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Comparison of maxillary first molar occlusal outlines of Neandertals from the Meuse River Basin of Belgium using elliptical Fourier analysis

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ABSTRACT: Several Neandertals derive from the karstic caves of the Meuse river tributaries of Belgium, including Engis 2, Scladina 4A-4 and Spy 1. These may form a group that is distinct in maxillary first molar occlusal outlines compared to La Quina 5 from Southwest France. Alternatively, chronological differences may separate individuals given that Scladina 4A-4 from MIS 5 is older than the others from MIS 3. Neolithic samples (n = 42) from Belgium (Maurenne Caverne de la Cave, Hastière Caverne M, Hastière Trou Garçon, Sclaigneaux and Bois Madame) dated to 4.6–3.9 kyr provide a context for the Neandertals. Dental casts were prepared from dental impressions of the original maxillary molars. Crown and occlusal areas as well as mesiodistal lengths were measured by calibrated Motic 3.0 microscope cameras. Occlusal outlines of the casts were captured through photostereomicroscopy and non-landmark smooth tracing methods. Occlusal outlines were processed using elliptical Fourier analysis within SHAPE v1.3 which reduced amplitudes of the harmonics into principal components (PC) axes. The first two PC axes group the Neandertals, although Scladina 4A-4 falls nearly outside the convex hull for the Neolithic sample. Neandertals are imperfectly separated from the Neolithic sample on PC3 and PC4, and completely distinct on PC5 and PC6. Scladina 4A-4 differs from the other Neandertals on most PC axes. Chronology may best explain the separation of Scladina 4A-4 from the more recent fossils, and particularly Spy 1 and La Quina 5 which are the most similar in maxillary first molar occlusal outline shape.

KEY WORDS: Engis 2; Scladina 4A-4; Spy 1; La Quina 5; Neolithic Belgium

Introduction

Neandertal-bearing sites in Belgium are distributed across several ecogeographic zones, and are dated from the last interglacial period to the relatively intense glacial perturbations occurring thereafter, from Marine Isotope Stage (MIS) 5 to MIS 3 (Di Modica et al. 2016). Unlike the Netherlands, Britain and Germany, Belgium was never glaciated during the last ice age and the varied landscape and presence of lithic outcroppings allowed Neandertals to effectively exploit the re-

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gion (Di Modica et al. 2016). The MIS 3 period is associated with abundant caves containing Mousterian tools and Neandertal remains from a total of 46 Middle Paleolithic sites in Belgium (Di Modica 2010). Many are <40 m from rivers and have large entrances and expansive internal galleries (Daujeard et al. 2016). This study examines three individuals from caves found within the Meuse River Basin of Belgium: Engis 2, Scladina 4A-4 and Spy 1. These three together represent a fifth of the 15 Neandertals discovered from a total of eight Middle Paleolithic sites in Belgium (Toussaint et al. 2011). The three include nearly the entire sample of well-preserved maxillary first molars.

Southwestern France also includes a rich assortment of cave sites and rock-shelters dating from MIS 5 to MIS 3, many with Quina-type Mousterian industries (Discamps and Royer 2017). La Quina cave, where this artifact complex was originally described, has multiple beds containing a sequence of anthropogenic deposits from Middle to Upper Paleolithic levels (Debénath and Jelinek 1998) and includes the well-known La Quina 5 remains (Petite-Marie et al. 1971). Middle Paleolithic peoples of the Meuse basin of Belgium and Southwest France both favored caves which were exploited seasonally by group members, although short-term encampments were also utilized to hunt, forage and procure locally available resources and raw lithic material (Daujeard et al. 2016; Di Modica et al. 2016). These two core areas may represent relatively stable populations with only episodic contact with groups from remote areas.

Estimating affinity using occlusal outlines

Neandertals may have lived in small closely-related groups (Lalueza-Fox et al. 2011; Kelso and Prüfer 2014). If true, then related Neandertals should resemble one another more closely than those from more distant locations. Close genetic relationships have been shown to be manifested in dental morphology. For example, occlusal surfaces, represented by two-dimensional images, have been shown to be highly heritable (Hlusko et al. 2007). Additionally, area measurements and molar crown area estimates are highly heritable in a known lineage of baboons with 55% of the variance explained by genetic mechanisms, including additive effects (Hlusko et al. 2002), as are scored dental traits of the cingulum, such as the interconulus and interconulid (Hlusko and Mahaney 2003). Dental traits, including remnants of the cingulum (i.e., Carabelli's cusp), are likely to be selectively neutral and thus serve to approximate genetic relationships (Turner et al. 1991; Scott and Irish 2017), and have been shown to differentiate Neandertals and recent humans (Bailey 2004; 2006).

In this study, we compare the occlusal outlines of the maxillary first molars of Engis 2, Scladina 4A-4, Spy 1 and La Quina 5 using elliptical Fourier analysis. As a comparative sample, we include Neolithic humans from the karstic caves of the Meuse River tributaries of Belgium (n = 42) dated to the brink of the Bronze Age, circa 4.6 to 3.9 kyr. The Neolithic cave burials are situated in close proximity to the Middle Paleolithic sites of Belgium, providing an ecological control, albeit from the warmer Holocene period.

Materials and Methods

Study populations

Original maxillary molars of Neandertals were examined by FLW at the Musée de l'Homme, the Université de Liège, the Institut royal des Sciences naturalles de Belgique and the Scladina Cave Archaeological Centre (Table 1). The Neolithic remains were examined at the Institut royal des Sciences naturalles de Belgique.

Engis 2

The second cave of Engis (Schmerling Cave) from which Engis 2 derives, represents multiple levels, including Middle Paleolithic deposits (Toussaint et al. 2011). The taphonomic context of Engis 2 is poorly known owing to its discovery in the winter of 1829–1830, prior to the development of precise excavation techniques (Twiesselmann 1971; Semal et al. 2013; Toussaint and Pirson 2006; Tousiant et al. 2011). Radiocarbon dates of 26,830 ± 430 and 30,460 ± 210 years BP from the parietal bone are believed to be too recent, and do not accord with the artifact assemblage (Toussaint and Pirson 2006; 2014; Toussaint et al. 2011; Di Modica et al. 2016). Engis 2 includes a calvarium and an isolated maxillary fragment of a child aged 4–5 years (Tillier 1983; Toussaint and Pirson 2006; 2014; Williams 2013), and is associated with an unworn, probably unerupted, right maxillary permanent first molar (Fig. 1) with slightly less than 1 mm of root development.

Table 1. Neandertal fossils utilized in this study

Individual	Ecogeographic Region	Chronology
Engis 2	Meuse River Basin, Belgium	MIS 3
La Quina 5	Charente, Southwest France	MIS 3
Scladina 4A-4	Meuse River Basin, Belgium	MIS 5
Spy 1	Meuse River Basin, Belgium	MIS 3

Scladina 4A-4

The MIS 5 deposits of 4A-CHE yielded Scladina 1–4A, comprising 19 Neandertal remains, including demi-mandibles, a partial maxilla and 11 teeth from a single individual (Toussaint 2014a; Toussaint and Pirson 2014; Toussaint et al. 2014). The level from which Scladina 1–4A was excavated is separated from the MIS 3 deposition which occurred between 40 and 37 kyr (Bonjean et al. 2011; Daujeard et al. 2016). The MIS 3 deposits contained black pigments and the remains of burnt animal bones, but no Neandertal fossils have been discovered (Bonjean et al. 2015). The Neandertal child from MIS 5, Scladina 1–4A, was dated using gamma-spectrometry to circa 127 kyr; although, using a chronostratigraphic framework and the Greenland Record as context, it is likely that the Scladina 1–4A Neandertal is either from MIS 5a circa 80 kyr or MIS 5b circa 87 kyr (Pirson et al. 2014; Toussaint and Pirson 2014; Di Modica et al. 2016). Scladina 4A-4 is the right maxillary permanent first molar of Scladina 1–4A (Bonjean et al. 2011; Toussaint 2014b) (Fig. 1). The fossil has been identified as an older child, aged to 8-11 years (Smith et al. 2007; 2014; Williams 2013; Toussaint and Pirson 2014).

Spy 1

Two adult partial skeletons of Neandertals (Spy 1 and Spy 2) were discovered in 1886 in Spy cave (Semal et al. 2013). The Spy assemblage is dated to relatively recently, circa 36 kyr (Semal et al. 2009), and may represent intrusive burials from the second fossiliferous level into the third level (Semal et al. 2013). The adult remains from Spy can be dated to the terminus of the Middle Paleolithic or possibly, though less likely, to the transitional Lincombian-Ranisian-Jerzmanowician artifact assemblage (Toussaint and Pirson 2014). Spy 1 has been aged as a young adult of ~35 years and includes a lower maxilla, mandible and calvarium (Twiesselmann 1971; Semal et al. 2009; 2011; 2013; Williams 2013; Toussaint and Pirson 2014), as well as a well preserved right maxillary first molar, Spy-C (Fig. 1).

La Quina 5

La Quina 5 is from Level 3 of Station Amont of La Quina Cave. Level 3 is associated with a middle Mousterian industry and has been dated to circa 43–47 kyr which corresponds to MIS 3 (Discamps and Royer 2017). La Quina 5 is represented by a partial skeleton, including a calotte, isolated maxilla and mandibular corpus (Williams 2013). The individual was previously suggested to be an elderly female (Petite-Marie et al. 1971), although this sex assessment has been recently challenged (Trinkaus 2016). The teeth exhibit substantial attrition with exposures of dentin present on most teeth, all of which are worn to a single functional plane. The left maxillary first molar was examined because the attrition is greater on the right side (Fig. 1).

Neolithic humans

The Neolithic remains (n = 42) include those from Maurenne Caverne de la Cave (n = 9), Hastière Caverne M (n = 7), Hastière Trou Garçon (n = 5), Sclaigneaux (n = 11) and Bois Madame (n = 10). These caves are among the nearly 200 rockshelters and caverns of the Meuse River Basin of Belgium which were utilized as burial chambers. The majority of the remains found were brought to the caves during the Late Neolithic period (Semal et al. 1999; Toussaint et al. 2001; Toussaint 2007; Polet 2011). Four dates have been obtained for Maurenne Caverne de la Cave, spanning 4,635 to 3,830 years BP, suggesting the burial chamber may have been in use for at least 800 years (Vanderveken 1997; Bronk-Ramsey et al. 2002; Tous-

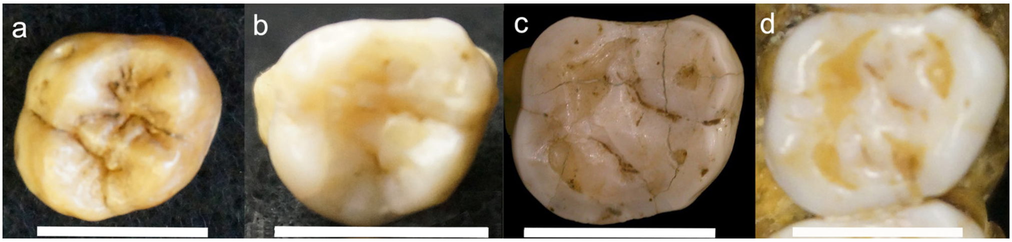

Fig. 1. Neandertal maxillary first molars in this study include (a) Engis 2, represented by an unworn (Stage 1; Smith 1984) right M1 and dated to MIS 3; (b) Scladina 4A-4, a right M1 from a child of 8–11 years which is relatively unworn (Stage 2; Smith 1984) and dated to MIS 5; (c) Spy 1 (Spy-C), represented by a relatively worn (Stage 5; Smith 1984) right M1 and dated to circa 36 kyr (MIS 3); and (d) La Quina 5, a somewhat worn (Stage 5; Smith 1984) left M1 dated to MIS 3. All right molars were flipped horizontally. The molars were positioned such that mesial is toward the top of the image. Scale bar = 1 cm

saint 2007). Hastière Caverne M is estimated to date 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). Both of the Hastière caves are middle Late Neolithic. In contrast, Sclaigneaux has been dated to 4,110 years BP which is toward the terminus of the Late Neolithic (Paepe 2007). The most recent Neolithic site sampled is Bois Madame which has yielded two dates (4,075 ± 38 and 3,910 ± 40 years BP), implying the possibility that this rockshelter was repeatedly used as a burial destination for more than 150 years (Bronk-Ramsey et al. 2002; Dumbruch 2003; 2007).

Data acquisition

Dental impressions of the fossil and Neolithic teeth, as well as a Scladina 4A-4 first generation resin cast on loan to FLW from the Scladina Archaeological Centre, were created by applying a thin layer of polyvinylsiloxane (President Jet Plus, medium body, Coltène-Whaledent) to the occlusal surface. Use of the dental resin cast of Scladina 4A-4 avoided taking into account the sliver of the crown which was removed to estimate age at death (Smith et al. 2007; 2014; Toussaint 2014b). A dental cast of Spy-C was created from a dental impression of the right maxillary first molar loaned to FLW from the Institut royal des Sciences naturalles de Belgique. Dental casts were prepared at the Bioarchaeology Lab of Georgia State University from dental impressions using epoxy resin and hardener (EpoxiCure, Buehler). The centrifuged mixture was poured into putty holding cups affixed beforehand with hardener (Buehler). The dental casts were left to dry for 24 hours at room temperature before extraction.

The maxillary occlusal outlines of the dental casts were examined using photostereomicroscopy and non-landmark smooth tracing methods in the Dental Microwear Laboratory of Georgia State University by a single observer (KML). Two-dimensional contours of the outer cuspal rim were imaged perpendicular to the occlusal surface, at a magnification of 10×, with an attached Moticam 3.0 megapixel trinocular camera and computer interface Motic SMZ-140TL. The outer cuspal rim was manually traced within Adobe Photoshop® (Fig. 2).

Three measurements were taken on each molar, including crown area, oc-

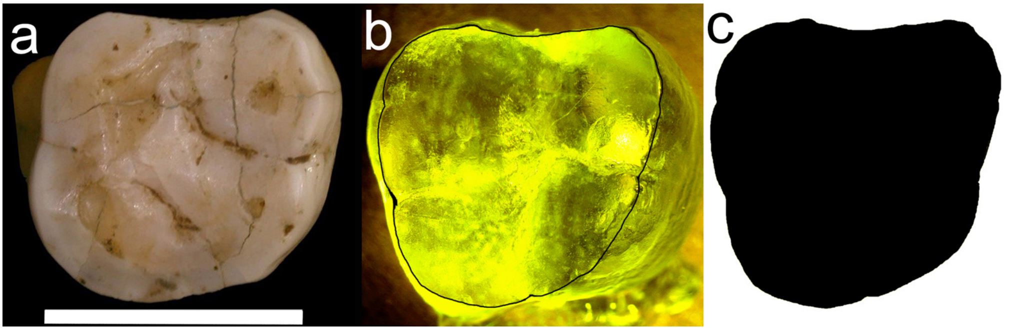

Fig. 2. Photographic image of (a) Spy 1 (Spy-C) juxtaposed with (b) the traced occlusal outline of the molar, and (c) a fully binarized image. Scale bar = 1 cm and mesial is toward the top of the image

clusal area and mesiodistal length (MD) using Motic tool functions. Crown area was captured by tracing the maximum visible crown surface, whereas occlusal area was defined as the extreme outline of the cuspal outer rim of the occlusal basin. The MD dimension was measured as the greatest distance between homologous points on the mesial and distal extremes that were parallel to the buccal and lingual surfaces.

Substantial dental wear may have impacted estimates of occlusal area more than crown area as attrition reduces the cusps and may have influenced differences between the unworn maxillary permanent first molar (M^1) of Engis 2 and those of Spy 1 and La Quina 5 which represent decades of wear. However, the notable buccolingual constriction of the occlusal basin in Engis 2 (Fig. 1) is likely to be a more profound difference than distinctions in wear.

Right antimeric outlines were mirrored horizontally within Adobe Photoshop® in order to standardize for siding, and the resultant images were imported into SHAPE v1.3. This program fully binarizes these images into a grid of only blank or filled pixels (Fig. 2), either black or white, and transcodes this into a Freeman chain-code of the image along all points where the pixel matrix changes, outputting a mathematical description of the contour (Iwata and Ukai 2002). This chain code was used to create the elliptical Fourier descriptors of each outline at a 20 harmonic resolution, by recording deviations of each individual outline shape from a normalized ellipse using trigonometric functions to calculate negative and positive perturbations. These are recorded as the amplitudes of the harmonics derived from four elliptical Fourier coefficients which describe subtle aspects of shape (Lestrel 1974; 1997; Kuhl and Giardina 1982; Haines and Crampton 2000; Iwata and Ukai 2002). Contour analysis of human posterior teeth has been previously conducted on Neandertals and modern humans (Benazzi et al. 2011a, b; 2012; Bailey et al. 2014; 2016; Bauer et al. 2016). Similar analyses have been conducted using elliptical Fourier functions to identify the degree of sexual dimorphism of human first molars (Ferrario et al. 1999) and to tooth crown shape of the mandibular permanent distal premolar (P_4) of Neandertals (Bailey and Lynch 2005). We apply a smooth-tracing, full resolution shape extraction in order to maximize the accuracy of specimen description and subsequent analysis using elliptical Fourier functions.

Statistical methods

Principal Components Analysis within SHAPE v1.3 was utilized to reduce the amplitudes of the harmonics to principal components (PC) scores for Neandertals and the Neolithic sample, both together and separately. For the Neolithic sample independent of the Neandertals, Kruskal-Wallis tests were included to compare each PC axis (dependent variable) with respect to the five Neolithic cave burial categories (independent variable) to ascertain whether significant differences could be identified, and when found, pair-wise Mann-Whitney U tests were run to identify inter-site distinctions.

When the total sample of Neolithic and Neandertal occlusal outlines were processed together within SHAPE v1.3, subsequent PC scores with eigenvalues greater than one and explaining at least 2.5% of the variance were plotted using

100% convex hulls to discern groupings. Pearson's correlations between PC scores and the measured variables were calculated to assist in interpreting the distribution of individuals across axes.

To examine the degree to which allometry influenced the results, regressions of the PC scores against log-transformed metric variables were calculated. The 95% confidence intervals of the regression coefficients were created using the standard error to test whether the slopes overlapped, with a zero value indicative of no change in shape as size increases.

Results

Neolithic sample

A Kolmogorov-Smirnov One Sample Test of the PC scores shows that the Neolithic human data are significantly different from a normal distribution justifying the use of nonparametric statistical tests of significance. The results of Kruskal-Wallis tests imply that there is no significant difference among the five Neolithic cave burials in the eight PC scores with eigenvalues greater than one, with the exception of PC6 (Table 2). The relatively high Kruskal-Wallis test statistic and significant p value ($p = 0.04$) for PC6 suggests some between-group distinctions are present (Table 2). However, PC6 accounts for only 2.2% of the variance explained. Mann-Whitney U tests for each pair-wise comparison of Neolithic cave burial categories shows that Bois Madame and Sclaigneaux are significantly different in PC6 scores ($p = 0.001$). None of the other comparisons between populations are significant. Given the lack of significant differences of PC scores among the cave burials generally, they are utilized as a single group to compare to the Neandertals.

Table 2. Kruskal-Wallis results for the PC scores of five Neolithic cave burials

PC Axes	KW[1] test statistic	P value
PC1 (43.7%)	3.586	0.465
PC2 (15.9%)	0.878	0.928
PC3 (12.7%)	2.463	0.651
PC4 (10%)	6.860	0.143
PC5 (4.1%)	1.176	0.882
PC6 (2.2%)	15.538	0.004
PC7 (1.7%)	4.484	0.385
PC8 (1.7%)	0.705	0.951

[1] Kruskal-Wallis

Neandertal and Neolithic samples

Elliptical Fourier analysis of the Neandertal and Neolithic samples yields 76 PC scores from the 20 harmonic descriptors. However, a total of nine PC axes exhibit an eigenvalue greater than one (91.7% of the variance). The occlusal outlines for the first six PC axes, cumulatively explaining 86.4% of the variance, were examined further. Overall differences among individuals can be visualized using the mean occlusal outline, plus and minus two standard deviations (Fig. 3).

Estimates of size and allometry

Metric variables indicative of size differ among Neandertals (Table 3). Furthermore, variation within Neandertals exceeds that for the Neolithic sample for crown and occlusal areas (Table 3). To examine the influence of size on the sample, tests of allometry are calculated. Coefficients for the three metric variables show that the null hypothesis of isometry cannot be refuted for 15 out of 18 PC scores (Fig. 4). Only three excep-

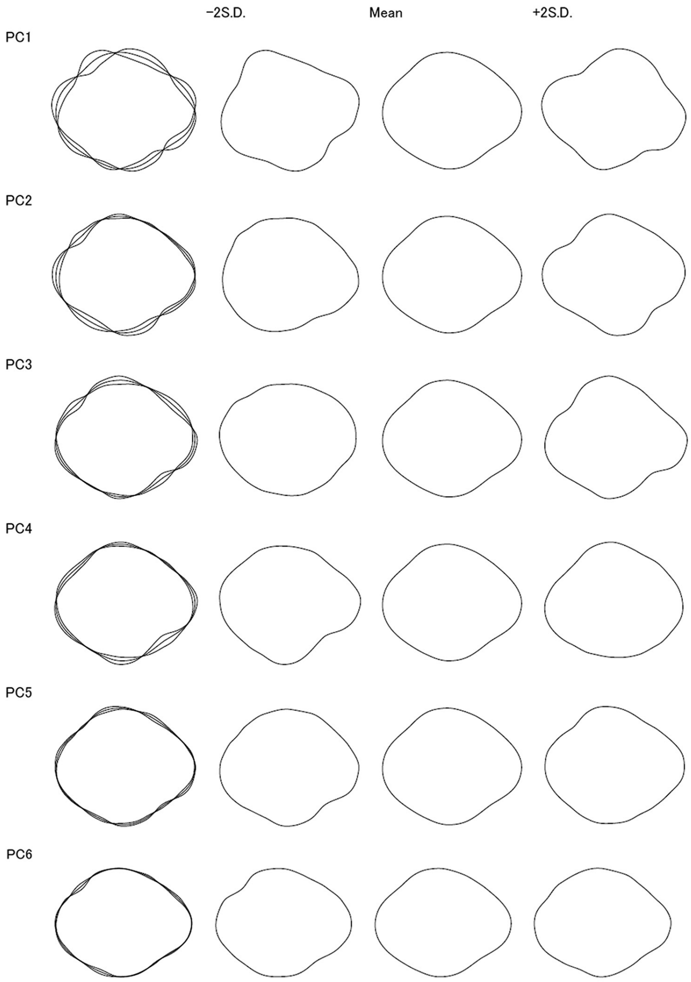

Fig. 3. Visualization of occlusal outlines for six PC axes characterizing the Neandertal and Neolithic combined sample, showing the mean plus and minus two standard deviations

Table 3. Metric values for individual Neandertals and descriptive statistics for samples

Neandertals and sample descriptive statistics[1]	Crown area (mm^2)	Occlusal area (mm^2)	MD (mm)
Engis 2	89.305	57.143	11.110
La Quina 5	102.736	95.879	10.328
Scladina 4A-4	88.674	80.718	10.728
Spy 1	119.593	94.497	11.130
Neandertals (n = 4)	100.077 (14.537)	82.059 (17.966)	10.823 (0.381)
Neolithic humans (n = 42)	92.336 (8.057)	77.744 (11.404)	10.029 (0.607)

[1] Samples associated with means and standard deviations (within parentheses).

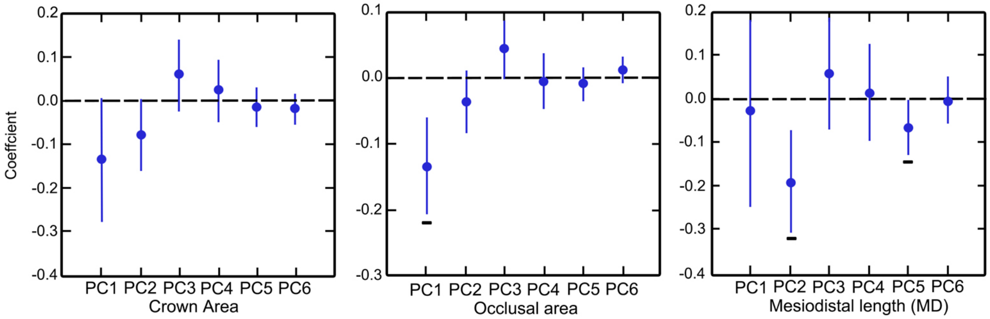

Fig. 4. Test of allometry comparing each PC axis to metric size variables including (left) crown area; (center) occlusal area; and (right) mesiodistal length (MD). The 95% confidence intervals (blue lines) of the coefficients (blue circles) largely overlap isometry, denoted by the dashed line, centered at zero, representing no change in shape as size increases. Three exceptions include PC1 and occlusal area, PC2 and MD, and PC5 and MD, each indicated by a minus sign, signifying negative allometry

Table 4. Pearson correlations of PC axes and metric variables for Neolithic and Neandertal samples[1]

	PC1	PC2	PC3	PC4	PC5	PC6	Crown area (mm^2)	Occlusal area (mm^2)
Crown area (mm^2)	–0.275	–0.289	–0.208	–0.108	–0.126	0.140	–	–
Occlusal area (mm^2)	**–0.480**	–0.259	–0.282	–0.038	–0.155	0.138	**0.664**	–
MD (mm)	0.034	**–0.455**	–0.120	–0.029	**–0.308**	–0.034	**0.700**	**0.505**

[1] Significant correlations are in bold

tions exist, all of which exhibit negative allometry and are significantly related: PC1 and occlusal area ($p = 0.01$), PC2 and MD ($p = 0.02$), and PC5 and MD ($p = 0.04$), where shape distinctions may be influenced by increasing size (Fig. 4). The measures of size are relatively highly correlated to one another compared to those involving PC scores (Table 4) and a significant correlation exists between all three metric variables ($p < 0.001$).

Principal components analysis

On the first two PC axes, the variation of the Neolithic sample is larger than that of the Neandertals (Fig. 5). Scladina 4A-4 falls nearly outside the convex hull representing 100% of the Neolithic sample. Engis 2 is situated more centrally within the Neolithic sample. Spy 1 and La Quina 5 are located between these two extremes, but closer to Engis 2 (Fig. 5). Neandertals, with generally larger crown areas (Table 3), are projected slightly positively on PC1 whereas the Neolithic sample is positioned both highly positively and negatively on this axis intimating that much variability exists in the size and shape of molar contour morphology in this human sample (Fig. 5, Table 4). On PC2, Scladina 4A-4 is separated from the other Neandertals.

On PC3 and PC4, the convex hulls for Neandertals and Neolithic humans overlap one another. However, Scladina 4A-4 and Spy 1 fall outside of the convex hull representing the Neolithic sample (Fig. 5). Spy 1 and La Quina 5 are both projected positively, whereas Engis 2 is

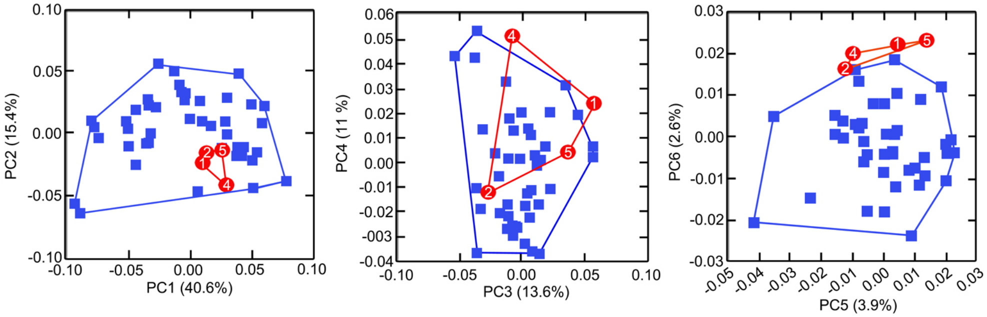

Fig. 5. Principal Components Axis 1 and PC2 (left); PC3 and PC4 (center); and PC5 and PC6 (right). Neandertals (red) and Neolithic humans (blue) are demarcated by convex hulls representing 100% of the samples. The symbols for the Neandertals are: Spy 1 = 1; Engis 2 =2; Scladina 4A-4 = 4 and La Quina 5 = 5

distinct from the other Neandertals and is positioned close to the opposite edge of the human range; Scladina 4A-4 is difficult to classify on PC3 (Fig. 5). On PC4, it is Scladina 4A-4 which is polarized from Engis 2. Spy 1 and La Quina 5 resemble one another on both PC3 and PC4 (Fig. 5).

On PC5 and PC6, the convex hull for Neandertals is distinct from that of Neolithic humans (Fig. 5). With respect to the Neandertal sample, Scladina 4A-4 and Engis 2 are separated on PC5, whereas on PC6, all of the Neandertals resemble one another, particularly Spy 1 and La Quina 5. Essentially, PC6 is a contrast vector projecting Neandertals with uniquely shaped, large molars from the Neolithic sample, most of whom exhibit relatively reduced MD dimensions (Fig. 5, Table 4).

Discussion

These results are limited by the size of the samples. With such small samples, the results may have been influenced by a few specimens. Furthermore, differential wear may affect occlusal and crown manual outlines (Benazzi et al. 2012; Bailey et al. 2016). Nevertheless, as has been shown by others, the Neandertals are distinct from Holocene humans in the shape of the post-canine teeth (Benazzi et al. 2011a, b; 2012; Bailey et al. 2014; 2016; Bauer et al. 2016).

Within the Neandertals, Spy 1 and La Quina 5 appear to share a relatively similar maxillary first molar occlusal contour when compared to those characterizing Scladina 4A-4 and Engis 2 (Fig. 5). Part of this relationship may stem from the relatively large size of the molars of Spy 1 and La Quina 5 compared to those of Engis 2 and Scladina 4A-4. However, none of the PC axes are as strongly correlated with measures of size compared to the correlations among the metric variables suggesting that subtle aspects of shape are far more important in distinguishing Neandertals from the Neolithic sample, and in identifying outliers among the fossils. Part of this resemblance may be borne out by the similarities in dental anatomy between Spy 1 and La Quina 5. For example, the paracone is rather large and projects buccally in both Spy 1 and La Quina 5. By comparison, the paracone of Scladina 4A-4 is relatively smaller and somewhat pinched buccolingually.

Although all of the Neandertals exhibit a large hypocone, those of Spy 1 and La Quina 5 are extensive (ASUDAS grade 6; Scott and Irish 2017), comprising nearly a fourth of the tooth (Fig. 1). Furthermore, the protocone is relatively prominent in Spy 1 and La Quina 5, particularly in comparison to that of Scladina 4A-4.

In most analyses, Scladina 4A-4 is distinct suggesting chronology rather than ecogeography may explain differences between individuals. The lengthy time span separating Scladina 4A-4, dated to MIS 5 (Pirson et al. 2014), from the MIS 3 Neandertals – a difference which may have exceeded 80–40,000 years – may help explain the distinctiveness of the sole individual from Scladina cave. What is perhaps the most surprising is the relative similarity in morphology between Spy 1 and La Quina 5 despite the considerable distances separating the two sites and the fact that Spy 1 may be substantially younger (Semal et al. 2009).

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Authors' contributions

FLW created the dental molds at museums in Belgium and France, assisted in creating the dental casts at Georgia State University, analysed the Principal Components scores and wrote the paper; KML traced the outlines and ran the results in SHAPE v1.3; WGA assisted in creating the dental casts and developed the experimental protocol using the Motic camera system and SHAPE v1.3 software packages.

Conflict of interest

The authors have no conflicts of interest to declare.

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