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Genetic Variability in Tooth Crown Characters: Analysis by the Tetrachoric Correlation Method

By

Yuji MIZOGUCHI

Department of Anthropology, National Science Museum, Tokyo

Most morphological characters in tooth crowns, e.g., the shovelling of the incisors and the CARABELLI's tubercles of the upper molars, show continuous variation in their phenotypes. Some students have described these continuous varations through several expressivities (HRDLIČKA, 1920; DIETZ, 1944; DAHLBERG, 1949; HANIHARA, 1961). Nevertheless, many authors have qualitatively, not quantitatively, analyzed these in order to clarify their genetic backgrounds (SIEMENS, 1928; KORKHAUS, 1930; SAHEKI, 1958; AOYAGI, 1967; BIGGERSTAFF, 1970, 1973). It would seem more reasonable for characters with continuity of expression to be analyzed by metric approaches (PORTIN and ALVESALO, 1974; STALEY and GREEN, 1974).

In practice, there are difficulties in measuring these characters because they are generally small in size or complicated in shape. This is the reason for their being called non-metric characters. However, some investigators have succeeded in measuring a few tooth crown characters. For example, DAHLBERG and MIKKELSEN (1947), CARBONELL (1963), HANIHARA *et al.* (1970b), and BLANCO and CHAKRABORTY (1976) directly measured the depth of the lingual fossae of the upper incisors, which had formerly been called shovelling as a non-metric character. To give another example, the size of some cusps, which had previously been classified into several grades as non-metric traits, was photographically measured in terms of their occlusal plane surface areas (ERDBRINK, 1965; BIGGERSTAFF, 1969, 1975; HANIHARA *et al.*, 1970a). But this photographic method continues to contain some difficulties because it is an indirect measuring method. At any rate in tooth crown morphology the directly measurable characters are very few, at least for the present.

If we can not use direct and/or indirect measuring methods, other approaches should be investigated in order to quantify non-metric characters. The purpose of this article is to estimate genetic and environmental variabilities of crown characters, and a tetrachoric correlation analysis was deemed to be one of the more suitable methods for carrying this out. This procedure was developed by PEARSON (1900) for estimating the correlation of non-metric traits on the basis of a "threshold model," but it was not widely used for some time because of its premises unsuited for some cases (YASUDA, 1969). Recently, however, EDWARDS (1960, 1969) re-evaluated this threshold model for non-metric traits in organisms, and BULMER (1970) recommended the tetrachoric correlation analysis method for estimating correlations of non-metric traits between relatives. CAVALLI-SFORZA and BODMER (1971) also introduced this threshold model as one of the best available in their publication. If this analysis is used, we can expect reasonable quantitative results for non-metric traits because the tetrachoric correlations are comparable to PEARSON's product-moment correlations for metric traits.

Although the concept of a threshold has already been introduced into some anthropological studies (SCHWIDETZKY, 1959; BERRY, 1968; SOFAER *et al.*, 1972), the tetrachoric correlation analysis has not been used in the field of genetics concerning human dentition. In the present paper, the phenotypic variations of several tooth crown characters will be separated into genetic and environmental variations by the tetrachoric correlation analysis on the basis of twin data.

Materials

The material consisted of 266 pairs of dental casts obtained from Japanese twins who lived in Tokyo and its surrounding areas and were of nine to sixteen years of age. There were 191 monozygotic (MZ) twin pairs and 75 like-sexed dizygotic (DZ) twin pairs: 98 of the MZ twin pairs were males and 93 were females; 42 of the DZ twin pairs were males and 33 were females. All of the casts belong to collections in the Department of Anatomy, the University of Tokyo. Zygosity was established on the basis of the SIEMENS-VERSCHUER's similarity diagnosis using morphological and serological characters. To check observational error, additional data were arbitrarily taken from dental casts from 61 Okinawa Islanders, part of the collection in the Department of Anthropology, the University of Tokyo. In the present study, observation was carried out on the right-side permanent dentition excluding the second and third molars.

Methods

Methods of observation

In order to be compared with the shovelling observed non-metrically, the depth of the lingual fossae in the upper central incisors was measured according to the method of HANIHARA, TANAKA and TAMADA (1970b), i.e. with a dial gauge with an accuracy of 0.01 mm.

The expressivities of 14 non-metric characters of tooth crowns were in principle divided into four grades ranging from absence to highly-developed in each character. The following are the observed characters and the criteria used for their classification.

(1) Shovelling of the upper incisors. HRDLIČKA's (1920) criteria were used.

0: no shovel (no),

1: trace-shovel for slight but distinct indications (tr),

2: semi-shovel for the relatively-well-developed grades (ss),

3: shovel for all the highly-developed grades (s).

The no-shovel corresponds to "a" of DAHLBERG's plaque, the trace-shovel to "b," the semi-shovel to "c" and "e," and the highly-developed shovel to "d, f, g" and "h."

(2) DE TERRA's tubercles of the upper premolars. SAHEKI's (1958) criteria were slightly modified before use.

0: no indication of the tubercle,

1: tubercle on the mesial marginal ridge encircled by the mesial marginal developmental groove and the buccal accessory groove, with the distal tip not reaching the mid point of the distance from the mesial margin of the crown to the center of the occlusal surface,

2: tubercle with the tip reaching the above-mentioned mid point,

3: tubercle with the tip reaching the center of the occlusal surface.

(3) CARABELLI's tubercles of the upper molars. The eight categories of HANIHARA's (1961) criteria were reduced to four classes.

0: no indication of the tubercle,

1: groove or pit without any swelling on the lingual surface,

2: a slightly-developed cusp or eminence extending smoothly to the rest of the lingual surface without interruption,

3: highly-developed tubercle encircled by a groove, looking like the "fifth cusp."

The grade "0" corresponds to "a" of DAHLBERG's plaque, "1" to "b" and "c," "2" to "d" and "e," and "3" to 'f, g" and "h." The present criteria corresponds to those of KRAUS (1951) and BAILIT *et al.* (1968), which were modified from those of DIETZ (1944).

(4) Degree of reduction of the hypocones in the upper molars. DAHLBERG's (1949) criteria for occlusal surface patterns of the upper molars were adopted in entirety.

0: four well-developed cusps (4),

1: four cusps with the hypocone reduced in size (4—),

2: no hypocone but a cuspule on the distal border (3+),

3: total absence of the hypocone (3).

(5) Mesiolingual accessory marginal tubercles of the upper molars. These are the tubercles referred to by SELENKA as *tuberculum accessorium anterius internum* (FUJITA, 1973). The criteria shown below were developed for the present study.

0: no indication of the tubercle,

1: a part of the mesial marginal ridge with little or no prominence contoured by the main mesial part of the mesiobuccal groove (FUJITA, 1973) and the small mesial groove diverging from the main mesial part of the mesiobuccal groove toward the mesiolingual side,

2: accessory marginal tubercle with slight prominence,

3: highly-developed marginal tubercle.

(6) Distobuccal accessory marginal tubercles of the upper molars. These are the tubercles referred to by SELENKA as *tuberculum accessorium posterius externum* (FUJITA, 1973). These criteria were also developed for the present study.

0: no trace of the tubercle,
1: distobuccal marginal ridge with slight prominence outlined dimly by the distal part of the distolingual groove (FUJITA, 1973) and the distal groove diverging from the distolingual groove toward the distobuccal side,
2: small cusp-like formation encircled clearly by the boundary grooves,
3: highly-developed marginal tubercle.

(7) Lingual accessory cusps of the lower premolars. SAHEKI's (1958) criteria were modified and used.

0: no indication of the accessory cusp,
1: small accessory cusp,
2: relatively-well-developed accessory cusp, smaller than the lingual main cusp,
3: well-developed accessory cusp, equal to or larger than the lingual main cusp.

(8) Protostylids of the lower molars. DAHLBERG's (1963) criteria were somewhat modified before use.

0: no structure other than the straight buccal groove,
1: only a distal gingival deviation of the buccal groove, or a large pit at the base of the buccal groove,
2: weak degree of prominence of the cusp,
3: well-developed protostylid.

The grade "0" defined here corresponds to "0" of DAHLBERG's plaque, "1" to "1" and "2" of the plaque, "2" to "3" and "4," and "3" to "5."

(9) Sixth cusps of the lower molars. SAHEKI's (1958) criteria were modified and used.

0: no trace of the sixth cusp,
1: slightly-swollen part of the distal marginal ridge between the entoconid and the hypoconulid encircled faintly by the boundary grooves,
2: small cusp-like formation outlined distinctly by the boundary grooves,
3: well-developed sixth cusp, nearly equal to the hypoconulid in size.

(10) Seventh cusps of the lower molars. HANIHARA's (1961) criteria were adopted, and only those cusps which seemed to be derived from the metaconids were recorded here.

0: no trace of the seventh cusp,
1: very weak, short groove extending downward from the lingual ridge of the metaconid, with no cusp-like formation,
2: small cusp-like formation between this descending groove and the lingual groove,
3: well-developed seventh cusp.

(11) Deflecting wrinkles of the lower molars. The criteria used here were defined according to the description of HANIHARA *et al.* (1964).

0: no deflection in the median ridge of the metaconid,
1: deflection of the median ridge as clear as in category "3," with the median ridge not as well developed,

2: distinctly-deflected and highly-developed median ridge with the obscure metaconid-hypoconid contact,

3: large, well-developed median ridge emerging from the tip of the metaconid and extending in the direction of the protoconid, there forming a right angle distally and finally resulting in a Y groove pattern (WEIDENREICH, 1945). In addition to this typical ridge, those deflected median ridges which are constricted in the middle of the course or show a two-stepped structure are also classified in this category.

(12) Degree of reduction of the hypoconulids in the lower molars. These criteria were defined after the manner of those of the hypocones described by DAHLBERG (1949).

0: five well-developed cusps,

1: five cusps with the hypoconulid reduced in size,

2: no hypoconulid but a cuspule on the distal border,

3: total absence of the hypoconulid.

(13) Groove patterns in the occlusal surfaces of the lower molars. JøRGENSEN's (1955) criteria were adopted as follows.

1: Y pattern: a linear, basal contact between the hypoconid and metaconid,

2: + pattern: a basal, point-shaped contact between the hypoconid-metaconid and protoconid-entoconid (the term "point-shaped contact," as used here, means that it cannot be determined with certainty which of the two diagonal paris of cusps has the longer basal contact, or that this contact does not exceed 0.2 mm),

3: X pattern: a basal, linear contact between the protoconid and entoconid.

(14) Distobuccal accessory marginal tubercles of the lower molars. These tubercles are those which were referred to by SELENKA as *tuberculum accessorium posterius externum* (FUJITA, 1973).

0: no trace of the tubercle,

1: buccal part of the distal marginal ridge with slight prominence between the entoconid or the sixth cusp and the hypoconulid, the boundary grooves being not distinct,

2: small cusp-like formation outlined clearly by the boundary grooves,

3: well-developed tubercle looking like an independent cusp.

Assessment of observational error

Mean measurement error variance was calculated on the depth of the lingual fossae of the upper central incisors by a double determination method (LUNDSTRÖM, 1948; OSBORNE *et al.*, 1958; GOOSE, 1963), using the following formula:

$$\frac{\sum d^2}{2n}, \qquad (1)$$

where d is the difference between two determinations for the same sample and n is the number of double determinations. In the present study, the duplicate measurements were carried out on 61 individuals at an interval of about seven months.

For each of the non-metric characters observed here, the reliability of observation was assessed on the basis of discordance between duplicate observations made at an interval of about eight months on dental casts obtained from 61 individuals. The discordances and concordances between double observations were compared with those between MZ twins to assess the reliability of observation of each non-metric character, using a chi-square test with 1 degree of freedom, if necessary, after YATES' correction.

Estimation of heritabilities

Various simple genetic models have been proposed by previous authors in order to estimate the heritability of quantitative characters. One of these models was used here under the following assumptions: there are many polymorphic genes controlling each dental character in a population, every one of which has a certain subtle effect on that character; the variation within those who have the same genotype is due to environmental factors; and variations due to genetic interaction (epistasis) and genotype-environment interaction do not exist.

Based on this model, the depth of the lingual fossae in the upper central incisors was first analyzed. For this metric character, mean intrapair variances and intraclass correlation coefficients were calculated on MZ and DZ twin paris to estimate heritability. Mean intrapair variances can be obtained by the use of the above-mentioned formula (1) where, in this case, d is the difference between the measurements on a twin pair and n is the number of twin pairs. Variance analyses based on these mean intrapair variances give information on the presence of genetic variability in a character and about the magnitude of measurement error variance. Heritability of a character was estimated by the following formula:

$$h^2=2(r_{MZ}-r_{DZ}), \qquad (2)$$

where r_{MZ} and r_{DZ} are the respective intraclass correlation coefficients of MZ and DZ twin pairs (BULMER, 1970; SMITH, 1974). This formula (2) provides an estimation of heritability corrected for common environmental factors between twins on the assumptions that there is no dominance variance for the character and that covariances due to environmental factors are the same for both MZ and DZ twins. This formula may be an indicator for large amounts of dominace variance at least when the heritability estimates exceed unity, because it is equivalent to $(V_A+\frac{3}{2}V_D)/V$, where V_A is the additive genetic variance, V_D is the dominance variance and V is the phenotypic variance (BULMER, 1970; SMITH, 1974). However, care should be taken concerning the rather large standard error of this formula, which is about $2\sqrt{2}$ times as large as that of the individual correlation coefficients (SMITH, 1974).

If $V_D=0$, the relative amount of the common environmental variance between twins, compared with the phenotypic variance, can be estimated by subtracting the h^2 estimate from the relevant correlation coefficient of MZ twins because this correlation coefficient is equivalent to $(V_A+V_D+V_C)/V$, where V_C is the common environmental variance within twin pairs.

For the non-metric characters observed, tetrachoric correlation coefficients were calculated on both MZ and DZ twin pairs. By putting these tetrachoric correlation coefficients in the above formula (2), heritability estimates can be obtained.

Incidentally, HOLZINGER's (1929) formula for estimating heritabilities was not used in the present study because some difficulties in interpreting the formula have been pointed out (BULMER, 1970; CAVALLI-SFORZA and BODMER, 1971; SMITH, 1974).

Method of tetrachoric correlation

The tetrachoric correlation method requires the assumption that the traits show the normal distribution of continuous variates, or of underlying continuous variates if the traits are phenotypically discrete. In the latter case, they must be analyzed on the basis of a threshold model which assumes that they are expressed only when the underlying continuous variates exceed a certain threshold.

According to PEARSON (1900) and EVERITT (1910), coefficients of tetrachoric correlation can be obtained on the basis of the following formula:

$$\frac{d}{N}=\frac{b+d}{N}\frac{c+d}{N}+\sum_{n=1}^{\infty}\left(\frac{r^n}{n!}HKv_{n-1}w_{n-1}\right), \qquad (3)$$

where r is the correlation coefficient, N is the total number of pairs, d is the absolute frequency of the affected concordant pairs, and b and c are those of the discordant pairs. H and K are the ordinates of the normal curve of area N corresponding to the abscissae h and k which are equivalent to the respective distances from the origin of two dividing planes on the axes x and y in a standardized bivariate normal distribution when the dividing plane perpendicular to the x axis divides a population into two parts, $(a+c)$ and $(b+d)$, and the plane perpendicular to the y axis divides that population into $(a+b)$ and $(c+d)$, in which a is the frequency of the non-affected concordant pairs. Finally, v and w are given by

$$v_n=hv_{n-1}-(n-1)v_{n-2} \quad (n=2, 3, \ldots);\ v_0=1,\ v_1=h,$$
$$w_n=kw_{n-1}-(n-1)w_{n-2} \quad (n=2, 3, \ldots);\ w_0=1,\ w_1=k.$$

The variance of r is expressed as follows:

$$\frac{1}{N\chi_0^2}\left[\frac{(a+d)(c+b)}{4N^2}+\Psi_2^2\frac{(a+c)(d+b)}{N^2}+\Psi_1^2\frac{(a+b)(d+c)}{N^2}\right.$$
$$\left.+2\Psi_1\Psi_2\frac{ad-bc}{N^2}-\Psi_2\frac{ab-cd}{N^2}-\Psi_1\frac{ac-bd}{N^2}\right], \qquad (4)$$

where

$$\chi_0=\frac{1}{2\pi}\frac{1}{\sqrt{1-r^2}}\exp\left(-\frac{h^2+k^2-2rhk}{2(1-r^2)}\right),$$

$$\Psi_1=\frac{1}{\sqrt{2\pi}}\int_0^{\beta_1}\exp\left(-\frac{1}{2}z^2\right)dz, \qquad \Psi_2=\frac{1}{\sqrt{2\pi}}\int_0^{\beta_2}\exp\left(-\frac{1}{2}z^2\right)dz,$$

$$\beta_1=\frac{h-rk}{\sqrt{1-r^2}}, \qquad \beta_2=\frac{k-rh}{\sqrt{1-r^2}}.$$

In this work, the terms of the first to the 35th degree in the above-mentioned equation (3) were used to estimate correlation coefficients.

The best estimates of tetrachoric correlation coefficients can be obtained when dividing planes, those which split a population into two parts, are located as near the origin as possible in the normal distribution (PEARSON, 1900). In the present study, therefore, the best location of a dividing plane was selected from the three possible locations between four expressivities of each trait.

Methods of calculation

The calculation involved was carried out by a HITAC 8800/8700 (OS–7) computer in the University of Tokyo Computer Centre using BASICl, MIVCRL, CLASS and TETRAC programs written in FORTRAN. The BASIC1 program and the NORMAL subroutine subprogram which was utilized in the MIVCRL and TETRAC programs were contained in the PLAS[1)] program library. The MIVCRL, CLASS, and TETRAC programs were coded by the present writer for the calculation of mean intrapair variances and intraclass correlation coefficients, for testing the homogeneity of two series of samples in a 2×2 contingency table, and for the calculation of tetrachoric correlation coefficients, respectively.

Results

First, the depth of the lingual fossae in the upper central incisors was analyzed by the procedure commonly used with metric traits to compare with the shovelling observed non-metrically. In order to show the process of analyses for non-metric characters, the analyses of the shovelling, as an example, will be outlined in more detail than those of the other characters observed. The results of all the non-metric characters except the shovelling are collectively listed in Tables 6, 7, 8 and 9. Tables 6 and 7 show the frequencies of the four expressivities of each character, and Tables 8 and 9 display the tetrachoric correlation coefficients between twins and a heritability estimate for each character.

To test for homogeneity of male and female samples or of MZ and DZ twin samples for each non-metric character, FISHER's exact test was utilized in a two-by-two table, where each of the two series of samples was divided into two parts in order to estimate a more accurate coefficient of tetrachoric correlation. The 5% level was in principle assigned for the significance tests used in this work.

1) Program Library for Anthropological Statistics (ed. K. HANIHARA, 1974).

Depth of the lingual fossae of the upper central incisors

Both the male and female data for this metric trait were incorporated because it was established by the *t*-test that there was no significant between-sex difference. The MZ and DZ twin samples also showed no significant difference. Therefore, a set of samples consisting of one member of each MZ twin pair was substituted as a control population because the sample size of the MZ twins was larger than that of the DZ twins.

The mean measurement error variance for the depth was significantly less at the 0.5% level than the mean intrapair variance of MZ twin pairs (Table 1). The *F*-ratio of the mean intrapair variance of DZ twins to that of MZ twins revealed that the former was significantly larger than the latter at the 0.5% level. This suggests that there was significant variation due to genetic components for the depth of the lingual fossae.

Table 1. Mean intrapair variances of depth of the lingual fossae of the upper central incisors observed in monozygotic and dizygotic twin data.

Mean intrapair variance				*F*-ratio		
Error (n)	MZ (n)	DZ (n)	Controls (n)	MZ/Error	DZ/MZ	Controls/DZ
.0019 (39)	.0147 (110)	.0447 (50)	.1144 (53)	7.7368*	3.0408*	2.5593*

* $P < .005$, by one-tailed *F*-test.

Intraclass correlation coefficients of MZ and DZ twins and an estimate of heritability are shown in Table 2. The coefficient of correlation within the DZ twin pairs of more than 0.5 suggests that the depth of the lingual fossae was influenced by environmental factors common between twins. The heritability estimate corrected for such factors was 0.52, and the relative amount of common environmental variance compared with the phenotypic variance was 0.35 with the assumption that there was no dominance variance.

Table 2. Intraclass correlation coefficients and a heritability estimate corrected for common environmental factors between twins for depth of the lingual fossae of the upper central incisors obtained from monozygotic and dizygotic twins.

Intraclass correlation coefficient			Heritability	Relative common environ. variance
MZ (n)	DZ (n)	Controls (n)		
.8614 (110)*	.6038 (50)*	−.0164 (53)	.52	.35

* $P < .01$.

Shovelling of the upper incisors

Table 3 shows the frequencies of four expressivities in the shovelling. From this, it is evident that the best location of a dividing plane to accurately estimate a

Table 3. Frequencies of four expressivities for the shovelling of the upper incisors[1)]

		No.	Expressivity (%)			
			0 (no)	1 (tr)	2 (ss)	3 (s)
I1:	Male	88	1.14	18.14	44.32	36.36
	Female	87	2.30	14.94	44.83	37.93
I2:	Male	89	1.12	23.60	42.70	32.58
	Female	87	8.05	18.39	42.53	31.03

1) Based on the samples consisting of one of each MZ twin pair.

tetrachoric correlation coefficient would be between the semi-shovel and the highly-developed shovel because this location is nearest to the origin of the distribution. The shovelling was, therefore, analyzed in terms of the frequencies of the highly-developed shovel and all the remaining expressivities.

In the cases of both the upper central and lateral incisors, FISHER's exact tests did not show any significant sex differences in incidences of a highly-developed shovel. Neither was the difference of this expressivity between MZ and DZ twin samples significant in the central and lateral incisors. Therefore the samples were combined for sexes, and a set of samples consisting of one of each MZ twin pair was again substituted as a control population because of the larger sample size of the MZ twins over that of the DZ twins.

The discordance between the double observations of the shovelling, as shown in Table 4, was not significantly different from the discordance between MZ twins in the central incisor or in the lateral incisor.

Table 4. Frequencies of within-pair discordance for the well-developed shovel of the upper incisors.

	Percent discordance[1)]				Probability[2)]		
	Double obs. (n)	MZ (n)	DZ (n)	Controls (n)	MZ/Dbl. obs.	DZ/MZ	Controls /DZ
I1	10.71 (56)	9.70 (165)	15.15 (66)	45.68 (81)	$>.80$	$>.20$	$<.001$
I2	12.28 (57)	12.05 (166)	28.13 (64)	40.24 (82)	$>.95$	$<.01$	$>.10$

1) The numbers in parentheses are those on which the relevant percentages are based.
2) Probability by a chi-square test in a two-by-two table where the number of concordant pairs affected plus non-affected and that of discordant paris are arranged in each series of samples.

Table 5 shows the coefficients of tetrachoric correlation within pairs and the estimates of heritability for the shovelling of the two upper incisors. In the central incisor, much influence due to twins' common environmental factors was inferred because of the correlation coefficient of more than 0.5 in DZ twins. After correction for these factors, a low heritability estimate of 0.22 was obtained. The relevant

Table 5. Tetrachoric correlation coefficients and heritability estimates corrected for common environmental factors between twins for the shovelling of the upper incisors obtained from monozygotic and dizygotic twin data.

	Tetrachoric correlation coefficient ± S.E.			Herita-bility	Relative common environ. variance
	MZ (n)	DZ (n)	Controls (n)		
I1	.9518±.0230 (165)	.8395±.0895 (66)	.1198±.1820 (79)	.22	.73
I2	.9119±.0362 (166)	.5345±.1661 (64)	.0282±.1909 (81)	.75	.16

common environmental variance was 73% of the phenotypic variance on the assumption that there was no dominance variance. Heritability of the shovelling in the lateral incisor was estimated to be as high as 0.75, and the common environmental variance was 16% of the phenotypic variance.

Table 6. Frequencies of four expressivities in tooth crown characters of maxillary permanent dentition.[1)]

Character			No.	Expressivity (%)			
				(0)	(1)	(2)	(3)
De Terra's tubercle							
	First premolar:	Male	74	54.05	2.70	40.54	2.70
		Female	69	71.01	4.35	24.64	0.00
	Second premolar:	Male	48	72.92	6.25	20.83	0.00
		Female	62	80.65	4.84	14.52	0.00
Carabelli's tubercle							
	First molar:	Male	95	15.79	21.05	43.16	20.00
		Female	79	22.78	25.32	41.77	10.13
Degree of reduction in hypocone							
	First molar:	Male	93	92.47	7.53	0.00	0.00
		Female	87	81.61	16.09	0.00	2.30
Mesiolingual accessory marginal tubercle							
	First molar:	Male	83	45.78	18.07	34.94	1.20
		Female	79	44.30	26.58	29.11	0.00
Distobuccal accessory marginal tubercle							
	First molar:	Male	77	38.96	35.06	25.97	0.00
		Female	72	41.67	37.50	20.83	0.00

1) These frequencies were based on the samples consisting of one member of each MZ twin pair.

De Terra's tubercles of the upper premolars

Significant sex difference was recognized for this tubercle of the first premolar. In the second premolar, however, this difference was not seen. Therefore, the male and female data were separately analyzed for the first premolar, and combined for the second premolar in order to increase the sample size. The derivations of the MZ and DZ twin samples were statistically ascertained to be the same for both the first and second premolars. Discordance between the double observations was significantly

Table 7. Frequencies of four expressivities in tooth crown characters of mandibular permanent dentition.[1)]

Character		No.	Expressivity (%)			
			(0)	(1)	(2)	(3)
Lingual accessory cusp						
First premolar:	Male	74	1.35	90.54	6.76	1.35
	Female	85	3.53	85.88	9.41	1.18
Second premolar:	Male	25	0.00	28.00	48.00	24.00
	Female	24	0.00	33.33	37.50	29.17
Protostylid						
First molar:	Male	69	26.09	33.33	40.58	0.00
	Female	70	22.86	37.14	38.57	1.43
Sixth cusp						
First molar:	Male	74	44.59	25.68	10.81	18.92
	Female	68	50.00	22.06	20.59	7.35
Seventh cusp						
First molar:	Male	36	63.89	27.78	8.33	0.00
	Female	28	78.57	17.86	0.00	3.57
Deflecting wrinkle						
First molar:	Male	65	84.62	1.54	4.62	9.23
	Female	68	83.82	2.94	2.94	10.29
Degree of reduction in hypoconulid						
First molar:	Male	82	78.05	21.95	0.00	0.00
	Female	75	77.33	18.67	2.67	1.33
Groove pattern						
First molar:	Male	37	—	70.27	27.03	2.70
	Female	26	—	65.38	34.62	0.00
Distobuccal accessory marginal tubercle						
First molar:	Male	36	91.67	2.78	2.78	2.78
	Female	27	92.59	0.00	3.70	3.70

1) Based on the samples consisting of one member of each MZ twin pair for all the characters except the lingual accessory cusp of the second premolar, the seventh cusp and the distobuccal accessory marginal tubercle of the first molar, whose frequencies were based on the samples consisting of one of each DZ twin pair.

less than the intrapair discordance of MZ twins for the tubercle of the first premolar in males. Concerning the first premolar in females and the second premolar, the discordances between these double observations were not significantly different from those within MZ twin pairs.

Heritability estimates of the DE TERRA's tubercles were 0.48 and 0.56 in the first premolar of males and females, respectively, and 0.43 in the second premolar (Table 8). Of the tetrachoric correlation coefficients obtained in advance, those of the DZ twin pairs for the first premolar in females and for the second premolar may not be completely reliable because the sample sizes were small. But these tentative findings do suggest that both the genetic and the environmental variabilities were nearly the same for the tubercles of the two premolars. Comparing the heritability estimates corrected for common environmental factors between twins with coefficients of correlation within MZ twin pairs, the data suggests that the variability due to common environmental factors was relatively limited for the DE TERRA's tubercles (Table 8).

Table 8. Tetrachoric correlation coefficients and heritability estimates corrected for common environmental factors between twins on tooth crown characters of maxillary permanent dentition obtained from MZ and DZ twin data.[1]

		Tetrachoric correlation coef. ± S.E.			Heritability	Relative common environ. variance
		MZ (n)	DZ (n)	Controls (n)		
DE TERRA's tubercle						
P1:	Male	.56±.15 (62)	.33±.28 (29)	.22±.29 (28)	.48	.09
	Female	.68±.16 (58)	.40±.28 (26)[2]	−.05±.35 (26)[2]	.56	.12
P2		.60±.14 (90)	.38±.29 (33)[2]	−.15±.36 (31)[2]	.43	.17
CARABELLI's tubercle						
M1		.69±.08 (157)	.46±.17 (61)	.12±.18 (78)	.46	.23
Degree of reduction in hypocone						
M1:	Male	.99±.02 (87)[2]	.92±.14 (40)[2]	.59±.33 (44)[2]	.12	.86
	Female	.97±.03 (78)[2]	.63±.35 (27)[2]	—	.69	.28
Mesiolingual accessory marginal tubercle						
M1		.60±.10 (134)	.52±.18 (52)	.07±.19 (68)	.16	.44
Distobuccal accessory marginal tubercle						
M1		.60±.11 (119)	.28±.22 (49)	−.04±.21 (58)	.64	−.04

1) Those values which are not on the list could not be obtained because no frequency of the affected concordant pairs was given.

2) One or more of four absolute frequencies in the fourfold correlation table were less than 5.

Carabelli's tubercles of the upper first molars

There was neither significant sex difference nor significant difference between MZ and DZ twin samples for this tubercle. The difference between the intrapair discordances of double observations and of MZ twin pairs was also not significant.

The heritability estimate for this tubercle was 0.46, as is shown in Table 8. The common environmental variance within twin pairs was estimated as 23% of the phenotypic variance on the assumption that there was no dominance variance.

Degree of reduction of the hypocones in the upper first molars

The between-sex difference was significant for this cusp. However the difference between the MZ and DZ twin samples was not significant. The discordance between double observations was not significantly different from the intrapair discordance of MZ twins.

The heritability estimates for the hypocones of the upper first molars must be carefully considered because the sample sizes were too small to reliably estimate coefficients of tetrachoric correlation. In particular, the frequencies of the affected concordant twin pairs were low because most of the hypocones were well developed in the first molars. In such a case, the dividing plane is located near the end of the distribution, not near the origin. Therefore, the tetrachoric correlation coefficients obtained for this cusp may not be completely reliable. However, if these values are accepted as correct, heritability of the hypocones would be estimated as 0.12 and 0.69 for males and females, respectively.

Mesiolingual accessory marginal tubercles of the upper first molars

No significant differences were detected between males and females nor between the MZ and DZ twin samples for this tubercle. The discordance between double observations was significantly less than was the discordance within MZ twin paris. Heritability was estimated at 0.16, and the common environmental variance between twins was 44% of the phenotypic variance (Table 8).

Distobuccal accessory marginal tubercles of the upper first molars

There was no significant difference either between males and females or between the MZ and DZ twin samples for this tubercle. Also, a comparison of the intrapair discordances within double observations and within MZ twin paris shows no significant differences. The heritability estimate was 0.64, and there seemed to be no common environmental variance within twin pairs for this tubercle, though the samples may be somewhat biased (Table 8).

Lingual accessory cusps of the lower premolars

There was no significant between-sex difference in either of the lower first and second premolars. The discordance between double observations was significantly less than the intrapair discordance between MZ twins for the second premolars but, for the first premolars, they were not significantly different from each other. In the first premolars, although the difference between the MZ and DZ twin samples was not significant, the heritability estimate of 0.50 for the lingual accessory cusps, as shown in Table 9, may not be completely dependable because of the small sample sizes used in estimating tetrachoric correlation coefficients.

In the second premolars, the hypothesis of homogeneity for the MZ and DZ twin samples was rejected for this accessory cusp. In a twin study, DZ twin samples are generally utilized as a control population when information about the general population is lacking. Therefore, a set of samples consisting of one of each DZ twin pair was here substituted as a control population, though the sample size was small. A heritability estimate of 0.71 was formally obtained, but it is difficult to accept this value because of the heterogeneity of the MZ and DZ twin samples (Table 9).

Protostylids of the lower first molars

No significant difference was recognized either between males and females or between the MZ and DZ twin samples for this character. The discordance of double observations was significantly less than the intrapair discordance between MZ twins.

Heritability was estimated at 0.17, while the relative amount of common environmental variance between twins was higher, 0.51 (Table 9).

Table 9. Tetrachoric correlation coefficients and heritability estimates corrected for common environmental factors between twins on tooth crown characters of mandibular permanent dentition obtained from MZ and DZ twin data.[1)]

	Tetrachoric correlation coef. ± S.E.			Herita-bility	Relative common environ. variance
	MZ (n)	DZ (n)	Controls[2)] (n)		
Lingual accessory cusp					
P1	.92±.05 (144)[3)]	.67±.21 (56)[3)]	−.82±.04 (65)[3)]	.50	.42
P2[4)]	.69±.10 (106)	.34±.24 (37)	−.39±.36 (19)[3)]	.71	−.02
Protostylid					
M1	.68±.10 (109)	.59±.16 (54)	−.35±.21 (52)	.17	.51
Sixth cusp					
M1	.88±.05 (112)	.07±.24 (43)	−.09±.21 (53)	1.63	−.74
Seventh cusp					
M1[4)]	.53±.16 (127)	.27±.24 (55)[3)]	−.49±.28 (28)[3)]	.52	.00
Deflecting wrinkle					
M1	.67±.14 (103)	.57±.25 (36)[3)]	.21±.30 (49)[3)]	.18	.48
Degree of reduction in hypoconulid					
M1	.87±.06 (133)	.62±.18 (54)	.19±.23 (64)	.49	.38
Groove pattern					
M1	.51±.30 (32)[3)]	—	−.08±.51 (11)[3)]	—	—
Distobuccal accessory marginal tubercle					
M1[4)]	.47±.29 (133)[3)]	.71±.29 (49)[3)]	—	−.47	.94

1) Those values which are not on the list could not be obtained because the frequencies of the affected concordant pairs were zero.

2) Control pairs randomly selected from one of each MZ twin pair for all the characters except for the lingual accessory cusp of the second premolar, the seventh cusp and the distobuccal accessory marginal tubercle of the first molar, whose controls were derived from DZ twins.

3) One or more of four absolute frequencies in the fourfold correlation table were less than 5.

4) The homogeneity hypothesis of MZ and DZ twin samples was rejected at the 5% level.

Sixth cusps of the lower first molars

For the sixth cusps, there was not significant difference either between males and females or between the MZ and DZ twin samples. Neither was the difference between the intrapair discordances of double observations and of MZ twin pairs significant.

The heritability estimate of 1.63 for this cusp, as shown in Table 9, is clearly an overestimation. The overestimation may have been caused simply by the biases in the samples, especially of the DZ twin pairs. But, as it was obtained on the basis of the formula $2(r_{MZ}-r_{DZ})=(V_A+\frac{3}{2}V_D)/V$, this estimate may indicate the presence of dominance variance for this cusp. If so, the additive genetic and environmental variances must be very small. It is difficult to determine whether the overestimation was due to dominance variance or sample biases, especially with only these data. However, it should be noted that, even if there was dominance variance for the sixth cusps, they would not necessarily be controlled by a single pair of dominant and recessive alleles.

Seventh cusps of the lower first molars

The seventh cusps had no significant between-sex difference. The discordance between double observations was not significantly different from the intrapair discordance of MZ twins. Because a hypothesis for the homogeneity of the MZ and DZ twin samples was rejected, it is difficult to compare the correlation coefficient of MZ twins with that of DZ twins. Although the heritability estimate formally obtained was consistent with the correlation coefficient between the MZ twins (Table 9), the value of the former is questionable because of the small sample size of the DZ twins and the heterogeneity of the MZ and DZ twin samples. However, the correlation coefficient of 0.53 for the MZ twins provides exact information on the genetic and common environmental complex variances of the seventh cusps.

Deflecting wrinkles of the lower first molars

For the deflecting wrinkles, there was no significant difference either between males and females or between the MZ and DZ twin samples. A comparison of the discordances in the double observations and in the MZ twin paris showed that they were not significantly different from each other.

Although the coefficient of tetrachoric correlation obtained within DZ twin pairs is somewhat questionable because of the small sample size, the deflecting wrinkle showed a low estimate of 0.18 for heritability (Table 9).

Degree of reduction of the hypoconulids in the lower first molars

FISHER's exact tests for the hypoconulids showed no significant difference either between males and females or between the MZ and DZ twin samples. It was ascertained by the chi-square test that the discordance of double observations was not significantly different from that of the MZ twin pairs.

Table 9 shows the heritability estimate of 0.49 for the degree of reduction in size of the hypoconulids. The relative amount of common environmental variance between twins was estimated as 0.38, which is equivalent to 76% of the total environmental variance for this cusp.

Groove patterns in the lower first molars

In the present study, three patterns, i.e., "Y," "+" and "X" patterns in the lower molars were regarded as the three most conveniently classified categories of a given continuous character.

For these groove patterns in the lower first molars, there was no significant difference either between males and females or between the MZ and DZ twin samples. There was also no significant difference between discordances of the double observations and of the MZ twin pairs.

Regretfully, a correlation coefficient within DZ twin pairs and therefore a heritability estimate corrected for common environmental factors between twins could not be calculated because of the small sample size which was mainly due to dental attrition. Although a correlation coefficient of 0.51 was obtained for the MZ twin pairs, it also is not completely reliable for the same reason.

Distobuccal accessory marginal tubercles of the lower first molars

There was no significant between-sex difference for this tubercle. Discordances of the double observations and the MZ twin pairs were not significantly different from each other. However, FISHER's exact test showed a significant difference between the MZ and DZ twin samples. Further, the sample sizes were too small to accurately estimate tetrachoric correlation coefficients for both the MZ and DZ twin paris. As a result, it is impossible to interpret the formally obtained heritability estimate of −0.47 for this tubercle.

Discussion

The continuous variation in phenotypes of tooth crown characters suggests polygenic inheritance. Thus, in the present study, all the characters observed non-metrically were uniformly analyzed by tetrachoric correlation on the premise that each of them was controlled by polygenes plus many environmental factors and, therefore, normally distributed in continuous or underlying continuous variates, according to the central limit theorem.

Although it is clear that the tetrachoric correlation method is theoretically available for non-metric characters, studies were made, before analyzing the non-metric traits, on how coefficients of tetrachoric correlation are in reality consistent with those of product-moment correlation by using the same data on the depth of the lingual fossae in the upper central incisors. The metric data of the lingual fossae were first converted to all-or-none data by a dividing plane located near the mean value and the tetrachoric correlation coefficients were calculated. Table 10 shows that the differences between the coefficients of tetrachoric correlation and those of product-moment correlation were not significant in any of the three examples for the MZ, DZ and

Table 10. Comparisons of coefficients of intraclass product-moment correlation with those of tetrachoric correlation for the depth of the lingual fossae in the upper central incisors.

	No. of pairs	Product-moment correlation	Tetrachoric correlation	Normal deviate of z-value[1]	Probability
MZ	110	0.8614	0.8970	1.5979	0.11
DZ	50	0.6038	0.5875	0.2465	0.80
Controls	53	−0.0164	0.1433	1.0854	0.28

1) Normal deviate was obtained after z-transformation of both the correlation coefficients under the assumption that the value of the tetrachoric correlation coefficient was a mean value of correlation coefficients in the population.

control pairs. This not only demonstrates that the tetrachoric correlation method is quite useful for the present investigation but, because this method is completely based on the assumption of normality, also indicates that the distribution of the depth of the lingual fossae does not deviate greatly from normality.

There are few previous reports which this work may support or refute, except for those on a few tooth crown characters such as the shovelling and the CARABELLI's tubercles.

SIEMENS (1928) and KORKHAUS (1930) investigated not only the CARABELLI's tubercles but also the so-called dental tubercles of the incisors to determine the modes of inheritance on the basis of twin data. WADA (1938) also investigated various tubercles on the occlusal surfaces of premolars and molars containing the central cusps, the DE TERRA's tubercles and so forth on the basis of family and twin data. He regarded these tubercles as a complex of dental anomalies and assigned a mode of dominant inheritance to this complex. However, the characters studied in these above-mentioned reports, except for the CARABELLI's tubercles, were not observed in the present study. BIGGERSTAFF (1970, 1975) attempted to clarify the genetic background of the occlusal surface pattern and the individual cusp size of the lower molars using twin data by his unique observational methods. However the differences of the methods and of the characters observed made comparisons between his results and the present ones impossible.

To assess the genetic and environmental influences on tooth crown characters, SAHEKI (1958) and AOYAGI (1967) investigated many characters, largely overlapping those studied here, on the basis of twin data. SAHEKI (1958) concluded from data on 285 twin paris that the characters most influenced by heredity were the shovelling of the incisors, the DE TERRA's tubercle of the upper premolar and a few others, while the lingual accessory cusp of the lower second premolar, the seventh cusp of the lower first molar, etc. were heavily influenced by environmental factors. AOYAGI (1967) stated on the basis of 201 twin pairs that genetic influence was more intensive in the shovelling of the upper central incisor, the groove pattern in the lower first molar and so forth. However, SAHEKI's results and part of AOYAGI's results were based on data which seem to have been taken from only one side of the dental arch for some twin pairs and, for the others, from both sides. This might have led to the same sort of biased results as one sees when doubly sampled data are taken from the same subjects.

On the other hand, in order to assess the usefulness of tooth crown characters in similarity diagnosis of twins, many authors have studied a variety of tooth crown characters (SHIMIZU, 1955; FUJITA and KASAI, 1956; NAGAI *et al.*, 1957; LUNDSTRÖM, 1963). In these studies, however, the influences of genetic and environmental factors were not discussed in terms of the individual characters.

This author's findings concerning the shovelling and the CARABELLI's tubercles, traits which have been frequently studied, will first be discussed in some depth.

Shovelling and the lingual fossae of the upper incisors

Although it was accepted quite some time ago that shovelling expressed continuous variation in its phenotypes, many students have disputed its mode of inheritance. Recently, PORTIN and ALVESALO (1974) examined several hypotheses on the mode of inheritance and showed that at least three hypotheses of the modes, i.e. due to a single intermediate autosomal gene, due to a single locus with more than two alleles involved, and due to polygenes, could not be rejected. As a result, they suggested that this character should in fact be attributed to polygenes. In the present study also, as was stated previously, the mode of inheritance was assumed to be polygenic on the basis of its continuity in expression.

In this way two characters, i.e. the shovelling observed non-metrically and the depth of the lingual fossa, were analyzed for the upper central incisor. The former showed a heritability estimate of 0.22 and the latter, 0.52. These two values were obtained separately through different correlation analyses, tetrachoric correlation for the former and product-moment correlation for the latter, which would have produced the same results if the two characters were substantially the same. The difference between these two characters was also verified by tetrachoric correlation coefficients. The correlation coefficients for the shovelling were considerably higher than those for the lingual fossae in both the MZ and the DZ twin pairs, though the differences were not significant (Table 11). This fact suggests that the character called shovelling does not strictly correspond to the character called depth of the lingual fossa. In any case, the heritability, relative genetic variability, was shown to be relatively low for both the shovelling and the depth of the lingual fossa in the upper central incisor.

Table 11. Comparisons of the depth of the lingual fossae with the shovelling in the upper central incisors on the basis of tetrachoric correlation coefficients

	Correlation coefficient ± S.E. (n)		Normal deviate[1)]	Probability
	Depth of fossa	Shovel observed		
MZ	.8970 ± .0468 (110)	.9518 ± .0230 (165)	1.0509	0.29
DZ	.5875 ± .1648 (50)	.8395 ± .0895 (66)	1.3438	0.18
Controls	.1433 ± .2130 (53)	.1198 ± .1820 (79)	0.0839	0.94

1) Normal deviate was directly obtained using tetrachoric correlation coefficients and their standard errors.

HANIHARA *et al.* (1970b) reported the correlation coefficients between relatives for the depth of the lingual fossae in the upper central incisors on the basis of 59 twin pairs and 69 sibling pairs. The correlation coefficients were 0.9297 for MZ twins, 0.7969 for DZ twins and 0.3869 for siblings. From these results, a heritability estimate corrected for common environmental factors between twins can be established at 0.27. This is between the values of 0.22 and 0.52 obtained as heritability estimates of the shovelling and the depth of the lingual fossa, respectively, in this present study. Incidentally, the results of HANIHARA *et al.* (1970b) suggest that if all the samples were derived from the same population, the difference between the correlation coefficients of DZ twins and those of siblings would indicate that the common environmental variance between twins is much larger than that of siblings because DZ twins and siblings are genetically homologous.

Further, HANIHARA *et al.* (1975) estimated the parent-offspring correlation coefficients for the depth of the lingual fossae in the upper central incisors. The coefficients given were 0.4103 for 27 father-son pairs, 0.4280 for 42 mother-son pairs, 0.4224 for 39 father-daughter pairs and 0.2453 for 52 mother-daughter paris. When these four parent-offspring correlation coefficients are compared with that of the siblings mentioned above (HANIHARA *et al.*, 1970b), it can be seen that there is no significant difference at the 5% level in any of these four cases. This may indicate that there was no dominance variance for the depth of the lingual fossae, if the derivations of all the samples were the same. By simply duplicating a correlation coefficient between siblings or between parent-offspring, a value of about 0.8 can be obtained as the heritability estimate for the depth of the lingual fossae in the upper central incisors. BLANCO and CHAKRABORTY (1976) presented similar heritability estimates for the shovel-shape-index, equivalent to the depth of the lingual fossae, in the upper central incisors using data taken from Chilean families. An estimate of 0.68 was obtained from parent-offspring data and 0.66 from full-sib data. These two reports suggested relatively high heritability for the depth of the lingual fossae in the upper central incisors, though the populations observed were quite different. In practice, however, the heritability of the lingual fossae in the central incisors would not be as high as in the above studies because common environmental variances, even if smaller than between twins, were probably present between siblings or between parents and offspring.

AOYAGI (1967) reported the frequencies of concordance and discordance between twins for the shovelling of the upper central incisors classified according to HRDLIČKA's criteria. Based on his data, further heritability estimates for the shovelling were obtained by tetrachoric correlation. Correlation coefficients of 0.97 and 0.75 were estimated by the present writer for MZ and DZ twin paris, respectively, on the basis of AOYAGI's (1967) data for right-side dentition of 98 MZ and 52 DZ twin pairs. From these two coefficients, a heritability estimate of 0.44 was obtained for the shovelling of the central incisors, and the common environmental variance between twins was estimated at 53% of the total phenotypic variance. These results are similar to those arrived at in this study.

As regards the shovelling of the upper lateral incisors, a somewhat higher heritability estimate of 0.75 was obtained in the present study. This means that the genetic variablity was much larger than the environmental variability for the shovelling of the lateral incisors, in contrast with the case of the central incisors. The difference in the genetic variability for the shovelling between the two upper incisors may be strongly related to the fact that the total size of the lateral incisors are, at least phenotypically, more variable than that of the central incisors.

It is most likely that the shovelling of the upper central incisors has lower genetic variability, or is genetically more stable, while the shovelling of the upper lateral incisors has a much higher genetic variability.

Carabelli's tubercles of the upper first molars

Many authors have investigated the CARABELLI's tubercles, some of them proposing simple dominance as their mode of inheritance. SIMENS (1928), for example, thought it to be dominant with limited variation in manifestation, and KORKHAUS (1930) presented a view of a simple dominant inheritance for it after comparing the concordance and discordance within MZ twin pairs with those within DZ twin paris. WADA (1938) inferred on the basis of 10 families' data that the CARABELLI's tubercle had a mode of dominant inheritance without sex linkage. Later, SHIMIZU (1939) suggested that the mode of inheritance for this tubercle was dominant after pedigree investigation. Similarly, on the basis of 28 Japanese pedigrees, TSUJI (1958) stated that the presence of the CARABELLI's tubercles was probably controlled by a simple Mendelian dominant gene with incomplete penetrance.

On the other hand, KRAUS (1951) maintained that the mode of inheritance was due to two allelic autosomal genes without dominance, or with intermediate dominance in heterozygotes, for this tubercle on the basis of eight pedigree data of Mexicans and Papago Indians.

It is rather difficult, however, to regard the CARABELLI's tubercle with widely varied phenotypes as a simple character. It would be more reasonable to suppose, as BIGGERSTAFF (1973) did, that morphological characters, in general, represent the end product of the interaction of a complex system of ontogenetic and environmental factors. He further suggested that the CARABELLI's tubercle did not have a high degree of heritability on the basis of twin data.

In the present study, a heritability estimate of 0.46 was given for the CARABELLI's tubercles of the upper first molars. This suggests that the genetic variability was slightly less than the environmental variability. Another heritability estimate was calculated by the present writer on the basis of AOYAGI's (1967) data from the right-side dentition of 112 MZ and 53 DZ twin pairs. The tetrachoric correlation coefficients obtained for the CARABELLI's tubercles of the upper first molars were 0.89 in MZ twins and 0.77 in DZ twins, and, therefore, a value of 0.23 was given as a heritability estimate corrected for the twins' common environmental factors. This means that in his population the genetic variability of the CARABELLI's tubercles was extremely low or that this tubercle was genetically very stable.

Those results obtained from the present and AOYAGI's (1967) samples are consistent with the view of BIGGERSTAFF (1973) that the genetic variability is not of high degree, though the populations on which they were based were not the same. In short, it is most likely that the genetic variability of the CARABELLI's tubercles in the upper first molars is approximately equal to or lower than the environmental variability.

General considerations on tooth crown characters

Of the non-metric characters observed here, those which seem to have been analyzed successfully in terms of the sample size were the shovelling of the two upper incisors, the DE TERRA's tubercle of the upper first premolar in the male samples, the CARABELLI's tubercle of the upper first molar, the mesiolingual accessory marginal tubercle of the upper first molar, the protostylid of the lower first molar, and the hypoconulid of the lower first molar. Of these seven characters, all but the shovelling of the upper lateral incisor showed relatively low heritability estimates ranging from 0 to 0.5. On the contrary, it is generally accepted that the mesiodistal crown diameters have relatively high heritabilities. Table 12 shows the heritability estimates, as

Table 12. Comparisons of crown components with the whole crown for heritability

Character		Heritability[1]
Upper M1:		
CARABELLI's tubercle		0.46
Mesiolingual accessory marginal tubercle		0.16
Mesiodistal crown diameter:[2]	Male	1.17
	Female	0.81
Lower M1:		
Protostylid		0.17
Hypoconulid		0.49
Mesiodistal crown diameter:[2]	Male	0.83
	Female	0.55

1) Heritability estimates corrected for common environmental factors between twins.
2) These metric characters were analyzed by intraclass correlation on the basis of the same twin samples as used in the present study (MIZOGUCHI, 1977).

an example, for the mesiodistal crown diameters of the upper and lower first molars (MIZOGUCHI, 1977) which were obtained from the same sample set used for the other characters in this paper. Although there were some sex differences for individual crown diameters and an overestimation of heritability for the upper first molar in males, there seems to be no doubt that the heritabilities of the crown diameters are higher than those of the component characters.

This is very interesting, if we take into consideration the fact that each of the non-metric characters studied here is a small part of a tooth crown and that each mesiodistal crown diameter, roughly, represents the whole of the tooth crown which consists of these small component parts (BIGGERSTAFF, 1970). The difference in heritability estimates between the components and the total size may be partly explained by the fact that a molar has a separate cap of enamel for each of the several cusps and that these eventually meet and merge into a compound crown (AREY, 1965). At least one metabolic pathway can be inferred in the process of development between a small component and the crown. If so, the tooth crowns would have a greater chance of being influenced by many more genes and at the same time by many more environmental factors than the small components. If this hypothesis is correct, it can be assumed from the previously-stated data in this paper that the pathway from the small components to the composite crown was more intensively influenced by genetic factors than environment in terms of variability, at least in the population studied here. In other words, it is likely that a small basic component is genetically more stable than a large composite. With this in mind, the lower genetic variability for the mesiodistal crown diameters of the canines as reported by OSBORNE *et al.* (1958) and MIZOGUCHI (1977) may similarly be explained, in addition to the "field concept" explanation, because the canines are simpler in structure than teeth such as molars.

In the present study, genetical analyses of the non-metric characters were quantitatively made by tetrachoric correlation. However, this method can also be utilized to elucidate interrelations between non-metric characters quantitatively. Although there are a few problems such as imperfection of objectivity in obtaining data, it is quite a useful method, at least until what are now called non-metric characters can be measured more easily and precisely. Finally, it should be mentioned that the results obtained here must be further ascertained on the basis of much more data, and, at the same time, that more exact models of dental morphogenesis must be examined from various viewpoints in the future.

Summary and conclusions

Some of the non-metric tooth crown characters were quantitatively analyzed by tetrachoric correlation on the basis of the dental casts from 266 Japanese twin pairs, and heritability estimates corrected for common environmental factors between twins were calculated. Those estimates having relatively high reliability are as follows: 0.22 and 0.75, respectively, for the shovelling of the upper central and lateral incisors, 0.48 for the DE TERRA's tubercle of the upper first premolar in the males, 0.46 for the CARABELLI's tubercle of the upper first molar, 0.16 for the mesiolingual accessory marginal tubercle of the upper first molar, 0.17 for the protostylid of the lower first molar, and 0.49 for the hypoconulid of the lower first molar. Of these characters, the shovelling and the CARABELLI's tubercles which had been studied most intensively were discussed in more detail than the others. Results show that it is likely that most of the tooth crown characters, as small components of a tooth crown, have relatively low genetic variability as compared to environmental variability. It is further suggested, at least in the molar teeth, that the small components have lower genetic variability than the mesiodistal crown diameters which, roughly, represent the whole crown size.

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