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Correlates of Enamel Hypoplasia With Human Dental Reduction

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ABSTRACT Human dental reduction has been manifested in evolutionary and secular trends, but it is not known to what degree each of these complementary processes contributes to changes in tooth size. Enamel hypoplasia is a marker of developmental stress that is often found to be of greater frequency and severity in populations undergoing dental size reduction. In order to test the developmental association of enamel hypoplasia with tooth size, measurements of bucco-lingual and mesio-distal diameters were taken on teeth of 54 black male skulls from southern Africa. Those dentitions that exhibited incisal enamel hypoplasia were significantly reduced in size as compared to those showing no signs of developmental stress. A distinct pattern of reduction emerged: the bucco-lingual diameters of the I^1, I^2, P^3, P^4, M^1, and M^2 were significantly reduced, whereas the mesio-distal diameters of only the I^2 and M^2 decreased in size. The I^2 and M^2 showed the greatest degree of reduction despite the lack of macroscopic enamel hypoplasia on the M^2. Application of the data to the variety of dental reduction patterns evinced in modern and ancient populations indicates that factors including tooth shape, developmental timing of stress, and genetic determinants of tooth size must be considered in order to partition evolutionary and secular trends in the dentition.

The emergence of modern *Homo sapiens* was shaped by the environmental and biological forces that affect all of organic evolution, but was profoundly augmented by the unique factors of human cultural behavior. The use of tools, shelter, food preparation, and environmental manipulation altered evolution's selective forces for our species, but also had a more direct effect on human growth and development by altering the means of nurturing growth. Opportunities to study the relative influences of evolutionary adaptations and developmental environments as well as the origins of modern variations in growth patterns are provided by the time depth represented in the human fossil record.

Human teeth are particularly revealing about the interactions of development with evolution. Evolution of the dentition in the genus *Homo* has involved a continuous reduction in total tooth size of 38% over the past 1.8 million years (Tobias, 1988). Throughout the evolution of *Homo erectus* to the Neandertals, it was the post-canine dentition which was differentially reduced as compared to the incisors (Sheets and Gavan, 1977). Over the past 100,000 years, all of the teeth have diminished in size, with an apparent acceleration of reduction at the time of the introduction of agriculture in the post-Pleistocene epoch (Brace et al., 1987; Calcagno, 1986; LeBlanc and Black, 1974; Macchiarelli and Bondioli, 1984, 1986a,b; Smith, 1982; Smith et al., 1984).

Early agricultural forms of subsistence had a peculiar effect on the human populations as represented in the fossil record: the general health of the populations declined (Cohen and Armelagos, 1984). The dental evidence for this deterioration is unambiguous, with increases in the frequency and severity of enamel hypoplasia and dental caries world-wide (Formicola, 1987; Goodman et al., 1980, 1984; Gordon, 1987; Hutchinson and Larsen, 1988; Martin et al., 1984; Smith et al., 1984; y'Edynak, 1989). This change in diet and health status was consistently accompanied by a reduction in the size of the dentition (Brace et al., 1987; Calcagno, 1986; Formicola, 1987; Frayer, 1978; Kennedy, 1984; Sciulli, 1979; y'Edynak, 1989).

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From this common coincidence of dental reduction with increased dental pathology at the beginnings of agriculture, the inference can be made that dietary changes and accompanying developmental stresses had a direct influence on tooth size (Guagliardo, 1982; Machiarrelli and Bondioli, 1984, 1986a,b; Smith et al., 1984; y'Edynak, 1989). If post-Pleistocene dental reduction can indeed be tied to the developmental differences caused by change in diet, then we are dealing with a negative secular trend (Tobias, 1985) and not necessarily an evolutionary trend alone.

A proper interpretation of the fossil record necessitates an understanding of the degree to which the post-Pleistocene change in diet may have affected tooth size. Although tooth size is thought to be highly heritable (Garn et al., 1965), the environment plays an important determinant role (Townsend and Brown, 1979; Kolakowski and Bailit, 1981). Garn et al. (1979) demonstrated that maternal health status can influence deciduous and permanent tooth size of the offspring. Studies on rats have shown that significant tooth size reductions are associated with induced developmental stress (Siegel et al., 1989).

Chronic and incidental stresses are sometimes "recorded" in the human teeth by enamel hypoplasia, which is defined as "a deficiency in enamel thickness due to a disruption of ameloblastic activity" (Goodman et al., 1980: 516). Thus if the incidence of enamel hypoplasia can be shown to have distinct correlations with tooth size reduction, and the possible degree of reduction can be ascertained, then the genetic and developmental components of tooth size can be better understood. By extrapolating this information to fossils that show decreased tooth size along with increased enamel hypoplasia, we can begin to partition evolutionary and secular trend components of human dental reduction.

Enamel hypoplasia of the maxillary central incisors has been associated with a significant reduction in the bucco-lingual width of the affected tooth as well as of the dimensions of the apparently non-hypoplastic second molar, as found in a preliminary study (McKee, 1989). These results suggest that the pattern of dental reduction depends on the developmental timing of the stress incident. In this paper we present an extension of the study to include all of the maxillary teeth in order to: a) further test the association of enamel hypoplasia with decreased tooth size, b) ascertain a potential degree of reduction, and c) understand the resulting pattern of reduction within the human dentition.

MATERIALS AND METHODS

Observations of dental health and tooth size were made on a series of 54 skulls of southern African black males selected from the Raymond A. Dart Collection of Human Skeletons. This collection comprises over 3,000 human skeletons derived primarily from dissected cadavers of known ages and racial affinities (Tal and Tau, 1983). Each of over 1,000 black male skulls, collected between 1923 and 1989, was inspected for selection in this study on the basis of dental health criteria and availability of maxillary teeth.

From the extensive collection, skulls were selected on the basis of dental criteria defining two groups. The first group showed no macroscopic signs of enamel hypoplasia on the maxillary teeth or, where available, on the mandibular dentition. Despite the large sample from which these skulls were selected, the high prevalence of enamel hypoplasia among the southern African blacks represented (Lunz, 1987) limited this group to 26 individuals that were available in the collection. The second group consisted of individuals with linear enamel hypoplasia on the maxillary central incisors, but no hypoplastic lines on the second or third molars. Teeth that would have been developing at the time of the stress insult represented by the incisal hypoplasia (i.e., I^2, C, P^3, P^4, and M^1) frequently showed hypoplastic lines, but these were not required for selection. The identification of enamel hypoplasia followed FDI standards (FDI, 1982), and cases with unclear or ambiguous dental health indicators were excluded from study.

Following the methods outlined by Tobias (1967), maximum mesio-distal and bucco-lingual diameters of all maxillary teeth were measured to the nearest 0.05 mm with Helios sliding calipers. The teeth were cleaned of calculus to ensure accuracy. The number of measurements for each tooth varied due to missing teeth, or due to exclusion based on damage or significant occlusal or approximal attrition.

Ten sets of left teeth were measured twice in order to establish the reliability of measurements. An analysis of variance was then used to assess the possible significance of measurement error.

Individual measurements as well as the product of the mesio-distal and bucco-lingual diameters were tested to see if the hypoplastic group had significantly smaller teeth. A non-parametric statistical test was deemed appropriate for the limited sample size; thus a one-tailed Mann-Whitney U test was employed (Blalock, 1979). The significance level for rejecting the null hypothesis, that the teeth of the hypoplastic group were not significantly smaller, was set at $P = .05$.

RESULTS

Measurement error for all dimensions was consistently less than 0.5 mm, and the average error was within a maximum of 2.2% of the mean for any one measurement. An analysis of variance for each tooth showed that measurement error accounted for less than 2% of the sample variation, and was not a significant source of variability ($P > 0.5$).

Enamel hypoplasia was associated with significant reductions in many of the dimensions measured, as shown in Table 1. All of the teeth except the third molars were significantly smaller in the bucco-lingual dimension on both the left and the right. The lateral incisors and second molars showed significant reduction in the mesio-distal dimension as well. Figure 1 illustrates the degree of reduction for the product of the mesio-distal and bucco-lingual dimensions, which can be taken as an index of maximum occlusal tooth area.

DISCUSSION

It is clear from the results that tooth size reduction is consistently and significantly associated with the occurrence of enamel

TABLE 1. Mean mesio-distal (M-D) and bucco-lingual (B-L) diameters (in mm) for samples with incisal hypoplasia or with "normal" non-hypoplastic dentitions

			Hypoplastic			Normal			%	
Tooth	Meas.	Side	N	Mean	Std	N	Mean	Std	reduction	$P < .05$
I^1	M-D	L	24	8.90	0.46	25	8.77	0.53	1.5	
		R	23	8.98	0.41	23	8.83	0.59	1.7	
	B-L	L	24	7.45	0.53	27	7.11	0.47	4.6	*
		R	23	7.44	0.50	27	7.10	0.48	4.5	*
I^2	M-D	L	22	7.22	0.53	25	6.82	0.55	5.5	*
		R	22	7.22	0.58	25	6.79	0.54	5.9	*
	B-L	L	23	6.85	0.51	26	6.33	0.48	7.5	*
		R	22	6.80	0.60	26	6.36	0.43	6.5	*
C	M-D	L	26	7.75	0.53	27	7.76	0.43	−0.1	
		R	23	7.66	0.54	28	7.76	0.47	−1.3	
	B-L	L	26	8.85	0.66	27	8.60	0.52	2.9	*
		R	23	8.85	0.68	28	8.56	0.52	3.2	*
P^3	M-D	L	23	7.13	0.38	25	7.06	0.47	0.9	
		R	26	7.20	0.43	27	7.02	0.42	2.5	
	B-L	L	23	9.81	0.59	26	9.43	0.51	3.9	*
		R	25	9.86	0.61	27	9.50	0.55	3.7	*
P^4	M-D	L	22	6.58	0.46	25	6.59	0.32	−0.1	
		R	26	6.60	0.53	28	6.60	0.39	0.0	
	B-L	L	22	9.80	0.67	26	9.52	0.55	2.8	*
		R	26	9.71	0.79	28	9.43	0.51	2.8	*
M^1	M-D	L	25	10.71	0.57	24	10.61	0.43	0.9	
		R	24	10.67	0.54	26	10.68	0.53	−0.1	
	B-L	L	26	11.53	0.48	24	11.24	0.37	2.5	*
		R	25	11.59	0.55	26	11.32	0.38	2.3	*
M^2	M-D	L	25	10.67	0.64	27	10.33	0.57	3.2	*
		R	26	10.72	0.75	27	10.40	0.59	3.0	*
	B-L	L	25	12.19	0.64	27	11.72	0.64	3.8	*
		R	26	12.29	0.77	27	11.72	0.61	4.7	*
M^3	M-D	L	22	9.76	0.84	21	9.60	0.64	1.6	
		R	21	9.59	0.76	21	9.27	0.72	3.3	
	B-L	L	22	11.81	0.77	21	11.61	0.61	1.7	
		R	21	11.79	0.85	22	11.47	0.88	2.7	

*Those measurements for which the hypoplastic sample has significantly smaller teeth.

hypoplasia. The distinct pattern of differential reduction among the teeth, and between the two dimensions of each tooth, leads to some important insights concerning dental development and evolution.

Dental development and the pattern of reduction

Stress insults that occur at a particular time, as represented by the incisal hypoplasia, may result in a particular pattern of reduction due to developmental timing. The hypoplastic lines on the central incisors usually appear on the cervical half of the enamel. Thus the stress insult occurred after completion of the greatest mesio-distal length near the occlusal edge, and is consistent with the lack of significant size difference between the two groups. The maximum bucco-lingual diameter is much closer to the cemento-enamel junction (Fig. 2), and its formation during or after the stress insult apparently resulted in a significant reduction. This pattern corresponds to that observed by Townsend (1987) on children with trisomy 21.

The lateral incisor develops slightly later and has a morphology with the maximum mesio-distal diameter closer to the midline between the occlusal edge and the cemento-enamel junction, thus forming after the stress insult. These combined factors account for the result that the I^2 shows the greatest reduction of all the teeth (Fig. 1).

Reduction of the canine, premolars, and first molar can be explained on a similar basis. As with the central incisor, the maximum mesio-distal diameters are close to the occlusal edge (Fig. 2), forming before the stress indicated by hypoplastic lines. The bucco-lingual bulge is completed later, near the cemento-enamel junction, and thus is significantly reduced by the stress insult. The small degree of reduction in the bucco-lingual diameter of the M^1 can be attributed to variations in developmental timing (Moorrees et al., 1963; Smith and Garn, 1987); in some individuals the M^1 enamel formation

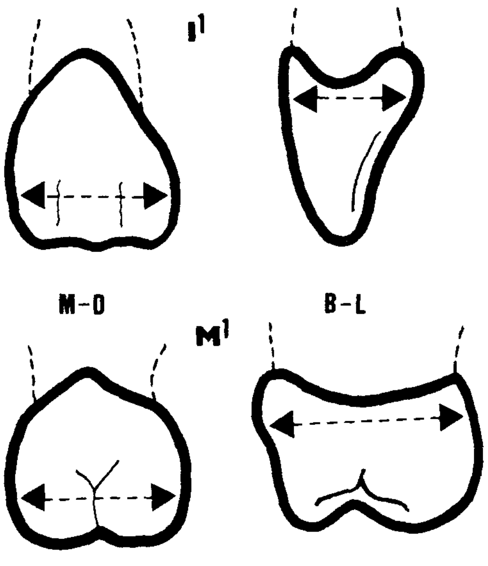

Fig. 2. Arrows indicate the region of maximum mesio-distal and bucco-lingual dimensions for the maxillary central incisors and first molars.

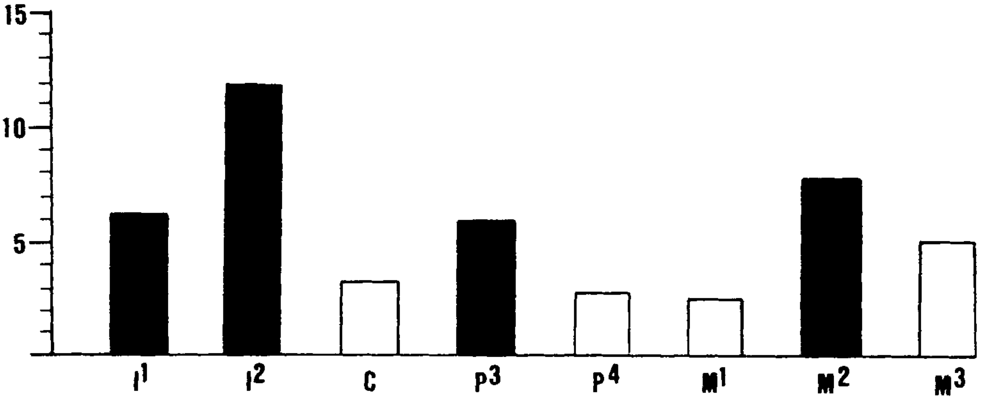

Fig. 1. Percentage of reduction in tooth size index for those with incisal hypoplasia relative to those with no enamel hypoplasia. The darkened bars indicate statistically significant reductions ($P < .05$).

would have been completed before the stress insult occurred.

Analysis of the large degree of reduction observed in the M^2 dimensions is most intriguing. The experimental design required that the M^2 show no macroscopic signs of enamel hypoplasia, yet it exceeds all but the I^2 in degree of reduction. The enamel organ of the M^2 begins formation at about 2½ to 3 years of age (DuBrul, 1980), at about the time when ameloblastic activity on the I^1 was interrupted. Thus it appears that the tooth germ can be hindered in its development by a stress insult without showing any defects other than size reduction. The later developing third molar would then be unaffected unless stress was chronic.

Utilization of our results in analyses of other populations requires careful assessment of developmental timing. It must be emphasized that the particular pattern of reduction found is limited to one type of stress, probably post-weaning stress. Chronic stress, or even post-weaning stress at a different age (due to different cultural practices of rearing children), could result in a different pattern. This cautionary note is well illustrated by the pattern of tooth size changes noted by Kieser et al. (1987), who detected a recent increase of tooth size among southern African blacks. The percentage increase calculated from their published data on skeletal populations shows greater change in the mesio-distal dimension as opposed to the data presented here, which was taken from the same skeletal collection. This could be due to improved nurturing before weaning, perhaps in the first 2 years of growth when the enamel of these teeth are beginning to develop and before the maximum mesio-distal diameter has been formed, or even during gestation when stress is known to affect the mesiodistal diameters of the permanent I^1, I^2, and M^1 (Garn et al., 1979). It also should be reiterated that Kieser et al. (1987) were studying temporal trends among a group with a mixed dental health status, whereas our observed differences were detected on the basis of apparent dental health alone.

Relevance to studies of secular trends and evolution

Meaningful applications of our data to long-term trends of dental reduction observed in the fossil record involve further complications, yet the evidence is strong that post-Pleistocene changes in tooth size may be partially due to developmental stresses. A clear example can be found in the post-Pleistocene dental reduction among Nubian archaeological populations. Calcagno (1986) has thoroughly documented metric trends among successive populations in Nubia at the introduction of agriculture in one of the few regions where an adequate sample size has been obtained. The pattern of reduction between Mesolithic and agriculturist phases is illustrated in Figure 3 alongside the pattern of reduction found in our sample. These patterns are remarkably similar, with the greatest discrepancies found in the canine, P^3, and M^1 mesio-distal diameters. Such a similarity, when considered in association with the dietary changes and increased stress (Martin et al., 1984; Smith and Shegev, 1988), strongly suggests that a substantial portion of the dental reduction may be attributable to developmental rather than evolutionary changes alone.

Additional support for an interpretation of stress-induced secular trends in post-Pleistocene populations is evidenced by the subsequent retardation and even reversals of the trends. Partial recovery of tooth size has been found in Early to Late Mesolithic transitions of Europe (Frayer, 1978) and in Neolithic to modern times in Italy (Macchiarelli and Bondioli, 1896a). Although the general trend through time is one of reduction, and a wide variety of reduction patterns exists, periodic increases in size at times of cultural innovation may indicate improved conditions and recovery from a more stressful period. It thus appears that the acceleration of dental reduction in the post-Pleistocene may have been a negative secular trend that accentuated the general evolutionary trend of tooth size decreases.

To confirm the secular nature of some post-Pleistocene dental changes we must go back and check tooth size against the health status of individual dentitions. This would require a particular diligence of observation because the developmental timing and duration of stress will affect both the distribution of hypoplastic lesions in the enamel (Goodman, 1988) as well as the pattern of reduction. Further complicating factors include the accompanying evolutionary forces as well as genetic variations in dental development and tooth shape among different populations. A thorough assessment of these complementary factors may elucidate the wide variety of dental reduction patterns evinced by the fossil record.

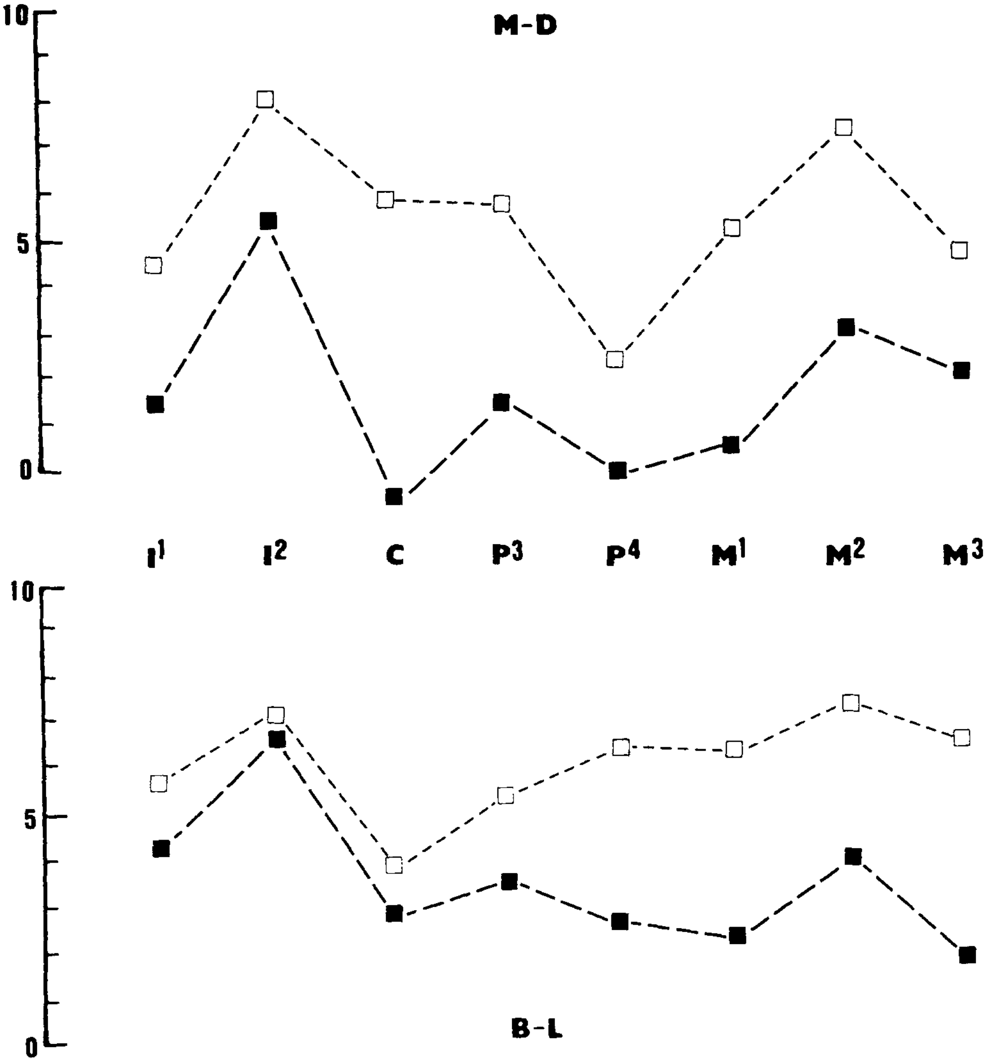

Fig. 3. Patterns of tooth size reduction in our sample from the Dart Collection (darkened boxes) as compared to the male Nubian sample published by Calcagno (1986). The scales indicate percentage of reduction for mesio-distal and bucco-lingual measurements of the maxillary dentition.

CONCLUSIONS

It can be concluded from the data presented in this paper that episodic postweaning stress may result in significant reductions in the bucco-lingual diameters of the maxillary I^1 to M^2, and that the I^2 and M^2 should show the greatest overall degree of reduction. Although tooth size decreases are clearly associated with the occurrence of enamel hypoplasia, a tooth can be reduced in size yet show no macroscopic sign of enamel defects if affected at an early developmental stage.

Characteristic patterns of enamel hypoplasia and tooth size decreases in modern and ancient populations vary according to the developmental timing of dietary and other stresses. Assiduous observations of populational trends may elucidate the nature of the nurturing environment at different times and places. When this is considered in association with long-term genetic adaptations, it may be possible to partition the effects of secular and evolutionary trends and better understand the human modes of biological adaptation.

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