Bull. Natn. Sci. Mus., Tokyo, Ser. D, 19, December 22, 1993

Adaptive Significance of the CARABELLI Trait*

By

Yuji MIZOGUCHI

Department of Anthropology, National Science Museum, Tokyo

Abstract Ecological correlations between the CARABELLI trait and environmental factors were estimated on the basis of the 23 pooled samples worldwide. These ecological correlations and the canonical correlation analyses of them suggest that those people who, or whose ancestors, have been adopting a lifeway with the milking in relatively dry regions have the narrower nose, buccolingually smaller molars, more highly-developed CARABELLI trait, and weaker incisor shoveling. From these findings and previous studies, it is inferable that the CARABELLI trait on the maxillary first molar was formed as a structure resisting excessive biomechanical stresses on the first molar itself which had already been reduced.

The CARABELLI trait is a dental character with the wide range of variation from a pit or groove to a tubercle or cusp that occasionally appears on the mesiolingual surface of the maxillary molar crown. In general, this character is said to have been described in 1842, for the first time, by Georg CARABELLI EDLEN VON LUNKASZPRIE, Professor of Dental Surgery at the Petrograd Academy and Dentist to the Court (KIESER, 1985). But, according to KORENHOF (1960), the CARABELLI trait may have already been noticed by L.F.E. ROUSSEAU as early as 1827, or even earlier, in 1755, by B. S. ALBINI.

Among dental characters, the CARABELLI trait has most frequently been studied by many authors from various viewpoints: geographical distribution (WEIDENREICH, 1937; TRATMAN, 1950; KRAUS, 1959; SCOTT, 1972, 1980; SUZUKI and SAKAI, 1973; HANIHARA *et al.*, 1975), the cingulum and CARABELLI trait in primates (WEIDENREICH, 1937; SAHEKI *et al.*, 1959; KORENHOF, 1960; FRISCH, 1963, 1965; SAHEKI, 1966; GODEFROIT, 1990), phylogenetic origin (WEIDENREICH, 1937; DAHLBERG, 1951; ROBINSON, 1956; KORENHOF, 1960; FRISCH, 1965; SAKAI and HANAMURA, 1967, 1971; SAKAI *et al.*, 1969–1970; HERSHKOVITZ, 1971; SUZUKI and SAKAI, 1973), ontogenetic origin (KRAUS and JORDAN, 1965), structures on the enamel-dentin junction (KORENHOF, 1960, 1982; SAKAI and HANAMURA, 1967, 1971), differences among the permanent molars (LASKER and LEE, 1957; KORENHOF, 1960), difference between the deciduous and permanent dentitions (TRATMAN, 1950; NOMURA, 1974; TOWNSEND and BROWN, 1981; TOWNSEND and BEOWN, 1983; KIESER, 1984; BERMÚDEZ DE CASTRO, 1989), sexual dimorphism (GARN *et al.*, 1966a; PINTO-CISTERNAS and FIGUEROA, 1968; TOWN-

* An earlier version of this paper was read at the 13th International Congress of Anthropological and Ethnological Sciences at Mexico City, Mexico, July 29, 1993.

SEND and BROWN, 1981; KIESER, 1984), mode of inheritance and heritability (SIEMENS, 1928; KORKHAUS, 1930; WADA, 1938; SHIMIZU, 1939; LASKER, 1950; KRAUS, 1951; TSUJI, 1958; DAHLBERG, 1963a; AOYAGI, 1967; TURNER, 1967a, 1969; GOOSE and LEE, 1971; LEE and GOOSE, 1972a; SOFAER *et al.*, 1972; BIGGERSTAFF, 1973; HARRIS, 1976; MIZOGUCHI, 1977; ZOUBOV and NIKITYUK, 1978; BERRY, 1978; KOLAKOWSKI *et al.*, 1980; TOWNSEND and BROWN, 1981; SCOTT and POTTER, 1984; NICHOL, 1989; TOWNSEND *et al.*, 1992), influence of genetic diseases (KIRVESKARI and ALVESALO, 1982; TOWNSEND and BROWN, 1983), influence of fluoride (COX *et al.*, 1961); influence of hybridization (HANIHARA, 1956, 1957, 1963, 1968; PINTO-CISTERNAS and FIGUEROA, 1968; HANIHARA and HANIHARA, 1989), associations with other characters (DIETZ, 1944; MOORREES, 1957; TSUJI, 1958; KORENHOF, 1960; PINTO-CISTERNAS and FIGUEROA, 1968; SAKAI *et al.*, 1969–1970; SOFAER *et al.*, 1972; SUZUKI and SAKAI, 1973; MIZOGUCHI, 1976, 1978, 1985; SCOTT, 1978; SCOTT and DAHLBERG, 1982), the significance of existence (DAHLBERG, 1951, 1963a, b; MOORREES, 1957; KORENHOF, 1960; GARN *et al.*, 1966b; KEENE, 1968; BANG and HASUND, 1972; LOMBARDI, 1975; REID *et al.*, 1991, 1992), *etc.*

As regards its adaptive significance or function, however, no systematic investigations have been pursued until now, though some of the above authors have discussed it on the basis of limited morphological observations. In the present study, the frequency data of the CARABELLI trait for about 550 samples of modern humans in the world were collected by literature search to elucidate its functional or adaptive role by estimating ecological correlations of the CARABELLI trait with some environmental factors.

Although many terms have been proposed or used to designate this variable trait [*e.g.*, according to MEREDITH and HIXON (1954), KORENHOF (1960) and others, "tuberculum anomalum (by CARABELLI, originally 'tuberculus anomalus')," "fifth lobe," "supplemental cusp," "accessory cusp," "mesiolingual elevation or prominence," "fifth cusp," "tuberculum CARABELLI," "CARABELLI's anomaly," "CARABELLI('s) tubercle," "CARABELLI('s) protuberance," "CARABELLI('s) cusp," "CARABELLI complex," "CARABELLI's polymorphism," "CARABELLI('s) trait," *etc.*], the "CARABELLI trait" is employed as a general term for this character in the present paper, with CARABELLI's "cusp," "tubercle," "groove (furrow)" or "pit" being used for each of various expressions of the CARABELLI trait.

Materials and Methods

As mentioned above, the frequency data of the CARABELLI trait on about 550 samples worldwide were first collected from the relevant literature. Then, in order to compare these data with one another as exactly as possible, they were transformed, once, to four-graded data according to the grading system of MIZOGUCHI (1977) and, finally, into presence-or-absence data.

In MIZOGUCHI's (1977) grading system, the continuous expressions of the CARA-

Table 1. Supposed inter-observer errors in three possible dichotomous classifications for the CARABELLI trait of the maxillary first molar.[1)]

Observers	No. of individuals or teeth	Frequency (%)					
		Classification A		B		C	
		Absence (0)	Presence (1+2+3)	Absence (0+1)	Presence (2+3)	Absence (0+1+2)	Presence (3)
Japanese population[2)]:							
TAKEHISA (1957)	4196	63.80	36.20	79.93	20.07	95.66	4.34
SAKAI & HANAMURA (1967)	78	42.31	57.69	69.23	30.77	87.18	12.82
MIZOGUCHI (1985)	301	10.96	89.04	35.22	64.78	88.04	11.96
Chi-square test							
D.F.		2		2		2	
χ^2-value		336.9		317.8		44.8	
Probability		<0.001		<0.001		<0.001	
European-derived American population[3)]:							
TAKEHISA (1957)	320	69.69	30.31	76.56	23.44	89.69	10.31
DAHLBERG (1963a)	140	15.00	85.00	37.14	62.86	45.71	54.29
MAYHALL *et al.* (1982)	90	24.44	75.56	47.78	52.22	93.33	6.67
Chi-square test							
D.F.		2		2		2	
χ^2-value		141.3		73.1		127.1	
Probability		<0.001		<0.001		<0.001	

[1)] All samples were assumed to be derived from the same population, Japanese or European-derived American.

[2)] The samples combined for sexes were used.

[3)] Only males were compared.

BELLI trait as a morphological character are partitioned as follows: total absence (grade 0), pit or groove (grade 1), slight tubercle (grade 2) and pronounced tubercle or cusp (grade 3). This grading system is basically the same as that of KRAUS (1951) and of BAILIT *et al.* (1968). Further, the grade "0" of MIZOGUCHI (1977) is equivalent to "a" of DAHLBERG (1963a) or "0" of TURNER (1979) and SCOTT (1980); the grade "1," to "b+c" or "1+2"; the grade "2," to "d+e" or "3+4"; and the grade "3," to "f+g+h" or "5+6+7."

In the present study, the transformation of data was carried out mainly to get the data which are as free as possible of the errors due to differences among classification methods. Further, for eliminating other errors, several samples from a population were pooled into one sample on the assumption that all possible errors such as sampling error, intra- and interobserver errors, *etc.* randomly affect the observed frequencies of a character in question. Here, the median was used as a value representing the frequency for the pooled sample or the original population.

The practical procedure of transformation from four-graded data to two-graded one is as follows. First, the best combination as the "presence" grade was sought among the three, *i.e.*, the combination of the grades 1+2+3, the combination of the grades 2+3, and the grade 3 only. For carrying this out, those populations from which many samples had been extracted were looked for among the samples collected. In result, the Japanese and European-derived American populations were found to be as such. On the assumption that the samples observed by different investigators were extracted from a homogeneous population, the chi-square test (SIEGEL, 1956) was applied to these data (Table 1). In the Japanese population, the least among-sample difference was found for the grade 3, but, in the case of the European-derived Americans, it was the combination of the grades 2+3. In the present study, therefore, both of them were adopted for the comparison of samples. As a result of this screening, the number of the samples available reduced to 346 (Table 2). Furthermore, these samples were pooled according to geographical regions, and, finally, only the data combined for sexes were used because the data combined for sexes had more frequently been reported by previous investigators than those of males or females alone. After all, the number of the pooled samples became only 23 (Table 3).

In the next place, for each of these twenty-three pooled samples, the data on mean values or frequencies of other dental characters, somatometric traits, climatic information and lifeway were collected, again, by literature search (Table 3). To evaluate the association of the CARABELLI trait with each of such morphological or environmental variables, SPEARMAN's and KENDALL's rank correlation coefficients (SIEGEL, 1956) as well as YULE's coefficient of association and the four-fold point correlation coefficient (YASUDA, 1969) were utilized. In the latter two cases, all the data were transformed into those of presence-or-absence on the basis of each median value in advance.

Furthermore, canonical correlation analyses (ANDERSON, 1958; ASANO, 1971; OKUNO *et al.*, 1971, 1976) were carried out to examine the overall interrelationships between the variable group of maxillary molar characters including the CARABELLI trait and that of environmental factors. In general, however, correlation coefficients based on sample means or frequencies, *i.e.*, ecological correlations (YASUDA, 1969), as used here, are not guaranteed to be normally distributed. The bootstrap method (EFRON, 1979a, b, 1982; DIACONIS and EFRON, 1983; MIZOGUCHI, 1993) was, therefore, used for the significance tests of the canonical correlation coefficients estimated in such a way.

The statistical calculations were conducted with the mainframe, HITAC M-880 (VOS3) System, of the Computer Centre, the University of Tokyo. The programs used here are X2TST, RKCNCT, CNDSFQ and CNCRSS, which were written by the present author in FORTRAN for chi-square tests, the estimation of rank correlation coefficients, the estimation of association coefficients between all-or-none attributes, and canonical correlation analyses, respectively.

Table 2. Incidence of the Carabelli trait of the maxillary first molar in modern human populations.

Ser. No.	Sample	Sex[1)]	No. of indiv.	No. of teeth	Frequency (%) Grades 2+3	Grade 3	Source
NORTH ASIA							
1	Nganasan (P-ov Taymyr, Russia)	M+F	103		11.6		Aksjanova ('79)
2	Nenets (N Siberia)	M+F	50		16.0		Subow ('72)
3	Nenets	M+F	898		21.7		Aksjanova ('74, '75, '76, '79)
4	Tatar (W Siberia)	M+F	87		27.5		Zoubov & Haldeyeva ('89)
5	Sel'kup (W Siberia)	M+F	216		15.3		Dubov ('85)
6	Ugrians (near the Urals)	M+F	140		35.7		Aksjanova ('74, '75, '76, '79)
7	Khakas (S Siberia)	M+F	376		28.5		Haldeyeva ('79)
8	Evenki (Siberia)	M+F	144		15.3		Dubov ('85)
9	Buryats	M+F	124		3.4		Haldeyeva ('79)
10	Mongolians	M+F	211		4.2		Batujeff (1896)
11	Mongolians	M+F		666	2.3		Masamori ('42)
12	Mongolians	M+F		392	23.0		Yabuki ('42)
13	Mongolians	M+F	241		25.3		Zoubov & Zolotareva ('80)
EAST ASIA							
14	Chinese (NE China)	M+F		1250	2.1		Oshima ('38)
15	Chinese (NE China)	M+F		80		17.5	T. Hanihara ('91a)
16	Chinese	M+F		2500	4.2		Oshima ('37)
17	Chinese	M+F	314		14.3	4.1	Takehisa ('57)
18	Chinese	M+F	604		20.7		Jien ('70)
19	Chinese	M+F	108		3.7		Lee & Goose ('72a)
20	Chinese	M+F	134		10.4		Lee & Goose ('72b)
21	Chinese (Canton & Hong Kong)	M+F	134		10.4	5.2	Goose ('77)
22	Chinese (Fucheng)	F+M		5649	7.0		Maruyama ('33)
23	Ami (Taiwan)	M		228	33.3	11.0	Liu ('77)
24	Ami (Taiwan)	F		86	39.5	9.3	Liu ('77)
25	Ami (Taiwan)	M+F		314	35.0	10.5	Liu ('77)
26	Aim (Taiwan)	M+F	146		38.4	21.2	Manabe *et al.* ('92)
27	Atayal (Taiwan)	M		114	36.8	0.0	Liu ('77)
28	Atayal (Taiwan)	F		74	32.4	9.5	Liu ('77)
29	Atayal (Taiwan)	M+F		188	35.1	3.7	Liu ('77)
30	Atayal (Taiwan)	M+F	335			2.7	Takei ('90)
31	Bunun (Taiwan)	M+F	94		43.6	21.3	Manabe *et al.* ('91)
32	Paiwan (Taiwan)	M+F		30	63.3		Ma ('39)
33	Yami (Taiwan)	M+F	197		33.0	12.7	Manabe ('89)
34	Koreans	M+F		78	28.2		Enishi ('39)
35	Koreans	M+F	388		17.3	2.6	Takehisa ('57)

Table 2. (Cont'd—2)

Ser No.	Sample	Sex[1)]	No. of indiv.	No. of teeth	Frequency (%) Grades 2+3	Frequency (%) Grade 3	Source
36	Koreans	M+F	109		24.8		SIKHIMBAEVA ('86, '87)
37	Sakhalin Ainu	M+F		36	5.6		MORIMOTO ('39)
38	Sakhalin Ainu	M+F	15		13.3		SUZUKI & SAKAI ('57)
39	Sakhalin Ainu	M+F		27		11.1	T. HANIHARA ('91b)
40	Ainu (Hidaka)	M+F	105			9.5	HANIHARA *et al.* ('75)
41	Ainu (of less than 1/8 non-Ainu admixture, Hokkaido)	M+F	77		15.6	10.4	TURNER & HANIHARA ('77)
42	Ainu (Japan)	M+F	51		4.0		MATSUMURA ('90)
43	Ainu (Central & E Hokkaido)	M+F		150		8.0	T. HANIHARA ('91a)
44	Ainu (SW Hokkaido)	M+F		90		2.2	T. HANIHARA ('91a)
45	Sakhalin Ainu-Japanese hybrids	M+F	10		10.0		SUZUKI & SAKAI ('57)
46	Japanese (Yamagata)	M	204		36.8	11.8	SAKAI *et al.* ('69–'70)
47	Japanese (Nagano)	M+F		418	12.4	0.7	KAMIJO *et al.* ('81)
48	Japanese (Chubu)	M	173		22.5		SUZUKI and SAKAI ('57)
49	Japanese (Nagano & Yamanashi)	M	286		28.0		SUZUKI and SAKAI ('73)
50	Japanese (Nagano & Yamanashi)	F	251		19.9		SUZUKI and SAKAI ('73)
51	Japanese (Nagano & Yamanashi)	M+F	537		24.2		SUZUKI and SAKAI ('73)
52	Japanese (Niigata)	M+F		110	32.7	2.7	KAMIJO *et al.* ('81)
53	Japanese (Toyama)	M+F		48	35.4	6.3	KAMIJO *et al.* ('81)
54	Japanese (Hokuriku)	M+F		393	17.6		YAMADA ('31)
55	Japanese (Ibaraki)	M+F		1727	39.1	2.7	KAMIJO *et al.* ('81)
56	Japanese (Saitama)	M+F		3224	33.3	4.6	KAMIJO *et al.* ('81)
57	Japanese (Chiba)	M+F		2756	35.2	4.6	KAMIJO *et al.* ('81)
58	Japanese (Tokyo)	M		55	30.9	9.1	KIMURA *et al.* ('78)
59	Japanese (Tokyo)	F		32	37.5	18.8	KIMURA *et al.* ('78)
60	Japanese (Tokyo)	M+F		87	33.3	12.6	KIMURA *et al.* ('78)
61	Japanese (Tokyo)	M+F		4445	26.2	2.7	KAMIJO *et al.* ('81)
62	Japanese (Tokyo)	M	160		65.0	17.5	MIZOGUCHI ('85)
63	Japanese (Tokyo)	F	141		64.5	5.7	MIZOGUCHI ('85)
64	Japanese (Tokyo)	M+F	301		64.8	12.0	MIZOGUCHI ('85)
65	Japanese (MZ twins, Tokyo)	M	132		63.6	18.9	MIZOGUCHI ('85)
66	Japanese (MZ twins, Tokyo)	F	118		50.8	7.6	MIZOGUCHI ('85)
67	Japanese (MZ twins, Tokyo)	M+F	250		57.6	13.6	MIZOGUCHI ('85)
68	Japanese (Kanagawa)	M+F		1711	19.6	1.2	KAMIJO *et al.* ('81)
69	Japanese (Kanto)	M+F	4196		20.1	4.3	TAKEHISA ('57)

Table 2. (Cont'd—3)

Ser. No.	Sample	Sex[1)]	No. of indiv.	No. of teeth	Frequency (%) Grades 2+3	Grade 3	Source
70	Japanese (Shizuoka)	M+F		1894	42.1	5.9	KAMIJO *et al.* ('81)
71	Japanese (W Japan)	M+F	44		36.4		KOBAYASHI ('89)
72	Japanese (Honshu)	M+F		72		6.5	T. HANIHARA ('91a)
73	Japanese (Tokyo & Hokkaido)	M+F	444			6.5	HANIHARA *et al.* ('75)
74	Japanese	M+F		190	13.7		SUZUKI ('20)
75	Japanese	M+F		954	12.3		MORI ('32)
76	Japanese	M+F	946		10.8		HIRAKAWA ('40)
77	Japanese	M+F	73		23.3		AOYAMA ('48)
78	Japanese	M+F		416	8.4		AOYAMA ('48)
79	Japanese	M		178	20.8		MA ('49)
80	Japanese	F		508	10.8		MA ('49)
81	Japanese	M+F		686	13.4		MA ('49)
82	Japanese	M		122	45.8		SHIKAI ('57)
83	Japanese	F		129	19.4		SHIKAI ('57)
84	Japanese	M+F		251	32.3		SHIKAI ('57)
85	Japanese	M		4737		44.5	SUMIYA ('59)
86	Japanese	F		3050		40.1	SUMIYA ('59)
87	Japanese	M+F		7787		42.7	SUMIYA ('59)
88	Japanese	M+F		78	30.8	12.8	SAKAI & HANAMURA ('67)
89	Japanese	M+F	89		33.7	14.6	SAKAI ('68)
90	Japanese	M+F	59		8.5		MATSUMURA ('90)
91	Japanese (Aogashima)	M+F		72		13.9	T. HANIHARA ('90)
92	Japanese (Amami Islands)	M+F	183			10.9	T. HANIHARA ('91c)
93	Japanese (Tokunoshima)	M		114		14.9	T. HANIHARA ('92)
94	Japanese (Okinawa)	M+F	60			5.0	HANIHARA *et al.* ('74)
95	Japanese (Okinawa)	M+F		66		9.1	T. HANIHARA ('91a)
96	Japanese (Nansei Islands)	M+F		89		4.5	T. HANIHARA ('91a)
97	Japanese (Ishigaki Island)	M		48	27.1	12.5	KIMURA *et al.* ('78)
98	Japanese (Ishigaki Island)	F		47	6.4	4.3	KIMURA *et al.* ('78)
99	Japanese (Ishigaki Island)	M+F		95	16.8	8.4	KIMURA *et al.* ('78)
100	Japanese (Sakishima Islands)	M+F	20			5.0	T. HANIHARA ('91c)
SOUTH ASIA							
101	Tibetans (Dharamsala, India)	M	33		0.0	0.0	SHARMA ('83)
102	Tibetans (Dharamsala, India)	F	36		0.0	0.0	SHARMA ('83)

Table 2. (Cont'd—4)

Ser. No.	Sample	Sex[1]	No. of indiv.	No. of teeth	Frequency (%) Grades 2+3	Grade 3	Source
103	Tibetans (Dharamsala, India)	M+F	69		0.0	0.0	SHARMA ('83)
104	Bhutanese	M		76	12.8	5.1	PRAKASH *et al.* ('79)
105	Indians (MZ twins, Chandigarh)	M+F		80[2]		2.5	KAUL *et al.* ('85)
106	Indians (DZ twins, Chandigarh)	M+F		120[2]		18.3	KAUL *et al.* ('85)
107	Jats (Haryana, India)	M	304		39.8	22.0	KAUL & PRAKASH ('81)
108	Jats (Haryana, India)	F	262		30.9	10.3	KAUL & PRAKASH ('81)
109	Jats (Haryana, India)	M+F	566		35.7	16.6	KAUL & PRAKASH ('81)
110	Hindus (Gujarat, India)	M+F		978		27	JOSHI *et al.* ('72)
111	Indians	M+F	136			7.4	NOMURA ('74)
112	Indians	M	101			8.9	SCOTT ('80)
113	Indians	F	95			9.5	SCOTT ('80)
114	Indians	M+F	196		30.6	9.2	SCOTT ('80)
115	Indians	M+F	1032		21.0		ZOUBOV & HALDEYEVA ('89)
116	Pashtuns (Afghanistan)	M	71		35.2	14.1	SAKAI *et al.* ('69–'70)
117	Tajiks (Afghanistan)	M	22		27.3	9.1	SAKAI *et al.* ('69–'70)
118	Tadjik	M+F	1708		34.3		ZOUBOV & HALDEYEVA ('89)
CENTRAL ASIA							
119	Kalmuck (N of Caspian Sea)	M+F	154		22.7		SIKHIMBAEVA ('86, '87)
120	Kazaks	M+F	3222		50.8		ZOUBOV & HALDEYEVA ('89)
121	Kirghiz	M+F	215		19.9		ZOUBOV & HALDEYEVA ('89)
122	Uzbek	M+F	413		33.0		ZOUBOV & HALDEYEVA ('89)
123	Turkmen	M+F	565		45.9		ZOUBOV & HALDEYEVA ('89)
124	Dagestan	M+F	1819		40.6		GADZHIEV ('79)
WEST ASIA							
125	Kurdish Jews (Iraq, Turkey & Iran)	M+F	156		83.3		SOFAER *et al.* ('86)
126	Turks	M+F	307		28.6		MINKOV ('77, '81)
127	Bedouins (Negev Desert, Israel)	M+F	77		59.7		SOFAER *et al.* ('86)
128	Circassians (K'far Kama, Israel)	M+F	56		75.0		SOFAER *et al.* ('86)

Table 2. (Cont'd—5)

Ser. No.	Sample	Sex[1)]	No. of indiv.	No. of teeth	Frequency (%) Grades 2+3	Grade 3	Source
129	Druse (Israel)	M+F	154		70.1		SOFAER *et al.* ('86)
130	Samaritans (Israel)	M+F	98		43.9		SOFAER *et al.* ('86)
131	Habbanite Jews (Yemen)	M+F	205		72.2		SOFAER *et al.* ('86)
132	Arab	M+F	235		34.5		ZOUBOV & HALDEYEVA ('89)
SOUTHEAST ASIA							
133	Vietnamese	M+F		192	16		GUIGUI ('74)
134	Vietnamese	M+F	373		23.2		AKSJANOVA *et al.* ('86)
135	Aeta (Philippines)	M+F		20		25.0	T. HANIHARA ('91a)
MELANESIA							
136	W Nakanai (New Britain)	M	46		17.4	6.5	TURNER & SWINDLER ('78)
137	Nasioi (Bougainville)	M+F	134		9.0	7.5	BAILIT *et al.* ('68)
138	Melanesians (Solomon Islands)	M	128			17.2	SCOTT ('80)
139	Melanesians (Solomon Islands)	F	153			15.7	SCOTT ('80)
140	Melanesians (Solomon Islands)	M+F	285		27.4	16.1	SCOTT ('80)
MICRONESIA							
141	Yapese (Yap Island)	M+F	24		16.7	4.2	HARRIS *et al.* ('75)
142	Micronesians (Guam)	M+F	89		12		LEIGH ('72)
143	Micronesians	M+F	134		19.0		ZOUBOV & HALDEYEVA ('89)
AUSTRALIA							
144	Aborigines (Kalumburu)	M+F	37			27.0	RICHARDS & TELFER ('79)
145	Aborigines (W Australia)	M+F		27		18.5	T. HANIHARA ('91a)
146	Aborigines (Yuendumu)	M+F	159			15.7	HANIHARA *et al.* ('75)
147	Aborigines (Yuendumu)	M+F	80			16.2	RICHARDS & TELFER ('79)
148	Aborigines (Yuendumu)	M	205			23.9	TOWNSEND & BROWN ('81)
149	Aborigines (Yuendumu)	F	161			14.3	TOWNSEND & BROWN ('81)
150	Aborigines (Yuendumu)	M+F	366			19.7	TOWNSEND & BROWN ('81)
151	Aborigines (Haast's Bluff)	M+F	35			14.3	RICHARDS & TELFER ('79)

Table 2. (Cont'd—6)

Ser. No.	Sample	Sex[1)]	No. of indiv.	No. of teeth	Frequency (%) Grades 2+3	Grade 3	Source
POLYNESIA							
152	Hawaiians	M+F	97		33.0	25.8	SCOTT ('80)
153	Pukapuka (Cook Islands)	M+F	39		30.8	2.6	KAWAMOTO ('89)
154	Rarotonga (Cook Islands)	M+F	36		38.9	5.6	KAWAMOTO ('89)
155	Mangaia (Cook Islands)	M+F	92		35.9	12.0	KAWAMOTO ('89)
156	S Cook Islanders	M+F	77		33.8	2.6	KAWAMOTO ('89)
157	Cook Islanders	M+F	34		38.2	8.8	KAWAMOTO ('89)
158	Easter Islanders	M+F	105		20.0	10.5	TURNER & SCOTT ('77)
159	Easter Islanders	M+F	98		15.3	6.1	SCOTT ('80)
ARCTIC							
160	Chukotski (Russia)	M+F	690		16.8		DUBOVA & TEGAKO ('83)
161	Inuits (Wainwright, Alaska)	M		103	60.2	26.2	HERSHEY ('79)
162	Inuits (Wainwright, Alaska)	F		125	71.2	26.4	HERSHEY ('79)
163	Inuits (Wainwright, Alaska)	M+F		228	66.2	26.3	HERSHEY ('79)
164	Inuits (Alaska)	M+F		96	16.7		BANG & HASUND ('72)
165	Inuits (Alaska)	M+F	23			13.0	HANIHARA *et al.* ('75)
166	NW Inuits	M+F	26			7.0	DAHLBERG ('51)
167	Inuits (Karluk, Kodiak Island)	M+F	61			16.4	TURNER ('67a)
168	Inuits (Old Harbor, Kodiak Island)	M+F	101			26.7	TURNER ('67a)
169	Inuits (Igloolik, Canada)	M	125		67.2	10.4	MAYHALL ('79)
170	Inuits (Igloolik, Canada)	F	99		59.6	7.1	MAYHALL ('79)
171	Inuits (Igloolik, Canada)	M+F	224		63.8	8.9	MAYHALL ('79)
172	Inuits (Hall Beach, Canda)	M	34		76.5	14.7	MAYHALL ('79)
173	Inuits (Hall Beach, Canada)	F	31		48.4	6.5	MAYHALL ('79)
174	Inuits (Hall Beach, Canada)	M+F	65		63.1	10.8	MAYHALL ('79)
175	Labrador Inuits (Canada)	M+F	23			0.0	DAHLBERG ('51)
176	Inuits (E Greenland)	M+F	25			0.0	PEDERSEN ('49)
177	Inuits (E Greenland)	M+F	106			0.0	PEDERSEN ('49)
178	Inuit-Aleut (USA)	M+F	112		15.2	0.9	SCOTT ('80)

Table 2. (Cont'd—7)

Ser. No.	Sample	Sex[1)]	No. of indiv.	No. of teeth	Frequency (%) Grades 2+3	Frequency (%) Grade 3	Source
NORTH AMERICA							
179	Blackfoot (N USA)	M+F	41			12.0	DAHLBERG ('51)
180	Pima	M+F	322			8.0	DAHLBERG ('51)
181	Pima (Arizona)	M		200	63.5	31.5	DAHLBERG ('63a)
182	Pima (Aizona)	F		200	48.5	17.0	DAHLBERG ('63a)
183	Pima (Arizona)	M+F		400	56.0	24.3	DAHLBERG ('63a)
184	Pima	M+F	216			6.9	HANIHARA *et al.* ('75)
185	Pima (Arizona)	M	609		15.8	1.2	SCOTT *et al.* ('83)
186	Pima (Arizona)	F	633		12.0	0.8	SCOTT *et al.* ('83)
187	Pima (Arizona)	M+F	1242		13.8	1.0	SCOTT *et al.* ('83)
188	Papago (Arizona)	M+F		560	17.0	2.0	KRAUS ('59)
189	Apache (Arizona)	M+F		100	4.0	0.0	KRAUS ('59)
190	Yaqui (Arizona)	M+F		81	17.3	1.2	KRAUS ('59)
191	Hopi (NE Arizona)	M+F	109			2.8	TURNER ('69)
192	SW U.S. Indians	M	165			3.0	SCOTT ('80)
193	SW U.S. Indians	F	273			5.5	SCOTT ('80)
194	SW U.S. Indians	M+F	438		22.8	4.5	SCOTT ('80)
195	Tarahumara (Mexico)	M	50		78.0	22.0	SNYDER *et al.* ('69)
196	Tarahumara (Mexico)	F	33		48.5	3.0	SNYDER *et al.* ('69)
197	Tarahumara (Mexico)	M+F	83		66.3	14.5	SNYDER *et al.* ('69)
198	European-Indian hybrids (Mexico)	M+F		96		14.6	KRAUS ('59)
199	Mestizos (Mexico)	M	17		64.7	17.6	SNYDER *et al.* ('69)
200	Mestizos (Mexico)	F	39		61.5	15.4	SNYDER *et al.* ('69)
201	Mestizos (Mexico)	M+F	56		62.5	16.1	SNYDER *et al.* ('69)
202	Queckchi (Guatemala)	M	250		30.4	12.0	ESCOBAR *et al.* ('77)
203	Queckchi (Guatemala)	F	194		27.8	8.8	ESCOBAR *et al.* ('77)
204	Queckchi (Guatemala)	M+F	444		29.3	10.6	ESCOBAR *et al.* ('77)
SOUTH AMERICA							
205	Yanomama (N Brazil & S Venezuela)	M+F		1124		29.5	BREWER-CARIAS *et al.* ('76)
206	Makiritare (N Brazil & S Venezuela)	M+F		114		19.3	BREWER-CARIAS *et al.* ('76)
207	Brazilians	M+F		93	7.4		DELLA SERRA ('51)
208	Peruvian Indians	M+F		97	12.4		GOAZ & MILLER ('66)
209	Lengua (Paraguay)	M		122	19.7	2.5	KIESER & PRESTON ('81)
210	Lengua (Paraguay)	F		119	47.9	19.3	KIESER & PRESTON ('81)

Table 2. (Cont'd—8)

Ser. No.	Sample	Sex[1)]	No. of indiv.	No. of teeth	Frequency (%) Grades 2+3	Grade 3	Source
211	Lengua (Paraguay)	M+F		241	33.6	10.8	KIESER & PRESTON ('81)
212	Andes (Argentine)	M+F	270		14.4		DEVOTO ('69)
213	Argentines (Buenos-Aires)	M+F	100		27		DEVOTO ('69)
EUROPE							
214	Kola Lapps (Russia)	M+F	124		28.3		SUBOW ('72)
215	Lapps	M+F		212	8.0		KAJAVA ('30)
216	N & Inari Lapps (Finland)	M	49		13.3		SUBOW ('72)
217	Skolt Lapps (Finland)	M	132		12.7		SUBOW ('72)
218	Skolt Lapps (Sevettijärvi, Finland)	M	77		54.5	16.9	KIRVESKARI ('74)
219	Skolt Lapps (Sevettijärvi, Finland)	F	65		41.5	12.3	KIRVESKARI ('74)
220	Skolt Lapps (Sevettijärvi, Finland)	M+F	142		48.6	14.8	KIRVESKARI ('74)
221	Skolt Lapps (Nellim, Finland)	M	17		47.1	17.6	KIRVESKARI ('74)
222	Skolt Lapps (Nellim, Finland)	F	22		50.0	22.7	KIRVESKARI ('74)
223	Skolt Lapps (Nellim, Finland)	M+F	39		48.7	20.5	KIRVESKARI ('74)
224	Skolt Lapps (Finnish Lapland)	M+F	182		15.9	1.6	KIRVESKARI ('78)
225	Skolt Lapp-Finn hybrids (Finland)	M	48		68.8	27.1	KIRVESKARI ('74)
226	Skolt Lapp-Finn hybrids (Finland)	F	40		47.5	7.5	KIRVESKARI ('74)
227	Skolt Lapp-Finn hybrids (Finland)	M+F	88		59.1	18.2	KIRVESKARI ('74)
228	Komi	M+F	55		34.0		SUBOW ('72)
229	Komi (Sysola)	M	78		24.4	7.7	AKSJANOVA *et al.* ('78?)
230	Komi (Low-Vychegda)	M	41		24.4	2.4	AKSJANOVA *et al.* ('78?)
231	Komi (Izhma)	M	56		33.9	3.6	AKSJANOVA *et al.* ('78?)
232	Komi (Vizinga & Zheshart)	M+F	82		25.6	4.9	AKSJANOVA *et al.* ('78?)
233	Komi (Izhma)	M+F	194		38.7	5.7	AKSJANOVA *et al.* ('78?)
234	Russians (Kola)	M+F	44		34.6		SUBOW ('72)
235	Russians (Moscow)	M+F	109		41.8		SUBOW ('72)
236	Russians	M+F	340		10.3		BATUJEFF (1896)
237	Russians	M+F	3731		33.4		ZOUBOV & HALDEYEVA ('89)
238	Belorussians	M+F	1127		42.2		TEGAKO & SALIVON ('79)
239	Estonians (W Estonia)	M+F	83		44.5		SUBOW ('72)

Table 2. (Cont'd—9)

Ser. No.	Sample	Sex[1]	No. of indiv.	No. of teeth	Frequency (%) Grades 2+3	Grade 3	Source
240	Estonians (E Estonia)	M+F	90		42.4		SUBOW ('72)
241	Estonians	M+F	1139		47.5		ZOUBOV & HALDEYEVA ('89)
242	Letts (E of Baltic Sea)	M+F	3936		41.0		ZOUBOV & HALDEYEVA ('89)
243	Lithua ians	M+F	158		54.9		SUBOW ('72)
244	Lithuanians	M+F	4857		49.8		ZOUBOV & HALDEYEVA ('89)
245	Ukrainians	M+F	1395		40.1		SEGEDA ('79)
246	Moldavians	M+F	145		49.2		ZOUBOV & HALDEYEVA ('89)
247	Azerbaijanis	M+F	2202		32.4		GASHIMOVA ('79)
248	Abkhazians (E of Black Sea)	M+F	729		38.9		AKSJANOVA ('82)
249	Nogai (W of Caspian Sea)	M+F	106		15.1		GADZHIEV ('79)
250	Mari (Mount. area)	M+F	105		35.5		SUBOW ('72)
251	Mari (Lowland area)	M+F	110		46.7		SUBOW ('72)
252	Finns	M+F	480		12.9		HELJMANN ('28)
253	Finns	M	91		33.3		SUBOW ('72)
254	Finns	M+F	233		19.7		ALVESALO *et al.* ('75)
255	Poles	M+F	168		35.4		KACZMAREK ('81)
256	Czechoslovaks	M	186		16.1	9.7	HANULÍK *et al.* ('66)
257	Czechoslovaks	F	234		11.1	2.6	HANULÍK *et al.* ('66)
258	Czechoslovaks	M+F	420		13.3	5.7	HANULÍK *et al.* ('66)
259	Hungarians	M+F	207		34.2		ZOUBOV & HALDEYEVA ('89)
260	Bulgarians	M+F		662	16.8		RAITCHINOVA ('72)
261	Bulgarians	M+F	3546		31.3		MINKOV ('77, '81)
262	Jews (E Europe)	M+F	119		78.2		SOFAER *et al.* ('86)
263	Greeks	M+F	93		36.5		MINKOV ('77, '81)
264	Germans	M+F	106		36		LENHOSSEK ('22)
265	Germans	M+F	155		19.2		FABIAN ('28)
266	Germans	M+F		1876	30.2		REINERS-KARSH ('64)
267	Germans (twins, Bonn)	M+F		127[2]		26.0	BERRY ('76)
268	Germans (twins, Heidelberg)	M+F		163[2]		19.6	BERRY ('76)
269	Germans (MZ twins, Bonn & Heidelberg)	M+F		326[2]		19.6	BERRY ('78)
270	Germans (DZ twins, Bonn & Heidelberg)	M+F		316[2]		27.8	BERRY ('78)
271	Dutch	M+F	2325		17.4		BOLK ('15)
272	Belgians	M+F	115		9.1		BRICHARD ('69)

Table 2. (Cont'd—10)

Ser. No.	Sample	Sex[1)]	No. of indiv.	No. of teeth	Frequency (%) Grades 2+3	Grade 3	Source
273	Swiss	M+F	313		17.6		DE TERRA ('05)
274	French	M+F	70		48.5		LEFEBVRE ('20)
275	SE England	M+F		207		10.6	BERRY ('76)
276	NW England	M+F		203		22.2	BERRY ('76)
277	Orkney Islands (UK)	M+F		205		12.7	BERRY ('76)
278	Shetland Islands (UK)	M+F		174		24.1	BERRY ('76)
279	British	M		326	21.8	10.7	GOOSE & LEE ('71)
280	British	F		276	15.2	7.2	GOOSE & LEE ('71)
281	British	M+F		602	18.8	9.1	GOOSE & LEE ('71)
282	Europeans	M+F		186	10.8		BRABANT ('71)
283	Europeans	M+F		186	27.4		GUIGUI ('74)
284	Europeans (Ohio, USA)	M	121		58.8	34.6	GARN *et al.* ('66a)
285	Europeans (Ohio, USA)	F	136		58.6	29.7	GARN *et al.* ('66a)
286	Europeans (Ohio, USA)	M+F	257		58.6	32.0	GARN *et al.* ('66a)
287	Europeans (Chicago, USA)	M		140	62.9	54.3	DAHLBERG ('63a)
288	Europeans (Chicago, USA)	F		140	70.7	55.0	DAHLBERG ('63a)
289	Europeans (Chicago, USA)	M+F		280	66.8	54.6	DAHLBERG ('63a)
290	Europeans (Chicago, USA)	M+F	59			39.0	HANIHARA *et al.* ('75)
291	Europeans (Iowa, USA)	M		100	90.0	66.0	MEREDITH & HIXON ('54)
292	Europeans (Iowa, USA)	F		100	77.0	53.0	MEREDITH & HIXON ('54)
293	Europeans (Iowa, USA)	M+F		200	83.5	59.5	MEREDITH & HIXON ('54)
294	Europeans (Tucson, USA)	M+F		600	45.2	16.2	KRAUS ('59)
295	Europeans (USA)	M+F	91			41.0	DAHLBERG ('51)
296	Europeans (USA)	M	320		23.4	10.3	TAKEHISA ('57)
297	Europeans (USA)	M+F	53		58.7		DAHLBERG ('65)
298	Europeans (USA)	M		773		21.9	KEENE ('68)
299	Europeans (USA)	M+F	113		62.8	32.7	SCOTT ('80)
300	Europeans (USA)	M+F	100		47.0	18.0	SCOTT & POTTER ('84)
301	Europeans (MZ twins, USA)	M+F	150[3)]		41.3	13.3	SCOTT & POTTER ('84)
302	Europeans (DZ twins, USA)	M+F	112[3)]		44.6	14.4	SCOTT & POTTER ('84)
303	Europeans (Burlington, Canada)	M	90		52.2	6.7	MAYHALL *et al.* ('82)

Table 2. (Cont'd—11)

Ser. No.	Sample	Sex[1)]	No. of indiv.	No. of teeth	Frequency (%) Grades 2+3	Grade 3	Source
304	Europeans (Burlington, Canada)	F	93		39.8	8.6	MAYHALL *et al.* ('82)
305	Europeans (Burlington, Canada)	M+F	183		45.9	7.7	MAYHALL *et al.* ('82)
306	Europeans (Australia)	M+F	77		32		CAMPBELL ('25)
307	Europeans (Australia)	M+F		77	26.1		CAMPBELL ('25)
308	Europeans (Australia)	M+F	189		61.9	25.9	TOWNSEND *et al.* ('92)
309	Europeans (MZ twins, Australia)	M+F	161[3)]		62.7	30.4	TOWNSEND *et al.* ('92)
310	Europeans (DZ twins, Australia)	M+F	152[3)]		62.5	23.7	TOWNSEND *et al.* ('92)
311	Europeans (Johannesburg, S Africa)	M	120		55.0	25.8	KIESER ('84)
312	Europeans (Johannesburg, S Africa)	F	120		53.3	29.2	KIESER ('84)
313	Europeans (Johannesburg, S Africa)	M+F	240		54.2	27.5	KIESER ('84)
314	Europeans (S Africa)	M+F		400	15.0		KIESER ('78)
315	Europeans (S Africa)	M	104			26.9	SCOTT ('80)
316	Europeans (S Africa)	F	103			20.4	SCOTT ('80)
317	Europeans (S Africa)	M+F	207		52.7	23.7	SCOTT ('80)
AFRICA							
318	Moroccans (mixed)	M+F	113		16.6		BRABANT & HUZAR ('66)
319	Moroccan Jews	M+F	161		83.2		SOFAER *et al.* ('86)
320	Shawiya (Algeria)	M+F	593		40.7		VERGER-PRATOUCY & REGNERE (n.d.)
321	Ethiopians	M+F	54		52.0		ZOUBOV & HALDEYEVA ('89)
322	Nubians (Sudan)	M+F	85		75.3		SOFAER *et al.* ('86)
323	Africans (mostly Bantu, Kenya)	M	647		31.7		HASSANALI ('82)
324	Africans (mostly Bantu, Kenya)	F	620		35.2		HASSANALI ('82)
325	Africans (mostly Bantu, Kenya)	M+F	1267		33.4		HASSANALI ('82)
326	Africans (mostly Bantu, Kenya)	M	143		43.4	11.2	HASSANALI ('82)
327	Africans (mostly Bantu, Kenya)	F	155		41.9	9.7	HASSANALI ('82)
328	Africans (mostly Bantu, Kenya)	M+F	298		42.6	10.4	HASSANALI ('82)

Table 2. (Cont'd—12)

Ser. No.	Sample	Sex[1]	No. of indiv.	No. of teeth	Frequency (%) Grades 2+3	Grade 3	Source
329	Africans (Nairobi, Kenya)	M+F	248		40.3	10.5	HASSANALI ('82)
330	Teso (Uganda)	M		7344		10.6	BARNES ('69)
331	Teso (Uganda)	F		2940		7.4	BARNES ('69)
332	Teso (Uganda)	M+F		10284		9.7	BARNES ('69)
333	Seres (Central Africa)	M+F	96		1.0		WAGEMAN ('76)
334	Bantu (S Africa)	M+F	389			2.0	SHAW ('31)
335	Bantu (S Africa)	M+F	163		6.7		SHAPIRO ('49)
336	Bantu	M	122			15.6	SCOTT ('80)
337	Bantu	F	120			7.5	SCOTT ('80)
338	Bantu	M+F	242		33.9	11.6	SCOTT ('80)
339	San-Negro hybrids (Namibia)	M+F		225	30.7	23.1	REID *et al.* ('91)
340	San	M+F	33		6.1		SHAPIRO ('49)
341	San	M+F	406		7		VAN REENEN ('64)
342	San	M+F	155		32.9	16.8	SCOTT ('80)
343	Pygmies	M+F	78		1.2		PALES ('38)
344	Pygmies	M+F		42	4.8		BRABANT ('76)
345	Afro-Americans (Washington, D.C.)	M+F	80			16.3	HANIHARA ('76)
346	Afro-Americans (Tucson)	M+F		548	29.9	15.0	KRAUS ('59)

[1] "M+F" also designates unknown-sex data.
[2] The right and left teeth of both twins are combined.
[3] Both twins of each twin pair are combined.

Results

The frequencies of the CARABELLI trait (grades 2 plus 3 as well as grade 3) in the 23 pooled samples are shown in Table 3. The medians among modern humans in the world were found to be about 30% for the tubercle-plus-cusp grade and about 10% for the cusp in the case of the data combined for sexes.

Shown in Table 4 are the SPEARMAN's and KENDALL's rank correlation coefficients of the CARABELLI trait with other dental characters, somatometric traits and climatic variables. In spite of the possible large interobserver errors, both data of the grade 3 and grades 2+3 revealed very similar tendencies in the pattern of associations. Namely, the CARABELLI trait seems inversely associated with the shoveling of the maxillary central incisor, and, further, relatively highly associated, in the same direction, with the average annual temperature and the average temperature in the coldest month, though statistically not significant. Moreover, the CARABELLI trait of the grades 2+3 has a relatively high inverse association with the nasal index.

Table 3. CARABELLI trait, other dental characters, somatological measurements, climatic factors and lifeways of modern human populations worldwide.[1)]

Group	Reference nos. of the samples in Table 2	Frequency of the CARABELLI trait of UM1 (%)					
		Male		Female		M+F	
		Grades 2+3	Grade 3	Grades 2+3	Grade 3	Grades 2+3	Grade 3
Mongolians	10– 13					14	
Chinese	14– 22					9	5
Taiwan Aborigines	23– 33	35	6	36	9	37	12
Koreans	34– 36					25	3
Ainu	37– 44					9	10
Japanese	46– 90	34	18	29	13	29	6
Okinawa Islanders	94– 96						5
Jats	107–109	40	22	31	10	36	17
Afghans	116–118	31	12			34	
Arabs	125–130					65	
Melanesians	136–140	17	12		16	18	12
Australian Aborigines	144–151		24		14		17
Polynesians	153–159					34	6
Hawaiians	152					33	26
Inuits	161–177	67	15	60	7	63	10
U.S. Indians	179–194	40	3	30	6	17	4
Mexican Indians	195–197	78	22	49	3	66	15
Guatemalan Indians	202–204	30	12	28	9	29	11
South Am. Indians	205, 206, 208–212	20	3	48	19	14	19
Northern Russia	2, 3. 228–233	24	4			26	5
Lapps	214–224	30	17	46	18	28	15
Europeans	234–317	52	24	53	25	40	24
Africans	322–338	38	11	39	8	34	10
Median value		34	12	39	10	29	11

The four-fold point correlation coefficients and YULE's coefficients of association (Table 5) also revealed almost the same tendencies as those seen in the rank correlation coefficients. In Table 5, furthermore, the associations with the ways of life are shown. The CARABELLI trait is relatively highly associated with the milking and agriculture for the grades 2+3, and, for the grade 3, to be inversely associated with the hunting-gathering.

The results of the canonical correlation analyses are shown in Tables 6 to 9. Tables 6 and 7 are concerned with the interrelationships between the variable group of maxillary molar characters and that of climatic variables, and Tables 8 and 9, with those between the maxillary molar variable group and the variable group of lifeways. Fig. 1 shows part of the results of these four canonical correlation analyses. Although any of the relevant canonical correlations was not significant at the 5% level, it is clear from Fig. 1 that the canonical variates correlated with the CARABELLI trait ex-

Table 3. (Cont'd—2)

Group	Mean tooth crown diameters in males[2)]					Frequency of UI1 shoveling $(tr+ss+s)$ in the combined sample for sexes (%)
	UM1 MD	UM2 MD	UM1 BL	UM2 BL	UI1 MD	
Mongolians						100
Chinese	10.30	9.90	11.50	11.70	8.60	92
Taiwan Aborigines	10.50	9.90	11.70	11.60	8.50	98
Koreans	10.20	9.80	11.60	11.80	8.70	84
Ainu	10.19	9.23	11.30	11.10	8.29	83
Japanese	10.66	9.81	11.92	11.56	8.74	94
Okinawa Islanders	10.57	9.64			8.54	97
Jats	10.76	9.83	11.21	10.69	8.78	87
Afghans	9.94	8.92	11.14	11.26	8.34	
Arabs	10.63	10.03	11.54	11.55	8.76	33
Melanesians	11.12	10.31	12.10	12.35	9.00	73
Australian Aborigines	11.20	10.83	12.55	12.77	9.36	68
Polynesians	10.68	10.09	11.95	12.22	8.72	82
Hawaiians	10.47		11.83		8.41	50
Inuits	11.10	10.40	11.80	11.80	8.70	100
U.S. Indians	11.03	10.46			9.14	98
Mexican Indians	10.34		11.40		8.55	
Guatemalan Indians						48
South Am. Indians	11.28	10.85	11.76	11.41	9.10	98
Northern Russia						
Lapps	10.53	9.87	11.73	11.66	8.79	44
Europeans	10.54	10.04	11.32	11.28	8.77	34
Africans	11.24	10.95	11.80	11.90	9.31	34
Median value	10.57	9.90	11.70	11.60	8.72	82

tracted from the data on the grade 3 are very similar to those extracted from the data on the grades 2+3. Such canonical variates seem to be inversely correlated with the buccolingual crown diameters of the maxillary first and second molars as well as with the amount of annual rainfall and, probably, also with the mean relative annual humidity, and, further, seem to be positively correlated with the milking.

Discussion

Environmental factors, in general, act on genes both in the ontogenetic process and in the phylogenetic one to produce a trait or to cause the change of a trait. Environmetal factors in the ontogenetic process may influence the individual variation of the trait in a population. On the other hand, environmental factors in the phylogenetic process may shift the average characteristic of the trait in a population to another one with genetic change, or, in other words, may cause an adaptive evolution

Table 3. (Cont'd—3)

Group	Somatometric variables in males			Latitude (°)	Average annual temp. (°C)	Average temp. in hottest month (°C)
	Stature (cm)	Cephalic index	Nasal index			
Mongolians	166	85		48 N	−3.1	16.1
Chinese	165	80	71	31 N	13.6	28.0
Taiwan Aborigines	161	79	94	24 N	23.5	28.1
Koreans	165	85	72	38 N	12.1	25.1
Ainu	160	77	78	43 N	7.1	20.0
Japanese	161	81	77	36 N	14.2	25.7
Okinawa Islanders	158	82	74	27 N	22.3	28.2
Jats	164	74	63	30 N	25.3	34.5
Afghans	166	86	65	33 N	15.0	26.8
Arabs	166	77	65	32 N	17.7	26.6
Melanesians	165	77	94	6 S	26.3	26.8
Australian Aborigines	167	74	108	24 S	20.7	28.2
Polynesians	171	81	76	20 S	26.7	27.6
Hawaiians	170	84	78	20 N	23.6	25.3
Inuits	163	82	68	69 N	−4.0	6.9
U.S. Indians	169	80	85	36 N	15.5	23.9
Mexican Indians	155	84		23 N	21.7	27.2
Guatemalan Indians	155	86	77	15 N	20.0	22.2
South Am. Indians	163	82		25 S	23.4	25.8
Northern Russia	159	83		68 N	0.2	14.1
Lapps	156	86	69	68 N	2.4	13.5
Europeans	169	83	67	54 N	7.1	17.1
Africans	167	76	120	5 S	25.5	26.1
Median value	164	81	75	31[4)]	20.0	25.7

through selection. The effect of the former environmental factors can be evaluated to some extent by estimating the environmental variance of the trait on the basis of family and twin data. And the effect of the environmental factors in the adaptive evolution may be assessed by calculating the differences in means or frequencies of the trait between populations in question. It should be noted here, however, that such differences can be caused not only by selection but also by the parallel changes in all members of a population due to the change of some environmental factors, like the rapid change of food habit seen in some countries, without accompanying genetic change (MIZOGUCHI, 1988).

In the present study, it was examined from a viewpoint of adaptive evolution whether the among-population variation of the CARABELLI trait could be explained by the among-population variations of some environmental factors. But, to begin with, the reliability of the present results should be argued because many data with various sources of errors were used here.

Table 3. (Cont'd—4)

Group	Average temp. in coldest month (°C)	Mean relative annual humidity (%)	Amount of annual rainfall (mm)	Lifeway in the 15th cent.[3]			
				Hunting-gathering	Stock raising	Milking	Agri-culture
Mongolians	−25.6	65	208	0	1	1	0
Chinese	−2.8	60	677	0	1	0	1
Taiwan Aborigines	17.9	80	2281	0	1	0	1
Koreans	−1.0	69	1126	0	1	0	1
Ainu	−5.5	78	1212	1	0	0	0
Japanese	2.6	72	1210	0	0	0	1
Okinawa Islanders	16.0	78	2118	0	1	0	1
Jats	14.3	49	715	0	1	1	1
Afhgans	1.8	50	258	0	1	1	1
Arabs	8.0	51	254	0	1	1	1
Melanesians	24.8	82	2055	0	1	0	1
Australian Aborigines	15.0	59	523	1	0	0	0
Polynesians	26.0	78	2224	0	1	0	1
Hawaiians	21.9	72	2013	0	1	0	1
Inuits	−19.9	82	236	1	0	0	0
U.S. Indians	6.5	48	309	1	0	0	0
Mexican Indians	14.2	66	726	0	0	0	1
Guatemalan Indians	17.2	77	1316	0	0	0	1
South Am. Indians	17.0	76	1531	0	1	0	1
Northern Russia	−11.7	80	464	0	1	0	0
Lapps	−6.9	78	713	0	1	0	0
Europeans	−2.2	83	594	0	1	1	1
Africans	24.4	80	1625	1	1	1	1
Median value	11.1	70	962				

[1] Each of the twenty-three groups listed was made up by pooling those samples which were supposed to be extracted from the same population. All the data except for the CARABELLI trait and tooth crown diameters were derived from MIZOGUCHI (1985).

[2] Data sources for the tooth crown diameters: BRACE *et al.* (1984) for Chinese; LIU (1977) for Taiwan Aborigines; BRACE and NAGAI (1982) for Koreans; HANIHARA (1976) and BRACE and NAGAI (1982) for Ainu; MIZOGUCHI (1986) for Japanese; MIZOGUCHI (1988) for Okinawa Islanders; BHASIN *et al.* (1985) for Jats; SAKAI *et al.* (1971) for Afghans; ROSENZWEIG and ZILBERMAN (1969) for Arabs; BAILIT *et al.* (1968) for Melanesians; TOWNSEND and BROWN (1979) for Australian Aborigines; YAMADA and SAKAI (1992) for Polynesians; YAMADA *et al.* (1979) for Hawaiians; MAYHALL (1979) for Inuits; HANIHARA (1976) for U.S. Indians; O'ROURKE and CRAWFORD (1980) for Mexican Indians; KIESER *et al.* (1985) for South American Indians; KIRVESKARI *et al.* (1978) for Lapps; DAHLBERG (1960) for Europeans; and KIESER *et al.* (1987) for Africans.

[3] 1 = Adoption; 0 = No adoption.

[4] The median of the absolute values regardless of whether data were from the Northern or Southern Hemisphere.

Table 4. Rank correlation coefficients between the CARABELLI trait and climatic variables, *etc.* based on the data of the frequencies or means in the samples from various regions in the world.[1]

	CARABELLI trait of UM1					
	Grades 2+3			Grade 3		
	No.	ρ[2]	τ[3]	No.	ρ[2]	τ[3]
UM1 CARABELLI trait (Grade 3)	18	0.40	0.30*			
UM1 MD crown diameter	18	0.05	0.03	18	0.20	0.17
UM2 MD crown diameter	16	0.08	0.06	16	0.32	0.22
UM1 BL crown diameter	17	−0.17	−0.11	16	−0.06	−0.04
UM2 BL crown diameter	15	−0.10	−0.08	14	−0.31	−0.16
UI1 MD crown diameter	18	−0.11	−0.09	18	0.12	0.11
UI1 shoveling	18	−0.33	−0.27	18	−0.39	−0.31*
Stature	21	0.05	0.01	20	0.07	0.10
Cephalic index	21	−0.04	−0.04	20	0.00	−0.03
Nasal index	17	−0.42*	−0.24	17	0.02	0.08
Latitude	21	−0.12	−0.08	20	−0.25	−0.16
Average annual temperature	21	0.22	0.16	20	0.26	0.18
Av. temp. in the hottest month	21	0.22	0.18	20	0.08	0.04
Av. temp. in the coldest month	21	0.24	0.16	20	0.25	0.17
Mean relative annual humidity	21	0.13	0.13	20	0.08	0.08
Amount of annual rainfall	21	−0.05	0.01	20	0.10	0.06

[1] See Table 3 for the data sources. For the CARABELLI trait, the data of the pooled samples for sexes were used.

[2] SPEARMAN's rank correlation coefficient.

[3] KENDALL's rank correlation coefficient.

* $P<0.10$.

Influence of errors

The chi-square tests for determining the range of the "presence" grade indicated the position of a dividing plane which could make the between-sample differences minimum (Table 1). The probabilities for the chi-square values are, however, very low even in such cases, implying that the between-sample differences are statistically highly significant and, therefore, that large errors due to some other factors, in addition to the real between-sample differences, may yet remain to be excluded.

In the present study, therefore, a further attempt was made to minimize errors by pooling samples for each population. If all errors such as sampling error, intra- and interobserver errors, etc. randomly affect the observed frequencies of a character in question, the median (also mean or mode) of many observed frequencies for a population can be expected to be a value representing the true frequency in the population. In the present study, the number of the samples pooled for a population varies considerably, as shown in Table 3. This indicates the heterogeneity in the elimination rate of errors among the pooled samples. The results of the present analyses should,

Table 5. Coefficients of association between the CARABELLI trait and climatic variables, *etc.* based on the data of the frequencies or means in the samples from various regions in the world.[1]

	CARABELLI trait of UM1					
	Grades 2+3			Grade 3		
	No.	Q[2]	r[3]	No.	Q[2]	r[3]
UM1 CARABELLI trait (Grade 3)	18	0.59	0.33*			
UM1 MD crown diameter	18	0.00	0.00	18	−0.43	−0.22
UM2 MD crown diameter	16	0.50	0.26	16	0.33	0.16
UM1 BL crown diameter	17	−0.14	−0.07	16	0.20	0.10
UM2 BL crown diameter	15	−0.38	−0.20	14	−0.54	−0.29
UI1 MD crown diameter	18	−0.43	−0.22	18	0.60	0.33*
UI1 shoveling	18	−0.59	−0.33*	18	−0.59	−0.33*
Stature	21	0.29	0.15	20	−0.02	−0.01
Cephalic index	21	−0.09	−0.05	20	0.20	0.10
Nasal index	17	−0.35	−0.18	17	−0.06	−0.03
Latitude	21	−0.45	−0.24	20	−0.62*	−0.33*
Average annual temperature	21	0.74*	0.43*	20	0.81*	0.50*
Av. temp. in the hottest month	21	0.61*	0.34*	20	0.41	0.21
Av. temp. in the coldest month	21	0.60	0.33*	20	0.72*	0.41*
Mean relative annual humidity	21	−0.08	−0.04	20	−0.14	−0.07
Amount of annual rainfall	21	−0.29	−0.15	20	−0.37	−0.19
Hunting-gathering	21	0.06	0.02	20	−0.64*	−0.29
Stock raising	21	0.39	0.18	20	0.49	0.24
Milking	21	0.82*	0.45*	20	0.48	0.18
Agriculture	21	0.76*	0.39*	20	0.33	0.15

1) See Table 3 for the data sources. For the CARABELLI trait, the data of the pooled samples for sexes were used.

2) YULE's coefficient of association.

3) Four-fold point correlation coefficient.

* Greater than 0.60 for Q or 0.30 for r in absolute value.

therefore, be interpreted with care in this respect.

In passing, some authors have showed their intra- and/or interobserver errors in observing the CARABELLI trait, and others have argued about observational methods. For example, SCOTT (1980) stated that, when the CARABELLI trait was scored as a presence-or-absence character, the concordance between duplicated observations by himself was 97.6% and an estimate of the rank order correlation coefficient between them was 0.96. MIZOGUCHI (1985) showed his intraobserver discordance rate of 15.25% for the CARABELLI trait (the cusp-plus-tubercle grade) on the first molar. NICHOL and TURNER (1986) reported the intra- and interobserver discordance percentages for the CARABELLI trait treated as a discrete character (the cusp, tubercle, and groove or pit grades combined), the former ranging from 5.1% to 12.8% for the

Table 6. Correlations between morphological characters of maxillary molars or climatic variables and the canonical variates extracted from them.[1]

Variable	Canonical variates			Total contribution (%)
	u_1	u_2	u_3	
UM1 CARABELLI trait (Grades 2+3)	0.37*	0.56*	0.57*	78.0
UM1 MD crown diameter	0.87*	−0.40*	−0.00	92.3
UM2 MD crown diameter	0.81*	−0.44*	−0.15	86.8
UM1 BL crown diameter	0.31*	−0.83*	0.43*	96.2
UM2 BL crown diameter	0.22	−0.65*	0.53*	75.6
Total contribution (%)	33.8	35.7	16.3	85.8
Cumulative proportion (%)	33.8	69.5	85.8	85.8
	v_1	v_2	v_3	T.c. (%)
Average annual temperature	0.25	−0.37*	−0.19	23.2
Average temperature in the hottest month	−0.12	−0.09	−0.39*	17.2
Average temperature in the coldest month	0.34*	−0.48*	−0.06	35.0
Mean relative annual humidity	0.23	−0.75*	0.13	63.1
Amount of annual rainfall	0.04	−0.93*	0.03	87.4
Total contribution (%)	4.9	36.2	4.1	45.2
Cumulative proportion (%)	4.9	41.0	45.2	45.2
Canonical correlation	0.95	0.77	0.66	
Probability[2]: P_F	0.68	0.87	0.90	
P_D	0.25	0.88	0.91	

1) The number of the populations used is 15.

2) The probability for a *z*-transformed canonical correlation coefficient was determined by the bootstrap method. Both P_F and P_D are bootstrap estimates of the probability in the two-tailed test, the former being based on the bootstrap standard deviation estimated using the ordinary formula for a standard deviation and the latter, based on the bootstrap standard deviation obtained by utilizing the cumulative frequency for one standard deviation in the normal distribution. The number of the bootstrap samples including the observed one is 497.

* Greater than 0.30 in absolute value.

first molar and from 7.0% to 16.3% for the second molar and the latter, from 8.6% to 17.1% for the first and from 9.5% to 16.7% for the second. Regarding observational methods, SCOTT (1980) and BERMÚDEZ DE CASTRO (1989) showed that the differences among the total tooth, unilateral, and individual count methods practically had no serious influence on recording of the CARABELLI trait. KIESER and VAN DER MERWE (1984) demonstrated that differences among some classification methods or observers affected the results of observation on the expression and frequency of the CARABELLI trait.

Within-group covariations

Regarding the occurrence of the CARABELLI trait, at least two major hypotheses have been contended. One is the "compensation" or "functional adaptation" hy-

Table 7. Correlations between morphological characters of maxillary molars or climatic variables and the canonical variates extracted from them.[1)]

Variable	Canonical variates			Total contribution (%)
	u_1	u_2	u_3	
UM1 CARABELLI trait (Grade 3)	0.54*	0.43*	0.51*	72.8
UM1 MD crown diameter	0.92*	−0.03	−0.28	93.2
UM2 MD crown diameter	0.88*	0.08	−0.07	79.3
UM1 BL crown diameter	0.35*	0.44*	−0.66*	75.1
UM2 BL crown diameter	0.26	0.51*	−0.61*	70.1
Total contribution (%)	42.3	12.7	23.1	78.1
Cumulative proportion (%)	42.3	55.0	78.1	78.1
	v_1	v_2	v_3	T.c. (%)
Average annual temperature	0.30*	−0.08	−0.28	17.6
Average temperature in the hottest month	−0.04	−0.15	−0.04	2.5
Average temperature in the coldest month	0.39*	0.08	−0.37*	29.7
Mean relative annual humidity	0.15	0.14	−0.21	8.4
Amount of annual rainfall	−0.02	−0.11	−0.55*	31.7
Total contribution (%)	5.3	1.3	11.3	18.0
Cumulative proportion (%)	5.3	6.7	18.0	18.0
Canonical correlation	0.99	0.72	0.53	
Probability[2)]: P_F	0.48	0.89	0.92	
P_D	0.02	0.89	0.93	

1) The number of the populations used is 14.

2) See the footnote to Table 6. However, the number of the bootstrap samples including the observed one is 1000.

* Greater than 0.30 in absolute value.

pothesis by BATUJEFF, DE TERRA, DAHLBERG and others, and the other is the "anti-compensation" or "evolutionary simplification" hypothesis by ADLOFF, DE JONGE, KEENE and others (DAHLBERG, 1951, 1963a, b; MOORREES, 1957; KORENHOF, 1960; KEENE, 1968). The compensation hypothesis says that the CARABELLI trait on the maxillary first molar tends to increase the occlusal surface of the whole dentition as an adaptive response to the loss of tooth material due to the reduction of the second and third molars. According to the evolutionary simplification hypothesis, the CARABELLI trait tends to reduce and disappear with the simplification of the occlusal surface represented by hypocone reduction. These hypotheses have been examined mainly by directly assessing the individual association coefficients between the CARABELLI trait and other characters, especially third molar agenesis and molar crown diameters (KEENE, 1968; BANG and HASUND, 1972; LOMBARDI, 1975; SCOTT, 1978; REID *et al.*, 1991, 1992; and others). But, as MIZOGUCHI (1983) suggested in the analysis of the third molar variation, there may be several components co-varying with other structures or external environmental factors also in the variation of the CARABELLI trait. In fact, MIZOGUCHI (1985) found, in some of the principal component analyses on

Table 8. Correlations between morphological characters of maxillary molars or lifeways and the canonical variates extracted from them.[1]

Variable	Canonical variates				Total contribution (%)
	u_1	u_2	u_3	u_4	
UM1 CARABELLI trait (Grades 2+3)	0.63*	0.62*	−0.04	0.19	81.9
UM1 MD crown diameter	0.18	0.02	0.75*	0.63*	99.8
UM2 MD crown diameter	−0.21	0.64*	0.65*	−0.19	91.3
UM1 BL crown diameter	−0.56*	−0.06	0.31*	0.56*	73.0
UM2 BL crown diameter	−0.68*	0.50*	−0.11	0.38*	86.6
Total contribution (%)	24.9	21.0	21.9	18.7	86.5
Cumulative proportion (%)	24.9	45.9	67.8	86.5	86.5
	v_1	v_2	v_3	v_4	T.c. (%)
Hunting-gathering	−0.04	0.28	−0.03	0.96*	100.0
Stock raising	−0.01	0.61*	−0.06	−0.79*	100.0
Milking	0.88*	0.46*	−0.09	−0.10	100.0
Agriculture	0.29	0.20	0.68*	−0.64*	100.0
Total contribution (%)	21.6	17.6	12.0	48.9	100.0
Cumulative proportion (%)	21.6	39.1	51.1	100.0	100.0
Canonical correlation	0.87	0.64	0.48	0.24	
Probability[2]: P_F	0.86	0.91	0.91	0.89	
P_D	0.87	0.93	0.11	0.40	

[1] The number of the populations used is 15. The ecological correlations between all the variables were estimated using the four-fold point correlation coefficient.

[2] See the footnote to Table 6. However, the number of the bootstrap samples including the observed one is 1000.

* Greater than 0.30 in absolute value.

twenty-two dental characters, that the CARABELLI trait had relatively high correlations not only with the principal component related to the hypocone and/or protostylid but also with the so-called general size factor related intensively to the mesiodistal diameters of all the teeth of the central incisors to the first molars in both jaws. Further, MIZOGUCHI (1983) had discovered, in other principal component analyses, that the principal component correlated with the mesiodistal diameters of all the permanent teeth but the third molars had inverse correlations with the third molar size. Thus it is likely that the CARABELLI trait is controlled by at least two factors which are independent of each other, one being correlated with the overall dental size except for the third molars and correlated inversely with the third molar size, and the other being a local common factor correlated with the hypocone, protostylid and others. Namely, from a viewpoint of within-group covariations, both compensation and evolutionary simplification hypotheses may be maintained to be reasonable. But it must be recalled here that such within-group covariations reflect only part of the results of evolution. Another aspect of the results may be explained through the analysis of the among-

Table 9. Correlations between morphological characters of maxillary molars or lifeways and the canonical variates extracted from them.[1]

Variable	Canonical variates				Total contribution (%)
	u_1	u_2	u_3	u_4	
UM1 CARABELLI trait (Grade 3)	−0.53*	0.44*	0.30*	−0.27	63.9
UM1 MD crown diameter	0.54*	−0.06	0.00	0.45*	49.4
UM2 MD crown diameter	0.18	−0.59*	0.58*	−0.35*	84.2
UM1 BL crown diameter	0.01	−0.48*	−0.40*	−0.06	39.1
UM2 BL crown diameter	−0.31*	−0.75*	0.13	0.57*	100.0
Total contribution (%)	13.9	26.7	12.2	14.5	67.3
Cumulative proportion (%)	13.9	40.6	52.8	67.3	67.3
	v_1	v_2	v_3	v_4	T.c. (%)
Hunting-gathering	0.30*	−0.39*	−0.06	0.87*	100.0
Stock raising	−0.40*	−0.00	0.72*	−0.56*	100.0
Milking	0.21	0.51*	0.79*	0.27	100.0
Agriculture	0.36*	0.15	0.49*	−0.78*	100.0
Total contribution (%)	10.7	10.9	34.9	43.6	100.0
Cumulative proportion (%)	10.7	21.6	56.4	100.0	100.0
Canonical correlation	0.85	0.73	0.50	0.19	
Probability[2]: P_F	0.86	0.88	0.84	0.73	
P_D	0.87	0.90	0.12	0.45	

[1] The number of the populations used is 14. The ecological correlations between all the variables were estimated using the four-fold point correlation coefficient.

[2] See the footnote to Table 6. However, the number of the bootstrap samples including the observed one is 1000.

* Greater than 0.30 in absolute value.

group covariations of characters in question.

Among-group covariations and adaptation

Some previous authors have already made between-group comparisons for each dental character like the CARABELLI trait or tooth crown diameter. For instance, SCOTT (1980), using the samples from ten populations in the world, showed that the frequency of the CARABELLI trait gradually decreased from European-derived populations through Asian Indians to Pacific Island peoples. On the other hand, HANIHARA *et al.* (1975), using CARABELLI's cusp and some other dental characters as markers for population classification, compared six samples worldwide by calculating multivariate biological distances between them.

Regarding ecological correlations between dental characters and environmental variables based on many sample means or frequencies, however, few investigations, except MIZOGUCHI's (1985, 1993), have been performed until now. In the present study, such correlations between the CARABELLI trait and other variables were first estimated using the four kinds of association coefficients on the basis of about 20 pooled samples (Tables 4 and 5). From these, it was elucidated that there was a relatively high inverse association between the CARABELLI trait (UM1) and shoveling (UI1). This confirms our empirical thesis that the incisor shoveling is less frequent in European and European-derived populations with high frequencies of CARABELLI's cusps. But MIZOGUCHI (1976) has found, in the cross twin analysis of the within-group covariations, that both genetic and environmental correlation coefficients between the CARABELLI trait (UM1) and shoveling (UI1) are extremely low. Further, in three of the four principal component analyses on the within-group covariations, MIZOGUCHI (1985) consistently found no high correlations between the CARABELLI trait (UM1) and shoveling (UI1 and UI2). It can be said from these findings that the results of among-group and within-group analyses are not necessarily compatible with each other. After all, it is likely that the CARABELLI trait and shoveling, which are ontogenetically or genetically independent of each other, occurred mainly in European-derived populations and in Asian-derived populations, respectively, in response to the respective adaptive demands, and that the inverse among-group association between these two dental characters was caused by some environmental factors taking an alternative value such as the lifeway, which could have produced the different adaptive demands for the different populations.

It was also suggested that there was an inverse among-group association between the CARABELLI trait (grades 2 plus 3) and nasal index. If this is correct, it can be said that people with the narrower nose tend to have well-developed CARABELLI's tubercles, conforming with the state seen in European or European-derived peoples. In this case, the association seems to have been caused indirectly by common environmental factors such as humidity.

As regards the associations with environmental factors (Tables 4 and 5), the CARABELLI trait appears to be relatively highly associated with the average annual temperature and the average temperature in the coldest month as well as with the milking and the agriculture for the grades 2+3, and inversely associated with the hunting-gathering for the grade 3. Regarding these environmental factors, the canonical correlation analyses further provided the information on their overall associations. According to the similar canonical variates (Fig. 1) obtained from the four canonical correlation analyses (Tables 6 to 9), the CARABELLI trait is likely correlated inversely with the buccolingual crown diameters of the maxillary first and second molars as well as with the amount of annual rainfall, and, further, positively correlated with the milking, though the relevant canonical correlations were not statistically significant. But, if the results of these canonical correlation analyses are accepted, it may be said that peoples having been taking a lifeway with the milking in relatively dry regions have buccolingually smaller molars and well-developed CARABELLI's cusps.

Although the association with the third molar agenesis was not estimated in the present analyses, part of the variation of the maxillary first and second molars seems to be inversely associated with the CARABELLI trait. In the within-group analyses,

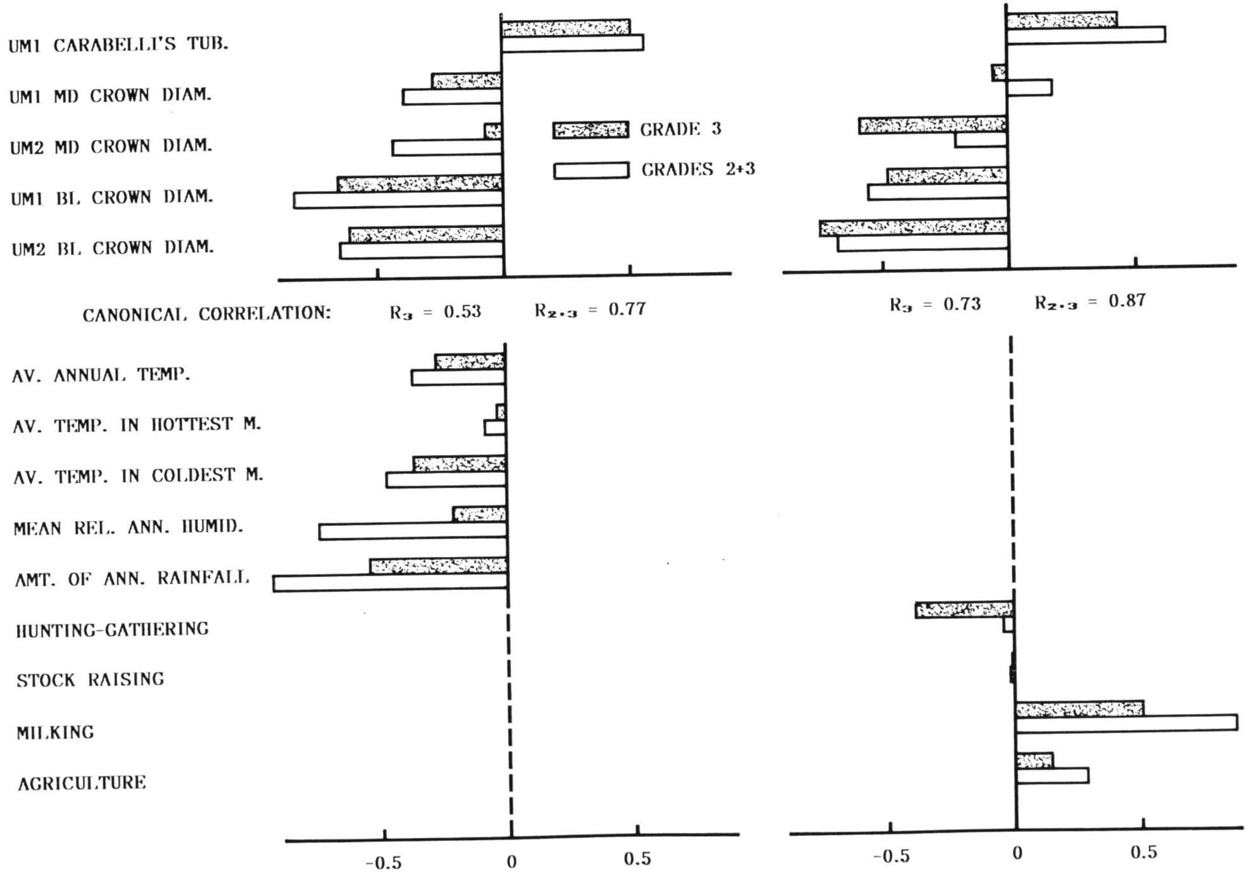

Fig. 1. Correlations between the original variables and the canonical variates correlated with the CARABELLI trait. This figure is based on the results of the four canonical correlation analyses (Tables 6 to 9).

both the compensation and the evolutionary simplification hypotheses were shown to be compatible with the results, as mentioned above. In the among-group analyses, especially in the canonical correlafion analyses, at first glance, the results appear to support the compensation hypotheis rather than the evolutionary simplification hypothesis. But the former hypothesis assumes that the CARABELLI trait compensates for the reduction of chewing surface areas in the second and third molars, not in the first molars. The present results of the among-group analyses, thereforc, do not support the so-called compensation hypothesis, either.

After all, from all the present results and previous findings, the following conclusions may be drawn. The people with well-developed CARABELLI's cusps have the buccolingually smaller molars, narrower nose, and weaker incisor shoveling. And they or their ancestors have been taking a lifeway with the milking in relatively dry regions. These conditions, in fact, seem comparable to those of European and Near Eastern peoples. The reduction in their overall dental size can be interpreted as an adaptation to the saving of energy in maintaining large structure in such an environment as a lifeway with the milking, where a higher level in nutrition is guaranteed by their livestock than in other ways of life like the hunting-gathering. The presence of the CARABELLI trait on the maxillary first molar is considered to have been caused, indirectly, by the reduction of the first molar associated with the tendency of the overall dental reduction, and, directly, by an adaptive demand for strengthening the lingual part of the first molar against the heaviest biomechanical stress which is generated in the position of the first molar within the tooth row in spite of the reduction of the tooth.

The hypothesis presented here may be supported by KORENHOF's (1960) finding that the CARABELLI trait of gorillas, when present, is always found on the maxillary second molar which is the largest of the molar teeth in gorillas. Further, the relatively high associations between the CARABELLI trait, hypocone and protostylid found in the within-group analyses (SCOTT, 1978; MIZOGUCHI, 1985) may also support this idea not only from a viewpoint of the common phylogenetic derivation, *i.e.*, cingulum, but from a biomechanical viewpoint as well. Namely, when a maxillary molar occludes with the mandibular counterpart, they touch each other on the lingual side for the former and on the buccal side for the latter. Both the CARABELLI trait and the hypocone occur on the lingual side of maxillary molars and the protostylid appears on the buccal side of mandibular molars. If these characters simultaneously enlarge their size, it is favorable for resisting powerful chewing stresses. In this context, the CARABELLI trait does not necessarily develop to a large cusp to occlude directly with the mandibular molar because even a small tubercle seems sufficiently buttress the lingual wall of the maxillary molar crown. This should however be ascertained through biomechanical experiments in the future.

Conclusions

If the results of the present analyses of the among-group covariations between dental traits and environmental factors are acceptable, we may say on the basis of them and previous studies as follows. Those people who, or whose ancestors, have been adopting a lifeway with the milking in relatively dry regions, like the peoples of the Near East and Europe, have the narrower nose, buccolingually smaller maxillary molars, larger CARABELLI's tubercles, and weaker incisor shoveling. The occurrence of the well-developed CARABELLI trait on the first molar in these people is the result of adaptation to their natural and sociocultural environments. Namely, first, the overall dental size decreased as an adaptation to a lifeway with a heavy reliance on dairy products. And, next, the still remaining intensive biomechanical demand for the reduced first molar caused the strengthening of the first molar in the buccolingual direction through the enlargement of the CARABELLI trait.

Acknowledgments

I would like to thank Dr. Bin YAMAGUCHI, Director of the Department of Anthropology, National Science Museum, Tokyo, for his invaluable comments on this manuscript. And I am also grateful to Miss Akiko NAKATSUKA for drawing the figure.

References

AKSJANOVA, G. A., 1974, 1975, 1976, 1979, 1982. Cited by ZOUBOV and HALDEYEVA (1989).

AKSJANOVA, G. A., A. A. ZOUBOV and R. S. KOCHIEV, 1978?. Odontological description of the Komi-Zyrians. *In*: (the title unknown). pp. 65–75.

AKSJANOVA, G. A., I. M. ZOLOTAREVA and A. A. ZOUBOV, 1986. Cited by ZOUBOV and HALDEYEVA (1989).

ALVESALO, L., M. NUUTILA and P. PORTIN, 1975. Cited by ESCOBAR *et al.* (1977), KIESER and PRESTON (1981) and BERMÚDEZ DE CASTRO (1989).

ANDERSON, T. W., 1958. An Introduction to Multivariate Statistical Analysis. New York, John Wiley & Sons.

AOYAGI, F., 1967. Morpho-genetical studies on similarities in the teeth and dental occlusion of twins: II. Shape of the teeth. *J. Tokyo Dent. Col. Soc.*, **67**: 606–624. (In Japanese with English summary.)

AOYAMA, T., 1948. Cited by SAKAI and HANAMURA (1967).

ASANO, C., 1971. Inshi-Bunsekiho-Tsuron (Outlines of Factor Analysis Methods). Tokyo, Kyoritsu-Shuppan. (In Japanese.)

BAILIT, H. L., S. J. DEWITT and R. A. LEIGH, 1968. The size and morphology of the Nasioi dentition. *Am. J. Phys. Anthrop.*, **28**: 271–287.

BANG, G., and A. HASUND, 1972. Morphologic characteristics of the Alaskan Eskimo dentition: II. Carabelli's cusp. *Am. J. Phys. Anthrop.*, **37**: 35–39.

BARNES, D. S., 1969. Tooth morphology and other aspects of the Teso dentition. *Am. J. Phys. Anthrop.*, **30**: 183–193.

BATUJEFF, N., 1896. Cited by SAKAI *et al.* (1969–1970) and VERGER-PRATOUCY (1981–1982).

BERMÚDEZ DE CASTRO, J. M., 1989. The Carabelli trait in human prehistoric populations of the Canary Islands. *Hum. Biol.*, **61**: 117–131.
BERRY, A. C., 1976. The anthropological value of minor variants of the dental crown. *Am. J. Phys. Anthrop.*, **45**: 257–267.
BERRY, A. C., 1978. Anthropological and family studies on minor variants of the dental crown. *In*: Development, Function and Evolution of Teeth, ed. P. M. BUTLER and K. A. JOYSEY. London, Academic Press. pp. 81–98.
BHASIN, M. K., A. SHARMA, I. P. SINGH and H. WALTER, 1985. Morphological and metric dental study on Indians. *Z. Morph. Anthrop.*, **76**: 77–90.
BIGGERSTAFF, R. H., 1973. Heritability of the Carabelli cusp in twins. *J. Dent. Res.*, **52**: 40–44.
BOLK, I., 1915. Cited by SAKAI and HANAMURA (1967) and VERGER-PRATOUCY (1981–1982).
BRABANT, 1971, 1976. Cited by VERGER-PRATOUCY (1981–1982).
BRABANT and HUZAR, 1966. Cited by VERGER-PRATOUCY (1981–1982).
BRACE, C. L., and M. NAGAI, 1982. Japanese tooth size: Past and present. *Am. J. Phys. Anthrop.*, **59**: 399–411.
BRACE, C. L., X.-q. SHAO and Z.-b. ZHANG, 1984. Prehistoric and modern tooth size in China. *In*: The Origins of Modern Humans: A World Survey of the Fossil Evidence, ed. F. H. SMITH and F. SPENCER. New York, Alan R. Liss. pp. 485–516.
BREWER-CARIAS, C. A., S. LE BLANC and J. V. NEEL, 1976. Genetic structure of a tribal population, the Yanomama Indians: XIII. Dental microdifferentiation. *Am. J. Phys. Anthrop.*, **44**: 5–14.
BRICHARD, 1969. Cited by VERGER-PRATOUCY (1981–1982).
CAMPBELL, T. D., 1925. Cited by SOFAER *et al.* (1972) and VERGER-PRATOUCY (1981–1982).
COX, G. J., S. B. FINN and D. B. AST, 1961. Effect of fluoride ingestion on the size of the cusp of Carabelli during tooth formation. *J. Dent. Res.*, **40**: 393–395.
DAHLBERG, A. A., 1951. The dentition of the American Indian. *In*: Papers on the Physical Anthropology of the American Indian, ed. W. S. LAUGHLIN. New York, Viking Fund. pp. 138–176.
DAHLBERG, A. A., 1960. The dentition of the first agriculturists (Jarmo, Iraq). *Am. J. Phys. Anthrop.*, **18**: 243–256.
DAHLBERG, A. A., 1963a. Analysis of the American Indian dentition. *In*: Dental Anthropology, ed. D. R. Brothwell. Oxford, Pergamon Press. pp. 149–177.
DAHLBERG, A. A., 1963b. Dental evolution and culture. *Hum. Biol.*, **35**: 237–249.
DAHLBERG, A. A., 1965. Cited by ZOUBOV and HALDEYEVA (1989).
DELLA SERRA, 1951. Cited by VERGER-PRATOUCY (1981–1982).
DE TERRA, M., 1905. Cited by SAKAI *et al.* (1969–1970) and VERGER-PRATOUCY (1981–1982).
DEVOTO, 1969. Cited by VERGER-PRATOUCY (1981–1982).
DIACONIS, P., and B. EFRON, 1983. Computer-intensive methods in statistics. *Scientific American*, **248**: 96–108, 138.
DIETZ, V. H., 1944. A common dental morphotropic factor: the Carabelli cusp. *J. Am. Dent. Assoc.*, **31**: 784–789.
DUBOV, A. I., 1985. Cited by ZOUBOV and HALDEYEVA (1989).
DUBOVA, N. A., and L. I. TEGAKO, 1983. Cited by ZOUBOV and HALDEYEVA (1989).
EFRON, B., 1979a. Bootstrap methods: Another look at the jackknife. *Ann. Statist.*, **7**: 1–26.
EFRON, B., 1979b. Computers and the theory of statistics: Thinking the unthinkable. *SIAM Rev.*, **21**: 460–480.
EFRON, B., 1982. The Jackknife, the Bootstrap and Other Resampling Plans. Philadelphia, Society for Industrial and Applied Mathematics.
ELLICOTT, D. F., 1979. The incidence of Carabelli's cusp in the Australian aboriginal. *Archaeol. Phys. Anthrop. Oceania*, **14**: 118–122.
ENISHI, J., 1939. Cited by SAKAI and HANAMURA (1967) and SAKAI *et al.* (1969–1970).

ESCOBAR, V., P. M. CONNEALLY and C. LOPEZ, 1977. The dentition of the Queckchi Indians: Anthropological aspects. *Am. J. Phys. Anthrop.*, **47**: 443–451.

FABIAN, 1928. Cited by VERGER-PRATOUCY (1981–1982).

FRISCH, J. E., 1963. Dental variability in a population of gibbons (*Hylobates lar*). *In*: Dental Anthropology, ed D. R. BROTHWELL. Oxford, Pergamon Press. pp. 15–28.

FRISCH, J. E., 1965. Trends in the Evolution of the Hominoid Dentition (Bibliotheca Primatologica, Fasc. 3). Basel, S. Karger.

GADZHIEV, Y. M., 1979. Cited by HAEUSSLER and TURNER (1992) and ZOUBOV and HALDEYEVA (1989).

GARN, S. M., R. S. KEREWSKY and A. B. LEWIS, 1966a. Extent of sex influence on Carabelli's polymorphism. *J. Dent. Res.*, **45**: 1823.

GARN, S. M., A. B. LEWIS, R. S. KEREWSKY and A. A. DAHLBERG, 1966b. Genetic independence of Carabelli's trait from tooth size or crown morphology. *Archs. Oral Biol.*, **11**: 745–747.

GASHIMOVA, U. F., 1979. Cited by ZOUBOV and HALDEYEVA (1989).

GOAZ, P. W., and M. C. MILLER III, 1966. A preliminary description of the dental morphology of the Peruvian Indian. *J. Dent. Res.*, **45**: 106–119.

GODEFROIT, P., 1990. Dental variation in the genus *Pan*. *Z. Morph. Anthrop.*, **78**: 175–195.

GOOSE, D. H., 1977. The dental condition of Chinese living in Liverpool. *In*: Orofacial Growth and Development, ed. A. A. DAHLBERG and T. M. GRABER. The Hague, Mouton. pp. 183–194.

GOOSE, D. H., and G. T. R. LEE, 1971. The mode of inheritance of Carabelli's trait. *Hum. Biol.*, **43**: 64–69.

GUIGUI, 1974. Cited by VERGER-PRATOUCY (1981–1982).

HAEUSSLER, A. M., and C. G. TURNER II, 1992. The dentition of Soviet Central Asians and the quest for New World ancestors. *In*: Culture, Ecology and Dental Anthropology, ed. J. R. LUKACS. Delhi, Kamla-Raj Enterprises. pp. 273–297.

HALDEYEVA, N. I., 1979. Cited by ZOUBOV and HALDEYEVA (1989).

HANIHARA, K., 1956. Studies on the deciduous dentition of the Japanese and the Japanese-American hybrids: IV. Deciduous upper molars. *J. Anthrop. Soc. Nippon*, **65**: 67–87. (In Japanese with English summary.)

HANIHARA, K., 1957. Studies on the deciduous dentition of the Japanese and the Japanese-American hybrids: V. General conclusion. *J. Anthrop. Soc. Nippon*, **65**: 151–164. (In Japanese with English summary.)

HANIHARA, K., 1963. Crown characters of the deciduous dentition of the Japanese-American hybrids. *In*: Dental Anthropology, ed. D. R. BROTHWELL. Oxford, Pergamon Press. pp. 105–124.

HANIHARA, K., 1968. Morphological pattern of the deciduous dentition in the Japanese-American hybrids. *J. Anthrop. Soc. Nippon*, **76**: 114–121.

HANIHARA, K., 1976. Statistical and comparative studies of the Australian Aboriginal dentition. *University Museum, University of Tokyo Bulletin*, (11): 1–57.

HANIHARA, K., and T. HANIHARA, 1989. Multivariate analysis of tooth crown morphology in Japanese-American F1 hybrids. *Hum. Evol.*, **4**: 417–427.

HAHIHARA, K., T. MASUDA and T. TANAKA, 1974. Affinities of dental characteristics in the Okinawa Islanders. *J. Anthrop. Soc. Nippon*, **82**: 75–82.

HAHIHARA, K., T. MASUDA, T. TANAKA and M. TAMADA, 1975. Comparative studies of dentition. *In*: JIBP Synthesis, Vol. 2: Anthropological and Genetic Studies on the Japanese, Part III: Anthropological and Genetic Studies of the Ainu, ed. S. WATANABE, S. KONDO and E. MATSUNAGA. Tokyo, Univ. of Tokyo Press. pp. 256–264.

HANIHARA, T., 1990. Dental anthropological evidence of affinities among the Oceania and the Pan-Pacific populations: The basic populations in East Asia, II. *J. Anthrop. Soc. Nippon*, **98**: 233–246.

HANIHARA, T., 1991a. Dental and cranial evidence on the affinities of the East Asian and Pacific populations. *In*: Japanese as a Member of the Asian and Pacific Populations, ed. K. HANIHARA. Kyoto, International Research Center for Japanese Studies. pp. 119–137.

HANIHARA, T., 1991b. The origin and microevolution of Ainu as viewed from dentition: the basic populations in East Asia, VIII. *J. Anthrop. Soc. Nippon*, **99**: 345–361.

HANIHARA, T., 1991c. Dentition of Nansei Islanders and peopling of the Japanese Archipelago: The basic populations in East Asia, IX. *J. Anthrop. Soc. Nippon*, **99**: 399–409.

HANIHARA, T., 1992. Dental and cranial affinities among populations of East Asia and the Pacific: The basic populations in East Asia, IV. *Am. J. Phys. Anthrop.*, **88**: 163–182.

HANULÍK, M., A. BACHRATÝ und P. ANDRIK, 1966. Bemerkungen zum Vorkommen des Tuberculum anomale Carabelli. *Z. Morph. Anthrop.*, **57**: 168–172.

HARRIS, E. F., 1976. Quasi-continuous variation in dental morphology. Paper presented at the Forty-Fifth Annual Meeting of the American Association of Physical Anthropologists, St. Louis, Missouri.

HARRIS, E. F., C. G. TURNER II and J. H. UNDERWOOD, 1975. Dental morphology of living Yap Islanders, Micronesia. *Arch. & Phys. Anthrop. in Oceania*, **10**: 218–234.

HASSANALI, J., 1982. Incidence of Carabelli's trait in Kenyan Africans and Asians. *Am. J. Phys. Anthrop.*, **59**: 317–319.

HELJMANN, 1928. Cited by VERGER-PRATOUCY (1981–1982).

HERSHEY, S. E., 1979. Morphology of the Wainwright Eskimo dentition: Carabelli's structures. *Ossa*, **6**: 115–124.

HERSHKOVITZ, P., 1971. Basic crown patterns and cusp homologies of mammalian teeth. *In*: Dental Morphology and Evolution, ed. A. A. DAHLBERG. Chicago, The Univ. of Chicago Press. pp. 95–150.

HIRAKAWA, 1940. Cited by VERGER-PRATOUCY (1981–1982).

JIEN, 1970. Cited by VERGER-PRATOUCY (1981–1982).

JOSHI, M. R., R. N. GODIAWALA and A. DUTIA, 1972. Cited by HERSHEY (1979) and VERGER-PRATOUCY (1981–1982).

KACZMAREK, M., 1981. Cited by ZOUBOV and HALDEYEVA (1989).

KAJAVA, 1930. Cited by VERGER-PRATOUCY (1981–1982).

KAMIJO, Y., T. HAGA, K. SATO, H. MORI, T. IWATA and S. KASHIWAGI, 1981. Hihonjin seitai shiga no kenkyu: Karaberi kessetsu ni tsuite (A study of the teeth of living Japanese: On the Carabelli trait). *In*: Kamijo Yasuhiko Kyoju Gyosekishu. Tokyo, Kamijo Yasuhiko Kyoju Gyosekishu Kanko Iinkai. pp. 203–207. (In Japanese.)

KAUL, S. S., K. SHARMA, J. C. SHARMA and R. S. CORRUCCINI, 1985. Non-metric variants of the permanent dental crown in human monozygous and dizygous twins. *In*: Dental Anthropology: Application and Methods, ed. V. RAMI REDDY. New Delhi, Inter-India Publications. pp. 187–193.

KAUL, V., and S. PRAKASH, 1981. Morphological features of Jat dentition. *Am. J. Phys. Anthrop.*, **54**: 123–127.

KAWAMOTO, K., 1989. The dental morphology of the Polynesians in the Cook Islands. *Aichi-Gakuin J. Dent. Sci.*, **27**: 855–883. (In Japanese with English summary.)

KEENE, H. J., 1968. The relationship between Carabelli's trait and the size, number and morphology of the maxillary molars. *Archs. Oral Biol.*, **13**: 1023–1025.

KIESER, J. A., 1978. Cited by KIESER and PRESTON (1981) and BERMÚDEZ DE CASTRO (1989).

KIESER, J. A., 1984. An analysis of the Carabelli trait in the mixed deciduous and permanent human dentition. *Archs. Oral Biol.*, **29**: 403–406.

KIESER, J. A., 1985. Congenital syphilis and the Carabelli cusp. *J. History of Med. and Allied Sci.*, **40**: 346–348.

KIESER, J. A., N. CAMERON and H. T. GROENEVELD, 1987. Evidence for a secular trend in the Negro dentition. *Annals of Human Biol.*, **14**: 517–532.

KIESER, J. A., H. T. GROENEVELD and C. B. PRESTON, 1985. An odontometric analysis of the Lengua Indian dentition. *Hum. Biol.*, **57**: 611–620.

KIESER, J. A., and C. B. PRESTON, 1981. The dentition of the Lengua Indians of Paraguay. *Am. J. Phys. Anthrop.*, **55**: 485–490.

KIESER, J. A., and C. A. VAN DER MERWE, 1984. Classificatory reliability of the Carabelli trait in man. *Archs. Oral Biol.*, **29**: 795–801.

KIMURA, K., M. KONISHI and S. TANAKA, 1978. Dental characteristics in the Ishigaki Islanders. *J. Natl. Def. Med. Coll.*, **3**: 145–151. (In Japanese with English summary.)

KIRVESKARI, P., 1974. Morphological traits in the permanent dentition of living Skolt Lapps. *Proc. Finn. Dent. Soc.*, **70** (Suppl. II): 1–90.

KIRVESKARI, P., 1978. Racial traits in the dentition of living Skolt Lapps. *In*: Development, Function and Evolution of Teeth, ed. P. M. BUTLER and K. A. JOYSEY. London, Academic Press. pp. 59–68.

KIRVESKARI, P., and L. ALVESALO, 1982. Dental morphology in Turner's syndrome (45,X females). *In*: Teeth: Form, Function, and Evolution, ed. B. KURTÉN. New York, Columbia Univ. Press. pp. 298–303.

KIRVESKARI, P., H. HANSSON, B. HEDEGARD and U. KARLSSON, 1978. Crown size and hypodontia in the permanent dentition of modern Skolt Lapps. *Am. J. Phys. Anthrop.*, **48**: 107–112.

KOBAYASHI, A., 1989. The temporal change of non-metric dental traits in Japan. *Anthrop. Reports*, (48): 65–101. (In Japanese with English summary.)

KOLAKOWSKI, D., E. F. HARRIS and H. L. BAILIT, 1980. Complex segregation analysis of Carabelli's trait in a Melanesian population. *Am. J. Phys. Anthrop.*, **53**: 301–308.

KORENHOF, C. A. W., 1960. Morphogenetical Aspects of the Human Upper Molar. Utrecht, Acad. proefschrift, Uitgeversmaatschappij Neerlandia.

KORENHOF, C. A. W., 1982. Evolutionary trends of the inner enamel anatomy of deciduous molars from Sangiran (Java, Indonesia). *In*: Teeth: Form, Function, and Evolution, ed. B. KURTÉN. New York, Columbia Univ. Press. pp. 350–365.

KORKHAUS, G., 1930. Die Vererbung der Kronenform und -grösse menschlicher Zähne. *Z. Anat. u. Entw.*, **91**: 594–617.

KRAUS, B. S., 1951. Carabelli's anomaly of the maxillary molar teeth: Observations on Mexicans and Papago Indians and an interpretation of the inheritance. *Am. J. Hum. Genet.*, **3**: 348–355.

KRAUS, B. S., 1959. Occurrence of the Carabelli trait in Southwest ethnic groups. *Am. J. Phys. Anthrop.*, **17**: 117–123.

KRAUS, B. S., and R. E. JORDAN, 1965. The Human Dentition Before Birth. Philadelphia, Lea & Febiger.

LASKER, G. W., 1950. Genetic analysis of racial traits of the teeth. *In*: Cold Spring Harbor Symposia on Quantitative Biology, Vol. 15: Origin and Evolution of Man. Cold Spring Harbor, The Biological Laboratory. pp. 191–203.

LASKER, G. W., and M. M. C. LEE, 1957. Racial traits in the human teeth. *J. Forensic Sci.*, **2**: 401–419.

LEE, G. T. R., and D. H. GOOSE, 1972a. The inheritance of dental traits in a Chinese population in the United Kingdom. *J. Med. Genet.*, **9**: 336–339.

LEE, G. T. R., and D. H. GOOSE, 1972b. Cited by BERMÚDEZ DE CASTRO (1989).

LEFEBVRE, 1920. Cited by VERGER-PRATOUCY (1981–1982).

LEIGH, 1972. Cited by VERGER-PRATOUCY (1981–1982).

LENHOSSEK, M., 1922. Cited by SAKAI *et al.* (1969–1970) and VERGER-PRATOUCY (1981–1982).

LIU, K.-L., 1977. Dental condition of two tribes of Taiwan Aborigines: Ami and Atayal. *J. Dent.*

Res., **56**: 117–127.

LOMBARDI, A. V., 1975. Tooth size associations of three morphologic dental traits in a Melanesian population. *J. Dent. Res.*, **54**: 239–243.

MA, C., 1939, 1949. Cited by SAKAI and HANAMURA (1967).

MANABE, Y., 1989. Dental characteristics in the Yami tribe, Taiwan Aborigine. *J. Kyushu Dent. Soc.*, **43**: 489–522. (In Japanese with English summary.)

MANABE, Y., A. ROKUTANDA and Y. KITAGAWA, 1992. Nometric tooth crown traits in the Ami tribe, Taiwan Aborigines: Comparisons with other East Asian populations. *Hum. Biol.*, **64**: 717–726.

MANABE, Y., A. ROKUTANDA, Y. KITAGAWA and J. OYAMADA, 1991. Genealogical position of native Taiwanese (Bunun Tribe) in East Asian populations based on tooth crown morphology. *J. Anthrop. Soc. Nippon*, **99**: 33–47.

MARUYAMA, Y., 1933. Cited by SAKAI and HANAMURA (1967).

MASAMORI, T., 1942. Cited by SAKAI and HANAMURA (1967).

MATSUMURA, H., 1990. Geographical variation of dental characteristics in the Japanese of the protohistoric Kofun period. *J. Anthrop. Soc. Nippon*, **98**: 439–449.

MAYHALL, J. T., 1979. The dental morphology of the Inuit of the Canadian Central Arctic. *Ossa*, **6**: 199–218.

MAYHALL, J. T., S. R. SAUNDERS and P. L. BELIER, 1982. The dental morphology of North American whites: A reappraisal. *In*: Teeth: Form, Function, and Evolution, ed. B. KURTÉN. New York, Columbia Univ. Press. pp. 245–258.

MEREDITH, H. V., and E. H. HIXON, 1954. Frequency, size, and bilateralism of Carabelli's tubercle. *J. Dent. Res.*, **33**: 435–440.

MINKOV, C. B., 1977, 1981. Cited by ZOUBOV and HALDEYEVA (1989).

MIZOGUCHI, Y., 1976. On the interrelation between the shovelling and the Carabelli's tubercle as quantitative characters. *J. Anthrop. Soc. Nippon*, **84**: 297. (In Japanese.)

MIZOGUCHI, Y., 1977. Genetic variability in tooth crown characters: Analysis by the tetrachoric correlation method. *Bull. Natn. Sci. Mus., Tokyo, Ser. D*, **3**: 37–62.

MIZOGUCHI, Y., 1978. Jogaku daikyushi ni okeru 2, 3 no kessetsu no sogo-kankei ni tsuite (On the interrelations between a few tubercles in the maxillary molar). *J. Anthrop. Soc. Nippon*, **86**: 142–143. (In Japanese.)

MIZOGUCHI, Y., 1983. Influences of the earlier developing teeth upon the later developing teeth. *Bull. Natn. Sci. Mus., Tokyo, Ser. D*, **9**: 33–45.

MIZOGUCHI, Y., 1985. Shovelling: A Statistical Analysis of Its Morphology. Tokyo, Univ. of Tokyo Press.

MIZOGUCHI, Y., 1986. Correlated asymmetries detected in the tooth crown diameters of human permanent teeth. *Bull. Natn. Tokyo, Ser. D*, **12**: 25–45.

MIZOGUCHI, Y., 1988. A Statistical Analysis of Geographical Variation in Dental Size. Report of the research supported by a Grant-in-Aid for Scientific Research from the Ministry of Education, Science and Culture, Japan. (In Japanese.)

MIZOGUCHI, Y., 1993. Overall associations between dental size and foodstuff intakes in modern human populations. *Homo*, **44**: 37–73.

MOORREES, C. F. A., 1957. The Aleut Dentition. Cambridge, Harvard Univ. Press.

MORI, T., 1932. Cited by SAKAI and HANAMURA (1967).

MORIMOTO, K., 1939. Cited by SAKAI and HANAMURA (1967).

NOMURA, J., 1974. Morphological studies on the first permanent molar and the second deciduous molar: 2. On the shape of the crown. *Shikwa Gakuho*, **74**: 620–634. (In Japanese with English summary.)

NICHOL, C. R., 1989. Complexing segregation analysis of dental morphological variants. *Am. J. Phys. Anthrop.*, **78**: 37–59.

NICHOL, C. R., and C. G. TURNER II, 1986. Intra- and interobserver concordance in classifying dental morphology. *Am. J. Phys. Anthrop.*, **69**: 299–315.

OKUNO, T., T. HAGA, K. YAJIMA, C. OKUNO, S. HASHIMOTO and Y. FURUKAWA, 1976. Zoku-Tahenryo-Kaisekiho (Multivariate Analysis Methods, Part 2). Tokyo, Nikkagiren. (In Japanese.)

OKUNO, T., H. KUME, T. HAGA and T. YOSHIZAWA, 1971. Tahenryo-Kaisekiho (Multivariate Analysis Methods). Tokyo, Nikkagiren. (In Japanese.)

O'ROURKE, D. H., and M. H. CRAWFORD, 1980. Odontometric microdifferentiation of transplanted Mexican Indian populations: Cuanalan and Saltillo. *Am. J. Phys. Anthrop.*, **52**: 421–434.

OSHIMA, S., 1937. Cited by SAKAI and HANAMURA (1967).

OSHIMA, S., 1938. Cited by ELLICOTT (1979) and KIESER and PRESTON (1981).

PALES, 1938. Cited by VERGER-PRATOUCY (1981–1982).

PEARSON, K., 1900. I. Mathematical contribution to the theory of evolution: VII. On the correlation of characters not quantitatively measurable. *Phil. Trans. R. Soc., A*, **195**: 1–47.

PEDERSEN, P. O., 1949. Cited by DAHLBERG (1951), GOOSE (1977), HERSHEY (1979), and VERGER-PRATOUCY (1981–1982).

PINTO-CISTERNAS, J., and H. FIGUEROA, 1968. Genetic structure of a population of Valparaiso: II. Distribution of two dental traits with anthropological importance. *Am. J. Phys. Anthrop.*, **29**: 339–348.

PRAKASH, S., V. KAUL and S. KANTA, 1979. Observations on Bhutanese dentition. *Hum. Biol.*, **51**: 23–30.

RAITCHINOVA, 1972. Cited by VERGER-PRATOUCY (1981–1982).

REID, C., J. F. VAN REENEN and H. T. GROENEVELD, 1991. Tooth size and the Carabelli trait. *Am. J. Phys. Anthrop.*, **84**: 427–432.

REID, C., J. F. VAN REENEN and H. T. GROENEVELD, 1992. The Carabelli trait and maxillary molar cusp and crown base areas. *In*: Structure, Function and Evolution of Teeth, ed. P. SMITH and E. TCHERNOV. London, Freund Publishing House Ltd. pp. 451–466.

REINERS-KARSH, M., 1964. Cited by KIESER and PRESTON (1981) and BERMÚDEZ DE CASTRO (1989).

RICHARDS, L. C., and P. J. TELFER, 1979. The use of dental characters in the assessment of genetic distance in Australia. *Archaeol. & Phys. Anthrop. in Oceania*, **14**: 184–194.

ROBINSON, J. T., 1956. The Dentition of the Australopithecinae. Pretoria, Transvaal Museum.

ROSENZWEIG, K. A., and Y. ZILBERMAN, 1969. Dentition of Bedouin in Israel. II. Morphology. *Am. J. Phys. Anthrop.*, **31**: 199–204.

SAHEKI, M., 1966. Morphological studies of *Macaca fuscata*: IV. Dentition. *Primates*, **7**: 407–422.

SAHEKI, M., K. TASHIRO and S. HAYAMA, 1959. Morphological study on the dentition of the macaque. *Primates*, **2**: 100–107.

SAKAI, T., 1968. Cited by SAKAI *et al.* (1969–1970).

SAKAI, T., and H. HANAMURA, 1967. A morphological analysis of Carabelli's cusp. *Aichi-Gakuin Daigaku Shigakukaishi*, **5**: 60–72. (In Japanese with English summary.)

SAKAI, T., and H. HANAMURA, 1971. A morphological study of enamel-dentin border on the Japanese dentition: V. Maxillary molar. *J. Anthrop. Soc. Nippon*, **79**: 297–322. (In Japanese with English summary.)

SAKAI, T., H. HANAMURA and N. OHNO, 1969–1970. The dentition of the Pashtun and Tajik in Afghanistan. *Aichi-Gakuin Daigaku Shigakukaishi*, **7**: 106–137, 265–314. (In Japanese with English summary.)

SAKAI, T., H. HANAMURA and N. OHNO, 1971. Tooth size of the Pashtun and Tajik in Afghanistan. *J. Anthrop. Soc. Nippon*, **79**: 159–177. (In Japanese with English summary.)

SCOTT, G. R., 1972. An analysis of population and family data on Carabelli's trait and shovel-shaped incisors. *Am. J. Phys. Anthrop.*, **37**: 449.

SCOTT, G. R., 1978. The relationship between Carabelli's trait and the protostylid. *J. Dent. Res.*, **57**: 570.

SCOTT, G. R., 1980. Population variation of Carabelli's trait. *Hum. Biol.*, **52**: 63–78.

SCOTT, G. R., and A. A. DAHLBERG, 1982. Microdifferentiation in tooth crown morphology among Indians of the American Southwest. *In*: Teeth: Form, Function, and Evolution, ed. B. KURTÉN. New York, Columbia Univ. Press. pp. 259–291.

SCOTT, G. R., and R. H. Y. POTTER, 1984. An analysis of tooth crown morphology in American white twins. *Anthropologie*, **22**: 223–231.

SCOTT, G. R., R. H. Y. POTTER, J. F. NOSS, A. A. DAHLBERG and T. DAHLBERG, 1983. The dental morphology of Pima Indians. *Am. J. Phys. Anthrop.*, **61**: 13–31.

SEGEDA, S. P., 1979. Cited by ZOUBOV and HALDEYEVA (1989).

SHAPIRO, M. M. J., 1949. Cited by KIESER and PRESTON (1981) and VERGER-PRATOUCY (1981–1982).

SHARMA, J. C., 1983. Dental morphology and odontometry of the Tibetan immigrants. *Am. J. Phys. Anthrop.*, **61**: 495–505.

SHAW, J. C. M., 1931. Cited by DAHLBERG (1951) and SOFAER *et al.* (1972).

SHIKAI, K., 1957. Cited by SAKAI and HANAMURA (1967).

SHIMIZU, K., 1939. Observations of family data on the supernumerary teeth and tubercles occurring in the molar parts of both jaws. *J. Nippon Dent. Assoc.*, **32**: 170–176. (In Japanese.)

SIEGEL, S., 1956. Nonparametric Statistics for the Behavioral Sciences. Tokyo, McGraw-Hill Kogakusha.

SIEMENS, H. W., 1928. Die Vererbungspathologie der Mundhöhle. *München. Med. Wschr.*, **41**: 1747–1750.

SIKHIMBAEVA, K. B., 1986, 1987. Cited by ZOUBOV and HALDEYEVA (1989).

SNYDER, R. G., A. A. DAHLBERG, C. C. SNOW and T. DAHLBERG, 1969. Trait analysis of the dentition of the Tarahumara Indians and Mestizos of the Sierra Madre Occidental, Mexico. *Am. J. Phys. Anthrop.*, **31**: 65–76.

SOFAER, J. A., C. J. MACLEAN and H. L. BAILIT, 1972. Heredity and morphological variation in early and late developing human teeth of the same morphological class. *Archs. Oral Biol.*, **17**: 811–816.

SOFAER, J. A., P. SMITH and E. KAYE, 1986. Affinities between contemporary and skeletal Jewish and non-Jewish groups based on tooth morphology. *Am. J. Phys. Anthrop.*, **70**: 265–275.

SUBOW, A. A., 1972. Einige Angaben der dentalen Anthropologie über die Bevölkerung Finnlands. *Annales Academiae Scientiarum Fennicae, Ser. A, V. Medica*, **150**: 1–12.

SUMIYA, Y., 1959. Statistic study on dental anomalies in the Japanese. *J. Anthrop. Soc. Nippon*, **67**: 215–233. (In Japanese with English summary.)

SUZUKI, B., 1920. Cited by SAKAI and HANAMURA (1967).

SUZUKI, M., and T. SAKAI, 1957. The living Sakhalin Ainu dentition. *Anthrop. Reports* (*Niigata Univ.*), (18): 303–346. (In Japanese with English summary.)

SUZUKI, M., and T. SAKAI, 1973. The Japanese Dentition: Morphological Study of the Dental Characteristics of the Permanent Teeth in Recent Japanese. Matsumoto, Shinshu University School of Medicine.

TAKEHISA, S., 1957. Anatomical and anthropological studies on the teeth of the American white races and Japanese. *Shika Gakuho*, **57** (Supplement): 1–41. (In Japanese.)

TAKEI, T., 1990. An anthropological study on the tooth crown morphology in the Atayal tribe of Taiwan Aborigines: Comparative analysis between Atayal and some Asian-Pacific populations. *J. Anthrop. Soc. Nippon*, **98**: 337–351. (In Japanese with English summary.)

TEGAKO, L. I., and I. I. SALIVON, 1979. Cited by ZOUBOV and HALDEYEVA (1989).

TOWNSEND, G. C., and R. H. BROWN, 1983. Tooth morphology in Down's syndrome: evidence for retardation in growth. *J. Ment. Defic. Res.*, **27**: 159–169.

TOWNSEND, G. C., and T. BROWN, 1979. Tooth size characteristics of Australian Aborigines. *In*:

Occasional Papers in Human Biology, No. 1. Canberra, Australian Institute of Aboriginal Studies. pp. 17–38.

TOWNSEND, G. C., and T. BROWN, 1981. The Carabelli trait in Australian Aboriginal dentition. *Archs. Oral Biol.*, **26**: 809–814.

TOWNSEND, G. C., L. C. RICHARDS, T. BROWN, V. B. BURGESS, G. R. TRAVAN and J. R. ROGERS, 1992. Genetic studies of dental morphology in South Australian twins. *In*: Structure, Function and Evolution of Teeth, ed. P. SMITH and E. TCHERNOV. London, Freund Publishing House Ltd. pp. 501–518.

TRATMAN, E. K., 1950. A comparison of the teeth of people: Indo-European racial stock with the Mongoloid racial stock. *Dental Record*, **70**: 31–53, 63–88.

TSUJI, T., 1958. Incidence and inheritance of the Carabelli's cusp in a Japanese population. *Jap. J. Hum. Genet.*, **3**: 21–31.

TURNER, C. G., II, 1967a. Dental genetics and microevolution in prehistoric and living Koniag Eskimo. *J. Dent. Res.*, **46** (Supplement to No. 5): 911–917.

TURNER, C. G., II, 1969. Microevolutionary interpretations from the dentition. *Am. J. Phys. Anthrop.*, **30**: 421–426.

TURNER, C. G., II, 1979. Dental anthropological indications of agriculture among the Jomon people of central Japan: X. Peopling of the Pacific. *Am. J. Phys. Anthrop.*, **51**: 619–635.

TURNER, C. G., II, and K. HANIHARA, 1977. Additional features of Ainu dentition: V. Peopling of the Pacific. *Am. J. Phys. Anthrop.*, **46**: 13–24.

TURNER, C. G., II, and G. R. SCOTT, 1977. Dentition of Easter Islanders. *In*: Orofacial Growth and Development, ed. A. A. DAHLBERG and T. A. GRABER. The Hague, Mouton. pp. 229–249.

TURNER, C. G., II, and D. R. SWINDLER, 1978. The dentition of New Britain West Nakanai Melanesians: VIII. Peopling of the Pacific. *Am. J. Phys. Anthrop.*, **49**: 361–371.

VAN REENEN, 1964. Cited by VERGER-PRATOUCY (1981–1982).

VERGER-PRATOUCY, J.-C., 1981–1982. Anomalies dentaires et tubercules anomaux. *L'Anthropologie*, **85/86**: 683–697.

VERGER-PRATOUCY and REGNERE, n.d. Cited by VERGER-PRATOUCY (1981–1982).

WADA, N., 1938. Genetical research in the field of odontology: III. Genetical studies on dental arch, dental dimension, and dental morphology. *J. Juzen Med. Soc.*, **43**: 715–902. (In Japanese.)

WAGEMAN, G., 1976. Cited by VERGER-PRATOUCY (1981–1982).

WEIDENREICH, F., 1937. The Dentition of *Sinanthropus pekinensis*: A Comparative Odontography of the Hominids. *Palaeontologia Sinica*, *N. S. D*, No. 1. (Whole Ser. No. 101): 1–180, with Atlas of 121 pp.

YABUKI, S., 1942. Cited by SAKAI and HANAMURA (1967).

YAMADA, E., 1931. Cited by SAKAI and HANAMURA (1967).

YAMADA, H., N. OHNO and T. SAKAI, 1979. A research on multivariate biological affinity of tooth crowns. *J. Anthrop. Soc. Nippon*, **87**: 457–471.

YAMADA, H., and T. SAKAI, 1992. Sexual dimorphism in tooth crown diameter of the Cook Islanders. *In*: Structure, Function and Evolution of Teeth, ed. P. SMITH and E. TCHERNOV. London, Freund Publishing House Ltd. pp. 437–449.

YASUDA, S., 1969. Shakai-Tokeigaku (Social Statistics). Tokyo, Maruzen. (In Japanese.)

ZOUBOV, A. A., and N. I. HALDEYEVA, 1989. Odontologiya v Sovremennoy Antropologii. Moscow, Nauka. (In Russian.)

ZOUBOV, A. A., and B. A. NIKITYUK, 1978. Prospects for the application of dental morphology in twin type analysis. *J. Hum. Evol.*, **7**: 519–524.

ZOUBOV, A. A., and I. M. ZOLOTAREVA, 1980. Cited by ZOUBOV and HALDEYEVA (1989).