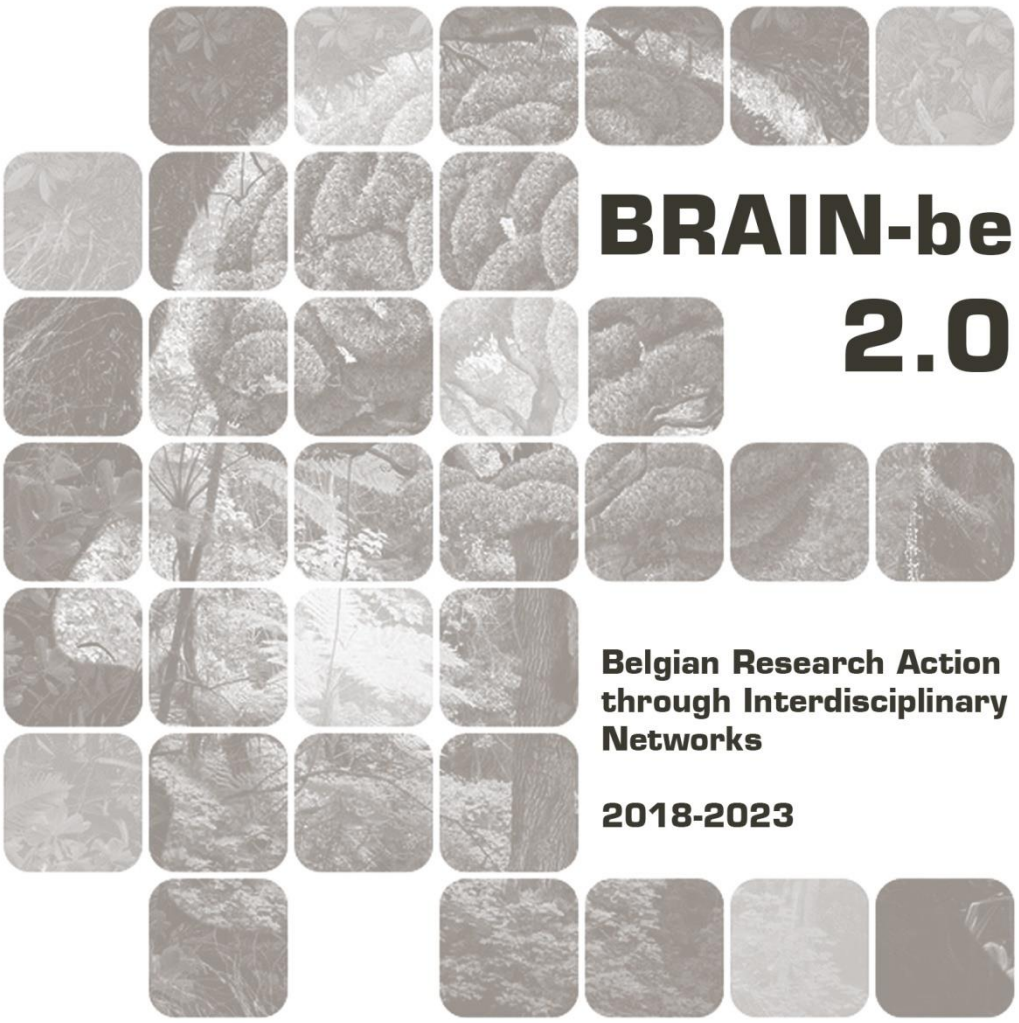


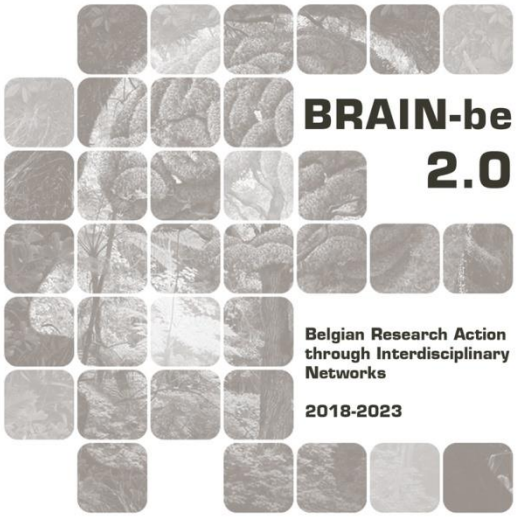
ICHIE

Interconnectivity of large Carnivores, Humans and Ice Age Environments

GERMONPRE, Mietje (Royal Belgian Institute of Natural Sciences), JIMENEZ, Elodie-Laure (Royal Belgian Institute of Natural Sciences), BOUDIN, Mathieu (Royal Institute for Cultural Heritage)

Pillar 2: Heritage science

belspo .be



NETWORK PROJECT

ICHIE

Interconnectivity of large Carnivores, Humans and Ice Age Environments

Contract - B2/ 191 / P2 / ICHIE

FINAL REPORT

PROMOTORS: Mietje Germonpré (Royal Belgian Institute of Natural Sciences)
Mathieu Boudin (Royal Institute for Cultural Heritage)

AUTHORS: Mietje Germonpré (Royal Belgian Institute of Natural Sciences)
Elodie-Laure Jimenez (Royal Belgian Institute of Natural Sciences)
Mathieu Boudin (Royal Institute for Cultural Heritage)

Published in 2023 by the Belgian Science Policy Office
WTCIII
Simon Bolivarlaan 30 bus 7
Boulevard Simon Bolivar 30 bte 7
B-1000 Brussels
Belgium
Tel: +32 (0)2 238 34 11
http://www.belspo.be
http://www.belspo.be/brain-be

Contact person: Georges Jamart
Tel: +32 (0)2 238 36 90

GERMONPRE, M., JIMENEZ, E.-L., BOUDIN, M. ***Interconnectivity of large Carnivores, Humans and Ice Age Environments (ICHIE).*** Final Report. Brussels: Belgian Science Policy Office 2023 – 36 p. (BRAIN-be 2.0 - (Belgian Research Action through Interdisciplinary Networks))

TABLE OF CONTENTS

ABSTRACT

CONTEXT

The caves of Caverne Marie-Jeanne, Goyet, Trou Magrite and Spy were excavated by geologists and archaeologists from the Royal Belgian Institute of Natural Sciences (RBINS) in the 19th and 20th century. The rich Late Pleistocene mammal assemblages found at these natural and prehistoric sites have been stored in the palaeontological collections of the RBINS since then.

OBJECTIVES

The aim of the ICHIE BRAIN project was to use the palaeontological collections of Pleistocene mammals which are housed at the RBINS, to examen the zooarchaeological data, the cementum and isotope analyses from a selection of sites in order to further our understanding of human-environment relationships in north-west Europe and to explore the inter-connectivity between human and carnivore communities just before the extinctions at the end of the Pleistocene. Combining new zooarchaeological studies with the cementum analyses, isotopic studies and AMS dating allowed to explore the seasonal mobility of prey animals and their hunters, the temporal variation in the diet of the Pleistocene apex predators (hominins included), the evolution of their niche partitioning over time and the interactions between Palaeolithic humans and large carnivores.

CONCLUSIONS

The Belgian karst region was relatively densely populated during the Late Pleistocene. Several caves yielded material dating from the transition period between Neanderthals and Anatomically Modern Humans. The seasonality analyses highlighted the absence of seasonal pattern in cave hyaenas suggesting that hyaena populations were well established in the Belgian Ardennes and were attached to their territory despite seasonal pressures. Neanderthals frequented the territories of southern Belgium on a regular basis during this time notwithstanding the presence of potential competitors, showing that the risk/reward ratio was probably low overall, maybe thanks to spatial organisation. Multi-isotope analyses ($\delta^{13}C$, $\delta^{15}N$, $\delta^{34}S$) of the faunal remains from the studied natural and Palaeolithic sites permitted to place the top-predators within the Pleistocene food web in Belgium and the rest of Europe. Comparison of the subsistence and mobility of the large carnivore communities and their interconnectivity with the last Neanderthals and the first Modern Humans can be the key to understanding the replacement of the Neanderthals and the extinctions at the end of the Pleistocene. Moreover, the presence of Palaeolithic dogs - the only species domesticated during the Pleistocene with an early beginning of this process placed in the Aurignacian - possibly influenced the (local) Late Pleistocene extinctions of large predators, such as cave hyaenas, cave bears and cave lions.

KEYWORDS

Pleistocene, Cave hyaena, Cave lion, Wolf, Ungulates, Palaeolithic dogs, Neanderthals, Modern Humans, Zooarchaeology, Cementum analysis, Stable isotopes

1. INTRODUCTION

Over the course of the last 120,000 years, mid-latitude Europe went through a period of climatic instability characterized by amplitude fluctuations between cold and arid phases, and milder and more humid phases. Starting about 40,000 years ago the climatic decline culminated in the Last Glacial Maximum, an extremely cold and dry period dating from 23,000 years to 19,000 years ago. These climatic fluctuations influenced to a high degree the environment and impacted both plant and animal communities. Just as the large carnivores today, the Ice Age predators played central ecological roles from their position at the top of the food webs. Their feeding strategies had significant impacts on overall ecosystem health. Human (Neanderthals and Anatomically Modern Humans) and large carnivore (cave hyaenas, cave lions, cave bears, brown bears, Pleistocene wolves) communities were also at that time in competition for habitat and food (prey: mammoth, woolly rhinoceros, horse, steppe bison, reindeer, etc.; other: berries, nuts, honey, etc.). During this period in Belgium, the habitat formed by the tributary valleys of the Meuse and by the limestone cliffs and interfluvial plateaux attracted a biodiverse fauna. Many caves are present in the Carboniferous outcrops. The karstic systems are characterised by several caves that have close access to rivers, are situated less than 40 m above the valley floor and are characterised by small chambers, galleries and corridors that have a southern orientation. Wide circulation zones are present nearby made up by the Meuse valley and its tributaries, and by the overlying plateaus. Carnivores used the caves along these rivers as den sites, hide-outs or hibernation places. Palaeolithic hunter-gatherers exploited this biodiverse palaeo-hotspot and utilised the caves as camp sites. In the caves, many Palaeolithic artefacts, and numerous bones of Pleistocene mammals and human remains have been found. Several of these caves were excavated by Edouard Dupont in the 1860s and this material has been housed at the RBINS since. Zooarchaeological analyses demonstrated that Palaeolithic peoples brought to the caves body parts of their prey and skinned and dismembered there the carcasses, filleted the meat, extracted marrow and rendered grease from the bones as is testified by the cut and impact marks on the bones. Cave hyaenas used the caves as birth-sites. They transported to the caves the body parts of their prey. The assemblages accumulated by carnivores display much more carnivore gnawing traces, while anthropogenic traces are lacking, compared to the anthropogenic assemblages. Other carnivores such as the cave bear and brown bear used the caves as hibernation dens. Many succumbed during their winter sleep or fell victim to predators. Their remains accumulated inside the caves. About 40,000 years ago the last Neanderthal populations lived in the karstic region of Belgium, they were replaced by Anatomically Modern Humans. It is also during this period, leading up to the Last Glacial Maximum, that the cave hyaena and cave bear became extinct and that the cave lion underwent a dramatic demographic decline, while it seems that a symbiotic interaction between Modern Humans and Pleistocene wolves started to developed. The stable temperature inside the caves insured that the organic fraction of the bones is well preserved, permitting sophisticated analyses. New studies, based on biogeochemical analyses of bone samples from the Pleistocene fauna, help to clarify interspecific competition, niche partitioning, and subsistence strategies of the Pleistocene carnivore and human communities.

The ICHIE project joined together teams and skills from two Belgian federal scientific institutions (RBINS, RICH), two foreign universities (Biogeology, Geoscience Department of the University of Tübingen, Germany; department of Geosciences, University of Aberdeen, U.K.) and two foreign

institutes (the Moravian Museum, Czech Republic; the Zoological Institute RAS, Saint-Peterburg, Russia).

2. STATE OF THE ART AND OBJECTIVES

The Ice Age fauna, from the iconic mammoth to the intriguing cave hyaena and the interconnectivity of these mammals with prehistoric humans fascinate since long not only scholars, but also the general public and the media.

The main objectives of this project were to clarify the interconnectivity of carnivore and human populations during the Ice Age. How did the human and carnivore communities interreact? Did Anatomically Modern Humans adapt in a different way to the changing environment compared to the last Belgian Neanderthals? Did Palaeolithic dogs help Anatomically Modern Humans control carnivore populations? How did the intraguild relationship between the apex predators evolve during the time leading up to the Last Glacial Maximum? Did the apex predators show signs of distress on their way to (local) extinction? Did the demographics of the megaherbivores suffer from human hunting pressure?

To answer these important questions, the ICHIE-project studied zooarchaeological and taphonomic data, and cementum and isotope analyses from a selection of archaeological and palaeontological sites. Some key specimens were dated by AMS dating. To achieve this, a new sampling campaign was integrated with published analyses of human and mammal bones.

Aim 1. How did the interconnectivity of carnivore and human populations influence the trajectories of both populations during the time leading up to the Last Glacial Maximum?

Preliminary evidence of specific attitudes of Modern Humans regarding cave and brown bears and wolves, and comparisons of resource exploitation of cave hyaena, Modern Human and Neanderthal populations suggest an emerging picture of a human expansion influencing carnivore demography. The analyses of the zooarchaeological and taphonomic features of the carnivores and their prey found at geographical and temporal distinct sites can allow for a clearer understanding of the trajectories of the large predators during the time before their extinction or local disappearance and clarify the dynamic relationship between the Ice Age predators and contemporaneous human populations in the context of a deteriorating climate. Previously published results are integrated with the analyses of new material from the karstic region (Goyet, Trou Magrite, Caverne Marie-Jeanne, Walou cave) from Belgium and from European mid-Upper Palaeolithic open-air sites. Human influence on the faunal assemblages the Caverne Marie-Jeanne in the Belgian karstic region is practical nihil and this material can be considered to form an excellent reference set of a natural accumulated faunal assemblage. They are confronted with the faunal assemblages from the Belgian Palaeolithic sites (Trou Magrite, Spy, Goyet) and the European contemporaneous open-air sites (Předmostí, Kostenki) that were formed mainly through anthropogenic activities.

Aim 2. Did the declining large carnivore populations adapt by extending their home range or by exploring other food niches during the time leading up to the Last Glacial Maximum?

This question is being addressed by multi-isotope analyses ($\delta^{13}C$, $\delta^{15}N$, $\delta^{34}S$) of the faunal remains from the diachronic sites to place the top-predators within the Pleistocene food web in Belgium and the rest of Europe. Did the large carnivores hunt other prey than their preferred ones once the latter

suffered from the climatic deterioration and the human hunting pressures? Studies that integrate the Pleistocene carnivores in the food web have already started for the Belgian Palaeolithic sites of Spy and Goyet, and the Czech Předmostí site, but have not yet been undertaken in detail for the Belgian Trou Magrite, Walou cave and Caverne Marie-Jeanne sites. However, comparison of the subsistence and mobility of the last Neanderthals, the first Modern Humans and the last large carnivore communities are key to understanding the extinctions at the end of the Pleistocene. Moreover, the presence of Palaeolithic dogs, the only species domesticated during the Pleistocene prior to the emergence of agriculture possibly had an effect on carnivore-human interferences and the Late Pleistocene extinction of large predators and this aspect deserves further investigation. Based on methods used in palaeoecology and modern ecology (multi-isotope analysis), and compiling isotopic data from published studies and new samples on herbivore and human ecology, the ICHIE-project examined ecological conservation and plasticity in predator behaviours during the Late Pleistocene in collaboration with national and international experts.

The ICHIE-project further demonstrates the need for a continued study of the palaeontological collections of the Pleistocene fauna at the RBINS by the following: the detailed comparison of the multi-isotope analyses of top predators such as the cave hyaena and the cave lion to verify trends in their choice of prey animals in the run-up to the Last Glacial Maximum. Furthermore, based on the results of the isotope analyses, a selection for the dating of the specimens can be made to find the last occurrences of these species to infer the time and tempo of their disappearances in our regions.

3. METHODOLOGY

The ICHIE-project analysed from a zooarchaeological point of view the palaeontological collections of the RBINS and the Moravian Museum in Brno. The skeletal elements of the Pleistocene mammal assemblages are counted as Number of Identified Specimens (NISP) and as Minimum Number of Individuals (MNI) (Lyman, 1994). The anthropogenic cut and impact marks and the carnivoran gnawing traces on the mammal remains are identified based on the descriptions in Binford (1981), Lyman (1994) and Fernández-Jalvo & Andrews (2016). Measurements of the skulls, teeth and bones are carried out according to von den Driesch (1976) to be compared to reference collections. All data are compiled in Excel data bases.

In addition to the zooarchaeological methods, the ICHIE-project used multi-isotope analyses of archaeological faunal bone and teeth from diachronic, newly-dated sites to explore conservation and plasticity in carnivore behaviour during the late Pleistocene and includes data that were generated from sites previously investigated for herbivore isotope ecology and/or human data. Isotope analyses are employed to produce primary data for the ICHIE-project. Carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope analysis of preserved bulk bone collagen is utilized to evidence dietary niche (Bocherens, 2003). Sulphur isotope ratios are also explored to provide information on palaeo-diet and migration. All bone samples for these isotopic studies were prepared following the collagen extraction method of Longin (Longin, 1971), with modifications based on the recommendations of Collins and Galley (Collins and Galley, 1998), with the addition of an ultrafiltration step (Brown et al., 1988), as described in Britton et al. (2012). The collagen was analysed by mass spectrometry in order to obtain Carbon, Nitrogen, and Sulphur ratios.

The combination of these modern palaeoecological analyses permitted to clarify the adaptability and variability of the top-predators towards the changing behaviour of their prey at the end of the

Pleistocene. Furthermore, a selection of bones was selected based on their excellent preservation and their direct connection with humans (e.g. cut marks) or carnivores (e.g. gnawing traces) for AMS dating.

References

Binford, L. R., 1981. Bones. Ancient men and modern myths. Academic Press, New York.

Bocherens, H., 2003. Isotopic biogeochemistry and the palaeoecology of the mammoth steppe fauna. Deinsea, 57-76.

Britton, K., Gaudzinski-Windheuser, S., Roebroeks, W., Kindler, L., Richards, M.P., 2012. Stable isotope analysis of well-preserved 120,000-year-old herbivore bone collagen from the Middle Palaeolithic site of Neumark-Nord 2, Germany reveals niche separation between bovids and equids. Palaeogeogr. Palaeoclimatol. Palaeoecol. 333-334, 168-177.

Brown, T.A., Nelson, D.E., Vogel, J.S., Southon, J.R., 1988. Improved collagen extraction by modified Longin method. Radiocarbon 30, 171-177.

Collins, M.J., Galley, P., 1998. Towards an optimal method of archaeological collagen extraction: the influence of pH and grinding. Ancient Biomolecules 2, 209-222.

Fernández-Jalvo, Y., Andrews, P., 2016. Atlas of taphonomic identifications: 1001+ Images of Fossil and Recent Mammal Bone Modification. Springer, Dordrecht.

Longin, R., 1971. New method of collagen extraction for radiocarbon dating. Nature 230, 241-242.

Lyman, R. L., 1994. Vertebrate taphonomy (Cambridge Manuals in Archaeology). Cambridge University Press, Cambridge.

von den Driesch, A., 1976. A guide to the measurement of animal bones from archaeological sites (Peabody Museum Bulletin 1). Peabody Museum Press, Cambridge (Massachusetts).

4. SCIENTIFIC RESULTS AND RECOMMENDATIONS

The project was divided into three different work packages. First the tasks that were specified in the project are detailed, then the results achieved are described.

4.1. WORK PACKAGE 1: CONSTRUCTION OF A CONCEPTUAL AND CONTEXTUAL FRAMEWORK

4.1.1.Task 1.1.: Exploring of existing theories (RBINS)

Specific attitudes of Anatomically Modern Humans regarding cave and brown bears and wolves, and the comparisons of resource exploitation by cave hyaena, Modern Human and Neanderthal populations suggest that the human demographic expansion in the course of the Late Pleistocene influenced carnivore demography. Approaches from archaeology, biology, palaeontology and ethnography have been used and explored in our published papers. The zooarchaeological and taphonomic analyses of carnivorous and anthropogenic assemblages found at geographical and temporal distinct sites explain the trajectories of the large predators during the time before their

extinction or local disappearance and clarify the dynamic relationship between the Ice Age predators and contemporaneous human populations in the context of a deteriorating climate. This integrative approach helped re-framing Palaeolithic lifeways by understanding the ecology of the key-species (humans and carnivores) and therefore decipher the complex interactions between co-evolving species within this guild and redefine the socioecology of the human species (Neanderthal and *Homo sapiens*). This approach has inspired other researchers to explore these complex aspects of the Palaeolithic life. Furthermore, the organization of the United Kingdom Archaeological Sciences Conference in Aberdeen in April 2022 and the session chairing of "Animals, Humans and the Environment" helped ELJ to gain more insights into modern paleoecology studies within the European context, grasp the potential of such studies and understand the challenges that will frame the future of isotope analyses.

Work Package 1.1: Activities realized and results achieved

The existing theories were discussed during the follow up committee meetings (31/08/2021; 11/01/23). The adaptations following the recommendations of the steering members were then used in the papers detailing the results of the work packages.

4.1.2.Task 1.2. Context and archaeology of the studied sites

The majority of the material considered for this project was excavated in the 19th and the 20th century from prehistoric and natural caves (Goyet, Trou Magrite, Caverne Marie-Jeanne, Spy) that are part of the large karstic systems developed in limestone cliffs in the Mosan basin (Figure 1). This collection consists of anthropogenic and carnivorous assemblages, stored at the RBINS. Unfortunately, the excavation methods deployed at that time do not meet today's standards, and the stratigraphic attribution assigned to the specimens should be verified for key specimens by absolute dating (AMS dating). All available data regarding the site history and archives, stratigraphy, the environment and archaeology of the palaeontological and Palaeolithic sites were studied and brought together, thanks to RBINS documentation and with the help of Annelise Folie, the collection manager of the palaeontological collections of the RBINS, along with data from other Belgian and foreign scientific institutions.

Work Package 1.2: Activities realized and results achieved

All available data from the different palaeontological and Palaeolithic sites in Belgium and the Czech Republic were brought together describing their stratigraphy, the palaeoenvironment and archaeology. Here below a summary is given of the most important features of the sites of Caverne Marie-Jeanne, Trou Magrite, Goyet, Spy and Walou Cave from Belgium and Předmostí from the Czech Republic (Figure 1). The results of the ICHIE-project on the Belgian Pleistocene fauna are confronted with the Palaeolithic assemblages from European contemporaneous open-air sites (Předmostí, Kostenki, Yudinovo) that were formed mainly through anthropogenic activities.

Figure 1: Map of the main Pleistocene sites in Belgium

The site of Caverne Marie-Jeanne (CMJ) is located in Hastière-Lavaux (Province of Namur, Belgium), on the right bank of the Féron, a small tributary of the Meuse River. Now partially destroyed, this small south-facing cave was located below the Insemont plateau at the top of a former quarry about 25 m above the Féron riverbed. The cave was composed of a long 'corridor' (Figure 2). During the summer of 1943, a small team from the RBINS led by palaeontologist Maxime Glibert, started the excavation of these deposits. The finds are housed at the RBINS under General Inventory number 14 138 from 4 September 1943. Ten Quaternary layers in the approximately 8 m-thick sequence of CMJ were recognized (Figure 2). The layers are sometimes separated by breccia, conglomerates, concretions and speleothems. Layers 10 to 7, which do not contain any faunal or artefact remains, suggest that the cave was most likely unoccupied during their deposition. The overlain layers (Layers 6 to 2) are mainly composed of aeolian deposits (silt sands) and contain the vast majority of the faunal remains. Radiocarbon dates on lemmings from Layers 6 to 4 suggest that the deposits accumulated around 47.6–43k a BP (early/mid-MIS 3). Layer 3 has not been dated yet, but the fauna – very similar to Layer 4's – suggest that this deposit too can be associated with the Late Pleistocene period/MIS 3. The large amount of faunal remains in Layers 4 and 3 shows that the cave was intensely occupied during the formation of these deposits, and the excellent preservation of the osseous material also shows that they were rapidly covered by aeolian deposits. The radiocarbon dating from remains of Layer 2 shows that this layer formed during MIS 2. Layer 1 seems heavily reworked, and is composed of black clay soil mixed with both fossil and modern fauna. A few Medieval pottery fragments were found in this uppermost Layer. In total, about 20 lithic 'artefacts'

were originally identified across the whole sequence by the excavator Glibert, but the anthropogenic origin of most of them remains highly debatable (lack of distinctive pieces, high degree of edge damage and abrasion). The scarcity of the lithic artefacts, and the complete absence of anthropogenic marks on the faunal material suggest that the lithic pieces and the faunal remains have accumulated independently, and that their association is probably fortuitous. Recent palaeoenvironmental reconstructions based on herpetofauna and small mammal analysis revealed cold conditions throughout the stratigraphy, with Layer 4 being relatively dry but still more humid than Layer 2 (LGM) when the conditions were slightly colder and drier. The landscape around the site was patchy when Layer 4 accumulated, with a mixed habitat dominated by open woodland formations and open dry meadows.

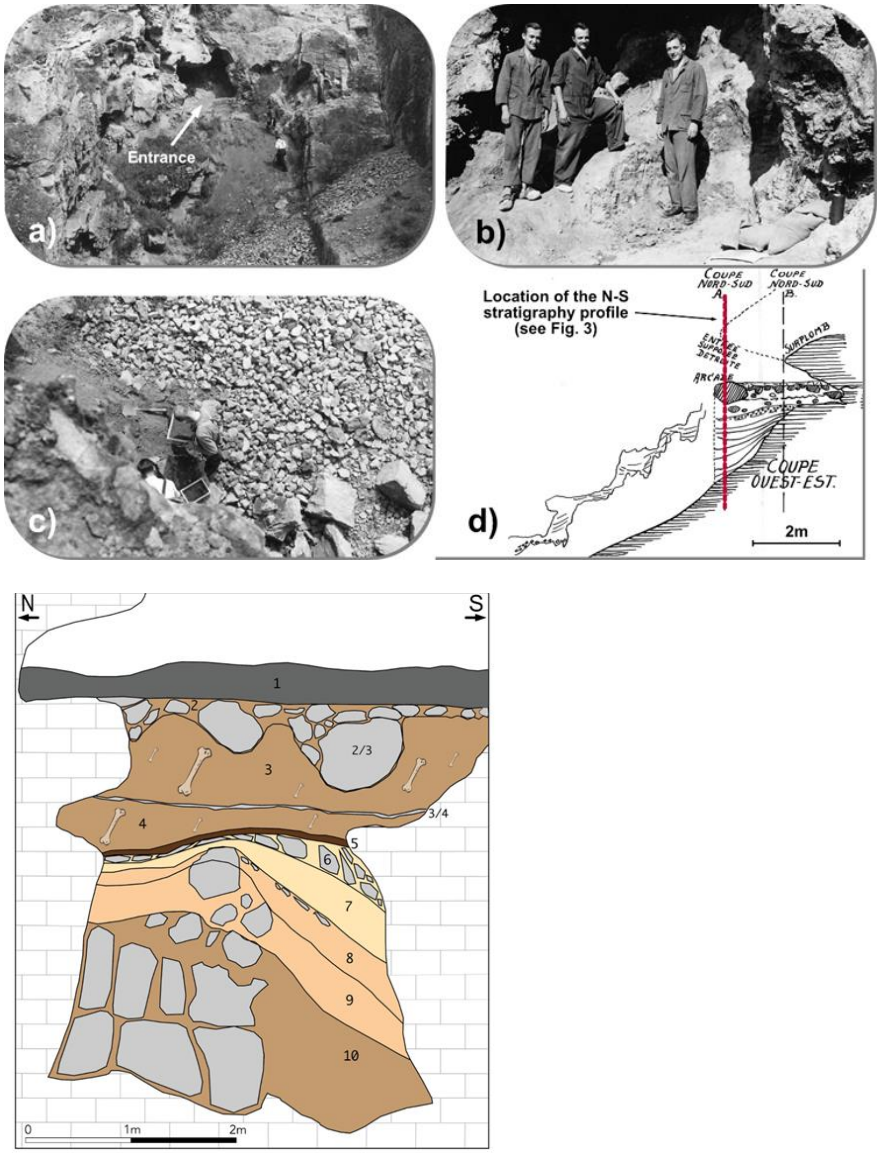


Figure 2: Historic documentation on Caverne Marie-Jeanne, Belgium, and reconstructed stratigraphy based on RBINS archives

Trou Magrite is a cave site located at Pont-à-Lesse in the Lesse Valley, commune of Dinant, Belgium. It was mainly excavated by E. Dupont during the 1860s. Dupont recognizes three sedimentary entities: the first, located at the top of the stratigraphy and approximately 1 m thick, is composed of

"boulder clay", the second of "stratified clayey-sandy deposits" with a thickness of 2.50 m, and the third of “Ardennes rolled pebbles” with a thickness of 1 m. Within the second set, E. Dupont described four archaeological bone levels. The two top levels contain many remains from reindeer and horse, the two lower levels are characterized by remains from the megafauna. Dupont also collected during these excavations two elements of portable art, an anthropomorphic figurine and an engraved reindeer antler, in the third bone level. The archaeological record covers a broad time range spanning from the Middle and Upper Palaeolithic to the Mesolithic, Neolithic, and Iron Age. An important Middle Palaeolithic collection is present, probably representing several occupation phases. Several human remains were also recovered and identified as Palaeolithic humans by E. Dupont. The faunal assemblage is dominated by remains from horse, reindeer and woolly rhinoceros. The large carnivores are represented by canids and hyaenas. Recent AMS dates, done on human modified bones, range from c. 43,000 till 30,300 BP. The majority of the faunal material of the Dupont collection is stored in the conservatories of the RBINS.

Figure 3: Terrace and entrance of Trou Magrite (photo: Rutot, taken around 1913, archives: RBINS)

Figure 4: Engraved reindeer antler found by E. Dupont in his third bone level of Trou Magrite in 1867

The third cave of Goyet, excavated in the latter half of the 19th and beginning of the 20th century, and again at the end of the 1990s, is part of a large cave system located in the Mosan Basin. It is situated at an altitude of 130 m in a limestone cliff 15 m above the river Samson, near the confluence of the Strouvia with the latter. It is about 120 meters deep and consists of several chambers. Chamber A lies at the entrance of the cave and is connected to Chamber B by a small gallery, with Chamber C situated at the back of the cave. The most extensive excavations were carried out by Edouard Dupont in the 1860s. The cave yielded a rich archaeological sequence with Middle and Upper Palaeolithic deposits containing mammal and human remains, and Middle Palaeolithic, Aurignacian, Gravettian and Magdalenian artefacts as well as younger material. Published AMS dates range from c. 41,200 y BP till 10,600 y BP. Unfortunately not much information is available on the stratigraphy and spatial distribution of the finds. The excavation methods by Dupont do not meet today's standards, and the levels described by Dupont likely represent a mix of material from different periods. In Chamber A, Dupont (1873) distinguished four bone levels. A sterile clay horizon separated the third and second bone horizon. The second and first bone horizon were also separated by a sterile horizon. Aurignacian ivory beads were discovered in Level 3. Other spectacular finds include "batons de commandement", perforated teeth and shells from the Magdalenian (Level 2 and 1) and a bone harpoon from Level 1. Furthermore, the upper three bone levels contained many bones from human refuse. The remains are among others from horse, reindeer, bison, ibex, muskox, mammoth, rhinoceros, wolf and arctic fox. In these levels, the bones were often fractured for marrow extraction, have cut marks or ochre stains, indicating that these animals were likely hunted and butchered by prehistoric humans. The faunal assemblages from Levels 3, 2 and 1 are therefore largely anthropogenic in origin. Bone level 3 was well developed near the entrance: "...*ce niveau renfermait en effet une grande quantité d'ossements... il renfermait aussi beaucoup de S. taillés, des objets de parure, des os carbonisés; le tout particulièrement vers l'entrée, c'est à dire la partie éclairée du souterrain*" (Dupont, unpublished notes). Based on the zooarchaeological records and isotopic analyses, the Neanderthals and Upper Palaeolithic Modern Humans preyed upon terrestrial herbivores, including mammoths with a special preference for mammoth calves and their mothers. The bear, lion and hyaena assemblages from bone Levels 1, 2 and 3 in Chamber A were found more to the back of the chamber and appear not to be related to the human refuse assemblages in the front of the Chamber. In his unpublished notes, Dupont mentions that the bear and hyaena remains from Level 2 were found deep in the cave. Chamber B lies behind Chamber A and has a length of circa 13 m. Bone horizon 5, which was seemingly only present in Chamber B, yielded remains from cave bear, brown bear and cave lion. According to Dupont (unpublished notes), this horizon had a wide extension: "*Le cinquième, qui est par conséquent l'inférieur, fut d'abord un repaire de Lion, dans l'anfractuosité B … il faut noter que, tandis que le Lion se tenait dans les premières galeries obscures (en B), l'Ours occupait la Caverne jusque dans ses parties les plus reculées, même à 100 m et plus de l'entrée*". Dupont (unpublished notes) assigns Level 4 mainly to Chamber B. Palaeolithic artefacts were apparently lacking from this level and the majority of the bones derives from cave bears. The mortality pattern of the cave bear assemblages from Goyet is dominated by young and old individuals. They likely died during hibernation, from starvation or from other attritional factors such as predation by cave lions. Although the age distribution of the remains at Goyet clearly shows that the bulk of the bear material is derived from animals dying of natural causes, it is possible that the bear bones with anthropogenic marks (cut marks, red stains) are from hunted bears that were, after skinning and/or consumption, deposited inside the cave. Level 4 includes further herbivore remains from horse,

reindeer and bison. The herbivore assemblage comes from body parts of prey animals brought to the cave by cave hyaenas, of which the skeletal elements occur as well in Chamber B, and is unrelated to the anthropogenic assemblages from Chamber A, given the presence of numerous carnivore traces on these remains and comparatively less human-modified material. A complete skull of a fossil canid was found in Level 4; not in Chamber B, but in a side gallery of the cave, together with remains from mammoth, lynx, red deer and large canids. This skull has been described as from a Palaeolithic dog (Figure 5), and with a calibrated age of about 35,500 years BP it is the oldest indication of human-wolf interactions. Although this specimen is not an ancestor of the present-day dogs, it is likely the outcome of an early domestication process. The mammal assemblage from Chamber C contains remains of, amongst others, cave bear, cave hyaena, horse and reindeer.

Figure 5: The canid skull excavated by Edouard Dupont in the 1860s in the Third cave of Goyet, described as from a Palaeolithic dog

The large faunal sample from Spy, a Belgian cave site famous for its Neanderthal remains, includes a wide spectrum of Pleistocene species. AMS dates on the fauna range from c. 44,400 BP to c. 25,700 BP. Horse, cave hyaena, mammoth, woolly rhinoceros and reindeer are the primary taxa. The Spy cave was used by both prehistoric humans and Pleistocene carnivores. Gnawed mammoth and rhinoceros postcranial bones and cervid antlers testify of the scavenging activities by cave hyaenas. Bears used the cave as a hibernation den as evidenced by remains of cubs, and of female and male adult bears. Indications of human manipulation (cut marks, ochre traces, worked bone/tooth) occur especially on remains from foxes, mammoth and deer. The age profile of the mammoth is dominated by calves. This selective mortality suggests that they were hunted by prehistoric people. The Spy bone assemblage therefore accumulated through a series of agents, such as cave hyaena, Neanderthals and Modern Humans, over a long period of the Pleniglacial. The mammoth assemblage, though, was, on the basis of AMS dates, the stratigraphic position of a number of mammoth molars, the isotopic signal in the Neanderthal bones and the absence of red stains on the mammoth molars, accumulated by Neanderthals rather than Anatomically Modern Humans.

Walou Cave (grotte Walou, Trooz, province of Liège, Belgium) is a major Palaeolithic site with deposits showing an important stratigraphic sequence, mostly dating from the Late Pleistocene. The site is located on the Magne River, a small tributary of the Vesdre River. The first campaign was

conducted from 1985 to 1990 by the Société Wallonne de Palethnologie (SoWaP), under the direction of Michel Dewez, and the second campaign from 1996 to 2004 under the direction of Christelle Draily. This campaign allowed to collect a tremendous amount of faunal remains, especially large carnivores like cave hyaena and cave bear. Unit C-I corresponds to the beginning of the Upper Palaeolithic (27-42 ka BP). Alongside a tooth of a Neanderthal found at the bottom of the unit, many faunal remains were excavated (55,5% cave bear and 6,8% cave hyaena). Unit C-II was dated by ESR at around 45-50 ka BP. In this unit, 61% of the remains belong to cave bear and 11% to cave hyaena. In both units, the faunal material is highly altered by hyaena activities. Units C-I and C-II yielded an interesting amount of juvenile remains of rhino and mammoth, heavily gnawed by cave hyaenas, suggesting that the site served as a hyaena den for a long period of time. Although the material from this site does not belong to RBINS collections, it is a crucial comparison point for our study for many reasons. Firstly, it is one of the very few Pleistocene sites in Belgium that was excavated with modern methods, thus the material was gathered with reliable contextual data. Secondly, it has a long stratigraphy that covers most of the Late Pleistocene, allowing a diachronic study spanning from the end of the Middle Palaeolithic to the beginning of the Upper Palaeolithic, a key period in Late Pleistocene studies; and finally, the main levels were highly occupied by predators, both large carnivores (hyaenas and bears) and humans (Neanderthals and Modern Humans). For these reasons, Walou cave is without a doubt the best comparison point for our ICHIE corpus.

Předmostí is located in the Moravian Corridor, Czech Republic. It is a complex Gravettian open-air site that was occupied in the period from 30,000 till 25,000 years BP and is characterized by a list of features such as the presence of human burials and female humanoid engravings, indirect evidence of mammoth hunting, original bladelet productions with characteristic tools, portable art and ornaments, and utilitarian and ritual modifications of canid remains. A large part of the fossil mammal assemblage is stored at the Moravian Museum at Brno. Since the 19th century, the Předmostí canid assemblage has been considered as evidence for the beginnings of the wolf domestication process with supportive studies using morphometrics, dietary isotopes and behaviour signals. The mammal assemblage is dominated by the mammoth with remains from more than 1000 individuals. In the mammoth age profile, young females aged from 20 to 30 years are preponderant. This suggests a selective mortality, which is probably due to a selective hunting of inexperienced female mammoths with their calves. Mammoth meat was an important staple food for the Předmostí people, based on the overwhelming presence of the mammoth remains in the assemblage and the stable isotope analysis of a human jaw. Skeletal elements from other large herbivores such as horse, bison and reindeer, are present in low frequencies. Large canids are the second most abundant group with the remains of more than 100 individuals. Based on multivariate analysis of complete skulls and mandibles, two canid morphotypes are present Předmostí, namely the Palaeolithic dog morphotype and the Pleistocene wolf morphotype. Three complete skulls and several mandibles from Předmostí were described as from Palaeolithic dogs, characterized by short skull lengths, short snouts, wide palates and braincases and sturdy mandibles relative to wild wolves. Also remains of Pleistocene wolves are well represented. The presence of the Palaeolithic dog morphotype (Figure 6), and the anthropogenic modifications of canid skulls and dentition point to a specific relationship between humans and large canids at this Gravettian site.

Figure 6: Palaeolithic dog from the Předmostí site, Czech Republic (collections of the Moravian Museum Anthropos Institute, Brno) with a piece of bone inserted between its teeth; photo credit: Mietje Germonpré

Work Package 1: Recommendations

Our studies combining archaeology, palaeontology, ecology, other related biological sciences and ethnography helped bridging the gap between several disciplines that are usually compartmentalized. Our analyses also showed that using old collections can be a great medium to explore scientific key questions from a modern perspective. Bridging this gap between different theoretical concepts allowed us to recompose our vision of past ecologies in all their complexity, in Belgium and other parts of north-western Europe. This work has already inspired other types of research by our peers and is participating in questioning Palaeolithic studies as a rigid and compartmented discipline. The data obtained through the ICHIE-project permits to continue the research on the interconnectivity of large carnivores and prehistoric humans, with several manuscripts published, forthcoming and in preparation (see below).

4.2.WORK PACKAGE 2: ZOOARCHAEOLOGICAL STUDIES

4.2.1.Task 2.1. Identification of the animal remains (RBINS)

Specimens from the palaeontological collections from Caverne Marie-Jeanne, Goyet and Trou Magrite have been identified. These newly obtained results are combined with the results of some assemblages that have been published in the past.

Work Package 2.1: Activities realized and results achieved

Identification lists of the specimens, including descriptions of anthropogenic and carnivorous modifications of the bones, from the different sites were compiled based on new analyses, unpublished reports and published papers.

4.2.2.Task 2.2. Interpretation of the zooarchaeological data

The data compiled by task 2.1. were compared among the different sites and evaluated against the site context (task 1.2.).

Work Package 2.2.: Activities realized and results achieved

Cementum analyses and seasonal competition between hominins and cave hyaenas (published)

In order to explore the dynamics of interspecific competition, niche partitioning and settlement patterns between large predators in the Meuse Valley, seasonality of predation was explored through classic methods and cementum analysis (in collaboration with the French project ANR "CemeNTAA" led by William Rendu and Lionel Gourichon). We undertook a multi-taxon, multi-site cementochronological study in the region, and tested season-at-death of different prey accumulated by either hyaenas or hominins during the second half of MIS 3 in the Belgian Ardennes. Following sites were included in this research: Caverne Marie-Jeanne and Trou Magrite (RBINS collections) alongside with Tiène des Maulins (ULB collections). In conjunction with a classic seasonal study conducted on ungulate species, the specificity of this study lies in the fact that carnivore (hyaena) dental cementum (NR=4) and dental cementum of their prey (large bovids) (NR=4) were tested (Figure 7). In total, we analysed 19 teeth from mostly anthropogenic (Trou Magrite) and mostly hyaena-accumulated (Caverne Marie-Jeanne, Trou Magrite, Tiène des Maulins) assemblages. The novelty of this study relies in the fact that cementum analysis were performed on cave hyaena teeth for the first time. Despite a quite low proportion of interpretable data (ROI found in two hyaena individuals out of four), this attempt shows that cave hyaena teeth can yield seasonal information and can successfully be analysed in order to explore top-predators' differential spatial strategies. In combination with cementum analyses on their prey, this study suggests that cave hyaenas in this region and time span do not show a specific pattern in their seasonal distribution and that they likely were present all year-round. The results are published as a peer-reviewed chapter by ELJ and MG in the book "Cementum in Anthropology" edited by S. Naji, W. Rendu and L. Gourichon for Cambridge University Press that was released in 2022. In the same book another chapter is also published related to the advances of the methodology itself, called "Cementochronology protocol for selecting a Region of Interest in zooarchaeology", of which ELJ is a co-author.

Figure 7: Reindeer tooth from Trou Magrite (Belgium) VERT-00493 were used for cementum analyses (from Jimenez and Germonpré, 2022) and shows that the animal was preyed on in the first half of the "warm" season. This specimen also shows butchery marks, suggesting that humans killed it and processed the carcass.

Cave hyaenas from Caverne Marie-Jeanne, Hastière-Lavaux, Belgium (published)

The faunal analysis of cave hyaena den Caverne Marie-Jeanne Level 4 (housed at the RBINS) led to the identification of 20,812 remains. A thorough faunal and taphonomical analysis was conducted on

each fragment in order to understand the site function(s) as well as hyaenas feeding and territorial behaviours. Alongside with prey specimens that were brought and eaten by the hyaenas, more than 300 juvenile hyaena cubs were identified in this level. This exceptional number of cave hyaena cubs in this level indicates that this site served as a natal den (Figures 8-10). The contextual data suggest that these remains accumulated in a relative short period of time, showing that the den was reused many times for the same purpose between 60 and 40 ka BP. This study sheds new light on cave hyaenas' reproductive behaviour, territory management and local adaptation and helps us further our knowledge of cave hyaena ethology and understand how apex predators of the Pleistocene adapted to local northern environments. A podium presentation of these results was given at the 7th International Geologica Belgica Meeting that took place in September 2021 at the Africa Museum in Tervuren. The paper detailing these results was published in 2022.

Figure 8: Drawer from the RBINS collections showing a part of the juvenile cave hyaena material from Caverne Marie-Jeanne level 4 (photo credit: Jimenez)

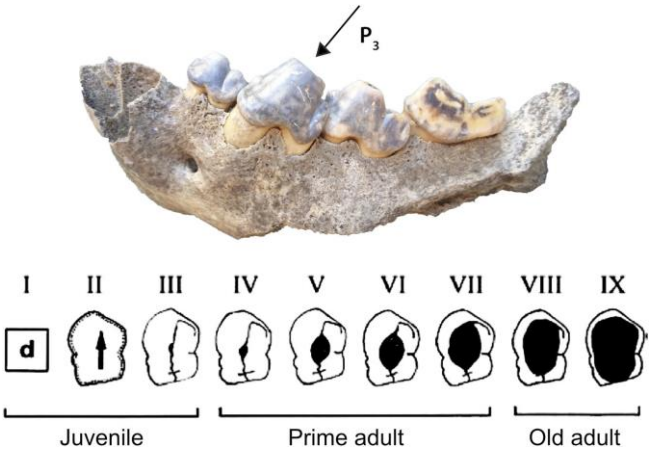


Figure 9: Hyaena (*Crocuta crocuta*) tooth eruption/wear sequence based on the lower deciduous premolar/third premolar (from Stiner, 2004) with adult cave hyaena jaw from Caverne Marie Jeanne (from Jimenez et al., 2022)

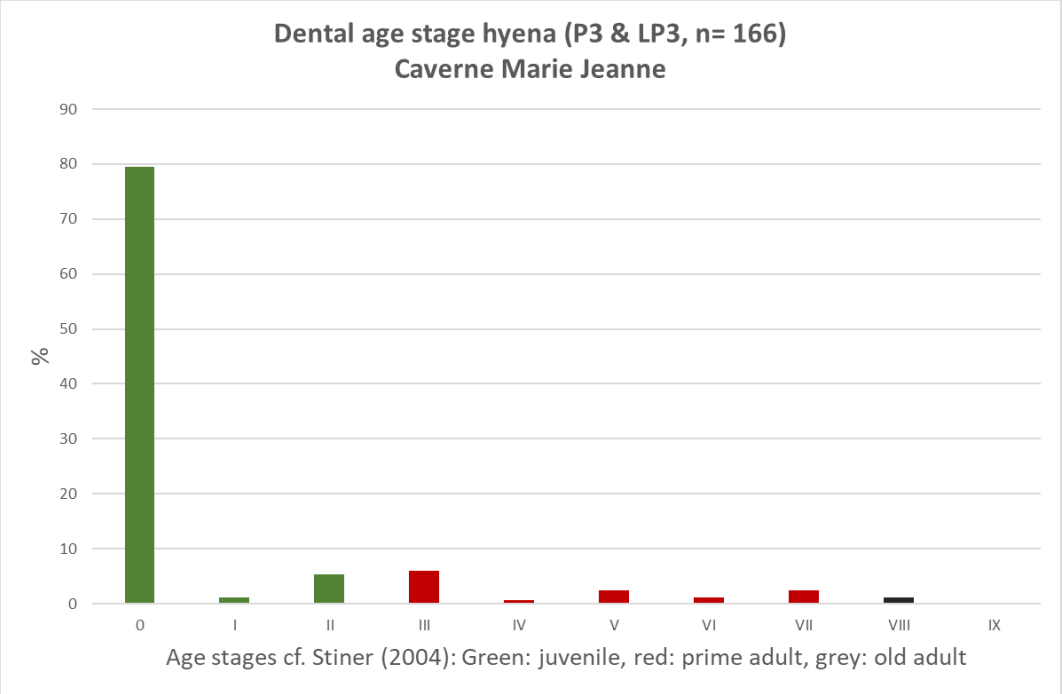


Figure 10: Age attribution of the hyaena assemblage (based on the deciduous p3 and permanent p3) (after Jimenez et al., 2022)

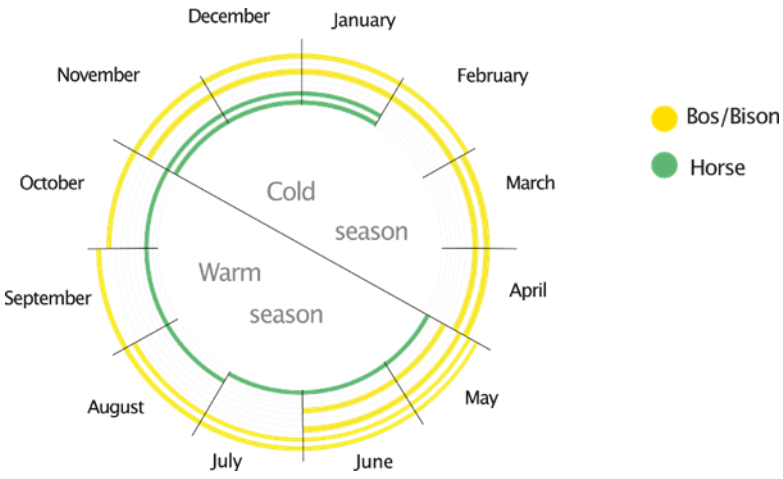


Figure 11: Season of death per species obtained on the material of Caverne Marie-Jeanne level 4 through cementum analyses and zooarchaeological study (from Jimenez et al., 2022)

A Late Glacial Palaeolithic dog from Goyet (third cave, bone level A1), Belgium (published)

The large canid remains of the first bone layer from the third cave of Goyet (Belgium) were analysed in detail. Several canid bones from the first layer were modified by Upper Palaeolithic humans, indicating that the carcasses of some animals were skinned, dismembered and filleted, presumably in order to obtain the skin and meat. Other elements were perforated or stained with red powder. A direct AMS 14C date (ca. 13,500 cal BP) of a canid ulna demonstrates that this animal lived during the Bølling/Allerød interstadial. The size of the ulna permits to describe this element as from a Palaeolithic dog. Human and carnivore modifications of the bone indicate that the animal was

dismembered by a contemporaneous human individual, likely to obtain its meat, and then gnawed by a canid-sized carnivore (Figure 12). With an estimated body mass of ~ 20 kg it is comparable in size to other Late Palaeolithic dogs from Western Europe. The manuscript with the detailed results of this analysis was published by MG, ELG and MB as a peer-reviewed book chapter in a book called "The Beef behind all possible pasts" in December 2021.

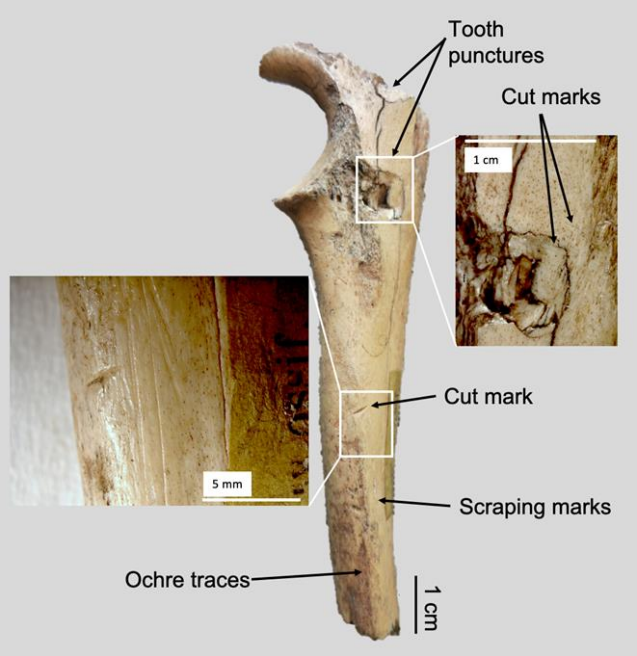


Figure 12: Ulna Vert00-247/2812-6 described as from a Palaeolithic dog with cut marks underlying one of the tooth impressions, with a transversal cut-mark, with scraping on the distal half of the diaphysis and with red stains on the distal half and the proximal end (from Germonpré et al., 2021)

Grey wolf genomic history reveals a dual ancestry of dogs (published)

The osteometry of a mandible from a large canid from the first bone horizon of the third cave of Goyet (Belgium) shows that this jaw can be described as from a Pleistocene wolf. Genetic analyses and AMS dating revealed that this element is from a female wolf that lived about 34,000 years ago. The results of these analyses are published in Nature in a paper by Bergström et al. (2022) of which MG is a co-author. In this paper several ancient wolf genomes were analysed, including the wolf from Goyet (Belgium), and compared to the genomes of prehistoric and modern dogs. Interestingly, modern dogs are more closely related to ancient wolves from eastern Eurasia than to those from western Eurasia, suggesting a domestication process in the east. However, dogs in the Near East and Africa derive part of their ancestry from a distinct population related to modern southwest Eurasian wolves, reflecting either an independent domestication process or admixture from local wolves (Figure 13). None of the analysed ancient wolf genomes is a direct match for either of these dog ancestries, meaning that the exact progenitor populations remain to be located. The media picked up this research and MG was interviewed in the Knack (13 July 2022) on this.

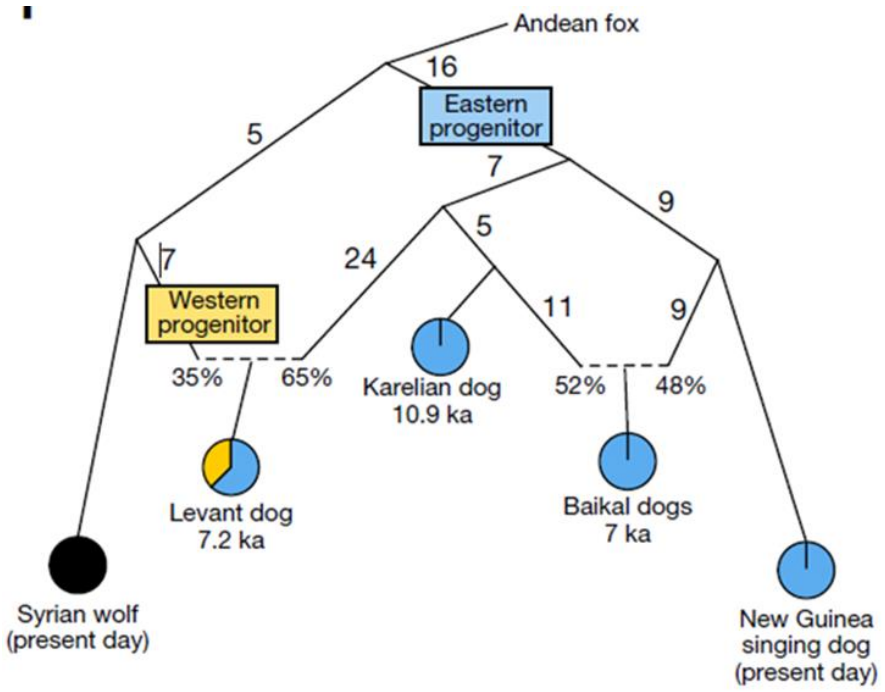


Figure 13: Admixture graph model of major dog lineage relationships (from Bergström et al., 2022)

A perspective on the first steps of the Palaeolithic domestication of the wolf utilising Aboriginal people's relations with dingoes (published)

In this paper, the human-initiated hypothesis of wolf domestication was expanded based on a consideration of human (indigenous people)-dingo relations in Australia. Two key points were addressed: (1) the conceptualization of how early hunter-gatherers in Eurasia might have interacted with socialized wolves that had reached breeding age; and (2) how wild-caught, human-raised, socialized wolves could have become reproductively isolated from wild populations — giving rise to early dogs (Figure 14). This perspective highlights the importance of the large seasonal hunting/aggregation camps, like those associated with mammoth sites in Gravettian/Epigravettian central Europe in the context of the first steps of the domestication process of the wolf. At these sites, large numbers of foragers gathered over long periods during spring, when wolves were giving birth. This permitted to the hunter-gatherers to routinely raid wild wolf dens for pre-weaned pups, which were then socialized to humans and kept in camp as tamed companions. These traditions might have been the catalyst for the early changes leading to the first domesticated dogs. This paper was published in 2023 in the research topic "Domestication and Evolution in Dogs: Current Issues and Questions That Remain" in Frontiers of Psychology.

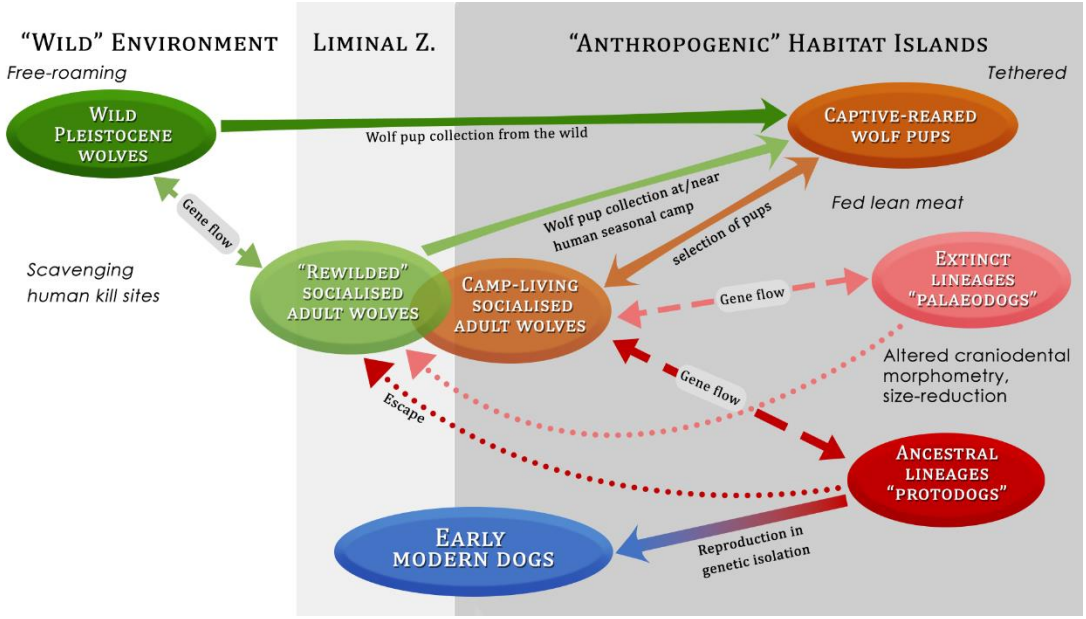


Figure 14: model presenting possible pathways in the domestication process of dogs from wolves showing several factors such as environment, selection, protection, food and provisioning (from Brumm et al., 2023)

The Advantages of Owning a Palaeolithic Dog (forthcoming)

This paper details the close relationships that could have existed between prehistoric humans and the first domestic canids, based on archaeological and zooarchaeological data gathered from Upper Palaeolithic sites combined with ethnographic information on forager societies from the circumpolar north. Likely, the presence of Palaeolithic dogs at camp sites and gathering localities conveyed some selective advantage to their owners. The Palaeolithic dogs could have been very useful as guards, by warning of the approach of predators or unfamiliar humans through vocalisations; this would have provided protection to the inhabitants of the camps and to the gatherers away from the settlements when accompanied by Palaeolithic dogs. Furthermore, Palaeolithic dogs could potentially have been suitable to increase the level of mobility of their people, helping with the transportation of firewood, lithics, gear, body parts of prey, etc. In addition, the anthropogenic manipulations of several Palaeolithic dog skulls, such as the perforation of the brain case or the insertion of objects in the mouth cavity (Figure 6), testify of the special standing these canids held within some Upper Palaeolithic societies. This manuscript, written by MG and three members of the follow-up committee (MLG, MS, HB), was accepted to be published as a book chapter in the book "Dogs, Past and Present, An Interdisciplinary Perspective".

The archaeological potential of Wogan Cavern (Pembroke, UK): results of the first fieldwork season (published)

The Wogan Cavern, lying beneath Pembroke Castle (Pembroke, UK), has been subject to several historic phases of antiquarian investigation. The results of the 2021 fieldwork at the site indicate that Wogan Cavern has significant archaeological potential. An Early Holocene archaeological layer contained diagnostic Mesolithic artefacts in the eastern part of the cave. Underlying this stratigraphically, securely within Pleistocene deposits, is a layer containing palaeontological and possible archaeological material. Overall, the nature of the archaeological remains, as well as the existence of Pleistocene fauna, including remains from mammoth, horse and reindeer, and possible

presence of an intact Palaeolithic layer, demonstrate its importance as an early prehistoric site. Our new excavations in 2022 have shown that Wogan Cavern is an important archaeological site, especially for its record of early prehistoric occupation. These first results were published in 2022. Another manuscript has been submitted.

The cave lions of the Gravettian Předmostí site (Czech Republic): taphonomy and osteometry (in preparation)

At the Gravettian open-air site of Předmostí, beside the presence of a large number of wolf remains, another large carnivore, the cave lion, occurs in high frequency in the faunal assemblage. We want to test whether the cave lions and their remains were considered and treated in the same way as the large canids by the Gravettian inhabitants of the site. Most skeletal parts of the cave lions have been found: skull, mandibles, long bones, foot bones including the third phalanges; axial elements are somewhat less well represented. Complete lion bodies were likely brought to the site by the Gravettian inhabitants. Several age groups are present from cubs to older adults. This is comparable to the presence of complete wolf skeletons at the site, but the rarity of anthropogenic cut marks on the lion material precludes that lion meat, in contrast to wolf meat, was consumed by the Palaeolithic people. Quite a few lion bones display carnivore gnawing marks, likely from canids (Figure 15). Human modified bones include two large “daggers/awls” made from fibulae (Figure 16). However, in contrast with the wolf dentition and postcranial bones, no perforated lion canines or decorated bones are present. This hints at another position of the cave lion in the symbolic world of the people from Předmostí compared to the one the large canids (Pleistocene wolves and Palaeolithic dogs) occupied. This manuscript is in preparation by MG and two members of the follow-up committee (MLG, HB). The taphonomy, osteometrics, anthropogenic and carnivorous modification and isotope analyses of the cave lion remains from Předmostí will be compared with those of the cave lion assemblage from the third cave of Goyet.

Figure 15: cave lion metatarsals (hind paw) with gnawing marks on their distal ends

Figure 16: cave lion fibula modified to “dagger/awl”

Work Package 2: Recommendations

The RBINS facilities allowed very efficient work on the faunal collections. However, the restrictions during the pandemic, the limited sampling possibilities and the long absence of Mietje Germonpré, due to sick leave, have somewhat limited the amount of work that could be done. Nevertheless, a great amount a work has been done in order to overcome the delays and catch up with lost time.

Caverne Marie-Jeanne Layer 4 (Hastière, Belgium) is one of the best-preserved palaeontological sites in the region. The cementum analysis study on this faunal assemblage led us to understand the seasonality of the most common carnivores in southern Belgium (hyaenas), and to compare it with the one of hominins. We found that hyaenas seem to have lived in the region all year-round and therefore were likely in high competition with hominins who were also present at different seasons, as has been shown by the age distribution of the mammoth, one of their prey animals, at the sites of Goyet and Spy. This suggests that a spatial and temporal niche partitioning between the two groups of predators probably occurred.

Furthermore, our study of the faunal assemblage from Layer 4 of Caverne Marie-Jeanne showed, for the first time, that the remains of an exceptional number of hyaena neonates (minimum number of individuals >300) accumulated here. This permitted to conclude that a Late Pleistocene hyaena birth-site was reused here over a long period of time around 47.6–43k a BP. By bridging the gap between archaeology and palaeontology, we explored the potential of carnivore socio-spatial organisation and denning habits as an ecological proxy and discussed how these new unique data could help us further understand hominins’ spatial strategy in southern Belgium and how human and mammal predators shared their environment. Future work could focus on the study of level 3 which looks very complementary to level 4.

Although the timing of the onset of the domestication process of the wolf is highly debated, most researchers agree that by the end of the Pleistocene domestic dogs were part of the daily life of prehistoric hunter-gatherers. The studies undertaken during the ICHIE-project showed that the handling of the canid bodies and bones at Goyet hints to the existence of a complex relationship, including cynophagy, between humans and large and medium-sized canids during the Late Palaeolithic. Furthermore, new DNA results of analyses of skeletal material from several sites in Eurasia, including from Goyet (Belgium), suggest that the origin of the first early dogs can be situated in Central or Eastern Asia and Southwest Asia. There are two competing hypotheses on the origin of wolf domestication: (1) wolves self-domesticated by adapting genetically to anthropogenic environments as commensal scavengers; and (2) wolf domestication emerged from the process of hunter-gatherers taking wolf pups from wild dens and hand-raising them as companions (“pets”).

The assumption of a self-domestication model of the wolf that proposes that less wary wolves were attracted to prehistoric human camp sites to scavenge stored food or refuse dumps, eventually becoming habituated to humans and colonizing the human dominated environment, is gaining favour. According to this premise, the descendants of the habituated wolves would become domesticated through more intensive human selection. In contrast, the human-initiated model suggests that wolf pups were taken from their dens by Upper Palaeolithic hunters and brought to the camps to be raised for different motivations (pet, fur, symbolic realm); the most sociable, less fearful and aggressive pups could have survived until adulthood and reproduced; a selection on sociable behaviour in subsequent generations could have led in the long run to Palaeolithic dogs. A possible pathway can be detailed from the way Aboriginal people in Australia interact with adult and pup dingoes. Such a domestication process could have started in several hunter-gatherer societies over northern Eurasia during the Upper Palaeolithic. Indeed, our work on the evidence of early Palaeolithic dogs in Western Europe demonstrates that the circumstances for dog domestication were not unique to one place or time, but on the contrary were likely supported by cultural traditions with long durations over large realms. The domestication of the wolf should thus be seen as a complex, slow and long-term process of different types of interactions between humans and canids that began gradually and had many dead ends before the first modern dogs emerged. The recent analyses of the genomes of Pleistocene wolves revealed that indeed two wolf populations, one in Central/Eastern Asia and one in Southwestern Asia, contributed to present-day dogs. Palaeolithic dogs, whether or not the ancestors of present-day dogs, likely began to transform the way of life of the Upper Palaeolithic people with whom they resided and contributed with many advantages to improve the daily lives of their owners.

The study on the taphonomy and zooarchaeology of another carnivore taxon, the cave lion, from the Gravettian Předmostí site in the Czech Republic, is underway. In parallel with the large canids from this site, also complete bodies of cave lions were here deposited and several age groups, from juvenile to old age, are present. Several cave lion bones were gnawed by carnivores (canids?), a few display human modification. The characteristics of the carnivores assemblages from Předmostí suggest that a specific relationship between humans and predators, including cave lions, existed during the Gravettian. Our results will bring more details to light.

So far, we published our results on the cementum analysis of several taxa from Caverne Marie-Jeanne, on the zooarchaeological and palaeontological analysis of Caverne Marie-Jeanne level 4, on the zooarchaeology and taphonomy of the large canids from Level 1 of the Goyet cave, on the genetics of fossil and prehistoric large canids, including material from Goyet, on the hypotheses of the domestication process of the wolf and the first results of excavations at the prehistoric Wogan Cavern in the UK. Task 2 has been successfully complete.

Future Prospects and Planning

Task 2 will be extended by the publication of the results of the taphonomic and osteometric analyses of the cave lion assemblage from Předmostí and the new results from excavations at the Wogan cavern. Furthermore, Mathieu Boudin (KIK/IRPA) will perform further AMS dating on RBINS material and this will allow to contextualise a few key specimens in their chronology. The extinction of the cave hyaena is of special interest. One of the latest occurrence of this carnivore in Eurasia, at c. 31,300 cal BP, was dated at Goyet. The results of new AMS dates from hyaenas found at Goyet,

Trou Magrite, and Caverne Marie-Jeanne and Tiène des Maulins will be integrated in future publications and hopefully detail the extinction path of this important predator.

4.3.WORK PACKAGE 3: ISOTOPE STUDIES

4.3.1.Task 3.1. Selection of animal samples (RBINS)

The isotope analysis part of the project was unfortunately greatly hindered by the pandemic restrictions. Once the restrictions lifted, we took into account the research questions, the available material, the requests of material for destructive analysis, granted by Annelise Folie, and the budgetary constraints, and a total of 28 bones from the RBINS collections (CMJ) were sampled: three bones each from hyaena, bison, horse and deer, five bones each from rhino and fox and one bone from a bear.

4.3.2.Task 3.2. Sample preparation and measuring (RBINS, KIK-IRPA)

The bone samples for AMS dating were prepared at the KIK-IRPA. Bone samples for isotopic studies were prepared at the laboratory of the Aberdeen university (member of the committee Dr Kate Britton's lab) by ELJ. The bone samples were prepared following the bulk bone collagen extraction method of Longin (Longin, 1971), with modifications based on the recommendations of Collins and Galley (Collins and Galley, 1998), with the addition of an ultrafiltration step (Brown, et al., 1988), as described in Britton et al. (2012). Samples were demineralized in 0.5M hydrochloric acid at 6-8°C for 3-10 days with acid changed at regular intervals. They were then rinsed to neutrality with de-ionized water and gelatinized in a weak acidic (pH 3) HCl solution at 70oC for 48hrs. The liquid fraction containing the gelatinized protein was isolated through filtration using 5-8µm Ezee® mesh filters, and then purified using ultrafilters (>30,000kD). The remaining solution was then frozen and lyophilized, and the collagen analysed by mass spectrometry in order to obtain Carbon, Nitrogen and Sulphur ratios.

4.3.3.Task 3.3. AMS dating (KIK-IRPA)

All samples were transformed into graphite using the automatic graphitization device AGE (Němec et al. 2010) and 14C concentrations were measured with accelerated mass spectrometry (AMS - Micadas) at the Royal Institute for Cultural Heritage (KIK-IRPA, Brussels).

4.3.4.Task 3.4. Data analyses and interpretation (RBINS, KIK-IRPA)

The results obtained by tasks 3.2. and 3.3. were compared among the different sites and evaluated against the site context (task 1.2.) and interpreted and discussed by the different collaborators.

Work Package 3: Activities realized and results achieved

The diet of the carnivore guild in Belgium during the Late Pleistocene: a comparison between natural and Palaeolithic cave sites (in preparation)

Huge advances in biochemical methods over the past three decades has made it possible to decipher in detail the dynamic processes of sharing ecological niches, the organization of food webs and the mobility of Pleistocene megafaunal species (e.g. mammoths, woolly rhinos, reindeer, lions, bears and cave hyaenas). The analysis of carbon ($\delta^{13}C$), nitrogen ($\delta^{15}N$) and sulfur ($\delta^{34}S$) isotopes from the

bone collagen of key species now opens up research horizons hitherto out of reach, in particular when these methods are applied to museum collections excavated without - or with little - sedimentary and/or geoarchaeological context. The results of isotopic analyzes carried out on material from two Belgian natural sites - with hyaena-accumulated assemblages - Caverne Marie-Jeanne (old excavations) and Walou Cave (modern excavations) are currently being studied. At Caverne Marie-Jeanne (Figure 17), the cave hyaenas present the most positive values of the nitrogen ($\delta^{15}N$) isotopes in the faunal assemblage, followed by the value of the wolf that is slightly more positive than the mean of the mammoths that have more elevated $\delta^{15}N$ values than the rest of the herbivores and also than the foxes. The bear, mammoths and rhinos have the most negative $\delta^{13}C$ values, while the reindeer have the most positive $\delta^{13}C$ values in the data set of Caverne Marie-Jeanne. These results (Figure 17) will be compared to the results of the Walou cave, Spy and Goyet faunal assemblages, all dating from MIS3. The isotopic results and the Bayesian models carried out on these values will make it possible to better understand how large carnivores shared their ecological niches in the Meuse valley and what were the migratory strategies of their main prey.

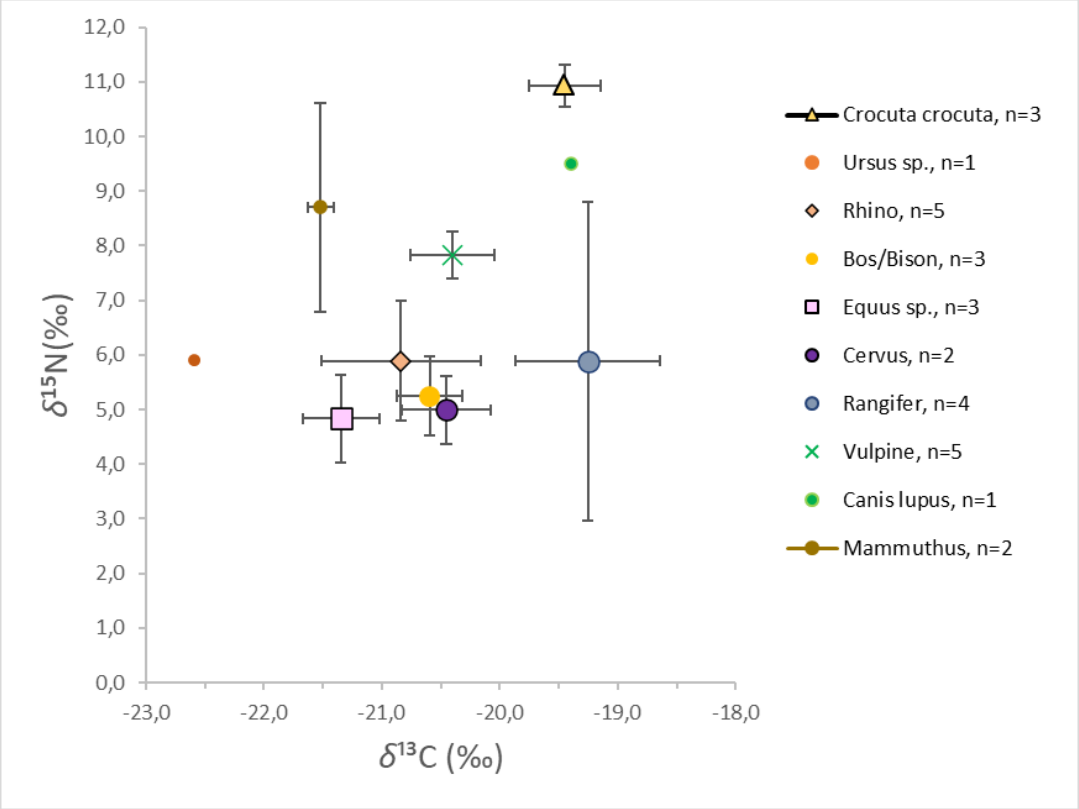


Figure 17: Stable isotopes (Carbon and Nitrogen) from the faunal assemblage from Caverne Marie-Jeanne

Work Package 3: Recommendations

Once institutions reopened fully after the lockdowns related to the Covid pandemic, we finally managed to access the collections at RBINS and sample our collections with the help of Annelise Folie. Despite a long waiting list, collagen extraction took place in Aberdeen in 2022 and isotopic ratios have been obtained on 28 samples. In combination with other previous (published + unpublished) studies, this allowed an efficient contextualization and a better understanding of the palaeoecology of MIS3 Belgium, especially from a carnivore perspective, an underexplored aspect of research. For the work in progress on the stable isotopes of faunal remains from Caverne Marie-

Jeanne, Walou Cave, Goyet and Spy, and the cave lions assemblage from Předmostí, additional specimens, with a special interest on the cave hyaenas and cave lions, after being granted for destructive sampling by Annelise Folie, will be dated.

4.4.WORK PACKAGE 4: INTERPRETATION AND VALORISATION OF THE RESULTS

4.4.1.Task 4.1. General meetings and reporting (RBINS, KIK-IRPA)

The project members met in order to exchange and integrate the results and ideas, to evaluate what further steps must be taken, and to evaluate, interpret and report the results. The meetings were organized by the project coordinator. Due to her long absence caused by health issues, only two meetings could be organised in the course of the project.

4.4.2.Task 4.2. Writing and presentations (RBINS, KIK-IRPA)

Manuscripts were prepared and are in preparation, based on the interpretations and reports obtained in Tasks 1.2., 2.2.,3.4. and 4.1., in collaboration with all members.

Furthermore, presentations were given by the members at international scientific congresses, but also at meetings of citizen science groups. In addition, interviews with the press helped to communicate the results of the ICHIE-project. (see point 5 & 6 here below for more details)

4.4.3.Task 4.3. Database (RBINS)

The data generated by the project were compiled in Excel data bases. They will be added, under the direction of Annelise Folie, to the digital data bases of the palaeontological collections of the RBINS, once our results have been published.

Work Package 4: Recommendations

Several manuscripts have been submitted and published. Some are still in the process of being written. The first results of the ICHIE BRAIN-project contributed to expand our knowledge of human-carnivore interactions, carnivore ethology and seasonality in north-western Europe during the Upper Palaeolithic. We are now working on recontextualising and interpreting our results from isotope analyses, and can add the data from our new excavations in the UK (i.e. Wogan cavern, Wales) in order to understand how apex predators of the Pleistocene adapted to local northern environments and to other members of their guild and how the presence of Upper Palaeolithic people, and their companions the palaeodogs, could have influenced the (local) disappearance of certain species.

Our attention is now focused on interpreting the recently obtained lab data and writing and publishing our final results.

5. DISSEMINATION AND VALORISATION

5.1.PARTICIPATION TO INTERNATIONAL CONFERENCES AND WORKSHOPS

-“1st virtual Conference for Women in Archaeology and Palaeontology”: Jimenez, E.L., Germonpré, M. “Carnivore dens as ecological proxies during the Late Pleistocene? The case of Caverne Marie-Jeanne (Belgium), a unique MIS3 hyaena natal den.” (9/03/21)

-“Science communication for Archaeologists” workshop by Oklahoma University (20/03/21) attended by ELJ

-“The 62nd Annual Meeting Hugo Obermaier Society for Quaternary Research and Archaeology of the Stone Age” 06/-08/04/2021, online meeting housed at the Moravian Museum, Brno, Online Presentatie: Nývltová Fišáková, M.; Germonpré, M.; Lázničková-Galetová, M.: “Seasonality in the fossil large canids from Předmostí”, oral presentation by MG

-“The 7th International Geologica Belgica Meeting 15-17 September 2021”: Jimenez, E.L., Germonpré, M. “Caverne Marie-Jeanne (Belgium): How an old collection from the Royal Belgian Institute of Natural Sciences sheds new light on cave hyaenas’ behaviour and adaptation”. (September 2021)

-UKAS (United Kingdom Archaeological Sciences Conference) 20-22 April 2022

.ELJ was part of the organizing committee

.ELJ chaired the session “Animals, Humans and the Environment”

.Poster presentation: Sarah Barakat, Elodie-Laure Jimenez, Mael Le Corre, Emmanuel Discamps, Kate Britton. “Sulphur isoscapes and faunal spatial palaeoecology: developing, refining, and applying isoscape-based sulphur analyses to Late Pleistocene fauna.”

-“The 28th European Association of Archaeologists Annual conference”, Budapest August 30-Septembre 3, 2022. ELJ was co-presenting “Combining Strontium And Sulphur Isotopic Analysis With Isoscape Modelling To Better Understand Faunal Mobility And Spatiality” by Sarah Barakat (Aberdeen university)

5.2.PARTICIPATION TO NATIONAL CONFERENCES

-“BELQUA conference 2022” in Brussels March 29, 2022, attended by ELJ

- North Sea Fossil Day at the VLIZ in Ostend, October 14, 2022. ELJ and MG presented “The Ice Age fauna from the North Sea: collections from the RBINS”.

5.3.SEMINARS AND LECTURES: DISSEMINATION TO UNIVERSITY STUDENTS AND SCHOLARS

5.3.1.Lecturing activities

.October 2020 - Lecture “Archaeology in the Cave” (University of Aberdeen) by ELJ

.October/November 2020 - Tutorials “Archaeology in Action” (University of Aberdeen) by ELJ

.January 2021 - Lecture - Archaeology of the North “Hunter-gatherer life ways in Palaeolithic Europe Part I” (University of Aberdeen) by ELJ

.February 2021 - Lecture - Archaeology of the North “Hunter-gatherer life ways in Palaeolithic Europe Part II” (University of Aberdeen) by ELJ

.February 2021 - Lecture - Past Lives “Scientific argumentation” (University of Aberdeen) by ELJ

.December 2021 - Seminar « Relations homme-loup au Paléolithique supérieur : vers une domestication? » for Master students (Muséum National d'Histoire Naturelle, Spécialité Quaternaire et Préhistoire, Institut de Paléontologie Humaine (IPH)) by MG

.January 2022 - Lecture - Archaeology of the North "Hunter-gatherer life ways in Palaeolithic Europe Part I & II" (University of Aberdeen) by ELJ

.February 2022 - Lecture - "The Other Human" (University of Aberdeen) by ELJ

.February 2022 - Tutorials "Archaeology in Action" (University of Aberdeen) by ELJ

.February 2022 - MOOC (Massive Online Open Courses) "Large Carnivores" by ELJ
https://www.youtube.com/watch?v=fWjFxTDXGjY

.December 2022 - Seminar « Relations homme-loup au Paléolithique supérieur : vers une domestication? » for Master students (Muséum National d'Histoire Naturelle, Spécialité Quaternaire et Préhistoire, Institut de Paléontologie Humaine (IPH)) by MG

5.3.2.Participation to Q&A

Theme: Archaeology of the North, Neanderthals and their environment(s) – University of Aberdeen (17/02/2021) by ELJ

5.4.DISSEMINATION TOWARDS MUSEUMS

-Scientific advisor for the Permanent exhibition Musée de Treignes, Belgium: ELJ

-Scientific advisors for the exhibition Giants (RBINS) (October 2022 -): MG & ELJ

-"Object of the month" for Musée du Malgré-Tout, Treignes, Belgium, June 2022 organised by ELJ. This object was a woolly rhinoceros molar and ELJ created content for social media and answered questions for the public.

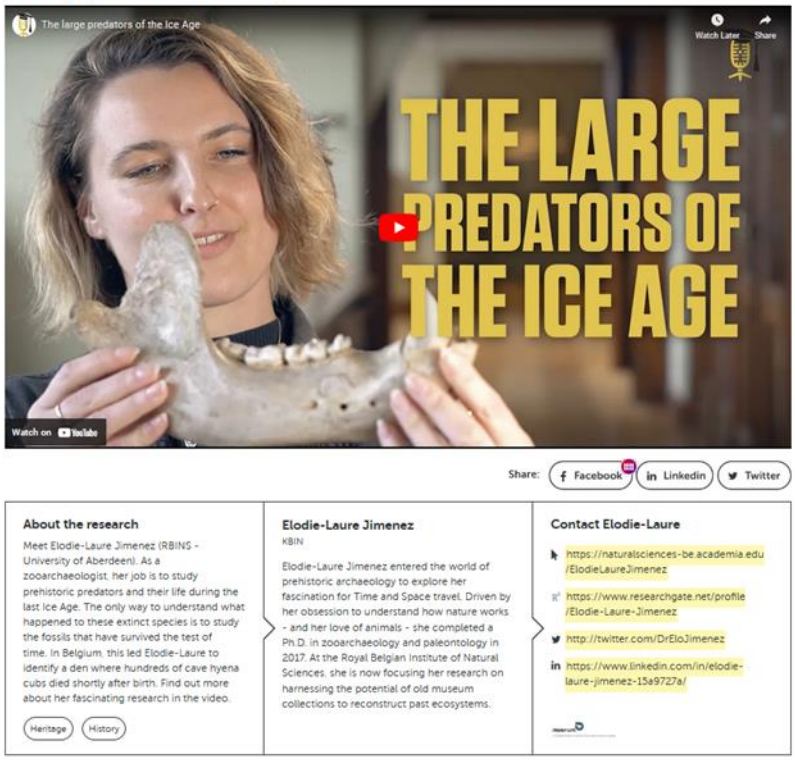
5.5. MEDIA APPEARANCES AND OUTREACH

Great emphasise on media and public outreach was given throughout the span of the ICHIE project. Not only this allowed us to communicate the last discoveries about our research, but it also promoted a better knowledge of the Ice Age to the public, which has always been a central hobbyhorse of ours.

5.5.1.Documentaries

- "The Large Predators of the Ice Age" (2021) filmed by Science Figured Out (Scriptie vzw) http://www.sciencefiguredout.be/large-predators-ice-age ;
https://www.youtube.com/watch?v=l602TXCTCf8

The large predators of the Ice Age



- The RBINS published on many social media an archeo-vlog documentary in 2 parts on the excavations at Wogan cavern in 2022:
https://www.instagram.com/reel/ClOrUggOcZk/?igshid=NTc4MTIwNjQ2YQ%3D%3D

5.5.2.Interviews and coverage in the press

-The paper “New insights into cave hyaena ethology and the implications for territorial competition with hominins in Late Pleistocene north-west Europe: the case of Caverne Marie-Jeanne (Belgium)” published in JQS was featured on a double page in “Science Connection: BELSPO magazine” n°67. In both Dutch and French.
http://www.belspo.be/belspo/organisation/publ/pub_ostc/sciencecon/67sci_nl.pdf

This paper had a great media coverage, in both French and Dutch speaking media. Some examples here:

- https://www.knack.be/nieuws/wetenschap/grot-in-hastiere-lavaux-was-kraamkamer-voor-ondertussen-uitgestorven-grottenhyena/

- https://www.vrt.be/vrtnws/nl/2022/02/03/grottenhyaena-s-stonden-45-000-jaar-geleden-onder-grote-ecologisc/

- https://www.dhnet.be/regions/namur/dinant-ciney/2022/02/03/300-squelettes-de-hyenes-des-cavernes-juveniles-decouverts-en-1943-a-dinant-temoignent-des-pressions-ecologiques-7QWUXHWW2VBN3NZIAFBNOUFHCE/

- https://www.lavenir.net/regions/namur/dinant/2022/02/03/des-squelettes-de-hyenes-decouverts-en-wallonie-temoignent-des-pressions-ecologiques-BTA4BEGQK5BCPE7Q5RT6YQJPGI/

- https://www.rtbf.be/article/des-squelettes-de-hyenes-decouverts-pres-de-dinant-temoignent-des-pressions-ecologiques-il-y-a-45000-ans-10927356

- The paper "Grey wolf genomic history reveals a dual ancestry of dogs" published in Nature prompted Dirk Draulans, journalist of the Knack, to interview MG (12/07/2022): 'Kleine honden denken soms dat ze nog in een wolvenlijf zitten', https://www.knack.be/nieuws/wetenschap/paleontoloog-mietje-germonpre-kleine-honden-denken-soms-dat-ze-nog-in-een-wolvenlijf-zitten/

- Jimenez, E.-L. (2023). Le chien descend-il vraiment du loup ? The Conversation, https://theconversation.com/le-chien-descend-il-vraiment-du-loup-195836

- "Pembroke: Archaeologists hunt for Ice Age life under castle" (2022): https://www.bbc.com/news/uk-wales-62065475

- "Pembroke Castle cave dig may uncover more evidence of Ice Age life" (2022), with an BBC live interview of ELJ: https://www.bbc.com/news/uk-wales-61822620

Pembroke: Archaeologists hunt for Ice Age life under castle
BBC News
A very nice BBC article and interview about our field work in Wales in July 2022

6. PUBLICATIONS

6.1. PEER REVIEWED PAPERS IN A1 JOURNALS

Bergström, A., Stanton, D.W.G., Taron, U.H. et al., 2022. Grey wolf genomic history reveals a dual ancestry of dogs. Nature 607, 313–320 https://doi.org/10.1038/s41586-022-04824-9 (M. Germonpré is co-author)

Brumm, A., **Germonpré, M.**, Koungoulos, L., 2023. The human-initiated model of wolf domestication – an expansion based on human-dingo relations in Aboriginal Australia. Front. Psychol. Sec. Comparative Psychology 14, https://doi:10.3389/fpsyg.2023.1082338

Jimenez, E.-L., **Germonpré, M., Boudin, M.**, 2021. New insights into cave hyaena ethology and the implications for territorial competition with hominins in Late Pleistocene north-west Europe: the case of Caverne Marie-Jeanne (Belgium). Journal of Quaternary Science 37 (4), 593-611. https://doi.org/10.1002/jqs.3404

6.2. PEER-REVIEWED BOOK CHAPTERS

Germonpré, M., **Jimenez, E.-L**, **Boudin, M.**, 2021. A Late Glacial Palaeolithic dog from Goyet (third cave, bone level A1), Belgium. In: S. Gaudzinski-Windheuser and O. Jöris (Eds), The Beef behind all Possible Pasts. The Tandem-Festschrift in Honour of Elaine Turner and Martin Street. Monographien des RGZM 157, Mainz, Leibniz-Research-Institute for Archaeology, pp. 505-520. https://doi.org/10.11588/propylaeum.950.c12576

Germonpré, M., **Lázničková-Galetová, M., Sablin, M.V., Hervé Bocherens**, H., **forthcoming**. The Advantages of Owning a Palaeolithic Dog. In: I. Fiore and F. Lugli (Eds), Dogs, Past and Present, An Interdisciplinary Perspective. Oxford, Archaeopress, pp. 63-71.

Jimenez, E.-L., Germonpré, M., 2022. Investigating seasonal competition between hominins and cave hyaenas in the Belgian Ardennes during the late Pleistocene: insights from cementum analyses. In: S. Naji, W. Rendu and L. Gourichon (Eds), Cementum in Anthropology. Cambridge, Cambridge University Press, pp. 288-305. https://doi.org/10.1017/9781108569507.020

Rendu, W., Naji, S., Pubert, E., Sánchez-Hernández, C., Vuillien, M., Alarashi, H., Discamps, E., **Jimenez, E.-L**., Rigaud, S., Gourichon, L. (2022). Cementochronology protocol for selecting a Region of Interest in zooarchaeology. In S. Naji, W. Rendu and L. Gourichon (Eds), Cementum in Anthropology. Cambridge: Cambridge University Press, pp. 201-214. https://doi.org/10.1017/9781108569507.013

6.3.OTHER

Dinnis, R., Boulton, J., Bates, M., Chamberlain, A.T., Davies, J., Hopkins, R., **Jimenez, E.L**., Masson-MacLean, E., Mogg, J., Parfitt, S., Payne, N., Pickard, C., Stringer, C., Walker, E.A., Williams, D., French, J.C., **submitted**. Report on the 2022 excavations at Wogan Cavern (Pembroke, Pembrokeshire, UK). Cave and Karst Science.

Jimenez, E.-L., Bocherens, H., Britton, K., Christoph Wissing, Christelle Draily, **Boudin, M., Germonpré, M**., **in preparation**. The diet of the carnivore guild in Belgium during the Late Pleistocene: a comparison between natural and Palaeolithic cave sites.

Germonpré, M., Lázničková-Galetová, M., Roblíčková, M., **Bocherens, H., Jimenez, E.L**. et al., **in preparation**. The cave lions of the Gravettian Předmostí site (Czech Republic): taphonomy and osteometry.

Dinnis, R. et al., 2022. The archaeological potential of Wogan Cavern (Pembroke, UK): results of the first fieldwork season. Cave and Karst Science 49 (2), pp. 65-72. (E.-L. Jimenez is co-author)

Jimenez, E.-L. (2023). Le chien descend-il vraiment du loup ? The Conversation, https://theconversation.com/le-chien-descend-il-vraiment-du-loup-195836

Wogan cave website (in English and Welsh): https://wogancavern.weebly.com/

7. ACKNOWLEDGEMENTS

We would like to thank the members of the scientific follow-up committee for providing us with interesting ideas and feedback throughout the project.

- Hervé Bocherens, Biogeology, Geoscience Department of the University of Tübingen
- Kate Britton, Department of Geosciences, University of Aberdeen
- Martina Lázničková-Galetová, Moravian Museum, Brno, Czech Republic
- Mikhail Sablin, Zoological Institute of the Russian Academy of Sciences, St. Petersburg, Russian Federation

We thank Annelise Folie and Cécilia Cousin for their help to make the faunal material in the paleontological collections of the RBINS accessible for our research.

We thank Christelle Draily from the AWAP, Service Public de Wallonie, Belgium for allowing us access to the faunal assemblage and its data from Walou Cave.

We thank Martina Roblíčková from the Moravian Museum, Czech Republic for granting us access to the cave lion assemblage from Předmostí.

We would also like to thank Georges Jamart from BELSPO for his follow-up, guidance, help and understanding throughout the project.

We are grateful to all the very helpful people at the University of Aberdeen for their material, technical and mental support throughout the pandemic, their generosity regarding lab access, and so much more: Kate Britton, Orsolya Czére, Joshua Wright, Mael le Corre, Sarah Barakat, Eléa Gutierrez, Edouard Masson-McLean, and all the staff members.

We would like to thank Rob Dinnis and Jennifer French for inviting ELJ to join the excavating and scientific team at Wogan cavern, and allowing her to be in charge of the palaeolithic faunal material.