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AN ANALYSIS OF TOOTH CROWN MORPHOLOGY IN AMERICAN WHITE TWINS

ABSTRACT. — The limited studies conducted to date on tooth crown morphology in twins have generally focussed on concordance rates and zygosity determination. Such efforts have not provided estimates of heritability for crown traits nor have they taken into account the possibility of greater environmental covariance in monozygotic twins. For the present study, we observed ten crown traits on 14 teeth in a series of American white monozygotic and dizygotic twins and analyzed these data through analysis of variance techniques. Specific assumptions regarding the variance among and within twin pairs were tested to sort out those traits which may show greater environmental covariance in MZ twins. The trait's distributions were also examined in a control series. Only seven of the 14 variables met all assumptions of the model and, for these traits, genetic variance estimates were highly significant. Heritability estimates for this set of traits were of similar magnitude, indicating that between one-third and one half of the phenotypic variance in expression can be attributed to genetic causes. While these traits do show a significant component of genetic variation, surficial crown morphology has an element of plasticity which may account, in part, for certain long-term hominid dental trends.

KEY WORDS: Dental morphology — Twins heredity — Genetic variability — Hominid dental trends.

In human population biology, tooth crown morphology has been utilized to make microevolutionary inferences and assess relative population relationships, but our knowledge of the genetic mechanisms underlying the development of such crown traits remains incomplete. Dental researchers have studied twins, families and populations in an attempt to determine modes of inheritance and degree of genetic determination, but debates continue over these issues. Some authors have suggested that particular traits may be inherited in a simple Mendelian manner (Kraus 1951, Tsuji, 1958, Turner 1967, Portin and Alvesalo 1974). Others contend that the inheritance patterns of dental morphologic traits are complex, or polygenic (Goose and Lee 1971, Lee and Goose 1972, Sofaer et al. 1972, Scott 1973, Alvesalo et al. 1975, Harris 1977) with a significant environmental component underlying their development.

Twin studies of tooth crown traits in human samples have been limited in scope compared to all other types of studies dealing with dental morphology. Because of the discrete nature of such crown traits, they have not been subjected to the complex methods of analysis devised for work in quantitative genetics. Approaches have centered basically on the analysis of concordance frequencies in *MZ* and *DZ* twins (Ludwig 1957, Biggerstaff 1970, 1973, Berry 1978) and the use of crown morphology in zygosity determination (Lundstrom 1963, Wood and Green 1969). Neither method actually results in an estimate of genetic variance but rather provides only a general type of information on whether or not such traits have some degree of genetic determination. A more thorough analysis of crown morphology in twins was conducted by Mizoguchi (1977) who utilized tetrachoric correlation coefficients to estimate heritability for 14 morphologic crown traits. Although family studies have not yielded clear results on the modes of inheritance of tooth crown morphology in most instances familial correlations indicate some genetic component. Twin studies can provide further insight into the genetic component of variance and contribute to our overall understanding of the developmental basis of tooth crown morphology.

MATERIAL AND METHODS

The sample of twins examined in this study represents part of the Indiana University twin panel. One aspect of major research efforts on this panel has been zygosity determination through genetic markers and dermatoglyphic variables. Stone casts were obtained from 79 monozygotic twin pairs and 59 sets of dizygotic twins. Observations were made on all these pairs, but sample sizes vary from trait to trait as some individual teeth could not be scored due to fillings, crowns, casting error, and unerupted or missing teeth. Most of the individuals in this series were between the ages of six and 16 at the time impressions were made so attrition was not a major impediment to observation. The total series was about equally divided between male and female twins. In addition to making observations on *MZ* and *DZ* twins, individuals from a general American white sample were matched randomly to create a control series of 50 unrelated pairs.

The trait set observed on the twin and control series was comprised of 10 crown traits observed on 14 teeth. Traits considered were: Shoveling (UI1, UI2), *tuberculum dentale* (UI1, UI2), the canine tubercle (UC), the hypocone (UM1, UM2), Carabelli's trait (UM1), the metaconule (UM1), multiple lingual cusps (LP1, LP2), the hypoconulid (LM1), cusp 6 (LM1), and cusp 7 (LM1). All traits were scored through the use of ranked scales developed by A. A. Dahlberg, C. G. Turner II, and G. R. Scott. Classifications included absence and four to seven degrees of trait presence, with size being the primary classificatory criterion (Dahlberg 1956, 1963, Turner 1970, Scott 1973, Scott and Dahlberg 1982). Going beyond the standardized scales, an attempt was made to score a threshold level of expression which marks a very fine observational line between trait absence and a low level expression of presence. It should be noted that in the first table, grade 1 represents trait absence, grade 2 represents the threshold level of expression, and grades 3 and above represent slight to increasingly pronounced degrees of phenotypic trait expression. Observations were made on both right and left antimeres for all traits, but for purposes of analysis, the individual count method was utilized (Turner and Scott 1977, Scott 1980).

Methods of analysis involved basically two strategies. A conservative strategy followed traditional efforts to estimate and compare concordance rates between *MZ* and *DZ* twins and the control series of unrelated pairs. In the analysis of concordance rates in *MZ* and *DZ* twins, the following procedure was adopted. First, concordance rates were calculated in the standard manner which involves dividing the number of concordant pairs by the total number of pairs (Berry 1978). For this analysis, phenotype expression was broken down by absence (0) and presence (+) so that twin pairs exhibiting (0—0) or (+—+) were classified as concordant with cases of (0—+) or (+—0) classified as discordant. Concordance rates for commonly occurring traits, however, provide little information by themselves because a high frequency of concordance can be achieved by chance. For example, for a trait in a frequency of 50 % in a population, chance alone would result in the following proportions in randomly matched pairs: (0—0) 25 %; (+—+) 25 %; (0—+ or +—0) 50 %. The concordance rate in this case is 50 %. Thus, to estimate the significance of a given concordance rate, expected values of concordance and discordance were estimated using the frequency of trait presence in a sample (performed separately for *MZ* twins, *DZ* twins, and the control series) as p and the frequency of absence as q in the binomial expansion $(p + q)^2$. The expected values of p^2 (+—+), $2pq$ (0—+ and +—0) and q^2 (0—0) were then compared to the observed cases of concordance and discordance, with chi-square used to test whether or not the observed concordance rate differed significantly from the expected rate. One degree of freedom is available for this test.

While concordance analysis is the standard method for dealing with presence—absence variables in twins (Smith 1970, 1974), information on the variation in the expression of presence is lost when considering tooth crown traits. Moreover, it is difficult to interpret concordance rates in terms of genetic variance as they mask within and among twin variation. In fact, intraclass correlation coefficients, routinely used to estimate heritability for quantitative traits, also conceal phenotypic variation which is evident both among and within twin pairs in the two twin types. In response to certain problems inherent in traditional methods of twin analysis, Kempthorne and Osborne (1961), Haseman and Elston (1970), Christian et al. (1974), Christian and Norton (1977), Kang et al. (1978), and Christian (1979) have developed new twin methodologies centering on analysis of variance techniques. Focus is on the estimates of among mean squares (AMS_{MZ} and AMS_{DZ}) and within mean squares (WMS_{MZ} and WMS_{DZ}) and the relationships among these variance estimates.

In contrast to earlier methods which involved deriving heritability estimates from intraclass correlation coefficients without regard for the pattern of variation within and among twin pairs, the analysis of variance methodology involves testing explicit assumptions about these patterns. If the assumptions of the model are not met, then heritability and genetic variance estimates are biased. The assumptions are as follows:

(1) There should be no significant difference in the means between *MZ* and *DZ* twins. If such a difference does exist, it could indicate inherent differences in the twinning process. To test this assumption, the modified *t* test of Christian and Norton (1977) was utilized. This method takes into account the nested hierarchical nature of twin pairs and should be used rather than the standard independent samples *t* test.

(2) There should be no significant variance inequality between the two twin types. Considering the four mean squares obtained from a twin analysis (AMS_{MZ}, WMS_{MZ}, AMS_{DZ}, WMS_{DZ}) the ratio for

TABLE 1. *Tooth crown trait class frequency distributions for American white twins and control series.*

Trait	Tooth	Sample	*n*	Expression (grade) in % 1	2	3	4	5	6	7	8	9	X^{2+}
		MZ twins	150	14.0	36.0	37.3	10.7	2.0	0.0	0.0	0.0	0.0	
Shoveling	I¹	*DZ* twins	110	15.5	23.6	43.6	10.9	6.4	0.0	0.0	0.0	0.0	5.36
		Control ser.	100	27.0	27.0	34.0	11.0	0.0	0.0	1.0	0.0	0.0	
		MZ twins	126	19.8	38.9	34.1	6.4	0.8	0.0	0.0	0.0	0.0	
Shoveling	I²	*DZ* twins	90	16.7	30.0	38.9	12.2	2.2	0.0	0.0	0.0	0.0	10.62
		Control ser.	100	39.0	25.0	22.0	13.0	1.0	0.0	0.0	0.0	0.0	*
Tuberculum		*MZ* twins	136	27.2	12.5	20.6	36.8	2.9	—	—	—	—	
dentale	I¹	*DZ* twins	98	20.4	12.2	25.5	35.7	6.1	—	—	—	—	15.73
		Control ser.	100	36.0	23.0	13.0	27.0	1.0	—	—	—	—	**
Tuberculum		*MZ* twins	106	43.4	21.7	13.2	10.4	5.7	1.9	0.9	2.8		
dentale	I²	*DZ* twins	80	31.3	21.3	13.8	11.3	5.0	6.3	6.3	5.0	—	6.18
		Control ser.	100	32.0	18.0	18.0	5.0	4.0	13.0	8.0	2.0	—	
Canine		*MZ* twins	78	42.3	10.3	14.1	14.1	12.8	3.9	2.6	0.0	—	
tubercle	*C*	*DZ* twins	52	26.9	30.8	15.4	9.6	11.5	3.9	1.9	0.0	—	7.53
		Control ser.	100	28.0	11.0	20.0	23.0	9.0	7.0	2.0	0.0	—	
Carabelli's		*MZ* twins	150	13.3	14.0	23.3	8.0	16.0	12.0	8.0	3.3	2.0	
trait	M¹	*DZ* twins	112	17.0	13.4	16.1	8.9	15.2	15.2	4.5	5.4	4.5	1.83
		Control ser.	100	14.0	12.0	21.0	6.0	17.0	12.0	5.0	5.0	8.0	
		MZ twins	124	81.5	8.9	3.2	4.0	2.4	0.0	0.0	—	—	
Metaconule	M¹	*DZ* twins	98	72.5	15.3	2.0	9.2	1.0	0.0	0.0	—	—	2.70
		Control ser.	100	67.0	16.0	3.0	13.0	1.0	0.0	0.0			
		MZ twins	150	0.0	0.0	0.7	2.0	16.7	63.3	17.3	—	—	
Hypocone	M¹	*DZ* twins	110	0.0	0.0	0.0	0.9	15.5	69.1	14.6	—	—	1.76
		Control ser.	100	0.0	0.0	0.0	0.0	16.0	64.0	20.0	—	—	
		MZ twins	82	12.2	7.3	14.6	17.1	34.2	12.2	2.4	—	—	
Hypocone	M²	*DZ* twins	44	13.6	11.4	13.6	13.6	38.6	9.1	0.0	—	—	6.77
		Control ser.	100	2.0	10.0	12.0	13.0	35.0	26.0	2.0	—	—	
Multiple		*MZ* twins	114	61.4	13.2	2.6	9.7	4.4	1.8	1.8	5.3	—	
lingual	P₁	*DZ* twins	70	61.4	15.7	1.4	7.1	7.1	1.4	2.9	2.9	—	1.64
cusps		Control ser.	100	68.0	2.0	3.0	11.0	6.0	3.0	3.0	4.0	—	
Multiple		*MZ* twins	88	21.6	6.8	11.4	29.6	15.0	15.9	10.2	4.6	—	—
lingual	P₂	*DZ* twins	60	21.7	13.3	11.7	26.7	11.7	6.7	3.3	5.0	—	4.42
cusps		Control ser.	100	36.0	2.0	15.0	13.0	20.0	12.0	2.0	0.0	—	
		MZ twins	132	13.6	0.8	2.3	13.6	31.8	28.0	9.9	—	—	
Hypoconulid	M₁	*DZ* twins	106	12.3	4.7	0.0	12.3	21.7	37.7	11.3	—	—	2.02
		Control ser.	100	13.0	4.0	2.0	8.0	25.0	37.0	11.0	—	—	
		MZ twins	122	78.7	9.0	4.9	6.6	0.8	0.0	0.0	—	—	
Cusp 6	M₁	*DZ* twins	102	81.4	13.7	1.0	1.0	2.9	0.0	0.0	—	—	4.68
		Control ser.	100	78.0	11.0	3.0	6.0	2.0	0.0	0.0	—	—	
		MZ twins	148	56.1	28.4	8.8	3.4	2.0	1.4	0.0	—	—	
Cusp 7	M₁	*DZ* twins	114	49.1	29.0	9.7	3.5	5.3	1.8	1.8	—	—	3.31
		Control ser.	100	53.0	24.0	18.0	2.0	1.0	2.0	0.0	—	—	

+ *With the exception of the metaconule which has 2 d.f., all other chi-square values based on 4 d.f.*
* *Significant at 0.05 level*
** *Significant at 0.01 level*

total mean squares between the twin types should not significantly differ from 1.0. The appropriate F test, given by Haseman and Elston (1970) and Christian (1979), is arrived at by taking the ratio of the total mean squares of MZ and DZ twins with the larger of the two values serving as the numerator of a 2-tailed F test and the probability double that shown in the usual F tables. Degrees of freedom available for this F test were approximated following the method of Christian et al. (1974). Variance equality between twin types is important because significantly lower total variance for MZ twins would suggest greater environmental covariance for this twin type.

(3) The ratio of AMS_{DZ} to WMS_{DZ} should yield an F value that is significantly larger than 1.0. As Christian et al. (1975) noted, if this ratio does not differ appreciably from 1.0, "it seems unlikely that any substantial proportion of total variance is genetic."

To determine whether or not the general analysis of variance model holds for the type of dental morphologic data under analysis, the control series of 50 unrelated pairs was subjected to an analysis parallel to that conducted for the twin samples. For this series, two assumptions were tested. First, if the analysis for a given trait is to be valid, there should be equal among and within mean squares for the control series. To test this, an F value was computed from the ratio AMS_{CS}/WMS_{CS}. If this ratio differed significantly from 1.0 in a 2-tailed F test, potential bias exists in the twin analysis due to the trait's frequency and/or distribution in the population. The second assumption is that there should be significantly less variance within DZ pairs than within randomly matched pairs. To test this, an F value was computed from the ratio WMS_{CS}/WMS_{DZ}.

When all of the above assumptions are met, it is possible to determine whether or not there is significant genetic variance for a given trait. Significance in this case is determined by an F value derived from the ratio WMS_{DZ}/WMS_{MZ} (Christian et al. 1974). If this F value differed significantly from 1.0, genetic variance was estimated by subtracting the WMS of MZ twins from the WMS of DZ twins. Heritability was estimated by the following formula (Corruccini and Potter 1980):

$$h^2 = \frac{WMS_{DZ} - WMS_{MZ}}{(TMS_{MZ} + TMS_{DZ})/4}$$

Typically, these heritability estimates are more conservative than those based on intraclass correlation coefficients. One can, however, be more confident of the results when all variance components are considered and all assumptions are met.

RESULTS

The class frequency distributions for the entire trait set are shown in *Table 1* for MZ twins, DZ twins, and the control series. In the table, n represents the total number of individuals in each series and not the number of pairs. The size of the scale for each trait can be determined from the position of dashed lines. For example, Carabelli's trait was classified as absent (1), threshold expression (2), or in one of seven grades (3—9) indicating varying magnitudes of expression. In contrast, cusp 6 was classified using two fewer grades so dashed lines are evident under 8 and 9. The chi-square values used to test the differences in these distributions generally involved 3 × 3 contingency tables through combining grades 1 and 2, treating 3 separately, and combining 4-n grades.

In general, crown traits varied between 20 and 80 percent in these American white series. MZ and DZ twins show very similar class frequency distributions, although DZ twins do tend to have higher frequencies of dental tubercles on the upper incisors and canine. The only significant differences among the three series as determined by chi-square values were for shoveling of the upper lateral incisor and *tuberculum dentale* of the upper central incisor. Most of the divergence in these cases was due to lower frequencies in the control series. For the most part, the three samples exhibit similar class frequency distributions.

Shoveling appears to be exceptionally frequent in these samples compared to other characterizations of American white and European dentitions. It should be noted, however, that combining grades 1 (absence) and 2 (threshold expression) results in a total trait frequency of about 50 %. The threshold grade of this trait is manifested as very subtle marginal ridges and has not been considered as part of the shoveling complex by most workers.

Table 2 illustrates the concordance rates in MZ twins, DZ twins, and the control series. Rates are not given for the hypocone of the upper first molar as the frequency of this trait is invariant (100 %) in these series.

For MZ twins, concordance rates vary generally between 70 and 90 %. With the exception of multiple lingual cusps of the lower second premolar, all MZ concordance rates are significant at the .01 level. In all cases but one, DZ concordance rates are lower than the respective rates shown by MZ twins although the difference between twin types is often slight. In contrast to the relatively small absolute differences in concordance rates, DZ twins consistently show much lower chi-square values and, in seven instances, these values are nonsignificant. Except for the hypocone of the upper second molar which has a high concordance rate (96 %) due entirely to its high trait frequency (98 %), the concordance rates for unrelated pairs are notably smaller than the rates for MZ and DZ twins. These rates, which vary between 42 and 74 %, are all nonsignificant except for the metaconule. Even in this case, the significance is due to an excess of discordant pairs rather than concordant pairs as was always the case for the two twin types. The small chi-square values for the control series suggest that randomly matched pairs closely approximate the categories of concordance and discordance expected by chance alone.

TABLE 2. *Concordance rates in MZ twins, DZ twins, and unrelated pairs.*

Trait	Tooth	*MZ* twins		*DZ* twins		Control Series (unrelated pairs)	
		% Conc.	X^2	% Conc.	X^2	% Conc.	X^2
Shoveling	I^1	88.0	18.44**	87.0	9.68**	58.0	0.19
Shoveling	I^2	85.7	18.49**	84.4	8.28**	46.0	0.90
Tuberculum dentale	I^1	80.9	20.98**	83.7	12.44**	52.0	0.10
Tuberculum dentale	I^2	81.1	20.01**	72.5	5.21	60.0	0.34
Canine tubercle	C	92.3	25.70**	69.2	1.20	52.0	1.99
Carabelli's trait	M^1	84.4	6.88**	76.8	1.77	72.0	1.36
Metaconule	M^1	88.7	24.71**	69.4	2.66	42.0	4.81*+
Hypocone	M^1	—	—	—	—	—	—
Hypocone	M^2	90.5	12.40**	72.7	0.54	96.0	0.02
Multiple lingual cusps	P_1	71.9	9.45**	62.9	1.65	60.0	0.34
Multiple lingual cusps	P_2	75.0	2.89	70.0	0.42	44.0	2.35
Hypoconulid	M_1	94.1	51.44**	83.0	2.34	74.0	1.12
Cusp 6	M_1	90.5	39.40**	82.4	8.65**	64.0	0.12
Cusp 7	M_1	68.9	10.00**	68.4	7.75**	50.0	0.00

* *Significant at 0.05 level*
** *Significant at 0.01 level*
\+ *Significant due to excess of discordant pairs*

TABLE 3. *Mean trait expression and among and within mean squares (AMS and WMS) for MZ twins, DZ twins, and control series.*

Trait	Tooth	*MZ* twins				*DZ* twins				Control series			
		n_{MZ}	Mean	*AMS*	*WMS*	n_{DZ}	Mean	*AMS*	*WMS*	n_{CS}	Mean	*AMS*	*WMS*
Shoveling	I^1	75	2.5	1.56	0.19	55	2.7	1.73	0.55	50	2.4	1.33	1.07
Shoveling	I^2	63	2.3	1.37	0.20	45	2.5	1.42	0.53	50	2.1	1.46	0.98
Tuberculum dentale	I^1	68	2.8	2.86	0.46	49	3.0	2.13	0.99	50	2.3	1.58	1.54
Tuberculum dentale	I^2*	53	2.4	5.23	0.69	40	3.1	6.34	2.99	50	3.1	4.77	4.54
Canine tubercle	C	39	2.7	5.80	0.54	26	2.7	3.68	1.44	50	3.0	2.78	2.81
Carabelli's trait	M^1	75	4.0	8.18	0.69	56	4.1	8.29	2.55	50	4.3	5.37	6.27
Metaconule	M^1	62	1.4	1.57	0.11	49	1.5	0.97	0.98	50	1.7	0.99	1.41
Hypocone	M^1	75	6.0	0.83	0.13	55	6.0	0.37	0.30	50	6.0	0.35	0.38
Hypocone	M^2	41	4.0	4.60	0.68	22	3.8	2.37	2.80	50	4.6	2.19	1.79
Multiple lingual cusps	P_1	57	2.2	6.05	2.04	35	2.1	3.98	3.16	50	2.3	5.13	3.56
Multiple lingual cusps	P_2	44	3.6	5.18	1.24	30	3.5	4.40	3.45	50	3.2	3.60	3.96
Hypoconulid	M_1	61	4.7	5.81	0.42	53	4.9	5.01	1.72	50	4.8	3.63	3.21
Cusp 6	M_1	61	1.4	1.54	0.14	51	1.3	1.02	0.28	50	1.4	0.82	1.01
Cusp 7	M_1	74	1.7	1.69	0.53	57	2.0	2.67	1.22	50	1.8	0.98	1.36

* Tuberculum dentale, I^2 is only trait that shows a significant difference in means between *MZ* and *DZ* twins ($t' = 1.92$, $p = 0.061$)

TABLE 4. *F tests for assumptions of the analysis-of-variance twin model.*

Trait	Tooth	$\sigma_{MZ^2} = \sigma_{DZ^2}$		AMS_{DZ}/WMS_{DZ}		AMS_{CS}/WMS_{CS}		WMS_{CS}/WMS_{DZ}	
		F	P	F	P	F	P	F	P
Shoveling	I^1	1.30	NS	3.17	<.01	1.25	NS	1.96	<.01
Shoveling	I^2	1.24	NS	2.66	<.01	1.49	NS	1.84	<.01
Tuberculum dentale	I^1	1.06	NS	2.15	<.01	1.03	NS	1.56	.01—.05
Tuberculum dentale	I^2	1.58	.05—.10	2.12	<.01	1.05	NS	1.52	.01—.05
Canine tubercle	C	1.24	NS	2.55	<.01	0.99	NS	1.95	<.01
Carabelli's trait	M^1	1.22	NS	3.25	<.01	0.86	NS	2.46	<.01
Metaconule	M^1	1.16	NS	0.99	NS	0.70	NS	1.44	.01—.05
Hypocone	M^1	1.44	.05—.10	1.23	NS	0.91	NS	1.27	NS
Hypocone	M^2	1.02	NS	0.85	NS	1.22	NS	0.64	NS
Multiple lingual cusps	P_1	1.13	NS	1.26	NS	1.44	NS	1.13	NS
Multiple lingual cusps	P_2	1.22	NS	1.27	NS	0.91	NS	1.15	NS
Hypoconulid	M_1	1.08	NS	2.92	<.01	1.13	NS	1.87	<.01
Cusp 6	M_1	1.29	NS	3.60	<.01	0.81	NS	3.56	<.01
Cusp 7	M_1	1.75	<.01	2.19	<.01	0.72	NS	1.12	NS

Table 3 presents the basic summary statistics used in the analysis of variance twin model. This includes number of pairs, mean trait expression, and among *(AMS)* and within *(WMS)* mean squares for *MZ* and *DZ* twins and unrelated pairs. Although these figures serve as the basis for all subsequent analyses, a few general points should be noted.

For *MZ* twins, the *WMS* is typically small in magnitude indicating that *MZ* twins are very similar phenotypically. The *AMS* for *MZ* twins is consistently much higher than the *WMS*. For *DZ* twins, there is always more variance within twin pairs when compared on a trait by trait basis with the *WMS* of *MZ* twins. For *DZ* twins, 12 of 14 traits show less variance within than among twin pairs. In sharp contrast to either twin type, the control series shows among and within mean squares of similar magnitudes. The highest mean square is evenly divided between *AMS* and *WMS* for the 14 traits.

Regarding mean trait expression in *MZ* and *DZ* twins, only *tuberculum dentale* of the upper lateral incisor shows a significant difference between twin types. As recommended by Christian (1979), the level significance for this test is .10 rather than .05. For all others traits, *MZ* and *DZ* mean trait expression is similar (differences range from 0.0 to 0.3).

In *Table 4*, *F* values and associated probabilities are shown for the tests of assumptions of the analysis of variance twin model. For a trait to meet these assumptions, it should have *F* values that do not differ significantly from 1.0 for total variance equality (column 1) or for the ratio of among to within mean squares for the control series (column 3). In contrast, the ratios of AMS_{DZ}/WMS_{DZ} (column 2) and WMS_{CS}/WMS_{DZ} (column 4), should yield *F* values that depart significantly from 1.0.

Crown traits which meet all the assumptions of the twin model are: shoveling of the upper central and lateral incisors, *tuberculum dentale* of the upper central incisor, the canine tubercle of the upper canine, Carabelli's trait of the upper first molar, and the hypoconulid and cusp 6 of the lower first molar. *Tuberculum dentale* of the upper lateral incisor violates the assumption of variance equality as *DZ* twins show significantly greater total variance. In addition, this was the only trait that showed a significant difference in mean trait expression between *MZ* and *DZ* twins. The metaconule of the upper first molar, while meeting three assumptions of the model, fails to show a significant difference in the ratio of among to within means squares for *DZ* twins. The hypocone of both upper molars and multiple lingual cusps of both lower premolars fail to meet the assumptions of greater among than within variance for *DZ* twins and greater within mean squares for the control series than for *DZ* twins. The hypocone of the upper first molar also shows significant variance inequality. Cusp 7 of the lower first molar shows significant variance inequality between twin types and also fails to show a significantly larger within mean square for the control series than for *DZ* twins.

Genetic variance and heritability estimates were calculated for only those traits that met all assumptions of the analysis of variance twin model. These values are shown in *Table 5*. For the seven traits that meet the assumptions of the model, all show a highly significant genetic component of variance. Genetic variance, estimated by the remainder of variance when WMS_{MZ} is subtracted from WMS_{DZ}, varies between 0.14 for cusp 6 to 1.86 for Carabelli's trait. Of course, these genetic variance estimates must be considered relative to the total variance shown within and among twin types. To standardize these estimates for intertrait comparison, genetic variance is divided by the average of the four mean squares For *MZ* and *DZ* twins. This standardized value is one method to esimate heritability using all relevant variance components (Corruccini and Potter 1980). The seven traits that met all assumptions of the twin model show heritability estimates that are of the same general magnitude. Only cusp 6 shows a value (.19) that falls outside the range of .32 to .40.

DISCUSSION

Concordance analysis of presence-absence variables in twins, while perhaps a more conservative approach than analysis of variance, appears to have

TABLE 5. *Tests of significance for genetic variance and genetic variance and heritability estimates for those trais meeting assumptions of analysis-of-variance twin model.*

Trait	Tooth	1. WMS_{DZ}/WMS_{MZ} F	P	2. $WMS_{DZ}—WMS_{MZ}$	3. Heritability $\frac{WMS_{DZ} — WMS_{MZ}}{(TMS_{DZ} + TMS_{MZ})/4}$
Shoveling	I^1	2.92	<.01	.36	.36
Shoveling	I^2	2.69	<.01	.33	.38
Tuberculum dentale	I^1	2.14	<.01	.53	.33
Canine tubercle	C	2.68	<.01	.90	.32
Carabelli's trait	M^1	3.69	<.01	1.86	.38
Hypoconulid	M_1	4.05	<.01	1.30	.40
Cusp 6	M_1	2.04	<.01	.14	.19

1. *F* test for significance of genetic variance
2. Estimate of genetic variance
3. Estimate of heritability

major limitations when applied to morphologic dental variables. Berry (1978) analyzed European twin series for a large number of dental traits and found basically the same pattern noted here; concordance rates are higher in *MZ* twins than *DZ* twins and are higher in *DZ* twins than in a series of unrelated pairs. Her analysis, however, included no tests of significance so it is difficult to assess these results except in general terms. In his study of American white twins, Biggerstaff (1970, 1973) found that for lower molar cusp number and groove pattern and for Carabelli's trait, *MZ* and *DZ* twins did not differ significantly in concordance rates. On this basis, he concluded these traits did not have high levels of heritability. Biggerstaff's analysis however, was based on 2×2 contingency tables (*MZ* twins, *DZ* twins; concordance, discordance) and this method masks the two different types of concordance (0—0 and +—+). When a similar analysis was performed for the twin series in this study, only two of 14 traits differed significantly between twin types. This result stands in contrast to the results of the goodness of fit tests. For example, concordance rates do not differ significantly between *MZ* and *DZ* twins for the hypoconulid in a 2×2 contingency analysis, but the concordance rate is highly significant for *MZ* twins and nonsignificant for *DZ* twins when assessed by goodness of fit. The methods of Smith (1970, 1974) show that concordance rates are related to total population frequencies and both must be considered, particularly when heritability is estimated. For example, a concordance rate of only 30 % in *MZ* twins indicates high heritability in cases where trait frequency in low (e.g. 1 %). As population frequencies increase, it becomes increasingly difficult to estimate heritability from concordance analysis. Considering the high population frequencies of morphologic crown traits and the insensitivity of the concordance analysis approach to among and within twin variation, it does not appear that this is the most suitable method available.

The results from analysis of variance are much more informative than those obtained from the concordance approach. The use of this method for tooth crown traits can be justified, in part, by the analysis of unrelated pairs. If a trait's population incidence and/or class frequency distribution biased results in a patterned way, this would be reflected in the mean squares among and within pairs. None of the AMS_{CS}/WMS_{CS} ratios differed significantly from 1.0, and, in fact, when all 14 F values were averaged, the mean F was 1.02 (the expected mean assuming random effect is 1.0). These results are in clear contrast to the pattern of among and within mean squares for the two twin types.

In contrast to most, if not all, prior twin studies of tooth crown traits, we have tested a specific set of assumptions which relate to the predicted magnitudes of the variance components for *MZ* and *DZ* twins. Other studies present results for full trait sets without distinguishing among traits which may be biased by greater environmental covariance in *MZ* twins. The question remains why some traits violate assumptions of the model while others do not. One could conclude that different dental traits show varying degrees of genetic determination and this may indeed be the case for some traits. There are, however, alternative explanations. For example, two traits which violated more than one assumption of the model were the hypocone (both upper molars) and multiple lingual cusps (both lower premolars). For these traits, the classification used to score trait expression may be in part responsible. The hypocone is difficult to rank consistently because, in the classification system used, the size of the hypocone is judged relative to the size of the other major cusps of the upper molar crown. Such relative judgements are difficult to make consistently. The scoring standard developed for multiple lingual cusps of the lower premolars (Scott 1973) represents an attempt to characterize phenotypic variation by the presence and relative size of an accessory distolingual cusp. While this system was thought to be an improvement over the Kraus and Furr (1953) dichotomous classification which considered any accessory cusp, regardless of placement or size, as characteristic of multiple lingual cusps, the more complex classification used here may not adequately reflect the developmental parameters of this trait. *Tuberculum dentale* of the upper lateral incisor violated the assumptions of equal twin means and total variances. This variable, at the same time, is difficult to classify and also shows a high degree of asymmetry. The problem with this variant may relate to both the classificatory scheme and a significant element of environmentally induced variance. For both the metaconule and cusp 7, observing low levels of expression is difficult and as these traits are rarely pronounced in size, the problem may be due to level of observation. Basically, the traits that violate one or more assumptions of the twin model may (1) actually reflect varying degrees of genetic determination among tooth crown traits, (2) indicate that the classification systems established for scoring trait expression do not correspond to the underlying biologic basis of the trait, and/or (3) suggest difficulties in making consistent observations, especially for those traits manifested in very subtle degrees. It is possible that a twin analysis such as this is a good method to determine the validity of specific trait classification systems and indicate areas where there is a problem with consistent observation.

For the set of traits that did meet all assumptions of the analysis of variance twin model, the heritability estimates were comparable in magnitude. Somewhat less than half of the variance in expression among and within twins could be attributed to genotypic variance. Problems of classification and observation could have contributed to lowering these estimates, but their internal consistency, considered in concert with other findings, suggest they are reliable estimates of population heritability. Although heritability estimates are specific to the population sampled, the results noted here are in agreement with those of Mizoguchi (1977) who analyzed a large Japanese twin sample. Excluding only two of 18 heritability estimates derived from this sample (one exceeded unity while another was negative), the mean h^2 value for his remaining 16 crown traits was .44 (range: .12—.75).

From twin studies, one can only estimate heritability in "the broad sense" which means that total genotypic variance is assessed in terms of its relationship to the environment (Kang et al. 1978). To derive "narrow sense" heritability, which is the ratio of additive genetic variance to total phenotypic variance, it is necessary to use intergenerational correlations, as in family studies. Theoretically, heritability can range from 0 to 1.0. An h^2 of 0 indicates that all phenotypic variance can be attributed to environmental causes. At the other extreme, an h^2 of 1.0 would suggest that phenotypic variance was due entirely to genotypic variance. Most attributes of the dentition, including tooth crown size and morphology, have heritabilities that fall between 0 and 1.0 (cf. Mizoguchi 1977, Townsend and Brown 1978). Although the dentition is often viewed as a highly canalized developmental system, twin and family studies show consistently that variation in tooth size and morphology has an environmental component. Significant secular trends in families have been shown for crown size (Hanna et al. 1963, Potter et al 1968, Garn et al. 1968, Bowden and Goose 1969), with improved nutritional status generally implicated as the most important causative factor (Potter 1976). Studies of antimeric asymmetry provide another line of evidence implicating environmental factors in dental development. Twin studies have shown that fluctuating asymmetry in the dentition has no appreciable genetic component (Staley and Green 1974, Potter and Nance 1976). Such asymmetry is often thought to reflect subtle differences in the timing of development, both prenatal and postnatal, between the sides of the dentition. Such differences in timing between left and right sides which generate asymmetry might be analogous to slight developmental differences between *MZ* twins which result in discordance. The mean intraclass correlation for *MZ* twins for the 14 variables in this study was .742. In an analysis of asymmetry for eight molar crown traits (observed on 16 teeth) in a large Pima Indian sample, the average correlation (Kendall's *tau*) between antimeres was .788 for males and .761 for females (Noss et al. 1983). Ideally, one should study the same trait set in a single ethnic group to compare degrees of asymmetry and *MZ* discordance, but the similarity between these correlations is noteworthy.

While the dentition is not often considered in discussions of human plasticity, it is becoming increasingly apparent that we cannot simply view the dentition as a system solely under the control of genetic factors. General crown form is clearly under strict developmental control as mediated by genetic factors, but the subtle differences in size and morphology that are of anthropological interest can be influenced to a degree by environmental variables (e.g. maternal diet, various types of stress, postnatal dietary factors, including trace elements, etc.). Major differences exhibited among groups in, say, shovel-shaped incisors or Carabelli's trait reflect underlying genetic differences. From a long-term evolutionary standpoint, however, groups are not totally inflexible in terms of dental adaptations to new or changing environmental regimes. In fact, Waddington's (1957) concept of genetic assimilation may be applicable to the dentition as well as to other more plastic systems. That is, if a group migrates to a region and this move involves dietary or other changes, the dental system has some latitude for minor environmentally induced phenotypic adjustments which, if selected for, could eventually involve genetic changes in the population. This would occur if there was some selective advantage to those individuals with genotypes which allowed for such adjustments. Considering the general stability and conservatism of the dentition, the suggestion of plasticity in the size and surficial morphology of teeth might be of greatest utility in enhancing our understanding of hominid dental trends (e.g. decreasing crown size, increasing agenesis, and morphological simplification in European and Asiatic Indian dentitions).

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