Diagnostic Differences in Mandibular P4 Shape Between Neandertals and Anatomically Modern Humans

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ABSTRACT   This study uses elliptical Fourier analysis to quantify shape differences observed in the P_4 crown of Neandertals and anatomically modern humans. Previously, P_4 shape was assessed qualitatively, and results suggested marked differences between Neandertals and anatomically modern humans (Bailey [2002] New Anat. *269:*148–156). The goal of this study was to investigate the P_4 shape in more detail, quantifying it in order to determine its utility for taxonomic classification and phylogenetic analysis. A comparison of mean shapes confirms that the mesiolingual portion of the P_4 is truncated in Neandertals, and that this produces a distinctively asymmetrical P_4. A randomization test confirms that the shape difference between Neandertals and anatomically modern humans is significant. Principal component and discriminant function analyses indicate that the relative size of the lingual portion of the tooth also affects tooth shape, with the lingual portion of the Neandertal P_4 being narrower than that of anatomically modern humans. Classification of P_4 crown shapes using discriminant functions analysis is far from perfect. While 86.4% of the teeth were correctly classified, classification was much better for anatomically modern humans (98.1%) than it was for Neandertals (65%). Fortunately, crown shape is but one of several diagnostic characters of the P_4 crown. P_4 crown asymmetry can be added to the growing list of dental morphological characters distinguishing Neandertals from anatomically modern humans. Moreover, based on a comparison of mean tooth shapes in fossil and recent humans, symmetry, rather than asymmetry, appears to be the primitive state, and the high frequency of P_4 asymmetry is likely derived in Neandertals. Am J Phys Anthropol 126:268–277, 2005.   © 2004 Wiley-Liss, Inc.

The use of minor tooth crown variants to address the role of Neandertals in modern human origins is relatively recent (Crummett, 1994; Bailey, 2000, 2002b). Traditionally, paleoanthropologists focused, instead, on information gathered from the skull and/or postcrania to address this important question. The identification of Neandertal apomorphies (derived characters) has played an important part in this research (Hublin, 1978; Rak, 1986; Hublin et al., 1996; Rak et al., 1996, 2002; Schwartz and Tattersall, 1996). Considering the relative frequency with which teeth are found in the fossil record and that taxonomic identification must sometimes be made based on teeth alone, it is important that efforts be made to recognize dental characters or patterns that can be used to identify fossil hominids. This study focuses on one tooth whose morphology appears to be particularly useful for taxonomic identification: the mandibular P4 (P_4).

Although there are possibly 200 or more dental crown traits that can be observed in the human dentition (Morris, 1965), few have received as much attention as the presence of taurodont roots (those with unusually large pulp chambers) and shovel-shaped incisors. Descriptions of Neandertal morphology typically identify variably present taurodontism as one of the traits that distinguishes

them from other hominins (e.g., Day, 1977; Hillson, 1986; Stringer and Gamble, 1993; Klein, 1999). Likewise, marked incisor shoveling has long been recognized as a distinctive Neandertal trait (Gorjanovic-Kramberger, 1906). More recently, a combination of incisor traits (shoveling, lingual tubercles, and labial convexity) was identified as characterizing Neandertals (Crummett, 1995; Bailey, 2000).

Although some researchers alluded to the presence of additional unique dental characters in Neandertals (e.g., Patte, 1959; Genet-Varcin, 1966; Zubov, 1992a,b), until recently, little had been done to pursue these suggestions in a comparative context. Instead, descriptive studies of particular fossils dominated the literature (Fraipont and Lohest,
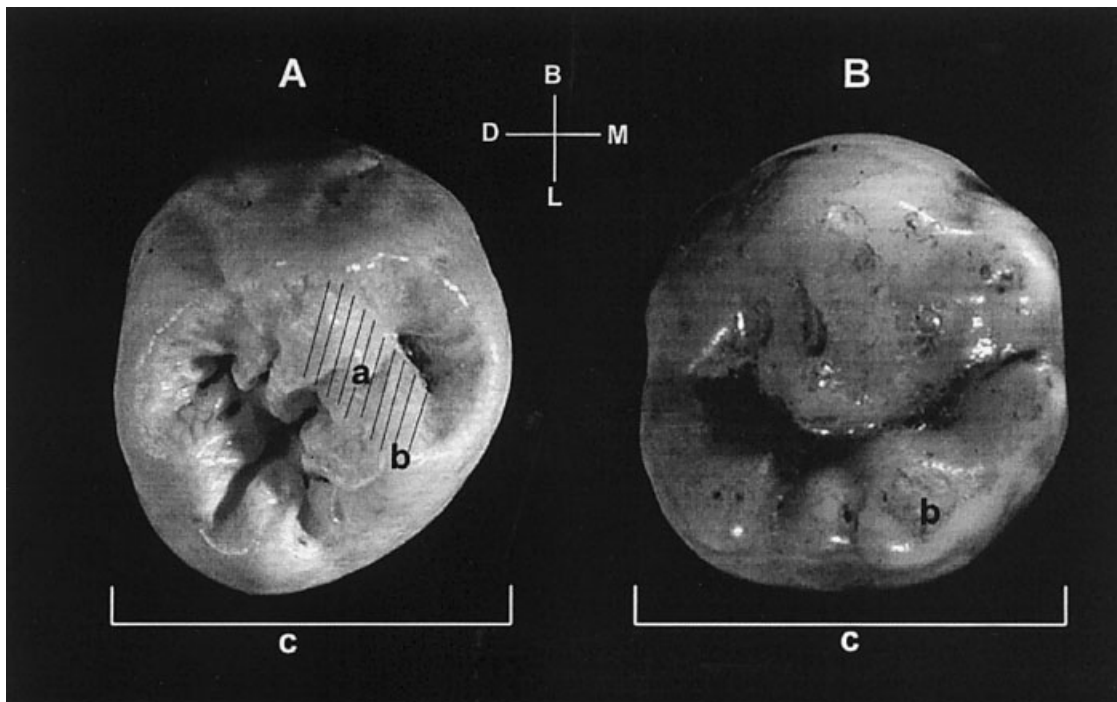
Fig. 1. Comparison of a typical Neandertal left P_4 (**A**) showing a strong transverse crest (a, hatched area), well-developed and mesially placed metaconid (b), and asymmetrical lingual contour (c), and a left P_4 from a contemporary Australian (**B**) lacking a transverse crest, with more weakly developed metaconid (b) and symmetrical lingual contour (c).

1887; Fraipont, 1936; Piveteau, 1959; Bordes and Lafille, 1962; Piveteau et al., 1963; Lumley et al., 1972; Tillier, 1983).

Recent work on Neandertal dental morphology (Bailey, 2002a,b) led to the identification of a number of dental crown traits that have not been studied in great detail but that are potentially useful for sorting out taxonomic status and relationships among Middle-Late Pleistocene hominins. Based on this work, it is apparent that P_4 is a particularly useful tooth for taxonomic purposes, in that it exhibits a number of crown traits that distinguish Neandertals from modern humans and other fossil hominins (Bailey, 2002b). These traits include the combination of a strong transverse crest, a well-developed and mesially placed metaconid, and a truncated mesiolingual lobe that results in crown asymmetry (Fig. 1). While each trait can be found in anatomically modern humans and other fossil hominins, the frequency with which these three traits occur together in a single tooth (59% in Neandertals, and 0% in anatomically modern humans) distinguishes Neandertals from both contemporary and fossil humans (Bailey, 2002a). One of these, crown asymmetry, is considered in greater detail here.

Dental anthropologists frequently rely on qualitative methods such as the Arizona State University dental anthropology system (ASUDAS; Turner et al., 1991) to make morphological assessments. This method uses a graded scoring system to measure trait expression, but these quasicontinuous data are ultimately dichotomized into presence/absence data

for most analyses. When P_4 shape (which is not currently one of the ASUDAS traits) was dichotomized into presence (asymmetrical) and absence (symmetrical) states in an earlier study (Bailey, 2002a), the result was marked differences of trait frequency in Neandertals and anatomically modern humans (96% vs. 0–6%). In that study, the degree of asymmetry was not evaluated, and it was not possible to test whether the mean P_4 shape of the two groups differed significantly.

The primary goal of this study was to quantify P_4 shape in order to address some unanswered questions of the previous study (Bailey, 2002a). Specifically, we were interested in determining if the differences observed between Neandertals and anatomically modern humans in the first study were statistically significant. To this end, we used elliptic Fourier analysis to quantify the P_4 occlusal outline and obtain mean P_4 shapes. With elliptic Fourier analysis, the entirety of the tooth's occlusal outline could be evaluated and considered in a multivariate analysis. In this way, the statistical significance of the differences in mean P_4 shape could be evaluated. This method of determining mean shapes also allowed us to compare the mean P_4 shape of Neandertals to that of other fossil hominins, and assess earlier conclusions that the morphology observed in Neandertals P_4s is derived (Bailey, 2002a).

Finally, we were interested in determining how well P_4 occlusal crown shape, alone, distinguishes Neandertals from anatomically modern humans. This is particularly important, given the frequency

TABLE 1. Samples used in this study and their composition

Group	Individuals/population
Homo erectus (n = 8)	Zhoukoudian 29, 90 KNM ER-15000, 992 OH 22 Ternigif 825, 286 Thomas Quarries
Archaic *Homo sapiens* (n = 3)	Arago 28, 13 Mauer
Neanderthals (n = 20)	Krapina D26, D30, D31, D32, D35, D50, D113, D118, MdE, F, H, J Le Moustier Pontnewydd 5 Régourdou Tabun 1 Hortus 2 Brno Spy 1, 2
Early anatomically modern *Homo sapiens* (n = 4)	Qafzeh 7, 8, 9 Skhul
Upper Paleolithic *Homo sapiens* (n = 6)	Dolni Věstonice 13, 14, 15 Gough's Cave 1 Forneau de Diable 2 Bruniquel
Contemporary *Homo sapiens* (n = 95)	North Africa (n = 3) West Africa (n = 20) Europe (n = 26) Northeast Asia (n = 7) Near East (n = 7) India (n = 14) Australasia (n = 18)

with which taxonomic identification must be made based solely on dental remains. To this end, we used discriminant function analysis to examine whether P_4 occlusal crown shape is a useful tool for elucidating the taxonomy of an isolated P_4 found in an archaeological context.

MATERIALS AND METHODS
Data acquisition

Two-dimensional coordinate data describing P_4 shape were acquired by taking digital images of the P_4 occlusal crowns of 136 individuals representing six hominin groups (*Homo erectus* (n = 8), archaic *Homo sapiens*, a.k.a. *H. heidelbergensis* (n = 3), Neandertals (n = 20), Upper Paleolithic modern humans (n = 6), early anatomically modern humans (n = 4), and contemporary modern humans (n = 95); Table 1). Images were taken with a Nikon CoolPix 950 digital camera, using a macro setting. The camera was attached to a camera stand or tripod, and a leveling device was used to ensure a consistent camera angle. Each tooth was positioned so that the cervical line was approximately perpendicular to the camera's focal point, and all images were composed using the LCD monitor to control for camera parallax.

Because the samples in this study were derived from archaeological and fossil contexts it was rare to find individuals in which P_4s from both sides of the jaw were preserved. Teeth from the left side were arbitrarily chosen for the focus of the analysis, but to maximize sample sizes a tooth from the right side was used when the left tooth was absent or damaged. In these cases, Adobe® Photoshop® was used to mirror image teeth from the right side so that they could be analyzed along with those from the left. Generally speaking, there was a high degree of concordance in P_4 shape between the left and right sides of the jaw. This appears to be true of most dental morphological traits: when differences in expression are observed, they tend to be minor (Scott and Turner, 1997, p. 99).

Images were downloaded onto an IBM-compatible personal computer, and Adobe® Photoshop® was used for editing. Photo editing involved mirror imaging (where necessary) and orienting each tooth horizontally along its mesio-distal axis (parallel to the x-axis). Editing software was also used to obtain a well-defined distinction between "tooth" and "background" by deleting the background and increasing the contrast of each image. Although tooth asymmetry was generally not affected by interproximal wear, the overall outline of the tooth could be affected (e.g., mesial and/or distal borders may be flattened with wear). In order to avoid confounding the results, in some cases, conservative corrections for interproximal wear were made by reconstructing the original mesial and/or distal crown margins based on the total crown shape and the buccolingual extent of the wear facet(s) (Fig. 2).

Digital images were uploaded into TPSdig (Rohlf, 2001), and the "trace" option was used to trace the occlusal crown and obtain coordinate data for the outline. All tooth traces began at the most buccal point of the tooth outline. The coordinate data describing the outline shapes were imported into Morpheus (Slice, 2000) to obtain elliptic Fourier coefficients.
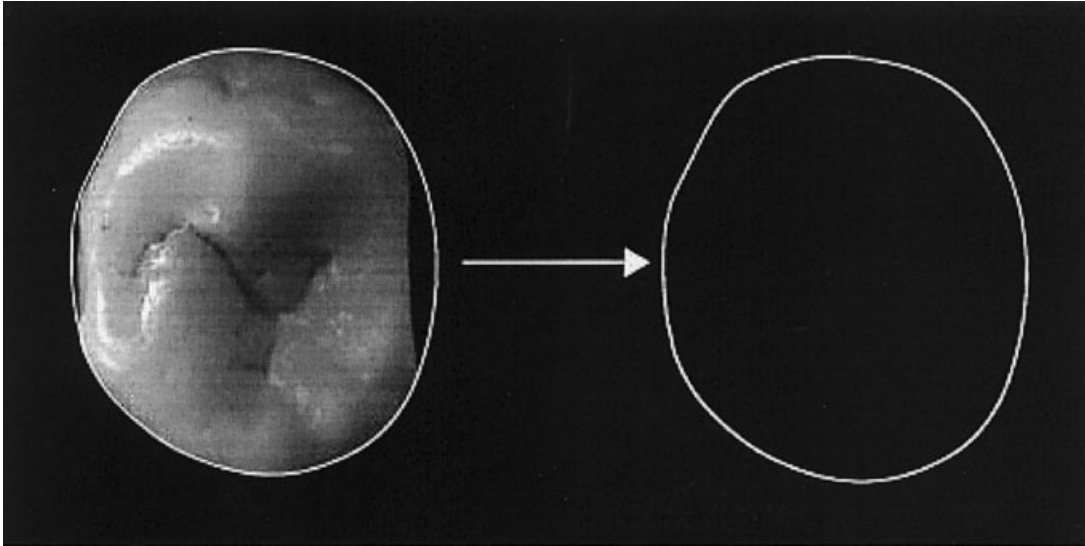
Fig. 2. Example of interproximal wear correction for obtaining P_4 outline shape (right). Note that symmetry of lingual surface is not affected by correction.

ANALYSIS

Elliptic fourier analysis

Elliptic Fourier analysis (EFA) is a process used to describe the outline of a two-dimensional closed curve (Kuhl and Giardina, 1982; Lestrel, 1997). It is based on fitting elliptic Fourier harmonics to closed outlines. Each harmonic defines ellipses that become smaller and smaller as they describe the outline shape in greater detail. Each harmonic is described by four elliptic Fourier coefficients. The elliptic Fourier coefficients are derived from a set of x- and y-coordinates that define a particular shape. These coefficients can be used as morphometric variables in multivariate analyses, thus allowing one to make quantitative statements about differences among groups of interest. Elliptic Fourier description is able to both describe complex forms and identify rather subtle differences among very similar oval shapes (e.g., Lestrel, 1974; Ferson et al., 1985; Chen et al., 2000; Seiffert and Kappelman, 2001). In the latter sense, it is particularly useful for analyzing differences in P_4 shape, as defined by occlusal crown outlines (which are essentially variations on an oval theme).

Fourier analyses were made invariant of size, position, and rotation, and used all eight harmonics (32 Fourier coefficients). To obtain mean P_4 shapes, the outlines from each group were analyzed separately. The results from the separate fossil and contemporary modern human analyses were then merged for subsequent multivariate analyses of differences between the P_4 shape of Neandertals and of anatomically modern humans.

Multivariate analyses

The 32 elliptic Fourier coefficients for each specimen were treated as variables in principal component and discriminant function analyses. Principal component analysis was used to identify significant sources of variation without a priori grouping of specimens, while discriminant function analysis was used to determine the probability that Neandertals could be correctly assigned to their group based solely on P_4 shape outline. Discrimination, in this case, was based on calculating Mahalanobis distances of individuals to group centers and then assigning each individual to the group to which it was closest.

In order to test the significance of the shape differences between anatomically modern humans and Neandertals, MANOVA was used to obtain Wilks' lambda, a measure of the difference between groups. A randomization test was used to estimate the significance of Wilks' lambda. To do this, the elliptic Fourier coefficients were randomly reassigned to taxa 10,000 times. Each time, the 125 cases (sets of coefficients) were reassigned to anatomically modern human and Neandertal groups (keeping the group sizes 20 and 105), and a new lambda value was obtained. These new values were then compared to the one obtained between Neandertals and anatomically modern humans (see results below).

RESULTS

Mean tooth shape

The mean tooth shape (outline) for each group was calculated using all eight harmonics. Each mean shape is an oval variant, and the differences among shapes are small (Fig. 3). The Neandertal P_4 differs from that of the other groups most notably in its truncated mesiolingual lobe, which gives the tooth an asymmetrical shape and a relatively narrower lingual portion of the crown. The mean tooth shapes of the other hominins are more symmetrical, both along the mesiodistal and buccolingual axes. In fact, those of Upper Paleolithic and contemporary hu-
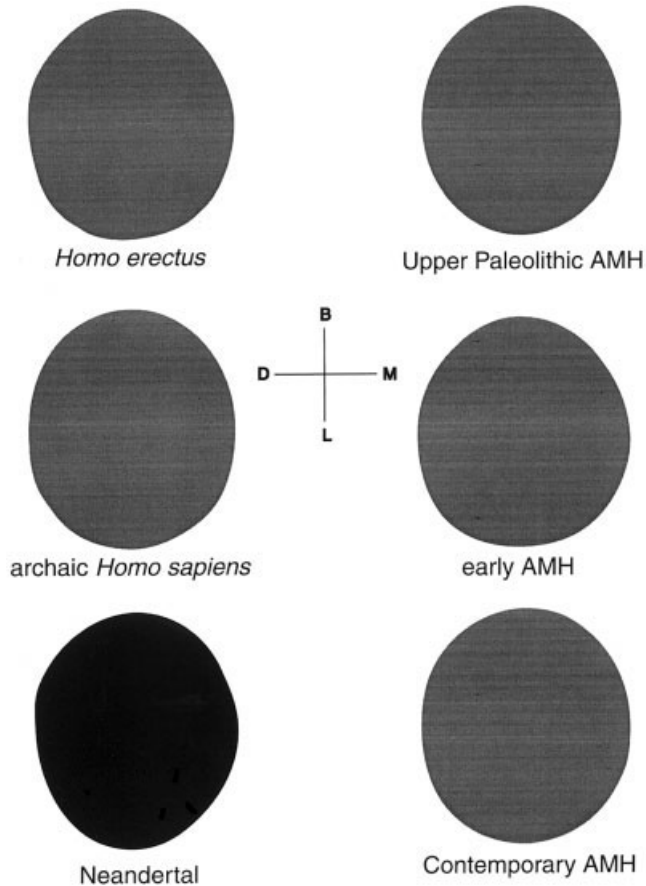
Fig. 3. Mean P_4 shapes derived from elliptic Fourier analysis. Excepting the Neandertal tooth, all mean shapes are symmetrical along buccolingual and mesiodistal axes, and possess a lingual crown that is as wide or wider than the buccal cusp. For orientation: B, buccal; L, lingual; M, mesial; D, distal.
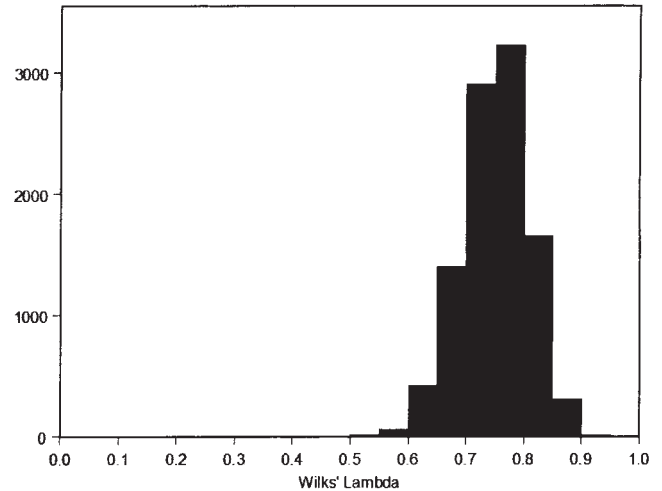

Fig. 4. Histogram of Wilks' lambda values (0 is equal to complete dissimilarity, 1 is equal to equality). Neandertal-anatomically modern human score is 0.55384, which is not exceeded more than 110 times out of 10,000 random trials ($P = 0.00110$).

mans are nearly perfect ovals. In contrast to the relatively narrow lingual crown of Neandertals, the P_4s of early anatomically modern humans exhibit a lingual crown that is wide relative to its buccal cusp, while those of other hominins are subequal in size. The mean shape obtained for the small (n = 3) archaic *Homo sapiens* sample is more similar to that of the anatomically modern humans than it is like that of the Neandertals, with a symmetrical crown and subequal buccal and lingual moieties.

Small sample sizes precluded the statistical analysis of all but the Neandertal and anatomically modern human (pooled) samples. The results of MANOVA confirm that the difference between these two groups is not particularly large. Our lambda value of 0.55384 is in the middle of possible values (0 to 1; values close to 0 indicate inequality of group means, and values close to 1 indicate equality). However, this value was found to be significantly smaller than those obtained from 10,000 randomizations ($P = 0.00110$) (Fig. 4). Thus, the difference in mean shape of Neandertal and anatomically modern human P_4s, though relatively slight, is statistically significant even when we take into account the disparate sample sizes.

Although we could not test this statistically, inspection of the P_4 mean shapes in Figure 3 indicates that the P_4 shape of anatomically modern humans is more similar to that of *Homo erectus* than that of Neandertals. This suggests that P_4 symmetry, rather than asymmetry, is the primitive condition, and that the high frequency and expression of asymmetry are derived characters in Neandertals.

Principal component analysis

The analysis of mean tooth shapes confirms that Neandertals and anatomically modern humans differ from one another in a statistically significant way. The remaining multivariate analyses are aimed at investigating how these shapes vary within groups and how well they discriminate between groups.

Using the Sidak method (a conservative post hoc test similar to Bonferroni, which takes into account multiple hypothesis tests), we estimated the significance of the Fourier coefficients. The results indicate that the differences in 8 of 32 coefficients are significantly different from zero. These variables were then used in a principal component analysis.

The first three factors in the principal component (PC) analysis have significant eigenvalues. Combined, they account for more than 80% of the total variation. The first two principal components account for 37.3% and 26.8%, respectively, for a total of 64% of the total variation.

Figure 5 provides a graphic representation of the individuals arranged according to the degrees of their projections onto the first two principal component axes. Clearly, there is a considerable amount of overlap in the distributions of Neandertal and anatomically modern human teeth. This is primarily due to the wide range of variation in contemporary modern humans, although the range of variation in fossil anatomically modern humans appears to be
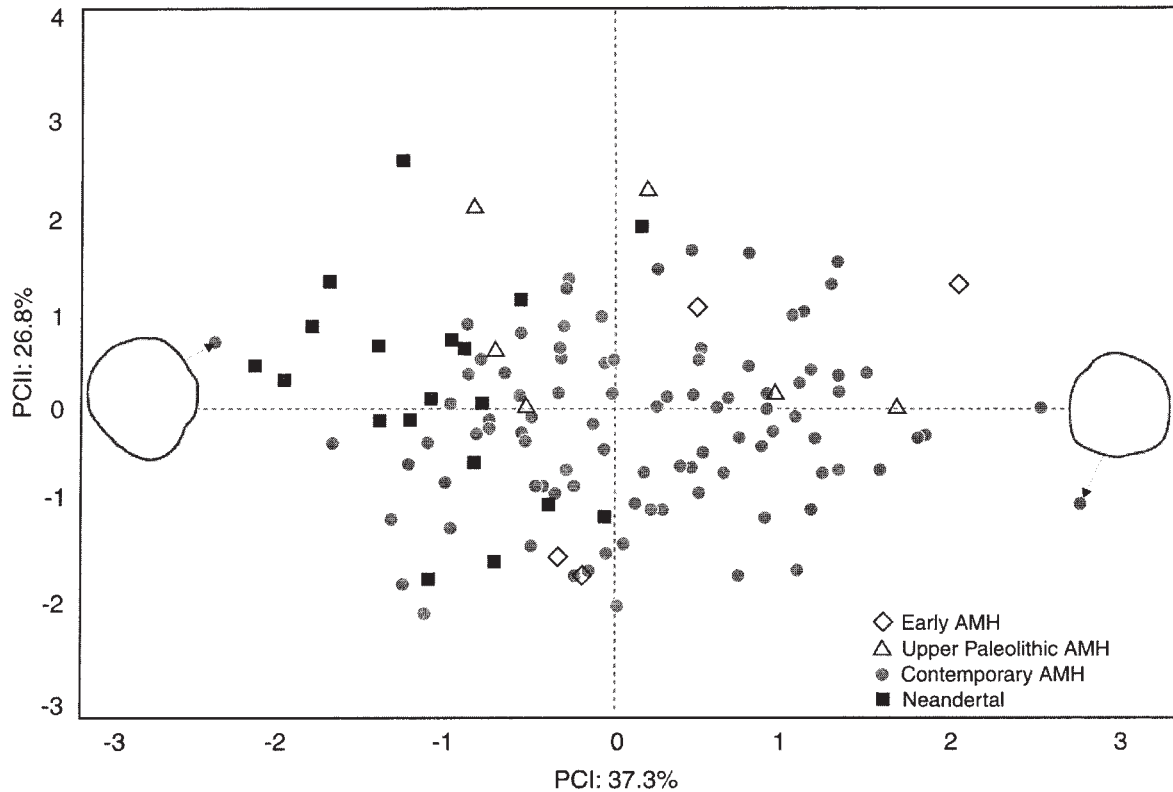
Fig. 5. Projection of individual P$_4$ crowns on PCI and PCII. Shape outlines indicate extremes along PCI. AMH, anatomically modern humans.

large as well. The contemporary modern humans are scattered randomly, occupying positions at all four extremes on the two axes. The Upper Paleolithic modern humans are concentrated on the upper half, with positive or neutral values for PCII, but they are widely spread along PCI. In contrast, Neandertals exhibit a much smaller range of variation; indeed, with only one exception, all Neandertals have negative eigenvalues for PCI and fall toward the negative pole. Like the contemporary modern humans, fossil anatomically modern humans are also quite variable in their morphology. Two of the four early anatomically modern humans have positive values for PCI, aligning them more closely with contemporary modern humans. The other two fall in an area of overlap between anatomically modern humans and Neandertals. Upper Paleolithic individuals are also highly variable. Two individuals fall on the positive side of PCI, while the other three fall on the negative side. One of these appears to be closer to Neandertals, while the other two are in the area of overlap between Neandertals and contemporary modern humans.

Examination of the Neandertal specimens with the highest negative values for PCI revealed that these teeth (Tabun, Le Moustier, and Krapina D50) possess a strongly asymmetrical crown contour. The single Neandertal P$_4$ that has a positive eigenvalue for PCI (Spy 2) is a symmetrical tooth with buccal and lingual moieties that are subequal in width.

Among the anatomically modern humans, the individual with the highest negative value for PCI (from India) is an outlier among all groups. The lingual portion of this tooth is notably narrow, but it lacks the characteristic asymmetry of Neandertal teeth. The individual with the highest positive value for PCI is a contemporary modern human from West Africa. This tooth is symmetrical, with an exceptionally wide lingual breadth. It appears that there is a continuum along PCI that reflects both tooth asymmetry and relative lingual crown width, and that separating these variables from each other may be difficult.

Principal component II is not easily interpreted, and there is little pattern to how the individuals are arrayed along this axis. Higher numbered principal components contribute little to understanding differences in P$_4$ shapes. Plots of individuals along these components show complete intermixing of the data points.

Discriminant functions analysis

All 32 elliptic Fourier coefficients were used in a two-group discriminant functions analysis to investigate the differences observed in the mean tooth shapes of Neandertals and anatomically modern humans. Figure 6 presents the distribution of the discriminant scores for the two groups. There is a clear bimodal distribution in the variation, with overlap between the two morphs. Shape outlines on the his-
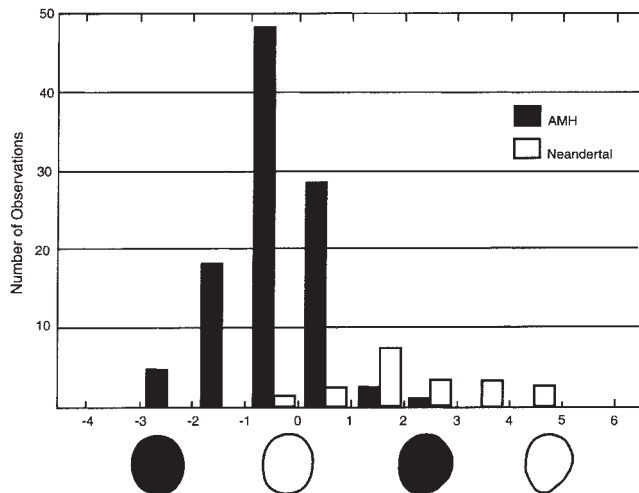
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Fig. 6. Distribution of discriminant function scores for Neandertals and anatomically modern humans (AMH). Tooth shapes associated with extremes of both distributions are plotted along the x-axis.

Fig. 7. Variation of P_4 shape within the Krapina sample, from least asymmetrical (**A:** D20) to most asymmetrical (**B:** Mandible F). Although it lacks asymmetry typical of Neandertal P_4s, tooth A possesses other traits common to Neandertals (e.g., strong transverse crest and well-developed metaconid). Likewise, the transverse crest of tooth B is less well-developed than in many Neandertals, but the tooth possesses a well-developed metaconid and markedly asymmetrical shape. Presence of at least two of these three characters (asymmetry, well-developed metaconid, and strong transverse crest) has been found in 92% of Neandertals (Bailey, 2002a).

TABLE 2. *Classification matrix based on discriminant functions analysis*

	Percent correct	Anatomically modern humans (pooled)	Neandertal
Anatomically modern humans (pooled)	98.1	105	2
Neandertal	65.0	7	13

togram depict the "most" Neandertal (Le Moustier), "least" Neandertal (Spy 2), "most" anatomically modern human (from Austria), and "least" anatomically modern human (from Jericho) teeth. Moving from left to right ("least Neandertal" to "most Neandertal"), it is easy to observe a gradual change in shape, from a very slight distal asymmetry (i.e., slight truncation of the distolingual lobe) to a strong mesial asymmetry (i.e., strong truncation of the mesiolingual lobe). The relative width of the lingual crown also becomes progressively smaller, moving from left to right, supporting the idea that the groups differ not only in degree of asymmetry, but also in relative size of the lingual crown.

The discriminant function analysis shows that occlusal outline shape alone can successfully discriminate the P_4 of Neandertals and anatomically modern humans in 86.4% of the cases. Fifteen of the 110 crown shapes were misclassified, resulting in an average a posteriori error rate of 13.6%. However, inspection of a classification matrix of the two groups (Table 2) shows that anatomically modern P_4s are much more likely to be classified correctly than are Neandertal P_4s. In the case of anatomically modern humans, only 2 of 105 crown shapes were misclassified, resulting in a 1.9% error rate. In contrast, 7 of 20 Neandertal P_4s were misclassified, resulting in a 35% error rate. There appears to be no
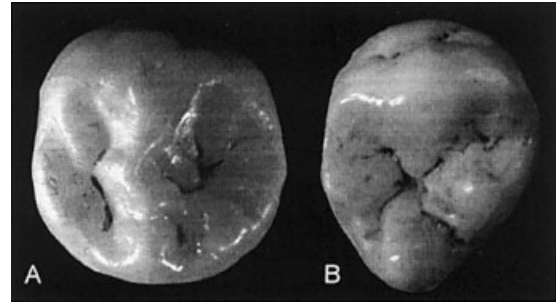
left-right bias for crown shape in this sample, as P_4s from the right side (e.g., teeth that were mirror imaged) were as likely (3/7) to be misclassified as those from the left.

Of the two anatomically modern human teeth that were misclassified, one came from an Upper Paleolithic site (Dolní Věstonice), and the other came from a contemporary human population (India). In both cases, the P_4s possess narrow, rather than asymmetrical, lingual crowns. Misclassified Neandertal teeth tended to be more symmetrical and to have wider lingual crowns than the correctly classified Neandertals. Interestingly, more than half (5) of the misclassified Neandertal P_4s came from a single site (Krapina). Clearly, this sample, which includes some of the most asymmetrical (Mandible F) and least asymmetrical (D26) teeth (Fig. 7), is variable with regard to P_4 shape.

DISCUSSION

The results of this study substantiate the perceived differences in P_4 crown shape in Neandertals and anatomically modern humans. Quantifying the data allowed the differences in these two groups to be explored in greater detail. An analysis of P_4 mean shape indicates that Neandertals and anatomically modern humans differ in two key ways: 1) their crown symmetry, and 2) the relative size of the lingual crown. While variation within each sample exists, on average, Neandertal P_4s are asymmetrical, while those of anatomically modern humans are symmetrical. The P_4 asymmetry of Neandertals appears to be the product of a mesial truncation of the lingual crown rather than a distal expansion. This mesial truncation explains why the lingual crown is, on average, somewhat narrower in Neandertal P_4s than in those of anatomically modern humans.

Results from multivariate statistics indicate that while the difference in mean P_4 shape of Neander-

tals and anatomically modern humans appears slight, it is highly significant. Therefore, while it was evident from an earlier study that marked differences exist in the frequency of asymmetrical P_4s (96% in Neandertals and up to 6% in anatomically modern humans) (Bailey, 2002a), the present study supports the idea that the mean shapes of the two groups differ significantly as well.

Results from the principal component analysis suggest that, while mean shapes between Neandertals and anatomically modern humans differ significantly, samples are highly variable in their overall P_4 shape. This is especially true of the contemporary modern human sample, and may not be surprising given that it is derived from seven different geographic populations. The Neandertal sample is also variable, but less so than that of the contemporary modern humans. This may be expected given the smaller Neandertal sample size; however, it is notable given the geographic and temporal variability of the individuals that make up the sample.

Although not explicitly tested here, it is generally accepted that much of the dental morphological variation observed in human populations is due to genetic drift rather than environmental pressures (i.e., natural selection). There are no significant differences in the P_4 crown areas of the teeth in this study (Bailey, unpublished data), and variation is therefore not linked to tooth size differences. Neither are there obvious morphological changes in the maxillary P^3 and P^4 (which occlude on P_4) that would suggest a functional complex is being selected for. While it remains to be tested, it is highly likely that, like many other dental traits (Nichol, 1989), crown shape is not inherited as a simple Mendelian trait, and that multiple genes code for its expression. Different distributions of these genes could be responsible for the variation in tooth shapes observed.

The somewhat mediocre success in classifying Neandertal teeth is surprising, considering previous findings (Bailey, 2002a). A reexamination of Neandertal teeth scored as "asymmetrical" in the previous study but misclassified in the discriminant analysis reveals that their crowns are indeed asymmetrical, albeit less so than teeth that were not misclassified. This indicates that the elliptical Fourier analysis (EFA) picked up on aspects of the tooth's shape that the discrete analysis did not. Most likely this difference is related to the fact that the EFA took into account the entirety of the tooth's outline and did not focus solely on the region of the tooth that differs most between Neandertals and anatomically modern humans.

It is evident from this analysis that while P_4 shape differs significantly in these two groups, P_4 crown asymmetry is not a "magical character" that can be used to classify hominins with complete accuracy. However, no character (dental or otherwise) should be considered in isolation, as individual characters rarely discriminate as well as several characters combined. Indeed, it is dental "complexes," and not individual characters, that tend to differentiate contemporary human groups (Mayhall et al., 1982; Townsend et al., 1990; Turner, 1992; Irish, 1994; Hawkey, 1998).

Fortunately, tooth shape is not the only morphological character that can be assessed on P_4. The utility of P_4 shape for taxonomic diagnosis increases when it is used in combination with some of these other characters. Focusing on three discrete dental characters (well-developed metaconid, transverse crest, and crown asymmetry), an earlier study demonstrated that when the frequency with which two or three traits occurred in combination is compared, there is a marked difference between Neandertals and anatomically modern humans (Bailey, 2002a). In Neandertals, 92% of the sample exhibited two or three P_4 characters in combination (36% and 56%, respectively), while in contemporary modern humans, two traits occurred in combination in 2.4% of the sample, while three traits were never observed in combination.

Based on these results, P_4 is likely to be the most diagnostic tooth of the postcanine dentition, at least in Middle-Late Pleistocene hominins. Even a worn isolated P_4 can be assigned to the Neandertal group with confidence if it shows marked asymmetry; those isolated P_4s that show less extreme morphology have an excellent chance of being assigned to the correct taxonomic group when more than one character is considered.

While it is clear that Neandertals possess a distinctive P_4 crown outline and a unique combination of crown traits, what does this mean? Are Neandertals just a population with some distinct traits, or are these dental differences greater than those that separate modern human populations? In addition to the morphologically distinctive P_4, other studies have found that Neandertals possess a dental pattern that is distinct and unlike any found in contemporary human populations (Coppa et al., 2001; Bailey, 2002b). In fact, based on measures of biological distance (e.g., mean measure of divergence), the Neandertal dental pattern was found to be 2–3 times more different from any modern human population than the most distinctive populations were from each other (Bailey, 2000, 2002b). In addition, *Homo erectus* and early and Upper Paleolithic anatomically modern humans appear to be more similar to contemporary humans than Neandertals in dental pattern (Bailey, 2000, 2002b) and P_4 shape (Bailey, 2002a,b). This suggests that beyond being distinct, the dental morphology and dental pattern are quite likely uniquely derived in their lineage.

Researchers for whom the presence of derived morphology in Neandertals is enough to warrant assigning them to their own species (e.g., Hublin, 1978; Rak, 1986; Hublin et al., 1996; Schwartz and Tattersall, 1996; Rak et al., 2002) may find the dental evidence presented here to be consistent with the hypothesis that *Homo neanderthalensis* is a valid species. For others (e.g., Trinkaus, 1986; Wolpoff,

1994, 1996; Franciscus and Trinkaus, 1995; Franciscus, 1999), the morphological differences and unique dental pattern may not be enough. Ultimately, the answer to the "species question" will most likely come from investigations of intra- and interspecific variation (Bailey, unpublished data; Harvati, 2002, 2003).

CONCLUSIONS

This study uses elliptic Fourier analysis in a quantitative assessment of the Neandertal P_4 occlusal crown contour. This method is particularly satisfying because it can be used to assess the shape of a tooth's occlusal outline, and because it provides an objective measure of shape differences. Inspection of mean shapes derived from elliptic Fourier coefficients confirms that Neandertals possess asymmetrical P_4s, and a randomization test confirms that the differences between Neandertals and anatomically modern humans are significant. Multivariate analyses suggest that the shape differences between Neandertals and anatomically modern humans go beyond asymmetry and include relative size of the lingual crown. While classification based on discriminant functions analysis was not perfect, it does appear that Neandertals can be identified based on their distinctive P_4 shape. Ultimately, this study demonstrates that the P_4 is one of the best teeth for discriminating between taxonomic groups in a Middle-Late Pleistocene context.

ACKNOWLEDGMENTS

LITERATURE CITED

Bailey SE. 2000. Dental morphological affinities among late Pleistocene and recent humans. Dent Anthropol 14:1–8.

Bailey SE. 2002a. A closer look at Neanderthal postcanine dental morphology. I. The mandibular dentition. New Anat 269:148–156.

Bailey SE. 2002b. Neandertal dental morphology: implications for modern human origins. PhD dissertation, Arizona State University, Tempe.

Bordes F, Lafille J. 1962. Découverte d'un squelette d'enfant moustérien dans le gisement de Roc de Marsal, commune de Campagne-du-Bugue (Dordogne). C R Acad Sci Paris 254:714–715.

Chen SYY, Lestrel PE, Kerr WJS, McColl JH. 2000. Describing shape changes in the human mandible using elliptical Fourier functions. Eur J Orthod 22:205–216.

Coppa A, Dicintip F, Vargiu R, Lucci M, Cucina A. 2001. Morphological dental traits to reconstruct phenetic relationships between Late Pleistocene-ancient Holocene human groups from Eurasia and North Africa [abstract]. Am J Phys Anthropol [Suppl] 32:54.

Crummett T. 1994. The evolution of shovel shaping: regional and temporal variation in human incisor morphology. Ph.D. dissertation, University of Michigan, Ann Arbor.

Crummett T. 1995. The three dimensions of shovel-shaping. In: Moggi-Cecchi J, editor. Aspects of dental biology: palaeontology, anthropology and evolution. Florence: International Institute for the Study of Man. p 305–313.

Day M. 1977. Guide to fossil man. London: Cassell.

Ferson S, Rohlf FJ, Koehn RK. 1985. Measuring shape variation of two-dimensional outlines. Syst Zool 34:59–68.

Fraipont C. 1936. Les hommes fossiles d'Engis. Arch Inst Paléontol Hum 16:1–52.

Fraipont J, Lohest M. 1887. La race humaine de Néanderthal ou de Canstadt en Belgique. Arch Biol 7:587–757.

Franciscus R. 1999. Neandertal nasal structures and upper respiratory tract "specialization." Proc Natl Acad Sci USA 96:1805–1809.

Franciscus R, Trinkaus E. 1995. Determinants of retromolar space presence in Pleistocene *Homo* mandibles. J Hum Evol 28:577–595.

Genet-Varcin E. 1966. Étude des dents permanentes provenant du gisement moustérien de la crose de Dua. Ann Paléontol (Vert) 52:89–114.

Gorjanovic-Kramberger K. 1906. Der Diluviale Mensch von Krapina in Kroatien. Wiesbaden: Kreidel.

Harvati K. 2002. Models of shape variation between and within species and the Neanderthal's taxonomic position: a 3D geometric morphometrics approach based on temporal bone morphology. BAR Int Ser 1049:25–30.

Harvati K. 2003. The Neanderthal taxonomic position: models of intra and inter-specific craniofacial variation. J Hum Evol 44: 107–132.

Hawkey D. 1998. Out of Asia: dental evidence for affinities and microevolution of early populations from India/Sri Lanka. Ph.D. dissertation, Arizona State University, Tempe.

Hillson S. 1986. Teeth. Cambridge: Cambridge University Press.

Hublin J-J. 1978. Quelques caractères apomorphes du crâne néandertalien et leur interprétation phylogénique. C R Acad Sci Paris 287:923–926.

Hublin J-J, Spoor F, Braun M, Zonneveld FW, Condemi S. 1996. A late Neanderthal associated with Upper Palaeolithic aftefacts. Nature 381:224–226.

Irish J. 1994. The African dental complex: diagnostic morphological variants of modern sub-Saharan populations [abstract]. Am J Phys Anthropol [Suppl] 18:112.

Klein R. 1999. The human career. Chicago: University of Chicago Press.

Kuhl FP, Giardina CR. 1982. Elliptic Fourier analysis of a closed contour. Comput Graph Imag Proc 18:259–278.

Lestrel PE. 1974. Some problems in the assessment of morphological shape differences. Yrbk Phys Anthropol 18:140–162.

Lestrel PE, editor. 1997. Fourier descriptors and their applications in biology. New York: Cambridge University Press.

Lumley H de, Lumley M-A de, Brandi R, Guerrier E, Pillard F, Pillard B. 1972. La Grotte moustérienne de Hortus. Marseille: Editions du Laboratoire de Paléontologie Humaine et de Préhistoire.

Mayhall J, Saunders S, Belier P. 1982. The dental morphology of North American whites: a reappraisal. In: Kurten B, editor. Teeth: form, function, and evolution. New York: Columbia University Press. p 245–258.

Morris DH. 1965. The anthropological utility of dental morphology. PhD dissertation. University of Arizona, Tucson.

Nichol C. 1989. Complex segregation analysis of dental morphological variants. Am J Phys Anthropol 78:37–59.

Patte E. 1959. La dentition des Néandertaliens. Ann Paléontol (Vert) 45.

Piveteau J. 1959. Les restes humains de la grotte du Régourdou (Dordogne). C R Hebd Séanc Acad Sci Paris 248:40–44.

Piveteau J, Lumley H de, Lumley M-A de. 1963. Découverte de restes néandertaliens dans la grotte de l'Hortus (Valflaunes, Herault). C R Hebd Seanc Acad Sci Paris 256:40–44.

Rak Y. 1986. The Neandertal: a new look at an old face. J Hum Evol 15:151–164.

Rak Y, Ginzburg A, Geffen E. 2002. Does *Homo neanderthalensis* play a role in modern human ancestry? The mandibular evidence. Am J Phys Anthropol 119:199–204.

Rak Y, Kimbel W, Hovers E. 1996. On Neandertal autapomorphies discernible in Neandertal infants: a response to Creed-Miles et al. J Hum Evol 30:155–158.

Rohlf FJ. 2001. TPSDig. Stony Brook, NY: Department of Ecology and Evolution, State University of New York at Stony Brook.

Schwartz J, Tattersall I. 1996. Significance of some previously unrecognized apomorphies in the nasal region of *Homo neanderthalensis*. Proc Natl Acad Sci USA 93:10852–10854.

Scott GR, Turner CG II. 1997. The anthropology of modern human teeth: dental morphology and its variation in recent human populations. Cambridge: Cambridge University Press.

Seiffert ER, Kappelman J. 2001. Morphometric variation in the hominoid orbital aperture: a case study with implications for the use of variable characters in Miocene catarrhine systematics. J Hum Evol 40:301–318.

Slice DE. 2000. Morpheus et al.: Software for morphometric research. Revision 01-31-00. New York: Department of Ecology and Evolution, State University of New York.

Stringer C, Gamble C. 1993. In search of Neanderthals: solving the puzzle of human origins. London: Thames & Hudson.

Tillier A-M. 1983. Le crâne d'enfant d'Engis 2: un exemple de distribution des caractères juvéniles, primitifs et néandertaliens. Bull Soc R Belge Anthropol Préhist 94:51–75.

Townsend G, Yamada H, Smith P. 1990. Expression of the entoconulid (sixth cusp) on mandibular molar teeth of an Australian Aboriginal population. Am J Phys Anthropol 82:267–274.

Trinkaus E. 1986) The Neandertals and modern human origins. Annu Rev Anthropol 15:193–218.

Turner CG II. 1992. Sundadont and sinodonty in Japan: the dental basis for a dual origin hypothesis for the peopling of the Japanese Islands. In: Hanihara K, editor. International Symposium on Japanese as a Member of the Asian and Pacific Populations. Kyoto: International Research Center for Japanese Studies. p 96–112.

Turner CG II, Nichol CR, Scott GR. 1991. Scoring procedures for key morphological traits of the permanent dentition: the Arizona State University dental anthropology system. In: Kelley M, Larsen C, editors. Advances in dental anthropology. New York: Wiley-Liss. p 13–31.

Wolpoff M. 1994. Time and phylogeny. Evol Anthropol 3:38–39.

Wolpoff MH. 1996. Neandertals of the Upper Paleolithic. In: Carbonell E, Vaquero M, editors. The last Neandertals, the first anatomically modern humans. Cultural change and human evolution: the crisis at 40 Ky B.P. Tarragona: Universitat Rovira i Virgili. p 51–76.

Zubov A. 1992a. The epicristid or middle trigonid crest defined. Dent Anthropol Newslett 6:9–10.

Zubov A. 1992b. Some dental traits in different evolutionary lines leading to modern man. Dent Anthropol Newslett 6:4–8.