FRANK L'ENGLE WILLIAMS, JULIET K. BROPHY, GREGORY MATHEWS, EMILEE HART, MARIE-ANTOINETTE DE LUMLEY, GAËL BECAM

NEANDERTAL MANDIBULAR MOLARS FROM HORTUS CAVE, FRANCE: A COMPARISON OF CROWN SHAPES USING ELLIPTICAL FOURIER ANALYSIS

ABSTRACT: Neandertal permanent mandibular molars are well represented at Hortus Cave, France, Sub-Phase IVb and Vb, providing an opportunity to assess intrapopulation and intersite shape variation. We expected the mandibular molars from Hortus cave, comprising Hortus II, Hortus IV, Hortus V and Hortus VI to cluster together, compared to Neandertals close in proximity, such as Malarnaud and La Quina 5 as well as those more distantly located such as Arcy-sur-Cure 1, Engis 2 and Scladina 4A-1. A single Neolithic cave burial from Maurenne Caverne de la Cave, Belgium (n = 11) is used to contextualize the degree of variation in the Hortus assemblage. From photographic images of the permanent molars, crown shapes were digitized and binarized. The resulting images were processed in R using elliptical Fourier analysis and the resulting amplitudes of the harmonics were subjected to principal components analysis and hierarchical clustering. Hortus II and Hortus V, both from Sub-Phase Vb, are relatively similar to one another in M_1 crown shape, and are secondarily grouped with Hortus IV from Sub-Phase IVb. Maurenne Caverne de la Cave has a larger degree of variation in crown shape than the Hortus assemblage, and the Neandertals imperfectly cluster together and apart from the Neolithic sample for some multivariate comparisons. Variance in Neandertal molar crown shape can be primarily explained as the result of chronology. Hortus consistently groups with other MIS 3 Neandertals such as La Quina 5 and Engis 2, while those from MIS 5, represented by Scladina 4A-1 and Malarnaud are distinct as is Arcy-sur-Cure 1 from late MIS 3. Across the molars, the Hortus assemblage is most similar to La Quina 5 from Charente, Southwest France.

KEY WORDS: Arcy-Sur-Cure 1 - Engis 2 - La Quina 5 - Malarnaud - Scladina 4A-1 - Maurenne Caverne de la Cave

INTRODUCTION

Hortus Cave - located about 30 km north of Montpellier - is situated south of the Languedoc Mountains in the piedmont region that separates the Massif Central from the Mediterranean littoral (Lumley 1972, Lumley 1973). Several phases of occupation exist at this location, each containing assemblages of Neandertal material remains (Lumley 1972, Lumley 1973). Phase III and Sub-Phase IVa are butchering sites preserving the carcasses of animals as well as the tools utilized to process the prey (Lebègue *et al*. 2010, Lebègue 2012, Lumley 1972, Lumley 1973, Lumley, Licht 1972, Pillard 1972). The sites were likely occupied for a short duration and indicate a nearly exclusive focus on ibex hunting and processing (Pillard 1972, Lebègue *et al*. 2010). These hunting camps were utilized mainly by small hunting parties (Lebègue *et al*. 2012, Lumley 1972). This type of habitation was eventually replaced with a seasonal exploitation of the site (Sub-Phase IVb and the sub-phases of Phase V) whereby a greater emphasis was placed on the movement of the group as demonstrated by a diversity of activities as opposed to solely the butchering of animals (Lebègue *et al*. 2010, Lebègue 2012, Lumley, Licht 1972). Sub-Phase IVb and Sub-Phases Va, Vb and Vc evidence the remnants of temporary camps, including repeatedly used hearths. The camps were economically self-sufficient and occurred during a single season. The presence of children and adults in these later phases suggests a social unit such as a micro-band and not just a hunting party (Lebègue *et al*. 2010).

If the remains at Hortus represent successive micro-bands of a single population or tribe, who repeatedly occupied the cave, then the individuals from Hortus Sub-Phase IVb and Sub-Phase Vb, should be more similar morphologically compared to individuals from more distant locations and time periods. Several approaches have been employed to reconstruct the relationships among individual fossils, including measurements of molar crown lengths and areas, crown and cervical outlines, three-dimensional digitization and geomorphometrics (Bailey 2000, 2002, 2006, Bailey, Lynch 2005, Bailey *et al*. 2014, 2016, Bauer *et al*. 2016, Benazzi *et al*. 2011a, 2011b, Gómez-Robles *et al*. 2007). Dental traits such as remnants of the cingulum in higher primates (e.g., Carabelli's cusp) are likely to be nonadaptive and thus serve as a proxy for genetic relationships among individuals (Turner *et al*. 1991). Furthermore, area measurements of molar crowns have been shown to be highly heritable in baboons, as have basal molar cusp areas from 2-D images of the occlusal surface and scored dental traits of the cingulum (Hlusko *et al*. 2002, 2007, Hlusko, Mahaney 2003). Both maxillary cusp size from 2-D images and nonmetric dental traits have been shown to partition Neandertals and humans (Bailey 2000, 2002, 2006, Bailey, Lynch 2005).

In this paper, we assess the extent to which individuals are similar to each other using a crown outline shape analysis. The crown shapes were captured using elliptical Fourier analysis (EFA). This method is outline-based and specifically designed for irregular morphologies (Kuhl, Giardina 1982, Lestrel 1974). An EFA allows for the quantification of tooth crown shapes and enables a multivariate statistical assessment of their distribution. The method was chosen because it has proven useful in differentiating taxa and assessing variation when investigating ostensibly similar shapes (Athreya 2006, Bailey, Lynch 2005, Caple *et al*. 2017, Claude 2013, Corny, Détroit 2014, Daegling, Jungers 2000, de Ruiter *et al*. 2013, Schmittbuhl *et al*. 2007). This particular method also allows for the inclusion of a broader range of ages than studies using cusp areas or nonmetric traits, and can include both worn and moderately worn teeth. Extreme dental wear characterizing adults substantially decreases the sample sizes for studies aimed at identifying affinity using dental trait scores, or restricts the samples to unworn teeth (Turner *et al*. 1991). The teeth used in this study range in wear from unworn to moderately worn (stages 1-5 in Molnar 1971) with minor estimates made to account for any interproximal wear.

Neandertals may have lived in small, relatively isolated social groups (Kelso, Prüfer 2014, Lalueza-Fox *et al*. 2011). If true, group contact may have occurred with respect to ecogeographic distance. Barriers to contact may have included the periodic expansion and contraction of glaciers of the Massif Central corresponding to climate variability and changing topography of the terrain (Goër de Herve, Veyret 1976, Miskovsky 1976). Alternatively, chronology may differentiate geologically younger fossils from older ones. The purpose of this study is to explore the variation in molar crown shape among individuals recovered from Hortus cave vis-à-vis other Western European Neandertals from Marine Isotope Stage (MIS) 5 to MIS 3 and a comparative Neolithic sample. We expect the individuals examined from Hortus cave, Hortus II, Hortus IV, Hortus V and Hortus VI to be more similar to one another than any is to an individual from another site.

MATERIALS

In total, we examine 32 molars including M_1 (n = 17), M_2 (n = 9) and M_3 (n = 6) deriving from Hortus cave, isolated Neandertal sites and a Neolithic comparative sample.

Hortus assemblage

The permanent mandibular molars in this study included Hortus II and Hortus V, both from Sub-Phase Vb, Hortus IV from Sub-Phase IVb of Hortus cave and Hortus VI which is unassociated with respect to phase (Lumley 1973) (n = 6, *Table 1*). Hortus II comprises a mandibular mental symphyseal region adjoining the dental arcade to the second deciduous molars, and includes an isolated permanent right first molar (M_1) (Lumley 1973). The child has been aged to about 6.5–7.9 years (Ramírez Rozzi 2005). The Hortus II mandible is associated with the Hortus III partial maxilla (Lumley 1973, 1976, Ramírez Rozzi 2005). Hortus IV consists of a relatively complete mandibular corpus with the first and second molars (M_1 and M_2) as well as the right canine and first premolar *in situ*. This late subadult/young adult is aged to 17–30 years (Lumley 1973). Hortus V includes a small left distal corpus fragment and several isolated teeth, including the right first and third molars (M_1 and M_3), aged to 18–25 years (Lumley 1973). Hortus VI, represented by a right third molar (M_3), is also included (*Table 1*).

Isolated Neandertal sites

The Hortus remains are compared to Neandertal molars (n = 7) from isolated sites, and include those relatively close in proximity, such as Malarnaud of the Pyrenees region and La Quina 5 of southwest France (*Table 1*). Malarnaud is a nearly complete adolescent mandible. The right first molar (M_1) is fully erupted and preserved *in situ*. This subadult has been aged to 14-15 years (Petite-Marie *et al.* 1971). Malarnaud was discovered in 1888 and is dated to the Riss-Würm interval (Petite-Marie *et al.* 1971), approximately equivalent to MIS 5e. La Quina 5 is from the Middle Paleolithic deposits of La Quina cave Level 3, near Charente in the Dordogne of southwest France (*Table 1*). La Quina cave has proven to be an area of intense use during the Upper Pleistocene, yielding, among many others, La Quina 5, the craniofacial remains of an older adult Neandertal, with a full permanent dentition worn to a single functional plane (Petite-Marie *et al.* 1971, Williams 2013). La Quina 5 is associated with a middle Mousterian date of 43-47 Ka,

corresponding to MIS 3 (Discamps, Royer 2017) and was previously considered to be female although this sex attribution has been challenged (Trinkaus 2016).

The sample also included fossils located a considerable distance away from Hortus cave such as Arcy-sur-Cure 1 of central France (Yvonne), and Engis 2 and Scladina 4A-1, two Neandertal fossils from the Meuse River tributaries of Belgium (*Table 1*). Arcy-sur-Cure 1 comprises a partial mandibular corpus with the right first molar (M_1) *in situ*. This adult has been dated to the Upper Pleistocene (Petite-Marie *et al.* 1971). Engis 2 consists of a relatively complete calotte (calvarium), isolated partial maxilla and unerupted right permanent first molars (M_1 and M^1). The child has been aged to between 4–5 years (Toussaint, Pirson 2006, Twiesselmann 1971). Radiocarbon dates of the parietal bone ($26,830 \pm 430$ and $30,460 \pm 210$ years before present (BP) are considered to be too recent, and do not correspond to the associated Mousterian artefact assemblage from MIS 3 (Di Modica *et al.* 2016, Toussaint *et al.* 2011, Toussaint, Pirson 2014). The Scladina 4A-1 mandibular fragment includes a right mandibular second molar (M_2) of the Scladina 1-4A child, which comprises demi-mandibles, a right maxillary fragment and a mixed dentition, and has been aged to between 8-11 years (Smith *et al.* 2014; Williams 2013). Scladina 1-4A has been dated to between 127–130 Ka using gamma-ray spectrometry, although chronostratigraphic methods within the context of the Greenland Record suggest the individual is 80–87 Ka, corresponding to MIS 5a or MIS 5b (Pirson *et al.* 2014, Toussaint, Pirson 2014) (*Table 1*).

Neolithic human sample

A comparative sample from Maurenne Caverne de la Cave (n = 11), a Neolithic site from the Hastière rockshelter of the Meuse Basin of Belgium, was utilized to provide a context for assessing the variation in crown shape within the Hortus assemblage (*Table 2*). The radiocarbon dates from Maurenne Caverne de la Cave span over 800 years suggesting the cave was used as a burial chamber for nearly a millennium. One of these dates, $4,635 \pm 45$ years BP, is from the Middle Neolithic. The other three, including $4,160 \pm 45$ years BP, $3,950 \pm 70$ years BP and $3,830 \pm 90$ years BP are Final/Late Neolithic (Bronk-Ramsey *et al.* 2002, Toussaint 2007). Maurenne Caverne de la Cave mimics the Hortus assemblage in several important ways, including the fragmentary nature of the remains which primarily consist of small gnathic fragments with molars *in situ* (*Table 2*). Like Hortus, both adults and

children are represented at Maurenne Caverne de la Cave in multiple internments over a large span of time (Vanderveken 1997) (*Table 2*).

METHODS

The occlusal surface of the molars was photographed using a Sony Nex-6 equipped with a 3.5–5.6 OpticLens at the EPCC-Centre Européen Recherches Préhistoriques de Tautavel, Musée de l'Homme (Paris), Université de Liège, the Centre Archéologique de la Grotte Scladina of Belgium (*Table 1*) and the Institut Royal des Sciences Naturelles de Belgique (Brussels)

(*Table 2*). The camera was positioned directly above the tooth and was levelled to be parallel to the table surface. Each tooth was placed such that the cervical line was perpendicular to the camera. A standard distance between the tooth and the camera of 30–35 cm with automatic zoom was maintained to offset the effects of parallax (Corny, Détroit 2014). Left teeth were used in the analysis; when the right side was better preserved than its antimere, it was used by flipping the image horizontally in Adobe Photoshop®.

The outline of each tooth was captured using the freeware GIMP (www.gimp.org). Points are placed around the outside of the tooth using the lasso tool. The image is then converted into a black and white image

TABLE 1: List of fossils examined. [a] RM = right molar; LM = left molar.

Fossil	Molar[a]	Dental age	Chronology
Arcy-sur-Cure 1	RM_1	Young adult	MIS 3
Engis 2	RM_1	Child (4–5 years)	MIS 3
La Quina 5	LM_1, LM_2, LM_3	Adult (25–30 years)	MIS 3
Hortus II (1265)	RM_1	Child (6.5–7.9 years)	MIS 3
Hortus IV (1436)	RM_1, RM_2	Subadult/adult (17–30 years)	MIS 3
Hortus V (988, 796)	RM_1, RM_3	Adult (18–25 years)	MIS 3
Hortus VI (13)	LM_3	Adult (22–30 years)	MIS 3
Malarnaud	RM_1	Subadult (14–15 years)	MIS 5
Scladina 4A-1	RM_2	Juvenile (8–11 years)	MIS 5

TABLE 2: Neolithic sample from Maurenne Caverne de la Cave, Belgium.

Individual	Molar	Preservation
Maurenne 1	M_1, M_2, M_3	Nearly complete mandible with right M_1, M_2 and M_3 *in situ*
Maurenne 15	M_1, M_2, M_3	Right corpus fragment with M_1, M_2 and M_3 *in situ*
Maurenne 26	M_2	Left partial corpus and ramus to P_3 crypt with M_2 *in situ*
Maurenne 29	M_1, M_2	Left partial corpus and ramus to P_3 crypt with M_1 and M_2 *in situ*
Maurenne 31	M_1, M_2	Left corpus fragment with M_1 and M_2 *in situ* and M_3 (damaged)
Maurenne 32	M_1, M_2, M_3	Right corpus fragment with M_1, M_2 and M_3 *in situ*
Maurenne 79	M_1	Right corpus fragment with M_1 *in situ*
Maurenne 85	M_1	Corpus from right I_1 crypt to left unerupted M_2 with M_1 *in situ*
Maurenne 91	M_1	Right corpus and partial ramus with dm_1, dm_2 and M_1 *in situ*
Maurenne 92	M_1	Right ramus and corpus fragment with dm_2 and M_1 *in situ*
Maurenne 93	M_1	Left ramus to right canine holding dm_1, dm_2 and M_1 *in situ*

with the bucket fill tool (*Figure 1*). Conservative estimates were made for teeth that had interproximal wear or damage to the crown. For each tooth (i.e., M_1, M_2 and M_3), the binarized black and white images of the teeth were loaded into the R statistical programming language (R Core Team, 2017) using the "import_jpg" function from the "Momocs" (Bonhomme *et al.* 2014) library which extracts points along the edge of the shape of the tooth. An EFA was then performed on the shape of the outline of the occlusal surface in order to produce amplitudes of the harmonics. The amplitudes are the degrees of deviation between the object in question and an original ellipse (Brophy *et al.* 2014, Caple *et al.* 2017, Claude 2013, Corny, Détroit 2014, Kuhl, Giardina 1982, Lestrel 1971, 1989). The harmonic coefficients from EFA were generated using R. Specifically, the "efourier" function from the R package "Momocs" was used to approximate the shape of each tooth using 8 harmonics with the size standardization option implemented. Size standardization in EFA is achieved by rotating, translating and scaling the first ellipse such that differences in magnitude are minimized.

Observer error study

An intraobserver error study was conducted to demonstrate measurement precision and the reliability of the method. The same observer traced the contours of each tooth type in this study twice, and the resulting outlines were visually compared to ascertain differences between the two trials. Although it is not possible to conduct a Mann-Whitney U test on observations done by the same observer since they are not independent, we did conduct Mann-Whitney U tests on PC scores derived from two observers (JKB and EH) on the same molars.

Analytical tools

To examine whether the individuals from Hortus cave cluster together or whether they were dispersed compared to other Neandertals and with respect to the Neolithic sample, a principal components (PC) analysis was performed on M_1, M_2 and M_3 using the Fourier coefficients as input vectors. For each molar, at least half (>50%) of the variance explained in the PC scores is presented, and plots are shown with convex hulls demarcating Maurenne Caverne de la Cave, and for M_1, the Hortus sample as well. To further estimate affinity, a hierarchical cluster analysis was performed on the scaled harmonic coefficients generated by each molar with the distance matrix computed by measuring Euclidean distances between vectors of Fourier coefficients defining each shape and single linkage used to join clusters.

RESULTS

Observer error study

Differences between trials of the intraobserver error study are represented by the outlines of the first molar (M_1) from Hortus II, V and IV superimposed on each other (*Figure 2*). The trials are quite close to one another suggesting the crown outline tracing method is highly repeatable. In addition, non-significant p values were obtained from Mann-Whitney U tests when the PC scores were compared between two observers.

Principal components analysis

The first two PC axes describing 31.3% of the variance in the crown shape of the mandibular first molars cluster the Hortus Neandertals on both vectors, together with Engis 2, Malarnaud and to a lesser extent,
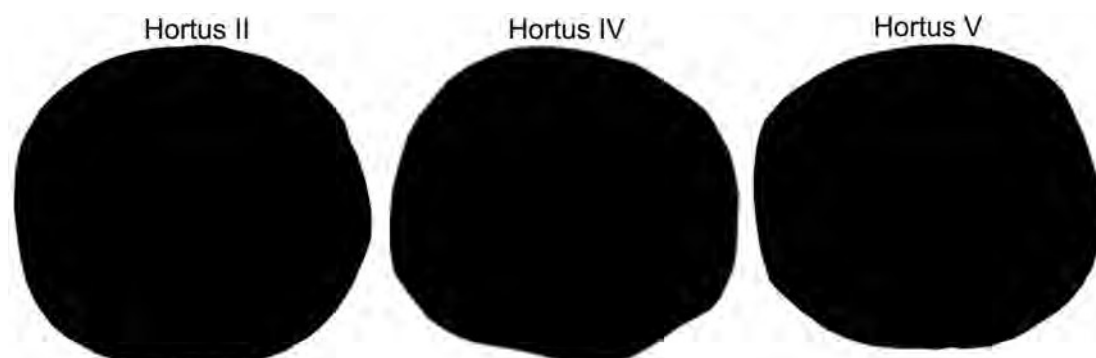

FIGURE 1: Binarized images of the mandibular first molars (M_1) of Hortus II, Hortus IV and Hortus V; all molars flipped from right to left, and aligned with the mesial cusps to the right and buccal as top side.
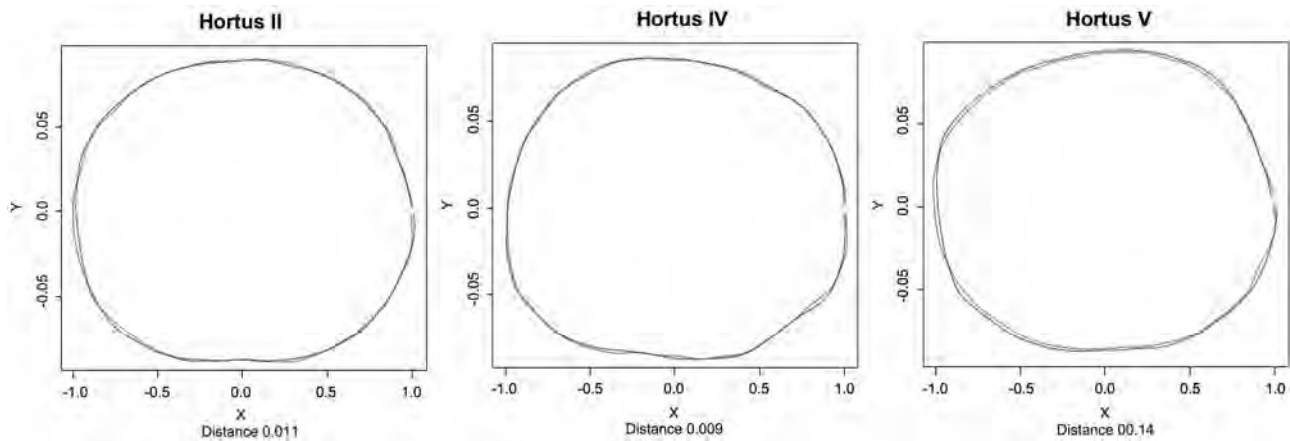
FIGURE 2: Two tracings of Hortus II, Hortus IV and Hortus V (M_1) conducted by the same observer show nearly identical outlines; all molars flipped from right to left, and aligned with the mesial cusps to the right and buccal as top side.

La Quina 5. Arcy-sur-Cure 1 appears as an outlier on both axes. The variation within the Maurenne Caverne de la Cave is much larger than that observed for Hortus and the other Neandertals with the exception of Arcy-sur-Cure 1 (*Figure 3*).

On PC3 and PC4, explaining 21.9% of the variance, Hortus II and Hortus V are positioned together and are closest to La Quina 5, whereas Hortus IV is projected farther in a positive direction. However, on PC4, Hortus IV is nearly identical to Hortus II and the two are similar to Hortus V. On PC3, Engis 2 is an outlier but on PC4 it is similar to the Hortus assemblage. Malaranud is closest to Hortus IV on PC3, whereas on

PC4 it is an extreme outlier. Arcy-sur-Cure 1 is the most similar to Hortus IV. The size of the Neolithic convex hull greatly surpasses the hull for Hortus (*Figure 3*).

For the second molar, PC1 and PC2 together explain 39.1% of the variance. Only Hortus IV is available and it is found outside the margin of the convex hull for Maurenne Caverne de la Cave (*Figure 4*). The other Neandertals are found along the border of the Neolithic distribution. With respect to the Neandertals, Hortus IV is relatively close to La Quina 5 and the two are polarized from Scladina 4A-1. On PC2, all of the Neandertals are similarly positioned and distinct from all but one individual from the Neolithic sample (*Figure 4*).
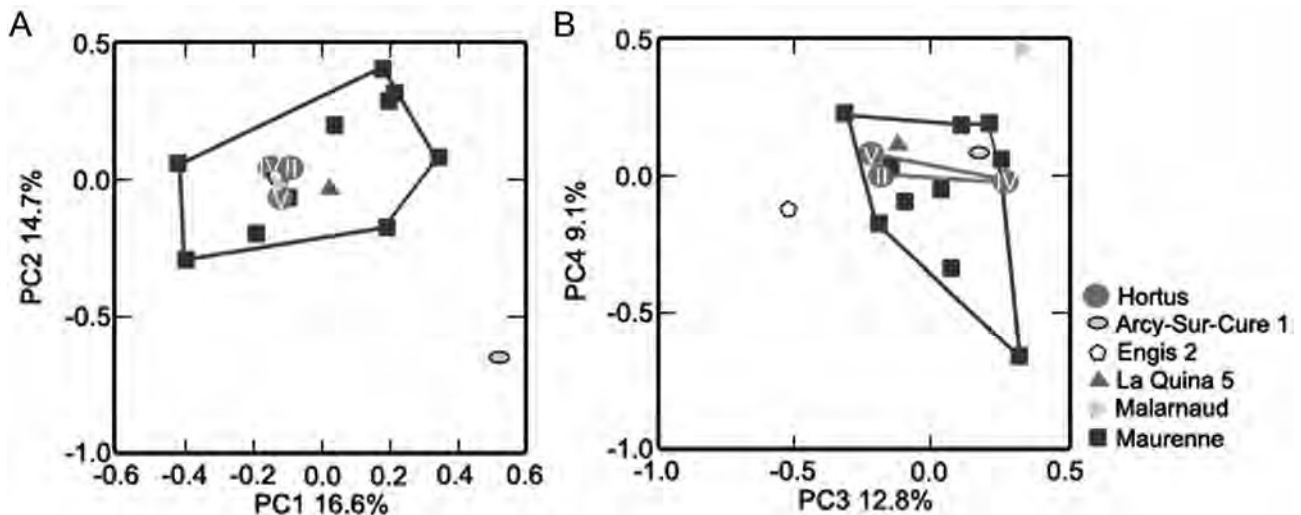

FIGURE 3: Principal components of the scaled amplitudes of the harmonics for M_1 (A) PC1 and PC2 and (B) PC3 and PC4; Hortus and Maurenne Caverne de la Cave are demarcated by a convex hull comprising 100% of the variation for each sample.
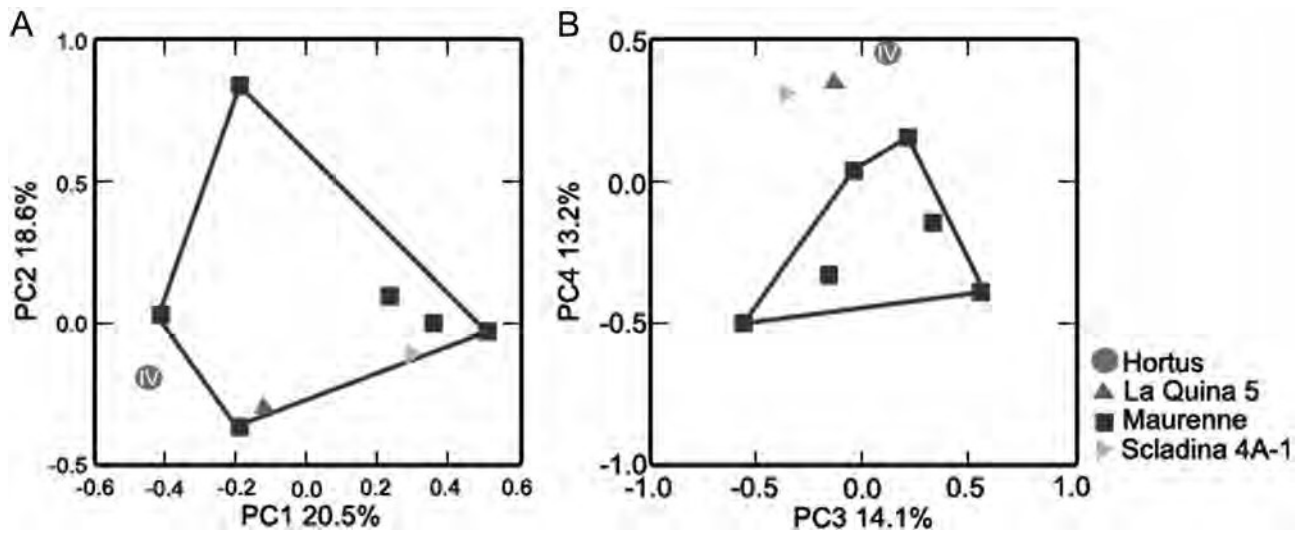
FIGURE 4: Principal components of the scaled amplitudes of the harmonics for M_2 (A) PC1 and PC2 and (B) PC3 and PC4; Maurenne Caverne de la Cave is demarcated by a convex hull comprising 100% of the variation of the Neolithic sample.

For PC3 and PC4, explaining 27.3% of the variance, all of the Neandertal fall outside of the convex hull for Maurenne Caverne de la Cave. On both axes, La Quina 5 is most similar to Hortus IV, particularly on PC3 where both differ from Scladina 4A-1 (*Figure 4*).

For the third molar, the first two axes PC1 and PC2 account for 53.5% of the variation in crown shape (*Figure 5*). Again, the Neandertals all fall outside the convex hull for the small number of Neolithic individuals represented. La Quina 5 is closest to Hortus VI on PC1 and is very close to Hortus V on PC2 (*Figure 5*). For PC3 and PC4, describing 34.1% of the variance, the Neandertals are also outside the convex hull for Maurenne Caverne de la Cave (*Figure 5*). On PC3 Hortus V is positioned between Hortus VI and La Quina 5, whereas on PC4 the two individuals from Hortus are close to one another as is the case for PC5 (not shown) explaining 12.3% of the variance.
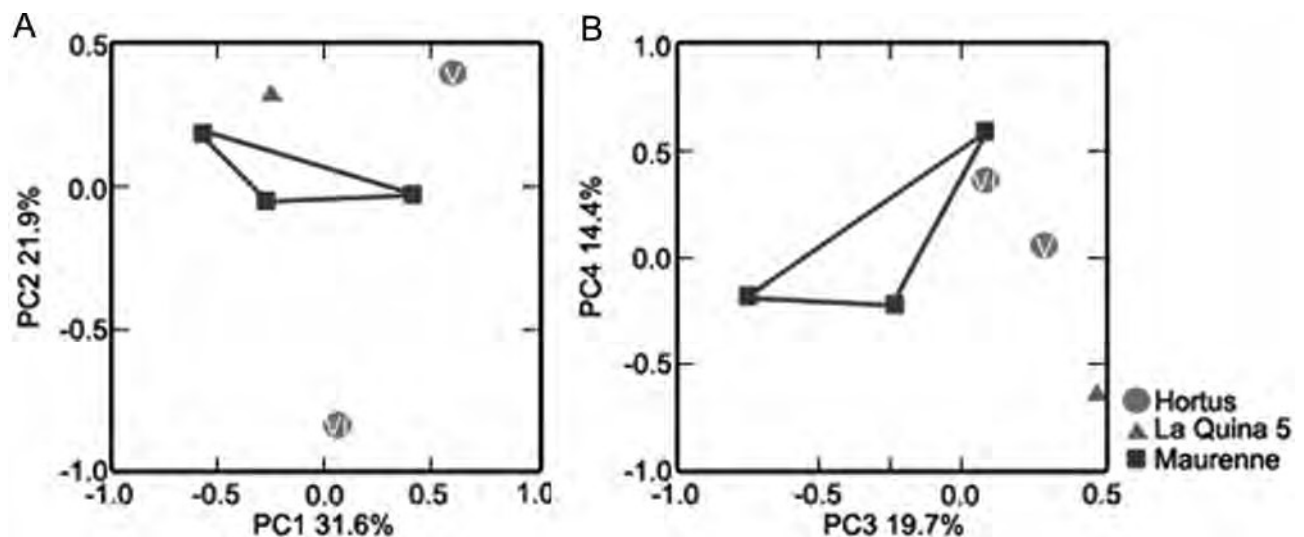

FIGURE 5: Principal components of the scaled amplitudes of the harmonics for M_3 (A) PC1 and PC2 and (B) PC3 and PC4; Maurenne Caverne de la Cave is demarcated by a convex hull comprising 100% of the variation of the Neolithic sample.

Hierarchical cluster analysis

A hierarchical cluster analysis run on the amplitudes of the harmonics for M_1 shows that relatively short distances are found between Hortus V, Hortus II and La Quina 5 and to a lesser extent with Engis 2 (*Figure 6*). Hortus II and La Quina 5 are the most similar, followed by Hortus V whereas Engis 2 is the next nearest branch. This entire group is exclusively from MIS 3. A short branch joins Malarnaud and Hortus IV. These two branches are joined by a relatively long branch that separates all of the Hortus Neandertals and the others from the most distinct fossil, Arcy-sur-Cure 1 which is separated from the rest by the longest branch (*Figure 6*). The distribution of Maurenne Caverne de la Cave is much larger than observed for the Hortus assemblage. For M_2, a short distance links Hortus IV and La Quina 5 (*Figure 6*). This cluster is joined to Scladina 4A-1 by a relatively long branch length (*Figure 6*). The Neolithic sample contains a greater amount of variation than is observed for the M_2 crown shape of the Neandertals. For M_3, the three Neandertals examined are clustered into two groups, one of these contains Hortus V. On the other, Hortus VI is similar to La Quina 5, but not particularly so with respect to the widely dispersed Neolithic sample (*Figure 6*).
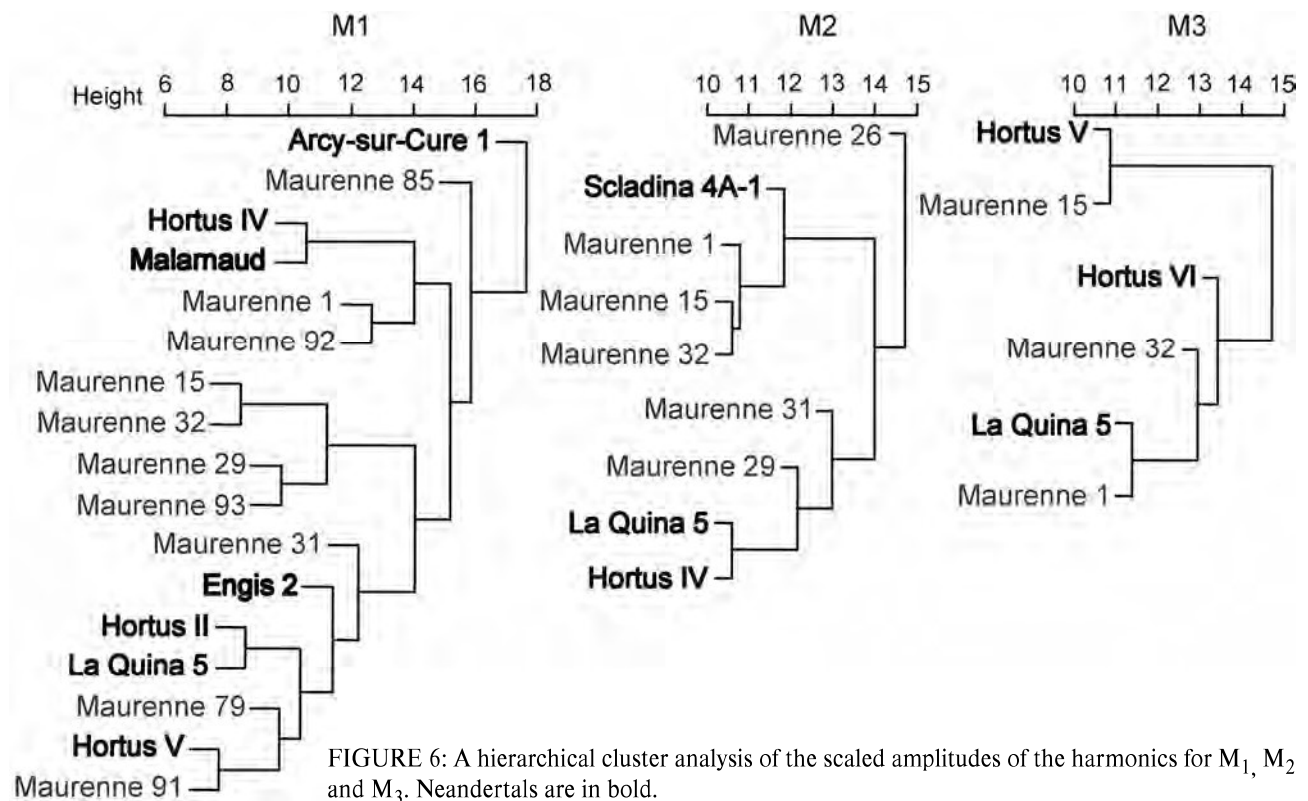
DISCUSSION

In the cluster analysis for M_1, MIS 3 Neandertals are separate from the others in the sample (*Figure 6*). The Hortus Neandertals are divided such that Hortus II and Hortus V, both from Sub-Phase Vb, are grouped closely together and are distinct from Hortus IV from Sub-Phase IVb. In the analysis of the first molar (M_1), the individual with the most distinctive crown shape is Arcy-sur-Cure 1 (*Figures 3, 5*).

The cluster analyses for the second and third molars (M_2 and M_3) reveal that the Hortus assemblage (Hortus IV, Hortus V and Hortus VI) repeatedly groups with La Quina 5 (*Figure 6*). The PC axes confirm the similarity between Hortus VI and La Quina 5 for the third molar (*Figure 4*). However, on other PC axes, the M_3 crown shape of Hortus VI is most similar to Hortus V (*Figure 4*).

The suggestion that chronology influenced the results of this analysis is corroborated by the differences found

FIGURE 6: A hierarchical cluster analysis of the scaled amplitudes of the harmonics for M_1, M_2 and M_3. Neandertals are in bold.

between Scladina 4A-1 and other Neandertals. Scladina 4A-1 is distinct from the MIS 3 Neandertals in the PC axes and cluster analysis for M_2 (*Figures 4, 6*). The position of Arcy-sur-Cure 1 may also be influenced by chronology, given its distinctive crown shape as shown in the cluster analysis for M_1 (*Figure 6*). On both PC1 and PC2, Arcy-sur-Cure 1 is an extreme outlier (*Figure 3*). Arcy-sur-Cure 1 was discovered in the Grotte des Fées in 1859, and its dating is not well established (Petite-Marie *et al.* 1971). If Arcy-sur-Cure 1 is from an Upper Paleolithic context, its divergent crown shape vis-à-vis the Neandertals would be explained.

As demonstrated by the PC axes, the individuals within the Hortus assemblage are relatively similar to one another and are closest in mandibular first molar shape to La Quina 5, followed by Engis 2 (*Figure 3*). The assemblage from Hortus cave has been dated to MIS 3. The periodic glaciation of the Languedoc Mountains, particularly during MIS 4 and MIS 3, may have partially restricted contact between populations living between the piedmont of the Massif Central and the Mediterranean coast, such as Hortus, and those living in the Dordogne region of southwest France. The Mousterian industry preserved at Hortus is most similar to those of the southeast of France (Lumley 1973). The degree of contact between Hortus cave and areas outside of the Mediterranean region may have been impacted by intermittent intense cold and dry conditions, which also characterized southwest France during MIS 3 (Laville 1976). Nevertheless, the Dordogne may have been a core area and refugia for Neandertals from MIS 5 to MIS 3 and could have influenced other regions to the northeast and south, such as Hortus cave.

Chronology and/or ecogeography may also explain the distinctive crown shape of the mandibular first molar (M_1) of Malarnaud from the lower Pyrenees (*Figure 3*). In terms of distance, Malarnaud is the closest site in the sample to Hortus cave. However, Malarnaud is relatively distinct in its crown shape from Hortus II, Hortus IV and Hortus V which together form a relatively cohesive group (*Figure 3*). However, Malarnaud also shares some shape similarities with Hortus IV (*Figure 6*).

The Neolithic collective burial of Maurenne Caverne de la Cave shows greater variation in molar crown shape than do the individuals from Hortus cave in all comparisons. Although the existence of a multi-generation subgroup or micro-band represented by the Neandertal remains from Hortus cannot be demonstrated by these analyses, it is certainly not possible to refute such an assertion (Lebègue *et al.* 2010).

CONCLUSION

The results of this study demonstrate that Hortus II, Hortus IV and Hortus V are relatively similar to each other. This similarity is particularly true of Hortus II and Hortus V, both of which derive from Sub-Phase Vb of Hortus cave. The variation in molar crown shape of a Middle to Final/Late Neolithic sample from Maurenne Caverne de la Cave (Belgium), a collective burial spanning perhaps more than 800 years, far exceeds that noted for the Hortus assemblage consistent with the suggestion that these teeth of Hortus may represent the remains of a micro-band or social group over time. La Quina 5 resembles the Hortus Neandertals in crown shape across all of the molars. The crown shape analysis of the remaining teeth in the sample is not as easily explained by chronology or ecogeography.

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Frank L'Engle Williams*
Department of Anthropology
Georgia State University
USA
E-mail: frankwilliams@gsu.edu

Juliet K. Brophy
Emilee Hart
Department of Geography &
Anthropology
Louisiana State University
USA
E-mail: jbrophy@lsu.edu
E-mail: emileehart94@gmail.com

Gregory Mathews
Department of Mathematics and
Statistics
Loyola University
USA
E-mail: gjm112@gmail.com

Marie-Antoinette de Lumley
Institut de Paléontologie Humaine,
Paris,
FRANCE
E-mail: marie-antoinette.malumley@mnhn.fr

Gaël Becam
Université de Perpignan
EPCC-Centre Européen de Préhistore
de Tautavel
avenue Léon Jean Grégory, 66720
Tautavel
FRANCE
E-mail: gael.becam@cerptautavel.com

*Corresponding author.