

Contents lists available at [ScienceDirect](https://www.sciencedirect.com)

Journal of Archaeological Science

journal homepage: <http://www.elsevier.com/locate/jas>

Cannibals in the forest: A comment on Defleur and Desclaux (2019)

Ludovic Slimak^{a,**}, Christopher Nicholson^{b,*}^a CNRS UMR 5608 TRACES, Université Toulouse Jean Jaurès, Maison de la Recherche, 31058, Toulouse Cedex 9, France^b Center for Digital Antiquity, School of Human Evolution and Social Change, Arizona State University, PO 872402, Tempe, AZ, 85287, USA

ARTICLE INFO

Keywords

Cannibalism
Neanderthals
Eemian
Eurasia
France

ABSTRACT

Though rare in the archaeological record, cannibalism has been documented among many different hominin populations; however, the mechanisms driving such behaviors remains poorly understood. Recent research that evaluates the hypothesized Neanderthal nutritional cannibalism at the Middle Palaeolithic cave site of Baume Moula-Guercy (BMG) in Mediterranean France, is one case that, in our opinion, is not fully substantiated by the evidence put forth by Defleur and Desclaux (2019). Using site occurrence data from the Last Interglacial (MIS 5e), the biogeography of extinct reptile species, and cut mark taphonomic evidence, Defleur and Desclaux (2019) suggest that the Neanderthal remains found in Layer XV of the cave are the result of nutritional cannibalism. The authors argue that a regional collapse of Neanderthal populations was the result of a depletion of prey biomass, caused by a profound upheaval of local environmental conditions, thus causing the Neanderthals at BMG to resort to cannibalism. In this response paper, we attempt to show that the methods and materials used by Defleur and Desclaux 1) do not reflect the known number of Eemian-aged sites, 2) do not present sufficient evidence related to the environmental stress conditions at BMG that would warrant cannibalism, and 3) taphonomic evidence on Neanderthal remains does not strictly support the argument for nutritional cannibalism. Additional study of the BMG remains is necessary before ruling out other processes related to the post-mortem treatment of the Neanderthal corpses.

1. Introduction

The topic of cannibalism in prehistory is the subject of much controversy (Chaline, 1972; Gibbons, 1997; Hurlbut, 2000; Marlar et al., 2000; Saladié and Rodríguez-Hidalgo, 2017; Stoneking, 2003; Villa, 1992; White, 2001, Yustos and de los Terreros, 2015), thus the physical evidence and methods used to justify such a conclusion at a site must be robust, and replicable. Because of the delicate nature of the topic, this response paper addresses several issues that we have identified with the Defleur and Desclaux (2019) hypothesis of nutritional cannibalism at the Middle Palaeolithic site of Baume Moula-Guercy, France (BMG). The onus of distinguishing cannibalism, whether done for nutritional purposes or resulting from alternative behaviors, requires substantial evidence related to the differential treatment of *Homo* remains from other species, a precise understanding of the depositional context of the remains, and evidence that the remains were not deposited as the result of some culturally specific mortuary practices (Villa, 1992). Based on the requisite evidence to support such straightforward conclusions, we

propose that Defleur and Desclaux (2019) do not meet these criteria and we discuss why the BMG data may be indicative of other complex behaviors.

A central tenant of Defleur and Desclaux (2019) focuses on the notion that there was wide spread population collapse in western Eurasia during the Last Interglacial, with only a few regions of the European continent able to maintain sufficient populations. Their hypothesis is, in part, based on the assumption that “(t)he distribution of Eemian Interglacial-aged sites is sporadic throughout Western Europe” noting that localities from northern Germany “form a fairly dense group, in contrast to the general scarcity of Eemian sites in the rest of Western Europe” (2019:114). Furthermore, because of a paucity of sites, the authors 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” (2019:115) and “paleoanthropological sites of Eemian age are extremely rare due to a drastic decline in the European human population during this period” (2019:115). Though we agree that there are

* Corresponding author.

** Corresponding author.

E-mail addresses: slimak@univ-tlse2.fr (L. Slimak), Christopher.M.Nicholson@asu.edu (C. Nicholson).<https://doi.org/10.1016/j.jas.2019.105034>

Received 13 May 2019; Received in revised form 11 October 2019; Accepted 19 October 2019

Available online 10 May 2020

0305-4403/© 2019 Elsevier Ltd. All rights reserved.

Table 1
Site names, countries, Eemian layer, and references for 85 MIS 5e sites.

Site	Country	Eemian Layer	Reference
Ailly sur Noye	France	Unspecified	Locht et al. (2016)
Ambrona	Spain	Layer AS1	(Howell et al., 1991; Markova and Puzachenko, 2018; Villa et al., 2001)
Arenero de Arriaga	Spain	Layer 1.1	Markova and Puzachenko (2018)
Arlampe	Spain	Level D	Rios-Garaizar et al. (2013)
Auteuil	France	Level 1	Goval et al. (2016)
Balzi Rossi/Menton	Italy	Unspecified	Wenzel (2007)
Baume de Gigny	France	Levels XII-XV	(Richter, 2005; Slimak et al., 2010)
Baume Flandin	France	Unspecified	Cregut-Bonnoure et al. (2010)
Beharovce-Sobotisko	Slovakia	Unspecified	Wenzel (2007)
Belokuzminovka	Ukraine	Unspecified	Richter (2005)
Bisnik Cave	Poland	Level A3	Cyrek et al. (2014)
Bockstein	Germany	BS III (Layers h & i)	https://www.nespos.org/display/PublicNesposSpace/Bockstein
Bojnice III	Slovakia	Layer X and XI	Neruda (2012)
Bolomor	Spain	Layer II	(Fernández Peris et al., 2012; Markova and Puzachenko, 2018)
Burgtonna	Germany	Unspecified	Speelers (2000)
Can Costella	Spain	Geological horizon MA-GR	https://www.nespos.org/display/PublicNesposSpace/Can+Costella
Caours	France	Level 4	(Antoine, 2012; Sier et al., 2015)
Cova del Rinocerot	Spain	Layers IIIa,b	Markova and Puzachenko (2018)
Cova Eiros	Spain	Layer 3	(Álvarez et al., 2011; Grandal-d' Anglade, 1993)
Crvena Stijena	Montenegro	Layer XXIV (XXIX-XVIII)	(Musil, 2010; Wenzel, 2007)
Cueva del Angel	Spain	Layer I-XIII	Barroso Ruiz et al. (2011)
Cueva Negra del Estrecho	Spain	Layer 15	(Markova and Puzachenko, 2018; Walker et al., 1998)
Ehringsdorf	Germany	Unspecified	(Richter, 2016; Weber et al., 1996)
El Castillo	Spain	Layers 24-26	(Richter, 2005); https://www.nespos.org/display/PublicNesposSpace/El+Castillo
Elaea	Greece	Unspecified	(Harvati et al., 2009; Richter, 2005)
Elbeuf I	France	Level 4	(Cliquet et al., 2009; Cliquet et al., 2003)
Estret de Trago	Spain	Layer UA3	https://www.nespos.org/pages/viewpage.action?pageId=29886295
Fontchevade	France	Level C	(Cheylan, 1981; McPherron et al., 2012)
Ganovce	Slovakia	Layer 3	(Richter, 2005; Wenzel, 2007)
Gouberville	France	Unspecified	Speelers, 2000(Speelers, 2000)
Grabschutz	Germany	Unspecified	(Gaudzinski-Windheuser and Roebroeks, 2011; van Kolfschoten, 2002)
Grobern	Germany	Layer 4	(Gaudzinski-Windheuser and Roebroeks, 2011); https://www.nespos.org/pages/viewpage.action?pageId=5701
Grossoeuvre	France	Unspecified	(Cliquet et al., 2003; Locht et al., 2016)
Grotte Mandrin	France	Layer I	(Slimak, unpublished)
Hangenbieten I	Germany	Unspecified	(Bosinski, 1967; Richter, 2016)
Horka-Ondrej	Slovakia	Unspecified	Wenzel (2007)
Hranovnica-Hincava	Slovakia	Unspecified	Wenzel (2007)
Ilskaya	Russia	Levels VI-VIII	Golovanova and Doronichev (2003)
Kabazi	Ukraine	Unit V/VI	(Chabai et al., 2005; Richter, 2005)
Karain Cave	Turkey	Unspecified	Richter (2005)
Krapina	Croatia	Layer 8 (Layer 4?)	(Gaudzinski-Windheuser and Roebroeks, 2011); https://www.nespos.org/display/PublicNesposSpace/Krapina
Kulna Cave (Sloup)	Czech Republic	Layer 11-13a	(Musil, 2010; Richter, 2005)
Lazaret	France	Level CIII	Valensi (2000)
Le Grand Abri aux Puces	France	Level 2	Slimak et al. (2010)
Lehringen	Germany	Layer IV	(Gaudzinski-Windheuser and Roebroeks, 2011); https://www.nespos.org/display/PublicNesposSpace/Lehringen
Lezetxiki	Spain	Level Vb	(Arriolabengoa et al., 2018; Falgueres et al., 2005)
Montfarville - Anse de Quéry	France	Unspecified	(Coutard and Cliquet, 2005; Locht et al., 2016)
Moravský Krumlov IV	Slovakia	Layer 2	Neruda and Nerudová (2010)
Moula-Guercy	France	Layer XIV-XV	Valensi et al. (2012)
Neumark-Nord	Germany	Layer 2	(Gaudzinski-Windheuser and Roebroeks, 2011) https://www.nespos.org/display/PublicNesposSpace/Neumark
Payre	France	Layer D	Rivals et al. (2009)
Phoben	Germany	Unspecified	Wenzel (2007)
Port-Racine	France	Unspecified	Wenzel (2007)
Predmostf I-III	Czech Republic	Unspecified	https://www.nespos.org/pages/viewpage.action?pageId=65404992
Rabutz	Germany	Unspecified	(Gaudzinski-Windheuser and Roebroeks, 2011; van Kolfschoten, 2002)
Ramandils	France	Level IV	Moles and Boutié (2009)
Rheindahlen	Germany	Layer B	https://www.nespos.org/display/PublicNesposSpace/Rheindahlen
Rochelot	France	Niveau d1	https://www.nespos.org/display/PublicNesposSpace/Rochelot
Roisel	France	Unspecified	(Gautier, 1989; Swinnen et al., 1996)
Saccopastore	Italy	Layer 2a	https://www.nespos.org/display/PublicNesposSpace/Saccopastore
Saint-Germain-des-Vaux	France	D2A	Bocquet-Appel and Tuffreau (2009)
Saint-Vaast-la-Hougue	France	Unspecified	Speelers (2000)
Sclayn	Belgium	Layer 4	(Gaudzinski-Windheuser and Roebroeks, 2011); https://www.nespos.org/display/PublicNesposSpace/Scladina
Seclin	France	Unspecified	(Conard, 1990; Tuffreau et al., 1985)
Seelberg	Germany	Unspecified	Speelers (2000)

(continued on next page)

Table 1 (continued)

Site	Country	Eemian Layer	Reference
Sesselfelsgrötte, Untere Schichten	Germany	Unspecified	(Richter, 2016; Weißmüller, 1995)
St. Marcel	France	Level U	(Cregut-Bonnoure et al., 2010; Slimak et al., 2010; Wenzel, 2007)
Stajnia Cave	Poland	D1 Layer	http://www.fossilized.org/Human_paleontology/sites_expanded.php?locality=Stajnia%20Cave&primy_key=1037
Steinmühle	Germany	Unspecified	Wenzel (2007)
Stuttgart-Bad Cannstatt	Germany	Unspecified	(Richter, 2016; Wenzel, 1998)
Stuttgart-Untertürkheim	Germany	Unspecified	(Gaudzinski-Windheuser and Roebroeks, 2011)
Taubach	Germany	Level XI	(Gaudzinski-Windheuser and Roebroeks, 2011); https://www.nespos.org/display/PublicNesposSpace/Taubach
Theopetra	Greece	Level II	Facorellis et al. (2013)
Treauville	France	Unspecified	Speelers (2000)
Vaufrey	France	Layers II-IV	Hernandez et al. (2014)
Veldwezelt–Hezerwater	Belgium	Layer B1	Vanmonfort et al. (1998)
Veltheim	Germany	Unspecified	Speelers (2000)
Veternica Cave	Croatia	Layer J	(Musil, 2010; Wenzel, 2007)
Vindija Cave	Croatia	Layer G3	https://www.nespos.org/display/PublicNesposSpace/Vindija
Vogelherd, Hohlensohle	Germany	Unspecified	(Richter, 2016; Wenzel, 1998)
Wallertheim	Germany	Wal A & B	Adler et al. (2003)
Waziers	France	Unspecified	(Locht et al., 2016; Verleijdonk, 2018)
Weimar-Parktravertin	Germany	Lower Travertine	(Gaudzinski-Windheuser and Roebroeks, 2011); https://www.nespos.org/display/PublicNesposSpace/Weimar
Yezupil	Ukraine	Level III	(Lanczont et al., 2009; Richter, 2005)

fewer Eemian-aged sites in western Eurasia than in later periods, the collection of sites that Defleur and Desclaux present, in our opinion, do not reflect all of the sites with a known MIS 5e component, thus leading to erroneous conclusions related to different population dynamics. Here, we attempt to show that the methods and materials used by Defleur and Desclaux 1) do not accurately reflect the number of known sites on the landscape during the MIS 5e Last Interglacial, 2) do not present sufficient evidence related to the environmental conditions at BMG that indicate “stress” conditions that would warrant cannibalism, and 3) their taphonomic evidence of the Neanderthal remains does not strictly support the argument for nutritional cannibalism or even cannibalism *sensu lato* at BMG.

2. Eemian-aged sites and components

Generally, and for a variety of taphonomic reasons, sites from older periods are less well-preserved than those that are more recent, and the Eemian record in western Eurasia is no exception. However, sites with a MIS 5e component are more ubiquitous than those cited by Defleur and Desclaux. In their narrative, Defleur and Desclaux identify only 10 sites in western Eurasia (Gröbern, Rabütz, Grabschütz, Taubach, Neumark Nord and Lehringen, Caours, Krapina, Bolomor Cave and BMG) as having stratigraphic layers dating to MIS 5e. Regarding BMG, the authors note that “only layer XV of BMG is confidently and unambiguously attributed to MIS 5e” in Southern France” (2019:119). The authors contend that Neanderthals had likely abandoned most parts of Europe because of a lack of natural resources when compared to the previous and subsequent periods, and because low population density groups were of insufficient size to allow for adequate human reproduction. With the exception of Saccopastore, in Italy, the authors do not provide evidence as to why only 10 sites are used in their analysis, when numerous studies have documented far more sites (Chabai et al., 2005, Gaudzinski-Windheuser and Roebroeks, 2011, Nicholson, 2017, Richter, 2005, Richter, 2008, Richter, 2016, Speelers, 2000, Wenzel, 1998, Wenzel, 2007). Instead of 10 sites in the region, an overview of the literature shows that there are approximately 85 sites with a cultural layer attributable to the Eemian (Table 1 and Fig. 1). Based on this increased number of sites, it is possible to glean a sense of the distribution of Neanderthal populations throughout western Eurasia and how these populations were able to adapt to numerous climatic zones, showing a preference for warm temperate and mesic climates (Nicholson, 2017). As radiometric dating improves, it is possible that subsequent research

could disprove the presence of an Eemian component at some of these sites. It is even possible such future evidence could demonstrate that only 10 sites “unambiguously” date to MIS 5e, however, excluding 75 other sites with no discussion, prompts questions regarding the hypothesis and methods of the authors aforementioned. Furthermore, their attribution of BMG Layers XIV-XV as dating to MIS 5e is not itself exempt of serious questions.

The biostratigraphic context at BMG is indeed indicative of a warm climate, signifying that Layers XIV-XV are from a warm phase of the Last Interglacial. Radiometric dating should help to clarify the classified MIS 5e layers at BMG; unfortunately, the obtained measures do not directly support a MIS 5e attribution for Layers XIV-XV. In terms of the radiometric dates collected from the site, these layers could be correlated with one of the other warm sub-stages (e.g., 5a or 5c) rather than the warmer 5e stage. Only one radiometric measure with a reported date is consistent with having an Eemian designation in Layer XV. Defleur and Desclaux note that “(r)ecent U-series and ESR dating provided a minimum date of 119 ± 13 ky for Layer XV. The probable age range is approximately 120–130 ky” (Willmes et al., 2016) (Defleur and Desclaux, 2019:118). However, the chronology of layers XIV to XV has been documented as being jumbled, making their chronological position unclear.

In another recent study of BMG, Willmes et al. (2016:318) note that “the CSUS/ESR ages for Layer XIV (n = 2) are not conclusive, with one age estimate at 70 ± 4 ka and another at 97 ± 6 ka. The younger age estimate for Layer XIV does not agree with the stratigraphy and biostratigraphy of the site, and more direct dating of material from this layer is needed to resolve this discrepancy”. These dates do not effectively match with the BMG XIV attribution to MIS 5e but could be congruent with one of the most recent warm sub-stages from MIS 5. Regarding Layer XV, Willmes et al. (2016:318) demonstrate that “the age estimates of the Neanderthal fossil bearing Layer XV are based on 3 faunal teeth (3039, 3041, 3042), yielding consistent ESR age estimates ranging between 97 ± 10 ka and 119 ± 13 ka”. The large sigma values assigned to these dates indicates that the layer could encompass both MIS 5e and MIS 5c. An assignment of the layer to MIS 5c could explain the presence of species that prefer continental and cooler conditions (*infra*) versus the warmer temperatures at the peak of MIS 5e. This alternative attribution of layers would also be congruent with additional BMG U-series dates of two Neanderthal teeth from Layer XV that “agree with an age for Layer XV corresponding to at least MIS 5 *sensu lato*” (Willmes et al., 2016:318). The precise determination of Layers XIV-XV,

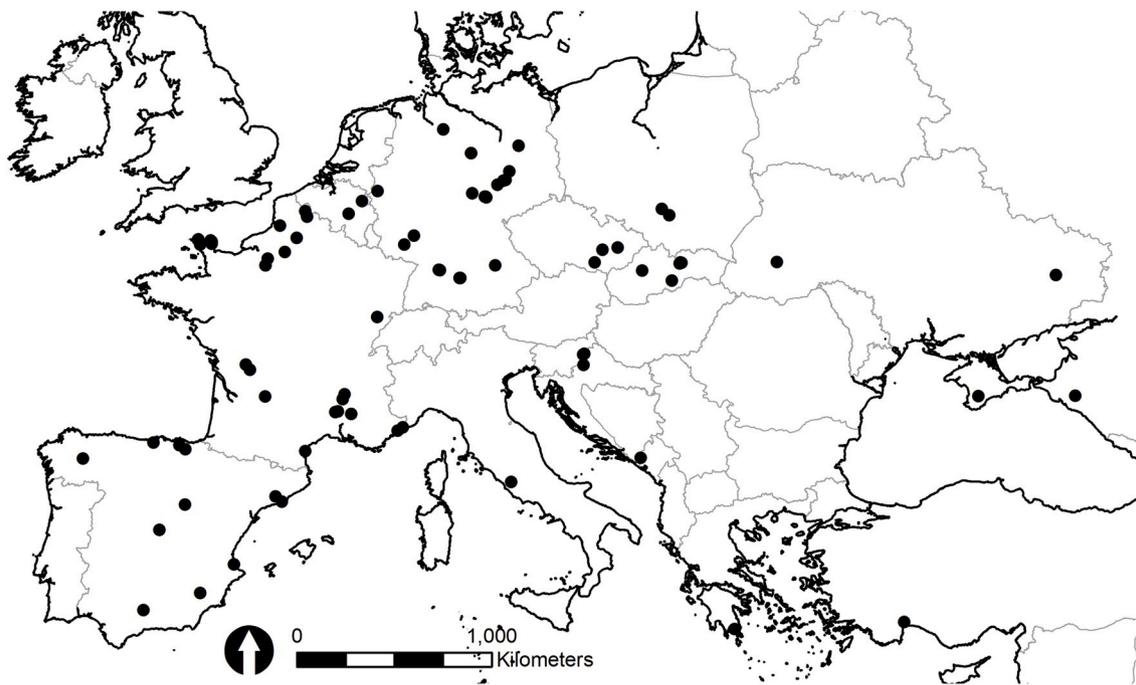


Fig. 1. Location of 85 sites with a component dating to MIS 5e (see Table 1 for site names and references).

especially in terms of chronological position and assignment strictly to MIS 5e require further testing and more precise radiometric dating.

Whatever the true chronological position of BMG XIV-XV Defleur and Desclaux conclude, based on 10 selected sites, that their “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” (Defleur and Desclaux,

2019:122). However, this assumption is not based on a summed probability distribution model of population nor any spatial analysis of the distribution of the Mousterian sites in region. Rather it is built on a visual comparison of the distribution of select sites dating to MIS 6 and MIS 4/3 sites. Their Figure 5 presents a non-exhaustive list of prehistoric sites (mostly stratified cave sites) from MIS 6 thru MIS 3 in southern France, which collectively plots ~92 sites, though no database or list of

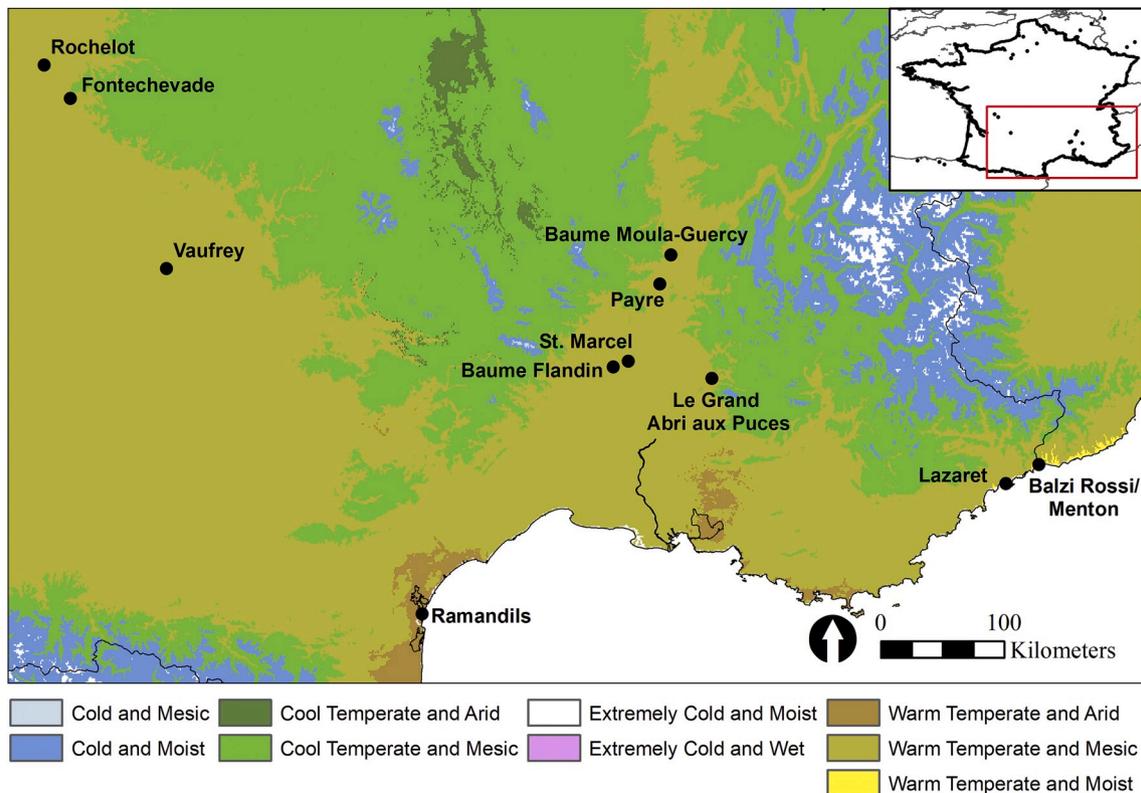


Fig. 2. Map of southern France with MIS 5e sites and Eemian paleoclimate zones.

sites is provided; therefore none of these maps are reproducible. These maps attempt to compare the spatial distribution of Neanderthal populations that have very different durations on the landscape, with ~15ky assigned to MIS 5e, ~70ky to MIS6, and ~50ky covering MIS4/3. These spatial and temporal scales are not easily comparable without some statistical manipulation of the data, though none of the data are presented.

In southern France, we identify ~10 sites with a cultural component dating to MIS 5e (Table 1 and Fig. 2). However, we are unable to perform a statistical comparison of Defleur and Desclaux's site data to ours. Proportionally there appear to be more than twice as many MIS 5e sites compared to their attribution of MIS6 sites. Based on this rudimentary comparison, one could conclude that the warmer Eemian period was particularly favorable to the expansion of Neanderthal populations across the region, with a rapidly growing population and expansion in the previously abandoned latitudes of northern Germany.

This anecdotal example is not robust, but could be tested using spatial analyses with a more exhaustive list of sites dating to MIS6 through 5 (or even 3). However, since the authors do not provide site dates, nor do they include climate/environmental data associated with these periods, their correlation between a warming climate and population collapse is not supported. Upon closer inspection, the data in fact may well support quite an opposite conclusion, with an expansion of the Neanderthal populations over the previous cold MIS6 phase.

3. Climate and biogeography

The MIS 5 climatic period spans roughly 50,000 years, whereas MIS 5e is far shorter spanning approximately 15,000 years. Defleur and Desclaux state that MIS 5e is warmer than the peak of the Holocene, therefore these temperatures serve as a diagnostic value when evaluating the presence of three species of extinct reptile identified in BMG Layer XV (*Testudo hermanni*, *Malpolon monspessulanus*, and *Rhinechis scalaris*). These reptiles are believed to prefer Mediterranean climates and are no longer found in the BMG area of the Soyons region. The authors note that the presence of these species indicates that the climate around the cave during the MIS 5e period was warmer and drier than at present, with the Mediterranean climate extending further north than the present day, following the Rhône Valley. The authors also note that Layer XIV contains the remains of *Testudo hermanni*, suggesting a relative stability of climatic conditions in the area throughout the duration of the Eemian and that the northern-most range of the Hermann tortoise is more than 100 km south of BMG.

The distribution of extinct species in a region may be correlated with the current or past distributions of a species, but the authors provide no evidence of this. Current environmental conditions in the Middle Rhône Valley are affected by a high degree of anthropogenic modification and are directly impacted by human activities related to deforestation, conversion of landscapes to pastures, and fire suppression; these anthropogenic processes have been at play since the beginning of the Holocene (Delhon et al., 2010) and could have impacted the distribution of these species. The past distribution of these reptiles in the more northern regions of their known Holocene distribution does not represent a direct proxy for a warmer phase for BMG XIV-XV, and the adaptive capabilities of the species to different and no-analog environments across the Holocene remains largely unknown. Additionally, the actual distribution of *Malpolon monspessulanus* does encompass slightly more northerly latitudes than BMG (Pottier et al., 2006). Focusing on Pleistocene data, *Rhinechis scalaris* remains have been recovered from a Middle Pleistocene sequence at the L'Igue des Rameaux site in the Tarn-et-Garonne area of France, far from Mediterranean climates and in a much more cool temperate Atlantic climatic context (Jeannot and Mein, 2016). *Rhinechis scalaris* is itself documented throughout the different climatic phases of the BMG sequence including Layers XIX, XVII, XVI attributed to the cold MIS6 phase, along with remains found in Layer VIII, in cold MIS4 conditions (Manzano, 2015).

A Pleistocene Atlantic distribution for *Testudo hermanni* is also documented at the site of Aven de la Fage, in Corrèze (Mourer et al., 1975) and in Fontéchevade in Charente (Cheylan, 1981; Hervet, 2000), both of which are located north of BMG and in a cooler Atlantic climate context. The Pleistocene distribution of these reptiles is not straight forward or indicative of a more Mediterranean climate, rather it corresponds to the phenotypic plasticity of these species to adapt to climates not directly comparable with their actual distribution (Geniez and Cheylan, 2012).

BMG XV also contains the remains of *Triturus cristatus*, *Rana temporaria* and *Pelobates fuscus*, which have a distribution indicative of continental and colder conditions (Manzano, 2015). The presence of these microfauna, which can inhabit no-analog cold and/or warm climates could indicate that the Middle Rhône Valley served as a natural north-south corridor recording Mediterranean influences well into southern France (Manzano, 2015). It may be the case that the reptile remains at BMG do not record the MIS 5e optimal warm period, rather one of the subsequent, and less warm, MIS 5 sub-stages. The lines denoting the approximate distribution over time of three thermophilous reptiles identified in level XV in Defleur and Desclaux's Figure 3 (2019) remain arbitrary and are not supported with any climatic or ecological data. Using gridded global climate model data, Nicholson (2017) recreated paleoclimate zones of western Eurasia which shows that BMG was located in a Warm Temperate and Mesic climate during MIS 5e as mentioned by Defleur and Desclaux (Fig. 2). However, Defleur and Desclaux's hand-drawn approximation of the geographic extent of the three extinct species is not based on any quantitative biogeographical analysis that attempts to accurately delineate where those warmer climate zones may have been located.

The question of the persistence of MIS6-adapted mammals and micromammals in Layers XIV-XV is particularly interesting, however their presence should not be used as a demonstration or definitive proof of a MIS 5e age for these layers, as the precise timing of these species' extinction is also unknown. The presence of *P. lenki*, *A. bursae* and *M. brecciensis* in Layers XIVa to XV is cited by Defleur and Desclaux as "not previously found in association in any late Pleistocene layers in Western Europe" (2019:116), however their distribution is known to exist at several localities post MIS 5, including more recent phases of the Upper Pleistocene (Chaline, 1970; Chaline, 1972; Defleur et al., 2001; Marquet, 1989). The presence of these species itself does not lead to an unambiguous and confident conclusion supporting a MIS 5e attribution of these layers.

4. Cannibalism

The debate over the evidence and meaning behind Neanderthal cannibalism has gone on for more than 150 years. In 1871, Carl Vogt argued that far from being a mark of savagery, one could infer that anthropophagy was commonly considered a sign of some degree of civilization (Vogt, 1871). The Baron de Lubac in 1873 noted that the evidence of Neanderthal cannibalism from the Grotte de Néron (a Mousterian cave site located less than 30 m from BMG) (Slimak, 2004) was likely "only by chance, and strange as this assertion may seem, the 'Cave Peoples' would not have been civilized enough to be cannibals" (de Lubac, 1873). The same may be true today, in that we still do not have a good understanding behind all of the behavioral mechanisms related to prehistoric cannibalism.

To begin, Defleur and Desclaux make a case for nutritional stress based on the presence of linear enamel hypoplasia (LEH) on teeth. The presence of LEH's, however, appear to be common throughout Neanderthal and AMH hunter-gatherer populations (Guatelli-Steinberg et al., 2014) and does not present definitive evidence of nutritional stress related to cannibalism.

Regarding the taphonomic evidence for cannibalism at BMG, Defleur and Desclaux note that there is a higher percentage of cut marks on Neanderthal remains (~50%) compared to those on red deer (*Cervus*

elaphus) remains (~26%) implying that the Neanderthals occupying these layers were especially careful when cutting up the Neanderthal corpses (Defleur et al., 1999; Valensi et al., 2012). These differences in the percent of cut marks between Neanderthal and red deer bones is remarkable as the remains from these two species were found in direct spatial association (Defleur et al., 1999). These differences could be interpreted in two divergent ways. If the activities in BMG Layer XV represent a nutritional cannibalism event, then the high prevalence of cut marks on Neanderthal remains may well be supported by Defleur and Desclaux's hypothesis, as it would reflect the need to exploit all available protein from the Neanderthal corpses, as well as all other procured fauna. However, "low utility" Neanderthal bones, such as metapodials, phalanges, clavicle, and mandible, record a high number of cut marks (~45%), fitting with the Burger et al. (2005) prey as patch model of bad nutritional times, while only 17% of the corresponding red deer remains exhibit similar cut mark frequencies, an indication that the group was not under nutritional stress. It is very possible that the Neanderthal and red deer remains were not defleshed during the same occupational event, as red deer remains were clearly not over processed.

The Neanderthal and red deer remains seem to have been processed in a specific manner and do not share a quantitative equivalence with other faunal remains. The "over-treatment" of Neanderthal remains is not documented elsewhere in Layer XV. Other artiodactyl and perissodactyl remains from the same layer are less abundant (but of comparable size with 97 remains, compared to 193 for *C. elaphus* and 120 Neanderthal remains). This diverse faunal assemblage includes the remains from at least 12 other species of medium- and large-size ungulates (*Capra*, *Capreolus*, *Rangifer*, *Equus*, *Megaloceros giganteus*, and *Bos*) that do not record comparable cut marks.

In a separate analysis of the faunal assemblage at BMG, Valensi et al. (2012) state that the high percentage of cut marks on Neanderthal remains indicates that great care was taken in cutting up the corpses; whereas Defleur and Desclaux suggest the opposite, that the high frequency of cut marks points to an "exacerbated need for protein". The fact that the associated ungulates were not treated as intensively, or carefully, as the Neanderthal corpses should be further explored. This pattern suggests that there could have been several occupational phases comprising Layer XV. There were likely short temporal differences between occupational phases when Neanderthals would have butchered ungulates for food and when the Neanderthal bodies were defleshed and disarticulated.

If Layer XV does reflect several hominin occupations then the scarcity of lithics also needs to be explained, as they do not support repeated occupations at the site. There are remarkably few lithic remains from Layer XV, totaling 227 lithic artifacts (>2.5 cm) which includes a limited number of retouched tools (n = 57) (Defleur, 2015). This lithic assemblage represents less than one tool for every two Neanderthal remains, or one tool for every 100 pieces of bone (from all species combined).

If the BMG Neanderthal corpses were defleshed and disarticulated for consumption then there should be distinct taphonomic signatures between the associated faunal and Neanderthal remains, though several lines of evidence to unravel these differences have gone unexplored. For instance, though Defleur et al., 's 1999 research shows images from a scan electron microscope (SEM), it does not appear that they investigate the micromorphology of the cut marks. A recent SEM analysis of cut marks on human remains at Gough's Cave site in the United Kingdom and the Lepenski Vir, Padina, and Vlasac sites in Serbia (Bello et al., 2016) attempt to determine the timing of cut marks based on their width, depth and opening angle of the cut mark and whether or not they were inflicted long after death. This type of analysis was also done by Garralda et al. (2005) to determine possible cannibalism practices at Combe-Grenal and Marillac (France). In this case, Garralda and colleagues propose that the cut marks were the result of "social/ritual" practices and not nutritional, and that there were potential funerary rituals that involved defleshing and dismemberment (Garralda et al., 2005). This type of analysis does not appear to have been done with the

BMG Neanderthal remains.

The possibility of dismemberment of corpses for secondary burial as described by Bello et al. (2016) should also be further explored. Bello and colleagues describe funerary practices that consist of the initial burial of dead bodies in the ground, followed by a period of decay, and finally the exhumation of remains and dismemberment for reburial or other ritual practices that have no relationship to caloric needs, a common case in ethnography. Because Defleur (2015) and Defleur et al. (1999) do not provide sufficient data and information for reanalysis, it is difficult to provide an alternative hypothesis other than the corpses may have been disarticulated for some ritualized purpose.

Finally, evaluating the nutritional content of different prey species has been one way of assessing the diet breadth of different human populations (Binford, 1978; Jones and Metcalfe, 1988; Lupo, 1998, 2006; Madrigal and Holt, 2002), and this line of evidence was recently explored by Cole (2017) who derived nutritional values for different hominins according to their body weight. Based on the caloric value of the six Neanderthal corpses at BMG (Cole, 2017), the amount of available calories to feed a Neanderthal group was low, especially given that of the six individuals only one is a large adult, one is a small adult, two are sub-adults, and two juveniles. The number of calories available would be nominal and would only feed a small Neanderthal population of 25 adult males for 1.13 days (Cole, 2017).

If fauna and Neanderthal remains from Layer XV were utilized in the same phase of occupation, the discrepancy in their respective exploitation indicates that this cannibalism event was likely not a nutritional episode. The treatment of the Neanderthal bodies related to the extraction of all soft tissues, including appendicular skeletal elements, points to a distinct treatment of the Neanderthal remains versus the associated fauna, a proxy that could be indicative of more complex cannibalistic practices, including the potential for ritualized treatment of the bodies, though the exact practice remains unknown (Fraye et al., 2006; Saladié and Rodríguez-Hidalgo, 2017; Yustos and de los Terreros, 2015). Taphonomic evidence of dismemberment of a corpse does not necessarily correlate with cannibalism events. Rather than a nutritional act, the dismemberment of the Neanderthal bodies may well be indicative of complex and ritualized social behaviors or territorial behavior that remains to be precisely documented among this still misunderstood population (Bahn, 1992; Carbonell et al., 2010; Conklin, 2001; Vilaca, 2000).

To some extent, Defleur and Desclaux neglect to discuss Neanderthal foraging during MIS 5e and the large body of literature that paints a different picture of food resources available to these populations. Richter (2016) clearly illustrates the relationship between Eemian Neanderthals hunting in forested regions with low-prey biomass versus hunting in open landscapes with high-prey biomass. Richter notes that even if encounter rates in forested areas with large-prey were low, because of a low Neanderthal population density, the impact of fewer prey items on the landscape should not affect human nutrition. Although herds of large-prey like mammoth, woolly rhino, reindeer and horse were not as abundant in forested areas, fauna such as *Bos primigenius*, *Capreolus capreolus*, *Cervus elaphus*, *Dama dama*, *Equus ferus*, and *Sus scrofa* (Gaudzinski-Windheuser and Kindler, 2012; Gaudzinski-Windheuser and Roebroeks, 2011; Gaudzinski, 2004; Rivals et al., 2009) were well adapted to these environments, likely providing a sufficient source of protein for a small Human population. In addition to large-prey, more evidence is being uncovered regarding the importance of plants in Neanderthal diets' (El Zaatari et al., 2016; Wenzel, 1998; Wenzel, 2007) as well as other small fauna (Cochard et al., 2012; Morin et al., 2019). With population estimates in the region estimated as ranging between 1000 and 12,000 (Briggs et al., 2009; Dennell et al., 2011; Green et al., 2006; Sørensen, 2011) throughout Europe, it seems unlikely that the landscape could not nutritionally support such small groups.

5. Conclusion

The evidence for nutritional cannibalism at BMG put forth by Defleur and Desclaux, which includes an important lack of Eemian-aged sites in western Eurasia, a warmer climate for Layer XV as evidenced by extinct reptiles, and taphonomic evidence on Neanderthal and other faunal remains, does not support the hypothesis of the authors and is at best tentative. Here, we have attempted to demonstrate that there are several more Eemian-aged sites in western Eurasia than mentioned by the authors, with as many as 85 sites representing Neanderthal populations across the regions, counteracting their inclusion of a mere 10. We have also addressed the issue of biostratigraphy for Layer XV, noting that the presence of the three extinct reptile species does not lead to the conclusion that Layer XV is attributable to MIS 5e, especially given the other radiometric dating issues with the said layers at the site. Finally, while we do not question the presence of the cut mark evidence on Neanderthal remains, we do question Defleur and Desclaux's hypothesis that it represents a nutritional cannibalism event or even the result of cannibalistic practices *sensu lato*. Given that the frequency of cut marks on low utility elements is not equivalent between Neanderthal and faunal remains, the dismemberment of Neanderthal corpses may be the result of more complex cultural rites that archaeologists have yet to understand and/or document. Furthermore, given that the total Neanderthal population on the landscape was quite low, these widespread groups were thus likely to have been well adapted to hunting forested prey-species (as well as gathering and collecting), and with their overall feeble numbers, gaining access to adequate game to meet their caloric and nutritional needs, was not at all likely an issue. The evidence presented by Defleur and Desclaux, while interesting, is far from conclusive and unfortunately uses data that, in themselves, do not validate the authors hypothesis of Neanderthal cannibalism at BMG.

Declaration of competing interest

We, Ludovic Slimak and Christopher Nicholson, certify that all authors have seen and approved the final version of the manuscript being submitted. The article is the authors' original work, and hasn't received prior publication and isn't under consideration for publication elsewhere.

Furthermore, we declare that there is no financial/personal interest or belief that could affect our objectivity.

Acknowledgements

We would like to thank Rob Hope and Sally Starkey for their input and valuable suggestions.

References

- Adler, D., Prindiville, T., Conard, N.J., 2003. Patterns of spatial organization and land use during the Eemian interglacial in the Rhineland: new data for Wallertheim, Germany. *Eurasian PreHistory* 1, 25–78.
- Álvarez, X.R., de Lombera Hermida, A., Valcarlos, R.F., Fernández, T.L., 2011. The Upper Pleistocene Site of Cova Eirós (Triacastela, Lugo, Galicia), to the West of Spanish Cantabria: the Palaeolithic Settlement of Galicia. *British Archaeological Reports (BAR)*, Archaeopress Oxford, pp. 123–132.
- Antoine, P., 2012. First evidence of Human occupation during the Eemian interglacial (MIS 5e) in Northern France at Caours (Somme Basin). *Quat. Int.* 279–280, 21.
- Arriolabengoa, M., Iriarte, E., Aranburu, A., Yusta, I., Arnold, L.J., Demuro, M., Arrizabalaga, A., 2018. Reconstructing the sedimentary history of Lezetxiki II cave (Basque Country, northern Iberian Peninsula) using micromorphological analysis. *Sediment. Geol.* 372, 96–111.
- Bahn, P., 1992. Cannibalism or Ritual Dismemberment. *Cambridge encyclopedia of human evolution*, p. 330.
- Barroso Ruiz, C., Botella Ortega, D., Caparrós, M., Moigne, A.M., Celiberti, V., Testu, A., Barsky, D., Nötter, O., Riquelme Cantal, J.A., Rodríguez, M.P., Carretero León, M.I., Monge Gómez, G., Khatib, S., Saos, T., Gregoire, S., Bailón, S., García Solano, J.A., Cabral Mesa, A.L., Djerrab, A., George Hedley, I., Abdessadok, S., Batalla Llasat, G., Astier, N., Bertin, L., Boulbes, N., Cauche, D., Filoux, A., Hanquet, C., Milizica, C., Moutoussamy, J., Rossoni, E., Verdú Bermejo, L., de Lumley, H., 2011. The Cueva del Angel (Lucena, Spain): an Acheulean hunters habitat in the South of the Iberian Peninsula. *Quat. Int.* 243, 105–126.
- Bello, S.M., Wallduck, R., Dimitrijević, V., Živaljević, I., Stringer, C.B., 2016. Cannibalism versus funerary defleshing and disarticulation after a period of decay: comparisons of bone modifications from four prehistoric sites. *Am. J. Phys. Anthropol.* 161, 722–743.
- Binford, L.R., 1978. *Nunamiut: Ethnoarchaeology*. Academic Press, New York.
- Bocquet-Appel, J.-P., Tuffreau, A., 2009. Technological responses of Neanderthals to macroclimatic variations (240,000–40,000 BP). *Hum. Biol.* 81, 287–307.
- Bosinski, G., 1967. Die mittelpaläolithischen Funde im westlichen Mitteleuropa, Böhlau.
- Briggs, A.W., Good, J.M., Green, R.E., Krause, J., Maricic, T., Stenzel, U., Lalueza-Fox, C., Rudan, P., Brajković, D., Kučan, Ž., Gusić, I., Schmitz, R., Doronichev, V.B., Golovanova, L.V., de la Rasilga, M., Fortea, J., Rosas, A., Pääbo, S., 2009. Targeted retrieval and analysis of five neandertal mtDNA genomes. *Science* 325, 318–321.
- Burger, O., Hamilton, M.J., Walker, R., 2005. The prey as patch model: optimal handling of resources with diminishing returns. *J. Archaeol. Sci.* 32, 1147–1158.
- Carbonell, E., Cáceres, I., Lozano, M., Saladié, P., Rosell, J., Lorenzo, C., Vallverdú, J., Huguet, R., Canals, A., Bermúdez de Castro, J.M., 2010. Cultural cannibalism as a paleoeconomic system in the European lower Pleistocene: the case of level TD6 of gran dolina (sierra de Atapuerca, Burgos, Spain). *Curr. Anthropol.* 51, 539–549.
- Chabai, V., Richter, J., Uthmeier, T., 2005. Uthmeier, 2005. *Kabazi II: Last Interglacial Occupation, Environment and Subsistence: Paleolithic Sites of Crimea*, vol. 1 (Simferopol, Cologne).
- Chaline, J., 1970. *Pliomys lenki, forme relique du Pléistocène supérieur de la grotte de Lezetxiki (Guipuzcoa, Espagne)*. *Munibe* 22, 43–49.
- Chaline, J., 1972. Les rongeurs du Wurmien II de la grotte de l'Hortus (Valfrances, Herault). *Etud. Quat.* 1, 233–240.
- Cheylin, M., 1981. *Biologie et écologie de la tortue d'Hermann Testudo hermanni, Gmelin 1789: contribution de l'espèce à la connaissance des climats quaternaires de la France*, Ecole pratique des hautes études.
- Cliquet, D., Mercier, N., Valladas, H., Froget, L., Michel, D., Vliet-Lanoë, B.V., Vilgrain, G., 2003. Apport de la thermoluminescence sur silex chauffés à la chronologie de site paléolithiques de Normandie : nouvelles données et interprétations [Thermoluminescence dating of burnt flints from Palaeolithic sites of Normandy recent advances]. *Quaternaire*, pp. 51–64.
- Cliquet, D., Lautridou, J.-P., Antoine, P., Lamothe, M., Leroyer, M., Limondin-Lozouet, N., Mercier, N., 2009. La séquence loessique de Saint-Pierre-lès-Elbeuf (Normandie, France): nouvelles données archéologiques, géochronologiques et paléontologiques. *Quaternaire*. *Revue de l'Association française pour l'étude du Quaternaire* 20, 321–343.
- Cochard, D., Brugal, J.-P., Morin, E., Meignen, L., 2012. Evidence of small fast game exploitation in the middle paleolithic of les canalettes aveyron, France. *Quat. Int.* 264, 32–51.
- Cole, J., 2017. Assessing the calorific significance of episodes of human cannibalism in the Palaeolithic. *Sci. Rep.* 7, 44707.
- Conard, N.J., 1990. Laminar lithic assemblages from the last interglacial complex in northwestern Europe. *J. Anthropol. Res.* 46, 243–262.
- Conklin, B.A., 2001. *Consuming Grief: Compassionate Cannibalism in an Amazonian Society*. University of Texas Press.
- Coutard, S., Cliquet, D., 2005. Chronostratigraphie des formations pléistocènes et peuplement paléolithique en contexte littoral : le Val de Saire (Normandie). *Bull. Soc. Prehist. Fr.* 477–499.
- Cregut-Bonnaire, 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, 227–248.
- Cyrek, K., Sudol, M., Czyżewski, Ł., Osipowicz, G., Grelowska, M., 2014. Middle palaeolithic cultural levels from middle and late Pleistocene sediments of biśnik cave, Poland. *Quat. Int.* 326–327, 20–63.
- Defleur, A., 2015. Les industries lithiques moustériennes de la Baume moula-guercy (Soyons, ardèche). *Fouilles 1993–1999*. *L'Anthropologie* 119, 170–253.
- Defleur, A., Desclaux, E., 2019. Impact of the last interglacial climate change on ecosystems and Neanderthals behavior at Baume Moula-Guercy, Ardèche, France. *J. Archaeol. Sci.* 104, 114–124.
- Defleur, A., White, T., Valensi, P., Slimak, L., Cregut-Bonnaire, É., 1999. Neanderthal cannibalism at moula-guercy, Ardèche, France. *Science* 286, 128–131.
- Defleur, A., Cregut-Bonnaire, É., Desclaux, E., Thion, M., 2001. Présentation paléoenvironnementale du remplissage de la Baume Moula-Guercy à Soyons (Ardèche) : implications paléoclimatiques et chronologiques. *L'Anthropologie* 105, 369–408.
- Delhon, C., Thiébaud, S., Brochier, J.L., Berger, J.F., 2010. Dynamiques de végétation au Tardiglaciaire et à l'Holocène ancien en moyenne vallée du Rhône d'après les données anthracologiques. *Quaternaire*. *Revue de l'Association française pour l'étude du Quaternaire* 21, 281–293.
- Dennell, R.W., Martín-Torres, M., Bermúdez de Castro, J.M., 2011. Hominin variability, climatic instability and population demography in Middle Pleistocene Europe. *Quat. Sci. Rev.* 30, 1511–1524.
- El Zaatari, S., Grine, F.E., Ungar, P.S., Hublin, J.-J., 2016. Neandertal versus modern human dietary responses to climatic fluctuations. *PLoS One* 11, e0153277.
- Facorellis, Y., Karkanas, P., Higham, T., Brock, F., Ntinou, M., Kyparissi-Apostolika, N., 2013. Interpreting radiocarbon dates from the Paleolithic layers of Theopetra cave in Thessaly, Greece. *Radiocarbon* 55, 1432–1442.
- Falgueres, C., Yokoyama, Y., Arrizabalaga, A., 2005. La Geocronología del yacimiento pleistocénico de Lezetxiki (Arrasate, País Vasco). *Crítica de las dataciones existentes y algunas nuevas aportaciones*. *Munibe* 57, 93–106.
- Fernández Peris, J., González, V.B., Blasco, R., Cuartero, F., Fluck, H., Sañudo, P., Verdascó, C., 2012. The earliest evidence of hearths in southern Europe: the case of bolomor cave (valencia, Spain). *Quat. Int.* 247, 267–277.

- Frayer, D.W., Orschiedt, J., Cook, J., Russell, M.D., Radovčić, J., 2006. Krapina 3: Cut Marks and Ritual Behavior?.
- Garralda, M., Giacobini, G., Vandermeersch, B., 2005. Nenderthal cutmarks: combe-grenal and marillac (France): a SEM analysis. *Anthropologie* 43, 189–198.
- Gaudzinski, S., 2004. A matter of high resolution? The Eemian Interglacial (OIS 5e) in north-central Europe and Middle Palaeolithic subsistence. *Int. J. Osteoarchaeol.* 14, 201–211.
- Gaudzinski-Windheuser, S., Kindler, L., 2012. Research perspectives for the study of Neandertal subsistence strategies based on the analysis of archaeozoological assemblages. *Quat. Int.* 247, 59–68.
- Gaudzinski-Windheuser, S., Roebroeks, W., 2011. On Neandertal subsistence in last interglacial forested environments in northern Europe. In: Conard, N.J., Richter, J. (Eds.), *Neandertal Lifeways, Subsistence and Technology: One Hundred Fifty Years of Neandertal Study, Vertebrate Paleobiology and Paleoanthropology*. Springer, New York, pp. 61–70.
- Gautier, C., 1989. Technologie de l'industrie Moustérienne de Roisel (Somme), *Paléolithique et Mésolithique du Nord de la France: nouvelles recherches*. Université des Sciences et des Technologies de Lille Flandre-Artois, Lille, France, pp. 61–68.
- Geniez, P., Cheylan, M., 2012. Les amphibiens et les reptiles du Languedoc-Roussillon et régions limitrophes: atlas biogéographique. *Biotope*.
- Gibbons, A., 1997. Archaeologists rediscover cannibals. *Science* 277, 635–637.
- Golovanova, L.V., Doronichev, V.B., 2003. The middle paleolithic of the caucasus. *J. World PreHistory* 17, 71–140.
- Goval, E., Hérison, D., Locht, J.-L., Coudenneau, A., 2016. Levallois points and triangular flakes during the Middle Palaeolithic in northwestern Europe: considerations on the status of these pieces in the Neandertal hunting toolkit in northern France. *Quat. Int.* 411, 216–232.
- Grandal-d'Anglade, A., 1993. El Oso de las cavernas en Galicia, el yacimiento de Cova Eirós. *Ser. Nova Terra* 8, 1–285.
- Green, R.E., Krause, J., Ptak, S.E., Briggs, A.W., Ronan, M.T., Simons, J.F., Du, L., Egholm, M., Rothberg, J.M., Paunovic, M., Pääbo, S., 2006. Analysis of one million base pairs of Neandertal DNA. *Nature* 444, 330–336.
- Guatelli-Steinberg, D., Stinespring-Harris, A., Reid, D.J., Larsen, C.S., Hutchinson, D.L., Smith, T.M., 2014. Chronology of linear enamel hypoplasia formation in the Krapina Neandertals. *PaleoAnthropology* 431, 445.
- Harvati, K., Panagopoulou, E., Runnels, C., 2009. The paleoanthropology of Greece. *Evol. Anthropol. Issues, News, Rev.* 18, 131–143.
- Hernandez, M., Mercier, N., Rigaud, J.-P., Texier, J.-P., Delpech, F., 2014. A revised chronology for the Grotte Vaufray (Dordogne, France) based on TT-OSL dating of sedimentary quartz. *J. Hum. Evol.* 75, 53–63.
- Hervet, S., 2000. Tortues du Quaternaire de France: critères de détermination, répartitions chronologique et géographique. *Mesogee* 58, 3–47.
- Howell, F.C., Butzer, K.W., Freeman, L.G., Klein, R.G., 1991. Observations on the Acheulean occupation site of Ambrona (Soria Province, Spain) with particular reference to recent investigations (1980–1983) and the lower occupation. In: MAINZ, Y.o.t.R.-G.C.M. (Ed.), *Zentralmuseum, Romisch-Germanisches, Mainz, Germany*.
- Hurlbut, S.A., 2000. The taphonomy of cannibalism: a review of anthropogenic bone modification in the American Southwest. *Int. J. Osteoarchaeol.* 10, 4–26.
- Jeannot, M., Mein, P., 2016. Les Muridae (Mammalia, Rodentia) du Pléistocène moyen de l'Igüe des Rameaux (Tarn-et-Garonne, France). *PALEO. Revue d'archéologie préhistorique* 177–205.
- Jones, K.T., Metcalfe, D., 1988. Bare bones archaeology: bone marrow indices and efficiency. *J. Archaeol. Sci.* 15, 415–423.
- Locht, J.-L., Hérison, D., Goval, E., Cliquet, D., Huet, B., Coutard, S., Antoine, P., Feray, P., 2016. Timescales, space and culture during the Middle Palaeolithic in northwestern France. *Quat. Int.* 411 (A), 129–148.
- Lupo, K.D., 1998. Experimentally derived extraction rates for marrow: implications for body Part Exploitation strategies of plio-pleistocene hominid scavengers. *J. Archaeol. Sci.* 25, 657–675.
- Lupo, K.D., 2006. What explains the carcass field processing and transport decisions of contemporary hunter-gatherers? Measures of economic anatomy and zooarchaeological skeletal Part Representation. *J. Archaeol. Method Theory* 13, 19–66.
- Madrigal, T.C., Holt, J.Z., 2002. White-tailed deer meat and marrow return rates and their application to eastern woodlands archaeology. *Am. Antiq.* 67, 745–759.
- Manzano, A., 2015. Les amphibiens et les reptiles des sites du Pléistocène moyen et supérieur du pourtour méditerranéen (Caune de l'Arago, grotte du Lazaret, Baume Moula-Guercy). *Etude d'herpétofaunes et reconstitutions paléoclimatiques et paléoenvironnementales*.
- Markova, A., Puzachenko, A., 2018. Preliminary analysis of European small mammal faunas of the eemian interglacial: species composition and species diversity at a regional scale. *Quaternary* 1, 9.
- Marlar, R.A., Leonard, B.L., Billman, B.R., Lambert, P.M., Marlar, J.E., 2000. Biochemical evidence of cannibalism at a prehistoric Puebloan site in southwestern Colorado. *Nature* 407, 74–78.
- Marquet, J.-C., 1989. Paléoenvironnement et chronologie des sites du domaine atlantique français d'âge Pléistocène moyen et supérieur d'après l'étude des rongeurs, Dijon.
- McPherron, S.P., Dibble, H.L., Chiotti, L., Chase, P., Debénath, A., Farrand, W.R., 2012. Processus de formation des sites et concept du Tayacien : l'exemple de Fontéchevade (Charente, France). *L'Anthropologie* 116, 321–347.
- Moles, V., Boutié, P., 2009. Contribution to the definition of middle paleolithic micro-production. The lithic assemblage from ramandils cave (port-La nouvelle, aude, France). *L'Anthropologie* 113, 356–380.
- Morin, E., Meier, J., El Guennoui, K., Moigne, A.-M., Lebreton, L., Rusch, L., Valensi, P., Conolly, J., Cochard, D., 2019. New evidence of broader diets for archaic Homo populations in the northwestern Mediterranean. *Sci. Adv.* 5, eaav9106.
- Mourer, C., Balleisio, R., Beden, M., Bouchud, J., Chaline, J., David, L., Guérin, C., Huguency, M., Jammot, D., Mein, P., 1975. In: *Conclusions générales sur les faunes de l'Aven 1 des Abîmes de la Fage à Noailles (Corrèze)*, vol. 13. Publications du musée des Confluences, pp. 123–129.
- Musil, R., 2010. The environment of the middle palaeolithic sites in central and eastern Europe. *Acta Universitatis Wratislaviensis, Studia Archaeologica* 41, 121-179-121-179.
- Neruda, P., 2012. Impact of raw materials on the interpretation of Middle Palaeolithic assemblages. *Anthropologie et Préhistoire* 50, 345–360.
- Neruda, P., Nerudová, Z., 2010. Moravský Krumlov IV—a new multilayer palaeolithic site in moravia. *Archaol. Korresp.* 40, 155–174.
- Nicholson, C.M., 2017. Eemian paleoclimate zones and Neandertal landscape-use: a GIS model of settlement patterning during the last interglacial. *Quat. Int.* 438, 144–157.
- Pottier, G., Vacher, J.-P., Savine, N., 2006. Interrogations sur l'existence contemporaine de la Couleuvre de Montpellier Malpolon monspessulanus (Hermann, 1804) (Reptilia, Colubridae) en région Midi-Pyrénées (France). *Bull. Soc. Herp. Fr* 120, 33–56.
- Richter, J., 2005. Hasty foragers: the crimea island and Europe during the last interglacial. In: Chabai, V., Richter, J., Uthmeier, T. (Eds.), *Kabazi II: Last Interglacial Occupation, Environment & Subsistence*. University of Cologne, Cologne, pp. 275–285.
- Richter, J., 2008. Neandertals in their landscape. In: Demars, B., Otte, M. (Eds.), *Neandertals in Europe. Proceedings of the International Conference*. ATVATVCA, Tongeren, pp. 17–32.
- Richter, J., 2016. Leave at the height of the party: a critical review of the Middle Paleolithic in Western Central Europe from its beginnings to its rapid decline. *Quat. Int.* 411, 107–128.
- Rios-Garaizar, J., Maidagan, D.G., Gómez-Olivencia, A., Avilés, E.I., 2013. Archaeological research in arlanpe cave (Lemoa, biscay). *La cueva de Arlanpe (Lemoa)* 5.
- Rivals, F., Moncel, M.-H., Patou-Mathis, M., 2009. Seasonality and intra-site variation of Neandertal occupations in the Middle Palaeolithic locality of Payre (Ardèche, France) using dental wear analyses. *J. Archaeol. Sci.* 36, 1070–1078.
- Saladié, P., Rodríguez-Hidalgo, A., 2017. Archaeological evidence for cannibalism in prehistoric western Europe: from Homo antecessor to the bronze age. *J. Archaeol. Method Theory* 24, 1034–1071.
- Sier, M.J., Parés, 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. *Quat. Int.* 357, 149–157.
- Slimak, L., 2004. *La grotte de Néron à Soyons (Ardèche)*, 26ème Congrès préhistorique de France " Congrès du Centenaire", Société préhistorique française, pp. 165–175.
- Slimak, L., Lewis, J.E., Crégut-Bonnoure, E., Metz, L., Ollivier, V., André, P., Chrzavetz, J., Giraud, Y., Jeannot, M., Magnin, F., 2010. Le Grand Abri aux Puces, a Mousterian site from the Last Interglacial: paleogeography, paleoenvironment, and new excavation results. *J. Archaeol. Sci.* 37, 2747–2761.
- Sonier de Lubac, J., 1873. L'homme au premier age des cavernes. *Epoque du Moustiers. Revue de France* 1873, 841-562.
- Sørensen, B., 2011. Demography and the extinction of european Neandertals. *J. Anthropol. Archaeol.* 30, 17–29.
- Speelers, B., 2000. The relevance of the Eemian for the study of the palaeolithic occupation of Europe. *Neth. J. Geosci.* 7, 283–290.
- Stonking, M., 2003. Widespread prehistoric human cannibalism: easier to swallow? *Trends Ecol. Evol.* 18, 489–490.
- Swinen, C., Locht, J.-L., Antoine, P., 1996. Le gisement moustérien D'auteuil (Oise). *Bull. Soc. Prehist. Fr.* 93, 173–181.
- Tuffreau, A., Révillon, S., Somme, J., Aitken, M., Huxtable, J., LEROI-GOURHAN, A., 1985. Le gisement paléolithique moyen de Seclin (Nord, France). *Archaol. Korresp.* 15, 131–138.
- Valensi, P., 2000. The archaeozoology of lazaret cave (nice, France). *Int. J. Osteoarchaeol.* 10, 357–367.
- Valensi, P., Crégut-Bonnoure, E., Defleur, A., 2012. Archaeozoological data from the Mousterian level from Moula-Guercy (Ardèche, France) bearing cannibalised Neandertal remains. *Quat. Int.* 252, 48–55.
- van Kolfschoten, T., 2002. The Eemian mammal fauna of the northwestern and central European continent. In: Tuffreau, A., Roebroeks, W. (Eds.), *Le Dernier Interglacière et les occupations humaines du Paléolithique moyen*. CERP, Lille, pp. 21–30.
- Vanmonfort, B., Vermeersch, P.M., Groenedijk, A.J., Meijs, E.P.M., De Warrimont, J.P., Gullentops, F., 1998. The middle palaeolithic site of hezerwater at veldwezelt, Belgian limburg. *Notae Praehistoricae* 18, 5–11.
- Verleijsonk, B., 2018. Early Hominin Activity in Waziers. Reconstructing the Environment of the Somme Valley, France during the Eemian Interglacial.
- Vilaca, A., 2000. Relations between funerary cannibalism and warfare cannibalism: the question of predation. *Ethnos* 65, 83–106.
- Villa, P., 1992. Cannibalism in prehistoric Europe. *Evol. Anthropol. Issues News Rev.* 1, 93–104.
- Vogt, C., 1871. Anthropophagie et sacrifices humains. In: *Congrès International d'anthropologie et d'archéologie préhistorique*, (Session) Bologne, pp. 295–328.
- Villa, P., Soto, E., Pérez-González, A., Mora, R., 2001. Taphonomy at ambrona: new perspectives. In: Cavarretta, G., Gioia, P., Mussi, M., Palombo, M.R. (Eds.), *Proceedings of the First International Congress, the World of Elephants*. Consiglio Nazionale delle Ricerche, Rome, pp. 617–619.

- Walker, M., Gibert, J., Sánchez, F., Lombardi, A., SERRANO, J., Eastham, A., Ribot, F., Arribas, A., Sánchez-Cabeza, J., GARCÍA-ORELLANA, J., 1998. Two SE Spanish middle palaeolithic sites with Neanderthal remains: sima de las Palomas del Cabezo Gordo and Cueva Negra del Estrecho del Río Quípar (Murcia province). *Internet Archaeol.* 5.
- Weber, T., Litt, T., Schäfer, D., 1996. Neue Untersuchungen zum älteren paläolithikum in mitteleuropa. *Terra and Prehistoria*—Beiträge zur Ur-und Frühgeschichte Mitteleuropas 9, 13–19.
- Weißmüller, W., 1995. Sesselfelsgrötte II, Die Silexartefakte der Unteren Schichten der Sesselfelsgrötte. Ein Beitrag zum Problem des Moustérien. *Quartär-Bibliothek* 6.
- Wenzel, S., 1998. Die Funde aus dem Travertin von Stuttgart-Untertürkheim und die Archäologie der letzten Warmzeit in Mitteleuropa, Habelt.
- Wenzel, S., 2007. Neanderthal presence and behaviour in central and northwestern Europe during MIS5e. In: Sirocko, F., Clausen, M., Sanches Goni, M.F., T, L. (Eds.), *The Climate of Past Interglacials*. Oxford University Press, Oxford, pp. 173–193.
- White, T.D., 2001. Once were CANNIBALS. *Sci. Am.* 285, 58–65.
- Willmes, M., Grün, R., Douka, K., Michel, V., Armstrong, R.A., Benson, A., Crégut-Bonnoure, E., Desclaux, E., Fang, F., Kinsley, L., Saos, T., Defleur, A.R., 2016. A comprehensive chronology of the Neanderthal site Moula-Guercy, Ardèche, France. *J. Archaeol. Sci.: Report* 9, 309–319.
- Yustos, M., de los Terreros, J.Y.S., 2015. Cannibalism in the neanderthal world: an exhaustive revision. *J. Taphonomy* 13, 33–52.
- Łanczont, M., Fedorowicz, S., Kusiak, S., Boguckij, A., Sytnyk, O., 2009. TL age of loess deposits in the yezupil I palaeolithic site on the upper dniester river (Ukraine). *Geologija* 51, 86–96.