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Abstract - Earth's climate experienced a major warming during the last interglacial period (Eemian, MIS 5e, LIG 128 to 114 ky). The rapid climate change altered ecosystems causing a geographical redistribution of flora and fauna. Due to the scarcity of archaeological sites representing this period, the effect of these events on the behavior of Neanderthal hunter-gatherers in Western Europe has been poorly understood. New evidence from a well-preserved archaeological layer (XV) at Baume Moula-Guercy cave in Southeastern France, attributed to the optimum Eemian Interglacial, allows us to consider the challenges Neanderthals faced as these new ecosystems and ecological communities formed. We argue that, on the European continent, the human population collapsed, maintaining itself only in a few regions. We further suggest that these environmental upheavals, including depletion of prey biomass at the beginning of the Upper Pleistocene, contributed to the rise of cannibalistic behavior in Neanderthals, as exhibited among remains found at the Baume Moula-Guercy cave.

Keywords – Last interglacial, MIS 5e, Climate change, ecosystems, Neanderthals, behavior, cannibalism.

1 - Introduction

Throughout the past 400,000 years, the last interglacial period (Eemian, MIS 5e, LIG 128 to 114 ky) was the warmest (Working Group of PAGES, 2016), with a temperature about 2 degrees higher than the present, and a sea level rise between 6 - 9 meters above the last century level (Dutton *et al.*, 2015). This warm climatic oscillation (Milankovitch, 1941) is documented in marine sediment cores (Emiliani, 1955, Shackleton, 1969), ice cores (Northgrip-members, 2004, NEEM community members, 2013,) and terrestrial records from long sequences in middle-Europe (de Beaulieu and Reille, 1989, Brewer *et al.*, 2008). Due to the scarcity of Western European sites with precisely dated stratigraphic sequences bearing stone tools, faunal remains, and reliable ecological data, little is known of the biotopes and landscape changes associated with global warming during this period. Understanding how European Neanderthal hunter-gatherer communities, having adapted for tens of thousands of years to an earlier cold climate, were able to adjust to the major climatic change of the MIS 5e, has been elusive.

The distribution of Eemian Interglacial-aged sites is sporadic throughout Western Europe. There are none in Britain (Roebroeks *et al.*, 1992, Ashton, 2002). Some authors argue that their absence is due to inaccessibility resulting from rapid sea level rise rather than to the development, during MIS 5e, of habitats inhospitable to Neanderthals (Roebroeks *et al.*, 1992, Roebroeks and Speleers, 2002). However, we know that Britain was occupied during the earlier interglacial periods (Robert *et al.*, 1995, Stringer and Hublin, 1999).

In Northern Germany several open-air sites (i.e. Gröbern, Rabütz, Grabschütz, Taubach, Neumark Nord and Lehringen), characterized by a temperate fauna and flora, are attributed to the optimum Eemian Interglacial. The site of Lehringen is famous for a well-preserved yew spear found with a *Palaeoloxodon antiquus* carcass (Thieme and Veil, 1985, Wenzel, 2007). This

discovery documents the recolonization of this area by temperate-adapted species following the strong climatic improvement that occurred during MIS 5e. Among similar sites, Neumark-North has yielded the widest spectrum of temperate-adapted fauna (Gaudzinski-Windheuser and Roebroeks, 2011, Gaudzinski-Windheuser *et al.*, 2014). Most of these sites are located in an area previously completely covered by the MIS 6 Scandinavian ice sheet, and these localities form a fairly dense group, in contrast to the general scarcity of Eemian sites in the rest of Western Europe.

In Southern Europe few Eemian Interglacial-aged (MIS 5e) sites have been found, including Krapina (Gorjanovic-Kramberger, 1906, Malez and Malez, 1988), in Croatia, and Bolomor cave (Arsuaga *et al.*, 2012, Sanudo *et al.,* 2016), in Spain. Saccopastore, in Italy, had previously been attributed to the Eemian but is now considered much older (Masa *et al*., 2015).

In France two Eemian sites are known. In the north is the site of Caours, (Antoine *et al.*, 2006, Sier *et al*., 2015). In the south, only Baume Moula-Guercy (BMG) is attributed with certainty to MIS 5e.

BMG is located near the village of Soyons in Ardèche (Southeastern France), between the Alps and the Massif Central, on the west bank of the Rhône River (**Fig. 1, 3**). Stratigraphic and biochronologic analyses (Saos *et al.,* 2014) allowed subdivision of the 8 meter thick deposits into 19 layers. These layers were then associated with three main climatic phases corresponding to MIS 6 to MIS 4. MIS 5 is represented by layers XV to XI and MIS 5e by layers XV and XIV. Layer XV, the most important layer of this cave, comprises a silty-sand sediment about 40 cm thick that covers approximately 30-40 m^2. The excellent state of bone and charcoal preservation in this layer has enabled reconstruction of the natural environment and landscapes that Neanderthals experienced during the Eemian period.

The quest to understand the causes of Paleolithic cannibalism is almost as old as prehistory itself (Piette, 1871), and continues to be a widely discussed topic in

prehistory and paleoanthropology. In a recent study Cole (2017) notes: *In the majority of studies, the interpretation is that cannibalism was practiced for nutritional reasons, although there has never been a way to quantify how nutritional these episodes may be*. Here we propose that the Neanderthal cannibalism evident at BMG cave layer XV is a nutritional cannibalism that emerged in response to the profound upheaval of their previously enduring environmental conditions. We also suggest that paleoanthropological sites of Eemian age are extremely rare due to a drastic decline in the European human population during this period.

2 – Methods

The initial discovery of human remains from Baume Moula-Guercy layer XV revealed characteristic traces suggesting an episode of Neanderthal cannibalism (Defleur *et al*., 1999). Simultaneously, observation of the associated fauna from layer XV indicated that it corresponded to a temperate episode, in contrast to the cold-adapted fauna found in overlying layers (Defleur *et al*., 1998). Using a paleoanthropological (interdisciplinary) approach to our investigation of BMG, the recovered samples and geological context were analyzed and compared with relevant publications. Topics assessed include; 1) delineating characteristics that distinguish cannibalism from other forms of bone damage - paleopathology (linear enamel hypoplasia: LEH), taphonomy, typology of lithic artefacts, and paleoethnography; 2) describing faunal and floral remains - vertebrate and invertebrate palaeontology (systematic, biostratigraphy and especially paleoecology including the cenogram method), palaeoanthropology, palaoebotany (anthracology), archaeozoology; 3) determining applicable dating methods - isotopic geochemistry (radiocarbon dating analysis: $^{40}Ar/^{39}Ar$, Uranium-series and ESR, Strontium isotope ratios ($^{87}Sr/^{86}Sr$) applied on tooth enamel of tooth enamel); 4) establishing stratigraphic context - archaeostratigraphy, quaternary geology (sedimentology and stratigraphy).

3 - Results

3.1 – The Layer XV: a deep reconfiguration of ecosystems

During the Pleistocene, climate change resulted in a general reconfiguration of ecosystems and redistribution of all living species on the European continent (Pecl *et al.*, 2017) from plants and insects to large mammals. The fauna of BMG documents these climatic fluctuations during the Eemian period.

Mammal species characteristic of cold biotopes such as reindeer (*Rangifer tarandus*), woolly mammoths (*Mammuthus primigenius*), collared Lemmings (*Dicrostonyx torquatus*) and northern birch mice (*Sicista betulina*) dominate the upper (IV and VIII) and lower (XVI) layers of the cave.

Alternatively, the layer XV sample reveals a significant increase in the presence, following the Rhône Valley, of Mesogean species that found refuge in the Mediterranean peninsula during the glacial phases. The layer XV fauna comprises large mammals characteristic of a temperate climate: deer (*Cervus elaphus*), fallow deer (*Dama* sp.), roe deer (*Capreolus capreolus*), giant deer (*Megaloceros giganteus*), straight-tusked elephant (*Palaeoloxodon antiquus*), narrow-nosed rhinoceros (*Stephanorhinus hemitoechus*), asiatic black bear (*Ursus thibetanus*) and many carnivores. This association is similar at other interglacial sites (**Fig. 1**).

The layer XV faunal sample is represented by a small number of individuals. Neanderthals (6 individuals) and deer (5 individuals) are the best represented. Reindeer (*Rangifer tarandus*) in this layer probably represent a relict species of the previous cold period (MIS 6). Bear cheek teeth and bones exhibit a mixture of anatomical traits specific to *Ursus deningeri* and *Ursus spelaeus*, and characteristic of the late European Middle Pleistocene (Crégut-Bonnoure *et al.*, 2010). Several rodent species, not previously found in association in any late Pleistocene layers in Western Europe, include *Hystrix* cf. *vinogradovi* and three species typical of the Middle Pleistocene (*Allocricetus bursae, Pliomys lenki* and

Microtus (*Iberomys*) *brecciensis*). Other micromammals indicate a predominance of forest areas and a temperate climate. These include: *Rhinolophus ferrumequinum*, *Miniopterus schreibersii*, *Pipistrellus pipistrellus*, *Nyctalus noctula*, *Nyctalus lasiopterus*, *Barbatella barbastellus*, *Glis glis*, *Eliomys quercinus*, *Apodemus sylvaticus*, *Muscardinus avellanarius* and *Clethrionomys glareolus*.

The cenogram method (**Fig. 2**) confirms that layer XV is consistent with a temperate climate with a predominance of mixed forest biotopes under well-marked warm conditions. The Hermann tortoise (*Testudo hermanni*) was also recovered from Layer XV. This tortoise is currently limited to the Mediterranean coastline and has not been reported to be in the Baume Moula-Guercy area in historic or prehistoric times. Currently, the northern-most range of the Hermann tortoise derives from a Holocene locality that is d more than 100 km south (Forest and Cheylan, 2015) of BMG. Two other reptile species, the Montpellier snake (*Malpolon monspessulanus*) and ladder snake (*Rhinechis scalaris*) are no longer dispersed in the study area and have a more southerly distribution (Manzano, 2015). The presence and current ecological requirements of these three species of reptiles indicates that the climate of this region was warmer and probably drier than at present.

A climatic shift to warmer and drier conditions, inferred from the reptiles recovered at BMG correlates with the study of chironomids assemblages (aquatic insects families which respond rapidly to environmental changes). These insect remains were recovered from the pollen sequence at the Les Echets mire (130 km to the north of BMG) (Gandouin *et al.,* 2007).

Charcoal recovered from a cave in the vicinity of BMG (MIS 4) only represents the remains of a single species of pine (*Pinus* type *silvestris*) (Defleur *et al.,*

1994). Flora remains recovered around hearths (Layer XV) belong to several species. These include: deciduous oak (*Quercus* sp.), beech (*Fagus sylvatica*), yew (*Taxus baccata*), elm (*Ulmus sp.*), dogwood (*Cornus mas*), holly (*Ilex aquifolium*), scots pine (*Pinus* type *silvestris*), common juniper (*Juniperus communis*), wired broadleaf (*Phillyrea latifolia*), buckthorn (*Ramnus saxatilis*), blackthorn (*Prunus spinosa*), ivy (*Hedera helix*), and common wild rose (*Rosa* sp.) (Defleur *et al*., 2001). All of these species indicate a deciduous forest environment. They are characteristic of a temperate climate similar to that of the present, although wired broadleaf is a typically Mediterranean species. The rapid warming of the climate at the end of MIS 6 led to the development of a thick deciduous forest throughout the continent, including the northern areas previously occupied by glaciers and permafrost (Gaudzinski-Windheuser *et al.,* 2014). The present local climate is significantly affected by the Rhône Valley corridor as it has resulted in Mediterranean climatic conditions extending to within 50 km to the south of the cave. The presence of Hermann tortoise in this part of France in the Eemian period indicates that the hot and dry Mediterranean climate must have reached much farther north than at present (**Fig. 3**).

These findings allow us to attribute the chronological position of layer XV to the initial phase of MIS 5e. Recent U-series and ESR dating has provided a minimum date of 119 ± 13 ky for Layer XV. The probable age range is approximately 120-130 ky (Willmes *et al*., 2016). This result is in accordance with palaeoecological and biochronological data provided by both the large and small vertebrate fauna.

3.2 - Rare cases of Neanderthal cannibalism

It is commonly accepted that inferences of prehistoric human cannibalism are best based upon similarity of butchery techniques found on human and ungulate remains, (skinning, defleshing, disarticulation), the same mode of breakage of long bones and skulls for the extraction of marrow and brains, and the same

discard pattern and context. When numerous human remains are discovered on an undisturbed living floor, with similar patterns of damage, mixed with animal remains, stone tools, and fireplaces they can legitimately be interpreted as evidence of cannibalism. (Villa *et al.,* 1986, White, 1992, Defleur *et al.*, 1999, Rosas *et al.*, 2006). The archaeological material ideally must have remained *in situ* since its abandonment and must have been recovered in a precise stratigraphic framework with meticulous excavation and recovery methods.

An inventory carried out in 2008 shows that about 220 European sites have yielded human remains belonging to the Neanderthal lineage (Mann and Maureille, 2008). The large majority of these vestiges are isolated human remains (teeth, fragments of skulls or long bones).

The issue of cannibalism currently arises for four Neanderthal sites, all located in Western Europe: Krapina in Croatia (Gorjanovic-Kramberger, 1906) BMG in France (Defleur *et al.,* 1999), El Sidron in Spain (Rosas *et al.*, 2006) and La Troisième caverne de Goyet in Belgium (Rougier *et al.,* 2016) (**Fig. 4**). However, the ideal criteria outlined above are not all present in each case. For example, at El Sidron, all the human remains are in a secondary position and the faunal remains are scarce, but the evidence of cannibal behavior is not in dispute.

At La Troisième caverne and Krapina, excavations were carried out between 1865-1868 and 1899-1905 and the contextual association between the human bones and their environmental contexts are not equivalent to those of sites excavated recently.

Other sites, also few in number, show traces of specific activities involving the deceased. Most of these cases have cut marks on cranial and sometimes post-cranial remains: Vindija (Malez and Ullrich, 1982), Combe-Grenal (Garralda *et al*., 2005), Zafarraya (Finlayson *et al.,* 2006).

However, if cut marks on human remains are a necessary criteria, they are not sufficient to support the hypothesis of cannibalism. Indeed, these traces can also

result from peri or post mortem manipulation of corpses associated with secondary funerary practices. Such funeral practices can include the preservation of skulls or other bones of the deceased for symbolic or other purposes as it is probably the case in Kebara (Bar-Yosef and Vandermeersch, 1991).

At the site of Marillac/Les Pradelles in northwestern France a sample of 95 human remains have been recovered (Garralda *et al.*, 2005). Review of the published data for this site shows that the human remains come from five different stratigraphic layers and the ages obtained for these layers cover a significant span of time (50-70 ky). Tooth marks and digestive traces (acid etching) associated with large carnivores were recognized on some bones. We note also the absence of trunk elements and pelvic and scapular girdles. While some of the bones possess cut marks from stone tools, percussion marks have not been observed (Garralda *et al.*, 2005). In a taphonomic study of these human remains Mussini (2011) considers this site as "*a probable case of cannibalism*".

3.3 - Evidence for a nutritional cannibalism at BMG layer XV

In BMG layer XV, the 120 human remains from 6 individuals (2 adults, 2 adolescents ($\approx$ 12/15 years) and 2 children ($\approx$ 4/5 and $\approx$ 7/8 years) exhibit all the criteria characteristic of Neanderthal cannibalism: *in situ* material on an undisturbed living floor, with fireplaces, fauna and a lithic industry, precise stratigraphic framework and modern excavations. Preservation of the osteological surfaces is excellent. The bone remains show neither the action of carnivores nor weathering alteration. Cut marks are spread over 50% of the human remains and distributed over the entire skeleton from the cranium and mandible to the metapodials and phalanges. Percussion marks are visible on all the skulls, all the long bones and other bones of adults and children. Some anvil striae, adhering flakes, internal vault release, crushing, and peeling (White, 1992) and probable Neanderthal chewing on two hand phalanges were also

observed. The human remains were recovered in a mixed context with faunal remains on a few square meters near the east wall of the cave (Defleur *et al.*, 1999). The numerous refitting pieces and projections indicate that there was probably only a single episode of cannibalism in this layer. The fact that skeletal elements from all regions of the body suggests that they were intact prior to the human butchery event. Further, none of the remains is in anatomical relationship to one another, indicating the body were completely dismembered.

The low number of unretouched flint flakes (Defleur, 2015) and large mammals, in addition to other zooarchaeological data suggest a succession of temporary hunting camps with occupation occurring during the summer or autumn (Valensi *et al.,* 2012).

For over a century, different hypotheses have been suggested to explain Neanderthal cannibalism: consumption of individuals from the group (endo-cannibalism) or outside the group (exo-cannibalism), and survival cannibalism. In the case of the BMG layer XV several arguments accredit the survival necessity cannibalism thesis:

BMG Cannibalism Not Mortuary Practice

- Neanderthal burials, a hallmark of Mousterian culture, come from 17 sites (34 individuals) and cover almost the entire Neanderthal dissemination area from the Atlantic Ocean to the Middle East and Central Asia (Defleur, 1993). All were discovered at cave sites. However, many areas (Italy, Spain, Balkan countries and Central Europe) have yet to produce evidence of Neanderthal burials, possibly reflecting different funerary behaviors such as burial outside of caves. In contrast, Neanderthal cannibalism is limited to four localities in Western Europe (Fig. 4). Thus, cannibalism, unlike burial, was probably not a usual mortuary practice of the Neanderthals.

Cannibalism Due to Lifestyle Adjustments

- Two of the four examples of Neanderthal cannibalism, Baume Moula-

Guercy and Krapina (Rink *et al.,* 1995), come from the MIS 5e, a short but significant period of climatic and ecological change representing only about 10% of Neanderthal existence during the Upper Pleistocene, as compared to 90% lived in cold or very cold phases.

- Changes in ecosystems reported above affect the lifestyles of human communities. As today, Pleistocene interglacial deciduous forests exhibited a high primary biomass predominantly represented by trees, vegetation, invertebrates and non-mammalian vertebrates (Ramade, 1984**;** Gamble, 1986; Kelly, 1995). The medium-sized ungulate biomass was much lower and more dispersed in contrast to open steppe formation where a rich pasturage favored abundant species, Mammoth being a typical representative. Throughout Neanderthal history, the open steppe biome was largely dominant.

- BMG layers above and below layer XV include open steppe and wooded prairie biotopes where small, medium-sized and large species were available (*cf. supra*) as Neanderthal prey.

  In contrast, the BMG Layer XV was located between a largely dominant interglacial forest environment providing a small number of medium sized mammal species difficult to kill, and rare open landscapes with powerful and dangerous animals. This change in availability would have disrupted the traditional way of life and behavior of Neanderthal communities hitherto accustomed to abundant large prey.

Few Occupation Sites Due to Population Stress

- The small number of sites attributable to MIS 5 in general and to the 5e in particular on the European continent cannot be explained by taphonomic causes (as suggested by Surovell and Brantigham, 2007, Surovell *et al*., 2009). Rather it is probably due to a sharp demographic contraction (i.e. Richter, 2006; Speller, 2000; Gaudzinski-Windheuser and Roebroeks, 2011, Williams, 2012, Rolland, 2015, Nielsen *et al*., 2017).

Some authors (Roebroeks *et al.*, 1992, Roebroeks and Speleers 2002) hypothesis that the rarity of Neanderthal traces during MIS 5e results from various factors, including its short duration, and a combination of geological and historical research factors.

Archaeological research conducted over more than a century in southern France - which is probably one of the regions of Europe where Neanderthal occupation was the most intense - shows that the hypothesis of an historically based lack of research does not correspond to the archaeological reality. In Southern France, the deposits are numerous to deliver occupation of MIS 6 the 4 and 3, exceptionally of MIS 5d,c,b,a, and never of MIS 5e. Hitherto, only layer XV of BMG is confidently and unambiguously attributed to MIS 5e in this region.

Neanderthals had likely abandoned most parts of Europe because of lack of natural resources compared to the previous and subsequent periods, and because the low population density of the groups was insufficient to allow adequate human reproduction. However, some regions such as the southeast of France may have remained permanently inhabited (**Fig. 5**).

Dependence on Protein from Meat

- Isotopic analyses show that Neanderthals were at the top of the food chain; meat and fat were their main food sources (Richards *et al.*, 2000, Wissing *et al.*, 2016), thus their population density had to be small. They had a robust skeleton and their average muscular mass was higher than that observed in modern people, implying a high-energy cost for travel and activities. Their DEE (daily energy expenditure) has been estimated (Churchill, 2006) between 3,500 and 5,000 kcal per day for men, a much higher expenditure than the average DEE of recent hunter-gatherer populations. This resulted in a greater dependence on the flesh and fat of large herbivores, with very little exploitation of small game. Populations would have been more vulnerable during periods when animal protein

became scarce. Although protein was a dominant component of their diet, it may have taken exceptional circumstances for human flesh to become meat. Hunger likely induced this behavior. "*People usually eat because they are hungry, and most prehistoric cannibals were therefore probably hungry.*" (White, 2003), and even more so during abrupt climate change.

- In layer XV, potential secondary preys are only represented by porcupine, Hermann tortoise and fishes. While fish remains have been recovered in only a small number of Mousterian sites, the study of fish bones from layer XV suggests that this group fish from the Rhône River. The rabbit (*Oryctolagus cuniculus*), which is widely represented in the contemporary layer IV at Bolomor cave in Spain (Blasco and Fernandez Peris, 2012) is not represented in layer XV.

- In layer XV, the percentage of cut marks on human bones (>50%) is much higher than on the remains of deer (14%), which is the most abundant and largest mammal recovered (Valensi *et al*., 2012). These findings indicate that human carcasses were exploited more than those of large mammals, suggesting an exacerbated need for protein. Cut marks on metapodials and phalanges confirm this observation.

- Faunal remains are scarce. Only 290 fragments of ungulates have been taxonomically identified and 193 are deer (66.5 %) (Valensi *et al*., 2012). The extent of the identified fauna could be misleading. This is because it corresponds to both a palimpsest of short-lived human occupations and, in small part, to the faunal remains left by carnivores during periods of Neanderthal absence. For example, we have no proof that the rare remains of elephant and rhinoceros correspond to prey hunted by humans. The presence in this layer of the fallow and roe deer are possibly also linked to carnivore activities (Valensi *et al*., 2013). Thus, contrary to assumption made by Yustos et al. (2015), the faunal list cannot be used as an argument to think that Neanderthals have never missed animal proteins

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at BMG layer XV (**Fig. 6**).

- The layer XV episode was of short duration. The total consumable soft tissue of the six individuals recovered does not exceed in caloric value that of a deer and an ibex (Cole, 2017). It is suggested by be about the equivalent of two days of meat consumption for a group of 15 to 25 people (Hayden, 2012), or 4 days by rationing.

Endured Episodes of Famine

- Study of the teeth of several individuals from layer XV shows defects in enamel development called "linear enamel hypoplasia" (LEH) (Hlusko *et al.*, 2013) at a frequency comparable to that observed on the cannibalized individuals of Krapina (Hutchinson *et al.* 1999). LEH can result from any number of physiological stresses, such as severe illness or malnutrition, signs of frequent nutritional stress (Hlusko *et al.*, op. cit.). A recent study of LEH in the Hadza in Tanzania shows that LEH occurrence is most often associated with malnutrition (Ungar *et al.*, 2017). Although observed in other sites (Ogilvie *et al.*, 1989), LEHs are expressed at Baume Moula-Guercy on molars, a finding that could indicate long periods of physiological stress and support the hypothesis of severe famines. These signs of developmental arrest or insufficient development are also present at El Sidron cave "*almost all individuals in El Sidrón associated with dental remains have at least one episode of physiological stress stigmatized by tooth enamel hypoplasia (HED) that affects two or three teeth*" (Rosas *et al*., 2012).   Of the four cases of cannibalism found in Neanderthals, at least three show signs of hypoplasia attesting that these populations had to endure periods of food stress. No equivalent study has been published for the fourth site.

- Data from study of the microwear on molar teeth suggests that BMG layer XV individuals likely had a diverse diet. While meat was included in their diet they may have had a comparatively richer plant resource base

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(Hlusko *et al.*, 2013). These observations suggest that this population could have been faced with episodes of dietary stress and that they regularly consumed plant resources provided by their environment.

Consumption of Deceased

- Unlike Krapina and other sites, such as the Sima de los Huesos (Bocquet-Appel and Arsuaga, 1999*)*, at BMG layer XV the individuals were not selected from any age group. Younger people aged under 15-16 years represent 2/3 of cannibalized individuals, along with an elderly robust individual and another gracile young-adult possibly female (Defleur *et al.*, 1999**,** Hlusko *et al.*, 2013, Mersey *et al.*, 2013a, Mersey *et al.*, 2013b). All age classes are close to natural mortality cases observed in recent hunter-gatherers (Gurven and Kaplan, 2007). In this case, cannibalism could have been an opportunistic consumption of the deceased of a human group, or part of it.

- In all known societies, cannibalism is accompanied by practices designed to dispel guilt. No evidence of social gestures of this nature have been recovered from the XV layer, though searches in this layer are as yet incomplete.

4 - Discussion

Analysis of the data found in BMG layer XV provides a benchmark for establishing the temperate conditions of the last interglacial, which is previously not documented for the European continent. The consistency of these data fills a gap for terrestrial climate change of the last interglacial. Our findings relate to reconstructing paleoenvironments and landscapes and human behavior from this period.

Firstly, we provide an additional terrestrial argument in favor of higher temperatures for the Eemian period than during peak Holocene. The three species of reptile found in layer XV; *Testudo hermanni*, *Malpolon*

monspessulanus, and *Rhinechis scalaris*, are specifically Mediterranean and are no longer living in the Soyons region. These bioclimatic markers show that the climate around the cave during the MIS 5e period was warmer and probably drier than at present, and at least comparable to that of the current Mediterranean coast. The Mediterranean climate extended more widely to the north than in the present day, following the Rhône Valley. Layer XIV also contains remains of *Testudo hermanni*, suggesting a relative stability of climatic conditions in this area throughout the duration of the Eemian, as shown by pollen data in the south of the European continent (Brewer *et al.*, 2008).

Secondly, our study fills a void in defining landscape features during MIS 5e. At this time, the cave surroundings corresponded to a mosaic landscape inhabited by a fauna that is now either gone extinct, has disappeared from the region, or is similar to that existing today. The vast deciduous forest sheltered a fauna still present today, apart from the fallow deer which disappeared from the region at the end of MIS 5. Relict groups such as the giant deer, straight-tusked elephant and narrow-nosed rhinoceros inhabited the wooded prairie. Open sunlit areas of bushy vegetation were inhabited by Mediterranean reptiles as well as the porcupine (*Hystrix* cf. *vinogradovi*). These species are now extinct or located several tens of kilometers to the south. Stratigraphic analysis suggests that the transition between the cold, arid climate of MIS 6 and the temperate, humid climate of the MIS 5e occurred rapidly, as has been observed elsewhere (Velichko *et al.*, 2007). The arctic lemming (*Dicrostonyx torquatus*), adapted to a circumpolar climate, disappears with layer XVI, whereas the Hermann tortoise, whose distribution is strictly Mediterranean, appears with layer XV. These paleoenvironmental data potentially sheds light on changes that our current ecosystems might undergo if our planet experiences global warming in the future.

Thirdly**,** as some authors have pointed out (Kelly, 1983, Bailley *et al.*, 1989, Kelly, 1995, Bindford, 2001), tropical or temperate forests are hostile living

environments for all hunter-gatherer groups today, as in the past, because protein from medium-sized ungulates is much less than from prey found in an open Mammoth steppe formation. Based on study of the human teeth (Hlusko *et al.,* 2013), this population was subject to frequent nutritional stresses and the presence of cannibalistic behaviour which, unlike ritual burial practices, is the exception for European Neanderthals.

Fourthly, our inventory of Mousterian sites attributed to MIS 5e in the southern half of France and elsewhere in Europe shows a collapse of the human population during the Eemian period of global warming.

According to Prüfer *et al.* (2017), the Neanderthal population has been low throughout the life of this species, on the order of tens of thousands of individuals, even at its peak and contrary to what one might suppose by referring to the many artifacts collected on the Eurasian continent.

Climate-environmental episodes encountered by this human population during its history on the European continent have certainly influenced its periodic demographic collapses, as successive bottleneck events lead to genetic weaknesses, rapid evolution and low variability in Neanderthals (e.g. Briggs et al., 2009, Premo and Hublin, 2009, Bocquet-Appel and Degiovani, 2013, Rogers *et al.*, 2017).

Using a model from sub-contemporary hunter-gatherer populations, Neanderthals were probably divided into autonomous groups of 15 to 25 individuals related to 10 or 20 other allied groups (Hayden, 2012, Lalueza *et al*., 2011, Rosas *et al.*, 2012).

During the Eemian period, networks of exchange and alliances, established for millennia among these human groups, may have been disrupted by new geographical barriers, as melting ice increased river volume and forests dominated the landscape. The scarcity of large prey species may have resulted in increased residential mobility and possibly disrupted old social connections, as

their high trophic level and high energy requirements forced expanded hunting forays in search of widely dispersed medium-sized mammals (Verpoorte, 2006). At Baume Moula-Guercy, situated along the Rhône River, fishery resources may have mitigated these phenomena (Guillaud in progress, Kelly, 1995, Roselló-Izquierdo and Morales-Muñiz, 2005). A few regions in Europe, such as the southeast of France, remained inhabited and could represent one of the population pools from which the Neanderthal groups of Western Europe reconstituted. The first $^{87}Sr/^{86}Sr$ isotopic analysis carried out on two Neanderthal teeth from layer XV provides direct evidence of a childhood food source from within the Rhône Valley (Willmes, 2015, Willmes *et al.*, 2016) and a local origin for this population.

Many recent works have changed the image of Neanderthals by showing their aptitude for language (D'Anastasio *et al.,* 2013, Krause *et al.,* 2007), the complexity of their lithic technology, shared with anatomically modern humans, the first known processing technology with the complex manufacturing of birch pitch, (Koller *et al.,* 2001), the use of natural pigments (Peter *et al.,* 2016), the use of ornamental objects (Radovcic *et al.,* 2015), their assistance of weak individuals (Schultz, 2006), and the practice of ritual burial (Defleur, 1993)**.** The available data show that from a technical, cognitive, symbolic, emotional, and analytical (ability to abstract, anticipate and reflect on complex situations) perspective, the Neanderthals were likely similar to modern humans, who replaced them on the European continent around 40-35 ky ago. Their remarkable adaptability allowed them to live in very different environments and climates, from the Atlantic to the Altai Mountains and even more to the east (Li *et al.,* 2017), for more than 300,000 years.

Cannibalism is not behaviour exclusive to Neanderthals; it has been practiced by many forms of hominids from the early Palaeolithic to the Bronze Age (Saladié and Rodriguez-Hidalgo, 2017) and beyond. The behaviour is also associated with many tragic situations that punctuate recent history. The cannibalism

highlighted at Baume Moula-Guercy is not a mark of bestiality or sub-humanity. The synthesis of the data makes it possible to interpret this occurrence as a short and single episode of survival endo-cannibalism in response to nutritional stress induced by rapid and radical environmental changes.

Following this episode, the same human cultural group continued to include this site in its seasonal cycle throughout the Eemian period (Defleur, 2015). This site demonstrates the practice of cannibalism by Neanderthals (Defleur *et al.,* 1999) and provides a credible explanation for this behaviour.

Competing interests

The authors have no competing interests

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References

Antoine, P., Limondin-Lozouet, N., Auguste, P., Locht, J.-L., Galheb, G., Reyss, J.-L., Escude, E., Carbonel, P., Mercier, N., Bahain, J.-J., Falguères, C., Voinchet, P., 2006: Le tuf de Caours (Somme, France) : mise en évidence d'une séquence éémienne et d'un site paléolithique associé. *Quaternaire*, 17, 4, 281-320.

Arsuaga, J.-L., Peris, J.-F., Garcia-Téllez, A., Quam, R., Carretero, J.-M., Gonzalez, V.B., Blasco, R., Cuartero, F., Sanudo, P. 2012 : Fossil human remains from Bolomor cave (Valensia, Spain). *Journal of Human Evolution*, 62, 629-639.

Ashton, N.M., 2002: The absence of humans from Last Interglacial Britain. *In : Le Dernier Interglaciaire et les occupations humaines du Paléolithique*, Roebroeks W, Tuffreau A (eds). Centre d'Etudes et Recherches Préhistoriques: Lille, 93-103.

Bailey, R. C., Head, G., Jenike, M., Owen, B., Rechtman, R., Zechenter, E. 1989: Hunting and gathering in tropical rain forest: Is it possible? *American Anthropologist*, 91, 59–82.

Bar-Yosef, O., Vandermeersch, B., Eds. 1991: *Le squelette moustérien de Kébara 2*, Cahiers de Paléoanthropologie, CNRS, Paris.

Beaulieu, J.-L. de Reille, M., 1989: The transition from temperate phases to stadials in the long upper Pleistocene sequence from Les Echets (France). *Palaeogeography, Palaeoclimatology, Palaeoecology*, 72, 147-159 (1989).

Benito, B., Gil-Romera, G. 2009: Eemian repartition of Neanderthals. *Authora*, 1.

Benito B. M., Svenning, J.-C., Kellberg-Nielsen, T., Reide, F., Gil-Romera, G., Mailund, T., Kjaergaards, P.C., Sandel, B.S. 2017: The ecological niche and distribution of Neanderthals during the Last Interglacial. *Journal of Biogeography*, 44, 51-61. DOI: 10.1111/jbi.12845

Binford, L.R, 2001: *Constructing Frames of Reference: An Analytical Method for Archaeological Theory Building Using Ethnographic and Environmental Data Sets*. University of California Press, Berkeley.

Blasco, R., Fernandez Peris, J. 2012: Small and large game: human use of

diverse faunal ressources at level IV of Bolomor cave (Valencia, Spain). *C.R. Palevol*, 11, 265-282, doi: 10.1016/j.crpv.2012.01.003.

Bocquet-Appel, J.-P., Arsuaga, J.-P. 1999: Age Distribution of Hominid Samples at Atapuerca (SH) and Krapina, could indicate Accumulation by Catastrophe. *Journal of Archeological Science*, 26, 327, doi: org:10.1006/jasc.1998.0370.

Bocquet-Appel, J.-P., Degioanni A. 2013: Neanderthal Demographic Estimates. *Current Anthropology*, 8:202-S213. DOI: 10.1086/673725

Brewer, S., Guiot J. Sanchez-Goni, M.-F., Klotz, S., 2008: The climate in Europe during the. Eemian: a multi-method approach using pollen data. *Quaternary Science Rev*iew, 27, 2303-2315, doi:10.1016/j.quascirev.2008.08.029

Briggs, A.W., Good, J.M., Green, R.E., Kraise, J., Maricic, T., Stenzel, U., Lalueza-Fox, C., Rudan, P., Brajkovic, D., Kucan, Z., Gusic, I., Schmitz, R., Doronichev, V.D., Golanova, L.V., Rasilla, M. de la, Fortea, J., Rosas, A., Paabo, S. Targeted retrieval and analysis of multiple Neandertal genomes, *Science*, 325, 2009, pp : 218-221.

Churchill, S.E., 2006: Bioenergetic perspectives on Neanderthals thermoregulatory and activity budgets, in Harvati K., Harrison T. (Eds) *Neanderthals revisited: New approaches and perspectives*, Springer, Dordrecht, 113-134.

Cole, J. 2017: Assessing the calorific significance of episodes of human cannibalism in the Palaeolithic. *Scientific Reports,* **7**, 44707, 1-9, doi:10.1038/srep44707.

Crégut-Bonnoure, E., Boulbes, N, Daujeard, C., Fernandez, P., Valensi, P., 2010: New data on the large mammals fauna from the Eemian in the Southeast of France. *Quaternaire*, 21, 3, 227-248.

D'Anastasio, R., Wroe, S., Tuniz, C., Mancini, L., Cesana D.T., Dreossi, D., Ravichandiran, M., Attard, M., Parr, W.C., Agur, A., and Luigi Capasso, L. 2013: Micro-Biomechanics of the Kebara 2 Hyoid and Its Implications for Speech in Neanderthals. *PloS One,* 8, (12). doi:org/10.1371/journal.pone.0082261.

Defleur, A., 1993 : *Les sépultures moustériennes*, Ed. CNRS, Paris.

Defleur, A., 2015 : Mousterian lithic assemblages from Moula-Guercy cave (Soyons, Ardèche). Excavations 1993-1999. *L'Anthropologie*, 119, 170-253, doi:

10.1016/j.anthro.2015.04.002.

Defleur, A., Bez, J.-F., Crégut-Bonnoure, E., Fontugne, M., Jeannet, M., Magnin, F., Talon, B., Thinon, M., Combier, J. 1994: Industries, biostratigraphie, restes humains et datation du gisement moustérien de la Baume Néron (Soyons, Ardèche). *C.R. Académie des Sciences Paris*, 318, série II, 1409-1414

Defleur, A., Dutour, O., Valladas, H., Vandermeermersch, B. 1995: Cannibals among the Neanderthals? *Nature*, 362, 214, doi:10.1038/362214a0.

Defleur, A., Crégut-Bonnoure, E., Desclaux, M., 1998: Première mise en évidence d'une séquence éémienne à restes humains dans le remplissage de la Baume Moula-Guercy (Soyons, Ardèche), *C.R. Acad. Sci Paris*, 326, 453-458, DOI10.1016/S1251-8050(98)80070-0.

Defleur, A., White, T., Valensi, P., Slimak, L., Crégut-Bonnoure, E., 1999: Neanderthal Cannibalism at Moula-Guercy, Ardèche, France. *Science* 286, 128-131, doi: 10.1126/science.286.5437.128.

Defleur, A., Crégut-Bonnoure, E., Desclaux, E., Thinon, M., 2001: Présentation paléo-environnementale du remplissage de la Baume Moula-Guercy à Soyons (Ardèche) : implications paléoclimatiques et chronologiques. *L'Anthropologie*, 105, 369-408, doi: 10.1016/S0003-5521(01)80022-4.

Dutton, A., Carlson, A. E., Long, A. J., Milne, G. A., Clark, P. U., DeConto, R, Horton, B., Rahmstorf, P. S., M. E. Raymo, M. E. 2015: Sea-level rise due to polar ice-sheet mass loss during past warm periods. *Science* 349, 6244, doi: 10.1126/science.aaa4019.

Emiliani, C., 1955: Pleistocene temperatures. *Journal of Geology*, 63, 538-578.

Forest, V., Cheylan, M. 2015: Le lièvre, la tortue et l'aurochs. *In Archéologie et Culture. L'environnement en mémoire*, Bardot-Combot A., Tranoy L., Eds, 25-43.

Gamble, C., 1986: The Paleolithic settlement of Europe. Cambridge, Cambridge University Press.

Gandouin, E., Ponel, P., Andrieu-Ponel, V., Franquet, E., De Beaulieu, J.-L., Reille, M., Guiter, F., Brulhet, J., Lallier-Vergès, E., Kéravis, D. 2007: Past environment and climate changes at the last Interglacial/Glacial transition (Les Échets, France) inferred from subfossil chironomids (Insecta) *C.R. Geoscience*, 339, 337-346, doi: 10.1016/j.crte.2007.03.002

Garralda, M. D, Giacobini, G., Vandermeersch, B. 2005: Neanderthal cut marks: Combe-Grenal and Marillac (France). A SEM analysis. *Anthropologie (Brno)*, 43, 189-197.

Gaudzinski-Windheuser, S., Roebroeks, W., 2011: On Neanderthal Subsistence in Last Interglacial Forested Environments in Western Europe (2011, in Conard & Richter, eds., *Neanderthal Lifeways, Subsistence and Technology*: One Hundred and Fifty Years of Neanderthal Study. Springer, Dordrecht, 61-71.

Gaudzinski-Windheuser, S., Kindler, L., Pop E., Roebroeks, W., Smith, G., 2014: The Eemian Interglacial lake-landscape at Neumark-Nord (Germany) and its potential for our knowledge of hominin subsistence strategies. Quaternary International, 331, 31-38, doi:10.1016/j.quaint.2013.07.023.

Gorjanovic-Kramberger, D., 1906: *Der diluviale Mensch von Krapina Kraotien*. Wiesbaden, C.W. Kreidels, Verlag.

Gurven, M., Kaplan, H., 2007: Longevity among Hunter-Gatherers: A Cross-Cultural Examination. *Population and development review*, 33, 321-365, doi: 10.1111/j.1728-4457.2007.00171.x.

Hayden, B., 2012: Neandertal Social Structure? *Oxford Journal of Archaeology*, 31, 1, 1-26, doi: 10.1111/j.1468-0092.2011.00376.

Hlusko, LJ, Carlson, JP, Guatelli-Steinberg, D, Krueger, KL, Mersey, B, Ungar, PS, Defleur, A. 2013: Neanderthal teeth from Moula-Guercy, Ardèche, France. *American Journal of Physical Anthropology*, 151, 477-491, doi: 10.1002/ajpa.22291.

Hutchinson, D.L., Larsen, C.S., Choi, I. 1997: Stressed to the max? Physiological perturbation in the Krapina Neanderthals. *Current Anthropology*, 38, 904–914.

Koller, J., Baumer, U., Mania, D., 2001: High-Tech in the Middle Palaeolithic: Neandertal-Manufactured Pitch Identified. *European Journal of Archaeology*, 1, 385-397, doi:10.1177/146195710100400315.

Kelly, R.I., 1983: Hunter-gatherer mobility strategies. Journal of Anthropological Research, 39, 277-306.

Kelly, R. L., 1995: The foraging spectrum. Diversity in hunter-gatherer lifeways. Washington/London: Smithonian Institution Press.

Krause, J., *et al*., 2007: The Derived FOXP2 Variant of Modern Humans Was Shared with Neanderthals. Current Biology, 17, 21, 1908-1912, doi: 10.1016/j.cub.2007.10.008.

Li, F., Kuhn, S.L., Chen, F., Wang, Y., Southon, J., Peng, F., Shan, M., Wang, C., Ge, J., Wang, X., Yun, T., Gao, X. 2017: The easternmost Middle Paleolithic (Mousterian) from Jinsitai Cave, North China. *Journal of Human Evolution*, 114:76-84. doi: 10.1016

Malez, M., Malez, V. 1988: The Upper Pleistocene fauna from the Neanderthal man site in Krapina (Croatia, Yougoslavia). *Geoloski Vjesnik*, 42, 49-57.

Malez, M., Ullrich, H., 1982: Neuere paläo-anthropologische Untersuchungen am material aus der HoleVindija (Kroatien). Paleontogian Jugoslavica, 29, 1-44.

Manzano, A. 2015: *Les amphibiens et les reptiles des sites du Pléistocène moyen et supérieur du pourtour méditérranéen (Caune de l'Arago, grotte du Lazaret, Baume Moula-Guercy). Etude d'herpétofaunes et reconstitutions paléoclimatiques et paléoenvironnementales.* PhD thesis, Université de Perpignan

Mann, A., Maureille, B., 2008: Les Néandertaliens européens. *In: Les Néandertaliens. Biologie et cultures*. Editions du CTHS, Paris, 69-85.

Marra, F., Ceruleo, P., Jicha, B., Pandolfi, L., Petronio, C., Salari, L., 2015: A new age within MIS 7 for the Homo neanderthalensis of Saccopastore in the glacio-eustatically forced sedimentary successions of the Aniene River Valley, Rome. *Quaternary Science Reviews*, 129, 260-274, doi:10.1016/j.quascirev.2015.10.027.

Mersey, B., Jabbour, R. S., Brudvik, K., Defleur, A., 2013a: Neanderthal Hand and Foot Remains From Moula-Guercy, Ardèche, France. *American Journal of Physical Anthropology*, 152, 516, doi: 10.1002/ajpa.22389.

Mersey, B., Brudvik, K., Black, M.T., Defleur, A., 2013b: Neanderthal axial and appendicular remains from Moula-Guercy, Ardèche, France. *American Journal of Physical Anthropology*, 152, 530-542, doi: 10.1002/ajpa.22388.

Mussini, C., 2011: *Les restes humains moustériens des Pradelles (Marillac-le-Franc, Charente, France): étude morphométrique et réflexions sur un aspect comportemental des Néandertaliens*. PhD thesis, Université de Bordeaux.

NEEM community members, 2013: Eemian interglacial reconstructed from a Greenland folded ice core. *Nature*, 493, 489-494, doi:10.1038/nature11789.

Northgrip-members, 2004: High-resolution record of Northern Hemisphere climate extending into the last interglacial period. *Nature*, 431, 147-151, doi:10.1038/nature02805.

Pecl, G. T. *et al.*, 2017: Biodiversity redistribution under climate change: Impacts on ecosystems and human well-being. *Science*, 355, eaai9214, 1389, doi: 10.1126/science.aai9214.

Ogilvie, M.D., Curran, B.K., Trinkaus, E., 1989. Incidence and patterning of dental enamel hypoplasia among the Neanderthals. *American Journal of Physical Anthropology*, 79, 5-41.

Peter, J. Heyes *et al.* 2016: Selection and Use of Manganese Dioxide by Neanderthals. *Scientific Reports* 6, 1-9, 22159, doi: 10.1038/srep22159.

Piette E., 1871: Les grottes de Gourdan (Haute-Garonne). *Bulletin de la Société d'Anthropologie de Paris*, 6, 247-263.

Premo, L.S., Hublin. J.-J., 2009: Culture, population structure, and low genetic diversity in Pleistocene hominins. *PNAS*, 106, 33-37 (2009).

Radovčić, D., Sršen, A. O., Radovčić, J. Frayer, D. W. 2015: Evidence for Neandertal Jewelry: Modified White-Tailed Eagle Claws at Krapina. *PLoS One* 10, e0119802, doi: 10.1371/journal.pone.0119802.

Ramade, F., 1984: *Éléments d'Écologie. Écologie fondamentale*, 4e éd., Dunod, Paris.

Richards, M.P., Pettitt, P.B., Trinkaus, E., Smith, F.H., Paunović, M., Karavanić, I. 2000: Neanderthal diet at Vindija and Neanderthal predation: The evidence from stable isotopes. *PNAS*, 97, 7663-7666; doi.org/10.1073/pnas.120178997.

Richter, J., 2008. Neanderthals in their landscape. In: Demars, B., Otte, M. (Eds.), Neanderthals in Europe. Proceedings of the International Conference. ATVATVCA, Tongeren, pp. 17-32.

Rink, W. J., Schwarcz H.P., Smith H., Radovcic J. 1995: ESR ages for Krapina hominids. *Nature*, 378, 24.

Roberts, M. B., Gamble C. S., Bridgeland, D. R., 1995: The earliest occupations

of Europe: the British Isles. In: Roebroeks W., Van Kolfschoten T. (Eds), *The earliest occupation of Europe*. Leiden, University of Leiden: 165-191.

Roebroeks, W., Conard, N.J., van Kolfschoten, T., Dennell, R.W., Dunnell, R.C., Gamble, C., Graves, P., Jacobs, K., Otte, M., Roe, D., Svoboda, J., Ji, X., xed, Svoboda, Tuffreau, A., Voytek, B.A., Wenban-Smith, F., Wymer, J.J. 1992: Dense forests, cold steppes, and the palaeolithic settlement of northern Europe [and comments and replies]. *Current Anthropology,* 33, 551-586.

Roebroeks, W., B.P. Speleers, B.P. 2002: Last interglacial (eemian) occupation of the North European plain and adjacent areas. In: Tuffreau, A., Roebroeks, W. (Eds.), Publications du CERP. Universite des sciences et technologies de Lille, Villeneuve-d'Ascq, France, pp. 31-39 Richter, J., 2008. Neanderthals in their landscape In: Demars, B., Otte, M. (Eds.), Neanderthals in Europe. Proceedings of the International Conference. ATVATVCA, Tongeren, pp. 17-32.

Rogers, A.R, Bohlender, R.J., Chad, C.D. 2017: history of Neanderthals and Denisovans. *PNAS*, 114, 9859-9863. doi.org/10.1073.

Rosas, A., Martínez-Maza, C., Bastir, M., García-Tabernero, A., Lalueza-Fox, C., Huguet, R., Ortiz, J.E., Juliá, R., Soler, V., De Torres, T., Martínez, E., Cañaveras, J.C., Sánchez-Moral, S., Cuezva, S., Lario, J., Santamaría, D., de la Rasilla, M., Fortea, J. 2006: Paleobiology and comparative morphology of a late Neandertal sample from El Sidrón, Asturias, Spain. *PNAS,* USA, 103, 51, 19266-19271, doi: 10.1073/pnas.0609662104.

Rosas, A., Estalrrich, A., García-Tabernero, A., Markus Bastir, M. Samuel García-Vargas, S., Andrea Sánchez-Meseguer, A. Huguet, R., Lalueza-Fox, C., Peña-Melián, A., Kranioti, E. F., Santamaría, D., de la Rasilla M., Fortea J.,J. 2012: The Neandertals from El Sidrón (Asturias, Spain).Updating of a new sample. *L'Anthropologie*, 116, 57-76.

Roselló-Izquierdo, E., Morales-Muñiz, A., 2005 : Ictiofaunas Musterienses de la peninsula Iberica: ¿Evidencias de pesca Neandertal? Munibe, 57, 183-195.

Rougier, H., Crevecoeur, I., Beauval, C., Posth, C., Flas, D., Wißing, C., Furtwängler, A., Germonpré, M. , Asier Gómez-Olivencia, A.,, Patrick Semal, P., Johannes van der Plicht, J., Bocherens, H., & Johannes Krause, J., 2016: Neanderthal cannibalism and Neanderthal bones used as tools in Northern Europe. *Scientific Reports*, 6, 29005, 1-11, doi:10.1038/srep29005.

Saladié, P., Rodriguez-Hidalgo, A. 2017: Archaeological Evidence for Cannibalism in Prehistoric Western Europe: from Homo antecessor to the Bronze Age. *Journal of Archaeological Method and Theory*, 24, 1034–1071,

doi:10.1007/s10816-016-9306-y.

Sanudo, P., Blasc R., Fernández-Peris, J. 2016: Site formation dynamics and human occupations at Bolomor Cave (Valencia, Spain); An archaeostratigraphic analysis of level I to XII (100-200 ka). *Quaternary International*, 417, 94-104, doi : I10.1016/j.quaint.2015.09.044.

Saos, Th, Djerrab, A., Defleur, A. 2014: Stratigraphical, sedimentological and magnetic study of middle and upper pleistocene infilling of Baume Moula‑Guercy (Soyons, Ardèche). *Quaternaire*, 25, 3, 237-251.

Shackleton, N. J., 1969: The last interglacial in the marine and terrestrial records. *Proceeding of the Royal Society of London B*, 174, 135-154.

Schultz M., 2006. *Results of the anatomical-palaeopathological investigations on the Neanderthal skeleton from Kleine Feldhofer Grotte (1856) including the new discovery from 1997/2000*. In: R. W. Schmitz, G. Bonani ed., Neanderthal 1856-2006, Mainz, Verlag Philipp Von Zabern, p. 277-318.

Sier M.J., Pares, J.M., Antoine, P., Locht, J.-L., Dekkers, M.J., Limondin-Lozouet, N.,, Roebroeks, W. 2015: Evidence for the Blake Event recorded at the Eemian archaeological site of Caours, France. *Quaternary International*, 357, 149-157.

Speelers, B., 2000: The relevance of the Eemian for the study of Palaeolithic occupation of Europe. *Neth. J. Geosciences,* 7, 283-290.

Stringer C.B., Hublin J.-J., 1999: New age estimates for the Swanscombe hominid, and their significance for human evolution. *Journal of Human Evolution*, 37, 873-877

Surovell, T.A., Brantingham, P.J., 2007: A note on the use of temporal frequency distributions in studies of prehistoric demography. *J. Archaeol. Sci.* 34, 1868e1877.

Surovell, T.A., Byrd Finley, J., Smith, G.M., Brantingham, P.J., Kelly, R., 2009: Correcting temporal frequency distributions for taphonomic bias. *J. Archaeol. Sci.*, 36, 1715-1724.

Thieme, H. Von, Veil, S., 1985: Neue Untersuchungen zum eemzeitlichen Elefanten-Jagdplatz Lehringen, Ldkr. Verden? Die Kunde N. F.; 36, 11-58

Ungar P. S., Crittenden A.N., Rose J. C., 2017: Toddlers in Transition: Linear Enamel Hypoplasias in the Hadza of Tanzania. *International Journal of Osteoarchaeology*, **27**, 638-649, doi: 10.1002/oa.2586 .

Verpoorte, A. 2006: Neanderthal energetics and spatial behavior. *Before farming: The Archaeology and Anthropology of Hunter-Gatherer*, 3, 1-6. https://doi.org/10.3828/bfarm.2006.3.2

Valensi, P., Crégut-Bonnoure, E., Defleur, A., 2012: Archaeozoological data from the Mousterian level from Moula-Guercy (Ardèche, France) bearing cannibalized Néanderthals remains. *Quaternary International*, 252, 48-55, doi: 10.1016/j.quaint.2011.07.028.

Velichko, A.A., Novenko, E.Y., Zelikson, E. M., Boettger, T. F., Junge, F. W. 2007: *Comparative analysis of vegetation and climate changes during the Eemian interglacial in Central and Eastern Europe* In: The Climate of Past Interglacials, F. Sirocko, M. Claussen, M.-F. & Sánchez Goñi, Eds. Thomas Litt, Developments in Quaternary Sciences, **7**, 255-264.

Villa, P., Bouville, C., Courtin, J., Helmer, D, Mahieu E., Shipman P., Belluomini G., Branca M. 1986: Cannibalism in the Neolithic. *Science*, 233, 431-437.

Wendel, S. 2007: Neanderthals presence and behavior in Central and Northwestern Europe during MIS 5e. In Sirocko F., Glaucen M., Sanchez-Goni M.-F., Litt T. (Eds) *The climate of past interglacials*, Elsevier, 172-189.

Williams, A.N., 2012: The use of summed radiocarbon probability distributions in archaeology: a review of methods. *J. Archaeol. Sci.* 39, 578-589.

Willmes, M. 2015: *Strontium isotope tracing of prehistoric human mobility in France*. PhD Thesis, Australian national University.

Willmes, M., Grün, R., Douka, K., Michel, V., Armstrong, R.A., Benson, A., Crégut-bonnoure, E., Desclaux, E., Fang, F., Kosley, L., Saos, T., Defleur, A. 2016: A comprehensive chronology of the Neanderthal site Moula-Guercy, Ardèche, France. *Journal of Archaeological Science*: Reports, 9, 309-319, doi:10.1016/j.jasrep.2016.08.003.

White, T.D. 1992: *Prehistoric cannibalism at Mancos 5MTUMR-2346*. Princeton University Press, Princeton NJ.

White, T. D., 2003: Once were Cannibals. *Scientific American*, 285, 2, 86.

Working Group of PAGES, 2016: Interglacials of the last 800,000 years. *Rev. Geophys.* 54, 162-219, doi:10.1002/2015RG000482

Wissing, C., Rougier, H., Crevecoeur, I., Germonpré M., Naito, Y.I., Semal, P., Boscherens , H., 2016: Isotopic evidence for dietary ecology of late Neandertals in North-Western Europe. *Quaternary International*, 411, 327-345, doi: 10.1016/j.quaint.2015.09.091.

Yustos, M., Yravedra Sainz de los Terreros, J., 2015: Cannibalism in the Neanderthal world: An Extensive Revision. *Journal of Taphonomy*, 13, 33-52.

Caption of figures

Fig. 1: Vertebrate faunas of the MIS 5e in Western Europe.

Fig. 2: Cenograms of the levels XV to IV of Baume Moula-Guercy, showing a gradual opening of the environment. This method corresponds to the study of the weight distribution of species in a mammalian community, at the exception of bats and carnivores. A cenogram is built by putting the logarithm of the mean body weight of each species of the community on the Y-axis; and the species classified in decreasing order of size on the X-axis. Four main categories of cenograms have been distinguished end it is possible to characterize the type of environments (open or closed) and the climatic conditions (arid or humid). Thus, a continuous distribution of weight is characteristic of a closed habitat. On the other hand, the lack of medium-weight species (between 500 g and 8 kg) is seen in faunas of open landscapes. Otherwise, an abundance of large-size species (over 8 kg) characterizes humid conditions, whereas a steep slope is associated with arid conditions. The slope for the small species reflects the temperature. A large number of small species (a gentle slope) indicates a rather warm climate.

Fig. 3: Distribution over time of three thermophilous reptiles (*Testudo hermanni*, *Rhinechis scalaris* and *Malpolon monspessulanus*) identified in level XV of Baume Moula-Guercy.

Fig. 4: Sites with Neanderhal cannibalism (letters) and burials (numbers). With : A= Baume Moula-Guercy, B=El Sidron, C=La Troisième caverne de Goyet, D=Krapina, 1=Roche à Pierrot, 2=La Ferrassie, 3=Le Regourdou, 4=La Chapelle-aux-Saints, 5=Le Moustier, 6=Roc-de-Marsal, 7=La Quina, 8=Spy, 9=Feldhofer, 10=Kilk-Koba, 11=Mezmalskaya, 12=Dederyeh, 13=Shanidar, 14=Amud, 15=Kebara, 16=Tabun and 17=Teshik Tash.

Fig. 5: Prehistoric sites (stratified cave sites) from MIS 6 to MIS 3 in southern France (south of the 46th parallel). This region is one of the richest in Middle Palaeolithic sites of Europe. The presence of sites from all periods from the end of MIS 6 to the end of MIS 3 suggests a clear decline or collapse in human demography during MIS 5e.

Fig. 6: Quantification of the large mammal species of the level XV of Baume Moula-Guercy, in terms of NISP (number of identified specimens) and MNI (minimal number of individuals). With: A = relative proportions of ungulates, carnivores and *Homo neanderthalensis* according to NISP; B = relative proportions of species consumed by humans according to MNI and C = comparison between MNI and NISP of species consumed by humans.
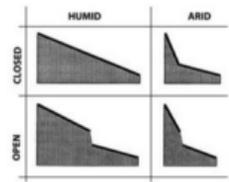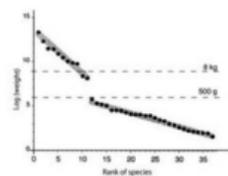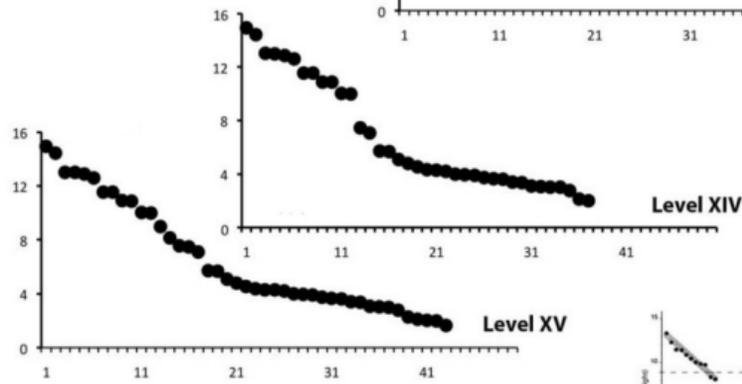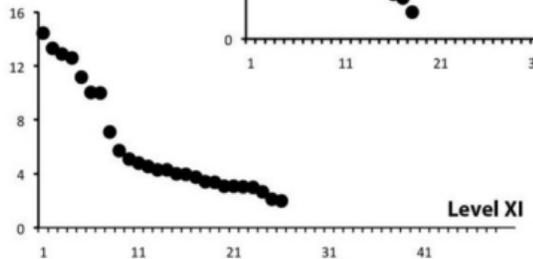
Lehringen

Neumark-Nord

Caours

Moula-Guercy

Krapina

Bolomor

Testudo hermanni

Malpolon monspessulanus

Rhinechis scalaris
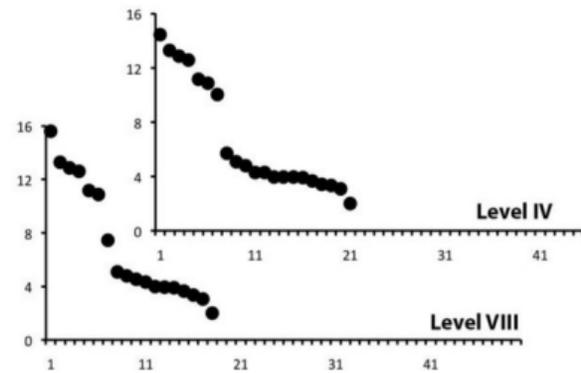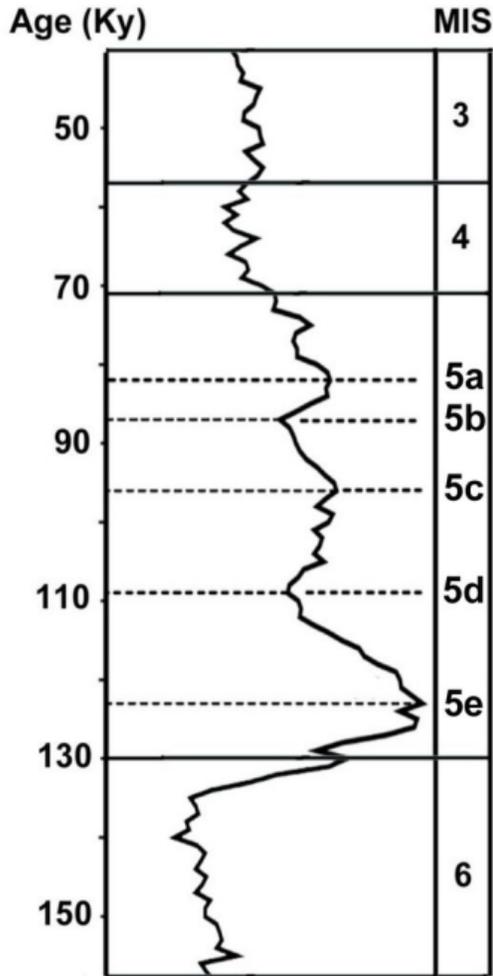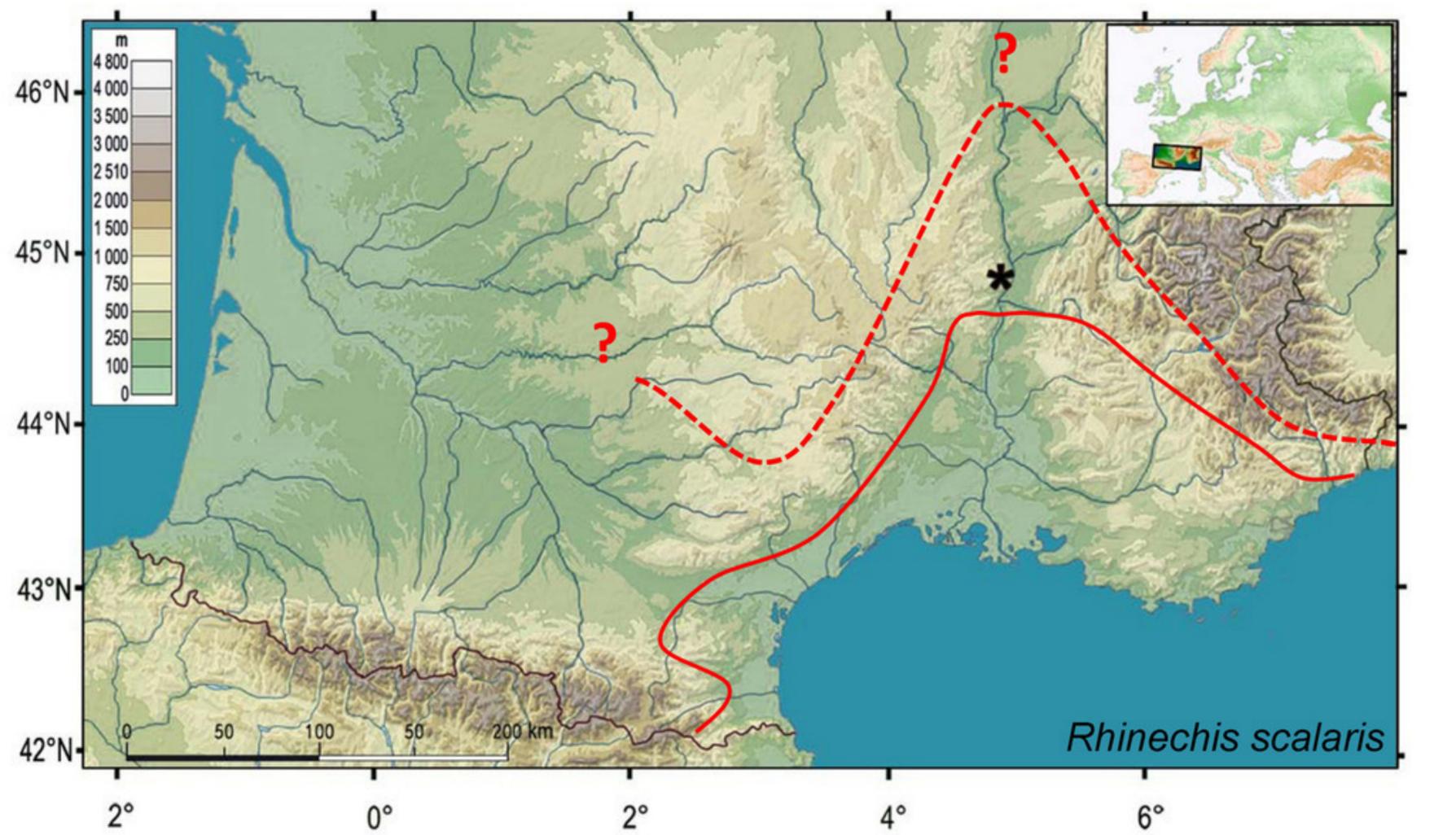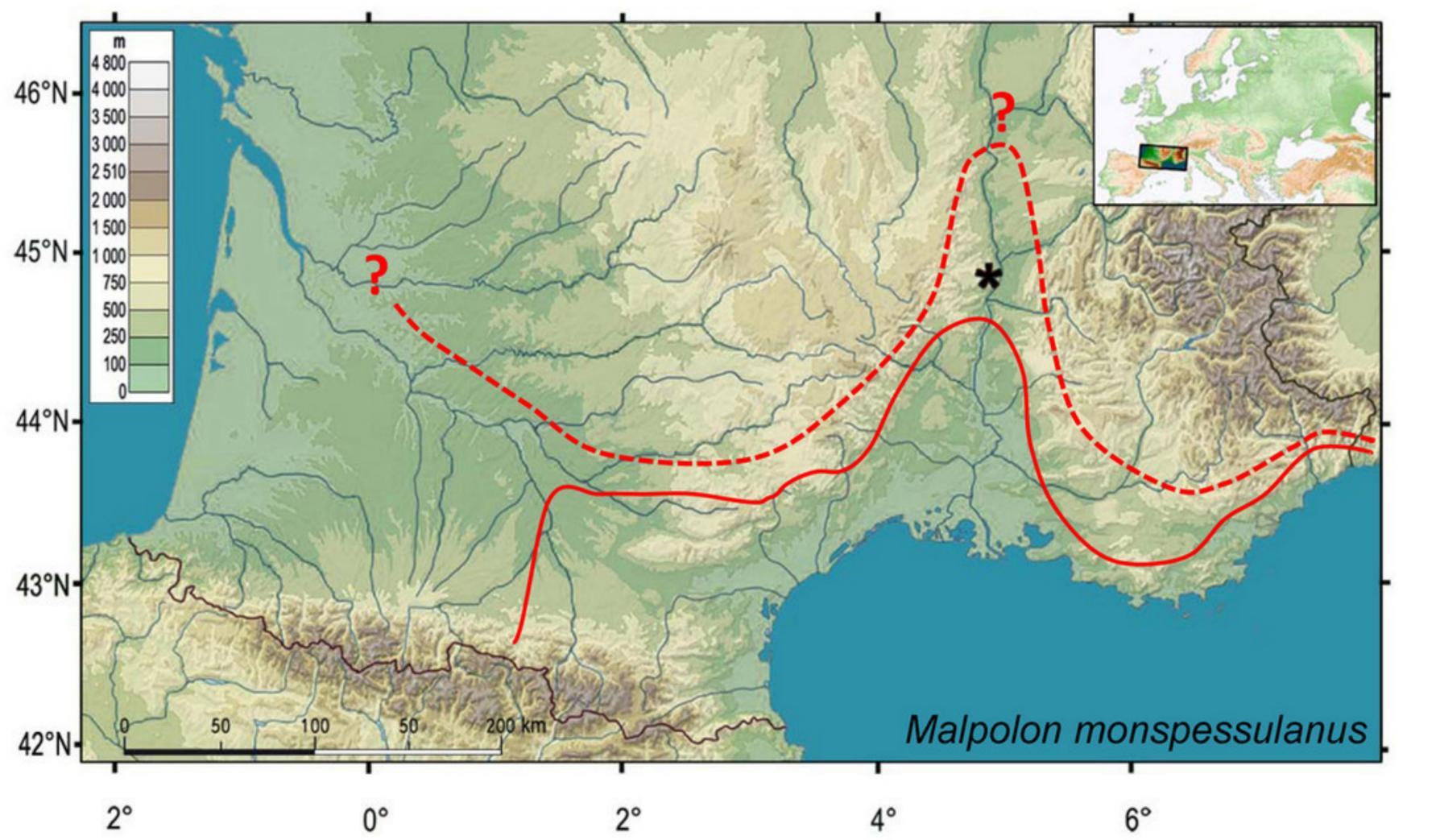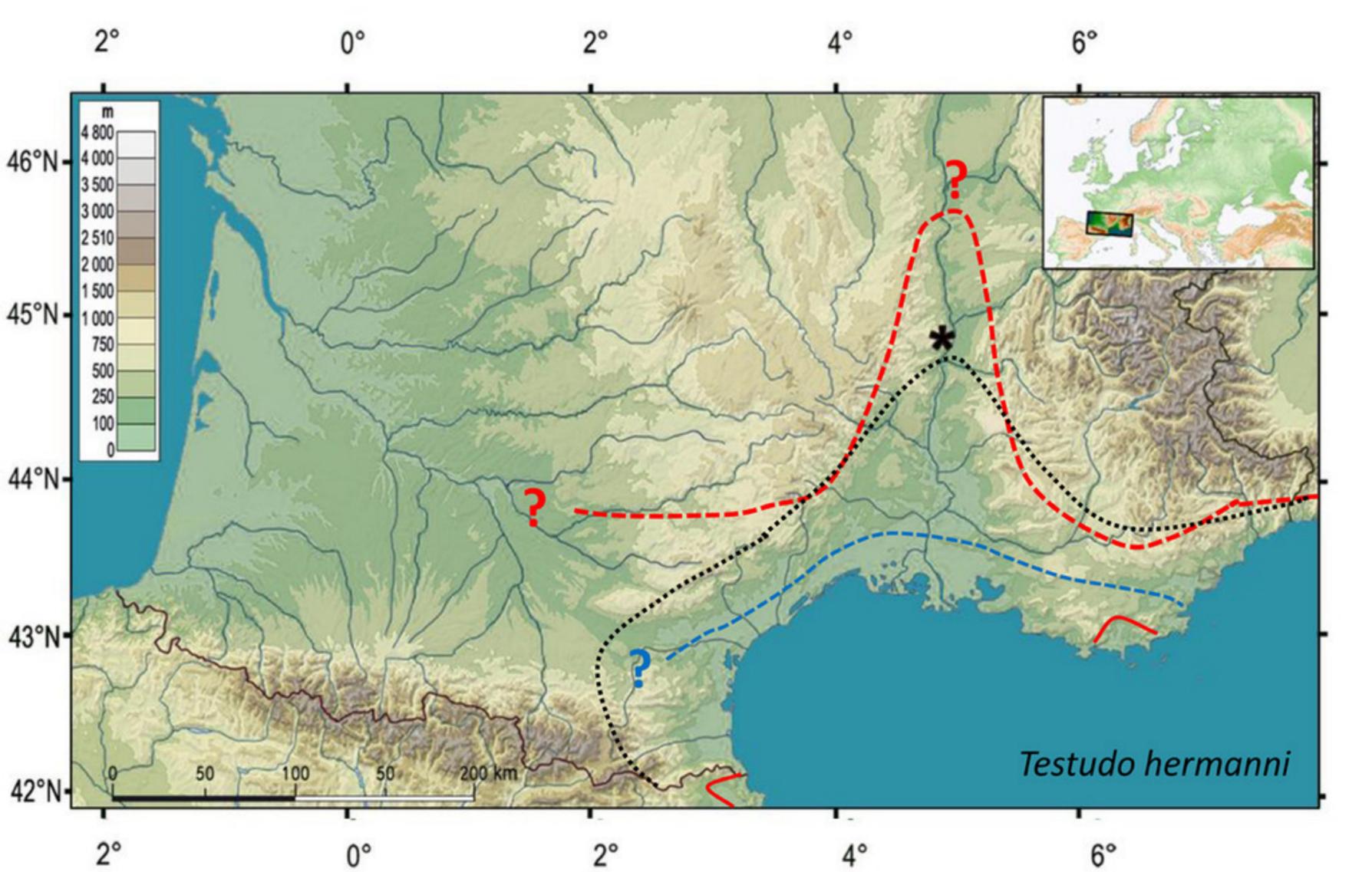
- - - - Distribution during MIS 5e
———— Actual distribution
- - - - Distribution during the Holocene
············· Limit of the Mediterranean climate

MIS 4 - MIS 3

MIS 5e(✱)-MIS 5(•)

MIS 6

A

B

Carnivores

Herbivores

Eauus caballus

Megaloceros giganteus

Sus scrofa

Rangifer tarandus

Bos primigenius

Homo neanderthalensis

Cervus elaphus

Capra sp.

C

Homo neanderthalensis, Cervus elaphus, Capra sp., Bos primigenius, Rangifer tarandus, Sus scrofa, Megaloceros giganteus, Equus caballus

MNI
NISP