

Fitting Genetic Models to Carabelli Trait Data in South Australian Twins

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This study aimed to clarify genetic and environmental contributions to Carabelli trait variation on permanent first molar teeth in a large sample of South Australian twins. Estimates of polychoric correlations were obtained between pairs of monozygous (MZ) and dizygous (DZ) twins for Carabelli data and various gene-environment models fitted by a weighted least-squares approach. The favored model included additive genetic effects together with both a general environmental component and an environmental effect specific to each side. An estimate of heritability around 90% indicated a very strong genetic contribution to observed variation. The pattern of correlations for MZ and DZ data suggested that further studies involving other types of relatives would be worthwhile for detection of possible non-additive genetic effects of dominance or epistasis.

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Introduction.

Although a considerable amount has been written in the anthropological literature about the Carabelli trait, its genetic basis remains unclear. The trait occurs on the palatal surfaces of the mesiopalatal cusps of maxillary molar teeth, particularly deciduous second and permanent first molars, with expression ranging from pits and grooves to protuberances and free cusps.

Based on pedigree studies, some early researchers proposed a simple autosomal mode of inheritance (*e.g.*, Kraus, 1951), although more recent studies have supported a polygenic model (Goose and Lee, 1971; Townsend and Brown, 1981). There have also been suggestions of major gene involvement (Kolakowski *et al.*, 1980; Nichol, 1989a). Estimates of heritability for the Carabelli trait are conflicting, some studies providing high estimates (Skrinjaric *et al.*, 1985), others yielding low estimates (Biggerstaff, 1973; Alvesalo *et al.*, 1975; Mizoguchi, 1977; Scott and Potter, 1984).

Given the limitations in study designs associated with most investigations of the Carabelli trait (*e.g.*, small sample sizes and methods of analysis which make inefficient use of the data), it is not surprising that there is still considerable confusion relating to the influence of genetic factors on this feature. A basic assumption implicit in studies of human population affinities and migratory patterns (*e.g.*, Turner, 1986) is that dental crown features, such as the Carabelli trait, have a strong genetic basis. Therefore, it is appropriate that more powerful methods of genetic model-fitting now be applied to dental data from large samples of related individuals.

Eaves (1982) has clearly described the value of twin studies in clarifying the relative contributions of genetic and environmental effects on phenotypic variability. Furthermore, he has stressed the importance of "model-building" and "model-fitting" to determine statistically whether data are consistent with theory and also to enable estimation of model parameters to be carried out. A number of researchers have now applied the LISREL software package along with the pre-processor PRELIS [developed by Jöreskog and Sörbom (1986, 1989)] to fit genotype-environment models to twin data (Martin *et al.*, 1989). The use of LISREL is facilitated by a working knowledge of path analysis which enables path diagrams

to be generated that relate measured and latent variables representing genetic and environmental causes of individual differences. Various genetic models can be fitted to summary covariance or correlation matrices by maximum likelihood or other methods. These models can then be tested by chi-square for goodness-of-fit, and estimates of the model parameters and their standard errors can also be determined (Heath *et al.*, 1989).

The present research used PRELIS and LISREL for analysis of data on the Carabelli trait in a large sample of South Australian twins.

Materials and methods.

Carabelli trait was scored on right and left permanent maxillary first molars from dental models collected as part of an ongoing study of dento-facial variability in South Australian twins (Townsend *et al.*, 1986; Brown *et al.*, 1987). A total of 448 sets of dental models [representing 122 pairs of monozygous (MZ) and 102 pairs of dizygous (DZ) twins] was examined, although a few individuals for whom the Carabelli trait could not be scored were subsequently excluded from analysis. Subjects ranged in age from ten to 46 years, with the majority being teenagers. Zygosity was confirmed by comparison of a number of genetic markers in the blood (ABO, Rh, Fy, Jk, MNS), together with several serum enzyme polymorphisms (GLO, ESD, PGM1, PGD, ACP, GPT, PGP, AK1) and protein polymorphisms (HP, C3, PI, GC). The probability of dizygosity, given concordance for all systems, was less than 1%.

The method of Dahlberg (1963) was applied for classification of the Carabelli trait on an eight-grade scale, ranging from absence through seven grades of presence, including single grooves and pits, double and Y-shaped grooves, and various sizes of cusps. When degrees of expression were determined, reference was made to a plaster replica of the plaque, labeled p12*, which was issued by Dahlberg to facilitate standardization in scoring the Carabelli trait within and between observers. Assessments were made for all subjects on two separate occasions, providing test/re-test data. Where discrepancies were noted between first and second determinations, a third assessment was made, and the corrected data were then used for determination of frequencies of occurrence of the trait.

The frequency of occurrence and degree of expression of the Carabelli trait were determined for right and left sides in males and females separately, associations between genders being tested by chi-square analysis. The software package for structural equation modeling [LISREL version 7.16 (Jöreskog and Sörbom, 1989)], along with its pre-processor PRELIS, were then applied to the Carabelli data. For analysis, subjects were divided into five zygosity groups: MZ males (46 pairs), MZ females (62 pairs), DZ males (25 pairs), DZ females (28 pairs), and DZ male-female pairs (41 pairs), with only those subjects having Carabelli scores for both right and left sides being included.

PRELIS enabled estimates of polychoric correlations for right and left Carabelli trait to be made in the different twin groups. Polychoric correlations (literally, "many spaces") represent a generalization of the familiar tetrachoric correlation and are more appropriate in quantifying associations for the ordinal Carabelli data (which include a number of categories) than the usual Pearson correlation for continuous data (Olsson, 1979). Estimation of polychoric correlations implies the assumption that the discontinuous distribution of Carabelli scores reflects an under-

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Results.

Table 1 gives the frequency of male and female twin individuals showing various degrees of expression of the Carabelli trait. There was no significant heterogeneity of trait-score distributions in males and females, for either the left or right sides, indicating no sexual dimorphism. Around 85% of subjects displayed the trait in some form, approximately 30% showing the cuspal form. Fig. 2 shows dental models of a pair of identical twins showing the most marked expression of the Carabelli trait (grade 7).

The joint distribution of right and left Carabelli trait scores for 423 twin individuals is given in Table 2. The hypothesis of an underlying bivariate-normal distribution was retained at the 5% probability level, with a polychoric correlation of 0.87 ± 0.014 .

Polychoric correlations for right and left Carabelli trait data in the different twin groups are summarized in Tables 3a, b, and c. Values of correlations between opposite sides of individual MZ twins were of a magnitude similar to those between corresponding sides of MZ twin pairs, averaging around 0.9. Correlations between right and left sides of individual DZ twins also averaged around 0.9, although those between corresponding sides of DZ twin pairs averaged near 0.4. When these values were compared with the polychoric correlations derived between the test/re-test data (0.94 ± 0.008 for the left and 0.96 ± 0.005 for the right side), the correlations between repeated Carabelli scores were similar in magnitude to those between right and left sides of individuals, and only slightly greater than those between corresponding sides of MZ twins.

Model fitting.—When the full model was fitted to the two female correlation matrices, it gave a fit of $\chi^2_5 = 3.89$, and the same model fitted to the males gave a fit of $\chi^2_5 = 1.57$. This model, fitted jointly to all four same-gender matrices, gave $\chi^2_7 = 12.33$. Subtracting the sum of the fits to the genders considered separately from the joint fit gave a heterogeneity of $\chi^2_7 = 6.87$, indicating that the sources of variation and covariation in the two genders were at least quantitatively similar. To test whether they were also qualitatively similar, the matrix for DZ male-female pairs was added and the model re-fitted, yielding $\chi^2_{23} = 19.30$, an increase of $\chi^2 = 6.97$ for 6 df. This suggested that the opposite-gender pairs revealed no new striking heterogeneity in causes of variation of the Carabelli trait, and that the sources of variation and covariation were similar in males and females, in both size and kind. If they were different in kind, one would expect the DZ male-female correlations to be significantly lower than those for DZ

same-gender pairs. In fact, the DZ male-female correlations were somewhat higher than those for DZ same-gender pairs, although apparently not significantly so.

The results of the full model fitted to all five correlation matrices are shown as Model 1 in Table 4, and this model became a benchmark for testing certain simplifying hypotheses. First, a test of whether dominance variation was needed at all was performed by eliminating both general and specific

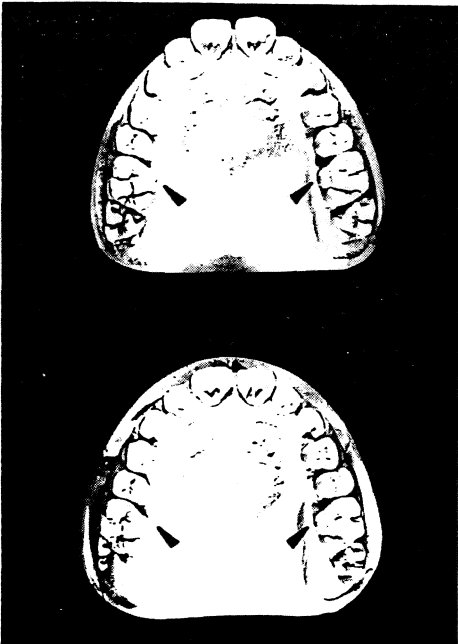


Fig. 2—Dental models of a pair of monozygous twins, both showing the most marked expression of Carabelli trait (grade 7) on maxillary first permanent molars.

dominance effects, and, in Model 2, the χ^2 increased only by 0.90 for 3 df, indicating that genetic non-additivity could be omitted (Table 5). This is not to say that non-additive variation did not exist for the Carabelli trait, merely that there was insufficient power to detect it. Martin *et al.* (1978) showed that very large sample sizes are required to detect even substantial amounts of genetic non-additivity when only twin correlations are available. Addition of parent-offspring or half-sibling data would greatly enhance the power to detect non-additivity, and these data are presently being collected.

Model 2 then became the benchmark against which further simplifying hypotheses were tested. Specifically, it was of interest to determine whether genetic variation may contribute to fluctuating asymmetry, as measured by imperfect covariation between Carabelli trait on left and that on right teeth. In model 3, this was

TABLE 2
JOINT DISTRIBUTION OF RIGHT AND LEFT CARABELLI TRAIT SCORES FOR 423 TWIN INDIVIDUALS

		Left							
		0	1	2	3	4	5	6	7
Right	0	39	10	0	3	2	0	0	0
	1	15	70	2	4	7	1	0	0
	2	0	1	1	1	0	1	0	0
	3	4	9	1	23	6	4	0	0
	4	1	4	1	10	54	4	1	0
	5	2	6	1	12	12	57	2	0
	6	0	0	0	1	1	5	29	0
	7	0	0	0	1	1	1	2	11

Polychoric correlation 0.87 ± 0.014 .

tested by dropping the genetic specific, and it was noticed that χ^2 increased by 5.74 for 1 df (Table 5), indicating that, indeed, genetic factors were involved in left-right differentiation for this trait. Similarly, the hypothesis that any environmental influence on one side of the dentition also affects the other to the same extent was tested; this was done by setting the environmental specific to zero (model 4 in Table 4, Hypothesis C in Table 5), and it was noted that this caused no significant increase in χ^2 over model 2. It was observed, however, that the loadings of the environmental factor were now quite disparate, with this factor accounting for 4% of variance in the left molar and 13% in the right. In model 2, however, the factor loadings were very similar, and apparently 6-8% of the variance in either trait was due to environmental influences which

act on both sides of the mouth, with a further 6% apparently specific to either tooth (arbitrarily assigned here to the right molar); this latter term also included uncorrelated scoring error.

Next, a test of whether genetic and environmental factors were both needed to explain covariation between the Carabelli trait on left and right sides was performed. In model 5, omission of the cross-loading of the genetic factor on the other tooth led to a drastic increase in χ^2 to 1027 (Table 4); clearly, genetic factors were the major source of covariation. The influence of environmental factors on both cusps was less important, but their omission (model 6) caused a significant deterioration in chi-square ($\chi^2 = 6.97$, Table 5).

Finally, the simplest possible model for variation and covariation—a single additive genetic loading constrained to be the

TABLE 3
POLYCHORIC CORRELATIONS (x100) FOR RIGHT AND LEFT CARABELLI TRAIT IN TWINS

(a) MZ females above diagonal, DZ females below				
MZ females (62 pairs)				
	Twin 1		Twin 2	
	R1	L1	R2	L2
R1	-	88	84	76
L1	94	-	78	85
R2	23	21	-	84
L2	25	27	92	-
DZ females (28 pairs)				
Standard errors range from 0.03 to 0.06 for MZ pairs and from 0.03 to 0.20 for DZ pairs.				
(b) MZ males above diagonal, DZ males below				
MZ males (46 pairs)				
	Twin 1		Twin 2	
	R1	L1	R2	L2
R1	-	88	95	85
L1	85	-	85	86
R2	46	27	-	90
L2	26	29	79	-
DZ males (25 pairs)				
Standard errors range from 0.02 to 0.05 for MZ pairs and from 0.07 to 0.20 for DZ pairs.				
(c) opposite-sex twins below diagonal (41 pairs)				
	Twin 1		Twin 2	
	R1	L1	R2	L2
R1	-			
L1	84	-		
R2	51	40	-	
L2	54	47	93	-
Standard errors range from 0.03 to 0.14.				

same for both sides without any environmental covariation—was tested (model 7). While this model gave a perfectly acceptable fit to the data ($p = 0.265$, Table 4), it was significantly worse than that of model 2, which allowed for genetic and environmental contributions to asymmetry and for environmental covariation. The preferred model allowed estimation of a genetic correlation from the computer program for the Carabelli trait between left and right molars of 0.93, while the equivalent environmental correlation was 0.76. The heritability of the Carabelli trait, from model 2, was simply 94% for the left molar and 86% ($74 + 12\%$) for the right, but no significance should be attached to the slight differences in these estimates. It should be noted that these high heritability estimates have no bearing in themselves on the question of whether variation in the Carabelli trait is produced by one or many genes. Different techniques involving segregation analysis—preferably with the addition of parent and sibling data—are needed to address this question.

Discussion.

Frequencies of occurrence of the Carabelli trait in this sample of South Australian twins were similar to those reported for American Whites (Scott, 1980), confirming that the feature is very common in Caucasian populations. The lack of sexual dimorphism for the trait is consistent with results of a number of other studies (e.g., Garn *et al.*, 1966; Turner, 1967), although different frequencies and expressions between the genders have been reported in other ethnic groups, suggesting that sexual dimorphism in the character varies among human populations (Townsend and Brown, 1981).

The trait tended to display symmetrical expression with very few individuals (only 12 of 423) displaying expressions categorized

as grade 2 or more on one side of the mouth, with no evidence of the trait on the other. Indeed, only two individuals were classified as showing a cuspal form of the Carabelli trait on one side, but no expression at all on the other. Among those individuals displaying asymmetrical expression, there was no evidence of expression on one side being consistently larger or smaller than that on the other, *i.e.*, there was no consistent directional asymmetry.

Biggerstaff (1973) proposed that different genetic factors might control trait expression on each side of the dental arch. Baume and Crawford (1980) noted population differences in the asymmetry of dental traits, including the Carabelli trait, and concluded that common genetic factors are more likely to influence dental characters on both sides of the dental arch, phenotypic expression being influenced either by local environmental conditions within the jaw or by more general intra-uterine developmental effects. These authors stressed, however, that a genetic basis for asymmetry could not be completely discounted.

In this regard, the results of this genetic analysis, which indicates that genetic factors are involved in left-right differentiation for the Carabelli trait, are of some interest. As Biggerstaff (1979) has described, the final morphology of a dental crown represents the outcome of complex interactions between developmental events during odontogenesis, including both soft-tissue proliferation and the onset and spread of calcification. Previous twin studies have failed to disclose an appreciable genetic basis to fluctuating asymmetry in the dentition (e.g., Potter and Nance, 1976), and it is generally assumed that minor phenotypic differences between antimeric tooth crowns reflect subtle differences in the timing of development, both pre-natal and post-natal, between the sides of the dentition (Scott and Potter, 1984). However, as Saunders and

TABLE 4

RESULTS OF BIVARIATE MODEL-FITTING (% VARIANCE) TO CARABELLI TRAIT DATA FOR RIGHT AND LEFT SIDES

Model		Additive		Non-additive		Unique		χ^2	df	P
		Factor	Genetic Specific	Factor	Genetic Specific	Factor	Environment Specific			
(1) Full model	L	80	-	14	-	6	-	19.30	23	0.684
	R	53	9	25	0 *	7	6			
(2) Drop dominance	L	94	-	-	-	6	-	20.20	26	0.782
	R	74	12	-	-	8	6			
(3) Model 2 and drop genetic specific	L	93	-	-	-	7	-	25.94	27	0.522
	R	84	-	-	-	1	15			
(4) Model 2 and drop environmental specific	L	94	-	-	-	4	-	20.31	27	0.817
	R	74	13	-	-	13	-			
(5) Model 2 and drop genetic covariation	L	53	-	-	-	47	-	1027	27	0.000
	R	-	40	-	-	60	0 *			
(6) Model 2 and drop environmental covariation	L	94	-	-	-	6	-	27.17	27	0.454
	R	86	2	-	-	-	12			
(7) A single additive factor with R&L loadings constrained equal. Specific environmental influences	L	91	-	-	-	-	9	33.31	29	0.265
	R	91	-	-	-	-	9			

*Parameter on lower boundary.

Mayhall (1982) have noted, different genotypic combinations can produce individuals or populations who are either poorly- or well-canalized against environmental stress (Mather, 1953; Waddington, 1957). For example, it has been shown that individuals with chromosomal abnormalities display greater fluctuating dental asymmetry, presumably reflecting a reduction in developmental stability or "buffering" (Townsend, 1983), and it is generally believed that the degree of heterozygosity of individuals in normal populations is related to developmental stability (Harrison, 1988). It would seem, then, from our results, that an individual's genotype may influence the degree of asymmetrical expression observed in the Carabelli trait.

Harris (1977) has shown that the Carabelli trait fulfills the criterion of a quasi-continuous variable, *i.e.*, it shows a continuous range of expression with a superimposed threshold below which it is undetectable. The quasi-continuous model assumes an underlying scale of continuous variation, resulting from the operation of both genetic and environmental factors, which is directly related to the expression of the character. Falconer (1965) referred to the polygenic attribute as a liability, and most recent studies of dental traits have been based on this assumption.

Complex segregation analysis has been applied to Carabelli trait data in an attempt to distinguish between single-gene and polygenic models. For example, Kolakowski *et al.* (1980) and Nichol (1989a) both found some evidence of a major gene influence, although environmental effects also appeared to contribute significantly to observed variability. However, Nichol pointed out that, while his study supported the concept of an important role for environmental factors in the development of crown morphology, difficulties associated with the ability to classify the expression of dental traits could lead to an overestimation of the importance of environmental influences. Attempts to overcome this problem have included the use of analysis of variance methods proposed by Christian and colleagues (*e.g.*, Christian, 1979) to test various assumptions of the twin model and to derive heritability estimates (Scott and Potter, 1984) and also the application of the tetrachoric correlation method to categorical Carabelli data (Mizoguchi, 1977).

This study is among the first to apply recently developed sophisticated genetic model-fitting approaches to dental data (*cf.* Potter *et al.*, 1983; Nichol, 1989b). An eight-grade scale to describe the Carabelli trait has been used which enabled polychoric correlations to be calculated and tests of bivariate normality to be applied. A number of genetic models have been fitted to the data and tested statistically for goodness-of-fit. The favored model for explanation of the variation observed in the Carabelli trait within and between the twins is one incorporating additive genetic effects, together with both a general environmental component and an environmental effect specific to each side. An estimate of heritability around 90% would suggest a very strong genetic contribution to observed varia-

tion. Although non-additive genetic effects could be omitted from the full model without significantly worsening fit, the pattern of correlations obtained for MZ and DZ data suggests that a future study including data from other types of relatives would be very worthwhile in an attempt to detect either dominance or epistasis. Heath *et al.* (1984) have provided evidence for polygenic epistatic interactions in human dermatoglyphic data, and it seems possible that features like the Carabelli trait—that may be either present or not, but show a range of expression—could be influenced by genes interacting at the same or different loci.

Although the genetic analysis presented in this paper has been applied to a dental morphological feature that is of primarily anthropological interest, model-fitting methods such as LISREL can also provide a potentially powerful means of analyzing twin and family data relating to common dental problems such as caries, periodontal disease, and malocclusion. These problems have complex, multifactorial etiologies leading to a continuous range of phenotypes from normal to abnormal (Potter, 1989, 1990), but the clinical data obtained to describe them are often ordinal and categorized as gradients, rather than being quantitative. As Potter (1990) has pointed out, information about genetic and shared environmental risks to dental diseases that can be obtained by the application of new genetic models and epidemiological designs should be of value in the development of future preventive strategies.

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TABLE 5
TESTS OF HYPOTHESES BASED ON DIFFERENCES BETWEEN GOODNESS-OF-FIT
CHI-SQUARE VALUES OF THE FULL AND REDUCED MODELS

Hypothesis	Model Comparison	LR χ^2	df	P
A. No dominance	2 vs. 1	0.90	3	0.825
B. No genetic contribution to asymmetry	3 vs. 2	5.74	1	0.017
C. No environmental contribution to asymmetry	4 vs. 2	0.11	1	0.740
D. No genetic covariation between L&R traits	5 vs. 2	1007	1	0.000
E. No environmental covariation between L&R traits	6 vs. 2	6.97	1	0.008
F. No asymmetry, no environmental covariation	7 vs. 2	13.11	3	0.004

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