REVISTA
ESTOMATOLOGIA

Racial diferences in tooth crown size gradients within morphogenetic fields

Diferencias raciales en el gradiente del tamaño de la corona dental dentro de los campos morfogenéticos

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RESUMEN

Los dientes se arreglan en campos morfogenéticos, los cuales son ubicaciones anatómicas en los maxilares que regulan tipos de dientes, específicamente incisivos, caninos, premolares y molares en primates. Cada campo está compuesto por dos o tres dientes (salvo el canino aislado), y hay una gradiente de tamaño característica correspondiente a la direccionalidad dentro de cada campo, generalmente con el diente mesial siendo más grande y más estable que el diente distal, variable. El presente estudio se enfoca en las diferencias raciales en la inclinación de las gradientes mesio-distales del tamaño coronal. Grupos con gradientes "inclinadas" demuestran una reducción apreciable del tamaño desde el diente estable al variable, mientras que otros grupos, con gradientes "planas", tienen dimensiones coronales más similares a través del campo. Esta encuesta de estudios publicados en todo el mundo (107 grupos) evalúa variación entre grupos (en vez de entre individuos) de las gradientes calculadas para los incisivos, premolares y molares en cada arcada. Los caucásicos suelen tener las gradientes más inclinadas; los indígenas de Australia las más planas. Las correlaciones entre las diferentes gradientes de los distintos tipos de diente son significativos estadísticamente, pero menores, lo cual sugiere que factores microevolucionarios han influido sobre las gradientes de los distintos grupos de maneras diferentes. De los siete grupos geográficos evaluados, los Amerindios son los más distintivos. Especulamos brevemente sobre la naturaleza del señalamiento molecular en el desarrollo que determina estas gradientes.

Palabras clave: Tamaño dental, odontometría, campos morfogéneticos, variación humana.

SUMMARY

Teeth are arranged in morphogenetic fields, which are anatomical locations in the jaws that regulate tooth types, namely incisors, canines, premolars, and molars in primates. Each field is composed of two or three teeth (except for the isolated canine), and there is a characteristic size gradient corresponding to directionality within each field, generally with the mesial tooth being larger and more stable than the distal, variable tooth. Focus of the present study is on racial differences in the steepness of these mesial-distal crown size gradients. Groups with "steep" gradients have appreciable size reduction from the stable to the variable tooth, while other groups, with "shallow" gradients, have more similar crown dimensions across a field. This worldwide survey of published studies (107 groups) assessed intergroup (rather than inter-individual) variation in size gradients calculated for the incisors, premolars, and molars in each arcade. Caucasians tend to have the steepest gradients; aboriginal Australians tend to have the most shallow gradients. Correlations among the gradients of different tooth types are significant statistically, but modest, suggesting that microevolutionary factors have influenced the gradients of different groups differently. Of the seven geographic groupings evaluated, Amerindians are the most distinctive. We briefly speculate on the nature of the developmental molecular signaling that determines these gradients.

Key words: Tooth size, odontometrics, morphogenetic fields, human variation.

INTRODUCTION

Tooth crown dimensions commonly are viewed as polygenic traits substantially controlled by the person's genotype (1,2) making them useful for the study of biological and anthropological issues. Numerous studies over the past century have explored the patterns of tooth crown size variation among extant and recent human groups (3-5). The rationales for these various studies differ considerably, but, often, the intent has been to document geographic (ethnohistorical) patterns of variation or to reconstruct human migrations. Almost all of these analyses have used individual tooth dimensions as the units of study.

This approach has been productive, but it ignores the fact that teeth are apportioned into morphogenetic fields and teeth within

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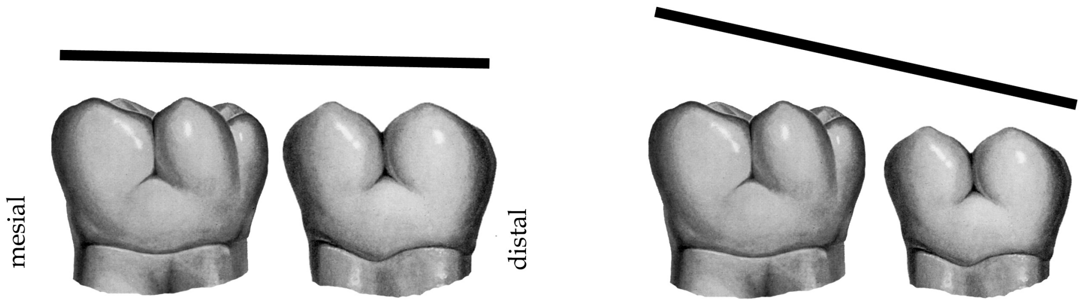

Figure 1. Illustrative examples of inter-tooth within-field gradients. Buccal views of mandibular first and second molars are pictured. Left: When the mesial and distal teeth are nearly equivalent in size, the shallow gradient will have a ratio near one. Across populations, there can be a considerable, continuous spectrum of gradients. Right: With a steep gradient, the variable tooth (generally the distal tooth) within the field is appreciably smaller than the pole tooth, so the first-to-second tooth ratio is well above unity.

a field share considerable similarities in function, size, shape, and time of formation (6-8). Indeed, the orderly arrangement of dental elements by size and shape within a field is a prime example of merism as described by Bateson (9), namely the repetition of anatomical units (such as vertebrae in the spinal column, phalanges in a finger, and teeth in a morphogenetic field).

Purpose of the present study is to assess population differences in what we term steepness of the size gradients of teeth within a field (Figure 1). We use a brief historical note to illustrate this issue. When Moorrees wrote his classic dental study of the Aleuts (10), he included a section comparing Aleut tooth sizes with published reports on other peoples. In spite of the numerous univariate tests performed (aided by Kalevi Koski), one of the few conclusions drawn by Moorrees was that Caucasians are characterized by a small maxillary lateral incisors in comparison to their central incisor. We label this as an example of a steep incisor-field gradient. In contrast, as an example, American Indians (11) characteristically have shallow maxillary incisor size gradients because the lateral incisor is absolutely smaller than but comparatively large relative to the central incisor.

A field gradient can easily be quantified for several tooth types, namely the incisors (I1/I2), premolars (P1/P2), and molars (M1/M2) in each of the two dental arcades. This study assesses population differences in the steepness of mesiodistal size gradients within these six morphogenetic fields.

MATERIALS AND METHODS

Descriptive mesiodistal tooth crown size statistics were collected from the literature; this worldwide survey is based on 107 samples (Table 1). Groups are modern, living peoples or from the recent archeological past, so only fully-modern humans are considered. In this initial survey, sex differences were not investigated. If published, descriptive statistics for the overall sample (males + females) were used; if sexes were described separately, the unweighted averages of the means were used. Groups were then categorized into seven geographic races (12) using the same criteria described by Harris and Rathbun (4) and Harris and Lease (13).

Three morphogenetic fields in each arch in the human dentition possess at least two teeth, namely the incisors, premolars, and molars, and we quantified the size gradient in each field simply as the mesial tooth's mean mesiodistal diameter divided by the mean of the distal tooth. Since (aside from the mandibular incisors) the mesial tooth is the larger of the two, most size ratios ("gradients") have values above 1.0.

An obvious detraction in this preliminary analysis is that there was no statistical adjustment for differences in sample sizes, though groups described from very small samples (less than roughly 20 individuals) were excluded. Not adjusting for sample sizes means that smaller samples (with less precise sample estimates) are compared to larger samples where the mean is estimated with greater accuracy. Also, these group averages obscure inter-individual variability in tooth size differences. Still, we believe that these data provide a roughly objective means of addressing the biological question, and finer discrimination can be obtained with subsequent analysis.

One-way factorial analysis of variance was used to test for significant differences in the mean size gradients among the seven geographic-racial groupings (14). The Tukey-Kramer HSD post hoc test was used to determine the source(s) of statistical significance.

RESULTS

Maxillary incisors

The analysis of variance test for a difference among groups for the I1-to-I2 size gradient was highly significant (Table 2). Box plots of the data (Figure 2A) show that American Indians, as a group, have among the lowest ratios (i.e., most similar I1-to-I2 widths). Peoples of European extraction (Caucasian), at the other extreme, have steep gradients because I2 widths are appreciably smaller than those of the

Table 1. Compilation of the 107 groups studied, along with the six within-field mesiodistal size gradients.

	Maxilla			Mandible			
Group	I1/I2	P1/P2	M1/M2	I1/I2	P1/P2	M1/M2	Reference
				Africa			
Africa	1.157	1.032	1.006	0.864	0.988	1.011	Hanihara 1998 (5)
Bushman Tribe	1.239	1.046	1.021	0.893	0.986	1.028	Drennan 1929 (39)
Griqua, South Africa	1.211	1.040	1.072	0.881	1.024	1.073	Kieser 1990 (1)
Bushmen	1.239	1.045	1.048	0.909	0.958	1.000	Abel 1933 (40)
Hottentot	1.277	1.030	1.019	0.839	0.986	1.018	Abel 1933 (40)
Nubia, Agriculturalists	1.280	1.049	1.071	0.900	0.989	1.043	Calcagno 1989 (30)
Nubia, Final Paleolithic	1.265	1.090	1.042	0.918	1.010	1.032	Calcagno 1989 (30)
Nubia, Intensive Agriculture	1.262	1.049	1.081	0.897	0.997	1.047	Calcagno 1989 (30)
Rwanda Pygmees	1.343	1.068	1.033	0.871	0.988	1.067	Brabant 1965 (41)
So Carolina Blacks	1.242	1.015	1.050	0.865	0.949	1.049	Harris, Rathbun 1989 (42)
South Africa, living	1.241	1.035	1.030	0.869	0.987	1.026	Kieser et al. 1987 (43)
South Africa, skeletal	1.238	1.044	1.032	0.880	0.990	1.034	Kieser et al. 1987 (43)
South African Negroes	1.244	1.068	1.035	0.882	0.992	1.030	Jacobson 1982 (44)
West Africa: Teso	1.236	1.019	1.087	0.937	0.994	1.039	Barnes 1969 (45)
				Asia			
Ainu	1.175	1.065	1.071	0.919	1.013	1.070	Hanihara 1998 (5)
Bronze Chinese	1.213	1.089	1.058	0.887	1.010	1.033	Brace 1978 (46)
Bronze Javanese	1.270	1.034	1.067	0.903	1.012	1.034	Brace 1978 (46)
Bronze Thai	1.231	1.076	1.106	0.884	0.997	1.071	Brace 1978 (46)
Chinese	1.165	1.084	1.059	0.880	1.007	1.052	Hanihara 1998 (5)
Dayak	1.291	1.080	1.085	0.795	1.003	1.100	Hanihara 1998 (5)
Early Thai	1.197	1.071	1.081	0.893	0.996	1.065	Hanihara 1998 (5)
Filipino	1.227	1.055	1.052	0.907	0.982	1.062	Hanihara 1998 (5)
Filipino	1.237	1.080	1.038	0.891	0.993	1.051	Potter et al. 1981 (47)
Gilimanuk, Bali	1.279	1.070	1.080	0.918	1.027	1.045	Jacob 1967 (48)
Guam	1.252	1.053	1.106	0.893	1.005	1.079	Hanihara 1998 (5)
Hawaii	1.231	1.086	1.042	0.876	1.004	1.049	Hanihara 1998 (5)
Japanese	1.192	1.071	1.027	0.900	1.003	1.039	Hanihara 1998 (5)
Japanese	1.221	1.057	1.076	0.890	0.986	1.038	Gonda 1959 (49)
Javanese	1.226	1.065	1.087	0.886	1.000	1.066	Mijsberg 1931 (50)
Jomon	1.218	1.072	1.103	0.915	0.991	1.082	Hanihara 1998 (5)
Kwaio	1.187	1.071	1.048	0.881	0.983	1.056	Harris, Bailit 1987 (51)
Modern Japanese, Kyoto	1.214	1.028	1.062	0.893	0.993	1.018	Brace, Nagai 1982 (52)
Modern Chinese	1.217	1.075	1.077	0.883	0.997	1.020	Brace 1978 (46)
Modern Javanese	1.222	1.060	1.082	0.890	1.013	1.076	Brace 1978 (46)

Modern Thai	1.194	1.089	1.076	0.896	0.993	1.050	Brace 1978 (46)
Negrito	1.213	1.048	1.094	0.896	0.983	1.101	Hanihara 1998 (5)
Ontong Java	1.227	1.030	1.066	0.874	0.959	1.087	Harris, Bailit 1987 (51)
Pre-Agriculture Jomon	1.212	1.071	1.087	0.904	0.993	1.061	Brace, Nagai 1982 (52)
Prehistoric Yayoi	1.185	1.065	1.050	0.893	0.986	1.045	Brace, Nagai 1982 (52)
Recent Koreans	1.230	1.051	1.046	0.983	1.007	1.018	Brace, Nagai 1982 (52)
Southeast Asia	1.180	1.065	1.052	0.888	0.988	1.054	Hanihara 1998 (5)
Australia							
Australian Aborigines	1.225	1.080	1.046	0.896	0.987	0.984	Campbell 1925 (20)
Broadbeach	1.286	1.039	1.026	0.870	0.988	0.984	Smith et al. 1981 (53)
Early Australians	1.261	1.031	1.035	0.895	0.982	0.984	Hanihara 1998 (5)
Recent Australians	1.240	1.034	1.014	0.878	0.984	0.970	Hanihara 1998 (5)
Swanport	1.211	1.041	1.056	0.938	0.974	1.000	Smith et al. 1981 (53)
Yuendumu	1.242	1.069	1.036	0.887	0.991	1.045	Townsend, Brown 1979 (54)
Europe							
Aeboholt Danes	1.297	1.021	1.112	0.864	0.984	1.081	Lunt 1969 (15)
American Whites	1.315	1.046	1.016	0.905	0.994	1.071	Garn et al. 1968 (55)
American Whites	1.287	1.014	1.135	0.920	0.957	1.078	Moyers et al. 1976 (17)
Australian Whites	1.279	1.044	1.033	0.906	0.986	1.044	Townsend, Alvesalo 1985 (56)
Belgian Whites	1.291	1.022	1.129	0.885	0.979	1.076	Brabant, Twiesselmann 1960 (16)
British Whites	1.313	0.985	1.115	0.902	0.986	1.085	Lavelle 1972 (57)
Czech	1.307	1.048	1.088	0.904	1.003	1.028	Hanihara 1998 (5)
Early Iran	1.256	1.047	1.058	0.872	0.977	1.025	Hanihara 1998 (5)
German	1.245	1.047	1.063	0.895	0.975	1.027	Hanihara 1998 (5)
Hailuoto Finns	1.296	1.044	1.025	0.912	0.989	1.050	Alvesalo 1970 (58)
Icelanders	1.291	1.039	1.092	0.910	0.996	1.037	Axelsson, Kirveskari 1983 (59)
Karelian USSR	1.242	1.062	1.041	0.885	1.042	1.031	Jacobs, Price 1991 (60)
Mesolithic Europe	1.314	1.045	1.072	0.898	1.014	1.056	Frayer 1977 (61)
Mesolithic	1.314	1.045	1.072	0.898	1.014	1.056	Frayer 1977 (61)
Naestved Danes	1.302	1.039	1.134	0.919	0.996	1.078	Lunt 1969 (15)
Norwegian Lapps	1.235	1.041	1.105	0.898	0.998	1.048	Selmer-Olson 1949 (62)
Russian	1.261	1.050	1.072	0.875	0.947	1.035	Hanihara 1998 (5)
Skolt Lapps	1.281	1.048	1.061	0.910	0.996	1.036	Kirveskari et al. 1978 (63)
Yugoslave Mesolithic	1.312	0.959	1.087	0.884	0.981	1.021	y'Edynak 1989 (64)
Melanesia							
Aita	1.200	1.087	1.074	0.885	1.006	1.061	Harris, Bailit 1987 (51)
Eivo	1.213	1.099	1.080	0.898	1.006	1.094	Harris, Bailit 1987 (51)
Goroko PNG	1.211	1.094	1.082	0.884	1.009	1.069	Doran, Freedman 1974 (65)
Island Melanesia	1.215	1.048	1.074	0.885	0.980	1.051	Hanihara 1998 (5)
Lufa PNG	1.227	1.078	1.044	0.926	1.033	1.045	Doran, Freedman 1974 (65)

Nagovisi	1.189	1.088	1.126	0.908	1.000	1.088	Harris, Bailit 1987 (51)
Neu-Pommern	1.200	1.080	1.095	0.873	0.979	1.061	Janzer 1927 (66)
New Britain	1.231	1.046	1.096	0.896	0.928	1.043	Wolpoff 1971 (67)
Papua New Guinea	1.300	1.031	1.081	0.870	1.000	1.049	Hanihara 1998 (5)
Mideast							
Bengalis	1.252	1.063	1.045	0.907	0.999	1.073	Hemphill 1991 (68)
Chalcolithic India	1.277	1.049	1.051	0.911	0.960	1.031	Lukacs, Hemphill 1991 (69)
Chenchu	1.267	1.100	1.081	0.886	1.023	1.132	Hemphill 1991 (68)
Gampadhompti	1.259	1.054	1.044	0.883	0.993	1.100	Hemphill 1991 (68)
Maharashtrans	1.253	1.055	1.039	0.905	0.983	1.072	Hemphill 1991 (68)
Neolithic Mehrgarh	1.225	1.035	1.069	0.897	0.982	1.062	Lukacs, Hemphill 1991 (69)
Pakanati	1.250	1.063	1.054	0.898	0.990	1.104	Hemphill 1991 (68)
Eastern Arabian Coast	1.244	1.024	1.082	0.918	0.975	1.033	Macchiarelli 1989 (70)
New World							
Adena	1.183	1.039	1.080	0.840	0.996	1.022	Sciulli 1979 (71)
Aleuts	1.134	1.036	1.090	0.877	0.964	1.058	Turner 1967 (72)
Archaic HSS	1.193	1.078	1.052	0.852	0.969	0.998	Hinton et al. 1980 (73)
Arctic Indians	1.064	1.058	1.119	0.853	1.004	1.050	Turner 1967 (72)
Classic Mexico	1.231	1.061	1.058	0.889	0.979	1.053	Christensen 1998 (74)
Coastal Peru	1.161	1.024	1.035	0.846	0.991	1.011	Scott 1979 (75)
Dickson Mounds	1.186	1.048	1.054	0.856	0.955	1.012	Wolpoff 1971 (67)
Early Formative Mexico	1.198	1.069	1.049	0.861	0.981	1.044	Christensen 1998 (74)
Eskimo-Aleut	1.153	1.054	1.089	0.865	0.995	1.052	Turner 1967 (72)
Eskimo	1.173	1.068	1.089	0.848	1.019	1.049	Turner 1967 (72)
Glacial Kame	1.210	1.060	1.087	0.841	0.984	1.042	Sciulli 1979 (71)
Hall Beach Eskimo	1.178	1.071	1.077	0.833	1.011	1.063	Mayhall 1979 (76)
Hopewell	1.182	1.062	1.082	0.856	0.966	1.031	Sciulli 1979 (71)
Igloolik Eskimo	1.204	1.074	1.069	0.841	0.993	1.032	Mayhall 1979 (76)
Indian Knoll	1.162	1.038	1.104	0.867	0.978	1.046	Perzigian 1976 (77)
Late Formative Mexico	1.206	1.035	1.069	0.862	0.982	1.056	Christensen 1998 (74)
Middle Formative Mexico	1.199	1.015	1.064	0.867	0.992	1.059	Christensen 1998 (74)
Mississippi HSS	1.195	1.056	1.058	0.849	0.985	1.017	Hinton et al. 1980 (73)
Ohio Adena	1.186	1.042	1.077	0.840	0.999	1.021	Sciulli 1979 (71)
Ohio Glacial Kame	1.210	1.061	1.088	0.840	0.984	1.043	Sciulli 1979 (71)
Ohio Hopewell	1.184	1.060	1.082	0.857	0.965	1.030	Sciulli 1979 (71)
Pecos Pueblo	1.228	1.060	1.080	0.899	0.964	1.048	Nelson 1938 (11)
Postclassic Mexico	1.210	1.044	1.061	0.882	0.985	1.050	Christensen 1998 (74)
Woodland HSS	1.241	1.043	1.060	0.821	1.000	1.017	Hinton et al. 1980 (73)

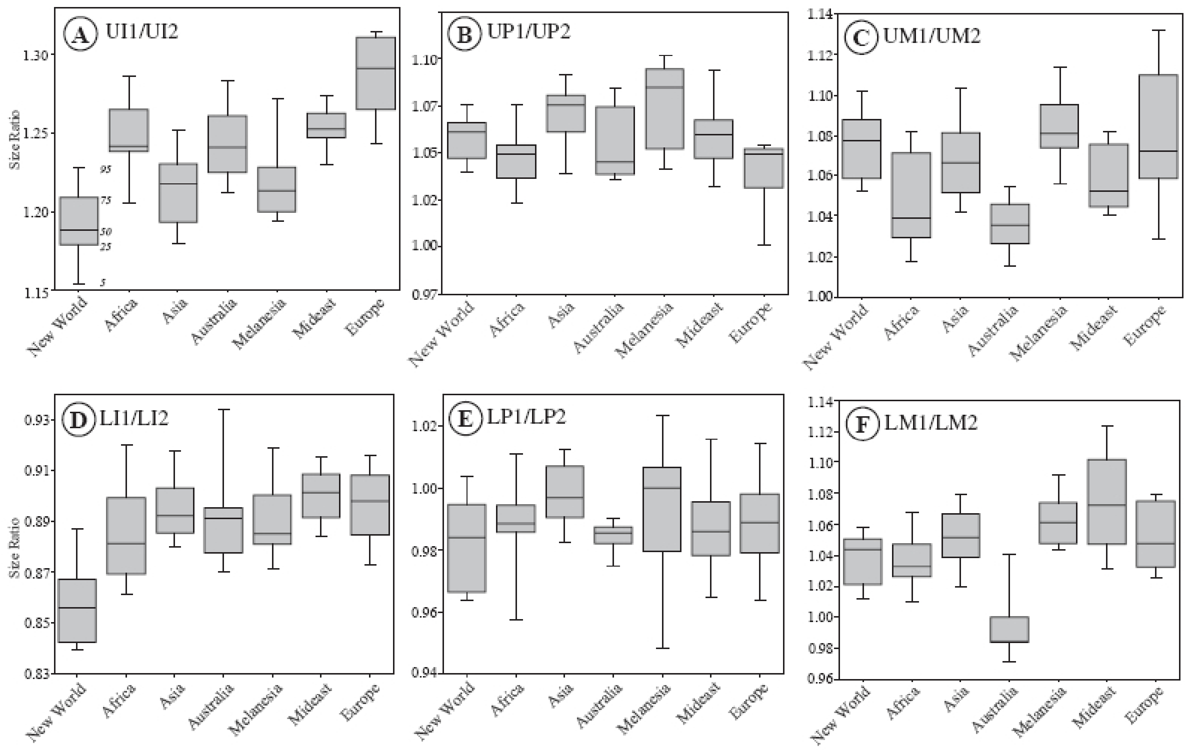

Figure 2. Box plots of the sample distributions for the six tooth size gradients. In each case, the mesial tooth's mean size is divided by mean size of the distal tooth: (A) maxillary incisors (I1/I2), (B) maxillary premolars (P1/P2), (C) maxillary molars (m1/m2), (D) mandibular incisors (I1/I2), (E) mandibular premolars (P1/P2), and (F) mandibular molars (M1/M2). Percentiles of the distributions are denoted by the horizontal lines on each box plot, as labeled for the New World samples in panel A.

central incisors. Post hoc tests show that there are three statistically distinct groupings of the seven geographic categories, namely (A) European and derived groups at the upper extreme, (B) Melanesians, Asians, and Amerindians are combined phenotypically at the lower extreme, and (C) an array of intermediate groups (notably Australians and Africans). As a group, New World Indians have the most shallow gradient (i.e., largest I2 widths relative to I1), and, as is obvious from Figure 2A, European groups are most extreme in their preferential reduction of I2.

Maxillary premolars

The maxillary premolar gradient is highly significantly different among groups (Table 2; Figure 2B), and the extremes are Europeans with P1 dimensions only slightly larger than P2 (so their P1-P2 ratio is closest to 1.0) and Melanesians at the other extreme with comparatively steep gradients (seemingly due to relatively small P2 dimensions rather than excessive P1 dimensions). These extreme groups make an important point: While some peoples, like Melanesians, are characterized by large tooth sizes, tooth size is only loosely tied developmentally to the size gradients examined here.

Maxillary molars

The source of the highly significant differences in molar gradients (Figure 2C) is primarily due to a dichotomization of the seven racial groupings, namely those with steep gradients (notably New World groups, Europeans, and Melanesians) and those with shallow gradients (notably Sub-Saharan Africans and native Australians). This leaves the other two geographic groupings (Asia, Mideast) as statistically intermediate. Figure 2C shows that some European samples have the steepest molar gradients found in this survey. Groups with the steepest molar gradients -about 1.1 to 1.4- are Danes (15), Belgians (16) and American whites (17).

Mandibular incisors

Dahlberg (18) was among the first to publish data on the field reversal in the mandibular incisors, where the lateral incisor is larger and metrically more stable than the central incisor. This reversal is mirrored here in all of the I1-to-I2 size ratios being less than 1.0 (Figure 2D). As suggested by this graph, New World Indians are unique in this global survey with their significantly steeper gradient (i.e., I1 is uncharacteristically small in Amerindians compared to I2).

For the samples studied, I1 is just 86% as wide as I2 in Amerindians, while all of the other geographic groupings are closer

Table 2. Correlation matrices among size gradients*

	Maxilla			Mandible		
	I1/I2	P1/P2	M1/M2	I1/I2	P1/P2	M1/M2
Max I1/I2	--	-0.292	-0.072	0.304	0.049	0.116
Max P1/P2	-0.381	--	-0.080	-0.017	0.350	0.210
Max M1/M2	-0.212	-0.235	--	0.007	-0.019	0.455
Mand I1/I2	0.289	0.044	0.022	--	0.103	0.096
Mand P1/P2	0.105	0.320	-0.051	0.063	--	0.222
Mand M1/M2	0.234	0.280	0.516	0.021	0.139	--

*Upper right: full Pearson product-moment correlations; lower left: partial correlations.

Table 3. Results of one-way analyses of variance testing for differences in mesiodistal size gradients by tooth type among the seven geographic groupings.*

Variable	df	Sum of Squares	Mean Square	Adjusted r^2 (%)	F-Ratio	P-Value
			Maxilla			
Incisors (I1/I2)	6	0.123	0.021	53.2	21.27	< 0.0001
Premolars (P1/P2)	6	0.015	0.002	23.0	6.32	< 0.0001
Molars (M1/M2)	6	0.020	0.003	21.3	5.83	< 0.0001
			Mandible			
Incisors (I1/I2)	6	0.029	0.005	38.6	12.19	< 0.0001
Premolars (P1/P2)	6	0.003	0.001	3.0	1.54	0.1716
Molars (M1/M2)	6	0.030	0.005	36.3	11.15	< 0.0001

*The seven groups are listed in Table 1; adjusted r^2 is the percentage of the total variance due to among-group differences in the size gradients.

to 90%. It is speculative, but the decidedly steeper gradient in American Indians compared to Asians from whom they are descended (19) suggests this alteration occurred after the migrations into the New World, when Indians became a separate racial group (12).

Mandibular premolars

The mandibular premolars are the one situation of the six gradients tested that disclosed no significant difference among groups (Table 2; Figure 2E).

One cause of this nonsignificance could be that there is considerable within-group variance. However, inspection of the ranges in Figure 2 shows that, instead, the nonsignificance is due to uniformity (diminished variability) within and among groups for these two premolar tooth types. The range of the worldwide distribution of size gradients (i.e., the distance along the vertical axis) is on the order of 0.15 for most of the graphs (Figure 2), but just 0.08 for the mandibular premolar. In other words, these mandibular premolars stand out in these analyses with their considerable uniformity in mesiodistal dimensions, with most groups exhibiting P2 diameters just slightly smaller (ca. 98%) than the mesial premolar.

Mandibular molars

There is considerable "sameness" for all of the M1-to-M2 gradients in human groups (Figure 2F) with the obvious exception of native Australians who have shallow gradients very close to 1.0. The other six geographic groups have steeper gradients because M2 tends to be noticeably shorter mesiodistally than M1, the pole tooth.

Associations among gradients

From the foregoing, one gets the impression that the racial differences vary appreciably from analysis of one gradient to the next. This in fact seems to be the case (Table 2). The correlations are moderate-to-low among the gradients in the various morphogenetic fields (Table 3). Indeed, the strongest associations are among gradients in the same tooth types between the two arcades, and even here the partial correlations are only on the order of 0.3 to 0.5. We interpret these low correlations to indicate that the gradients among fields have developed essentially independently of one another as opposed to being modulated by any overarching control mechanism (though the comparatively high within-tooth-type correlations between arches is noteworthy).

DISCUSSION

Metrically, human dentitions can vary according to absolute size or, as studied here, relative sizes of teeth one to the other. In terms of absolute sizes, it is well known that native Australians possess the largest crown sizes of any extant or recent group (3,20,21). This holds true both for the primary and permanent dentitions (4,13). Size, in itself, however generally is of little discriminatory power in anthropological contexts unless the differences are large (22,23). Also, since tooth crown dimensions characteristically are positively intercorrelated (24,25), size differences among tooth types are largely redundant in both the statistical and the biological sense. "Shape" differences -differences in proportionalities among variables- often are more informative in addressing anthropological issues.

Readers will appreciate that several researchers have already focused on one aspect of size gradients, namely molar size sequence -reviewed in Townsend and Brown (26)-.

Table 4. Correlations between tooth size (sum of the 14 tooth types and tooth size gradients.*

Variables	r	P-Value	rho	P-Value
Maxilla				
Size and I1/I2	-0.283	0.0027	-0.352	0.0002
Size and P1/P2	0.079	0.4131	0.019	0.8436
Size and M1/M2	-0.224	0.0187	-0.138	0.1507
Mandible				
Size and I1/I2	-0.094	0.3276	-0.205	0.0317
Size and P1/P2	-0.085	0.3780	-0.112	0.2439
Size and M1/M2	-0.410	0.0000	-0.271	0.0042

*Correlations are based on 107 samples; r is Pearson's product-m oment correlation coefficient, while rho is Spearman's rank correlation coefficient.

Garn and coworkers (27) showed (A) that M2>M1 is common in modern humans (ca. 1/3 in maxilla and 10-20% in mandible) and (B) that, within a group, people with large teeth are more likely to possess M1>M2 than individuals with small teeth. Subsequent studies show that there is considerable intergroup variation in humans (just as confirmed in Figure 2C, F).

Dahlberg (28), among others, recognized that crown size is associated with crown complexity in a population -see Garn (29) for a fuller explication-, which implies that tooth reduction might well be accompanied by morphological simplification. In a related vein, several studies have shown that human tooth dimensions have gotten smaller since the Pleistocene, but (A) rates vary considerably in different culture areas and (B) tooth types have diminished at different rates within a phylogeny, typically with the variable distal tooth reducing more -reviewed in Calcagno (30)-.

We speculate from these various findings that tooth size gradients would be steeper in contemporary human groups who have experienced greater crown size reductions. This was explored using the present data set (Table 4) by testing for associations between tooth size and "steepness" of the size gradients in each field. Expectation is that groups with large teeth have more shallow gradients and, thus, smaller ratios. A dentition-wide measure of tooth size is used (i.e., summation of the 7 maxillary plus the 7 mandibular mesiodistal means) so that "size" is not defined by just the teeth in a field, which would produce spurious associations (31). Tooth size is not distributed normally in the data set, so the nonparametric results -Spearman's rho (32)- are more reliable than Pearson's r.

Two of the correlations are highly significant statistically -namely maxillary incisors and mandibular molars- and the associations are negative, as predicted, meaning that groups with large teeth tend to have shallow tooth gradients. Conversely, groups with small teeth tend to have steeper gradients (i.e., higher ratios) because the distal tooth is appreciably smaller than the pole tooth. It merits emphasizing that these associations are based on comparisons between groups; it would be of interest, as well, to analyze inter-individual relationships within groups. We speculate that the same associations occur, but for different biological reasons (33).

There is speculation in the dental literature about the kind and nature of control mechanisms governing tooth size and morphology within a morphogenetic field -reviewed in Kieser (1)-. But, in spite of the huge recent advances in understanding the cascades of chemical events that determine crown morphology (34-36), we remain mostly in the dark concerning control mechanisms among teeth in a field. Teeth, especially within a field, can be viewed as meristic series (9,37) -referring to the duplication of homologous structures, often along a size gradient, such as the branchial arches, vertebrae, and the phalanges within a ray-. Nature of a morphogenetic field seems to be biochemical (38), and the "steepness" of a field, we suppose, reflects how sharply the molecular gradient drops with distance and, as well, with time.

This is an exciting time for the analysis of tooth size and shape because prospects are good that developmental biology will soon inform us about the underpinning control mechanisms. This will let us better understand the very nature of the mechanisms that cause the phenotypic variability dental researchers have so assiduously been measuring. In turn, this will permit the intellectual leap forward of integrating tooth size and shape with the molecular signaling that controls them.

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