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DENTAL MORPHOLOGY AND DIET USE-WEAR OF THE BELGIAN NEOLITHIC: A
STUDY OF MASS CAVE BURIALS IN THE MEUSE RIVER BASIN

by

KATHERINE E. SHERRILL

Under the Direction of Frank L'Engle Williams, Ph.D.

ABSTRACT

In order to reconstruct relationships between cave burials in the Meuse River Basin of Belgium during the Middle to Terminal Neolithic, dental remains from five sites are compared. Because molar morphology and the presence or absence of nonadaptive dental traits are highly heritable and biologically neutral, they can potentially yield clues as to the chronological and spatial relationships between sites and the variation within these collective burials. Dental microwear is brought to bear on the dietary proclivities of the individuals represented in the caves and is compared to the variation in molar morphology.

INDEX WORDS: dental microwear, molar; Neolithic, Europe, ASUDAS, cave

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by

KATHERINE E. SHERRILL

A Thesis Submitted in Partial Fulfillment of the Requirements for the Degree of

Master of Arts

in the College of Arts and Sciences

Georgia State University

2018

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Katherine Elizabeth Sherrill
2018

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STUDY OF MASS CAVE BURIALS IN THE MEUSE RIVER BASIN

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May 2018

DEDICATION

I dedicate this thesis to the memory of my grandmother, my *Nagymama*, Katalin Barath Ertavi. The determination and perseverance you showed throughout your life were a beacon of hope for me in moments of fear, guiding me back to confidence when I doubted myself. You once told me, “learn as much as you possibly can; it’s the one thing that can *never* be taken from you.” Well, I took your advice. This is for you.

Ezt a disszertációt a nagymamám, Ertavy Barath Katalin emlékére adom. Az az elszántság és kitartás, amelyet egész életemben megmutáltál, reményt hozott a szívemhez, és visszavezetett a bizalomra, amikor kételkedtem magamban. Egyszer, kislánykoromban, azt mondtad nekem: "tanulj annyit, amennyit csak tudsz; ez az egyetlen dolog, amit senki soha nem vehet el tőled." Nos, vettem a tanácsodat. Ez a tied.

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TABLE OF CONTENTS

ACKNOWLEDGEMENTS	V
LIST OF TABLES	IX
LIST OF FIGURES	X
LIST OF ABBREVIATIONS	XI
1 INTRODUCTION	1
1.1 The Wave of Advance Model	5
1.2 Hypotheses and Research Design	8
<i>1.2.1 Samples.....</i>	<i>9</i>
<i>1.2.2 Mortuary Context and Material Culture.....</i>	<i>10</i>
1.3 Contextualizing Subsistence and Diet in the Meuse Region.....	12
<i>1.3.1 Stable and Radiogenic Isotopes</i>	<i>12</i>
<i>1.3.2 Zooarchaeology and Faunal Remains</i>	<i>13</i>
<i>1.3.3 Microbotanical Remains.....</i>	<i>14</i>
2 METHODS.....	15
2.1 Dental Microwear Analysis	15
<i>2.1.1 Statistical Analyses of Dental Microwear Traits</i>	<i>19</i>
2.2 Scoring Nonmetric Dental Traits.....	19
3 RESULTS	21
3.1 Dental Microwear Analysis	21

3.1.1	<i>Intercemetery Comparisons</i>	22
3.1.2	<i>Intracemetery Comparisons</i>	25
3.2	Scoring Nonmetric Dental Traits	26
3.2.1	<i>Frequency</i>	26
3.2.2	<i>Rates of Expression</i>	30
4	DISCUSSION AND CONCLUSIONS	33
4.1	Dental Microwear	33
4.2	Nonmetric Dental Traits	34
	REFERENCES	37
	APPENDICES	44
A.1:	Complete List of Individuals (n=158)	44
A.1.1:	<i>Sclaigneaux (n=56)</i>	44
A.1.2:	<i>Hastière Caverne M (n=24)</i>	44
A.1.3:	<i>Hastière Trou Garçon C (n=6)</i>	44
A.1.4:	<i>Bois Madame (n=34)</i>	45
A.1.5:	<i>Maurenne Caverne de la Cave (n=38)</i>	45
A.2:	Molars Used in Dental Microwear Analysis	45
A.2.1:	<i>Sclaigneaux (n=18)</i>	45
A.2.2:	<i>Hastière Caverne M (n=15)</i>	46
A.2.3:	<i>Hastière Trou Garçon C (n=2)</i>	46

<i>A.2.4: Bois Madame (n=15)</i>	46
<i>A.2.5: Maurenne Caverne de la Cave (n=16)</i>	46
A.3 Molars Used in Nonmetric Dental Trait Scoring	46
<i>A.3.1 Sclaigneaux (n=46)</i>	46
<i>A.3.2: Hastière Caverne M (n=29)</i>	47
<i>A.3.3: Hastière Trou Garçon C (n=2)</i>	47
<i>A.3.4: Bois Madame (n=33)</i>	47
<i>A.3.5: Maurenne Caverne de la Cave (n=40)</i>	47

LIST OF TABLES

Table 1 Number of individuals identified from each burial site	9
Table 2 Nonadaptive dental traits scored.....	21
Table 3 One-Way ANOVA with Tukey's Post-Hoc Test	22
Table 4 Jackknife classification rates	25
Table 5 Mandibular trait mean frequencies	27
Table 6 Maxillary mean trait frequencies	29

LIST OF FIGURES

Figure 1 Radiocarbon dates (Bronk-Ramsey, et al. 2002).....	3
Figure 2 Meuse river rockshelters.....	4
Figure 3 Site locations; 01: Hastière (Caverne M, Trou Garçon C, Maurenne Caverne de la Cave), 02: Bois Madame, 03: Sclaigneaux.....	4
Figure 4 Wave of advance model after Ammerman and Cavalli-Sforza (1984, 59).....	7
Figure 5 Resin cast (left) and photograph (right) of Maurenne Caverne de la Cave 8URM1-M210	
Figure 6 Dental microscopy indicating fine scratches and small pits.....	18
Figure 7 Discriminant Function Analysis; 95% confidence ellipses around group centroids.....	23
Figure 8 Cluster analysis.....	24
Figure 9 Mandibular trait frequency.....	27
Figure 10 Mandibular groove pattern.....	28
Figure 11 Maxillary trait frequency.....	30
Figure 12 Maxillary trait expression 1-3.....	31
Figure 13 Maxillary trait expression 4-7.....	31
Figure 14 Mandibular trait expression 1-3.....	32
Figure 15 Mandibular trait expression 4-7.....	33

LIST OF ABBREVIATIONS

Specimen identification key:

L: Lower (Mandibular)

U: Upper (Maxillary)

R: Right

L: Left

P: Premolar

M: Molar

dm: Deciduous Molar

Ex: 43(ID no.) L(lower) L(left) dm(deciduous molar) 1 = 43LLdm1

1 INTRODUCTION

The practice of farming in Western Europe slowly replaced earlier subsistence strategies of hunting and gathering, likely having filtered in from the east after the retreat of the Würm glaciation (Marine Isotope Stage 2) approximately 12,000 years BP. As the megafauna that had sustained Paleolithic European foraging populations lost their niche habitat, their dwindling populations could no longer provide the nutritional and caloric intake that foraging necessitated. As the ecosystem changed around them, humans did what they do best – they changed the environment to suit their needs. Neolithic farmers typically lived in small communities and depended considerably on locally available foods and game. Relationships among these small-scale farmers is inferred from shared pottery styles and tool technology.

Though agriculture replaced their earlier subsistence traditions, some vestiges of the previous era persisted throughout northern Atlantic Europe. Throughout the Neolithic, farmers inhabiting modern-day Belgium continued to make use of the wealth of natural caves and caverns their landscape offered as burial grounds; many of them were in continued usage for centuries. This project examines five such sites, located in Wallonia, central Belgium: Sclaigneaux, Hastière Caverne M, Hastière Trou Garçon C, Hastière Maurenne Caverne de la Cave and Bois Madame (Figures 2-3). All of these cave burials are from the Late Neolithic period, radiocarbon dated from ~4,600 to ~3,800 years BP (Bronk-Ramsey, et al. 2002), and are among the largest and most complete of the collective burials for the period in Belgium.

This period of time in Northern Europe may have been an interval of intense change for these small-scale farmers given the incipient Bronze Age that their descendants were to experience. Although human remains have been recovered from hundreds of caves in Belgium dating from the Middle Paleolithic to the cusp of the historical age, more of them derived from the Middle to

Late Neolithic periods (~ 5,000 – 1,000 BP) suggesting intense and possibly repeated use of these sites as collective burial locations (Toussaint, et al. 2001; Williams and Polet 2017). Some sites may have been in use for over 800 years as suggested by the four dates obtained from Maurenne Caverne de la Cave (Bronk-Ramsey, et al. 2002). Maurenne Caverne de la Cave includes both the earliest and latest (4,635 – 3,830 BP) of the five caves examined.

Radiocarbon estimates place the Meuse burials in a date range from about 4,600 to 3,800 years BP (Bronk-Ramsey, et al. 2002; Toussaint 2007). Most represent a single burial event or a few events within a relatively short time frame, perhaps a generation or two (Williams and Polet 2017). Four samples taken from Maurenne Caverne de la Cave were dated to $4,635 \pm 45$; $4,160 \pm 45$; $3,950 \pm 70$, and $3,830 \pm 90$. Two dates were taken from Bois Madame with resulting dates of $4,075 \pm 38$ and $3,910 \pm 40$. Hastière Caverne M, Hastière Trou Garçon C, and Sclaigneaux were each dated once, to $4,345 \pm 60$, $4,220 \pm 45$, and $4,155 \pm 35$ respectively (Figure 1).

The purpose of this study is to examine the molars found at these sites to determine whether the individuals of Maurenne Caverne de la Cave cluster as a group and whether they are more similar to the earlier sites of Hastière Caverne M and Hastière Trou Garçon C or the later sites of Bois Madame and Sclaigneaux, given the extended time frame of burials relative to the others. The details of the archaeological information and context is reported elsewhere (Semal et al., 1999; Toussaint et al., 2001; Dumbruch, 2007; Toussaint, 2007; Polet, 2011; Williams and Polet, 2017). Using microscopy of dental casts, microwear analysis is performed to examine dietary patterns which may reflect relationships among groups in terms of subsistence strategies.

Dietary variation may correspond to the cluster of groups based on dental morphology. Size, shape, and the presence or absence of nonadaptive dental morphology represent evolutionarily-neutral genetic traits which aid in determining genetic distance, although any interpretation of the

results must be tempered with caution given the small and uneven sample sizes of the collective burials (Palomino, Chakraborty and Rothhammer 1977; Pilloud and Kenyhercz 2016; Edgar 2017). Differences in the patterns of variation between Maurenne Caverne de la Cave and the other sites may suggest that the individuals buried there were not of the same population as their neighbors. Two hypotheses are given to potentially explain the variation noted at Maurenne Caverne de la Cave.

Figure 1 Radiocarbon dates (Bronk-Ramsey, et al. 2002)

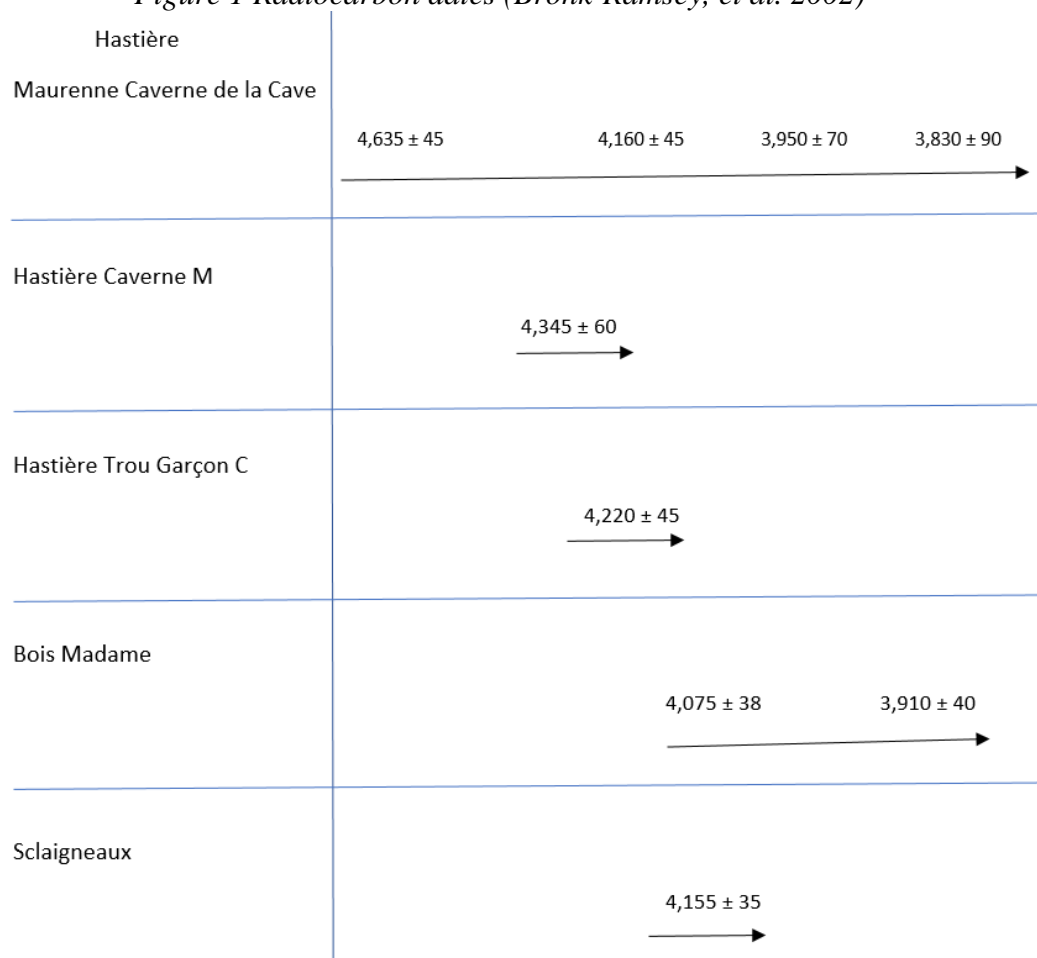




Figure 2 Meuse river rockshelters

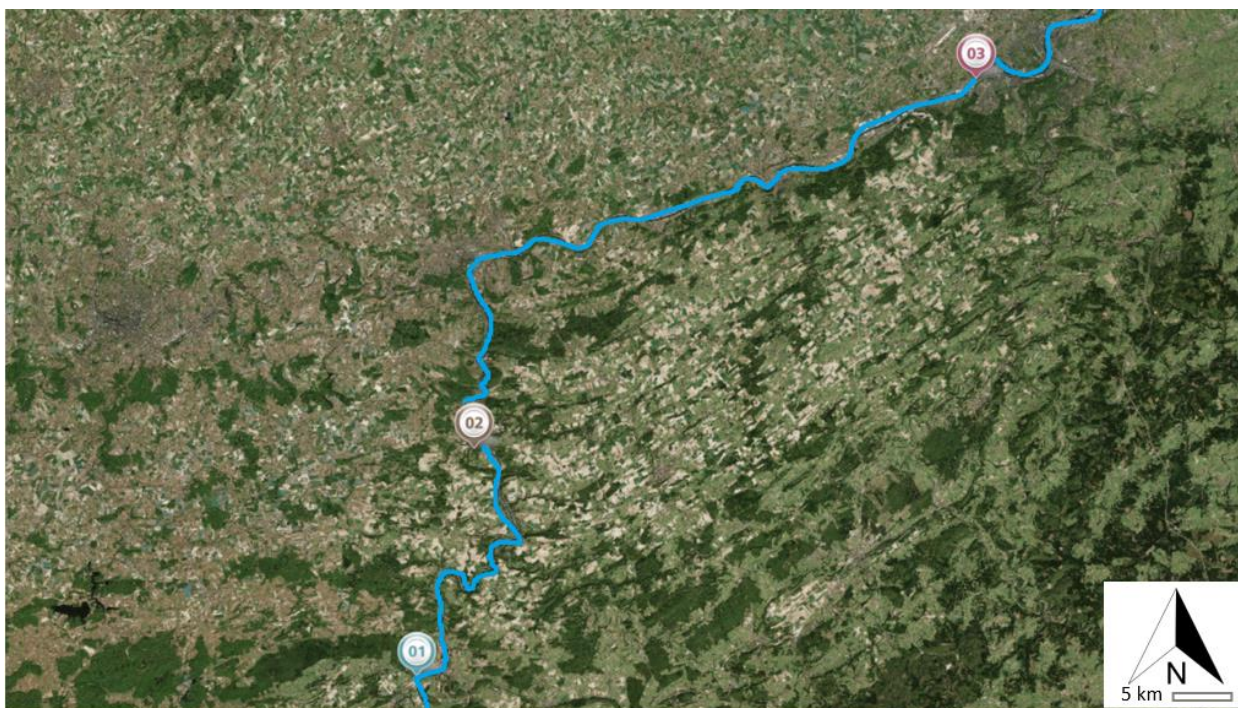


Figure 3 Site locations; 01: Hastière (Caverne M, Trou Garçon C, Maurenne Caverne de la Cave), 02: Bois Madame, 03: Sclaigneaux

One hypothesis is that Maurenne Caverne de la Cave represents a communal burial ground for several local groups over many generations and that these individuals were not necessarily tied to a specific population. Alternatively, it may be that Maurenne Caverne de la Cave represents a discrete population that is distinct from other Late Neolithic groups in terms of dietary proclivities and molar morphology, perhaps implying a single cultural group that utilized the same cave site as a burial chamber for over 800 years. This hypothesis would be supported by distinct wear patterns and nonmetric trait expressions at Maurenne Caverne de la Cave if individuals from this cave cluster separately from the other groups. In other words, it is expected that Hastière Caverne M, Hastière Trou Garçon C, Bois Madame, and Sclaigneaux will show more similarities to each other in both behavioral (wear) and genetic (nonmetric trait expression) than any of them do to Maurenne Caverne de la Cave.

1.1 The Wave of Advance Model

To determine the origins and time frame of the adoption of domestication in Europe, Ammerman and Cavalli-Sforza (1984) utilized radiocarbon dates to analyze and map the chronological and temporal spread of farming practices. The resulting map indicated a “wave of advance” of agricultural technology from the Fertile Crescent into Europe, beginning in southern and eastern Europe around 7,000 years before present (BP), reaching present-day Belgium by approximately 5,500 years BP (Figure 4). The radiocarbon dates were generated from preserved microbotanical remains, specifically of early domesticated variants of wheat, which is the most commonly farmed cereal grain in Europe and Western Asia (Mangelsdorf 1953; Ammerman and Cavalli-Sforza 1971).

This model of westward diffusion, dubbed by V. Gordon Childe *ex oriente lux* or “light from the east” (Childe 1925) reinforces antiquated ideas about the nature of cultural change; diffusionism, the culture-historical model, and the concept of archaeological cultures have since fallen out of fashion in favor of more democratic models of independent invention (Trigger 2006, 306-309) which uphold post-processual concepts of agency and intellectual equality. Models of cultural diffusion reinforce power dynamics wherein “civilized” or “advanced” peoples share their enlightenment with less sophisticated, “savage” groups (Shennan 1989). Ammerman and Cavalli-Sforza (1984) address concerns regarding the suggestion of cultural diffusion as a major factor in the domestication of Europe while maintaining the position that the existing evidence overwhelmingly supports cultural, if not necessarily demic, diffusion in this instance. The extension of Ammerman and Cavalli-Sforza’s model to Neolithic Belgium is supported by the abundance of archaeological material found in Belgium that is unique to Neolithic lifeways, including pottery and farming tools found in context with human remains at the site of Bois Madame (Dumbruch 2007).

Popular narratives of the “march of progress” conjure images of agricultural economies rapidly replacing hunting and gathering by virtue of the new economy’s ability to produce enough food surplus to allow for leisure time to dedicate to art and philosophy. However, farming populations express higher rates of dental decay and overall decline in health relative to hunter-gatherers. Paleopathological analyses suggest that the transition from a foraging lifestyle to an agricultural one is responsible for significant differences in the skeletal remains of farming versus hunting and gathering populations (Larsen 1995; Lillie 1996; Cohen and Crane-Kramer 2007; Eshed, et al. 2010). Despite dramatic increases in population, overall health and quality of life in Neolithic populations frequently declined (Armstrong, Goodman and Jacobs 1991).



Figure 4 Wave of advance model after Ammerman and Cavalli-Sforza (1984, 59)

A dependence on a narrow selection of plant and animal specials, particularly an abundance of simple starches, results in a range of pathologies from dental caries and abscesses to enamel hypoplasia as a result of early childhood malnutrition. Simple starches are broken down into glucose during mastication, and overconsumption of these at the expense of other nutritional sources can eventually result in decay of the enamel and dentin. If the pulp of the tooth is exposed, the tooth is at risk of infection. Dental disease and other stress or malnutrition-induced skeletal pathologies common to early farmers, e.g. cribra orbitalia, porotic hyperostosis, and severe arthritis (Eshed, et al. 2010; Roberts and Manchester 2013) are rarely found in either extinct or extant foraging populations. In actuality, contemporary and historical foragers have been documented to work less on average (a few hours per day), and also to consume a wider

variety of foods than farmers. Agriculturalists work harder and longer and depend on a limited range of plant and animal species (Sahlins 1974), increasing the risk of inadequate nutrition, especially if a harvest fails or livestock die unexpectedly.

Diffusion of intensive farming from the east does not negate the likelihood of pre-agricultural Europeans engaging in small-scale horticultural or domestication activities. As Pringle (1998) illuminates, proto-domestication of plants (primarily grasses, but also squashes in the Americas) as a supplementary practice to traditional hunting and gathering methods predate intensive agriculture by up to several thousand years. Pringle's "slow birth" model also implies that the use of wild plants and animals did not suddenly cease with the adoption of cultivation practices. Analysis of microbotanical remains from Neolithic Iberia (5400-2300 cal BP) suggests that wild fruits continued to be a dietary staple even as agriculture intensified as the dominant economic subsistence model in Western Europe (Antolin and Jacomet 2015). Dietary reconstruction based on microphytological analysis will be further discussed in the methods chapter. These historical processes eventually gave birth to the sedentary farming lifeways associated with the Neolithic that would persist until the early Bronze Age. The sites included in this study represent the cultural (and possibly biological) descendants of these early European farmers.

1.2 Hypotheses and Research Design

The relationships among individuals from Maurenne Caverne de la Cave compared to their Neolithic neighbors can be reconstructed via the frequency and expression of nonadaptive dental traits to determine whether the site was being used by the same group over generations or as a common, regional burial site. Additionally, dental microwear can provide

information about the dietary changes in the Belgian Neolithic. Not much variation in diet is expected between groups, but the possibility that the large number of burial sites represent distinct populations with potentially different subsistence practices cannot be excluded. Moreover, given that Maurenne Caverne de la Cave represents both ends of the temporal spectrum of the Belgian Late Neolithic, analysis of dental microwear may illuminate the nature and time frame of changing subsistence patterns of this period at the brink of the early Bronze Age.

1.2.1 Samples

A total of 158 individuals have been identified from the five sites (Table 1). The samples included in this study are high-fidelity resin casts of gnathic remains from each mass grave. The molds were collected by Dr. Frank Williams at the Laboratory of Anthropology and Prehistory of the Royal Belgian Institute of Natural Sciences and casts were created at the Bioarchaeology Laboratory of Georgia State University.

Table 1 Number of individuals identified from each burial site

Meuse River cave burial	Number of individuals identified
Sclaigneaux	56
Hastière Caverne M	24
Hastière Trou Garçon C	6
Hastière Maurenne Caverne de la Cave	38
Bois Madame	34

In addition to resin casts, high-resolution photographs of the teeth collected by Dr. Frank Williams aided in analysis (Figure 5). The transparency of the casting resin can render small

details difficult to see, even with the aid of magnification. Photographs of the actual molars provide additional contrast, allowing for a higher degree of accuracy.



Figure 5 Resin cast (left) and photograph (right) of Maurenne Caverne de la Cave 8URM1-M2

For dental microwear analysis, adult molars were selected by the amount of visible, diagnostic microwear and the absence of postmortem taphonomy consisting of irregular features atypical of ante-mortem use wear. With respect to dental morphology, all molars are scored using the Arizona State University Dental Anthropology System (ASUDAS) (Scott and Irish 2017), excluding those exhibiting extreme wear or breakage.

1.2.2 Mortuary Context and Material Culture

Understanding local mortuary practices is crucial in identifying biological and cultural similarities and differences. The use of caves as burial grounds was common practice throughout European prehistory (Bergsvik and Skeates 2012, 6; Manem 2012; Weiss-Krejci 2012), and the

conditions present in such locations are typically conducive to the preservation of bone and material goods (Harrold 1980, 196), providing the best possible glimpse into prehistoric mortuary practices.

The five sites included in this study are not all single caves, but constitute discrete burial units. They are all found within karstic caverns (limestone cave systems created by underground water erosion) or rockshelters containing mass or collective burials. The region includes approximately 3,000 caverns, 250 of which are currently known to contain prehistoric human remains (Polet 2011). In Belgium, and specifically the burial sites in the Meuse cave system, there are substantially more cave or rockshelter burials from the Neolithic than either the earlier Upper Paleolithic, the Mesolithic or later Early Bronze Age, and most of the buried individuals were discovered in various states of disarticulation and commingling. Maxillae were often found separate from the cranium (Polet 2011). Natural processes that would damage the bone enough to separate the maxilla would likely destroy the teeth, but this is not the case. Teeth remain in these maxillae, suggesting intentional removal possibly related to burial rites. Most of the skeletons have been identified as female, suggesting that these burials do not represent the average funerary treatment applied to most members of these populations (Polet 2011). The dramatic uptick in such burials toward the end of the Neolithic may reflect a resurgence in popularity of the practice, or a special funerary rite reserved for elite persons or unusual circumstances. Additionally, materials associated with burial goods including lithics, pottery, and animal remains were also found in some of the burials, though they are sparse (Toussaint 2007).

1.3 Contextualizing Subsistence and Diet in the Meuse Region

In addition to skeletal evidence of diet-related pathologies, dietary patterns have been reconstructed through multiple approaches. Methods of determining dietary proclivities are heavily dependent on the antiquity and state of preservation of organic material. Small, ancient sites with limited resources such as the Meuse burials necessitate inferences drawn from similar sites which allow for more complex interpretations.

1.3.1 Stable and Radiogenic Isotopes

The presence of specific isotopes (typically carbon, but also strontium, nitrogen, and oxygen) in dental tissue can aid in determining what kind of plants were frequently utilized for food (Borić and Price 2013). Carbon isotopes unique to certain grasses, for example, will also be present in human tissue if the humans ate herbivores that, in turn, ate a diet of grass (Lam 1994; Lillie 1996, 136). Carbon decays at a steady, predictable rate, which is why C14 dating is reliable within an increasing margin of error depending on the antiquity of the sample. However, the process of fossilization replaces organic compounds with mineral deposits, so carbon isotopes are typically utilized for analysis on more recent populations that have not had time to fossilize completely. Occasionally, ancient dental fossils, through a serendipitous set of environmental conditions and events, will retain enough carbon to reconstruct basic dietary behaviors of early hominins (Sponheimer, et al. 2013). This method is commonly used with Neolithic populations, as it can provide dietary data when observable diagnostic features are obscured by extreme wear or damage. Isotopic analyses of nitrogen from the Bois Madame burials indicate a diet abundant in freshwater fish. Oxygen and nitrogen isotopic analyses show greater dietary similarities

between humans and carnivores than herbivores, suggesting consumption of terrestrial animals (Semal, Garcia Martin and Polet 1999).

Moreover, isotopic analysis of oxygen 13 can aid in mapping mobility in individuals (Boric and Price 2013); if enough data are gathered, it is possible to reconstruct larger migratory and subsistence patterns. Isotopic analysis of lipid biomarkers derived from Atlantic European Neolithic pottery reveals that utilization of wild plant and marine resources persisted well into the Neolithic (Craig, et al. 2011). Conversely, similar studies from contemporaneous sites in the northern Atlantic archipelagos suggest that marine resources were quickly abandoned in favor of dairy (Cramp, et al. 2014). These differences are likely due to subtle ecological differences that can exist even within small regions; settlements that lie more inland are less likely to consume large amounts of marine foods than coastal habitation zones. Therefore, ecology is considered in the analysis of dietary proclivities within the approximately thirty-kilometer radius of the Meuse river basin samples examined in this study.

1.3.2 Zooarchaeology and Faunal Remains

Zooarchaeology is the study of animal remains in archaeological contexts. As humans increasingly interfered with animal breeding, livestock became morphologically and genetically distinct from their wild ancestors. Zooarchaeologists are trained to distinguish these differences. The presence of wild versus domesticated animal remains indicate whether a population primarily procured meat from hunting wild game or breeding domesticates. Égüez et al. (2016), using micromorphological evidence in conjunction with radiocarbon analysis, investigated sheep and goat husbandry in a cave in Middle Neolithic Iberia (5320-5170 years BP), concluding that humans and domestic livestock cohabitated in very close quarters. As animal husbandry

increased, the subsequent sustained direct contact with livestock introduced new pathogens into human populations (Diamond 1997, 205). Zoonoses (pathogens derived from contact with animals) can leave distinct evidence of disease on human skeletal remains (Torrey and Yolken 2005, 33-43).

Faunal remains found in Bois Madame include “horses, pigs, bovids, cervids, goats, dogs, cats (domestic and wild), rabbits, hares, insectivores, bats, birds, amphibians as well as mollusks (Dumbruch 2003; Williams and Polet 2017, 45-46). The presence of animals typically associated with animal husbandry such as horses, pigs and goats alongside mollusks and rabbits which are often associated with hunting and foraging suggest that the inhabitants of the region during the burial period at Bois Madame participated in both farming and hunting to some degree. The presence of birds, bats, and amphibians are likely not associated with the burials; these animals inhabit cave environments and likely lived and died in the caves before and after the site was used as a burial ground. The inclusion of animal remains may be evidence of feasting or other funerary rites. Their presence alone indicates a broad, mosaic subsistence pattern in the Belgian Neolithic consisting of both wild and domestic food sources.

1.3.3 Microbotanical Remains

Microbotany – the study of microscopic plant fossils – also informs the reconstruction of ancient diets. Analysis of fossilized pollens and phytoliths (silica bodies that give plants their rigidity) are often found on pottery that was used to store grains or other plant foods or in the soil surrounding food storage or cooking areas (Rosen 1995). Other plant remains, including seeds, husks, and pits are less likely to preserve over long periods of time. As with animals, the distinction between wild and domesticated plants is discernable by comparing changes in pollen

and phytoliths. In her discussion of proto-domestication prior to intensive agriculture, Pringle (1998) analyzed phytoliths from early plant domesticates on every continent. As mentioned earlier, this method has also been used to determine that Neolithic farmers in Europe continued to augment their diets with wild plants (Antolin and Jacomet 2015; Fernandez, et al. 2015). To date, there has been no research published on microbotanical remains from the Meuse burials, though it is possible that future analysis of the lithics and ceramics will yield data regarding specific wild and domestic plants that were utilized by Neolithic peoples.

These methods provide valuable context for research in the Meuse sites, given the relatively small sample size and sparse material culture from which to gather data. Human activity does not occur in a vacuum; therefore, all geographic, archaeological, and biological processes must be evaluated in order to piece together an accurate reflection of the past.

2 METHODS

Similarities in farming practices reconstructed archaeologically suggest cultural affinities, or at least a measure of contact between nearby settlements wherein cultural information was exchanged (Ammerman and Cavalli-Sforza 1971; Golitko 2015; Olalde, et al. 2018) . This study utilizes two methods of collecting data. One is based on the prevalence of molar traits within and across sites and another is an analysis of dietary use-wear patterns on the molars using the same individuals.

2.1 Dental Microwear Analysis

Dental microwear has been captured and analyzed to reconstruct dietary patterns in all manner of mammals and is especially useful for reconstructing the diets of extinct nonhuman

primates and human ancestral forms (Ungar 2012; Williams and Geissler 2014, 483). Enamel wear studies originated in the 1920s as a gross estimation of dietary and paramasticatory wear, scored by the exposure of dentine on the occlusal surface (Rose and Ungar 1998, 354). During the 1980s, microwear analysis became an increasingly important tool in reconstructing diet on the individual and population level. Rose (1998) pioneered this aspect of microwear analysis by matching abrasion features with types of masticatory behavior, laying a foundation for dental microscopy as a tool for environmental and biological sciences. Dental microwear can provide valuable behavioral information; however, it does not inform biological relationships.

With respect to dental microwear, increased consumption of grains can be inferred by the presence of pitting caused by small stone particles from ground-stones and other grinding tools used to pound grain into flour or remove the tough outer shell (Wright 1994; Weiss, et al. 2004). Harvesting and processing grain is a labor-intensive practice with little nutritional payoff; however, grains are relatively stable crops with long shelf-lives. As such, foragers in the area were unlikely to have depended heavily on wild grains as a core food source, especially considering that large grinding stones and stores of food are not easily portable. High frequencies of fine scratches alongside pitting would suggest that farmers produced relatively soft foods that had been processed with tools like mortars and pestles – e.g. gritty bread. Conversely, high frequencies of heavy microwear would indicate a diet of harder foods with less processing. Scanning electron microscopy of buccal microwear from Bois Madame conflicts with isotope results conducted by Semal et. al (1999). Microwear features were heavier than expected, though the authors interpret coarse scratches as the result of the ingestion of fish scales, which could explain the discrepancy (Semal, Garcia Martin and Polet 1999); all available methods and previous research are considered in order to thoroughly contextualize the data.

Across continental Europe, diets of Neolithic peoples share similar patterns; as grain crops and dairy were introduced, populations adapted to them to varying degrees depending on their location, needs, and ecosystem. From Denmark to Ukraine, freshwater and terrestrial animals (wild and domesticated) continued to be utilized as staple foods from the Mesolithic through the Neolithic, augmented by dairy and cereal grains (Lillie 1996; Richards, Price and Koch 2003; Nystrom 2008; Nehlich, et al. 2014).

Counts of the dental microwear features were observed at two locations on the paracone and protoconid when available and the two observations were averaged and subsequently utilized as the raw dental microwear data for statistical analysis (Figure 6). Diagnostic microwear features include hypercoarse scratches, coarse scratches, fine scratches, puncture pits, large pits, and small pits. Hypercoarse scratches appear as wide, deep, straight, trench-like lines. Coarse scratches are also deep lines; however, they are narrower than hypercoarse scratches. Fine scratches typically appear in clusters. They are thinner and shallower than coarse scratches. Puncture pits appear as large, deep, unreflective holes. Large pits are smaller than puncture pits and approximately twice the size of small pits (Williams and Geissler 2014). Under a microscope, fine features are generally reflective.

These features can be caused by a variety of sources; there does not exist a 1-1 correlation between a specific substance and a given microwear feature; however, heavier microwear is associated with heavy consumption of harder foods or an abundance of grit contaminating the food (Walker, Hoeck and Perez 1978; Williams and Geissler 2014). The frequencies of each of these features indicate the kinds of foods consumed by an organism within the final weeks before death. The first molar from each individual was prioritized, because this tooth is generally the most diagnostic for microwear, followed by the second molar. When

chewing, food comes into contact with these teeth frequently. Third molars can also be used to assess microwear, but they tend to exhibit less wear due to their extreme distal position in the mouth. Premolars and deciduous teeth are excluded from this method of analysis for two reasons: premolars tend to exhibit paramasticatory wear that wears down enamel and obscures dental microwear, and deciduous teeth come from small children; this can skew the data due to the different dietary requirements of children versus adults.

Dental microwear patterns are expected to be homogeneous within and between all sample populations due to the proximity of the burials. Subsistence practices in the same geographic region are assumed to be unrelated to genetic proximity between groups. This method will determine whether the population at Maurenne Caverne de la Cave, given its long timespan, deviated from the rest in terms of their patterns of subsistence, giving insight into the adoption of agriculture in Neolithic Northern Europe.

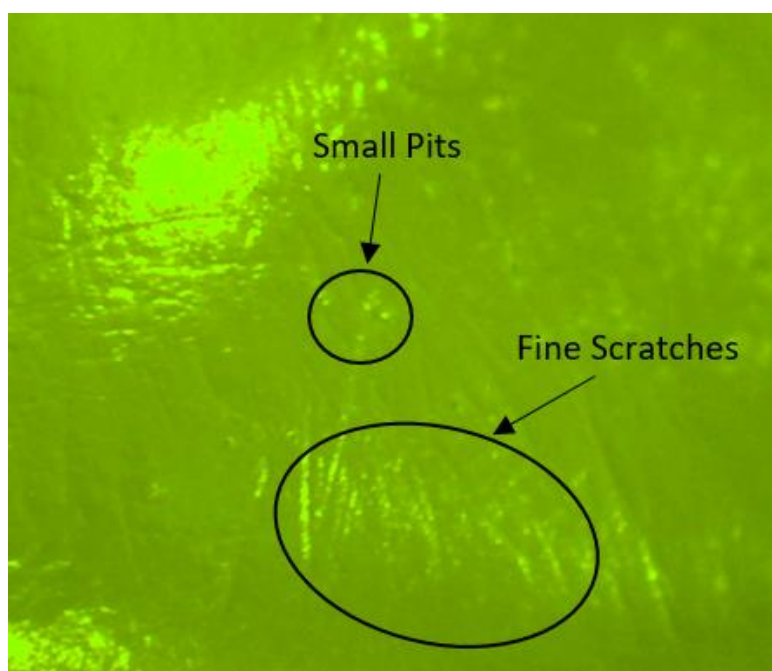


Figure 6 Dental microscopy indicating fine scratches and small pits

2.1.1 Statistical Analyses of Dental Microwear Traits

Univariate analysis is performed in the form of ANOVA by microwear feature with the addition of Tukey's post-hoc test. Multivariate analyses are also performed. Discriminant function analysis is utilized to calculate canonical scores wherein 95% confidence ellipses around group centroids are constructed. The means for each microwear feature per cave burial were compared in a cluster analysis using a single linkage of Euclidean distances.

2.2 Scoring Nonmetric Dental Traits

The likelihood of relatedness within and between groups can be inferred using the frequency and types of nonadaptive dental traits present for each sample population. Because these traits are neutral to natural selection yet highly heritable (Hillson 1996, 100; Pilloud and Kenyhercz 2016, 140), they are excellent proxies to use in mapping potential relationships on a population scale. Therefore, these data allow for assessment regarding the degree to which these cave burials represent distinct groups of people. The standardized scoring procedures used in this study are detailed by the Arizona State University Dental Anthropology System (ASUDAS) (Turner, Nichol and Scott 1991; Scott and Irish 2017). For the purposes of reconstructing relationships on the population level, metric analyses of adult teeth can be unreliable because tooth size is more variable and adaptive than nonmetric traits (Kieser 1990, 20).

Intact genetic materials from ancient skeletal remains are few and far between, limiting the range of possibilities to accurately reconstruct ancient demographic structures. Living populations are the closest analog available in many cases (Ammerman and Cavalli-Sforza 1984, 84). Pilloud and Kenyhercz identify two modes of determining relatedness in archaeological contexts – “intracemetery analysis employing dental morphological data can address regional

questions such as the relationship between cemetery structure and biological relationships. Intercemetery approaches can be used to explore broader population relationships and migration” (Pilloud and Kenyhercz 2016, 122-123). For the purposes of this study, primarily intercemetery or population-scale analyses are conducted; a larger sample size is more likely to produce accurate statistical data than a smaller sample size, such as within a cemetery. The relatively small sample size available for analysis in this study precludes extensive intracemetery study until further excavation and investigation is conducted at these sites. However, intracemetery analysis is utilized where applicable to estimate relatedness between individuals within a single burial site.

A selection of samples was scored for diagnostic nonadaptive molar traits using the criteria stipulated by the ASUDAS. Samples were chosen by the degree of preservation, giving priority to deciduous first molars because they are the least likely to exhibit severe attrition which would obscure the expression of traits. In the absence of well-preserved deciduous molars, adult M1 was consulted, followed by M2. If only M3 was present or well-preserved enough, it was scored. Individuals exhibiting extreme wear were excluded.

These ASUDAS traits scored include the metacone, hypocone, metaconule, Carabelli’s trait (or Carabelli’s cusp), and parastyle in the maxilla. Mandibular traits scored include the anterior fovea, groove pattern, protostylid, hypoconulid (cusp 5), entoconulid (cusp 6), and the metaconulid (cusp 7) (Table 2). Although incisors, canines, and premolars also exhibit nonadaptive traits, molars are generally better preserved. Only molars found within gnathic remains were examined by Dr. Williams.

Table 2 Nonadaptive dental traits scored

Maxillary	Mandibular
Metacone (cusp 3)	Anterior Fovea
Hypocone (cusp 4)	Groove Pattern
Metaconule (cusp 5)	Protostylid
Carabelli's Trait	Hypoconulid (cusp 5)
Parastyle	Entoconulid (cusp 6)
	Metaconulid (cusp 7)

Relatedness between individuals within a single burial site can be inferred through these methods, as well as differences between groups. However, mortuary archaeology is so complex that social inferences based on material remains in mortuary contexts are highly subjective and speculative, and therefore murky at best (Binford 1971). The archaeological record cannot show activities and rituals that do not leave tangible remains, and it cannot be assumed that any given archaeological population will reflect the living population. Given this limitation, any initial demographic reconstruction will be tentative until more data are recovered and analyzed.

3 RESULTS

3.1 Dental Microwear Analysis

The most common microwear features across all groups are fine scratches and small pits, both spatially and temporally. Fine use-wear patterns are associated with agriculturalists. The presence, frequency, and distribution of these features suggest that the inhabitants of the Meuse river region maintained an agricultural subsistence strategy from ~4,600 to ~3,800 years BP.

3.1.1 Intercemetery Comparisons

A One-Way Analysis of Variance test (ANOVA) was performed on the microwear samples as a univariate analysis to determine similarities between and within groups examined that would suggest variance in diet (Aron, Aron and Coups 2008, 312-317)(Table3). *F* ratios of puncture pits ($F = 2.023$) and fine scratches ($F = 3.444$) suggest greater between-group variation than within-group variation, with the most extreme differences between Maurenne Caverne de la Cave and Hastière Caverne M; however, these differences are not significant ($p = 0.104$). Tukey's post-hoc tests indicate significant differences in the frequency of light scratches between the populations at Maurenne Caverne de la Cave and Sclaigneaux ($p = 0.014$) but no other significant differences between the groups are present. Discriminant function analysis of microwear samples showed groups clustering by location, albeit loosely.

Table 3 One-Way ANOVA with Tukey's Post-Hoc Test

		ANOVA				
		Sum of Squares	df	Mean Square	F	Sig.
Fine Scratches	Between Groups	244.680	4	61.170	3.444	.014
	Within Groups	994.755	56	17.763		
	Total	1239.434	60			
Coarse Scratches	Between Groups	.720	4	.180	.220	.926
	Within Groups	45.731	56	.817		
	Total	46.451	60			
Hypercoarse Scratches	Between Groups	.914	4	.229	.521	.721
	Within Groups	24.569	56	.439		
	Total	25.484	60			
Small Pits	Between Groups	10.257	4	2.564	.126	.972
	Within Groups	1139.333	56	20.345		
	Total	1149.590	60			
Large Pits	Between Groups	21.069	4	5.267	1.720	.158
	Within Groups	171.458	56	3.062		
	Total	192.527	60			
Puncture Pits	Between Groups	1.048	4	.262	2.023	.104
	Within Groups	7.255	56	.130		
	Total	8.303	60			

Canonical scores axes calculated from discriminant function analysis were used to calculate 95% confidence ellipses around each group centroid (Figure 7). This provides more detailed insight into the relationships between and within groups. Axis 1 explains 81.3% of the total variation within and between groups where axis 2 explains 12.1%. In total, these axes account for 93.4% of all variation in dental microwear patterns among the sites surveyed.

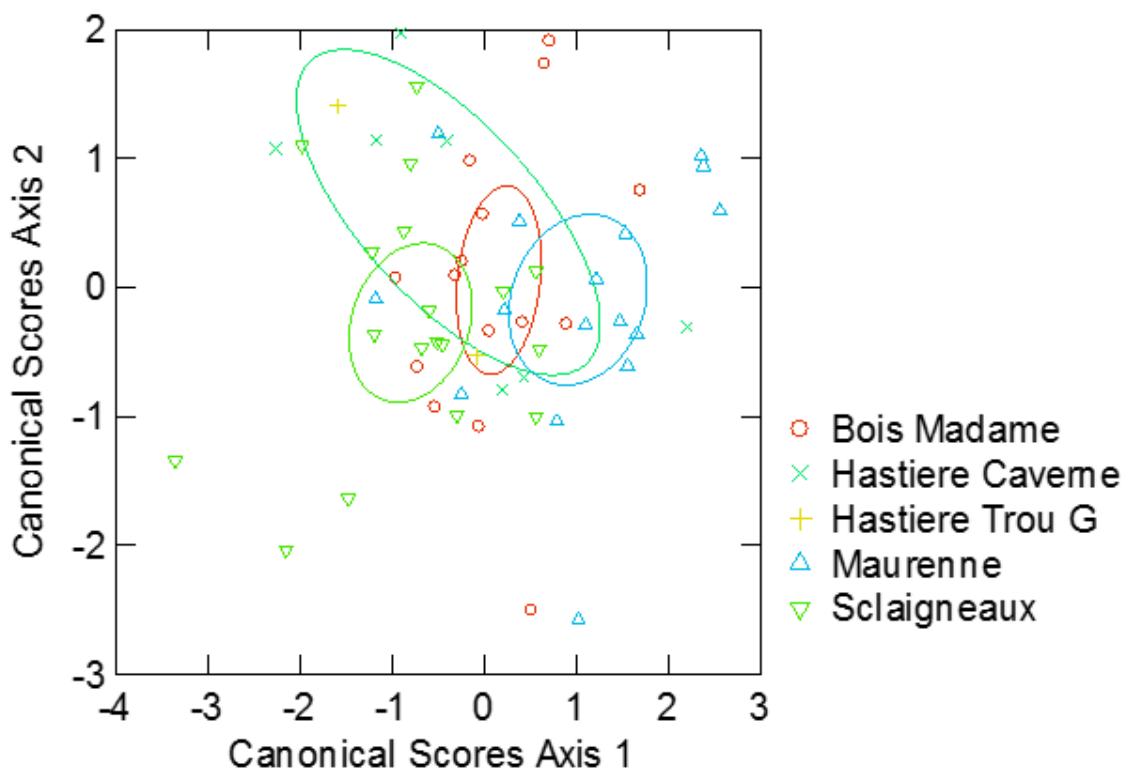


Figure 7 Discriminant Function Analysis; 95% confidence ellipses around group centroids

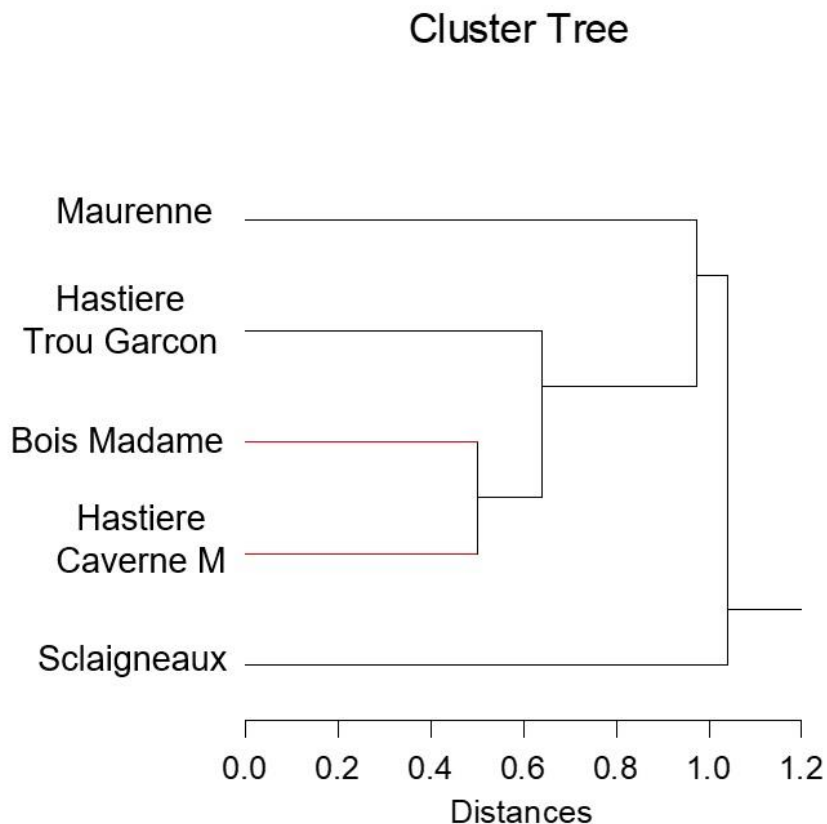


Figure 8 Cluster analysis

The results show that in terms of dental microwear patterns, Bois Madame is imperfectly separate from, but also between, Maurenne Caverne de la Cave and Sclaigieux. Hastière Caverne M overlaps all groups but has a larger confidence ellipse than the others and extends further in the negative direction. These indicate outliers. A cluster tree reinforces these classifications and illuminates both the relationships between groups and the extent of Sclaigieux's distance from the intercemetery mean (Figure 8). Maurenne Caverne de la Cave and Sclaigieux are most dissimilar from each other and Maurenne Caverne de la Cave is most similar to Hastière Trou Garçon C and Bois Madame, which remains firmly centered in terms of variation.

3.1.2 *Intracemetery Comparisons*

Multivariate analyses include classification rates, canonical scores taken from discriminant function analyses, and cluster analysis. Given the small sample size, only the more rigorous jackknife classification was consulted. According to jackknife classifications, 30% of individuals were correctly classified. Nine of the sixteen individuals from Maurenne Caverne de la Cave were correctly classified; this produces the highest correct classification score. Two individuals each from the Hastière groups were classified into Caverne M and Trou Garçon C. Bois Madame, however, shows no such tight classification, with six placed in the Hastière Caverne M group, five in Maurenne Caverne de la Cave, five in Sclaigneaux, and one in Hastière Trou Garçon C (Table 4).

These results indicate that Maurenne Caverne de la Cave exhibits the most distinct microwear patterns as a group. The other groups show wide degrees of variation – especially Bois Madame, where individuals have been classified into every other group; Bois Madame is also the most centrally located among the rockshelters included in this study.

Location	Correctly Classified
Maurenne Caverne de la Cave	56%
Hastière Caverne M	38%
Hastière Trou Garçon	0%
Sclaigneaux	33%
Bois Madame	0%

Table 4 Jackknife classification rates

3.2 Scoring Nonmetric Dental Traits

Casts were scored according to the standards set by Arizona State University Dental Anthropology System (Edgar 2017) (Scott and Irish 2017).

3.2.1 Frequency

To refine and analyze the data set, trait frequencies were calculated, then converted to percentages (Table 5). This shows the frequency of each trait by site, allowing comparisons to be made within and between sites; however, this only shows the presence or absence of a trait, not the level of expression. Only two mandibular and three maxillary samples were observable from Hastière Trou Garçon C, thus they were excluded from analysis to prevent uneven results.

3.2.1.1 Mandibular Nonmetric Trait Frequencies

In the mandible, the protostylid is the most consistent, hovering around 15% expression across sites, with Sclaigneaux and Bois Madame nearly identical at 16%, Hastière Caverne M at 15%, and Maurenne Caverne de la Cave showing the least expression. The hypoconulid (cusp 5) is slightly more variable than the protostylid, with Hastière Caverne M showing the highest rate of expression at 15% and Sclaigneaux showing the lowest at 12% frequency. The entoconulid (cusp 6) shows low expression across sites, with the exception of Hastière Caverne M at 15%; Maurenne Caverne de la Cave showing the lowest at 5%. The anterior fovea is expressed often across sites and is also the most frequent within sites (with the exception of Hastière Caverne M at 10%, the lowest expressed trait from that sample) (Figure 9).

Table 5 Mandibular trait mean frequencies

Location	Anterior Fovea	Protostylid	Hypoconulid (cusp 5)	Entoconulid (cusp 6)	Metaconulid (cusp 7)
Sclaigneaux	30.00%	16.66%	10.94%	9.38%	9.38%
Hastière CM	10.00%	15.00%	15.00%	15.00%	0.00%
Bois Madame	20.45%	16.67%	13.64%	6.82%	9.09%
Maurenne Caverne de la Cave	18.00%	13.33%	12.59%	5.00%	9.26%

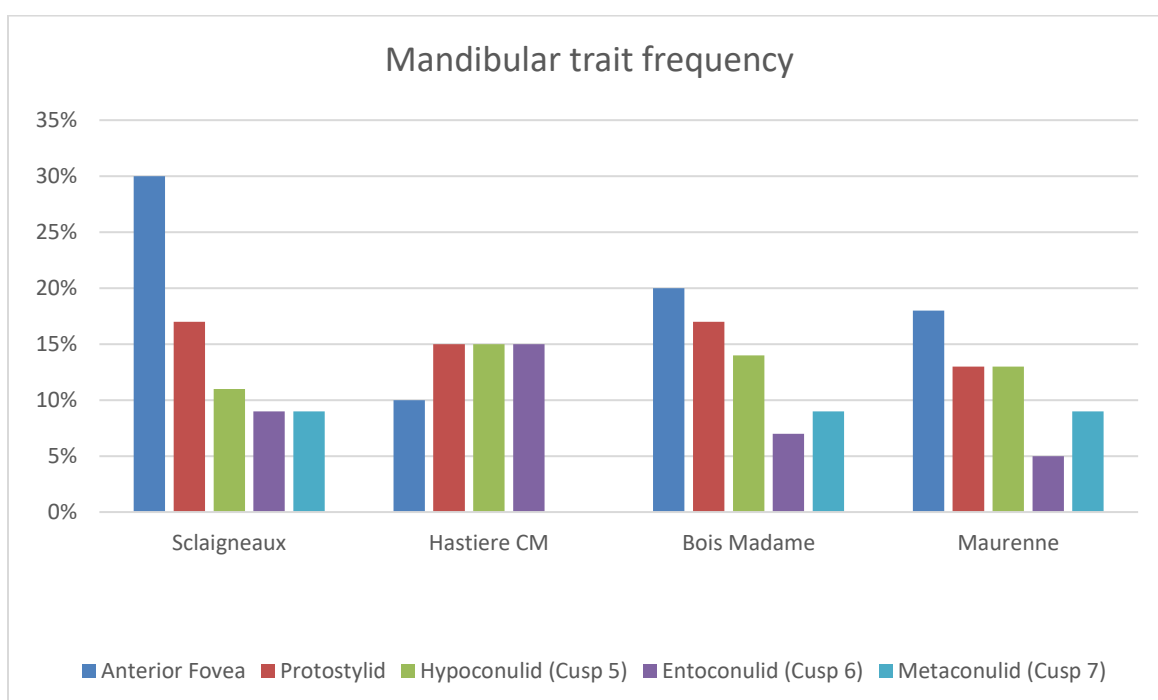


Figure 9 Mandibular trait frequency

The groove pattern on the lower molars describes the contact between cusps. A “Y” pattern describes contact between the metaconid and hypoconid; an “X” pattern is contact between the protoconid and entoconid; a “+” pattern is contact between all cusps at the center of the tooth, forming a plus-sign shape. Distribution of groove-pattern types are fairly even in Maurenne Caverne de la Cave and Sclaigneaux. The “Y” and “+” patterns are more commonly

expressed in Bois Madame with few expressing the “X” pattern. In Hastière Caverne M, “X” and “Y” are frequent where “+” is not. Maurenne Caverne de la Cave and Sclaigieux are almost identical regarding the distribution of groove-pattern traits (Figure 10).

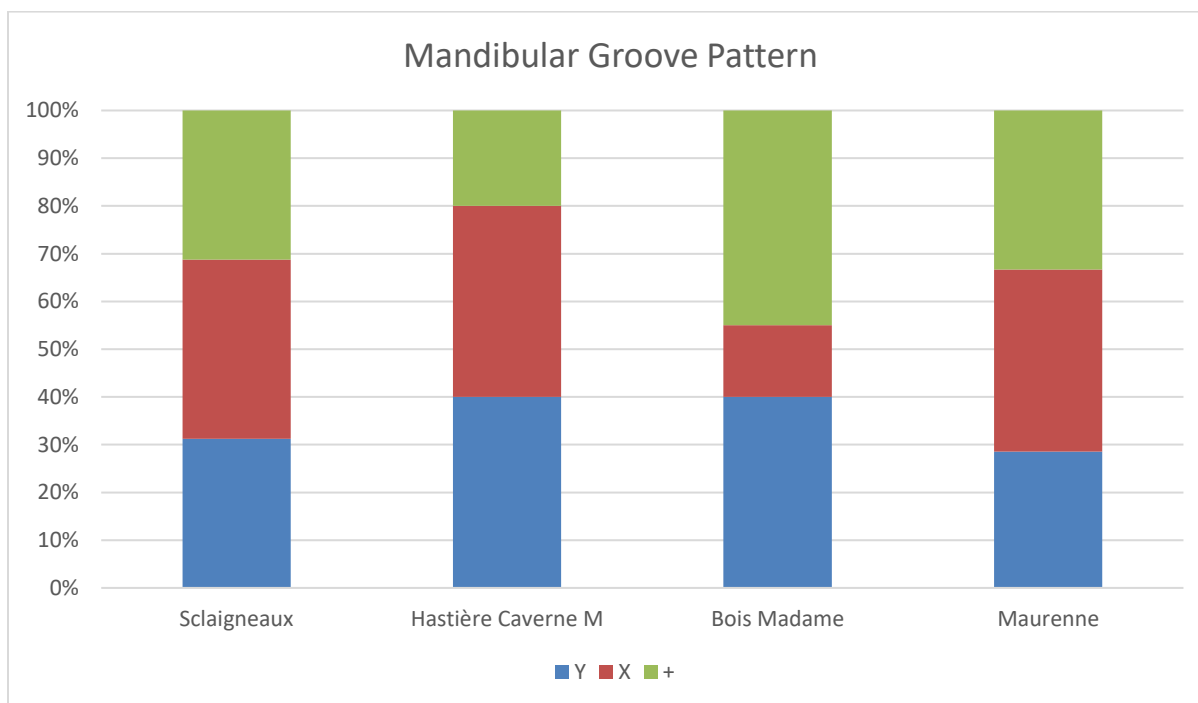


Figure 10 Mandibular groove pattern

The frequencies of mandibular traits are strikingly similar between Bois Madame and Maurenne Caverne de la Cave. Sclaigieux is more similar to both of these than any of them are to Hastière Caverne M, which appears to be an outlier with respect to the frequencies of the anterior fovea and entoconulid.

3.2.1.2 Maxillary Nonmetric Trait Frequencies

Maxillary traits are considerably more variable across and within sites than mandibular traits. The metacone is the most consistent, appearing between 16% and 18% of the time, with

the exception of Bois Madame, which shows a significantly higher rate of expression at 25%. The hypocone shows relatively high expression; highest at Maurenne Caverne de la Cave and lowest at Sclaigieux (Table 6). With regards to similarities, Sclaigieux and Hastière Caverne M both show approximately 15% rates of expression where Bois Madame and Maurenne Caverne de la Cave show approximately 20%. Carabelli's cusp and the metaconulid are the most variable. Carabelli's cusp is the least frequently expressed trait from the Sclaigieux sample at 7% where the parastyle is the most frequently expressed at 24%. Sclaigieux is the only site where this is the case; in Bois Madame, the opposite is shown, where Carabelli's cusp is frequently expressed but the parastyle is not (Figure 11). Overall, the frequency of maxillary traits is most similar between Maurenne Caverne de la Cave and Hastière Caverne M. Bois Madame is more similar to the former two than Sclaigieux is to any of them.

Table 6 Maxillary mean trait frequencies

Location	Metacone	Hypocone	Metaconule	Carabelli's Cusp	Parastyle
Sclaigieux	18.67%	15.43%	15.38%	7.14%	23.81%
Hastière CM	18.75%	15.63%	13.34%	10.00%	12.50%
Bois Madame	25.00%	20.00%	18.18%	18.18%	9.09%
Maurenne Caverne de la Cave	18.40%	21.25%	13.80%	13.33%	33.33%

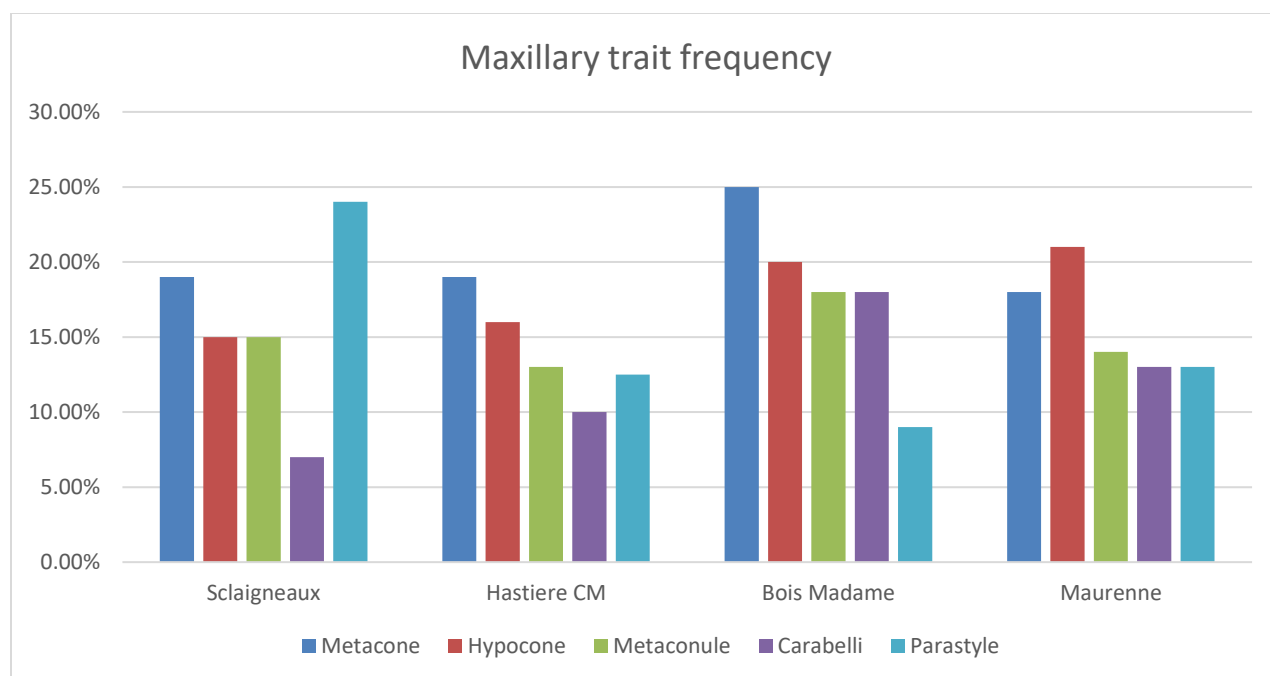


Figure 11 Maxillary trait frequency

3.2.2 Rates of Expression

In addition to determining the presence or absence of dental traits, the rate at which each is expressed was analyzed. This is done in order to illuminate the degree of relatedness among individuals from each site, as well as the similarities and differences between groups.

3.2.2.1 Maxillary Nonmetric Trait Expression

In the maxilla, the metaconule and Carabelli's cusp show the lowest rates of expression. Carabelli's cusp is either absent or faint in 80% to 100% of samples. The metacone shows a mild degree of variation, appearing in low grades in approximately 40% of all samples. The hypocone shows low rates of expression in Maurenne Caverne de la Cave and Sclaigieux, also about 40%. In all sites, the hypocone and metacone show high rates of expression, Bois Madame

showing the highest at 80% and 90%, respectively. Both are highly expressed (< 50%) across sites. Carabelli's cusp shows low rates of expression across sites, hovering around 25%. The metaconule is very slightly expressed; peaking at 15% at Maurenne Caverne de la Cave and only appears in high expression (ASUDAS grade < 4) at Bois Madame (Figures 12-13).

Figure 12 Maxillary trait expression 1-3

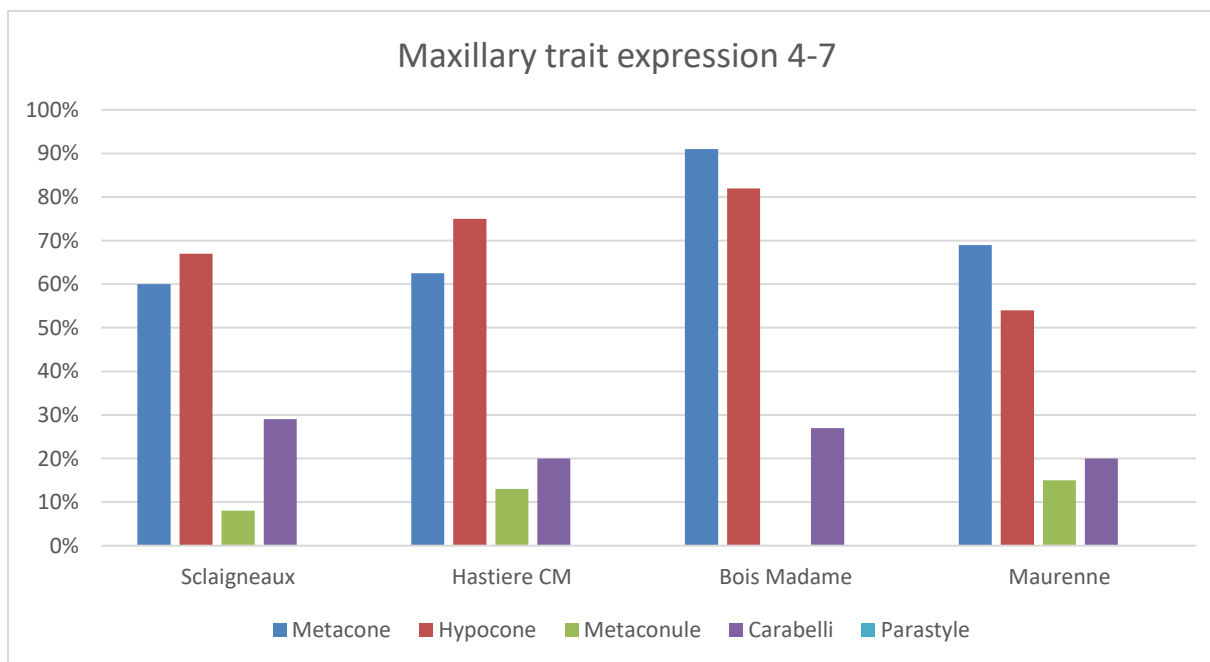
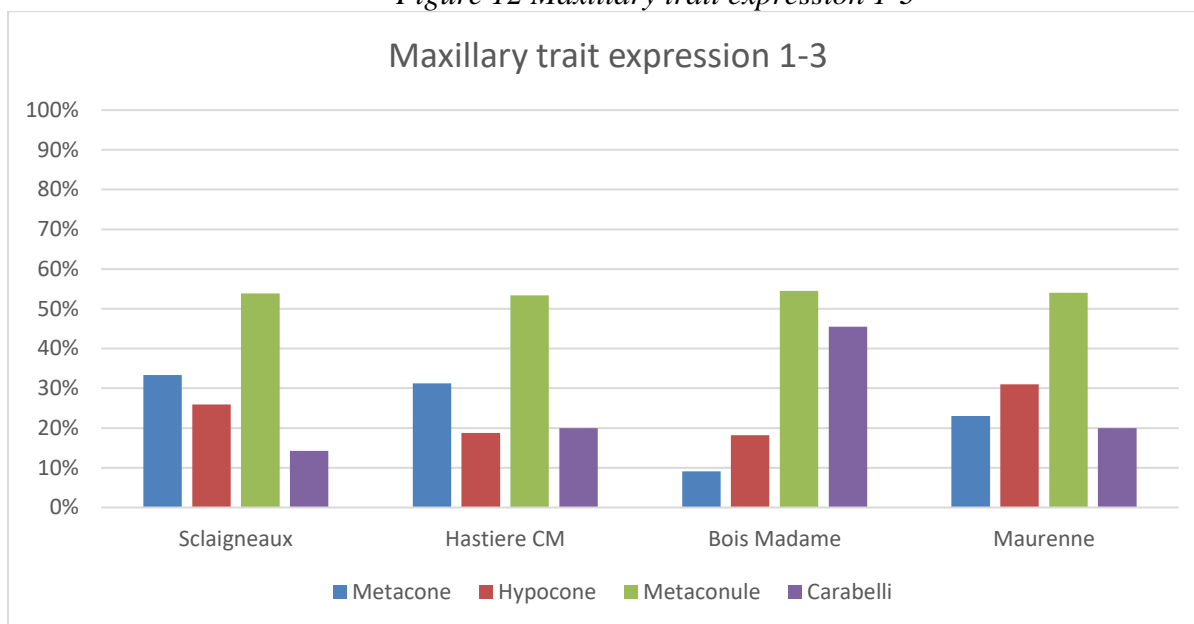


Figure 13 Maxillary trait expression 4-7

3.2.2.2 Mandibular Nonmetric Trait Expression

Variation in the expression of mandibular traits is more extreme than in maxillary traits. The anterior fovea, protostylid, and cusp 7 all show low rates of expression (zero or 1-3) where cusp number is very highly expressed, only dipping under ASUDAS grade 3 in Hastière Caverne M with 10% of samples exhibiting 4 or fewer cusps. The hypoconulid (cusp 5) and entoconulid (cusp 6) also show low expression but more variation between ASUDAS grades 1 and 3. The hypoconulid (cusp 5) is expressed in the low range approximately 70% of the time except in Hastière Caverne M where it is at 100%. Bois Madame and Maurenne Caverne de la Cave show considerable similarities in rates of expression. Hastière Caverne M is more similar to both of these, where Sclaigieux is a minor outlier (Figures 14-15).

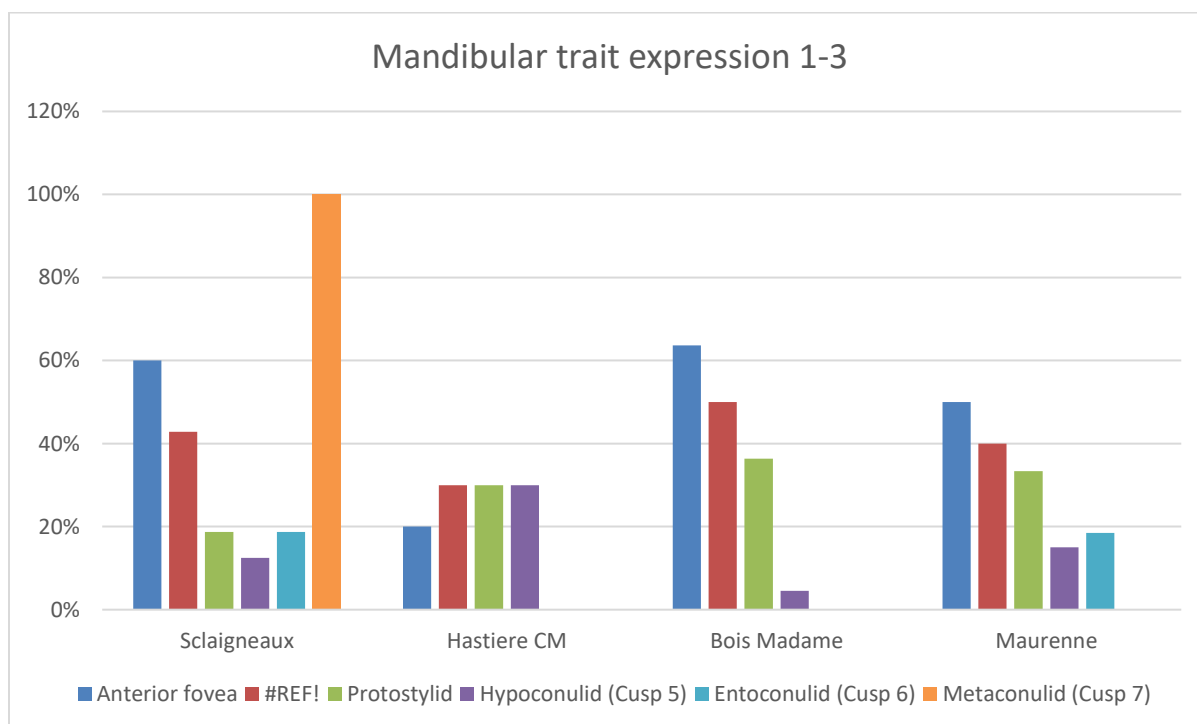


Figure 14 Mandibular trait expression 1-3

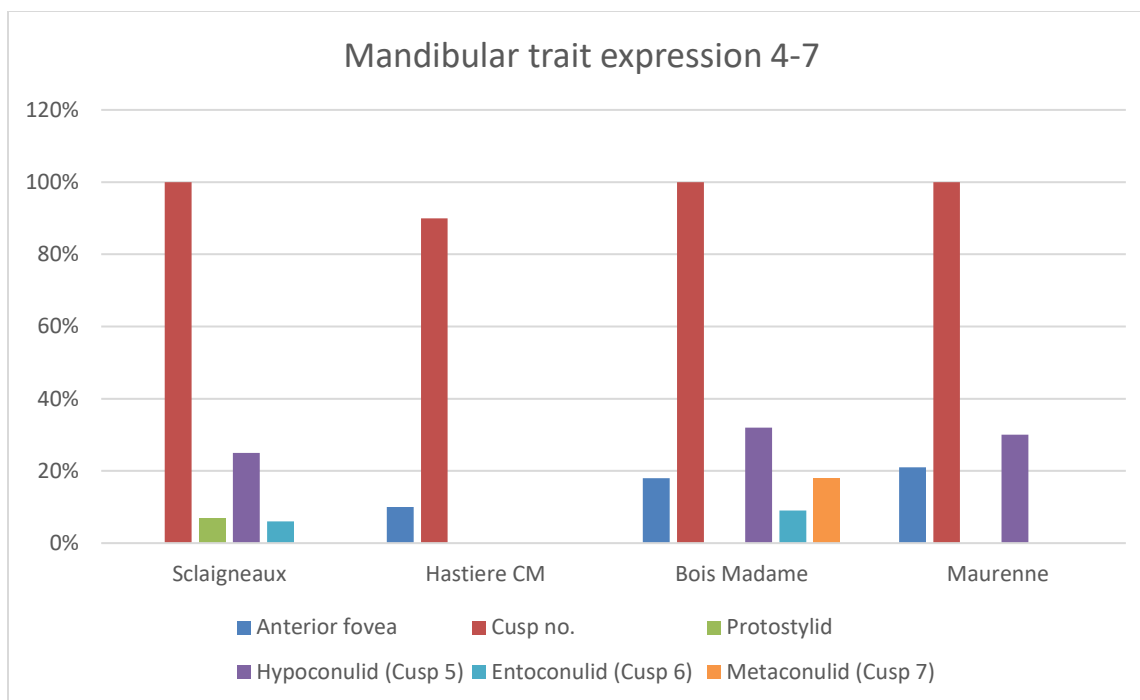


Figure 15 Mandibular trait expression 4-7

4 DISCUSSION AND CONCLUSIONS

4.1 Dental Microwear

The Neolithic abundance of “lighter” microwear features relative to Mesolithic populations from the same region is consistent with early farming populations worldwide (Pinhasi and Stock, 2011). The fine scratches indicate a diet rich in fibrous terrestrial plants, likely domesticated cereal grains. Another common feature, small pits, can possibly be attributed to the presence of small stone particles that made their way into grain flour during the grinding process. By comparison, an abundance of large pits and coarse scratches are caused by “dirty” food such as wild fruits and vegetables or freshly-pulled underground storage organs, and

consistent with European Neandertal populations and other hunter-gatherers (El Zataari, et al. 2011; Schmidt 2016) and therefore would not be expected here.

Individuals from Maurenne Caverne de la Cave and Sclaigneaux exhibit the only significant differences in microwear; they are also more distant from each other than any of the other sites, being separated by approximately 35 km. Subtle ecological variation could have presented each population with a slightly different pool of potential food sources. Moreover, given that Maurenne Caverne de la Cave is the most distant cave both geographically and temporally (it was in use before and contemporaneously with the other sites), shifts in the local ecology or changes in technology (i.e. paramasticatory behavior) could also explain the subtle differences in enamel wear. The results from the dental microwear analyses track with the geographic landscape. Additionally, they support the expectation that the inhabitants of this region during the Middle to Terminal Neolithic consumed a relatively homogenous diet with minor variation between the most distant sites.

4.2 Nonmetric Dental Traits

Maxillary traits show significantly more variation in frequency and rate of expression within and between sites; however, this variation lies within a small margin, suggesting close genetic relationships between groups. For example, Carabelli's trait is common in European, Native American, and Pacific groups, though its frequency and mean rate of expression are highly correlated in Europeans but the two are not correlated in other groups (Scott and Irish 2017, 111). The high frequency of additional cusps indicates a trend toward square molars except in Sclaigneaux, where additional cusps are less frequent, and molars tend to be elongated and triangular.

Analysis of nonmetric dental traits suggests that the inhabitants of the Meuse River Region from the Middle to Terminal Neolithic were very closely related, if not the same biological population. While variation in molar shape and trait expression exists between sites, they are subtle enough to be explained by normal variation over the course of several generations (Palomino, Chakraborty and Rothhammer 1977). Moreover, the variations exist along a continuum that matches the geographic distances between sites. Bois Madame, the most centrally located burial site, also lies in the median of dental microwear patterns and nonmetric trait expression. The most geographically distant sites from each other, Sclaigneaux and Maurenne Caverne de la Cave, are the most different from each other.

These results suggest that the locations of these burials reflect the population in the immediate area. The inhabitants of this region were generally sedentary and may have lived within the same several-kilometer radius for most, if not all, of their lives. The slight variation in dental trait expression across the landscape suggests that there were several related yet distinct settlements in close but limited contact with one another, and that the regional gene pool remained relatively stable through the Neolithic with no evidence of large-scale genetic interruptions or assimilations (Robb 2013).

The evidence suggests that the burials at Maurenne Caverne de la Cave do not represent a single population distinct from its neighbors. Although dietary behaviors and genetic proxies cluster according to the burial site in which they were found, the similarities between sites significantly outweigh any in-group variation. The changes that took place in Belgium during the Middle to Terminal Neolithic reflect *in-situ* cultural change. As groups became increasingly reliant on crops and livestock, they settled down in villages on arable land with a fresh water source. It is likely that many small settlements sprang up along the Meuse river as they did along

the Danube (Květina and Hrnčír 2013) and Körös rivers (Gyucha, Duffy and Parkinson 2013) in Central Europe and that these neighboring communities were in contact with each other more frequently than nomadic foraging groups would have been, allowing for increases in exchanges in technology and culture (Gabel 1958) (Golitzko 2015). The evidence also suggests that each village may have had its own burial ground, though they were in close enough proximity to share burial practices and grave goods as evidenced by the continuity of comingled bones, lithics, pottery, and separated maxillae among the sites.

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APPENDICES

A.1: Complete List of Individuals (n=158)

A.1.1: *Sclaigneaux (n=56)*

92ULP3-M3, 1LRM1-M2, 31LRM1-M2, 15LRM1-M3, 58LLM3, 124URdm1-M1, 126URdm1, 73bLRdm1, 103UM1-M3, 93URM1-M2, 115URdm1-dm2, 47LLM1-M2, 34LRM1-M3, 11LRM1-M2, 28LRM1, 23LRM1-M2, 35LRM1-M2, 42LRM1-M3, 62LLm2-M3, 50LLM1, 63LLM2-M3, 4LRM1, 118ULdm2-M1, 73LRdm1, 120ULdm1, 122ULdm1-dm2, 18LRM1-M2, 82LLdm1-dm2, 56LLM1-M2, 46LLM1-M2, 21LRM1-M3, 40LRM2, 8LRM1-M3, 33LRM1, 108ULM1-M2, 116ULdm1-dm2, 125LRdm1-dm2, 59LLM2, 19LRM3, 3LRM1-M3, 26LRM1-M2, 99ULM1-M2, 97URM1-M2, 90LLM1, 49LLM3, 117ULdm1-dm2, 88LLdm2-M1, 98URM1, 119ULdm1-M1, 5LLdm2-M1, 85LRdm2, 64LLM3, 121ULdm1-dm2, 100URM1, 66LLM1, 91URM1-M3

A.1.2: *Hastière Caverne M (n=24)*

17LLM1-M2, 5LLM1, 14LLM3, 25URM1, 19LRdm2, 15LLM1, 36URM2, 35ULM1-M2, 38(1)LLdm1-dm2, 28URM1-M2, 18LLdm1-dm2, 38ULdm1-dm2, 39URdm1-dm2, 16LRM1-M2, 29ULM2-M3, (?)LRM1-M2, 3LLM1-M2, 34ULM1-M2, 10LRM2-M3, 13LLM1-M2, 31ULM2, 27URM1, 6LRM3, 32URM1-M2

A.1.3: *Hastière Trou Garçon C (n=6)*

HTG3LRM1-M2, HTG9LM1-M3, HTG387LLM1-M3, HTG5 No.6 IG 3873URM1-M2, HTG2LRM2-M3, HTG1ULM1

A.1.4: Bois Madame (n=34)

32LLdm1-dm2, 41Lldm1, 9ULM1-M2, 13URM1-M2, 21ULM2-M3, 16URM2-M3, 27LRdm1-M1, 6URM1-M2, 37LRdm1-dm2, 1URM1-M2, 11URM1-M2, 20LLM2, 10ULM1, 33LLdm1-M1, 65URM2, 27ULdm1-M1, 11LLM1-M3, 29LLM1, 2LRM1-M3, 6LRM1-M2, 28LRdm1-dm2, 4LRM2-M3, 18LLM1-M2, 1LLM2-M3, 13LLM1-M2, 38LRdm1-dm2, 31LLdm2-M1, 36LLdm1-dm2, 19LLM1, 5LRM2, 30LRdm2, 34LLdm1-dm1, 10LRM2-M3, 17LLM2

A.1.5: Maurenne Caverne de la Cave (n=38)

91LRdm1-M1, 31LLM1-LM2, 93LLdm1-M1, 7LRM1-M2, 8LLM1, 8URM1-M2, 85LLdm1-M1, 2LLdm1-dm2, 82LRdm1-dm2, 7LRM1-M3, 15LRM1-M3, 43LRM1-M2, 23LLM1-M2, 79LRM1, 1LRM1-M3, 92LRdm2-M1, 26LLM2, 4ULM1-M3, 29LLM1-M2, 10URM1-M3, 65LLM1, 90LRdm2-M1, 18LLM1-M2, 11ULM1, 15ULM1-M2, 39LRM2, 32LRM1-M3, 34LRM1-M3, 25URdm1-M1, 23URdm1-dm2, 27URdm1, 22URdm1-dm2, 26ULdm1-dm2, 6ULM1, 83LRdm1-dm2, 21ULdm1-M1, 24URdm1-dm2, 17URM1

A.2: Molars Used in Dental Microwear Analysis**A.2.1: Sclaigneaux (n=18)**

100URM1, 91URM1, 66LLM1, 59LLM2, 3LRM2, 99ULM2, 98URM1, 42LRM2, 18LRM2, 56LLM2, 46LLM2, 8LRM2, 50LLM1, 92ULM2, 31LRM2, 35LRM2, 11LRM2, 47LLM2

A.2.2: *Hastière Caverne M (n=15)*

17LRM1, 4 URM2, 29ULM2, 10LRM2, 18LLM2, 32URM2, 15LLM2, 6URM1, 31ULM2,
15LRM2, 23 LLM2, 27ULM2, 36ULM2, 35ULM2, 28URM2

A.2.3: *Hastière Trou Garçon C (n=2)*

HTG4URM2, HTG3LRM2

A.2.4: *Bois Madame (n=15)*

11LLM3, 11LLM2, 2LRM3, 2LRM2, 9ULM2, 21ULM2, 16URM2, 10ULM1, 17LRM1,
12URM1, 20LLM2, 29LLM1, 4LRM2, 18LLM1, 13LLM2

A.2.5: *Maurenne Caverne de la Cave (n=16)*

17URM1, 4ULM2, 29LLM2, 10URM2, 65LLM1, 18LLM2, 32LRM2, 15LRM2, 6ULM1, 31L
LM2, 7LRM2, 8URM2, 15LRM2, 43LRM2, 23LLM2, 26LLM2

A.3 Molars Used in Nonmetric Dental Trait Scoring**A.3.1 *Sclaigneaux (n=46)***

100URM1, 108ULM1, 108ULM2, 116ULdm1, 116ULdm2, 117ULdm1, 117ULdm2,
119ULdm1, 119ULdm2, 119ULM1, 125URdm1, 125URdm2, 91URM1, 91URM2, 91URM3,
97URM2, 99ULM1, 99ULM2, 92ULM1, 92ULM2, 92ULM3, 124URdm1, 124URdm2,
124URM1, 115URdm1, 115URdm2, 103URM2, 103URM3, 93URM1, 93URM2, 19LRM3,
49LLM3, 59LLM2, 64LLM3, 66LLM1, 88LRdm2, 88LRM1, 90LLM1, 1LRM1, 1LRM2,
31LRM1, 31LRM2, 15LRM3, 58LLM3, 35LRM1, 35LRM2

A.3.2: *Hastière Caverne M (n=29)*

36URM1, 36URM2, 35ULM1, 35ULM2, 38ULdm1, 38ULdm2, 39URdm1, 39URdm2,
 29ULM3, 34ULM1, 34ULM2, 25URM1 HTG20ZURM1, HTG6URM1, HTG6URM2,
 HCM32URM1, HGC32URM2, HCM31ULM2, HCM27URM1, 38LLdm2, 18LLdm1,
 18LLdm2, 16LRM1, 16LRM2, 3LRM1, 3LRM2, 13LLM2, 17LLM1, 17LLM2

A.3.3: *Hastière Trou Garçon C (n=2)*

HTG3LRM2, HTG5LLM3

A.3.4: *Bois Madame (n=33)*

9ULM1, 9ULM2, 13URM1, 13URM2, 6URM1, 6URM2, 1URM1, 26ULdm2, 11URM1,
 10ULM1, 65URM2, 20LLM2, 18LLM1, 18LLM2, 5LRM2, 32LLM1, 21LLM3, 27LRM1,
 37LRdm1, 37LRdm2, 11LLM1, 11LLM2, 11LLM3, 29LLM1, 18LLM1, 18LLM2, 13LLM1,
 13LLM2, 31LLM1, 10LRM2, 10LRM3, 27LRM1, 33LLM1

A.3.5: *Maurenne Caverne de la Cave (n=40)*

17URM1, 24URdm1, 24URdm2, 21ULdm1, 21ULdm2, 21ULM1, 8URM1, 8URM2, 4ULM2,
 4ULM3, 11ULM1, 15ULM1, 15ULM2, 83LRdm1, 83LRdm2, 91LRdm1, 91LRdm2, 91LRM1,
 93LLdm1, 93LLdm2, 93LLM1, 81LLM1, 85LLM1, 82LRdm1, 82LRdm2, 15LRM1, 15LRM2,

15LRM3, 43LRM2, 23LLM2, 79LRM1, 1LRM2, 1LRM3, 92LRM1, 29LLM1, 29LLM2,
65LLM1, 90LRM1, 18LLM1, 18LLM2