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Comparing maxillary first molar crown shape using elliptical Fourier analysis in the Late Neolithic cave burials of Belgium

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ABSTRACT: The Belgian Meuse karstic basin holds more than 200 Late Neolithic collective burials. Four of the largest include Hastière Caverne M, Hastière Trou Garçon C, Sclaigneaux and Bois Madame. The remains from these caves are commingled and fragmentary. However, *in situ* maxillary molars are well preserved permitting an investigation of molar crown shape within and across sites.
Crown outlines from the burials are compared using elliptical Fourier analysis to capture shape distinctions in the relatively numerous first maxillary molars (n = 27). Elliptical Fourier analysis is designed to compare deviations between each shape outline and an idealized ellipse, recorded as amplitudes of the harmonics which are reduced to principal components (PC) scores. We expect individuals from each site will be more similar to one another than to other internments in PC scores, and that the sites will be distributed along PC axes according to differences in chronology and geographic location.
Principal components analysis reveals that individuals tend to cluster together based on cave burial as well as time period. Geographic distance only differentiates the final/late Neolithic cave burials. The earliest of the sites, Hastière Caverne M, is distinctive and includes multiple outliers. Hastière Trou Garçon C from earlier in the Late Neolithic does not cluster with Hastière Caverne M as expected. Instead, this cave burial groups with Sclaigneaux, the most geographically distant site but chronologically the closest to Hastière Trou Garçon C. Although the limited sample sizes for each site must be considered, it appears that early farmers of the Belgian Meuse basin exhibited intricate human population dynamics which may have included small, semi-isolated groups early in the Late Neolithic and larger communities with greater contact toward the onset of the northern European Bronze Age.

KEY WORDS: Hastière Caverne M, Hastière Trou Garçon C, Sclaigneaux, Bois Madame, final/late Neolithic, molar outlines

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Introduction

The Neolithic is associated with increased population density, greater variability in settlement patterns, and noteworthy human-made alterations to the landscape seemingly all tied to an intensification of food production (Golitko 2010; Bocquet-Appel 2011; Zimmermann 2012; Teuber et al. 2017). As Neolithic settlement patterns expanded, peoples of Eurasia increasingly began to create collective burials. The significance of these collective burials is uncertain, although the shifting dynamic of burial styles occurs in concert with changes in settlement types (McLaughlin et al. 2016). Burial patterns during this period reveal several noteworthy findings regarding the relationship between the living and the dead. Collective funerary practices are found in a variety of locations, including Iberia, Catalonia, Italy, Poland and Siberia (Subirà et al. 2014; Waters-Rist et al. 2016; López-Onaindia et al. 2018; Sarasketa-Gartzia et al. 2018; Silvestri et al. 2020).

In Belgium there are more than 230 collective burials radiocarbon dated to the Middle and Late Neolithic (Bronk-Ramsey et al. 2002; Bocherens et al. 2007; De Paep and Polet 2007; Toussaint 2007). These sites are located within the vast karst cave system found along the Meuse River, a major northern European watershed. The increasing intensity of collective cave and rockshelter burials in Belgium during the Late Neolithic parallels discoveries along the Seine and Rhine rivers (Toussaint 2007). These cave sites display a variety of mortuary features. For instance, there is variation in the method of burial and body orientation as well as evidence of commingling, cremation, cut-marks and the manipulation of remains (Toussaint et al. 2003; Toussaint 2007; Polet 2011). Most of the cave burials found in Belgium contain only a few to more than a dozen internments (Polet 2011). Others such as Sclaigneaux include the remains of a minimum of 58 individuals (De Paepe 2007). A third to more than a half of individuals represented in these collective burials are children (De Paepe and Polet 2007; Toussaint 2007; Polet 2011), suggesting this part of northern Europe was experiencing a demographic transition typical of early farming communities elsewhere (Bocquet-Appel 2011). The final/late Neolithic collective burials may indicate changes in social organization and reflect influences emerging from increased trade networks across northern Europe (Toussaint 2007; de Reu 2014). These early farmers lived at a critical junction of human history where the Neolithic transitioned into the Bronze Age. This transition represents a long-term process of adaptation towards agricultural patterns of subsistence and away from a previous foraging way of life (Semal et al. 1999; Toussaint et al. 2001; Bocherens et al. 2007), and was marked by large migrations of peoples and innovations in weapons of war (Nørgaard 2018).

Although most of the Late Neolithic cave burials are represented by fragmentary remains, *in situ* molars are relatively well preserved. In particular, maxillary alveolar fragments that include the first molar are often available. We examine four well-studied cave burials of the Belgian Meuse basin, radiocarbon dated to the Late Neolithic, that preserve maxillary molars, including Hastière Caverne M (Vanderveken 1997; 2007), Hastière Trou Garçon C (Orban et al. 2000), Sclaigneaux (De Paep 2007; De

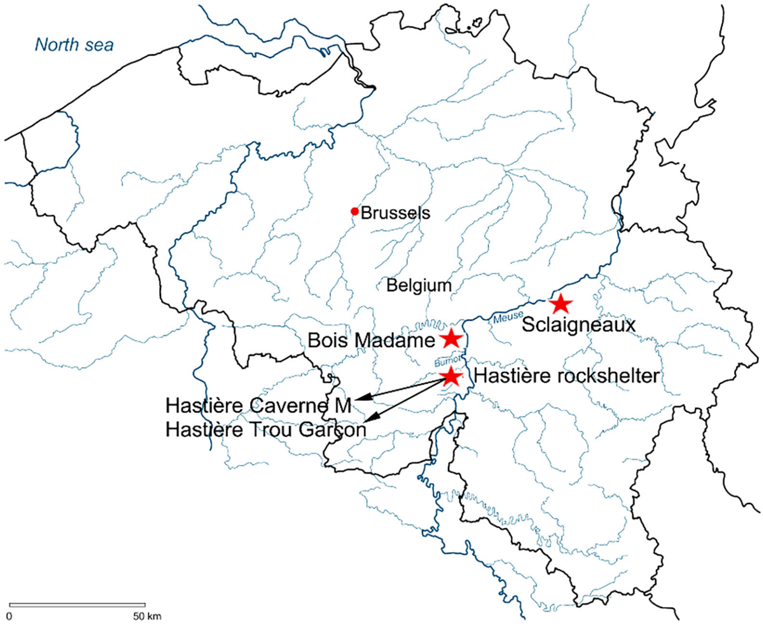

Fig. 1. Map of Belgium showing the location of the cave burials featured in this study. Sclaigneaux and Bois Madame have been dated to the final/late Neolithic [4,155 ± 35 years BP for the former, and 4,075 ± 38 years BP & 3,910 ± 40 years BP for the latter] while Hastière Caverne M and Hastière Trou Garçon C are dated to earlier in the Late Neolithic (4,345 ± 60 years BP & 4,220 ± 45 years BP, respectively)

Paepe and Polet 2007) and Bois Madame (Dumbruch 2003) (Fig. 1). The four caves singled out for analysis encompass several hundred years of habitation. More specifically, two final/late Neolithic sites, Sclaigneaux (4,155 ± 35 years BP) and Bois Madame (4,075 ± 38 years BP & 3,910 ± 40 years BP) are contrasted to Hastière Caverne M (4,345 ± 60 years BP) and Hastière Trou Garçon C (4,220 ± 45 years BP) from earlier in the Late Neolithic. The radiocarbon dates are acquired through accelerator mass spectrometry (AMS) at Oxford University for the Hastière rockshelter sites and Bois Madame (Bronk-Ramsey et al. 2002; Toussaint 2007) and at the University of Groningen for Sclaigneaux (De Paep and Polet 2007).

Research questions

Due to the heritable formation of dental morphology and crown shape, closely related individuals are more similar to one another than those sharing fewer ancestors in common (Turner et al. 1992; Scott and Turner 1997; Hlusko et al. 2002; 2007; Hlusko and Mahaney 2003; Scott and Irish 2013; Paul and Stojanowski 2015; 2017; Scott et al. 2018; Stojanowski et al. 2018; Trakinienė et al. 2019). This estimate of affinity is imperfect however, as crown form is also subject to extrinsic factors during development (Scott et al. 2018). To the degree to which maxillary molar crown form reflects affinity – and with the assumption that cave burials include relatives – it is expected that members of each cave burial should be more similar to one another than to individuals from other sites.

Our second hypothesis concerns chronology. Each of the caves sites is chronologically distinct. However, Hastière Trou Garçon C is situated temporally midway between Hastière Caverne M and Sclaigneaux. The latest dates derive from Bois Madame. To the extent that chronology distinguishes the sites, it is predicted that Hastière Caverne M should be the most different from Bois Madame in maxillary first molar crown form, followed by Sclaigneaux. Similarly, Hastière Trou Garçon C should be similar to Hastière Caverne M in some ways and to Sclaigneaux in others, but also distinct from Bois Madame.

Geographic location may also explain the partitioning of molar crown shape. To the extent to which geography accounts for the difference among individuals, Hastière Trou Garçon C and Hastière Caverne M should be the most similar to one another since they are both found within Hastière rockshelter. Meanwhile, Sclaigneaux is separated by a distance of about 35 km away from the rockshelter at Hastière (Williams et al. 2018). If geographic distance is a proxy for relatedness, then Sclaigneaux should be distinctive from the two burials from Hastière rockshelter. Meanwhile, Bois Madame is ~15 km from Hastière rockshelter and both are to the west of Sclaigneaux. Therefore, it may be the case that Bois Madame is more similar to the two burials from Hastière rockshelter than to Sclaigneaux.

Elliptical Fourier analysis

There are several methods to capture the shape of the molar crown, including geometric morphometrics using a generalized Procrustes approach, linear descriptive measurements and dental morphology (Turner et al. 1991; Gómez-Robles et al. 2007; Pilloud and Larsen 2011; Scott and Irish 2017). The semi-circular closed contour of the molar occlusal surface has also been traced or landmarked to capture the shape of the crown, and multiple mathematical approaches have been applied to compare human individuals, including elliptical Fourier analysis (Ferrario et al. 1999; Corny and Détroit 2014; Williams et al. 2017; 2019). However, most methods require unworn teeth. In contrast, a higher degree of dental attrition is possible with elliptical Fourier analysis of crown shape since the unit of analysis is the molar margin rather than cusp morphology (Brophy et al. 2014). The inclusion of a greater number of individuals can be particularly advantageous when only limited sample sizes are available. Such is the case for the Late Neolithic cave burials from the Belgian Meuse basin.

Elliptical Fourier analysis is utilized in this study to estimate the similarity of molar crown shape by comparing each individual to an idealized ellipse. Elliptical Fourier analysis utilizes harmonics to accurately represent a shape contour. During this process, the outline conforms to the ellipse by a series of increasingly accurate transitions of shape (Fig. 2). The number of harmonics is contingent on the overall distinctiveness of the shape and each harmonic in the series explains a unique feature. There is an increase in complexity during the progression of the harmonics beginning with a simple ellipsis that approximates the size of a polygon (Latham et al. 2017). The progression continues until the contour more closely resembles the original shape of the object (Fig. 2).

Elliptical Fourier analysis can describe any shape as long as it is closed and two-dimensional (Lestrel 1974, 1989; Iwata and Ukai 2002). The first maxillary molar crown shapes examined here are approximated using an outline method (Ferrario et al. 1999; Brophy et al. 2014; Williams et al. 2017; 2019). The deviations between each molar and the standard sphere are recorded as amplitudes of the harmonics using trigonometric functions, which are then reduced using multivariate tools (Fig. 3). Late Neolithic individuals from four cave burials are compared to address whether there is a clustering of individuals per site; whether cave burials differ with respect to chronological age; and whether geography accounts for the distribution of individuals across multivariate axes.

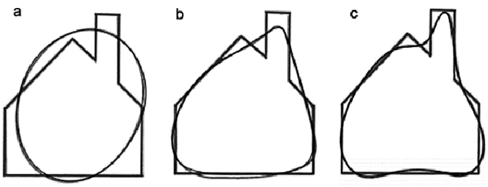

Fig. 2. Harmonic progression series to approximate a polygon; the first harmonic is a simple ellipsis that approximates the size of the object (a), the second harmonic warps the ellipse to more closely fill the area (b), by the fifth harmonic, nearly all of the complexity of the polygon has been captured (c); image adapted from Kuhl and Giardina (1982)

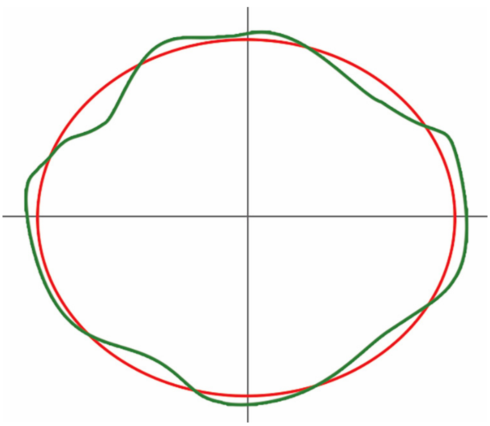

Fig. 3. Comparison between a sample maxillary molar crown and an idealized ellipse

Material and methods

A total of 27 first maxillary molars are included from Hastière Caverne M and Hastière Trou Garçon C from Hastière rockshelter, Sclaigneaux and Bois Madame (Table 1). The dental elements were photographed at the Royal Belgian Institute of Natural Sciences, Brussels using a Sony Nex-6 equipped with a 3.5–5.6 OpticLens. The camera was held at a distance of 30–35 cm directly parallel to the occlusal surface to avoid as much as possible the effects of parallax (Corny and Détroit 2014). The sample was restricted to molars preserved within the alveolus to prevent incorrect attributions from biasing the results, and only molars lacking substantial attrition comprising wear stages 1–5 (Smith 1984) were included (Fig. 4). The great majority of the sample consists of small, one-sided, fragmentary maxillary remains which often preserved the first molar. In cases where the alveolus was relatively intact, the left side was chosen unless the right side was better preserved or exhibited less wear. In some cases, only the right

Table 1. List and number of individuals (n = 27) from each cave burial examined

Cave burial	Numbering of individuals	Total
Hastière Caverne M	24, 25, 32, 34, 35, 36	6
Hastière Trou Garçon C	1, 4, 6, 9	4
Sclaigneaux	92, 93, 97, 98, 99, 100, 103, 122	8
Bois Madame (Mx)	1, 5, 6, 9, 11, 12, 13, 17, 27	9

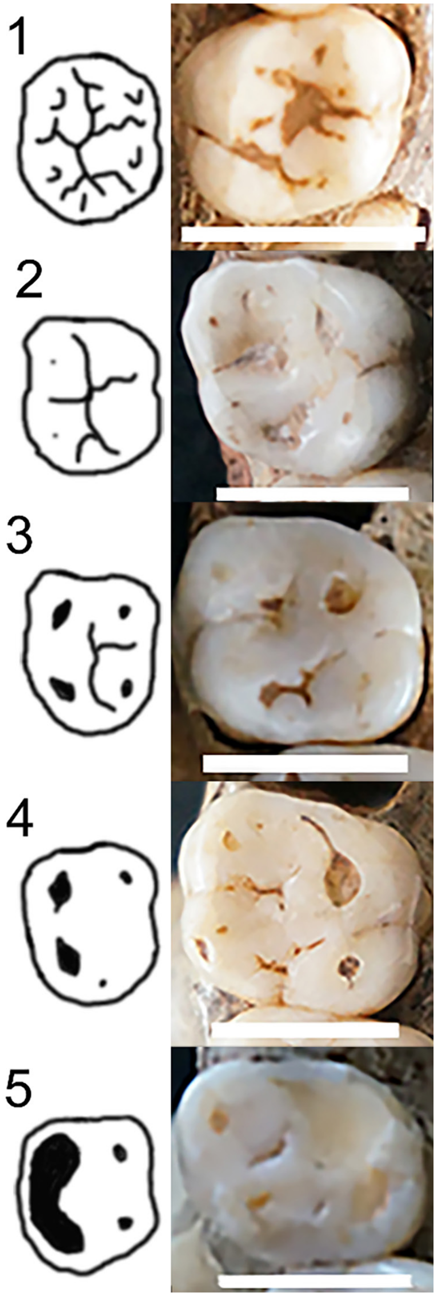

Fig. 4. Dental wear stages 1–5, including 1: BM Mx 27; 2: Hastière Caverne M 36; 3: BM Mx 1; 4: BM Mx 6; 5: Hastière Trou Garçon C 4; line drawings adapted from Smith (1984) for mandibular molars

maxillary molars remained. All of the right molars were flipped horizontally in media editing software to match the left ones prior to the comparison of the crown outlines.

Data capture

Photographs of the crown surfaces of the molars were imported into GIMP, a free image editing software, and the crown outlines were traced using the paths tool. The dental arcade was oriented such that mesial was the uppermost surface, defined by the crown margins of the paracone and protocone. The paths tool allows the user to place landmarks along the outline of an object. Between 150 and 200 landmarks were needed to outline the molars (Fig. 5). Once the landmarks were placed and examined for accuracy, they were merged to form a single tracing of the molar crown.

The outlines were converted into high-contrast black and white images (Fig. 6). The outline and the crown surface were rendered exclusively black, whereas the background negative space was transformed to entirely white. This sharp contrast allowed for the closed contour to be translated into chain code

Fig. 5. Landmarks surrounding M^1 of Bois Madame Mx 13 shown to demonstrate the process of creating crown outlines

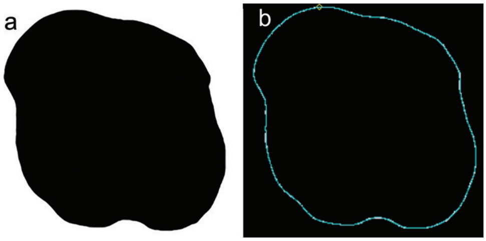

Fig. 6. Binarized image of Bois Madame Mx 27 (a); the outer margin of the binarized image of Mx 27 has been captured in SHAPE v2 as chain code (b)

using SHAPE v.2, a series of free software programs specifically designed to conduct elliptical Fourier analysis (Fig. 6). In SHAPE v.2, the black/white distinction allows for an outline to be deconstructed in vector format in which changes in directions occur at fixed lengths (Iwata and Ukai 2002).

Elliptical Fourier analysis was then utilized to approximate the shape using curve fitting techniques in which the perimeter of the molar is estimated by summing the multiple sine and cosine waves that account for the outline of the sphere. This process allows the perimeter of an object to be characterized iteratively until the ellipse is complete (Caple et al. 2017). SHAPE v.2 calculates the coefficients of elliptical Fourier descriptors from the chain code description of the outline. The coefficients were then converted into principal components (PC) scores along a series of vectors, the first of which explains the largest percent of the variation. Each subsequent axis describes less of the variation, until eventually all of the variance was explained.

Individuals were compared across the PC axes on bivariate plots using convex hulls inclusive of 100% of the variation per site. To further approximate the degree to which individual crown shapes were grouped according to site, a cluster analysis using single linkages of Euclidean distances was calculated using the PC axes as input vectors. The outline method was validated in a previous study by comparing the tracings from two observers and the results were not significantly different (Williams et al. 2019).

Results

Four of the total 76 principal components (PC) scores account for 79% of the variation among maxillary first molar crown shapes. The first two axes, PC 1 and PC 2, explain 59.8% of the variance and exhibit the largest standard deviations surrounding the mean (Fig. 7). In comparison to the first two axes, PC 3 and PC 4 together explain 19.2% of the variance. Subsequent PC axes explaining less of the variation were excluded from further investigation.

All of the Hastière Caverne M molars have positive values on PC 1, representing 38.5% of variation, and in this way are completely separated from individuals from Sclaigneaux and Hastière Trou Garçon C who are associated with primarily negative PC scores. Bois Madame is intermediate with respect to the other sites, but has a greater number of individuals with negative scores. However, there is no overlap on PC 1 between Bois Madame, excepting BM Mx 27, and Hastière Caverne M. In this way, PC 1 can be considered a polarizing vector that effectively separates Hastière Caverne M from nearly all other individuals (Fig. 8).

On PC 2, Hastière Caverne M 32 and 35 contrast with all others, including additional individuals from Hastière Caverne M, positioned at the extreme negative end of this axis (Fig. 8). Hastière Trou Garçon C parallels this extensive

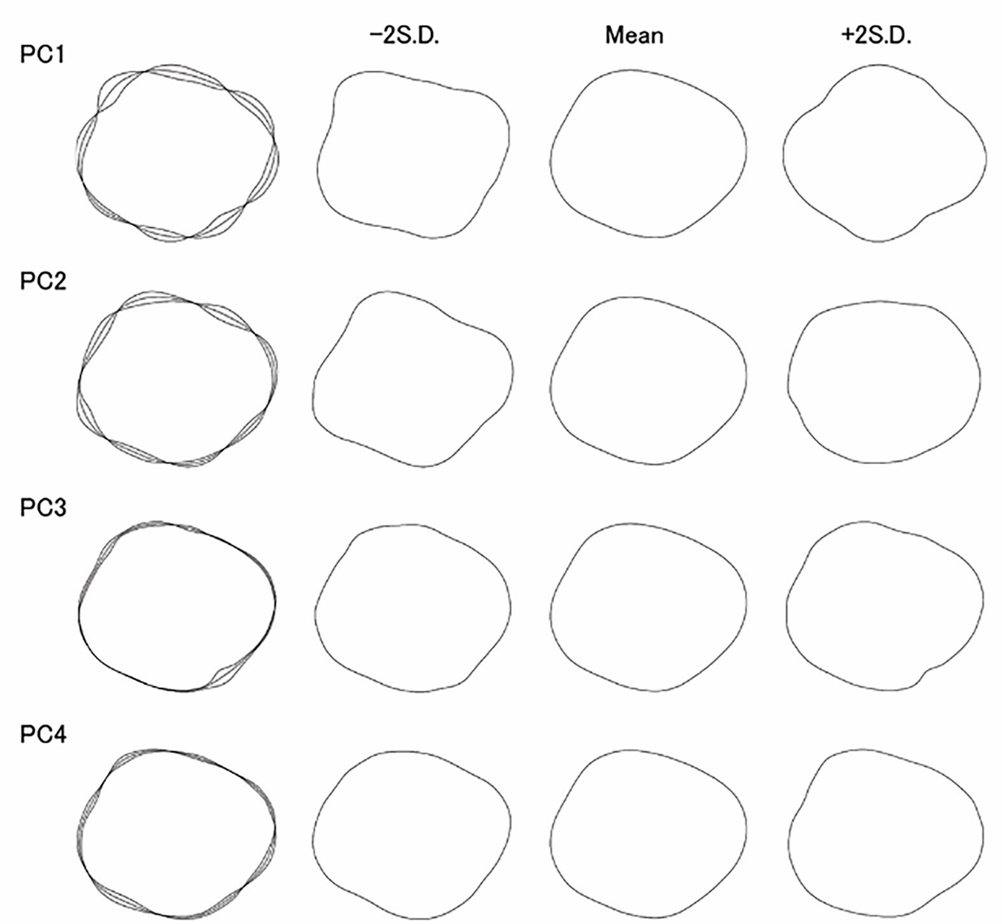

Fig. 7. Mean and two standard deviations for the first four PC axes together explaining 79% of the variance

variation with high positive scores for numbers 6, 9 and 1 and a high negative score for number 4. In fact, with the exception of number 4, Hastière Trou Garçon C is completely separated from Sclaigneaux and Bois Madame on PC 2 (Fig. 8). Sclaigneaux and secondarily Bois Madame are the most tightly clustered of the sites on PC 2.

On PC 3, a polarization exists between Hastière Caverne M 22 and 24; these individuals are positioned on the high negative and positive extremes of PC 3, respectively (Fig. 8). However, with the exception of Hastière Caverne M 22, all other individuals of this cave burial are projected positively. Meanwhile, the molars of Bois Madame cluster relatively tightly together as do those from Hastière Trou Garçon C and Sclaigneaux (Fig. 8).

Most individuals from Bois Madame exhibit negative scores on PC 4, culminating in an extreme value for BM Mx 13 (Fig. 9). In this way, Bois Madame, excepting BM Mx 11, Mx 12 and Mx 17 with positive PC scores, is distinct from the other sites. Hastière Trou Garçon C is tightly clustered on PC 4, followed by Hastière Caverne M and Sclaigneaux (Fig. 8).

When chronology in years BP is compared to PC1, there is much overlap between Hastière Trou Garçon C and Sclaigneaux. While Bois Madame, with the exception of BM Mx 27, is similar in PC1 scores to Hastière Trou Garçon C and Sclaigneaux, it differs in chronology. Hastière Caverne M differs from the others in both chronology and PC1 scores (Fig. 9).

A cluster analysis using all of the PC axes corroborates the uniqueness of Hastière Caverne M which is represented by numerous outliers. None of the individuals from the other sites exhibit outliers with the possible exception of BM Mx 27, but even in this case the branch length is relatively short (Fig. 9). There are several short branch lengths among pairs of individuals from the same cave, including Hastière Trou Garçon C 5 and

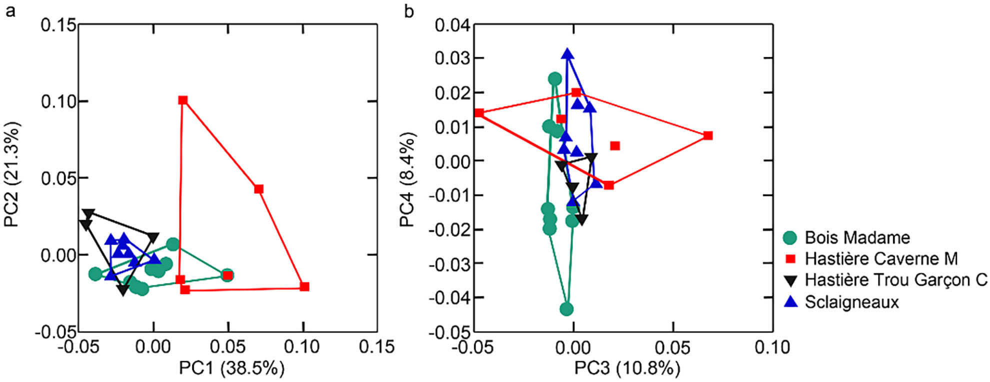

Fig. 8. Bivariate comparisons with convex hulls comprising 100% of each burial sample for PC 1 and PC 2 (a); PC 3 and PC 4 (b)

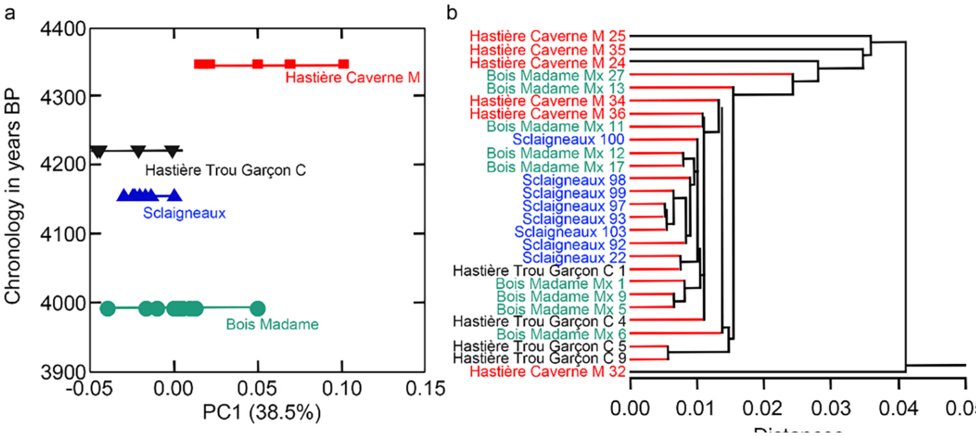

Fig. 9. Chronology compared to PC1 (a); cluster analysis with relatively short branches shown in red (b)

9, Bois Madame BM Mx 9 and 5, as well as between Sclaigneaux 93, 97, 103 and 99. In fact, all Sclaigneaux individuals exhibit relatively short distances (Fig. 9).

Discussion

The similarity of Hastière Trou Garçon C and Sclaigneaux along most of the PC axes suggests time period, rather than geography, accounts for a greater share of the variance among individuals. Meanwhile, the two most disparate sites in terms of chronology are Hastière Caverne M and Bois Madame, with a difference of around 600 years between the two. The two cave burials tend to cluster discretely along the first two PC axes, presenting two distinct distributions. However, PC 3 and PC 4 shows considerable variability in Hastière Caverne M while Bois Madame is more consistently clustered, particularly on PC 3.

Hastière Caverne M, as the oldest site of the group, appears to be highly variable yet is distinct from all other cave burials (Figs. 8 and 9). Individuals from Hastière Caverne M are represented by outliers for each comparison, and this contributes to a lack of clustering compared to the other sites. The presence of outliers from Hastière Caverne M raises questions about their relationship to the other individuals. Several individuals are consistently on the periphery of the PC axes and are represented by outliers in the cluster analysis (Fig. 9). However, some individuals from Bois Madame, such as Mx 13 and Mx 27, also exhibit relatively extreme values. Such observations cast some doubt about the extent to which Hastière Caverne M is distinct from the final/late Neolithic sites. However, the overall tight clustering of Bois Madame, especially along PC 3, bolsters the suggestion that this final/late Neolithic site represents a discrete community.

The distinctiveness of Hastière Caverne M indicates that chronology explains more of the variance than geographic distance. The narrow time interval between – and grouping of – Sclaigneaux and Hastière Trou Garçon C, despite a distance of roughly 35 kilometers, as well as the separation of the two sites within Hastière rockshelter, corroborates the importance of chronology to account for the differences among sites in maxillary first molar crown shape. The deciduous molars of Hastière Caverne M also differ from those of final/late Neolithic sites by the near ubiquity and large size of Carabelli's cusp and the expression of a protostylid (Williams et al. 2018).

Studies of dental morphology have shown similarities among individuals buried in the same graves (Alt et al. 1997) whereas others have suggested that practical kin rather than affinal relatives were buried together (Pilloud and Larson 2011). Both processes may explain the general overlap of individuals and the extensive variation at some sites such as Bois Madame and Hastière Caverne M. Although the tight clustering of Sclaigneaux and pairs of individuals from Hastière Trou Garçon C and Bois Madame may represent cases of affinity, differences, such as the distinctiveness of Hastière Caverne M, are probably more important than similarities in explaining the variation across sites.

Limitations of the study

Several studies have suggested that dental tissues are highly heritable (Hlesko et al. 2002; 2007; Hlesko and Mahaney 2003; Paul and Stojanowski 2015; 2017; Stojanowski et al. 2018; Hardin 2019).

This is particularly true of the first molar (Hlesko et al. 2007; Stojanowski et al. 2018; Hardin 2019). Crown outlines should therefore also be under strong genetic control like other markers of dental morphology. However, it is also possible that environmental or developmental factors could have limited the degree to which crown outlines are heritable over multiple generations. Additionally, a critique of elliptical Fourier analysis is warranted. While the use of outlines alleviates some of the problems inherent in selecting biologically relevant landmarks in geometric morphometrics, as well as in capturing shape features between landmarks, the method may also overemphasize representation of within-group variation compared to the variation between groups (Frieß and Baylac 2003; Baylac and Frieß 2005). This problem is further compounded by mixing within- and between-group variation in a principal components analysis (Baylac and Frieß 2005). Although the between-group variation seems to be greater than the within-group variation for most of the cave burial, the lack of statistical testing and classification rates from the limited size of the samples has reduced confidence in the validity of the results. Additionally, potential bias could have resulted from selecting relatively unworn and well preserved *in situ* molars. The resulting small and uneven sample sizes certainly affected the principal components analysis by allowing unusual individuals to have a disproportionate influence on the distribution of values on the PC axes.

Conclusion

We initially asked whether the crown shape of maxillary first molars from Late Neolithic Belgian sites would cluster based on the assumption that a greater number of relatives would be interred together within each burial. We also asked whether chronological age and/or geographical location would explain the results. Although there is some clustering of individuals per burial, extensive variation in crown shape within and between cave sites is the primary pattern. However, Hastière Caverne M does appear distinctive in maxillary first molar crown shape compared to the other cave burials, suggesting the PC axes have captured chronological differences. Bois Madame and Sclaigneaux differ from one another on some of the PC axes suggesting geography may partly explain the distinctions in molar crown shape among the final/late Neolithic sites. In contrast to Bois Madame, Sclaigneaux appears to largely overlap with Hastière Trou Garçon C. In this way, the distinctiveness of the final/late Neolithic sites should be reconsidered. More specifically, Hastière Trou Garçon C may be better described as a final/late Neolithic cave burial. Hastière Trou Garçon C and Hastière Caverne M do not group together in any discernable manner despite the fact that they are both from Hastière rockshelter. Indeed Hastière Caverne M may derive from a variable culture group that was distinct from the final/late Neolithic cave burials.

Nevertheless, these distinctions are subtle and suggest extensive interaction occurred among peoples living along the Meuse River of Belgium and its tributaries during the Late Neolithic. Although the funerary behaviors vary across Late Neolithic cave sites, the burial practices of this period are fundamentally distinct from subsequent Bronze Age internments where collective burials are rare or nonexistent. This seems to be the case at other locations as well where collective Neolithic burial practices were supplanted by individual internments with grave goods reflective of status distinctions and cultural identity (de Reu 2014; Waters-Rist et al. 2016; López-Onaindia and Subirà 2017; López-Onaindia et al. 2018).

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The Authors' contribution

BCB captured and processed the data as part of his MA thesis in Anthropology at Georgia State University. FLW created the photographic images at the Royal Belgian Museum of Natural Sciences as a Fulbright grantee and developed the research protocol. Both authors participated in writing the manuscript.

Conflict of interest

The authors declare that there is no conflict of interest.

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