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FESTSCHRIFT

Univ. Prof. Dr. Gernot Rabeder
zum 80. Geburtstag

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universität wien

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Dedication

This volume is dedicated to Gernot Rabeder on the occasion of his 80th birthday. We, his friends, colleagues and students wish him all the best and hope he enjoys this compilation in his honour.

Gernot Rabeder was born on September 11th 1939 in Linz (Upper Austria) just minutes before his twin brother Gisbert. Both went to the primary school in Bad Ischl where it was safer for children during the Second World War. There his love of and interest in the Alpine area evolved and, therefore, it is no surprise that Gernot decided to join the mountain troops during his military service between 1958 and 1959. The brothers became experts in mountaineering and wrote several books about hiking routes in the Austrian Alps (Totes Gebirge, Dachstein, Niedere Tauern).

In 1959 Gernot Rabeder enrolled in the study of college training for biology and mathematics at the University of Vienna but during his Ph.D. he strictly focused on the field of palaeontology and finished in 1970 with the topic “Die Insectivora und Chiroptera von Hundsheim (Alt-Pleistozän)”.

Six years later his habilitation followed with a detailed description of the complex karstic fissures of Deutsch-Altenburg and its carnivores (Early Pleistocene) supervised by Erich Thenius, an expert in mammalian palaeontology.

Stratigraphic work continued in various loess sites such as Stranzendorf and Krems and lead to a fruitful cooperation between the Department of Pre- and Early History, Department of Anthropology and the Department of Isotopic Research at the University of Vienna.

In 1979 Gernot Rabeder, still enthusiastic about micro-mammals, concentrated on the probably most important mammal in the Austrian Pleistocene, the cave bear. His first excavation started in the Ramesch Knochenhöhle 40 years ago where the remains of this cave bear showed significant differences to other cave bears. Many years of excavation followed in Austria as well as abroad (Switzerland, Germany, Italy, Croatia, Slovenia, Slovakia, Ukraine and Greece).

The cooperation with Michael Hofreiter accelerated his insights into this fascinating group and genetic analyses of the cave bears changed the systematics completely. To give this new information a stronger platform he, together with Jörg Müller (Chur), initialised the first International Cave Bear Symposium 25 years ago and it has had a meeting every year since with participants from Spain to Russia and from Greece to Sweden.

He focused more on the Pleistocene and included in his studies different aspects of bears such as brown bear evolution or bear teeth as jewellery in Palaeolithic sites. He broadened his research from beavers in France to woolly rhinos from Germany, always looking for palaeoecological as well as palaeogeographical information.

In 1988 Gernot Rabeder became full professor for palaeobiology at the Department of Palaeontology at the University of Vienna. Twice he was named president of the Austrian Palaeontological Society (1988-1990 and 1996-1998), was Head of the Department of Palaeontology from 1995-1999 and Head of the Commission for Quaternary Research at the Austria Academy of Sciences from 1992 till 2014. Gernot Rabeder gained emeritus status in 2007.

An important part of his life was the communication of research in form of exhibitions. He organized, and was the scientific advisor of, several exhibitions in Linz, Grundlsee, Bad Aussee, Salzburg and San Kassian (South Tirol) just to name a few.

He held over 15 different lectures at the university all concerning palaeontology, speleology and evolution. Gernot Rabeder supervised many master students, Ph.D. students and, as the curriculum changed, also bachelor students. He nurtured their interest in caves and fossils, taught them how to excavate and inspired them to publish their thesis, and most importantly, he always supported their scientific career. No wonder most of them are still his friends and colleagues, always returning to take part in fieldwork or conferences. A Festschrift was compiled in 2005 (his 65th birthday) and a note of honour in 2009 (his 70th birthday).

His retirement/rest has nothing to do with rest but as he puts it ‘it is more of an unrestment’.
Many excavations and publications followed such as Ajdovska Jama and Vazecka cave (Slovenia), Steigelfadbalm near Luzern, Wildkirchli, Wildenmannisloch and Drachenloch (Switzerland), Arzberghöhle, Torsteinhöhlen, Pendling-Bärenhöhle, Gauerblick-Höhle, Leopoldinen-Höhle, Frauenhöhle, Repolusthöhle, Lurgrotte, Bärenfalle (Totes Gebirge), Flatzer Bärenhöhle and the most recent one: the Schwaigerhöhle.

We, his friends, colleagues and students, want to thank him for all he has done for us, for his knowledge, inspiration, insight, patience, help and most of all his humour. We hope to share this for many more years to come!

Doris Nagel, Nadja Kavcik-Graumann, Doris Döppes, Martina Pacher

emer. Univ. Prof. Dr. Gernot Rabeder
Department of Palaeontology
University of Vienna

Curriculum vitae

Born 11. September 1939 in Linz/ Donau (Upper Austria).
Parents: Dkfm. Friedrich and Maria Rabeder, 4 brothers and sisters
1969: Married to Ilse, born Plech
1970: Birth of daughter Sigrid
1981: Birth of daughter Sibylle
four grand-children

Education:

1945 – 1949: Primary school (Volksschule) in Bad Ischl and Linz – Urfahr
1949 – 1950: Elementary school (Hauptschule) in Linz – Urfahr
1950 – 1958: High school (Bundesgymnasium) in Linz, Spittelwiese
1958 – 1959: Military service (mountain troops)
1959 – 1966: Study of college training-degree at the Faculty of Philosophy/University of Vienna
1966: Teachership-degree for biology and mathematics
1966 – 1970: Studying for Doctoral degree
1970: Doctor of Philosophy (Paleontology and Geology). Thesis: “The insectivores and chiropteres from Hundsheim (Early Pleistocene)“

Career:

1966 – 1967: Assistant at the Institute of Paleontology/University of Vienna
1967 – 1988: Assistant professor at the Department of Paleontology/University of Vienna
1976: Habilitation: Thesis “The carnivores from Deutsch Altenburg 2 (Early Pleistocene), with contributions to the systematic of mustelides and canides”. Venia legendi in paleozoology
1985: Qualification as senior lecturer (Extraordinarius)
1988: Full professor of paleontology and paleobiology at the Department of Palaeontology (University of Vienna)
1992: Head Commission of Quarternary Research Austrian Academy of Sciences
1995 – 1999: Head of the Department of Palaeontology, University of Vienna
1988 – 1990 and 1996–1998: President of the Austrian Palaeontological Association
2007: Emeritus status

Publications since 2005:

2018

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Rabeder, G., & Kavcik, N. (2013). “Drachenhöhle” Mixnitz.. 27-28. Beitrag in 19th International Cave Bear Symposium Semriach (Styria, Austria), Semriach, Styria, Austria, Österreich.

Prost, S., Klietmann, J., Van Kolfschoten, T., Guralnick, R. P., Waltari, E., Vrieling, K., ... Sommer, R. S. (2013). Effects of late quaternary climate change on Palearcticshrews. Global Change Biology, 19, 1865-1874. https://doi.org/10.1111/geb.12153

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Contents

Bärenfalle – Gernots jüngste hochalpine Höhlengrabung

Bärenfalle – Gernot‘s latest high alpine cave excavation

Doris Döppes [1], Sebastian Krutter [2] & Annett Werner [3]

In den Jahren 2015-2016 konnten in der Bärenfalle (1511/169), einer hochalpinen Höhle auf rund 2.100 m Seehöhe im Tennengebirge (Salzburg, Österreich), Grabungskampagnen durchgeführt werden. Mit der folgenden Fotoretrospektive möchten wir uns im Namen des gesamten Grabungsteams – bestehend aus Christine Frischauf, Sebastian Krutter, Doris Döppes, Annett Werner, Claudia Gstöttl, Wolfgang Strasser, Josef Ries, Daniel Brandner, Andreas Gremmel, Barbara-Melanie Stary, Karin Hackl, Sebastian Heiland, Anke Oertel und Alfred Schlagbauer – für die erlebnisreiche Zeit am Tennengebirge bedanken und Gernot Rabeder sehr herzlich zu seinem 80. Geburtstag gratulieren.
Im Anhang wurde die Literatur, die aus diesen Grabungskampagnen entstand, zusammengefasst.
Bilder sagen mehr als tausend Worte!

In the years 2015-2016, excavation campaigns were carried out in the Bärenfalle (1511/169), a high alpine cave at about 2,100 m above sea level in the Tennen Mountains (Salzburg, Austria).
With the following photo retrospective we would like to thank Gernot Rabeder on behalf of the entire excavation team - consisting of Christine Frischauf, Sebastian Krutter, Doris Döppes, Annett Werner, Claudia Gstöttl, Wolfgang Strasser, Josef Ries, Daniel Brandner, Andreas Gremmel, Barbara-Melanie Stary, Karin Hackl, Sebastian Heiland, Anke Oertel and Alfred Schlagbauer - for the exciting and instructive time at Tennen Mountains and congratulate on his 80th birthday.
The appendix summarizes the literature that emerged from these excavation campaigns.
Pictures say more than a thousand words!

Abb. 1: Gernot und der Hubschrauberpilot von Heli Austria besprechen die Flugroute vom Pass Lueg ins Tennengebirge, Juli 2016.
Fig. 1: Gernot and the helicopter pilot of Heli Austria talking about the flight route from the Pass Lueg up to the Tennen Mountains, July 2016. © Sebastian Krutter

Abb. 2: Gernot am Hubschrauberlandeplatz hinter dem Leopold-Happisch-Hut, Juli 2016.
Fig. 2: Gernot at the helicopter landing place behind the Leopold-Happisch hut, July 2016.
© Sebastian Krutter

Abb. 3: Gernot und Christine beim täglichen rund 30 Minuten dauernden Aufstieg zur Bärenfalle, Juli 2015.
Fig. 3: Gernot and Christine during the daily approx. 30-minute ascent to the Bärenfalle, July 2015.
© Daniel Brandner

Abb. 4: Gernot und Doris bei der Montage der Seilsicherung für den Aufstieg zum Höhleneingang, Juli 2015.
Fig. 4: Gernot and Doris during the mounting of the safety rope for ascent to the cave entrance, July 2015.
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Abb. 5: Sebastian beim Kübeltransport mit der Grabungsstelle im Hintergrund, Juli 2015.
Fig. 5: Sebastian carrying buckets, the excavation site in the background, July 2015.
© Daniel Brandner

Abb. 6: Christine und Andreas bei Vermessungsarbeiten an der Grabungsstelle in der Bärenfalle, Juli 2016.
Fig. 6: Christine and Andreas doing survey work at the excavation site inside the Bärenfalle, July 2016.
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Abb. 7: Claudia und Barbara in der Grabungsstelle in der Bärenfalle, Juli 2016.
Fig. 7: Claudia and Barbara in the excavation site inside the Bärenfalle, July 2016.
© Josef Ries

Abb. 8: Gernot am Aussuchtisch im Eingangsbereich der Bärenfalle, Juli 2015.
Fig. 8: Gernot at the selection-table in the entrance area of the Bärenfalle, July 2015.
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Abb. 9: Wolfgang und Annett beim Verpacken von Fossilmaterial im Eingangsbereich der Bärenfalle, im Hintergrund Andreas und Sebastian, Juli 2016.
Fig. 9: Wolfgang and Annett packing fossil material in the entrance area of the Bärenfalle, in the background Andreas and Sebastian, July 2016.
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Abb. 10: Annett, Doris, Christine, Wolfgang und Joe bei der Mittagspause unterhalb des Höhleneinganges, Juli 2016.
Fig. 10: Annett, Doris, Christine, Wolfgang und Joe during lunch break below the cave entrance, July 2016.
© Sebastian Krutter

Abb. 11: Wolfgang und Gernot während einer fachlichen Diskussion – das darf auch nicht fehlen – bei der Mittagspause unterhalb des Höhleneinganges, Juli 2015.
Fig. 11: Wolfgang and Gernot during a scientific discussion – that even must not be missing – at lunch break below the cave entrance, July 2015. © Sebastian Krutter

Abb. 12: Tea time im Eingangsbereich der Bärenfalle, Juli 2016.
Fig. 12: Tea time in the entrance area of the Bärenfalle, July 2016.
© Sebastian Krutter

Abb. 13: Doris, Gernot und Annett bei Sonnenuntergang vor dem Leopold-Happisch-Haus, Juli 2016.
Fig. 13: Doris, Gernot and Annett at sunset in front of the Leopold-Happisch hut, July 2016.
© Sebastian Krutter

Abb. 14: Unser Basecamp während der Grabungen in der Bärenfalle: das Leopold-Happisch-Haus, März 2019.
Fig. 14: Our base camp during the excavations in the Bärenfalle: the Leopold-Happisch-Hut, March 2019.
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The complete skeleton of the bear n°2 from the Galerie des Aiglons of the Azé Cave (Saône-et-Loire, France): *Ursus spelaeus ladinicus*

L'ours complet N°2 de la Galerie des Aiglons de la grotte d'Azé 1 (Saône-et-Loire, France): *Ursus spelaeus ladinicus*

Alain Argant [1,2,5], Thierry Argant [2,3], Lionel Barriquand [2,4,5] & Jacqueline Argant [1,2]

Abstract

Between 1990 and 1997, excavations by R. Villeneuve in Azé 1 led to the discovery of the presence of a gallery parallel to the Azé 1 cave, the Galerie des Aiglons, as well as the complete skeletons of several bears in the gallery joining these two caves (Azé 1-6). It was possible to carry out a rather complete morphometric study of two of these bears, Bear N°2, a female, and an adjacent bear cub, despite the extensive concretion of the remains requiring painstaking removal which nevertheless could only be partial. As a result, an individual of *Ursus spelaeus ladinicus* was identified, the most recent bear species found at Azé 1. The dating remains imprecise, but based on the general evolution of the cavity, it lies between the end of isotopic stage OIS.6 and the upper limit of 14C-AMS (about 50 ka), at the latest, stage OIS.4. The bear from Azé, which had previously provided a mtDNA analysis came from a group of remains in proximity to Bear N°2. This bear belongs to haplogroup A, as does the sequence of bears at Conturines (Italy) which is precisely *Ursus spelaeus ladinicu*s.

Résumé

Entre 1990 et 1997, les fouilles de R. Villeneuve à Azé 1 ont permis de découvrir l'existence d'une galerie parallèle à la grotte d'Azé 1, la Galerie des Aiglons et le squelette complet de plusieurs ours dans la galerie de jonction (Azé 1-6). L'ours N°2, une femelle, et un ourson, permettent une étude morphométrique assez complète malgré l'état très concrétionné des vestiges recueillis nécessitant un long travail de dégagement qui n'a pu être que partiel. Il est possible de déterminer un individu d'*Ursus spelaeus ladinicus*, sous-espèce d'ours la plus récente d'Azé 1. La datation en reste imprécise mais d'après le fonctionnement général de la cavité, elle se situe entre la fin du stade isotopique OIS.6 et la limite supérieure du 14C-AMS (50000 ans environ), au plus tard au stade OIS.4. L'ours d'Azé ayant fourni auparavant une analyse d'ADN-mt correspond au stock en relation avec cet individu N°2. Il appartient à l'haplogroupe A, comme la séquence de l'ours des Conturines (Italie) qui est justement *Ursus spelaeus ladinicus*.

Key-words: *Ursus spelaeus ladinicus*, Azé 1, single individual, morphometry, chronology.

Mots-clés: *Ursus spelaeus ladinicu*s, Azé 1, unique individu, morphométrie, chronologie.

1. Introduction

From a geological, palaeontological and archaeological perspective, Azé is a very rich site (Fig. 1). Two main caves and six other much smaller ones open onto a south-facing cliff overlooking the valley of the Mouge. The upper cave, Azé 1, known as the "Prehistoric Cave", contains the famous palaeontological deposit of cave bear and lion remains (excavations A.J. Argant, 1982 to 1985) as well as the oldest prehistoric site in Burgundy (Lower Palaeolithic, excavations J. Combier, 1966 to 1970) (Fig. 2).

The removal of obstructions to enable tourist activities, followed by several scientific excavations, led to a good knowledge of the cave fillings, dating for the most part from the Middle Pleistocene. In 1990, a team led by René Villeneuve (specialist teacher in charge of a group of children with difficulties, the "Aiglons") began to empty out a small rounded recess, the Fosse Rotonde, on the eastern side of the main gallery of the tourist cave, about 30 metres from its entrance. In 1991, they discovered and very carefully removed two bears in anatomical connection. Then from 1991 to 1993 they emptied out the Boyau Ouest (= Connexion Galery, Junction Galery, Azé 1-6). In 1993, they reached, further below, the Salle des Pétoux, in reality the Galerie des Aiglons, which they proceeded to empty out until they reached the exterior on 16th August 1993, only a few metres below the entrance to the tourist gallery of Azé 1.

The Galerie des Aiglons is parallel to Azé 1 in the general north-south axis of this karst-area. Its entrance had been hidden by slope deposits and was totally invisible until 1993. From 1998 to 2002, adding to the work done by R. Villeneuve, L. and J. Barriquand conducted four excavation campaigns during which they drew cross-section diagrams of all the sediments and carried out sedimentological studies (Barriquand et al., 2011). The fauna collected, identified by A. Argant, is much more diverse than in the rest of the cave and clearly indicates the presence of *Crocuta spelaea*, until then only known through a few remains in the upper gallery of Azé 1. This fauna, at least in part, consists of a mixture of fossils from the upper gallery with those from the Galerie des Aiglons, which occurred because of drainage at a number of points, some known and probably many others unknown.

The Fosse Rotonde marks the beginning of a small gallery, the Boyau Ouest (Azé 1-6), which connects with the lower gallery about twenty metres from its exit at the cliff face. This connecting gallery is narrow. It acted as a passageway and as a channel for the periodic evacuation of water from the upper gallery during times of flooding. It is probable that at such times there was a flushing action which drew into this channel the bodies of dead bears still connected by their ligaments, but the possibility of animals being trapped or killed in their place of hibernation cannot be completely ruled out. In any case, later water flows have removed nearly all the small bones such as carpal, tarsal and metapodial bones, phalanxes, sesamoids and incisors (the few exceptions being 1 calcaneus, 1 metapodial bone, 2 phalanxes and 1 incisor). The trampling of the skeleton by the passage of other bears has very probably contributed to its crushing and the severe cracking of the skull and long bones.

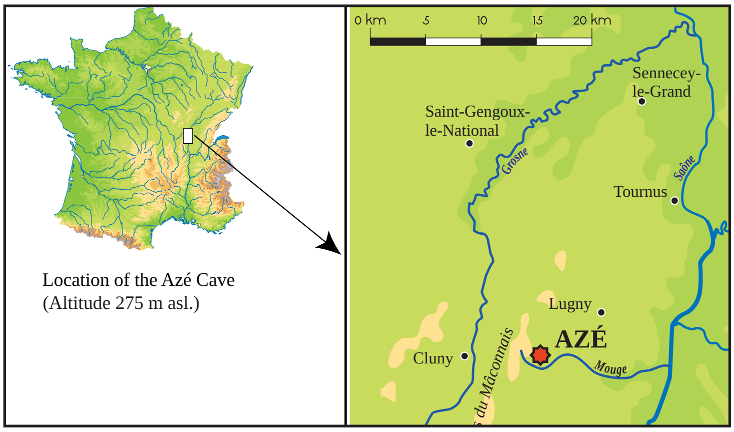


Fig. 1: Location of Azé (Saône-et-Loire, France).
Fig. 1: Situation d'Azé (Saône-et-Loire, France).

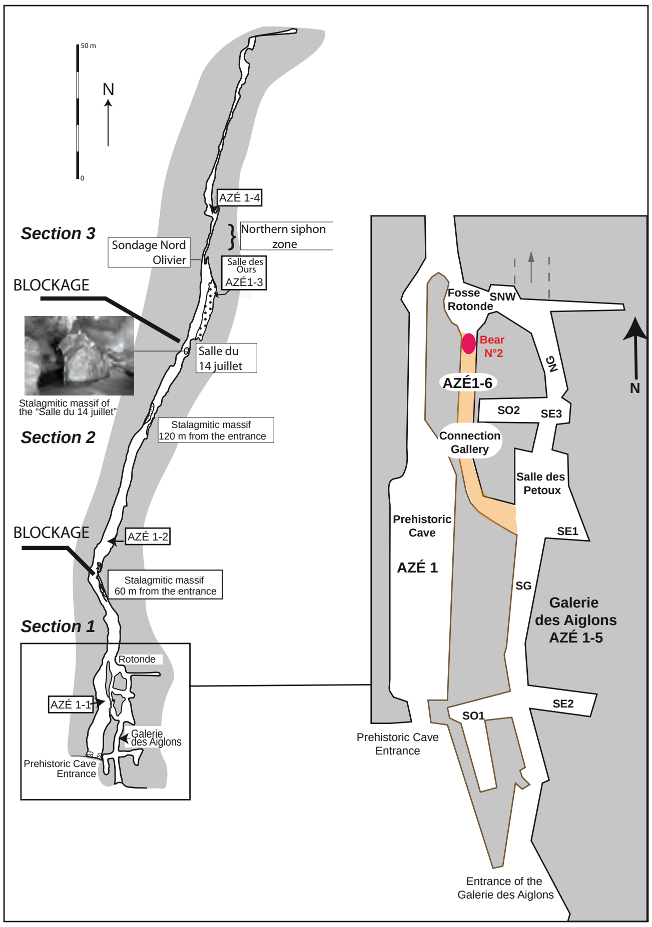


Fig. 2: Sketch of the Azé 1 cave and detail of Sectin 1 and of the Galerie des Aiglons. The connecting gallery Azé 1-6 and the location of Bear N°2.
Fig. 2: Plan de la grotte d'Azé 1 et détail du tronçon n°1 et de la Galerie des Aiglons. Galerie de jonction Azé 1-6 et position de l'ours N°2.

2. The complete bear N°2

Bear N°1, lying along the eastern wall at the beginning of the Fosse Rotonde, was the first individual found in anatomical connection, but in the same location were the scattered bones of several other individuals. The alignment of bones along the side indicates a “wall effect”, a consequence of trampling by bears moving regularly through the passageway, pushing bones to the side. This is not the case for Bear N°2 which affords us the certainty of a single individual, a female wedged across the gallery with the skull of a bear cub at its side (Fig. 3). These sorts of finds are too rare at Azé, as elsewhere, to not try to make use of their morphometric data. In order to be complete, the existence should be noted of other individuals in anatomical connection (at least partial) still in place to the south of Bear N°2 in the connecting gallery (Azé 1-6) before it opens into the Galerie des Aiglons.

Fig. 3: Photo of Bear N°2 in situ in the junction gallery Azé 1-6 (photo J. Argant)
Fig. 3: Photo de l’ours N°2 en place dans la galerie de jonction Azé 1-6 (photo J. Argant).

Figure 3 shows the placement of the bones after their clearing by the Aiglons team. The bones are in anatomical connection, the animal lying on its side, head to the west, fore limbs towards the north, hind limbs towards the south, the spinal column in an arc across the gallery. The skeleton is in contact with the limestone wall on each side. It has been flattened horizontally but is clearly visible in the upper part of the filling of this small gallery a little more than a metre wide. All the bones are represented, but are in very poor condition for two main reasons. Firstly, after their trampling, the bones underwent a long stagnation in water which is the cause of the calcite concretions around most of them, requiring a lengthy period of removal and cleaning. A second reason relates to the in-situ exhibition to the public between 1991 and 2001 of two of the bears excavated by R. Villeneuve. This aggravated the cracking and splitting of the bones. In 2001, given the worrying state of the skeleton, the decision was taken to extract it. T. Argant was responsible for the extraction as part of the excavations of L. Barriquand (1998 - 2002). He mapped the area and plotted the spatial distribution of the remains (Fig. 4). He measured the pieces in situ in case they were damaged during extraction, numbered each of them and recorded their coordinates with a view to later study, then removed and archived them all.

In 2012, as part of a post-doctorate in the laboratory of M. Hofreiter at Oxford (England), C. Frischauf attempted a DNA analysis on a fragment of the femur of Bear N°2 and a 14C-AMS dating. Both attempts ended in failure because of a lack of collagen, emphasising the age of this bear, greater than the limits of these two methods.

3. Morphometric data

Advice to readers:
All the measurements in this study are in mm and this unit does not appear in the tables.
Abbreviations used:
* about (after a measure)
APD = antero-posterior diameter = length or DAP = diamètre antéro-postérieur
Dentition: I = incisive; C = canine; P = premolar; M = molar
DPD = dorso-palmar or dorso-plantar diameter = height
or DDP = diamètre dorso-palmaire ou
dorso-plantaire (= hauteur)
inf.; sup.; ant.; post.; med.; art.= inferior; superior; anterior; posterior; median; articular
L or R = left or right (= droit ou gauche)
MD = mesio-distal diameter = length (for a tooth)
min., max. = minimum; maximum
Mtt = metatarsal bone; Mtt 3 = 3rd metatarsal bone
P/2 = second lower premolar
P2/ = second upper premolar
PUEMA (Plan Ursidés d‘Enregistrement Morphométrique Argant) = Plan Argant for morphometric record of Ursids.
prox.; ext.= proximal extremity; dist. ext. = distal extremity
TD = transverse diameter or DT = diamètre transverse
TN = transfer number (in a table, a figure, a caption)
VL = vestibulo-lingual diameter = width (for a tooth) HC = heigtht of the crown

The state of the palaeontological material from Bear N°2 did not allow the usual finesse of measurement according to the PUEMA plan for Ursids (Argant, 2010). Therefore, the measurements taken before dismantling played an essential role especially when later measurements could add to their precision. It was not possible to remove the calcite encrustations from all the pieces, except in a few cases where painstaking removal using a diamond bur or acetic acid enabled key observations and measurements to be made. Most of the material consisted of fragments which in some cases could be glued back together. Nevertheless, it was possible to carry out a relatively complete morphometric study of Bear N°2 in order to establish its characteristics.

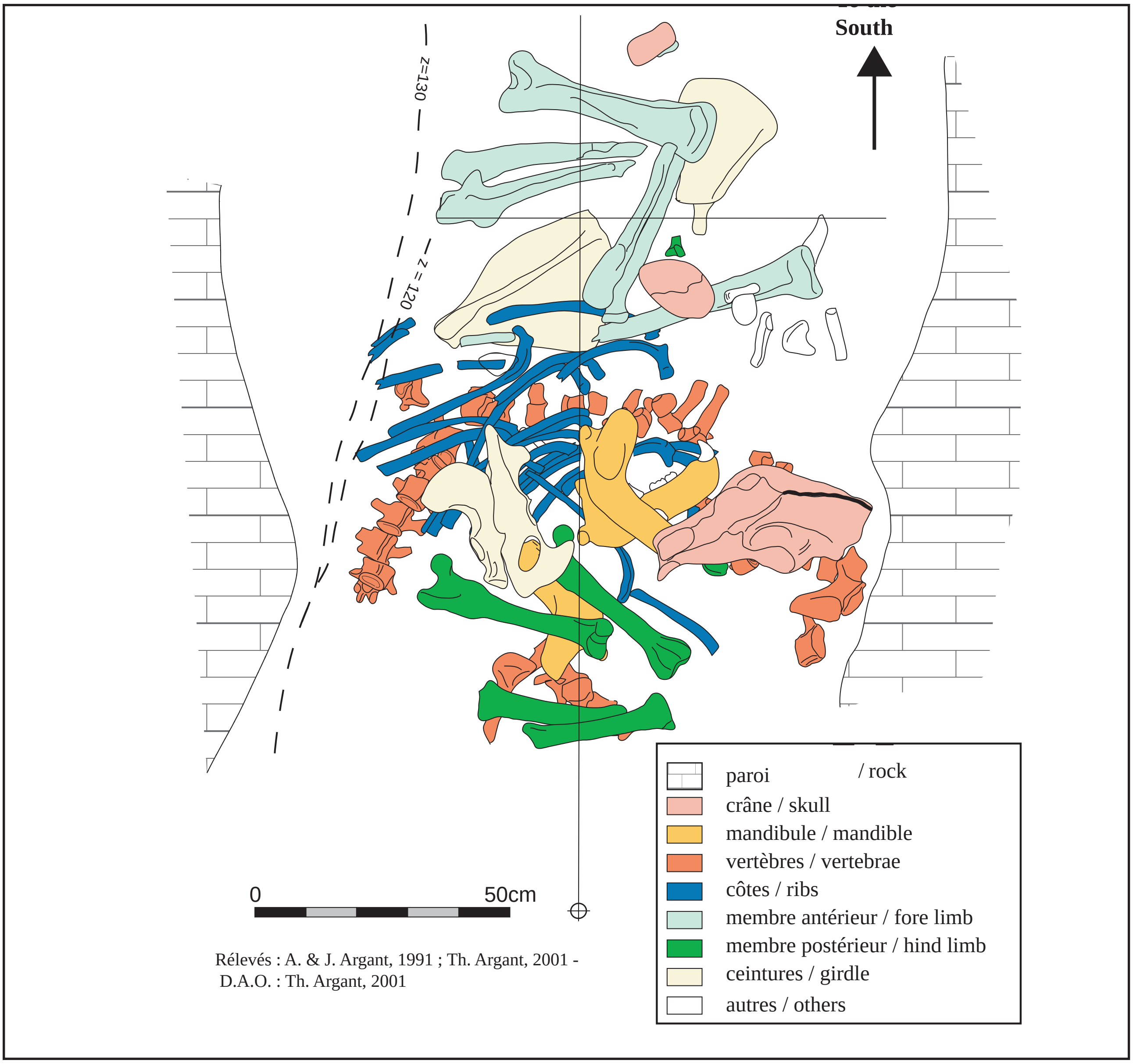


Fig. 4: Sketch of the Bear N°2 in situ in the connecting gallery Azé 1-6 (plan T. Argant).

Fig. 4: Plan de l‘ours N°2 en place dans la galerie de jonction Azé 1-6 (plan T. Argant).

3.1. The adult

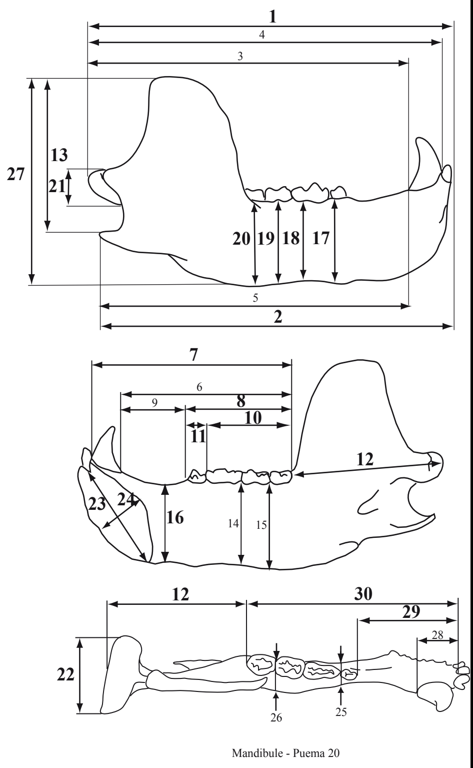
This is a large bear, a female, given the relatively small dimensions of its long and thin canines and the slenderness of its mandible. Its long bones, though large, have neither the massiveness nor proportions of typiquely spelaean forms. Unfortunately, numerous identifying observations have not been possible because of the difficulties encountered in cleaning them.

- the cranium: it is unfortunately extremely fragmented. Only a few pieces are able to provide information. The very brechified incisor segment has however two upper canines in place, and part of the incisor bone is visible along with most of the empty alveoli of the incisors (Tab. 1). The complete upper left canine is long and has a relatively long and slender root. This confirms that the bear is indeed a female. On the left maxilla, also very concretionned, it was possible to clean the two upper molars, M1/ and M2/. The left P4/, also well-cleaned, was on a separate fragment (Fig. 5, Tab. 2).

Bear N°2 - *Ursus spelaeus ladinicus* - Azé 1-6

Cranium	Bear N°2 - adult - TA 06	PUEMA 10	33	Breadth of incisors row (at exterior of I3/)	68
		PUEMA 100	2	Breadth min. of maxilla	88
			3	Breadth of maxilla at the canines	95,3*
			5	Length, anterior of canine - posterior of the M2/	161
			6	Length, posterior of canine - posterior of M2/	138
			7	Length of the cheek teeth	89
	Bear cub TA.50	PUEMA 10	6	Neuro-cranial length: Acrocranion-frontal medial (F)	88
			17	Breadth max. of neurocranium Euryon-Euryon	99
			20	Breadth max. of frontal Ectorbiital-Ectorbital	78

Hemi-mandible	Bear N°2 - adult - L = TA.07b; R = TA.07		PUEMA 20	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**
		L		306,0	-	-	-	-	-	-	-	-	-	-
		R		306,6	280	-	-	-	-	179	91,7	-	77	16
				12	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**
		L		-	-	-	-	59,7	-	-	-	-	64.0	20.2
		R		119,2	126,5*	-	-	-	70,3	67,1	68,1	69	-	-
				23	**24**	**25**	**26**	**27**	**28**	**29**	**30**	**31**	**32**	**33**
		L		90,8	40,6	-	-	-	-	-	-	-	-	-
		R		-	-	-	-	151	-	91,7*	180	-	-	-



Tab. 1: Bear N°2, Azé 1-6, *Ursus spelaeus ladinicus*, skull (PUEMA 10 & 100) and hemi-mandibles (PUEMA 20).
Tab. 1: Ours N°2, Azé 1-6, *Ursus spelaeus ladinicus*, crâne (PUEMA 10 & 100) et hémi-mandibules (PUEMA 20).

- P4/: the crown of this premolar is simple, with three well-individualized cusps dominated by the paracone. The metacone has a slight bulge at the rear. The deuterocone, simple and small in size, stands out on the internal edge of the crown a little towards the rear of the tooth.

Fig. 5: Bear N°2, Azé 1-6, *Ursus spelaeus ladinicus*, left cheek teeth, lingual (a) and occlusal (b) views.
Fig. 5: Ours N°2, Azé 1-6, *Ursus spelaeus ladinicus*, dents jugales supérieures gauches, vues linguale (a) et occlusale (b).

A slight cingulum lies below this edge essentially in its anteromedial part. The two crests of the paracone and metacone are not aligned but form between them an angle of about 150° (Fig. 5).
- M1/: on the crown the metacone slightly dominates the metacone. These cusps are simple, with smooth sides and no significant grooves. The occlusal surface is also smooth, without furrows or ridges. A small parastyle lies at the front of the molar. The metastyle stands out more prominently at the rear. The internal edge of the crown is well developped and has a relatively low gradient (Fig. 5).
- M2/: this is a large, long and simple tooth with a flat occlusal surface and parallel and relatively narrow edges. The paracone clearly dominates the metacone. These two cusps are simple, with smooth sides and a relatively low volume. The talon is slightly granular. On the lingual edge a small cingulum extends as far as the talon. The anteromedial widening is marked but not very developed (Fig. 5).

- the mandible: (Fig. 6)

The two hemimandibles lie flattened one upon the other, the right one above having pivoted 35° under the weight of the skull. The point of the upper right canine is embedded in the hardened sediment surrounding the mandible below. These rest on a tangle of ribs, all in the same block.
There is considerable mineralisation, and though very cracked, the bones have been consolidated by the varnish applied before extraction. All the cheek teeth are present, but only partially visible in lateral view, and impossible to remove in the available time because of their fragility and the hardness of the sediment. Only the incisors and the right M/2 are missing.
Both lower canines are embedded in sediment but only the right one is visible, in lateral view. It is long and slender. The dimensions are those of a large animal. The slender canines as well as the elongated form and not very massive body of the mandible indicate that this individual is female (ARGANT, 1991).

Fig. 6: Bear N°2, Azé 1-6, *Ursus spelaeus ladinicus,* concretionary hemi mandibles connected with ribs.
Fig. 6: Ours N°2, Azé 1-6, *Ursus spelaeus ladinicus,* hémi mandibules concrétionnées et soudées à des côtes.

- post-cranial skeleton (Tab. 3, 4, 5; Fig. 7)
The right tibia has been entirely reconstitued and has provided the usual dimensions (Fig. 7, Tab. 4). It is relatively elongated and not as massive as typical of *Ursus spelaeus*. The index of massivity is 24.2, which is even close to that of *Ursus deningeroides* (= *U. spelaeus deningeroides* Mottl, 1964) from Repolusthöhle (Austria) (Kavcik & Rabeder, 2004, Fig.8)

3.2. The bear cub

Four pieces from a young bear cub - two fragments of the skull, a left mandible and a right ulna (Tab. 5) - were found wedged in the skeleton of Bear N°2. Part of a calcite endocranial cast can be seen through an opening (Fig. 8). The fragment of the right maxilla holds the fully erupted M1/, not at all worn, as well as the partly erupted canine, only the tip of the crown appearing above the level of the maxillary bone (Fig. 9, Tab. 2). The M/3 has not emerged and the roots of the M/2 are visible through a break in the body of the right hemimandible.
They show that only the anterior part of the M/2 has emerged. The occlusal surfaces of these cheek teeth are not observable because of a covering of hardened sediment.
An age of 8 to 10 months can be attributed to this bear cub (Debeljak, 1996). It means that the cub died at the end of autumn, at the beginning of its second period of hibernation in the cave with its mother.
The dimensions and morphology of the first upper molar of the bear cub match perfectly those of the adult, but here the relief of the crown is clearly evident because of the complete absence of wear. The rather smooth appearance of the M/1 of the female is due to pronounced wear (U = 3).
In contrast, the M/1 of the cub (U = 0) has a noticeably granular functional surface (Fig. 9).

Is the female N°2 the mother of this cub? The close association of the complete skeleton of the adult with the remains of a cub immediately makes us wonder about a filial relationship. The cub is not a foetus, but is at least 8 months old.

Bear N°2 - *Ursus spelaeus ladinicus* - Azé 1-6

		Ref.	Lat.	Length	Width	HC	HT	Wearness	Paracone length	Metacone length
Upper teeth	**P4/**	TA.06	L	17.3	12.5	10.7	32.8	1.0	11.4	
	M1/	TA.06	L	25.0	19.0	10.0	31.5	1.5	9.7	9.6
	M2/	TA.06	L	48.2	24.5	11.1	36.6*	1.5	15.3	11.9
Lower teeth	**C**	TA.07	R	20.0*	-	41.5*	-	1.0		
	P/4	TA.07	L	14.5	-	-	-	-		
		TA.07	R	14.9	-	9.0	-	-		
	M/1	TA.07	L	25.4	-	-	-	-		
		TA.07	R	25.9	-	-	-	-		
	M/2	TA.07	L	-	-	8.7	-	-		
	M/3	TA.07	R	25.3	18.7	9.6	-	1.0		
Cub	**M1/**	TA.50	R	26.2	19.6	10.8	27.8	0.0	10.8	10.7

Tab. 2: Bear N°2, Azé 1-6, *Ursus spelaeus ladinicus*, upper and lower teeth.
Tab. 2: Ours N°2, Azé 1-6, *Ursus spelaeus ladinicus*, dents supérieures et inférieures.

It would have been entering its second winter with its mother, hardly ever away from her, especially in a cave. The M1/, the only dental element usable, reveals a perfect morphometric correspondance between the two individuals.

Although it is not possible to be certain, the likelihood that the cub was lying close to its mother seems high and perhaps can be validly assumed.

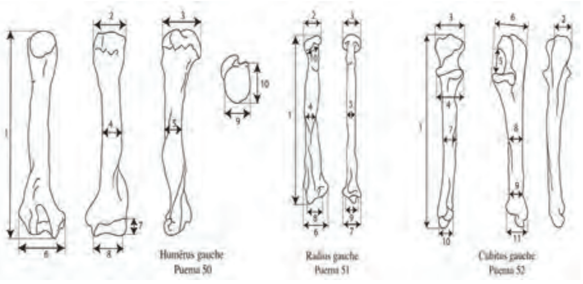
3.3. How to determine the species of Bear N°2?

Available evidence consists of morphometric comparison with bears from other loci in Azé 1 and the age of this bear which is beyond the limits of 14C dating. Right at the back of the cave (220 m from the entrance), Azé 1-4 delivered *Ursus deningeri*, as did Azé 1-3.

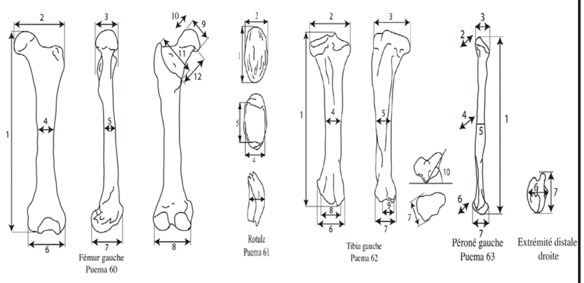
The latter was originally identified as *Ursus spelaeus deningeroides* Mottl, 1964 (Argant, 1991) in order to show its closeness to the ancestral form as well as its characteristics more recent than those of forms from the median Middle Pleistocene. Because of its morphological features, the skull of the cave lion contemporaneous with these bears belongs to the ancient form *Panthera (Leo) spelaea fossilis* (Sotnikova & Nikolskyi, 2006, Argant & Brugal, 2017).

The stalagmitic blockage of this part of the cave (terminal for bears) began at the end of OIS.7 but mainly occurred during OIS.6.

Fore limb - *Ursus spelaeus ladinicus* - Azé 1-6					
Reference TA			L	R	Cub (R)
Humerus L = TA.27 R = TA.31	1	L	-	376.0	
	2	prox.TD	77.0	78.4	
	3	prox. APD	92.7	95.3*	
	4	med. TD	-	38.8	
	5	median APD	-	43.0	
	6	dist. TD	-	119.7	
	7	dist. max. APD	-	76.0*	
	8	max.dist.art. TD	-	82.8	
	9	caput TD	-	64.4	
	10	caput APD	-	78.1	
Radius L = TA.26 R = TA.24	1	L	250.0*	252.0*	
	2	prox.TD	-	37.8	
	3	prox. APD	-	47.3	
	4	med. TD	-	20.9*	
	5	median APD	-	32.1*	
	6	dist. TD	-	-	
	7	dist. APD	-	-	
	8	dist.art. TD	-	-	
Ulna L = TA.25 R = TA.24 Cub (R) = TA.58	1	L	352.6	352.6*	132.0*
	2	olecranon TD	46.8	-	
	3	olecranon APD	80.7*	-	
	4	prox.art. TD	54.5	-	
	5	prox.art. APD	33.0	-	
	6	prox. APD	-	-	
	7	med. TD	30.5	-	11.3*
	8	median APD	38.2	-	19.3
	9	min. diaphysis APD	29.0	-	
	10	dist. TD	26.8	-	
	11	dist. APD	46.4	-	



Hind limb - *Ursus spelaeus ladinicus* - Azé 1-6				
Reference			L	R
Femur L = TA.03 R = TA.04	1	L	409.8	-
	2	prox.TD	112.3	-
	3	prox. APD	59.0	-
	4	med. TD	42.8	43.6
	5	median APD	32.5	-
	6	dist. TD	88.0	90.5
	7	dist. APD	77.2	76.8
	8	dist. art. TD	79.8	76.6
	9	caput art. TD	51.2*	-
	10	aput art. APD	53.8	-
	11	inter trochanter L	94.9	-
	12	neck L	73.4	-
Patella	1	DPD	-	61.0
	2	max. TD	-	45.0
	3	APD	-	-
	4	art. TD	-	-
	5	art. APD	-	-
Tibia L = TA.01 R = TA.02	1	L	-	296.7
	2	prox.TD	-	95.8
	3	prox. APD	-	-
	4	med. TD	33,0	30.7
	5	median APD	-	36.1
	6	dist. TD	-	71.7
	7	dist. APD	-	38.4
	8	dist. art. TD	-	54.3
Fibula R = TA.57	1	L	-	-
	2	prox.TD	-	-
	3	prox. APD	-	-
	4	med. TD	-	-
	5	median APD	-	-
	6	dist. TD	-	23.4
	7	dist. APD	-	30.9



Tab. 3: Bear N°2, Azé 1-6, *Ursus spelaeus ladinicus*, fore limb (PUEMA 50, 51 & 52).
Tab. 3: Ours N°2, Azé 1-6, *Ursus spelaeus ladinicus*, membre antérieur (PUEMA 50, 51 & 52).

Tab. 4: Bear N°2, Azé 1-6, *Ursus spelaeus ladinicus*, hind limb (PUEMA 60, 61 & 62).
Tab. 4: Ours N°2, Azé 1-6, *Ursus spelaeus ladinicu*s, membre postérieur (PUEMA 60, 61 & 62).

The age of the bears from Azé 1-3 is consistent with this chronology and the determination *Ursus deningeri* must be retained. In the median part of the cave (from 90 to 100 m from the entrance), Azé 1-2 yielded a large collection of bear remains. These are more recent than Azé 1-3 based on a dental study (ARGANT, 1991, Fig.36) confirming the presence of two different morphotypes for the M2/, an important tooth for characterizing a species. The first morphotype is that of *Ursus deningeroïdes*, very similar to the photo of an M2/ from Repolusthöhle (RABEDER et al., 2016, Fig. 4-1). The second morphotype (for two M2/) is clearly different and corresponds to a short M2/ with parallel edges, but by its shortness it is different from that of *Ursus spelaeus ladinicus*. This collection from Azé 1-2 can be linked to the recent Middle Pleistocene because of the microfauna found above the remains, such as an *Arvicola* whose M/1 has the dental characteristics of Middle Pleistocene forms (JEANNET, 1980).

This is also confirmed by the presence of *Paleoperdrix* (MOURER-CHAUVIRE, 1975).

Fig. 7: Bear N°2, Azé 1-6,
Ursus spelaeus ladinicus, right tibia, posterior view.
Fig. 7: Ours N°2, Azé 1-6,
Ursus spelaeus ladinicus, tibia droit, vue postérieure.

Fig. 8: Cub, Bear N°2, Azé 1-6,
Ursus spelaeus ladinicus, skull, neurocranium with the opening showing the endocranium partially casted by calcite.
Fig. 8: Ourson, Ours N°2, Azé 1-6,
Ursus spelaeus ladinicus, crâne, neurocrâne avec ouverture montrant un moulage partiel de l‘endocrâne par la calcite.

Bear N°2 - *Ursus spelaeus ladinicus* - AZE 1-6										
Vertebrae	**Cervical vert.**		**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**
			DPD	**TD**	**APD**	**art. cran. TD**	**caud. Art. TD**	**max. APD**	**dors. min. APD**	**vent. min. APD**
		Atlas TA. 49	60,3	160,0*	-	87,3	-	-	-	-
			1	**2**	**3**	**4**	**5**	**6**	**7**	**8**
			cranial vert. body TD	**cranial vert. body DPD**	**caud. vert. body TD**	**caud. vert. body DPD**	**max.vert. body APD**	**Rank**	**Total length with apophysis**	
		CV TA.83	43.9	31.2	-	27.9	35.6	4	-	
	Thoracic vert.	TA.68	-	-	62.7	45.3	40.4	11	74.1*	
	Lombar vert.	TA.60	61.9	39.9	61.4	61.6	45.0	6	-	
Scapula	**left**		**1**	**2**	**3**	**5**	**6**	**7**	**8**	**9**
			L	**max L. (with spina**	**APD**	**max. prox. TD**	**articular TD**	**articular DPD**	**APD neck**	**acromion width**
		TA.20	280.0	260.0	230.0	81.0	71.2	36.7	83.8	31.6
Patella			**L**	**l**						
		TA.47	61.0	45.0						
Calcaneum	**right**		**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**
			L	**astr..art. TD**	**tuber calc. TD**	**tuber calc. DPD**	**max. prox. TD**	**max. prox. DPD**	**min. diaphysisTD**	**min. diaphysis APD**
		TA.30	88.7	46.9	36.9	41.6	64.2	45.1	18.8*	34.5*
Metatarsus			**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**
			L.	**prox. TD**	**prox. APD**	**med. TD**	**med. APD**	**dist. TD**	**dist. APD**	**dist.art. TD**
	Mtt.2 (left)	TA.32	64.3	12.2*	22.3	13.5	10.4	19.8	16.4	16.7
	Mtt.3 (right)	TA.59	72.5*	19.8	-	13.6	13.3	22.1	19.3	19.4
Phalanx 2			**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**
			L.	**prox. TD**	**prox. APD**	**med. TD**	**med. APD**	**dist. TD**	**dist.APD**	**dist.art. TD**
		TA.48	25.8	16.6	12.4*	12.1	8.4	14.5	11.4	12.8

Tab. 5: Bear N°2, Azé 1-6,
Ursus spelaeus ladinicus, post-cranial (diverse).
Tab. 5: Ours N°2, Azé 1-6,
Ursus spelaeus ladinicus, post-cranial (divers).

Fig. 9: Bear N°2, Azé 1-6,
Ursus spelaeus ladinicus, fragment of the right maxilla with M1/ and C.
Fig. 9: Ourson, Ours N°2, Azé 1-6,
Ursus spelaeus ladinicus, fragment du maxillaire droit avec M1/ et C.

It is interesting that the entrance chamber, Azé 1-1 (excavation J. Combier), has provided *Ursus deningeri*, a more ancient form than that of Azé 1-2, as well as very crude artefacts from the Lower Palaeolithic, evidence of the passage of prehistoric Man (Combier et al., 2000). Bear N°2 from Azé 1-6 corresponds neither to *Ursus deningeri* nor to *Ursus spelaeus deningeroïdes*. It is a large bear, with a longer and less massive tibia, proportionally similar to that of *Ursus deningeroïdes*.

The M2/ is very similar to the one in photography of the skull of *Ursus spelaeus ladinicus* from the Conturines (Italy) (Rabeder & Kavcik, 2014). In the Galerie des Aiglons, just below the Fosse Rotonde, a group of two complete bear skulls was excavated. The southernmost, upside down, displayed a row of teeth morphologically very similar to those observed on Bear N°2, with a right P3/ clearly visible, but with the corresponding left part of the maxilla hidden under encrustations. The presence of a P3/ is also encountered in *Ursus spelaeus ladinicus* (about 30%, Rabeder et al., 2004) and is undoubtedly more frequent in ancient forms of this species. Here it is encountered chronologically well before the limit of 14C dating. In any case, Azé 1-6 (connecting gallery) and Azé1-5 (Galerie des Aiglons) contained the most recent of the bears found in Azé 1, which at this time could only reach the upper gallery of Azé 1 by passing through the Galerie des Aiglons and the connecting gallery.

4. Elements for dating

Most of the sedimentary filling still in place in the Azé 1 cave clearly dates to the Middle Pleistocene, principally characterised by important phases of concretion beginning during OIS 6. These phases partitioned the gallery into three sections, which then functioned separately but nevertheless also in ways that were determined by connection with the Galerie des Aiglons, including its parts still unknown. These concretions are probably linked to modifications of the surrounding limestone due to particularly strong erosion during OIS.6 at the time of the second last glacial period. Indirect evidence is provided by the relative chronology of these events. The oldest corresponds to the stalagmitic system of the Salle du 14 Juillet blocking the Salle des Ours of Azé 1-3, and dated by U/Th at 190.7 ka, 158.1 ka and 113.1 ka. It lies below the highest part of the Plateau de Rochebin. We can imagine maximum erosive action on the high part of the plateau during the severe cold of OIS. 6, dismantling the more impermeable upper layers of limestone. The stalagmitic blockage 60 m from the entrance occurred later. Nine U/Th datings: 134.6 ka; 114.6 ka; 63.4 ka; 58.9 ka; 53.5 ka and four more recent ones relate it to OIS.3 and then OIS.2. This blockage was clearly more to the south and lies below some of the large slope deposits which further down had closed the entrance to Aze 1. The dismantling of the surface in this location occurred later. Here the concretions began to form after the particularly severe stage OIS. 6, mostly during stage OIS. 4.

The second characteristic is the existence of the Galerie des Aiglons (Azé 1-5) a few meters below and to the east of Azé 1 and parallel to it. These two galleries are connected at a number of points. We had already become certain of the existence of a lower network during our excavations in Azé 1-2 (1978) and especially in Azé 1-3 (1982-1985) because of the presence of several drainage points in each of these cave sections where water which had accumulated over winter disappeared. Later in Azé 1-3, the dip of the bear and lion layer towards the north was confirmed (Argant et al., 2007), and explained a posteriori by the discovery of the drainage point at the “bayonet” in Azé 1-4 where a large number of bear remains had accumulated. Towards the entrance, the regular drainage of water from the filling of the Fosse Rotonde led to the discovery of a succession of parallel lines of bones directly below Bear N°1, separated by sterile layers of clay. This clearly indicated that lines of bones originally in the same position as Bear N°1 had gradually sunk against the west wall of the Fosse Rotonde (excavations L. Barriquand). Electric tomography carried out later by O. Kaufman clearly confirms the extension of the Galerie des Aiglons northwards, at least as far as the far end of Azé 3, as well as the presence of large voids upstream of the current terminal cross-section of the Galerie des Aiglons (Barriquand et al., 2016).

- The complete bears from the connecting gallery Azé 1-6 are geologically too old to be dated by 14C-AMS. Two separate attempts, one directly on Bear N°2, ended with the same negative result, “date beyond the limit of the method” (about 50 ka). That left only two other dating methods that could be used, the sufficiently characteristic evolutionary stage of Bear N°2, and dating based on the evolution and functioning of the connecting gallery between Azé 1 (tourist gallery) and the Galerie des Aiglons (Azé 1-5), using all available data.

- Section 1 of the front part of Azé 1 terminated at the stalagmitic blockage 60 m from its entrance. For a very long time this blockage was where the cave ended and it was broken through by speleologists only in 1963. It began to form during OIS.5e after the second last glaciation, ultimately preventing the arrival of any water from sections of the cave to the north. Running water in this part of the cave would have prevented or dismantled any deposit of calcite. Therefore, from this time, Section 1 of the cave functioned independently.

- The presence of prehistoric Man in Azé 1-1 (excavations J. Combier) indicates that he entered the front chamber of the cave directly from the outside and in daylight, but this occurred largely before OIS.6. The bear found here is *Ursus deningeri*. Later, the entrance of Azé 1 was blocked by slope deposits. The cave contained a body of water (permanent or temporary?) in which bones rolled along by the current were deposited by progradation (Argant, 2004). At a certain point in time, only the connecting gallery (Azé 1-6) allowed communication with the exterior through the Galerie des Aiglons (Azé 1-5). This explains the greater age and good preservation of the filling of the entrance chamber (Salle d’entrée, Azé 1-1).

- During major flooding, water could only enter Azé 1-1 from the lower Galerie des Aiglons via the connecting gallery, Azé 1-6, and other points of connection. In these conditions, rapid falls in the water level could have flushed Bear N°2, still intact and attached by its ligaments, into the connecting gallery where it became jammed between the walls. Later, bears passed through this gallery and currents of water carried away smaller bones. Those left behind were covered by fine sediments and extensive concretions which protected them.

- The use of only Section 1 of the cave by bears to hibernate should be placed at the end of the recent Middle Pleistocene (OIS.6), at stage OIS.5, or at the latest, at stage OIS.4. *Ursus spelaeus ladinicus* is found neither in Azé 1-1, nor in Azé 1-3, nor in Azé 1-4. Azé 1-2 indicates the presence of *Ursus spelaeus deningeroides* which at that time could still reach Section 2 upstream of the stalagmitic blockage at 60 m which started at 134.6 ka and by OIS.5 was sufficiently developed to prevent the entry of large fauna. The use of the connecting gallery, Azé 1-6, as the only means of entering the upper gallery corresponds to this period. At this time *Ursus spelaeus ladinicus* was the only bear there. The bear from Azé which provided mtDNA comes from the palaeontological stock collected in Section 1, from near the Fosse Rotonde (Orlando et al., 2002, Fig.4). It is contemporaneous with Bear N°2 and its location would indicate that its species is the most recent of those from Azé 1. The genetic study shows that it belongs to haplogroup A, along with the sequences from Scladina (Belgium), Prélétang and les Merveilleuses (France), and Conturines (Italy). This constitutes a sound confirmation of the determination that Bear N°2 is *Ursus spelaeus ladinicus*.

- The cave hyaena, *Crocuta spelaea*, is found in the Brèche de Château (Saône-et-Loire) at OIS. 6, and is not usually encountered in Burgundy before this stage. It has always been rare in Burgundy and only became more widespread from OIS.4 until OIS.2. In Azé 1, a metapodial bone and some coprolites found in Azé 1-2 confirm its presence there but nothing has been found north of this locus. It is present in Section 1, downstream from the blockage at 60 m but in layers lower than the stalagmitic deposit which, because of their stratigraphic position, must correspond chronologically to those of Azé 1-2. It is represented there by several hemimandibles. The concretions at 60 m began to form at the very beginning of OIS. 5e, about 130 ka. Therefore, the presence of the cave hyaena in Azé 1 occurred before these concretions, during OIS.6, and was contemporaneous with *Ursus spelaeus deningeroïdes* and *Ursus spelaeus ladinicus* in Azé 1-2.

The excavation by L. Barriquand below the Fosse Rotonde encountered lines of bones directly below Bear N°1, descending progressively from the upper gallery towards the Galerie des Aiglons. The fauna, still under study, is particularly diversified (ARGANT et al., 2011). Such diversity is surprising at Azé 1, which for a long time, had been only a bear den, with only the usual visites by cave lions. Classically, only two potential factors could explain such diversity, either man or cave hyaenas. Prehistoric man did indeed leave traces at Azé, very crude Clactonian type artefacts, much too ancient to be contemporary with *Ursus spelaeus ladinicus*. Evidence of the Middle Palaeolithic has not been found in Azé 1, although it has been found outside at Azé 2 (COMBIER & MERLE, 1999). Fragments of flint attributed to the Upper Palaeolithic were found in Azé 1 before the stalagmitic blockage at 60 m, and at the present end of the Galerie des Aiglons, proof of the possible penetration by Man at this time (FLOSS & HOYER, 2010).

But these rare indices are not sufficient to explain the abundance and the diversity of the fauna and they are more recent than the cave hyaena, *Crocuta spelaea* (OIS 6- OIS 5), which therefore remains as the only explanation for that.

Bears N°1 and N°2 in Azé 1-6 (connecting gallery) were situated above these lines of bones and had not time to be affected by the same subsidence towards the lower network. Chronologically, this places them after the activity of hyeanas began, and later than Azé 1-2, which took place before the stalagmitic blockage at 60 m.

- Previous searches for fossilized pollen in the Azé sediments had always been disappointing, hardly surprising given that the conditions for their deposit and preservation were far from favourable (ARGANT, 1990).

However, in the case of the connecting gallery it was worth a try. Pollen could have ended up embedded in sediment because it had been on the fur or in the digestive tracts of buried animals. In the case of Bear N°2 and the cub, it appeared that conditions were favourable to the preservation of pollen because of the rapidity with which their bones were buried and then covered by concretions which would have protected them from the action of oxygen. Two samples of very compact concretions, one adhering to the skull of the bear N°2 (TA.06), the other to the skull of the cub (TA.22) were chosen for pollen analysis.

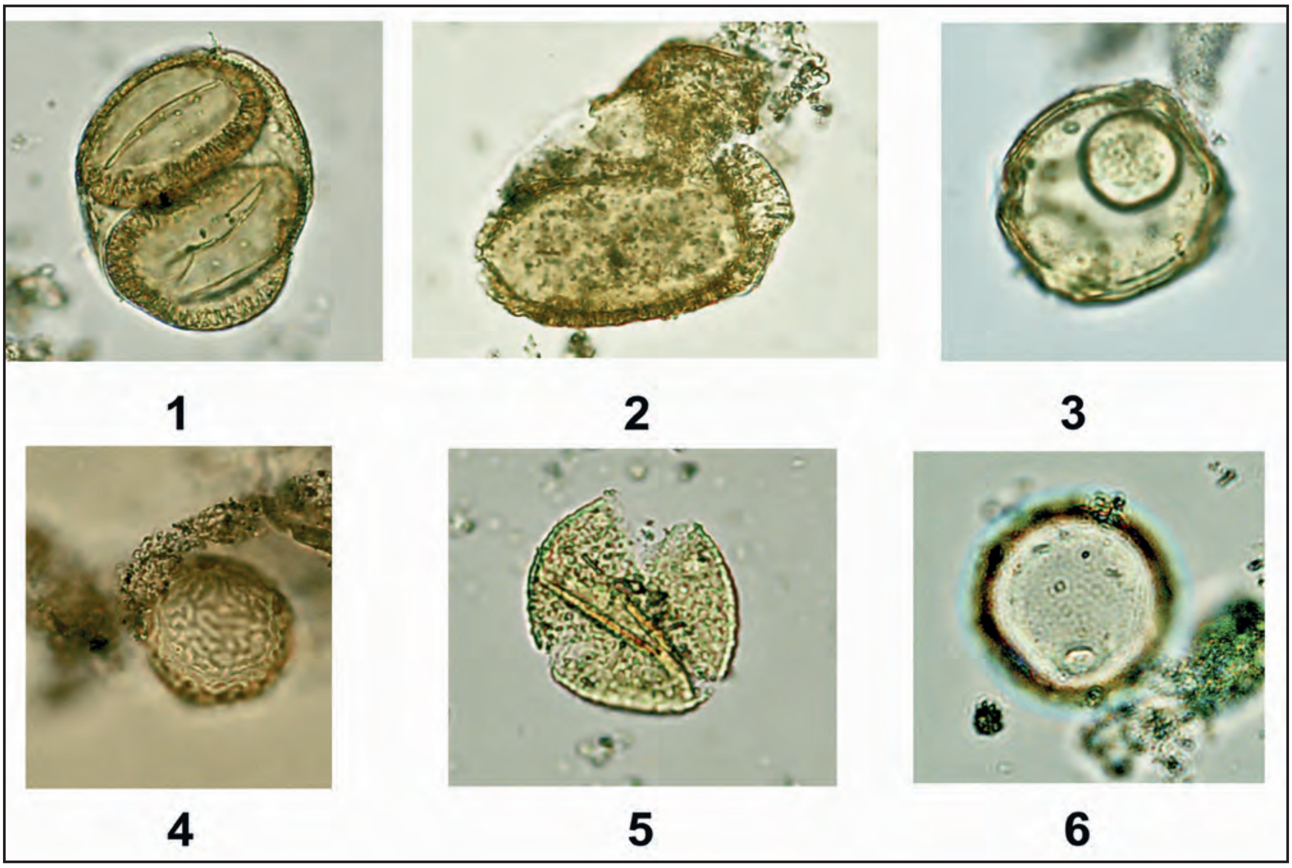


Fig. 10: Bear N°2, Azé 1-6, pollen grains from the samples of concretions in contact with the skulls (adult and cub).
1- *Pinus* (60 µm); 2- *Cedrus* (damaged), (60 µm); 3- *Alnus* (22 µm); 4- *Ulmus* (24 µm); 5-*Quercus* (20 µm); 6- Poaceae (25 µm) (Photos J. Argant).

Fig. 10: Ours N°2, Azé 1-6, grains de pollen des échantillons de concrétions en contact avec les crânes (adulte et ourson).
1- *Pinus* (60 µm) ; 2- *Cedrus* (abîmé), (60 µm) ; 3- *Alnus* (22 µm) ; 4- *Ulmus* (24 µm) ; 5- *Quercus* (20 µm) ; 6- Poaceae (25 µm) (Photos J. Argant).

They both provided pollen in very good condition and of a similar type, of which 34 were identifiable (Fig. 10, Tab. 6). They are essentially from trees, among them four types of conifers (pine, cedar, juniper and one undetermined), but the pollen grains of mesothermophilous broadleaved trees largely dominate: alder, hazelnut, deciduous oak, elm, hornbeam, ash. They indicate temperate conditions, and in the case of alder, water-logged soils essential for their growth.

Azé 1-6. Bear N°2	TA-06	TA-22
	Adult	Cub
Pinus	1	
Cedrus	1	1
Undet. Conifer	1	
Betula		1
Juniperus	1	
Alnus	5	2
Corylus	3	
Quercus	3	
Ulmus	3	
Carpinus		1
Fraxinus	1	
Ranunculaceae	5	1
Poaceae	2	
Brassicaceae	1	
Chenopodiaceae		1
Undetermined	5	
Total	32	7
AP	**19**	**5**
NAP	**8**	**2**

Tab. 6: Bear N°2, Azé 1-6, *Ursus spelaeus ladinicus*, result of pollen analysis of the two samples.
Tab. 6: Ours N°2, Azé 1-6, *Ursus spelaeus ladinicus*, résultat de l‘analyse pollinique des deux échantillons.

Though not enabling a reconstruction of the landscape, these results do however support the hypothesis that the bones were deposited and covered by concretions during a clearly temperate phase consistent with OIS.5, and rule out OIS.4 which is considerably cold.

The Galerie des Aiglons is probably the major gallery of the karstic system of Azé 1. It has been active for a very long time, just as much as the upper tourist gallery, and continued to function long after the latter was closed by slope deposits.

A study of cryophilic microfauna by M. Jeannet indicates a glacial period dated by 14C-AMS at 15,945 ± 65 BP (OxA-12455).

A fragment of bear bone from the layer below this microfauna could not be dated because it was older than the limit of the method (Barriquand et al., 2011). A stalagmitic floor dated by U/Th at 8.1 (± 1.2) ka BP sealed the filling. The entrance of the Aiglons therefore disappeared behind slope deposits at the latest in OIS.1, or even before the end of the Tardiglacial period, in OIS.2.

Finally, Bear N°2 from Azé 1-6, *Ursus spelaeus ladinicus*, occurred between the end of OIS.6 and at the latest OIS.4, in any case before the 50-ka upper limit of the 14C-AMS method. Pollen analysis indicates a warm temperate period attributable to OIS.5.

5. Conclusion

The complete skeleton of Bear N°2 provides a reference point within a relatively precise chronological range in the evolution of cave bears in Burgundy (Tab. 7).

Chronology (after Gamble, 1999)	**Ka**	**478**	**427**	**410**	**375**	**320**	**230**	**200**	**130**	**75**	**50**	**30**	**10**
	OIS	**OIS.12**	**OIS.11**	**OIS.10**	**OIS.9**	**OIS.8**	**OIS.7**	**OIS.6**	**OIS.5**	**OIS.4**	**OIS.3**	**OIS.2**	**OIS.1**
Loci in Azé 1	AZÉ 1-1	?	▨	▨	▨	▨	▨						
	AZÉ 1-2	?	▨	▨	▨	▨	▨	▨					
	AZÉ 1-3	?	▨	▨	▨	▨	▨						
	AZÉ 1-4	?	▨	▨	▨	▨							
	AZÉ 1-5	?	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	
	AZÉ 1-6	?	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	
Bears	*U. deningeri*	?	+	+	+	+	+						
	U. spelaeus deningeroides							+					
	U. spelaeus ladinicus							?	+	?			
	U. arctos								+				
Crocuta spelaea								+ Azé 1-2 Azé 1-5	+ Azé 1-5	+ Azé 1-5			
Stalagmitic blockages 🟥 Salle du 14 juillet Section 3 isolated		?	+	+	+	+	+	🟥					
Blockage at 60 m Section 2 isolated		?	+	+	+	+	+	+ 🟥					
Blockage of the entrance of Azé 1-1		?	+	+	+	+	+	🟥					re-opening
Functioning of Azé 1-5 and Azé 1-6 possible		?	+	+	+	+	+	+	+	+	+	+ 🟥	
Presence of Man possible Azé 1-1 : Lower Paleolithic				+	+	+	+						
Azé 1-5 ; Upper Paleolithic											+	+	
Bronze Age Azé 1 - Section 1													+
Gallo-roman Azé 1 - Section 1													+
Middle Ages Historical period Azé 1 - Section 1													+
Bear N°2 **Azé 1-6**								?	**+**	?			

Tab. 7: Azé 1 chronological synthesis. Various chronological marks and position of the various bears following each other.

Tab. 7: Azé 1, synthèse chronologique. Différents repères chronologiques et position des différents ours s‘y succédant.

Azé 1 establishes the direct and continuous links in the evolutionary stages and in the dynamics of the populations of bears in the course of time, from the form *U. deningeri* at the end of median Middle Pleistocene (since OIS.9 or even before) in the entrance of Azé 1-1, in Azé 1-4, and at the end of Azé 1-3, then *U. spelaeus deningeroides* during the recent Middle Pleistocene (OIS.6) in Azé 1-2 (ARGANT, 1991).

Ursus spelaeus ladinicus form occurred later in Azé 1-5 and Azé 1-6, probably during OIS. 5, at the latest during OIS.4, but in any case, before the limit of 14C. This latter subsisted until much later, for example in the Alps: Cuvée des Ours, Chapareillan (Isère, France), 1,641 m asl, 13,990±50 BP, Ly-2545 (OxA) (ARGANT et al., 2018).

The site of Azé has been well studied in a wide range of fields (prehistory, palaeontology, history, dating, karstology, underground biology, botany).

Palaeontology provides elements of dating which can enable a better understanding of the evolution and functioning of this very particular karstic system, neither too large, nor too small, on the human scale of speleologists and scientists, and even of bears!

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Cave bears and ancient DNA: a mutually beneficial relationship

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Abstract

For almost 30 years, cave bears and paleogenetic research have shared a mutually beneficial relationship. Due to the abundance and frequently good preservation of cave bear bones, they have often been the tissue of choice to develop and test molecular approaches aimed at recovering and sequencing DNA from ancient remains. Our understanding of cave bear biology has similarly profited from the molecular data produced through paleogenetic studies. DNA data has complemented morphological data to provide insights into the evolution and phylogeny of cave bears. Molecular population dynamic studies have helped develop hypotheses explaining the extinction of cave bears, and new genomic data is now promising to shed light on evolutionary and population genetic processes that could previously only be obtained from living species. Here we evaluate and review the role cave bears have played in the development of paleogenetic research as well as the role that paleogenetic research has had in understanding cave bear biology. We provide a perspective on where this mutually beneficial relationship is likely to take us in the near future.

Zusammenfassung

Seit fast 30 Jahren verbindet die Höhlenbären- und paläogenetische Forschung eine, für beide Seiten vorteilhafte, Beziehung. Aufgrund der Fülle und häufig guten Erhaltung von Höhlenbär-Knochen waren sie häufig das Material der Wahl, um molekulare Ansätze zur Extraktion und Sequenzierung von DNA aus Fossilien zu entwickeln und zu testen. Unser Verständnis der Biologie des Höhlenbären hat in ähnlicher Weise von den molekularen Daten aus paläogenetischen Studien profitiert. DNA-Daten haben morphologische Daten ergänzt, um Einblicke in die Evolution und Phylogenie des Höhlenbären zu erhalten. Molekulare Studien zur Populationsdynamik haben dazu beigetragen, Hypothesen zum Aussterben der Höhlenbären zu entwickeln und neue Genomdaten versprechen nun Aufschluss über evolutionäre und populationsgenetische Prozesse, die bisher nur an noch lebenden Arten untersucht werden konnten. In diesem Artikel untersuchen und diskutieren wir die Rolle, die Höhlenbären bei der Entwicklung der paläogenetischen Forschung gespielt haben, wie auch die Rolle, die die paläogenetische Forschung beim Verständnis der Biologie der Höhlenbären gespielt hat. Es wird ein Überblick darüber gegeben, wohin uns diese, für beide Seiten vorteilhafte, Beziehung in naher Zukunft führen wird.

Key words: *Ursus spelaeus*, megafaunal extinction, molecular palaeontology, cave bear taxonomy, paleogenomics, paleogenetics

Introduction

The study of ancient DNA, i.e. DNA mostly derived from subfossil bones less than 1 million years old, has fascinated scientists and the public alike ever since the first reports on its feasibility were published more than 30 years ago (HIGUCHI, BOWMAN, FREIBERGER, RYDER & WILSON, 1984). By now, DNA data from thousands of specimens have been published, ranging from short snippets of mitochondrial DNA to multifold coverage of the nuclear genome. These data have been used to address a variety of questions, including identification of samples to species (DALÉN et al., 2017), phylogenetic relationships of extinct species to their extant relatives (DABNEY et al., 2013, KRAUSE et al., 2006, MEYER et al., 2012), identification of morphological traits and their genetic basis, especially traits that do not fossilize (BURGER, KIRCHNER, BRAMANTI, HAAK & THOMAS, 2007, FORTES, SPELLER, HOFREITER & KING, 2013, OLALDE et al., 2014, RÖMPLER et al., 2006), and various population genetic analyses (SHAPIRO et al., 2004), such as changes in genetic diversity over time (STILLER et al., 2013), gene flow (BARLOW, CAHILL et al., 2018) and population replacements (COLLINS et al., 2014, HOFREITER et al., 2007; RAWLENCE et al., 2017).

However, despite the wide range of research that can be conducted using ancient DNA and the spectacular successes obtained through it, retrieving DNA sequences from fossils is not trivial. DNA degrades rapidly in the fossil record, resulting in three main obstacles for analysis. First, many bones simply contain no DNA of interest (i.e. that from the individual a bone originates from, also called “endogenous DNA”). The older a bone and the warmer the climate in the place it originates from, the less likely it is that a sample still contains DNA (PÄÄBO et al., 2004). The age limit for aDNA retrieval at the moments lies around 400,000 years (DABNEY et al., 2013) outside the permafrost and around 700,000 years for permafrost samples (ORLANDO et al., 2013). Second, even if DNA is preserved, often the endogenous DNA is far rarer than DNA originating from microorganisms that have lived on the bone any time between the death of an animal and the analysis of the bone. And third, ancient DNA molecules are short, often in the range of 30-50 basepairs (KISTLER WARE, SMITH, COLLINS & ALLABY, 2017, ROHLAND, GLOCKE, AXIMU-PETRI & MEYER, 2018) meaning puzzling together useful data sets is a major task even though this is now done by computer programs. In fact, modern high-throughput sequencing datasets contain so many short DNA sequencing reads that assembling them into their respective genome regions can often not be achieved without very powerful “super” computers.

So clearly some issues that need paying attention to if ancient DNA is analysed. Providing this is done, successful ancient DNA analysis are, as in any scientific endeavour, then simply a combination of asking the right questions, obtaining the right samples (as much as this is possible to know in advance), applying the right methods for analysis (both in the laboratory and at the computer) and having the required amount of luck. Cave bears are a particularly suitable species for ancient DNA analyses, which has to do mainly with where and how they lived. Cave bears probably represent the Pleistocene species with the richest fossil record of all. This is mainly the case since they used karstic caves for hibernation, which means their bones can be found in large numbers and are usually well preserved. They also went extinct only about 27,000 years ago (Pacher & Stuart, 2009) and diverged from their sister species, the common ancestor of brown bears and polar bears between 1.2 and 1.6 million years ago (Knapp et al., 2009), meaning that a substantial part of their evolutionary history falls in the time range for which ancient DNA analyses are possible. Furthermore, within the family Ursidae, there are several quite closely related species, most of which are more or less well studied genetically and genomically, so that comparative genetic data are available (Barlow, Cahill et al., 2018, Cahill et al., 2013). And finally, the cave bear is a well-known and charismatic species, and its evolution as well as the causes that led to its demise are of interest not only to scientists but also to the broader public.

Part 1: Contributions of cave bears to ancient DNA

Our understanding of cave bear evolutionary history has benefitted tremendously from ancient DNA analyses, but at the same time, ancient DNA as a research field has also benefitted tremendously from analyses of cave bear samples. Thus, the first short DNA segments analysed from cave bears and published in 1994 (Hänni, Laudet, Stehelin, Taberlet, 1994) also represented the first reproducible Pleistocene DNA sequences obtained for any species from outside the permafrost. Although alleged sabretooth cat sequences had been published in 1992 (Janczewski, Yuhki, Gilbert, Jefferson & O'Brien, 1992), these have been shown to be incorrect (Barnett et al., 2005) and are now widely accepted to represent contamination with modern DNA from the lab, in which the analyses were performed.

Cave bears also hold the records for the oldest sample outside of permafrost from which DNA has been firstly recovered, and subsequently sequenced. Both records go back to the same bone, a 400,000 year old cave bear bone from the Spanish site Sima de los Huesos (Dabney et al., 2013). A 2006 study had already managed to type single nucleotide polymorphisms of the mitochondrial genome from this sample, an achievement clearly ahead of its time (Valdiosera et al., 2006). The data was later confirmed by sequencing of the entire mitochondrial genome from this specimen using next generation sequencing in combination with DNA hybridization capture in 2013 (Dabney et al., 2013).

Moreover, the first Pleistocene mitochondrial genome from samples outside the permafrost was also obtained from a cave bear (Krause et al., 2008). In fact, since one of the current authors was principal investigator on this study, we are able to point out that the cave bear mitochondrial genome was in fact the first Pleistocene mitochondrial genome obtained ever, even predating the mammoth (Krause et al., 2006) that was published earlier. Publication of the cave bear mitochondrial genome was simply delayed by a lack of comparative data from the related species at the time, and obtaining these required substantial time. Even earlier, studies on larger sets of cave bear bones demonstrated both the feasibility and richness of insights that can be achieved using Pleistocene population genetics based on mitochondrial DNA (Hofreiter et al., 2002, 2007, 2004, Loreille et al., 2001, Orlando et al., 2002).

Cave bear fossils were not only instrumental in development of mitochondrial DNA studies, the first Pleistocene nuclear DNA sequences were also obtained from a cave bear bone (Greenwood, Capelli, Possnert & Pääbo, 1999) as was the first genomic study from ancient DNA (Noonan et al., 2005). Thus, it was cave bears that started the field of paleogenomics. Within this field of research, thanks to the above mentioned advantages, cave bears continue to play an important role, for example as the first undisputed species for which partial genomic survival in an extant relative, the brown bear, has been demonstrated (Barlow, Cahill et al., 2018).

Finally, thanks to their abundance, cave bear fossils have played a pivotal role in the development of molecular techniques for ancient DNA, especially in improving DNA extraction techniques for ancient DNA (Dabney et al., 2013; Rohland & Hofreiter, 2007, Rohland, Siedel & Hofreiter, 2009). More recently, cave bear bones have been used to develop CT-scanning as a technology for choosing the best region of a bone for ancient DNA sampling (Alberti et al., 2018).

Thus, it is no exaggeration to state that cave bear fossils have been absolutely instrumental for progress and numerous – both technical and conceptual – developments in ancient DNA research.

Part 2: Contributions of ancient DNA to cave bear biology and evolution

Just like cave bears have contributed greatly to progress in ancient DNA research, paleogenetic data has had an impact on our understanding of cave bear ecology, biogeography and evolution.

While early genetic analyses of cave bear remains were limited by the amount of DNA sequence data that could be obtained using traditional Sanger sequencing technology, they have been useful in complementing and evaluating information retrieved from morphological analyses. For example, cave bears across Late Pleistocene Europe were phenotypically diverse. Based on morphological data, they were subdivided into at least six different groups, *Ursus spelaeus spelaeus, U. s. eremus, U. s. ladinicus, U. ingressus, U. rossicus* and *U. kudarensis* (Baryshnikov & Puzachenko, 2011, Hofrei-

TER et al., 2004, RABEDER & HOFREITER 2004). Interpretations of this diversity reached from all types belonging to a single, phenotypically diverse species to cave bears representing multiple different species.

A recent publication (STILLER et al., 2013) summarized previously published and new mitochondrial control region data from 142 cave bear samples representing all of the six different groups listed above. Their phylogenetic reconstruction of relationships between the different groups of cave bears showed that samples identified as *Ursus s. spelaeus*, *U. s. ladinicus*, *U. ingressus*, *U. rossicus* and *U. kudarensis,* respectively, belonged to distinct, reciprocally monophyletic lineages. *Ursus s. eremus,* on the other hand, could not be confirmed as single lineage. Different samples were found to either form a sister clade to just the *U. s. spelaeus* and *U. s. ladinicus* clades or a much earlier diverging sister clade to all European cave bear lineages. The latter placement was confirmed by more recent nuclear genome studies, which also recovered a sister group relationship of *spelaeus* and *ingressus* (BARLOW, CAHILL et al., 2018), in accordance with morphological data (BARYSHNIKO & PUZACHENKO, 2011), suggesting that conflicting mitochondrial data may be a result of incomplete lineage sorting and / or introgression, a phenomenon also observed in polar bears and brown bears (CAHILL et al., 2015).

While these results are consistent with the different cave bear groups forming different subspecies or even species, the conflicting data highlights that studies of mitochondrial lineages alone are not suitable to unequivocally confirm reproductive isolation and therefore species status of the different groups. Mitochondrial DNA is maternally inherited only, precluding any formal evaluation of gene flow or admixture between groups or individuals.

Nevertheless, taken together with morphological data, mitochondrial phylogenies can yield information which, if not unequivocal, is at least strong evidence for reproductive isolation between groups. For example, morphological analyses of phenotypically distinct populations of cave bears in two Austrian caves that were only 10 km apart showed that phenotypic differences between bears in these two caves appeared to be consistent for 15,000 years (HOFREITER et al., 2004). Genetic analyses revealed that the bears represented distinct mitochondrial lineages, *U. s. eremus* and *U. ingressus*, respectively, with no evidence of genetic exchange between the caves for more than 15,000 years. In other words, the mitochondrial lineage characteristic for one cave was never found in the respective other cave. Morphological data did not provide any evidence that phenotypic differences between the two caves diminished through time, as would be expected if gene flow occurred between caves. As the caves were certainly close enough for the cave bears to encounter each other, the observed pattern was most likely explained by reproductive isolation between the two populations, an indication that *U. s. eremus* and *U. ingressus* were at least different subspecies if not species. A speculative, but not unjustified extension of this conclusion would be to hypothesise that if *U. s. eremus* and *U. ingressus* were reproductively isolated subspecies or species, then *U. kudarensis*, the Caucasus cave bear, which was a distinct sister taxon to the *spelaeus/ingressus* clade, must have also been a separate subspecies or species. This hypothesis is at least consistent with recent genome wide data (Barlow, Cahill et al., 2018). However, the authors were cautious about making firm taxonomic conclusions based on their data. An informative amount of nuclear genome data from a broad taxonomic range of samples will be required to shed more light on the relationships within the Pleistocene cave bear complex. Nevertheless, the study raises expectations that state-of-the-art sequencing technologies have brought such studies within reach of cave bear researchers.

Beyond addressing taxonomic questions, molecular data has made significant contributions to reconstructing cave bear population dynamics and potential causes of extinction. For example, Stiller et al. (2010) reconstructed Late Pleistocene population dynamics of brown bears and cave bears and found that only cave bears seem to have suffered a population decline, starting from approximately 50,000 years before present. The study concluded that ecological differences between brown bears and cave bears, and in particularly different hibernation strategies, might have contributed to the different fates of the two species. If cave bears were more dependent on caves for hibernation and birth, they would have been more affected by the increased human activity in Eurasian caves starting from about 50,000 years before present. While these conclusions were rather speculative, a recent study found further evidence to support the hypothesis (Fortes et al., 2016). Analysing mitochondrial data, the study found that cave bears, very unlike brown bears, displayed “homing” behavior, returning to the cave of their birth for hibernation year after year. Such behavior would increase the detrimental effects of competition for cave sites with the growing human population.

Taken together with sample age information from radiocarbon dating, ancient DNA has also contributed to reconstructing population movements through time. Stiller et al. (2013) showed that the cave bear range appeared to become increasingly restricted in Asia and Eastern Europe as the last glaciation proceeded. Consistent with these findings, a replacement of the western *U. s. spelaeu*s mitochondrial lineage by the eastern *U. ingressus* lineage in several German caves in the Ach valley at about 28,000 years bp had previously been shown (Hofreiter et al., 2007). These results suggest that the loss of range in the east was not only a result of eastern populations dying out, but also of active westwards movements of eastern populations.

Technical improvements now allow for analyses of unprecedented amounts of nuclear genome data from extinct species. While most paleogenomic studies have focused on reconstructing our own history and evolution, first paleogenomic studies into cave bears are now providing insights into cave bear biology that had previously remained hidden. Barlow, Cahill et al. (2018) investigated potential admixture of brown bears and cave bears and found evidence that parts of the cave bear genome have survived to the present day in modern brown bears. The findings mirror those from Neanderthals and modern humans and paint a more complex picture of relationships between the Pleistocene cave bear complex and brown bears as well as within the cave bear complex itself.

Part 3: The future of cave bear paleogenomics

Given the considerable advances in our knowledge of cave bear biology facilitated by ancient DNA thus far, one could imagine that the rate of new discoveries will start to slow in the coming years and decades. However, we argue the opposite: that we are in fact on the brink of a new era of cave bear research facilitated by the emerging field of paleogenomics. Currently, analysis of the petrous bone appears to be the most efficient approach for the recovery of genome-level data from Pleistocene mammals outside of permafrost regions. This requirement for a specific, small skeletal element will be a limiting factor for taxa which are poorly represented in the fossil record; however, the sheer volume of cave bear bones deposited in their hibernation caves means this is unlikely to apply to cave bears. Thus, at least in principal, the potential for paleogenomic research on cave bears is huge.

One area where genome-level data can clearly contribute is our basic understanding of the relationships among cave bear taxa. Although relationships at the mitochondrial level are well established (STILLER et al., 2013), conflicting relationships recently inferred from paleogenomes (BARLOW, CAHILL et al., 2018) call into question the accepted view of cave bear evolution and taxonomy. Priorities for future studies include comprehensive geographic sampling of cave bear morphotypes to allow tests of monophyly as well as phylogeny. The challenge for these studies will be to extract phylogenetic information from typically low coverage and error-rich paleogenomic datasets (BARLOW, HARTMANN, GONZALEZ, HOFREITER & PAIJMANS, 2018), as well as separating population histories from more recent admixture and ancestral genetic polymorphisms (WEÇEK et al., 2017). Nonetheless, such knowledge is essential to identify macroevolutionary processes such as convergent or parallel evolution, as well as allowing the formulation of basic hypotheses on other aspects of cave bear evolution.

In addition to phylogeny, gene flow or admixture between populations provides an additional factor shaping their genetic variation. For cave bears, mitochondrial DNA has been used as evidence for a lack of gene flow (HOFREITER et al., 2004), but this evidence is indirect and cannot unequivocally exclude, for example, very low level or male-biased gene flow. Genome-level data, in contrast, can provide direct evidence of gene flow even involving ancestors occurring hundreds of generations in the past (FU et al., 2015, PRÜFER et al., 2014). Careful analysis can further elucidate the direction of gene flow as well as differences in the frequency that males and females admixed. Given the well-established evidence of admixture occurring within the genus *Ursus* (CAHILL et al., 2015, KUMAR et al., 2017), including between cave bears and brown bears (Barlow, Cahil et al., 2018), it may be tentatively hypothesized that different cave bear taxa also admixed over the course of their evolution. These questions represent priorities for future paleogenomics studies of cave bears, with populations occurring at contact zones between taxa (Hofreiter et al., 2007, Münzel et al., 2011) representing a logical starting point.

As well as improving geographic sampling of cave bear paleogenomes, another goal of future studies should be to extend their temporal sampling. Successful sequencing of Middle Pleistocene cave bear mitochondrial DNA (Dabney et al., 2013, Stiller et al., 2013) suggests that retrieving paleogenomic data for Middle Pleistocene cave bears may be possible. A fascinating aspect of cave bear evolution is their morphological change through time, for example the small bodied Middle Pleistocene *U. deningeri*, which is thought to have given rise to several Late Pleistocene forms including the very large bodied *U. ingressus* and *U. s. spelaeus* (García, Arsuaga & Torres, 1997). Sequencing the genomes of ancestor and descendent may thus allow the genomic changes underpinning this morphological evolution to be uncovered. This idea leads to a completely new avenue for cave bear genetic research, which has been largely unexplored, namely identifying evidence of selection on specific genes or genome regions which have facilitated adaptive evolution. In addition to body size, adaptations evolving in response to the cave bear’s herbivorous diet, in contrast to their close relatives the carnivorous polar bears and omnivorous brown bears, would be of key evolutionary interest.

A final noteworthy area for future paleogenomics research on cave bears are their population dynamics, encompassing the occurrence of their populations through space and time, the size and composition of these populations, and the factors that shaped them. At a microgeographic scale, a recent study based on mitochondrial DNA found evidence that behavioural processes – specifically homing behaviour – shaped patterns of genetic variation within a single cave bear population in Late Pleistocene Northern Spain (Fortes et al., 2016). In this population, the timing of establishment of the hibernation cave groups, group size, and level (of lack) of migration between cave groups appears to have existed simultaneously at the perfect level to result in the clear segregation of mitochondrial haplotypes among hibernation groups. Critically, any major deviation in any of these population parameters could render this behaviour undetectable using mitochondrial DNA. Paleogenomes, in contrast, provide much higher sensitivity and would allow generally applicable tests for homing behaviour in other cave bear populations.

In terms of global population dynamics, mitochondrial DNA has similarly provided key initial insights, specifically on the timing of the cave bear population decline. With paleogenomes, similar inferences are possible from a high coverage genome of a single individual (Li & Durbin, 2011). This offers several advantages over demographic inference based on mitochondrial DNA. Paleogenomic data has the potential to recover older events and, since inferences are based on a single individual, the potential confounding factor of population structure among the sampled individuals is avoided. Moreover, sampling of multiple paleogenomes would allow the demography of different cave bear taxa to be investigated, providing a more complete and complex view of the processes leading to their extinction.

Conclusions

Cave bear research and ancient DNA research have enjoyed a mutually beneficially relationship for more than two decades. The most significant results with implications for our understanding of evolutionary processes in general and for the evolution of cave bears in particular are likely still to come. In fact, some of the new ancient DNA sequencing technologies that are now promising unprecedented insights into cave bear biology have been developed using cave bear samples. The cave bear might be extinct in nature, but as an essential model species in evolutionary biology, it remains very much alive.

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Predation on *Allactaga major* (Teufelslucke, Lower Austria, Upper Pleistocene): carnivores or birds of prey

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Abstract

The first documented excavation of the Fuchsenlucke, also known as Teufelslucke (located in Lower Austria, Austria, northeast of Eggenburg, 314 m above sea level), started in 1890. During these years several excavations have been conducted uncovering a variety of fossil bones of different Upper Pleistocene age species. Cave bears, cave lions, and hyenas are among the findings of bigger vertebrates as well as their prey. Additionally, birds and other small mammals have been found. A stratigraphic classification, however, proved to be more difficult. In this article the mostly fragmented but only findings (postcranial elements) of *Allactaga major* (Kerr, 1792), syn. *Allactaga jaculus* (Pallas, 1779), will be analysed and discussed as leftovers from specific predators found on-site (*Bubo bubo* and *Vulpes vulpes*). The focus lies on recent information on *Allactaga major* combined with the assumption that most fossil findings of *Allactaga* are prey leftovers.

Zusammenfassung

Die ersten nachweislichen Grabungen der „Fuchsenlucken", auch als Teufelslucken bekannt (Lage: Niederösterreich, Österreich, nordöstlich von Eggenburg, 314 m über dem Meerespiegel), begannen um 1890. Im Laufe der Jahre brachten diese eine Vielzahl an Knochen diverser Tiere oberpleistozänen Alters hervor. Unter den Großsäugern befinden sich unter anderem Höhlenbären, Höhlenlöwen und die Hyänen sowie deren Beutetiere. Es wurden auch Kleinsäuger und Vögel entdeckt, jedoch gestaltet sich eine stratigraphische Klassifizierung dieser schwieriger. In diesem Artikel werden die hauptsächlich fragmentierten und einzigen Funde (postcraniale Elemente) von *Allactaga major* (Kerr, 1792), syn. *Allactaga jaculus* (Pallas, 1779), als Speisereste von spezifischen Prädatoren (*Bubo bubo* und *Vulpes vulpes*) analysiert und diskutiert. Der Fokus liegt auf rezenten Informationen von *Allactaga major* kombiniert mit der Annahme, dass die meisten fossilen Funde von *Allactaga* Speisereste sind.

Key words: *Allactaga*, Dipodidae, Upper Pleistocene, Teufelslucke

1. Introduction

The Teufels- or Fuchsenlucke in Lower Austria is placed at the northern side of the Koenigsberg near Roggendorf in Lower Austria. The cave has been known since 1890. It is famous for its cave hyena remains as well as for its huge variety in different taxa (Adam et al., 1966, Döppes & Rabeder, 1997). Naturally the question occurred whether or not all these findings are of the same age since Adam et al. (1966) already distinguished three different layers. Radiocarbon-dating was executed on cave hyena remains during the ancient DNA investigation of these animals and yielded an age around 38.060 +900/-810 years BP (VERA 2536) (Rohland et al., 2005); similar results gave the dating of the cave lion. Micromammals on the contrary were never tried and only judged on their evolutionary level between 13.000 to 10.000 years BP (Döppes & Rabeder, 1997).

Today, specimens from the genus *Allactaga* are mainly distributed in Asia and Eastern Europe (China, Mongolia, Pakistan, Afghanistan, Armenia, Azerbaijan, Georgia, Kazakhstan, Uzbekistan, Turkmenistan, Tajikistan, Syria, Iraq, Iran, Jordan, Saudi Arabia, Russia, Ukraine) (Don & Reeder, 2005). *Allactaga major*, the great Jerboa, is a typical inhabitant of steppes and fossil findings show temporary immigrations into Europe, one of them in the Late Glacial (Vauthey et al., 1973, Janossy, 1961). Therefore, a steppe layer was defined for a Late Glacial period in the Teufelslucke (Döppes & Rabeder, 1997). Since *Allactaga* is bound to very specific climatic conditions and habitat characteristics (dry steppes, low vegetation), the species was presumed to reach only western and central parts of Europe for short periods of the younger ice age (Kahlke, 1981). Radiocarbon datings are still missing to confirm this.

1.2. Material and Method

Allactaga major from the Teufelslucke is known by the following elements: a total number of 6 pelvic fragments, 7 right (3 juvenile, 4 fragments) and 11 left femora (3 complete, 8 fragments), 8 tibiae (2 complete, 6 fragments), 6 metapodia (4 complete, 2 fragments), 5 phalanges (partially fragmented). The materials are housed today in the Krahuletz-Museum (Eggenburg) and the Höbarth Museum (Horn), both in Lower Austria.

Micromammal assemblages are nowadays evaluated in archaeological excavations to analyse the paleoenvironment. In areas where Dipodidae are common, like Asia Minor, the general assumption is that they result from owl pellets (Hashemi, 2006, Cupere et al., 2009, Tal et al. 2018). Taphonomic processes without animal activities are also evaluated. The bones were judged by their bones surface modification, styles of limb bone breakage (Andrews & Cook, 1990, Schipman et al., 1981) and acid damage (Tal et al., 2018, Cupere et al., 2009, Weissbrod et al., 2005).

2. Results and comparison

There is a complete lack of cranial elements of *Allactaga* from the Teufelslucke as only postcranial bones were recovered during the excavations.

As a result, the adscription to *Allactaga* spp. happened solely according to the morphology of the larger postcranial elements and can be considered as *Allactaga major.* With the exception of one humerus fragment, the findings are strictly comprised of hind limb elements: femora with additional tibiae, metapodia and pelvic fragments. Judging from the size, some of them probably belonged together.

The pelvic remains were often fractured with stepped or even sawtoothed marks. Femora are mostly represented by the proximal part, four are complete and three more belong to juveniles, the distal epiphysis missing. Six tibiae are fractured at an obtuse angle, the other two are not broken. All remains show very few bone flaking and pittings. No gnawing or bite marks could be observed as well as no acid/digestive damage. In general, the bone surface is very well preserved (Fig. 1). Hence, reptilians like snakes and bigger lizards are ruled out as possible predators because they have strong acid-digestive juices affecting surfaces of bones and teeth (Czaplewski, 2011, Fisher, 1981). Therefore, animals leaving little to no digestive traces were closely considered.

Fig. 1: Fossil *Allactaga major* leftovers from Teufelslucke cave, Austria. a1: femora sin., a2: femora dex., b: metapodials, c: tibiae, d: humerus fragment.

a) Carnivores. Terrestrial carnivores such as the fox (*Vulpes vulpes*) or various mustelids were found in the Teufelslucke. These carnivores crush the bones significantly and leave typical bite marks

(Andrews & Cook, 1990, Wettstein-Westersheimb, 1966). Fossil findings from *Allactaga major* from the Villa Seckendorff, Stuttgart, show these conical impressions most likely from small predators such as the red fox (Koenigswald, 1985). Jerboa remains from the Teufelslucke, however, have no bite marks whatsoever and can therefore be ruled out (Fig. 2).

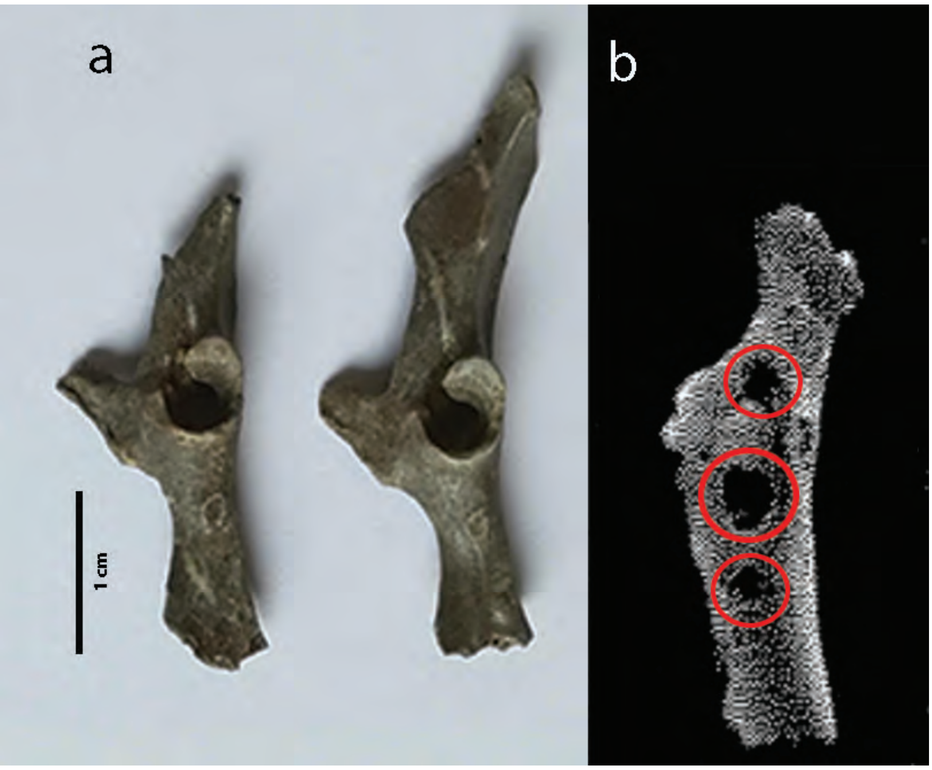

Fig. 2: a) Pelvic fragments without any bite mark traces from Teufelslucke cave. b) Fossil *Allactaga major* pelvic fragments from Villa Seckendorff with conical teeth impressions (Koenigswald, 1985).

b) Diurnal birds. These do not swallow their prey as a whole but work their way from the head to the bottom, often leaving parts when not hungry enough or if parts are of no nutritional value (Andrews & Cook, 1990). If bones are eaten, then the articulations surface is often completely dissolved depending on the species (Bochenski et al., 1998, Geng et al., 2009, Cupere et al., 2009, Tal et al., 2018). In the Teufelslucke, *Aquila heliaca* (eastern imperial eagle), *Buteo buteo* (common buzzard) and *Falco tinnunculus* (common kestrel) are documented. Kestrels specialize on small prey ranging from 20g to 40g (Geng et al., 2009) and *Allactaga major* is well out of reach with an adult weight of 300g to 350g (Tsytsulina et al., 2016). Buzzards seem to favour voles and lagomorphs but in case of low mammalian prey, they concentrate on birds and reptiles (Selas, 2001). In any case, they prefer diurnal prey, while *Allactaga* is crepuscular to nocturnal. The imperial eagle has a wide variety of prey, just like the buzzards, and in Europe they are known to hunt ground squirrels, hamsters, lagomorphs but also birds and reptiles. The fragmentation and digestive traces they produce is much higher than in the eagle owl (Bochenski et al., 1998). Therefore, it seems reasonable to rule out the eagle as a possible predator of *Allactaga*.

c) Eagle owl (*Bubo bubo*). In connection with *Allactaga*, birds of prey such as owls and more specifically the eagle owl (*Bubo bubo* (Linnaeus, 1758)) are potential predators and were also described to be found in the same layers (Wettstein-Westersheimb, 1966).

Bubo bubo inhabits mountainous areas with rocky ground but also occurs in open lowlands often close to rivers and lakes where it nests in trees. Both cover and perches overlooking wide areas are important for this species. Closed forests often appear to be less nutritious with respect to micromammals and as a result the eagle owl today prefers border areas of forested areas and open areas (Piechock, 1985).

Especially small to medium-sized mammal species dominate the diet of *Bubo bubo* (in West-Mongolia), including Cricetidae, Dipodidae and Arvicolidae (Hoffmann, 1988).

The fossil bones from *Allactaga major*, however, show no traces of any digestive juices (Fig. 3).

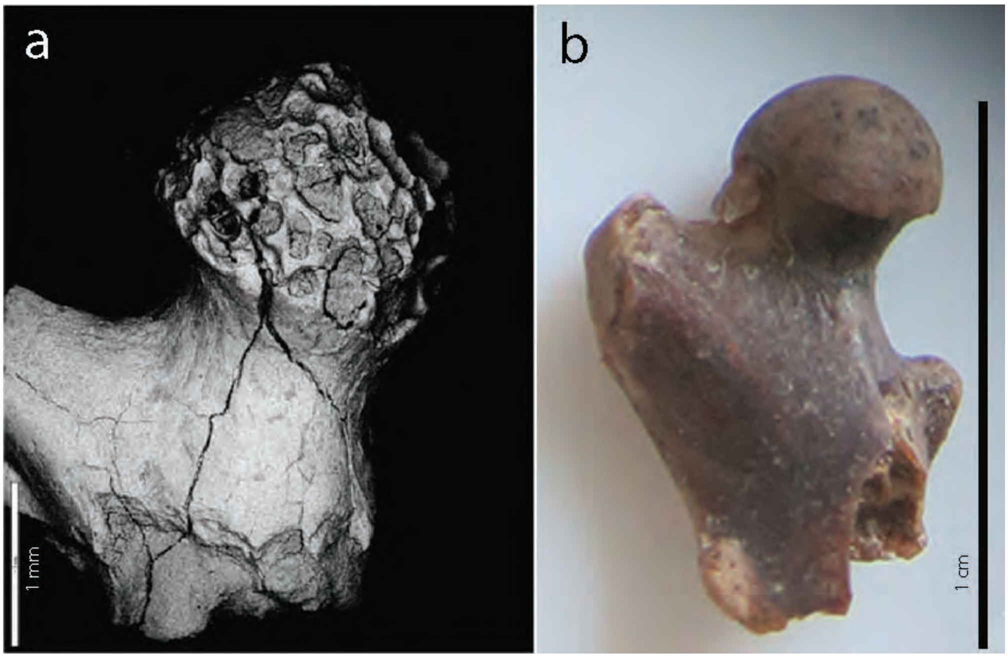

Fig. 3: a) Femur head from the Niche assemblage with acid digestion marks from ed-Wal Terrace (Weissbrod et al., 2005). b) Femur head without any digestion marks from *Allactaga major* from Teufelslucke cave.

The lack of these missing structures and the actually good preservation of the fragmented bones could be an indicator for an eagle owl as they typically leave little chemical or physical damage to prey bones in comparison to other birds of prey (Czaplewski, 2011, Glue, 1970). Larger prey is often torn apart by *Bubo bubo* (Bezzel & Obst, 1976, Hoffman, 1988) and similar to large diurnal birds, they tear off elements of no nutritious value and discard them. This might be the reason for most findings being limb bones.

Fossil findings of *Bubo bubo* bones from the Teufelslucke reinforce this idea as both eagle owl and great jerboa remains were found in the same site (Adam et al., 1966)
Bubo bubo has an enormous diversity in its diet, unlike other owls that hunt for specific animals (Piechocki & März, 1985). Leftovers from *Allactaga* are underrepresented in pellets from eagle owls in Mongolia even though this area is the species' main distribution site (Koenigswald, 1985), which would explain the very few *Allactaga* remains in the Teufelslucke compared to other rodents.

3. Conclusion

Only the hind limb bones of *Allactaga major* were recovered in the Teufelslucke and they consist primarily of femora suggesting a selected accumulation by a predator. As findings show neither digestive nor bite marks many predators can be excluded. Judging from the bone damage only *Bubo bubo* comes into question as possible predator. This includes the possibility that prey was torn apart while eating and the bones where not digested at all.

4. Acknowledgement

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This work is dedicated to Univ.Prof. Dr. Gernot Rabeder on the occasion of his 80th birthday who was very involved in the recovery and determination of the material from the Teufelslucke.

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Ektopodon, an enigmatic phalangeroid marsupial: its enamel microstructue and mastication pattern

Wighart v. Koenigswald

Abstract

The molars of the Late Oligocene *Ektopodon stirtoni* (Phalageroidea, Marsupialia) have a unique lophodont morphology that differs from all other marsupials and has no parallel in Placentalia. Teeth with a unique morphology often show specific modifications of the enamel. Therefore, the enamel of *Ektopodon* was investigated and compared with the enamel in other Marsupialia. The schmelzmuster of *Ektopodon* is formed mainly by radial enamel with some modifications. A differentiation of the enamel in the leading or trailing edges could not be identified. The distribution of the various enamel types differs among the various marsupial families and is partially diagnostic.

Zusammenfassung

Die Morphologie der lophodonten Molaren des oberoligozänen *Ektopodon stirtoni* (Phalageroidea, Marsupialia) ist einmalig und unterscheidet sich grundlegend von denen andere Marsupialia. Sie hat auch keine Parallele bei den Placentalia. Zähne mit einer stark abweichenden Morphologie zeigen oft auch Sonderbildungen im Schmelz. Deswegen wurde die Mikrostruktur des Schmelzes von *Ektopodon* untersucht und mit dem Schmelz anderer Marsupialia verglichen. Das Schmelzmuster der Molaren von *Ektopodon* wird aber weitgehend von Radialschmelz gebildet, zeigt aber einige Modifizierungen. Eine Differenzierung zwischen dem luvseitigen und leeseitigen Schmelz konnte aber nicht beobachtet werden. Die Verbreitung der Schmelztypen variiert in den verschiedenen Familien der Marsupialia und ist teilweise diagnostisch.

Key-words: *Ektopodon*, Marsupialia, Late Oligocene, enamel microstructure

1. Introduction

Ektopodontidae with the eponymous genus *Ektopodon* are a family within the phalangeroid marsupials from Australia. The fossil record reaches from the upper Oligocene to the Pliocene (Woodburne & Clemens, 1986a, b, Woodburne, 1987, Pledge, 1982, 1986, 2016, Pledge et al., 1999, Rich et al., 2006). Besides their stratigraphic occurrence, Ektopodontidae raised a special interest because of the conspicuous molar dentition. The molars have transverse lophs (Fig. 1A), these lophs, however, are modified into a series of laterally compressed cusps. Such molars have no parallel in metatherian or placental dentitions. The first three upper and lower molars of *Ektopodon* have two or three modified transverse lophs; the lophs are reduced on the fourth molars. In the genus *Ektopodon* the number of cusps per loph varies between 8 and 10 according to the tooth position (Pledge, 2016).

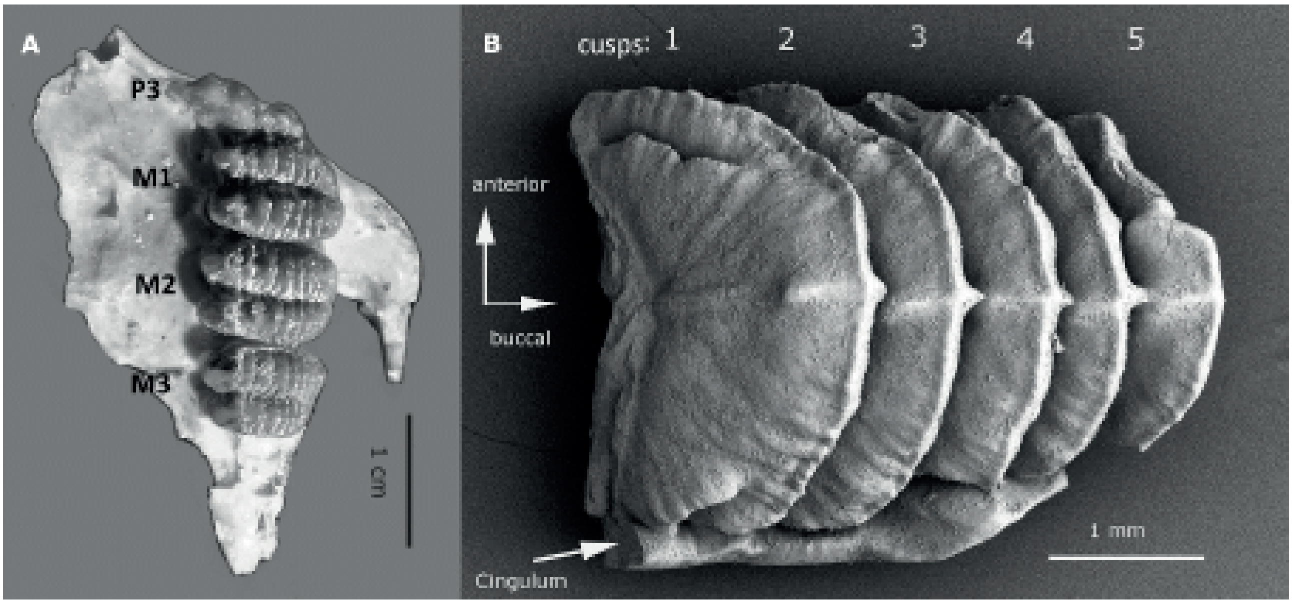

Fig. 1: *Ektopodon stirtoni*, A - Left maxilla with three molars (M1-M3), and alveolus for the fourth (SAM 35309). B – The investigated tooth fragment (KOE 1733), interpreted as a partial metaloph of a left upper molar (?M2).
Both specimens are from Mammalon Hill (SAM locality PL7611; the Type Locality for the species), northwestern shore of Lake Palankarinna, South Australia.

According to the state of art, Ektopodontidae diversified into two genera, *Chunia* with three species (*C. illuminata, C. omega, and C.* sp.) and *Ektopodon* with five species (*E. serratus, E. tommosi, E. stirtoni, E. litolophus, and E. paucicristata*). In most localities only a single species is represented and remains are generally very rare. Pledge (1986, 1991, 2016) actualized the data on Ektopodontidae and completed the earlier monograph edited by Woodburne & Clemens (1986).

Ektopodontidae retained the general morphology of their molars during their time range from the Late Oligocene to Pliocene. The number of cusps per loph on the molars increased only slightly and thus the molars became somewhat larger (Pledge, 2016). So far, no postcranial bones are known, but because of their relation to Phalangeroidea, such as *Phalanger*, an arboreal way of life is very plausible. The body-tail length is estimated 40 cm.

In placental dentitions, teeth with a strongly modified morphology often show a specialized enamel microstructure. Therefore, the aberrant morphology of *Ektopodon* molars is challenging to investigate the schmelzmuster (the three-dimensional arrangement of enamel types within a tooth) in comparison with the enamel microstructure of other marsupials (Koenigswald, 1994).

So far, only a very limited analysis of the enamel has been done by M. Moss, stating some “tubular or fibrous structure”, as communicated by Clemens (Woodburne & Clemens, 1986). Neville Pledge generously presented me a small tooth fragment for the destructive investigation of the enamel. The results are discussed here.

The closely arranged cusps on the lophs of the Ektopodon molars show in their grinding function some similarities to elephant molars, and among rodents, to arvicolid molars, having a highly differentiated schmelzmuster (Koenigswald, 1980). Gernot Rabeder, to whom this volume is dedicated, used in his PhD thesis the differentiation of the schmelzmuster in arvicolid molars to shed new light into the systematics of these rodents (Rabeder, 1981)

2. Material and methods

*Ektopodon stirtoni (*Pledge, 1986), molar fragment KOE 1733, Late Oligocene, Mammalon Hill (SAM locality PL7611; the Type Locality for the species), northwestern shore of Lake Palankarinna, South Australia (SAM Adelaide - Neville Pledge)
Phalanger cf. vestitus (Milne-Edwards, 1877), mandible KOE 1693, Recent, Sepik-district, Papua New Guinea (AM Sydney - T. Flannery).
The molar fragment available for the enamel investigation is about 3 mm in width and 4 mm in length. The fragment was assigned as *Ektopodon stirtoni* by Neville Pledge. Because of the inclination of the cusps and a partially preserved cingulum, the fragment was interpreted as a partial metaloph of a left upper molar (M2). The molar fragment is unworn and thus the cusps show their initial enamel surface. The cusps distinctly inclined towards the buccal side. Even if it is unclear if the most lingual cusp is preserved, the remaining cusps are numbered as cusp 1 to 5 for easier identification (Fig. 1B). The profile of each cusp is highly domed in an antero-distal direction. On both sides little struits link the cusps at their highest point (Pledge, 2016), but they do not merge into each other but touch each other on the side. The anterior and posterior crests of the cusps 1 show a bifurcation in its lower part (Fig. 1B). Such additional crests were named precrista and postcrista (Pledge, 1986).

For the interpretation of the enamel microstructure, sections in vertical, transverse, and tangential planes are optimal. All three aspects together – studied at various magnifications - allow a secure reconstruction of the schmelzmuster of a tooth. Isolated photos may show details but provide an incomplete picture. With rare fossils, the number of sections has to be adjusted to the available material. In the case of the tooth fragment of *Ektopodon*, fractioning of the specimen prior to the embedding was a reasonable way to increase the possible number of sections. Cusps 1 and 2 were separated from cusps 3 to 5. That allowed an individual embedment and further treatment of both parts. Cusps 1 and 2 (KOE 1733 A) provided a longitudinal sections in a linguo-buccal direction (Fig. 2A), and cusps 3 to 5 (KOE1733 B) provided a transverse section perpendicular to the growing axis (Fig. 2B).

The routine preparation of the two fragments includes an embedding into an artificial resin (epoxy) because such delicate teeth neither can be sectioned or ground. The resin blocks are cut with a saw in the direction of the desired section, but outside of the tooth fragments. Using this cut surface, further grinding was done on sand paper until the desired section was nearly reached. Grinding was continued with grinding powder (1000 grid) on a piece of glass. After washing in an ultrasonic device, the dried surface was etched with 10% hydrochloric acid (HCl) for about 3 seconds. After sputter-coating the enamel was investigated under the SEM.

The process of grinding with sandpaper, grinding powder and the subsequent etching and sputter coating was repeated several times in order to correct a poor preparation, such as scratches or an unsuitable etching. The repeated grinding allows to study the enamel in various different levels in the height of the tooth.

Enamel can be investigated at different levels of complexity (Koenigswald & Clemens, 1992). The investigation concentrated on two levels, the occurring types of enamel and their arrangement in the schmelzmuster. Enamel types are characterized by the orientation of the prisms (P) and the interprismatic matrix (IPM). The schmelzmuster describes the distribution of the enamel types in the architecture of the tooth. Because only a molar fragment was investigated, potential differences in the enamel on the dentition level, such as differences between molars and incisors, remain unknown.

Different enamel types are mostly arranged more or less parallel to the enamel dentin junction (EDJ). If different enamel types are separated by a sharp border, they are described as layers. If there is a more gentle transition the term zones is used.

The schmelzmuster of various genera of different marsupials was surveyed earlier (Koenigswald, 1994, 1995), providing the background for characterizing the enamel of *Ektopodon*.

2.1 Used abbreviations

AM	Australian Museum, Sidney
EDJ	enamel dentin junction
IPM	interprimatix matrix
KOE	Enamel collection at Institut für Geowissenschaften (Paläontologie), Universität Bonn
OES	outer enamel surface
P	prism
PLEX	prism less external enamel

SAM	South Australian Museum, Adelaide
SEM	Scanning electron microscope

A glossary of the terminology used for the enamel description was provided by Koenigswald & Sander (1997a).

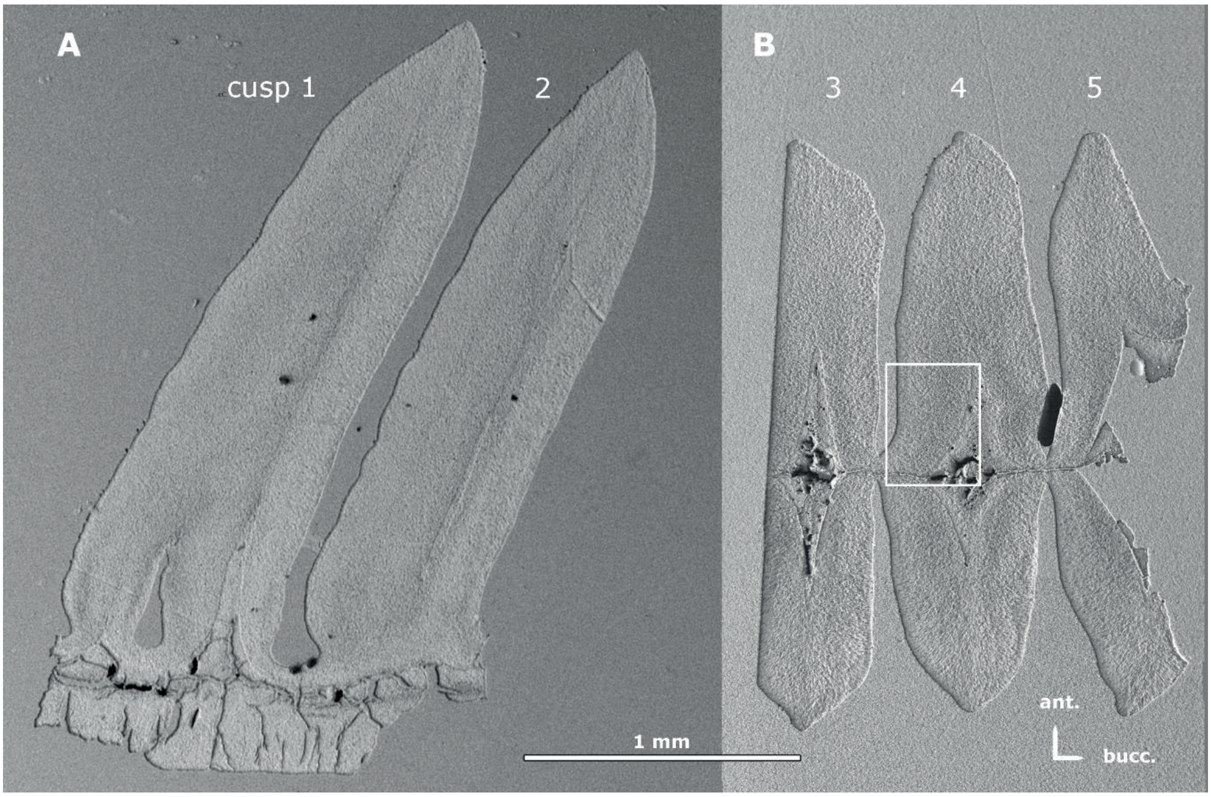

Fig. 2: *Ektopodon stirtoni*, A, vertical section of cusps 1 and 2 (KOE 1733A) showing the deep separation of the cusps. B, transverse section of cusps 3 to 5 (KOE 1733B) at a depth where the dentine core is met and the cusps are just beginning to fuse. The frame indicates the position of Figure 3.

3. Results

The schmelzmuster of *Ektopodon* is dominated by radial enamel that can be divided into three zones between EDJ and OES. The inner and the middle layer zones have a prismatic enamel, whereas the thin outer zone is formed by prism-less enamel (PLEX).
The thickness of these three zones varies and their separation is vague. Therefore, they are described as zones, whereas layers are separated more sharply.

The inner and the middle zone are made of radial enamel, with prisms generally arising from the EDJ towards the OES. The two zones differ distinctly in the orientation of the IPM.
In the inner zone, close to the EDJ, prisms are arranged in radial rows separated by thin sheets of IPM.

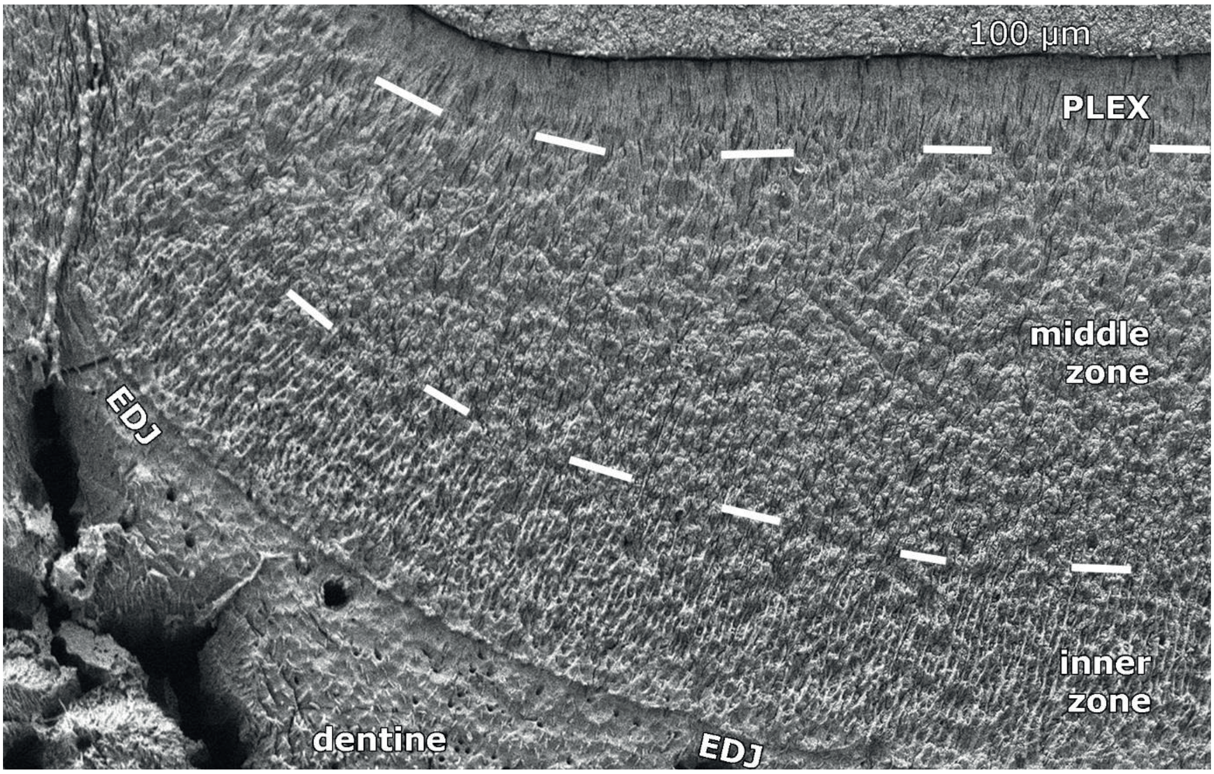

Fig. 3: Transverse section of the central part in cusp 4 in *Ektopodon stirtoni*. The inner zone is marked by sheets of IPM between radial rows of prisms. In the middle zone the IPM is less organized. The outer zone is formed by PLEX. EDJ - enamel dentine junction, PLEX - prism less external enamel.

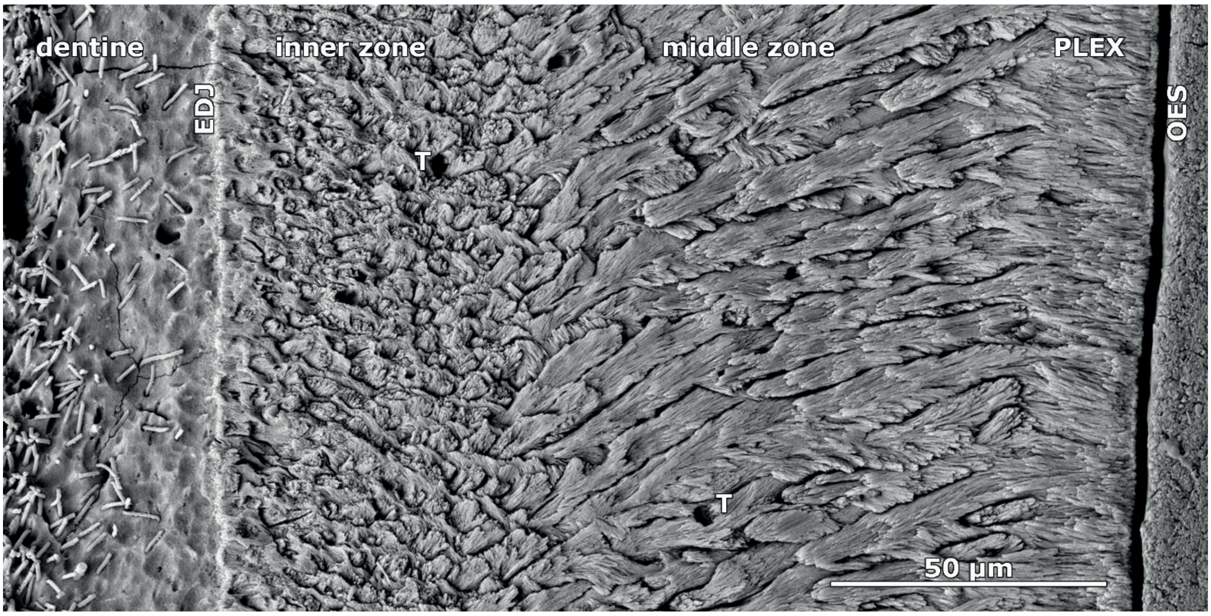

Fig. 4: Vertical section of one side of the cusp 2 in *Ektopodon stirtoni*. The dentine is on the left side. The enamel can be differentiated into three zones parallel to the EDJ. The inner zone and the middle zone are formed by radial enamel, whereas the outer zone is a PLEX. Abbreviations: EDJ - enamel dentine junction, PLEX - prism less external enamel, T - tubuli.

In the transverse section (Fig. 3), close to the EDJ, the IPM is visible as light lines between the prisms that are seen in cross-section. This specific modification was described as radial enamel with inter-row sheets (REIS) occurring in Eulipotyphla, especially in Soricinae (Koenigswald & Reumer, in press). In the lophs of *Ektopodon*, the thickness of this inner zone varies.

In the studied transverse section, the REIS is thickest and seen best in the middle of the cusps, and gets thinner towards the anterior and posterior margins. In the vertical sections, the REIS of the inner zone is less obvious, because the section was in an angle to the rows of prisms and not parallel (Fig. 4). A more detailed view (Fig. 5), however, shows the large angle between the IPM and the prisms. The prisms are rising from the EDJ at about 45° and the IPM is oriented perpendicularly.

The middle zone differs in the transverse and the vertical sections (Figs 3 and 4) distinctly from the inner zone. The inter-row sheets are missing and the prisms are less arranged in rows. The prisms continue to rise towards the OES but at a lower angle. In the transverse their cross-section appears to be stretched. The vertical section shows that the prisms reduce their inclination after leaving the inner zone and point towards the OES almost perpendicularly. In the same way, the IPM reduces its angle with the prisms (Fig. 4) and continues in the outer zone. The middle zone is two or three times as thick as the inner zone. In the anterior and posterior loops of the enamel it covers the entire thickness of the enamel except the thin outer zone.

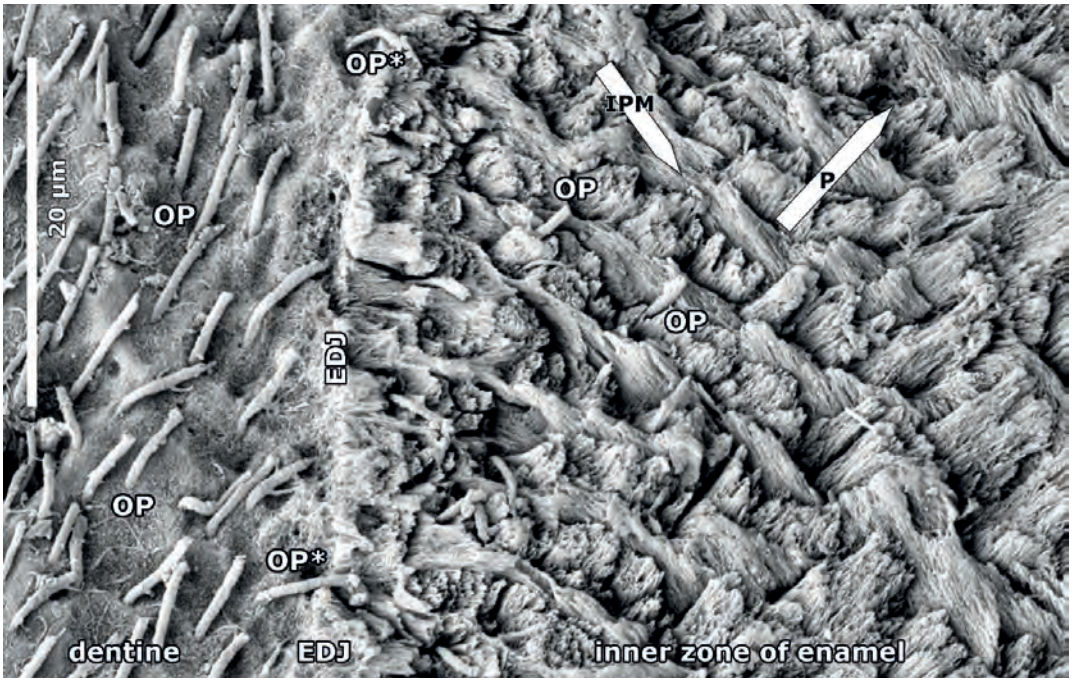

Fig. 5: Enamel and dentine in *Ektopodon stirtoni*. The dentine (left side) shows odontoblastic processes with ramifications. Some of the odontoblastic processes cross (OP*) the EDJ and occur within the enamel. There, they are seen parallel to the prisms of the inner zone of the enamel. Abbreviations: EDJ - enamel dentine junction, IPM - direction of the interprismatic matrix, OP - odontoblastic processes, P - prism direction.

The thin outer zone formed by a prism-less enamel is formed by crystallites driving from the prism and the IPM. The prism sheath surrounding the prisms in the middle vanishes, and thus its crystallites are not discernable from those of the IPM anymore. All crystallites are parallel and perpendicularly to the OES. The thickness of the outer zone is variable.

The described enamel schmelzmuster is somewhat generalized and does not include possible differentiations on the very base of the tooth cusps. Similarly the extent of the inner zone may be different in basal part. However, the available material did not allow a more comprehensive investigation, but the observed results allow a comparison with other marsupial animals.

One specialty of marsupial enamel is the occurrence of tubules within the mineralized tissue (e.g. GILKESON, 1997). The tubules are visible as holes in the sections (Fig. 4). They are containing odontoblastic processes. The odontoblastic processes are well seen in the dentine (Fig. 5) and show some ramification. The main axes are similar in thickness, slightly less than 0.5 μm. The applied etching during preparation was relatively mild and preserved the mineralized odontoblastic processes, while the surrounding dentine was removed. Most probably, the mineralization of the odontoblastic processes occurred during fossilization. Similarly mineralized odontoblastic processes within the dentine have been observed in several Eutheria (e.g. KALTHOFF et al., 2011).

In *Ektopodon* (Fig. 5), as typical for marsupials, these odontoblastic processes can be observed crossing the EDJ and penetrating into the enamel. Within the enamel the processes occur always with the same orientation as the prisms. This strengthens the idea that they are bound to the prisms. According to the observed, tubuli might extend into the middle zone.

4. Discussion

4.1 Comparison of the enamel microstructure

A survey of the enamel microstructure on the schmelzmuster level was given by KOENIGSWALD (1994) for recent and fossil marsupials from Australia. Observations on various fossil marsupials from Australia, South America and Antarctica were added (KOENIGSWALD & GOIN, 2000, GOIN et al., 2006). Thus a general outline of the enamel microstructure in marsupials is known, although some dentitions may provide additional specializations. Despite similarities some basic differences separate marsupial enamel from placental enamel (KOENIGSWALD, 1995).

The enamel of *Ektopodon* shows a schmelzmuster with three zones. Two zones are formed by two modifications of radial enamel. The outer zone is a PLEX. The combination of different enamel types in the schmelzmuster occurs in placentals as well as marsupials, although such a differentiation might have evolved independently. Both groups include taxa with a simpler schmelzmuster.

The radial enamel dominating the schmelzmuster of *Ektopodon* is regarded as the basal enamel type of prismatic enamel in theria. The two modifications are present in both groups as well.
The radial enamel with inter-row sheets occurs in various marsupial families (Tab. 1). This enamel type was found in placental mammals and described as REIS, for example in Soricinae (KOENIGSWALD & REUMER, in press).

Marsupial family	Tooth type	Radial enamel	Inter-row sheets	Simultaneous turn of prisms	HSB	Zipper enamel	Borderline	Irregular enamel
Didelphidae	M	●●						
Dasyuridae	M C	●● ●●						(●)
Thylacinidae	M C	●● ●●						●● ●●
Peramelidae	M	●●	●●					
Phascolarctidae	M I	●● ●●					●●	
Diprotodontidae	M I	●● ●●	●●	●●		●●		 ●●
Vombatidae	M I	●● ●●			●● ●●			
Thylacoleonidae	P I	●● ●●	●●	●●				(●) ●●
Phalangeridae	M I	●● ●●	●●	●●			(●)	
Ektopodontidae	M	●●	●●	●			●	
Potoroidae	M I	●● ●●	●● ●●	●● ●●		●● ●●		
Macropodidae	M I	●● ●●	●● ●●	●● ●●		●● ●●		(●)
Pseudocheiridae	M I	●● ●●	●● ●●	●● ●●			(●)	
Petauridae	M I	●● ●●	●● ●●	●● ●●				
Acrobatidae	M I	●● ●●						

Tab. 1: The occurrence of specific characters of the enamel in the marsupial families (modified from Koenigswald 1994). C - canines, I - incisors, M - molars.

One characteristic of the marsupial enamel is the dominance of parallel prisms without decussation. The crystallites of the IPM, forming inter-row sheets or anastomosing between prisms, are often oriented at a large angle to the prisms and thus providing a decussating structure, basically different from the decussating layers of prisms in Placentalia. Such decussating layers of prisms, called Hunter-Schreger bands, occur in Marsupialia only sporadically (e.g. in *Vombatidae*).
A unique kind of prism decussation in marsupials, called zipper enamel, has been found in the crests of molars and incisors, e.g. in Macropodidae. Two fields of radial enamel meet at the crest. The prisms

of both fields interfinger in vertical layers for a short distances. This enamel type was called zipper enamel. Special attention was paid to the crests of enamel in *Ektopodon* but no zipper enamel was identified. In placentals a zipper enamel was never found. There the enamel surrounds even sharp edges of the dentine.

In the marsupial enamel prisms may perform simultaneous turns without decussating. Such simultaneous turns may occur repeatedly several times between the EDJ and the OES, but without any decussation of the prisms.

In some marsupial teeth a distinct structure between fields of radial enamel was detected, e.g., in Phascolarctidae, and called borderline (Koenigswald, 1994). It described the contact between two fields of enamel. In *Ektopodon* no typical borderlines were observed, but that might be due to the limited number of sections. One suspect structure occurs where the two fields of radial enamel meet in the crests of the cusps. But the available sections do not provide enough details. Another unusual structure is the line in the enamel between the anterior and the posterior half of the cusps. The wavy structure reminds strongly of the borderline found in *Phascolarctos* (Koenigswald, 1994, Figs. 28 & 29). A borderline structure similar to the zipper enamel has never been seen in placental enamel. Obviously, placental enamel surrounds sharp edges of the dentine core with fewer problems.

The enamel of *Ektopodon* has typical elements occurring in Marsupialia. In a premolar and molar of *Phalanger* cf. *vestitu*s, a representative of the nearest related extant group, an inner zone of REIS superimposed by a thicker zone of radial enamel and a variable PLEX near the OES were recognized. Thus the basis agreement with Phalangeridae is confirmed (Tab. 1). The schmelzmuster alone, however, would not allow the exclusion of several other marsupials.

4.2 The mastication pattern

Pledge (2016) postulated a transverse jaw movement in *Ektopodon*, because the lophs and the valleys of upper and lower molars are oriented transversely. During the power stroke the mandible is moved in bucco-lingual direction. The inclination of the cusps strengthens this reconstructed direction during the mastication process. In upper and lower molars, the cusps are inclined towards the moving antagonist. In such a lateral movement is combined with an alternative occlusion of only one side at a time, the left or the right jaws. The power stroke, which in primitive mammals consist of two phases separated by a central occlusion (Hiiemäe & Kay, 1972, Kay & Hiiemäe, 1974), is in *Ektopodon* continuous. Phase 1 and 2 cannot be discerned because there is not central occlusion. Such a perfect alignment of phases I and II in direction and inclination is a derived pattern that occurs in various herbivorous mammals (Koenigswald et al., 2013).

The concluded jaw movement is only possible, if the lophids of the lower jaw and the lophs of the uppers are oriented parallel. In the reconstruction of the palatine (Pledge, 1986, Plate 3.3 D and E) the lophs of the upper molars are directed almost perpendicular to the sagittal axis whereas those of the lower molars are much more angled in mesial direction. This discrepancy is unlikely, because it would hinder a smooth function. Only more complete material will correct this discrepancy.

A transverse jaw movement of *Ektopodon* is not common in marsupials but occurs, for instance, in *Vombatus*. The transverse jaw movement is indicated there by the position of the enamel. It covers only the trailing sides of upper and lower molars. Striations in the dentine core confirm the transverse movements.

In contrast, the lophodont molars of *Macropus* occlude in a very different way. The lower jaw is moved upwards and slightly forward, so that the shearing crests of the transverse lophs cut against each other during phase 1 of the power stroke. The weak longitudinal crests show slight facets that indicate a transverse movement during phase 2. But this lateral movement is distinctly less important than the proal movement during phase 1. In placental mammals similar lophodont dentitions with transverse cutting edges are seen in various unrelated taxa, e.g. in *Deinotherium, Pyrotherium*, and *Tapir*. The main function happens similarly during phase 1, whereas phase 2 in these dentitions is insignificant or missing.

4.3 Leading and trailing edges

The unusual morphology of *Ektopodon* molars led to the expectation that the enamel might show a differentiation of the enamel between leading and trailing edges in the conspicuous transverse lophs. Such differentiations were observed in various molars of placental mammals (Koenigswald & Sander, 1997b). In the molars of the rodent *Otomys*, for instance, the transverse lophs are strongly inclined comparable to those of *Ektopodon*. In each loph the enamel is much thicker on the trailing side, which functions as a crest, whereas the enamel of the leading side is very thin but nevertheless of a more complex schmelzmuster (Koenigswald, 1980). The trailing side is so thin that it does not reach the occlusal surface. In arvicolid molars the half-lophs are more or less vertical and both sides, the leading and the trailing side are functioning. Nevertheless the schmelzmuster is characterized by different enamel types on both sides (Koenigswald, 1980, Rabeder, 1981).

In the molar enamel of *Ektopodon*, however, no differentiation between the lingual and the buccal sides of the cusps could be detected. In *Ektopodon* the problem is solved in a different way. The dentine core is surprisingly small and the main height of the tooth is formed by the enamel cap. Thus the dentine is exposed only in a late stage of the life history. Neither the leading side nor the trailing side are thickened, but both together have to withstand the stress during mastication. Therefore a differentiation of the enamel was not necessary. It is difficult to estimate the stress because the kind of diet is not known. The occlusal stress, however, may have been limited, because most of the teeth figured by PLEDGE (2016) are fresh. The valley between the lophs never seems to be intensively worn or flattened. That indicates that the enamel of *Ektopodon* teeth was not specialized for an abrasive diet.

5. Summary

The schmelzmuster of the *Ektopodon* molars is dominated by radial enamel but separated into three zones. The inner one shows a radial enamel with inter-row sheets (REIS), the middle one is thickest and has unspecialized radial enamel. The outer zone is formed by PLEX of varying thickness. This pattern is typical for marsupials and occurs in the *Phalanger* as well. The expectation of a differentiation between the enamels of the leading and the trailing edges was not fulfilled. The different extent of the dentine cores in the lophs may be provide an explanation.

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Ein inneralpiner Neufund des Wollhaarmammuts (*Mammuthus primigenius*) aus dem Abtenauer Becken (Salzburg, Österreich)

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Abstract

In 2017 in the river bed of the Zwieselbach in the inneralpine Abtenau Basin a fossil tusk fragment was found, which is assigned to an adult male woolly mammoth (*Mammuthus primigenius*). According to a radiocarbon date of about 31,000 cal BP the tusk fragment dates to the beginning Late Würmian of the Upper Pleistocene and prove still ice-free conditions in the Abtenau Basin in the onset of the Last Glacial Maximum (LGM, 29,000-19,000 BP). The carbon ($\delta^{13}C_{coll}$) and nitrogen ($\delta^{15}N_{coll}$) stable isotope values indicate a cold steppe environment with permafrost and a grass-dominated nutrition of the woolly mammoth. The tusk fragment originally deposited probably in fine sediments of a stillwater area within pre LGM gravel deposits, while the preservation condition and the discovery site indicate a secondary dislocation into the river bed of the Zwieselbach and a short transport within the fluvial gravel in the Holocene. If the woolly mammoth was captured by carnivores or died naturally remains unclear, whereas an influence of Palaeolithic hunters seems very unlikely. Nevertheless, the tusk fragment from the Zwieselbachgraben in the Abtenau Basin currently is the youngest dated woolly mammoth find from inneralpine regions of the Eastern Alps.

Zusammenfassung

Im Jahr 2017 wurde im Bachbett des Zwieselbachgrabens im inneralpinen Abtenauer Becken ein fossiles Stoßzahnfragment eines adulten männlichen Individuums des Wollhaarmammuts (*Mammuthus primigenius*) entdeckt. Ein ^{14}C-Datum von rund 31.000 cal BP datiert den Fossilrest in das Spätwürm des Jungpleistozäns und zeigt eisfreie Umweltbedingungen für das Abtenauer Becken im unmittelbaren Vorfeld der letzten Maximalvereisung (LGM, 29.000-19.000 BP) an. Die stabilen Isotopen von Kohlenstoff ($\delta^{13}C_{coll}$) und Stickstoff ($\delta^{15}N_{coll}$) belegen eine kalt-trockene Steppenlandschaft mit Permafrost sowie eine von Gräsern dominierte Ernährung des Wollhaarmammuts. Der Stoßzahn wurde ursprünglich vermutlich in einem von Feinsediment geprägten Stillwasserbereich in präglazialem Schotter abgelagert, während der Erhaltungszustand und die Fundstelle eine sekundäre Verfrachtung in das Bachbett des Zwieselbaches sowie einen kurzzeitigen Transport im fluviatilen Schotter anzeigen. Während ein anthropogener Einfluss des paläolithischen Menschen als sehr unwahrscheinlich gelten kann, ist unklar, ob das Wollhaarmammut von Carnivoren erbeutet wurde oder eines natürli-

chen Todes verendete. Ungeachtet dessen, ist das aus dem Zwieselbachgraben stammende Stoßzahnfragment der bislang jüngste datierte Fossilrest des Wollhaarmammuts aus den inneralpinen Regionen der Ostalpen.

Schlüsselwörter: *Mammuthus primigenius,* Ostalpen, Spätwürm, ^{14}C-Datierung, stabile Isotopen, Paläoklima
Key words: *Mammuthus primigenius*, Eastern Alps, Late Würmian, radiocarbon dating, stable isotopes, palaeoclimate

1. Einleitung

Das Wollhaarmammut (*Mammuthus primigenius* Blumenbach, 1799) gilt als prominentester Vertreter der jungpleistozänen Megafauna und zugleich als eponymes Taxon einer als „Mammutsteppe“ bezeichneten, artenreichen, kalt-trockenen Steppenlandschaft in Eurasien (Kahlke, 1994, 2014). Das äußere Erscheinungsbild des Wollhaarmammuts wird von einer charakteristisch geformten Rückenlinie geprägt, wobei männliche Individuen eine Schulterhöhe bis zu 3,40 m und ein Gewicht von bis zu sechs Tonnen erreichen konnten. Weibliche Individuen waren hingegen kleiner und erreichten nur eine Schulterhöhe von 2,90 m. Für das in kleinen, matriarchalisch geführten Herden lebende Wollhaarmammut wird eine Lebenserwartung von bis zu 60 Jahren angenommen (Haynes, 1991, Joger & Kamcke, 2005, Lister & Bahn, 2009). Eine dicke Haut mit 10 cm dickem Unterfettgewebe, ein dichtes Fell mit bis zu 100 cm langen, dunkel- bis gelbbraunen Deckhaaren mit dichter Unterwolle sowie kleine Ohren zur Minimierung von Wärmeverlusten gelten als spezialisierte Anpassungen an kalte Umweltbedingungen (Boeskorov et al., 2016). Charakteristisch für das Wollhaarmammut sind aus den Incisivi des Oberkiefers entstandene, lange, bogenförmig gekrümmte Stoßzähne mit zueinander weisenden Spitzen, welche anhand typischer Schliffmarken unter anderem zum Freilegen von Vegetation unter der Schneedecke dienten. Auch bei den Stoßzähnen zeigt sich hinsichtlich der Morphologie und Dimensionierung ein deutlicher Geschlechtsdiphormismus, wonach die Stoßzähne männlicher Individuen eine Länge von bis zu 5 m und ein Einzelgewicht von bis zu 90 kg erreichten, während weibliche Individuen deutlich kürzere, dünnere und weniger gekrümmte Stoßzähne ausbildeten. Milchstoßzähne juveniler Individuen erreichten eine durchschnittliche Länge von 10 cm und wurden im Alter von 12-18 Monaten durch dauerhafte Stoßzähne ersetzt (Maschenko, 2002, Rountrey et al., 2012, Mol et al., 2018). Stoßzähne sind aus zahlreichen, im Jahresrhythmus gebildeten, Wachstumskegeln aus Elfenbein aufgebaut, deren unterschiedliche Breiten auf jahreszeitlich bedingte Unterschiede in der Ernährung hindeuten und zudem Rückschlüsse auf Reproduktions- und Laktationsphasen von weiblichen Individuen erlauben (Fisher et al., 2003). Spezifische Abnutzungsmuster an den Molaren, botanische Makroreste und Pollen aus dem Verdauungstrakt von Mammutkadavern aus dem Permafrost sowie stabile Isotopen belegen, dass die Ernährung des Wollhaarmammuts primär aus Gräsern und Seggen bestand, während Moose, Kräuter und junge Zweige der Zwergformen von *Larix*, *Salix*, *Alnus* und *Betula* nur fallweise konsumiert wurden. Die effiziente Verwertung großer Mengen dieser allgemein nährstoff- und proteinarmen, jedoch ballaststoffreichen Futterpflanzen, ist letztlich als weitere spezialisierte, physiologische Anpassung sowie ökologische Nischenbesetzung anzusehen (Vereshchagin & Baryshnikov, 1982, Mead et al., 1986, Bocherens, 2003, Tütken et al., 2007, van Geel et al., 2008, Rivals et al., 2012, Schwartz-Narbonne et al., 2015).

Der evolutionäre Ursprung des Wollhaarmammuts liegt mit *Mammuthus subplanifrons* in Ostafrika, dessen älteste Fossilreste in das beginnende Pliozän datieren. Im späten Pliozän (3,5-2,5 mya BP) tritt die Gattung mit *Mammuthus rumanus*, dessen Fossilreste in Rumänien entdeckt wurden, erstmals in Südeuropa auf. Als unmittelbarer Nachfahre gilt der Südelefant (*Mammuthus meridionalis*), welcher sich über Eurasien verbreitete, über die Beringbrücke nach Nordamerika einwanderte und sich zum Präriemammut (*Mammuthus columbi*) entwickelte. Im Ältestpleistozän ging in Ostasien aus dem Südelefanten das Steppenmammut (*Mammuthus trogontherii*) hervor, dessen Fossilreste erstmals um 750.000 BP in Mitteleuropa nachweisbar sind. Aus letzterem entwickelte sich um 700.000 BP in Ostsibirien das Wollhaarmammut (*Mammuthus primigenius*), welches schließlich um 200.000 BP im Mittelpleistozän erstmals in Mitteleuropa auftritt (Lister & Sher, 2001, 2015, Lister et al., 2005, van der Made, 2010). Die geografische Verbreitung des Wollhaarmammuts erstreckte sich über das gesamte nördliche Eurasien von der Iberischen Halbinsel, Irland, Doggerland und Mitteleuropa im Westen bis nach Sibirien und Beringia im Osten. Lediglich während des Riß-Würm-Interglazials (Eem) zog sich das Wollhaarmammut nach Sibirien zurück, ehe es am Beginn des Würm-Glazials wieder nach Europa einwanderte und in dieser Phase bis zu seinem Aussterben die größte geografische Verbreitung erreichte (Ukkonen et al., 2011, Kahlke, 2015, Puzachenko et al., 2017). Die einsetzende Klimaerwärmung, das Verschwinden der offenen, kalt-trockenen Steppenlandschaft, die einsetzende Bewaldung sowie die anthropogene Bejagung führten nach der letzten Maximalvereisung zu einem sukzessiven Aussterben des Wollhaarmammuts (Nogués-Bravo et al., 2008, Cooper et al., 2015, Drucker et al., 2018). In Mitteleuropa verschwand das Wollhaarmammut bereits um 13.800 cal BP, während es im nördlichen Sibirien auf der Taimyr-Halbinsel noch bis um 11.000 cal BP bis in das Frühholozän überleben konnte (Stuart et al., 2002, MacPhee et al., 2002, Stuart et al., 2004, Stuart, 2005, Stuart & Lister, 2007, Kuzmin, 2010, Markova et al., 2010, Stuart, 2015). Von der St.-Paul-Insel im Beringmeer sowie der sibirischen Wrangel-Insel stammende Fossilreste verzwergter Wollhaarmammute belegen letztlich noch einen Fortbestand einiger isolierter Restpopulationen bis in das Mittelholozän um 4.000 cal BP (Vartanyan et al., 1993, 2008, Enk et al., 2009).

Im Ostenalpenraum tritt das Wollhaarmammut insbesondere in pleistozänen Löss- und Schotterablagerungen des flachen Alpenvorlandes sowie entlang der Donau auf (Ziegler, 1994, Kohl, 1999, Darga, 2009) und einige weitere Fossilreste stammen als eingetragene Beutereste der Höhlenhyäne (*Crocuta crocuta spelaea*) aus Höhlen wie der Teufelslucke bei Eggenburg oder der Griffener Tropfsteinhöhle (Döppes & Rabeder, 1997). Die Mehrheit der Fossilreste stammt hingegen aus jungpaläolithischen Freilandstationen des Donauraumes, wozu allen voran die Stationen von Ruppersthal und Langmannersdorf zu nennen sind (Salcher-Jedrasiak & Umgeher-Mayer, 2010). Während die Mehrheit der Fossilreste im Alpenvorland und im Donauraum auftreten, liegen aus den großen inneralpinen Tälern der Ostalpen bislang nur vergleichsweise wenige Nachweise des Wollhaarmammuts vor (Stadler, 2003, Patzelt, 2014, Spötl et al., 2018).

2. Abtenauer Becken

Das Abtenauer Becken ist eine im Lammertal gelegene, inneralpine Beckenlandschaft der Nördlichen Kalkalpen, welche über das voralpine Salzachtal an das Alpenvorland angeschlossen ist. Begrenzt durch die Osterhorngruppe im Norden, das Tennengebirge im Süden und durch die beiden markanten Geländerücken des Roadberges und Flichtlhofberges im Westen, erstreckt sich das Abtenauer Becken auf einer Fläche von rund 45 km^2 und liegt auf durchschnittlich 600-900 m Seehöhe (Abb. 1).

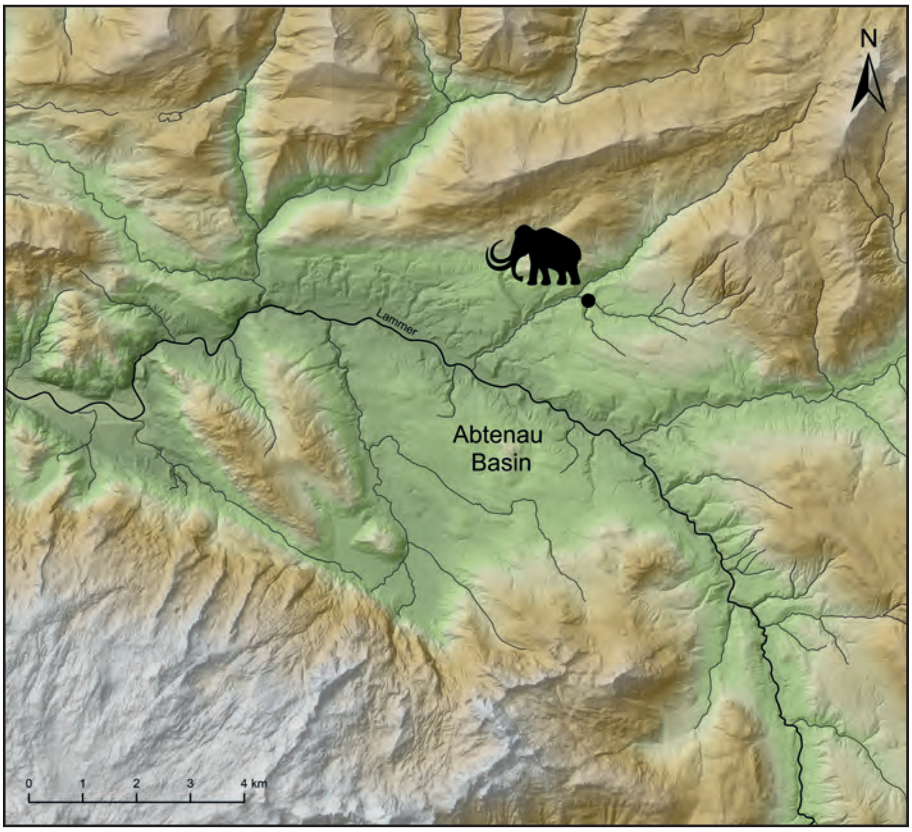

Abb. 1: Abtenauer Becken mit der Fundstelle des Stoßzahnfragmentes des Wollhaarmammuts (*Mammuthus primigenius*) im Zwieselbachgraben.
Fig. 1: Abtenau Basin with discovery site of the tusk fragment of woolly mammoth (*Mammuthus primigenius*) in the Zwieselbachgraben.
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Während der präquartäre Untergrund des Abtenauer Beckens aus Haselgebirge, Dolomit sowie triassischem Schiefergestein der Werfen-Formation aufgebaut ist, wird die rezente, flach-hügelige Geländemorphologie des Abtenauer Beckens maßgeblich durch glaziale Ablagerungen des Jungpleistozäns geprägt: Vor der letzten Maximalvereisung (29.000-19.000 BP, STARNBERGER et al., 2011) kam es ab dem Beginn des Spätwürm (um 34.000 BP) in den Hochlagen aufgrund eines klimatisch indizierten Vegetationsrückganges sowie verstärkter Frostverwitterung zu einer vermehrten Schuttbildung, infolgedessen in den Tallagen eine massive Ablagerung so genannter „Vorstoßschotter" (VAN HUSEN & REITNER, 2011) erfolgte, wodurch das anstehende Grundgestein im Abtenauer Becken mit bis zu 40 m mächtigen fluviatilen Schottern überdeckt wurde. Typisch für derartige Vorstoßschotter ist eine Zusammensetzung aus primär autochthonen Gesteinen sowie unregelmäßige Lagerungsverhältnisse, welche rasch wechselnde Sedimentationsprozesse im Gletschervorfeld anzeigen (VAN HUSEN, 1979, KALS, 1984; persön. Mitteilung VAN HUSEN).

Abb. 2: Panorama über die Hügellandschaft an den Ausläufern des Radochsberges oberhalb des Zwieselbachgrabens mit dem Tennengebirge (links) und der Osterhorngruppe (rechts) im Hintergrund.
Fig. 2: Panoramic view over the hilly landscape at the foothills of the Radochsberg above the Zwieselbachgraben with the Tennengebir-ge (left) and the Osterhorngruppe (right) in the background.
© Sebastian Krutter

Während der letzten Maximalvereisung des Würmhochglaziales wurden diese Vorstoßschotter schließlich großflächig durch bis zu 60 m mächtige Grundmoränen überdeckt, welche sich aus allochthonen Geröllen der Gosau-Schichten sowie autochthonen Gesteinen zusammensetzen. Langgestreckte, nordwestlich orientierte Drumlins sowie glazial überformte Rundbuckel des Grundgesteins zeigen hierbei die Fließrichtung der Eismassen nach Nordwesten an, welche nördlich des Tennengebirges, dessen höchste Gipfel als Nunataker aus dem Eisschild ragten, über das Lammertal abflossen und sich im Bereich des Gollinger Beckens mit dem Salzachgletscher vereinten (VAN HUSEN, 1979, PLÖCHINGER et al., 1982, KALS, 1984).
Mit dem einsetzenden Zerfall des Eisstromnetzes im Spätglazial blieb im Abtenauer Becken, wie für inneralpine Becken oftmals nachweisbar (GAREIS, 1981), eine isolierte Toteisvergletscherung zurück, an dessen Kontaktzonen zu den Talrändern sich durch abfließende Schmelzwässer charakteristische Eisrandterrassen ausbildeten. Bei einem neuerlichen, spätglazialen Gletschervorstoß, dem Wolfs-

grub-Stand, wurden nochmals weite Bereiche des Abtenauer Beckens mit Eismassen bedeckt. Der dem Schwarzberg-Stand angehörende mächtige Moränenwall im Südosten des Abtenauer Beckens zeigt an, dass im Gschnitz-Stadial (16.000 BP, Ivy-Ochs et al., 2006) nochmals einzelne Gletscherzungen vom Plateau des Tennengebirges bis in das Abtenauer Becken hinabreichten (Kals, 1984). Im ausgehenden Spätglazial und Holozän formten sich schließlich durch fluviatile Zerschneidung der mächtigen Grundmoränendecke sowie Tiefenerosion im unterlagernden Grundgestein tief eingeschnittene Gräben, wie unter anderem auch der Zwieselbachgraben (Abb. 2-3), worin der hier untersuchte Fossilrest entdeckt wurde.

Abb. 3: Fundstelle des Stoßzahnfragmentes des Wollhaarmammuts (*Mammuthus primigenius*) im Bachbett des Zwieselbachgrabens.
Fig. 3: Discovery site of the tusk fragment of woolly mammoth (*Mammuthus primigenius*) in the river bed of the Zwieselbachgraben.
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Abb. 4: Stoßzahnfragment des Wollhaarmammuts (*Mammuthus primigenius*) aus dem Zwieselbachgraben in medialer (oben) und lateraler (unten) Ansicht mit der Position der osteometrischen Messstrecken. Abkürzungen: GPD/GPC = größter proximaler Durch-messer und Umfang, GMD/GMC = größter medialer Durchmesser und Umfang, GDD/GDC = größter distaler Durchmesser und Umfang.
Fig. 4: Tusk fragment of woolly mammoth (*Mammuthus primigenius*) from the Zwieselbachgraben in medial (above) and lateral (below) view with the position of osteometric measurements. Abbreviations: GPD/GPC = greatest proximal diameter and circumference, GMD/GMC = greatest medial diameter and circumference, GDD/GDC = greatest distal diameter and circumference. © Sebastian Krutter

3. Fossilmaterial

Im Norden des Abtenauer Beckens an den Ausläufern der Osterhorngruppe liegt der rund 70 m tief eingeschnittene Zwieselbachgraben, in dessen Bachbett im Jahr 2017 durch Alfons Klamm auf rund 700 m Seehöhe ein isoliertes Fragment eines Stoßzahnes entdeckt wurde, welches rund 30 cm aus dem fluviatilen Geröll und Feinsediment des Bachbettes herausragte (Abb. 4). Der Fossilrest ist anhand der Krümmung in der Horizontalachse als linker Stoßzahn (I2 sin.) bestimmbar und weist entlang der äußeren Krümmung eine erhaltene Länge von 130 cm auf, wobei dessen distales sowie proximales Ende mit der Pulpahöhle und dem in der Alveole befindlichen Bereich nicht erhalten sind.

Abb. 5: Wollhaarmammut (*Mammuthus primigenius*) vor einer jungpleistozänen inneralpinen Beckenlandschaft.
Fig. 5: Woolly mammoth (*Mammuthus primigenius*) in front of an Upper Pleistocene inneralpine basin landscape.
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An der lateralen Seite zeigt der Fossilrest eine hellweiße Farbgebung, einige größere Risse sowie eine fein geglättet-verrundete Oberfläche. Medial sind hingegen jeweils am proximalen und distalen Ende größere Ausbrüche vorhanden, worin die von Trocknungsrissen durchzogene innere Struktur des Stoßzahnes offenliegt. Die Oberfläche weist mehrere kleinere, flächige Absplitterungen und Verfärbungen auf, wobei sich zumindest an einer Stelle die ursprüngliche, für Elfenbein typische, hellbeige Farbgebung erhalten hat. Anhand osteomorphologischer Merkmale, der Datierung sowie paläoökologischer Aspekte kann der hier untersuchte Fossilrest aus taxonomischer Sicht eindeutig dem Wollhaarmammut (*Mammuthus primigenius*) zugewiesen werden.

Eine ergänzende taxonomische Bestimmung mittels der für dieses Taxon spezifisch ausgeprägten Schreger-Linien im Dentin konnte aufgrund des Erhaltungszustandes des Stoßzahnfragmentes nicht vorgenommen werden (Trapani & Fisher, 2003, Abelova, 2008). Der im pleistozänen Mitteleuropa ebenfalls vorkommende Waldelefant (*Palaeoloxodon antiquus*) kann aufgrund des ausschließlich interglazialen Auftretens dieses Taxons sowie anhand der Datierung ausgeschlossen werden (Stuart, 2005). Die eingeschränkte Aussagekraft des isolierten Fossilrestes sowie das Fehlen von weiterem assoziierbarem Fossilmaterial, ermöglichen vorerst keine weiteren, detaillierten Aussagen über das hier fassbare Individuum. Zumindest aber ein Vergleich der osteometrischen Daten (Tab. 1) mit

Stoßzähnen jungpleistozäner Mammutfaunen aus Sibirien zeigt an, dass es sich hier um ein adultes, männliches Individuum im Alter von rund 30-50 Jahren gehandelt haben könnte (Vereshchagin & Tikhonov, 1986, 1999, Haynes, 1991, Averianov, 1996, Smith & Fisher, 2011, 2013).

GL1	GL2	GPD	GMD	GDD	GPC	GMC	GDC	ADPC	AD
1300	1130	130	120	80	400	380	(260)	–	–

Tab. 1: Osteometrische Messstrecken (basierend auf Vereshchagin & Tikhonov, 1986, 1999, Smith & Fisher, 2011, 2013) des Stoßzahnfragmentes des Wollhaarmammuts (*Mammuthus primigenius*) aus dem Zwieselbachgraben. Abkürzungen: GL1 = größte erhaltene Länge an der äußeren Krümmung, GL2 = größte erhaltene Länge an der inneren Krümmung, GPD = größter proximaler Durchmesser, GMD = größter medialer Durchmesser, GDD = größter distaler Durchmesser, GPC = größter proximaler Umfang, GMC = größter medialer Umfang, GDC = größter distaler Umfang, ADPC = axiale Tiefe der Pulpahöhle, AD = Tiefe der Alveole. Alle Maße in Millimetern; Maße in Klammern stellen Schätzwerte dar.

Tab. 1: Osteometric measurements (based on Vereshchagin & Tikhono, 1986, 1999, Smith & Fisher, 2011, 2013) of the tusk fragment of woolly mammoth (*Mammuthus primigenius*) from the Zwieselbachgraben. Abbreviations: GL1 = greatest preserved length along the outer curvature, GL2 = greatest preserved length along the inner curvature, GPD = greatest proximal diameter, GMD = great-est medial diameter, GDD = greatest distal diameter, GPC = greatest proximal circumference, GMC = greatest medial circumference, GDC = greatest distal circumference, ADPC = axial depth of pulp cavity, AD = alveolar depth. All measurements in millimetre; measurements in parenthesis are estimated values.

4. Datierung und Paläoumwelt

Zur Datierung des Stoßzahnfragmentes wurde am Curt-Engelhorn-Zentrum für Archäometrie in Mannheim eine ^{14}C-Analyse (Tab. 2) durchgeführt, wofür einige lose Elfenbeinfragmente als Probenmaterial verwendet wurden. Aus der Probe wurde Kollagen extrahiert und mittels Ultrafiltration die Fraktion > 30 kD abgetrennt, gefriergetrocknet und in einem Elementaranalysator zu CO_2 verbrannt. Das entstandene CO_2 wurde katalytisch zu Graphit reduziert und anschließend der ^{14}C-Gehalt mit einem MICADAS-Beschleuniger gemessen (Kromer et al., 2013). Die ^{14}C-Alter werden in BP (before present), in Jahren vor 1950, angegeben.

LabNr.	^{14}C-Alter	cal BP [1σ]	cal BP [2σ]	C:N$_{coll}$	C$_{coll}$ [%]	Coll. [%]
MAMS-31890	26.970 ± 100	31.140-30.950	31.220-30.840	3,2	41,1	1,63

Tab. 2: ^{14}C-Datierung des Wollhaarmammuts (*Mammuthus primigenius*) aus dem Zwieselbachgraben.

Tab. 2: Radiocarbon analysis of woolly mammoth (*Mammuthus primigenius*) from the Zwieselbachgraben.

Das ^{14}C-Alter muss kalibriert werden, um Kalenderalter angeben zu können, wobei das kalibrierte Alter jeweils für den 1σ-Bereich (68,2 %) und für den 2σ-Bereich (95,4 %) angegeben wird. Die Kalibrierung des ^{14}C-Alters erfolgte mit dem Datensatz INTCAL13 (Reimer et al., 2013) und der Software OxCal 4.3. Das ermittelte C:N-Verhältnis liegt mit 3,2 innerhalb des Bereichs für eine gute

Erhaltung des Knochenkollagens und auch die relative Kollagenmenge von 1,63 % zeigt eine zuverlässige Datierung an (van Klinken, 1999).

LabNr.	$\delta^{13}C_{coll}$ [‰]	$\delta^{15}N_{coll}$ [‰]	$C:N_{coll}$	C_{coll} [%]	N_{coll} [%]
MA-175013	-20,92	9,25	3,2	38,68	14,16

Tab. 3: Stabile Isotopenwerte des Wollhaarmammuts (*Mammuthus primigenius*) aus dem Zwieselbachgraben.
Tab. 3: Stable isotope values of woolly mammoth (*Mammuthus primigenius*) from the Zwieselbachgraben.

Die Analyse der stabilen Isotopen (Tab. 3) erfolgte ebenfalls am Curt-Engelhorn-Zentrum für Archäometrie in Mannheim an einem vario PYRO cube CNSOH-Elementaranalysator und einem precisION Isotopenverhältnis-Massenspektrometer, wobei die Rohdaten auf die Standards USGS40 und USGS41 normiert wurden (Paul et al., 2007). Die externe Reproduzierbarkeit der $\delta^{13}C$ und $\delta^{15}N$-Werte liegt bei 0,04 ‰ oder besser. Die Quantität des Kohlenstoffs (C_{coll}) entspricht mit 38,68 % jenen Werten aus frischen Knochen (25 %). Das C:N-Verhältnis von 3,2 liegt hierbei im akzeptablen Bereich von 2,9 bis 3,6 (DeNiro, 1985) und auch der Stickstoffgehalt (N_{coll}) > 5 % untermauert das Ergebnis der Isotopenanalyse.

Das hier untersuchte Stoßzahnfragment des Wollhaarmammuts (*Mammuthus primigenius*) aus dem Zwieselbachgraben weist ein kalibriertes ^{14}C-Alter von 31.220-30.840 cal BP auf und ist demnach in die erste Phase des jungpleistozänen Spätwürm einzuordnen, welche allgemein als Mammutsteppenzeit (34.000-13.000 BP, Döppes & Rabeder, 1997) bezeichnet wird. Diese Phase charakterisiert sich durch eine, über das nördliche Eurasien verbreitete, baumlose, von Permafrost geprägte, kalttrockene Steppenlandschaft mit einer nährstoffreichen, von Gräsern und Kräutern dominierten Vegetation sowie einer, der rezenten afrikanischen Savanne ähnlichen, hohen Artenvielfalt (Vereshchagin & Baryshnikov, 1982, Guthrie, 1982, 2001, Zimov et al., 2012).

Die stabilen Isotope von Kohlenstoff ($\delta^{13}C$) und Stickstoff ($\delta^{15}N$) aus dem Kollagen von Herbivoren liefern paläoökologische Hinweise, indem sie die konsumierten Futterpflanzen wiederspiegeln, deren Isotopensignaturen wiederum durch Umweltbedingungen wie Temperatur, Trockenheit und Höhenlage beeinflusst werden. So zeigen niedrige $\delta^{13}C_{coll}$-Werte Futterpflanzen aus einer dicht bewaldeten Umwelt an, während erhöhte $\delta^{13}C_{coll}$-Werte auf offene, baumlose Landschaften schließen lassen, wie dies an der von Flechten dominierten Ernährung von Rentieren (*Rangifer tarandus*) ersichtlich ist (Drucker et al., 2011). Die niedrigen $\delta^{13}C_{coll}$-Werte des Wollhaarmammuts sind nicht als Indikator einer dicht bewaldeten Paläoumwelt interpretierbar, sondern resultieren aus der physiologischen Eigenschaft einer vermehrten Nutzung von eingelagertem, ^{13}C-armem Körperfett (Bocherens, 2003, 2015). Die $\delta^{15}N_{coll}$-Werte geben hingegen Hinweise auf das Klima und die Bodenbeschaffenheit und gelten auf Basis sinkender Temperaturen sowie ansteigender Trockenheit als Indikator für die Intensität von Permafrostböden und die räumliche Nähe zu vergletscherten Gebieten, wobei das Wollhaarmammut im Vergleich zu anderen Herbivoren der jungpleistozänen Megafauna stets signifikant erhöhte, aus einer von trockenen Gräsern dominierten Ernährung resultierende $\delta^{15}N_{coll}$-Werte aufweist (Bocherens, 2003, 2015). Für die Phase des Mittel- und Spätwürm sind für das Wollhaarmammut in Eurasien allgemein sehr geringvariable Isotopensignaturen belegt, welche infolgedessen weitgehend konstante Umweltbedingungen anzeigen (Kuitems et al., 2019). Auch die Isotopensignaturen des hier untersuchten Fossilrestes aus dem Zwieselbachgraben geben für jungpleistozäne Wollhaarmammute typische Werte wieder, indem sie eine von Gräsern dominierte Ernährung belegen und für das Abtenauer Becken für den Zeitbereich um 31.000 cal BP eine, als Mammutsteppe zu charakterisierende, offene, baumlose und von Permafrost geprägte, kalt-trockene Steppenlandschaft anzeigen. Die geologischen Erkenntnisse belegen, dass das Abtenauer Becken in dieser Phase bereits durch großflächige fluviatile Ablagerungen an Vorstoßschottern eingenommen wurde, während sich die Vergletscherung noch auf die hochalpinen Kare und das Plateau des Tennengebirges beschränkte (Abb. 5).

Das hier untersuchte Stoßzahnfragment gilt als jüngster, bislang datierter Fossilrest des Wollhaarmammuts aus den inneralpinen Tälern der Ostalpen (Spötl et al., 2018) und belegt infolgedessen, dass das Wollhaarmammut noch im beginnenden Spätwürm in große inneralpine Täler und deren Seitentäler eingewandert ist. In Kontext der paläoökologischen Daten fungiert der Fossilrest als Klimaproxy für noch eisfreie Umweltbedingungen um 31.000 cal BP im Abtenauer Becken im unmittelbaren Vorfeld der letzten Maximalvereisung (29.000-19.000 BP, Starnberger et al., 2011) und gibt folglich einen *terminus post quem* für das endgültige Vorstoßen der würmzeitlichen Vergletscherung im Lammertal. Somit ist das hier fassbare Individuum aus dem Zwieselbachgraben wohl als eines der letzten Wollhaarmammute anzusehen, welche im Vorfeld der letzten Maximalvereisung aus dem Alpenvorland bis in das inneralpine Abtenauer Becken vorgedrungen sind, ehe dieses von bis zu 1.000 m mächtigen Eismassen überfahren wurde (Kals, 1984, Gamerith & Heuberger, 1999).

5. Taphonomie

Der Erhaltungszustand des hier untersuchten Stoßzahnfragmentes des Wollhaarmammuts (*Mammuthus primigenius*) lässt aus taphonomischer Sicht eine sekundäre Verlagerung konstatieren, wonach der Fossilrest an der Abbruchkante der oberhalb des Zwieselbachgrabens lagernden jungpleistozänen Sedimente aus seinem ursprünglichen Ablagerungsort auserodiert und über die rund 45° geneigten Abhänge in den Zwieselbachgraben abgerutscht ist sowie in die fluviatilen Schotter des Bachbettes gelangte. Der verhältnismäßig gute Erhaltungszustand belegt zudem, dass dieser sekundäre Umlagerungsprozess erst in den letzten Jahren erfolgt sein muss, da der Fossilrest bei einem längeren Transport im fluviatilen Schotter durch mechanische Erosionsprozesse nicht mehr erhalten gewesen wäre oder eine zumindest stärker ausgeprägte Fragmentierung aufgewiesen hätte. Über die taphonomischen Prozesse der ursprünglichen Ablagerung können hingegen nur Vermutungen angestellt werden, wonach der Stoßzahn möglicherweise in einem von Feinsediment geprägten Stillwasserbereich in den Vorstoßschottern abgelagert worden sein könnte, wie dies auch für das Stoßzahnfragment von Bischofshofen anzunehmen ist (Tichy, 1989). Unklar ist, ob der Stoßzahn sowie das übrige Fossilmaterial des hier fassbaren Individuums an einer Stelle gemeinsam abgelagert oder bereits zuvor durch fluviatile Prozesse weitflächig disloziert wurden. Zumindest die hellweiße Farbgebung und die fein geglättet-verrundete Oberfläche an der lateralen Seite des Fossilrestes lassen vermuten, dass der Stoßzahn irgendwann im Laufe des taphonomischen Prozesses für längere Zeit oberflächlich freiliegend der Witterung und direkten Sonneneinstrahlung ausgesetzt war. In jedem Fall muss die Einbettung in die Vorstoßschotter vor dem Beginn der letzten Maximalvereisung (29.000-19.000 BP, Starnberger et al., 2011) erfolgt sein, zumal der Stoßzahn eine direkte Überfahrung durch das Gletschereis sowie eine Verfrachtung innerhalb der Grundmoräne nicht überstanden hätte.

Ob das hier fassbare Individuum auf natürliche Weise verendete, durch Carnivoren erbeutet oder durch eine paläolithische Jägergruppe erlegt wurde, ist anhand des einzelnen Fossilrestes nur schwer rekonstruierbar. Die fehlenden zoogenen Bissspuren an dem Fossilrest erlauben diesbezüglich keine Rückschlüsse, da an den fleischlosen Stoßzähnen naturgemäß keine derartigen Spuren zu erwarten sind, weshalb angesichts der fehlenden postcranialen Fossilreste eine Aktivität von Carnivoren weder zu bestätigen noch auszuschließen ist. Zumindest aber ein anthropogener Kontext mag als unwahrscheinlich gelten, da im Abtenauer Becken bislang keinerlei paläolithisches Fundmaterial nachweisbar ist und auch im angrenzenden Salzachtal paläolithische Fundstellen nur sehr selten belegt sind (Ehrenberg, 1974, Abel, 1978, Hell & Moosleitner, 1980-1981, Rettenbacher, 1998, Mais, 1990). Zudem erscheint es untypisch, dass ein Stoßzahn eines erlegten ‚Wollhaarmammuts durch eine paläolithische Jägergruppe zurückgelassen worden wäre, zumal Elfenbein im Paläolithikum als ein überaus begehrtes sowie vielseitig nutzbares Rohmaterial galt (Pfeifer et al., 2019). Infolgedessen ist zu postulieren, dass das hier fassbare Individuum womöglich durch Carnivoren erbeutet wurde oder auf natürliche Weise verendete, indem es beispielsweise in morastigem Boden stecken geblieben, ertrunken oder über eine Geländekante abgestürzt ist. Sofern keine unmittelbare Sedimentüberdeckung erfolgte, wäre auch in letzterem Fall an den, bislang nicht überlieferten, postcranialen Fossilresten mit entsprechenden zoogenen Bissspuren von Carnivoren und Nekrophagen zu rechnen.

6. Wollhaarmammutfunde aus dem Salzachtal

Aus dem Alpenvorland und Donauraum sind unzählige Fossilreste des Wollhaarmammuts (*Mammuthus primigenius*) überliefert, wohingegen Fossilreste aus den großen inneralpinen Tälern nur selten vorliegen (Spötl et al., 2018). Dies ist einerseits auf eine vollständige Vergletscherung der Ostalpen während der letzten Maximalvereisung zurückzuführen, wodurch die alpinen Täler, konträr zu den periglazialen Gebieten, für das Wollhaarmammut nicht zugänglich waren. Andererseits wirkte sich die glaziale Erosion negativ auf die Erhaltung von abgelagerten Fossilresten aus, womit sich diese lediglich an natürlichen, vor glazialer Erosion geschützten Geländesituationen erhalten konnten.

Infolgedessen sind auch aus dem alpinen Salzachtal und dessen Seitentälern bislang nur sehr wenige Fossilreste des Wollhaarmammuts überliefert, wobei sich für das nördliche Salzachtal am Übergang in das weitläufige Alpenvorland eine erhöhte Funddichte abzeichnet (Tab. 4). Bei dem vorliegenden Fossilmaterial handelt es sich mehrheitlich um isolierte Molare, welche anhand der kompakten Struktur in ihrer Erhaltung deutlich begünstigt sind und zumeist aus fluviatilen, teils durch den Schotterabbau aufgeschlossenen, Schotterablagerungen entlang der Salzach sowie aus grabenartig eingetieften Bachläufen, wie dem Kroisbachgraben bei Nußdorf (Tichy, 1989), stammen. Stoßzahnfragmente sind bislang mit fünf Fossilresten vertreten, welche wiederum mehrheitlich aus fluviatilen Schotterablagerungen entlang der Salzach überliefert sind. Erwähnenswert ist insbesondere ein rund 1 m langes Stoßzahnfragment vom Buchberg bei Bischofshofen im inneralpinen Salzachtal, welches rund 15 m unter der Geländeoberkante in sandigem Sediment aufgefunden wurde und wobei es sich um den südlichsten bislang bekannten Fossilrest des Wollhaarmammuts im inneralpinen Salzachtal handelt. Wenn auch dessen Datierung um 32.400 cal BP zuletzt kritisch bewertet wurde (Tichy, 1989, Spötl et al., 2018), so ist diese angesichts des hier untersuchten Stoßzahnfragmentes aus dem Abtenauer Becken als grundlegend plausibel zu erachten, zumal auch dieser Fossilrest als Beleg eines letztmaligen, inneralpinen Vordringens des Wollhaarmammuts im Vorfeld der letzten Maximalvereisung (29.000-19.000 BP, Starnberger et al., 2011) gelten mag.

Fundstelle	**Fossilmaterial**	**Verbleib, InvNr.**	**Literatur**
Oberndorf	zwei Stoßzahnfragmente	HdN, 31960, 31961	Hell, 1936
Lamprechtshausen	Molar	HdN	Hell, 1936
Salzburg (?)	Scapula, Humerus	HdN	Hell, 1936
Salzburg, Aigen	M2 inf. dex.	HdN, 27/1969	Tichy, 1989
Nußdorf, Kroisbachgraben	M3 inf. dex.	HdN, 6/1968	Tichy, 1989
Bischofshofen, Buchberg	Stoßzahnfragment	MB, 1	Tichy, 1989
Oberndorf	zwei Molare	MBG, IN851	unpubl.
Bergheim	Stoßzahnfragment	MBG, IN4716	unpubl.
Elsbethen	Molar	MBG, IN4728	unpubl.
Abtenau, Zwieselbachgraben	Stoßzahnfragment	MBG, IN4570	diese Arbeit
Berchtesgaden, Nesseltalgraben			Spötl et al., 2018

Tab. 4: Zusammenstellung von Fossilresten des Wollhaarmammuts (*Mammuthus primigenius*) aus dem Salzachtal und Seitentälern. Abkürzungen: HdN = Haus der Natur Salzburg, MB = Museum Bischofshofen, MBG = Museum Burg Golling.

Tab. 4: Compilation of fossil remains of woolly mammoth (*Mammuthus primigenius*) from the Salzach Valley and tributary valleys. Abbreviations: HdN = Haus der Natur Salzburg, MB = Museum Bischofshofen, MBG = Museum Burg Golling.

Während craniale Fossilreste mit Molaren und Stoßzähnen vergleichsweise häufig vorliegen, sind postcraniale Elemente bislang nur mit einer Scapula und einem Humerus belegt, welche vermutlich aus dem Salzburger Becken stammen (Hell, 1936). Weitere, derzeit noch nicht im Detail vorgelegte Fossilreste des Wollhaarmammuts stammen aus den lakustrinen Ablagerungen des Nesseltalgrabens im Berchtesgadener Becken, welches westlich an das Salzachtal anschließt (Mayr et al., 2017, Spötl et al., 2018).

7. Fazit

Das aus dem Zwieselbachgraben im Abtenauer Becken stammende linke Stoßzahnfragment eines vermutlich adulten, männlichen Individuums des Wollhaarmammuts (*Mammuthus primigenius*) datiert mit rund 31.000 cal BP in die erste Phase des jungpleistozänen Spätwürms, welche allgemein als Mammutsteppenzeit bezeichnet wird. Das Stoßzahnfragment gilt als bislang jüngster Fossilrest des Wollhaarmammuts aus den inneralpinen Tälern der Ostalpen (Spötl et al., 2018) und ist vermutlich als eines der letzten Wollhaarmammute anzusehen, welche im Vorfeld der letzten Maximalvereisung (29.000-19.000 BP, Starnberger et al., 2011) bis in das inneralpine Abtenauer Becken vorgedrungen sind.

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Brown bear remains in prehistoric and early historic societies: case studies from Austria

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Abstract

Remains of brown bear (*Ursus arctos* LINNAEUS, 1758) are seldom recovered within archaeological assemblages. Nonetheless, interactions with bears and remains from this animal in past human societies are diverse, as will be reflected in this paper through the discussion of a number of archaeozoological case studies from Austria. The aim of this study was to detect the varying roles of bears in pre- and early historic agricultural societies and to identify the importance of 'rare' elements. The study presents an investigation of the osteological indications of this particular species, within a defined area and across time. Bears did not supply an important contribution to daily consumption but this species was incorporated within varying contexts, suggesting a variety of different practices.

Zusammenfassung

Überreste von Braunbären (*Ursus arctos* LINNAEUS, 1758) werden in archäologischen Fundstellen selten geborgen. Interaktionen mit Bären und deren Überresten sind in früheren menschlichen Gesellschaften dennoch vielfältig, wie in diesem Artikel anhand einer Reihe von archäozoologischen Beispielen aus Österreich gezeigt wird. Ziel dieser Studie ist es, die unterschiedlichen Rollen von Bären in vor- und frühzeitlich historischen landwirtschaftlichen Gesellschaften zu erkennen und die Bedeutung von „seltenen“ Elementen zu identifizieren. Die Arbeit präsentiert eine Untersuchung der osteologischen Indikationen dieser besonderen Art in einem abgegrenzten Gebiet und über die Zeit hinweg. Bären lieferten keinen wichtigen Beitrag bei der täglichen Nahrungsaufnahme, sind jedoch in unterschiedlichen Kontexten eingebunden, was auf eine Vielzahl unterschiedlicher Praktiken hindeutet.

Key words: Brown bear, *Ursus arctos,* archaeozoology, human interaction, Austria

Introduction

Nearly driven to the edge of extinction in many parts of Europe, brown bear populations are recovering slightly today. Probably since the time of their first encounter, the relationship between bears and humans has been inconsistent and fallen somewhere between respect, fear and condemnation.
In contexts as early as the Palaeolithic, modified bear bones and teeth indicate skinning, meat con-

sumption and use as pendants (Pacher, 2005). Occasionally brown bears occur in Palaeolithic cave art. Late Glacial and Mesolithic finds of associated human and bear skeletons from Central Europe (Morel, 1993), as well as bone points created from these animals (Bárta, 1990), may provide evidence that this species was actually hunted. Other relationships are also apparent: a possible example of a tamed bear is proposed at a Mesolithic site in France (see Chaix et al., 1997).

In Austria, bear bones occur regularly in archaeological assemblages from the Neolithic period (c. 5600-2000 BC, including the Copper Age or Chalcolithic c. 4000-2000 BC) to the High Medieval period (c. AD 907-1250). Apparently, there are no important bone assemblages containing bear remains from later historical periods but information concerning human-bear relationships can be obtained from written sources and visual imagery, such as rock art. Aside from Palaeolithic cave art (see above), such additional sources are provided from Roman times onwards, such as the stone reliefs from the Roman town of Virunum (Gugl, 2004) and Medieval petroglyphs from Upper Austria depicting a bear hunt (Mandl, 2004). From neighbouring Germany, a vivid illustration of a market scene with a butchered bear can be found in the so-called Richenthal Chronicle (dating to the late fifteenth century AD; Richental, 1964).

In archaeozoological contexts the remains of bear bones and teeth provide the primary evidence for human-bear relationships, although exceptional cases, such as the fur cap of the Tyrolean Iceman (Egg & Spindler, 1992), can provide further evidence. Bear bones are easily identified because of their large size and morphological characteristics and only occasionally can they be confused with other animal or human bones; for example in cremation burial contexts (Wahl, 2001). Bones from single individuals are easy to recognize and to refit and operation chains (sequences of human actions), such as the processes of skinning, dismembering and filleting, can be reconstructed from preservation patterns and bone modifications.

The brown bear in the Austrian archaeological record

Archaeological sites with brown bear remains are not equally distributed across the territory of present-day Austria (Fig. 1). This picture is related to former human settlement patterns and archaeological activities rather than to the historical distribution of this species. Current knowledge of recent bear populations connects the occurrence of these animals with sparsely populated, ‘remote’ (i.e. inner-Alpine) areas, where archaeological data are often ephemeral and faunal remains are largely restricted to natural places, such as caves. Hence, the recent known modern-age distribution of the brown bear, before its extinction as regularly reproducing species, exhibits little congruence with the identified distribution patterns present in the archaeological record of prehistoric and early historic times, as bear remains have been recovered in a variety of landscape contexts.

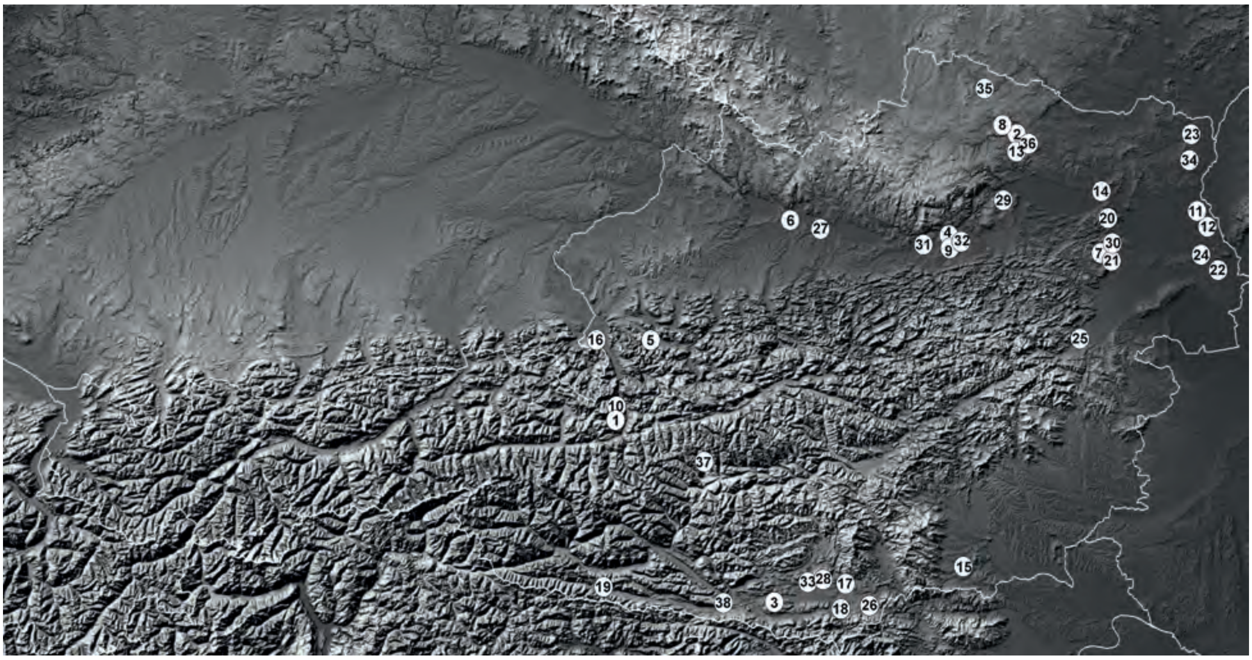

Fig. 1: archaeological sites with brown bear remains from Austria. Neolithic: 1 - Götschenberg, 2 - Ertl, 3 - Keutschach, 4 - Melk-Winden, 5 - Mondsee, 6 - Ölkam, 7 - Perchtoldsdorf, 8 - Poigen, 9 - Nussdorf. Bronze Age: 10 - Bischofshofen, 11 - Buhuberg, 12 - Stillfried, 13 - Thunau, 14 - Unterhautzental. Iron Age: 15 - Burgstallkogel, 16 - Dürrnberg, 17 - Führholz, 18 - Gracarca, 19 - Gurina, 20 - Leopoldsberg, 21- Perchtoldsdorf, 22 - Prellenkirchen. Roman period: 23 - Bernhardsthal, 24 - Carnuntum, 25 - Gerasdorf, 26 - Hemmaberg, 27 - Lauriacum, 28 - Magdalensberg, 29 - Mautern, 30 - Perchtoldsdorf, 31 - Pöchlarn, 32 - Traismauer, 33 - Virunum. Medieval: 34 - Gaiselberg, 35 - Sand, 36 - Thunau, 37 - Thurnschall, 38 - Villach.

It may, nevertheless, be the case that bears became rare or extinct in the densely settled and farmed lowlands much earlier (Spitzenberger, 2001), as has been suggested for the Roman period in neighbouring Switzerland (Deschler-Erb, 2001). Likewise, in the area of Perchtoldsdorf, situated just south of Vienna, which has been continuously populated since the Early Neolithic, bear remains have been found in five archaeological sites dating from the Neolithic, Iron Age and Early and Late Roman periods.

Altogether, 15 localities in Austria are known to have yielded 5 or more identified bone fragments (NISP > 5) of *Ursus arctos* (Figs. 2 and 3). Apart from a Middle Neolithic circular ditch, all belong to some type of settlement structure. As some sites were excavated in the early twentieth century or even earlier, the quality of the materials and the character of the resulting publications differ markedly and context information is rarely provided for the assemblages. In several of the settlements, the bone material could not be attributed to defined features and, as a consequence, the bone samples could not be categorised into context groups and were treated as one assemblage. The collections from the lakeside dwelling Mondsee yielded the largest samples. They resulted from underwater surveys or were dredged from the lake bottom but appeared, nevertheless, suited for further analysis, including small fragments and broken specimens (Pucher & Engl, 1997, Wolff, 1977; Fig. 4).

Considered chronologically, the majority of the bear material from the 15 Austrian sites discussed can be attributed, in roughly equal amounts to either Neolithic or Roman sites (c. 200 identified bone specimens within each category).

Site	Period	Type	Mammals	Wild Mammals		Brown Bear				source
			n	n	% total	n	% total	n corr.	% wild	
Ölkam	Middle Neolithic	circular ditch	3462	3145	90,8	15	0,4	15	0,5	Schmitzberger 2001
Melk-Winden	Middle Neolithic	rural	2204	1478	67,1	5	0,2	5	0,3	Pucher 2004
Mondsee 1	Late Neolithic	lakeside	8688	3341	38,5	108	1,2	108	3,2	Wolff 1977
Mondsee 2	Late Neolithic	lakeside	5094	1514	29,7	47	0,9	47	3,1	Pucher & Engl 1997
Keutschach	Late Neolithic	lakeside	838	599	71,5	14	1,7	14	2,3	Pucher 2003
Götschenberg	Late Neolithic	hilltop	1695	322	19,0	7	0,4	7	2,2	Peters 1992
Buhuberg	Bronze Age	rural	1738	305	17,5	8	0,5	8	2,6	Pucher 1996
Magdalensberg	Early Roman	urban/hilltop	59526	3215	5,4	87	0,1	87	2,7	Hornberger 1970, Ehret 1964
Gerasdorf	Early Roman	?	82	45	54,9	7	8,5	7	15,6	Kunst, unpublished
Traismauer	Roman	vicus	12607	162	1,3	15	0,1	13	8,0	Riedel 1993
Virunum	Roman	urban/theatre	3461	255	7,4	89	1,5	48	18,8	Galik 2004
Hemmaberg	Late Roman	sanctuary	7734	202	2,6	10	0,1	10	5,0	Gaggl 1996
Perchtoldsdorf	Late Roman	rural	150	14	9,3	6	4,0	1	7,1	Kunst 2005
Sand	Early Medieval	hilltop	3137	1293	41,2	16	0,2	16	1,2	Pucher & Schmitzberger 1999
Thunau	Early Medieval	hilltop	2672	330	12,4	23	0,9	23	7,0	Kanelutti 1990, 1993

Fig. 2: Austrian archaeological sites with >5 brown bear remains (NISP); n corr.: reduced number for samples with articulated units; Middle Neolithic c. 4700-4000 BC; Late Neolithic c. 4000-2000 BC; Bronze Age 2000-750 BC; Early Roman (here) c. 50 BC – 70 AD; Roman 15 BC – 476 AD; Late Roman 378-476 AD; Early Medieval (here) c. 600-1000 AD.

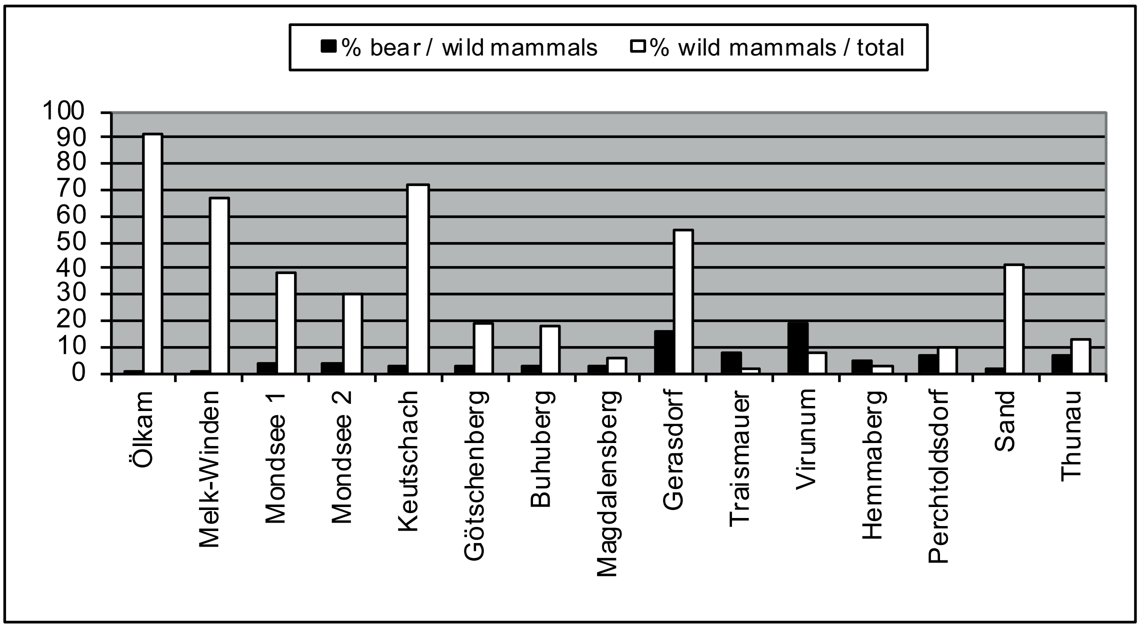

Fig. 3: percentages of bears/wild mammals and of wild mammals/total mammals for sites mentioned in Fig. 2.

Although this may be partly linked to the fact that these two periods have received most scholarly attention and often yield large samples, this abundance evidently reflects human behaviour as well. In the case of the Roman material, the large number may also be attributed to the occurrence of articulated units and the bear assemblages exhibit more signs of patterning as well (Fig. 5). A third, smaller, 'peak' in sample sizes can be found for the two Early Medieval hilltop settlements.

The total number of bear remains used for this study, either from the literature or inspected individually, amounted to a reduced (taking account of the articulated bones) NISP of 425 from the collections, including smaller samples which contained less than five bear bones. Compared with the main domesticates and other wild mammals, such as hare and red deer, the brown bear can be regarded as a rare, but consistently appearing element of faunal materials from Austria. At two sites, Perchtoldsdorf-Aspetten (Middle Neolithic) and Prellenkirchen (La-Tène), human engagements with the remains of brown bear is evidenced through the recovery of a bone tool and an ornamental worked claw bone, respectively (Kunst, 2005, Karwowski, 2010). The faunal record for the Mesolithic is, in contrast, rather poorly known in Austria, and no comparisons regarding the importance of the brown bear in pre-agricultural societies can therefore be drawn.

Bone samples and the human-bear relationship

The primary question for this study can be defined as follows: what can a 'rare' species tell us about human-animal interactions from an archaeozoological viewpoint? Studies of large bone assemblages are the most revealing in this respect. For instance, in the Germanic settlement of Bernhardsthal (c. second and third centuries AD; Riedel, 1996), two bear bones, a fragmented radius and an ulna, were recovered and these two specimens make up c. 0.01% of the whole sample, which numbered nearly 8000 identified remains. These bear fragments exhibit some taphonomical modifications, such as abrasion and carnivore damage, and contribute little historical information other than extending the species list. Their very occurrence may simply be a 'side-effect' of the overall large faunal assemblage from this locality. At the other extreme, the 47 brown bear specimens from the excavations of the Late Neolithic site of Mondsee (Pucher & Engl, 1997), which included some complete long bones, has been most informative, revealing data on age and skeletal part distribution, osteometrics, and bone modifications (Fig. 4). Some clues regarding human consumption and disposal behaviour regarding this species could therefore be obtained. In some cases, however, a small number of specimens provided certain insights as well. Examples include the partly connected, heavily butchered elements of a forelimb from Perchtoldsdorf-Aspetten (Kunst, 2005) and several instances where bear remains appear as grave-goods or artefacts (see according chapters below).

When examining the literature and some of the material, the criteria listed below appeared to be most relevant in characterizing the bear bone samples. In general, they did not differ from ordinary procedures in faunal analysis, but some were particularly useful for the present study (Fig. 6), while others played only a minor role. For example, metric variation was found to be great, even within the same materials (e.g. Mondsee and Magdalensberg; Hornberger, 1970, cf. Pucher & Engl, 1997, Wolff, 1977). This feature is common in bears but was not thought to be important for the present investigation regarding human-bear interaction.

Fig. 4: overview of the brown bear remains from the Neolithic lakeside dwelling Mondsee, recent excavations (Natural History Museum Vienna, Archaeozoological Collection).

Absolute and relative frequency

It must be kept in mind that the different assemblages are not comparable in terms of the excavation and recovery techniques and overall numbers. However, what is noteworthy is the frequency of other wild mammals within the assemblages, especially the occurrence of other large carnivores (e.g. wolf and lynx).

Age structure

Occurrences of juvenile (infant) and sub-adult individuals were noted. As the brown bear reaches full skeletal maturity at a comparatively late age, bones with incompletely fused epiphyses are frequent.

1. **Skeletal part distribution**

Any over-representation of certain body parts or elements may provide clues regarding human interactions with the carcass. If three bones out of a sample of eight are claws, this is not a major trend in a statistical sense, but it is nevertheless an important observation.

2. **Articulated units or bones from the same individual**

In rare species, it is easier to check an assemblage for articulating bones, an occlusal fit of tooth rows or matching pairs of symmetric elements; sometimes, articulated units are in fact reported by the excavator.

3. **Butchery marks**

Cut and chop marks provide immediate evidence of carcass treatment. In many situations, particular types of procedure (e.g. skinning and dismemberment) can be reconstructed.

4. **Special modifications**

Bones may display anthropogenic manipulation other than that related to butchering, such as manipulation into artefacts, unfinished objects and any bones exhibiting wear or polish. Within this group of criteria, two aspects deserve particular attention in the case of bears: the presence of claw bones or other elements with traces of heat influence; and the use of canine teeth, including their possible intentional extraction from the skull and mandible.

5. **Pathological conditions**

Pathological conditions, such as exostoses or dental diseases, were worth noting.

Faunal samples with bear remains

The following overview of Austrian faunal assemblages containing brown bear remains, grouped by archaeological periods, is certainly incomplete, but contains all the published and unpublished post-Mesolithic occurrences of *Ursus arctos* within archaeological contexts known to the authors. The abbreviations ‘LA’ and ‘UA’ stand for Lower Austria and Upper Austria respectively.

The Neolithic

Bear remains were present in the settlement debris from the Early Neolithic site of Franzhausen (LA; Lenneis, 1995). In this period, wild species are often poorly represented in archaeological assemblages. For the Middle Neolithic (the ‘Lengyel Culture’), the single-context site at Melk-Winden (LA; Pucher, 2004) and the circular ditch at Ölkam (UA; Schmitzberger, 2001) produced a few specimens. The species is also represented in a similar ditch context at Perchtoldsdorf (LA; Kunst, 2005). As already mentioned, important materials have been collected from Late Neolithic lakeside dwellings, now all submerged, particularly from a number of sites at Mondsee (UA; Pucher & Engl, 1997; Wolff, 1977) and from Lake Keutschach (Carinthia; Pucher, 2003). From the contemporaneous hilltop settlements at Götschenberg (Salzburg; Peters, 1992) and Ertl (Schweighofer Mauer, LA; Maurer, 2011, 2014), there were seven bear bones and two worked bear teeth, respectively.

The Bronze Age

There are no large samples of brown bear from this period in the study area. Hence, the Early Bronze Age settlement at Buhuberg (LA; Pucher, 1996), which produced eight bones, may be regarded as an important site in this respect. The Early Bronze Age site Unterhautzenthal (LA; Pucher, 2001), and the two Late Bronze Age (Urnfield period) fortified settlements, Thunau (LA; Kanelutti, 1993) and Stillfried (LA; Pucher, 1982), yielded less than five bear bones per site. Regarding the inner Alpine area, the recently published Middle Bronze Age site of Saalfelden-Katzentauern (Salzburg; Pucher, 2019; not indicated in the map), which produced a single bear remain, has to be added.

The Iron Age

In this period, *Ursus* is also only occasionally present in archaeological assemblages. The species occurred in small number at the Hallstatt period hilltop settlements of Gurina and Gracarca (both Carinthia; Galik, 1998), Burgstallkogel (Styria; Peters & Smolnik 1994) and Leopoldsberg (Vienna; Kunst, unpublished), at the Celtic salt miners' occupation site of Dürrnberg (Salzburg; Pucher, 1999; Schmitzberger, 2012) and at the lowland late Hallstatt period settlement of Perchtoldsdorf (LA; Talaa, 1993, Christandl, 1998). Another lowland, but La-Tène period site, Prellenkirchen, produced a single worked clawbone (LA; Karwowski, 2010). The apparent absence of the species from other Iron Age lowland settlements of the area (LA: Göttlesbrunn, Roseldorf) is otherwise remarkable. A concentration of burnt bear bones from the Hallstatt period cremation cemetery Führholz (Carinthia) contained two middle phalanges (Kanelutti in Renhart, 1990).

The Roman period

Regarding context types and configuration of the skeletal assemblages, this period is the most diverse of all; it also includes the greatest number of sites with bear remains. Bernhardsthal, the only site outside the Roman Empire, and north of the Danube, has been described above. From the Early Roman period, the small bone assemblage from the rural context of Gerasdorf/Steinfeld (LA; Kunst, unpublished) and the Late La-Tène/Roman town on the Magdalensberg (Carinthia; Ehret, 1964, Hornberger, 1970), were both rich in bear remains, but represent very different archaeological situations. Parts of the latter site were excavated in the middle of the twentieth century, and Ehret (1964) mentions the possible occurrence of infantile bear bones within a ritual context, being deposited inside an urn. Later, more 'typical', Roman sites contained large bone collections, such as the *vicus* of Traismauer/Augustiana (LA; Riedel, 1993), which produced 15 bear remains, with some deriving from the same individuals.

The species was also present at other sites along the Danubian Limes, such as at the civilian settlements of Mautern/Favianis (LA; Kunst, 2006), Pöchlarn/Arelape (LA; Hofer, pers. comm.) and Lorch/Lauriacum (UA; Müller, 1967, Böhm, pers. comm.). In the town of Carnuntum, ten, possibly connected, remains were recovered from rubble layers underlying a street pavement.

Fig. 5: overview of the brown bear remains from the Roman vicus of Traismauer
(Natural History Museum Vienna, Archaeozoological Collection).

The only well stratified item, a metapodial bone, is from a restoration layer dating to the second century AD (Radbauer & Humer, 2004). More recently, bear remains were identified from further contexts of the civil town of Carnuntum (baths, house II: Kirchengast, pers. comm.), and from a pit within the sanctuary of Jupiter Heliopolitanus (Gál, pers. comm.). The most peculiar

Roman period bear assemblages, however, were collected from debris in the area of the amphitheatre of Virunum (Carinthia; Galik, 2004, Gostenčnik, 2008). It comprises more than 50 specimens, mainly attributable to articulated units or residual skeletons. Elements of an articulated unit were also found within a Late Roman settlement structure from Perchtoldsdorf (LA; Kunst, 2005), and a first century AD pit from an earlier phase of the same settlement produced a single bone. Another Late Roman site, the Early Christian sanctuary Hemmaberg (Carinthia; Gaggl, 1996), yielded a moderate number of bear remains. A bear skull was reported from layers dating to the second - third century AD from the Roman town of Aguntum (East Tyrol). It was interpreted as a sacrifice or an apotropaic device by the excavator (Kofler, 1979).

Although the number of Roman sites studied archaeozoologically in Austria is far smaller than in neighbouring Switzerland, and the state of research is, therefore, not strictly comparable, the percentage of Roman sites with bear remains appears higher in Austria. In Switzerland, less than 5% of all bone assemblages from this period yielded bear bones (SCHIBLER et al., 2002).

site	skeletal parts overrepresented	articulated units	mark types	tools	burnt claws	pathologies	juveniles & subadults	other Carnivores		
								wolf	lynx	n other species
Ölkam	balanced, few autopodials		?	+				+		3
Melk-Winden	long bones		?cut				+		+	4
Mondsee 1	isolated teeth, front leg, autopodium		perforation, cut	+	+	+	+	+	+	6
Mondsee 2	balanced; limbs		?	+	+		+		+	5
Keutschach	limbs	+	cut, ?chop	?					+	4
Götschenberg										
Buhuberg	autopodium, clawbone		cut, polish	?	+			+	+	
Magdalensberg			?				+			5
Gerasdorf	forelimb		cut				+			
Traismauer	skull, mandible	+	cut			+	+	+		1
Virunum	balanced?	+	cut, chop			+	?	?		1
Carnuntum	balanced	+	chop				+			
Hemmaberg	balanced		many; type?				+			
Perchtoldsdorf	hindlimb	+	cut, chop							1
Sand	balanced		cut, chop	?	+					4
Thunau	skull; balanced		cut, chop, sawn	+		+	+	+		

Fig. 6: archaeological sites with >5 brown bear remains, showing additional features of bear remains and associated carnivore species.

Medieval

The only noteworthy medieval assemblages are from two similar sites from the same area in northern Austria. One is the Early Medieval hilltop settlements of Thunau (LA; KANELUTTI, 1993) and the other is the settlement Sand/Oberpfaffendorf (LA; PUCHER & SCHMITZBERGER, 1999). The sites were regional centres and both were destroyed in the tenth century AD. The High and Late Medieval records are surprisingly poor in bear remains. Thurnschall Castle (Salzburg; ZOHMANN, 2005), Villach (Carinthia; GALIK, pers. comm.) and a motte-and-bailey at Gaiselberg (LA; SPITZENBERGER, 1983) are the only sites which have produced brown bear bone specimens. This may reflect local extinctions of the species, as well as other issues, which led to a decline in brown bear populations in this period. It must be stated, however, that these later periods, as well as the post-Medieval period, are insufficiently studied.

The characteristics of the different assemblages will now be discussed in terms of the criteria outlined above (Fig. 6). It will become evident that some of the criteria work only on the scale of large assem blages, and are not always applicable to small samples, where they may nevertheless exhibit some kind of patterning.

Absolute and relative frequency of material

In Figure 2, the absolute and relative specimen counts are given for assemblages with at least five bear remains. Carnuntum had to be omitted because overall faunal data were lacking and the Mondsee material was divided into old (Mondsee 1; Wolff, 1977) and new (Mondsee 2; Pucher & Engl, 1997) elements. For Virunum, Traismauer and Perchtoldsdorf, the presence of articulated units was demonstrated and a reduced specimen number was used for further calculations, counting associated units as single specimens. Again, it must be remembered that the materials from the various sites differ markedly, not only in terms of overall numbers, but also in terms of archaeological context. For example, some sites are represented by a single context only (e.g. Melk-Winden, Gerasdorf) while others contain a complex stratigraphy, and some of the assemblages (e.g. from Magdalensberg) were collected over the course of many years of excavation. The percentage of bear remains varies from between 0.1% and 8.5% of the total mammal material and between 0.3% and 18.8% of the wild mammals (the maximum values were displayed in the samples from Gerasdorf and Virunum, respectively). The correlation between overall wild mammal percentages and the role of bears among the wild species is shown in Figure 3. Generally, Central European sites with important relative amounts of wild species are confined to older prehistory, especially to certain Neolithic periods or cultures (Pucher, 2004, Benecke, 1994), although it is difficult to recognize a uniform trend. Furthermore, the trends shown in Figures 2 and 3 may be somewhat biased, as only bone assemblages containing bear remains were included in this study. Regarding more recent periods, Gerasdorf is a small sample from the first century AD and probably contains specialized hunter's refuse, and Sand has been defined as a high-status site with a rather diverse wild fauna assemblage (Pucher & Schmitzberger, 1999, Saliari & Felgenhauer-Schmiedt, 2017). It appears that high bear frequencies among wild species are not linked to high values for game in general (Fig. 3), as Ölkam and Melk-Winden produced particularly low values for bears. In Neolithic and Bronze Age assemblages, the maximum values for bears among the wild species were slightly higher than 3% (Mondsee 1), being somewhat lower in four other sites. It is only in the Roman and Early Medieval periods that higher percentages are reached. Among the richer materials (excluding Gerasdorf and Perchtoldsdorf), Virunum produced the highest figures (18.8%), followed by Traismauer, Thunau and Hemmaberg (8-5%). Magdalensberg displayed equally low figures for both wild species and bears. Ironically, the game-rich assemblage from Sand produced the lowest percentage of bear remains out of all the early historic sites considered. As for its prehistoric counterparts (Ölkam, Melk-Winden and Keutschach), this pattern was caused by the high amount of artiodactyls, mainly red deer, remains. In Sand, there was also a large percentage of European bison. It therefore appears that societies relying to a greater extent on wild animals, or engaging in prestige hunting, accumulate greater amounts of wild herbivore bones in their domestic refuse, causing low values of rarer elements, such as bears. On the other hand, the hunting of wild artiodactyls plays a less important role in most of the Roman sites and in Thunau, allowing bears, possibly also acquired for other reasons, to reach higher relative percentages. Bear or bear products may have been held in higher esteem in these latter sites for various reasons. Possible explanations include bears being held as captive animals (Virunum, Thunau) or being consumed in greater quantities due to a preference for bear hide and meat (Traismauer, Perchtoldsdorf). For example, in Thunau, the remains of three individuals were found within one single context (KANELUTTI, 1990), and two incomplete skeletons were associated in Virunum (GOSTENČNIK, 2008). In most of the prehistoric assemblages, the bear bones were accompanied by the remains of wolf or lynx, or both of these species, often occurring together with smaller carnivores (e.g. red fox, wild cat and various mustelids). There is far less regularity concerning the simultaneous appearance of these species in the Early Historic sites, again pointing towards a more specific role of the bear in these later periods.

Age distribution

Given the rather long adolescence in bears, sub-adult bone specimens with unfused epiphyses are a common feature in most of the richer assemblages (Fig. 6), with Keutschach and Sand being the only possible exceptions. The presence of actual bear cubs or of individuals in their first year, however, is only mentioned for Magdalensberg (EHRET, 1964, HORNBERGER, 1970), Virunum (GOSTENČNIK, 2008) and Early Medieval Thunau (KANELUTTI, 1990). According to WOLFF (1977), ‘young’ animals account for one-fourth of the total sample from Mondsee.

Skeletal part representation

The prehistoric period

Among the large prehistoric assemblages assessed by the authors, the sample from the Late Neolithic site of Mondsee, stored at the Natural History Museum (PUCHER & ENGL, 1997), appears to be relatively balanced, in that all body parts are represented, although a prevalence of long bones is indicated. The relative scarcity of vertebrae and ribs is possibly explained as a result of taphonomical loss; a common feature in many archaeological bone samples. In comparison with other sites, head elements appear slightly underrepresented. Judging from the literature, the opposite is true for the material from the older excavations, where isolated teeth account for almost half of the 106 remains (WOLFF, 1977). However, long bones, mainly from the front leg, and distal limb parts, figure prominently as well. The sample from the other lakeside dwelling, Keutschach, very much resembles Mondsee in its state of preservation, but is almost entirely built up of greater parts of long bones and metapodials. The material from Ölkam comprises skull and axial elements and long bones, but is almost devoid of autopodial elements. Among the smaller prehistoric samples, some patterning is recognizable in the Middle Neolithic assemblage from Melk-Winden, where there is a prevalence of proximal, potentially meat-bearing, leg parts, and also in the Bronze Age assemblage from Buhuberg, where autopodial elements, especially clawbones (three out of a total of eight bones) prevail. In Götschenberg, more than half of the remains are from the distal limbs. There is a marked difference in average fragment size between the 'protective' lake sediments, where even complete long bones occur, and settlement sites, where the influence of taphonomic processes is more strongly felt.

The Roman period

Judging from the literature (Ehret, 1964, Hornberger, 1970), the material from the Iron Age/Early Roman site of Magdalensberg appears to be relatively balanced, although there is some emphasis on the head parts and the forelimb, and the vertebral column is entirely absent from the assemblage. In Traismauer (Fig. 5), skull and mandible fragments dominate the assemblage; the remaining bones consist of proximal and distal limb elements. Some elements are connected, consisting of articulated units, and this phenomenon is discussed further below along with the remains from Virunum, Perchtoldsdorf and Carnuntum. For the remaining Roman samples, a trend can be observed in Gerasdorf, where five out of the seven bear remains consist of long bone fragments from the (lower) forelimb. It must be remembered, however, that in ursids, certain long bone shafts, such as the radius and ulna, are still well recognizable when in a broken condition, more so than other elements or in other species, and this may explain the good representation of these skeletal parts within several samples.

The Medieval period

The Early Medieval assemblage from Sand comprises, apart from a rib fragment, mandibles and isolated teeth, meat-bearing limb bones, and autopodials in almost equal portions. Whereas the autopodials (three consist of phalanges) are complete, the other remains are fragmented or butchered. A very similar distribution of body regions was observed in the assemblage from Thunau, although in this instance, there were also largely complete skull parts (Kanelutti, 1993, Böhm & Kunst, 2007) and the axial skeleton was not recorded. The Late Medieval sample from Gaiselberg is unique as it only comprises three rib fragments.

Articulated anatomical units and bones from the same individual

It seems likely that some metacarpals from Keutschach belong to the same paw, indicating little skeletal dispersal after disposal. Articulated bone groups are more frequent in the Roman materials, and examples of anatomical units exist in the assemblages from Virunum, Traismauer, Perchtoldsdorf and probably also from Carnuntum. Galik (2004) describes three different sets of articulated elements in the Virunum assemblage. These were documented by the excavators and comprise the following sets: one cervical and thoracic vertebral column with an associated pair of mandibles; one partial cervical column and the residual of a skeleton made up of ribs; one humerus and the pelvis. A similar situation was found in the backfill of a water supply system beneath a city street in Carnuntum, although this unit exhibits some traces of butchering. Eleven bones (vertebrae, ribs, a near-complete scapula, femur with proximal epiphysis, various autopodial elements) were found associated within the same structure. These bones presumably belong to a single sub-adult individual, being compatible in size and ontogenetic developmental stage and forming the only bear remains within this excavation trench. A similar interpretation may be offered for a set of six, partially butchered, elements from a left hindlimb (femur, two tarsals, two metatarsals, proximal phalanx) which were recovered within a Late Roman pit from Perchtoldsdorf (Kunst, 2005). In this instance, direct re-articulation was possible among some of the autopodial elements. In the vicus of Traismauer, a maxilla fragment and a pair of mandibles with most of the dentition in place could be reassembled (Fig. 7). A special case of refitting was reported from the Neolithic site of Ölkam (Schmitzberger, 2001). Here, two fragments of the same bear humerus were found to be matching, and these parts were deposited in the concentric inner and outer circular ditches of the system, possibly demonstrating the contemporaneity of the ditch fills. Bears are not represented among the spectacular Late Bronze Age depositions of wild mammals at Stillfried, which mainly comprise skeletons of red deer and wolf (e.g. Pucher, 2017).

Anthropogenic marks and human activities

Anthropogenic bone modifications may be considered as primary evidence of carcass treatment. Marks concerning the processing of carcasses, as well as the production of tools and other artefacts, are discussed in this chapter. According to an analysis of the literature and to the personal experience of the authors, the presence of human marks on bear bones appears to be a widespread phenomenon. Even in small sample sets, bone modifications can usually be observed (e.g. Gulde, 1985, Zeiler, 1997). Therefore, for the present study, a considerable amount of data, not necessarily mentioned in detail in the respective reports, could be collected from the accessible samples. Some of these marks may be partly caused by certain constraints imposed by the anatomy of a bear carcass. Firstly, in comparison with most similar-sized ungulates, the muscle mass is more evenly distributed along the extremities and hence bone modifications should be expected equally on all limb bones. Secondly, some body parts, such as claws, hide, and teeth are often held in high esteem, and their removal and processing is frequently accompanied by specific marks. Even without experimental testing, the characters of the cut and chop marks are usually self-explanatory and interpreted as evidence for particular activities, such as disarticulation, filetting or skinning.

The prehistoric period: marks related to carcass treatment

Among the Neolithic and Bronze Age materials, the remains from the lakeside dwellings at Mondsee 2 (Pucher & Engl, 1997) and Keutschach (Pucher, 2003) were analysed and the study proved very revealing; Mondsee 2 yielded 15 modified specimens (32% of the bear sample) and Keutschach yielded 7 (50% of the bear sample). The modifications found were, almost exclusively, cut marks inflicted with stone tools. Usually, the cut marks occurred as dense groups of short parallel grooves (Fig. 8), but cut marks were also sometimes loosely scattered across the bone surfaces. At Mondsee, such marks were found on the zygomatic arch of a skull fragment, laterally on a mandible corpus, on the cranial articular area of a lumbar vertebra and on the corpora of two ribs. All other modified elements were limb bones (scapula, two ulnae, three radii, tibia, two metapodials and a proximal phalanx). These marks imply a range of activities, but most appear to be related to butchery (e.g. disarticulation and filetting). The potential skinning marks appear on the skull, mandible, phalanx and possibly on the metapodials, but these latter modifications are mostly on the proximal parts and point, instead, at a dissection of the hand and feet for culinary purposes. On a distal juvenile tibia and a complete adult radius, three and four discrete clusters of cut marks were observed, indicating intense butchering activities at these spots (Fig. 9). In the case of the radius, the modifications left the bones relatively intact and the marks were located close to the proximal articulation (Fig. 8) or coincided with areas possessing muscle attachments, as indicated by Davis (1964) for *Ailuropoda*.

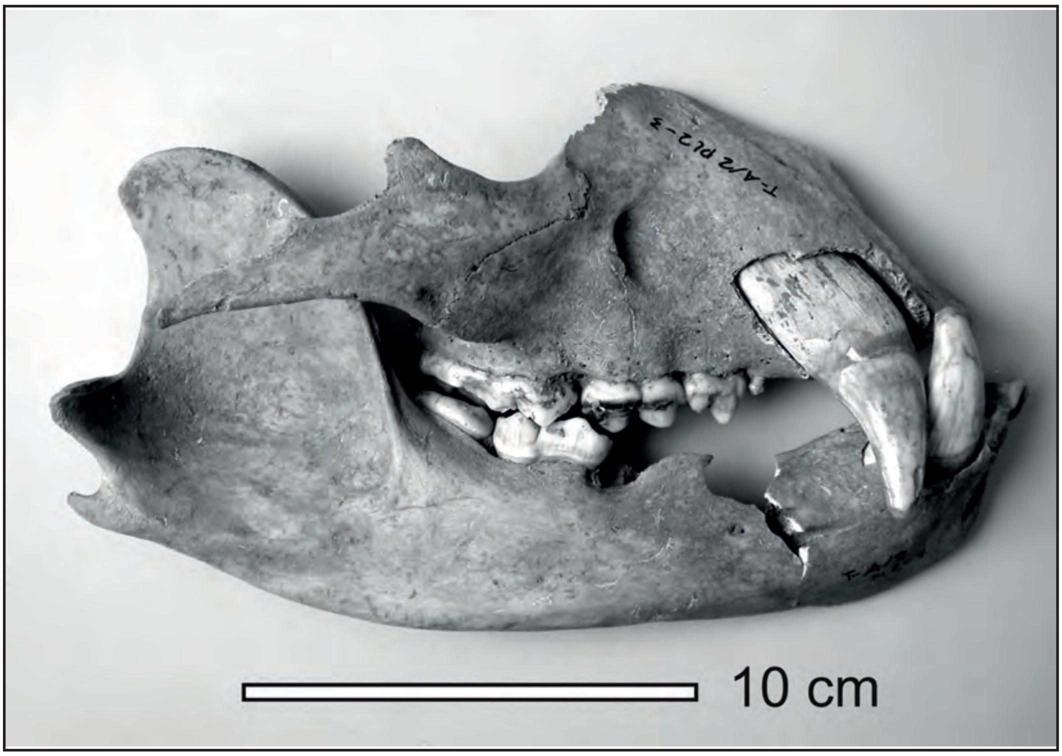

Fig. 7: re-assembled skull and mandible of brown bear from the Roman vicus of Traismauer (Natural History Museum Vienna, Archaeozoological Collection).

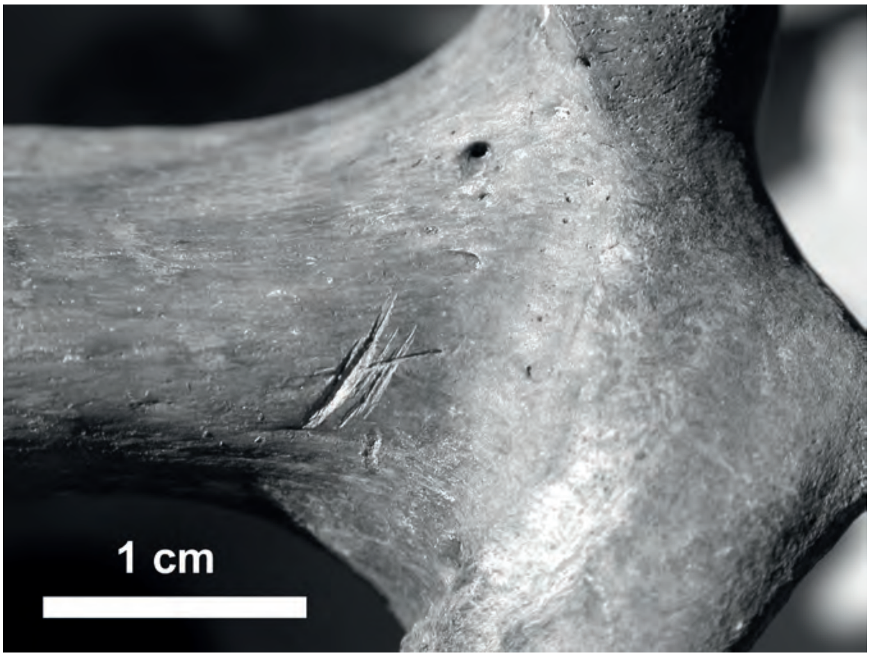

Fig. 8: tightly clustered group of cut marks on a right radius of brown bear from Mondsee, medio-proximal end (Inv.Nr. MS 29/J, Natural History Museum Vienna, Archaeozoological Collection).

There was one more complete radius and one radius diaphysis with cut marks from Mondsee, and another complete specimen with two sets of traces from Keutschach.

Jéquier (1963), Wolff (1977) and Pucher & Engl (1997) have observed that bear bones from lakeside dwellings are generally less fragmented than bones from large artiodactyls (see also Fig. 4). If the bones were incorporated within consumption activities, it is possible that bear long bones were not fractured for marrow, as allegedly these bones contain limited quantities of bone marrow which are difficult to access (Jéquier, 1963). It is also tempting to argue that bear bones were left intact deliberately, possibly due to some cosmological scheme, as this behaviour has been observed in recent Siberian hunter-gatherer groups (e.g. Jordan, 2003). Whatever the reason, the fact that long bones may survive intact seems the most noteworthy observation regarding the processing of bear bones at the lakeside dwellings of Mondsee and Keutschach. The pattern of cut marks found in Keutschach strongly follows the situation in Mondsee, although at the former site there is one modification on a pelvic bone which resembles a chop mark. Because of the skeletal part representation, the locations of the marks are completely restricted to the articular areas and shafts of long bones and also to distal metacarpals, indicating butchering and possibly skinning.

Modification patterns are not so clear in the remaining early prehistoric samples, and only shallow striations were observed on some of the bones from the Middle Neolithic site at Melk-Winden and the Early Bronze Age site at Buhuberg. It is only in the Late Bronze Age that unequivocal cut marks become apparent once again, such as on the material from Stillfried.

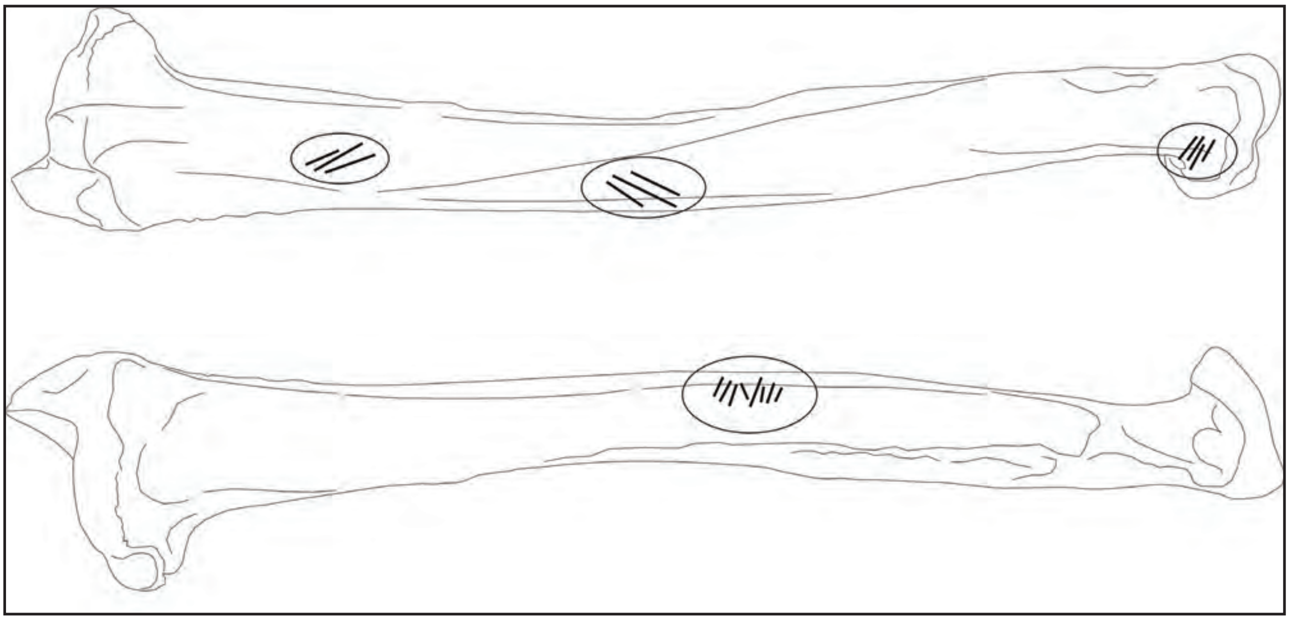

Fig. 9: distribution of cut marks on a right radius of a brown bear from Mondsee: top; dorsal view, bottom; palmar view (Inv.Nr. MS 29/J, Natural History Museum Vienna, Archaeozoological Collection).

In this case, the marks were clearly inflicted by metal, i.e. bronze, blades. A sequence of fine cut marks was observed on the body of a rib and proximally on an ulna, the diaphysis of which was chopped through distally. These marks represent the earliest observation of two-step butchering, involving different types of action and, possibly, tools, on a single bear bone.

The Roman period: marks related to carcass treatment

Anthropogenic modifications were present in all Roman materials analysed in this study and, with the exception of Magdalensberg, observations of cut marks are frequently reported in the publications. In Traismauer, 9 out of 15 remains show traces in the form of knife cuts. For the skulls and mandibles, fine and short cut marks were found on the zygomatic arch, and, in particular, in the snout area of both the upper and lower jaws. Such marks were exhibited on all three elements of the re-articulated, young adult skull fragment described above, comprising the right maxilla and mandibles. Another maxilla possessed a set of long cut lines which ran parallel to the border of the maxillary and the nasal bone. It therefore appears that the patterns on the skulls and mandibles indicate a skinning procedure carried out by a skilled butcher. Taking into account the fineness of the lines, which were often almost invisible to the naked eye, it would appear that people engaging in skinning activities at this time were eager to avoid any unnecessary contact between the knife and the bone, possibly to avoid dulling the blade. Given the rostral position of the cuts in the first individual, it appears that a major aim was to remove the skin as complete as possible. There are no signs of deliberate dissection of skulls and mandibles from one another and most teeth were left in place.

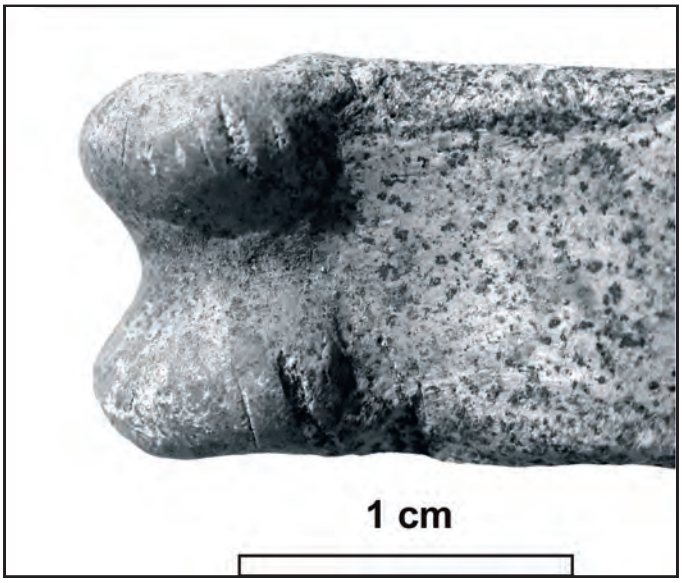

Fig. 10: proximal phalanx of brown bear, distal part in plantar view, with cut marks on distal articulation; Roman vicus of Traismauer (Natural History Museum Vienna, Archaeozoological Collection).

Fig. 11: left femur of brown bear, proximal view, chop marks on femoral neck (left) and greater trochanter (right); Perchtoldsdorf-Aspetten, Late Roman period. Scale in cm

A dense cluster of transversally running cut marks on the palmar/plantar side of a distal articulation of a proximal phalanx points at the disarticulation of the proximal interphalangeal joint, also produced during the skinning process (Fig. 10). The other marks observed in the sample from Traismauer appear more related to butchering, e.g. to the severing of the scapula from the rib cage, and to the filetting of meat along the femoral shaft area. It would appear that knives were the only tools employed in the processing of bear carcasses at Traismauer. A similar pattern is evident at the first century AD site at Gerasdorf, where a cut mark on a radius was the only one observed in the collection. The range of marks and their locations found among the red deer bones from the same site, including both cut and chop marks, suggest a versatile attitude to the processing of the carcasses of other wild mammals.

Two different types of cut marks could be discerned on two preserved elements of a left hindlimb from the Late Roman site at Perchtoldsdorf. On the proximal femur, the greater trochanter and caput were severed from the rest of the bone by several heavy blows (Fig. 11), indicating dismemberment. The implement involved was probably a chopping tool with a heavy blade, an instrument which was commonly used in Roman butchery. Moving to the distal elements of the limb, on the proximal phalanx of the first digit, there are very fine, parallel cut marks running diagonally on the plantar side and on the distal articulation. They are probably related to either skinning or slicing flesh off the paw area by using a knife. These two sets of marks, generated in the course of processing a single carcass, were interpreted as elements of an operational sequence (chaîne opératoire; Kunst, 2005). This type of two-step butchering, involving two different types of tools, is common in Roman butchery, particularly of larger domestic species, such as cattle.

The associated bear bones from the Carnuntum sewer, which included an almost complete scapula, are devoid of modifications except for one femur fragment. This latter piece received several chop marks on its diaphysis, which would eventually lead to its breakage at midshaft. This pattern is not easily explained, apparently most of the bones of this putative skeleton have been lost.

Galik (2004) reports that many bear bones from Virunum exhibit chop and cut marks which indicate systematized disarticulation and the consumption of bear meat. At Hemmaberg, 6 out of 10 remains displayed signs of butchering (Gaggl, 1996).

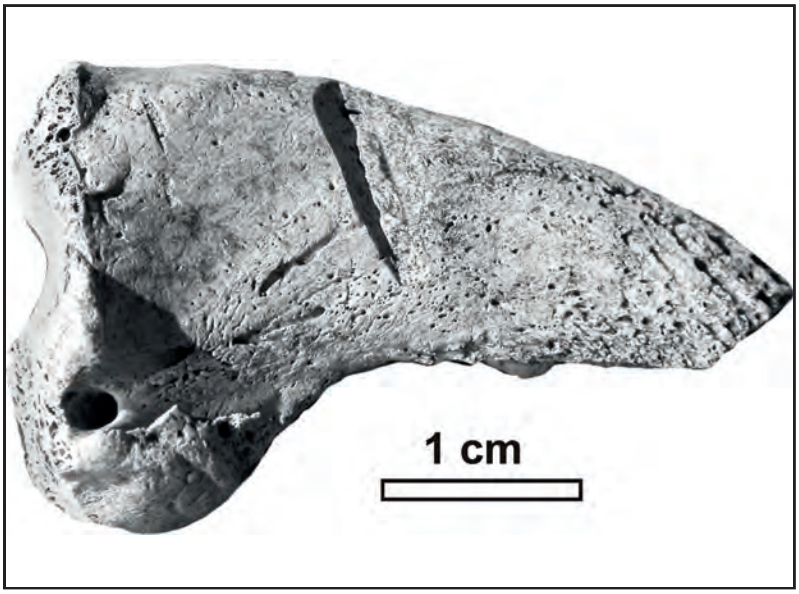

Fig. 12: distal phalanx (claw bone) of brown bear with chop marks; Sand/Oberpfaffendorf, Early Medieval (Natural History Museum Vienna, Archaeozoological Collection).

Therefore, in Roman bear processing, three combinations of butchering marks can be observed: cut marks; chop marks (e.g. Carnuntum); and a combination of these two categories. It must be noted that the presence of certain marks is doubtlessly also related to skeletal part representation. In most cases, the processing of a bear carcass may have been an exceptional event, thus lacking a defined ‘butchering tradition’ as, e.g. in cattle.

The Medieval period: marks related to carcass treatment

The two Early Medieval hilltop settlements Sand and Thunau provide a wide array of anthropogenic marks allowing for a range of processes to be reconstructed. In Sand, half of the remains are modified, mostly by cut marks. The modified bones are all from the limbs, comprising both proximal and distal elements and indicating different human actions. Knife cuts suggest the severance of articular areas and bones from one another (scapula from thorax, elbow joint). Once again, the presence of very fine and short knife cuts in the autopodial area (corpus of metacarpal, os pisiforme) cannot be interpreted easily, although it may be related to the skinning or butchering of the paws. One of the claw bones displayed a deep cut or chop mark which may possibly result from this practice (Fig. 12).

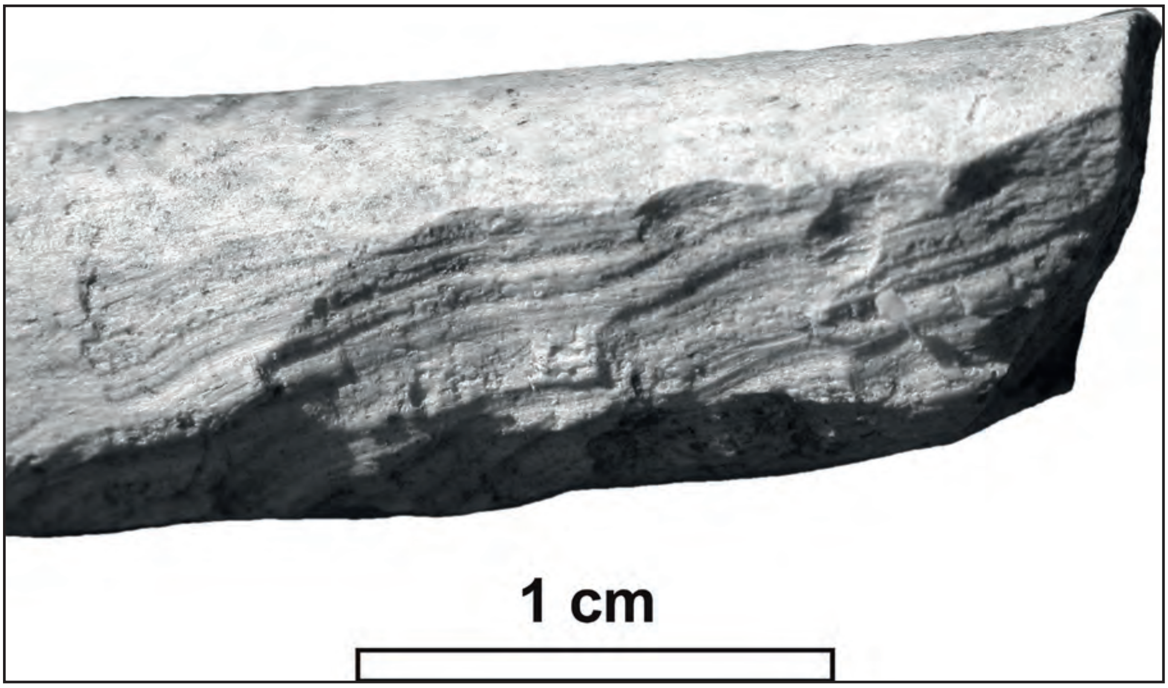

Fig.:13: distal fragment of an ulna of brown bear, proximal end, fracture edge reworked with metal blade; Sand/Oberpfaffendorf, Early Medieval (Natural History Museum Vienna, Archaeozoological Collection).

Scar-lines also indicate that swing percussion was applied from the side, with the obvious intention of removing the claw from the rest of the paw. On the same claw bone and on a second, burnt, specimen, additional cut marks in the articulation area can be discerned. These examples demonstrate that paw elements were sometimes dissected from the rest of the skeleton.

The most peculiar example, however, is represented by an ulna from Sand, comprising about the distal two-thirds of the shaft (Fig. 13). Fine transversal knife cuts on the medial side, close to the distal end of the diaphysis, may be related to skinning, or to the severing of muscle attachments, on the palmar side of the carpal joint. Major parts of the fractured edges delimiting the fragment proximally, however, have been purposefully reworked by a series of blows generated by a metal blade.

These chop marks, characterised by internal striations produced by nicks in the blade, were directed in a distal-proximal direction. As the existing edges of the distal ulna had already been reshaped, it is difficult to identify a possible reason for this activity. Moreover, this body part does not appear to be well suited for being worked into a tool, and there are no traces of use-wear. It is possible that the whole, skeletonised or dried distal segment of the forelimb served some unknown symbolic purpose, for example as a trophy. Kanelutti (1990, 1993) also reports a special treatment of certain bones from Thunau. The upper part of one skull and the ascending ramus of one mandible were sawn or chopped off, possibly for decorative reasons. These examples may, in a way, be regarded as borderline examples of bone artefacts. There are, however, many more traces among the Thunau material, mostly comprising cut marks on skulls, mandibles and limb bones that are clearly related to skinning and butchery. In one instance, a skull was separated from the cervical column by a series of oblique blows, aimed at the occipital and directed from the basal side (Kanelutti, 1990).

Marks related to symbolic, ornamental and artefactual use of skeletal parts

As noted above, it is not always easy to draw a clear distinction between marks related to definite butchery and carcass treatment, and more special manipulations where certain elements are formed into objects. There are, nevertheless, clear examples of parts of the bear skeleton being utilised as ornaments, or worked into decorative pieces or bone tools. Such objects are often associated with unworked bear remains within the same sites (e.g. Mondsee and Thunau). There are, however, some samples which are devoid of worked specimens (e.g. Traismauer) or contain only indirect evidence for such activities (e.g. Virunum), as well as two prehistoric sites where the bear is only represented by artefacts (e.g. Perchtoldsdorf-Aspetten and Prellenkirchen).

Generally speaking, there are two skeletal elements that are more likely to be selected for manipulation into valued objects: teeth, especially canines, and the claw bones or claws (distal phalanges). Modified objects, and marks related to the extraction of these elements from the rest of the carcass, also appear in the archaeological record. In certain periods and regions, such as the Iron Age of northern France, the brown bear is only represented through canine pendants and burnt claw bones from burial contexts; this species is alternatively completely absent in occupation deposits at settlements (Méniel, 2001). The following discussion will consider the individual types of bone modification present in our data sets.

Canines and other teeth

Bear canines have been worked into pendants or other decorative objects from the Palaeolithic period onwards (see Pacher, 2005 for a recent overview). Normally, canine pendants are easily recognized by the excavators and do not find their way into faunal assemblages investigated by archaeozoologists. Among the literature studied, there appears to be only one exception from Mondsee (Wolff, 1977). An overview of their chronological and geographical distribution is, therefore, beyond the scope of this paper. Within the collection analysed at the University of Vienna (Department of Prehistory and Historical Archaeology), at least one specimen was identified – this example derived from the Late Bronze Age settlement at Thunau, and the root of the specimen had been fully perforated. A mandible from this site exhibited some partial destruction of the area of the canine alveolus, possibly indicating the intentional extraction of the canine. Similar damage is reported for mandibles from Virunum (Galik, 2004) and was also observed in the collection from Sand. In the Early Medieval period at Thunau, some tool marks were observed in the alveolar region of some specimens and have been interpreted in the same way (Kanelutti, 1993). In contrast, some collections display no evidence for such practices, such as Traismauer and other examples from Virunum (see also Gostenčnik, 2008), where the canines were left in their original positions in both upper and lower jaws. This situation is likely to indicate an indifference towards the canine as a valued object, unless these particular skulls and mandibles were deliberately left intact, being used as a trophy. This latter interpretation may be offered for the mandible from Thunau, which exhibited a sawn-off ramus (see above), and which still possessed its canine. Admittedly, in one of the skulls from Virunum presented by Gostenčnik (2008) one canine, still *in situ*, had been heavily worn down, thus becoming unattractive for further use or display.

Among the more recent excavations, the site Schweighofer Mauer (LA; Maurer, 2011, 2014) must be mentioned. From the debris accumulated down the slope underneath a hilltop settlement of the Late Neolithic Mondsee group, besides fox and wild boar tooth pendants, three worked bear teeth could be collected (Maurer, 2011: Table 15, Maurer, 2014: Fig. 26-28). Apart from a classical canine pendant with a perforated root, a canine from a young individual had the surface of its partly undeveloped and hollow root covered all over with small pits. These exhibit a very regular arrangement. The shiny surface of the tooth indicates its use as a pendant. Maurer (2011) reports a very similar object from 19th c. excavations at the classical site of Mondsee. In this case, the pits still exhibited traces of a black colouring resulting from birch tar. These may therefore also have been present originally in the specimen from Schweighofer Mauer. The third worked bear tooth from this site was made from a second lower molar (M_2). Its occlusal surface and one root were completely smoothed or grinded down, and the remaining root was perforated. This object, which somehow resembles the miniature model of a modern mountain boot (Maurer, 2011), was therefore also used as pendant.

Modified claw bones

Distal phalanges with special alterations are present in prehistoric, Roman and Medieval contexts. In one specimen from an Early Bronze Age context at Buhuberg, the tip of the claw bone had been evenly smoothed. Evidently, a fine-grained abrasive surface had created this affect, as no scratch lines were visible, and it is possible that the polishing represents use-wear, with the specimen forming part of a garment or personal adornment that was worn for a long period of time. Partial smoothing of the articulation area of another claw bone was reported in an Early Medieval context at Thunau. In this case, the claw bone served as a natural socket for the claw itself, which protected the distal part of the bone from abrasion. A similar pattern was observed on one specimen from the La-Tène settlement at Prellenkirchen. Here, the articular area displayed evidence of heavy abrasion and was slightly polished, whereas the distal area of the phalanx remained in an unworn condition. There are, however, two mediolateral perforations with a diameter of 4-5mm (Karwowski, 2010). These latter two examples clearly indicate the ornamental use of claw bones which possessed claws *in situ*.

Burnt claw bones

Claw bones with traces of burning are present at the sites of Mondsee (several specimens; Fig. 4), Buhuberg and Sand, and the intensity of the heat influence on the bones ranges from local blackening to total calcination. The presence of burnt claw bones deserves attention; they are often reported in cremation burials (e.g. Lehmkuhl, 1987), and they are usually interpreted as representing the remains of skins with third phalanges still attached, which were burnt together during cremation ceremonies

(e.g. Méniel, 2001). In the sites under discussion, however, the material was not recovered in defined grave contexts. It is unclear why these elements have been more regularly exposed to heat than any other bone. Alternative explanations for this pattern include some form of roasting procedure involving paw elements, or alternatively, this abundance may be related to the better preservation of the compact bones during burning. For instance, in an Iron Age cremation burial mound at Führholz (Carinthia; Kanelutti in Renhart, 1990), two calcined middle phalanges were recovered, and these bones were associated with other autopodial elements (astragali, phalanges, sesamoids) from cattle and sheep/goat.

Bone tools

Although not particularly apt for working into tools, there are many examples of long bone diaphyses, particularly from the lower extremities, being worked into points and chisels, and rich assemblages have been recovered from the Swiss Neolithic lakeside dwellings (see Schibler, 1980). At least one proximal tibia fragment from the Late Neolithic collection from Mondsee can be interpreted as a haft: the bone was broken at the midshaft, and the fracture edges were well rounded. Another object made from a proximal tibia was recovered from the Middle Neolithic circular ditch at Perchtoldsdorf-Aspetten (Kunst, 2005), representing the only bear remain from this structure (Fig. 14).

In this instance, the central shaft was ground down with stone tools and shaped into a wedge-like tip. This object was possibly also used as a haft or as a socket for some kind of point. In comparison with long bones and metapodials of ruminants, the marrow cavity of the bear tibia is rather narrow in its central area and appears particularly useful for the insertion of a fine point.

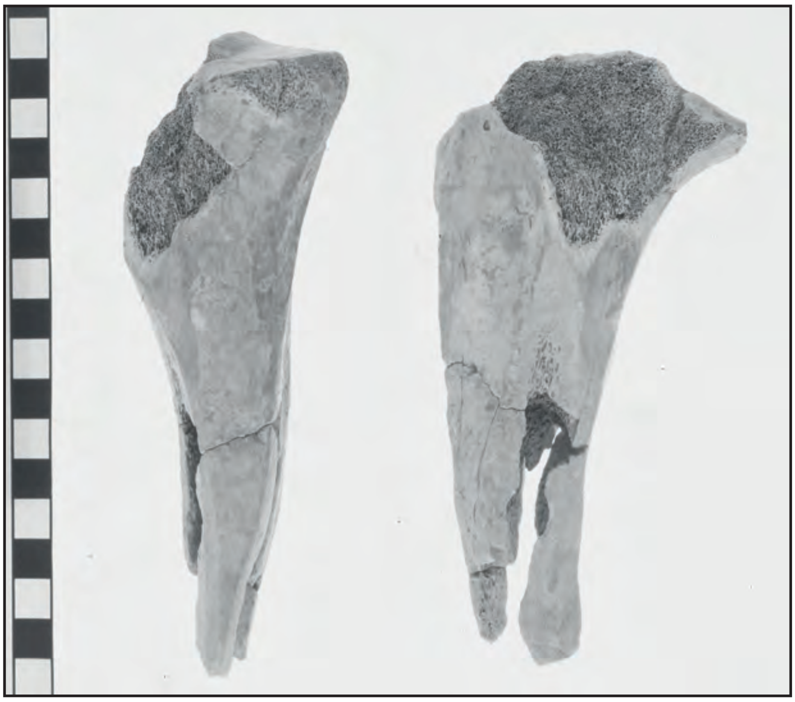

Fig. 14: bone tool made from a left tibia of brown bear - plantar and lateral view; Perchtoldsdorf-Aspetten, Middle Neolithic (Photo: R. Gold).

Pathological conditions and their implications

Being a powerful and sturdy omnivore, the brown bear can easily survive pathological conditions that are lethal in other carnivores and herbivores which depend on, for example, fast locomotion or an intact dentition. Therefore, bear remains exhibiting loss of teeth, minor pathological lesions such as exostoses on metapodials, or even healed fractures of long bones, are frequently reported from both cultural and non-cultural contexts. For instance, WOLFF (1977) reports several examples among the old collections from Mondsee. In Virunum, a distal humerus and a rib from the same animal were characterized by arthritic deformations, and a further individual exhibited heavy lesions in the upper dentition (GALIK, 2004). Two other sites deserve further discussion here – Traismauer and Thunau – as some elements of the assemblages displayed pathologies that were interpreted as illuminating specific human-bear relationships. On the right mandible of the associated maxilla and mandible pair from Traismauer, a deep furrow is visible between the first and second molar, and this was accompanied by the loss of the fourth premolar on its left counterpart (Fig. 7). According to RIEDEL (1993), these conditions are reminiscent of modern zoo animals and it can be argued that this particular animal was held in captivity, as has previously been suggested for similar observations at other Roman sites (e.g. GULDE, 1985). The furrow present on the mandible is also similar to a deformation observed by

Chaix et al. (1997) on a Mesolithic specimen from France. In this instance, it appears that a thong had been tied around the mandible. In the Early Medieval assemblage from Thunau, the high frequency of pathological conditions found in the bear remains differs from the low frequency identified on domestic mammals, with more than one-fourth of the bear bones being affected (Kanelutti, 1993). These frequencies are unusual and are considered to be too high for a wild population. The lesions observed comprise loss of teeth, inflammation in the area of the tooth rows, hyperostosis of long bone shafts and badly healed fractures. Some of these conditions are interpreted as resulting from malnutrition, and hence it has been argued that some of the animals may have spent longer periods of time in captivity. In contrast, no pathologies were identified in the assemblage from Sand, which is located nearby and is roughly contemporaneous with Thunau (Pucher & Schmitzberger, 1999). This suggests that the bears at Thunau were exposed to different, seemingly special, conditions. The frequency of pathologies in wild brown bear populations, however, is poorly studied and while it is, therefore, difficult to draw comparisons between bears kept in captivity and those living under natural conditions, the significance of these patterns should not be underestimated.

Concluding remarks

The evaluation of the occurrence of a ‘rare’ species, such as the brown bear, in the archaeological record from a specific geographical region, can provide invaluable insights which are relevant to both cultural and faunal history. For instance, if we consider another wild, but not necessarily ‘rare’, mammal, the brown hare (*Lepus europaeus*), the repeated occurrence of (partial) skeletons within settlement pits has been recognized as a widespread phenomenon in the Middle Neolithic and Early Bronze age of Europe (Manhart & Vagedes, 1999, Schmitzberger, 2009). Certain trends, however, may appear more defined for ‘rare’ species in comparison to the assemblages of the main domesticates, where the large amount of bone material often obscures individual, specific preservation patterns. On the other hand, the low occurrence of ‘rare’ species in archaeological assemblages often leads to the recovery of small sample sets, the compositions of which are likely to be driven by chance, and may not therefore exhibit any patterning. The observations of the sample characteristics of brown bear assemblages discussed in this paper, such as complete long bones in lakeside dwellings, or the high frequencies of burnt phalanges and human modifications elsewhere, is, therefore, remarkable. Potential human influences on the assemblages must be considered against other taphonomic agents, such as differential destruction and the overall impact of the immediate archaeological and sedimentary environments (e.g. buildings, settlement layers).

As the main differences found between the samples and/or periods analysed here concern the relative abundance and frequency of skeletal parts, the issue of data quality has to be addressed first. Among all the European game animals, bears present some particularly unique features. In contrast to the wild species of artiodactyls, equids and canids, bear remains cannot be confused with domesticated congeners. Unlike the brown hare and birds, they appear to be little affected by recovery biases and preservation conditions. The data quality may, therefore, be regarded as generally good – an absence of bear remains within a large bone sample may therefore indicate that this animal had little or no relevance to local residents. Such an issue touches upon an important question: can the distribution, extinction or rarefying of a species be inferred from the archaeological record? In a recent survey, SCHMITZBERGER (2009) analysed 101 Neolithic sites from the Austrian Danube area, 22 of which yielded bear remains. If NISP-counts for the 30 sites with more than 50 determinable bones are calculated, bear remains account for 0.25% of the total. These figures appear moderate for a period when the distribution of the species was widespread, but its availability or importance, for whatever reason, was limited. Nevertheless, there are very few rich prehistoric assemblages that do not contain bear remains. An interesting exception was the Late Iron Age sanctuary at Frauenberg (Styria; URBAN, 2000) which had an NISP of over 23,000 faunal remains, including several species of large wild mammals and birds (GRILL, 2009). It is against this prehistoric background that the more complex picture of the Roman period can be interpreted. Here, we have rural contexts, which exhibit a sensible reliance on hunting (Perchtoldsdorf), sometimes even producing specialized hunters' refuse (Gerasdorf; although poorly documented), and military and civilian centres which display a varying reliance on natural resources. For example, in Mautern-Favianis, the bear, like other large carnivores, was an exceptional element and was not found within the contexts selected for study. However, red deer remains were consistently found within large refuse pits, with a NISP ranging from 0.5% to 4% of the main domesticates (KUNST, 2006). At the similar setting at Traismauer-Augustiana (RIEDEL, 1993), red deer was once again the dominant species among the wild mammals (0.7% of total NISP). The respective value for the bear was, in contrast, c. 0.1%. At both sites, the remains of this species occurred mostly as anatomical sets, underlining the exceptional status of this material against the more even distributed, processed remains of red deer. A very different picture was rendered by the large bone assemblage (NISP >12.000) from the substructures of a city street from Carnuntum, which mirrored the consumption and discard behaviours of an urban population. A single bear bone with documented stratigraphic affiliation resulted in less than 0.01% of the total NISP from this site, but the other large game species (e.g. red deer, roe deer and wild boar) were only slightly more frequent. Generally, the contexts excavated (e.g. the backfill of sewers or construction horizons) provided a favourable taphonomic environment for small fragments, but also for primary butchery refuse and kitchen remains. The diversity of fish and wild birds, therefore, was high, with animals such as the brown hare rivalling in numbers with domestic fowl within certain layers, while large wild mammals occurred in smaller numbers than in both sites described above. Thus, in the Roman period, reliance on natural resources in general (e.g. Carnuntum) and large wild mammals in special circumstances (e.g. Mautern) are not necessarily linked with an occurrence of bears. Significant quantities of bear remains normally appear with larger-than-average quantities of wild mammals (e.g. Gerasdorf and Perchtoldsdorf), with Hemmaberg and Traismauer being possible exceptions. At this latter site, bears may have played a certain role within the local economy and social life. This can certainly be proposed for the amphi-theatre of Virunum, which has produced the most important bear assemblage from Austria: raised absolute and relative NISP abundances may be interpreted as being directly linked to the function of this site (Galik, 2004).

In regards to faunal history, the presence of bears is neither linked to topography nor to the geographical distribution of the sites. The highest numbers of brown bear either derived from densely populated areas (e.g. Perchtoldsdorf and Traismauer) or from administrative centres (e.g. Virunum). These patterns may also reflect trading networks, rather than real distribution patterns of this species, with the animals or their parts entering the sites as exchange items. Although it must be stated that there are no Roman sites yielding bear remains as worked objects only. It must further be added that wild mammals are generally rare in Germanic sites from the area north of the Danube, which was never included into the Roman Empire. At the Early Medieval hillforts, bears show up as minor elements among high NISP abundances of wild mammals (e.g. Sand) or exhibit high absolute values themselves (e.g. Thunau). Contrary to the Roman samples and in accordance with some prehistoric materials, butchered remains and worked bones and teeth appear to be equally important. Both sites represent small central strongholds within a hitherto sparsely populated area, and the wild mammal remains probably reflect the hunting activities of the local elite. Bear bones occurred at these sites, alongside other ‘rare’ elements, such as the European bison, aurochs and European elk. These species, despite surviving the Roman period in the areas to the north and south of the Danube, possibly became extinct in the territory of present-day Austria, not long after AD 1000 (Spitzenberger, 2001). Hence, the animal bone samples from those sites may indeed reflect the over-exploitation of the local wild fauna. From the High Medieval onwards, written sources provide more detailed information concerning human–bear relationships. No remains of this species have been recorded among bone samples from Late Medieval and Early Modern layers from urban centres. This pattern may be attributable to the state of archaeological research in these periods, the dwindling numbers of bears in general or their decreasing availability, brought about by particular legal restrictions.

From the Neolithic onwards, the NISP-percentages of bears within archaeological samples in Austria are likely to reflect the amount of interaction between some people in these communities and these animals, rather than the actual population and distribution patterns of these animals. Following the Neolithic lakeside dwellings, it is only in the ‘developed’ societies of the Roman and Early Medieval periods that bears appear both in greater relative numbers and in peculiar configurations, such as complete skulls, articulated units, and so on. Therefore it seems that at least until the High Medieval, no regional extinctions occurred. Nevertheless, whereas bear remains can be expected in earlier prehistoric assemblages, later prehistoric assemblages, in particular from the Iron Age, may often be devoid of this species, suggesting a range of human-bear relationships which are specific to particular periods, regions and sites.

The archaeological bone record should, therefore, be treated with caution in the reconstruction of faunal history (e.g. Kunst, 2014). Wild animals portray a different pattern and ‘behaviour’ in the archaeological assemblages than domesticates. For example, species like the European pond terrapin, the European elk, the aurochs and the European bison became rare in later Austrian prehistory, being mostly absent during the Roman period, only to ‘reappear’ in the Early medieval period.

Further insights have been provided in this paper through the consideration of a single ‘rare’ species. Similar to the treatment of red deer antler and bones, a dichotomy can be constructed for body parts of the bear with a potential symbolic or decorative value, such as teeth, skulls and claws, and the post-cranial skeleton incorporated within food consumption activities. In contrast to red deer, which is often represented by antler alone, bear is usually represented by both ‘symbolic’ and ‘mundane’ remains, at least in settlement contexts. Only at the Neolithic site of Perchtoldsdorf and the Iron Age site of Prellenkirchen, evidence for brown bear was indicated exclusively by the presence of worked objects – with only one specimen being recovered from each site. Similar to worked antler, these objects could represent objects that were highly valued and exchanged. Another important observation is the high frequency of anthropogenic modifications present on bear bones in general, which can be expected on virtually any skeletal element. This pattern, known from the Late Palaeolithic onwards (see Fiore & Tagliacozzo, 2008 for a recent example), is probably related to the practicalities of engaging with the peculiarities of the ursid anatomy (e.g. butchery marks) and the high esteem held for certain body parts (e.g. skinning marks, extraction of teeth and claws).

More work is needed, however, so that certain questions can be addressed. The low fragmentation of bear long bones in the Late Neolithic lakeside dwellings of Mondsee and Keutschach stands in contrast to the Swiss site of Arbon-Bleiche, where fragmentation was reportedly intensive, being similar to the cattle remains from the same site (Deschler-Erb & Marti-Grädel, 2004). It is unknown whether differences in carcass treatment, or in taphonomic pathways, are responsible for these different patterns. Likewise, it is undecided whether the high frequency of burnt claw bones outside of burial contexts in different periods, is due to the differential preservation rates of these materials or to specific human behaviours associated with the treatment of bear claws.

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Large mammals except cave-bears from the Loutra Almopias Cave, Late Pleistocene, Macedonia, Greece

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Abstract

Excavations in the Loutra Almopias cave yielded a large amount of different vertebrate taxa assigned to two different time horizons. Here we describe the carnivores, with the exception of the cave bear, and herbivores found in the cave. Special focus lies on the mustelids, not evaluated previously, and the comparison of leopard, hyena and chamois. The composition of the mustelids in the isolated chamber Ia confirms its chronological assignment into the Late Glacial, while most of the larger mammals, such as *Crocuta*, *Panthera* and *Rupicapra*, fit into the time before the Last Glacial Maximum (LGM).

Zusammenfassung

Die Grabungen in der Loutra Almopias Höhle ergaben eine große Anzahl an unterschiedlichen Vertebraten, die zwei verschiedenen Zeithorizonten zugeordnet werden. Wir beschreiben hier die Carnivora, mit Ausnahme des Höhlenbären, und die Herbivoren aus der Höhle. Der Schwerpunkt liegt auf den bis jetzt unbearbeiteten Musteliden, sowie auf dem morphologischen Vergleich der Hyäne, des Leoparden und der Gämse. Die Zusammensetzung der Musteliden aus der isolierten Kammer Ia bestätigt die zeitliche Einstufung in das Spätglazial, während die meisten Großsäuger, wie *Crocuta*, *Panthera* und *Rupicapra*, in die Zeit vor dem letzten Vereisungshöhepunkt im Glazcial (LGM) zu stellen sind.

Key words: Carnivora, Artiodactyla, Almopias cave, Late Pleistocene, Greece

1. Introduction

The cave is situated in the Almopia Speleopark in Macedonia (Greece), which holds a group of caves of scientific interest. It is embedded in Maastrichian limestone. During the Quaternary, the intramontane basin of Almopia experienced extensive karstification, thus leading to the formation of the cave (Lazaridis, 2005).

Scientific investigations took place from 1990 to 2012 and yielded more than 20.000 specimens, most of them belong to the cave bear, making it the richest Pleistocene fossil cave in Greece. The cave is structured into different chambers. LAC Ia, the smallest chamber, is less than a square meter, difficult to access and completely separated from the others.

Sedimentation in the cave changed between warm and humid intervals with calcareous crusts and tufas and colder sections with clastic sediments (Tsoukala et al., 2006).

Dating the material proved difficult since most of the bones had too few or no collagen at all. Only one femur of *Ursus* (GrN-7573) revealed a reliable radiocarbon result of 37.880 +370/-360 (cal 42.361±378) years before present (a BP). Sediments and sinter (dated with various methods such as OSL, LUM, U/Th and C14) fill the time gap with results from 29.900 to 11.500 a BP. The micromammals from LAC Ia yielded an age between 11.230 ± 110 (VERA-0060) and 12.350 ± 40 (VERA-5631) a BP. A charcoal remain from LAC Ic is dated around 5.000 a BP (Zacharias et al., 2008). Therefore most of the animal remains from the cave come from the Middle Weichselian (OIS 3) with the exception of smaller mammals from LAC Ia, which are placed into the Late Glacial (Tsoukala et al., 2006).

Descriptions of the Pleistocene material from Loutra Almopias were made by Tsoukala et al. (2001), Tsoukala & Rabeder (2005) and Tsoukala et al. (2006) with overviews of the setting, excavation and the main findings. In this work, the focus lies on the description of all non-ursid and non-micromammal material with a special focus on the carnivores and artiodactyls. It includes a detailed evaluation of the distribution of these taxa in the different parts of the cave.

Abbreviations

PIUW – Department of Palaeontology Vienna
LAC – Loutra Almopias cave
MIN – minimum number of individuals
LAC I, Ia, Ib, Ic, II and III refer to the chambers, where the specimens were found. For a detailed description of the chambers see Tsoukala et al., 2006.

Measurements

Capital letters are used for upper teeth (e.g. M – upper molars, P – upper premolars) small letters are used for lower teeth (e.g. m – lower molars, p – lower premolars)

DO – smallest depth of the ulna at the olecranon

Dpa – smallest depth above the processus anconaeus

Hcrown – crown height of the canine, measured from the enamel band

Hroot – root height of the canine, measured from the enamel band

L ant.-post – length measured anterior-posterior

Wp – maximal width proximally

Dp – maximal depth proximally

Wd – maximal width distally

Dd – maximal depth distally

mL – maximal length

mW – maximal width

mL art – maximal length of the articulation

mW art – maximal width of the articulationm

H – maximal height

sD – smallest diaphyses width

BT - width of trochlea

WoP – width over processus anconeus

nt-post – long bones measured anteroposterior

2. Methods

Measurements were taken with a calliper up to 0.1mm and follow VON DEN DRIESCH (1976). Measurements given in tables are in millimetre. Measurements were only taken on dental and/or postcranial material of taxonomic value. If only few elements per taxa are present, the measurements are given in the list of the material; otherwise, separate tables are provided. Photos and plates were made by Rudolf Gold (PIUW).

3. Systematic description

Order: Carnivora (Bowdwich, 1821)

Family: Mustelidae (Fischer, 1817)

Subfamily: Mustelinae (Fischer, 1817)

The subfamily includes a variety of carnivores with different food and hunting preferences ranging from the largest mustelid, the wolverine to the smallest, the least weasel and from the African honey badger to the South American Eira.

Today the mustelid fauna in Greece consists of *Meles meles* (badger), *Martes martes* (pine marten), *Martes foina* (stone marten), *Vormela peregusna* (marbled polecat), *Mustela lutreola* (European mink), *Mustela putorius* (European polecat), *Mustela erminea* (ermine) and *Mustela nivalis* (least weasel). Recorded from some Greek islands is *Lutra lutra* (European otter) (Massetti, 1995). In the Loutra Almopias caves four of the nine extant known species could be identified.

Genus: *Mustela* (Linnaeus, 1758)

Members of the genus *Mustela* live in Europe, Asia, North and South America and Africa. It was introduced to Australia by men. In Europe during the Pleistocene, the following taxa have been known so far: *M. nivalis* (least weasel), *M. erminea* (stoat), *M. eversmanni* (steppe pole cat), *M. lutreola* (European mink) and *M. putorius* (European polecat) (Spitzenberger, 2001).

Mustela nivalis (Linnaeus, 1758)

Material (all from chamber Ia): LAC 1292 right maxilla fragment with Csup and P2; LAC 10503 left P4; LAC 1290a left mandible fragment with p2-p4 (Plate 1, Fig. 1a & b); LAC 3850 left mandible fragment with m1 broken; LAC 3851 right mandible fragment with alveoli of p3-p4, m1, alveoli of m2; LAC 3852 right dp4; LAC 10524 left mandible fragment with broken p3, p4-m1; LAC 10520 I fragment; LAC 2910 left m1. Measurements of 1290a, 10524 see Table 1.

The smallest of the mustelids is represented by a number of single teeth, permanent and milk teeth, by a right lower mandible fragment with p2-p3 and a right upper maxilla fragment with I2, Csup, root fragment of P2 and P3. Only *M. nivalis* is of that size and it was the smallest predator in the Loutra Almopias caves, only found in chamber Ia.

Mustela (*Putorius*) *putorius* (Linnaeus, 1758)

Material (all from chamber Ia): LAC 10518 maxilla fragment with a right I1 and left I1-2, alveolus for I3; LAC 4269 right maxilla fragment with Csup, P1-P4 and M1 (Plate 1, Fig. 4); LAC 2905 left

Csup.; LAC 2904 and LAC 4265 right Csup.; LAC 3839 right P3; LAC 2906 left mandible with root of broken canine, p2–p4, m1-m2; LAC 4268 left mandible fragment with root of broken canine, p2, p3, distal part of p4, m1 and m2 (Plate 1, Fig 3a-c); LAC 3833 left cinf and LAC 2911 right cinf. Measurements of LAC 4269, 2906, and 4268 see Table 1.

The maxilla fragment (LAC 4269) is broken mesially in front of the I2, the alveolus for I3 still present. The tooth row from Csup to M1 is quite well preserved. Only the tip of the upper canine is broken; the paracone on the P4 is slightly worn. This mustelid material in this size group is either *M. putorius* or *M. eversmanni* but in the latter the protocone on the P4 is slightly larger and more rounded.

The left mandible (LAC 2906) is broken mesially, with the alveolus of i3 still visible; the canine is broken with its root still in place, and the ramus ascendens is damaged. The other left mandible (LAC 4268) is as well only preserved from the alveolus of the i3 to the m2, the ramus ascendens broken. Its canine is broken but the root still present. The mandible was broken at the position of the p4 and the anterior part of p3 is missing. The m1 is very small and the metaconid missing on the carnassial, which is typical for *M. putorius*. Therefore the material is assigned to *M. putorius*.

All specimens were found in the isolated chamber Ia The polecat is not present in Greece today.

Genus: *Martes* (Pinel, 1792)

Members of the genus *Martes* live today in the northern deciduous forests of Europe, Asia and North America. In Europe, during the Pleistocene, the following taxa have been known so far: *M. foina* (stone marten), *M. martes* (pine marten), *M. zibellina* (sable). They are carnivorous to omnivorous and not as specialized on meat as their smaller relatives from the *Mustela*-group (Grupe & Krüger, 1990).

Martes foina (Erxleben, 1777)

Material: LAC 6938 left M1 (I); LAC 10480 left M1 (III); LAC 14481 right P4 (Ib); LAC 2892 left mandible fragment with alveolus for cinf and p2-p3, p4 broken (Ia); LAC 3829 left mandible with cinf, alveolus of p1, p2-m1 (Ia) (Plate 1 Fig 2a&b). Measurements see Table 1.

The occlusal surface of both M1 is well preserved and roots are missing. The buccal shape of the M1 with a more pronounced paracone and metacone allows an assignment to *M. foina*. The P4 is slightly worn and the protocone is missing but the shelf in front of the paracone is very small so the protocone was probably very closely attached, as typical in *M. foina*. On the mandible (LAC 3829) the protoconid and paraconid of the m1 are already worn, as well as the hypoconid. Otherwise only the tips of the remaining teeth show signs of wear. On the m1 the metaconid is closed attached to the protoconid and the paraconid is also extended lingually, as known from *M. foina*.

The material was found in the chamber Ia as well as in the main chambers of the Loutra Almopias cave. The migration of *M. foina* into Europe seems to have started from Asia and it probably arrived during the Latest Pleistocene (Anderson, 1970 in Buskirk et al., 1994 in Spitzenberger, 2001).

Martes martes (Erxleben, 1777)

Material: LAC 7481 left M1, 6.9 x 9.6 mm (III) (Plate 1, Fig. 7); The upper molar is buccal less grooved as typical for *M. martes*, therefore the assignment. LAC 3830 is a right mandible fragment with cinf to p3 (Ia). The M1 was found in the main part of the Loutra Almopias cave in chamber III and the mandible in Ia. The pine marten today is found in most parts of Europe with decent vegetation. Therefore, it is not distributed in the arid areas such as south of the Pyrenees, the Pindos mountains and southern Ukraine (www.arkive.org, retrieved 08.2017).

Martes sp.

Since remains of the pine marten and the beech marten, which are of similar size, co-occurred in the Loutra Almopias cave area, it was not possible to distinguish the material, when no diagnostic features were present. Therefore the following material is only assigned to the genus *Martes*: LAC 3831 right Csup. (Ia); LAC 3832 right cinf. (Ia); LAC 2878 (left mandible fragment with alveoli for m1-m2 (Ic); LAC 3821 right tibia fragment (Ia); LAC 3822 left tibia fragment (Ia); LAC 3823 left radius fragment (Ia). Measurements see Table 1.

Genus: *Meles (*Linnaeus, 1758)

The badger is a wide spread animal in the holarctic area. A study on the mitochondrial DNA (Del Cerra et al. 2010) concluded four different phylogeographic groups (European, Continental Asia, Southwest Asian and North-East Asian). They suggest an independent evolution of these types since the Pliocene. For the last glacial part, they see no indication that the European, as well as the Russian regions, were recolonised by the Southwest Asian badgers, except maybe the Crete island population which is more closely related to the Southwest-Asian type. Baryshnikov (2009) commented on these results, that there is not enough morphological evidence for a separation on a species level. Therefore we refer to the European badger here as *Meles meles*.

Subfamily: Melinae (Linnaeus, 1758)

Genus: *Meles* (Linnaeus, 1758)

Meles meles (Linnaeus, 1758)

Material: LAC 7409 left maxilla fragment with P3-M1(III) (Plate 1, Fig. 5); LAC 204 left i3 (II); LAC 8704 right i3 (III). Measurements see Table 1.

The badger is not very common in the Almopias cave but the specimens were found in the main part of the cave in chamber III. Only one maxilla fragment and three single teeth were preserved. The maxilla fragment consists of the P2 to P4 and the alveoli of M1, parts missing on the lingual-posterior side. The teeth are not very worn. Part of the alveolus of the canine is preserved but there is not enough space between it and the P2. Therefore no P1 was present on this specimen. This tooth is missing in about 50% of the extant badgers (Baryshnikov, 2009)

The P4 resembles that of a recent badger in morphology and size and does not differ in its size range from other Late Pleistocene badgers. Baryshnikov (2009) described the extensive sample from Kudaro cave and Binagady, Caucasus. The ones from Kudaro are slightly larger while the material from Binagady is about the same size as the material from Loutra Almopias. With the small sample, no information about sexual dimorphism or possible differences on a subspecies level can be given.

Mustelidae indet.

Several specimens belong to mustelids but cannot be identified further. Among them are phalanges of small to very small size, tooth fragments and tooth germs.

Family: Canidae *(*Fisher von Waldheim, 1817)

Genus: *Canis* (Linnaeus, 1758)

Canis lupus (Linnaeus, 1758)

Material: LAC 13701 right P4 fragment (mL = 23,8 mm, mW = 11,8 mm) (I) (Table 2, Plate 1, Fig 10); LAC 3912 caput femori (Ic); LAC 2888 right metacarpal 5 (Ia); LAC 3931, 3932 and LAC 3933 first phalanges (Ia).

The paracone and the metacone blade on the P4 are very worn, the protocone and its root are broken. Further damaged are the buccal and posterior side, as well as parts below the paracone. The tooth is rather worn but the overall morphology is that of a canid carnassial, too small for a lion or hyena and not slender enough for a leopard. It is far too worn to give any indication whether it may have belonged to a male or female wolf. The postcranial material is fragmentary with only one complete metacarpal 5. Metrically, the phalanges found in LAC Ia, are very small, even dog-size.

Canis lupus, the wolf, was distributed in the Mediterranean area until the end of the Sub-Atlantic (Sablin & Khlopachev, 2002, Sommer & Benecke, 2005). It retreated later on further north.

Genus: *Vulpes (*Frisch, 1775)

Vulpes vulpes (Linnaeus, 1758)

Material: Upper dentition; LAC 7646 right I3 (III); LAC 3825 right Csup (Ia); LAC 3647 right P4 fragment (Ia); LAC 2900 left M1 buccal side only (Ia); LAC 5719 left M2 (I); Lower dentition; LAC 4267 and LAC 2901 refitted, juvenile left mandible fragment with p4 in crypt, m1-m2 and m3 in crypt (Ia) (Plate 1, Fig. 6a&b); LAC 3826 left mandible fragment with alveoli for cinf to m1 (Ia); LAC 3835 left i3 (Ia); LAC 1291 right i3 (Ia); LAC 4939 left i2 (II); LAC 2893 left cinf (Ia); LAC 3827 left p2 (Ia); LAC 4266 right p2 (Ia); LAC 3828 left p4 (Ia); LAC 2897 right m1 both roots damaged (Ia); LAC 2896 left m1 posterior root broken (Ia). Postcranial elements: LAC 3820 right humerus fragment, only distal part preserved (Ia); Measurements see Table 2.

Two left mandible fragments, LAC 2901 and LAC 4267, belong together. The symphysis fits together perfectly. The p4 is still in crypt as well as the m3. The m2 is not fully erupted; m2 as well as m1 are not worn. The individual was of semi-adult age. LAC 2896 and LAC 2897, one left and right m1 probably belong to a second individual and they are equally unworn. The postcranial material is very fragmented. Apart from a distal fragment of a right humerus, only a broken part of a phalange and the proximal part of a metapodial could be identified. Metrically as well as morphologically, the material fits into the *Vulpes* range. All the material came from the chamber Ia. It consists at least of two individuals.

Family: Felidae (Gray, 1821)

Felis silvestris aff. *catus* (Linnaeus, 1758)

Material: LAC 1292c (Ia) left upper carnassial fragment.

The P4 fragment consists of the buccal part of the paracone and the metastyle blade. The lingual and anterior part is missing, as well as the anterior root. The tooth was found in LAC Ia, a chamber of the cave where mainly remains of Holocene smaller animals were found. The specimen is of very small size and probably also of Holocene age, thus the affiliation to the domestic cat rather than the feral one.

Genus: *Panthera (*Oken, 1816)

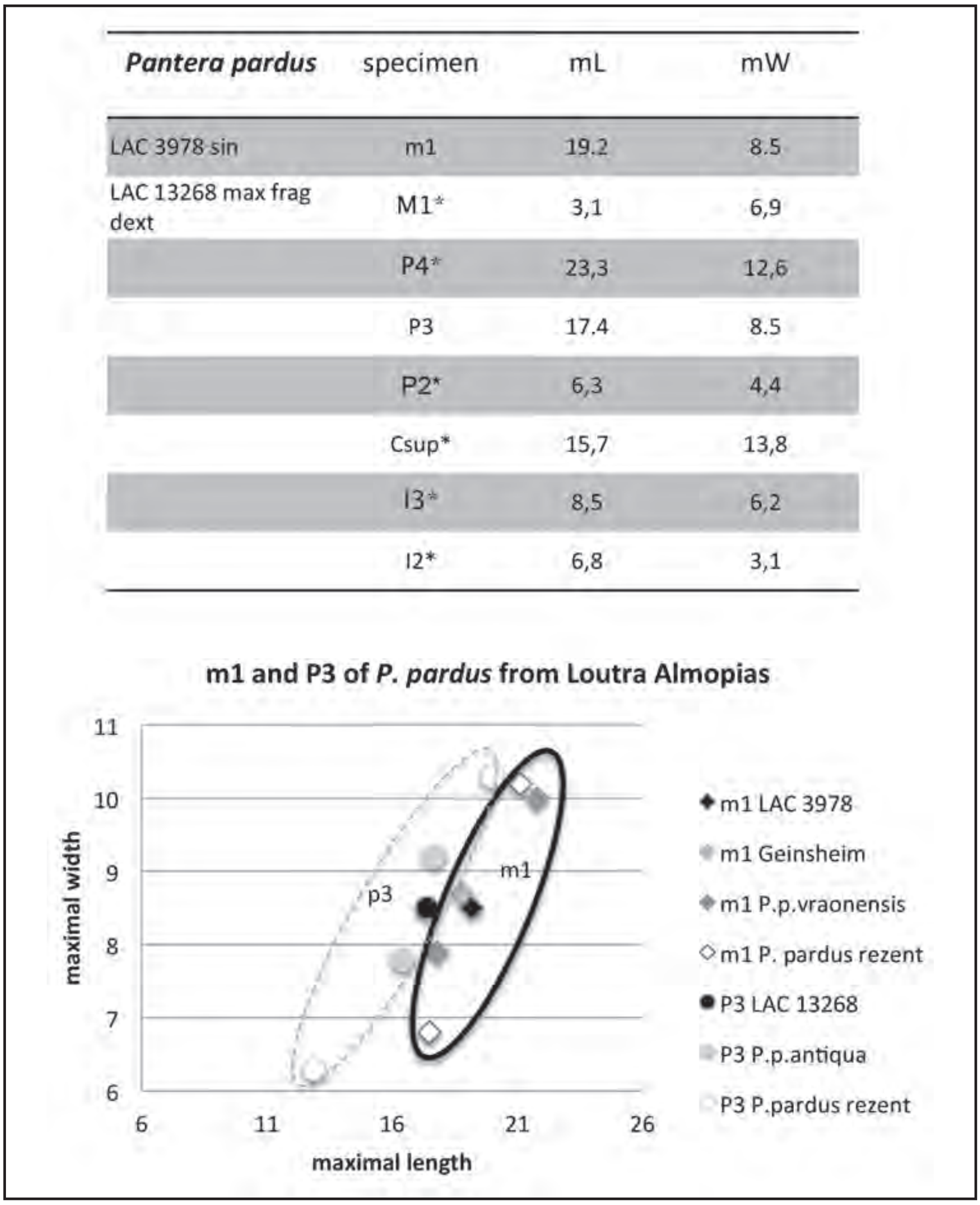
Panthera pardus (Linnaeus, 1758)

Material: LAC 13268 right cranium fragment with P3 (Ic) (Plate 2, Fig. 1a&b), LAC 9980 right Csup (Ic), LAC 3978 left m1 (Ic) (Table 1, Plate 1, Fig. 8a & b), LAC 13530 left radius proximal fragment (Ic), LAC 13284 left radius (Ic), LAC 11779 left ulna proximal fragment (Ic), LAC 8385 left ulna proximal fragment (I), LAC 12102 left trapezium (Ic), LAC 14918 left tarsale 3 and cuniforme (Ic), LAC 3913 right proximal part metatarsal 3 fragment (Ic) LAC 4170 left first digit (II), LAC 2628, 5813 second digits (Ic, I).

The most of the leopard specimens were found in LAC Ic. Only the complete ulna (LAC 8385) and the intermediate phalange (LAC 5813) was recovered from chamber I; the posterior phalange (LAC

4170) from champer II. Since two left radius and ulna fragments were found, the material seems to belong to two individuals (MNI = 2). A metrical comparison (Fig. 1) of the m1 and P3 indicates leopards of average size.

Fossil remains from the Pleistocene leopard are scarce. Nevertheless, material is known in the entire of Europe (e.g. Fischer, 2000, Pacher & Rabeder, 2016). While it probably co-existed with a similar large felid, *Panthera onca gombaszögensis,* during the Middle Pleistocene (Hemmer, 1971, Hemmer et al., 2010, Fischer, 2000). The leopard is the only felid of this size in the Late Pleistocene (Wolsan, 1993, Sommer & Benecke, 2005) and the Holocene (De Grossi Mazzorin, 1995, Žuravlev, 1999) in Europe.



Pantera pardus	specimen	mL	mW
LAC 3978 sin	m1	19.2	8.5
LAC 13268 max frag dext	M1*	3,1	6,9
	P4*	23,3	12,6
	P3	17.4	8.5
	P2*	6,3	4,4
	Csup*	15,7	13,8
	I3*	8,5	6,2
	I2*	6,8	3,1

Fig. 1: Scatter diagram of m1 and P3 of *Panthera pardus* from Loutra Almopias caves in comparison (Schmid, 1940, Nagel, 1999, Del Campana, 1954, Koenigswald et al., 2006).

Several fossil subspecies have been described from Europe: *P. p. sickenbergi* (SCHÜTT, 1969) and *P. p. lunellensis* (BONIFAY, 1971) from the Middle Pleistocene, *P. p. antiqua* (DEL CAMPANA, 1954), and *P. p. vraonensis* (NAGEL, 1999) from the Late Pleistocene. Genetic investigations of the fossil leopards will be necessary to confirm or refute the taxonomic value of these subspecies. We therefore, refer the material from Almopias cave to *Panthera pardus* (Fig. 1).

The specimens fit morphologically as well as metrically into the *P. pardus* group. The upper canine is with a minimum height of 62 mm of average to larger size; the fossil and extant leopards range from 50 to 80 mm (SCHMID, 1940) The same is true for the upper P3 (Plate 2, Fig. 1). The postcranial material, specially radius and ulna, range metrically more on the upper end of the scale and may indicate that one of the individuals was a male. Since only one incomplete metapodial was found, a comparison with the material from Vraona (*P. p. vraonensis*) is not possible (DEL CAMPANA 1954, NAGEL, 1999, SCHMID, 1940).

Suborder Feloidea (SIMPSON, 1931)

Family: Hyaenidae (GRAY, 1869)

Genus: *Crocuta* (KAUP, 1828)

Crocuta crocuta spelaea (GOLDFUSS, 1832)

Material (Plate 1, Fig. 9, Plate 2, Figs. 2-5, 8a & b), all from chamber Ib; exceptions are mentioned in brackets. LAC 9150 left upper canine; LAC 6629 right first incisor; LAC 11788 left first incisor; LAC 6862 left second incisor; LAC 11823 right third incisor (I); LAC 8475 right p4 (I); LAC 7097 right lower canine. Vertebrae: LAC 9500 cervical v.; LAC 6129, 6679, 6838, 12379, 11454 thoracic v.; LAC 7107, 8427, 9293, 11310 lumbal v.; LAC 6284 right pelvis fragment; LAC 11287 left acetabulum; LAC 9172 left humerus; LAC 11060 left femur; left caput femori LAC 11235 left and 11334 right; LAC 6282 left radius; LAC 7225 right radius; LAC 13675 right ulna fragment proximal with diaphysis; LAC 9283 right tibia; LAC 8177 left patella; LAC 8263 right scapholunatum; LAC left 9504 left pyramidal; LAC 6681 right capitulum; LAC 7171 left hamatum; LAC 8179a left calcaneus; LAC 6680, 7034 left and LAC 7185 right naviculars ; LAC 7712 right tarsal 3; LAC 9365 left metacarpal 2; LAC 6274 right metacarpal 3; LAC 9002 left and 7047 right metacarpals 4; LAC 13638 right and 12632 left metacarpals 5; LAC 9003 left metatarsal 2; LAC 6285 left metatarsal 3; LAC 9007 right and LAC 6050 left metatarsals 4; LAC 4313, 6134, 6310, 6815, 6839, 7045, 7048, 7106, 9530 phalanges 1, LAC 8825, 14898 (subadult, Ic) phalange 1; LAC 10130 phalange 2 (Ic); LAC 6291, 8072, 11582 phalanges 3, LAC 7953b, 8042 two coprolites. Re-measured or new material see Table 3; otherwise see TSOUKALA et al. 2006.

The cave hyena is present with more than 60 specimens, including cranial and postcranial material. From the skull, only part of the cranium is preserved. No jaws were found, only single teeth. The bones show no signs of gnaw marks. Most of the vertebrae lack on one or both sides the epiphyses. Four metapodials fit together and seem to be from one individual (LAC 9365, 6274, 7047, 13638) (Plate 2, Fig. 8a & b). One metatarsal is slightly pathological, being thicker and more rugose in the diaphysis. Left and right limb bones as well as carpal and tarsal bones are of similar size. The minimum individual number is therefore only two. Judging from the state of the bones, it was probably one semi-adult and one adult individual; the latter older or maybe sick.

One major factor to separate *Crocuta* into a fossil and an extant form was size. The fourth premolar has a total length of 22.7mm and a width of 14.4mm. Extant ones range from 19 to 23mm and 10 to 12mm; fossil ones can go up to 25mm and 15mm. Tibias from fossil hyenas are about 200mm to 210mm long (Engelbrecht, 2011), the one from Loutra reaches 193mm. So the material from Loutra Almopias is in general larger than the extant hyenas but average in size when compared to fossil ones.

Almost all the material came from chamber LAC Ib, only two teeth were found in the adjacent chamber I and III, potentially transported there by water or other animals (Fig. 2).

The cave hyena is a well-known member of the Late Pleistocene fauna and the only hyaenid species in the Late Pleistocene in Eurasia. Investigations regarding the genome, place the Eurasian population within the extant one, granting it a subspecies status. The latest occurrence in Europa is up to 30,000 maybe 25,000 years before present (Hofreiter & Stuart, 2009, Rohland et al., 2005, Sheng et al., 2014).

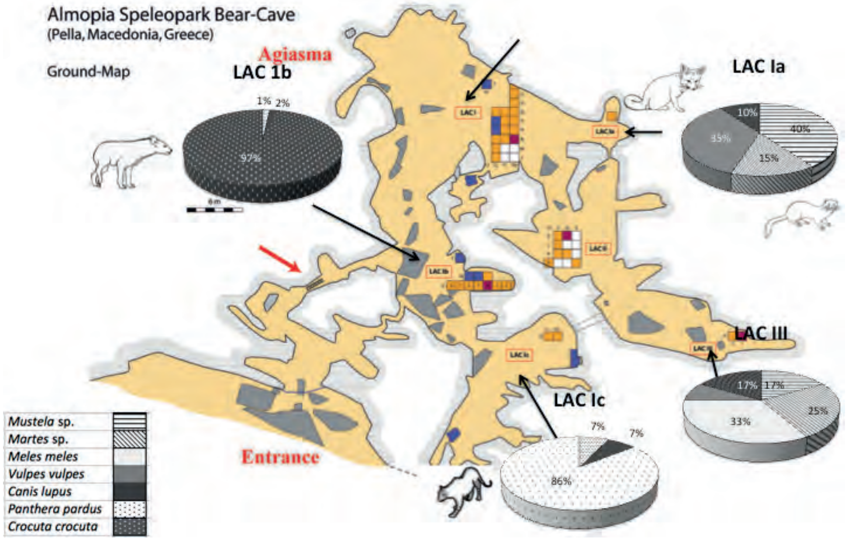


Fig. 2: Carnivore distribution in the Loutra Almopias caves

Order: Artiodactyla

Family: Bovidae (Gray, 1821)

Subfamily: (Caprinae Gill, 1872)

Genus: *Capra* (Linnaeus, 1758)

*Capra ibex (*Linnaeus, 1758)

Material: LAC 6840 (Ib) right 3, 4. upper premolar; LAC 1820 (II) and 6536 (I) two i1,2; LAC 9303 & 9308 left (Ib) radius; LAC 1833 left (II) capitatotrapezoid (same individual with LAC 905)*; LAC 14940 (I) astragalus prox. right; LAC 8826 (Ib); cuneiform right; LAC 905 left (II) Mc 3+4 (same male individual with LAC 1833); LAC 6790 right (III) Mt3+4, female juvenile; LAC 13818 (I) Mp3+4 distal; LAC 6340, 6341 (Ib) 2 first Phalange (same individual?); LAC 11268 (Ic) Ph1; LAC 5590, 5591, 5595, 5596, 3090 Ph 1 (Ia).

Ibex remains are found in all chambers of the cave implying a rather heterogenous fossil history of the assemblage further strengthen by their differing preservation quality. None of the remains shows traces of carnivore activity. *Ibex* went extinct in Greece during the Holocene (Geskos, 2013).

Genus: *Rupicapra (*Blainville, 1816)
Rupicapra rupicapra (Linnaeus, 1758)
Material: LAC 8796 phalange 2 (Ib) 2; LAC 10095 phalange 2(Ic); LAC 11800 astragalus (Ic).
The three bones attributed to *Rupicapra rupicapra* are the first evidence of this species in the Pleistocene of Greece (Tsoukala, 1992a). A comparison of the remains with material from the collection of the Institute of Palaeontology, Vienna confirms the determination (Plate 2, Figs. 6 & 7).
The remains come from chamber Ib and Ic but their chronological age is unknown. Especially the astragalus shows clear traces of bone abrasion due to transport.
Today, the subspecies *R. rupicapra balcanica* is an endangered taxa in Greece. It survived in dispersed small populations like those in the Pindos and Rhodope mountains, Sterea Ellada or Mount Olympus (Papaioannou & Kati, 2007).

Family: Cervidae (Gray 1821)

Genus: *Cervus* (Linnaeus, 1758)

Cervus elaphus (Linnaeus, 1758)

Material. LAC 11425 phalange 2; LAC 9992 phalange 3 (Ic); LAC 15500 phalange 2 (I), LAC 6680 left semilunar bone (Ib).

The red deer is represented by two middle phalanges and a distal phalange. Phalanges LAC 11425 and 9992 are from the same individual. They show no trace of carnivore activity. Two middle phalanges come from chamber Ia and might therefore represent Late Glacial/Holocene remains of the red deer in the Loutra Almopias cave.

Genus: *Dama (*Frisch, 1775)

Dama dama (Linnaeus, 1758)

Material: LAC 13122 Antler frag. (Ic); LAC 6338 left (I) and LAC 4302 (Ib) left scapula fragments; LAC 10096 metapodial trochlea (Ib).

While the fallow deer is today native in Eurasia, the occurrence in the Mediterranean area, especially in Greece during the Last Glacial is discussed (e.g. Massetti, 2012). Since the age determination of the material is not clear, no further information on this topic can be added.

Subfamily: Bovinae (Gill, 1872)

Genus: *Bos (*Linnaeus, 1758)

*Bos primigenius (*Bojanus, 1827)

Material: LAC 9319 proximal phalange (Ib), LAC 5597 phalange 1 prox. epiphysis fragment (Ia).

This extinct species is a typical element of the European Late Pleistocene and is known till the Holocene when it was domesticated into cattle breeds. The specimen shows clear traces of gastric acids, typical for a bone that passed the digestive system of a carnivore (Andrews & Cook, 1990). It was found in LAC Ib where most of the *Crocuta* remains come from. The proximal epiphyseal fragment from a large bovid comes from chamber Ia and shows a different porous preservation. Its age assignment is unclear.

4. Discussion and Conclusion:

The Mediterranean as well as the Balkan area have been important refugia for larger mammals during colder periods and only recently more attention has been given to migration tendencies of the small carnivores as well (Sommer & Benecke, 2005, Sommer & Nadachowski , 2006, Miracle & Brajkovic, 2010). Therefore the assignment of the various groups of carnivores from the Loutra Almopias cave to the different chambers and so to different time events was of importance. It was only a short-term hyena cave since the hyena findings are from two individuals only and only two coprolites were found mostly in chamber Ib. The remains from the leopard, maybe two individuals, were mainly found in chamber Ic and almost no other carnivore remains were retrieved from chamber I, since it was mostly used by cave bears, judging from the number of bones found there. The isolated chamber Ia was the main site where specimens of mustelids were deposited (Fig. 2). Therefore it is very unlikely, that all these carnivores used the cave at the same time.

The single phalange from *B. primigenius* shows traces of hyena activity. Bones of other herbivores are rare and bear no traces of bite marks, while several unidentified long bone fragments show green bone fractures and partly gnawing activity.

The lion, reported in Tsoukala et al. (2006) had to be reassigned to *Ursus*. *Panthera pardus* remains were found from two individuals. The wolf is only represented by one carnassial. Given the large amount of cave bear bones found in Loutra Almopias, this cave system was inhabited by cave bears, with the hyena and other carnivores as occasional guests.

The smaller carnivores include *M. nivalis*, *M.* (*Putorius*) *putorius*, *M. foina*, *M. martes* and *M. meles*. With the exception of *Putorius*, all taxa are present in Greece today as well, at least in the Northern part in the Rhodope mountains. Regarding their size, they all are in the extant size range. The least weasel (*nivalis*) seems to be more often found in the Late Glacial than in the time before or after while *Putorius* has rarely been found in Late Glacial sites in Europe but the species is mentioned from Spain and Italy (Altuna, 1972, Tozzi, 1971 in Sommer & Benecke, 2005). This is the first record from Greece from the Late Glacial, whereas the giant polecat *Mustela putorius* has been recorded in the Late Pleistocene hyenid den of Agios Georgios Cave (Kilkis) (Tsoukala, 1992b). *Martes* and *Meles* are at least once recorded in one fossil Greek site (Julien, 1973 in Sommer & Benecke, 2005). All these faunal elements prefer a temperate to cool environment with bushy and rocky areas; *M. foina* is not known from the northern parts of Europe.

Since this material seems to come mainly from the isolated chamber Ia, dated into the Late Glacial, these remains probably are from a cooler phase, maybe Dryas II. This part of the cave was probably used by smaller carnivores, mustelids. Therefore, this area was also used as a glacial refuge for taxa such as the badger, the marten and the European polecat. The fact that *M. nivalis* was also present indicates somewhat lower temperature than today.

Middle-sized carnivores such as the red fox (*V. vulpes*) and the arctic fox (*Alopex lagopus*) existed sympatrically during the Pleni-Glacial and in some areas even during the Late-Glacial in Greece, but only the red fox is known from the fossil record so far. *V. vulpes* has a very large range of habitats and is not specialised in its diet (Sommer & Benecke, 2005).

C. crocuta and *P. pardus* are typical elements of the Late Pleistocene. Genetic analyses indicate a close relationship of the fossil *Crocuta* with the extant ones (Barnett et al., 2009, Rohland et al., 2005). The size of these taxa from Loutra Arideas does not even exceed the values of the extant ones.

Ecologically, hyenas and leopards today inhabit subtropical semi-arid deserts to dry forests. Although they are not very dependent on water, they are not able to live in deserts (Honer et al., 2008, Varela et al., 2010). In the Late Pleistocene, hyenas seem to be present in Europe during drier conditions (Nagel et al., 2017). Clearly, these larger carnivores came from a different time span than the mustelids from chamber Ia.

Among the herbivores chamois is the most important finding. It is the first record of this species in Greece and it is a typical form for mountainous areas. *C. ibex*, *C. elaphus* and *D. dama* were probably food remains of the occasional large predator seeking shelter in the cave.

5. Acknowledgments

We are thankful to Rudolf Gold (photographer Department of Palaeontology, University Vienna) for the photos and the compilation of the plates. We are grateful to Dr. Vangelis Vlachos (Aristotle University, Thessaloniki) for the co-ordination of information during the research progress. We thank the Austrian Academy of Sciences, Commission of Quaternary Research, for their long term financial support of the excavations as well as the local authorities for the partial financial support.

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Mustela nivalis	specimen	ml	mW
LAC 1290a mandible fragment sin	p2	1.3	0.9
	p3	1.9	0.9
	p4	2.6	1.2
LAC 10524 sin mandible fragment	p3	broken	
	p4	1.9	0.9
	m1	4.8	1.4

Mustela (*P.*) *putorius*		ml	mW
LAC 4269 maxillar fragment dext	I3*	3.3	2.1
	Csup	4.1	4.2
	P2	2.8	1.9
	P3	4.5	2.5
	P4	8.1	4.3
	M1	3.2	6.2
LAC 2906 manidible fragment sin	i3*	1.1	1.2
	cinf	4.5	3.8
	p2	2.5	1.5
	p3	4.6	2.0
	p4	4.8	2.7
	m1	8.8	5.5
	m2	2.6	2.1
	p2-m2	20.4	
	H below m1	8.1	
LAC 4268 mandible fragment sin	cinf	4.7	3.7
	p2	2.4	2.2
	p3	4.0	2.5
	p4	broken	
	m1	8.8	3.3
	m2	2.4	1.8
	H below m1	9.1	

Martes foina		ml	mW
LAC 6938	M1	5.3	7.6
LAC 10480	M1	5.2	7.7
LAC 14481	P4	9.2	broken
LAC 2892 mandible fragment sin	p1	4,5	2,7
	p2	5,7	2,8
	p3	broken	
LAC 3829	cinf	3.9	3.4
	p1*	1.3	1.5
	p2	4.2	2.6
	p3	5.3	2.6
	p4	6.0	2.8
	m1	9.4	4.2

Meles meles		ml	mW
LAC 7409 maxillar fragment sin	P2	4.4	3.1
	P3	5.7	3.8
	P4	8.6	7.9
LAC 7646	I3	4.6	3.3

Tab. 1: Measurements of the Late Pleistocene mustelid remains from Loutra Almopias (Greece). Measurements in mm and as defined in von den Driesch (1976); * = measurements taken at the alveoli.

Canis lupus	specimen	mL	mW
LAC 13701	P4 fragment	23.8	11.8
LAC 3933	phalange 1	35.4	SD 7.2
LAC 3931		34.8	SD 6.7
Vulpes vulpes	specimen	mL	mW
LAC 7646 dext	I3	3.7	3.0
LAC 3825 dext	Csup	5.6	3.9
LAC 2900 sin	M1	9.9	broken
LAC 5719 sin	M2	5.6	8.4
LAC 2893 sin	cinf	-	4.0
LAC 2897 dext	m1	15.5	5.9
LAC 2896 sin	m1	15.7	5.6
LAC 3827 sin	p2	8.0	3.2
LAC 4266 dext	p2	8.1	3.0
LAC 3828 sin	p4	8.8	4.0
LAC 3826 md sin	p1	(4.0)	
alveoli only	p2	(7.3)	
	p3	(9.3)	
	p4	(9.9)	
LAC 2901+4267 md sin	p4 in crypt		
refitted	m1	16.5	6.0
	m2	7.6	5.1
	m3	in crypt	

Tab. 2: Measurements of the Late Pleistocene canid remains from Loutra Almopias (Greece). Measurements in mm and as defined in von den Driesch (1976); * = measurements taken at the alveoli.

Panthera pardus	specimen	mL	mW	mH
LAC 13268 mx frag. dext.	M1*	3.1	6.9	
	P4*	23.3	12.6	
*measured at the alveolus	P3	17.4	8.5	
() minmal	P2*	6.3	4.4	
	Csup*	15.7	13.8	
	I3*	8.5	6.2	
	I2*	6.8	3.1	
LAC 9980 dext	Csup	13.5	10.7	(61.9)
LAC 3978 sin	m1	19.2	8.5	
Postcranial remains		mL	Lp	Wp
LAC 13284 sin	radius	196	24.7	16.6
LAC 13530 sin	radius frag.	-	24.6	18.4
		mL	DPa	DO
LAC 8385b sin	ulna		35.3	30.5
LAC 18779 sin	ulna		(30.4)	(30.1)
			Lp	Wp
LAC 3913 dext	metatarsale 3		16.0	11.5
LAC 4170 dext	phalange 1		35.5	
LAC 2628	phalange 2		30.2	
LAC 5813	phalange 2		30.Mai	

Crocuta crocuta	specimen	mL	mW	mH
LAC 9150 sin	Csup	15.2	13.0	63.3
LAC 6629 dext.	I1	7.4	5.2	
LAC 11788 sin	I1	7.1	5.4	
LAC 6862 sin	I2	8.7	6.5	
LAC 11823 dext	I3	8,9	8.0	
LAC 7097 dext	Cinf	15.7	12.9	63.5
LAC 8475 dext	p4	22.7	14.4	worn
Postcranial remains		mL	Wp	Wd
LAC 9172 sin	humerus	-	-	59.3 x 44.5
LAC 13675 dext.	ulna	-		
LAC 6282 sin	radius	224.8	-	43.7 x 27.3
LAC 7225 dext.	radius	227.3	36.6 x 20.6	42.4 x 26.2
LAC 11060 sin	femur	236.0	(59.7 x 25.4)	(40.3 x 30.3)
LAC 9283 detx.	tibia	193.3	- x 57.1	34.2 x 26.1
LAC 8179 sin	calcaneus	61.5	27.7 (mW)	
LAC 9365 sin	Mc 2	79.61	15.6 x 19.0	16.6 x 16.6
LAC 7047 dext.	Mc 4	82.26	11.9 x 20.2	14.1 x 14.1
LAC 9002 sin	Mc 4	82.43	10.9 x 18.0	13.7 x 17.7
LAC 12632 sin	Mc 5	68.83	12.2 x 18.6	12.7 x 13.1
LAC 13638 dext.	Mc 5	68.73	12.4 x 18.9	12.9 x 13.4

Tab. 3: Measurements of the Late Pleistocene felids and *Crocuta crocuta* remains from Loutra Almopias (Greece). Measurements in mm and as defined in von den Driesch (1976); * = measurements taken at the alveolie.

Plate 1

Fig. 1. *Mustela nivalis* LAC 1290a, left mandible fragment with p2-p4; a – buccal view; b – lingual view.

Fig. 2. *Martes foina* LAC 3829, left mandible fragment with cinf, alveolus of p1, p2-m1; a – buccal view; b – lingual view.

Fig. 3. *Mustela* (*Putorius*) *putorius* LAC 4268, left mandible fragment with root of broken canine, p2, p3, distal part of p4, m1 and m2; a – buccal view; b – lingual view; c – occlusal view.

Fig. 4. *Mustela* (*Putorius*) *putorius* LAC 4269, right maxillar fragment with Csup, P1-P4 and M1; occlusal view.

Fig. 5. *Meles meles* LAC 7409, left maxillar fragment refitted with P3-M1 (alv.); occlusal view.

Fig. 6. *Vulpes vulpes* LAC 2901 and LAC 4267, refitted; left mandible with p4 and m3 still in crypt and m2 not fully erupted; a – buccal view; b – lingual view.

Fig. 7. *Martes martes* LAC 7481, isolated left M1; occlusal view.

Fig. 8. *Panthera pardus* LAC 3978 left m1; a – buccal view; b – lingual view.

Fig. 9. *Crocuta crocuta* LAC 8475 right p4; a – buccal view; b – lingual view.

Fig. 10. *Canis lupus* LAC 13701 right P4 fragment, lingual view.

Plate 1

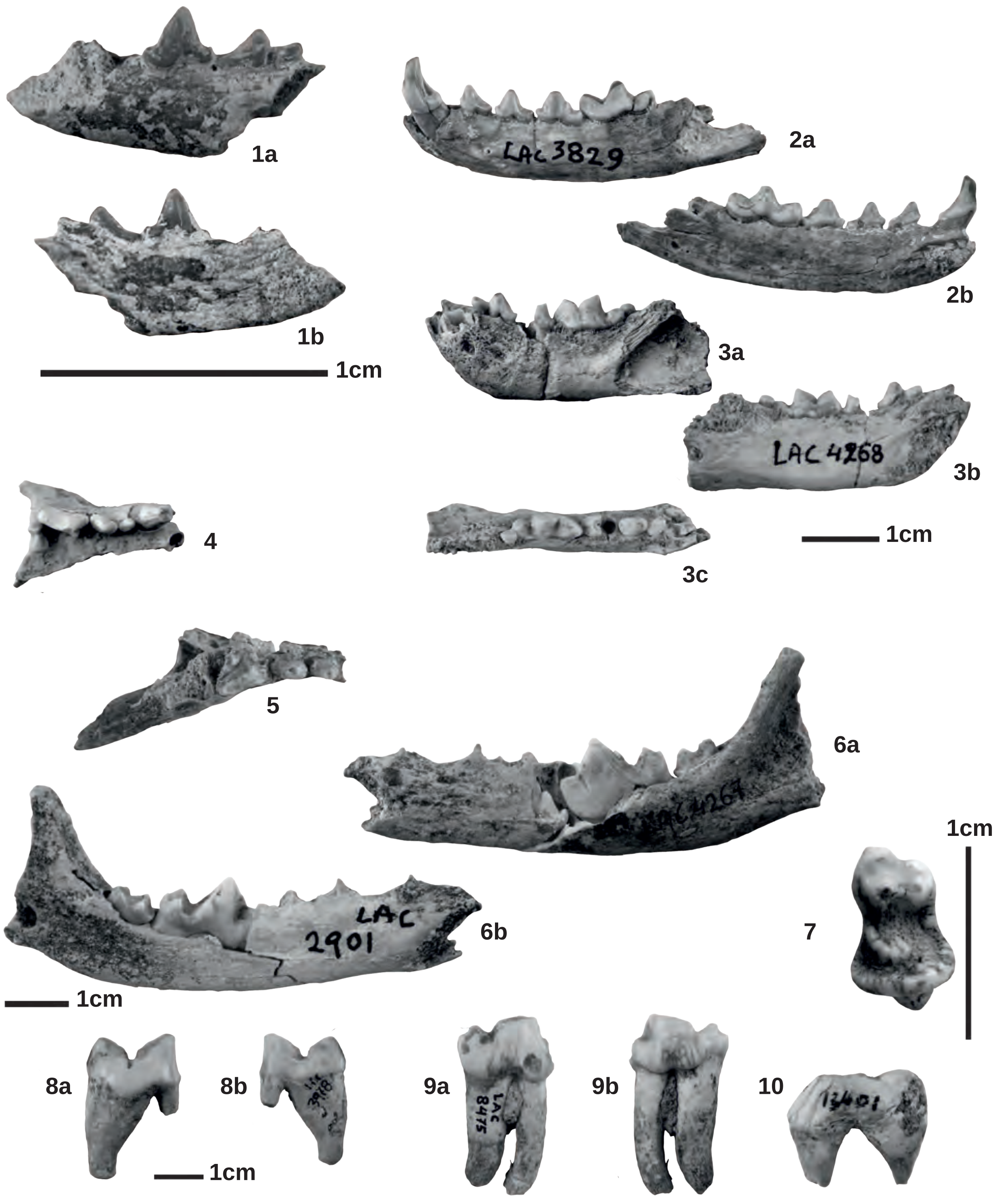

1a
1b
1cm
2a
LAC 3829
2b
3a
3b
LAC 4268
3c
1cm
4
5
6a
LAC 4267
6b
LAC 2901
1cm
7
1cm
8a
8b
LAC 3918
1cm
9a
LAC 8475
9b
10
13401

Plate 2

Fig. 1. *Panthera pardus* LAC 13268 right cranium fragment with P3; a – buccal view; b – lingual view.

Fig. 2. *Crocuta crocuta* LAC 9172 left humerus.

Fig. 3. *Crocuta crocuta* LAC 7225 right radius and LAC 13675 right ulna.

Fig. 4. *Crocuta crocuta* LAC 8179a left calcaneus.

Fig. 5. *Crocuta crocuta* LAC 9283 right tibia.

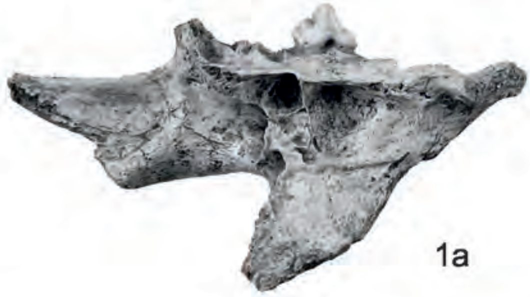
Fig. 6. Comparison of astragalus of *Rupicapra rupicapra*. 6a - LAC 11800, 6b - PIUW 1882.

Fig. 7. Comparison of middle phalanx of *Rupicapra rupicapra*. 7a - LAC 8796, 7b - PIUW 1773.

Fig. 8. *Crocuta crocuta* LAC 9365 Mc 2, LAC 6274 Mc 3, LAC 7047 Mc4 and LAC 13638 Mc 5; probably from one individual. a – proximal joint facets, b – anterior view.

Scale = 1 cm

Plate 2



1a

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2

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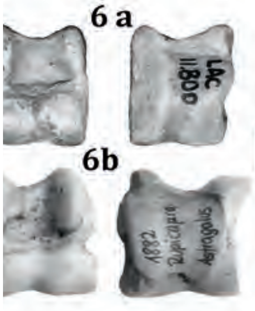

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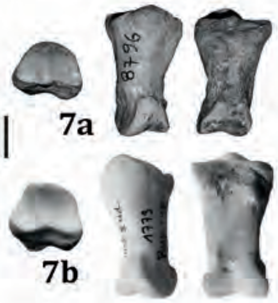

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The highlights of the cave bear research in Slovakian Western Carpathians

Martin Sabol [1] & Branislav Šmída [2]

Abstract

Fossil remains of cave bears (*Ursus* ex gr. *spelaeus*) are known from Slovak caves at least from the Middle Age. Originally attributed to dragons and giants, these have been the object of the scientific study for almost 300 years. This research yielded so far many data on the taxonomy, phylogeny, palaeoecology, and palaeobiology of this one of the most famous extinct Pleistocene animals. The most important highlights of this cave bear research in the Slovakian Western Carpathians are presented.

Zusammenfassung

Fossile Überreste von Höhlenbären (*Ursus* ex gr. *spelaeus*) sind aus slowakischen Höhlen zumindest seit dem Mittelalter bekannt. Ursprünglich Drachen und Riesen zugeschrieben, sind sie seit fast 300 Jahren Gegenstand der Wissenschaft. Bis heute liefert die Forschung eines der berühmtesten ausgestrobenen pleistozänen Tieres, Daten zur Taxonomie, Phylogenie, Paläoökologie und Paläobiologie. Die wichtigsten Erkenntnisse der Höhlenbärenforschung in den slowakischen Westkarpaten werden hier vorgestellt.

Key words: cave bear, Pleistocene, Western Carpathians, Slovakia

1. Introduction

Nearly 300 years of cave bear research in Slovakia, i.e. research focused on the fossils of bears from the *spelaeus*-group (Sabol, 2017), yielded many important data on these animals inseparably connected with European Late Pleistocene mammalian communities. Fossils of cave bears occur in every larger horizontal cave. To date their dental and skeletal remains have been found in deposits of more than one hundred Slovak karst sites, and other new localities are reported every year (Sabol, 2001). Simultaneously with that, new approaches in the field and laboratory researches based on modern methods and technologies are applied thus yielding new information about “old dragon bones”.

2. Highlights (Fig. 1)

The stratigraphically earliest fossil record of cave bears in the Slovak territory of the Western Carpathians is probably reported from Trojuholník Cave in the Borinka Karst (Malé Karpaty Mts.) near Bratislava capital city. Although fossil remains were attributed to cave bears probably from the Middle Pleniglacial (Sabol, 2005), these show also several primitive characters in dentition, with the predominance of rather simpler morphotypes in premolars (A, A/D, B in P4s and C1 and C3 in p4s). Also smaller dimensions of teeth, comparable rather with those of *Ursus deningeri*, and some taphonomic phenomena, such as a skull deformed by overlying sediments, indicating a longer sedimentary history, can point out a different taxonomic position of these cave bear fossils (*U. spelaeus* ssp.) than in cases of finds from other Slovak sites (*U. ingressus*).

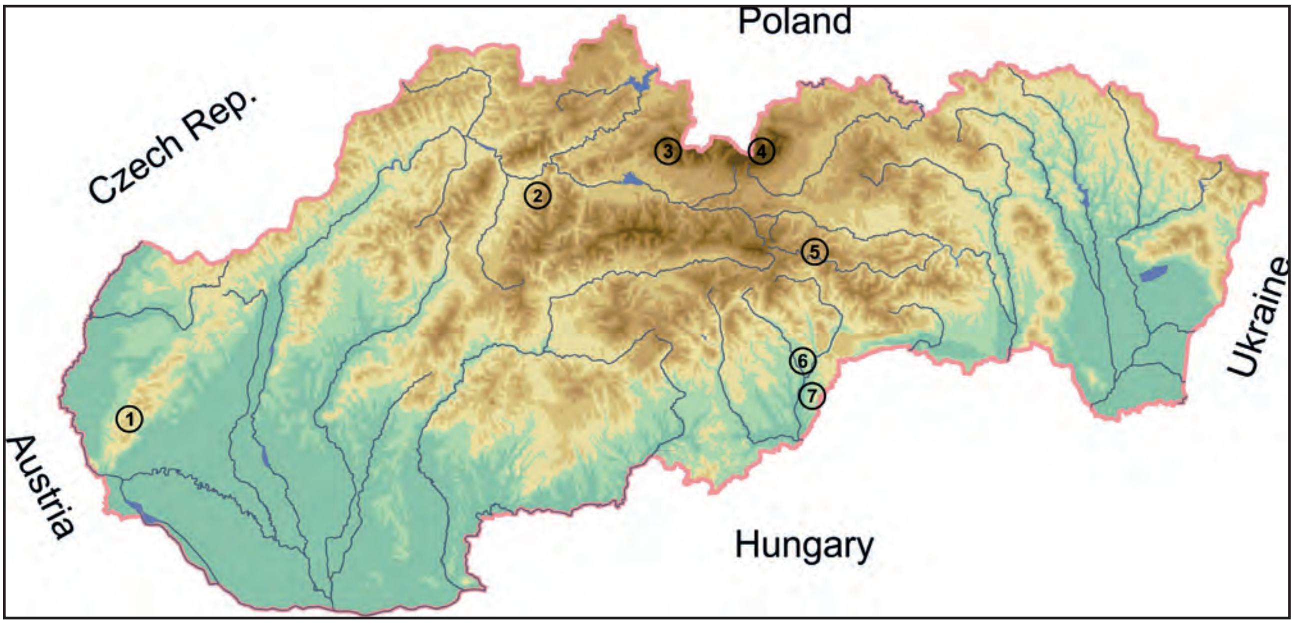

Fig. 1: Location of Slovak cave bear sites mentioned in the text.
1) Trojuholník Cave, 2) Jaskyňa Izabely Textorisovej Cave, 3) Medvedia jaskyňa Cave in the Západné Tatry Mts., 4) Javorinka Cave and Mesačný tieň Cave, 5) Medvedia jaskyňa Cave in the Slovenský raj Mts., 6) Peško Cave, 7) Činčianska jaskyňa Cave.

So far the last occurrence of cave bears in the Slovak territory of the Western Carpathians is recorded from Jaskyňa Izabely Textorisovej Cave in the Veľká Fatra Mts. near Turčiansky Svätý Martin town. The ^{14}C-AMS dating of two metapodial bones in the Vienna VERA-Laboratory yielded radiometric dates 26,460 ± 180 (VERA-5680) and 24,640 ± 170 (VERA-5679) years BP (Sabol et al., 2014). These data indicate the possible extinction period of cave bears in Western Carpathians just before the beginning of the Last Glacial Maximum or during its initial phase which is in good concordance with data on the species disappearing in the Alps and adjacent areas (Pacher & Stuart, 2009).

The highest occurrence of cave bear fossil remains in Slovakia has until recently been reported from Javorinka Cave in the western part of the Kolový Úplaz Massif on the western slope of the Javorová dolina Valley on the northern side of the Tatry Mts. (Sabol et al., 2014). The cave bear fossils, dated to 51,000 + 4,500 / - 2,900 years BP, have been found here at altitudes between 1,525 and 1,559 m. However, new discoveries in Mesačný tieň Cave with its entrance at 1,767 metres above sea level yielded updated information about the highest situated Slovak fossil record of cave bears (Fig. 2). The cave, situated in the Javorinská Široká Massif in the Tatry Mts., is the second longest (34,085 m) and the third deepest (-451 m) cave in Slovakia. The highest located fossils of cave bears, attributed to *U. ingressus* (Popović et al., 2015), have been found in the Medvedia chodba cave part at an elevation of 1,587 metres. Their first radiometric dating yielded an age of 49,110 years BP (Popović et al., 2016), which corresponds relatively well with the age of fossil record from Javorinka Cave, indicating the MIS 3 period.

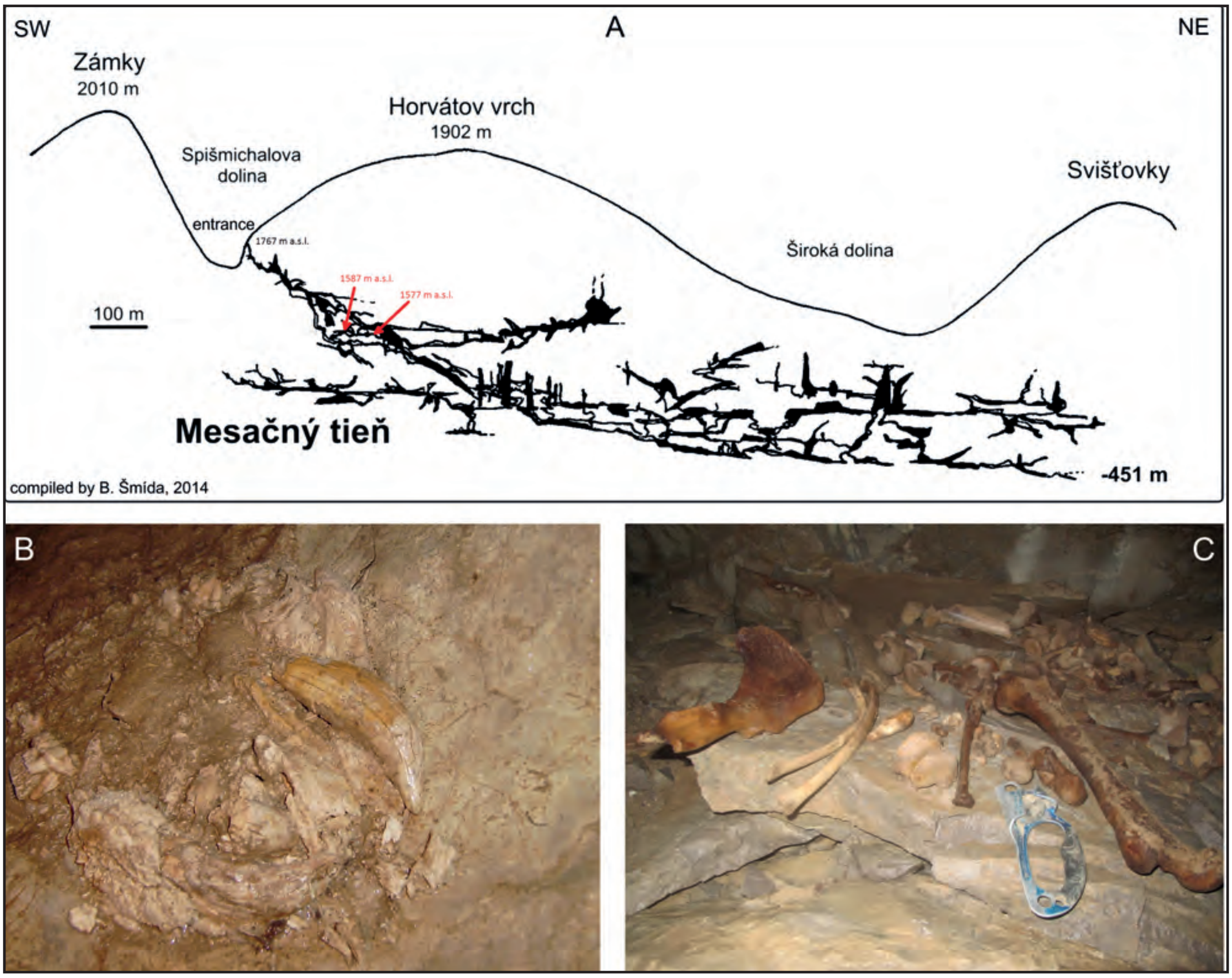

Fig. 2: The high-alpine fossil record of cave bears in Mesačný tieň Cave.

A) cross-section of the Javorinská Široká Massif with the cave and highlighted places, where cave bear fossils have been found, B) cave bear fossil record at an altitude 1,577 metres, C) cave bear fossil record at an altitude 1,587 metres. Cross-section and photos: B. Šmída.

Against the abovementioned, the lowest recorded occurrence of cave bear fossils in the Slovak territory is so far reported from two caves situated in southern Slovakia at about 200 metres altitude. The lower situated site is 17 metres long fluvial-karst Peško Cave in the Rimavská kotlina Basin (Rožňava district) with its entrance at 200 metres above sea level. Ložek et al., (1989) found here a fragment of cave bear upper canine (*Ursus* cf. *spelaeus*) in complex of three layers (10 to 12) with a vertebrate fossil assemblage from the Last Glacial (originally dated to W2-W3).

The larger quantity of cave bear fossil remains is known from Čenčianska jaskyňa Cave in the Bodvianska pahorkatina Upland, Revúca district. The entrance of this 28 metres long fluvial-karst cave is located at of 215 metres altitude.

The fossil material, discovered at the site in 1978 and consisting of 26 teeth, five cranial fragments and one fragmented mandible of cave bears from the Last Glacial, was later evaluated by Sabol (1997, 2000).

The fossil record of cave bears is relatively multifarious in Slovak caves – from several isolated finds of teeth or bones up to more or less completely preserved skeletons of individuals of different ages, sexes and sizes. Up to now, the largest cave bear specimen is from Medvedia jaskyňa Cave in the Slovenský raj Mts. in Eastern Slovakia. It is a skull belonging to a huge adult male. The maximum length of this cranial fossil, housed in the Slovak Museum of Nature Protection and Speleology in Liptovský Mikuláš (No. 501/77) is 571.4 mm, with the condylobasal length 513.0 mm (Sabol, 2002). The weight of this male could certainly reach over 500 kg.

Medvedia jaskyňa Cave in the Slovenský raj Mts. is also the site where the largest quantity of cave bear fossil remains have been found in the Slovak territory of the Western Carpathians. The palaeontological record of this cave, discovered in 1952, was preliminarily investigated by Fejfar (1953) and later by Janáčik & Schmidt (1965) as well as by Sabol (1997, 2000, 2002). However, the systematic field campaign – the first modern one within the Slovakian cave bear research – was carried out by a scientific team composed of experts from Austria (Vienna University and Austrian Academy of Sciences) and Slovakia (Comenius University in Bratislava) under the direction of Prof. Gernot Rabeder (Sabol et al., 2008b). During the triennial campaign (2007-2009), more than 4,300 samples of fossils were excavated from three pits with the participation of 57 European researchers and students.

From the time of the first scientific reports on cave bear findings in the territory of Slovakian Western Carpathians (Sabol, 2017), many new sites with fossil remains of this extraordinary extinct animal have been discovered. In a few cases, research has revealed several peculiar finds. The fossil remains of cave bears influenced by various taphonomic and pathological processes, belong among the most interesting ones within this group of finds. One of the most exceptional is a skeleton of a three-legged cave bear female in Jaskyňa Izabely Textorisovej Cave (Sabol et al., 2008a). Her left forearm have been attacked by large predator or violently removed in the case of injury, and the preserved part of the limb consisted only of a damaged humerus. The bone was pathologically modified by chronic inflammatory processes, which resulted in limited movement of this animal during its remaining life in the harsh conditions of the Last Glacial wilds. Another extraordinary, so far not detailed described findings are fossil remains of cave bear female and (her?) cub in one small hall of Medvedia jaskyňa Cave in the Západné Tatry Mts. together with the skeleton of a prime adult male of cave lion (Sabol et al., 2018). Their common presence in one cave part could indicate a prehistoric wildlife drama that took place over 40,000 years ago.

3. Conclusion

The Slovak territory of the Western Carpathians with more than 4,000 caves is rich in finds of cave bear fossils. However, the future research has to bring more detailed analyses, focused predominantly on taxonomical studies based on palaeogenetic (ancient DNA) data, on the reconstruction of cave bear palaeoenvironment on the basis of isotopic data, as well as on the study of population structure, age of death, causes of death, and extinction reasons of this bear species. More detailed taphonomic data can yield other information for its interaction with other species and environment. To prevent the return of cave bear research in Slovakia to the level of 20th century, a sufficient financial funding and cooperation with researchers from various world scientific institutions will be needed. Only then can it yield other interesting and important data about West Carpathian bears from the *spelaeus*-group.

4. Acknowledgements

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Hunting horse at the Danube – A Late Pleistocene cannon bone with cut-marks from Vienna-Nussdorf and its (re)discovery

Oliver Schmitsberger [1], Florian A. Fladerer [2], Marc Händel [1], Konstantina Saliari [3], Ursula Göhlich [3], Rachel Hopkins [4], Gerhard Forstenpointner [5], William Davies [6], Christine Neugebauer-Maresch [1]

Abstract

A main goal of the project "Gog & Magog – the Time of Mammoth Hunters in Vienna" was establishing a database for recording Pleistocene mammal bones from different public collections. Main attention was laid on anthropogenic manipulation signatures such as cut-marks or fire influence - with the goal to gather information concerning formerly unknown Palaeolithic sites. ^{14}C-dating of a horse metacarpal bone with skinning marks produced an age of roughly 38,700 - 36,500 cal BC. This is the first evidence for the presence of Early Upper Palaeolithic hunter-gatherers in Vienna.

Zusammenfassung

Im Rahmen des Projekts „Gog & Magog – Die Mammutjägerzeit in Wien" wurde eine Datenbank der in unterschiedlichen öffentlichen Sammlungen vorhandenen pleistozänen Tierknochen aus Wien erstellt. Ein Hauptaugenmerk wurde dabei auf anthropogene Manipulationsspuren wie Schnittmarken und Feuereinwirkung gelegt, um Hinweise auf bislang unbekannte paläolithische Fundstellen zu erlangen. Die ^{14}C-Datierung eines Pferde-Metacarpales mit Schnittspuren, wie sie bei der Fellablösung entstehen, ergab ein Alter von 38.700 - 36.500 cal BC. Dies ist der erste sichere Nachweis für die Anwesenheit von Wildbeutern des älteren Aurignacien auf dem Gebiet des heutigen Wien.

Key words: *Equus* sp., Late Pleistocene, cut marks, Early Upper Palaeolithic, Aurignacian, Vienna, ^{14}C-dating

1. Introduction

1.1 Basic situation

In terms of the archaeological evidence Vienna is mainly renowned for its rich Roman and Medieval heritage. Due to its geographic position, the city, however, has at all times attracted both large herbivores and humans. It is therefore not surprising that also rich prehistoric remains have been recorded. This is mainly due to the position at the east-west-transition along the Danube, as well as the prominent geomorphological situation with landmarks such as the Bisamberg and the Leopoldsberg hills in the north or the Wienerberg and the Laaer Berg hills in the south.

As always the case at popular settlement locations, intensive construction works caused massive destruction of archaeological information early on. On the other hand, earthwork shed light on the earliest prehistoric period in our region, the Palaeolithic. Best known of all these finds is a mammoth bone, which was recovered during the construction of the north tower of St. Stephen`s cathedral (Stephansdom) in the late Middle Ages. It was exhibited on the outer church wall for a long time, labelled with “AEIOU“ (the motto of emperor Friedrich III) and “1443“, the year of its discovery. In those times, long before Pleistocene megafauna fossils became commonly known, mammoth bones were interpreted as remains of giants. Systematic research on human lifeways during the Ice Age was never conducted in Vienna until now. Only scattered artefacts from insecure archaeological context, which could only roughly be assigned to the Upper Palaeolithic, were known so far (see Schmitsberger & Neugebauer-Maresch 2016a, 2016b), and there is only one publication specifically dedicated to mammoths, the “giants of the ice age” (Vávra 2002).

In 2015-2016, the Cultural Administration Office of the City of Vienna (MA 7) funded the documentation of old finds from museums and other scientific collections, their interpretation and additional field surveys (Project “Gog & Magog – the Time of Mammoth Hunters in Vienna”, 1.1.2015-31.8.2016, directed by C. Neugebauer-Maresch). The project, named after the biblical giants, was hosted at the Institute for Oriental and European Archaeology (OREA) of the Austrian Academy of Sciences (ÖAW). Its goal was the reconstruction of a Palaeolithic find landscape in the Vienna area with the additional objective to define relevant areas of high archaeological potential, and to officially protect these if necessary.

Palaeolithic research is commonly interdisciplinary because only the reconstruction of the environmental conditions and the available resources allow assessments concerning the way of life of Ice Age human societies. Accordingly, this work was conducted in cooperation with various specialists from different research fields. The archaeological part was carried out by O. Schmitsberger and the palaeontological work by K. Saliari, with the support of U. Göhlich and F. A. Fladerer. Additionally collaborations were established with M. Penz (Stadtarchäologie Vienna) and R. Hopkins (at that time affiliated at Oxford University), who was responsible for the dating of the bones in the framework of her dissertation. Furthermore, there was cooperation with the Federal Monuments Authority Austria (BDA, C. Blesl) and E. Pucher (1st Zoological Department, Archaeozoological Collection of the NHMW/Natural History Museum Vienna).

1.2 Projects aims and approach

Summarizing the state of the art in 2015 nearly no secured information resp. only very sparse hints for the presence of Palaeolithic people in Vienna existed. Given the geographical position at the east-west passage of the Danube valley and specifically the striking geomorphological bottleneck situation of the Vienna Gate (cut of the Danube river through the Northern Alpine – i.e. the Rheno-Danubian

- Flysch Zone) between the Bisamberg and the Leopoldsberg (Fig. 1), encampments of Palaeolithic hunter-gatherer groups definitely had to be assumed. Moreover, the presence of such groups had to be expected due to the spatial extent of the study area and the generally favourable environmental conditions.

Therefore, the primary goal of the project was the compilation of indicators for (Upper-) Palaeolithic sites in Vienna, their verification or falsification and the dating of insecure/problematic old assemblages, as well as field investigations. The project was structured in three main work-steps. The first comprised delimitation and definition of promising areas or hot spots based on old collections of archaeological and especially palaeontological/archaeozoological finds including topographic and geological information. This also included creating a database of Pleistocene faunal remains from Vienna with the main goal to document 1) find concentrations, and 2) processing traces on fossil animal bones, which would allow us to infer the presence of Palaeolithic hunter-gatherer-groups in this area. The second stage included field surveys. Lastly, core drillings (at two different locations) and the recording of a loess profile (at a third one) for the recognition of potential Palaeolithic cultural layers were conducted (SCHMITSBERGER & NEUGEBAUER-MARESCH 2016a, 2016b).

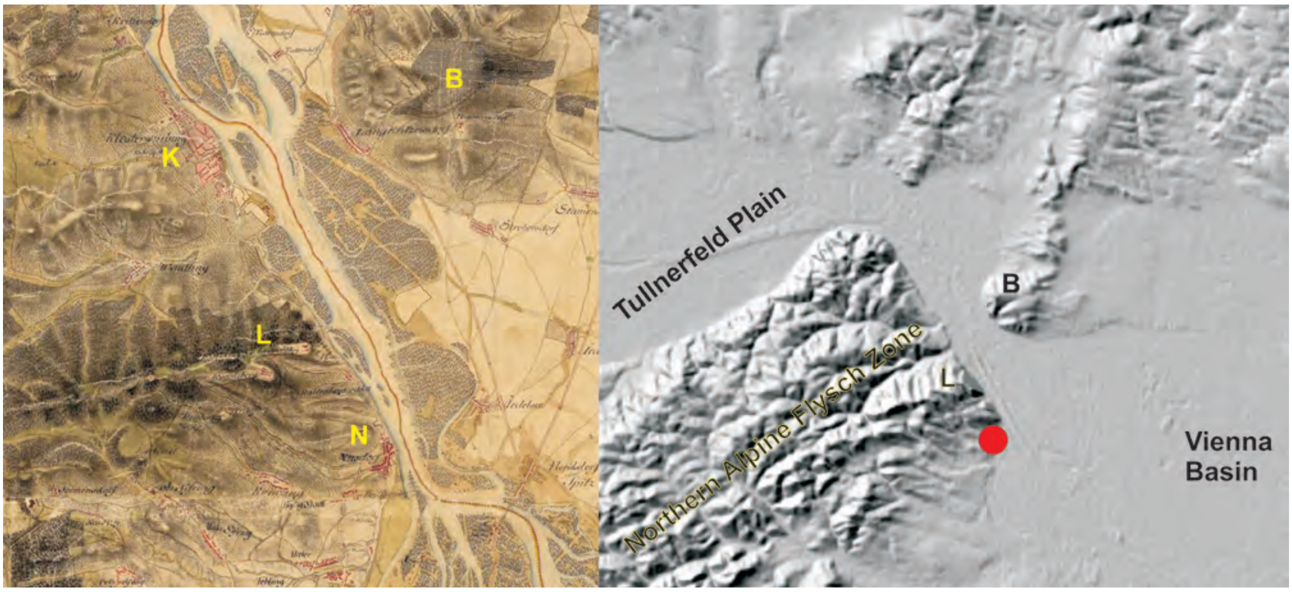

Fig. 1: Left: the Vienna Gate between Kahlenberg/Leopoldsberg (L) and Bisamberg (B) resp. Klosterneuburg (K) and Vienna-Nussdorf (N) (map: Josephinische Landesaufnahme 1763-1785). Right: Geomorphological situation of the region surrounding the Vienna Gate at smaller scale (Airborne Laser Scan © Amap Austrian Map/BEV), red dot marks Nussdorf.

Due to the notable concentration of Pleistocene mammal bones discovered at the loess covered Wienerwald foothills located close to the Danube in the 19th district of Vienna (especially at the localities Heiligenstadt, Nussdorf and Hohe Warte) (see 3.) it was assumed that they were, at least partially, accumulated by humans. Therefore, bone finds still available today were examined for possible manipulation marks. Many of these fossils were recovered in the 19th century. It is not surprising, that only eye-catching animal bones were collected and inconspicuous but supposedly present stone tools were ignored, as they were not recognized by the workers. One of the reasons is that prehistoric archaeology, especially the Palaeolithic, was at its very infancy at this time and the appearance (i.e. morphology) of stone artefacts – at least in Austria – largely not even known.

The survey of the animal bones primarily focused on the detection of manipulation marks like incisions or fire influence. Although some specimens could be classified as „potentially anthropogenically manipulated“ (see below), F. A. Fladerer was only able to verify cut marks on one horse metacarpal. All others were either not anthropogenic (e.g. bite marks), or so called excavation artefacts and therefore recent damages.

2. Recording the Pleistocene animal bones from Vienna in a database

2.1 Materials and methods of documentation

The faunal remains are almost exclusively accidental finds from construction sites and brickyards. Most of them were found in the 19th and the beginning of the 20th century. It cannot be excluded that Pleistocene bones were mixed with younger ones at some sites.

The material of the current study is housed in the following collections: Natural History Museum Vienna (NHMW), Wien Museum (Depot Himberg), University of Vienna (Department of Palaeontology), Geological Survey of Austria, and from the city district museums of Floridsdorf, Liesing, Hietzing, Döbling and Simmering. The individual collections differ significantly in terms of available information.

Altogether, approximately 810 datasets were recorded, comprising both individual bones and partial skeletons, the latter counting also only as one dataset. Additionally, the finds were mapped using a GIS-program.

The most important information recorded when documenting the bones were: a) Name of the actual collection and, if there had been a transfer, the name of the original collection; b) inventory number (and any information written on the bones); c) faunal information (species, skeletal elements, number of elements and fragments); d) site location; e) any kind of taphonomic observations; f) geological setting/type of sediment (loess, gravel); g) dating; h) references; i) additional observations.

The steps of documentation were 1) inventory creation, followed by 2) quantification and 3) determination. The quantification of the material is based on the number of bones and fragments. Unfortunately it was not possible to interpret the minimal numbers of individuals. Skeletons and partial skeletons were noted as well. Only a part of the bones had aready be determined. If possible, additional determinations were conducted in the course of the documentation work. The majority of the material consisted of bones which could not clearly be assigned to a species and had to be lumped together in groups: large mammals (in the size range of mammoth and rhinos), medium sized mammals (approximately of Equidae size), and small mammals.

Similar to the classification of bones according to faunal size groups, the skeletal elements were grouped into the following categories: small bones, long bones, flat/tabular bones, skull fragments and indeterminable fragments.

2.2 Analysis on family level - the equids

In the investigated assemblage, Equids constitute the second most common family after Elephantidae. The majority of horse remains are teeth, metapodials and phalanges. Following the previous determinations, the most common species would be so-called "*Equus ferus fossilis*", however, also *Equus hydruntinus*, *Equus woldrichi*, and "*Equus abeli*" occur. Some fragments were only identified as "Equidae indet". It has to be noted that there were problems with some previous determinations such as "*Equus abeli*". According to Nobis (1971), the description of "*Equus abeli*" by Antonius (1913) is fundamentally wrong: Nobis (1971) reviewed the measurements of Equus abeli and observed that for the description of this "species" remains of different horse individuals were combined, partly even from medieval animals. "*Equus woldrichi*" is also problematic. There exist only very few fossils assigned to this species which are not described adequately and following the literature these remains are additionally of insecure date (Forsten & Dimitrijević, 2004).

The distribution of the equids differs from that of the mammoths – horses derive predominantly from Nussdorf/Heiligenstadt and the Laaerberg locality (Frank & Rabeder 1997a, 1997b).

Only for a little number of bones there is specific information regarding the geological setting; most of them had been preserved in a loess milieu and only very few derive from gravelly sediments.

2.3 Manipulation marks - proof of human activity

It was only possible in a few cases to clearly decide whether breakages on bones were recent or old. Another difficulty was the partly poor preservation of the fossils. Some surfaces were eroded to such an extent that potential manipulation marks could not be determined anymore. As mentioned above, some bones with questionable manipulation marks were detected in the course of the recording (e.g. a Phalanx 1 and a calcaneus of *Bison priscus* from Heiligenstadt). Only the marks on a horse metacarpal stood up to scrutiny and were verified to be actual anthropogenic cut-marks (Fig. 2).

Although the preservation of the animal remains depends on various factors, a dominating presence of specific bones can be observed (see above).

This observation could be of significance regarding natural or anthropogenic selection, however further interpretations are hampered by lacking context information.

With the exception of the Titlgasse site in the 13th district/Hietzing (Schmitsberger & Neugebauer Maresch, 2016b), no cultural layers or secure Palaeolithic stone tools have been recorded in Vienna to date. A possible explanation could be that many of the bones were found in the 19th century and possible associated artefacts were not recognised (see 1.2).

Fig. 2: Equus sp., metacarpal. a medial view, b dorsal view, c palmar view, d lateral view, e proximal view (with borehole from ^{14}C-sampling), f distal view, g: detail of cranial view with incision marks (all photos by A. Schumacher, NHMW).

2.4 Geographical distribution of Pleistocene animal bone finds in Vienna

Pleistocene animal bones are not uniformly distributed throughout Vienna, but show clear find concentrations, especially in Nussdorf/Heiligenstadt (Figs. 3 & 4) and at the Laaerberg hill. The find distribution pattern is governed by several factors. One of the more important aspects is the location of brickyards in 19th century Vienna.

Many of the finds stem from the clay pits of these brickyards, and it is therefore not surprising that especially the above mentioned localities are proportionally richer in animal bones than other areas since many large clay pits were located there.

There are not only geographical deviations in the distribution and number of bone finds, but also regarding the composition of the faunal remains.

To interpret this, a more detailed palaeontological investigation would be necessary. Here, only the find areas of Nussdorf and Heiligenstadt will be adressed.

A wide range of different families and species is represented in the faunal material from Heiligenstadt/Nussdorf.

Fig. 3: Mapping of Pleistocene animal bones in the north-western part of Vienna with a concentration in the Heiligenstadt-Nussdorf area (yellow: with exact location, violet: with approximate location; GIS-graph by K. Saliari).

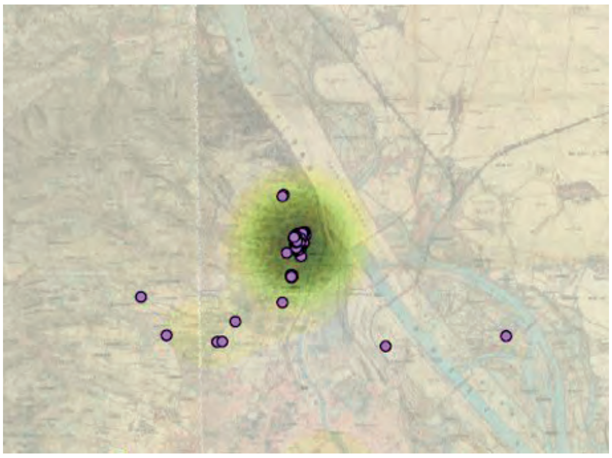

Fig. 4: Kernel Density for bones without exact location shows a clear centre (of altogether two in Vienna) in Nussdorf/Heiligenstadt (GIS-graph by K. Saliari).

It has to be emphasized, that most of these determinations refer to the already existing labels and have not been reviewed in the course of the documentation work, and therefore need not necessarily to be correct in each single case. Determined animal remains belong to Elephantidae (*Mammuthus primigenius, Mammuthus meridionalis*), Equidae (*Equus ferus, Equus hydruntinus*), Bovidae (*Bos primigenius*, *Bison priscus*), Cervidae (*Rangifer tarandus*, *Cervus elaphus*, *Megaloceros giganteus*, *Capreolus capreolus* and possibly *Alces alces*), Rhinocerotidae (*Coeleodonta antiquitatis*), Canidae (*Canis lupus*), Ursidae (*Ursus* sp.), Hyaenidae (*Crocuta spelaea*), Talpidae (*Talpa europaea*), Cricetidae (*Microtus* sp., *Arvicola* sp.), Leporidae (*Lepus europaeus*) and Soricidae (*Sorex* sp.).

According to Frank & Rabeder (1997b), the Nussdorf/Heiligenstadt fauna predominantly dates to the younger part of the Middle Pleistocene. This assessment is mainly based on the small mammals. The main subject of the current paper, the horse metacarpal, shows, that at least in Nussdorf there are Late Pleistocene faunal fossils too.

3. The horse metacarpal from Nussdorf in the palaeontological collection of the NHM Vienna

The fossil (Metacarpale III dext. of a horse *Equus* sp.) was originally located in the collection of the “Imperial & Royal Polytechnic Institute of Vienna” (founded in 1815), nowadays the Vienna Technical University. It is not known, when the specimen was incorporated to collection of the NHMW. The metacarpal was inventoried with the No. NHMW 2016/0111/0001 in the course of sampling for the ^{14}C-dating.

The caption on the historical label (Fig. 5) reads:

> 1870
> Hinterer Metatarsus von
> Equus fossilis (Equus adamiticus Schloth. [=Schlotheim])
> Durchstich bei Nussdorf

K. K. polyt. Institut.
Jahr der Acq. 1870. No ....
Hinterer Metatarsus von
Equus fossilis
(Equus Adamiticus Schloth.)
Durchstich bei
Nussdorf
[illegible]. geol. Sammlung.

Fig. 5: The historic label of the cannon bone (photo by U. Göhlich).

In the same box two more fragments of metapodials are kept, a distal half and a proximal half. The latter derives from a young animal, because it misses the proximal epiphysis. Both of them cannot securely be determined either as metacarpal or as metatarsal.

Equus adamiticus is not a valid species. Also, *Equus fossilis* most likely only indicates that it is a fossil (and not a recent) horse.

The term “Durchstich“ most likely refers to the inlet of the Danube channel. According to these indications, the bone does not seem to have originated from one of the Nussdorf brickyards, where most of the other fossil Nussdorf specimens were recovered.

4. Find location - attempt of reconstruction and geochronological assignment

4.1 Location

Although the label reads “Acquiriert (acquired) 1870“, the year 1870 is not necessarily also the year of the bone`s recovery. The Danube in present day Vienna comprises three (main) river branches; the so-called “Alte Donau”, the former main stream which is not an active branch anymore, the so-called “Neue Donau” (New Danube, the actual/regulated main stream) and the “Donaukanal” (Danube channel).

What is now the Danube channel, was originally a natural side stream of the Danube river, which branched off the old river bed which only existed until 1870 (Fig. 6; see also: Donaukanal, n.d.; For a detailed history of the Viennese Danube river and its streambed changes see Hohensinner et al., 2013a, 2013b, Haidvogl et al., 2013, Sonnlechner et al. , 2013).

The construction of the channel commenced as early as 1598 with an initial channel puncture in the “Wolfsau”. In 1832, an additional channel puncture was carried out at the present day Ostbahnbrücke.

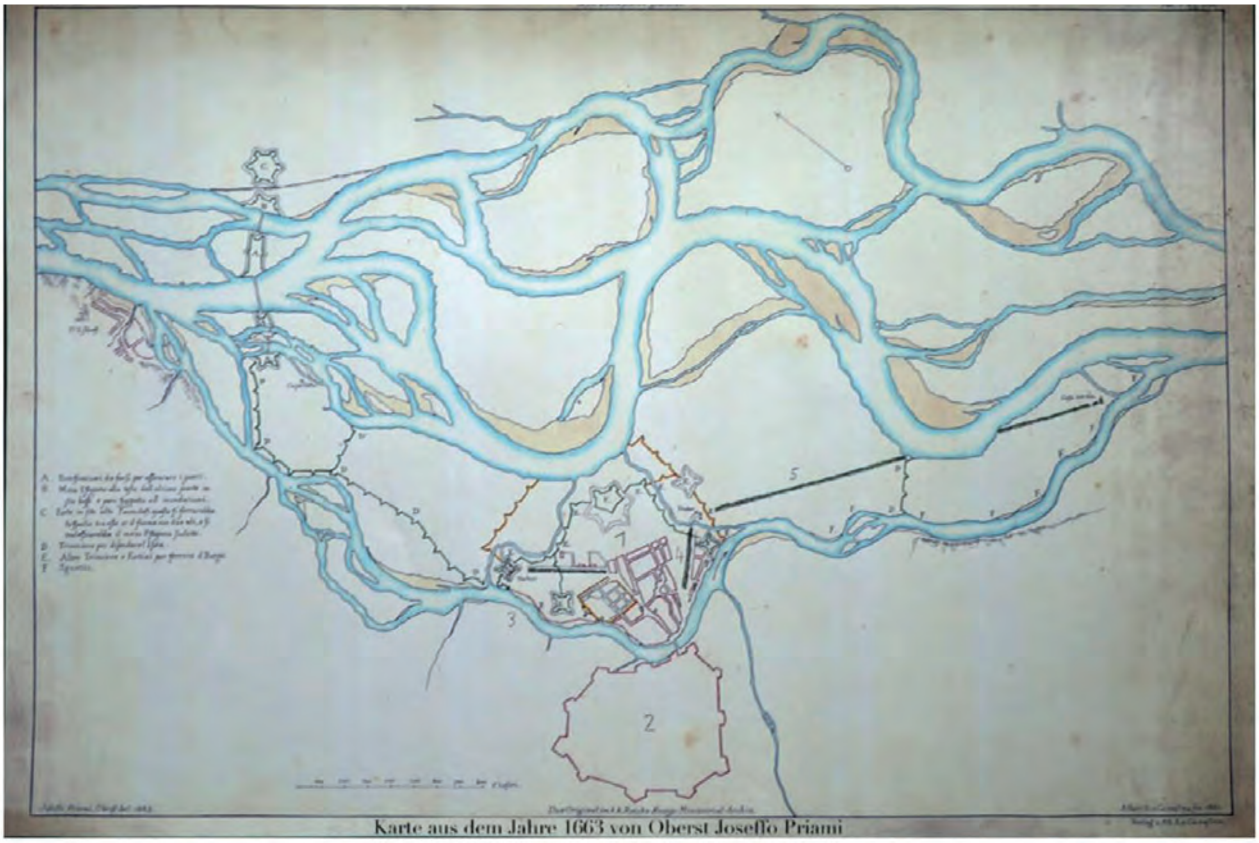

Fig. 6: Map of the Danube in Vienna from 1663 (Joseffo Priami, “Abriß zu Wien zu Versicherung der Brükhen“, earliest detailed illustration of the Danube from Nussdorf to Simmering). The southernmost side stream represents the modern Danube channel; the presumable find spot is located where it branches off the main river (at the left edge, where the former Nussdorf village is also indicated on the map).
© Österreichisches Staatsarchiv / Kartensammlung des Kriegsarchivs.

In the years 1894-1898 intensified construction activities took place in Nussdorf, which is clearly too late for our find.

Most likely the bone was found in the course of the general Danube river regulation 1870-1875 (see: DONAUREGULIERUNG, n.d.). The reason for the regulation of the Danube riverbed between Nussdorf and Albern (today Neue Donau/New Danube) was the frequent flooding of the area. In the course of the creation of the New Danube, the entire new stream bed, which is running between the flood embankments, was named “Wiener Durchstich”. Hence, the find location indicated on the label, is not necessarily related to the Danube channel cutting, although this is very likely.
The modern Danube channel branches off the new main stream, commissioned in 1875, at Nussdorf shortly before the Nussdorf sluice complex (Figs. 7 & 8).
As already mentioned, the “Durchstich” (cutting/puncture) created in the course of the regulation of the Danube between 1868/1870 and 1875 does not predominantly refer to the Danube channel but rather to the New Danube, which now constitutes the main river bed.

Fig. 7: View from the eastern Nussberg foothill towards the Old Danube (left in the background) and the regulated Danube (in the centre). The branch in the foreground, immediately behind the houses of the Nussdorf village, is the Danube channel. The find spot is most likely located at the very left edge at the channel inlet. Drawing by Hugo Darnaut. Vorzeichnung zum „Kronprinzenwerk“ (Die österreichisch-ungarische Monarchie in Wort und Bild, Wien 1886-1902), Bd. „Wien“, 1886, 323; vor 1886. © ÖNB Bildarchiv und Grafiksammlung - http://data.onb.ac.at/rec/baa12956209

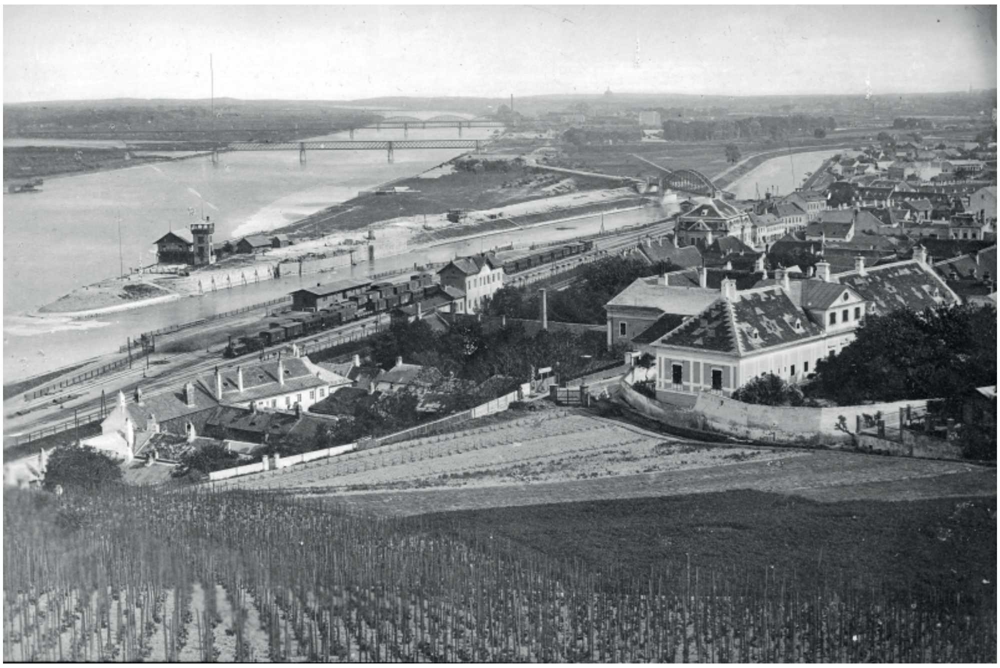

Fig. 8: View from the slope of the Nussberg hill towards the Nussdorf village, the “Brigittaspitz“ and the Danube bridges. The old Nussdorf sluice complex is located in the centre. Photo before 1894, the find spot is again in the foreground to the very left.
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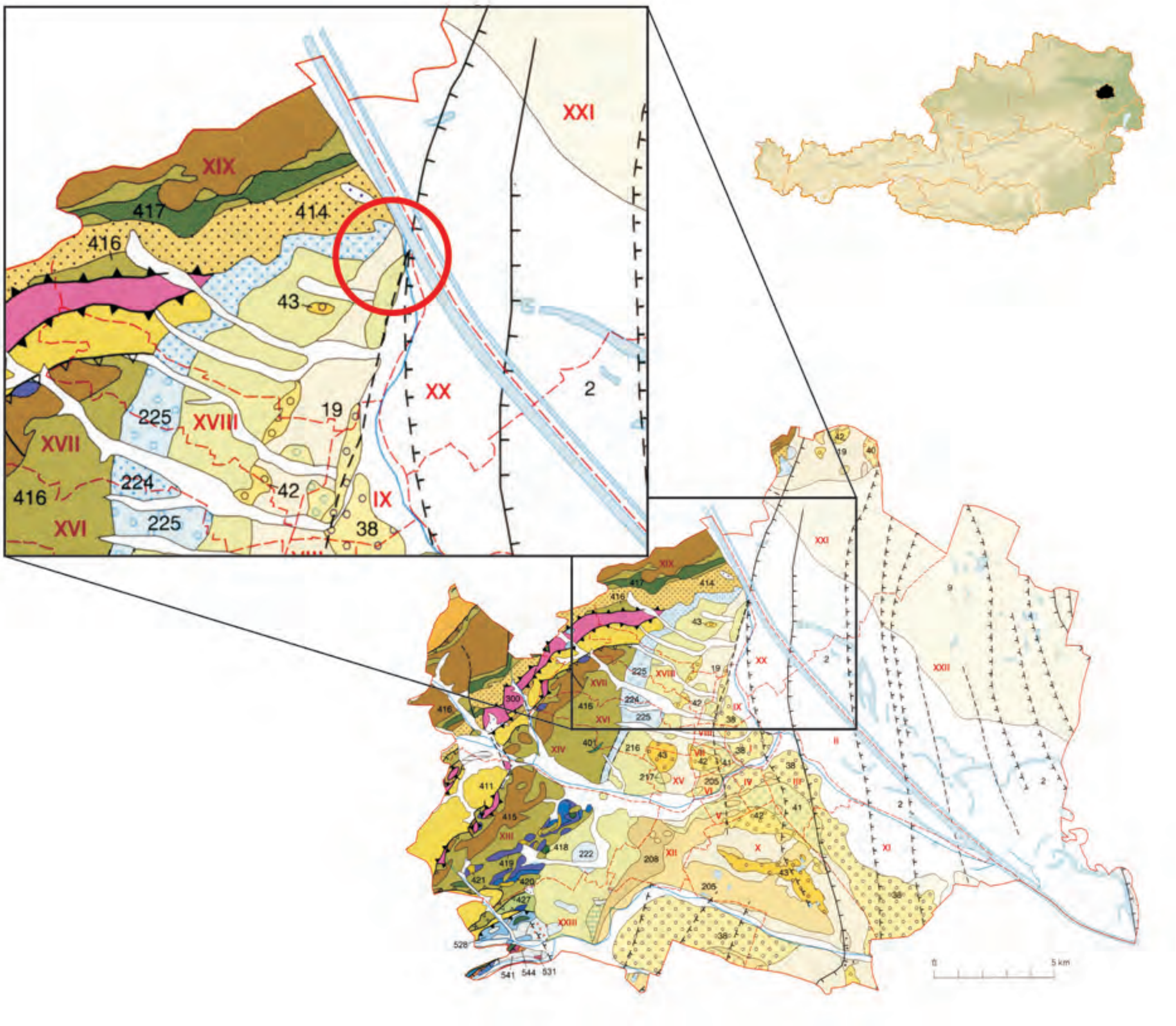

Fig. 9: Geological map of Vienna (modified after Summesberger, 2011, 63; based on Geological Map of Lower Austria 1:200.000, Schnabel et al, 2002). 19: loess; 38: Stadt terrace; 40-43: earlier Pleistocene Danube terraces; 2, 9: Prater terrace and Holocene gravels; light blue (especially 224) and light green (especially 216): Neogene sediments (Badenian and Sarmatian).

Therefore, due to the terminological confusion of the term “Durchstich” and its use for both the Danube channel as well as the New Danube, the meaning of this term on the label for the bone is insecure. In principle, the bone could therefore either have derived from the cutting of the New Danube, or from the channel inlet. In any case it was discovered at the eastern foothills of the Nussberg.However, in the course of the Danube regulation 1868-1875 the Danube channel was again expanded, especially the inlet construction at Nussdorf and also the outlet at Albern (Gaube, n.d.). This fits perfectly with the indications of “Durchstich bei Nussdorf“ (inlet) and “Acquiriert 1870“.

The loess cover only reaches the Danube in the very small area where the channel branches off the river. Since the bone (and the two additional specimens from this find post) must have been associated with loess and certainly not with gravel (state of preservation, no fluvial rounding, etc.), the find location can be reconstructed quite accurately: directly at the eastern foothills of the Nussberg at the inlet of the Danube channel, the only point in Vienna, where the loess cover reaches the Danube, immediately above its riparian zone. Hence it most likely derives from the lowest loess deposits above the river (Fig. 9). This situation corresponds to the entrance resp. exit of the geomorphological significant bottleneck of the Vienna Gate.

4.2 Geochronological assignment

The exact original site location is unknown, but we argue that it must have been located in/near the former Nussdorf village on the so called Stadt terrace of Rissian (resp. Saalian) age (Pfleiderer, 2008a, 114, Summesberger, 2011). This terrace, attested only through core drillings, represents the lowermost glacial terrace in this area, and is only partly preserved exposing underlying Neogene sediments (Pfleiderer, 2008a, Figs. 1 & 4). These geological units are covered by Wuermian (resp. Weichselian) loess deposits, which represent the find context of the bone.

The loess sediments can be roughly correlated with (or are somewhat older than) the gravels of the Wuermian Prater terrace, which is however not developed in this area, but only north of the pronounced meander zone of the Holocene Danube and maybe partially also beneath the gravels of the Holocene meander zone (Pfleiderer, 2008a, 2008b, Fig. 2). This youngest of the glacial terraces (Prater terrace) shows no more loess cover. For varying maps of the geological situation in this area see also Fuchs, 1873 Pl. XIX, Brix, 1972, and Fuchs, 1985.

5. Palaeontological and archaeozoological investigations and scenario reconstruction

5.1 Measurements and description

Equus ferus (NHMW Department of Geology & Palaeontology 2016/0111/0001)

Measurements (von den Driesch 1982)
Greatest length (GL): 245 mm
Lateral length on the outer side (Llat): 234 mm
Proximal width (Wp): 52.1 mm

Proximal (cranio-caudal) depth (Dp): 36.8 mm
Smallest diaphyseal width (SD): 39.9 mm
Distal width (Wd): 50.7 mm
Distal depth (Td): 27.9 mm

Fig. 10: Details of the cannon bone with marked incision groups A, B, C (photos A. Schumacher, NHMW).

The right metacarpal III, the cannon bone in popular vocabulary, is completely preserved. No epiphyseal scar is visible, hence the specimen represents an adult prime-aged individual. Slight damages are visible on the proximal end and on the dorsal as well as the palmar facies of the distal trochlea. Furthermore there are spallings and desiccation cracks on the shaft, as well as a narrow groove between the middle and the distal third of the diaphysis which can not be verified as a palaeolithic modification of the bone. The most striking and indicative taphonomic features are parallel cuts on the distomedial side of the shaft.

On the frontal or dorsal facies of the shaft, within the inner, the medial half, between 7 and 6 cm distant from the distal end, a group of three distinct more or less parallel cut-marks is situated, inclined to the longitudinal shaft axis by about 45°. The microscopic view shows a corrosion grade that is identical with the corrosion of the outer surface. This provides a taphonomic proof of the identical age of the bone and the modification: the lesion of the surface happened to the fresh bone.

The first proximal cut is 8.5 mm long (Fig. 10 Position A). About 1 cm downwards two merging cuts comprise a total length of 13.0 mm (Fig. 10 Position B).

The cuts display an asymmetrical profile or cross-section with more flattened distal cut faces (Fig. 11). The steep proximal face of the cut in position A shows chipped off micro-flakes causing a “ragged appearance” (sensu Binford, 1981, Fig. 2 Position A).

There are further parallel lineaments between the two positions (see Fig. 11 upper picture), as well as below, versus the trochlea (Fig. 10 Position C).

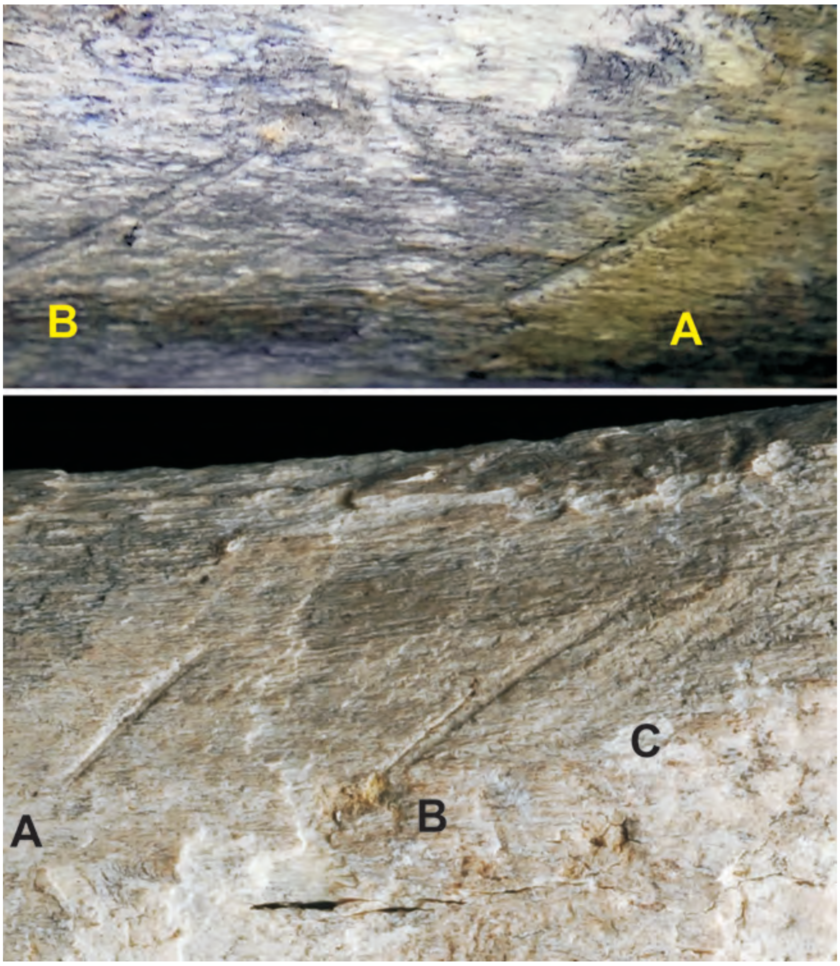

Fig. 11: Micro- (above) and Macro-photos (below) of the cut-marks from different views (photographs by F. A. Fladerer and A. Schumacher, NHMW).

They may derive from shallower cuts that did not completely penetrate the periosteum. On the posterior, palmar side of the metacarpal further lineaments can be observed, but an anthropogenic cause seems not very likely.

5.2 Discussion of bone dimension and species attribution

The greatest length measurement of the Vienna-Nussdorf specimen is 245 mm. An osteometric survey lists data of 123 Würmian horses, the means of greatest length is around 230 mm (Eisenmann, 1991b). Another study of the same author provides means of 222 mm calculated from 16 Late Pleistocene *E. germanicus*- and 215.5 mm from 36 recent *E. przewalskii*-specimens (Eisenmann, 1991a). Forsten & Ziegler (1995) report greatest length means of 239+-0.1 from 34 *E. germanicus*-metacarpals, and proximal width means of 56 mm. The distal width of the Nussdorf specimen of 50.7 mm obviously exceeds the range of the Przewalski-horses (x = 44.2, n = 88; Eisenmann, 2016). Compared to these data the Nussdorf horse is identified as a large individual.

Interpolated to a more recent survey of Late Pleistocene horses (Kagaan, 2000, Fig. 5.13) the metacarpal from Nussdorf again is grouped among the largest specimens of the studied sample from continental Ice-age Europe fossils. Three horse metacarpals from the camp site Alberndorf 1 (for chronol-

ogy see 6.3) yield measurements of 226, 234 and 269 mm, proving a rather broad intraspecific variability within only one assemblage (Fladerer,1996) and similar to data sets of domestic horse types. Nevertheless, available data suggest an at least coarse conclusion: the Vienna-Nussdorf individual is within the range of moderate large Late Pleistocene horses, and it was definitely not stout, but rather slender. According to the Kiesewalter-method (WH = lateral length of the metacarpal III * 6.41; e.g. Cramer, 2002) the withers height of the Nussdorf horse can be rated as 150 cm. Using the factor 5.77, specific for Przewalski horses, the calculated withers height amounts to 141 cm (Eisenmann, 2009).
Concerning the species attribution as *E. ferus*, caballine (caballoid) horses from West to Central European Late Pleistocene assemblages often are addressed as *E. germanicus* (compare Forsten & Ziegler, 1995), *E. gallicus*, *E. remagensis, E. solutreensis* or on subspecies-level as *E. caballus* (the guidelines of the International Commission on Zoological Nomenclature - ICZN 2003 state that the species name *E. caballus* should only be used for domesticated animals). Therefore a more reliable denomination might be *E. ferus* (e.g. *E. ferus 'solutreensis'*, e.g. Rabeder, 1996). A general decrease of size from the Middle Pleistocene towards the last Glacial Maximum is observed (e.g. Forsten, 1991) and ecomorphologic size and stoutness variation triggered by glacial vs. more humid conditions are taken into account (e.g van Asperen, 2010, van Asperen & Stefaniak, 2011).

5.3 Archaeozoological interpretation

The cannon bone (German: Röhrbein) is the third longest front-limb element. It is positioned in the autopodium between the carpals and the first phalanx, the long pastern bone. There are strong joints connecting the element, proximally the carpal, and distally the metacarpo-phalangeal joint. The cannon bone contains in its medullary cavity a relative high amount of marrow, holding the fifth position behind femur, tibia, radius and humerus (e.g. Outram & Rowley-Conwy, 1998). The complete status of the bone proofs that the marrow had not been exploited, yet anthropogenic manipulation proven by a series of parallel cut-marks on the dorsomedial side of the diaphysis indicates result-oriented human behaviour. This position marks the cutaneous plane of the metacarpal, where the shaft of the bone is only covered by hide. The distinct asymmetric profile of the cut-marks, with the flat distal faces and micro-flaking of the steep proximal face indicates cutting from a distal position.
Cut-marks derive from various stages during processing an animal carcass - or its separated parts -, following an experienced sequence, between the kill of the animal and final acts within residential camps.
Considering the anatomical features of equine autopodials we suggest an interpretation of the cut-mark series as consequence of skin removal.
The medial part of its dorsal facies is the only position of the metacarpal where the hide is not separated from the bone by other structures like sinews or ligaments and cutting will therefore harm the bony surface very easily.

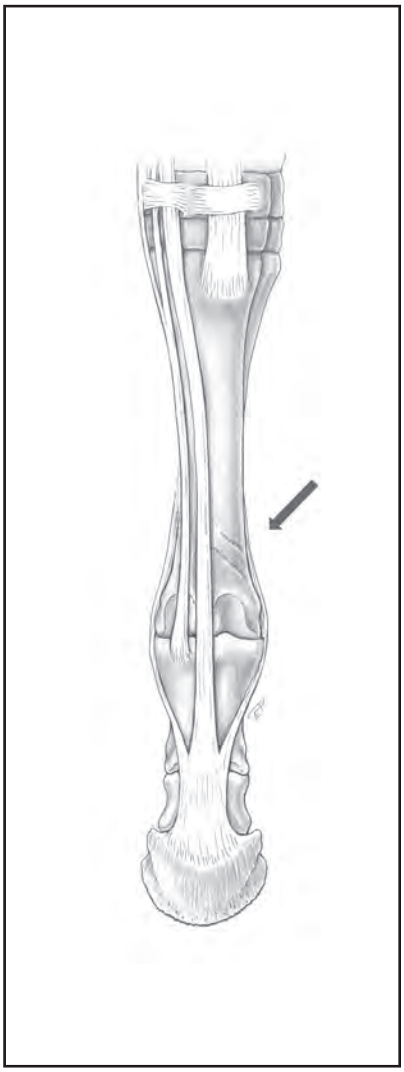

Fig. 12: Anatomical position of the cannon bone and adjoining tendons (Drawing by E. Polsterer).

The position of the cut-marks in their anatomical context is depicted in figure 12. Potentially, but not proven by indicative cut-marks, the metapodial has been cut out and the phalanges remained attached to the hide, as this helps to transport the hide and butchered meat by using the distal bones as handles. This behaviour might also be responsible for the under-representation of distal phalanges in kill site assemblages (compare Fladerer, 1996) while metapodials of horses are frequently observed in archaeological assemblages, at hunting or kill-sites as well as at residential sites (e.g. Niven, 2007, Soulier, 2014) and they often bear cut-marks (e.g. Niven, 2007, Brasser, 2012). At an Early Upper Palaeolithic site in Southern France (Soulier, 2014), rather isochronous to Vienna-Nussdorf, frequent oblique cut-marks are interpreted as caused during detachment of the skin and they are present over the entire length of the metapodial diaphysis. Additionally, short and transverse cut-marks are thought to indicate the removal of the strong tendon of the extensor muscle, as tendons are valued by indigenous people for their usefulness for cordage and also hafting (e.g. Binford, 1981).

5.4. A possible kill site/butchering site?

There are arguments for a “real“ archaeological site at this locality: two additional horse bones, presumably (but not certainly) from the same site, are kept in the same box. They represent animals of different age and therefore at least two individuals. According to one of the authors (U. Göhlich) the three bones do not belong to the same find complex. This assumption is based on a slightly differing preservation which could indicate a deposition in different sediments. This however does not exclude the possibility of the same find location, which in such a case could have been a seasonally used kill site at the banks of the Danube River. Because long bones of horses - compared to those of other large herbivores - contain very little marrow, they were often left behind at kill sites (West, 1996). The location at a geomorphological bottleneck situation (narrow section of the Danube valley) would have been predestined for a hunting spot. Since at the time of discovery only bones were kept for the natural scientific collections, potential stone tools would not have been noticed (see chapter 1.2).
Removing the skin from the carcass of large-sized ungulates like equids is part of the most initial

butchery tasks. The bodies must be partly dismembered at the kill-site or a nearby butchering site (see, e.g., SIVERTSEN, 1980), at least within a Palaeolithic spatial organisation. Selected parts are then transported to residential camps. The unbroken shaft of the Nussdorf-specimen testifies that the marrow cavity has not been opened by the hunters. Actually, the bone-marrow is one of the most attractive substances because of its nutritional value, containing high quantities (up to 70%) of unsaturated fatty acids. These are known to be highest between late summer and early winter, while being rather depleted from late winter on (compare e.g. OUTRAM & ROWLEY-CONWY, 1998). Compared to reindeer or bison, horse bones contain much smaller marrow quantities (BLUMENSHINE & MADRIGAL, 1993), but the butchery and marrow exploitations patterns seem rather consistent (NIVEN, 2007). In the highly seasonal Pleniglacial annual climate course, and hence the hunter-gatherer`s subsistence cycles, we would expect marrow exploitation between late summer and mid-winter when marrow quality is best. Complete horse metapodials seem by far under-represented or even absent in Early to Mid Upper Palaeolithic residential sites, but there is clear evidence of broken specimens, very probably for marrow exploitation (NIVEN, 2007) which is similar to younger evidence from the Middle Danube Region (WEST, 1996). A large river system and the vicinity of low mountain ranges is surely a preffered landscape for Early Aurignacian spatial behaviour (HUSSAIN & FLOSS, 2016). We suggest a scenario where the Vienna-Nussdorf horse specimen derives from a hunting a,nd primary butchery episode of a local or regional population, probably carried out close to the Danube banks and maybe between mid-winter and early summer.

6. Radiocarbon dating and chrono-stratigraphic placement

6.1 Method

The specimen was sampled at the Natural History Museum in Vienna. Although documentation of restoration or preservation work is not available, visual inspection indicated that it had been heavily treated in the past. The cannon bone seemed to be coated with a thick layer of glue, omitting a smell reminiscent of acetone.

To prevent contamination of the radiocarbon sample, a circular surface area of ca. 1 cm^2 was cleaned with a drill before sampling. Bone powder for radiocarbon dating was obtained using key-hole drilling, a minimal invasive sampling technique collecting material from the interior of the specimens, while keeping the exterior largely intact (Fig. 2e).

The bone powder sample (696.92 mg) was treated and radiocarbon dated at the Oxford Radiocarbon Accelerator Unit (ORAU). First, a solvent wash protocol was applied to remove possible contamination deriving from conservation and restoration materials: 30 min in acetone, 30 min in methanol (both in a heating block at 40°C), 30 min in chloroform at RT. The sample was centrifuged and decanted between each step, and finally left to dry overnight in a heating bloc at 40°C.

Subsequently, the dried sample was pre-treated using the standard ORAU protocol for bone using acid-base-acid steps followed by gelatinisation and the use of Ezee-filters™ (Brock et al., 2010). A freeze-drying step was added after Ezee-filtering to assess whether collagen preservation is sufficient for ultrafiltration. The sample yield was adequate, and the unpurified collagen thus hydrolysed with 10 mL Milli-Q™ water and ultra-filtered. All remaining steps, graphitisation and AMS measurement, followed standard lab procedures as described by Brock et al. (2010) and Bronk Ramsey et al. (2004).

6.2 Result

The specimen was successfully dated to 34,550 ± 600 BP (Ox-A 34405). Collagen preservation was very good (Tab. 1), resulting in a collagen yield after ultrafiltration (AF*) of 9.19 wt%. The C:N ratio of 3.2 is consistent with collagen. All quality control measurements suggest a reliable radiocarbon age.

Sample-no	Site	Species	Treat	Yield (mg)	Yield (%)	Lab/P-no	$F^{14}C$	^{14}C age	%C	C:N	$\delta^{15}N$	$\delta^{13}C$
2016/0111/0001	Wien-Nussdorf	*Equus*	AF*	64.03	9.19	OxA- 34405 / P41690	0.01354 ± 0.00102	34550 ± 600	43	3.2	6.6	-22.1

Tab. 1: Radiocarbon result for specimen Inv.-nr. 2016/0111/0001, pre-treatment applied (* stands for solvent wash, AF for treatment with ultrafiltration; for ORAU codes see Brock et al. 2010), listing collagen yield after pre-treatment, Lab-code, radiocarbon measurement in fraction modern (F14C) with 1σ error and conventional radiocarbon date in BP, %C on combustion, carbon to nitrogen ratio and stable nitrogen and carbon isotope ratios.

Using the IntCal13 calibration curve the radiocarbon age calibrates to 40,600-37,700 cal BP at a confidence interval of 95.4% (Fig. 13).

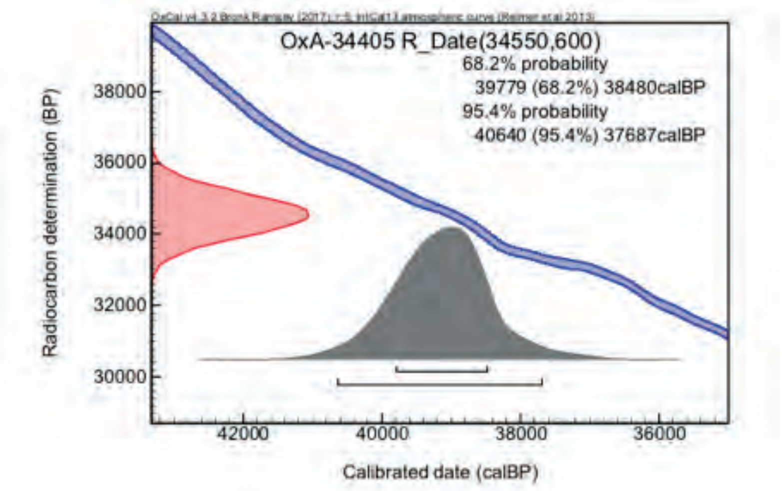

Fig. 13: Calibrated radiocarbon age obtained from the horse Metacarpale III dext. with anthropogenic marks using OxCal 4.3 (Bronk Ramsey, 2009). Red: conventional radiocarbon age for OxA-34405 (1σ). Blue: IntCal13 calibration curve (Reimer et al. , 2013). Black: calibrated radiocarbon age with both the 68.2% and 95.4% confidence interval marked.

6.3 Discussion and chrono-stratigraphic placement

Since no archaeological context was recorded for the anthropogenically modified horse Metacarpale III dext specimen of Vienna-Nussdorf (Inv.-nr. 2016/0111/0001), the obtained radiocarbon age is – beside the geographic location – of utmost importance for the reconstruction of a cultural and chrono-stratigraphic framework. In a broader sense, the radiocarbon age of 34,550 ± 600 BP for the Vienna horse specimen is in agreement with prevalent chronological assessment and hypotheses regarding the dispersal of early anatomically modern humans (AMH) into Europe (Conard & Bolus, 2003, Jöris et al., 2010, Chu, 2018, Hopkins, 2019). It can therefore be assumed that the anthropogenic modification of the bone, and thus also hunting, processing, and consumption of the horse was carried out by anatomically modern humans. The age of 40,600-37,700 cal BP (IntCal13) resp. 41,700-37,800 cal BP (CalPal-2007-Hulu) – both ranges given for the 95.4% confidence interval – corresponds to ages obtained for the regional early Aurignacian assessed at the northeast Austrian open-air sites Willendorf II, Senftenberg, and Krems-Hundssteig. The ages presented here (Tab. 2, Fig. 14) only include dates produced for unambiguous Aurignacian complexes, or – in some cases – only ages that clearly fall within the Aurignacian range.

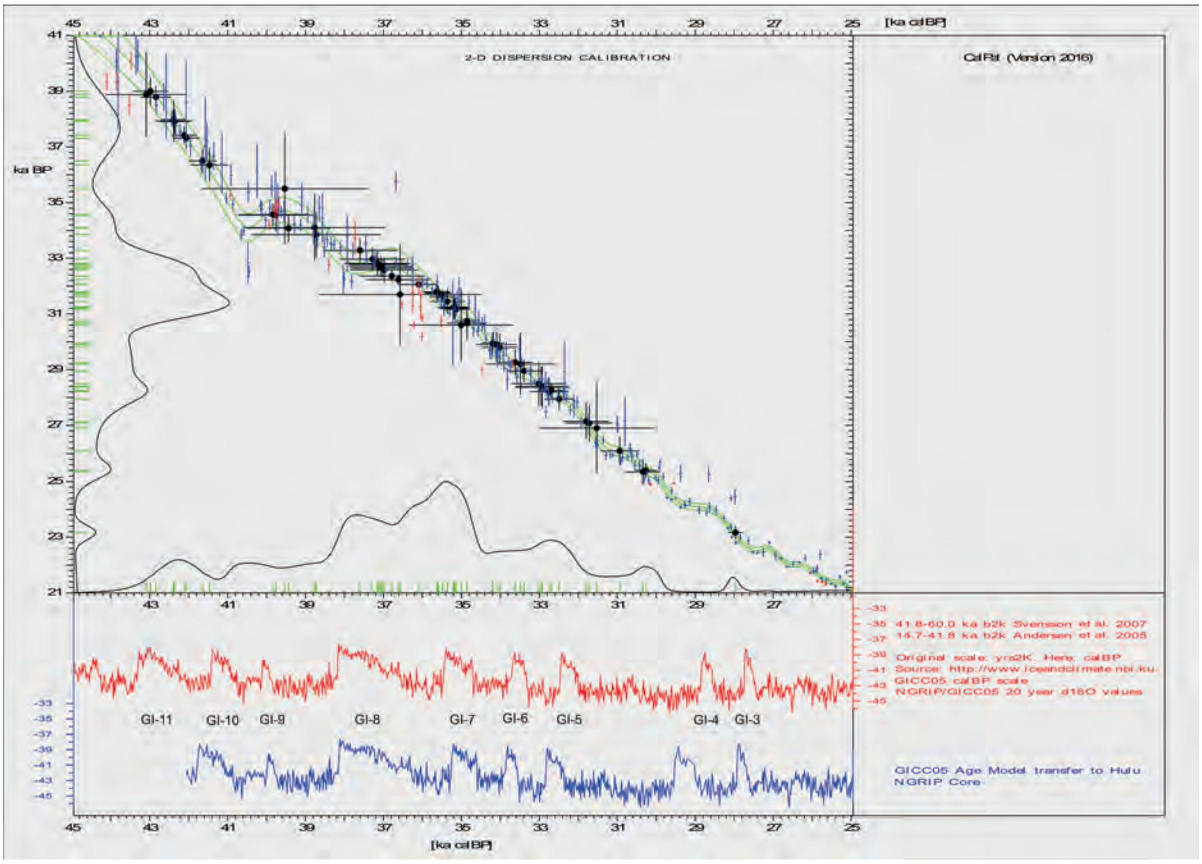

Fig. 14: Graphic representation of the data presented in Table 2 with the exception of samples VRI-1373, OxA-8511, and OxA-4595. Calibration was carried out with CalPal-Beyond the Ghost, Version 2016.2, http://monrepos rgzm.de/forschung/ausstattung.html#calpal (Weninger & Jöris, 2008). The Calpal-2007-Hulu calibration curve is given in green together with the underlying reference data. Beneath, the GICC05 timescale (Greenland Ice Core Chronology 2005, 15 - 42 ka; 20 yr δ 18O, http://www.iceandclimate.nbi.ku.dk, as well as a version of the GICC05 timescale adapted to the Hulu data) is provided as climate reference.

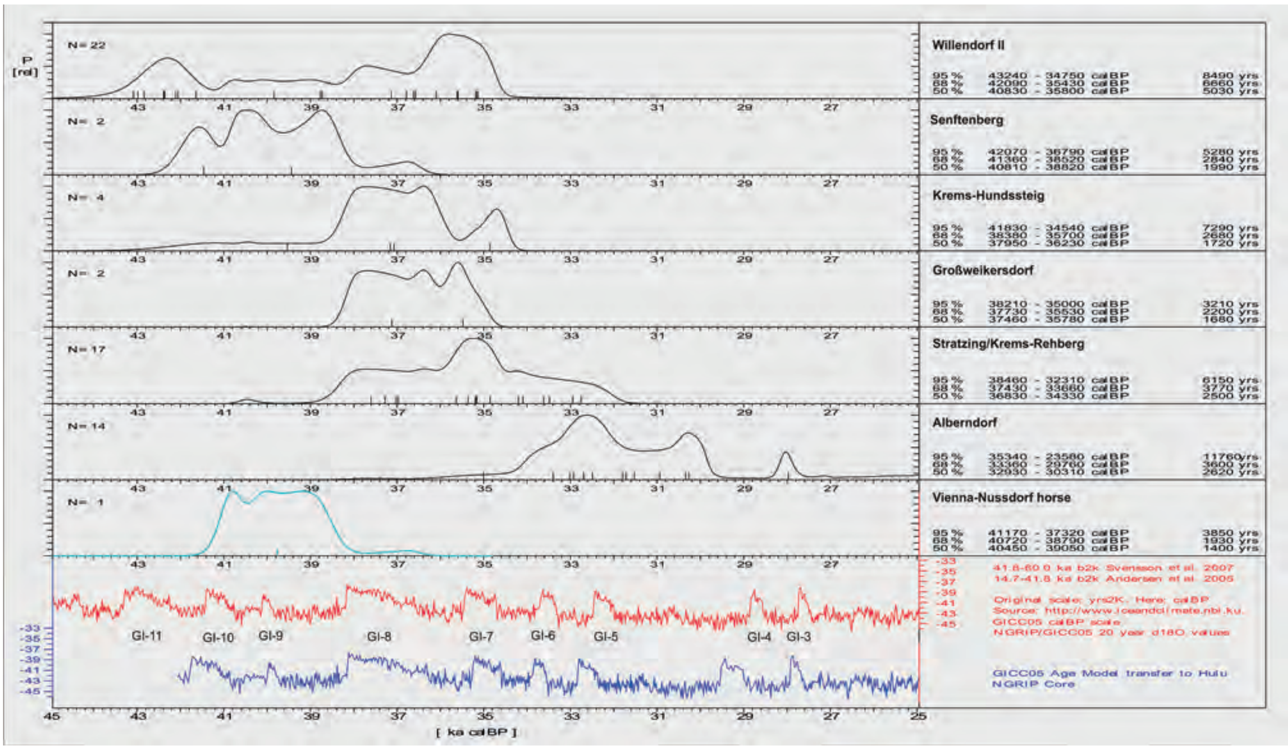

Fig. 15: Multigroup graph with sum plots of probability distributions of calibrated 14C dates (calBP) of Aurignacian contexts of northeast Austria produced with CalPal-Beyond the Ghost, Version 2016.2, http://monrepos-rgzm.de/forschung/ausstattung.html#calpal (Weninger & Jöris, 2008). The dates have been grouped according to sites. Beneath, the GICC05 timescale (Greenland Ice Core Chronology 2005, 15 - 42 ka; 20 yr δ 18O, http://www.iceandclimate.nbi.ku.dk, as well as a version of the GICC05 timescale adapted to the Hulu data) is provided as climate reference. Chronologically, the Vienna-Nussdorf specimen is clearly attributable to the earlier, i.e. pre Greenland Interstadial 8 phase of the Aurignacian.

Therefore, regarding Willendorf II, archaeological horizons 3 and 4, but not lithostratigraphic complex D, are considered here (Haesaerts et al., 1996, Haesaerts & Teyssandier, 2003, Nigst et al., 2014, Teyssandier & Zilhão, 2018).

This does not imply that we categorically reject considerably earlier dates for a Proto-Aurignacian, but we see no necessity to extend our discussion in this direction.

The ages presented for Krems-Hundssteig are not sensu stricto connected to stratified Aurignacian artefacts but rather represent dates from stratigraphically plausible positions at a site with evidenced Aurignacian industry (Hahn, 1977, Neugebauer-Maresch, 2008, Händel, 2017). The other radiocarbon-dated Aurignacian open-air sites in northeast Austria, namely Großweikersdorf, Stratzing/Krems-Rehberg, and Alberndorf, postdate the Vienna-Nussdorf horse. Sample ETH-6026 from Stratzing/Krems-Rehberg is included in the model although it derives from layer 3 since the age it provides clearly falls within the Aurignacian range.

Whereas Stratzing/Krems-Rehberg and Großweikersdorf overlap with the younger Aurignacian strata of Willendorf II and Krems-Hundssteig and represent well-dated contexts of the later regional Aurignacian, the majority of the (considerably younger) ages obtained for Alberndorf, provoked discussions regarding a prolonged duration of the regional Aurignacian. More recently produced dates, however, show chronological congruency with the later part of Stratzing/Krems-Rehberg's age range (Trnka, 2005, Jöris et al., 2010, Davies et al., 2015).

Radiocarbon ages are grouped by site (Fig. 15) and graphed with CalPal-Beyond the Ghost, Version 2016.2. The GICC05 timescale (Greenland Ice Core Chronology 2005, 15 - 42 ka; 20 yr δ 18O, http://www.iceandclimate.nbi.ku.dk; given in cal BP; as well as a version of the GICC05 timescale adapted to the Hulu data) was added to the multiple group graph to reference climate data (Andersen et al., 2006, Svensson et al., 2008). Assuming a temporal succession from the Aurignacian to the Gravettian, we must at least reject all ages postdating Greenland Interstadial GI-6 as too young when taking the well-dated, stratigraphically controlled, as well as artefact- and finding-supported Early Gravettian sequence of the Krems sites into account (Händel, 2017).

A third model (Fig. 16) considers only ages produced for horse remains. As there are currently only four directly radiocarbon-dated horse specimens for Austria in the time span of interest (namely from Krems-Hundssteig, Stratzing/Krems-Rehberg, Senftenberg, and of course the Vienna-Nussdorf specimen presented here), the model also includes ages produced for horses from Germany (Hohle Fels, Geissenklösterle and Vogelherd). Two dates from Germany were excluded from the model but are listed in Table 2: OxA-4595 produced on a femur provided a very early date, and OxA-8511 produced on a pelvis from Breitenbach B (too young, possibly due to poorly understood diagenesis).

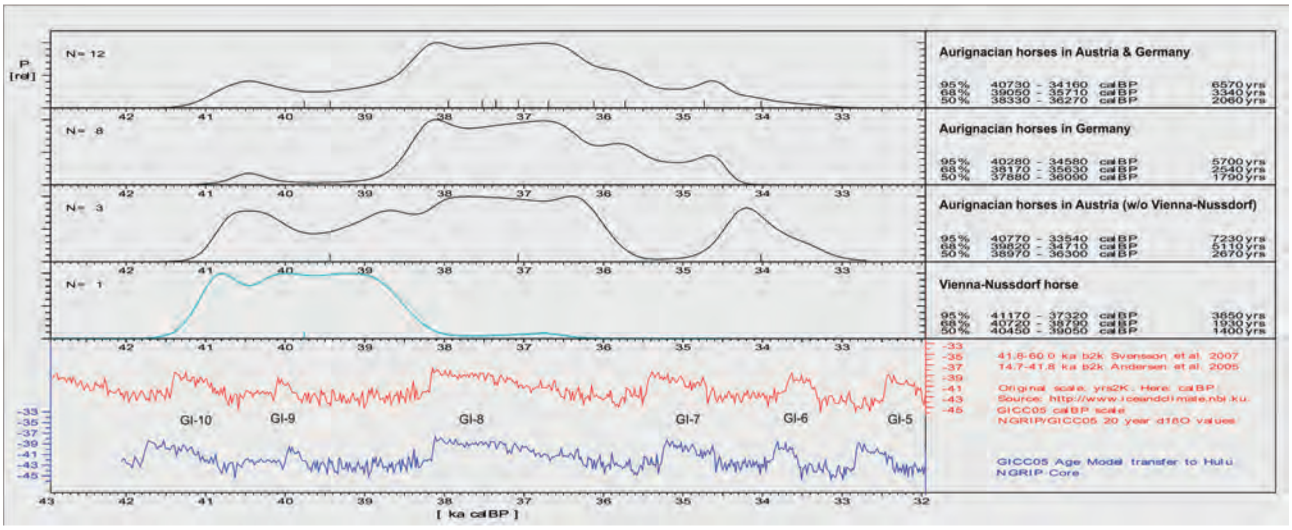

Fig. 16: Multigroup graph with sum plots of probability distributions of calibrated 14C dates (calBP) of Aurignacian horses of Austria and Germany (exceptions see text) produced with CalPal-Beyond the Ghost, Version 2016.2, http://monrepos-rgzm.de/forschung/ausstattung.html#calpal (Weninger & Jöris, 2008). Beneath, the GICC05 timescale (Greenland Ice Core Chronology 2005, 15 - 42 ka; 20 yr δ 18O, http://www.iceandclimate.nbi.ku.dk, as well as a version of the GICC05 timescale adapted to the Hulu data) is provided as climate reference.

It should also be noted that two potential horse specimens from Alberndorf are not considered in Figure 16 (but listed in Table 2). For both, species determination seems uncertain (Jöris et al., 2010). The sample with lab code VRI-1373 only provided a minimal age while sample ETH-13041 produced an age that is clearly too young (see discussion on Alberndorf above).

Noticeably, in this group, the Vienna-Nussdorf specimen provided – together with the horse from Senftenberg – the earliest dates. Chrono-stratigraphically, these fall into the range of GI-10 to GI-9, and include GS-9 (Andersen et al., 2006). Referring to the refined INTIMATE event stratigraphy by Rasmussen et al. (2014), the 41,700-37,800 cal BP (CalPal-2007-Hulu) range given for the Vienna-Nussdorf specimen starts with the onset of GI-10 and ends before the start of GI-8b. Focussing on the 68.2% confidence interval (40,700-39,000 cal BP) reduces the range to between the start of GS-10 and the end of GS-9. Transition from GS-10 to GI-9 is considered atypical because the onset of GI-9 is more gradual than in neighbouring transitions. This could indicate that GI-9 and GI-10 can be considered parts of the same interstadial period (Rasmussen et al., 2014). In any case is the more distinct GS-9 – parallelized with Heinrich event 4 – included in the range so that placement of the Vienna-Nussdorf horse both in an interstadial and in a pronounced stadial context remains within the bounds of possibility.

7. Conclusive remarks

Clearly human-made incision marks on a horse metacarpal provide the first definite, unambiguous evidence for the presence of (anatomically modern) humans on the territory of present-day Vienna in the Early Upper Palaeolithic. ^{14}C-dating established a time range (68%) between 40,650 – 38,850 cal BP (CalPal) resp. 39,800 – 38,500 cal BP (OxCal) for which the presence of AMH is extensively attested for in the wider region, and which postdates any evidenced regional Neanderthal occurrence. From a geographic perspective, the presence of hunter-gatherer groups in this area was not unexpected due to the physiographic characteristics in the surroundings of the Vienna Gate and its location in the so-called Danube corridor. The results of this study securely establish such presence for the first time. When compared to the earliest dates claimed for the Upper Palaeolithic resp. AMH presence along the Danube, it seems, that the occupation represented by the Vienna-Nussdorf horse does not belong to this very earliest presence, but attests for a time very soon thereafter.

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Lab-Nr	14C age	14C STD	Material	Species	Site	Techno-culture	Remark	cal BC	S p(68%)	cal BP p(95%)	Reference
VRI-1272	20500	1400	antler	reindeer	Alberndorf	Final Aurignacian?		22750	1740	28180 - 21220	Trnka 2005
VRI-1374	26900	1600	bone	mammoth	Alberndorf	Final Aurignacian?	long bone (compacta)	29580	1470	34470 - 28590	Trnka 2005
VRI-1536	25350	450	bone	mammoth	Alberndorf	Final Aurignacian?	Ulna	28390	450	31240 - 29440	Trnka 2005
VRI-1537	26100	500	bone	mammoth	Alberndorf	Final Aurignacian?	Tibia (same sample as VERA-0006)	28990	490	31920 - 29960	Trnka 2005
ETH-13040	25400	260	bone	reindeer?	Alberndorf	Final Aurignacian?	rib	28320	270	30810 - 29730	Trnka 2005
VERA-0006	28250	250	bone	mammoth	Alberndorf	Final Aurignacian?	Tibia (same sample as VRI-1537)	30740	320	33330 - 32050	Trnka 2005
GrA-5223	27140	650	charcoal	nd	Alberndorf	Final Aurignacian?		29850	580	32960 - 30640	Trnka 2005
GrA-5224	28360	760	charcoal	nd	Alberndorf	Final Aurignacian?		30980	690	34310 - 31550	Trnka 2005
GrA-5241	28490	780	charcoal	nd	Alberndorf	Final Aurignacian?		31060	710	34430 - 31590	Trnka 2005
GrA-5242	27080	650	charcoal	nd	Alberndorf	Final Aurignacian?		29770	590	32900 - 30540	Trnka 2005
OxA-X-2191-43	30600	1300	bone	reindeer	Alberndorf	Final Aurignacian?	reindeer antler "handle"	33060	1340	37690 - 32330	Davies et al. 2015
OxA-18523	28950	400	bone	reindeer	Alberndorf	Final Aurignacian?	reindeer antler "handle"	31450	450	34300 - 32500	Davies et al. 2015
OxA-X-2199-15	27940	390	bone	reindeer	Alberndorf	Final Aurignacian?	reindeer longbone fragment (modified?)	30540	380	33250 -31730	*W. Davies*
GrN-16263	32770	240	charcoal	nd	Grossweikersdorf	Aurignacian?	lower layer	35170	760	38640 -35600	Neugebauer-Maresch 1993
GrN-16244	31630	240	charcoal	nd	Grossweikersdorf	Aurignacian?	upper layer	33530	330	36140 -34820	Neugebauer-Maresch 1993
VERA-1616	30750	290	charcoal	nd	Krems-Hundssteig	Aurignacian?	HU2000-2002, ID 9003	32910	320	35500 - 34220	Neugebauer-Maresch 2008
VERA-2289	32810	450	charcoal	nd	Krems-Hundssteig	Aurignacian?	HU2000-2002, ID 232001	35210	850	38860 - 35460	Neugebauer-Maresch 2008
KN-654	35500	2000	charcoal	nd	Krems-Hundssteig	Aurignacian?	HU1895-1904	37580	2150	43830 - 35230	Hahn 1977
GrN-16887	36350	600	charcoal	nd	Senftenberg	Aurignacian		39510	490	42440 - 40480	Djindjian et al. 1999
ETH-6023	29950	370	charcoal	nd	Stratzing/Krems-Rehberg	Aurignacian	layer 2	32250	300	34800 - 33600	Neugebauer-Maresch 1996
ETH-6024	31450	440	charcoal	nd	Stratzing/Krems-Rehberg	Aurignacian	layer 2	33410	450	36260 - 34460	Neugebauer-Maresch 1996
ETH-6025	31230	430	charcoal	nd	Stratzing/Krems-Rehberg	Aurignacian	layer 2	33250	420	36040 -34360	Neugebauer-Maresch 1996
ETH-6026	32640	330	charcoal	nd	Stratzing/Krems-Rehberg	Aurignacian	layer 3	35070	810	38640 - 35400	Neugebauer-Maresch 1996
GrN-15641	30670	600	charcoal	nd	Stratzing/Krems-Rehberg	Aurignacian	layer 2 (moved)	32900	500	35850 - 33850	Neugebauer-Maresch 1996
GrN-15642	31190	390	charcoal	nd	Stratzing/Krems-Rehberg	Aurignacian	layer 2 (moved)	33220	390	35950 - 34390	Neugebauer-Maresch 1996
GrN-15643	29200	1100	charcoal	nd	Stratzing/Krems-Rehberg	Aurignacian	layer 2 (moved)	31530	920	35320 - 31640	Neugebauer-Maresch 1996
GrN-16135	31790	280	charcoal	nd	Stratzing/Krems-Rehberg	Aurignacian	layer 2	33690	350	36340 - 34940	Neugebauer-Maresch 1996
KN-3941	28400	700	charcoal	nd	Stratzing/Krems-Rehberg	Aurignacian	layer 2 (moved)	31000	660	34270 - 31630	Neugebauer-Maresch 1996
KN-3942	29900	600	charcoal	nd	Stratzing/Krems-Rehberg	Aurignacian	layer 2 (moved)	32140	520	35130 - 33050	Neugebauer-Maresch 1996
KN-4140	29260	460	charcoal	nd	Stratzing/Krems-Rehberg	Aurignacian	layer 1 (moved)	31670	450	34520 - 32720	Neugebauer-Maresch 1996
KN-4141	28210	500	charcoal	nd	Stratzing/Krems-Rehberg	Aurignacian	layer 1 (moved)	30800	500	33750 - 31750	Neugebauer-Maresch 1996
VERA 965	33285	440	charcoal	nd	Stratzing/Krems-Rehberg	Aurignacian	layer 1, G3	35650	950	39500 - 35700	Jöris et al. 2010
VERA 966	31200	300	charcoal	nd	Stratzing/Krems-Rehberg	Aurignacian	layer 2, G3	33210	350	35860 - 34460	Jöris et al. 2010
VERA 964	31210	340	charcoal	Pinus sp.	Stratzing/Krems-Rehberg	Aurignacian	layer 2, (partially moved) hearth F	33220	370	35910 - 34430	Jöris et al. 2010
VERA 963	32580	450	charcoal	Pinus sp.	Stratzing/Krems-Rehberg	Aurignacian	layer 2	35030	870	38720 - 35240	Jöris et al. 2010
VERA 961	32970	420	charcoal	Pinus sp.	Stratzing/Krems-Rehberg	Aurignacian	layer 2 (moved)	35330	830	38940 - 35620	Jöris et al. 2010
GrA-501	31210	260	charcoal	nd	Willendorf II	Aurignacian		33220	330	35830 - 34510	Damblon et al. 1996
GrA-896	37930	750	charcoal	Picea	Willendorf II	Aurignacian	layer C8-2 (sample ID A-166 a)	40430	490	43360 - 41400	Damblon et al. 1996
GrN-11192	34100	1200	charcoal	nd	Willendorf II	Aurignacian	layer C8-2 (sample ID PH 1990)	36820	1800	42370 - 35170	Damblon et al. 1996
GrN-1273	32060	250	charcoal	nd	Willendorf II	Aurignacian	AH 4	34150	490	37080 - 35120	Damblon et al. 1996
GrN-17805	38880	1530	charcoal	Picea	Willendorf II	Aurignacian	layer C8-2 (sample ID A-166 b)	41140	1050	45190 - 40990	Damblon et al. 1996
H-249-1276	31700	1800	charcoal	nd	Willendorf II	Aurignacian	AH 4	34620	2070	40710 - 32430	Damblon et al. 1996
GrA-35403	31250	230	charcoal	Picea/Larix	Willendorf II	Aurignacian	layer C4-1 (sample ID A-1905)	33240	320	35830 - 34550	Nigst et al. 2008
GrA-35404	31770	250	charcoal	Picea/Larix	Willendorf II	Aurignacian	layer C4-1 (sample ID A-1906)	33670	330	36280 - 34960	Nigst et al. 2008
GrA-35406	31170	230	charcoal	Picea/Larix	Willendorf II	Aurignacian	layer C4-2 (sample ID A-1912 a)	33190	310	35760 - 34520	Nigst et al. 2008
OxA-17396	32230	190	charcoal	Picea/Larix	Willendorf II	Aurignacian	layer C4-2 (sample ID A-1912 b)	34670	810	38240 - 35000	Nigst et al. 2014
GrA-45804	32360	210	charcoal	Pinus t. cembra	Willendorf II	Aurignacian	layer C4-2 (sample ID A-2421 a)	34840	840	38470 - 35110	Nigst et al. 2014
GrA-45011	32790	210	charcoal	Pinus t. cembra	Willendorf II	Aurignacian	layer C4-2 (sample ID A-2421 a)	35180	740	38610 - 35650	Nigst et al. 2014
OxA-22294	31750	260	charcoal	Pinus t. cembra	Willendorf II	Aurignacian	layer C4-2 (sample ID A-2421 b)	33640	340	36270 - 34910	Nigst et al. 2014
OxA-23562	33850	800	charcoal	Pinus t. cembra	Willendorf II	Aurignacian	layer C4-2 (sample ID A-2421 c)	36770	1660	42040 - 35400	Nigst et al. 2014
GrA-38250	34570	410	charcoal	Picea	Willendorf II	Aurignacian	layer C8-2 (sample ID A-2131)	37890	860	41560 - 38120	Nigst et al. 2014
GrA-35411	37320	390	charcoal	Picea	Willendorf II	Aurignacian	layer C8-2 (sample ID A-2039)	40110	340	42740 - 41380	Nigst et al. 2014
OxA-17397	37980	300	charcoal	Picea	Willendorf II	Aurignacian	layer C8-2 (sample ID A-1933)	40440	330	43050 - 41730	Nigst et al. 2014
GrA-44894	37420	300	charcoal	Picea/Larix	Willendorf II	Aurignacian	layer C8-2 (sample ID A-1935 a)	40160	330	42770 - 41450	Nigst et al. 2014
GrA-35409	37910	440	charcoal	Picea/Larix	Willendorf II	Aurignacian	layer C8-2 (sample ID A-1935 b)	40410	370	43100 - 41620	Nigst et al. 2014
OxA-22295	36500	450	charcoal	Picea/Larix	Willendorf II	Aurignacian	layer C8-2 (sample ID A-1935 c2)	39690	360	42360 - 40920	Nigst et al. 2014
GrA-45012	38790	400	charcoal	Picea/Larix	Willendorf II	Aurignacian	layer C8-2 (sample ID A-1935 c1)	40890	390	43620 - 42060	Nigst et al. 2014
OxA-23520	39000	500	charcoal	Picea/Larix	Willendorf II	Aurignacian	layer C8-2 (sample ID A-1935 c3)	41030	460	43900 - 42060	Nigst et al. 2014
VRI-1373	>16600		bone	horse?	Alberndorf	Final Aurignacian?	long bone				Trnka 2005
ETH-13041	23170	230	bone	horse?	Alberndorf	Final Aurignacian?	skull	26020	190	28350 - 27590	Trnka 2005
OxA-18527	32700	370	bone	horse	Krems-Hundssteig	Aurignacian	HU1895-1904, metapodial with spiral break	35120	810	38690 - 35450	*W. Davies*
VERA-3217	34080	500	tooth	horse	Senftenberg	Aurignacian	Molar (excavation Hampl 1949)	37490	1070	41580 - 37300	Hinterwallner 2007
OxA-18528	29800	500	bone	horse	Stratzing//Krems-Rehberg	Aurignacian	tibia diaphyseal fragment with helical break	32070	440	34900 - 33140	*W. Davies*
OxA-34405/P41690	**34550**	**600**	**bone**	**horse**	**Vienna-Nussdorf**	**Aurignacian?**	**Metacarpale III dext with cutmarks**	**37810**	**960**	**41680 - 37840**	
OxA-8511	27480	340	bone	horse	Breitenbach B	Aurignacian	pelvis	30170	270	32660 - 31580	Street & Terberger 2000
KIA-16035	33090	260	bone	horse	Hohle Fels	Aurignacian	femur	35400	770	38890 - 35810	Conard & Bolus 2003
KIA-16036	33290	270	bone	horse	Hohle Fels	Aurignacian	femur (retoucher)	35580	830	39190 - 35870	Conard & Bolus 2003
KIA-16040	30640	190	bone	horse	Hohle Fels	Aurignacian	pelvis (cutmarks and impact)	32780	240	35210 - 34250	Conard & Bolus 2003
KIA-8958	31870	260	bone	horse	Geissenklösterle	Aurignacian	humerus (impact)	33780	330	36390 - 35070	Bocquet-Appel & Demars 2000
OxA-4595	40200	1600	bone	horse	Geissenklösterle	EUP	femur	42090	1210	46460 - 41620	Conard & Bolus 2003
OxA-5707	33200	800	bone	horse	Geissenklösterle	Aurignacian	scapula (impact and cutmarks)	36000	1490	40930 - 34970	Conard & Bolus 2003
OxA-6369	31750	650	bone	horse	Geissenklösterle	Aurignacian		34170	1040	38200 - 34040	Stevens & Hedges 2004
KIA-8970	33080	320	bone	horse	Vogelherd	Aurignacian	long bone fragment (impact)	35400	790	38930 - 35770	Conard & Bolus 2003
PL0001339A	32180	960	bone	horse	Vogelherd	Aurignacian	tibia (cutmarks and green break)	34740	1300	39290 - 34090	Conard & Bolus 2003

Tab. 2: Radiocarbon data produced for Aurignacian contexts of open-air sites in northeast Austria, as well as data obtained for Aurignacian horses from Austrian and German sites. Calibrated ages are produced with CalPal-Beyond the Ghost, Version 2016.2, http://monrepos rgzm.de/forschung/ausstattung.html#calpal using the Calpal-2007-Hulu calibration curve (WENINGER & JÖRIS, 2008), and given as cal BC p (68.2%) and cal BP with 2 Sigma ranges.

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