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Faculty of Sciences

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Editors
Evangelia Tsoukala
Gernot Rabeder

ARISTOTLE UNIVERSITY OF THESSALONIKI
FACULTY OF SCIENCES

ΑΡΙΣΤΟΤΕΛΕΙΟ ΠΑΝΕΠΙΣΤΗΜΙΟ ΘΕΣΣΑΛΟΝΙΚΗΣ
ΣΧΟΛΗ ΘΕΤΙΚΩΝ ΕΠΙΣΤΗΜΩΝ

SCIENTIFIC ANNALS OF THE SCHOOL OF GEOLOGY
SPECIAL VOLUME 98

ΕΠΙΣΤΗΜΟΝΙΚΗ ΕΠΕΤΗΡΙΔΑ ΤΟΥ ΤΜΗΜΑΤΟΣ ΓΕΩΛΟΓΙΑΣ
ΕΙΔΙΚΟΣ ΤΟΜΟΣ 98

PROCEEDINGS
Of the 12th International Cave Bear Symposium
2-5 NOVEMBER 2006, THESSALONIKI AND ARIDEA (PELLA, MACEDONIA)

ΠΡΑΚΤΙΚΑ
Του 12ου Διεθνούς Συμποσίου για την Αρκούδα των Σπηλαίων
2-5 ΝΟΕΜΒΡΙΟΥ 2006, ΘΕΣΣΑΛΟΝΙΚΗ ΚΑΙ ΑΡΙΔΑΙΑ (ΠΕΛΛΑ, ΜΑΚΕΔΟΝΙΑ)

Επιμέλεια Έκδοσης/Editors: Evangelia S. TSOUKALA and Gernot RABEDER

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PREFACE

The School of Geology of the Aristotle University of Thessaloniki accepted with pleasure the proposal of the Academic Prof. Gernot Rabeder, Director of the Paleontological Institute of Vienna University, for the 12th International Cave Bear Symposium (ICBS) to be held in Thessaloniki in 2006. It was an honour for the School and at the same time a challenge for the colleagues who were ready to organize and participate to the Symposium. The School of Geology not only accepted the organization of the Symposium but also contributed financially to its success. The ultimate proof is the present volume of the proceedings of the Symposium which is hosted in the Scientific Annals of the School of Geology.

The participation of thirty five European Universities and Institutions, the relatively high number of participants, the enthusiasm of our students, the high level of the scientific contributions and the interesting and well-organized excursions undoubtedly place the 12th ICBS among the successful paleontological events in Greece. Of particular interest were the visits to the Almopia Spelopark in the Aridea Natural History Museum and to the Loutra Physiographical Museum, where findings of the excavations of the last 16 years regarding the Cave Bear are displayed.

The Symposium gave the scientists the great opportunity to present and discuss their research on the Cave Bear, one of the best known Pleistocene mammals worldwide.

One of the most positive contributions of the 12th ICBS was the holding of the main part of it in Aridea, a lovely small town of the area in which materials of the Cave Bear were found. The local authorities participated in the Symposium and addressed it, making known to the local people and particularly to the politicians their will and their attempt to sensitize the society to geoparks and geotourism. The Symposium became a very good example of the development of collaboration of scientists with local authorities and local societies regarding this matter.

The prevalent opinion is that the 12th ICBS was very successful and very fruitful and of course its success is mainly related to the hard work of all the members of the Organizing Committee. A major part of the success is due to the enthusiastic group of our students, both under- and postgraduate, who made their best for the Symposium. The warm hospitality of the Aridea Municipality was among the factors which added greatly to the successful organization.

To all those who in whatever way offered their assistance to the Symposium, the School of Geology would like to express its gratitude and its sincere thanks. Special thanks are due to the President of the Organizing Committee, Mrs. Evangelia Tsoukala, Assistant Professor of the School of Geology, who spent valuable time to offer us the unforgettable 12th ICBS. I would also like to thank Prof. George Eleftheriadis, who, from the post of the President of the Committee of the Scientific Annals of the School of Geology, did his best for the publication of the volume of the Proceedings of the Symposium in the Scientific Annals.

In addition to the efforts of the Organizing Committee the Symposium benefited greatly from the financial support of Schools, Institutes, Organizations, Ministries, Prefectures, Municipalities and Museums. Since the economic support of a Symposium plays a major role in its success, on behalf of the School of Geology, I would like, at this point, to warmly thank all the sponsors.

Lastly, hoping that the present volume of the 12th ICBS Proceedings will be a valuable tool for the students and the scientists dealing with the Cave Bear research, I would like to thank all the participants who contributed, each with his/her on presentation, and altogether with their discussions and remarks, that the Thessaloniki - Aridea Symposium be considered as an outstanding Cave Bear Symposium.

Professor Georgios Christofides
Chairman of the School of Geology
Aristotle University of Thessaloniki

INTRODUCTORY NOTE

The Cave Bear is one of the best known Pleistocene mammals, whose remains have been excavated by hundreds and thousands in the European bear caves. There have been considerable advances in the research concerning this animal during the last decades. The International Cave Bear Symposiums (ICBS) have contributed substantially to this development. For the first time, this Symposium was held in Greece, at Thessaloniki and Aridea - Almopia Speleopark (district of Pella, Macedonia).

The paleontological research in the area started in 1990 and the excavation of the cave site in 1992, while the cooperation with the Vienna University and Austrian Academy of Sciences has started since 1996. The results of this research among others include: many scientific publications, popularized publications, presentations given at international congresses, dissertation theses, Master of Science theses, a Doctoral Thesis (under preparation), training of students of Geology and Archaeology, two paleontological exhibitions in Loutrá and in Aridéa, presentations in the media, a monograph (under preparation) and the book entitled "A guide to the Speleopark of Almopia".

For our work mentioned above, we were assigned the organization of the 12th ICBS and we were in the most pleasant position to welcome many distinguished scientists from at least 12 different countries and 35 Universities and Institutes in Europe. The participants visited the Paleontological Museum of the Geology School of Aristotle University, Thessaloniki and had the chance to look at the most important primate finds of Macedonia: the famous Petralona hominid skull as well as many *Ouranopithecus macedoniensis* and *Mesopithecus* specimens. Also, they presented their contributions in Aridea during the Work of the Symposium, they visited the specially organized exhibition of the cave bear collection derived from 16 years of research and excavations in Almopia Speleopark in the Aridea Natural History Museum, and in the Physiographical Museum of Loutra. Additionally, they visited the caves of the Speleopark (the Bear Cave was especially prepared) and finally some of them visited the Grevena proboscidean site and some the Agios Georgios cave (hyaena den) in Kilkis regarding the post symposium excursions.

Our sincerest and warmest thanks go to every student and colaborator who greatly contributed to the highly successful outcome of the 12th International Cave Bear Symposium. We are grateful to the Geology School which contributed by all means at its disposal to the Symposium and accepted the responsibility for publishing the proceedings in its Scientific Annals. We are also grateful to the Municipality of Aridea and to the people of the Loutra area who helped us enormously towards accommodation of the participants to whom we would like to express once more our great pleasure for honoring us with their visit to Greece.

Evangelia TSOUKALA
President of the Organizing Committee

Acknowledgements

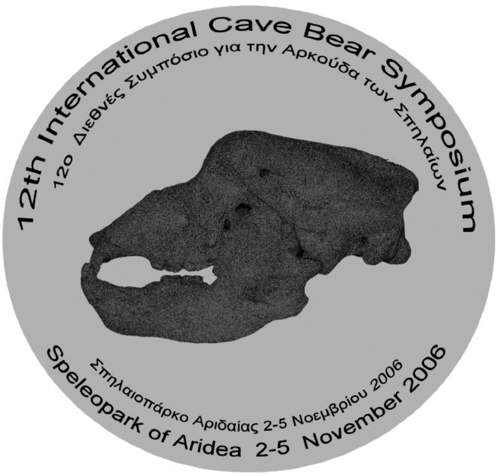
Special thanks should also be addressed to the following Organizers and Sponsors of the 12th Cave Bear Symposium:

- The School of Geology
- The Institute for Palaeontology, University of Vienna
- The Commission for Quaternary Research of Austrian Academy of Science
- The Municipality of Aridea
- The Physiographical Museum of Almopia
- The Prefecture of Pella
- The Hellenic Speleological Society, Department of Northern Greece
- The Ministry of Macedonia and Thrace
- The Research Committee of Aristotle University of Thessaloniki
- The Geotechnical Chamber of Greece

12th International Cave Bear Symposium

Thessaloniki, Aridea, Almopia Speleopark
(Macedonia, Greece)
2-5 November 2006

PROCEEDINGS



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12º International Cave Bear Symposium (ICBS), 2-5/11/ 2006, Thessaloniki/Aridea (Pella, Macedonia, Greece)

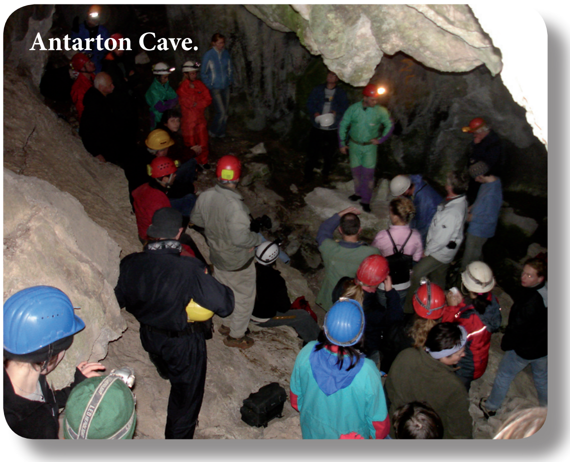
12º International Cave Bear Symposium 2-5/11/ 2006, Thessaloniki/Aridea (Pella, Macedonia, Greece).

Thessaloniki, School of Geology: Presentation of fossil primates from the Macedonia area including The Petralona Man, *Ouranopithecus macedoniensis,* and *Mesopithecus.*

Aridea, Ksenitidion Congress hall.

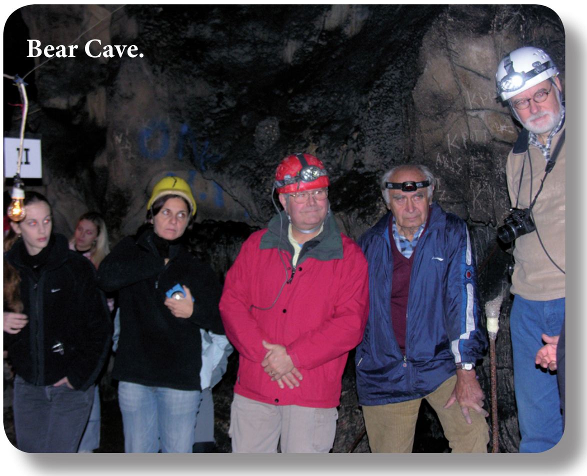
Natural History Museum of Aridea and Physiographical Museum of Almopia in Loutra.

Post Symposium main excursion.


Antarton Cave.


Entrance of the Varathron Cave.


Bear Cave.


Bear Cave.


Bear Cave.

Bear Cave.

Post Symposium excursions, Sunday 5 November 2006.

Grevena Proboscidean sites-Milia *Mammut borsoni.*

Agios Georgios Cave - Kilkis, hyaenid den.

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INTRODUCTION TO THE ALMOPIA SPELEOPARK

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THE GEOLOGY OF ALMOPIA SPELEOPARK

George ELEFTHERIADIS[1]

Abstract: The Almopia Speleopark is located on the boundary of two geological zones: the Almopia (Axios) zone eastwards and the Pelagonian zone westwards. The Almopia zone in the area of study is comprised of metamorphic rocks (schists, marbles and cipolines), ophiolites, limestones and clastic formations whereas the Pelagonian zone consist of carbonate rocks of Triassic-Jurassic age, sediments of Upper Cretaceous age and flysch of Upper Maastrictian-Lower Paleocene. In the area there are also travertine deposits of significant quantity and excellent quality. The seismicity in the area can be considered as not significant.

Key words: Almopia, Speleopark, geology, volcanology, seismicity.

INTRODUCTION

The Almopia area geotectonicaly belongs to the Almopia zone, which together with the Peonia and Paikon zones constitute the old Axios (Vardar) zone (Mercier, 1968). The Axios zone (Kossmat, 1924) is situated between the Pelagonian massif to the west and the Serbo-Macedonian massif to the east. The Almopia and Peonia zones, constituting the westernmost and easternmost parts of the Axios zone, respectively, were deep-water oceans separated by the shallow ocean of the Paikon zone, consisting of thick carbonate rocks of mainly Triassic to Cretaceous age.The Almopia zone is characterized by huge masses of ophiolites (Bebien *et al.,* 1994).

The Almopia zone was deformed during two orogenic periods: the Upper Jurassic-Lower Cretaceous and the Upper Cretaceous-Middle Eocene. During the first period the Almopia ocean closed, the Almopia zone emerged temporary until the Middle-Upper Cretaceous transgression and the ophiolitic rocks overthrusted on the Pelagonian platform westwards (Mercier, 1968). Between the Upper Cretaceous and the Middle Eocene (second orogenic period) the final emersion of Almopia zone took part. Because of the orogenic movements the Almopia rocks (older metamorphic rocks, ophiolites and upper Cretaceous transgression sediments) formed small to big dislocated slices in the form of units named usually according to the villages names. They are distinguished in different groups (Mountrakis, 1985; Mercier, 1968; fig. 1) such as:

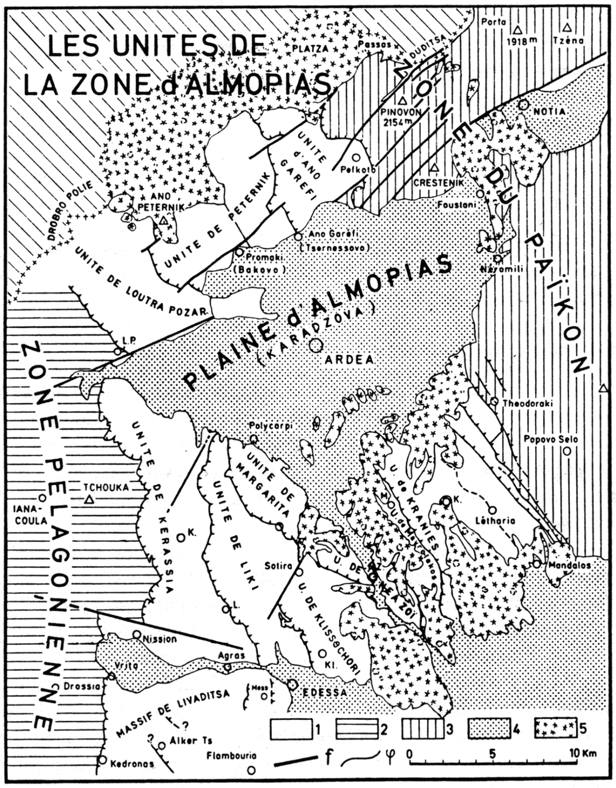

Figure 1. Sketch of Almopia zone units: 1. Almopia units; 2. Pelagonian zone; 3. Paikon zone; 4. Quarternary; 5. Post-alpine volcanic formations, f. Faults, Φ. Anomalous contacts (after Mountrakis, 1985 & Mercier, 1968).

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East Units	West Units	Middle Units	North Units
Ano Garefi	Kerassia	Liki	Peternik
Mavrolakkos	Kedronas	Margarita	Loutra
Kranies		Klissochori	
		Nea zoi	
		Messimeri	

In general, the Almopia zone formations show some differences from place to place reflecting maybe paleogeographic differences. The main formations from the lower to upper parts are (Mountrakis, 1985, fig. 2).

Al 1. Augen gneisses and amphibolites alternating in the upper parts with pre-alpine quartzites and amphibolitic-, mica- and chloritic-shists (Peternic unit).

Al 2. Metamorphic rocks consisting of continuous alternations calcic-, chloritic-, sericitic-schists, phyllites and marbles of Triassic to maybe Jurassic age.

Al 3. Metamorphic rocks of the same sedimentation (Triassic to Jurassic age) such as marbles, crystalline limestones and dolomites with intercalations of schists

Al 4. Tectonically emplaced on the previous formations there are mélanges ophiolitics. They consist of big or small marble and metamorphic blocks set in an ophiolitic mass. The age of the tectonic emplacement is considered to be Upper Jurassic. This formation appears in various places of the Almopias zone, especially in the area of Klissochori.

Al 5. Huge masses of ophiolites consisting of serpentines, basic laves, dolerites etc of Jurassic age.

Al 6,7,8. On the ophiolites or synfold with them there are sedimentary (6) volcanosedimentary (7) and clastic (8) formations.

Al 9. Basal conglomerate of Middle-Upper Cretaceous age.

Al 10. Gray to black limestones of Upper Cretaceous age.

Al 11. Flysch of Upper Maastrichtian-Lower Paleocene age.

GEOLOGICAL STRUCTURE OF SPELEOPARK

The Speleopark area is located at the boundary of two geotectonic zones that are: the Almopia zone, at the East and the Pelagonian one, at the West (Mountrakis, 1976, fig. 3).

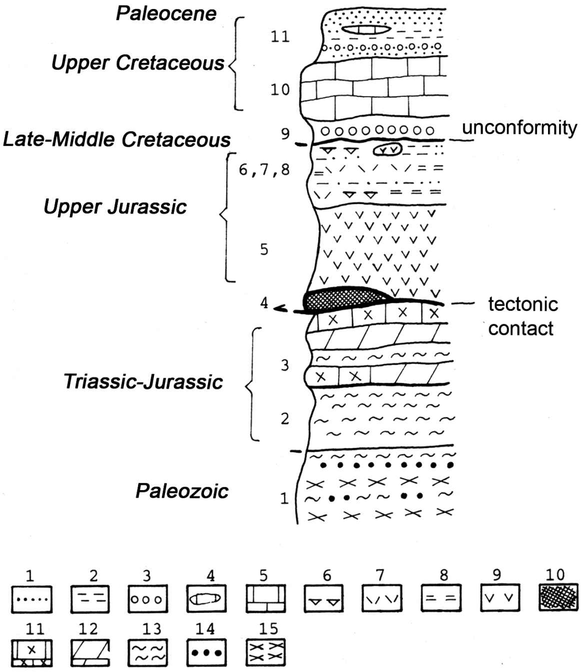

Figure 2. Modified generalized lithostratigraphic column of Almopia zone: 1. Sandstone; 2. Clay and slates; 3. Conglomerates and others clastic sediments; 4. Calcareous lenses; 5. Limestones; 6. Cherts; 7. Volcanic materials; 8. Tuffs and volcanoclastics; 9. Ophiolites; 10. Melanges ophiolitics; 11. Marbles and crystalline limestones; 12. Dolomites; 13. Slates; 14. Amphibolites; 15. Gneisses (after Mountrakis, 1985).

ALMOPIA ZONE

The Almopia rocks in the Loutra area are of the following rock types starting from the lower to upper formations:

Metamorphic system

It consists of alternating metamorphic rocks, such as phyllites, sericite schists, greenschists, amphibolitic schists, marbles and cipolines. The general direction of the metamorphic system is NW-SE with NE dip. The thickness of each member of this system varies from about 50 to 200 m. The metamorphic system is characterized by an ibricate structure that results in the repetition of the rock members. This system was formed during the Mesozoic time.

Ophiolites

There is a large mass of ophiolitic rocks and some smaller bodies in the area of Loutra. They generally consist of basic to ultra basic rocks that suffered intense serpenti-

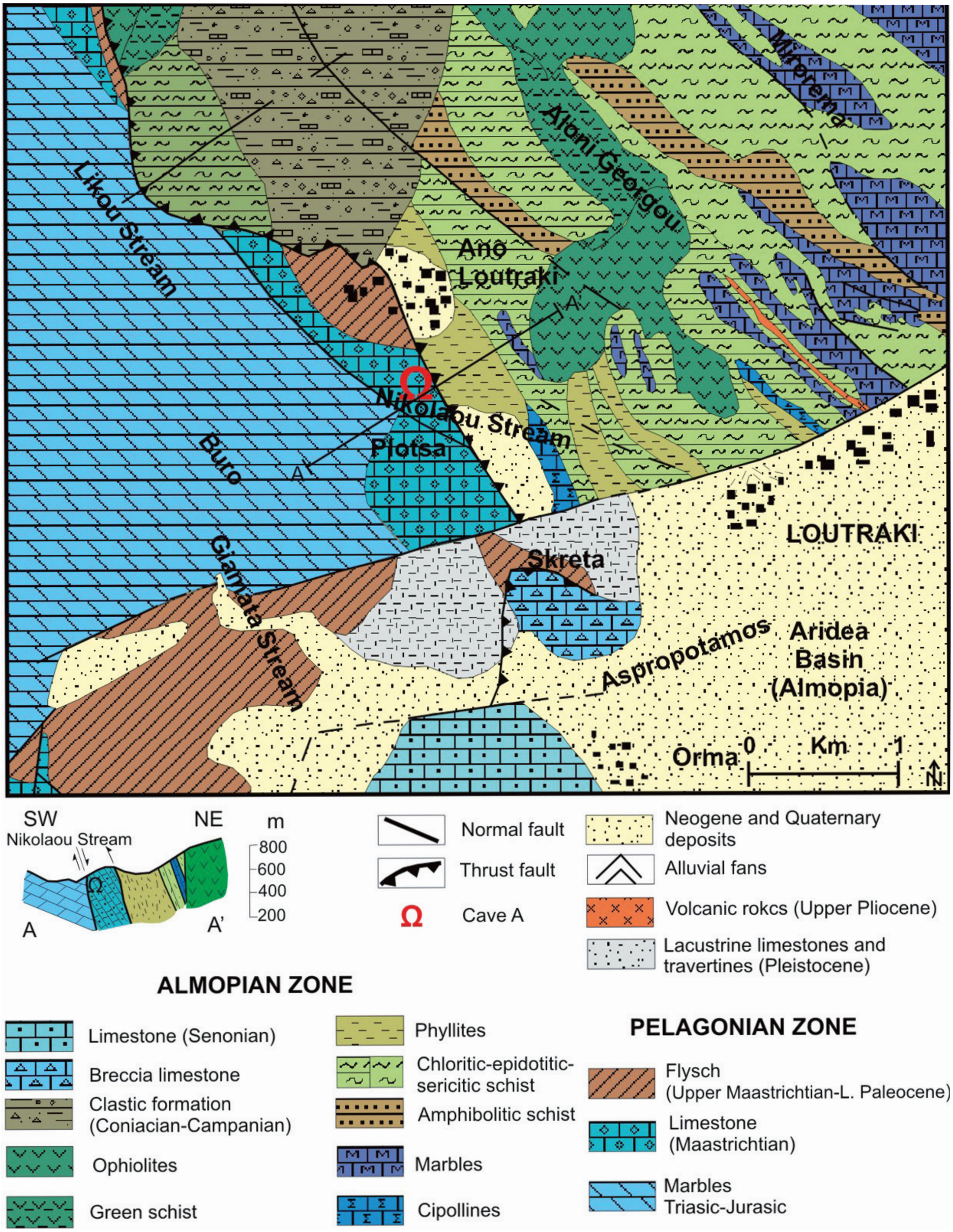

Figure 3. Geological map of the Loutra area (based on the map in Mountrakis, 1976, modified by K. Chatzopoulou and Ath. Vassiliadou).

nization. As is known the name “ophiolites” comes from their green color looking like the skin of a snake. The existence of these rocks and their age imply that the area was a large ocean during Upper Jurassic, about 150 million years ago.

The Diasselo Limestone

The Diasselo limestone is slightly green in color. As it is slightly recrystallized, the fossils that it contains have not been destroyed. It covers the ophiolites and its contact with the metamorphic system does not clearly have conformity. In general it is a very small outcrop, but very important because it proves the transgression of the sea during Middle Cretaceous, about 130 to 90 million years ago.

Clastic formation of Mariam

It is a sedimentary formation with intense tectonic deformation and slight metamorphism. It consists of alternations of fine- to coarse-grained sediments containing gneissic or ophiolitic pebbles. The coarse-grained character, as well as the foraminifera found in this formation reveal the coastal or neritic facies of sedimentation during Upper Cretaceous, probably Coniacian - Campanian, about 80 million years ago.

PELAGONIAN ZONE

The following rock outcrops are observed in the broader study area:

Carbonate cover of Triassic- Jurassic age

The carbonate cover consists of recrystallized carbonate sediments such as marbles, dolomitic marbles and dolomites of white and light grey color. This formation appears to be homogenous due to the effect of tectonic movements and the metamorphism which have distracted the boundaries between the different rock members and the pre-existing fossils.

Very close to the caves site, the rocks of the carbonate cover are intensely mylonitized.

Transgressional sediments of Upper Cretaceous

These sediments overlay the carbonate cover of Triassic-Jurassic age and are immediately in contact with rocks of the Almopia zone. They comprise the following formations from the lower to the upper parts:

i. The sediments of Upper Santonian-Campanian are slightly to darker gray in color and slightly recrystallized with fossils of the genus *Distefenella*.
ii. The Maastrichtian sediments are dark gray limestones, of a thickness more than 100 m, bearing foraminifera (*Orbitoides media)*.

In the area of Loutra the distinction between these limestones is not possible because the Pelagonian formations suffered intense tectonism by the overthrust of the Almopian rocks.

Flysch of Upper Maastrichtian - Lower Paleocene

The Pelagonian flysch is immediately below the thrust of the Almopia zone. In the broader area of study, the flysch consists of alternating dark clay-pelitic sediments with intercalation of calcitic and quartzitic sandstone. Near the Loutra area, the formation is more calcarinate and more tectonically disturbed.

VOLCANOLOGY

During Pliocene - Quaternary time tensile forces acted in the Almopia area and resulted in new faults and reactivated old ones that formed the Almopia basin and accommodated upwelling of magmas from the deeper parts of the earth giving rise to volcanism.

The Almopia volcanic rocks (AVRs) are located on the Voras Mt., and have been emplaced above the alpine metamorphic basement of the Almopia series, consisting mainly of greenschists, phyllites, limestones, gneisses, amphibolites, marbles and ophiolitic rocks.

The AVRs extend beyond the Greek - F.Y.R.O.M. boundaries covering an area of approximately 200 km^2. They belong to the widespread volcanic activity, which has affected the Aegean and the surrounding areas since Tertiary (Fytikas *et al.,* 1984). This volcanism is generally related to the subduction of the African plate underneath the southern margins of the Eurasian plate (Boccaletti *et al.,* 1974).

Based on pollen spores found in cineritic tuffs Mercier & Sauvage (1965) suggested an Upper Pliocene age for Almopia volcanism. This suggestion was supported by K/Ar dating on whole rock and mineral separates (biotite, hornblende) which have provided ages from 1.8 to 5.0 Ma (Bellon *et al.,* 1979; Kolios *et al.,* 1980). Ages up to 6.5 Ma have been published for the volcanic rocks in the F.Y.R.O.M. sector (Vougioukalakis, 2002).

On the basis of petrographical and petrochemical criteria the AVRs can be distinguished on six groups that are: high-K andesites-dacites, trachydacites, trachytes, latites, rhyolites and shoshonites (Vougioukalakis, 2002). The last group is found only as enclaves in the rest groups. All the rocks have a porphyritic texture mostly characterized by the presence of prismatic or tabular phenocrysts of sanidine, often of relatively large size (up to 2-3 cm). Moreover there are phenocrysts of plagioclase, biotite, hornblende and pyroxene. The AVRs have an intermediate chemical character and are enriched in potassium. They belong to the high-K calc-alkaline to shoshonite rock series.

The AVRs are connected with transversal faults of SW-NE and SE-NW directions. An extensional tectonic regime has being active in this area since the Neogene. The AVRs form several distinct centers, consisting of lava domes and subordinate lava flows and dikes. The eruptive centers are surrounded by large amounts of volcanoclastic materials. A characteristic feature of Almopia volcanism is the intense explosive activity and the huge amounts of volcanoclastic materials (Vougioukalakis, 2002).

According to the last author, the volcanic activity was manifested in three distinct chrononogically and magmatologically periods:

The first period was manifested between 6.5/5.6 and 5 Ma to the east and central sector of the volcanic field. It was fed by andesitic and dacitic magmas. The second period was manifested between 4.9 and 4.2 Ma in the central and west sector of the Voras Mt. fed by latitic and trachytic magmas and the third and last eruptive period occurred between 4 and 1.8 Ma. It was restricted to the SW sector of the volcanic field and was fed at the beginning by trachytic magmas (up to 3 Ma) and later by latitic magmas.

TRAVERTINE

One of the most important geological formations of the Almopia region is the travertine deposits found either in the caves of the Speleopark or in the broader area of Aridea, the significance of which comes as a result of their quantity and quality. The Almopia's travertine deposits hold the first place in the travertine deposits of Greece. These rocks have been unearthed, processed and exported all over the world. The major characteristics of the Almopia's travertines are their clearance and fine crystallization, as well as the absence of xenoliths.

SEISMICITY

Based on geologic observations, the Almopia region is regarded as an area with tectonic activity. However, there is absence of significant earthquakes and only in the broader area, during the last century, have been registered few of them varying from M= 4.0 to M= 5.3.

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ALMOPIA SPELEOPARK (PELLA, MACEDONIA, GREECE): MORPHOLOGY-SPELEOGENESIS OF THE CAVES

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Abstract: In the present study the morphology of Almopia Speleopark caves is described in order to discuss preliminarily their speleogenesis in relation to the hydrogeological zones. At least two phreatic phases seem to exist with respect to the observed speleogens. The presence of solution ceilings, cupolas, ridges, pendants, abruptly ending passages and the horizontal morphology of the caves suggest that speleogenesis was due to slowly convecting water bodies. As an exception, some caves contain scallops or other phreatic features that developed by forced flow along a pressure head. The former pattern of speleogenesis was related to the presence of thermal ascending water in the area, while the latter is related to the downcutting of the Thermopotamos stream.

Key words: Almopia Speleopark, Aridea, Macedonia, Greece, speleogenesis, cave morphology.

INTRODUCTION

The Almopia Speleopark is located in the inner-mountain Almopia basin, in Northern Greece (Macedonia), 120 km northwest of Thessaloniki and 2 km from the Kato Loutraki village, on the slopes of the Voras Mt. (2524 m high), one of the highest mountains of Greece. A number of caves, opened by the downcutting of the Thermopotamos River, are situated in the V-shaped Nicolaou valley of the Speleopark (fig. 1).

Speleological research in the Loutra Arideas area started in 1990, when the late speleologist K. Ataktidis reported finding of cave bear bones, that where dug up illegally by treasure hunters in Bear Cave. Due to the great paleontological interest the first excavation cycle was launched in 1992 by the Geology School of Aristotle University, Thessaloniki (AUTH) (E. Tsoukala), under the supervision of the Ephorate of Speleology and Paleoanthropology (ESP) of the Ministry of Culture, and in cooperation with archaeologist Prof. G. Chourmouziadis, and of the late Prof. Eitan Tchernov (University of Jerusalem). The excavations continued in 1993-1994 in cooperation with ESP (Dr. E. Kambouroglou). In 1996 and since 1999 the excavations have been carried out by the AUTH, the ESP, and in co-operation with the Vienna University (Profs G. Rabeder, S. Verginis and their team). The palaeontological specimens from Bear Cave recovered in these excavations can be attributed to *Ursus ingressus* RABEDER, HOFREITER, NAGEL & WITHALM, 2004 and to the associated fauna including spotted cave hyena, lion, leopard, wolf, fox, badger, mustelids, artiodactyles and micromammals, of Late Pleistocene age (TSOUKALA, 1994; TSOUKALA *et al.*, 1998; TSOUKALA *et al.*, 2001; TSOUKALA & RABEDER, 2005; CHATZOPOULOU, 2001; CHATZOPOULOU *et al.*, 2001; PAPPA *et al.*, 2005). There are also caves in both sides of the valley with archeological remains, mainly with Neolithic and Byzantine pottery.

In 1990, the late K. Ataktidis also made the first documentation of the caves and organized the first exploration of the Speleopark. During this expedition preliminary geological (Dr. Tsamandouridis, unpublished data) and paleontological (Tsoukala, unpublished data) results were reported. The late speleologist J. Ioannou, member of the first exploration, noted that the Loutra Arideas area is of high scientific and speleological interest; therefore he suggested that it could be the first speleological park ("Speleopark") in Greece. The next researchers supported his idea and it is well accepted now. In 2005, the speleological research continued. New discoveries and photographic documentation, surveys and observations enlarged the scientific knowledge of the area (LAZARIDIS, 2005). Today the speleological research is progressing well with the aim of completing the previous work as much as possible and to contribute to the palaeontological research in the area.

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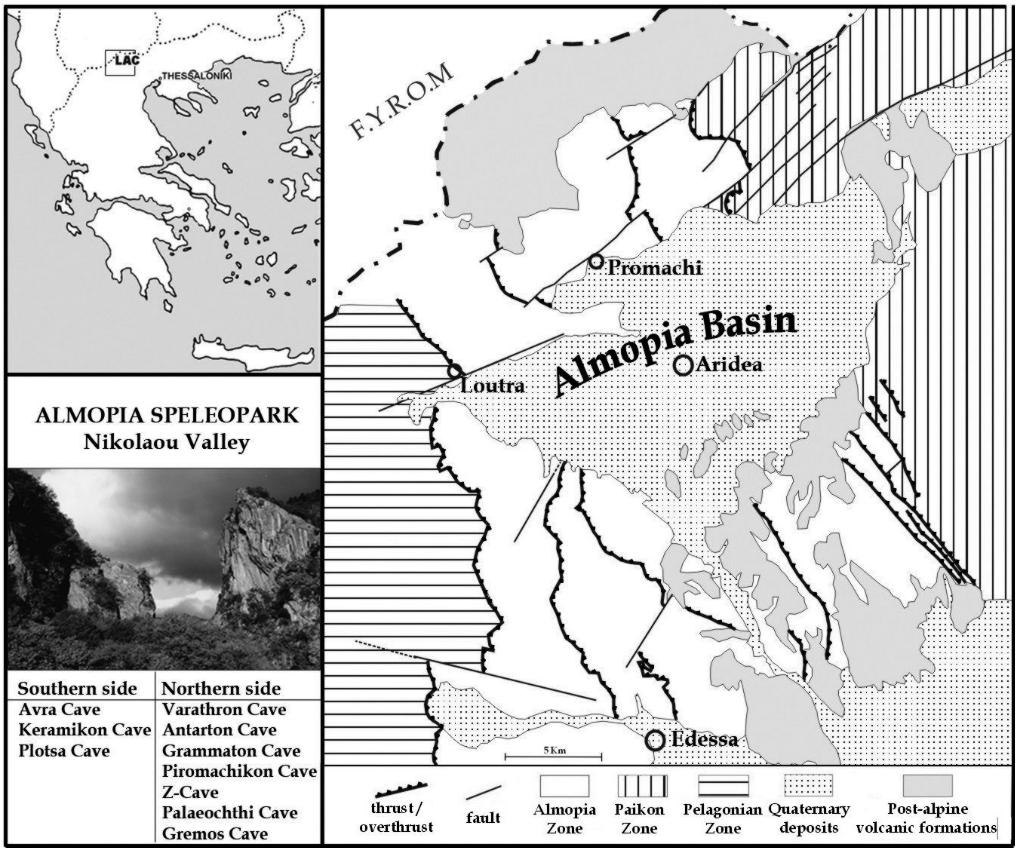


Southern side	Northern side
Avra Cave	Varathron Cave
Keramikon Cave	Antarton Cave
Plotsa Cave	Grammaton Cave
	Piromachikon Cave
	Z-Cave
	Palaeochthi Cave
	Gremos Cave

Figure 1. Left: Map of Greece with the Almopia Speleopark (LAC: Loutra Arideas Caves) and a view of the Nicolaou valley with the list of the caves on both sides. Right: geological sketch-map of Almopia (based on Mercier, 1968).

GEOLOGICAL SETTING

The general area is situated near the geological boundary between the Almopia Zone to the east and Pelagonian Zone to the west (Mercier, 1968; Mountrakis, 1976). It consists of Mesozoic metamorphic and sedimentary rocks, and more precisely the Nicolaou valley consists of Maastrichtian limestones of the Almopia zone. A NW-SE striking, ore-bearing fault zone and the ENE-WSW striking Loutraki Fault dominate the general area tectonically. The latter has a length of more than 10 km bounding the Aridea basin against the Voras Mt. (2524 m) (Mountrakis, 1976; Eleftheriadis, 1977; Chatzidimitriadis, 1974).

In the general area of the Almopia Speleopark on the Pelagonian massif, three uplifted denudation surfaces and one or two piedmont surfaces have been identified by Psilovikos & Kanetsi (1989). The former three surfaces were established in periods of a warm and humid climate prior or during the Neogene. The latter surfaces were formed in periods of warm and semiarid climate during the Villafranchian - Villanyian, or in glacial/interglacial climates during the Pleistocene. The entire northern part of the Pelagonian massif (Macedonia) has been uplifted at higher rates than its southern section. Above the caves there is a notable erosional surface, approximately at 700 m a.s.l. where the old Ano Loutraki village is located. According to the description by Psilovikos & Kanetsi (1989) of the erosional surfaces of the Pelagonian massif, this surface is probably an Early Pleistocene paleopediment.

Neotectonic activity of the Loutraki fault uplifted the Voras Mt. and the area of the Speleopark. As a result intense down-cutting of the Thermopotamos River occurred that formed the V-shaped Nikolaou valley and lifted the caves from the phreatic to the vadose zone successively.

Furthermore, a group of thermal springs exists due to the neotectonic activity and to the volcanism in the broader region (Mountrakis, 1976; Vougioukalakis, 2002; Patras, 1990). Mountrakis (1976) states that the origin of the travertine in the Loutra area, as well as at other localities nearby, is also due to these thermal springs either being active today or in the past. Patras (1990) calculated that the water rises from a depth of 600 m and its temperature at this depth ranges from 150 to 180°C. Today springs are located from 360 to 390 m of altitude. Their temperature varies between 30 and 37.5°C. The same researcher states also that the Na^+, K^+ and SO_4^{2-} concentrations decreased in correlation with a lowering of the spring water temperature, because possibly of their precipitation during their mixing with cooler water.

MORPHOLOGY AND SPELEOGENS OF THE CAVES

The Almopia Speleopark consists of six caves and four rock-shelters of similar morphology, the altitudes of which ranges between 460 m to 560 m a.s.l. (pl. 1). Additionally some small "isolated" chambers and many karst conduits occur as well. Presently they are "dry caves" in the vadose zone.

The caves described here as rock-shelters (pl. 2.1) are remnants of karst caves intersected by surface erosion. For this reason they developed as small chambers with many small conduits. Usually they contain a lot of breakdown boulders.

The larger caves have a maze-like pattern, structurally guided by joints. Maze caves can develop only if the growth rate is similar along many alternate flow paths. The maze pattern in general presents a variety of types. Six different types of linestone caves are differentiated: two branching types (curvilinear, rectilinear) and four maze types (anastomotic, network, spongework, ramiform) (Palmer, 2000; 2005). The plan morphology of the Almopia Speleopark caves reminds of ramiform mazes. This kind of plan pattern is due to local boosts in the water aggressiveness. Generally angular connections dominate where joints and faults are the principal structural guides of the conduits in contrast to curvilinear connections that dominate where the conduits develop primarily along bedding planes (Ford, 2000). The Almopia Speleopark caves present angular connections that indicate the significance of fracture control. However, they also show a ramiform pattern that illustrates the importance of the bedding partings in contrast to network types that show fracture control. The former refers mainly to the major passages of the caves. The latter is noticed in some large halls, in some small passages and in places where boneyard morphology (pl. 2.10) is observed. Generally the caves that developed on the northern slope represent large halls, except for the linear passages along joints, in contrast to the caves of the southern slope where large halls are absent. Large halls, connected by small "windows" are predominant in Bear Cave, Antarton Cave, Gremos Cave and Varathron Cave.

The predominant strike of the cave passages is NW-SE and NE-SW. The majority of the caves have more than one entrance developed by intersections of passages by surface erosion.

Cave genesis in general can occur either below the ground water table (i.e. in the phreatic zone) or in the unsaturated zone above the water table (i.e. in the vadose, where cavities are mostly filled with air). Both zones leave characteristic micro- and mesoscale morphological elements known as speleogens, that can be used to reconstruct the speleogenetic history of a cave or a cave area. In the case of the Almopia Speleopark, morphological indicators suggest that the bulk of the cavities developed under phreatic conditions and that vadose processes later altered the initial morphology.

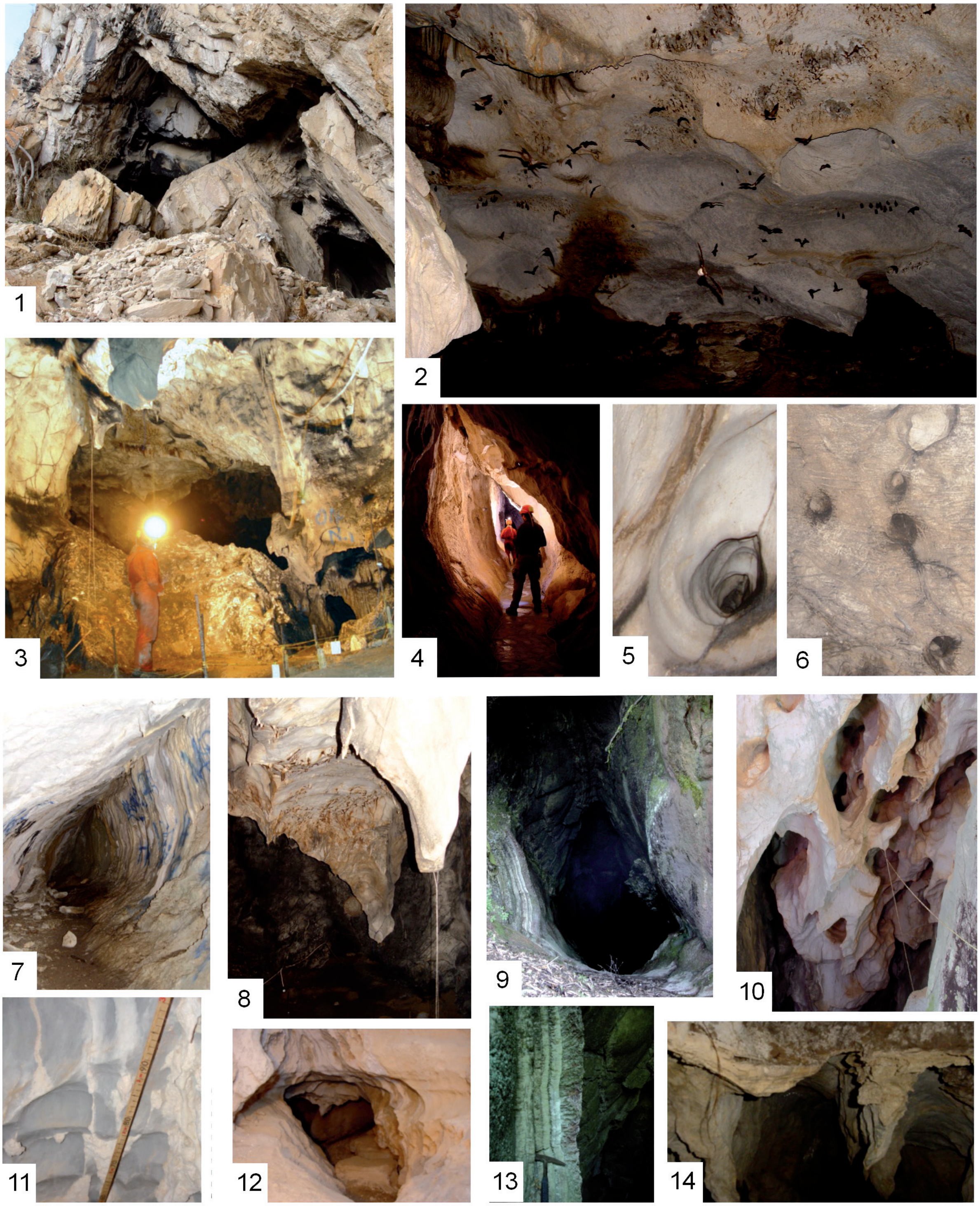
The phreatic origin of the caves (Kempe, pers. com.) is indicated by the following morphological elements (according to Kempe, 1970; Kempe *et al.,* 1975; Bögli, 1978; White & Deike, 1989; Lauritzen & Lundberg, 2000; White & White, 2000; Lundberg, 2005; Kempe *et al.,* 2006):

1. Solution ceilings (Laugdecken) either flat or concave formed by slowly convecting water bodies (pl. 2.2).
2. Walls sculptured by cupolas that grade downward into sloping side walls (facets) (pl. 2.2).
3. Bedrock ridges that separate the halls or interrupt the passages (pl. 2.3).
4. The presence of elliptical (lenticular) and symmetrical cave passages (in cross sections) that are controlled by high angle joints or by the intersection between two planes respectively (pl. 2.4; 2.7 and 2.9).
5. Many solution pockets that are present at the roof of some caves of the Speleopark; these are created by mixing corrosion along joints where water emerges into a passage filled with water of a different chemistry (pl. 2.5 and 2.6).
6. The presence of ceiling half-tubes, i.e. a channel in the ceiling of descending elliptical passages with a semicircular cross-section.
7. Scallops on ceilings and walls that develop by solution in a turbulent flow of groundwater filling the passage (pl. 2.11). They are absent in Bear Cave, Antarton Cave and Gremos Cave, while there is one passage with scallops in Varathron Cave. On the other hand, the caves of the southern slope contain abundant scallops that indicate a S-N flow direction from the caves outward to the river. On the contrary the scallops of Varathon Cave and Pyromachikon Cave show the same flow direction but from the river inward to the mountain.
8. Pendants that are remnants from removal of intervening rock through eddy dissolution (pl. 2.8 and 2.14).

Plate 1

Almopia Speleopark; surveys of the caves. Ground plans: 1a. Varathron Cave; 2. Antarton Cave; 3. Pyromachikon Cave; 4. Grammaton Cave; 5. Gremos Cave; 6. Z-Cave; 7. Bear Cave (based on Kampouroglou & Chatzitheodorou, 1999); 8. Avra Cave; 9. Plotsa Cave; 10. Keramikon Cave; 1b. Cross section of the main chamber of Varathron Cave.

Plate 2



Almopia Speleopark: 1. The "rock-shelter" morphology of the Speleopark Caves (Z-Cave); 2. Sculptured ceiling in Antarton Cave by slowly convecting water bodies (Kempe, pers. com.); 3. Bedrock ridge that separates two chambers of the Bear Cave; 4. Elliptical phreatic passage in Varathron Cave; 5. Solution pocket along a fracture; 6. A fracture guided group of pockets; 7. Elliptical phreatic passages that end abruptly (Avra Cave); 8. Pendants of more than 1.5 m length (Bear Cave); 9. Phreatic passage at the higher entrance (520 a.s.l.) of Varathron Cave; 10. Boneyard morphology (Bear Cave); 11. Scallops; 12. Keyhole passage (Keramikon Cave); 13. Detail of the phreatic coating that cover the passage of the higher entrance of Varathron Cave; 14. Pendants of approximately 0.5 m of length in Avra Cave.

Table 1
Almopia Speleopark. Morphology and location of the caves. Summary table.

	Bear Cave	**Antarton Cave**	**Varathron Cave**	**Avra Cave**	**Keramikon Cave**	**Piromachikon Cave**	**Grammaton Cave**	**Gremos Cave**	**Palaeocthi Cave**	**Cave Z**	**Plotsa Cave**
Southern (S) or Northern (N) slope	N	N	N	S	S	N	N	N	N	N	S
Altitude (m)	540	540	500-520	460	494	536	541	560	540	537	570
Entrances	1	2	3	2	4	1	2	3	1	1	1
Solution ceilings	+	+	+	-	-	-	-	-	-	-	-
Facets	+	+	+	-	-	-	-	-	-	-	-
Bedrock ridges	+	+	+	-	-	-	-	+	-	-	-
Elliptical & symmetrical passages	+	-	+	+	+	+	+	+	+	-	-
Ceiling half-tubes	-	-	-	-	+	-	-	-	-	-	-
Scallops	-	-	+	+	+	+	-	-	-	-	-
Pendants	+	+	+	+	-	-	-	-	-	-	-
Keyhole passages	-	-	-	-	+	-	-	-	-	-	-
Phreatic speleothems	-	-	+	-	-	-	-	-	-	-	-
Breakdown	+	+	+	-	+	-	-	+	-	+	-
False-floors	+	+	-	-	+	-	-	+	-	-	-

According to the presence or absence of these morphological elements, the initial development of the caves occurred in the phreatic zone. Once the caves drained because of the regional uplift, changes in the vadose zone followed:

1. The deposition of the speleothems as a process that takes place in airfilled caves. The inclined passage of the higher entrance of Varathron Cave is the only place at the Speleopark caves, where phreatic speleothem coating on the passage walls has been observed (pl. 2.9 and 2.13).
2. The filling of the caves with fluvial sediments. These sediments are well studied in Bear Cave. The dominant presence of Ca-Mg rich metamorphic minerals (clinozoisite, tremolite, talc, chlorite/vermiculite) in the fine-grained sediments of the cave floor is indicative of the composition of the weathering products of the parent rocks of the broader drainage basin, which have been weathered. The absence of smectite and kaolinite indicates that the sediments have not been transported a long distance (Tsirambides, 1998). The allochthonous origin of the cave sediments is recognised in general by the presence of non-carbonate pebbles.
3. Keyhole passages occur only in Keramikon Cave that represent the shift from the phreatic to the vadose conditions. This type of passages results in the combination of a symmetrical phreatic tube and a vadose canyon (pl. 2.12).
4. Post-phreatic breakdown modified walls and ceilings that lose their smooth surfaces, replacing it with a more angular morphology, and obstructing the floor by large blocks, diminishing the cross section of the cave.

DISCUSSION - CONCLUSION

At least two phreatic phases must have occurred because of the observed morphology and the presence or absence of the corresponding speleogens (tab. 1). The presence of solution ceilings, cupolas, bedrock ridges, pendants, abruptly ending passages and the overall horizontal development of the caves suggest the dominant phase of speleogenesis was due to slowly convecting water bodies in the phreatic zone. This morphology is characteristic for Bear Cave, Antarton Cave, Gremos Cave and Varathron Cave. Thermally ascending water most probably was responsible for the formation of the caves at this location. Additionally, all caves occur in a relatively small area, where even today thermal springs occur. As an exception some of them contain abundant scallops or some other phreatic features that are developed by forced flow along a pressure head. Only these caves or passages might correlate with a base level of the incising valley.

For the reason these two conditions above never happen simultaneously, a degeneration of the caves is possible. The development by convection is a deep-seated method of speleogenesis that may have taken place before the neotectonic activity in the area; therefore it probably took place before the formation of the erosional surfaces. While downcutting, took place near-surface groundwater or surface water could have entered the caves, thereby by passing the surface stream under pressure and re-sculpturing some of the walls under turbulent flow.

The predominant vadose modifications are the filling of the caves by sediments and the breakdown. Furthermore, the solutional or erosional vadose features present a minor development.

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PALEONTOLOGICAL AND STRATIGRAPHICAL RESEARCH IN LOUTRA ARIDEAS BEAR CAVE (ALMOPIA SPELEOPARK, PELLA, MACEDONIA, GREECE)

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ABSTRACT: Excavation in Loutra Arideas Bear Cave has yielded thousand of fossilized specimens, thus it can be considered one of the richest in Late Pleistocene paleontological material of Greece. The abundance of the cave bear remains is remarkable. The large mammalian associated fauna comprises of *Ursus ingressus, Crocuta crocuta spelaea, Panthera leo spelaea, Panthera pardus, Vulpes vulpes, Canis lupus, Meles meles,* mustelids, *Bos primigenius, Capra ibex, Cervus elaphus* and *Dama dama,* as well as of 25 species of micromammals, excluding bats. This excavation in the site during 1992-2006 involved in total: 90 participants (researchers, students and co-operators) in 12 systematic excavation seasons, 34 excavated squares with a total of 206 levels, resulting in 15 thousand specimens of large mammals and thousands of specimens of micromammals from the sieving procedure. The research on the cave bear continues with new techniques afforded by the use of the Scanning Electron Microscope (SEM) in milk carnassials, as well as in milk canines. The bear teeth and the metapodials are also discussed as well as comparisons between *Ursus ingressus* from Loutra and from Gamssulzen Cave in Upper Austria, the cave that is usually used as the standard for comparisons within the cave bear group.

Key words: Late Pleistocene Cave Fauna, Stratigraphy, Loutra Arideas, Macedonia, Greece.

INTRODUCTION

Location of the cave site

The cave-site of Loutrá (**LAC**: Loutrá Aridéas Caves) is located in northern Greece (Macedonia), NW of and about 120 km from Thessaloniki, 10 km from Aridéa and very near (2 km) Loutraki village, in the Almopia Speleopark (fig. 1). The co-ordinates of the site are: N 40° 58,267′, E 021° 54,850′.

The "Almopia Speleopark", the first speleological park in Greece, was named so by the speleologist J. Ioannou, in 1990. Administratively, it belongs to the Municipality of Aridéa, Prefecture of Pella, which has been named after the ancient Macedonian capital Pella, birthplace of Alexander the Great.

A system of caves has developed mainly on the northern slope of the V-shaped Nicolaou Rema gorge that is situated on the slopes of the Voras Mt. (2524 m), which is one of the highest mountains of Greece (the third one, after Olympus Mt., 2917 m and Smolikas Mt., 2637 m), very close to the border with former Yugoslavia. The Bear Cave or cave A is part of the "Almopia Speleopark" in the region of the Loutrá curative springs and spas. The Nicolaou Rema gorge consists of Mastrichtian limestone with intense karstic phenomena and the erosion resulted in a depth of about 150 m, to the bottom of which the Thermopotamos River flows. The temperature of the thermal water is about 37°C. Extended travertine occurrences characterize most of the Almopia broader area.

Both in the Speleopark caves or the broader area, calcareous sinter (calcium carbonate rock or deposits formed by precipitation from natural water, often from a hot or cold spring) is widespread. Their importance comes as a result of their quantity and quality as their

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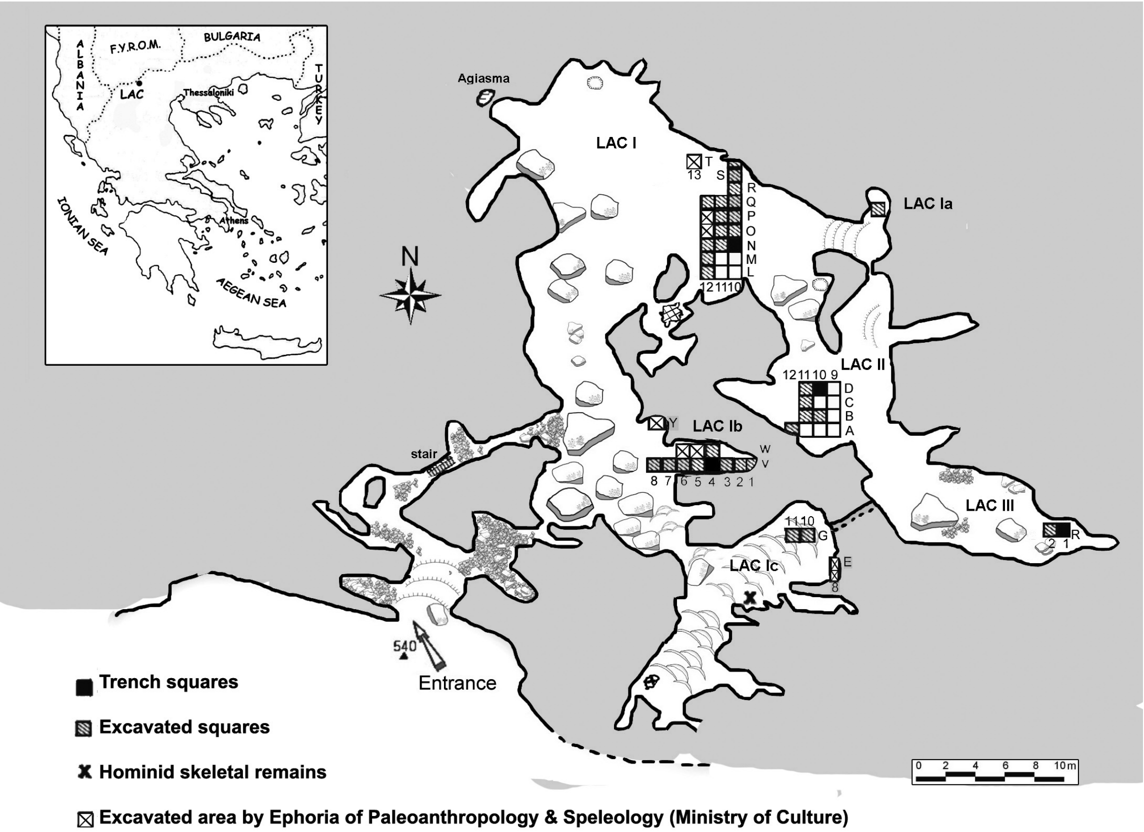


Figure 1. Ground plan of the Bear Cave with the excavating block of squares of the various chambers (1992-2006) [based on the topographic plan (Kambouroglou & Chatzitheodorou, 1999; Kambouroglou *et al.*, 2006, modified by G. Lazaridis and K. Chatzopoulou)].

clarity, the absence of xenoliths and fine crystallization are the major characteristics of them. The Almopia's travertine possesses the first position among the travertine deposits of Greece.

Historical overview

Paleontological research in the Speleopark started in 1990, when the late speleologist K. Ataktidis gave information to one of us (E.T.) about fossil bones of bear, which were brought to light by treasure seekers in the cave A or Bear Cave. It must be noted that in Z Cave of the Speleopark a fossilized maxilla bearing the broken left canine of the brown bear *Ursus* cf. *arctos* was found by the late K. Ataktidis. The first excavation face in the Bear Cave started in 1992 by the Geology School of Aristotle University, Thessaloniki (AUTH), under the supervision of the Ephorate of Paleoanthropology and Speleology (EPS, Ministry of Culture), in co-operation with Emer. Prof. G. Chourmouziadis of Archaeology, with the contribution of the late Prof. Eitan Tchernov (Jerusalem University). The excavations were continued in 1993-1994 in cooperation with EPS (Dr. E. Kambouroglou) and since 1996, 1999 till today the excavations have been carried out by Aristotle University, EPS, in co-operation with Prof. K. Kotsakis of Archaeology and Vienna University (Profs G. Rabeder, the late S. Verginis and their team) (Tsoukala, 1994; Tsoukala *et al.* 1998; 2001; Tsoukala & Rabeder, 2005). The research is still in progress.

Description of the Bear Cave - Methodology

To reach the Bear Cave, where the excavations have been carried out for twelve systematic excavation seasons, including micromammalian research, a narrow path with abrupt steps leads to the entrance of the cave. At the entrance of the cave there is a polished surface on a rock which may be due to chemical reasons or to the passing of many cave bears, which inhabited the cave. This is known reference to many bear caves in Europe, where there are polished surfaces in the narrow paths and passages of the caves too (Kurtén, 1976). Next

Figure 2. Right: The level of depth -(85-100) cm from the zero point of the square O10, excavated in 2000, was reconstructed exactly in the exhibition of the Aridéas Museum. The fossiliferous layer is rather homogenous and consists of brownish silty sediments of various thickness depending on the chamber (the thinner -about 40 cm- is in the main chamber and the thicker is about 140 cm in LAC Ic), deposited mainly under calm conditions of the paleoenvironment.
Left: The only pyrite artifact, found in 1993, in association with ursid remains of the third layer of B10 square, added another aspect to the excavations.

to the entrance, following a wooden staircase there is the first largest chamber - LAC I - of the cave, about 10 m in height, where the main excavation has been done (thirteen squares, the N10 being the trench square (fig. 1). The floor of this chamber is covered by bat guano resulting from the great number of bats which inhabit the cave. Many pottery and glass remains, from the Neolithic/Byzantine period up to the present are due to religious customs that concern a natural pool of water, called "Agiasma", in a small karstik basin, north of the chamber. The walls of the cave are grey-blackish, with "cave-corals", and less abundant, stalactite and stalagmite, fully developed speleothemes, as well as small gours (water pools).

Five smaller chambers present also special paleontological interest. The fossils are spread all over the floor of the cave. East of the main chamber there is the smallest chamber - LAC Ia, which is very difficult to reach, as it is more than 6 m above than the floor of the LAC I, on the top of a slippery rock. Ropes or stairs are necessary to visit this chamber, in which, a quick excavation in 1996, resulted in abundant material of macro- and micromammals of different taphonomy, probably of Holocene age.

In the small chamber LAC Ib, the V and W nine squares gave the most interesting material, from paleontological and taphonomical point of view. Large pebbles and stones, large ursid specimens, such as skulls, a complete pelvis, complete long bones and especially the majority of the hyaenid remains characterize this chamber. Unfortunately, two guide squares, which were left unexcavated for future reference and evidence for stratigraphy, were dug out by EPS of the Ministry of Culture.

In the gour area (chamber LAC Ic), calcite-covered recent cranial fragments and a mandible of a child were found. The sediments in this chamber include many pebbles and gravels, much more than in the other chambers. Only two squares were excavated in this chamber: the G10 that is a trench square and the G11. In the latter, the most complete, well preserved cranium of a bear was found in 2004.

The entrance of the second chamber LAC II is short, and about 70 cm in height. This chamber is much smaller, with no pottery remains on the floor.

It must be noted that in all chambers there are many disturbances caused by the treasure-seekers and many fossils had been destroyed or illegally collected.

The first excavations in this chamber started in 1992, due to fossils that were brought to light from the disturbances caused by the treasure seekers. The orientated block of squares and the datum (O) point were first fixed in this chamber, followed by the other chambers. Six squares have been excavated, the D10 being the trench square. In B10 square, very small juvenile metapodials, with no fusion of their epiphyses, were found in anatomical position. Finally, it must be noted that a stone artefact (fig. 2) was found in the same square, in association with the ursid remains. These findings added great taphonomical and archaeological interest to the excavations.

To the end of the easternmost branch of the cave, the third chamber LAC III has been almost destroyed by diggings of the treasure seekers. Only two squares (the R1 and R2, the former one being the trench square) have been excavated, characterized by thicker fossiliferous sediments with special micromammalian interest, but fewer large mammalian remains.

The excavation in the Bear Cave followed standard paleontological rules. After the definition of datum point, the three coordinates were measured of the bones. Photographs were taken for each layer (fig. 2), which was figured in mm paper and in the diary as well.

The sediments of each layer were collected, transported and washed separately through a double system of sieves, one for micromammals and smaller specimens

(0.8 mm) and the other (3 mm) for larger, mainly ursid remains including milk teeth. Concerning the large findings of the layers, they were carefully cleaned and consolidated. The classification of the bones and teeth in the archives of the excavation was recorded. All the paleontological material is stored in the Physiographical Museum of Loutra and the Natural History Museum of Aridea.

PALEONTOLOGY

The paleontological excavation and research during 1992-2006 in the Bear Cave of Almopia Speleopark has yielded more than 15 thousand fossil remains either from large or from small mammals. The major part of the large mammalian material belongs to the cave bear, while very little, but representative material belongs to eleven fossil species of carnivores and herbivores: the spotted cave hyaena, the cave lion, the leopard, the wolf, the fox, the badger, small mustelids, the red and the fallow deer, the auroch and ibex. The participation of the non ursid specimens per chamber are shown in fig. 9 and tab. 3. There are also thousands of deciduous teeth representing all the milk tooth-row, as well as of 25 species of micromammals-excluding bats.

Large mammals

Taxonomy

Order: CARNIVORA BOWDISH, 1821
Sub-order: Canoidea SIMPSON, 1931/Arctoidea FLOWER, 1969
Family: Ursidae GRAY, 1825
Genus: *Ursus* LINNAEUS, 1758
Ursus ingressus RABEDER, HOFREITER, NAGEL & WITHALM, 2004

Material-Description: Thousands of elements from the entire skeleton (bones and teeth): 3 skulls, 44 maxillary fragments, 93 mandibles and mandible fragments and many isolated teeth. Of the vertebras: 14 atlas, 9 epistropheus, 15 cervical, 34 thoracic, 25 lumbar, and 6 sacrals, many ribs, 9 sternum, 22 scapulae, 30 pelvis, 74 humeri, 98 femurs, 54 radii, 62 ulnae, 59 tibiae, 24 fibulae, 3 baculum, 208 ossa sesamoidea, 7 patellae, of the carpals: 25 pisiform, 21 scapholunatum, 15 pyramidal, 10 trapezium, 6 trapezoid, 14 magnum, 20 unciform. Of the tarsals: 25 astragali, 29 calcanei, 23 cuboid, 20 naviculars, 15 cuneiform 1, 8 cuneiform 2, 26 cuneiform 3, metapodials, 81 metapodial fragments, 332 first phalanges, 219 second phalanges, 175 third phalanges.

The bear remains are spread in all chambers, all over the cave floor. They represent few skulls, many mandibles, abundant isolated teeth and all elements of postcranial bones from animals of all ages. They mainly belong to very young animals or to juveniles as is commonly the case in bear caves.

The complete skulls are few (pl. 1.1), but there are enough complete or almost complete mandibles (pl. 1.2). The former are well preserved skulls of adults, found either in the main chamber LAC I and the most important skull, that shows clearly the characters of *U. ingressus* was found in G11 square of LAC Ic chamber (pl. 1.1), while a skull of a juvenile has been found at the end of chamber LAC Ib among other specimens of juveniles and subadults too. The abundance of the isolated teeth is remarkable and many of them have been found in all wear stages (unworn to completely worn- down to the middle of the root). Therefore the age structure of the cave bear population shows a variation with the extremes (very young and very old) predominating (pl. 1.3a-j).

The presence of both sexes has been established due to the sexual dimorphism either in the teeth (mainly canines) or in the postcranial skeleton, with a strong predominance of females over males (pl. 6.2).

The sex index (number of females/number of all canines x 100) is 77.14. More than three-quarters of canines are females (fig. 3).

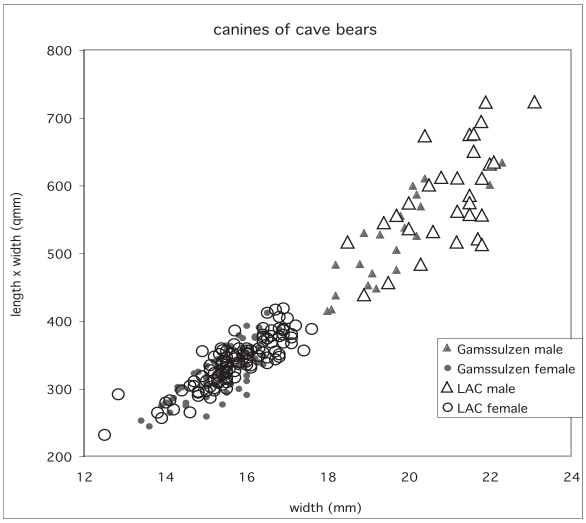


Figure 3. Scatter diagram of canine dimensions of LAC and Gamssulzen cave.

The dimensions of the teeth are relatively large. The means of length and width are similar to the values of Gamssulzen cave (Rabeder, 1995). A few means are a little smaller (I_1, I_3, premolars, M^1 and M_1) the other ones are a little bigger than the means of Gamssulzen bear.

The frequencies of morphotypes of the 4th premolars are:

Table 1.
Tooth measurements of *Ursus ingressus* from Loutra Arideas Bear Cave.

	mean	GS-standard	deviation	max	min	number
$I^{1,2}$ length	10.18	102.00	1.306	13.5	7.1	202
$I^{1,2}$ width	11.57	101.64	0.998	14.5	7.9	202
I^3 length	19.67	105.07	2.346	26.0	15.7	52
I^3 width	15.15	102.62	1.481	18.2	12.9	63
I^3 total height	50.90	103.47	3.916	57.9	41.3	23
I^3 calyx index	25.93	25.93	-	-	-	108
I_1 length	6.51	99.16	0.548	7.5	4.4	58
I_1 width	8.82	100.45	0.817	10.5	6.8	64
I_2 length	9.88	101.78	0.620	11.7	8.4	113
I_2 width	11.05	101.88	0.920	13.8	8.8	125
I_2 total height	38.45	104.88	2.262	44.0	35.7	28
I_3 length	12.66	95.88	0.987	15.0	10.5	107
I_3 width	11.82	94.97	1.009	14.1	9.0	124
I_3 total length	44.44	104.71	2.951	51.0	39.8	25
female canine length	21.71	106.42	1.592	28.5	18.2	111
female canine width	15.78	102.48	0.959	18.0	12.5	111
male canine length	27.67	109.80	2.829	33.0	23.2	30
male canine width	20.95	106.90	1.045	23.1	18.5	30
P^3 length	7.76	-	-	-	-	7
P^3 width	6.50	-	-	-	-	7
P^4 length	20.09	99.81	1.312	23.3	17.4	102
P^4 width	14.20	99.90	1.098	17.9	11.8	104
P^4 index	180.34	70.53	-	-	-	90
P4/4 index	**170.32**	**75.66**				
P_4 length	15.14	99.37	1.072	17.5	12.0	95
P_4 width	10.19	98.73	0.745	12.4	8.8	95
P_4 index	160.86	81.16				93
M_1 length	28.58	99.49	1.443	31.6	24.1	108
M_1 width	19.74	99.95	1.038	1.0	17.5	109
M_2 length	45.52	102.53	2.348	52.1	41.1	73
M_2 width	23.19	102.82	1.219	26.0	20.9	77
M_2 metaloph index	297.22	79.26	-	-	-	72
M_1 length	30.02	99.34	1.435	33.8	27.4	143
M_1 width	14.62	100.81	0.849	16.8	12.8	149
M_1 enthypoconid index	109.24	83.39	-	-	-	93
M_2 length	30.68	100.16	1.628	38.8	27.0	110
M_2 width	18.73	102.65	1.274	21.6	15.9	113
M_2 enthypoconid index	144.67	78.08	-	-	-	169
M_3 length	27.74	100.65	2.077	32.3	18.5	95
M_3 width	19.88	104.01	1.772	29.3	17.3	94

Table 2.
Measurements and indices of metapodial bones from Loutra Arideas Bear Cave.

Element	n	gl	pw	sdw	dw	dew	pd	sdd	dd	da	pa	sda	ip	K
Mc1	12	60.9	24.1	12.1	18.3	18.2	19.0	9.4	17.6	322.6	466.6	116.2	29.55	7.47
Mc2	17	76.6	18.7	17.7	21.4	25.0	28.3	12.4	21.1	466.6	540.6	220.7	32.15	6.97
Mc3	12	78.0	19.9	16.3	21.0	24.5	27.6	12.3	21.6	468.7	540.5	203.6	32.04	6.95
Mc4	9	82.2	21.4	18.0	23.0	27.1	31.5	13.4	23.7	522.1	549.1	215.8	31.53	6.92
Mc5	16	84.0	28.2	18.6	28.0	29.1	34.9	13.8	22.6	532.6	844.9	258.8	33.99	10.58
Mc	**66**	76.3	22.5	16.5	22.3	24.8	28.3	12.3	21.3	462.5	588.3	203.0	31.90	7.80
Mt1	14	52.1	20.8	11.0	16.3	16.4	23.3	9.0	15.6	264.2	492.5	101.2	30.83	9.59
Mt2	13	64.4	14.5	13.6	17.8	19.9	23.5	10.0	15.7	279.3	347.1	136.4	30.87	5.28
Mt3	16	75.3	18.6	14.8	18.4	21.2	29.3	10.4	18.1	353.5	560.6	152.1	28.20	7.40
Mt4	11	86.4	20.9	16.8	23.4	25.2	29.6	13.2	20.7	504.2	606.5	225.4	29.00	7.19
Mt5	15	87.5	27.3	13.7	23.6	23.5	28.8	12.0	17.6	408.3	819.0	175.7	27.04	9.23
Mt	**69**	73.2	20.4	14.0	19.9	21.2	26.9	10.9	17.5	361.9	565.1	158.2	29.20	7.70

gl: greatest length; pw: proximal width; sdw: smallest diaphyseal width; dw: distal width; dew: distal epicondyleal width; pd: proximal depth; sdd: smallest diaphyseal depth and dd: distal depth. Indices: da: distal area; pa: proximal area; sda: smallest diaphyseal area; ip: index of plumpness and K.

P^4: 4 A/D, 2 B, 13 B/D, 25 D, 8 D/F, 3 E, 1 E/F, 2 F. P4 sup., index: 180.34

P_4: 1 A, 2 B1/C1, 1 B1/C2, 1 B1/D1, 2 B1, 26 C1, 8 C1/C2, 15 C2, 2 D1/E1, 11 D1, 7 D1/d2, 8 D2, 1 D2/D3, 1 D3, 13 E1, p4 inf. Index: 160.86., P4/4 index 170.32 (standardised 75.66).

In both premolar groups the high developed morphotypes dominate. The simple forms A, A (B respectively A1, A1/B1, B1 are rare or missing.

All morphodynamic indices (M^2 metaloph, M_1 enthypoconid, M_2 enthypoconid, premolar indices) have evolutionary levels between 70 and 84% of Gamssulzen standard.

The bones are mostly well preserved, representing all biological ages (pl. 1.4). A few long bones are complete and very well preserved, the metapodials included.

Metapodial bones: There is only a small number of metapodial bones in Loutra Arideas Bear Cave (LAC), actual measurements of which were taken only from 66 metacarpals and 69 metatarsals and a few are still missing. So, the actual results are only preliminary ones. Eight measurements were taken according to Withalm (2001:175 ff.) and five indices were calculated (tab. 2).

When we take a closer look at the dimensions of metacarpus and metatarsus, we can see that the greatest length comes close to what is known from Gamssulzen Cave in Upper Austria, the cave that is usually used as a standard for comparisons within the cave bear group. The difference, on average, does not exceed 4 mm. The inner metacarpals and metatarsals (1-3) are smaller, whereas the outer ones are bigger than those from Gamssulzen bears.

The metapodial bones from LAC are in general less plump than their Austrian counterparts from Gamssulzen Cave. Whereas the metacarpals show a similar pattern to the Gamssulzen bears, the pattern diverges in the metatarsus as the 4th metatarsal is bigger than expected and thus produces a extra peak. It will be interesting to find out whether this is an artefact or a real difference that can probably be attributed to the different environmental conditions of the sites.

There are even bigger differences in the proportions of the smallest diaphyseal area. The sda in the metacarpus is in general smaller, with only one exception that shows a bigger value than the bears from Gamssulzen Cave is the 2nd metacarpal (tab. 2). This produces a different pattern in the diagram. The pattern of the metatarsus is more similar to those from Gamssulzen Cave but the 4th metatarsal shows a significantly higher value, whereas the 3rd metatarsals are significantly smaller than their counterparts.

Also the K-index is in general smaller than in the Gamssulzen bears and the patterns are more or less identical with a slight different trend in the three inner metacarpal bones (fig. 4-7).

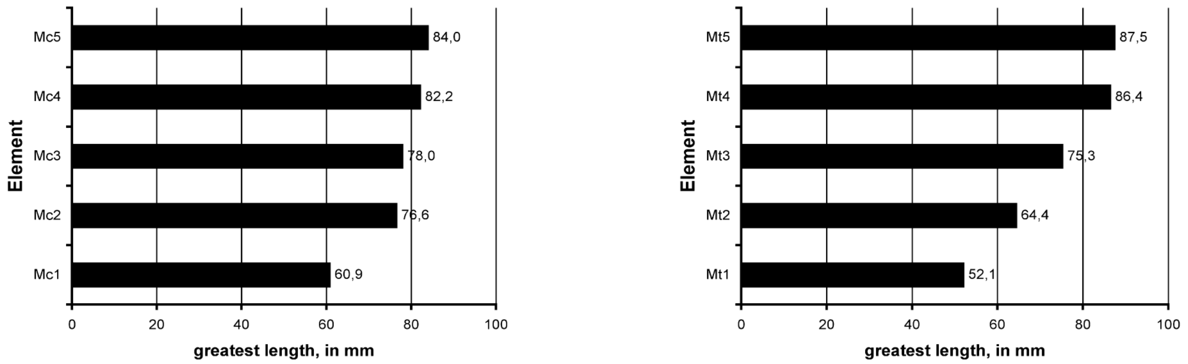


Figure 4. Proportions of metacarpus and metatarsus in respect of the greatest length (gl).

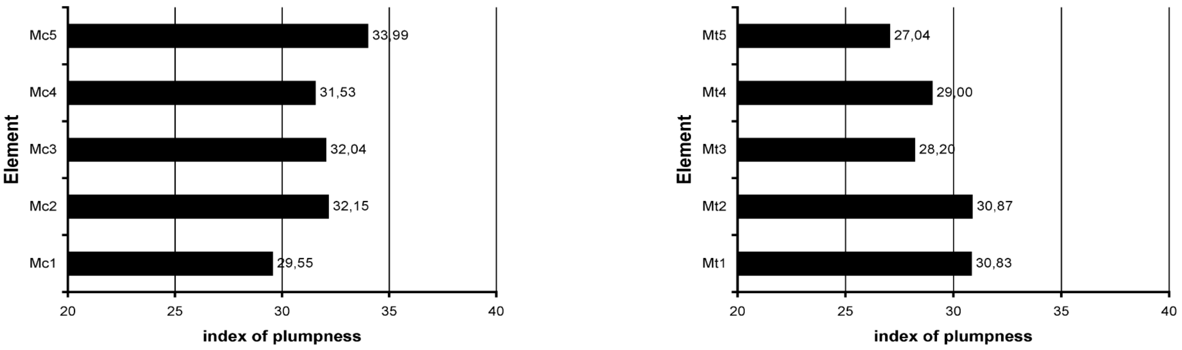


Figure 5. Proportions of metacarpus and metatarsus in respect of the index of plumpness (ip).

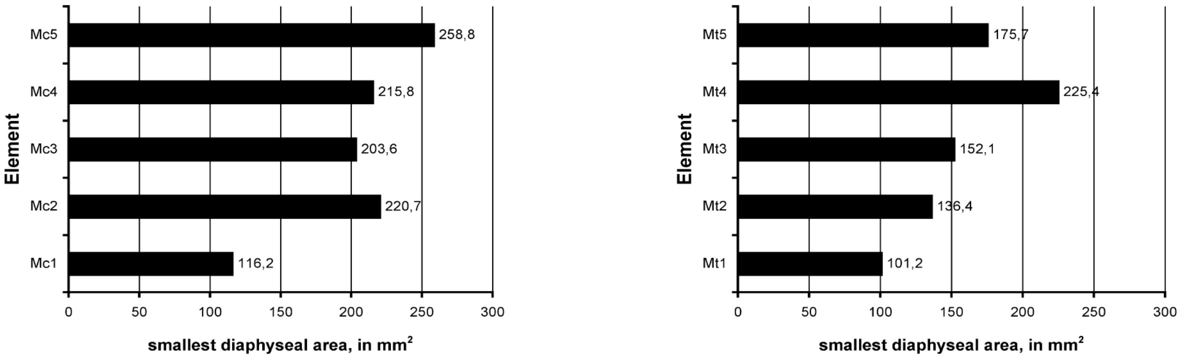


Figure 6. Proportions of metacarpus and metatarsus in respect of the smallest diaphyseal area (sda).

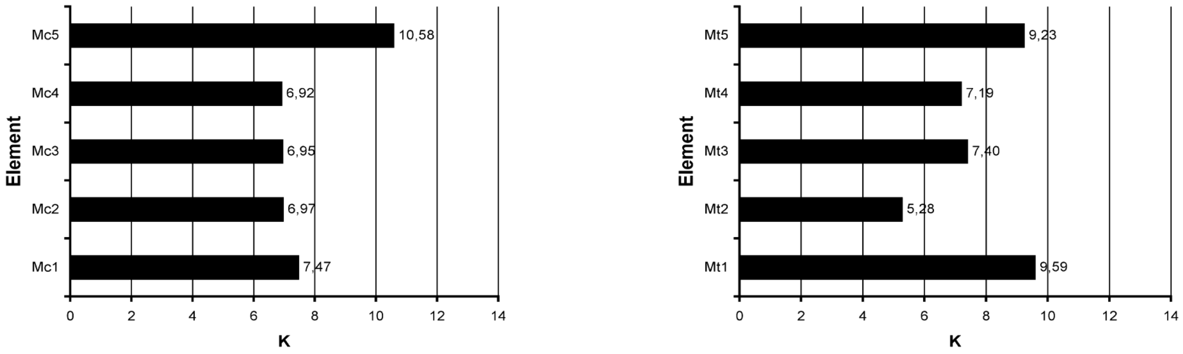


Figure 7. Proportions of metacarpus and metatarsus in respect of the index of K-index (K).

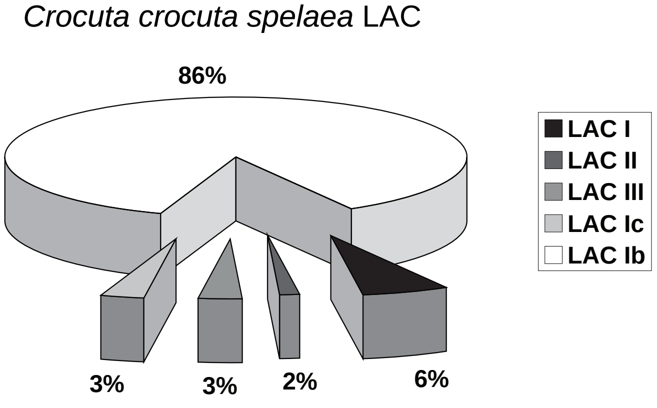


Figure 8. Loutra Arideas Bear Cave: The percentage of the cave hyena specimens in each chamber of the cave (see plan of the cave in fig. 1).

Overall there is a similar pattern in the metacarpus and metatarsus of the bears from LAC with those from Gamssulzen cave. There are also some differences that are probably local variations. The K-index of the 2nd metatarsal bone is 5.28 and is consistent with the picture that we already have.

We do have to bear in mind that there is only a small number of metapodial bones and that this deficit affects the reliability of the analysis. Further research on more complete material will certainly shed more light on metacarpus and metatarsus of this population.

Family: Canidae GRAY, 1821

Genus: *Canis* (LINNAEUS, 1758)

Canis lupus (LINNAEUS, 1758)

Material, Description: In the Bear Cave the Pleistocene wolf is very poorly represented by a right upper slightly worn carnassial (P^4), the protocone of which is missing (pl. 2.1, tab. 4). It was found in the small LAC Ib chamber.

Genus: *Vulpes* FRISCH, 1775

Vulpes vulpes (LINNAEUS, 1758)

Material, Description: The Pleistocene fox is poorly represented by few teeth: an upper left slightly worn canine (chamber LAC Ic) and two molars (M^2 chamber LAC I and M_2 chamber LAC II). Also, few post cranial bones are preserved: proximal fragments of humeri, metapodials and first phalanges (chambers LAC I, Ic and III). (pl. 2.2, tab. 4).

Family: Mustelidae FISCHER, 1817

Genus: *Meles* LINNAEUS, 1758

Meles meles LINNAEUS, 1758

Material, Description: Among the mustelid remains found in the cave (chambers LAC I, II, III and Ib), the badger is represented only by a left maxilla fragment with P^2-P^4 present, slightly worn and few post cranial bone fragments (chamber LAC III). The P^2 and P^3 are simple conical teeth, while the triangular carnassial has a prominent little worn blade with a large paracone, an ill-defined metacone and a well defined cingulum around the base of the crown. The foramen infraorbitale is well developed (Dmax=9.00, Dmin=7.57mm) (pl. 2.3, tab. 4).

Suborder Feloidea SIMPSON, 1931

Family: Hyaenidae GRAY, 1869

Genus: *Crocuta* KAUP, 1828

Crocuta crocuta spelaea (GOLDFUSS, 1832)

Material, Description: The cave spotted hyaena is the most abudant non-ursid material represented by 66 specimens. These comprise of canines, incisors, cheek teeth and many post cranial bones, such as vertebras, scapula, humerus, femur, radius, ulna, tibia carpals, tarsals, metapodials and phalanges, some of them with unfussed epiphyses.

The specimens are spread all over the five chambers of the cave; the percentage is shown in fig. 8. The animal probably lived in the cave for a short time and there are remains of juveniles, coprolites and typical food remains of this scavenger (pl. 2.4, tab. 4). On some bear bones there are bite traces marks of this scavenger (pl. 6.2). No significant diversion in size has been noted in comparison with the Petralona Middle Pleistocene and the Agios Georgios Kilkis Late Pleistocene crocuta. The cave hyena had a very large distribution area in the whole of Eurasia. Recent analyses allowed some discussion about different migration waves from Africa. The body size of these animals follow the Bergmann rule but there is also a decline in size till the end of the Pleistocene.

Family: Felidae GRAY, 1821

Genus: *Panthera* OKEN, 1816

Panthera pardus (LINNAEUS, 1758)

Material, Description: The cave leopard is well represented by ten specimens (chambers LAC I, II and Ic);

Table 3.
Loutra Arideas Bear Cave: the participation of the non ursid specimens per chamber

Taxa	Number of specimens	LAC I	LAC Ib	LAC Ic	LAC II	LAC III
Ursus	thousands	+	+	+	+	+
Crocuta	66	4	57	2	1	2
Panthera	10	3		6	1	
Panthera leo	1	1				
Vulpes	6	2		2	1	1
Canis	1		1			
Meles	1					1
Mustelidae	7	2	1		1	3
Bos	1		1			
Capra	16	4	6	3	3	
Cervus	4	1		3		
Dama	1		1			
TOTAL Non ursid	114	17	67	16	7	7

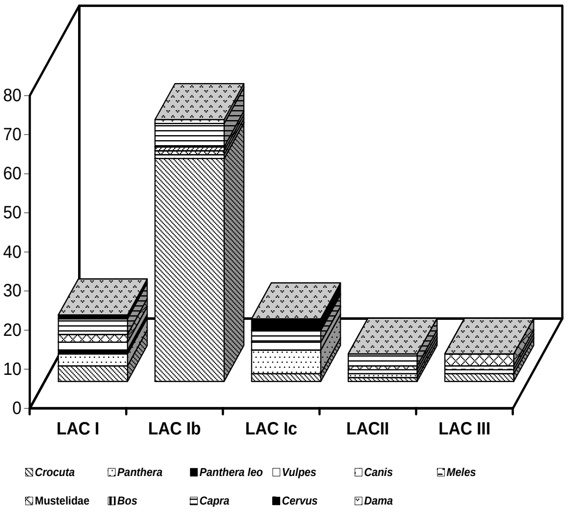


Figure 9. Loutra Arideas Bear Cave: Histogram with the participation of the non ursid specimens per chamber.

a right maxilla with P^3 that bears a large anterior and posterior accessory cusps, as well as a small posterior cingulum. The foramen infraorbitale is well developed (Dmax=11.11, Dmin= 8.45 mm). The canine is little worn with well distinguished labial and lingual longitudinal flutes. The root is well preserved. Of the post cranial bones the complete left radius is well preserved while the proximal fragment is a lesser degree. Of the left ulnas, two proximal parts with the olecranon are preserved (DTolecr.=15.18, DAPolecr.=33.84, DTprox.art.=21.90 and 26.49 mm). Of the carpals, a trapezium with dimensions 16.26 X 9.32 X 9.67 mm and of the tarsals a cuneiform 3 with dimensions 13.53 X 14.89 X 27.06 mm and the two phalanges, Ph I and Ph II, are well preserved (pl. 2.5, tab. 4). Knowledge of the leopard exists since the Middle Pleistocene when it migrated from Africa to Europe and co-existed with the European jaguar (*P. onca gombaszögensis*). In contrast to the latter, it survived even the last glacial maximum but retreated during historical time from Europe.

Panthera leo spelaea (OWEN, 1848)

Material, Description: The cave lion is poorly represented only by an upper canine found in the central chamber (LAC I). It is well preserved, complete and there is an intense longitudinal sulcus posterior of the root. The base of the crown is of circular shape and the typical flutes of the crown are well distinguished. It is rather slender, probably of a female individual (pl. 2.6, tab. 2). The cave lion is known from several European sites. It took over the ecological niche as a top predator from *P. onca gombaszögensis*. Findings from archaeological sites indicate a historical distribution of the lion but it is also possible, that this animal was traded from Asia or Africa.

Order: ARTIODACTYLA
Family: Bovidae GRAY, 1821
Subfamily: Bovinae GILL, 1872
Genus: *Bos* LINNAEUS, 1758
Bos primigenius BOJANUS, 1827

Material, Description: The aurochs is poorly represented by a first phalange: Ph I (chamber LAC Ib). A hole through the distal part of the bone shows a mark of carnivore canine (pl. 2.7, tab. 5).

Subfamily: Caprinae GILL, 1872
Genus: *Capra* LINNAEUS, 1758
Capra ibex LINNAEUS, 1758

Material, Description: The ibex is represented only (chambers LAC I, Ib and Ic) by two lower incisors, and an upper premolar), one carpal (os hamatum), a metacarpal Mc 3+4 of a male juvenile with infused epiphyses (both of the same individual)**,** a metatarsal Mt 3+4 of a female juvenile, also with infused epiphyses, 2Ph I, Ph II (pl. 2.8, tab. 5).

Family: Cervidae GRAY, 1821
Genus: *Cervus* LINNAEUS, 1758
Cervus elaphus LINNAEUS, 1758

Material, Description: The Almopia Pleistocene red deer is represented only by three phalanges: 2 Ph2 and Ph3 of the same individual (chambers LAC I and Ic). They are robust and well preserved (pl. 2.9, tab. 5)

Genus: *Dama* FRISCH, 1775
Dama dama (LINNAEUS, 1758)

Material, Description: The Almopia Pleistocene dama is represented only by a scapula fragment (pl. 2.10, tab. 5).

The milk teeth from the Loutra Arideas Bear Cave

During Pleistocene many of the caves served as lairs for cave bears for many years. An analysis of thousands of milk teeth from the Loutra Arideas Bear Cave gives us a picture of the dynamics of the bear population, of its balance between births and deaths as well as of their taphonomy. The sieving process and the systematic collection of the milk teeth from the washed sediments from both sieves with a mesh of 0.8 mm and of 3 mm started in 1993, and it has been continued up to now. All deciduous incisors, canines and premolars of *Ursus ingressus* RABEDER *et al.*, 2004, have been studied, drawn and measured; their occlusals have been described in detail, as well as their root structure (Pappa *et al.*, 2005, Pappa *et al.* in press). New techniques in the research of the milk teeth afforded by the use of the Scanning Electron Microscope (SEM).

Material: Among the 3260 specimens of juvenile and young bears, the complete mandibles are rare: a right mandible fragment with slightly worn dC_i, the lower milk carnassial D_4 and the germ first molar M_1 unerupted (pl. 3.1) and the mandible with I_3, C, M_1, M_2 and M_3 unerupted belongs to a bear of sixteen months old (after Dittrich in Andrews & Turner, 1992) (pl. 3.2). Also there are mandible fragments with unerupted C_i, with well preserved condylus or processus angularis. In certain mandibles of young bears, the distal corpus is intensely curved beneath M_2. The abudance of the isolated teeth is remarkable: 12 dI^1, 105 dI^2, 695 dI^3, 6 D^2, 26 D^3, 240 D^4, 52 dI_1, 29 dI_2, 180 dI_3, 7 D_2, 62 D_3, 285 D_4 and 1600 dC.

Abbr.: dI: deciduous incisor, dC: deciduous canine, D: deciduous premolar.

Description and Discussion

The dI^1 is a small and slender tooth. There is a well developed palatinal cingulum and the root is elongated, conical and slightly curved (pl. 3.3). The dI_1 is a very small tooth, with a small crown and a cylindrical root, the end of which is slightly convex (pl. 3.4). The dI^2 is much stronger than the first milk incisor, and also bears a well developed palatinal cingulum. The crown is curved and the conical root is anteriorly flattened. The dI_2 is more robust than the dI_1, with triangular shaped crown and elongated root. The second upper and lower milk incisors can be attributed to three categories according to the main attribution of the milk canines after Kurtén (1968; 1976). For the former there are a few germs consisting by an enamel cap and a root that has barely started to form (pl. 3.5a), few complete teeth with unworn occlusal and fully formed roots (pl. 3.5b) and finally a few teeth bearing very large crop of shed, the root of which seems to be dissolved completely (pl. 3.5c). For the latter, the three categories are: few germs consisting by an enamel cap up to almost complete root (pl. 3.6a), few complete teeth (among them unworn teeth) with fully formed roots (pl. 3.6b), and finally few teeth with a very large crop with dissolved root (pl. 3.6c). The dI^3 has a convex crown and intense palatinal cingulum and resembles closely the milk canine. It is the largest and most abundant among the milk teeth, after the milk canines. Four categories are distinguished: few germs consisting by an enamel cap and a root that has barely started to form (pl. 3.7a), few complete teeth (among them unworn teeth) with fully formed roots (pl. 3.7b), few complete teeth with roots showing resumption marks (pl. 3.7c), a preliminary stage of which being shed as the root is gradually dissolved by the osteoclast (Koby, 1952) and finally many teeth with a very large crop with completely dissolved root (pl. 3.7d). The dI_3 is the largest lower milk incisor with crown of triangular shape and well developed root. There are two lingual accessory cuspids, jointed with a small cingulum. Two categories can be distinguished: few germ teeth consisting by an enamel cap and a root that has barely started to form (pl. 3.8a, b) and very few teeth with completely dissolved root (pl. 3.8c).

The milk canines are long and flattened teeth, abundant in the LAC material, far more numerous than the other milk teeth. There are more than 1600 specimens of these pointed teeth. It is difficult to distinguish between maxillas and mandibles, thus both are described as dC *sensu lato*. They are distinguished in various wear stages according to Kurtén (1976), (Andrews & Turner, 1992): In a) unerupted, consisting by an enamel cap and a root that has barely started to form (unborn or newborn cubs), b) erupted complete teeth with unworn occlusal and fully formed roots, c) unworn complete teeth with root showing resumption marks d) slightly worn with

Table 4
Loutra Arideas Bear Cave: measurements of bones and teeth of the non ursid carnivores.

Canis lupus	
LP^4	23.79
BP^{4}mts	11.77

Meles meles	
LP^2	4.43
BP^2	3.12
LP^3	5.69
BP^3	3.80
LP^4	8.28
BP^4	7.68
L P^2 -P^4	18.29

Vulpes vulpes	
LC^s	6.88
BC^s	4.59
HC^s	29.69
LM^2	9.76
BM^2	5.89
LM$_2$	8.35
BM$_2$	6.14

Panthera leo spelaea	
LC^s	20.00
BC^s	17.92
HC^s	113.75
H crown	46.00
L root	27.65
B root	19.85

Crocuta crocuta spelaea

	C^s	C$_i$	I^1		I^2	I^3	dI^3	P$_4$
L	15.90	15.79	7.56	7.40	9.20	11.20	8.00	23.00
B	13.40	12.77	6.15	5.90	6.37	11.68	6.00	14.52
H	62.00	61.00				43.00		
H crown	28.38	28.30				15.65		

	Calcaneus	**Scaphoid**	**Cun3**	**Cuboid**	**Capitatum**	**Pyramidal**	**Lunatum**	**Hamatum**
L	60.52	13.34	15.80	22.57	17.35	13.96	24.00	19.85
DT	27.67	28.63	14.15	20.42	14.25	13.65	40.00	18.90
DAP	29.10	23.54	26.12	19.86	26.93	23.21	25.00	23.65

Panthera pardus

	Radius		**Ph1**	**Ph2**
L	196.00	-	36.29	30.43
DT pr.	24.73	24.23	12.34	12.79
DAP pr.	16.59	18.45	12.00	13.28
DT dia.	18.83		8.55	7.37
DAP dia.	12.47		-	7.79
DT dis.	36.29		10.46	11.12
DAP dis.	20.61		9.00	8.50
DT d.art.	29.78			
DAP d.art.	18.27			

Mx + P^3	
LP^3	17.16
BP^3	8.39
L I^1-P^4 alv.	86.81
L diast.	4.30
L P alv.	50.51

Canine	
LC$_i$	(13.5)
BC$_i$	10.70
HC$_i$	(62.00)
L root	16.52
B root	13.06

Crocuta crocuta spelaea

	Radius	**Tibia**
L	229.00	192.00
DT pr.	30.85	(50.00)
DAP pr.	20.72	56.00
DT dia.	23.57	18.85
DAP dia.	13.71	22.19
DT dis.	42.38	39.00
DAP dis.	26.04	27.00
DT d.art.	35.10	

Crocuta crocuta spelaea

	Mc2	**Mc3**	**Mc4**		**Mc5**	**Mt3**		**Mt4**		**Mt5**
L	79.61	93.99	93.23	92.12	69.73	82.64	79.11	82.43	82.26	68.81
DT pr.	15.55	16.58	12.77	13.00	12.37	14.52	-	10.95	11.87	12.22
DAP pr.	19.00	21.64	19.26	18.23	18.87	21.15	19.86	18.00	20.20	18.60
DT dia.	11.93	12.19	12.00	11.90	8.51	11.29	12.46	10.96	11.55	8.97
DAP dia.	9.68	10.35	9.32	9.41	11.31	10.16	11.80	9.53	10.00	10.68
DT dis.	16.59	16.51	15.43	15.54	12.87	15.00	14.35	13.68	14.10	12.07
DAP dis.	15.86	16.33	15.38	15.58	13.38	14.45	13.45	13.74	13.98	13.14

Ph1									
L	33.40	33.36	33.62	29.49	30.44	32.00	30.00	32.00	30.31
DT pr.	15.36	15.44	16.00	13.95	13.55	14.21	13.19	-	13.47
DAP pr.	14.46	13.87	14.82	13.00	12.26	13.19	12.10	12.25	12.30
DT dia.	11.00	10.69	11.16	10.00	9.73	9.83	8.85	9.83	8.90
DAP dia.	8.87	7.73	8.67	9.00	8.35	7. 66	7.90	8.30	7.90
DT dis.	13.45	13.30	13.55	14.00	11.90	12.73	11.00	12.67	11.54
DAP dis.	9.60	9.40	9.41	9.00	7.96	8.39	8.21	8.27	7.96

Ph3			
L	22.92	20.00	22.34
DT	13.82	10.75	12.90
H	15.57	12.40	14.85

Table 5
Loutra Arideas Bear Cave: measurements of bones and teeth of herbivores

	Bos primigenius	***Capra ibex***									
		Ph1			**Ph2**		**Radius**	**Mc3+4 ♂**	**Mt3+4 ♀**	**Os hamatum**	
L	74.50	45.47	45.33	45.07	32.27	34.11	228.00	-	-	L	13.95
DT pr.	35.72	18.48	17.12	16.62	13.50	14.67	45.27	35.92	24.76	DT	17.43
DAP pr.	41.84	20.34	17.49	17.38	14.00	16.33	22.16	23.94	23.25	DAP	23.19
DT dia.	33.85	15.09	14.57	14.90	9.02	10.51	27.94	(26.36)	(15.00)		
DAP dia.	29.38	15.74	15.60	15.22	-	-	17.71	(17.43)	(12.00)		
DT dis.	33.28	17.56	17.03	16.04	9.89	10.44	41.12				
DAP dis.	25.82	15.69	15.68	14.14	11.85	13.33	24.10				

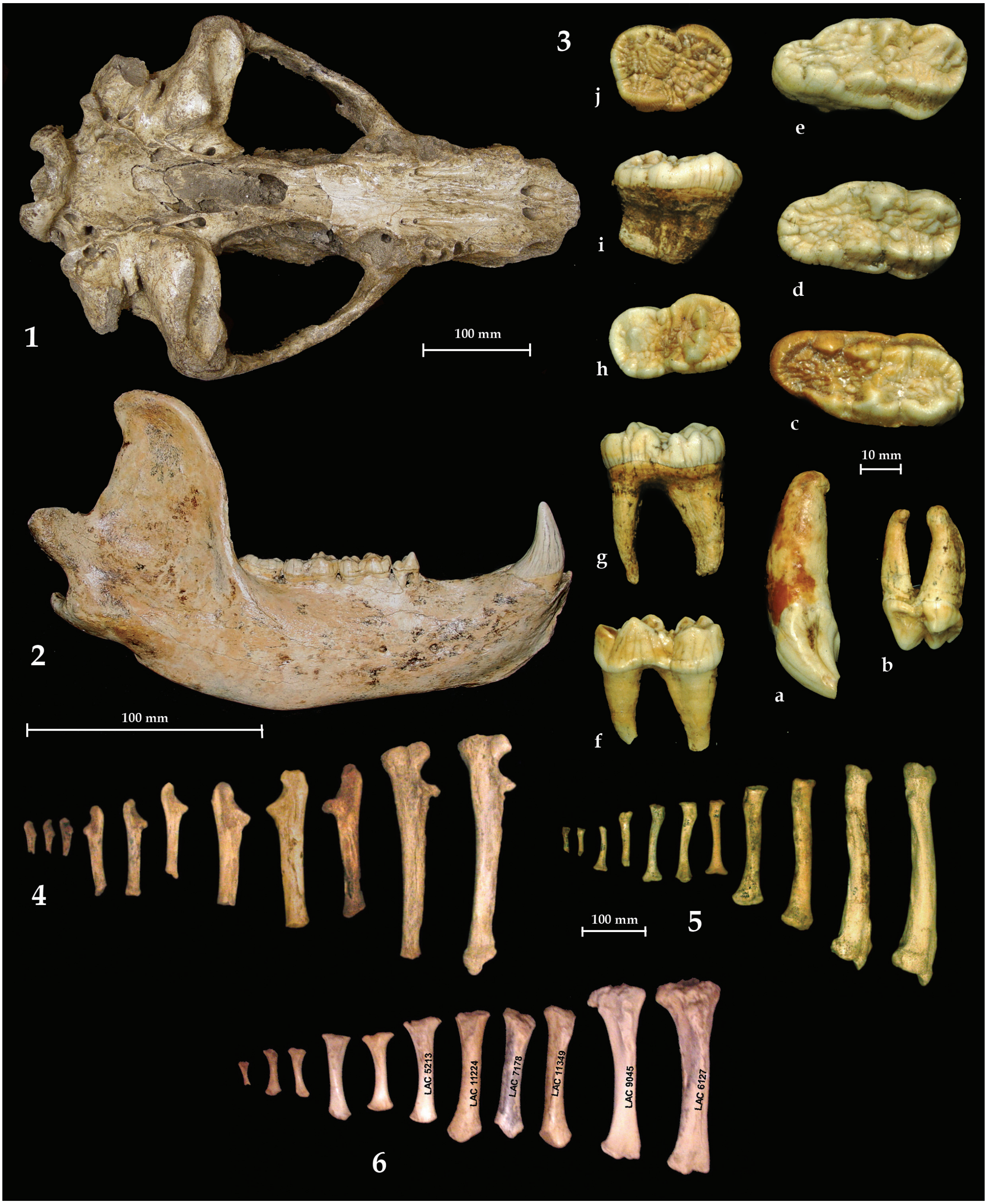
Cervus elaphus				
	Ph2		**Ph3**	
L	43.41	45.20	L	52.19
DT pr.	22.77	25.14	H	31.74
DAP pr.	27.52	30.40	DT	18.67
DT dia.	18.34	19.36	Dart.max	28.26
DAP dia.	24.11	22.67	Dart.min	17.68
DT dis.	19.84	20.83		
DAP dis.	28.91	27.67		

a very large crop of shed milk canines in which the root has dissolved completely, e) heavily worn, that includes the heavy wear stage of deciduous teeth and f) worn with resorbed root. Concerning the LAC milk canines, they can be attributed to: a) 132 unerupted (pl. 3.9a), b) 500 erupted (pl. 3.9b), c) 83 unworn in a preliminary stage to the tooth being shed and as the root is gradually dissolved by the osteoclast (pl. 3.9 c), d) 130 slightly worn (pl. 3.9d), e) 600 heavily worn and f) 155 worn (after Koby, 1952 whose hypothesis on the milk teeth has still to be tested as the research is still in progress).

The second premolars are the smallest of the cheek milk teeth and the less differentiated, the root of the D^2 being small and conical and the D$_2$ with inclined, growth (pl. 3.10 and 11). The D^3 is more differentiated with developed talon and two roots (pl. 3.12). The D$_3$ is of elongated crown, with two roots that are well separated or fused in some specimens Radulescu & Samson (1959) (pl. 3.13). The upper milk carnassial D^4 is the most important tooth because it contributes to the study of the evolutionary stage according to its morphotype (Rabeder, 1983; 1991; 1999). It is molar like and has one palatinal and two labial roots. The occlusal shape is rounded and sometimes there is a palatinal cuspid-like cingulum (pl. 3.14). The lower carnassials D$_4$ are much more various than that of the maxilla one, with crown bearing at least 5 cusps and two roots (pl. 3.15). The milk carnassials D^4 and D$_4$ are the most important deciduous teeth as the study of the morphotype can give evidence for their evolutionary stage (Rabeder, 1983). The D^4 LAC is molar like with one palatinal and two labial roots. The occlusal shape is rounded and sometimes there is a palatinal cuspid-like cingulum. The paracone is well developed and the metacone bears longitudinal palatinal crest. There is small parastyle while there is a trace of cingulum like metastyle. Finally there is a crest-like hypocone. The lower milk carnassials D$_4$ LAC are much more variable than those of the upper ones, with crown bearing at least 5 cuspids. Paraconid, metaconid and protoconid are well developed. There is a small hypoconid and endoconid.

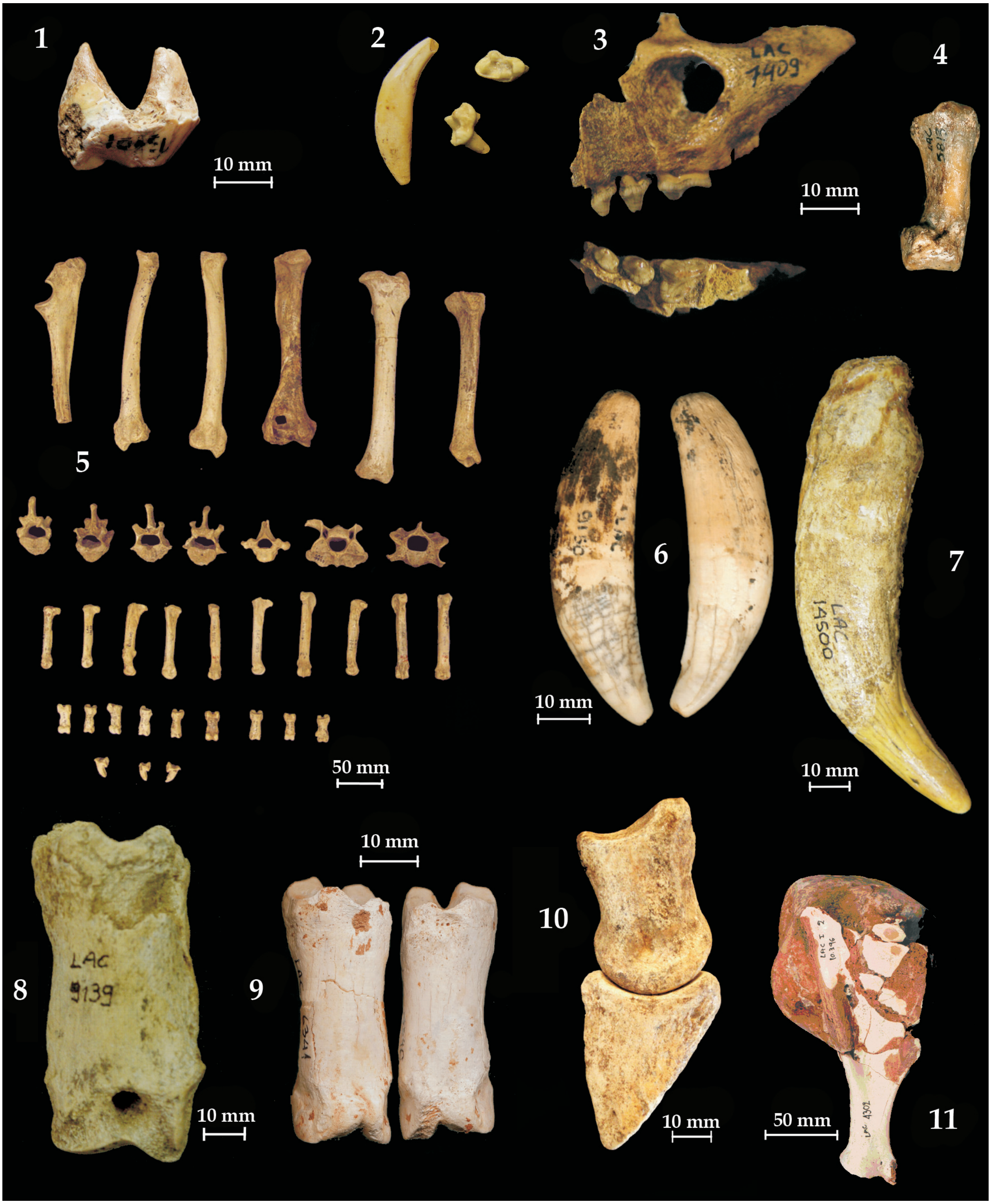
Research on the LAC cave bear continues with the upper and lower milk carnassials, as well as with the milk canine through the implementation of new techniques afforded by the use of the Scanning Electron Microscope (SEM). The aim is to document different modes of chewing and to remark the chemical analysis of various parts of the milk teeth. The digestion of food is the way animals acquire energy, and the organs involved with feeding are fundamental for survival. Existing literature points out that tooth wear is produced by two types of masticating behaviour (by Kay & Hiiemae, in Pinto *et al.,* 2005). Foodstuffs may be pulped through a series of cycles (puncture-crushing) that do not involve tooth to tooth contact, and this may result in an abrasive wear. Subsequent tooth to tooth contact produces attritional wear. The micrograph analysis in D^4 LAC 14600, showed the presence of: relatively intense accessory cusps focusing in metacone (pl. 4.1a), robust denticulate cingulum (pl. 4.1b), microscratches (with ~100μm analysis)(pl. 4.1c) and microprotuberances, the chemical analysis of which, by the

Plate 1



Ursus ingressus LAC: 1. Skull of an adult bear, basal view; 2. Mandible of a male with C_i, P_4-M_3 dex; 3. Isolated teeth: a) I^3 sin, b) P^4 dex, c,d) M^2 dex, e) M^2 sin, f) M_1 sin, g,i) M_2 sin, j,k) M_3 sin. Post cranial bones of various ages from very juvenile to fully adult: 4. ulnae; 5. radii; 8. tibiae.

Plate 2

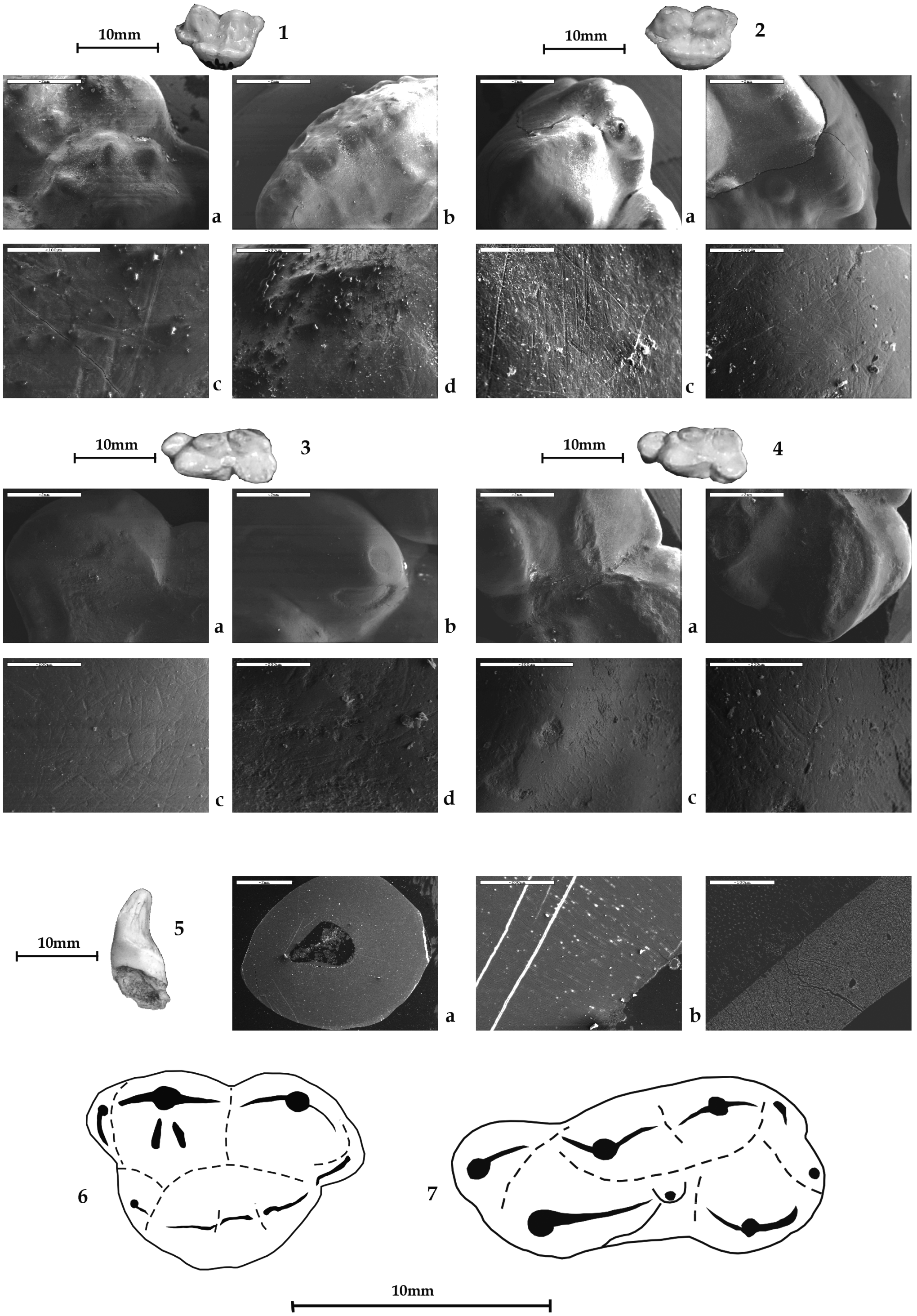


Loutra Arideas Bear Cave, non ursid mammalian remains: 1. *Canis lupus,* P^4 dex; 2. *Vulpes vulpes,* C^s sin, M^2 dex, M$_2$ sin; 3. *Meles meles,* maxilla frag. with P^2-P^4 sin; 4. *Panthera pardus* Ph 2; *Crocuta crocuta spelaea:* 5. postcranial bones (vertebras, metapodials, Ph 1 and Ph 3) and 6. C^s sin; 7. *Panthera leo spelaea* C^s sin; 8. *Bos primigenius,* Ph I; 9. *Capra ibex,* Ph I; 10. *Cervus elaphus,* Ph 2 and Ph 3 and 11. *Dama dama,* scapula fragment.

Plate 3

Ursus ingressus LAC, milk teeth: 1. Right mandible fragment with a slightly worn dCi, D_4 and the germ M_1 unerupted; 2. Mandible with I_3, C, M_1, M_2 and M_3 unerupted; 3. dI^1; 4. dI_1; 5. dI^2 (a-c: various categories); 6. dI_2 (a-c: various categories); 7. dI^3 (a-d: various categories); 8. dI_3 (a-c: various categories); 9. dC (a-d: various categories); 10. D^2; 11. D_2; 12. D^3; 13. D_3; 14. D^4; 15. D_4. For the various categories see in the text.

Plate 4



Ursus ingressus LAC, Scanning Electron Microscope (SEM): 1. Micrograph of D^4 LAC 14600. 1a. Metacone and accessory cuspids, 1b. Cingulum, 1c. Microscratches, 1d. Micro-protuberances; 2. Micrograph of D^4 LAC 14601. 2a. Paracone, 2b. Paracone and cingulum, 2c. Microscratches with ~100μm resolution, 2d. Microscratches with ~200μm resolution; 3. Micrograph of D_4 LAC 14603. 3a. Slightly worn hypoconid and endoconid, 3b. Protoconid, 3c. Microscratches with ~100μm resolution, 3d. Microscratches with ~200μm resolution; 4. Micrograph of D_4 LAC 14604. 4a. Completely worn hypoconid, 4b. All cuspids are worn, 4c. Microwear such as pits, 4d.Microscratches; 5. Micrograph analysis in dC LAC 14602. 5a. Section at the base of the crown, 5b. Close up to the dentine. 5c. Difference between dentine and cementum; 6. Morphology of the occlusal D^4 LAC 12557; 7. Morphology of the occlusal D_4 LAC 12560. The SEM photos were kindly provided by Dr. Labrini Papadopoulou.

Table 6
Chemical analysis of some micro-protuberances on the occlusal of D^4 LAC by the use of Scanning Electron Microscope (SEM)*.

Elmt	Spect Type	Element %	Atomic %	Nos. of ions
Mg K	ED	0.55	0.53 MgO	0.22
P K	ED	20.29	15.60 P_2O_5	6.55
Cl K	ED	0.68	0.45	0.19
Ca K	ED	36.64	21.77 CaO	9.14
			Cation sum	15.98

Table 7
Chemical analysis of cementum and dentine of dC LAC by the use of Scanning Electron Microscope (SEM)*.

Cementum				Dentine			
Elmt	Spect Type	Element %	Atomic %	Elmt	Spect Type	Element %	Atomic %
O K	ED	44.25	64.11	O K	ED	44.84	64.76
Na K	ED	0.64	0.64	Na K	ED	0.44	0.45
Mg K	ED	0.29	0.28	Mg K	ED	0.48	0.45
P K	ED	18.97	14.20	P K	ED	17.61	13.14
Cl K	ED	0.35	0.23	S K	ED	0.39	0.28
Ca K	ED	35.41	20.48	Ca K	ED	36.01	20.76

* The samples were analyzed by Dr. Labrini Papadopoulou.

tooth (pl. 4.1d, tab. 6). The micrograph analysis in D^4 LAC 14601 showed the paracone in detail (pl. 4.2a), the lesser intense cingulum (pl. 4.2b), microscratches on the paracone, with ~100μm (pl. 4.2c) and ~200μm analysis (pl. 4.2d). The micrograph analysis in D_4 LAC 14603, showed: slightly worn hypoconid and endoconid (pl. 4.3a), the tip of the protoconid greatly rounded, with a wear facet on the top and pit (pl. 4.3b), microscratches on the protoconid, with ~100μm (pl. 4.3c) and ~200μm analysis (pl. 4.3d). The micrograph analysis in D_4 LAC 14604 showed: eroded hypoconid (pl. 4.4a), completely worn cuspids (pl. 4.4b) as well as all the types of microwear such as pits (pl. 4.4c), polished surfaces and microscratches (pl. 4.4d). The micrograph chemical analysis by the use of SEM in dC LAC 14602 (cross section at the base of the crown is shown in pl. 4.5 a,b) showed slight divergence of cementum and dentine (pl. 4.5c, tab. 7).

Concerning the occlusal morphology of the milk carnassials D^4 (LAC 12557) and D_4 (LAC 12560), they are more similar to those from Gamssulzenhöhle (Rabeder, 1983) (pl. 4.6, 4.7).

The micromammals from the Loutra Arideas Bear Cave

The study the micromammalian fauna from the chosen squares N10 (LAC I), V4 & W4 (LAC Ib), B11 & D10 (LAC II) and R1 (LAC III) followed several steps. The sediments were first put into water and perhydrol and then all the material was washed through a double system of sieves, one for micromammals (0.8 mm) and the other (3 mm) for larger, mainly ursid remains. The total sediment that was washed through the sieves and collected in the second one, with a mesh of 0.8 mm for the study of the small mammals weighed 2000 kg. Then the material was dried, packed up and transported to the Aristotle University's labs for sorting, the teeth were placed in special plates and they were listed. The measurements of the teeth were taken using a WILD Photomakroskop M400 stereoscope. The teeth were figured in the Aristotle University. All the material is stored both in the Aristotle University of Thessaloniki and the local Physiographical Museum of Almopia.

The LAC assemblage consists of four orders of micromammals. The faunal list shows a remarkable abundance of the small mammals: 25 species belonging to 12 families, 18 of which identified at the species level (Chatzopoulou *et al.*, 2001; Chatzopoulou, 2003; 2005). The material presented in this research yielded a rich microfauna based on more than 1500 specimens. The material from LAC III shows the most remarkable diversity of taxa and great abundance of bones and teeth remains in the cave regarding micromammals. The assemblage of LAC II is relatively rich. In LAC I, the number of teeth and bones is reduced, while the material from LAC Ib is very poorly represented. Few complete mandibles were found up to now, as it is fragmentary material, bearing few teeth.

The insectivores are represented by two families, Erinaceidae and Soricidae. The remains of the former family confer to *Erinaceus* cf. *europaeus* (pl. 5.1). The structure of two isolated teeth of the upper jaw, found in the Bear Cave is exactly as in recent specimens of *E. europaeus*.

Soricidae are differentiated in two subfamilies Soricinae and Crocidurinae by the tooth pigmentation. Soricinae have red teeth. The mandible from LAC (pl. 5.4a-b) is attributable to the genus *Sorex* because the buccal cingulum is narrow, the talonid of M_1 is slightly shorter than trigonid and the mental foramen is placed below the trigonid of M_1 (Reumer, 1984). The large size (*S. araneus* group) and the morphological characteristics conform rather well to *S. araneus* (Reumer, 1996). Nevertheless, the study of a single specimen does not allow a secure identification at the species level. A small-sized representative of the genus *Sorex* was also recorded in the material of LAC III. The mental foramen, that is indicative for this species, is not visible because the mandible is damaged. The study of the LAC specimen (pl. 5.5a-b) showed that the size and the morphological characteristics conform rather well to *S. minutus* (Reumer, 1984). However, as the material is so extremely scanty, the LAC material is referred as *S.* cf. *minutus*.

Crocidurinae have white teeth. The lower incisor is acuspulate (pl. 5.3), in the lower molars the buccal reentrant valley opens high above the cingulum, the entoconid crest is low to nearly absent (pl. 5.2b), the buccal cingulum is narrow but well pronounced and undulating in M_1 (pl. 5.5a). These characteristics determine the genus *Crocidura* (Reumer, 1984). No P^4 has been preserved in the LAC material in order to define the species.

A small-sized representative of Sciuridae has been also recorded. The high protocone and the U-shaped occlusal surface of upper molars (pl. 5.7) as well as the strong entoconid and the presence of trigonid basin in M_3 (pl. 5.8), conform to the genus *Spermophilus* [=*Citellus*] (Miller, 1912). Distinction of small-sized species is based on the number of roots of P_4. Since this tooth has not been found up to now, therefore, LAC remains are attributed to *Spermophilus* sp.

Two isolated teeth found in LAC III belong to the genus *Sicista*, which is characterized by brachyodont molars with simple morphology (pl. 5.6) (Koliadimou, 1996). *S. subtilis* shows a low degree of enamel folding. Its simple molar structure and its dimensions, which are considerably variable in size in recent *S. subtilis*, characterize the LAC material.

The remarkable abundance of arvicolids is described by six different species. The large-sized hypsodont molars (pl. 5.29a) belong to the genus *Arvicola*. The symmetry and the simple structure of the anteroconid of M_1 (Chaline, 1974) conform to *Arvicola terrestris* (pl. 5.29b).

The best-represented *Microtus* is *M. nivalis*. The M_1s have four closed triangles and the shape of the anteroconid looks like a shaft (pl. 5.30-31). The M^3s are massive and show simple structure (pl. 5.32). Lots of arvicolid teeth are attributed to *Microtus arvalis* or *M. agrestis* due to the structure of the anteroconid of the M_1. Differentiation between the latter of the voles is problematic since their structure and dimensions overlap to a large extent. Among the teeth attributed to *Microtus arvalis* (pl. 5.34-35), there are specimens whose length of M_1 is more than 3.10mm (pl. 5.33). According to Nadachowski (1982) these specimens belong to *M. agrestis*.

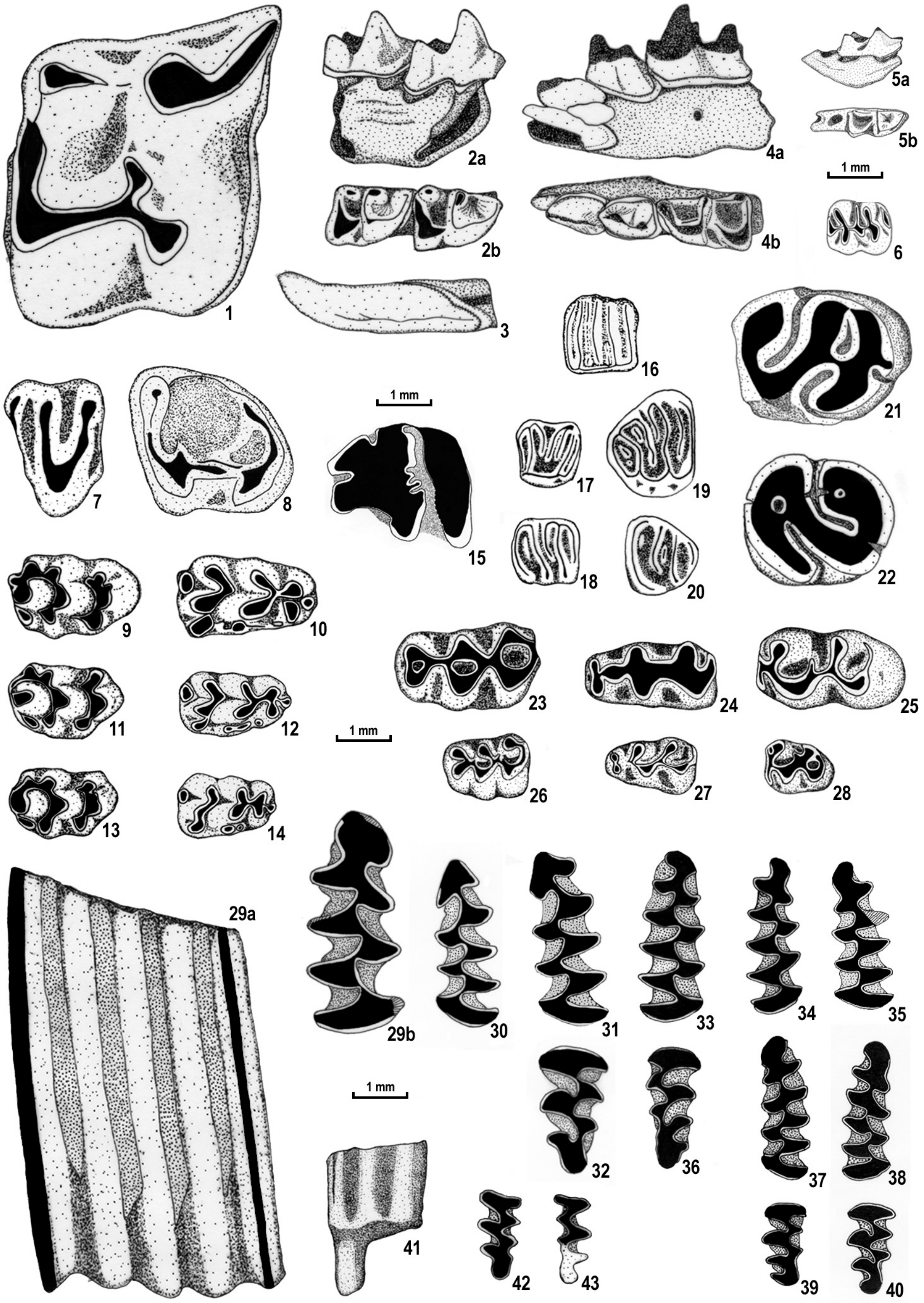
The distinction between *Microtus (Pitymys) multiplex* and *Microtus (Pitymys) subterraneus* is based on the structure of the anteroconid of M_1 (Chaline, 1972). The LAC specimens have an open connection between the anteroconid and triangles T6 and T7. In 57% of the M_1 T9 is well developed. These characteristics conform to *M. (P.) multiplex* (pl. 5.37-38). The arvicolid molars bearing roots and having a more slender structure (Miller, 1912) are attributed to the genus *Clethrionomys*. Since the LAC material is poor, it is identified as *Clethrionomys* sp (pl. 5.41-43).

The murids are very prevalent and are represented by three different species. The large-sized teeth attribute to *Apodemus mystacinus* (pl. 5.9-10). Nevertheless their size is considerably smaller than that of other *A. mystacinus* populations. The small-sized *Apodemus* teeth are attributed to the group *Apodemus sylvaticus/flavicollis* (pl. 5.11-12) since the distinction between these species is difficult. Some M^1 and M_1 (pl. 5.13-14) are very small and can be assigned to *A. sylvaticus*.

Two hamsters have been recorded in LAC material. The small-sized cricetid (pl. 5.26-28), which is morphologically similar to recent *Cricetulus migratorius*, is slightly smaller than other *C. migratorius* from the Balkans. The large-sized teeth (pl. 5.23-25) fall within the range of *Mesocricetus newtoni*. The Romanian Hamster, which probably originated in the Middle East, is assumed to have crossed the Bosporus at the lowest sea level stand during the last glaciation (Santel & Koenigswald, 1998).

The glirids are represented by three species. The most abundant of all, *Dryomys nitedula* is characterized by the prominence and the number of the main ridges of the molars (pl. 5.17-18). *D. nitedula* in Greece shows an average-complexity of the occlusal surface (Daams, 1981). The complex morphology and the large size of the occlusal surface of the LAC specimens conform to *Glis glis* (pl. 5.19-20). The long transversal, continuous ridges of LAC material conform rather well to recent *M. avellanarius* (Storch, 1978). However, as the material is extremely scanty, the LAC material is referred to as *M.*cf. *avellanarius* (pl. 5.16).

Plate 5



LAC micromammals: *Erinaceus* cf. *europaeus*. 1. M^1 sin. *Crocidura* sp.; 2. Mandible with M$_1$-M$_2$ dex. 2a. labial view, 2b. occlusal view; 3. I^{sup} dex (lateral view). *Sorex* sp.; 4. Mandible with I$_{inf}$ frag, A, P$_4$, M$_1$ dex. 4a. labial view, 4b. occlusal view. *Sorex* cf. *minutus*.; 5. Mandible with M$_2$ dex. 5a. labial view, 5b. occlusal view. *Sicista subtilis*.; 6. M$_2$ sin. *Spermophilus* sp.; 7. M^1 sin; 8. M$_3$ sin. *Apodemus* aff. *mystacinus*; 9. M^1 dex; 10. M$_1$ dex. *Apodemus sylvaticus/flavicollis;* 11. M^1 dex; 12. M$_1$ dex. *Apodemus sylvaticus*; 13. M^1 dex; 14. M$_1$ dex. *Lepus* cf. *europaeus;* 15. P$_3$ sin. *Muscardinus* cf. *avellanarius*; 16. M^2 dex. *Dryomys nitedula*; 17. M^1 dex; 18. M$_2$ dex. *Glis glis*; 19. M^3 dex; 20. P$_4$ dex. *Spalax leucodon*.;21. M^1 dex; 22. M$_1$ dex. *Mesocricetus newtoni*; 23. M^1 sin; 24. M$_1$ sin; 25. M$_3$ sin. *Cricetulus migratorius*; 26. M^1 sin; 27. M$_1$ sin; 28. M$_3$ sin. *Arvicola terrestris*; 29. M$_1$ sin. 29a. lingual view, 29b. occlusal view. *Microtus nivalis*; 30. M$_1$ sin; 31. M$_1$ sin; 32. M^3 sin. *Microtus agrestis*; 33. M$_1$ dex; 34. M^3 dex. *Microtus arvalis*; 35. M$_1$ dex; 36. M$_1$ sin. *Microtus (Pitymys)*cf. *multiplex*; 37. M$_1$ sin; 38. M$_1$ dex; 39. M^3 sin; 40. M^3 sin. *Clethrionomys* sp.; 41. M^2 dex (lingual view); 42. M^3 sin; 43. M^3 dex.

Table 8
Presence of the mammalian remains in the four chambers of the Loutra Arideas Bear Cave.

	Chiroptera	*Erinaceus* cf. *europaeus*	*Sorex* sp. (group *S. araneus*)	*Sorex* cf. *minutus*	*Crocidura* sp.	*Spermophilus* sp.	*Sicista subtilis*	*Arvicola terrestris*	*Microtus arvalis/agrestis*	*Microtus nivalis*	*Microtus (Pitymys)* cf. *multiplex*	*Clethrionomys* sp.	*Apodemus* aff. *mystacinus*	*Apodemus sylvaticus/flavicollis*	*Cricetulus migratorius*	*Mesocricetus newtoni*	*Dryomys nitedula*	*Glis glis*	*Muscardinus* cf. *avellanarius*	*Spalax leucodon*	*Lepus* cf. *europaeus*
LAC I	+	-	-	-	+	-	-	+	+	+	+	-	+	+	+	+	+	-	-	+	-
LAC Ib	+	-	-	-	+	+	-	-	+	+	-	-	+	+	+	+	-	-	-	+	-
LAC II	+	+	+	-	+	+	-	+	+	+	+	+	+	+	+	+	+	+	+	+	+
LAC III	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+

The mole-rats are represented by *Spalax leucodon*. The LAC assemblage is characterized by the relatively simple morphology, the medium size of the occlusal surface and the diagonal position of the labial loops (pl. 5.21-22) (Kowalski & Nadachowski, 1982).

Hares are scarce, as only one lower third premolar indicates accurately its presence in the assemblage of Bear Cave. The margin of the P_3 from LAC is an intermediate form between the elongated *L. timidus* (Fladerer, 1992) and the rounded *L. europaeus* (Palacios & Lopez-martinez, 1980). The structure of P_3 found in the Bear Cave resembles to recent specimens of *L. europaeus* (pl. 5.15). Therefore, the LAC material is referred to as *L.* cf. *europaeus*. In the microfauna, chiropters (*Rhinolophus* sp., *Myotis* sp. and *Miniopterus* sp. were identified preliminarily by G. Rabeder) as well as amphibians, reptiles and fish were also found.

Discussion

The LAC assemblage shows a remarkable abundance of the small mammals: 25 species belonging to 12 families, 18 of which identified at a species level. According to the ecology of each animal, the micromammals from the Bear Cave were divided into three groups: A) animals that live in open dry environment [*M. nivalis*, *A. mystacinus*, *M. newtoni*, *C. migratorius*, *Spermophilus*, *S. leucodon* and *Sicista subtilis*], B) animals that inhabit forest [*A. sylvaticus*, *A. flavicollis*, *Clethrionomys*, *D. nitedula*, *G. glis* and *M. avellanarius*] and C) animals that can adjust to various environments [*E. europaeus*, *Sorex*, *Crocidura*, *A. terrestris, M. arvalis*, *M. agrestis*, *M. (P.) multiplex* and *L. europaeus*]. A pie diagram of the environmental distribution (fig. 10) was constructed based on the minimum number of individuals for each micromammal. The LAC fauna contains predominantly species that are associated with open vegetation (50%). 24% of the micromammals indicate the presence of deciduous and mixed forests, while the rest (26%) live in various climatic conditions. The surroundings of the Bear Cave are geomorphologicaly very complex; forest peaks, rocky slopes, vast fields and mountain plateaus alternate in a small area. Just like today, geomorphological density had to result in vegetational and faunal variety.

The presence of *Arvicola terrestris,* as well as the taxon range zones of the micromammals of the Eastern Europe-MNQ 26 after Guérin (Guérin & Patou-mathis, 1996), implies a Late Pleistocene to Holocene age for the fauna of the Bear Cave. The majority of the species also shows an advanced evolutionary stage.

The presence of *M. arvalis, Pitymys, Clethrionomys, M. avellanarius, G. glis, Crocidura,* as well as the small size of *A. mystacinus* (Bergman's rule) indicate a rather temperate climate. The study of seeds found during sieving, which are typical Mediterranean plants (Tsoukala *et al.*, 2001), confirms this conclusion. During the colder phases of Würm, while central Europe was covered with ice, it seems that the Balkans was a refuge for many animals (Pradel, 1989).

The material from LAC III shows the most remarkable diversity of taxa, and great abundance of bones and teeth remains in the cave regarding micromammals (tab. 8). The assemblage of LAC II is relatively rich. In LAC I the number of teeth and bones is reduced, while the material from LAC Ib is very poor. Moreover, some teeth and bones of both macro and micromammals show traces of transportation by water (pl. 6.3). This observation related to the taphonomy of the macromammals could be the result of the increase of water mass surface flowing inside the cave. A rock shelter, 50 m west of Bear Cave, at the same altitude, presents a cohesive conglomerate,

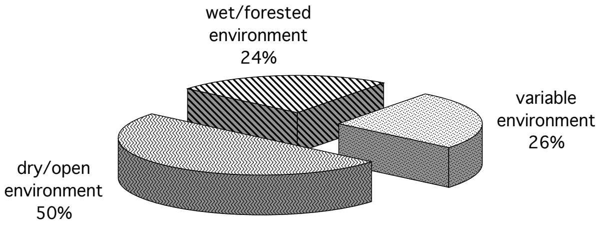


Figure 10. Pie diagram of the enviromental distribution based on the minimum number of individuals of the micromammals of the Bear Cave.

remains of an old river-bed. During Late Pleistocene the Thermopotamos stream was probably flowing 80 m above its today's level. It is likely that during floods of the river, micro and macromammalian remains were scattered inside the cave or entered the cave. Heavier material (long bones, skulls and large pebbles) was deposited close to the supply of the sediments in the cave, while lighter fine-grained assemblages (sediments and micromammalian remains) were transported into deeper parts of the cave.

Micromammals could be the food remains of various predatory-owls and others raptors that primarily feed on small mammals hunting over a variety of habitats and returning to the cave to digest and regurgitate their meals, and mammal carnivores which carried carcasses of their pray into the cave. Among the numerous bones and teeth, there were sometimes more or less complete mandibles, but no complete skull is found, which is characteristic for owl pellets (Andrews, 1989). This source of origin is also supported by the presence of erosion on the enamel and dentine in many teeth due to indigestion by predatory birds (pl. 6.3).

STRATIGRAPHY AND SEDIMENTS OF THE BEAR CAVE

The study of a stratigraphical column provides important information about the taphonomy and the circumstances, such as environment and climate that occurred in the area and aims to collect data regarding the composition and the formation of the sediments of the cave, as well as their depositional conditions. The aim of the research is to correlate the sediments and the paleontological material of all chambers. During the excavation's progress, all observations were continuously marked, the layers were drawn and photographed and samples of the sediments were collected. Every change in the color, the composition and the cohesion of the sediment grains was noted. The excavation proceeds in predefined levels, consulting these remarks. All columns from chambers LAC Ic, LAC Ib, LAC I, LAC II and LAC III have been described by Chatzopoulou (2001; 2003; 2005).

Chamber LAC Ic. The chamber of gours is situated very close to the today's cave entrance. The floor is covered with gour structures and it is situated at the highest level among all chambers. The reddish and gray sterile sediments overlie the fossiliferous beds. The fossiliferous stratum layer appears to be the thickest (~140 cm) among all chambers, although the fossil material is relatively scarce. A great number of middle-sized pebbles were observed throughout the brownish layer although there are fewer and smaller ones to the bottom of it. The external surface of the stones of the lower fossiliferous beds shows an alteration probably due to weathering. A sequence of thin sinter layers with gray sand underlies the fossiliferous layer. All beds show a slight SW inclination towards the center of the chamber. All the sediments of this chamber are penetrated by plant roots probably due to its closeness to the open-air slope of the gorge.

Chamber LAC Ib. It is the smallest excavated chamber of the cave. Actually, it is an extension of the main chamber showing great paleontological interest regarding the abundance of large mammal bone remains among them non ursids (tab.1, fig. 4). The sedimentation is mainly clastic. All beds display the maximum thickness at V4 square and they are wedging out towards the walls of the cave and the connection to the main chamber (LAC I). The reddish and gray sediments that overly the fossiliferous beds are similar to those of LAC Ic (G10 square). A great accumulation of large stones and pebbles of different lithological composition was observed at the superior beds of the fossiliferous layer in V4. The fossiliferous layer is relatively thin (~40 cm). Thick gray sterile micaceus sand underlies the fossiliferous layer.

Chamber LAC I. The central chamber is the larger one, while the level of the floor is the lowest in the cave. The diversity of sediments makes it the most remarkable of all chambers. In trench-square N10, the clastic material dominates, although there are four thin sinter layers interposed. The sediments are mainly brownish and small grained (clay and silt). Below 250 cm from the reference-zero point, a sandy layer with many pebbles seems to be the deepest one in the entire cave. The fossiliferous layer is very close to the surface (<20 cm). It is thin (~25 cm) and the upper beds are consolidated to crust, sometimes with enclosed fossils.

Chamber LAC II. The alternation of clastic and chemical sediments is evident in D10. The sinter layers (fig. 11, oblique stripes) were deposited during warm and humid intervals, while the clastic sediments (sand, clay and silt) were accumulated during colder periods. The study of the small grain size of the clastic sedimentation of the floor of the Bear Cave is evidence of slow water flow in the deposition site. This is the result of the surface increase of water mass flowing inside the cave, as well as of probable climatic changes from wet to dry (Tsirambides, 1998). The surface beds, fig. 11, (above the dotted line) are disturbed by unauthorized diggings, resulting in an unequal thickness (25-60 cm) of the fossiliferous layer.

Chamber LAC III. This chamber is the deepest area of the cave, although there is a passage that links LAC III with the gour chamber (LAC Ic) (fig. 11). At first, the trench square R1 was excavated. The sedimentation is mainly clastic and rather monotonous. The fossiliferous layer appears to be very thick (~120cm). It is mainly a brownish sandy clay dotted with white calcareous pebbles and gravels. Some blackish lenses appear close to the surface of the column. The fossiliferous layer ends on the bedrock of the cave. The small mammals in this square are abundant (Chatzopoulou, 2005), while the remains of large mammals are scarce and poorly preserved. The excavation of R2 added new data when a series of layers were revealed. All beds show a SW inclination (dip angle 30°) and they are wedging out towards the walls of the cave. The fossiliferous layer is less extended, ending on a sinter. This crust represents a paleo-floor of the cave since a stalagmite *in situ* (consolidated to the upper part of the crust) is preserved. The fossiliferous beds must have filled this part of the cave subsequently at a later stage. The gray and reddish sterile sediments underlying the fossiliferous beds show no similarity to those of other chambers. Sedimentation ends on the limestone (bedrock) of the cave.

In conclusion, it is obvious that the fossiliferous layer in the stratigraphical columns from the trench-squares G10, V4, N10, D10 and R2 of the chambers LAC Ic, LAC Ib, LAC I, LAC II and LAC III respectively (fig. 11) is placed at the same depth (-130cm) in the cave, despite the distinctly different sedimentation and the deviation in thickness. The only safe chronological and sedimentological correlation of the five trenches is the fossiliferous layer that is characterized by the presence of *Ursus ingressus* (Tsoukala & Rabeder, 2005). The accumulation of sediments in the cave was in cyclic intervals (clastic and chemical sediments). During warm and humid intervals, sinter layers were deposited, while during colder periods clastic sediments were accumulated. The alternation of the sediments is more evident in chamber LAC II, while clastic sedimentation dominates in LAC Ic and LAC Ib. Chambers LAC I and LAC III stand in between. The lithological composition of the fine-grained depositions as well as the pebbles of the cave represents the eroded rocks of the surrounding area (limestones, dolomites, marbles, schists, phyllites, ophiolites).

CONCLUDING REMARKS AND TAPHONOMY

The Loutrá Aridéas Bear Cave is an important site with very rich paleontological material. The research over 16 years and the excavations in the site followed the paleontological rules strictly, and today it can be considered as the biggest systematic excavation with cave bear remains in Greece. Since 1990, twelve excavating seasons took place in 34 squares with total 206 levels and approximately 15000 specimens (mostly indeterminable) were brought to light. Twelve species of large mammals and 25 taxa of small mammals were determined, the latter derived from the washed sediment that weighted two tons. Furthermore, in Z Cave of the Speleopark a fossilized maxilla with a broken left canine of *Ursus* cf. *arctos* was found.

- The large mammalian fauna consists of: *Ursus ingressus*, *Crocuta crocuta spelaea, Panthera leo spelaea, Panthera pardus, Vulpes vulpes, Canis lupus, Meles meles,* mustelids, *Bos primigenius, Capra ibex, Cervus elaphus* and *Dama dama.*
- The small mammalian fauna consists of insectivores, rodents, lagomorphs and bats. Insectivora: *Erinaceus* cf. *europaeus*, *Sorex* sp. (cf. *araneus*), *Sorex* cf. *minutus, Crocidura* sp. Rodents: *Spermophilus* sp., *Arvicola terrestris, Microtus arvalis & agrestis, Microtus nivalis, Microtus (Pitymys)* cf. *multiplex, Clethrionomys* sp., *Apodemus* aff. *mystacinus*, *Apodemus sylvaticus* & *flavicollis, Cricetulus migratorius, Mesocricetus newtoni, Dryomys nitedula, Glis glis, Muscardinus* cf. *avellanarius, Sicista subtilis, Spalax leucodon*, lagomorpha: *Lepus* cf. *europaeus*, Chiroptera: *Rhinolophus* sp., *Miniopterus* sp., *Myotis* sp.
- Carnivores are scarcely despersed, but ursids are extremely abundant.
- The study of the best preserved bone fragments and teeth of the bears i.e., the most representative, showed the presence of the *U. ingressus* for first time in Greece. Its position in the evolutionary tree of the bears during Quaternary is shown in fig. 12.
- The complete skulls are few, but there are enough complete or almost complete mandibles. The former are well preserved skulls of adults, found either in the main chamber LAC I. The most important skull that shows clearly the characters of *U. ingressus*, was found in G11 square of LAC Ic chamber, whereas a skull of a juvenile has been found at the end of chamber LAC Ib among other specimens of juveniles and sub-adults.
- Concerning teeth, in both upper and lower fourth premolar groups the high developed morphotypes

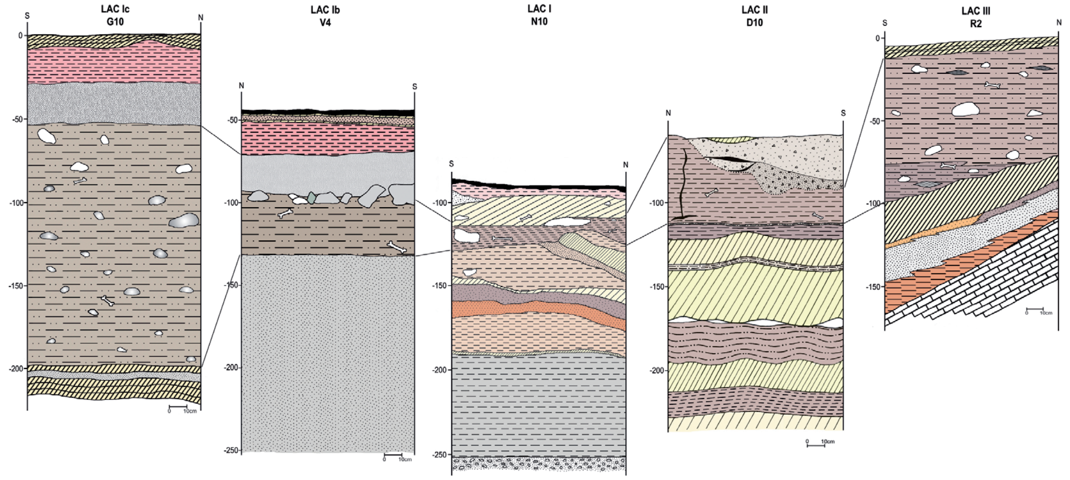


Figure 11. Stratigraphical columns of trench-squares G10 (LAC Ic), V4 (LAC Ib), N10 (LAC I), D10 (LAC II), and R2 (LAC III). The depth in all the sections is considered from the reference-zero point of the cave and it is counted in cm. The fossiliferous layer appears to be thicker in G10 (~140cm). Despite the distinctly different sedimentation in the five square-trenches and the variation in thickness, the fossiliferous layer is found at the same level (-130cm) in the cave (CHATZOPOULOU, in press).

are dominating. All morphodynamic indices (M^2 metaloph, M_1 enthypoconid, M_2 enthypoconid, premolar indices) have evolutionary levels between 70 and 84% of Gamssulzen Cave (Upper Austria) standard.

- Concerning metapodials from Bear Cave there is a similar pattern in the metacarpus and metatarsus with those of the bears from Gamssulzen Cave. There are also some differences that are probably local variations.
- The bones are mostly well preserved, representing all biological ages. Few long bones are complete and very well preserved.
- Many isolated teeth have been found of all wear stages (unworn to completely worn- down to the root) therefore the age structure of the cave bear population shows a variability with the extremes - very young and old- predominating (pl. 6.1).
- The majority of the tooth and bone remains belong to juveniles and sub-adults, while very few belong to very old individuals and few to adults, indicating thus an extremely high incidence of juvenile and neonate mortality. There are many bear carcasses as a result of death during hibernation. The abundance of the milk teeth, in spite of their fragility, is very remarkable thus the Loutrá Arideas site can be considered as the most important place of Greece where so abundant and well stratified cave bear deciduous teeth have been collected from 206 excavated layers.
- The Bear Cave is very rich in ursid milk teeth and the MNI (minimum number of individuals) of the juveniles, based on the left dI^3, is calculated to 355 individuals.
- The morphotypes of D^4 and D_4 seem to be similar to those of *U. ingressus* from Gamssulzenhöhle (Austria) and the analysis from the micrographs by the use of the Scanning Electron Microscope (SEM) of the occlusal microwear showed polished surfaces, microscratches and pits.
- All ages from juvenile to senile individuals are present. Among the material there are many postcranial bones, including metapodials, with their epiphyses unfused.
- Milk teeth that have just been substituted show clearly that the bears used occasionally the cave as a den. The study of the milk teeth showed also the presence of unborn bears. All this evidence supports the hypothesis that the cave was inhabited by bears. Also, many milk teeth as well as teeth of micromammals were transported into the cave along with the sediments.
- A few bones bear traces of large carnivore teeth and this can be explained either by the presence of other carnivores (felid, hyaenid, canid) or by cannibalism (pl. 6.2).
- In some bones gnawing marks appear, which are probably due to many rodents. On certain micrommamal bones corrosion has been noted due to action of water, and stomach liquids of animals that digested them (pl. 6.3).

- The rounding and abrasion of some bones such as metapodials, phalanges and patellas also establish the action of flowing water. The poor preservation of certain remains, as well as their orientation within the sediments, indicate a moderate water flow as few were found in situ over the deposit.
- Very few bones, such as metapodials with unfused epiphyses, found in anatomical position, in B10 square (LAC II chamber) but the majority has been found scattered, and this is due either to animals activity or to the action of flowing water (pl. 6.4).
- The presence of corrosion on the enamel and dentine of many of the teeth under study due to digestion by raptors implies that some small mammals comprised the meal of predators that visited the cave. Bats must have inhabited the cave.
- The presence of both sexes has been established due to the sexual dimorphism either of the teeth (mainly canines) or of the postcranial skeleton, with a strong predominance of females over males (fig. 3, pl. 6.5).
- Paleopathologies are evident on certain bones, especially on metapodials.
- The micromammalian fauna shows a remarkable diversity of taxa and a great abundance of bones and teeth remains implying a Würmian (Late Pleistocene) age (tab. 8, pl. 6.6).
- The age of the paleofauna according to the radiometric data is estimated to 37.880 years before present (Rabeder *et al.*, 2006).
- During washing of the sediments from the various excavating squares, seeds were collected by the floatation method, which the late archaeologist Maria Mangafá identified as: *Rumex crispus*, *Picris echioides, Matricaria chamomilla (Chamomila recutita)*, and Compositae. All seem recent, typical Mediterranean plants. The first one is the most common and loam, clay and nutrient indicator. The second is a stony waste land indicator and the third one indicates fresh or sandy loams, rich in nutrients and saline soils.
- The fauna of the Bear Cave lived during a milder episode of the last glacial period or Würmian glacial period that was not so severe in Greece. The presence of small mammals that are indicators of temperate climate and the typical Mediterranean flora confirm that during the colder phases of Würm, the Balkans was a refuge for many animals, while central Europe was covered by ice.
- The paleoenvironment seems to be predominantly open with deciduous and mixed forests. The surroundings of the Bear Cave are geomorphologicaly very complex-forest peaks, rocky slopes, vast fields and mountain plateaus alternating in a small area. Just like today, in the Late Pleistocene geomorphological density had to result in certain vegetational and faunal variety.

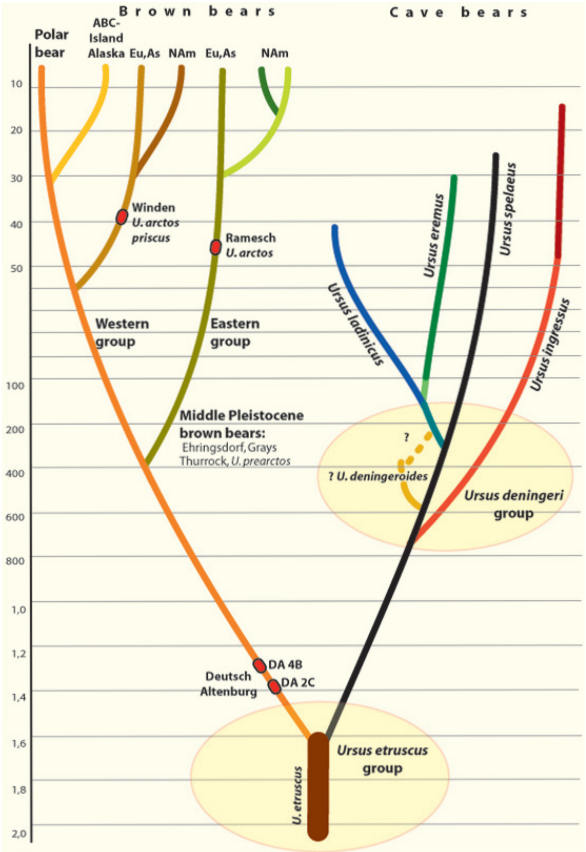
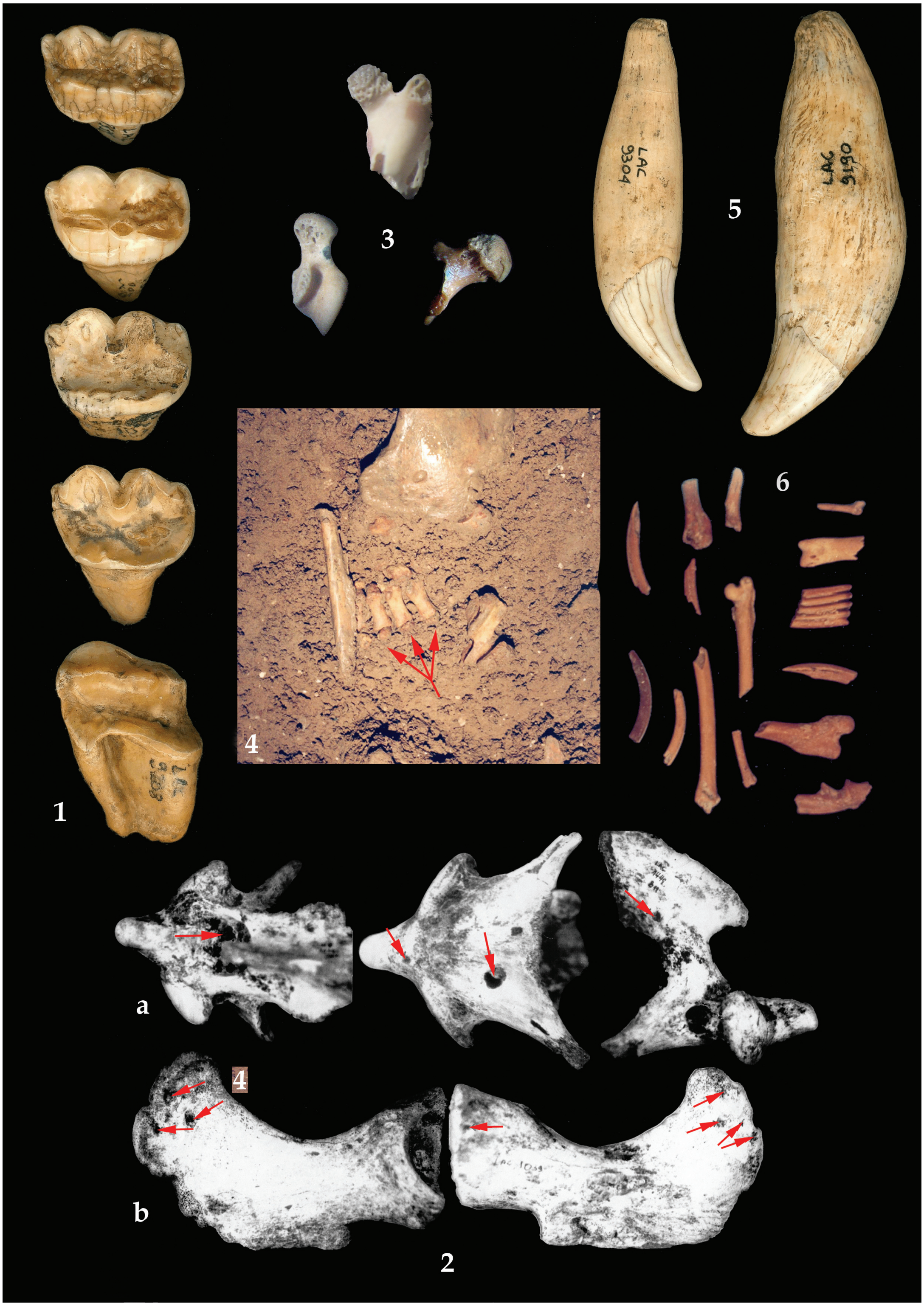


Figure 12. *Ursus ingressus*: its position according to the special taxonomy of the cave bears based on their genetics, morphology and chronology is given by RABEDER & HOFREITER (2004).

- The paleogeomorphology of the surroundings of the Bear Cave were very complex: forest peaks, rocky slopes, vast fields and mountain plateaus alternate in a small area. There were shrubs and mixed woods. The climate appears to be relatively arid. Nevertheless, there were streams that attracted many animals'. The thermal springs possibly affected the local climate by making it more tolerable.
- The cave does not seem to have been used by humans, as only one lithic (pyrite) artifact has been found up to now, in B10 square of LAC II chamber. Neolithic period is also evidenced by the presence of burned wood or of pottery remains in V8 square of LAC Ib chamber.

Plate 6



Ursus ingressus LAC: 1. M^1 of various wear stages; 2. Axis (epistrophaeus) (a) and pelvis (b) with bite marks by a scavenger; 3. Micrommamal bones with corrosion due to action of water and stomach liquids of animals that diggested them; 4. Metapodials in anatomical position of a juvenile with unfused epiphyses, in B10 square; 5. Canines of a male (right) and female (left) showing the sexual dimorphism in the Loutra material; 6. Paleopathology on the metapodials; 7. Bones and teeth of micromammals are of great abundance among the LAC material.

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CHRONOLOGICAL AND SYSTEMATIC POSITION OF CAVE BEARS FROM LOUTRÁ ARIDÉAS (PELLA, MACEDONIA, GREECE)

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Abstract: The cave bears from Loutrá Aridéas cave most likely belong to the species *Ursus ingressus* (Rabeder *et al.* 2004). This emanates from metrical and morphological comparisons. Radiometric data show that these cave bears lived at least 37.000 years ago. Between 34.000 and 32.000 years B.P. the fossil remains of bears and other large mammals were relocated from their initial deposit, which is completely destroyed today, and were dispersed on nearly all the ground of the cave.

Key words: Loutrá Aridéas Cave, *Ursus ingressus*, radiometric datings, Taphonomy.

INTRODUCTION

The cave-site of Loutrá (LAC: Loutrá Aridéas Caves) is located in Northern Greece (Macedonia), 120 km northwest of Thessaloniki and 2 km from the Loutraki village, in the so called "Almopia Speleopark". The research in the area started in 1990 and in twelve systematic excavation circles, under strict paleontological rules, including micromammalian research, was carried out by the Geology School of Aristotle University, in cooperation with the Ephorate of Paleoanthropology and Speleology of the Ministry of Culture. Since 1996 the excavations continued in co-operation with the Vienna University (Tsoukala, 1994; Tsoukala, Rabeder & Verginis, 2001; Tsoukala & Rabeder, 2006). All the paleontological material is stored in the local Physiographical Museums of Almopia in the Loutrá area and Aridéa town. All the sediments of the 206 levels (about 5 cm of thickness each) have been washed through a system of double sieves, for micromammals with a mesh of 0.8 mm and for large mammal remains and milk teeth of 3 mm (Chatzopoulou, 2006; Pappa *et al.* 2006).

MATERIAL

The cave bear remains consist of abundant isolated teeth, bone fragments, while there are several mandibles and a very few skulls. For studies on the evolutionary level and systematic position, about 1500 teeth were measured: 202 I1 and I2, 68 I3, 64 i1, 125 i2, 124 i3, 141 canines (111 female, 30 male), 7 P3, 104 P4, 95 p4, 109 M1, 77 M2, 149 M1, 169 M2, 95 M3.

METHODS

For age determination of the cave bear remains several bone fragments were dated using AMS and two sinter samples were analysed using conventional radiocarbon dating.

Since we know, that at least 4 cave bear lines inhabited Europe in the Late Pleistocene, the question of affiliation to different cave bear species is a contemporary issue. DNA analysis of the bears from Loutrá was not successful; therefore we compare the mean values and morphological indices with other populations and try to find out the classification into one of three possible taxa. For the problem of local adaption and the appropriate evolution, specific criteria of dentition are very interesting. So it is necessary to find out the significant metrics and morphodynamic indices of teeth and to use them for systematic classification. Typical faunas of *Ursus ingressus* (Gamssulzenhöhle), of *Ursus eremus* (Ramesch-Knochenhöhle) and of *Ursus ladinicus* (Conturineshöhle) as well as other representative populations were compared. Only DNA analysed or morphologically classifiable material was used for comparison.

That is:

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Table 1

Lab.	Lab.-nr.	material	sample nr.	Campaign	sector	square	depth (cm)	^{14}C Age	1 sigma		^{13}C
									+	-	$(^0/_{00})$
GrN	22770	sinter	Loutraki 1	1996	LAC I	N 10	15	**32.060**	520	490	+5,77
GrA	7573	bear femur	Loutraki 2	1996	LAC I	N 10	40	**37.880**	370	360	-21,35
GrN	22772	sinter	Loutraki 3	1996	LAC I	N 10	80	**33.910**	590	550	+5,25
VERA	-	bear Mt5	LAC 7005	2000	LAC Ib	W/V 4	170-175		no collagen		
VERA	-	bear Mt2	LAC 7023	2000	LAC Ib	W/V 4	170-175		no collagen		
VERA	-	bear Mc1	LAC 7068	2000	LAC I	O 10	85-100		no collagen		
VERA	-	bear Mt4	LAC 7079	2000	LAC I	O 10	85-100		no collagen		
VERA	-	bear Mc4	LAC 7170	2000	LAC Ib	V 4	180-185		no collagen		
VERA	-	bear bone	LAC III	2001	LAC III		32		no collagen		

Abbreviations: GrA and GrN - Centre for Isotope Research, University of Groningen (NL), VERA - Vienna Environmental Research Accelerator, University of Vienna.

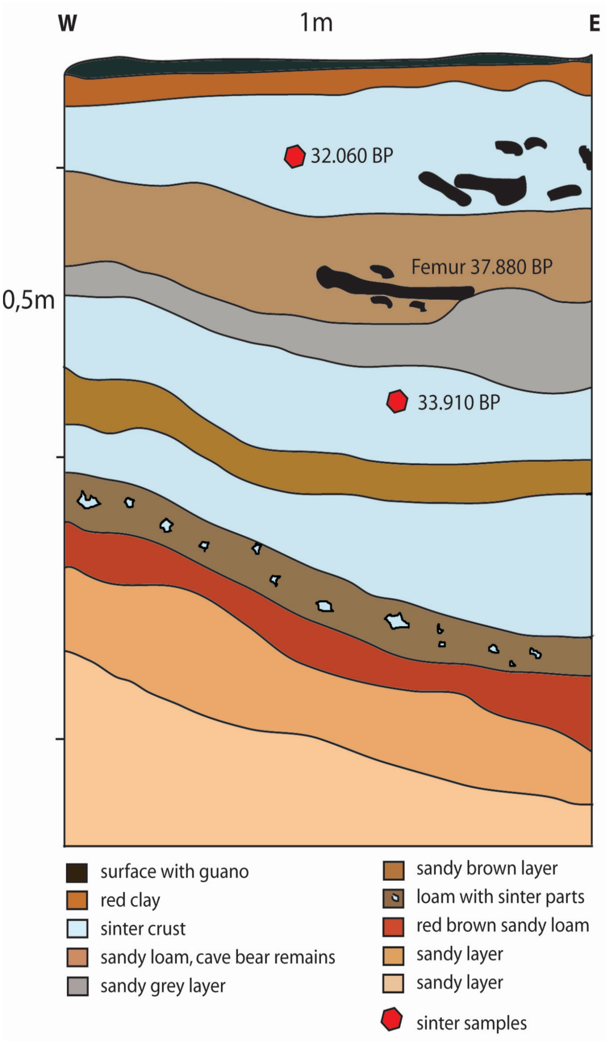

Figure 1. Profile of excavation site LAC I (first chamber), boundary of square N10 to O10, with position of dated sinter samples and cave bear femur.

Ursus ingressus: Gamssulzenhöhle (locus typicus), Hartelsgrabenhöhle, Herdengelhöhle layers 5-6, Ilianka, Krizna jama, Lieglloch, Merkensteinhöhle, Mokriska jama, Nixloch, Potocka zijalka, Vindija G.

Ursus eremus: Ramesch-Knochenhöhle (locus typicus), Ochsenhalthöhle, Pocala, Salzofenhöhle, Schreiberwandhöhle, Schwabenreith-Höhle.

Ursus ladinicus: Conturineshöhle (typical fauna), Brieglersberghöhle, Grotte Merveilleuse, Sulzfluh-Höhle

Ursus spelaeus: Zoolithenhöhle (locus typicus), Erpfingen, Weinberghöhle bei Mauern

s. Döppes & Rabeder (1997), Hofreiter *et al.* (2004), Pacher *et al.* (2004), Rabeder (1989; 1999; 2005), Rabeder & *et al.* (2004,) Rabeder & Hofreiter (2004).

RESULTS

1. **Radiometric datings (tab. 1)**

Interpretation: Taphonomic studies during the excavations showed that the fossil remains of ursids, hyaenids and felids were on secondary deposits in all parts of the cave. This is concluded from the alignment of limb bones and fragments and from the sediments, which contains allochthon elements, like crystalline debris (especially in site LAC Ib). The extensive presence of Ca-Mg rich primary and secondary minerals (clinozoisite, tremolite, talc, chlorite, chlorite/vermiculite) in the fine-grained sediments of the cave floor indicates the composition of the parent rocks of the broader drainage basin, which have been weathered (Tsirambides, 1998). Large mammals in original deposit have not been found up to now anywhere in the present preserved parts of the cave (except for an almost complete right anterior paw of a juve-

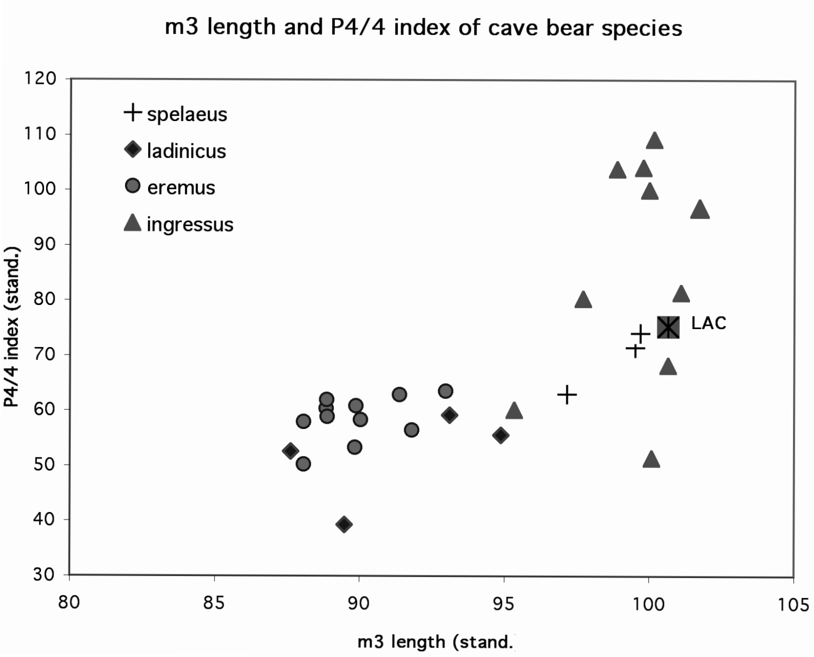

Figure 2. Comparison of means and index values of typical members of cave bear group in Europe.

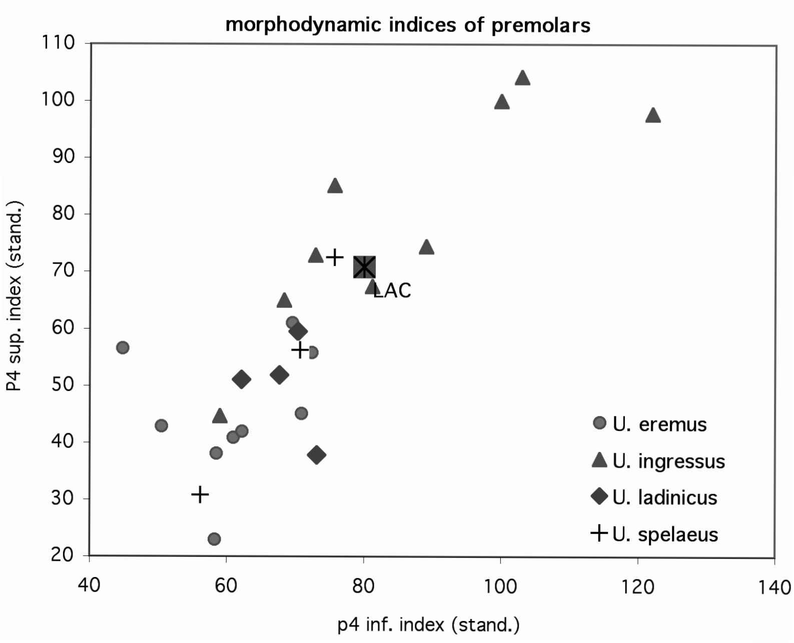

Figure 3. Comparison of index values of 4th premolars of typical members of the cave bears in Europe.

nile found *in situ,* in B10 square, in the second chamber LAC II). The fossils originate from other places or cavities. Between 34.000 and 32.000 B.P. they were moved from those places, where the cave bears bones were initially deposited, to their present sites. This removal was caused by floodwater, which invaded the cave and brought also a large amount of rubble. After this event the deposit of mountain milk was continued.

2. **Measuring teeth**: The means of the teeth length show that the bears of Loutrá Aridéas cave were as large

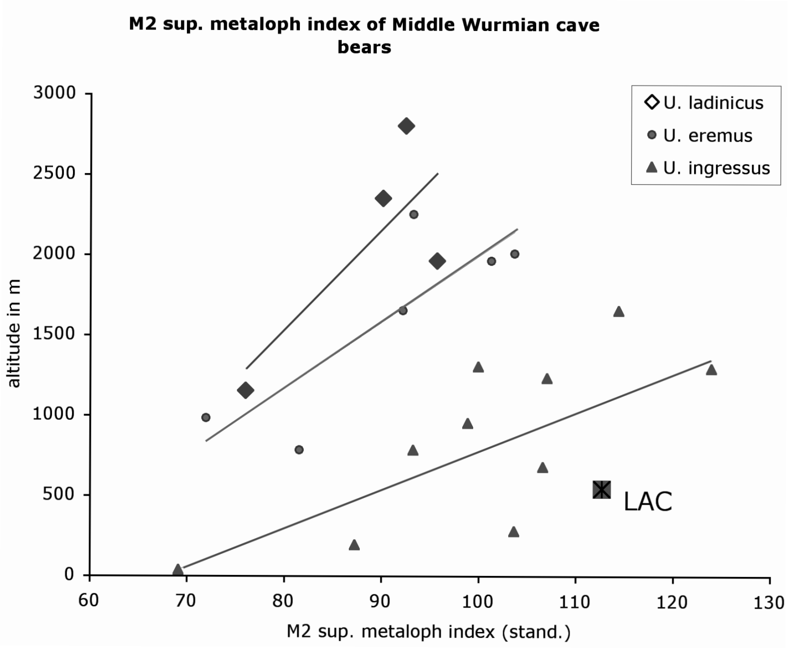

Figure 4. The relation between morphodynamic index values and altitudes of cave entrances.

as the bears from Gamssulzenhöhle and therefore a good deal bigger than *Ursus eremus* and *Ursus ladinicus* from the Alps. Representatives of the typical *Ursus spelaeus* from caves in Germany also reach these dimensions (as example m3 length, fig. 2). This points out that it is not possible to make a classification only by dimension.

3. **Morphodynamic indices** of premolars and molars (s. RABEDER, 1999).

The morphodynamic indices of premolars show that the bears from Loutrá Aridéas have much higher values then *U. eremus* and *U. ladinicus*, so these species are not represented in the cave, but there is an overlap (fig. 2 and 3) with the highly developed *Ursus spelaeus* (such as from Guloloch in Zoolithenhöhle and Bärenhöhle in Erpfingen), for other morphodynamic indices no data exists for *Ursus spelaeus*. The index values of the three cave bear species from the Alps show a dependence on the altitude of the cave. The higher the cave is situated, the higher are the index values. This is most obviously in *U. ingressus* and less in *U. ladinicus* (fig. 4).

The values of the bears from Loutrá Aridéas point to *U. ingressus*. This also applies to the enthypoconid index of m2 inf.

The occurrence of *Ursus spelaeus* in Eastern Europe is not verified through DNA analysis, but *Ursus ingressus* was found in many cases, so we can assume that the bears from Loutrá Aridéas belong to the species *Ursus ingressus*.

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THE SEDIMENTOLOGY OF THE BEAR CAVE OF ALMOPIA SPELEOPARK (PELLA, MACEDONIA, GREECE)

Ananias TSIRAMBIDES[1]

Abstract: The small grain size of the clastic sediments in the floor of Bear Cave is evidence of slow water flow in the deposition site, which is the result of the increase of water mass surface flowing inside the cave, as well as of probable climate change from wet to dry. The filling of floor cavities with claysilt material indicates that these holes were formed before the deposition of fluvial-terrestrial sediments from the adjacent area during Pleistocene. The extended presence of Ca-Mg rich primary and secondary minerals (clinozoisite, tremolite, talc, chlorite, chlorite/vermiculite) in the fine-grained sediments of the cave floor is indicative of the composition of the parent rocks of the broader drainage basin, which have been weathered. The absence of the discrete minerals smectite and kaolinite from the examined sediments means there was action of weathering factors of limited time duration, as well as small distance of transportation from the adjacent environment to the interior of the cave.

Key words: Climate, claysilt, Ca-Mg minerals, Bear Cave, Macedonia, Greece, Pleistocene.

INTRODUCTION

The sediments found in the floor cavities of karstic caves, present important evidence of their evolution in relation to the broader area of their occurrence. The creation of these cavities is the result of karstic weathering of carbonate rocks from meteoric waters flowing downwards along faults, fissures and bed surfaces. The genesis of cavities is always followed by deposition of clastic and chemical sediments under different conditions. Vavliakis *et al.* (1995) studying the grain size distribution and the mineralogical composition of the sediments from floor cavities of the Eptamyloi Cave (Serres), found that they are influenced greatly by the increase or decrease of the water flow rate at the deposition site. The examined Bear Cave is located at an elevation of 540 m and has an area of about 875 m^2 (Apostolou *et al.*, 1995).

In this work the conditions and the environment under which the sediments of the floor cavities were formed, using granulometric and mineralogical analyses, are studied.

GEOLOGICAL SETTING

The broader area of the Bear Cave which is flowed through by streams, consists of a great variety of lithological formations such as limestones, dolomites, marbles, schists (chloritic, epidotitic, sericitic), phyllites, flysch, ophiolites, as well as clastic sediments with various granulometric and mineralogical composition (Tsirambides, 1998).

MATERIALS AND METHODS

A thin section of one sample from the Cave floor crust was prepared for optical examination. Another four samples were collected from different depths of a floor site (D) and were analyzed in detail using petrographic and X-ray diffraction (XRD) techniques. Prior to mineralogical analysis samples were dried overnight in an oven at about 65°C and then were disaggregated by use of an agate mortar and pestle. Disaggregation was done gently in order to retain, to the extent possible, the intrinsic grain sizes of the samples. A 20 g split of the <2 mm fraction of each sample was subjected to the following chemical treatments (Jackson, 1979) to remove the non-silicate phases: 1N sodium acetate-acetic acid buffer solution (pH = 5.0) for carbonate removal; 30% H_2O_2 for organic matter and Mn- oxides removal; and 0.3M sodium citrate-1M $NaHCO_3$ buffer solution (pH = 7.3), to which 4 g of $Na_2S_2O_4$ were added during digestion in a water-bath

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Table 1
Depth (cm) from the cave floor and grain size distribution (wt.%) of the samples analyzed.

Sample	Depth	C.O.I.[1]	>20 μm	20-2 μm	<2 μm
D_1	70-83	36	30	11	23
D_2	83-86	21	46	12	21
D_3	93-104	15	29	17	39
D_4	117-122	19	56	14	11

[1] Total percentage of undesirable materials [Carbonates + Organics + Fe oxides + (Fe + Al hydroxides)].

Table 2
Mineralogical composition of separated size fractions (μm) of the samples analyzed.

Sample	Size	Q	F	M	Tr	Clz	Ch	T	C	D
D_1	whole	E	X	E	X	E	E	E	E	E
	20-2	X	X	E	X	X	E	E	-	-
	<2	-	-	E	X	-	E	E	-	-
D_2	whole	E	E	E	X	E	E	X	X	X
	20-2	E	E	E	E	X	E	E	-	-
	<2	-	-	E	X	-	E	E	-	-
D_3	whole	Y	X	E	X	E	E	X	E	E
	20-2	E	X	E	E	X	E	E	-	-
	<2	-	-	E	E	-	E	E	-	-
D_4	whole	E	X	E	X	X	X	X	Y	X
	20-2	E	E	X	E	X	E	E	-	-
	<2	-	-	E	E	-	E	E	-	-

Y: >40%, E: 40-10%, X: <10%.
Q=quartz, F=feldspars, M=mica (illite in <2 μm), Tr=tremolite, Clz=clinozoisite, Ch=chlorite (+ vermiculite + interstratified chlorite/vermiculite), T=talc, C=calcite, D=dolomite.

at 75-80°C, to remove free Fe-oxides and interlayer Fe- and Al-hydroxides.

The cleaned residues were separated into three size fractions (>20 μm, 20-2 μm and <2 μm) by gravity settling and centrifugation and were dried overnight in an oven at about 65°C. X-ray diffraction was performed using a Philips diffractometer with Ni-filtered CuK_α radiation. Both randomly oriented samples and samples with preferred orientation were scanned over the interval 3° to 43° 2θ at a scanning speed of 1° per minute. Some samples were re-analyzed after overnight glycolation. Semi-quantitative estimation of the amounts of minerals present is based on peak heights and intensity factors on XRD patterns of randomly oriented powder samples, using the method of Klug & Alexander (1974). XRD patterns taken from preferentially oriented and glycolated samples were used for the semi-quantitative estimation of clay mineral phases using specific reflections and intensity factors (Moore & Reynolds, 1997).

RESULTS

The microscopic study of thin sections of the cave floor crusts revealed that they consist of elongated calcite crystals with radial arrangement and size up to 1 mm. In the rest mass sparitic calcite crystals predominate (size up to 0.2 mm), as well as many micritic calcite crystals (size smaller than 4 μm). Noteworthy is the presence of dolomite crystals, too.

Among the non carbonate minerals and in small percentages, angular crystals of quartz, needle crystals of muscovite (length <0.2 mm) and fine aggregates of metallic minerals, predominate. The last give in some crust horizons a red brown tint.

The total percentage of the undesirable materials is significant (tab. 1) as expected for a cave environment. The carbonate salts, organic matter, Fe oxides and Fe and Al hydroxides are abundant, because of the easy transportation and deposition with the rest fine grained constituents.

The most important non carbonate minerals in the untreated whole samples are (tab. 2): quartz, sericite, clinozoisite and chlorite (+vermiculite + interstratified chlorite/vermiculite). Feldspars (especially plagioclases), tremolite and talc follow in abundance. Calcite is the predominant carbonate mineral with dolomite in second place. In the treated 20-2 μm and <2 μm fractions the clay minerals predominate (carbonate minerals have been dissolved and removed through repeated centrifugations).

CONCLUSIONS

The small grain size of the clastic sediments in the floor of the Bear Cave is evidence of slow water flow in the deposition site, which is the result of the increase of water mass surface flowing inside the cave, as well as of probable climate change from wet to dry.

The filling of the floor cavities with claysilt material indicates that these holes were formed before the deposition of the fluvial - terrestrial Pleistocene sediments transported from the adjacent area. The great consolidation they present is secondary and is due to the deposition of cement material (calcite) during or after the deposition of this material.

The high participation of carbonate salts, organic matter, Fe oxides and Fe and Al hydroxides in the floor sediments indicates an environment of low oxidation potential (Eh) during the processes of weathering, transportation and deposition.

Usually the dark coloured horizons consist of fine grains (they contain mainly clay minerals and organic matter) and represent periods of high humidity. The light coloured horizons consist of coarser grains and represent periods of extended dryness.

The extended presence of Ca-Mg rich primary and secondary minerals (clinozoisite, tremolite, talc, chlorite, chlorite/vermiculite) in the fine-grained sediments of the cave floor is indicative of the composition of the parent rocks of the broader drainage basin, which have been weathered.

The predominance of Mg-chlorite over Fe-chlorite is confirmed from the higher peaks of odd order reflections of this mineral in the XRD patterns taken.

The absence of the discrete minerals smectite and kaolinite from the examined sediments means action of weathering factors of limited time duration, as well as small distance of transportation from the adjacent environment to the interior of the cave.

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SECOND PART

THE CONTRIBUTIONS

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MORPHOMETRICAL VARIABILITY OF CHEEK TEETH IN CAVE BEARS

Gennady BARYSHNIKOV[1]

Abstract: As a result of the morphometric study, tooth samples examined in 17 sites of Western and Eastern Europe and the Caucasus were distributed into two groups. The first group is formed by teeth from localities of the Middle Pleistocene and from the Late Pleistocene layers 3-4 of Kudaro 3 Cave, which were identified as *Ursus deningeri*. The second group united specimens from the Late Pleistocene localities attributed to *U. spelaeus*. The sample from Furtins Cave in France was shown to occupy a transitional position. The teeth from Bacton Forest Bed in England and from Kizel Cave in the Ural Mountains resemble those in the first group, revealing, nevertheless, some difference; despite the produced analysis allows no confidence in the establishment of their species attribution, these may be tentatively referred to *U. savini*.

Key words: Cave bear, *Ursus,* teeth, variability, Pleistocene.

INTRODUCTION

It is generally known that cheek teeth provide reliable characters for the purposes of diagnostics and taxonomy of Ursidae. The study of the tooth morphometry and morphology has usually led to dividing cave bears into 2 species: *Ursus deningeri* VON REICHENAU and *U. spelaeus* ROSENMÜLLER (Kurtén, 1968; Rabeder, 1999). Other studies of the dental characters, on the contrary, suggest uniting the cave bears into a single species, *U. spelaeus* (Grandal d'Anglade & López-Gonzáles, 2004).

In the cave bears, cheek teeth demonstrate progressive modification of the occlusal surface during the Pleistocene, the temps of such changes growing toward the finish of this epoch (Rabeder & Tsoukala, 1990; Rabeder, 1999). It has been also revealed that the sites of equal age were geographically grouped with regards to the cave bear dental measurements; this phenomenon may be explained by regional peculiarities in the bear diet (Baryshnikov *et al.,* 2003).

The aim of the present study is to give morphometrical analysis of the tooth samples from the European and Caucasian sites of different geological ages and geographical positions in order to elucidate stratigraphic and geographic variability of teeth in the cave bears.

MATERIAL AND METHODS

The work embraces tooth collection from 17 sites of the Western and Eastern Europe and the Caucasus, which are dated at the Middle and Late Pleistocene.

The Middle Pleistocene sites are Westbury-sub-Mendip Fissure in England, Jagsthausen Cave, Mosbach (terra typica for *U. deningeri*) and Einhorn Cave in Germany, Kudaro 1 Cave (layer 5) in Georgia. The examined collection from Einhorn comes from the early excavations having no stratigraphic division; however, later excavations have exhibited the presence of several stratigraphic levels in the cave, with the oldest one dated more that 100 thousands years (Nielbock, 1987).

The Late Pleistocene sites comprise Eiros in Spain, Arcy-sur-Cure in France, Zoolithen Cave (terra typica for *U. spelaeus*) and Rübeland in Germany, Nietoperzowa Cave in Poland, Odessa in Ukraine, Kudaro 3 Cave (layer 3-4) in Georgia, Secrets Cave and Medvezhiya Cave in Russia (the Ural Mountains) (fig. 1). Their geological dates correspond to the time of the late glacial. In Arcy-sur-Cure, the teeth originating from the layers of the Middle and Late Paleolithic reveal no reliable difference in size (Baryshnikov & David, 2000), being, therefore, examined together.

The age of deposits in the Furtins Cave in France is somewhat elder. It is estimated as beginning of the Late

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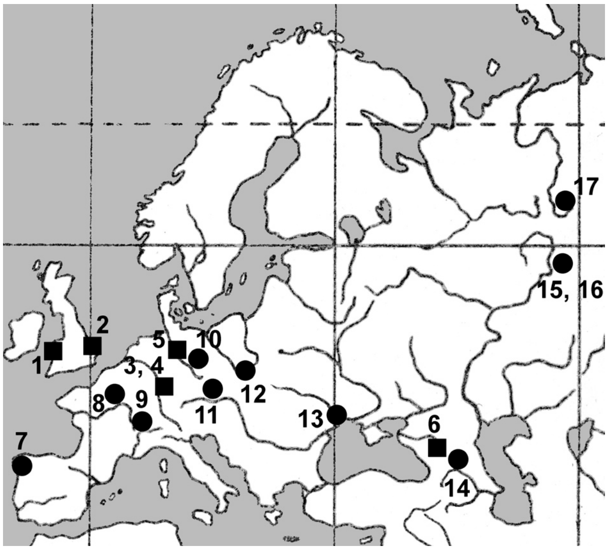

Figure 1. Distribution of examined localities from the Middle Pleistocene (quadrate) and Late Pleistocene (circle). 1 - Wesrtbury; 2 - Bacton Forest Bed; 3 - Jagsthausen; 4 - Mosbach; 5 - Einhorn Cave; 6 - Kudaro 1 Cave; 7 - Eiros; 8 - Arcy-sur-Cure; 9 - Furtins Cave; 10 - Rübeland; 11 - Zoolithen Cave; 12 - Nietoperzowa Cave; 13 - Odessa; 14 - Kudaro 3 Cave; 15 - Kizel Cave; 16 - Secrets Cave; 17 - Medvezhiya Cave.

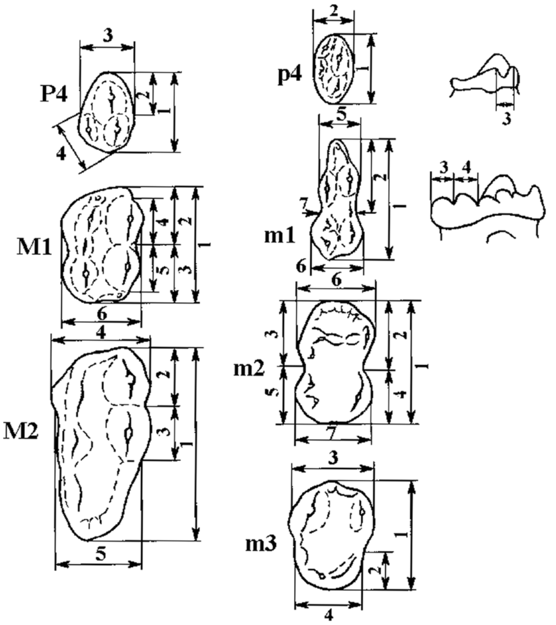

Figure 2. Scheme of measurements of upper (P4-M2) and lower (P4-m3) cheek teeth. Designations of measurements are shown in tab. 1-14.

Pleistocene (late interglacial or early late glacial) (Argant, 1991).

In addition, two small tooth collections have been examined. One of them originates from Bacton Forest Bed in England, which is dated at the early Middle Pleistocene (Sutcliffe, Kowalski, 1976). This collection represents the type material of *U. savini* (Andrews, 1922) whose status of being a separate species is not always accepted (Kurtén, 1968). The other one was collected in the Late Pleistocene sediments of Kizel Cave in the Ural Mountains (Russia). This material was described as *U. uralensis* Vereshchagin, but later the taxon has been referred to *U. rossicus* BORISSIAK as a subspecies (Vereshchagin & Baryshnikov, 2000).

Since the examined samples predominantly consisted of the isolated teeth, their comparison was carried out separately for each cheek tooth. The specimens, which are retained in the jaws, were also used. In total, more than 1750 upper teeth and more than 2350 lower teeth have been measured.

Each sample (with rare exceptions) includes as many as 10 specimens. Teeth were measured by calipers with accuracy 0.05 mm according to the scheme given in fig. 2. The metric data are summarized in tables 1-14.

For processing the obtained data, the Dicriminant Analysis and Cluster Analysis from STATISTICA 6.0 were used. The examined samples were classified basing on the means of the standardized variables. In the Discriminat Analysis, the forward stepwise method was applied. The dendrograms of similarity were built according to Squared Mahalanobis Distances.

RESULTS

Sexual dimorphism. For the analysis, the cheek teeth were not sexed, as sexual dimorphism in the tooth size of cave bears seems to be weakly developed (Kurtén, 1955). At the same time, morphometric study of teeth in the recent brown bear (*U. arctos* L.) from Hokkaido Island revealed that males and females differ in the upper (P4) and lower (m1) average carnassial length (Baryshnikov *et al.*, 2005).

In order to elucidate whether sexual dimorphism in the cave bears is pronounced in the size of cheek teeth, the upper and lower jaws where cheek teeth were associated with the upper or lower canine were used, since males of cave bears are differ reliably from females in the canine width (Kurtén, 1955).

In the material from Mosbach, the upper canine width was 20.5-17.3 mm in males (n=8) and 16.7-13.3 mm in females (n=10); whereas the lower canine width varied from 18.9-16.7 mm in males (n=5) to 16.0-13.9 mm in females (n=7). In the material from Zoolithen, these dimensions were correspondingly 25.5-20.5 mm (n=6) and 17.9-15.4 mm (n=11) for the upper canine and 23.7-18.7 mm (n=11) and 17.2-14.6 mm (n=17) for the lower canine. These measurements reflect that *U. spelaeus* possessed more robust canines in comparison with *U. deningeri*, the sexual dimorphism in the canine size in *U. spelaeus* being more developed, as Kurtén (1969) noted.

After the material has been examined on sexing, it was found out that in the sample from Mosbach the length of the upper tooth row P4-M2 represents 80.4-101.5, M=89.65 mm (n=6) in males and 79.6-89.7, M=83.87 mm (n=12) in females; whereas in the sample from Zoolithen it is measured as 89.7-101.5, M=96.70 mm (n=10) in males and 82.5-91.2, M=87.15 mm (n=22) in females. The length of the lower tooth row p4-m3 from Mosbach represents 97.0-106.8, M=100.71 mm (n=7) in males and 86.0-98.7, M=92.21 mm (n=8) in females; in the sample from Zoolithen it is 98.6-110.5, M=103.95 mm (n=11) in males and 92.9-99.8, M=96.84 mm (n=10) in females. In the both sites, in the means of length of the tooth row males were larger than females, though in the overlapping of the sample extremes occurred. Therefore, unsexed tooth samples may demonstrate difference in the average size with regard of the ratio of male and female teeth, as has been already hypothesized (Grandal d'Anglade, 2001; Baryshnikov *et al.*, 2003).

Size. The comparison of the samples, which have been sexed by the length of the upper teeth P4-M2 and lower teeth p4-m3, revealed that both the males and females from the Middle Pleistocene on average demonstrate longer tooth rows than those from the Late Pleistocene, i.e. the Late Pleistocene cave bears possessed more robust teeth than the Middle Pleistocene bears. At the same time, in the length of P4-M2 (88.4-95.5, M=90.72 mm, n=5) and the length of p4-m3 (98.1-103.4, M=101.07 mm, n=6), males from the Late Pleistocene site of Kudaro 3 (layers 3-4) in Caucasus resemble males from the Middle Pleistocene site of Mosbach in Europe.

It should be, however, noted that in the material from Kizel Cave, where males were not separated from females, the length of P4-M2 (74.0-82.0, M=77.29 mm, n=8) and that of p4-m3 (85.9-91.6, M=88.23 mm, n=6) were markedly smaller than those dimensions even in the females from the Middle Pleistocene sites. Similar dimensions were recorded in the unsexed sample from Bacton (76.4, 81.5 mm, n=2 and 78.3-91.3, M=87.09 mm, n=7, correspondingly).

Relative size. I failed to find any reliable difference between relative length of the cheek teeth in the cave bears from the Middle and Late Pleistocene.

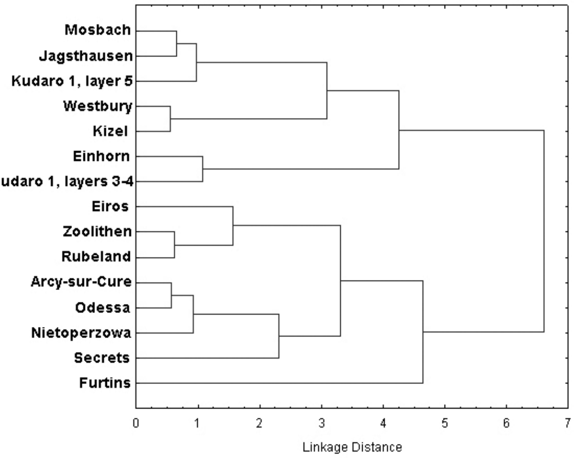

Figure 3. Hierarchical tree plot for P4 of cave bear.

In the upper tooth row P4-M2, the length of each tooth constitutes: 21.2-21.9% (P4), 29.4-30.7% (M1) and 47.8-49.6% (M2). The sample of *U. savini* from Bacton represents an exception, demonstrating robust upper carnassial tooth P4 (22.8%) and small last lower molar m3 (45.2%). By these indices, *U. savini* seems to be more archaic as compared not only to other cave bears examined from the Middle and Late Pleistocene, but even in comparison with *U. rodei* from the locality of Untermassfeld in Germany, which is dated by the late Early Pleistocene (Musil, 2001).

In the lower tooth row p4-m3, each tooth occupies 14.6-15.9% (p4), 28.5-29.7% (m1), 29.2-30.2% (m2) and 25.6-26.5% (m3) of the tooth row total length. Similar proportion has been found in the cave bear from Kizel Cave (15.1-28.8-29.7-26.3%) as well as in *U. rodei* from Untermassfeld (15.5-29.4-30.3-24.8%), despite that the latter species possesses shorter m3 (Musil, 2001). On the contrary, the sample from Bacton (16.1-28.8-28.2-26.9%) is characterized by the combination of primitive characters (robust p4, m1 longer than m2) with derivative one (enlarged m3).

Variability of the upper cheek teeth. In the measurements of the upper carnassial tooth P4, the examined samples were united into two groups predominantly divided by the paracone length (fig. 3). The first group incorporates all the specimens from the Middle Pleistocene as well as from Kudaro 3 and Kizel Cave. The teeth from localities of Kudaro 3 and Einhorn occupied the isolated position within this group, characterizing in the pronounced distance between the anterior margin of protocone and posterior margin of the tooth crown. The second group comprises the samples from the Late Pleistocene localities, including Furtins. The material from

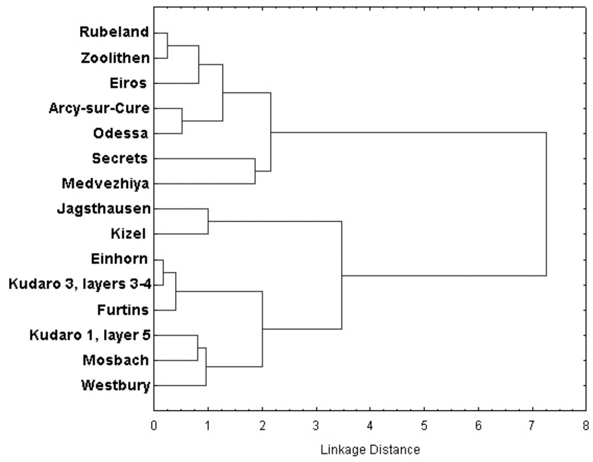

Figure 4. Hierarchical tree plot for M1 of cave bear.

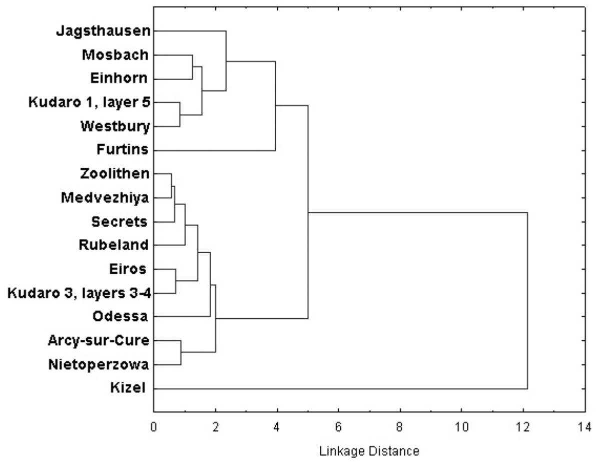

Figure 5. Hierarchical tree plot for M2 of cave bear.

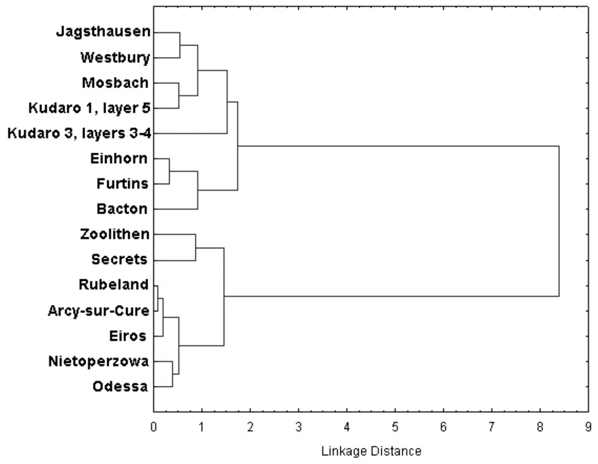

Figure 6. Hierarchical tree plot for p4 of cave bear.

the latter locality forms an isolated subgroup, since P4 from Furtins demonstrate marked shift of the protocone backwards.

The morphometric analysis of the first upper molar M1 has grouped all Middle Pleistocene samples together with teeth from Kudaro 3, Furtins and Kizel Cave (fig. 4). M1 from Kizel Cave and Jagsthausen are similar to each other in the greatest width of the tooth crown. The second group is formed by remaining samples from the Late Pleistocene localities. Both groups are diverged in the greatest length M1 and the length of the posterior portion of its crown.

In the measurements of the second upper molar M2, the analyzed samples form three groups (fig. 5). The first group contains teeth from the Middle Pleistocene sites and Furtins. The second one consists of the samples from the localities of the Late Pleistocene, including Kudaro 3. Both groups are divided due to the anterior width and posterior width of the tooth. The third group is formed by the teeth from Kizel Cave, which possess shortened metacone.

Variability of the lower cheek teeth. The analysis of measurements of the forth lower premolar p4 provided distribution of the samples examined into two groups, within each of which no reliable difference has been established between teeth from various localities (fig. 6). The first group incorporates samples from the Middle Pleistocene localities as well as from Furtins and Kudaro 3. The second group unites remaining Late Pleistocene samples. The difference between groups is pronounced in the greatest width of p4. The analyzed teeth from Bacton Forest Bed can be grouped together with those from the Middle Pleistocene sites.

The examined samples of the lower carnassial tooth m1 (with the exception of measurements 3 and 4) similarly form two groups diverging in the tooth greatest length (fig. 7). The first group unites the samples from the Middle Pleistocene localities as well as Bacton, Kizel Cave, Kudaro 3 and Furtins. Within this group, the isolating position is revealed for the samples from the localities of younger geological age (Einhorn, Furtins), and Kudaro 1, where teeth are larger and comparatively more narrow across trigonid. The second group comprises samples from other Late Pleistocene sites, which show no noticeable difference.

The analysis of measurements of the second lower molar m2 has demonstrated somewhat different distribution of the samples. These are united into three groups, diverging in the greatest length m2 and width of its trigonid. The first group consists of the teeth from the localities of the Middle Pleistocene and specimens from Kizel Cave and Kudaro 3 as well as teeth from Zoolithen and Medvezhiya Cave that is unusual (fig. 8). Within this group, the teeth from Kizel Cave form an isolated subgroup which is distinguished by the greatest length and lingual length of talonid. The second group involves all remaining samples from the Late Pleistocene sites. Lastly, the third group consists of the teeth from Bacton, which are, on the average, smallest.

The samples of the third lower molar m3 are split into two groups according to the length and width of talonid, differences between groups being inconspicuous (fig. 9). The first group contains specimens from the localities of the Middle Pleistocene, including Bacton and Kudaro 3 as well as Medvezhiya Cave. The second group involves specimens from other localities of the Late Pleistocene, including Furtins.

DISCUSSION

As a result of the analysis, a clear tendency in the time distribution of the examined samples was revealed, which is observed for each cheek tooth. The samples form two well-isolated clusters. The first cluster contains samples from the Middle Pleistocene sites, whereas the second one consists of specimens from the Late Pleistocene sites. However several samples do not fall into groups that correspond to their geological age.

Within the Middle Pleistocene group, the specimens from Jagsthausen and Mosbach are grouped together. According to the P4/p4-index, the sample from Jagsthausen seems to be the most archaic in Europe (Rabeder & Tsoukala, 1990). This is according to the shape of the lower carnassial tooth m1 whose entoconid looks like large, inconspicuously divided cusp (fig. 10). The most distanced from this cluster is the sample from Einhorn, which is, in several cases, united with the samples of a later geological age (with Kudaro 3 for P4 and Furtins for p4 and m1).

The sample from layers 3-4 of Kudaro 3 is most often placed by the morphometric analysis within the Middle Pleistocene group, in spite of these cave layers dated by the Late Pleistocene. Only by the metric characteristics of M2 does this site belong to the second group. This result is consistent with the opinion on the preservation of the archaic dentition in the Caucasian cave bears as late as almost the finish of the Pleistocene (Baryshnikov, 1998). The entoconid portion of the lower carnassial tooth m1 from layers 3-4 in Kudaro 3 is divided into three cusps successively becoming higher posteriorly, as in *U. deningeri* (fig. 11, *3-5*).

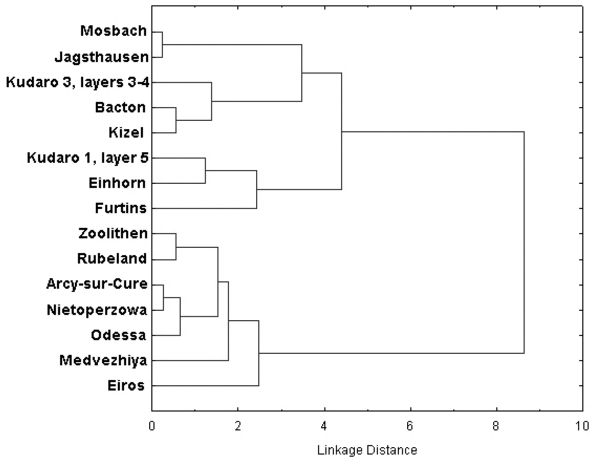

Figure 7. Hierarchical tree plot for m1 of cave bear.

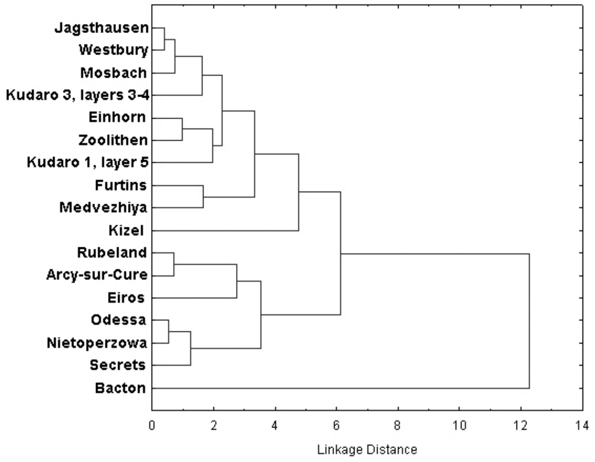

Figure 8. Hierarchical tree plot for m2 of cave bear.

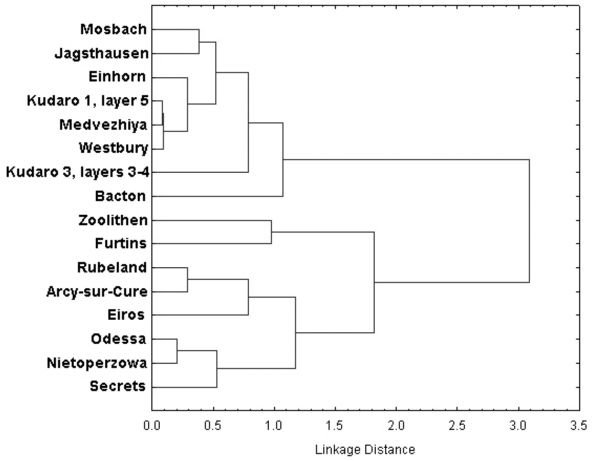

Figure 9. Hierarchical tree plot for m3 of cave bear.

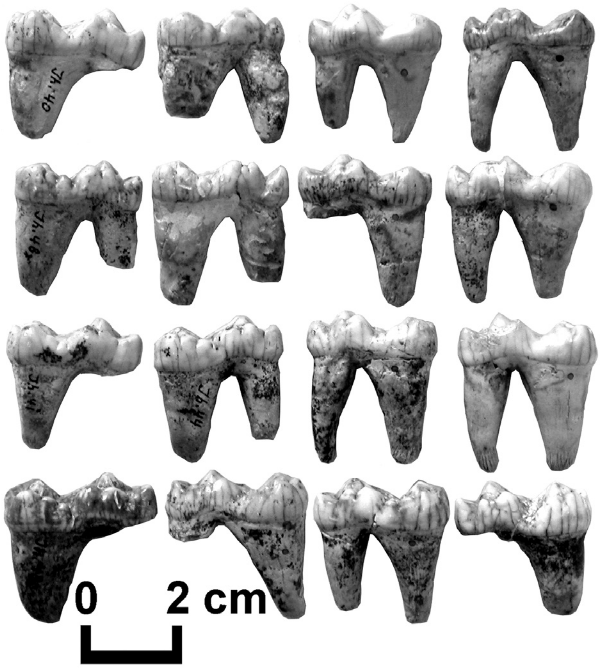

Figure 10. *Ursus deningeri*, lower carnassial tooth m1 from Jagsthausen (SMNS 31101, Staatlichen Museum für Naturkunde, Stuttgart). Lingual view.

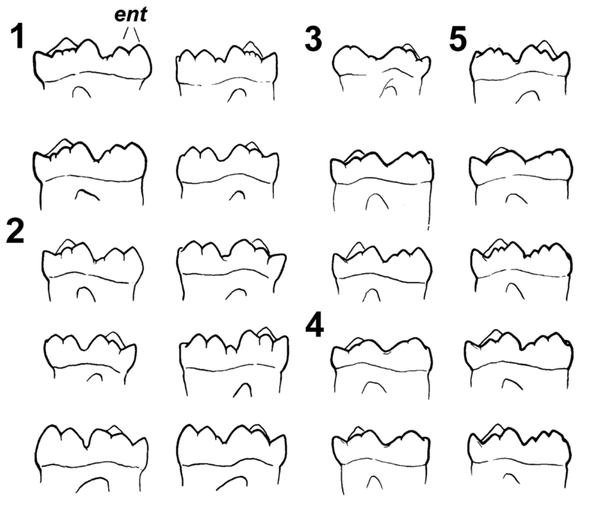

Figure 11. Structure of entoconid (*ent*) of lower carnassial tooth m1 of *Ursus spelaeus* (1, 2) and *U. deningeri* (3-5) (coll. Zoological Institute, Russian Academy of Sciences, St. Petersburg; ZIN). 1 - Medvezhiya Cave; 2 - Odessa; 3 - Kudaro 3 Cave, layer 3; 4 - Kudaro 3 Cave, layer 4 (horizons 1-4); 5 - Kudaro 3 Cave, layer 4 (horizons 5-6).

Within the second group, which is formed by the samples from localities of the Late Pleistocene, no units associated with the age or geographic position of the sites were revealed. It should be mentioned that in the characters of several teeth the samples from the Ural Mountains (Secrets Cave and Medvezhiya Cave, by measurements of M1) as well as the samples from Germany (Zoolithen and Rübeland, by measurements of P4, M1 and m1) form distinct groups; however, all these sites are closely placed according to M2 dimensions. The specimens from Medvezhiya Cave and Odessa possess entoconid of m1 consisting of two distanced cusps that is typical of *U. spelaeus* (fig. 11, *1-2*).

The sample from Furtins Cave either falls into the Middle Pleistocene teeth (on the basis of metric characters of M1, M2, p4 and m1) or groups together with the Late Pleistocene teeth (by measurements of P4, m2 and m3). Such variability indicates a transitional position of this sample and agrees with the geological age of the cave. The dental morphometry in specimens from Furtins indicates the transition from the Middle Pleistocene cave bears to the Late Pleistocene animals.

Two other Late Pleistocene samples, by measurements of m2 (Zoolithen, Medvezhiya) and m3 (Medvezhiya), are associated with the Middle Pleistocene group, whereas the Middle Pleistocene sample (Kudaro 1) by metric characters of m2 is placed within specimens from the localities of the Late Pleistocene. The obtained data disagree with the age of the localities as well as with dimensions of other teeth. This contradiction may be explained by the inaccuracy in the teeth measuring or tooth composition in a sample (the ratio between the isolated teeth and teeth fixed in jaws, presence of the tooth crowns without roots belonging to young bears, etc.).

The average values of measurements markedly vary in the different samples, which is obviously substantiated by the ratio between male and female teeth within each sample. The lower means of tooth dimensions in Secrets Cave and Medvezhiya Cave implies the predominance of females, whereas higher means of tooth measurements in Arcy-sur-Cure indicate prevalence of male teeth.

In the average, the teeth from Kudaro 1 (layer 5) are found to be smaller than those from Kudaro 3, the first site containing, however, the largest individual specimens. Most likely, predominantly males perished in Kudaro 3, whereas mainly females died in Kudaro 1. This hypothesis is confirmed by findings of numerous milk teeth in layer 5 of Kudaro 1 (Baryshnikov, 1999). Therefore this cave was used by bears as a den.

In spite of the predominance of male mortality being hypothesized for the Arcy-sur-Cure site, numerous milk teeth have been found there (Baryshnikov & David, 2000). Most probably, in different times of bears exploiting this cave, it was a winter shelter of males or den for females with cubs. Similarly, it had been found that the Goyet site in Belgium that it was occupied by males in the colder stages of the Pleistocene and by females in the warmer stages (Germonpré, 2004).

Rather small samples of the cheek teeth from Bacton Forest Bed (*U. savini*) and Kizel Cave (*U. rossicus uralensis*) are distributed into the Middle Pleistocene group or, with regard to M2 for Kizel Cave and m2 for Bacton, form a distinct group. In the structure of lower carnassial tooth m1 whose entoconid is divided into two or, more seldom, three crowded cusps, the cave bear from Kizel Cave exhibits resemblance with *U. deningeri* (fig. 12). In the metric characteristics of m1, the samples from Bacton and Kizel Cave are distributed close to each other, occurring in the different groups by the measurements of m2. Therefore, the conducted analysis gives no clear reply to the degree of similarity of these samples. At the same time, these samples are well distanced from other groups.

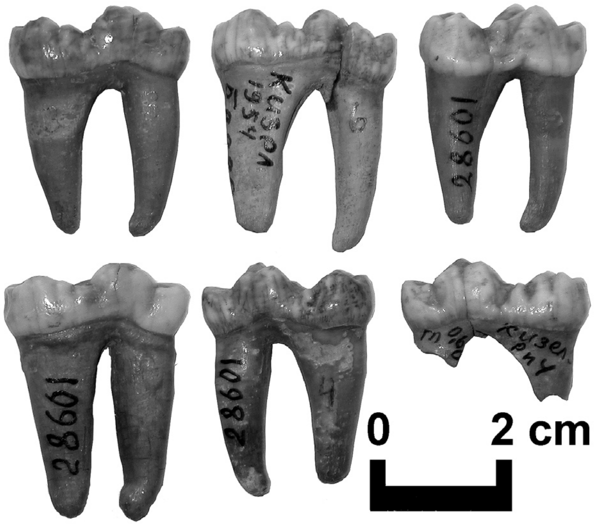

Figure 12. *Ursus savini uralensis*, lower carnassial tooth m1 from Kizel Cave (ZIN 28601). Lingual view.

CONCLUSION

Thus the peculiarities of grouping of the examined tooth samples resulting from the morphometric analysis substantiate the difference in the dentition between cave bears from the Middle and Late Pleistocene. A group of samples from Mosbach, Jagsthausen, Westbury, Einhorn, Kudaro 1 (layer 5), and Kudaro 3 (layers 3-4) belongs to *U. deningeri*, whereas other group (Zoolithen, Rübeland, Arcy-sur-Cure, Eiros, Nietoperzowa, Odessa, Secrets, Medvezhiya) is attributed to *U. spelaeus*. In addition, the sample with characters transitional between teeth of these species (Furtins) has been revealed.

U. spelaeus stratigraphically replaces *U. deningeri*, the boundary between these species roughly coinciding in Europe with the boundary between the Middle and Late Pleistocene, as has been already stated (Musil, 1981; Rabeder *et al.,* 2000; Petronio *et al.,* 2003). However, in the Caucasus, cave bears with the tooth characters similar to those in *U. deningeri* survived till the Late Pleistocene.

The systematic position of *U. savini* and *U. rossicus* remains unclear. Both species share a model of dental transformation (combination of the modified p4 and archaic m1) that is unusual for other cave bears. In addition, *U. rossicus* differs from *U. deningeri* and *U. spelaeus* by a smaller cranial size and structure of baculum (Vereshchagin & Baryshnikov, 2000). *U. savini* and *U. rossicus* are placed closely to each other in the phylogenetic scheme of the genus *Ursus* (Baryshnikov & Foronova, 2001), being, probably, a single species.

Meanwhile it should be noted that such an interpretation of the cave bear taxonomy is based mainly on the dental characters. No reliable cranial features distinguishing *U. deningeri* from *U. spelaeus* as well as from *U. savini/rossicus* is known. The smaller size of *U. rossicus* may be of adaptive nature (adaptation to steppe environmental conditions). It is not excluded that all cave bears could belong to a polytypical species, *U. spelaeus*, which is characterized in the pronounced stratigraphic and geographic variability.

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Table 1
Measurements (in mm) of upper premolar P4 of Middle Pleistocene cave bears.

Localities		Greatest length (1)	Length of paracone (2)	Greatest width (3)	Least distance between frontal ridge of protocone and caudal side of crown (4)
Jagsthausen	n	22	22	21	22
	min	16.6	10.4	10.8	12.2
	max	21.4	13.2	15.0	18.0
	M	18.32	11.35	12.49	14.09
	SD	1.13	0.70	0.99	1.40
Mosbach	n	37	37	36	36
	min	15.6	9.8	10.4	11.8
	max	21.6	14.9	15.4	17.2
	M	18.47	11.70	13.05	14.43
	SD	1.49	1.22	1.29	1.52
Westbury	n	48	48	48	48
	min	16.2	10.1	11.0	11.8
	max	21.4	14.5	15.7	17.6
	M	18.54	12.28	13.20	14.65
	SD	1.18	1.04	1.03	1.30
Kudaro 1, layer 5	n	77	77	80	80
	min	16.5	9.7	11.3	12.8
	max	23.7	14.8	16.9	18.8
	M	19.25	11.84	13.54	15.13
	SD	1.33	0.97	1.09	1.34
Einhorn	n	52	52	52	52
	min	17.0	10.4	11.4	12.8
	max	22.2	13.9	17.3	19.9
	M	19.12	12.04	14.10	15.66
	SD	1.23	0.84	1.09	1.40
Furtins	n	16	16	16	15
	min	16.8	10.4	11.1	11.2
	max	20.1	12.8	15.0	15.3
	M	18.74	11.67	13.47	13.25
	SD	1.10	0.72	0.91	1.04

Table 2
Measurements (in mm) of upper premolar P4 of Late Pleistocene cave bears.

Localities		Greatest length (1)	Length of paracone (2)	Greatest width (3)	Least distance between frontal ridge of protocone and caudal side of crown (4)
Zoolithen	n	62	62	62	62
	min	17.7	11.5	11.6	12.4
	max	22.1	14.7	15.8	17.4
	M	20.04	13.23	13.71	14.81
	SD	1.16	0.74	0.93	1.17
Rübeland	n	37	37	37	37
	min	16.7	10.2	12.4	13.3
	max	23.8	15.7	16.5	17.7
	M	20.25	13.20	14.28	15.35
	SD	1.49	1.07	0.93	1.10
Arcy-sur-Cure	n	31	31	31	31
	min	18.9	11.6	12.7	13.3
	max	23.4	15.3	16.9	17.3
	M	21.08	13.50	14.95	15.28
	SD	1.26	0.91	1.03	1.26
Eirós	n	17	17	17	17
	min	18.1	10.9	12.5	13.8
	max	21.8	14.2	16.0	17.9
	M	20.41	12.87	14.38	15.84
	SD	1.20	0.87	1.10	1.29
Nietoperzowa	n	30	30	30	31
	min	18.1	12.0	12.6	12.2
	max	23.5	15.0	16.3	18.0
	M	20.83	13.45	14.31	14.89
	SD	1.43	0.98	0.98	1.38
Odessa	n	50	50	50	50
	min	18.2	10.3	12.8	9.9
	max	24.0	16.4	17.1	18.5
	M	21.30	13.66	14.83	14.80
	SD	1.49	1.18	1.07	1.64
Secrets Cave	n	19	19	19	18
	min	17.3	10.7	12.0	10.3
	max	22.7	14.8	17.6	16.3
	M	19.70	13.01	14.09	13.84
	SD	1.60	1.10	1.62	1.84
Kudaro 3, layer 3-4	n	13	14	14	13
	min	17.2	10.0	12.5	13.8
	max	21.8	13.9	16.8	18.7
	M	19.47	12.19	14.80	16.09
	SD	1.47	1.05	1.21	1.47
Kizel	n	21	21	22	21
	min	15.5	10.0	10.9	11.1
	max	19.5	13.8	14.3	15.8
	M	17.82	11.95	12.55	13.71
	SD	1.13	0.93	0.83	1.11

Table 3
Measurements (in mm) of upper molar M1 of Middle Pleistocene cave bears.

Localities		Greatest length (1)	Length of frontal part (2)	Length of caudal part (3)	Length of paracone (4)	Length of metacone (5)	Greatest width (6)
Jagsthausen	n	14	14	14	14	14	14
	min	22.7	11.1	10.9	7.9	7.6	15.4
	max	27.2	13.3	13.7	10.5	10.4	20.0
	M	24.91	12.19	12.43	9.22	8.52	17.30
	SD	1.01	0.60	0.84	0.75	0.77	1.13
Mosbach	n	47	47	47	47	47	47
	min	21.2	9.7	10.5	7.7	6.9	15.4
	max	28.9	13.7	14.9	11.3	10.4	22.3
	M	23.38	12.04	12.90	9.20	8.74	18.35
	SD	1.89	0.89	1.08	0.83	0.86	1.46
Westbury	n	34	34	34	34	34	34
	min	23.7	11.0	11.6	7.5	7.5	16.6
	max	28.4	15.4	15.1	10.4	11.1	21.0
	M	25.70	12.43	13.38	9.27	9.00	18.85
	SD	1.19	0.84	0.90	0.58	0.76	1.08
Kudaro 1, layer 5	n	75	67	71	67	69	83
	min	22.2	10.5	10.9	8.1	7.5	16.8
	max	29.7	15.9	15.8	11.5	11.7	22.5
	M	26.02	12.61	13.36	9.75	8.77	18.91
	SD	1.53	0.80	0.94	0.69	0.76	1.27
Einhorn	n	55	55	55	55	55	55
	min	23.4	11.7	11.1	8.4	7.9	16.5
	max	29.6	14.7	15.3	11.7	10.5	22.3
	M	26.74	13.09	13.27	9.89	9.16	19.35
	SD	1.44	0.66	0.94	0.67	0.57	1.26
Furtins	n	38	38	38	38	38	38
	min	23.7	11.7	10.7	8.2	7.8	16.8
	max	31.5	15.2	15.7	11.5	12.0	21.5
	M	26.85	13.17	13.24	10.14	9.61	19.37
	SD	1.65	0.74	1.04	0.75	0.83	1.18

Table 4
Measurements (in mm) of upper molar M1 of Late Pleistocene cave bears.

Localities		Greatest length (1)	Length of frontal part (2)	Length of caudal part (3)	Length of paracone (4)	Length of metacone (5)	Greatest width (6)
Zoolithen	n	62	62	62	62	62	62
	min	25.3	11.6	12.7	8.3	8.0	18.1
	max	31.8	15.6	17.7	11.9	11.6	23.2
	M	28.61	13.75	14.63	10.51	9.59	19.74
	SD	1.45	0.82	1.04	0.76	0.71	1.14
Rübeland	n	45	45	45	45	45	45
	min	25.3	12.3	12.7	9.2	8.5	17.4
	max	32.4	15.4	16.9	11.7	11.0	23.0
	M	29.05	13.87	14.91	10.45	9.72	19.93
	SD	1.57	0.72	0.95	0.65	0.61	1.28
Arcy-sur-Cure	n	31	31	31	31	30	31
	min	24.9	11.5	13.1	8.6	8.5	18.3
	max	32.0	15.3	17.1	12.0	11.7	22.9
	M	29.09	13.79	15.22	10.63	10.17	20.38
	SD	1.89	0.93	1.28	0.84	0.78	1.38
Eirós	n	26	26	26	26	26	26
	min	26.0	12.0	13.1	9.0	8.6	16.9
	max	30.8	14.6	16.4	11.4	10.7	21.7
	M	28.43	13.56	14.72	10.06	9.58	19.85
	SD	1.32	0.69	0.86	0.53	0.57	1.23
Odessa	n	53	53	53	53	53	52
	min	27.6	13.1	13.9	9.9	9.2	18.5
	max	33.4	16.0	18.0	12.4	11.8	23.6
	M	29.82	14.14	15.59	11.08	10.37	20.83
	SD	1.35	0.69	0.91	0.60	0.50	1.11
Secrets Cave	n	20	20	20	20	20	20
	min	25.7	12.5	13.1	9.0	8.5	17.2
	max	30.7	14.9	17.4	11.5	11.4	22.1
	M	27.91	13.61	14.97	10.13	9.74	19.24
	SD	1.56	0.67	1.12	0.67	0.71	1.37
Medvezhiya Cave	n	22	22	22	22	22	22
	min	26.4	12.5	12.9	9.3	8.6	18.2
	max	32.6	17.5	17.7	11.4	10.7	22.0
	M	29.31	14.23	15.25	10.22	9.85	20.16
	SD	1.54	0.98	1.20	0.59	0.56	0.98
Kudaro 3, layer 3-4	n	20	20	19	18	17	20
	min	23.7	11.6	12.0	8.6	7.7	17.6
	max	28.5	13.9	14.9	10.7	10.1	21.1
	M	26.50	12.76	13.19	9.67	8.83	19.13
	SD	1.16	0.64	0.76	0.58	0.59	0.89
Kizel	n	29	27	28	27	28	29
	min	22.2	10.8	9.8	7.8	6.9	15.2
	max	29.0	12.7	13.8	9.4	10.0	19.4
	M	24.44	11.89	12.11	8.61	7.98	17.10
	SD	1.21	0.52	0.85	0.41	0.60	1.05

Table 5
Measurements (in mm) of upper molar M2 of Middle Pleistocene cave bears.

Localities		Greatest length (1)	Length of paracone (2)	Length of metacone (3)	Greatest width (4)	Width through hypocone (5)
Jagsthausen	n	11	11	11	11	11
	min	37.4	10.0	8.2	18.4	16.0
	max	46.1	14.3	11.9	22.6	19.9
	M	40.38	11.74	10.26	19.94	18.14
	SD	2.61	1.43	0.97	1.16	1.12
Mosbach	n	52	53	53	53	52
	min	35.2	9.2	7.4	18.0	15.3
	max	50.1	15.8	14.2	24.2	20.5
	M	40.81	12.08	10.57	20.84	17.88
	SD	3.03	1.31	1.40	1.39	1.24
Westbury	n	37	37	37	37	37
	min	35.1	9.3	8.0	19.0	16.4
	max	50.8	15.1	13.8	24.0	23.4
	M	43.42	12.20	11.03	21.32	19.04
	SD	3.44	1.45	1.42	1.30	1.53
Kudaro 1, layer 5	n	47	50	51	57	49
	min	37.7	10.3	7.0	19.3	15.4
	max	49.7	15.9	13.9	25.1	22.6
	M	43.49	12.88	11.44	21.84	18.83
	SD	2.54	1.13	1.40	1.30	1.41
Einhorn	n	54	54	54	54	54
	min	38.5	10.8	8.1	19.7	15.9
	max	49.1	15.8	14.2	24.1	21.8
	M	43.14	12.98	10.69	21.90	18.56
	SD	2.52	0.95	1.21	1.13	1.16
Furtins	n	32	32	32	31	32
	min	34.9	10.2	6.6	19.4	17.4
	max	48.5	14.6	12.7	24.3	20.7
	M	42.79	12.20	9.32	21.97	19.00
	SD	2.82	1.05	1.36	1.32	1.00

Table 6
Measurements (in mm) of upper molar M2 of Late Pleistocene cave bears.

Localities		Greatest length (1)	Length of paracone (2)	Length of metacone (3)	Greatest width (4)	Width through hypocone (5)
Zoolithen	n	65	65	65	65	65
	min	39.1	10.7	8.9	20.2	17.7
	max	50.4	15.3	13.5	25.9	23.7
	M	44.54	13.07	11.13	22.87	20.28
	SD	2.55	1.03	1.10	1.27	1.16
Rübeland	n	55	55	55	55	55
	min	40.4	11.4	9.7	20.9	18.6
	max	52.1	15.6	14.6	25.5	23.6
	M	45.64	13.79	11.74	23.11	20.81
	SD	2.54	0.99	1.30	1.08	1.16
Arcy-sur-Cure	n	32	32	32	32	32
	min	38.5	11.8	8.3	21.4	19.3
	max	56.4	15.5	14.2	26.7	25.3
	M	46.61	13.41	10.70	23.44	21.61
	SD	3.56	1.03	1.41	1.31	1.34
Eirós	n	25	25	25	25	25
	min	41.4	11.0	7.6	20.3	17.8
	max	47.1	14.7	12.1	25.1	21.6
	M	44.71	12.96	10.22	22.61	20.27
	SD	1.52	0.92	1.05	0.92	0.78
Nietoperzowa	n	31	37	36	39	31
	min	42.0	12.3	8.3	21.0	18.5
	max	51.3	15.1	14.8	27.7	24.4
	M	46.65	13.66	11.33	23.94	21.64
	SD	2.44	0.83	1.40	1.35	1.25
Odessa	n	53	53	53	52	53
	min	36.7	12.0	8.7	19.9	16.0
	max	51.9	15.4	15.0	27.1	23.0
	M	46.32	13.55	11.40	23.73	20.42
	SD	2.87	0.81	1.46	1.61	1.53
Secrets Cave	n	83	75	79	83	82
	min	41.3	10.6	8.4	20.4	18.3
	max	49.4	15.0	13.4	25.8	25.8
	M	44.49	12.54	11.11	22.71	20.68
	SD	1.98	0.81	0.94	1.08	0.99
Medvezhiya Cave	n	21	21	21	21	21
	min	39.1	11.3	10.1	19.9	18.1
	max	52.6	18.4	14.4	27.7	24.5
	M	44.10	13.03	11.71	22.72	20.50
	SD	3.14	1.48	1.07	1.52	1.51
Kudaro 3, layer 3-4	n	24	26	25	25	23
	min	39.0	9.6	7.4	19.2	17.9
	max	47.8	14.9	12.2	24.7	23.5
	M	42.91	12.61	10.46	21.97	19.94
	SD	2.17	1.56	1.15	1.35	1.49
Kizel	n	29	28	28	29	28
	min	35.4	9.3	7.0	17.5	13.7
	max	42.3	13.2	9.8	21.8	18.4
	M	39.24	10.54	8.21	19.13	17.01
	SD	2.08	0.92	0.66	1.12	1.07

Table 7
Measurements (in mm) of lower premolar p4 of Middle Pleistocene cave bears.

Localities		Greatest length (1)	Greatest width (2)	Distance between peak of paraconid and peak of metaconid (3)
Jagsthausen	n	21	21	14
	min	12.4	7.6	4.0
	max	15.7	9.9	7.6
	M	14.21	8.81	5.76
	SD	0.98	0.63	1.00
Mosbach	n	20	20	14
	min	13.5	7.7	4.7
	max	17.2	9.9	8.2
	M	14.99	8.80	6.09
	SD	0.92	0.63	1.10
Westbury	n	20	20	8
	min	12.5	6.9	4.5
	max	16.7	10.2	6.6
	M	14.53	8.77	5.45
	SD	1.03	0.87	0.70
Kudaro 1, layer 5	n	68	67	40
	min	11.1	7.7	3.7
	max	17.9	10.6	8.1
	M	15.08	9.09	6.16
	SD	1.26	0.73	1.03
Einhorn	n	28	28	19
	min	11.8	8.1	3.8
	max	16.3	11.3	6.8
	M	14.30	9.43	5.15
	SD	1.07	0.85	0.79
Furtins	n	12	12	9
	min	12.3	8.4	3.4
	max	16.8	12.0	9.0
	M	14.93	9.46	5.11
	SD	1.30	0.94	0.922
Bacton Forest Bed	n	14	14	10
	min	12.7	7.9	6.1
	max	16.8	10.4	10.0
	M	14.53	8.81	4.82
	SD	1.05	0.78	1.03

Table 8
Measurements (in mm) of lower premolar p4 of Late Pleistocene cave bears.

Localities		Greatest length (1)	Greatest width (2)	Distance between peak of paraconid and peak of metaconid (3)
Zoolithen	n	55	55	52
	min	11.9	8.6	3.2
	max	19.7	12.8	6.8
	M	15.61	10.31	4.90
	SD	1.26	0.91	0.95
Rübeland	n	38	38	38
	min	12.5	8.5	2.7
	max	19.0	14.2	5.7
	M	15.49	10.69	4.06
	SD	1.44	1.16	0.75
Arcy-sur-Cure	n	41	41	41
	min	11.5	9.4	2.4
	max	17.6	12.9	5.8
	M	15.47	10.85	4.10
	SD	1.17	0.96	0.79
Eirós	n	17	17	17
	min	11.3	8.9	2.4
	max	17.8	12.4	5.1
	M	15.52	10.64	3.83
	SD	1.63	0.92	0.69
Nietoperzowa	n	34	34	35
	min	14.0	9.4	3.2
	max	18.0	13.3	5.8
	M	16.26	10.88	4.21
	SD	1.02	0.77	0.71
Odessa	n	56	56	52
	min	12.9	9.5	2.1
	max	18.5	13.0	6.3
	M	16.14	11.24	5.00
	SD	1.27	0.83	0.98
Secrets Cave	n	24	24	23
	min	14.8	9.6	3.3
	max	18.5	12.0	6.2
	M	16.51	10.65	4.64
	SD	1.19	0.69	0.80
Kudaro 3, layer 3-4	n	10	11	10
	min	12.6	8.9	3.9
	max	16.2	10.5	9.7
	M	14.62	9.59	6.03
	SD	1.11	0.52	1.60
Kizel	n	17	10	
	min	10.1	7.3	
	max	15.4	10.6	
	M	13.35	9.09	
	SD	1.59	0.97	

Table 9
Measurements (in mm) of lower molar m1 of Middle Pleistocene cave bears.

Localities		Greatest length (1)	Length of trigonid (2)	Length of entoconid 1 (3)	Length of entoconid 2 (4)	Width of trigonid (5)	Width of talonid (6)	Least width in middle part (7)
Jagsthausen	n	27	27	20	20	27	27	27
	min	25.0	15.6	4.6	1.7	9.0	11.6	9.1
	max	30.4	19.8	7.8	6.0	11.3	13.6	11.6
	M	27.20	17.40	5.80	3.51	10.14	12.77	10.21
	SD	1.29	1.05	0.76	1.01	0.59	0.57	0.61
Mosbach	n	20	17	12	12	17	20	17
	min	24.5	16.0	4.1	3.1	9.4	11.7	9.5
	max	31.1	21.0	7.3	5.7	11.2	14.5	11.6
	M	27.34	17.53	5.35	4.05	10.22	13.04	10.39
	SD	1.70	1.23	0.97	0.76	0.57	0.89	0.55
Westbury	n	6	6	4	4	6	6	6
	min	25.8	16.1	3.9	3.8	9.9	11.5	9.6
	max	27.5	18.2	5.8	6.0	11.3	13.6	11.1
	M	26.77	16.88	4.80	4.73	10.5	12.78	10.28
	SD	0.65	0.77	0.80	0.93	0.49	0.95	0.59
Kudaro 1, layer 5	n	88	75	52	52	76	123	104
	min	25.3	15.5	2.3	2.8	8.7	11.6	9.0
	max	32.7	21.2	7.1	7.3	12.6	15.8	12.9
	M	28.51	18.12	4.66	4.82	10.93	13.57	10.91
	SD	1.60	1.32	1.08	0.97	0.76	0.88	0.80
Einhorn	n	42	42	42	42	42	42	42
	min	25.5	15.9	3.2	2.8	9.9	12.3	9.4
	max	33.4	21.4	7.4	5.6	13.6	17.6	13.7
	M	28.82	18.20	5.21	4.17	11.48	14.13	11.43
	SD	1.57	1.11	0.87	0.66	0.73	0.93	0.77
Furtins	n	38	38	38	38	38	38	38
	min	25.6	14.7	2.3	2.7	9.9	12.0	9.7
	max	30.9	19.7	6.2	5.9	13.0	15.4	13.0
	M	28.26	17.43	4.15	4.09	11.65	13.69	11.43
	SD	1.30	1.01	0.70	0.75	0.77	0.92	0.88
Bacton Forest Bed	n	11	11	7	7	11	11	11
	min	24.6	15.6	3.1	3.2	9.7	11.9	9.8
	max	28.1	18.5	6.3	5.0	11.7	15.5	12.8
	M	26.00	16.72	4.69	4.26	10.53	13.12	10.86
	SD	1.29	0.99	0.98	0.62	0.66	0.98	0.87

Table 10
Measurements (in mm) of lower molar m1 of Late Pleistocene cave bears.

Localities		Greatest length (1)	Length of trigonid (2)	Length of entoconid 1 (3)	Length of entoconid 2 (4)	Width of trigonid (5)	Width of talonid (6)	Least width in middle part (7)
Zoolithen	n	51	51	51	51	51	51	51
	min	26.8	16.8	3.5	4.0	9.8	11.7	9.9
	max	34.3	21.8	7.1	6.9	13.5	17.2	13.3
	M	29.85	18.78	5.53	5.15	11.56	14.20	11.29
	SD	1.76	1.10	0.76	0.68	0.83	1.06	0.80
Rübeland	n	39	39	39	39	39	39	39
	min	28.2	17.5	4.1	3.7	10.3	12.9	9.9
	max	33.7	21.8	7.8	6.6	13.4	16.6	12.8
	M	30.69	19.27	6.10	5.28	11.88	14.80	11.54
	SD	1.43	0.99	0.84	0.66	0.77	0.94	0.71
Arcy-sur-Cure	n	31	31	31	31	31	31	31
	min	27.3	17.2	3.4	3.8	10.7	13.1	10.2
	max	33.4	20.7	6.3	7.1	13.9	16.7	12.9
	M	30.75	19.29	5.31	5.68	12.33	14.98	11.57
	SD	1.43	0.94	0.66	0.75	0.68	0.83	0.60
Eirós	n	25	25	25	25	25	25	25
	min	27.7	17.3	4.3	3.8	10.4	13.4	10.4
	max	34.0	21.1	7.0	7.2	13.1	16.0	12.6
	M	31.32	19.42	5.34	5.36	11.67	14.81	11.19
	SD	1.48	0.94	0.86	0.77	0.69	0.76	0.55
Nietoperzowa	n	18	19	19	20	19	19	20
	min	27.5	17.4	4.0	4.0	10.2	12.0	10.4
	max	33.5	21.4	6.8	6.4	13.3	17.1	13.0
	M	30.53	19.26	5.24	5.20	12.27	14.68	11.54
	SD	1.79	1.05	0.74	0.70	0.87	1.18	0.74
Odessa	n	45	42	40	40	45	45	45
	min	28.0	10.2	4.5	4.2	10.8	13.8	10.9
	max	34.1	26.0	7.5	8.2	14.4	17.2	14.1
	M	31.24	19.72	5.54	5.59	12.60	15.40	11.98
	SD	1.53	2.08	0.68	0.83	0.82	0.77	0.64
Medvezhiya Cave	n	24	24	24	24	24	24	24
	min	26.9	17.3	4.8	4.0	10.8	12.8	9.8
	max	33.9	21.5	9.6	6.4	12.4	16.2	12.0
	M	30.11	19.24	6.04	5.14	11.73	14.36	10.96
	SD	1.68	1.15	1.06	0.63	0.58	0.96	0.60
Kudaro 3, layer 3-4	n	22	22	16	16	23	23	23
	min	24.7	15.0	2.5	2.6	9.5	12.5	9.9
	max	29.7	18.9	5.9	6.9	11.7	14.8	12.4
	M	27.08	17.00	4.56	4.19	10.94	13.74	11.09
	SD	1.30	0.90	1.03	1.22	0.63	0.62	0.62
Kizel	n	14	14	12	13	13	14	13
	min	24.2	15.4	3.9	2.5	9.0	11.6	9.1
	max	27.2	17.4	7.3	3.9	11.7	14.1	11.0
	M	25.48	16.34	5.68	2.99	10.19	12.75	10.36
	SD	0.87	0.69	0.96	0.36	0.75	0.63	0.56

Table 11
Measurements (in mm) of lower molar m2 of Middle Pleistocene cave bears.

Localities		Greatest length (1)	Labial length of trigonid (2)	Lingual length of trigonid (3)	Labial length of talonid (4)	Lingual length of talonid (5)	Width of trigonid (6)	Width of talonid (7)
Jagsthausen	n	27	27	27	27	27	27	27
	min	25.2	15.1	13.0	8.6	10.2	14.1	14.8
	max	32.5	19.9	18.0	11.7	15.2	18.3	20.1
	M	28.46	16.91	14.91	10.14	12.31	16.46	17.48
	SD	2.04	1.33	1.49	0.82	1.35	1.06	1.33
Mosbach	n	42	39	39	39	39	40	42
	min	24.6	13.7	11.6	7.8	8.9	13.4	14.1
	max	31.1	18.5	16.1	12.5	13.9	18.5	20.0
	M	27.43	16.19	14.18	9.57	11.48	15.91	17.08
	SD	1.46	1.20	1.10	1.00	1.24	1.04	1.31
Westbury	n	31	31	31	31	31	31	31
	min	23.6	13.8	11.4	9.0	9.3	13.3	14.6
	max	33.0	20.1	18.3	12.2	15.0	19.2	20.0
	M	28.53	17.05	14.78	10.49	12.32	16.36	17.61
	SD	2.17	1.50	1.60	0.77	1.54	1.36	1.46
Kudaro 1, layer 5	n	72	72	72	72	72	72	72
	min	25.1	14.6	13.1	9.9	10.1	14.8	15.3
	max	34.4	21.1	18.2	14.0	16.7	19.8	20.9
	M	29.56	17.63	15.37	11.43	13.37	16.86	18.05
	SD	1.92	1.50	1.11	0.98	1.24	1.20	1.27
Einhorn	n	42	42	42	42	42	42	42
	min	24.2	14.0	13.0	9.0	10.0	13.5	13.5
	max	32.0	19.6	17.4	13.0	15.0	19.2	20.9
	M	29.07	16.79	14.87	10.86	12.27	16.96	17.59
	SD	1.67	1.38	1.03	0.98	1.08	1.21	1.44
Furtins	n	44	43	44	44	44	44	44
	min	25.8	14.1	12.5	9.1	9.0	14.6	14.8
	max	31.0	18.5	19.4	12.0	13.5	19.2	19.3
	M	28.08	16.51	15.48	10.57	11.39	16.65	17.06
	SD	1.39	1.15	1.21	0.73	1.04	0.85	1.00
Bacton Forest Bed	n	10	10	10	10	10	10	10
	min	23.3	14.4	13.2	7.5	9.5	13.8	15.3
	max	28.3	18.1	15.2	9.6	11.2	17.0	18.1
	M	25.38	16.12	13.96	8.72	10.42	15.46	16.39
	SD	1.43	1.20	0.71	0.89	0.64	1.03	0.78

Table 12
Measurements (in mm) of lower molar m2 in of Late Pleistocene cave bears.

Localities		Greatest length (1)	Labial length of trigonid (2)	Lingual length of trigonid (3)	Labial length of talonid (4)	Lingual length of talonid (5)	Width of trigonid (6)	Width of talonid (7)
Zoolithen	n	57	57	56	57	56	56	57
	min	25.7	14.9	12.3	8.9	9.4	14.9	15.6
	max	36.3	21.7	18.8	16.8	17.1	20.2	21.9
	M	29.70	17.66	15.31	11.36	12.55	17.54	18.44
	SD	2.24	1.51	1.49	1.45	1.53	1.20	1.44
Rübeland	n	39	39	39	39	39	39	39
	min	27.8	14.6	13.5	9.2	10.5	15.9	16.4
	max	34.3	20.1	18.3	13.7	15.0	20.3	22.1
	M	31.18	18.14	16.14	11.73	13.01	18.11	18.43
	SD	1.67	1.18	1.17	0.98	0.97	1.04	1.18
Arcy-sur-Cure	n	44	44	44	44	44	44	44
	min	28.0	16.2	13.2	9.6	10.1	15.8	16.0
	max	34.2	20.6	19.2	14.9	15.3	21.0	21.4
	M	31.29	18.48	16.34	11.84	12.71	18.26	18.89
	SD	1.62	1.00	1.22	1.19	1.23	1.13	1.26
Eirós	n	24	24	24	24	24	24	24
	min	28.3	15.7	14.4	10.3	11.4	15.5	17.1
	max	34.5	19.9	17.7	14.3	16.0	20.5	22.8
	M	31.36	17.56	15.77	12.48	13.33	17.66	19.12
	SD	1.42	1.18	0.84	0.94	1.17	1.04	1.27
Nietoperzowa	n	31	31	31	31	31	31	31
	min	27.0	16.6	13.0	10.0	11.3	16.3	16.0
	max	34.7	21.2	18.7	14.4	17.1	20.5	22.3
	M	31.18	18.84	16.14	12.77	14.46	18.59	19.18
	SD	1.76	1.20	1.37	1.00	1.39	1.00	1.29
Odessa	n	89	89	89	89	89	89	89
	min	27.5	16.4	13.5	9.9	10.8	16.4	17.1
	max	35.7	21.9	19.6	15.2	18.0	20.9	22.1
	M	31.26	18.73	16.44	12.74	13.99	18.44	19.30
	SD	1.64	1.27	1.29	1.21	1.54	1.01	1.09
Secrets Cave	n	62	62	62	62	62	62	62
	min	27.3	14.9	13.6	10.1	11.9	15.0	17.0
	max	37.3	23.4	20.3	18.7	18.8	24.0	26.0
	M	31.61	18.94	16.02	12.44	14.78	18.69	19.75
	SD	2.08	1.91	1.73	1.80	1.88	1.94	1.93
Medvezhiya Cave	n	15	15	15	15	15	15	15
	min	27.4	15.3	14.5	10.0	9.7	15.5	15.6
	max	31.9	18.9	17.2	14.2	15.7	18.6	19.9
	M	29.17	17.02	15.73	11.76	12.60	17.04	17.49
	SD	1.35	0.88	0.79	1.26	1.43	0.89	1.32
Kudaro 3, layer 3-4	n	20	20	20	20	20	20	20
	min	25.3	15.8	12.1	9.4	10.5	14.7	15.7
	max	30.9	18.8	16.6	12.1	14.5	18.2	19.3
	M	28.24	17.23	14.67	10.78	12.21	16.78	17.87
	SD	1.46	0.88	1.08	0.75	0.93	0.83	0.96
Kizel	n	12	12	12	12	12	12	12
	min	24.2	13.9	12.4	8.2	9.2	14.0	15.2
	max	27.5	17.2	14.3	11.1	13.3	16.3	17.2
	M	26.22	15.49	13.37	9.36	11.72	14.90	16.02
	SD	0.98	1.03	0.61	0.79	1.16	0.63	0.75

Table 13
Measurements (in mm) of lower molar m3 of Middle Pleistocene cave bears.

Localities		Greatest length (1)	Length of talonid (2)	Greatest width (3)	Width of talonid (4)
Jagsthausen	n	37	37	37	37
	min	20.9	7.4	15.7	8.0
	max	30.1	14.1	19.9	18.2
	M	24.44	9.86	17.77	15.81
	SD	2.04	1.71	1.10	1.74
Mosbach	n	34	31	32	32
	min	19.8	6.5	15.3	13.0
	max	29.8	14.4	20.8	19.4
	M	24.28	10.20	17.90	15.84
	SD	2.33	2.02	1.26	1.60
Westbury	n	50	47	50	47
	min	18.2	7.2	14.9	11.8
	max	30.0	14.4	21.3	20.2
	M	24.72	10.42	18.24	16.39
	SD	2.49	1.67	1.47	1.97
Kudaro 1, layer 5	n	124	111	131	111
	min	20.7	7.5	15.7	13.0
	max	30.6	14.5	22.0	21.1
	M	25.26	10.84	18.42	16.63
	SD	2.01	1.46	1.18	1.52
Einhorn	n	42	42	42	42
	min	22.3	7.5	15.5	14.1
	max	31.3	13.5	21.6	21.0
	M	25.12	10.41	18.70	17.08
	SD	1.90	1.30	1.34	1.51
Furtins	n	8	8	8	8
	min	22.5	10.5	18.0	16.8
	max	29.9	15.1	21.4	19.8
	M	25.61	11.79	19.25	18.57
	SD	2.66	1.47	1.26	1.20
Bacton Forest Bed	n	10	10	10	10
	min	21.8	7.4	15.4	14.2
	max	27.1	13.5	20.7	18.0
	M	24.20	10.39	17.57	16.19
	SD	1.70	1.75	1.63	1.31

Table 14
Measurements (in mm) of lower molar m3 of Late Pleistocene cave bears.

Localities		Greatest length (1)	Length of talonid (2)	Greatest width (3)	Width of talonid (4)
Zoolithen	n	55	55	55	55
	min	21.4	8.5	16.9	13.8
	max	31.1	16.0	22.4	21.5
	M	25.87	12.63	18.92	18.02
	SD	2.02	1.73	1.12	1.80
Rübeland	n	33	33	33	33
	min	22.2	9.4	16.6	15.3
	max	30.8	16.2	21.5	22.4
	M	26.97	12.11	18.89	17.99
	SD	2.46	1.75	1.27	1.77
Arcy-sur-Cure	n	41	41	41	41
	min	23.8	9.6	17.1	15.6
	max	31.7	15.2	22.2	22.0
	M	27.91	12.68	19.53	18.73
	SD	1.78	1.23	1.18	1.32
Eirós	n	12	12	12	12
	min	25.2	10.6	17.4	14.8
	max	30.1	14.6	21.0	20.3
	M	27.20	12.45	19.32	17.70
	SD	1.78	1.40	1.17	1.65
Nietoperzowa	n	30	31	30	31
	min	24.8	8.4	17.2	16.0
	max	33.0	18.7	23.6	23.6
	M	28.08	13.65	20.08	19.26
	SD	2.21	2.16	1.38	1.83
Odessa	n	100	100	99	99
	min	21.0	8.1	17.5	14.1
	max	31.4	16.7	22.7	22.0
	M	27.33	12.86	19.91	18.79
	SD	2.10	1.45	1.24	1.48
Secrets Cave	n	18	18	18	18
	min	22.9	9.1	16.2	14.6
	max	31.4	15.0	22.4	21.0
	M	27.46	12.40	20.19	18.73
	SD	2.39	1.81	1.48	1.61
Medvezhiya Cave	n	22	22	22	22
	min	21.5	8.8	15.7	13.3
	max	29.7	13.1	21.4	19.5
	M	25.36	10.72	18.59	16.86
	SD	2.14	1.15	1.42	1.69
Kudaro 3, layer 3-4	n	24	24	24	23
	min	20.7	8.3	16.5	13.2
	max	28.1	13.3	21.1	19.3
	M	24.87	10.74	18.68	17.20
	SD	2.08	1.32	1.14	1.54
Kizel	n	19		19	
	min	21.0		14.8	
	max	25.2		18.0	
	M	23.25		16.82	
	SD	1.12		0.81	

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COMPARATIVE DENTAL MICROWEAR ANALYSIS OF CAVE BEARS *URSUS SPELAEUS* ROSENMÜLLER, 1794 AND BROWN BEARS *URSUS ARCTOS* LINNAEUS, 1758

Ana C. PINTO LLONA[1]

ABSTRACT: Dental Microwear Analyses (DMA) studies diet-related microscopic dental wear features, offering an additional and fresh insight into the diet of extinct animals. Most DMA studies have been carried on primates and hominines, as well as on herbivores. Very few approach carnivores and none to our knowledge studies bears. One of the chief drawbacks of DMA studies is that different authors choose different teeth, tooth areas, and methods rendering comparison across works difficult. Here we describe the methodology that we have devised for the analyses of dental microwear features in brown bears *Ursus arctos* and cave bears *U. spelaeus*, which could be applied to any species of bear. The diet of extant European brown bears is well known, and the comparison of their dental wear with that one seen on cave bears allows for some inferences. Although the collection of bear teeth analyzed here was small, we are hoping that the same methods may be adopted by other scientists researching on bear DMA.

Key words: Pleistocene, *Ursus spelaeus, Ursus arctos,* dental microwear, diet, molars, SEM.

INTRODUCTION

The diet of the extinct cave bear *Ursus spelaeus* is still greatly unknown, although we do have some clues: the morphological features of their chewing apparatus (for review see Pinto Llona *et al.,* 2005; pages 87-121, 597-600 and Sacco & Van Valkenburgh, 2004) suggest both, non-predatory behaviour, and important adaptations to a tough vegetarian diet.

Comparative analyses of gross-wear features on the teeth of extant European brown bears *Ursus arctos* whose diet is known, with those on cave bear teeth, shows that tubers were in fact absent from their diet (Pinto & Andrews, 2001) and therefore tubers are not responsible for the extreme wear seen in cave bear teeth.

Taphonomic analyses of carnivore produced modifications on cave bear bones at several cave bear sites has shown that they actively scavenged on the carcasses of their con-specifics, both adult and infant, at all sites analysed, and also that they did so by following a very homogeneous and identifiable pattern that is peculiar to cave bears. This pattern is very distinct from the one produced by other large carnivores (Pinto & Andrews, 2004; Pinto Llona *et al.*, 2005) including brown bears.

However, results obtained on the stable isotopic yield of cave bear bones are interpreted as indicators of a diet even more vegetarian than that of contemporary herbivore taxa (Bocherens *et al.*, 1994). It is possible that the cannibalistic scavenging carried out by cave bears constituted a minor part of an otherwise chiefly vegetarian diet, thus leaving no identifiable isotopic signature in their bones. On the other hand the metabolism of bears during hibernation and its effect on their isotopic signature is, to this day, poorly understood. It is thought that it involves significant mobilization of Nitrogen as discussed elsewhere (Pinto & Andrews, 2004; Pinto Llona *et al. op. cit.*) and thus the metabolism of hibernation could be responsible of the apparent anomaly in that chemical signature.

A new line of evidence, complementary to the ones above, can offer fresh insights on the cave bear diet. Dental Microwear Analyses (DMA) is based on the assumption that different foodstuffs produce different and identifiable patterns of wear (Walker *et al.,* 1978). DMA studies the varying percentages, length and width of *pits* and *scratches* on tooth enamel surfaces and their relative proportions.

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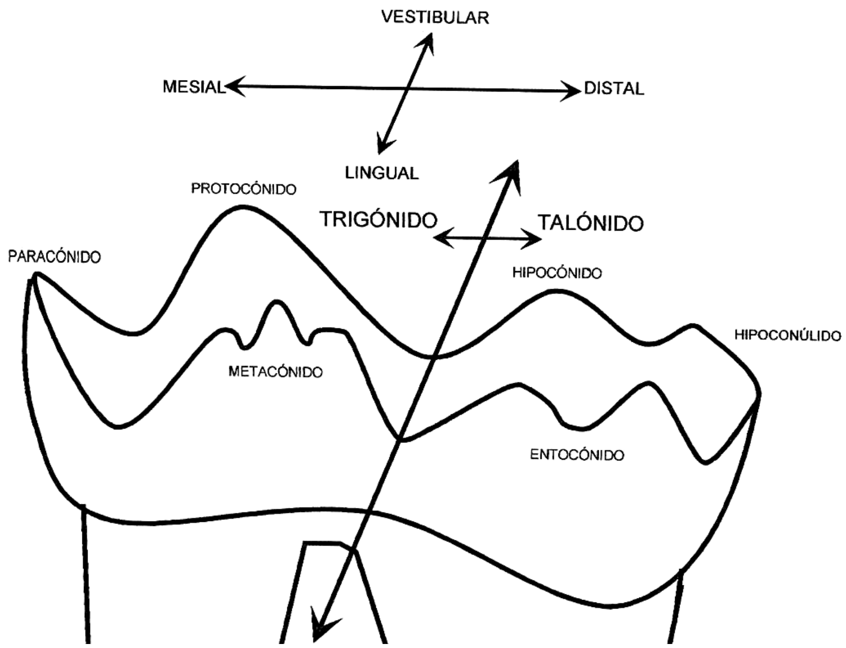

Figure 1. Right M_1 of *Ursus*. Mesially, the three cusps of the trigonid: protoconid, paraconid and metaconid. Distally, the three cusps of the tabloid: hypoconid, hypoconulid and entoconid.

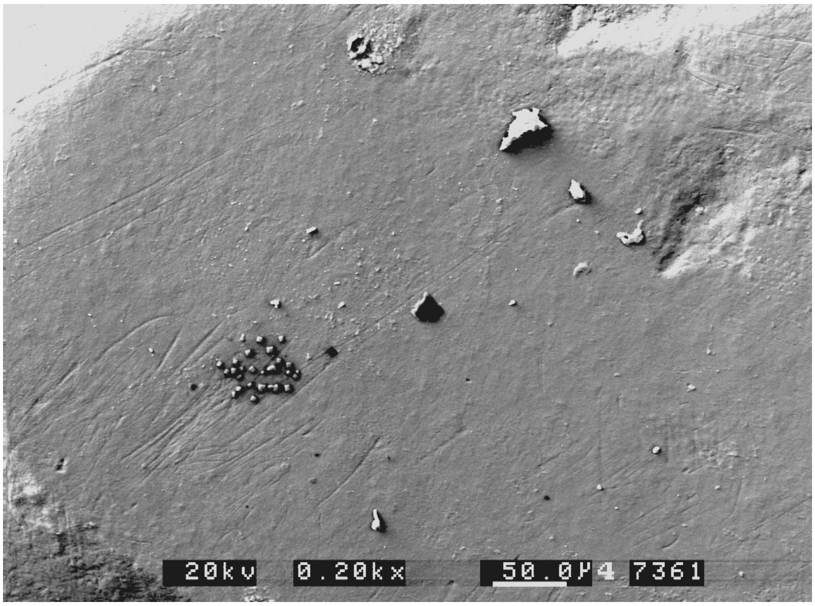

Figure 2. Micrograph of the protoconid distal facet of a cave bear from Troskaeta. During hibernation bears do not eat, drink, urinate or defecate. In the shut mouth of the bear, dental microwear marks disappear during the hibernation, leaving featureless surfaces where sometimes the prisms of enamel can be distinguished as if after acid treatment. The facet above appears flat but for a few structures visible, probably plant silica phytoliths of a last mouthful of grass just after leaving hibernation and als just before dying, and the scratches produced by them.

DMA had not been carried out before on bears, and only a few works approach it on other carnivores; amongst these are the works by Van Valkenburgh *et al.* (1990) on the carnassial facet of several carnivores, Taylor & Hannam (1987) on the buccal surface of the upper carnassial P4 of several species of African viverrids, Strait (1993) comparing microwear on several primates and quiroptera and others.

Here we present our approach to the bear DMA. We choose to perform it on the low 1st molar, on a sample of cave bears and also of both fossil and extant brown bears, because of the evolutionary stability of this tooth.

MATERIALS AND METHODS

Although initially we revised large collections of low M1 from several cave bear collections, the usable sample was limited by three factors: (1) Teeth showing any taphonomic post-depositional alteration were excluded from

Table 1
Facet denomination according to Butler (1952) and, between brackets, Kay (1977). From Hunter & Fortelius (1994).

FACET	UPPER MOLAR	LOWER MOLAR
1(2)	Distal Metacone	Mesial protoconid
2(1)	Mesial Paracone	Distal protoconid
3(5)	Mesial Protocone	Distal metaconid
4(7n)	Distal Hypocone	Lingual metaconid
5(10n)	Buccal Hypocone	Lingual protoconid
6(3)	Distal Paracone	Mesial hypoconid
7(4)	Mesial Metacone	Distal hypoconid
8(8)	Mesial Hypocone	Distal entoconid
9(6)	Distal Protocone	Mesial entoconid
10(9)	Buccal Protocone	Lingual hypoconid

the sample following King *et al.,* (1999). Furthermore, this type of analyses is carried out on enamel, thus (2) our sample was limited to teeth conserving it on the occlusal surfaces, presumably those of relatively young adults. Additionally, (3) some specimens belonged to animals that died during or soon after hibernation: according to our observations (Pinto *et al.,* 2005), dental microwear features are erased by long hibernation periods, during which time bears do not eat nor drink at all for several months each year. The obliteration of all dental microwear features, as well as the noticeable exposure of the enamel prisms in these specimens suggests that the acidity in the mouth of the bears is greater during hibernation (fig. 2).

Having discounted the specimens that for one or other of the above reasons were unsuitable for this type of analyses, the sample finally employed included six extant brown bear low M1 plus four Holocene ones, both from the Cantabrian mountains of Asturias, and seven cave bear specimens, from Troskaeta cave in the Basque country. All of these locations are in northern Spain.

Since our objective was to compare dental wear in brown and cave bears, a set of facets had to be chosen that homogeneously appear in both species of bears. On the selected specimens we therefore recorded exhaustively the presence or absence of discrete wear facets in each of the cusps -paraconid, metaconid, protoconid, entoconid, hypoconid and hypoconulid (fig. 1).

One interesting observation derived from this approach was that none of the cave bears in the sample has a carnassial facet -that is, the wear facet that forms by the shearing occlusion of the upper P4 (lingually) and the lower M1 (bucally) in carnivores. In contrast, all fossil brown bear low M1 specimens have it, while only 60% of extant brown bears from the northern Iberian Peninsula, whose diet has a very important vegetarian component (Pinto *et al.,* 2001; 2005) showed a carnassial facet, corresponding with assessed predatory behaviour in each of these types of bears (Couturier, 1954).

Occlusal facets and facet denomination have been the object of several studies (for a review see Hunter & Fortelius, 1994). Following the advice of these authors, we adapted facet denomination from extant literature by Butler (1952) and Kay (1977). Tab. 1 shows these denominations, and fig. 3 is our adaptation of it to the bear low M1.

Once assessed the homogeneity of their presence on both brown and cave bear teeth, we choose to carry out the analyses in two facets, that is one Trigonid facet and one Talonid facet, since those are thought to have different functions during mastication. The facets employed throughout the analyses were the distal facet of the protoconid Facet 2(1), and the lingual facet of the hypoconid Facet 10(9) (fig. 3).

High precision Coltene™ moulds or peelings were taken from the occlusal surfaces and reinforced with dental putty. The resulting moulds were then positivated by using slow curing Araldit™. These Araldit™ replicas were then gold or platinum coated and Scanning Electron Microscope micrographs were taken of the chosen facets. The settings employed for the SEM throughout the study were x 200 magnification, 35 mm working distance, and 20 Kv potency -since the resin casts would fuse with higher potency.

The pictures thus obtained were then digitised and analysed by using Microwear 2.2 software developed by Dr. Ungar (Ungar *et al.*, 1991; Ungar, 1995a; Ungar, 1995b) and available to the author. For the bears we used a *pit* to *scratch* ratio of 1:4, that is, marks whose width is more than ¼ of the length are classified as pits. The software records individual features and classifies them according to our settings, in so doing performing some basic statistics.

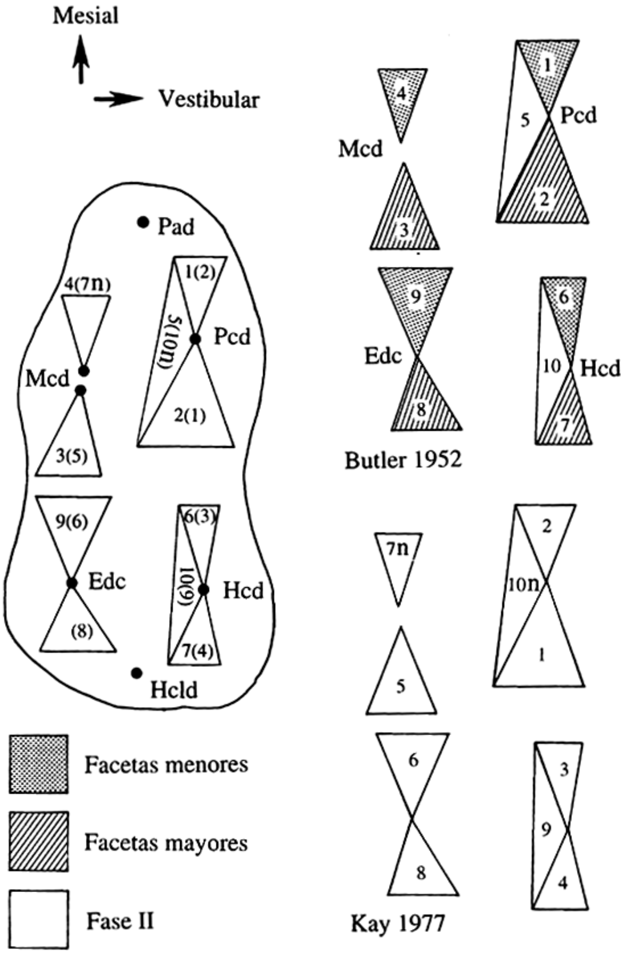

Figure 3. Occlusal view of a bear right low M1, showing facet location and denomination according to the frameworks by Butler (1952) and Kay (1977).

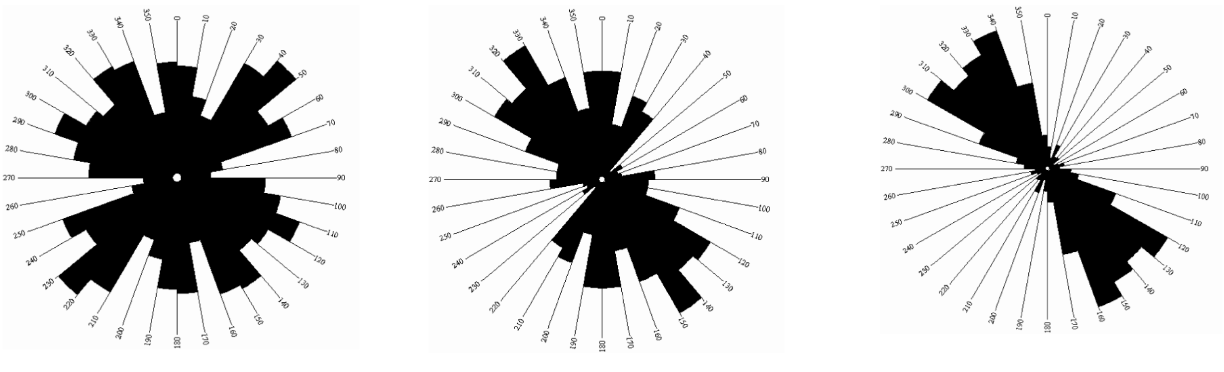

Figure 4. Orientation of dental microwear features in Facet 2(1). Left, extant brown bear, middle Holocene fossil brown bear, right cave bear. If puncture-crushing of hard objects is responsible for the diverging orientation of wear marks, it could be suggested that cave bears do not practice it. Orientation diverges most between the two bears of allegedly most similar diets, chiefly vegetarian.

RESULTS

Having measured and classified dental microwear features in these extant brown bears, Holocene fossil brown bears and Troskaeta cave bears, we effected the following observations:

Cave bears have more marks in both facets than either extant or fossil brown bears: average number of marks in Facet 2(1) in extant brown bears is 80.1, in fossil brown bears is 99.3 and in cave bears is 163.7; average number of marks in facet 10(9) in extant brown bears is 87.4, in fossil brown bears is 131.3 and in cave bears is 153.4.

Both types of brown bears tend to have a greater proportion of *scratches* relative to *pits* than cave bears: Facet 2(1) average number of pits and scratches in extant brown bears is 22.6% and 77.4% respectively; in fossil brown bears is 6.3% and 93%, and in cave bears is 33.4% and 66.6% respectively. As for Facet 10(9), extant brown bears 26.5% and 73.5%, fossil brown bears 18.7% and 81.3% and cave bears 49.5% and 50.1%.

Regarding scratch size, cave bears have the shortest and widest scratches in Facet 2(1) (extant brown bears 63.72 μ x 2.69 μ, fossil brown bears 72.27 μ x 2.99 μ and cave bears 48.23μ x 3.73μ) and pit size is similar in both fossil brown and cave bears (extant brown bears 31.05μ x 18.66μ, fossil brown bears 23.92 μ x 12.53 μ, cave bears 23.13 μ x 11.18 μ). As for Facet 10(9), scratch sizes are more homogeneous amongst the three types of bears (extant brown 56.96 μ x 2.92 μ, fossil brown 62.83 μ x 2.79 μ, cave bears 57.83 μ x 4.24 μ), while pit sizes are smaller for cave bears (extant brown 23.7 μ x 12.86 μ, fossil brown 21.56 μ x 12.06 μ, cave bears 20.31 μ x 10.56 μ).

SUMMARY AND DISCUSSION

We present here a standardized method for the Dental Microwear Analyses of the 1st low Molar of the bear, devised with the aim of shedding complementary light on the dietary habits of the extinct cave bear by comparing its dental wear with that of modern bears of known diet. The number of specimens available to this study was limited because of the excessive wear leading to enamel loss on occlusal surfaces and by the obliteration of dental wear features presumably during hibernation. A small collection of low M1, of modern and Holocene fossil brown bears, as well as cave bears from Troskaeta, were analyzed. On these we choose to analyze the distal facet of the protoconid in the Trigonid and the lingual facet of the hypoconid in the Talonid. Cave bears showed to have significantly more marks than brown bears in both facets.

In the three types of bear, pits are more numerous on facet 10(9) than in facet 2(1), pointing to the superior grinding function of the Talonid. In brown bears, scratches in facet 2(1) are longer than those in 10(9). Numerous long narrow scratches are sometimes related with grazing behaviours; we know that brown bears do graze. Conversely, cave bears have the longer and wider scratches in facet 10(9) suggesting a different feeding behaviour than that of brown bears at least relating to grazing. On the other hand pits are on average larger on facet 2(1) than in the Talonid facet, in the three groups of bears considered.

Cave bears show a marked preference in the orientation of the marks, that is more erratic for brown bears, and this must be related to the dynamics of chewing as well as to the foodstuffs ingested.

Val Valkenburgh *et al.* (1990), when assessing bone chewing behaviours in carnivores, showed that dental microwear marks in hyaenas have a combination of relatively long marks and a larger proportion of pits than scratches. Felids, that eat less bone, had narrow scratches with few pits. Taylor & Hannam (1987) concluded that faunivore animals tend to have greater mark density than fruit or leaf eaters, although such differences did not prove statistically consistent.

Of the three bear types considered, cave bears *U. spelaeus* have the highest proportion of pits relative to scratches in both facets, and also the greater mark density. A large concentration of scratches is thought to be associated with the ingestion of grass because of the opal phytoliths contained in it. Brown bears are known grass eaters and had larger percentages of scratches on both facets.

In view of the observations on dental wear in other carnivores, and of our observations here, we believe that our results are consistent with dietary behaviours that include a greater consumption of bone on the part of cave bears relative to brown bears, as has also been assessed by the taphonomic analyses of carnivore produced bone modification on cave and brown bear bone deposits.

Acknowledgements: This research has been made possible by grants awarded to the author by FICYT (Fundación Investigación Ciencia y Tecnología de Asturias) and by a joint agreement Fundación Oso de Asturias, DuPont and the Natural History Museum. Use of the Scanning Electron Microscope at the NHM was possible with support of the European Commission Large Scale Facilities, Training and Mobility for Researchers Programme. Thanks to Dr. J. Naves that provided access to teeth of extant brown bears, to Sociedad Ciencias Aranzadi that keeps the Troskaeta collection, to Dr. T. King for insights on replication and feedback, to Dr. P. Ungar for sharing his software, and to the SEM staff at the Natural History Museum.

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ABOUT THE ABSENCE OF CAVE BEAR IN PROVENCE (SE FRANCE) AND THE VALLESCURE EXCEPTION

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Abstract: The Provence region in the South-East of France, delimitated by the Alps to the East and the Rhône River to the North and the West, is characterized by a relative endemism of its Pleistocene fauna. Compared with Italy and the West Rhône River, relevant ungulate taxa of cold plains are very rare. The carnivore representation is also specific to this region with scarce evidences of *Crocuta crocuta spelaea, Cuon alpinus europaeus, Gulo spelaeus* and *Ursus spelaeus*, while *Ursus arctos* and *Ursus thibetanus* are well known. During Late Pleistocene, the Vallescure locality is the only site to have registered the presence of carnivore taxa absent from the rest of Provence. In this cave, carnivore remains are abundant and represented by twelve species: *Canis lupus*, *Cuon alpinus europaeus*, *Vulpes vulpes*, *Alopex lagopus*, *Ursus spelaeus*, *Ursus arctos*, *Gulo spelaeus*, *Crocuta spelaea*, *Panthera* (*Leo*) *spelaea*, *Panthera pardus*, *Lynx spelaea*, *Felis silvestris*. *Capra ibex* is the only herbivore present. The morphological study of cave bear teeth highlights the geographical isolation of Provence during the Late Pleistocene. Convergent arguments on ungulate and carnivore taxa, in particular cave bear, are relevant to demonstrate that the Rhône River acted as a major paleobiogeographical limit, seeming to be active since the OIS 4, at least for *U. spelaeus*.

Key words: *Ursus spelaeus,* Late Pleistocene, France, South-East, geographical isolation.

INTRODUCTION

The Provence region, in the South-East of France, is a karstic area abundantly provided with caves, in which archaeological and paleontological remains are known existing since more or less 1 Ma. The Pleistocene fauna is various (Brugal & Crégut-Bonnoure, 1994; Crégut-Bonnoure, 1995a; 2004a,b; Crégut-Bonnoure & Fernandez, 2004,) and Ursidae are represented by four species:

- *Ursus thibetanus* in three caves: "Les Cèdres" (OIS 6, Plan d' Aups, Var, Crégut-Bonnoure, 1995b), Bérigoule (OIS 6, Murs, Vaucluse; Crégut-Bonnoure, 1997), Cimay (OIS 7, Saint-Anne-d' Evenos, Var, Crégut-Bonnoure, 1997);
- *U. arctos* in twenty six localities: Adaouste (OIS 5d, Jouques, Bouches-du-Rhône, Defleur *et al*., 1994), «Bau de l' Aubesier» (OIS 4, Monieux, Vaucluse, Crégut-Bonnoure *et al*., 1994), "Baume des Peyrards" (OIS 4, Buoux, Vaucluse; Gagnière, 1957), "La Masque" (OIS 4, Entrechaux, Vaucluse; Gagnière *in* Lumley-Woodyear, 1969), «Les Cèdres» (Crégut-Bonnoure, 1995b), Vallescure (OIS 4, Gagnière & Germand, 1934), «Grotte aux Puces» (Cabasse, Var, Gagnière, 1954), Lazaret (OIS 6, Alpes-Maritimes, Patou, 1984), «Grotte Murée» (Holocene, Montpezat, Alpes-de-Haute-Provence, Helmer, 1979), "Aven de Vauclare" (Holocene, Esparron-de-Verdon, Alpes-de-Haute-Provence, Courtin, 1974), La Fare (Holocene, Alpes-de-Haute-Provence, E. Blaise, pers.com.), "Les Gras" (Escragnolles, Alpes-Maritimes, Crégut-Bonnoure, 2002), Espiguières (Var, Aups, Courtin pers. com.), "Aven de Contadoux" (Holocene, Sault, Vaucluse, Buisson-Catil & Crégut-Bonnoure, 1995), "La Clairière" (Holocene, la Roque-sur-Perne, Vaucluse, Blaise *et al.,* 2004), "La Balance" (Holocene, Avignon; Vaucluse, Helmer, 1979), Mont Ventoux (Holocene, ten traps, Brantes and Savoillan, Vaucluse, Crégut-Bonnoure *et al*., 2005);

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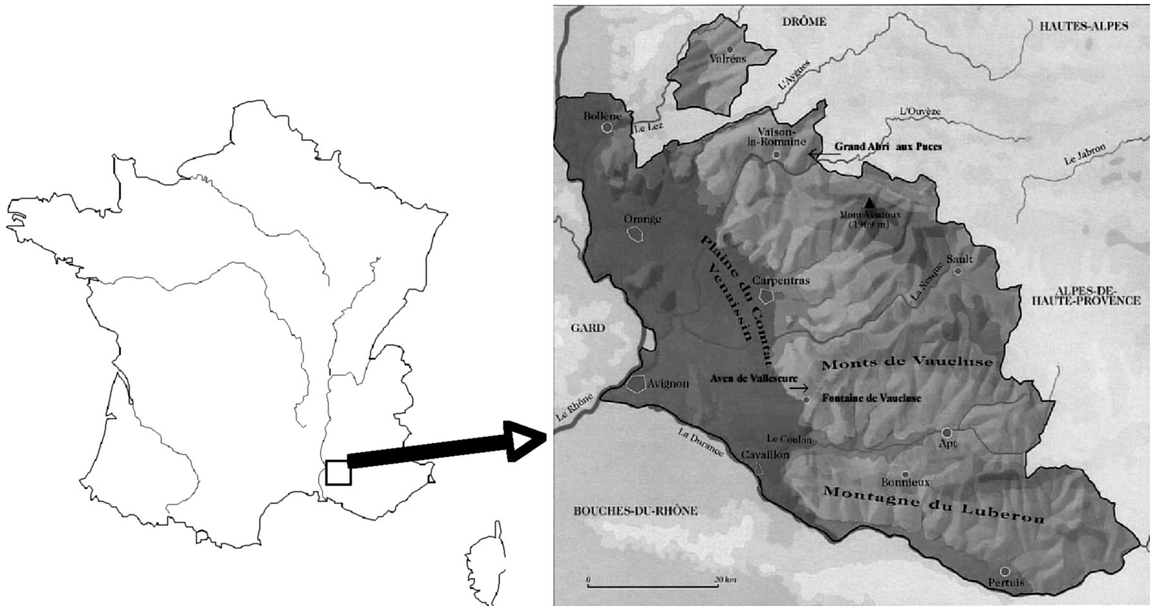


Figure 1. Geographical localization of "Grand Abri des Puces" and Vallescure. Modified from Olive (*in* Buisson-Catil *et al.,* 2004).

- *U. deningeri* in three caves: Vallonnet (Lower Pleistocene; Roquebrune-Cap-Martin, Alpes-Maritimes; Moullé, 1992), Escale (Lower Middle Pleistocene; Saint-Estève-Janson, Bouches-du-Rhône, Bonifay, 1971) and "Les Cèdres" (Crégut-Bonnoure, 1995b),
- *U. spelaeus* in three localities: Vallescure, perhaps «Grand Abri des Puces» (OIS 4, Entrechaux, Vaucluse; Crégut-Bonnoure, 2002), «L' Albarea» (Late Pleistocene, Sospel, Alpes-Maritimes, Moullé *et al.,* 2000).

Compared with other regions of France, *U. thibetanus* and *U. arctos* are relatively abundant while *U. deningeri* and *U. spelaeus* are poorly represented. The scarcity of cave bear, which is particularly numerous within the all Europe with more than a thousand of sites known, is under question.

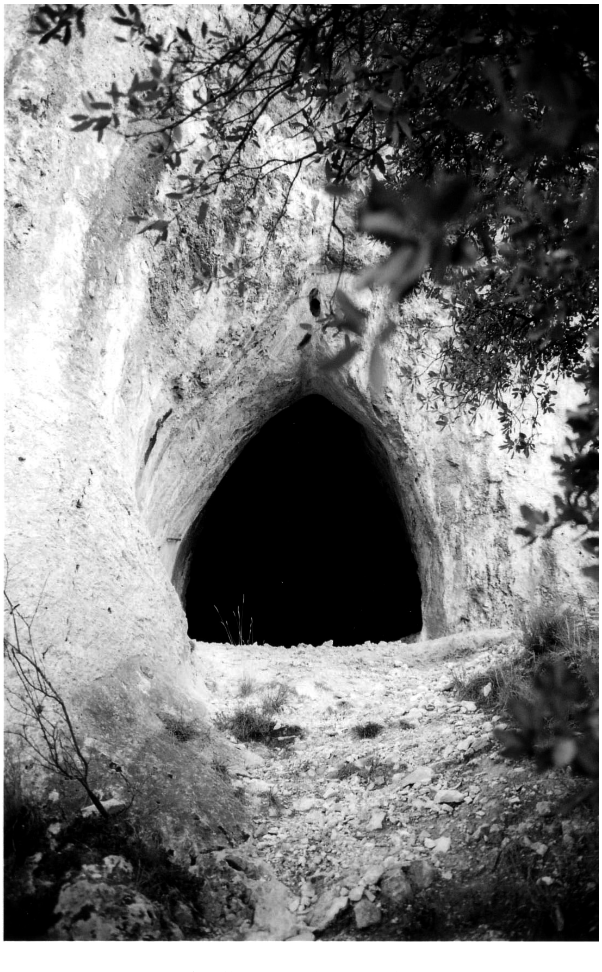


Figure 2. Entrance of Vallescure. Photograph E. Cregut-Bonnoure.

VALLESCURE AND "GRAND ABRI DES PUCES" LOCALITIES

Vallescure (or Valescure) and "Grand Abri des Puces" (or Grotte Basse) are situated in the western border of Provence, called Vaucluse (fig. 1).

The Vallescure cave belongs to the Cretaceous karstic context of the famous Fontaine-de-Vaucluse. Two entrance porches give access to a 50 m² room, where a rich paleontological assemblage, dated from the OIS 4 (Gagnière & Germand, 1934) and associated with Mouste-

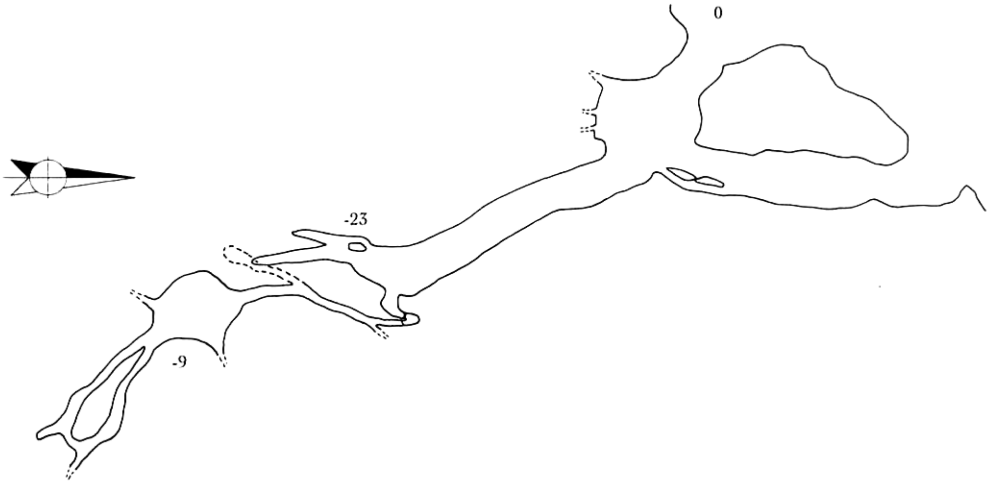


Figure 3. Plan of Vallescure after Groupe spéléologique de Fontaine-de-Vaucluse (LE FAHLER & FRADIN, 1995). Scale 16 mm for 10 m.

rian artefacts (LUMLEY-WOODYEAR, 1969) (fig. 2, 3) was discovered . The major part of the infilling and by consequence of the faunal material was destroyed during phosphates exploitation of the site. First scientific excavations were made by C. Chatelet, S. Gagnière, L. Germand, B. Girerd and D. Helmer, the collections of which are conserved in the Museum Requien of Avignon.

Carnivore remains are represented by twelve species: *Canis lupus*, *Cuon alpinus europaeus*, *Vulpes vulpes*, *Alopex lagopus*, *U. spelaeus*, *U. arctos*, *Gulo spelaeus*, *Crocuta crocuta spelaea*, *Panthera* (*Leo*) *spelaea*, *P. pardus*, *Lynx spelaea* and *Felix silvestris*. *Capra ibex* is the only Pleistocene herbivore present. All the material was found at the bottom of the entrance room, except wolverine bones found in a 15 m deep hole, corresponding to the beginning of a small horizontal gallery (fig. 4). This hole, used by local farmers, is also showing recent remains of *C. familiaris, Bos taurus* and *Ovis aries*. Bones of *Cervus elaphus* and *Sus scrofa*, less fossilized than the Pleistocene assemblage, are also present.

The "Grand Abri des Puces" is located just near the village of Entrechaux and the Ouvèze River, near the "La Masque" cave. This rock shelter was formed between two layers of Miocene limestone, and it is 10 m long and 5 m wide. Discovered by S. Gagnière, surface remains are composed by Mousterian artefacts and bones of ten mammal species: *C. lupus*, *U.* cf. *spelaeus*, *P.* (*L.*) *spelaea*, *Equus* sp. (*caballus sensu*), *Capreolus capreolus*, *Bos* or *Bison*, *C. ibex*, *Castor fiber*, an unidentified *Testudo* and *Emys orbicularis* (CRÉGUT-BONNOURE, 2002; CHEYLAN, 1981; HERVET, 2000). This fauna is also conserved in the Museum Requien of Avignon.

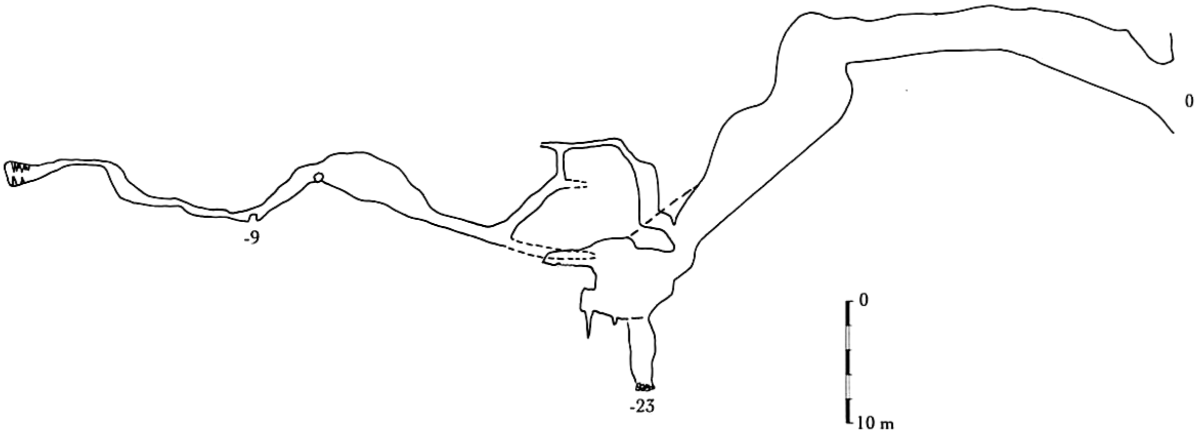


Figure 4. Section of Vallescure after Groupe spéléologique de Fontaine-de-Vaucluse (LE FAHLER & FRADIN, 1995).

Table 1
Skeletal representation of *U. spelaeus* remains from Vallescure.

	Adult	young		Adult	young adult	young		Adult	young adult	young		Adult	young adult
skull fragments	9	4	incomplete scapula	4			incomplete coxal	5			first phalanxes	54	
premaxillae	1		incomplete humerus	9	4		incomplete femur	5	11		second phalanxes	14	
fragmentary mandibles	3	2	incomplete radius	5	1	2	incomplete tibia	6	5	1	third phalanxes	55	
fragmentary canine	13	6	incomplete ulna	5	3	2	incomplete fibula	2	2	1	hyoid bones	2	
upper I1	1		pyramidal	3			patella	3			sternebrae	10	
upper I3	3		pisiform	3	2		talus	5	1		incomplete vertebrae	20	2
upper P4	5		scapholunar	7			calcaneus	4	5	1	sacrum	1	
upper M1	5		unciform	3			cuboid	4			incomplete rib	2	
upper M2	9		magnum	3	1		navicular	3	1				
lower I1	2		trapeze	2			cuneiform III	2					
lower I2	1		trapezoid	3			metatarsal I	3	1				
lower I3	8		metacarpal I	1			metatarsal II	1	1				
lower P4	2		metacarpal II	5	2		metatarsal III	4					
lower M1	6		metacarpal III	7			metatarsal IV	7	1				
lower M2	5		metacarpal IV	10	1		metatarsal V	5	3				
lower M3	4		metacarpal V	6	1		frag m. metapodials	10	4				
Total	77	12		76	15	4		69	35	3		158	2

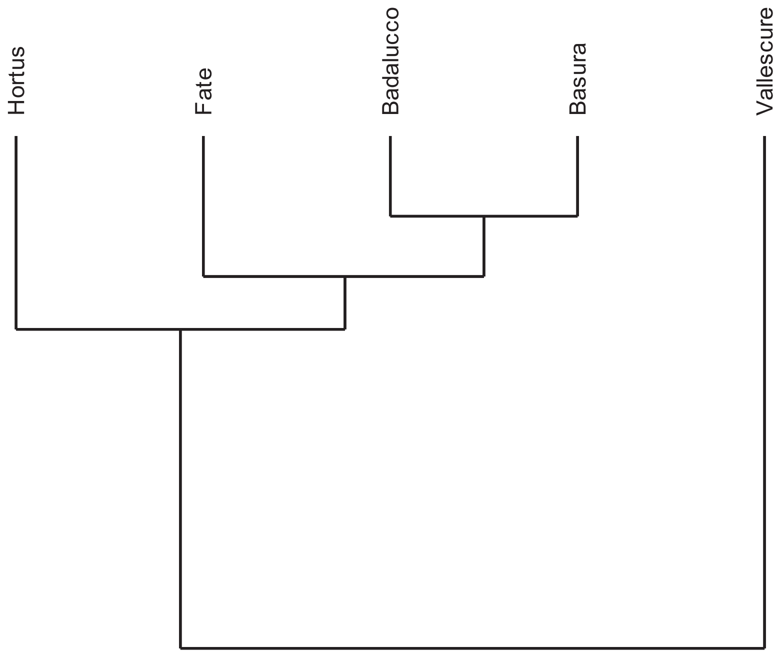


Figure 5. Cluster analysis on data from table 3 with Ward's algorithm (10000 bootstraps).

DESCRIPTION OF THE MATERIAL

"Grand Abri des Puces":

The cave bear material is scarce and composed of an isolated and incomplete mandible of an old adult (left; MR 4.01.681) (pl. 1a). The *ramus* is broken on the base of the canine and on the *fossa masseterica*. M/2 and M/3 are entire but their enamel has disappeared. Crown contours are showing characteristic constructions for spelaean bears, with a clear medial constriction of M/2 giving an "8" shape to the tooth, and the biconvexity of the labial part of the M3/. Even if Mousterian artefacts were found in the same level, diagnostic elements present on this bone are only sufficient enough to attribute it to *U.* cf. *spelaeus*.

Vallescure:

The material of Vallescure is known to be a sample of the original assemblage, due to uncontrolled lootings soon after discovery. The 451 remains of *U. spelaeus* belong to at least thirteen individuals (tab. 1). Unfortunately, important elements like skulls, mandibles and limb bones are incomplete and unusable for a paleontological characterisation. The biochronology based on P4 morphotypes (see Rabeder, 1999) is not reliable enough. Indeed, an amount of twenty teeth for each P4 is needed, and only four P4/ and two P/4 are available in this site (pl.1c to e and m, n). The strong sexual dimorphism and the high intraspecific variability, highlighted by many authors for cave bear (see Quilès, 2003 for details), invalidate the use of measurements comparisons.

A morphological grid of analysis on teeth has been preferred to define the Vallescure's sample (tab. 2). This grid summarizes 62 morphological criteria on upper and lower premolars and molars. Each criteria is divided using different coefficients (0, 1, 2…) in order to provide a quantified index (Number x Coefficient) in percentage of total occurrences of the criteria.

The Provence region is delimitated by the Alps in the East and the Rhône River in the West and the North. North Italian (Fate, Basura, Badalucco) and West of the Rhône River (Hortus) sites have been selected for comparisons with Vallescure. Given the high amount of cave bear individuals in each sites, cross comparisons over 62 criteria are reliable (tab. 3). Synthetic results are presented on a cluster tree made using Ward's algorithm during 10,000 bootstraps (fig. 5). Hortus cave (West of the Rhône) and North Italian populations are more closely related than with Vallescure lineage, even though distant from the Hortus locality by only 150 km. This isolation is effective given the OIS 4, represented by the cave bear assemblage from Fate.

Table 2
Morphodynamic study of cave bear teeth from Vallescure.

Coefficients	0	1	1.5	2	2.5	3	3.5	4	Total	Im
P4 sup.									4	
Morphotypes of the occlusal surface (Rabeder, 1999)				1		1		1	3	300
Angulation between para and metacone crests (0=strong, 2=flat)		1		2					3	166.7
Position of the deuterocone (0=very distal, 1=distal, 2=medial)		4							4	100
Development of the deuterocone (0=weak, 2=strong)				3					3	200
Individualisation of the deuterocone (0=valley, 1=cusp, 2=crest)	1			2					3	133.3
M1 sup.									5	
Development of para and metastyls (0=weak, 2=very strong)	3	1		1					5	60
Individualisation of para and metastyls (0=weak, 2=very strong)	3			2					5	80
Morphotypes of the lingual flanc of paracone (Rabeder, 1999)				1		2			3	266.7
Morphotypes of the lingual flanc of metacone (Rabeder, 1999)		3		1					4	125
Development and number of metaconule's cusps (0=weak+1,4= =very strong+3)			1	2			1		4	225
Link between protocone and metaconule (0=weak, 2=very strong)		5							5	100
Morphotypes of protocone (Rabeder, 1999)				1			2		3	300
Morphotypes of the basal cingulum (Rabeder, 1999)					2	2			4	275
Morphotypes of the talon's ornementation (Rabeder, 1999)		1		3					4	175
M2 sup.									9	
Shape of the distal margin of the talon (0=round, 1=sharp, 2=vestibular reduction)	2			4					6	133.3
Number of convexities on the lingual flanc				1		3			4	275
Morphotypes of the parastyle (Rabeder, 1999)	1	2		2					5	120
Morphotypes of the lingual flanc of paracone (Rabeder, 1999)		1	2	2					5	160
Morphotypes of the protocone (Rabeder, 1999)		2		3					5	160
Development of proto-meta-hypocones' crest (0=none,3=very strong)	1			1		2			4	200
Number of cusps on proto-meta-hypocones' crest						3			3	300
Morphotypes of the proto-meta-hypocones' crest (Rabeder, 1999)						1		2	3	366.7
Morphotypes of the link between para - and metacone (Rabeder, 1999)				4					4	200
Morphotypes of the link between metastyle and hypocone (Rabeder, 1999)		3							3	100
Morphotypes of the link between metastyle and hypostyle (Rabeder, 1999)		1		3					4	175
Morphotypes of the basal cingulum (Rabeder, 1999)					4				4	250
Morphotypes of the talon's crest (Rabeder, 1999)	1			4					5	160
Morphotypes of the talon's ornementation (Rabeder, 1999)				4					4	200

continued

Table 2 *(continued)*

P4 inf.									2	
Morphotypes of the occlusal surface (Rabeder, 1999)						2			2	300
Number of roots				2					2	200
Shape of the occlusal surface (0=ovoïd, 1=rectangular)		2							2	100
Position of the maximum height of protoconid (0=central, 2=mesial)				2					2	200
Number of antero-lingual cusps				1		1			2	250
Number of cusps on talonid		1		1					2	150
M1 inf.									5	
Morphotypes of metastylids (Rabeder, 1999)		2	1						3	116.7
Morphotypes of the entoconid (Rabeder, 1999)					1	2			3	283.3
Morphotypes of the entoconid (Argant, 1995)				1	2	1			4	250
Convexity of the vestibular flanc of the metaconid (0=weak, 2=very strong)	1	2							3	66.7
Orientation of mesial (mc) and distal (dc) crests of protoconid (0=equal, 1=mc>dc)		3							3	100
Individualisation of the paraconid (0=weak, 2=very strong)	1	1		1					3	100
Development of medio-lingual contraction (0=very weak, 3=very strong)						4			4	300
Morphotypes of the valley on talonid (Rabeder, 1999)						4			4	300
Morphotypes of the hypoconid (Rabeder, 1999)				3					3	200
Morphotypes of the lingual flanc of entoconid (Rabeder, 1999)								3	3	400
M2 inf.									5	
Development of the medial contraction (0=weak, 2=very strong)				4					4	200
Development of the basal cingulum (0=very weak, 3=very strong)		2		1					3	133.3
Number of cups on the medial crest				2					2	200
Morphotypes of the mesial crest (Rabeder, 1999)				2					2	200
Morphotypes of the trigonid (Rabeder, 1999)						1			1	300
Morphotypes of the distal crest of protoconid (Rabeder, 1999)		1	1						2	125
Number of cups on the inner flanc of the hypoconid				1		1			2	250
Morphotypes of the hypoconid (RABEDER, 1999)						2			2	300
Number of cusps on the mesial part of metaconid				1					1	200
Number of cusps on the distal part of metaconid		2							1	200
Number of cusps on the entoconid (0=1 cusp, 2= 3 cusps)		1		1					2	150
M3 inf.									4	
Morphotypes of crown's shape (Rabeder, 1999)		2		1					3	133.3
Number of lingual convexities		3							3	100
Number of vestibular convexities		1		2					3	166.7
Morphotypes of the lingual flanc of metaconid (Rabeder, 1999)	1			1					2	100
Morphotypes of the talonid (Rabeder, 1999)				1		1			2	250
Morphotypes of the entoconid (Rabeder, 1999)	1	1							2	50
Morphotypes of the hypoconid (Rabeder, 1999)			1						1	150

Table 3
Comparison of cave bear teeth morphotype indices between Vallescure, Fate, Badalucco, Hortus and Basura (after Quilès, 2003).

	Vallescure		Fate		Badalucco		Hortus		Basura	
	n	Im	n	Im	n	Im	n	Im	n	Im
P4 sup.										
Morphotypes of the occlusal surface (Rabeder, 1999)	3	300	127	102.8	14	171.4	10	215.0	64	269.5
Angulation between para and metacone crests (0=strong, 2=flat)	3	166.7	126	91.3	15	126.7	10	150.0	66	150.0
Position of the deuterocone (0=very distal, 1=distal, 2=medial)	4	100	94	147.9	14	150.0	10	100.0	65	167.7
Development of the deuterocone (0=weak, 2=strong)	3	200	98	128.6	14	114.3	10	140.0	64	156.2
Individualisation of the deuterocone (0=valley, 1=cusp, 2=crest)	3	133.3	104	101.9	14	135.7	10	130.0	64	187.5
M1 sup.										
Development of para and metastyles (0=weak, 2=very strong)	5	60	50	168.0	13	153.8	9	200.0	73	178.1
Individualisation of para and metastyles (0=weak, 2=very strong)	5	80	58	119.0	13	130.8	9	166.7	71	180.3
Morphotypes of the lingual flanc of paracone (Rabeder, 1999)	3	266.7	28	119.6	7	135.7	9	161.1	67	194.8
Morphotypes of the lingual flanc of metacone (Rabeder, 1999)	4	125	31	167.7	7	171.4	9	150.0	65	213.1
Development and number of metaconule's cusps (0=weak+1,4=very strong+3)	4	225	47	183.0	8	275.0	9	216.7	73	221.2
Link between protocone and metaconule (0=weak, 2=very strong)	5	100	41	131.7	8	162.5	9	77.8	71	160.6
Morphotypes of the protocone (Rabeder, 1999)	3	300	33	180.3	7	221.4	8	203.1	68	283.1
Morphotypes of the basal cingulum (Rabeder, 1999)	4	275	45	239.4	13	223.1	9	244.4	72	238.2
Morphotypes of the talon's ornementation (Rabeder, 1999)	4	175	37	200.0	8	175.0	9	200.0	72	194.4
M2 sup.										
Shape of the distal margin of the talon (0=round, 1=sharp, 2=vestibular reduction)	6	133.3	98	231.6	26	269.2	5	460.0	82	236.6
Number of convexities on the lingual flanc	4	275	58	200.0	25	224.0	4	275.0	83	225.3
Morphotypes of the parastyle (Rabeder, 1999)	5	120	46	171.7	13	238.5	5	220.0	95	208.9
Morphotypes of the lingual flanc of the paracone (Rabeder, 1999)	5	160	49	122.4	13	146.2	7	128.6	99	145.5
Morphotypes of the protocone (Rabeder, 1999)	5	160	45	128.9	14	150.0	7	121.4	90	152.2
Development of proto-meta-hypocones' crest (0=none,3=very strong)	4	200	60	225.0	19	205.3	6	183.3	88	234.1
Number of cusps on proto-meta-hypocones' crest	3	300	48	383.3	17	364.7	6	466.7	85	400.0
Morphotypes of the proto-meta-hypocones' crest (Rabeder, 1999)	3	366.7	47	380.9	18	452.8	6	366.7	94	435.6
Morphotypes of the link between para - and metacone (Rabeder, 1999)	4	200	44	92.1	21	209.5	6	208.3	90	172.8
Morphotypes of the link between metastyle and hypocone (Rabeder, 1999)	3	100	37	183.8	13	153.8	6	150.0	89	215.7
Morphotypes of the link between metastyle and hypostyle (Rabeder1999)	4	175	61	160.7	16	175.0	4	150.0	88	170.5
Morphotypes of the basal cingulum (Rabeder, 1999)	4	250	61	174.2	25	158.0	5	140.0	91	189.8
Morphotypes of the talon's crest (Rabeder, 1999)	5	160	52	116.3	16	106.2	4	150.0	84	132.1
Morphotypes of the talon's ornementation (Rabeder, 1999)	4	200	56	198.2	22	190.9	7	200.0	87	197.7

continued

Table 3 *(continued)*

P4 inf.									
Morphotypes of the occlusal surface (Rabeder, 1999)	2	300	151	136.4	25	157.0	12	152.1	35	162.1
Number of roots	2	200	167	65.3	27	88.9	12	41.7	35	88.6
Shape of the occlusal surface (0=ovoïd, 1=rectangular)	2	100	137	60.6	26	57.7	7	42.9	34	58.8
Position of the maximum height of protoconid (0=central, 2=mesial)	2	200	138	132.6	26	161.5	10	150.0	34	150.0
Number of antero-lingual cusps	2	250	138	207.2	26	184.6	10	240.0	34	197.1
Number of cusps on talonid	2	150	136	83.8	25	104.0	7	157.1	34	97.1
M1 inf.									
Morphotypes of metastylids (Rabeder, 1999)	3	116.7	107	173.8	33	216.7	11	181.8	76	221.1
Morphotypes of the entoconid (Rabeder, 1999)	3	283.3	115	235.2	36	247.2	15	256.7	77	259.4
Morphotypes of the entoconid (ARGANT, 1995)	4	250	144	225.7	36	245.8	23	269.6	78	243.6
Convexity of the vestibular flanc of the metaconid (0=weak, 2=very strong)	3	66.7	71	126.8	34	105.9	10	80.0	65	129.2
Orientation of mesial (mc) and distal (dc) crests of protoconid (0=equal, 1=mc>dc)	3	100	52	84.6	27	74.1	10	70.0	72	86.1
Individualisation of the paraconid (0=weak, 2=very strong)	3	100	102	56.9	36	119.4	8	150.0	75	124.0
Development of medio-lingual contraction (0=very weak, 3=very strong)	4	300	78	248.7	40	215.0	7	214.3	78	223.1
Morphotypes of the valley on talonid (Rabeder, 1999)	4	300	113	300.0	37	294.6	15	300.0	75	298.7
Morphotypes of the hypoconid (Rabeder, 1999)	3	200	67	114.6	23	126.1	14	110.7	72	122.2
Morphotypes of the lingual flanc of entoconid (Rabeder, 1999)	3	400	29	150.0	21	226.2	13	153.8	56	225.9
M2 inf.									
Development of the medial contraction (0=weak, 2=very strong)	4	200	62	161.3	40	120.0	13	138.5	90	130.0
Development of the basal cingulum (0=very weak, 3=very strong)	3	133.3	49	202.0	38	178.9	12	158.3	91	131.9
Number of cups on the medial crest	2	200	91	157.1	31	161.3	16	193.8	95	172.6
Morphotypes of the mesial crest (Rabeder, 1999)	2	200	61	173.8	29	187.9	16	193.8	95	208.9
Morphotypes of the trigonid (Rabeder, 1999)	1	300	55	257.3	28	303.6	16	231.2	95	265.3
Morphotypes of the distal crest of protoconid (Rabeder, 1999)	2	125	55	115.5	33	139.4	16	118.8	92	161.4
Number of cusps on the inner flanc of the hypoconid	2	250	94	164.9	22	195.5	15	186.7	91	231.9
Morphotypes of the hypoconid (Rabeder, 1999)	2	300	58	148.3	22	161.4	15	156.7	90	207.8
Number of cusps on the mesial part of metaconid	1	200	69	184.1	40	200.0	17	188.2	93	210.8
Number of cusps on the distal part of metaconid	1	200	71	115.5	40	127.5	18	111.1	79	110.1
Number of cusps on the entoconid (0=1 cusp, 2= 3 cusps)	2	150	72	112.5	37	100.0	16	93.8	91	102.2
M3 inf.									
Morphotypes of crown's shape (Rabeder, 1999)	3	133.3	85	148.8	49	138.8	3	166.7	58	170.7
Number of lingual convexities	3	100	126	110.3	49	118.4	2	200.0	61	113.1
Number of vestibular convexities	3	166.7	126	167.5	50	200.0	3	166.7	61	200.0
Morphotypes of the lingual flanc of metaconid (Rabeder, 1999)	2	100	51	196.1	25	268.0	3	216.7	52	287.5
Morphotypes of the talonid (Rabeder, 1999)	2	250	61	199.2	29	262.1	2	250.0	49	250.5
Morphotypes of the entoconid (Rabeder, 1999)	2	50	74	135.1	25	178.0	3	200.0	50	172.0
Morphotypes of the hypoconid (Rabeder, 1999)	1	150	50	190.0	23	278.3	3	283.3	53	284.0

DISCUSSION

The morphological study of cave bear regional lineages is demonstrates the role of the Rhône River during the Late Pleistocene as a paleobiogeographical limit, isolating Provence from around regions. Convergent arguments on ungulate and carnivore taxa are relevant to demonstrate this role at different times. The geographical context and the climate of Provence have also to be considered in the repartitioning of Pleistocene species, because:

- the area is mountainous and plains are restricted to

the Mediterranean coastal margin and to the Rhône margin,
- the Rhodanian corridor (Rhône River valley) has favoured North winds and dryness.

During the Middle Pleistocene, some species well developed to the West of the Rhône River are scarce in Provence: *U. deningeri* restricted in two caves (cf. *supra*), the Reindeer *R. tarandus* ("Les Cèdres", Crégut-Bonnoure, 1995b, Lazaret, Patou, 1984) and the Woolly Rhinoceros *Coelodonta antiquitatis* only determined in the Lazaret cave (Guérin, 1980). On the other side, the density of low to middle altitude mountains explains the largely represented species of rupicol ungulates like:

- *Hemitragus bonali*, identified in Escale cave (Bonifay, 1974-75), Terra Amata (Mourer-Chauviré & Renault-Miskovsky, 1980), "Baume Bonne" (OIS 8, Quinson, Alpes-de-Haute-Provence; Psathi, 1996) and Bérigoule (Crégut-Bonnoure, 1996).
- *H. cedrensis* recognized in "Les Cèdres", Cimay, Rigabe (Artigues, Var) (Crégut-Bonnoure, 1989; 1995b) and "Bau de l'Aubesier" (Fernandez, 2001; 2006).

Morphometrical analysis indicate that *H. cedrensis* derives from the evolution of *H. bonali* in Provence during the Middle Pleistocene (OIS 7) (Crégut-Bonnoure, 2002), demonstrating the role of the Rhône River as an ecological barrier at the end of the Middle Pleistocene (OIS 6). The same phenomena are perceptible with the Tibetan's bear *U. thibetanus,* present in three localities (cf. *supra*): morphology and proportions of the upper teeth being distinct in West of the Rhône River populations (Crégut-Bonnoure, 1996; 1997). The geographic isolation is well known for Lagomorphs (Les Cèdres; Crégut-Bonnoure, 1995c) and Rodents as the *Arvicola* from Lazaret (Desclaux *et al.* 2000) and *Pliomys* gr. *episcopalis* recognized until the OIS 6 in Provence (Les Cèdres and Lazaret; Radulescu, 1995).

The cold period of the early Late Pleistocene is responsible for the presence in Vaucluse of *A. lagopus* and *G. spelaeus*, both identified in Vallescure (Gagnière & Germand, 1934; Crégut-Bonnoure *in* Brugal & Crégut-Bonnoure, 1994), and of polar fox in "Auzières II" near Méthamis (Crégut-Bonnoure *et al.*, 1983). Therefore, these two taxa are totally absent from the rest of Provence, whereas they are identified in several localities at the West of the Rhône River. Cave hyena, *C. crocuta spelaea*, is also uncommon with three sites in Vaucluse: Vallescure (Gagnière & Germand, 1934), "Auzières II" (Crégut-Bonnoure *et al.*, 1983), "Baume des Peyrards" (Rambert, 2000) and one site in Alpes-Maritimes at "Baume Périgaud" (Tourrette-Levens, Crégut-Bonnoure, 2004c) and another in Bouches-du-Rhône at "Le Tonneau" (La Bouilladisse; Crégut-Bonnoure, 2002). The painted dog's status, *C. alpinus europaeus*, is quite similar, recognized in Vallescure (Crégut-Bonnoure *in* Brugal & Crégut-Bonnoure, 1994), "Baume des Peyrards" (Crégut-Bonnoure *in* Rambert, 2000) and Mars cave (Vence, Alpes-Maritimes; Copin-Vathaire, 1966).

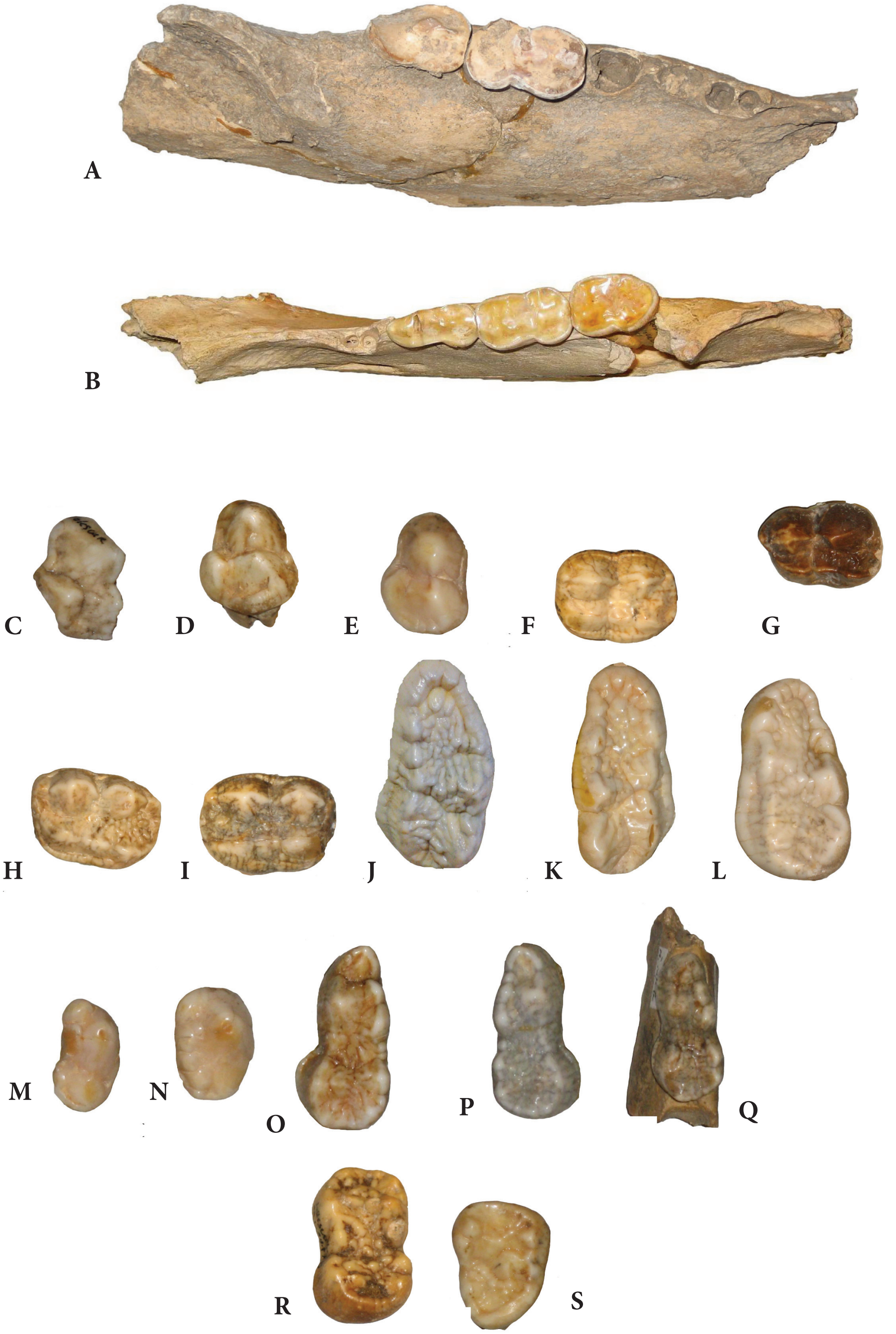
The Woolly Rhinoceros, which with Mammoth and Reindeer, is part of the classic cold faunal association of France Late Pleistocene, is again exceptional, determined only in "Auzières II" (Crégut-Bonnoure *et al.*, 1983). The Mammoth *Mammuthus primigenius*, well developed to the West of the Rhône River and on the western side of the Rhodanian corridor (Rousselières 2006), is restricted to the Vauclusian area, in the locality of "Auzières II" (OIS 4, Monchot, pers. com.) and Chinchon I (OIS 2, Crégut-Bonnoure & Paccard, 1998). The Reindeer, highly common prey of Magdalenian hunters to the West of the Rhône River (Crégut-Bonnoure, 1991), is only identified in six Provence sites. Two date from the beginning of this period: "Grotte aux Puces" (Gagnière, 1954) and Adaouste (Defleur *et al.*, 1994). In Vaucluse, Reindeer is signalled in the archaeological sites of: "Bau de l' Aubesier" (Fernandez, 2001; 2006), Chinchon I (Crégut-Bonnoure & Paccard, 1998) and Roquefure (OIS 2; Bonnieux; Gagnière *in* Paccard 1963; Crégut-Bonnoure & Paccard, 1998). The Vauclusian aven of "Les Planes" at Monieux possesses a complete skeleton of a young male (Aujard-Catot *et al.* 1979), dated of 12660 ± 75 BP (Lyon 3138). At the exception of this skeleton, in all of the other sites mentioned, the species is represented by one or two rests only, rarely more.

In contrast, Ibexes are abundant with two species:

- *C. caucasica praepyrenaica*, the Caucasian ibex discovered in Adaouste (Defleur *et al.*, 1994) and "Bau de l' Aubesier" (Fernandez, 2001; 2006);
- *C. ibex*, the Alpine ibex present in c.a. thirteen localities dated from the OIS 7 to Holocene (Crégut-Bonnoure, 2002; 2006 a & b).

Morphometrical analysis indicates that early Late Pleistocene (OIS 4) populations of Alpine ibexes from each side of the Rhône River constitute distinct biometrical entities. The Eastern group (Vallescure, "Baume des Peyrards", "Le Tonneau" populations) has short lower M_1 and M_2 and extended M_3, while the Western group ("Les Pêcheurs", Mialet, "La Sartanette" population) shows the opposite and is characterized by a less triangular horn core section (Crégut-Bonnoure, 2002; 2006 a & b).

Plate 1



A-Ursus cf. *spelaeus*, Grand Abri des Puces. Left mandible MR 4.01.681.
B to S: *Ursus spelaeus*, Vallescure. B: right mandible MR 4.00.401+4.00.729+4.00.768; C: left upper P4 MR 4.04.411; D: left upper P4 MR 4.00.782; E: left upper P4 MR 4.00.772; F: left upper M1 MR 4.00.786; G: left upper M1 MR 4.00.795; H: left upper M1 MR 4.00.781; I: right upper M1 MR 4.00.044 bis; J: right upper M2 MR 4.04.405; K: left upper M2 MR 4.00.789; L: right upper M2 MR 4.00.788; M: right lower P4 MR 4.00.773; N: right lower P4 MR 4.04.404; O: left lower M1 MR 4.04.399; P: left lower M1 MR 4.04.400; Q: left lower M1 MR 4.00.790; R: left lower M2 MR 4.00.778, S: left lower M3 MR 4.00.779.

From the OIS 3 to the beginning of the Holocene, the metaconid of the P/3 is dilating in the population of South Eastern France (Provence area) and the P/2 disappears (Crégut-Bonnoure, 1992) connected with a geographic isolation as in extant Spanish *C. pyrenaica* (Crégut-Bonnoure, 2002).

To summarize, ungulate and carnivore representations are clearly different between Provence and its surrounding regions since the Middle Pleistocene. For several taxa such as ibexes and cave bears, an evident lack of exchanges between populations across the Rhône River reflects a geographical isolation since the OIS 4 (Crégut-Bonnoure, 1992; 1997; 2002; 2006 a & b).

CONCLUSIONS

The Vaucluse is distinguishable from the eastern part of Provence by a greater biodiversity. The rich paleontological assemblage of Vallescure appears as an exception for its carnivore assemblage, registering the presence of taxa absent from the rest of Provence. The analysis of cave bear teeth morphology demonstrates a distinct lineage since the OIS 4, compared with around regions of the West of Rhône River and North Italy, documenting a geographical isolation. Other taxa like the Caprini *Hemitragus* and *Capra*, the Ursid *U. thibetanus* as well as Rodents and Lagomorphs indicate a recurrent endemism in Provence, which takes place from the end of the Middle Pleistocene to the Holocene. The probable scenario is that repeated periods of isolation occurred and alternated with periods of exchanges, in close correlation with glacial and interglacial oscillations and with the Rhône River fluctuations of the water level. During cold phases of Middle and Late Pleistocene, the Rhône acted as a major paleobiogeographical limit. The general mechanism of isolation of Provence lineages is now better understood, but there is no convenient issue to the presence of cave bear in Vallescure, that either reflect an ancestral eemian population or of a punctual passage across the Rhône River during the OIS 4.

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MIGRATION PATTERN INFERRED FROM *URSUS SPELAEUS* ROSENMÜLLER TOOTH FROM TMAVÁ SKALA CAVE (SLOVAK REPUBLIC) USING STRONTIUM ISOTOPE ANALYSES

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Abstract: Isotopes of Sr were employed in the study of *Ursus spelaeus* second upper molar M^2 from Late Weichselian bear cave Tmavá skala (Little Carpathians, Slovak Rebublic). Samples of enamel and dentine were used for the analyses. Variations in the strontium isotope ratio ($^{87}Sr/^{86}Sr$) were used to examine the migration patterns. The $^{87}Sr/^{86}Sr$ ratio of *Ursus spelaeus* dentin is 0.70913, $^{87}Sr/^{86}Sr$ ratio of enamel is 0.70930. Dentine values are close to the enamel values, suggesting little movement or migration during life.

Key words: Strontium Isotopes, Migration, Teeth, *Ursus spelaeus*, Late Pleistocene.

INTRODUCTION

To date the interest in recording seasonal and short-term climatic changes and their impact to local ecosystems has been increasing. One powerful tool enabling the reconstructing of these short-term climatic fluctuations is isotope analysis of biominerals.

After an animal's burial, its unaltered tissue can be studied to gain valuable evidence about its paleo-environment through chemical isotopic analysis.

Teeth and bones both contain biogenic phosphate (i.e. hydroxyapatite), the target substance most readily available for the study. Bone phosphate, however, is highly porous and therefore allows infiltration of water and other impurities. Subsequent alteration leads to difficulties in direct study of such matter. Tooth enamel, on the other hand, is dense and has low porosity. Such properties bolster resistance to change, making tooth enamel a strong candidate for study (Koch *et al.,* 1994).

An understanding of the migration patterns and home-range sizes of extinct animals is critical for evaluating hypotheses of extinction, speciation, evolutionary change, and paleoclimatic or paleoenvironmental studies based on fossil remains (Hoppe *et al.,* 1999).

During the Pleistocene, bears were important members of mammalian faunas. The last cave bear population of Slovakia in the area of West Carpathians began to die out in the time span between 15.000-10.000 BP (Schmidt, 1970). But it is not excluded, that some parts of Slovakia (Slovak Paradise and Low Tatras) were one of the last refugias of relative large cave bears in Central Europe between the end of Last Glacial and beginning of the Holocene (Sabol, 2001).

Cave bear teeth appear to preserve their original isotope composition, can be dated, and occur in abundance in many locations of Europe and the Near East. The abundance of the teeth and their large size allows samples used for paleoclimate studies to be restricted to enamel/dentine of one type of tooth. They provide a good potential source of material for detailed investigation of Pleistocene paleo-environment.

Here we asses the bears movements through analyses of the **$^{87}Sr/^{86}Sr$** ratios of tooth enamel and dentine. The $^{87}Sr/^{86}Sr$ ratio of an animal, and thus its teeth, equals the average $^{87}Sr/^{86}Sr$ ratio of ingested plants (Lenihan *et al.,* 1967; Price *et al.,* 1985). The ratios of plants, in turn, equal the soluble Sr in soils, which is derived from bedrock weathering and atmospheric deposition (e.g., erosols, and precipitation) (Gosz & Moore, 1989; Miller *et al.,* 1993). Environmental $^{87}Sr/^{86}Sr$ ratios thus vary with differences in bedrock age, bedrock composition, and atmospheric input.

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LOCALITY

Tmavá skala cave is situated southeastwards of the Plavecký Mikuláš village, on the Plavecký karst territory in the Malé Karpaty Mountains (Slovak Republic) under the Polámané hill, 445 m above sea level (Šmída, 1996). The cave is about 50 m long. Maximum width reaches 8,5 m and it is 1,5 to 4 m high. Its opening is oriented to the northwest. The opening to the Tmavá skala cave is in the rocky wall 3-10 m high. The wall is represented by Anisian-Annaberian limestone and underlying Verfenian siliceous sandstone.

The origin of the cave system is related to a supposed autochtonous stream (Šmída, 1996). The cave probably represents an old occasional rise, activity of which was related with changing of groundwater level, which was connected with climatic changes during Late Pleistocene. Humic soils with pebbles and osteologic material accumulated through fluvial activity of ground stream during interglacial Riss/Würm and interstadials of Würm. The groundwater level decreased during the periods of cold Würmian oscilations. On the formation of the cave sediments mainly the eolic activity took part, which created loess series. Occasional rise stopped its function in the consequence of the groundwater decrease after the Late Würm. After this time, there was Holocene sedimentation of humic soil with sharp fragments falling from the cave roof (Liška, 1973).

FOSSIL AND SUBFOSSIL FAUNA OF THE CAVE

There was a fossil gastropod and vertebrate fauna discovered in the sedimentary filling. The gastropod fauna (*Helix pomatia, Limax* sp., *Macrogastra* cf. *latestriata* (uv.), *Oxychilus depressus*, *O. inopinatus*) represents termophilous, mostly woodland gastropod fauna from Middle to Late Holocene). The vertebrate fauna (Salientia, Reptilia, Insectivora, Chiroptera, Rodentia, Carnivora, Perissodactyla, Artiodactyla) represents mixed elements from the ecological point of view (karst - woodland - open land - mountain areas) and from the stratigrafic point of view (Pleistocene - Holocene - Recent) too (Holec *et al.*, 1998).

The osteological remains of cave bears represent the largest portion of the fossil material. Due to finding circumstances (secondary redeposition of the original sediments) the ages of the fossil remains were dated only as the Late Pleistocene (Riss/Würm - Late Würm). The gastropod and other vertebrate fauna, occuring together with the fossil remains of Late Pleistocene cave bears, included mostly indifferent elements, that are characteristic for warm and woodland environment of the Holocene. It demonstrates the secondary redeposition of the original cave sediments too (Sabol, 1997).

More concrete paleoclimatic conclusions could not be carried out, as polles grains of the determined taxa (*Abies, Pinus, Tsuga, Tilia, Quercus*) were found in very small quantity in the samples (Holec *et al.*, 1998).

Tmavá skala cave is a typical bear cave with relatively stable temperature, more spacious subhorizontal space and with sufficient water quantity in the past. Therefore the cave was utilized by tens to hundreds (perhaps) of individuals of the species *Ursus spelaeus* for hibernation and birth of cubs during the Late Pleistocene (Sabol, 1997).

MATERIAL

We analyzed *Ursus spelaeus* second upper molar enamel and dentine of one individual from Tmavá skala cave in Little Carpathians, Slovak Rebublic (fig. 2.). On the base of dental cementum analyses we determined the individual age of the studied animal. The individual age of the animal is about 4,5 years and the season of the death is summer.

Shells of molluscs served for determination of migrations as geological niveau. They were represented by one species i.e. *Helix pomatia* (LINNAEUS, 1758). This species is endemic in the given locality.

Table 1

Ratio results of $^{87}Sr/^{86}Sr$ of *Ursus spelaeus* dentine and enamel and *Helix pomatia* (geological benchmark) from Tmavá skala cave.

	87Sr/86Sr	1 sigma	2S(M)
Ursus spelaeus dentin	0.70913	0.000051	0.000008
Ursus spelaeus enamel	0.70930	0.000063	0.000019
Helix pomatia shell	0.70842	0.000062	0.000013

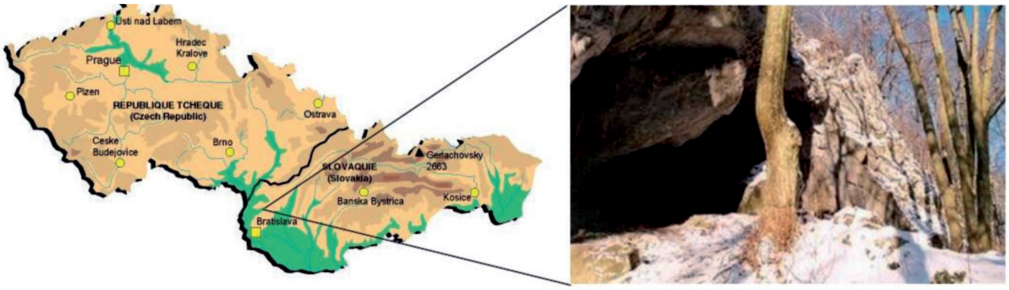

Figure 1. Tmavá skala cave, Little Carpathians, Slovak Rebublic (Photo Vodička, 2003).

METHODS

The method is based on the principle that the ratio of Sr isotopes in the tissues reflects the isotopic ratio in the diet in the time of its origin. If the tooth enamel and the dentine (or compact bone) give different values of the strontium isotopes it can be supposed that the examined animal passed the early years of the life and pre-mortal years in different geochemical kinds of environments (Bentley *et al.,* 2002).

For determination of $^{87}Sr/^{86}Sr$ ratios we used the following methodology. Samples of teeth and shells are cleaned up ultrasonically in distilled water for 15 minutes to remove alien dirts. Then sufficient amount of sample is drilled out with a dental drill. The fragments are cleaned up with ultrasonically in distilled water and in 5% acetic acid. Acetic acid should also secure that the thin surface layer is dissolved (because this layer might be contaminated by the environment in which the sample was found.) After that the fragments were dried in the laminar box. Dry material was burned at 825° for 8 hours. Obtained ash was dissolved at concentrated HNO_3, evaporated to dry, again dissolved at 6M HCl and evaporated to dry. Then follow the last dissolution and evaporating in concentrated $HNO_{3.}$ Vapour was dissolved at 2M $HNO_{3.}$ Separation ran at chromatographical columns with using ionex SR firm Eichron. (Methodology of sample preparing is partially adopted from Price, Manzanilla & Middleton (2000) (with some modifications).

The value of $^{87}Sr/^{86}Sr$ ratio was determined in a mass spectrometer with ionization from the solid phase MAT 262, mark Finnigan, in dynamic mode and in two-fibre arrangement. Thermal fractionalization was corrected by normalization to supposed value of the ratio of $^{88}Sr/^{86}Sr$ = 8,375209.

Reproducibility is checked by measurement of ratio $^{87}Sr/^{86}Sr$ isotopes of the standard NBS 987 whose long-time mean is 0.710248, with standard deviation 0.000013 (at 23 repeating).

RESULTS

Determination of mobility

Tab. 1 and fig. 3 provides a summary of results. The

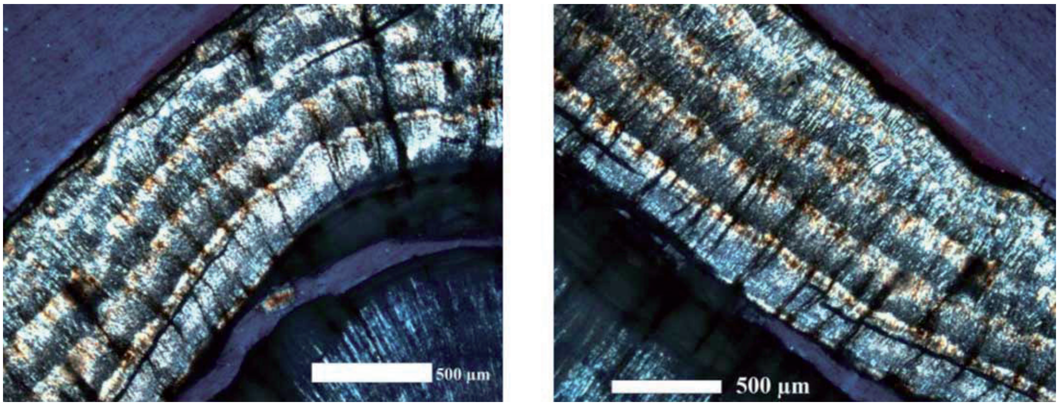

Figure 2. Transverse cross section of investigated *Ursus spelaeus* tooth (M^2) used for isotopic analyses in this study. Photo expose the dentine/cementum junction and annual increments in the cementum. Individual age estimation and season of death on the base of dental cementum analysis: about 4,5 years, death season: summer. (Photo author).

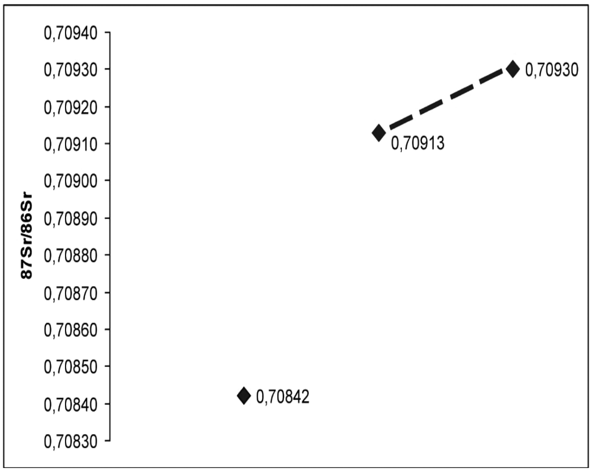

Figure 3. $^{87}Sr/^{86}Sr$ in tooth enamel and dentine of *Ursus spelaeus* from Tmavá skala cave. (*Helix pomatia* is used as a geological benchmark).

$^{87}Sr/^{86}Sr$ ratio is plotted on the y axis and *Ursus spelaeus* dentine and enamel across the x-axis (fig. 3). The $^{87}Sr/^{86}Sr$ ratio of *Ursus spelaeus* dentin is 0.70913, $^{87}Sr/^{86}Sr$ ratio of enamel is 0.70930. The $^{87}Sr/^{86}Sr$ ratio of *Helix pomatia* shell is 0.70842 (tab. 1, fig. 3).

DISCUSSION AND CONCLUSION

When we look at the $^{87}Sr/^{86}Sr$ ratio results of *Ursus spelaeus* enamel (0.70930) and dentin (0,70913) we could tell that the dentine values are close to the enamel values, suggesting little or no movement or migration during life.

Helix pomatia served for determination of migrations as geological niveau. The $^{87}Sr/^{86}Sr$ ratio from his shell (0.70842) is a little bit different from the values of *Ursus spelaeus* enamel and dentine, but this difference is not so great when we take into account the somewhat different life style of the bears and snails.

Using the procedure outlined above, the study of samples on a much larger scale could shed some light on the paleomovements of the animals.

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A LIST OF CRANIODENTAL MATERIAL OF PLIOCENE URSIDS (GENUS *URSUS*) IN THE COLLECTION OF NATURHISTORISCHES MUSEUM BASEL

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Abstract: Craniodental ursine material deposited in Naturhistorisches Museum Basel from five Ruscinian to Villanyian localities (Montpellier - MN 14a; Vialette - MN 16a; Les Pardines, St. Vallier, Senèze - MN 17) is listed. A basic description as well as a short discussion of their taxonomic status are given. Bears from Montpellier, Vialette, and Senèze can be determined, with some uncertainty, as members of *Ursus* gr. *minimus-thibetanus*, that from Les Pardines and St. Vallier as *Ursus* aff. *etruscus*.

Key words: *Ursus minimus*, *Ursus etruscus*, Ruscinian, Villanyian, France, Europe.

INTRODUCTION

During my visit to Naturhistorisches Museum Basel (NHMB) in summer 2006 I had the opportunity to study in detail the craniodental material of Pliocene ursids. Most of these specimens have already been mentioned in the literature before, but none of these was figured or described in detail. Therefore, a list of these specimens with short comments on their morphology and taxonomical status are given below.

MATERIAL AND METHODS

The material, including its inv. num., is listed separately for each locality in the following section.

The teeth measurements are defined according to Rode (1935) (see tab. 1 and 2), the terminology of their morphology is adopted from Rabeder (1983; 1989; 1999). Material was measured by a caliper. Each measuring was repeated three times and the median was used.

STUDIED LOCALITIES

MONTPELLIER

Material: Mesial fragment of M^2 sin (M. P. 509), coll. in 1932; M^2 sin (M. P. 848), coll. in 1937.

Both specimens, including their inv. nr., are mentioned in Viret (1954; p. 45 - a footnote). For the specimen M. P. 848 the maximal length and breadth were noted.

Stratigraphical position of the locality: The locality is of the Lower Ruscinian age - MN 14 (Fejfar *et al.,* 1997) or MN 14a (Fejfar & Heinrich, 1990), respectively. Therefore, the absolute age falls within the range of 4.9 and 4.5 M. A. (Fejfar *et al.,* 1997). Although, it is necessary to mention that exact stratigraphical positioning is unsure in the old collections. The contamination of the Uppermost Miocene elements is not excluded (Fejfar in verb. 2006).

Description of the studied material: M. P. 509: A hard abraded trigonid part of M^2 sin. Fossilization is grayish, in some places yellowish. Cingulum is preserved below the protocone-complex and below the mesial part of hypocone. There was probably a metaloph present between the top of metacone and protocone 2. Perhaps it was also connected with a medialwards crest of hypocone. Protocone-complex is approximately in the same line as the hypocone. It seems that there was a good developed posthypocone. (pl. 1: 1).

M. P. 848: A hard abraded, dark pink to brownish fossilized M^2 sin. Cingulum is present below the protocone-complex and the hypocone on linqual side and below paracone and metacone-complex on the buccal

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Table 1
Dimensions of the upper teeth of *Ursus* spp. from studied localities.

	Montpellier		Pardines			St. Vallier							Senèze
	M. P. 509	M. P. 848	L. P. 199, dex	L. P. 199, sin	L. P. 199	St. V. 290, dex	St. V. 290, sin	St. V. 292	St. V. 293	St. V. 755, dex	St. V. 755, sin	St. V. 970	Se 1505
Cs/: poster-anterior diameter on crown basis	-	-	-	-	17.9	-	-	-	-	22.6	22.6	-	22.6
Cs/: medio-lateral diameter on crown basis	-	-	-	-	11.4	-	-	-	-	16.1	16.3	-	15.7
Cs/: posterior crown hight	-	-	-	33.2	-	-	-	-	-	-	34.0	-	35.9
Cs/: anterior crown hight	-	-	-	-	-	-	-	-	-	-	30.5	-	34.6
Cs/: poster-anterior diameter of root	-	-	-	-	-	-	-	-	-	-	-	-	24.6
Cs/: medio-lateral diameter of root	-	-	-	-	-	-	-	-	-	-	-	-	15.7
P1/: maximal length	-	-	-	-	-	-	-	6.0	-	-	-	-	-
P1/: maximal breadth	-	-	-	-	-	-	-	5.3	-	-	-	-	-
P2/: maximal length	-	-	5.9	6.4	-	-	-	-	-	-	-	-	-
P2/: maximal breadth	-	-	4.2	4.3	-	-	-	-	-	-	-	-	-
P3/: maximal length	-	-	7.6	7.2	-	-	-	-	-	-	-	-	-
P3/: maximal breadth	-	-	5.0	4.6	-	-	-	-	-	-	-	-	-
P4/: maximal length	-	-	-	-	-	-	16.1	-	16.4	16.5	-	14.9	-
P4/: maximal breadth	-	-	-	-	-	-	11.7	-	11.2	12.1	12.1	10.4	-
P4/: breadth of constriction	-	-	8.3	8.1	-	-	10.4	-	-	11.6	-	10.2	-
M1/: maximal length	-	-	19.6	19.5	-	-	ca.21.4	22.2	20.3	22.4	22.6	20.9	-
M1/: breadth of anterior lobe	-	-	-	15.0	-	-	16.5	17.3	16.5	16.7	16.5	15.6	-
M1/: breadth of posterior lobe	-	-	15.0	15.0	-	-	16.2	17.7	16.9	16.4	16.2	16.1	-
M1/: breadth of constriction	-	-	14.7	14.9	-	-	15.9	16.8	16.3	16.0	15.9	14.6	-
M1/: length of paracone	-	-	6.9	6.9	-	-	8.3	8.0	8.1	8.9	8.3	8.4	-
M1/: length of metacone	-	-	7.0	6.7	-	-	8.0	7.6	7.6	8.0	8.0	7.6	-
M2/: maximal length	-	20.8	27.6	27.7	-	31.7	31.1	-	-	31.1	31.1	31.2	-
M2/: buccal length of trigon	ca.15.1	14.9	-	-	-	-	-	-	-	-	-	20.3	-
M2/: buccal length of talon	-	8.2	-	-	-	-	-	-	-	-	-	11.0	-
M2/: maximal anterior breadth (ovar Pa)	14.6	13.9	16.1	16.4	-	17.9	17.8	-	-	17.6	17.8	17.5	-
M2/: maximal breadth behind constriction	14.1	13.3	15.6	15.7	-	16.9	17.2	-	-	16.8	16.8	17.1	-
M2/: maximal breadth of constriction	14.0	13.4	15.8	15.6	-	16.4	16.6	-	-	17.3	-	16.9	-

one. The buccal cingulum is weak. Both buccal and lingual cusp lines are a little medialwards bent in their distal part. The protocone-hypocone boundary is placed more medialwards than usually in *Ursus*. Metalophid was present. But due to abrasion, it is not clear if it was connected with paracone 2 or/and with hypocone. Talon is short and strongly rotated. Viret (1954) gives measurements 21.2 x 13.8 for this specimen. According to the author, the maximal length is 20.8 and frontal width 13.9. The differences in maximal length are probably caused by a slightly different orientation of the tooth during measuring. (pl. 1: 2).

Comparsion and discussion: The finds of *Ursus*-remains from Montpelier are the world's-oldest record of the genus. In Asia there is the oldest find of *Ursus* sp. recorded from the Gaozhung Formation (Yushe area, China) (Qiu, 2003). The age of this faunal assemblage is thought to be about 4.0 M. A. (Flynn *et al.,* 1991; Flynn & Wu, 2001) or between 4.5 and 4.1 (Qiu, 2003), respectively. The first record (determined as *Ursus abstrusus*) in North America comes from the White Bluffs fauna (Washington, USA), that is about 4.3 M. A. old (Hunt, 1998). Approximately of the same age (or a little older) is a find from Gray Site (Washington, USA), determined as "? *Ursus* sp."(Parmalee *et al.,* 2002). Tedford & Harrington (2003) mentioned an Early Pliocene (5.0 - 4.0 M. A.) fauna from Ellesmere Island (Nunavut, Canada) that also includes a bear called *Ursus abstrusus*.

The mesial fragment (M. P. 209) is similar in both, morphology and size to the M^2 from Baróth-Köpecz (=Baraolt-Căpeni, Romania) (Maier von Mayerfels, 1929; Ryziewicz, 1969). Similarity with a bear from Per-

Table 2
Dimensions of the lower teeth of *Ursus* spp. from studied localities.

	Vialette	St. Vallier					Senèze
	Vt. 94	St. V. 291	St. V. 294	St. V. 295	St. V. 296	St. V. 793	Se 1714
c/i: postero-anterior diameter on crown basis	21.5	22.4	-	-	-	-	-
c/i: medio-lateral diameter on crown basis	ca.13.7	16.5	14.2	-	-	-	-
c/i: postero-anterior diameter of root	23.3	-	-	-	-	-	-
c/i: medio-lateral diameter of root	15.5	-	-	-	-	-	-
p/2: maximal length	-	-	-	-	5.8	5.4	5.8
p/2: maximal breadth	-	-	-	-	4.6	5.3	3.2
p/3: maximal length	-	-	-	-	-	-	6.2
p/3: maximal breadth	-	-	-	-	-	-	4.5
p/4: maximal length	-	10.7	-	12.8	-	-	-
p/4: maximal breadth	-	7.2	-	7.4	-	-	7.3
p/4: hight of protoconid	-	-	-	8.4	-	-	-
m/1: maximal length	-	23.0	-	-	-	-	-
m/1: buccal length of trigonid	-	14.9	-	-	-	-	-
m/1: buccal length of talonid	-	8.1	-	-	-	-	8.3
m/1: lingual length of talonid	-	-	-	-	-	-	8.7
m/1: maximal breadth of trigonid	-	9.9	-	-	-	-	9.7
m/1: maximal breadth of talonid	-	-	-	-	-	-	11.1
m/1: breadth of constriction	-	10.4	-	-	-	-	10.2
m/2: maximal length	-	23.2	-	-	-	-	23.1
m/2: buccal length of trigonid	-	14.3	-	-	-	-	14.8
m/2: buccal length of talonid	-	9.1	-	-	-	-	8.2
m/2: maximal breadth of trigonid	-	14.4	-	-	-	-	14.0
m/2: maximal breadth of talonid	-	-	-	-	-	-	14.8
m/2: breadth of constriction	-	14.9	-	-	-	-	13.8

pignan (France) is mentioned by VIRET (1954). In general character, this tooth is inside a known variability for bears of Ruscinian to Lower Villanyian. Due to a state of abrasion and a fragmentariness of the specimen, no more detail comparison is possible.

The complete left M^2 (M. P. 848) is more atypical. The general form of the tooth (e. g. more closed distal end of trigon, relatively medialy placed Pr/Hy boundary or short talon beginning almost immediately behind the metacone tip) as well as its small size, are unusual among Pliocene ursines, for which, among others, more opened trigon, more elongated talon and maximal length ^{3} 23.00 mm are prevalent. Only a left M^2 (specimen no. 2) from Odesskie Katakomby is similar in size (maximal length 21.0 mm), but it has a more reduced talon (ROŠČIN, 1956). Fine morphology is not very recognizable from a published photo, but it seems little different. The age of Odesskie Katakomby is correlated to terminal Ruscinian or a transition Ruscinian-Villanyian (VANGENGEIM *et al.,* 1996). The states of characters mentioned above are thought to be of plesiomorphic character and are known, in a more intensive development, in genus *Ursavus*. The assignment to the genus *Ursus* is problematic and it is not possible to exclude, for this time, that this specimen belongs to an advanced form of genus *Ursavus*.

Based on the above mentioned, the author supposes that both specimens could belong to the same paleopopulation of archaic bears of genus *Ursus*, representing two different poles within the intraspecific variability. The plesiomorphic characters of M. P. 848, indicating an *Ursavus*-like morphology for ancestral taxon of *Ursus*, has never been recorded in *Ursus* before (some parallels could be seen only in sbg. *Helarctos*). The taxonomical status of bear from Montpellier has already been discussed for several times. The latest revisions (BARYSHNIKOV, 1991; MAZZA & RUSTIONI, 1994a; MORLO & KUNDRÁT, 2001) synonymized this bear with *U. minimus* (the last one with *U. m. boeckhi*). New data shows, at least, that there exists a larger variability among Lower Pliocene ursids than was previously thought and therefore a new revision in detail of these forms seems to be necessary for a more precise taxonomical determination.

Table 3
Dimensions of the mandibles of *Ursus* spp. from studied localities.

	St. Vallier	Senèze
	St. V. 291	Se 1714
length of cheek teeth row p4/ - m/3	-	76.7
p4/ - ci/ diastema length	-	34.7
p1/ - p2/ diastema length	-	2.5
p2/ - p3/ diastema length	12.0	7.4
p3/ - p4/ diastema leng th	4.4	7.3
labial hight of the horizonal ramus under m2-3/	44.3	53.5
labial hight of the horizonal ramus under m1/	43.3	49.3
breadth of the horizonal ramus between p4/ - m1/	19.3	16.4
breadth of the horizonal ramus between m2/ - m3/	20.9	23.1

VIALETTE

Material: C_i sin (Vt. 94), coll. in 1906.

An isolated canine from this locality is mentioned in Dubois & Stehlin (1933; p. 62). This specimen was listed in Heintz *et al.* (1974; p. 177), including its inv. nr., but without any description.

Stratigraphical position of the locality: The locality is of the Lower Villanyian age - MN 16a (Fejfar & Heinrich, 1990; Fejfar, 2001). According to these authors, based on the micromammals, this locality is approximately of the same age as Arondelli-Triversa (Italy) or Hajnáčka (Slovakia). The same stratigraphical position, as an equivalent of Triversa F. U. (first Villafranchian faunal unit in the Italian faunal succession schema), is for Vialette proposed by Azzaroli *et al.* (1988) based on macrommamals. The Ruscinian/Villafranchian boundary is identified with MN 15/MN 16 boundary (Palombo *et al.* 2000-2002) and characterized by "*Leptobos*-event" - FAD of *Leptobos* in (southwest) Europe (Azzaroli *et al.* 1988). In this context it is remarkable that Heintz *et al.* (1974) revised the Vialette fauna and resulted that there is no *Leptobos* present. These authors included Vialette into "Zones des Etouaires" together with classical locality Etouaires but older than the last one. They proposed for Vialette an absolute age of about 3.8 M. A. But this date seems to be overvalued, because the MN 15/MN 16 boundary used to be placed at the Gilbert/Gauss paleomagnetic boundary - ca. 3.58 M. A. (Fejfar *et al.,* 1998) or even later (Albianelli *et al.,* 1997). According to Bandet *et al.* (1978) the age of Vialette fauna is between 3.3 M. A. and 2.6 M. A., but an age younger than 3.1 M. A. seems to be very improbable (see Fejfar *et al.,* 1998; Albianelli *et al.,* 1997).

Description of the studied material: Vt. 94: The enamel has a beige fossilization, the bone is brownish, in some places black. An abrasion is intermediate, evident only on the top of the crown. The enamel is missing in the lower half of an anteromedial wall of the crown and in the place of a posterior enamel crest. There is a weak damage at the top of the tooth's root.

The posterior enamel crest is preserved only in a small area below the crown's top. The enamel margin of the crown is, due to the damage, indistinct in a medial half. A spiral rotation, typical for ursid lower canines, is very vague. (pl. 2: 1).

Comparison and discussion: An isolated canine can not be used for taxonomical results. A lateral enamel border seems to be less steep than that in the specimen from Wölfersheim (Morlo & Kundrát, 2001) or Baróth-Köpecz, that could theoretically support its higher evolutionary stage in comparison to the Ruscinian forms.

Bears from this stratigraphical niveau (MN 16a) are relatively rare. Probably the best preserved material comes from Gaville (Castelnuovo lacustrine phase of Upper Valdarno, Italy) described in detail and determined as *U. minimus* by Berzi (1966), but no measurements or detailed figure is given for canines. The same bear species is also mentioned from Triversa (Italy) but without any information about material (Azzaroli, 1977; Palombo *et al.,* 2000-2002). Azzaroli *et al.* (1986) listed this species also in Arondelli local fauna (Italy), that is adopted with some doubtfulness by Rustioni & Mazza (1993) and Mazza & Rustioni (1994a). But neither Berzi *et al.* (1970) nor Azzaroli (1977) mentioned any *Ursus* in this fauna. Sabol (2004) mentioned one isolated anterior premolar from the locality Hajnáčka I (Slovakia) determined as Ursidae gen. et sp. indet. and mentioned some similarities with black bears‘ anterior premolars. From Vialett itself a bear was listed under a name *U. etruscus* by Heintz & al. (1974, this authors included into this species also *U. minimus*).

Based on the above mentioned it seems probably that this canine belongs to a bear from *Ursus* gr. *minimus-thibetanus* sensu Mazza & Rustioni (1994a), although this result is not possible on the specimen itself.

LES PARDINES

Material: Maxillary fragment with an almost complete set of cheek teeth (L. P. 199), coll. in 1935; C^s sin. and a small fragment of canine root (both L. P. 228), coll. in 1939.

Heintz *et al.* (1974; p. 177) mentioned a specimen inv. nr. L. P. 199 (without any description) but incorrectly wrote, that this is a mandible.

Stratigraphical position of the locality: The locality is of the Upper Villanyian age - MN 17, probably of its lower part (Fejfar *et al.,* 1997) but the exact position within this zone remains open. It is younger than Roccaneyra, the basal fauna of MN 17 zone with faunal assemblage of transitional character between MN 16b and MN 17 zones (e. g. present of *Leptobos elatus* or *Hipparion* sp. instead of *Equus* spp.; Heinz *et al.,* 1974). The absolute age of Roccaneyra is indicated between 2.5 M. A. (Bout, 1970) and 2.35 to 2.00 M. A. (Bonifay, 1990). The locality Les Pardines is connected with a later volcanic phase in Perrier plateau than that of Roccaneyra, with the age proposed about 2.00 M. A. (Bonifay, 1990). The fauna of Pardines contains no more archaic (MN 16b) elements (although Kurtén (1963) mentioned co-occurence of *Equus* and *Hipparion* in this locality, Heintz *et al.* (1974) listed no *Hipparion* among taxa from Pardines). The faunal assemblage is thought to be similar to that of St. Vallier (Heintz *et al.,* 1974) or somewhat older (Guérin & Faure, 2002; Torre *et al.,* 2002). The higher age of Pardines is supported also by an absence of *Gallogoral*, that occurs for the first time in St. Vallier (Grégut-Bonnoure, 2002).

Description of the studied material: L. P. 199: Maxillopalatal fragment of skull with I^3 dex, C^s dex., P^2-M^2 dex. et sin., and an alveolus of P^1 dex. The enamel is fossilized from dark greyish to black, the bone mainly brownish. Most of palatal part is missing, the rostral part is damaged. All teeth, but P^{2-3} sin. et dex, are well worn.

Teeth are relatively small. Due to the abrasion no fine morphological structures are preserved. M^2s bear an intermediately developed cingulum approximately below protocone-complex and anterior half of hypocone on the lingual side and below paracone on the buccal one. These two parts were probably connected together by a mesial margin (= Mesialrand sensu Rabeder, 1999). There was probably no parastyle present at the contact between a mesial margin and paracone but the cingulum gets stronger in this region. No accessory cusps are evident on the buccal side. Talon is relatively short. M^1s bear cingulum along the buccal side (there is not a clear state on the lingual one due to an abrasion). Both, parastyle and metastyle are present. Metastyle is well developed, parastyle is weak. P^4s bear cingulum along the buccal side and in front of protocone on the lingual one. Both fourth premolars are hard worn on the messial slope of the paracone, the left one is moreover damaged in this part. Protocone is situated approximately opposite the groove between paracone and metacone. Protocone bears no accessory cusps. Anterior premolars are well developed, separated by fairly wide diastemata. Canine possesses an abrupt tip of crown. A posterior enamel crest is marked. (pl. 1: 3-4; pl. 2: 3).

L. P. 228: C^s sin. The enamel is fossilized greyish, the bone yellow-brownish and greyish. Abrasion is weak. Approximately central third of the tooth (both, root and crown) is badly damaged in its anterior half. A posterior enamel crest is marked in all crown's length, although it is damaged in its lower part. (pl. 2: 2).

Comparison and discussion: The dimensions are relatively small, under the values obtained for St. Vallier bears deposited in NHMB but still within the variability found out by Viret (1954). A hard abrasion makes impossible any more detailed comparison. But the gross morphology is the same as in the bears from St. Vallier. Anterior premolars were well developed. Kurtén (1963) and Heintz *et al.* (1974) listed this bear under *U. etruscus*. The author finds it more suitable to call it, preliminary, *Ursus* aff. *etruscus* sensu Mazza & Rustioni (1992).

ST. VALLIER

Material: Fragment of skull (St. V. 290), coll. in 1952; right hemimandible (St. V. 291), coll. in 1952; M^1 sin. (St. V. 292), coll. in 1952, left maxillary fragment with P^4-M^1 (St. V. 293), coll. in 1952, fragment of C (St. V. 294), coll. in 1952; P_4 dex. (St. V. 295), coll. in 1952, anterior P (St. V. 296), coll. in 1952, fragment of skull (St. V. 755), coll. in 1952; fragment of anterior P (St. V. 792), coll. in 1953, anterior P (St. V. 793), coll. in 1953, left maxillary fragment with P^4-M^1 (St. V. 970), coll. in 1954.

Viret (1954; p. 40) only the mandible described in detail (St. V. 291), but gave no picture. Torres (1992) used this material for comparison with that from Venta Micena. Mazza & Rustioni (1992) studied it in detail following specimens and gave their measurements: St. V. 291-296, 792 and 970. None of these was figured.

Stratigraphical position of the locality: The locality is of the Upper Villanyian age - MN 17 (Fejfar *et al.,* 1997). This is a type locality for MN 17 zone and the Middle

Villafranchian sensu AZZAROLI (1970; 1977). Through the new excavation two fossiliferous horizons were indicated, both approximately of the same age (DEBARD *et al.,* 1994). Most of authors proposed for this locality age about 2.0 M. A. (see GUÉRIN & FAURE (2002) for an overview).

Description of the studied material: In all specimens, but St. V. 290, enamel is fossilized whitish, bone yellow-whitish. The different color of bone in St. V. 290 could be caused by the type of conservation.

St. V. 290: A weakly deformed skull fragment without occipital, rostral a distal part of palatal region as well as zygomatic arches, with M^2 dex., P^4-M^2 sin., and alveoli of P^3-M^1 dex. and P^3 sin. Enamel is fossilized whitish, a bone yelowish. All teeth are very well abraded.

In M^2s there is preserved only a rest of cingulum on the buccal side below a mesial half of paracone. Talons are short but wide. In M^1, there is missing most of the buccal slope of paracone and almost a complete parastyle. Cingulum remains only below metacone. Metastyle is well developed, parastyle was probably only weak. P^4 has an oval, mesially pointed shape. Cingulum is present along a buccal side and continues uninterruptedly on the lingual one as far as protocone. Protocone is placed approximately opposite the groove between paracone and metacone. No metastyle is evident. (pl. 3: 2).

St. V. 291: A right mandible with present C_i and P_4-M_2, alveolus of M_3, and a rest of alveolus of P_1. All teeth are well abraded. Most part of ascending ramus is broken off. Symphysis is damaged in its mesial part. There are present 2 - 3 foramina mentalia; the largest one is situated below P_4, the smaller one below P_3. There is probably still the third one below P_2, but this is unclean due to a state of preservation.

There is damaged buccal side of hypoconid in M_2. Entoconid-complex extends relatively messialwards in M_2, as compared to hypoconid. M_1 is damaged on the buccal slope of hypoconid and weakly also in the area between metaconid and entoconid. A very weak cinugulum is present below the paraconid/protoconid as well as trigonid/talonid boundary on the buccal side. There is a mesial metastylid developed. Between the metastylid and paraconid there is a small accessory cusp of uncertain origin present. The distal arm of metaconid turns medialwards, without reaching entoconid. Entoconid is unicuspid, well developed, placed on the linguo-distal corner. P_4 is unicuspid with a well developed protoconid. Protoconid bears sharp mesial and distal arm. Approximately in the half of the last one is a short lingualwards crest present. Almost around all the tooth is a cingulum present. In C_i there is developed a posterior enamel crest only very weakly. (pl. 1: 11-13; pl. 2: 6; tab. 3).

St. V. 292: An isolated M^1 sin. Hard abraded, damaged on the buccal slope of paracone and on the mesial basis of protocone. Cingulum is present along the both, lingual and buccal side. Buccal and lingual lines of cusps are approximately parallel. There are present good developed mesocone as well as parastyle and metastyle, the last one is the larger. (pl. 1: 10).

St. V. 293: A small maxillary fragment with P^4-M^1 sin., intermediately abraded. Cingulum is present along the both, lingual and buccal sides. Buccal and lingual lines of cusps are approximately parallel or slightly converge distalwards. There are good developed mesocone and metastyle present, parastyle extremly weak. P^4 has damaged linguo-messial side and the top of metacone. Cingulum is present around the whole crown, but on the distal end of metacone. Protocone is placed mesially from the groove between paracone and metacone. No metastyle is evident. (pl. 1: 8-9).

St. V. 294: A crown of canine, probably inf. dex., with damaged crown's basis on the medial and posterior side. Abrasion is only very weak. A posterior enamel crest is well marked in all the crown's length.

St. V. 295: An isolated P_4 dex. with a damaged crown's basis in some places. A weak cingulum located in distal half of the tooth. Protoconid bears sharp serrated mesial and distal arms. Approximately in the half of the last one there is a short linguo-distalwards crest present. Protoconid is dominant, very weak hypoconid and entoconid are present as swellings of distal or disto-lingual cingulum, respectively.

St. V. 296: An isolated anterior premolar. It was determined as P_3 in MAZZA et RUSTIONI (1992). But according to the author, the determination as P_2 or P^2 seems to be more probable. Abrasion is weak to intermediate. The tooth is oval without a cingulum. Only one main cusp is developed, with its point divided by a shallow notch.

St. V. 755: A skull fragment is medio-lateraly deformed, with missing occipital part as well as zygomatic arches. I^1 dex., I^{1-3} sin., C^s dex. et sin., P^1 sin., P^4-M^2 dex. et sin. are present, moreover an anterior premolar is stuck on the position of P^3 dex. Alveoli of P^{1-2} dex. and P^{2-3} sin. are free and relatively well preserved. An anterior premolar on the position of P^3 dex. is a left one, perhaps P^3 sin. Also P^1 sin. seems to be secondary stuck and it is not excluded that this is P^2 sin. All teeth are well abraded. This specimen was not listed in MAZZA & RUSTIONI (1992).

In M^2 sin., there is damaged crown's basis below metacone. Due to a hard abrasion, neither in right nor in left

M^2 is a clear extent of cingulum. Only in the left one, is there a small part of cingulum preserved below a mesial half of paracone. In both M^2s, paracone bears a mesial accessory cusp and probably also parastyle was present. Talons are short and get quickly narrow. M^1 dex. has a damaged buccal slope of paracone and the basis below hypocone. The left one has a slight damage on the buccal slope of paracone. Both M^1s are very similar from the morphological point of view. Buccal and lingual lines of cusps are approximately parallel, metastyle and parastyle are present. The last one is smaller. Mesocone is only a small cusp wedging in between hypocone and two-pointed protocone. In P^4 sin. the mesial end of the tooth is broken off. Both P^4s are triangular in occlusal view, with cingulum around all tooth, protocone placed messialy from paracone/metacone boundary, and with metastyle. In both canines a posterior enamel crest is present. (pl. 2: 4; pl. 3: 1).

St. V. 792: A fragment of anterior premolar. Mazza & Rustioni (1992) determined this specimen as P^2. The author does not believe that such an exact determination of this fragment is possible.

St. V. 793: An anterior premolar, probably P2 inf. or sup. Not mentioned in Mazza & Rustioni (1992).

St. V. 970: A fragment of left maxilla with P^4-M^2 and probably an alveolus of P^3. An abrasion is only very weak. M^2 bears relatively weak cingulum below protocone-complex and hypocone. A small granulation is presented on the buccal wall between the paracone and metacone. Paracone is large with a strong central crest extending to a basis of protocone 1. In front of the paracone, there is a small accessory cusp that is in contact with a very weak parastyle. Metastyle is not present. A relatively strong metaloph is developed, connecting the top of metacone and a distal end of the protocone-complex. The last one is divided into two main parts but without dominant points. Hypocone is well developed, a posthypocone is not present. Talon is short but relatively huge. M^1 bears cingulum along the both, lingual and buccal side. Buccal and lingual lines of cusps converge slightly messialwards. Parastyle is very weak, metastyle pronounced with a very small distal accessory cusp-like structure. Mesocone is divided into two parts, the mesial one is smaller. P^4 bears a cingulum around whole tooth. Protocone is placed messialy from paracone/metacone boundary. Metacone had divided its top. Metastyle was not present. (pl. 1: 6-7; pl. 2: 5).

Two more specimens are preserved in the NHMB collection as incisives of *Ursus* - St. V. 297 and St. V. 298. The first one is indetermined as I^2 in Mazza & Rustioni (1992). The author did not include these two teeth in this overview due to their doubtful status.

Comparison and discussion: The bears from St. Valliers have been studied in detail repeatedly since Viret‘s (1954) monograph. All of these specimen, but skull fragment St. V. 755, were also included in the revision of *U.* gr. *etruscus* by Mazza & Rustioni (1992). No important additional information was obtained in the present revision and the author can only support the idea (Baryshnikov, 1991; Mazza & Rustioni, 1992) of separation of these bears from the typical *U. etruscus* from Upper Valdarno. The designations of *Ursus etruscus* subsp. sensu Baryshnikov (1991) or *Ursus* aff. *etruscus* sensu Mazza & Rustioni (1992) seems to be adequate.

When we compare the dimensions of the same specimens published e. g. in Mazza & Rustioni (1992) and those in the present paper, in some cases relative large differences can be found. The author thinks that this is not due to an inaccuracy of work. It is caused by a subjective element (e. g. orientation of tooth, decision of placing the measurement point, etc.) that is a principal and inseparable component of any measurement process (especially when someone works with bunodont teeth). This fact restricts the value of metrical characteristic as well as the possibility of comparison of data published by different authors.

SENÈZE

Material: Left hemimandible (Se 1714), coll. in 1928; C^s sin. (Se 1505); fragment of C (? sup. sin.) (Se 1581), coll. in 1914); fragment of C (? sup. dex.) (Se 1660), coll. in 1920.

The mandible is briefly discussed in Dubois & Stehlin (1933; p. 63) (there are a few measurements given, but no figure). Torres (1992) used this material for comparison with that from Venta Micena. The left mandible could be an original of a cast discussed in Mazza & Rustioni (1992; p. 114). But neither this paper nor Mazza & Rustioni (1994b) specify this item enough or figure it.

Stratigraphical position of the locality: The age of fauna is uncertain. Two different niveaus are present: the earlier one of the Upper Villanyian age (younger than St. Vallier) and the later one of the Biharian age (see Mazza & Rustioni (1994b) and Spassov (2002) for an overview). It is not clear to which faunal assemblange several taxa belong, including the bear (Mazza & Rustioni, 1994b). Mazza & Rustioni (1994b) discussed both possibilities (based on the character of preservation of bear material, the Pleistocene age would be more probable), on the other hand, Guérin (in Spassov, 2002) presumed an Pliocene age for most of fauna.

Description of the studied material: Se 1714: A left hemimandible with a fragment of C_i, P_2-M_2 and alveoli of P_1 and M_3. Most part of the ascending ramus is broken off. The enamel is fossilized yellowish, the bone mainly brownish. An alveolus of M_3 is slightly inclined and partly placed in the ascending ramus. There are three foramina mentalia present. The most distal one is located below a distal root of P_4, the largest one below P_3, and the smallest one below P_2. All three anterior premolars were present. The spacing of premolars is very similar to that of the mandible figured in Mazza & Rustioni (1994b). All teeth, but $P_{2\text{-}3}$, are badly abraded.

M_2 has the lingual half of damaged distal wall. A very short segment of cingulum is present on a buccal boundary of trigonid/talonid. A large mesial metastylid is present. A mesolophid is well developed. M_1 is with a broken paraconid. There is a weak cingulum below the hypoconid and the mesial end of protoconid-complex. In front of metaconid there is a large messial metastylid present. A complete medial slope of protoconid is covered by the body of metaconid-complex. There is a small accesosoric cusp in the notch between paraconid and metaconid-complex. Entoconid-complex is formed by a large main distal cusp and two small cuspids on a messial edge. P_4 is damaged at its distal end. The tooth is oval in the occlusal view, only protoconid is developed. Distal arm bifurcates in its distal half. (pl. 1: 14-16; pl. 2: 8; tab. 3).

Se 1505: Slightly abraded, good preserved canine with whitish to yellowish fossilized enamel and dark brownish bone. A posterior enamel crest is well marked in all crown's length. (pl. 2: 7).

Se 1581 and 1660: Two badly preserved fragments of canines with badly damaged crowns.

Comparison and discussion: Although the material from Senèze is very scanty and badly preserved, the author supports the opinion of Mazza & Rustioni (1994b) that this bear belongs rather to *Ursus* gr. *minimus-thibetanus* than to *Ursus* gr. *etruscus*. One of the reasons, not mentioned in Mazza & Rustioni (1994b), is a character of entoconid-complex. In the specimen from Senèze, it has a character of a main distal cusp with a mesially decreasing crest bearing two small cusp-like structures. On the contrary, for *U. etruscus* one well emergated cusp without any accesory cusps or crests is more characteristic.

Correspondence in mandible and teeth measurements as well as in position of anterior premolars in right hemimandible described in Mazza & Rustioni (1994b) and the left one from NHMB supports the idea that these two specimens belong to the same individual.

RESULTS

Craniodental material of *Ursus* spp. from five Pliocene localities displayed in the Naturhistorisches Museus Basel was newly redescribed and its taxonomic status shortly discussed. Based on the above mentioned findings, the following results showed:

1) Bears from Montpellier represent the world-oldest known record of genus *Ursus*. It seems that this paleopopulation include more derived morphotypes known also in the other Ruscinian bears as well as more plesiomorphic ones that has never been described in *Ursus* before. Similarities with members of *Ursus* gr. *minimimus-thibetanus* are notable.

2) An isolated and damaged canine from Vialette can not be used for detail taxonomical determination. But based on the stratigraphical position of the locality, it seems probable that it belongs to *Ursus* gr. *minimimus-thibetanus*.

3) Based on both morphological and metrical characters, the material from Les Pardines can be preliminarily determined as *Ursus* aff. *etruscus*.

4) Restudy of material from St. Vallier confirmed its distinction from typical *U. etruscus* from Upper Valdarno and supported the determination as *Ursus* aff. *etruscus*.

5) Badly preserved material from Senèze can support an idea presented by Mazza & Rustioni (1994b) that this bear belongs to *Ursus* gr. *minimimus-thibetanus*.

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Plate 1

Ursus sp. from Montpellier. 1. M^2 sin. (M. P. 509) - occlusal view. 2. M^2 sin. (M. P. 848) - occlusal view. *Ursus* aff. *etruscus* from Les Pardines. 3. M^2 sin. (L. P. 199) - occlusal view. 4. M^1 sin. (L. P. 199) - a: occlusal view; b: buccal view. 5. P^4 sin. (L. P. 199) - occlusal view. *Ursus* aff. *etruscus* from St. Vallier. 6. M^2 sin. (St. V. 970) - occlusal view. 7. M^1 sin. (St. V. 970) - a: occlusal view; b: buccal view. 8. M^1 sin. (St. V. 293) - a: occlusal view; b: buccal view. 9. P^4 sin. (St. V. 293) - occlusal view. 10. M^1 sin. (St. V. 292) - a: occlusal view; b: buccal view. 11. M_1 dex. (St. V. 291) - a: occlusal view; b: lingual view. 12. M_2 dex. (St. V. 291) - occlusal view. 13. P_4 dex. (St. V. 291) - lingual view. *Ursus* ex gr. *minimus-thibetanus* from Senèze. 14. M_1 sin. (St. V. 1714) - a: occlusal view; b: lingual view. 15. M_2 sin. (St. V. 1714) - occlusal view. 16. P_4 sin. (St. V. 1714) - a: occlusal view; b: lingual view (1-2, 6-16 - photo O. Fejfar; 3-4 - photo J. W.).

Plate 1

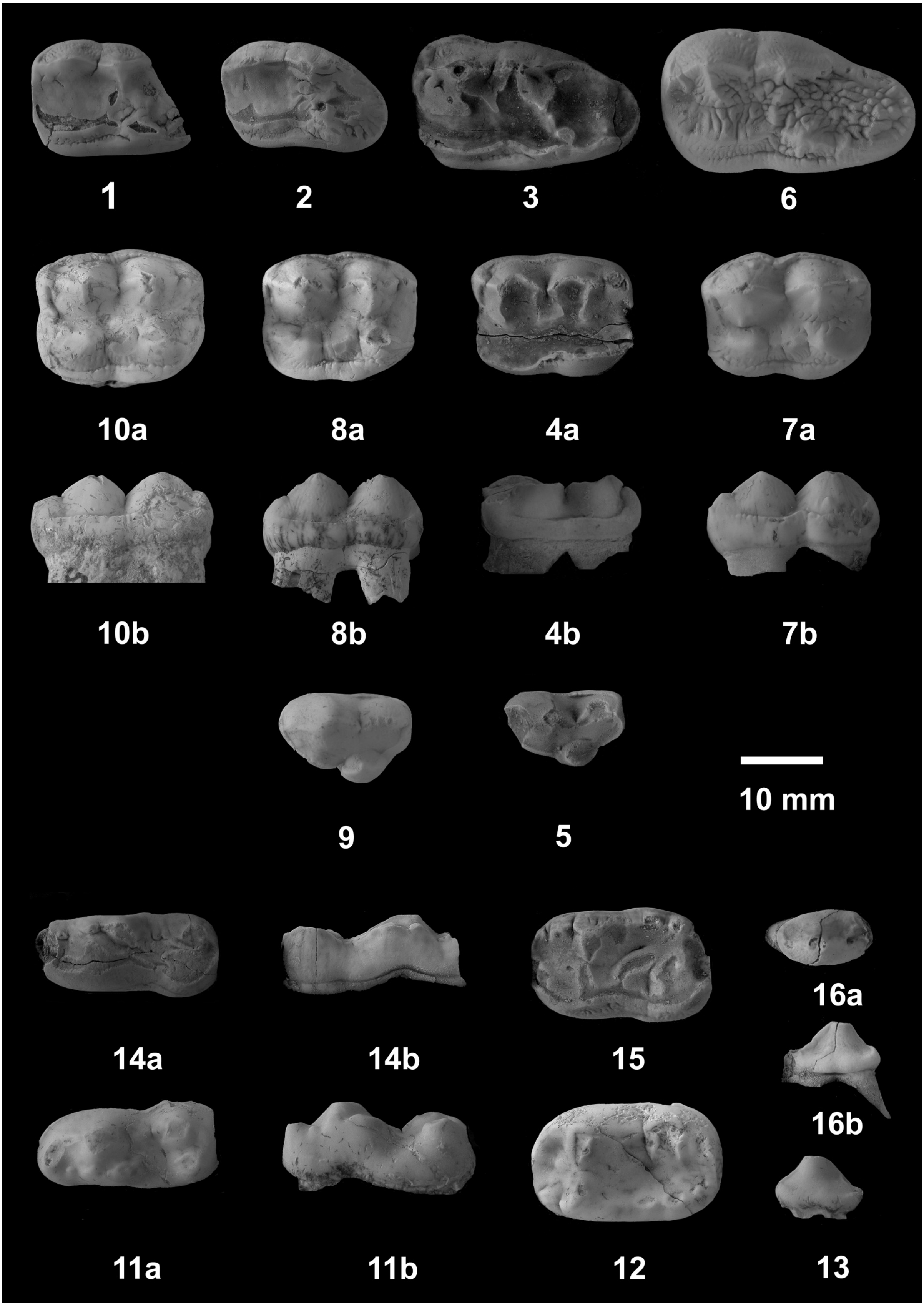
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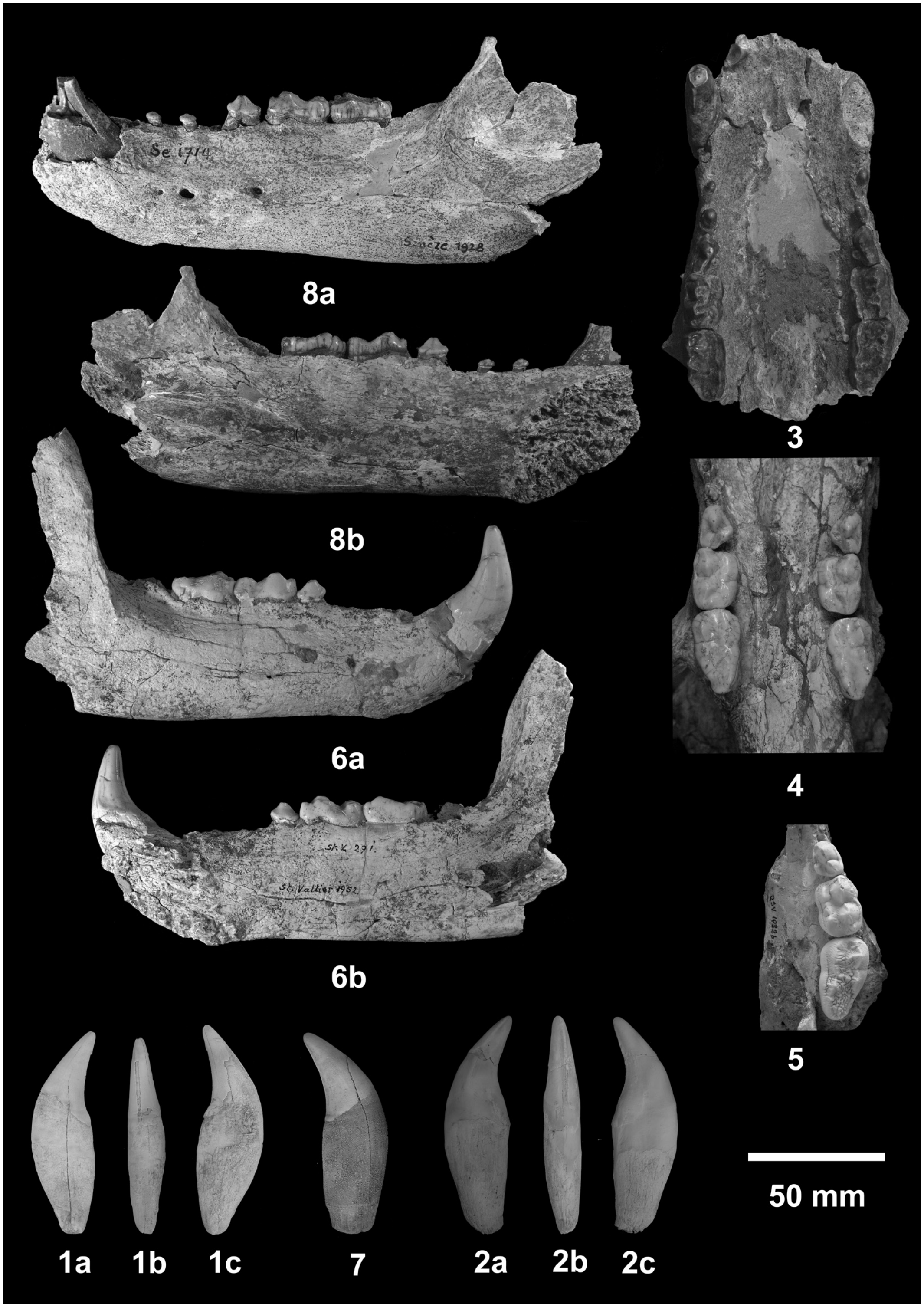
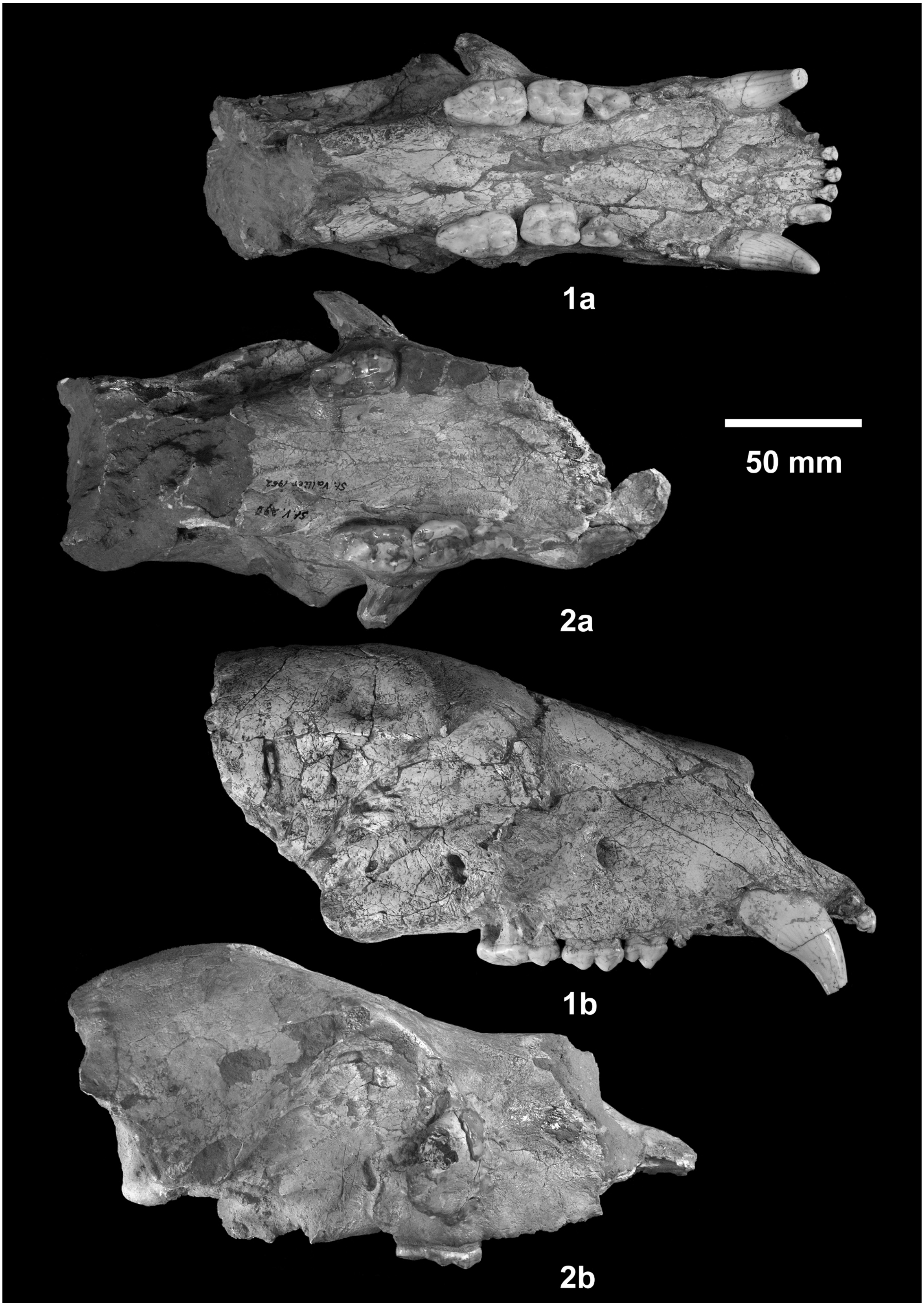
Plate 2



Ursus sp. from Vialette. 1. C_i sin. (Vt. 94): a: lateral view; b: posterior view; c: medial view. *Ursus* aff. *etruscus* from Les Pardines. 2. C^s sin. (L. P. 228): a: lateral view; b: posterior view; c: medial view. 3. maxillar fragment with P^2-M^2 sin et dex (L. P. 199): ventral view. *Ursus* aff. *etruscus* from St. Vallier. 4. maxillar part with P^4-M^2 sin. et dex. (St. V. 755): ventral view. 5. maxillar fragment with P^4-M^2 sin (St. V. 970): ventral view. 6. mandible dex with P_4-M_2 (St. V. 291): a: lateral view; b: medial view. *Ursus* ex gr. *minimus-thibetanus* from Senèze. 7. C^s sin. (Se 1505): lateral view. 8. mandible sin with P_2-M_2 (Se 1714): a: lateral view; b: medial view. (1-2 - photo J. W.; 3-8 - photo O. Fejfar).

Plate 3



Ursus aff. *etruscus* from St. Vallier. 1: cranium (St. V. 755): a: ventral view; b: lateral view. 2: cranium (St. V. 290): a: ventral view; b: lateral view. (photo O. Fejfar).

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HIGH-RESOLUTION X-RAY COMPUTED TOMOGRAPHY APPLIED TO THE STUDY OF SOME ENDOCRANIAL TRAITS IN CAVE AND BROWN BEARS

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José Miguel CARRETERO[2,3]

ABSTRACT: A complete skull of *Ursus deningeri* recovered from Sima de los Huesos (Middle Pleistocene) of Sierra de Atapuerca (Spain) (Torres, 1988; Arsuaga *et al.*, 1997; García *et al.*, 1997; García, 2003) was studied by using X-ray Computed Tomography (CT). This technique allowed the extraction of new relevant information from the endocranial structures, while avoiding any damage (Conroy & Vannier, 1984; Brochu, 2000; Ketcham & Carlson, 2001; Marino *et al.*, 2001). An undescribed endocranial cavity of *U. deningeri* was compared with related species such as *Ursus spelaeus* and *Ursus arctos*. The characters studied included the braincase morphology and also quantitative measurements which are only available with this technique. The surface of the frontal sinuses and the brain cavity, the shape of the ethmoid bone, and the basioccipital pneumatization were analyzed. The resulting analysis supports the relationship of the two ursids included in the cave bear lineage (*U. deningeri* and *U. spelaeus*), as among others, being similar in the endocranial roof or the palatine profile. Moreover, some endocranial morphologies observed in brown bears such as, thin basioccipital, elongated frontal sinuses and very rounded olfactory bulbs, differ from cave bears, and are here interpreted as plesiomorphies. New endocranial traits are described which will be very useful in the study of the ursid phylogeny.

Key words: *Ursus deningeri,* Atapuerca, CT scan, endocranium, frontal sinus, basioccipital, pneumatization.

INTRODUCTION

In the mid-1970s and 1980s new methods, such as the use of high-resolution X-ray Computed Tomography (CT), were applied for the first time in palaeontology (Jungers & Minns, 1979; Conroy & Vannier, 1984). This technique allows for the non-destructive analysis and measurement of internal structures and cavities in fossil remains (Joeckel, 1998; Brochu, 2000; Marino *et al.*, 2001). The use of CT is particularly useful for reconstructing the virtual endocast in well preserved fossil skulls (Rowe *et al.*, 1997; Brochu, 2000; Franzosa & Rowe, 2005).

The Sierra de Atapuerca is a complex system of cavities located at 14 km at the east of Burgos (Spain) (fig. 1), and represents one of the most important Pleistocene localities in Europe, due to a continuous human presence and abundant faunal record ranging from around 1.2 Ma up to the present. Several cave fillings have yielded fossils and/or artefacts, among the trench (Trinchera) deposits and also in Sima de los Huesos (SH), (fig. 2).

The Sima de los Huesos (SH) site is located deep inside the Cueva Mayor-Cueva del Silo cave system, far removed from any modern day surface entrance. The site has yielded the well-preserved skeletal remains of dozens of human individuals (Arsuaga *et al.*, 1997) lying stratigraphically below a jumble of bones of the Middle Pleis-

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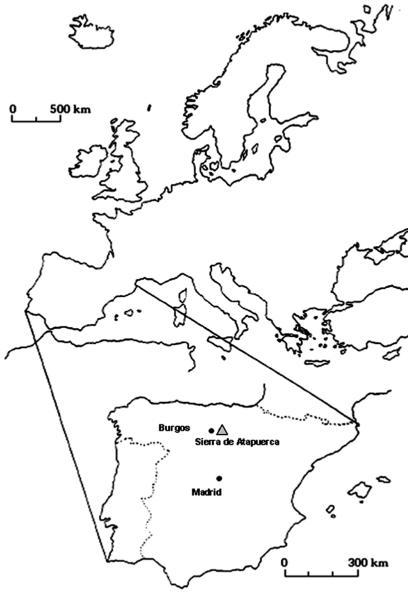

Figure 1. Sierra de Atapuerca, location.

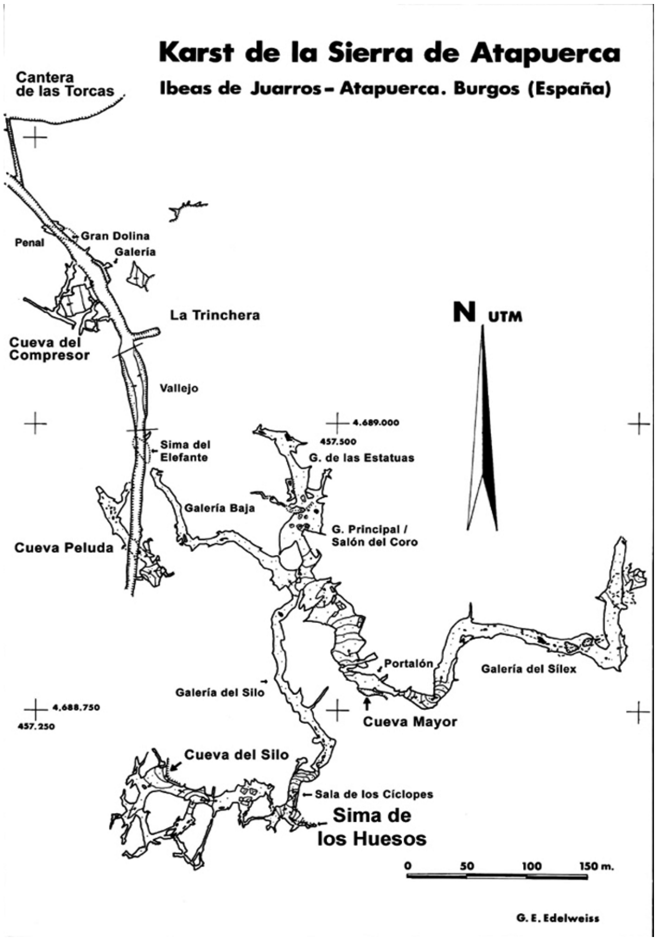

Figure 2. Plan of the Sierra de Atapuerca cave system (G.E. Edelweis).

tocene cave bear *Ursus deningeri* (García *et al.*, 1997; García, 2003). No herbivores are present among the faunal assemblage from the site, contrasting with their common occurrence at hominid occupation sites.

In the 1999 field session a nearly complete skull (SH99 T/U-13/14-68) from the Sima de los Huesos (fig. 3) was recovered in association with postcranial elements. A study of the cranial morphology of this specimen was undertaken through CT scanning and virtual reconstruction. Several endocranial traits have been analyzed and their expression across taxa has been investigated to determine their usefulness in reconstructing phylogenetic relationships within the ursid evolutionary lineage.

The *U. spelaeus* skull is characterized in classic descriptions by a strong development in the frontal area (glabella), showing a very distinctive doming of the forehead (convex forehead), which is strongly vaulted, with bulging tubera frontalis (Marinelli, 1931; Kurtén, 1968; 1972; Cordy, 1972; Torres, 1988; Mazza & Rustioni, 1994). This profile has also been observed in the *U. deningeri* skulls from Mauer, Mosbach (von Reichenau, 1904; 1906), Petralona (Kurtén & Poulianos, 1977; 1981; Tsoukala, 1989) and la Fage (Bonifay, 1975). This feature results in a characteristic step-profile in lateral view. The inner part of the frontal bone presents a large frontal sinus (FS). This character readily distinguishes both *U. deningeri and U. spelaeus* from the living brown bear *U. arctos* (Kurtén, 1968; Mazza & Rustioni, 1994).

MATERIAL AND METHODS

The *U. deningeri* cranium (SH99 T/U-13/14-68) from the Sima de los Huesos, was scanned, in the coronal axis, at the Hospital General Yagüe (Burgos, Spain), with the following parameters: scanner energy was 120 kV and 150 mA, slice thickness 0.5 mm, and inter-slice spacing was 0.5 mm. The slices were obtained in DICOM format.

For comparative purposes, two *Ursus spelaeus* (Cantabria, Spain) and seven *Ursus arctos* (north of Spain) specimens have also been scanned and virtually reconstructed (tab. 1). All specimens were scanned in the coronal axis using either a Helicoidal Asteion CT scanner at the Hos-

Table 1
Specimens scanned *= unknown origin.

Specimen	Sex	Age	Chronology	Locality
U. deningeri SH99 T/ U-13/14-68	♂	Non fully-adult	Middle Pleistocene	Atapuerca (Burgos, Spain)
U. spelaeus 1	♂	Non fully-adult	Late Pleistocene	* (Cantabria, Spain)
U. spelaeus 2	♀	Adult	Late Pleistocene	Las Monedas Cave (Puente Viesgo, Cantabria, Spain)
U. arctos 1	♀	Adult	Holocene	Maza Cotina (Burgos, Spain)
U. arctos 2	♂	Adult	Holocene	* (north of Spain)
U. arctos 3	♂	Adult	Holocene	La Machorra Cave (Burgos, Spain)
U. arctos 4	♂	Adult	Holocene	Las Motas 33 Cave (Burgos, Spain)
U. arctos 5	♂	Adult	Holocene	Las Motas 33 Cave (Burgos, Spain)
U. arctos 6	♀	Adult	Holocene	* (north of Spain)
U. arctos 7	♀	Adult	Holocene	Palencia (Spain)

pital General Yagüe (Burgos, Spain) or an YXLON MU 2000-CT scanner at the University of Burgos (Spain). The sex determination of the specimens was made using the anteroposterior diameter of the canine.

The slices were used to create three-dimensional computer models of the objects using the Mimics 8.1 (Materialise N.V.) and VGStudio MAX 1.2 (Volume Graphics GmbH) software packages. This software allows the taking of volumetric and linear measurements in both 2D and 3D. To check on the reliability of the virtual measurements, selected dimensions were also measured with standard sliding callipers, and no significant differences were found.

DESCRIPTION

The skull of a non-fully adult specimen of *Ursus deningeri* (SH99 T/U-13/14-68), from the Sima de los Huesos, presents a doming of the forehead also observed in the adult specimens of *U. deningeri* from Petralona Cave (Kurtén & Poulianos, 1977; 1981; Tsoukala, 1989), Mauer, Mosbach (von Reichenau, 1904; 1906) and la Fage (Bonifay, 1975). This feature does not occur in *U. arctos* (Bonifay, 1975; Mazza & Rustioni, 1994). The skull profile in the SH specimen is interrupted at the orbital region, like in *U. spelaeus*, dividing the facial skeleton from the braincase and giving a stepped appearance (fig. 4).

Frontal Bone and Frontal Sinuses

The frontal bones are broad and forming part of the brain cavity and the olfactory tract. The enlargement of the anterior part of the frontal bones and the vaulted forehead in the SH specimen, both typical traits of *U. spelaeus*, reveals large frontal sinuses (FS). The FS are asymmetric, divided by a variable number of bony septa and connected to the middle meatus via the frontal recess. The anterior part of the FS is anteroposteriorly elongated, and the caudal portion is more rounded (fig. 5).

The FS are dorsoventrally enlarged in the SH specimen and *U. spelaeus*, while in *U. arctos*, they are anteroposteriorly elongated. The vaulted forehead observed in the SH frontal bone is reflected in the shape of the rostral frontal sinuses (RFS) which is rounded in both the SH skull and *U. spelaeus*. This region in *U. arctos* is completely different, being much more receding.

Palatine

In sagittal view the palatine profile of the SH specimen is thick and curved. This profile in *U. spelaeus* is thicker and less arched, while in *U. arctos* is thin and practically straight. In ventral view this bone is convex in both cave bears and slightly concave in brown bears.

Basioccipital

The basioccipital bone shows clear differences between *U. speleaus*, which is very thick and pneumatized, and *U. arctos*, which is much thinner and shows no signs of pneumatization (Torres, 1988). The basioccipital in the non-fully adult specimen of *U. deningeri* from SH is thick (as in *U. spelaeus*) but is not pneumatized (as *U. arctos*) (fig. 6).

Ethmoid bone and cribriform plate

The morphology of the ethmoid bone, particularly the cribriform plate (CP), showing taxonomic variation (Torres, 1988), and it is correlated to the structure of the brain. In *U. arctos*, the CP is globular. In *U. spelaeus*, the CP is ellipsoid and strangulated. The *U. deningeri* skull,

Figure 3. *U. deningeri* skull from Sima de los Huesos (Sierra de Atapuerca).

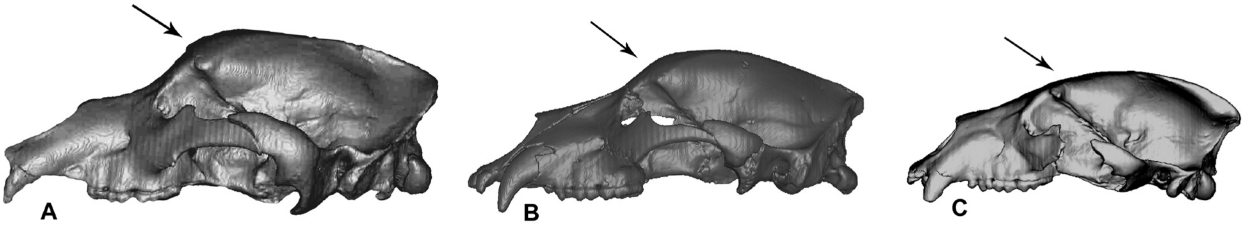

Figure 4. A. *U. spelaeus* 2, B: *U. deningeri* cranium from the Sima de los Huesos and C: *U. arctos* 1. The arrows indicate the stepped forehead in both cave bear and the absence of this trait in brown bear.

Figure 5. Digital image of the *Ursus deningeri* skull from Sima de los Huesos. Top: sagittal view. Bottom: frontal sinuses area in detail. Right: dorsal view. The images show the frontal sinuses filling the vaulted forehead.

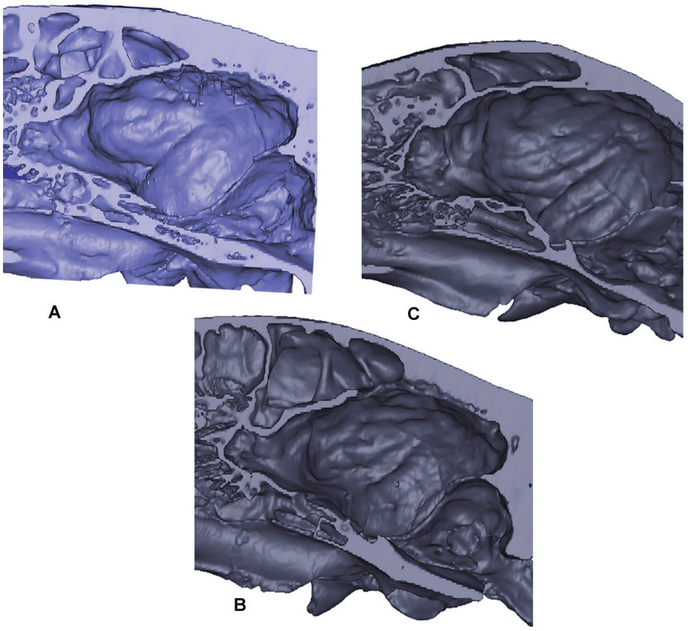

Figure 6. Parasagittal sections of skulls, in which the basioccipital bone and the profile of the brain cavity can be seen. A: *Ursus spelaeus*. B: *Ursus deningeri*. C: *Ursus arctos*.

Profile of brain cavity

In *U. arctos*, the antero-dorsal profile of the brain cavity describes a pronounced curve, while in *U. spelaeus* this contour is clearly straight (fig. 6). In the SH cranium, the antero-dorsal outline of the brain cavity is intermediate between both morphologies, although it more closely approaches the condition seen in *U. spelaeus*.

CONCLUSIONS

High resolution CT scanning of fossil specimens is a non-destructive method which allows the description of new anatomical features of the endocranium. This technique will allow future investigations on the internal cranial anatomy of ursids for a better understanding of their phylogeny and adaptations.

In this preliminary approach we were able to observe some derived traits in the *Ursus deningeri* from SH that are shared with the analyzed *U. spelaeus* specimens, and which differ from *U. arctos*:

- A stepped forehead.
- A cranial vault with a straight profile,
- A rostral endocranial fossa clearly independent from the rest of the brain cavity.
- A thick basioccipital
- A thick palatine.
- A rounded frontal sinuses.

Furthermore the SH skull shows, for a number of traits, an intermediate stage between *U. arctos* and *U. spelaeus*, but in all the cases is closer to the later species:

- Palatine more curved (than *U. spelaeus)*.
- Basioccipital not pneumatized.
- The antero-dorsal outline of the brain cavity is intermediate between both morphologies.
- The joint between the frontal and ethmoid bones are more constricted (than *U. spelaeus*).

The endocranial traits here analyzed show two different patterns of expression between the cave bear and brown bear lineages. The SH *U. deningeri* skull can be aligned within the cave bear pattern in all the traits, and support the hypothesis that *U. deningeri* represents an initial evolutionary stage within the cave bear phylogenetic lineage.

Acknowledgments: CT scanning was carried out by F. Montes and J. M. Nieto, at the Hospital General Yagüe, and L. Rodriguez helped during the CT scanning process, at the University of Burgos High-Resolution X-ray Computed Tomography Facility (Burgos, Spain). We thank our colleagues from Centro Mixto UCM-ISCIII sobre Evolución y Comportamiento Humanos and the Laboratorio de Evolución Humana at Burgos University, for their help in the field and laboratory works. We are grateful to A. I. Ortega from the Edelweiss Speleologic Group and F. Alférez from UCM for providing access to some specimens of ursids used in this study. We are very grateful to G. Withalm for his constructive comments and L. Laughlan who revised the English version. This study has been funded by the Dirección General de Investigación Científica y Técnica de España (Project nº.BOS2003-08938-C03-01) and by the Consejería de Educación de la Junta de Castilla y León (Project nº. BU032A06). E. Santos received a grant from the Fundación Siglo para las Artes of the Junta de Castilla y León (Spain).

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CAVE BEAR METAPODIALS FROM DIVJE BABE I (WESTERN SLOVENIA)

Borut TOŠKAN[1]

Abstract: The excavation of the Late Pleistocene cave site of Divje babe I (Western Slovenia) yielded several thousand cave bear metapodials. Multivariate statistical analysis of metric data for 1,598 metacarpals and metatarsals allowed these bones to be grouped according to sex. The differences in sex ratio between the samples from OIS 5a-5d and OIS 3 are explained with the increased intersexual competition for lairs in OIS 3 due to more severe climatic conditions.

Key words: Divje babe I, cave bear, metapodials, sex structure, palaeoclimate.

INTRODUCTION

The cave-bear group is by far the best represented animal taxonomic unit in the fauna of the Late Pleistocene cave site of Divje babe I. The majority of remains probably belonged to animals that died during or just after hibernation. The high number of finds enabled a detailed biometric analysis of many skeletal elements, from long bones (Jambrešić & Turk, in press) and isolated teeth (Debeljak, 2002a) to skulls (Toškan, in press (a)). The excavated material also includes several thousand metapodials. These hefty, compact bones are relatively numerous in many Late Pleistocene sites and are therefore often subject of detailed morphometric analyses (for example Rakovec, 1967; Pohar, 1981; Krklec, 1997; Gužvica & Radanović-Gužvica, 2000; Withalm, 2001; 2004; 2005). Considering their role in the biomechanics of walking (Opavský, 1990), such attention is justified in principle, though conducting such analyses without knowing the sex ratio of the sample raises many doubts. Namely, the cave bear shows well-marked sexual dimorphism (*cf.* Kurtén, 1955; Reisinger & Hohenegger, 1998; Grandal d'Anglade, 1993; 2000; Rabeder, 2001; Baryshnikov *et al.*, 2003), which was surely reflected also on the metatarsals and (particularly) on the metacarpals. For this reason, the method for sexing cave bear metapodials based on their size is presented below.

MATERIAL AND METHODS

Divje babe I is a 45 m long and up to 15 m wide horizontal cave, opening towards the north-west, and lies 230 m above the bed of the Idrijca River near Cerkno (western Slovenia; 450 m above sea level). The thickness of the Pleistocene clastic sediments exceeds 13 m. They are composed mostly of autochthonous dolomite blocks, rubble, sand and silt (Turk, 1997). There were 26 layers determined during excavation (time span: approx. 115.000 - 35.000/40.000 years B.C.), which are mostly difficult to set apart macroscopically. Turk (2003) therefore substituted the *ad hoc* delineated geological layers with new basic stratigraphic units, the so-called facies A to C. The substitution is based on the analysis of the vertical distribution of structural aggregates (0.5 - 3 mm) and bone remains (> 3 mm) along several profiles and in two blocks of sediments. More than 90 (Nelson & Ku, 1997; Lau *et al.*, 1997; Turk *et al.*, 2001; 2006; Blackwell *et al.*, in press) available ESR and ^{14}C (AMS) dates have shown that facies A and B correspond to the Oxygen Isotopic Stage 3 (= OIS 3; i.e. Interpleniglacial) and facies C to OIS 5a-5d (i.e. Early Glacial). Four U/Th dates are also available (Nelson & T.-L. Ku, 1997) but since extended gaps in sedimentation greatly influenced mobilisation and absorbtion of U, thus leading to its remobilisation, the determination of age by U series method proved inaccurate in this case (Turk *et al.*, 2003). The

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OIS 4 (i.e. Pleniglacial I) is almost not represented in the cave, since a pause in sedimentation occurred at the time. The transition between facies A and B corresponds with the former layer 7 (i.e. approx. 50.000 years B.C.) and the transition between facies B and C with the former layer 11/12 (i.e. approx. 74.000 B.C.), thereby corresponding to the radiometrically determined chronological border between OIS 5 and OIS 4 (Turk *et al*., 2001; Blackwell *et al*., in press). Although the facies C begun to form already around 115,000 years B.C., the most ancient metapodials included in this study originate from the layer 16a, being dated to 75,000 - 85,000 years B.C. (Blackwell *et al*., in press).

Although radiometric datations are not without pitfalls, the high number of available dates (>90) in combination with the methodology used (e.g. assessment of the total dose rate from external environment in ESR dating using the neutron activation analysis; *cf.* Blackwell & Blickstein, 2000) do give the assurance of a relatively reliable chronology of the site. According to latest data (Turk *et al.,* 2006; Blackwell *et al*., in press) radiocarbon datations seem to be reliable for layers 2 - 6 (although a shift of +2-3 ka due to calibration in calendar years is necessary), while ESR datations proved trustworthy for layers 2 - 23. Nevertheless, since no radiometric method provides a chronology which is in itself of sufficient reliability for detailed archaeological interpretation, the available datations were considered also in the context of the site stratigraphy (with sedimentological, paleobotanical and paleontological data taken into account). The results, however, fully confirmed the reliability of the radiometric datations (Turk, in press).

Following the new basic stratigraphic units (= facies), the available sample of cave bear metapodials was divided into three subsamples: Db-A (includes metapodials of facies A), Db-B (facies B) and Db-C (facies C). Due to unpredictable objective reasons (*cf.* Turk, 2003), it was possible to observe the vertical distribution of structural aggregates and bone remains (whose distribution served as the basis for the substitution of *ad hoc* delineated geological layers with facies) only on a part of the excavation field. For this reason only the metapodials from that part of the excavation field were metrically analyzed. The initial sample of several thousand specimens thus decreased to 1,598 metacarpals and metatarsals, only. Nevertheless, each of the three subsamples (i.e. Db-A, Db-B and Db-C) included a sufficient number of specimens of individual skeletal elements (i.e. metacarpus I - V, metatarsus I - V) so as to enable the application of multivariate statistical methods.

Eight different measurements were taken from each metapodial (Withalm, 2001; fig. 1): greatest length (gL), medio-lateral breadth of the proximal epiphysis (pB), antero-posterior breath of the proximal epiphysis (pH), smallest medio-lateral breadth of the diaphysis (sDB), smallest dorso-palmar or dorso-plantar breadth of the diaphysis (sDH), greatest medio-lateral breadth of the distal epiphysis (gDB), medio-lateral breadth of the articular surface of the distal epiphysis (dB) and antero-posterior breadth of the distal epiphysis (dH). Only specimens with fused epiphyses were included in the analysis. It must be pointed out that several studies of skeletons of ungulates have indicated the possibility of a considerable growth of bone tissue also in bones with fused epiphyses (Legge & Rowley-Conwy, 1988; Payne & Bull, 1988; Luff, 1993). However, this occurred mostly on skeletal elements that ossify very early in the ontogenetic development (e.g. scapulas, distal parts of humeri, astragali), which is not the case with metapodials. Nevertheless, metacarpals and metatarsals with visible exostoses were excluded from the analysis by way of precaution.

The analyses of the X-ray images of the paws of the black bear (*Ursus americanus*) have shown that the fusion of epiphyses in metacarpals terminates when the animal reaches two years of age. In the following months the ridge of the distal epiphysis becomes fully shaped (Marks & Erickson, 1966). The metapodial development in the cave bear is though to conclude on average somewhat later (supposedly just before reaching three years of age), since the ontogenetic development of the skeleton in the cave bear is though to be slower (*cf.* Debeljak, 2002b). Beside this, the tempo of the epiphyses fusion in the study by Marks and Erickson is most probably somewhat overestimated, since their conclusions are based on the analysis of X-ray images (1966; see also Moran & O'Connor, 1994).

The analysed samples mostly include complete metapodials where all eight measurements could be taken. Partly damaged metacarpals and metatarsals, where one of the measurements could not be taken, were also analyzed. The missing data were substituted by estimates, which were obtained using forward stepwise regression (StatSoft Inc., 2001). The efficiency of the method was tested on undamaged specimens: the absence of statistically significant differences between the measured and estimated values (F-test: $p < 0.05$) indicated the appropriateness of the method used.

Metapodials were sexed based on the results of the principal component analysis (PCA). This method enables a satisfactory explanation of the variation of certain

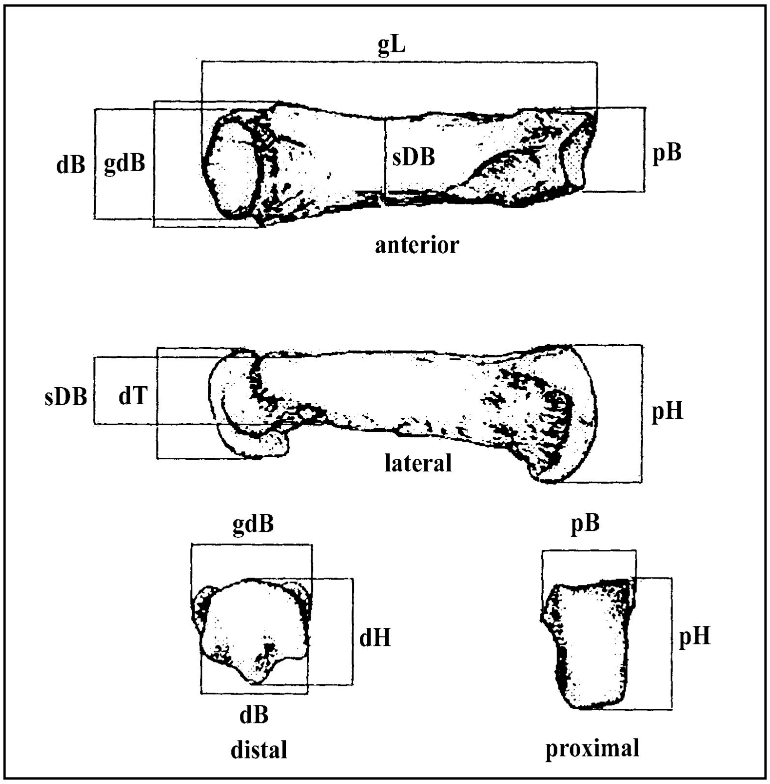

Figure 1. Cave bear (*Ursus spelaeus*) metapodial with indicated measurements. For definitions of individual measurements see the text.

number of basic *X* variables with a (considerably) smaller number of principal components (Pc_i), which renders the interpretation of the intrasample variability considerably easier (MANLY, 1994; STATSOFT INC., 2001). Prior to the principal component analysis the available metric data were first standardized (*cf.* ALBARELLA, 2002). Thus only the relative deviations of individual specimens from the average value of each of the eight measurements in the reference sample (deviations are expressed in standard deviations) were transferred to subsequent analyses. Consequentially, all metacarpals/metatarsals could have been pooled together to form a uniform statistical sample, rendering it considerably more representative. Metric data were standardized using the formula:

$$\text{Standardized value} = (x - M)/S$$

where x represents individual measurements to be standardized and M and S the average and the standard deviation for the same measurement in the reference sample.

In statistical analyses the StatSoft 2001, Statistica for Windows software package, version 6.0 was used. The analyzed material is held at the National Museum of Slovenia in Ljubljana.

RESULTS

The weight of the cave bear male is supposed to be a third above the weight of the female (VIRANTA, 1994), which indicates a well-marked sexual dimorphism. In spite of this, the analysis of 4,459 metacarpals and metatarsals of *U. spelaeus* and *U. deningeri* from eight Austrian and one Italian site has shown that sexing the metapodials on the basis of any single linear measurement is not possible (WITHALM, 2001). Better results were expected by using the principal component analysis, since this method enables the simultaneous consideration of several (in this case all eight) parameters. Due to the previous standardization of metrical data it was possible to compare the variability in the size of metapodials on a unified sample of all five metacarpals/metatarsals. The metapodials from facies B were used as reference sample in standardization, since they fall between the specimens from facies A and facies C in their size.

The correlation matrix of standardized values of all eight parameters was used as input data for the PCA, separately for metacarpals and metatarsals. The first principal component accounts for 83.7 percent of the variability of the basic data set for metacarpals and 72.8 percent for

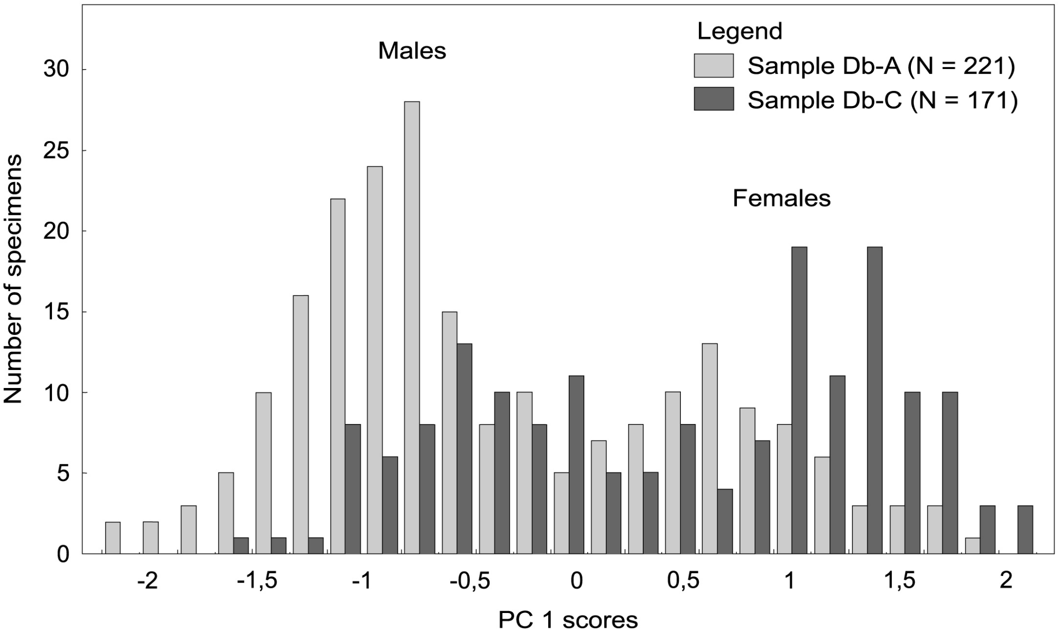

Figure 2. Distribution of the first principal component (PC 1) scores, calculated on the basis of a correlation matrix of standardized data for eight measurements of cave bear (*Ursus spelaeus*) metacarpals from Divje babe I: samples Db-A and Db-C. Scores were standardized using the data of the sample Db-B, which is thus not represented on the figure. Due to negative factor loadings, the large (i.e. male-ascribed) metacarpals form the left of the two peaks and the small (i.e. female-ascribed) metacarpals the right one.

metatarsals. Factor loadings of all eight parameters are negative and vary between the values of -0.76 and -0.94. The communalities are high and the residual correlations low. Due to the above, the major part of the basic data set could accurately be represented already with the first principal component.

The distribution of PC 1 scores is distinctly bimodal for metacarpals/metatarsals from the Db-A sample as well as for those from the Db-C sample (fig. 2, fig. 3). Such a distribution reflects the sexual dimorphism and enables at least an approximate estimate of the sex ratio. Overlapping of the scores of both sexes is slightly higher for the metatarsals than for the metacarpals. This observation is quite expected considering the constitution of the cave bear and was proven also on long bones of both pairs of limbs (Reisinger & Hohenegger, 1998).

The distribution of the PC 1 scores indicates that the number of metacarpals and metatarsals of both sexes was roughly equal in the sample from OIS 5a-5d (= sample Db-C). As opposed to that, the material from the OIS 3 (=sample Db-A) shows an approximate two-thirds majority of male specimens. None of the metapodials (i.e. Mc I - V, Mt I - V) show significant deviations in that sense. In three of the five metacarpals the differences in sex ratio between the samples Db-A and Db-C are even highly statistically significant (χ^2 test: $p < 0.01$; tab. 1). The sex ratio was estimated without considering the anatomical orientation of specimens (i.e. without distinguishing between left and right metacarpals / metatarsals), since the available samples were not large enough. The only exception in this sense is represented by second metacarpals, which are the most numerous among all metapodials in the studied sample (Mc II: N = 96). Also in this case, however, the results confirmed the balanced sex ratio in the Db-C sample and a predominance of male-ascribed second metacarpals in the Db-A sample (tab. 2).

The results mentioned so far refer exclusively to the material from the middle part of OIS 3 (= Db-A sample) and from OIS 5a-5d (= Db-C sample), since the metapodials from the initial part of OIS 3 (= Db-B sample) were used as the reference sample in the standardization of metric data. In order to provide an estimate of the sex ratio also for the Db-B sample, metric data of the metapodials from that sample were standardized using the data of the entire fossil sample from Divje babe I (Db-A + Db-B + Db-C) as reference. The results clearly showed a predominance of males (fig. 4), thereby confirming the hypothesis made above on the majority of metapodials in the OIS 3 material being ascribed to males.

The sex ratio of cave bear assemblages is usualy esti-

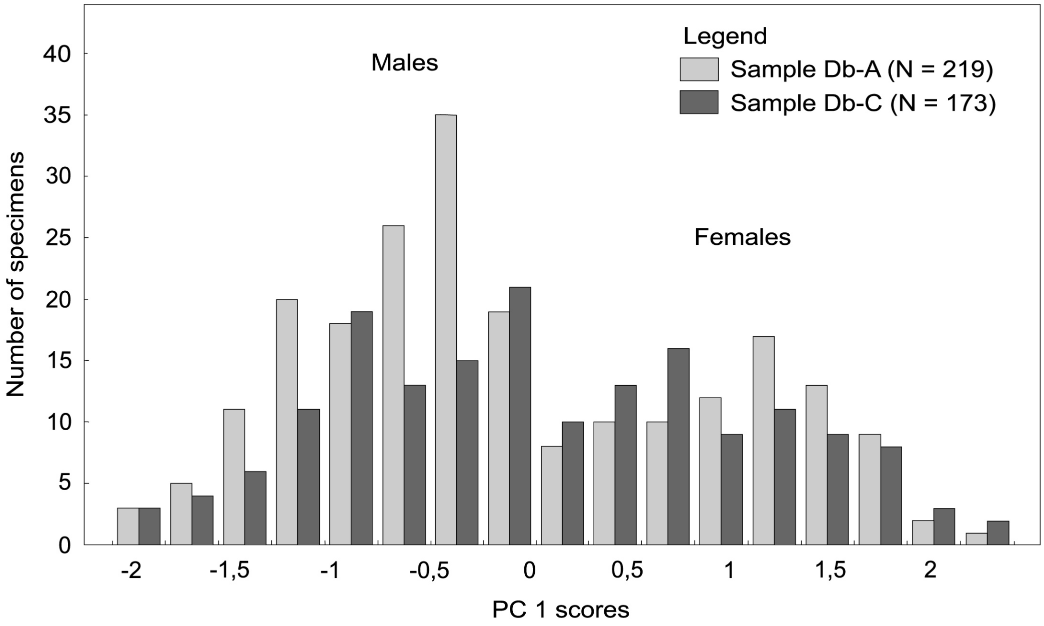

Figure 3. Distribution of the first principal component (PC 1) scores, calculated on the basis of a correlation matrix of standardized data for eight measurements of cave bear (*Ursus spelaeus*) metatarsals from Divje babe I: samples Db-A and Db-C. Scores were standardized using the data of the sample Db-B, which is thus not represented on the figure. Due to negative factor loadings, the large (i.e. male-ascribed) metatarsals form the left of the two peaks and the small (i.e. female-ascribed) metatarsals the right one.

Table 1
The number of male- and female-ascribed cave bear (*Ursus spelaeus*) metacarpals from Divje babe I: samples Db-A and Db-C. Statistically significant differences in the sex ratio between the two samples are shaded.

Mc	Sample Db-A		Sample Db-C		Total			χ^2 test
	♂	♀	♂	♀	♂	♀	♂ + ♀	
Mc I	22	9	9	23	31	42	73	χ^2=26.20 p= 0.00
Mc II	44	13	19	20	63	33	96	χ^2= 8.32 p= 0.00
Mc III	36	16	20	12	56	28	84	χ^2= 0.40 p= 0.52
Mc IV	19	15	18	19	37	34	71	χ^2=37.00 p= 0.54
Mc V	25	12	10	21	35	33	68	χ^2= 8.42 p= 0.00
Total	146	75	76	95	222	170	392	χ^2=18.30 p= 0.00

mated by using metric data of canines, since they show a well pronounced sexual dimorphism (e.g. Kurtén, 1955). For the material from Divje babe I such an analysis was performed by Debeljak (2002b). Her results indicate a roughly equal share of male and female specimens not only in facies C, but also in facies A and B, thus contrasting the conclusions based on the study of metapodials. The discrepancy between the two approaches, however, can be convincingly explained with the lack of canines of (sub)adult cave bears (compared to cheeck-teeth and to most postcranial elements) in certain layers from facies A and B (Turk & Dirjec, in press; Toškan, in press (b)). Namely, because of the lack of canines the sample studied by Debeljak was actually non-representative, making the resulting sex ratio estimates questonable.

The lack of canines is really only evident in layers with

Table 2
Statistical testing of differences in the sex ratio of all cave bear (*Ursus spelaeus*) metacarpals from the Db-A and Db-C samples on one side and only the second metacarpals (Mc II) of the same species from the same two samples (Db-A and Db-C) on the other side.

Sample Db-A	♂	♀	Total	χ^2 test
Mc II (left)	21	6	27	$\chi^2 = 1.50$
All metacarpals	146 (= 65.7%)	76 (= 34.3%)	222	p = 0.220
Sample Db-A	♂	♀	**Total**	**χ^2 test**
Mc II (right)	23	7	30	$\chi^2 = 1.35$
All metacarpals	146 (65.7%)	76 (= 34.3%)	222	p = 0.245
Sample Db-C	♂	♀	**Total**	**χ^2 test**
Mc II (left)	14	12	26	$\chi^2 = 0.80$
All metacarpals	76 (= 44.4%)	95 (= 55.6%)	171	p = 0.370
Sample Db-C	♂	♀	**Total**	**χ^2 test**
Mc II (right)	5	8	15	$\chi^2 = 0.18$
All metacarpals	76 (= 44.4%)	95 (= 55.6%)	171	p = 0.675

hearths and/or above-average number of stone artefacts. The relativelly lower number of canines in these layers could thus be related to Palaeolithic man, who might have collected the larger (= male) specimens as some sort of trophies and transported them elsewhere (Turk & Dirjec, in press; Toškan, in press (b)). Such a conclusion is corroborated by the results of taphonomic analyses, showing that the lack of canines cannot be explained by differential post-depositional fragmentation (Toškan, in press (b)). In addition to this it should be emphasize that the estimated sex ratio emerging from the study of metapodials corresponds to the results of metric analyses of long bones (Jambrešić & Turk, in press) and skulls (Toškan, in press (a)).

DISCUSSION

Sexing the cave bear metapodials from Divje babe I offered an interesting point of departure for a detailed insight into the biology of the species. The accumulation of cave bear remains in caves is usually related to natural mortality during the period of lethargy (*cf.* Pohar, 1981; Stiner, 1998; Weinstock, 2000; Debeljak, 2002b). Such inferences are drawn from data on the high energetic cost of hibernation in recent bears (Watts & Jonkel, 1988) and by considering the supposed comparability of metabolisms of brown and cave bears (Nelson *et al.*, 1998; Lidén & Angerbjörn, 1999; Fernández-Mosquera *et al.*, 2001; but see also Jenkins *et al.*, 2001).

The physiological readiness for entering hibernation in recent bears is determined by the circannual rhythm tied to the seasonal cycle of vegetation (Ewer, 1973). This is responsible for an approximate timing of the beginning of hibernation, while the actual transition to the lethargic state is thought to be triggered by an interaction of certain climatic factors (amount and frequency of precipitation, dense clouds, general deterioration of weather) and smaller quantities of available food (Johnson & Pelton, 1980). What about the choice of lair? For the present-day black and brown bears it is known that the first to occupy a lair in good climatic conditions are pregnant females, which are followed by subadult individuals and finally by males (Slobodyan, 1976; Pasitschniak-Arts, 1993). Postponement (in males sometimes even a complete absence) of the beginning of hibernation can be caused by abundant crops of beech-nuts, acorns and the like (Johnson & Pelton, 1980; Germonpré & Sablin, 2001). In accordance with the above, we might infer that females have a wider choice of appropriate lair in mild winters and/or in periods of relatively large amounts of available food. A different picture emerges at the onset of severe climatic conditions and/or shortage of food. In these cases, males enter the hibernation approximately contemporaneously to the subadult individuals and pregnant females (Slobodyan, 1976; Pasitschniak-Arts, 1993), thus significantly increasing the intersexual competition for appropriate lairs (Johnson & Pelton, 1980; Stiner, 1998). Since pregnant females and females with subadult young usually avoid solitary males when choosing a lair (Slobodyan, 1976; Wielgus & Bunnell, 1994), the onset of climatically severe conditions undoubtedly favours males.

Similar behaviour was probably present also in the cave bear, as is indicated by the increased δ^{15}N values in males from the cold phases of Würm (Fernández

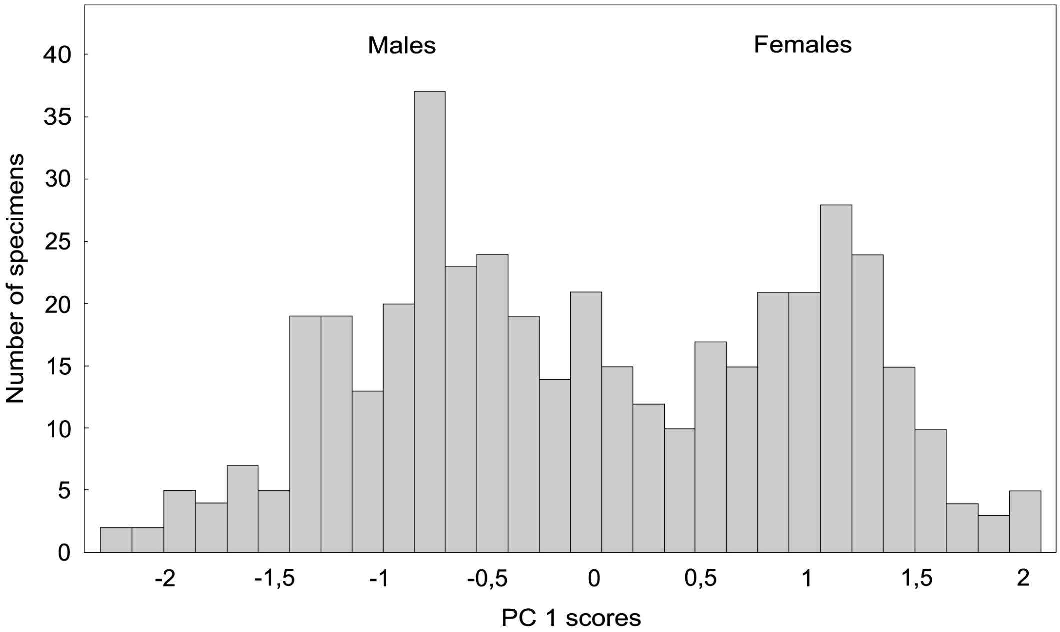

Figure 4. Distribution of the first principal component (PC 1) scores, calculated on the basis of a correlation matrix of standardized data for eight measurements of cave bear (*Ursus spelaeus*) metacarpals from Divje babe I: sample Db-B (N = 434). Scores were standardized using the data of the entire fossil sample from Divje babe I (Db-A + Db-B + Db-C). Due to negative factor loadings, the large (i.e. male-ascribed) metacarpals form the left of the two peaks and the small (i.e. female-ascribed) metacarpals the right one. PC 1 explains 77.0% of the variance accounted for by the basic data set.

MOSQUERA *et al.*, 2000; 2001). The increased δ^{15}N values are thought to be tied to the earlier beginning (and thereby longer duration) of hibernation, during which urea recycling in amino acid synthesis occurs. Although the metabolism in the black/brown and cave bear might well have diverged to some extent (i.e. cave bears being more tied to hibernation) the transition to the letargic state seems to have been triggered by climatic factors in cave bears, too. The presumption of a sex-specific timing of the actual beginning of hibernation in cave bears is thus to be considered as a legitimate one (*cf.* GERMONPRE & SABLIN, 2001). This realisation is important in the context of the observed sex ratio of cave bears from Divje babe I. There is, in fact, no doubt that the climatic conditions in OIS 5a-5d south of the Alpine glaciation were significantly more favourable and more stable than those in OIS 3. This is shown by sedimentologic analysis (TURK *et al.*, 2001; 2002), palaeobotanic research (ŠERCELJ & CULIBERG, 1991) and by the study of the small mammals' remains (KRYŠTUFEK, 1997; TOŠKAN, 2002; TOŠKAN & KRYŠTUFEK, in press). It is therefore to be expected that pregnant females and females with subadult young went into hibernation before the males in OIS 5a-5d. This provided them with much more freedom in choosing a lair. Namely, though in recent bears females use to avoid males when looking for a lair, males also usually do not occupy the already occupied caves, even when inhabited by females (SLOBODYAN, 1976; WIELGUS & BUNNELL, 1994). An approximately equal representation of both sexes in the Db-C sample from Divje babe I (fig. 2, fig. 3, tab. 1, tab. 2) could thus be efficiently explained with the wider choice of females in looking for a lair. Since in mild winters males of the present-day brown and black bear often make their lair in the open (for example in a thicket of young trees or in a shelter of a fallen tree; ROGERS, 1981; SLOBODYAN, 1976; GROFF *et al.*, 1998), an even lower share of male metapodials in the Db-C sample could be expected. The reasons for this not being the case are to be sought in the ethology of the cave bear, since it was supposedly more prone to hibernating in caves than the present-day representatives of the *Ursus* genus (COUTURIER, 1954; FOSSE *et al.*, 2002).

A colder and more humid climate in OIS 3 surely contributed to a more pronounced seasonal availability of vegetable food. The winters of that period are thought to have been longer and substantially more abundant in snowfall (TURK *et al.*, 2002). For the (predominantly) herbivorous (*cf.* BOCHERENS *et al.*, 1994; 1997; NELSON *et al.*, 1998) cave bear, this environment probably led to a more or less synchronous autumnal occupation of caves from individuals of both sexes. Pregnant females or females with subadult young probably avoided solitary males in choosing their lairs and the latter probably occupied also those caves that used to be occupied by females in the warmer and less humid OIS 5a-5d. The increased share of males choosing Divje babe I as their lair in OIS 3 seems thus not to be problematic.

Lately morphological and metrical differences between several alpine cave bear associations of the same geological age were considered large enough by some authorities (Rabeder, 2004; Rabeder *et al.*, 2004a; Hofreiter *et al.*, 2002; 2004) to suspect more than one evolutionary line. Analyses of fossil DNA indicated at least three different lineages within the cave-bear group, two of these groups showing evidence of reproductive isolation (Rabeder *et al.*, 2004a; 2004b; Hofreiter *et al.* 2004; Noonan *et al.*, 2005; but see also: Peatkau, 1998; Orlando *et al.*, 2002). It was thus suggested that *Ursus spelaeus* Rosenmüller, 1794 comprised at least two species, of which *Ursus ingressus* Rabeder *et al.*, 2004 occurred in the eastern parts of the Alpine region and the Dinarids of Slovenia and Croatia. For two other morphological forms, subspecific status with *U. spelaeus ladinicus* and *U. spelaeus eremus* was suggested (Rabeder *et al.*, 2004a). In line with this thesis the appearance (or predominance) of larger individuals of cave bear in Interpleniglacial (≈OIS 3) layers of e.g. Potočka zijalka, Vindija and Gamssulzenhöhle was explained by immigration of the considerably larger *U. ingressus* (Rabeder *et al.*, 2004a; 2004b; Withalm, 2004; 2005). The latter species is assumed to have immigrated into the Alps around 50.000 years BP, subsequently replacing the other two forms of cave bears (Rabeder & Hofreiter, 2004).

According to the above the predominance of larger individuals in the upper layers (i.e. facies A) of Divje babe I could also be explained by immigration of a considerably larger cave bear species (*U. ingressus*), thus resulting in the pretence of an asymmetrical distribution between sexes. Unfortunately data about aDNA are not yet available for the cave bear from Divje babe I. Nevertheless, detailed morphometrical analysis of metapodials pointed out a complete lack of statistically significant differences between specimens from the three facies once the “size” component has been discarded (Burnaby’s method) from the metric data [Toškan, in press (b)]. Since *U. ingressus* is supposed to differ from *U. spelaeus* in the metapodial bone proportions (Rabeder *et al.*, 2004a; Hofreiter *et al.*, 2004; (see supplement data available with the article online), Withalm, 2004; 2005) the lack of such differences in the material from Divje babe I speaks against the hypothesis of the immigration of *U. ingressus*. Moreover, according to Rabeder *et al.* (2004a) the differences in the index of plumpness (Ip = gDB/gL; see fig. 1) of the first metacarpal and metatarsal bones seem to be the most striking and therefore best usable indicator for diagnostic use. It is thus important to note that the comparison of the first metacarpals and metatarsals ascribed to *U. ingressus* from Potočka zijalka (Withalm, 2004) with those from facies A (≈ 35/40 - 50 ky BP) of Divje babe I does not show statistically significant differences in *Ip* values (t-test: $p > 0.05$). But the same also holds true for the comparison of *Ip* values for the first metacarpal/metatarsal bones from Potočka zijalka with those from Divje babe’s facies B (≈ 50 - 70 ky BP) and facies C (≈ 70 - 85 ky BP), which deposited before the assumed immigration of *U. ingressus* into the Alps (Rabeder & Hofreiter, 2004). Differences in *Ip* values of the first metacarpals between male-/female- ascribed specimens from facies A and those from facies C are not statistically significant neither (t-test): males (facies A) vs. males (facies C: p = 0,891; females (facies A) vs. females (facies C): p = 0,627), as would be expected if the predominance of larger individuals in the upper layers (i.e. facies A) would be related to the immigration of *U. ingressus*. By taking the above into account it thus seems legitimate to explain the bimodal distributions of PC 1 scores by the sexual dimorphism.

CONCLUSION

The use of multivariate statistical methods in analysing cave bear metapodials from Divje babe I enabled us to sex them. As already mentioned above, the estimated sex ratio differs somewhat from the one that is based on the metric data of canine teeth (Debeljak, 2002b), but corresponds exactly to the results of the metric analysis of long bones (Jambrešić & Turk, in press) and skulls (Toškan, in press (a)). The presented method can therefore serve, among other uses, also as an independent control of the otherwise more popular approach to estimate the sex ratio, i.e. by using metric data of canines.

A comparable share of male and female metapodials in the sample from OIS 5a-5d as opposed to the almost two-thirds majority of male-ascribed metacarpals and metatarsals in OIS 3 can be explained with a more severe climate in OIS 3. Longer and colder winters with a thick and longer-lasting snow cover caused the males to begin their hibernation more or less contemporaneously with subadult individuals and (pregnant) females, which

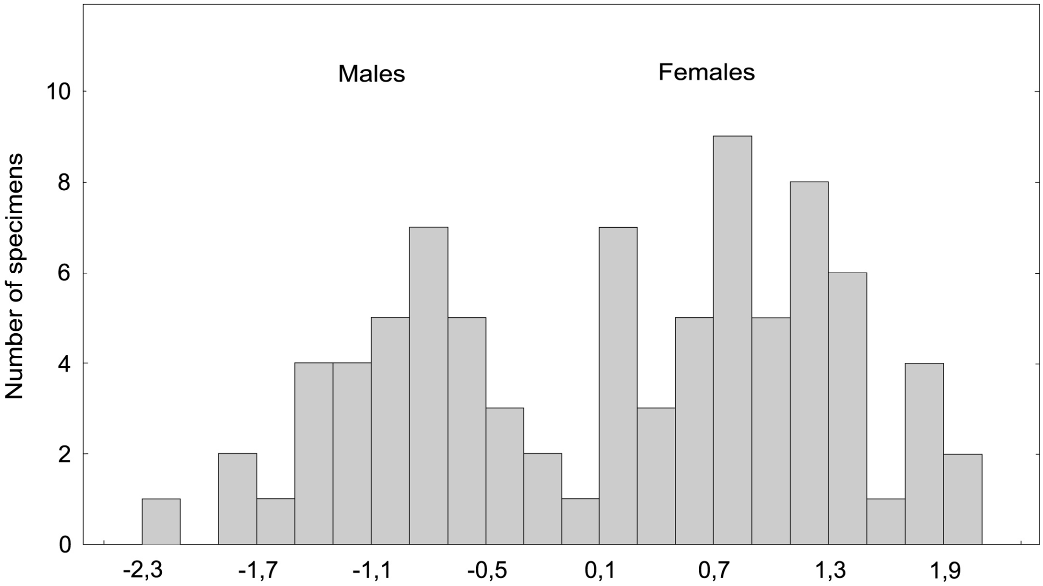

Figure 5. Distribution of the first principal component (PC 1) scores, calculated on the basis of a correlation matrix of standardized data for eight measurements of cave bear (*Ursus spelaeus*) metacarpals from Divje babe I: specimens from layers 6 and 7 (N = 85). Scores were standardized using the data of the sample Db-B. Due to negative factor loadings, the large (i.e. male-ascribed) metacarpals form the left of the two peaks and the small (i.e. female-ascribed) metacarpals the right one. PC 1 explains 72.8% of the variance accounted for by the basic data set.

substantially increased the intersexual competition for appropriate lairs. Such a thesis is corroborated by the fact that the sex ratio in metapodials from the only two relatively warm and/or arid phases of OIS 3 (i.e. the set of layers 2-5 without layers 5a and layer 6-7; *cf.* TURK *et al.*, 2001; 2002; in press) does not show a majority share of males otherwise characteristic of the rest of the material from OIS 3. Instead, the share of males in the material of the two above-mentioned phases is practically equal to the share of females, just like in the Db-C sample from the relatively warm OIS 5a-5d (fig. 5; see also fig. 2, fig. 3 and fig. 4).

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BIOSTATISTICAL INVESTIGATION OF LONG BONES AND METAPODIAL BONES OF *URSUS SPELAEUS* AND *URSUS DENINGERI*

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Abstract: This paper is on multivariate testing for species differentiation between *Ursus deningeri* and *Ursus spelaeus*. Significant results were achieved with twelve combinations of variables on nine postcranial elements in the discriminant analysis. These are attributed to a difference in locomotion habits, correlated to the differing diet of each species. These measurements were then used for the calculation of classification probabilities for the fossil finds of uncertain affiliation from the Einhornhöhle/Germany. A dominance of the geologically older *U. deningeri* is postulated here.

Key words: Ursids, Europe, Pleistocene, postcranial, statistics, species separation.

INTRODUCTION

Following a recent publication (Athen & Pfretzschner, 2005) data were evaluated from the Pleistocene *Ursus deningeri* and *Ursus spelaeus.* The data were gathered using 249 particular measurements on the skeletal elements humerus, ulna, radius, metacarpalia I-V, femur, tibia, fibula and metatarsalia I-V. For each of the 16 postcranial skeletal elements to be analysed between 8 and 25 variables and up to 56 instances per site are present. A new aspect of this study is that, along with the usual measurements, width and depth of the joint surfaces were also measured. The 2,890 specimens examined were from 12 sites in central Europe (fig. 1) and exclusively from adult individuals. The data was analysed using uni- and multivariate methods. The analyses have two goals. One is to discover species-defining characteristics. The other is to classify the finds from the Einhornhöhle (Unicorn Cave)/Germany as belonging to either species, *Ursus deningeri* or *Ursus spelaeus*.

Therefore, first all tests were applied to 2,295 specimens, excluding the finds from the Einhornhöhle. Next, the 595 specimens from Einhornhöhle were analysed. The statistical evaluation consisted of tests for normal distribution (Shapiro and Wilk's test) and variance (Levene test, ANOVA, Kruskal-Wallis test), of univariate (two sample tests for species distinction, *t*-test, Welch's *t*-test and the Mann-Whitney *U*-test) and multivariate main analyses (regression analysis, discriminant analysis, correlation analysis, factor analysis). The data from each species were examined in their entirety without subgroups (male/female).

RESULTS

The results of the univariate two sample tests determined significant differences between *Ursus deningeri* and *Ursus spelaeus* in 10.44% of the 249 analysed variables.

The multivariate discriminant analysis, requiring no normal distribution or homogeneous variances, could be applied to all data. The most important variables were the greatest length, proximal and distal breadth and thickness of the bones, also and especially of the joint facets. Using discriminant analysis of the logarithmized 249 variables twelve variable combinations could be identified which made a clear and certain division of the data into two groups possible, *Ursus deningeri* and *Ursus spelaeus.* In the data sets used here species separation was 100% accurate.

In a further examination process, those variables were eliminated which showed a strong correlation, as providing no significant information and being a possible source of inaccuracy. Factor analysis was used to pinpoint those combinations of factors indicating species separation. The combinations thus found were then examined again using discriminant analysis. The estimated

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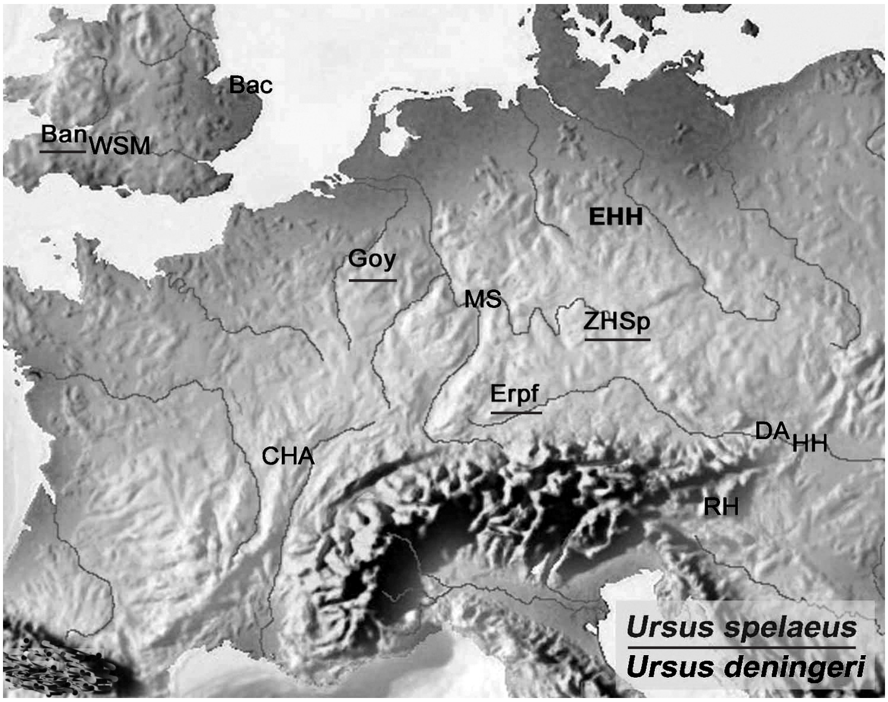

Figure 1. The location of the fossil sites in Europe. Finds of *Ursus deningeri* from Bacton/Nor-folk/United Kingdom (Bac), Château/Saône-et-Loire/France (CHA), Deutsch-Altenburg/Lower Austria (DA), Hundsheim/Lower Austria (HH), Mosbach-Sande/Wiesbaden/Germany (MS), Repolusthöhle/Styria/Austria (RH), Westbury-sub-Mendip/Somerset/United Kingdom (WSM). Selected fossil sites with finds of *Ursus spelaeus* from Banwell Bone Cave/Somerset/United Kingdom (Ban), Erpfingen/Swabian Alb/Germany (Erpf), Goyet/Condroz/Ardennes/Belgium (Goy), Zoolithenhöhle/Franconian Alb/Germany (ZHSp). The classification case is Einhornhöhle/Scharzfeld/Harz/Germany (EHH).

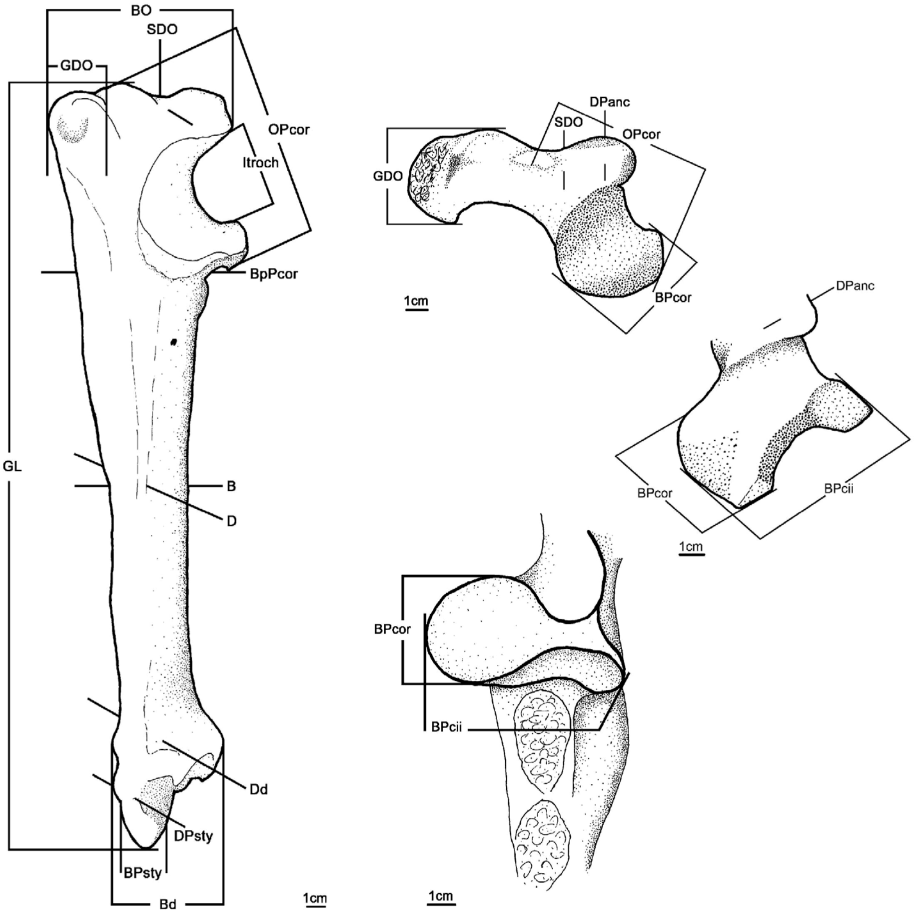

Figure 2. Ulna sinister, *Ursus spelaeus* specimen GPIT/MA/104 from Erpfingen, 16 measurements, GL (greatest length), B (breadth of diaphysis), D (thickness of diaphysis), BO (greatest breadth of the *Olecranon*), GDO (greatest thickness of the *Olecranon*), SDO (smallest thickness of the *Olecranon*), OPcor (from the most proximal part of the *Olecranon* to the *Processus coronoideus*), Itroch (distance of the outer margins of the *Incisura trochlearis* [*Cavitas sigmoides major*]), BpPcor (proximal breadth of the ulna at the level with *Processus coronoideus*), DPanc (greatest thickness of the *Processus anconaeus*), BPcor (greatest breadth of the *Processus coronoideus*), BPcii (greatest breadth of both *Processi coronarii*), Bd (greatest distal breadth), Dd (greatest thickness of the distal epiphysis), BPsty (breadth at the mean of the *Processus styloideus*), DPsty (thickness at the mean of the *Processus styloideus*). Most measurements were taken from DUERST (1926) and VON DEN DRIESCH (1976).

values of the first three factors discovered through factor analysis were again subjected to discriminant analysis, in order to find variable combinations with factors leading to species separation. Based on these results, ten variable combinations on humerus, ulna, metacarpalia I, metacarpalia III, metacarpalia V, femur and metatarsalia V were worked out. Because of the small number of instances, the fibula was deemed less useful for this purpose than the other 15 skeletal elements. Five of these variable combinations were identical to the above discovered in the first discriminant analysis process. One will be taken as an example: ulna having the logarithmized variables of smallest depth of the *Olecranon* (ln_SDO), greatest thickness of the *Processus anconaeus* (ln_DPanc), greatest breadth of the *Olecranon* (ln_BO), from the most proximal part of the *Olecranon* to the *Processus coronoideus* (ln_OPcor), proximal breadth of the ulna at the level with *Processus coronoideus* (ln_BpPcor), greatest breadth of the *Processus coronoideus* (ln_BPcor), breadth at the mean of the *Processus styloideus* (ln_BPsty) (fig. 2, 3).

In both ursid species the ulna had its highest factor scores in the measurement OPcor, determined from the most proximal part of the *Olecranon* to the *Processus coronoideus*, and in its distal area. *Ursus deningeri* had a high factor score on the *Processi*, whereas in *Ursus spelaeus* there lay more emphasis on the greatest length of the bone and the smallest thickness of the *Olecranon* (SDO). The *t*-test, Welch's *t*-test and the *U*-test found significant differences between the two species in two variables with high factor scores on the proximal breadth of the ulna at the level with *Processus coronoideus* (BpPcor) and on the distance of the outer margins of the *Incisura trochlearis* (*Cavitas sigmoides major*, Itroch). Furthermore, opposite trends in both groups were found in the variable SDO: *Ursus spelaeus* showed a decrease, *Ursus deningeri* an increase in size during the time span from the geologically older finds (900,000 years) to the younger finds (30,000 years). The reason for this observation is not yet fully understood.

The results showed that all changing variables in the factor analysis were also good distinguishing features for species separation in the discriminant analysis. The results of the discriminant analysis and factor analysis match those of the *t*-test, Welch's *t*-test and the *U*-test. In both univariate and multivariate methods it is consistently the same set out of the 249 variables, which shows differences between the species - based on the mean values.

The above discovered significant variable combinations for reliable species separation were then used for classification of the fossil finds from the Einhornhöhle (EHH, fig. 1). A lack of detailed stratigraphic information regarding the material from old excavations, which makes up the largest part of the 595 findings, has lead to some disagreement concerning species affiliation. So far it has not been possible to ascertain the absolute geological age of the fossils found. The discriminant analysis calculates probabilities for a correct classification of the material to either species. In these tests c. 60% of the processed postcranial material data from the Einhornhöhle could be identified as *Ursus deningeri* and c. 40% as *Ursus spelaeus.* Irrelevant for this classification was whether the finds originated from old or new excavations.

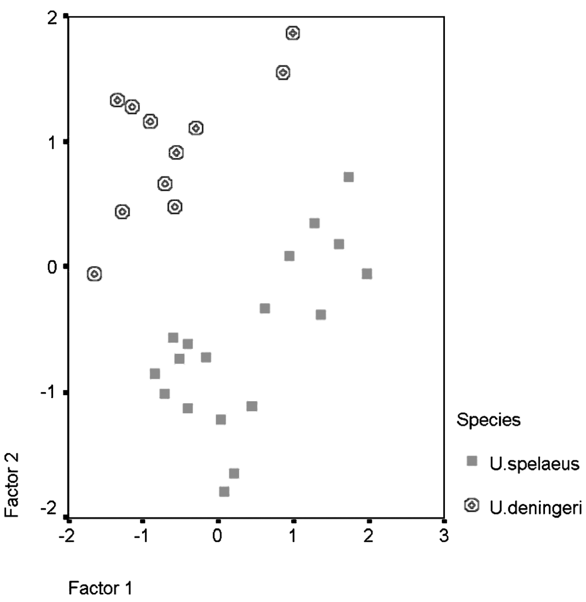

Figure 3. Plot of factor1 to factor2 in the factor analysis of the ulna (logarithmized data of GL, SDO, BO, OPcor, BpPcor, Itroch, Bpsty).

CONCLUSION

In this study species separation was possible on the above listed postcranial elements of 2,295 specimens of *Ursus deningeri* and *Ursus spelaeus*, unlike in some studies on dental material (GRANDAL D'ANGLADE & LÓPEZ GONZALEZ, 2004). The results show that in the stylopodium, zygopodium and metapodium mostly the shaft width and thickness were significantly different. This is associated with increased roaming activity over large distances. Interestingly, species classification and factor extraction was possible especially with measurements of the proximal and distal joint surfaces. Within the scope of this investigation an observed lengthening of the zygopodium in relation to the stylopodium also indicates an increased cursoriality. The mean values of the data sets analysed here also show that *Ursus spelaeus* was generally larger than *Ursus deningeri.* This is associated with increased herbivory and a genetic change, possibly due to migration especially of *Ursus deningeri*. The interpretation of the observations in this study is that the factor behind the differences, the cause, is a change in locomotion habits. The weight-supporting elements were strengthened, especially the anterior extremities, which would have been used increasingly to dig for roots and other food. It could be, that the ursids retreated south (southeast or southwest) and re-immigrated later in a more developed form. Climatic influence and subsequent changes in alimentation are also conceivable.

The majority of 595 fossil finds from the Einhornhöhle/Germany points towards a dominance of the *Ursus deningeri*-morphology group. There are different explanations for this observation. The fossil finds probably had accumulated over a long geological time span. Perhaps it was during the period of time, when *Ursus spelaeus* relieved *Ursus deningeri*. Possibly the specimens show the transition interpretation (von Koenigswald & Heinrich, 1999; Carls, Groiss & Rabeder, 1988) or a local variety (Rode, 1935). Apparently the Einhornhöhle was mainly populated by the geologically older *Ursus deningeri* whose remains during the course of sedimentation became mixed with those of the younger *Ursus spelaeus.*

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TITO BUSTILLO, A NEW *URSUS SPELAEUS* ROSENMÜLLER, 1794 CAVE ASSEMBLAGE IN ASTURIAS (NORTHERN SPAIN)

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Abstract: The cave named Tito Bustillo (Ribadesella, Asturias, Spain) has been known for decades because of its Magdalenian rock-art. It is a large karstic system by the Atlantic shore of northern Spain; the entrance is almost at sea level and its lower levels are submitted to tidal action. Currently a show cave, an assemblage of bear *Ursus spelaeus* bones was discovered when improving on the walkways in the 80's, and subsequently excavations were carried out. This is the only cave bear site documented so far in the Asturias region of northern Spain. Here we describe the site and the bear population excavated, and briefly compare it with other cave bear sites in the neighbouring regions.

Key words: *Ursus spelaeus*, *U. s. parvilatipedis,* Cantabrian mountains, Late Pleistocene.

INTRODUCTION

Cave bears were probably present throughout the Atlantic regions of northern Spain. Several cave bear sites have been excavated and published, most of these either in the eastern range of the area, at the Basque Country region (eg. Arrikrutz, Ekain, Letxetxiki, Troskaeta) (Torres, 1984; Torres *et al.,* 1988; Torres & Salazar, 1991) and others in the western area of the range, in the Galician region (eg. Eirós, Liñares, A Ceza) (Grandal d'anglade, 1993a; 1993b; 1993c; Grandal d'Anglade & Vidal Romaní, 1997; Grandal d'Anglade & López González, 1998). Here we describe a new cave bear cave, so far the only one recorded in the Asturias region of the Cantabrian Mountains, centrally occupying a position regarding other cave bear sites to the west (Eirós, Galicia) and to the east in the Basque country (fig. 1).

Tito Bustillo is a long cave (fig. 2), almost at sea level by the Atlantic coast, in the karstified carboniferous limestone of the eastern Asturias, and is part of the massif know as Macizo de Ardines. It was carved by the river San Miguel that still runs through its lower levels. At times of strong rain, the river overflows into the main gallery and if this was the case in the past it may have affected too the cave bear assemblage as discussed later.

The cave itself is renowned by its outstanding Magdalenian rock and mobile art (Moure Romanillo, 1992; Balbín *et al.,* 2003) and can be visited as a show cave. The cave bear assemblage is in the central area of the cave, quite separated from the archaeological site. It seems that the cave bear occupation of Tito Bustillo is much earlier in age than these Magdalenian occupations and quite unrelated to them.

Works carried out at the main gallery of the cave, aiming on improving public access, unearthed an assemblage of bones found to be of cave bears. Excavations were carried out there in 1998 and 1999, using the archaeological method (Pinto Llona, 2001; Pinto *et al.,* 2005). Cave bears are the only species so far identified in this assemblage.

The excavation was carried in a limited area bordering the access path (Paso Turistas in fig. 3), and extending to the wall in the north (Cata Norte). We carried out a test excavation at square B4 that reached 3 m. depth; only one fertile level was found, in the upper part of the sequence. Excavations were carried then in an extension of 20 m^2 and cave bear bones were recovered in a single cave earth layer, from depths ranging -29 cm to -124 cm.

A flowstone sealed the deposits, and it has been dated by Uranium series analysis, yielding an age older than 61±

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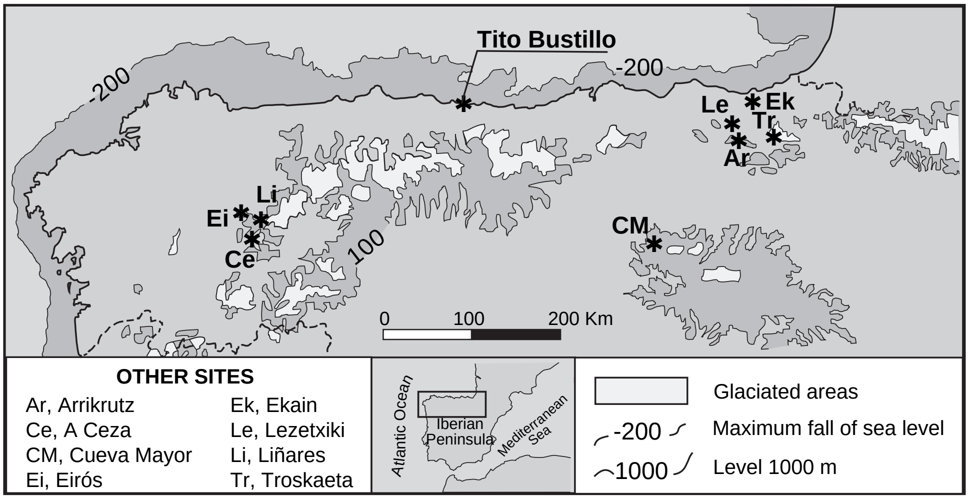


Figure 1. Bottom left: The Iberian Peninsula and the Cantabrian area in northern Spain. Above, localization of the cave bear sites mentioned in the text. Right cluster, sites in the Basque Country; left cluster sites in the Galician region; Tito Bustillo is at the present coastline and almost at sea level, in the Asturias region, the most mountainous. CM are *Ursus deningeri* from Cueva Mayor (Atapuerca), a site that is placed more southerly, in the region of Burgos.

3 ka BP (Schwarcz, TB99-1). C14 AMS analyses offered a coincident date older than 55.300 BP (OxA-9689).

The cave is periodically submitted to inundations from the river San Miguel that flows in the lower galleries. Therefore, it can not be discarded that the fossil assemblage may have been submitted to some degree of transport. However we have found limb bones in anatomical connexion (femur plus tibia plus patella, series of vertebras) suggesting that secondary movements, if any, could have been limited in extent.

MATERIALS AND METHODS

During the excavations, 1015 cave bear bones were recovered and plotted three-dimensionally; of these 228 were long bones (95 of adults and 133 of infants), representing (MNI) a minimum of 13 adults/subadults and 20 infants. In general the bones are complete or almost complete, although upon drying they proved to be in very poor condition, requiring routine use of preservers. No complete skull has been recovered although some could be restored by adding artificial filling materials. Sediment

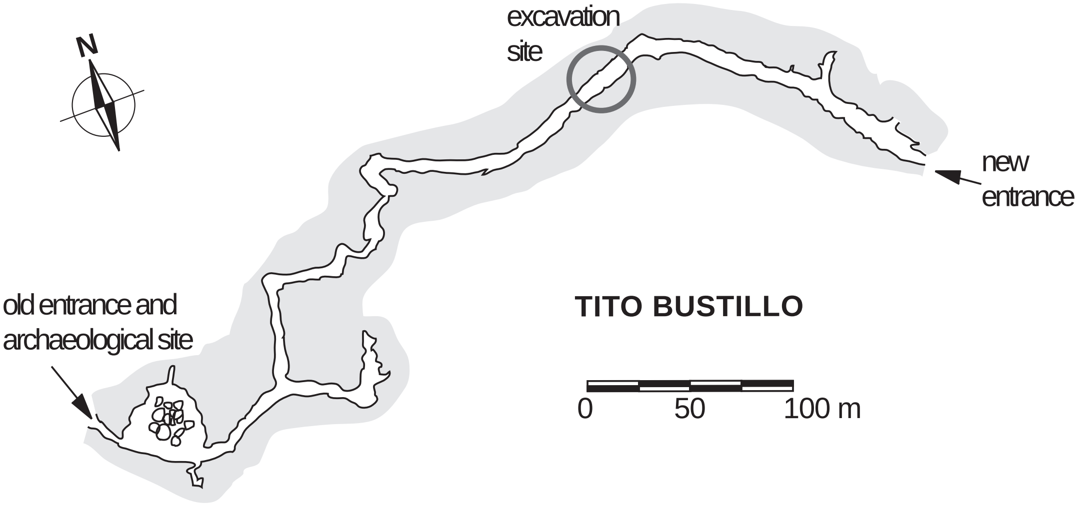


Figure 2. Plan map of Tito Bustillo. The new entrance is an artificial tunnel, with a succession of iron gates blocking air flow from the exterior. Rock art -painting and also engraving- appear throughout the cave, and an archaeological assemblage was excavated in the western area (original entrance to the cave) dated the Magdalenian.

Table 1
Sites discussed in the text, suggested dates, altitude over sea level and references.

Tito Bustillo	c. 60 Ky BP	At sea level	Pinto & Andrews, 2004
Cova Eirós	c. 24 Ky BP	780 m.	Grandal & Vidal, 1997
A Ceza	c. 35 Ky BP	1004 m.	Grandal & Lopez, 1998
Liñares	c. 35 Ky BP	1115 m.	Grandal & Lopez, 1998
Troskaeta	c. 58 Ky BP	580 m.	Torres *et al.,* 1991 2003
Ekain	Upper Pleistocene	90 m.	Torres, 1984
Arrikrutz	Upper Pleistocene	450 m.	Torres, 1984
Lezetxiki	Middle Pleistocene		Altuna, 1972
Cueva Mayor	Middle Pleistocene		Torres, 1988

samples that were taken, dried and sieved yielded no further materials or any microfauna.

Earlier research on scavenging modifications on the bones of the Tito Bustillo bears has shown that they did scavenge to a degree on the carcasses of other bears, and that this scavenging was carried out following a readily identifiable pattern, that affects in the same manner both adult and infant bones, and that is neatly distinct from scavenging patterns by other large carnivores. Identical scavenging pattern has been found to affect to other mono-specific cave bear sites of northern Spain, and it differs greatly when other carnivores such as wolves or hyenas were also at play modifying bones. (Pinto LLona, 2001; Pinto Llona & Andrews, 2004a; 2004b; Pinto Llona *et al.,* 2005).

Bone measurements have been taken for Tito Bustillo and then compared with those published for other cave bear sites in northern Spain. For bone measurements we followed generally Von den Driesch (1976) and the measures proposed by Tsoukala & Grandal d'Anglade (2002) on long bones, including metapodials, and on the 1st low molar. We choose this tooth because of its special interest from an evolutionary point of view: it reflects better the evolutionary degree, and is also most adequate to characterize each population (Grandal d'Anglade, 1993a; 1993b; 1993c; Grandal d'Anglade & López González, 2004). The number of lower M1's measured is as follows: Tito Bustillo, 22, Troskaeta 9, Ekain 23, Arrikrutz 16, Eiros 35, Liñares 10, A Ceza 11. Mean data of Lezetxiki and Cueva Mayor are from the literature (Altuna, 1972; Torres, 1988). Table 1 shows known dates, altitudes over sea level and references on these sites.

RESULTS

Metric analyses of Tito Bustillo adult long bones has shown that these belong chiefly to females. All the long bones appear within the range represented by females in other peninsula samples. Some metapodials reach sizes that are typical for males within the Iberian Peninsula, and therefore there were also some males at Tito Bustillo (tab 2). The presence of a majority of females amongst the adults of Tito Bustillo is consistent with the important presence of infants.

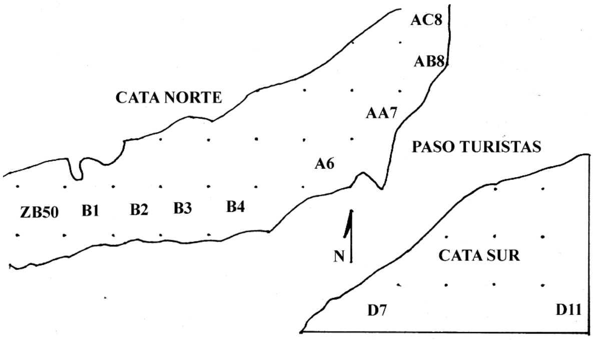


Figure 3. Excavation trenches at Tito Bustillo. The remains analyzed here proceed chiefly from the "Cata Norte" (north trench). Points signal the grid of 1m^2 squares.

The Tito Bustillo metapodials are on average of smaller size than those of other cave bear collections from northern Spain (tab. 3), and similar to the smaller subspecies *Ursus spelaeus parvilatipedis* described by Torres and colleagues in Troskaeta cave (Basque Country) (Torres *et al.,* 1991).

The average values of the measures on the lower 1st molar are also similar to the smaller sub-species *U. s. parvilatipedis* (tab. 4 and fig. 4). The Talonid Convergence Index (CI Tal) correlates well with the chronology offered for these populations and with the degree of dental evolution in each one of them (Grandal D'Anglade & López González, 2004) which also is similar to the one reached by the Troskaeta bears.

Table 2

HUMERUS

Measure	mean	std. Dev.	Min.	Max.	n
L abs	378.60	11.24	367.00	391.00	5
DAP cap	83.06	3.82	80.36	85.76	2
DAP prox	90.28	3.53	87.79	92.78	2
DT cap	66.77	3.67	64.54	71.01	3
DT prox	73.64	3.25	70.84	78.17	4
DT dia inf	42.57	1.09	40.97	43.90	5
DT dist	103.82	3.37	100.19	109.05	6
DT art dist	75.75	2.44	72.12	78.57	5
Alt art	32.88	1.63	30.51	35.60	6

ULNA

Measure	mean	std. Dev.	Min.	Max.	n
L	330.25	11.90	314.00	342.00	4
DT ol	39.23	2.20	36.69	40.50	3
DAP ol	69.09	2.01	67.26	70.92	4
DT pr.art.	51.32	11.12	34.82	58.74	4
D int.sem.	39.16	3.88	36.24	46.57	6
DAP dia	35.34	1.41	33.54	37.40	6

RADIUS

Measure	mean	std. Dev.	Min.	Max.	n
L abs	249.42	40,39	228.20	310.00	4
DT prox	44.09	-	44.09	44.09	1
DAP prox	43.27	3.31	40.44	48.87	5
DT dia	31.36	0.67	30.46	32.04	6
DT dist	65.61	1.84	64.10	68.25	4
DAP dist	40.62	0.75	39.88	41.66	4
DT art dist	46.73	1.56	45.44	48.71	4
DAP art dist	34.52	1.79	32.18	36.35	4
DT coll	33.84	1.31	32.19	35.07	5

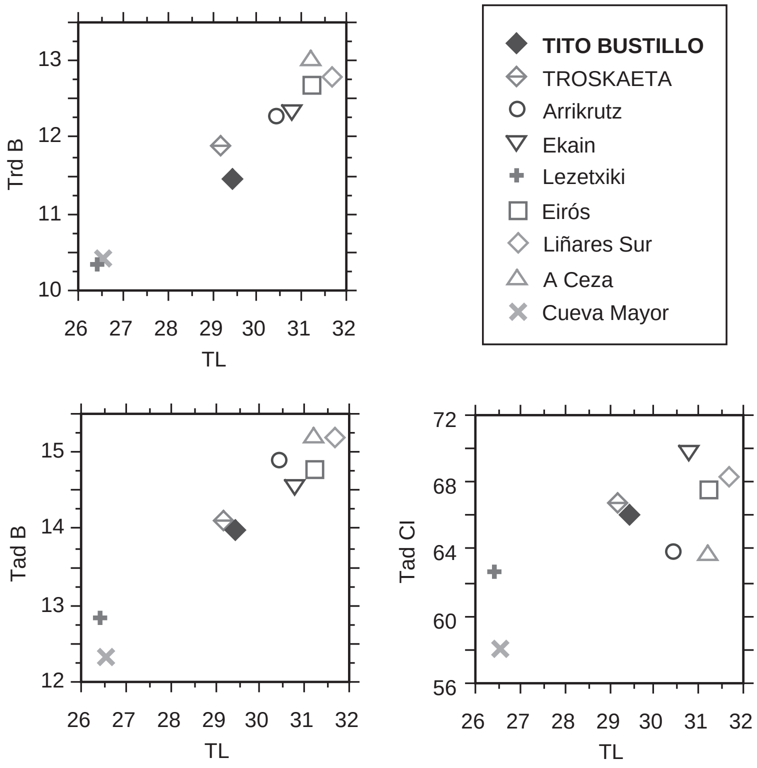
FEMUR

Measure	mean	std. Dev.	Min.	Max.	n
L abs	377.00	-	377.00	377.00	1
L int troc	85.55	6.47	77.20	91.23	4
L collum	73.98	3.26	71.25	78.38	4
DT prox	103.00	2.77	99.12	105.50	4
DT caput	47.83	2.40	45.98	51.36	4
DT dist	84.64	2.02	81.45	87.04	5
DT dia	38.23	3.06	36.06	40.39	2
DAP dist	76.18	3.60	71.59	80.34	4
DT epicond	86.05	1.25	84.21	86.87	4

TIBIA

Measure	mean	std. Dev.	Min.	Max.	n
L abs	267.25	15.61	255.00	290.00	4
DAP prox	68.80	0.44	68.49	69.11	2
DT dia	30.89	3.46	28.82	34.88	3
DT prox	83.01	5.45	75.04	87.30	4
DT dist	65.56	2.39	63.67	69.05	4
DAP dist	36.04	4.43	29.58	39.62	4
DAP art dist	30.33	4.05	24.53	33.28	4
DT art dist	50.67	1.44	49.48	52.27	3

Figure 4. Metric data (mean values) of the Lower Carnassial from Tito Bustillo and other sites in the northern Iberian Peninsula. Talonid Convergence Index was calculated as distance Hypoconid-entoconid *100/Talonid breadth.



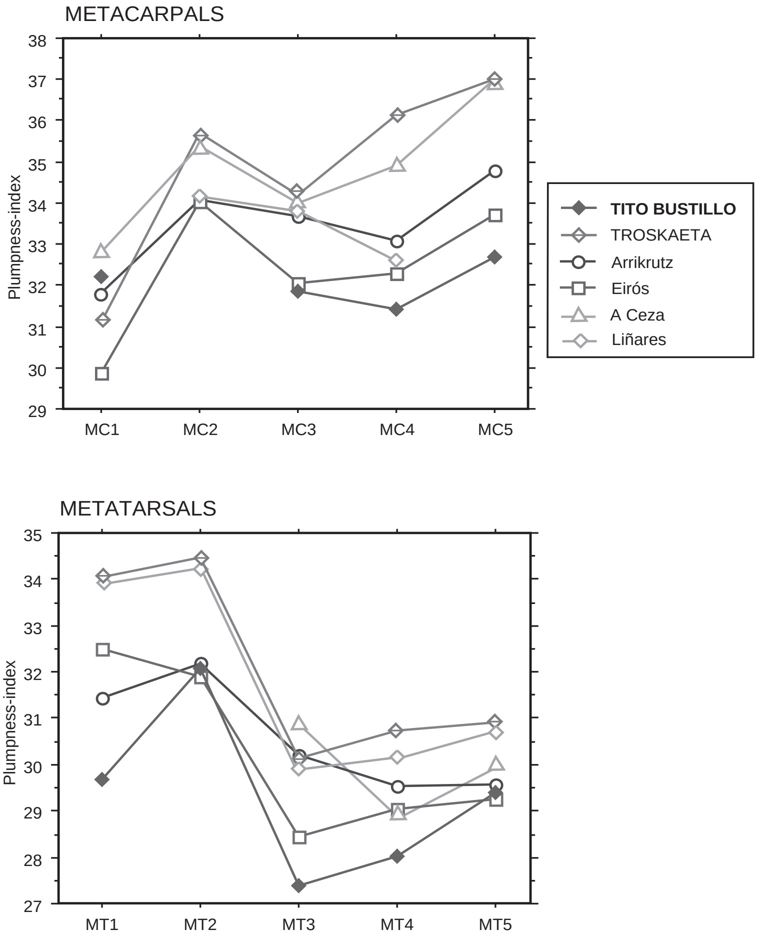


Figure 5. Plumpness index of the metapodials from Tito Bustillo and other sites calculated following WITHALM (2001): PI=Distal transversal diameter*100/Absolute length.

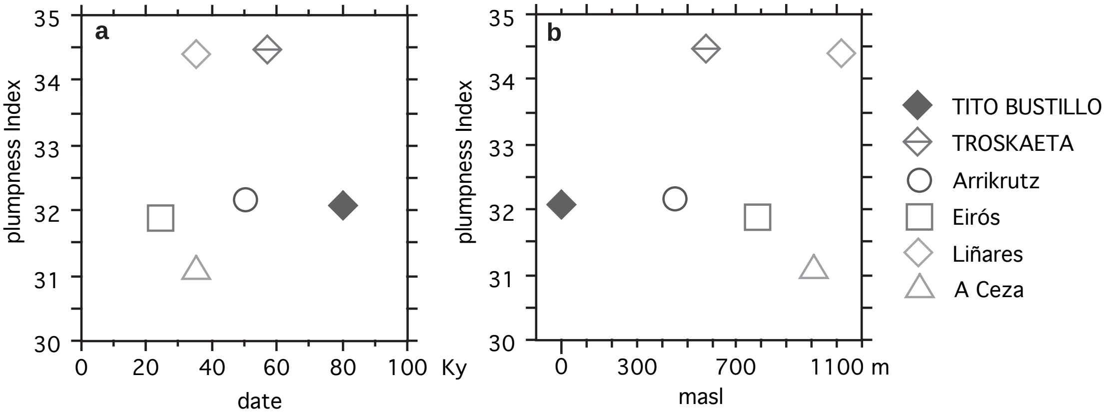


Figure 6. Average plumpness index versus chronology (a) and altitude above sea level (b).

All the above withstanding, the long bones and also the metapodials from Tito Bustillo are more gracile than those of Troskaeta, which typically are robust. We applied the Plumpness Index (Withalm, 2001) to Tito Bustillo and other Iberian cave bear sites; Tito Bustillo metapodials are rather gracile when compared with the more robust ones from Troskaeta and the other sites considered here (fig. 5). The Plumpness Index was considered by Withalm (2001) as a bio-stratigraphic index that correlates well with the age of the Alpine cave bear populations studied by the author. According to his work, robustness increases with recentness of population. However we applied this Index to several cave bear sites at the Iberian Peninsula and there does not exist a comparable correlation. The regression of the Average Plumpness Index and the age of each site yields a value of R2 = 0,111 which suggests the low correlation amongst both parameters (fig. 6 a). Particularly noteworthy is the disparity in robustness between Tito Bustillo and Troskaeta, despite bears at both sites being of smaller size, both being chronologically very close and with a very similar morphology of their 1st low molar.

It could be suggested that metapodial robustness is an adaptation to high or rough country, thus the metapodials of bears from higher caves or rougher landscapes would be more robust. However, as fig. 6 b shows, there does not appear to be any clear relation amongst the altitude of the bear caves and the robustness (R2 = 0,231). Alternately, this feature could relate to the roughness of the country the bears lived on, independently of altitude.

Pinto *et al* (2005) linked the presence of slight pathologies in the arm bones of cave bears from the same sites of northern Spain (Tito Bustillo 10,2%; Troskaeta 36,4%, Arrikrutz 34%, Eirós 29,9%) with behaviours that could relate either to digging or mountain climbing. In an earlier study (Pinto & Andrews, 2001) comparing gross dental wear features in 1st low molars of cave bears from the same sites and Holocene and extant brown bears of known diet from the same region and known diet, digging for tubers was discarded as an activity of the cave bears since they do not seem to eat tubers at all, although they could dig for other reasons.

The Tito Bustillo cave bears have the smallest percentage of pathological arm bones, which in the light of their metapodial gracility, suggests that these bears inhabited and obtained their resources in the coastal plateau of the north Atlantic coast of the Peninsula, and avoided the rougher terrain of the neighbouring Picos de Europa Mountains, where limestone caves abound but a cave bear site has not yet been documented to our knowledge.

DISCUSSION

Tito Bustillo is a long cave by the coast and at sea level in the Asturias region of northern Spain. The cave is well known by its rich cave art of Magdalenian age.

Older deposits in the cave contain a cave bear *Ursus spelaeus* assemblage. Despite Asturias being the most mountainous part of the Cantabrian Peninsula, with most of the Cantabrian mountains within its territory, and despite these mountains being chiefly limestone, with thousands of caves and many being explored and mapped by speleologists every year, no cave bear cave had been so far described there. Tito Bustillo is the first one, and is placed almost at sea level and by the present coastline.

Earlier research on the cave bears at Tito Bustillo suggests that a degree of patterned cannibalistic scavenging was part of their behaviour. The assemblage made up

Table 3

METACARPALS

FIRST METACARPAL

Measure	mean	std. Dev.	Min.	Max.	n
TL	51.77	5.17	48.12	55.43	2
DT prox	20.68	1.39	19.69	21.66	2
DAP prox	19.16	-	19.16	19.16	1
DT dia	11.18	0.83	10.60	11.77	2
DAP dia	11.55	0.35	11.30	11.80	2
DT dist	16.70	2.00	15.28	18.11	2
DAP dist	15.33	-	15.33	15.33	1
Plumpness-I	32.21	0.65	31.75	32.67	2

SECOND METACARPAL

Measure	mean	std. Dev.	Min.	Max.	n
TL	64.45				1
DT prox	13.58				1
DAP prox	22.67				1
DT dia	13.09				1
DAP dia	9.31				1
DT dist	18.81				1
DAP dist	15.04				1
Plumpness-I	29.19				1

THIRD METACARPAL

Measure	mean	std. Dev.	Min.	Max.	n
TL			73.69	85.05	2
DT prox			19.20	24.93	2
DAP prox			28.71	33.30	2
DT dia			17.07	21.58	2
DAP dia			13.47	16.30	2
DT dist			20.99	29.97	2
DAP dist			19.21	24.05	2
Plumpness-I			28.48	35.24	2

FOURTH METACARPAL

Measure	mean	std. Dev.	Min.	Max.	n
TL	78.34	7.86	72.60	89.49	4
DT prox	22.16	2.45	20.12	25.69	4
DAP prox	31.83	4.02	28.76	37.74	4
DT dia	17.39	1.67	15.70	19.68	4
DAP dia	15.37	1.78	13.90	17.96	4
DT dist	24.56	2.10	22.60	27.53	4
DAP dist	20.73	2.20	19.41	24.02	4
Plumpness-I	31.40	1.30	30.56	33.33	4

FIFTH METACARPAL

Measure	mean	std. Dev.	Min.	Max.	n
TL	78.16	3.29	73.73	81.38	5
DT prox	27.31	0.90	26.70	28.65	4
DAP prox	29.67	1.21	27.96	31.33	5
DT dia	17.38	1.07	15.70	18.23	5
DAP dia	15.18	0.99	14.02	16.59	5
DT dist	25.53	1.02	24.16	26.75	5
DAP dist	19.37	0.30	18.95	19.60	4
Plumpness-I	32.68	0.82	31.63	33.83	5

continued

Table 3 *(continued)*

METATARSALS

FIRST METATARSAL

Measure	mean	std. Dev.	Min.	Max.	n
TL	60.167	0.978	59.040	60.800	3
DT prox	23.450	1.811	21.380	24.740	3
DAP prox	19.497	1.736	17.730	21.200	3
DT dia	13.010	1.594	11.170	13.970	3
DAP dia	11.133	0.958	10.060	11.900	3
DT dist	17.867	1.387	16.270	18.770	3
DAP dist	16.183	0.208	15.950	16.350	3
Plumpness-I	29.675	1.839	27.558	30.872	3

SECOND METATARSAL

Measure	mean	std. Dev.	Min.	Max.	n
TL	69.560	4.172	66.610	72.510	2
DT prox	16.267	1.106	15.080	17.270	3
DAP prox	25.137	1.159	23.850	26.100	3
DT dia	16.550	1.510	15.400	18.260	3
DAP dia	12.530	0.411	12.070	12.860	3
DT dist	23.040	1.336	22.190	24.580	3
DAP dist	18.910	0.652	18.320	19.610	3
Plumpness-I	32.078	2.087	30.603	33.554	2

THIRD METATARSAL

Measure	mean	std. Dev.	Min.	Max.	n
TL	72.565	1.438	70.730	74.160	4
DT prox	17.708	0.801	16.790	18.680	4
DAP prox	27.725	1.502	25.710	29.330	4
DT dia	15.072	0.485	14.760	15.790	4
DAP dia	10.730	0.181	10.490	10.880	4
DT dist	19.860	0.924	18.540	20.520	4
DAP dist	16.155	0.143	16.030	16.320	4
Plumpness-I	27.376	1.368	25.380	28.374	4

FOURTH METATARSAL

Measure	mean	std. Dev.	Min.	Max.	n
TL	79.828	5.763	75.870	89.890	5
DT prox	21.310	2.208	18.960	24.230	5
DAP prox	27.322	3.448	24.440	33.130	5
DT dia	16.171	1.646	14.120	18.660	7
DAP dia	14.104	2.935	11.930	20.150	7
DT dist	22.277	1.710	21.190	26.020	7
DAP dist	17.856	1.880	16.710	21.870	7
Plumpness-I	28.034	0.724	27.163	28.946	5

FIFTH METATARSAL

Measure	mean	std. Dev.	Min.	Max.	n
TL	80.490	2.315	78.200	84.380	5
DT prox	26.056	1.666	23.230	27.660	5
DAP prox	25.354	1.343	23.480	26.850	5
DT dia	12.984	0.590	12.220	13.870	5
DAP dia	14.908	1.432	13.180	16.830	5
DT dist	23.624	0.807	22.580	24.690	5
DAP dist	16.898	0.563	16.240	17.740	5
Plumpness-I	29.385	1.671	26.760	30.844	5

Table 4

FIRST LOWER MOLAR

Measure	mean	std. Dev.	Min.	Max.	n
TL	29.454	1.680	25.240	31.960	24
TridB	11.472	0.877	9.860	13.080	27
TaldB	13.994	0.992	11.710	15.690	26
Hyd-End	9.394	0.864	7.810	10.760	22
Tad.CI	66.124	2.896	60.727	71.370	22

chiefly by females and infants. The smaller size of their metapodials reminds of the measures published for the smaller sub-species *U. S. parvilatipedis* from Troskaeta cave in the Basque Country, although more gracile.

The dates obtained for the cave bear use of the cave, and its present position almost at sea level and by the coast, suggest that the bears inhabited the cave in a cold stage earlier than the last glacial maximum (MIS 2). At such time the sea level would be lower than it is today, the coastline would have been further to the north, and the surrounding landscape would be a dry continental platform with smooth and worn relief. This landscape could explain the gracility in the metapodials of the cave bears from Tito Bustillo, when compared with those from other caves or similar or more recent dates, but that are in more abrupt and mountainous areas.

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O REBOLAL: A NEW CAVE IN GALICIA (NW SPAIN) WITH RECENT CAVE BEAR REMAINS: PRELIMINARY REPORT

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Marcos VAQUEIRO-GONZÁLEZ[2] & **Eduardo MÉNDEZ**[2]

Abstract: In this paper we describe a new cave with cave bear remains located at the NW of Spain in which the most recent cave bears, up to now, from the Iberian Peninsula were found. The range of ages varies from 30,000 to 13,000 years BP. In the material recovered it is possible to recognise different individuals of all ages. The cave walls also show scratches made by the young bears that inhabited the cave. All these would indicate that the bears used the cave frequently as a winter den for a long period of occupation. The southerly location of this cave and the range of ages allow us to interpret this site as a refugium for the cave bears during the Last Glacial Maximum, and where the bears survived along the postglacial until the beginning of the Holocene.

Key words: *Ursus spelaeus*, Galicia, glacial refugium, postglacial, bear scratches.

INTRODUCTION

Galicia is a region situated in the Northwest of the Iberian Peninsula in which cave bear remains of recent age were found into several karstic caves. These sites correspond to the westernmost populations of this species. Some of the sites have been extensively studied, such as Eirós (Grandal-D'Anglade 1993; Grandal-D'Anglade & Vidal 1997), Liñares (Grandal-D'Anglade *et al* 2000; Grandal-D'Anglade & López-González 1998; López-González & Grandal-D'Anglade 2001; López-González, 2003) and A Ceza (Grandal-D'Anglade *et al* 2000; López-González & Grandal-D'Anglade 2001; Grandal-D'Anglade & López-González 1998). In recent times, a new site was found in a cave situated more southerly than the above mentioned. This is the Rebolal Cave, in the nearby of the village Cobas (Rubiá, Ourense) (fig. 1).

This karstic cave opens out in a rocky wall facing north, at 505 m a.s.l. and presents a complicated topography (fig. 2).

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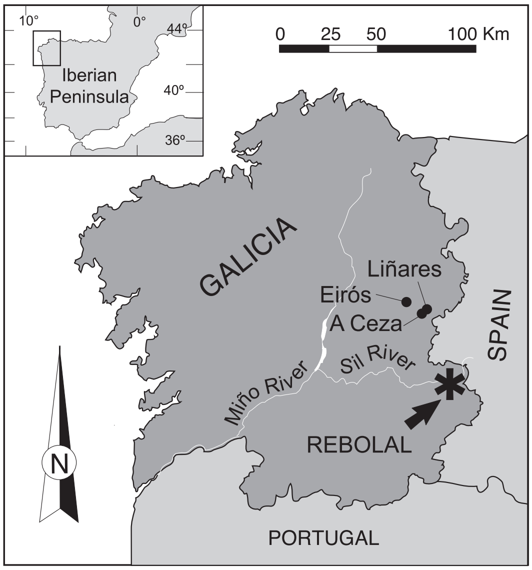

Figure 1. Situation map indicating other Galician cave bear sites.

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one of the entrances of the cave. All but two were identified as belonging to *Ursus spelaeus*.

The bones had become integrated into sediment together with quartzitic pebbles and fragments of stalagmitic crust. All of this seems to indicate that the material comes from an old excavation in the entrance probable dating from the Spanish war, as was documented in other caves of this area (fig. 3).

The bone remains were identified (tab. 1) and cleaned, and some samples were taken for different analysis. The bones were then consolidated and some of them measured (those that were in good conditions).

DESCRIPTION-DISCUSSION

The morphology of two upper P4 is different, one of them being simple according to the morphodynamic classification after Rabeder (1999). The other, although broken, seems more complex (fig. 4).

The bone sample, although scarce, includes senile, adult and juvenile specimens. This indicates that the cave was not an occasional refuge for bears, but a fully cave bear den, used at least by females with cubs.

Another clue that lead to this cave being considered as a typical bear den is the presence of bear scratches in the cave. However these scratches according to their dimensions were made by the young bears. The breadth of the scratches (four fingers or toes) is up to 32 mm. The breadth of those that are full grown (five fingers or toes) is about 42 mm.

The scratches were found in a cave wall and also in blocks (fig. 5 a & b). The situation of some of the scratches suggests that they were made with paws and also with the feet, as if the cubs were trying to climb up the cave wall.

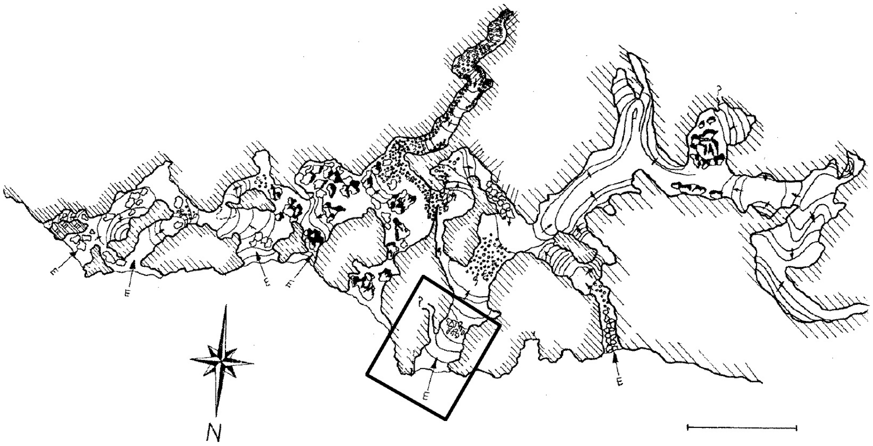

Figure 2. Topography of Rebolal Cave (GES Ártabros, 1979). The square marks the gallery detailed in fig. 3.

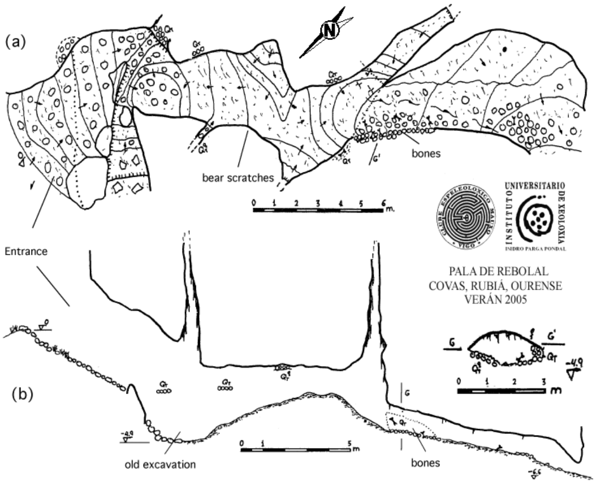

Figure 3. Rebolal Cave. (a) Topography and (b) section of the gallery where the bones and scratches were found (Clube Espeleolóxico Maúxo, 2005).

Table 1
List of bones recovered in the cave.

Num	Bone	Side	Age	Conservation	Observations
RC-1,2,3	Maxilar (fragment)	dex	adult	P4 broken M1 good M2 broken and worn out	M1 root dated
RC-4	Upper canine	dex	adult	just root	
RC-5	Jaw	dex	adult	no teeth, just canine rooth (4) very fragmented. with concretions	sampled and dated
RC-6	Jaw	dex	senile	m3 & m2 very worn out. very fragmented	small size
RC-7	Upper P4	dex	adult	good	primitive morphotype
RC-8	First phalanx	-	adult	good	
RC-9	Tibia	sin	adult	distal half	
RC-10	Tibia	sin	adult	distal epiphysis	same than 9?
RC-11	Tibia	sin	adult	proximal epiphysis	
RC-12	Long bone		adult	fragment	humerus?
RC-13	Long bone		adult	fragment	diaphysis
RC-14	Rib		adult	fragment	
RC-15	Humerus	sin	subadult	regular	sampled and dated
RC-16	Femur	dex	juvenile	diaphysis	sampled.and dated
RC-17	Femur	dex	adult	broken, *Cervus elaphus*	distal fragment
RC-18 to 26	Indet. fragments				
RC-27	Long bone	-	adult	(same than 28??)	
RC-28	Humerus	-	adult	fragment, lacking prox epiphysis	
RC-29	Humerus?	-	adult	broken	fragment prox epiphysis?
RC-30 to 33	Vertebrae	-	adult	fragment	
RC-34 to 37	Ribs	-	adult	fragment	
RC-38	Palatine	-	adult	broken	
RC-39	Skull		subadult	parietal, temporal and occipitalis	3+1 pieces
RC-40 to 46	Indet. fragments				
RC-47	Humerus	-	adult	fragment	small sized carnivore

Table 2
Ages of the dated bones.

Sample	bone	age	Lab. reference
RC-2	root of M1	13,785 ± 110 (cal 14,600 BC)	Ua-24252
RC-5	adult jaw	22,915 ± 445	Ua-24939
RC-16	juvenile femur	27,970 ± 600	Ua-24941
RC-15	subadult humerus	30,455 ± 795	Ua-24940

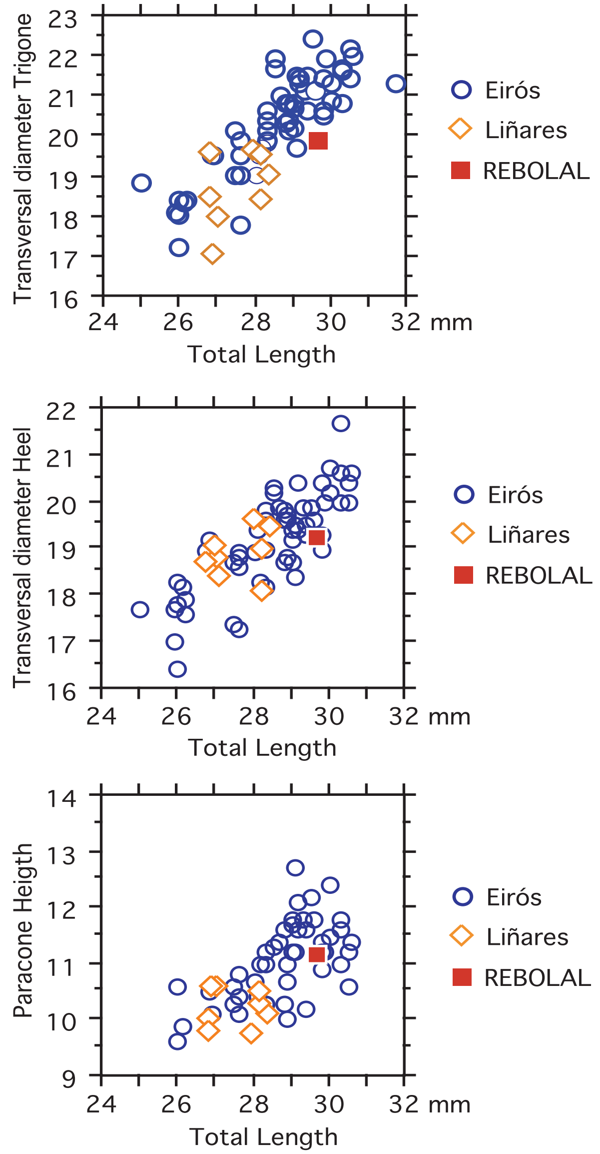

Figure 6. Bivariate diagrams of the main dimensions of the upper first molar of Rebolal and other Galician sites.

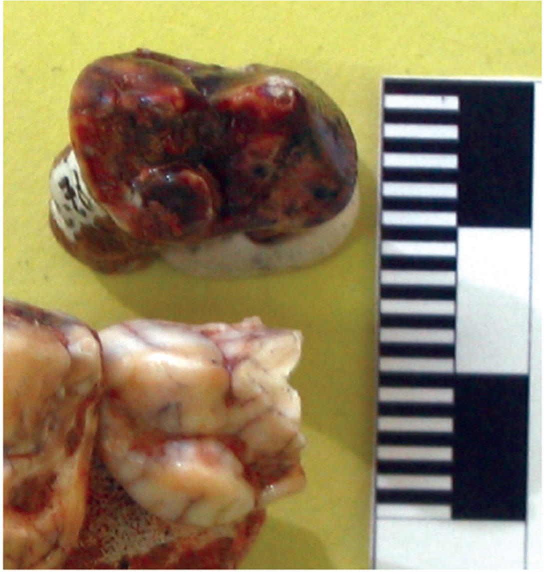

Figure 4. Two fourth upper premolars showing different morphologies.

Figure 7. The upper first molar dated in 13,785 ± 110 BP.

Figure 5. Scratches of young cave bears on the cave wall (a) and blocks (b).

CONCLUSIONS

Four radiocarbon datings (AMS 14C) were made, yielding ages between 13.5 and 30.5 Ky BP, indicating a long occupation of the cave by the bears, and the youngest ages known in the Iberian Peninsula for this species (tab. 2). The youngest age was yielded by an upper first molar with undoubtful *U. spelaeus* size (fig. 6) and morphology (fig. 7).

During 2007 it is planned to start palaeontological excavations in the cave for the localization of the main site, since the bones here studied come from sediments removed in the past by unknown people, probably partisans from the Spanish Civil War. Due to the material found so far, we expect to find a large deposit of cave bear bones dating at least from the last glacial period to the very beginning of the Holocene. That could represent a remnant population at the southwest of the cave bear distribution that probably reached this latitude in the last glacial maximum, and survived in what could be considered a glacial refuge for this species.

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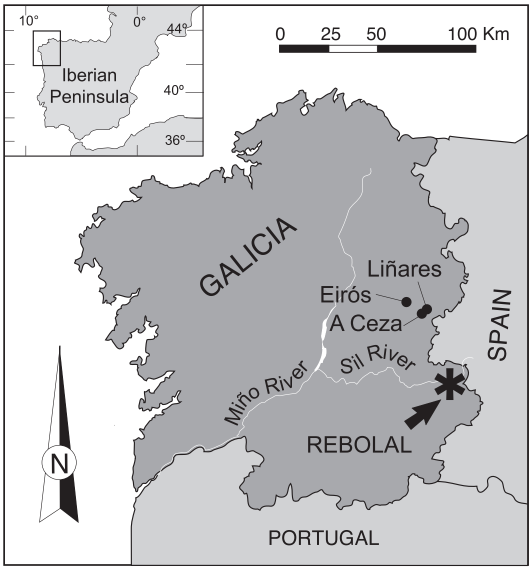

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NEW EVIDENCE FROM THE BEARS OF THE VENETO REGION (NORTHERN ITALY) IN THE EVOLUTIONARY PICTURE OF THE ITALIAN CAVE BEARS

Giuseppe SANTI[1] & Mario ROSSI[2]

Abstract: New morphological and morphometric data concerning the mandibular and dental (P_4 and M_1) remains of *Ursus* gr. *deningeri-spelaeus* from Grotta del Cerè and Covoli di Velo (Veneto region, Northern Italy) have allowed further consideration of the phyletic step reached by the cave bears in this part of Italy. Based on the new data, the *U.* gr. *deningeri-spelaeus* remains from Grotta del Cerè should be at least Middle Pleistocene in age, while those from Covoli di Velo are ascribed to the Upper Pleistocene. A question occurs concerning the possible distinction of the two species *U. deningeri* and *U. spelaeus*. In this first analysis the few observed morphological differences indicate the hypothesis of a unique species of *Ursus* (*spelaeus*) but divided into 'old' and 'modern' rather than two distinct species (*deningeri* and *spelaeus*).

Key words: *Ursus* gr. *deningeri-spelaeus*, mandibles, dentition, phylogenetic degree, Pleistocene, Northern Italy.

INTRODUCTION

Ursus spelaeus Rosenmüller, 1794 left a great amount of fossil evidence within the caves of northern Italy. Those mainly studied to date are, in the Lombardy region, the Caverna Generosa, Grotta Sopra Fontana Marella (Varese Province) (Perego *et al.,* 2001; Bona, 2004), and Grotta del Buco dell'Orso (Laglio, Como) (Rossi & Santi, 2001a,b; Santi & Rossi, 2001; Santi *et al.,* 2003) and in the Veneto region, the Grotta del Cerè and the Covoli di Velo (Verona Province) (Zorzin & Bona, 2002; Zorzin *et al.,* 2003; 2004; 2005; Galli *et al.,* 2005) (fig. 1). Less well known are the caves in the Piedmont (Grotta delle Streghe-Sambughetto Valstrona-Mt. Fenera, Vercelli Province) (Santi *et al.,* 2005) and in the Liguria (Grotta delle Fate) (Quiles, 2004). Until now the Grotta delle Ossa (Zandobbio, Bergamo Province, Lombardy) and the Grotta del Bandito (Cuneo Province, Piedmont) have been even less studied (Bonin *et al.,* 2005; Zunino & Pavia, 2005). Notwithstanding that further work is required, on the basis of the abundant analysed remains it is possible to drawn a coherent phyletic picture of the "Italian cave bears" pertaining to the *deningeri-spelaeus* group.

URSUS DENINGERI VON REICHENAU, 1906 AND *URSUS SPELAEUS* ROSENMÜLLER, 1794 IN THE VENETO

In northern Italy *Ursus deningeri* Von Reichenau, 1906 did not colonise wide areas, as its remains show. In fact, based on the current data, only rare fossils (particularly of the skull and mandibles) pertain to this species. They were only discovered within the Grotta del Cerè (Verona), a place in which more abundant fossils of *U. spelaeus* and less frequently *U. arctos* LINNAEUS, 1758, have been gathered. This cave holds many bone remains, forming a very rich association: Amphibia indet., Reptilia indet., Aves indet., *Sorex* sp., *Talpa* sp., *Marmota marmota*, *Evotomys* [recte *Clethrionomys*] sp., *Dolomys* [recte *Dinaromys*] *bogdanovi*, *Arvicola* sp., *Allophaiomis* sp., *Microtus agrestis*, *Microtus arvalis*, *Microtus nivalis*, *Microtus* sp., *Apodemus sylvaticus*, *Glis glis*, *Canis lupus*, *Canis lupus* aff. *mosbachensis*, *Canis* sp., *Vulpes vulpes*, *Vulpes vulpes crucigera*, *Vulpes* sp., *Ursus arctos*, *Ursus spelaeus*, *Ursus spelaeus minor*, *Ursus* sp., *Mustela putorius*, *Gulo gulo*, *Martes martes*, *Martes* sp., *Panthera leo spelea*, *Panthera* cf. *pardus*, *Panthera* sp., *Sus priscus*,

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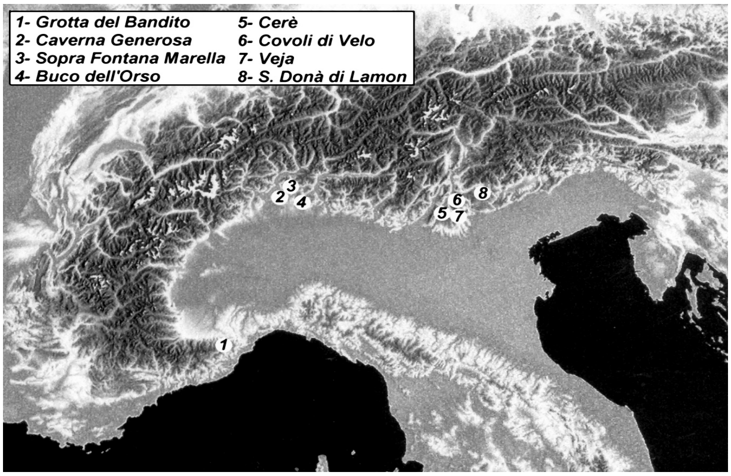

Figure 1. Distribution of the main caves in northern Italy containing remains of *Ursus* gr. *deningeri-spelaeus*.

Sus scrofa, *Sus* sp., *Cervus elaphus*, *Cervus* sp., *Bos* sp., *Rupicapra rupicapra*, *Capra ibex* and *Capra* sp. (Bon *et al.,* 1991). The presence of the three species of bear mirrored a long inhabitation of the cave by this vertebrate: considering the other species allied to the bear remains, particularly the micromammals, it is likely that the older fossils are at least 400.000-500.000 years old. Globally the Cerè's fauna might be referred to the uppermost Galerian?-Aurelian. Fossils from Covoli di Velo are certainly more recent, pertaining to the Late Pleistocene.

A distribution of the fossil bears in northern Italy can be listed: Piedmont: (1) Grotta delle Streghe: *Ursus spelaeus*; (2) Mt. Fenera: *Ursus spelaeus*; (3) Grotta del Bandito: *Ursus spelaeus*. Lombardy: (1) Grotta Sopra Fontana Marella: *Ursus spelaeus*, *Ursus arctos*; (2) Grotta Generosa: *Ursus spelaeus*, *Ursus arctos*; (3) Grotta Buco dell'Orso: *Ursus spelaeus*, *Ursus arctos*; (4) Grotta delle Ossa: *Ursus spelaeus*, *Ursus arctos*. Veneto: (1) Cerè: *Ursus deningeri*, *U. spelaeus*, *U. arctos*; (2) Covoli di Velo: *Ursus spelaeus*; (3) Veja: *Ursus spelaeus*; (4) S. Donà di Lamon: *Ursus spelaeus*. Considering the rarity of *Ursus deningeri* not only in northern Italy, but also in the whole Italian peninsula (other fossils are found in Central Italy), its presence within the Grotta del Cerè has great importance. There are possible signs of this species even in the Grotta delle Ossa in neighbouring Zandobbio village (Bergamo Province, north of Milan, Lombardy), but we need to wait for the conclusions of the research in order to confirm the eventual presence of this species. If future research confirms the uniqueness of the discovery in the Grotta del Cerè, it might become even more significant. In fact, on the basis of these data, this area could represent at least a regional expansion nucleus.

The possibility that the species *Ursus deningeri* Von Reichenau, 1906 and *Ursus spelaeus* Rosenmüller, 1794 should not really be two different taxa, but of the same taxon, has been advanced by several authors previously, and is still an unsolved problem. In recent years more detailed studies have been conducted, examining morphological and morphometric features for a distinct separation of the two species. Referring to the bears from Veneto, the first step involved the mandibles from Grotta del Cerè; a range of fundamental taxonomic elements were noted, above all concerning the vertical branch and the dentition. The main features are: (1) high condyle and angular process; (2) large masseteric fossae with right posterior border; (3) great diminution of the conic portion of the condyle; (4) complication of the masticatory surfaces.

Morphologically the main differences occurred in the vertical branch: in *U. deningeri* there is less elevation of the condyle and angular process compared with *U. spelaeus*. Morphometrically *U. deningeri* (compared with *U. spelaeus*) presents: (1) less sturdiness of the horizontal branch, either vertically or horizontally; (2) less height of the condyle; (3) less breadth of P_4. On the basis of current data, a distinction between the two species is not clear, and the transition between *U. deningeri* and *U. spelaeus* is gradual and almost insignificant. This may confirm the hypothesis that, at least for the *deningeri-spelaeus* group in Italy as well as in other European areas, we cannot speak of two clearly different species (Grandal d'Anglade & López González, 2004), but rather of an intraspecifical variability. In future, new studies on the material will give us further knowledge in order to confirm this belief.

Morphology: Referring to the bears from Grotta del Cerè and Covoli di Velo (the most significant caves for this study) it is possible to summarize as follows. Fossils from Cerè show features globally approximating to those typical of the cave bears group (in the widest view)

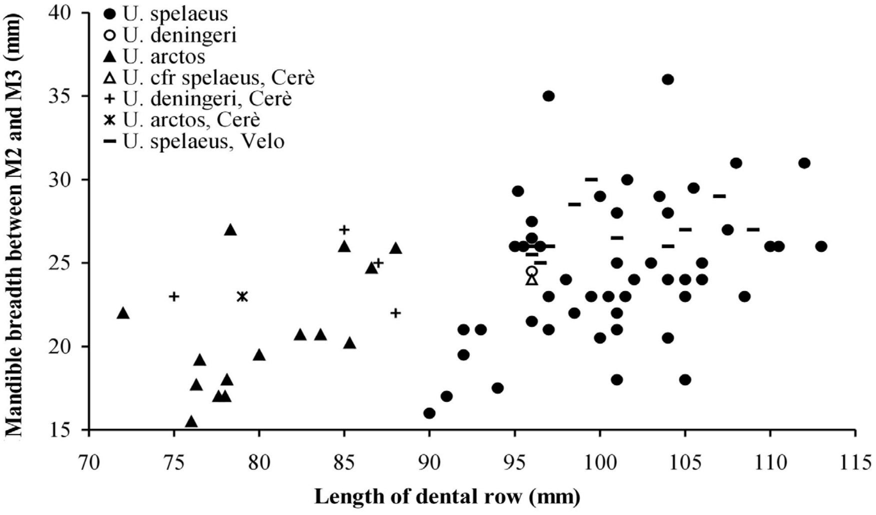

Figure 2. "Length of the dental row" and "Breadth of the mandible between M_2 and M_3" relationships in cave bears from Veneto and other caves.

comprising the two species *U. deningeri* and *U. spelaeus* (Kurtén, 1976; Ficcarelli, 1979; Ballesio, 1983; Torres Perez-Hidalgo, 1988; Argant, 1991; Mazza & Rustioni, 1994; Ballesio *et al.,* 2004). The vertical branch is characterized by rising of the condyle and angular process with consequent undertaking on the horizontal branch of the same. Except the smallest remain where the P_1 alveolus is still observable and the diastema shows a great concavity, the horizontal branch maintains the almost sturdy proportions. In all cases condyles show strong development of the cylindrical portion compared with the conic one.

Spelean bear remains from Covoli di Velo can be divided into two main groups: a group related to the female and juvenile elements, with the horizontal branch of the mandible being longer and less sturdy, and a second ascribed to the adult males with a more sturdy morphology and a shorter horizontal branch. The vertical branch always is more or less greatly leaning against the horizontal branch, with consequent rising of the condyle and of the angular process. Condyles are sturdy and more developed in the cylindrical portion than in the conic one.

Morphometry: Referring to the bears from Cerè and Covoli di Velo, utilising the more meaningful parameters indicated by Torres Perez-Hidalgo (1988) and their more important relationships, it is possible to introduce some considerations.

(1) Firstly, considering the relationship between the mandibular parameters (breadth of the mandible between M_2 and M_3 and length of the dental row) (fig. 2), in a general viewpoint the sizes of *U. deningeri* are approximately the same as those of a great brown bear, except for one mandible having a smaller size. The nearly complete lack of data concerning *U. deningeri* from other caves does not allow for much comparison; therefore in the former analysis the Deninger bears from Cerè overlap the dimensional range of the Spanish populations. For all mandibles the size of the horizontal branch compared with the length of the dental row seems to show the mandibular branch reinforcement typical of the speloid evolutionary line. This trend is confirmed by data of the mandible from Covoli di Velo, featuring strong development in a transversal line of the horizontal branch. The increase in size reached by *U. deningeri* at the *U. spelaeus* transition (Torres Perez-Hidalgo, 1988) allows us to consider the Cerè's deningerians as almost primitive forms, particularly the specimen having a smaller size characterised by an almost frail horizontal branch.

(2) The morphometric analysis of the condyles (fig. 3) confirms all previous data. In particular, main heights in the *spelaeus* bears are shown, while in *U. deningeri* the sizes and dimensions are intermediate between the two species. The fossil from Grotta del Cerè has the smallest size, smaller than typical of the species (Torres Perez-Hidalgo, 1988). This might be a consequence of two factors: lack of comparative data, or a particularly small individual for this species. However, the designation as *U. deningeri* for this fossil is defined by the morphology of the condyle. Fossils from Covoli di Velo, even if characterised by squashed condyles, are within the dimensional

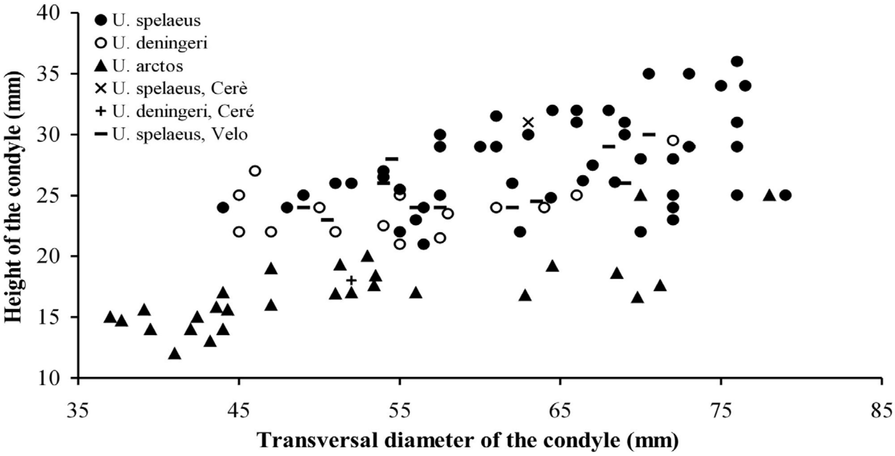

Figure 3. "Transversal diameter of the condyle" and "Height of the condyle" relationship in cave bears from Veneto and other caves.

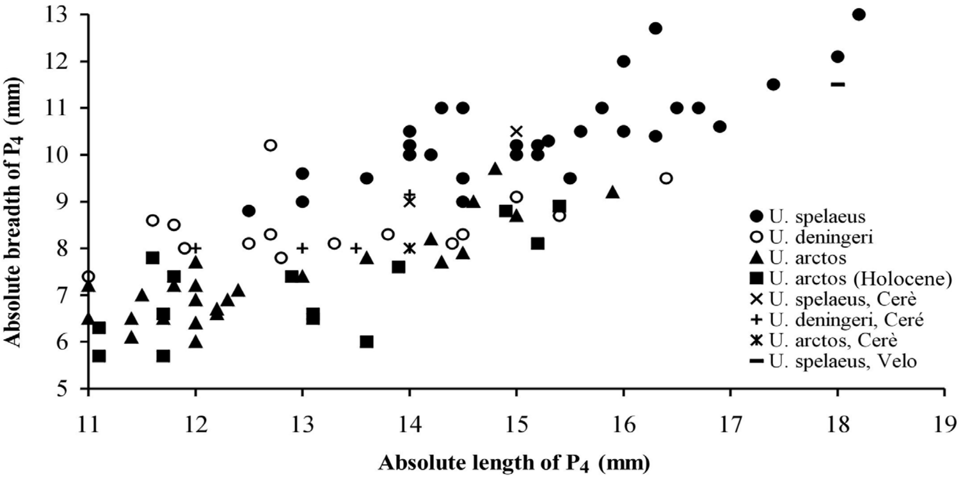

Figure 4. "Absolute length of P_4" and "Absolute breadth of P_4" relationship in cave bears from Veneto and other caves.

range typical of the cave bears.

(3) To conclude, concerning the dimensional parameters of P_4 (fig. 4) with the same absolute length, the breadth values are higher in *U. spelaeus* than *U. arctos*, while in *U. deningeri*, intermediate values occurred. Also in this case the data confirm those of the morphology: in fact, the crown boundary that more usually is shown within the three species is ellipsoidal acute in the arctoid forms, ellipsoidal large in the deningerians, and sub-circular in the speleoid specimens too. Some of the fossils from Grotta del Cerè overlap with the variability of *U. deningeri*, also showing low values even for this species, and in two cases corresponding to the *U. spelaeus* dimensions, indicating a medium-small size.

MORPHODYNAMIC ANALYSIS OF P_4 AND M_1

The morphodynamic analysis of P_4 and M_1 *sensu* Rabeder (1999) and Grandal d'Anglade & López González (2004) is the key for establishing the step reached by the cave bear in its phyletic path. This approach was applied on teeth coming either from the various Italian caves (i.e. Bona, 2004; Quiles, 2004; Zunino & Pavia, 2005; Stoppini *et al.*, 2005 an so on) or others (Grandal d'Anglade & López González, 2004).

Bears from Cerè pertaining to *U. deningeri* show P_4 with a very simple morphology characterised by a few developed paraconids and with two accessory tubercles (lingual and postero-lingual). They show some analogies either with fossils from Petralona of the Middle Pleis-

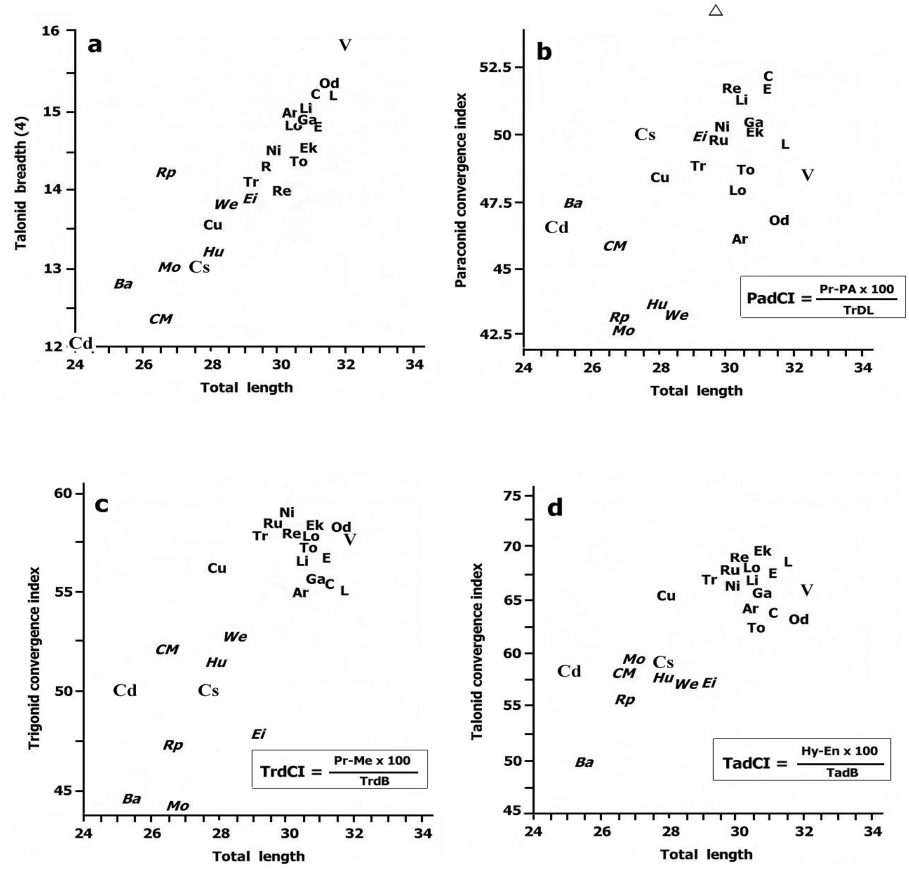

Figure 5. a. Relationship between the "Total length" and "Total breadth", b. Relationship between the "Total length" and the "Paraconid convergence index", c. Relationship between the "Total length" and the "Trigonid convergence index", d. Relationship between the "Total length" and the "Talonid convergence index" in M_1 from Italian and other caves (from Grandal D'Anglade & López-González, 2004, mod.) Symbol legend for M_1 from Italian caves: Cd, Cerè *deningeri*; Cs, Cerè *spelaeus*; V, Covoli di Velo. Other sites: IBERIAN PENINSULA: E, Eirós; C, A Ceza; L, Liñares; Ar, Arrikrutz; Tr, Troskaeta; Ek, Ekain; To, Toll; Re, Reguerillo; CM, Atapuerca (Cueva Mayor). BRITISH ISLES: Ba, Bacton; We, Westbury. CENTRAL EUROPE: Ei, Einhornhöhle (Scharzfeld); Rp, Repolust; Ru, Rubeland; Ga, Gailenreuther (Zoolithenhöhle); Hu, Hundsheim; Ni, Nixloch; Li, Liegllocħ; Cu, Conturines. EAST: Lo, Loutraki (Greece); Od, Odessa (Ukraine).

tocene (Rabeder & Tsoukala, 1990) or with those ascribed to *U. deningeri* from "Grotte des Fées" (Ballesio *et al.,* 2004). The *U. spelaeus* premolar corresponds to the C1 morphotype *sensu* Rabeder (1999).

P_4 from Covoli di Velo have a more evolute morphology approximating to the C1 morphotype or even more evolute ones, characterised by the appearance of secondary cusps and ridges.

According to Grandal d'Anglade & López González's (2004) interpretation of *spelaeus* bears, two typologies of M_1 exist: one typical of the "primitive" bears and a second concerning the more "modern" ones. In these last the hypothetical trigonid section (protoconid-metaconid) shows a more dipped border, and the surface having these two elements as extremities is wider. Passage from protoconid (where the apex within the modern speleians is more blunted) to metaconid is identified by a less dipped boundary; the metaconid is not directly linked to the protoconid, but it is lightly separated. In the hypoconid side the talonid section (hypoconid-entoconid) shows a much more dipped boundary than in the older populations, and above all, there is a little collar with an inflated appearance. This defines the crown base having a more wavy boundary in the more modern populations. In modern bears the passage from the hypoconid to entoconid, with less blunted apex, is more indented (depending on a prominent hypoconulid).

Globally the morphological features of the tooth correspond to those shown in the evolutionary schema of Grandal d'Anglade & López González (2004, fig.

2). In fact, the *U. deningeri* teeth have the more primitive features, as well as the acute paraconid and fewer of the accessory cusps that, in contrast, appear within the *U. spelaeus* teeth. All remains from Covoli di Velo belong to *U. spelaeus*, and globally show evolutionary features either in the morphology of the cusps or in the complexity of the masticatory surface.

Figs 5 a,b,c,d mirror the relationship between the "*Total Length*" and the "*Talonid Breadth*" of M_1 and those between the "*Total Length*" and the "*Convergence Index*" respectively of the paraconid, trigonid and talonid (*sensu* Grandal d'Anglade & López González, 2004).

1) In the former, the smaller size of the remains pertaining to *U. deningeri* from Cerè is shown, with fewer teeth coming from Bacton, a deposit of Early Pleistocene age (Kurtén, 1969; Bishop, 1982). Those of *U. spelaeus* have a size similar to those of Mosbach and Hundsheim, both ascribed to the Middle Pleistocene (Zapfe, 1946; Kurtén, 1969). Teeth from Covoli di Velo have a large size as well as those of speleians from the caves of the Late Pleistocene.

2) Observing the other diagrams, as already indicated by Grandal d'Anglade & López González (2004), schemas labelled with "C" and "D" are those that best show the evolutionary trend. The remains pertaining to *U. spelaeus* have a lower convergence degree for the paraconid than the bears of the Late Pleistocene caves. Convergence indices of the talonid and trigonid are, instead, very similar for the two species compared with those of the Middle Pleistocene deposits. Probably, the former of these graphs is biased by the morphological variability of this part of the tooth, while referring to the talonid and trigonid, the model is more defined. Hence, based on these data the Cerè cave's speleoid and deningerian forms might be closer together and placed on the transition interval between the two species.

3) Concerning the teeth from Covoli di Velo, they have a convergence index corresponding to those typical of the Late Pleistocene deposits.

CONCLUSIONS

Fossils from Grotta del Cerè and Covoli di Velo seem to represent the opposite extremes of the phyletic line of the cave bear. From the former come remains pertaining to the species *U. deningeri* and almost primitive forms of *U. spelaeus*. From the latter come only fossils with morphological and morphometric features typical of the more evolved speleans.

Confirmation of this in particular comes from the morphological and morphometrical features of P_4 and M_1. Comparison with material from other caves seems to confirm this deduction, suggesting for the older fossils from Cerè a chronological data in the Middle Pleistocene, and confirming that already advanced by Zorzin *et al.* (2005) for remains from Covoli di Velo. At the last, even the data concerning the faunal association of these caves seem to agree with this hypothesis.

Inside the Grotta del Cerè, *U. arctos* remains have been also gathered; it surely inhabited this cave successive to the *U. spelaeus* extinction. Paucity of remains pertaining to the more evolved forms of *spelaeus* is probably fortuitous, perhaps linked to the low number of fossils discovered in previous field surveys.

The presence of *U. deningeri* inside the Grotta del Cerè only, may underline the hypothesis that this population was an original stem from where other populations of the caves within the Verona area (i. e. Covoli di Velo and Veja) descended. It will be important to carry out some studies on the mtDNA of these populations, even if the first investigations on Austria's populations seem to indicate substantial isolation among almost closed populations (Hofreiter *et al.,* 2004).

Furthermore, study of the fossils from these caves has indicated some useful morphological and morphometrical features for separating the species *U. deningeri* from *U. spelaeus,* and included these data in the debate about the validity of these two species. Transition between *U. deningeri-U. spelaeus* occurred gradually and independently in the different European areas, and in a general view, cannot be chronologically established for the different sectors of Europe. Therefore it is difficult to show the separation between the two species (Grandal d'Anglade & López González, 2004 and references therein; Rossi & Santi, 2005). Previous authors (Kurtén, 1976; Andrews & Turner, 1992; Mazza & Rustioni, 1994; Vila Taboada & Grandal d'Anglade, 2001) have raised the possibility that the fossils represent not two different taxa, but the first and the last form of the same taxon. This is still an unsolved question. Morphologically the main differences are shown in the vertical branch of the mandible (*U. deningeri* has a lower condyle and angular process than in *U. spelaeus*). Morphometrically in *U. deningeri* the horizontal branch is less sturdy either vertically or horizontally than in *U. spelaeus*, with a lower condyle and narrower P_4 dimensions. This might enhance the hypothesis of a single taxon as suggested by Mazza & Rustioni (1994) and Vila Taboada & Grandal d'Anglade (2001). Fossils from Grotta del Cerè, as well as those of the other populations from Veneto (i.e. S. Donà di Lamon, Veja and Covoli di Velo) and Lombardy (Buco dell'Orso-Laglio, Como Province north of Milan), show morphological and morphometric features that seem to suggest the presence of a unique species. It is possible to distinguish the "old" forms (corresponding to *U. deningeri* and early *U. spelaeus*) and the "modern" ones. Data concerning the metapodial bones from the Busa di Bernardo (Predazzo, Trento Province, Trentino Alto Adige) (data in progress) seem to confirm this. In contrast, recent studies on the mtDNA have caused several authors to exclude the species *U. deningeri* as the ancestor of *U. spelaeus,* rather considering it as a "sister group" of the same (ORLANDO *et al.,* 2000). Studies yielded by TORRES PEREZ-HIDALGO *et al.* (1991) and RABEDER *et al.* (2004) show a strong differentiation within the speloid phyletic branch, with the appearance of several species and subspecies. Surely the great variability within the cave bear, much clearer within these recently studied populations, and maybe even dependent on the particular geographical situation, is at present still an open question.

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CAVE BEAR OPEN AIR SITE REMAINS AND DEN CAVES FROM THE UPPER PLEISTOCENE OF CENTRAL BOHEMIA (CZECH REPUBLIC)

Cajus DIEDRICH[1]

Abstract: A few Upper Pleistocene cave bear remains from six open air loess sites around Praha found in the 19th century and important cave bear den sites in the Bohemian Karst of the central Czech Republic are described. The few *U.* cf. *spelaeus* bones from the open air sites consist of cranial and postcranial bones whereas the female material dominates with 60%. The cave bear remains were found generally at Ice Age spotted hyena *C. crocuta spelaea* activity zones or den sites which are proved by strong chewing on woolly rhinoceros and other macromammal bones including some cave bear bones. The bone accumulations at many open air loess sites, especially along the Moldavian river and branching valleys, seems to be in most cases the result of hyena activity. *Crocuta crocuta spelaea* used many caves in the Bohemian Karst as their den and prey deposit sites, whereas cave bear scavenging by hyenas can be proved at three horizontal cave bear den caves in the Bohemian Karst. The Upper Pleistocene fauna of the sites includes only few *M. primigenius*, but commonly *C. antiquitatis*, *B. priscus*, *M. giganteus*, *C. elaphus*, *R. tarandus*, *E. ferus przewalskii*, *E. hydruntinus*, *C. ibex*, *R. rupricapra*, *P. leo spelaea*, *C. lupus*, and sometimes *G. gulo* which indicate the influence of a mountainous and alpine macrofaunal assemblage.

Key words: Cave bears, open air sites, cave dens, Upper Pleistocene, Central Bohemia, Czech Republic.

INTRODUCTION

Thousands of large Pleistocene animal bones were found in the Bohemian Karst caves and karst depressions and around Praha at open air sites, which are only partly mentioned or figured in local Czech journals (e.g. Woldřich, 1893; Kafka, 1903; Petrbok, 1939).

None of the publications have described or interpreted the Bohemian cave sites as hyena den or prey depot caves or have subdivided cave bear dens or hyena den caves or open air prey depot sites in former times. These old interpretations were revised recently by the new study of Upper Pleistocene hyena *Crocuta crocuta spelaea* (GOLDFUSS) bone accumulations in the Czech Republic (fig. 1, Diedrich & Žák, 2006) as a first result of a new collections management of the National Museum Praha Pleistocene bone collection.

In between many non-carnivore bones a few carnivore material of cave bears were rediscovered in the open air sites material. Only 0.1% of the open air site bones from localities around Praha (fig. 1), which have delivered more then 1.000 macromammal bones, are from cave bears.

These few cave bear bones from Central Bohemia are important for the understanding of the bone taphonomy at open air and cave sites and finally the cave bear demography and palaeoecology.

The caves which were used during the Upper Pleistocene in the Bohemian Karst and around Praha by cave bears (fig. 1) are the horizontal caves Axamitova Brána Cave at Tmaň, Turská Maštal Cave at Tetín, Nad Kačákem Cave at Hostím, and Praha Hlubočepy-Svatoprokopská Cave, whereas the few left bone remains and destruction of the locality Praha-Podoli makes it difficult to decide its history. In these caves about 500 cave bear bones are present in the collections.

In contrast to the cave bear “bone rich” caves only seven bones from six different open air sites are known. These are all loess sites around Praha at which the clay was explored for the brick works during the 19th century with the growth of the city. The six cave bear open air

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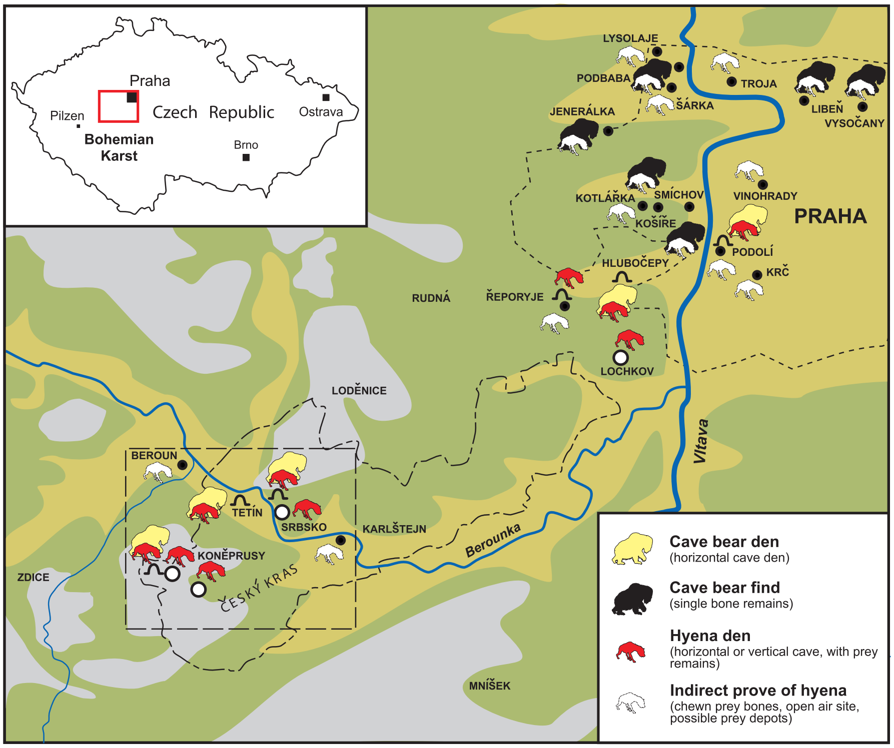

Figure 1. Geographical position of the Upper Pleistocene cave bear remains from open air loess sites around Praha (Praha-Smíchov, Praha-Jenerálka, Praha-Libeň, Praha-Podbaba, Praha-Vysočany and Praha Košíře) and important cave bear and hyena den sites in the Bohemian Karst. The cave bear remains were found at sites at which also Ice Age spotted hyena *C. crocuta spelaea* activity is proved by strong chewing on woolly rhinoceros and on some other macromammal bones. At all sites many bones of the Upper Pleistocene fauna including *M. primigenius*, *C. antiquitatis*, *B. priscus*, *E. ferus przewalskii*, *E. hemionus*, *R. tarandus*, *C. ibex*, *P. leo spelaea*, *C. lupus*, and *G. gulo* were found mainly in the 19th century (after DIEDRICH & ŽÁK 2006).

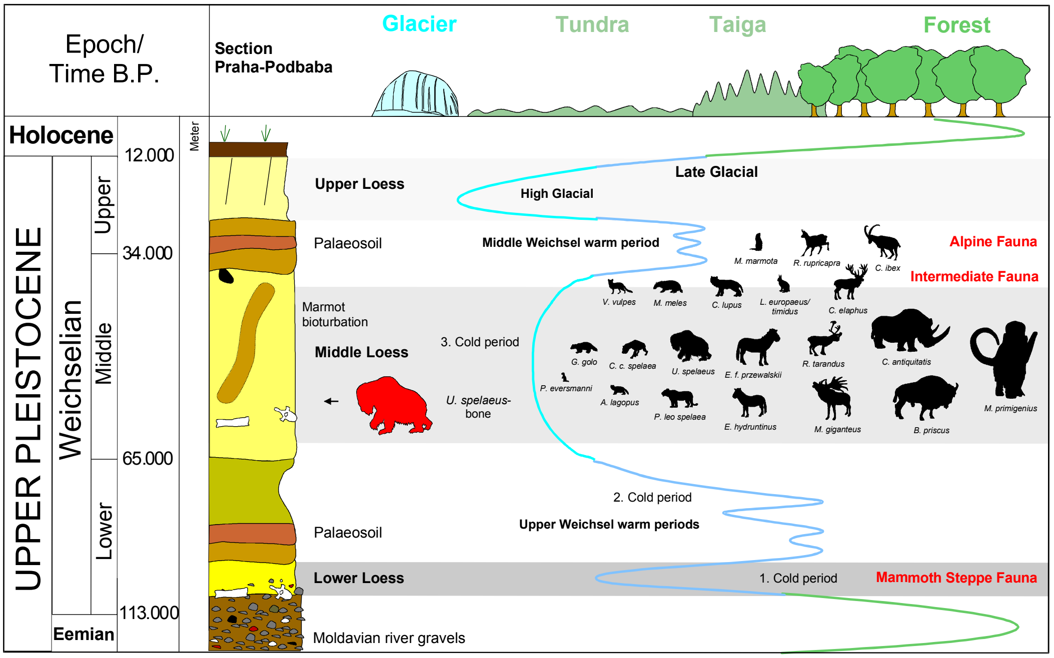

Figure 2. Geological and palaeontological history of the loess section at the Upper Pleistocene bone site Praha-Podbaba, Czech Republic (section redrawn after KAFKA (1903), with new interpretation). At this very bone rich locality by hyena chewn woolly rhinoceros bones and two cave bear bones (two ulnae, see tab. 1) were found in the 19th century.

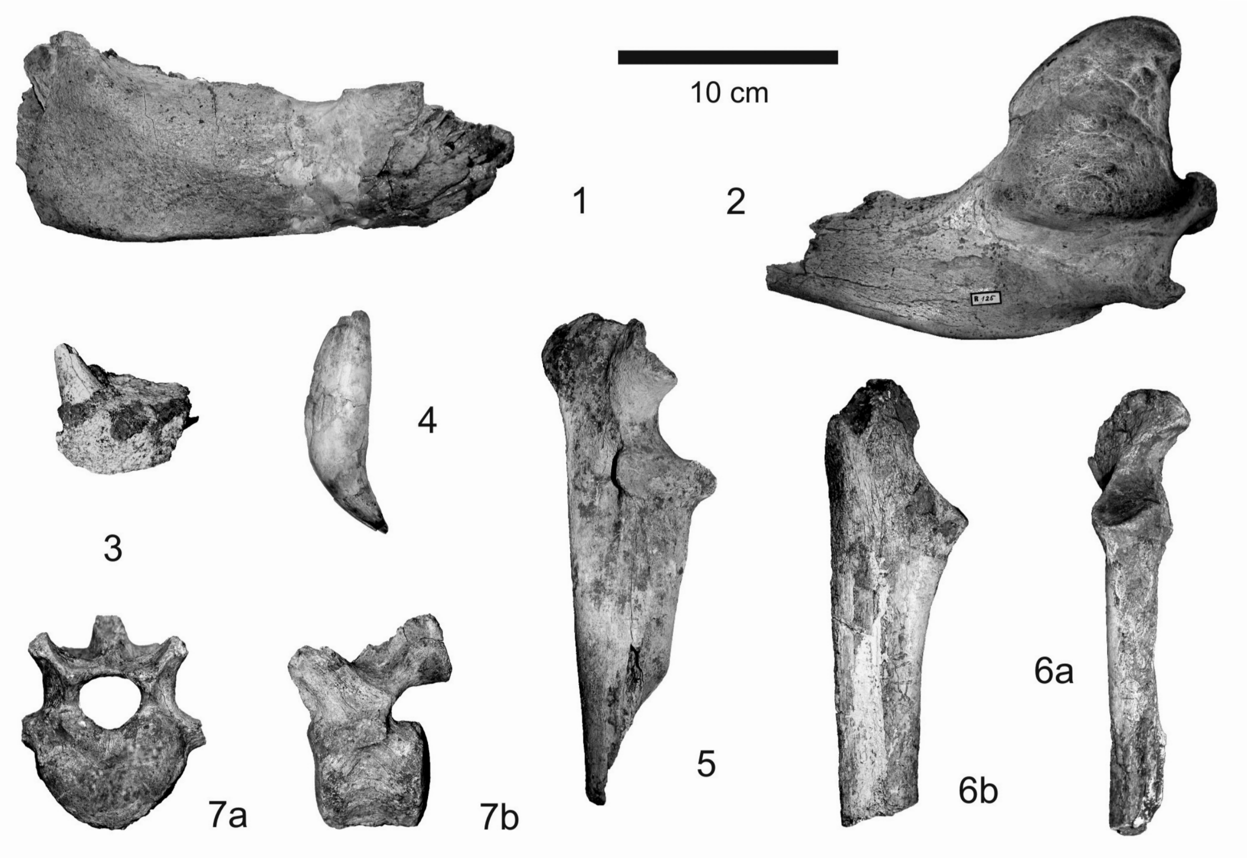

Figure 3. *Ursus* cf. *spelaeus:* Bone remains from Upper Pleistocene Bohemian open air sites around Praha. 1. Right mandible of an adult ?male animal from Praha-Smíchov (NMP, No. R 126), lateral. 2. Left mandible of an adult ?female animal from Praha-Libeň, Báně (NMP, No. R 125), lateral. 3. Left mandible of a juvenile animal from Praha-Jenerálka (NMP, No. R 6588), lateral. 4. Canine of an adult female from Praha-Vysočany (NMP, No. R 1312), a. lingual. 5. Right ulna of an adult male from Praha-Podbaba (NMP, No. R 78), lateral. 6. Left ulna of an adult female or juvenile male from Praha-Podbaba (NMP, No. R 78), a. lateral, b. cranial. 7. Lumbar vertebra of an adult ?male animal from Praha Košíře (NMP, No. R 6804), a. cranial, b. lateral.

localities Praha-Smíchov, Praha-Libeň, Praha-Jenerálka, Praha-Vysočany, Praha-Podbaba, Praha-Košíře are all situated along the Moldavian river and its branching valleys.

At all open air sites many other Upper Pleistocene macromammal bones of few *M. primigenius*, but commonly *C. antiquitatis*, *B. priscus*, *M. giganteus*, *C. elaphus*, *R. tarandus*, *E. ferus przewalskii*, *E. hydruntinus*, *C. ibex*, *R. rupricapra*, *P. leo spelaea*, *C. lupus*, and sometimes *G. gulo* were collected about hundred years ago. The little presence of the mammoth or giant deer seems to be a result of the mountainous situation. In this region the woolly rhinoceros and horses were quite abundant. Finally animals such as *C. ibex*, *R. rupricapra*, and *M. marmota* indicate alpine faunal influences during the Upper Pleistocene in Central Bohemia.

GEOLOGY AND DATATION

All cave bear bones are from loess clay pits around Praha and are situated on the old Moldavian river terraces. The macrofaunal assemblages and the finding situation in loess deposits above the Moldavian river gravels of the pre-Weichselian periods let them date generally only into the Weichselian of the Upper Pleistocene, whereas possibly material could range into the Saalian Ice Age.

The documented section of the open air site Praha-Podbaba is important for the geological history. It is the only of the six cave bear loess localities which was figured and described well by Kafka (1893; 1903). This section of Podbaba, which is very similar to the Upper Pleistocene section at the hyena open air loess depot site Bad Wildungen Biedensteg in northern Germany (cf. Diedrich, 2006b) is redrawn here with a new and detailed geological and palaeontological interpretation (fig. 2).

Table 1
Cave bear *U.* cf. *spelaeus* remains from Upper Pleistocene open air loess sites around Praha (Czech Republic).

No.	Coll.-No.	Locality	Bone type	Commentary	Left	Right	Sex	Age	Bite marks	Original	Collection
1	R 126	Praha-Smíchov	Mandible	Without dentition, incomplete		x	Male	Adult		x	National Museum Praha
2	R 125	Praha-Libeň, Báně	Mandible	Without dentition, incomplete	x		Female	Adult		x	National Museum Praha
3	R 6588	Praha-Jenerálka	Mandible	Anterior fragment, with canine	x			Juvenile		x	National Museum Praha
4	R 1312	Praha-Vysočany	Dens	Canine			Female	Adult		x	National Museum Praha
5	R 77	Praha-Podbaba	Ulna	Shaft, without joints	x		Female	Adult	x	x	National Museum Praha
6	R 78	Praha-Podbaba	Ulna	Shaft, without joints		x	Male	Adult	x	x	National Museum Praha
7	R 6804	Praha-Košíře	Vertebra	Lumbar				Adult		x	National Museum Praha

The section at Podbaba starts with the river gravels of the Moldavian river which belong to the Eemian warm period. On this, thin Loess, here called "Lower Loess" was first deposited during the first cold period of the Lower Weichselian. In the "Lower Loess" a mammoth fauna was recognized with *M. primigenius*, *C. antiquitatis*, but also a *G. gulo* skeleton remain and a partial *P. leo spelaea* skeleton find were mentioned. For this part *A. saliens,* being typical for the Lower and Middle Upper Pleistocene, was figured (Kafka, 1893). Many of the bone material was discovered in the here so-called "Middle Loess", including the two cave bear ulnae (figs. 3.5-6), which seems to represent the Middle Upper Pleistocene. Here marmot bioturbation was frequent; also burrows of other cold period micromammals (cf. Kafka, 1893). The here subdivided "Upper Loess", which could have been accumulated at the end of the Weichselian has delivered no macrofauna at this locality.

PALAEONTOLOGY

Family: *Ursidae* GRAY, 1825

Genus: *Ursus* LINNÉ, 1758

Ursus cf. spelaeus

Material: The limited material is listed in tab. 1. Seven bones are present from six different localities around Praha: Praha-Smíchov, Praha-Libeň, Praha-Jenerálka, Praha-Vysočany, Praha-Podbaba, Praha-Košíře. The bones are in a similar state of preservation. They are mostly grey to red-brown in colour and have in some cases rests of caliche incrustation on the surface (fig. 3.3). In many cases roots of plants have left with their roots a bizarre and non-smooth bone surface bioerosion structure by dissolution. Such preservations are very typical for loess sites and are generally absent in cave localities.

The cranial material consists of one isolated canine tooth and three mandible fragments. The first right mandible (fig. 3.1) from Praha-Smíchov has no teeth (but some roots are left in the alveoli) and lacks also the ramus. The height of the mandible (behind the M3) let the belief that this jaw is from a male individual. The second left mandible (fig. 3.2) from Praha-Libeň lacks all teeth again and is missing the anterior part. The alveoli of the last molar teeth are present. The ramus is nearly complete. In the proportions (height behind M3) the fragmented jaw fits more to a female animal. From a third left mandible of Praha-Jenerálka the anterior part is preserved with the canine (fig. 3.3). The lower height of the symphyses and the incompletely changed canine indicate a cub. The isolated canine (fig. 3.4) from an adult animal fits in its small proportions to the female canines.

Two ulnae and one lumbar vertebra are present from the postcranial. The first ulna (fig. 3.5) from Praha-Podbaba is lacking both joints. The shaft seemed to be cracked, whereas the proximal parts might be chewn off.

In particular the width of the shaft fits to male cave bears. The second incomplete ulna (fig. 3.6) from Praha-Podbaba is also lacking both joints, whereas the distal part must have been lost in modern times. The proximal part has again chewing marks. The less narrower width could fit to female bones, but possibly this incomplete bone belongs to a juvenile *U.* cf. *spelaeus*. Finally a lumbar vertebra (fig. 3.7) was found in Praha-Košíře which is from an adult cave bear.

The cave bear remains figured here (fig. 3) are deposited in the Pleistocene collection of the National Museum Praha (Abbreviation = NMP). The open air site bones were compared to complete bones of the famous Upper Pleistocene cave bear den site "Sloup Cave" in Moravia, from which material is deposited in the National Museum Praha.

DISCUSSION

Upper Pleistocene bone accumulations in caves of the Bohemian Karst, Czech Republic, are classified as several types of hyena dens or bone deposits and cave bear dens (fig. 1, DIEDRICH & ŽÁK, 2006).

The bone material of at least several tens of thousands of bones of this region, including about 1.000 Upper Pleistocene hyena and about 500 cave bear bone remains, is at most sites strongly fragmented by bone cracking, chewing or nibbling, very typical of hyena activities, or by improper excavations.

The cave localities can be subdivided to horizontal caves and vertical caves and karst depressions, which each have similar yet different mechanisms of bone accumulations. With the comparison of hyena cave den sites bone accumulations at open air loess sites, around Praha and the Bohemian Karst seem to be in many cases the result of hyena activity, in which also cave bear remains occur.

In the Upper Pleistocene many caves in the Bohemian Karst were used by hyenas of *Crocuta crocuta spelaea* as den and prey storages but also in some cases by cave bears for hibernating, especially along the Berounka River and the branching valleys (fig. 1). Upper Pleistocene cave bears were scavenged postmortally by the Ice Age spotted hyena in three cave sites: Axamitova Brána Cave near Tmaň, Nad Kačákem Cave near Hostím and Turská Maštal at Tetín. The intensive cave bear scavenging by hyenas in three Bohemian Karst caves is documented here additionally to some northern German Sauerland caves (e.g. Perick caves, DIEDRICH, 2005b).

The cave bear open air sites along the Moldavian river and their branching valleys are loess deposit and possibly hyena bone accumulation sites. The presence of chewing marks on woolly rhinoceros and other bones led to the belief they were of hyena prey deposit origin. A comparative situation can be found close to the cave rich mountainous area in northern Germany where freeland sites were partly studied in the Münster Bay, a flatland region north of the Sauerland cave rich mountains. Here thousands of bones were found in gravel pits at different localities mostly from the Upper Pleistocene (Weichselian). At two famous Upper Pleistocene sites Herten-Stuckenbusch and Selm-Ternsche it became obvious, that hyenas were partly or mainly responsible for big bone accumulations along rivers, in that case the Lippe and Emscher rivers (DIEDRICH, 2005a). Besides hyena skeleton remains many prey bones are similar "badly" preserved such as the bones found in the open air sites around Praha. Especially the strongly chewn and nibbled woolly rhinoceros bones are markers to identify hyena scavenging or den sites, which were later proved at the hyena open air loess site Bad Wildungen-Biedensteg in northern Germany (DIEDRICH, 2006b). Also in the Berounka valley such chewn woolly rhinoceros bones were observed in Beroun, but also at some places along the Moldavian River around Praha, which prove hyenas indirectly (fig. 1).

As for freeland sites it is difficult to discuss the male-female percentages, but the material from the females are more dominant (60% females, 40% males) at the Bohemian sites. The same cave bear sex ratio is described for open air sites in Westphalia in northern Germany (DIEDRICH, 2004; 2005a). At the open air hyena prey deposit site Bad Wildungen-Biedensteg (DIEDRICH, 2006a) all cave bear remains seems to be of female origin. More and more open air finds indicate a higher percentage of female carcasses outside the caves, whereas in caves more bones of males were found, but this can be proved only though a much higher amount of open air site bone remains in future. Also the amount of juveniles is much less in open air sites, then in caves. At the Praha sites only one jaw belongs to a few months old cub. The other bones seem to be from adult animals. Also at the German open air sites only bones from adult bears were found (DIEDRICH, 2005a; 2006a).

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ICE AGE SPOTTED HYENAS ?HUNTING OR ONLY SCAVENGING THE CAVE BEAR *URSUS SPELAEUS* ROSENMÜLLER AT THE ICE AGE SPOTTED HYENA OPEN AIR DEN AND PREY DEPOSIT SITE BAD WILDUNGEN-BIEDENSTEG (HESSIA, GERMANY)

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Abstract: Some remarkable cranial and postcranial bones of Upper Pleistocene cave bear *Ursus* cf. *spelaeus* Rosenmüller, 1794 from a *Crocuta crocuta spelaea* (Goldfuss, 1823) hyena den and prey deposit open air site at Biedensteg near Bad Wildungen (Hess) in Northern Germany represent prey remains. The taphonomical study of the bite, chew and nibbling marks being present on all cave bear bones are similar to those found on bones from the hyena Perick Cave den site in Hemer (Sauerland, NW Germany). Fore limb bones such as a scapula, humerus, ulna and a femur fragment, are from a female adult cave bear and belong possibly to one individual. Both fore limbs must have been removed from a carcass, whereas it is unclear whether the carcass was found by the hyaenas in the mammoth steppe or in a cave of the cave bear rich Sauerland mountainous region. It is possible that the female cave bear died naturally. Another possible scenario is an active successful hunting. The cave bear remains indicate that hyaenas have fed on cave bears not only in the caves, such as the Perick Caves in the Sauerland which have impressively proved hundreds of chewn and cracked cave bear bones. The hyenas could have transported from these topographically close related caves their cave bear prey remains to freeland mud deposit sites. If true, this is a unique proof of the feeding strategies of *Crocuta crocuta spelaea* on the cave bears and completes the recently studied knowledge of the palaeoecology of the hyenas and their impact on the taphonomy of cave bear carcasses in Central Europe.

Key words: Cave bear, hyenas, scavenging, open air site, Upper Pleistocene, Northern Germany.

INTRODUCTION

The cave bears *Ursus spelaeus* ROSENMÜLLER, 1794 from Northwest-German have been listed and not well described since the 18th century with the mentioning of thousands of bones from more than ten caves of the Sauerland (cf. Siegfried in 1983; Zygowski in 1988; Hammerschmidt *et al.* in 1995) whereas studies of cave bear populations have started to become more detailed (Diedrich, 2005a).

The few freeland remains of *U. spelaeus* in northern Germany were first described from river gravel deposits and one hyena mud deposit site north of the Sauerland in the Münsterland Bay and in the Weserbergland from only three localities (Diedrich, 2004).

Now new freeland cave bear finds at a very important ice age spotted hyena prey deposit site can be added in a palaeoecological study about the hyaenas *Crocuta crocuta spelaea* (GOLDFUSS, 1823). Their main cave den sites in the northern Sauerland mountainous region were recently described by Diedrich (2004; 2005a). An indirect proof of these ice age carnivores was also shown by chewn, nibbled and gnawn macromammal prey bones at some other freeland sites, where no hyena bones were found (cf. Diedrich, 2005c). A subdividing of hyena den sites from cave bear dens is of importance to understand the palaeoecology of both extinct animals in detail. In particular the question of the feeding habits or specialization of the hyenas onto ice age animals and the possible use of caves of both animals at the same time or even period will become clearer.

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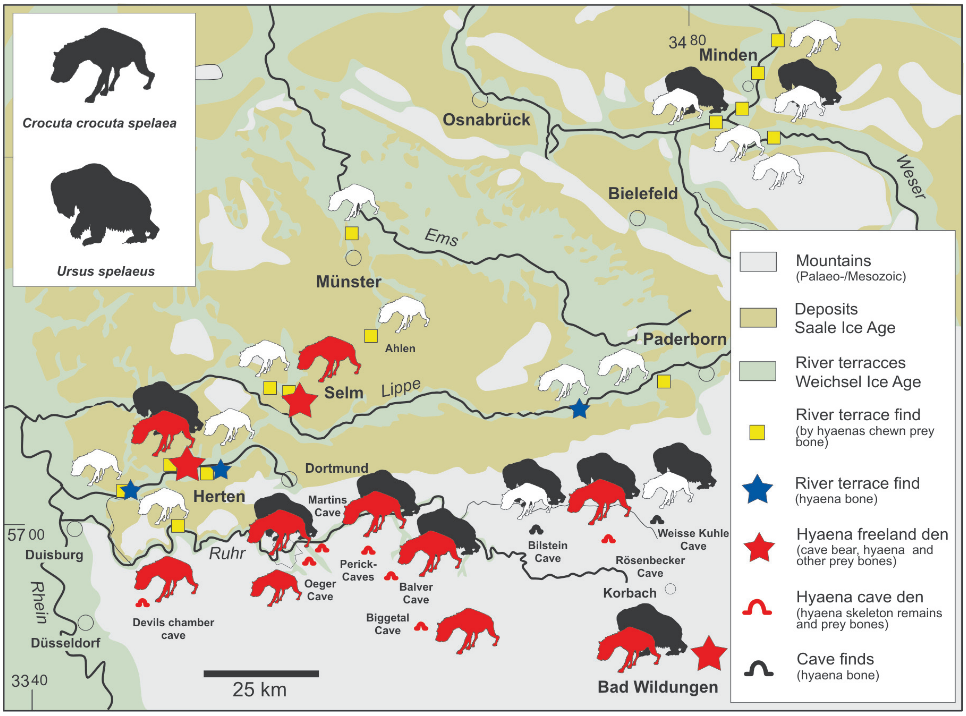

Figure 1. Position of the Upper Pleistocene hyena and cave bear den caves (Perick Caves, Martins Cave, Deutmecker Cave, Roesenbeck Cave, Balve Cave etc.), the new freeland site Bad Wildungen-Biedensteg and other open air sites in the Münster Basin. Hyena gnawn bones of *Coelodonta antiquitatis* were found at many non-cave sites being an indirect proof of these animals in the Münster Basin and northern the Wiehengebirge during the mammoth steppe period of the late Weichselian. In the Perick Caves and Martins Cave e.g. hyenas fed strongly on the cave bear carcasses.

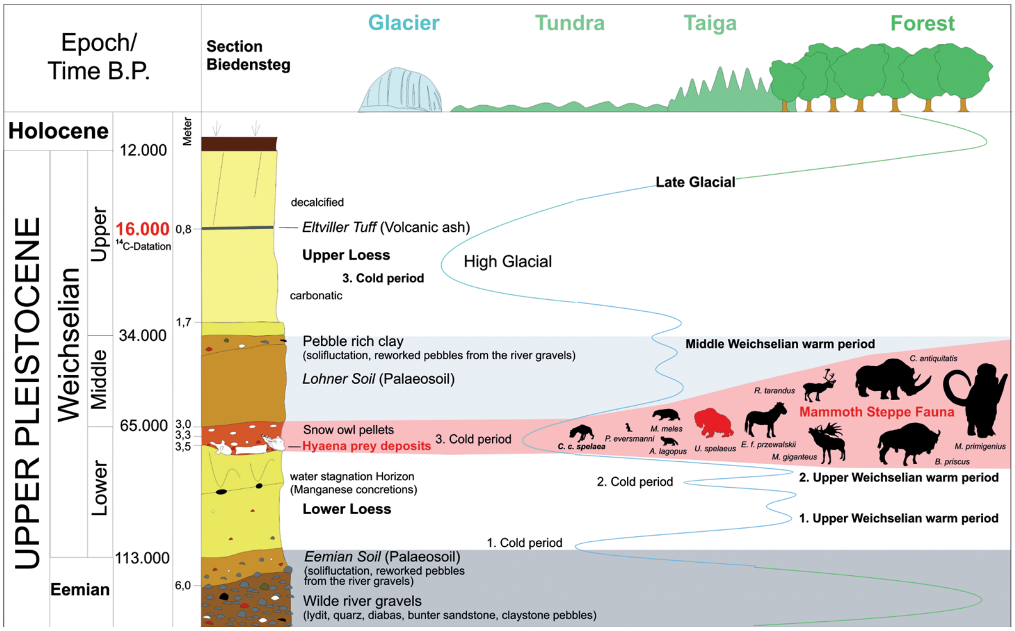

Figure. 2. Generalized section at the Ice Age Spotted Hyena *Crocuta crocuta spelaea* (Goldfuss, 1823) prey deposit site Biedensteg (Bad Wildungen, Hess, NW-Germany). The macrofauna deposited by the hyenas during the Lower Weichselian are dominated by woolly rhinoceros bones, while the rest of the prey fauna is a typical Mammoth steppe fauna consisting of *M. primigenius*, *C. antiquitatis*, *B. priscus*, *M. giganteus*, *R. tarandus*, *C. elaphus*, *E. f. przewalskii*, *U. spelaeus*, *A. lagopus*, *M. meles*, *P. eversmanni*, *L. lagopus*, *L. timidus* and *C. c. spelaea*.

The first bones in the clay pit site "Ziegeleigrube Biedensteg" in Bad Wildungen (northern Hess, Central Germany, fig. 1, coordinates: lat. 35,1058, long. 56,6550) were discovered in 1932 by F. Pusch who collected and excavated many bones, especially of macro mammals. In 1952, E. Jacobshagen and R. Lorenz found snow owl pellets in a "pellet horizon", but the latter also had two hyena skulls. Jacobshagen described in 1963 this fauna, mainly of the micromammals, whereas Huckriede & Jacobshagen published the first section which was studied with addition of new results by Semmel (1968) and Kulick (1973). Finally Storch (1969) conducted paleontological research on snow owl pellet material.

Since that time the not well determined macrofauna was forgotten and not studied in detail. Therefore a very important Ice Age hyena prey deposit and den freeland site in Europe was not understood, although first thoughts about hyena gnawing and bone deposits were mentioned by Jacobshagen (1963). None of the here described cave bear bones from Biedensteg were described as such, because of non- or misidentification as "*U. arctos*" (cf. Jacobshagen 1963).

At the site at Biedensteg mainly woolly rhinoceros *Coelodonta antiquitatis* bones were found (Diedrich, 2006) and only a few bones of other macromammals such as *Mammuthus primigenius*, *Equus ferus przewalskii*, *Rangifer tarandus*, *Megaloceros giganteus*, *Cervus elaphus*, *Meles meles*, *Alopex lagopus, Putorius eversmanni, Lepus timidus, Lagopus lagopus*, many micromammals and *Crocuta crocuta spelaea* itself. In this study the cave bear remains are described separately because of their special importance.

The material from two old collections, the Kurmuseum Bad Wildungen and the University Marbung (old coll. Jacobshagen, mainly micromammals), including all here figured cave bear remains, are now exposed in the Biedensteg exhibition of the Kurmuseum Bad Wildungen.

GEOLOGY AND DATATION

The geological situation at the hyena deposit site "Lehmgrube Biedensteg" was published by Huckriede & Jacobshagen (1963), Semmel (1968) and Kulick (1973). The overview of the redrawn sketch of the outcrop section with a combination with all published results and new own interpretations about the hyena deposits is newly presented here in fig. 2.

The Wilde river gravels at the base of the section are of the Eemian interglacial period. They consist of red bunter sandstone- and claystone-, lydit-, quartz-, diabas-pebbles. These deposits are overlain by a palaeosoil resulting of solifluctation. In this "Eem-Soil" the river pebbles are resedimented with reddish-brown loess. The Lower Loess is from the early to middle Lower Weichselian and a product of the first maximum Glaciation where in this mountainous region loess was deposited in a mammoth steppe environment. Some snails were found in the Lower Loess by Jacobshagen (1963) whereas the loess soil snail *Pupilla muscornum* (MÜLLER) fits to the climatic and environment interpretation.

In the middle and at the end of the Lower Weichselian a climatic stagnation resulted a palaeosoil along the Wilde river gravels which were at that time on the shore of a small lake. This lake was caused by subsurface salt dissolution and positioned in a doline. The lake was fed by the Wilde river a fact what can be proved by the presence of many aquatic species such as frogs (*Rana agiloides* BRUNNER, 1951) but mainly by salmonid fish (cf. Jacobshagen, 1963) that need fluent water. The lake shore was used by the Ice Age spotted hyenas as mud pit prey deposit sites. Bones from animals of the mammoth steppe macrofauna was deposited here, whereas "bone nests" were mentioned in the publication of Jacobshagen (1963). The sedimentary depression structures in the bone rich loess horizon described by Kulick (1973) as "cryoturbation and channels" also could be at least partially of bioturbation origin and were possibly caused by the hyenas who deposited animal prey remains into the soft soil. The main bones are from *Coelodonta antiquitatis* (BLUMENBACH) as shown in this description. Other animals such as *Mammuthus primigenius* (BLUMENBACH), *Megaloceros giganteus* (BLUMENBACH), *Rangifer tarandus* LINNÉ, *Equus ferus przewalskii* POLJAKOFF, *Bison priscus* (BOJANUS), *Ursus spelaeus* (ROSENMÜLLER), *Meles meles* (LINNÉ), *Alopex lagopus* (LINNÉ) or *Putorius eversmanni* (LESSON), but also snow hare *Lepus timidus* (LINNÉ) are present in the maximum glaciation fauna.

Additionally there are many steppe environment typical micromammal rodents such as *Lemmus lemmus* (LINNÉ), *Dicrostonyx henseli* (Hinton), *Microtus gregalis* (PALLAS), *Alactaga saliens* (GMELIN) or birds such as *Lagopus lagopus* (LINNÉ) listed with many other species by Jacobshagen (1963). Also the hyena *Crocuta crocuta spelaea* (GOLDFUSS, 1823) itself is present with skulls, postcranial and many coprolithes (Diedrich, 2007). The bioturbation interpretation would fit into the "hyena prey deposit site", but cannot be studied or proved anymore because of the refilled clay pit Biedensteg. In the section (fig. 2) such depressions are figured here as hyena

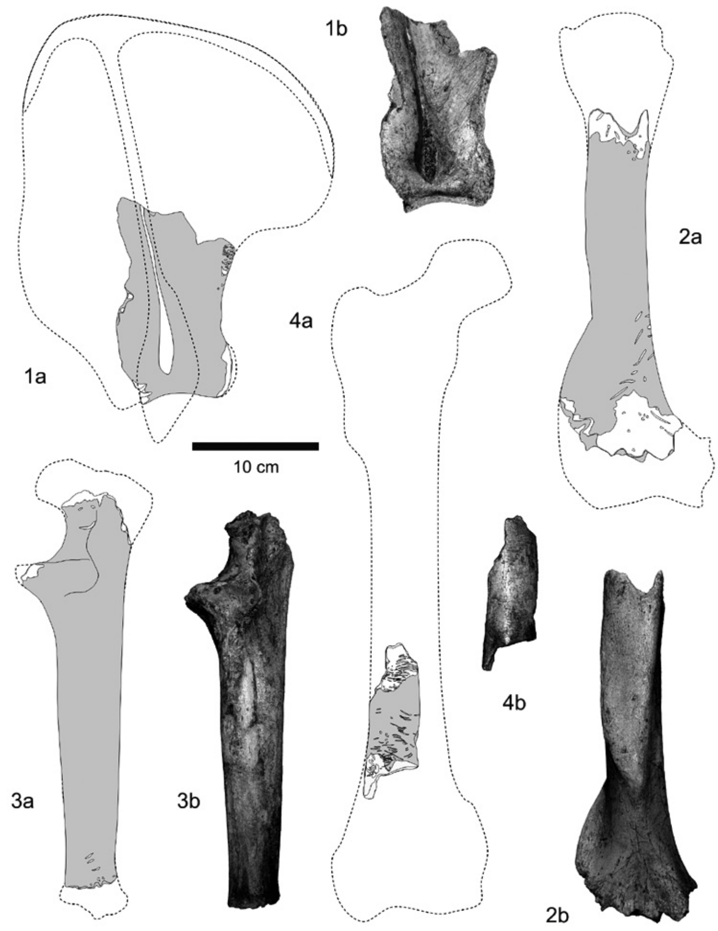

Figure 3. *Ursus spelaeus* Rosenmüller 1794 bones from the ice age spotted hyena prey deposit open air den site Biedensteg near Bad Wildungen (NW Germany). The bones from the adult animal seemed to belong to one adult female individual. **1.** Left scapular fragment (No. Bi-52/227), lateral. **2.** Right humerus shaft (No. Bi-52/2), cranial. **3.** Left ulnar shaft (No. Bi-52/241), lateral. **4.** Right (?) femora shaft fragment and "nibbling stick" (No. Bi-52/242), cranial.

bone depots. Possibly a later cryoturbation, fitting into the environment and climatic situation of that time, was responsible for the secondary overprint of the primary sediment structures.

The "pellet horizon" is figured differently in the publications (cf. Jacobshagen *et al.* 1963; Kulick, 1973). For sure the pellets are not only from snow owls, because they do not feed on anures or fishes. The high amount of frog bones must have resulted from some other large water birds and other predators which also left pellets and bone remains at the lake shore. The section of Kulick (1973) indicates that the pellets and the macromammal bones are mixed in a single horizon. A proof of that are caliche concretions around hyena coprolites in which also micromammal bones and teeth are cemented. The "hyena prey deposit site" and the "pellet horizon" are from the same period and are dated relatively into the late Middle Lower Weichselian (65.000-90.000 BP, see. fig. 2). Therefore the complete micro- and macrofauna and its taphonomy have to be newly studied to understand the lake and its surroundings and climatic situation of a mammoth steppe environment.

The bone rich horizon is overlain by another palaeosoil, in that case the "Lohner Soil", which can be found in the region at different sections (Semmel, 1968; Kulick, 1973). After their interpretations a solifluctation of Loess and Wilde river gravel material took place in the Middle Weichselian warmer period (cf. fig. 2). It seems, that some mammal species, which are also described from the "bone rich horizon" are from that time. *Vulpes vulpes* and *Meles meles* are the dominating faunal elements, besides *Lepus europaeus* and *Cervus elaphus*. This warm period

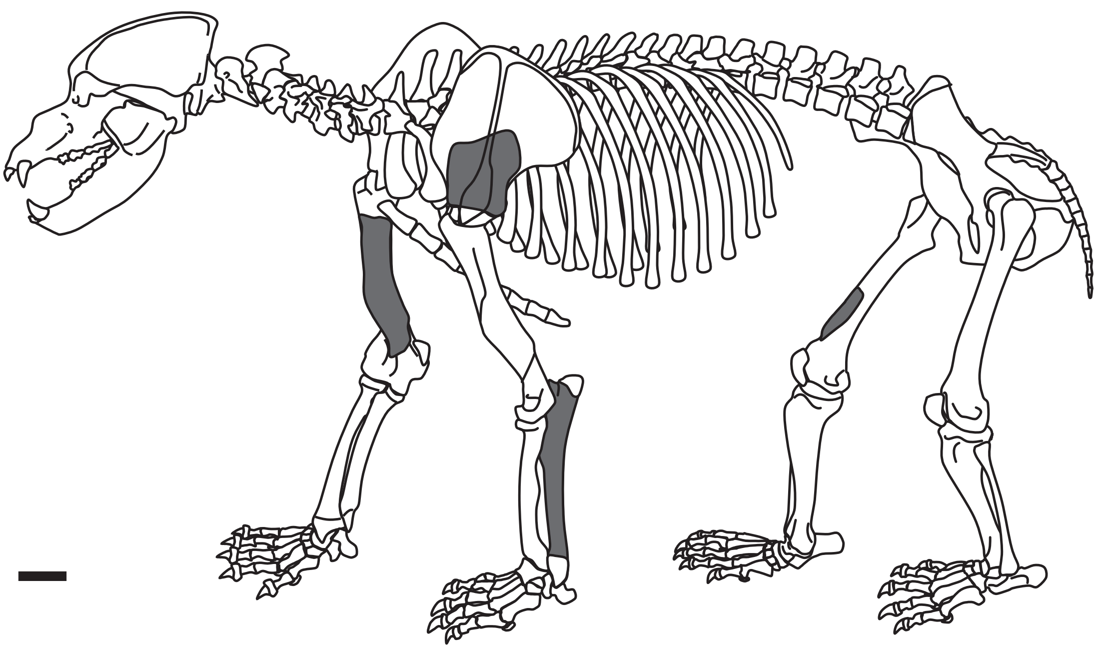

Figure 4. Present bones (grey) of an adult female *Ursus spelaeus* ROSENMÜLLER, 1794 from the Ice Age spotted hyena prey deposit open air site Biedensteg near Bad Wildungen (NW Germany).

fauna fits to *Meles/Vulpes* den sites in loess soils, in front of which they often left some prey bones. The large cave systems are often up to some meters deep burrowed and would have reached therefore the "bone rich horizon" of the hyena prey deposits. It seems obvious, that such *Meles/Vulpes* cave systems have caused a faunal mixing of the arctic and warm period mammal fauna, which was not excavated and documented in detail. This problem was not discussed in Jacobshagen (1963).

Finally the Upper Loess was sedimented, whereas the upper part was decalcified during the Holocene period. The "Eltviller Tuff" is a one to two centimetres thin layer in the Upper Loess and the only dated horizon with an age of 20.000 BP (Semmel, 1968). This proves an interpretation of the Upper Loess of its sedimentation during the Maximum Glaciation (fig. 2).

PALAEONTOLOGY

Family: Ursidae GRAY, 1825
Genus: *Ursus* LINNÉ, 1758
Ursus spelaeus ROSENMÜLLER, 1794

Material: The five cave bear bones and fragments are listed in Tab. 1 and are all figured here (figs. 3, 4).

The left scapula (fig. 3.2) of an adult female animal lacks all distal parts, which seemed to be cracked off by the hyenas. The small diameter of the glenoid with 7.5 cm fits into female cave bear scapulae of that Lower Weichselian time. Hyena gnawing and bite marks are visible at the glenoid.

A right humerus shaft (fig. 3.3) lacks the joints as a result of strong hyena chewing. At the ends and in the lower middle of the shaft bite marks are present (fig. 3.3). The small diameter of the bone shaft (4.9 cm) and the

Table 1
Bone material list of *Ursus spelaeus* ROSENMÜLLER, 1794 from the freeland prey deposit site. Bad Wildungen-Biedensteg (Hessia, NW-Germany).

No.	Coll.-No.	Bone type	Commentary	left	right	Age	Bite marks	Original	Collection
1	52/227	Scapula	Without distal part	x		Adult	x	x	Rudolf-Lorenz-Stiftung
2	52/2	Humerus	Shaft		x	Adult	x	x	Rudolf-Lorenz-Stiftung
3	52/241	Ulna	Incomplete	x		Adult	x	x	Rudolf-Lorenz-Stiftung
4	52/14	Femur	Fragment		?	Adult	x	x	Rudolf-Lorenz-Stiftung

proportions fits to femora dimensions of female cave bears of the Lower Pleistocene.

From one left incomplete ulna (fig. 3.4) the distal parts and joints were chewn by the hyenas, which also left some bite marks. In the middle of the shaft the 5 cm in maximum with ulna fits more to smaller female cave bear ulnae.

Finally a fragment of a femur (fig. 3.5) with strong chewing indicate the cracking of the femur shaft by the hyenas and further use of the bone fragment as a “nibbling stick”. The fragment does not allow a clear identification of a male or female.

Discussion: The postcranial bones of adult animals seem to belong to one skeleton of a female adult cave bear, whereas this can not be proven for the femora fragment. This fragment was compared to some hundred femur fragments from the Perick Caves hyena den, and to complete femora of that site. The thickness of the bone compact layer, the internal structures and the form do fit mostly to the cave bear. Compared bone fragments and complete bones of Bovidae, Cervidae from the Perick Caves are different in the thickness and internal structures, for sure also mammoth and rhinoceros bones. Also in the Perick Caves some cave bear femur fragment nibbling sticks are present (Diedrich, 2005a), which are very similar to the nibbling stick of Bad Wildungen-Biedensteg.

DISCUSSION

The site Bad Wildungen Biedensteg is one of the best studied yet little known open air hyena prey deposit and loess den sites in Europe. The use of that place over longer periods is documented by the presence of hyena bone and skull material, but also by their many coprolites and massive chewing, gnawing and nibbling marks on nearly all macromammal bones that were found at that site.

As shown for the main prey, the woolly rhinoceros *Coelodonta antiquitatis* (BLUMENBACH), on the one hand there must have been animals, which died or were killed by carnivores at the margin of the ancient small lake. On these carcasses the hyenas scavenged strongly and destroyed by this the skeleton articulations. One nice example is a female adult woolly rhinoceros carcass.

On the other hand prey remains were transported into the mud close to the Wilde river or small lake at Bad Wildungen. From this study of the non-cave bear material a mixture of prey deposit and lake hunting site can be figured out for the hyena site Bad Wildungen Biedensteg.

On the other hand prey remains were hidden in the mud close to the Wilde river or small lake at Bad Wildungen. From this study of the non-cave bear material a mixture of prey deposit and lake hunting site can be figured out for the hyena den site Bad Wildungen Biedensteg.

But what happened to the cave bears exactly? Certainly there must have been one female animal that was at least eaten by hyenas. Typically only massive bones such as skull fragments or longbones were left by hyenas. The presence of longbone remains indicate, such as for the woolly rhinoceros female carcass, that the bear seems to have died close to the lake or Wilde river or even at the hyena prey depot. At small lakes many large mammals would search for water, died sometimes here a natural death but were hunted here also by large carnivores.

For sure some different scenarios can be speculated on now. In the freeland at Biedensteg the female cave bear died possibly naturally or was hunted by carnivores such as the steppe lion or the hyenas.

This is the most spectacular scenario, but is not unusual, if compared to the hunting strategies of the recent spotted hyenas. The last possibility is a transportation of cave bear carcass material from caves of the Sauerland region and deposit of those at Biedensteg. This is not strongly provable, but the strong cave bear scavenging at e.g. the Perick Caves in the Sauerland give the impulse for such a theory.

At least the most logical theory seems to be, that a female cave bear searched for fresh water at the Biedensteg lake or Wilde river. Here the animal died however, and was at least scavenged by hyenas. These left only the most massive bones such as longbones.

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HYENA CAVES IN JORDAN

Stephan KEMPE[1], Ahmad AL-MALABEH[2], Doris DÖPPES[3], Mahmoud FREHAT[4], Horst-Volker HENSCHEL[5] & Wilfried ROSENDAHL[6]

Abstract: Of 14 lava caves discovered and explored since 2003 in the Jordanian volcanic Al-Shaam Harrat, eight contain traces of usage by the striped hyena (*Hyaena hyaena*). Three caves have a particularly rich record: Al-Fahda, Dabié and Al-Hayya Caves. Hyena cave usage left abundant deposits of camel bones with bones from other animals in the minority (by weight), bones and skulls of the hyena, hyena dens, coprolite deposits, paw traces and polished rocks. Hyenas penetrated caves all the way to their ends, i.e. up to 490 m from the entrance. The habit to carry large bones into caves is similar to that of the extinct European *Crocuta crocuta spelaea*, but unlike the extant African *Crocuta crocuta* and *Hyaena brunnea*. The Jordanian striped hyena may therefore be a good model to use to study the taphonomy of the cave hyena as well as its own cave-related ethology.

Key words: *Hyaena hyaena, Crocuta crocuta spelaea*, caves, lava caves, bone deposits, camel bones, dens, Jordan.

INTRODUCTION

Hyenas account for a large part of the Pleistocene bone deposits in caves in Europe (e.g., BUCKLAND, 1823; ZAPFE, 1954; ROSENDAHL, 1995; ROSENDAHL *et al.*, 2007). Among the earliest anatomically correct pictures of a bone from an extinct Pleistocene animal was a jaw fragment of a hyena from the Baumann's Cave, Harz Mountains, Germany, collected in 1708 by Johann Christian KUNDMANN and published in 1737 (KUNDMANN, 1737; KEMPE, 2004). In 1805, CUVIER recognized these teeth as those of a hyena, larger than the living species and finding it more similar to the "hyéne du Cap" than to the "hyéne du Levant". GOLDFUSS depicted a fossil hyena skull in 1810, and, in 1823, named the fossil species *Hyäna spelaea* (GOLDFUSS, 1823). It is a distinctly larger subspecies of the extant African spotted hyena (*Crocuta crocuta*) (ROHLAND *et al.,* 2005). Hyenas can feed on bones; but to consume large bones, it may be of advantage to carry them to a protected den. *C. crocuta spelaea* therefore carried bones, mostly of large Pleistocene herbivores, individually into caves where they were consumed (e.g., ZAPFE, 1939). Glacial "hyena den caves" therefore contain a variety of large, partly consumed, individual bones of those animals living nearby, but they never contain complete skeletons. Because cave hyenas are climate indifferent, these bone deposits can represent both glacial and interglacial faunas.

The ethology of *C. crocuta spelaea* (GOLDFUSS, 1823) with respect to caves cannot be studied anymore. It is therefore interesting to look at the recent species of hyenas (spotted hyena *Crocuta crocuta*, ERXLEBEN, 1777; striped hyena *Hyaena hyaena,* LINNAEUS, 1758; and brown hyena *Hyaena (Parahyaena) brunnea,* THUNBERG, 1820) and study their cave usage. This opportunity arose when, during a survey of Jordanian caves, we realized that most

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Table 1
List of currently (May 2006) known and surveyed lava caves in Jordan, sorted by total passage length (after Kempe *et al.,* 2006).
H = hyena cave.

Name of Cave	Latitude	Longitude	H	Stations	Length m	Stations	Depth m	Direction	Altitude m	Type
Al-Fahda Cave	32°18′	37°07′	+++	Complex	**923.5**	2 to 54	6.7	SW-NE	832	Lava Tunnel
Al-Badia Cave	32°07′	36°49′	-	32 to 23	**445.0**	1 to 23	17.2	NW-SE		Lava Tunnel
Hashemite University Cave	32°14′	36°34′	++	21 to 35	**231.1**	1 to 23	10.0	NW-SE		Lava Tunnel
Al-Ameed Cave	32°13′	36°33′	++	Complex	**208.0**	2 to 31	4.0	SW-NE		Pressure Ridge
Dabié Cave	32°10′	36°55′	+++	0 to 14	**193.6**	0 1to 13	1.8	NW-SE	893	Lava Tunnel
Abu Al-Kursi East	32°15′	36°39′	++	20 to 34	**153.7**	1 to 34	12.2	W-E		Lava Tunnel
Al-Howa	32°18′	36°37′	-	Complex	**97.1**	2 to 6	10.8	SW-NE		Lava Tunnel
Al-Hayya Cave	32°17′	36°34′	++	1 to 11	**81.3**	1to 9	4.2	NW-SE	911	Pressure Ridge
Abu Al-Kursi West	32°15′	36°39′	++	2 to 18	**77.1**	2 to 18	8.1	N-S		Lava Tunnel
Azzam Cave	32°17′	36°36′	-	13 to 25	**44.1**	1 to 25	4.2	NNW-SSE		Pressure Ridge
Al-Ra'ye Cave	32°17′	36°34′	-	1 to 6	**42.0**	1 to 34	3.5	NW-SE	911	Pressure Ridge
Dahdal Cave	32°17′	36°35′	+	5 to 12	**28.9**	1 to 12	0.0	SW-NE		Pressure Ridge
Beer Al-Wisad	31°46′	37°28′	-	11-3-7	**11.4**	1-2-7	11.5	NE-SW	615	Pit (unknown)
Treasure Pit	30°51′	35°24′	-	Complex	**7.2**	2 to 11	5.8	NE-SW	960	Tunnel ?
Total					**2,544**					

of the caves encountered in Jordan's deserts were hyena caves. This observation is in accordance with findings in Saudi Arabia, where hyena traces are also observed in lava caves of similar settings (Pint, 2006).

LAVA CAVES IN JORDAN

The eastern part of the Hashemite Kingdom of Jordan forms a vast stony desert, partly occupied by volcanic terrain. It is a section of a large intra-continental lava plateau called the Harrat Al-Shaam, stretching from Syria through Jordan into Saudi Arabia, build up by eruptive activity that started in the Oligocene (fig. 1). Its centre is formed by young alkali olivine basaltic lava flows (Al-Malabeh, 1998). The top-most and therefore youngest flows are about 400,000 years old (Tarawneh *et al.,* 2000). They are associated with recognizable eruptive centers such as the Quis Volcano Group (Al-Malabeh *et al.,* 2002), the Al-Bishriyya flow field (Al-Malabeh, 2003) or the Al-Fahda (Jawa) eruption center (Ibrahim & Al-Malabeh, 2006) (from west to east). Their surface is characterized by local playas between ridges that give the terrain a "mottled" appearance. Drainage networks have not yet developed, unlike on the underlying older lavas that feature extensive wadi systems. Younger and older lavas of the Harrat Al-Shaam are covered by a layer of loess, often over one meter thick. In these lavas we explored, surveyed and studied a total of 14 lava caves since September 2003. 2,544 m of passages were surveyed as of May 2006 (tab. 1) (Kempe *et al.,* 2006).

The discovery of so many lava caves in the Jordanian Harrat by A. Al-Malabeh in the period between 1986 and 2006 came as a surprise, first because of the high age of these lavas and second because loess, washed into the caves, could easily seal them in a geologically short period. Al-Fahda Cave, Al-Badia Cave (Beer Al-Hamam), Dabié Cave and the two Abu Al-Kursi Caves are all terminated by sediments. Hashemite University Cave ends with a lava seal. Most of the larger caves are lava tunnels, i.e. former lava conduits in which lava was transported from the volcanic vent towards the flow front (e.g., Hon *et al.,* 1994; Kempe, 2002). Other caves that lack signs of laterally flowing lava are summarized as pressure ridge caves. They seem to be created by upward doming of lava sheets by lateral pressure or by injection and consecutive draining of lava underneath still pliable lava strata. These caves tend to be smaller in extent, but Al-Ameed Cave is a sizeable example of this type of cave formed by two wide but low cavities connected by a 30 m long and 8 m wide crawl passage. Beer Al-Wisad finally is an 11 m deep pit of unknown origin in massive lavas (possibly pillow lavas) of Miocene age. Shifting sand should have filled it a long time ago. An anthropogenic origin of the cave can therefore not be excluded entirely even though the form of the shaft does not at all support such a conclusion.

Upper Cretaceous and lower Tertiary formations underlay the Al-Shaam basalts. These rocks crop out in the southern and eastern part of the Jordanian desert. They contain countless chert beds that form an almost continuous cover of nodules and flakes on top of the calcareous country rock. In these areas we found so far one natural cave (a large overhanging sinkhole) and several artificial cavities that have been used for housing, for stables or to extract flint.

HYENA CAVES

Even more astonishing than the fact that these caves are still accessible are the almost ubiquitous signs that the caves were or are used by hyenas (*Hyaena hyaena*, LINNAEUS, 1758). Specifically Al-Fahda Cave, Hashemite University Cave, Dabié (Arabic for "hyena") Cave, Abu Al-Kursi Caves, Al-Ameed Cave, Al-Hayya Cave, and Dahdal Cave can be classified as hyena caves. Al-Badia Cave and Beer Al-Wisad have overhanging entrance pits unsuitable for hyenas. They are used instead by pigeons. Al-Howa has been opened for us in 2004 and no traces of a former hyena occupation were found. Azzam Cave and Al-Ra'ye Cave are sheep pens, a usage that may have obliterated formerly present hyena traces. Column "H" (tab. 1) classifies the caves so far explored by the intensity of hyena traces. Hyena-transported bones with gnaw marks were also found in one of the artificial caves, making it the ninth hyena cave so far encountered.

Hyenas still live in Jordan, both in the Jordan Valley and in the eastern desert (Al-Younis, 1993; Amr *et al.*, 1996; Nissim, 1985; Qumsiyeh *et al.*, 1993; Searight, 1987). In May 2006 the authors saw a hyena from a distance in an area of Wadi Aritain around Jabal Hassan Volcano which lies between Azraq and Al-Safawi. This is in accordance with the ethology of the striped hyena that roams solitarily. Hunting hyenas is not permitted in Syria, so that hyenas can also immigrate from the north in search of food. Overall they do not seem to be plentiful, since we also found carcasses of sheep and camels in the southern desert that did not show evidence of hyena scavenging.

Evidence of hyena usage of caves

Hyena usage of caves has left several lines of evidence:

- Skulls and other bones of hyenas (fig. 2), including one mummified hyena (in Dabié Cave) and a few almost complete skeletons,
- large amounts of bones of other animals, mostly of

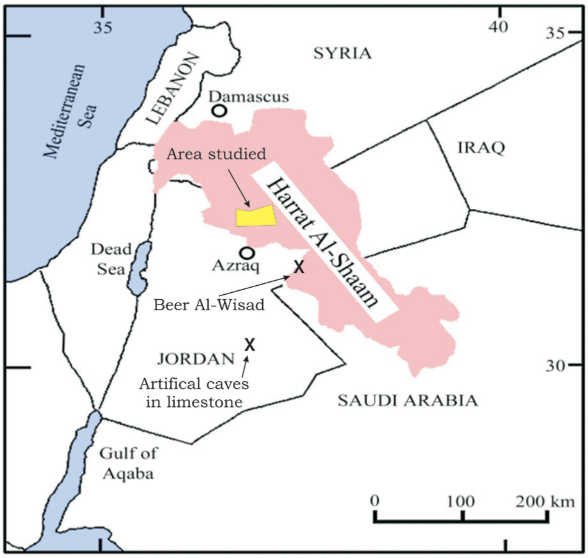

Figure 1. Study area and extent of Harrat Al-Shaam (altered after Al-Malabeh, 1994).

Figure 2. Upper jaw and skull of a hyena from Al-Hayya Cave (2005).

Figure 3. Section of Dabié Cave (2004). The floor is almost continuously covered by bones brought in by hyenas.

Figure 4. Hyena coprolite with the typical conical protrusion in a field of decomposed coprolites and camel bones in various stages of consumption (Al-Fahda Cave, 2005).

Figure 5. Hyena den almost at the upslope end of Al-Fahda Cave.

Figure 6. Pit (smaller than den) dug by a hyena or fox at a fissure, possibly in search of water (Al-Fahda upslope section near station 73).

camels, including entire legs and skulls, but also of sheep and/or goats and occasionally antelope with abundant gnaw marks and in all stages of consumption (fig. 3),

- abundant hyena coprolites (fig. 4),
- hyena dens, i.e. shallow pits dug mostly along the sides of the passages and occasionally in the centre of the cave floors (fig. 5),
- excavation pits, dug either in search of water or even in search of cave continuation (fig. 6),
- imprints of feet in soft mud (Al-Ameed Cave), and
- polished corners of rocks ("hyenaschliffe" already mentioned by Nöggerath, 1824; for Kirkdale Cave and Sundwig) at places of regular hyena traffic (Hashemite University Cave).

Caves are also used by fenneks (*Vulpes zerda*, ZIMMERMANN, 1780) (one for example was feeding on the hyena mummy) and possibly by wolves. Bedouins used to close hyena caves with rocks to keep hyenas and wolves out of their area and away from herds.

HYENAS IN AL-FAHDA CAVE

One of the most surprising observations was that hyenas have penetrated the caves all the way to their ends. In Al-Fahda hyenas have visited and lefts dens, coprolites and bones at both ends, 490 and 190 m, respectively, from the entrance (fig. 7). This appears to be the furthest documented penetration of hyenas into caves yet (literature search by the authors). Similar deep ventures of hyenas into caves are reported from Saudi Arabia: 390 m in Kahf Al Shuwaymis and 315 m in Hibashi Cave (pers. com. J. Pint). In reaching those final chambers the animals had to crawl through some tight passages that we had to enlarge to fit through. This suggests that hyenas negotiate spaces as low as 30 cm (fig. 8). At the upslope (western) end of the cave hyenas have dug extensively, moving sediment in the amount of >0.1 m^3. Possibly they tried to follow an air draft. At the downslope end we found a dead, decayed hyena in its den. This suggests that no other hyena or fox had penetrated this far into the cave recently, disturbing the carcass. Interestingly the body is not mummified, but decayed with the bones also mostly disintegrated to a mush (fig. 9). This may be due to the fact that drip water was present even at the end of September.

Al-Fahda cave is very wide (on average 7.51 m) but rather low (tab. 2), unusual proportions for a lava tunnel. It therefore has a very large floor area, about 7000 m^2 (total length times average width). Hyenas did concentrate their feeding places to certain sites not distributing the bones evenly across the floor. Since they could not have

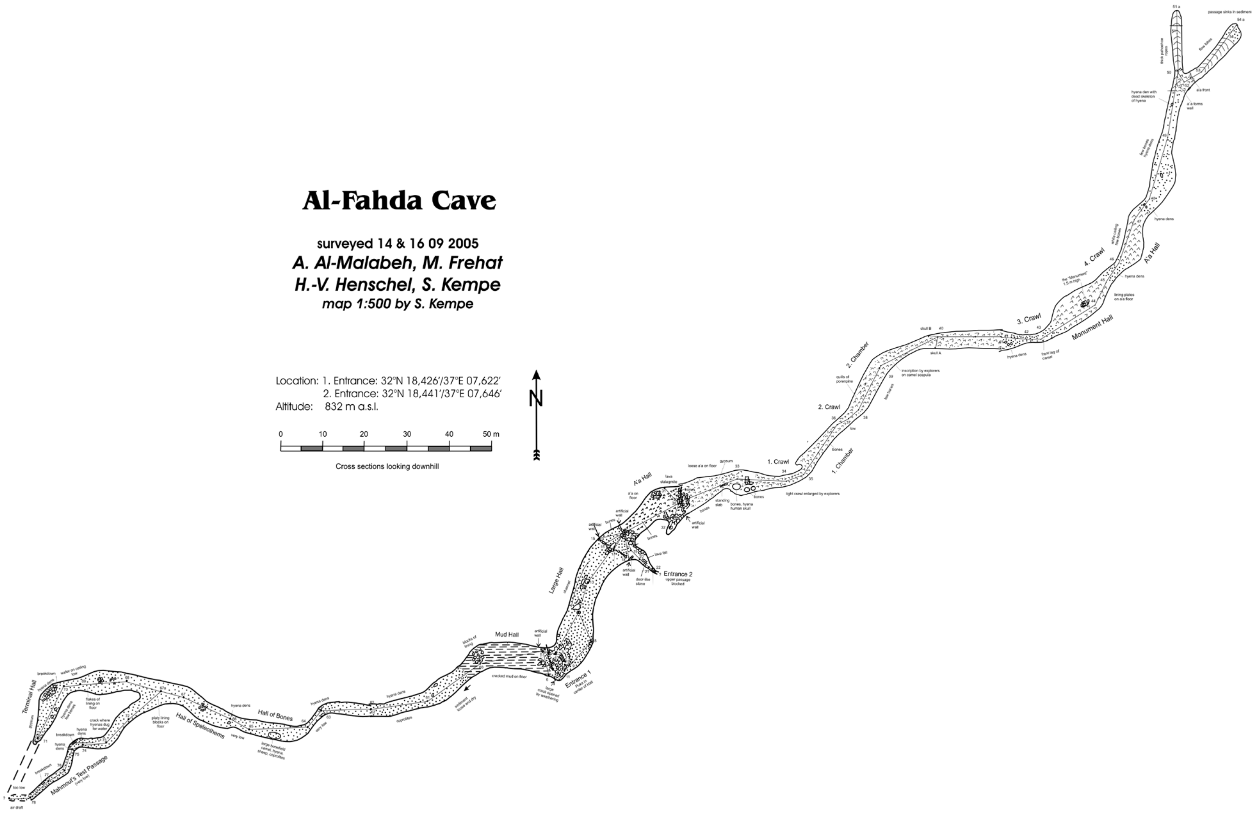

Figure 7. Composite map of the Al-Fahda Cave. It is currently the longest lava cave known on the Arabian Plate.

brought the large amount of camel bones at any single site at one time (fig. 10), these feeding places were repeatedly visited (by the same individual or different ones?). There is no clear link between feeding places and dens, most of the dens do not have bones associated with them. Normally the bones seem to be in no context with each other; at one place however, it can be shown that a hyena dragged in an upper front leg consisting of a humerus

Figure 8. Surveying in one of the low crawls in the lower section (eastern) of Al-Fahda Cave.

Figure 9. A dead hyena in its den very near to the lower end of Al-Fahda Cave.

Figure 10. A typical hyena feeding place with a collection of large camel bones in the downslope section of Al-Fahda Cave.

Figure 11. Human skull cap A near Station 40 in Al-Fahda Cave.

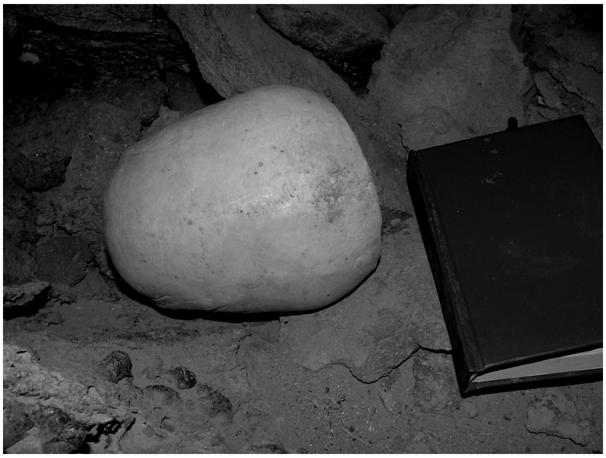

Figure 12. Human skull cap B near Station 40 in Al-Fahda Cave.

and radius/ulna. Entire camel skulls are also found far into the caves.

Table 2
Width and height of Al-Fahda Cave (Kempe *et al.*, 2006).

Width	Maximal at St. 8	17.5 m
	Minimal at St. 64	3.55 m
	Mean width main passage (39 stations)	7.51 m
Height	Maximal St. 14	4.67 m
	Mean height main passage (39 stations)	1.21 m

The cave floor is covered 100 % by sediment upslope of the entrance and to an estimated 30 % downslope of the entrance. These sediments derive from the main entrance (Bedouins once build a channel to feed water into the cave during winter), from a now buried upper entrance or by being transported through ceiling cracks with drip water. In some parts, one can see mud-stalactites at the ceiling: The sediment is re-deposited fine-grained quartz-containing aeolian sediment, probably glacial loess. In these sediments the hyenas have dug many dens, about 20 cm deep and 1 m across. Preferentially these dens are located at the wall and in low passages, sometimes even behind breakdown rocks. Apparently such a situation offers the most protection to the hyena. Often the ceiling height of the passage is lowest in the middle, due to the sediment piled up there from the dens fringing the walls.

Since most of the cave is in total darkness, the question of how the hyenas oriented themselves arises. We have seen a few rocks that seem to be "wet", possibly wetted with urine for markers. Hyaenidae also have an anal gland, the excretion of which is used for frequent territorial marking (e.g., Mills, 1989). Other possibilities are that the hyenas orient themselves by feeling the air-draft in the cave, by echoes and/or by feeling their way with their facial whiskers.

We also found three human skull caps in the cave, two of them at the perimeter of the cave across each other (figs. 11, 12). A first inspection does not suggest that they have been consumed by hyenas. Humans have previously explored the cave beyond the sites of the skull caps and left a stack of rocks (see "the Monument" on fig. 7) in the middle of the passage. There are no traces of burials or any other human bones in the cave. In addition, we found remains of a porcupine.

HYENAS IN DABIÉ CAVE

Dabié Cave is far shorter (194 m) and narrower than (on average 3.6 m of 13 stations) Al-Fahda Cave (fig. 13). The area of the cave is about 700 m^2, one tenth of Al-Fahda. In

Table 3
Bone dimensions measured in Abu Al-Kursi (East) Cave (AAK) compared to the measurements given in WALKER (1985) (REF, last column). Letters (A) and (B) refer to the sketches in WALKER (1985) for exact placement of measurements.

Bone	Measurement	AAK cm	REF cm
Humerus (right)	Total length	33.2	37.6
(proximal epiphysis loose)	Proximal width (A)	11.15	10.5
	Proximal thickness (B)	8.03	6.05
	Distal width (A)	7.97	8.15
	Distal thickness (B)	4.20	3.85
Humerus (proximal epiphysis missing)	Width of role (A)	7.92	8.15
	Thickness between rolls	4.51	3.85
Ulna & Radius (proximal end missing)	Distal width (A)	7.52	7.9
Ulna & Radius	Proximal gap (A)	4.46	3.80
	Proximal width (B)	9.65	7.65
	Length (without distal end)	51.5	51.2
Ulna & Radius	Overall length	55.5	51.2
	Proximal gap (A)	4.43	3.80
	Proximal width (B)	8.85	7.65
Metacarpal	Overall length	36.6	36.5
	Proximal width (A)	7.25	6.7
	Distal width left roll (B)	4.02	3.85
Tibia & Fibula (left)	Overall length	46.5	44.2
	Proximal width (A)	11.65	11.1
	Proximal thickness (B)	4.7	4.0
	Distal width (A)	8.97	8.35
	Distal thickness (B)	4.90	3.95
	Smallest thickness	4.98	
	Smallest width	3.17	
Tibia & Fibula (right)	Overall length	46.1	44.2
	Proximal width (A)	11.48	11.1
	Proximal thickness (B)	4.15	4.0
	Distal width (A)	8.02	8.35
	Distal thickness (B)	4.33	3.95
	Smallest thickness	4.51	
	Smallest width	2.85	

consequence, the back part of the cave, beginning a few meters inside of Station 11, is covered almost continuously with bones. Hyena dens begin at about 80 m inside. The last ones occur at the very end where bones and sediments almost fill the cave to the ceiling.

When the authors were shown to the cave by a local Bedouin, the entrance was blocked by stones to keep hyenas out of the cave. Formerly, a short channel diverted water into the cave from the wadi that perpendicularly cut the lava flow. When we entered the cave, a strong putrid smell filled the cave. It came from a half-consumed hyena mummy located ca. 40 m from the end of the cave (fig. 14). The hyena is missing its front teeth (fig. 15). We can only speculate how this happened. Either the animal was trapped in the cave when rocks were placed over the entrance and when it tried feverishly to dig its way out, or it lost the teeth in a fight or accident (e.g., with a car) and withdrew to the cave to die. When we returned one and a half years later (fig. 16), we found the mummy split in two. A fennek was in the cave and left it in panic. Apparently it had fed on the remains of the mummy. We collected the remains for further study and as a specimen in the exhibition on mummies planed for 2007 at the Reiss-Engelhorn-Museen at Mannheim, Germany.

In Dabié cave the majority of bones (at least by weight if not necessarily by number) to be camel bones. We also noticed sheep or goat bones, sheep wool and a few hyena bones. Coprolites of both hyenas and foxes occurred as well.

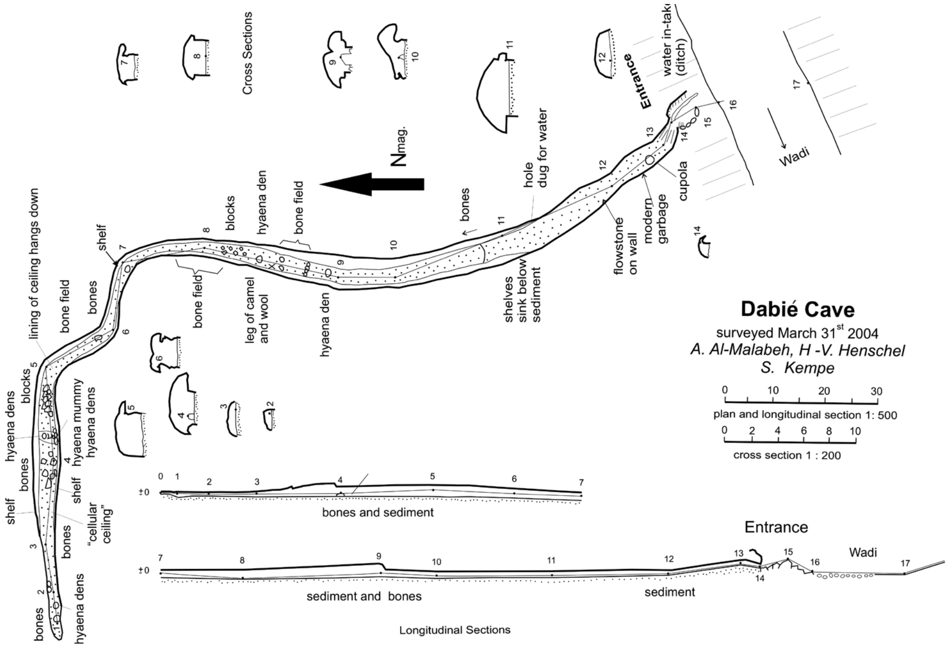

Figure 13. Map of Dabié Cave.

HYENAS IN AL-HAYYA CAVE

Al-Hayya Cave is an 80 m long passage, interrupted by a few blocks of breakdown. It was named after its only live inhabitant, a harmless mouse-eating snake: *Spalerosophis diadema cliffordii,* SCHLEGEL, 1837 (Arab: Bou m'raiat or ar'am (arkam) ahmar, German: Diademnatter, English: Clifford's snake or Diadem snake; pers. comm. Prof. Dr. Wolfgang Böhme of the Museum König in Bonn). The cave floor is covered by dry sediment in which a few hyena dens have been dug. The cave contains quite a lot of bones, among them wolf or dog (fig. 17), hyena, camel, cattle, horse and another human skull cap. We also found a dry mummy of a fennek (fig. 18) that was sent to Mannheim as well for the upcoming exhibition.

FIRST OBSERVATIONS ON HYENA BONE CONSUMPTION

The large amount of bones and coprolites offers the opportunity to study hyena bone consumption. First observations suggest that - at least by weight - camel bones dominate in the cave deposits. In order to be sure of this conclusion (i.e. excluding other large sized animals, like

Figure 14. Dry mummy of a hyena, found in Dabié Cave, March 31st, 2004.

Figure 15. Head of hyena mummy from Dabié Cave; note missing front teeth.

Table 4
Chemical analysis of coprolites (fraction<1 mm); results are weight percentages.

	Ca %	Mg %	PO_4 %	C %	N %	S %	C/N	N/S	Total %
Coprolite 1				10.65	2.20	0.49	4.84	4.49	
4.8 g				10.70	2.23	0.42	4.81	5.31	
				11.48	2.40	0.46	4.79	5.22	
Mean	**22.5**	**0.55**	**30.8**	**10.94**	**2.27**	**0.45**	**4.81**	**5.04**	**67.51**
St. deviation				0.46	0.11	0.036	0.028	-	
Coprolite 2				10.24	1.92	0.31	5.33	6.19	
4.7 g				9.82	1.69	0.17	5.80	9.94	
				10.21	1.88	0.24	5.43	7.83	
Mean	**18.9**	**0.61**	**21.4**	**10.09**	**1.83**	**0.24**	**5.52**	**7.65**	**53.07**
St. deviation				0.24	0.12	0.069	0.25	-	

Figure 16. State of hyena mummy on September 19th, 2005.

Figure 18. Mummy of Fennek from Al-Hayya Cave, September 2005.

Figure 17. Four skulls of wolves or dogs and two of hyenas (to the right) from Al-Hayya Cave, September 2005.

horses or cattle) we measured a few bones in Abu-Al Kursi (eastern section) with a caliper (tab. 3) and compared their dimensions and morphology with published *Camelus* data (Walker, 1985). The measured limb bones are with certainty bones of *Camelus*. Apart from the two humeri which are from subadult individuals, all bones are slightly larger than the respective animal measured by Walker (1985). This applies not so much to the overall length but to the sizes of the epiphyses.

The next observation is that metacarpals and metatarsals seem specifically common and complete. This may be explained by the enormous thickness of the cortical part of the bones, their small joints and their low cancellous bone component, rendering them difficult to gnaw. They are therefore left behind. In contrasts to this the larger (by volume) femuri and humeri are consumed starting with their cancellous epiphyses. These parts of the bone, in spite of their larger diameter, appear easier to get at. In the end, sharply pointed cortical bone fragments, so typical for hyena feeding, remain.

The “end product” of the hyena bone processing is the coprolite. It is typically white in color, indicative of the large percentage of bone-derived apatite. Two coprolites from Dabié Cave, collected in September 2005, were analyzed (tab. 4). Both were similar in weight and contained only a few bone fragments > 1 mm in size (26 fragments with a total of 106.7 mg and 9 fragments with 47.5 mg and a stone with 51.0 mg, for coprolite 1 and 2, respectively). Each sample was analyzed for calcium, magnesium and phosphate with ion chromatography and four times for C, N, S with a Vario-EL Elemental Analyzer. Results show that the coprolites contain high percentages of bone apatite (53.3 and 41.3 %, respectively) and about 25 % (percent C multiplied by an “organic factor” of 2.5) of organic matter. Much of that could be undigested hair that was also macroscopically visible in the samples. Hair may also be responsible for the high sulfur values in the samples (cystine of the hair-protein keratin). The repeated analyses of C, N, S content allow to calculate standard deviations, showing that the composition of the two coprolites is statistically significantly different. Coprolite 1 has a higher C and N content but a lower S content and a lower C/N ratio than Coprolite 2. C/N ratios are quite low, i.e. in the range of proteins, suggesting that not all of the available protein was consumed by the hyena, such as keratin for example. The low N/S values support this conclusion.

DATING THE DEPOSITS

One of questions remaining is that of the age of the bone deposits. At the Reiss-Engelhorn Museen an incisive of one of the collected hyena skulls was dated (sample No. ETH-32026/REM-M18). The age proved to be negative (-185±40 aBP), i.e. bomb-^{14}C contaminated, making the sample younger than AD 1950. Overall, all of the bone deposits appear not very old. Specifically the presence of so many camel-bones is puzzling. Camels have only been present in the Near-East in the last 3000 years (Klingel, 1988, reported that they have been present in Mesopotamia since 1500 BC). Thus, older deposits without camel bones should be found underneath the present layers. For example, one should expect gazelle bones to be dominating in Neolithic times.

Whether these older layers exist or not appears doubtful. In the Hashemite University Cave we found two treasure hunter pits in the cave, less than a meter deep. They contained white layers of disintegrated coprolites but no larger bone fragments. Should the older bones have been dissolved after all? Or should hyena consume all the bones available by and by, specifically if they are not large camel bones?

CONCLUSIONS

The reasons why the desert caves in Jordan have been used so intensively by hyenas may include:

- Use as a cool shelter (the caves have a temperature range from 18 to 24°C) during the hot daytime (maximum temperature may reach up to 45°C);
- To store large bones for later consumption;
- To feed on bones undisturbed;
- To give birth and to raise cubs;
- To die; or
- To search for water (some of the caves still have drip water on the ceiling at the end of September).

Because of the excellent preservation of bones, coprolites, dens and other traces, many additional questions can be studied in these newly discovered and largely undisturbed caves:

- What is the spectrum of animals consumed by hyenas in the caves and what are their proportions;
- What is the role of the few human skull caps found in Al-Fahda and Al-Hayya Caves;
- Which other animals regularly visit the caves;
- What is the stratigraphy of the bone deposits, do older non-camel-dominated strata occur;
- What is the manner of consumption of large bones, does every bone have a different pattern of consumption;
- Which bones are preferentially consumed, which are left over;
- What amount of proteins are extracted from the bone,

(a question answerable by comparing N-Analyses of bones and coprolites);

- How old can bones be and still be consumed by hyenas at a profit (a question answerable by analyzing the bones for collagen);
- Do we find insect or plant remains in the coprolites, since some hyenas regularly consume insects and plants as well (a question answerable by microscopic investigation of the coprolites);
- What is the frequency of visits by males and females, (a question answerable by analyzing coprolites for hormones);
- What is the range in composition in the coprolites and what can they tell us about the animals fed on by the hyenas;
- Can we map out scent trails, marked by urea or anal gland paste?

In comparative studies between brown hyenas and spotted hyenas in the Kalahari, Mills (1989) pointed out a few differences between the two species: *Crocuta* for example has a small sexual dimorphism (the females being larger and dominant) which is not true for hyena; *Crocuta* hunts large animals (antelopes) in packs for about 50% of its food, while the striped hyena is mostly a solitarily scavenger for carrion, hunting only rarely for small game and supplements its diet with fruits and insects. *Crocuta* is not storing food, hyena does bury excess. Females tend to be territorial in both species (with *Crocuta* using the larger one) while males are more migratory. In *Crocuta* nomadic males mate with clan females while in *Hyaena* the males are immigrants. Both species form female-bonded matrilineal clans. Both species have very long gestation periods and keep the cubs in dens for 15 months, weaning them as late as 12-15 months of age. *Crocuta* does not bring meat to cubs; *Hyaena* does, starting when the cubs are 12 weeks old. *Crocuta* has two cubs on average, *Hyaena* three and mothers may suckle other cubs occasionally. Cubs are raised in both species in dens that are small and narrow, just large enough for the cubs.

This short list of behavioral facts raises several questions with regard to the Jordanian cave-using striped hyena. First of all, their ability to carry large bones into caves makes them similar to the European *C. crocuta spelaea*, but not at all alike either the African extant spotted or the brown hyenas that do not stash large bones. Possibly the hyena had to adapt to a human-dominated desert ecology, where medium-sized (antelopes) and small wild animals are hunted by humans almost to extinction, while humans would leave on the other hand the big bones behind after loosing or slaughtering camels or sheep. Feeding big bones to cubs does not make sense, therefore the question remains, as to if the caves are used for raising cubs at all. Cubs would be protected from most other animals, but not from other hyenas or foxes. Digging pits for sleeping also seems to be an unreported habit (though we did not search the entire literature on the topic yet). Overall the ethology of the striped hyena appears not to be well studied (Mills, 1989) but seems not to be that much different from the other two species.

We hope to investigate these caves and their hyena-related remains in greater detail and answer some of these questions in order to compare the results with hyena traces of the Upper Pleistocene *C. crocuta spelaea* in Central Europe.

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THE BAUMANN'S CAVE AT RÜBELAND/HARZ, GERMANY, ONE OF THE CAVES NOTED IN EARLY SCIENCE HISTORY FOR ITS CAVE BEAR AND CAVE HYENA BONE DEPOSITS

Stephan KEMPE[1]

A SHORT HISTORY OF THE BAUMANN'S CAVE

The Baumann's Cave at Rübeland near Elbingerode/Harz is ubiquitous in the early scientific and travel literature (e.g., Kempe 1999; 2000; 2004; Kempe & Reinboth, 2001; Kempe *et al.,* 1999; 2004). It has been open to the public since the end of the 16th century and is the oldest regularly visited and guided show cave.

In Baroque times, the Baumann's Cave represented - even though only 150 m long and small compared its presently known extent (fig. 1) - a singular geological object causing wide-spread curiosity. All reports agree that it was discovered by a miner named "Baumann", who was searching for iron ore in the Bode Valley in the late 15th century. The cave was originally decorated profusely with speleothems and once contained extensive cave bear bone deposits, mined for medical *unicornu fossile.*

The Baumann's Cave was first mentioned in the middle of the 16th century by Agricola, Matthesius and Gesner (with the first two citations not fully verified as yet) (Kempe, 2004; Kempe *et al.,* 2004). Heinrich Eckstorm wrote the first longer account of the cave in 1589 in Latin (published 1620). His report was cited extensively by later authors, even though Eckstorm used local information and did never visit the cave himself. Johannes Letzner - a contemporary of Eckstorm - also wrote a short account about the cave but based on his own visit to the cave in 1599 (or shortly later). Both Eckstorm and Letzner gave descriptions of the first hall only.

In the first half of the 17th century, the Baumann's Cave was mentioned several times in connection with its *unicornu fossile* deposits. Merian published the first longer descriptions in German in 1650 and 1654. The latter text is also accompanied by three copperplates showing the Bode valley with Rübeland and the entrance of the cave, a detailed picture of the entrance, and a picture of the interior of the first section of the cave, including the "Ross" (horse) in the background, a large breakdown block that visitors had to straddle to reach the descent to the deeper parts of the cave. This picture is the first of the interior of any cave ever published (fig. 2).

In 1656, Olearius, an official of the city of Halle, visited the cave accompanied by the young student Von Alvensleben. Olearius left a manuscript in German (published by Bürger, 1929) with a description of the cave and von Alvensleben sketched the ground plan of the cave on two sheets showing sections one and two (fig. 3a,b). These sketch-maps are the first cave maps still preserved world-wide (Stolberg, 1930; Reinboth, 1982; Shaw, 1992; Kempe *et al.,* 2004).

Also, in 1656, Horst published a short note on fossil bones from the Unicorn Cave near Scharzfeld mentioning that similar bones have been taken from the Cave at Elbingerode as well, i.e., from the Baumann's Cave. In this note he suggested that the bones were "similar" to those of "bears, lions, and humans", which is the first anatomically correct interpretation of the unicorn bones (Kempe *et al.,* 2005).

Kircher (1665) mentioned the cave in his famous "*Mundus subterraneus*" also in connection with the fossil bones. In 1666, Lachmund visited the cave and published a short Latin description in his book "*Oryktographia Hildesheimensis*", which appeared 1669. In the same year Praetorius also printed a short account of a cave visit. Towards the end of the century Leibniz visited the cave and wrote about it, its formations and bone deposits. His Latin text was included in the "*Protogaea*", a book published 1749, more than 50 years after his visit.

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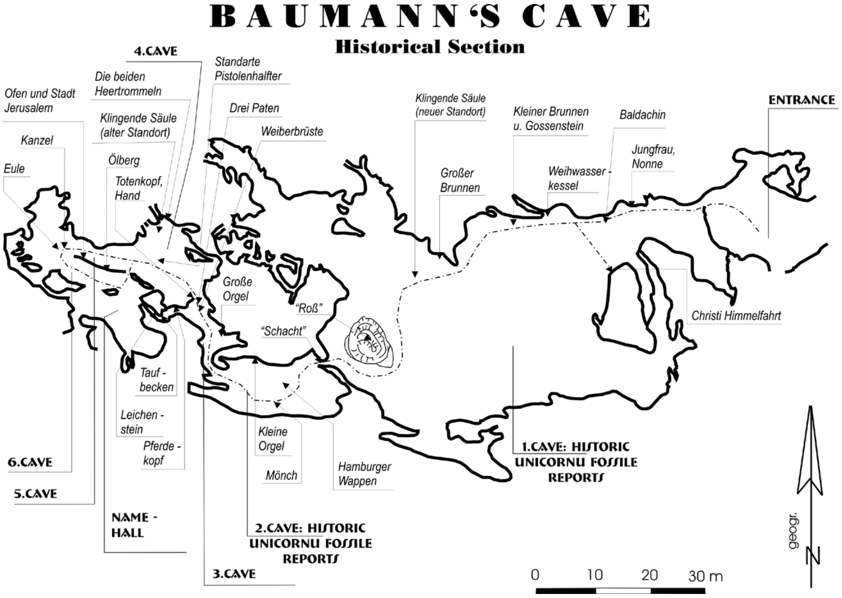

Figure 1. Map of the historical section of the Baumann's Cave and its division into six „caves". The locations and historic names of the flowstone figures presented in guided tours are indicated as far as they have been identified. Historically fossil bones have been dug in the first and second section; today, bones are visible only in a corner of the second cave (altered after Kempe *et al.,* 1999).

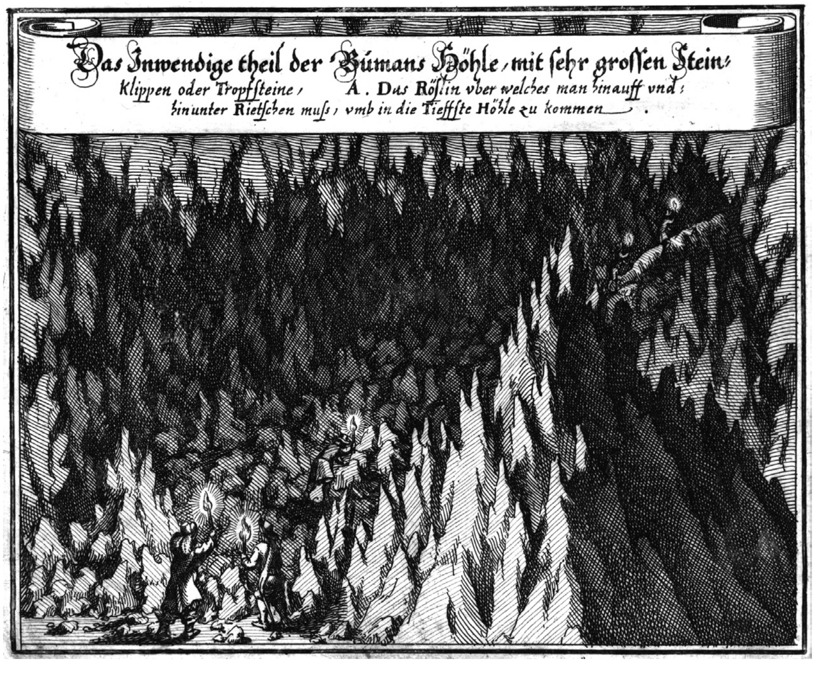

Figure 2. Merian etching of 1654 showing the interior of the Baumann's Cave with the titel: "Der Inwendige theil der Bumans Höhle, mit sehr grossen Stein-Klippen oder Tropfsteine, A Das Röslin uber welches man hinauff und hinunter Rietschen muss, umb in die Tieffste Höhle zu kommen". (The inner part of the Baumann's Cave with very large stone cliffs and flowstones. A: the Horse, across which one has to slide to get to the deepest cave). This figure is the oldest figure depicting the interior of a natural cave published world-wide. The view is into the first section of the historic cave (today named "Goethe Saal") from the southwest with the northeast wall removed so that one can look into the cave. The three persons in the foreground have just entered the cave, the two "cavers" in the background "ride up" across the big breakdown block named "Ross (Horse)" to get to the continuation of the cave (today "Saal des Hamburger Wappens"). The etching was drawn by Conrad Buno by personal instruction of Duke August der Jüngere and published in the Merian "*Topographia Braunschweig-Lüneburg*". (Original: collection Kempe).

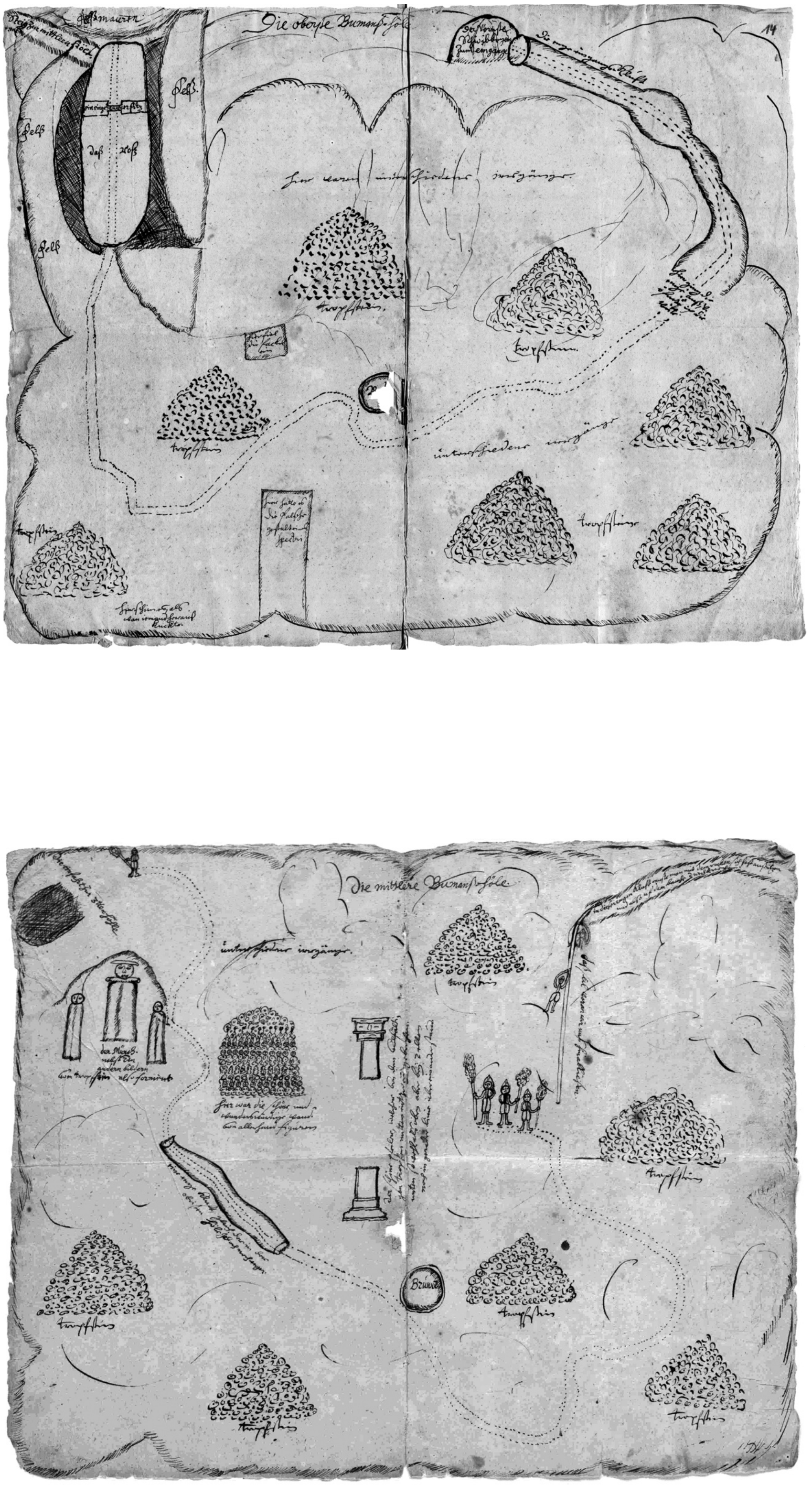

Figure 3 a,b. The student von Alvensleben drew this sketch after a visit of the Baumann's Cave together with the superintendent Olearius, 1665. The maps are kept today in the state archive in Magdeburg. They are the first preserved maps of a natural cave world-wide. For the translations of the texts see Kempe *et al.,* 2004. (Printed by permit of the Landeshauptarchiv Sachen-Anhalt).

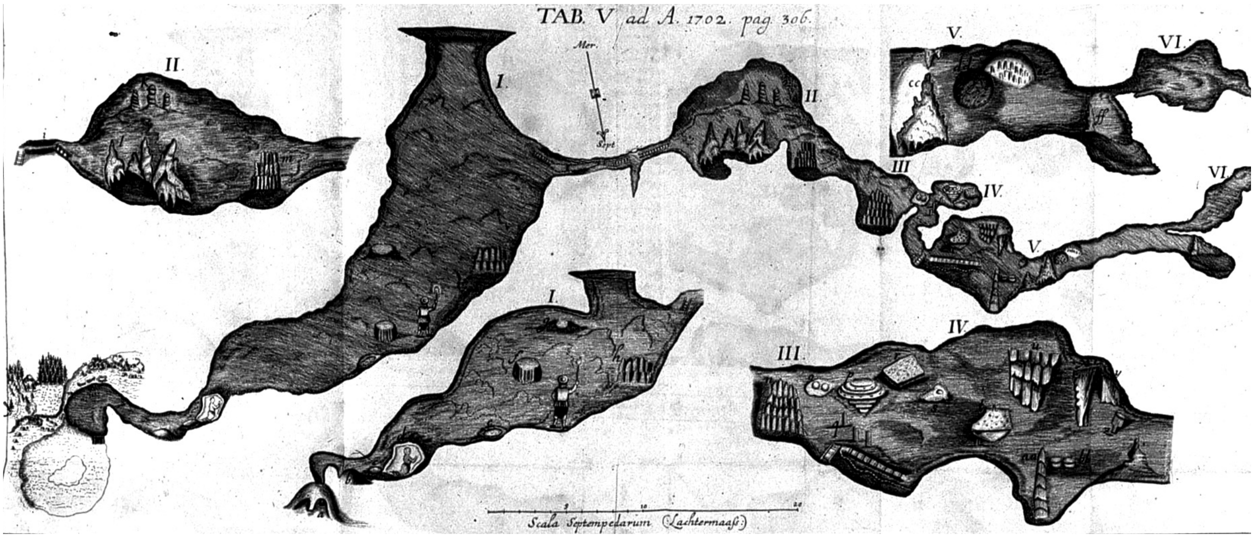

Figure 4. This map of the Baumann's Cave was published as a copper etching by v. d. Hard in the "*Acta eruditorum*", 1702. The map is oriented to the south and has already a north arrow and a scale (in Harzer Lachter; 1 HL = ca. 2 m). There is a plan view and four longitudinal sections of certain parts of the cave. The letters refer to the individual flowstone formations shown to the visitor (For details see Kempe *et al.,* 2004. (Original: collection Kempe).

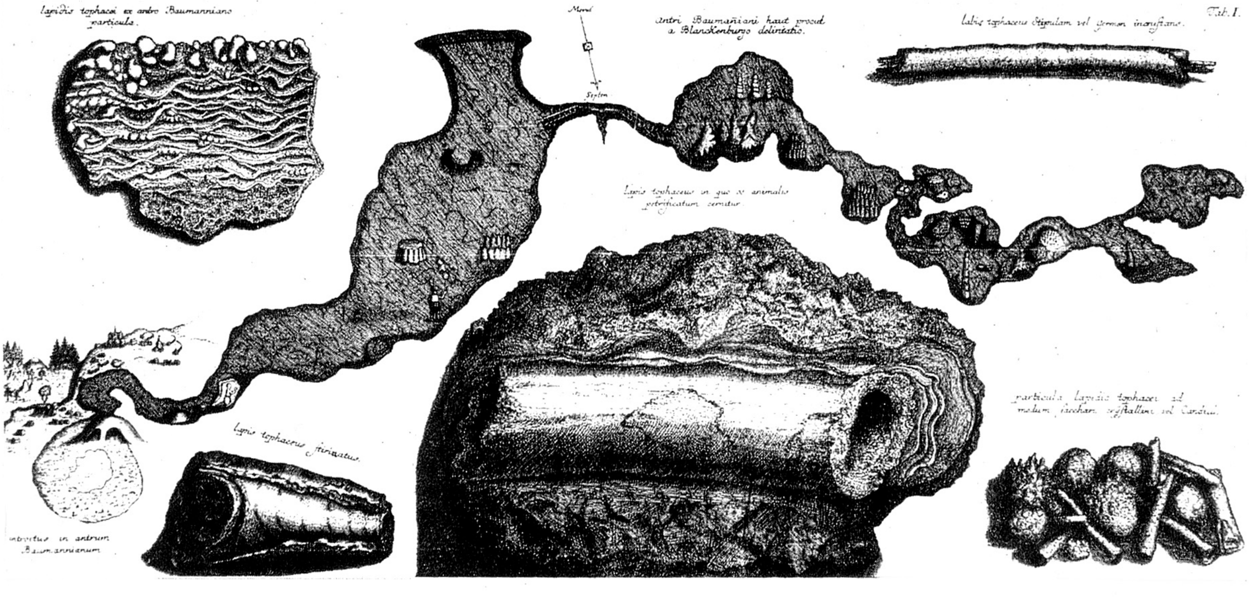

Abb. 59 *Lageplan und Aufriß der Baumannshöhle* · Kupferstich; 21,5 × 47 cm · aus: Leibniz, Protogaea, 1749, Tab. I

Figure 5. The map of the Baumann's Cave re-printed in Leibniz "*Protogaea*", published 1749. (After the translation of the "*Protogaea*" by Engelhardt, 1949).

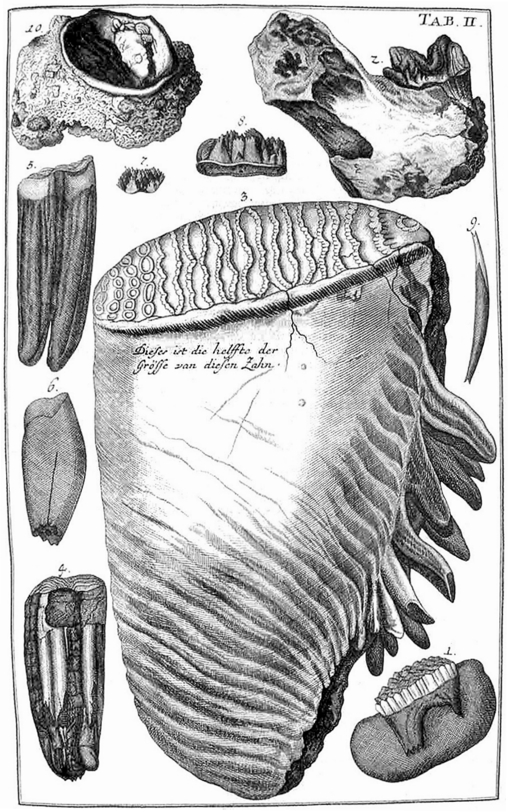

Figure 6. The copperplate No. 2 from Kundmann's curiosity opus, published in 1737, depicting fossil bones. The ones in the right corners were the bones he had, as a young person, collected himself in the Baumann's Cave, second section; they are depicted at a scale 1:1. (Original: Universitäts- and Landesbibliothek, Darmstadt).

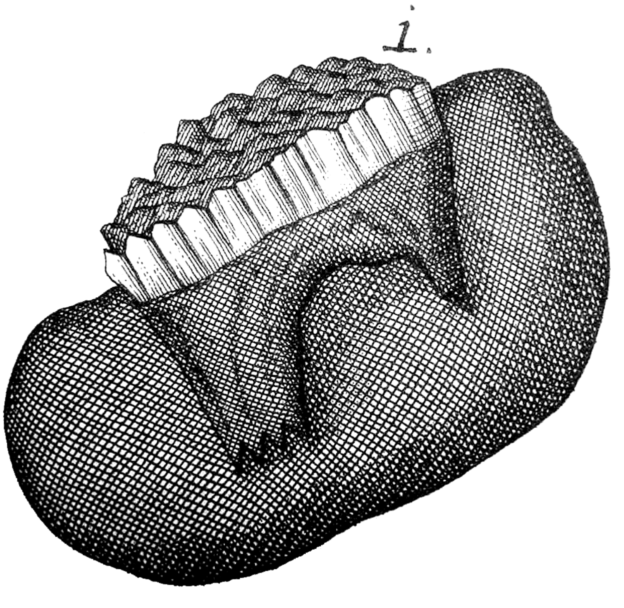

Figure 7. Etching of an abraded molar, most probably of a cave bear. It was identified as a tooth of a horse by Kundmann (1737: Taf. 2, item 1). (Original: Universitäts- and Landesbibliothek, Darmstadt).

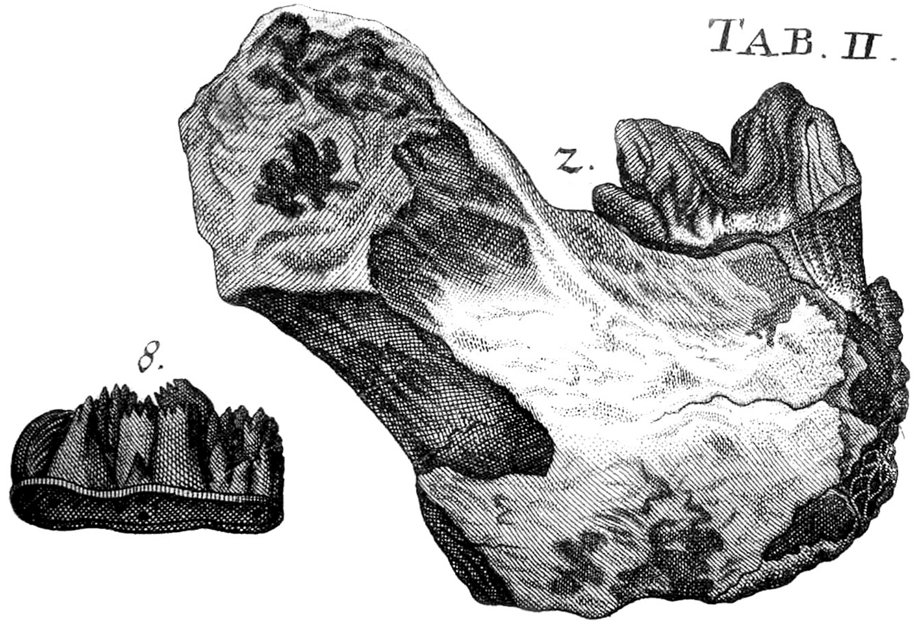

Figure 8. Etching of the last molar in a left lower jaw of the cave hyena. It was identified as the jaw of a calf by Kundmann (1737: Taf. 2, item 2). (Original: Universitäts- and Landesbibliothek, Darmstadt).

In the early 18th century three more reports of the cave were published, those of Behrens (1703), Hellwig (1702) and Von Der Hardt (1702). Behrens' account does not relate much more information about the cave than the Eckstorm-text, and Hellwig copied the Olearius-report, but Von Der Hardt published the first map and longitudinal sections of the cave based on a rough survey (fig. 4). His Latin report appeared in the "*Acta Eruditorum*", the most influential scientific magazine of the time. It contained for the first time a detailed description of all the formations (cross-referenced with the map) usually shown to the visitors by guides (Reinboth, 1986; Kempe *et al.,* 2004). It also established the division of the cave into five (later enlarged to six) sections, a practice followed by all the later authors. A copy of this map was reproduced by Leibniz (1749) (fig. 5) and Linné (1779).

In 1708, Johann Christian Kundmann (1684-1751) visited the cave and retrieved several pieces of bone. Kundmann was a physician and a collector of - among other things - natural curiosities. His visit is described and the bones are depicted in the catalogue of his cabinet of natural curiosities: "*Naturae et Artis item in Re Medica, oder Seltenheiten der Natur und Kunst des Kundmannischen Naturalien-Kabinets wie auch in der Arzeney-Wissenschafft*" published in 1737 (fig. 6). Kundmann, however, was not able to correctly determine which animals these bones belong to. One of the pictures shows (most probably) a cave bear tooth (fig. 7), while the other depicts a fragment of the lower jaw of a hyena (fig. 8). This picture is most probably the earliest of a cave hyena bone. Cuvier (first in 1805) correctly attributed it to a large hyena. Goldfuss also referred to the Kundmann picture when discussing fossil hyena bones in 1810 and when he established the cave hyena as a separate species in 1823 as *Hyäna spelaea* (now *Crocuta crocuta spelaea).*

The last one to describe the bones from the Baumann's Cave without clearly recognizing which animal they belonged to was the physician Johann Friedrich Zückert (1763) (Kempe, 1999; 2000; Kempe *et al.,* 1999). Shortly after the extinct bear species was established as *Ursus spelaeus* by Rosenmüller, 1794. The steps which led to this benchmark in early Paleontology have been illustrated in detail by Kempe *et al.* (2005).

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LAST GLACIAL (OIS 4, OIS 3 AND OIS 2) PALEOENVIRONMENTAL ANALYSIS FOR WESTERN LOMBARDY (NORTH ITALY) CAVE BEAR SITES

Fabio BONA[1]

Abstract: For the first time we propose a tentative paleoclimatic and paleoenvironmental reconstruction for the Prealps area located in the middle-western Lombardy (North Italy), using the small mammals yielded by the *Ursus spelaeus* fossiliferous levels.

The data set is from two caves studied by the Dipartimento di Scienze della Terra "A. Desio", UNIMI, over the last two decades: 1- Caverna Generosa (Como); 2- Grotta sopra Fontana Marella (Varese) which are less than 30 km from each other.

The long and complete stratigraphical sequences kept in both caves allowed the analysis of a time span covering more or less the last 50 Ky, from more than 50 Ky to Holocene-recent.

Paleontological analysis of the sequences of Caverna Generosa and Grotta sopra Fontana Marella highlights for the Insubrian area (North-western Lombardy - North Italy) a well represented climatic and environmental change in the last 50 Ky. Exactly about 50 Ky the environment was a cold grassland; about 45-46 Ky this situation changed when wooded environment taxa, found in the "Sala Terminale" of Caverna Generosa, became dominant on open habitat taxa. The environmental and climatic situation was probably still favourable until 26 Ky; the Grotta sopra Fontana Marella sequence shows a new climate worsening testified by dominance of cold and grassland species. *Ursus spelaeus* attendance in the Insubrian area is confirmed beginning from more than 50 Ky to at least 25 Ky.

Key words: *Ursus speleaus*, North-Western Lombardy, Italy, small mammals, Late Pleistocene, paleoenvironment.

INTRODUCTION

The aim of this work is to propose, for the first time, a tentative paleoclimatic and paleoenvironmental reconstruction for the Prealps area located in the middle-western Lombardy (North Italy), using the small mammals yielded by the *Ursus spelaeus* fossiliferous levels.

During the last two decades numerous studies on Quaternary fossil mammals from western Lombardy pre-Alps have contributed to the paleoclimatic and paleoenvironmental reconstructions. Fossiliferous cave deposits with *Ursus spelaeus* remains are widespread in the Alps, but today, in Italy, only few caves have been exploited with stratigraphical criteria; in most cases the excavations in cave bear sites have been carried out in the nineteenth century, when the stratigraphical importance of the finds was not clearly known by the majority of researchers.

This study is focused on small mammal remains coming from two cave bear caves well studied, in the last fifteen years, by students of Università degli Studi di Milano: 1- Caverna Generosa (Como) (Bona, 2003; 2004; 2005; Bona *et al.*, in press), 2- Grotta sopra Fontana Marella (Varese) (Zanalda *et al.*, 1997; Perego *et al.*, 2001), which are less than 30 km from each other. For both caves, studies carried out on palaeontological material testify as the most common large mammal was *Ursus spelaeus*. Remains of small mammals (voles, dormouses, mouses, shrews and moles) have also been recovered in the same levels, and they turned out to be essential for this work.

GEOGRAPHICAL SETTING

The Grotta sopra Fontana Marella cave is located in the north-western Lombardy (Northern Italy) (fig. 1), 1040

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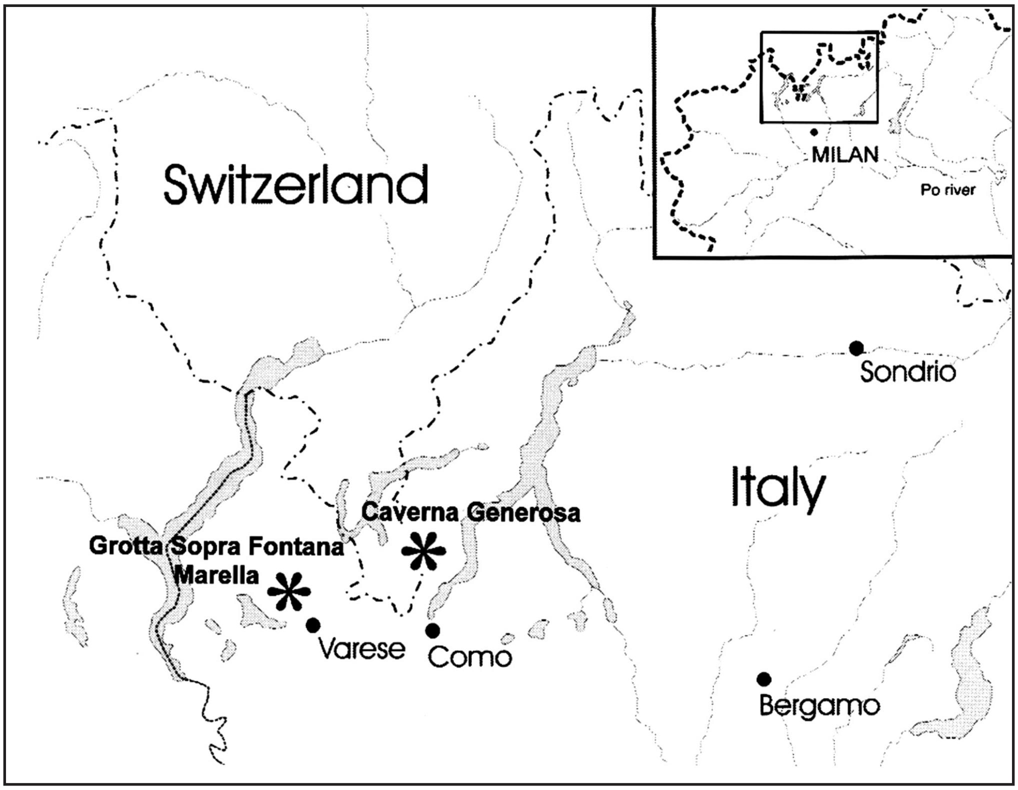

Figure 1. Map of the middle-western Lombardy with the geographical position of Grotta sopra Fontana Marella and Caverna Generosa.

m a.s.l. on the north-eastern slope of the calcareous-dolomitic massif of Monte Campo dei Fiori (maximum elevation 1226 m a.s.l.), Varese province. It is located in Lombardian Pre-Alps facing the Po Plain. It is laterally limited by two deep valleys: Olona Valley and Valcuvia.

Also the Caverna Generosa is situated in the north-western Lombardian Pre-Alps, but a few kilometres East of Grotta sopra Fontana Marella cave, in the Como province. The Caverna Generosa opens at 1450 m a.s.l on the Italian eastern site of Monte Generoso (maximum elevation 1701 m a.s.l.), near the boundary between Italy and Switzerland (fig. 1). The Monte Generoso is a calcareous massif, located between the Lugano and the Como lakes, largely made of Calcare di Moltrasio limestone (Lower Jurassic).

The stratigraphic sequence of Grotta sopra Fontana Marella is about 2 m thick and it has been subdivided in 12 levels. The uppermost four levels have been attributed to Upper Pleistocene according to C14 dating (Zanalda *et al.,* 1997). Its four levels yielding cave bear remains represent a time span not well known for lacking of C14 dates of the lowest level (FM4). Probably FM4 is synchronous with "Sala Terminale" upper levels. Levels FM2 and FM1 have been dated respectively to 26, 266 and 25, 688 years Bp calibrate C14 dating (Perego *et al.,* 2001).

The "Sala Terminale" stratigraphical sequence of Caverna Generosa is about 3 m thick and has been subdivided in 13 levels. The "Sala Terminale" sequence is the most complete and covers the most wide temporal interval. In fact, the uppermost 6 levels have been dated from more than 50 Ky to 38 Ky (Bona *et al.,* in press); the lowermost 7 levels have not been dated because of their old age excess the possibility of C14 method even if, probably, they could reach more than 60 Ky at the bottom.

A new stratigraphical sequence along the shaft, 15 meters from the entrance of the Caverna Generosa has been recently analysed (Cunicolo - MG CUN). So far, no C14 dating are available for this sequence. The presence of a cryoclastic angular limestone deposit at the surface (MG CUN 0 - Holocene-recent) suggests an age close to the last maximum glacial for MG CUN I and MG CUN II (levels with *Ursus spelaeus* dominant). Presence of the Holocene is supported also by the finds of remains of large domestic mammals such as goats and cows (Laurenti, in progress). Probably, according to small mammals frequency, MG CUN IV and MG CUN V could be connected with MG1 and MG2 of "Sala Terminale".

MATERIAL AND METHODS

The paleoenvironmental interpretations suggested in the present paper are based on 665 remains of small mammals (118 from Grotta sopra Fontana Marella, 140 from Caverna Generosa "Sala Terminale" and 407 from Caverna Generosa "Cunicolo"). For the counting of the voles right and left lower first molars have been added. For the other species it has been used the normal counting of MNI using the more represented skeleton portion.

The method used to collect these small remains consists in two phases:

1. The sieving of sediments during field work, with 1 mm mesh sieves, reporting stratigraphical and planimetric indications for each sample;
2. More accurate sieving, in the laboratory of Università degli Studi di Milano, and picking of samples.

The remains found are divided by skeletal constituents using a binocular microscope Wild Heerbrugg M3 with enlargement zoom from 6,4x to 40x and afterwards determined following mainly Chaline *et al.* (1974), Niethammer & Krapp (1978; 1982; 1990).

SMALL MAMMALS DATA

Grotta sopra Fontana Marella (tab. 1)

Concerning the Late Pleistocene levels of Grotta sopra Fontana Marella (Zanalda *et al.*, 1997), in the level FM 4 we have scarce remains: the glirids are the most represented. With some doubts this could be interpreted as a sign of wood extensions and probably small open areas, underlined by a single specimen of vole *Microtus agrestis*.

In the level FM 3 the presence in the same ratio of voles and glirids could testify a mixed wood and grassland environment with scarce *Sorex* sp. and *Arvicola terrestris* attesting the presence of limited humid areas.

During the first field excavation pollen analysis has been carried out. Data collected for levels FM 3-4 of Grotta sopra Fontana Marella (Perego, 1993) shows a large spreading of forest trees, mainly *Betula* and *Pinus*, on the surroundings of Campo dei Fiori slope where Grotta sopra Fontana Marella opens.

With level FM 2 and FM 1 the presence of micromammals typical of cold (*Chionomys nivalis*) and open (*Microtus arvalis* and *Microtus agrestis*) environments, besides the presence of *Marmota marmota* and the com-

Table 1
Grotta sopra Fontana Marella: remains (n) and percentages (%) of small mammals.

FM	Level	1		2		3		4		Tot	
		n	%	n	%	n	%	n	%	n	%
TAXON											
Microtinae											
Arvicola terrestris		6	14	2	20	1	6.7			9	12.5
Chionomys nivalis		7	16.3							7	9.7
Cletrionomys sp.		1	2.3	1	10					2	2.7
Microtus agrestis		7	16.3					1	25	8	11.1
Microtus arvalis		20	46.5	5	50	4	26.5			29	40.3
Muridinae											
Apodemus sp.						1	6.7			1	1.4
Sciuridae											
Marmota marmota		1	2.3							1	1.4
Gliridae											
Muscadinus avellanarius								1	25	1	1.4
Glis glis				1	10	6	40.1	2	50	9	12.5
Leporidae						1	6.7			1	1.4
Insectivora											
Sorex sp.						1	6.7			1	1.4
Talpa cf. *europaea*		1	2.3	1	10	1	6.7			3	4.2

plete absence of wooded taxa from the pollens, could be interpreted as an abrupt transition towards a colder climate, with a sudden decrease of arboreal vegetation and a increase of the soil erosion.

The palynological data for FM1 and FM2 (Perego, 1993) show a floral arrangement typical of grassland and steppe, with the species: *Artemisia* sp., *Ephedra fragilis*, *Centaurea* sp., *Alchemilla* sp., *Poligonum viviparum* and *Echinops* sp.

Caverna Generosa: "Sala Terminale" (tab. 2)

In the "Sala Terminale" of Caverna Generosa levels with the same chronological and sedimentological characteristics have been grouped, owing to the scarcity of remains, in order to obtain significant paleoecological data (Bona, 2006; Bona *et al.,* in press).

Levels MG 10, 11 and 12 (group 4); small mammals are very poorly represented in this group of levels. Only 8 remains have been determined (2 *Arvicola terrestris*; 3 *Terricola* gr. *multiplex-subterraneus*; 3 *Microtus arvalis*) for this time interval, so that it's impossible to make some paleoenvironmental analysis.

Levels MG 5, 6, 8, 9 and III (Group 3) are characterized by an assemblage of *Terricola gr. multiplex-subterraneus* (5,9%), *Chionomys nivalis* (23,5%), *Arvicola terrestris* (29,4%) and *Microtus arvalis* (35,2%). The large presence of *Chionomys nivalis* and *Microtus arvalis*, correlated to a scarcity of wooded taxa allows to suppose that the Monte Generoso area was characterized by open areas with exposed rocks and reduced wooded areas. The climate would have been cold and dry.

For levels MG 3, 4 and II (Group 2) the number of remains is scarce. The best represented taxa are *Terricola* gr. *multiplex-subterraneus* (31,2%) and *Cletrionomys glareolus* (25,0%). Another important taxon is *Apodemus* gr. *sylvaticus/flavicollis* (18,8%). This latter is considered

Table 2
Caverna Generosa "Sala Terminale": remains (n) and percentages (%) of small mammals.

MG "Sala Terminale"	Level	Group 1		Group 2		Group 3		Group 4		Tot	
		n	%	n	%	n	%	n	%	n	%
TAXON											
Microtinae											
Arvicola terrestris		16	20	1	4.8	6	19.3	2	25	25	17.8
Chionomys nivalis		1	1.2			8	25.8			9	6.4
Clethrionomis glareolus		2	2.5	7	33.3					9	6.4
Microtus agrestis											
Microtus arvalis		8	10	1	4.8	11	35.5	3	37.5	23	16.4
Terricola gr. *multiplex-subterraneus*		38	47.6	5	23.8	4	12.9	3	37.5	50	35.7
Terricola cf. *savii*		1	1.2							1	0.7
Muridinae											
Apodemus gr. *silvaticus-flavicollis*		4	5	5	23.8	1	3.2			10	7.1
Gliridae											
Glis glis		3	3.7							3	2.2
Muscradinus avellanarius				1	4.8					1	0.7
Insectivora											
Sorex araneus				1	4.8					1	0.7
Soricidae ind.											
Sorex alpinus		1	1.2							1	0.7
Sorex minutus		1	1.2							1	0.7
Crocidura sp.											
Sorex sp.											
Talpa caeca		2	2.5			1	3.2			3	2.2
Talpa sp.		3	3.7							3	2.2

ubiquitous, so it is not useful for paleoenvironmental considerations. Also *Arvicola terrestris, Microtus arvalis, Sorex araneus* represented each by a single find, are not useful for paleoenvirommetal interpretation.

According to the data above presented it is possible to suppose that the surroundings of Monte Generoso, about 46 Ky ago, were characterized by wide wooded areas with dense underbrush (significant is the presence of *Muscardinus avellanarius*).

Levels MG 0, 1, 2, 2b, A, B and I (Group 1); the collected data underline the presence of wooded conditions in the cave neighbourhood about 38-40 Ky. This interpretation is supported by numerous remains of *Terricola* gr. *multiplex-subterraneus* (49,3 %) and by scarce *Clethrionomys glareolus* (2,7 %) and *Glis glis* (4,1%). It is possible to consider the presence of small open areas alternated by wooded ones owing to the presence of *Microtus arvalis* (11,0%) and of one specimen of *Chionomys nivalis*; the occurrence of *Arvicola terrestris* (16,4%), an animal today living near fresh water like rivers, lakes but also less aquatic habitat, confirms the presence of wet environment, probably nearby the watershed.

Caverna Generosa: Cunicolo, meters 13, 14 and 15 (tab. 3)

At 13m to 15m of Cunicolo of Caverna Generosa the situation is quite different; although we have not C14 dating yet it is possible indicatively to correlate the lower MG CUN V and MG CUN IV with the MG1 and MG2 by using sedimentology and small mammals assemblages. In fact, during the sequence to MG CUN V to MG CUN I it is possible to remark an important climate change.

MG CUN V, MG CUN IV are characterized by mixed wood and open areas, probably with a not so cold a climate.

Table 3
Caverna Generosa "Cunicolo", meters 13, 14 and 15: remains (n) and percentages (%) of small mammals.

MG CUN Level	0		I		II		III		IV		V		Tot	
	n	%	n	%	n	%	n	%	n	%	n	%	n	%
TAXON														
Microtinae														
Arvicola terrestris	3	1.9	4	9.1	10	23.2	32	22.2	2	11.8			51	12.5
Chionomys nivalis	5	3.2	10	22.7	5	11.6	18	12.5	1	5.9			39	9.6
Clethrionomis glareolus	9	5.8			1	2.3							10	2.5
Microtus agrestis			1	2.3			7	4.9					8	2
Microtus arvalis	15	9.6	14	31.8	17	39.6	47	32.6	4	23.5	1	50	98	24.1
Terricola gr. *multiplex-subterraneus*	76	48.7	8	18.1	7	16.4	31	21.5	8	47	1	50	131	32.2
Muridinae														
Apodemus gr. *silvaticus-flavicollis*	7	4.6			1		1	0.7					9	2.2
Gliridae														
Glis glis	9	5.8	3	6.8	1	2.3							13	3.2
Insectivora														
Sorex araneus	1	0.6	1	2.3	1	2.3	2	1.4					5	1.2
Soricidae indet.	1	0.6											1	0.2
Sorex alpinus	1	0.6											1	0.2
Sorex minutus	1	0.6											1	0.2
Sorex sp.	1	0.6	1	2.3	1		1	0.7					4	1
Crocidura sp.	1	0.6											1	0.2
Talpa caeca	23	14.7	2	4.6	1	2.3	3	2.1	2	11.8			30	7.4
Talpa sp.	2	1.3					2	1.4					4	1
Chiroptera	1	0.6											1	0.2

During deposition of MG CUN III there is an increasing presence of voles typical of open, dry, and probably cold, climate (*Microtus agrestis* is abundant and *Chionomys nivalis* is well represented); some wooded areas however continue to exist (*Arvicola terrestris*).

The dominance of voles typical of open and cold environment (*Microtus arvalis* and *agrestis*, *Chionomys nivalis*), together with the cryoclastic angular limestone blocks deposit at the top of the sequence, testifies for MG CUN II and MG CUN I an age near to the last maximum glacial.

CONCLUSIONS

Data obtained by the study of small mammals, coming from Caverna Generosa and Grotta sopra Fontana Marella, allow to propose the following paleoenvironmental interpretations, mainly for the Insubrian area (Como and Varese provinces, Western Lombardy Prealps), during the last glacial period and Holocene:

- Before 50 Ky the paleoenvironmental situation is not yet clear, owing to the poor amount of remains.
- About 50 Ky (levels MG5-6-8-9 and III), *Chionomys nivalis* and *Microtus arvalis* are dominant, with scarce presence of arboreal species. This suggests that climate was cold and that the area was characterized by an open land with scarce arboreal cover.
- Around 45-46 Ky (levels MG3-4 and II), arboreal species such as *Terricola* gr. *multiplex-subterraneus*, *Clethrionomys glareolus* and *Muscardinus avellanarius* stand out on previous ones. An increase of wooded areas in a milder and wetter climate is suggested by this association of species.
- Levels dated about 40 Ky (Levels MG0-1-2 and probably levels FM3-4) confirm the situation described above. Pollens analysis for levels FM3-4 of Grotta sopra Fontana Marella (Perego, 1993), probably synchronous with MG1 and MG2 (Tintori, pers. com.), shows a large spreading of forest trees, mainly *Betula* and *Pinus*, on the Campo dei Fiori slope where Grotta sopra Fontana Marella opens.
- About 26 Ky (level FM2) *Microtus arvalis* dominance with scarce *Glis glis*, *Cletrionomys glareolus* and *Arvicola terrestris* testifies an important environmental change with wide open land and restricted wooded areas. Near 25 Ky (level FM1) the environment and climate did not change and species typical of cold and open habitats were still dominant. The climatic deterioration is testified by the presence of *Microtus arvalis*, *Microtus agrestis*, *Chionomys nivalis* and *Marmota marmota*. *Cletrionomys glareolus* and subordinate *Arvicola terrestris* prove that small covered areas were still present. FM1 and FM2 palynological data (Perego, 1993) show a floral arrangement typical of grassland and steppe, with the species: *Artemisia* sp., *Ephedra fragilis*, *Centaurea* sp., *Alchemilla* sp., *Poligonum viviparum* and *Echinops* sp.
- Also for MG CUN II and MG CUN I of Caverna Generosa *Microtus arvalis*, *Microtus agrestis* and *Chionomys nivalis* testify an environmental situation similar to that of FM1 e FM2 with grassland and cold climate.
- The Postglacial and Holocene association of MG CUN 0 shows a clear increase of wood with *M. (Terricola)* gr. *multiplex-subterraneus* well represented. Unfortunately at present it is impossible to make more detailed reconstruction for this period.

Paleontological analysis of the sequences of Caverna Generosa and Grotta sopra Fontana Marella highlight for the Insubrian area (North-western Lombardy - North Italy) a well recognizable climatic and environmental change in the last 50 Ky. About 50 Ky the environment was probably represented by a cold grassland; around 45-46 Ky this situation changed when wooded environment taxa became dominant. Environmental and climatic situation was probably still favourable until 26 Ky; the Grotta sopra Fontana Marella sequence shows a new climate worsening testified by dominance of cold and grassland species. *Ursus spelaeus* attendance in the Insubrian area is confirmed at least from 50 Ky to 25 Ky.

Very important for this area is the irregular presence of Neandertal man at 1450 m. a.s.l. in the Caverna Generosa testified by six flint tools (Bona *et al.,* in press). After the last maximum glacial and the disappearance of *Ursus spelaeus* the Insubrian area sees the new spreading of luxuriant wood, modified only recently by human activity (Bona, 2006).

In the sediments of Ciota Ciara cave (Monfenera - Piedmont), a cave characterized by the presence of *Ursus spelaeus* and *Homo neanderthalensis* and located few kilometres West to the Grotta sopra Fontana Marella and the Caverna Generosa, the macromammals remains testified a trend similar to the two caves object of this paper, but the ancient excavation and the incompleteness of the work do not allow an absolute correlation (Fedele, 1968; 1972) within the three stratigraphical sequences presented in this paper.

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FIRST PALEO-ENVIRONMENTAL CONSIDERATIONS ON THE PLEISTOCENE DEPOSITS OF THE LOWER CAVE OF COVOLI DI VELO (VR - ITALY)

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ABSTRACT: From 2001 until today over 2.000 remains of *Ursus spelaeus*, cave bear of this karstic system, have emerged from the five year excavation in the Lower Cave of Covoli di Velo. Therefore this cavity has returned a real paleonthological patrimony, on which important studies have already been performed in order to get data on the population of cave bears of this karstic system.

Unfortunately, during this five year research we did not have similar luck with other species, despite evidence by various authors of the presence of a rich fauna of vertebrates in these caves in the past. In fact, few finds have been retrieved, revealing only three macro-mammal species: *Canis lupus*, *Crocuta crocuta spelaea* and *Capra ibex*.

Therefore, in these last campaigns we decided to sample different sectors and levels of excavation B, in order to get information about the micro-mammals of these Pleistocene deposits. However, the amount of determinable material, retrieved by sifting sediment, is very scarce. It was, in fact, only a few teeth and jaws that led us to identify the following species: *Glis glis*, *Microtus arvalis*, *Microtus agrestis*, *Microtus oeconomus*, *Chionomys nivalis*, *Dinaromys bogdanovi*, *Terricola* sp. (Rodentia), *Sorex minutus* (Insectivora), *Myotis blythi*, *Myotis* sp., *Miniopterus schreibersi*, *Rhinolophus* sp. (Chiroptera).

We then tried to cross examine these results with those of the pollen analysis of three samples taken from different depths of sector B. The results obtained from the pollen, combined with those of the fauna, give us interesting matters of discussion and further ideas on the possible paleo-environment of Covoli di Velo during Late Pleistocene.

Key words: Grotta inferiore, Covoli di Velo, *Ursus spelaeus*, micro-mammals, pollen, paleo-environment.

THE LOWER CAVE OF COVOLI DI VELO

The karstic system of Covoli di Velo consists of three principal cavities ("Upper Cave", "Lower Cave" or "Cave of the bear" and "Covolo dell'Acqua") and of some smaller hollows, situated in the so-called Valle del Covolo, between the villages of Velo Veronese and Selva di Progno, between 860 and 890 m a.s.l. (fig. 1).

The caves were formed by the water inside the "Grey Limestones of Noriglio" (Lower Jurassic) and consist of oolitic calcarenite, intensely and locally dolomitised, with oyster shell beds or lumachelles, laminated micrites and micrites with shale intercalations.

About 545 meters of karst net have been explored, of which 364 m belong to the system of the Upper Cave - Lower Cave, 65 m to the Covolo dell' Acqua, 40 m to the Covolo dell' Atrio and the last 75 m to the smaller hollows.

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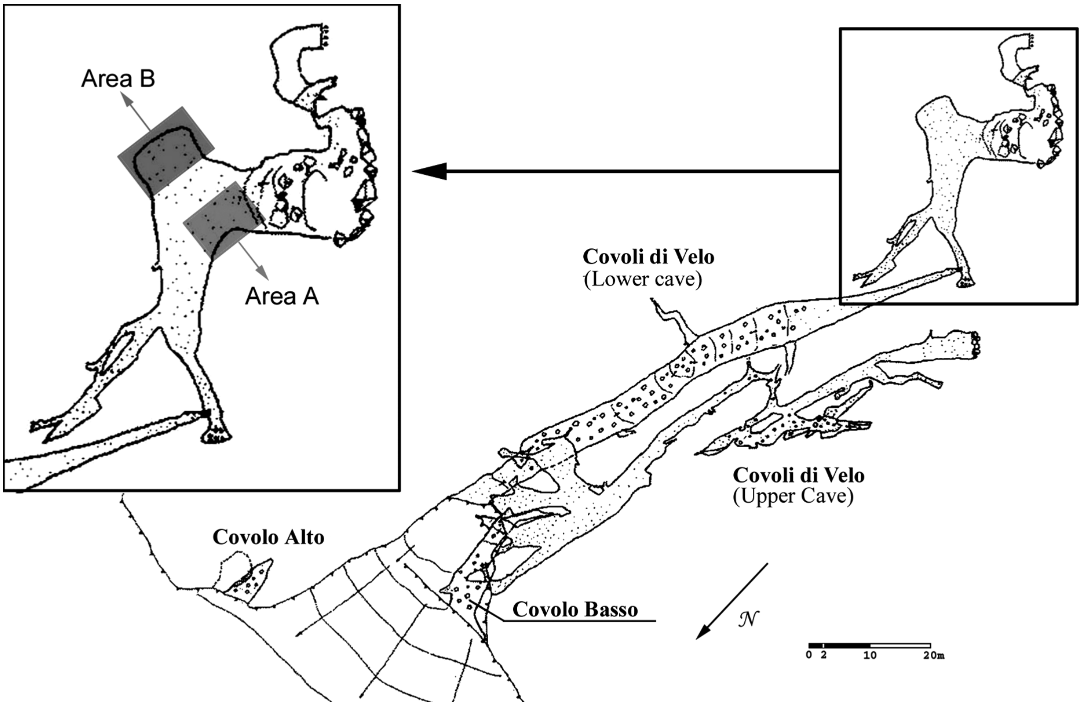

Figure 1. Planimetry of the karst system of Covoli di Velo with excavation sectors A and B (Image by G. Rossi and R. Zorzin).

The first part of the cavities is sub-horizontal and rich in alluvial sediments. The accessible parts of the complex and the presumable connections between cavities are limited due to the large alluvial and collapse deposits, which block the galleries in different places (Zorzin & Rossi, 1999; Zorzin & Bona, 2002).

At the beginning of 2001, in that one chamber, situated around 150 m from the entrance, the Section of Geology and Paleontology of the Civic Museum of Natural History in Verona undertook a series of excavations. These excavations concerned two small portions of ground, one along the west side and the other along the east side, respectively denominate sector A and sector B (fig. 2).

In sector A, an area of about 12 m^2, the following stratigraphical levels emerge: level 0, consisting of blocks of landslide of varying dimensions; levels 1 and 1b, com-

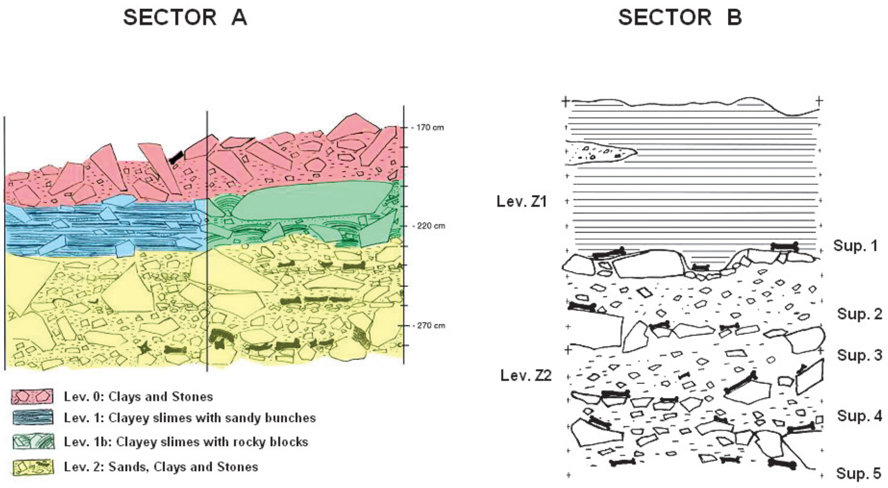

Figure 2. Stratigraphy of sectors A and B (Images by F. Bona).

Table 1.
Finds of micro-mammals recovered in excavations of Covoli di Velo.

N°	SPECIMEN	SPECIES	LEVEL
1	Hemimandible sx.	*Myotis blythi*	A3/2 (2001)
2	Hemimandible dx.	*Miniopterus schreibersi*	A3/2 (2001)
3	Hemimandible sx.	*Rhinolophus (?)*	A3/2 (2001)
4	Hemimandible dx.	*Myotis* sp.	N2/Z1 (2002)
5	M Sup.	*Myotis (?)*	N2/Z1 (2002)
6	Hemimandible dx.	*Glis glis*	N2/Z1 (2002)
7	M^1 sx.	*Glis glis*	N2/Z1 (2002)
8	P^4 sx.	*Glis glis*	N2/Z1 (2002)
9	M_1 dx.	*Glis glis*	N2/Z1 (2002)
10	M_3 dx.	*Glis glis*	N2/Z1 (2002)
11	M^3 sx.	*Glis glis*	N2/Z1 (2002)
12	P^4 sx.	*Glis glis*	N2/Z1 (2002)
13	P_4 dx.	*Glis glis*	N2/Z1 (2002)
14	M_1 dx.	*Glis glis*	M00/Z1
15	M_1 sx.	*Terricola* sp.	M00/Z1 25-50 cm
16	M_1 sx.	*Microtus agrestis*	M00/Z1 50-75 cm
17	M_1 sx.	*Microtus* gr. *arvalis-agrestis*	N1/Z1 50-75 cm
18	Hemimandible dx.	*Sorex minutus*	M00/Z1 50-75 cm
19	Hemimandible dx.	*Sorex minutus*	L2/Z1 - rehandled
20	M_1 sx.	*Microtus agrestis*	L2/Z1 - rehandled
21	M^3 dx.	*Dinaromys bogdanovi*	L2/Z1 - rehandled
22	M_1 sx.	*Microtus agrestis*	L2/Z2 Sup.2
23	M_1 dx.	*Chionomys nivalis*	N1/Z2 Sup.2
24	M_1 dx.	*Dinaromys bogdanovi*	N1/Z2 Sup.2
25	M_1 dx.	*Microtus arvalis*	L2/Z2 Sup.3
26	M_1 sx.	*Microtus arvalis*	L3/Z2 Sup.3
27	M_1 sx.	*Dinaromys bogdanovi*	L3/Z2 Sup.3
28	Hemimandible sx.	*Chionomys nivalis*	L3/Z2 Sup.4
29	M_1 sx.	*Microtus agrestis*	L2/Z2 Sup.5
30	M^s	*Dinaromys bogdanovi*	L2/Z2 Sup.5
31	M_1 sx.	*Microtus arvalis*	L3/Z2 Sup.5
32	M_1 dx.	*Microtus agrestis*	L3/Z2 Sup.5
33	M1	*Microtus oeconomus*	L3/Z2 Sup.5
34	M_1 sx.	*Chionomys nivalis*	L3/Z2 Sup.5
35	M^s	*Dinaromys bogdanovi*	N2/Z2 Sup.5

posed of clay slime and sandy bunches, with landslidden blocks in the second; level 2, formed by surfaces of clasts and alternate bones to slow of clayey slime. Sector B, of around 9 m^2, shows a stratigraphy consisting of 2 main levels: level Z1, constituted mainly by rolled clayey slime with some sandy bunches and the level Z2, formed by surfaces of clasts and alternate bones to slow clayey slime. Given the evident stratigraphical similarity, respectively between the levels 1 and 2 of the sector A and the levels Z1 and Z2 of the sector B, their correspondence is almost certain. According to these considerations, layer Z1 in sector B is designed under the new term "Unity of the slimes" and layer Z2 "Unity of the blocks". In both sectors of excavation almost 3 m below level zero of the cave is reached.

SMALL MAMMALS FAUNA

A small quantity of micro-mammals, coming to the following species, was recovered during the last campaign by sifting samples of sediment from all the squares and levels of sector B: *Glis glis*, *Microtus arvalis*, *Microtus agrestis*, *Microtus oeconomus*, *Chionomys nivalis*, *Dinaromys bogdanovi*, *Terricola* sp., *Sorex minutus*, *Myotis blythi*, *Myotis* sp., *Miniopterus schreibersi*, *Rhinolophus* sp. (tab. 1).

Some of the determined rests originate from the sifting of samples withdrawn for granulometric analysis (Accordini, 2003-2004) during the excavations 2002 and 2003 and have been found to belong to the dormouse and the bat. All other finds derive from a long sifting operation consisting of around sixty picked samples of sediment in the two following campaigns (2004 and 2005). However, the particular position of area B has not given us a great number of finds. Nevertheless, thanks to this enormous work we have succeeded in drawing a small but meaningful collection of micro-mammals (Muridae, Gliridae, Soricidae and Chiroptera).

Considering the sector B only, since sector A seems to a large extent to have been rehandled, the distribution of the various recognized species is the following (fig. 3):

"Unity of the "slimes" (level Z1): *Glis glis*, *Microtus arvalis*, *Microtus agrestis*, *Terricola* sp., *Sorex minutus*, *Myotis* sp.

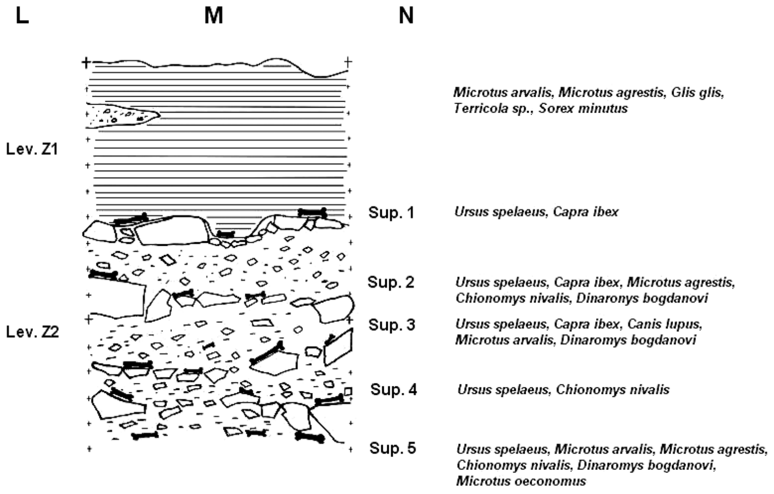

Figure 3. Distribution of determinated species in levels of sector B (Image by M. Accordini and F. Bona).

"Unity of the "blocks" (level Z2): *Ursus spelaeus*, *Canis lupus*, *Capra ibex*, *Microtus arvalis*, *Microtus agrestis*, *Microtus oeconomus*, *Chionomys nivalis*, *Dinaromys bogdanovi*, *Myotis blythi*, *Miniopterus schreibersi*, *Rhinolophus* sp.

PRELIMINARY PALEO-ENVIRONMENTAL CONSIDERATIONS ON THE SMALL MAMMALS FAUNA

The macro-fauna recognized in the Lower Cave of Covoli di Velo is composed, besides the cave bear, of *Crocuta crocuta spelaea*, *Canis lupus* and *Capra ibex*. The micro-fauna, though not very abundant, shows a higher number of species.

The constant presence of the cave bear in the lower cave allows us to report our levels to a glacial period: this kind of bear, in fact, reached its maximum development and widest distribution during the last great Würm Glaciation, extinguishing itself probably around 18-20.000 years ago.

In our evaluations we have decided not to take the wolf and the bear into account because, as is the case with most carnivores, they do not usually give precise indications from a paleo-environmental point of view.

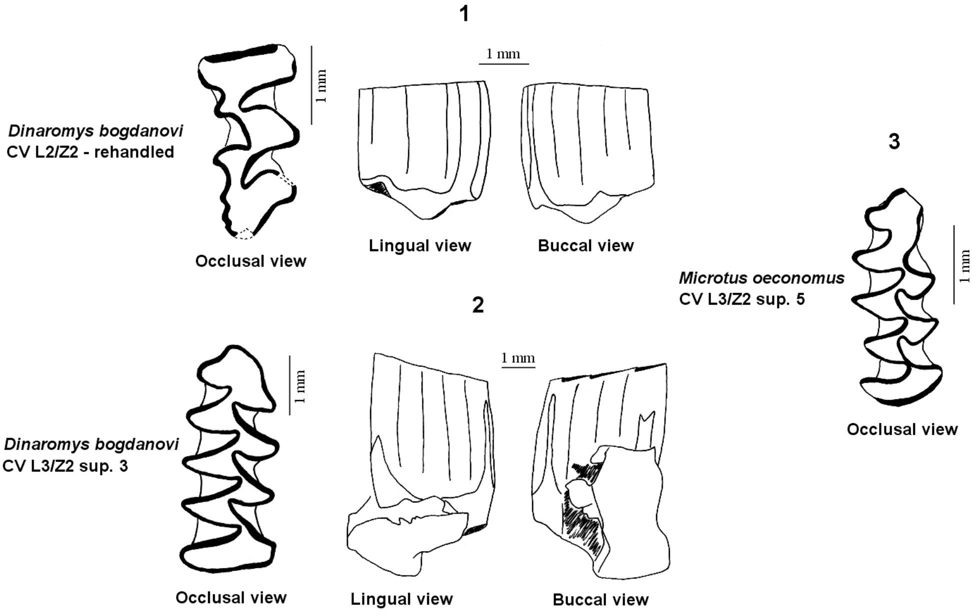

Figure 4. Molars of some rodents recovered in the Lower Cave: 1) M^3 dx. of *Dinaromys bogdanovi* (occlusal, lingual and buccal view); 2) M_1 dx. of *Dinaromys bogdanovi* (occlusal, lingual and buccal view), 3) M_1 dx. of *Microtus oeconomus* (occlusal view) (Images by F. Bona).

Other than these considerations, the presence of the ibex could also be meaningful. This species currently lives at an altitude between 1.600 and 3.000 m a.s.l., inhabiting grassy and rocky slopes above the limit of arboreal vegetation. The presence of this animal indicates open expanses with scarce vegetation, typical of a cold and arid climate. Its recovery at a lower altitude, around 880 m a.s.l., leads us to suppose that vegetation was scarce around the cave with the timber line situated much lower than it is today (Zorzin *et al.*, 2005a).

Besides the ibex, we have considered of fundamental importance the rests of micro-mammals, particularly those belonging to the rodent group (fig. 4). Above all we wish to underline the presence of various species belonging to the Microtinae subfamily, which is mainly known to inhabit meadows and alpine pastures at the borders of forests or rocky slants above the tree-line, some also reaching elevated stations up to the limit of the snows. The dormouse seems to be the only rodent, among those discoveries, which was well adapted to the woody environment in hilly and mountainous areas.

From our observations on the fauna determined up to this point, we can draw some important paleo-environmental considerations about the Karstic area of Covoli di Velo during the period of deposition of the two main levels (Unity of the "slimes" and Unity of the "blocks") of the last chamber of the Lower Cave. The presence of the ibex in the first three surfaces of level Z2 (Unity of the "blocks") leads us to hypothesize the presence of a number of open spaces with scarce forest coverage where the limit of forest extension was surely found lower than it is today. In this geological phase the climate had to be cold and the landscape rather arid. The environmental evaluations given by the ibex are also confirmed by the rests of *Chionomys nivalis* and *Dinaromys bogdanovi*, two species belonging to a cold environment which at present live on rocky mountain slopes up to elevated altitude. The other voles recovered in sector B also seem to indicate a predominantly open environment partly damp ground, above all given by the presence of *Microtus oeconomus*, besides *Microtus arvalis* and *agrestis*.

Conditions seem to change somehow in the superior level, the Z1 (Unity of the "slimes"), where the species which mostly characterize the cold environment of Z2 (*Capra ibex*, *Chionomys nivalis*, *Dinaromys bogdanovi* and *Microtus oeconomus*) disappear. The disappearance of these species and the appearance of *Glis glis* in the most superficial layer, denote without any doubt an increase of woody coverage, probably due to a phase of increasing temperature. Therefore the limit of the forest would have been at higher altitudes compared to the scenario of the underlying level. In the level of slimes *Microtus arvalis* and *agrestis* have also been found, besides the species *Terricola* and *Sorex minutes*. These species testify the existence of wide open spaces at the borders or inside the wood, where they could live.

As a result, we can hypothesize the existence of two geological periods corresponding to the first two levels dug in sector B. The first level (Unity of the "blocks"), seems to correspond to a geological phase characterized by a cold, alpine type environment, with wide open spaces and scarce forest coverage; the second level (Unity of the "slimes") seems to depict a more recent geological period, in which an increase of the temperature led to higher extension of the timber line and subsequently the return of arboreal species to the area of Covoli di Velo. Nevertheless, these considerations can only be considered preliminary and hypothetical due to the limited data currently available.

POLLEN ANALYSIS AND FLORAL-VEGETATION CONSIDERATIONS

In the 2004 campaign, besides the samples of sediment for studies on the micro-mammal finds, three core borings were performed in section B sector from which a number of samples for pollen analysis were taken. The samples, denominated 1-2-3, have been picked from the quadrant L1. The levels involved in the sampling are: level Z1 - "Unity slimes" (Sample 1), level Z2 sup.3 - "Unity blocks" (Sample 2) and level Z2 sup.5 - "Unity blocks" (Sample 3).

Samples of ca. 15-17 gs have been treated for the extraction of pollen and microchar-coals, following routine methods which include the following steps (Lowe *et al.*, 1996): addition of spores of *Lycopodium* for the calculation of concentrations (number of granules/gram = p/g), Na-pyrophosphate, HCl 10%, sifting with 7 μms nylon mesh filter, acetolysis, enrichment with liquid heavy Na-metatungstate I, HF 40%, ethanol 98%, addition of few drops of glycerine, drying in heater, assemblage of the residue with glycerinated glaze in brittle permanent. Pollen identification was performed in optic light transmitted 400x and 1000x microscope, with the aid of Palinoteca and morphological keys/atlases/works (for example: Faegri & Iversen, 1989; Moore *et al.* 1991; Reille 1992; 1995; 1998). Pollen spectra percentages have been calculated on a Pollen Sum that excludes the overrepresented Cichorioideae. The Cichorioideae have been calculated in percentage to the Pollen Sum plus themselves, in accordance to Berglund & Ralska-Jasiewiczowa (1986). The sum of categories held profitable for the discussion is represented in a histograms graph (fig. 5). The botanical

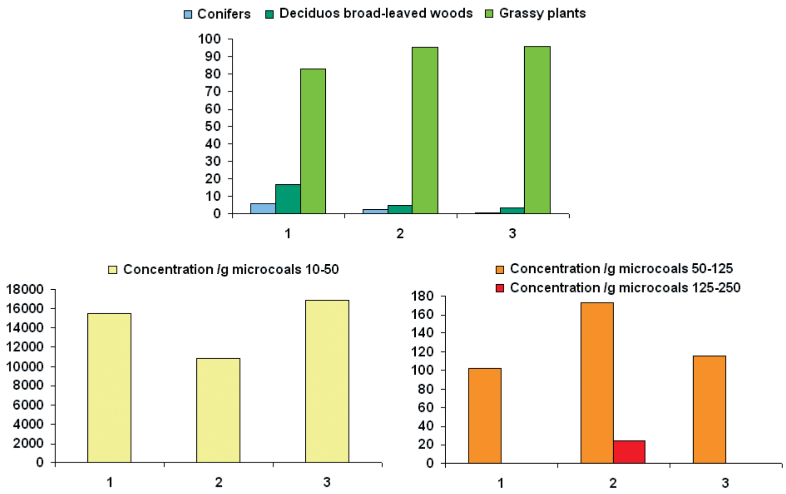

Figure 5. Up: Diagram of the percentages of the pollens of conifers, deciduous broad-leaved woods and grassy plants in the 3 samples of sediment picked in the sector B. Down: Diagrams of the concentrations of the different types of microcoals in the 3 samples (Diagrams by C. A. Accorsi *et al.*).

nomenclature is in accordance to Pignatti (1982).

The pollen contained is uniform and low, around 10^3-10^4. The highest value, around 13.000 granules/gs, has been observed in the Sample 2. In the presence stage of analyses, conditions of the grains suggest notable influxes to be attribuited to air, water, animals and eventually humans who have frequented the cave (Dimbleby, 1985; Faegri & Iversen, 1989). A high number of entomophilious taxa, among which melliferous, could be connected to the bears (for example: pollen in the fur, in coprolites...).

GENERAL CHARACTERS OF THE POLLEN SPECTRA

The pollen spectra of the three samples have a physiognomy in some ways similar (tab. 2):

1. Grassy plants clearly dominate the spectrum. In fact, they always exceed 80% and in the samples 2 and 3 (level Z2) they even exceed 90% (95-96%).

2. Grasses include a range of floral species (38-46 taxa), above all Gramineae (38-47%), Cichorioideae (10-66%), Umbelliferae (4.5-20%).

3. Woody plants, trees and bushes, are represented by more than 10 taxa in each sample. Some coniferous and various deciduous broad-leaved trees are also present. Six taxa are found in all three samples: *Alnus*, *Betula*, *Hyppophae*, *Pinus*, *Quercus deciduous*, *Salix*.

The pollen spectra also show differences that point out an overall "vegetation trend":

- progressive increase of woody plants upward, both in abundance and in diversity, as indicated by the percentage of the woody ones (4, 5, 17% in the samples 3, 2, 1 respectively) and by the number of taxa (13, 14, 18 taxa in the samples 3, 2, 1 respectively),

- an increase, from lower levels upward, of woody plants subjected to damp environments, above all meaningful in the sample 1 (6%).

Within this trend there is higher similarity between the two leading samples, 2 and 3, while sample 1 differs from both.

THE FLORA

The flora testified in the pollen spectra is quite rich, containing around a hundred types of pollen, two of which grassy plants and one woody.

Among the woody plants some conifers appear: *Pinus* (with indications of *P. mugo*), *Picea excelsa*, *Taxus* and *Juniperus* cf., and various deciduous trees, *Betula*, *Fagus*, *Castanea*, *Quercus deciduous*, *Tilia*, *Ulmus*, *Fraxinus*, *Carpinus*, *Salix*, *Corylus*, *Hipphophae*, *Ligustrum*, *Alnus*, *Populus*. In sample 2 *Quercus ilex*, a woody Mediterranean evergreen is present. The grassy flora is very rich: Gramineae, Compositae (among which very abundant Cichorioideae in the superior sample, followed by *Artemisia*, *Aster* type and *Cirsium*, always well represented), very abundant Umbelliferae in the two inferior samples, then Cruciferae, *Campanula* type, Leguminosae, Labiatae etc., every family being represented by numerous pollen types.

Table 2.
Pollen spectra of the Lower Cave of Covoli di Velo (VR - Italy).

Samples n°			**1**	**2**	**3**
Depht (cm)			50	100	150
Stratigraphic Unity			Z1	Z2 sup. 3	Z2 sup. 5
Concentration (poll/g)			**1787,5**	**12626,4**	**6137,4**
WOODS-BUSHES					
BETULACEAE	*Alnus* cf. *glutinosa*	A/ar,LD,IG	1,1		
	A. cf. *incana*	A/ar,LD,IG		0,2	
	A. undiff.	A/ar,LD,IG	1,1	0,2	0,7
	Betula	A/ar,LD	1,4	0,2	0,6
CISTACEAE	*Helianthemum*	ar,LD		0,2	
CORYLACEAE	*Corylus avellana*	A/ar,LD,Q	0,3		0,3
	Carpinus betulus	A,LD,Q			0,1
CUPRESSACEAE	*Juniperus* type	ar,CF	0,5	0,4	
	Juniperus cf.	ar,CF	0,5	0,1	
ELAEGNACEAE	*Hippophae* cf.	ar	0,3	0,1	0,4
EPHEDRACEAE	*Ephedra* cf.	ar,CF	0,5		
FAGACEAE	*Castanea*	A,LD,C	0,3		0,1
	Fagus sylvatica	A,LD	0,3		
	Quercus decidue	A,LD,Q	1,6	0,1	0,4
	Quercus ilex type	A/ar,M		0,2	
OLEACEAE	*Fraxinus ornus*	A,LD,Q	0,8		
	Fraxinus cf.	A,LD,Q	0,3		
	Ligustrum	ar,LD, Q	0,3		
PINACEAE	*Picea*	A,CF	0,3		
	Pinus	A,CF	4,1	2,0	0,2
ROSACEAE	*Rubus* cf. *chamaemorus*	ar/LD			0,3
	Rubus undiff.	ar,LD		0,1	
SALICACEAE	*Salix*	A/ar,LD,IG	3,0	0,5	0,2
TAXACEAE	*Taxus* cf.	ar/A,CF			0,1
TILIACEAE	*Tilia* cf. *platyphyllos*	A,LD,Q		0,1	0,1
ULMACEAE	*Ulmus*	A,LD,Q		0,1	0,1
THYMELEACEAE	*Daphne*	ar/LD	0,3		
Forest coverage			***16,8***	***4,8***	***3,8***
GRASSY PLANTS					
ALISMATACEAE	*Alisma*			0,2	
BORAGINACEAE	Boraginaceae			0,1	0,1
CAMPANULACEAE	*Campanula*		1,1	1,5	2,7
CARYOPHYLLACEAE	*Cerastium fontanum* type	As	0,3		0,4
	Caryophyllaceae undiff.		0,5	1,0	1,3
CHENOPODIACEAE	Chenopodiaceae	As	3,5	0,4	0,6
COMPOSITAE	*Ambrosia* type		0,3	0,5	
	Anthemis type	As	2,2	0,7	3,6
	Artemisia	As	4,3	5,7	3,9
	Aster type		6,3	1,6	6,3
	Centaurea nigra type	As	1,9	0,5	0,8
	Cirsium	As	2,7	1,6	3,8
	Asteroideae undiff.			0,7	1,1
	Cichorioideae	***As***	***66,0***	***10,2***	***10,0***
CONVOLVULACEAE	*Convolvulus*	As			0,3
	Cuscuta cf.	As		0,2	0,6
CRASSULACEAE	*Sedum* cf.		0,5		
CRUCIFERAE	*Brassica* type		0,3		
	Hornungia type		3,3	0,1	0,8
	Cruciferae undiff.				
CYPERACEAE	Cyperaceae	ig	0,8	1,1	0,3
DIPSACACEAE	Dipsacaceae			0,2	0,2
GENTIANACEAE	*Gentianella*				0,1
GRAMINEAE	*Hordeum* group	c,cer	0,3	0,1	0,3
	Glyceria cf.	ig			0,3
	Phragmites type		0,8	2,6	2,2
	Gramineae spontaneous group		36,7	44,5	37,0
HALORAGACEAE	*Myriophyllum*	id/el		0,1	
HYPERICACEAE	*Hypericum*			0,1	0,1
LABIATAE	*Mentha* type			0,1	0,1
	Stachys type		0,3	0,5	
	Labiatae undiff.		1,4	1,0	0,2
LEGUMINOSAE	*Hedysarum* cf.			0,2	
LEGUMINOSAE	*Lotus*		0,5		
	Onobrychis cf.			0,2	
	Leguminosae undiff.		1,4	0,6	0,7
LILIACEAE	Liliaceae		0,3		
MENYANTHACEAE	*Menyanthes*				0,1
PLANTAGINACEAE	*Plantago media/major* type	As	1,6		0,1
	P. undiff.	As	1,4	0,9	1,0
POLEMONIACEAE	*Polemonium*				0,1

continued

Table 2 *(continued)*

POLYGONACEAE	*Polygonum aviculare* type	As	0,3		0,3
	Rumex	As		0,1	
RANUNCULACEAE	*Aconitum*			0,1	0,2
	Actaea			0,1	
	Anemone type		0,3	0,7	
	Clematis cf.		0,3		
	Consolida				0,1
	Ranunculus type		0,8		0,2
	Thalictrum flavum type		1,4	0,7	0,4
	Ranunculaceae undiff.		0,5	1,1	2,1
ROSACEAE	*Aphanes/Alchemilla* type	As		0,2	0,9
	Filipendula			0,2	
	Fragaria cf.		0,3	0,1	0,2
	Potentilla type		0,8		
	Rosaceae undiff.		0,3	1,1	1,2
RUBIACEAE	*Galium* type		0,8	1,5	0,3
SAGITTARIACEAE	*Sagittaria* cf.	ig		0,5	
SAXIFRAGACEAE	*Saxifraga* cf.				0,4
SCROPHULARIACEAE	*Melampyrum*				0,1
	Scrophulariaceae undiff.			0,2	0,1
UMBELLIFERAE	*Bupleurum* cf.		0,8		
	Umbelliferae undiff.		3,5	20,1	19,9
URTICACEAE	*Thesium*			0,1	
	Urtica dioica type	As	0,5	0,2	
VALERIANACEAE	*Valeriana*			0,1	0,1
Grassy plants sum					
Pollen counts			***1082***	***898***	***990***
POLLEN SUM (Cichorioideae excluded)			***368***	***806***	***900***
NUMBER OF TAXA			**56**	**60**	**58**
INDETERMINABLE					1,0
PTERIDOPHYTA					
HYPOLEPIDACEAE	*Pteridium*		1,1	2,0	
MONOLETE undiff.			5,2	7,0	2,0
TRILETE undiff.			0,5	1,0	
TOTAL			*6,8*	*10,1*	*2,0*
ALIA					
Spores of mushrooms			++	+	++
Sphagnum			+	+	+
Concentrycistes			+	+	+
Secondary deposition			+	+	
Rehandled				+	
SUMMARY					
Woods		A	14,4	3,8	2,9
Bushes		ar	2,4	1,0	0,9
Conifers		CF	6,0	2,5	0,3
Deciduous broad-leaved woods		LD (A+ar)	16,8	4,8	3,8
Quercetum (*Acer campestre* type + *Carpinus betulus* + *Ostrya carp./Carpin. orientalis* +*Fraxinus excelsior* type+ F. *ornus*+*Quercus* dec. + *Tilia* + *Ulmus*)		Q	3,3	0,4	1,1
Mediterranean plants		M		0,2	
Hydrophyle woods		IG	5,2	1,0	0,9
Cultivated grassy plants		C	0,3		0,1
Grassy plants		E	83,2	95,0	96,0
Hydrophytes + elophytes grassy plants		ig+id/el	0,8	1,7	0,7
Cultivated/cultivable grass		c	0,3	0,1	0,3
Cereals		ce	0,3	0,1	0,3
Grassy anthropic indicator plants		As	18,8	10,7	16,2
Damp environments (Total hydro-hygro-elophytes)		IG+ig+id/el	6,0	2,7	1,6
Cultivated areas (Total cultivated plants)		C + c	0,5	0,1	0,4
Anthropic environment (Total anthropic indicators)		C + c+ As	16,3	9,3	11,2

Various finds of nitrophilious plants such as Chenopodiaceae, *Rumex*, *Urtica dioica* type, which can be connected to the circulation of animals and/or to the anthropic frequentation, appear as well. These belong to the group of anthropogenetic indicators, in which pollens of *Hordeum* group, recovered in the three samples, are also present, possibly indicating the presence of cereals in compatible contexts. Plants belonging to damp environments, represented by hydrophytes and hygrophytes/elophytes (*Alisma*, *Menyanthes trifoliata*, *Myriophyllum*, *Nymphaea*, *Phragmites* type, Cyperaceae), added to trees such as willows, alder-trees and poplars have modest, but meaningful presences. Particularly interesting are the water clover (*Menyanthes trifoliata*), a northern species growing in swamps and marshes on the damp environment vegetation which was found in the leading sample, and *Sphagnum*, found in all samples, mostly typical of peat-bogs.

LANDSCAPE PATTERNS OF VEGETATION AND HYPOTHESIS ON CHRONOLOGY

Landscape patterns of vegetation are connected to pollen spectra samples (from the cave), whose formation, as already reminded, influxed due to the frequentation of animals privileging entomophile entities (above all grassy plants), to loss of the anemophile ones, among which the greatest part of recovered woody plants reverts, could have contributed notably. Also keeping in mind the possible bottom respect to the eolic influx in the two inferior samples, the vegetation is characterized by grassy formations, probably primary grasslands, above the tree-line. Such grasslands are dominated by Gramineae, as well as a vast number of other grassy plants, among which Campanulaceae, Compositae, Cruciferae, Leguminosae, Liliaceae, Rosaceae, Ranunculaceae, Umbelliferae.

Therefore the landscape would appear to depict wide open spaces, typical of alpine landscape, characterized by grasslands, with a few watercourses or water mirrors that could account for the presence of hydro/hygrophytes: a scenario in accordance with our faunistic finds. Forest formations are situated in foundation, presumably to lower quotas of Covoli di Velo, which leads us to hypothesize a descent of the forest due to the rigidity of the climate that appears severe, cold and arid.

Nevertheless, we noticed that the woody plants are quite different, containing testimonies of broad-leaved woods from pollen which is not particularly widespread (for example *Tilia*). Together with pollen documents of the ilex, this could signal the proximity of a place of shelter. However, we cannot exclude the influx from a long distance, particularly for the ilex. In the superior sample an increase in broad-leaved woods, particular the mesophile, signals a climatic improvement in terms of temperature, with an increase of damp too, testimonied by the sensitive growth of woody plants associated to damp grounds.

The pollen spectra seem to testify the existence of geological time period, during which, or rather, at the end of which, meaningful climatic changes brought warmer and damper conditions. Even though much caution is required in setting hypothesis of chronology, given the limited number of samples, the two inferior samples can be compatible with a Pleistocene age around the maximum glacial (around 18.000 years 14C from the present), while the superior sample is, at the moment, hardly connected to a precise chronological phase.

MICRO-COALS

The micro-coals have been read according to the method adjusted by Bosi and Accorsi (in press). Carbonaceous particles, in modest concentrations (max 10^4) in all samples, signal the possibility of a constant presence of regional fires, although it cannot be specified whether the typology is natural or anthropic. Coals of the two smaller classes (inferior to 125 μms) are always present, more abundant in samples 1 and 3; class size “very large” (>250 μms) is always absent, whereas class size “large” (125-250 μms) is present only in sample 2. For this reason we can imagine the presence of fires, anthropic or not, in the immediate proximities of the cave (Mooney *et al.,* 2001) and to the casual transport of traces of these fires in the cave aside, for instance, of the great mammals which frequented it.

CONCLUSIONS

Among the over 2.000 rests recovered and determined during five years’ excavations, 99% belong to *Ursus spelaeus* (fig. 6). A morphological and morphometric analysis of this species has brought the followings results: analysis of the long bones reveal that the lowest number of bears frequenting the cave is estimated to be around ninety individuals. The greater part belongs to cubs at different phases of growth and to young animals, whereas the adults are fewer in number; among adult individuals, females are more numerous than males (Zorzin *et al.,* 2005b).

The other species of macro-vertebrates are *Canis lupus*, *Crocuta crocuta spelaea* and *Capra ibex*. The fauna of micro-mammals is composed of: *Glis glis*, *Microtus arvalis*, *Microtus agrestis*, *Microtus oeconomus*, *Chionomys*

Figure 6. Finds of cave bear emerged in the excavation (Photo by F. Bona).

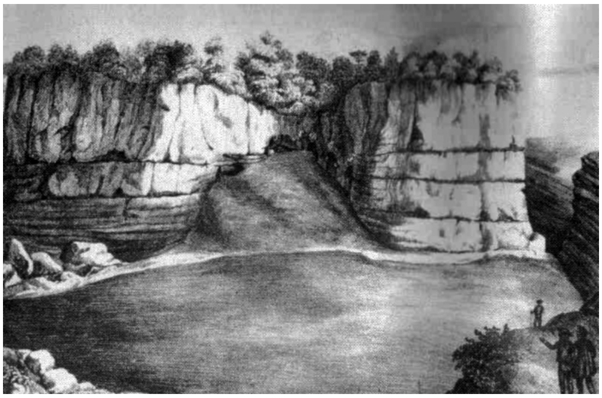

Figure 7. Landscape of Covoli di Velo (Figure by A. Massalongo, 1851).

nivalis, *Dinaromys bogdanovi*, *Terricola* sp., *Sorex minutus*, *Myotis blythi*, *Myotis sp.*, *Miniopterus schreibersi*, *Rhinolophus* sp.

Analysis of pollen present in levels of sector B have allowed us to identify the following species: *Pinus*, *Picea excelsa*, *Taxus* and *Juniperus* (conifers), *Betula*, *Fagus*, *Castanea*, *Quercus*, *Tilia*, *Ulmus*, *Fraxinus*, *Carpinus*, *Salix*, *Corylus*, *Hipphophae*, *Ligustrum*, *Alnus*, *Populus* (broad-leaved trees), *Quercus ilex* (Sample 2); Gramineae, Compositae, Brassicaceae, Campanulaceae, Fabaceae, Liliaceae, Rosaceae, Ranunculaceae, Umbellifere Apiaceae, Cyperaceae, Lamiaceae, Chenopodiaceae, hydrophyte and hygrophyte plants, *Sphagnum*.

Combining the observations on the fauna with the results of the pollen analyses a few important preliminary paleo-environmental considerations can be made. In Unity of the "blocks", the rodents and the ibex, combined with pollen data, reveal an open, grassy alpine-type landscape (fig. 7), with meadows among the rocks, few trees, and a rather cold climate. In Unity of the "slimes", the dormouse, which lives in areas covered by broad-leaved woods and conifers, is abundant, confirming the increase of woody plants in this layer as shown by the pollen. Despite the forest landscape, areas of open expanses are left on the borders or inside the woods, as demonstrated by rests of Microtinae found in this layer. This gives evidence of a climatic change from cold to warmer and more humid conditions. However, these conclusions would need to be confirmed by further studies on more samples. Given the importance of Covoli di Velo as a site of paleontological interest, it would be advisable to collect many new samples for pollen and microfauna study, which will be one of the priorities of the following excavations.

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TRACE FOSSILS FROM BEARS IN CAVES OF GERMANY AND AUSTRIA

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Abstract: The article gives an overview of trace fossils from bears in caves of Germany and Austria. Recorded trace fossils are Bärenschliffe, bear dens, scratch marks and kidney stones. The trace fossils were found in 22 different cave sites of Germany and in only five cave sites of Austria. All traces cannot be attributed to either the cave or the brown bear, they can neither be dated.

Key words: Bärenschliff, trace fossils, bears, caves, Germany, Austria, Quaternary.

INTRODUCTION

Fossil bones of bears, particularly those of the cave bear, are commonly found in caves of Germany and Austria. Traces of bears and their usage of caves are, however, rare. The following traces of bears have been recorded in caves: (i) polished rock surfaces (so-called "Bärenschliffe"), (ii) bear dens, (iii) scratch marks of claws and (iv) bear kidney stones. The first three traces arise from the activity of the bears in the cave, while (iv) are remains of the metabolism of bears.

Outside of the two countries, footprints of bears have also been reported, for example from the Grotte de Bruniquel in France (Rouzaud *et al.,* 1995). Late glacial brown bear footprints have, however, been discovered at the open-air site Mertloch, Eifel, preserved in volcanic ashes (Baales & Berg, 1997).

(i) The "Bärenschliffe" are smooth, polished and often shining surfaces, thought to be caused by passing bears, rubbing their fur along the walls. These surfaces do not only occur in narrow passages, where the bear would come into contact with the walls, but also at corners or rocks in wider passages.

The oldest known mention of animal polished rock surfaces are given in a report from the Austrian Erzherzog Rainer, in which he describes his visit to the Mixnitzer Drachenhöhle at the 13th of October 1806 (Abel, 1931). In the report is written: "…in the deeper and narrower part of the cave the rocks are partly polished like marble, probably done by rubbing of large animals, unthinkable times ago".

The scientific introduction of the matter of fact and the term "Bärenschliff" was given in 1826 by Johann Jacob Nöggerath (Nöggerath, 1826), geologist at the Bonn University, according to his observations in the "Alte-Höhle" near the village of Sundwig in the Sauerland/Northrhine-Westfalia (Nöggerath, 1823).

(ii) The bear dens are elliptical, shallow pits, on average between one and three meters in diameter and a couple of decimetres deep. These are interpreted as formed by the bears as resting dens for hibernation.

(iii) The scratch marks attest to the habit of bears - as is typical for clawed carnivores - to wear down their claws by dragging them across rough surfaces.

(iv) Bear kidney stones were first described without recognizing what they were by Rath (1834): He referred to them as unusually shaped, globulous mineral deposits. However the concentric structure and the chemical composition revealed that these objects were biologic in origin (Edinger, 1933; Bausch *et al.,* 1997).

All traces cannot be attributed to either the cave or the brown bear, nor can they be dated.

SITES AND GROUPS OF LIFE TRACES

1. Germany

1.1. Bärenschliffe

1.1.1. Vogelherd/Swabian Alb, Baden-Wuerttemberg

The Vogelherd, near the village of Stetten in the Lone Valley, 25 km northeast from Ulm, is one of the most important Upper Palaeolithic cave sites in Central Europe. The site was discovered in 1930 and excavated in 1931 (Riek, 1932). Because of several animal ivory figures from the

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Aurignacian layers (FLOSS, 2000) the 41 m long cave is known worldwide. A perfect, preserved Bärenschliff is located on the left cave wall of the southwestern entrance (pl. 1.1), around 2 m above the ground (i.e. RATHGEBER, 1993).

1.1.2. Bärenhöhle in the Höhlenstein/Swabian Alb, Baden-Wuerttemberg

The Bärenhöhle is situated in the rocks of the so-called Höhlenstein, near the village of Öllingen in the Lone Valley, 24 km northeast of Ulm. The cave is 72 m long and 14 m wide. Oscar Fraas undertook first excavations in 1861 (FRAAS, 1862). During the excavations Fraas recognized smooth, polished rock surfaces, which he interpreted as Bärenschliffe (FRAAS, 1862: 187, RATHGEBER, 1993). One Bärenschliff from this site is exhibited in the Höhlenkundemusem at the Laichinger Tiefenhöhle (pl. 1.2).

1.1.3. Charlottenhöhle/Swabian Alb, Baden-Wuerttemberg

The Charlottenhöhle was discovered in 1893 and is situated near the village of Giengen, 30 km northeast of Ulm. With a total length of 587 m the cave is the longest tourist cave of the Swabian Alb. Bärenschliffe are located on a part of the cave wall near the entrance (BLEICH, 1968; RATHGEBER, 1993; pl. 1.3).

1.1.4. Hohle Fels/Swabian Alb, Baden-Wuerttemberg

One of the most important cave sites in the Aach Valley is the Hohle Fels near the village of Schelklingen, 20 km west of Ulm. The cave is 120 m long and has in its back part a hall to the size of 6000 m^3, one of the biggest cave halls of the Swabian Alb. The first bones were discovered in 1830 and O. Fraas undertook the first excavations in 1870/71. Till today archaeological excavation is taking place in the cave. In total a 5 m thick sediment section displays a stratigraphic sequence with layers from the Middle Palaeolithic to the Magdalenian. The cave is one of the most important archaeological cave sites in Central Europe, not only because of several animal ivory figures from the Aurignacian layer (i.e. BLUMENTRITT & HAHN, 1991; CONARD, 2003).

During the excavations in all Upper Palaeolithic layers from the cave wall splintered Bärenschliffe (pl. 1.4) were discovered (HAHN, 1993). Most important of these finds are Bärenschliffe from the Gravettian layers. They show difference by palaeolithic human produced engravings (HAHN, 1993, pl. 1.5).

1.1.5. Kleine Scheuer in the Rosenstein/Swabian Alb, Baden-Wuerttemberg

The Kleine Scheuer is a cave situated in the Rosenstein, a rock massif near the village of Heubach, 40 km northwest from Ulm. The first excavations in the 26 m long cave were undertaken in 1906 (KELLER, 1933; MAIER, 1936). Bärenschliffe are located on the left wall near the entrance, on a boulder in the back part of the cave and on the back wall (KELLER, 1933).

1.1.6 Bären- und Karlshöhle/Swabian Alb, Baden-Wuerttemberg

The Bären- und Karlshöhle (Bear's and Charles' Cave) is situated 2,5 km northeast of the village of Erpfingen, 20 km southeast of Tübingen. The total length of the tourist cave is 292 m. While the Karlshöhle (Charles' Cave), the first part of the cave system, was discovered in 1834, the Bear's Cave, the second cave part, was discovered only in 1949, at the end of the last hall of the Karlshöhle. Both caves have an importance in quaternary palaeontology (RATHGEBER, 2003). A Bärenschliff is located direct behind the small connection passage between the two cave parts (RATHGEBER, 2003).

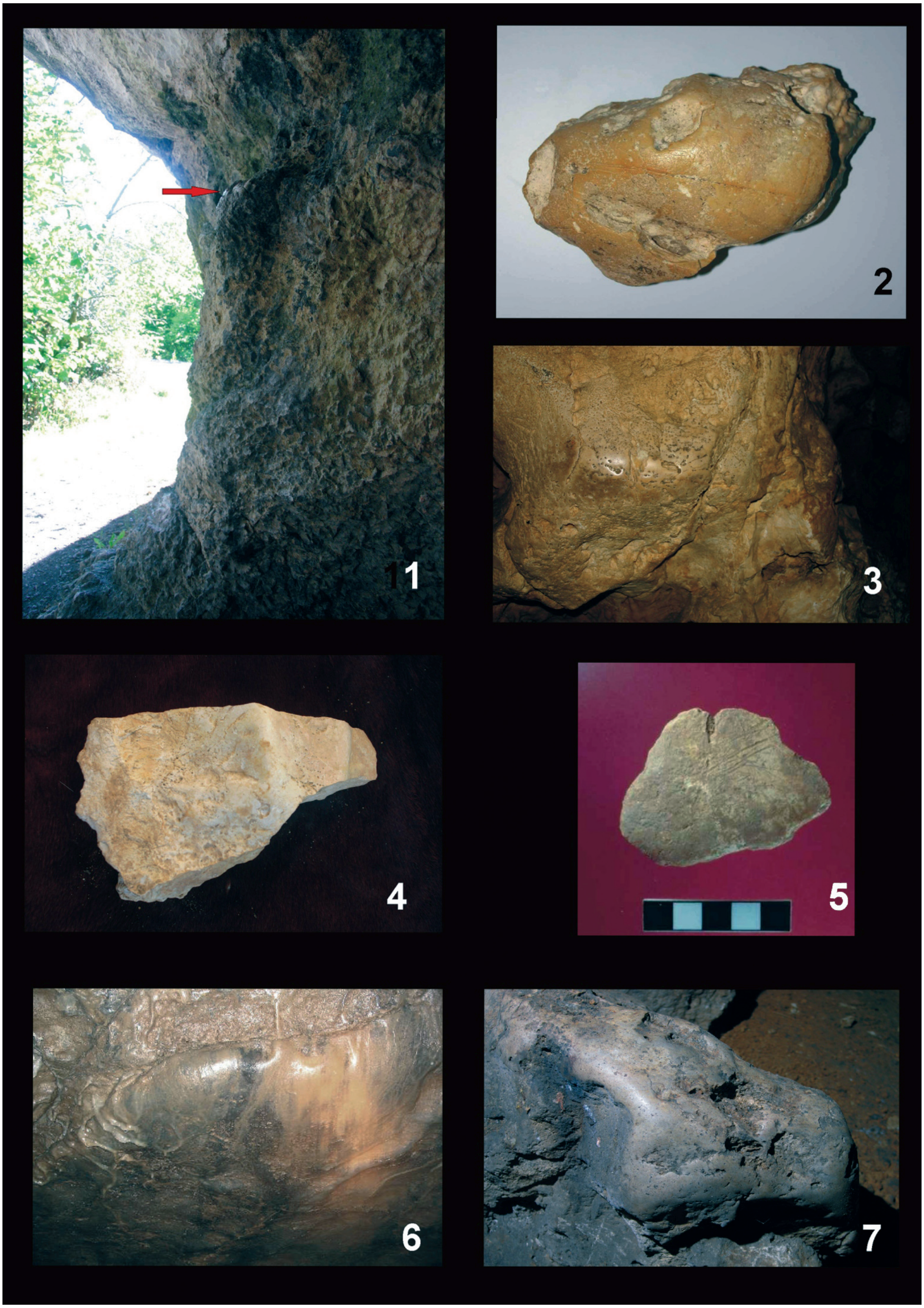
1.1.7. Sundwiger Höhle/Sauerland, Northrhine-Westfalia

The Sundwiger Höhle is situated in the village of Hemer-Sundwig, 30 km northwest of Dortmund. Together with the Heinrichshöhle (today a tourist cave) the Sundwiger Höhle is part of a huge cave system called Perick-Höhle, which is altogether over 3 kilometres long. The Sundwiger Höhle is an important site in science history and very well known since the 19th century (e. g. CUVIER, 1806; NÖGGERATH, 1823). J. J. NÖGGERATH did the first scientific description of Bärenschliffe after observations in this cave (NÖGGERATH, 1826). Several Bärenschliffe are located on the wall of a 50 long cave channel part, 150 m far from the entrance (pl. 1.6).

1.1.8. Großes Schulerloch/Franconian Alb, Bavaria

The cave Großes Schulerloch is situated in the Altmühl Valley between the villages of Kehlheim and Essing, 22 km southwest Regensburg. In 1824 the 420 m long cave was opened as a tourist cave (ILLMANN, 1984). During excavations near the entrance of the cave, F. Birkner discovered pleistocene faunal remains and Mousterian artifacts (KAULICH, 1984). Several Bärenschliffe are located on the eastern wall of a lateral channel in northwestern direction, 200 m far from the entrance (ILLMANN, 1984).

Plate 1



Bärenschliffe from different localities: 1. Vogelherd, 2. Bärenhöhle in the Höhlenstein, 3. Charlottenhöhle, 4. Hohle Fels (from the Aurignacian layer), 5. Hohle Fels (from the Gravettian layer, with human produced ingravings), 6. Sundwiger Höhle, 7. Großes Rohrnloch. (Photos: W. Rosendahl, 1, 2, 3, 4, 7; H.W. Weber, 6; Universität Tübingen, 5).

1.1.9. Zahnloch near Steifling/Franconian Alb, Bavaria

The Zahnloch cave is situated 500 m southeast of the village of Steifling, 36 km northeast of Erlangen. First palaeontological excavations in the 80 m long cave were undertaken in the second half of the 18th century. In some publications Bärenschliffe are reported on the surface of a larger rock (called Magnetblock) in the central part of the cave (i.e. Herrmann, 1991). Recent observations in the cave couldn't confirm this.

1.1.10. Großes Rohrnloch near Viehofen/Franconian Alb, Bavaria

The cave Großes Rohrnloch is situated in the Kupfer Valley, 1 km northeast of the village of Viehofen, 40 km east of Erlangen. The cave is 67 m long (Lang, 2002) and several Bärenschliffe are located in different levels along the walls (Cramer, 1931), mainly in the first half of the cave (pl. 1.7).

1.1.11. Großes Teufelsloch near Krögelstein/Franconian Alb, Bavaria

The cave Großes Teufelsloch is situated 1.5 km west of the village Krögelstein, 20 km east of Bamberg. The cave has been known for a long time, is only 26 m long and built by a small channel. Several Bärenschliffe are located in the first half of the cave, on the left and right cave wall (pl. 2.1), at a level of around 20 cm over the floor.

1.1.12. Kleines Höhlloch near St. Wolfgang/Franconian Alb, Bavaria

The cave is situated 110 m north of the village St. Wolfgang, 50 km southeast of Nuremberg. The cave is characterised by a 34 m long main channel and three lateral channels. All together the cave has a length of 113.50 m. Palaeontological and archaeological excavations were started at the end of the 19th century and ended in 1935. Several Bärenschliffe are located on the walls in the first half of the main channel and on the walls at the beginning oft first left lateral channel (pl. 2.2). The polished rock parts are always found on the upper part of the walls, between 30 and 50 cm over the floor.

1.1.13. Große Kuhsteinhöhle near Gößmannsberg/Franconian Alb, Bavaria

The Große Kuhsteinhöhle is situated on a slope of the Aufseß Valley, 1350 m east of the village Gößmannsberg, 20 km east of Bamberg. The cave opens with a huge entrance (12 m broad and 3.50 m high) and has a total length of 35 m. From a wide-open main part two smaller cave channels (a left and a right one) goes in a westerly direction. Bärenschliffe are located mainly on the left and right wall of the junction from the main cave part to the left lateral cave passage (pl. 2.3).

1.1.14. Geisloch near Oberfellendorf/Franconian Alb, Bavaria

The Geisloch is situated 500 m east of the village Oberfellendorf, 30 km northeast of Erlangen. The cave was discovered in 1972 and has a total length of 700 m (Teschner & Geyer, 1981). The essential part of the cave is a large, speleothem rich hall, from which eight lateral channels (between 20 and 50 m length) branch off in different directions. A Bärenschliff without any specific localisation in the cave (pl. 2.4) is shown in Rosendahl *et al.* (2000).

1.1.15. Breitenwinner Höhle/Franconian Alb, Bavaria

The cave is situated today in the central part of the military area "Hohenfels", 15 km northwest of the village Hohenfels and 45 km northwest of Regensburg. A visit to the cave is only possible with a special permit. Before closing the area for military use, the cave was in parts opened for the public. The oldest description of the cave is known from the 16th century (Hagen, 1892).

Bärenschliffe are mentioned by Hagen (1892) and Cramer (1931), without any specific localisation in the cave. One Bärenschliff is located in the first part of the main cave channel (pl. 2.5), on the right wall of a more narrow part (Lorenz, pers. comment).

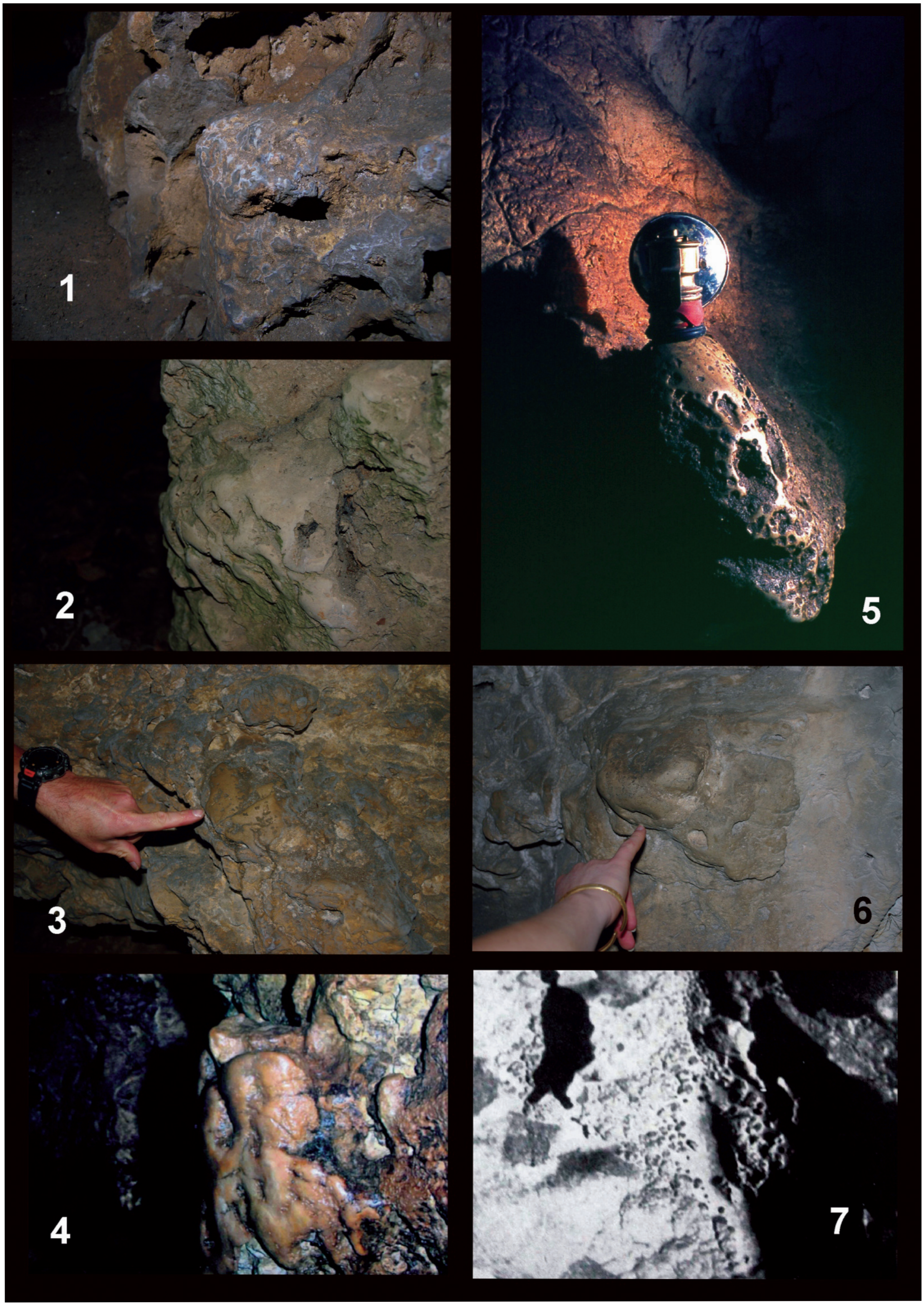
1.1.16. Obere Höhle in the Höhlenknock near Draisendorf/Franconian Alb, Bavaria

The Obere Höhle in the Höhlenknock (Höhlenknock in the local franconian dialect means irregular rock massif with caves) is situated 1225 m northeast of the village Draisendorf, 36 km northeast of Erlangen. The 67 m long tunnel like cave is built by a main channel with two lateral passages at the western side. The cave opens with three entrances. Several Bärenschliffe are situated on left and right wall of the lateral passage (pl. 2.6), which opens with the third entrance (the second smaller and higher entrance from the northern part of the Höhlenknock rock massif). The presence of Bärenschliffe in the cave is also mentioned by Kaulich & Hilpert (2005).

1.1.17. Petershöhle near Hartenstein, Bavaria

The Petershöhle is situated on the northeastern slope of a hill called Kreitsberg, 1 km northeast of the village Hartenstein and 40 km east of Erlagen. The total length of the cave is 110 m. Bärenschliffe are mentioned by Cramer (1931) and Huber (1967), without any specific localisation in the cave.

Plate 2



Bärenschliffe from different localities: 1. Großes Teufelsloch near Krögelstein, 2. Kleines Höhlloch near St. Wolfgang, 3. Große Kuhsteinhöhle near Gößmannsberg, 4. Geisloch near Oberfellendorf, 5. Breitenwinner Höhle, 6. Obere Höhle in the Höhlenknock near Draisendorf, 7. Mixnitzer Drachenhöhle. (Photos: W. Rosendahl, 1, 2, 3, 6. H. Schabdach, 4. G. Lorenz, 5. after Abel & Kyrle 1931, 7).

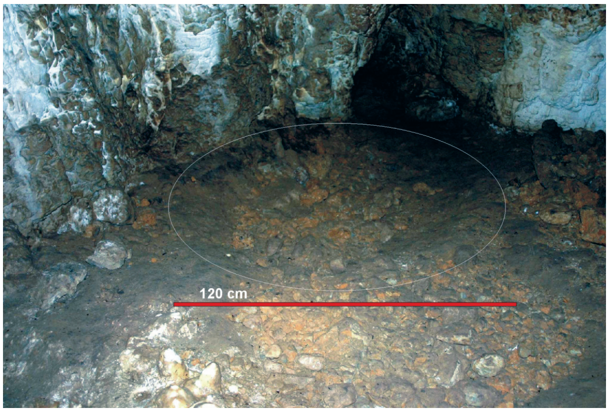


Figure 1. Bear den in the Jubiläumshöhle (Photo: W. Rosendahl).

Figure 2. Bear den in the Große Klingerberghöhle (Photo: B. Kaulich).

Figure 3. Scratch marks in the Neue-Laubenstein-Bärenhöhle (left: Photo W. Rosendahl) and in the Mixnitzer Drachenhöhle (right: after Abel & Kyrle, 1931).

1.1.18. Osterloch near Hegendorf, Bavaria

The Osterloch, a 66 m long cave, is situated 150 m north of the village Hegendorf, 40 km east of Nuremberg. Bärenschliffe are mentioned by Cramer (1931) and in the documents of the franconian cave register. After the documents Bärenschliffe are located in a narrow passage leading into the "speleothem chamber".

1.1.19. Bodenberghöhle near Neutras, Bavaria

The Bodenberghöhle is situated in the northeastern slope of a hill called Bodenberg, 850 m northeast of the village Neutras and 45 km east of Nuremberg. Bärenschliffe are mentioned in the 23.50 m long cave by Cramer (1931) and in the documents of the franconian cave register, without any specific localisation in the cave.

1.2. Bear dens

1.2.1. Neu-Laubenstein-Bärenhöhle, Chiemgau Alps, Bavaria

The Neue-Laubenstein-Bärenhöhle (NLB) is situated in the Laubenstein region in the Chiemgau Alps (Bavarian Alps), 100 km south of Munich (Rosendahl *et al.,* 2000). The cave was discovered in 1996 and has a total length of 120 m and maximum depth of 58 m. It is the first alpine cave bear bearing cave in Germany (Rosendahl & Darga, 2003). In the back part of the first hall are two oval depressions on the floor that are possibly bear dens. The cave floor is built by loam and limestone debris.

1.2.2. Jubiläumshöhle/Franconian Alb, Bavaria

The Jubiläumshöhle is situated on the left upper part of the Püttlach Valley, 1500 m northeast of the village Elbersberg, 36 km northeast of Erlangen. The cave was discovered in 1974 and is built mainly by one big hall with 40 m length, 11 m width and 9 m height. On several places of the cave, mostly close to the walls, round-oval hollows were observed (Auer, 1974). Some of them are today destroyed, but some can be still interpreted as bear dens (fig. 1).

1.2.3. Große Klingerberg Höhle/Franconian Alb, Bavaria

The Große Klingerberg Höhle is situated 1 km southeast of the village Berghausen, 30 km south of Amberg. The 230 m long cave was discovered in 1953 and consist of a lower and upper level (Leja, 1994). Baer dens are located only in the 55 m long horizontal lower level. Altogether eight bear dens with a round-oval form were observed in the loamy cave floor (fig. 2; Leja, 1999). The depth is

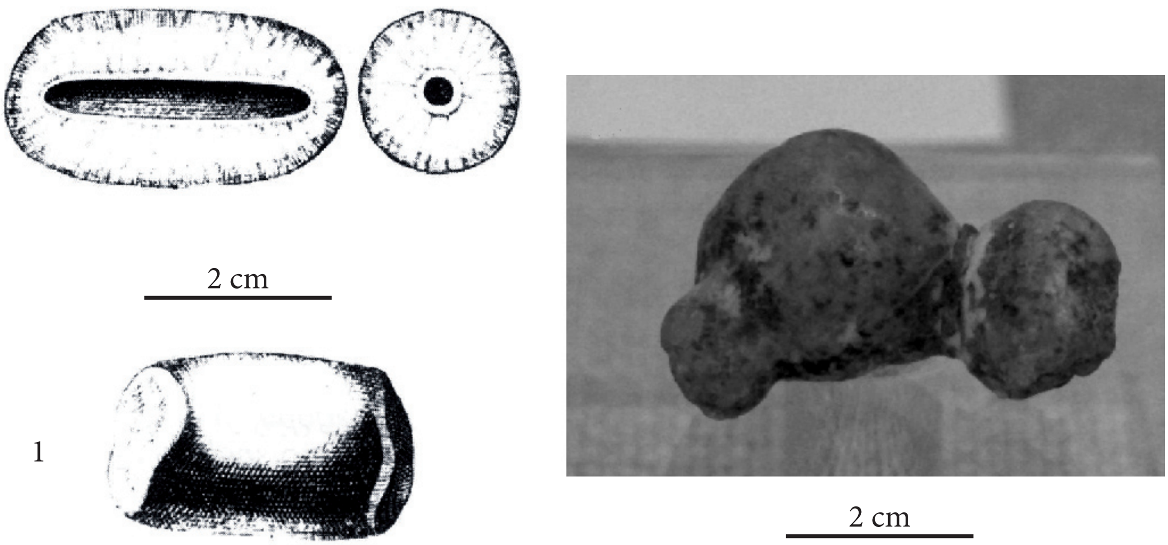


Figure 4. Kidney stones from the Bären- und Karlshöhle (left: after Rath, 1834) and from the Zahnloch (right: Photo W. Rosendahl).

between 20 and 25 cm, the diameters of the hollows are between 1.2 m and 2.5 m.

1.3. Scratch marks

1.3.1. Bären- und Karlshöhle/Swabian Alb, Baden-Wuerttemberg

For general cave informations see 1.1.6.

Scratch marks are located close to the Bärenschliff, direct behind the small connection passage between the Karls- and Bärenhöhle (Rathgeber, 2003).

1.3.2. Neu-Laubenstein-Bärenhöhle/Chiemgau Alps, Bavaria

For general cave informations see 1.2.1.

The scratch marks are in the first hall, close to the descent in the deeper part of the cave (fig. 3), around 1.5 m over the cave floor (Rosendahl *et al.,* 2000).

1.4. Kidney stones

1.4.1. Bären- und Karlshöhle, Swabian Alb, Baden-Wuerttemberg

For general cave informations see 1.1.6.

Already in the first description of the cave part of the Karlshöhle, written by C. Rath (1834), beside cave bears bones and teeth also rollers-shaped stones were described (fig. 4). In 1933 T. Edinger could prove, that the stones were biological in origin, which means kidney stones (Edinger, 1933). Today the whereabouts of the findings is unknown (Rathgeber, 2003).

1.4.2. Zahnloch near Steifling/Franconian Alb, Bavaria

For general cave informations see 1.1.9.

During the historical excavations in the cave also an unusually formed concretion was found. In 1997, Bausch *et al.* could prove by XRD-analyses, that the concretion is a kidney stone, probably from *Ursus spelaeus* (Bausch *et al.,* 1997). Today the find is displayed in the Fränkische Schweiz Museum in Tüchersfeld (fig. 4).

2. Austria

2.1. Bärenschliffe

2.1.1. Drachenhöhle near Mixnitz, Styria

The Drachenhöhle is situated in the Mur Valley near the village Mixnitz, 40 km north of Graz. The entrance is 20 m broad and 20 m high. The horizontal cave has a total length of 710 m and three huge rock falls divide it in four parts. The Drachenhöhle has been visited at least since the Middle Ages. The cave was excavated between 1919 and 1923 (Abel & Kyrle, 1931). The cave is well known because of the discovery of several thousands cave bear individuals during the excavations of the 10 m thick sediments.

Several Bärenschliffe are present in six different parts of the cave. They are located on cave walls and on several big blocks (pl. 2.7). After the first rock fall (“1. Versturz”), approximately 115 m from the entrance, the first Bärenschliff occurs. Bärenschliffe can be found even in the very back of the cave (“Ostergang”) (Abel & Kyrle, 1931).

2.1.2. Bockhöhle, Styria

The Bockhöhle is situated in the Mur Valley near the village Peggau, 24 km north of Graz. The cave has two entrances, is 101 m long and was rediscovered in 1967. Excavations took place in 1997 in the eastern part of the cave (Kusch, 1998). Five polished rock surfaces (maybe Bärenschliffe, see Kusch, 1998:29) are located in the main corridor, 35 m far from the entrance (Kusch, 1998; fig. 2).

2.1.3. Schottloch, Styria

The Schottloch is situated on the Plateau of the Dachstein Massif, near the village Haus im Ennstal, 70 km southwest of Salzburg. The narrow but 5 m broad entrance leads into two small rooms.

During the first scientific excavations in 1881 a Bärenschliff from the entrance wall was removed to widen the entrance. After Kraus (1881), it should be stored in the collections of the Geological Survey of Austria.

2.1.4. Bärenhöhle im Hartelsgraben, Styria

The Bärenhöhle im Hartelsgraben is situated in the western slope of the Schalenkogel, a part of the Gesäuse Mountains, southwest of Hieflau and 100 km northwest of Graz. The cave consists of three chambers whose first two are divided by a big rock fall (“Trümmerberg”). First scientific excavations took place in 1982 (Rabeder, 1997). Several Bärenschliffe are located on the right wall in the second chamber, directly after the big rock fall (G. Stummer, pers. comment).

2.1.5. Arzberghöhle, Styria

The Arzberghöhle is situated in the Salza Valley between the villages Wildalpen and Fachwerk, around 75 km northwest of Graz.

Several holes in the ceiling of the entrance chamber lead on one hand to the next higher cave system and on the other hand to the outside.

Mottl (1947) described Bärenschliffe from the centre of a narrow passage, which was blocked by rock fall. Several Bärenschliffe are also located in the back of the 278 m long cave system (G. Stummer, pers. comment).

2.2. Scratch marks

2.2.1. Drachenhöhle near Mixnitz, Styria

For general cave information see 2.1.1.

Scratch marks are located at the so-called “Färtenwand”, a part of the cave wall at the eastern side of the last big cave chamber (“Großer Dom”, Abel & Kyrle, 1931; fig. 3).

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ALPINE CAVE BEARS AND CLIMATE IN MARINE ISOTOPE STAGE 3

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Abstract: The Eastern Alps were covered with ice during the last glaciation (Würmian) but glaciers fluctuated and there was no constant ice cover all over the Alpine region. Direct dated cave bear remains document animals within the glaciated area of the Alps during the last glacial cycle. Ice-free conditions are assumed as a prerequisite for a visit of the cave. But no clear succession in time of faunal evidence and climatic conditions has been reconstructed so far. In this study direct dates from cave bears, Greenland Stadials and Interstadials and well defined pollen profiles from south and west of the Alpine arc are compared.

Key words: Alps, cave bear, pollen, climate, Greenland Stadials and Interstadials, ice extent.

INTRODUCTION

Terrestrial information about the Marine Isotope Stage (MIS) 3 is rare because the global Last Glacial Maximum (LGM) during MIS 2 eroded a lot of the evidence from MIS 3. Some pollen sites around the Alpine arc (fig. 1) display long palynological and climatic records covering MIS 3. The interpretation of these continuous pollen profiles offers a possibility to learn more about vegetational and climatic changes in the Alpine area.

Numerous cave fillings in and around the Alpine arc survived the erosion during the LGM as well. Cave bears were the most abundant species in these caves accompanied by a few additional faunal elements, mainly carnivores such as wolves and cave lions. Some of the sites even lie in high alpine areas up to an elevation of 2750 m a.s.l. Direct dates place the remains mainly in MIS 3. Ice-free conditions seem to be a prerequisite for the visit of distinct caves but little is known about the ice extent during MIS 3 (van Husen, 2000). Eleven well dated cave sites (tab. 1) from France, Italy, Slovenia, and Austria are compared to define well continuous pollen sites spanning MIS 4 to MIS 2 in order to understand more about cave bear distribution and climatic conditions during MIS 3.

METHODOLOGY

3-D reconstructions of the LGM ice cover and entrances of the cave sites will act as starting points for modelling of ice fluctuations during the last glacial cycle including MIS 3. For the 3-D reconstruction of the ice cover a triangular irregular network (TIN) data model is created from the digitised point data of the mapped features and digitised contour lines of the map published by van Husen (1987) using the GIS program ArcGIS. The TIN surface model is converted to a grid-based model in order to compare this model with the grid-based digital elevation model (DEM) of the present land topography. Examples of the spatial situation of cave entrances in comparison with the ice are provided in fig. 2 and 3.

Data from several caves were compiled in Tab. 1:

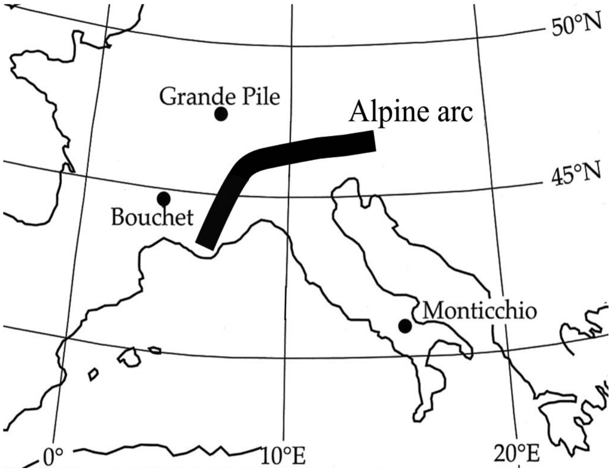

Figure 1. Sites with continuous pollen profiles in the west and south of the Alpine arc (modified after van Andel, 2003:12).

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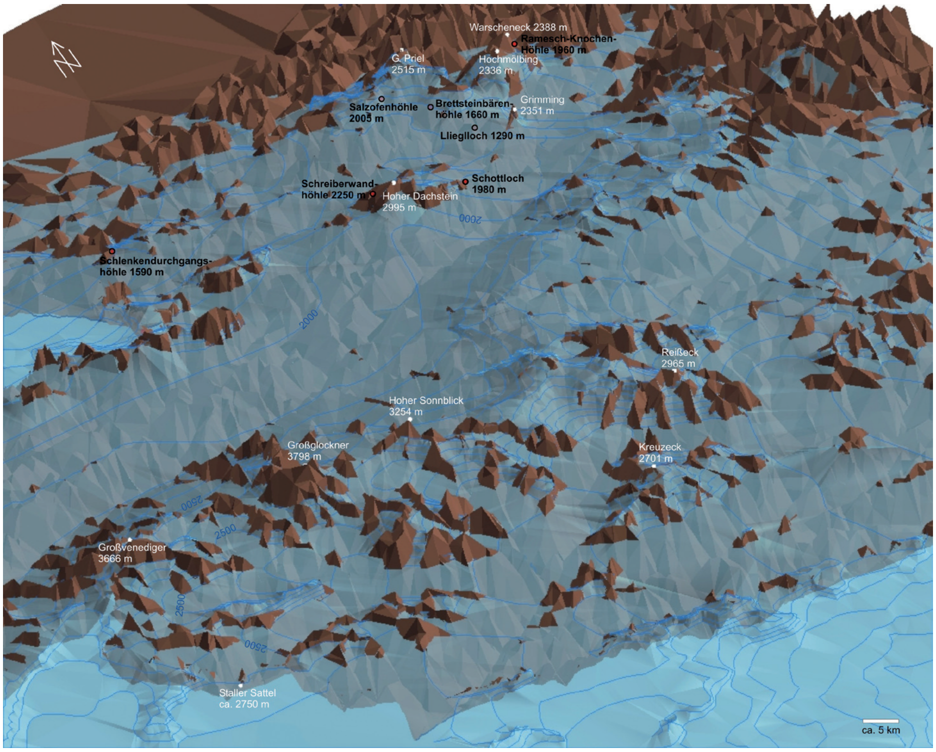

Figure 2. A 3-D reconstruction of the LGM ice elevation in the Eastern Alps and position of selected cave bear sites (digitised after van HUSEN, 1987). Contour lines of ice elevation have the equidistance of 100 m. The Enns valley is visible in the middle of this illustration (compare fig. 3).

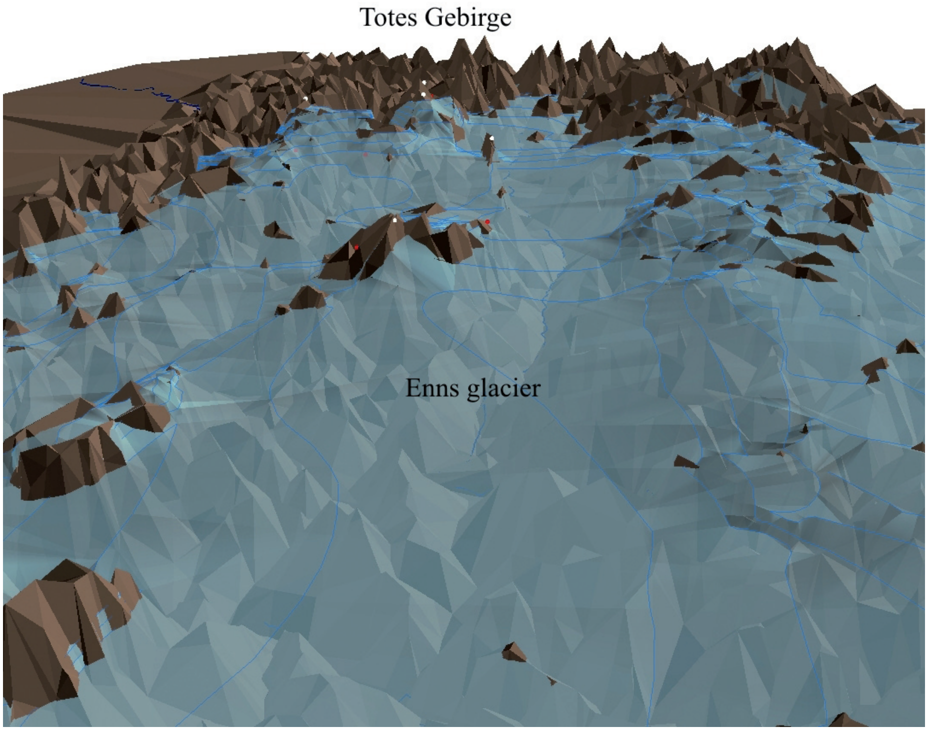

Figure 3. View of the Enns valley towards Totes Gebirge in the north-east of the Alps. The position of most of the caves of Totes Gebirge is very close to the border of the Alpine glaciation during LGM. The nunatak in the middle of the reconstruction is the Hohe Dachstein (2995 m), with the red dots indicating Schottloch and Schreiberwandhöhle (compare fig. 2).

Table 1

Direct radiocarbon dates of cave bear samples from selected cave sites [dates after Blant et al. (2004), Morel *et al.* (1997), Pacher (2003), Philippe (2003), Rabeder *et al.* (2005)]. Palaeoclimate information from Greenland after Rousseau *et al.* (2006) showing the synchronicity of the data to Greenland Stadials (GS) or Greenland Ínterstadials (GIS); in brackets the range of the data considering the period of the error.

	Site	**a.s.l.**	**Lab.no**	**Dates**	**CalPal**	**Palaeoclimate**
F	Balme à Collomb	1700	OxA-3946	24160+/-370	29111+/-528	GS4 (GIS4-GS4)
CH	Bärenloch	1645	ETH	26520+/-240	31057+/-169	GS4
A	Lieglloch	1290	VERA-2184	26390+/-110	31017+/-141	GS4
A	Gamssulzen	1300	VRI-1159	25090+/-640	29887+/-675	GS4
A	Gamssulzen	1300	Hv-16893	25965+/-780	30552+/-605	GS4
SI	Potocka zijalka	1700	Beta-143240	26900+110/-100	31257+/-102	GS4
A	Gamssulzen	1300	Hv-16892	27520+/-645	32358+/-897	GIS5 (GS4-GS5)
A	Ochsenhalt	1660	VERA-2191	28370+/-140	32956+/-657	GS5 (GIS5-GIS6)
A	Lieglloch	1290	Ua-15978	28130+/-600	32846+/-979	GS5 (GS4-GS6)
SI	Potocka zijalka	1700	GrN-23501	29130+570/-530	34001+/-922	GS6 (GS5-GIS7)
SI	Potocka zijalka	1700	VERA-0659	29310+750/-250	34083+/-1086	GS6 (GS5-GIS7)
SI	Potocka zijalka	1700	GrN-23500	29600+/-290	34798+/-438	GIS7 (GS6-GIS7)
SI	Potocka zijalka	1700	VERA-0661	29810+/-270	35070+/-372	GIS7 (GS6-GIS7)
SI	Potocka zijalka	1700	VERA-0660	30980+330/-310	36099+/-361	GS7
SI	Potocka zijalka	1700	VERA-2194	31730+210/-200	36692+/-270	GS7
CH	Frueteli	1775	ETH-14476	31740+/-430	36829+/-523	GS7 (GS7-GIS8)
A	Ramesch	1960	Beta-157670	31140+/-310	36320+/-332	GS7
CH	Frueteli	1775	ETH-11357	33140+/-420	38265+/-770	GIS 8 Denekamp (GIS8-GS8)
A	Gamssulzen	1300	VRI-1226	31500+1300/1100	37009+/-1567	GIS8 Denekamp (GIS7-GIS8)
A	Gamssulzen	1300	Beta-157659	32190+/-330	37691+/-853	GIS8 Denekamp (GS7-GIS8)
A	Gamssulzen	1300	Beta-157660	32010+/-320	37408+/-755	GIS8 Denekamp (GS7-GIS8)
A	Gamssulzen	1300	VRI-1228	34300+2400/-1900	39223+/-2243	GS8 (GS7-GIS10)
A	Ramesch	1960	VRI-776	34900+1800/-1500	39762+/-1851	GS8 (GIS8-GIS10)
A	Lieglloch	1290	VERA-2185	33500+/-240	38506+/-888	GS8 (GIS7-GS8)
SI	Potocka zijalka	1700	GrN-22335	35720+650/-600	40996+/-910	GS9 (GS8-GIS10)
A	Ramesch	1960	VRI-792	37200+1900/1600	41760+/-1703	GIS10 (GS8-GIS11)
A	Ochsenhalt	1660	VERA-1601	36240+670/-620	41671+/-503	GIS10 (GS9-GS10)
A	Gamssulzen	1300	VRI-1227	3800+3300/-2300	42163+/-2879	GS10 (GS8-GIS12)
A	Gamssulzen	1300	VRI-1326	3800+2000/-1900	42552+/-1515	GS10 (GS9-GS11)
A	Gamssulzen	1300	Beta-157661	37310+/-580	42380+/-357	GS10
A	Ochsenhalt	1660	VERA-2190	39620+500/-470	43657+/-568	GIS11 (GIS11-GS11)
A	Gamssulzen	1300	Beta-157664	41060+/-920	44715+/-958	GS11 (GIS11-GIS12)
A	Ochsenhalt	1660	KIA-25283	42290+970/-870	45886+/-1198	GIS12 Hengelo (GS11-GIS12)
A	Ramesch	1960	Beta-143242	43610+/-1800	47222+/-2066	GIS12 Hengelo (GIS12-GIS13)
A	Ramesch	1960	Beta-157667	43700+/-1270	47169+/-1771	GIS12 Hengelo (GIS12-GS12)
A	Gamssulzen	1300	KIA-25287	44160+1400/-1190	47547+/-1876	GIS12 Hengelo (GIS12-GIS13)
I	Conturines	2750	Beta-143246	44260+/-900	47532+/-1638	GIS12 Hengelo (GIS12-GS12)
A	Gamssulzen	1300	Beta-157662	44400+/-1380	47742+/-1893	GS12 (GIS12-GIS13)
A	Gamssulzen	1300	Beta-157663	45410+/-1560	48863+/-2285	GS12 (GIS12-GS13)
A	Gamssulzen	1300	Beta-157665	47300+/-1970	50791+/-2685	GS13 (GS12-GS14)
A	Ramesch	1960	Beta-157669	47600+/-2060	51053+/-2696	GS13 (GS12-GIS14)
A	Brieglersberg	1960	VERA-2857	49700+2400/-1800	53069+/-2882	GIS 14 Glinde (GS13-GIS15)
A	Ramesch	1960	Beta-143241	49520+/-1600	52802+/-2207	GIS 14 Glinde (GS13-GIS14)

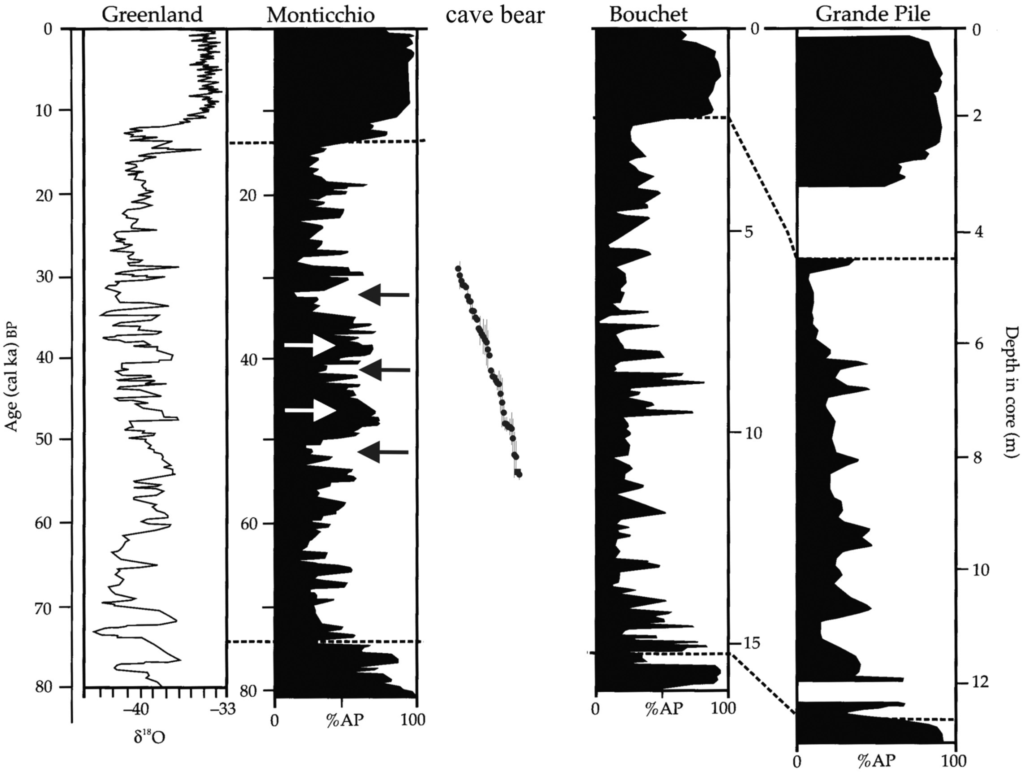

Figure 4. Comparison between calibrated cave bear dates from table 1 and arboreal pollen distribution in the profiles Monticchio, Bouchet and Grande Pile (modified after van ANDEL, 2003:14). Severe changes in the vegetation pattern of Italy (white arrows - increase in arboreal pollen, black arrows - strong decrease) are not reflected in the cave bear occurrence of the Alpine region.

Conturines cave (11°60′/46°63′50′′), Potočka zijalka (14°40'/46°26'), Gamssulzenhöhle (14°17′52′/47°40′56′′), Ramesch-Knochenhöhle (14°15′/47°39′), Ochsenhalt cave (14°10′/47°50′), Brettsteinbärenhöhle (13°59′/47° 37′19"), Brieglersberg (14°03′07′′/47°37′12′′), Liegl-loch (14°/47°34′23′′), Frueteli (8°26′/46°76′), Bärenloch (7°24′ 40′′/46°58′10′′), and Balme à Collomb (5°/45°).

On the base of ROUSSEAU *et al.* (2006) cave bear dates and GRIP events are compared. In addition, the calibrated dates are compared to data from continuous pollen sites south and west of the Alps. Together with considerations of the circulation pattern during the last glacial cycle a picture of the climatic situation during the cave bear occurrence in high Alpine areas is attempted.

RESULTS

The glacier extent as reconstructed by van HUSEN (1987) for the LGM is illustrated in figure 2. Some of the cave sites entrances have been covered by LGM ice, e.g. Brettsteinbärenhöhle, Salzofenhöhle, Liegloch. Other caves, like Ramesch-Knochenhöhle, were never covered by ice, not even during the high stand of the last glacial cycle, the LGM.

Dates are calibrated using CalPal (http://www.calpal.de), and then sorted according to Greenland Stadials (GS) and Greenland Interstadial (GIS) after ROUSSEAU *et al.* (2006). The ranges of the dates lie between GS 4 to GIS 14. Taking the dates without error 26 samples date into a GS (60,5 %) and 17 samples fall into a GIS (39,5 %). Considering the error range, only 9 samples date completely into a GS while 34 samples are indifferent.

Severe vegetational changes are indicated in the profiles from Monticchio, Bouchet and Grande Pile (fig. 4). Cave bear distribution in the Alpine region does not follow this pattern. Their occurrence seems to be independent of the vegetational and climatic fluctuations indicated in the pollen profiles to the south and in the west of the Alps.

In figure 5 an assumed pattern of winter atmospheric circulation during the LGM is presented. It seems that the transport of moisture towards the Alps comes mainly from the Mediterranean Sea because of a very southern position of the polar front (FLORINETH, 1998). For other

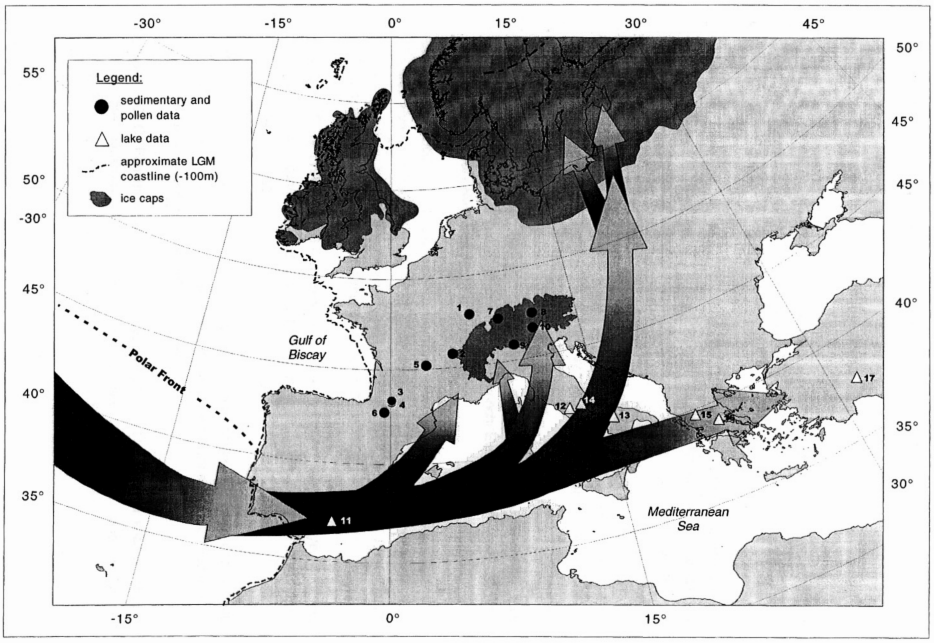

Figure 5. Sketch map of Europe during the LGM with the assumed characteristics of the winter atmospheric circulation pattern. Locality 1 - Grande Pile, locality 13 - Monticchio (from Florineth, 1998).

periods of the last glacial cycle, like stage 3 more westerly transport directions can be assumed. The selected pollen profiles to the south and west of the Alps (Grande Pile, Bouchet, Monticchio) are lying in the main transport direction of moisture during stage 3 and 2. Thus, it seems to be unlikely that the high Alpine climate around the cave bear sites was independent of conditions reflected in these pollen profiles.

CONCLUSION

The calibrated dates of the cave bear occurrences point to a more or less even distribution (60% to 40%) over the periods of Greenland Stadials and Interstadials. Considering the whole error ranges of the dates clear statements concerning correlations especially to the very short interstadials are not possible. The comparison of the pollen profiles and the cave bear occurrences seems to confirm the cave bear distribution over stadials and interstadials. There is no correlation between the severe vegetation changes in the profiles of Monticchio, Bouchet and Grande Pile and the occupation of the high Alpine region by cave bears.

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HUMAN MODIFICATIONS ON CAVE BEAR BONES FROM THE GARGAS CAVE (HAUTES-PYRÉNÉES, FRANCE)

Carole VERCOUTÈRE[1], Cristina SAN JUAN-FOUCHER[2] & Pascal FOUCHER[3]

Abstract: In this paper, we are going to examine seven cave bear remains modified by prehistoric men. These remains come from the Aurignacian and Gravettian levels of the Gargas Cave (Hautes-Pyrénées, France). They were discovered during the excavations carried out by H. Breuil and E. Cartailhac from 1911 to 1913. One Aurignacian artefact and three Gravettian objects were unpublished and other pieces were only briefly described in the 1958 publication (Breuil & Cheynier, 1958). These osseous artefacts allow us to discuss the status of *Ursus spelaeus* for the Aurignacian and Gravettian human populations, which lived in the Gargas Cave.

Key words: *Ursus spelaeus*, modified remains, bear status, Gargas Cave, Aurignacian, Gravettian.

INTRODUCTION

The site of Gargas (Aventignan, Hautes-Pyrénées, France) is located in the centre of the Pyrenean piedmont (fig. 1) at the same distance from the Mediterranean zone (to the east), the Atlantic one (to the west) and the Périgord (to the north).

It's a cave that became famous for its painted hands, discovered 100 years ago. The studies about the Gargas Cave are a part of a collective research project, which deals with the Gravettian-Solutrean complex in the Pyrenees. It includes multidisciplinary studies on the archaeological material from old collections (Breuil & Cheynier, 1958; San Juan-Foucher, 2003; 2004; Foucher, 2004; San Juan-Foucher & Vercoutère, 2005) and from new excavations in order to:

- elaborate a detailed chronostratigraphic sequence that takes the palaeoenvironmental data into account;
- obtain a better characterization of the regional lithic and bone industries;
- understand the relations between rock art and settlement levels (Foucher & San Juan, 2004; Foucher, 2006).

The bottomset clay bed of Gargas (older than the Mousterian level; fig. 2) is rich in cave bear remains. The cave was then a den for bears that came there to hibernate. Over the centuries, these carnivores left some traces: wallows, claw marks on the walls and polishing of certain narrow ways. During the Upper Palaeolithic, Man and carnivore have alternately lived in the cave. Sometimes, the former used the remains of the latter as raw material.

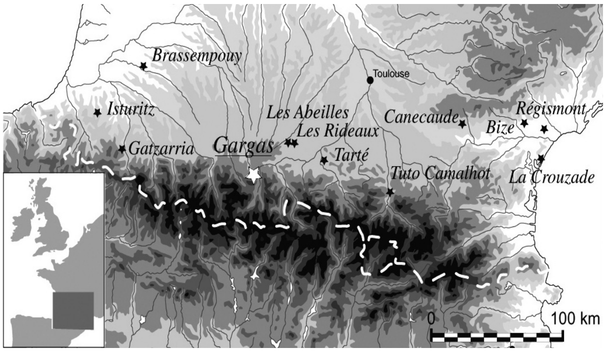

Figure 1. Geographical localisation of the Gargas Cave (Hautes-Pyrénées, France; star) and of the other Aurignacian and Gravettian sites of the Pyrenean piedmont (Map background: F. Tessier; Data: P. Foucher).

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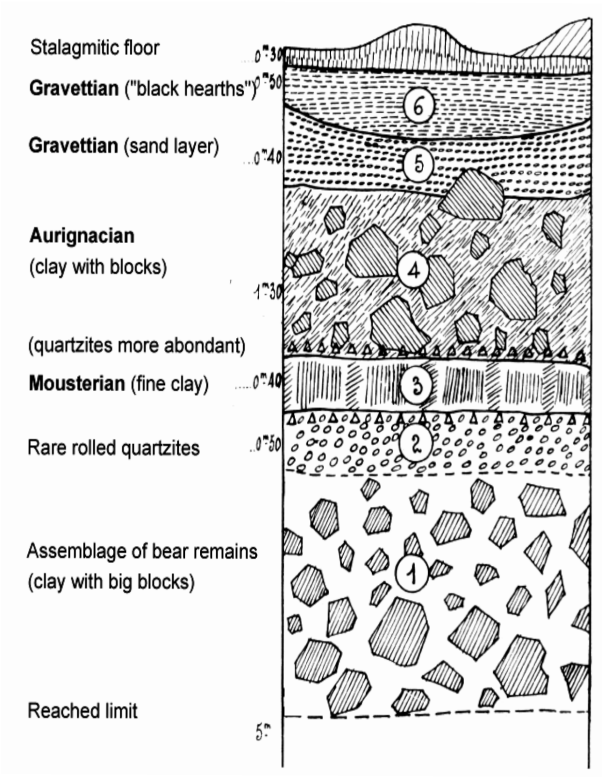

Figure 2. Stratigraphic sequence (after Breuil & Cheynier, 1958).

Moreover, there is a stalagmitic concretion in the lower part of the cave, the form of which takes on a bear, hence the name of the "Salle de l'Ours". Therefore, everyone understands the special status of the cave bear, both for the prehistoric men and for the prehistorians who studied and are still studying this famous Pyrenean cave.

MODIFIED CAVE BEAR REMAINS

The archaeological material from the old excavations composes the Breuil-Cartailhac collection, which is retained at the Institute of Human Palaeontology (Paris) and at the Toulouse Museum of Natural History.

We have one radiocarbon (AMS) date for the Early Aurignacian level: 31 540 BP ± 720 (GRA-19731/Lyon 1624; Foucher, 2004) got from a fragment of a *Bos*/*Bison* long bone. Also, two radiocarbon (AMS) dates are available for the Middle Gravettian level:

- 26 860 BP ± 460 (Clottes *et al.,* 1992) obtained from a piece of bone pushed into a crack of the "Panneau des Mains" in the main chamber;
- 25 050 BP ± 170 (GRA-19506/Lyon 1625; Foucher, 2004) taken from a reindeer antler fragment.

The osseous artefacts from the Breuil-Cartailhac collection are studied by two of us (C. V. for the Aurignacian objects and C. S. J. - F. for the Gravettian ones). Among these pieces, seven correspond to *Ursus spelaeus* remains modified by prehistoric men:

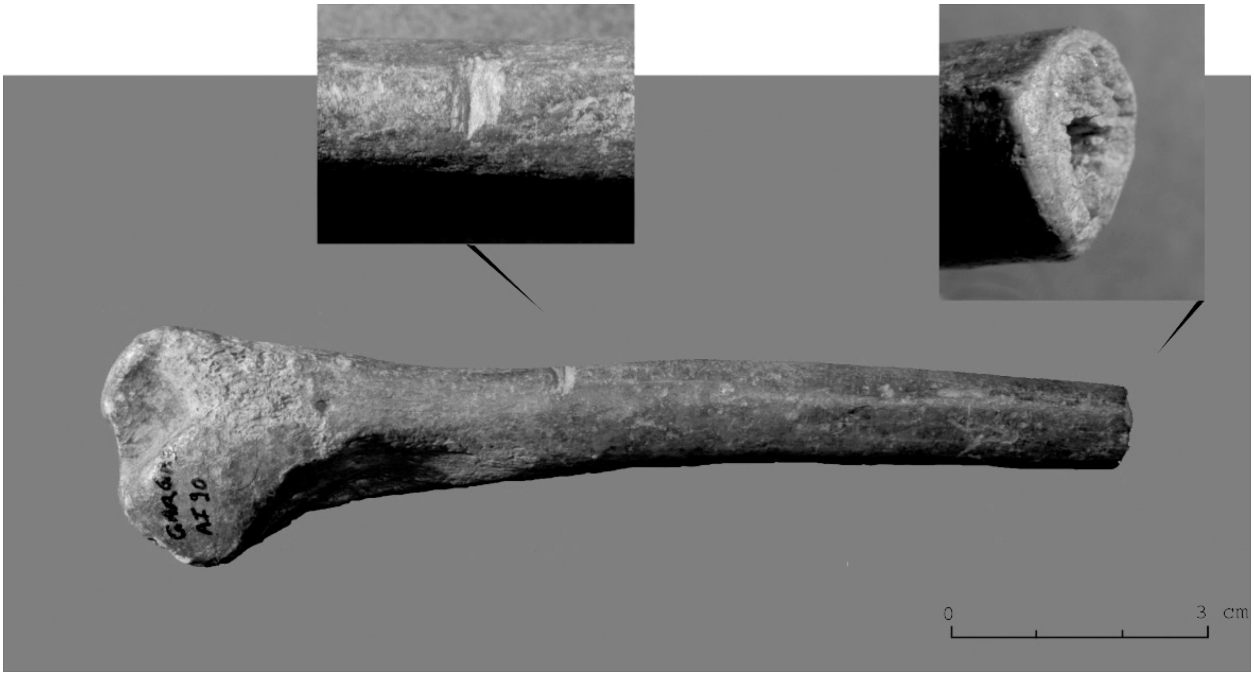

Figure 3. Gargas, Aurignacian level - Cave bear fibula sawn by prehistoric men: IPH-90 (Breuil & Cheynier, 1958, p. 359, Pl. VIII, 90), distal part of a left fibula with the same red patina as *Ursus spelaeus* bones from the bottomset clay layer (Pictures: P. Foucher, 2006).

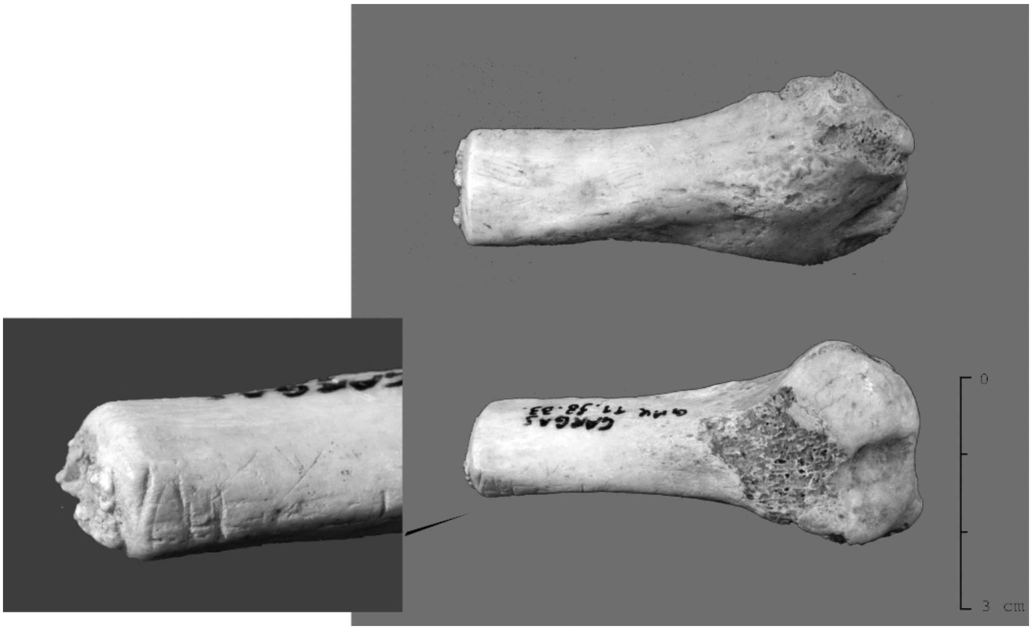

Figure 4. Gargas, Aurignacian level - Cave bear fibula sawn by prehistoric men: MHNT 99.38.33 (Breuil & Cheynier, 1958, p. 361, Pl. IX, 112), distal part of a left fibula with cutmarks probably due to the "cleaning" of the bone to make the sawing easier (Pictures: P. Foucher, 2006).

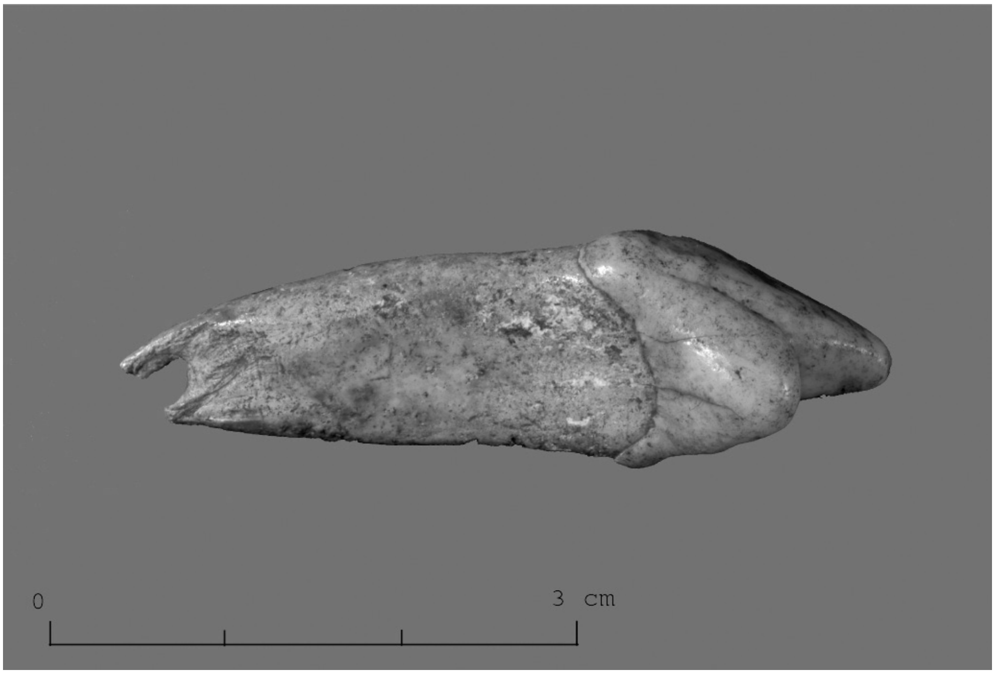

Figure 5. Gargas, Gravettian level - Cave bear tooth modified by prehistoric men: IPH-298 (Breuil & Cheynier, 1958; p. 378, Pl. XVIII, 298), pierced lower left third incisor (Picture: P. Foucher, 2006).

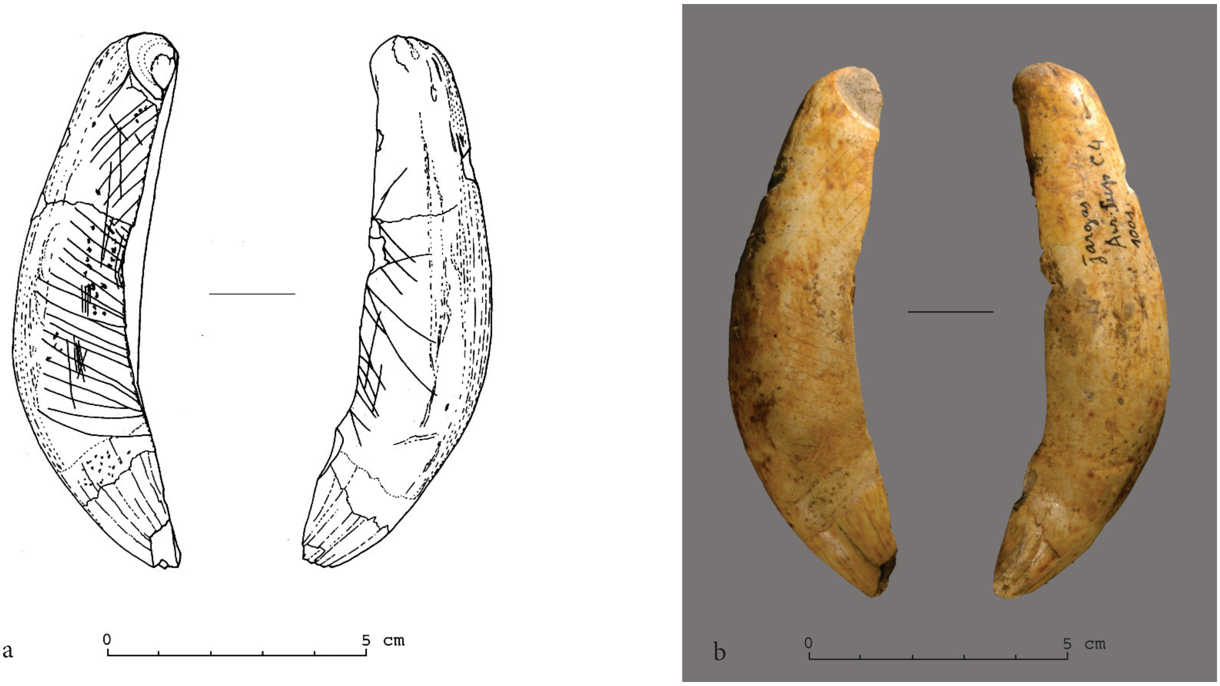

Figure 6. Gargas, Gravettian level - Cave bear tooth modified by prehistoric men: a & b IPH-1001, engraved canine longitudinally split (Drawings: C. San Juan-Foucher; Pictures: P. Foucher, 2006).

Figure 7. Gargas, Gravettian level - Cave bear tooth modified by prehistoric men: IPH-1778, canine with elongated impact scars resulting from knapping (Pictures: P. Foucher, 2006).

Figure 8. Gargas, Gravettian level - Cave bear tooth modified by prehistoric men: IPH-1787, canine with man-made striae (Pictures: P. Foucher, 2006).

- three Aurignacian fibulas were sawn and seem to be blanks for tubes or tubular beads (fig. 3 & 4);
- four Gravettian teeth were also used: one incisor served as a pendant (fig. 5), one engraved canine (fig. 6), one canine with elongated impact scars resulting from knapping (fig. 7), one canine with man-made striae (fig. 8).

Furthermore, the taphonomic study allowed us to point out at least two origins for the Aurignacian artefact blanks. One of the fibulas (IPH-90; fig. 3) has the same red patina as the *Ursus spelaeus* bones from the bottom-set clay layer (fig. 2), where it was probably picked up by the Aurignacian before being modified (note that the sawing marks have not the same red colour as the surface of the bone). The fibula MHNT 99.38.33 (fig. 4) doesn't present this red patina but seems to come from a more recent bear carcass. Its distal shaft shows cutmarks probably due to the "cleaning" of the bone to make the sawing easier.

CONCLUSION

We have never observed any cutmarks on *Ursus spelaeus* bones that could give us some clues about the consumption of bear meat by Aurignacian and/or Gravettian men from the Gargas Cave. Indeed, the majority of bear remains from both levels (Aurignacian and Gravettian) corresponds with bones and teeth picked up by prehistoric men on the carcasses of the carnivores that had died there of natural causes for a more or less long time. The only remains voluntarily modified by men are those that served as raw material for the manufacture of seven objects. Because of the artefact small number and the nature of the osseous objects (six pieces linked with adornment and also one utilitarian tool), we are not able to put forward any hypothesis about the exact status of cave bear either for the Aurignacian or for the Gravettian human settlements.

The 2005 excavations near the cave entrance provided two fragments of Gravettian cave bear crania (Foucher & San Juan, 2005). These crania wear some impact marks that prove a breakage by prehistoric men, who might have taken the front part of these heavy bones with teeth and especially canines served as raw material. Therefore, the continuation of the old collections studies and the analysis of the material from the recent excavations should give us more information about the "image" of this impressive carnivore for the Aurignacian and Gravettian populations that lived in the Gargas Cave.

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ABRI CASTANET (DORDOGNE, FRANCE): AN AURIGNACIAN SITE WITH BEAR PROCUREMENT. BEAR EXPLOITATION IN PALEOLITHIC TIME

Dominique ARMAND[1]

Abstract: The abri Castanet is located in Sergeac (Dordogne, France). At the beginning of the last century, the Abri Castanet was excavated by Peyrony who described 2 Aurignacian levels (Peyrony, 1935). The first one stands on the bed-rock and shows split based points and has been attributed to the Aurignacian 1 by Denis Peyrony. The examination of this material at the Musée National de Préhistoire in les Eyzies (France) allowed us to discover the existence of a bear phalanx with cutmarks. So the Abri Castanet can be considered as a new site with butchery marks on bear remains, which add to the about thirty examples known. When we examine these sites in literature, it seems that different bear procurement modalities can be shown.

Key words: Bear exploitation, Castanet site, Aurignacian, Upper Pleistocene, Southwestern France.

PRESENTATION OF THE SITE

Abri Castanet is located in Sergeac (Dordogne, France), at the bottom of a cliff by the Vézère River. It is one of a series of such sites that includes the Abri des Merveilles, the Abri Blanchard, and la Souquette.

The Abri Castanet stands on a bedrock terrace. Before the first excavations, it was covered by large limestone blocks. In the nineteen thirties, the site was excavated by Peyrony, who described two Aurignacian levels (Peyrony, 1935).

On top, was an Aurignacian II level that contained a lithic industry with blades, notches, scrapers, and burins, a poor bone industry with flattened lozenge-shaped points and awls, and engraved limestone blocks. Faunal remains were rare. Reindeer dominated, followed by horse, bovids, wolf, fox, and brown bear.

Below this, resting on bedrock, an Aurignacian I level yielded a blade industry very rich in scrapers and poor in burins, with a number of other tool types. At this level, the fauna was dominated by reindeer and included roe deer, horse, bovids, deer, wild boar, ibex, lion, hyena, wolf, fox, wild cat, lynx, brown bear, and seal. Harlé made the identification of brown bear on the basis of a canine (peyrony, 1935).

During recent work for the new museum project at the Musée National de Préhistoire in les Eyzies, Stéphane Madeleine discovered a bear phalanx with cut marks in the Castanet Aurignacian I collection. In collections from recent excavations (by Pellegrin and White) there are no bear remains (J.-C. Castel, personal communication).

FAUNA FROM THE AURIGNACIAN I (PEYRONY COLLECTION)

The remains consist of primarily of teeth, of the ends of long bones, and of small bones. There are only a few shaft fragments. There was probably a selection made during excavations. Some of the remains mentioned by Peyrony (1935) are absent from the Musée National de Préhistoire collections, such as the canine of *Ursus arctos,* and there are no remains of lynx nor of wild cat.

BEAR IN THE AURIGNACIAN I COLLECTION

There are four specimens of bear in the Aurignacian I: a fragment of a canine, an upper second molar, and two first phalanges.

The upper M2 has an almost straight mesio-distal axis, while this axis is curved in the cave bear (Prat &

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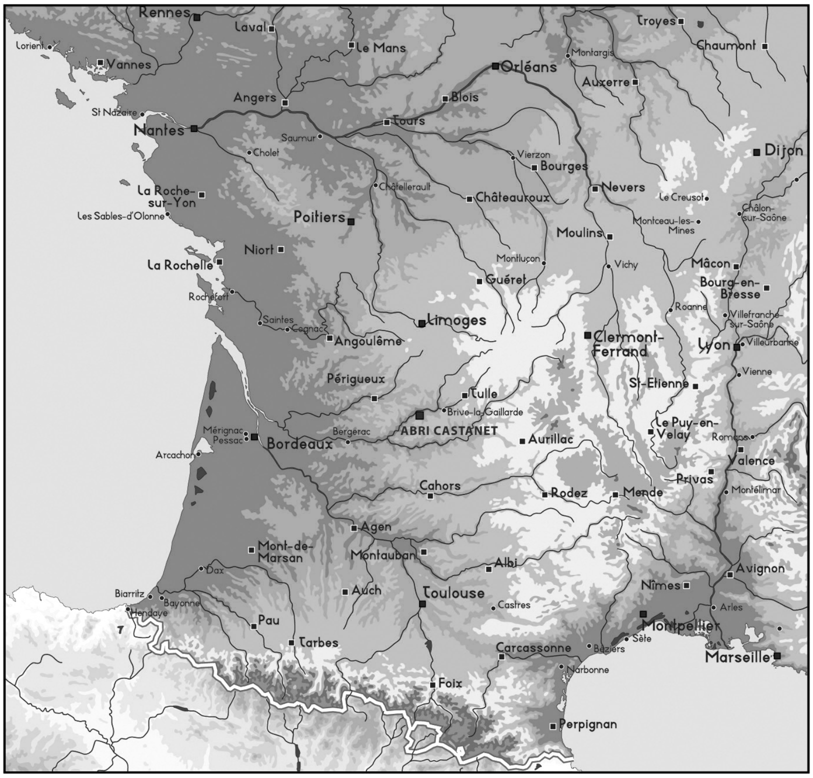

Figure 1. Map of France with the location of the abri Castanet.

THIBAULT, 1976). The distal part is small with a limited number of reliefs (fig. 2), and it is smaller than the upper M2 of the cave bear studied by PRAT & THIBAULT (*op. cit.*).

The *Ursus arctos* M^2 measured by TORRES (1984) have mesio-distal diameters ranging from 20 to 42 mm, with values peaking between 34 and 36 mm, while the mesio-distal diameters of cave bear are greater than 38 mm. Thus, on both morphological and biometric grounds, this tooth can be assigned to *Ursus arctos*. It displays one particularity, a supplementary cusp on the mesio-buccal side just above the base of the crown (fig. 2).

It should also be noted that this tooth served as an ornament - the distal root was perforated.

The dimensions of the first phalanx, which bears cut marks, are shown in tab. 3 (the height cannot be measured because of heavy erosion of the edges). It is difficult to determine the species on the basis of dimensions of the first phalanx. The data provided by TORRES (1984) overlap for *Ursus spelaeus* and *Ursus arctos,* and our specimen stands in the overlapping area. This specimen seems to be rather slender and may therefore belong to a brown bear.

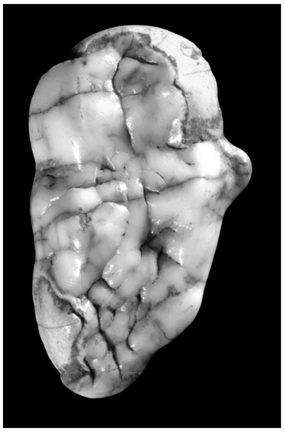

Figure 2. *Ursus arctos*: Second upper molar, occlusal view (photograph by P. Jugie, MNP, les Eyzies, France).

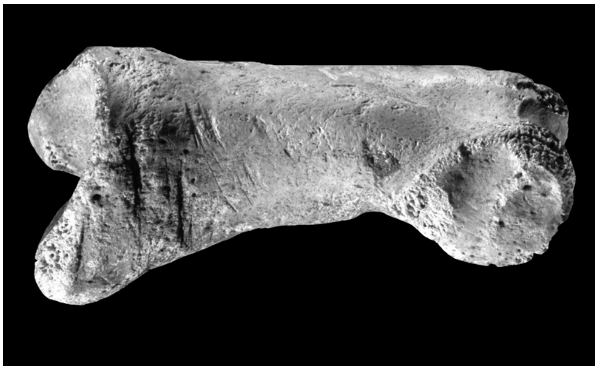

Figure 3. *Ursus arctos:* cut marks on the first phalanx (photograph by P. Jugie, MNP, les Eyzies, France).

Table 1
Faunal data from the Aurignacian I, Abri Castanet.

Taxon	NISP
Crocuta spelaea	1
Canis lupus	52
Vulpes/Alopex	15
Ursus sp.	4
Cervus elaphus	7
Rangifer tarandus	336
Rupicapra rupicapra	2
Capra ibex	1
Bovinae	16
Equus sp.	32

Table 2
Ursus sp. Measurements of the second upper molar.

	Mesio-distal diameter (1)	Bucco-lingual diameter (2)	2/1
Castanet	35.2	20.8	59.09
Ursus spelaeus	75		75
Prat & Thibault, 1976	37.5-52		47.3-58.2
	44.95+/-0.65		51.82+/-0.53

Table 3
Ursus sp. Measurements of the first phalanx.

Ph 1	Proximal transversal diameter	Proximal antero-posterior diameter	Minimum transversal diameter	Distal transversal diameter
Castanet	21.8	18.6	14.2	16.7

The cutmarks (fig. 3) are located on the dorsal face and on one lateral face of the first phalanx described above. Some are superficial, but most are very deep. These marks indicate use of the hide. In general, carnivore hides are usually taken at the beginning of winter, when they are at their best.

This gives no idea of the way in which the bears were used, and it is more or less impossible here to make such a determination. Given the small number of remains, one may surmise that this was not the place where the animal died, nor even the location where the carcass was processed.

EXPLOITATION OF BEARS IN THE PALEOLITHIC

The site of Castanet can be added to the list of paleolithic sites yielding evidence for the exploitation of bears (Armand *et al.*, 2004).

Up until recently the exploitation of bears in the Paleolithic had been denied, however most researchers now agree that bears were indeed occasionally used by prehistoric populations (Fosse *et al.,* 2002; Auguste, 2003; Quilès, 2003 and 2004).

Stiner (1994) has suggested a predation model based on ethnographic observations of Native American Indians: according to her, prehistoric groups may have also opportunistically collected bears during the first stages of hibernation.

Pacher (2000) *in* Münzel & Conard (2004) analyzing ethnographic data on bear hunting since the 17th century shows also that winter was generally the favoured season for hunting bears.

The archaeological data does not always allow determining the mode and season of procurement. For Stiner *et al.* (1996), on a hibernation site it is taphonomically difficult to distinguish between attacks on a living bear from those on an already dead animal. But, if the animal's skin was removed, then this means that the bear died very shortly before being skinned, either because it was killed or because scavenging took place not long after its death. It was probably a planned activity that took place during denning time. However in the case of meat and marrow extraction, the timeframe for consumption is not strictly fixed, as it depends on taste preferences and food tolerance which cannot be known today. And we can have any certitude about the strategy and the period of procurement. Additionally, remains of young individuals may also indicate the season.

We have surveyed zooarchaeological studies which deal with bear procurement in order to find any patterns in the available data which may confirm this scenario and be used to elucidate the reasons behind such exploitation.

BEARS AS RESOURCES

Cutmarks interpreted as representing the removal of the animal's skin were found on cranial fragments at Höhle Fels (Münzel & Conard, 2004), on a mandible at Madonna dell' Arma (Quilès, 2003), and at Taubach (Bratlund, 1999), and on a skull and mandible at Biache-Saint-Vaast (Auguste, 1995).

Striations observed on a patella from the Aurignacian levels at Arcy have been interpreted as the result of a skinning process (or disarticulation) (David & Poulain, 2002).

In the carpal region, marks found on a pisiform at Goyet (Germompré & Sablin, 2001), and on a pyramidal at Badalucco (Quilès, 2003) are interpreted as being tied to a skinning activity, while Bratlund (1999) hesitates between meat processing and skinning for the marks found on a pisiform at Taubach.

With regards to evidence from the tarsals, the only indication is of a calcaneum at Taubach (Bratlund, *op. cit.*).

Marks found on metapodials are more frequent: there is mention of them at Biache-Saint-Vaast (Auguste, 1992), at Goyet (Germompré & SABLIN, 2001), at Arcy (Roblin-Jouve, 2002; David & Poulain, 2002), at Höhle Fels (Münzel *et al*. 2001 and Münzel & Conard, 2004), at Divje Babe (from an illustration *in* Turk & Kavur, 1997) and at Taubach (bratlund, 1999).

The fractured metapodials at Arcy are also interpreted by David & Poulain (2002) as a result of an activity linked to acquisition of hides.

SEASONS OF PROCUREMENT

In Font-de-Gaume cave (Armand *et al.*, 2004), the bone remains with butchery marks were found on a hibernation site, and indicate a meat and marrow extraction process. We therefore have no indication of the season.

In the cave of Les Cèdres, milk canines imply an occupation of the site in the winter months (Crégut-Bonnoure, 1995).

For David & Poulain (2002), the Aurignacian levels of Arcy are the site of bear hibernation. The authors don't conclude on the season of procurement. Since the hides were used, we believe the bears were butchered during denning time. This would certainly be the case also at Moscerini, Sant' Agostino, Hayonim, sites studied by Stiner (1994 and 2005) and at Fate, la Caune de l' Arago, Badalucco and Madonna dell' Arma, sites studied by Quilès (2003).

At Madonna dell' Arma, for Quiles (2003), this would even be a case of hunting in a bear den.

In the case of the Castanet bear, as we mentioned earlier, it is not a hibernation site, and we have no indications about the seasonality of exploitation.

At the site of Hohle Fels, Münzel & Conard (2004) come to the conclusion that the site was occupied in the winter months, based on the data obtained from the tooth eruption stages of horses, and remains of cave bear cubs indicate "an interaction between humans and bears during the transition of winter to spring".

At the Pauline cave, young individuals carry butchery traces and according to the age indicated by the mandibules, Cordy (1974) thinks they died in the winter.

Similar conclusions were drawn for Geissenklösterle (Münzel *et al.*, 2001*)*: cutmarks were found on bear cubs aged 3-4 months, which would indicate the end of winter.

At Biache, Auguste (1995) observes that very young bear cubs are absent, while adults and sub-adults dominate, and «le rapport mâles/femelles en légère faveur pour les premiers indiquent une acquisition d'individus isolés; ceci correspond bien au comportement plutôt solitaire des ursidés et rejette un abattage des animaux hibernant». He puts forward the hypothesis of a spring hunt for the aurochs, with an intensive marrow extraction process to compensate for the poor quality of the meat in this season, and a fall hunt for the bear, as it is the meat, fatty in this season, which was mostly used.

BEAR PROCUREMENT STRATEGIES

Bear procurement strategies are often impossible to determine at sites where bear remains show butchery marks.

However, at Hohle Fels, bear hunting is proved by the presence of a lithic point inplanted in a vertebra (Münzel & Conard, *op. cit.*).

According to Auguste (2003), the presence of numerous cutmarks and an analysis of age cohorts (showing a peak for sub-adults and adults, which is not the pattern observed in dens) demonstrate that Biache is a kill site.

At Taubach, cutmark frequencies correspond to the values observed at hunting camps (Bratlund, 1999).

Bez (1995) also found striations on a metatarsal belonging to a bear of Tibet at the site of Les Cèdres. Since they are situated on the inferior side of the bones, he stresses that this may represent meat processing rather than skinning, as the underside of a bear paw is rich in meaty and fatty tissues. In his 14th century book on hunting, PHÉBUS (translated 1986), explains that "ses pieds sont meilleurs à manger que tout ce qu' il porte".

Butchery marks linked to the skinning process are rather frequent on the first phalanges. These are found at Castanet, as well as at Hayonim (STINER, 2005), at Badalucco and Fate (QUILES, 2003), at Sant' Agostino (STINER, 1994), in the Aurignacian layers of Arcy (DAVID & POULAIN, 2002 and ROBLIN-JOUVE, 2002), at Biache (AUGUSTE, 1995) and at Taubach (BRATLUND, 1999). At the Caune de l' Arago (QUILÈS, 2003), there is mention of cutmarks on a phalanx with no further precision.

Striations on the second phalanx were observed in just a few sites: at Moscerini (STINER, 1994), at Arcy (DAVID & POULAIN, 2002 and ROBLIN-JOUVE, 2002), at Biache (AUGUSTE, 1995) and at Taubach (BRATLUND, 1999).

The meat of the bear was used at Biache-Saint-Vaast (AUGUSTE, 1992), at Taubach where the cut marks are present on the entire skeleton (BRATLUND, 1999), at Hohle Fels, where the marks are found on humerus and pelvis (MÜNZEL & CONARD, 2004). At Font-de-Gaume, we find them on a femur, a humerus and ribs (ARMAND *et al.,* 2004), at the Caune de l' Arago and at Badalucco on ribs (QUILÈS, 2003), at Portel also on a rib (GARDEISEN, 1994), at Fate on a rib and 2 ulnas (QUILÈS, 2003) and probably at Divje Babe: although there is no mention of the use of bear meat in the site report, the illustrations show butchery marks on a rib (TURK & KAVUR, 1997).

Finally, the use of the animal's tongue is suggested by the cut marks found on a hyoid bone at Fate (QUILÈS, 2003).

The fracturation of bones in the following sites demonstrates marrow extraction: Hohle Fels (MÜNZEL & CONARD, 2004), Font-de-Gaume (ARMAND *et al.*, 2004), in the Aurignacian layers of Arcy (DAVID & POULAIN, 2002), Divje Babe (TURK & DIRJEC, 1997) and Goyet (GERMOMPRÉ & SABLIN, 2001).

The gravettian layers at Hohle Fels, rich in ash, contain large burned bones that are identified as bear remains. It seems that these bones were used as combustibles at this site (MÜNZEL & CONARD, 2004).

CONCLUSION AND PERSPECTIVES

The number of Paleolithic sites which attest to bear exploitation will surely increase. The recent analyses of old collections is of particular interest as it has brought to our attention 2 new cases (Font-de-Gaume and Castanet)

If the first phalanx with cut marks really belongs to a brown bear, the Aurignacian site of Castanet and the Epigravettian one of Polesini (STINER, 1994), at the current state of research, are the only ones which suggest that the brown bear was exploited in the Upper Paleolithic. For all other sites of this period, when exploitation took place, the species concerned was the cave bear (ARMAND *et al.,* 2004).

The use of hides, as illustrated at Castanet and other sites, seems to be the primary reason for exploiting bears. It is interesting to note that there is a notable variability in the location of cut marks.

For the season of exploitation, it is only possible to associate it with the period of hibernation. It is not very precise. GERMOMPRÉ & SABLIN (2001) demonstrate that the timing and length for the dormancy period varied with climatic conditions, but not in contradiction with the theory of exploitation during the first stages of hibernation.

Exploitation during the fall hunt at Biache does not contradict this hypothesis. However, the records at Geissenklösterle and Hohle Fels, where exploitation occurred during the winter/spring transition, contradict this idea.

In order to further understand the notion of seasonal bear exploitation, it would be useful to carry out skeletochronological studies.

Bear-specific procurement strategies are not always opportunistic. Bears were hunted at Biache, Taubach and Hohle Fels. However hide procurement was probably a planned activity. Nonetheless bear exploitation still appears to have been a marginal activity when compared to herbivores procurement.

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TAPHONOMIC RESULTS FROM PETRLAŠKA CAVE, EASTERN SERBIA

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Abstract: Taphonomy is a very important scientific discipline, not only for paleontologists, but for archeologists, especially for zooarcheologists. In Petrlaška Cave, in the central hall, 20 cm below the surface remains were found of a fireplace and fragments of pottery. In the lower cultural layer bone remains were found: two canines and a part of mandible of a cave bear. Recently revision of the cave brought new information about animals which lived during Pleistocene in this part of Eastern Serbia. In this paper are the preliminary taphonomic results. Unfortunately, the excavation was not done professionally-"treasure hunters" left bones on the surface of the cave. Because of that stratigraphic analysis is not possible.

Key words: *Ursus spelaeus,*Taphonomy, Eastern Serbia.

INTRODUCTION

Petrlaška Cave is situated on the southwestern brim of the Odorovačko field, on the alluvial level, just 10 m from the last active stream-sink (fig. 1). The large entrance of the cave is entrenched at 686 m a.s.l. The total length of the surveyed galleries is 480 m (Petrović, 1976).

In 2005, there was a new revision of the Petrlaška Cave and new fossil remains from three species were found: *Ursus spelaeus* ROSSENMÜLLER, 1794, *Equus ferus* BODDARET, 1785, *Cervus elaphus* LINNAEUS, 1758 of Pleistocene age. Carnivores or man brought a metacarpal bone of a tarpan and part of a red deer skull into the cave.

Remains of cave bear originate from at last three animals: two animals around one and half years old and one six month old cub. One of the remains is a skull from a one and half year old cave bear with a big aperture (16 x 20 mm) on the left frontal bone. Also porosity of osseous tissue of a left mandible belonging the same animal shows it to be in a very bad health condition. As the edge of aperture is smooth it could not have happened from a hit or bite. It was caused by some serious pathological disorder or infection.

The abundance of the remains of cave bears in caves is the consequence of the fact that the cave bear used caves for winter hibernation. As for the high mortality rate among immature bears, some or perhaps most of the deaths can be attributed to simple inexperience and inadequate summer feeding (Kurtén, 1978).

The most numerous group of underground karst phenomena on Vidlič Mt. are stream-sink caves and pits. There are 20 caves and 36 pits on the southwestern brim of Odorovačko Polje. Petrlaska Cave is one of them (fig. 2, 3). This was a human occupied cave and also shelter for Pleistocene mammals, especially for the cave bears. Most of the cave bears' remains in Pleistocene cave deposits of Serbia are found to be originating from animals hibernating in caves. The main question in this research is the reason of high mortality of immature bears, and the attempt to find out which pathological disorder caused the death of one of cubs.

Remains of other species, *Cervus elaphus* and *Equus ferus,* were brought into the cave as prey of carnivores or man.

MATERIAL AND DESCRIPTION

A total of ten bear bones were found at Petrlaska cave: a skull (cranium) of a young animal, with well preserved posterior part; a cranium with a broken oral frontal part, aboral in the occipital part; fragments of frontal (sin and dex), parietal (sin and dex), supraoccipital and fragments of temporal (sin. and dex.) are well preserved. The skull belonged to a very a young animal, which hadn't finished its growth. Also, the skull is small with open sutures. In the base of the left cheekbone there is a joint for process of right mandible.

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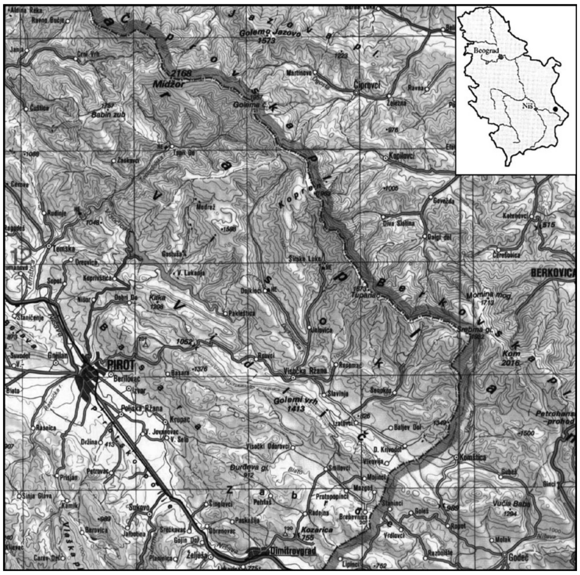

Figure 1. Map with the position of the Petrlaška Cave.

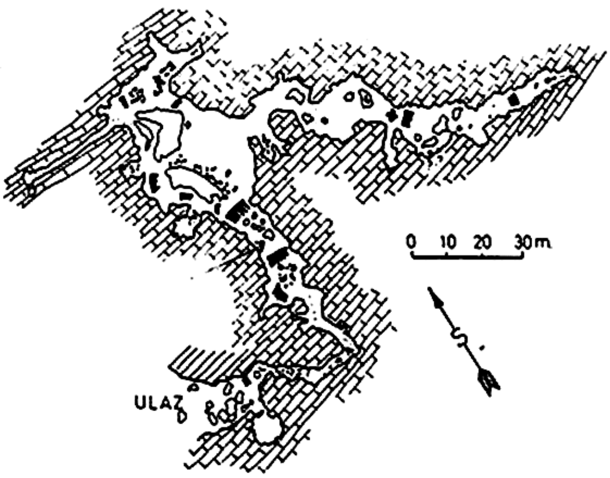

Figure 2. Scheme of the Petrlaška Cave.

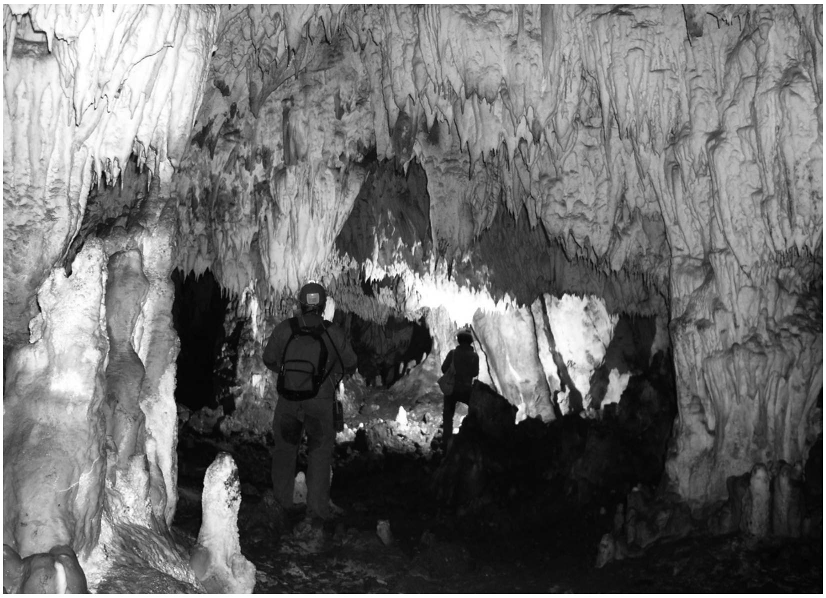

Figure 3. Inside of the Petrlaška Cave.

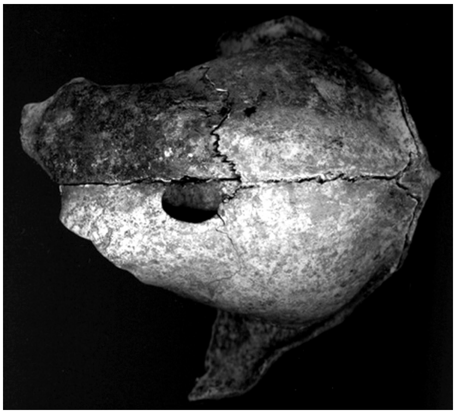

Figure 4. Petrlaška Cave: *Ursus spelaeus* ROSSENMÜLER, 1794. The skull of a one and half years old cub with a big aperture.

On the left frontal bone is a big aperture (16 x 20 mm). This was the cause of death of the cub (fig. 4).

The right mandible (mandibula dex) is oral broken at the level of the alveolus for the fourth premolar. The first and second molars are preserved and the alveolus for the third molar are preserved. The mandible belonged to the young animal, concluded from the size of the mandible, unworn tooth crowns and the alveolus for third molar which is placed in base of the coronoid.

Osseous tissue around the third molar shows porosity and indicates a bad health condition of the animal.

The skull and mandible belonged to the animals of the same age, around a year and a half. We can draw the conclusion that they are remains of the same animal, because the morphology and size of the processus articularis is suitable for skull cheekbone joint.

First lower, right molar (M_1 inf. dex) has the same degree of wear of tooth crown as the first molar from the mandible, which shows that they belonged to animals of the same age, but not to the same cub, because both molars are from a right mandible.

Third, low, right molar (M_3 inf.dex) belongs to an animal of the same age.

Fragment of left humerus (fr. humeri sin juv.) with preserved distal end is the bone of the remains of young animal.

Fragment of left femur (fr. femoris sin juv.) with a preserved parts of proximal and distal ends.

Fragment of left tibia (fr. tibiae sin juv.) of six months old cub.

Fragment of cranial vertebra (fr. vertebrae craniales juv.), then frag. vertebrae lumbalis and frag. costae; all are remains of very young animals.

TAPHONOMY

Remains of cave bear from Petrlaška Cave belong to three individuals at least. Most of the remains (cranium, mandibula dex, M_1 inf. dex, M_3 inf. dex, humerus and femur) originate from one and half year old animals. The fragment of tibia is from a six months old cub. Material was not transported. Abrasion refers to the rounding of natural and broken edges of of bones caused by rubbing against fine particles in a soil matrix. Abrasion may indicate the amount of traffic inside a site or geological rolling (Stiner, 1994). There are marks of tooth of carnivores, but doesn't exclude that bones were gnawed postmortal.

Bones were not burnt and there were not tool cut marks which indicate that cave bear and man did not use the cave in the same time. On the skull are marks of chemical corrosion process. All bones were covered by crystalline calcium carbonate which fell off easily.

Young bears used the cave for winter hibernation, after the feeding season. It could happen that winter was very long and deep and that cubs could not get enough fat for hibernation. Sometimes they did not have experience in feeding, sometimes they died from diseases, or from contact with hostile adults.

The aperture in the frontal bone of a young cave bear from Petrlaška Cave was not a result of brain tumor, because a tumor would make a whole net of channels in the cranial bones; similar channels would be caused by the making of a cyst. Some serious infection caused this aperture. Smooth edges of the aperture shows that it is not result of carnivore teeth or man tools. This is the effect of an inflammatory processes in the bone.

CONCLUSIONS

The Petrlaška Cave has not been well explored, yet, like many other caves and pits in Serbia. A high percentage of young cave bears' remains are registered in all localities (including those which yielded single or few fossils). Sexual dimorphism is notable in the cave bear population in Serbia, like as in other European regions. Skeletal elements on which pathological deformations can be recognized are seldom found in Serbia. Several long bones with pathological deformations and only more or less progressive osteoporosis on cave bear remains from other localities are reported (Dimitrijević, 1997). This finding of a very young cub which died from serious diseases is unique in Serbia, for now. It is necessary to give more attention on paleopathology of mammals which can open new views for us.

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QUATERNARY MAMMALIAN REMAINS FROM THE KITSELI POTHOLE (ALEA, NEMEA, PELOPONNESE)

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Katerina CHATZOPOULOU[1] & Georgios LAZARIDIS[1]

ABSTRACT: In the present study a new karstic cave in the Peloponnese, the Kitseli Pothole, is described for the first time. At its maximum depth of about 10 m, fossilized bones of a brown bear and a leopard have been found, which are best described as *Ursus arctos* and *Panthera pardus.* Additionally only a few micromammalian remains can be attributed to *Crocidura* sp., *Microtus (Microtus) arvalis*, *Microtus (Microtus)* cf. *nivalis, Microtus (Pitymys)* cf. *subterraneus/multiplex* and *Cricetulus migratorius.* Also, a maxillary fragment belongs to a small reptile. This is the first report of a fossil brown bear found in the Peloponnese and it expands the southernmost limits of the taxon. The bones of the leopard are consistent with the creation of the myth of the Nemean Lion that was killed by Hercules. The paleoenvironment and the biochronology are also discussed.

Key words: Kitseli Pothole, Quaternary fauna, Nemea, Peloponnese, Greece.

INTRODUCTION

The Kitseli Pothole is located near Alea village, in the Nemea area of the Peloponnese, South Greece (code of the site KNP: Kitseli Nemea Peloponnese) (fig. 1a). The name of the pothole is given by the present authors to honour the memory of Theodoros Kitselis who was a caver and first explored the caves of Alea, such as "Trypa tis Chionas" (Panagiotidis, 1978). Soon after the exploration of "Trypa tis Chionas" one of us (A.B.) explored the Kitseli Pothole where he found the bones presented here (fig. 1b, 2). The maximum depth of the pothole is 10

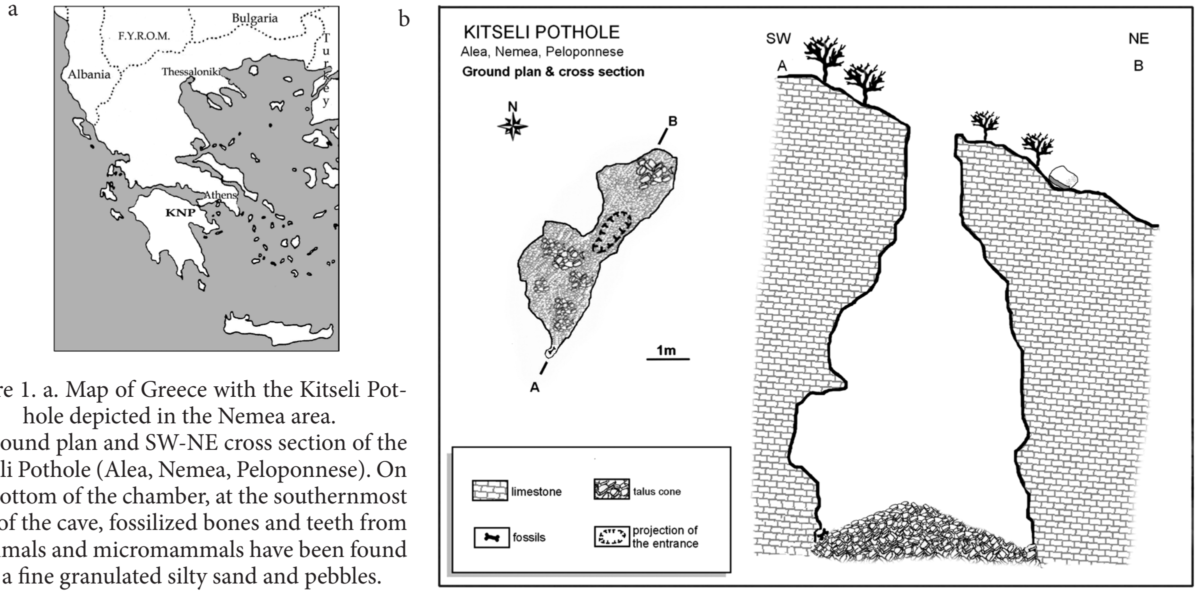

Figure 1. a. Map of Greece with the Kitseli Pothole depicted in the Nemea area.
b. Ground plan and SW-NE cross section of the Kitseli Pothole (Alea, Nemea, Peloponnese). On the bottom of the chamber, at the southernmost part of the cave, fossilized bones and teeth from mammals and micromammals have been found in a fine granulated silty sand and pebbles.

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m. It has a small entrance 40 X 80 cm (fig. 3). At the bottom of the pothole a small talus cone has been formed. The surface of the cave floor occupies an area of about 6 m^2 and is full of stones and has a maximum length of 5 m and a minimum breadth of 0.70 m (fig. 1b). The pothole is decorated with a few stalactites, stalagmites, flowstones and cave corals. Very few recent bones, mainly belonging to artiodactyles, were noted on the surface.

Figure 2. Animal bones at the bottom of the Kitseli Pothole.

Figure 3. The entrance of the Kitseli Pothole.

PALEONTOLOGY

Large Mammals

Taxonomy

Order: CARNIVORA BOWDISH, 1821
Sub-order: Canoidea SIMPSON, 1931
Arctoidea FLOWER, 1969
Family: Ursidae GRAY, 1825
Genus: *Ursus* LINNAEUS, 1758
Ursus arctos LINNAEUS, 1758

Material: 1 vertebra lumbar KNP 2, 1 vertebra sacral KNP 10, 2 vertebras/coccyx KNP 17 and 18, 2 pelvis frag. KNP 11 sin and 12 dex, 1 complete femur KNP 1 dex, 1 femur frag. KNP 13 sin, 2 tibia fragments KNP 3 dex and KNP 14 sin, 1 proximal frag. KNP 7, 2 fibula frag. KNP 4 and 16, calcaneus frag. KNP 15 dex, 1 cuneiform3 KNP 26 dex, metapodials: Mp distal KNP 29, 3Mp proximal KNP 28, 30 and 31, phalanges: 4 Ph1 KNP 19, 21, 22, and 20 for Mp 1, 1 Ph3 KNP 23, 2 sesamoids KNP 24 and 25.

Description: The ursid remains include only post cranial bones; most of them have not been identified confidently as they are incomplete or in small fragments. The right femur is the best preserved among the Kitseli specimens (pl. 1.1, tab. 1), the morphology and the dimensions of which point clearly to the presence of the brown bear (fig. 4). On the contrary, the left femur is very poorly preserved, a powder sample of which was XRD analysed, in order to assess the degree of fossilization. Both acetabulums are preserved, the left one being more complete, the

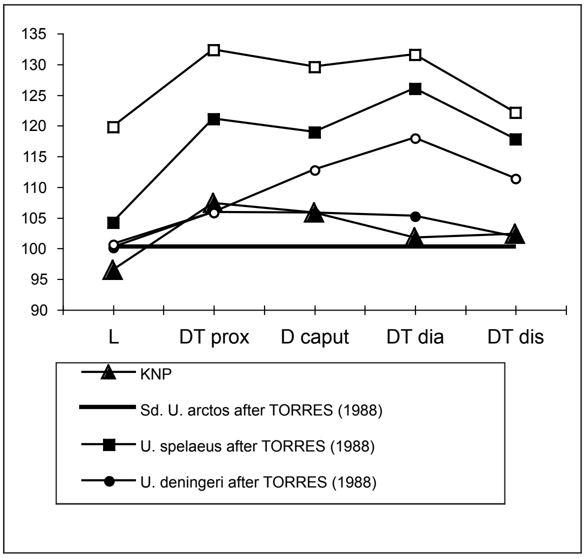


Figure 4. Comparative diagram with the femur dimensions of various species of *Ursus*. The Kitseli bear (KNP) falls within the range of the arctoid bears. Standard *Ursus arctos*, Spain (Torres, 1988).

tuber ischiadicum of which seems to be unfused, showing thus a sub-adult individual. The vertebral column is well represented by an almost complete sacral (pl. 1.2), the *alae* of which are missing, an almost complete lumbar (pl. 1.3) and two complete caudal vertebras (pl. 1.4 and 5). Only parts of the shaft of the right and left tibias are preserved. Of the fibulas, the shaft (pl. 1.6) and a proximal part are preserved. Of the relatively small and slender calcaneus the tuber, the shaft and the *sustentaculum tali* are preserved, while the distal part is missing (pl. 1.7). Of the rest tarsals, only a right incomplete third cuneiform is preserved. The metapodials are badly preserved –two shafts and a distal epiphysis (KNP 29: DTXDAPdist.art.= 17.44 X 16.55 mm, I(DAP/DT)X100= 94.90), while three first phalanges-one for the first metapodial (pl. 1.8) and the other two (pl. 1.9 and 10) are well preserved. Only one Ph3 (pl. 1.11) is poorly preserved.

Sub-order Feloidea SIMPSON, 1931
Family: Felidae GRAY, 1821
Genus: *Panthera* OKEN, 1816
Panthera pardus (LINNAEUS, 1758)

Material: Tibia diaphysis frag. KNP 46 dex, metapodial distal frag. KNP 27.

Description: The diaphysis of the tibia is slender, curved with intense *linea* m. *poplitea,* a feature noted in felids (pl. 1.12). The metapodial distal part is distinguished by the rounded distal trochlea, from the rather flattened ursid trochlea. (KNP 27: DTXDAPdist.art.=(14.54)X14.40 mm, I(DAP/DT)X100= 99.04) (tab. 1).

Discussion

The Kitseli Pothole fauna is composed of two species of carnivores and various micromammals: many skeletal elements of the brown bear *Ursus arctos* and only two bones from the leopard *Panthera pardus* a tibia diaphysis and a distal metapodial (fig. 3). The latter two are slenderer than those specimens reported from Vraona Cave, Attiki that have been dated to 7-25 Ka old (Nagel, 1995 and 1999). Comparing to bears, felids are more frequent in the Peloponnese: leopard, lynx and wild cat have been found in the same context in the Middle Pleistocene cave of Apidima, Mani peninsula in the Southern Peloponnese (Tsoukala, 1989). Also, two skeletons of leopards were found in Dyros cave one of which is about 28 Ka old (Bassiakos, 1993; Georgiadou - Dikaioulia *et al.* 2002).

The broader area of the Kitseli Pothole is of historical importance as in Greek Mythology Hercules killed the famous lion of Nemea. In a myth told by Hesiod, the Nemean Lion was the son of Orthos - a giant dog - and according to Pausanias, people believed that the Nemean Lion came out of the ground. Mayor (2000) suggested that the bones of mythological super sized animals are none other than the fossil remains of extinct animals. Hence, it is possible that the ancient people mistook a fossil skeleton of a leopard as that of a lion, thus how the myth of Nemean Lion might have come about. Thus the bones of *Panthera pardus* reported here are the only material evidence so far as to the existence and nature of the Nemean Lion. Indeed, Hercules killed the Nemean Lion in a cave (Apollodorus B′ V 1). It is interesting to note, that no fossil bone from *Panthera leo spelaea* (GOLDFUSS, 1810) has ever been reported from the Peloponnese, except the presence of its ancestor *Panthera leo fossilis* (REICHENAU) of Early Biharian (Middle Pleistocene) from Megalopolis-Marathousa (Sickenberg, 1976).

Brown bear does not live in the Peloponnese nowadays but its presence had been reported by travellers until the 17th century (Papavassileiou, 1963; Simopoulos, 1984). Fossil brown bear has not been reported earlier from the Peloponnese until the present paper while its Early Pleistocene ascendant *Ursus cf. etruscus* has been reported from Kastritsi, Achaia by Symeonidis *et al.* (1985/1986). The presence of fossil brown bear is rather rare in Greece. It has been recorded in Vraona, Attiki by Symeonidis *et al.* (1980) and Rabeder (1995), as well as in Kouklesi, Epirus by Theodorou (1992), and in Petralona Cave by Tsoukala (1989) and Almopia Speleopark.

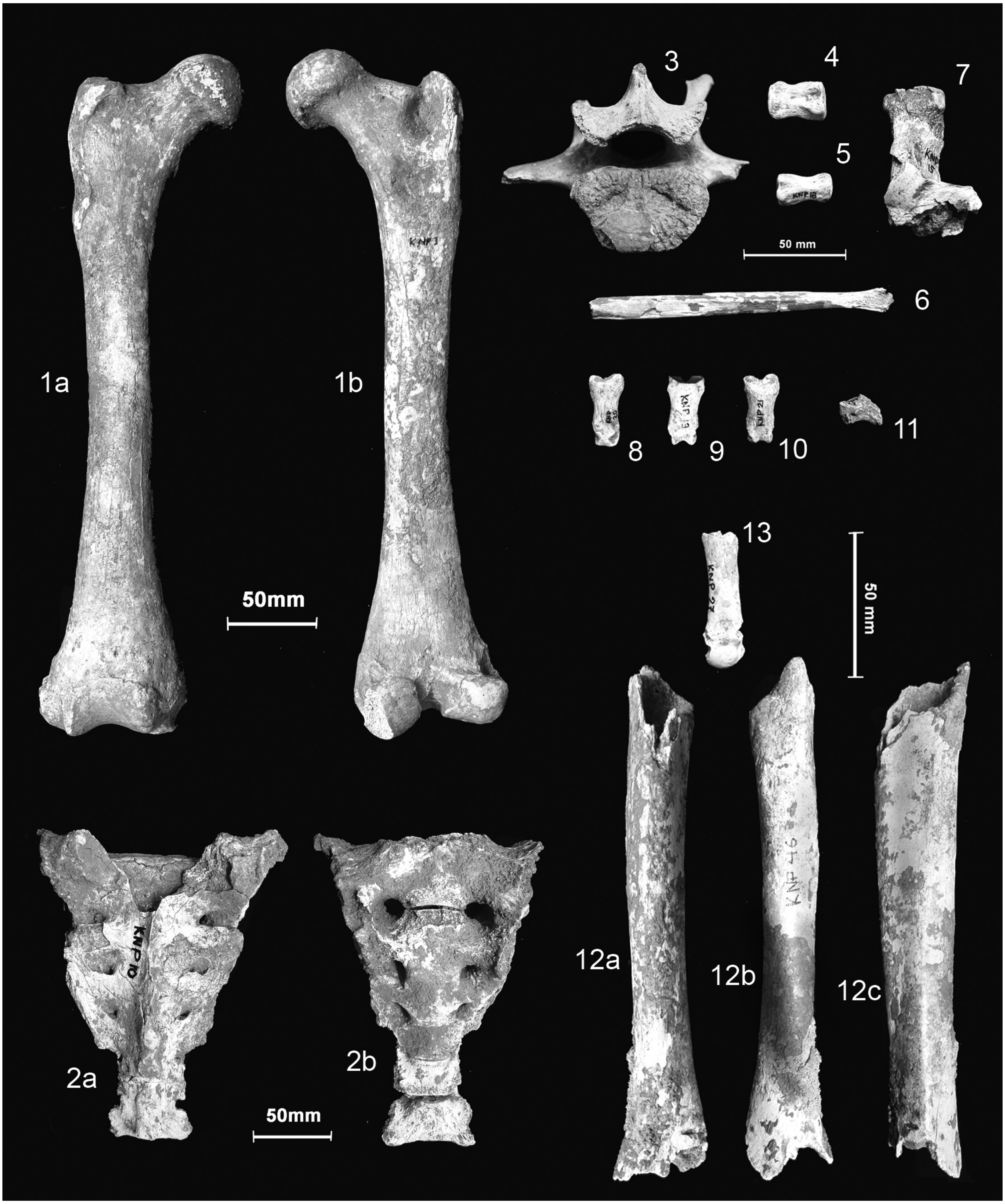
Brown bear still lives in the mountainous areas of Northern Greece and its early presence in Nemea is consistent with this environment.

The leopard entered Europe in the Middle Pleistocene (Cromerian, Kurtén, 1968) with a wide distribution but more restricted than the cave lion. The possible existence of the leopard in the Holocene in the Balkans is discussed by Spassov & Raychev (1997) according to zoogeographic, climate and environmental conditions. A systematic study of material that comes from archaeological sites of Greece would provide evidence of its existence during this period.

The spread of modern humans over the whole planet played a main role in the Late Pleistocene megafaunal extinction. A number of Late Pleistocene survivors such as leopard disappeared from Europe in historical times. Others were severely enlarged having become considerably restricted in their original habitat as was the case of brown bear (Agusti & Anton, 2002).

The geological age of the Kitseli Pothole large mammalian fauna presented here might be of Late Pleistocene.

Plate 1



Ursus arctos KNP: 1. Right femur KNP 1: a) anterior and b) posterior view); 2. Sacral bone KNP 10: a) dorsal and b) ventral view; 3. Lumbar KNP 2; 4 and 5. Coccyx KNP 17 and 18 vertebras; 6. Fibula diaphysis frag. KNP 16; 7. Left calcaneus KNP 15, anterior view; 8. Ph1 for Mp1 KNP 20; 9 and 10. Ph1 KNP 19 and 21, anterior view; 11. Ph3 lateral view. *Panthera pardus* KNP: 12. Right tibia (diaphysis): a) anterior, b) posterior and c) lateral view; 13. Metapodial distal frag. KNP 27, anterior view.

Table 1
Ursus arctos and *Panthera pardus* KNP: Measurements of the postcranial bones.

Ursus arctos	**Femur**	**Ph1**		
	KNP 1	KNP19	KNP 21	KNP 20 (Mp 1)
L	382.00	34.21	34.57	35.63
DT prox.	97.80	17.78	17.67	17.50
DAP troch.	40.50	14.84	15.55	13.99
DT dia.	35.33	13.03	12.90	12.14
DAP dia.	31.88	9.83	11.23	10.51
DT dist..	82.96	14.78	13.97	13.66
DAP dist..	62.88	8.81	9.36	8.87
D caput	47.87			
L trochas	78.08			
L collum	55.95			

Calcaneus	
KNP 15	
L	-
DT	(42.75)
DT tuber	28.77
DAP tuber	35.17
L manubrium	43.55
DT min	17.28

Fibula	
DT prox.	23.42
DAP prox.	18.79
DT dia.	(10.33)
DAP dia.	(13.45)

Cuneiform 3	
KNP 26	
L	14.82
DT	19.26
DAP	27.00

Tibia	
DT dia.	(27.00)
DAP dia.	(33.52)

Pelvis	
D acetab.	49.30
D pubic min	33.67

Sacrum	
KNP 10	
L	178.00
DT min	33.20
DT S6	51.00
DAP S6	22.50

Panthera pardus		
	KNP	***LAO****
Tibia		
DT dia.	(18.40)	*19.00*
DAP dia.	(24.90)	*22.20*
Metapodials	**Mp**	***Mc V***
DT dia.	min 10.44	*7.80*
DAP dia.	10.50	*8.20*
DT dist.	14.34	*12.30*
DAP dist.	14.42	*12.50*
DT d.art.	14.30	*12.00*
DAP d.art.	14.42	*12.50*

LAO* *Panthera pardus* from Apidima Cave (South Peloponnese)(Tsoukala, 1999)

The micromammals from the Kitseli Pothole

The matrix sampled has been screen-washed through sieves with a mesh of 0.5 mm. The micromammalian elements were picked out of the residue and studied under a light microscope. The measurements of the teeth were taken using a Wild Photomakroskop M400 stereoscope. The drawings were made using a light microscope with a camera lucida attached. The terminology and the measuring method used for each taxon are recorded in text. The material is stored in the Geology and Paleontology Laboratory, the Geology School, Aristotle University of Thessaloniki, Greece.

Taxonomy

Order: INSECTIVORA BOWDICH, 1821
Family: Soricidae FISHER VON WALDHEIM, 1817
Sub-family: Crocidurinae MILNE-EDWARDS, 1872
Genus: *Crocidura* WAGLER, 1832
Crocidura sp.

Material: M^1 sin KNP 65, M^2 sin KNP 66, M^2 frag dex KNP 67, mandible with M_2 dex KNP 58.

Measurements (in mm): The measurements (table 2) and terminology are according to Reumer (1984) and Koliadimou (1996). Dimensions of M_2: L=1.402, TAW=0.917, TRW=0.861.

Description: M^1 (pl. 2.2): The first molar is relatively broad and short of a slender appearance. The hypocone is poorly developed and separated from the protocone by a valley. There is no metaloph, hence the protocone has an L-shape. The parastyle shows a little knob. The postero-buccal corner protrudes strongly.

M^2 (pl. 2.3): The shape of M^2 is trapezoidal. The protocone is connected to the paracone. The mesostyle is well developed.

M_2 (pl. 2.1): A mandible fragment bearing a lightly worn second molar was found. Part of the anterior root of M_3 is preserved. The mental foramen is not visible because the mandible is damaged. The protoconid is the highest cusp of M_2. The lingual cusps are shorter. The buccal re-entrant valley opens high above the cingulum. The entoconid crest is rather low. The buccal cingulum is narrow but well pronounced. The lingual one is weak. Both cingula are straight.

Discussion: The subfamily Crocidurinae has white teeth. In the lower molars the buccal re-entrant valley opens

Table 2
Crocidura sp. (KNP): Dimensions (in mm) of the first and second upper molars.

	BL	LL	PE	AW	PW
KNP 65	1.731	1.549	1.260	1.728	2.022
KNP 66	1.380	1.279	1.119	1.933	1.662
KNP 67	1.374	1.335	1.095	-	1.730

high above the cingulum (plate 1.1b), the entoconid crest is low to nearly absent (pl. 2.1c), and the buccal cingulum is narrow but well pronounced (pl. 2.1b). These characteristics are consistent with the genus *Crocidura* (Reumer, 1984).

Crocidura russula is characterized by a constriction in the buccal cingulum of M_2 (Reumer, 1986), which is absent in the KNP specimen. The position of protocone on P^4 is indicative for this species. Since no P^4 has been preserved in the KNP material, an identification at a species level is uncertain. Although there are only a few KNP specimens, it seems that M_2 belongs to a smaller individual/species (smaller than *C. kornfeldi* and *C. zimmermanni*) (fig. 5), than the upper molars from Kitseli (larger than *C. kornfeldi* and *C. zimmermanni*) (fig. 6). Nevertheless, these differences in size can be explained by the range of variation of a single species.

Order: RODENTIA BOWDICH, 1821
Family: Arvicolidae GRAY, 1821
Sub-family: Arvicolinae GRAY, 1821
Tribe: Microtini SIMPSON, 1945
Genus: *Microtus* SCHRANK, 1798
Microtus (Microtus) arvalis (PALLAS, 1778)

Material: mandible with M_1, M_2, M_3 frag sin KNP 59, M^3 sin KNP 53, M^3 frag sin KNP 56, M^3 dex KNP 51.

Measurements: The measurements (table 3) and terminology are according to Van Kolfschoten & Roebroeks from Koliadimou, 1996 and Rabeder, 1981.

Description: One of the specimens is a mandible fragment bearing all the cheek-teeth. The incisor and the posterior lobe of M_3 are broken. The occlusal surface of the teeth was covered with calcite crust. Most of the cement in the triangles is not revealed, because the cleaning could break the fragile enamel. There are no roots.

M_1 (pl. 2.4)**:** It consists of the posterior lobe, five closed triangles and the anteroconid complex. There are five lingual and four buccal synclines with crown cement. BSA5 and LSA6 are developed to the same degree. The triangle T6 is widely connected with T7. The constriction between anteroconid AC3 and T6-T7 complex is relatively narrow (morphotype C6 according to Nadachowski, 1982). AC3 is rather symmetrical.

M^3: It consists of the anterior lobe, three triangles and the posterior cap. There are three lingual and three buccal synclines with crown cement. The specimen KNP3

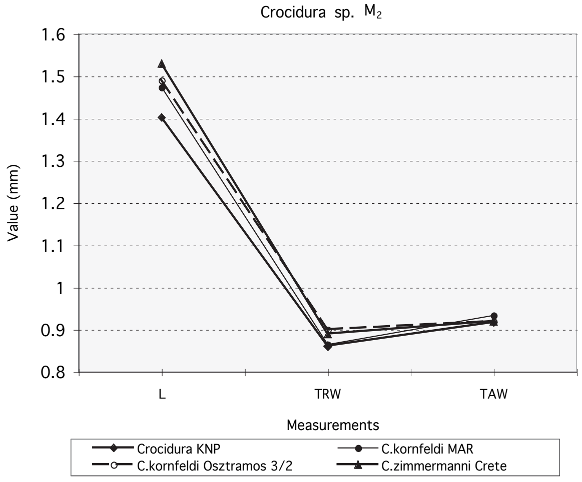


Figure 5. Line diagram comparing the dimensions of M_2 of *Crocidura* sp. from KNP, *Crocidura kornfeldi* from Marathousa (Koufos *et al.,* 2001), Osztramos 3/2 (Reumer, 1984) and *C. zimmermanni* from Crete (Reumer,1986).

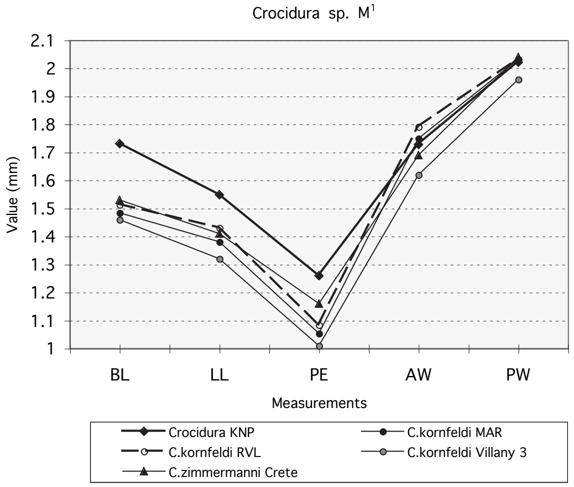


Figure 6. Line diagram comparing the dimensions of M^1 of *Crocidura* sp. from KNP, *Crocidura kornfeldi* from Marathousa (Koufos *et al.,* 2001), Rema Voulgaraki (Koliadimou, 1996), Villany 3 (Reumer, 1984) and *C. zimmermanni* from Crete (Reumer, 1986).

Table 3
Microtus arvalis (KNP): Dimensions (in mm) of the lower first molar and upper third molars.

Maximum occlusal length (L-L')	L=2.768
Length of the anteroconid complex (a-L)	a=1.473
Width of the anteroconid complex (w-w')	W=1.010
Shortest distance between BRA4 and LRA5 (d-d')	d=0.143
Shortest distance between BSA4 and LSA5 (e-e')	e=0.781
Maximum occlusal length of M^3	l=1.939 & l=1.817

(pl. 2.5) shows a very deep LRA4 resulting distinct T5 and T7. LRA4 is weaker in specimens KNP1 and KNP6 (Plate 2.6-7) showing T5 blended with PC (morphotype "artimultiplex" according to Rabeder, 1981). There are no roots.

Discussion: The morphological characteristics and the size of the M_1 conform rather well to *M. arvalis* or *M. agrestis*. Differentiation between the Common Vole (*M. arvalis*) and the Field Vole (*M. agrestis*) is problematic since their structure and dimensions overlap to a large extent. According to Dienske, it is not possible to separate *M. arvalis* from *M. agrestis* on the basis of the M_1 structure only and according to Fedyk and Ruprecht the teeth of the Common Vole are smaller and lighter than the molars of the Field Vole (Nadachowski, 1982). Dimension of teeth overlap, but still there is a difference which enables us to assign KNP specimen to *M. arvalis* (fig. 7). Additionally, the M^2s that have been studied, lack small postero-lingual lobe, which is characteristic of *M. agrestis* (Chaline, 1974).

The Common Vole is one of the most frequent rodents in Europe in the last glaciation, especially during warmer phases. At present this species inhabits mainly cultivated fields. During Pleistocene it was probably connected with open areas (Nadachowski, 1982).

Microtus (Microtus) cf. *nivalis* (MARTINS, 1842)

Material: M^3 dex KNP 55.

Measurements (in mm)**:** l=1,828.

Description: M^3 (pl. 2.8)**:** The molar is rather massive. It consists of the anterior lobe, three triangles and the posterior cap. There are two lingual and two buccal synclines with crown cement. Triangle T2, T3 and T4 are slightly interconnected since the triangles are not completely closed. T4, T5 and PC have confluent dentine fields with incipient BRA3 and LRA4 (morphotype "simplex" according to Rabeder, 1981). There are no roots.

Discussion: In comparison with other species of *Microtus* found in the Kitseli Pothole, the enamel in the grinding surface of the molars studied here is relatively thicker and the enamel triangles are massive. Nevertheless, these features are not sufficient for secure specific identification as it is the morphological pattern of the occlusal surface of lower first molar. No M_1 has been found in the KNP material. Based on the simple structure ("simplex" morphotype) of the single M^3 and the slightly confluent dentine fields of the tooth (Chaline, 1974), the specimen is referred to as *Microtus* cf. *nivalis*.

At present, the Snow Vole is found in the mountains. Its inhabitat is the high slopes above the timber line. During Late Pleistocene it was widespread in Europe (Kurtén, 1968).

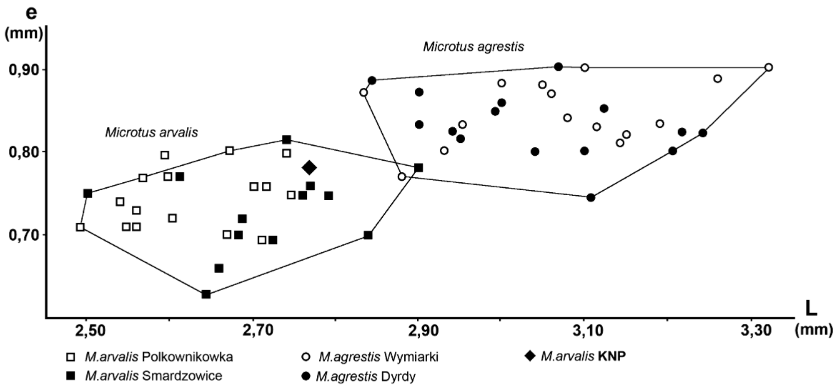


Figure 7. The ratio of the maximum occlusal length of M_1 (L) to the shorter distance between BSA4 and LSA5 (e) in recent species *Microtus arvalis* (squares) and *Microtus agrestis* (circles) from Poland (Nadachowski, 1982). The KNP specimen marked with rhomb.

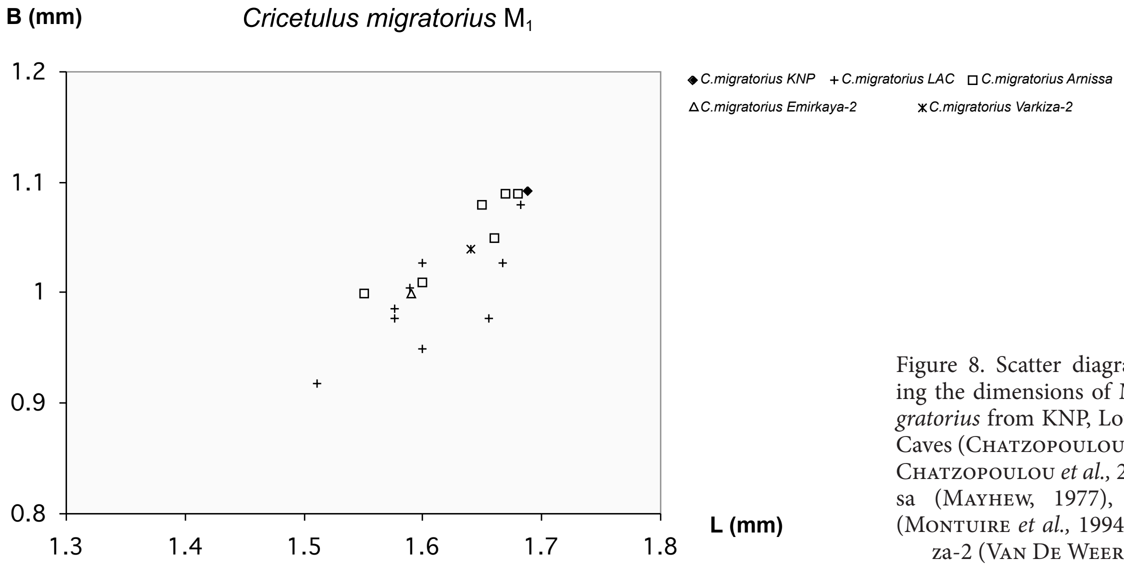


Figure 8. Scatter diagram comparing the dimensions of M_1 of *C. migratorius* from KNP, Loutra Arideas Caves (Chatzopoulou, 2001; 2003; Chatzopoulou *et al.,* 2001), Arnissa (Mayhew, 1977), Emirkaya-2 (Montuire *et al.,* 1994) and Varkiza-2 (Van De Weerd, 1973).

Sub-genus: *Pitymys* McMURTIE, 1831
cf. *Microtus (Pitymys) subterraneus/multiplex*

Material: M^3 sin KNP 52, M^3 frag dex KNP 54.
Measurements (in mm): l=1,684 & l=1,673.

Description: **M^3:** It consists of the anterior lobe, three triangles and the posterior cap. There are three lingual and three buccal synclines with crown cement. Both specimens (pl. 2.9-10) show a deep LRA4 resulting in a distinct T5 and T7 widely interconnected. PC is distinct (morphotype "arvalis" according to Rabeder, 1981). Dentine fields of T4 and T5 are slightly confluent. The enamel occurs on the whole lateral surface of the teeth (lack of the enamel-free areas) except the PC. All samples are smaller and lighter than all other M^3s studied.

Discussion: The light structure and the morphology of the M^3s are consistent rather well with subspecies *Pitymys*. The Pine Voles are difficult to determine since the morphological features show faint differences. The structure of M^3 permits the separation of two groups. The M^3s of "complex" structure (two clearly closed triangles and T4 slightly open to the posterior part of the tooth) are attributed to *subterraneus/multiplex* group. The M^3s of "simplex" structure (triangles T2 and T3 are often interconnected and T4 broadly confluent with the posterior part of the tooth) are attributed to *duodecimcostatus* group (Chaline, 1974). The KNP samples are consistent with the *"arvalis"* morphotype, which is a form of the "complex" structure (Rabeder, 1981). However, since the material is so extremely scanty, farther classification cannot be achieved. It must be noted that the limited enamel-free areas imply that these teeth belong to a young animal (Nadachowski, 1982).

The Pine Vole inhabits differentiated environments; open fields, forests. In the southern part of its distribution this species is connected with moist habitats. During Late Pleistocene it can be regarded as an indicator of the warming-up of the climate (Nadachowski, 1982).

Family: Cricetidae ROCHENBRUNE, 1883
Sub-family: Cricetinae MURRAY, 1886
Genus: *Cricetulus* MILNE-EDWARDS, 1867
Cricetulus migratorius (PALLAS, 1773)

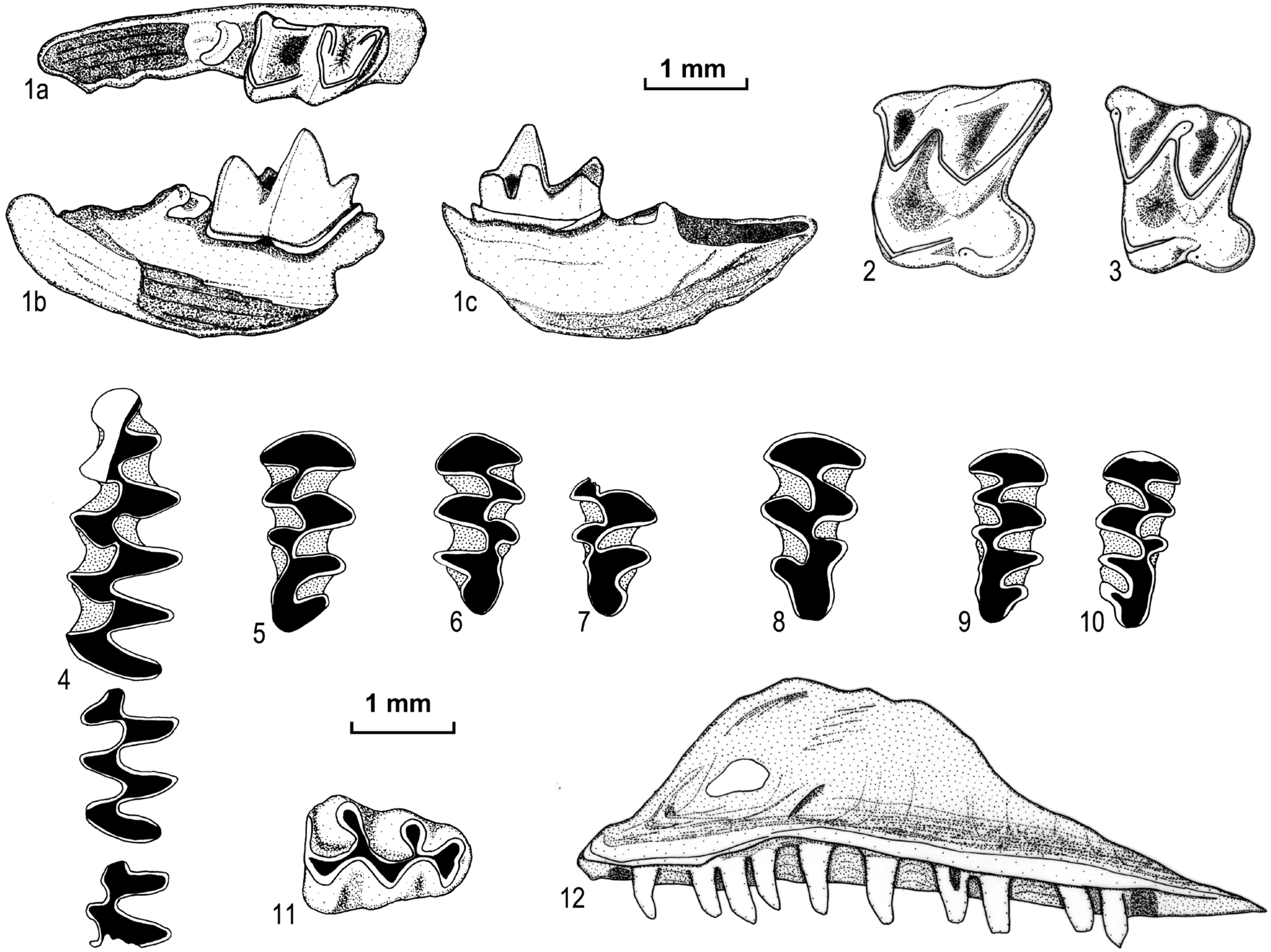
Material: M_1 dex KNP 57.

Measurements (in mm): L=1,688 and B=1,092. The measurements and terminology are according to Mein & Freudental and Hir from Koliadimou, 1996.

Description: **M_1** (pl. 2.11)**:** The anteroconid consists of two developed cuspules that are merged due to the advanced stage of wear. The anterolophid connects with the anterior cuspules to the protoconid. The entoconid joins the protoconid with the ectolophid. The posterolophid is well developed and reaches the postero-lingual margin of the tooth. The posterosinus is closed and crescent. The labial sinuses are wider than the lingual ones. The labial and lingual cingula are well developed. There are two roots.

Discussion: The lower first molar from the Kitseli Pothole shows no morphological differences from recent species. The size of the tooth is considerably larger than that of other *C. migratorius* populations (fig. 8), yet still lies in the variation range of the species. The Grey Hamster inhabits open areas, especially steppes and semi-deserts (Nadachowski, 1982).

Plate 2



Kitseli Nemea Peloponesse. *Crocidura* sp. 1. KNP 58 - Mandible with M_2 dex. 1a. occlusal view, 1b. lateral view, 1c. lingual view; 2. KNP 65 - M^1 sin; 3. KNP 66 - M^2 sin; *Microtus arvalis* 4. KNP 59 - Mandible with M_1-M_3 frag sin; 5. KNP 53 - M^3 sin; 6. KNP 51 - M^3 dex; 7. KNP 56 - M^3 frag. sin; *Microtus* cf. *nivalis* 8. KNP 55 - M^3 dex; *Microtus (Pitymys)* cf. *subterraneus/multiplex* 9. KNP 52 - M^3 sin; 10. KNP 54 - M^3 frag. dex; *Cricetulus migratorius* 11. KNP 57 - M_1 dex; Reptilia 12. KNP 68 - maxilla.

DEGREE OF FOSSILIZATION

To assess the degree of fossilization, the Crystallinity Index (I) of one modern bear bone (FL1) and one bear bone from the Kitseli Pothole (KNP) were measured according to the method of X-ray diffraction used by Bartsiokas & Middleton (1992). The Index of the former is 6.4 and of latter 6.7. The only conspicuous difference between the two bones is in the amount of calcite that is appreciably higher in the bear bone from the Kitseli Pothole that in the modern bear bone (fig. 9). Systematic measurements of a number of bear bone specimens should be made before one can make any conclusive arguments.

CONCLUSIONS

- The Kitseli Pothole (Nemea, Peloponnese) is a karstic cave with paleontological interest that is described and mapped for the first time here.
- The fossilized bones belong mainly to *Ursus arctos* L. that were found either complete and well preserved or fragmented.
- A tibia diaphysis and a distal metapodial are best described as *Panthera pardus* (L.). These leopard bones from Nemea constitute the first hard evidence as to the origin of the Nemean lion mythology.
- The micromammalian remains belong to the following rodents: *Crocidura* sp., *Microtus (Microtus) arvalis* (PALLAS, 1778), *Microtus (Microtus)* cf. *nivalis* (MARTINS, 1842), *Microtus (Pitymys)* cf. *subterraneus/multiplex*, *Cricetulus migratorius* (PALLAS, 1773). A maxilla fragment belongs to a small reptile.
- The fossil brown bear is referred to for the first time in the Peloponnese, while its Early Pleistocene ascendant *Ursus cf. etruscus* has already been reported from Achaia. However, felids have already been reported in the Peloponnese: leopard, lynx and wild cat are found in the same context in the Middle Pleistocene site of Apidima (Mani peninsula) to the south. Also, two leopard skeletons were found in the Dyros Cave.
- The brown bear that still lives in Greece is indicative of a mountainous environment and this is consistent with the environment of the Kitseli Pothole.
- Of the KNP micromammals, the presence of *Microtus* with three species implies a Middle Pleistocene to Holocene age for the fauna of Kitseli, while the micromammalian assemblage suggests a temperate climatic phase.
- The association of a brown bear, a leopard as well as of the rodents *Microtus nivalis* and *Cricetulus migratorius* has been also determined in the Late Pleistocene fauna the Vraona Cave (Attiki).
- The geological age of the Kitseli Pothole fauna is Late Pleistocene.

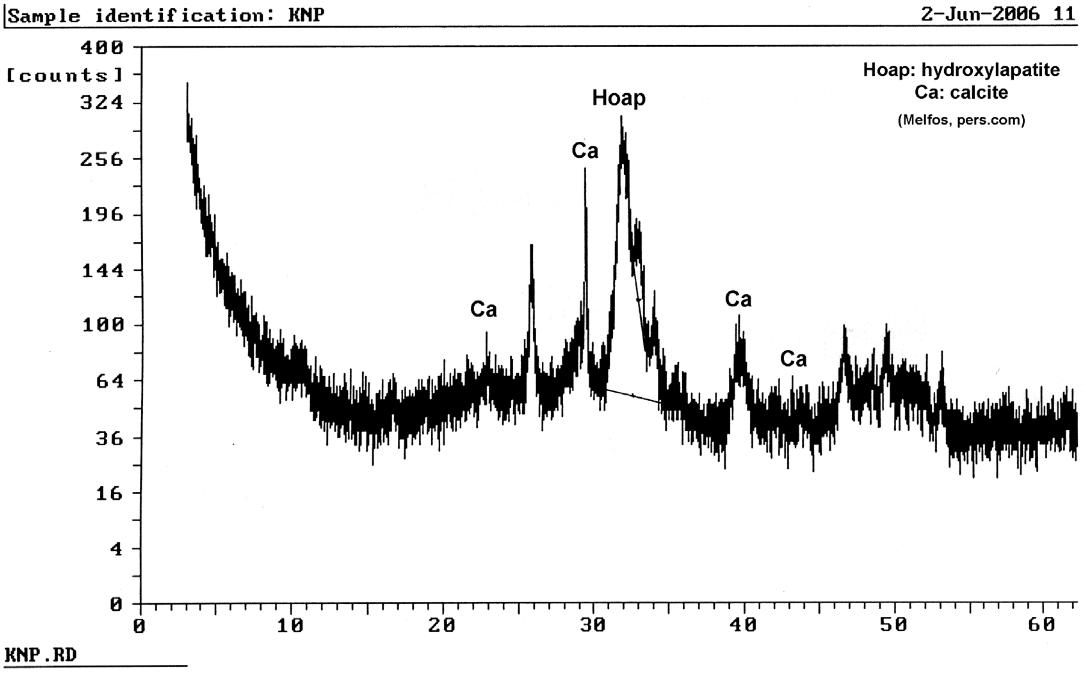


Figure 9. The XRD profile of bear bone powder (KNP). The Crystallinity Index is measured according to the method of X-Ray diffraction (used by Bartsiokas & Middleton, 1992) in order to access the degree of fossilization. The sample was analyzed by Dr B. Melfos.

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THE GREEK LATE NEOGENE-QUATERNARY URSIDS IN RELATION TO PALAEOGEOGRAPHY AND PALAEOENVIRONMENT

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Abstract: The family Ursidae appears to be a sensitive mammal group, promptly reflecting large but also small scale changes in global environmental conditions. Although the Greek ursid record is extremely incomplete, especially regarding the late Miocene-early Pliocene period, it is evident that the main evolutionary and ecological trends of the family are roughly depicted. The presence of Ursidae in Greece, and the southern Balkans in general, is highly controlled by palaeoecological factors concerning primarily climatic and vegetational changes.

Key words: Ursidae, Greece, palaeoenvironment, distribution, Cenozoic.

INTRODUCTION

The Greek Neogene/Quaternary continental record exhibits an important archive of fossil mammal assemblages spanning in time from the middle Miocene up to the late Pleistocene. Although most large mammal families occur regularly, the presence of Ursidae shows strong fluctuations in time and space. Of the three recognized European Neogene Ursidae subfamilies (Ginsburg, 1999), Phoberocyoninae (MN1-MN6) and Hemicyoninae (MN1-MN7/8) have never been recorded in Greece, whereas Ursinae (MN3-recent) are exceptionally rare in late Miocene and middle-late Pliocene assemblages, but quite common in middle-late Pleistocene ones. In this short communication, the presence of ursids in Greece is discussed with respect to the general palaeozoogeographic dynamics of the family during Neogene and Quaternary.

Starting with *Phoberogale bonali,* the oldest European occurrence of the family Ursidae, discovered in French late Paleogene deposits (Ginsburg, 1999), the chronological and geographical distribution of ursids in Europe appears to be highly heterogeneous, reflecting major environmental changes. Therefore, the Greek ursids are also regarded in relation to their palaeoenvironment, as it is extracted from the palaeoecological spectra of the accompanied large mammal faunas.

THE GREEK URSIDAE RECORD

Apart from their presence in middle-late Pleistocene cave deposits, ursids are usually rare in the Greek fossil record both in number of specimens and species. Currently, three genera with eight species are known from 19 large mammal faunas spanning in time from the middle Turolian (~7.5 Ma) to the latest Pleistocene (~10,000 years) (tab. 1, fig. 1). *Bosdagius felinus* Sickenberg, 1968 from Volakas is considered to be synonymous with the widespread *Ursus etruscus,* whereas *Ursavus ehrenbergi* THENIUS, 1947 from Halmyropotamos is regarded as a valid species, although its relations with other representatives of the genus are still uncertain.

Ursids appear in Greece during middle Turolian and from middle-late Villafranchian onwards (fig. 1). Two main factors are responsible for the significant gap in the Greek ursid record during latest Miocene-middle Pliocene (tab. 1, fig. 1). The absence of Ursids from the well-known and rich large mammal faunas of Dytiko (MN13, late Miocene; Axios valley), Maramena (MN13/14, latest Miocene-earliest Pliocene; Serres basin) and Megalo Emvolon (MN15, early Pliocene; Thermaikos basin) is possibly related to the environmental changes at the beginning of Pliocene, as will be discussed below. On the other hand, their absence during the early Villafranchian

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Table 1
Chronological distribution of Greek ursids.

Epochs		Ages	Localities	Species
Pleistocene	Late		Vraona	*Ursus arctos*
			Agrapha Cave	*Ursus spelaeus*-group
			Ioannina Cave	*Ursus spelaeus*-group
			Loutra Arideas Cave A	*Ursus ingressus* **
	Middle		Drama	*Ursus spelaeus*-group
			Petralona Cave	*Ursus* cf. *deningeri; Ursus spelaeus*-group
			Makinia	*Ursus* cf. *etruscus*
	Early	Villafranchian	Kastritsi (Achaia)	*Ursus* cf. *etruscus*
			Apollonia	*Ursus etruscus*
			Libakos	*Ursus* sp.
Pliocene	Late		Vassiloudi	*Ursus etruscus*
			Volakas	*[Bosdagius felinus]**
	Middle		Dafnero	*Ursus etruscus*
			Sesklo	*Ursus etruscus*
	Early	Ruscinian		
Late Miocene	Late			
	Middle	Turolian	Pikermi	*Ursavus* sp., *Indarctos atticus*
			Samos	*Ursavus* cf. *depereti*, *Indarctos atticus*
			Halmyropotamos	*Ursavus ehrenbergi*
			Perivolaki	*Ursavus depereti*
	Early			

*=nomen nudum; **=*Ursus arctos* is also mentioned but outside cave A. Data from: de Bonis & Koufos, 1999; Koufos & Kostopoulos, 1997; Rabeder & Tsoukala, 1990, Tsoukala, 1992, Tsoukala & Rabeder, 2006.

(MN16, middle Pliocene) is evidently due to the scarcity of contemporaneous faunas in SE Europe of this age.

DISCUSSION

During the early Miocene (MN1-MN3), ursids were restricted in the laurophyllus evergreen forests of central-western Europe (France, Spain, Germany, Austria), represented mostly by carnivorous species with running ability (fig. 2). Their limited spatial distribution suggests strong dependence on environmental factors (e.g. climate, vegetation), whereas the Eastern Paratethys and the active Fore-Carpathian basins (Popov *et al.,* 2006) must have prevented a southward migration.

From the end of early Miocene to the end of middle Miocene (MN4-MN7+8), ursids show their widest geographic expansion from Turkey to Spain, and their greatest species diversification (especially during MN5) (fig. 2). The abundance of omnivorous ursids in relation to carnivorous ones shows a general trend to increase throughout this period (fig. 3), contrasting the pattern of general decrease in number of ursid species after MN5 (fig. 2). Although the extended land between the Eastern Paratethys and the Mediterranean was connected with the European mainland both from the east and west (Popov *et al.,* 2006), ursids did not invade this area, being restricted northwards of the Alpine Chain.

During the Vallesian, the middle Miocene warm subtropical conditions in Europe came to an end and tropical forests were replaced by deciduous and sclerophyllus ones, while grassy/bushy landscapes gradually extended from the east to the west (Koufos, 2006a and literature therein). As a result, the European ursids declined drastically (fig. 2); phoberocyonines and hemicyonines permanently disappeared, whereas forest-dependent primitive omnivorous ursines remained in several refuge areas of Western Europe, causing a high signal during MN9 (fig. 3). Nevertheless, at the end of the Vallesian (MN10), the carnivorous ursine genus *Indarctos*, already known from MN7+8 assemblages, predominated (fig. 3) and for the first time *Indarctos arctoides,* a medium-sized (160 kg) meat eater, invaded the eastern Balkan area (Moldova

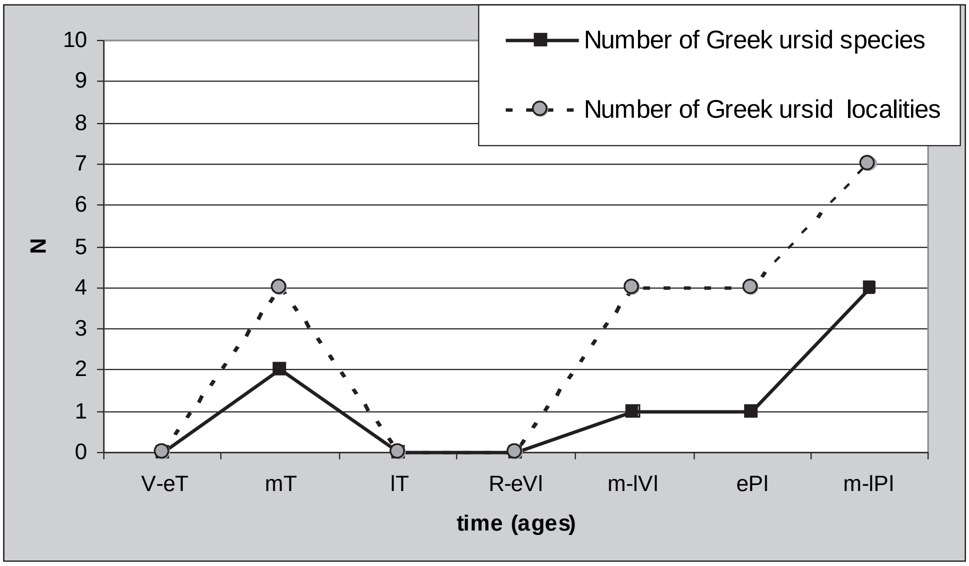

Figure 1. Time distribution of Greek ursids. Data from Koufos & Kostopoulos, 1997 and pers. obs. Abbreviations: V: Vallesian; T: Turolian; R: Ruscinian; Vl: Villafranchian; Pl: Pleistocene; e: early; m: middle; l: late.

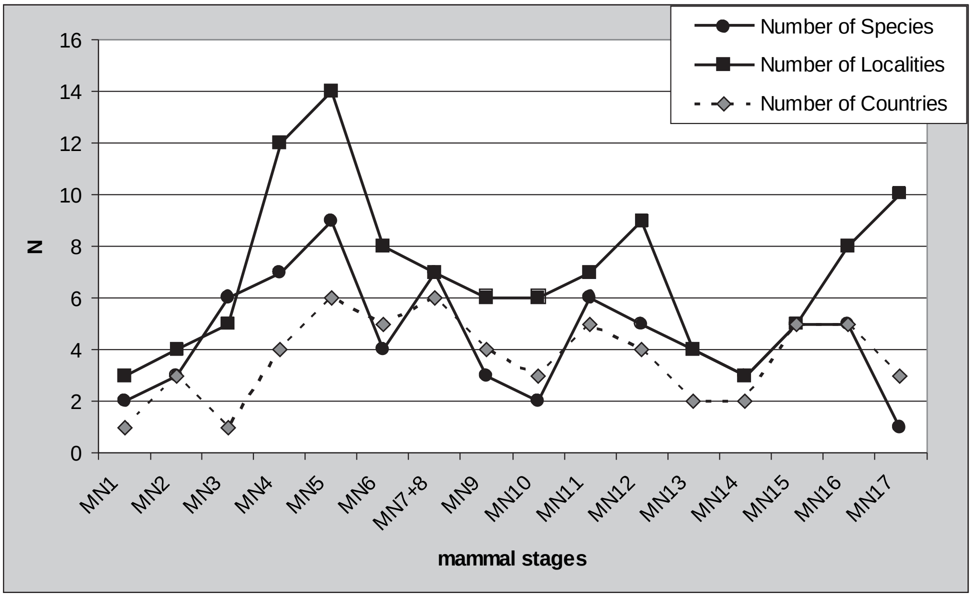

Figure 2. Time distribution of European ursids. Data from NOW 2003 and pers. obs.

and Thrace) probably through a forest corridor along the east-Aegean shore (Geraads *et al.*, 2005) (fig. 4).

From the beginning of Turolian (MN11) until MN12, the SE of Europe enters into a more arid phase, during which sclerophyllus and xerophytic plants became more abundant and parkland environments prevailed (Agusti & Antón, 2002). Omnivorous and carnivorous ursines recovered significantly (figs. 2, 3), but for the first time their signal became stronger in east than in west Europe (fig. 4). During this period, ursines occupied the Balkans (Hungary, Greece, Bulgaria) and penetrated Italy.

Following the general tendency of the subfamily Ursinae to move southwards, the large omnivorous *Ursavus depereti* (~100 kg), already known from the late Vallesian-early Turolian of central-western Europe (Solbay, Melchingen, Dork Dürkheim) (Now, 2003), appears in the fauna of Perivolaki (central Greece), dated at the beginning of MN12 (middle Turolian) or before 7.5 Ma

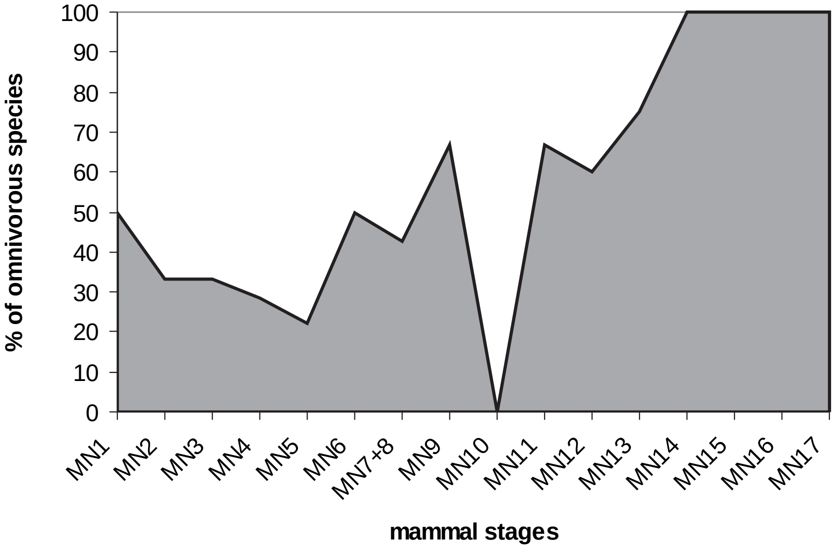

Figure 3. Time distribution of European omnivorous Ursidae. Data from NOW 2003 and pers. obs.

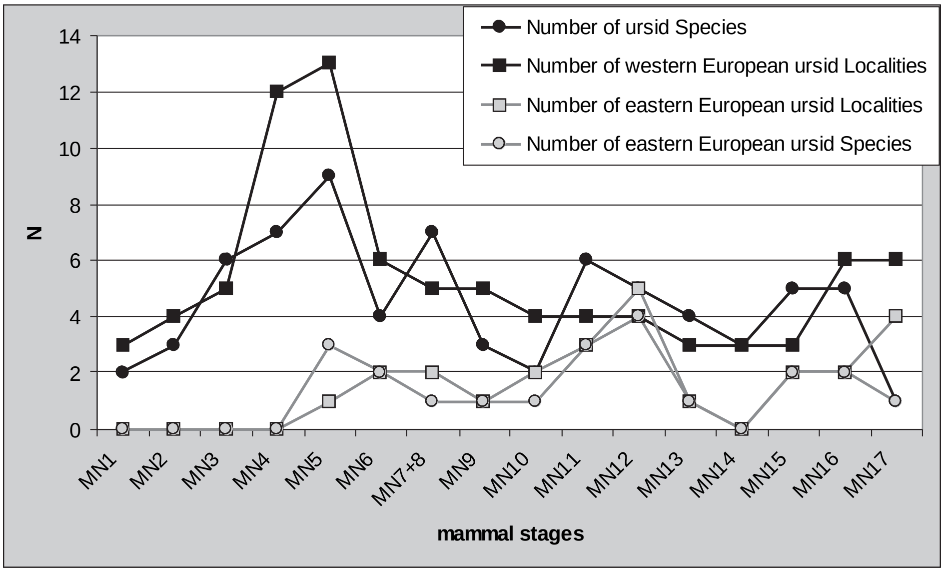

Figure 4. Comparison between the time distribution of ursids in western and eastern Europe. Data from Now (2003) and pers. obs.

(Koufos, 2006b). The palaeoecological reconstruction of Perivolaki and the contemporaneous fauna of Hadjidimovo in Bulgaria (Koufos *et al.*, 2006, Merceron *et al.*, 2006) support an open bushy/woody landscape with grassy undergrowth, in which meal-by-meal mixed feeding bovids and grazing-mixed feeding hipparions predominate in a fauna that can still support browsers.

Perivolaki and Hadjidimovo represent the last phase of the early Turolian east European large mammal association, toward the classical "pikermian biome" of MN12, characterized by a more advanced stage of the opening of tree cover. Such a seasonal environment with grassy vegetation and bushy/wooded patches (Bonis *et al.*, 1992, Koufos *et al.*, 2006, Merceron *et al.*, 2006), with a diverse fauna of mostly open dwellers, such as *Helladotherium, Microstonyx, Gazella, Prostrepsiceros, Tragoportax, Palaeoryx, Pachytragus/Protoryx* and slender *Hipparion* morphotypes, can support more varied omnivore assemblages. As a result, a new ailuropodine ursid, *Indarctos atticus* arrived in the Balkan area (Kalimanci, Bulgaria)

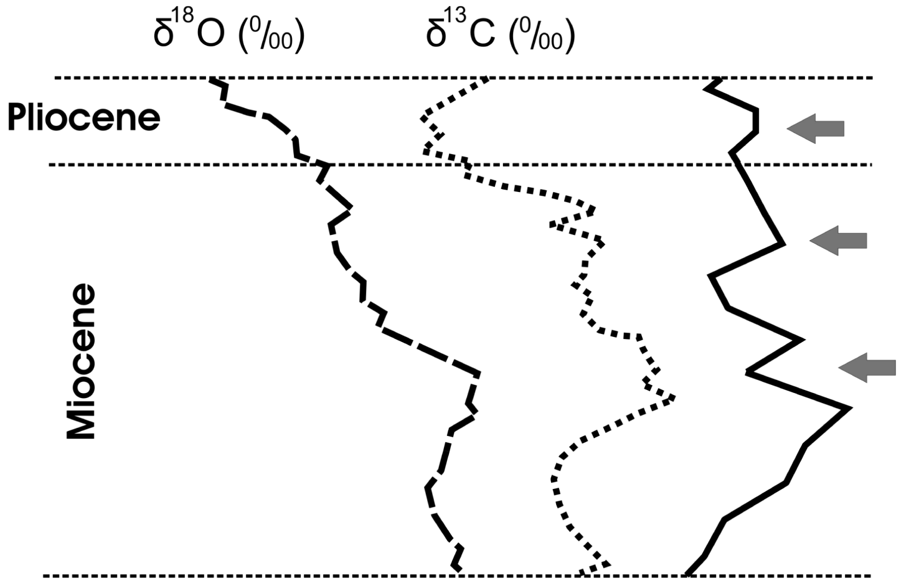

Figure 5. Comparison between the global deep-sea oxygen (dash-line) and carbon isotope (dot-line) records with the ursid diversity during Neogene (black line). (Curves adapted from ZACHOS et al., 2001).

and accompanied *Ursavus* in the late middle Turolian Greek faunas (Pikermi, Samos). This terrestrial species was much larger in size than the Vallesian representatives of the genus, reaching 350 kg in weight and had flexible feeding habits, adapted to switch between a plant dominated and meat dominated diet (VIRANTA, 2004).

From the end of the Miocene (MN13) to the beginning of the Pliocene (MN14), a new phase of warm-humid climate with low amplitude changes allowed ursids to undergo a second decline (fig. 2), during which carnivorous species were permanently replaced by omnivorous ones (fig. 3). The effects of this environmental inversion seem to be stronger in east Europe (fig. 4). At the same time, the rare MN11-MN12 ailuropodine *Agriotherium* spread rapidly. Although *Agriotherium* was considered to be a carnivorous genus, it was later shown that its diet mostly consisted of plants, together with animal material obtained by scavenging (SORKIN, 2006 and literature therein). As a response to the climatic shift toward more humid conditions and following the general trend of the family, both *Ursavus* and *Indarctos* disappeared from the latest Miocene-early Pliocene Greek record (localities Dytiko, Maramena). Indeed, during this period, Greece, and the Balkans in general, entered into a wet phase, which is directly reflected in the extended lignitogenesis of the beginning of Pliocene. Wooded/bushy landscapes alternate with some grassy ones (MERCERON *et al.,* 2005 and literature therein) and forest-dependent species such as tragulids, cervids and chalicotheres re-appeared in the area. In Western Europe, small and primitive representatives of the genus *Ursus* made their first appearance in the established evergreen/mixed forests dominated by Taxodiaceae (AGUSTI & ANTÓN, 2002). *Ursus minimus*, the first member of the *U. arctos/U. thibetanus* lineage, was a temperate-forest dweller originated probably from an Asian ursavi ancestor (AGUSTI & ANTÓN, 2002). *Agriotherium* and primitive *Ursus* widely overlap in time but they rarely co-exist, suggesting quite different ecological profiles and habitats.

Since the early Pliocene, the Greek mammal record (MN14-MN16) is rather poor (KOUFOS & KOSTOPOULOS, 1997), it is not clear if the absence of ursids from Greece is due to taphonomic biases or environmental factors. The presence of omnivorous ursines in Western Europe significantly increased during MN15, but from MN16 to the end of Pliocene, the number of species decreased drastically (figs. 2, 4). This was certainly the effect of the first glaciation process in the Northern Hemisphere, which allowed an important European faunal turnover, highly controlled by the new climatic conditions and the establishment of a double seasonality model.

Most European ursine species failed to survive until the end of Pliocene (MN17). From 2.5 Ma onwards (MN16 -MN17), the southern Balkans and neighboring areas entered into a new arid phase, related to the glacial-interglacial dynamic established in the Northern Hemisphere. During the middle-late Villafranchian (MN17), the mammal faunas from Greece already show a more open and arid character than the contemporaneous faunas of west Europe (Kostopoulos & Koufos, 2000): *Gazella* persisted here associated with the new Asian immigrant *Gallogoral*, the widespread *Gazellospira* and the giraffid *Mitilanotherium*, all indicative of open/bushy landscapes. These conditions were expanded southwestwards until the end of Pliocene (Kostopoulos *et al.,* 2002; Agusti & Antón, 2002). At the same time, ursines re-appeared in the southern Balkans: a species intermediate between *Ursus minimus* and *U. etruscus* is recorded in the Bulgarian locality of Varshets (early MN17) (Spassov, 2002). From MN17 to the end of early Pleistocene, *U. etruscus,* a medium-sized (~90 kg) close relative of the living black and brown bear, became the single representative of the family (figs. 2, 4), occupying the entire territory south to the Alpine Chain, from Spain to Greece and also probably to China. The post-Olduvai expansion of steppes and cooler temperate conditions in southern Eurasia seem to have favored the widespread of the species, which is more rapidly spreading in the east (fig. 4). Although the *U. etruscus* record remains scarce in the Balkans, the species is present in the Greek land until the end of the early Pleistocene, contributing to the open landscape mammal faunas of this period, which were dominated by primitive bisons, large ovibovines, large stenonoid horses, praemegacerids, hippos etc (Koufos & Kostopoulos, 1997).

Early middle Pleistocene faunas seem to be missing from Greece. In central-western Europe this period is characterized by a new warm phase of alternations of mild glacial intervals with warm interglacial ones, allowing European forests to recover and temperate elements to (re-)enter (Agusti & Antón, 2002). From middle Pleistocene onwards, the establishment of the bipolar climate in the North Alpine areas forced the south European environment to alternate between Mediterranean arid and mild-temperate, allowing the modernization of the mammal fauna, which now includes true wolfs and foxes, large bovines, goats, asine horses, elephants, rhinos, fallow, red deer etc. Under these conditions, *U. etruscus* gave rise to two branches: an Asian one leading to the late Pleistocene *U. arctos-U. maritimus* and a European one leading to the early-middle Pleistocene *U. dolinensis-U. savini* and their middle Pleistocene descendant *U. deningeri* (Kurten, 1976; Garcia & Arsuaga, 2001; Agusti & Antón, 2002). Although both *U. deningeri* and *U. arctos* were highly omnivorous and not very distinct from a dietary point of view (Stiner *et al.,* 1998), the robust and mainly vegetarian *U. deningeri* already exhibited excavating and scavenging habits that were later fully expressed in its offspring, the cave bear. In Greece, *Ursus deningeri* is only known from the lower levels of the Petralona cave (~600,000 years) (Tsoukala, 1989; Rabeder & Tsoukala, 1990).

During the last late Pleistocene interglacial-glacial cycles, the European environmental conditions rapidly interchanged between cold-temperate and the steppe/tundra biome predominated. In Europe and the Balkans, the mammal fauna is characterized by specialized grazing bovids and equids and mixed deciduous-pine forest cervids, all together indicating a strong altitudinal control. In this context *U. deningeri* gave rise to the low altitude cave bear *U. ingressus* and the high altitude cave bear *U. spelaeus* ssp. (Rabeder & Hofreiter, 2004). The cave bear was a primarily herbivorous and specialized cave dweller (Bocherens *et al.,* 1994; Pinto & Andrews, 2004), about 30% larger than the more carnivorous brown bear, with which it coexisted in the mountain areas until the end of the last ice age.

The diversity curve of ursid species throughout Neogene fit pretty well with those of the global deep-sea oxygen and carbon isotope records (fig. 5), suggesting a high dependence on climatic conditions. Ursids positively correspond to the mid-Miocene climatic optimum, the Turolian dry warming and the early Pliocene increase of temperature and humidity, whereas they seem to react negatively to the Serravalian and Pleistocene cooling.

CONCLUSIONS

The present day record of Greek Ursidae lacks homogeneity in time distribution. However, the gaps in the data-continuum are only partly due to taphonomic biases (i.e., during early Villafranchian or early middle Pleistocene), whereas in most cases they roughly reflect general palaeoecological and palaeozoogeographical trends, related to the response of the family to global environmental changes. Ursid diversity was always low in Greece, with a maximum of two co-existing species during MN12 and late Pleistocene. The analysis shows that the presence of Ursidae in Greece together with the southern Balkans, is highly controlled by palaeoecological factors, concerning primarily large-scaled climatic and vegetational changes in Europe. Both the middle Turolian and middle Villafranchian - early Pleistocene species that appeared in Greece represent medium to large-sized highly omnivorous or flexible carnivorous offshoots of central-western European ursines, adapted to open bushy landscapes. From middle Pleistocene onwards the presence of ursids in continental Greece is constant and comparable with other south European countries, regulated by the succession of Pleistocene stadials and interstadials.

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KARL MEULI'S "GRIECHISCHE OPFERBRÄUCHE" - TOWARDS AN ETHOLOGY OF RELIGION

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Abstract: On a first view, the academical disciplines "history of religions" and "ethology" have little in common. As recently as 1945 the philologist and historian of religions Karl Meuli (1891-1968) has been able to prove that religions as distinct from one another as the religions of ancient Greece, imperial Rome, recent arctic hunter-gatherers, and probably even prehistoric hunters, shared similar ritual customs. In spite of the prevailing paradigm Meuli concluded that these similar manifestations of sacrificial practices must originate in an innate behavior pattern acquired during human evolution.

Key words: Anthropology, Etholology of Religion**.**

INTRODUCTION

During the last few years the alleged new discipline of cultural studies determined the discourse within the humanities as much as the demand for interdisciplinarity. This postulation was associated with the strong conviction of the personal progressiveness of the scholars under question. This self-assessment, however, is not in accordance with the facts. Even the specialization of the natural sciences and the humanities into disciplines and subdisciplines is a phenomenon mainly of the last fifty years and, therefore, quite new. Already during the beginning of this development, clear-sighted scholars tried to bridge the gap between the sciences and the humanities. Not astonishingly, many of those scholars came from the discipline of anthropology that has to deal with both scientific and scholarly approaches. One of the most renowned proponents of this approach was the skilled anthropologist Victor Witter Turner, who wrote as early as in the seventies: "One remedy would be to seek means to overcome the overspecialization of departments and the atomism of funding. My paper indicates that a new breakthrough in anthropology depends upon a serious sustained effort by the proponents of severely segregated subdisciplines… to relate the best findings of their segregated years." (TURNER, 1977). Even if Turners' postulation may have sounded uncommon to many of his contemporaries, he stood nevertheless in a strong tradition of outstanding researchers, who had never abandoned the approaches and results of more or less related disciplines who continued to consider anything qualified for broadening the scientific horizon.

Usually, in this connection a scientific transfer from the sciences into the humanities is brought into consideration, as the history of natural science easily proves. Famous philosophers and anthropologists such as Antoine de Condorcet (1743-1794), Herbert Spencer (1820-1903) or Edward Burnett Tylor (1832-1917) stressed the results of contemporary biology (having then discussed theories of the French biologist Jean-Baptiste de Lamarck), to develop their ideas of human evolution and the related development of society. In contrast, it is mostly forgotten that even the humanities have had a strong impact on biological science: No one less than Charles Darwin (1809-1882) and Alfred Russel Wallace (1823-1913) have developed their theory of natural selection (1858) in dependence on the work of the famous economist Robert Malthus (1766-1834) and his observation of the coherence of population-growth and available resources (Malthus; Essay on the Principle of Population, 1798).

A broader discussion of this interesting topic, however, would go too far within a symposium dedicated to the cave-bear and, to a lesser account, to phenomena related

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to its temporal and geographical environment. Therefore, I decided to introduce the work of a scholar, who stressed the same arguments and saw new approaches not only in the field of anthropology and philology, but in biology as well. Additionally, his research focused on Greece in historic and prehistoric times, and, therefore, is in the geographical and chronological range of our symposium. Karl Meuli's "Griechische Opferbräuche" (Greek Sacrifices), therefore, is meant as a hommage to our hosts and a plea for the entity of science.

THE ROOTS OF ETHOLOGY

On a first view, cultural anthropology including religious studies and ethology has little in common. Whilst historians of religion use hermeneutical methods, ethology has a strong foothold in biology including scientific methodology.

The historical roots of ethology can be traced to Charles Darwin's theory of evolution. In his book The Expression of the Emotions in Man and Animals (1872) he recognized that the role of instinct is just as important for the survival of the species as the adaptation of morphological structures in the course of their phylogenetic histories. During the following decades, however, the Darwinian approach continued to be disregarded. On the contrary, a scientific school with roots in psychology dominated the study of animal and human behavior. This so-called behaviorism was based on the premise that psychology should be regarded as the science of behavior, rather than the science of mental life. Proceeding from the assumption that behavior is a product of learning, American behaviorists focused on the study of observable behavior and the ascertainable or contrived circumstances of its occurrence. As a result, behaviorists were successful in all kinds of research with regard to general laws of learning, but failed to take evolutionary approaches into account. Until the 1970s, most behaviorists and sociologists were convinced that the behavior of humans and animals was mainly a product of their environment and education (HINDE, 1982).

Within the scientific climate at that time, anthropology and the study of religions developed approaches of cultural relativism that considered human culture as phenomena upon which the biological heritage had no influence. This opinion first came into question when the experienced philologist Karl Meuli (1891-1968) was able to prove that religions as distinct from one another as the religions of ancient Greece, imperial Rome, recent arctic hunter-gatherers, and probably even prehistoric hunters, shared similar ritual customs. This observation was unintelligible from an environmental point of view. In spite of the prevailing paradigm Meuli concluded that these similar manifestations of sacrificial practices must originate in an innate behavior pattern acquired during human evolution.

Karl Meuli

Karl Meuli, the classical philologist at the university of Basel, did not merely make his name as an exponent of philological research, but followed the tradition of such famous predecessors as Hermann Usener (1834-1905) from Bern or Johann Jacob Bachofen (1815-1887) from Basel. Even if these scholars had been outstanding exponents of philological research in the nineteenth century, they owe their lasting fame in the realm of the humanities to specific approaches that crossed the borders of their particular discipline. While Bachofen had stressed the historical approach to shed light on the development of Greek and Roman religion in general and the role of mother-goddesses in particular, Hermann Usener went so far as to conjecture about the origin of religious ideas in general. He thereby stressed the results of contemporary psychology and, as a result, saw that religion is mainly found in the natural fright of threatening apparitions such as lightning or thunderstorms. These were typically unexplainable until a first term was found that named the phenomenon, making it acceptable to the human mind and, as a result, less frightening. Only later did these items become personalized, growing into the gods and goddesses of ancient times - so far Usener. In this context it may be interesting to mention that the skilled art-historian Aby Warburg used that approach later to develop his own ideas, that partly founded in Darwin's The Expression of the Emotions ... Warburg's essay A Serpent Ritual and his Mnemosyne Atlas, actually undergo a renaissance, even if their importance was hardly valued during the time of their first publication (FORSTER, 1999, WUNN, 2005).

Something similar to this happened to the non-philological work of Karl Meuli. Considerable internal and external obstacles have stood in the way of any thorough understanding of Meuli's non-philological writings. Almost his entire scholarly output was published in German, and, therefore, was seldom cited, even when closely relevant. Even if one cannot say that Meuli's initiatives attracted no attention - for the discipline of the history of religions the contrary is true (BÖHME, 2001) - but the pioneering ideas of his approach were not discerned until today.

Any contemporary interest in Meuli, therefore, should not arise mainly in connexion with his philological research, but from issues connected with the decipherment of general patterns of human behavior as adapted during human evolution.

GREEK SACRIFICES - GRIECHISCHE OPFERBRÄUCHE

Not only recent generations, but also the Greek people of ancient times feared their own myths and hardly understood meaning and reason of their sacrifices. Not only did the narratives speak about cruelties such as the emasculating and laceration of a god or the ravage of a town, but were improper to give meaning to a pious life. In addition to that people consistently came across antilogies and discrepancies in myths as well as in rituals (Most, 1991, Meuli, 1946). This mostly concerned the sacrifice on behalf of the Olympic gods. A common offering was divided into a nearly valueless part for the gods containing mainly the bones and the gall, whilst the humans received the precious meat.

Whereas Greek mythology tried to explain this unreasonable way of sharing with the help of the legend of a former deceit of Prometheus, philological research was confronted with a mystery that absorbed the effort of countless researchers past and contemporary. For Meuli, the answer seemed to come into reach by not only bringing the results of the new discipline of archaeology into account, but also by using a genuine scientific approach. His search for human universals included both generalization and reductionism that are usual procedures in the sciences, but abandoned in the humanities.

Concretely, Meuli first stressed a comparison of different types of sacrifices at ancient Greece, before making an excursus deep into Greek history and prehistory, when the predecessors of the Greeks still had made their living as hunter-gatherers in the steppe of Eurasia.

Analogies among different types of sacrifice proved that the various sacrifices common in ancient Greece such as in hero worship or ancestor worship were meant as aliment and support. Therefore, the receivers of the offering had not to be content with bones, but should receive proper meals from their worshipers. Only later, when the whole community had taken on the duty of worship, even the gods and goddesses knew the promise of meals in which outstanding members of the community took part.

Shortly after this, the whole demos became participant in the sacrifice and the following meal. The derivation of sacrifice with respect to elder customs such as the worship of the dead may explain its origin as well as the joint meal, but fails to explain the unjust distribution of goods. ("Eine Speisegabe kann das olympische Opfer ursprünglich nicht gewesen sein." Meuli, 1946: 214.) This phenomenon is explicable only, if hunting customs of contemporary and ancient hunter-gatherers of the arctic zone are brought into account (Meuli, 1946: 223). If an animal is hunted and killed by hunter-gatherers, the carcass is transported into the village and treated with care. The dead animal is often showered with gifts and always treated with honour. After certain ceremonies and the meal, the left-overs, especially the skeleton of the animal is treated in a specific way. Sometimes the bones are collected, sometimes one tries to reconstruct the appearance of the former animal. These ceremonies serve the purpose that a certain god-like being such as a master of animals or a pothnia theron may use the remnants to recreate the animal and, therefore, will continue to provide the community with meat (Wunn, 2005).

Meuli was convinced that similar customs were widely common even among prehistoric hunter-gatherer communities. Contemporary proceedings of prehistoric research reinterpreted assemblies of bones in certain caves as the remnants of hunting rituals among prehistoric tribes and Meuli had no reason to distrust those results provided by Emil BÄCHLER and Konrad HÖRMANN (Pacher, 1997; Wunn, 2005). According to Meuli, the specific form of the olympic sacrifice should to be seen as a so-called survival from prehistoric times, that was adapted to the needs of later generations without loosing its characteristics. Especially those relicts from ancient times make the sacrifices look strange even in the classical period.

As a result, Meuli explained that even social behavior as a process of adaptation during evolution obeys biological rules. According to Meuli, adaptive stategies have to result not only in physiology and morphology, but also in adaptive behavior, and, finally, in culture.

RECENT APPROACHES

Before discussing Karl Meuli's impact on modern anthropological research, a short overview about the recent knowledge concerning the origin of Greek sacrifices should be given. Even if it is obvious that Greek offering rituals in their classical form must have had a long history, their rooting in Neanderthal hunting customs is not very likely. Later investigations of supposed remains of a cave bear worship in the Paleolithic (Pacher, 1997; Wunn, 2005) or related rituals for example at Monte Circeo did not bring any evidence for such an assumption. On the contrary, is it most unlikely that religious practice and feelings developed earlier than during the Upper Palaeolithic period. On any other aspect of the question Meuli seems to be correct: His assumption that Greek offering customs may be originated in inherited hunter-gatherer-customs is most probably correct. Even if the sacrifice of bones is not as widely spread as he assumed, it was probably common within a region from where the indoeuropean Greek people originated, so that a historical relation to hunter-gatherer-customs seems most likely. On the other hand it is commonplace among psychologists that the killing of a being, be it human or non-human, is strongly related to feelings of guilt that have to be appeased in specific rituals. Besides that, many researchers even of the later decades referred to Meuli's approach of the display of pretended innocence that serves the purpose to be released from guilt. From a psychological point of view, this part of the sacrifice is supposed to have a cathartic effect insofar, as the ritualized killing is suitable for preventing uncontrolled outbursts of violence (Girard, 1992).

MEULI'S SUCCESSORS

According to Darwin, any behavior pattern is adaptive in the sense that it contributes to the reproductive success or to the survival of the individual, the group, or finally the species. In that sense, well adapted religious activities also promote the success of a culture. MEULI was the first who referred explicitly to the results of human ethology (a discipline that hardly existed during his time) when tracing rituals and other activities within the scope of religious behavior to their supposed biological origins. Several basic elements of religious practice and thought, and, in particular, sacrifice, have to be seen as being inherited from predecessors, where they may contribute to the survival of the individual or the group in dangerous situations. While Meuli placed emphasis on the origin of religion in strategies of survival, recent anthropologists such as Marvin Harris (1927-2001) see religious behavior as the result of the adaptation of a culture to its specific ecological niche. In this context, the occurrence of rites of passage, especially seen in male initiation, can be traced to biological roots. Especially in societies with a low-protein diet prolonged nursing is a necessity. This, however, results in a postpartum sex taboo that leads to polygeny. The resulting mother-child households, together with prolonged nursing, lead to an intensive bonding between mother and child and, finally, to cross-sex identification. Severe male initiation ceremonies that include circumcision or other forms of ritual torture and mind control are then required to break the prepubescent identity in order to allow for later identification with fathers and other males.

A similar approach scaped the work of Roy Rappaport (1926-1997). His famous book Pigs for the Ancestors is a classic case study of human ecology in a tribal society, focusing on the the role of ritual in local and regional resource management. Rappaport describes the role of a religious ceremony among the Tsembaga, a community of horticulturalists in New Guinea. After warfare, the Tsembaga used to perform a ritual in which a large number of pigs were slaughtered in order to offer the pork to their ancestors. As Rappaport found out, the ritual was articulated with the ecological relationship among people, pigs, local food supplies, and warfare. Warfare and the succeeding ritual occurred, when the pig population had grown to a certain extent. This means, that the ritual kept the number of pigs within the capacity of the natural environment and prevented land degradation. Even warfare had its certain place within the ecological relationship among people, pigs, local food supplies, and social relationships, because it caused the necessity of finding allies among the neighboring villagers, that had to be impressed by hospitality and wealth, displayed by the amount of meat served to them during the ritual.

Even if Harris, Rappaport and other proponents of the so-called cultural materialism sometimes overstrain their approach and ('sometimes' may be replaced with 'possibly') loose sight of historical relations, they succeeded in directing the attention of a too often over-specialized discipline of cultural anthropology to regularities occurring among all human societies and cultures.

UNITY OF THE SCIENCES

By adopting and establishing a new approach in the humanities, Meuli still proves to be the underestimated proponent of a genuine biological conception of human cultural behavior including the various religions and related customs. During a time formed by behaviorism and therefore by a scientific paradigm reducing culture to learned behavioral patterns, he emphasized on the strong roots of human behavior to its biological heritage, its adaptive value and its evolution during history. For this reason Meuli became the proponent of a discipline that was not appreciated until twenty years later, when Konrad Lorenz and Niko Tinbergen or Huxley and Robert Hinde made ethology popular.

Meuli should have set standards in anthropology. Solely because his revolutionary approach was hardly understood in the humanities, Meuli is a nearly forgotten figure in cultural anthropology. Most certainly, Meuli is well regarded as long as research on Greek religion is in demand, and equally, his research on ritual is hardly questioned. Especially the German historian of religions, Walter Burkert, has recently stressed Meuli's approaches to develop his own concept of the origins of religion.

On the other hand, it remained overlooked that Meuli could develop a biological and evolutionary approach on religions. Similarly, his understanding of religion as a behavior pattern rooted in human biology was not understood by his contemporaries. His conviction that religious activity has to be seen as an adaptive reaction to requirements of the environment was to peregrine to be accepted. Only his (few and often criticized) successors succeeded in developing his approach and making it aware. Nevertheless, heavy criticism did not fail to appear.

In the meantime ethological approaches to the study of religions have helped to gain insight into the ways multiple cultural systems are related to the biology of the human species. It may not be disregarded, however, that the stress on universals runs the risk of deflecting attention from the characteristics of a given society and its religion that make it a solitary system of conceptions and deeds acquired throughout the course of history. At this point the evolutionary approach comes into the focus of attention, if the specific history of a society and its religion shapes the spiritual universe of a people and modifies certain psychological attitudes, which have retroactive effects on religious behavior and thought.

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THE YUKAGIR MAMMOTH: BRIEF HISTORY, 14C DATES, INDIVIDUAL AGE, GENDER, SIZE, PHYSICAL AND ENVIRONMENTAL CONDITIONS AND STORAGE

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BRIEF HISTORY

The Yukagir Mammoth consists of a unique, well-preserved partial carcass of a woolly mammoth, *Mammuthus primigenius* (BLUMENBACH, 1799). This specimen was discovered in the autumn of 2002 by Mr. V. Gorokhov and sons near the Maxunuokha River in northern Yakutia, Arctic Siberia, Russia (GPS 71° 52′ 988" North - 140° 34′ 873′′ East) (Lazarev *et al.,* 2004 and Mol et. al., 2004).

In September 2002, the head of this mammoth without the trunk, but otherwise almost completely covered with skin, was extracted from the permafrost. In June 2003 a team from CERPOLEX/Mammuthus, headed by Mr. Bernard Buigues, conducted a brief survey of the Yukagir Mammoth site in close cooperation with scientists of the Mammoth Museum in Yakutsk, Yakutia, and the scientific secretary of the Russian Mammoth Committee, Saint Petersburg, Russia. More remains of the Yukagir Mammoth were discovered. Soon it became evident that even more remains of this specimen are in the permafrost, not far below the surface, apparently in anatomical order and in well-preserved condition.

In the beginning of September 2003 a small team travelled to the site and excavated the left front leg of the Yukagir Mammoth. This leg was in anatomical position (fig. 1) and frozen solid, with ice crystals covering some parts. The radius/ulna and the complete foot are covered with soft tissue, skin and hair, and the "toes" are clearly delineated. In addition, parts of the intestines were salvaged.

In June 2004, a team of Russian, Yakutian, Japanese and other scientists visited the site of the Yukagir Mammoth. The objective of this expedition was to clean and to protect the site for the coming summer. A thick layer of frozen snow was removed, exposing some fur and underfur of the Yukagir Mammoth.

Figure 1. Excavation of the entire left front leg of the Yukagir Mammoth. Photograph: Francis Latreille.

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[7] Mammoth Site of Hot Springs, South Dakota, United States of America.

Table 1

Field number	Sample	Laboratory number	Results
CM-DM-64	Bone (rib)	GrN-28258	18,510 +/- 80 BP
CM-DM-65	Skin	GrN-28259	18,510 +/- 100 BP
CM-DM-66	Hair	GrA-24288	18,680 +/- 100 BP

GrN = Groningen Conventional radiocarbon dating
GrA = Groningen AMS radiocarbon dating

Table 2

Field number	Sample	Laboratory number	Results
	Bone (rib), same sample as CM-DM-64	AA-59602	18,160 +/- 110 BP

Table 3

Field number	Sample	Laboratory number	Results
	Bone	GIN-12719	18,200 +/- 60 BP

The final expedition for extraction of remains of the Yukagir Mammoth took place in the first half of September 2004. Remains of the vertebral column and the rib cage were recovered, as well as remains of the intestine. Samples of sediments and vegetation, above and beneath the mammoth remains were collected to analyze the environment of this mammoth. The Yukagir Mammoth has been added to the inventory of the Mammoth Museum of Yakutsk, Yakutia, Institute of Applied Ecology, Academy of Sciences of Sakha (Yakutia) Republic (Lenina prospekt, 39, 677891 Yakutsk, Russia) and it is currently kept frozen in an ice cave in Yakutsk.

14C DATES

Three samples of bone, skin and hair from the June 2003 expedition were sent to Dr. Johannes van der Plicht, Groningen University, the Netherlands, for 14C dating. The results are in tab. 1.

Average value of these measurements: 18,560 +/- 50 BP which calibrates into ca. 22,500 calendar years ago from today, expressed as 22,500 cal. BP.

A 14C cross-check (AMS) has been run in Tucson, Arizona, USA, initiated by Dr. Alexei Tikhonov, the results are in tab. 2.

Another 14C cross-check (conventional) has been run in Moscow by Dr. L. Sulerzhitsky, the results are in tab. 3.

THE INDIVIDUAL AGE

Estimation of the individual age of a woolly mammoth is based on the assumption that the life span of a woolly mammoth is similar to that of modern elephants in Africa and Asia. To estimate the individual age of a woolly mammoth, molars in the mandible are compared to those of an African elephant of which the individual age is known. As an example, the estimated individual age for the Jarkov Mammoth, Taimyr Peninsula, is 47-49 African Elephant Years (AEY).

The head of the Yukagir Mammoth (fig. 2, 3, 4, and 5) is extremely well preserved; almost the entire head, including the mandible, is still covered with thick skin and the mouth is closed, Tikhonov, 2004. Consequently, the molars in the upper and lower jaws are not exposed, and it is not possible at this stage, to inspect the molars of this mammoth, without inflicting damage. Based on the size and the curvature of the tusks, however, the Yukagir Mammoth could be identified as a mature individual with remnants of the lower and upper m/M 3's in occlusion. Non-destructive investigations on the skull of the Yukagir Mammoth using a CT-scan and three-dimensional images of the upper and lower molars during the World Expo 2005 in Japan, will shed new light on the individual age of this mammoth compared to AEY. These studies will also allow more detailed investigations of the dental wear pattern in occlusion.

THE GENDER

Considering the size of the head and its long and spirally twisted tusks, the Yukagir Mammoth was probably a male. No remains of the pelvic girdle have been traced, which could have provided confirmation on the gender of the animal. Investigation of the right tusk of the Yukagir Mammoth in September 2004 by Daniel C. Fisher corroborated the identification of a male individual.

Figure 2. Lateral view of the head of the Yukagir Mammoth. Photograph: Francis Latreille.

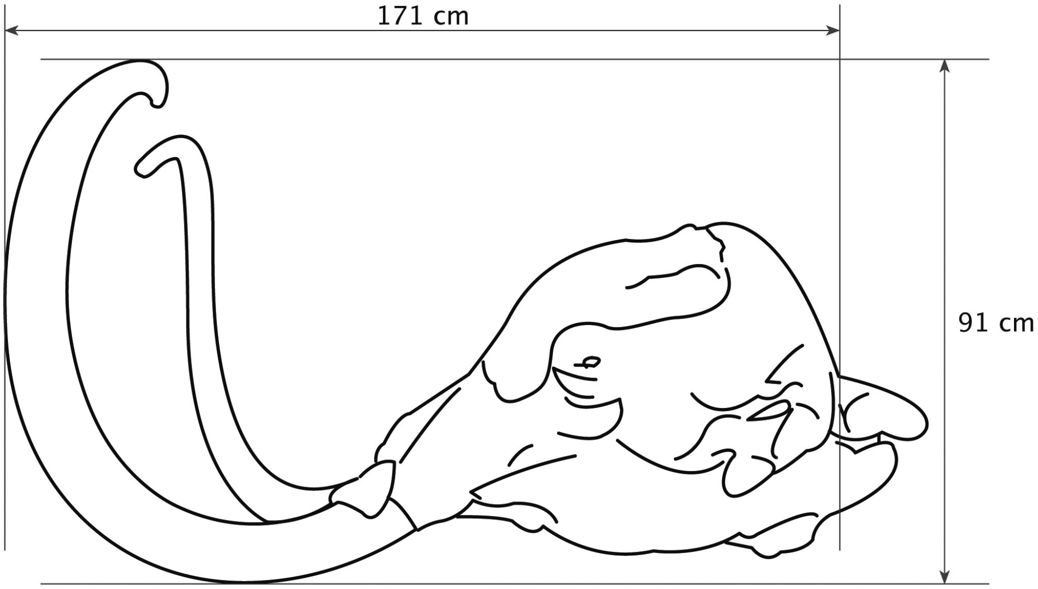

Figure 3. Measurements (lateral) of the head of the Yukagir Mammoth.

Figure 4. Frontal view of the head of the Yukagir Mammoth. Photograph: Francis Latreille.

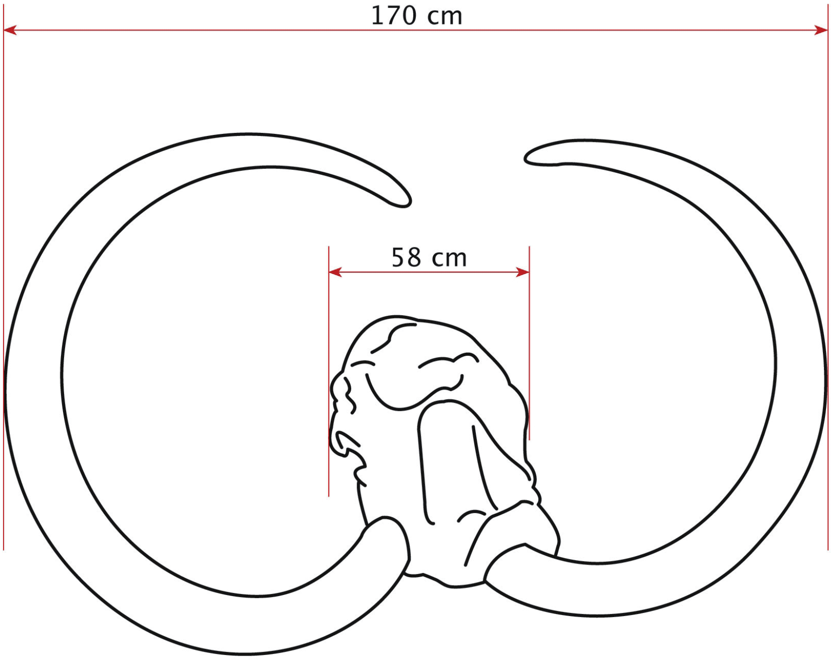

Figure 5. Measurements (frontal) of the head of the Yukagir Mammoth.

THE SIZE

The Yukagir Mammoth was average-sized for a male woolly mammoth. It had large spirally-twisted tusks (Cat. No. Mammoth Museum: N 7865), typical for an old individual. The shoulder height of the Yukagir Mammoth is estimated to have been 272.5 cm based on the measurements of the entire left front leg in anatomical position including 13 cm added for missing soft tissue at the shoulder (measurements see below). However, based on combined data from the entire left front leg and the forefoot circumference, the estimated shoulder height is 282.9 cm (Shoshani & Mol, 2004).

The excellent state of preservation of the Yukagir Mammoth provided a wealth of information on the exterior of a "woolly mammoth": the left side of the cranium is entirely covered with skin. Both the entire ear (fig. 6 and 7) and the eye opening (fig. 8), including eyelashes as well as the temporal gland opening are preserved (for measurements, see fig. 7).

The ear dimensions

Comparing the dimensions of the pinna, or external ear, of the Yukagir Mammoth (data given below) to those of an African elephant (after Shoshani *et al.,* 1987), we note the following. The height of the left ear Yukagir Mammoth is 30.7 cm, and that of the African elephant ("Ahmed") is 133.0 cm; the anterior-posterior distances of the ears are 17.5 cm and 90.0 cm, respectively; and the maximum thicknesses are 40.8 mm and about 10 mm, respectively. The surface area of the left ear of the Yukagir Mammoth is 537.25 square cm, and the surface area of the left ear of Ahmed is 11,970 square cm. It emerges that the surface area of Ahmed, the African elephant, is about 22 times larger than that of the Yukagir Mammoth. To our knowledge, this kind of comparison of the surface areas between the extinct mammoth and the living African elephant was not published previously.

Temporal gland

In living elephants this gland is known to function in establishing a hierarchy among males during breeding season (Easa, 2000; Poole, 2000; Schmidt, 2000). The gland secretes a chemical substance "temporin", which informs other males that the secretor with the highest chemical composition is in full musth (a word of Hindi origin, that means 'intoxicated', implying that the owner is in madness to win an estrus female), and this male is ready to mate with an estrus female. Among the lines of research under consideration is to search for temporin secretion in the woolly mammoth gland, if it did not decompose.

Figure 6. Complete ear of the Yukagir Mammoth. Photograph: Dick Mol.

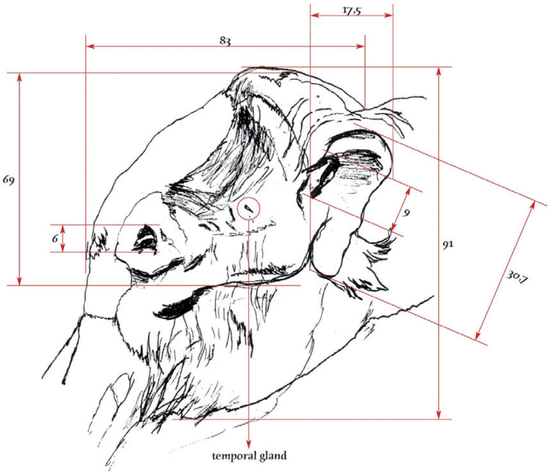

Figure 7. Measurements of the head, including the left ear, of the Yukagir Mammoth. Note the small size (30.7 cm) of the length of the ear. The position of the temporal gland opening indicated.

Figure 8. Eye of the Yukagir Mammoth. Photograph: Francis Latreille.

Figure 9. III, IV and V thoratic vertebrae of the Yukagir Mammoth. IV and V thoratic vertebrae are fused through bony outgrowths. Top: Ventral view of the vertebrae bodies. Below: Fused dorsal spines. Photograph: Dick Mol.

CT-scan of the Yukagir Mammoth head during World Expo 2005 in Japan will provide data on the interior ear organs (Suzuki, 2004). During the examination of the cranium in the Mammoth Museum in Yakutsk, June 2004, the left stylohyoideum was discovered *in situ*.

THE PHYSICAL CONDITION

The Yukagir Mammoth had backbone/spine problems. Thoracic vertebrae IV and V showed abnormal growth possibly as a result of auto-immune reaction to an inflammation somewhere else in the body. Only the thorn-shaped extremities of the two subsequent thoracic vertebrae (thoracic vertebrae VI and VII, No. 7885 and No. 7886) have been retrieved; these were naturally cut off just above the neural canal and were strongly deformed, showing some pus channels. The available vertebrae before and after these pathologically-modified specimens were in good condition. Dr. Erwin Kompanje of the Erasmus Medical Center and the Natural History Museum in Rotterdam, The Netherlands, diagnosed a form of Spondylarthropathy (also known as (Ankylosing) Spondylitis or Rheumatoid spondylitis) in the 4th and 5th thoracic vertebrae (fig. 9). Unfortunately, the pelvis bone and the sacrum bone are missing. Generally, this disease shows most clearly in the joint between these two bones.

Spondylarthropathy includes a group of inflammatory diseases comprising Reiter's syndrome, reactive arthritis, psoriatic arthritis and arthritis associated with inflammatory bowel disease. The bony outgrowths found on the vertebrae of affected individuals are called syndesmophytes (Francois *et al.,* 1995).

These are slim, bony outgrowths, parallel to the vertebral column, which replace the outer parts of the annulus fibrosus (part of the intervertebral disc) and the shorter and longer perivertebral ligaments, thus leading to an intervertebral bridge by means of complex processes involving ossification. The syndesmophytes can be distinguished from the vertical and chunky osteophytes (bone spurs) in degenerative vertebral disease, and the often bizarre new bone formation associated with primary bacterial infections.

These abnormal bony outgrowths on two thoracic vertebrae (IV and V) of the Yukagir Mammoth resemble the syndesmophytes usually found in Spondylarthropathy in man and other mammals (Rothschild, 1994; Kompanje, 1999; Kompanje *et al.,* 2000) A diagnosis of Reactive spondylarthropathy, most probably associated with inflammatory bowel disease seems plausible in this case.

These inflammations would have caused pain, especially in the early stages of abnormal bone growth but this was most likely not related to death. The event or condition triggering this growth might have occurred several years earlier. It will be interesting to see if Daniel Fisher finds signs of this event in the growth of the tusk, where a daily history of life is stored as variations in structural and compositional properties.

PLANT REMAINS IN THE YUKAGIR MAMMOTH DUNG AND AN ENVIRONMENTAL RECONSTRUCTION

Samples from the intestinal tract (fig. 10, 11 and 12) of the Yukagir Mammoth were studied for pollen, spores and macroscopic botanical remains (van Geel *et al.,* 2004). The dung consisted of compact plant material, mainly fibres and thin willow twigs, mixed with small mineral particles. Many of the observed mosses showed soil dust, caught between the leaves. The pollen record from the soil dust component reflects a mixed pollen deposition over a number of years. The pollen spectra demonstrate a typical biased distribution, related to the different pollen production and dispersal strategies of the various species. Wind-dispersed taxa such as grasses and *Artemisia* are overrepresented, whereas insect-pollinated species have been underrepresented. The pollen grains are well preserved. The dominance of pollen of grasses (Poaceae) and *Artemisia*, in combination with *Plantago*, *Armeria*, *Polemonium* and Caryophyllaceae, and the absence of tree pollen suggest a treeless steppe vegetation. Ascospores of the coprophilous (dung-inhabiting) fungus *Sporormiella* were recorded in the microfossil slides. *Sporormiella* does not form spores inside the gastrointestinal tract, implying that the spores were ingested together with the food plants. Earlier palynological studies (e.g. the study of the Jarkov Mammoth) have shown that spores of coprophilous fungi are common in the microfossil record of the mammoth steppe (MOL *et al.,* 2001; 2003 and *in press).* The presence of these spores is related to the availability of herbivore dung as a substrate.

The record of macroscopic plant remains is strongly influenced by the food choice of the mammoth during its last meal (UKRAINTSEVA, 1993), but the species composition supports and extends the reconstruction of the landscape based on the pollen record. Willow (*Salix*) twigs formed an important component of the meal. Species identification of the willow remains was not possible, but it was evident that small-leaved dwarf species had been consumed. Willow twigs were 1-2 (< 4) mm in diameter, and up to 7.5 cm in length. Thicker twigs had more than 20 year rings. Thinner twigs showed scars from where leaf stalks had originally been attached. Based on the observation that no remains of leaf stalks were connected with willow twigs, we infer that the Yukagir Mammoth died between two growing seasons (during the period from autumn to late winter). Fruits and many axillary buds of willow were recorded, some of the buds still in connection with twigs. The yellow-brown, thin twigs and axillary buds showed the typical cell pattern of willow epidermis, with numerous pits (originally bearing hairs). The preservation of willow leaves was poor; in most cases only fragments of the venation were preserved. Rarely, leaf cuticles were preserved and these showed the characteristic *Salix* cell pattern. As leaves are the softest parts of the willows, the degradation of the leaves may have partly been caused by the digestion process in the mammoth's gastrointestinal tract. Stem fragments of grasses (Poaceae) were common. The spectrum of the recorded fruits and seeds is indicative of a grassy willow-shrub landscape, but this does not contradict the steppe character of the

Figure 10. Part of the preserved intestine. Photograph: Jan van Arkel, University of Amsterdam.

Figure 11. Dung of the Yukagir Mammoth extracted from the intestine fragment (figure 10). Photograph: Jan van Arkel, University of Amsterdam.

Figure 12. Enlargement of the dung (figure 11). Photograph: Jan van Arkel, University of Amsterdam.

Figure 13. Storage of the Yukagir Mammoth remains in an artifical ice cave in Yakutsk, Yakutia, Russia. Photograph: Francis Latreille.

vegetation. In addition to the *Salix* fruits, we recorded, among others, *Poa* cf *arctica*, cf *Agrostis* sp., cf *Hordeum* sp., *Potentilla* sp., *Rumex acetosella*, several *Carex* spp., *Papaver* sp., Caryophyllaceae, Brassicaceae, Primulaceae (*Lysimachia*?) and possibly Asteraceae. The mosses (*Drepanocladus*/*Campylium*, *Polytrichum* sp., *Bryum* sp., and Pottiaceae) indicate a variety of environments, ranging from moist to dry conditions.

Based on the botanical record we conclude that the Yukagir mammoth died during the cold season in a treeless steppe. Grazing pressure and trampling by large herbivores, combined with the cold climate caused open patches of soils where mineral dust was eroded and deposited by wind extensively over the landscape and its vegetation (van Geel *et al.,* 2004). Based on the preservation of the willow twigs (broken, but not squashed), we question the ability of the Yukagir mammoth to absorb sufficient nutrients from its food.

THE STORAGE OF THE YUKAGIR MAMMOTH

The remains of the Yukagir Mammoth are stored in the collections of the Mammoth Museum in Yakutsk, the capital of Yakutia. The Mammoth Museum belongs to the Institute of Applied Ecology of the North, Academy of Sciences of the Sakha Republic (Yakutia), and is located in the capital of Yakutia, Yakutsk.

Permafrost creates unique conditions for preservation, not only of skeletal parts but also of soft tissues of extinct animals. Many of the permafrost fossils dating to the Quaternary have been found in the territory of the Sakha Republic (Yakutia) which occupies most of Eastern Siberia. The most interesting and spectacular collections of fossil mammals from the Quaternary are kept in museums in Yakutsk. The most important collections are housed in the following museums: the Regional Nature Museum, the Geological Museum of the Institute of Geology of Diamonds and Precious Metals of the Siberian Division of the Russian Academy of Sciences, and the Mammoth Museum (Boeskorov & Mol, 2004).

In 1991, the Mammoth Museum was founded; it specializes in mammoths and the mammoth fauna. The aim of this museum is to study the mammoth fauna and its environment during the Pleistocene. The collection of the Mammoth Museum consists of more than 1,000 remains of the larger mammals of the mammoth fauna. This collection needs further study to improve understanding of the late Pleistocene and the extinction of many large mammals at the end of the Pleistocene and the beginning of the Holocene.

The condition of many of the remains of the Yukagir Mammoth is excellent, and many soft parts have been collected, like the complete skin covering of the head, partly covered with fur. Therefore, it was decided to store the remains under the best possible conditions. Cerpolex/Mammuthus had experienced good results with the ice cave in Khatanga, where all the fossils of the Pleistocene mammals are stored at a constant temperature of -11 degrees Celsius. It was decided initially to store the Yukagir Mammoth remains in an artificial freezer at temperatures of about -15 degrees Celsius. However this proved to be too cold and too dry and it resulted in slowly freeze-drying the remains. So, the remains were transferred to an ice cave in the center of Yakutsk (fig. 13) where the temperature is not that low. It was still possible to carry out extensive examinations of the head in the cave.

INVENTORY OF THE YUKAGIR MAMMOTH REMAINS

SCAPULA SINISTER (Cat. # Mammoth Museum: N 7861/19)

Maximum length	79.4 cm
Maximum length a/p glenoid	18.7 cm
Maximum width m/l glenoid	9.5 cm
Antero-posterior diameter neck	20.5 cm
General remarks	Damaged by excavation activities No soft tissue remains

HUMERUS SINISTER (Cat. # Mammoth Museum: N 7861/21)

Maximum length	85.5 cm
Maximum width, distal epiphysis	24.8 cm
Maximum width, proximal epiphysis	21.6 cm
Minimum circumference shaft	33 cm
General remarks	Both epiphyses are fused, indicating a full grown animal No soft tissue remains

HUMERUS DEXTER (Cat. # Mammoth Museum: N 7894). Excavated September 2004.

Maximum length	89 cm
Maximum width, distal epiphysis	26 cm
Maximum width, proximal epiphysis	23.6 cm
Minimum circumference shaft	34 cm
General remarks	Both epiphyses are fused, indicating a full grown animal No soft tissue remains. Excavated in disturbed sediments just below the water level in September 2004. Some damage at distal epiphysis and proximal part of the shaft.

SCAPULA DEXTER (Cat. # Mammoth Museum: N 7861/20)

Maximum length	79.4 cm
Maximum length a/p glenoid	18.7 cm
Maximum width m/l glenoid	9.5 cm
Antero-posterior diameter neck	20.5 cm
General remarks	Damaged by excavation activities No soft tissue remains

Scapula sinister and humerus sinister together, in anatomical position, have a maximum length of 160 cm.

RADIUS-ULNA and COMPLETE FRONT FOOT SINISTER (Cat. # Mammoth Museum: N 7863)

General remarks on this part of the left front leg	• Completely covered with soft tissue like skin, fur and underfur, due to an ice-wedge in close proximity to this part of the disarticulated Yukagir Mammoth body • Muscles in good conditions • Excellent state of preservation • 3 Nails/hooves are preserved in good condition • X-ray is necessary
Maximum width of the proximal epiphysis of the left Ulna	21 cm
Maximum height of radius-ulna plus foot	99.5 cm
Number of nails/hooves	3 on the digits 2,3 and 4
Maximum width of nail/hoof III	14.5 cm
Maximum height of nail/hoof III	5 cm
Measurements of the left foot	
Antero-posterior diameter	42 cm
Medial-lateral diameter	50 cm
General remark	The foot is extremely big compared to the shoulder height

Professor Naoki Suzuki, a member of our research team from Tokyo, will investigate the head of the Yukagir thoroughly by CAT-scan when the remains are in Japan for Expo 2005. In this way we should obtain more details about the cranial cavity, the inner ear and other features. The condition of the molars in the upper and lower jaws, particularly wear patterns, should also be revealed. This will allow us to compare the Yukagir with known-age African elephants. With this information we can improve our estimate of the age of the Yukagir Mammoth.

Just before the start of the first scientific conference, "The Yukagir Mammoth: Outcome of the First Stage of Work" in Yakutsk (2004), we did a test on the foreleg or arm of the Yukagir Mammoth which had the complete foot, fully intact with muscles, skin and hair. The medical staff had agreed to scan this part of the animal with a CAT-scan. We were lucky; the foot barely fit. Any larger and it would not have been possible. The scans were made and a few moments later we had a very good impression of the lower foreleg and foot. The computer screen showed clearly that there were no fractures or abnormal growth. We also noticed that the radius and ulna had not fused (synostosis) as happens sometimes with mammoth of very advanced ages.

The scans of the foot (fig. 14) resulted in some outstanding images, and new facts were revealed. The forefoot wrist bones were clearly visible, the five metacarpal bones I - V were nicely arranged just as we see in modern elephants. The number of phalanges and sesamoids was clearly displayed. We see that the first metacarpal I (representing the thumb) has only one sesamoid but no phalanges as can be noticed in modern elephants (Neuville, 1935). Apparently the Yukagir Mammoth had no thumbs. We have seen this in isolated or separate first metacarpal bones. It seems that the woolly mammoth often had four digits on its forefoot.

CONCLUDING REMARKS

Skeletal remains of mammoths are not very rare; they have been found in many places in the world, except in Australia and Antarctica. Rarer are discoveries of whole carcasses or soft tissues of 40-20,000 years old mammoths that are found in the permafrost of Siberia, remains of which have been discovered since the 18th century. The Yukagir Mammoth, exposed in the autumn of 2002, is one example. This excellently preserved specimen has provided unique opportunity to study ancient tissues and retrieve valuable direct data and inferences. Some of our findings are summarized here. The Yukagir Mammoth was an adult male with estimated shoulder height of 282.9 cm and weighed between four and five tones; it lived in the late Pleistocene, approximately 18,560 years ago. This specimen is one of the best-preserved mammoths ever found because the head, partially covered with skin and hair with magnificent pair of tusks and includes a complete ear with all the features found in modern elephants. Also preserved are the external surface of the eye, and the external opening of the temporal gland. In living elephants this gland is known to function in establishing a hierarchy among males during breeding season. Some postcranial elements were also found, a few with soft tissues attached. In addition one of the stylohyoid bones was found *in situ*. The ecosystem of the Yukagir Mammoth at the end of the Pleistocene consisted of a steppe - grassland, treeless, except for ribbons and patches of forest. Today, this region is tundra - void of trees, but mosses and lichen thrive. Additional findings are presented by other contributors. The Yukagir Mammoth was displayed in EXPO 2005, held in Aichi prefecture in Japan. There are many mammothine projects to be conducted, and exciting discoveries are looming. Data from living elephants help us better understand life histories of mammoth and vice versa.

Figure 14. Scan of the left front foot of the Yukagir Mammoth, showing the inside of the left manus. Photograph: Francis Latreille.

METACARPAL BONE	Mc I	Mc II	Mc III	Mc IV	Mc V
Number of sesamoids	1	2	2	2	2
Number of phalanges	0	3	3	3	1
Hoofs or nails	?	X	X	X	?

X = Hoof or "nail" present, (the middle finger "nail" is 14 cm wide (5 1/2")

? = Hoof or "nail" not present but it appears that a hoof or nail was present before but it was lost in the decay process or a rodent may have scavenged it. Even though there are no phalanges on the first metacarpal bone, there appears to have been a hoof or nail at the end.

VERTEBRAL COLUMN
(Fig. 15 and 16)

Figure 15. Part of the vertebral column of the Yukagir Mammoth. Photograph: Dick Mol.

Figure 16. III, IV and IV thoratic vertebrae of the Yukagir Mammoth. Photograph: Dick Mol.

VERTEBRAL COLUMN YUKAGIR MAMMOTH

Vertebra	Mammoth Museum Number	Max. height (cm)	Max. width (cm)	Remarks
Atlas	(Cat. # Mammoth Museum: N 7861/1)	18.6	32.5	
Epistropheus or axis	(Cat. # Mammoth Museum: N 7861/13)	22.8	23.5	Some soft tissue on the top of the dorsal spine
Vertebra cervicalis III	(Cat. # Mammoth Museum: N 7861/14)	20.0	24.4	
Vertebra cervicalis IV	(Cat. # Mammoth Museum: N 7861/2)	21.0	24.5	
Vertebra cervicalis V	(Cat. # Mammoth Museum: N 7861/3)	24.7	24.0	
Vertebra cervicalis VI	(Cat. # Mammoth Museum: N7861/15)	29.2	25.1	Some soft tissue on the top of the dorsal spine
Vertebra cervicalis VII	(Cat. # Mammoth Museum: N 7861/4)	32.5	25.8	
Vertebra thoracalis I	(Cat. # Mammoth Museum: N 7861/16)	38.5	27.6	
Vertebra thoracalis II	(Cat. # Mammoth Museum: N 7861/5)	Damaged Since Sept. 2004 complete.	27.5	Dorsal spine is broken. Distal end which was missing is found at the site in September 2004.
Vertebra thoracalis III	(Cat. # Mammoth Museum: N 7861/17)	42.5	27.5	
Vertebra thoracalis IV	(Cat. # Mammoth Museum: N 7861/18)	42.5	Damaged	Fused with Vertebra thoracalis V
Vertebra thoracalis V	(Cat. # Mammoth Museum: N 7861/18)	42.5	Damaged	Fused with Vertebra thoracalis IV
Vertebra thoracalis VI	(Cat. # Mammoth Museum: N 7885)		Only the pathological neural spine Max. height 19.8	Excavated Sept. 2004.
Vertebra thoracalis VII	(Cat. # Mammoth Museum: N 7886)		Only the pathological neural spine Max. height 23.5	Excavated Sept. 2004.
Vertebra thoracalis VIII	(Cat. # Mammoth Museum: N 7887)		Complete vertebra 24.1	Excavated Sept. 2004.
Vertebra thoracalis IX	(Cat. # Mammoth Museum: N 7888) & # 7861/24		Now complete	7861/24 is vertebra body excavated Sept. 2003 Neural arch excavated Sept. 2004.
Vertebra thoracalis X	(Cat. # Mammoth Museum: N 7889)		Complete vertebra 21.3	Excavated Sept. 2004.
Vertebra thoracalis XI	Missing	XXXX	XXXX	XXXX
Vertebra thoracalis XII	(Cat. # Mammoth Museum: N 7890)		Complete vertebra 20.2	Excavated Sept. 2004.
Vertebra thoracalis XIII	Missing	XXXX	XXXX	XXXX
Vertebra thoracalis XIV	(Cat. # Mammoth Museum: N 7891)		Complete vertebra 19.2	Excavated Sept. 2004.
Vertebra thoracalis XV	Missing	XXXX	XXXX	XXXX
Vertebra thoracalis XVI	(Cat. # Mammoth Museum: N 7892)		Complete vertebra 16.8	Excavated Sept. 2004.
Vertebra thoracalis XVII	Missing	XXXX	XXXX	XXXX
Vertebra thoracalis XVIII	(Cat. # Mammoth Museum: N 7893)		Complete vertebra 15.9	Excavated Sept. 2004.

RIB CAGE REMAINS

Left side of the carcass	Rib #	Mammoth Museum Number	Remarks
	3	(Cat. # Mammoth Museum: N 7861/23)	Excavated Sept. 2003 Distal end damaged
	7 or 8	(Cat. # Mammoth Museum: N 7861/11)	Excavated Sept. 2003 Proximal portion missing
	16 or 17	(Cat. # Mammoth Museum: N 7884)	Excavated September 2004 expedition. Complete rib

Right side of the carcass	Rib #	Mammoth Museum Number	Remarks
	1	(Cat. # Mammoth Museum: N 7861/22)	Excavated Sept. 2003
	5	(Cat. # Mammoth Museum: N 7861/9)	Excavated Sept. 2003
	6	(Cat. # Mammoth Museum: N 7861/10 (2003) = fragment7876 (2004))	Excavated Sept. 2003. Fragment, Proximal portion.
	7	(Cat. # Mammoth Museum: N 7877)	Excavated September 2004 expedition. Complete rib
	8	(Cat. # Mammoth Museum: N 7878)	Excavated September 2004 expedition. Complete rib, length 108.6 cm
	9	(Cat. # Mammoth Museum: N 7879)	Excavated September 2004 expedition. Distal end missing.
	10	(Cat. # Mammoth Museum: N 7861/8 (2003) = fragment 7880 (2004))	Excavated September 2004 expedition. Distal end missing.
	11	(Cat. # Mammoth Museum: N 7881)	Excavated September 2004 expedition. Complete rib, length 99.4 cm
	12	(Cat. # Mammoth Museum: N 7882)	Excavated September 2004 expedition. Complete rib, length 92.3 cm
	13	(Cat. # Mammoth Museum: N 7883)	Excavated September 2004 expedition. Fragment, proximal portion.
General remarks			Ribs ## 7 – 13 all broken at the same position (solifluction??)

REMAINS OF THE HIND LEGS

Element	Cat. # Mammoth Museum	Remarks
Patella sinister	(Cat. # Mammoth Museum: N 7909)	Damaged, soft tissue on the internal side of the patella.

CRANIUM AND TUSKS

The tip of the right tusk was slightly damaged during the life of the animal. A chip of ivory is missing. The surface of the tusk tip is polished during the life of the animal after the tusk sustained damage.

The right tusk was taken from the cranium to obtain the following measurements. The left tusk is still in its original position in the cranium.

Dr. Daniel C. Fisher took samples from the right tusk of this mammoth. Examination of these samples would provide chemical and isotopic data and details about the life history of the animal (see Fisher, 2004).

Measurements of the right tusk of the Yukagir Mammoth
(Cat. # Mammoth Museum: N 7864)

Maximum length, measured along the outer curvature	316.4 cm
Maximum circumference at the end of alveolus	45 cm @ 73.4 cm measured from beginning of pulp cavity
Maximum diameter at the end of the alveolus	11.6 cm
Depth of the pulp cavity	26 cm
Maximum distance of the tip to the edge of the pulp cavity	112 cm
Straight line from the tip to the end of the part which was hidden in the alveolous	100.6 cm
Depth of the alveolus	>45 cm
Yakutsk, September 3, 2004	11 samples (cores) drilled by Dr Daniel C. Fisher for tusk analysis More measurements taken by Daniel C. Fisher on September 2nd, 2004

Measurements of the left tusk and the cranium of the Yukagir Mammoth
(Cat. # Mammoth Museum: N 7865)

Maximum length, measured along the outer curvature (from where it erupts from the alveolus)	296 cm
Maximum circumference at the end of alveolus	46 cm
Maximum width of both alveoli with skin cover	55 cm
Maximum thickness of skin near the nasal opening	3 cm
Maximum width of both tusks when in anatomical position in the alveoli	170 cm
Measurements of the cranium	See figure 3, 5 and 7
Maximum antereo-posterior length	83 cm
Maximum height including mandibula	91 cm
Maximum height lower side jugale to top of cranium	69 cm
Maximum diameter left eye	6 cm
Distance left eye to temporal gland opening	21 cm
Distance temporal gland opening ear opening	13 cm
Maximum length ear opening	9 cm
Maximum height left ear	30.7 cm
Maximum a-p diameter left ear	17.5 cm
Thickness of left ear from the top to the lower end	40.8 mm, 30.8 mm and 28.8 mm

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