2021

Elliptical Fourier Analysis of Crown Shape in Permanent Mandibular Molars From The Late Neolithic Cave Burials of Belgium

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ANTHROPOLOGIE • LIX/1 • pp. 1–14 • 2021

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ELLIPTICAL FOURIER ANALYSIS OF CROWN SHAPE IN PERMANENT MANDIBULAR MOLARS FROM THE LATE NEOLITHIC CAVE BURIALS OF BELGIUM

ABSTRACT: Prehistoric remains from caves and rockshelters are known from more than 250 sites situated along the Meuse River Basin of Belgium. Most of these osteological remnants date to the Late Neolithic period beginning after 4,500 years before present (BP), and five of these cave burials have been subject to intensive study, including Hastière Caverne M and Hastière Trou Garçon C from an earlier period of the Late Neolithic (4,345 ± 60 to 4,220 ± 45 years BP), Sclaigneaux and Bois Madame from the final/late Neolithic (4,155 ± 35 to 3,910 ± 40 years BP) and Maurenne Caverne de la Cave which dates to the final/late Neolithic period, 4,160 ± 45 to 3,830 ± 90 years BP and Middle Neolithic, 4,635 ± 45 years BP. Since the majority of the remains comprise gnathic fragments with in situ dental elements, comparisons between the caves are largely restricted to the teeth. Elliptical Fourier analysis of 40 permanent mandibular molar crown outlines from 27 individuals is utilized to address the degree to which chronology and ecogeography can explain the variation in crown shape across the caves. Although the sample sizes are limited, the cave burial of Hastière Caverne M appears to be distinctive. The variation within the cave burials of Sclaigneaux and Maurenne Caverne de la Cave is extensive, and a pronounced overlapping characterizes some of the sites. The results may provide evidence for increasingly broader contact between Late Neolithic farming communities of the Belgian Meuse basin prior to the Bronze Age.

KEY WORDS: Hastière Caverne M – Hastière Trou Garçon C – Sclaigneaux – Bois Madame – Maurenne Caverne de la Cave – Final/Late Neolithic – Elliptical Fourier functions – Occlusal shape – Molar contours – Crown form

Received 12 November 2019; accepted 9 April 2020.

DOI: https://doi.org.10.26720/anthro.20.07.14.1

INTRODUCTION

Copper and tin alloys were common in southeastern Europe by the 4th millennium. However, in northern Europe, the transition to the Bronze Age occurred more than two thousand years later (Nørgaard 2018). The use of metals, which fundamentally transformed human political organization through weapons of war, was preceded in many parts of northern Europe by nearly two millennia of Neolithic settlements, some which developed distinctive funerary practices involving the internment of multiple individuals within caves and rockshelters. A wealth of these Neolithic burial remains – radiocarbon dated from ~5,345 to ~3,390 years BP (before present) – have been discovered within the karstic formations along the Meuse river basin of Wallonia, Belgium, of which the great majority date to the Late Neolithic beginning at 4,500 years BP (Bronk-Ramsey *et al.* 2002, Orban *et al.* 2000, Toussaint 2007).

The earliest of these caves to be formally excavated was Schmerling Cave, or the second cave of Engis, during the winter of 1829–1830, which yielded the Engis 2 Neandertal child as well as the intrusive Neolithic remains of Engis 1 (Toussaint *et al.* 2011). This discovery spawned interest in the caves of the Belgian Meuse basin, and others were excavated in the late 19th century, such as Hastière rockshelter (Orban *et al.* 2000, Toussaint 2007, Toussaint *et al.* 2011) and Maurenne Caverne de la Cave (Vanderveken 2007). Presently, over 230 funerary sites in Belgium are known to date to the Middle and Late Neolithic (Toussaint *et al.* 2001). Some of these burials comprise one to two individuals, although most contain five or more, but fewer than 15 (Polet 2011). The largest Late Neolithic collective burials tally more than 55 individuals, such as Sclaigneaux (De Paep 2007, Polet 2011, Toussaint 2007). Funerary behaviors include deposition, cut-marks, burial, secondary reburial, regrouping of elements and cremation (Polet 2011, Toussaint 2007, Toussaint *et al.* 2001). While some of the burials are found at the entrance of caves and within rockshelters where sunlight is visible, others are placed deep within caverns in dark recesses (Toussaint 2007). Some of these Late Neolithic burials are found at principle points along the Meuse River. Others are found within small valley tributaries. Often the burials are positioned in crevices within the karst cliffs close to the summit, or within fissures in the cliff walls (Toussaint 2007). In some caves, all of the available fissure area is utilized, whereas in other locations, these crevices are only partly filled with human remains.

The larger collective burials contain adult females and males as well as immature remains which comprise a third to one half of the individuals (Polet 2011, Toussaint 2007). These funerary deposits are valuable for understanding the composition of individuals and their relation to others buried during this time period (Polet 2011, Toussaint 2007), and include Hastière Caverne M, Hastière Trou Garçon C, Sclaigneaux, Bois Madame and Maurenne Caverne de la Cave (*Figure 1*). All of these five collective burials are dated to the Late Neolithic using radiocarbon dating (*Table 1*). One exception is Maurenne Caverne de la Cave which yields three dates from the Late Neolithic (4,160 ± 45; 3,950 ± 70; 3,830 ± 90 years BP), and a single date deriving from the Middle Neolithic (4,635 ± 45 years BP). The variation in radiocarbon dates could suggest Maurenne Caverne de la Cave was utilized as a burial chamber for <800 years (Bronk-Ramsey *et al.* 2002, Toussaint 2007, Vanderveken 1997, 2007). However, there is no association between the four isolated bone samples utilized for radiocarbon dating and the gnathic fragments, obscuring the chronological attribution of individuals from Maurenne Caverne de la Cave (Vanderveken 2007).

Hastière rockshelter was utilized for burials by various Neolithic peoples over the span of 5,180 ± 45 years BP to 4,155 ± 50 years BP (Orban *et al.* 2000). The cave was excavated from approximately 1867 to 1873, and includes Hastière B, Hastière L, Hastière Fanfan, Hastière Caverne M, Hastière Trou Garçon C, Hastière Petite Caverne, and these are adjacent to Maurenne Caverne de la Cave (Orban *et al.* 2000, Vanderveken 2007). Two of these deposits, Hastière Caverne M and Hastière Trou Garçon C, are dated to earlier in the Late Neolithic (*Figure 1, Table 1*). Hastière Caverne M dates to 4,345 ± 60 years BP whereas Hastière Trou Garçon C is dated to 4,220 ± 45 years BP (Bronk-Ramsey *et al.* 2002, Toussaint 2007).

Two caves from the final/late Neolithic period include Sclaigneaux and Bois Madame. Sclaigneaux is dated to 4,155 ± 35 years BP (De Paepe 2007). Two dates are known for Bois Madame, 4,075 ± 38 years BP and 3,910 ± 40 years BP, perhaps indicating more than 150 years of use. Both of the dates for Bois Madame are from the terminus of the Neolithic preceding the Bronze Age (Bronk-Ramsey *et al.* 2002, Dumbruch 2007).

Comparing Neolithic cave burials of Belgium

Although the remains are largely fragmentary and commingled, hundreds of individuals are represented

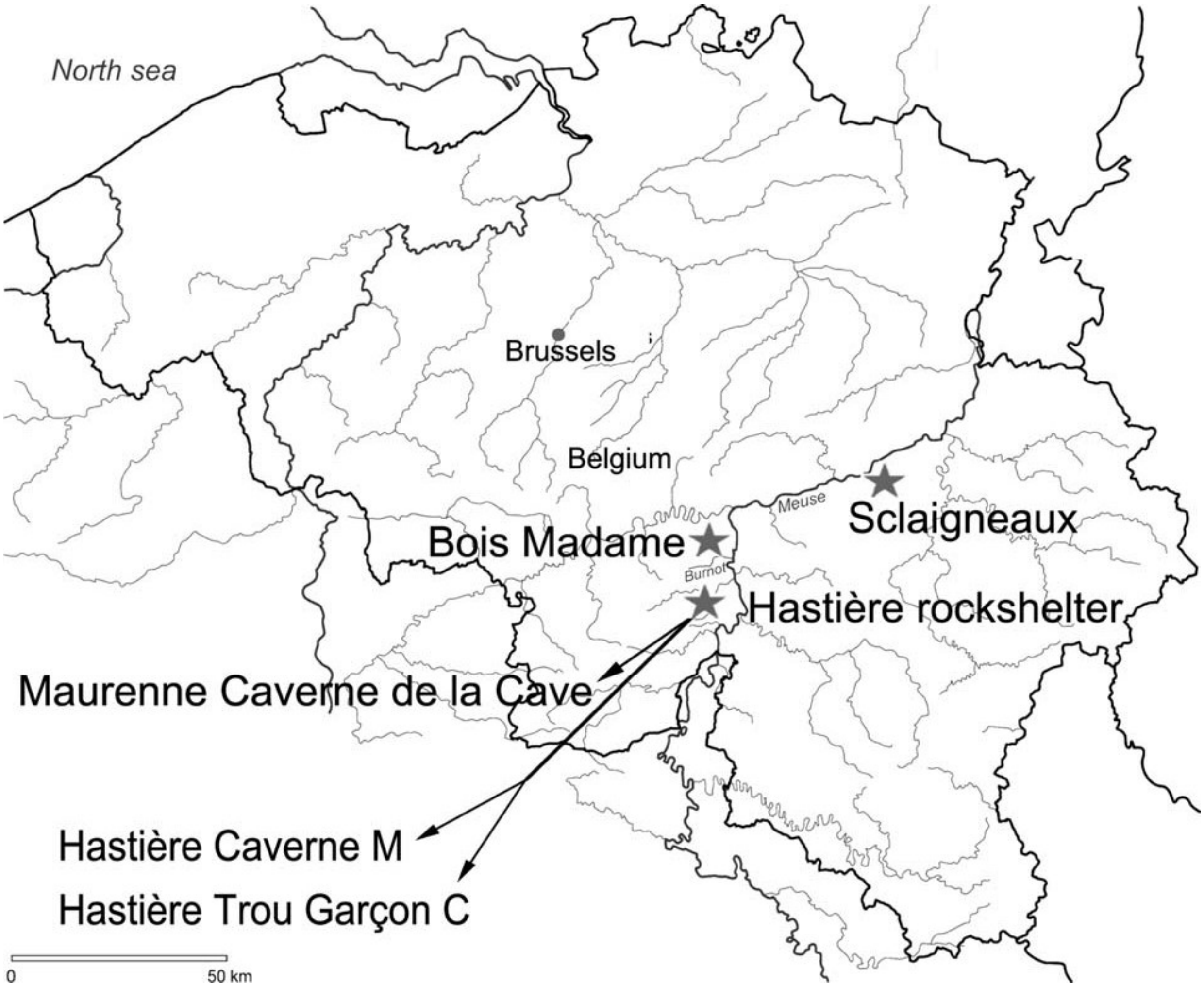

FIGURE 1: Map of Belgium showing the location of the five cave burials featured in this study.

TABLE 1: Radiocarbon dates for five cave burials of the Belgian Meuse basin, from earliest to latest, using Accelerated Mass Spectrometry (AMS) at Oxford University, UK (OxA) and Rijksniversiteit Groningen, the Netherlands (GrA), and conventional methods at the University of Louvain, Belgium (Lv). [a]Bronk Ramsey *et al.* 2002, [b]Toussaint 2007, [c]De Paepe and Polet 2007.

Neolithic cave burial	Sample number	Date in years BP
Maurenne Caverne de la Cave	AMS OxA-9025[a, b]	4,635 ± 45
Hastière Caverne M	AMS OxA-6558[a, b]	4,345 ± 60
Hastière Trou Garçon C	AMS OxA-6853[a, b]	4,220 ± 45
Maurenne Caverne de la Cave	AMS OxA-9026[a, b]	4,160 ± 45
Sclaigneaux	GrA-32975[c]	4,155 ± 35
Bois Madame	AMS OxA 10831[b]	4,075 ± 38
Maurenne Caverne de la Cave	Lv-1483[b]	3,950 ± 70
Bois Madame	AMS OxA 10830[b]	3,910 ± 40
Maurenne Caverne de la Cave	Lv-1482[b]	3,830 ± 90

by mandibular remains with molars in situ, allowing for variation in crown shape across sites to be examined. Dietary reconstructions have shown that the farmers from these Late Neolithic caves of Belgium did not exhibit substantial differences between sites in terms of the mechanical properties of the foods consumed (García Martín 2000, Semal *et al.* 1999). In contrast, funerary practices are tremendously variable (Toussaint *et al.* 2001), and some differences in stature have been noted (Orban *et al.* 2000). For example, the mean of six stature estimates of the metatarsals of Hastière Trou Garçon C is nearly 4 cm higher than for Maurenne Caverne de la Cave which exhibits the greatest amount of variation of all of the caves of Hastière rockshelter in terms of stature (Orban *et al.* 2000). Hastière Caverne M presents a slightly higher range of stature estimates compared to Maurenne Caverne de la Cave. In addition to the higher stature estimated for Hastière Trou Garçon C, this site preserves nearly complete crania in contrast to the fragmentary condition of most of the gnathic remains from the other sites.

Although Hastière Caverne M and Hastière Trou Garçon C differ in stature as well as funerary behavior, it is reasonable to assume that cave burials from earlier in the Late Neolithic will be more similar in crown shape to one another than either will be to Sclaigneaux or Bois Madame. Similarly, the final/late cave burials should be more similar to each other than either is to sites from earlier in the Late Neolithic. Since three out of four radiocarbon dates for Maurenne Caverne de la Cave are from the final/late Neolithic, this collective burial should be more similar to Bois Madame and Sclaigneaux than to the earlier Late Neolithic sites of Hastière Caverne M and Hastière Trou Garçon C.

In addition to chronology, ecogeographic distance may also account for the variation in crown shape. Since three of the burials are situated within or close to Hastière rockshelter (Hastière Caverne M, Hastière Trou Garçon C and Maurenne Caverne de la Cave), it is possible that they will be the most similar to one another, and perhaps to nearby Bois Madame of the Burnot valley. Meanwhile, Sclaigneaux is the most distant site, about 35 km from Hastière rockshelter, and this collective internment should be the most distinct if ecogeography explains the differences in crown shape among the cave burials (*Figure 1*).

Crown shape is likely to demonstrate affinity since features of tooth form are known to be shared among close relatives (Alt *et al.* 1997, Scott, Turner 1997, Scott *et al.* 2018). Dental traits are highly heritable, including measurements of molar crown lengths and areas (Hlusko *et al.* 2002). In pedigreed baboons, area measurements of molar crowns are shown to be highly heritable with more than 55% of the variance explained by the additive effects of genetic mechanisms (Hlusko *et al.* 2002). Basal molar cusp areas from 2-D images of the occlusal surface are also reported to be highly heritable (Hlusko *et al.* 2007). Scored dental traits of the cingulum, such as the interconulus and interconulid of baboons demonstrate high heritability (Hlusko, Mahaney 2003), further implying that dental variation is largely under genetic control. Dental traits such as remnants of the cingulum in higher primates (i.e., Carabelli's cusp) are likely to be nonadaptive and thus serve as a proxy for genetic relationships among individuals (Turner *et al.* 1991). Both maxillary cusp size from 2-D images and nonmetric dental traits have been shown to partition fossil and recent humans (Bailey 2000, 2002, 2006). Crown form also partitions groups (Bailey, Lynch 2005, Bailey *et al.* 2014, Bauer *et al.* 2016, Bennazi *et al.* 2011a, b), but not human females and males, which differ in size but not molar outline shape (Ferrario *et al.* 1999).

In order to assess variation within and between molars in these Neolithic sites, we use elliptical Fourier analysis to compare crown outlines. Elliptical Fourier analysis has been utilized previously as a tool to compare differences in morphology (Athreya 2006, Carlo *et al.* 2011, Daegling, Jungers 2000, de Ruiter *et al.* 2013, Kuhl, Giardina 1982, Lestrel 1974, 1989), and for assessing the variation in molar crown shape (Bailey, Lynch 2005, Bauer *et al.* 2016, Brophy *et al.* 2014, Corny, Détroit 2014, Ferrario *et al.* 1999, Williams *et al.* 2019). The technique can be utilized with slightly worn molars in contrast to the examination of nonmetric dental traits using the Arizona State University Dental Anthropology System (ASUDAS) or the collection of 3-D landmark (Gómez-Robles *et al.* 2000, Turner *et al.* 1991).

MATERIALS

A total of 40 mandibular permanent molars from 27 individuals were examined at the Institut Royal des Sciences Naturelles de Belgique, Bruxelles (Royal Belgian Institute of Natural Sciences, Brussels), including M_1 (n = 15), M_2 (n = 14) and M_3 (n = 11) from Hastière Caverne M, Hastière Trou Garçon C, Sclaigneaux, Bois Madame and Maurenne Caverne de la Cave, (De Paepe and Polet 2007, Dumbruch 2003, Toussaint 2007, Toussaint *et al.* 2001, Vanderveken 1997, 2007; *Figure 1, Table 2*). A total of 17 individuals have only one molar included whereas ten others are represented by two or three permanent molars (*Table 3, Figure 2*). Only complete molar crowns with relatively little attrition were incorporated, inclusive of Smith's (1984) stages 1–5. We only considered in situ molars so that errors of attribution could be avoided.

Sex estimation was conducted using standard osteological techniques (Buikstra, Ubelaker 1994). However, in the majority of cases, the attribution should be considered tentative given the fragmentary nature of most of the mandibular remains. The sample included four males from Hastière Caverne M and one from Hastière Trou Garçon C, as well as three males and two females from Sclaigneaux, and one male and four females from Maurenne Caverne de la Cave (Table 3). Three individuals were represented by corpus fragments too small to assess sex attribution. For the analysis of M_1, nine children were included, five of whom derive from Maurenne Caverne de la Cave (*Table 3*).

TABLE 2: Number of molars and individuals included for each Neolithic cave burial.

Neolithic cave site	N molars	N individuals
Hastière Caverne M	6	4
Hastière Trou Garçon C	2	1
Sclaigneaux	9	7
Bois Madame	4	2
Maurenne Caverne de la Cave	19	13
Total	40	27

METHODS

Photographic images of the molar occlusal surface were taken with a Sony Nex-6 coupled with a 3.5–5.6 OpticLens. To limit parallax, the camera lens was situated a distance of 30–35 cm from the specimen and levelled to be parallel to the occlusal surface and perpendicular to the cervical line (Corny, Détroit 2014). Left molars were utilized except when only the right molar was available, or when the right was less worn or better preserved. In these instances, the right molar was flipped horizontally prior to analysis using media editing software.

To capture the outline of each molar, the freeware GIMP program (www.gimp.org) was employed. The lasso tool was utilized to place points on the outer margin of the molar crown positioned with the buccal surface as superior. Interproximal attrition or crown damage was mitigated by making conservative estimates of the crown outline. The bucket fill tool binarized the image to black (inner) and white (outer) parts separated by the crown outline (*Figure 3*). Using the "import_jpg" function from the "Momocs" library, the binarized images for each molar were input into the R statistical programming language (Bonhomme *et al.* 2014, R Core Team 2017). This process extracts points along the outer margin of the molar crown which were subjected to elliptical Fourier analysis (EFA) to yield amplitudes of the harmonics. These amplitudes represent the differences between each of the samples and an idealized ellipse (Brophy *et al.* 2014, Caple *et al.* 2017, Carlo *et al.* 2011, Claude 2013, Corny, Détroit 2014, Kuhl, Giardina 1982, Lestrel 1974, 1989).

To obtain EFA harmonic coefficients, the "efourier" function within the "Momocs" R package was employed and eight harmonics with size standardization were sufficient to capture the shape of the molars. Standardizing by size within EFA is

TABLE 3: Neolithic cave burials by molar, showing sample numbers and sex attributions. ^{c} – child; ^{cf} – corpus fragment lacking sex characteristics.

Molar	Hastière Caverne M	Hastière Trou Garçon C	Sclaigneaux	Bois Madame	Maurenne Caverne de la Cave
M_1	13^c		88^c, 90^c	11^{cf}, 32^c	1♂, 15^{cf}, 29♀, 31♀, 32♀, 79^c, 85^c, 91^c, 92^c, 93^c
M_2	2♂, 16♂, 10♂, 13♂	1♂	15♂, 62♀	11^{cf}	1♂, 15^{cf}, 26♀, 29♀, 32♀, 31♀
M_3	10♂	1♂	15♂, 19♂, 58^{cf}, 62♀, 64♂	11^{cf}	1♂, 15^{cf}, 32♀

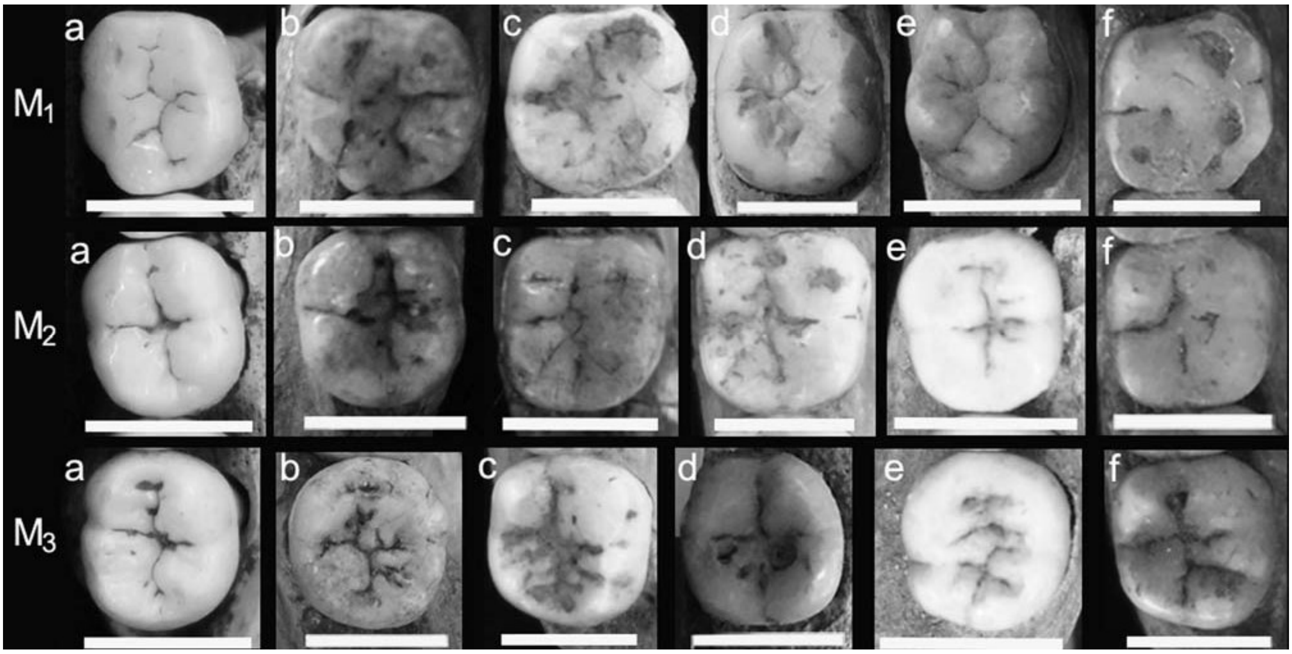

FIGURE 2: Representative images of mandibular remains from the caves, oriented with mesial above and distal below. Top row (M_1): (a) Bois Madame BM 11, left M_1; (b) Hastière M 13, left M_1; (c) Maurenne 1, right M_1; (d) Maurenne 91, right M_1; (e) Maurenne 92 right M_1; (f) Sclaigneaux 15, left M_1. Middle row (M_2): (a) Bois Madame BM 11, left M_2; (b) Hastière M 13, left M_2; (c) Hastière M 16, right M_2; (d) Maurenne 1, right M_2; (e) Sclaigneaux 62, left M_2; (f) Sclaigneaux 15, left M_2. Bottom row (M_3): (a) Bois Madame BM 11, left M_3; (b) Hastière M 10, right M_3; (c) Maurenne 1, right M_3; (d) Sclaigneaux 58, left M_3; (e) Sclaigneaux 62, left M_3; (f) Sclaigneaux 15, left M_3.

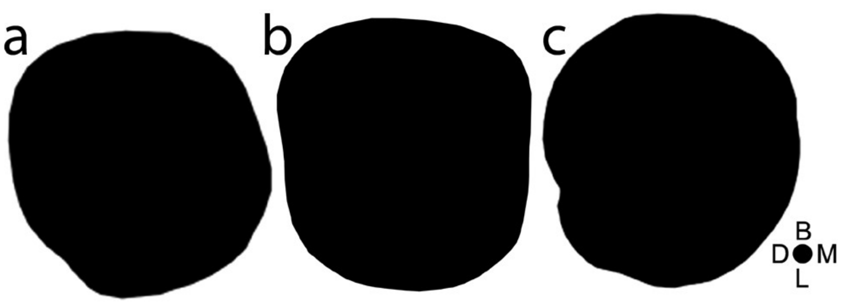

FIGURE 3: Binarized images of (a) M_1 of Hastière M 13, (b) M_2 of Maurenne 1, and (c) M_3 of Sclaigneaux 58 showing characteristic shapes of the molars; B = buccal; L = lingual; D = distal; M = mesial.

performed by scaling, rotating and translating the first ellipse to limit the degree to which differences in magnitude affect the results.

We conducted a principal components (PC) analysis to explore the variation in crown shape among the Late Neolithic cave burials. The PC analysis was performed separately for each molar (M_1, M_2 and M_3) with the use of Fourier coefficients as input trajectories. For each of the molars, plots with convex hulls, comprising 100% of the variation of a sample, are depicted for each cave burial comprising more than two individuals. A convex hull for Maurenne Caverne de la Cave is shown for all three molars, given the larger sample sizes for this cave burial. Hastière Caverne M exhibits a convex hull for M_2, and M_3, and there is one for Sclaigneaux for M_3, while Bois Madame and

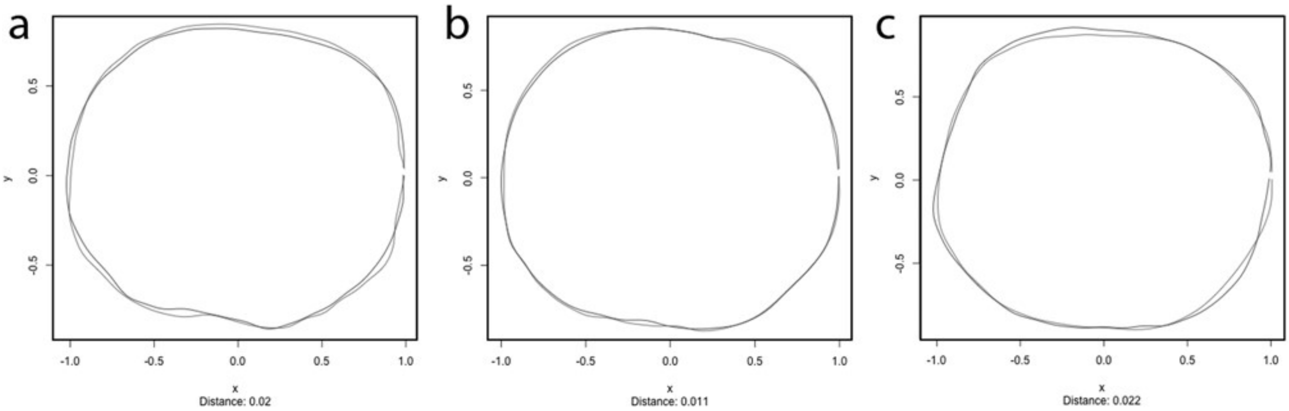

FIGURE 4: An intraobserver error study demonstrates consistency in tracing the crown shape of molars using a Middle Paleolithic sample from the Pyrenees of France, including (a) the right M_1 of Malarnaud, (b) the left M_1 of Montmaurin, and (c) the right M_2 of Montmaurin.

Hastière Trou Garçon C cave burials are represented solely by individuals. Group centroids are shown to compare all of the cave burials to one another regardless of sample size.

An intraobserver error study was employed to assess reliability and measurement precision (*Figure 4*). The same observer created outlines of each molar twice. The outlines were compared visually to detect differences between observations. In a previous study, interobserver error of the same method was assessed using a Mann Whitney U test of PC scores from two observers which yielded non-significance probability values (Williams *et al.* 2019). These prior results and Figure 4 demonstrate the precision of the tracing method employed in the present study.

RESULTS

Principal components analysis for M_1

In *Figure 5*, component 1 separates the centroids of Hastière Caverne M and Bois Madame from Sclaigneaux and Maurenne Caverne de la Cave. However, the individuals from Maurenne Caverne de la Cave exhibit a large amount of variation. For example, Maurenne 79, Maurenne 29 and Maurenne 92 are more similar to the centroids for Hastière Caverne M and Bois Madame and separated from Maurenne 1 and Maurenne 85. An individual from Bois Madame, BM Md 11, is quite distinctive on component 1, and has no overlap with the convex hull of Maurenne Caverne de la Cave (*Figure 5*). In fact, much of the separation of individuals on component 1 derives from the differences seen in Bois Madame BM 11 with respect to Maurenne 1 (*Figure 5*). Bois Madame BM 11 is markedly buccolingually compressed but with a rounded and elongated hypoconulid, and a pronounced entoconid with respect to the metaconid which is rather small. In contrast, Maurenne 1 is expanded buccolingually with an absent hypoconulid and a prominent metaconid (*Figure 2 and Figure 5*).

On component 2, BM Md 11 from Bois Madame is also distinct and is projected positively, only surpassed by Maurenne 91 (*Figure 5*). These two are polarized from Hastière Caverne M 13, and secondarily from Bois Madame BM Md 32 which are all projected negatively. Maurenne 91 can be also described as buccolingually compressed but not nearly to the degree that is present in Bois Madame BM 11. In contrast, Hastière Caverne M 13, on the negative extreme of component 2, exhibits a relatively elongated molar, but with a protoconid that projects into the buccal plane, and an entoconid which extends farther distally than does the hypoconid (*Figure 2 and Figure 5*). There is very little variation in the two individuals from Sclaigneaux, Sclaigneaux 88 and Sclaigneaux 90, and the centroid for this cave burial is situated positively, like that of Bois Madame, and unlike that of Hastière Caverne M which is projected on the negative extreme of component 2 (*Figure 5*).

Principal components analysis for M_2

Component 1 serves as a contrast vector separating the centroid values for Hastière Caverne M, Hastière Trou

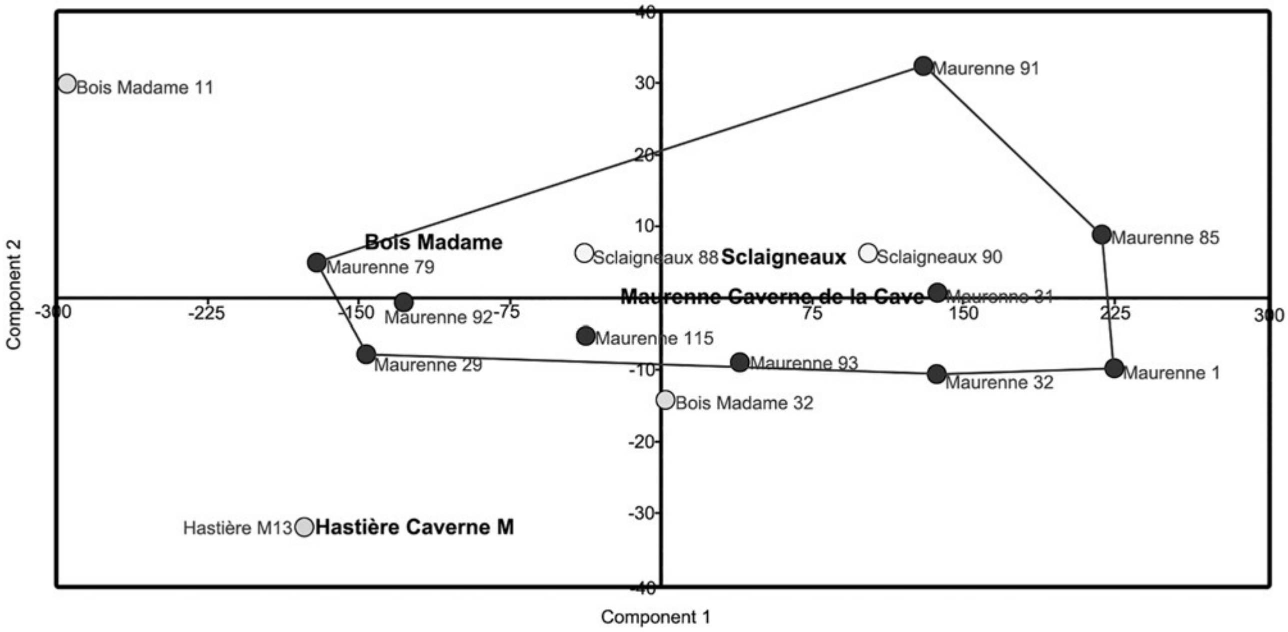

FIGURE 5: Principal components analysis for M_1 showing Bois Madame BM Md 11 at the negative pole and Maurenne 1 at the positive extreme of component 1, and Hastière M 13 and Maurenne 91 at negative and positive ends of component 2, respectively. Centroids in bold.

Garçon C and Bois Madame, all of which are negatively projected, from those associated with Maurenne Caverne de la Cave and Sclaigneaux which are both positive. Much of this contrast can be explained by the polarization of Hastière M 16 and Maurenne 1. Hastière M 16 presents a rather rounded buccal margin in contrast to that of Maurenne 1 which is somewhat flattened. Additionally, the hypoconid is more pronounced on Maurenne 1, and the molar is buccolingually expanded, compared to the crown shape of Hastière M 16 (*Figure 2 and Figure 6*).

On the first component for M_2, the convex hulls for Maurenne Caverne de la Cave and Hastière Caverne M are imperfectly separated owing to the position of Maurenne 26, which is an outlier for this cave burial, and is found within the distribution of values for the Hastière Caverne M sample. The other individuals of Maurenne Caverne de la Cave are positively projected in contrast to those from Hastière Caverne M which are all negative (*Figure 6*). Bois Madame, BM Md 11, is positioned as more similar to the Hastière Caverne M sample than is Hastière Trou Garçon C1 which falls outside of the convex hull for Hastière Caverne M. There is a complete overlap between Sclaigneaux and Maurenne Caverne de la Cave on component 1.

Component 2 shows very little variation within Hastière Caverne M and Maurenne Caverne de la Cave compared to the polarization of the two individuals from Sclaigneaux cave, where Sclaigneaux 15 is negatively projected and Sclaigneaux 62 is highly positive. Part of this distinction is borne out from the buccally deflected protoconid of Sclaigneaux 62, coupled with the pronounced distal extension of the molar, albeit lacking a hypoconulid (*Figure 2 and Figure 6*). In contrast, Sclaigneaux 15 presents a rather square-shaped M_2 with a flat distal margin (*Figure 2 and Figure 6*). There is also a distinction on component 1 between BM Md 11 from Bois Madame which is negative and Hastière Trou Garçon C1 which is positive, and close to the centroid for Sclaigneaux (*Figure 6*).

Principal components analysis for M_3

The M_3 sample for Sclaigneaux is larger than for the other cave burials, and extends from the positive to the negative extremes of component 1. Hastière Trou Garçon C1 and the small convex hull for Maurenne Caverne de la Cave - with the exception of Maurenne 1- all overlap that of Sclaigneaux (*Figure 7*). On the negative extreme is Sclaigneaux 58 which is polarized

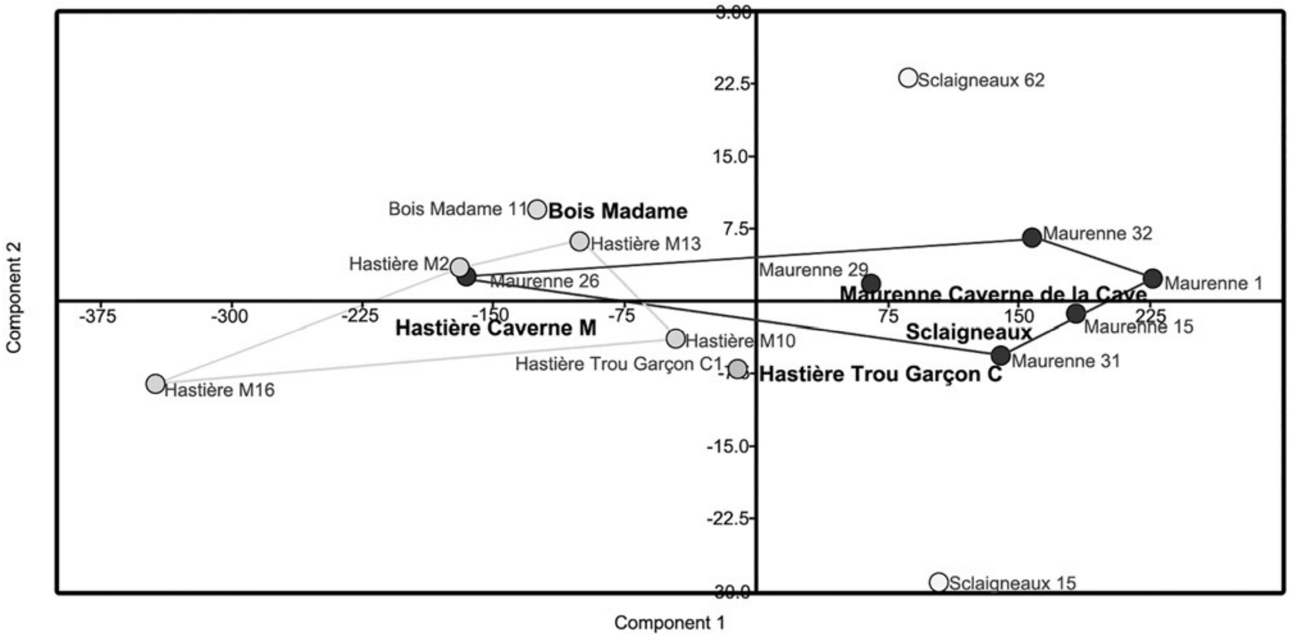

FIGURE 6: Principal components analysis for M_2 showing Hastière M 16 and Maurenne 1 at the negative and positive extremes of component 1, respectively, and the polarization of Sclaigneaux 15 (negative) and Sclaigneaux 62 (positive) on component 2. Centroids in bold.

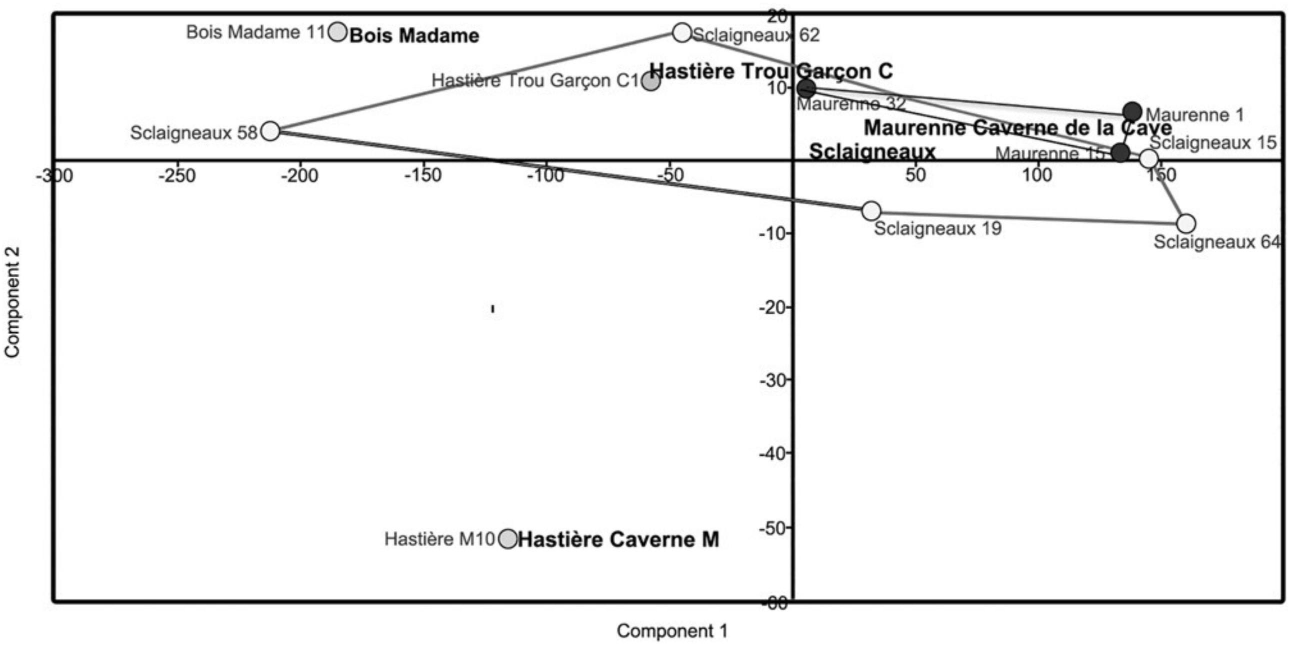

FIGURE 7: Principal components analysis for M_3 showing Sclaigneaux 58 at the negative end and Sclaigneaux 62 at the positive extreme of component 1, and Hastière M 10 and Bois Madame BM 11 at negative and positive poles of component 2, respectively. Centroids in bold.

from Sclaigneaux 62, and to a lesser extent by Sclaigneaux 15. Sclaigneaux 58 exhibits a prominent metaconid which projects mesially with respect to the protoconid, and presents a buccal margin which is rounded with a shallow and short buccal groove (*Figure 2 and Figure 7*). In Sclaigneaux 62, it is the protoconid which is large and the crown presents a mesiobuccal flattening while the buccal border is sharply pinched owing to a deep buccal developmental groove and mesially rotated hypoconid (*Figure 2 and Figure 7*).

On component 2, Hastière Caverne M 10 and BM Md 11 are completely outside of the convex hull for Sclaigneaux, and are polarized from one another. In fact, it is Hastière Caverne M 10 that is distinct in crown shape from all other individuals across cave sites, deriving from a somewhat mesiodistally compressed and round crown shape, but with a somewhat flattened buccodistal margin (*Figure 2 and Figure 7*). By way of comparison, the M_3 of Bois Madame BM 11 has a more distinctive protoconid which is demarcated buccally by a pinched buccal margin coupled with a deep developmental groove (*Figure 2 and Figure 7*). On the positive extreme, the unique crown form of Bois Madame BM Md 11 is only approximated by Sclaigneaux 62 (*Figure 2 and Figure 7*). Meanwhile, the negative projection of Hastière Caverne M 10 contrasts with the positive placement of the centroids for Bois Madame, Hastière Trou Garçon C and Maurenne Caverne de la Cave. The variation along component 2 for Sclaigneaux is not as extreme as noted on component 1 given the differences present between Hastière Caverne M 10 and all other individuals.

DISCUSSION

Hastière Caverne M is distinct from the other caves for most comparisons. Although the final/late Neolithic collective burials of Sclaigneaux and Maurenne Caverne de la Cave present extensive variation in molar crown shape, they rarely overlap that of Hastière Caverne M. Bois Madame also appears to differ from Sclaigneaux and Maurenne Caverne de la Cave. This is particularly true for one individual from Bois Madame, BM Md 11, who is quite distinctive across the molars and has no overlap with the convex hull of Maurenne Caverne de la Cave or Sclaigneaux. The same could be said for Hastière Caverne M 13, M 16 and M 10 which are separated from the other cave burials for M_1, M_2 and M_3, respectively. However, the samples sizes for Hastiere Caverne M and Bois Madame are limited. If a greater number of individuals were present for these two cave burials, they might mimic the distribution of values characterizing Maurenne Caverne de la Cave and Sclaigneaux.

Chronology and ecogeography

Chronology helps to explain the separation of individuals from Hastiere Caverne M from the final/late Neolithic collective burials. However, Hastière Caverne M was not paired in any discernable way with Hastière Trou Garçon C1 which was considered a priori as earlier Late Neolithic. In fact, it seems Hastière Trou Garçon C1 is most similar to Sclaigneaux. These two cave burials are possibly less than 70 years apart (*Table 1*), further suggesting that chronology, rather than ecogeography, accounts for the variation in crown shape.

While it is tempting to assume a close affinity between individuals who are similar in crown shape, epigenetic factors that occur in the expression of the crown during growth and development also need to be taken into consideration (Scott *et al.* 2018). Differences may be more informative than similarities in terms of affinity. The extreme variation present at Sclaigneaux is noteworthy and suggests a variety of crown forms across the molars are present. The same could be said for Maurenne Caverne de la Cave for M_1 and M_2 but not for M_3.

Sex differences

On the first component for M_2, males of Hastière Caverne M and Hastière Trou Garçon C appear distinct from the predominately female sample from Maurenne Caverne de la Cave (*Figure 6*). However, the projection of female Maurenne 26 within the convex hull formed by males of Hastière Caverne M, coupled with the placement of the lone male from this cave burial, Maurenne 1, on the far positive extreme of component 1 cast doubt on the degree to which the distribution of individuals is the result of sex attribution. In addition, there does not appear to be a strong differentiation with respect to sex attribution for any of the other PC axes, corroborating an earlier study of human molars (Ferrario *et al.* 1999). However, since the sample included nine children and three small mandibular corpus fragments, the sex of only 55.6% or 15 of 27 individuals could be estimated. Thus, the full extent to which sex-based crown shape differences partition these Neolithic cave burials remains unknown.

Comparison with other studies

Several analyses have been conducted on these Late Neolithic collective burials, including diet reconstructions (García Martín 2000, Semal *et al.* 1999, Toussaint *et al.* 2001, Bocherens *et al.* 2007), funerary behavior (Toussaint 2007, Vanderveken 2007), stature (Orban *et al.* 2000) and paleopathology (Polet 2011, Williams, Polet 2017). These studies have shown extensive variation characterizes these collective burials. For example, stable isotopes do not indicate a strong signal for the differentiation of sites (Semal *et al.* 1999, Bocherens *et al.* 2007). A study of buccal (vestibular) dental microwear using Scanning Electron Microscopy also showed overlap among these Late Neolithic cave internments (García Martín 2000, Toussaint *et al.* 2001). The few long bones and metatarsals preserved from the Late Neolithic of Belgium exhibited greater overlap than separation in stature estimates, although this may be a result of females comprising the majority of the sample available (Orban *et al.* 2000). The funerary practices are so varied that patterns with respect to location or chronology of the Late Neolithic have not been forthcoming (Toussaint 2007). This study of crown shape as approximated using crown outlines subjected to EFA supports the aforementioned studies in that extensive variation is the rule rather than the exception for these cave burials. However, some nuances do appear between the earlier Late Neolithic cave burial of Hastière Caverne M and the final/late Neolithic sites. Indeed Hastière Caverne M appears distinctive in other dental features, such as the pronounced expression of Carabelli's cusp and the protostylid on deciduous molars (Williams *et al.* 2018). However, such observations must be tempered with caution given the fragmentary nature of the remains, and the uneven and limited sample sizes. These caveats must be considered when differences between individuals and groups are asserted for these Neolithic remains.

CONCLUSIONS

The Late Neolithic cave burials of Belgium represent poorly differentiated units, supporting previous studies of diet and funerary practices. The samples are limited in size so it is not possible to make definitive statements about the relationship of individuals within and between cave sites. However, it appears that the earlier Late Neolithic site of Hastière Caverne M may be distinct from the other sites for M_1 and M_3 but has an overlap of values with Maurenne Caverne de la Cave for M_2. The final/late Neolithic cave burial of Sclaigneaux exhibits substantial variation in crown form for M_2 and M_3, perhaps indicative of a larger population from which the inhabitants of the caves represent. Hastière Caverne M may have come from a smaller population compared to the larger ones characterizing the final/late Neolithic peoples situated at the brink of the Bronze Age.

ACKNOWLEDGEMENTS

We are extremely grateful to Patrick Semal, Chief Heritage Officer, Anthropologie et Préhistoire, Royal Belgian Institute of Natural Sciences, Brussels (Institut Royal des Sciences Naturelles de Belgique, Bruxelles) who granted permission to examine these remains. At the Royal Belgian Institute of Natural Sciences, we would like to thank Caroline Polet who kindly provided osteological expertise and the literature pertaining to the Neolithic caves in Belgium; and Laurence Cammaert who expertly created the map of Belgium adapted for Figure 1, which we use with permission. This research was generously funded by Fulbright-Belgium and the Commission for Educational Exchange between the US, Belgium and Luxembourg.

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