A Study of Cusp Base Areas in the Maxillary Permanent Molars of American Whites

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ABSTRACT The focus of this descriptive study was to explore the patterns of variation of base crown areas for the four major cusps on the maxillary first and second permanent molars in a cohort of contemporary North American whites of western European descent. A computer-assisted photogrammetric method was used to measure two-dimensional areas of the cusps. Ranking of mean cusp size was the same for M1 and M2, namely protocone > paracone > metacone > hypocone. In concert with field theory, size decreased while variability (CV) increased across this same sequence. Overall area of M1 (97 mm^2) is 13% larger than M2 (86 mm^2) in this sample. Most cusps exhibited significant sexual dimorphism, with greater differences for the distal cusps within a tooth and from M1 to M2. Intercorrelations of cusp areas were notably low (r^2 < 15%) both within and between M1 and M2, suggesting considerable independence in formative rates of each cusp and low morphological integration of these constituents of the occlusal table. Limited comparative material in the literature suggests that cusp areas may valuably extend the quantitative comparisons for genetic and biological studies beyond conventional tooth crown width and length. *Dental Anthropology* 2005;18:22-29.

Much of a molar's morphological complexity occurs on its occlusal surface, yet conventional measurements are made on the later-forming collum of the tooth. Maximum mesiodistal and buccolingual tooth crown diameters and similar dimensions (*e.g.*, Goose, 1963) primarily have been chosen based on their ease of measurement and their repeatability—not on any true biological criterion. Researchers have investigated other sorts of tooth crown variables, notably Biggerstaff (1969a,b) who devised an array of distances, angles, and areas that can be measured on the occlusal table of teeth in the buccal segments. As with some previous researchers (*e.g.*, Biggerstaff, 1975; Corruccini, 1979; Townsend, 1985; Townsend *et al*., 2003; Bailey, 2004), we were motivated to explore the patterns of variation of the occlusal tables of maxillary molars, largely to investigate whether additional information can be gained compared to the conventional lengths and widths of crowns.

Maxillary molars were chosen because their occlusal morphology is a bit simpler than in the mandible and because there is considerable research by embryologists on how the number and arrangement of enamel knots determines a tooth's occlusal morphology. Considerable importance now is attributed to primary and secondary enamel knots that direct the folding of the inner enamel epithelium (IEE) that determines a tooth's crown morphology (Jernvall *et al*., 1994; Thesleff *et al*., 2001). Enamel knots are transitory condensations of the IEE that cause growth of that site to cease (thereby creating a presumptive cusp tip) while at the same time promoting cell proliferation of adjacent regions that causes the IEE to fold (Jernvall *et al*., 1994, 1998, 2000; Luuko *et al*., 2003). Regional differences in proliferative rates account for the angularity of cusps, at least at the enamal-dentin interface.

Purpose of the present study, which is predominantly descriptive and exploratory, was to characterize the basal cusp areas of the main cusps on the maxillary first and second molars in a sample of North American whites. Basal cusp area is a term coined by Biggerstaff (1969b) to refer to the two-dimensional area defined by a cusp in occlusal view, demarcated by the major developmental grooves (*e.g.*, Zeisz and Nuckolls, 1949) and ranging to the periphery of the occlusal table. In fact, Biggerstaff actually used polygons defined by several anatomic landmarks as proxies for the anatomic configuration of a cusp area because of the technical difficulties involved in computing the area of a free-form object. Wood and colleagues (Wood and Abbott, 1983; Wood *et al*., 1983) used a planimeter to measure basal cusp areas. More recently, Macho and Moggi-Cecchi (1992), Bailey (2004) and others used computer systems that obviate the tedium of semi-mechanical approaches.

MATERIALS AND METHODS

Data were collected from full-mouth dental casts of adult North American whites. Individuals were phenotypically normal. There were 112 females and 88 males

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in the sample (200 individuals total).

Cusp base areas were measured on the maxillary first and second permanent molars. There were very few third molars in this sample because of the common clinical practice of extracting them prophylactically. Not every tooth was usable because of dental restorations that obscured key morphological features. Restorations were, by far, the predominant reason for excluding teeth, and the comparatively high frequency of restorations on the first molars accounts for the larger usable samples for variables on M2.

A high-resolution digital photograph was taken of each molar individually (described in Harris and Dinh, n.d.). These images were stored on a computer, and data were collected using ProScan 5.0 (SAS Institute, NC). Cusp outlines were traced using the computer's mouse in a fashion analogous to using a planimeter (Wood and Abbott, 1983; Wood *et al*., 1983). The four main cusps were measured individually (Fig. 1). The fifth cusp (the metaconule[1]; Harris and Bailit, 1980) was also measured, though it occurred too infrequent to permit statistical analysis. When the hypocone was absent, it was scored as "missing," not zero. The base area of Carabelli's trait (*e.g*., Kraus, 1959; Turner and Hawkey, 1998) was included as part of the area of the protocone because we found it difficult to distinguish the occlusal component of Carabelli's trait from that of the protocone except when this cingular feature exhibited a large separate cusp. Inclusion of Carabelli's trait accounts for the protocone's large coefficient of variation, especially on M2 where the trait (and trait size) is more variable.

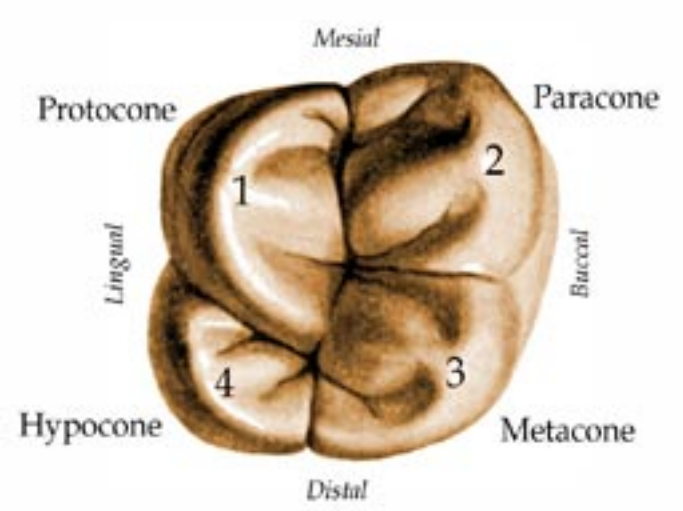

Fig. 1. Terminology used for the maxillary molars. This cusp numbering system was introduced by Gregory (1916); numbering is only used as a shorthand device since this numbering sequence is not the mineralization sequence noted by embryologists (*e.g*., Kraus and Jordan, 1965).

RESULTS

Descriptive statistics (Table 1) show that the modal cusp base areas is the same as the phylogenetic acquisition of the cusps, namely that the protocone is the largest and the sequence of reduction is protocone > paracone > metacone > hypocone, which is the same ranking of sizes described in texts on contemporary anatomy (*e.g*., Zeisz and Nuckolls, 1949; Ash, 1993).

Two rankings are of note on the first molar: (1) size of the cusp base area diminishes sequentially from the protocone through the hypocone and (2) size variability (CV) increase in this same sequence. The same patterns of variability hold for the second molar (recalling that we included Carabelli's trait as part of the protocone base area). In addition, as predicted from dental field theory (Dahlberg, 1951), cusp areas on M2 (the later forming tooth) are more variable than homologous features on M1.

Tests for sexual dimorphism (Table 1) show that males characteristically have larger cusp base areas, though not invariably so. The protocone on M1 is not dimorphic ($P = 0.71$) nor is the base area for the metacone ($P = 0.20$). The other two cusps on M1 and all four cusps on M2 exhibit statistically significant sexual dimorphism. On a percentage basis, the overall crown area of M1 is about 5% larger in males ($P < 0.01$) and this difference increases to about 10% for the later-forming M2 ($P < 0.01$).

Correlations were computed between the cusp areas (Table 2). This was done pairwise so the absence of the hypocone on about half of the second molars did not affect the other sample sizes. The weakness of the correlations seems striking; the strongest correlations are only on the order of 0.3 to 0.4 and most are appreciably lower. These low correlations are indicative of "loose" morphological integration of the cusps that compose the occlusal tables (Olson and Miller, 1958). Correlations between cusps on M1, the pole tooth, achieve statistical significance because of the fairly large sample sizes, but they explain little of the variation between areas (all with $r^2 < 15\%$). There is no discernible patterning of the correlations within M1 or within M2. Correlations are even smaller for the M2 comparisons than on M1.

Comparing between M1 and M2, the correlations are no stronger between the homologous cusps than for the other pairings, and, again, the explained variation (r^2) between cusp areas on the two molars is invariably less than 15%.

[1]Mizoguchi (1988:45) correctly notes that this cusp actually is the "tuberculum accessorium posterius externum" described by Selenka (1898, cited in Korenhof, 1960) that Mizoguchi himself terms the "distobuccal accessory marginal tubercle." The true metaconule is a different feature.

TABLE 1. Descriptive statistics and tests for sexual dimorphism[1]

	Total				Male			Female					
Variable	n	$\bar{x}$	sd	CV	n	$\bar{x}$	sd	n	$\bar{x}$	sd	%SD	F Ratio	Prob > F
Maxillary First Molar													
Protocone	160	32.23	4.78	14.83	68	32.40	5.34	92	32.11	4.34	0.9	0.14	0.7109
Paracone	160	24.06	3.41	14.18	68	25.36	3.46	92	23.09	3.05	9.8	19.25	< 0.0001
Metacone	160	21.46	3.09	14.41	68	21.83	3.14	92	21.19	3.05	3.0	1.65	0.2005
Hypocone	160	19.35	3.83	19.80	68	20.26	4.28	92	18.68	3.33	8.5	6.90	0.0094
Metaconule	1	4.59	--	--	0	--	--	1	4.59	--	--	--	--
Crown Area	160	96.94	10.45	10.78	68	99.85	11.30	92	94.78	9.25	5.3	9.70	0.0024
Maxillary Second Molar													
Protocone	183	36.97	7.48	20.22	78	38.50	7.98	105	35.83	6.90	7.5	5.88	0.0163
Paracone	183	25.47	3.65	14.32	78	26.21	3.49	105	24.92	3.68	5.2	5.78	0.0172
Metacone	183	16.07	3.15	19.58	78	16.90	3.56	105	15.46	2.66	9.3	9.81	0.0020
Hypocone	102	14.58	5.29	36.28	43	16.06	5.86	59	13.50	4.59	18.9	6.09	0.0153
Metaconule	2	20.51	11.43	--	2	20.51	11.43	0	--	--	--	--	--
Crown Area	183	85.67	11.90	13.90	78	90.37	14.28	105	82.18	8.26	10.0	23.85	< 0.0001

[1]Descriptive statistics are: sample size (n), arithmetic mean ($\bar{x}$), standard deviation (sd) and coefficient of variation (CV). "%SD" is percent sexual dimorphism calculated as $\left(\frac{\bar{x}_M - \bar{x}_F}{\bar{x}_F}\right)100$. The F ratios test for sexual dimorphism.

The occlusal table of M2 is about 13% smaller than that of the first molar (Table 3), but this summary statistic hides some interesting variations. The mesial pair of cusps (the protocone and paracone) actually is significantly larger on M2 than M1. In contrast, the decreases in average cusp sizes are dramatic for the metacone and hypocone; both basal areas are about one-third smaller on M2. These distal cusps are, however, smaller absolutely than their mesial counterparts, so, the M1-to-M2 difference for the whole occlusal table is a decrease of about 13%. We also included a molar-by-sex interaction term in the ANOVA tests in Table 3, but it was not significant for any variable, which confirms that the size gradients between M1 and M2 are equivalent (proportionate) in males and females.

DISCUSSION

There are several contributors to a cusp's basal area, though little is known about their specific control mechanisms. The number and presumptive spatial relationships of cusps are defined by primary and secondary enamel knots (Thesleff and Jernvall, 1997; Jernvall and Thesleff, 2000; Sharpe, 2001; Thesleff *et al.*, 2001). The histological occurrence of enamel knots has been known for over a century (reviewed in Butler, 1956), but their function was recognized only recently. Enamel knots are sites in the stellate reticulum adjacent to the inner enamel epithelium. They are sites without mitotic activity that initiate cusp tip formation at the enamel–dentin interface.

While enamel knots define the number and fundamental arrangement of cusps, there is considerable growth of the tooth from the cap stage (when knots develop) into the bell stage when amelogenesis progresses down the slopes of the cusps and, eventually, the intercuspal regions mineralize, thereby "freezing" the distances between cusps, at least at the enamel-dentin junction. Information on the growth of the teeth (primarily intercuspal distances between the early-forming stable cusps) shows that there are considerable increases in dimensions of the occlusal table during these phases and that the rates of growth differ among cusps, among teeth, and with time (*e.g.*, Butler, 1967a,b, 1968). Butler's data (1967b) for UM1 show that the paracone-metacone distance increases from about 1 mm when the cusps are first discernible to about 4 mm when they have both mineralized. Butler comments that the intercuspal distances

TABLE 2. Pairwise correlations between cusp areas within and between the two maxillary molars[1]

Variable	Variable	n	r^2	r	P Value	tau	P Value
			Within First Molar				
M1 Protocone	M1 Paracone	160	0.042	0.205	0.0095	0.158	0.0031
M1 Protocone	M1 Metacone	160	0.078	0.278	0.0004	0.166	0.0019
M1 Protocone	M1 Hypocone	160	0.059	0.243	0.0020	0.203	0.0001
M1 Paracone	M1 Metacone	160	0.090	0.301	0.0001	0.177	0.0009
M1 Paracone	M1 Hypocone	160	0.110	0.332	< 0.0001	0.223	< 0.0001
M1 Metacone	M1 Hypocone	160	0.132	0.364	< 0.0001	0.241	< 0.0001
			Within Second Molar				
M2 Protocone	M2 Paracone	183	0.080	0.283	0.0001	0.176	0.0004
M2 Protocone	M2 Metacone	183	0.001	0.029	0.6974	0.025	0.6198
M2 Protocone	M2 Hypocone	102	0.032	0.179	0.0719	0.056	0.4050
M2 Paracone	M2 Metacone	183	0.077	0.278	0.0001	0.182	0.0003
M2 Paracone	M2 Hypocone	102	0.005	0.073	0.4669	0.080	0.2313
M2 Metacone	M2 Hypocone	102	0.029	0.171	0.0856	0.120	0.0749
			Between Molars				
M1 Protocone	M2 Protocone	141	0.050	0.224	0.0076	0.163	0.0041
M1 Protocone	M2 Paracone	141	0.091	0.302	0.0003	0.215	0.0002
M1 Protocone	M2 Metacone	141	0.035	0.187	0.0264	0.139	0.0148
M1 Protocone	M2 Hypocone	76	0.060	0.246	0.0325	0.190	0.0151
M1 Paracone	M2 Paracone	141	0.107	0.327	0.0001	0.219	0.0001
M1 Paracone	M2 Protocone	141	0.004	0.064	0.4498	0.030	0.5953
M1 Paracone	M2 Metacone	141	0.065	0.255	0.0023	0.170	0.0028
M1 Paracone	M2 Hypocone	76	0.043	0.208	0.0714	0.087	0.2679
M1 Metacone	M2 Protocone	141	0.022	0.147	0.0821	0.092	0.1063
M1 Metacone	M2 Paracone	141	0.121	0.348	< 0.0001	0.241	< 0.0001
M1 Metacone	M2 Metacone	141	0.155	0.394	< 0.0001	0.318	< 0.0001
M1 Metacone	M2 Hypocone	76	0.123	0.351	0.0019	0.205	0.0089
M1 Hypocone	M2 Protocone	141	0.002	0.045	0.5943	0.011	0.8459
M1 Hypocone	M2 Paracone	141	0.050	0.224	0.0076	0.180	0.0016
M1 Hypocone	M2 Metacone	141	0.108	0.329	0.0001	0.238	< 0.0001
M1 Hypocone	M2 Hypocone	76	0.149	0.386	0.0006	0.311	< 0.0001

[1]The Pearson product-moment correlation coefficients (r) and coefficients of determination (r^2) are listed, along with Kendall's tau, a nonparametric measure of association. Sample sizes are number of pairs of observations.

have the highest growth rates. "The cusp tips separate more rapidly than can be accounted for by enlargement of the bases on which the cusps stand" (1967b:990). In other words, the cusps migrate toward the sides of the tooth (buccally and lingually) with growth because of faster mitotic rates in the central basin. Additional increases in intercuspal distance and basal cusp area occur after bridging of the cusps because amelogenesis is eccentric, meaning that enamel deposition proceeds "in such a manner that the completed enamel apices are dispersed linguobuccally more than mesiodistally relative to their dentine analogs" (Kraus, 1952). It also is well documented that enamel deposition (amelogenesis) initiates on different cusps at different times and bridging between cusps occurs at different times (Kraus and Jordan, 1965), so the definitive size of cusps at the enamel-dentin junction reflects a collage of events ranging a span of time—where it is likely that this "span" varies among tooth types and among individuals and among populations (Bailey, 2004). Indeed, data collected by Kraus and Jordan (1965) and by Moss and Applebaum (1962) clearly shows these allometric patterns of growth. Similarly, Rosenzweig's (1970) study of crown index (BL/MD times 100) confirms intergroup differences in completed tooth crown shape, along with the trend for males to have larger indices (*i.e.*, greater BL width in comparison to MD length) than females within a group.

Viewed occlusally, cusp area includes the sloping margins of the crowns, down to what, clinically are

TABLE 3. Results of mixed-model ANOVA testing for sexual dimorphism and size difference between cusps on M1 and M2[1]

	Sex Difference			M1-M2 Difference			
Variable	df	F-Ratio	Prob > F	df	F-Ratio	Prob > F	Percent Difference
Protocone	1, 139	2.37	0.1258	1, 139	51.43	< 0.0001	+12.8
Paracone	1, 139	22.50	< 0.0001	1, 139	14.09	0.0003	+5.5
Metacone	1, 139	6.86	0.0098	1, 139	375.61	< 0.0001	-33.5
Hypocone	1, 74	8.83	0.0040	1, 74	126.34	< 0.0001	-32.7
Crown Area	1, 139	21.27	< 0.0001	1, 139	298.91	< 0.0001	-13.2

[1]Sex was included in the model to account for the observed sexual dimorphism in cusp areas. Sex is a fixed effect while the cusp areas on M1 and M2 are a repeated-measure in the ANOVA tests.

termed the heights of contour (Zeisz and Nuckolls, 1949; Ash, 1993). These heights correspond to the bulges (convexities) on the crowns that operationally define the maximum mesiodistal and buccolingual tooth crown dimensions that have been used so extensively in the anthropological study of teeth (Wolpoff, 1971; Swindler, 1976, 2002; Kieser, 1990). These maxima occur at various heights of the crowns depending on tooth type. On human molars, maximum mesiodistal height occurs near the midsection of the crown's height, while buccolingual width occurs close to the gingival margin. Some portions of these crown heights are included in an occlusal projection of a cusp's area even though the collum of the crown mineralizes at some time appreciably later than the occlusal table (Moorrees, Fanning and Hunt, 1963). Macho and Spears (1999) note that there is a mesiodistal gradient among the molars such that first molars have considerably thinner enamel than second and third molars and that the first molar tends to have more sloping (less upright) sides of the crown, buccally and lingually, than the distal molars. One would suppose that these buccal and lingual slopes on M1 would reposition the maximum heights of contour apically and have the effect of increasing occlusal areas when viewing the crown occlusally. Little is known about growth control mechanisms that regulate development of the cervical loop—that region of the crown apical to the occlusal table that progressively undergoes dentinogenesis—and, subsequently, amelogenesis until the crown is complete at the cementoenamel junction (Keene, 1982).

In the present study, we were struck by the low levels of correlation among the basal cusp areas (Table 2). While all of the correlations were positive and many achieved statistical significance because of the large sample sizes, they do not account for much of the observed variation (all $r^2 < 15\%$). The typical interpretation of low biological correlations is that the variables have separate developmental causes (separate etiologies) and that seems to be the case here. The conventional measurement of crown size (*e.g.*, Goose, 1963) has traditionally been viewed as a composite measure of the constituent basal cusp area. The occlusal morphology of a tooth, especially that of a molar, is so distinctive that there rarely is any question as to its arcade, side, or placement in the tooth row. It seems to us that these features have bolstered the supposition that the constituent cusp areas are strongly tied to overall tooth size (also see Garn, 1977). The present study suggests a different scenario: Growth of the basal cusp areas is only weakly coordinated. Low correlations imply weak morphological integration among the main cusps (Olson and Miller, 1958), seemingly because each cusp's growth depends on (largely) independent regulatory mechanisms (Salazar-Ciudad and Jernvall, 2002).

Low correlations among the cusps—weak "morphological integration" of the regions of the occlusal table—are in fact the rule rather than the exception. Biggerstaff commented on these weak associations in his landmark work in this area (1975), and subsequent researchers (Garn, 1977; Corruccini and Potter, 1981; Townsend, 1985; Townsend *et al.*, 2003) have each remarked on it. The consensus is that the constituent regions of the occlusal table show weaker levels of intercorrelation, greater coefficients of variation, greater left-right asymmetry, and lower genetic control (greater environmental variation) than overall crown size. Townsend *et al.* (2003:350) studied intercuspal distances instead of areas, but they concluded equivalently that, "Our finding of high phenotypic variation in intercuspal distances with only moderate genetic contribution is consistent

with substantial epigenetic influence on the progressive folding of the internal enamel epithelium, following formation of the primary and secondary enamel knots."

Most of the basal cusp areas on both M1 and on M2 are sexually dimorphic in the present sample of American whites. In fact, percentage dimorphism (Table 1) tends to be greater for these areas than for corresponding sex differences in overall mesiodistal and buccolingual tooth dimensions measured on the same teeth, namely 2.8% and 1.8% for M1 and M2 dimensions mesiodistally and 5.0% and 2.9% for M1 and M2 buccolingually (Harris and Burris, 2003). Again, we attribute the high variability and absence of sexual dimorphism of the protocone on M1 to including the variable size of Carabelli's trait with this cusp. It is of note that the degrees of sexual dimorphism are larger for the second molar whose occlusal table mineralizes around four and a half years of age (Harris and Buck, 2002) than on M1 where mineralization occurs by one-half year. For both molars, the morphologically variable hypocone shows a high degree of sexual dimorphism. This difference in area of the hypocone is part of the morphogenetic field effect, where there is a steeper decline in average size (and occurrence) in females than males (*e.g.*, Moorrees, 1957; Jacobson, 1982).

These findings (Table 1) are at odds with Biggerstaff's finding (1975) that there were "suggestions" of sexual dimorphism in cusp areas but that they seldom attained statistical significance. Biggerstaff did not provide statistics in this regard, but his graphs suggest that, indeed, most means for males and females were within one standard deviation of each other. Subsequent studies of intercuspal distances (Garn, 1977; Townsend, 1985; Townsend *et al.*, 2003) also comment on the low level of sexual dimorphism in these constituent components of crown size.

Biggerstaff's results were hampered by partitioning his sample into small groups based on molar cusp configurations, and he did not actually measure cusp area. Instead, he calculated the areas of polygons defined by several landmarks, none of which was truly peripheral on the occlusal table, so his values variably underestimate "basal cusp area" as viewed occlusally.

The computer-assisted method used in the present study is comparable to that used by Macho and Moggi-Cecchi (1992) to measure cusp areas of maxillary molars of South African blacks (Fig. 2). Analogous to studies of conventional crown diameters (*e.g.*, Richardson and Malhotra, 1975; Jacobson, 1982), the cusp areas of these Sub-Saharan blacks are obviously larger than the present sample of North American whites of western European descent, but not uniformly so. For several cusp areas there is greater sexual dimorphism in the blacks. Protocone size is the same in the two groups for M1 and larger in whites on M2. Paracone areas appear to be equivalent in the two groups, while the metacone and hypocone are appreciably larger in the blacks. Since there is not just a difference in scale between these two groups, additional studies may provide informative patterns of size variation well beyond the simple blacks > whites suggested by overall crown sizes (*e.g.*, Harris and Rathbun, 1991).

Prior studies (*e.g.*, Macho and Moggi-Cecchi, 1992) have asked the somewhat rhetorical question of whether there is uniform (isometric) scaling of cuspal features from M1 to M2 to M3. Obviously, the decisive answer is "no." There are obvious allometric differences. In the present study that compares just M1 and M2 (Table 3), there are highly significant changes for all four-cusp areas. An isometric reduction from M1 to M2 would mean that M2 is merely a "scaled-down" version of M1, the pole tooth. Instead, the protocone and paracone have significantly larger basal areas on M2, while the metacone and hypocone are clearly smaller on M2. The

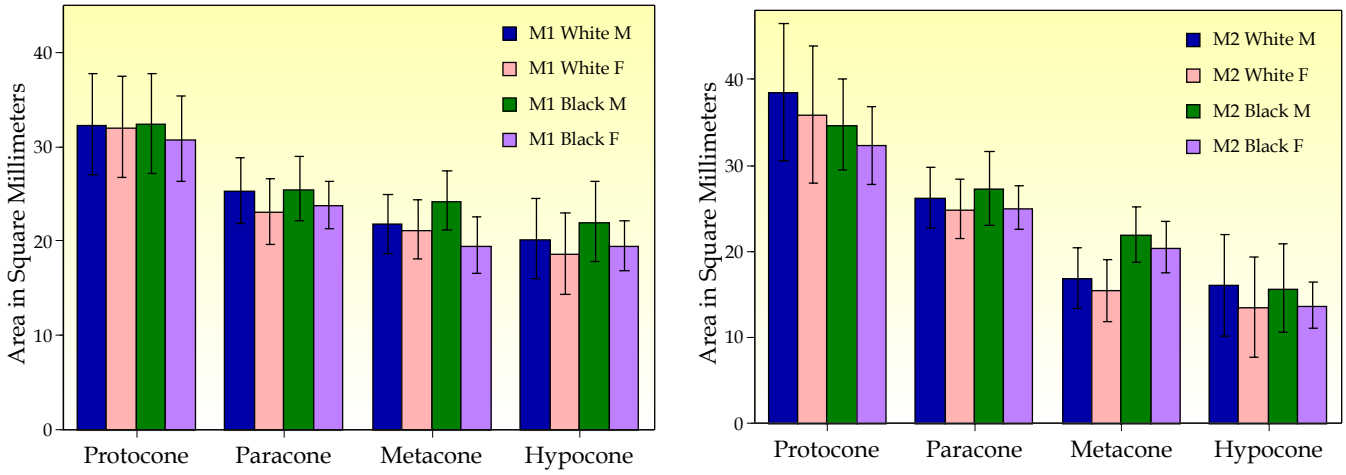

Fig. 2. Average basal cusp areas for the present sample of American whites compared to data published by Macho and Moggi-Cecchi (1992) for South African blacks. Error bars are ±1 standard deviation. Overall crown area was about 3% larger in blacks than whites for M1 and 11% larger for M2.

metacone and hypocone (Table 3) differ in their degrees of size reduction, perhaps because the metacone is part of the molar's comparatively stable trigon, while the hypocone is the sole cusp of the talon in humans (Osborn, 1907; Gregory, 1922). The metacone's variability seems to be expressed wholly as size variation; there was no instance on M1 or M2 where this cusp was absent. In contrast, the hypocone was always present on M1 in some form, but was absent in about half (47%; 66/140) of the M2 sample. Consequently, the size variation calculated here is just for the half of the M2 where the hypocone is present. Other studies that have quantified occlusal areas also have commented on the especial variability of the hypocone (*e.g.*, Biggerstaff, 1975; Peretz *et al.*, 1998; Yamada and Brown, 1998). To note just that M2 has a smaller occlusal table than M1 (a 13% reduction on average) hides the considerable variability within the constituent cusps.

We have explored here some of the biological features of cusp areas on maxillary molars. Our motivation was to extend the battery of biologically (and anthropologically and genetically) useful features that can be studied beyond the hackneyed use of maximum MD and BL crown diameters. Moreover, work by embryologists (*e.g.*, Jernvall and Thesleff, 2000; Salazar-Ciudad and Jernvall, 2002) suggests that regulation of events that define morphology of the occlusal table probably are different than those acting later to form the collum of the crown where conventional diameters are measured, thus providing additional and different biological information. In contrast to the enormously time- and effort-intensive computer methods initiated by Biggerstaff (*e.g.*, 1969a,b), the computer hardware and software now available make the study of crown components comparatively quite feasible.

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LITERATURE CITED

Ash MM Jr. 1993. Wheeler's dental anatomy, physiology and occlusion, 7th ed. Philadelphia: WB Saunders.

Bailey SE. 2004. A morphometric analysis of maxillary molar crowns of Middle-Late Pleistocene hominins. J Hum Evol 47:183-198.

Biggerstaff RH. 1969a. The basal area of posterior tooth crown components: the assessment of within tooth variations of premolars and molars. Am J Phys Anthropol 31:163-170.

Biggerstaff RH. 1969b. Electronic methods for the analysis of the human post-canine dentition. Am J Phys Anthropol 31:235-242.

Biggerstaff RH. 1975. Cusp size, sexual dimorphism, and heritability of cusp size in twins. Am J Phys Anthropol 42:127-139.

Butler PM. 1956. Ontogeny of the molar pattern. Biol Rev 31:30-70.

Butler PM. 1967a. The prenatal development of the human upper permanent molar. Arch Oral Biol 12: 551-563.

Butler PM. 1967b. Relative growth within the human first upper permanent molar during the prenatal period. Arch Oral Biol 12:983-992.

Butler PM. 1968. Growth of the human second lower deciduous molar. Arch Oral Biol 13:671-682.

Corruccini RS. 1979. Molar cusp-size variability in relation to odontogenesis in hominoid primates. Arch Oral Biol 24:633-634.

Corruccini RS, Potter RHY. 1981. Developmental correlates of crown component asymmetry and occlusal discrepancy. Am J Phys Anthropol 55:21-31.

Dahlberg AA. 1951. The dentition of the American Indian. In: Laughlin WS, editor. The physical anthropology of the American Indian. New York: Viking Fund Inc., p 138-176.

Garn SM. 1977. Genetics of tooth development. In: McNamara JA, editor. The biology of occlusal development. Ann Arbor, MI: Craniofaical Growth Series, p 61-88.

Goose DH. 1963. Dental measurements: an assessment of its value in anthropological studies. In: Brothwell DR, editor. Dental anthropology. Oxford: Pergamon Press, p 125-148.

Gregory WK. 1916. Studies on the evolution of the primates. I. The Cope-Osborn 'theory of trituberculy' and the ancestral molar patterns of the Primates. Bull Am Mus Natl Hist 35:239-257.

Gregory WK. 1922. The origin and evolution of the human dentition. Baltimore: Williams & Wilkins Company.

Harris EF, Bailit HL. 1980. The metaconule: A morphologic and familial analysis of a molar cusp in humans. Am J Phys Anthropol 53:349-358.

Harris EF, Buck A. 2002. Tooth mineralization: a technical note on the Moorrees-Fanning-Hunt standards. Dental Anthropology 16:15-20.

Harris EF, Burris BG. 2003. Contemporary permanent tooth dimensions, with comparisons to G. V. Black's data. J Tenn Dent Assoc 83:25-29.

Harris EF, Dinh DP. n.d. Intercusp relationships of the maxillary first and second molars in American whites. Am J Phys Anthropol [In Press].

Harris EF, Rathbun TA. 1991. Ethnic differences in the apportionment of tooth sizes. In: Kelley MA and Larsen CS, editors. Advances in dental anthropology. New York: Alan R. Liss, Inc., p 121-142.

Jacobson A. 1982. The dentition of the South African Negro. Anniston, AL: Higginbotham, Inc.

Jernvall J, Aberg T, Kettunen P, Keranen S, Thesleff I. 1998. The life history of an embryonic signaling center: BMP-4 induces p21 and is associated with

apoptosis in the mouse tooth enamel knot. Development 125:161-169.
Jernvall J, Keränen SV, Thesleff I. 2000. Evolutionary modification of development in mammalian teeth: quantifying gene expression patterns and topography. Proc Natl Acad Sci U S A 97:14444-14448.
Jernvall J, Kettunen P, Karavanova I, Martin LB, Thesleff I. 1994. Evidence for the role of the enamel knot as a control center in mammalian tooth cusp formation: non-dividing cells express growth stimulating Fgf-4 gene. Int J Dev Biol 38:463-469.
Jernvall J, Thesleff I. 2000. Reiterative signaling and patterning during mammalian tooth morphogenesis. Mech Dev 92:19-29.
Keene HJ. 1982. The morphogenetic triangle: a new conceptual tooth for application to problems in dental morphogenesis. Am J Phys Anthropol 59:281-287.
Kieser JA. 1990. Human adult odontometrics: the study of variation in adult tooth size. New York: Cambridge University Press.
Korenhof CAW. 1960. Morphogenetical aspects of the human upper molar. Utrecht: Uitgeversmaatschappij Neerlandia.
Kraus BS. 1952. Morphologic relationships between enamel and dentin surfaces of the lower first molar teeth. J Dent Res 31:248-256.
Kraus BS. 1959. Occurrence of the Carabelli trait in Southwest ethnic groups. Am J Phys Anthropol 17:117-123.
Kraus BS, Jordan RE. 1965. The human dentition before birth. Philadelphia: Lea and Febiger.
Luukko K, Loes S, Furmanek T, Fjeld K, Kvinnsland IH, Kettunen P. 2003. Identification of a novel putative signaling center, the tertiary enamel knot in the postnatal mouse molar tooth. Mech Dev 120:270-276.
Macho GA, Moggi-Cecchi J. 1992. Reduction of maxillary molars in Homo sapiens sapiens: a different perspective. Am J Phys Anthropol 87:151-160.
Macho GA, Spears IR. 1999. Effects of loading on the biomechanical [correction of biochemical] behavior of molars of Homo, Pan, and Pongo. Am J Phys Anthropol 109:211-227.
Mizoguchi Y. 1988. Degree of bilateral asymmetry of nonmetric tooth crown characters quantified by the tetrachoric correlation method. Bull Nat Sci Mus, Tokyo, Series D 14:29-49.
Moorrees CFA. 1957. The Aleut dentition: a correlative study of dental characteristics in an Eskimoid people. Cambridge: Harvard University Press.
Moorrees CFA, Fanning EA, Hunt EE Jr. 1963. Age variation of formation stages for ten permanent teeth. J Dent Res 42:1490-1502.
Moss ML, Applebaum E. 1962. Differential growth analysis of vertebrate teeth. J Dent Res 36:644-651.
Olson EC, Miller RL. 1958. Morphological integration. Chicago: University of Chicago Press.
Osborn HF. 1907. Evolution of mammalian molar teeth to and from the triangular type. New York: Macmillan.
Peretz B, Nevis N, Smith P. 1998. Morphometric analysis of developing crowns of maxillary primary second molars and permanent first molars in humans. Arch Oral Biol 43:525-533.
Richardson ER, Malhotra SK. 1975. Mesiodistal crown dimension of the permanent dentition of American Negroes. Am J Orthod 68:157-164.
Rosenzweig KA. 1970. Tooth form as a distinguishing trait between sexes and human populations. J Dent Res 49:1423-1426.
Salazar-Ciudad I, Jernvall J. 2002. A gene network model accounting for development and evolution of mammalian teeth. Proc Natl Acad Sci U S A 99:8116-8120.
Sharpe PT. 2001. Neural crest and tooth morphogenesis. Adv Dent Res ;15:4-7.
Swindler DR. 1976. Dentition of living primates. New York: Academic Press.
Swindler DR. 2002. Primate dentition: an introduction to the teeth of non-human primates. Cambridge: Cambridge University Press.
Thesleff I, Jernvall J. 1997. The enamel knot: a putative signaling center regulating tooth development. Cold Spring Harb Symp Quant Biol 62:257-267.
Thesleff I, Keranen S, Jernvall J. 2001. Enamel knots as signaling centers linking tooth morphogenesis and odontoblast differentiation. Adv Dent Res 15:14-18.
Townsend GC. 1985. Intercuspal distances of maxillary pre-molar teeth in Australian aboriginals. J Dent Res 64:443-446.
Townsend G, Richards L, Hughes T. 2003. Molar intercuspal dimensions: genetic input to phenotypic variation. J Dent Res 82:350-355.
Turner CG II, Hawkey DE. 1998. Whose teeth are these? Carabelli's trait. In: Lukacs JR, editor. Human dental development, morphology, and pathology: a tribute to Albert A. Dahlberg. Eugene: University of Oregon Anthropological Papers, no 54, p 41-50.
Wolpoff MH. 1971. Metric trends in hominid dental evolution. Studies in anthropology, no. 2. Cleveland: Case Western Reserve University Press.
Wood BA, Abbott SA. 1983. Analysis of the dental morphology of Plio-pleistocene hominids. I. Mandibular molars: crown area measurements and morphological traits. J Anat 136 (Pt 1):197-219.
Wood BA, Abbott SA, Graham SH. 1983. Analysis of the dental morphology of Plio-Pleistocene hominids. II. Mandibular molars—study of cusp areas, fissure pattern and cross sectional shape of the crown. J Anat 137 (Pt 2):287-314.
Yamada H, Brown T. 1988. Contours of maxillary molars studied in Australian aboriginals. Am J Phys Anthropol 76:399-407.
Zeisz RC, Nuckolls J. 1949. Dental anatomy. St Louis: CV Mosby Company.