e-Research Reports
of Museum Burg Golling
Vol. 9 | 2022

MUSEUM BURG GOLLING
Das regionale WeltenMuseum
MBG

New subfossil findings of wisent (*Bos bonasus*) in caves of the Northern Calcareous Alps (Upper Austria)

Teresa Schaer[1], **Doris Döppes**[2], **Doris Nagel**[3], **Susanne Lindauer**[4] & **Gernot Rabeder**[3]

[1] Schullersiedlung 10, 4645 Grünau im Almtal, Austria

[2] Reiss-Engelhorn-Museen, Zeughaus, C5, 68159 Mannheim, Germany

[3] University of Vienna, Department of Palaeontology, Geozentrum/UZAII, Althanstraße 14, 1090 Vienna, Austria

[4] Curt-Engelhorn-Centre Archaeometry, C4/8, 68159 Mannheim, Germany

✉ schaer.teresa@gmail.com

Published: 09.09.2022

Citation: Schaer, T., Döppes, D., Nagel, D., Lindauer, S. & Rabeder, G. (2022): New subfossil findings of wisent (*Bos bonasus*) in caves of the Northern Calcareous Alps (Upper Austria). — e-Research Reports of Museum Burg Golling 9: 1-5.

Published by
Museum Burg Golling
Markt 1
5440 Golling a.d. Salzach
AUSTRIA
office@museumgolling.at
www.museumgolling.at

wisent | Totes Gebirge | radiocarbon dating | climate reconstruction | Holocene
Wisent | Totes Gebirge | Radiokohlenstoffdatierung | Klimarekonstruktion | Holozän

Abstract: New subfossil finds of wisent (*Bos bonasus*), including a complete skeleton, from two caves in the Totes Gebirge (Upper Austria) allowed a new evaluation of the »wisent time« and preferred altitude of these animals. Since they needed deciduous plants in their nutrition the restricted occurrence between 1,400 and 2,000 m above sea level indicates warmer temperatures from the Neolithic time to the Early Middle Age than today.

Kurzfassung: Neue subfossile Funde von Wisenten (*Bos bonasus*), darunter ein komplettes Skelett, aus zwei Höhlen im Toten Gebirge (Oberösterreich) erlauben eine neue Einschätzung der »Wisentzeit« und der bevorzugten Höhenlage dieser Tiere. Da sie für ihre Ernährung Laubpflanzen benötigten, deutet das eingeschränkte Vorkommen zwischen 1.400 und 2.000 m Seehöhe auf wärmere Temperaturen von der Jungsteinzeit bis zum Frühmittelalter hin als heute.

Introduction

Wisent remains have been known for a long time from caves in the alpine karst regions of Austria. The radiocarbon data so far (12 samples) are exclusively from the Holocene (BAUER, 2001). *Bos bonasus* on the other hand has never been verified in the Pleistocene faunas of Austria (DÖPPES & RABEDER, 1997). The remains from the new sites were removed in 2020 and 2021 but scientific excavations were neither possible nor necessary. These are single findings with no additional faunal elements. The assignment of the specimens to wisent (*Bos bonasus*) results from the dimensions and the shape of the horn-cores, but also from the shape of the last mandibular molars (m3 inf) and the plumpness of the metapodial bones.

Ur or Aurochs (*Bos primigenius*) and domestic cattle (*Bos p. taurus*) can be excluded because of the differently shaped horn-cores and teeth. Contrary to earlier opinions (see BAUER, 2001), the wisent is neither closely related to the American buffalo (*Bison bison*) nor the fossil steppe bison (*Bison priscus*). According to DNA data, the bison is closest to the Ur (*Bos primigenius*), the ancestral form of domestic cattle (HASSANIN & ROPIQUET, 2005; PALACIO et al., 2017; MARSOLIER-KERGOAT & ELALOUF, 2017). DNA analyses of the new bison finds are in progress. Remarkable is not only the temporal restriction of the wisent from the Neolithic to the Early Middle Ages, but also the spatial restriction to altitudes between 1,400 m and 2,000 m. With the inclusion of the new specimens and their data, an attempt is made to clarify the special circumstances of these findings.

New locations

Wisentschacht on the Kasberg near Grünau in the Alm valley (Upper Austria). Altitude of shaft entrance 1,530 m a.s.l., length 153.37 m. This shaft is over 30 metres deep and opens into a horizontal cave. With its vertical walls, it forms a natural animal trap. Only one individual was found, a wisent bull, dated to about 1,350 years before present (**Fig. 2**). Klufthöhle in Mandlkar near Hinterstoder (Upper Austria). Altitude of the entrance: 1,611 m a.s.l., length: 136 m. This narrow and only moderately steep sloping cave (**Fig. 2**) is inconceivable as a natural animal trap. The accumulation of bones here can only be explained by the activity of a large predator or humans. Two individuals were identified.

Discovery and recovery

The skull found in the Wisentschacht was discovered and recovered by speleologists on December 27th 2020 while surveying the cave. In the first and second week of January 2021, the 30-meter-deep shaft was subjected to a local inspection by a team of biologists, mountain rescuers and speleologists. Within 3 days in January 2021 about 95 % of the individual was recovered. The Klufthöhle in Mandlkar was discovered by a speleologist on January 26th, 2021. The remains were sighted and the cave was examined. The bones were recovered later on June 19th, 2021 by a team of specialists. The two sites are only about 15 km apart (beeline).

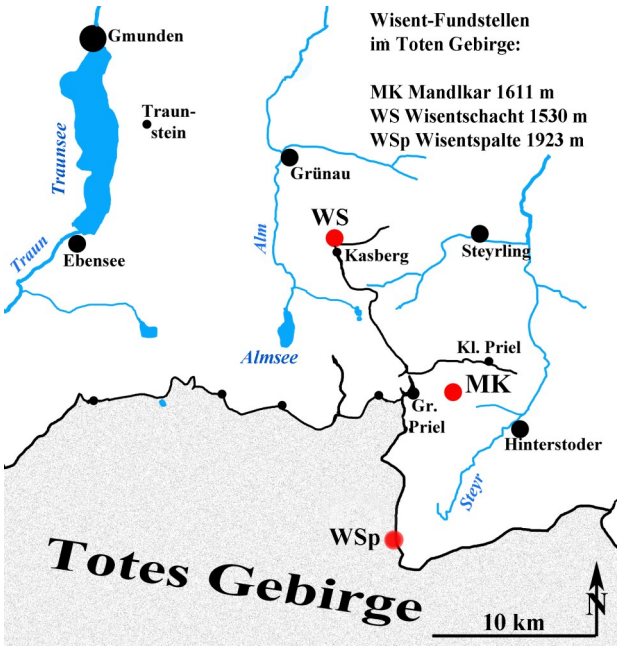

Fig. 1: Location sketch of the wisent sites in the Toten Gebirge (Upper Austria). MK = Klufthöhle in Mandlkar 1,611 m, WS = Wisentschacht 1,530 m, WSp = Wisent-Spalte 1,923 m. | **Abb.1**: Lage der Wisent-Fundstellen im Toten Gebirge (Oberösterreich).

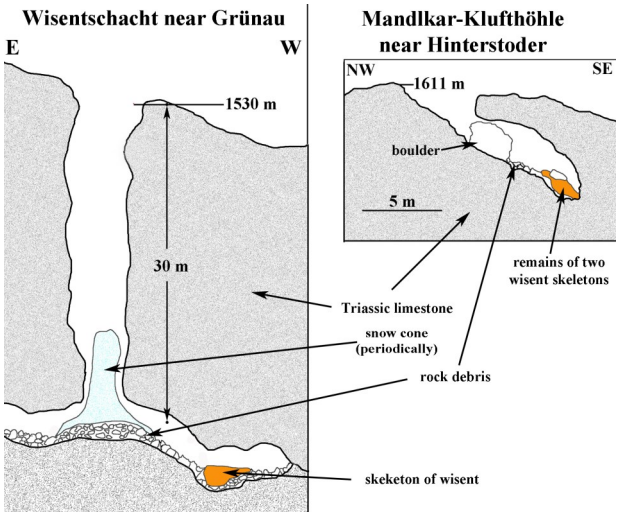

Fig. 2: Simplified longitudinal sections of the two new wisent sites in the Totes Gebirge. According to plans by Manfred Jäger, Landesverein für Höhlenkunde in Oberösterreich, research group Gmunden. | **Abb. 2**: Vereinfachter Längsschnitt der beiden neuen Wisent-Fundstellen im Toten Gebirge (nach den Plänen von Manfred Jäger, Landesverein für Höhlenkunde in Oberösterreich, research group Gmunden).

Material

The recovered wisent (*Bos bonasus* L.) remains can be assigned to a total of three individuals. Wisentschacht: an almost complete skeleton (SCHAER et al., 2022). Klufthöhle in Mandlkar: 2 cranium fragments, 4 maxillar fragments, 4 mandibular fragments (2 dext, 2 sin), 3 ossa hyalia, 2 atlantes, 2 epistrophei, 2 humeri, 3 radii + ulnae, 2 femora, 3 tibiae, 3 calcanei, 2 centralia tarsi, 1 metacarpale 3+4, 2 metatarsalia 3+4, 10 phalanges (2 basal, 4 medial, 4 terminal), 1 os sesamoides and fragments of ribs and vertebrae.

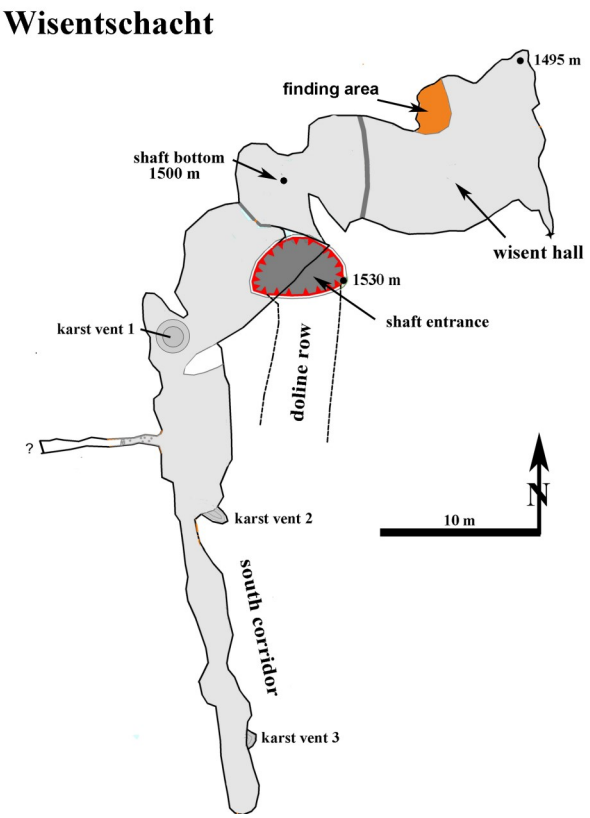

Fig. 3: Simplified ground plan of the Wisentschacht on the Kasberg near Grünau/Almtal. According to a plan by M. Jäger, Landesvereins für Höhlenkunde in Oberösterreich, research group Gmunden. | **Abb. 3**: Vereinfachter Grundriss des Wisentschachtes am Kasberg bei Grünau im Almtal (nach dem Plan von M. Jäger, Landesverein für Höhlenkunde in Oberösterreich, Forschergruppe Gmunden).

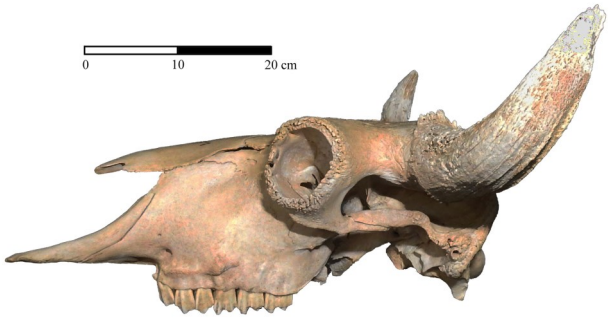

Fig. 4: Skull of *Bos bonasus* L. from the Wisentschacht on the Kasberg near Grünau/Almtal (lateral view). Photo: Teresa Schaer. | **Abb. 4**: Schädel des Wisents vom Wisentschacht am Kasberg near Grünau/Almtal (Seitenansicht). Foto: Teresa Schaer

Fig. 5: Metatarsal bone (metatarsale 3+4 dex, MK-13) with cut marks. Photo: Teresa Schaer. | **Abb. 5**: Metatarsalia dex (MK-13) mit Schnittspuren. Foto: Teresa Schaer

Measurements

The dimensions of the skull, horn-cores and metapodials (**Tab. 1**), show great differences to the fossil remains of *Bos primigenius* (Pandolfi et al., 2011).

Animal trap and cut marks

The way in which the two sites work are fundamentally different. While the Wisentschacht is an animal trap and the animal died in a 30-meter fall, the remains of the two wisents in the Klufthöhle in Mandlkar are most likely the result of human intervention. This cave is much too small and shallow for an animal to have died here in a fall. Cut marks on a metapodium (**Fig. 5**) lead us to the assumption that the wisent died as a result of medieval hunting. The small cave in the Mandlkar probably served as a dumping ground.

Radiocarbon dating

Six samples were taken from the two caves and sent to the Curt-Engelhorn-Zentrum Archäometrie in Mannheim. Results are presented in **Tab. 2**. For dating, the collagen fraction of the bone material was extracted. The collagen preservation of the six samples was good showing no degeneration of the collagen and therefore the ages are reliable. The wisent from the Wisentschacht dates from the Early Middle Ages, while the two wisents from the Mandlkar are almost the same age and date much earlier to the Iron Age.

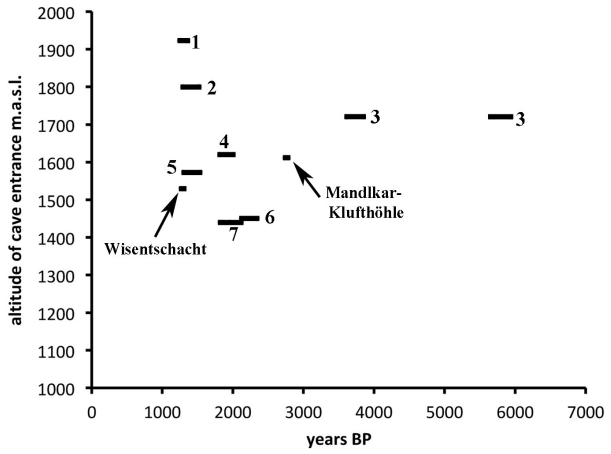

Fig. 6: Chronological position and altitude of the sites of bison remains from the karst regions of Austria: 1 = Wisentspalte near Hinterstoder, highest site of wisent remains; 2 = Wildes Loch, Grebenzen; 3 = Gläserkogelschacht, Neuberg/Mürz; 4 = Zwergweidendoline, Tauplitz; 5 = STUB-Schacht-194, Tragöß; 6 = Schneeeloch, Hinteralm; 7 = Stainzenkogelschacht, Lunz am See. | **Abb. 6**: Geologisches Alter und Seehöhe der Wisent-Fundstellen aus den Karstgebieten Österreichs.

element	cranium	cranium fragment	cranium fragment	cranium fragment	cranium fragment	cranium fragment
inventary number	WS-1	MK-1	MK-2	MK-38	MK-39	MK-40
total length incl. horn cones	543.0	fr	fr	fr	fr	fr
condylobasal length	521.0	fr	fr	fr	fr	fr
distance of horn-core peaks	710.0	fr	608.0	fr	fr	fr
distance of horn-core bases	230.5	273.0	240.0	fr	fr	fr
orbital width	327.0	344.0	313.0	fr	fr	fr
circumference of horn-core base	292.0	250.0	fr	fr	fr	fr
length of tooth row P2-M3	139.0	149.4	138.6	149.3	138.6	149.5
length of tooth row M1-M3	83.3	90.0	85.1	88.0	85.1	91.5

mandible	WS-2	WS-3	MK-43	MK-44	MK-45	MK-47
condylar length	443.0	442.0	fr	fr	fr	fr
tooth row p2-m3	146.8	148.3	159.0	144.7	161.0	154.0
tooth row m1-m3	95.2	96.0	96.8	99.5	96.1	89.7

element	mc 3+4	mc 3+4	mc 3+4	mt 3+4	mt 3+4	mt 3+4	mt 3+4
inv. nr.	WS-74	WS-75	MK-15	WS-76	WS-77	MK-13	MK-14
side	sin	dex	sin	sin	dex	dex	sin
length	221.0	222.0	241.0	273.0	273.0	285.0	271.0
distal width	79.0	78.4	81.0	70.4	71.1	74.0	72.0
distal depth	42.5	42.7	50.0	42.2	40.3	fr	42.0

Tab. 1: Selected values of skull and metapodial measurements of subfossil wisent (*Bos bonasus*) remains from the Wisentschacht (WS) and the Klufthöhle in Mandlkar (MK) in the Totes Gebirge (Upper Austria). | **Tab.1**: Ausgewählte Messungen am Schädel und Metapodien von den subfossilen Wisenten aus der Wisentschacht (WS) und der Klufthöhle im Mandlkar (MK) im Toten Gebirge (Oberösterreich).

Lab.Nr.	sample name	C^{14} age yBP	error ±	$\delta^{13}C$ AMS [‰]	probability 68%	probability 95%	C:N	C (%)	collagen (%)	material
50542	Wisentschacht Kasberg WS-51	1470	21	-23.8	579-637 AD	567-642 AD	3.2	45.6	11.6	tibia dex
50543	Wisentschacht Kasberg WS-68, MK-1	1470	21	-24.4	579-637 AD	567-642 AD	3.2	44.6	11.7	calcaneus dex
50541	Klufthöhle Mandlkar KHM-1, MK-2	2481	23	-27.8	752-545 BC	769-492 BC	3.3	45.8	5.3	petrosa
51824	Klufthöhle Mandlkar KHM-3	2486	23	-23.1	755-546 BC	770-520 BC	3.3	42.7	13.3	tooth root
53295	Klufthöhle Mandlkar KHM-2	2499	22	-25.3	760-552 BC	772-544 BC	3.3	44.9	8.3	tooth root
53294	Klufthöhle Mandlkar MK-13	2464	23	-23.8	749-518 BC	756-421 BC	3.2	44.3	15.6	mt

Tab. 2: Radiometric data of wisent bones from two caves in the Totes Gebirge (Upper Austria). | **Tab. 2**: AMS datierte Wisent Knochen von den zwei neuen Höhlen im Toten Gebirge (Oberösterreich).

Discussion and conclusion

The taxonomic assignment to *Bos bonasus* is unambiguously based on the morphology of the horn-cores and the teeth. The special feature of these finds is the altitude of the sites and the absolute age of the bones. According to the chronological position they are part of the »wisent time« in the Eastern Alps (Bauer, 2001). The samples dated so far range from 6,000 to 1,200 years before present (4,000 a BC to 700 AD) and from elevations between 1,440 and 1,923 m a.s.l..

The European »bison« (wisent, *Bos bonasus* L.) is an inhabitant of deciduous or mixed deciduous-coniferous forests, where foliage, small twigs, and bark of deciduous trees play a major role (Bauer, 2001). In the Alps today, bison would prefer colline (mixed oak forest) and montane (mixed beech-fir forest) vegetation stages. These wisent remains from alpine caves are all from sites now in the subalpine to alpine zone. From this it can be concluded that the beech limit but also the forest line during the »wisent time« (6,000 to 1,200 years before today) was much higher and the average summer temperature had to be at least 3 to 6 °C higher than today. Remarkable is a palynological record (Ressl, 1980) from the shaft cave Stainzerkogelschaft near Lunz am See. Remains of wisent were found in the shaft (1,463 m, see **Tab. 3**). The clay with a skull fragment with horn-cores inside was examined palynologically. The dominating pollen were from alder (*Alnus*), oak (*Quercus*) and linden tree (*Tilia*). The oak boundary (boundary between colline and montane vegetation stages) today lies between 400 and 800 metres in the Northern Alpine Alps (Grabherr et al., 2004). Oaks (*Quercus*) at an altitude of 1,450 metres around 2,000 years ago also indicate a climate approximately 4 to 7 °C warmer than today. Investigations of dated stone pines (*Pinus cembra*) in the Central Alps support this climatological interpretation (Nicolussi & Patzelt, 2006). The results underline the importance of post glacial findings to understand the alpine climatic history of the early Holocene.

Cave name	Local community	Lab. Nr.	altitude	aBP	error ±	2 sigma calBP	archaeolog. times 2 sigma BC/AD	archaeolog. units	Lit.
Wisentspalte	Hinterstoder	VERA-0143	1923 m	1370	50	1242-1357	593-708 AD	Early middle age	1
Wisentschacht Kasberg	Grünau	MAMS-50542	1530 m	1470	21	1265-1302	567-642 AD	Early middle age	2
Wisentschacht Kasberg	Grünau	MAMS-50543	1530 m	1470	21	1308-1383	567-642 AD	Early middle age	2
Wildes Loch	Grebenzen	VERA-0145	1800 m	1480	70	1289-1520	430-661 AD	Early middle age	1
STUB-Schacht-194	Tragöß	VERA-0144	1567 m	1530	70	1303-1535	415-647 AD	Early Middle Age	1
Stainzenkogelschacht	Lunz/See	VERA-0146	1463 m	1980	60	1864-1950	86 BC-0	Roman period	1
Zwergweidendoline	Tauplitz	VERA-0142	1620 m	1980	45	1817-2003	133 BC-53 AD	Roman period	1
Stainzenkogelschacht	Lunz/See	VERA-0140	1463 m	2010	60	1819-2120	170 BC-131 AD	Roman period	1
Schneeloch/Hinteralm	Mürzsteg	LTI-3900A	1450 m	2228	50	2120-2345	400-180 BC	Iron Age	3
Klufthöhle Mandlkar	Hinterstoder	MAMS-51824	1611 m	2486	23	2720-2470	770-520 BC	Iron Age	2
Klufthöhle Mandlkar	Hinterstoder	MAMS-50541	1611 m	2481	23	2719-2442	769-492 BC	Iron Age	2
Klufthöhle Mandlkar	Hinterstoder	MAMS-53295	1611 m	2499	22	2722-2493	772-544 BC	Iron Age	2
Klufthöhle Mandlkar	Hinterstoder	MAMS-53294	1611 m	2464	23	2706-2370	756-421 BC	Iron Age	2
Gläserkogelschacht	Neuberg/Mürz	VERA-0148	1725 m	3470	50	3614-3851	1901-1664 BC	Bronze Age	1
Gläserkogelschacht	Neuberg/Mürz	VERA-0147	1725 m	5060	70	5651-5931	3981-3701 BC	Neolithic	1
Gläserkogelschacht	Neuberg/Mürz	VERA-0141	1725 m	5090	60	5705-5938	3755-3988	Neolithic	1

Tab. 3: Radiocarbon (AMS) ages of subfossil bone fragments of *Bos bonasus* from Austrian caves, sorted by geological age of cave finds. ^{14}C data according to 1 Bauer (2001), 2 new and 3 Herrmann et al. (2010), calibrieded after Stuiver et al. (2021). | **Tab. 3**: AMS datierte Reste von Wisenten (*Bos bonasus*) aus den Karstgebieten Österreichs, geordnet nach geologischem Alter (1 Bauer (2001), 2 new, 3 Herrmann et al. (2010), kalibriert nach Stuiver et al. (2021).

Acknowledgements

We want to thank Franz Rührlinger and Franz Moser, Heli Steinmassl for sharing the information and recovering the material. The following institutions supported the operations in the field: Bergrettungsdienst Ortsstelle Grünau; Petzl Österreich; Verband österr. Höhlenforscher Sektion Oberösterreich; Fleischerei Silmbroth; Gemeinde Grünau im Almtal; Cumberland Wildpark Grünau; Forstverwaltung Württemberg; Markus Pernkopf and his family. The Department of Palaeontology at the University of Vienna provided excavation and preparation equipment and facilities. We are grateful to the whole excavation teams for their help. And finally Eva-Maria Geigl and her team from the Institut Jacques Monod (Epigenome and Paleogenome, Paris) for the possibility to study the aDNA from the wisent material.

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