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# Additive and non-additive genetic variance in odontometric traits in crosses of seven inbred lines of house mice

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SUMMARY

A least-squares diallel analysis of the offspring of crosses of seven inbred lines of house mice was performed for the mean widths of the second ($M_2$) and third ($M_3$) mandibular molars. Significant differences among lines, as well as between inbreds and hybrids (positive heterosis) were found for these characters. Estimates of the heritabilities (from general combining ability variances) were high for both teeth as were estimates of maternal effects. Specific combining ability and reciprocal effects were significant only for the $M_3$. Additionally, X-irradiation reduced the mean number of individuals per litter, and thereby indirectly influenced the widths of both molars.

## 1. INTRODUCTION

Assessment of the magnitude of the components of genetic variance – both additive and non-additive – for characters of economic importance has proven of enormous practical value. For other characters, good examples of which are dental traits in mammals, this knowledge is of considerable taxonomic and evolutionary significance. Calculation of the relative contribution of a number of genetic and environmental categories to the total variation in the widths of mandibular molars has been achieved both in house mice (Bader, 1965*a*; Larson, 1971), and in *Peromyscus leucopus* (Leamy & Bader, 1968).

Diallel analyses, however, have not been previously applied to odontometric traits in house mice, even though the technique has been utilized in this species for a variety of other traits (for example, see Chai, 1971). In the diallel method, a number of inbred lines are crossed in all possible ways, and the variation among the progeny is ascribed to general and specific combining abilities, maternal effects, and reciprocal residuum. The basic theory of genetic combining ability and of the diallel analysis in general has been developed by Henderson (1948), Hayman (1954), Griffing (1956*a*, *b*, 1958), and Kempthorne (1956).

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This paper reports the results of a diallel analysis of the variation in mandibular molar widths in crosses of a number of inbred lines of house mice. Among other estimates, the analysis provides (for the first time for these dental characters) direct estimates of the contribution of non-additive and reciprocal components, as well as an assessment of the effects of X-irradiation.

## 2. MATERIALS AND METHODS

Seven inbred lines of house mice – C57BL/6J, RF/J, CBA/J, A/J, C57BL/10J, C57BR/cdJ, C3HeB/FeJ – utilized in this study were received in November 1965 from the Jackson Laboratory. The approximate number of generations inbred ranged from 38 (RF/J) to 136 (CBA/J and A/J) so that all were assumed to be isogenic or nearly so. Each line was maintained separately in standard fashion in an animal room at room temperature. Food and water were provided *ad libitum*, the food consisting of Rockland rat/mouse complete diet from the Teklad Corporation, Monmouth, Illinois.

When most of the individuals were from six to eight weeks old, one-half of the males from each inbred line were chosen at random for X-irradiation. Irradiation was accomplished by placing several males at one time in containers at a distance of 150 cm from the source of the beam. The level of irradiation was maintained at 150 r for a period of 30 min.

All 49 possible single-pair matings of sires and dams among the seven lines were then made for both the irradiated and non-irradiated groups. An attempt was made to obtain three replications for each of the crosses for both groups, but a number of the crosses were unsuccessful. Individuals producing no litters by the time they had reached 80 days of age were regarded as sterile and were discarded.

All offspring resulting from such matings were sacrificed at 42 days of age. First litters only were utilized, these being kindly provided by A. S. Singer who reared all of the mice for purposes of a separate diallel analysis (Singer, 1967). Three individuals from each litter were randomly chosen for measurement except that both sexes were selected where possible. In those litters with less than three individuals present, all available were used. The total number of mice measured was 537; 268 males and 269 females. The skulls and teeth were prepared by the papain digestion technique (Luther, 1949).

The dentition of *Mus musculus* consists of two incisors and six molars in both the upper and lower jaws. Since previous studies (Bader, 1965*a*; Wallace, 1968) had shown a general similarity of the widths of the first and second molars with an independence of the third molar, it was decided to measure only the second ($M_2$) and the third ($M_3$) mandibular molars. Both the left and the right $M_2$ and $M_3$ were measured. Width measurements were taken in microns with a Gaertner travelling microscope. The $M_3$s were removed from the jaws although the $M_2$s were left intact for purposes of measurement. All measurements were made from the labial edge of the protoconid to the lingual edge of the metaconid, essentially at right angles to the anterior–posterior axis of the teeth. Repeatability was generally within 5 $\mu$ of the original measurement.

The basic statistical design employed was that of the least-squares diallel analysis of Harvey (1960) with an extension to include effects of X-irradiation and of the number of individuals per litter. Effects of X-irradiation were measured simply as one-half of the difference between the irradiated and non-irradiated groups. Litter size (measured over all individuals) was treated as a covariate, differences in litter size being adjusted for by the use of the overall regression for individuals. Differences between the mean of inbreds and the mean of hybrids provided an estimate of heterosis (H). In addition, deviations of the mean of any particular inbred line from the grand inbred mean constituted the category of lines (L), and were useful in describing the variation among the seven lines.

The four more usual categories in a diallel analysis (general combining ability, specific combining ability, maternal effects, and reciprocal effects) are all measured only over the crossbred progeny. The general combining ability (G.C.A.) of a particular line (of sires or dams) measures the deviation of the progeny of that line from the mean of crossbred progeny from all other lines. Maternal effects (M.E.) are measured simply as the difference between the G.C.A. for a line of dam minus the G.C.A. for the same line of sire. The specific combining ability (S.C.A.) effects are expressed as the mean deviation of the hybrid progeny (both reciprocals included) of a particular cross from the mean of the G.C.A.s of the two strains involved in the cross. Finally, reciprocal effects (R.E.) are measured as the difference between the two reciprocal crosses for any two lines after account has been taken of general maternal effects.

With replications nested within each combination of the various levels of sire, dam, and X-irradiation, the basic error variance may be partitioned into between litter (replicate) and within litter components. If the between litter mean square proves to be greater than that within litters, then it is the appropriate error term for significance testing in the analysis of variance. If the litters and lines are regarded as random, specific estimates of the percentage contribution of the genetic combining abilities, and maternal, reciprocal, and between litter effects are possible. The analysis of variance table with the expected mean squares for these random components is shown in Table 1.

Table 1. *The analysis of variance for the random components*

($p$ = the number of inbred lines, $a$ = the number of replicates, and $n$ = the number of individuals per litter.)

| Source of variation | D.F. | M.S. | $E$(M.S.) |
|---|---|---|---|
| General combining ability | $p-1$ | M.S.$_g$ | $\sigma_w^2+n\sigma_b^2+k_6\sigma_r^2+k_7\sigma_c^2+k_8\sigma_g^2$ |
| Maternal effects | $p-1$ | M.S.$_m$ | $\sigma_w^2+n\sigma_b^2+k_4\sigma_r^2+k_5\sigma_m^2$ |
| Specific combining ability | $\frac{p(p-3)}{2}$ | M.S.$_c$ | $\sigma_w^2+n\sigma_b^2+k_2\sigma_r^2+k_3\sigma_c^2$ |
| Reciprocal effects | $\frac{p(p-3)}{2}+1$ | M.S.$_r$ | $\sigma_w^2+n\sigma_b^2+k_1\sigma_r^2$ |
| Between litters | $2p^2(a-1)$ | M.S.$_b$ | $\sigma_w^2+n\sigma_b^2$ |
| Within litters | $2p^2a(n-1)$ | M.S.$_w$ | $\sigma_w^2$ |

$k_1 = 16{\cdot}26$, $k_2 = 11{\cdot}14$, $k_3 = 31{\cdot}54$, $k_4 = 8{\cdot}98$,
$k_5 = 21{\cdot}86$, $k_6 = 9{\cdot}42$, $k_7 = 11{\cdot}83$, $k_8 = 47{\cdot}27$.

## 3. RESULTS

Table 2 gives the means ($\bar{\chi}$), variances ($s^2$), coefficients of variation (C.V.), and correlations ($r$) for the left and right $M_2$ and $M_3$ in each sex. The mean $M_3$ is about two-thirds the width of the mean $M_2$ (0·636 compared with 0·960 mm on the average), but has a greater coefficient of variation (4·56 compared with 3·30). The greater size variability of the third molars has been ascribed to their semi-vestigial nature (Bader, 1965*a*). The basic statistics for the separate sexes show a close similarity. Results of all Student $t$ tests for differences in molar means between the sexes as well as $F$ tests of differences in variances were non-significant ($P > 0{\cdot}05$). Bader (1965*a*) and Wallace (1968) found little or no sexual dimorphism in molar widths or variances in house mice.

Table 2. *Means* ($\bar{\chi}$), *variances* ($s^2$), *coefficients of variation* (C.V.), *and correlations* ($r$) *of each side for the widths of the second and third mandibular molars for the separate sexes*

(In all cases the sample size = 267. Means and variances are expressed in microns.)

| | | Males | Females |
|---|---|---|---|
| $LM_2$ | $\bar{\chi}$ | 959·3 | 960·9 |
| | $s^2$ | 1077·22 | 1018·57 |
| | C.V. | 3·42 | 3·32 |
| $RM_2$ | $\bar{\chi}$ | 958·8 | 960·8 |
| | $s^2$ | 1068·64 | 965·47 |
| | C.V. | 3·41 | 3·23 |
| $LM_3$ | $\bar{\chi}$ | 633·6 | 638·7 |
| | $s^2$ | 863·07 | 946·24 |
| | C.V. | 4·64 | 4·82 |
| $RM_3$ | $\bar{\chi}$ | 633·0 | 637·0 |
| | $s^2$ | 849·78 | 844·25 |
| | C.V. | 4·61 | 4·56 |
| $r$ | $LM_2$–$LM_3$ | 0·49 | 0·53 |
| | $RM_2$–$RM_3$ | 0·50 | 0·51 |
| | $LM_2$–$RM_2$ | 0·96 | 0·94 |
| | $LM_3$–$RM_3$ | 0·91 | 0·90 |

The similarity of mean widths for each side for both molars ($P > 0{\cdot}05$ in both paired $t$-tests) implies that what asymmetry is present is of a fluctuating type, a conclusion in accord with previous results for these same characters in house mice (Bader, 1965*b*; Wallace, 1968). The asymmetry component contributing to the total variance is approximately $1-r$ (Bader, 1965*b*), the values in this case being 5% ($M_2$) and 9% ($M_3$). The inter-dental correlations (measured over all progeny) are moderately high, and are remarkably close to similar estimates made by Bader (1965*c*) for the same characters.

The mean squares for each of the sources of variation in the combined analysis of variance for the mean of the two sides for the $M_2$ and $M_3$ are listed in Table 3. For each tooth, the mean of the two sides (rather than either the left or the right

side) is used throughout since comparability of the two sides was previously shown. Similarly, the sexes are pooled together in the analysis since significant sexual dimorphism was not indicated. In some cases, the degrees of freedom are less than expected because of missing treatment combinations. The between litter mean squares for both molars are highly significant, and thus are utilized as the errors in the significance tests.

Table 3. *Mean squares for each of the sources of variation in the analysis of variance for the mean of the sides for the second and third molars*

(** Significance at the 1 % probability level, * significance at the 5 % level.)

| | | Mean squares | |
|---|---|---|---|
| Source of variation | D.F. | Mean $M_2$ | Mean $M_3$ |
| X-ray (X) | 1 | 493 | 521 |
| Heterosis (H) | 1 | 13510** | 14179** |
| Among lines (L) | 6 | 16220** | 4448** |
| General combining ability (G.C.A.) | 6 | 10738** | 6545** |
| Maternal effect (M.E.) | 6 | 5179** | 2259** |
| Specific combining ability (S.C.A.) | 14 | 881 | 2658** |
| Reciprocal effect (R.E.) | 14 | 572 | 1003* |
| X by H | 1 | 1307 | 378 |
| X by L | 4 | 1551* | 563 |
| X by G.C.A. | 6 | 562 | 621 |
| X by M.E. | 6 | 727 | 287 |
| X by S.C.A. | 14 | 478 | 370 |
| X by R.E. | 8 | 506 | 618 |
| Litter size | 1 | 2777* | 2910* |
| Between litters | 98 (95) | 604** | 445** |
| Within litters | 350 | 125 | 132 |

As seen in Table 3, significant effects are present for both molars for the categories of heterosis, lines, general combining ability, maternal and between litter effects, and litter size. However, significant specific combining ability and reciprocal effects are present only for the $M_3$. Neither mean square for the X-irradiation category reaches significance, and only one of the X-irradiation interactions does so. The significant heterosis category implies a real difference between the mean of the inbreds and the mean of the crossbreds. The significant among lines category indicates that the inbred lines show a considerable diversity in mean molar widths. The majority of the next five random factors (the general combining abilities, maternal, reciprocal, and between litter effects) contribute heavily to the variances, and specific estimates of their relative effects are given below. Treatment of litter size as a covariate in the analysis evidently was worthwhile, since this factor also contributed significantly to the variance.

Estimates of the percentage contribution of each of the five random factors previously mentioned are given in Table 4. Calculation of the coefficients in the expected mean squares was done according to Harvey (1960). The degrees of freedom for R.E. (14) is one less than expected because of a missing cell. The total variances as seen in the table are considerably less than those given previously

principally because of the elimination of the variance of line effects in this analysis. Heritability estimates were computed by doubling the general combining ability percentages.

Table 4. *The analysis of variance of the widths of the second and third molars for the random factors*

(Heritability values ($h^2$) are estimated by 2 × G.C.A.%. *Significance at the 5% probability level, ** significance at the 1% probability level.)

| Source | D.F. | M.S. | Variance component | % of total variance |
|---|---|---|---|---|
| | | Mean $M_2$ width | | |
| G.C.A. | 6 | 10738** | 212·2 | 29·2 $h^2$ = 0·58 |
| Maternal effect | 6 | 5179** | 209·3 | 28·8 |
| S.C.A. | 14 | 881 | 8·8 | 1·2 |
| Reciprocal effect | 14 | 572 | 0 | 0 |
| Between litters | 98 | 604** | 171·4 | 23·6 |
| Within litters | 350 | 125 | 125·3 | 17·2 |
| Totals | 488 | — | 727·0 | 100·0 |
| | | Mean $M_3$ width | | |
| G.C.A. | 6 | 6545** | 107·7 | 21·0 $h^2$ = 0·42 |
| Maternal effect | 6 | 2259** | 68·9 | 13·4 |
| S.C.A. | 14 | 2658** | 58·0 | 11·3 |
| Reciprocal effect | 14 | 1003* | 34·3 | 6·7 |
| Between litters | 95 | 445** | 112·2 | 21·9 |
| Within litters | 350 | 132 | 131·8 | 25·7 |
| Totals | 485 | — | 512·9 | 100·0 |

Both molars exhibit high heritabilities (although that for the $M_2$ is greater), indicating that a substantial portion of the total phenotypic variance is additive genetic. Maternal effects are also quite prominent for both teeth, but are over twice as important for the $M_2$. Specific combining ability effects – indicative of non-additive genetic variation – account for just 1% of the variance of the $M_2$, but 11% of that of the $M_3$. Reciprocal effects were not detected for the $M_2$ although they contribute nearly 7% to the total variation of the $M_3$. Between litter effects account for roughly one-quarter of the variation in each molar. In general, maternal, between litter, and general combining ability effects are quite important for both teeth (although more so for the $M_2$) whereas reciprocal effects and specific combining ability effects are more noticeable in the $M_3$. About 83 and 74% of the total variation in the $M_2$ and $M_3$, respectively, is ascribable to these five components.

The least-squares constants for the mean of the sides for the $M_2$s and $M_3$s for heterosis, number per litter, lines, G.C.A., and maternal effects are shown in Table 5. These values indicate the magnitude of the effect of the particular category in terms of the number of microns deviation from the appropriate least-squares mean. For the category of heterosis, the mean of the inbreds is 10 $\mu$ less, and that of the crossbreds 10 $\mu$ more, than the grand mean. Both molars were consistent in showing a decrease of 1·7 $\mu$ from the overall mean for each unit increase in the

Table 5. *Constant estimates for the categories of heterosis, number/litter, lines,* G.C.A., *and maternal effects for the means of the second and third mandibular molars*

(The values for heterotic effects and number/litter represent deviations in microns from the grand mean of all individuals, those for line effects are deviations from the grand inbred mean, and those for G.C.A. and maternal effects are deviations from the grand crossbred mean.)

| | Mean $M_2$ | Mean $M_3$ |
|---|---|---|
| Heterosis ... | +10·1 | +10·4 |
| Number/litter ... | −1·7 | −1·7 |

| | Lines | | G.C.A. | | Maternal effect | |
|---|---|---|---|---|---|---|
| | $M_2$ | $M_3$ | $M_2$ | $M_3$ | $M_2$ | $M_3$ |
| C57BL/6J | −80·2 | −15·3 | −5·5 | +15·7 | −21·7 | −13·6 |
| RF/J | +13·5 | +5·7 | +3·6 | −0·5 | +10·3 | +9·1 |
| CBA/J | +36·9 | −26·1 | +15·6 | −2·2 | +11·5 | +3·2 |
| A/J | −30·9 | −33·4 | −9·0 | −19·4 | −13·1 | −9·4 |
| C57BL/10J | +22·5 | +49·6 | +18·0 | +25·2 | −12·8 | −0·5 |
| C57BR/cdJ | −19·9 | +11·2 | −35·2 | −8·9 | +10·7 | −1·6 |
| C3HeB/FeJ | +58·1 | +8·4 | +12·5 | −9·8 | +15·1 | +12·8 |

number of individuals per litter over the grand litter mean. The exact magnitude of the increase or decrease could be found from the appropriate regression, but in general there is a decrease in tooth width with increase in this covariable. The constants for the lines show a considerable diversity (the two sublines of the C57BL strain are surprisingly different), and even those for G.C.A. and M.E. effects diverge appreciably.

The estimates of the constants for lines, G.C.A., and maternal effects were derived for each inbred line, and thus permit comparisons to be made between lines. Although only a small number of degrees of freedom is involved, it is instructive to compute correlations between some of the combinations. The correlation between the $M_2$ and $M_3$ constants for maternal effects is quite high ($r_M = +0{\cdot}86$); that between lines is considerably lower (+0·35). This implies that a considerable difference exists between the lines with respect to the magnitude of the differences of $M_2$ and $M_3$ widths, but that all are quite similar with regard to the maternal influences operative on both the $M_2$s and $M_3$s.

Inasmuch as the G.C.A.s are equivalent to the breeding values of the lines, their correlation is an estimate of the genetic correlation, $r_A$ (Falconer, 1960). This correlation (+0·40) includes only the additive effects of pleiotropic genes common to both molars. When the correlation of maternal effects ($r_M$) is accounted for, only an environmental correlation ($r_E$) remains, this latter being due to environmental differences between lines and/or non-additive genetic effects. The $r_E$ for the $M_2$-$M_3$ combination may be calculated from the following expression:

$$r_P = h_x h_y r_A + m_x m_y r_M + e_x e_y r_E,$$

where $r_P$ is the phenotypic correlation (in this case the correlation of line effects: +0·35), $h_x$ and $h_y$ are the square roots of the heritabilities of the $M_2$ and $M_3$, $m_x$ and

$m_y$ are the square roots of the maternal effects, and $e^2 = 1-h^2-m^2$. The genetic and maternal correlations for the $M_2$-$M_3$ are high, but the residual environmental correlation calculated from the above is negative ($r_E = -0{\cdot}26$).

## 4. DISCUSSION

The only major restriction normally applicable to the diallel technique concerns the interpretation of the generality of the results. Since the inbred lines in the present analysis were not all originally derived from a single outbred population, then estimates of the various components are applicable strictly to these seven lines. However, this restriction really does not detract substantially from the usefulness of the results, since the crossbred progeny (although 'artificial') are probably a fair representation of the genetic diversity found in many randombred populations. Both the constant estimates for the lines, and the highly significant lines category in the analysis of variance attest to the magnitude of this diversity. Furthermore, the results of this analysis are similar (to a satisfactory degree) with those obtained by Bader (1965*a*) for the same characters in a 'randombred' population of house mice.

The heritability estimates (0·58 and 0·42, respectively, for the $M_2$ and $M_3$) would be considered high in comparison with the majority of such estimates for other traits (Falconer, 1960). However, they are in excellent agreement with previous estimates for these same characters obtained both in house mice via a half-sib analysis (Bader, 1965*c*) and via artificial selection (Larson, 1971), and in *Peromyscus leucopus* by parent–offspring regression techniques (Leamy & Bader, 1968).

The non-additive genetic variance was much more prominent in the $M_3$ (11%) as compared with the $M_2$ (1%). Bader (1965*a*) failed to detect any non-additive genetic variance in an indirect estimate of this component for these same characters in house mice. However, some was undoubtedly present since the means of the hybrids were generally greater than the means of the inbred parents in his study.

Since the bulk of the genetic variance for the $M_2$ and $M_3$ is additive, it might be surmised that these characters are 'neutral', or nearly neutral, with respect to fitness (Falconer, 1960). However, even though this hypothesis is in accord with previous thoughts on these same characters (Bader, 1965*c*), it must be regarded at best as merely a crude indicator. This is particularly so in view of reports of selection acting on molar widths both in wild house mice (Van Valen, 1965) and *Peromyscus leucopus* (Leamy & Bader, 1970).

Undoubtedly dominance did contribute to the non-additive genetic variance for both molars since both exhibited a significant amount of heterosis. Heterosis depends, in part, upon the presence of directional dominance (Falconer, 1960). It is interesting that the relative importance of heterosis (as evidenced by the variance ratios in the analysis of variance) is roughly the same for both teeth despite the differences in magnitude of the non-additive genetic component. It is possible either that the directional components are nearly the same in both molars, or that the greater differences among lines for the $M_2$ reflect truly greater allelic differences

upon which heterotic effects may be manifested. Alternatively, the disparity might be explained on the basis of an interaction from maternal effects. Since characters subject to maternal effects are among the most susceptible to inbreeding (Falconer, 1960), the $M_2$ should be more depressed, and thus show more recovery upon outcrossing.

The magnitude of the maternal effect was greater in the $M_2$ than in the $M_3$, which is in accord with the trend in the same molars in *Peromyscus leucopus* (Leamy & Bader, 1968), but is opposite to that found by Bader (1965*c*) in house mice. The trend in the present study may well be a manifestation of the ontogenetic sequence of development of these molars. In general, the $M_3$ lags behind the $M_2$ in all stages of development (Cohn, 1957), and in fact has not even erupted by the time of weaning. Thus prenatal effects should be more pronounced in the $M_2$s, whereas the $M_3$s should be more sensitive to the postnatal environment. The fact that the maternal effect constants among the lines were quite erratic in magnitude for the $M_3$ as compared with the $M_2$ would seem to support this contention. In a cross-fostering experiment, Tenczar & Bader (1966) did find a high postnatal component of the general maternal variance in the $M_3$ width in the C57BL/10 strain of mice.

Reciprocal effects contain a non-genetic maternal component as well as a genetic sex-linked component although in the present analysis the relative importance of two components is, of course, unknown. Reciprocal effects (detected for the $M_3$ only) are probably of minor importance in molar widths, a conclusion in accord with those of the majority of investigations of other characters (for example, see Eisen *et al.* 1967).

The high contribution to the total variance of both molars by the between litter component was somewhat of a surprise. This partition of the original (replicates ignored) total error showed that considerable local differences, presumably primarily environmental in nature, are present between litters of crosses involving the same inbred lines. Furthermore, it is apparent that the between-litter component represents the appropriate error in this design; the total error mean square would be an under-assessment, and its use would result in the promotion to significance of more categories, especially the X-ray interactions.

There was no *a priori* hypothesis that the linear effects of X-irradiation on both the $M_2$ and $M_3$ would be insignificant. Significant effects of irradiation on dental characters in mice are known (Searle, 1964). Actually linear effects of X-irradiation in the present study were highly significant in a preliminary analysis of variance performed before adjustment was made for the effects of litter size. This would indicate that the effects of irradiation are primarily mediated through this covariable. The mean number of offspring per litter for the non-irradiated and the irradiated groups, respectively, was 6·31 and 5·14.

The negative relationship between litter size and tooth size could be accounted for in either or both of two ways: (1) there could be a greater milk supply per mouse for the smaller litters, or (2) there could be a negative pleiotropic relationship between the two variables. Leamy & Bader (1970) found a positive relationship between tooth size and litter size in *Peromyscus leucopus*.

The moderately high (+0·40) genetic correlation between the two molars is similar to a comparable estimate (+0·57) made by Bader (1965*c*), and is good evidence that some of the same genes are affecting both teeth. Maternal effect correlations have not been previously estimated in dental traits of mice, but the extremely high value obtained is not really surprising. It implies that the environmental sources positively influencing both teeth are primarily manifested through the mothering abilities of dams of the various lines.

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