EVOLUTION

INTERNATIONAL JOURNAL OF ORGANIC EVOLUTION

PUBLISHED BY

THE SOCIETY FOR THE STUDY OF EVOLUTION

Vol. 38 **September, 1984** **No. 5**

Evolution, 38(5), 1984, pp. 921–930

MORPHOLOGICAL AND PHYLOGENETIC RELATIONS AMONG THE DARWIN'S FINCHES

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Received February 16, 1984. Revised April 1, 1984

Despite the ecological and evolutionary significance of the Darwin's finches (Lack, 1947; Bowman, 1961; Abbott et al., 1977; Boag and Grant, 1981; Schluter and Grant, 1984), their phylogenetic relationships are incompletely understood. Yang and Patton's (1981) electrophoretic study on 11 of the 13 Galápagos species supported Lack's (1947) division of the finches into three major groups (Fig. 1): ground finches (*Geospiza*), tree finches (*Camarhynchus* and *Platyspiza*), and the warbler finch (*Certhidea olivacea*). Biochemical differences within these groups were slight, however, leaving details of species relationships largely unresolved. In this report I use a new method to estimate evolutionary relationships among the finches based on morphological data. The analysis includes all 13 Galápagos species and *Pinaroloxias inornata* from Cocos Island, putatively a warbler finch (Lack, 1947).

Ecological studies have indicated that morphology in the Darwin's finches has been strongly influenced by natural selection (Boag and Grant, 1981; Price and Grant, 1984; Schluter and Grant, 1984). Under these conditions morphological differences between species might be expected to reflect differences in environmental history rather than evolutionary relationships (Barrowclough, 1983). Indeed, poor concordance between estimates of phylogeny based on morphological data and estimates based on biochemical data (ostensibly neutral) has been noted in other groups (e.g., Zink, 1982) as well as in the Darwin's finches (Barrowclough, 1983). However, most standard measures of morphological distance (e.g., Cherry et al., 1982) lack explicit evolutionary justification, and this may partly explain poor concordance when it is observed. Here I employ a measure of morphological distance based on a theoretical study of multivariate evolution (Lande, 1979). The resulting evolutionary relationships inferred agree reasonably well with both the biochemical (Yang and Patton, 1981) and the traditional estimates (Lack, 1947), where comparison is possible.

Morphological Distance

Determining an appropriate measure of evolutionary distance between two forms hinges on finding a solution to two outstanding problems in phylogenetic inference: how to weight characters by their susceptibility to change, and how to ac-

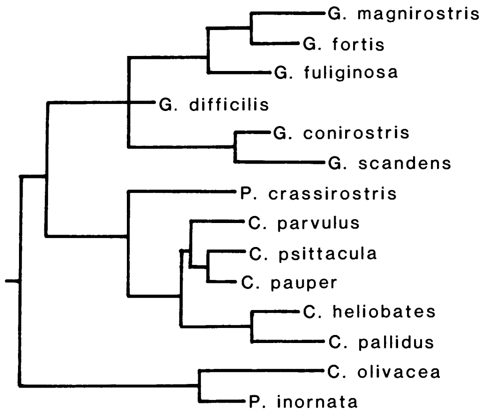

FIG. 1. Lack's (1947) phylogenetic tree, with branch lengths approximately as he drew them.

count for correlations between characters (Felsenstein, 1982). Recent models for the evolution of mean phenotype in populations (Lande, 1979) provide ways to deal with both these factors simultaneously, at least for morphological data. Under multivariate selection:

$$\beta = \mathbf{G}^{-1}[z(t) - z(0)]. \qquad (1)$$

$z(0)$ and $z(t)$ are vectors of character means in the population at times 0 and t. $\mathbf{G}$ is a matrix of genetic variances and covariances among characters, and it is assumed to remain constant through time. β is the net selection gradient, a vector whose elements β_i are the net forces of directional selection which have acted on each character i in order to produce the observed overall change in z. The magnitudes of individual β_i depend on the genetic variance in character i: a given change in the mean of a character requires more selection when genetic variance is low, than when it is high. Secondly, each β_i depends on the magnitude and direction of the indirect effects on z_i resulting from selection on genetically correlated characters. For example, a given increase in size in two characters z_1 and z_2 requires more selection if they are negatively correlated, than if they are uncorrelated or positively correlated (Lande, 1979). The length of the vector can be measured by the Euclidean distance,

$$B = [\Sigma\beta_i^2]^{1/2}, \qquad (2)$$

which represents the total net force of directional selection that has acted to shift mean morphology from $z(0)$ to $z(t)$.

The above result can be applied to any modern group of related species, for example the Darwin's finches. For the pair of species a and b, mean morphologies $z(a)$ and $z(b)$ are substituted in place of $z(0)$ and $z(t)$ in (1) (examples are given in Price et al., 1984). In this situation B is a measure of "selection distance" between the two species: it estimates the total net force of directional selection which would be required to produce their observed morphological differences. In many situations B will therefore be an appropriate measure of morphological distance between them.

Because it is explicitly a measure of evolutionary distance, B may be used to estimate phylogenetic relations among the species. Such an application requires one further assumption: B will be directly proportional to t, the time interval involved in evolutionary change only if the total net force of directional selection averaged over generations (i.e., B/t) is approximately constant. Clearly there is no a priori reason to accept this assumption. However, the assumption is certainly worth stating as a null hypothesis, one which could be tested through comparison with independent estimates of phylogeny (e.g., Barrowclough, 1983).

Note that if we transform means for the original morphological characters z to yield $z' = \mathbf{G}^{-1}z$, then for two species a and b,

$$\beta = z'(a) - z'(b)$$

and

$$B = [\Sigma\ (z_i'(a) - z_i'(b))^2]^{1/2}. \qquad (3)$$

Hence, B is simply the Euclidean distance applied to the transformed mean vectors z', and it is given in units^{-1} of the original variables. A related distance is B^*, computed as in (3) using the standardized uncorrelated characters $z^* = \mathbf{G}^{-1/2}z$. In this case B^* is the "generalized genetic distance" between two species (Lande, 1979), and it is dimensionless.

Whether one should use B or B^* as the measure of selection distance will depend on whether the selective environment is best described in terms of the units of the original variables (B), or in terms of population standard deviations (B^*). The latter distance is appropriate under the special case of artificial selection, or truncation selection (Lande, 1979), but B may be appropriate when dealing with natural environments. All analyses of the Darwin's finches were performed using both distance measures, and they gave very similar results. For this reason I present only results based on the unstandardized measure (B) in this report.

Note finally that the methods for computing selection distance account for only those characters included in the analysis. Hence there can be no certainty that inclusion of another character would not alter the estimates of individual and combined selection intensities (Lande and Arnold, 1983). The problem presented by unmeasured characters is not unique to the present distance measure; as always, a partial resolution is better than none (Lande and Arnold, 1983).

METHODS

Measurements of eight characters (Abbott et al., 1977) are available for all 14 species of Darwin's finches. These eight characters summarize most of the morphological differences between the species (Price et al., 1984). They are wing length (WNG), tarsus length (TRS), upper mandible length (UML), width (UMW) and depth (UMD), and lower mandible length (LML), width (LMW) and depth (LMD), all in mm. Measurements were made from museum specimens, and most populations of each species were included, 88 in all (Grant et al., unpubl.). Ground finches (*Geospiza*) were measured by I. J. Abbott and P. R. Grant; at least ten, and up to 278 individuals were measured per sex, per population available. Tree and warbler finches (including *Pinaroloxias*) were measured by P. R. Grant and R. L. Curry; ten adult individuals of each sex were measured per population. Identical methods were used throughout. All measurements were converted to the log(e) scale. Males are generally larger than females (Price, 1984; Grant et al., unpubl.), and I used only males when computing population means. Means for species are unweighted averages of (male) population means. Phenotypic variances and covariances within species were computed by pooling individuals across sexes and populations, scaling for differences in subgroup means.

The distance measure, B, assumes that genetic variances and covariances remained approximately constant during divergence (Lande, 1979). Phenotypic covariance matrices for different species were compared, by investigating the factor loadings of the different characters on the first two principal components (PC's). In general, character loadings were similar within the tree finches and ground finches, but differed slightly between the two groups. In all cases variables loaded positively onto PC1, but the highest loadings on both PC1 and PC2 were for LMD in the tree finches, and for UMD in the ground finches. Relative to other characters UMD in the ground finches generally had a negative loading on PC2 and LMD had a positive loading. The signs were usually reversed in the tree finches. For this reason, a different covariance matrix was used to measure divergence within each of the two finch groups.

I used phenotypic variances and covariances in *G. fortis* and *C. psittacula* as representative of their respective groups, rather than a pooled sample of species. Each of these two species is intermediate in size in all measured characters with respect to other members of their group. Choice of these two species avoids high relative measurement error associated with the smaller species (Rohlf et al., 1983). Also, both species have a large number of individuals on which to base

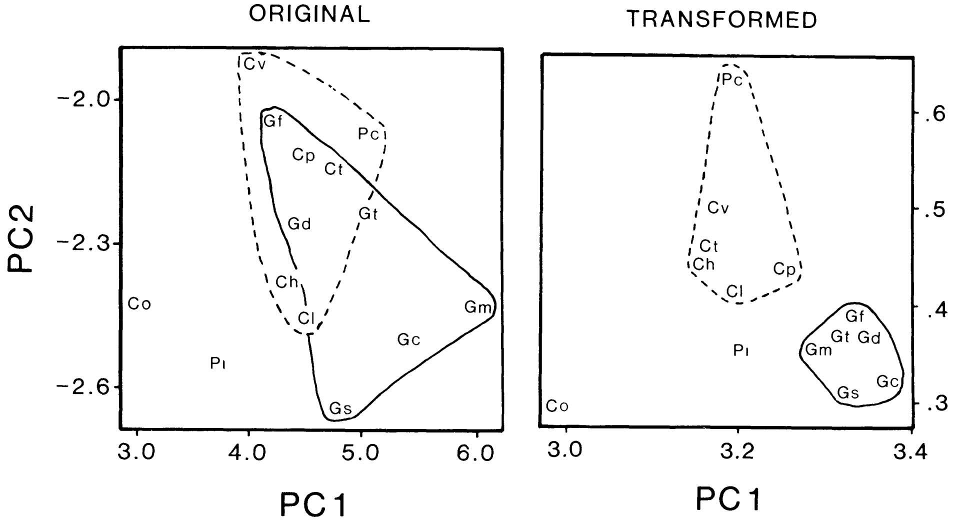

FIG. 2. Species means along the first two principal components (PC's) derived from original (z) and transformed (z') population means. Lines delimit means for the ground finches (solid) and tree finches (dashed). Symbols are *Geospiza magnirostris* (Gm), *G. fortis* (Gt), *G. fuliginosa* (Gf), *G. difficilis* (Gd), *G. conirostris* (Gc), *G. scandens* (Gs), *Chamarynchus parvulus* (Cv), *C. pauper* (Cp), *C. psittacula* (Ct), *C. heliobates* (Ch), *C. pallidus* (Cl), *Platyspiza crassirostris* (Pc), *Certhidea olivacea* (Co), and *Pinaroloxias inornata* (Pi).

estimates of variance and covariance. *Geospiza fortis* is further appropriate in that some genetic parameters are known (Boag, 1983).

In *G. fortis,* I used two different estimates of **G**, the matrix of genetic variances and covariances. In the first, genetic values were estimated from their phenotypic values. Genetic values for five characters were computed directly from data in Boag (1983): WNG, TRS, UML, LMW, and beak depth (UMD + LMD). Phenotypic variances and covariances recorded in the present study were correlated with the genetic variances ($r = .98$, $N = 5$) and covariances ($r = .99$, $N = 10$) in Boag (1983). Genetic parameters for the remaining characters could thus be estimated using least squares regression.

For the second estimate of **G** in *G. fortis* I simply used the phenotypic values. Both estimates gave very similar results in the evolutionary analyses, due to the similarity between the genetic and phenotypic matrices (Boag, 1983). I present results from only the first estimate. Because no genetic parameters are known for *C. psittacula,* and because the genetic and phenotypic parameters gave similar results in the ground finches, I used only the phenotypic values in the tree finches.

Phylogenetic relationships were inferred by computing minimum-length Wagner trees (Kluge and Farris, 1969) in PHYSYS (Farris and Mickevich, unpubl.) directly from the transformed mean characters for species (z'). I used this procedure instead of an alternative one suggested by Felsenstein (1981) primarily because his model of random divergence is inappropriate in this case. Divergence in the Galápagos finches probably occurred instead through sequential, stepwise adaptation to unoccupied feeding niches (i.e., stationary optima) along previously existing resource axes (Lack, 1947; Schluter and Grant, 1984; Price et al., 1984). Hence, though the statistical validity of parsimony remains questionable, this criterion seems intuitively the more appropriate for the adaptive model.

Unfortunately there are no procedures

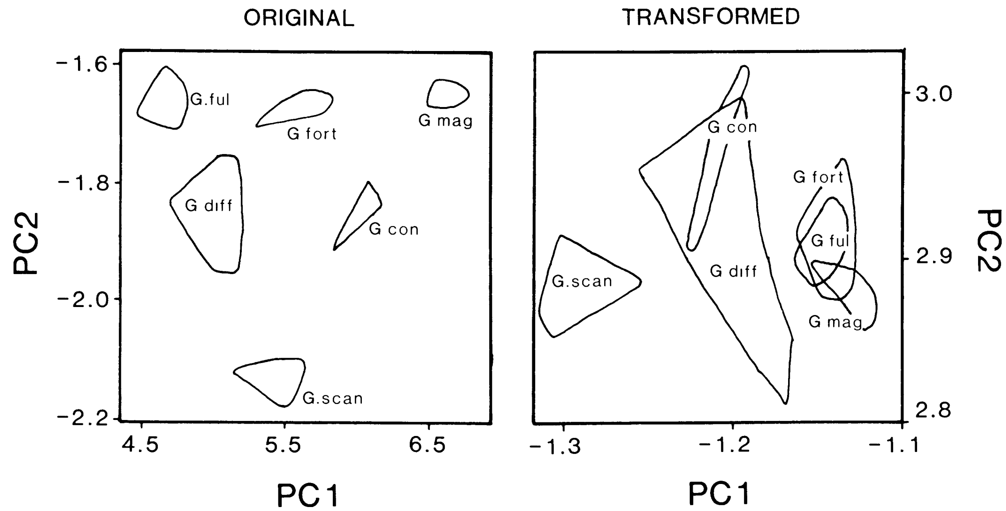

FIG. 3. Population means for the ground finches along the first two PC's derived from original and transformed data sets. Lines delimit means for separate species. Species abbreviations are for *G. magnirostris, G. fortis, G. fuliginosa, G. difficilis, G. conirostris,* and *G. scandens.*

for computing minimum-length Wagner trees that use Euclidean distances. The phylogenetic trees presented here are based on Manhattan distances between species. However, Distance-Wagner procedures (Farris, 1972) using either distance metric gave essentially identical results.

The warbler finch, *Certhidea olivacea,* was used as an outgroup in both the ground finch and the tree finch analyses: Lack (1947) suggested that the warbler finches, *C. olivacea* and *P. inornata,* branched off prior to the ground finch-tree finch division (Fig. 1), and this is supported by Yang and Patton's (1981) results. *Pinaroloxias inornata* was also included in both analyses. Results were the same when it was excluded, or when it was used as an outgroup instead of *C. olivacea.*

RESULTS

Morphological Differences.—Principal components analysis (Pimentel, 1979; Ricklefs and Travis, 1980) was used to represent morphological relationships among populations and species. The advantage of this procedure is that morphological relationships can be represented without distortion using a small number of dimensions. In the first analysis, populations of all 14 species were combined, in order to investigate morphological relationships between the ground, tree, and warbler finches. Components were determined on both the original means for populations (z) and on means transformed using genetic parameters derived from the ground finches (z'). Relationships among the three groups were similar when data were transformed using the corresponding matrix for the tree finches. Additional analyses were performed on the ground finches and tree finches separately, to more closely investigate patterns of divergence within the two main groups. Factor loadings for the ground finches and tree finches are listed in Tables 1 and 2, respectively. Mean species positions along the first two components (PC's) are shown in Figure 2 for the combined analysis. Population positions within the tree finches and ground finches are shown in Figures 3 and 4.

In all analyses PC1 and PC2 together accounted for at least 78% of the total variance among means. Hence PC1 and

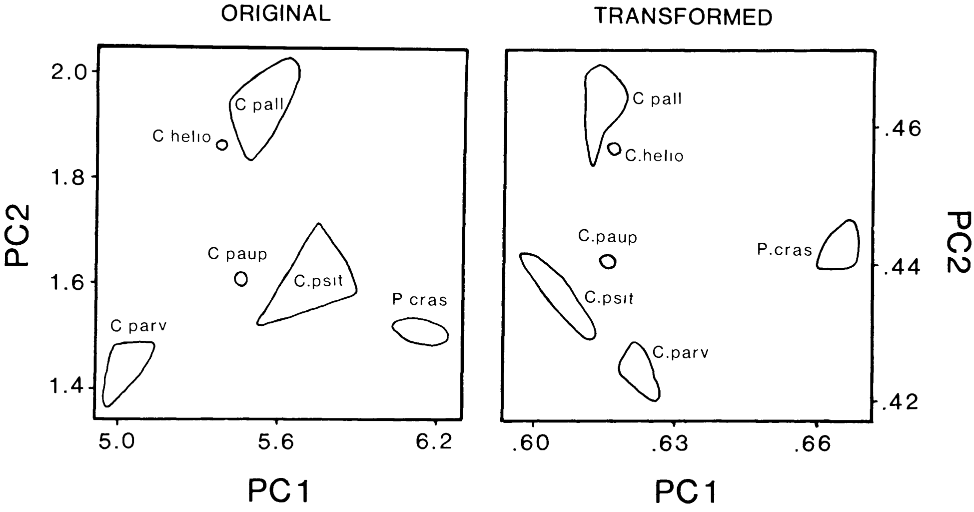

FIG. 4. Population means for the tree finches along the first two PC's derived from original and transformed data sets. Lines delimit means for species. Species abbreviations are for *C. parvulus, C. pauper, C. psittacula, C. heliobates, C. pallidus,* and *Platyspiza crassirostris.*

PC2 summarize the major trends of variation among populations and species (Figs. 2–4). In the combined analysis, 97% of the variance among untransformed means is accounted for by these two components. Figure 2 shows that the tree finches and ground finches overlap broadly along these dimensions (see also Grant et al., unpubl.). However, the two components derived from transformed means account for 85% of the variance but succeed in separating the two main groups (Fig. 2).

Factor loadings on principal components derived from the original means identify traits along which populations are morphologically most differentiated. Factor loadings on components derived from the transformed means (z') identify the traits subject to the greatest net force of selection during morphological differentiation. Because different traits within populations are not equally genetically variable, and because traits are correlated, these factor loadings are unlikely to correspond to those for the components derived from the original variables. Differences between loadings are evident in the ground and tree finch analyses. In both groups all untransformed variables load positively onto PC1 (Tables 1, 2), separating species by "size" (Figs. 3, 4). PC2 represents "shape" variation among species, particularly beak length relative to other variables. In contrast, principal components derived from the transformed variables indicate that variation in shape predominates along both axes. In the ground finches, the analysis indicates signifiant shape variation within species, particularly in *G. difficilis* (Fig. 3).

Some pairwise differences between species in a group also vary in the two analyses. For example, *C. psittacula* is morphologically more similar to *P. crassirostris* than to *C. parvulus,* with respect to the original variables (Fig. 4). However, the net force of selection necessary to actually bridge the difference between *C. psittacula* and *P. crassirostris* would be much greater than between the other pair, as indicated by their relative differences with respect to the transformed variables. Similarly, more net selection separates *G. fuliginosa* from *G. scandens* than from *G. magnirostris* (Fig. 3). With respect to the untransformed variables,

TABLE 1. Factor loadings on the first three principal components derived from the original (z) and transformed (z') population means, for the ground finches.

	Original			Transformed		
Variable	I	II	III	I	II	III
WNG	.14	−.08	.36	−.23	.46	−.74
UML	.34	−.60	−.17	−.51	−.12	.12
LML	.32	−.60	−.17	−.54	.14	.53
UMD	.44	.16	.35	.05	.17	.05
LMD	.49	.40	−.57	.19	.18	.06
UMW	.35	.11	.35	.00	−.76	−.22
LMW	.43	.25	.01	.60	.16	.28
TRS	.12	−.10	.50	.06	−.30	−.16
% variance	90.8	98.9	99.7	56.3	78.0	92.8

these comparisons indicate that shape is considerably more difficult to alter than size, a consequence of strong, positive genetic correlations between traits (Price et al., 1984).

With respect to the transformed variables, *C. olivacea* is quite distinct from both the tree finches and the ground finches (Fig. 2); *P. inornata* is less distinct. *G. fuliginosa, G. fortis,* and *G. magnirostris* form a cluster in the ground finches. *Geospiza conirostris* and *G. difficilis* are also close to one another, and *G. scandens* is relatively isolated. In the tree finches, *C. pauper, C. parvulus,* and *C. psittacula* form an apparent cluster as do *C. pallidus* and *C. heliobates. Platyspiza crassirostris* is distinct from both of these.

These relationships are similar to those suggested by the biochemical data (Yang and Patton, 1981). A full comparison is not possible since their analyses did not include *C. heliobates, C. psittacula,* and *P. inornata.* Also, in order to compare tree finches with ground finches, only one of the respective covariance matrices can be used to transform both data sets. Since more ground finch pairs than tree finch pairs are available in Yang and Patton's analysis, I used parameters for the ground finches (Fig. 2). Pairwise morphological distances between species (B) are strongly correlated with the biochemical distances given in Yang and Patton (Rogers' D; $r = .74$; $N = 55$). This correlation probably underestimates the actual correspondence between morphological and biochemical differences: some of the residual variance can be attributed to a greater morphological distance between species in pairs of tree finches than in pairs of

TABLE 2. Factor loadings on the first three principal components derived from the original (z) and transformed (z') population means, for the tree finches.

	Original			Transformed		
Variable	I	II	III	I	II	III
WNG	.25	.00	.37	.50	.38	.32
UML	.28	.62	.14	.19	.35	.35
LML	.19	.69	−.10	−.50	.75	−.22
UMD	.36	−.05	−.73	−.42	−.14	.58
LMD	.55	−.32	.07	.20	−.24	.19
UMW	.38	−.08	−.16	.18	.06	.00
LMW	.43	−.16	.12	.16	−.11	−.60
TRS	.25	−.05	.50	.44	.27	−.08
% variance	79.6	95.5	99.4	72.5	93.9	97.4

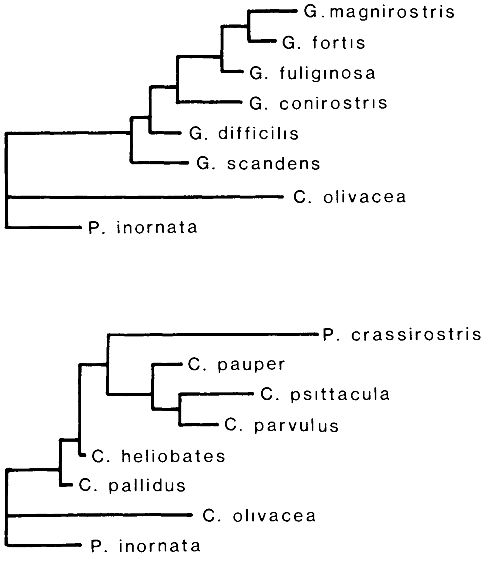

FIG. 5. Minimum-length Wagner trees for tree finches and ground finches, using *C. olivacea* as outgroup. Branch lengths for the two trees were scaled relative to the length of the *P. inornata* segment.

ground finches for a given value of Rogers' *D*. This may be an artifact of using **G** based on the ground finches to compare morphological distances in both groups.

B^* is also correlated with Rogers' *D* ($r = .68$). Standard Euclidean distances between species, based on the untransformed measurement means, are more weakly correlated with Rogers' *D* ($r = .39$).

Phylogenetic Relationships.—I computed minimum-length Wagner trees, using the transformed variables, for the tree finches and ground finches separately. Since the original character means were transformed differently in the two groups, the two trees are also presented separately, in Figure 5. At present I can think of no method which would allow me to combine the three groups into a single tree; the arrangement shown in Figure 1 remains a viable possibility. Consistencies (Kluge and Farris, 1969) in the two trees were .67 and .80, respectively.

Overall, phylogenetic relationships within the tree finches and ground finches in Figure 5 are similar to those of Lack's tree (Fig. 1), which was based on morphology, plumage, and dietary considerations. They are also similar to relationships suggested by Yang and Patton's (1981) branching phenogram based on biochemical distances among 11 of these species. Similarities include the inference that *C. parvulus, C. psittacula,* and *C. pauper* in the tree finches, and *G. fuliginosa, G. fortis* and *G. magnirostris* in the ground finches form monophyletic trios. *Chamarynchus pallidus* and *C. heliobates,* and *P. inornata* and *C. olivacea,* are grouped in both Lack's and my reconstructions. Figure 5 suggests that *C. pallidus* and *C. heliobates* are not monophyletic, as in Figure 1, but branch segments are short, and hence the local configuration uncertain.

Relationships among some species differ in Lack's and my reconstructions. For example Lack considered *G. conirostris* and *G. scandens* to be very closely related, but in terms of the transformed morphological variables *G. conirostris* is closer to *G. difficilis* than to *G. scandens.* Lack also suggested that *C. pallidus* and *C. heliobates* were highly modified forms (Fig. 1). However, morphologically they are closer to the hypothetical ancestral condition than are the other tree finches (Fig. 5).

DISCUSSION

In practice it is difficult to estimate **G**, the genetic covariance matrix. However, since phenotypic correlations tend systematically to underestimate genetic correlations (Cheverud, 1982; Cheverud et al., 1983; Boag, 1983; Grant, 1983), it will often be possible to estimate **G** from the phenotypic values. In other cases the observed phenotypic covariance matrix **P** can substitute for **G** when estimating selection distance. This assumes the phenotypic matrix to be a simpler scalar multiple of the genetic matrix. While unlikely, the resemblance will sometimes be great enough for **P** and **G** to yield similar results, as in the present study.

The correspondence between morphological (*B*) and biochemical estimates of evolutionary relationships in the present study is intriguing. It is especially surprising given the importance of ecological factors, mainly food, in determining morphology in these finches (Boag and Grant, 1981; Price and Grant, 1984; Schluter and Grant, 1984), and given the observation that natural selection can substantially affect mean morphology within one generation (Boag and Grant, 1981). Recall that the reliability of the present approach depends on the validity of the assumption that B/t is approximately constant, where t is the time since separation. Unless morphological and biochemical data do not provide independent estimates of phylogeny, this assumption is supported: in the Darwin's finches, morphological changes requiring more selection (e.g., changes in shape) indeed appear to have required more time than other changes involving less selection (e.g., changes in size). Differences in the amounts of selection required for specific morphological changes are determined entirely by **G**, the genetic covariance matrix. Hence, though selection has been responsible for morphological divergence in the Darwin's finches, the results are evidence that genetic parameters have exerted a powerful role in determining the direction and rate of change.

The results also suggest that an appropriate measure of morphological distance (i.e., *B*) may often allow reliable inference of phylogenetic relationships. Indeed, in some situations morphological data may have some advantages over biochemical data in estimating phylogeny. For example, rates of morphological divergence do not usually depend on effective population size, unlike short-term divergence rates in neutral characters (Lande, 1979; Felsenstein, 1981). Also, among closely related species (e.g., the Darwin's finches), estimates of relationships based on morphology will not be greatly influenced by small amounts of hybridization. Under neutrality, measured differences could reflect frequency of hybridization as much as actual phylogenetic distance.

Of course, good reasons remain why morphology will not always reflect phylogeny. For example, relationships may be obscured by morphological convergence, or by variable rates of morphological evolution. Morphological data may thus be most useful for phylogenetic purposes in providing complementary information to that derived from biochemical and other independent methods. However, even in situations where these other methods are thought to provide the true phylogenetic picture, it will be interesting to compare results with those of morphological analyses (Barrowclough, 1983). In this way it may be possible to clarify the importance of convergence and variable evolutionary rates in the history of morphological change. In such circumstances, because of its simple evolutionary interpretation, *B* may be a more appropriate measure of morphological distance than other more commonly used measures.

SUMMARY

A new measure of morphological distance is used to estimate morphological and phylogenetic relations among the Darwin's finches. The measure, *B,* is based on a model for multivariate evolution (Lande, 1979), and it estimates the total net force of directional selection acting on characters that is required to bridge the differences between any two species. This force depends on the amount of genetic variance in traits, and on genetic correlations between traits. "Selection distance" between species is shown to be correlated with biochemical distance, and the method produces a phylogenetic tree similar to the one originally suggested by Lack (1947). The results indicate that, in addition to natural selection, genetic parameters have strongly influenced the direction and rate of morphological divergence in the Darwin's finches.

ACKNOWLEDGMENTS

I thank P. Grant and I. Abbott for providing the morphological data, and J. Felsenstein, N. Heckman, R. Lande, and

T. Price for valuable discussion and advice. D. Brooks, J. Farris and R. O'Grady helped construct the phylogenetic trees. I. Abbott, G. Barrowclough, N. Barton, P. Grant, R. Lande, T. Price, and J. Smith read and commented on the manuscript. Computer funds were provided by the Institute of Animal Resource Ecology at UBC, and by the Division of Biological Sciences at The University of Michigan.

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