



# ARAGONIT

**vedecký a odborný časopis Správy slovenských jaskýň**

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- pôvodné vedecké príspevky z geologického, geomorfologického, klimatologického, hydrologického, biologického, archeologického a historického výskumu krasu a jaskýň, najmä z územia Slovenska
- odborné príspevky zo speleologického prieskumu, dokumentácie a ochrany jaskýň
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- (2) Medvedia jaskyňa Cave. Foto: P. Staník
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## 23rd International Cave Bear Symposium (ICBS 2017)

Liptovský Mikuláš, Slovakia  
October 4–7, 2017

### Organized by

Department of Geology and Palaeontology, Comenius University in Bratislava  
Slovak Museum of Nature Protection and Speleology in Liptovský Mikuláš  
State Nature Conservancy of the Slovak Republic, Slovak Caves Administration in Liptovský Mikuláš



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# A SHORT HISTORY OF CAVE BEAR RESEARCH IN SLOVAKIA

*Martin Sabol*

Department of Geology and Palaeontology, Faculty of Natural Sciences, Comenius University,  
Ilkovičova 6, 842 15 Bratislava, Slovakia; sabol@fns.uniba.sk

Fossil remains of ursids (hemicyonine-, agriotherine-, chiefly ursine bears) are very frequently found in the Late Cenozoic deposits (mainly in the karst and fluvial ones) of the Slovak part of the Western Carpathians. Most of them belong to cave bears (*Ursus* ex gr. *spelaeus* Rosenmüller, 1794) from the Late Pleistocene, fossils of which are predominantly located in cave sediments.

Originally, cave bear bones in caves were believed to be the remains of cave-dwelling giants, dragons or other mythological beasts. This fact was mirrored in names of many "dragon caves" across Europe, famous especially in Switzerland (e. g. Drachenloch Cave in the canton of St. Gallen), Austria (e. g. Drachenhöhle Cave at Mixnitz in Styria), or Slovakia (e. g. Dračia jaskyňa Cave, today's Demänovská ľadová jaskyňa Cave) near Liptovský Mikuláš) (Rosendahl & Döppes, 2012). Finds of these "dragon bones" in Slovak caves have been reported at least since the Middle Age, first by word of mouth and then later also by reports on "dragons" and other "natural curiosities" published in many historical annals and chronicles also from later periods. The evidence about that can be found for instance in the Ostrihom Abbey documents from 1229 (Kučera et al., 1981) or in publications such as "De draconum Carpathicorum cavernis" by P. J. Hain in 1672 (Fig. 1), "Danubius Pannonico-Mysicus, observationibus geographicis, astronomicis, hydrographicis, historicis, physicis, perlustratus et in VI tomos digestus, cum tabulis aeri incisis" by F. Marsigli from 1726, or "Antra draconum Liptovensis" by F. Brückmann from 1739 (Schmidt, 1970). Even in the first half of 18th century, the Technical Museum in Dresden exhibited a "dragon skeleton" from the Demänovská ľadová jaskyňa Cave (Fig. 2), which was sent there by J. Buchholtz Jr., who studied the cave between 1714 and 1724 (Kučera et al., 1981; Lalkovič & Komorová, 1991). Curiously, the debates on fossils from caves had appeared in the literature even after a new extinct species of bear (*Ursus spelaeus*) was described by J. C. Rosenmüller in 1794 from Zoolithenhöhle near Gailenreuth in Germany. This was related to the demand for exploration of nature and its history at the scientific level which

had become increasingly important in Europe at the beginning of the 18th century and was also reflected in the study on caves and bear osteological remains from the Slovak territory as can be for example found in the publication

by M. Bel "Hungariae antiquae et novae prodromus" from 1723 (Kučera et al., 1981). However, the first who recognized the bear bones among fossils in Slovak caves was English mineralogist and traveler R. Townson who vis-

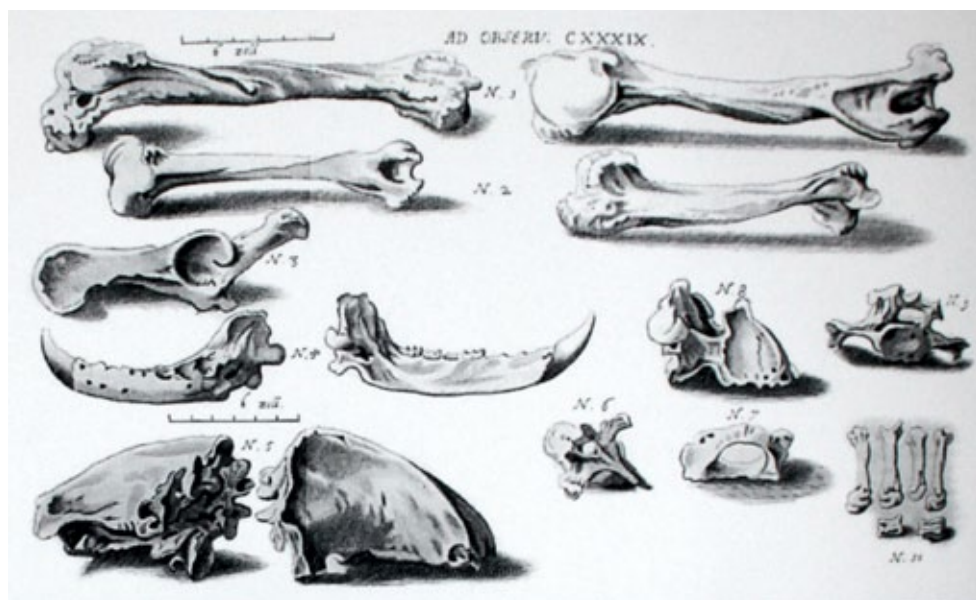


Fig. 1. "Dragon bones" from a cave in the Carpathian Mountains, figured by P. J. Hain in 1672 (Rosendahl & Döppes, 2012; poster).

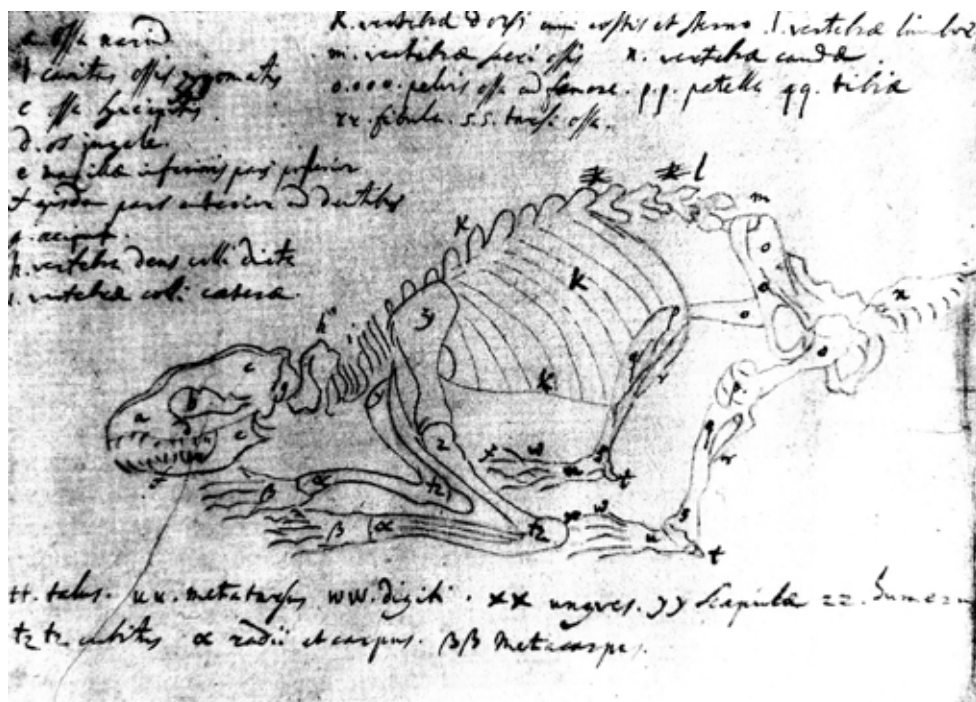


Fig. 2. Illustration of "dragon skeleton" from the Demänovská ľadová jaskyňa Cave, sent by J. Buchholtz Jr. to the Technical Museum in Dresden in the first half of 18th century (Lalkovič & Komorová, 1991).

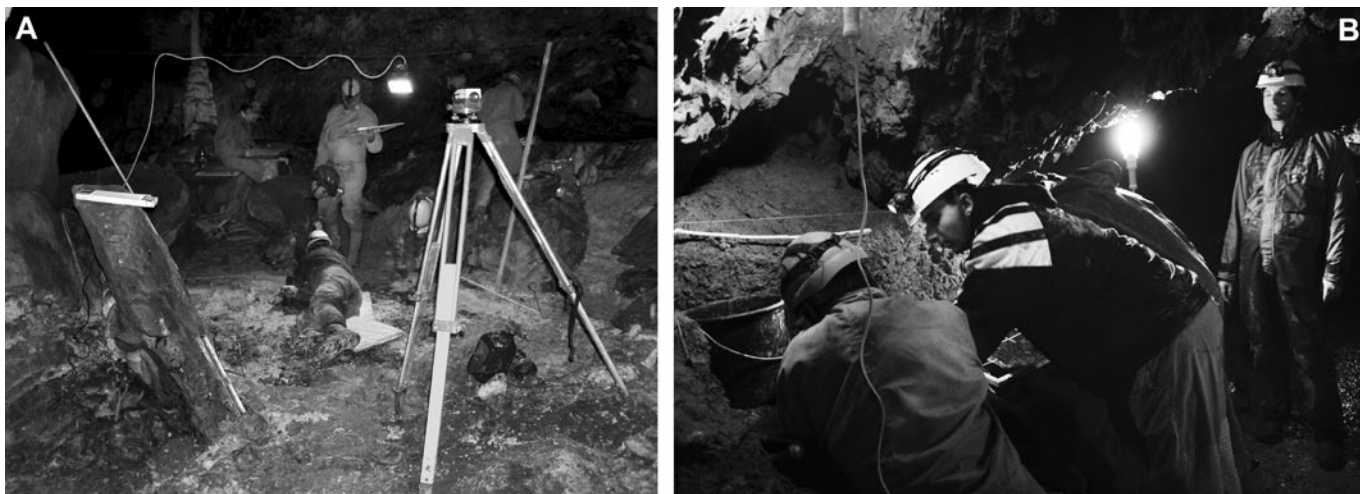


Fig. 3. Field campaigns: A – in the Medvedia jaskyňa Cave in the Slovenský raj Mts. in 2007 and B – in the Važecká jaskyňa Cave in 2011. Photo Archive: M. Sabol

ited the Demänovská Valley in 1797 (Schmidt, 1970). The research continued in this scientific spirit during the whole upcoming 19th century, when more scientific works were appeared.

Many fossil records of bears from Slovak caves are also mentioned in period manse- and castle notes (Skutil, 1938). Reports on the frequent occurrence of cave bear skeletal remains continued to be interesting also in the Austro-Hungarian Empire (Bredetzky, 1805) as well as abroad (Cuvier, 1806). In following years, bear fossils were reported from karst sites of the southern- (Zipser, 1858), western- (Paul, 1863; Štúr, 1870), northern- (Fuchs, 1872; Nehring, 1880), and central Slovakia (Petrikovich, 1897). However, Primics (1890) was the first who listed all localities with the fossil record of cave bears in the eastern (Hungarian) part of the former Monarchy.

In the late 19th century, but especially in the first half of 20th century, important foreign publications led to the revision and re-study of the bear fossil material from previous collectings and excavations. More and more, new specialized works focusing mainly on phylogeny, anatomy, morphology, histology, ecology, pathology as well as biostratigraphic importance of the various ursid fossils were appeared. This also mirrored in the study of cave bears which resulted in publication of synthesis works from various fields of research (geological, geographical, archaeological, and biological ones).

During the first third of 20th century, many authors followed these new trends in cave bear research also in Slovakia, especially those connected with (zoo-)archaeological- (Hillebrand, 1919; Bábor, 1929; Eisner, 1933; Skutil, 1938) and palaeontological researches (Kmeť & Rizner, 1903; Petrikovich, 1907; Éhik, 1913; Kormos, 1914; Sigmeth-Horusitsky, 1914; Volko-Starohorský, 1927, 1929). Later on, mainly after the World War II, papers focused on the solution of genetic and ecological relations between cave bear fossils and cave sediments were published (Kretzoi, 1938; Hokr, 1946; Augusta & Hokr, 1948a, b; Fejfar, 1953; Musil, 1953, 1956; Ložek et al., 1957; Fejfar & Sekyra, 1964; Bárta, 1965; Prikryl & Schmidt, 1965; Janáček & Schmidt, 1965) and many of them also described morphology (predominantly dental one) and ontogeny of cave bears.

In addition to archaeological excavations at various sites, in this period, an extensive paleontological research was carried out more or less only in the Jasovská jaskyňa Cave (Ložek et al., 1957) and in the Medvedia jaskyňa Cave in the Slovenský raj Mts. (Fejfar, 1953; Janáček & Schmidt, 1965). Apart from morphological, stratigraphic, and biogeographical questions (Schmidt, 1970), these researches tried to solve also a problem of the first and the last occurrence of cave bears in the territory of Slovakia. In this regard, the first attempt to date exactly the cave bear fossils using the radiocarbon method was made (Schmidt & Chrapan, 1970). Despite of the questionable datum of cave bear remnants from the Medvedia jaskyňa in the Slovenský raj Mts. (>15,000 years BP), another cave bear fossils from the Psie diery (Dog's Holes Cave) were dated (Pomorský, 1993) and showed similar ages ( $15,490 \pm 780$  to  $17,530 \pm 900$  years BP).

In the final third of 20th century, the research of cave bears, especially in the level of  $\alpha$ -taxonomy based on the basic morphometric analysis (especially of dental remains) continued (Musil, 1996; Holec et al., 1998; Sabol 1998, 1999; Holec, 2000), and most of older findings housed in Slovak museums were revised (Sabol, 1997, 2000).

The beginning of the new millenium has brought new impulses in the cave bear research in Slovakia focusing mainly on the radiometric dating of cave bear fossils and on the isotopic and aDNA analyses. In addition to the traditional works aimed at the determination and description of bear fossils from Slovak caves (Sabol, 2002a, b, 2005; Sabol & Struhár, 2002; Vlček et al., 2005; Vlček & Sabol, 2006; Bendík & Sabol, 2007; Sabol & Kozáková, 2007; Sabol & Višňovská, 2007; Sabol et al., 2008a, 2009; Bendík et al., 2009; Štuller et al., 2011; Čeklovský & Sabol, 2012; Čeklovský et al., 2013) or their geographical distribution (Sabol, 2001), the publications included various analytical results, inspired by the new research of cave bears in the Alps region (Sabol & Šándorová, 2007; Ábelová & Sabol, 2009), whence three new cave bear taxa (*Ursus ingressus*, *U. spelaeus ladinicus*, and *U. spelaeus eremus*) were described on the basis of morphometric and morphodynamic analysis as well as palaeogenetic analysis of ancient DNA (Rabeder et al., 2004). This stimulated a successful cooperation with the Geocentre and the VERA Laboratory of the Vienna University and the Austrian Academy of Sciences (Prof. Gernot Rabeder and his research team), which resulted in a new systematic palaeontological research of the Medvedia jaskyňa Cave in the



Fig. 4. Cave bear – realistic model in the Važecká jaskyňa Cave. Photo: M. Rengevič

Slovenský raj Mts. during three field campaigns in 2007–2009 (Fig. 3A) and the Važecká jaskyňa Cave during three winter seasons between 2011 and 2013 (Figs. 3B, 4). Preliminary results on the age (~50,000 – 30,000 years BP), taxonomy (*U. ingressus*), and taphonomy of cave bear records from these studied cave sites have already been published (Sabol et al., 2008b, 2011; Laughlan et al., 2012; Sabol & Rabeder, 2012), but finalization of the research in the form of monographic outputs is still in progress. Fossils of cave bears from the Medvedia jaskyňa Cave in the Slovenský raj Mts. were also used for the study of isotopic variability across Europe during MIS 3 – a warmer phase of the Last Glacial (Krajcarz et al., 2016).

Similarly to the cave bear research in the Alps area, an attempt to find first high-mountain cave bear assemblage in Slovakian Western Carpathians was realized. So far, it has been carried out in the Javorinka Cave in the Vysoké Tatry Mts., where fossils of cave bears (*U. ingressus*) were discovered at the elevation of 1,525 to 1,559 m a. s. l., although Fejfar and Sekyra (1964) described a weathered ursid canine at the same altitude from the Muránska jaskyňa Cave. The exact taxonomic determination of this canine is, however, still questionable. Simultaneously with this survey, the last occurrence of cave bears in Slovakia was documented in the Jaskyňa Izabely Textorisovej Cave in the Veľká Fatra Mts. with calibrated radiocarbon ages 30,181 and 30,190 years BP (Sabol et al., 2014).

At present, a study of cave bear fossil remains in the territory of Slovakia is carried out from several localities (Fig. 5). This research is, however, very limited by financial funds, and if no significant change in

the financing of the Slovak science will occur in near future, there is a serious concern that the level of cave bear investigation will fall again to the level of research in the 20th century.

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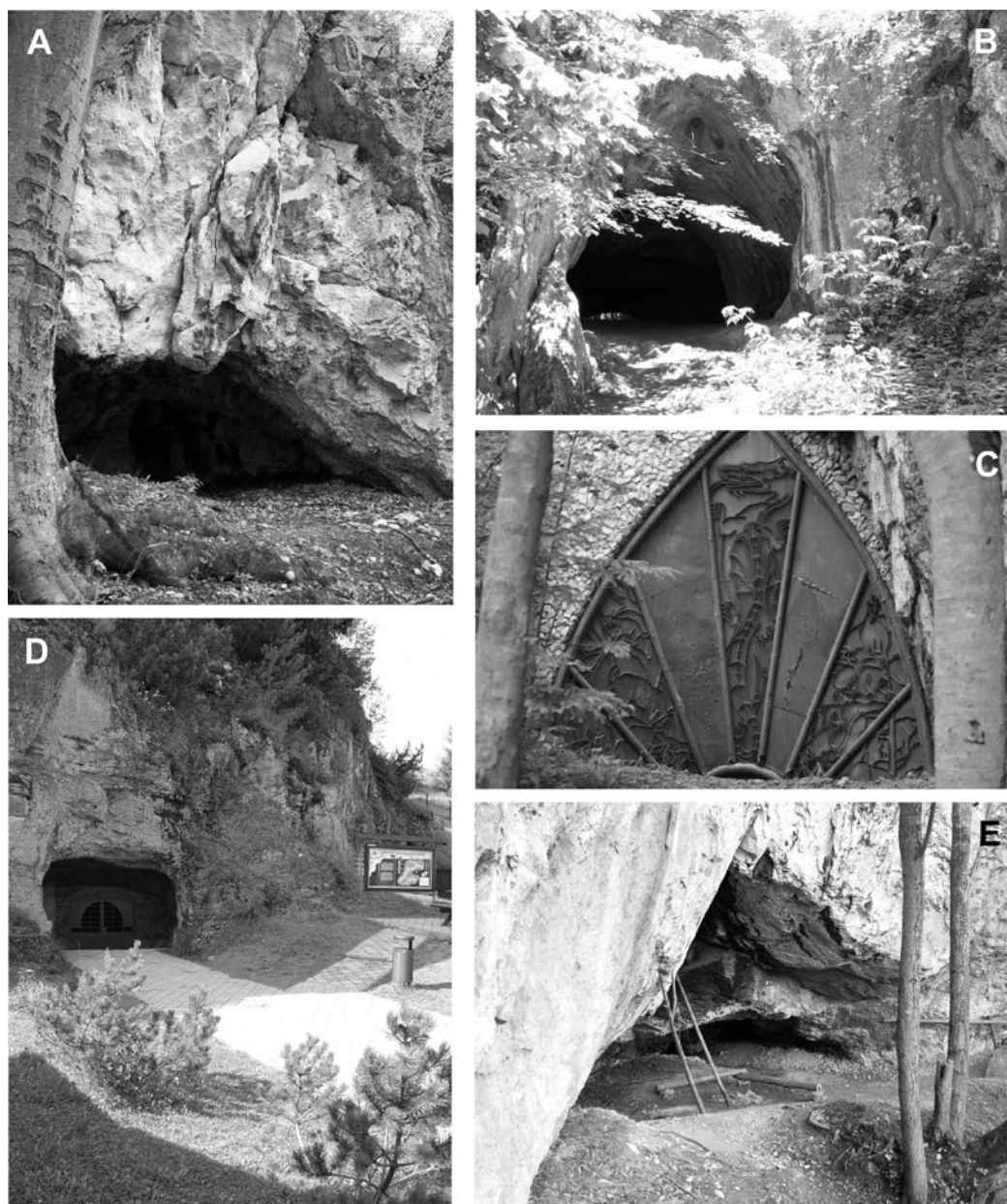


Fig. 5. Some most important Slovak sites with the fossil record of cave bears: A – Tmavá skala Cave, B – Čertova pec Cave, C – Demänovská ľadová jaskyňa Cave, D – Važecká jaskyňa Cave and E – Medvedia jaskyňa Cave in the Slovenský raj Mts. Photo: M. Sabol (A–B and D–E), <https://www.kamnavikend.eu/demanovska-ladova-jaskyňa/> (C)

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# JÁN VOLKO-STAROHORSKÝ AND NATURE CONSERVATION

**Leonard Ambróz<sup>1</sup> – Martin Sabol<sup>2</sup> – Michal Rendoš<sup>3</sup>**

<sup>1</sup> Slovak Museum of Nature Protection and Speleology, Školská 4, 031 01 Liptovský Mikuláš, Slovakia; leonard.ambroz@smopaj.sk

<sup>2</sup> Department of Geology and Palaeontology, Faculty of Natural Sciences, Comenius University, Ilkovičova 6, 842 15 Bratislava, Slovakia; sabol@fns.uniba.sk

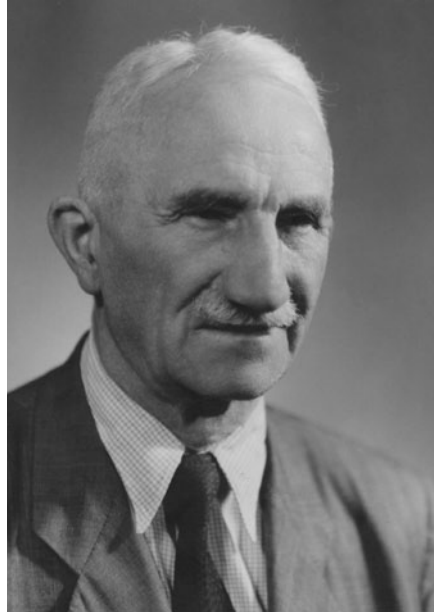
<sup>3</sup> State Nature Conservancy, Slovak Caves Administration, Hodžova 11, 031 01 Liptovský Mikuláš, Slovakia; michal.rendos@ssj.sk

Ján Volko-Starohorský was born on the 31st of July 1880 in Liptovský Mikuláš, in a district called Nižný Hušták, which is today's Moyzesova Street. He attended a five-year primary school under the supervision of outstanding teachers – Rehor Uram Podtatranský, music composer Karol Ruppeldt and mineral collector Mieroslav Kovalevsky. A couple of years later, J. Volko-Starohorský continued his education at the secondary school in Levoča, where he began to be keenly interested in astronomy. After graduating from the high school in 1900, he joined the Domestic Vienna Regiment (Hoch und Deutchermeister No 4), where he completed his one-year volunteer service. After being released from the service, J. Volko-Starohorský was promoted to the rank of "Cadett aspirant". He wanted to attend further studies at Charles University in Prague, where at that time; however, the graduates of Hungarian secondary schools could not be admitted for studies. In January 1902, he enrolled instead in the second semester at University of Budapest, where he began his studies of natural sciences, particularly geology taught at that time by professors Antal Koch and Imre Lörenthey. In the course of the university studies, J. Volko-Starohorský took part in several geological excursions from which, he collected various geological materials deposited later at the Museum of Slovak Karst in Liptovský Mikuláš.

J. Volko-Starohorský was employed for some time as an assistant of professor A. Koch. Subsequently, he was assigned by the Hungarian Cartographic State Geological Institute to the geological mapping work in Banat. In December 1908, he passed the final pedagogical exam and received his professorship. J. Volko-Starohorský served as a teacher at Evangelical Elementary School in Hybe. Afterwards, he worked for Dessewffy noble family in the Hungarian village of Vanyarc, the state schools in the towns of Topolčany, Brezno, Abrud (Transylvania) and Poľný Berinčok (Hungary), where he was commissioned by the municipality to drill an artesian well. At the end of his career, J. Volko-Starohorský taught in the Romanian city of Deve.

On 26 August 1914, J. Volko-Starohorský enlisted in the World War I army, where he remained until 1918. During the war, he reached the rank of lieutenant, was transferred from infantry to meteorologists and became a member of the Imperial Military Geographic Institute in Vienna.

After the war, between 1918 and 1939, J. Volko-Starohorský worked as a part time



assistant teacher at Gymnasium in Liptovský Mikuláš thanks to which, he could engage in scientific work and conservation activities.

At the Museum of Slovak Karst, in foundation of which J. Volko-Starohorský actively participated, he created the Natural Sciences Corps, part of which was the Nature Conservation Department. The aim of this department was to give impetus to the beautification, landscaping and greening of public and abandoned areas as well as to draw attention to an illegal woodcutting. The founding meeting of the Natural Sciences Corps took place on 29 November 1932. The so-called "Beautification and Afforestation Commandments", adopted at the meeting, were used by J. Volko-Starohorský as an educational tool for the teaching of nature conservation at Gymnasium in Liptovský Mikuláš. The commands were as follows:

1. Everything you see around you, all nature, has its life goal, which you have as well.
2. Treat the plants gently, fondly and sensibly. The plants can grow only noble, good and soulful people. Unlearned, crude, spoiled and angry people always decimate the plants.
3. Beautify our dwellings, yards, streets, villages and cemeteries with the flowers. Set to grow the trees and shrub along the roads and river banks, and do not tolerate destroying flowers and trees. Be public defender of the arousing plants, save what the others have created.

4. The plant lives, feels, rejoices and is built up of cells, just like the bodies of humans do. Plants are living creatures and their life is in common with human life. Plants are also susceptible to diseases and thus, we must not only grow them but also protect them and treat them when needed.

5. The plant breathes and feeds through the leaves. When you destroy the leaves and branches of the tree, you take away its beauty and destroy its life.

6. The skin protects an animal from the discomfort. When you cut the skin off the animal, it gets sick and dies. The bark protects a plant from the discomfort. When you strip the bark off the tree, or if you damage bast fibers and wood with knife and nail, you then open deep wounds and paths to deadly diseases and destroy nice, joyful and hopeful lives.

7. The singing birds clean the trees from the insects. Lure them by food and build them nest boxes in the gardens.

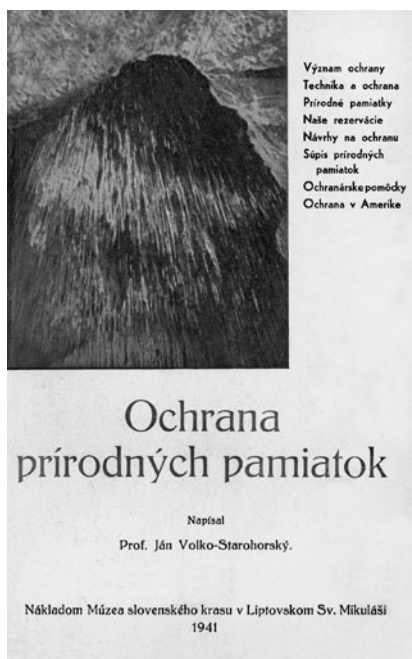
8. The plants not only beautify our surroundings, clean the air, pick up the dust that damages our lungs, but they also give us a lot of benefits. The plants mitigate the floods, regulate the springs, moderate the climate, and equalize the precipitation, electricity and air. The plants fill the air with a scent and pleasantly cool us in hot summer. The plants nourish us, treat our enfeebled health, give us wood, and heat us in winter. We would not be able to live without plants. The world without plants would be just a desert.

9. Every ignorant, calculating, selfish and fraudulent person is capable of chop down the trees, break and destroy the plants. Only educated and noble-minded people can afforest, repair and beautify destroyed forest edges. According to the plants cultivated, we considered the maturity, culture and education of the nations.

10. The mountains are the temples of nature; they are the rock cliffs sanctuaries. Love our mountains. Set to grow the young trees on the clearings. Protect the seedlings.

Professor Ján Volko-Starohorský devoted himself to the nature conservation already at the time when almost no one was aware of its importance. He considered the protection of nature and natural monuments as something "magnificent, generous, beautiful, humane, moral and educational". At the





Cover page of "Conservation of Natural Heritage". A book by J. Volko-Starohorský published in 1941.

museological course held at Slovak National Museum in Martin between the 8th and 10th February 1941, J. Volko-Starohorský stated that "nature conservation is a majestic performance that can be conducted only by a man who perfectly knows nature. The nature conservation shapes man and forms a nation. It has many in common with Christian religion; it does not harm anyone, but on the other hand, it commands to treat nature with love and to honour the Almighty in His magnificent creation". During World War II, when nature conservation in Slovakia stagnating, J. Volko-Starohorský presented his 15-article proposal on "Protection of Natural Monuments" in the introduction of which, he states: "We must finally be able to attain at least the same level of nature conservation in our homeland as we have already achieved. However, it would be even more desirable if we dare to surpass this achieved level".



Ján Volko-Starohorský educates the youth. Photo: Archive of SMOPaJ Liptovský Mikuláš



Ján Volko-Starohorský with a guide T. Jurišová in the Demänovská jaskyňa slobody Cave in 1974. Photo: Archive of SMOPaJ Liptovský Mikuláš

Ján Volko-Starohorský was inspired by scientific works of Dionýz Štúr, Andrej Kmeť, and journalistic work of Gustáv Kazimír Zechenter-Laskomerský. At the same time, he cooperated with the outstanding Czech scientists – Prof. Dr. Jiří Daneš, Prof. Ján Eisner, Dr. Radim Kettner and Prof. Dr. František Vításek. In addition to pedagogy and engaging in nature conservation, J. Volko-Starohorský was interested in associational activities, social issues, rail transport, balneology, museology, astronomy, cartography, geography, geology and speleology. He participated in paleontological research in several Slovak caves. His discoveries of fossil remains of cave bears and other extinct Pleistocene mammals in the Jasovská jaskyňa Cave in eastern Slovakia and in the Okno Cave in Demänovská Valley in the twenties of the last century (1925, 1927, 1929) are among the most significant. He wrote more than 160 papers published in various scientific and science popularization journals as well as

in scientific collections. Many of J. Volko-Starohorský ideas about nature conservation were eventually realized. These included, for instance, the adoption of the Nature Conservation Act in 1955, which he considered to be "the culmination of nature conservation efforts". His desire to establish a department of nature conservation and speleology at some of the Slovak universities remained unfulfilled.

During his life, J. Volko-Starohorský was a member of several scientific societies:

- co-founder of Matica Slovenská, Slovak scientific and cultural institution focusing on topics around the Slovak nation
- member of committee of Czechoslovak Geographical Society and Natural History Club in Prague
- member of Society for Mineralogy and Geology in Prague
- founding member of Enlightenment and Protection Society in Prague
- editor of Museum Library of Slovak Karst Museum in Liptovský Mikuláš
- external associate of State Geological Institute in Prague (since 1918)
- professor at Technical University in Košice (since 1938)
- chairman of Matica Slovenská Natural Sciences Department
- vice-chairman of Scientific Committee of Demänovské Caves in Liptovský Mikuláš
- head of scientific departments of Slovak Karst Museum in Liptovský Mikuláš
- chairman of department of Natural History Museum in Bratislava
- member of Scientific Czechoslovak-Polish Commission for Geology in the Tatra Reserve, Červený Kláštor
- member of commission for commercialization of Demänovské Caves
- honorary member of Slovak Geological Society, Slovak Academy of Sciences
- member of Šafárik's learned society in Bratislava
- honorary member of Slovak Nature and Landscape Conservation Union
- member of Railway Research Commission, Handlová – Horná Štubňa
- member of Commission for construction of observatory on the Lomnický štít Peak

Ján Volko-Starohorský died on the 17th December 1977 in Bratislava at the age of 97 and was buried at the Vrčica Cemetery in his natal Liptovský Mikuláš.

The most substantial publications of J. Volko-Starohorský dealing with nature conservation and research of extinct cave fauna in the Jasovská jaskyňa Cave and Okno Cave are as follows:

VOLKO-STAROHORSKÝ, J. 1925. *Diluválne náplavy v Jaskyni „Okne“ v Demänovskej doline. (Liptov na Slovensku) [Diluvial deposits in the Okno Cave in the Demänovská Valley (Liptov Region in Slovakia)].* *Věstník Státního Geologického ústavu*, 1, 2, 24–39 (in Slovak)

VOLKO-STAROHORSKÝ, J. 1927. *Vykopávky v jaskyni „Okne“ (Demänovská dolina, Liptov). Zpráva o nálezisku [Excavations in the Okno Cave, (Demänovská Valley, Liptov Region). Report on the site].* *Sborník Muzeálnej slovenskej spoločnosti*, 21, 24–39 (in Slovak)

VOLKO-STAROHORSKÝ, J. 1929. *Zpráva o výskume Jasovskej jaskyne [Report on research in Jasovská Cave].* *Sborník Muzeálnej slovenskej spoločnosti*, 23, 41–70 (in Slovak).

VOLKO-STAROHORSKÝ, J. 1941. *Ochrana prírodných pamiatok [Conservation of natural heritage].* *Archív slovenského múzea ochrany prírody a jaskyniarstva, fond J. Volko-Starohorský, Liptovský Mikuláš*, 53 p. (in Slovak)

# ABSTRACTS

## 23rd INTERNATIONAL CAVE BEAR SYMPOSIUM (ICBS 2017)

Liptovský Mikuláš, Slovakia,

October 4–7, 2017

### OPTIMISING DNA RECOVERY FROM CAVE BEAR BONES

Federica Alberti<sup>1</sup> – Javier Gonzalez<sup>1</sup> – Johanna L. A. Paijmans<sup>1</sup> –  
Nikolas Basler<sup>1</sup> – Michaela Preick<sup>1</sup> – Kirstin Henneberger<sup>1</sup> –  
Alexandra Trinks<sup>1</sup> – Guido Fritsch<sup>2</sup> – Thomas Hildebrandt<sup>2</sup> –  
Gernot Rabeder<sup>3</sup> – Susanne C. Münzel<sup>4</sup> – Ulrich Joger<sup>5</sup> –  
Michael Hofreiter<sup>1</sup> – Axel Barlow<sup>1</sup>

<sup>1</sup> Institute for Biochemistry and Biology, University of Potsdam, 14476  
Potsdam, Germany; falberti@uni-potsdam.de, j.gonzalez@uni-potsdam.de,  
paijmans.jla@gmail.com, nbasler@uni-potsdam.de,  
michaela.preick@uni-potsdam.de, kihenneb@uni-potsdam.de,  
Michael.hofreiter@uni-potsdam.de, axel.barlow.ab@gmail.com

<sup>2</sup> Leibniz Institute for Zoo and Wildlife Research (IZW), Alfred-Kowalke-Straße 17,  
10315 Berlin, Germany; fritsch@izw-berlin.de, hildebrandt@izw-berlin.de

<sup>3</sup> Department of Palaeontology, Geozentrum, University of Vienna, UZA II  
Althanstraße 14, A – 1090 Vienna, Austria; gernot.rabeder@univie.ac.at

<sup>4</sup> Institute for Archaeological Sciences, Archaeozoology, University of  
Tübingen, Rümelinstraße 23, 72070 Tübingen, Germany;  
susanne.muenzel@uni-tuebingen.de

<sup>5</sup> State Museum of Natural History, Postfach 3309, 38023 Braunschweig,  
Germany; Ulrich.Joger@snhm.Niedersachsen.de

The study of ancient genomes has greatly enhanced our understanding of evolutionary processes and population dynamics through time. Cave bears (*Ursus spelaeus* group) are an ideal candidate for genetic analysis. Modern molecular-genetics approaches applied to their rich fossil record have even allowed investigation of the population genomics of this extinct species. These efforts have been reliant on petrous bone samples, and some important evolutionary questions remain unsolved due to the unavailability of this specific sample type. Sequencing paleogenomes from samples other than the petrous bone is still extremely challenging due to the massive fraction of external contaminant DNA (~99% of total DNA molecules) typically associated with these samples. Obtaining even modest amounts of endogenous data thus requires greatly increased sequencing effort which incurs a parallel increase in sequencing costs. Here, we present a new sampling approach that we have developed to increase the relative endogenous DNA fraction by targeting specific bone or skeletal regions associated with low levels of contamination. The targeting approach has already led to substantial progress as the discovery of mammalian petrous bone as a source of pure endogenous DNA (Gamba et al., 2014; Pinhasi et al., 2015) with the difference that our method is highly consistent, reproducible, and more important, applicable across a wide range of bone types, ages and species. With this approach, new genomic data from cave bears have been produced that was not possible prior to the development of this method, allowing further investigations of the species' population dynamics. This discovery will greatly extend the potential to study ancient populations and species in the genomics era.

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### RECENT ADVANCES IN CAVE BEAR GENOMICS

Axel Barlow

Institute for Biochemistry and Biology, University of Potsdam, Karl-Liebknecht  
Straße 24-25, 14476 Potsdam, Germany; axel.barlow.ab@gmail.com

Cave bears have played a central role in ancient DNA research, and recovery of their mitochondrial sequences has provided many new insights on their biology, evolution and extinction. In 2013, at the 19th International Cave

Bear Symposium, I announced an ambitious project to sequence the complete nuclear genome of the cave bear. Although this undertaking has presented considerable challenges, our success has exceeded all expectations and, to date, we have recovered the nuclear genomes of twenty cave bears. New discoveries provided by these data have been frequent, and in many cases unexpected, including ancient hybridisation between cave bears and brown bears, relationships among cave bears contradicting that inferred previously using mitochondrial DNA, as well as relationships between Middle Pleistocene cave bears and their Late Pleistocene counterparts. Moreover, our established laboratory procedures now provide rapid sample processing with consistently high rates of success, providing the framework for future sequencing of hundreds of cave bears. Now our project is nearing completion, I look forward at new directions and priorities in the study of cave bear genomes. Although extinct for many tens of thousands of years, in the field of palaeogenomics, cave bears have an exciting future.

### OF FOXES AND HUMANS – AN ISOTOPIC STUDY ABOUT THEIR INTERACTION DURING THE UPPER PALEOLITHIC OF THE SWABIAN JURA (GERMANY)

Chris Baumann<sup>1</sup> – Dorothee G. Drucker<sup>2,3</sup>  
– Susanne C. Münzel<sup>1</sup> – Britt M. Starkovich<sup>1,3</sup>  
– Hervé Bocherens<sup>2,3</sup> – Nicholas J. Conard<sup>3,4</sup>

<sup>1</sup> Institut für Naturwissenschaftliche Archäologie, University of Tübingen,  
Rümelinstraße 23, 72070 Tübingen, Germany;

Chris.baumann@uni-tuebingen.de, susanne.muenzel@uni-tuebingen.de

<sup>2</sup> Institut für Geowissenschaften, Hölderlinstraße 12,  
72070 Tübingen, Germany

<sup>3</sup> Senckenberg Center of Human Evolution and Paleoenvironment, University  
of Tübingen, Rümelinstraße 23, 72070 Tübingen, Germany;

dorothee.drucker@senckenberg.de, britt.starkovich@senckenberg.de,  
herve.bocherens@uni-tuebingen.de, nicholas.conard@uni-tuebingen.de

<sup>4</sup> Institut für ältere Urgeschichte, Burgsteige 11, 72070 Tübingen, Germany

Humans occupied the cave sites of the Swabian Jura during the Aurignacian and Gravettian. Many remains of their hunting activities were found in these sites. Not only bones of large prey were recognized; in addition, bones from red and arctic foxes were deposited in the caves (Conard et al., 2013). Fox teeth were an important raw material for pendants during the Gravettian, but not the only sign of small carnivore usage by humans. Indeed, some of the fox bones from Hohle Fels showed human bite marks (Camarós et al., 2016; Fernández-Jalvo & Andrews, 2011; Saladié et al., 2013). Additionally, cut marks on fox bones from Geißenklösterle cave reflect the skinning and defleshing process of foxes. Therefore, upper Paleolithic humans did not only consume the meat of large mammals, but also the meat of small carnivores, such as foxes.

In general, most studies about interaction of humans with foxes are based on "classical" zooarchaeological methods (e. g. Fairnell & Barrett, 2006; Maher et al., 2011; Stahl, 2012; Yeshurun et al., 2009), which provide a good view on the human use of foxes, but they do not consider the symbiotic relationship between the two, and how foxes could have benefited from humans.

In the presented study, we analyzed the  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values from collagen of four arctic foxes (*Vulpes lagopus*) and three red foxes (*Vulpes vulpes*). With the isotopic data from related isotopic studies from the Swabian Jura during the Upper Paleolithic (e. g. Bocherens et al., 2011; Drucker et al., 2011a; Drucker et al., 2011b; Drucker et al., 2015; Münzel et al. 2014), it was possible to reconstruct the dietary spectrum of these foxes and place them within the Upper Paleolithic food-web.

We could reconstruct the anthropogenic resources that were accessible for small scavengers including foxes. The combination of both, the reconstructed anthropogenic resources and the paleo-diet of the analyzed foxes, allow us to build and test hypotheses on how, when and why foxes fed on the refuse left behind by the Upper Paleolithic inhabitants of the Swabian Caves. Within the framework of these hypotheses, we provide numerical estimates for the diet of foxes present in the Aurignacian and Gravettian faunal assemblages from Hohle Fels and Geißenklösterle and consider the syn- and diachronic variability in these data.

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## THE “SMOPAJ” FOSSIL COLLECTIONS OF THE PLEISTOCENE LARGE CARNIVORES

Tomáš Čeklovský

Slovak Museum of Nature Protection and Speleology, Školská 4, 031 01 Liptovský Mikuláš, Slovakia; tomas.cekvsky@gmail.com

Up to the present, the Slovak Museum of Nature Protection and Speleology in Liptovský Mikuláš (Slovakia) has owned 4,632 registered items within Palaeontological collections. Of this number, 768 items present the fossil material of four large carnivore taxa: *Ursus ex gr. spelaeus* (Rosenmüller, 1794), *Ursus arctos* (Linnaeus, 1758), *Crocota crocota spelaea* (Goldfuss, 1823) and *Panthera spelaea* (Goldfuss, 1810).

So far, these fossil remains have been found in the Upper Pleistocene sediments of 27 Slovak cave localities. The most important is especially one skull from Medvedia jaskyňa, Slovenský raj (The Bear Cave, Slovak Paradise) and the fossil record from Medvedia jaskyňa, Západné Tatry (The Bear Cave, Western Tatras). The skull from Slovenský raj belongs to a cave bear adult male and represents one of the largest skulls of the species in Slovakia (cranium length ~57 cm). The found fossils from Západné Tatry represent 70 % of the entire skeleton of a cave lion prime adult male, and it is one of the most complex and largest individuals of the species in Europe (cranium length ~45 cm).

Some fossil material of these carnivores has already been expertly analysed and the results have been published in scientific papers (e. g. Sabol, 2000, 2011).

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## THE EARLIEST OCCURRENCE OF *URSUS ARCTOS* IN THE MIDDLE PLEISTOCENE OF ITALY AND ITS COEXISTENCE WITH *URSUS DENINGERI* IN THE SITE OF FONTANA RANUCCIO (ANAGNI BASIN, CENTRAL ITALY)

Jacopo Conti<sup>1,3</sup> – Luca Bellucci<sup>2,3</sup> – Raffaele Sardella<sup>1,3</sup>

<sup>1</sup> Dipartimento di Scienze della Terra, Sapienza Università di Roma, P. le Aldo Moro, 5, 00185, Roma, Italy; jacopo.conti@uniroma1.it, raffaele.sardella@uniroma1.it

<sup>2</sup> Polo museale, Sapienza Università di Roma, P. le Aldo Moro, 5, 00185, Roma, Italy; luca.bellucci@uniroma1.it

<sup>3</sup> Paleofactory, Sapienza Università di Roma, P. le Aldo Moro, 5, 00185, Roma, Italy

The presence of *Ursus arctos* in the Middle Pleistocene of Europe is relatively well documented even if its origin and evolution is still debated (Rabeder et al., 2010). The occurrence of the brown bear in Italy is less documented and unclear. *Ursus arctos* is diffused in northern and central Italy in the late Middle-Late Pleistocene but, even if rare, this species reached the southern Italy and is documented in Sicily too (Marra, 2003).

In Italy, during the Middle Pleistocene two other groups of ursids occur: 1) the rare and small *Ursus thibetanus*, 2) the cave bear lineage.

Cave bears are represented in the early Middle Pleistocene (Galerian) assemblages by *Ursus deningeri* that has been found at Ceré and Visogliano, Isernia La Pineta, and Fontana Ranuccio (Rossi & Santi, 2011; Falguères et al., 2008; Coltorti et al., 2000; Sardella et al., 2006). The occurrence of the true cave bear *Ursus spelaeus* in the late Middle Pleistocene has been considered by (Gliozzi et al., 1997) as the bioevent characterizing the beginning of the Aurelian Mammal Age.

The site of Fontana Ranuccio (Frosinone, central Italy) was discovered in the late 1970s by Italian Institute of Human Palaeontology (ISIPU) researchers. The very rich faunal assemblage of Fontana Ranuccio, dated approximately to 0.45 My (Biddittu et al., 1979; Muttoni et al., 2009), consists of more than 20,000 faunal remains, besides four human teeth (Rubini et al., 2014) and several lithic and bone artefact. The detailed analysis of this material is still in progress.

Here we present the revision of the *Ursus* material of Fontana Ranuccio that has been chosen as Faunal Unit for the late Galerian. The material consists of five isolated teeth: two first upper molars, the fourth lower premolar, the second lower molar and the third lower molar. These were described and compared with other specimens of *U. arctos*, *U. deningeri*, *U. spelaeus* and *U. thibetanus* from Middle and Late Pleistocene Italian localities (Capasso-Barbato et al., 1990 and references therein, Crégut-Bonnoure, 1997).

The morphological analyses suggest that in the Fontana Ranuccio assemblage two different species occurred: *Ursus arctos* and *Ursus deningeri*. In order to better analyze the occlusal surface, we produced also 3D models of the selected specimens thanks to the photogrammetry using Agisoft Photoscan and Cloud Compare software.

Azzaroli (1983) reported in a faunal list about Fontana Ranuccio the occurrence of *Ursus arctos* but not of *Ursus deningeri* without any description of the fossils. After the analysis of the fossil teeth stored at ISIPU labs in Anagni we are able to confirm the occurrence at Fontana Ranuccio of both the species.

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- <sup>1</sup> *Institute for Archaeological Sciences, University of Tübingen, Rümelinstraße 23, D-72070, Tübingen, Germany; joscha.gretzinger@student.uni-tuebingen.de, ella.reiter@uni-tuebingen.de, ch.urban@student.uni-tuebingen.de, verena.schuenemann@ifu.uni-tuebingen.de, johannes.krause@uni-tuebingen.de*  
<sup>2</sup> *Fachbereich Geowissenschaften, Biologie, University of Tübingen, Hölderlinstr. 12, 72074 Tübingen, Germany; herve.bocherens@uni-tuebingen.de*  
<sup>3</sup> *Senckenberg Center for Human Evolution and Palaeoenvironment, University of Tübingen, Tübingen, Germany*  
<sup>4</sup> *Department of Geology and Palaeontology, Faculty of Natural Sciences, Comenius University, Ilkovičova 6, 842 15 Bratislava, Slovakia; sabol@fns.uniba.sk*  
<sup>5</sup> *Max Planck Institute for the Science of Human History, Jena, Germany; krause@shh.mpg.de*

The subsistence of extinct cave bear *Ursus spelaeus* sensu lato was research focus of numerous interdisciplinary studies and so far, all cave bear populations studied were referred to as virtually pure herbivores (e. g. Bocherens et al., 2011; Krajcarz et al., 2016). But yet, in the last years results of isotopic studies of Romanian samples were published, disagreeing with this assumption and postulating dietary flexibility based on nitrogen ( $\delta^{15}\text{N}$ ) isotopic values, but not carbon ( $\delta^{13}\text{C}$ ) isotopic values (e. g. Robu et al., 2013). However, until now there was no specimen among European Pleistocene cave bears showing both high  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values characteristic of carnivorous or omnivorous diet.

The focus of this analysis is a bear long bone excavated at Prepošská Cave in Prievidza, western Slovakia, preliminary dated to the Middle Weichselian, featuring unique high carbon and nitrogen isotopic compositions similar to those of mammoth steppe predators like wolf *Canis lupus* or cave lion *Panthera spelaea* (Bocherens et al., 2013).

Using a silica-based extraction protocol (Dabney et al., 2013) in combination with aDNA library preparation (Meyer & Kircher, 2010; Kircher et al., 2012) and in-solution target enrichment (Maricic et al., 2010) we were able to reconstruct the full mitochondrial genome and compare it to 69 published Eurasian (Knapp et al., 2009; Fortes et al., 2016) as well as 39 new Spanish, Serbian, Swiss, French and German bear sequences ranging from Middle Pleistocene to the Lateglacial.

Phylogenetic reconstructions indicate that the bear sequence from Prepošská Cave forms together with Bulgarian and Austrian brown bear specimens a sister lineage to a published Pleistocene samples from France, belonging to clade 1 in the western lineage (Taberlet & Bouvet, 1994), within the species *Ursus arctos*.

Nevertheless, overall it is shown that there is still no evidence for carnivorous-like isotopic signatures in eastern European cave bears. Further analysis of the recently obtained Mitogenomes from Western Europe and the Balkans will shed light on the biogeography of *Ursus spelaeus* sensu lato haplogroups during the Late Pleistocene.

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## INSIGHTS INTO BEAR BEHAVIOUR FROM aDNA DATA

**Gloria G. Fortes<sup>1,2,3,9</sup> – Aurora Grandal-d’Anglade<sup>3</sup> – Ben Kolbe<sup>1</sup> – Daniel Fernandes<sup>4</sup> – Ioana N. Meleg<sup>5</sup> – Ana García-Vázquez<sup>3</sup> – Ana C. Pinto-Llona<sup>6</sup> – Silviu Constantin<sup>5</sup> – Trino J. de Torres<sup>7</sup> – Jose E. Ortiz<sup>7</sup> – Christine Frischau<sup>8</sup> – Gernot Rabeder<sup>8</sup> – Michael Hofreiter<sup>1,9</sup> – Axel Barlow<sup>1,9</sup>**

<sup>1</sup> *Institute for Biochemistry and Biology, University of Potsdam, Karl-Liebknecht Straße 24-25, 14476 Potsdam, Germany; ggfortes14@gmail.com, Michael.hofreiter@uni-potsdam.de, axel.barlow.ab@gmail.com*

<sup>2</sup> *Department of Biology and Evolution, University of Ferrara, 44121 Ferrara, Italy*

<sup>3</sup> *Instituto Universitario de Xeoloxía, Universidade da Coruña, Campus de Elviña s/n, 15081 A Coruña, Spain; xeauroara@udc.es*

<sup>4</sup> *School of Archaeology and Earth Institute, University College Dublin, Dublin Belfield, Dublin 4, Ireland*

<sup>5</sup> *“Emil Racoviță” Institute of Speleology, Frumosa 31, R-010986, Bucharest, Romania; karstology@gmail.com*

<sup>6</sup> *Instituto de Historia, Consejo Superior de Investigaciones Científicas, 28037 Madrid, Spain*

<sup>7</sup> *Depto de Ingeniería Geológica y Minera, Universidad Politécnica de Madrid, 28003 Madrid, Spain; trinidad.torres@upm.es, joseeugenio.ortiz@upm.es*

<sup>8</sup> *Institute of Palaeontology, University of Vienna, Althanstraße 14, A-1090 Vienna, Austria; christine.f@gmx.at, gernot.rabeder@univie.ac.at*

<sup>9</sup> *Department of Biology, The University of York, YO10 5DD, United Kingdom*

Although ancient DNA has revolutionised the study of extinct species and populations, inferences on their behaviour and sociality have been rare. In this study, we investigate the complete mitochondrial genomes of extinct Late Pleistocene cave bears and middle Holocene brown bears that each inhabited multiple geographically proximate caves in northern Spain. In cave bears, we find that each cave almost exclusively contains a unique lineage of closely related haplotypes, suggesting that cave bears returned to the caves within which they were born for hibernation. In contrast, we do not find such an association in brown bears indicating an important behavioural difference between these two species. We argue that this behavioural difference could represent a key factor explaining the extinction of the cave bear and the survival of the sympatric brown bear at a time in which competition for caves between bears and humans was likely intense. Our study demonstrates the potential of ancient DNA to uncover patterns of behaviour and sociality in ancient species and populations, even those that went extinct many tens of thousands of years ago.

## GENETIC ANALYSIS OF A CAVE BEAR-MORPHOTYPE SPECIMEN FROM PREPOŠSKÁ CAVE, SLOVAKIA FEATURING CARNIVOROUS-LIKE ISOTOPIC SIGNATURE

**Joscha Gretzinger<sup>1</sup> – Ella Reiter<sup>1</sup> – Christian Urban<sup>1</sup> – Hervé Bocherens<sup>2,3</sup> – Martin Sabol<sup>4</sup> – Verena J. Schuenemann<sup>1,3</sup> – Johannes Krause<sup>1,3,5</sup>**

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## MORAVIAN KARST CAVE LION – POPULATION ON THE CROSSROAD, WHAT WE KNOW ABOUT IT?

Vlastislav Káňa<sup>1,2</sup> – Martina Robličková<sup>3</sup>

<sup>1</sup> Masaryk University, Faculty of Science, Department of Geological Sciences, Kotlářská 2, 611 37 Brno, Czech Republic; kanabat@email.cz

<sup>2</sup> Muzeum Blanenska, p. o., Zámek 1, 678 01 Blansko, Czech Republic

<sup>3</sup> Moravian Museum, Historical Museum, Anthropos Institute, Zelný trh 6, 659 37 Brno, Czech Republic; mroblickova@mzm.cz

The first records of large felid bones, possible to be classified now as the cave lion (*Panthera spelaea*, Goldfuss 1810), in sediments of Moravian Karst caves origin from the second half of 19th century and then mentioned as the description of private collections items (Kříž & Koudelka, 1900), where Sloupské Caves represent the main locality. The first steps in paleontological, stratigraphical and taphonomical description follow at the beginning of 20th century by Szombathy, Knies, Kříž (Musil, 2002). Some next localities were set as “lion-dwelling” caves, Výpustek Cave above all. Some other, smaller in length and space, were established as cave lion bones finding sites, Balcarka Cave, Kateřinská Cave, Pod Hradem Cave, Kůlna, Švédův Stůl Cave, Pekárna, Jáchymka Cave. Two main shapes of lion bone in-cave localities were established: “natural” ones (without the influence of man) and “human settlements” with prey animals bone remains (Kůlna and Pekárna Caves above all). The most of old collections disappeared in time, excluding samples of Szombathy, Knies and some small ones, mostly from Výpustek Cave (contemporary preserved in NHM Wien and MZM Brno collections). The richest sites were almost completely emptied, as the bone sediments were mined for industrial use, milled to use in refinery or used as a fertilizer along with phosphates. Only small number of finds was saved: long bones, well preserved jaws, metapodials (crashed bones and fragments were thrown out), cranial bones stayed ignored or reconstructed without care. The “most interesting” finds (largest ones, adult male metapodials, vertebrae and jaws for example) were collected first. The collections of finds from this period have stayed unrepresentative at all.

Widely managed excavations and paleontological/speleoarchaeological research within the area of Moravian Karst Protected Landscape Area (established in 1952) in the second half of 20th century yielded new collections from traditional sites as well as from the new ones. They set first indirect stratigraphical or archaeological datation between 50 ka BP and 12 ka BP for archaeological finds in Kůlna Cave and other (Musil, 2002; Valoch, 2011). However, these finds were entangled with hunting activity of either Neanderthal and Magdalenian inhabitants of Moravian Karst caves. Also the datation from one of the most important sites – Švédův stůl stays indirect and unsharp, as the precise stratigraphical position of cave lion bones stays unknown or arguable. Two kinds of non-human in-cave bone assemblage were recognized that time: 1) large, bone rich caves with high dominance of the cave bear (*Ursus ex. gr. spelaeus*), named as “Bear Caves” (Musil, 1959, 1960), represented by Sloupské Caves and Pod Hradem Cave in the northern part of Moravian Karst and by Výpustek Cave and Barová Cave in the central part (Křtinské – Josefovské Valley), 2) smaller localities, short caves or cavities with varied fauna including cave hyena (*Crocota c. spelaea*), brown bear (*Ursus arctos*) and prey bone remains, mostly rhinoceros, horse, reindeer, red deer, smaller ungulates and rodents (*Coelodonta antiquitatis*, *Equus* sp., *Rangifer tarandus*, *Cervus* sp., etc.). These smaller caves changed in time from the hyena den (Diedrich, 2011; Robličková, 2011) to small bear wintering site, used by animals often until recent.

Newly explored localities also negated that classification, as the medium-size caves (tens to hundreds of meters), showed either hibernating or occasional den use for more species of predators, scavenger and mostly herbivorous bears. Large hibernacula like Sloupské Caves or Výpustek consist then of several self-standing habitats, where large cave bear hibernacula occurs in the most in-cave part of the underground system. Changes in time could be very frequent and periods of bear inhabitation repeated (Seitl, 1998). The hypothesis, that some predation and/or scavenging on hibernating bears was the important reason for cave lion to get inside these cave systems was set after all. Also the theory of interspecific conflicts in cave lion, hyenas and bears based on finds of such assemblages of bones from in-cave sediments, along with bite mark or traces research and comparison (Diedrich, 2011).

Altogether, fourteen caves in Moravian Karst yielded cave lion bones studied by authors until now. The number of discovered, yet unpublished or newly described varies from one (Pod Suchdolskou Cave) to app. 260 (Barová Cave, this research is mentioned by authors in the other abstract on 23rd

ICBS). The available datation shows, that large felid bones from Moravian Karst caves (without presence of man) belong to the period from 50 ka BP to 45–35 ka BP (directly Barová Cave, indirectly Výpustek Cave, Pod Hradem Cave, Sloupské Caves). We expect further datation from Barová Cave and some others. Faunal assemblages suggest that the caves hosted the same or very similar association. As the period was one of changing in the history of last glaciation cave lion population (Barnett et al., 2011), including east-west migrations or re-inhabiting of the new areas, the morphometrical, molecular and palaeoecological data are important.

The preliminary results of morphometrical analysis (now in progress) show high variability in postcranial and cranial skeleton, in body mass and shape. Cranial characteristics (sensu Sabol et al., 2016) suggest the intermedial state between western and eastern Eurasian populations, sadly the preservation state of the bone material is unfavourable, artificial reconstructions wiped most of characters away or made non-realistic ones. This is the situation in all the skull material from Výpustek Cave (with one exception) and Sloupské Caves. The most recent finds from Barová Cave, although well preserved) show damages, that complicate the comparison, preliminarily they show intermedial characters, too. The shape of mandibular characteristics clusters Moravian Karst finds together with assemblages from archaeological sites Předmostí, dolní Věstonice and Pavlov and differs deeply from that in extant lion (*Panthera leo*), being closer to *Panthera fossilis*. In the light of that, former designation as *Panthera leo* for some cave samples stays invalid.

The ecology of Moravian Karst cave lion populations depend on prey offer, which had to be rich in the period of karst find datation. Sadly, no complex collection covering both predator and prey bone remains from one locality exist from Moravian Karst, with one exception: Barová Cave. The locality yielded bone remains of at least 8 individual (MNI 8), the total number of bones still grows, as the excavation continues. The remains belong to 3 males, 3 females, the sex of last two individuals is uncertain; as they are represented by single poorly preserved bones, presumably here is one female and one male, so the sex ratio is here 1:1. The most preserved is the young, subadult female here, represented with 74 bones and fragments. Two female individuals represent adult ones (presumed age 3 and 5 yrs.). One male individual here is presumably fully adult, two individuals show the age past the prime (9.5–11 yrs., see the other paper of the authors). Pathological bones suggest the survival strategy in society (Robličková & Káňa, 2013). The bite marks and traces on prey bones inside the cave suggest that lions at least occasionally entered the cave to prey or scavenge on wintering bears. The second reason to entry the cave was the shelter here. Localities in Moravian Karst did not reveal any bone remains of newborn or foetal individual yet; juvenile individuals are known (Výpustek Cave). We do not presume that cave lions used the caves as the nursery, at least in Moravian Karst. The bite marks and traces on the cave lion bones do not allow us to state the scavenger here, the comparison with recent traces suggests, that such bite marks could be even the result of casual cannibalism or post mortal bone cracking. The traces on bones from Barová Cave (and some rare from other localities) lead us to suspect, that there were no (or rare) interspecific conflict between predators or scavengers. Predator – prey relations between lions and bears probably occurred more frequently.

Moravian Karst cave lion population is one of the most in-time and in-space coherent in Europe. The specific environment of Moravian Karst valleys, water springs and plateaus supported numerous prey animals on the crossroad of migration trails. The in-cave sediments preserved here whole-population sample, the consequence of unsuccessful predation in large bear wintering caves, the remains of temporary shelter in the small ones. The population here shows intermedial characters and high variability in many ways. Cave lions dwelling or hunting in caves of Moravian Karst preceded the ones, which were hunted or slaughtered by gravettian or Magdalenian people.

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## A NEW HYENA CAVE IN ST. MARGARETHEN (BURGENLAND, AUSTRIA)

Nicole Kanta<sup>1</sup> – Nadja Kavcik-Graumann<sup>2</sup> – Julius Lindenbauer<sup>1</sup> – Martina Pacher<sup>1</sup> – Gernot Rabeder<sup>1</sup>

<sup>1</sup> Institute of Palaeontology, University Vienna, Althanstraße 14, A-1090, Vienna, Austria; ju-li@gmx.at, martina.pacher@univie.ac.at, gernot.rabeder@univie.ac.at

<sup>2</sup> Department of Cognition Biology, University Vienna, Althanstrasse 14, A-1090 Vienna, Austria; nadja.kavcik@univie.ac.at

The material represents the last remains of a former larger assemblage found in 1979 in the well-known quarry of St. Margarethen, Burgenland (Fig. 1). Unfortunately several remains have been sold to tourists over the years, leaving only a small part of a once more numerous assemblage. Finally, the local collector Josef Gossy informed the Landeamt für Denkmalkunde, Burgenland and in 2015 a team from the Austrian Academy of



Fig. 1. Map of fossil hyena caves in Austria: 1 – Schusterlucke, 2 – Teufelslucke near Eggenburg, 3 – Bärenhöhle von Winden, 4 – Hyänenspalte of St. Margarethen, 5 – Dripstone cave of Flatz, 6 – Klein St. Paul, 7 – Dripstone cave of Griffen.

Sciences respectively Institute of Palaeontology, Vienna consisting of Martina Pacher, Marc Händel and Ulrich Simon could visit the site. Its exact locality is not known but must be near the former tavern of the quarry, where a large and heavily overgrown debris cone is still visible. According to Josef Gossy the remains were found by workers in debris cone, caused by mining, while the modern cone further increased by ongoing



Fig. 2. Fragment of right maxillare with P4 and P3 dext. of *Crocuta crocuta spelaea* from Hyänenspalte of St. Margarethen. Photo: R. Gold

mining activity and erosion. Nonetheless, the remains must have come from former cave and/or shaft, structures which are common in this quarry. The new hyena site was named “Hyänenspalte von St. Margarethen”. The fossil remains were metrically and morphologically analyzed in two Baccalaureus thesis at the Institute of Palaeontology at the University of Vienna. The material included cave hyena (Fig. 2), brown bear, cave bear, woolly rhinoceros, onager (Fig. 3), wild horse, red deer, capricorn and steppe bison. Some of the bone fragments show gnawing marks that are probably caused by hyenas. The faunal composition is typical for a Late Pleistocene hyena cave. Particularly interesting are the well-preserved remains of an onager, which recent relatives are restricted to dry areas in subtropical and tropical conditions. Previously the taxonomic status of this “European wild ass” was *Equus hydruntinus*.



Fig. 3. Fragment of mandible sin. (P3-M2) of *Equus hemionus hydruntinus*, occlusal from Hyänenspalte St. Margarethen. Photo: R. Gold

## THE CAVE BEARS FROM SCHLENKEN-DURCHGANGSHÖHLE (SCHLENKEN PASSAGE CAVE, OSTERHORN MASSIF, SALZBURG, AUSTRIA)

Tatjana Knaus<sup>1</sup> – Bernd Schopf<sup>1</sup> – Christine Frischauf<sup>1</sup> – Nadja Kavcik-Graumann<sup>2</sup> – Gernot Rabeder<sup>1</sup>

<sup>1</sup> Institute of Palaeontology, University Vienna, Althanstraße 14, A-1090, Vienna, Austria; tatjana.knaus@gmx.at, christine.f@gmx.at, gernot.rabeder@univie.ac.at

<sup>2</sup> Department of Cognition Biology, University Vienna, Althanstraße 14, A-1090 Vienna, Austria; nadja.kavcik@univie.ac.at

Schlenken-Durchgangshöhle (Fig. 1) is an Alpine bear cave located in the eastern ridge of the Schlenken (1649 m), community Bad Vigaun, about 15 km south of the city of Salzburg. During 20 years of excavation under the leadership of Kurt Ehrenberg and Karl Mais plenty of cave bear material could be collected. However, the material was not accessible for scientific research until the present time.

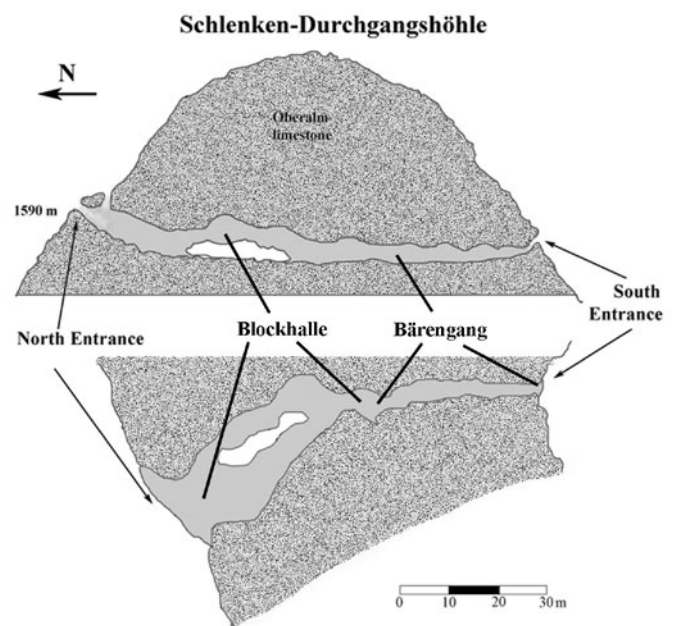


Fig. 1. Cross section and ground plan of Schlenken-Durchgangshöhle.

As a first step in the scientific processing of the material, statistically meaningful amounts of the teeth and the metapodia were inventoried, measured and morphologically analyzed.

Only small bones like the metapodia and teeth could be found in a whole, bigger bones were only fragmentary. In order to standardize values for a better comparability, mean values and morphological indices (teeth) of *Ursus ingressus*, which inhabits the Gamssulzen Cave, were used as reference for the material of the Schlenken-Durchgangshöhle.

Comparisons of our data with values obtained from Alpine cave faunas from different altitudes allowed taxonomic determination of *U. spelaeus eremus*, using morphological indices and ratios.

This determination is mainly due to the large-scale correlation of teeth and metapodia (LHD-diagram) and the morphological differences of the second hypodermoid (enthypoconid index).

The incisors, as well as the canines were then examined for grinding marks to draw conclusions on food and climate. Due to the enormous number of grinding marks on the canines caused by pulling off grass, it can be assumed that the cave bears of Schlenken-Durchgangshöhle were forced to use grass as a food source, which suggests a dry local clima.

## COLLAGEN-COLLAGEN PREY-PREDATOR ISOTOPIC ENRICHMENT – A STUDY OF A SUBFOSSIL RED FOX DEN

Maciej T. Krajcarz<sup>1</sup> – Magdalena Krajcarz<sup>1,2</sup> –  
Hervé Bocherens<sup>3,4</sup>

<sup>1</sup> Institute of Geological Sciences, Polish Academy of Sciences, Research Centre in Warszawa, Twarda 51/55, 00-818 Warszawa, Poland; mkrajcarz@twarda.pan.pl

<sup>2</sup> Institute of Archaeology, Nicolaus Copernicus University in Toruń, Szosa Bydgoska 44/48, 87-100 Toruń, Poland; magkrajcarz@twarda.pan.pl

<sup>3</sup> Fachbereich Geowissenschaften, Paläobiologie (Biogeologie), Universität Tübingen, Hölderlinstr. 12, 72074 Tübingen, Germany; herve.bocherens@uni-tuebingen.de

<sup>4</sup> Senckenberg Center for Human Evolution and Palaeoenvironment (HEP), Universität Tübingen

Stable isotope analysis found number of applications in ecological and palaeoecological study, one of which is to evaluate quantitatively the contribution of different prey in the diet of predators (e. g., Hilderbrand et al., 1996; Bocherens et al., 1995, 2005, 2011, 2015, 2016; Fox-Dobbs et al., 2007; Guiry, 2012; Yeakel et al., 2013; Bocherens, 2015; Wiśning et al., 2015). The main parameter used in isotopic trophic ecology is the Trophic Enrichments Factor (TEF, i. e., the difference in isotopic ratio between consumer tissues and diet). TEF values can be derived from specimens subjected to experimental feeding in which all dietary items can be monitored for their isotopic composition, or from free-ranging specimens which dietary behaviour is well monitored (Caut et al., 2009). TEFs between diet and animals may be measured for different tissues of animal body (e. g., Roth & Hobson, 2000; Voigt et al., 2014). In palaeoecological studies the bones and teeth are the only tissues preserved. Unfortunately, very few studies of modern vertebrates include bone collagen, probably due to difficulties in sampling that may not be conducted on living animals. The direct collagen-collagen TEF is however a key parameter for fossil material and needs to be well constrained in order to make the palaeodietary models reliable. Uncertainties in the values of TEFs may lead to errors in the calculation of prey proportions and therefore efforts should be made to improve the determination of these factors. For  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values of bone collagen, the collagen-collagen TEFs have been provided either as average values or ranges of values (Schoeninger & DeNiro, 1984; Szepanski et al., 1999; Bocherens & Drucker, 2003; Fox-Dobbs et al., 2007).

Studies of TEF in the wild are difficult as they require access to both the tissues of predator and tissues of its prey, and knowledge on the participation of particular prey in the diet. Especially unique and valuable situation is when we have directly access to these specimens of prey that were hunted and eaten by a given predator. Usually such situations are rare and researchers may only analyse other specimens in the population of prey species than those actually consumed by the analysed predators. Only occasionally we find the remains of long-term predator's nourishing in its natural environment, and this was the case of red fox den in Potok-Senderki, Poland (Krajcarz & Krajcarz, 2014). That site offers an unique opportunity for isotopic study of bone assemblage representing the population of fox and wide spectrum of its prey. Due to the relatively great number of remains, the participation of particular prey species in the predator's diet can be estimated on the basis of bone representation. This provides an opportunity to investigate the bone collagen of predator population together with the bone collagen of specimens that were eaten by the studied predators. In addition, the presence of young and adult individuals of fox allows us to study the difference in isotopic enrichment according to the age class of a predator.

The objective of this study was to report  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  collagen data for both wild-living red foxes and their prey measured for subfossil bone accumulation. We use these data to calculate a prey-predator collagen-collagen TEF.

The research material includes 15 bones of red fox (*Vulpes vulpes*), both of adult, subadult and juvenile individuals; as well as 60 bones of fox's prey, including adult (domestic chicken, common pheasant, domestic goose, hooded crow, common kestrel, cat, European badger, European hare, domestic

rabbit and roe deer) and juvenile individuals (roe deer, red deer, wild boar or domestic pig, and European hare or domestic rabbit). All bone specimens were chosen from the collection from Potok-Senderki, stored in the Institute of Geological Sciences, Polish Academy of Sciences (Warsaw, Poland). Only the bones identifiable to species or genus level, large enough to ensure the sufficient amount of collagen and representing as many different individuals as possible, were chosen. The isotopic measurements were performed on the purified collagen (well-established protocols by Ambrose, 1990; Bocherens et al., 1997) at the geochemical unit of the Geoscience Faculty at the University of Tübingen (Germany), using an elemental analyser NC 2500 connected to a Thermo Quest Delta+ XL mass spectrometer.

We used four taphonomic indexes to quantify the input of particular prey species on the total biomass in fox diet: NISP (number of identified specimens), MNI (minimum number of individuals), weight of bone (a total weight of dry remains), and weight of edible parts (assumed mass of body parts connected to the preserved remains that were edible, calculated according to the method by Reitz & Wing, 2008).

The measured  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values of the fox collagen, both of adult, subadult and juvenile animals, are higher than bone collagen of most of the prey taxa (Fig. 1). This difference clearly indicates the presence of isotopic trophic enrichment in foxes. TEFs values calculated for adult and subadult foxes ranged from 0.84 ‰ to 1.28 ‰ for  $\delta^{13}\text{C}$  and from 2.07 ‰ to 3.61 ‰ for  $\delta^{15}\text{N}$ , according to different taphonomic indexes used to estimate the mean values for prey.

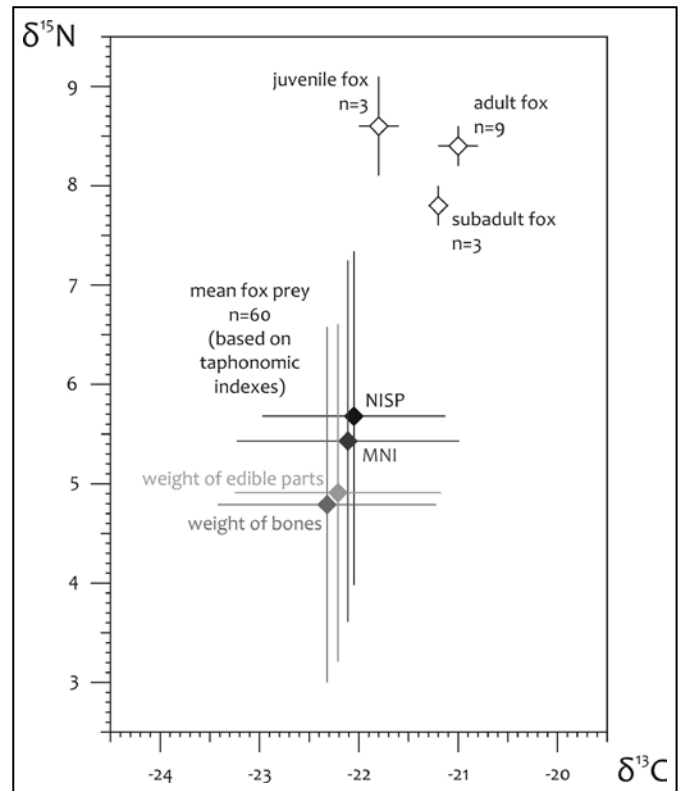


Fig. 1. Means (diamonds) and standard deviations (lines) for isotopic signature of foxes and their prey from the subfossil fox den in Potok-Senderki.

The main conclusion of the presented study is that red fox exhibits collagen-collagen TEF similar to that shown by wolf and lynx (Szepanski et al., 1999; Bocherens & Drucker, 2003; Fox-Dobbs et al., 2007) and used in palaeoecological studies (TEF ca. 0.8–1.3 ‰ for  $\delta^{13}\text{C}$  and 3–5 ‰ for  $\delta^{15}\text{N}$ , e. g., Bocherens, 2015; Bocherens & Drucker, 2003; Bocherens et al., 2015; Wiśning et al., 2015). This suggests that TEF values for terrestrial mammalian carnivores are probably universal (are not species relevant) and may be transposed to other species, including extinct ones.

This new data will provide important information for interpreting stable isotope fractionation in terrestrial food webs and will allow more accurate use of isotopic signal measured in fossil mammalian bones to reconstruct ancient trophic relationships.

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## INTRA-INDIVIDUAL AND INTER-SEX ISOTOPIC SIGNATURE ( $\delta^{13}\text{C}$ , $\delta^{15}\text{N}$ ) OF CAVE BEAR DENTINE COLLAGEN

Magdalena Krajcarz<sup>1,2</sup> – Maciej T. Krajcarz<sup>2</sup> – Piotr Wojtal<sup>3</sup> – Hervé Bocherens<sup>4,5</sup>

<sup>1</sup> Institute of Archaeology, Nicolaus Copernicus University in Toruń, Szosa Bydgoska 44/48, 87-100 Toruń, Poland; magkrajcarz@twarda.pan.pl

<sup>2</sup> Institute of Geological Sciences, Polish Academy of Sciences, Research Centre in Warszawa, Twarda 51/55, 00-818 Warszawa, Poland; mkrajcarz@twarda.pan.pl

<sup>3</sup> Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Sławkowska 17, PL-31016 Kraków, Poland; wojtal@isez.pan.krakow.pl

<sup>4</sup> Fachbereich Geowissenschaften, Paläobiologie (Biogeologie), Universität Tübingen, Hölderlinstraße 12, 72074 Tübingen, Germany; herve.bocherens@uni-tuebingen.de

<sup>5</sup> Senckenberg Center for Human Evolution and Palaeoenvironment (HEP), Universität Tübingen, Germany

Carbon and nitrogen isotopic signatures of fossil animal tissues have been used for decades as a useful tool for reconstructing paleoclimate, paleoenvironment and dietary habits (e. g., DeNiro & Epstein, 1978; Ambrose & DeNiro, 1986; Bocherens et al., 1994, 2011; Hilderbrand et al., 1996; Stiner et al., 1998; Vila Toaboda et al., 2001; Drucker et al., 2011; Richards et al., 2008; Chritz et al., 2009; García García et al., 2009). Among Pleistocene mammals, the cave bear was the first extinct species for which stable isotopes were used to document diet (Bocherens et al., 1991). However, bears are among the most difficult species concerning the ecological reconstructions based on isotopes. It is because bears use to hibernate, and the physiological effects of dormancy on the isotopic signal recorded in tissues must be taken in consideration. These effects are crucial in case of diet-related studies, as animal body metabolises the fat reserves during hibernation instead of normal feeding–excretion (Nelson et al., 1975). Hibernation may therefore produce an isotopic signal overlapping the warm-season diet-related signature (Fernández-Mosquera et al., 2001).

It is known that the bone records the long-term isotopic signature of body and usually represents the generalized isotopic signal from several years (Hindelang et al., 2002; Huja & Beck, 2007). Due to that, the bone cannot be used to detect the details of the isotopic history of an animal, neither to compare the impact of physiology and ecology on the isotopic signature during life. Teeth however record the isotopic signal in another way than bones. It is known that tooth reaches its definitive volume after several years into the lifetime of an animal. During life, the layers of dentin are accumulated inside the pulp cavity, resulting in diameter decreasing. In ursid canines, the dentin layers are deposited progressively toward the pulp cavity interior, sealing almost the entire cavity in old specimens (Torres & Garcia, 1997; Hillson, 2005). Dentin in canines is accumulated in concentric rings, what creates an opportunity to derive the information on the isotopic changes during animal lifespan via the sequence sampling across the rings. Because of the periodic deposition of dentin and its potential to record subsequent years of life, authors decided to examine the inner isotopic variability of this tissue.

The main objective of the study was to track the  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  signature in cave bear teeth in order to determine changes of isotopic signal during lifespan of cave bear and to check the possible differences of isotopic intra-tooth variation in both sexes. In the study we used 6 cave bear canines (3 of males and 3 of females) from Nietoperzowa Cave (southern Poland). All teeth were radiocarbon dated to around 35–46 ky (Krajcarz et al., 2017). The method of sex determination was based on morphometric discrepancy between sexes in bears as reported by Kurtén (1955). The isotopic measurements were performed on the purified collagen (protocols by Ambrose, 1990 and Bocherens et al., 1997) at the geochemical unit of the Geoscience Faculty at the University of Tübingen (Germany), using an elemental analyser NC 2500 connected to a Thermo Quest Delta+ XL mass spectrometer.

The measured  $\delta^{13}\text{C}$  values of dentine collagen sampled across the canines gave very consistent results among samples, from -23.2 to -21.4 ‰. The values for  $\delta^{15}\text{N}$  ranged from 1.5 to 7.0 ‰. The highest values of  $\delta^{15}\text{N}$  were measured both in case of male and female teeth. The isotopic signature of  $\delta^{13}\text{C}$  within tooth of one individual shows small variation during life, however a weak growing trend toward the tooth interior can be observed (Fig. 1) in each studied individual. The intra-individual record of  $\delta^{15}\text{N}$  is more variable. Among studied teeth, no sex-related pattern of  $\delta^{13}\text{C}$  or  $\delta^{15}\text{N}$  distribution or absolute values was observed. Correlative analysis of C and N isotopic values in the whole set of samples reveals a weak negative correlation ( $R^2 = 0.5$ ) between  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ : the samples with higher  $\delta^{13}\text{C}$  exhibit lower  $\delta^{15}\text{N}$  values. We cannot exclude some ecological (dietary) causes of this relationship; how-

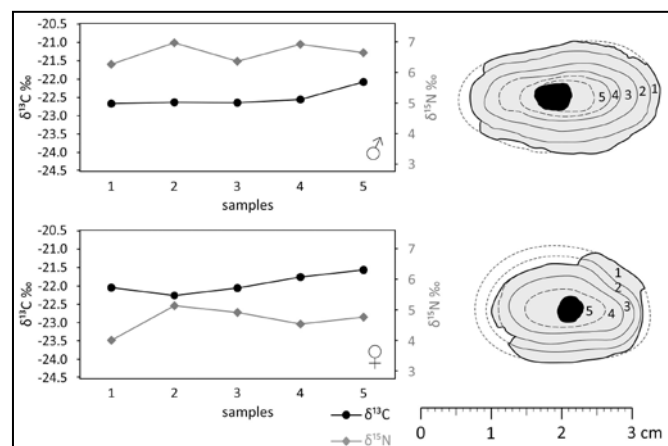


Fig. 1. The exemplary isotopic signatures for subsequent samples of cave bear dentine measured for male and female canine. Schematic cross-sections show the position of samples in the root.



ever the herbivory-carnivory drifts usually give the same direction of C and N isotopic shift (Bocherens, 2015). The observed pattern of negative  $\delta^{13}\text{C}/\delta^{15}\text{N}$  correlation is similar to physiological influence of hibernation on the isotopic composition of tissues (Nelson et al., 1975; Fernández-Mosquera et al., 2001), expected to cause the depletion in  $^{13}\text{C}$  due to mobilisation of fat resources and relative increase in  $^{15}\text{N}$  due to urine recycling.

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## POST-DEPOSITIONAL BONE DESTRUCTION IN CAVE SEDIMENT – A CASE OF LOWER WEICHSELIAN CAVE BEAR STRATA IN BIŚNIK CAVE, POLAND

Magdalena Krajcarz<sup>1,2</sup> – Maciej T. Krajcarz<sup>2</sup>

<sup>1</sup> Institute of Archaeology, Nicolaus Copernicus University in Toruń, Szosa Bydgoska 44/48, 87-100 Toruń, Poland; magkrajcarz@twarda.pan.pl

<sup>2</sup> Institute of Geological Sciences, Polish Academy of Sciences, Research Centre in Warszawa, Twarda 51/55, 00-818 Warszawa, Poland; mkrajcarz@twarda.pan.pl

Accumulations of animal bones are abundant in cave sediments, and reasons for deposition of bones are usually well understood. However, little is known about the post-depositional processes affected the bones in caves, although such processes could play important role in the current preservation state and sedimentological features of accumulations. From geological point of view, it is crucial to depict post-depositional effects on the site to enable the reconstruction of primary sedimentary processes. In this study, we tried to describe the post-depositional features of the Lower Weichselian cave bear strata from Biśnik Cave, southern Poland, bearing abundant and highly fragmented bones.

This part of Biśnik Cave sequence includes archaeological layers: 9, 10a, 10 and 11. Strata were dated to Lower Weichselian, MIS 5a-5d, around 70–90 ka (Krajcarz et al., 2014). These sediments exhibit no sedimentological traces of water transport (Mirosław-Grabowska, 2002); instead, traces of temporary stagnation of water ponds were identified (Krajcarz et al., 2014). These layers contain over 20 % of limestone clasts and about 20 % of sand.

Occupation over thousands of years by cave bears has resulted in huge quantities of bones being accumulated in layers of Biśnik Cave dated to Lower Weichselian. The bones accumulated in those strata are highly fragmented; the complete large bones are almost absent. Only small bones like metapodials, phalanges, carpals and tarsals, and also loose teeth, are usually complete. The surface of bones bears traces of intensive abrasion. The edges of broken bones as well as prominent parts of small ones are rounded, such as some fossils became rounded pebbles. The study of bone surface with use of SEM (scanning electron microscope) revealed traces similar to those caused by

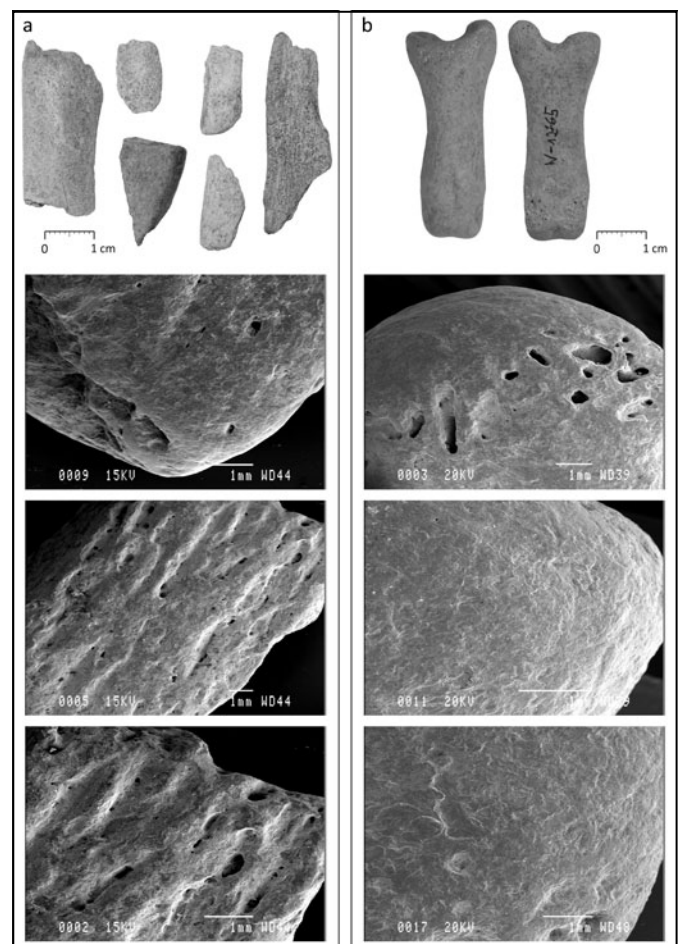


Fig. 1. Exemplary macrophotographs of bones from layer 9 of Biśnik Cave, and SEM photographs of magnified details of the bone surface: a – fragmented large long and flat bones, b – phalanx preserved as a whole.

water abrasion in sandy or silty sediments (Andrews, 1995; Fernández-Jalvo & Andrews, 2003, 2016). The bone surface is polished, usually without linear traces. In all studied cases, the entire surfaces of bones were affected by an abrading agent. Probably the already fossilized bones underwent that destruction, as the mineral precipitations and cracks are also abraded (Fig. 1). Due to lack of any sedimentological record of geological transport, we may assume that bones were most probably abraded in situ, in dry sediment. The preliminary hypothesis on the origin of bone modification observed in studied layers is joint interaction of animal trampling and pressure of surrounding sediment rich in limestone clasts.

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## WHAT IN FACT WAS THE STEPPE BROWN BEAR *URSUS ARCTOS PRISCUS* GOLDFUSS, 1818?

Adrian Marciszak<sup>1</sup> – Charles Schouwenbourg<sup>2</sup> –  
Wiktor Gornig<sup>1</sup>

<sup>1</sup> *Department of Paleozoology, Institute of Environmental Biology, Faculty of Biological Sciences, University of Wrocław, Sienkiewicza 21, 50-335 Wrocław, Poland; adrian.marciszak@uwr.edu.pl, wiktor.gornig@uwr.edu.pl*

<sup>2</sup> *Dorpsstraat 53, 3238BB Zwartewaal, Netherlands; c.schouwenbourg@upcmail.nl*

Steppe brown bear *Ursus arctos priscus* is a very particular kind of bear. This giant arctoid bear (Fig. 1), was a rare but permanent member of open grasslands mammal palaeocommunities. Described almost two centuries ago, till recent there are no sharply defined metrical and morphological features characterising this form. Many authors proposed in the past factors like great size, robust build, massive metapodials and a significant amount of speleoid features in morphology, especially dentition. But till now, partially because not a sufficient number of specimens, partially because of the enormous variability of the brown bear as a species.

Obtained so far by us data showed that genetic analysis is no answer, what in fact is steppe brown bear. Our metrical and morphological analysis revealed that it is an example of the plasticity of *Ursus arctos* and answer of the species for the availability of the large amount of meat in open grasslands in steppe-tundra. It should be considered as a different chronoform/ecomorph, which features like immense posture and broad teeth are an expression of specialisation to scavenge. Moreover, the bear remains in somewhat older faunal assemblages, often coexisted with thermophile species such as *Palaeoloxodon*



Fig. 1. Size comparison of three bears from Niedźwiedzia Cave, compared with man 1.8 m tall (from left to right): European brown bear *Ursus arctos arctos* Linnaeus, 1758, cave bear *Ursus ingressus* Rabeder et al., 2004 and the steppe brown bear *Ursus arctos priscus* Goldfuss, 1818. All animals are drawn in the same scale. Drawing: W. Gornig

*antiquus* or *Stephanorhinus kirchbergensis*, might indicate the presence of another form, closely related to the steppe brown bear. The Taubach bear *Ursus arctos taubachensis* Rode, 1935, which appeared already in the late Middle Pleistocene, is a characteristic component of European interglacial faunas like Taubach, Weimar Ehringsdorf, Kent's Cavern or Tornewton Cave (Kurtén, 1957). Sometimes synonymised with *Ursus arctos priscus*, it differs nevertheless in some metric and morphological features (Baryshnikov, 2007), which points to a distinct form (Marciszak et al., 2017). The problem needs further aDNA analysis, which may resolve the presence of other bear forms in Silesian open sites.

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## LATE PLEISTOCENE FAUNAL ASSEMBLAGE FROM NIEDŹWIEDZIA GÓRNA CAVE (SOUTHERN POLAND)

Adrian Marciszak<sup>1</sup> – Urszula Ratajczak<sup>1</sup> – Wiktor Gornig<sup>1</sup> –  
Magdalena Stupińska<sup>2</sup> – Mariusz Polok<sup>2</sup> – Jerzy Zygmunt<sup>2</sup> –  
Andrzej Tyc<sup>2</sup> – Krzysztof Stefaniak<sup>1</sup>

<sup>1</sup> *Department of Paleozoology, Institute of Environmental Biology, Faculty of Biological Sciences, University of Wrocław, Sienkiewicza 21, 50-335 Wrocław, Poland; adrian.marciszak@uwr.edu.pl, urszula.ratajczak@uwr.edu.pl, wiktor.gornig@uwr.edu.pl, krzysztof.stefaniak@uwr.edu.pl*

<sup>2</sup> *Polish Speleology Foundation, Będzińska 65, 41-200 Sosnowiec, Poland; speleologiapolska@gmail.com*

<sup>3</sup> *Department of Geomorphology, Faculty of Earth Sciences, University of Silesia, Będzińska 60, 41-200 Sosnowiec, Poland; andrzej.tyc@us.edu.pl*

Niedźwiedzia Górna Cave, located in Silesia Voivodeship is long (ca. 635 m) and newly discovered cave. The entrance is situated ca. 310 m a. s. l. in Złoty Potok area and recently the site is closed to protect against destroying. During field research, the abundant paleontological material was collected, mainly from the surface of the cave silt. The state of preservation is surprisingly good; the bones are primarily lightly in colour, with some thin coating of calcite. All skeletal elements were found, with a domination of cranial bones, long and metacarpal/metatarsal bones. Carnivores dominate faunal assemblage, and among them, ursids are the most numerous. Also, juvenile specimens found. The whole assemblage can be divided into two, differ in age and species composition. In the upper horizon, near Krasieński hall and in the vicinity of the entrance the postglacial and Holocene fauna have been found. Bones are light and poorly fossilised. Apart from typical elements like *Vulpes vulpes*, *Felis silvestris*, *Martes martes*, *Capreolus capreolus*, *Lepus europaeus* and some micromammals, also relatively rare faunal elements appeared. Very rarely found in Polish cave sediments *Lynx lynx* and *Gulo gulo* (a probable survivor from the last glacial) together with *Ursus arctos arctos* are the most interesting among them.

The second assemblage, found in the lower horizon, is represented by Late Pleistocene large carnivores like *Ursus ingressus*, *Ursus arctos priscus* and *Panthera spelaea spelaea* (Fig. 1). Obtained for these species so far C<sup>14</sup> dates showed, that they dated on MIS 3. Among them, especially interesting is the presence of high percentage (proportionally) of the cave lion, which is represented so far by MNI = 4. Such accumulation of remains may suggest that the species is not cave dweller, penetrated caves in search of food like hibernating cave bears.

Preliminary data (DNA and isotopic analysis, successful C<sup>14</sup> dating), the number of the bones, their stage of preservation and numerous of species decided of the uniqueness of the site. In the future, it is planned to take regular excavations.



Fig. 1. Why cave lion is so common in Niedźwiedzia Górna Cave and possible answer.

## STEPPE BROWN BEAR *URSUS ARCTOS PRISCUS* GOLDFUSS, 1818 – HUGE SCAVENGER OF LATE PLEISTOCENE GRASSLANDS PALEOCOMMUNITIES

Adrian Marciszak<sup>1</sup> – Charles Schouwenbourg<sup>2</sup> –  
Grzegorz Lipecki<sup>3</sup> – Wiktoria Gornig<sup>1</sup> – Vlastislav Káňa<sup>4</sup> –  
Martina Robličková<sup>4</sup>

<sup>1</sup> Department of Paleozoology, Institute of Environmental Biology, Faculty of Biological Sciences, University of Wrocław, Sienkiewicza 21, 50-335 Wrocław, Poland; adrian.marciszak@uw.edu.pl, wiktoria.gornig@uw.edu.pl

<sup>2</sup> Dorpsstraat 53, 3238BB Zwartewaal, Netherlands; c.schouwenbourg@upcm.nl

<sup>3</sup> Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Sławkowska 17, 31-016 Kraków, Poland; lipecki@isez.pan.krakow.pl

<sup>4</sup> Moravian Museum, Anthropos Institute, Zelný trh 6, 659 37 Brno, Czech Republic; mroblickova@mzm.cz, kanabat@email.cz

With opportunistic behaviour, extremely broad diet, ability to adapt to various habitats ranging from semi-deserts to Arctic tundra, including arid and mountain areas, *Ursus arctos* could adapt to the changes of environmental conditions. The brown bear remains from many European sites document the occurrence of a very particular kind of bear. This giant bear, called steppe brown bear *Ursus arctos priscus*, was a rare but permanent member of open grasslands mammal palaeocommunities. It is very characteristic that this form is always strangely difficult to find not only in open sites but also in caves. Compared to other carnivores, the steppe brown bear was never common in one locality and tended to be a solitary hunter and scavenger, which required large expanses of open grassland. This bear was a scavenger and kleptoparasit, whose huge size gave it advantage over other predators (also ancient hunters) (Fig. 1). It also followed herds of herbivores and took animals which died naturally or in another way. Occasionally it also hunted. In its behaviour, it resembled the modern *Ursus maritimus* or *Arctodus simus* from North America in the past. It can be conjectured that, except pregnant females, the steppe brown bear was active year-round following herbivores and other carnivores in search of food.

Isotopic analysis shows that brown bears were highly carnivorous till the late glacial and became more omnivorous with the change of climate and environmental conditions. The last postglacial warming brought about a shrinkage of open grasslands, disappearance of ungulate herds and expansion of forests. The largest species like mammoths, rhinoceros, and some bovids became entirely extinct, other forms lived in smaller herds or small groups, and carcasses were much harder to obtain than previously. The density was much lower, and the amount of available food much smaller. There was not enough food and space for such a huge bear. During the postglacial times, the brown bear slowly dwarfed, and also smaller bears similar to the nominate subspecies entered from the south and southeast. The dwarfing process, however, was not the same in entire Europe, since in some regions large, robust bears of *priscus*-type survived longer. The form is only a smaller descendant of the Late Pleistocene form, which occurred till the early Holocene over the coast of the North and Baltic Seas as well as in some parts of Germany and Poland. Some populations slowly retreated to the northeast, while others were genetically swamped by the modern European bear. Finally, in the early Holocene, the modern brown bear appeared and became the sole bear species in Europe.



Fig. 1. Visit the kill plave by not-welcome guest at the famous mammoths hunter-camp Spadzista street near Kraków.

## A POSSIBLE MAGDALENIAN DOG FROM GNIRSHÖHLE NEAR ENGEN (HEGAU, SW-GERMANY)

Susanne C. Münzel<sup>1</sup> – Chris Baumann<sup>1</sup> – Gerd Albrecht<sup>2</sup> –  
Catherine C. Bauer<sup>3</sup> – Hervé Bocherens<sup>3, 4</sup>

<sup>1</sup> Archaeological Science, Archaeozoology, University Tübingen, Rümelinstraße 23, D-72070, Tübingen, Germany; susanne.muenzel@uni-tuebingen.de, chris.baumann@uni-tuebingen.de

<sup>2</sup> Palaeolithic archeologist, 794 10 Badenweiler, Germany; gerd-albrecht@t-online.de

<sup>3</sup> Department of Geosciences, Palaeobiology, Biogeology, Eberhard Karls University of Tübingen, Hölderlinstraße 12, 72070 Tübingen, Germany; catherine.bauer@ifu.uni-tuebingen.de

<sup>4</sup> Senckenberg Center of Human Evolution and Palaeoenvironment, University of Tübingen, Rümelinstraße 23, 72070 Tübingen, Germany; herve.bocherens@uni-tuebingen.de

The beginning of dog domestication remains hotly debated, partly because of the difficulty to decipher this behavioural change. Morphological diversity in the canid family is already recognizable in the Early Upper Palaeolithic (Germonpré et al., 2009; Ovodov et al., 2011; Germonpré et al., 2012; Thalmann et al., 2013; Bocherens et al., 2015). We will present a new case of a possible Magdalenian dog, from a time when dogs probably were daily companions of the hunters.

Gnirshöhle is a small cave site in the Bruder Valley near Engen/Hegau (SW-Germany) with a Magdalenian occupation (Albrecht et al., 1977). Petersfels cave is situated on the opposite site of the valley and is well-known for its intensive Magdalenian occupation and for its jewellery, such as jet pendants in the shape of 'Venus' figurine (Albrecht et al., 1983).

The Magdalenian occupation in both sites dates between 12 and 13 ka BP. Dominant game species of the hunters were reindeer (*Rangifer tarandus*), horse (*Equus* sp.) and hare (*Lepus timidus*). Beside foxes (*Vulpes* sp.), a mandible of a middle-sized canid was found in Gnirshöhle Cave, which was suggested to be a dog (Napierala & Uerpman, 2010). The faunal report mentions heavy carnivore gnawing on the bones from Gnirshöhle Cave (Albrecht, 2002), thus we may consider wolves or dogs as bone destructors.

Two other Magdalenian canid finds in this region are of importance as possible evidence for the presence of dogs. It is a maxilla from Kesslerloch (Switzerland) and one from Hohle Fels in the Ach Valley near Ulm (Napierala, 2008; Napierala & Uerpman, 2010; Camarós et al., 2016). The maxilla from Kesslerloch was directly dated at 12,225±45 BP (KIA-33350). The find is metrically below the size variability of wolves and shows slight morphological differences with wolves from the site (Napierala & Uerpman, 2010). However, genetic analysis places the putative dog from Kesslerloch to the wolf clade, which is highly variable (Thalmann et al., 2013). The canid maxilla from Hohle Fels was considered a putative dog by Camarós et al. (2016). However, analysis of the mitochondrial DNA also placed this specimen in the wolf clade (Feuerborn, 2016). These examples demonstrate the difficulties to draw conclusions about the state of domestication in canids, as morphometric and genetic methods may give apparently different results.

An important tool to get further insight into the state of domestication is the stable isotope-analysis of the diet of canids in human settlements. Isotope tracking may elucidate the potential control that Palaeolithic hunters had on the canids. Isotope studies have been conducted on canids from the archaeological site Předmostí in the Czech Republic. Distinct differences in diet between 'Palaeolithic dogs', humans, and 'Pleistocene wolves' were recognized here (Bocherens et al., 2015). Based on these dietary differences it was hypothesised that the 'Palaeolithic dogs' had a limited dietary variation compared to the 'Pleistocene wolves'.

We will present morphometrical and stable-isotope data from the putative dog from Gnirshöhle Cave and of coeval canids to reconstruct the place of the Gnirshöhle specimen in the local Magdalenian food web and to draw conclusion on the state of domestication.

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

Doris Nagel<sup>1</sup> – Nadja Kavcik-Graumann<sup>2</sup> – Gernot Rabeder<sup>1</sup>

<sup>1</sup> Institute of Palaeontology, University of Vienna, Althanstraße 14, A-1090, Vienna, Austria; [doris.nagel@univie.ac.at](mailto:doris.nagel@univie.ac.at), [gernot.rabeder@univie.ac.at](mailto:gernot.rabeder@univie.ac.at)

<sup>2</sup> Department of Cognitive Biology, University of Vienna, Althanstraße 14, A-1090, Vienna, Austria; [nadja.kavcik@univie.ac.at](mailto:nadja.kavcik@univie.ac.at)

The discovery of a new fossil cave hyena fauna in a cave at the eastern boarder of the Alps has been the reason to re-evaluate the chronology and the genetic data of hyenas. Radiocarbon dates of predators, like the fossil hyenas, as well as the remains of their prey yielded values between 41,000 and 50,000 years before present (calBP). Only one results with >48,500 a BP lies probably above the 50 ka boarder and indicates the presents of the cave hyena already before 50,000 in Middle Europe.

The remains of these Upper Pleistocene hyena sites consists mainly of hyena remains, fractured bones with gnawing marks from large herbivores as well as other predators, such as lions, leopards and brown bears, which used the cave occasionally. The faunal list of these sites includes taxa which have extant relatives living in the tropical and/or subtropical steppe region today: onager, porcupine, blind mole-rats, lion, leopard and of course the hyena. According to the genetic investigations, these taxa, formerly seen as separated species, are actually quite close to their extant relatives; so close that a species distinction does not seem justified. Therefore we assume that their ecological preferences were comparable to the moderen taxa and cave hyena areas between 40 to 50 ka was warmer and drier than today (Fig. 1). However, some prey of the cave hyena were large herbivores of the arctic steppe-tundra of the peniglacial time, such as mammoth, woolly rhino, steppe bison, horses and the Irish elk. The contemporaneous occurrence of boreal and subtropical elements in the food source of the hyenas could be explained by seasonal migration of these steppe elements.

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Fig. 1. Distribution areas of spotted hyena and onager during the Holocene and the positions of fossil hyena fauna sites with the Radiocarbon results in Eastern Middle Europe (Denzau, 1999; modified).

## NEW URSID REMAINS FROM THE MOSBACH SANDS, GERMANY

Martina Pacher<sup>1</sup> – Thomas Keller<sup>2</sup>

<sup>1</sup> University of Vienna, Institute of Palaeontology, Althanstraße 14, A-1090, Vienna, Austria; [martina.pacher@univie.ac.at](mailto:martina.pacher@univie.ac.at)

<sup>2</sup> Am Ebbefeld 135, 60488 Frankfurt, Germany; [thomas.60488@web.de](mailto:thomas.60488@web.de)

The term “Mosbach Sands” comprises accumulation mainly from the rivers Rhine and Main and accounts for a variety of fossil localities along an ancient river bank, now part of the town of Wiesbaden (e. g., Keller, 1994). The rich Middle Pleistocene fauna contains several large mammals, among them the first known remains of *Ursus deningeri* described by von Reichenau (1906). In course of the regular routine of visits to localities of the Mosbach Sande members of the Landesamt für Denkmalpflege Hessen found and documented more than 20 remains of bears at different localities among them a well preserved skull of *Ursus deningeri* (Fig. 1). As far as possible the stratigraphical position of the finds was interpreted based on the new division from Mosbach in Radtke & Keller (2007). Preservation of the remains suggests a partly intense taphonomical history.



Fig. 1. Find situation of the bear skull LDK 22/95. Photo: Thomas Keller

Finally, metrical and morphological characteristics of the finds have been examined. The results are then compared to several ursid remains from Europe, which allowed a broader view on the variability of these Middle Pleistocene bears.

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## WOLVERINE POPULATION DYNAMICS SINCE THE LATE PLEISTOCENE BASED ON ANCIENT MITOGENOMES

Johanna L. A. Pajmans<sup>1</sup> – Axel Barlow<sup>1</sup> – Kirstin Henneberger<sup>1</sup> – Doris Döppes<sup>2</sup> – Michael Hofreiter<sup>1</sup>

<sup>1</sup> Institute for Biochemistry and Biology, University of Potsdam, Karl-Liebknecht-Straße 24-25, 14476 Potsdam, Germany;

[pajmans.jla@gmail.com](mailto:pajmans.jla@gmail.com), [axel.barlow.ab@gmail.com](mailto:axel.barlow.ab@gmail.com), [kihenneb@uni-potsdam.de](mailto:kihenneb@uni-potsdam.de), [Michael.hofreiter@uni-potsdam.de](mailto:Michael.hofreiter@uni-potsdam.de)

<sup>2</sup> Reiss-Engelhorn-Museen, C4, 8, 68159 Mannheim, Germany; [doris.doeppes@mannheim.de](mailto:doris.doeppes@mannheim.de)

The wolverine (*Gulo gulo*) is the largest member of the weasel family and has a widespread, circumpolar distribution. Although wolverines are currently designated ‘Least Concern’ on the IUCN Red List of Threatened Species, the mustelid is affected by many potentially detrimental anthropogenic effects such as hunting and predator poisoning, contributing to a steady population decline observed over the past decades. The Scandinavian wolverine in particular has experienced severe population reductions, and although their relationship to

Asian wolverines is unclear, they have been shown to be quite distinct from American populations, suggesting they have been isolated in Scandinavia for some time. During the Late Pleistocene, wolverines inhabited many parts of Eurasia where they no longer exist today, with fossils recovered from European localities as far south as the Iberian Peninsula. Whether these Pleistocene European populations went extinct before the start of the Holocene, or instead migrated to more suitable habitats (a process known as 'habitat-tracking'), is not known. Morphological differences between ancient and modern wolverines may reflect a lack of population continuity between Pleistocene populations and those that occur today (size and dentition); however, this has not yet been tested using ancient DNA. Here, we present full mitochondrial genomes from wolverines throughout the Eurasian continent. Our data encompasses both ancient (Late Pleistocene and Early Holocene) as well as historical samples, thus allowing for a detailed assessment of the population history of maternal lineages over time. The mitogenomic data is used to infer population dynamics during the severe climatic fluctuations that marked the end of the Pleistocene. In particular, we investigate the origins of the Scandinavian wolverines, and the fate of the Pleistocene European populations, by comparing their mitochondrial haplotypes with those found in the rest of Eurasia and America. The results from our study can provide insights into the process of habitat-tracking, and the responses of arctic carnivores faced with climate fluctuations.

## MORPHOMETRICAL ANALYSES OF CAVE BEAR POPULATIONS FROM BAROVÁ CAVE IN MORAVIAN KARST (CZECH REPUBLIC)

Aleš Plichta<sup>1</sup> – Martina Roblíčková<sup>3</sup> – Vlastislav Káňa<sup>1,2</sup>

<sup>1</sup> Masaryk University, Department of Geological Sciences of Faculty of Science, Kotlářská 2, 611 37 Brno, Czech Republic; plichta.ales@mail.muni.cz

<sup>2</sup> Muzeum Blanenska, p. o., Zámek 1, 678 01 Blansko, Czech Republic; kanabat@email.cz

<sup>3</sup> Moravian Museum, Anthropos Institute, Zelný trh 6, 659 37 Brno, Czech Republic; mroblickova@mzm.cz

The Barová Cave is located in right slope of Křtiny Valley in central part of Moravian Karst in the Czech Republic. The Barová Cave was discovered in 1947 by Dr. Sobol and group of his students, who had dug on the bottom of Křtiny skála (Raven Rock), near well-known archaeological site, the Býčí skála Cave (Bull Rock Cave). The Barová Cave and the Býčí skála (Bull Rock) Cave together make a one connected cave system. More details about the Barová Cave are described by Roblíčková et al. at another place of this volume. The bone material from the Barová Cave was excavated during several researches, with a focus on material from a Dr. Seitz's research (Seitz, 1988) and material from a new research proceeding by Káňa & Roblíčková which has been started in the cave since 2011 (Roblíčková & Káňa, 2013a, b; Roblíčková et al., 2017).

The sedimentary sequence – debris cone of fossiliferous sediments with bones was sorted into three layers (A, B, C), meanwhile a fourth layer (D) forms sterile bedrock. Each layer represents one period of debris cone creating. Despite of the fact that the periods are time-separated, we suppose that the bones belong to the same time period in all three layers.

The Barová Cave was a wintering ground for cave bear, and bones from different ages are found here – from fetus to senile individuals, males and females. Bones of cave bears represent approximately 90 % of total amount of all bones dug out from Barová Cave, so it is a typical bear-cave. Total quantity of all individuals of bears is estimated at about 150 to 200. The total number of bones excavated from the Barová Cave is in thousands (Roblíčková, pers. comm).

Radiocarbon dating of bones identify age at approximately 46 +/- 2 t. years, which responds to the last Weichselian Glacial, Hengelo Interstadial (MIS 3). Dating by this method could be incorrect though, because of possible contamination by carbon from the cave environment. Therefore, samples were sent for U/Th dating, but results are not known yet.

It is not possible to determine clearly whether it is a cooler or warmer fluctuation because the interstadial species were found only sporadically in several pieces (aurochs/bison, deer, lynx, etc.). The abstract of Roblíčková et al. deals with the fossil assemblage of Barová Cave is at another part of this volume.

In accordance with Sabol (2008), the largest representative of genus *Ursus* was the cave bear, but this is not consistent with Marciszak (pers. comm) claim, that the largest representative of this genus was *Ursus arctos priscus*. The cave bears represent the final developmental stage of speleoid family branch. There are rarely preserved third premolars in teeth (P3 sup. et inf.) and the fourth premolars are significantly molarized. A typical teeth formula of cave bear is 3I-1C-1P-2M in upper jaw and 3I-1C-1P-3M in lower jaw (Fig. 1).

In recent years, opinions on the systematic division of cave bears have undergone a great development. Originally, it was assumed that there is only one species of cave bear, *Ursus spelaeus* Rosenmüller (1794). Rosenmüller described a holotype of cave bear from the Bavarian Zoolithen Cave. However, the holotype was lost. Diedrich (2009) thinks that the lost holotype has reappeared in the Rosenmüller's collections which are housed in Berlin and presents its detailed description. According to Wagner (pers. comm), however, the authenticity of this specimen cannot be verified.

Rabeder et al. (2008) published a study based on a large number of statistical data from over than 30 alpine and extra-alpine bear populations (Austria,

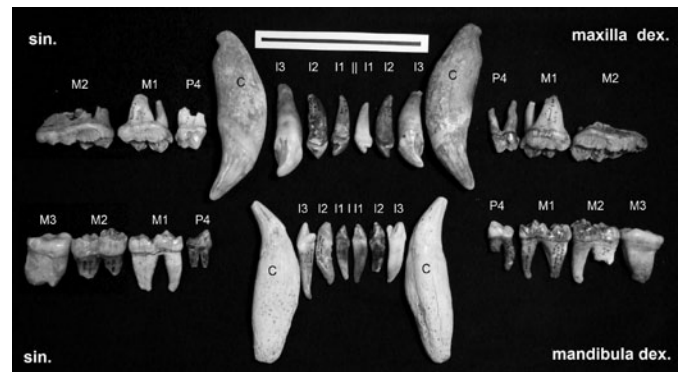


Fig. 1. Teeth of cave bear with typical dentition.

Slovakia, Italy, France, Switzerland). They emphasize the differences between individual populations that are distinguishable by morphometric analysis and subsequently these differences were confirmed by mtDNA analyses. The entire group of alpine cave bears was thus divided into four species – *Ursus spelaeus*, *U. eremus*, *U. ladinicus* and *U. ingressus*. Some of the species seem to react to their place of occurrence (especially to altitude). What is really interesting is the coexistence of the species *U. ingressus* and *U. eremus* in the Austrian Alps for 15,000 years, when *U. ingressus* lived in the lower and *U. eremus* in higher altitudes, although there was no genetic cross between the two populations.

According to DNA analyses carried out by Polish colleagues (Popović et al., 2016) it was discovered that only *Ursus ingressus* (Fig. 2) was found in caves of Moravian karst (Barová Cave (6 samples), Pod Hradem (3 samples), Kateřinská (1 sample), Sloupské (2 samples) and Výpustek (1 sample)).



Fig. 2. Complete skull of cave bear *Ursus cf. ingressus* from Barová Cave. Photo: V. Káňa

**Methods:** The fourth upper and lower premolar (P4 sup. et inf.) were used for morphometrical analysis and all molars were also used (M1 et M2 sup., m1, m2 et m3 inf.). Various dimensions are measured on each tooth. On the upper fourth premolars (P4 sup.), there are measured length, width, lingual length or height of the paracone. On the lower fourth premolar (p4 inf.), there were measured length, width, the paraconid-metacconid distance or height of the protoconid. In the lower first molar (also in the second one) (m1 et m2 inf.), the following dimensions were measured: the total length of the tooth, the width and the length of the trigonide and the talonid (as for the length both of the buccal and the lingual side), the width of the constriction between the trigonide and the talonid, the length of the entoconid complex and the length of each entoconid separately. On the lower third molar (m3 inf.), only the length, width and buccal length of the talonid were measured. First upper molar (M1 sup.) – length, width of the front (trigon) and back (talon), width of the constriction, length of the paracone and metacone without stylides, and with stylides and height of the paracone and metacone were measured. In the second upper molar, the total length, width against the paracone and metacone, the width of the constriction, and the width of the "talon" were measured against the top of the posthypocone.

Only morphotypes of the fourth premolars (P4 sup. et inf.) (Table 1) and P4/4 index (ratio P4 and p4 index) (Fig. 3) can be evaluated at this time. P4/4 index was plotted and compared with data from the Alps, published by Rabeder (1999). The obtained result – P4 index 158.3 and p4 index 120.85 after plotting is not deviated and fits among the other bear populations of the Alps and their surroundings. The gained data of other teeth will be processed by multidimensional statistic. If there is only *U. ingressus* in Barová Cave, as supported by

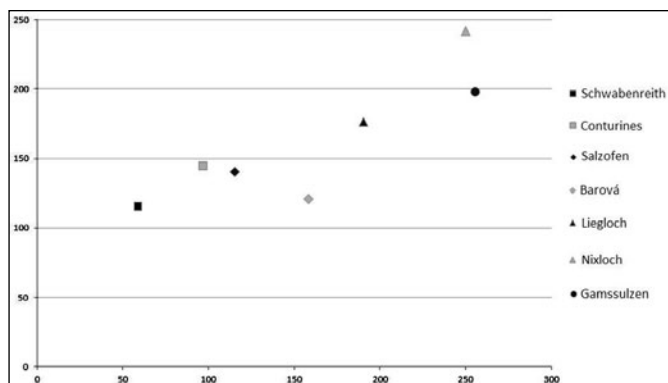


Fig. 3. Graphic view of P4/4 index in context of the other fossil sites (modified by Rabeder, 1999).

genetic analysis, the points in the individual point charts, which will be the final outcome, will be likely grouped into the one area. In case of presence of any other bear's (*U. spelaeus*) relics, division into two or more groups can be assumed. In case of several species or morphotypes / morphotaxa respectively, it would be appropriate to send extreme results for mtDNA analyses.

Table 1. Representation of the individual morphotypes of the fourth upper and lower premolars and calculation of P4/4 index.

P4 sup. (sin., total quantity = 24)				
Type	quantity	%	factor	product
D	8	33.33	2	66.66
A	6	25	0	0
A/D	3	12.5	1	12.5
C	2	8.33	2	16.66
E	2	8.33	3	24.99
F	2	8.33	4	33.32
B	1	4.17	1	4.17
total	24	100		158.3
p4 inf. (sin., total quantity = 29)				
Type	quantity	%	factor	product
C1	19	65.52	1	65.52
C2	4	13.79	2	28.58
B2	2	6.90	1,5	10.35
B1	1	3.45	0,5	1.73
C1/C2	1	3.45	1,5	5.18
C1/D1	1	3.45	1,25	4.31
D1	1	3.45	1,5	5.18
total	29	100		120.85

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## EXTINCTION PATTERN OF ALPINE CAVE BEARS. NEW DATA AND CLIMATOLOGICAL INTERPRETATION

Gernot Rabeder<sup>1</sup> – Doris Döppes<sup>2</sup> – Frischauf Christine<sup>1</sup> – Kavcik-Graumann Nadja<sup>3</sup> – Kromer Bernd<sup>4</sup> – Lindauer Susanne<sup>4</sup> – Ronny Friedrich<sup>4</sup> – Rosendahl Wilfried<sup>2</sup>

<sup>1</sup> Institute of Palaeontology, University Vienna, Althanstraße 14, A-1090 Vienna, Austria; gernot.rabeder@univie.ac.at, christine.f@gmx.at

<sup>2</sup> Reiss-Engelhorn-Museen, Zeughaus, C5, 68159 Mannheim, Germany; doris.doepes@mannheim.de, wilfried.rosendahl@mannheim.de

<sup>3</sup> Department of Cognition Biology, University Vienna, Althanstraße 14, 1090 Vienna, Austria; nadja.kavcik@univie.ac.at

<sup>4</sup> Klaus-Tschira-Archäometrie-Zentrum, Institute of CEZ Archäometrie gGmbH, C4, 8, 68159 Mannheim, Germany; susanne.lindauer@cez-archaeometrie.de, ronny.friedrich@cez-archaeometrie.de

The cave bears of the Alps have disappeared from the different altitudes at different times (Fig. 1). The progress of the HDEL (Height Dependant Extinction Line) – which combines the geologically most recent radiocarbon dates per altitude stage – is not consistent with the general cooling of the temperatures from about 45,000 years BP. The cave-bear sites with the most recent radiocarbon ages do not lie in the lowlands but in the caves, which have altitudes of 1,500 m to 1,700 m.

With the help of new radiocarbon dates, done at the Klaus-Tschira Archeometry Center at the Reiss-Engelhorn museums in Mannheim (Germany), the HDEL can be determined much more precisely. The causes of gradual extinction are also better understood. The comparison of stable carbon and nitrogen isotopes as well as the different frequencies of grinding marks allows conclusions about the composition of the food at different elevation levels. There is a suspicion that the food of the cave bears in the intermediate elevations consisted mainly of relatively soft plant parts (herbs, leaves), while the caves in the lower locations had to accept a higher proportion of hard plants (grasses). The HDEL descends from an altitude of 2,800 m by about 50,000 years BP to a height of about 1600–1700 m by 25,000 years calBP, which can be explained by the general cooling of the climate. In the lowlands, the cave bears – according to the course of the HDEL – have disappeared much earlier. In order to explain this phenomenon, we offer the hypothesis that the aridity derived from Alpine foothills by the occurrence of typical steppe elements (*Mammuthus*, *Coelodonta*, *Equus*, *Bison priscus* etc.) has also gradually effected the inner valleys of the Alps. The food sources of the cave bears have declined so that they have first disappeared from the lowlands and then increasing from the regions up to 1,600 m. There is no evidence for the theory that the Paleolithic man had influenced the extinction pattern of the Alpine cave bear.

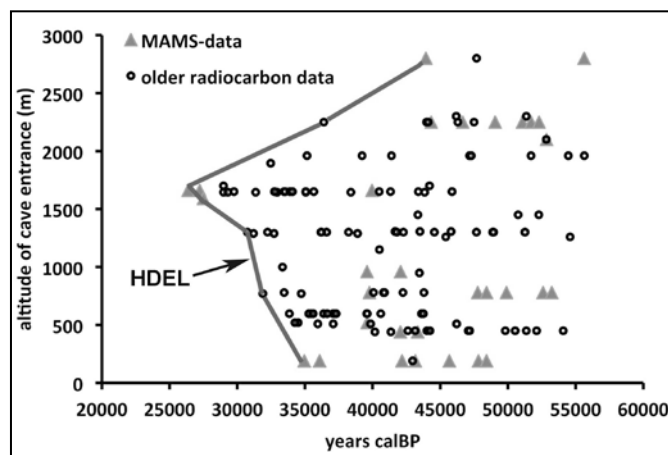


Fig. 1. Radiocarbon dates of cave bears from Alpine caves and the Height dependent extinction line (HDEL) of cave bears. Old and new AMS data.

## LAST GLACIAL MAMMALIAN ASSEMBLAGE FROM BAROVÁ CAVE (MORAVIA KARST, CZECH REPUBLIC) – NEW FINDINGS

Martina Roblíčková<sup>1</sup> – Miriam Nývltová Fišáková<sup>2</sup> – Vlastislav Káňa<sup>3,4</sup>

<sup>1</sup> Moravian Museum, Historical Museum, Anthropos Institute, Zelný trh 6, 659 37 Brno, Czech Republic; mroblickova@mzm.cz

<sup>2</sup> Institute of Archaeology of the CAS, Brno, Čechyřská 363/19, 602 00 Brno, Czech Republic; nylvtova@arub.cz

<sup>3</sup> Muzeum Blanenska, p. o., Zámek 1, 678 01, Blansko, Czech Republic; kanabat@email.cz

<sup>4</sup> Masaryk University, Faculty of Science, Department of Geological Sciences, Kotlářská 267/2, 611 37 Brno, Czech Republic

The Barová Cave is situated in the central part of the Moravian Karst (Czech Republic) on the right bank of the Křtiny Creek in the Josefůvské Valley. The cave entrance is located in the foot of the Krkavčí skála (Raven Rock) rock cliff. It is the outflow part of the cave system Rudické propadání (Rudice Sink) – Býčí skála (Bull Rock); the cave system is formed in Josefův and Lažánky limestone of the Devonian Macocha formation. The cave was discovered and described by Antonín Sobol and his colleagues in 1947 (Sobol, 1948, 1952). Already at that time there were found fossil bones of the Pleistocene fauna in sediments between the entrance and the so-called Second Shaft (Strnad, 1949).

The Barová Cave is an indented polygenetic karst cavity flowed through by the Jedovnický Creek. It comprises three levels (floors) with a total denivelation of about 80 m and a length of approximately 1,000 m. The upper floor is formed by vertical to sub-horizontal spaces of a vadose zone; the lower floor is the current creek bed of the Jedovnický Creek. The middle floor interconnects the other two floors and it is formed by surface of sediments which fill in a large karst cavity. There are six dome-like natural depressions called "Shafts" in sediments filling. These sediments form the bedrock of studied fossiliferous layers. Between the First and Second Shaft (app. 40 m from the cave entrance) the bedrock sediments are covered with a younger debris cone consisting of a layer of Pleistocene (and maybe of Holocene too in an upper part) sediments with numerous bones of Pleistocene fauna.

In general the sediments of the cone can be stratified as follows: above the highest part of the bedrock there is a layer C – fossiliferous layer on the basis of the sedimentary tongue which contains numerous bones of large carnivores (mostly bears from the group of cave bears). The layer B lies above the layer C, this is the main body of sedimentary cone. Bone remains of mainly large carnivores are also quite abundant in layer B, however, they are scattered. The bones of the layer B are damaged not only by the pressure of overlying sediment, but also by the transport in the sediment or on its surface. The transport presumably proceeded over longer distances. The layer A has been largely destroyed or excavated in the previous years. In case that layer A occurs, it contains bone material only seldom (Sobol, 1952; Roblíčková & Káňa, 2013b; Roblíčková et al., 2017).

In the fossiliferous sediments of the Barová Cave two waves of paleontological researches took place before 2011, namely the excavations by R. Musil in 1958 (Musil, 1959, 1960) and the archaeological-paleontological research by J. Svoboda and L. Seitl in the eighties, under which they also examined the sediment containing bones of Pleistocene fauna in space called Medvědí síňka (Bear Little Hall; Seitl, 1988). A landslide of sediments in the summer

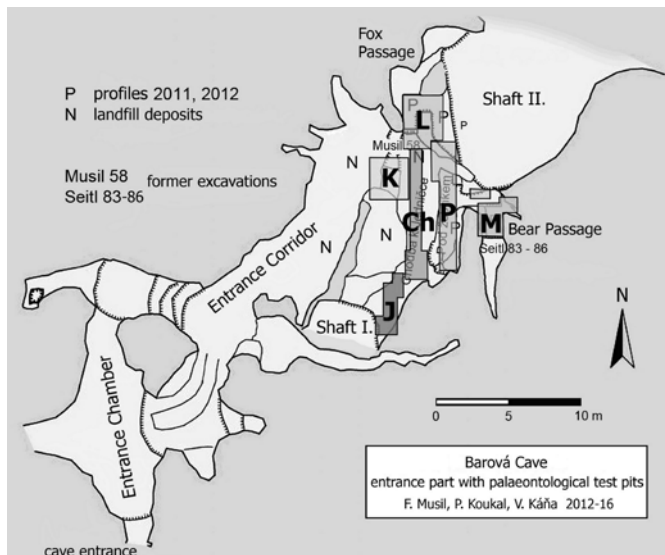
of 2011 revealed yet unexamined fossiliferous positions in the Upper Pleistocene sediments and meant the beginning of the current research activity. Six paleontological test pits (Fox Passage, Under the Ladder, Bear Passage, Passage to the Shaft I, Shaft I and Chimney Dome) were laid in the fossiliferous sediments of the Barová Cave during the current research activity in years 2011–2016 (Fig. 1; for more see Káňa et al., 2013; Roblíčková & Káňa, 2013a, 2013b; Roblíčková et al., 2017).

There were discovered skeletal remains of 21 taxa of animals in the Barová Cave between 2011 and 2017. Bears from the group of cave bears (*Ursus* ex gr. *spelaeus*) completely dominate (thousands pieces of their bones were found); other carnivores found in the cave include cave lions (*Panthera spelaea*) and wolves (*Canis lupus*) with hundreds of bones and cave hyenas (*Crocuta crocuta spelaea*) with tens of pieces of bones. Osteological remains of other five taxa of carnivores, namely the brown bear (*Ursus arctos*), lynx (*Lynx lynx*), wolverine (*Gulo gulo*), fox, probably red (*Vulpes cf. vulpes*) and marten (*Martes cf. martes*), were found only in units of pieces. Several bones of seven taxa of ungulates were found, namely the alpine ibex (*Capra ibex*), chamois (*Rupicapra rupicapra*), aurochs or bison (*Bos primigenius / Bison priscus*), reindeer (*Rangifer tarandus*), red deer (*Cervus elaphus*), horse (*Equus* sp.) and woolly rhinoceros (*Coelodonta antiquitatis*). Just several bone remains the Barová Cave provided also in case of the hare (*Lepus* sp.), lemming (*Dicrostonyx* sp.), red vole (*Clethrionomys* sp.), jackdaw (*Corvus monedula*) and probably northern pintail (*Anas aff. acuta*).

Animal osteological material from the sectors 2, 3, 4 and R4 from the Under the Ladder test pit is analyzed in detail in this paper. The largest number of bones found in these sectors came from bears from the group of cave bears (3,663 pieces of bones). Together with the worse identifiable fragments determined only as very likely of the bears of the cave bear group (*Ursus* cf. ex gr. *spelaeus*) the total sum of bones determined as bone of bears from the group of cave bears make up nearly 95 % of all determined material (Table 1). The cave lion was the second most abundant species in the monitored sectors; its bones comprise nearly 3 % of the determined material. Bones of the wolf represent about 1.2 % of the determined findings; bones of the cave hyena represent approximately 0.5 %. There were found a rib fragment of an individual from the mustelids and several skeletal remains of ungulates too, specifically of the chamois, the red deer, the reindeer and the horse. There were also found two rodent lower jaws and bones from one skeleton of a jackdaw in the monitored sectors (Table 1).

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

Taxon	pieces of bones	%	% from determined	MNI	% MNI
<i>Ursus</i> ex gr. <i>spelaeus</i>	3663	48.29	71.60	40	70.18
<i>Ursus</i> cf. ex gr. <i>spelaeus</i>	1196	15.77	23.37		
<i>Ursus</i> sp.	6	0.08	0.12		
cf. <i>Ursus</i> sp.	1	0.01	0.02		
<i>Panthera spelaea</i>	147	1.94	2.87	4	7.02
<i>Canis lupus</i>	58	0.76	1.13	2	3.51
<i>Canis</i> cf. <i>lupus</i>	3	0.04	0.06		
<i>Crocuta c. spelaea</i>	27	0.36	0.53	3	5.26
Mustelidae	1	0.01	0.02		
<i>Rupicapra rupicapra</i>	5	0.07	0.10	1	1.75
<i>Cervus elaphus</i>	2	0.03	0.04	2	3.51
<i>Rangifer tarandus</i>	1	0.01	0.02	1	1.75
<i>Rangifer</i> cf. <i>tarandus</i>	1	0.01	0.02		
<i>Equus</i> sp.	1	0.01	0.02	1	1.75
<i>Dicrostonyx</i> sp.	1	0.01	0.02	1	1.75
<i>Clethrionomys</i> sp.	1	0.01	0.02	1	1.75
<i>Corvus monedula</i>	1	0.01	0.02	1	1.75
Aves	1	0.01	0.02		
Total of determined bones / total of MNI	<b>5116</b>	<b>67.45</b>	<b>100.00</b>	<b>57</b>	<b>100.00</b>
Undetermined bones	2469	32.55			
<b>Total of bones</b>	<b>7585</b>	<b>100.00</b>			



**Fig. 1. The cut-out of Barová Cave map focused on the palaeontological excavations. Single test pits are marked by letters: Ch – Passage to the Shaft I test pit, J – Shaft I test pit, K – Chimney Dome test pit, L – Fox Passage test pit, M – Bear Passage test pit, P – Under the Ladder test pit.**

Bones of the bears from the group of the cave bears from the sectors 2, 3, 4 and R4 of the Under the Ladder test pit belonged to at least 40 individuals (MNI = 40, Table 1). All age categories of bears from the group of cave bears were present, from newborn to older adults. Molar abrasion indicates a high mortality rate among young bears, 47.5 % of all individuals of bear from cave bear group died in period 2–7 years. These results correspond to Musil (2014). He states that in most bear caves findings of bones of such young bear individuals reach up to 70 % (Musil, 2014). Both males and females of bears from the group of cave bears occurred in the cave. The five bear cubs which died or were killed at the age of the newborn to maximally 3 months proved that the cave served the females as the birthplace of their offspring. The cave lion bones from the sectors 2, 3, 4 and R4 of the Under the Ladder test pit represent the remains of at least four individuals (MNI = 4, Table 1), two of them were probably males and two females. The first of the individuals is a subadult female, which is represented by uniquely preserved almost completed skull, including large part of postcranial skeleton. The remaining three lion individuals died or were killed as adult. Wolf bone remains originate from at least two adult individuals (MNI = 2, Table 1), the first one was young adult individual, the second was older. The cave hyena bones originate from at least three adult individuals (MNI = 3, Table 1), presumably two females and one male. All other taxa from the sectors 2, 3, 4, and R4 of the Under the Ladder test pit are represented by single individuals (MNI = 1) only the bone remains of the red deer come from two differently aged adults (MNI = 2, Table 1). Determined osteological material from the sectors 2, 3, 4, and R4 from the Under the Ladder test pit originate from at least 57 individuals, however, especially in case of the taxa, which are represented by a greater number of the found bones it is more than likely that the actual number of individuals was higher.

Some bones of the bears from the group of the cave bear show evidence of food activity of carnivores or scavengers. There are teeth marks on the bear bones, bite and gnawing marks by wolves, cave hyenas, cave lions and maybe even cave bears. However, the number of bones with definite or probable gnaw marks is more or less low. On the bear bones from the layer B, it is possible to observe definite and probable gnaw or bite marks in total on 9.63 % of these bones. In the intermediate layer B+C the gnawing marks were found on 5.28 % of the bear bones and in the layer C the traces of food activity of carnivores were found on 5.42 % of bones of bears from group of cave bears. The traces of gnawing of another carnivore or scavenger were rarely found on some bones of the cave lion, wolf and cave hyena too. Still, a rather steady, even though small, portion of the gnawed, chewed or bitten bones suggests that this food source was of some importance to the carnivores.

Eight permanent teeth of various mammals from the Barová Cave were used to determine the seasonality and the dental age of the given individual. The method is based on the analysis of cemental increments on the teeth roots and exploits the fact that the rate of increment of the cement is not the same in various seasons. Increment is more intense during the growing summer season (May to October) and less intense during the dormant winter season (November to April). Moreover, the summer growth is bright and the winter growth is dark, due to a various activity of cementoblasts. The thickness of the last increment indicates the time elapsed since the beginning of its formation, i. e. from May or November. To calculate the dental age using the cement increment method, the time elapsed between the birth of the animal and the eruption of a particular permanent tooth has to be added (more in Lieberman et al., 1990; Carlson, 1991; Lakota-Moskalewska, 1997; Debeljak, 1997, 2000; Curci & Tagliacozzo, 2000; Ábelová, 2005; Hillson, 2005; Nývltová-Fišáková, 2007, 2013). The first individual of the cave lion, whose tooth was studied, died during April / May at 11 years, the second died in March at the age of 3 year and the third individual died in the autumn at the turn of October and November at the age of 9.5 years. Both the cave hyena individuals whose teeth were studied died in spring at the turn of April and May at the age of 5 and 9 years. One surveyed individual of the bear from group of cave bears died at the turn of April and May at the age of 14.3 years and one individual of wolf died also in spring (at the turn of April and May) at the age of 5 years. A single analyzed individual of the red deer died at the turn of April and May too at the age of 8 years. The seasonality of studied animal teeth suggests that the time of death varies the most frequently near the end of wintering season.

The tremendous amount of especially bear bone material leads to the consideration that the bears from the group of the cave bears wintered in the Barová Cave over a period of several thousand years. Dating of osteological material shows no contradiction with this assumption either. The peak of this inhabitancy is probably between 45,000 and 50,000 years BP according to radiocarbon dating. Considering the reasons for the death of the bear individuals in the Barová Cave, they were probably quite natural in the most cases, i. e. inadequate nutrition, injury, illness or higher age. Predation was not abundant as a reason for the death here, scavenging was possibly more regular. The way of deposition of the animal bones in the B-layer and C-layer sediments of the 2, 3, 4 and R4 sectors of the Under the Ladder test pit, together with the C14 dating results, put the local cave bears, lions and all other fauna in the same period of the more or less uninterrupted cave settlement. The found bone remains form logical thanatocoenosis.

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## CAVE BEARS IN THE VENETO REGION (N. ITALY): THE STATE OF THE ART

Mario Rossi<sup>1</sup> – Roberto Zorzin<sup>1</sup> – Giuseppe Santi<sup>2</sup>

<sup>1</sup> Department of Geology and Paleontology, Civic Museum of Natural History, Lungadige Porta Vittoria 9, 37100 Verona, Italy; mario.rush@tiscali.it, roberto.zorzin@comune.verona.it

<sup>2</sup> Department of Earth and Environmental Sciences, University of Pavia, Via Ferrata 1, 27100 Pavia, Italy; gsanti@unipv.it

Among the studies of the Italian populations of *U. spelaeus*, the bears of the Veneto region (N. Italy) (Fig. 1) are surely very interesting; in fact they show some evolutionary tendencies which characterize the populations of the Italian peninsula and more in particular those of the central-eastern sector of the Alps. The populations mainly studied come from Covoli di Velo (Verona Province) (Fig. 2) and Grotta of S. Donà di Lamon (Belluno Province). The most important and typical characteristic of these populations is the simultaneous presence of archaic characters principally in the denture, and modern features in both the metapodial bones and in size. The premolars when compared with those from the Gamssulzen cave (Austria) (the locality-type of the *U. ingressus* species), have less complicated morphotypes with less crests and accessory cusps; this is identified especially in the populations from both Grotta del Cerè and S. Donà di Lamon. In the Covoli di Velo population the P<sup>3</sup> is present, with about 42 %, a not negligible frequency. In general the bears have a middle-big size, when compared with those of cave bear populations with greater sizes and surely they are on the way of the evolutionary trend typical of *U. spelaeus*. The metapodial analyses support similar conclusions; in fact the plumpness indices of the metacarpal and metatarsi are similar to



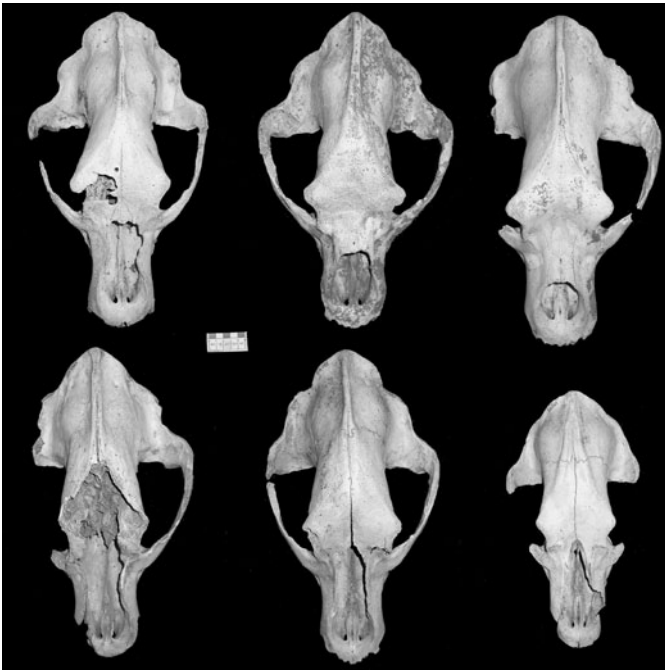


Fig. 1. Some specimens of skulls of cave bears from Covoli di Velo (Verona Province, Veneto).



Fig. 2. A room of the Covoli di Velo cave.

those of the more evolved populations. In general these features are very similar to those of some populations that inhabited the eastern sector of the Alps (Conturines and Pocala caves), while in the western ones; a more variegated situation is individuated. In fact, in the latter, populations with more evolved features, typical of the forms that lived in the central-eastern Europe (*U. ingressus*) have been individuated. This picture suggests the possibility that the Italian forms evolved with a conservative trend and the migratory ways toward the Alps involved almost exclusively the western sector, where the bear populations mix archaic and modern traits.

### THE METAPODIA AND PHALANGES OF THE CAVE BEAR FROM BUCO DELL'ORSO (LAGLIO, LOMBARDY, N. ITALY): A SINGLE POPULATION OR MORE POPULATIONS?

Mario Rossi<sup>1</sup> – Giuseppe Santi<sup>2</sup>

<sup>1</sup> Museo Civico di Storia Naturale, Lungadige di Porta Vittoria 9, 37100 Verona, Italy; mario.rush@tiscali.it

<sup>2</sup> Dipartimento di Scienze della Terra e dell'Ambiente, University of Pavia, Via Ferrata 1, 27100 Pavia, Italy; gsanti@unipv.it

Recently, the research and studies on the Buco dell'Orso remains (Laglio, Lombardy, N. Italy) have had as a topic of study new fossils of cave bears, namely the metapodia and phalanges. For the first time the latter are analysed and the results are partially in contrast with those known for the skulls,

mandibles and more superficially for the teeth. An unexpected dualism exists! Several argumentations are newly confirmed, namely considering the metapodia, in which the speleian population have a small-medium size, or that their evolutionary step is of an intermediate degree. The phalanges, in particular the 1° phalanx, are bigger in size, and this collides with the conclusions principally emerged from the skulls, mandibles and metapodia analyses. No morphometrical differences between the three species of cave bear (*U. ingressus*, *U. eremus* and *U. ladinicus*) and the population of Buco dell'Orso, have been found; we do not have clear elements that these Italian bears belong to one of these species. Are these differences in size the consequences of a morphometric variability of one population medially composed by elements with small or medium size? Or do these phalanges represent the remains of a different population that was partially coeval with the original of the Buco dell'Orso? The simpler answer is that the fossils represent the morphometric variability of the population, but the second hypothesis can be supported by the study of the succession of the bear populations inside Fontana Marella cave (Varese, Lombardy), a place near the Buco dell'Orso. In fact, in this cave a substitution of speleians with a lower evolutionary degree respect to the original population, is documented. Could it be possible that this "new" population is partially mixed with the original one of Buco dell'Orso? Perhaps both the chronological and genetic data will give a definitive answer.

### A JUVENILE SKULL OF CAVE HYENA FROM THE JASOVSKÁ JASKYŇA CAVE

Martin Sabol – Vlasta Petrovič

Department of Geology and Palaeontology, Faculty of Natural Sciences, Comenius University, Ilkovičova 6, 842 15 Bratislava, Slovakia; sabol@fns.uniba.sk, vlastapetrovic@gmail.com

The fossil record of cave hyenas (*Crocota crocuta spelaea* (Goldfuss, 1823)) from Slovakia is relatively rare, limited more or less to Late Pleistocene deposits of Čertova pec Cave, Dzeravá skala Cave, Gánovce-Hrádok, Jasovská jaskyňa Cave, Malá ľadnica Cave, Okno Cave, Prepoštská jaskyňa Cave, Salovec near Gombasek, Silická Brezová, and Tmavá skala Cave (Volko-Starohorský, 1927, 1929; Skutil, 1938; Hokr, 1951; Musil, 1996; Ďurišová, 2005; Holec, 2007; Sabol, 2008).

The Jasovská jaskyňa Cave (known also as Okno Cave or Takáčová jaskyňa Cave), one of the ten documented Slovak sites with fossil remains of cave hyenas, is situated near Jasov village in the Medzev Hills (Medzevská pahorkatina), approximately 20 km S-SW from Košice town (48° 40' 36" N, 20° 58' 35" E) (Fig. 1). The entrance of this 2,811 m long and 55 m deep fluvio-karst cave is situated at an elevation of 257 metres (Bella et al., 2007).



Fig. 1. Location of the Jasovská jaskyňa Cave (black arrow / white circle) in south-eastern Slovakia.

The first fossils of cave hyenas from this cave were mentioned by Volko-Starohorský (1929). He described briefly the third lower incisor (i3) together with several fragments of other teeth from the "second" dark-yellow to brown loam layer of excavated pit in the "Klinová chodba", situated above the "lower" reddish loam layer with the dominance of cave bear remains. However, the most spectacular cave hyena record from the Jasovská jaskyňa Cave is a skull of juvenile individual which had to be found later, after the excavations mentioned by Volko-Starohorský.

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 skull are known. Since Ložek et al. (1956) who carried out the last field campaign in the cave in 1955 reported no fossils of cave hyenas from the site, the skull was probably found here sometime between 1925 and 1955 during an archaeological prospection, although no report on that is maintained.

The gray to yellow skull of the juvenile cave hyena is damaged, especially in the anterior part and on the left side. Distinctly visible cranial sutures are not yet fully grown. The skull is relatively high, with a slightly arched frontal

area (*pars frontalis*) and with a rounded parietal part (*pars parietalis*) in the center of which, a short and low sagittal ridge runs at the dorsal side. Nasal and incisor bones are missing together with the anterior part of the palatal bones, of which only a wide posterior part with a pair of medium-sized palatal foramina and a more pronounced right sulcus (*sulcus palatinus dexter*) are preserved. Undamaged auditory bullae are large, oval and convex. The neurocranial part is markedly narrower than the visceral one in which, a wide palatal bones and a massive right zygomatic arc dominate.

Only the not-fully erupted third upper premolars are preserved from the dentition. The crown tip of P3 dext. is broken and P3 sin. is damaged and slightly worn. On both teeth, the massive conical paracone dominates; with an antero-lingual and a posterior ridge passing into the cingular accessory cusp. The cingulum is developed on the posterior, lingual, and anterior margins of the crowns of both P3. Only alveoli of other teeth are preserved; P1 was single-rooted, P2 was two-rooted, and P4 was three-rooted.

Based on the level of teeth change, when permanent premolars have already been cut (although their roots were not fully developed), the skull probably belonged to an individual younger than one year (Schütt, 1974).

In a morphological comparison with the skull of an approximately equally old spotted hyena individual (*C. crocuta intermedia*) from the Middle Pleistocene (Holsteinian) of French site Lunel-Viel, several major differences can be observed (Fig. 2). The most important one is the relatively smaller length and the higher height of the skull of the Late Pleistocene specimen (*C. crocuta spelaea*) in which, a significant expansion of the palatal and zygomatic areas can be observed. These differences are likely the 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, such as cave bears (Diedrich, 2005), mammoths, and woolly rhinoceroses.

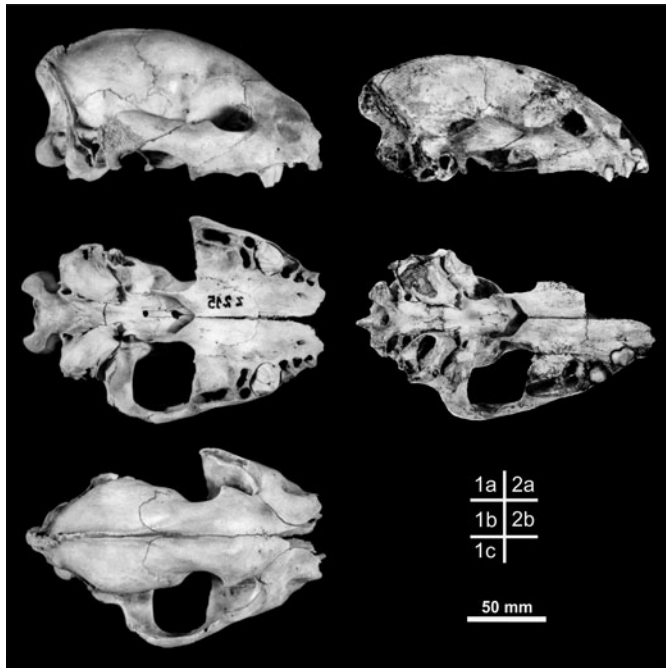


Fig. 2. Skulls of juvenile representatives of spotted hyena from the European Pleistocene: 1 – *Crocota crocuta spelaea* (Goldfuss, 1823), Jasovská jaskyňa Cave, Vistulian (Z 215; a – lateral view, b – ventral view, c – dorsal view), 2 – *Crocota crocuta intermedia* de Serres, 1828, Lunel-Viel, Holsteinian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

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## EVOLUTIONARY DEGREE OF CAVE BEAR FROM THE GROTTA DEL BANDITO (CUNEO-PIEDMONT, N. ITALY)

Giuseppe Santi<sup>1</sup> – Mario Rossi<sup>2</sup>

<sup>1</sup> Dipartimento di Scienze della Terra e dell'Ambiente, University of Pavia, Via Ferrata 1, 27100 Pavia, Italy; gsanti@unipv.it

<sup>2</sup> Museo Civico di Storia Naturale, Lungadige di Porta Vittoria, 9, 37100 Verona, Italy; mario.rush@tiscali.it

The Grotta del Bandito (Cuneo Province, Piedmont, N. Italy) is a rich deposit of cave bear remains; these are spelaeians and at present only the teeth have been deeply studied: the comparison of the different morphometric features with other species of cave bear (*ingressus*, *eremus*, *ladinicus*) doesn't show significant differences among them. The Bandito bears convergent features of different species in particular in the conformation of the teeth; in some cases these elements appear to be primitive, in others, on the contrary, they are more evolved. To indicate a dominant species is difficult because their individuation is principally genetic, but not morphometrical. We prefer to indicate for the Bandito cave bears the gr. *spelaeus* as a single species and no relationship with the altitude of the cave is noted. From a general point of view these bears occupy an intermediate evolutionary step, and therefore the more modern individuals are also present. In fact, overall in the fourth premolars some higher morphotypes have been found, more so than in other "Italian" populations where they are very rare. The explanation of this discrepancy is not easy, but the closeness of the Basura Cave (Liguria) in which more modern bears are found can induce us to postulate the hypothesis of the attempt of replacement of the "old" bears with the "modern" ones. If in the Basura Cave the disappearance of the older bear seems clearer, in the Bandito Cave it is softer. In other words, during the Late Pleistocene, close to the time of extinction of the speleians in the Bandito area maybe two different populations probably cohabited for a short period, one of these composed by old bears and a second, formed by few, but more modern elements. Therefore, the complete substitution did not occur all at once because the cave bears vanished and became extinct. This problem is still open.

## A NEW PLEISTOCENE MAMMAL FAUNA FROM BOTTICINO AREA (BRESCIA-LOMBARDY, N. ITALY). PRELIMINARY REMARKS

Paolo Schirolli<sup>1</sup> – Mario Rossi<sup>2</sup> – Giuseppe Santi<sup>3</sup> – Elisabetta Caserini<sup>3</sup> – Sigrid Huld<sup>3</sup> – Davide Casali<sup>1</sup>

<sup>1</sup> Museo Civico di Scienze Naturali, Via Ozanam 4, 25100 Brescia, Italy; pschirolli@comune.brescia.it

<sup>2</sup> Museo Civico di Storia Naturale, Lungadige di Porta Vittoria, 9, 37100 Verona, Italy; mario.rush@tiscali.it

<sup>3</sup> Dipartimento di Scienze della Terra e dell'Ambiente, University of Pavia, Via Ferrata 1, 27100 Pavia, Italy; gsanti@unipv.it

The Botticino area consists of a series of quarries placed toward the eastern surroundings of the city of Brescia (Lombardy, N. Italy) where the "Corna"

limestone is extracted under the name of "Botticino Classico". Inside this formation, several karst cavities and holes have filled with sediments and animal bones. Chronologically, these fossils are principally referred to the Middle Pleistocene, according to the biochronological data from small mammal assemblages (Bona et al., 2016). Fossils mainly have been gathered in three of the eleven levels known up to now: two of them are at the base (the most ancient) and one is in an intermediate position (the most recent) in the karst fissure-fill deposits exposed in the Quecchia Quarry in Botticino. Remains are, for the most part, still integrated in the sediment; only a minor part of them has been isolated. The matrix is composed of terrigenous sediments cemented with both calcareous and siliceous fragments. Often, the big fossils are complete or lacking only in their most frail parts. The most fragile bones, especially of micromammals, which are often complete, are in very great amounts to the point of forming an organogenic rock, as a consequence of low reworking and fast cementation. Remains of *Ursus gr. spelaeus*, *Panthera leo* and *Macaca sylvanus* represent the more important vertebrates identified together with bats, marmots, foxes, deer, goats, mustelidae, *Ursus arctos*. At the moment the faunal assemblage is under study.

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## ANCIENT DNA FROM CANIDS

Ulrike H. Taron<sup>1</sup> – Virgil Dragusin<sup>2</sup> – Stefan Vasile<sup>3</sup> –  
Michaela Preick<sup>1</sup> – Michael Hofreiter<sup>1</sup> – Johanna L. A. Pajmans<sup>1</sup>

<sup>1</sup> Institute for Biochemistry and Biology, University of Potsdam, Karl-Liebknecht Straße 24-25, 14476 Potsdam, Germany; [ulrike.taron@gmx.net](mailto:ulrike.taron@gmx.net), [michaela.preick@uni-potsdam.de](mailto:michaela.preick@uni-potsdam.de), [Michael.hofreiter@uni-potsdam.de](mailto:Michael.hofreiter@uni-potsdam.de), [pajmans.jla@gmail.com](mailto:pajmans.jla@gmail.com)

<sup>2</sup> Romanian Academy, Emil Racoviță Institute of Speleology, 31 Frumoasă, 010986 Bucharest, Romania; [virgil.dragusin@iser.ro](mailto:virgil.dragusin@iser.ro)

<sup>3</sup> University of Bucharest, Faculty of Geology and Geophysics, Department of Geology, 1 Nicolae Bălcescu Avenue, 010041 Bucharest, Romania; [stefan.vasile@gg.unibuc.ro](mailto:stefan.vasile@gg.unibuc.ro)

The dhole (*Cuon alpinus*) is the only extant species in the genus *Cuon*. Its current distribution encompasses South, East and Southeast Asia and includes a wide variety of habitats (tropical deciduous forests to mountainous alpine regions; IUCN, 2015). Due to severe population declines caused by habitat loss and fragmentation, decreasing prey availability, persecution by humans and possible infections with diseases of domestic dogs, the actual range and population size is not clearly known (IUCN, 2015). Based on pelage colour and length, up to eleven subspecies have been distinguished (Cohen, 1978; IUCN, 2015). However, patterns found in mitochondrial and nuclear DNA variation did not correspond with these subspecies designations, but rather supported two broad geographical groupings (Iyengar et al., 2005). During the Pleistocene the dhole was widely distributed across North America, Europe and Asia but became restricted to Asia at the end of the Late Pleistocene (Thenius, 1954; Cohen, 1978; Ghezze & Rook, 2014). Based on several morphological features, such as dental structure, multiple extinct species have been described (Petrucci et al., 2012; Ghezze & Rook, 2014). Better knowledge of genetic variability within and among these extinct species, as well as their relation to the extant *C. alpinus*, would greatly contribute to our understanding of glacial as well as post-glacial populations dynamics in dholes. Here, we present mitogenomic data from three metapodial remains from a Late Pleistocene cave site in Romania, that were considered to have belonged to *Cuon* sp. Ongoing morphological analysis of these specimens places them at the limit between wolves and dholes, while the discovery of a right *Cuon* hemimandible at the site is definitive evidence for *Cuon* presence here (Drăgușin et al., in preparation). We have successfully reconstructed near-complete mitochondrial genomes for these samples. The relationships between Pleistocene European dholes and modern dholes were assessed through the comparison to published dhole mitochondrial genomes, as well as other canids. As the mitochondrial genome is uniparentally inherited, it provides limited insight into the genetic association between the specimens under investigation, and their relation to other canids. To fully characterise relationships between ancient and extant dholes, broader sampling and the addition of nuclear data would be required.

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CAVE BEAR (*URSUS SPELAEUS*) EXTINCTION IN NORTHEASTERN ITALY: ANTHROPIC IMPACT, STABLE ISOTOPE EVIDENCE AND EXTINCTION CHRONOLOGY

Gabriele Terlato<sup>1,2</sup> – Matteo Romandini<sup>1,3</sup> – Nicola Nannini<sup>1,4</sup> –  
Marco Peresani<sup>1</sup> – Hervé Bocherens<sup>5,6</sup>

<sup>1</sup> Università degli Studi di Ferrara, Dipartimento di Studi Umanistici, Sezione di Scienze Preistoriche e Antropologiche, Corso Ercole I d'Este 32, 44100 Ferrara, Italy; [gabriele.terlato@gmail.com](mailto:gabriele.terlato@gmail.com), [ncl.nannini@gmail.com](mailto:ncl.nannini@gmail.com), [psm@unife.it](mailto:psm@unife.it)

<sup>2</sup> Area de Prehistoria, Universitat Rovira i Virgili (URV), Avinguda de Catalunya 35, 43002 Tarragona, Spain

<sup>3</sup> Dipartimento di Beni Culturali, Università di Bologna, Via degli Ariani 1, Ravenna 48121, Italy; [matteo.romandini@unibo.it](mailto:matteo.romandini@unibo.it)

<sup>4</sup> MuSe – Museo delle Scienze, Corso del Lavoro e della Scienza 3, 38123 Trento, Italy

<sup>5</sup> Department of Geosciences, Biogeology, University of Tübingen, Hölderlinstraße 12, Tübingen, 72074, Germany; [herve.bocherens@uni-tuebingen.de](mailto:herve.bocherens@uni-tuebingen.de)

<sup>6</sup> Senckenberg Center for Human Evolution and Palaeoenvironment (HEP), University of Tübingen, Hölderlinstraße 12, Tübingen, 72074, Germany

The disappearance of the cave bear (*Ursus spelaeus*) is one of many spectacular megafaunal extinctions that occurred during the last 30,000 years in Europe. The largest amount of remains has been recovered from many caves, most of which associated with human deposits in archaeological sites. In order to address the reasons for extinction and paleoecology of cave bear, we present taphonomic and isotopic analyses of Upper Pleistocene *Ursus spelaeus* (26–18 ka BP) from three cave sites in northeastern Italy (Berici Hills – Vicenza): Grotta di Paina, Buso doppio del Broion and Covolo fortificato di Trene. In some of these caves, taphonomic analyses suggest close interactions between humans and bears, which used the caves as dens during wintering. Numerous bear remains reveal several well preserved traces of human modification such as cut marks, which enable a reconstruction of the main steps of the butchering process and fur recovery. In preparation of isotopic analyses, 49 cave bear bones were screened for collagen preservation by measuring their nitrogen content. The results demonstrated the very good quality of collagen preservation. The carbon and nitrogen isotopic analysis of this bone collagen will allow a palaeodietary reconstruction of these cave bears, as well as direct radiocarbon dating. The broad range of plant types available and the favorable location of Berici Hills may have played an important role in the range expansion of cave bears and their interaction with the Paleolithic hunters who frequented the area.

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REVISION OF EARLY ASIATIC BLACK BEAR (*URSUS THIBETANUS*) – ITS MORPHOLOGICAL, PHYLOGENETICAL AND TAXONOMICAL RESULTS

Jan Wagner<sup>1,2</sup> – Qigao Jiangzuo<sup>3,4</sup> – Jinyi Liu<sup>3</sup>

<sup>1</sup> Department of Palaeontology, National Museum, Cirkusová 1740, 193 00 Prague 9, Czech Republic; [jan\\_wagner@nm.cz](mailto:jan_wagner@nm.cz)

<sup>2</sup> Institute of Geology of the CAS, v. v. i., Rozvojová 269, 165 00 Prague 6, Czech Republic

<sup>3</sup> Key Laboratory of Vertebrate Evolution and Human Origins of Chinese Academy of Sciences, Institute of Vertebrate Palaeontology and Paleoanthropology CAS, Xizhimenwai Street 142, Beijing, China; [jiangzuo@ivpp.ac.cn](mailto:jiangzuo@ivpp.ac.cn), [liujinyi@ivpp.ac.cn](mailto:liujinyi@ivpp.ac.cn)

<sup>4</sup> University of Chinese Academy of Sciences, Beijing 100049

Asiatic black bear (*Ursus thibetanus* Cuvier, 1823) is an extant bear species inhabiting areas in South and East Asia. Present distribution ranges from

southeastern Iran on the west to Japan on the east and from Southeast Asia mainland (except Malaysia) on the south to southern Russian Far East on the north. But in the past, distribution of *U. thibetanus* was more extensive, reaching to the Western Europe, Caucasus, and Middle Ural Mountains (Crégut-Bonnoure, 1997; Baryshnikov, 2002, 2010, and references therein). But it seems that distribution centre was always in the southern part of East Asia.

Although the origin of this species was discussed several times in the past, in fact, no relevant evidence about it was available until recently. For a long time, Middle and Late Pleistocene fossil record represented almost all the fossil material available for this species, with only few exceptions (e. g., Liucheng *Gigantopithecus* Cave (= Juyuangong Cave); Pei, 1987). Neither molecular studies, despite producing many new and important data, provide more accurate basis for solving this problem. They estimate splitting time of *U. thibetanus*-lineage from other extant ursines from 4.4 Ma (Kumar et al., 2017) to 1.56 Ma (Kutcher et al., 2014). The knowledge about early evolutionary history of the species was therefore very limited, until discovering several new Early Pleistocene localities with *U. thibetanus* (Renzidong Cave, Tuozhi Cave, Longgupo, Longgudong Cave) during last two decades. Up to now, the Early Pleistocene record of *U. thibetanus* is exclusively limited to the territory of China, from where also a new Gelasian subspecies, *U. t. primitivus* Liu et Qiu, 2009, was described (Liu & Qiu, 2009). Moreover, several Early Pliocene specimens from Europe were assigned to this lineage (e. g., Mazza & Rustioni, 1994; Baryshnikov & Zakharov, 2013).

We revisited dental material from 9 Early Pleistocene localities (with the largest samples from Gelasian Liucheng *Gigantopithecus* Cave (in Liucheng, Guangxi Province, Southernmost China) and Calabrian Longgudong Cave (in Jiangshi, Hubei Province, northern part of Southern China) and compared it with Middle Pleistocene and extant representatives of the species from China and Europe as well as with assumed Pliocene Asiatic black bears. The preliminary results are as followed:

1. Concerning dental material, the Pliocene specimens assigned to *U. thibetanus*-lineage (a) do not bear *thibetanus*-like morphology in m1 and (b) although parastyle in M1 is similar to that of Middle Pleistocene (and later) *U. thibetanus*, it is more developed than in Gelasian representatives. We therefore resulted that the similarities are results of convergent evolution and not an evidence of ancestral position.
2. The characters typical for modern *U. thibetanus*, e. g. morphology of End area in m1, are still much more polymorphic in Gelasian population with morphotypes absent in the species since Middle Pleistocene (or possibly from Calabrian).
3. There is possible to detect oriented morphometric changes from Gelasian to Middle Pleistocene. Latest from Middle Pleistocene the reached the extant morphological pattern.
4. During the Early Pleistocene, *U. thibetanus* distribution is almost exclusively limited to the southern parts of China. It expands northwards ca. during early Middle Pleistocene, which correlates surprisingly well with FAD of this species in Europe. But if we compared, more or less contemporary population from China (Zhoukoudian Loc. 1, Heshandong) and Europe (Mauer etc.), we see some fine differences in size and proportion of the teeth. It seems therefore probable, that source population for European colonization was not located in China (but probably in more southern regions).

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## ANCIENT NUCLEAR GENOMES UNRAVEL THE EVOLUTIONARY HISTORY OF *CROCUTA CROCUTA*

Michael Westbury<sup>1</sup> – Stefanie Hartmann<sup>1</sup> – Axel Barlow<sup>1</sup> – Rasmus Heller<sup>2</sup> – Michaela Preick<sup>1</sup> – Li Fang<sup>3</sup> – Guojie Zhang<sup>3</sup> – Arne Ludwig<sup>4</sup> – Bogdan Ridush<sup>5</sup> – Doris Nagel<sup>6</sup> – Thomas Rathgeber<sup>7</sup> – Reinhard Ziegler<sup>7</sup> – Gennedy Baryshnikov<sup>8</sup> – Guilian Sheng<sup>9</sup> – Ingrid Wiesel<sup>10</sup> – Love Dalen<sup>11</sup> – Michael Hofreiter<sup>1</sup>

<sup>1</sup> Institute for Biochemistry and Biology, University of Potsdam, Karl-Liebknecht-Strasse 14-15, 14476 Potsdam, Germany; westbury@uni-potsdam.de, axel.barlow.ab@gmail.com,

michaela.preick@uni-potsdam.de, Michael.hofreiter@uni-potsdam.de

<sup>2</sup> The Bioinformatics Centre, Department of Biology, University of Copenhagen, Ole Maaløes Vej 5, 2200 Copenhagen, Denmark; stefanie.hartmann@uni-potsdam.de

<sup>3</sup> BGI-Shenzhen, Beishan Industrial Zone, Yantian District, 518083, Shenzhen, China

<sup>4</sup> Department of Evolutionary Genetics, Leibniz Institute for Zoo and Wildlife Research, Alfred-Kowalle Straße 17, 10315 Berlin, Germany; ludwig@izw-berlin.de

<sup>5</sup> Department of Physical Geography and Natural Management, Geographical Faculty, Chernivtsi 'Yuriy Fed'kovych' National University, Kotsubynskogo 2, 58012 Chernivtsi, Ukraine; ridush@yahoo.com

<sup>6</sup> University Vienna, Department of Palaeontology, Althanstraße 14, A-1090 Vienna, Austria; doris.nagel@univie.ac.at

<sup>7</sup> Staatliches Museum für Naturkunde Stuttgart, Rosenstein 1, 70191 Stuttgart, Germany; ziegler.smns@naturkundemuseum-bw.de

<sup>8</sup> Laboratory of Theriology, Zoological Institute of the Russian Academy of Sciences, 1, Universitetskaya emb., 199034, Saint-Petersburg, Russia; ursus@zin.ru

<sup>9</sup> State Key Laboratory of Biogeology and Environmental Geology, China University of Geosciences, No. 388 Lumo Road, 430074 Wuhan, Hubei, China

<sup>10</sup> Brown Hyena Research Project, Luderitz, Namibia, Centre of Wildlife Management, University of Pretoria, Private bag X20, Hatfield 0028, South Africa; strandwolf@eivway.na

<sup>11</sup> Department of Bioinformatics and Genetics, Swedish Museum of Natural History, Box 50007, 104 05 Stockholm, Sweden; Love.Dalen@nrm.se

Cave hyena existed across Eurasia until the end of the Pleistocene. Initially, due to the distinctive morphologies, Eurasian cave hyena (*Crocota crocuta spelaea*) and modern African spotted hyena (*C. c. crocuta*) were considered different subspecies or even species. In contrast to this, a study using mitochondrial DNA (Rohland et al., 2005) found the Eurasian cave hyena and the African spotted hyena to be phylogenetically indistinct, with genetic differentiation of Northern and Southern African spotted hyena populations being greater than that occurring between Northern Africa spotted hyena and some Eurasian cave hyena. However, this study involved only a short marker of maternally inherited mtDNA so lacked the ability to detect the more extensive admixture potentially occurring between sympatric hyena populations as suggested by morphological evidence.

We have generated nuclear genomic data from a number of Late Pleistocene cave hyena individuals originating from across Eurasia as well as a number of modern spotted hyena individuals originating from across Africa. Nuclear data allows the detection of male mediated gene flow, and as male dispersal is known to play a large role in the breeding habits of modern spotted hyena, the inclusion of this would allow the detection of a potentially large force of interpopulational gene flow previously undetectable using just the maternally inherited mtDNA data.

By performing genetic comparisons between both cave and spotted hyena, we uncover a relationship more closely resembling the geographical and morphological evidence and unsurprisingly, with evidence for admixture between the two. In contrast, when investigating the population structure patterns within Eurasian cave hyena, we find a pattern more similar to that suggested in the mitochondrial evidence as opposed to what would be expected based on the geographic relationships of the individuals. On top of this, we find very little genetic differentiation within modern spotted hyena relative to cave hyena. This finding could represent that the cave hyena was the resident population hinting towards and into Africa dispersal or that there must have been a large bottleneck within the spotted hyena after the dispersal of the cave hyena out of Africa dispersal. The former being the more parsimonious of the two.

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## 23rd CAVE BEAR SYMPOSIUM – VENUE AND EXCURSION GUIDE

**Michal Rendoš<sup>1</sup> – Zuzana Višňovská<sup>1</sup> – Martin Sabol<sup>2</sup> – Peter Holúbek<sup>3</sup>**

<sup>1</sup> State Nature Conservancy of the Slovak Republic, Slovak Caves Administration, Hodžova 11, 031 01 Liptovský Mikuláš, Slovakia; [michal.rendos@ssj.sk](mailto:michal.rendos@ssj.sk), [zuzana.visnovska@ssj.sk](mailto:zuzana.visnovska@ssj.sk)

<sup>2</sup> Department of Geology and Palaeontology, Faculty of Natural Sciences, Comenius University, Ilkovičova 6, 842 15 Bratislava, Slovakia; [sabol@fns.uniba.sk](mailto:sabol@fns.uniba.sk)

<sup>3</sup> Slovak Museum of Nature Protection and Speleology, Školská 1124/4, 031 01 Liptovský Mikuláš, Slovakia; [peter.holubek@smopaj.sk](mailto:peter.holubek@smopaj.sk)

### SYMPOSIUM VENUE – LIPTOVSKÝ MIKULÁŠ

Liptovský Mikuláš, formerly called Liptovský Svätý Mikuláš (Liptovský Saint Nicholas in English) is a town in northern Slovakia, in the Liptov Basin surrounded by the Western Tatras in the north and the Low Tatras in the south and the Choč Mountains in the north-west (Fig. 1). The town extends mainly on the right bank of the Váh River, the longest river

right of self-determination of the Slovak nation within the Hungarian Empire. Ľudovít Štúr, the leader of the Slovak National Revival, publicly disclosed a document called “The demands of Slovak nation” in 1848 in Liptovský Mikuláš. The document was an official appeal to the leaders of Austrian-Hungarian Empire to help to solve the then existential problems of the Slovaks. In 1945, at the end of the World War II, one of the longest and most difficult liberation battles in the territory of former Czecho-

Slovakia and in case of show caves, their safe and sustainable use. Its administration is under direct management of the State Nature Conservancy of the Slovak Republic, which is a part of the Ministry of Environment of the Slovak Republic. Slovak Museum of Nature Protection and Speleology (<http://www.smopaj.sk>) (Fig. 2) is the museum specialized in nature protection and speleology in Slovakia and includes several permanent exhibitions on display protected fauna, flora, minerals and caves. Slovak



Fig. 1. Panoramic view of Liptovský Mikuláš and the Low Tatras in the background. Photo: M. Rengevič, source: Information Centre of the town Liptovský Mikuláš

within Slovakia, directly at its inlet to the Liptovská Mara artificial water dam. With a population of about 35,000, Liptovský Mikuláš is the most populous urban area in the Liptov Region and at the same time, it is an important tourist and cultural centre.

From the 10th century until 1918, the Liptov Region, as well as the rest of the territory of today's Slovakia was a part of the Kingdom of Hungary and the later Austro-Hungarian Empire. The first written mention of Liptovský Mikuláš dates back to 1286. In the 14th century, the originally parish settlement developed into a medieval town, which at the end of 17th century became the seat of the Liptov County. Since 1424, the town had the privilege to hold an annual fair, which greatly supported its economic and urban expansion. An interesting personage of national history, the most famous Slovak highwayman Juraj Jánošík often referred to as “the Slovak Robin Hood”, was imprisoned, sentenced to death and executed by being hung by the ribcage on a hook in Liptovský Mikuláš in 1713. According to the legend, Jánošík robbed nobles and gave the loot to the poor. During the period of 19th century, Liptovský Mikuláš was one of the Slovak National Movement centres. It was home to prominent Slovak romantic poet and national activist Janko Kráľ who was fighting for the

slovakia took place in Liptovský Mikuláš and its surroundings. The Czechoslovak and Soviet troops fought for liberation of the town for two months during which, more than 4.5 thousand soldiers deceased. This tragic event is commemorated today by the military monument and cemetery on the hill called Háj towering above the town.

Since the second half of 20th century, Liptovský Mikuláš has become an important centre of national speleology. It has been a seat of three major Slovak speleological institutions. Slovak Caves Administration (<http://www.ssj.sk>) is a specialized organization of nature protection managing the protection of all caves in

Speleological Society (<http://www.sss.sk>) is a professional civic association of Slovak voluntary spelunkers. Its main mission is to discover, register, document and protect caves as well as other karst phenomena.

### 1st EXCURSION DAY – OCTOBER 5, 2017 (THURSDAY)

#### DEMÄNOVSKÁ VALLEY

It is the most famous and most visited natural site of the Liptov Region lying approximately 10 km south of Liptovský Mikuláš, on the northern slopes of the Low Tatras – an extensive mountain range with a main ridge stretching over 82 km east-west. The 15 km long valley is a part of the Low Tatras National Park and extends northwards from the foot of dominant Chopok Peak (2,024 m a. s. l.) to the Liptov Basin (Fig. 3). From geological and geomorphological point of view, the Demänovská Valley is composed of the two different parts. The upper and wider part of the valley, near the main ridge of the Low Tatras, consists of granites and was predominantly formed by glaciers during the Pleistocene proof of which, is the Vrbické pleso moraine-dammed lake (Fig. 4). The lower limestone part of the valley is narrower and represents a karst canyon deepened particularly by the allochthonous Demänovka River.



Fig. 2. Symposium venue – Slovak Museum of Nature Protection and Speleology in Liptovský Mikuláš. Photo: Z. Višňovská



Fig. 3. Karstic part of the Demänovská Valley with the main ridge of the Low Tatras in the background. Photo: P. Bella



Fig. 4. Vrbické pleso moraine-dammed lake (1,113 m a. s. l.) in the Demänovská Valley. Photo: Z. Višňovská

### Karst and caves of the Demänovská Valley

Karst of the Demänovská Valley built on the Middle Triassic Gutenstein Limestones of the Krížna Nappe represents a contact dissected karst of monoclinial crests and ridges in the middle-mountain positions of the Western Carpathians. Prevailing karst features in this dissected mountain area relate to the subsurface phenomena. There are more than 200 caves of various genetic types known in the Demänovská Valley.

The dominant cave system on the right side of the valley, known as Demänovský Cave System (Fig. 5), was formed at nine levels chiefly by the sinking waters of Demänovka River. The development of cave levels is cor-

related with the development of river terraces on the surface in the north part of the valley and the adjacent part of Liptov Basin. However, the whole cave system is not morphologically homogenous. At the contact of non-karstic and karstic areas, several drawdown vadose passages lead from sinkholes or invasion sinkholes to a lower levelled river bed of main underground stream. With a total length of more than 40 km, Demänovský Cave System represents the longest cave system in Slovakia and consists of the Demänovská jaskyňa mieru Cave (ca 16.5 km), Demänovská jaskyňa slobody Cave (ca 11.1 km), Pustá jaskyňa Cave (ca 6.2 km), Demänovská ľadová jaskyňa Cave (ca 2.2 km) and other

smaller caves (Herich & Holúbek, 2015). Of these, the Demänovská jaskyňa slobody Cave and Demänovská ľadová jaskyňa Cave are open to the public.

In 2006, the caves of the Demänovská Valley were included in the list of internationally important wetlands within the commitment of the Ramsar Convention on Wetlands. This Ramsar site represents a unique subterranean system with the specific environmental conditions supporting the occurrence of many cave-adapted aquatic and terrestrial invertebrate species (e.g. subterranean crustaceans *Niphargus tatrensis* and *Bathynella natans* (Fig. 6), palpigrade *Eukoenia spe-laea* (Fig. 7), local endemic carabid beetle

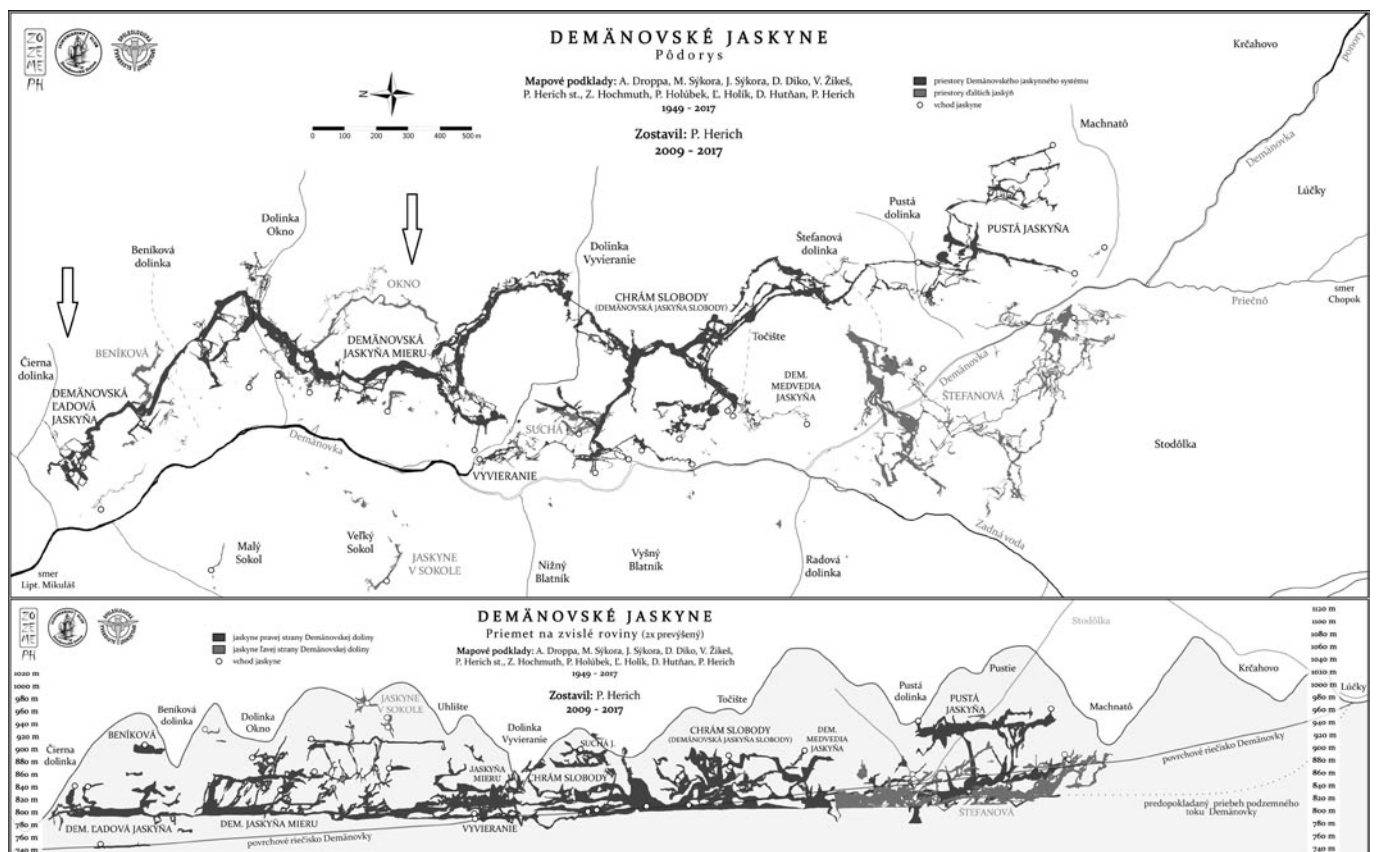


Fig. 5. Demänovský Cave System with arrow-marked position of Demänovská ľadová jaskyňa Cave and Okno Cave. Ground plan and side projection after Herich (2017).

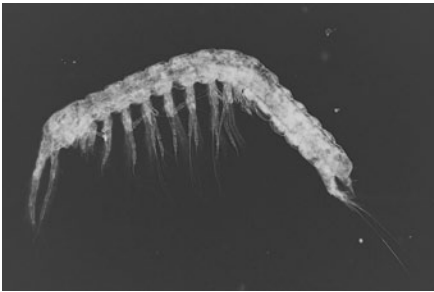


Fig. 6. Bathynellid crustacean *Bathynella natans* (Crustacea). Photo: Z. Višňovská



Fig. 7. Palpspider *Eukoenenia spelaea* (Arachnida). Photo: Ľ. Kováč & P. Luptáčik

*Duvalius microphthalmus spelaeus*, and the others). Several caves in the valley, and especially the Demänovská ľadová jaskyňa Cave, rank among the most important hibernation sites of cryophilic forest bat species, such as the Northern Bat (*Eptesicus nilssonii*, Fig. 8), Whiskered Bat (*Myotis mystacinus*) and Brandt's Bat (*Myotis brandtii*) in Slovakia.



Fig. 8. The Northern Bat – *Eptesicus nilssonii* (Chiroptera). Photo: Z. Višňovská

#### Demänovská ľadová jaskyňa Cave

The Demänovská ľadová jaskyňa Cave (Demänovská Ice Cave) is located on the right side of the Demänovská Valley. Its entrance (840 m a. s. l.) is about 90 m above the valley bottom, in the rock cliff called Bašta. The cave was eroded by the previous ponor flow of the Demänovka River inflowing here from the Demänovská jaskyňa mieru Cave. The cave (Fig. 9) represents the northern, previously resurgence part of the Demänovský Cave System. The total length of the measured parts is 2,174 m with elevation span of 80 m (Herich

& Holúbek, 2015). The cave spaces spread in three development levels and consist of oval, river-modelled passages with ceiling and side troughs, and dome spaces reshaped by collapse and frost weathering.

Permanent ice fill occurs in the lower parts of the cave, mostly in Kmetov dóm (Kmet's Dome). We can find there floor ice, ice columns, stalactites and stalagmites (Fig. 10). The conditions for glaciations have started after burying several openings to the surface in consequence of slope modelling processes by which, the air circulation was restricted. Heavi-

er cold air is kept in the lower parts of the cave. Seeping precipitation water freezes in overcooled underground spaces. Air temperature fluctuates in glaciated parts under 0 °C and in the direction back to the non-glaciated parts, it rises up to 6 °C. Relative air humidity ranges between 92 and 98 % in deeper parts of the cave. Original flowstone and dripstone fills were preserved mostly in the back of the cave where the effect of frost weathering is minimal or absent. Several of these formations have a dark colouring. This is due to the excessive use of tar torches, oil burners and paraffin

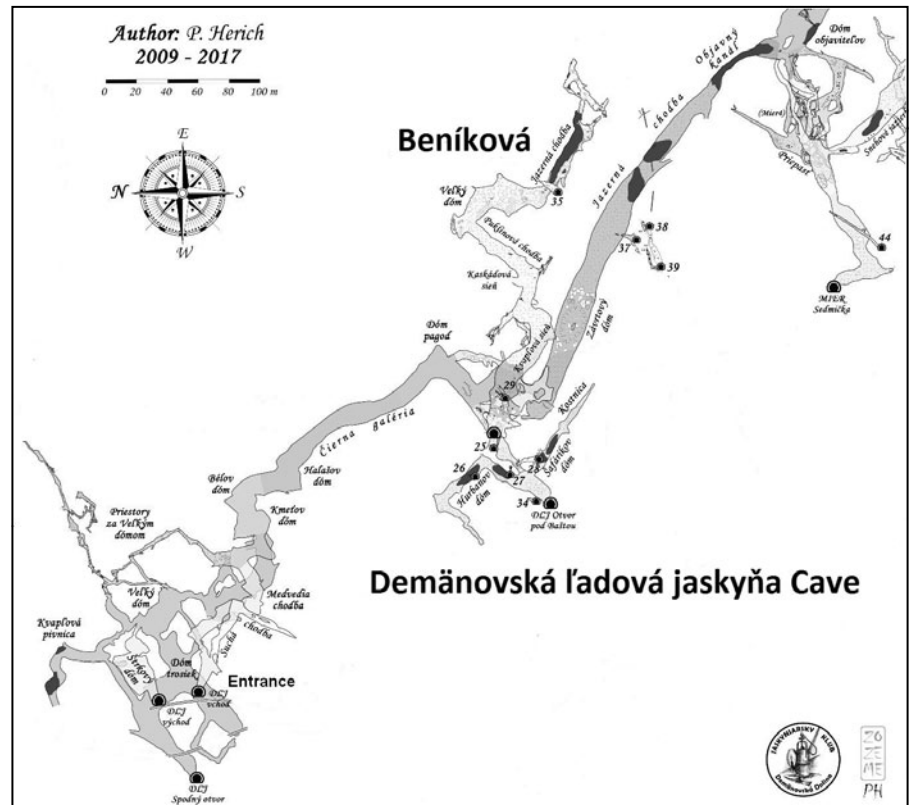


Fig. 9. Demänovská ľadová jaskyňa Cave. Ground plan after Herich (2017).



Fig. 10. Demänovská ľadová jaskyňa Cave – permanent ice fill in Kmet's Dome. Photo: Z. Višňovská



Fig. 11. Inscriptions on the walls of Demänovská ľadová jaskyňa Cave. Photo: Z. Višňovská

lamps that served to illuminate the cave in the past (until 1924).

The first written mention of the Demänovská ľadová jaskyňa Cave dates back to 1672 and is associated with the description of a cave near Liptovský Mikuláš. The description was compiled by Johann Paterson Hain, the first well-known Upper Hungarian scholar who was exploring the cave bears and their remains, considered at that time as the remains of the dragons. This is the reason why the cave was called “the Dragon Cave” in the past. Plenty of inscriptions on the cave walls (Fig. 11) and rich well-preserved literature indicate a great interest of the then scientific circles as well as general public in the Demänovská ľadová jaskyňa Cave. The primary opening of the cave to the public took place in the eighties of 19th century, but in 1924, when the Demänovská jaskyňa slobody Cave was made accessible, it was closed for the lack of interest. After new technical arrangements including the installation of electric lighting, the cave was reopened for the public in 1952. Of the total length of cave passages, the 650 m long section is available nowadays to visitors.

### Okno Cave

The entrance to the Okno Cave (Window Cave) is located in the same-name rock cliff, on the right side of the Demänovská Valley, at an altitude of 915 m a. s. l. Nearby the cave entrance, there are two interesting rock openings called Veľké Okno (Large Window) and Malé Okno (Small Window). The current known length of the Okno Cave is 2,676 m with a vertical span of 110 m (Herich, 2017). This inactive fluviokarst cave (Fig. 12), almost horizontal in a main long-section, represents the oldest and uppermost ninth level in the sequence of Demänovský Cave System development and is principally composed of former stream passages created by the Demänovka River. A fluvial origin of the main passages is supported by the presence of well-developed scallops on the walls of Sieň smútočnej vrby (Chamber of Sad Willow). Fluvial activity is also indicated by

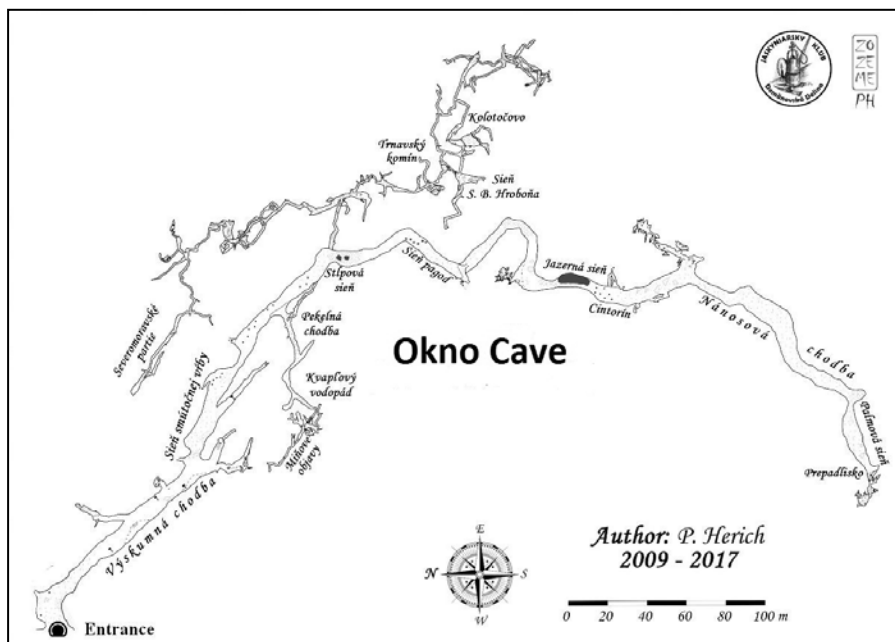


Fig. 12. Okno Cave. Ground plan after Herich (2017).



Fig. 13. Okno Cave – the lake in Jazerná sieň (Lake Corridor). Photo: Z. Višňovská

large deposits of strongly cemented clastic sediments composed of coarse sand and rounded pebbles. The cave corridors are characterized by a relatively rich cave fills with the exception of the entrance Výskumná chodba (Research Corridor), where it was destroyed by frost weathering as well as by vandals. Undoubtedly, one of the most beautiful cave features is a lake in Jazerná sieň (Lake Corridor) with a skeletal cave travertine on its bottom (Fig. 13). The cave air temperature ranges between 5.8 and 6.6 °C, with a relative humidity of 88 to 96 %.

The Okno Cave was described for the first time by Slovak polymath Matej Bel in 1723. Its deeper passages, rich in sinter decoration, were discovered by Prague scouts in 1921 and during exploratory works that took place between 1923 and 1925. The cave was made accessible to the general public in 1925 by Ladislav Povol-

ný, the owner of neighbouring land. However, the cave was closed a few years later due to the lack of interest. In the cave, several archaeological artefacts have been excavated, the oldest of which originate from the end of Copper Age (Eneolith), specifically from the period of Baden culture (ca 3600 – 2700 BC).

### Palaeontological discoveries in the Demänovská Valley

The Demänovská Valley is known not only for its karst phenomena but also for rich fossil content excavated in the passages of almost all larger horizontal caves (Volko-Starohorský, 1927; Skřivánek, 1954; Sabol, 2000, 2002; Sabol & Struhár, 2003). Osteological remains of extinct representatives of Ursidae family are among the most common palaeontological discoveries in the Demä-



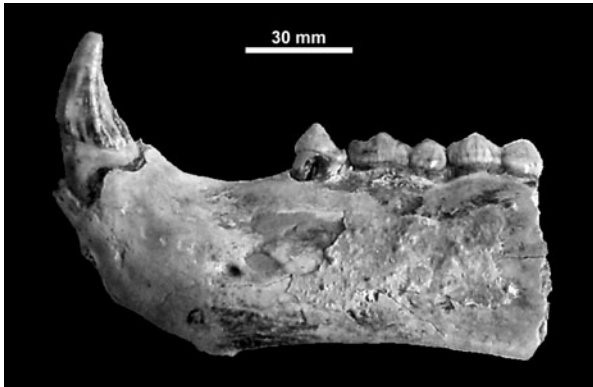


Fig. 14. Left mandible fragment with dentition of *Ursus ex gr. spelaeus* from the Late Pleistocene deposits of Demänovská medvedia jaskyňa Cave. Photo: M. Sabol

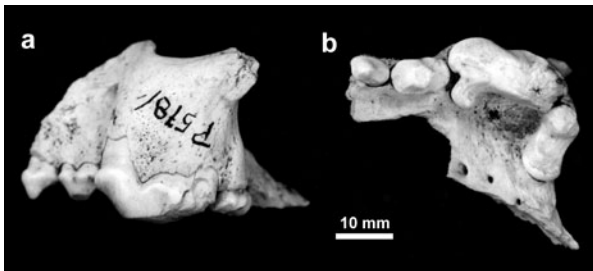


Fig. 15. Left maxillary fragment with P2 to M1 of *Gulo gulo* from the Late Pleistocene deposits of Okno Cave: a - buccal view, b - occlusal view. Photo: E. Klimešová

novská Valley. In the vast majority of cases, such remains have been found in the form of accumulation of isolated bones and teeth. The findings of the complete skeletons are still very rare. Hitherto, the fossil remains of the two forms of ursine carnivores have been found in the Demänovská Valley caves. The first form represents the larger and massive cave bears from *spelaeus* group (*Ursus ex gr. spelaeus*, Fig. 14) while the second one represents the brown bears (*Ursus ex gr. arctos*) that could belong to the extinct representatives of brown bear (*U. cf. priscus*) living during the Last Glacial period (Sabol, 1999, 2001). However, the species status of *U. priscus* was recently disputed as the type material has the characteristics of the modern brown bear (*U. arctos*) (Pacher, 2007).

The Okno Cave represents one of the most remarkable paleontological sites in the Demänovská Valley. Abundant fossil materials excavated in the cave coarse gravel sediments by naturalist Ján Volko-Starohorský is currently housed by Liptov Museum in Ružomberok (with its depository in Liptovský Mikuláš). Volko-Starohorský (1925) reported the fossils of "glacial" (*Lagopus albus* and *Vulpes lagopus*) and "postglacial" fauna (*Felis leo*, *F. pardus*, *Felis sp.*, *Hyaena crocuta*, *Canis lupus*, *Martes martes*, *Ursus spelaeus*, *U. arctos*, *Saiga* antelope, *Cervus dama*, and *Tarandus rangifer*) as well as discovery of *Homo sapiens* and the Holocene ruminants and *Cervus elaphus*. Later on, Volko-Starohorský (1927) described the fossil finds of *Ursus spelaeus*, *U. arctos*, *Canis lupus*, *Vulpes cf. lagopus*, *Hyaena crocuta*, *Felis sp.*, *F. pardus*, *F. leo*, *Saiga* antelope, *Cervus dama*, and *Lagopus alba* and mentioned a bone record of domestic animals from the surface of cave sediments.

Preliminary re-determination of the fossil material from the Liptov Museum depository confirmed the occurrence of *Canis lupus*, *Cuon cf. alpinus*, *Gulo gulo*, *Martes sp.*, *Meles meles*, *Mustelidae* indet., *Panthera spelaea*, *Ursus ex gr. arctos*, *U. ex gr. spelaeus* as well as so far undetermined fossil remains of mammals. Late Pleistocene finds of wolverine (*Gulo gulo*) (Fig. 15) and bears have already been described by Sabol (1999, 2006). However, bear fossils (171 teeth, 5 damaged jaws and 1 incomplete juvenile cranium) were determined only as *Ursus sp.* due to the presence of "arctoid" and "speleoid" characters on the teeth crowns and their dimensions (Sabol, 1999). Based on the radiocarbon dating (Ábelová & Sabol, 2009), the extinction of main megafaunal elements is assumed before the beginning of the Last Glacial Maximum (ca 25,000 years ago).

## 2nd EXCURSION DAY – OCTOBER 7, 2017 (SATURDAY)

### JÁNSKA VALLEY

The valley lies east of the Demänovská Valley and is a part of the national nature reserve being declared in 1928. With a length of almost 18 km, it represents one of the longest valleys of the Low Tatras stretching northwards from the foot of the Low Tatras highest peak Ďumbier (2,046 m a. s. l.) to the village of Liptovský Ján (Fig. 16).

The spa village of Liptovský Ján located 9 km east of Liptovský Mikuláš is known for its 14 mineral springs, some of which are warm with a water temperature ranging from 14.8

to 29.4 °C. The most popular is Teplica spring, familiarly called "Kaďa", containing approximately 830 mg/L of sulphates. These mineral waters are used for therapeutic purposes as well as for thermal water swimming pools open to the general public. The first written mention about the village dates back to 1327. The most striking historic site is the fortified Roman-Gothic Church dedicated to St. John the Baptist built at the end of 13th century.

### Karst and caves of the Jánska Valley

Similarly to the neighbouring Demänovská Valley, the upper granite part of the Jánska Valley underwent a significant glacial modelling during the Pleistocene glaciations. Monoclinic carbonate rocks of the Mesozoic Age are situated here directly on the crystalline granite rocks (Krakova Hoľa – 1,752 m a. s. l.). The lower section of the valley is built on the Middle Triassic Gutenstein Limestones of the Chočský Nappe and was primarily formed by the allochthonous Štiavnica River. At present time, more than 250 caves with a total length of more than 45 km are known in the valley. Of these, the most remarkable is the Slovak deepest cave system of Hipman's Caves (vertical span of 499 m), and Jaskyňa zlomísk Cave representing one of the longest Slovak caves (known length of 11.2 km) (Holúbek, 2015). With a length of more than 7 km, the Stanišovské Caves represent another large complex of underground spaces consisting of three mostly horizontal caves (Fig. 17). Malá stanišovská jaskyňa Cave (871 m) along with Stanišovská jaskyňa Cave (3.138 m) forms a single genetic system including also Nová stanišovská jaskyňa Cave (3.242 m) on the opposite side of the small side valley (Holúbek, 2015). These underground spaces were created mostly by erosion and corrosion activity of Štiavnica River penetrating the underground through several ponors and flowing along the tectonic faults.

### Malá stanišovská jaskyňa Cave

The Malá stanišovská jaskyňa Cave (Small Stanišovská Cave) is situated on the right side of the Jánska Valley, in the south-western slope of the Smrekovica Massif at an altitude of 766 m



Fig. 16. Karstic part of the Jánska Valley with the Liptov Basin in the background. Photo: L. Kunáková

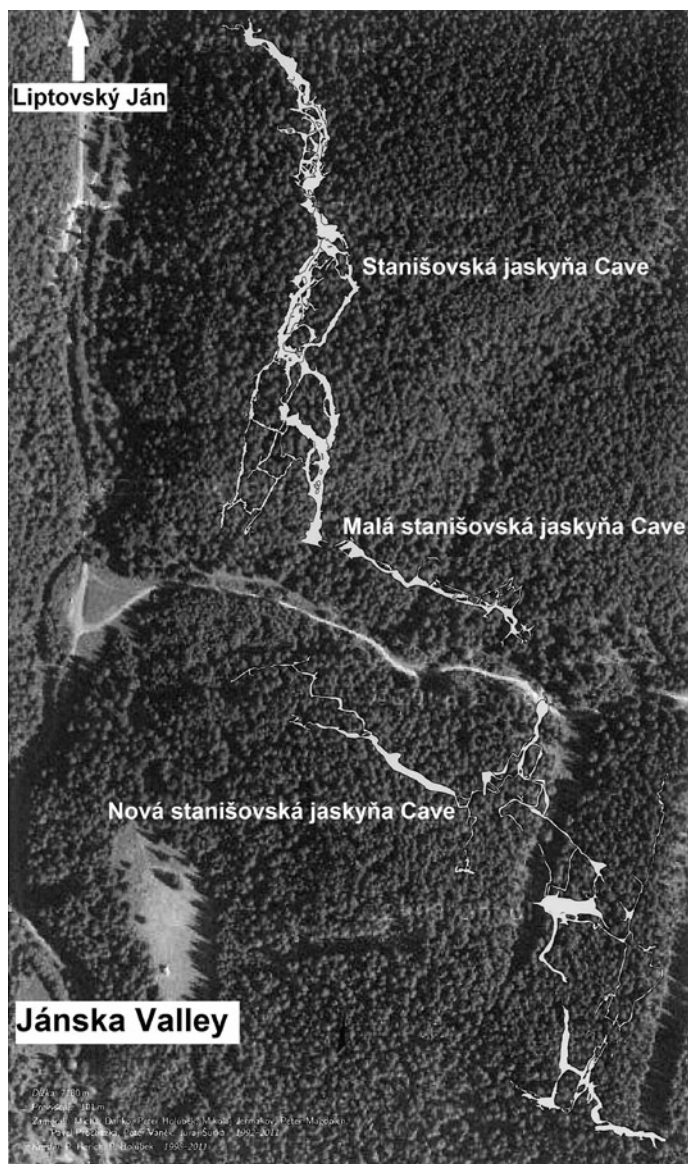


Fig. 17. Complex of Stanišovské Caves in the Jánka Valley. Ground plan after M. Biskupič (modified according to Z. Hochmuth, P. Holúbek & P. Herich).



Fig. 19. Entrance part of Malá stanišovská jaskyňa Cave with ice fill during winter. Photo: P. Vaněk

a. s. l., in the immediate vicinity of more famous and larger Stanišovská jaskyňa Cave. The main part of the cave represents an oval, mostly horizontal corridor with ceiling and sidewall streambeds, which indicates its former river modelling. Several shorter tubular corridors connect to the main passage (Fig. 18). The length of the cave passages is totally 871 m (Holúbek, 2011, 2015). In the past, the cave was relatively rich in dripstones which were, however, largely damaged by people who could freely

enter the cave. Nowadays, the sinter decoration in the cave is mostly formed by water from atmospheric precipitation. In some places, the cave walls are covered with a moonmilk, a white and creamy substance of calcium carbonate to which, several healing effects were attributed in the past. The cave air temperature is up to 6.1 °C. In winter, the frosty air flows into the front of the cave which ultimately causes the formation of numerous ice stalagmites (Fig. 19).

Both Malá stanišovská jaskyňa Cave and Stanišovská jaskyňa Cave have been known to the local inhabitants since time immemorial. The first written mention of the Stanišovské Caves dates back to 1689 when Martin Szentiványi, a professor from University of Trnava, wrote about the caves in the valley above the village of Liptovský Ján. In 1720, the cave was explored by Georg Buchholtz jr. In 1904, a work entitled "Stanišovská Dripstone Cave in Liptov District" was published by Hungarian geologist and palaeontologist Tivadar Kormos who made a detailed description of the cave. After frequent visits in the past, a number of inscriptions have been preserved on the cave walls the oldest of which, comes from the 19th century. A considerable amount of these inscriptions originate from the World War I and II when people used the cave as a shelter. The most notable are the signatures of Russian students, written in Cyrillic, who left their homeland after the revolutionary year of 1917 and the subsequent civil war in Russia, and the signature of members of the Jewish religion with the six-pointed David's Star originating from the inter-war period. At the turn of 20th and 21st century, the members of Slovak Speleological Society worked intensively in the Stanišovské Caves and discovered hundreds of meters of the new passages. After several unsuccessful attempts, the Malá stanišovská jaskyňa Cave was made available to the public in 2010 thanks to the effort of local volunteer cavers. The length of a show trail is 410 m.

**Medvedia jaskyňa Cave**

The Medvedia jaskyňa Cave (Bear Cave) is an inactive fluviokarst-collapsed cave situated on the left side of the Jánka Valley, in the massif of Krakova Hoľa, at an altitude of 878 m a. s. l. The cave is 1,420 m long and 44 m deep (Tencer, 2017) and consists of passages eroded by activity of the Štiavnica River, percolating water and at the entrance part, also

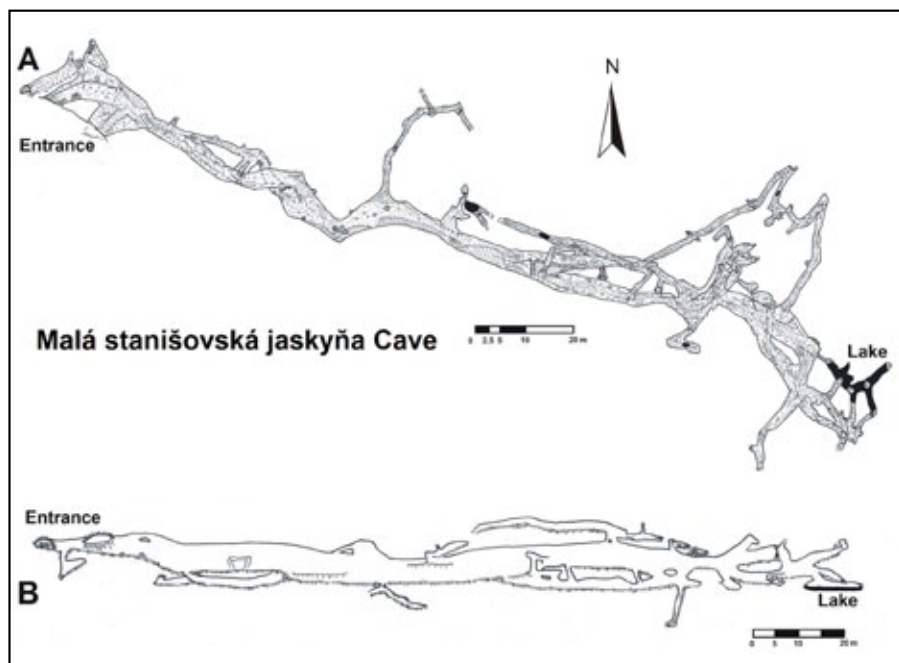


Fig. 18. Malá stanišovská jaskyňa Cave: A – ground plan and B – side projection after Holúbek (2011).

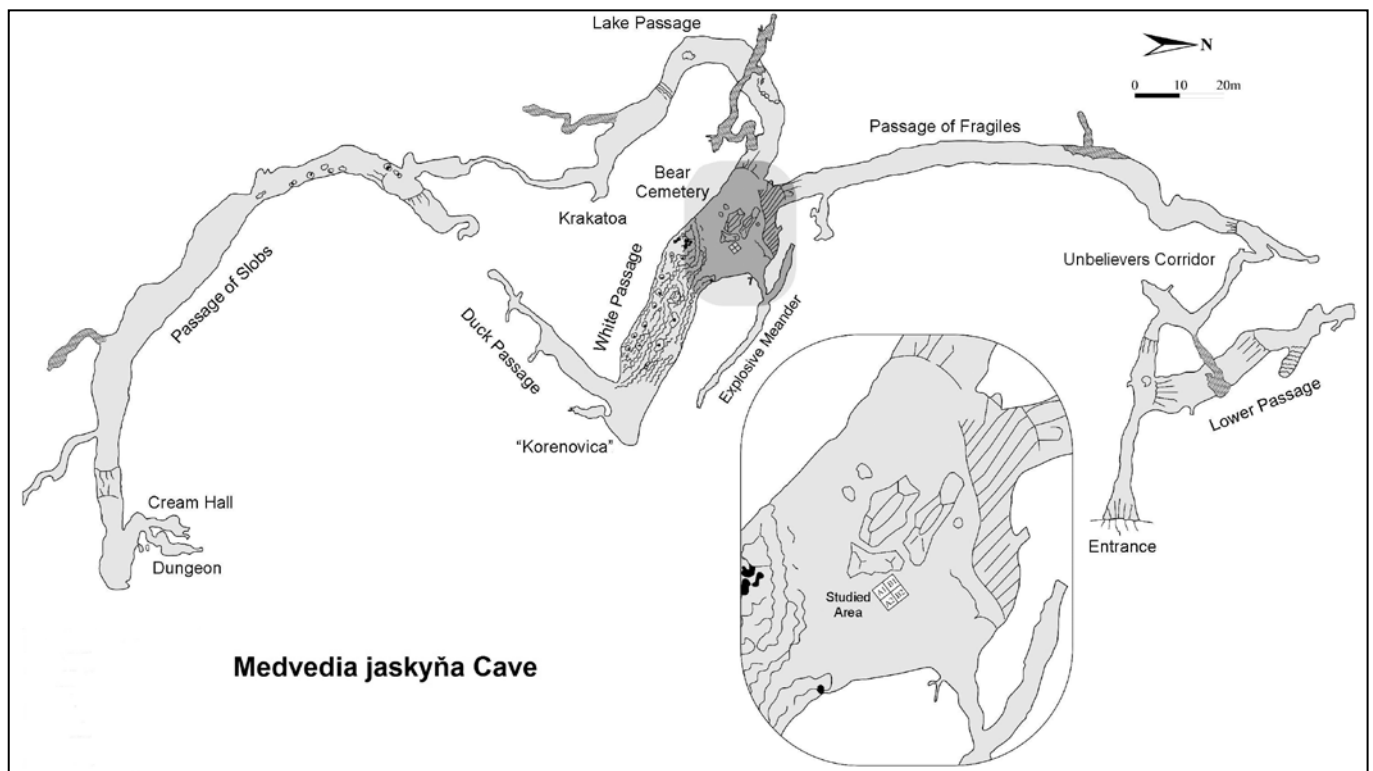


Fig. 20. Medvedia jaskyňa Cave. Ground plan after Sabol et al. (2009) (modified according to J. Vajs & P. Procházka)

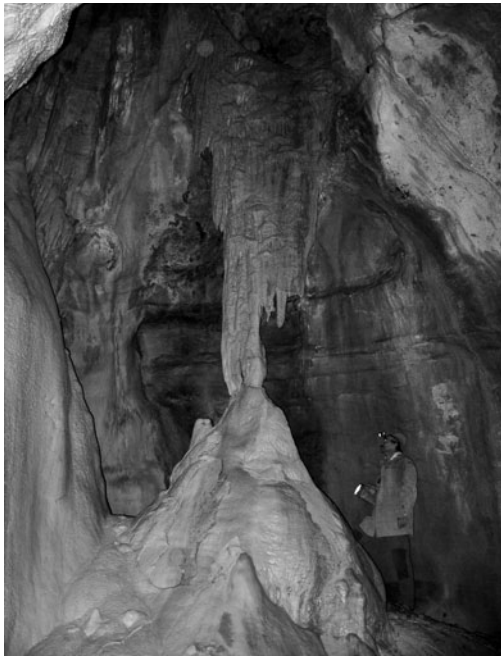


Fig. 21. Sinter column named after Krakatoa Volcano situated at the end of Jazerná chodba (Lake Passage) in Medvedia jaskyňa Cave. Photo: Z. Višňovská

by gradual frost weathering of the limestone layers (Fig. 20). The Medvedia jaskyňa Cave seems to be a fragment of extensive cave system with a potential connection to the nearby Jaskyňa zlomisk Cave which is more than 11 km long (Marušin, 2003; Holúbek, 2015).

The cave has not as rich history as the above-mentioned Stanišovské Caves. The reason for this is that the cave belonged to rather less attractive sites for speleologists in the past. Its more intensive research began only after the end of World War II. The oldest mention of the cave comes from 1947 and is related to the cor-

respondence of the two prominent Slovak speleologists Pavol Revaj and Vojtech Benický who mentioned a small and very cold cave in which, old ursine bones were found. Other famous Slovak geographer and speleologist Anton Droppa (1959) was the first who states the cave in scientific literature. In 1989, a group of volunteer speleologists from Liptovský Mikuláš discovered the new cave passages after three years of digging out of the sediments in the narrow Chodba bezvercov (Unbelievers Corridor) (Vajs, 1991; Vajs & Pocházka, 1998). The so-called Chodba krehotíniiek (Passage of Fragiles) was named after the small and fragile sinter formations on the walls and floor. Another interesting sinter fill was found in Jazerná chodba (Lake Passage) at the end of which, there is a stalagnate having a shape of erupting volcano. For this reason, this sinter column was named after Krakatoa, a world-famous active volcano on one of the Indonesian islands (Fig. 21). Based on the magnetostratigraphy, the underlying lower fluvial deposits in the Jazerná chodba have been dated to the time period 780 – 990 thousand years BP (Kadlec et al., 2004).

#### Palaeontological discoveries in the Jánska Valley

Until the discovery of the new deeper parts of Medvedia jaskyňa Cave, the fossil remains were being found only sporadically in the Jánska Valley caves. Nowadays, the Medvedia jaskyňa Cave represents one of the most notable cave bear sites in the region. The cave served as a cave bear den for certain time during the Late Pleistocene. The cave bear fossils have been mostly accumulated in Medvedí

cintorín (Bear Cemetery Chamber) where the excavation field campaign was held between 2002 and 2004 (Sabol et al., 2009). The excavation was conducted on a square area (2×2 m) divided into four quadrants with a size of 1×1 m (Fig. 20). During the excavation, the L-shaped vertical pit was dug out as the first including two profiles: M-5a with a depth up to 0.9 m and M-5b with a depth only to 0.5 m (Fig. 22). Afterwards, in a place bounded by vertical pit, a horizontal pit was dug out. The lower part of the profiles consists of gravels and sand of the riverbed facies of occasional underground stream. These deposits represent a filling of the highest riverbed part where dynamics of the underground stream was relatively weak. Based on analogy with the upper cave floor, it is assumed that basal part of the passage infill consists of boulder-shaped granite gravels. The upper profile part is formed by non-assorted loam with an admixture of tiny pebbles and rock fall. This part of both profiles, containing also vertebrate fossils, is considerably re-deposited which could be possibly caused by cryoturbation during the period of better communication between the cave and the surface. In this case, the whole process could be carried out in the time of cold air suction into the cave during winters (Sabol et al., 2001).

Based on sedimentary filling, three different evolution stages of the cave level are distinguished: (1) a period of predominant active evolution of the cave level – during this period, passages of the cave level were forming and filling up by deposits of permanent underground stream(-s); (2) a period of predominant inactive evolution of the cave level – during this period, passages of the cave level had already been situated above the erosive base level of underground stream and cave bear bones were transported as lightweight material within the

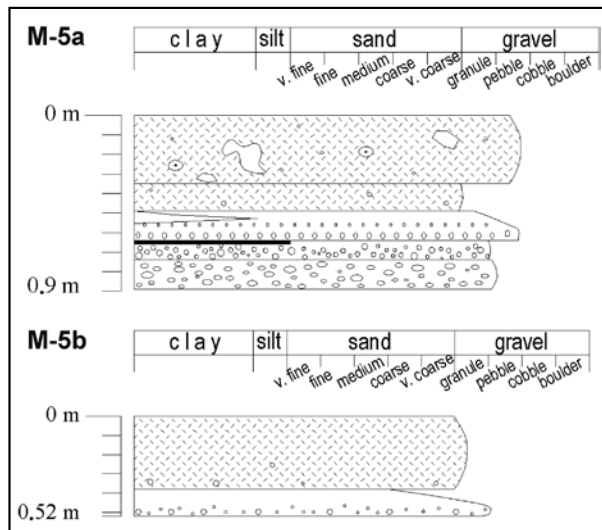


Fig. 22. Sedimentological profile of M-5a and M-5b layers excavated in Medvedí cintorín (Bear Cemetery Chamber) in Medvedia jaskyňa Cave. Drawing: Ľ. Sliva

sediment; and (3) a period of inactive evolution of the cave level – recent condition of the cave level, situated high above the river erosive base and beyond reach of floodwater too (Sabol et al., 2001, 2009). Regarding the formation of fossiliferous bed, the second period is the most important.

The cave bear fossils were predominantly found on the surface or in sediment up to the depth of approximately 30 cm. During the field campaign, 134 teeth or their fragments, 55 cranium fragments, 17 mandible fragments and 411

elements of postcranial skeleton or their fragments were excavated (Fig. 23). The morphological and metric characteristics of found teeth as well as bones indicate typical bears from the *spelaeus*-group and the entire assemblage can generally be determined as yearling/juvenile-dominating with outnumbering of females (sex index = 70; sex ratio = 2.3).

The basic taphonomic analysis demonstrated the presence of post-mortem processes such as a short-distance transport of fossils in aquatic environment or gnawing the bones by larger predators (lions), scavengers

(wolves) and rodents. The transport was presumably occasional and chaotic as indicated by orientation of fossils in the layers. From pathological point of view, the marks of some diseases (e. g. exostosis or bone deformation) were observed on some adult bones. The found fossil remains from the Medvedia jaskyňa Cave represent most likely a non-violent taphocoenosis of cave bears from the Last Glacial (the sample forwarded to VERA-Laboratory in Vienna for AMS dating did not yield adequate volume of collagen for exact age determination) the death of which, is related to their hibernation (Sabol et al., 2009).



Fig. 23. Cave bear mandibles from the Late Pleistocene deposits in Medvedia jaskyňa Cave: 1 – right (a) and left (b) mandible of the same neonate individual, 2 – left mandible with dentition of adult animal, 3 – mandible with dentition of adult male, consisting of left branch and fragmented right branch. Photo: M. Sabol

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## TWENTY-TWO SEASONS OF ICBS – A BACKWARD GLANCE

**Jan Wagner<sup>1</sup> – Doris Döppes<sup>2</sup> – Martin Sabol<sup>3</sup>**

<sup>1</sup> Department of Palaeontology, National Museum, Cirkusová 1740, 193 00 Prague 9, Czech Republic; jan\_wagner@nm.cz

<sup>2</sup> Reiss-Engelhorn-Museen, C4, 8, D – 68159 Mannheim, Germany; doris.doeppes@mannheim.de

<sup>3</sup> Department of Geology and Palaeontology, Faculty of Natural Sciences, Comenius University, Ilkovičova 6, 842 15 Bratislava, Slovakia; sabol@fns.uniba.sk

International Cave Bear Symposium or Höhlenbären-Symposium or International Cave Bear-Meeting as it was called in the first years – is the reason why we meet together this year again, this time in Slovakia, already for the 23rd time. In 1993, **Gernot Rabeder** summoned for the first time the cave bear specialists from the whole Europe and ICBS was born. Each year, it is rather a small, familiar and friendly meeting attended by many students and young scientists as well as by respected specialists who have been studying cave bears for many years. It is a beautiful place for informal talks, sharing new ideas or old problems. But when we look back, we will still see something more than only pleasant memories. In fact, since 1993, almost each important discovery, each new method or opinion concerning cave bears have been presented at ICBS. In many cases, it is possible to see how the idea or research changes/continues from meeting to meeting, year by year. Almost each person who is now involved in cave bear research presented her/his results at ICBS regularly and in many cases, it is possible to see that ICBS was the starting point of her/his career. We see this fact as very unique and hope that it will continue also in the next years. We would like to use this place to thank prof. G. Rabeder for starting and supporting ICBS during all those past years.

Going through the past ICBS abstracts and proceedings, we decided to remind, on a few lines below, some colleagues, some ideas and some memories connected to ICBS. It was not possible to mention all people and presentations, so we apology to all friends and colleagues who will not agree with our choice – and we are looking forward to their criticism.

The **1st meeting** (“Der Höhlenbär in den Alpen”) connected to the evaluation of the cave bear finds from the Sulzfluh was held on November 18 and 19, 1993 in Chur, Switzerland. It was the beginning of the astounding tradition of common meetings of European scientists dealing not only with cave bears but also interested in the research of Pleistocene carnivores and other members of Ice Age fauna.

The following year, the **2nd International Cave Bear Meeting** was held from September 15 to 18 in Alta Badia, Italy. The excursion to the Conturines Cave was realized on Friday September 16, and the lectures followed next day. Saturday morning, lectures concerned on the news from the Conturines Cave research (these were presented for instance by G. Rabeder, M. Pacher, and G. Withalm) and during the afternoon session, the research results from other areas were presented; e.g., from

Italy (P. Mazza), Spain (A. Grandal d’Anglade), and Greece (E. Tsoukala).

The **3rd symposium** began on November 2, 1995 in Lunz am See, Austria and continued until November 4. The lecture sessions were on Friday and Saturday morning, the excursions to Herdengelhöhle Cave und Schwabeneithöhle Cave took place on Friday afternoon. Except for the Austrian researchers (G. Rabeder, M. Pacher, G. Withalm and F. Fladerer), bear specialists from the Czech Republic (R. Musil), Slovenia (V. Pohar), Croatia (M. Purnović) and Spain (T. de Torres) presented also their contributions.

After three years, the **4th International Cave Bear Symposium** was held from September 17 to 20, 1998 in Velenje, Slovenia. The lectures were presented on Friday, September 18. Inter alia, I. Debeljak presented her results about using dental cementum for cave bear aging. G. Rabeder reported about the evolution changes in cave bear incisors and F. Cimerman et al. about supposed find of cave bear hairs. The excursions to Potočka zijalka Cave and Divje babe I Cave took place on Saturday and Sunday, respectively. Since this year, the symposia have been held regularly every year.

Next year, “cave-bearlogists” (or arctologists dealing with cave bears) had a meeting in Bad Mitterndorf, Austria. This **5th ICBS** was held from September 24 to 26, 1999. During the symposium, Brettsteinbärenhöhle Cave, Salzofenhöhle Cave, and Liegloch Cave were visited. Among many lectures, contributions by G. Baryshnikov about Akhstyrskaya Cave, by A. Argant about Château Cave, by Villa Taboada et al. about stable isotopes from cave bear bone collagen or by M. Sabol about cave bears from Slovakia can be mentioned.

The **6th symposium** was held in a peaceful place near O Castro town in Galicia from September 27 to 30, 2000. Although the number of participants was slightly smaller than usual, many interesting contributions were presented on Wednesday, September 27. Among others, A. Angerbjörn et al. presented results of palaeogenetic studies on cave bear for the first time at ICBS, G. Baryshnikov reported about his revision of *U. rossicus* from South Siberia, A. Grandal d’Anglade (the main organizer of the symposium) presented a review about the problem of sexual dimorphism in cave bears and G. Rabeder presented his taxonomic interpretation about Austrian cave bears that time based still solely on morphometric and, of course, morphodynamic analyses. Except for the participants from many European countries, R. A. Nelson, a zoologist from the USA studying the metabolism and physiology of American black bears, took also part in the symposium. During the excursion days, seven

Galician caves yielded bear fossils were visited, including the famous Eirós Cave.

The Trieste meeting (**7th ICBS**, Italy) started on Friday, October 5, 2001 by excursions to the nearby Slovenian caves including the famous Križna jama Cave. Next day was the lecture day. Among the lecture and poster presentations, we can mention the lectures about ancient DNA by L. Orlando and C. Hänni or lecture about metapodial bones evolution within cave bears by G. Withalm. The group from University Erlangen (B. Kaulich, B. Hilpert and D. Ambros) presented news from Hunas excavations. Ph. Fosse has an unannounced presentation (in the first session after lunch) about Chauvet Cave which was included neither in the program nor in the abstract book. On Sunday, the Pocala Cave was visited. This site was in the centrum of research interest of R. Calligaris, the main organizer of this meeting.

On Thursday September 19, 2002 the **8th symposium** began in Kirchheim unter Teck, Germany. The next excursion day included among other sites also the visit to Erpfinger Bärenhöhle Cave. During Saturday, many interesting lectures and posters were presented. We can remind the presentation by A. Argant and J. Argant about bears from Château Cave, with the important evidence of early presence of *U. arctos*. M. Hofreiter presented his palaeogenetic research for the first time at ICBS and G. Rabeder et al. presented new view on Alpine cave bears taxonomy with integrated preliminary palaeogenetic (mtDNA) results. In addition, we can mention the presentation of K. Athen about cave bear postcranial bones, or record of brown bear in Hunas reported by B. Hilpert. The last conference day offered several possibilities including visit to Sybillen Cave (a type locality of *Ursus spelaeus sibiricus* E. Fraas, 1899).

The **9th symposium** was held in the beautiful area of “Cave Bear Museum” in Entremont-le-Vieux, France from September 25 to 27, 2003. It came to a meeting of many old friends and a lot of new information. The first two days were devoted to the excursions, including the visit to Balme à Collomb Cave and official visit to Musée de l’Ours des cavernes. On Saturday, September 27, many interesting lectures and posters were presented, so it is complicated to mention only some of them. M. Hofreiter spoke about the aDNA from Siberian cave bears, Ph. Fosse presented actualistic study about denning behaviour of brown bears, T. de Torres reported news from his research on Spanish cave bears. V. Pohar et al. introduced their starting research on *deningeri*-like bears from Herkova jama Cave, W. Hamdine reported about the finds of brown bear from north Algeria, E. Turner

informed about her research on *U. thibetanus* from Miesenheim I locality and D. Nagel et al. reported about the excavations of Nerubajskoe locality (Ukraine). Last but not least, it is necessary to mention the presentation by Rabeder et al. about the final taxonomic concept for Alpine cave bears. In subsequent proceedings, three new cave bear taxa were described.

Similarly, the **10th ICBS** took place in France (Mas d'Azil, September 29 to October 3, 2004). Talks and posters were presented on Thursday, September 30. Inter alia, we can remind the lecture by J. Quiles et al. about cave bear sex ratio determination, study on femur cross sections by G. Jambrešić, or new radiocarbon dating from several bear caves from Germany reported by Rosendahl et al. Next three days, several excursions including the visit to Mas d'Azil Cave were realized.

The **11th ICBS** was hosted by Pommelsbrunn (Germany, September 29 to October 2, 2005), a village with a bear in its coat of arms. After Friday excursion, Saturday was a day of presentations. Among many interesting contributions, we can mention lecture presented by B. Hilpert about her revision of bears from Hunas. R. Musil presented his summarizing view on taxonomy of European fossil bears, M. Sabol presented news from Za Hájovnou Cave excavation (Middle Pleistocene), and C. Schouwenburg presented an overview about the carnivore fossil record from the North Sea. The poster session was also very inspiring, S. Pappa presented her first results on cave bear milk teeth, K. Athen presented results of biometrical analysis of fossil ursid postcranial elements, and G. Rabeder reported about assignment of bears from Herkova jama Cave to *U. deningeroides*. Next day, the excursion included also two crucial localities for bear research – Early Pleistocene Windloch Cave near Sackdilling (type locality of *U. sackdillingensis* Heller, 1955) and the birthplace of scientific research on cave bears – Zoolithenhöhle Cave – type locality of *Ursus spelaeus* Rosenmüller, 1794!

In order, the **12th symposium** was held for the first time in Greece (Aridéa/Loutrá), unusually from November 2 to 5, 2006. After arrival in Thessaloniki, each participant received a certification of her/his participation in symposium signed by G. Rabeder and E. Tsoukala, the main organizers of this meeting (supported by her students K. Chatzopoulou, S. Pappa and the others). On Thursday evening, we moved to the place of conference and Friday, November 3, was the presentation day full of interesting contributions. Very interesting and well prepared lecture about endocrinology of cave bear was presented by E. Santos. G. Baryshnikov presented his results about morphometric variability of cave bear cheek teeth, based on many years long research. G. Rabeder and G. Withalm presented their research of Early Pleistocene bears from Deutsch-Altenburg, A. Grandal d'Anglade et al. informed about rather late record of cave bear from O Rebolal Cave, M. Hofreiter and M. Stiller reported about news in aDNA research as well as about the new palaeogenetic and stable isotopes results from Peștera cu Oase Cave, and many other interesting

contributions could be added. Next day, the excursion to Loutrá Aridéa area was realized, connected with the visit to Bear Cave.

The first cave bear symposium in the Czech Republic (**13th ICBS**) was held from September 20 to 24, 2007 in Brno (Moravia). Friday, September 21, was the presentation day. Among other contributions, A. Argant et al. gave a presentation about Azé Cave, M. Pacher reported about news from Peștera cu Oase Cave, H. Bocherens et al. spoke about the usage of stable isotopes in cave bear palaeoecology reconstruction and M. Sabol with his colleagues presented news from several cave bear sites in Slovakia. Excursion on Saturday under the leadership of R. Musil, the main organizer, comprised several stops within the Moravian Karst. September 23 and 24 were devoted to the post-conference field trip, including several caves in Moravian, e.g. Javoříčko Cave and Mladeč Caves.

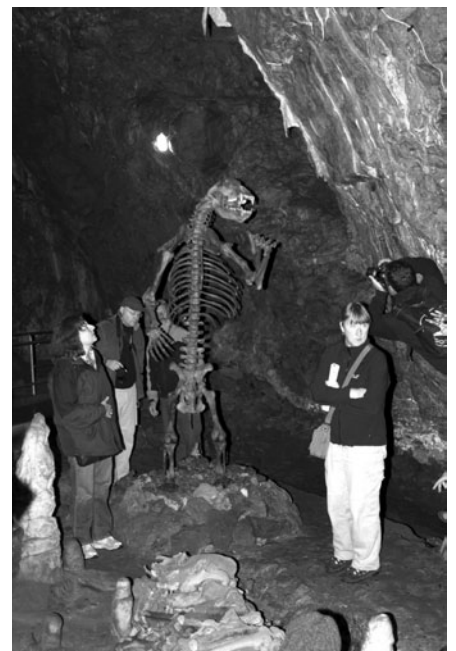
Appenzell, a Swiss village with a bear in its coat of arms, was the place of the **14th ICBS** from September 18 to 22, 2008. The presentations were held on Friday, September 19. Among many interesting contributions, we can remind the lectures by A. Argant and J. Argant about the large carnivore assemblage from Château Cave, G. Baryshnikov about *U. kudarensis* from Akhstyrskaya Cave, H. Goubel about using geometric morphometry for differentiating m1 of Pleistocene bear species or B. Toškan about size variability in cave bears from Divje babe I Cave. M. Stiller and M. Hofreiter reported about the progress in aDNA studies and successfully newly sequenced cave bears from several localities, including Kizel Cave, Bolshoi Glukhoy Grotto Cave, Secrets Cave, Medvezhiya Cave, Hovk Cave or Baumannshöhle Cave. Saturday and Sunday were excursion days during which, the Wildkirchli Cave was visited.

The **15th ICBS** was held in Slovakia (Spišská Nová Ves) for the first time from September 17 to 20, 2009. The presentations took place on Friday, September 18. M. Pacher et al. reported about research on Ural fossil bears (incl. *U. uralensis*) and new radiocarbon dates were presented, G. Withalm presented his research on endocranial morphology of brown bear from Winden (using CT scanner), with interesting finding of *U. spelaeus*-like *sinus frontalis*. A. H. van Heteren presented preliminary results about functional morphology of bear mandibles using 3D geometric-morphometric approach, S. C. Münzel (in co-operation with K. Athen) had a lecture about correlating biometrical and genetic analysis of metapodial bones of cave bears from the Ach Valley, A. Nadachowski et al. presented new radiocarbon dating that gave an evidence of brown bear presence in Poland during LGM. Next day, Važecká jaskyňa Cave and Medvedia jaskyňa Cave were visited during the excursion.

The **16th symposium** was interesting by its first connection with the cave lion symposium (**International Cave Bear and Lion Symposium**). It took place from September 22 to 26, 2010 in Azé, France. On Thursday, September 23, the Cave Bear Symposium presentations were held, providing a lot of news from bear research. J. Madurell-Malapeira informed

about *U. deningeri* from Early Pleistocene localities Cal Guardiola and Vallparadís, K. Athen reported about metapodial bone potential for the gender separation in recent brown bears, H. Goubel presented dental shape variability analysis using geometric morphometry approach and E. Crégut-Bonnoure spoke about Pleistocene brown bears in Vaucluse. Next day, the participants visited Azé, Château and Blanot localities, the latter well known for its beautiful find of almost complete skull of *U. thibetanus mediterraneus* Major, 1873. On Saturday, September 25, the conference continues with the Lion Symposium and with the poster session for both symposia. We can remind at least the poster by A. Marciszak about bears from Bišník Cave and the poster by Ch. Frischauf et al. reporting, among other things, about the surprising combination of highly evolved cave bears from Balme Noire Cave with mtDNA haplotype ladinicus. On Sunday, the last excursion day was realized (speleology in Mâconnais or Museum and Roche de Solutré).

The **17th ICBS** was held once again in Germany. Friends of cave bear and cave fauna research met in Harz (Lower Saxony) from September 15 to 18, 2011. Friday, September 16, was the presentation day and brought a lot of news regarding bear research all around Europe. H. Bocherens et al. reported about the usage of oxygen stable isotope for reconstructing the cave bear hibernation behaviour under different climatic conditions, I. Debeljak spoke about longevity of cave bears, M. Pacher presented interesting review about the presence of supracondylar foramen in bears, M. Robu informed about news in research of Ursilor Cave, etc. Saturday and Sunday were devoted to excursions. Among other sites, well-known Baumannshöhle Cave, Hermannshöhle Cave, and Einhornhöhle Cave (the latter is the type locality of *U. deningeri hercynicus* Rode, 1934) were visited.



A cave bear skeleton reconstruction in the Hermannshöhle Cave, visited by participants of the 17th ICBS in Lower Saxony (Germany). Photo: archive of ICBS participants

Organizers of the **18th ICBS** joined the symposium with the international workshop "Fossil remains in karst and their role in reconstructing Quaternary paleoclimate and paleoenvironment". The conference, held in Băile Herculane (Romania), started on Thursday, September 20, 2012 with the first day of presentations. Among many important talks, we can especially remind the following ones: M. Hofreiter and his team presented the review of aDNA of cave bear as well as the perspectives for palaeogenetic studies, M. Baca et al. informed about palaeogenetic results from Niedźwiedzia Cave, H. Bocherens reviewed the state of art of stable isotopic studies in palaeoenvironmental research, and Ph. Fosse and E. Crégut-Bonnoure presented the study about brown bear ontogenetic development and its application for cave bear study. Next day was also devoted to oral and poster presentations. We can mention for instance the presentation by S. Münzel et al. about behavioural ecology of Late Pleistocene bears, presentation by Ph. Fosse and M. Robu about cave bear bioglyphs in France and Romania or interesting posters by M. Alscher et al. about Alpine cave bear phalanges or L. Holland about teeth wear stages in Alpine cave bears. The last day was reserved for the field trips to the Danube Gorge and Poncova Cave.

The **19th ICBS** was held in Semriach, Austria from October 3 to 6, 2013. The conference presentations started in familiar atmosphere on Friday, October 4. Among others, S. Pappa et al. presented preliminary results on brown bears from Tornewton, A. Barlow informed about a new-starting palaeogenomic project, or Ch. Frischauf et al. reported the first results about the *U. deningeroides* revision. During the next day of excursion, two important localities were visited – first Drachenhöhle Cave near Mixnitz, famous locality known for cave bears researchers especially due to the phenomenal monograph "Abel, O. & Kyrle, G. (1931) (eds): Die Drachenhöhle bei Mixnitz", which can be without an exaggeration called as the starting point of the modern cave bear research. The second locality visited was Repulsthöhle Cave, the type locality of *U. d. deningeroides* Mottl, 1964. The last conference day started with the poster session, where we can remind a poster presented by M. Sabol about the bear endocast from Gánovce or a preliminary report about the revision of cave bear from Drachenhöhle Cave near Mixnitz by P.-M. Liedl et al. The poster session was followed by a short excursion.

To celebrate the **20th** anniversary of beloved **Cave Bear Symposium**, the organizers decided to come back to the roots and organized the meeting in the same area as the 2nd symposium was. This anniversary symposium was held in Corvara (Italy) from September 11 to 13, 2014. The presentation day was on Thursday, September 11. G. Santi and M. Rossi reported about perspectives of cave bear research in northern Italy, M. Hofreiter and A. Barlow informed about news from palaeogenetic (and especially palaeogenomic) and M. Sabol presented a high-alpine record of cave bears from the territory of Slovakia. Within the poster session, we can mention for example



A common photo from the 20th ICBS what was held in Corvara (Italy). Photo: archive of ICBS participants



A common photo on the grounds of the Historyland Museum during the 21st ICBS in Netherland (Hellevoetsluis). Photo: archive of ICBS participants

presentation by M. Pacher et al. about the first results of cave bears revision from Bächler's cave sites. On Friday, the excursion was prepared to Conturines Cave, since 2004, the type locality of *U. s. ladinicus* Rabeder, Hofreiter, Nagel et Withalm, 2004. Next day, Museum Ladin *Ursus ladinicus* was visited. This museum was founded in 2011, under the scientific supervision of G. Rabeder, for the purpose to celebrate the beauty and importance of Conturines bear.

In the following year, the symposium was held in Netherlands (Leiden - Hellevoetsluis - Rotterdam) for the first time. This **21st ICBS** took place from September 10 to 13, 2015. Thursday, September 10, was the arrival day with several visits and lectures in Leiden (Naturalis, University) and next day, there was a field trip presenting, among other things, the so called

bone fishing. On Saturday, September 12, the presentations were held in the Historyland (Hellevoetsluis). Many interesting presentations were given, among them, we can mention for instance A. Barlow's presentation about a preliminary palaeogenomic results of his team detecting the hybridisation between brown and cave bears, the talk by J. Arroyo-Cabralles (Mexico) presenting a review about North American Quaternary bears, D. Popović et al. reported about genetic studies of cave bears



A common photo in front of the Niedźwiedzia Cave during the last 22nd ICBS in Poland (Kletno). Photo: archive of ICBS participants

from Eastern and Central Europe, and G. Rabeder presented a newly reviewed problems of grindings marks on cave bear C/c and I/i. During the last symposium day, participants visited the Rotterdam Natural History Museum.

So far the last symposium, **22nd ICBS**, was associated with the celebration of 50th anniversary of the Niedźwiedzia Cave discovering. It took place in Kletno, Poland from September 21 to 25, 2016. The conference was officially opened on Thursday, September 22 and the presentations started just after the opening. Although we still have this nice symposium in our memories, we can remind few presented results. M. Baca et al. presented news about the latest record of cave bears in Poland, G. Xenikoudakis et al. reported palaeogenomic

data of brown bears, Popović et al. presented phylogeographic model for cave bears from Central and Eastern Europe based on ancient mtDNA, and A. Marciszak reported about his interpretations of Late Pleistocene brown bear taxonomy. Compared to the previous ones, this ICBS was specific by strong presence of palaeogenetic presentations. The next two days were devoted to the excursions, including also the visit to Niedźwiedzia Cave.



A cave bear skeleton reconstruction in the Niedźwiedzia Cave (Poland). Photo: archive of ICBS participants

## THE LIST OF CAVE BEAR SYMPOSIA WITH THE LIST OF PUBLISHED ABSTRACT BOOKS (A) AND PROCEEDINGS (P)

### 1st ICBS: Chur (Graubünden, Switzerland), November 18–19, 1993

**Organizer:** Institut für Paläontologie, Universität Wien & Bündner Naturmuseum, Chur

### 2nd ICBS: Alta Badia (South Tyrol, Italy), September 15–18, 1994

**Organizer:** Turismesverband Alta Badia & Institut für Paläontologie, Universität Wien

**A:** Abstract book called just “Ursus Spelaeus” was comprised of unpaginated loose leaves and was in three language versions – German, Italian and English.

### 3rd ICBS: Lunz am See (Lower Austria, Austria), November 2–4, 1995

**Organizer:** Institut für Paläontologie, Universität Wien

**A:** RABEDER, G. – WITHALM, G. (Eds.). 1995. 3. Internationale Höhlenbären-Symposium in Lunz am See, Niederösterreich. Zusammenfassungen der Vorträge, Exkursionführer [3rd International Cave Bear-Meeting in Lunz am See, Lower Austria. Abstracts and excursion guide], 19 p.

Except for this formally published abstract book, there were unpaginated “Abstracts” available. The unpaginated version included also the programme, two short abstracts by G. Withalm and N. K. Vereshchagin, English translation in some abstracts and lacked Introduction presented in the formally printed version.

### 4th ICBS: Velenje (Slovenia), September 17–20, 1998

**Organizer:** Oddelek za geologijo, Naravoslovnotehniška fakulteta, Univerza v Ljubljani; Institut für Paläontologie, Universität Wien; Premogovnik Velenje, d.d.

**A:** POHAR, V. – PAVLOVEC, R. (Eds.). 1998. 4. Mednarodni simpozij o jamskem medvedu. Program, izvlečki referatov, ekskurzije [4th International “Cave-Bear” Symposium. Program, abstracts, excursion], 53 p.

**P:** RABEDER, G. – RIEDEL, A. – ŽERDIN, F. – PAVLOVEC, R. – POHAR, V. – ŠKARIA, B. (Eds.). 2000. Zbornik 4. Mednarodni simpozij o jamskem medvedu [Proceedings. 4th International Cave Bear Symposium]. Geološki zbornik, 15, 1–135.

### 5th ICBS: Bad Mitterndorf (Styria, Austria), September 24–26, 1999

**Organizer:** Verein für Höhlenkunde in Obersteier; Institut für Paläontologie der Universität Wien; Kommission für Quartärforschung d. Österr. Akademie der Wissenschaften

**A:** DÖPPES, D. – NAGEL, D. (Eds.). 1999. 5. Internationales Höhlenbären-Symposium, Bad Mitterndorf, Steiermark, Österreich. Exkursionführer, Zusammenfassungen der Vorträge und Poster [5th International Cave Bear-Meeting in Bad Mitterndorf, Styria. Excursion guide – Abstracts], 26 unnumbered leaves printed on one side.

**P:** [no editors] 2000. Proceedings of the 5th International Cave Bear Symposium, 1999. Beiträge zur Paläontologie, 25, 144–185.

Proceedings were published as a part of volume 25, including the papers unrelated to ICBS.

### 6th ICBS: O Castro (Galicia, Spain), September 27–30, 2000

**Organizer:** Instituto Universitario de Xeoloxía, Universidade da Coruña – Laboratorio Xeolóxico de Laxe & Institut für Paläontologie, Universität Wien

**A:** [no editors] 2000. 6th International Cave Bear Symposium. Communications, Excursion guide, 100 p.

**P:** [no editors] 2001. In: Caderos, Cadernos do Laboratorio Xeolóxico de Laxe, Revista de xeoloxía galega e do hercínico peninsular, 26, 281–507. <https://dialnet.unirioja.es/ejemplar/10694>

The contributions were published without separate title list or dedication to ICBS as a part of volume 25 including also other papers.

### 7th ICBS: Trieste (Italy), October 5–7, 2001

**Organizer:** Natural History Museum of Trieste & Institut für Paläontologie, Universität Wien

**A:** [no editors] 2001. 7th International Cave Bear Symposium. 109 unnumbered leaves printed on one side.

There is no publication date stated in this abstract book.

[no editors] 2001. 7th International Cave Bear Symposium. Estratti dei lavori riguardanti la grotto Pocala di Aurisina. 27 p.

This volume consists of copies of four previously published papers concerning the Pocala Cave. In all cases, their author or co-author is R. Calligaris. Except for this volume, excursion guides for Krížna jama Cave by G. Rabeder and G. Withalm (4 p.) and for Betalov spodnomol by V. Pohar (2 p.) on loose leaves were available to participants.

**P:** [no editors] 2003. 7th International Cave Bear Symposium, Trieste 5-6-7 ottobre 2001. Atti del Museo civico di storia natural di Trieste, Supplemento al vol. 49, 1–140.

### 8th ICBS: Kirchheim unter Teck (Baden-Württemberg, Germany), September 19–22, 2002

**Organizer:** Institut für Angewandte Geowissenschaften, Technische Universität Darmstadt & Institut für Paläontologie, Universität Wien

**CV:** Rosendahl, W. – Morgan, M. – López Correa, M. (Eds.). 2002. Cave-Bear-Researches/Höhlen-Bären-Forschungen. Abhandlungen zur Karst- und Höhlenkunde, 34, 1–112.

For the first time, Proceedings were published still before the symposium, so no abstracts were needed.

### 9th ICBS: Entremont-le-Vieux (Savoie, France), September 25–27, 2003

**Organizer:** Institut Dolomieu, Grenoble; Museum d’Histoire naturelle, Lyon & Institut für Paläontologie, Universität Wien

**A:** ARGANT, A. – PHILIPPE, M. (Eds.). 2003. 9ème Symposium International Ours des Cavernes, 25 – 27 septembre 2003, Livret guide, Résumés des communications et posters [9th International Cave Bear Symposium, 25 – 27 September 2003, Guide book, Abstracts of lectures and posters], 107 p.

A. Argant and M. Philippe are not explicitly cited as the editors, but both are the main organizers and authors of the volume preface.

**P:** PHILIPPE, M. – ARGANT, A. – ARGANT, J. (Eds.). 2004. Actes du 9e Symposium international sur l’ours des cavernes [Proceedings of the 9th International Cave Bear Symposium]. Cahiers scientifiques, Hors série, 2, 1–208.

In Abstract book as well as in Proceedings, there is written September 27 as the last day of symposium. In the Circulars, there was date September 25–28, but September 28 has already been only departure day.

### 10th ICBS: Mas d’Azil (Ariège, France), September 29 – October 3, 2004

**Organizer:** UMR 5608 CNRS; Université de Toulouse le Mirail & Institut für Paläontologie, Universität Wien

**A:** [no editors] 2004. 10th International Cave Bear Symposium. Guide book/Livret guide, 55 p. + Annexe.

Annexe is comprised of selected pages (concerning the caves of this area) from A. Leroi-Gourhan’s book from 1984 “L’Art des cavernes. Atlas des grottes ornées paléolithiques françaises” (together 38 p.). The abstract for oral presentation by L. Kindler “Balve Cave (North Rhine-Westphalia, Germany): Competition between Bears and Neanderthals in the occupation of a cave?” was submitted too late and therefore, it is not included in the abstract book. It was distributed to the ICBS participants on the separate unnumbered sheet.



**P:** [no editors] 2005. In: *Bulletin de la Société d'histoire naturelle de Toulouse et de Midi-Pyrenees*, 141(1), 5–54.

Papers from the ICBS are included in this volume together with 4 other papers. Conference papers are marked as "Article présenté au 10ème Colloque International sur l'Ours des Cavernes (Mas d'Azil, 23-26 septembre 2004)". In most of the papers, it is erroneously stated "l'Ours des Pyrénées" instead of "l'Ours des Cavernes" and this note is missing in Rosendahl et al. But all the papers on pp. 5–54 were presented at 10th ICBS as apparent from the abstract book. No special title page or editors are present in this volume.

**11th ICBS: Pommelsbrunn (Bavaria, Germany), September 29 – October 2, 2005**

**Organizer:** Förderverein Hunas – Archiv des Eiszeitalters e.V.; Institute for Prehistory, University of Erlangen-Nürnberg; Institute for Palaeontology, University of Erlangen-Nürnberg; Naturhistorische Gesellschaft Nürnberg e.V., Abteilung für Karst- und Höhlenkunde

**P:** AMBROS, D. – GROPP, CH. – HILPERT, B. – KAULICH, B. (Eds.). 2005. Neue Forschungen zum Höhlenbären in Europa. 11. Internationales Höhlenbären-Symposium. 29. September – 2. Oktober 2005 in Pommelsbrunn (Landkreis Nürnberg Land). Abhandlung, Naturhistorische Gesellschaft Nürnberg e.V., 45, 1–391.

The Proceedings were still published before the conference (although they were distributed to participants only on CD due to the printing delay), so no abstracts were needed.

**12th ICBS: Aridéa/Loutrá (Macedonia, Greece), November 2–5, 2006**

**Organizer:** School of Geology, Aristotle University of Thessaloniki; Institute for Palaeontology, University of Vienna; Commission for Quaternary Research of Austrian Academy of Science; Municipality of Aridéa; Prefecture of Pella; Physiographical Museum of Almopia; Hellenic Speleological Society, Department of North Greece

**A:** [no editors] 2005. 12ο ΔΙΕΘΝΕΣ ΣΥΜΠΟΣΙΟ (ΔΙ.Σ.Α.Σ.), Η ΑΡΚΟΪΔΑ ΤΩΝ ΣΠΗΛΛΑΙΩΝ [12th International Cave Bear Symposium (ICBS), Abstract book], 78 p.

**P:** TSOUKALA, E. – RABEDER, G. (Eds.) 2006. Proceedings of the 12th International Cave Bear Symposium (I.C.B.S.). *Scientific Annals of the School of Geology, Aristotle University of Thessaloniki (AUTH)*, Special volume 98, 1–315.

**13th ICBS: Brno (Moravia, the Czech Republic), September 20–24, 2007**

**Organizer:** Department of Geological Sciences, Faculty of Sciences, Masaryk University

**P:** MUSIL, R. – VÁVRA, V. 2007. Proceedings of the 13th International Cave Bear Symposium, September 20–24, 2007, Brno, Czech Republic. *Scripta Facultatis Scientiarum Naturalium Universitatis Masarykianae Brunensis, Geology*, 35, 1–169.

This volume was published before the conference, so no abstract book was needed. Nevertheless, although called Proceedings, contributions in this volume have rather character of extended abstracts than the regular papers.

**14th ICBS: Appenzell (Switzerland), September 18–22, 2008**

**Organizer:** Natural History Museum St. Gall; Museum Appenzell; St. Gall Society of Natural Sciences; Archaeological Service Canton St. Gall; Institute for Prehistory and Archaeological Science (IPAS), Basel University; Swiss Institute for Speleology and Karst Studies (SISKA), La Chaux-de-Fonds; Höhlenclub Alpstein (section of the Swiss Speleological Society)

**A:** [no editors] 2008. 14th International Cave Bear Symposium. Abstracts. 34 p.

Abstracts of G. Baryshnikov "New data on the cave bear from Akhstyrskaya cave (North-western Caucasus, Russia)" (1 p.) and of S. C. Münzel, M. Hofreiter, M. Stiller, N. J. Conrad and H. Bocherens "New Results on the Palaeobiology of Bears on the Swabian Alb (Chronology, Isotopic Geochemistry and Palaeogenetics)" (3 p.) were added on the loose leaves to the abstract book.

**P:** [no editors] 2008. Das 14. Internationale Höhlenbären-Symposium in Appenzell, Schweiz, 18.–22. September 2008/Le XI<sup>Ve</sup> Symposium international sur l'Ours des cavernes à Appenzell, Suisse, 18 au 22 septembre 2008 [The 14th International Cave Bear Symposium at Appenzell, Switzerland, 18–22 of September 2008]. *Stalactite*, 58, 2, 1–83.

Proceedings were published in fact in 2009.

**15th ICBS: Spišská Nová Ves (Slovakia), September 17–22, 2009**

**Organizer:** Department of Geology & Palaeontology, Comenius University in Bratislava; Museum of Spiš in Spišská Nová Ves; State Geological Institute of Dionýz Štúr; State Nature Conservancy of the Slovak Republic – Slovak Caves Administration & National Park Slovenský raj

**A:** ŠABOL, M. (Ed.) 2009. 15th International Cave Bear Symposium. Abstract Book, 68 p.

An abstract to a presentation by A. García-Vázquez, M. Pérez-Rama and A. Grandal d'Anglade "On the different types of carnivore marks on cave bear bones from Cova Eirós (NW of Spain)" was added as Addendum on a separate sheet.

**P:** ŠABOL, M. – VIŠŇOVSKÁ, Z. – VLČEK, L. (Eds.). 2009. European Cave Bear Researches. *Slovenský kras*, 47, suppl. 1, 1–127. <http://www.ssj.sk/sk/clanok/59-slovensky-kras-47-suppl-1-2009>

**16th ICBS: Azé (Saône-et-Loire, France), September 22–26, 2010**

**Organizer:** LAMPEA – UMR 6636, Grenoble; A.R.P.A., Université C. Bernard Lyon 1 & Institut für Paläontologie, Universität Wien

**A:** ARGANT, A. (Ed.). 2010. 16ème Symposium International de l'Ours et du Lion des Cavernes. Programme – Livret guide des excursions [16th International Cave Bear and Lion Symposium. Program – Guide book of excursions], 93 p.

The abstract to the talk by E. Crégut-Bonnoure, J. E. Lewis, L. Slimak and J.-E. Brochier "New data on the Pleistocene localities with *Ursus arctos* in Vaucluse (Southern France)" (3 p.) was added separately to the abstract book.

**BARRIQUAND, J. – BARRIQUAND, L.** 2010. Azé the Mâconnais. Geology and karst/Human occupation (from the Prehistory to Antiquity) / Palaeontology / Environment / History of research. A.R.P.A., Université C. Bernard, Villeurbanne, Association Culturelle des Grottes d'Azé, Azé, 208 p.

**P:** ARGANT, A. – ARGANT, J. (Eds.) 2011. 16th International Cave Bear and Lion Symposium. Azé (Saône-et-Loire, France), 22–26 septembre 2010. *Quaternaire, Hors-séries*, 4, 1–324. Proceedings were published in fact at the beginning of 2012.

**17th ICBS: Einhornhöhle (Lower Saxony, Germany), September 15–18, 2011**

**Organizer:** Reiss-Engelhorn-Museen; Staatliches Naturhistorisches Museum, Braunschweig & Gesellschaft Unicornu fossile e.V.

**A:** [no editors] 2011. 17th International Cave Bear Symposium. Abstracts – Excursion Guide, 36 p.

Although no editors are indicated, D. Döppes, U. Joger, R. Niellbock and W. Rosendahl are listed as the organizers. D. Döppes and W. Rosendahl are authors of Excursion Guide.

**P:** [no editors] 2012. In: *Braunschweiger Naturkundliche Schriften*, 11, 1–142.

**18th ICBS: Băile Herculane (Romania), September 20–22, 2012**

**Organizer:** The "Emil Racoviță" Institute of Speleology & the Romanian Society for Speleology and Karstology

**A:** CONSTANTIN, S. (Ed.). 2012. The 18th International Cave Bear Symposium. Program – Abstracts – Field trip, 87 p.

**P:** CONSTANTIN, S. (Ed.) 2014. Fossil remains in karst and their role in reconstructing Quaternary paleoclimate and paleoenvironment. *Quaternary International*, 339–340, 1–300. <http://www.sciencedirect.com/science/journal/10406182/339?sd=1>

Not all papers published in this volume were presented at ICBS, but these mostly fit into the conference thematic scope, with the exception of the paper by Wang et al.

**19th ICBS: Semriach (Styria, Austria), October 3–6, 2013**

**Organizer:** Institut für Paläontologie, Universität Wien & Landesverein für Höhlenkunde in der Steiermark

**A:** RABEDER, G. – KAVCIK, N. (Eds.). 2013. 19th International Cave Bear Symposium. Abstracts & Excursions. 39 p.

**20th ICBS: Corvara (South Tyrol, Italy), September 10–13, 2014**

**Organizer:** Institut für Paläontologie, Universität Wien; Museum Ladin Ursus ladinicus & Tourismusverband Alta Badia

**A:** RABEDER, G. – KAVCIK, N. (Eds.). 2014. XX. International Cave Bear Symposium, 2014. Abstracts & Excursion-guide. XII + 45 p.

**21th ICBS: Hellevoetsluis (the Netherlands), September 10–13, 2015**

**Organizer:** Werkgroep Pleistocene Zoogdieren & Speleo Nederland

**A:** [no editors] 2015. 21st International Cave Bear Symposium 2015. Programme & Abstracts. 33 p.

**P:** [no editors] 2016. Proceedings of the 21st International Cave Bear Symposium. *Cranium*, 33, 1, 1–66.

**22th ICBS: Kletno (Poland), September 21–25, 2016**

**Organizer:** Department of Paleozoology, Institute of Environmental Biology, Faculty of Biological Sciences, University of Wrocław & Department of Genomics, The Faculty of Biotechnology, University of Wrocław

**A:** [no editors] 2016: 22nd ICBS. Kletno, Poland, 2016, 47 p.

**P:** under preparation (*Acta zoologica cracoviensia*)

