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Degree of Bilateral Asymmetry of Nonmetric Tooth Crown Characters Quantified by the Tetrachoric Correlation Method

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Abstract The directional and fluctuating asymmetries of fourteen nonmetric tooth crown characters including shoveling, CARABELLI's tubercle, *etc.* were examined in a Japanese sample. No significant directional asymmetry was found for most of the characters examined. The fluctuating asymmetries were confirmed to be significant for about one third of the characters examined. Tetrachoric correlation coefficients between right and left sides suggested tendencies for relative fluctuating asymmetry in several nonmetric tooth crown characters to be greater in females than in males and to be smaller in the mesial tooth than in the distal one within a morphological tooth class. Furthermore, the relative fluctuating asymmetries of most nonmetric tooth crown characters of cheek teeth were greater than those of the mesiodistal and/or buccolingual crown diameters of the same teeth. After all, it was suggested that the degrees of fluctuating asymmetry in crown components or overall crown size were associated with the adaptive significance of the characters, and that the developmental pathways from most of the crown components to the composite crown which were more intensively influenced by genetic factors than by environmental ones existed during the calcification period.

If the asymmetry of a certain bilateral trait continually exists in a certain species, it should have some adaptive significance for the species. In the entire size of tooth crowns, however, neither directional asymmetry nor antisymmetry of biological origin has been found (MIZOGUCHI, 1986). The asymmetry that certainly exists in the crown size is only fluctuating asymmetry. Regarding this fluctuating asymmetry, there are many investigations (See MIZOGUCHI, 1986, for the historical sketch). In them, the fluctuating asymmetry had been assumed to be caused by random environmental factors without any definite evidence until POTTER and NANCE (1976) and MIZOGUCHI (1987) found that the right-left differences of tooth crown diameters had no or little genetic basis with respect to their variation. Consequently, it seems also unlikely that the nonmetric tooth crown characters which constitute parts of the tooth crowns but are not always present show directional asymmetry or antisymmetry in response to some adaptive demands. What is expected for them, therefore, also seems only fluctuating asymmetry.

In analyzing the fluctuating asymmetries of nonmetric characters, however, there is a problem that the frequencies of asymmetry occurrence can not be compared between different populations under the same conditions when the total incidence of the trait varies from population to population. Although SAUNDERS and MAYHALL (1982) and MAYHALL and SAUNDERS (1986) have proposed a calculation method for estimating the asymmetry frequency of a bilateral trait by removing the category of absence/absence from the data to diminish the effect of the varying population incidences, their method clearly contains another serious problem beacuse the same value can be estimated for the percent right-left discordance in either case with a low total trait incidence and a high inter-side correlation or with a high incidence and a low correlation.

The use of KENDALL's (BAUME and CRAWFORD, 1980; NOSS *et al.*, 1983) or SPEARMAN's (HARRIS and BAILIT, 1980) rank correlation coefficient may be a strategy to overcome the above problem in between-population comparisons. As was stated by MIZOGUCHI (1985), however, the results obtained by such coefficients of association may be affected by the grading procedures. For quantitatively estimating the degrees of fluctuating asymmetry in a nonmetric character which are comparable to one another among the samples obtained by different observers from different populations, the tetrachoric correlation method (PEARSON, 1900; EVERITT, 1910), after all, is deemed the best for the present, though this method is unavailable unless a threshold model can be set up for the character. A drawback that the absolute extent of the fluctuating asymmetry can not be known, however, is shared by this and the PEARSON's product-moment correlation method for metric characters.

Regarding the right-left asymmetry of nonmetric dental traits, many authors have contributed not only toward clarifying the frequencies of asymmetry in various populations (TSUJI, 1958; GARN *et al.*, 1966; SUZUKI and SAKAI, 1973; NOMURA, 1974b; SAUNDERS and MAYHALL, 1982; MAYHALL and SAUNDERS, 1986) but also toward examining the genetic background of the asymmetry (SIEMENS, 1928; COHEN *et al.*, 1970; BIGGERSTAFF, 1973; STALEY and GREEN, 1974; TOWNSEND and BROWN, 1983). Further, some have attempted to measure the degree of the fluctuating asymmetry by using rank correlation coefficients (BAUME and CRAWFORD, 1980; HARRIS and BAILIT, 1980; NOSS *et al.*, 1983), as mentioned above, or by directly quantifying the size of tooth crown components (NOMURA, 1974a; BIGGERSTAFF, 1975; AAS and RISNES, 1979; CORRUCCINI and POTTER, 1981; AAS, 1982a, b). Except for the latter studies, however, the fluctuating asymmetry of the tooth crown characters observed nonmetrically has not been quantified convincingly.

In the present study, the statistical significance for the existence of directional asymmetry is firstly tested for fourteen nonmetric tooth crown characters including shoveling, CARABELLI's tubercle, *etc.* After that, the degrees of fluctuating asymmetry in these characters are estimated by the use of the tetrachoric correlation coefficient. As regards the antisymmetry of the nonmetric tooth crown characters, however, nothing will be done because the number of the grades in expression used here for them is too small to detect the antisymmetry even though it would exist.

Materials and Methods

Two series of samples were used, one being the JP series and the other the OK series. The JP series consists of 161 male and 144 female Japanese from Tokyo, and the OK series is composed of 61 male and female Japanese from Okinawa. The dental plaster casts of these samples were collected by Prof. K. HANIHARA of International Research Center for Japanese Studies, Kyoto, and are now housed in the Department of Anthropology and Prehistory, University Museum, University of Tokyo. The JP and the OK series were used to assess bilateral asymmetry and intraobserver error, respectively, in nonmetric tooth crown characters. Observations were carried out by the present author.

The grading methods for the development of the fourteen nonmetric tooth crown characters analyzed here (Table 1) are all described in MIZOGUCHI (1977). The number of grades for each character is in principle four: absence (0), slightly developed (1), relatively-well-developed (2) and highly-developed (3) expressivities. The well-known grades "*no*, *tr*, *ss* and *s*" for shoveling defined by HRDLIČKA (1920) are completely corresponding to "0, 1, 2 and 3" in the present study. Similarly, "4, 4−, 3+ and 3" in DAHLBERG's (1951) classification for the occlusal surface patterns of maxillary molars correspond to the grades "0, 1, 2 and 3" for the reduction of the hypocone, and the groove patterns "Y, + and X" of mandibular molars defined by JØRGENSEN (1955) to "1, 2 and 3" in the present system.

In addition to the observation of the nonmetric tooth crown characters, the data of the crown diameters were also used to compare the crown components and the overall size of the same crown in their right-left correlations. The materials for this are the JP series. The crown diameters, mesiodistal and buccolingual, were measured by the present author after FUJITA (1949). The details of the crown size asymmetries in the JP series have been reported in MIZOGUCHI (1986).

Directional asymmetry in the nonmetric tooth crown characters was grossly examined using the χ^2-test. Namely, the frequencies of four grades for each character were compared between right and left sides. Then between-sex differences were tested for the frequencies of right-left concordance and discordance also by the use of the χ^2-test on the basis of the direct differences between the grades of right and left sides or ranked asymmetries, not of presence-or-absence data.

For testing the significance of fluctuating asymmetry in each nonmetric trait, the total discordance rate between sides or the total frequency of ranked asymmetries was calculated as follows:

$$\text{Total discordance rate } (\%) = \frac{\sum_{i=1}^{n} |\text{sign } (R_i - L_i)|}{n} \times 100 , \qquad (1)$$

where R_i or L_i is the grade for the right or left side of the i-th individual, n is the sample size, and

Table 1. Significance tests for the directional asymmetry of nonmetric tooth crown characters in males.

Character	Tooth	Side	Sample size[1)]	Expressivity (%)				χ^2-test[2)]	
				0	1	2	3	d.f.	χ^2
Shoveling	UI1	R	158	5.70	18.35	46.84	29.11		
		L	158	5.06	17.72	48.73	28.48	3	0.15
	UI2	R	157	8.92	19.11	47.77	24.20		
		L	157	8.28	21.66	45.22	24.84	3	0.41
DE TERRA'S tubercle	UP1	R	145	63.45	8.97	26.21	1.38		
		L	145	65.52	6.90	26.21	1.38	2	0.44
	UP2	R	136	84.56	5.15	8.82	1.47		
		L	136	83.82	8.82	5.88	1.47	2	1.99
CARABELLI'S tubercle	UM1	R	158	15.19	18.99	48.10	17.72		
		L	158	16.46	21.52	50.00	12.03	3	2.11
	UM2	R	107	66.36	18.69	14.02	0.93		
		L	107	58.88	24.30	14.95	1.87	2	1.38
Reduced hypocone	UM1	R	155	94.84	3.87	0.65	0.65		
		L	155	96.77	1.94	0.00	1.29	1	0.32
	UM2	R	94	5.32	67.02	21.28	6.38		
		L	94	7.45	65.96	18.09	8.51	3	0.87
Mes.-lin. acc. mar. tub.	UM1	R	73	45.21	21.92	26.03	6.85		
		L	73	42.47	31.51	21.92	4.11	2	1.90
	UM2	R	107	92.52	5.61	1.87	0.00		
		L	107	87.85	6.54	4.67	0.93	1	0.84
Dis.-buc. acc. mar. tub.	UM1	R	116	37.07	37.07	25.00	0.86		
		L	116	43.10	32.76	23.28	0.86	2	0.90
	UM2	R	68	70.59	26.47	2.94	0.00		
		L	68	88.24	7.35	4.41	0.00	1	5.44*
Protostylid	LM1	R	144	30.56	20.14	45.14	4.17		
		L	144	32.64	25.00	39.58	2.78	3	1.78
	LM2	R	114	67.54	20.18	12.28	0.00		
		L	114	66.67	16.67	15.79	0.88	2	1.15
Sixth cusp	LM1	R	136	47.79	13.24	14.71	24.26		
		L	136	47.79	19.12	12.50	20.59	3	2.11
	LM2	R	78	60.26	1.28	8.97	29.49		
		L	78	61.54	5.13	3.85	29.49	2	0.08
Seventh cusp	LM1	R	148	90.54	4.05	2.03	3.38		
		L	148	87.16	9.46	0.68	2.70	2	3.99
	LM2	R	109	97.25	2.75	0.00	0.00		
		L	109	96.33	3.67	0.00	0.00	1	0.00
Deflecting wrinkle	LM1	R	127	66.93	5.51	3.15	24.41		
		L	127	74.02	7.87	1.57	16.54	2	3.46
	LM2	R	125	98.40	0.80	0.80	0.00		
		L	125	100.00	0.00	0.00	0.00	1	0.50
Lingual acc. cusp	LP1	R	158	6.96	76.58	15.19	1.27		
		L	158	3.80	79.75	14.56	1.90	2	1.57
	LP2	R	147	6.12	20.41	47.62	25.85		
		L	147	6.12	15.65	53.06	25.17	3	1.37

Table 1. (Continued)

Character	Tooth	Side	Sample size[1]	Expressivity (%)				χ^2-test[2]	
				0	1	2	3	d.f.	χ^2
Reduced	LM1	R	147	84.35	15.65	0.00	0.00		
hypoconulid		L	147	81.63	18.37	0.00	0.00	1	0.22
	LM2	R	87	25.29	42.53	5.75	26.44		
		L	87	29.89	32.18	5.75	32.18	3	2.07
Groove	LM1	R	90	—	83.33	11.11	5.56		
pattern		L	90	—	81.11	13.33	5.56	2	0.21
	LM2	R	53	—	3.77	43.40	52.83		
		L	53	—	7.55	41.51	50.94	1	0.00
Dis.-buc.	LM1	R	134	97.01	0.00	2.24	0.75		
acc. mar. tub.		L	134	96.27	0.00	2.24	1.49	1	0.00
	LM2	R	76	92.11	0.00	2.63	5.26		
		L	76	89.47	1.32	1.32	7.89	1	0.08

[1] The individuals whose right and left teeth were intact enough to observe a character in question were selected.

[2] When the expected value for a certain absolute frequency was less than five or in the limited cases noted by COCHRAN (SIEGEL, 1956), two or more expressivities were grouped into one. In a 2×2 table, YATES' correction (SIEGEL, 1956) was made.

* $P<0.05$; ** $P<0.01$; *** $P<0.001$.

$$\mathrm{sign}\,(x)=\begin{cases}-1 & \text{for } x<0\\ 0 & \text{for } x=0\,.\\ 1 & \text{for } x>0\end{cases}$$

The significance of the total discordance rate between sides was tested using FISHER's (1958) exact probability test on the basis of the total error discordance rate for the same character which can be calculated by substituting double observations on the same subject for R_i and L_i of the formula (1). In the present sutdy, both right and left teeth of the OK series were observed twice at an interval of about eight months and used for this purpose.

Intraclass correlation coefficients between right and left sides were estimated to quantify the degree of fluctuating asymmetry in nonmetric tooth crown characters by the tetrachoric correlation method (PEARSON, 1900; EVERITT, 1910; MIZOGUCHI, 1977). In order to obtain the best estimate of a tetrachoric correlation coefficient, it has been suggested by PEARSON (1900) that a dividing plane which splits a sample into two groups should be located as close to the origin as possible in the normal distribution. The dividing plane was therefore set at the closest location to the origin among the three possible ones between the four expressivities for each trait in the present study. Needless to say, a tetrachoric correlation coefficient can exactly be estimated only where a threshold model with an abrupt threshold in a normal distribution is reasonable, and, if so, is completely comparable to the PEARSON's product-moment correlation coefficient. For estimating intraclass correlation coefficients on tooth crown diameters,

Table 2. Significance tests for the directional asymmetry of nonmetric tooth crown characters in females.

Character	Tooth	Side	Sample size[1)]	Expressivity (%)				χ^2-test[2)]	
				0	1	2	3	d.f.	χ^2
Shoveling	UI1	R	140	2.86	12.86	47.86	36.43		
		L	140	2.86	15.00	41.43	40.71	2	1.17
	UI2	R	138	7.25	20.29	47.83	24.64		
		L	138	7.97	19.57	47.10	25.36	3	0.09
DE TERRA's tubercle	UP1	R	134	64.18	4.48	28.36	2.99		
		L	134	60.45	5.22	33.58	0.75	2	0.41
	UP2	R	104	77.88	5.77	8.65	7.69		
		L	104	78.85	5.77	9.62	5.77	3	0.34
CARABELLI's tubercle	UM1	R	138	5.07	29.71	59.42	5.80		
		L	138	4.35	21.74	68.84	5.07	3	2.80
	UM2	R	95	41.05	34.74	24.21	0.00		
		L	95	48.42	20.00	31.58	0.00	2	5.27
Reduced hypocone	UM1	R	141	94.33	4.96	0.71	0.00		
		L	141	96.45	2.84	0.71	0.00	1	0.32
	UM2	R	93	3.23	53.76	20.43	22.58		
		L	93	8.60	54.84	20.43	16.13	3	3.28
Mes.-lin. acc. mar. tub.	UM1	R	84	51.19	25.00	23.81	0.00		
		L	84	38.10	32.14	29.76	0.00	2	2.92
	UM2	R	91	87.91	10.99	1.10	0.00		
		L	91	87.91	7.69	4.40	0.00	1	0.05
Dis.-buc. acc. mar. tub.	UM1	R	90	30.00	46.67	23.33	0.00		
		L	90	48.89	22.22	28.89	0.00	2	12.41**
	UM2	R	69	63.77	27.54	8.70	0.00		
		L	69	81.16	13.04	4.35	1.45	2	5.41
Protostylid	LM1	R	124	8.06	29.84	62.10	0.00		
		L	124	15.32	21.77	62.10	0.81	2	4.36
	LM2	R	103	58.25	19.42	20.39	1.94		
		L	103	47.57	23.30	28.16	0.97	2	2.40
Sixth cusp	LM1	R	120	37.50	17.50	30.00	15.00		
		L	120	50.00	14.17	19.17	16.67	3	5.53
	LM2	R	86	68.60	5.81	11.63	13.95		
		L	86	66.28	4.65	12.79	16.28	2	0.19
Seventh cusp	LM1	R	128	87.50	10.94	0.00	1.56		
		L	128	89.84	7.81	0.78	1.56	1	0.16
	LM2	R	108	95.37	2.78	1.85	0.00		
		L	108	97.22	2.78	0.00	0.00	1	0.13
Deflecting wrinkle	LM1	R	117	70.09	10.26	3.42	16.24		
		L	117	76.07	8.55	0.85	14.53	2	1.08
	LM2	R	122	100.00	0.00	0.00	0.00		
		L	122	100.00	0.00	0.00	0.00	1	0.00
Lingual acc. cusp	LP1	R	141	0.00	79.43	17.02	3.55		
		L	141	1.42	79.43	15.60	3.55	2	0.10
	LP2	R	123	5.69	20.33	47.97	26.02		
		L	123	5.69	13.01	52.03	29.27	3	2.41

Table 2. (Continued)

Character	Tooth	Side	Sample size[1]	Expressivity (%) 0	1	2	3	χ^2-test[2] d.f.	χ^2
Reduced hypoconulid	LM1	R	132	84.85	13.64	0.00	1.52		
		L	132	80.30	18.18	0.00	1.52	1	0.66
	LM2	R	98	30.61	25.51	0.00	43.88		
		L	98	35.71	31.63	2.04	30.61	2	2.64
Groove pattern	LM1	R	61	—	72.13	22.95	4.92		
		L	61	—	78.69	18.03	3.28	1	0.40
	LM2	R	32	—	3.13	34.38	62.50		
		L	32	—	6.25	46.88	46.88	1	1.01
Dis.-buc. acc. mar. tub.	LM1	R	120	93.33	0.00	6.67	0.00		
		L	120	95.00	1.67	1.67	1.67	1	0.08
	LM2	R	86	93.02	1.16	4.65	1.16		
		L	86	94.19	0.00	4.65	1.16	1	0.00

[1] and [2] See the footnote to Table 1.
* $P<0.05$; ** $P<0.01$; *** $P<0.001$.

the PEARSON's product-moment correlation method was used in practice.

The statistical calculations were carried out with the HITAC M680H/M682H (VOS3) System of the Computer Centre, University of Tokyo. The programs used are X2TST for χ^2-tests and FISHER's exact probability tests, CNDSFQ for total discordance rates, TETRAC for tetrachoric correlation coefficients, and MIVCRL for intraclass product-moment correlation coefficients. These programs were all written in FORTRAN by the present author.

Results

No significant directional asymmetry was found at the 5% level for the nonmetric tooth crown characters examined except the disto-buccal accessory marginal tubercles of the female upper first molar and male upper second molar in the JP series, for which the incidence was higher in the right teeth than in the left (Tables 1 and 2). This trend was also shown for the same trait of the male upper first and female upper second molars (Tables 1 and 2), though not significant statistically. In the OK series, there was no significant directional asymmetry at the 5% level in any nonmetric tooth crown character. But, again in this case, the incidence of the disto-buccal accessory marginal tubercle tends to be higher in the right teeth than in the left, as seen in the JP series.

In 21 of the 28 items, the frequencies of discordance between sides seem to be slightly higher in females than in males, though this tendency is not significant at the 5% level except for the sixth cusp of the mandibular second molar (Table 3).

In Table 4, total discordance rates between right and left sides are compared with the error discordance rates between duplicate observations. Of the 28 items,

Table 3. Significance tests for between-sex differences in the frequencies of right-left concordance and discordance of nonmetric tooth crown characters.

Character	Tooth	Sex	Sample size	Frequency (%)			χ^2-test[1)]	
				$L>R$	$L=R$	$L<R$	d.f.	χ^2
Shoveling	UI1	M	158	1.90	97.47	0.63		
		F	140	5.71	90.71	3.57	1	2.06
	UI2	M	157	8.92	82.80	8.28		
		F	138	10.14	80.43	9.42	2	0.28
DE TERRA's tubercle	UP1	M	145	11.03	74.48	14.48		
		F	134	18.66	65.67	15.67	2	3.59
	UP2	M	136	11.76	75.00	13.24		
		F	104	18.27	63.46	18.27	2	3.80
CARABELLI's tubercle	UM1	M	158	12.03	67.09	20.89		
		F	138	19.57	67.39	13.04	2	5.33
	UM2	M	107	25.23	58.88	15.89		
		F	95	27.37	44.21	28.42	2	5.80
Reduced hypocone	UM1	M	155	1.29	96.13	2.58		
		F	141	0.00	97.87	2.13	1	0.02
	UM2	M	94	9.57	78.72	11.70		
		F	93	8.60	66.67	24.73	2	5.35
Mes.-lin. acc. mar. tub.	UM1	M	73	15.07	67.12	17.81		
		F	84	27.38	59.52	13.10	2	3.66
	UM2	M	107	9.35	85.98	4.67		
		F	91	7.69	86.81	5.49	2	0.23
Dis.-buc. acc. mar. tub.	UM1	M	116	14.66	62.93	22.41		
		F	90	18.89	53.33	27.78	2	1.93
	UM2	M	68	7.35	67.65	25.00		
		F	69	7.25	66.67	26.09	1	0.00
Protostylid	LM1	M	144	13.89	65.97	20.14		
		F	124	12.10	73.39	14.52	2	1.89
	LM2	M	114	17.54	68.42	14.04		
		F	103	26.21	57.28	16.50	2	3.16
Sixth cusp	LM1	M	136	11.03	69.12	19.85		
		F	120	10.00	68.33	21.67	2	0.17
	LM2	M	78	5.13	87.18	7.69		
		F	86	17.44	69.77	12.79	2	7.97*
Seventh cusp	LM1	M	148	7.43	87.16	5.41		
		F	128	4.69	88.28	7.03	2	1.14
	LM2	M	109	3.67	93.58	2.75		
		F	108	2.78	92.59	4.63	1	0.14
Deflecting wrinkle	LM1	M	127	6.30	77.17	16.54		
		F	117	6.84	79.49	13.68	2	0.40
	LM2	M	125	0.00	98.40	1.60		
		F	122	0.00	100.00	0.00	1	0.48
Lingual acc. cusp	LP1	M	158	10.13	82.91	6.96		
		F	141	7.80	81.56	10.64	2	1.62
	LP2	M	147	18.37	66.67	14.97		
		F	123	21.95	64.23	13.82	2	0.55

Table 3. (Continued)

Character	Tooth	Sex	Sample size	Frequency (%)			χ^2-test[1)]	
				L>R	L=R	L<R	d.f.	χ^2
Reduced	LM1	M	147	6.80	89.12	4.08		
hypoconulid		F	132	9.09	86.36	4.55	2	0.56
	LM2	M	87	17.24	68.97	13.79		
		F	98	10.20	65.31	24.49	2	4.49
Groove	LM1	M	90	12.22	76.67	11.11		
pattern		F	61	11.48	70.49	18.03	2	1.46
	LM2	M	53	15.09	67.92	16.98		
		F	32	12.50	53.13	34.38	1	2.46
Dis.-buc.	LM1	M	134	2.24	97.01	0.75		
acc. mar. tub.		F	120	3.33	92.50	4.17	1	1.90
	LM2	M	76	3.95	94.74	1.32		
		F	86	2.33	93.02	4.65	1	0.59

1) See the footnote 2) to Table 1.
* $P<0.05$; ** $P<0.01$; *** $P<0.001$.

nine were found to show significant total discordance rates in males, and twelve in females.

The intraclass correlation coefficients between sides of the nonmetric tooth crown characters were estimated by the tetrachoric correlation methods (Table 5). The between-sex differences in the correlation coefficients were significant for only three of the 28 items at the 5% level. In these items, the correlation coefficients of females were consistently lower than those of males. This tendency, however, is also detectable in many other items, that is, fourteen items in addition to the above three, though not significant, and compatible with the results shown in Tables 3 and 4. Regarding differences between the mesial and distal teeth within a morphological tooth class, four of the twelve nonmetric tooth crown characters which could be compared showed significant differences at the 5% level in males or females or both of them. If non-significant differences were taken into account, a total of eleven traits would show the same trend among the twelve traits. That is, the right-left correlation coefficients of the nonmetric tooth crown characters tend to be higher in the mesial teeth than in the distal ones within the same morphological tooth classes.

In Table 5, the right-left correlation coefficients are also compared with the intraclass correlation coefficients within monozygotic (MZ) twin pairs (MIZOGUCHI, 1985). The results show that the former is slightly higher than the latter in thirteen out of the eighteen items examined, but any of these except the CARABELLI's tubercle of the male upper first molar does not have a significant difference between the two kinds of correlation coefficients at the 5% level.

Finally, in order to compare the right-left correlations of the nonmetric tooth crown characters with those of the entire crown size of the same teeth, intraclass product-moment correlation coefficients between sides were estimated for the crown

Table 4. Significance tests for the total discordance rates between right and left sides of nonmetric tooth crown characters.

Character	Tooth	Total discordance rate (%)[1]			Probability[2]	
		Double obs. (*n*)	Male (*n*)	Female (*n*)	Male/ D. obs.	Fem./ D. obs.
Shoveling	UI1	14.15 (106)	2.53 (158)	9.29 (140)	0.00[3]	0.16[3]
	UI2	18.42 (114)	17.20 (157)	19.57 (138)	0.66[3]	0.47
DE TERRA's	UP1	6.60 (106)	25.52 (145)	34.33 (134)	0.00*	0.00*
tubercle	UP2	18.37 (98)	25.00 (136)	36.54 (104)	0.15	0.00*
CARABELLI's	UM1	26.32 (114)	32.91 (158)	32.61 (138)	0.15	0.17
tubercle	UM2	25.00 (68)	41.12 (107)	55.79 (95)	0.02*	0.00*
Reduced	UM1	8.47 (118)	3.87 (155)	2.13 (141)	0.09[3]	0.02[3]
hypocone	UM2	15.22 (46)	21.28 (94)	33.33 (93)	0.27	0.02*
Mes.-lin.	UM1	13.64 (66)	32.88 (73)	40.48 (84)	0.01*	0.00*
acc. mar. tub.	UM2	15.38 (78)	14.02 (107)[4]	13.19 (91)[4]	0.68[3]	0.74[3]
Dis.-buc.	UM1	20.59 (68)	37.07 (116)[4]	46.67 (90)	0.01*	0.00*
acc. mar. tub.	UM2	17.65 (34)	32.35 (68)	33.33 (69)	0.09	0.07
Protostylid	LM1	31.11 (90)	34.03 (144)	26.61 (124)	0.38	0.81[3]
	LM2	15.71 (70)	31.58 (114)	42.72 (103)	0.01*	0.00*
Sixth cusp	LM1	17.02 (94)	30.88 (136)	31.67 (120)[4]	0.01*	0.01*
	LM2	25.00 (44)	12.82 (78)	30.23 (86)	0.07[3]	0.34
Seventh cusp	LM1	8.70 (92)	12.84 (148)	11.72 (128)	0.22	0.31
	LM2	8.06 (62)	6.42 (109)	7.41 (108)	0.76[3]	0.68[3]
Deflecting	LM1	8.33 (84)	22.83 (127)	20.51 (117)	0.00*	0.01*
wrinkle	LM2	1.96 (102)	1.60 (125)	0.00 (122)	0.70[3]	0.08[3]
Lingual	LP1	17.27 (110)	17.09 (158)	18.44 (141)[4]	0.58[3]	0.47
acc. cusp	LP2	32.65 (98)	33.33 (147)[4]	35.77 (123)[4]	0.51	0.37
Reduced	LM1	18.87 (106)	10.88 (147)	13.64 (132)	0.05[3]	0.18[3]
hypoconulid	LM2	11.29 (62)	31.03 (87)[4]	34.69 (98)[4]	0.00*	0.00*
Groove	LM1	0.00 (24)	23.33 (90)	29.51 (61)	0.00*	0.00*
pattern	LM2	12.50 (16)	32.08 (53)	46.88 (32)	0.11	0.02*
Dis.-buc.	LM1	5.77 (104)	2.99 (134)	7.50 (120)	0.23[3]	0.40
acc. mar. tub.	LM2	6.45 (62)	5.26 (76)	6.98 (86)	0.74[3]	0.58

1) Total discordance rates between double observations on both sides of the OK series as well as between right and left sides in the males and females of the JP series. The numerals in parentheses are the numbers of pairs on which the relevant percentages are based.

2) Probability (one-tailed) by FISHER's (1958) exact probability test for a two-by-two table in which the numbers of concordance and discordance pairs for two samples are arranged.

3) The right-left discordance rate was less than the error discordance rate.

4) There is a significant sample difference between the OK and JP series at the 5% level in the frequencies of expressivities of the right teeth. This means that the significance test for the total discordance rate of the relevant character is not so sensitive.

* Probability showing a significant total discordance rate between right and left sides at the level of 5% or less.

diameters (Table 6). The intraclass correlations for shoveling were found to be significantly higher than those for the mesiodistal crown diameters of the central and lateral incisors of both sexes. On the other hand, most of the nonmetric characters of cheek teeth except the reduced hypocones of the upper molars and a few others showed significantly lower intraclass correlations than the tooth crown diameters.

Discussion

As expected by analogy from the findings on tooth crown diameters (MIZOGUCHI, 1986), no significant directional asymmetry was found in the nonmetric tooth crown characters examined except the distobuccal accessory marginal tubercles of the upper molars (Tables 1 and 2). The systematic asymmetry to the right direction of the distobuccal accessory marginal tubercles can be found commonly in all the cases observed, that is, in the upper first and second molars of both males and females from not only the JP but also the OK series if both statistically significant and non-significant asymmetries are taken into account. The simplest explanation for this fact may be that the directional asymmetry of the distobuccal accessory marginal tubercle is due to the systematic intraobserver error of the present author. If it is not the case, we should think up another explanation to the problem of why only this trait among the fourteen nonmetric ones must show such directional asymmetry or what kind of adaptive demands cause the directional asymmetry. Although some authors have reported directional asymmetries for the depth of lingual fossa in the maxillary central incisor (AAS and RISNES, 1979), the protoconid (CORRUCCINI and POTTER, 1981) and hypoconulid (NOSS *et al.*, 1983) of the mandibular first molar, they seem to be accidental phenomena because most of the other traits observed by these authors have no consistent directional asymmetry. For the present, therefore, it seems safe to regard the directional asymmetry detected in the distobuccal accessory marginal tubercles of the maxillary molars as caused by the present author's systematic observational error. The between-sex difference in the frequencies of right-left concordance and discordance found only for the sixth cusp of the mandibular second molar (Table 3) is also considered to be due to some observational errors because the error discordance rate for this trait is considerably high, resulting in the non-significant discordance rates between sides in both males and females (Table 4).

It was suggested by the significance tests for total discordance rates between sides (Table 4) that the fluctuating asymmetries of most nonmetric tooth crown characters tended to be slightly greater in females than in males. NOSS *et al.* (1983) stated, on the basis of the data from a large sample of 1,528 Pima Indians, that there was no significant between-sex difference in percentage of asymmetry occurrence either for the crown diameters or for the nonmetric crown characters of upper and lower molars. In their table for the percentage asymmetries of eight nonmetric characters of the maxillary or mandibular first and second molars (sixteen cases in total), however, it is shown that the percentage asymmetry of females is greater than that of males in eleven of the

Table 5. Intraclass correlation coefficients between right and left sides for nonmetric tooth crown characters by the tetrachoric correlation method.

Character	Tooth	Sex	Tetrachoric corr. coef. ±S.E. (*n*)		Normal deviate[1]		
			Right & left	MZ twins[2]	Male/ Female	Mesial/ Distal	R-L/ MZ
Shoveling	UI1	M	.999999926 (158)[3]	.9488±.0280 (119)			1.2930
		F	.9882±.0098 (140)	.9650±.0217 (119)	0.8514		0.9744
	UI2	M	.9557±.0236 (157)	.8837±.0509 (118)		1.3273	1.2833
		F	.9285±.0356 (138)	.9034±.0456 (120)	0.6368	1.6168	0.4339
DE TERRA's tubercle	UP1	M	.7506±.0753 (145)	.5943±.1287 (83)			1.0482
		F	.4849±.1157 (134)	.6159±.1358 (89)	1.9247		0.7343
	UP2	M	.2859±.1752 (136)			2.4369*	
		F	.0147±.1929 (104)		1.0407	2.0904*	
CARABELLI's tubercle	UM1	M	.8285±.0567 (158)	.5441±.1191 (126)			2.1560*
		F	.5863±.1071 (138)	.8134±.0724 (102)	1.9986*		1.7567
	UM2	M	.4915±.1289 (107)			2.3931*	
		F	.1332±.1601 (95)		1.7432	2.3523*	
Reduced hypocone	UM1	M	.8944±.0871 (155)	.9583±.0404 (123)			0.6655
		F	.9635±.0413 (141)	.9835±.0179 (116)	0.7168		0.4443
	UM2	M	.8214±.0806 (94)			0.6151	
		F	.9136±.0458 (93)		0.9946	0.8091	
Mes.-lin. acc. mar. tubercle	UM1	M	.8664±.0688 (73)				
		F	.4575±.1461 (84)		2.5321*		
	UM2	M	.5905±.1810 (107)			1.4248	
		F	.7613±.1293 (91)		0.7678	1.5572	
Dis.-buc. acc. mar. tubercle	UM1	M	.7277±.0870 (116)				
		F	.6162±.1206 (90)		0.7498		
	UM2	M	.0212±.2435 (68)			2.7323**	
		F	.3357±.1944 (69)		1.0094	1.2261	
Protostylid	LM1	M	.7911±.0654 (144)	.5109±.1402 (82)			1.8112
		F	.8470±.0590 (124)	.5728±.1340 (80)	0.6346		1.8728
	LM2	M	.5817±.1163 (114)			1.5694	
		F	.6317±.1082 (103)		0.3148	1.7470	

Sixth cusp	LM1	M	.8733±.0484 (136)	.7651±.0937 (84)			1.0260
		F	.8758±.0511 (120)	.8682±.0653 (79)	0.0355		0.0917
	LM2	M	.9591±.0299 (78)			1.5082	
		F	.5571±.1383 (86)		2.8411**	2.1616*	
Seventh cusp	LM1	M	.7042±.1199 (148)				
		F	.7759±.1072 (128)		0.4458		
	LM2	M	—			—	
		F	—		—	—	
Deflecting wrinkle	LM1	M	.7893±.0754 (127)				
		F	.7734±.0843 (117)		0.1406		
	LM2	M	—			—	
		F	—		—	—	
Lingual accessory cusp	LP1	M	.8690±.0589 (158)				
		F	.7985±.0781 (141)		0.7207		
	LP2	M	.8744±.0518 (147)	.5871±.1506 (60)		0.0688	1.8040
		F	.8828±.0529 (123)	.7384±.0977 (89)	0.1135	0.8937	1.2997
Reduced hypoconulid	LM1	M	.8550±.0647 (147)	.8438±.0713 (104)			0.1163
		F	.7798±.0892 (132)	.8554±.0743 (92)	0.6824		0.6512
	LM2	M	.9401±.0375 (87)			1.1380	
		F	.7615±.0879 (98)		1.8689	0.1461	
Groove pattern	LM1	M	.4312±.1855 (90)				
		F	.3491±.2127 (61)		0.2909		
	LM2	M	.6293±.1512 (53)			0.8278	
		F	.2804±.2633 (32)		1.1491	0.2030	
Dis.-buc. acc. mar. tubercle	LM1	M	.9279±.0784 (134)				
		F	.8497±.1104 (120)		0.5775		
	LM2	M	.9198±.0747 (76)			0.0748	
		F	.8235±.1402 (86)		0.6062	0.1468	

1) The normal deviates for the differences of two tetrachoric correlation coefficients were estimated between sexes in right-left correlations; between mesial and distal teeth within the same tooth class in right-left correlations for each sex; and between right-left and MZ twin correlations in each sex, directly using the tetrachoric correlation coefficients and their standard errors, though this method is not so exact because correlation coefficients do not necessarily have normal distributions.

2) Intraclass correlation coefficients within monozygotic twin pairs based on the right teeth alone (Mizoguchi, 1985).

3) Approximation by Pearson's cosine method (Arkin and Colton, 1956; Yasuda, 1969) because the number of the discordance pairs was too small to estimate a tetrachoric correlation coefficient by the ordinary method.

* $P<0.05$; ** $P<0.01$; *** $P<0.001$, by the two-tailed test.

Table 6. Comparisons of nonmetric tooth crown characters with the crown diameters of the teeth carrying the nonmetric ones in intraclass correlation coefficients between right and left sides.

Tooth	Sex	Character	Intraclass corr. coef.[1] (*n*)	Normal deviate[2]	
				MD[3]	BL[4]
UI1	M	Shoveling	1.0000 (158)	62.7562***	
		MD[3]	0.8980 (158)		
	F	Shoveling	0.9882 (140)	8.3817***	
		MD	0.9154 (142)		
UI2	M	Shoveling	0.9557 (157)	4.4448***	
		MD	0.8831 (157)		
	F	Shoveling	0.9285 (138)	2.7546**	
		MD	0.8659 (142)		
UP1	M	DE TERRA's tubercle	0.7506 (145)	−3.8777***	−4.5999***
		MD	0.8906 (155)		
		BL[4]	0.9070 (153)		
	F	DE TERRA's tubercle	0.4849 (134)	−8.3724***	−7.9568***
		MD	0.9127 (142)		
		BL	0.9042 (141)		
UP2	M	DE TERRA's tubercle	0.2859 (136)	−8.2175***	−7.6637***
		MD	0.8545 (150)		
		BL	0.8379 (145)		
	F	DE TERRA's tubercle	0.0147 (104)	−9.4716***	−9.7137***
		MD	0.8599 (120)		
		BL	0.8688 (119)		
UM1	M	CARABELLI's tubercle	0.8285 (158)	−1.1078	1.2006
		Reduced hypocone	0.8944 (155)	1.1735	3.4671***
		M.-l. acc. mar. tub.	0.8664 (73)	0.0892	1.9214
		D.-b. acc. mar. tub.	0.7277 (116)	−3.1087**	−0.9813
		MD	0.8641 (154)		
		BL	0.7804 (153)		
	F	CARABELLI's tubercle	0.5863 (138)	−5.8329***	−3.6566***
		Reduced hypocone	0.9635 (141)	5.0835***	7.1238***
		M.-l. acc. mar. tub.	0.4575 (84)	−6.3220***	−4.4299***
		D.-b. acc. mar. tub.	0.6162 (90)	−4.8184***	−2.9005**
		MD	0.8808 (137)		
		BL	0.8080 (130)		
UM2	M	CARABELLI's tubercle	0.4915 (107)	−3.4939***	−4.2228***
		Reduced hypocone	0.8214 (94)	0.7686	−0.6142
		M.-l. acc. mar. tub.	0.5905 (107)	−2.5291*	−3.4136***
		D.-b. acc. mar. tub.	0.0212 (68)	−6.2539***	−6.6024***
		MD	0.7800 (87)		
		BL	0.8525 (50)		
	F	CARABELLI's tubercle	0.1332 (95)	−4.4222***	−6.6415***
		Reduced hypocone	0.9136 (93)	5.0643***	1.4031
		M.-l. acc. mar. tub.	0.7613 (91)	1.3821	−1.7043
		D.-b. acc. mar. tub.	0.3357 (69)	−2.7192**	−5.0777***

Table 6. (Cont'd-2)

Tooth	Sex	Character	Intraclass corr. coef.[1] (n)	Normal deviate[2] MD[3]	Normal deviate[2] BL[4]
		MD	0.6592 (89)		
		BL	0.8609 (51)		
LP1	M	Ling. acc. cusp	0.8690 (158)	−0.7514	0.5790
		MD	0.8883 (159)		
		BL	0.8520 (157)		
	F	Ling. acc. cusp	0.7985 (141)	−2.2796*	−3.2258**
		MD	0.8781 (141)		
		BL	0.9016 (141)		
LP2	M	Ling. acc. cusp	0.8744 (147)	1.1718	−1.5791
		MD	0.8379 (147)		
		BL	0.9115 (148)		
	F	Ling. acc. cusp	0.8828 (123)	1.0947	0.4974
		MD	0.8475 (121)		
		BL	0.8679 (123)		
LM1	M	Protostylid	0.7911 (144)	−2.5722*	−2.5918**
		Sixth cusp	0.8733 (136)	−0.2511	−0.2627
		Seventh cusp	0.7042 (148)	−4.2923***	−4.3179***
		Deflecting wrinkle	0.7893 (127)	−2.5237*	−2.5422*
		Red. hypoconulid	0.8550 (147)	−0.8768	−0.8908
		Groove pattern	0.4312 (90)	−6.7855***	−6.8124***
		D.-b. acc. mar. tub.	0.9279 (134)	2.2214*	2.2178*
		MD	0.8803 (148)		
		BL	0.8806 (150)		
	F	Protostylid	0.8470 (124)	−1.1032	−3.1697**
		Sixth cusp	0.8758 (120)	−0.2051	−2.2536*
		Seventh cusp	0.7759 (128)	−2.8096**	−4.8933***
		Deflecting wrinkle	0.7734 (117)	−2.7896**	−4.8241***
		Red. hypoconulid	0.7798 (132)	−2.7527**	−4.8530***
		Groove pattern	0.3491 (61)	−6.5105***	−8.1692***
		D.-b. acc. mar. tub.	0.8497 (120)	−1.0163	−3.0647**
		MD	0.8818 (135)		
		BL	0.9278 (135)		
LM2	M	Protostylid	0.5817 (114)	−4.0267***	−4.4001***
		Sixth cusp	0.9591 (78)	3.3826***	3.3864***
		Seventh cusp	—		
		Deflecting wrinkle	—		
		Red. hypoconulid	0.9401 (87)	2.3321*	2.2899*
		Groove pattern	0.6293 (53)	−3.0140**	−3.2617**
		D.-b. acc. mar. tub.	0.9198 (76)	1.4296	1.3452
		MD	0.8690 (55)		
		BL	0.8754 (64)		
	F	Protostylid	0.6317 (103)	−2.8840**	−3.7266***
		Sixth cusp	0.5571 (86)	−3.4599***	−4.2805***
		Seventh cusp	—		
		Deflecting wrinkle	—		

Table 6. (Cont'd-3)

Tooth	Sex	Character	Intraclass corr. coef.[1] (*n*)	Normal deviate[2]	
				MD[3]	BL[4]
		Red. hypoconulid	0.7615 (98)	−1.3050	−2.1070*
		Groove pattern	0.2804 (32)	−4.1133***	−4.7270***
		D.-b. acc. mar. tub.	0.8235 (86)	−0.2751	−1.0352
		MD	0.8372 (61)		
		BL	0.8711 (65)		

1) Tetrachoric correlation coefficients for nonmetric characters and PEARSON's product-moment correlation coefficients for tooth crown diameters.

2) Significance test for the difference in correlation coefficients between the nonmetric character and the mesiodistal or buccolingual diameter of the same tooth based on the normal deviates of the *z*-values for two intraclass correlation coefficients (FISHER, 1958).

3) Mesiodistal tooth crown diameter.

4) Buccolingual tooth crown diameter.

* $P<0.05$; ** $P<0.01$; *** $P<0.001$, by the two-tailed test.

sixteen cases, though not all the differences may be statistically significant. This is consistent with the above findings in the present study. If these results are accepted, it may be said that females generally have a little greater instability in the formation of tooth crown components than males. The rough significance tests for sex differences in right-left correlations appear also to support this hypothesis at least for the CARABELLI's tubercle and mesiolingual accessory marginal tubercle of the upper first molar and for the sixth cusp of the lower second molar (Table 5). It should be noted here again, however, that the error discordance rates for the CARABELLI's tubercle (UM1) and sixth cusp (LM2) are not so low compared with their total discordance rates between sides (Table 4).

In the present study, it was found that at least four nonmetric tooth crown characters revealed significantly higher right-left correlations in the mesial teeth than in the distal ones within the same morphological tooth classes. This implies that such crown components of mesial teeth have lower relative fluctuating asymmetries than those of distal teeth. The same trend has been reported not only for tooth crown diameters (TOWNSEND and BROWN, 1980; MIZOGUCHI, 1986; and others) but for the depth of lingual fossa of incisors (AAS and RISNES, 1979; AAS, 1982a) as well. Also regarding nonmetric tooth crown characters, SAUNDERS and MAYHALL (1982) and MAYHALL and SAUNDERS (1986) have asserted on the basis of the asymmetry frequencies calculated without the bilateral absence category that in such dental traits as CARABELLI's tubercle, protostylid, *etc.*, fluctuating asymmetry generally increases as one goes distally in a tooth field. The results obtained by them, however, are not necessarily accepted because of the ambiguity of their calculation method for percentage asymmetry due to the various combinations of population incidences and population correlations between sides, as was stated previously. But their assertion itself seems to be supported by the present results. Noss *et al.* (1983) have also stated, using Kendall's rank correlation coefficient, that in seven of the eight nonmetric tooth crown characters of maxillary and mandibular molars, the right-left correlations of the second molar are lower than those of the first molar. Furthermore, Harris and Bailit (1980), using Spearman's rank correlation coefficient, have found a similar trend in the "metaconules"[1] of maxillary molars. But, because rank correlation coefficients may be influenced by grading procedures and population incidence and because of the difference of the adopted methods, the rank correlation coefficients presented by them can not directly be compared with the tetrachoric correlation coefficients obtained in the present study. The qualitative tendency is, however, certainly similar in these samples. As regards this gradient within a morphological tooth class, Saunders and Mayhall (1982) and Noss *et al.* (1983) supposed it to be caused by the differences of the environmental factors associated with the timing or period of dental formation, and Mayhall and Saunders (1986) suggested a field effect. This effect, if any, is assumed to provide differential developmental processes for tooth buds. For the present, these thoughts seem not so remote from the truth. That is, it seems likely that the gradient of fluctuating asymmetry of crown components or entire crown size within a tooth class is produced by the mechanisms which may be explained by the field hypothesis (Butler, 1939; Dahlberg, 1945, 1951). Furthermore, according to Corruccini and Potter (1981), the absolute fluctuating asymmetry (in the form of standard deviation or coefficient of variation) in the size of the earlier developing protoconid of the mandibular first molar is smaller than that in the size of the later developing hypoconid or hypoconulid. That is, the protoconid is considered to be environmentally more stable than the hypoconid or hypoconulid. This seems basically the same phenomenon as in the variation of mesiodistal tooth crown diameters expected from the field hypothesis (Butler, 1939; Dahlberg, 1945, 1951). In other words, it is likely that a tooth or a tooth crown component with the most significant adaptive value is both genetically and environmentally least variable or most stable, resulting in the lowest absolute fluctuating asymmetry, and, if the genetic variability is extremely low compared with the environmental one as often expected for such a trait, in the highest relative fluctuating asymmetry or lowest correlation between sides or relatives or in the lowest heritability.

If the right and left parts of a bilateral character are controlled by the same genes as in the case of the like sides of MZ twins, the comparisons of the right-left and MZ twin correlations (Table 5) suggest that the common environmental variance between sides tends to be greater than the common environmental variance between the two members of a MZ twin pair, as expected, though the rough significance tests based on the standard errors of tetrachoric correlation coefficients might not give definite significance to the differences.

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[1] The "metaconule" observed by Harris and Bailit (1980) is probably not a metaconule but the "*tuberculum accessorium posterius externum*" called by Selenka in 1898 (Korenhof, 1960; Fujita, 1973) or distobuccal accessory marginal tubercle in the present study.

Through the comparisons of nonmetric crown characters with the entire crown size of the teeth carrying the nonmetric ones, it is suggested that the relative fluctuating asymmetries of most nonmetric crown components tend to be greater than those of the entire crown size except for a few characters such as the shoveling and reduced hypocone (Table 6). In general, an intraclass correlation coefficient between sides is assumed to be composed of the relative genetic variance and the relative common environmental variance between sides. Then, if the variances due to environmental factors common to both sides can be assumed to be of the same degree for all characters compared to the total variances, the intraclass correlation coefficients between sides may roughly represent the upper limits of the relative genetic variances or heritabilities in a strict sense, and are comparable to one another. If so, most of the nonmetric tooth crown characters are inferred to be genetically more stable or environmentally more variable than the overall crown size. On the basis of Japanese twin data, in fact, MIZOGUCHI (1977) has reported that the heritabilities corrected for common environmental factors between twins are lower in the CARABELLI's tubercle and mesiolingual accessory marginal tubercle of the maxillary first molar and the protostylid and hypoconulid of the mandibular first molar than in the mesiodistal crown diameters of the corresponding teeth. For these findings, MIZOGUCHI (1977) has argued that if at least one metabolic pathway can be assumed in the process of development from a small component to the compound tooth crown, the latter would have a greater chance of being influenced both by many more genes and by many more environmental factors than the former; if so, it can be supposed from the findings that the pathway from a small component to the composite crown is more intensively influenced by genetic factors than by environmental ones in terms of variability. On the other hand, MIZOGUCHI (1980), using the exploratory maximum likelihood factor analysis, has suggested that the environmental variation in the mesiodistal crown diameters of human permanent teeth is caused chiefly during the developmental period before calcification. According to CHRISTENSEN (CORRUCCINI and POTTER, 1981; NOSS *et al.*, 1983), tooth buds before calcification are more asymmetric than the fully calcified teeth. Further, KURISU (1977) has demonstrated on the basis of the molar teeth of mice that the relative fluctuating asymmetry in the calcium ratio, which is the relative calcium content at a developmental stage compared to the final calcium content, increases as the calcification proceeds; then reaches the maximum at the beginning of growth spurt of calcification; and decreases with the further calcification process. From these three findings, it is most likely that the susceptibility of a tooth to environmental factors is highest around or before the beginning of calcification spurt.

After all, integrating all the above findings and hypotheses, it seems that the developmental pathways from most crown components to the composite crown which are more intensively influenced by genetic factors than by environmental ones exist during the calcification period rather than before calcification period, and that the magnitude of fluctuating asymmetry in crown components or overall size is associated with the adaptive significance of the characters or the timing of appearance in the ontogenetic processes. It should be noted, however, that the degree of fluctuating asymmetry can also be changed by congenital abnormalities (CORRUCCINI and POTTER, 1981; TOWNSEND and BROWN, 1983) or various environmental stressors generated experimentally (SIEGEL and MOONEY, 1987).

Conclusions

In most nonmetric tooth crown characters, it is probable that there is no significant directional asymmetry. The degree of fluctuating asymmetry in crown components or overall crown size seems to be associated with the adaptive significance of the characters. The developmental pathways from most of crown components to the composite crown which are more intensively influenced by genetic factors than by environmental ones are inferred to exist during the calcification period.

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