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Identifying Metameric Variation in Extant Hominoid and Fossil Hominid Mandibular Molars

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KEY WORDS *Australopithecus africanus*; morphometrics; Euclidean distance matrix analysis; Sterkfontein; South Africa

ABSTRACT Landmark data were collected from cross sections and occlusal images of mandibular molar crowns, and Euclidean distance matrix analysis (EDMA) was used to identify metameric morphological variation between the first and second mandibular molars of living taxa: *Gorilla gorilla* (n = 30), *Pan troglodytes* (n = 34), and *Homo sapiens* (n = 26). Two patterns of metameric variation were identified, one unique to humans and the other shared by chimpanzees and gorillas.

In order to assess the utility of this type of analysis for the interpretation of the hominid fossil record, 19 mandibular molars from Sterkfontein Member 4, South Africa, were examined. The pattern of metameric variation of the Sterkfontein molars resembled that of the African great apes, and differed from the modern human pattern. These results demonstrate that data on metameric variation may provide information regarding function or developmental processes previously indiscernible from fossil material. Am J Phys Anthropol 118:86–97, 2002.
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Well over 100 years ago, Bateson (1894) named the repetition of segments *merism* and the variation that accompanies this repetition *metameric variation*. These terminologies were developed to assist in the discussion of variation within an organism, between organisms in the same species, and between species. Weiss (1990) described how slight, genetically determined physiological differences (through changes, e.g., in growth factors, inhibitors, or homeobox genes) can result in phenotypic differences between repeated regions of anatomy, or rather segments. It is these slight, genetically determined differences that result in metameric variation in the phenotype. Weiss (1990) describes this as "duplication with variation." An obvious example of metameric variation is the vertebral column, where the basic vertebral morphology is modified between the different regions. This patterned variation corresponds with differential expression of members of the Hox gene family (Condie and Capecchi, 1993; Kessel and Gruss, 1991). The dentition is another example of repeated segments in anatomy, and it is therefore not surprising to find metameric variation within tooth categories, such as molars.

The developmental genetic processes that result in teeth are not yet fully understood (for reviews of dental development see Zhao et al., 2000; Peters and Balling, 1999; Weiss et al., 1998; Stock et al., 1997; Thesleff and Sharpe, 1995). However, there is little doubt that, at least within the same tooth category, teeth are the product of merism, the repetition of segments (Bateson, 1894). Butler (1939, 1967) linked this observation to his morphogenetic field theory of dental development. Osborn (1978) later proposed the clone theory for dental development. Though these two developmental models differ in the location of the control mechanism, they both acknowledge that teeth demonstrate serial differences. Thomas and Sharpe (1998) proposed that the pattern of mouse dentition is determined by overlapping domains of homeobox gene expression, i.e., a "code" of gene expression that gives rise to specific traits, similar to that seen in the vertebral column and the Hox gene family "code." Other researchers argued against this *odontogenic code* model for dental patterning (Kulesa and Murray, 1995; Kulesa et al., 1996; Weiss et al., 1998), and proposed that dental patterning is caused by a *reaction diffusion* process instead, as described by Turing (1952).

In this paper, I do not focus on the developmental mechanism that results in these serial differences, but rather, show how the mechanism (whatever it may ultimately prove to be) expresses itself in mandibular molar shape (in contrast to the extensive investigation of size differences, e.g., Garn et al.,

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1968a,b, 1969). Bateson (1894) described meristic or metameric variation as being evidence of intrinsic biology distinct from phylogenetic variation. The focus of this paper is the identification of this type of variation in hominid molars, and the benefits to paleontology that result from this recognition.

The recognition that there is more than one type of variation allows us to ask the appropriate questions of what developmental mechanisms underlie this variation. The identification of metameric variation by no means implies that the developmental mechanism behind it is understood. Bateson (1894) himself said that the study of variation is "an empirical means of getting at the outward and visible phenomena which constitute Evolution." The identification of this type of variation in hominoid molars enables us to pose questions about genetic and developmental mechanisms, and allows us to proceed with morphological studies, knowing that we are not mistaking meristic variation for more phylogenetically relevant variation.

BACKGROUND

Previous investigations of cross-sectional molar morphology have been largely qualitative. Variation in cross-sectional molar morphology has been noted frequently in the hominid paleontological literature, and has been provisionally used as a character with which to sort taxa. Robinson (1956) commented on the "flatter" buccal surface of the gracile South African mandibular molars compared to *A. robustus*. Wood et al. (1983) reported that the East African *Homo* molars have more vertical sides than do the South African robusts. Leakey et al. (1995) included in their diagnosis of *Australopithecus anamensis* a differentiation from *A. afarensis* teeth, in that the *A. anamensis* lower molars have more sloping buccal sides and the upper molars have more sloping lingual sides. Though qualitative assessments of cross-sectional shape continue to be noted (e.g., Ward et al., 1999), as yet there has been no attempt to quantify it.

Though the study of variation specifically related to metamerism is new, the analysis of two-dimensional occlusal molar morphology is not. Wood and Abbott (1983) analyzed morphological features of Plio-Pleistocene mandibular molars (excluding the Omo collection); they included occlusal cusp area relationships and nonparametric scoring. Hartman (1989) also investigated occlusal molar morphology, finding that phenetic differences between the hominoids do not reflect known phylogenetic relationships. Suwa (1996) and Suwa et al. (1996) investigated isolated teeth from the 2–3-myr Shungura Formation, Omo, Ethiopia collection. These two studies used sets of discriminant functions (based on cusp area, linear variables of cusps, and linear or angular variables of fissure pattern all taken in occlusal view) from confidently categorized specimens to sort mandibular molars of undecided taxonomic affinity into known taxa.

In this paper, occlusal and cross-sectional shape differences among samples of relatively unworn mandibular molars were quantified using Euclidean distance matrix analysis (as developed by Lele, 1991, 1993; Lele and Cole, 1996; Lele and Richtsmeier, 1990, 1991, 1992, 1995; Richstmeier and Lele, 1993). There have been various applications of this analytical method to evolutionary questions (Richtsmeier and Walker, 1993; O'Leary, 1996; Hlusko, 1999; Lague and Jungers, 1999). The most pertinent to this paper is the analysis carried out on occlusal molar morphology of an isolated 6-mya mandibular molar from the Baringo area of Kenya (KNM-LU 335, the "Lukeino molar;" Ungar et al., 1994). This molar crown shows close taxonomic affinities to a tooth now included as part of the *Australopithecus anamensis* hypodigm (Leakey et al., 1995). The authors used EDMA to compare distances between 11 three-dimensional (3-D) occlusal landmarks on KNM-LU 335 with the same landmarks on *Pan troglodytes* and *Homo sapiens* mandibular molars. Their results found no statistical difference between the cusp tip pattern of KNM-LU 335 with that of *P. troglodytes*. They reported some shorter intercusp fissures on the occlusal surface of KNM-LU 335 compared with *H. sapiens* and *P. troglodytes*. Though the Lukeino tooth crown is incompletely formed, they noted a dramatic buccal flaring which far exceeds that of either *P. troglodytes* or *H. sapiens*, and is more pronounced than is seen in more recent *Australopithecus* specimens. Ungar et al. (1994) demonstrated that a quantification of such morphology would be informative, especially in cases where other morphological and metric analyses are ambiguous.

All of the research described above focused on interspecific variation. Advances in developmental biology have led paleontologists to rethink our approaches to fossil studies, as fossils hold the key to the time dimension of evolutionary developmental biology research (e.g., Jernvall, 1995; Lovejoy et al., 1999; McCollum, 1999; Polly, 1998; Raff, 1996; Shubin et al., 1997). The application of EDMA to cross-sectional and occlusal molar morphology facilitates the search for developmental information within hominid molar morphology. This can be done by looking for patterns of metameric variation.

PURPOSE OF THIS STUDY

This paper tests three hypotheses.

Hypothesis 1

If cross-sectional and occlusal mandibular molar morphology in an individual results from similar yet slightly different developmental processes, then these slight developmental differences will result in morphological variation between first and second molars within that individual. These differences between first and second molars within one individual will be similar in all individuals of the same species,

given that members of the same species have the same basic developmental mechanism. Therefore, metameric variation should exist between the first and second molars of individuals of the same species.

Hypothesis 2

If hypothesis 1 is supported, similarities and differences between species' metameric patterns should reflect known phylogenetic relationships. Given that human dental morphology is derived compared to the African great apes, the metameric patterns of the African great apes are expected to be most similar to each other, and the human metmeric pattern should be distinctive.

Hypothesis 3

If hypotheses 1 and 2 are supported, the metameric pattern of fossil hominids should provide information about the timing of the origin of any distinctive human-like pattern. One of the underlying mechanisms of metameric variation may correlate with the development of thick enamel. Therefore, the thick-enameled Sterkfontein fossil hominid sample should demonstrate the same metameric pattern as seen in their descendants, humans (assuming that *Australopithecus africanus* is in the same clade as modern humans, a point that will not be discussed further in this paper).

The following materials and methods were used to test these three hypotheses.

MATERIALS AND METHODS

Samples consist of unworn or hardly worn lower first and second molars from modern humans (n = 26, equal numbers of males and females, Smithsonian National Museum of Natural History Terry Collection), and *Pan troglodytes* (n = 34, 12 male, 15 female, 7 juvenile) and *Gorilla gorilla* (n = 30, 18 male, 10 female, 2 juvenile) from the Smithsonian National Museum of Natural History and the Cleveland Museum of Natural History collections. Since EDMA removes the analysis of size from the analysis of shape (described below), we do not need to be concerned with size differences resulting from sexual dimorphism, but only shape differences between males and females. Therefore, the samples comprise approximately half males and half females.

Nineteen mandibular molars from Sterkfontein Member 4 were used in this analysis. Ten of the Sterkfontein molars are antimeres (there are five pairs). Analyses with and without the antimeres were virtually identical, though only the results from those not including antimeres are presented, so as not to artificially inflate sample sizes and, consequently, significance values. Table 1 lists the specimen numbers for the fossil teeth used in these analyses and the tooth row position designated for each one. Note that three of the specimens have new catalogue numbers, reflecting their recently recognized antimeric relationships (Moggi-Cecchi, personal communication). The sexual composition of the fossil sample is unknown.

TABLE 1. Specimen numbers of Sterkfontein fossils used in the analyses[1]

First molars	Second molars
Stw 106b	Stw 120b
Stw 123	Stw 133
Stw 123b (Stw 130)	*Stw 412a*
Stw 145	*Stw 412b (Stw 419)*
Stw 151	Stw 487a
Stw 151b (Stw 158)	*Stw 560d*
Stw 246	*Stw 560e*
Stw 309a	Sts 9
Stw 421a	
Stw 421b	
Sts 24	
N = 11 (8)	N = 8 (6)

[1] Antimeres are italicized.

Within the Sterkfontein Formation, 6 members are recognized (Partridge, 1978), of which both Members 4 and 5 yield significant numbers of hominid remains. The teeth used in this study all derive from Member 4. Faunal dating of Member 4 has given an age estimate of between 2.8–2.3 mya (Vrba, 1982, 1985; Delson, 1984, 1988).

Over 680 hominid specimens have been recovered from the Member 4 deposit, and the vast majority have been allocated to the species *Australopithecus africanus*. However, several recent studies suggest that some specimens may represent another taxon (Clarke, 1988, 1994; Kimbel and Rak, 1993; Calgano et al., 1997; Lockwood, 1997; Lockwood and Moggi-Cecchi, 1998). Others (Kimbel and White, 1988; Suwa, 1990; Wood, 1991; Calgano et al., 1999) found no evidence to reject the hypothesis that the Sterkfontein Member 4 hominid sample is taxonomically homogeneous. In this analysis, all of the molars are considered to be members of one species, *A. africanus*.

Collection of 2-D cross-sectional and occlusal landmarks

Molds were made of the mesial aspect of these molars with Coltène President© putty. Using a scalpel and microscope, the molds were coronally sliced directly through the tips of the protoconid and metaconid, though this plane was not always directly perpendicular to the mesial-distal axis of the tooth. The outlines of the tooth crowns were then captured by Optimas© software (Media Cybernetics, 1999), using a digital camera (Fig. 1). Cross sections were imaged so that the buccal surface was always to the right. X and Y coordinates were recorded for seven cross-species landmarks (as established by Lele and Richtsmeier, 1991, 1992), with the origin consistently placed at the lingual cervix and the X-axis running horizontally through the buccal cervix. All images were calibrated and points taken to the tenth of a millimeter. Coordinates were recorded three times for each specimen and averaged.

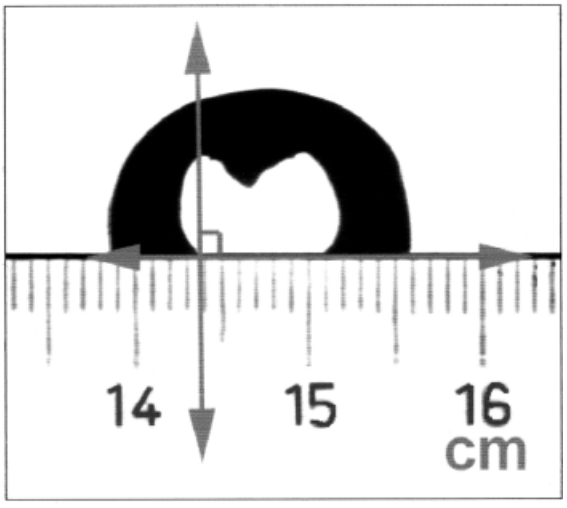

Fig. 1. Digitizing protocol. Coronal outline of tooth taken through the mesial cusps is captured digitally using Optimas© software. Lingual side is at left. Origin is placed at lingual cervical margin.

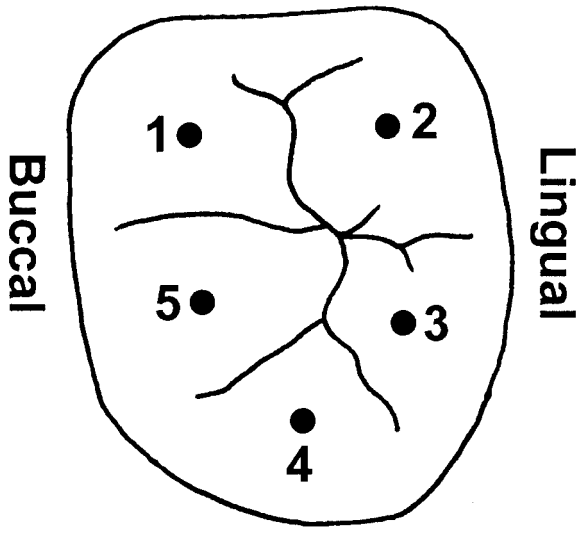

Fig. 3. 2-D occlusal landmarks. 1, protoconid cusp tip; 2, metaconid cusp tip; 3, entoconid cusp tip; 4, hypoconulid cusp tip; 5, hypoconid cusp tip.

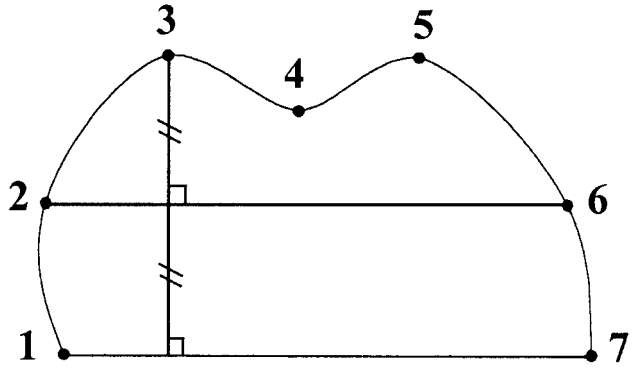

Fig. 2. Cross-sectional landmarks. 1, lingual cervix; 2, lingual midpoint defined as point on crown that marks half the distance between cervical line and tip of the metaconid; 3, metaconid cusp tip; 4, deepest point of central groove; 5, protoconid cusp tip; 6, buccal midpoint, defined as shown here; 7, buccal cervix.

The seven landmarks measured were the lingual cervix, midpoint of the lingual side, tip of the metaconid, central groove, tip of the protoconid, midpoint of the buccal side, and buccal cervix (Fig. 2). The midpoints on each side are not proper biological landmarks, but were recorded to capture some of the shape between the other landmarks. All seven landmarks were chosen because they are easily repeated and adequately summarize the shape of the cross section.

The entire procedure was repeated for 10 teeth to test reliability. The differences between the two sets of X, Y coordinates averaged less than 0.4 mm; using a standard *t*-test, the difference from zero is not significant.

The same teeth were used for the occlusal analyses. Occlusal views of the casts were captured digitally using the same camera and Optimas© software, as for the cross-sectional study. The teeth were calibrated, and X, Y coordinates to the tenth of a millimeter were recorded three times for each of the landmarks and averaged. Five landmarks were considered for all of the first molars and for gorilla, chimpanzee, and Sterkfontein second molars (Fig. 3). The protoconid (landmark 1) was used as origin, with the X axis running through the metaconid. Only four landmarks were included in the second molar comparisons of humans, as modern-human second mandibular molars typically do not have hypoconulids. Reproducibility was calculated for 11 molars, and measurement error found to be less than 0.1mm. A standard *t*-test shows that this measurement error is not significantly different from zero.

Euclidean distance matrix analysis

All landmark data, cross-sectional and occlusal, were analyzed using the program SHAPE version 1.0, written by Tim Cole (see Lele and Cole, 1996), a Euclidean distance matrix analysis (EDMA). With EDMA, coordinate data are used to derive matrices of distances between all possible pairs of landmarks for each specimen, and then for each sample. The matrices of distances are then subjected to analysis. EDMA-II was chosen for the following analyses because it provides a coordinate-free approach for comparing landmark data. The reader is referred to Cole and Richtsmeier (1998) for a discussion of the advantages of EDMA over other coordinate system-invariant methods. The advantage of being coordinate-free is that implicit or explicit coordinate systems are not imposed on the form, and the form is not affected by nuisance parameters (e.g., reflection, translation, or rotation; Lele, 1993; Cole and Richtsmeier, 1998). Rohlf (2000) criticized EDMA-II primarily for not being the uniformly most powerful test. But as Lele and Richtsmeier (2001) pointed out, neither EDMA-I nor EDMA-II was claimed to be the

TABLE 2. Significant shape difference matrix values calculated using bootrapped EDMA for the comparisons of cross-sectional interlandmark distances between first and second molars of humans, chimpanzees, gorillas, and Sterkfontein Member 4 hominids[1]

Interlandmark distance	Human M1 vs. M2	Chimpanzee M1 vs. M2	Gorilla M1 vs. M2	Stw M1 vs. M2	Stw* M1 vs. M2
1–2	0.046^	0.052^+	0.041^+	0.051	0.051
1–3	—	0.103^+	0.083^+	0.088	0.088
1–4	—	0.078	0.047	—	0.061
1–5	—	—	—	—	—
1–6	−0.091^+	—	—	—	—
1–7	−0.132^+	—	—	—	—
2–3	—	0.075^+	0.043^+	—	—
2–4	—	—	—	—	—
2–5	—	—	—	—	−0.048
2–6	—	—	—	—	—
2–7	—	—	—	—	—
3–4	—	−0.091^+	—	—	—
3–5	0.070^+	−0.124^+	−0.073^	−0.054	−0.048
3–6	—	—	—	—	—
3–7	—	—	—	—	—
4–5	—	−0.066^+	−0.041	—	−0.054
4–6	—	—	—	—	—
4–7	—	—	—	—	—
5–6	−0.059^+	—	—	—	—
5–7	—	0.075	0.052^	—	—
6–7	—	0.046	0.039^+	—	0.044

[1] First column refers to interlandmark distances defined in Figure 2. Second and third columns from left refer to intraspecific first and second molar comparisons of species noted in heading. −, nonsignificant values. Positive values indicate that first molar distance is greater than second molar distance. Negative values indicate that second molar distance is greater than first molar distance. *P*-value = 0.10 (two-tailed), as per Lele and Cole (1996), except for the Sterkfontein analysis, Stw*. See text for explanation. M1, first mandibular molar; M2, second mandibular molar.
^ All pairwise distances significant at 0.05.
+ All pairwise distance significant at 0.01.

uniformly most powerful test. This does not invalidate the EDMA approach to shape analysis, since no multivariate statistical procedure is the most powerful in every circumstance. More importantly, EDMA is the *only* test that allows for two populations to be compared when they have different covariance matrices (Lele and Richtsmeier, 2001). Given the properties of EDMA (coordinate-free test of landmark data, and the need to not assume equal covariance matrices), this analytical technique was deemed the most appropriate for this study.

In EDMA, matrices of distances between all possible pairs of landmarks are created for each specimen and then for each sample. In these analyses, each sample is scaled using its geometric mean, thereby removing the analysis of size from the analysis of shape. The geometric mean was chosen as the scaling factor because no one edge of the shape seemed most appropriate for scaling the shape of either the cross section or the occlusal cusp arrangement. The mean shape (or form) matrix of one sample is compared to another, creating a mean shape (or form) difference matrix. Bootstrapping allows the iteration of these difference matrices numerous times, calculating the statistical significance for each distance. All analyses performed here were bootstrapped (100 times) in order to calculate significance values, i.e., the analysis was performed 100 times using different subsets of the original sample (for more on bootstrapping, see Sokal and Rohlf, 1995; Mooney and Duval, 1993; Efron and Tibshirani, 1991). An alpha value of 0.10 was used for all analyses, as recommended by Lele and Cole (1996). The reader is referred to the following references for a more in-depth description of these Euclidean distance matrix analyses (Cole and Richstmeier, 1998; Lele, 1991, 1993; Lele and Cole, 1996; Lele and Richtsmeier, 1990, 1991, 1992,

The one main drawback to EDMA is the difficulty of visualizing the results (Cole and Richtsmeier, 1998). To circumvent this, results of pairwise comparisons are reported in table format, and the main pattern of results is drawn in an accompanying figure.

RESULTS

Cross-sectional landmarks

There are significant differences in the pairwise comparison of cross-sectional interlandmark distances of first and second molars of the same species for all species analyzed (Table 2). Significance was calculated through the bootstrapping of EDMA (Lele and Cole, 1996), using their suggested two-tailed confidence interval of 90%. Table 2 shows the significant differences found when first and second molars of the same species are compared. The first column on the left notes the interlandmark distance being compared (see Fig. 2). For example, "interlandmark distance 1–3" means the distance from the lingual cervix to the tip of the metaconid. "Interlandmark distance 3–5" means the distance between the tips of the metaconid and protoconid. All reported values are significant. Cells without a numerical value in-

dicate that this pairwise interlandmark distance comparison between first and second molars was not significantly different. A positive value indicates a greater distance in the first molar compared to the second molar. A negative value indicates a greater distance in the second molar compared to the first molar.

The pattern of significant differences ($\alpha = 0.1$; two-tailed tests, with $\alpha_1 = 0.05$, and $\alpha_2 = 0.05$) between first and second molars is similar for both chimpanzee and gorilla. These can be summarized as: 1) the second molar cusp tips are farther apart than first molar cusp tips; and 2) the buccal and lingual sides of the first molar are more expanded than those of the second molar. Actual distance values are reported in Table 2, and the pattern is represented diagrammatically in Figure 4a. This pattern is labeled *metameric pattern A*.

The modern human first/second molar comparison shows a different pattern. The intercusp tip distance is greater in the first molar relative to the second molar; this is the opposite of what is seen in the great ape samples. The buccal side of the human second molar bulges more than does the first molar. This is in contrast to the pattern seen in great ape samples. However, as in chimpanzees and gorillas, the lingual midpoint of the first molar is more expanded than in the second. Actual distances are reported in Table 2 and represented diagrammatically in Figure 4b. This pattern is labeled *metameric pattern B*.

When the Sterkfontein first and second molars are compared using the same procedure as for the extant samples, the results show that the lingual aspect of first molars is more expanded than in second molars. Additionally, the mesial fovea is more open in second molars compared to first molars. See Table 2 and Figure 4c.

The Sterkfonein sample was then analyzed at a *P*-value of 0.2. The reason for using this different critical level is outlined in the Discussion. The results from this analysis show that the cusp tips are farther apart on the second molar than on the first, and the first molar buccal and lingual sides are more expanded than are those of the second molar. See Table 2, far right.

Occlusal landmarks

When intraspecific first and second molars were compared using occlusal landmarks, no significant differences were found for either the modern human or Sterkfontein samples. Because no pairwise interlandmark distance comparisons were found to be significant, Table 3 reports only the results for the chimpanzee and gorilla analyses.

The results in Table 3 are reported in the same manner as were those for the cross-sectional analyses. The reader is refered to Figure 3 for the definition of landmark numbers. The first column on the left notes the interlandmark distance being compared. For example, "interlandmark distance 1–2" means the distance from the tip of the protoconid to the tip of the metaconid. "Interlandmark distance 1–4" means the distance between the tips of the protoconid and hyponconulid. All reported values are significant. Cells without a numerical value indicate that this pairwise interlandmark distance comparison between first and second molars was not significantly different. A positive value indicates a greater distance in the first molar compared to the second molar. A negative value indicates a greater distance in the second molar compared to the first molar.

TABLE 3. Significant shape difference matrix values calculated using bootrapped EDMA for comparisons of occlusal interlandmark distances between first and second molars of chimpanzees and gorillas[1]

Interlandmark distance	Chimpanzee M1 vs. M2	Gorilla M1 vs. M2
1–2	−0.217	−0.167
1–3	—	—
1–4	0.080	—
1–5	0.072	0.143
2–3	—	—
2–4	—	—
2–5	−0.123	—
3–4	—	—
3–5	—	—
4–5	—	—

[1] First column refers to interlandmark distances defined in Figure 3. Second and third columns from left refer to intraspecific first and second molar comparisons of species noted in heading. −, nonsignificant values. Positive values indicate that first molar distance is greater than second molar distance. Negative values indicate that second molar distance is greater than first molar distance. *P*-value = 0.10 (two-tailed), as per Lele and Cole (1996). Results are not reported for the human and Sterkfontein fossil samples because no significant differences were found. M1, first mandibular molar; M2, second mandibular molar.

Two significant differences were found when gorilla first and second molars were compared: the protoconid and hypconid are relatively farther apart in first molars than in second molars, and the mesial fovea is more open in second molars (Table 3).

Four pairwise interlandmark distances were found to be significantly different between chipmanzee first and second molars (Table 3). These differences show that chimpanzees also have more open mesial foveas on their second mandibular molars, i.e., the protoconid and metaconid cusp tips are closer together on the first molar compared to the second molar. Additionally for chimpanzees, the hypoconid and hypoconulid are closer to the protoconid in the second molars. This reveals that in chimpanzees, the distobuccal aspect of the tooth is more compressed and the hypoconid is oriented more buccally on the second molar than on the first. This may also be the case in humans, where the second molar usually lacks the hypoconulid. When only four landmarks were analyzed for chimpanzees, the distance between the protoconid and hypoconid was found to be relatively shorter in second molars, bolstering the findings from the five-landmark analysis. See Table 3.

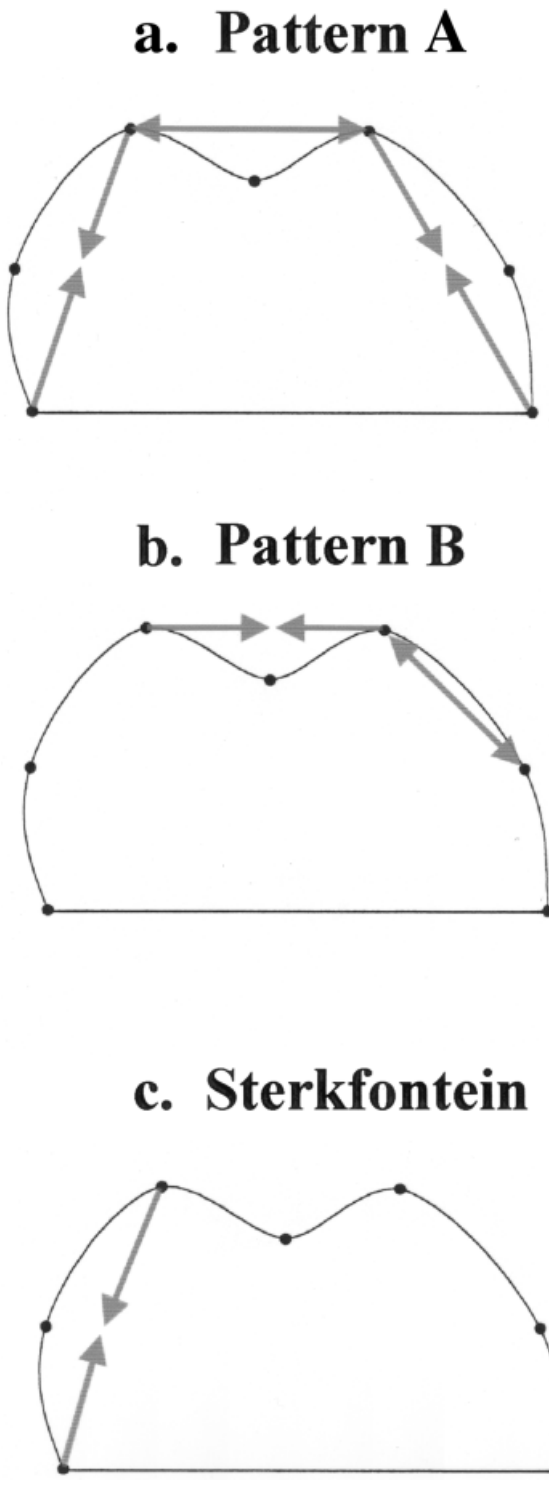

Fig. 4. Cross-sectional metameric patterns. See text for explanation. Lingual is at left.

The overall trend for both great apes shows that in second molars, the mesial fovea is more open and the buccal cusps are more compressed. This translates into the lingual side of the tooth being more expanded on the first molar. See Figure 5 for a diagrammatic representation of these results.

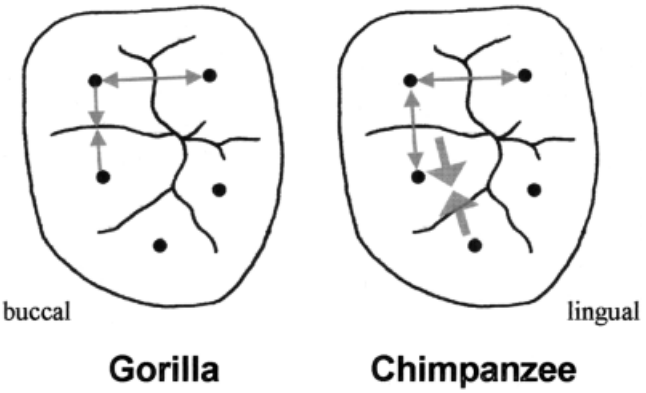

Fig. 5. Occlusal metameric patterns. See text for explanation. Lingual is at right.

DISCUSSION

The results presented here demonstrate that there are significant cross-sectional shape differences between the first and second molars in the samples of chimpanzees, gorillas, modern humans, and Sterkfontein hominids studied here. Significant differences were also found between the occlusal morphologies of the first and second molars of the chimpanzee and gorilla samples. These significant differences are interpreted as metameric variation. Therefore, these results support hypothesis 1, i.e., that there is metameric variation within the two-dimensional cross-sectional morphology of first vs. second mandibular molars. The evidence for metameric variation in two-dimensional occlusal morphology using the landmarks in Figure 3 is less convincing.

The lack of evidence for occlusal metameric variation for modern humans and the fossil hominids may be an effect of small sample sizes. However, several other factors may influence these results. For the Sterkfontein sample, the first and second molars may both be highly variable, therefore overlapping in morphological differences between the two. Or, the Sterkfontein first and second molars may not vary greatly in the relative positions of cusp tips. For the human samples, the distal aspect of the molar crown may be more variable (e.g., Macho and Moggi-Cecchi, 1992; Brown and Townsend, 1984; Sekikawa et al., 1988). Therefore, by not analyzing the hypoconulid landmarks, I may have selectively removed the most highly variable region, and consequently artificially homogenized the first and second molar morphologies of humans. Different types of analyses will be required to find the answer.

With respect to hypothesis 2, these data suggest that metameric variation may be shared among some species. The results from this study support the interpretation that there are patterns of cross-sectional metameric variation in the samples of extant taxa studied. The significant differences in cross-sectional shape (metameric pattern A) are virtually the same for gorillas and chimpanzees.

Metameric pattern A is different from the pattern identified for first and second molars in modern humans, called metameric pattern B. The reader is referred to Figure 4a,b for a representation of these two patterns. In summary, metameric pattern A is characterized by the lingual cusp of the first molar being more expanded than in second molars, and second molars having more open mesial foveae. This pattern is distinct from metameric pattern B, in which the first molar mesial foveae are more expanded, i.e., the opposite of metameric pattern A.

Assuming the hypothesis that there are two metameric patterns, and that for reasons of parsimony metameric pattern B is derived compared to metameric pattern A, the next step is to determine when during human evolution this pattern emerged. Do early hominids demonstrate metameric pattern A or metameric pattern B? A logical hypothesis is that the shift in enamel thickness seen in human evolution would correspond with other dental developmental changes that might result in a different metameric pattern. Therefore, thick-enameled hominids would have the same metameric pattern as do their thick-enameled descendants. The Sterkfontein hominid sample was used to test hypothesis 3. Is the metameric pattern of the fossil hominids representative of metameric pattern A or metameric pattern B, or is it unique?

There are at least two interpretations of the fossil data. First, the Sterkfontein metameric pattern could be interpreted as a third pattern distinct from metameric pattern A or metameric pattern B. If there are indeed three patterns, then metameric patterns, and the developmental processes that underlie them, are highly plastic or labile. As such, they may not be informative to phylogeny, even in very closely related taxa.

However, there is no strong evidence for this interpretation. There are only three significant differences between first and second Sterkfontein molars (with a two-tailed confidence interval of 90%; see Table 2). All three of these are included in metameric pattern A. It would not be prudent to conclude that an entirely different metameric pattern is present, given that it is comprised of a subset of the differences included in metameric pattern A. The more conservative conclusion is that these data suggest that the Sterkfontein sample is consistent with metameric pattern A (Fig. 4c).

This more cautious interpretation is given further support if we are more liberal with the statistical techniques employed. Lele and Cole (1996) recommended a *P*-value of 0.10, which was used in all of the analyses reported above. However, when this constraint on the confidence interval for bootstrapping is relaxed to 0.20, the analysis of the Sterkfontein sample reveals many more significant differences. These differences, as reported in the far right of Table 2, further demonstrate similarities with metameric pattern A.

The most prudent interpretation of the data presented here is that there are two patterns of cross-sectional metameric variation, one that characterizes modern humans (metameric pattern B), and one that characterizes the African great apes and the fossil hominids from Sterkfontein (metameric pattern A).

As discussed previously, metameric variation results from slight alterations in the developmental process, creating what Weiss (1990) described as "duplication with variation." Though the presence of metameric variation is not particularly surprising, patterns of metamerism are of interest, especially to the paleontologist. Why is metameric variation the same for some hominid taxa and different for others?

The first possibility is that the change in cross-sectional metameric pattern is caused by the change in the developmental mechanism that produced thick enamel in the hominid lineage. However, enamel thickness does not appear to correlate with the metameric pattern. As demonstrated in Table 2, the Sterkfontein Member 4 sample has a metameric pattern almost identical to that of the African great apes, and is distinctly different from the human pattern. Therefore, thick enamel does not correlate with the human pattern, as *A. africanus* molars have thick enamel but also display the metameric pattern of gorillas and chimpanzees. Data on enamel thickness are provided to further support this point. Figure 6 shows data taken from Shellis et al. (1998). This paper was an investigation of the enamel thickness of extant prosimians and anthropoids. Figure 6 shows a log/log regression of average enamel thickness on the square root of dentine area for anthropoids, using the least squares regression method. Chimpanzee enamel thickness is as predicted, given the anthropoid regression. Orangutan enamel is thin, and gorilla enamel is very thin. Humans have thick enamel.

Data on the enamel thickness of South African *Australopithecus* specimens from Grine and Martin (1988) are plotted on the graph as well. These two fossils (Stw 284 and Stw 402) also have thick enamel. The fossil and modern human residual values are 1.035, 1.506, and 1.146, respectively. This demonstrates that both early hominids and humans had thick enamel. Note that the thick-enamel hominids share the same pattern with chimpanzees that have a residual value of 0.089, and with gorillas whose residual value is −2.433. Therefore, cross-sectional shape pattern is not correlated with a species' enamel thickness.

Because the metameric pattern within the Sterkfontein sample is quite similar to that of the extant African great apes, these early hominids must have shared either the developmental process that causes this metameric pattern in modern chimpanzees and gorillas, or the functional constraints that select for such a pattern. The latter may be more likely, given

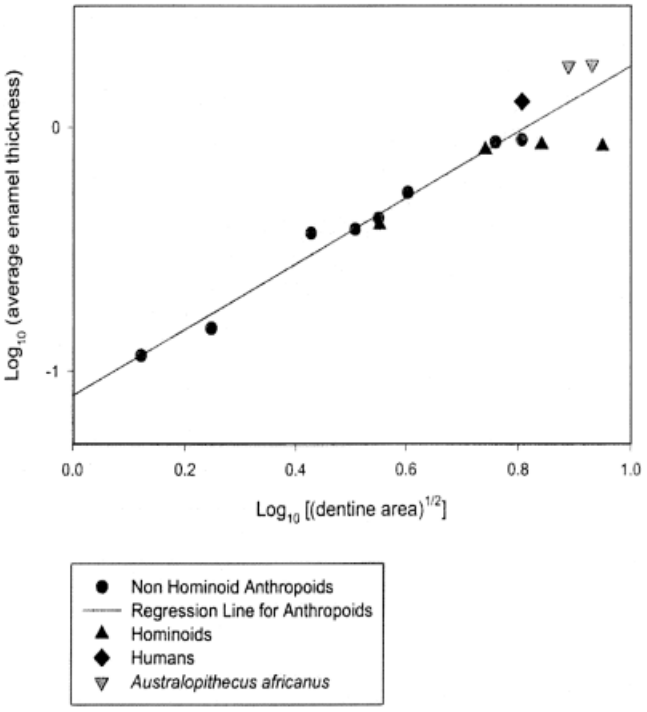

Fig. 6. Data on anthropoid enamel thickness relative to dentine area. Gorillas are the farthest outlier, with thin enamel for hominoids. Humans and *A. africanus* fall about an equal distance above the anthropoid regression line. Data for extant primates are from Shellis et al. (1998); *A. africanus* data are from Grine and Martin (1988).

the complexity of differences between gorilla and chimpanzee dental development.

Recent work by Spears and Macho (1998) and Macho and Spears (1999) suggested the possibility of interpreting functional differences from cross-sectional morphological differences. Macho and Spears (1999) noted that the buccal cusps of hominoid mandibular molars are better at dissipating loads than are lingual cusps, and that bite forces increase from anterior to posterior. However, given the different arrangements of orofacial anatomy in humans and chimpanzees, there are likely to be differences in the functional morphology of molars. Therefore, humans would have a unique pattern of morphological adaptation, given our unique orofacial arrangement. Perhaps the metameric differences between the first and second mandibular cross-sectional morphology found in this analysis are indicative of functional responses to the size of food particles, direction or magnitude of bite force, or possibly all three. Given that the general orofacial arrangement of *A. africanus* more closely resembles that of chimpanzees and gorillas and that they share a common ancestor, it would be expected that the adapted functional response of the molars may also be similar. Humans, therefore, may have a derived metameric pattern from these other hominids/hominoids as a functional response to the rearrangement of the orofacial anatomy caused by an enlarged brain and/or different masticatory mechanisms.

Selection, of course, acts on the phenotype and not necessarily on the process that forms that phenotype. Therefore, if the functional demands on molar crown morphology are rather specific, as Spears and Macho (1999) suggested, then we can understand possible variation of the developmental process so long as the ultimate morphology remains the same. Such variation is noted when chimpanzee and gorilla tooth development patterns are considered individually.

In general, the initiation of great ape molar crown calcification is sequential. For chimpanzees, the first molar crown starts to mineralize prior to birth, the second molar crown begins at about 1.95 years of age, and the third molar crown starts mineralization around 3.75 years of age (Reid et al., 1998a). This is similar to the gorilla pattern, though the initiation times are later (Beynon et al., 1991). Also, each crown takes longer to form than the previous one, such that second molars take longer to form than the first, and third molars take longer than the second. This pattern is distinct from that in humans. Human molar crown formation times are debatably more similar in duration time (Ried et al., 1998b; but see Dean et al., 1993) and follow each other sequentially. This sequence, however, is more spread out, possibly due to the prolonged duration of childhood (but see Fanning and Moorrees, 1969). This demonstrates an overall pattern that is shared between apes and that differs from humans.

However, the two African apes are not identical. For example, gorillas have distinctively thin enamel, based on the findings in Figure 3. Though gorilla and chimpanzee molars erupt at the same time and take approximately the same amount of time to form, they do so quite a bit differently. First, gorilla molars are much larger than chimpanzee molars. However, gorilla molar crowns do not take longer to form. Also, chimpanzee molar crown formation times overlap, and those of gorillas do not. Therefore, chimpanzee molars reach crown initiation earlier than do gorilla molars, take about the same time to form (if not a little longer), and form smaller crowns (gorilla crown initiation ages and duration times can be found in Beynon et al., 1991, and chimpanzee information in Reid et al., 1998a; also see Macho and Wood, 1995, their Table 1). The growth and development picture is not a simple one. Chimpanzees and gorillas share a similar metameric morphological pattern that can be argued through parsimony to be the primitive condition for the ape/human clade. However, we currently do not know if it is evidence of a shared functional constraint or a shared developmental process. Understanding the underlying causes of these shared metameric patterns will be a critical step in exploiting the information that metamerism can provide about evolutionary history.

There are many possible reasons for the selection of different metameric patterns. Unfortunately, at this point we can only speculate about some causal

factors and rule out others, such as enamel thickness. Further studies of the genetic bases for morphological variation will probably provide answers in the relatively near future.

CONCLUSIONS

The analyses reported here demonstrate that metameric variation does exist in mandibular molars. The metameric variation between first and second molars of the same species is virtually identical in chimpanzees and gorillas. The human pattern is distinct. The fossil hominids from the Sterkfontein sample demonstrate a metameric pattern more similar to the African great apes than to humans, suggesting that whatever mechanism underlies the distinctive modern human pattern had not evolved yet in the hominids from Sterkfontein. However, research on functional dental morphology suggests that metameric patterns in cross-sectional shape may not result from a common developmental mechanism, but rather from functional constraints from overall orofacial structure.

Two important points derive from the identification of metameric variation. First, when working with samples of combined first, second, and third molars, we need to be cautious if they are biased with a particular molar in the series, as intraindividual variation could be mistaken for taxonomic level variation.

Second, shared patterns, such as are seen between chimpanzees and gorillas, may evince homologous developmental processes. Richtsmeier and Lele (1993) noted that growth patterns are genetically inherited and can be used as a phylogenetic character. The analyses presented here show that metameric patterns that are genetically inherited could additionally be used as phylogenetic characters. Metameric pattern A, as seen in modern chimpanzees, gorillas, and *Australopithecus africanus*, could be interpreted as a symplesiomorphic trait. Metameric pattern B, found in humans, would then be autapomorphic.

Though much remains to be answered in terms of underlying mechanisms, and more formal and complete descriptions of this type of variation are needed, the identification of metameric variation in mandibular molar morphology may prove to be a useful tool for unlocking paleobiological/paleodevelopmental information from fossils, thus furthering our understanding of both phylogeny and the process of evolution

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