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Some paleontological evidence of cave lion biology

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ŠTÚDIE A VEDECKÉ SPRÁVY – SCIENTIFIC PAPERS

EVOLUTIONARY LEVEL OF THE CAVE BEAR FROM THE GROTTA DEL BANDITO (PIEDMONT, N. ITALY)

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G. Santi, M. Rossi: Evolutionary level of the cave bear from the Grotta del Bandito (Piedmont, N. Italy)

Abstract: The Grotta del Bandito (Piedmont, North Italy) in northern Italy represents very interesting cave for several reasons, the most important of which is the geographical position near the French border from where, the most "evolved" cave bears could originate. In this cave, *Ursus* gr. *spelaeus* remains were collected. In this note, the first preliminary study of teeth, mandibles and metapodia has been elaborated in order to advance some news about the evolutionary level of these bears. The morphodynamics characteristic of teeth and the main indices of the metapodia (IP and K-I) indicate these bears to occupy an intermediate step in the evolutionary scale. This is not surprising because, from an evolutionary point of view, they are similar to the other Italian cave bears. Distinctly from the other populations that lived in N. Italy, the presence of more evolved morphotypes has been found compared to the other fossils from the Alpine localities (the most important are: the Buco dell'Orso, Buco del Frate, Cerè, Covoli di Velo and so on). Can this be a signal of the substitution by more modern cave bears?

Key words: *Ursus* gr. *spelaeus*, Grotta del Bandito, North Italy, evolutionary level, Late Pleistocene

INTRODUCTION

In Piedmont (North Italy), contrarily to other alpine regions, the caves and holes in which the fossils of cave bears have been found are less known. Of these, one of the most studied is the Grotta del Bandito (Cuneo Province). Nowadays, as a consequence of palaeogenetic research, we are witnessing a great and rapid enlargement of the knowledge on the spelaeoid bears. In fact, in recent years, using mtDNA, the phyletic tree of the cave bears is being continuously modified with the individuation and addition of new taxa (*ingressus*, *eremus* and *ladinicus*) in many places of Europe (Rabeder et al., 2004; Baca et al., 2012, 2013, 2017 and references therein; Bocherens et al., 2013; Baryshnikov & Puzachenko, 2017). In North Italy, studies on the spelaeoid bears have been restricted to a few places in the Alps and many questions still have to be answered. In this context, the Grotta del Bandito is surely very important place not only for its geographical position (next to the boundary with France from where, the most "evolved" cave bears could come), but also for the richness of fossils that allows us to ameliorate the knowledge about the evolution of the Italian bears and to study the possible relationship between the populations of Italy and France. This work is a preliminary study of the teeth, mandibles and metapodial bones, from the Grotta del Bandito. It aimsis toimprove some notes on these bears after those (a small amount) only superficially introduced (Zunino & Pavia, 2005).

THE GROTTA DEL BANDITO

Geographically, this cave is located on the right side of the Valle del Gesso Valley (Fig. 1b), with the entrance at 726 m a.s.l. The cave is eroded in Jurassic limestone and consists of east-west corridor (217 m), three main chambers and other smaller adjacent chambes. Zunino & Pavia (2005) divided the cave into two sections on the basis of different sedimentary infilling: (1) the first section, named the eastern branch, is composed of sandy-clay with gravel sedimentsand (2) the second section, very similar to the first one in the sediments composition, occupies the western part of the cave. The authors made three surveys (named L, M, and N respectively) (Fig. 1c) in different sections of the cave.

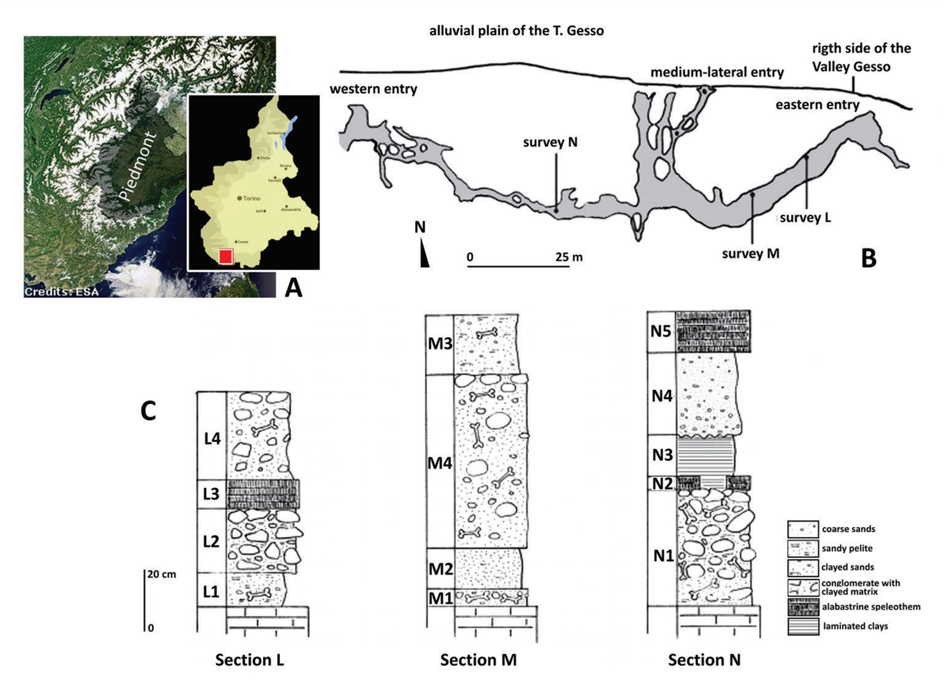

Fig. 1. Grotta del Bandito (Cuneo, Piedmont), Italy. A: Geographic position of the site. B: Map of the cave, and C: sections performed in the cave (from Zunino & Pavia, 2005 mod.)

MATERIALS AND METHODS

Teeth, mandibles, and metapodial bones are the elements of the skeleton under study; these fossils are deposited in the Museo Civico di Storia Naturale of Milan. The teeth analyzed include all types of the teeth: incisors, canines, premolars, and molars, and the morphometric parameters have been used for the latter according to Tsoukala & Grandal d'Anglade (1997), while the morphodynamic indices are those of Rabeder (1989, 1999) and Grandal d'Anglade & López-González (2004). Previously Zunino & Pavia (2005) studied some specimens of P4 and p4 from this cave and proposed some general considerations.

The mandibles and metapodia represent new and important material. We studied them both morphologically and morphometrically; for the metapodia we use the parameters codified by Withalm (2001) and both the Plumpness Index and K-I index have also been calculated. In order to have better overview, the comparisons with data of different species of cave bears from European localities are also presented.

RESULTS AND DISCUSSION

Both the morphometry with the morphodynamic analyses of the teeth (*sensu* Rabeder, 1999) and the Plumpness index with the K-I index for the metapodia place these bears within the spelaeoid bears group. For a better comprehension, we have subdivided the discussion into the single components of the skeleton starting with the teeth.

Teeth – The low morphotypes of the incisors (e.g. the morphotype "p" for the "Fossa lunaris-Cingulum" of I2, or morphotype "0" for the *Kalyx distalis* in I3 and so on, or also the "B/C" morphotype for the "*Sulcus mesialis*" of i3) are the most abundant ones. The most derived morphotypes are totally lacking. As for the P4 and p4, the morphotypes are also low, which is also the case for other spelaeoid bear populations in Lombardy and Veneto. On the contrary to the incisors that constantly show low morphotypes, for the P4 and p4 some of the highest morphotypes (D or E and in the specimens from Bossea, a cave next to the Grotta del Bandito the F-type also) have been identified. In Fig. 2, the position of the fourth premolars of the Grotta del Bandito is indicated, and the relative point is well inserted in the cloud of the Italian bears with the exception of the Cerè (Veneto) and Basura (Liguria) specimens. For these localities, two different explanations are possible. In the first cave, the three species of *Ursus* (*deningeri*, *spelaeus* and *arctos*) have been discovered and the primitivity of the speleians has been supported (i.e. Rossi & Santi, 2001, 2011; Santi & Rossi, 2008). In the second cave, the most modern cave bears have been only found (Quiles, 2004).

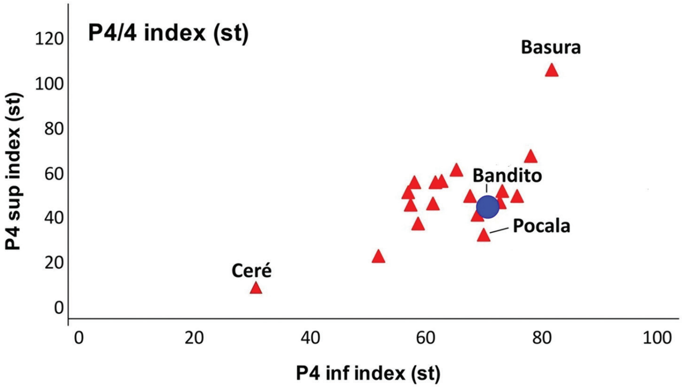

Fig. 2. Relationship between the morphodynamic indices (std) for the upper/lower fourth premolars from Grotta del Bandito and some other caves in Italy

The characteristic of m1 is that basically, the bears are advanced bears (e.g. in the relationships "Paraconid convergence index-Total length", or in the "Trigonid convergence index-Total length" and in the "Talonid convergence index-Total length", *sensu* Grandal d'Anglade & López-González, 2004), with some features of both the masticatory surface and of morphometry (e.g. the "Total Length-Talonid Width" relationship, Fig. 3), typical of the ancient bears (*sensu* Grandal d'Anglade & López-González, 2004). The same characteristics are shown in the other kinds of teeth. This combination is typical of the Italian spelaeoid bears.

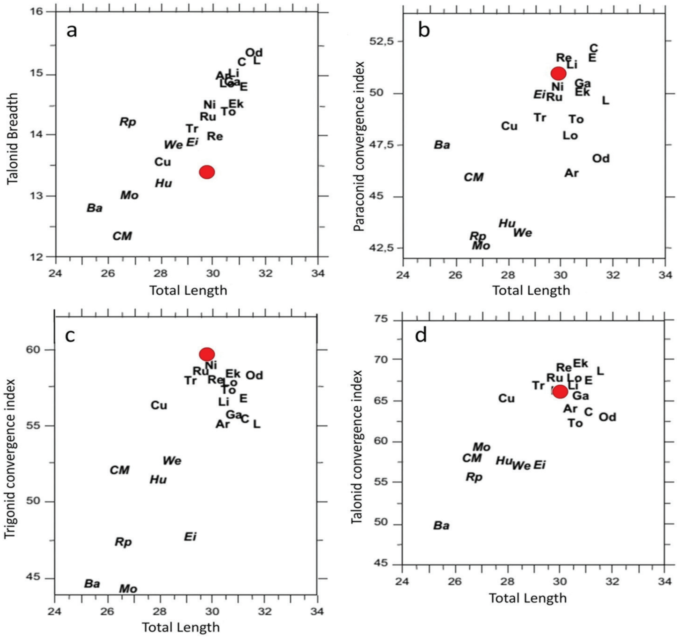

Fig. 3. Position of the m1 from Grotta del Bandito (red point) utilizing the relationships between the main convergence indices and "Length" (from Grandal d'Anglade & López-González, 2004 mod.). Abbreviations: Ar: Arrikrutz, Ba: Bacton, C: A Ceza, CM: Atapuerca, (Cueva Mayor), Cu: Conturines, E: Eirós, Ei: Einhornhöhle (Scharzfeld), Ek: Ekain, Ga: Gailenreuther (Zoolithenhöhle), Hu: Hundsheim, L: Liñares, Li: Lieglloch, Lo: Loutraki, Ni: Nixloch, Od: Odessa, Re: Reguerillo, Ru: Rubeland, To: Toll, Tr: Troskaeta, We: Westbury

Mandibles – Metric characteristics of several mandibles are reported in Fig. 4, where some important parameters are placed in relationship and compared with fossils of both Italian and foreign localities. From a general point of view, the mandibles of the Grotta del Bandito bears are within the distribution of other caves; few points indicate bears with a small size; they probably are females. If these specimens are representative of the Bandito population, they are very similar to others distributed in the Alps (in this case that of the Buco del Frate – Brescia, Lombardy), more particularly to the population of *U. ingressus* from Gamssulzen and other foreign localities (Fig. 4a). Furthermore, a particular comparison with the fossils from Grotta del Cerè (Verona) in which, besides *U. spelaeus*, both *U. deningeri* and *U. arctos* (the bears with "small" size) have been found, is shown in Fig. 4b, in which the "Length of the dental row" and the "Breadth of the mandible between m2 and m3" are placed in relationship. From this diagram, the belonging of these bears to the *spelaeus* group seems also clear; their distribution is wide and few specimens only have a size similar to both the *deningeri* from Cerè and to *U. arctos*. The

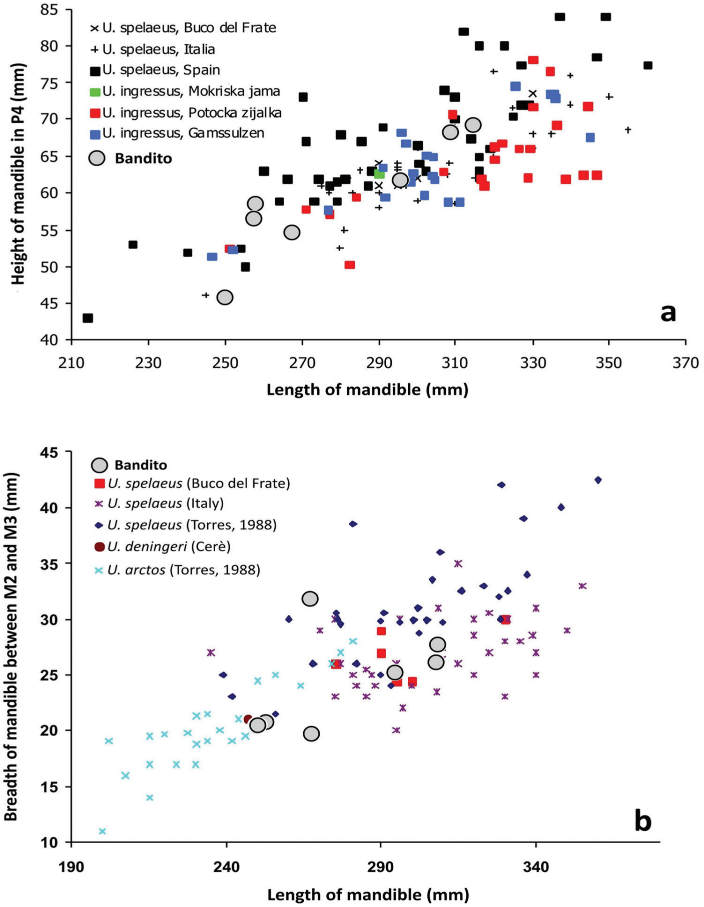

Fig. 4. Some relationships between parameters of the mandibles from Grotta del Bandito and cave bears from Italian and foreign localities (Torres Pérez Hidalgo, 1988, for diagram a, Rossi & Santi, 2013 mod.)

latter are probably females as also proposed for the other diagrams and we can confirm that the Bandito cave bears are similar in size to other populations of cave bears (*Ursus* gr. *spelaeus*) of the Italian Alps. Utilizing only the size, we don't have concrete tools to individuate the *Ursus* species; therefore the morphology is unequivocally spelaeoid.

Metapodia – In this first note, a comparison with the bears from Gamssulzen (*U. ingressus*), Buco dell'Orso (Laglio) and Conturines (*U. ladinicus*) is performed. This choice has been made because the bears from Gamssulzen cave have always been considered the reference cave population and it is also the type locality of the *U. ingressus*; the Buco dell'Orso is one of the main caves known in NW Italy, and the Conturines (Tyrol) is the cave placed at the highest altitude and the type locality of *U. ladinicus*. The IP values are shown in Fig. 5a-b ; we observed that the distribution is similar for all localities but when referred to the Bandito specimens, the values are the lowest and very similar to those of the Urşilor cave bear (Romania) (47-39 ky; Robu, 2016) and Risovača bear (Serbia, Late Pleistocene) (Cvetković & Dimitrijević, 2014). When observing the distribution

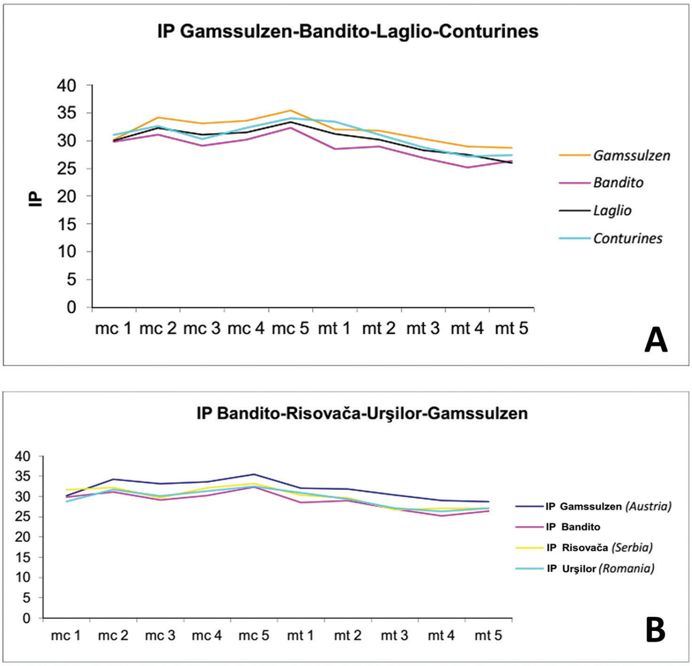

Fig. 5. A – Distribution of the IP index of the metapodia from Grotta del Bandito, Buco dell'Orso (Laglio), Gamssulzen and Conturines caves (for these last caves data from Withalm, 2001) and B – from Urşilor and Risovača caves (data from Robu, 2016; Cvetković & Dimitrijević, 2014)

of K-I (comparison Bandito-Gamssulzen-Laglio) (Fig. 6), the same considerations can be put forward: the Bandito bears have the lowest values of this index. In the comparison between the speleians from Buco dell'Orso and those from Grotta del Bandito another consideration can be advanced for the mt 2 (considered the most important metapodium from an evolutionary aspect): a significant correlation does not exist between its Length and K-I (Fig. 7). Curiously, again referring to what occurs with the Bandito bears in

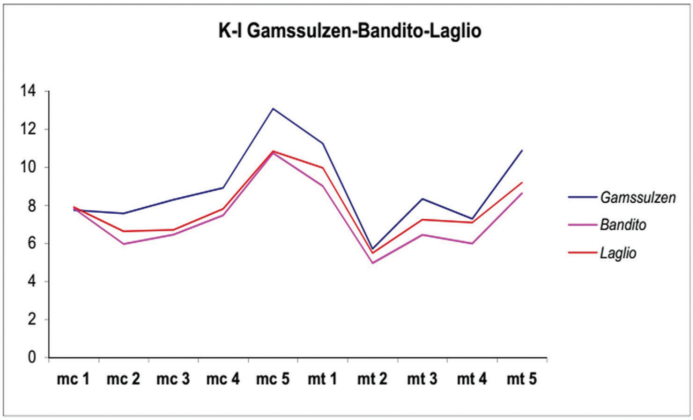

Fig. 6. Distribution of the K-I index of the metapodia from Grotta del Bandito, Buco dell'Orso (Laglio) and Gamssulzen caves (for this last cave, data from Withalm, 2001)

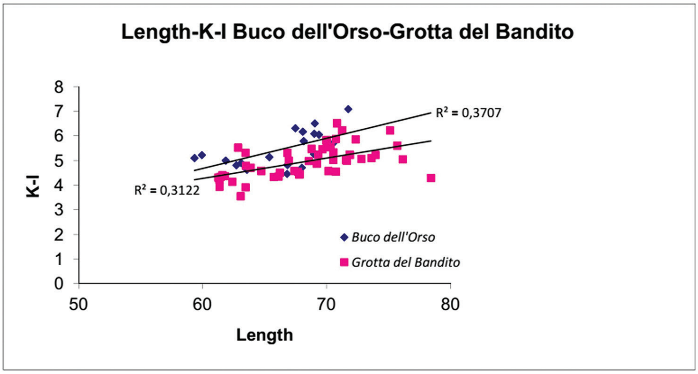

Fig. 7. Relationship between the Length and K-I index of the mt 2 of cave bears from Grotta del Bandito and Buco dell'Orso (Laglio)

the IP/K-I relationship (Fig. 8) a correlation between the two above discussed indices ($R^2 = 0.39$) is absent contrarily to the Buco dell'Orso specimens ($R^2 = 0.89$). Observing the Fig. 9, another important consideration can be deduced: the indices, when in relationship (P4/4 and K-I) are the lowest and the position of the Bandito bears is far separate from the distribution of that of the other caves. The value of K-I is similar to that of bears from Repolust cave, the type-locality of *U. deningeroides* (Rabeder & Temmel, 1997), but with a greater complexity of the fourth premolar. This can indicate that the Bandito bears are morphometrically rather similar to the bears from Repolust, but with more evolved teeth. More in general, the population is morphometrically, and in an evolutionary sense, very similar to the other Italian populations (Santi & Rossi, 2014). With these features, some questions arise: 1) Is this population the original one from the Grotta del Bandito? 2) Is this a migrant population coming from a foreign region? 3) Is it possible to establish a species of cave bear for the fossils from the Bandito cave? At the present, we do not have any answers to these questions but hopefully, the future excavations in this cave might shed more light to the above subjects.

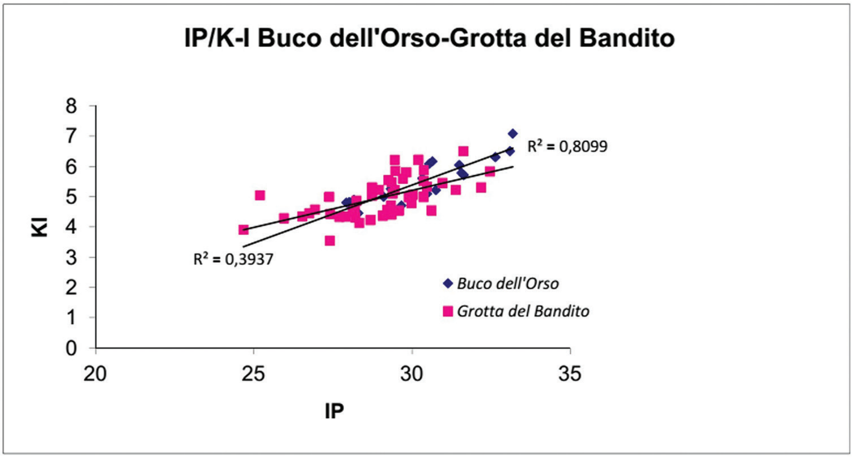

Fig. 8. Relationship between the IP and K-I indices of the mt 2 of cave bears from Grotta del Bandito and Buco dell'Orso (Laglio)

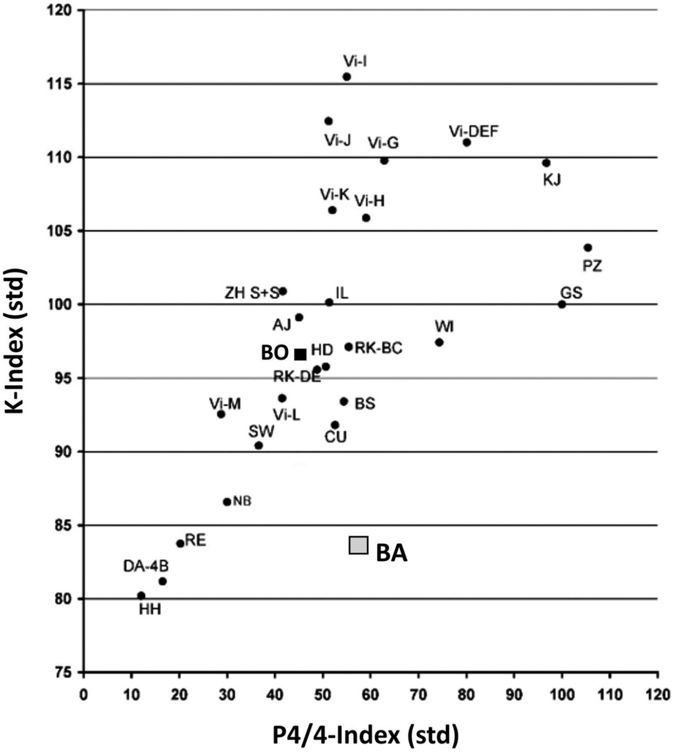

Fig. 9. Plot of K-index (std) and P4/4 index (std) of cave bear from different European caves and the speleians from Grotta del Bandito (BA) and Buco dell'Orso (BO) (from Withalm, 2011, mod.). Abbreviations: AJ: Ajdovska jama (Slovenia), BS: Brettstein Bärenhöhle (Styria, Austria), CU: Conturines (South Tyrol, Italy), DA-4B: Bad Deutsch Altenburg (Lower Austria), GS: Gamssulzen-Höhle (Upper Austria), HD: Herdengelhöhle (Lower Austria), HH: Hundsheim (Lower Austria), IY: Ilianka cave (Ukraine), KJ: Krizna jama (Slovenia), MV: Grotte de Merveilleuse (France), NB: Nerubajskoe (Ukraine), PZ: Potočka zijalka (Slovenia), Rep: Repolusthöhle (Styria, Austria), VI M-D/E/F:Vindija, layers M-D (Croatia), RK D/E: Ramesch Knochenhöhle, lower layers (Upper Austria), RK B/C: Ramesch Knochenhöhle, upper layers (Upper Austria), SR: Schreiberwandhöhle (Upper Austria), SW: Schwabenreithhöhle (Lower Austria), WI: Windener Bärenhöhle (Burgenland, Austria)

CONCLUSIVE REMARKS

With this first analysis of the teeth, mandibles and metapodia from the Grotta del Bandito (Cuneo Province, Piedmont, N. Italy), some preliminary conclusions useful for the future discussions and insights can be advanced. In general, the bears from the Bandito cave are aligned with other populations of the Alpine regions, namely in the morphodynamic indices of the teeth which are rather low or intermediate in the mixed characteristics of both "ancient" and "advanced" speleians and in the most important indices of the metapodia (IP and K-I). In light of this first analysis, with these data, the population of Grotta del Bandito shows at least an intermediate degree on an evolutionary scale; perhaps the IP and K-I indices which are rather low, could be a characteristic of this population. Many explanations can be proposed to justify those aspects, and surely the most suggestive one is to invoke the "Lilliput effect" that in the past, we often proposed to explain the small or medium size of the bears. From a systematic point of view, no decisive characteristic allows us to determine the species (*ingressus*, *eremus*, *ladinicus*). It is important to point out the presence of the highest morphotypes in the Bossea cave nearby the Bandito cave (Zunino & Pavia, 2005) which could be a symptom of a first attempt of substitution of "new cave bears" among the original population. In fact, near the Grotta del Bandito in the Liguria region as well as the bears that lived in the Basura cave show the highest morphotypes of the P4 and p4. Does a correlation between the Bossea and Bandito cave bears exist? This is a problem that is to be studied in the future with a global and comprehensive morphometric, radiometric and DNA analyses.

Acknowledgements. The authors thank Dr. Alessandro Garassino (Milan) for access to Museo Civico di Storia Naturale of Milan, Dr. Martin Sabol (Bratislava), Dr. Jan Wagner (Prague), for the comments, Prof. Gernot Rabeder (Wien) for the useful help, and the Dr. Nicoletta Benedetta Carlo-Stella (Cleveland) is also thanked for help with English.

EVOLUČNÁ ÚROVEŇ MEDVEĎOV JASKYNNÝCH Z GROTTA DEL BANDITO (PIEDMONT, SEVERNÉ TALIANSKO)

Resume

Grotta del Bandito (Piedmont, severné Taliansko) je zaujímavá jaskyňa z viacerých dôvodov, z ktorých najdôležitejší je zemepisná poloha pri francúzskych hraniciach, kde sa mohli vyvinúť najodvodenejšie formy medveďov jaskynných. V jaskyni sa našli fosílne zvyšky *Ursus* gr. *spelaeus*, z ktorých zuby, sánky a metapódia boli predbežné študované za účelom získania údajov o evolučnej úrovni týchto medveďov. Morfodynamické znaky na korunkách zubov a hlavné indexy metapódií (IP a K-I) poukazujú, že tieto medvede tvorili prechodné štádium v evolučnej línii medveďov zo skupiny *spelaeus*. Nie je to prekvapujúce, pretože z evolučného hľadiska sú podobné ďalším medveďom jaskynným z Talianska. Avšak na rozdiel od ostatných populácií, ktoré žili v severnom Taliansku, vykazujú evolučne vyššiu úroveň morfotypov, ktoré sú porovnateľné s morfotypmi z alpských lokalít (k najvýznamnejším patria: Buco dell'Orso, Buco del Frate, Cerè, či Covoli di Velo). Môže to byť signál pre nahradenie viac odvodenejšími medveďmi jaskynnými?

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THE METAPODIA AND PHALANGES OF THE CAVE BEAR FROM BUCO DELL'ORSO AREA (LOMBARDY, NORTHERN ITALY)

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M. Rossi, G. Santi: The metapodia and phalanges of the cave bear from Buco dell´Orso (Lombardy, Northern Italy)

Abstract: The Buco dell'Orso Cave (Lombardy, N. Italy) is a rich deposit of cave bear remains. We present the analysis of metapodia and the phalanges with the aim to obtain data on the evolutionary degree of the bears. The cave bears are surely speleians, but a dualism in the size of these components is observed; the results of the metapodia study conform with the skulls and mandibles but, the phalanges are medially larger and sturdier. The Plumpness Index, K-Index and P4/4 morphodynamic data show that the evolutionary step of bears from Buco dell'Orso is indicatively in a median position, but a confirmation can be had only with a complete study comprehensive of mtDNA and radiometric chronology.

Key words: Metapodia, phalanges, cave bears, Buco dell'Orso, Late Pleistocene

INTRODUCTION

Up to now the major part of research on the cave bear (*Ursus spelaeus*) has been focalized on mtDNA analyses with the identification of new mitospecies (*U. ingressus*, *U. spelaeus eremus* and *U. spelaeus ladinicus* (Orlando et al., 2002; Rabeder et al., 2004; Baca et al., 2012, 2013, 2017 and reference therein; Bocherens et al., 2013; Dabney et al., 2013 etc.). Genetics and morphometry have still not reached a contact point to effectively individuate the different taxa of cave bears; in fact using the morphometry of the different components of the skeleton, in particular the skulls, mandibles, teeth and metapodia, few differences have been observed and can be considered as attributable to intraspecific variations (i.e. Santi & Rossi, 2014). However, some kinds of bones have not been studied in depth, including the phalanges which could be a useful tool to further advance some information on the evolutionary step of the cave bear.

The Buco dell'Orso Cave is one of the famous holes found in Lombardy (N. Italy) in which a rich amount of cave bear fossils, have been gathered. In the most recent past this material was the topic of many studies, but only the skulls and mandibles had been deeply analysed (Santi & Rossi, 2001, 2005).

With this study we introduce new insights to the bears from Buco dell'Orso and more precisely we study preliminarily the metapodia and the phalanges to place them, at least indicatively, in the systematic and evolutionary position after a few highlights that were presented before (Rossi & Santi, 2001; Santi & Rossi, 2001; 2014; Santi et al., 2003).

In particular the 1^{st} basal phalanges have been compared with those of the *ingressus* (Gamssulzen Cave, age 38 – 25.4 ka), *ladinicus* (Conturines Cave, age, 107.2 – 41.9 ka) and *eremus* (Schwabenreith Cave, age 34 – 48 ka) (Rabeder, 1999; Döppes et al., 2016), the three known species of "speleian". In order to study these aspects we have utilised the data from different caves distributed in Europe, in particular the Gamssulzen Cave (Austria) often considered as a reference cave (i.e. Rabeder, 1999). In the future a more detailed study about these metapodia will be developed.

BUCO DELL'ORSO CAVE

On more than a single occasion in the past a short description of the cave has been proposed: geographically this cave opens into the neighbourhood of the Laglio village (Como Province, Lombardy) at 648 m a.s.l. (Fig. 1). The cave is about 300 m. long, 15 m tall and is opened in the micritic limestone rocks of the Lower-Middle Liassic intersected by a series of faults; initially its direction is ENE – WSW changing to WNW – ESE. Only Cornalia (1850, 1858 – 1871) performed a detailed stratigraphy, and individuated 6 levels; and from the base, only the second one was fossiliferous. At the present the Buco dell'Orso is closed and excavations are impossible to perform.

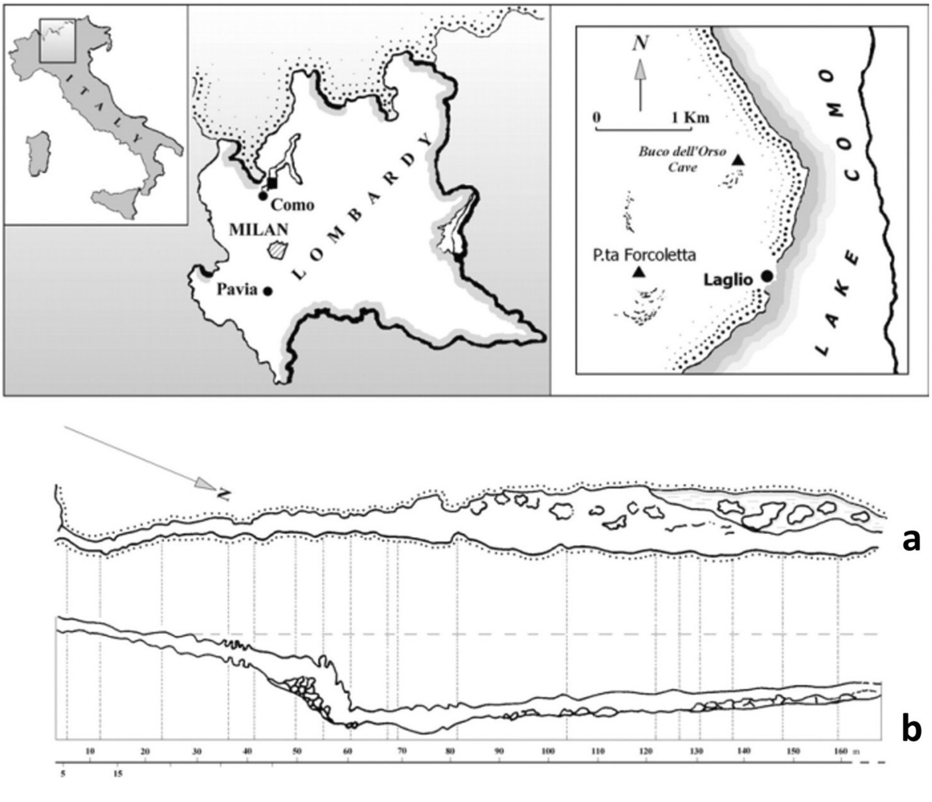
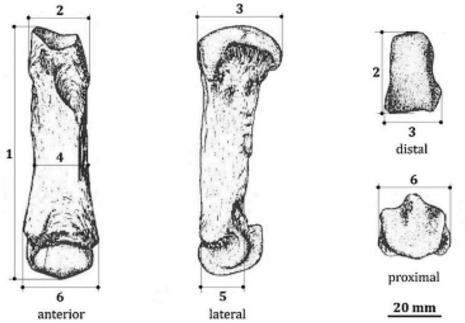


Fig. 1. Geographic position of the Buco dell'Orso cave (North Italy). Ground plan (a) and transversal section (b) of the cave (Cornalia, 1858 – 1871, mod.)

MATERIALS AND METHODS

The complete series of metapodia (metacarpi and metatarsi) is represented. They are stored in the Museo Civico di Storia Naturale of Milan (Lombardy) and different parameters of measurement are individuated on them following the Withalm (2001) indications. The metapodia are well preserved and only in a few cases some specimens are incomplete or partially destroyed, with no pathologies or attack marks, being individuated; this allowed us the possibility to take measurements on a great amount of specimens. Plumpness Index and K-I index are also calculated, but the main discussion is referred to the 2nd metatarsus because it is an element which is less subject to sexual dimorphism or ontogenetic variability as opposed to the other metapodia (Withalm, 2004; Robu, 2016). Table 1 shows an overview of the main numerical features and indices of the Buco dell'Orso metapodia.

Tab. 1. Means of measurements and indices of metapodia from Buco dell'Orso (Laglio, Lombardy, N. Italy)



1 -Total Length
2 - Proximal width
3 - Proximal depth
4 - Smallest diaphyseal width
5 - Max. diameter antero-post. diaphyseal
6 - Distal epicondyleal width

IP = DT dist x 100/T L
K-I = DT prox x DAP prox/T L

Metapodia	**n**	**T L (1)**	**DT prox. (2)**	**DAP prox. (3)**	**DT dia. min. (4)**	**Dap dia. (5)**	**DT dist. (6)**	**IP**	**K-I**
Mc1	16	62.23	24.28	20.25	13.06	9,95	18.65	30.02	7.89
Mc2	13	76.02	18.85	26.62	17.1	12.34	24.6	32.3	6.62
Mc3	22	75.49	19	26.42	15.75	11.78	23.45	31.09	6.7
Mc4	26	82.04	21.52	29.8	17.62	13	25.76	31.49	7.8
Mc5	25	78.93	27.8	30,9	17.82	12.99	26.28	33.35	10.83
Tot. metac.	**102**							**31.65**	**7.97**
Mt1	12	55.12	23.4	23.63	12.08	10.23	17.32	31.23	9.95
Mt2	20	66.5	15.33	23.69	14.03	10.68	20.12	30.21	5.47
Mt3	18	77.51	18.66	29.91	15.78	11.64	22.18	28.28	7.23
Mt4	22	85.62	20.46	29.48	15.72	12.63	23.54	27.48	7.08
Mt5	21	85.76	27.81	28.28	13.34	12.48	22.31	25.99	9.18
Tot. metat.	**93**							**28.64**	**7.78**

The phalanges are a part of the skeleton that have not been studied in depth; in fact recently, only Alscher & Rabeder (2012) morphometrically analysed this anatomic component of the Alpine cave bears. Among the fossils from the Buco dell'Orso Cave, specimens of phalanges have been found. This material, as for the metapodia, is also stored in the Museo Civico di Storia Naturale of Milan. The morphometry of the 1st-2nd and 3rd phalanx has been studied utilising the parameters codified by Alscher (2013, unpublished) and Hilpert (2006, unpublished), (Fig. 2): the greater part of the analysed fossils concerns the 1st basal phalanx; the data are reported in Table 2. In order to facilitate the comprehension of the data a comparison with those of *ingressus*, *ladinicus* and *eremus* species and with other Europeans caves has also been elaborated.

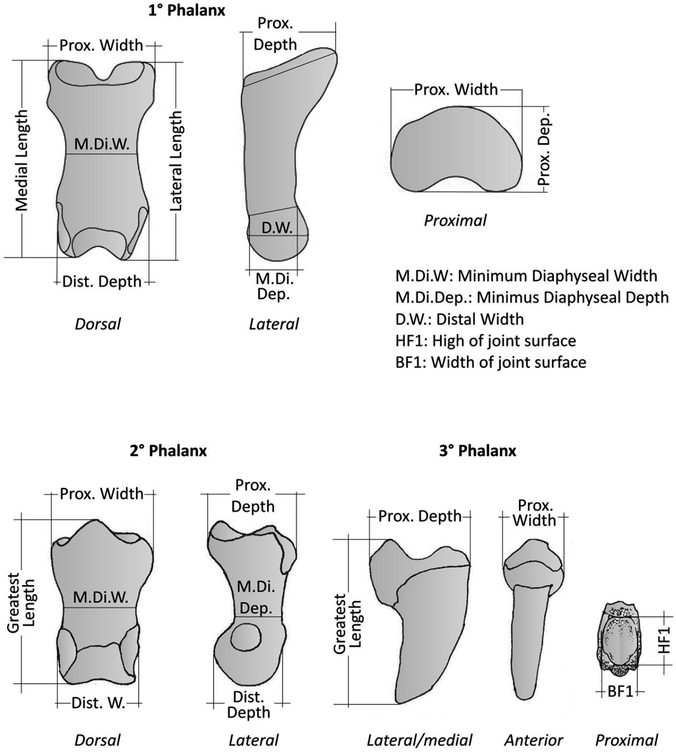


Fig. 2. Parameters of measurements of the phalanges (Hilpert, 2006, unpublished mod.; Alscher, 2013, unpublished mod.)

RESULTS

Metapodia

General considerations – The metacarpi (1 – 5; Fig. 3) belong to the distribution formed by the bears from Deutsch-Altenburg, Hundsheim (*eremus*) and only partially from Valdarno (*etruscus*). Bears from Schwabenreith (*deningeri*) form a single and well defined cloud; the elements from Buco dell'Orso are surely cave bears with a small size; in fact the recent bear (*U. a. horribilis*) is clearly separate. This is compatible with the cranial and mandible sizes (Santi & Rossi, 2001), but is strongly in contrast with the size of the phalanges, in particular the first phalanx. Also observing the diagram (Fig. 4) the *U. spelaeus* species is confirmed.

A second consideration can be advanced by observing the diagrams (Fig. 5) in which both the Plumpness Index (IP) and K-I index of the metapodia from Buco dell'Orso, Gamssulzen (Austria) (*U. ingressus*) and Conturines (Italy) (*U. ladinicus*), are compared. Referring to IP of the metatarsi, a few differences among the studied populations are observed, while for the metacarpi, the Gamssulzen population generally shows much higher values, whereas the Buco dell'Orso population the IP values are the lowest with the exception of Mc III. The values of K-I are homogenous in both the metacarpi and metatarsi, but higher values are observed for the Gamssulzen bears and similar values are obtained for both Buco dell'Orso and Conturines populations. It is possible that the differences between metacarpi and metatarsi are to be linked to intraspecific variability. The presence of a mix of females and males is shown in Figure 6 where a comparison of the 3rd metatarsus from two localities in France is indicated.

2nd metatarsal – Among the metapodia components the 2nd is the one less linked to sexual dimorphism or ontogentic variability and in this view it is considered to be a metapodium of reference. The correlations between some significant indices and

Tab. 2. Morphometrical measurements and main indices of the phalanges from Buco dell'Orso

Medial Length	Lateral Length	Proximal Width	Proximal Depth	Min. Diaph. Width	Min. Diaph. Depth	Distal Width	Distal Depth	Prox. Area	IP
47.98	45.67	25.79	18.78	16.69	9.94	18.26	14.19	484.34	53.75
47.81	47.23	24.96	21.1	16.67	11.45	20.98	14.38	526.66	52.21
40.91	38	23.25	15.46	15.23	9.5	16.24	12.94	359.45	56.83
44.66	43.55	26.54	18.62	19.37	10.7	20.19	13.73	494.17	59.43
43.51	39.75	23.73	16.21	15.38	10.28	17.26	13.6	384.66	54.54
47.52	45.73	26.64	18.24	16..49	11.39	18.86	13.38	485.91	56.06
47.85	46.77	26.51	17.59	16.93	10	18.67	13.85	466.31	55.4
43.3	41.02	23.8	16.84	15.39	9.77	17.09	13.75	400.79	54.97
40.98	40.78	21.36	16.16	15.08	10.09	16.48	12.66	359.7	52.12
46.86	45.33	23.93	17.58	17.38	10.53	18	13.32	420.69	51.07
44.59	40.25	24.11	16.97	16.47	10.06	17.29	13.72	409.15	54.07
42.68	40.36	24.26	15.85	15.23	9.81	17.57	12.97	384.52	56.84
38.6	37.41	21.37	15.92	12.88	8.68	15.64	12.91	340.21	55.36
43.69	41.05	24.31	16.68	14.8	9.02	16.99	13.32	405.49	55.64
42.73	39.2	20.58	17.06	12.41	10.17	15.02	10.75	351.09	48.16
44.22	41.89	24.57	18.38	15.46	11.34	17.66	13.89	451.6	55.56
42.41	39.19	24.67	17.1	15.28	10.75	17.97	13.92	421.86	58.17
46.85	43.36	24.49	18.02	15.25	11.06	17.25	13.01	441.31	52.27
37.07	34.98	20.58	13.21	12.62	9.32	14.71	11.96	271.86	55.52
42.5	40.28	23.79	16.26	14.1	9.46	17.43	13.2	386.83	55.98
42.07	38.52	23.99	16.05	14.87	9.02	17.05	13.31	385.04	57.02
41.17	39.34	22.05	15.56	14.63	9.3	16.85	12.26	343.1	53.56
36.32	32.97	18.94	14.26	12.04	9.35	15.35	8.91	270.08	52.15
31.88	29.9	17.81	13.81	11.12	8.44	12.99	9.54	245.96	55.86
43.14	42.88	24.53	18.13	16.57	9.35	17.12	13.32	444.73	56.86
38.25	37.35	22.56	15.55	13.27	9.71	15.73	12.81	350.81	58.98
35.88	36.26	19.96	14.37	12.6	8	15.56	11.71	286.83	55.63
36.23	35.23	19.91	15.47	12.69	9.16	14.55	11.61	308.01	54.95
37.01	36.63	20.15	16.08	13.37	9.95	15.23	12.12	324.01	54.44
45.21	43.39	25.84	19.29	18.18	10.69	19.86	14.34	498.45	57.16
40.91	39.16	20.85	16.51	14.22	9.74	16.79	12.79	344.23	50.96
39.1	37.82	21.8	16.18	13.37	9.09	16.75	12.32	352.72	55.75
34.22	33.94	18.07	13.65	11.71	6.85	13.2	10.35	246.66	52.81
44.94	42.94	24.52	18.37	16.51	10.95	18.24	12.92	450.43	54.56
33.14	31.38	18.88	13.14	11.01	7.4	13	10.91	248.08	56.97
38.66	36.94	21.57	15.08	12.94	9.27	15.55	12.03	325.28	55.79
41.86	40.46	23.57	15.72	14.82	9.65	15.6	12.91	370.52	56.31
32.82	32.49	17.94	12.8	11.14	6.69	12.73	10.55	229.63	54.66
37.63	34,99	20.23	14.74	12.24	7.87	15.36	11.91	298.19	53.76
41.28	37.6	24.02	15.77	14.35	9.72	16.43	13.57	378.8	58.19
32.17	30.48	18.89	14.1	11.75	7.8	14.08	11.35	266.35	58.72
33.44	32.73	18.27	11.92	11.61	7.67	13.2		217.78	54.64
32.31	31.5	17.48	13.8	11.7	8.15	13.92	11.66	241.22	54.1
47.98	46.9	26.01	20.44	16.72	10.54	20.26	14.42	531.64	54.21
41.45	39.42	22.91		14.58	9.78	17.17	12.8		55.27
39.04	36.51	21.79	14.4	13.2	8.3	15.16	12.56	313.78	55.81
34.67	34.05	21.05	15.36	14.04	9.48	15.66	11.98	323.33	60.72
41.25	38.45	23.18	15.86	13.31	8.76	16.81	12.76	367.73	56.19
37.45	36.82	19.74	16.08	14.51	8.8	16.19	12.13	317.42	52.71
35.47	35.22	19.45	12.77	11.65	7.47	13.26	11.54	248.38	54.84
34.04	33.47	18.29	13.85	11.65	6.95	13.05	10.64	253.32	53.73
	39.3	21.4	15.36	13.95	8.51			328.7	
44.27	43.12	23.36		15.66	9.34	17.46	12.47	398.29	52.77
41.36				16.03	10.18	17.01	12.45		
	44.89	27.06	18.26	18.7	10.48			494.12	
43.08	40.66	24.27	17.36	15.92	10	16.85	12.75	421.33	56.34
	40.5			15.19	8.08	17.73	12.64		
		21.74	16.53	13.95				359.36	

TAB. 2 – 1st PHALANX

Statistical Parameters 1st phalanx	Medial Length	Lateral Length	Proximal Width	Proximal Depth	Min. Diaph. Width	Min. Diaph. Depth	Distal Width	Distal Depth	Prox. Area	IP
mean	40.4893	38.8573	22.345	16.1036	14.4117	9.36509	16.38.75	12.5517	364.197	55.1013
st dev.	4.6118	4.3531	2.5999	1.9214	1.9974	1.1578	1.9295	1.1908	81.6125	2.2619

TAB. 2 – 2nd PHALANX

GL	Proximal Width	Proximal Depth	Min. Diaph. Width	Min. Diaph. Depth	Distal Width	Distal Depth	Prox. Area	IP
28.53	15.32	10.58	12.58	7.64	12.73		162.09	53.7
22	15.05	12.81	10.9	7.09	12.41	9.88	192.79	68.41
21.77	15.35	11.84	11.85	7.65	12.25	8.73	181.74	70.51
23.28	16.64	12.92	11.74	8.11	13.2	9.09	215	71.48

TAB. 2 – 3rd PHALANX

GL	Proximal Width	Proximal Depth	HF1	BF1	Prox. Area	IP
26.1	10.29	15.67	10.61	9.84	161.24	39.43
22.46		15.46	10.02	7.93		
29.98		17.66	10.43	7.65		
25.67	10.15	17.71	11.8	8.3	179.76	39.54
17.35	7.07	12.15	9.51	7.22	85.9	40.75

parameters are shown in Fig. 7. In some cases we observe a significant correlation (i.e. DAP with K-I, or DT prox with K-I, or DT dist with DAP prox as well). In others, the correlation is weak (i. e. Length with K-I, or DT prox and DA prox, or Length and DT prox as well). As previously reported by Robu (2016) K-I is a “robusticity indicator” of the metapodium; in fact the correlation between the K-I and the Length is strongly or weakly associated with the robusticity depending only on the proximal part of the metapodium but not on its length. A significant correlation is also observed in the relationship between the K-I and DT dist (R = 0.77); an increase of the distal part of the metapodium corresponds to a similar increase in size of the proximal end. Therefore an indicator of the evolutionary degree is the relation between the morphodynamic indices of the P4/4 and the indices

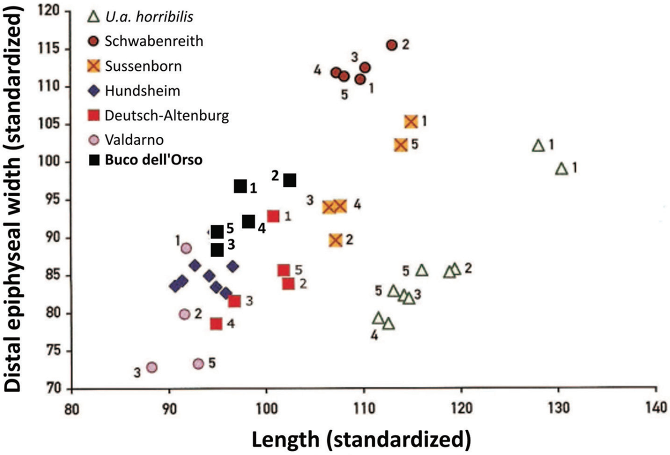


Fig. 3. Relationship between the length (std) and distal epiphyseal width (std) of cave bears from different caves in Europe and Buco dell’Orso cave (Rabeder et al., 2010, mod.)

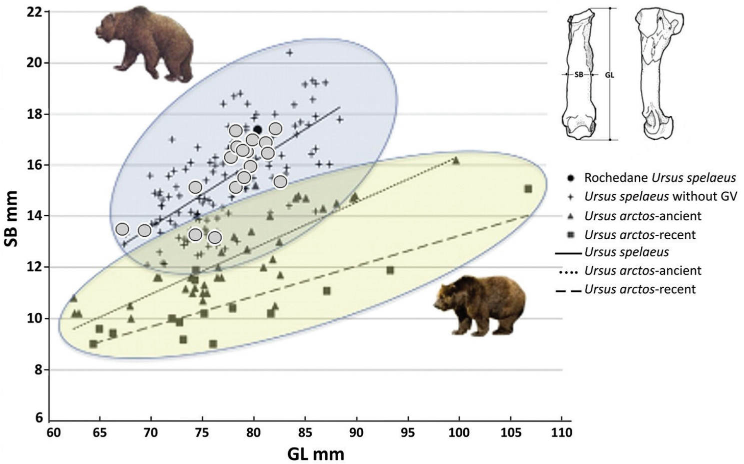


Fig. 4. Relationship between the length and smallest breadth of the 3^{th} metatarsus from Buco dell'Orso (grey dots) and metatarsals from different caves (Bocherens et al., 2014, mod.)

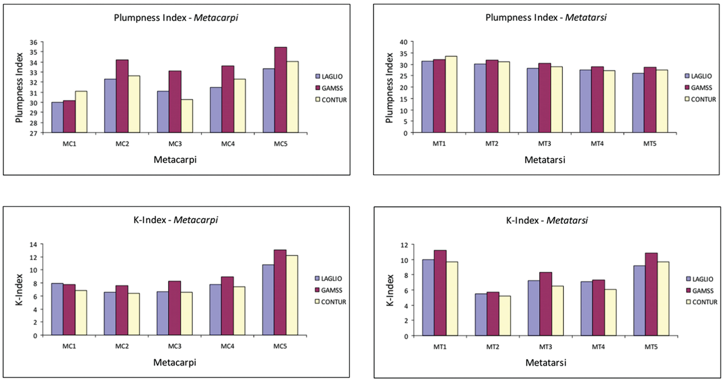


Fig. 5. Comparison of the Plumpness index of the metapodia of cave bears from Buco dell'Orso and those from Gamssulzen and Conturines caves (Gamssulzen data Rabeder pers. com., Conturines data from Withalm, 2001)

of the metapodium (IP and K-I). Fig. 8 shows as an example, a correlation between the main indices of the Buco dell'Orso bears and those from many other sites of Europe. In the diagrams the position of the Buco dell'Orso is near that of the cave bears of Hendergel (40 ka), Ramesch (53 ka) and slightly lower to those of Ajdovska (50 ka). If the correlation between the P4/4 index and IP or K-I indices is a sign of an evolutionary trait, Buco dell'Orso bears have in a preliminary approximation, an evolutionary level similar to the bears of 40 – 50 ka.

Phalanges

Globally, the analysed fossils are well preserved**,** and complete; specimens of the 1^{st} phalanx are the most abundant (n. 58) and, the discussion will be based on them.

Some comparisons between the Buco dell'Orso population and those typical of the *U. ingressus* (Gamssulzen, type-locality), *U. ladinicus* (Conturines, type-locality) and *U. eremus* (Schwabenreith) species, are shown in Figure 9. The box plots relating to the

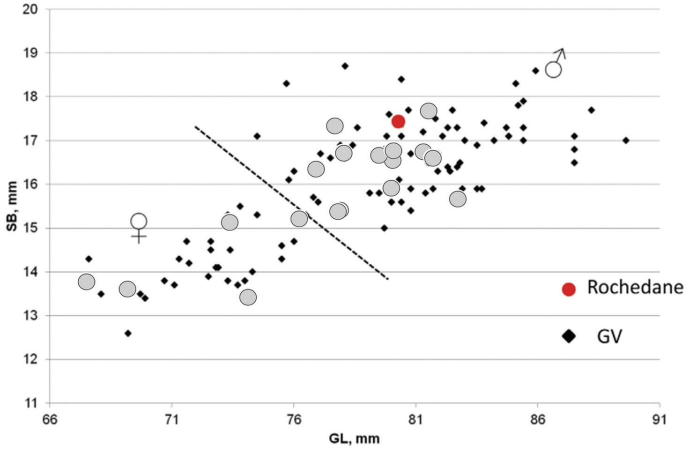


Fig. 6. Distribution of males and females based on the measurements of the 3th metatarsus from Buco dell'Orso (grey dots) and specimens from Rochedane and Vaucluse (France) (Bocherens et al., 2014, mod.)

"Medial Length" are shown in Fig. 9a. In the comparison between the three populations, a general homogeneity is noted, but the bears from Buco dell'Orso and Schwabenreith have a slightly larger size. Also the range of the variability is similar for the populations analysed. On the contrary, the box-plot relating to the "Transversal breadth of the proximal epiphyses" (Fig. 9b) shows the differences between the studied populations. The range of the variability is similar in both the Buco dell'Orso and Schwabenreith populations (it is lower for the others), but the main differences can be seen in their sizes. The bear population from Buco dell'Orso shows clearly higher values than the others populations of cave bears. Similar observations can be advanced for the "Antero-posterior breadth of the proximal epiphyses" (Fig. 9c). The consequences of the larger sizes of these parameters are a larger articular proximal surface and a higher value of the Plumpness indices in the Buco dell'Orso population than in the other ones (Figs. 9d – e). The analysis of the Plumpness Index is highly interesting: comparing the different populations, the Gamssulzen population shows minimum values; but the comparison of the transversal breadth of the diaphysis and the transversal breadth of the distal epiphyses (Figs. 9f – g) shows that the Buco dell'Orso population has larger sizes than the other populations.

The "Proximal area" (Proximal Width x Proximal Depth) and, as well as was for the metapodia, the "Plumpess index" (IP = Proximal Width/Medial Length x 100) are two useful and important parameters to understand the morphometry of the 1st phalanx of the *ingressus* (Gamssulzen), *ladinicus* (Conturines), *eremus* (Schwabenreith) and Buco dell'Orso bear. In the diagram (Fig. 10) the distribution of the 1st phalanges of the Buco dell'Orso is rather homogeneous and we can hypothesize that the examined population belongs to the same species of cave bear with no sexual differences observed.

Considering these parameters, a comparison between the different species of cave bears confirms the conclusions obtained by observing the box-plots (Fig. 9); apart from some specimens from Schwabenreith with a size that does not reach the maximum size of the bears from Buco dell'Orso, the overlap between the Buco dell'Orso population and the others is light and regards the specimens with smaller sizes. In fact, with the same

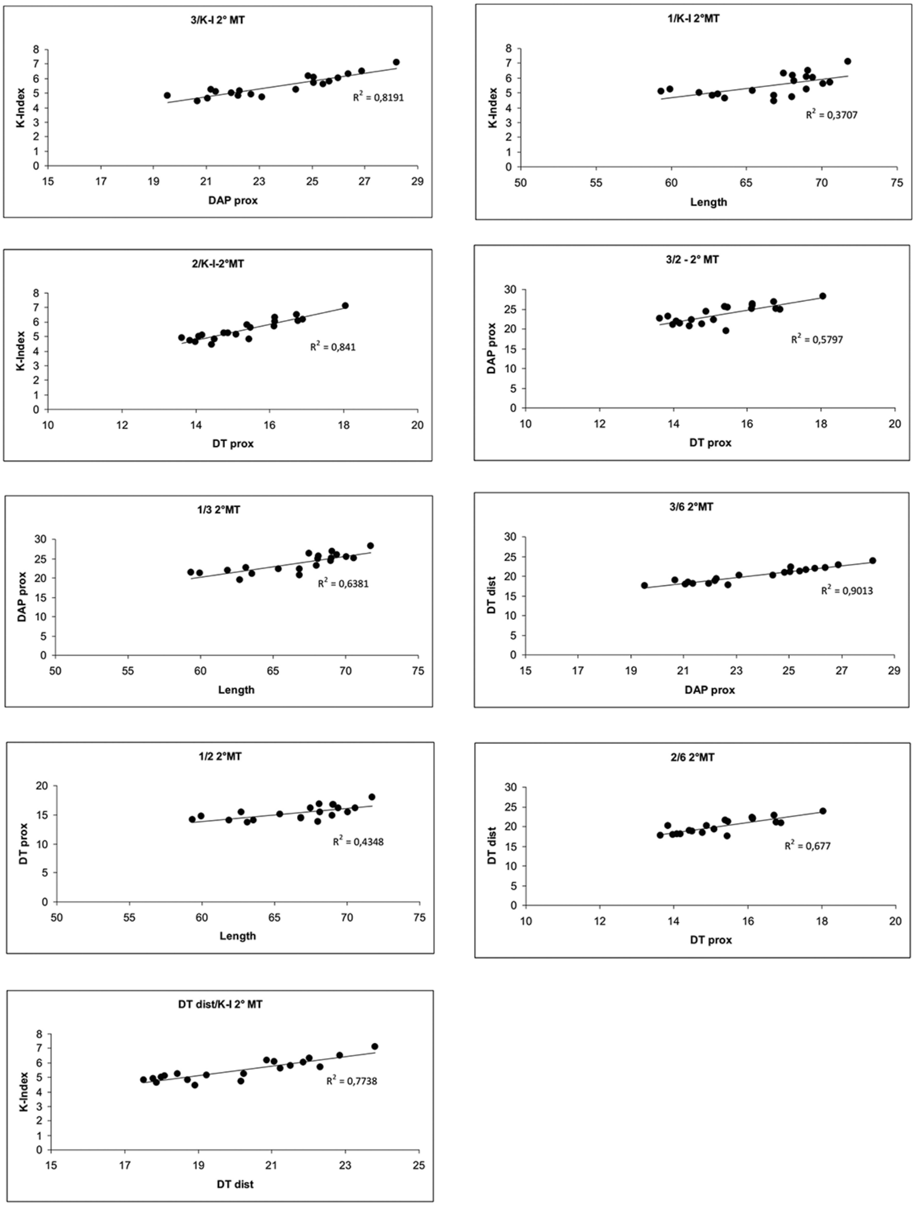


Fig. 7. Some relationships between indices and parameters of the 2nd metatarsus of Buco dell'Orso cave bears

IP, the bears from Buco dell'Orso with greater sizes, also have a larger proximal area. The "Medial Length" and the "Transversal breadth of the distal epiphyses" relationship is shown in Figure 11. In this case as well the Buco dell'Orso population is different compared to the other populations; with a same medial length, the transversal breadth is higher. This characteristic is substantially similar as evidenced by the other diagrams. In general, the morphometrical analysis shows a medial length whose values are within

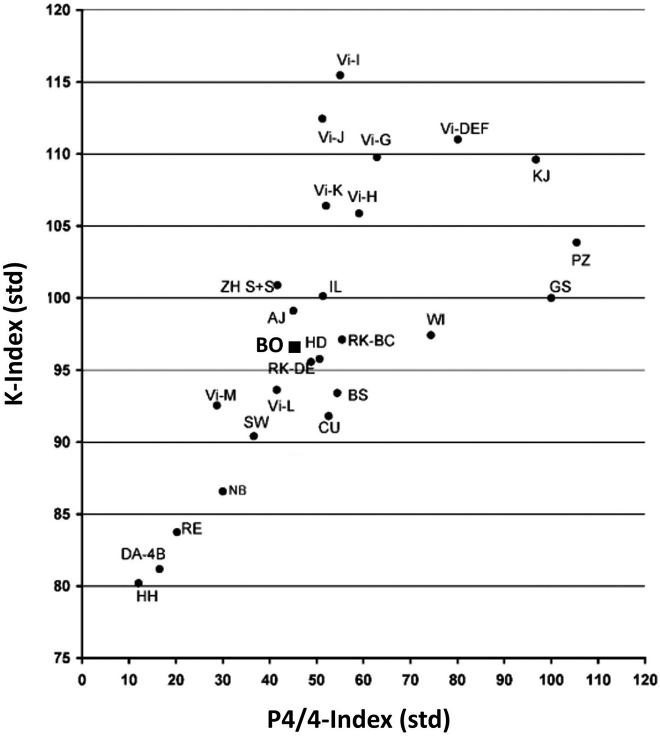


Fig. 8. Plot of K-index (std) and P4/4 index (std) of cave bear from different European caves and the speleians from Buco dell'Orso (Withalm, 2011, mod.)

the range of the values typical for the species, but with a higher breadth that indicates a greater robustness of the bones.

DISCUSSION AND CONCLUSIONS

This work is a study of the metapodia and phalanges from Buco dell'Orso Cave (Laglio, Como Province, Lombardy) to preliminarily allocate these bears in the evolutionary picture of the Italian and European cave bears. Considering the morphometric parameters of the metapodia, the bears of the Buco dell'Orso have a small or medium size in conformity with the sizes of both the skulls and mandibles. Therefore, an exception is found in the phalanges (mainly in the first phalanx) that show specimens of greater size. This collides with the general size of the Buco dell'Orso population. At the present we do not have a plausible explanation for this dualism. Morphometry and indices (IP and K-I) are relatively low compared with those of many other bears from Europe and together with the low morphodynamic index of the P4/4, are symptoms of an intermediate evolution for the Buco dell'Orso bears. Robu (2016) discusses the validity of the use of the indices: the P4/4 morphodynamic index, Plumpness index and K-index, as tools for the assessment of the bears evolution, concluding that these indices can be of regional validity, but not on a larger scale (Europe). They can be a very useful tool if considered together with the radiometric data and mtDNA analyses. At the present, if the future data will confirm an

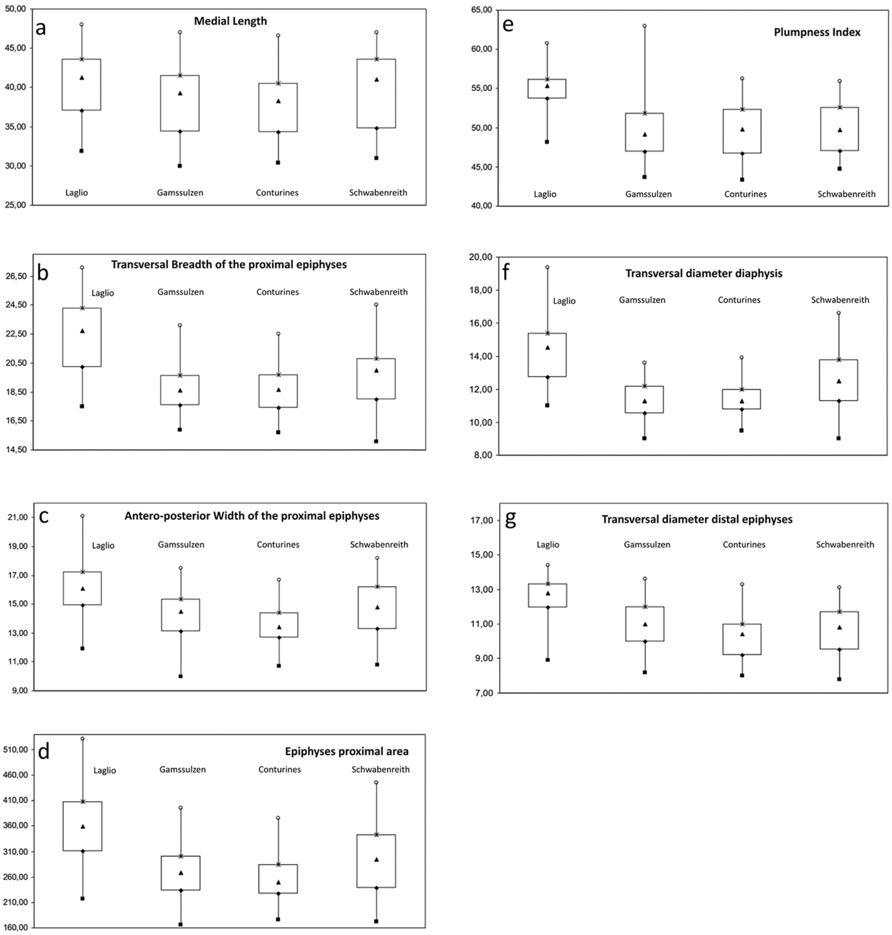


Fig. 9. Box-plots of the main parameters of the 1st phalanges from Buco dell'Orso, Gamssulzen, Conturines and Schwabenreith caves (Alscher, 2013, unpublished)

intermediate position in the evolutionary scale of the Italian cave bears, the population of the Buco dell'Orso is very similar to those of other sites (Grotta del Bandito, Buco del Frate, Venetian caves) in Italy.

Compared to those of *ingressus*, *ladinicus* and *eremus* the 1st phalanges of the bears from Buco dell'Orso are larger in size, and also more robust. This is an unexpected result because in different studies on the skulls and mandibles the adults of the Buco dell'Orso population had a smaller size compared to other Italian and European populations (Rossi & Santi, 2015).

Considering that the *Ursus spelaeus* remains found in the Buco dell'Orso come from a single level (Cornalia (1850, 1858 – 1871), it is possible that when the collection was assembled the specimens were divided, grouping the bigger cranial and mandibular ones in to another collection of which the knowledge is lost. In fact, we know of the presence of a single skull with a larger size exposed in the Museo di Storia Naturale of Milan. The data on the phalanges show that the studied population has a great size, similar to the others

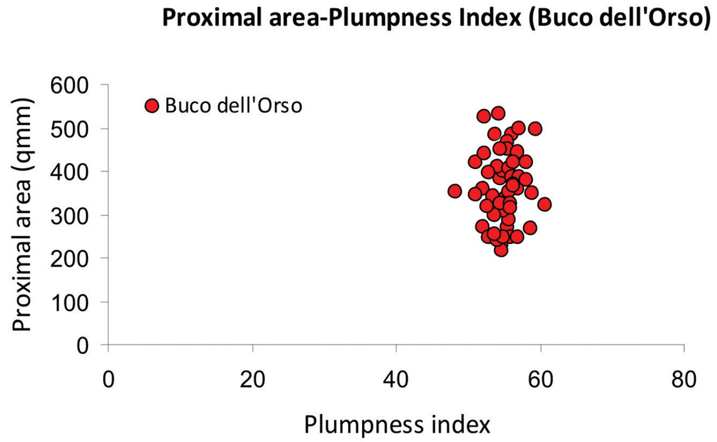


Fig. 10. Relationship between the Proximal area and the Plumpness index of the 1st phalanges from Buco dell'Orso

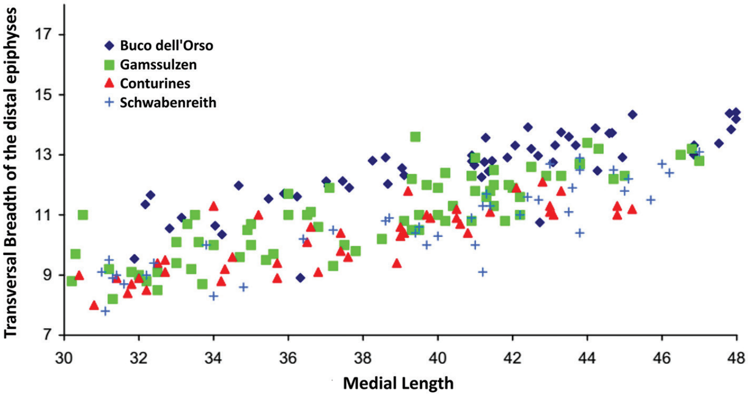


Fig. 11. Relationship between the Medial Length and the Transversal breadth of the distal epiphyses of the 1st phalanges from Buco dell'Orso, Gamssulzen, Conturines and Schwabenreith caves (data from Alscher, 2013, unpublished)

of the bigger populations and confirming the evolutionary trend toward the greater size typical of the most recent forms of cave bears. In this view the data agrees with those for the other Italian populations, particularly for those from the central and eastern sectors of the Alps (S. Donà di Lamon, Covoli di Velo and Grotta Pocala). Up to now, since the morphodynamic indices of molars are lacking, it is not possible to surely affirm that the Buco dell'Orso population can be included in the more specialized cave bears (*U. ingressus* sensu Rabeder et al., 2004) rather than in the group with a more primitive morphology that characterizes different populations of the central-eastern sectors of the Alps. The population effectively is placed in a contact zone between these two forms (*U. spelaeus* and *U. ingressus*), and this zone seems to be the last boundary for the penetration of the more specialized populations in Italy. More studies are necessary to further define the evolutionary place of Buco dell'Orso bears and to enlarge the knowledge on the migratory flow schemes that the study of the Italian populations seem to show.

Acknowledgements. The Authors thank Dr. Alessandro Garassino (Milan) for access to Museo Civico di Storia Naturale of Milan, Dr. Martin Sabol (Bratislava) for the comments and Dr. Nicoletta Benedetta Carlo-Stella (Cleveland) for help with English.

METAPÓDIA A PRSTOVÉ ČLÁNKY MEDVEĎOV JASKYNNÝCH Z BUCO DELL´ORSO (LOMBARDSKO, SEVERNÉ TALIANSKO)

Resume

Jaskyňa Buco dell'Orso (Lombardsko, severné Taliansko) je bohaté nálezisko fosílnych zvyškov medveďov jaskynných. Za účelom získania údajov o evolučnej úrovni miestnych medveďov boli analyzované ich metapódia a prstové články. Medvede z tejto lokality patria do skupiny *spelaeus*, hoci skúmané osteologické zvyšky vykazujú istý dualizmus vo veľkosti. Zatiaľ čo výsledky získané z analýzy metapódií potvrdzujú údaje zo štúdia lebiek a sánok, prstové články sú väčšie a mohutnejšie. Index zaoblenosti (the plumpness index), K-Index a údaje z P4/4 morfodynamickej analýzy ukazujú, že medvede z Buco dell'Orso zaberajú strednú pozíciu z hľadiska evolúcie tejto skupiny medveďov. Potvrdenie alebo vyvrátenie tohto predbežného záveru bude možné len po kompletnom štúdiu mtDNA a po rádiometrickom datovaní nálezov.

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SLOVENSKÝ KRAS ACTA CARSOLOGICA SLOVACA	56/1	29 – 46	LIPTOVSKÝ MIKULÁŠ 2018

FOSÍLNE NÁLEZY LEVA JASKYNNÉHO (*PANTHERA SPELAEA* GOLDFUSS, 1810) A MEDVEĎA JASKYNNÉHO (*URSUS* EX GR. *SPELAEUS* ROSENMÜLLER, 1794) Z HARMANECKEJ JASKYNE (VEĽKÁ FATRA)

TOMÁŠ ČEKLOVSKÝ

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T. Čeklovský: The fossil record of cave lion (*Panthera spelaea* Goldfuss, 1810) and cave bear (*Ursus* ex gr. *spelaeus* Rosenmüller, 1794) from the Harmanec Cave (Veľká Fatra Mts.)

Abstract: Studied bear fossils from the Harmanec Cave (southern part of the Veľká Fatra Mts.) belong to the bear from "*spelaeus*" group (*Ursus* ex gr. *spelaeus*), who died at maximum 3 years of age. This bear used the site probably as a place for hibernation. In addition, the Harmanec Cave is also new Slovak site with the fossil record of cave lion (*Panthera spelaea*). Lion remains belonged to an adult male. Both carnivores lived probably in an interstadial phase during the Last Glacial.

Key words: the Harmanec Cave, cave lion, cave bear, the Veľká Fatra Mts., osteology, morphometry, taphonomy, Last Glacial

ÚVOD

Harmanecká jaskyňa sa nachádza v južnej časti geomorfologického celku Veľká Fatra. Situovaná je v severozápadnom úbočí krasového masívu Kotolnica, v katastri obce Dolný Harmanec (48°48´50,41´´ S a 19°02´24,08´´ V) (obr. 1).

Lokalitu tvorí fluviokrasový inaktívny jaskynný priestor s dĺžkou 3 216 m, vertikálnym rozpätím 75 m a celkovým smerom jaskyne SSV – JJZ (obr. 2). Podzemné priestory boli vytvorené v tmavých gutensteinských vápencoch stredného triasu pozdĺž predisponovaných tektonických porúch (Polák et al., 2003). Priestory s korózno-rútivým charakterom sa činnosťou vody formovali počas pliocénu (Lenčo, 1950). Jaskynnú výzdobu tvoria veľké pagodovité stalagmity, sintrové vodopády a najmä speleotémy bieleho mäkkého sintra, ktorý tu vytvára jedinečné formy.

Vchod do jaskyne leží v nadmorskej výške 821 m. Vstupná sieň je pod názvom „Izbica“ známa od nepamäti. Využívali ju drevorubači a lesní robotníci ako úkryt v nepriaznivom počasí. Ďalšie priestory objavil dňa 22. júna 1932 Michal Bacúrik, keď sa prekopal do snehobielej siene nazvanej „Dóm objaviteľa“ (Bacúrik, 1950). Ďalšie objavné práce vykonali v rokoch 1938 až 1953 V. Kovalčík, O. Ondroušek, L. Šperka, K. Absolon a V. Lenčo (Šperka, 1947; Lenčo, 1950). Prvý biospeleologický výskum v jaskyni vykonal v r. 1946 Dr. Wagner a prvý geologický výskum J. Kukla (1951). Na staršie výskumy nadväzovali v druhej polovici 20. storočia práce členov Slovenskej speleologickej spoločnosti, pri ktorých sa našli 4 fragmenty lebkových kostí a ďalšie kosti človeka (Majko, 1959). Posledný geologický výskum na lokalite vykonala Ľ. Luhová (2013).

Obr. 1. Situovanie Harmaneckej jaskyne na výseku mapy strednej Európy
(zdroj: https://www.bing.com/maps, © 2018 Microsoft)
Fig. 1. Location of the Harmanec Cave on the map section of the Central Europe
(source: https://www.bing.com/maps, © 2018 Microsoft)

Terénne záznamy z horeuvedených výskumov neobsahujú žiadne zmienky o pozostatkoch pleistocénnej fauny. V súčasnosti žije v jaskyni niekoľko druhov netopierov a bezstavovcov (Bobáková a Hapl, 2002; Kováč et al., 2003). Jaskyňa je od 3. septembra 1950 sprístupnená pre verejnosť v dĺžke 720 m a v súčasnosti má štatút národnej prírodnej pamiatky (Karcolová, 1984).

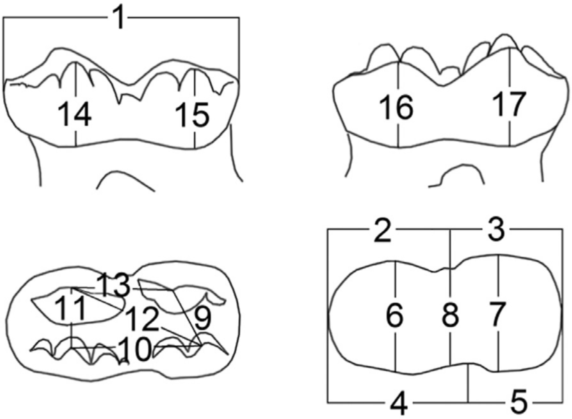
MATERIÁL A METODIKA

Skúmaný osteologický materiál v počte 14 kusov je uložený v depozitári Slovenského múzea ochrany prírody a jaskyniarstva (SMOPaJ) v Liptovskom Mikuláši pod evidenčnými číslami P00697 – 9 a prírastkovými číslami 697 – 9/77. Podľa prírastkovej knihy múzea z roku 1969 boli všetky kusy zozbierané v Izbici a zaevidované pod názvom „Kosti medveďa jaskynného“. Fosílne zvyšky boli po nadobudnutí múzeom zakonzervované neznámou chemickou látkou. Ďalšie informácie spojené s nadobudnutím a ani dokumentácia nálezových okolností sa nezachovali. Zuby medveďa jaskynného uložené v múzeu SMOPaJ s číslami P00699/1 – 3 už vo svojej diplomovej práci opísal M. Sabol (1997).

Nálezy boli najprv spracované pomocou morfometrickej analýzy. Na určovanie typu kosti a taxónu som použil prácu Palesa et al. (1981) a anatomická terminológia použitá

Obr. 2. Pôdorys Harmaneckej jaskyne s vyznačenou vstupnou sieňou s fosílnymi nálezmi (prekreslené z podkladov L. Krumpa; Zimák et al., 2001)
Fig. 2. Ground plan of the Harmanec Cave with the marked entrance hall with fossil record (redrawn from the documents of L. Krump; Zimák et al., 2001)

pri opise jednotlivých kostí je z práce Danka et al. (2013). Zuby medveďov boli morfologicky opísané podľa Musila (2005) a stupeň abrázie žuvacích plôch medvedích zubov bol stanovený podľa Stinerovej (1998). Základná morfometrická terminológia kostí vychádza z prác Gonzálesa (2003) (obr. 3) a Withalma (2001) (obr. 4).

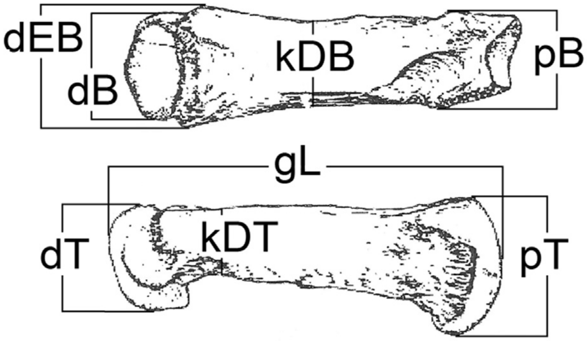


Obr. 3. Základný spôsob merania medvedej stoličky m2 (Gonzáles, 2003; upravené). **1** – maximálna dĺžka, **2** – labiálna dĺžka trigonidu, **3** – labiálna dĺžka talonidu, **4** – lingválna dĺžka trigonidu, **5** – lingválna dĺžka talonidu, **6** – šírka trigonidu, **7** – šírka talonidu, **8** – šírka stredovej zúženiny, **9** – vzdialenosť medzi hypokonidom a entokonidom, **10** – vzdialenosť medzi metakonidom a entokonidom, **11** – vzdialenosť medzi protokonidom a metakonidom, **12** – vzdialenosť medzi protokonidom a entokonidom, **13** – vzdialenosť medzi protokonidom a hypokonidom, **14** – výška metakonidu, **15** – výška entokonidu, **16** – výška hypokonidu, **17** – výška protokonidu
Fig 3. The basic measuring method of bear molar m2 (Gonzáles, 2003; modified). **1.** maximum length **2.** labial length of the trigonid **3.** labial length of the talonid **4.** lingual length of the trigonid **5.** lingual length of the talonid **6.** width of the trigonid **7.** width of the talonid **8.** width in the central constriction **9.** distance between hypoconid and entoconid **10.** distance between metaconid and entoconid **11.** distance between protoconid and metaconid **12.** distance between protoconid and entoconid **13.** distance between protoconid and hypoconid **14.** height of the metaconid **15.** height of the entoconid **16.** height of the hypoconid **17.** height of the protoconid

Na meranie bolo použité posuvné meradlo s maximálnym dosahom 13 cm a s presnosťou na 0,1 mm. Smerodajná odchýlka, rozptyl a náhodná chyba 10-krát opakovaného merania jedného rozmeru sa vypočítali pomocou programu PAST: Paleontological Statistics, verzia 3.18 (Hammer et al., 2001), (tabuľka 1). Všetky namerané hodnoty sú uvádzané v mm.

Tabuľka 1. Smerodajná odchýlka, rozptyl a náhodná chyba pri meraniach
Table 1. Standard deviation, dispersion and random error of measurements

Vzorka	**Rozmer**	**N**	**Smerodajná odchýlka**	**Rozptyl**	**Náhodná chyba**
Mc V (P00697/2)	max. dĺžka	10	0,1852926	0,03433333	0,05859465



Obr. 4. Základný spôsob merania záprstných kostí medveďov (Withalm, 2001; upravené). **gL** – maximálna dĺžka, **pB** – šírka proximálnej epifýzy, **pT** – výška proximálnej epifýzy, **kDB** – minimálna šírka diafýzy, **kDT** – minimálna výška diafýzy, **dB** – šírka distálnej hlavice (kladky), **dEB** – šírka distálnej epifýzy, **dT** – výška distálnej epifýzy
Fig. 4. The basic measuring method of bear metacarpal bones (Withalm, 2001; modified). **gL** – maximum length, **pB** – transversal diameter of the proximal epiphysis, **pT** – anteroposterior diameter of the proximal epiphysis, **kDB** – minimum transversal diameter of the diaphysis, **kDT** – minimum anteroposterior diameter of the diaphysis, **dB** – transversal diameter of the distal head, **dEB** – transversal diameter of the distal epiphysis, **dT** – anteroposterior diameter of the distal epiphysis

Fosílny materiál sa následne skúmal z tafonomického hľadiska, zameraného na kvantifikáciu skúmaného materiálu (celkový počet určených vzoriek, minimálny počet jedincov), ako aj na determináciu stôp po činnosti abiotických (sedimentácia, chemizmus) a biotických činiteľov (človek), ktoré sa na skúmanom materiáli zachovali. Tafonomické činitele boli determinované podľa prác Binforda (1981) a Lymana (1994).

Terénna časť bola vykonaná v marci 2018 a spočívala v obhliadke lokality s odobratím vzoriek sedimentov.

SYSTEMATICKÁ PALEONTOLÓGIA

Trieda Mammalia Linnaeus, 1758
Rad Carnivora Bowdich, 1821
Čeľaď Felidae Fischer de Waldheim, 1817
Rod *Panthera* Oken, 1816
Panthera spelaea Goldfuss, 1810

Holotyp: lebka dospelého samca (118 Qu Kat. p. 64) uložená v Prírodovednom múzeu Humboldtovej univerzity v Berlíne
Typová lokalita: jaskyňa Zoolithenhöhle pri Burggaillenreuthe, Nemecko
Stratigrafické rozšírenie: stredný až vrchný pleistocén (MQ 2)
Materiál: *os metacarpale* IV sin. (P00697/1), *os metacarpale* V sin. (P00697/2), *os naviculare* dext. (P00698/3), *phalanx proximalis* (P00698/1), *phalanx medialis* (P00698/2), *os metacarpale / metatarsale* (P00698/4); (Obr. 5, Tab. 2 – 3).
Opis materiálu: Proximálna hlavica Mc IV je ukončená kĺbovou plôškou oblúkovitého tvaru, na jej mediálnej strane sa nachádza výrazná kĺbová plôška pre skĺbenie s Mc III

a na laterálnej strane hlboká jama pre skĺbenie s Mc V; diafýza (telo kosti) je dlhá, okrúhleho prierezu; distálna hlavica je tvorená kladkou, ktorej chýba useknutá mediálna časť. Proximálna hlavica Mc V je ukončená kĺbovou plôškou oblúkovitého tvaru výrazne sa zužujúcou dorzálnym smerom, na jej mediálnej strane sa nachádza výrazná kĺbová plôška pre skĺbenie s Mc IV; diafýza je kratšia ako pri Mc IV, oválneho prierezu; distálna hlavica je tvorená kladkou, ktorá je rozdelená na dve časti výrazným sagitálnym hrebeňom; na laterálnej aj mediálnej strane je kladka lemovaná úponovými plôškami, od ktorých proximálne ležia malé hrboľčeky.

Člnkovitá kosť (*os naviculare*) a proximálny prstový článok sú zachované v celku. Mediálnemu prstovému článku chýba časť distálnej hlavice. Fragment neurčiteľného metapódia pozostáva z distálnej epifýzy s hlavicou a z časti tela kosti. Materiál patrí pravdepodobne tomu istému, dospelému jedincovi.

cf. *Panthera spelaea* Goldfuss, 1810

Materiál: fr. *vertebra cervicalis* (P00698/5), fr. *os* indet. (P00698/6)
Opis materiálu: Fragment krčného stavca pozostáva zo stavcového oblúku (*arcus vertebrae*) so zachovaným bočným výbežkom (*processus transversus*).

Tabuľka 2. Rozmery člnkovitej kosti leva jaskynného z Harmaneckej jaskyne. **1** – maximálna šírka, **2** – maximálna dĺžka, **3** – maximálna výška
Table 2. Measurements of the cave lion naviculare from the Harmanec Cave. **1.** maximum width **2.** maximum length **3.** maximum height

Taxón	Materiál	Evid. č.	1	2	3
Panthera spelaea	naviculare	P00698/3	40,5	51,6	24,1

Tabuľka 3. Rozmery záprstných kostí a prstových článkov leva jaskynného a medveďa jaskynného z Harmaneckej jaskyne. Rozmery sú opísané na obrázku č. 4
Table 3. Measurements of the cave lion and cave bear metacarpals and phalanges from the Harmanec Cave. Measurements are described in Figure 4

Taxón	Materiál	Evid. č.	gl	pB	pT	kDB	kDT	dB	dEB	dT
Panthera spelaea	Mc IV	P00697/1	*133,0*	27,0	28,4	16,2	17,9	-	-	-
Panthera spelaea	Mc V	P00697/2	119,9	30,2	29,5	18,8	15,0	23,6	26,1	24,7
Panthera spelaea	Px prox.	P00698/1	65,2	26,2	22,9	19,2	14,2	-----	20,1	16,2
Panthera spelaea	Px med.	P00698/2	-	21,6	24,4	17,1	15,3	-----	*27,2*	-
Ursus ex gr. *spelaeus* juv.	Mc II	P00698/8	-	12,6	20,5	10,4	9,4	-	-	-
Ursus ex gr. *spelaeus* juv.	Px med.	P00698/7	-	-	-	10,8	8,6	-----	15,6	12,0

Obr. 5. *Panthera spelaea*, Harmanecká jaskyňa. **1** – *phalanx medialis* (P00698/2), **2** – *phalanx proximalis* (P00698/1), **3** – *os naviculare* dext. (P00698/1), **4** – *os metacarpale* IV sin. (P00697/1), **5** – *os metacarpale* V sin. (P00697/2); pohľad zhora
Fig. 5. *Panthera spelaea*, the Harmanec Cave. **1** – *phalanx medialis* (P00698/2), **2** – *phalanx proximalis* (P00698/1), **3** – *os naviculare* dext. (P00698/1), **4** – *os metacarpale* IV sin. (P00697/1), **5** – *os metacarpale* V sin. (P00697/2); upper view

Čeľaď Ursidae Fischer de Waldheim, 1817
Rod *Ursus* Linnaeus, 1758
Ursus ex gr. *spelaeus* Rosenmüller, 1794

Holotyp: lebka mladého dospelého samca (MB Ma.5017) uložená v Prírodovednom múzeu Humboldtovej univerzity v Berlíne
Typová lokalita: jaskyňa Zoolithenhöhle pri Burggaillenreuthe, Nemecko
Stratigrafické rozšírenie: stredný až vrchný pleistocén (MQ 2)
Materiál: fr. *maxilla* sin. s I3 (P00699/1), I3 dext. (P00699/2), m2 dext. (699/3), *os metacarpale* II dext. (P00698/8), *phalanx medialis* (P00698/7), fr. *cranium* (P00699/4); (Obr. 6, Tab. 3 – 5).
Opis materiálu: Dentíciu už predbežne opísal Sabol (1997). Korunky rezákov sú v apikálnej časti neabradované; majú zachované aborálne bazálne cingulá, mierne zhrboľatené pri distálnom okraji, kde sa naň napája hrebeň; na meziálnej strane koruniek sú pri báze zachované výrazné plôšky po styku s I2; rezák č. 699/2 má koreň ulomený v strednej časti.

Tabuľka 4. Rozmery rezákov medveďa jaskynného z Harmaneckej jaskyne. **1** – priečny priemer korunky, **2** – pozdĺžny priemer korunky, **3** – výška korunky
Table 4. Measurements of the cave bear incisors from the Harmanec Cave. **1.** transversal diameter of crown **2.** anteroposterior diameter of crown **3.** crown height

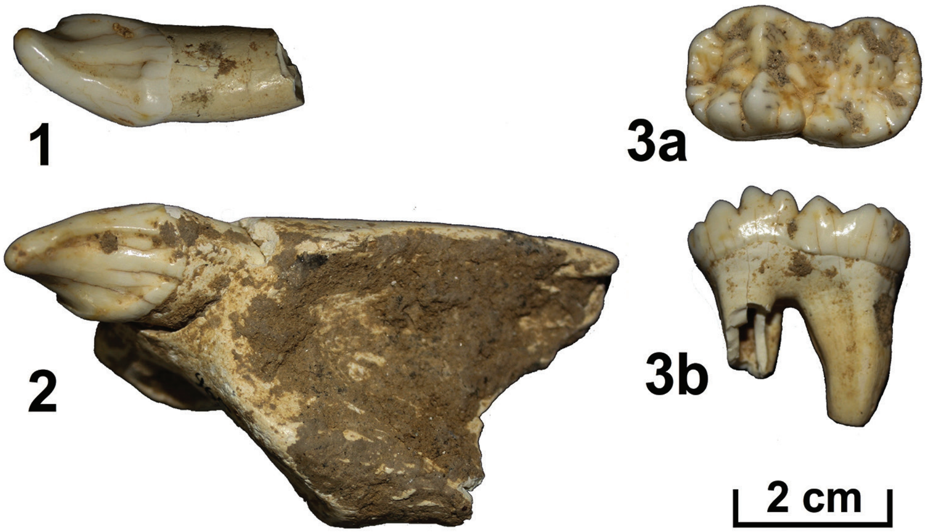
Taxón	**Materiál**	**Evid. č.**	**1**	**2**	**3**
Ursus ex gr. *spelaeus* juv.	I3 sin.	P00699/1	10,9	13,8	20,7
Ursus ex gr. *spelaeus* juv.	I3 dext.	P00699/2	11,2	14,0	19,0

Tabuľka 5. Rozmery stoličky medveďa jaskynného z Harmaneckej jaskyne. Rozmery sú opísané na obrázku č. 3
Table 5. Measurements of the cave bear molar from the Harmanec Cave. Measurements are described in Figure 3

Taxón	**Materiál**	**Evid. č.**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**
Ursus ex gr. *spelaeus* juv.	m2 dext.	P00699/3	29,1	13,5	14,2	13,5	15,0	16,3	16,2	14,1
		9	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**
		10,2	13,3	13,1	13,6	8,8	7,5	9,2	10,3	9,7

Žuvacia plocha stoličky (m2) je slabo abradovaná (stupeň abrázie II); parakonid splýva s hrboľčekmi na prednom okraji zuba; jednoduchý protokonid má vyvinutý hrebeňovitý entprotokonid na vnútornej strane; metakonid je s meziálnym aj distálnym metastylidom, s entmetakonidom a malým mezostylidom; entokonidový komplex pozostáva z dvoch hrboľčekov, z ktorých zadný je mohutnejší, v apikálnej časti ešte rozdvojený; hypokonid má vyvinutý enthypokonid na vnútornej strane spolu s hypostylidom, hypokonulid splýva s hrboľčekmi na zadnom okraji zuba, pričom je najväčší z nich, ležiaci pri hypokonide; cingulum je zachované na posterolabiálnom a posteriórnom okraji korunky; korene sú dva, duté, predný koreň je ulomený v strednej časti.

Proximálna hlavica Mc II je ukončená mierne oblou kĺbovou plôškou zužujúcou sa plantárnym smerom, na jej mediálnej strane sa nachádza kĺbová plôška pre skĺbenie s Mc I; diafýza je krátka, oválneho prierezu; nezrastená distálna hlavica chýba. Prstovému článku chýba nezrastená proximálna epifýza. Materiál patrí minimálne jednému juvenilnému jedincovi.



Obr. 6. *Ursus* ex gr. *spelaeus*, Harmanecká jaskyňa. **1** – I3 dext. (P00699/2), **2** – fr. *maxilla* s I3 sin. (P00699/1), **3** – m2 dext. (P00699/3; **a** – oklúzny pohľad, **b** – lingválny pohľad)
Fig. 6. *Ursus* ex gr. *spelaeus*, the Harmanec Cave. **1** – I3 dext. (P00699/2), **2** – fr. *maxilla* with I3 sin. (P00699/1), **3** – m2 dext. (P00699/3; **a** – occlusal view, **b** – lingual view)

Tabuľka 6. Počet kostrových pozostatkov z Harmaneckej jaskyne. **NISP –** celkový počet určených vzoriek, **MNI –** minimálny počet jedincov
Table 6. Number of bone elements from the Harmanec Cave. **NISP –** number of identified specimens **MNI –** minimum number of individuals

Taxón	**NISP**	**MNI**	**juvenilné**	**adultné**
Panthera spelaea / cf. *P. spelaea*	8	1	-	1
Ursus ex gr. *spelaeus*	6	1	1	-

ZÁKLADNÉ TAFONOMICKÉ VYHODNOTENIE

Skúmaný materiál je sfarbený do svetlých odtieňov žltej až bielej farby, ktorá je spôsobená fosilizáciou v mäkkom sintri. Svetlá farba povrchu kostí a drobné sintrové povlaky na povrchu kostí sú dobrým ukazovateľom pôvodnej akumulácie a fosilizácie kostí v prostredí Harmaneckej jaskyne. Pokrytie kostí povlakom sintra svedčí o tom, že kosti museli ležať istý čas na povrchu vo vnútri jaskynného priestoru. Materiál je na povrchu miestami tiež pokrytý čiernymi povlakmi, ktoré vytvárajú charakteristické dendritické vzory. Povlaky sú dôsledok prieniku zlúčenín Mn-Fe oxidov obsiahnutých v jaskynnej vode a v jaskynnom sedimente. Prímesi oxidov Fe a Mn v sedimentoch Harmaneckej jaskyne potvrdila aj optická mikroskopia, ktorú vykonala na pracovisku SMOPaJ v Liptovskom Mikuláši Ľ. Luhová (2013).

Skúmaný materiál vykazuje rôzne stupne poškodenia. V skúmanej vzorke sa nachádzajú stopy po výkopových prácach v podobe odštiepenia povrchu kosti – odlúpnutie alebo odseknutia celej časti kosti ostrejším predmetom.

DISKUSIA

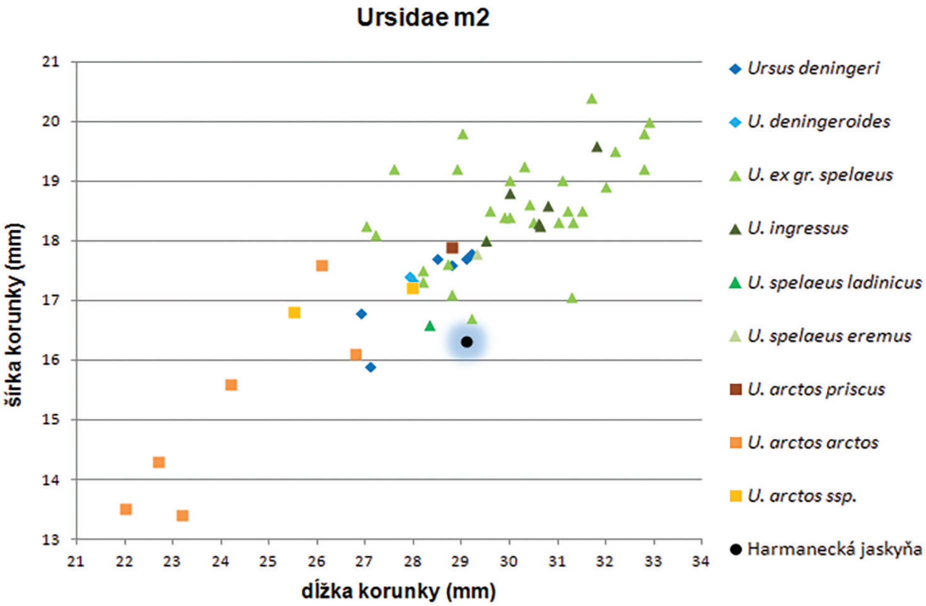
Na základe morfologickej analýzy sú nálezy medveďa z Harmaneckej jaskyne taxonomicky zaradené k medveďom zo skupiny *spelaeus*. Podľa DNA analýz vykonaných Stillerom et al. (2014) sa speleoidné medvede rozdeľujú do dvoch samostatných vývojových línií – *Ursus spelaeus* zo západnej časti Európy a *U. ingressus* z východnej časti Európy (vrátane Západných Karpát). Rabeder et al. (2004) rozdeľuje líniu *spelaeus* ešte do troch čiastkových línií – *U. s. spelaeus*, *U. s. ladinicus* a *U. s. eremus*. Taxóny sa vyznačujú istými metrickými rozdielmi ako výsledok adaptácie na rozdielne environmentálne podmienky. Vysokohorské medvede *U. s. ladinicus* a *U. s. eremus* boli o niečo menšie.

Stolička m2 medveďa jaskynného z predmetnej lokality bola metricky porovnaná s nálezmi medveďov z vybraných európskych pleistocénnych lokalít (*U. deningeri* – Aze I, Bilzingsleben, Einhornhöhle, Urdhöhle, Chateau, Stránska skála; *U.* „*deningeroides*“ – Aze I; *U.* ex gr. *spelaeus* – Berze, Saint-Aubin, Saint-Romain, Barová, Pod hradem, Švédův stůl, Činčianska jaskyňa, Domica, Homološova diera, Horná Túfna, Jánošíkova jaskyňa, Javorinka, Malá drienčanská jaskyňa, Malá ľadnica, Medvedia jaskyňa v Jánskej doline, Medvedia jaskyňa v Západných Tatrách, Moldavská jaskyňa, Psie diery, Šarkania diera, Teplica, Tmavá skala, Trojuholník, Važecká jaskyňa; *U. ingressus* – Gamssulzenhöhle, Medvedia jaskyňa v Slovenskom raji; *U. spelaeus ladinicus* – Conturines; *U. spelaeus eremus* – Ramesch; *U. arctos priscus* – Předmostí, *U. arctos arctos* – Pyreneje, Klenovec, Líščia jaskyňa, Lukáčova priepasť, Medvedia jaskyňa pri Hučiakoch, Očová; *U. arctos* ssp. – Kupčovie izbička, Moldavská jaskyňa). Porovnávané boli dĺžka a šírka korunky, ktorých hodnoty sa nachádzajú v tabuľke 5. Hoci stolička z Harmaneckej jaskyne patrila nedospelému jedincovi, porovnávací graf (obr. 7) potvrdzuje príslušnosť zuba k medveďovi zo skupiny *spelaeus* (*Ursus* ex gr. *spelaeus*).

Metricky porovnaná bola aj štvrtá záprstná kosť leva jaskynného s nálezmi levov z nemeckých vrchnopleistocénnych lokalít Bilstein (2 samci, 1 samica) a Neumark-Nord (1 samica). Porovnané boli maximálna dĺžka kosti a šírka proximálnej epifýzy, ktorých hodnoty sa nachádzajú v tabuľke 3. Na grafe (obr. 8) je zreteľné, že záprstná kosť zo skúmanej lokality je dlhšia aj robustnejšia a patrila mohutnejšiemu jedincovi, s najväčšou pravdepodobnosťou dospelému samcovi.

V blízkom okolí Harmaneckej jaskyne boli fosílie medveďov jaskynných nájdené aj v jaskyniach Dolná Túfna (935 m n. m.) a Horná Túfna (975 m n. m.), patriace predovšetkým senilným (starým) jedincom (Čeklovský, nepublik.). V skúmanej vzorke z Harmaneckej jaskyne sa vyskytujú pozostatky medveďa juvenilného veku (vek 1 až 3 rokov). Nenachádzajú sa na nich ani stopy po aktivite iných predátorov, ani patologické prejavy. Všeobecne, v jednotlivých tafocenózach medveďov jaskynných tvoria vo väčšine prípadov najväčšiu časť juvenilné a staré jedince. Považuje sa to za jasný ukazovateľ prirodzenej mortality spojenej s úhynom počas hibernácie (Kurtén, 1976; Stiner et al., 1998). Okolité územie Harmaneckej jaskyne má z geomorfologického hľadiska ráz stredohorského reliéfu s prudko sa zvažujúcimi úbočiami do údolia (obr. 10). Dolinu prehĺbil svojou erozívnou činnosťou Harmanecký potok. Jaskyňa leží 260 m nad potokom, resp. dnom doliny. Prítomnosť vody mohla zohrať významnú úlohu pri hľadaní vhodných miest na prezimovanie.

V jaskyniach na Slovensku ale aj celkovo v Európe sa najčastejšie nachádzajú fosílne zvyšky medveďov jaskynných (*Ursus* ex gr. *spelaeus*) z vrchného pleistocénu. Taxóny mäsožravcov slúžia ako dobrý indikátor paleoprostredia, ako aj na definovanie indivi-

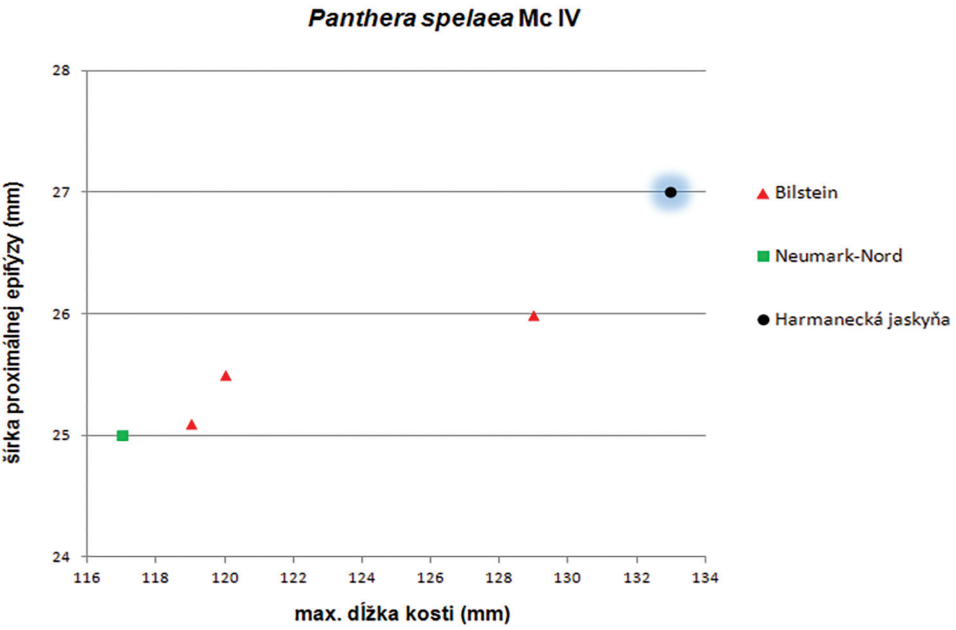


Obr. 7. Porovnanie rozmerov spodnej stoličky medveďa z Harmaneckej jaskyne s údajmi z vybraných európskych jaskýň (údaje prevzaté z prác Erdbrinka, 1953; Musila, 1959, 1962, 1965, 1972, 1991; Sabola, 1998, 2002, 2005; Rabedera et al. 2004; Vlčeka a Sabola, 2006; Sabola et al., 2009, 2014; Čeklovského, 2011)
Fig. 7. Comparision of measurements of lower molar of bear from the Harmanec Cave with data from selected European sites (data source: Erdbrink, 1953; Musil, 1959, 1962, 1965, 1972, 1991; Sabol, 1998, 2002, 2005; Rabeder et al. 2004; Vlček and Sabol, 2006; Sabol et al., 2009, 2014; Čeklovský, 2011)

duálnych časových horizontov a makrobiozonáciu (Sabol, 2000). Na Slovensku sú fosílie medveďov jaskynných známe z viac ako 60 jaskynných lokalít datovaných od konca stredného pleistocénu po obdobie posledného zaľadnenia (Sabol, 2001) a ich počet sa neustále zvyšuje. Z paleoekologického hľadiska je výskyt medveďov jaskynných spojený s oblasťami, kde najviac prevažovali ihličnaté a zmiešané lesy a neprístupný hornatý terén s prítomnosťou vody. V Západných Karpatoch sa najvyšší vertikálny výskyt medveďov jaskynných pohybuje v rozhraní od 1505 do 1559 m n. m., doložený nálezmi z Javorinky (Sabol et al., 2014; Čeklovský, nepublik.) vo Vysokých Tatrách.

Fosílne zvyšky levov jaskynných boli dosiaľ opísané z 12 slovenských lokalít z obdobia vrchného pleistocénu (Sabol, 2011; Čeklovský a Sabol, 2012; Laughlan et al., 2012). Harmanecká jaskyňa predstavuje ďalšiu lokalitu s nálezmi tejto vyhynutej mačkovitej šelmy (obr. 9). Lokality sú situované v nadmorskej výške od 240 do 1133 m (tabuľka 7). Lokality s nižšími nadmorskými výškami (Deravá skala, Čertova pec, Prepoštská jaskyňa) sú známe aj svojimi archeologickými nálezmi, kde prítomnosť fosílií leva mohla byť spôsobená akumuláciou človekom resp. inými predátormi (napr. hyena jaskynná; Čeklovský et al., 2016). Z tohto pohľadu sa spodná vertikálna hranica prirodzeného výskytu levov na Slovensku posúva na úroveň cca 500 m n. m.

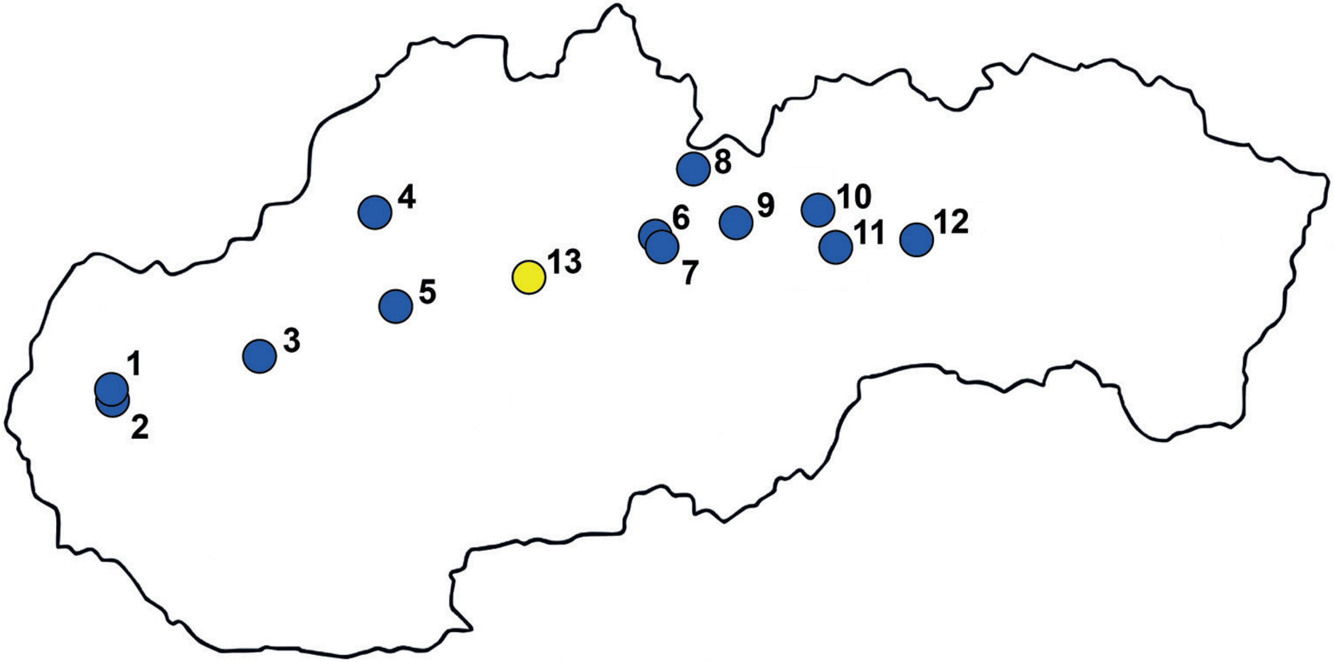
Lev jaskynný je ekologicky flexibilný druh. Prednosť dával boreálnym lesom aj otvoreným plochám, kde sa pohybovali stredne veľké až veľké rastlinožravce (Hublin, 1984). Podľa Musila (1986) prirodzene prenikal do vyšších nadmorských výšok.



Obr. 8. Porovnanie rozmerov záprstnej kosti leva z Harmaneckej jaskyne s údajmi z vybraných európskych jaskýň (údaje prevzaté z prác Diedricha, 2009 a 2011)
Fig. 8. Comparision of measurements of metacarpal bone of lion from the Harmanec Cave with data from selected European sites (data source: Diedrich, 2009 and 2011)

Európske populácie druhu *P. spelaea* žili v podhorských a horských oblastiach. Ich maximálne vertikálne rozšírenie v Európe počas posledného zaľadnenia varírovalo od 1460 m n. m. (Magurská jaskyňa; Kowalski, 1959) do 2800 m n. m. (Conturines; Rabeder et al., 2000). Harmanecká jaskyňa je výbornou strategickou polohou, odkiaľ mohol lev jaskynný bezpečne sledovať pohyb zveri, ktorá sa chodila napájať k vodnému zdroju.

Fosílne zvyšky cicavcov v jaskynných sedimentoch patria medzi najdôležitejšie údaje pre kvartérnu stratigrafiu. Okrem zvyškov malých cicavcov sa v slovenských jaskyniach najčastejšie nachádzajú kosti a zuby medveďov jaskynných. Fosilizácia kostí závisí od času, druhu sedimentu a od chemických procesov, ktoré v nich prebiehali. Skúmaný materiál je sfarbený do svetlých odtieňov žltej až bielej farby spôsobenej fosilizáciou mäkkým sintrom, ktorý vypĺňa veľkú časť priestorov Harmaneckej jaskyne. Mäkký sinter (angl. „moonmilk“) je zvláštny typ speleotémy, ktorý predstavuje biely, žltkastý alebo hnedastý agregát kalcitu. Mäkký sinter obsahuje veľké množstvo vody, spravidla medzi 40 – 80 %. Pokiaľ táto sintrová forma vyschne, tak je veľmi ľahká a má kriedový charakter (Bosák et al., 1988). Pokrýva steny, strop a miestami aj podlahu jaskyne. Navyše sa sinter tvorí len za istých klimatických podmienok, najmä v teplejších a vlhkejších obdobiach. Z uvedeného vyplýva, že nálezy z Harmaneckej jaskyne patrili jedincom, ktoré žili pravdepodobne v teplejšom a vlhkejšom období interštadiálneho charakteru počas posledného zaľadnenia (visla).



Obr. 9. Lokality s nálezmi leva jaskynného na Slovensku (Sabol, 2011; Čeklovský a Sabol, 2012; Laughlan et al., 2012; upravené).
1 – Deravá skala, Malé Karpaty, 2 – Tmavá skala, Malé Karpaty, 3 – Čertova pec, Považský Inovec, 4 – Pružinská Dúpna jaskyňa, Strážovské vrchy, 5 – Prepoštská jaskyňa, Hornonitrianska kotlina, 6 – Vyvieranie, Nízke Tatry, 7 – Okno, Nízke Tatry, 8 – Medvedia jaskyňa, Západné Tatry, 9 – Važecká jaskyňa, Kozie chrbty, 10 – Gánovce-Hrádok, Podtatranská kotlina, 11 – Medvedia jaskyňa, Slovenský raj, 12 – Šarkania diera, Volovské vrchy, 13 – Harmanecká jaskyňa, Veľká Fatra
Fig. 9. Slovak sites with the cave lion fossil record (Sabol, 2011; Čeklovský and Sabol, 2012; Laughlan et al., 2012; modified).
1. Deravá skala Cave, Malé Karpaty Mts. 2. Tmavá skala Cave, Malé Karpaty Mts. 3. Čertova pec Cave, Považský Inovec Mts. 4. Pružinská Dúpna Cave, Strážov Mts. 5. Prepoštská Cave, Horná Nitra Basin 6. Vyvieranie Cave, Nízke Tatry Mts. 7. Okno Cave, Nízke Tatry Mts. 8. Medvedia (Bear) Cave, Západné Tatry Mts. 9. Važec Cave, Kozie chrbty Mts. 10. Gánovce-Hrádok, Podtatranská Basin 11. Medvedia (Bear) Cave, Slovenský raj Mts. 12. Šarkania diera Cave, Volovské vrchy Mts. 13. Harmanec Cave, Veľká Fatra Mts.

Tabuľka 7. Vertikálne rozšírenie levov na Slovensku (údaje prevzaté z prác Bella et al., 2007; Sabol, 2011; Čeklovský a Sabol, 2012; Laughlan et al., 2012)
Table 7. Vertical distribution of lions in Slovakia (data source: Bella et al., 2007; Sabol, 2011; Čeklovský a Sabol, 2012; Laughlan et al., 2012)

Panthera spelaea	**Nadmorská výška**
Lokalita	**m n. m.**
Medvedia jaskyňa, ZT (8)	1133
Okno (7)	915
Medvedia jaskyňa, SR (11)	905
Harmanecká jaskyňa (13)	**821**
Vyvieranie (6)	791
Važecká jaskyňa (9)	784
Šarkania diera (12)	690
Gánovce-Hrádok (10)	642
Pružinská Dúpna jaskyňa (4)	590
Tmavá skala (2)	500
Deravá skala (1)	460
Prepoštská jaskyňa (5)	242
Čertova pec (3)	240
Priemerná nadmorská výška	*670,23*
Priemerná prirodzená nadm. výška	*792,11*

ZÁVER

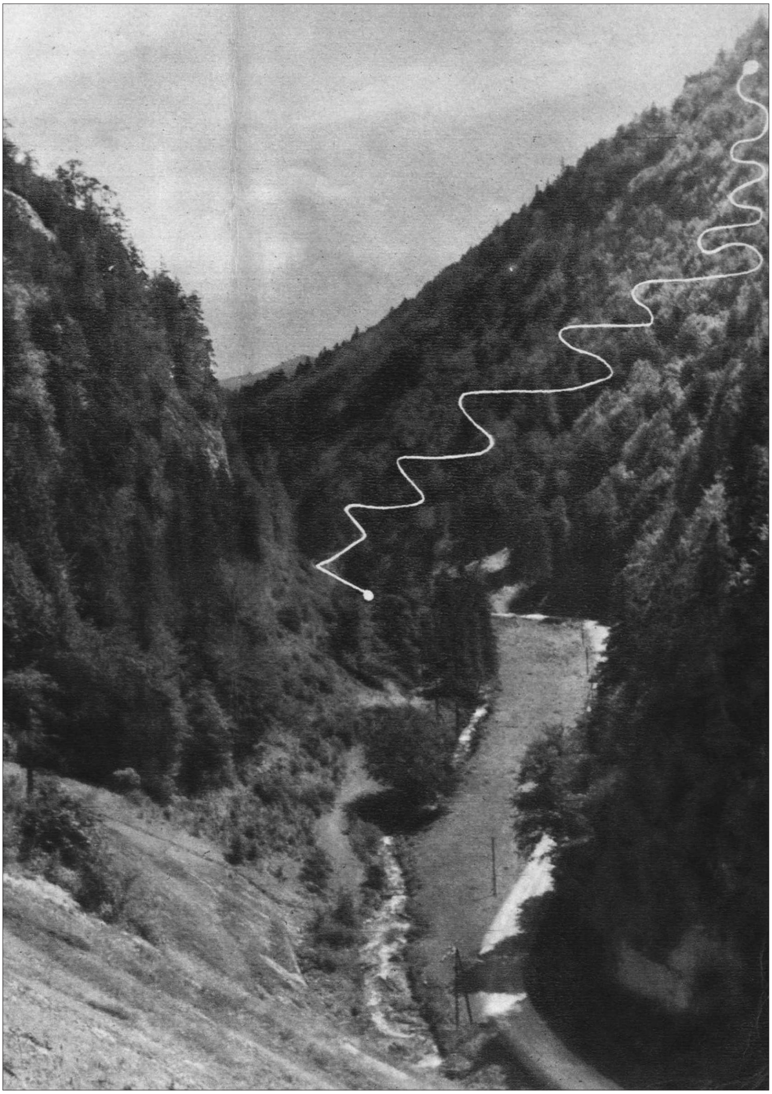
Predmetné medvedie fosílie patrili medveďovi zo skupiny *spelaeus* (*Ursus* ex gr. *spelaeus*), ktorý umrel vo veku maximálne 3 rokov. Lokalitu pravdepodobne využil ako miesto na prezimovanie, no zimnú hibernáciu neprežil. Harmanecká jaskyňa je zároveň v poradí 13. slovenskou lokalitou s nálezmi leva jaskynného (*Panthera spelaea*). Levie zvyšky patrili pravdepodobne dospelému samcovi. Obidva mäsožravce žili s najväčšou pravdepodobnosťou v interštadiálej fáze počas posledného zaľadnenia.

THE FOSSIL RECORD OF CAVE LION (*PANTHERA SPELAEA* GOLDFUSS, 1810) AND CAVE BEAR (*URSUS* EX GR. *SPELAEUS* ROSENMÜLLER, 1794) FROM THE HARMANEC CAVE (VEĽKÁ FATRA MTS.)

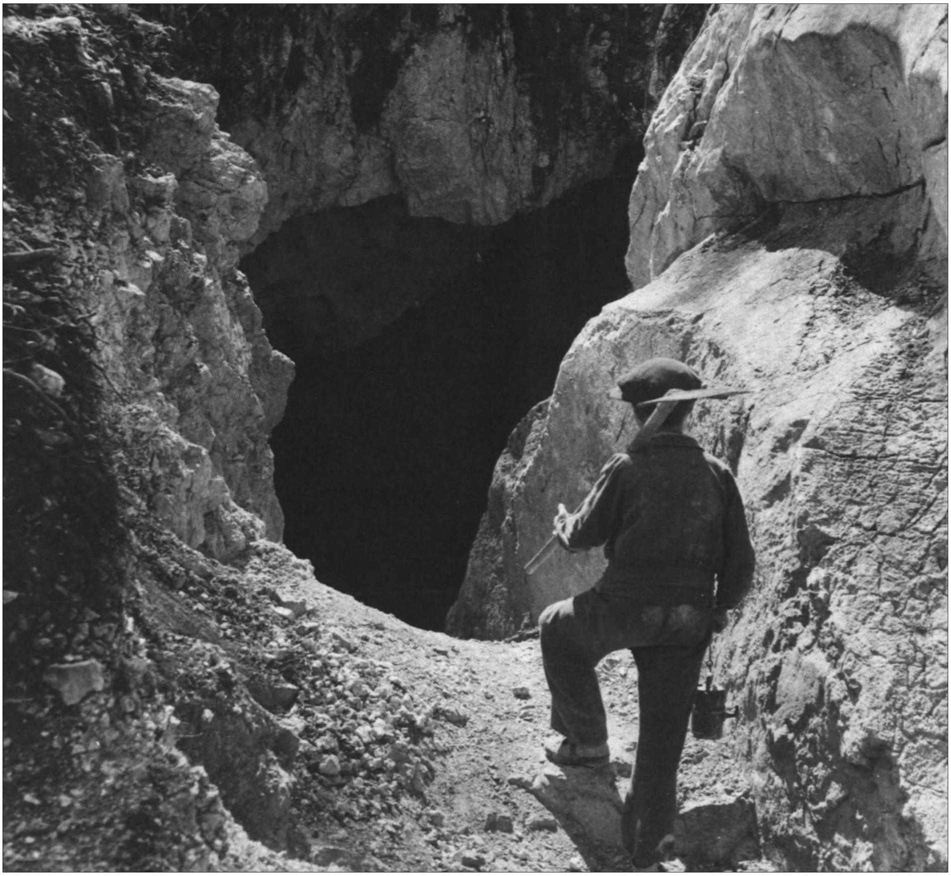
Summary

The Harmanec Cave is situated in southern part of the Veľká Fatra Mts. The site represents a fluvial-karst inactive cave system with 3.216 m of length and 75 m of vertical span, formed in the Gutenstein Limestone with an entrance altitude of 821 m above sea level. Studied osteological material from the site is stored in the depository of the Slovak Museum of Nature Protection and Speleology in Liptovský Mikuláš. Fossil material in the number of 14 pieces was studied by morphometric and taphonomic analyses. Analysed material is coloured in bright hues of yellow to white, which is caused by a fossilisation in moonmilk (soft) sinter and this is reliable indicator of the autochthonous accumulation and fossilisation of bones in the Harmanec Cave environment.

Fossil remains belong to a bear from „*spelaeus*“ group (*Ursus* ex gr. *spelaeus*) and to a cave lion (*Panthera spelaea*). The measurements of the cave bear molar and cave lion metacarpals were compared with data taken from several Late Pleistocene sites in Europe. Studied bear died at maximum 3 years of age and used the site probably as a place for hibernation. In the vicinitiy of the Harmanec Cave were bear fossils found also in the Dolná Túfna Cave (935 m a.s.l.) and Horná Túfna Cave (975 m a.s.l.). In addition, the Harmanec Cave is new Slovak site with the fossil record of cave lion. Lion fossils probably belonged to an adult male. The site under study was good strategic point from where the lion could safely watch the movement of the game that was going to feed to the stream. Both carnivores lived probably in an interstadial phase during the Last Glacial.



Obr. 10. Harmanecká dolina, pohľad z vlakovej zastávky. Biela farba vyznačuje trasu ku vchodu do jaskyne. Foto: Archív Slovenského múzea ochrany prírody a jaskyniarstva
Fig. 10. The Harmanecká Valley, view from the train stop. White color marked the path to cave entrance. Photo: Archive of the Slovak Museum of Nature Protection and Speleology



Obr. 11. Vchod do Harmaneckej jaskyne v čase sprístupňovacích prác. Foto: Archív Slovenského múzea ochrany prírody a jaskyniarstva
Fig. 11. The Harmanec Cave entrance at the time of commercial works. Photo: Archive of the Slovak Museum of Nature Protection and Speleology

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SLOVENSKÝ KRAS ACTA CARSOLOGICA SLOVACA	56/1	47 – 55	LIPTOVSKÝ MIKULÁŠ 2018

SOME PALEONTOLOGICAL EVIDENCE OF CAVE LION BIOLOGY

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I. V. Kirillova, F. K. Shidlovskiy, J. van der Plicht, O. F. Chernova: Some paleontological evidence of cave lion biology

Abstract: A skull of cave lion, *Panthera spelaea* (Goldfuss, 1810) was discovered in glacial deposits in north-eastern Russia. It reveals deep traces of canine teeth on its face, associated with suffocation by another lion. This was the real cause of death and one of the manners of modern lions killing. Radiocarbon dating shows that the skull is older than 48,500 calendar years. The observed features suggest biology similar to modern lions in social behaviour: hierarchy, competition between males, struggle for the territory, and pride formation. The dental system shows serious damages such ascaries, chipped broken parts, and extensive microwear on canines and carnassials. Such features are also observed on the other cave lion skulls. This suggests that, in addition to meat, the cave lion fed on bones of large prey, including frozen carcasses. The active combative behaviour of males, recorded paleontologically in tooth damage (besides lesions on soft tissues which are not traumatic), caused the decrease of their vitality. Therefore, males died at younger age than females. The latter could reach old age, even with strongly eroded or lost teeth.

Key words: N-E Russia, cave lion, dental damage, male combat

INTRODUCTION

The first scientific description of a cave lion skull was made by A. Goldfuss in 1810 and comes from southern Germany. The specimen was discovered in the cave No. D 106 named at that time as “Gailenreuther Höhle” currently known as “Zoolithenhöhle” (Goldfuss, 1810). Recently, the holotype was re-analysed, indicating the intravital V-shaped lesion on the cerebral part of the skull in the region of the sagittal crest as a trace from teeth of another large predator. Similar, but deeper lesions are noted on the skull of cave lion female from the Czech location “Srbsko” (Diedrich, 2008). The specific morphology of the remains, associated with pathology or attacks of the top predators, has been described by several authors (Barycka & Narojek, 2006; Rothschild & Diedrich, 2012).

In Russia, the first discovery of cave lion was made in northern Yakutia (Cherskiy, 1891). The author identified the femur incorrectly as belonging to a tiger, *Panthera* *tigris*. This error was caused by difficulties in distinguishing the bones of these two predators at that time . Cherskiy's identification was later corrected by other researchers. Vereshchagin (1971) summarized and systematized the data of different authors on cave lion remains, substantiated the status of independent species based mainly on the features of skeleton. In recent publications, the similarity between cave lion and lion was shown to be larger than the one between cave lion and tiger (Baryshnikov & Boeskorov, 2001; Sotnikova & Nikolsky, 2006; Boeskorov & Baryshnikov, 2013). This confirms the conclusion of Vereshchagin (1971) and the others. Based mainly on the "lions" features of the skull and skeleton, the authors assumed a social way of life similar to present lions. However, paleontological evidence for this is still lacking.

The goal of our work is to interpret paleontological data of a cave lion skull from the collection of the Museum of the Ice Age (IAM) in Moscow.

MATERIALS AND METHODS

The cave lion skull without lower jaw with collection number F-4142 was discovered on the Badyarikha River, right tributary of the Indigirka River, northern Yakutia, Russia (Fig. 1) in Pleistocene glacial deposits. A sample of the skull was dated by Radiocarbon in

Fig. 1. Location of cave lion skull with Coll. Number F-4142

Groningen, the Netherlands. The ^{14}C age is older than 45,000 BP, which is the background value of the dating method. After calibration (Reimer et al., 2013), the absolute age is more than 48,500 calBP (calendar years relative to 1950 AD). When studying the skull, we applied macro- and microscopic morphological methods. Images of the skull and teeth were obtained with different magnifications using a digital camera (Sony 5000) and a Keyence digital microscope.

DESCRIPTION AND DISCUSSION

The total length of the skull is about 39 cm. This is close to the length of the holotype skull from Zoolithenhöhle (40.2 cm) and other male from the Pleistocene of Western Europe. However, it significantly exceeds the length of cave lion skulls from Yakutia (30.3 cm in the holotype of a new subspecies, № ZIN 29398, Zoological Institute RAS – ZIN; 30.9 cm in the paratype, № YIG 3190/1, Yakutsk Institute of Geological Sciences, SB RAS). The small size of the cave lion skulls from northern Yakutia served as a basis to describe a north-eastern Late Pleistocene subspecies *P. s. vereshchagini* (Baryshnikov & Boeskorov, 2001). The skull belonged to a large adult male.

Macro- and microwear of the cave lion's CL's teeth during its life, sample F-4142

The right carnassial, P4, is entirely carious; its surrounding dental tissue has enlarged pores and it is loose and degraded, which is a result of inflammation of the periosteum. The left carnassial is absent but around it, the dental tissue is healthy and dense; probably the tooth was healthy. The crown of the left upper canine was broken during the life, approximately in the middle part, and eroded away as a result of further use; the pulp channel is open (Fig. 2); the right P3 and P4, and the left P3 have lifetime stubs which are clearly visible. All incisors are strongly worn (until to the pulpal canal), and the line of their vertices, when viewed from the front, is oblique to the side of the broken left canine. This is the result of uneven application of force during feeding. Microwear is visible by deep carious cavities on almost all teeth (Fig. 3). In addition, we found: (1) numerous chips of enamel of various sizes and configurations, (2) locally small

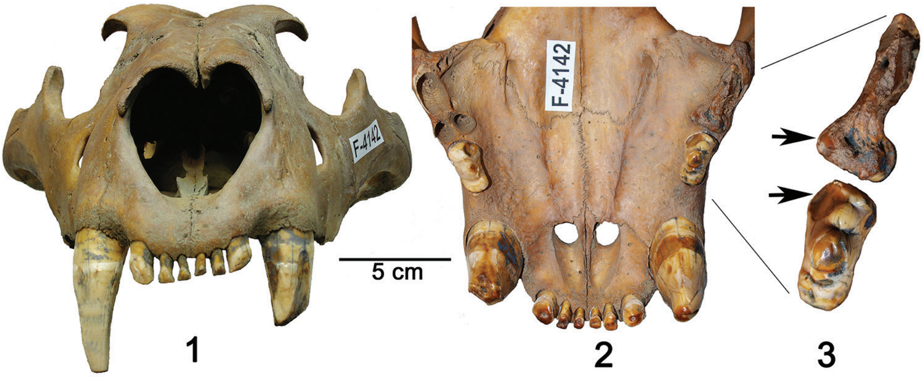

Fig. 2. The dentition of the cave lion male (specimen F-4142, IAM): 1 – front view, lifetime splitting of the left canine and a sloping line of the incisor's row; 2 – palatinal view, the erasure of teeth and splitting on the lingual side of the premolars P3 and P4; 3 – lifetime splitting on the inner side of the P3 and P4 (indicated by arrows), strong caries on P4

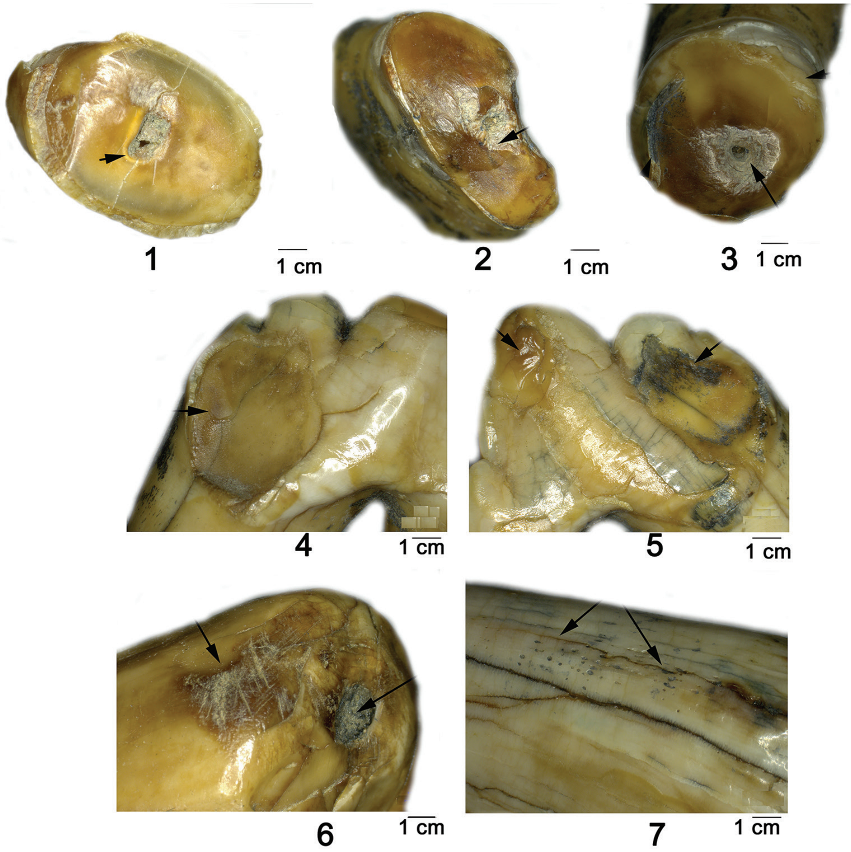

Fig. 3. Microwear of the cave lion's teeth (indicated by arrows) (sample F-4142, IAM): 1 – incisor I1; 2 – I2; 3 – I3; 4 – premolar P4; 5 – P3; 6 – top of left canine C1; 7 – lateral surface of the right canine C1

(0.1–0.3 mm) shallow pits on the right canine (Fig. 3), (3) small field (2 × 3 mm) with chaotically crossing short in-depth grooves at the top of the broken left canine. Thus, the morphology of the dental system of the skull F-4142 indicates that significant permanent load was applied on it during life. Obviously, the appearance of lesions on the lingual (inner) side of the teeth was caused by contact with more solid food than meat. This can be either bones or frozen soft tissue or it can be caused by contact with opposing teeth under a load from prey bones during eating. The lateral slope of the incisors profile and their damage indicate that these took over part of the load during eating, complementing the function of broken left canine.

In nature, the life expectancy of a male modern lion is usually less than that of females, as male is forced to guard the territory and the pride, and constantly enters into combats with competitors for his place. For instance, in the Serengeti, a female lion can live up to 18 years, whereas males typically live no longer than 12 years (https://www.sa-venues.com). In terms of the cave lion males, serious teeth damage also led to their earlier death . The latter can live to a very old age with deep-worn canines and complete loss or severe damage to the cheek teeth, up to the alveolar closure (Fig. 5). Regarding

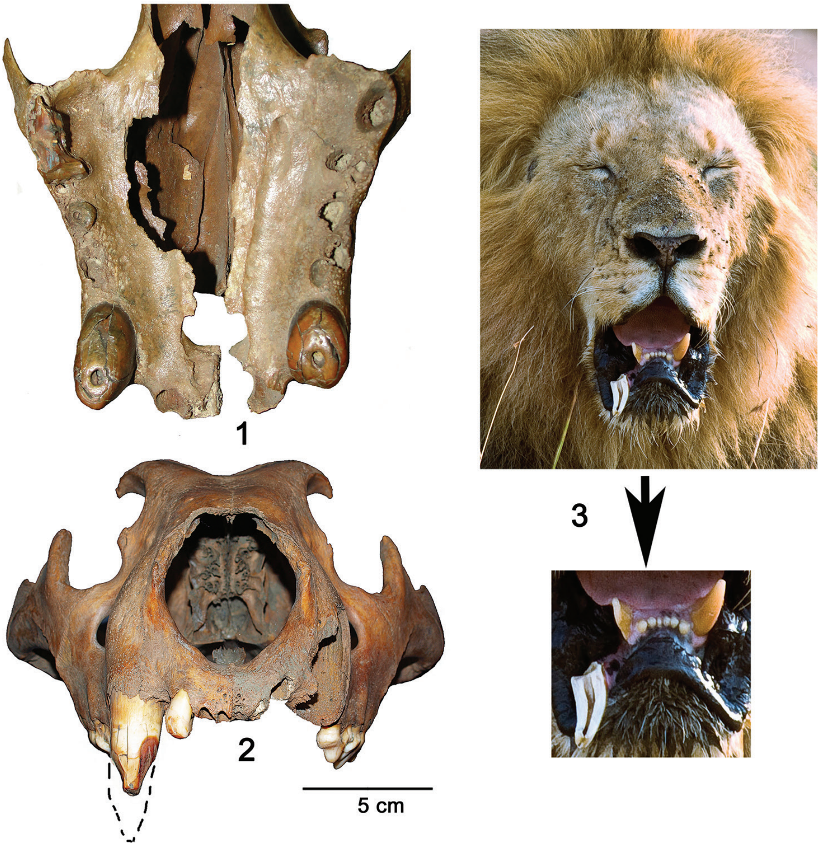

Fig. 4. Macrowear of the cave lion's teeth (indicated by arrows) (1, 2) and a modern lion (3): 1 – an old female's skull, teeth are destroyed to the base (coll. No. ZIN 3245); 2 – a skull of an adult male (sample F-3779, IAM), the right canine was broken during life. 3 – a wild adult male with half-broken right canine, (see the lower lip). Kenya. Photo (fragment) by Nikita Golovanov

a male, the loss or significant damage to a canine means "the beginning of the end", because it brings pain, problems with hunting, feeding, and in fights with competitors. As a result, their vital forces diminish, gradually or rapidly.

Initially, a lion with an injured canine may not suffer, but it is obvious that the consequences of the injury will be fatal. A photograph of N. Golovanov (Fig. 5) shows a situation where a male lost a half of its canine, and another half of the second part of the canine hung on the lip. The cause of such damage can be a fight with an enemy, resistance by a prey, rough food, etc. Tooth wear and breakage are normal in modern lion populations (Patterson et al., 2003). According to Van Valkenburgh (1988), in a modern lion population, 25% of individuals have one broken tooth; canines compose about 53% of these broken teeth, carnassials about 26.5%, and both incisors and premolar about 10%. The author states that more fracture occurrences in different fossil large carnivores happened in the past when use of carcasses and food stress were more intensive, and that more aggressive species did break their teeth more often.

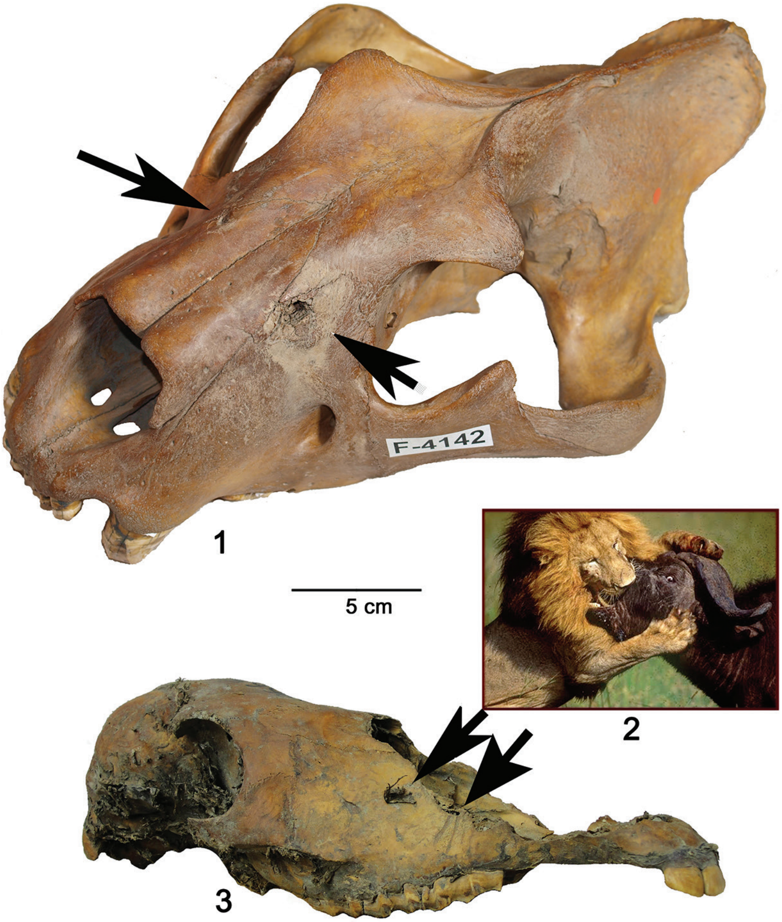

Fig. 5. Traces left by large cat's canines (indicated by arrows) on fossil skulls: 1 – the cave lion (sample F-4142, IAM); 3 – the foal (sample F-2665, IAM). 2 – a modern illustration: the death grip of the victim's muzzle by a lion

From ten skulls in the IAM collection, the canines of four of them are broken. In two cases, canines are lost post-mortem, and two skulls have only one canine each.

Apparently, the loss of canines is a common phenomenon in nature, and one of several ways of loss of male competitiveness in social and territorial animals. For example, during combat between males of the northern fur seal *Callorhinus ursinus*, we observed (unpublished data) that one of the opponents hits stone in an unsuccessful attack. As a result, the canine broke into small pieces; later, the seal had to give up his place to its competitor.

In comparison, a tiger, which is another large but not a social panther, eats its prey carefully, thereby avoiding tooth injuries. On the skulls of the wild Amur tigers, we did not observe such serious intravital injuries as those described above for the cave lion skulls. The same is observed for African man-eating lions (DeSantis & Patterson, 2017).

Damage to the skull bones on the sample F-4142

The facial part of the skull shows traces of lifetime bites, including several through the bone (Fig. 5). Similar traces are observed on other skulls of cave lion. For example, a similar but successfully healed canine track on the left nasal bone was found on the skull with IAM collection number F-4291 from the Yana River. Similar traces exist on the facial part of the skull of a fossil foal, IAM collection number F-2665, possibly a victim of a cave lion (Fig. 5). We assume that cave lion canines left these traces, because during the Pleistocene there were only two large predators in the North-East territory of modern Russia besides it: brown bears and polar bears. Bears are characterized by another type of killing a victim, which is to break a spine or rip open a belly. The damage of the skull of F-4142 (and F-2665) is similar in victims of modern lions. They testify that the ancient pantherins also killed their prey, using canines (and obviously also claws) (Fig. 5), grabbing and holding the victim by the muzzle, until it was weakened by suffocation. For this discussion, we have assumed perimortem (and not postmortem) circumstances; strangulation of a dead animal does not make sense.

Biological aspects.

The diet of cave lion was determined by stable isotope analysis for some locations in Western Europe. In some cases, the predominant prey during the pre-LGM period was a young cave bear *Ursus spelaeus*, in the others, during the LGM, the prey was a reindeer *Rangifer tarandus* (Bocherens et al., 2011). A mixed prey spectrum is characteristic for this predator in Northeast Asia, but here, the reindeer part was not dominant (Kirillova et al., 2015). In addition, regional features are most likely less important than local ones for "food preferences" of cave lion.

In present day large pantherins (lions and tigers), social relations depend on the abundance of basic resources such as food, territory, and females. Sufficient resources allow a relatively tolerant coexistence, which can easily be disturbed. After feeding, these predators leave behind remains such as tubular bones, ribs, spines, and skulls; traces of their teeth on the bones can be recognized. Large cats kill a victim, biting through the cervical vertebrae or throat; the existence of similar mechanisms in the past – breaking the neck closer to the skull – is confirmed from fossil materials (Kirillova et al., 2009). Another common method of killing is demonstrated by the skull F-4142 (Fig. 5), as discussed above.

A lack of resources leads to aggression and conflicts between predators. We argue that the traces from canine teeth on the facial part of the skull F-4142 (Fig. 5) are the result of a fatal battle with another male. This allows us to reconstruct the features of the social organization of cave lion in comparison with the modern lion. The latter lives in a complex social structure, and agonistic behaviour of males as struggle for their territory, pride, and prey is highly developed. This is different for tigers which lead a solitary way of life. They avoid direct conflicts, which prevents injuries which would result in decreasing viability. In present day lions, a pride is the most stable social group, consisting of adults, often related females, their cubs and one to three adult males. Prides enable more successful hunting, protection of the territory, protection against enemies, and reproduction. Besides lions living in prides, there are also solitary individuals as well as groups consisting of two or more females with their cubs. But these are less stable communities which can be transformed into other social forms. However, in the geological record only typical cases are preserved. The fossil record by itself does not prove direct evidence of pride formation, as there is only a limited amount of samples. But the conflicts between males as well as their way of life, as indicated by defects in their teeth, justifies the conclusion that prides did exist.

CONCLUSION

The absence or weak development of a characteristic mane in the cave lion male forces us to doubt the existence of pride, or to assume that its dimensions were small (Kays & Patterson, 2002; Chernova et al., 2016). However, the morphological features of the skull F-4142 we investigated, indicate a developed agonistic behaviour, and suggesting sociality: fights with competitors to protect the territory and probably life in a pride, similar to the modern lion. Also similar to the latter, females of cave lion lived longer than males.

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NIEKOĽKO PALEONTOLOGICKÝCH DÔKAZOV BIOLÓGIE LEVA JASKYNNÉHO

Resume

Lebka leva jaskynného, *Panthera spelaea* (Goldfuss, 1810), objavená v glaciálnych sedimentoch na severovýchode Ruska, nesie hlboké stopy po špičiakoch v prednej časti papule, čo poukazuje na činnosť iného leva, ktorý sa snažil svojho protivníka udusiť. To je bežná príčina smrti a jeden zo spôsobov ako dnešné levy zabíjajú svoju korisť či protivníkov. Rádiometrické datovanie ukazuje, že predmetná lebka je staršia než 48 500 rokov. Zistené stopy po činnosti iného jedinca podporujú rovnaké sociálne správanie sa levov jaskynných aké pozorujeme aj pri dnešných levoch, ako z hľadiska hierarchie vo svorke, súperenia medzi samcami, zápasov o teritórium, či formovania svorky. Dentícia skúmaného jedinca vykazuje vážne poškodenia, ako sú ulomené časti zubov alebo výrazné obrusy na špičiakoch a trhákoch. Takéto poškodenia sú často pozorované aj na iných lebkách levov jaskynných. To môže poukazovať, že levy jaskynné sa okrem mäsa, živili aj kosťami veľkej koristi, vrátane zamrznutých zdochlín. Aktívny konflikt medzi samcami, zaznamenaný na fosílnom materiáli v podobe poškodených zubov (okrem zranení na mäkkých tkanivách, ktoré nie sú traumatické) mohol viesť až k poklesu ich vitality. Z tohto dôvodu, samce pravdepodobne zomierali mladšie než samice, ktoré sa mohli dožiť vyššieho veku aj napriek silnej abrázii zubov, či dokonca ich strate.

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PROWLING THE MOUNTAINS – ALPINE CAVE LION (*PANTHERA SPELAEA*) DISTRIBUTION AND METRICS

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M. Pacher: Prowling the mountains – Alpine cave lion (*Panthera spelaea*) distribution and metrics

Abstract: Based on the Late Pleistocene cave lion distribution in the Alps (especially in the Eastern Alpine region and Eastern Swiss Alps), a compilation of records and metrical data from the Eastern Alps is given for the first time. The study yields data on the frequency of lion occurrence and its palaeobiological implications, mainly the possible prey pattern of Alpine lions. The possible size differences between the Eastern Alpine population and lions outside the Alps are also solved on the basis of metrical data compilation, which are analysed by two-dimensional plots and the LSI approach. The later approach allows to include also single specimen for a large comparison of populations as is frequently used in archaezoological context. For the better understanding of palaeobiology and metrical variability of Late Pleistocene Alpine lions, further approaches are needed.

Key words: cave lion, *Panthera spelaea*, Alps, distribution, morphometrics, Log size index, Late Pleistocene, Marine Isotope Stage 3

INTRODUCTION

The cave lion (*Panthera spelaea*) is a typical element of the Pleistocene megafauna that roamed across the Eurasian mammoth plane (e.g. Kahlke, 1994). Nonetheless, these large felids occur frequently in higher mountain areas as well. The aim of this study is a detailed compilation and metrical investigation of lion remains from the Eastern Alpine region, completed by records from the western and southern parts of the Alps.

The taxonomic position of the Ice Age lion has recently been discussed (see overview in Hemmer & Keller, 2011). They were either considered as subspecies of modern lions (e.g. Schütt, 1969; Kurtén, 1968) or regarded as distinct species (e.g. Kabitsch, 1960; Altuna, 1981). More recent investigations on its skull and tooth morphology argue for a division on species level (Baryshnikov & Boeskorov, 2001; Sotnikova & Nikolskiy, 2006). Studies based on mitochondrial DNA suggest genetic isolation of European Pleistocene populations from modern lions (*Panthera leo*) (Burger et al., 2004; Barnett et al., 2009; Ersmark et al., 2015). Male individuals miss the mane in Late Pleistocene cave art, which seems to confirm species diagnostic differences in modern and Ice Age lions. Development of the mane is correlated to thermoregulation and social behaviour of these large felids (Nagel et al., 2003).

The species status of cave lions implies its complete extinction and hitherto discussions about a possible merging of Ice Age groups into Holocene lion populations from the Balkan

Peninsula are obsolete. There, lion remains are found from Neolithic to Iron Age context (e.g. Gross, 1992; Forstenpointner et al., 2010). Direct radiometric dates suggest lions in south-eastern Europe probably as early as 8.0 cal ka BP and definitely from 6.5-6.0 cal BP into the Iron Age. The cave lion, on the other hand, disappeared 6.0 to 8.0 ka years earlier across Europe at 14.5-14.0 cal ka BP (Stuart & Lister, 2011).

EASTERN ALPINE AND EASTERN SWISS DISTRIBUTION

The Pleistocene lion occurs frequently at Eastern Alpine sites (Fig. 1). The highest elevated finds in the Alps comes from the Conturineshöhle, South-Tyrol, Italy. Skull remains of a juvenile individual (Rabeder, 1991: 112, fig. 95) prove *P. spelaea* at 2,800 m a.s.l, followed by records from the cave site Bärenfalle at 2,100 m a.s.l. and Salzofenhöhle at 2,005 m a.s.l., both in the Northern Calcareous Alps.

In summary, 39 cave sites revealed remains of this large felid but seldom more than one or two individuals are confirmed (Tab. 1). Exceptions are correlated to shaft situations within larger cave-systems. The pitfalls inside Repolusthöhle and Frauenhöhle, both near Graz, Styria, Austria account for more numerous and partly articulated remains (Mottl, 1949a, 1951; Pacher, 2014). A nearly complete skeleton was reported from the Löwenschacht (lion-shaft) in the cave-system of Salzofenhöhle, Totes Gebirge, Styria (Ehrenberg, 1950: 5). Another partial lion skeleton was found along a brook at the village Siegsdorf, Bavaria (Gross, 1992).

In course of this study, unpublished material from several sites was examined. Cave lion is verified for the first time at Einhornhöhle and Felsenkeller, both Lower Austria (Pacher & Rabeder, *in press*), Mathildengrotte and Geröllhöhle, Styria and Windener Bärenhöhle, Burgenland. Unfortunately, the remains from Tischoferhöhle, Tyrol (Schlosser, 1909: 425), Schlenkendurchgangshöhle (Frank & Rabeder, 1997), Lettenmayerhöhle, both Upper Austria (Ehrenberg, 1962: 396), Mehlwurmhöhle, Lower Austria (Mais & Rabeder, 1974: 143), Lurgrotte (Mottl, 1975: 173), Kleine Peggauerwandhöhle (Fladerer, 1997a: 326),

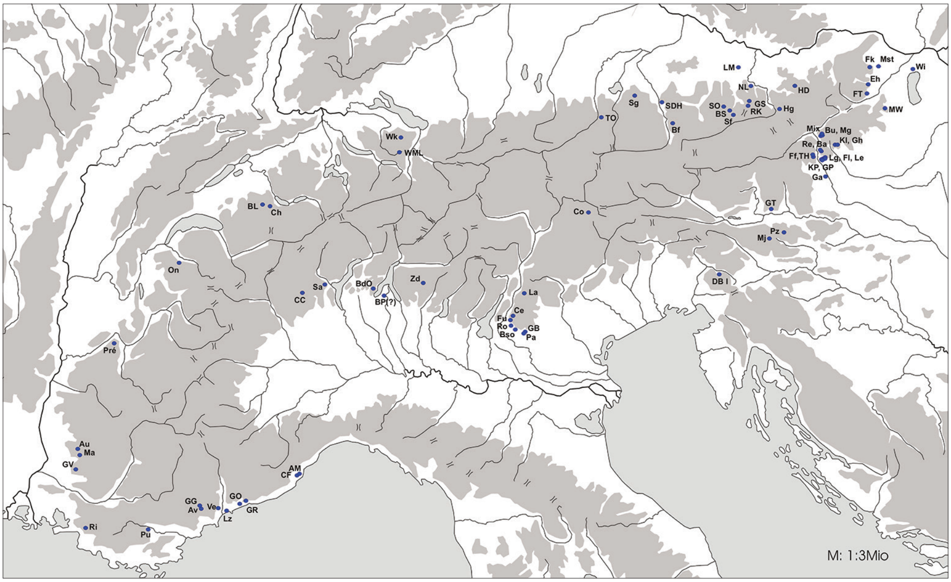

Fig. 1. Map of Alpine caves site with lion remains (Abbreviations as in Tab. 2)

Tab. 1. Skeletal element distribution of cave lions (*Panthera spelaea*) from Eastern Alpine and Eastern Swiss sites. Abbreviation of sites as in Tab. 2 (C – cranium, M – mandible, D – teeth, V – vertebra, S – scapula, H – humerus, R – radius, U – ulna, Ca – carpal bone, Mc – metacarpal bone, Co – pelvis, F – femur, T – tibia, Fi – fibula, Ta – tarsal bone, As – talus, Cl – calcaneus, Mt – metatarsal bone, Ph1 – phalanx proximal, Ph2 – phalanx medial, Ph3 – phalanx distal, Va – various other elements)

Site	**NISP (MNI)**	**C**	**M**	**D**	**V**	**S**	**H**	**R**	**U**	**Ca**	**Mc**	**Co**	**F**	**T**	**Fi**	**Ta**	**As**	**Cl**	**Mt**	**Ph1**	**Ph2**	**Ph3**	**Va***
Ba	30(1)	2	1	3	9		1			1				1				1	2	6	3		
Bf	28(1)	1	1	2			2			4	3					3			2	8	1		1
BS	12(1)	1		1	5														1 (+ 2 metapodials)	1	1		
Bu	1(1)				1																		
Co	3(1)	1	1	1																			
DB	18(1)			6	4										1		1		1		2	3	
Mix	55(3)			4	19			1		1	7			3			4	3	13				
Eh	1(1)																				1		
Fk	1(1)																						
FT	4(1)		1	1							1	1											
Fl	65(4)	1	2	5	13		2		2	1	4		1	1		2		1	4	14	9	1	
Ff	1(1)							1															
Ga	1(1)		1																				
GS	69(2)		1	8	14	1					5					2	3	2	5 (+1 metapodial)	4	5	3	5
Gh.	1(1)																		1				
GT	2(1)										1					1							
GP	>2 (1)																				1		
Hg	1(1)										1												

HD	61(2)	1	3	5	13	2	1	1	3	1	4		1		1	2			4	6	4	6	3
Kl	X																						
KP	X																						
Le	4(1)										2								1			1	
LM	3(1)																		3 metapodials				
Lg	X																						
Mg	2(1)		1	1																			
MW	x																						
Mst	12(1)	1	2		2						1			1					1	3			1
Mj	1(1)							1															
NL	1(1)			1																			
PZ	1(1)				1																		
RK	6(1)			1							1					2			1		1		
Re	10(1)			2				1		1	1				1					2	1		1
Sf	5(1)																			2		1	2
So	>22(>2)	1	1		8		1	1			2	2		1		1		1					3
SDH	x																						
Sg	63(1)	1	2		21								2	2	1	2	1	1	3				
TH	x																						
To	10(1)				3											1		1	2	2		1	
Wi	4(1)				1																3		

*varia: Bf – 1 patella; GS – 4 rib fragments, 1 sesamoid bone; HD – 1 rib, 1 patella, 1 se; Mst – 1 patella; Re – 1 sternum; Sf – 2 sesamoid bones; So – 3 rib fragments

Große Peggauerwandhöhle (Fladerer, 1997b: 322), Tropfsteinhöhle am Kugelstein (Fladerer & Frank, 1997: 344), Katerloch (Mottl, 1975: 173) and Schafsteinhöhle (Wolff, 1978: 62) all in Styria were not available.

Lion remains in the Eastern Alpine region come from different time periods. The karst fillings at Bad Deutsch-Altenburg, Lower Austria yield the oldest evidence. *Panthera* n. sp. from locality Deutsch-Altenburg 4B is referred to the Early Pleistocene (Rabeder, 1981; Nagel & Rabeder, 1997: 246). The Middle Pleistocene complex from Deutsch-Altenburg 1 contains a complete humerus classified as *Felis leo* var. *spelaea* (Freudenberg, 1914: 635), respectively as *P. spelaea* (Nagel & Rabeder, 1997: 235).

At Repolusthöhle, numerous lion remains referred to as *Felis spelaea* were uncovered from Middle Pleistocene sediments in the 9 m deep shaft, while only about 12 *Panthera spelaea* specimens come from two Late Pleistocene strata ("Early Würmian" and "Middle Würmian") and are included in this study (Mottl, 1951: 65; Pacher, 2014: 246). Based on peculiarities in tooth morphology, mainly the greater breadth of the cheek teeth and particular proportions of the fourth upper premolar the stratigraphical older lions from Repolusthöhle are seen as transitional population between *P. leo fossilis* of the Early Pleistocene and Late Pleistocene lions (Schütt & Hemmer, 1978: 245). The few non-stratified lion specimens from Flatzer Tropfsteinhöhle and Neue Höhle, Lower Austria represent probably older Late Pleistocene remains as suggested by their larger size and the total faunal composition of these caves (Thenius, 1949; Pacher & Rabeder, *in press*). All other Eastern Alpine sites bear typical Late Pleistocene *P. spelaea* remains ascribed to the Marine Isotope Stage 3 (MIS 3).

The same holds true for the lion remains from the Swiss and the French Alps. *P. spelaea* is confirmed at Wildkirchli and Wildenmannlisloch (Bächler, 1940: 211), Bärenloch (Blant et al., 2010) and Chilchihöhle (Koby, 1964: 154). The French Alps, Haute-Savoie yield several lion evidences (Tab. 2). An extraordinary rich assemblage is reported from Prélétang with remains of at least ten individuals (Lequatre, 1966: 12). In the Vaucluse region, the cave lion is a scarce faunal element and confirmed at least at Bau de l'Aubesier, Grotte de la Vallesqure and La Masque (Crégut-Bonnoure, 2011).

Middle Pleistocene lions are present along the southern Alpine Arc at the site complex from Brecce di Soave, Italy referred to as *Panthera* cf. *fossilis* (Bona & Sardella, 2012), from the Eemian ossiferous rubble at Zandobbio classified as *P. leo spelaea* (Bona, 2006), and mentioned at Serbaro di Romagnano (Bon et al., 1991). Grotta del Cerè yielded remains of at least seven juveniles classified as *P. leo spelaea* (Ghezzo et al., 2014). The Late Pleistocene lion is present with few elements at seven additional sites (Tab. 2). The proposed evidence at Buco del Piombo mentioned by Musil (1980: 40) stays unclear according to a remark in Döppes (2001). The Alpes-Maritimes, France and neighbouring Liguria, Italy witness again a frequent occurrence of lions from the Last Interglacial onwards, sometimes with unclear chronological position of the finds (see Bonifay, 1971; Valensi and Psathi, 2004, Crégut-Bonnoure, 2011).It seems, lions were more frequent in this region during end of the Middle Pleistocene and beginning of the Late Pleistocene than during MIS 3 (Crégut-Bonnoure, 2011)

So far, direct radiocarbon dates for the cave lion from the Alpine area have been available from five sites (see Stuart & Lister, 2011). A pelvic fragment from Tischoferhöhle, Tyrol gave an age of 31,890+/-300 BP and a bone from the Siegsdorf skeleton, Bavaria resulted at 47,180+1,190/-1,040 BP (Burger et al., 2004). A tibia from Gamssulzenhöhle, Upper Austria confirms the cave lion around 49,900+/-1,500 BP in the Northern Calcareous

Tab. 2. Remains of the cave lions from Alpine sites (LP – Late Pleistocene, MP – Middle Pleistocene, NISP – number of identified specimen, MNI – minimum number of individuals, a.s.l. – height at sea level)

Abbreviation	Site	Region	Chronology	m a.s.l.	NISP (MNI)	Reference
Eastern Alps						
Ba	Große Badlhöhle	Styria	LP	495 m	30(1)	Mottl, 1949a: 108, 1953: 16; Thenius, 1960: 42; own data
Bf	Bärenfalle	Salzburg	LP	2,100 m	28(1)	Tichy, 1985: 5; own data
BS	Brettsteinbärenhöhle	Styria	LP	1,660 m	14(1)	Ehrenberg, 1958: 6; Ehrenberg, 1970: 40; own data
Bu	Burstallwandhöhle I	Styria	LP	810 m	1(1)	Mottl, 1953: 33; own data
Co	Conturines cave	South Tyrol	LP	2,800 m	3(1)	Rabeder, 1991: 112; own data
DB	Divje babe I	Slovenia	LP	450 m	18(1)	Toškan, 2007: 257
Mix	Drachenhöhle bei Mixnitz	Styria	LP	949 m	55(3)	Sickenberg, 1931: 749; own data
Eh	Einhornhöhle	Lower Austria	LP	580 m	1(1)	own data
Fk	Felsenkeller	Lower Austria	LP	650 m	1(1)	own data
FT	Flatzer Tropfsteinhöhle	Lower Austria	LP	585 m	4(1)	Thenius, 1949: 291; own data
Fl	Frauenhöhle	Styria	LP	600 m	65(4)	Mottl, 1949a: 107; own data
Ff	Fünffenstergrotte	Styria	LP	441 m	1(1)	Mottl, 1953: 31; own data
Ga	Gaisberg	Styria	LP	640 m	1(1)	Mottl, 1949a: 108; own data
GS	Gamssulzenhöhle	Upper Austria	LP	1,300 m	69(2)	Ehrenberg, 1962: 412; own data
Gh	Geröllhöhle	Styria	LP	637 m	1(1)	own data
GT	Griffener Tropfsteinhöhle	Carinthia	LP	484 m	2(1)	Thenius, 1960: 42; own data
GP	Große Peggauerwandhöhle	Styria	LP	510 m	>2(1)	Fladerer, 1997b: 322
Hg	Bärenhöhle im Hartlesgraben	Styria	LP	1,230 m	1(1)	Mottl, 1949b: 20, own data
HD	Herdengelhöhle	Lower Austria	LP	878 m	61(2)	Pacher, 2009; own data
Kl	Katerloch	Styria	LP	900 m	mentioned	Mottl, 1975: 173

KP	Kleine Peggauerwandhöhle	Styria	LP	511 m	mentioned	Fladerer, 1997a: 326
Le	Leopoldinengrotte	Styria	LP	762 m	4(1)	Kusch et al., 2015: 73; own data
LM	Lettenmayerhöhle	Upper Austria	LP	380 m	3(1)	Ehrenberg, 1962: 396
Lg	Lurgrotte-Semriach	Styria	LP	642 m	mentioned	Mottl, 1975: 173
Mg	Mathildengrotte	Styria	LP	970 m	2(1)	own data
MW	Mehlwurmhöhle	Lower Austria	LP	390 m	mentioned	Mais & Rabeder, 1974: 143
Mst	Merkensteinhöhle	Lower Austria	LP	441 m	12(1)	Nagel, 1997; own data.
Mj	Mokriška jama	Slovenia	LP	1,500 m	1(1)	Brodar, 1960
NL	Nixloch	Upper Austria	LP	770 m	1(1)	Kunst, 1992: 111
Pz	Potočka zijalka	Slovenia	LP	1,700 m	1(1)	Krofel, 2004
RK	Ramesch-Knochenhöhle	Upper Austria	LP	1,960 m	6(1)	own data
Re	Repolusthöhle	Styria	MP/LP	525 m	237(17)/10(1)	Mottl, 1951: 65; own data
Sf	Schafsteinhöhle	Styria	LP	1,780 m	5(1)	Wolff, 1978: 62
SO	Salzofenhöhle	Styria	LP	2,005 m	>22(>2)	Ehrenberg, 1950: 4, 1964: 6; own data
SDH	Schlenkendurchgangshöhle	Salzburg	LP	1,590 m	mentioned	Frank & Rabeder, 1997: 220
Sg	Siegsdorf	Bavaria	LP	ca.700 m	63(1)	Gross, 1992
TH	Tropfsteinhöhle	Styria	LP	482 m	mentioned	Fladerer & Frank, 1997: 344
TO	Tischoferhöhle	Tyrol	LP	598 m	10(1)	Schlosser, 1909: 425
Wi	Windener Bärenhöhle	Burgenland	LP	190 m	4(1)	own data
Western Alps			LP			
BL	Bärenloch, Charmey	Préalpes fribourgeoises	LP	1,645 m	10(1)	Blant et al., 2010: 156
On	Baré d'Onnion	Haute-Savoie	LP	1,190 m	mentioned	Argant et al., 2012: 6
Au	Bau de l'Aubesier	Vaucluse	LP		1(1)	Crégut-Bonnoure, 2011: 238
Ch	Chilchi	Préalpes fribourgeoises	LP	1,810 m	1(1)	Koby, 1964: 188

GV	Grotte de la Vallescure	Vaucluse	LP		6(1)	Crégut-Bonnoure, 2011: 238
Ma	La Masque	Vaucluse	LP		2(1)	Crégut-Bonnoure, 2011: 241
Prè	Prélétang	Vercors	LP	1,208 m	MNI 10	Lequatre, 1966: 12
Wk	Wildkirchli	Säntis	LP	1,477 m	19(2)	Bächler, 1940: 211; own data
WML	Wildenmannlisloch	Selun	LP	1,628 m	4(1)	Bächler, 1940: 211; own data
Southern Alps						
BSo	Brecce di Soave-Mt. Tenda	Veneto	MP		1(1)	Bona & Sardella, 2012: 194
BSo	Brecce di Soave-Viatelle	Veneto	MP		1(1)	Bona & Sardella, 2012: 194
BSo	Brecce di Soave-Sentiero	Veneto	MP		10(1)	Bona & Sardella, 2012: 194
BSo	Brecce di Soave-Castello	Veneto	MP		1(1)	Bona & Sardella, 2012: 194
BSo	Brecce di Soave-Zopegga 1	Veneto	MP		mentioned	Bon et al., 1991: 188
(BP)	Buco del Piombo	Lombardy	LP	695 m	unclear	Musil, 1980: 40; Döppes, 2001: 48
BdO	Bucodell'Orso, Monte Generosa	Lombardy	LP	648 m	1(1)	Santi & Rossi, 2005: 21
CC	Ciota Ciara, Monte Fenera	Piedmont	LP	675 m	3(1)	Buccheri, 2014: 23
GB	Grotta del Broion	Veneto	LP	150 m	2(1)	Sala, 1980: 70; Bon et al., 1991: 200
Ce	Grotta del Cerè	Veneto	MP	750 m	13(7 juv)	Ghezzo et al., 2014: 82
Fu	Grotta di Fumane	Veneto	LP	350 m	1(1)	Romandini, 2011: 270- 271, fig. 4.1.3-6
Pa	Grotta di Paina	Veneto	LP	350 m	3(1)	Romandini, 2011: 23
La	Grotta di S. Donà di Lamon (Bus de la Bela)	Tesino	LP	1,150 m	mentioned	Bon et al., 1991: 202
Sa	Caverna delle Streghe, Sambughetto	Piedmont	LP		1(1)	Santi et al., 2004: 599
Ro	Serbaro di Romagnano	Veneto	MP		mentioned	Bon et al., 1991: 190
Zd	Zandobbio „Grotta delle Ossa“	Lombardy	Eemian	370 m	1(1)	Bona, 2006

Liguria-Alpes Maritimes						
AM	Arma dell Manie	Liguria	MP		1(1)	Valensi & Psathi, 2004: 259
Av	Aven de la Malle	Alpes-Maritimes	LP		1(1)	Crégut-Bonnoure, 2011: 237
GG	Grotte de Gras	Alpes-Maritimes	Eemian	820 m	55(1)	Crégut-Bonnoure, 2011: 241
GR	Grotte des Enfants	Monaco	LP	17 m	3(1)	Bonifay, 1971: 304
CF	Caverna delle Fate	Liguria	MP	280 m	19(6)	Valensi & Psathi, 2004: 259
Lz	Grotte du Lazaret	Nice	MP	26 m	7(3)	Valensi & Psathi, 2004: 259
GR	Grotte du Prince	Monaco	LP		mentioned	Bonifay, 1971: 304
Pu	Grotte aux Puces	Alpes-Maritimes	LP		mentioned	Crégut-Bonnoure, 2011: 238
Ri	Grotte de Rigabe	Alpes-Maritimes	MP/LP		4(1)	Crégut-Bonnoure, 2011: 237
Ve	Grotte de Mars, Vence	Nice	Eemian	950 m	1 skeleton	Crégut-Bonnoure, 2011: 237
GO	Grotte l'Observatoire	Monaco	LP	100 m	1(1)	Bonifay, 1971: 305

Alps (Barnett et al., 2009). Unfortunately, the sample from Griffener Tropfsteinhöhle, Carinthia failed (Gleirscher & Pacher, 2005). Recently, one sample from Bärenfalle, Salzburg has been submitted for dating (Döppes et al., 2016). In the western Alpine Arc, the lion from Bärenloch, Prélapes fribourgeoises yielded an age of 43,320+/-939 BP (ISSKA-SISKA, 2016). In addition, one direct date comes from Baré d'Onnion, Haute-Savoie. A tooth sample resulted at 34,600+/-1100 BP (Argant et al., 2012: 6).

The regular occurrence of this large carnivore in the high Alps above 1,000 m a.s.l. implies the presence of prey species in the area. In fact, little is known about the chronological distribution of Ungulates in the high Alps during the Pleistocene. Ibex, chamois or red deer are common remains of the Holocene period in high Alpine caves. At least three direct radiocarbon dates confirm the occurrence of *Capra ibex* in the western Alps during MIS 3. The sample from Bettchenhöhle, Switzerland gave an age of 36,540+/-530 BP, the one from Grotte de Alfredo, France resulted at 32,835+/-205 BP (Blant et al., 2012). At Barè d'Onnion at 1,190 m a.s.l, two samples of *Capra ibex* resulted in dates of 31,300+/-750 BP and 38,470+/-810 BP (Argant et al., 2012: 6), which subsequently fall into MIS 3 like the dated lion sample from this site.

The feeding behaviour of modern lions which tear meat from the carcass leaves few significant traces on bones. Mainly single (sub)-circular marks and deep furrows are recorded (Domínguez-Rodrigo, 1999). Other large carnivores constantly chew on bones and produce more severe and diverse modification patterns. The majority of marks produced stay insignificant and the consumption sequence of carcasses is similar. It is mainly the intensity of gnawing and the size of punctures and furrows that allows for identification of the taphonomic agent (e.g. Fourvel et al., 2014; Domínguez-Rodrigo & Piqueras, 2003; Haynes, 1983). The cave hyena (*Crocuta c. spelaea*) caused the most extensive modification and destruction of bones. This species never entered into high Alpine areas. The highest evidence comes from Tischoferhöhle, Tyrol at 598 m a.s.l. (Schlosser, 1909). The typical pattern of wolf activity is frequently recorded on cave bear bones from high elevated sites (e.g. Pacher, 2000, 2004), while traces of felid flesh consumption (e.g. Argant, 2000; Káňa & Roblíčková, 2017) have not been reported from Alpine caves, so far. Isotope signatures from *P. spelaea* samples from northwest Europe (Ardennes, Swabian Alb, Jura Mountains, Paris Basin) suggest reindeer (*Rangifer tarandus*) as common prey but also individualistic predatory behaviour with single individuals relying possible on juvenile cave bears (Bocherens et al., 2011). At the Central European loess area, lions showed again a preference for reindeer but probably added musk-oxen to their diet as based on results from Předmostí, Moravia (Bocherens et al., 2015). The reindeer never entered into higher elevated landscapes and the currently barely proven Pleistocene evidence for Ungulates at higher elevations suggests that lions in the high Alps might have relied more frequently on cave bears. This assumption still needs to be tested in order to better understand the Alpine faunal diversity and the food web of the Pleistocene high Alpine palaeoecosystem.

METRICAL ANALYSES

Late Pleistocene lions were larger than modern representatives, but they were of moderate size compared to Middle Pleistocene lions (*Panthera leo fossilis*). A comprehensive study of size variation by Marciszak et al. (2014) suggests a considerable decline in size at the end of the Late Pleistocene from MIS 3 to MIS 2. Nonetheless, the picture of a gradual size decline through time might be influenced by a pronounced sexual dimorphism in lions (e.g. Turner, 1984).

Based on associated faunal elements and the few direct dates, the studied Alpine remains are attributed to MIS 3 and hence represent typical Late Pleistocene cave lions. The metrical analyses of the Alpine lion material will show if it fits into the published size variations. The material consists mainly of small and dense skeletal elements such as tooth-bearing fragments, isolated teeth, metapodial bones, carpal and tarsal bones and phalanges. Long bones, mandibles and cranial remains are scarce. An unlabelled skull housed at the Regional museum in St. Pölten, Lower Austria might represent the mentioned skull from Merkensteinhöhle, Lower Austria (Wettstein & Mühlhofer, 1938: 526), which is listed with a question mark in the metrical data set (Supplement: Tab. 1 to 14). Metrical values of available elements are compared to Late Pleistocene lion values from outside the Alps. Therefore, scatterplots are used to compare dimensions of teeth and values of skeletal elements that provide a larger dataset. A second approach is used since the number of specimen and measurable fragments per site is often small. The LSI (log size index) is burrowed from archaeozoological studies. It allows for comparison of single specimen and measurements from different skeletal parts. A detailed description and discussion of the approach is given in Meadow (1999). First, all measurements are converted into logarithms. In this case log10 was used. The rather complete male individual from Arrikrutz, Basque country was chosen as reference specimen (Altuna, 1981). For each dimension the difference between the log value of the reference specimen and the log value of the measured specimen is calculated, which resulted in a LSI-value for each single measurement. The mean value of all breadth/depth measurements of a single specimen and the mean of length values calculated with the left and right body side of the reference specimen are plotted. Results are again compared to values from non-Alpine lion remains from Jaurens, France (Ballesio, 1980), Schusterlucke and Teufelslucke, both Lower Austria (Pacher & Rabeder, *in press*).

Results of teeth values show, that size variation is similar in Alpine and non-Alpine samples. Smaller and larger specimens are most likely attributable to males and females. This is well shown by the two groups observed in the metrical distribution of lower canines (Fig. 2). Nonetheless, segregation of sexes is not always straightforward. A slight tendency towards bisection in the lower m1 (Fig. 3) might exhibit a certain dimorphism, too (see Turner, 1984). Marciszak et al. (2014) explain large specimen with an evolutionary elongation process of carnassials in stratigraphical younger lions. Additional teeth, like the lower p4 exhibit size variability to the same extent as shown in Marciszak et al. (2014)

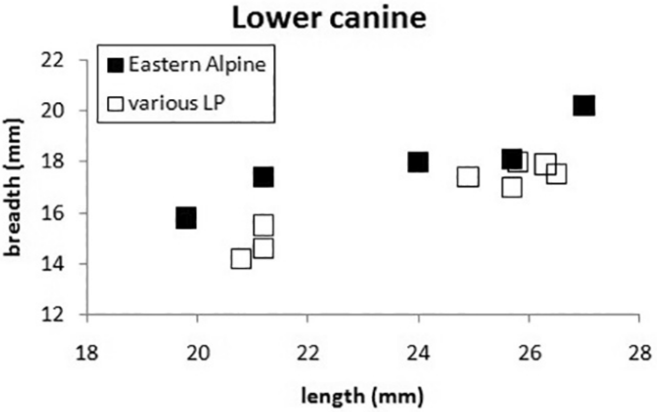

Fig. 2. Greatest length and greatest breadth of lower canines from Eastern Alpine cave lions (data from Supplement: tab. 2) and other Late Pleistocene (LP) finds: Jaurens (Ballesio, 1980) and La Fage (Ballesio, 1975)

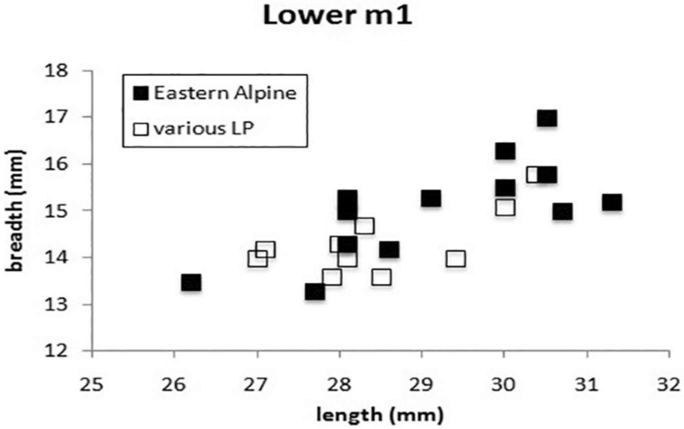

Fig. 3. Greatest crown length and breadth of lower m1 from Eastern Alpine cave lions (data from Supplement: tab. 2) and other Late Pleistocene (LP) finds: Jaurens (Ballesio, 1980), La Fage (Ballesio, 1975), and sites from Lower Austria (Pacher & Rabeder, *in press*)

but little evidence of clustering (Fig. 4). Postcranial elements such as the tibia or the *os metatarsale* 3 suggest also two size groups with some intermediate specimen (Figs. 5, 6). The *os metatarsale* 3 reveals two rather small but remarkable massive specimen from Drachenhöhle and Leopodinengrotte (Fig. 6).

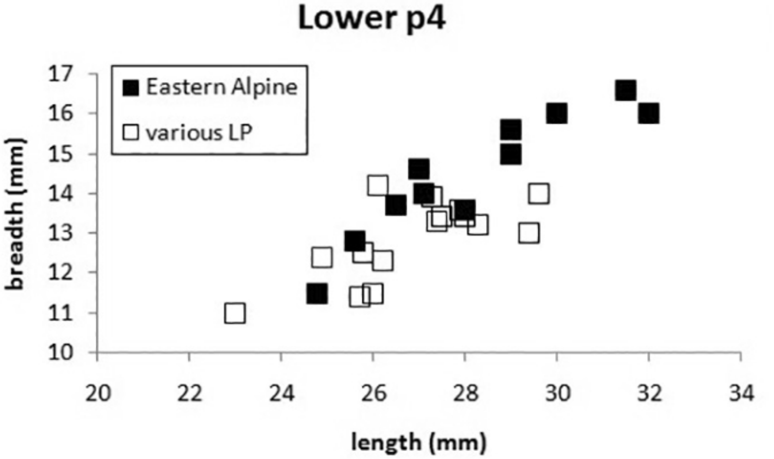

Fig. 4. Greatest length and breadth of lower p4 from Eastern Alpine cave lions (data from tab. 2) and other Late Pleistocene (LP) finds: Jaurens (Ballesio, 1980), La Fage (Ballesio, 1975), and sites from Lower Austria (Pacher & Rabeder, *in press*)

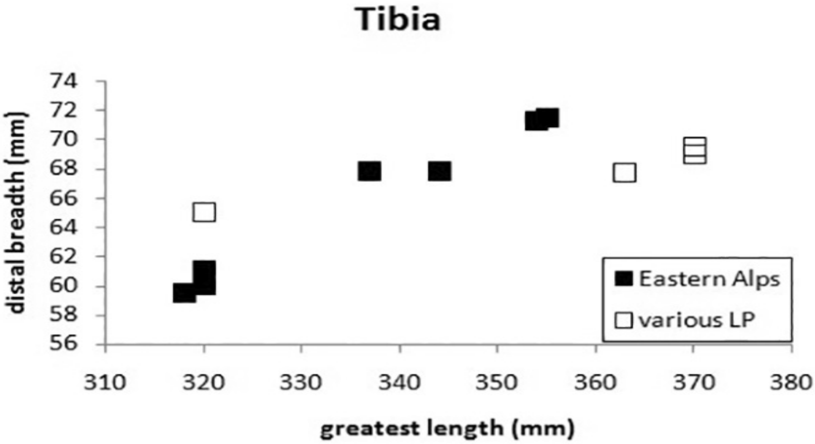

Fig. 5. Greatest length and distal breadth of tibiae from Eastern Alpine cave lions (data from Supplement: tab. 10) and other Late Pleistocene (LP) finds: Jaurens (Ballesio, 1980), Arrikrutz (Altuna, 1981) and Schusterlucke, Lower Austria (Pacher & Rabeder, *in press*)

LSI values of available long bones, metacarpal and metatarsal bones as well as talus and calcaneus confirm the picture obtained on scatterplots. Alpine and non-Alpine samples show an identical distribution range in length (Fig. 7) as well as in breadth values (Fig. 8). Mean and median values for both regional groups are nearly identical.

Length values are correlated to body height and show a rather bimodal pattern suggesting male and female specimen. The LSI obtained on breadth/depth values results

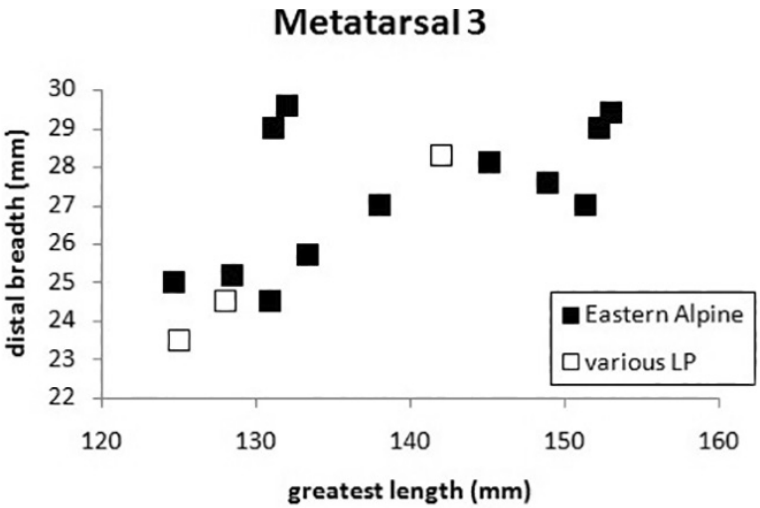

Fig. 6. Greatest length and distal breadth of *os metatarsale* 3 from Eastern Alpine cave lions (data from Supplement: tab. 13) and other Late Pleistocene (LP) finds: Jaurens (Ballesio, 1980) and Schusterlucke, Lower Austria (Pacher & Rabeder, *in press*)

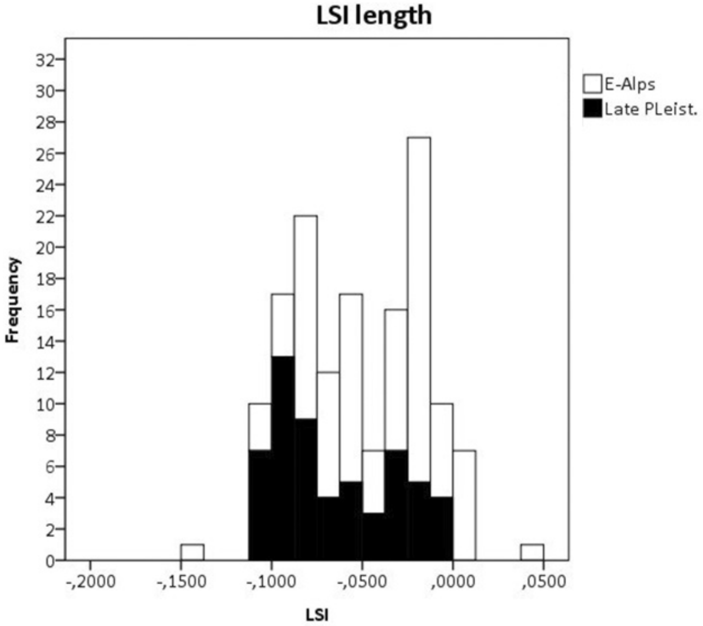

Fig. 7. LSI length values for Eastern Alpine and Eastern Swiss lions (n: 90, mean: -0,044, median: -0,037) and various Late Pleistocene lions (n: 57, mean: -0,065, median: -0,078).

again in a similar range for Alpine and non-Alpine specimen (Fig. 8) but shows a wider range of variability. This might be caused by the fact that several measurements per bone are combined and that the breadth of long bones is more correlated to body mass which is more affected by external conditions (Meadow 1999). LSI analysis confirms the higher variability in breadth values as suggested by values from the third metatarsal bone (Fig. 6).

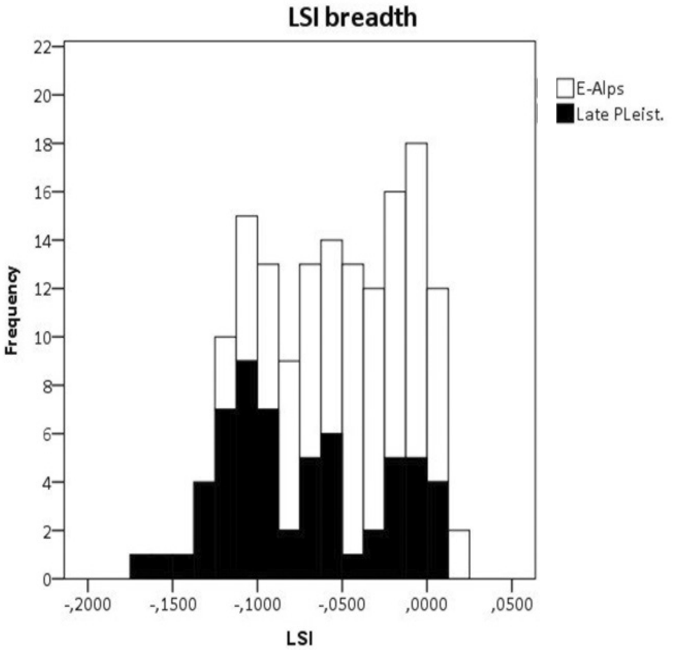

Fig. 8. LSI values for breadth measurements of Eastern Alpine and Eastern Swiss lions (n: 94, mean: -0,045, median: -0,039) and various Late Pleistocene lions (n: 60, mean: -0,074 median: -0,085)

CONCLUSION

Cave lions were widespread in the Eastern Alpine region and throughout the Alpine Arc during the Late Pleistocene. The majority of remains is attributed to MIS 3 as based on few direct dates and associated faunal remains. The frequent occurrence of *Panthera spelaea* in high Alpine areas implies the presence of prey species. While little is known about herbivores in the High Alps during MIS 3, cave bears (*Ursus spelaeus*-group) are abundant. Isotope data – so far only from outside the Alps – suggest a certain portion of cave bears in their diet (e.g. Bocherens et al., 2011). Due to felid behaviour of defleshing carcasses with rare appearance of significant bone modifications cave lion hunting activity has not been proven so far in Alpine caves.

Metrical analyses of available elements show size ranges typical for Late Pleistocene cave lions. Size values of Alpine lions fall well within the limits shown by Marciszak et al. (2014) for specimen from MIS 3. A certain degree of sexual dimorphism is observed and mainly recorded in length measurements while long bone breadth is more variable. The large size of scattered elements of a single individual from Schusterlucke, Lower Austria outside the Alpine Arc argues against the proposed size reduction of lions from MIS 3 to MIS 2 (Marciszak et al., 2014). Directly dated into the Late Glacial period (Stuart & Lister, 2011) the specimen falls within the range of large sized, probably male specimen with values of 142mm and 363mm greatest length for the *os metatarsale* 3 and the tibia (Pacher & Rabeder, *in press*). In summary, Alpine lion exhibit metrical characteristics of typical Late Pleistocene lions, while additional studies are needed to understand cave lion behaviour in the high Alpine areas and possible size variability of Pleistocene *Panthera spelaea* in various regions through time.

Acknowledgement. The study was inspired by a revision of the faunal material from “Emil Bächler’s” bear caves, housed at the Naturmuseum St. Gallen, His 150th anniversary was celebrated at the museum this year. The study would not have been possible without the kind help of several people who provided access and information on cave lion material, especially Alexander Bibl and Frank Zachos, Zoological Department of the Natural History Museum Vienna, Toni Bürgin from the Naturmuseum St. Gallen, Switzerland, Ursula Göhlich, Geological-Palaeontological Department of the Natural History Museum Vienna, Ingomar Fritz and Martin Gross from the Regional Museum Joanneum Graz, Nagel Doris and Gernot Rabeder from the Institute of Palaeontology, University of Vienna. The study is financed by the Naturmuseum St. Gallen in course of the revision of the three Eastern Swiss bear caves. It is also part of the project “Lunzer Bärenhöhlen” of the Institute of Palaeontology, University of Vienna and the Wasserkluster Lunz financed by the regional government of Lower Austria.

POĽOVAČKA V HORÁCH – ROZŠÍRENIE LEVA JASKYNNÉHO (*PANTHERA SPELAEA*) V ALPÁCH A METRIKA

Resume

Na základe vrchnopleistocénneho rozšírenia leva jaskynného v Alpách (najmä vo východoalpskej oblasti a vo Východných Švajčiarskych Alpách) je v článku podaný po prvýkrát prehľad nálezov a metrických údajov z Východných Álp. Štúdia prináša údaje o frekvencii výskytu levov a ich paleobiologické dôsledky, predovšetkým pre stanovenie koristi alpských levov. Možné veľkostné rozdiely medzi východoalpskými populáciami a levmi mimo územia Álp sú taktiež riešené na základe porovnania metrických údajov, ktoré sú analyzované pomocou dvojrozmerných grafov a LSI prístupu. Ten umožňuje zahrnúť do väčšieho porovnania populácií aj jediného jedinca (vzorku), ako sa to bežne používa pri archeozoologickom výskume. Pre lepšie porozumenie paleobiológie a metrickej variability alpských levov z obdobia vrchného pleistocénu sú potrebné ďalšie výskumy.

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Supplement: Measurement from cave lions *(Panthera spelaea)* of the Eastern Alpine region and Eastern Swiss Alps

Tab. 1. Measurements of upper teeth from cave lions (*Panthera spelaea*) of the Eastern Alpine region and Eastern Swiss Alps (Inv. no. – Inventory number, Pres. – preservation)

Site	Inv. no	Pres.	Element	Length	Breadth	Reference
Badlhöhle	LMJ 2174	maxilla	C sup.	23.5	16.6	new
Badlhöhle	LMJ 58262	isolated	C sup.	27.9	20.5	new
Gamssulzen	GS 129-2	isolated	C sup.	-	20.3	new
Gamssulzen	onr (1988)	isolated	C sup.	26.2	19.1	new
Frauenhöhle	LMJ 14134	maxilla	C sup.	26.2	18.7	new
Frauenhöhle	LMJ 58262	isolated	C sup.	27.8	20.7	new
Mathilden-grotte	LMJ 9587	isolated	C sup.	29.0	21.0	new
Siegsdorf	-	skull	C sup.	27.0	21.0	Gross, 1992: 114
Nixloch	NL 71/6	isolated	P2 sup.	8.2	6.0	Kunst, 1992: 111, tab. II, 7
Bärenfalle	BF 2	isolated	P3 sup.	23.3	11.7	new
Brettstein	LMJ77316	maxilla	P3 sup.	26.0	13.7	new
Gamssulzen	NHMW-2	isolated	P3 sup.	28.0	13.7	new
Frauenhöhle	LMJ 22785	isolated	P3 sup.	26.3		new
Frauenhöhle	LMJ 22624	isolated	P3 sup.	27.3		new
Frauenhöhle	LMJ 14134	maxilla	P3 sup.	26.9	13.9	new
Merkenstein ?*	F5164-F98 sin	skull	P3 sup.	22.8	11.4	new
Merkenstein ?*	F5164-F98 dext.	skull	P3 sup.	22.3	12.5	new
Siegsdorf		skull	P3 sup.	28.0	15.5	Gross, 1992: 114
Wildenmann-lisloch	Wm16	maxilla	P3 sup.	26.7	14.5	new
Badlhöhle	LMJ 2174	maxilla	P4 sup.	37.2	19.7	new
Badlhöhle	LMJ 58261	maxilla	P4 sup.	34.9		new
Divje babe		isolated	P4 sup.	33.2		Toškan, 2007: 233
Merkenstein ?*	F5164-F98 sin	skull	P4 sup.	32.9	16.4	new
Merkenstein ?*	F5164-F98 dext.	skull	P4 sup.	32.0	16.4	new
Siegsdorf	-	skull	P4 sup.	40.3	20.0	Gross, 1992: 114

*…site affiliation of the skull is assumed

Tab. 2. Teeth measurements of lower teeth from cave lion (*Panthera spelaea*) from the Eastern Alpine region and Eastern Swiss Alps (Inv. no. – Inventory number, Pres. – preservation)

Site	Inv. no.	Pres.	Element	Length	Breadth	Reference
Conturines	Cu 33	isolated	cd inf.	8.6	5.8	new
Bärenfalle	IN 850-1	mandible	C inf.	19.8	15.8	new
Frauenhöhle	LMJ 14137	mandible	C inf.	27.0	20.2	new
Herdengel	HD 371	mandible	C inf.	25.7	18.1	Pacher, 2009: tab. 1
Salzofen	A 3516	mandible	C inf.	21.2	17.7	new
Siegsdorf	-	mandible	C inf.	24.0	18.0	Gross, 1992: 115
Badlhöhle	LMJ 2175	mandible	p3 inf.	20.0	13.0	Mottl 1949a: 106, tab. 2
Bärenfalle	BF 37	isolated	p3 inf.	15.8	8.6	new
Gaisberg	LMJ 1655	mandible	p3 inf.	21.4	11.5	new
Gamssulzenhöhle	NHMW 3	isolated	p3 inf.	18.0	9.7	new
Frauenhöhle	LMJ 14136	mandible	p3 inf.	17.3	8.9	new
Frauenhöhle	LMJ 14137	mandible	p3 inf.	19.7	11.0	Mottl, 1949a: 106, tab. 2; new
Frauenhöhle	LMJ 14138	isolated	p3 inf.	18.8	9.8	new
Frauenhöhle	LMJ 14139	isolated	p3 inf.	17.0	10.3	new
Herdengelhöhle	HD 181	isolated	p3 inf.	15.0	8.7	new
Siegsdorf	-	mandible	p3 inf.	19.5	11.0	Gross, 1992: 115
Bärenfalle	IN 850-1	mandible	p4 inf.	24.8	11.5	new
Badlhöhle	LMJ 22651	isolated	p4 inf.	28.0	13.6	new
Badlhöhle	LMJ 2175	mandible	p4 inf.	30.0	16.0	Mottl, 1949a: 106, tab. 2
Divje babe		isolated	p4 inf.	28.0	13.3	Toškan, 2007: 233
Frauenhöhle	LMJ 14136	mandible	p4 inf.	25.6	12.8	new
Frauenhöhle	LMJ 14137	mandible	p4 inf.	26.5	13.7	Mottl, 1949a: 106, tab. 2; new
Gaisberg	LMJ 1655	mandible	p4 inf.	32.4	17.0	new
Herdengelhöhle	HD 371	mandible	p4 inf.	27.0	14.6	Pacher, 2009: tab. 1
Herdengelhöhle	HD 89	isolated	p4 inf.	29.0 ca.	15.6	new
Mathildengrotte	LMJ 9586	mandible	p4 inf.	31.5	16.6	new
Salzofen	A 3516	mandible	p4 inf.	27.1	14.0	new
Siegsdorf	-	mandible	p4 inf.	29.0	15.0	Gross, 1992: 115
Wildkirchli	I.S.O.M. 2,2	isolated	p4 inf.	32.0	16.0	new
Badlhöhle	LMJ 2175	mandible	m1 inf.	30.5	17.0	Mottl, 1949a: 106, tab. 2
Bärenfalle	IN 850-1	mandible	m1 inf.	26.2	13.5	Tichy, 1985: 848
Divje babe		isolated	m1 inf.	27.7	13.3	Toškan, 2007: 233
Drachenhöhle	3000/04/002	isolated	m1 inf.	29.1	15.3	new
Frauenhöhle	LMJ 14136	mandible	m1 inf.	28.1	15.3	new
Frauenhöhle	LMJ 14137	mandible	m1 inf.	28.6	14.2	Mottl, 1949a: 106, tab. 2; new
Gaisberg	LMJ 1655	mandible	m1 inf.	31.7	17.0	new
Gamssulzen	NHMW-1	isolated	m1 inf.	28.1	15.0	new
Herdengel	HD 371	mandible	m1 inf.	31.3	15.2	Pacher , 2009: 23, tab. 1
Mathildengrotte	LMJ 9586	mandible	m1 inf.	30.5	15.8	new
Salzofen	A 3516	mandible	m1 inf.	28.1	14.3	new
Siegsdorf	-	mandible	m1 inf.	30.0	15.5	Gross, 1992: 115
Wildkirchli	I.S.O.M 2,2	isolated	m1 inf.	30.0	16.3	new

Tab. 3. Measurements of mandibles from cave lion (*Panthera spelaea*) from the Eastern Alpine region and Eastern Swiss Alps (Inv. no. – inventory number, TL – total length, L-Id – length from indentation between the condyle process and the angular process towards the infradentale, Lm1c – Length behind m1 towards behind the canine, DL – length between canine and p3, Hp3 – height of mandible in front of p3, hm1 – height of mandible behind m1, CTL – length of cheek teeth row, m1a – length of m1 alveoli)

Site	**Inv. no.**	**TL**	**L-Id**	**Lm1c**	**DL**	**Hp3**	**Hm1**	**CTL**	**m1a**
Badlhöhle[1]	LMJ 2175						58.0		
Bärenfalle	IN 850-1			83.0	19.0	39.5	36.9	64.0	24.7
Frauenhöhle[1]	LMJ 14137			101.7	30.0	56.8	60.0	75.2	26.7
Frauenhöhle[1]	LMJ 14136						56.4	71.7	
Gaisberg[1]	LMJ 1655						74.0	78.6	27.7
Herdengelhöhle[2]	HD 371	230.0	207.0		18.0	49.7	46.4	77.1	31.0
Mathildengrotte	LMJ 9586								28.2
Salzofenhöhle	A 3516	270.0		29.0	30.3	56.6	57.8	75.9	
Siegsdorf[3]	-	263.0	213.0			51.5	55.0	82.0	29.0

[1]Mottl, 1949a: 106, tab. 2, [2]Pacher, 2009: 24, tab. 2, [3]Gross, 1992: 115

Tab. 4. Measurement of atlas from cave lion (*Panthera spelaea*) from the Eastern Alpine region and Eastern Swiss Alps (Inv.no.– inventory number, BFcr – breadth of the *facies articularis cranialis*, BFcd – breadth of the *facies articularis caudalis*, H – height, Lad – length of the *arcus dorsalis*, Lav – length of the *arcus ventralis*)

Site	**Inv.no**	**BFcr**	**BFcd**	**H**	**Lad**	**Lav**	**Reference**
Herdengelhöhle	HD 314	77.1	73.5	50.7		20.2	Pacher, 2009: 25, tab. 3
Potočka zijalka	-	67.7	65.8ca.	42.5		21.7	Krofel, 2004: 82, tab. 1
Siegsdorf	-	86.0	84.5	55.0	39.5	27.0	Gross, 1992: 117

Tab. 5. Measurement of humerus of cave lion (*Panthera spelaea*) from the Eastern Alpine region and Eastern Swiss Alps (Inv. no. – inventory number, gL – greatest length, pL – physiological length, Bp – proximal breadth, Dp – proximal depth, SD – smallest diaphyseal depth, Bd – distal breadth, BT– breath of the trochlea)

Site	**Inv. no.**	**gL**	**pL**	**Bp**	**Dp**	**SD**	**Bd**	**BT**	
Bärenfalle	850-2-1					28.4	83.6	56.9	new
Bärenfalle	850-2-2					29.0			new
Herdengelhöhle	IPUW	374.0	351.1	91.0	114.1	34.5	99.4	72.2	new
Wildkirchli	A4a1.3m						100.6	75.0	new

Tab. 6. Measurement of radius of cave lion (*Panthera spelaea*) from the Eastern Alpine region and Eastern Swiss Alps (Inv. no. – inventory number, gL – greatest length, Bp – proximal breadth, Bd – distal breadth)

Site	**Inv. no.**	**gL**	**Bp**	**Bd**	
Drachenhöhle		290.0		59.0	Sickenberg, 1931: 749
Herdengelhöhle	HD 597	327.0 ca.	46.1	65.0 ca.	Pacher, 2009: 25, tab. 5

Tab. 7. Measurement of ulna from cave lion (*Panthera spelaea*) from the Eastern Alpine region and Eastern Swiss Alps (Inv. no. – inventory number, Bpc – breadth across the coronoid process, SDO – smallest depth of the olecranon, gDO – greatest depth of the cranial border of the olecranon, Bd – distal breadth, SD – smallest depth of *incisura trochlearis* until *margo caudalis*, DPa – depth across the *processus anconeus*)

Site	**Inv. no.**	**Bpc**	**SDO**	**gDO**	**Bd**	**SD**	**DPa**
Frauenhöhle	LMJ 14100	49.0		57.0		49.0	76.7
Frauenhöhle	LMJ 14110	76.7	59.1			46.5	83.8
Herdengelhöhle	HD 316				38.6		
Herdengelhöhle	HD 558		65.1		42.0	46.0	76.7

Tab. 8. Measurement of metacarpals from cave lion (*Panthera spelaea*) from the Eastern Alpine region and Eastern Swiss Alps (Inv. no. – inventory number, gL – greatest length, Bp – proximal breadth, Dp – proximal depth, SD – smallest diaphyseal breadth, Bd – greatest distal breadth, Bda– breadth of distal articulation, dD – depth of the distal end, juv – juvenile)

Site	**Inv.no**	**Element**	**gL**	**Bp**	**Dp**	**SD**	**Bd**	**Bda**	**dD**
Gamssulzen	GS 133	Mc1	44.7				19..7		
Herdengelhöhle	HD 148	Mc1	36.8						
Leopoldinengrotte	LG 58	Mc1	42.5	18.4			18.5		
Bärenfalle	IN 850-4-1	Mc2		21.9	29.8				
Drachenhöhle	IPUW	Mc2	109.4	23.7	34.4	15.8	24.9	22.7	23.8
Drachenhöhle	LMJ 39733	Mc2	102.4	23.3	31.4	15.5	23.8	20.8	21.7
Drachenhöhle	LMJ 59491	Mc2	102.8	22.8	31.0	16.2	24.0		21.9
Frauenhöhle	LMJ 14118	Mc2	107.8	25.5	32.3	17.4	25.5	22.0	23.6
Gamssulzen	GS 129-29	Mc2	118.8			16.3	24.7		
Herdengelhöhle	HD 57	Mc2	96.2	25.1	31.0	14.3	21.9		20.2
Bärenfalle	850-3-1	Mc3		24.5	24.7	14.9			
Drachenhöhle	IPUW	Mc3		31.0	29.6	16.3			
Drachenhöhle	IPUW	Mc3	119.7	28.5	27.6	16.7	23.8	21.3	22.1
Frauenhöhle	LMJ 14116	Mc3	125.0	29.5	28.2	17.9	27.2		25.3
Frauenhöhle	LMJ 14117	Mc3	130.0	31.4	31.0	19.2	27.6	24.8	24
Gamssulzen	GS 26-83	Mc3	126.8			17.1	27.2	24.0	
Hartlesgrabenh.	LMJ 58267	Mc3	128.9	28.3	31.0	17.4	27.6	25.0	25.2
Herdengelhöhle[1]	HD 405	Mc3		32.2		18.8			
Leopoldinengrotte	LG 52-5	Mc3		25.6	28.9				
Wildenmannlisloch	Wm26	Mc3		25.4	27.5				
Bärenfalle	850-6-1	Mc4		24.7	32.2	16.8			
Drachenhöhle	IPUW	Mc4	126.0	27.1	30.2	16.7	23.0	23.1	26.3
Gamssulzen	GS 161-29	Mc4	145.7			19.2	25.9		25.7
Flatzer Tropfsteinh.	MNK 11500	Mc4	135.7	25.9	31.5	17.7	24.3		
Merkensteinh.[2]	-	Mc4	111.2	22.2		13.8	21.8		
Ramesch	IPUW	Mc4	118.0			14.0	21.0		
Drachenhöhle	LMJ 39053	Mc5	91.2	25.3	26.8	15.3	21.8		
Gamssulzen	GS 45-5	Mc5	106.0	30.2	29.9	16.8	25.9	23.3	25.0
Frauenhöhle	LMJ 14119	Mc5 juv		28.0	26.1	15.3			
Herdengel	HD 552	Mc5	105.8	29.0	29.7	18.3	25.9		25.0
Salzofenhöhle	IPUW	Mc5	86.9	24.7	25.7	14.5	20.0	18.8	21.1
Wildkirchli	V 1,9	Mc5	110.1	29.6	30.9	18.5	26.2	23.6	26.1

[1] Pacher, 2009: 26, tab. 6; [2] Nagel, 1997: 221, tab. 3

Tab. 9. Measurement of femora from cave lion (*Panthera spelaea*) from the Eastern Alpine region and Eastern Swiss Alps (Inv. no. – inventory number, gL – greatest length, gLc – greatest length from *caput femoris*, Bp – proximal breadth, Bp – proximal breadth, Dc – depth of *caput femoris*, CD – smallest circumference of diaphysis, SD – smallest diaphyseal breadth, Bd – distal breadth)

Site	Inv. no.	gL	gLc	Bp	Dc	CD	SD	Bd
Frauenhöhle	LMJ 14111			109.2	48.02		41.0	
Siegsdorf	left	410.0	410.0	106.0	48.0	117.0	38.0	86.5
Siegsdorf	right	409.0	407.0	106.0	48.0	116.5	38.0	85.5

Tab. 10. Measurement of tibia from cave lion (*Panthera spelaea*) from the Eastern Alpine region and Eastern Swiss Alps (Inv. no. – inventory number, gL – greatest length, Bp – proximal breadth, SD – smallest diaphyseal breadth, CD – smallest circumference of diaphysis, Bd – distal breadth, Dd – depth of the distal end)

Site	Inv. no.	Element	gL	Bp	SD	CD	Bd	Dd
Badlhöhle	IPUW 80	sin.	344.1	93.7	36.1	117.0	67.8	45.9
Drachenhöhle[1]	IPUW	dext.	320.0		33.8		60.0	42.7
Drachenhöhle[1]	IPUW	dext.	320.0		31.5		61.1	40.0
Drachenhöhle	LMJ 25094	sin.	337.0	91.2	37.5		67.8	43.9
Frauenhöhle	LMJ 14112						70.0	45.5
Merkensteinh.	NHMW	2014/0324/0001	318.0	80.0	32.0		59.5	39.0
Siegsdorf		sin.	354.0	92.0	36.0	110.0	71.25	45.5
Siegsdorf		dext.	355.0	92.5	35.0	110.0	71.5	45.0

[1] Sickenberg, 1931: 749

Tab. 11. Measurement of talus from cave lion (*Panthera spelaea*) from the Eastern Alpine region and Eastern Swiss Alps (Inv. no. – inventory number, gL – greatest length, GB – greatest breadth, BTa – breadth of trochlea, LTa – length of trochlea)

Site	Inv. no.	gL	GB	BTa	LTa
Divje babe[1]	D.b.554	57.0			
Drachenhöhle	IPUW-left	64.0		43.2	49.4
Drachenhöhle	IPUW-right	56.0	49.0	37.1	43.0
Drachenhöhle	LMJ 36825		53.0	41.0	
Drachenhöhle	LMJ 36817		53.0		
Gamssulzenhöhle	GS 26-150	67.0	57.0	43.0	
Gamssulzenhöhle	GS 33-1	58.0	56.0	38.0	
Siegsdorf[2]		65.0	55.0		

[1] Toškan, 2007: 271, [2] Gross, 1992: 126

Tab. 12. Measurement of calcaneus from cave lion (*Panthera spelaea*) from the Eastern Alpine region and Eastern Swiss Alps (Inv. no. – inventory number, gl – greatest length, GB – greatest breadth, HTc – height of *tuber calcanei*, SB – smallest breadth, Bcr – breadth of *facies articularis astragali*, gH – greatest height)

site	**Inv. no.**	**gL**	**GB**	**HTc**	**SB**	**Bcr**	**GH**
Badlhöhle	LMJ 1645	123.2	61.8	55.6	14.0	45.2	55.6
Drachenhöhle	IPUW-right	125.6	52.2	52.3	26.2	48.5	55.0
Drachenhöhle	IPUW-right	119.3	45.3	50.3	21.4	46.0	54.0
Drachenhöhle	IPUW-left	113.8	48.2	45.8	29.7	43.5	48.0
Frauenhöhle	LMJ 14113	122.0	55.3	53.2	25.0	46.8	56.7
Gamssulzenhöhle	GS 123-3	131.9	62.8	49.7		51.7	
Gamssulzenhöhle	GS 161-27					42.8	
Siegsdorf[1]	-	126.0	57.5	60.0			
Wildkirchli	WH m43	132.0	56.0	56.5		47.3	

[1] Gross, 1992: 126

Tab. 13. Measurement of metatarsals from cave lion (*Panthera spelaea*) from the Eastern Alpine region and Eastern Swiss Alps (Inv. no. – inventory number, gL – greatest length, Bp – proximal breadth, Dp – proximal depth, SD – smallest diaphyseal breadth, Bd – greatest distal breadth, Bda – breadth of distal articulation, dD – depth of the distal end, juv – juvenile)

site	**Inv. no.**	**Element**	**gL**	**Bp**	**Dp**	**SD**	**Bd**	**Bda**	**Dd**
Bärenfalle	850-5-1	Mt2		22.4	29.7	14.9			
Drachenhöhle	IPUW	Mt2	119.5	25.7	32.9	19.0	25.6	23.8	
Drachenhöhle	IPUW	Mt2	133.0	29.4	30.0	18.4	25.8	23.7	25.2
Frauenhöhle	LMJ 22847	Mt2	118.5	24.9	31.4	16.2	23.2	22.1	-
Gamssulzen	GS 28-1	Mt2	116.2			16.7	24.5	21.1	
Geröllhöhle	H1984-1	Mt2	126.8			13.7	23.1		20.7
Wildkirchli	WH 43m	Mt2	134.1	25.9		18.7	27.0	23.6	23.4
Divje babe[1]	D.b.564	Mt3	143.0	17.0		24.0		20.0	
Drachenhöhle	IPUW	Mt3	131.1	29.6	40.9	21.0	29.0	25.8	25.3
Drachenhöhle	IPUW	Mt3	130.9	28.1	35.6	18.9	24.5	22.3	23.4
Drachenhöhle	IPUW	Mt3	151.4	28.5	40.0	21.5	27.0	25.0	24.6
Drachenhöhle	LMJ 13367	Mt3	148.9	30.0	40.8	22.8	27.6		
Drachenhöhle	LMJ 13364	Mt3	124.7	25.4	34.2	18.4	25.0		22.3
Drachenhöhle	LMJ 13365	Mt3		27.7	38.1	19.5			
Gamssulzen	GS 26-84	Mt3	145.1	29.6	40.2	19.7	28.1		
Gamssulzen	GS 36-1	Mt3	128.5	27.4	36.5	17.6	25.2	22.7	
Herdengelh.[2]	HD 307	Mt3	152.3	29.0	40.5	20.0	29.0		26.3
Herdengelh.[2]	HD 636	Mt3	153.0	30.8	40.7	22.6	29.4		26.3
Leopoldinengr.	LG 88	Mt3	133.0	28.8	39.6	19.6	29.6	24.8	25.6
Siegsdorf[3]	-	Mt3	138.0	29.5		20.0	27.0		
Tropsteinhöhle	LMJ 60050	Mt3	133.4	26.9	36.4	18.4	25.7	23.2	23.5
Brettstein[4]	Aussee	Mt4	150.0	26.1				26.3	
Badlhöhle[4]	IPUW	Mt4	141.5	25.8				27.2	
Badlhöhle	LMJ 58269	Mt4		28.8	34.7	18.8			
Drachenhöhle	IPUW	Mt4	132.4	28.4	37.6	20.3	27.5	23.8	25.0
Drachenhöhle	IPUW	Mt4	140.3	27.5	36.6	18.3	24.2	20.7	
Drachenhöhle	IPUW	Mt4	125.4	25.3	31.0	16.3	23.0	20.2	21.6
Frauenhöhle	LMJ 14115	Mt4	149.6	30.3	36.2	20.4	26.7	24.4	24.7
Griffen[5]	KLM	Mt4			34.2	39.8			
Merkenstein[6]	IPUW	Mt4	132.7	25.9		16.1	22.5		
Siegsdorf[3]		Mt4	141.5	32.5	17.5		25.0		
Bärenfalle	IN 848-10	Mt5 juv		25.5	16.2	10.8			
Drachenhöhle	IPUW	Mt5	139.7	30.3	24.1	15.2	24.3	20.8	23.0
Drachenhöhle	IPUW	Mt5		27.6	20.7	13.2	21.5	18.6	19.8
Drachenhöhle	LMJ 13366	Mt5	128.6	29.8		13.5	22.8		21.9
Gamsulzen	GS 56-2	Mt5	118.7			14.0	21.1	18.3	
Gamsulzen	GS 161-30	Mt5	138.0			14.9	24.1	20.0	
Herdengel[2]	HD 94+91	Mt5	141.2	29.2		13.5	23.9		23.1
Herdengel[2]	HD 340	Mt5	140.0	28.8		13.5	24.0		22.9
Ramesch	IPUW	Mt5	130.0			12.0	20.0		
Siegsdorf[3]	-	Mt5	132.5	29.5		12.5	22.5		
Tropfsteinhöhle	LMJ 60051	Mt5	122.7	27.4	-	11.8	21.1	19.0	20.6

[1] Toškan, 2007: 271; [2] Pacher, 2009: 26, tab. 6; [3] Gross, 1992: 127; [4] Ehrenberg, 1958: 6; [5] Thenius, 1960: 43; [6] Nagel, 1997: 221, tab. 3

Table 14. Measurement of proximal phalanges from cave lion (*Panthera spelaea*) from the Eastern Alpine region and Eastern Swiss Alps (Inv. no. – inventory number, gL – greatest length, Bp – proximal breadth, Dp – proximal depth, SD – smallest diaphyseal depth, Bd – distal breadth)

Site	**Inv. no.**	**gL**	**Bp**	**Dp**	**SD**	**Bd**
Badlhöhle	LMJ 58237	61.2	26.9	19.5	18.9	19.0
Badlhöhle	LMJ 58274	55.3	23.0	20.0	13.9	17.0
Badlhöhle	LMJ 22626	55.3	23.8	18.6	18.6	19.0
Badlhöhle	LMJ 58263	54.1	23.4	17.3	17.3	17.5
Badlhöhle	LMJ 59264	60.4	24.0	18.8	15.5	19.0
Badlhöhle	LMJ 58265	54.7	23.6	17.6	15.8	17.9
Bärenfalle	IN 850-7-1	54.6	21.3		15.5	17.3
Bärenfalle	IN 850-7-2	45.4	17.8	15.0	11.3	15.2
Bärenfalle	IN 850-7-3	53.3	22.5	18.0	16.9	17.5
Bärenfalle	IN 850-7-4	57.0	22.0	17.3	15.5	17.2
Bärenfalle	BF 18	58.0	22.0	16.9	14.9	17.5
Bärenfalle	BF 21	51.6	22.0	17.7	15.5	17.0
Bärenfalle	BF 36	55.1	21.2	17.6	14.8	17.2
Bärenfalle	BF 34	48.7	20.0	16.8	12.3	16.3
Brettstein	BS 15	52.4	21.4	16.9	13.6	16.0
Frauenhöhle	LMJ 14121	65.5	26.4	21.9	18.7	20.8
Frauenhöhle	LMJ 22601	63.3	26.8	22.6	18.5	20.5
Frauenhöhle	LMJ 14122	63.0	15.2		16.4	19.0
Frauenhöhle	LMJ 19476	61.4	24.7	21.5	19.0	
Frauenhöhle	LMJ 19308	60.0			19.7	20.2
Frauenhöhle	LMJ 19363	60.8	25	21.8	19.5	20.5
Frauenhöhle	LMJ 19374	55	25	20.5	18	18
Frauenhöhle	LMJ 19269	51.5	20.5		14	18
Frauenhöhle	LMJ 19426	54.5	23	19	16	
Frauenhöhle	LMJ 19431	54	23	19.8	16.2	19
Frauenhöhle	LMJ 58264	58.9	24	18.3	15.5	19
Frauenhöhle	LMJ 58265	54.8	23.3	17.3	15.7	17.5
Frauenhöhle	LMJ 59263	54	23.3	17.3	17.2	17.4
Frauenhöhle	LMJ 22602	53.4	23.7	18.8	16.4	18
Frauenhöhle	LMJ 22603	57	22.6	19	15.4	17.4
Frauenhöhle	LMJ 14120	58.5	24.2	18.4	16.7	18.7
Frauenhöhle	LMJ 22598	50.8	20.7			16.5
Gamssulzenhöhle	GS 26-40	45.9			12.8	14.3
Gamssulzenhöhle	GS 34-2	50.5	22.7	19.0	16.2	17.6
Gamssulzenhöhle	GS 55-1	55.1	24.0	18.9	16.3	18.3
Herdengelhöhle	HD 324	63.5	26.2		17.4	19.5
Herdengelhöhle	HD 59	55.1	24.4		16.8	19.0
Herdengelhöhle	HD 338	47.0	22.0	20	14	20
Herdengelhöhle	HD 563	44.0	21	18	14	18
Herdengelhöhle	HD 181	39.0	18	17	11	20
Herdengelhöhle	HD 335	41.0				
Merkensteinhöhle[1]	IPUW	58.7	21.9		14.5	19.8
Merkensteinhöhle[1]	IPUW	60.6	24.0		15.6	18.5
Merkensteinhöhle	NHMW 2014/0324/0003				16.2	23.3
Tropfsteinhöhle	LMJ 60052	60.6	23.2	22.0	17.3	19.5
Tropfsteinhöhle	LMJ 60053	49.3	21.1	18.0	12.9	16.7
Wildkirchli	WKV 401-1	60.0	24.0	21.2	18.3	20.3
Wildkirchli	WKV 401-2	57.7	24.6	20.8	17.4	19.2

[1] Nagel 1997: 218

SLOVENSKÝ KRAS ACTA CARSOLOGICA SLOVACA	56/1	87 – 98	LIPTOVSKÝ MIKULÁŠ 2018

CRANIUM OF JUVENILE CAVE HYENA FROM THE JASOVSKÁ JASKYŇA CAVE (SLOVAKIA)

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M. Sabol, V. Petrovič, J. Šurka: Cranium of juvenile cave hyena from the Jasovská jaskyňa Cave

Abstract: The fossil record of cave hyenas (*Crocuta crocuta spelaea*) from Slovakia is relatively rare, limited so far only to 10 Late Pleistocene sites. A juvenile skull from the Jasovská jaskyňa Cave is the most complete cranial record of this species in the Slovak territory. Partially damaged, the skull probably belonged to an individual younger than one year on the basis of root development of not-fully erupted P3s. In morphological comparisons with the skull of an approximately equally old individual of the Middle Pleistocene *C. crocuta intermedia* from Lunel-Viel, the main difference is observed in the skull length and height, attended by different levels of the expansion of palatinal and zygomatic areas. These differences are likely to result of changes in species evolution during the Middle to Late Pleistocene associated with a gradual increase in body size and a more robust development of jaw musculature, what could be a possible consequence of not only the changing environment but also adaptation to crushing and biting of bones of larger animals.

Key words: *Crocuta crocuta spelaea*, craniology, environmental and behavioural changes, Pleistocene, Europe

INTRODUCTION

The cave hyena (*Crocuta crocuta spelaea* (Goldfuss, 1823)) is an extinct large subspecies of the spotted hyena (*C. crocuta* (Erxleben, 1777)) that evolved probably at the end of Middle Pleistocene in the Northern Hemisphere, presumably by hybridization of ancestral form *C. crocuta praespelaea* Schütt, 1971 with *C. crocuta intermedia* de Serres, 1828 (Barycka, 2008). Whereas *C. crocuta praespelaea* is a descendant of the first migration wave of spotted hyenas from Africa to Europe 1.5 to 1.3 Ma ago, *C. crocuta intermedia* is a representative of the second migration event dated back only 0.36 Ma ago (Rohland et al., 2005; Barycka, 2008). The subspecies status of cave hyena was confirmed by new analyses of partial DNA sequences of the mitochondrial cytochrome b, which showed also the presence of two mtDNA clades of cave hyenas – one is different from modern spotted hyenas (clade B) and the second is formed by intermixed sequences of Late Pleistocene Eurasian cave hyenas and modern spotted hyenas from Northern Africa (clade A) (Rohland et al., 2005). Although the morphological results revealed a phylogeographic pattern with a little geographic overlap between these clades, the genetic investigation suppresses these phylogenetic differences (Nagel et al., 2004). New generated nuclear genomic data from Eurasian Late Pleistocene cave hyenas and modern African spotted hyenas show very little genetic differentiation within modern spotted hyenas relative to cave hyenas. It could indicate a resident population status of cave hyenas and their possible dispersal to Africa or a large bottleneck took place within spotted hyenas after the dispersal of cave hyenas out of Africa (Westbury et al., 2017).

The fossil record of cave hyenas from Slovakia is relatively rare, limited more or less to the Late Pleistocene deposits of the Čertova pec Cave, Dzeravá skala Cave, Gánovce-Hrádok, Malá Ľadnica Cave, Okno Cave, Prepoštská jaskyňa Cave, Salovec near Gombasek, Silická Brezová, Tmavá skala Cave, and also Jasovská jaskyňa Cave (Volko-Starohorský, 1927, 1929; Skutil, 1938; Hokr, 1951; Musil, 1996; Ďurišová, 2005; Holec, 2007; Sabol, 2008).

LOCALITY

The Jasovská jaskyňa Cave (Jasov Cave, also known as Okno Cave or Takáčova (Menyhért Takács) Cave), as one of ten documented Slovak sites with fossil remains of cave hyenas, is situated near Jasov village in the Medzevská pahorkatina (Medzev Hills) of the Košická kotlina (Košice Basin), approximately 20 km W-SW from Košice town (48° 40′ 36′′ N, 20° 58′ 35′′ E) within the Slovenský kras National park (Fig. 1) (Bella, 2003; Bella et al., 2007b). The entrance of this 2,811 m long and 55 m deep fluvio-karst cave is situated at an elevation of 257 m (Bella et al., 2007b). The cave is formed in the Middle Triassic grey Guttenstein dolomite and light Steinalm limestone and dolomite of the Silica Nappe; it is connected with the Okno (Window) Cave and genetically related to the Oblúková jaskyňa Cave (Arc Cave), the Fajka (Pipe) Cave, and the Kamenná pivnica (Stone Cellar) Cave (Bella, 2003).

Although the cave has been known for centuries (for example, inscriptions on cave walls from 1452, 1571, 1576, 1619, or 1783; Bella, 2003; Lalkovič, 2006),it was only opened in 1846 by A. Richter (Bella, 2003) and the first detailed written records are known only from 1857 to 1864 (A. Kiss, J. Hunfalvy, S. J. Petényi).The first experimental excavations in the cave were carried out by J. Nyáry and Ľ. Thallóczy in 1878 (Bárta, 1978). Also K. Siegmeth paid great attention to the cave in his works in 1880s. In 1890, J. Primič devoted his attention to the finding of cave bears in caves of the Austro-Hungarian Monarchy, including also fossil remains from the Jasovská jaskyňa Cave. However, the first report on fossil (bear) bones found in Pleistocene sediments of the cave was brought by Bucko in 1915 and the first palaeontological excavation at the site was carried out by T. Kormos and his co-workers (Kőszeghy, Szombathy, Ráday, Vámos, Vécsey, and Bucko) in 1916. Many animal bones were also excavated by soldiers of Czecho-Slovak legions headed by General R. Gaida during the opening work at the locality. Later, the fossilifereous sediments in several parts of the Jasov Cave System (Fajka, Oblúková jaskyňa, and Klinová chodba (Wedge Corridor) Caves – the left part of original entrance area of the Jasovská jaskyňa Cave) were detailed explored by J. Eisner and J. Bábor in 1924, and by J. Eisner and J. Volko-Starohorský in 1925 (Volko-Starohorský, 1926, 1929; Skutil, 1938).

The last systematic palaeontological research of the Jasovská jaskyňa Cave,focused predominantly on the stratigraphy and the fossil record of cave sediments,was carried out by Czech scientists V. Ložek, J. Sekyra, J. Kukla, and O. Fejfar in 1955 (Ložek et al., 1957). The excavations were realized in the original cave entrance (today's cave exit), which was formerly assumed to be a part of the oldest of five cave levels (Droppa, 1971; Gaál, 2008), but today probably represents rather a portion of evolutional phase of the ponor part of cave system (Bella et al., 2007a).

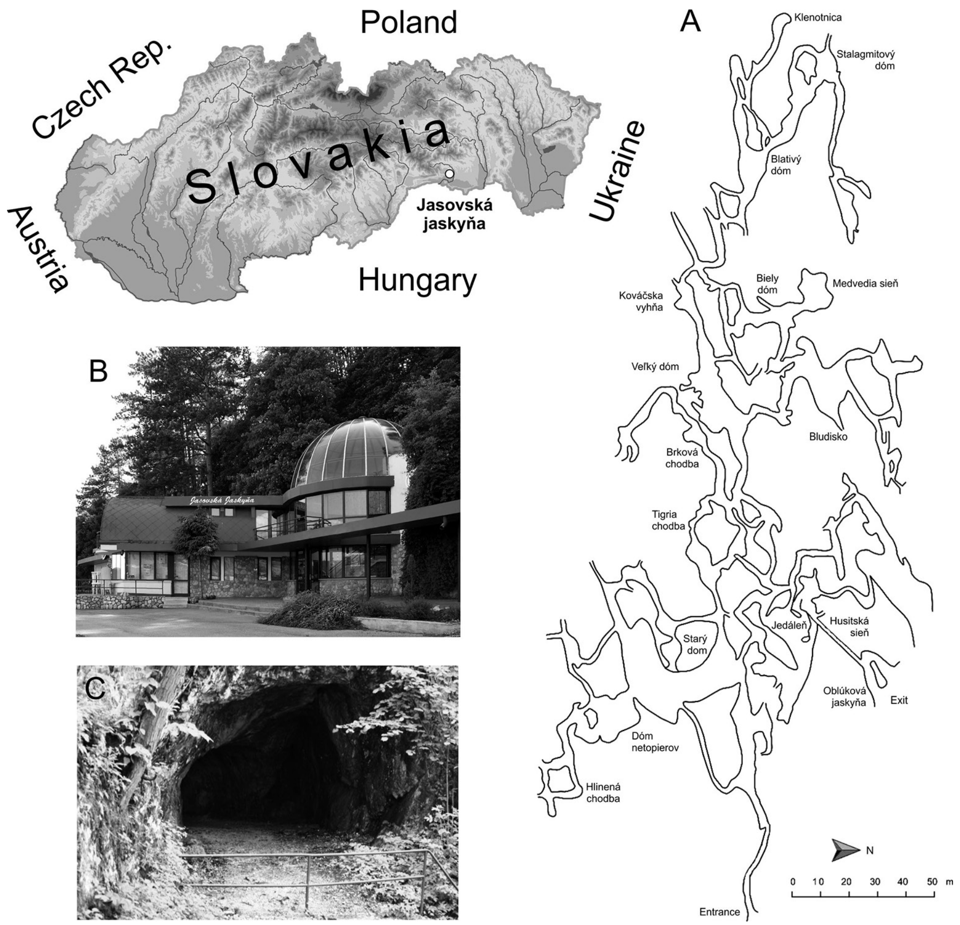

Fig. 1. The Jasovská jaskyňa Cave in south-eastern Slovakia. A: ground plan of the cave (http://www.ssj.sk/sk/jaskyna/11-jasovska-jaskyna), B: cave entrance (https://sk.wikipedia.org/wiki/S%C3%BAbor:Jasovsk%C3%A1_jasky%C5%88a,_vstupn%C3%BD_rozsah.jpg), C: cave exit (original cave entrance; http://www.slovensky-kras.eu/info/jaskyne-a-priepasti/jasovska-jaskyna/

MATERIAL AND METHODS

The first fossils of cave hyenas from the Jasovská jaskyňa Cave were mentioned by Volko-Starohorský (1929). He described briefly the third lower incisor (i3) together with several fragments of other teeth from the "middle diluvial" dark-yellow to brown loam layer of excavated pit in the "Klinová chodba" (extended Kormos's pit II), situated above the "lower" reddish loam layer with the dominance of cave bear remains. However, the most spectacular cave hyena record from the site is a skull of juvenile individual.

The skull, housed and exhibited today in the Slovak National Museum – Natural History Museum in Bratislava with the registration number Z 215 (P 1494/1961), was originally deposited in collections of the Archaeological Institute of the Slovak Academy of Sciences in Nitra until 1961. Unfortunately, no data on finding circumstances of this fossil remain are known and there are only circumstantial indications of its origin. Since

Ložek et al. (1957) did not publish any fossils of cave hyenas from this locality, the skull could be found here sometimes between 1925 (excavations of J. Eisner and J. Volko-Starohorský) and 1955 (excavations of Ložek et al.). On the other hand, the cave hyena skull could be found during archaeological prospections of J. Eisner and J. Bábor in 1924 (Anonymus, 1928), although no report on that is maintained. However, the Archaeological Institute of the Slovak Academy of Sciences in Nitra, where the skull was originally stored, originated only in 1953 from the formerly existing State Archaeological Institute, founded in 1939 in Martin. From this point of view, the deposition of the find in Nitra before 1953 is impossible and so its origin remains unknown, although its location at the Eisner's work places in Bratislava (Archaeological-historical section of Slovak Museum or State Archaeological Institute for Slovakia) before 1939 is not fully excluded.

Based on the colouring of the skull, it is possible to estimate at least the place of its original deposition in cave sediments. The find is coloured in grey to yellow with rusty (or red-brownish) stains. According to Volko-Starohorský (1929), fossils from the "lower" layer of reddish loam with fine gravel were light-yellow, whereas animal bones from the overlaying layer of brown-yellow gravelly loam were dark. This "lower" layer deposited at the depth of about 3.15 – 4.10 m with the thickness ranged from 0.85 to 0.95 m (Volko-Starohorský, 1929) could be correlated with lower layers (15 – 17, mainly with the 15a–c layer complex) of the back probe of Ložek et al. (1957) with the relatively rich fossil record of cave bears and the thermophilous forest molluscan assemblage with *Drobacia banatica* from the layer 15. Ložek et al. (1957) dated these lower layer to the Last Interglacial. On the other hand, it is not excluded that the found cave hyena skull comes from younger sediments, deposited during the Vistulian and correlated mainly with layers 7 and 8 of the back probe described by Ložek et al. (1957).However, assuming that the layers are properly dated, this supposition seems to be less likely than the abovementioned one also with the respect to the deposition depth of layers (see also "Discussion and Conclusion" chapter).

Traditional morphometric analysis was employed for precise determination of the cave hyena fossil find. The measured data is in millimeters; with measurements taken to the nearest 0.01 mm with engineering vernier calipers, 0.3 mm standard deviation, 0.1 mm dispersion, and 4.2% random error. The basic morphological terminology and measuring methods of the record under study were borrowed from Najbrt et al. (1980), Argant (1991), Gonzáles (2003), and Tseng (2013).

SYSTEMATIC PART

Family Hyaenidae Gray, 1821
Subfamily Hyaeninae Gray, 1821
Genus *Crocuta* Kaup, 1828
Crocuta crocuta spelaea (Goldfuss, 1823)
(Fig. 2, Tab. 1)

Type Locality: Zoolithenhöhle, Gailenreuth near Muggendorf (cave No. D 106), Germany (Diedrich, 2008).

Occurrence: late Middle Pleistocene to Late Pleistocene of Europe, Asia, and North Africa.

Characteristics: An extinct subspecies that differs from modern spotted hyena by a larger overall size, a large elongation of upper canines but a reduction in lower canines, a large elongation of P4 metastyle and wider and less prominent paracone, and smaller

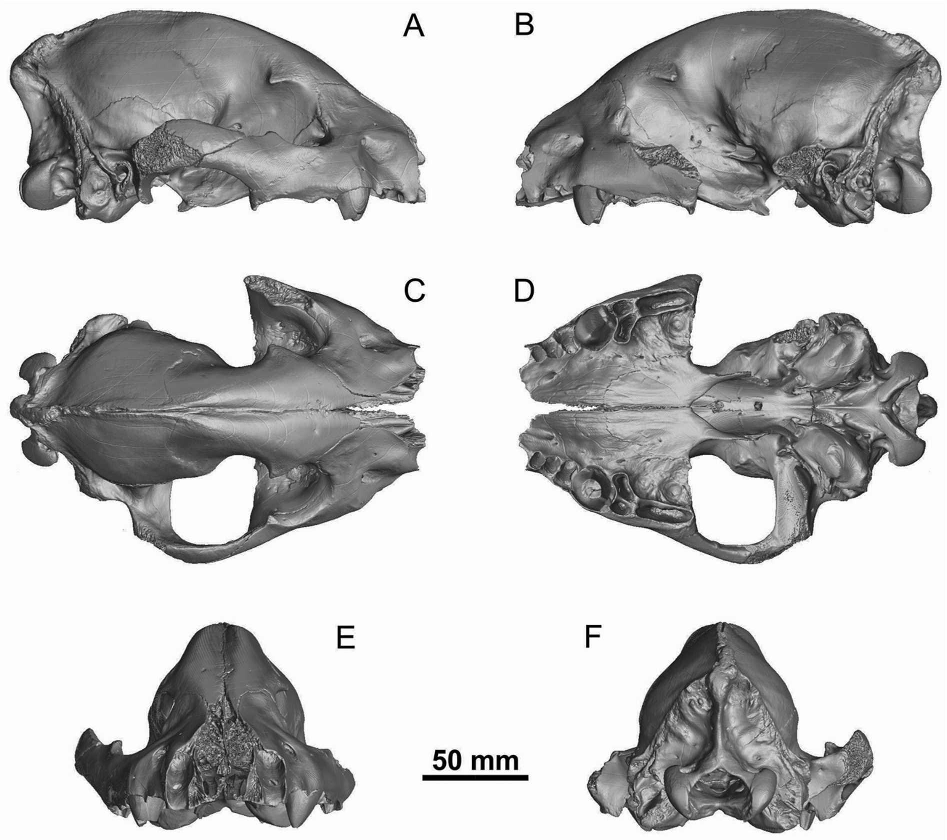

Fig. 2. Skull of juvenile cave hyena (*Crocuta crocuta spelaea* (Goldfuss, 1823)) from the Jasovská jaskyňa Cave (SNM – Z 215), Late Pleistocene.
A: lateral view (right side), B: lateral view (left side), C: dorsal view, D: ventral view, E: anterior view, F: posterior view

P1. The small protoconid is shifted more lingually on the wider p4. The lower carnassial (m1) is wider. The relative and absolute length of metapodial bones is smaller than in modern *Crocuta crocuta*. The cave hyena had a larger head and more massive forelimbs than modern spotted hyena. Compared to *Crocuta crocuta intermedia*, the cave hyena had a larger size, wider upper carnassials with the longer metastyle, and the longer p3. Compared to *Crocuta crocuta prespelaea*, it had wider upper carnassials with the longer metastyle, the longer p3, and the wider p4 (see Barycka, 2008).

Material: The skull of a juvenile with P3 dext. et sin. (SNM – Z 215), housed and exhibited in the Slovak National Museum – Natural History Museum in Bratislava. Skull measurements are in Table 1.

Description: The medium-long, relatively large and high skull with a slightly arched frontal area and with a rounded parietal part is damaged, especially in the anterior part (premaxilla and nasal bones are not preserved together with the anterior part of the palatinal bones) and on the left side (zygomatic arch is broken off). Distinctly visible cranial sutures are not yet fully joined.

Tab. 1. Measurements of the juvenile cave hyena skull (SNM – Z 215) from the Jasovská jaskyňa Cave

Length between basion and opistocranion	70.76 mm
Upper neurocranial length (acrocranion – frontal midpoint)	127.66 mm
Neurocranial length	98.90 mm
Length between nasion and acrocranion	160.95 mm
Basicranial length synsphenion – basion	62.33 mm
Length of palatal notch	33.40 mm
Posterior length dext.	66.44 mm
Posterior length sin.	66.19 mm
Medial length from canines to foramen magnum	171.21 mm
Rostrum breadth	60.56 mm
Breadth between infraorbital foramina	59.21 mm
Infraorbital constriction breadth	51.30 mm
Frontal breadth	64.30 mm
Postorbital constriction breadth	42.20 mm
Greatest neurocranium breadth	77.10 mm
Occipitale breadth	85.50 mm
Palatal breadth across P4 (outside)	103.58 mm
Palatal breadth across P4 (inside)	84.41 mm
Maximum palatal breadth across P4	113.53 mm
Anterior pterygoid breadth	29.90 mm
Posterior pterygoid breadth	27.77 mm
Greatest mastoid breadth	89.90 mm
Tympanic breadth	38.60 mm
Breadth between bulla ossae	17.56 mm
Greatest breadth on condyli occipitales	54.66 mm
Greatest breadth of the foramen magnum	30.86 mm
Maximum height of the zygomatic arch (dext.)	30.15 mm
Minimum height of the zygomatic arch (dext.)	19.70 mm
Skull height at the supraorbital processes	85.70 mm
Height of the occipital triangle	74.54 mm
Greatest inner height of the orbit	71.15 mm
Greatest inner length of the orbit	53.82 mm
C – P3 alveolar length	17.38 mm
Height of the foramen magnum	23.02 mm
Greatest diameter of the auditory bulla (length)	30.13 mm
Minimum diameter of the auditory bulla (breadth)	24.62 mm
Vertical diameter of the infraorbital foramina	10.28 mm
Horizontal diameter of the infraorbital foramina	8.88 mm
P3 – P4 alveola length (dext.)	80.82 mm
P3 – P4 alveola length (sin.)	81,33 mm

The maxilla is slightly damaged, with the high facial part and distinctly developed wide alveolar and robust palatinal processes. The infraorbital foramina are oval, with the medial margin more flat than the lateral margin. The maxillary foramina are relatively small, oval to circular. The exposed ethmoid bone separates the nasal cavity from the frontal sinus. Whereas *lamina perpendicularis* is not preserved, the labyrinth of the ethmoid bone forms the rest of nasal cavity. The facial part of the lacrimal bone has a smooth surface and its caudal process is short; the lacrimal bulla is developed on the lower side of the lacrimal bone. The both parts of the frontal bone with distinct zygomatic processes are connected by the sagittal suture in the medial plane and form the triangular-shaped forehead in the front, so far without the sagittal depression known in adult skulls. Parietal bones are distinctly wide and arch-shaped, dorsally forming the short and low sagittal crest. The triangular-shaped occipital bone is flat, with the conspicuous nuchal (lambdoid) crest and the blunt external occipital cusp. The large foramen magnum is laterally bordered by occipital condyles. The paracondylar processes are broken off. The jugular foramen is present together with ducts for hypoglossal nerves on the basioccipital skull portion. The left zygomatic process of the temporal bone is almost completely broken off, while the right one is only damaged together with the mastoid process. The both undamaged oval tympanic bullae are large, laterally flattened and convex (dome-shaped), with the hyoid processes close to them. The external auditory meatus and its porus are situated on the lateral sides in the tympanic portion of the temporal bone. The pterygoid bone is small and flat, situated on the skull base; its lower margin is more robust and caudally forms the distinguishable pterygoid hamulus with the lateral sulcus. The sphenoid forms a connection between the basioccipital bone and the presphenoid; the hypophysial fossa is present on the dorsal side of the sphenoid; basisphenoidal alae are relatively short and wide, while the pterygoid process is long; the sharp, but low sphenoid spine is situated caudally from oval foramen. Similarly as the sphenoid, the presphenoid is also laterally bordered by alae (in its rostral part). The vomer is connected with the maxilla and the palatinal bones; posteriorly is connected with the presphenoid through the *ala vomeris*. The thin palatine bones are in the shape of rounded irregular tetragon, with the concave surface, connected with the maxilla by the palatomaxillary suture; a pair of medium-sized palatinal foramina and a more pronounced right palatinal sulcus are distinguishable in the preserved posterior part of the palatine. The frontal process of the preserved, but damaged robust right zygomatic arch is small, not connected with the zygomatic process of the frontal bone and eye socket is caudally open; mandibular fossa is relatively shallow. Generally, the neurocranial part is markedly narrower than the visceral one, in which a wide mouth dominate.

Only the not-fully erupted third upper premolars (P3 dext. et sin.) are preserved from the dentition. The crown tip of P3 dext. is broken and the P3 sin. crown is damaged and already slightly worn. The massive, conical, more posteriorly bent paracone with more flat lingual side dominates on crowns of both teeth; it has an antero-lingual and a posterior ridge – the former is bifurcated at its base and runs into the anterior and the lingual cingulum, while the latter is separated by a notch from the cingular accessory cusp. The posterior cingulum is robust, forming a transverse, almost straight posterior limitation of the crown. The buccal cingulum is absent. The roots of both premolars are not yet developed, what indicates a juvenile individual.

Only alveoli of other teeth are preserved; P1s were single-rooted, P2s were two-rooted, and P4s were three-rooted. The individual alveoli are separated from each other by interalveolar septa. Palatinally from the posterior root alveoli of P4s, a circular depression is situated on both sides, representing probably the phantom alveoli of M1s. The existence of these phantom alveoli can be connected only with the early stage of hyenid ontogeny, although vestigial two-rooted M1s are also known from the fossil record of some adult cave hyenas (Ewer, 1954; Kurtén, 1956; Barycka, 2008).

DISCUSSION AND CONCLUSION

Although cranial remains of cave hyenas are often found in Pleistocene karst sediments (e.g. Bonifay, 1971; Codrea, 1990; Argant, 1991; García, 2003; Diedrich, 2005, 2007, 2008, 2012, 2014, 2016; Diedrich & Žák, 2006), the fossil record of juvenile skulls is relatively rare. In comparison with adult skulls, enlargement and elongation of the visceral skull part can be observed during the ontogeny. The change in the neurocranial part of skulls is more or less moderate, mainly associated with an increase in the region of the sagittal crest (see e.g. Arznov et al., 2010, fig. 4).

From the phylogenetic point of view, a morphological comparison with the skull of approximately equally old spotted hyena individual (*C. crocuta intermedia*) from Holsteinian (Middle Pleistocene)deposits of the French site Lunel-Viel is very interesting. This juvenile specimen (LVI-2-3), depicted by Bonifay (1971, Pl. XX/Fig. 2), shows several major differences from the studied skull from the Jasovská jaskyňa Cave (Fig. 3). The most

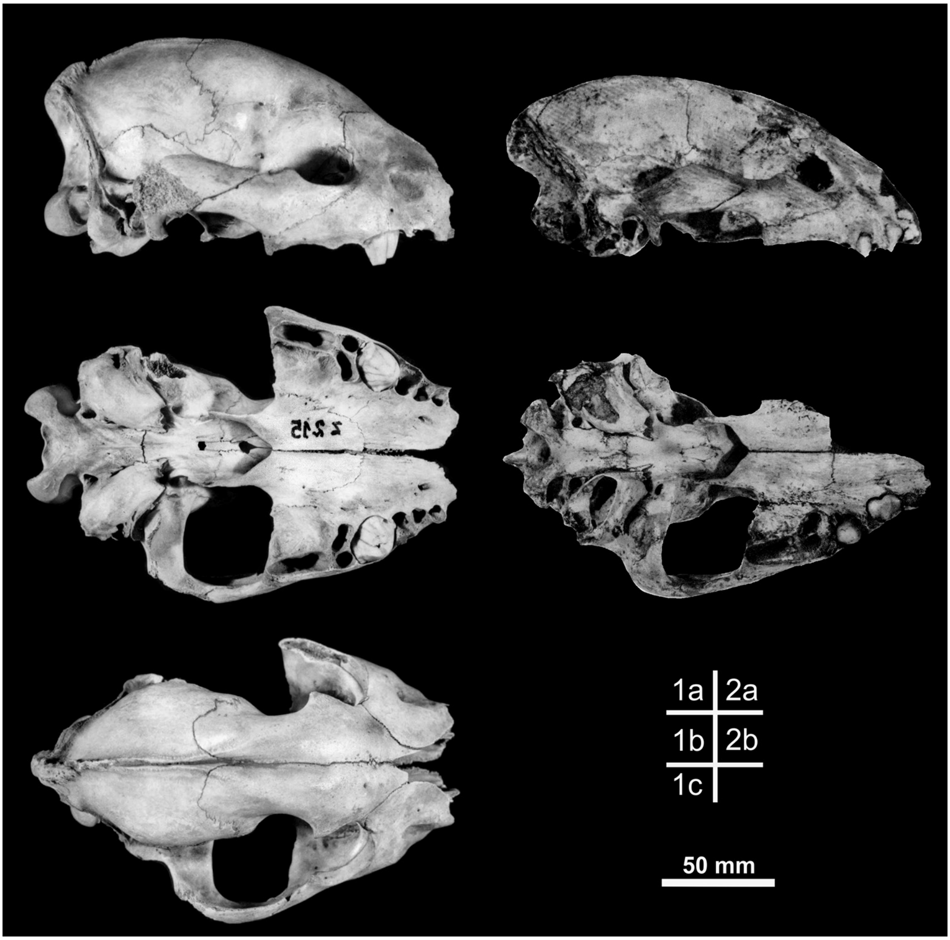

Fig. 3. Skulls of juvenile representatives of spotted hyena from the European Pleistocene.1: *Crocuta crocuta spelaea* (Goldfuss, 1823), Jasovská jaskyňa Cave, Late Pleistocene (SNM – Z 215; a – lateral view, b – ventral view (invert), c – dorsal view); 2: *Crocuta crocuta intermedia* de Serres, 1828, Lunel-Viel, Holsteinian (LVI-2-3; a – lateral view, b – ventral view; according to Bonifay, 1971)

significant difference can be observed in the relatively smaller length and the higher height of the juvenile skull from the Late Pleistocene (*C. crocuta spelaea*), connected with the lateral expansion of the palatino-maxillary and the zygomatic regions. These differences are likely to result of changes in species evolution during the Middle to Late Pleistocene associated with a gradual increase in body size and more robust development of jaw musculature, what could be a possible consequence of not only the changing environment but also adaptation to crushing and biting of bones of larger animals, such as cave bears, mammoths, and wooly rhinoceroses (Diedrich, 2005, 2014).

The borophagous P3s are longer than wider (base on the CT images, Fig. 4), what is typical character for cave hyenas from glacial periods unlike individuals from interglacials with the shorter and wider third upper premolars (Barycka, 2008). However, this is in contradiction to assumed stratigraphical position of the studied fossil dated rather to the

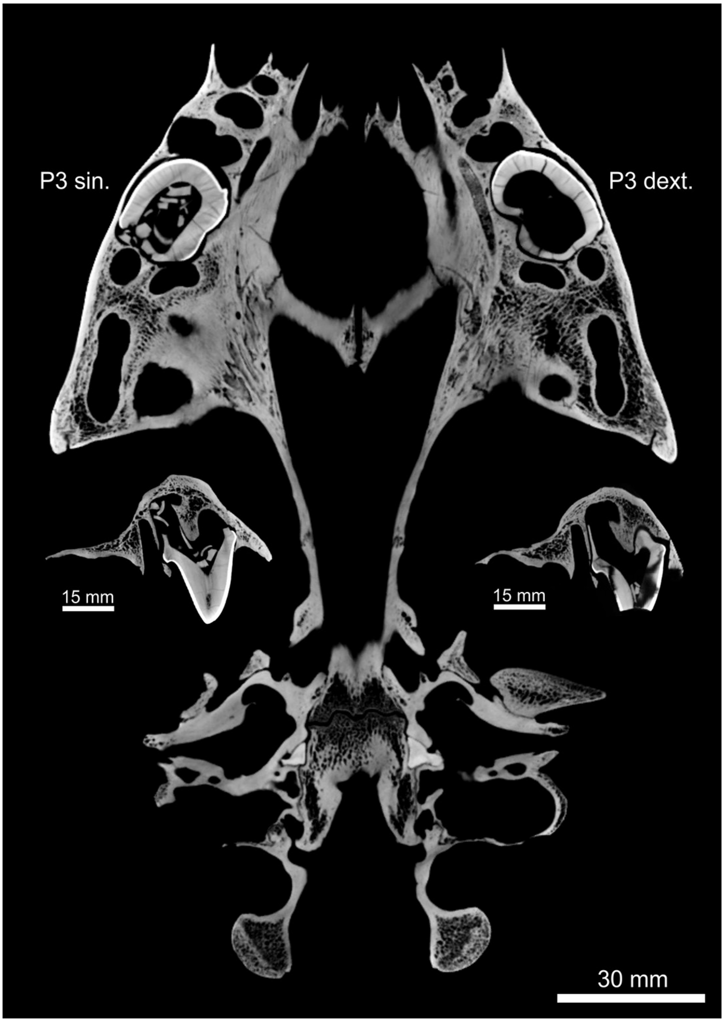

Fig. 4. CT dorsal view on the crown base cross-section of cave hyena P3s from the Jasovská jaskyňa Cave (SNM – Z 215) with CT images of their longitudinal cross-section

Eemian Interglacial than to the Early Vistulian on the basis of the correlation of the cave sedimentary record and the skull fossilization (see "Material and Methods" chapter). On the other hand, the existence of specimens with longer and narrower P3s in warmer Pleistocene periods is also not fully excluded and the found fossil can be only an exception to the rule of thumb.

Based on the abovementioned data, the skull of cave hyena juvenile from the Late Pleistocene sediments of the Jasovská jaskyňa Cave is an important fossil find that mirrors trends in the evolution of European Pleistocene spotted hyenas associated with the climatic changes and the advanced adaptation also on the scavengering (predation?) of large representatives of the Ice Age fauna (such as cave bears, mammuths, woolly rhinoceroses, etc.).

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LEBKA JUVENILNEJ HYENY JASKYNNEJ Z JASOVSKEJ JASKYNE

Resume

Fosílny záznam hyeny jaskynnej (*Crocuta crocuta spelaea*) je na Slovensku pomerne vzácny, obmedzený dosiaľ len na 10 lokalít (Čertova pec, Dzeravá skala, Gánovce-Hrádok, Malá Ľadnica, Okno, Prepoštská jaskyňa, Salovec pri Gombaseku, Silická Brezová, Tmavá skala a Jasovská jaskyňa) datovaných do obdobia neskorého pleistocénu. Lebka juvenilného jedinca z Jasovskej jaskyne (SNM – Z 215) reprezentuje najkompletnejší kraniálny nález druhu na našom území. Čiastočne poškodená lebka pravdepodobne patrila jedincovi mladšiemu ako jeden rok, čo bolo stanovené na základe rozvoja koreňovej sústavy ešte plne neprerezaných tretích vrchných premolárov (P3). Pri morfologickom porovnaní s lebkou približne rovnako starého jedinca taxónu *C. crocuta intermedia* zo stredopleistocénnych vrstiev lokality Lunel-Viel (LVI-2-3) je možné pozorovať niekoľko hlavných rozdielov, predovšetkým v dĺžke lebky a jej výške v spojitosti s odlišnou úrovňou rozvoja podnebných a jarmových kostí. Tieto rozdiely sú s najväčšou pravdepodobnosťou výsledkom zmien v evolúcii druhu počas stredného až vrchného pleistocénu, odzrkadľujúce sa v postupnom zväčšovaní telesných rozmerov a v robustnejšom rozvoji čeľustného svalstva, čo nemuselo súvisieť len so zmenami prostredia, ale aj s adaptáciou na drvenie a hryzenie kostí veľkých cicavcov, ako boli medvede jaskynné, nosorožce, či mamuty.

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SUBTROPICAL STEPPE INHABITANTS IN THE LATE PLEISTOCENE CAVE FAUNAS OF EASTERN MIDDLE EUROPE

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D. Nagel, J. Lindenbauer, N. Kavcik-Graumann, G. Rabeder: Subtropical steppe inhabitants in the Late Pleistocene cave faunas of eastern Middle Europe

Abstract: Investigations in cave hyena caves during the last decade encourage a re-interpretation of the Middle Wurmian ecology through new chronological and genetic data. Upper Pleistocene hyena fauna remains in Europe consists of megaherbivore bones, some of them with characteristic gnawing marks from hyenas as well as porcupines and predators (hyenas, lions, leopards and brown bears) that have occasionally used caves as shelters. These hyena faunas additionally includes rare elements such as onagers, porcupines and blind mole-rats, whose closest relatives now inhabit tropical to subtropical steppe areas. Datings of cave hyena remains from the Alpine area have yielded values covering the MIS 3 period of approximately 41,000 to 50,000 years (calBP). This allows a distinction between the cave bear area and the hyena area in the Alps; the latter ending earlier before the Last Glacial Maximum.

Key words: *Crocuta*, hyena caves, Middle Wurmian, subtropical steppe climate

INTRODUCTION

The Late Pleistocene hyena fauna of Europe consists of bones of large herbivores, accumulated by hyenas which left characteristic gnawing marks, as well as remains of the predators themselves. Additionally, other predators like lions, leopards and brown bears occasionally used caves as a shelter (Koenigswald 2002). The accumulated elements include amongst others onager, porcupine, mole-rat, lion and leopard. These fossil mammals have been attributed in general to a cold-temporal climate, because of the co-occurring arctic animals such as mammoth, wolverine and lemming (Kurten 1968, Koenigswald 2002). The general assumption therefore is also that the modern humans immigrated Europe during a cold steppe environment (Nigst et al. 2014).

During the last decade, investigation in Austrian caves and caves in adjacent countries, accumulated many new Radiocarbon dates. The Výpustek (Czech Republic) and Teufelslucke (Austria) caves are located on the Bohemian Massive. Other Austrian caves are situated on the eastern border of the Alps. The Pocala Cave is close to Trieste (Italy) and well-known caves at Miskolc (Szeleta), Kiskevély, and Igric are spread from Budapest to Romania (Fig.1). The altitude of these caves ranges from 100 to 600 m above the sea level.

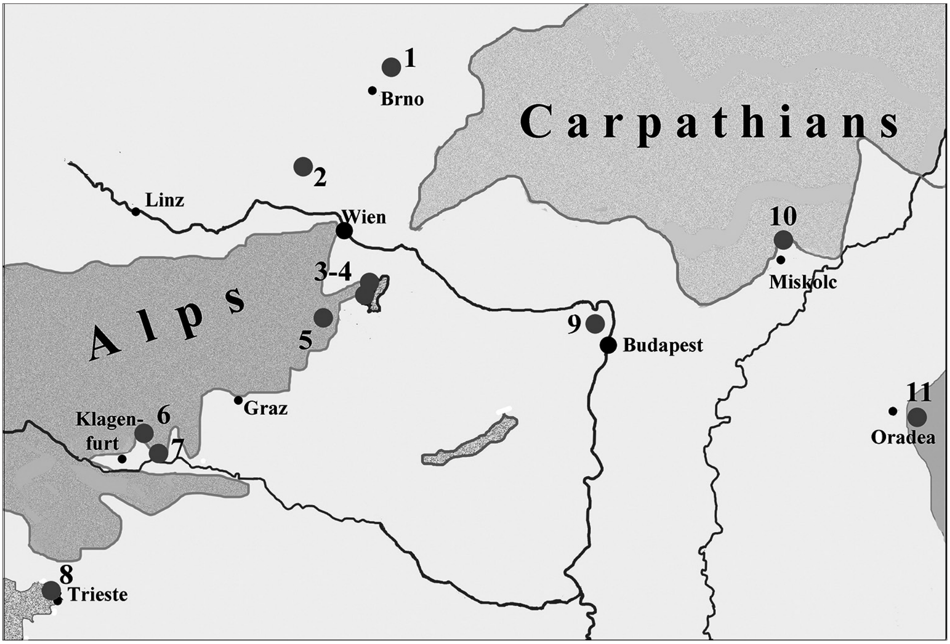

Fig. 1. Map of hyena caves of the Eastern Alps and comparable caves. 1. Výpustek Cave (Czech Republic), 2. Teufelslucke near Eggenburg (Austria), 3. Bear Cave of Winden (Austria), 4. Hyena Cave of St. Margarethen (Austria), 5. Mehlwurm Cave near Scheiblingkirchen (Austria), 6. Hyena cave of Klein St. Paul (Austria), 7. Dripstone Cave of Griffen (Austria), 8. Pocala near Aurisina (Italia), 9. Kiskevély Cave near Budapest (Hungary), 10. Szeleta Cave near Miskolc (Hungary), 11. Igric Cave near Oradea (Romania)

These radiometric datings have made it possible to detect the considerable time differences between the Mid-Würmian faunas of the cave-bear era and the Late Glacial faunas with Arctic and Alpine animals (Tab. 1) (Rohland et al. 2005, Döppes et al. 2016). The results range from approximately 36,000 to older than 49,000 years BP or 41,000 to older than 50,000 years calBP (Tab. 1). The cave hyena disappeared starting in the Far East; it vanished from Transbaikalia to Austria around 40,000 year BP but survived in the west and south of Europe till approximately 25,000 years BP (Stuart & Lister 2014).

MATERIAL AND METHOD

We herein discuss the taxonomic status of hyena, lion, leopard, hystrix and onager in order to show the close relationship between the fossil and extant taxa. Furthermore, the evaluation of the ecological preferences of the modern taxa is summarized in order to speculate about the inclination of the fossil ones. This has to be set in comparison to the Milankovitch curve as well as the Greenland ice-core climatic data.

2.1 Taxonomic status of "subtropical steppe elements" and their extant relatives

Recent genetic studies have shown that the Pleistocene hyena, lion, leopard and onager, which were originally described as independent species, differ only slightly from their extant relatives, and that these taxa can today only be assessed as subspecies of the modern species (Tab. 2). Furthermore, the genetic analyses indicate a quite recent immigration

Tab. 1. Radiometric ages of cave hyenas from nine caves in the Alps and in the Eastern foothills (Rohland et al., 2005)

Taxon	Cave	State	Laboratory nr.	C14 age	Error +/-	calBP	Error +/-	Altitude
Bison (bite tracks of Crocuta)	Mehlwurmhöhle	A	VERA-2540	35900	600	40975	978	390 m
Crocuta	Teufelslucke	A	VERA-2536	38060	900	42679	780	314 m
Crocuta	Grotta Pocala	I	VERA-2532	38220	920	42799	804	139 m
Crocuta	Winden	A	VERA-2538	38680	970	43072	805	190 m
Crocuta	Pestera Igriţa	RO	VERA-2534	41800	1400	45478	1478	328 m
Crocuta	Teufelslucke	A	VERA-1425	40170	920	45959	1267	314 m
Panthera	Teufelslucke	A	VERA-2545	46280	1800	46280	1955	314 m
Crocuta	Griffen	A	VERA-1833	44300	1800	47917	2251	348 m
Crocuta	Szeleta	H	VERA-2533	44400	1900	48050	2349	349 m
Crocuta	Griffen	A	VERA-2539	45300	2200	48560	1683	348 m
Crocuta	Vypustek	CZ	VERA-2531	46000	2400	49976	3200	388 m
Crocuta	Kiskevélyi	H	VERA-2535	>48500	–	>48500	–	253 m

period into Europe of some of the taxa mentioned above (Barnett et al. 2009, 2016, Orlando et al. 2009, Sheng et al. 2014).

The genetic differences between fossil cave hyenas and recent spotted hyenas are small and at most in the rank of a subspecies (Rohland et al. 2005, Sheng et al. 2014). Differences between a Southern and a Northern population can be seen in the modern African spotted hyenas. European fossil specimens are close mostly to the Southern genetic group with some tending more to the Northern population (Fig. 2A), which indicates multiple immigrations to Europe (Rohland et al. 2005). The Asian fossil hyena is separated from all other lines and therefore immigrated to China very early. An Asian origin is even discussed in Sheng et al. (2014).

The fossil *Panthera leo* findings are very close to the extant lion but populations can be distinguished (Fig. 2B). The European and the Beringian group seem to be more related than the American lion, *Panthera leo atrox* (Barnett et al. 2009). The differences between

Tab. 2. Table of "subtropical elements" in the Late Pleistocene of the Alps. The taxa listed below originally have not been described as own species or subspecies on the basis of morphological criteria but according to their different (usually larger) dimensions

Common name	Former scientific name		Current scientific name
cave lion	*Panthera spelaea* Goldfuss, 1810	=	*Panthera leo spelaea* Goldfuss, 1810
cave leopard	*Felis antiqua* Cuvier, 1825	=	*Panthera pardus* (L.)
cave leopard	*Panthera pardus spelaea* Bächler, 1936	=	*Panthera pardus* (L.)
cave hyena	*Crocuta spelaea* (Goldfuss, 1823)	=	*Crocuta crocuta* (Erxleben, 1777)
European wild ass	*Equus hydruntinus* Regalia, 1907	=	*Equus hemionus* Pallas, 1775
porcupine	*Hystrix vinogradovi* Argyropoulo, 1941	=	*Hystrix (Acanthion) brachyura* L.
lesser mole rat	*Spalax hungaricus* Nehring, 1897	=	*Spalax leucodon* Nordmann, 1840

leopard and lion is much larger as between the fossil lion and the extant one, but it is still controversial whether the genetic differences between fossil cave lions and extant lions are sufficient to regard them as a separate species or whether they are only to be classified as a subspecies (Burger et al 2004, Barnett et al 2009, 2016, Ersmark et al. 2015).

The fossil onager from Europe, formally described *Equus hydruntinus*, falls within the genetic distribution of the extant onager, *Equus hemionus*, that it can only be regarded as subspecies close to *E. h. kulan* (Orlando et al. 2009) (Fig. 2C).

From fossil *Hystrix* and *Spalax* genetic data are still missing, but morphological data indicate that the formerly described *H. vinogradovi* either has to be considered a subspecies of *H. brachyura* (Baryshnikov 2003) or synonymized with *H. brachyura* (e.g. van Weers 2005, Diedrich 2009).

2.2 Ecological adaption of extant spotted hyena, lion, leopard, hystrix and onager

Today, the herein mentioned taxa, lion, leopard, hyena, onager and porcupine are all living in a subtropical environment

Crocuta crocuta, the spotted hyena, is today only known from Africa (Fig. 3). As in most larger carnivores, it had a larger distribution area in former times. During the Pleistocene, hyenas even inhabited England. The extant spotted hyena prefers savanna, semi deserts and dry woodland but is absent in the tropical rainforest. It is known up to 4,100 m altitude. Water is needed to some extant (http://www.iucnredlist.org/details/5674/0 12.01.2018).

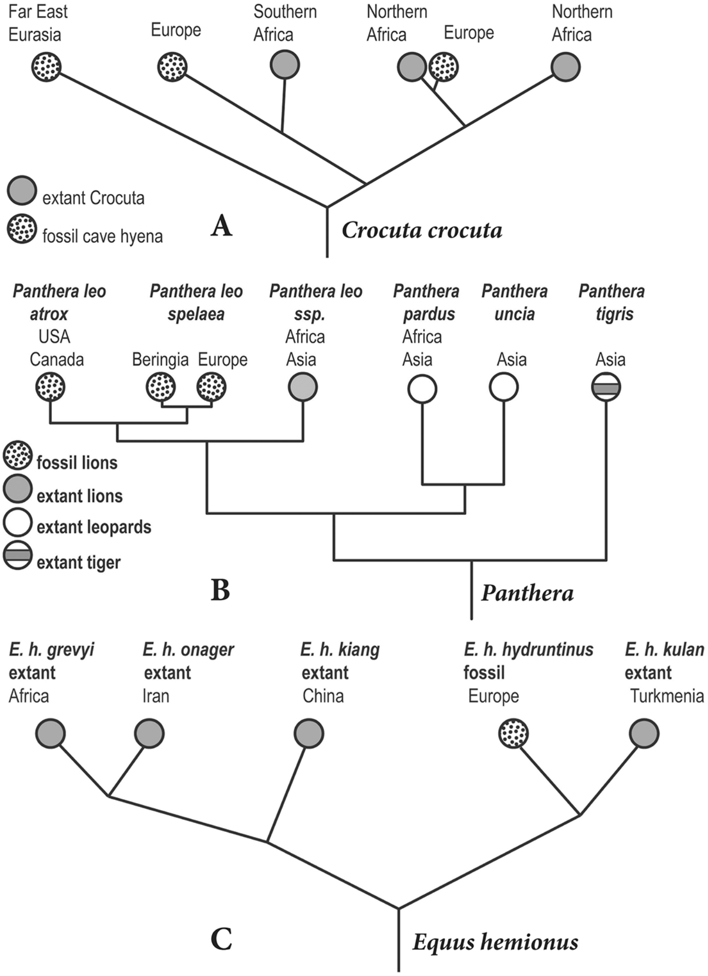

Fig. 2. A – Simplified genetic tree of extant spotted hyenas *Crocuta crocuta* and fossil cave hyenas *Crocuta crocuta* „*spelaea*“ (s. Sheng et al. 2014); B – Simplified genetic tree of extant lions, leopards and tiger so far so fossil cave lions (s. Barnett & al. 2009); C – Simplified genetic tree of extant onager subspecies and fossil European half ass *Equus „hydruntinus“* (s. Orlando & al. 2009)

Panthera leo, the lion, today is only found in the sub-saharan Africa and in the Gir Forest National park in India (Fig. 4). The decline of its range is probably as young as 2000 years, when it had to retreat from Europe (Nowell & Jackson 1996, Sunquist & Sunquist 2014). The lion prefers dry habitats and is therefore absent in the tropical rainforest parts. Although it cannot live the Saharan desert, it is able to obtain the necessary water from plants or its prey. Therefore it survives in areas with an annual precipitation as low as 100 mm (http://www.iucnredlist.org/details/15951/0 12.01.2018).

The leopard, *Panthera pardus*, with its various subspecies has the largest distribution area of the big cats today. The northernmost area is up to 45° northerly latitude and is known from Asia to Africa. They live from tropical rainforest with 1,500 mm precipitation to dry habitats such as the Arabian Peninsula with 150 mm in some parts. The Amur leopards lives in a temperate deciduous forest with approximately 500 m rainfall. Trees

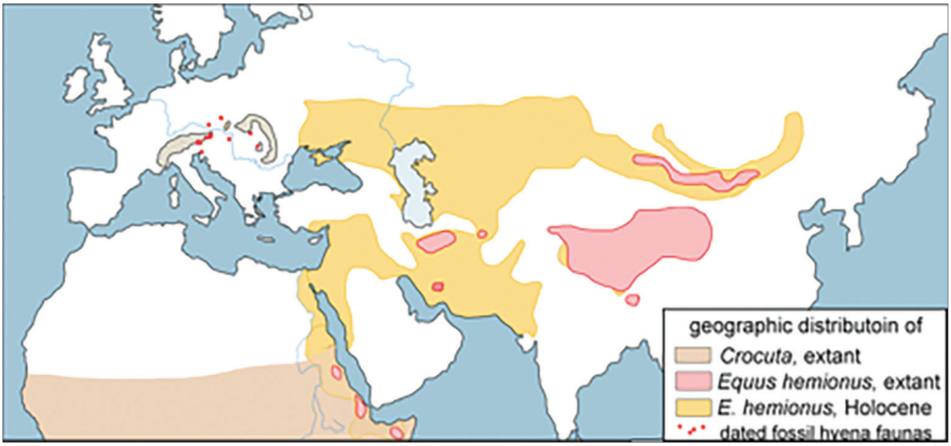

Fig. 3. Distribution areas of spotted hyena and onager in the Holocene and the positions of new dated fossil hyena faunas in Eastern Middle Europe (Sheng et al. 2014; Denzau & Denzau 1999)

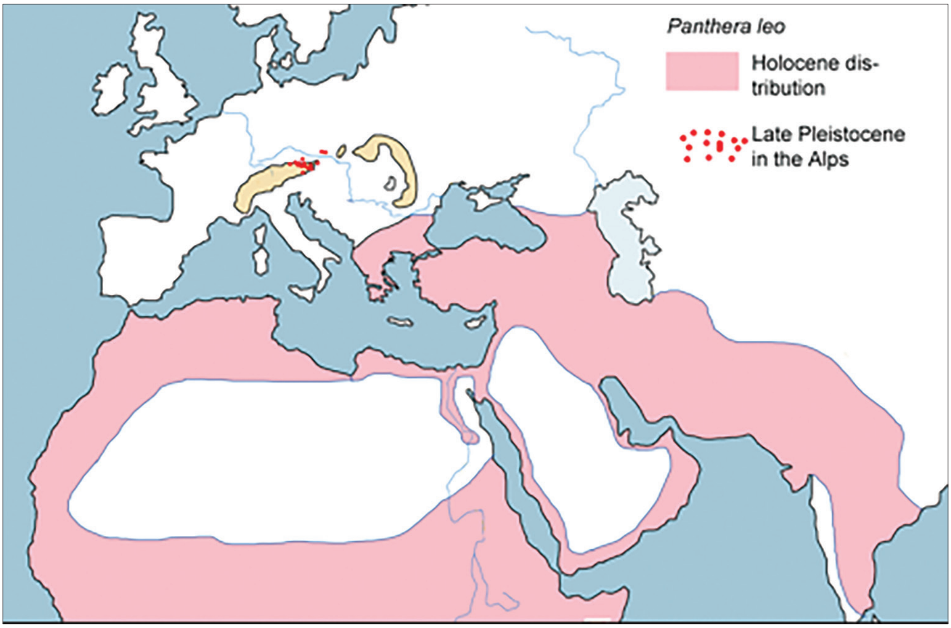

Fig. 4. Distribution map of lions, fossil and extant (Sommer & Benecke 2006)

are an important factor for their environment as deep snow is a limiting one (https://russia.wcs.org/en-us/Wildlife/Amur-Leopards/Ecology.aspx 12.01.2018; Jacobson et al. 2016).

The genus *Hystrix* (*Acanthion*) *brachyura* lives south of 35°N (van Weers 2005) and is restricted to south-east Asia. It prefers open to closed habitat. While it is not particularly critical about the density of vegetation, it needs rocky territory to create burrows or use burrows from other animals (www.iucnredlist.org/details/10749 12.01.2018).

The onager, *Equus hemionus*, inhabits today steppes and desert steppes, although water has to be present to some extent. In historic times, its habitat ranged from the East of Asia to Asia Minor with precipitation between 100 to 400 mm precipitations (Fig. 3). Today they are highly endangered and restricted to conservation areas (http://www.iucnredlist.org/details/7951/0 from 12.01.2018). These fragmented habitats stretch from the Tibetan plateau up to 5000 m above the sea level (ASL) to Turkmenistan as low as 600 m ASL (between 25° and 50° northern latidude). It can survive temperatures between +46° to -33°C and only starts to migrate when the dry season lasts too long or when snow fall in winter makes it difficult to find food. *Equus hydruntinus* is now seen as a subspecies of *E. hemionus* (s. Orlando et al. 2009) and therefore similar ecological conditions may apply (Denzau & Denzau, 1999).

Of similar interest to the mentioned taxa here is *Spalax leucodon*, which is also a rare faunal element in European sites. Since neither ancient genetic or radiometric data are known about this animal yet, further evaluation can only be done in future. Its ecological adaption to arid areas makes it important in the context of this work (Niethammer & Krapp 1993).

2.1. Milankovitch curve and Greenland Ice-core data

If the fossil taxa like hyena or onager had similar or the same ecological preferences as their extant relatives, then we can hypothesize about a similar climate in Alpine region between 50,000 and 40,000 years BP as known today in the steppe subtropics: warmer and drier.

Evidence for the climate during the Pleistocene comes from the Milankovitch curve and the Oxygen-Isotopic curve ($^{16}O/^{18}O$-curve). The Milankovitch curve represents the calculated insolation on our planet due to the shifting transfer orbit of our earth around the sun. The computed variations revealed a rhythmical pattern. Milankovitch results mirrored the results of the oxygen isotopic-curve. Figure 5 depicts the insolation-graph for summer during the Würmian at the 47th northern latitude (Berger et al. 1984, Hille & Rabeder 1986).

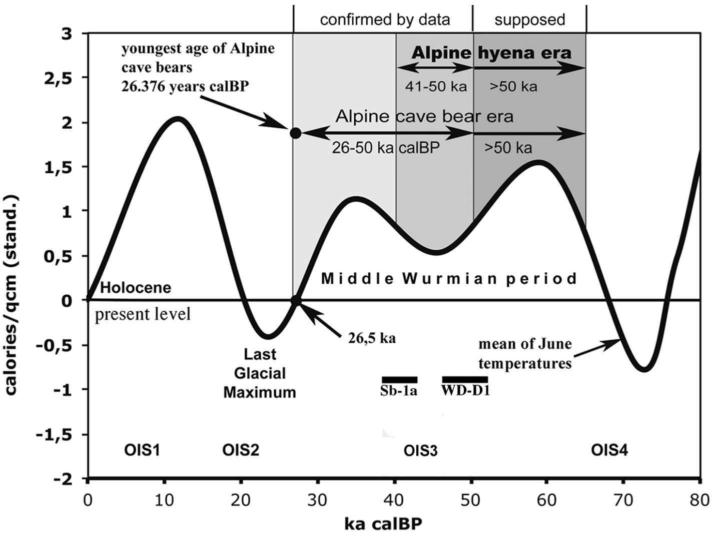

Fig. 5. Chronological position of "Cave hyena era" and "Cave bear era" in relation to the insolation curve by Milankovitch. Note the timely coincidence of the latest cave bear date with the decline of the summer temperatures to today's level. Black bars mark the Willendorf D1 (WD-D1) and Schwallenbach Ia (Sb-1a section from Nigst et al. (2014)

The evaluation (δ ^{18}O /^{16}O difference) is either done on the calciumcarbonate in shells of foraminifera from deep sea drills or from ice-cores, e.g. from Greenland ice-cores. The course of the ^{18}O isotope curve is very often understood as "palaeotemperature curve"; low values of the ^{18}O /^{16}O indicate low temperature averages. The values are calculated for marine conditions. Calculated values from speleothems are interpreted on the results of the marine ones (Spötl et al. 2006). This has led to an extreme discrepancy especially for the Middle Würmian. The mass occurrence of cave bear remnants in high alpine caves can only be explained by the assumption that at least the summer temperatures must have been higher on average than today (Döppes et al. 2011). The distribution of ^{18}O values in precipitation in terrestrial areas is not only determined by the temperature but also by the geographical position on the continent (see Fig. 6); a fact well known by researcher working on stable isotopes in mammal bones (e.g. Tütken et al. 2008).

The zones with the same ^{18}O values do not run parallel to the parallel arcs in Europe and western Eurasia, but from NW to SE. Obviously, the ^{18}O values also depend on the distance of the area from the sea, the farther the distance the lower the ^{18}O values. Using the example of the month of August, it can be seen that the ^{18}O values in the Alpine region

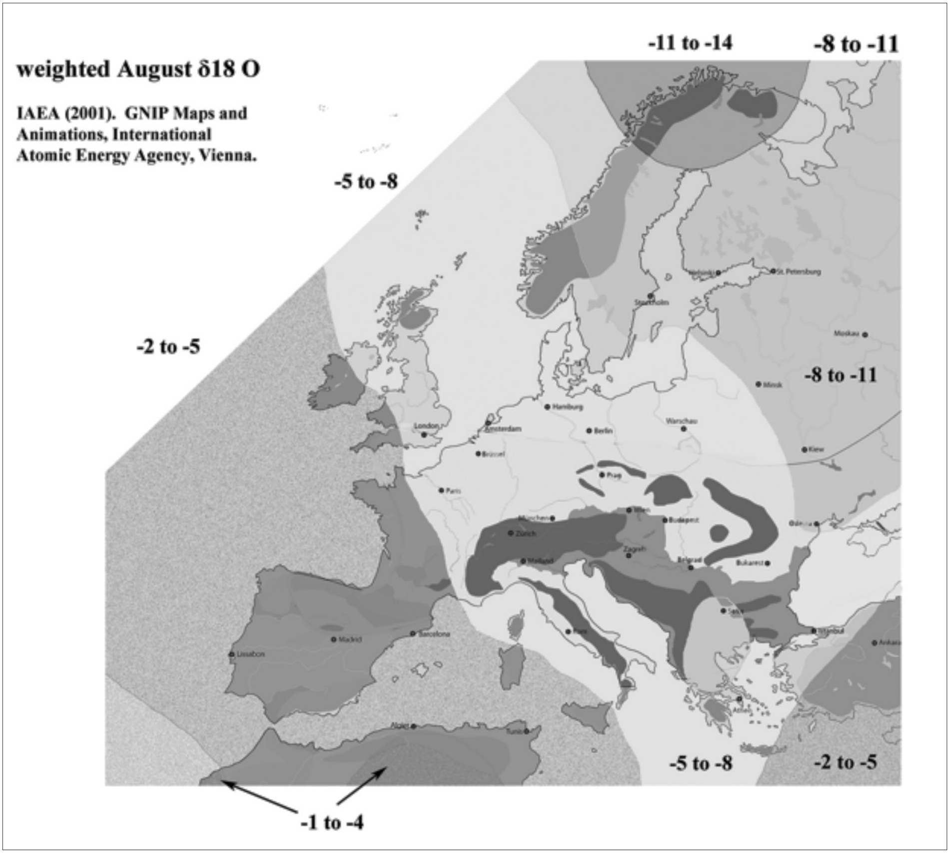

Fig. 6. The δ ^{18}O /^{16}O values in precipitation in the summer today (according to: graphical representations of the GNIP (Global Network for Isotopes in Precipitation) stable isotope database of IAEA (International Atomic Energy Agency);
http://www-naweb.iaea.org/napc/ih/documents/userupdate/Waterloo/ December 2017

are similar to those in subtropical areas, although the average summer temperatures there may be more than 10 °C higher than in Central Europe. In other words, in relatively warm continental areas, ^{18}O levels may be similar to oceanic, cold, and relatively wet areas.

Applied in figure 5 and 7 is the time range of the fossil cave hyena from cave evaluated in this investigation. Additionally marked are the time spans of Willendorf D1 and Schwallenbach Ia. These are important phases in the history of human settlement in Central Europe. The palaeoenvironment there was calculated through the lithological record as well as the ecological adaption of terrestrial molluscs and is interpreted as a medium-cold steppe environment with occasional boreal trees (Nigst et al. 2014). This interpretation is contradictory to the ecological evaluation of terrestrial molluscs (Döppes & Rabeder 1997: 73), which describes a climate that was warmer and more humid than today.

DISCUSSION AND CONCLUSION

According to available radiocarbon data (Tab. 1), the "hyena era" belongs to the Middle Würmian, which essentially coincides with the MIS3 (28,000 to 60,000 years BP). Palaeoecological construction paint this part of the Pleistocene as a cold or medium-cold steppe environment in Europe. The Milankovitch curve presents this time period as clearly warmer than the following LGM around 20,000 years BP. The Greenland ice core results reveal several fluctuations in the temperature; some interstadials follow in rapid succession from 47,000 to 35,000 years BP before the warming events became shorter till the LGM (Rasmussen et al. 2014).

Typical taxa of the ice age like cave hyenas and cave lions are in co-existence with other rare faunal elements such as hystrix, onager or the lesser mole rat (*Spalax*). All these taxa are known today from arid but warmer environments, so called subtropical steppes. It is very unlikely that they could thrive in the mammoth steppe. Judging from the living conditions of these animals today, the summer between 40,000 and 50,000 years ago

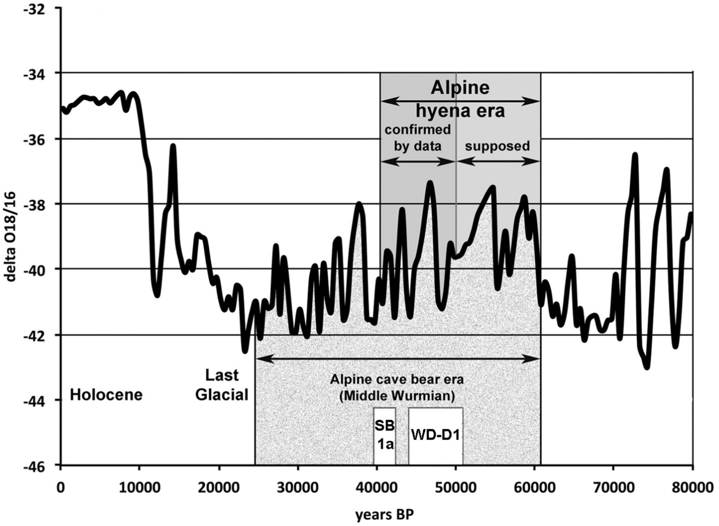

Fig. 7. The chronological position of the Alpine hyena faunas in comparison to a quincentennial isotope curve of the Greenland ice cores project GRIP (adapted from Ref). Black bars mark the Willendorf D1 (WD-D1) and Schwallenbach Ia (Sb-1a) section from Nigst et al. (2014)

was warmer and with less precipitation. Reduced precipitation would also explain the different $\delta^{18}O$ values, which lead to the conclusion of a cold climate. We assume, grass steppes and savannahs reached as far as to the Alpine foothills and a continental climate probably triggered the immigration wave of these "subtropical elements" together with the big steppe herbivores. Change in faunal elements during that time was reported from the Northern Black sea (Dodonov et al. 2006), Northern Caucasian as well as Transcaucasian localities (Baryshnikov 2003) and Transbaikalia (Erbajeva et al. 2014).

Maybe the immigration of *Ursus ingressus* and *Homo sapiens* was also initiated through this climate change. Around 50,000 to 40,000 years BP, the cave hyena era was shaped by a warm and dry climate, as typical for steppes and semi-deserts today.

SUBTROPICKÉ STEPNÉ PRVKY VO VRCHNOPLEISTOCÉNNEJ JASKYNNEJ FAUNE Z VÝCHODNEJ ČASTI STREDNEJ EURÓPY

Resume

Výskum hyeních jaskýň počas posledného desaťročia vyvolal opätovnú interpretáciu ekológie z obdobia posledného zaľadnenia (stredný würm / stredná visla) prostredníctvom získaných nových chronologických a genetických údajov. Fosílne zvyšky hyenej fauny z vrchného pleistocénu v Európe pozostávajú z kostí veľkých rastlinožravcov, z ktorých niektoré nesú charakteristické stopy po zuboch hyen, ale aj dikobrazov a predátorov (levy, leopardy a medvede hnedé), ktoré tiež príležitostne využívali jaskyne ako útočiska. Tieto hyenie fauny zahŕňali aj také vzácne elementy, ako sú osly, dikobrazy a slepce, ktorých dnešní najbližší príbuzní obývajú tropické a subtropické stepné oblasti. Datovanie fosílnych zvyškov hyeny jaskynnej z alpskej oblasti poskytlo údaje spadajúce do obdobia MIS 3 v rozmedzí približne od 50 000 do 41 000 rokov BP (kalibrovaný vek). To umožňuje v Alpách oddeliť oblasti s výskytom medveďov jaskynných od oblastí s výskytom hyen jaskynných, ktoré odtiaľ vymizli ešte pred posledným glaciálnym maximom (LGM).

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Crocuta crocuta http://www.iucnredlist.org/details/5674/0 from 12.01.2018

Panthera leo http://www.iucnredlist.org/details/15951/0 from 12.01.2018

Panthera pardus https://russia.wcs.org/en-us/Wildlife/Amur-Leopards/Ecology.aspx from 12.01.2018

Hystrix brachyura www.iucnredlist.org/details/10749 from 12.01.2018

Onager (http://www.iucnredlist.org/details/7951/0 from 12.01.2018)

SLOVENSKÝ KRAS ACTA CARSOLOGICA SLOVACA	56/1	111 – 116	LIPTOVSKÝ MIKULÁŠ 2018

A NEW PLEISTOCENE MAMMAL FAUNA FROM THE BOTTICINO AREA (BRESCIA-LOMBARDY, NORTHERN ITALY): PRELIMINARY REMARKS

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P. Schirolli, M. Rossi, G. Santi, E. Caserini, S. Huld, D. Casali: A new pleistocene mammal-fauna from the Botticino area (Brescia-Lombardy, Northern Italy): Preliminary remarks

Abstract: A rich deposit of fossils of mammals from the Quaternary has been recently discovered in the Botticino village located in the neighborhood of Brescia city (Lombardy, Northern Italy). Cavities and holes filled with macro- and micromammals were formed in the local Lower Jurassic limestone by karstification phenomena. In this note, the preliminary observations are advanced after the first study on *Macaca sylvanus* Linnaeus, 1758 remains published recently.

Key words: Mammal fauna, Botticino, Northern Italy, taphonomy, Pleistocene

INTRODUCTION

The studies on vertebrate fauna of the Quaternary give an important picture on the systematic composition, behaviour of association components but most of all, on their taphonomy. In particular, these three elements, composition, behaviour and taphonomy, assume a decisive importance if the faunal assemblage is found in caves and holes. This is the case of the “Botticino mammal association”, a new Pleistocene vertebrate fauna, gathered in the quarries near Brescia city (Lombardy, Northern Italy). In this study, some preliminary notes on this association are presented after the first published study on *Macaca sylvanus* Linnaeus, 1758 fossils (Bona et al., 2016). This material is deposited in the Museum of Natural Sciences in Brescia (Lombardy, Northern Italy). It is not easy to find an association composed of micro- and macro-vertebrates in the sediments of caves and holes and for this reason, the Botticino fauna assumes a very important role; in fact, the fauna is surely of the Middle-Upper Pleistocene, possibly with some remains of the Holocene.

A SHORT GEOLOGIC REVIEW OF THE BOTTICINO AREA

Vertebrate remains have been gathered and collected in the Botticino area, located in the eastern surroundings of Brescia city (Lombardy, Northern Italy) (Fig. 1a). This territory is characterised by plenty of quarries where the “Corna” formation is extracted under the name of “Botticino Classico”. “Corna” refers to a Lower Jurassic unit of very

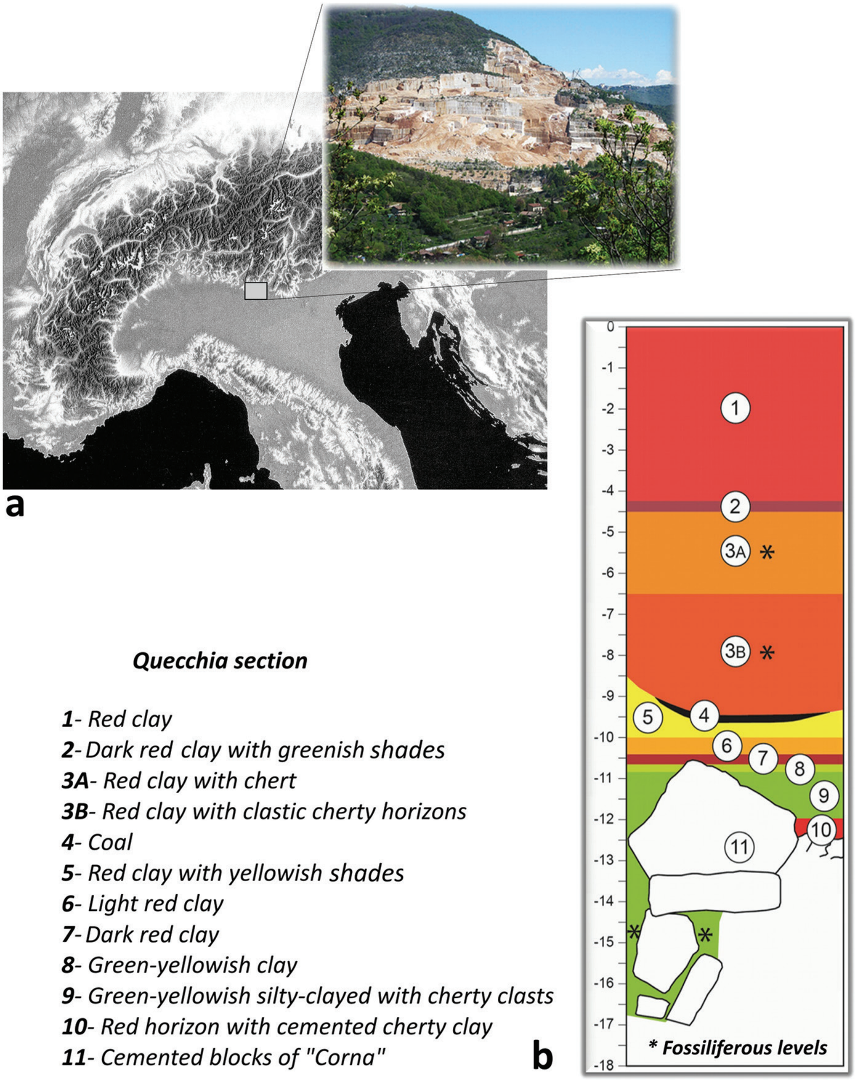

Fig. 1. Location of the Botticino quarries near to the Brescia city (Lombardy, Northern Italy) (a) and the schematic stratigraphic section of the Quecchia area (b)

thick-bedded limestones of platform environment. Inside the unit, several karst cavities and holes have been filled with sediments and animal bones.

Geological and paleontological studies on the Lower Jurassic carbonate succession of the Botticino area are referred to Bettoni (1900); Zaccagna (1915); Cantaluppi (1966); Cassinis & Cantaluppi (1967); Cantaluppi (1968); Cassinis (1968); Cantaluppi & Cassinis (1970); Cassinis & Schirolli (1995); Schirolli (1997); Dommergues et al. (1997); Schirolli (2002a, b); Schirolli (2007); Cassinis & Schirolli (2008); Meister et al. (2009) and Meister et al. (2017).

The first partial analysis of the vertebrate association was carried out by Bona et al. (2016) who described the *Macaca sylvanus* Linnaeus, 1758 remains. The main body of fossils comes from a series of holes inside the Quecchia quarry, the most abundant area in bone remains, as a consequence of karstification phenomena. In Fig. 1b, the first complete stratigraphic column described within a 12 m wide karst fissure filled with 17 m thick deposit is shown. This section, composed of 11 levels, refers to Middle Pleistocene up to the Holocene. The Middle Pleistocene age is in accordance with the micro-vertebrate assemblage on the "…occurrence of *Arvicola mosbachensis*, *Microtus* (*Terricola*) gr. *Multiplex-subterraneus*, *Pliomys coronensis* and *Microtus gregalis*..." (Bona et al., 2016, p. 2). Lastly, utilising the micro-vertebrate association, the climatic fluctuation was also examined; consequently, the layers 1 – 3, 6 – 7 and 10 corresponded to temperate and humid environment, while the layers 5 and 9 were deposited during the cooler climate with more open environment. Moreover, Bona et al. (2016) proposed a chronological correlation of the level 9 with MIS 9, levels 6 – 7 with MIS 7, 3A and 3B (in which large mammals were found) with MIS 7a.

THE FIRST TAPHONOMIC ANALYSIS

The holes and cavities filled with sediments and vertebrate bones were the traps for the remains of animals which lived in this area of the Italian Prealps during the Pleistocene; the inhabitants of caves (i.e. bats) are associated with big vertebrates that normally do not live in these habitats (i.e. horse). The particular features of the karst massif and the filling mechanisms have favoured the accumulation of a great amount of bones. Surely, the opening of these cavities and holes during the extraction activities in the "Corna" blocks facilitated the collection of the bones, also the frailer ones, and in many cases, they were still in the optimal condition (i.e. bats or birds). Remains are perfectly integrated and cemented in the matrix which is composed of residual red clay with fragments of chert and terrigenous sediments of different sizes (bone beds); the bone remains are often complete or lacking only the frailer parts. This modality of preservation is a proof that the zone of accumulation was not removed for a long way (both the incomplete and complete remains) and the cementation was rather quick. Naturally, the composition of the vertebrate association is defined by bones of different chronological ages as testified by different degrees of fossilization. The cave bear, probably the last of its kind living in the Alps, and Prealps together with the brown bear, horses, deer, marmots, artiodactyls, and mustelids, canids, bats, etc. (Fig. 2) are exponents of the faunas in "transformation" in their components during the last moments of the Pleistocene and during the beginning of the Holocene. Occasionally broken or pressed, the bones of the big vertebrates (i.e. *Ursus*) are in general well preserved. The main amount of fossils comes from the levels 3 and 9, and consequently, they are the most interesting. At present, it is difficult to advance a systematic classification of the elements that compose the "Botticino mammal fauna" with the only exception of *Macaca sylvanus* Linnaeus, 1758 studied by Bona et al. (2016). At the first observation, we found very heterogeneous association, therefore the presence of *Ursus* (*spelaeus*, *arctos*, and presumably *deningeri*) and *Macaca* represent the most important elements.

THE *URSUS* APPROACH

Ursus remains have been found along the complete development of the Quecchia section, but most frequently in the 3A, 3B and 9 levels. As previously annotated, the 3A and 3B are the most important levels correlated with the MIS 7a (about 200 ka) (Bona et al.,

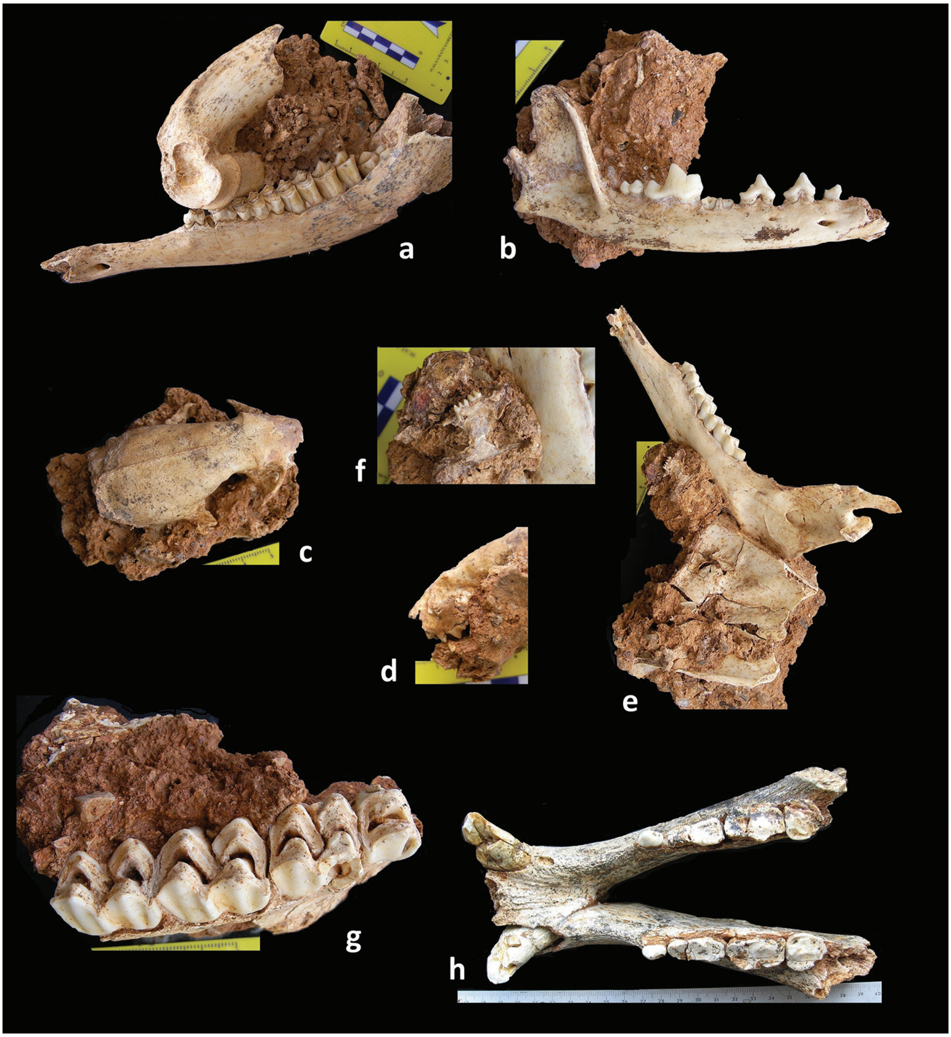

Fig. 2. Example of Quaternary bone remains from Quecchia quarry (Botticino, Brescia). a. Mandible of *Cervus elaphus* Linnaeus, 1758 and a fragment of an undetermined humerus (specimen n. MCSNBS-PA11163, layer 9, -14,5/15 m), b. Mandible of *Vulpes vulpes* Linnaeus, 1758 (specimen n. MCSNBS-PA11164, layer 9, -14,5/15 m), c. Skull of a mustelid, dorsal view (specimen n. MCSNBS-PA11165, layer 9, -14,5/15 m), d. Detail of the denture of the same mustelid specimen, e. Mandible of *Capra hircus* Linnaeus, 1758 with a mandible part of micromammal (cricetid?) (specimen n. MCSNBS-PA11166a, layer 9, -15 m), f. Detail of the micromammal mandible (specimen n. MNSNBS-PA11166b, layer 9, -15 m), g. Upper dentition of *Cervus elaphus* Linnaeus, 1758 (specimen n. MCSNBS-PA11167, not in place but coming from the levels above layer 4), h. Mandible of *Ursus arctos* Linnaeus, 1758 (specimen n. MCSNBS-11168). Photo: G. Santi

2016). The studies are just in a preliminary phase but some notes on the bears can be advanced. The components of the skeleton are very abundant and often complete. The chronological dating obtained using the micromammal association establishes a Middle Pleistocene age, and *Ursus* gr. *spelaeus* in the Botticino fauna is present. We have not individuated its direct ancestor *U. deningeri* which may be missing, but *U. arctos* is largely represented in the more recent levels. If the presence of *U. deningeri* is documented, then this will have the most important consequence because up to now, its presence in the Italian Alps/Prealps has surely been individuated only in the Cerè cave (Verona, Veneto region) (i.e. Rossi & Santi, 2005, 2007, 2011; Santi & Rossi, 2007 and so on) even though, its presence has been individuated to Central Italy (Sardella et al., 2006). This can open new and interesting views on the paths of colonization of *U. deningeri*. Future studies will be focused on the contemporary presence of the two (*deningeri-spelaeus*) or also three exponents of bears (*deningeri*, *spelaeus* and *arctos*) modifying the evolutionary modalities of the bears in Northern Italy.

PRELIMINARY CONCLUSIVE REMARKS

Within this note, the new site, Botticino area, near Brescia city (Northern Italy) was introduced. Its novelty lies in the presence of numerous holes of different sizes inside the Lower Jurassic limestones of the "Corna" filled with sediments and bone remains of macro- and micro-vertebrates, an association likely dated to Middle Pleistocene-Holocene. The Middle Pleistocene age was advanced by Bona et al. (2016) considering the presence of micro-vertebrate markers. The bone remains must be studied more comprehensively. Up to now, only fossils of *Macaca sylvanus* Linnaeus, 1758 have been analyzed in detail. As a first approach, it is interesting to note the abundance of *Ursus* remains (*spelaeus*, *arctos* and maybe *deningeri*) and the extreme rarity of other big vertebrates as well as big felines. The studies focalised on the bear bones, being the most abundant remains among the big vertebrates, are only in a preliminary phase and thus, no decisive conclusions can be deduced.

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NOVÁ FAUNA PLEISTOCÉNNYCH CICAVCOV Z OBLASTI BOTTICINO (BRESCIA--LOMBARDSKO, SEVERNÉ TALIANSKO): PREDBEŽNÉ POZNÁMKY

Resume

Bohaté nálezisko skamenelín cicavcov zo štvrtohôr bolo nedávno objavené v obci Botticino neďaleko mesta Brescia (Lombardsko, severné Taliansko). Dutiny a pukliny, vyplnené sedimentom so zvyškami malých aj veľkých cicavcov, boli vytvorené v miestnych spodnojurských vápencoch procesom krasovatenia. Po nedávnom publikovaní fosílnych zvyškov druhu *Macaca sylvanus* Linnaeus, 1758 sa rozvíja výskum aj ostatných nálezov cicavcov z lokality.

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SÚČASNÝ STAV PALEONTOLOGICKÝCH VÝSKUMOV V JASKYNIACH VEĽKEJ FATRY

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A. Bendík: The paleontological research in caves of the Veľká Fatra Mts. – a state of the art

Abstract: The article provides information about current paleontological research of the caves in the Veľká Fatra Mts. The research is realized since 2003 and it is carried out by Slovak National Museum in Martin – Andrej Kmeť Museum. During previous researches, osteological finds of brown bear from Došná 7 Cave, Sounder at the focal point Cave, HV-4 Cave and cave bear from Lôm Cave, Mažarná Cave, Biela jaskyňa Cave, Cave of I. Textorisova and M-1 Cave have been identified in the Veľká Fatra Mts. More of these finds are formed by isolated bones, but incomplete skeletons of cave bears were also discovered. Exceptional position between these caves belongs to Cave of I. Textorisova and M-1 Cave, where were discovered skeletons of cave bear *in situ* position. The latest research provides a new knowledge about taxonomic position of fossil Ursids in Slovakia. The fossil record is dated by radiocarbon dating to the 45 000 year ago (Last Glacial, probably to the period of OIS 3) and 30 190 (cal. BP age range) represent the last known occurrence of cave bears in the Slovakian Western Carpathians.

Key words: Veľká Fatra Mts., *Ursus* ex gr. *spelaeus*, *Ursus arctos*, Quaternary

ÚVOD

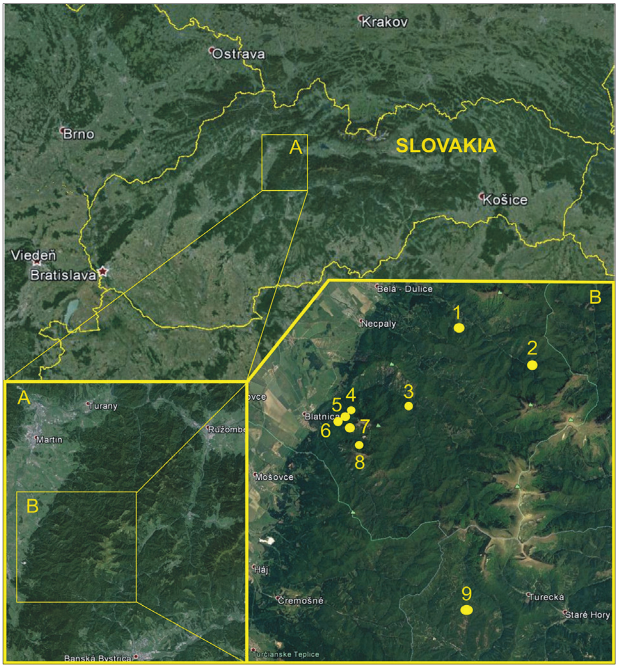
Podzemné krasové fenomény vo Veľkej Fatre lákali zvedavcov už od nepamäti. Jaskyne sa stávali častým cieľom návštev miestnych občanov z obcí v ich blízkosti, ako aj národne uvedomelých Slovákov a Čechov. Pri týchto výletoch sa stávalo, že návštevníci jaskýň si všimli rôzne kosti na dne jaskýň. Tí, ktorí správne pochopili vážnosť situácie, svoje nálezy oznámili povolaným osobám alebo vtedajším úradom, čo viedlo k prvým pionierskym výskumom jaskýň vo Veľkej Fatre.

Samotné výskumy z územia Veľkej Fatry je možné datovať do prvej polovice 19. storočia. Zatiaľ ako prvé sú zmienky o jaskyni „Vrchná Tufná“, kde v 30. – 40. rokoch 19. storočia uskutočnil výskum Chr. Andr. Zipser z Banskej Bystrice. Neskôr v jaskyni kopali Th. Kormos (v roku 1914), F. Schön (v rokoch 1931 – 1933, A. Liebus (Liebus, 1933 ex Skutil, 1938). Krátke správy o nálezoch kostí „jeskynního medvěda“ z Vrchnej Tufnej podáva J. Eisner (1926, 1928). Ďalšími preskúmanými jaskyňami vo Veľkej Fatre boli jaskyňa Mažarná (v roku 1868 v nej kopal P. Križko, 1884; v roku 1932 v nej kopali aj J. Silnický a J. Gregor) (Bárta, 1958), jaskyňa Lôm a jaskyňa na Balovom Grúni (Petrikovich, 1897, 1907). V 60. – 80. rokoch 20. storočia sa uskutočnil rozsiahly výskum krasu Gaderskej a Blatnickej doliny, ktorý mal cieľ zhodnotenie krasových javov na danom území, ich zameranie a zhodnotenie (Mitter, 1977), prípadne skúmanie fosílnej malakofauny (Ložek, 1980). Samostatné výskumy prebiehali aj v iných, menších jaskyniach, ale tie mali výhradne archeologický charakter (napr. jaskyňa Remová, Na Vyhni a iné).

Od roku 2003 prebieha systematickejší paleontologický výskum vo vybratých jaskyniach na území Veľkej Fatry (výskum vedie autor príspevku v rámci plnenia vedecko-výskumných úloh v Slovenskom národnom múzeu v Martine v spolupráci s Katedrou geológie a paleontológie Prírodovedeckej fakulty Univerzity Komenského v Bratislave). V poslednom období (rádovo 10 – 15 rokov) sú známe kostrové nálezy aj z iných jaskýň vo Veľkej Fatre, ale tie členovia jaskyniarskych skupín neohlásili, resp. ostali v ich vlastníctve bez možnosti preskúmania nájdených predmetov, čím sa často znehodnotili nálezové okolnosti, a tým sa znížil aj význam jaskyne ako takej.

LOKALIZÁCIA VÝSKUMNÝCH PRÁC

V príspevku sú opísané doterajšie výskumné práce, výsledky a ďalšia perspektíva výskumu jaskýň nachádzajúcich sa v Belianskej doline, Gaderskej doline a doline Túfna (obr. 1). V rámci krasu Belianskej doliny ide o jaskyňu Došná 7 a Sonda pri ohnisku. Z oblasti Blatnického krasu sú prezentované jaskyňa Lôm, Mažarná, Biela jaskyňa, Jaskyňa I. Textorisovej, jaskyňa HV-4 a jaskyňa M-1. Harmanecký kras zastupuje jaskyňa Horná Túfna. Všetky nálezy opisované v príspevku sú uložené v SNM v Martine – Múzeu Andreja Kmeťa.



Obr. 1. Lokalizácia skúmaných jaskýň vo Veľkej Fatre: 1. Sonda pri ohnisku, 2. Došná 7, 3. jaskyňa Lôm, 4. jaskyňa Mažarná, 5. Biela jaskyňa, 6. Jaskyňa I. Textorisovej, 7. jaskyňa HV-4, 8. jaskyňa M-1, 9. jaskyňa Horná Túfna

Fig. 1. Location of studied caves in Veľká Fatra Mts.: 1. Sounder at the focal point Cave, 2. Došná 7 Cave, 3. Lôm Cave, 4. Mažarná Cave, 5. Biela jaskyňa Cave, 6. Cave of I. Textorisova, 7. HV-4 Cave, 8. M-1 Cave, 9. Horná Túfna Cave

Došná 7

Jaskyňa sa nachádza v katastrálnom území obce Belá-Dulice, v závere Belianskej doliny a jej dĺžka je asi 8 metrov (obr. 2). V závere pomerne strmo klesajúcej chodby pri prieskumných prácach v roku 2012 členovia OS Veľká Fatra objavili kostrové zvyšky, na ktoré ma upozornili a spoločne sme vykonali ich odber. Išlo o dve lebky a sánky (obr. 3 a 4), kosti končatín a chodidiel, stavce a rebrá medveďa hnedého (*Ursus arctos*, ďalej MH), ktoré boli pokryté pomerne hrubou vrstvou sintra, čo môže naznačovať pomerne starý vek kostí (rádovo niekoľko tisíc rokov). Kosti pochádzajú minimálne z dvoch jedincov. Okrem kostí MH sa v jaskyni našli kosti ryšavky žltohrdlej (*Apodemus flavicollis*), krta podzemného (*Talpa europaea*), uchane čiernej (*Barbastella barbastellus*), salamandry škvrnitej (*Salamandra salamandra* – najhojnejšie nálezy) a juvenilných spevavcov (Passeriformes sp. juv.) (určil J. Obuch, Botanická záhrada UK, Blatnica).

Obr. 2. Vstupný otvor jaskyne Došná 7. Foto: A. Bendík
Fig. 2. Entrance of the Došná 7 Cave. Photo: A. Bendík

Obr. 3. Nahromadenie zasintrovaných kostí medveďa hnedého (*Ursus arctos*) v jaskyni Došná 7. Foto: A. Bendík
Fig. 3. Accumulation of brown bear bones (*Ursus arctos*) in the Došná 7 Cave. Photo: A. Bendík

Obr. 4. Sánka a časť lebky (*maxilla*) medveďa hnedého (*Ursus arctos*) z jaskyne Došná 7 po jej očistení. Foto: A. Bendík
Fig. 4. Mandible and part of the skull (*maxilla*) of brown bear (*Ursus arctos*) from the Došná 7 Cave after its conservation. Photo: A. Bendík

Sonda pri ohnisku

Jaskyňa (sonda) sa nachádza v katastrálnom území obce Belá-Dulice, v Belianskej doline, bočnej Žiarnej doline, pri jaskyni Žiarna 3 a jej dĺžka je v súčasnosti približne 15 m. Pri výkopových prácach v roku 2012 našli členovia JK Speleo Turiec kosti a fragmenty kostí horných aj dolných končatín (ramenná, lakťová, lýtková kosť, kosti chodidiel) a sánky a úlomky lebky MH. Vek kostí nebol stanovený, no s najväčšou pravdepodobnosťou pochádzajú z holocénu. Boli pokryté jemnou vrstvou sintra.

Jaskyňa Lôm

Obr. 5. Vstupný portál jaskyne Lôm.
Foto: A. Bendík
Fig. 5. Entrance of the Lôm Cave.
Photo: A. Bendík

Obr. 6. Priestory v jaskyni Lôm s historickými nápismi v bielom sintri a sintrovými jazierkami. Foto: A. Bendík
Fig. 6. The Lôm Cave space with historical inscriptions in white sinter and sinter lakes. Photo: A. Bendík

Jaskyňa sa nachádza v katastrálnom území obce Blatnica, v Gaderskej doline, v severných svahoch masívu Ľubenej, v nevýraznom skalnom páse. Jaskyňa pozostáva zo vstupnej chodby a veľkej siene s bielymi sintrami na stenách, sintrovými jazierkami a dominujúcou sintrovou vázou (obr. 5 a 6). Už v úvode bolo spomenuté, že jaskyňa sa po svojom objavení v roku 1896 stala cieľom výskumov Jána Petrikovicha a odvtedy je častým cieľom návštev (Bendík, 2017). Ako spomína J. Petrikovich, pri svojich výskumoch našiel počas kopacích prác veľké množstvo kostí medveďa jaskynného (*Ursus* ex gr. *spelaeus*, dnes pravdepodobne *U. ingressus*; ďalej MJ). Medzi nimi boli aj pomerne hojné lebky a sánky, ktoré sa neskôr stali ťažiskom prvej expozície v Slovenskom národnom múzeu v Martine v roku 1908. Časť zo zbierok sa zachovala v zbierkach Múzea Andreja Kmeťa, časť zbierky sa stratila.

Po predchádzajúcej návšteve v roku 2008 (povrchový zber), sa od roku 2016 začal revízny výskum jaskyne. V rámci výskumu sa vykonalo nové zameranie siene s paleontologickými nálezmi, priestor sa rozdelil na segmenty a boli vytipované oblasti s možným výskumom. Pri odkrývaní sedimentov sa našli solitérne vypadávajúce kosti MJ, pričom sa vyskytujú výhradne kosti chodidiel (predovšetkým juvenilné jedince) a vyseparované zuby. Celkovo sa podarilo získať viac ako 100 kusov kostrových zvyškov.

Jaskyňa Mažarná

Jaskyňa Mažarná patrí medzi najznámejšie jaskyne v Turci a bola osídlená minimálne od neskorej kamennej doby (eneolitu) (obr. 7). Jaskyňa sa nachádza v doline Vápenná, bočnej doline Gaderskej doliny, pod výrazným skalným bralom. Popri jaskyni vedie modro značený turistický chodník z Blatnice na vrchol Tlstej (TZT 2724). Orientácia jaskyne, priestory a prítomnosť vody umožnili jej využívanie pravekými ľuďmi, ale aj pravekými zvieratami. Z jaskyne pochádzajú pomerne časté nálezy izolovaných kostí MJ, ktoré sa našli pri archeologických vykopávkach v 19. – 20. storočí. Súčasný výskum v jaskyni sa dosiaľ sústredil len na povrchové zbery a záchranné zbery z ilegálnych výkopov realizovaných neznámymi osobami. Výkopové výskumné práce sa orientovali len na vytipované miesta s možnosťami ďalších postupov. V sedimentoch z výkopov sa nachádzali úlomky kostí MJ. Všeobecne však ide len o izolované kosti chodidiel, zuby (moláre) a fragmenty väčších kostí a rebier. Pokračovanie výskumu je plánované v priebehu 2 až 3 rokov, pričom bude potrebné skoordinovať možnosť výkopových prác s obdobiami s nižšou intenzitou návštev jaskyne turistami.

Biela jaskyňa

Biela jaskyňa sa nachádza v bralnom pásme Vápennej doliny nad Gaderskou dolinou. Tvorí ju nevýrazný znížený vchod, prechádzajúci do širších priestorov, ktoré dokonale chránili vnútorné priestory pred nepriaznivými vonkajšími poveternostnými vplyvmi počasia (obr. 8). Výskum bol zameraný na prekopávanie bočnej chodby s možným postupom (obr. 9). Pri kopaní sa našli pomerne dobre zachované izolované kosti MJ. Išlo o zachované veľké kosti (lýtková), stavce (atlas, hrudné, bedrové), úlomky panvy (dospelého aj juvenilného jedinca), rebrá, prstové články, izolované zuby (moláre, rezáky a očné zuby) a dve sánky. Zaujímavosťou je prítomnosť ľavej sánky s chýbajúcou dentíciou ako výsledok uzavretia alveol po vypadnutí zubov počas života jedinca (Bendík, et al., 2009; obr. 10). V jaskyni je plánovaný len sporadický výskum s cieľom záchrany možných kostrových nálezov.

Jaskyňa Izabely Textorisovej

Jaskyňa Izabely Textorisovej sa nachádza v údolí Konského dolu v Gaderskej doline. Jaskyňa pozostáva z veľkého portálového vstupu a troch siení (Sieň, Hrobka, Plazivka), viac-menej spojených horizontálnymi/uklonenými chodbami (obr. 11). Dno siení vytvára poväčšine ostrohranná drvina s hlinitými nánosmi, v jednom mieste s vrstvami guána (v súčasnosti prekrytom vykopanými sedimentmi). Pri spe-

Obr. 7. Vstupný portál jaskyne Mažarná, pohľad z vnútra. Foto: A. Bendík
Fig. 7. Entrance of the Mažarná Cave, view from inside. Photo: A. Bendík

Obr. 8. Vstupný portál jaskyne Biela.
Foto: A. Bendík
Fig. 8. Entrance of the Biela Cave.
Photo: A. Bendík

Obr. 9. Chodba v jaskyni Biela s osteologickými nálezmi medveď jaskynného (*Ursus* ex gr. *spelaeus*) vo fosiliferných hlinito-piesčitých pleistocénnych sedimentoch. Foto: A. Bendík
Fig. 9. Corridor in the Biela Cave with osteological finds of the cave bear (*Ursus* ex gr. *spelaeus*) in fossiliferous loamy-sandy Pleistocene sediments. Photo: A. Bendík

Obr. 10. Ľavá sánka (*mandibula*) medveďa jaskynného (*Ursus* ex gr. *spelaeus*) s viditeľnou chýbajúcou dentíciou ako výsledok degeneratívnej poruchy. Foto: A. Bendík
Fig. 10. Left mandible of the cave bear (*Ursus* ex gr. *spelaeus*) from the Biela Cave with a visible missing cheek teeth as a result of a degenerative disorder. Photo: A. Bendík

Obr. 11. Vstupný portál Jaskyne I. Textorisovej. Foto: A. Bendík
Fig. 11. Entrance of the Cave of I. Textorisova. Photo: A. Bendík

leologickom výskume Speleoklubu Malá Fatra sa našli kosti MJ a na tento nález som bol upozornený. Výskumné práce sa začali na jeseň roku 2004 a pokračujú dodnes (obr. 12 – 14). Z paleontologického hľadiska ide o najkomplexnejší výskum medveďov jaskynných na území Veľkej Fatry. Počet kostrových zvyškov dosahuje viac ako 1600 kusov. Výnimočnosť nálezu však nespočíva v množstve nájdených a zachránených kostí, ale v stave, v akom sa našli. Ide predovšetkým o nálezy takmer kompletných kostier minimálne 11 jedincov MJ, čo v podmienkach slovenskej paleontológie predstavuje unikát (obr. 15). Jedinečným je objav zachovaných fosílnych zvyškov jedincov v polohe, v akej zvieratá uhynuli (*in mortem*), čo v spojitosti s ďalšími údajmi umožňuje podrobnú tafonomickú analýzu nálezov a odhalenie príčin úhynu jednotlivých jedincov. Významné sú zistenia prítomnosti patologických javov na nájdených kostrách jedincov, ktoré dosiaľ neboli zaznamenané vo fosílnom zázname stavovcov vôbec (napr. nález kostry mladej samice, ktorá z dôvodu choroby alebo úrazu prišla ešte počas života o časť ľavej prednej končatiny) a pre vedu a spoločnosť prinášajú nové poznatky o tomto vyhynutom druhu z radu Carnivora (Bendík & Sabol, 2008; Sabol et al., 2009; Štuller et al., 2011). Predmetné nálezy majú veľký prínos pre taxonomický výskum fosílnych zvyškov

Obr. 12. Hrobka – miesto nálezov kostier medveďov jaskynných (*Ursus* ex gr. *spelaeus*) v Jaskyni I. Textorisovej. Foto: M. Sabol
Fig. 12. Tomb – finding place of cave bears skeletons (*Ursus* ex gr. *spelaeus*) in the Cave of I. Textorisova. Photo: M. Sabol

Obr. 13. Nález osteologických zvyškov kostry medveďa jaskynného (*Ursus* ex gr. *spelaeus*) z Jaskyne I. Textorisovej. Foto: M. Apfelová
Fig. 13. Find of osteological remains of cave bear (*Ursus* ex gr. *spelaeus*) from the Cave of I. Textorisova. Photo: M. Apfelová

Obr. 14. Nález lebky medveďa jaskynného (*Ursus* ex gr. *spelaeus*) z Jaskyne I. Textorisovej. Foto: M. Apfelová
Fig. 14. Find of a cave bear skull (*Ursus* ex gr. *spelaeus*) from the Cave of I. Textorisova. Photo: M. Apfelová

Obr. 15. Rekonštrukcia jednej z nájdených kostier medveďa jaskynného (*Ursus* ex gr. *spelaeus*) z Jaskyne I. Textorisovej. Foto: A. Bendík
Fig. 15. Reconstruction of one cave bear skeleton (*Ursus* ex gr. *spelaeus*) found in the Cave of I. Textorisova. Photo: A. Bendík

MJ na území Západných Karpát z hľadiska exaktného definovania druhového postavenia nálezov pomocou morfometrickej, morfodynamickej a paleogenetickej analýzy v spojitosti s biostratigrafickým kontextom. Analýzami stanovenia veku pomocou ^{14}C sa podarilo datovať kostrové zvyšky MJ z Jaskyne I. Textorisovej do obdobia spred 45 000 až 25 000 rokov (Bendík & Sabol, 2007), čím sa tieto nálezy radia medzi najmladšie datované kosti MJ na Slovensku a zároveň dokazujú dlhodobé využívanie jaskyne. Z piesčitej vrstvy, na ktorej sa nachádzali uložené kostrové zvyšky MJ, bola odobratá vzorka na palynologický rozbor, v ktorej sa objavili redeponované prvky kriedového veku (palynomorfy), čo môže poukazovať na obdobie tvorby prvotných procesov krasovatenia (Vaněková & Bendík, 2008).

Celkove je možné nález fosílií MJ v Jaskyni I. Textorisovej zhodnotiť ako unikátny nielen na území Slovenska, ale aj v rámci celej Európy, pričom prináša nové poznatky o vyhynutom druhu, na ktorý sa v posledných rokoch pohľad výrazne zmenil a rozšíril.

Výsledky výskumov boli úspešne prezentované v domácich aj zahraničných publikáciách a na medzinárodných sympóziách o MJ (napr. Bendík, 2005; Bendík, 2007a,b; Bendík, 2011a,b; Bendík, 2012; Sabol et al., 2014).

Obr. 16. Odber nálezov z jaskyne HV-4. Foto: A. Bendík
Fig. 16. Collecting of mammalian remains from the HV-4 Cave. Photo: A. Bendík

HV-4 (Gaderská dolina)

Jaskyňa sa nachádza v katastrálnom území obce Blatnica, na južnom svahu masívu Tlstej, nad záverom Havranej doliny. Vchod má rozmery 0,5 × 0,4 metra a dĺžku približne 20 metrov (obr. 16, zameral P. Pokrievka ml. v roku 2009). V jaskyni sa našla len jedna sánka MH a ohlodaný paroh jeleňa. Jaskyňa slúžila asi ako dočasné útočisko MH alebo líšky, ktorá si do nej dotiahla zvyšky svojej potravy, čomu by nasvedčovala absencia ostatných kostí. Podrobnejší prieskum dna jaskyne sa však neuskutočnil. Nálezy pochádzajú z roku 2011.

Jaskyňa M-1

Jaskyňa sa nachádza v Konskom dole v masíve Muráňa a tvorí ju výrazný vstupný portál s mohutným závalom vychádzajúcim z jaskyne (obr. 17). Skúmaný priestor (Medvedí cintorín) sa nachádza vo výraznej sieni za úzkou vstupnou chodbou (zapaženou v závale). Pri postupových prácach členovia JK Speleo Turiec objavili kosti, ktoré patrili MJ. Následne sa vykonávali výkopové práce na vytipovaných miestach siene, pri ktorých sa našli tri neúplné kostry MJ (z toho jeden juvenilný jedinec) a dve lebky MJ (obr. 18 a 19). Vplyvom tlaku nadložného závalu došlo k porušeniu výdrevy a v súčasnosti je prístup do jaskynných priestorov nemožný; výskum v závale pokračuje. Celkovo sa našlo necelých 500 kusov kostí MJ. Po vyhodnotení možných prienikov do jaskyne je plánované pokračovanie paleontologického výskumu.

Horná Túfna

Ako bolo uvedené v úvode, jaskyňa Horná Túfna je známa už od nepamäti a uskutočnili sa v nej viaceré odborné výskumy. Nachádza sa v katastrálnom území obce Dolný Harmanec, v doline Túfna. Jaskyňa s aktuálnou dĺžkou 85 metrov má výrazný vstupný portál so strmo uklonenou stúpajúcou chodbou, ktorá sa za výraznou hranou lomí nadol na ploché dno (obr. 20). Keďže leží pri výstupovom turistickom chodníku z Dolného Harmanca na Kráľovu studňu (TZT 5435), stáva sa často cieľom návštev a z toho dôvodu sú jaskynné priestory – sedimenty pomerne znehodnotené (prekopané). V jaskyni sa plánuje revízny výskum.

Obr. 17. Vstupný portál jaskyne M-1.
Foto: A. Bendík
Fig. 17. Entrance of the M-1 Cave.
Photo: A. Bendík

Obr. 18. Vstupný zával do siene Medvedí cintorín s vyčnievajúcimi kosťami medveďa jaskynného (*Ursus* ex gr. *spelaeus*) z jaskyne M-1. Foto: A. Bendík
Fig. 18. The entrance to the Bear cemetery with the protruding bones of the cave bear (*Ursus* ex gr. *spelaeus*) from the M-1 Cave. Photo: A. Bendík

Obr. 19. Nález lebiek medveďa jaskynného (*Ursus* ex gr. *spelaeus*) z jaskyne M-1.
Foto: A. Bendík
Fig. 19. Finding of cave bear skulls (*Ursus* ex gr. *spelaeus*) from the M-1 Cave.
Photo: A. Bendík

Obr. 20. Vstupný priestor jaskyne Horná Túfna.
Foto: A. Bendík
Fig. 20. Entrance area of the Horná Túfna Cave.
Photo: A. Bendík

ZHODNOTENIE

Opísané lokality s kostrovými nálezmi fosílnych – subfosílnych druhov sú pravdepodobne len časťou z celkových možných nálezov v jaskynných priestoroch (v súčasnosti sú nám známe nové jaskyne s výskytmi kostrových zvyškov). Pri takom veľkom množstve nálezov je však pomerne ťažká systematická práca na všetkých lokalitách súčasne; prioritou ostanú tie, v ktorých sa nachádza väčšie nahromadenie kostí, resp. tie, ktoré sa môžu stať terčom vykrádačov jaskýň. Nájdené kostrové zvyšky sú všeobecne v dobrom stave, pričom výnimočné postavenie v rámci nálezov má Jaskyňa I. Textorisovej a jaskyňa M-1. Táto skutočnosť bola podmienená pravdepodobne rýchlym prekrytím zahynutých tiel sedimentmi, malým prítokom vody, a tým nižšou vlhkosťou, ktorá degraduje kosti, zneprístupnením tiel pred nekrofágmi (zdochlinármi) a v neposlednom rade aj včasným ohlásením nálezov a ich záchranou. Najlepšie zachovanými kosťami sú menšie a väčšie kosti chodidiel, lebky, sánky a zuby. Menej odolné sú predovšetkým stavce, rebrá a kosti panvy. Dobré zachovanie kostrového materiálu umožňuje jeho využitie na rôzne druhy analýz (stanovenie veku, paleogenetická analýza (mtDNA), izotopová analýza). Aj keď v rámci osvetovej činnosti medzi jaskyniarmi apelujeme na záchranu paleontologického materiálu, z minulého aj súčasného pozorovania je zjavné, že kostrové zvyšky sa často stávajú ich „trofejami“, pričom končia v súkromných zbierkach, resp. dochádza k ich znehodnoteniu (nesprávna starostlivosť vedie k rozpadu kostí) a sú indície o ich predaji, čo je v rozpore so zákonom č. 647/2008 o chránených nerastoch a chránených skamenelinách a ich spoločenskom ohodnocovaní.

Poďakovanie. Za spoluprácu na doterajších výskumoch ďakujem členom Speleoklubu Malá Fatra, JS Speleo Turiec, OS Veľká Fatra a Mgr. Márii Apfelovej (Správa NP Veľká Fatra). Za odbornú pomoc a spoluprácu chcem poďakovať doc. Mgr. Martinovi Sabolovi, Ph.D., z Prírodovedeckej fakulty UK v Bratislave.

THE PALEONTOLOGICAL RESEARCH IN CAVES OF THE VEĽKÁ FATRA MTS. – A STATE OF THE ART

Summary

The research of the Veľká Fatra Mts. territory can be dated since the first half of the 19th century. Current research started in 2003 by scientists of the Slovak National Museum in Martin – Andrej Kmeť Museum in cooperation with the Department of Geology and Palaeontology of Faculty of Natural Sciences, Comenius University in Bratislava. Paleontological research is in progress in caves of Belianska valley, Gaderská valley and Túfna valley.

From the Došná 7 Cave and the Sounder at the focal point Cave in the Belianska valley come bones of brown bear (*Ursus arctos*) covered by a layer of sinter, which can indicate an older age (maybe a few thousand years). Findings from the Lôm Cave, Mažarná Cave, Biela Cave, Cave of I. Textorisova, HV-4 Cave, and M-1 Cave in the Gaderská valley are represented exclusively by fossil remains of cave bear (*Ursus* ex gr. *spelaeus*). It is unique to discover the preserved fossil remains of individuals in the place where they died (*in mortem*), which in connection with other data allow a detailed taphonomic analysis of the finds and the revelation of the causes of individual deaths. Determined age of cave bear fossils (45 000 and 25 000 year BP) from the Cave of I. Textorisová documents one of the youngest occurrence datum for cave bears in the Slovakia. The Horná Túfna Cave in Túfna valley was known from 19th century, when started the first scientific research, the result being depreciation of the cave sediments. In The Horná Túfna Cave is prepared a revisory research.

Total number of bones from studied caves of brown bear is about 100 specimens and of cave bears are about 2300 specimens. Good preservation of the skeletal material makes it possible to use them for various types of analyzes (determination of age, ancient DNA analysis, isotopic analysis).

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