GENETIC AND ENVIRONMENTAL CORRELATIONS OF MORPHOMETRIC TRAITS IN RANDOMBRED HOUSE MICE

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The phenotypic correlation coefficient (r_P) is regularly employed as a measure of association between metric traits in a variety of morphogenic studies. Multivariate techniques such as component analysis and factor analysis (Harman, 1967), extensively used with mammalian dental and/or skeletal systems (Jolicoeur and Mosimann, 1960; Wallace and Bader, 1967; Gould and Garwood, 1969; Riddle, 1971; Leamy, 1975), typically start with a matrix of such correlations. However, the phenotypic correlation between two traits is influenced by both genetic and environmental sources of variation in much the same way as is the total phenotypic variation in a single trait. Therefore, most such studies usually attempt to interpret factors, components, or forces which necessarily confound these sources.

An alternative approach, only rarely used (Bailey, 1956; Yap Potter et al., 1968), involves performing the appropriate multivariate technique on separate genetic and environmental correlations rather than on phenotypic correlations only. The genetic correlation (r_A) between two traits may be obtained in a conventional quantitative genetic analysis from the association of the two traits in related individuals. It is generated by the covariation of additive genetic values for the two traits, and if significantly different from 0, is an indicator of pleiotropy and/or linkage (Falconer, 1960). Genetic correlations are also of interest because they determine, in part, the amount of change which can be brought about in one character by artificial or natural selection for the other (correlated) character. Environmental sources of covariation are both many and varied, and may result in an environmental correlation (r_E) quite different from the genetic correlation in magnitude, and sometimes even in sign (see Falconer, 1960 for examples).

A recently completed experiment provided data suitable for a quantitative genetic analysis of 15 osteometric and 3 external metric traits in randombred house mice (Leamy, 1974), and for calculation of genetic and environmental correlations. The purpose of this paper is the presentation and analysis (by multivariate clustering and ordination techniques) of these correlations. The patterns of association are also compared to those previously found from a principal component analysis of the phenotypic correlations among these same traits (Leamy, 1975).

MATERIALS AND METHODS

Materials

House mice of strain CV1 (a randombred derivative of inbred strain 101) were utilized in this study. The original total population consisted of 200 families, each with two parents of age 5 months, and 6 offspring divided into 3 sublitters of 2 mice at each of three ages—1-month, 3-months, and 5-months (Leamy, 1974). Heritabilites of the 18 traits previously were calculated from the regressions of offspring of each age group on the parents, the means of the best estimates (combined regressions on sire) for all traits for the 1-month, 3-month, and 5-month groups being 0.21, 0.47, and 0.41 (Leamy, 1974). However, only those values estimated from parents and offspring of the same age (e.g., the 5-month individuals) were considered conventional estimates. For this reason also, genetic and environmental correlations in this study were calculated from the 5-month mice (male parents and male and female offspring) only.

The 15 osteometric and 3 external metric traits used have previously been described in detail (Leamy, 1974), and are listed below:

$\mathrm{Sk_L}$	skull length
$\mathrm{P_L}$	palate length
$\mathrm{ZF_L}$	zygomatic fenestral length
$\mathrm{M_L}$	mandible length
$\mathrm{Sk_W}$	skull width
$\mathrm{Z_W}$	zygomatic width
$\mathrm{IO_W}$	interorbital width
$\mathrm{In_L}$	innominate length
$\mathrm{Il_L}$	ilium length
$\mathrm{OF_L}$	obturator foramen length
$\mathrm{Sc_L}$	scapula length
$\mathrm{F_L}$	femur length
$\mathrm{Ti_L}$	tibia length
$\mathrm{H_L}$	humerus length
$\mathrm{RU_L}$	radioulna length
$\mathrm{Ta_L}$	tail length
$\mathrm{B_L}$	body length
W	body weight

Calculation of Genetic and Environmental Correlations

There are several alternative formulas for the computation of genetic correlations from parent-offspring data, although each employs covariances of each pair of traits. The following formula, considered preferable by Van Vleck and Henderson (1961), was used to calculate genetic correlations first for each of the separate sexes:

$$r_A = \frac{\tfrac{1}{2}(\mathrm{cov}\, xy' + \mathrm{cov}\, x'y)}{\sqrt{(\mathrm{cov}\, xx')\,(\mathrm{cov}\, yy')}}$$

where x and y are the values of a pair of traits in parents, and x' and y' are the values for the same traits in the offspring. Only covariances of offspring on sire were used in the computations, covariances on dams being generally inflated by non-genetic maternal effects (Leamy, 1974). Since the two "cross-covariances" in the numerator sometimes differed in sign because of sampling error, the arithmetic mean rather than the geometric mean (used in an alternate formula) was needed. The cross covariances for any given pair of traits were always computed from equal sample sizes, scattered missing data being omitted in the computer program. Sample sizes among pairs of traits, however, differed widely (Leamy, 1974). The genetic correlations so calculated exhibited acceptable agreement (non-significant differences) between the two sexes. Thus, the separate values for the sexes were pooled (simply by taking the unweighted mean) in order to give more stability, and thus hopefully more reliability, to the estimates. Body weight exhibited a negative heritability in males (Leamy, 1974), however, and it was necessary to pool covariances between the sexes prior to the calculation of all genetic correlations involving this trait.

Environmental correlations were calculated (also first for the separate sexes) for each pair of traits, x and y, by solving the following:

$$r_P = h_x h_y r_A + e_x e_y r_E$$

where r_P = the phenotypic correlation of the two traits, h_x and h_y are the square roots of the heritabilities of the two traits, and $e^2 = 1 - h^2$ (Falconer, 1960). The phenotypic correlation for each pair of traits was computed from the unweighted means of the r_P values for parents and offspring, the calculation using the usual z transformation (Fisher, 1958). Heritabilities used were those previously derived from twice the regression of offspring on sire (Leamy, 1974). The final r_E values were obtained as the unweighted means of the values for the two sexes. The only exception to this was for correlations with body weight, those being obtained by pooling the appropriate parameters before estimation of r_E.

Clustering and Ordination Methods

Principal component analysis, one of the more popular multivariate ordination techniques, describes the interrelationships of a large battery of characters in terms of a few (often causal) components. I originally intended to use this technique on the genetic and environmental correlation matrices for interpretation, and particularly for comparison both with each other and with previous results from component analysis of the phenotypic correlations (r_P) of the 18 characters (Leamy, 1975). Early trials employing component analysis (and factor analysis), even with several options, however, all managed to generate communalities exceeding unity, because both the genetic and environmental correlation matrices contained some values greater than 1, and thus neither matrix was amenable to the basic model of principal components. In addition, since the original correlations were calculated from essentially different sets of data, the matrices did not meet the criterion of being positive, semi-definite (Harman, 1967). A different ordination technique, described below, was used, although in conjunction with cluster analysis.

The technique of cluster analysis was chosen for use, particularly since it can accept a variety of similarity matrices (including genetic and environmental correlations), and produce meaningful groups or clusters (Anderberg, 1973; Sneath and Sokal, 1973; Everitt, 1974). Applications of cluster analysis in biology are found especially in numerical taxonomy (Sneath and Sokal, 1973), although there the emphasis is primarily in clustering individuals (*Q*-type analysis), rather than variables (*R*-type analysis) as in this study. Among the most popular clustering techniques used in biology are those which are sequential, agglomerative, hierarchic, and nonoverlapping, known by the acronym SAHN (Rohlf, 1970). Full details of the differences among such SAHN methods as single linkage clustering, complete linkage clustering, arithmetic average clustering, and the hierarchic grouping method of Ward (1963), may be found in Sneath and Sokal (1973).

One persistent concern in cluster analysis is whether or not the resultant clusters really are a satisfactory representation of the relationships in the original similarity matrix. One early measure developed to assess those relationships was the Pearsonian correlation of the elements of the original matrix with the so-called cophenetic values implied by the dendrogram. This value is known as the cophenetic correlation coefficient in numerical taxonomy, although more generally it is one of several types of matrix correlations (Sneath and Sokal, 1973). If in fact clustering of an original similarity matrix yields unsatisfactory results (as evidenced by a low matrix correlation or other comparable measure), then one possible way to refine the original solution is to perform an ordination, and then cluster on the reduced space created by the ordination (Sneath and Sokal, 1973).

Multidimensional scaling (MDS) represents a comparatively recent, but very promising field which encompasses a number of general ordination techniques (Shepard, 1962, 1966; Kruskal, 1964*a*, 1964*b*; Shepard et al., 1972). Essentially these techniques depict the structures or patterns inherent in a matrix of data by a geometrical picture. Even in low-dimensional solutions, spatial representations of the points (usually based on Euclidean distances between them) often reveal prominent features of the data. However, sometimes in these solutions there is a poor ordinal relationship between the original correlations and their corresponding derived distances. Poor relationship leads to a high "stress," the degree of which was first measured by a coefficient devised by Kruskal (1964*a*, 1964*b*). High stress (analogous to a low matrix correlation coefficient in cluster analysis) usually can be reduced with a higher dimensional solution (Shepard et al., 1972).

One of the great advantages of MDS is

TABLE 1. *Genetic correlations (above diagonal) and environmental correlations (below diagonal) for the 18 characters.*

	Sk$_L$	P$_L$	ZF$_L$	M$_L$	Sk$_W$	Z$_W$	IO$_W$	In$_L$	Il$_L$	OF$_L$	Sc$_L$	F$_L$	Ti$_L$	H$_L$	RU$_L$	Ta$_L$	B$_L$	W
Sk$_L$		0.51	0.77	0.41	–0.02	–0.02	0.22	0.75	0.72	0.90	0.14	0.06	0.14	–0.28	0.81	0.51	1.18	0.11
P$_L$	0.91		0.64	0.76	–0.08	0.37	0.03	0.71	0.36	0.75	0.19	0.30	0.45	0.18	0.53	0.50	0.62	0.14
ZF$_L$	0.67	0.43		0.53	–0.26	0.38	–0.01	0.58	0.22	0.43	–0.33	0.09	0.30	–0.20	0.29	0.03	0.89	0.30
M$_L$	0.82	0.41	0.65		0.36	0.64	–0.01	0.56	0.32	0.62	0.11	0.31	0.42	0.46	0.26	–0.06	0.94	0.64
Sk$_W$	0.63	0.56	0.62	0.42		0.45	0.00	0.82	0.55	0.01	0.49	0.26	–0.03	0.31	0.52	0.13	–0.10	–0.12
Z$_W$	0.75	0.53	0.74	0.60	0.63		0.24	1.05	0.42	0.57	0.27	0.01	0.19	0.06	–0.22	0.22	0.52	0.70
IO$_W$	0.33	0.21	0.26	0.17	0.61	0.43		0.01	–0.04	–0.00	0.45	0.17	–0.12	–0.09	0.02	0.20	0.62	0.59
In$_L$	0.77	0.61	0.35	0.53	0.42	0.33	–0.02		1.13	0.56	0.93	0.94	0.86	0.88	1.19	0.01	1.12	0.78
Il$_L$	0.84	0.56	0.65	0.67	0.52	0.43	0.37	0.73		0.61	0.65	0.49	0.46	0.61	0.67	0.02	0.71	0.08
OF$_L$	0.39	0.35	0.33	0.31	0.39	0.31	0.03	0.80	0.52		0.77	0.62	0.91	0.59	0.46	0.27	1.27	0.59
Sc$_L$	0.97	0.84	1.18	0.95	0.42	0.73	0.10	0.56	0.81	0.36		0.51	0.47	–0.35	0.50	–0.10	1.40	–0.30
F$_L$	0.87	0.76	0.76	0.66	0.52	0.82	0.27	0.66	0.83	0.28	0.85		0.85	0.77	1.11	0.60	0.61	0.43
Ti$_L$	0.85	0.83	0.62	0.57	0.61	0.66	0.32	0.84	0.88	0.33	0.85	0.90		0.32	0.86	0.78	1.12	0.79
H$_L$	1.15	0.78	1.06	0.58	0.46	0.81	0.45	0.64	0.78	0.46	1.35	0.90	0.97		1.15	–0.35	1.49	0.37
RU$_L$	0.81	0.70	0.89	1.00	0.70	1.28	0.56	0.24	0.86	0.91	1.03	0.61	1.03	0.51		0.69	1.50	0.46
Ta$_L$	0.36	0.12	0.55	0.46	0.33	0.41	0.20	0.43	0.49	0.30	0.64	0.48	0.39	0.80	0.16		0.76	0.35
B$_L$	0.55	0.45	0.37	0.41	0.41	0.54	0.16	0.51	0.50	0.27	0.29	0.59	0.52	0.35	0.55	0.07		0.96
W	0.59	0.29	0.60	0.39	0.44	0.51	0.06	0.21	0.50	0.35	0.35	0.43	0.37	0.46	0.50	0.18	0.54	

that, unlike factor-analytic methods which are based on assumptions of linearity, nonlinear relations among variables are accepted. Even though they produce quantitative, metric results, MDS methods are often known as "nonmetric" since they require no more than ordinal relations in the original correlation matrix (Shepard, 1962). For this reason, MDS techniques also seemed particularly attractive as a means of analyzing the genetic and environmental correlation matrices. As will be seen in the results, in fact, MDS proved quite useful and essential in converting the original correlation matrices into distance matrices more acceptable for clustering.

RESULTS

Genetic and Environmental Correlations

The ordination and clustering techniques described above used the genetic and environmental correlations given in Table 1. The genetic correlations (above diagonal) generally are positive and moderate to high in magnitude, ranging from –0.35 to +1.50. Those correlations exceeding the theoretical upper limit of +1.0 are especially noticeable among those associated with body length, undoubtedly a consequence of the particularly low estimates of heritability for this trait (Leamy, 1974). Although the emphasis here is not specifically on the precision of the estimates, it should be mentioned that standard errors of the genetic correlations were calculated, the majority being approximately 0.20. Environmental correlations (below diagonal) show a more restricted range (–0.02 to +1.35) compared to the genetic correlations, but again some (especially those associated with RU$_L$) exceed unity.

Original Clustering

The results of complete linkage clustering of the genetic correlation matrix are shown as a dendrogram in Figure 1. Although early trials utilizing single linkage and weighted and unweighted arithmetic average clustering methods gave results very similar to those of the complete link-

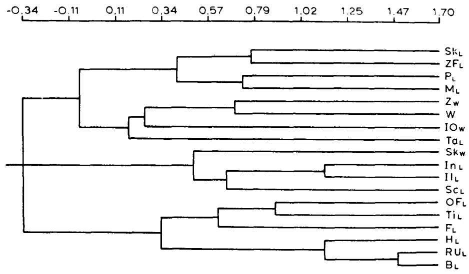

FIG. 1. Dendrogram derived from complete linkage clustering of the original genetic correlation matrix.

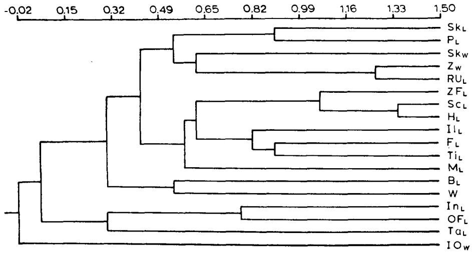

FIG. 2. Dendrogram derived from complete linkage clustering of the original environmental correlation matrix.

age clustering, this latter was chosen since it produced more separable, discrete clusters. The cophenetic correlation coefficient for this solution, however, was only 0.422, indicative of a poor agreement between the dendrogram and the original correlation matrix, and thus of the need for scaling.

At about the level of $r_A = 0.11$, four fairly well defined clusters may be seen in Figure 1. The first cluster contains the four skull lengths whereas the second contains two of the three skull widths, as well as body weight and tail length. Both of these clusters join together at a lower (negative) level of association to form an "axial" skeletal cluster. The third cluster basically is a "gridle" one which, however, also contains skull width, although this is the last dimension to join the cluster. The final cluster is essentially a limb bone cluster which also includes body length and obturator foramen length. Thus, the third and fourth clusters (which also join at a negative level of association) comprise an "appendicular" skeletal cluster.

In addition to these rather general patterns of association, more specific ones may be seen in Figure 1. Within the last (limb bone) cluster, for example, femur and tibia dimensions, and humerus and radioulna dimensions, first form separate pairs before all join as the limb cluster. Rather unexpected, perhaps, in this cluster (rather than in the girdle cluster) is the presence of $\mathrm{OF_L}$. Body length (also in the limb bone cluster), as might be expected, shows the highest level of association whereas $\mathrm{IO_W}$ and $\mathrm{Ta_L}$ exhibit the lowest. $\mathrm{In_L}$ and $\mathrm{Il_L}$ form an expectedly high union, although that between $\mathrm{Z_W}$ and W is not immediately explainable.

The complete linkage clustering pattern of the environmental correlation matrix, illustrated by the dendrogram in Figure 2, is noticeably different from that for the genetic correlations. At the level of $r_E = 0.32$, five clusters may be identified. The first contains 12 of the 18 characters, including all four skull lengths, two of the three skull widths, all four limb lengths, and humerus and ilium length. This cluster is also seen to be subdivisible into one cluster of 5 traits (3 skull lengths, one skull width, and $\mathrm{RU_L}$) and one of 7 (3 of the 4 limb bones, 2 skull lengths, plus scapula and humerus length). Thus, neither subcluster forms an intuitively appealing array of characters such as was found for the genetic correlations, but there is again at least a crude demarcation of axial and appendicular dimensions. The next cluster consists of body length and weight, the third includes inominate and obturator foramen lengths, and the fourth and fifth are single elements (not really clusters at this level), $\mathrm{Ta_L}$ and $\mathrm{IO_W}$. As was true for the genetic correlation clustering, these last two dimensions exhibit the lowest association of all the characters. The cophenetic correlation coefficient for the environmental correlations is 0.726, considerably higher than that for the genetic correlations.

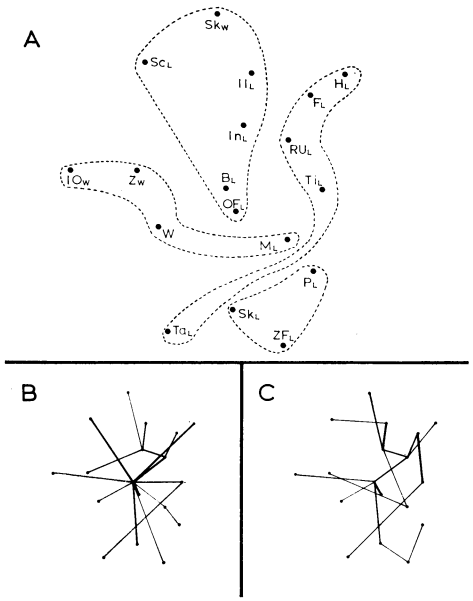

FIG. 3. Two-dimensional MDS solution for the original genetic correlations (A), and minimal spanning trees for the original genetic correlations (B), and for the final (six-dimensional MDS) genetic distances (C).

Ordination and Final Clustering

Since clustering of the original correlation matrices (especially the genetic correlations) yielded the anticipated rather low cophenetic correlations, I performed an ordination utilizing the technique of multidimensional scaling (Shepard, 1962), as previously described. The specific program used was the "smallest space analysis" devised by Guttman (1968) and Lingoes (1965, 1966) who also provided their own measure ("coefficient of alienation") as well as Kruskal's measure, of stress. The pattern of the coefficients of alienation for the genetic correlations was such that a six-dimensional solution seemed most appropriate (coefficient of alienation = 0.082), this being the solution on which the final clustering was performed.

Although it is obviously impossible to represent this solution graphically, the results of MDS of the genetic correlations for two dimensions may be depicted (Fig. 3A). The relative distances between each pair of points (characters) are an indication of their relative magnitude of association. There definitely is distortion at this level (coefficient of alienation = 0.319), but it is nevertheless useful to obtain some indication of the shape of the clusters in the character space. In general, the vertical axis (Fig. 3A) seems to differentiate particularly the skull lengths (and Ta_L) from the other dimensions whereas the horizontal axis distinguishes widths (including W) from lengths, IO_W being an especially conspicuous outlier. A somewhat oblique horizontal line tends to differentiate the axial from the appendicular elements. With the exception only of Sk_W, the positions of the characters in this space are quite compatible with the original clustering which gave rise to four discrete clusters.

Specific character groups indicated by the dashed lines (Fig. 3A) are those derived from the final clustering, described below. They are not quite so intuitively obvious from the ordination alone (note the distance covered to include Ta_L in the limb bone cluster), but it must be remembered that they are the results of a clustering process on the final six-dimensional solution.

An indication of the distortion in the original, compared with the final, solution may be seen by a comparison of the two minimal spanning trees in Figure 3 (B and C). Both represent the same set of points (18 characters as in 3A) in a two-dimensional space, but the construction of tree B is based on the results of single linkage clustering of the original correlations, whereas the tree in Figure 3C is based on results of comparable clustering of the final (six-dimensional) distances. Essentially, each pair of points is connected in sequence from those having the strongest to those having the weakest association. The strength of this association is indicated in the Figure by the relative thickness of the connecting lines, the thickest denoting the highest magnitude of association.

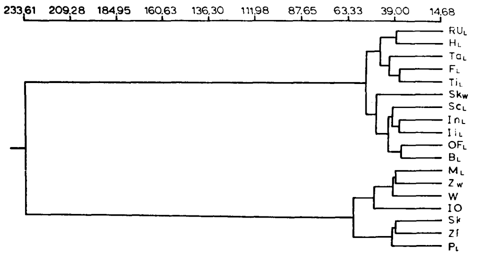

FIG. 4. Dendrogram derived from Ward's clustering of the final (six-dimensional MDS) genetic distances.

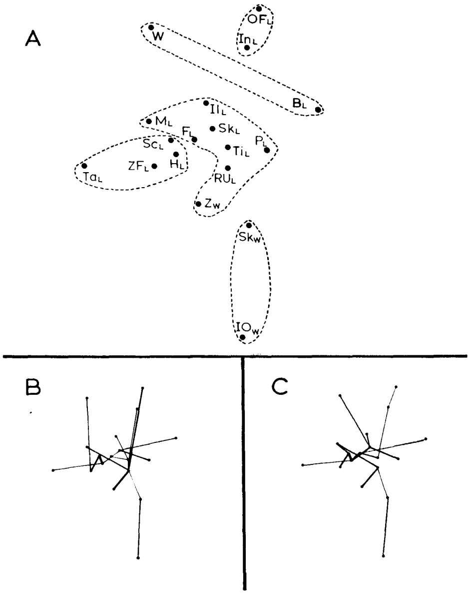

FIG. 5. Two-dimensional MDS solution for the original environmental correlations (A), and minimal spanning trees for the original environmental correlations (B) and for the final (seven-dimensional MDS) environmental distances (C).

A major feature of the minimal spanning tree of the original solution is that many of the lines emanate from one point, B_L, thereby confirming its (unwarranted) importance. This is entirely, of course, a result of the several genetic correlations involving this character exceeding unity. Although B_L is still important in the final tree (Fig. 3C), its overall importance is much reduced. Another primary difference between the two trees is the degree of correspondence between the magnitude of association (as judged by the thickness of the lines) and the distance between pairs of points, the correspondence being generally better in the final solution.

The hierarchical grouping method of Ward (1963) was used to produce clusters from the final six-dimensional distances, the dendrogram from which is shown in Figure 4. At each step, Ward's method minimizes the sum of squares of distances between points within clusters (maximizing the between cluster sum of squares), thus giving rise to sharply demarcated clusters (Everitt, 1974). Originally, complete linkage clustering was tried on the final scaled distances, and although the results were similar, those from Ward's method seemed most satisfactory. Incidentally, it should be mentioned that the nature of the metric scaling in the MDS process is such that although clustering on the final distances is an excellent way of depicting the final results, this may not necessarily be reflected in an increased cophenetic correlation. The cophenetic correlation for complete linkage of the final scaled distances, in fact, showed some improvement over the original correlation, but the increase was not dramatic.

The final clustering of the scaled genetic correlations (Fig. 4) is similar to the original solution in that four clusters are produced, but their composition has changed somewhat. The four limb lengths form an obvious cluster which this time includes Ta_L. The next cluster contains all four girdle elements as well as B_L, and as before, Sk_W. Both of these clusters unite in a rather distinct appendicular unit. The third cluster is essentially a skull width one which also contains one skull length and W, whereas the fourth cluster includes the remaining three skull lengths. The differentiation between the major axial and appendicular clusters is striking.

The MDS ordination of the environmental correlations for two dimensions is

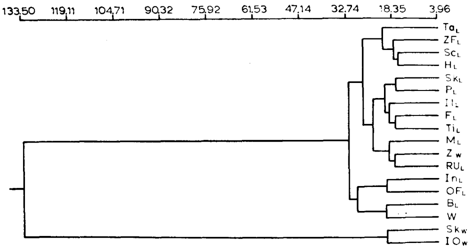

FIG. 6. Dendrogram derived from Ward's clustering of the final (seven-dimensional MDS) environmental distances.

shown in Figure 5A, with the minimal spanning trees for the original (5B) and final (5C) solutions also shown. The final solution achieved this time was a seven-dimensional one with a coefficient of alienation of 0.062. The two-dimensional space of the environmental distances (Fig. 5A) is quite different from that of the genetic correlations, the correlation coefficient of the appropriate distances for both two-dimensional solutions being only 0.11. The vertical axis seems to differentiate the three widths on the lower side and three other dimensions (W, In_L, OF_L) on the higher side from the remaining bulk of the dimensions which cluster approximately in the middle. The horizontal axis seems primarily to contrast B_L from Ta_L. The results again are quite compatible with the original clustering, including the presence of two obvious outliers, Ta_L and IO_W. The minimal spanning trees are also fairly similar, implying that the final seven-dimensional solution did not greatly alter the original clustering solution.

The results of Ward's clustering on the final solution, indicated by dashed lines in Figure 5A and by the dendrogram in Figure 6, are quite similar to the original clustering. The largest of the five clusters in Figure 6 contains 3 of the 4 skull lengths, 1 skull width (Z_W), 3 of the 4 limb lengths, and one girdle character (Il_L). Another closely associated cluster contains the remaining skull length and limb length as well as Sc_L and Ta_L. Both join as a cluster of 12 characters exactly the same as the original solution except that Ta_L rather than Sk_W is included. The remaining three clusters contain two elements each: In_L and OF_L, B_L and W, and Sk_W and IO_W. The last of these three clusters deviates from the original solution in that Ta_L and Sk_W are interchanged.

DISCUSSION

The results of clustering and ordination of the genetic and environmental correlations of the 18 morphometric characters allow greater insight into the architecture of the skeletal system. Single genetic correlations between different body dimensions probably have limited use, even in the prediction of correlated response to selection (Cock, 1969), but it is the interrelationships of such correlations which are of interest here. Presumably those clusters formed from the genetic correlations represent groups of characters which are in fact controlled by the same gene or gene complex in the hierarchical developmental pathway(s) appropriate for the skeletal system. In contrast, common environmental causes should have resulted in the character groupings seen in the environmental correlation clustering; it is of interest to compare these results with those from the genetic clustering.

Clustering rather than ordination by principal components or factor analysis was of course mandated by the nature of the correlation matrices. The original clustering produced an unacceptably low cophenetic correlation, however, and the rather sophisticated MDS process was utilized to "scale" these original (especially genetic) correlations into a matrix more suitable for clustering. In addition, although it possessed a rather high degree of stress, the two-dimensional MDS solution provided a useful representation of the data. Currently the desirability of first performing an ordination and then clustering on the reduced space is controversial, since meaningful information may be lost (Sneath and Sokal, 1973). However, clustering was depicted in the analysis both before and after

MDS ordination, and it should be recalled that the results were not dramatically different, even for the genetic correlations. It is assumed, then, that for both the genetic and environmental correlations, the final solution is the better representation of the complex of associations inherent in the matrices.

The final clustering solution for the genetic correlations produced a remarkably acceptable pattern of basically functional skeletal groups. Certainly it is easy to envision all 4 paired limbs as well as one unpaired appendage (Ta_L) coalescing into a locomotor group. The house mouse is a quadruped (with a plantigrade gait) which uses its 4 limbs reasonably evenly, so that it is understandable that there was no major subdivision into front versus hind limbs. The other subcluster of the appendicular cluster consisted mainly of girdle elements plus body length and skull width. The scapula and pelvic bones definitely serve as a cushion for shock absorption when jumping or other such activity takes place, and thus again a locomotor function is implied. Sk_W was a measure taken at roughly the thickest part of the skull, and where, in fact, the major task of holding the skull steady during locomotion must take place. It is of course also conceivable that the association of Sk_W in this group is spurious, but the huge axial-appendicular difference (and the pattern of original correlations) argues that it somehow is more of a member of the appendicular than of the axial group.

The masseter muscle complex is quite a prominent feature of rodent mastication (Young, 1950), and is probably responsible for linking together M_L, Z_W, IO_W, and W (seen as an axial subcluster) into a functional chewing complex. Initially it was puzzling why M_L should fall into this group of essentially skull widths (plus W) rather than into the other axial subcluster containing the 3 remaining skull lengths. This measure, however, was taken from the angular process of the mandible to the base of the first molar (Leamy, 1974), and so is really not a true "length." More importantly, one branch of the masseter muscle (zygomaticus) runs in about this same direction, originating on the zygomatic arch and inserting on the angular process, thus nicely linking together M_L and Z_W. Zygomatic width is also undoubtedly influenced by the masseter branches and the temporalis muscle, since they both pass through the zygomatic arch which thus must necessarily be wide enough to accomodate them. In addition, the major masseter branches originate on the side of the skull on and around the zygomatic arch, and it is easy to see how they could also influence IO_W development. Finally, even W may be influenced by the masseter complex, for the greater the muscle mass, the greater the ability to chew and presumably increase in body weight, although of course other explanations are possible.

The functional skeletal groups as just described are very much reminiscent of the morphologically integrated groups (***F***-groups) defined by Olson and Miller (1958) in terms of characters "related by some unifying factor." For the skeletal characters they employed, the unifying factor in some cases was function (as in the jaw movement, head orientation, axial, fore- and hindlimb locomotion, and intergroup functional groups in *Rana pipiens*, and the masticatory and head movement group in *Sciurus niger rufiventer*) whereas in other cases it was growth (skull complex in *Sciurus*) or ontogeny (nerve development skeletal complex in skull of *Sciurus*). In adult rats, functional locomotor, distal limb, and axial groups, as well as one proximity, growth group of the skull and jaws, were recognized (Olson and Miller, 1958). In the house mice of the present study, undoubtedly both the selection of characters, and the fact that the mice are mature in age, has tended to promote the primarily functional assemblages of characters.

One of the principal theses of morphological integration as propounded by Olson and Miller (1958) is that highly correlated groups of characters generally constitute

F-groups (especially functionally related *F*-groups). Despite some objections (Bock, 1960) to the method by which correlation coefficients were used by Olson and Miller, this basic thesis was nonetheless amply confirmed (Van Valen, 1965). The present results indicate that genetic correlations are rather sensitive indicators, perhaps even more so than phenotypic correlations, of the existence of such *F*-groups. As Van Valen (1965) has pointed out, however, correlations between morphological characters are directly produced only by ontogenetic processes, and thus it is logical that these associations should have a genetic basis. Function may well be a causative agent of these correlations (Gould and Garwood, 1969), but if this is true, it must be at the level of the evolution of the developmental system (Van Valen, 1965). This would seem to be one of the few studies which offers evidence for the existence of genes, long assumed present by a wide assortment of evolutionists, taxonomists and morphologists, which have been selected for developmental pathways which affect entire functional complexes.

These or similar genes controlling character complexes have long been known to animal breeders from the results of artificial selection experiments. Multivariate genetical studies in fowl (Cock, 1969), for example, clearly show the inheritance of complex body conformations or "shapes." The formulation of indices of selection (Hazel, 1943; Rouvier, 1969) is of course based on the concept of simultaneous selection for suites of characters. Theoretically, the skeletal traits of the randombred mice in this study should respond to artificial selection in a manner predictable from the results of the genetic clustering (Fig. 4). Thus, selection applied to any character in one of the four functional skeletal groups should also affect especially the remaining characters in that group, and, judging from the magnitude of the heritabilities for most of these characters (Leamy, 1974), the correlated responses would be appreciable (Falconer, 1960).

Unlike that for the genetic correlations, clustering of the environmental correlations was rather disappointing, at least from the standpoint of producing biologically meaningful clusters. Although there were some "logical" character bonds, the overall pattern was certainly not one of functionally or anatomically acceptable groups. The apparent differences in the patterns generated, however, are useful in emphasizing the need for a separation of genetic and environmental contributions to the phenotypic correlations. Bailey (1956) found a general similarity (although with some differences) of the first two principal components of the axis and mandible in mice for both genetic and environmental sources of control.

The clustering pattern generated by the environmental correlations is not too surprising when it is recalled that these correlations are calculated from phenotypic and genetic correlations. The genetic correlations are computed first (before the environmental correlations) from covariances of parents and offspring in a manner not unlike that used for the calculation of phenotypic correlations. The genetic correlations are then used to calculate the environmental correlations, and therefore very much influence their magnitude, almost to a point of these latter being basically "residuals." Furthermore, if the genetic correlations (and heritabilities) are in general high in magnitude (as they were in this study), whereas the phenotypic correlations are moderate in magnitude, then the genetic correlations contribute more than the environmental correlations to the phenotypic correlations (Pirchner, 1969). These facts help to explain both the greater range of the genetic correlations (Table 1) and the fact that the lowest genetic correlation between a pair of characters (H_L and Sc_L, –0.35) has resulted in the highest environmental correlation (+1.35) between these same characters. Other low genetic correlations (such as between Z_W and RU_L) are similarly associated with high environmental correlations, these in turn being reflected in the clustering process.

This same sort of reasoning also helps explain why the clustering pattern of the genetic rather than the environmental correlations is more similar to the pattern of factors found in a previous component analysis of the phenotypic correlations (Leamy, 1975). Thus, although in the previous study sexes were separated, in general, limb, girdle, skull length, skull width, and body (B_L and W) factors were delineated. The last factor was really the only one not found in the genetic clustering, but interestingly enough, this was one of the clusters found in the environmental clustering analysis. Both B_L and W exhibited rather low heritabilities (Leamy, 1974), however, and this would explain the greater importance of the environmental correlation for these characters. Similarly, Sk_W shows the lowest heritability of the three skull widths (Leamy, 1974), so perhaps it is not unreasonable that it is not found in the skull width cluster in the genetic solution. Z_W is also interesting in that for males in the factor solution (Leamy, 1975), it loads about equally on three different factors (width, body, and skull length-girdle) and also in the cluster analysis of the environmental correlations, it is associated with the skull and limb lengths. The highest loading of M_L for males in the component analysis is on the body factor, Z_W also loading moderately high with this factor. In the final clustering solution for the genetic correlations, M_L finds itself in the "skull width" cluster which incidentally also includes W.

As an alternative to the present approach, Rouvier (1966) and Hashiguchi and Morishima (1969) have devised methods for calculating genetic and environmental vectors from principal component analysis of the phenotypic correlations of characters. What is most interesting about their analysis is that the vectors calculated (Hashiguchi and Morishima, 1969) closely corresponded to the components derived from the same characters. In the present study, the similarities between the results of the component and clustering analysis as detailed above indicate that the factors themselves from the component analysis may really represent meaningful genetic (or in some cases, environmental) patterns of association. Admittedly, it would be nice to think that this might be true for the majority of future component or factor analysis performed for which there is some evidence that the characters involved have moderate to high heritabilities. As usual, however, this must await future verification.

Summary

Estimates of genetic and environmental correlation coefficients were made among 15 osteometric and 3 external metric characters in a randombred strain (CV1) of house mice five months of age. Genetic correlations were calculated from parent-offspring covariances pooled over both sexes. Previous estimates of heritabilities obtained from twice the regression of offspring on sire were utilized in the calculation of environmental correlations. Both the genetic and environmental correlation matrices were then subjected to multivariate cluster and ordination techniques in order to detect general patterns of association. Limb, girdle, skull width, and skull length genetic clusters were found, all of which were explained on a functional basis. Environmental clustering did not produce apparent anatomical or functional groups but did serve to emphasize the difference between genetic and environmental sources of covariation. The genetic (and to some extent, environmental) clusters compared favorably with previous factors found in a component analysis of the phenotypic correlations among these same characters.

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LITERATURE CITED

ANDERBERG, M. R. 1973. Cluster analysis for applications. Academic Press, New York. 359 p.

BAILEY, D. W. 1956. A comparison of genetic and environmental principal components of morphogenesis in mice. Growth 20:63–74.

BOCK, W. 1960. A critique of "Morphological Integration." Evolution 14:132–133.

COCK, A. G. 1969. Genetical studies on growth and form in the fowl. 2. The complexity of changes in skeletal proportions produced by selection. Genetical Research 14:237–247.

EVERITT, B. 1974. Cluster analysis. Wiley and Sons, New York. 122 p.

FALCONER, D. S. 1960. Introduction to quantitative genetics. Oliver and Boyd, Edinburgh. 365 p.

FISHER, R. A. 1958. Statistical methods for research workers. 13th ed. Hafner, New York. 356 p.

GOULD, S. J., AND R. A. GARWOOD. 1969. Levels of integration in mammalian dentitions: an analysis of correlations in *Nesophontes micrus* (Insectivora) and *Oryzomys couesi* (Rodentia). Evolution 23:276–300.

GUTTMAN, L. 1968. A general nonmetric technique for finding the smallest coordinate space for a configuration of points. Psychometrika 33:469–506.

HASHIGUCHI, S., AND H. MORISHIMA. 1969. Estimation of genetic contribution of principal components to individual variates concerned. Biometrics 25:9–15.

HARMAN, H. H. 1967. Modern factor analysis. Univ. of Chicago Press, Chicago. 346 p.

HAZEL, L. N. 1943. The genetic basis for constructing selection indices. Genetics 28:476–490.

JOLICOEUR, P., AND J. E. MOSIMANN. 1960. Size and shape variation in the painted turtle. A principal component analysis. Growth 24: 339–354.

KRUSKAL, J. B. 1964*a*. Multidimensional scaling by optimizing goodness of fit to a nonmetric hypothesis. Psychometrika 29:1–27.

——. 1964*b*. Nonmetric multidimensional scaling: a numerical method. Psychometrika 29: 115–129.

LEAMY, L. 1974. Heritability of osteometric traits in a randombred population of house mice. J. of Hered. 65:109–120.

——. 1975. Component analysis of osteometric traits in randombred house mice. Syst. Zool. 24:176–190.

LINGOES, J. C. 1965. An IBM-7090 program for Guttman-Lingoes smallest space analysis-I. Behav. Sci. 10:183–184.

——. 1966. New computer developments in pattern analysis and nonmetric techniques. *In* Uses of computers in psychological research. Gauthier-Villars, Paris. p. 1–22.

OLSON, E. C., AND R. L. MILLER. 1958. Morphological integration. Univ. of Chicago Press, Chicago. 317 p.

PIRCHNER, F. 1969. Population genetics in animal breeding. W. H. Freeman and Co., San Francisco. 274 p.

RIDDLE, R. A. 1971. Selection on odontometric and osteometric characters in natural populations of *Peromyscus californicus insignis*. M.S. thesis, Calif. State Univ., Long Beach.

ROHLF, F. J. 1970. Adaptive hierarchical clustering schemes. Syst. Zool. 19:58–82.

ROUVIER, R. R. 1966. L'analyse en composentes principales; son utilisation en genetique et ses rapports avec l'analyse discriminatoire. Biometrics 22:343–357.

——. 1969. Ponderation des valeurs genotypiques dans la selection par index sur plusieurs caracteres. Biometrics 25:295–307.

SHEPARD, R. H. 1962. The analysis of proximities: multidimensional scaling with an unknown distance function. I and II. Psychometrika 27:125–140, 219–246.

——. 1966. Metric structures in ordinal data. J. Math. Psychol. 3:287–315.

SHEPARD, R. N., A. K. ROMNEY, AND S. B. NERLOVE (eds.). 1972. Multidimensional scaling, vol. I. Seminar Press, New York. 261 p.

SNEATH, S. A., AND R. R. SOKAL. 1973. Numerical taxonomy. W. H. Freeman and Co., San Francisco. 573 p.

VAN VALEN, L. 1965. The study of morphological integration. Evolution 19:347–349.

VAN VLECK, L. D., AND C. R. HENDERSON. 1961. Empirical sampling estimates of genetic correlations. Biometrics 17:359–371.

WALLACE, J. T., AND R. S. BADER. 1967. Factor analysis in morphometric traits of the house mouse. Syst. Zool. 16:144–148.

Ward, J. H. 1963. Hierarchical grouping to optimize an objective function. J. Amer. Statist. Assoc. 58:236–244.

Yap Potter, R. H., Pao-Lo Yu, A. A. Dahlberg, A. D. Merritt, and P. M. Conneally. 1968. Genetic studies of tooth size factors in Pima Indian families. Amer. J. Human Genet. 20: 89–100.

Young, J. Z. 1950. The life of vertebrates. Oxford Univ. Press, London.