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THE GENUS: A MACROEVOLUTIONARY PROBLEM

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Although much of the recent work on macroevolution has centered on the fossil record (Gould, 1980), a few studies have addressed this concept using the morphology of living species as a data base (Ricklefs, 1980; Lemen and Freeman, 1981). The neontological record does lack the element of time that allows a researcher to follow change through time, but this deficiency is counterbalanced by the fact that living species represent one perfect slice of time. Admittedly systematists have not been able to collect and classify all extant species, but tests using the neontological record in the better known groups such as birds and mammals will not suffer the problems of incomplete data sets or uncertain chronologies as badly as is probable with the paleontological record. One way to use neontological data is to study how species are arranged in morphological space. The evolutionary diversification of a clade can be seen as a tree that spreads with morphological change and branches with cladogenesis. In such a vision living species are one cross-sectional slice of the tree. The problem is to find what this cross section reveals about the structure of the tree. Perhaps the best way to start visualizing this approach is by considering that all clades ultimately trace their ancestry to a single species. Therefore, one can imagine a clade evolving from one species to many and filling morphological space through time in a certain way that is based on the number of species in the clade and the individual morphologies of the species. The specific morphologies of these species are not

predictable because they are the products of the unique environment, history and stochastic processes that species face. However, if all clades share certain fundamental evolutionary processes, then some repeated patterns that depend on these shared processes might be expected in all clades.

This paper centers on the macroevolutionary problem surrounding the concept of the vertebrate genus. We have been fascinated by the apparent tendency of members of a genus to have the same shape in contrast to the great differences in shape among genera at the family level. If this is true, genera would be considered shape conservative groups. Our initial view of this contrast in shape variation within and among genera leads us to question whether the same evolutionary processes that produce genera can simply be extended to produce families. To approach this question two things need to be done. First, the morphology of genera must be quantified to yield a more exact idea of how the morphological variation of a family is partitioned into genera. And second, evolutionary models need to be built that make different assumptions about how evolution proceeds. Our quantification of the morphology of genera will involve looking at size and shape variation at the familial and generic levels with multivariate methods. The evolutionary models will be used to make predictions of size and shape variation in families and genera under different evolutionary assumptions. As will be presented below, our models make clearly different predictions of how species will

come to fill morphological space. Based on a comparison with real data we can reject some types of evolutionary models as incompatible with real data.

Before the evolutionary models are introduced, we give attention to how genera are actually formed. This point must be dealt with because, no matter what the underlying evolutionary processes, the method used to form genera will affect the properties of genera. As an example, if genera are formed by randomly selecting species from the family, they will have very different properties from groups formed on the basis of monophyly. Since the exact nature of the formation of genera is not known, a variety of possibilities must be taken into account to determine their effects on our models' predictions. We will investigate two alternative views of the genus. The first view will be that genera are strictly monophyletic groups within the family. This may seem an unwarranted assumption, but because it is the ideal definition to most evolutionary biologists, and because it will allow us to investigate the properties of subclades within clades, which is of theoretical interest, we will use it as an assumption here. The second view will be that genera are formed phenetically to make groups of similarly shaped species, but not necessarily species of the same body size. This assumption may be very close to the method actually used historically by systematists to form genera. Another reason for this second definition of genus formation is that one of our basic findings will be that some models of evolution cannot produce groups that are as conservative in shape as are found in real genera. Because the degree of shape conservatism is important in this study, we need a method of forming genera that will minimize the variance in shape within groups.

We take no stand on how genera are actually formed, or on how genera should be formed; nor do we maintain that these two approaches are the only possibilities. Rather these definitions of genera are viewed as opposite ends of a spectrum of possibilities. As such we can use these extreme views for a sensitivity analysis of our models' predictions. And because our evolutionary models do make consistently different predictions, no matter what the definition of the genus, we can be far more confident in these differences for generating macroevolutionary tests using the neontological data.

The Models

The first is the uni-modal model. The basic assumption behind this model is that the expected change in morphology of a character through time has a normal distribution. This model is similar to those developed by Raup and Gould (1974). The uni-modal model can be viewed as neutral morphological change by drift or as a complex deterministic process where, because many interacting factors are affecting the species in a clade, the whole process is indistinguishable from a random walk model. Although the uni-modal model of evolution may appear to be simplistic, data from the fossil record often seem compatible or nearly compatible with random models (Raup and Crick, 1981). Also, Raup and Gould (1974) have shown that random morphological change can produce high within-subclade similarity and low among-subclade similarity, just as one might expect with real data. Therefore, we decided to consider the uni-modal model of evolution in our work because of the interest shown to such models in previous studies and the apparent robustness of these simple models. Perhaps a caveat should be inserted here: the uni-modal model is not our attempt to generate the gradualistic model of evolution. Any effort to model gradualism would be very difficult because of the diversity of approaches that could be used. The uni-modal model qualifies as a gradualistic model, but it is only one of many possibilities.

The next set of models considered assumes there are two kinds of evolutionary events producing morphological change. The first to be considered is the decoupled model. The basic assumption

behind this model is that the two modes of evolution are size-coupled and size-decoupled change. Change coupled to size is defined as a change in which all characters tend to have a similar direction of change that is correlated with an underlying change in size. Such size changes may be easy for evolution to produce (Hallam, 1978). Change decoupled from size occurs when characters normally correlated with each other become decoupled and change independently. This kind of change may be more difficult for selection to produce (Dickerson, 1955). Thus evolution might proceed as in Figure 1.

Another possible interpretation of Figure 1 can be cast in an ecological context so that the morphology of species in genera reflect adaptive zones (Simpson, 1944). The high morphological similarity of congeneric species would reflect the ecological pressures of adaptive zones to confine morphological divergence. Escape of a species from one adaptive zone to another could be viewed as a basically different evolutionary event from speciation within an adaptive zone. If it is assumed that changes in size alone typically do not cause a shift in adaptive zone (Simpson, 1944 p. 92; Freeman, 1981 p. 103), and that a change in shape is required to shift to a new adaptive zone, then the similarity between this model and the decoupled model is clear. The main difference is the mechanism that tends to produce shape conservative groups. In the case of the decoupled model the mechanism may be a genetic-developmental constraint, and in the case of the adaptive zone model it is an ecological constraint. Based on the kind of morphological analysis we perform in this study, these two models are indistinguishable. So while these two hypotheses may operate very differently, they are lumped in this paper as the decoupled/ adaptive zone model. Only the decoupled model will be described in detail. By substituting the concepts of a speciation event that produces a new species in the same adaptive zone for coupled evolu-
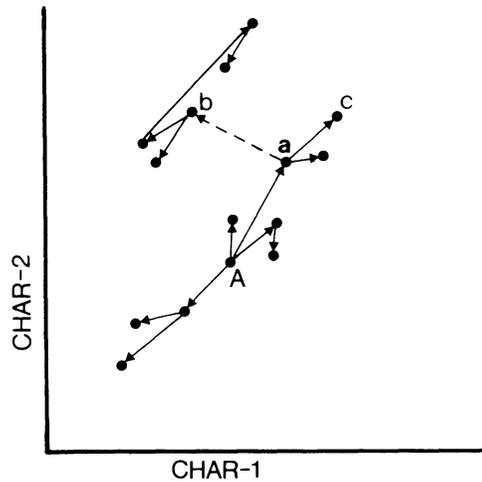

FIG. 1. This clade is produced by 13 coupled speciation events and one decoupled event (a to b). Defining groups on the basis of decoupled events (dashed line) will produce two groups, one founded by species A and the other by b.

tion and evolutionary events that produce new species in a different adaptive zone for decoupled evolution, the similarity of the models can be seen.

The last model we consider is the saltational model. This model is similar to the decoupled model just discussed in that it assumes two different kinds of evolutionary events. First, there can be change that is correlated with size, the same basic mechanism of evolution in both the uni-modal and the decoupled model. Second, at rare, random intervals a species can undergo a saltational event. The saltational move is similar to the size-correlated change just mentioned except there is an increase in the magnitude of the change. The correlation between characters is still maintained, contrary to a decoupled event.

The decoupled/adaptive zone model and the saltational model have some similarities to the punctuated equilibria hypothesis (Eldredge and Gould, 1972) in that all postulate a dual nature to evolutionary change. The two modes in our models are either saltational and non-saltational or decoupled and coupled evolution. In the case of the punctuated

equilibria hypothesis the two modes are changes in small, isolated populations that can produce large shifts in morphology and new species, and changes within large populations that typically produce relatively small shifts in morphology.

In this paper we use computer models to simulate the uni-modal model, the decoupled/adaptive zone model and the saltational model to compare their predictions to the morphological structure of three families of bats, the Phyllostomidae, the Emballonuridae, and the Molossidae. Our results indicate that the decoupled model is the only model capable of producing groups that are consistent with real genera. We conclude that real morphological data are consistent with the idea that shape change within a genus is qualitatively different from the mechanism that leads to changes in shape among genera. It should be noted that our conclusions are based on a mammalian data set. Other groups may not show similar patterns, and further study would be needed to verify our findings in other taxa.

MATERIALS AND METHODS

The approach used here follows that of Raup and Gould (1974) in that it uses computer models to simulate how evolution might proceed. We create three different computer programs: the uni-modal model, the decoupled/adaptive zone model and the saltational model. The computer simulates phylogenies and species morphologies based on certain assumptions. These hypothetical clades can be analyzed to see if these models of evolution give different results.

The main emphasis is to monitor changes in morphology within the clade. One of the basic ideas in morphometrics is that size and shape are separable concepts (Jolicoeur and Mosimann, 1960). The concepts of size and shape are intuitive to all, but a problem can arise in actually quantifying a specific difference in morphology into its size and shape components. One of the main difficulties

is that growth in biological systems is normally allometric and not isometric. To define this pattern of consistent shape change with size change, an allometric growth curve can be found for a group of organisms (Gould, 1966). Although morphologies that are plotted along such a line are rarely isometric, they are often interpreted as being the same "biological shape." If we use this definition of shape, then points along the allometric growth curve differ only in size from one another. Likewise, points that are not on the line represent different shapes from the one defined by the curve. Points along a line perpendicular to the allometric curve represent morphologies that are the same size as the morphology at the point of intersection of the two lines. The degree of shape difference along this perpendicular line increases linearly with distance from the intersection point.

In this paper we will be using allometric growth curves and the concept of "biological shape" just described. Caution must be exercised when using this approach because the actual allometric equations for a group of species are normally empirical. In the extreme case any two morphologies can always be connected and their differences in morphology be defined away as allometric growth. Even with possible difficulties, based on the work of Gould (1966), Lande (1979) and many others as well, as a consideration of the morphological characters used in this study, we will use the allometric growth curve as a method of separating and defining size and shape. When we refer to a change in size alone, that means along an allometric growth curve. Similarly, a change in shape is a change perpendicular to a specific allometric growth curve.

Our morphological data sets, both real and simulated, are used to create variance-covariance matrices. The largest eigenvector and eigenvalue extracted represents the allometric curve and the variance in size it explains. This occurs because all characters in our data sets are highly correlated with size. All the rest

of the variation in the matrix is attributed to shape differences, and there is no allowance for an error term. However, there is surely some error term in the real data sets. The problem can be reduced somewhat by measuring several individuals of each species and using the mean values for a species in the calculations of the variation at the genus and family levels. It should also be remembered that because of the nature of the data, errors in measurements will tend to inflate the variation in shape at the genus level relatively more than at the family level. Thus, errors will tend to make genera appear less shape conservative than they actually are. Even in the face of this problem real genera are found to be quite shape conservative relative to the family.

To compare the uni-modal model, the decoupled/adaptive zone model and the saltational model we must define them. The defining process involves simplifications, but we feel the following simulations have biological validity. It is important for the reader to be critically aware of the assumptions used in our models, because once these assumptions are made all conclusions are fixed. The assumptions follow.

Uni-modal Model

1) This model is not constrained to have a constant rate of morphological change through time; rather, the rate of morphological evolution is determined by a random number generator. Each species has a data set of characters, where X_i is the linear dimension of an artificial character i. In every time unit the morphology of a species is modified by a morphological divergence function so that the new morphology of each character, X_i', is equal to

$$X_1' = X_1 SD_1$$
$$X_2' = X_2 SD_2 \dots$$
$$X_n' = X_n SD_n,$$

where S is randomly selected from a normal distribution with mean .0 and standard deviation of y. S is selected new each time unit for each species but is the same for all characters within a species. The D_i's are a series of numbers selected randomly from a normal distribution with mean of .0 and standard deviation of z. The logic behind this method of the evolution of characters is to simulate changes that are along the allometric growth curve (size change) and those that are not (shape change). The S value represents the change in size each time period, and D_i is a shape change in character i for the same time period. By changing the relative size of y and z, the amount of size versus shape change can be altered. When y is large relative to z all characters become highly correlated with size and by default with each other as well. If y is zero, the average correlation between characters is zero, because each character is only modified by the independent D_i's. It is important to remember that the values of y and z not only determine the way a species changes through time but also determine the pattern of size and shape diversification in the whole clade. Therefore the values used in our simulations must be able to produce average correlations among characters that are consistent with the average intercharacter correlations found in the families of bats studied. The exact values chosen within the expected range of correlations does not substantially affect our analysis. This mode of evolution, the only method of change in the uni-modal model, is also used as one of the modes of evolution in both the decoupled model and the saltational model. We will refer to this mechanism of change as the coupled mode of evolution. The name *coupled* drives from the fact that in this mode of evolution most change is correlated with size.

2) As there is no correlation among successive time periods in the values of S or D_i's, no long term trends in evolution are knowingly modeled into the simulation. Each character behaves as a random walk, but as predicted by Raup and Gould (1974), we find some species have consistent, apparently directed changes through time by chance alone.

3) The chance of one species splitting into two is the same for all species; no particular morphology or past history produces high rates of speciation in a species or group of species. Likewise, the risk of extinction is the same for all; therefore, such parameters as morphology, speciation rate, and length of existence have no effect on survival. Because both extinction and speciation are random, there is a great variety in the number of descendants produced by species and the time each species endures. In some runs, the rates of extinction and speciation are changed to produce periods of increase or decrease in the number of species.

4) The speciation events do not in themselves produce large morphological shifts. There is no tendency for the mother species to be more similar to ancestral size or shape than a daughter species. When a speciation event occurs, the new morphology of each sibling species is determined by its own randomly selected S and D_i's.

5) A single seed species is used to generate the clade. At time zero this species is assigned a data set of X_i's. All species generated in the analysis can have their ancestry traced to this one species.

6) Two modifications of the uni-modal model are considered. First, the uni-modal model is modified to run at an equilibrium number of species. When the simulation starts, the number of species rapidly increases from 1 to about 100 (the speciation rate is set much higher than the extinction rate). Then the rates are made equal so that the number of species extant remains around 100 (a negative feedback system on the extinction and speciation rates is used to keep the species diversity from wandering away from 100 by drift). After a total of 200 time units the simulation is stopped. At that time there are an average of 100 species extant, which represents an average of about 2% of the total species created in the simulation; the other 98% have gone extinct before the end of the run.

Second, the speciation rate is modeled to be a heritable characteristic. The method is to assign each newly formed species the speciation rate of its mother species. On rare and randomly selected occasions the rate of speciation is altered. In our simulations we divided the speciation rates into two categories, low and high. Once set, this rate is constant for a species and its descendents except for those rare events (1 in 10 by random chance) when it is altered to the other rate. This simulation produces two kinds of groups, those with high speciation rates that are increasing explosively and those with low speciation rates that are increasing slowly.

Decoupled Model

The only change that is needed to transform the uni-modal model into the decoupled/adaptive zone model is to assume there are two different kinds of evolutionary events, coupled and decoupled. During coupled evolution, the morphology of a species is determined exactly as in the uni-modal model, while in decoupled events S is replaced by a series of S_i's.

$$X_1' = X_1 S_1 D_1$$
$$X_2' = X_2 S_2 D_2 \ldots$$
$$X_n' = X_n S_n D_n.$$

Each S_i is determined by a random number generator with mean .0 and standard deviation of y, using the same algorithm that produces the single S values during coupled speciation. Using a series of S_i's decouples the correlation of characters at this kind of evolutionary event and is our computer program's equivalent of a genetic revolution (or a shift in adaptive zone). The proportion of evolutionary events that are decoupled is set at the beginning of the computer run. If the probability is zero, this model is the same as the uni-modal model. The occurrence of a decoupled evolutionary event in time and lineage is a matter of chance, and determined by a random number generator.

Saltational Model

As in the decoupled model there are two kinds of evolutionary events in the saltational model. The first mode of evolution in this model is coupled evolution, exactly the same as used in the uni-modal model and decoupled model. The second mode of evolution in this model is the saltational event. The saltational event involves changes that are correlated with size. However, the magnitude of change possible is greater than expected in the coupled events. When a saltational event occurs the new morphology of a species is given by the following equations

$$X'_1 = X_1 S^*_1 D^*_1$$
$$X'_2 = X_2 S^*_2 D^*_2 \ldots$$
$$X'_n = X_n S^*_n D^*_n.$$

S^*_i's are determined by a random number generator with a mean of .0 and a standard deviation of Ky (K is a constant greater than 1). This means the range of change is K times greater than in the coupled events. Likewise the D^*_i's values are enlarged by a factor of K. The percentage of saltational events versus coupled events is set at the beginning of the computer run. The exact time and place of these events is a matter of chance using a random number generator.

The Microchiropteran Data Set

The analyses performed in this paper are based on morphometric data from two sources. The phyllostomid data set is from Swanepoel and Genoways (1979) and includes eight measurements of 139 species most of which have eight replicates per species. The eight measurements taken are forearm length, greatest length of skull, condylobasal length, zygomatic breadth, postorbital constriction, breadth of braincase, length of maxillary toothrow, and breadth across upper molars. Fifty genera are represented. Data sets for the molossids and emballonurids are taken from Lemen and Freeman (1981) and include 42 measurements on a single specimen (usually male) of each of 111 species, representing 22 genera (see

Freeman, 1981 and Lemen and Freeman, 1981 for full description of these characters). Six out of the 42 characters measured on the molossids and emballonurids are common to the phyllostomid data set. The characters in common are forearm length, greatest length of skull, zygomatic breadth, postorbital constriction, breadth of braincase, and length of maxillary toothrow.

RESULTS

The Microchiropteran Data

The morphological variation in size and shape that is found in a family can be broken into three levels: variation among individuals within a species, variation among species within a genus, and variation among genera within a family. Variation within species is calculated here using all species with a sample size greater than six individuals. Variation within genera is found by using the species averages of genera that contain more than four species. Finally, the family level variation is calculated using the means of all species. In Figure 2 the variances in size and shape are shown for these three taxonomic levels for all characters for the family Phyllostomidae. Note that size variation within a genus is highly variable: at the lowest point, little more than that found within a species; at the greatest, almost as much as found in the whole family. Shape variation operates in a different manner. The shape component of the genus is small. In fact, it is similar to the shape variance found within the species. However, the variance in shape of the whole family Phyllostomidae is 15 times greater than the average variance in shape found in its genera.

A way to see the relationship between size and shape in the bivariate case is to plot them as ellipses (Fig. 3). Here the major axis of each ellipse is size and the minor axis shape. The ellipses are centered at their genus means, and the slope of each ellipse is the ratio of the standard deviations of the two morphological characters in that genus (the reduced ma-
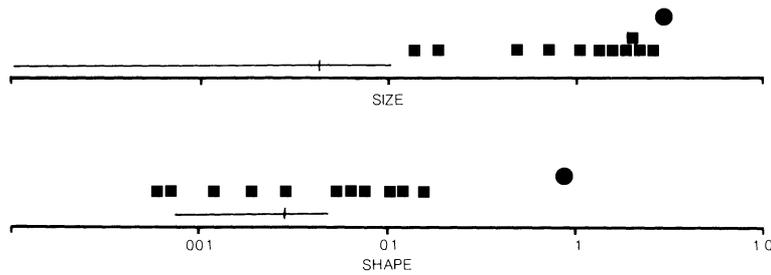
FIG. 2.   In this figure the variances in size and shape are compared at different taxonomic levels for the Phyllostomidae. All eight variables are used to generate these variances. The solid lines represent the mean ± 2 SD for intraspecific variances in size and shape. The squares are the variances for the generic level and the circles for the family level.

jor axis method, Kermack and Haldane, 1950). There is a striking similarity in the slopes of these ellipses but great differences in their elevations. It is the shift in elevation that produces the high shape diversity of the family, and it is this shift that may represent decoupled events (Fig. 1). For comparison, we have also plotted the variance in size and shape of the whole family. The ellipse F, representing the size and shape variation of the family, is more circular because of the high shape variance present at the family level.

The relationship between the variation in size and shape and the number of species in a phyllostomid genus for all eight morphological characters is shown in Figure 4. The size and shape variances of the genera can be expressed as percentages of the size and shape variances of the family (this percentage will be referred to as relative variance in size and shape). The relative variances give an index of how conservative the variances of genera are relative to the family. The relative variance in size averages 35% in the phyllostomids. Six of the eleven genera used (some genera had to be deleted from the multivariate analysis because of missing data) have relative variances in size over 50%. A different pattern exists for the variation in shape. The average relative variance in shape is only 1.5%. No genus has a relative shape variance over 50%. The clear difference in the behavior of size and shape can be seen by

inspection of Figure 4 or it can be quantified with a Mann-Whitney U test (comparison of relative size and shape variation, $n_1 = n_2 = 11$, $U = 120$, $P < .001$). A contingency table can be used to compare the number of genera with relative variances in size and shape above and below 50% ($\chi^2_1 = 8.5$; $P < .005$).

Data sets for the Emballonuridae and the Molossidae have more characters measured, but there is only one specimen per species. As before a comparison of the variation in size and shape in a genus can be plotted against the number of species in the genus (Fig. 5). In the Molossidae the average relative variation in size and shape is 54.2% and 28.4%, respectively. In the Emballonuridae the values are 19.2% and 49.7%. Of the eight genera studied in the Molossidae, four have relative variances in size over 50%, while none have relative variances in shape over 50%. In the Emballonuridae none of the four genera studied have a relative variance in size over 50%, but one genus does have a relative variance in shape that is over 50% (see discussion below).

The Uni-modal Model

The artificial clades generated by the uni-modal model are analyzed for variation in size and shape using groups that are based on both monophyly and clustering techniques based on shape (shape groups). We have just established that
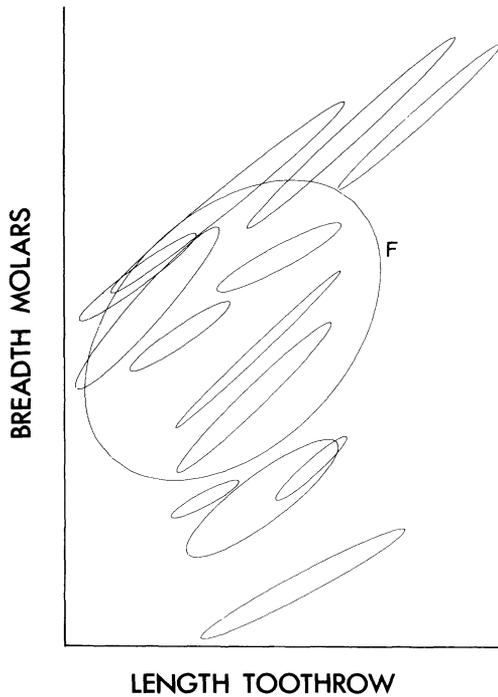
BREADTH MOLARS

LENGTH TOOTHROW

FIG. 3. The genera of the Phyllostomidae are represented as size and shape ellipses for a bivariate case. The large ellipse (F) represents the whole family. Note that the standard deviations of size and shape are used here and not the variances.
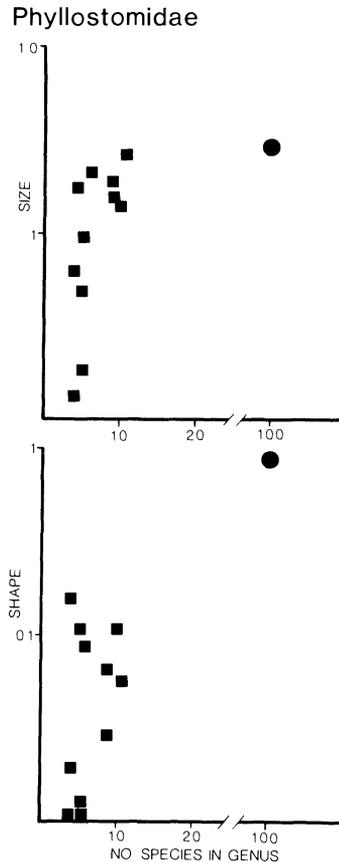
Phyllostomidae

FIG. 4. The relationships between the variances in size and shape with the number of species in a genus are shown here for the Phyllostomidae as squares. The variances at the family level are represented by circles. The variances are generated using all eight characters available.

real genera are shape conservative, and here we will find that the species generated by the uni-modal model can not be divided into either clades or shape groups that resemble real genera.

First we quantify the behavior of monophyletic groups under the uni-modal model. The most straightforward way to investigate the morphological properties of monophyletic groups is to monitor the changes in the variance of size and shape as the whole clade increases in number of species. If genera and families are nested monophyletic groups and change is coupled, then real clades should conform to the same pattern of morphological diversification predicted by this computer model.

We investigate the properties of clades under two conditions. First, we consider the rapid increase simulation when the speciation rate is set higher than the extinction rate and there is a rapid increase in the number of species in the clade. At the end of each time unit the existing species are analyzed for size and shape variance. When the clade reaches approximately 200 species the computer run is terminated. Thus our view of size and shape for this simulation is from a clade that is always in a rapid growth phase. The second condition is to run the simulation as before to a maximum clade size, but at that point the extinction rate is raised above the speciation rate. This
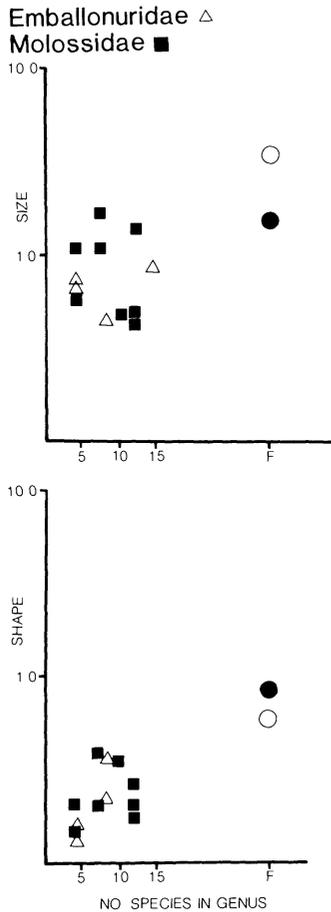
Emballonuridae △
Molossidae ■

FIG. 5. The relationships between the variances in size and shape with the number of species in a genus are shown here for the Molossidae and the Emballonuridae. The variances at the family level are also shown for the Molossidae (solid circles) and the Emballonuridae (open circles).
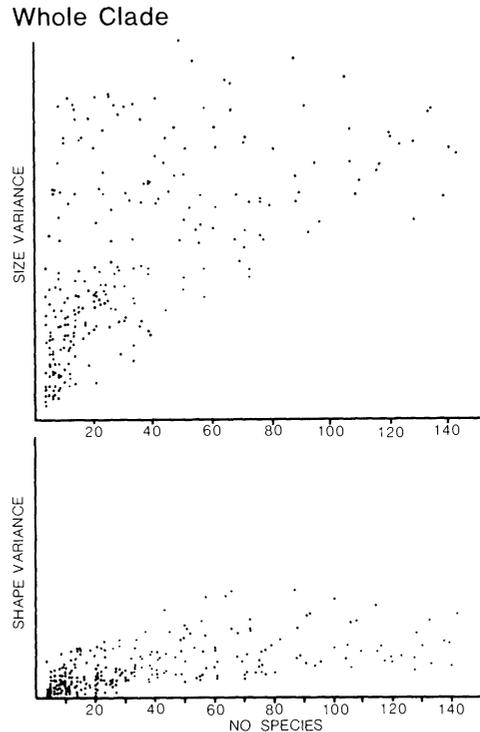
Whole Clade

FIG. 6. The uni-modal model with a rapid increase in the number of species produced these results. The variances in size and shape of the whole clade are calculated and plotted for each time unit of the simulation. Then the simulation is repeated several times to get the results of many runs. Note the rapid increase in the variances with increasing clade size.

causes the number of species in the clade to decrease to zero.

Results of these two simulations are similar, and only the results found within the rapidly increasing clade are shown (Fig. 6). The pattern found within a rapidly increasing clade is an asymptotic approach to a maximum variance in both size and shape. The important feature of Figure 6 is the speed at which the variances of size and shape approach the asymptotic maximum. At clade sizes of only 10–15 species there is already a large

overlap in the expected variances for size and shape with those found for clades of 200 species. Changing the computer simulation to allow the clade not only to increase to a maximum but also to decrease back to zero only increases the expected overlap of size and shape variances found in small monophyletic groups with the variances in larger clades. This occurs because extinction is random with respect to size and shape, and as a result those monophyletic groups that are left at the end of the decline will not necessarily involve species that are closely related. They are simply all that is left of the mostly extinct clade.

Therefore in both of these cases clades quickly approach an asymptote of size

and shape variation with increasing numbers of species in the group. These results are not consistent with the real data, Figure 4. This may mean that evolution is not adequately modeled by this form of the uni-modal model, or it may mean that genera are not clades. Because the monophyletic groups are not sufficiently shape conservative and size variable we now turn to shape groups. If shape groups cannot match real data for shape conservatism we must reject this form of the uni-modal model as a viable explanation of evolution.

The method of forming groups based on shape involves using a sizeout analysis (Lemen, 1983) and phenograms (UPGMA in Sneath and Sokal, 1973 p. 230). The goal is to remove the effect of size by eliminating the first principal component. The data are then used to construct a phenogram, and clusters of species are formed by setting a level of similarity as a cutoff point for inclusion in a shape group. The level of overall similarity is somewhat arbitrary, but if too high a similarity is insisted upon, then there will only be one or two members in each group, and there will be many groups. Likewise if only low similarity is demanded, then only one group will be formed, and it will contain all the species. We considered the entire range of similarities that can give a distribution and mean number of species in shape groups that are similar to that found in the genera of bats.

We first investigate the morphological properties of shape groups from data generated by the uni-modal model with data from the rapid increase simulation. The shape groups are made using three, five, ten and 16 of the variables in the data set. The relationship between size and shape diversity in these groups can be seen in Figure 7. As the number of variables used in the shape analysis increases, the ability of the computer to form shape-conservative groups decreases. By the time 16 variables are entered into the analysis there is little difference in the properties of monophyletic groups and
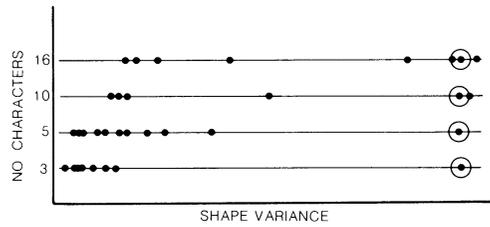

FIG. 7. Shape groups (dots) are formed using data generated from the uni-modal model with a rapidly increasing clade and analyzed for shape variance. The variances can then be compared to the variance in shape of the whole clade (circled dots). The same artificial species are put into shape groups using 3, 5, 10 and 16 characters. As more characters are used, the shape groups become less conservative.

shape groups, both fail to produce groups that are as conservative in shape as the real genera.

One of the factors we felt might affect the variance of size and shape in a clade is the length of time the simulation ran. Perhaps if the clade is maintained over a long period of time at an equilibrium number of species, results more like real data can be obtained. We felt this procedure would more closely simulate clades that are at long-term species diversity equilibrium, and might produce more distinctive shape groups as groups became more isolated with time. However, this modification of the uni-modal model fails to create shape groups consistent with real genera (Fig. 8). The shape groups formed have an average relative variance in shape of 18%. The average relative variance in size is 28%. This difference is statistically significant (Mann-Whitney $U = 221$, $n_1 = n_2 = 17$, $P < .01$). However, this difference is less than that found in real data sets. Special note should be made of the fact that neither relative variation in size nor shape rises above 50%. Based on this criterion both size and shape are conservative in these shape groups. This happens because the members of shape groups are typically closely related (all had a recent ancestor in the simulation), and the reason they occurred in the same shape group is be-
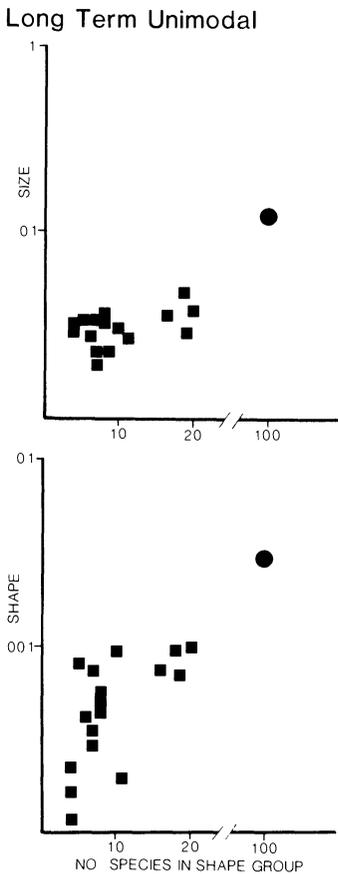
Long Term Unimodal

FIG. 8. These size and shape variances are generated using data from the uni-modal model with the long term simulation. The species have been placed into shape groups, and the size and shape variances of these groups are plotted (squares). The variances of the whole clade are also plotted (circles). Note that the variance in size and shape of the shape groups falls below the family levels of variances.

cause insufficient time has passed to allow them to diverge away from the ancestral shape. For exactly the same reason, these species tend to be about the same size as well. Because of the hyperdimensionality of the shape analysis, the convergence of two shape groups to a similar shape, but with different sizes, is rare. The fusion of two such shape groups is necessary to produce the size-variable and shape-conservative groups that are con-

sistent with real genera (see the discussion below).

The last alteration of the uni-modal model is to make the speciation rate heritable. Because the rate of morphological change is unaltered by increased speciation in the uni-modal model, the average morphological similarity is high in the rapidly increasing groups. However, these groups are not size-variable, shape-conservative groups as are real genera. Both slow-increasing and fast-increasing groups expand in size and shape in the same proportions. Therefore, the explosive groups are not overly shape conservative relative to their size variance. Using the clustering method described above once again proved ineffective at producing size-variable and shape-conservative groups with the appropriate number of species.

The Decoupled Model

The decoupled model has two modes of evolution and therefore has an alternative criterion for group formation. New groups are formed by decoupled events, while coupled events only increase the number of species in a genus. To investigate the morphological properties of these decoupled groups we can plot the changes of size and shape variances as a function of the number of species in these groups. Also plotted are the size and shape variances for the whole clade (Fig. 9). Figure 9 can be interpreted most easily by remembering the coupled/decoupled dichotomy of our model. Within a decoupled group the change of morphology is generated solely by coupled events. The differences among decoupled groups are produced largely by decoupled events. The decoupled groups are analyzed in the same way as shape groups. The relative variance in size and shape averages 33% and 5.2%, respectively. This difference is statistically significant (Mann-Whitney $U = 142,000$, $n_1 = n_2 = 388$, $P < .001$). Of a total of 388 decoupled groups, 58 have relative variances in size that exceed 50% while no decoupled group has
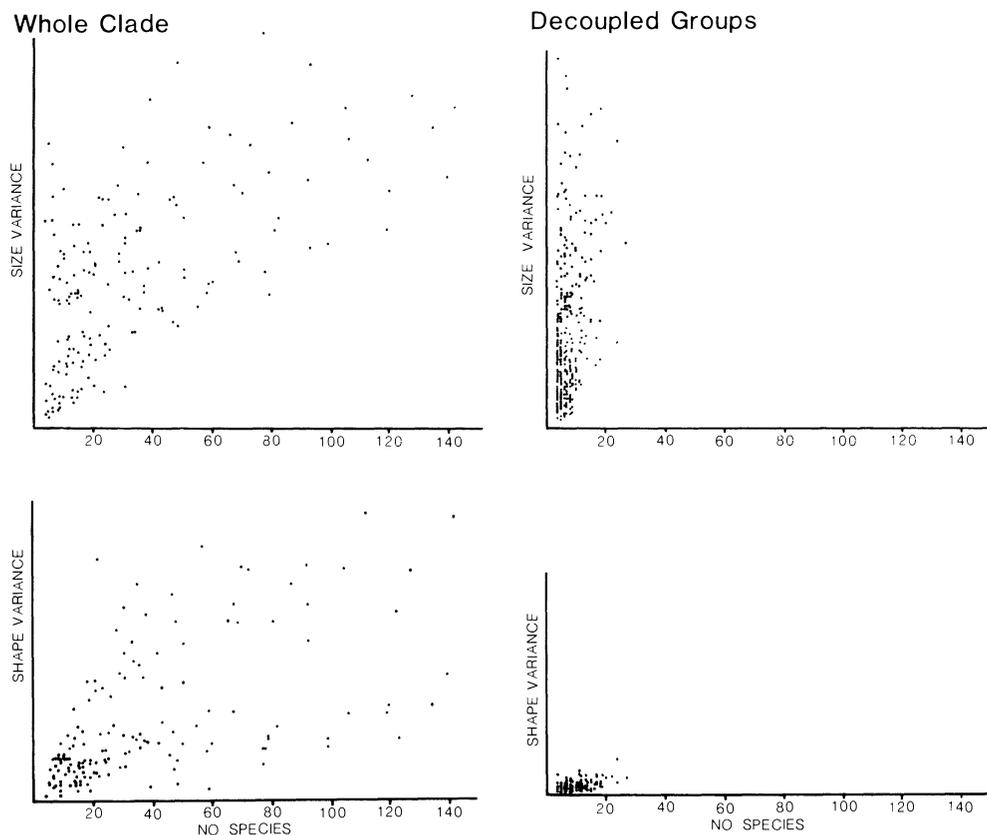
Whole Clade
Decoupled Groups

FIG. 9. The size and shape variances of whole clades and the decoupled groups within them are compared here. The plots of the whole clade are produced just as in Figure 6. At the end of each simulation the decoupled groups are analyzed for size and shape variances. Note that the variances in size of some of the decoupled groups are in the same range as the variances of clades with over 100 species. This is not true of the variance in shape.

a relative variance in shape that is greater than 50%. This difference in distribution is statistically significant ($\chi^2 = 62.6$, $P < .001$).

Results of the decoupled model can be summarized as follows: 1) size variances within decoupled groups quickly approach the size variance of the whole clade as the number of species in a group increases and 2) shape variances within these groups quickly approach an asymptote as well, but this asymptote is below the shape diversity of the whole clade. The reason that the shape variation of the decoupled group does not approach the variation in shape of the whole

clade is that the variance in shape at the group level only includes coupled events while the family level includes both coupled and decoupled events. The exact relationship between the asymptote of the shape variance of the whole clade and the asymptote of the decoupled groups is a function of the frequency of decoupled events.

The Saltational Model

The saltational model also has two modes of evolutionary change and likewise an additional criterion for forming new groups. Saltational groups are formed by saltational events, while coupled
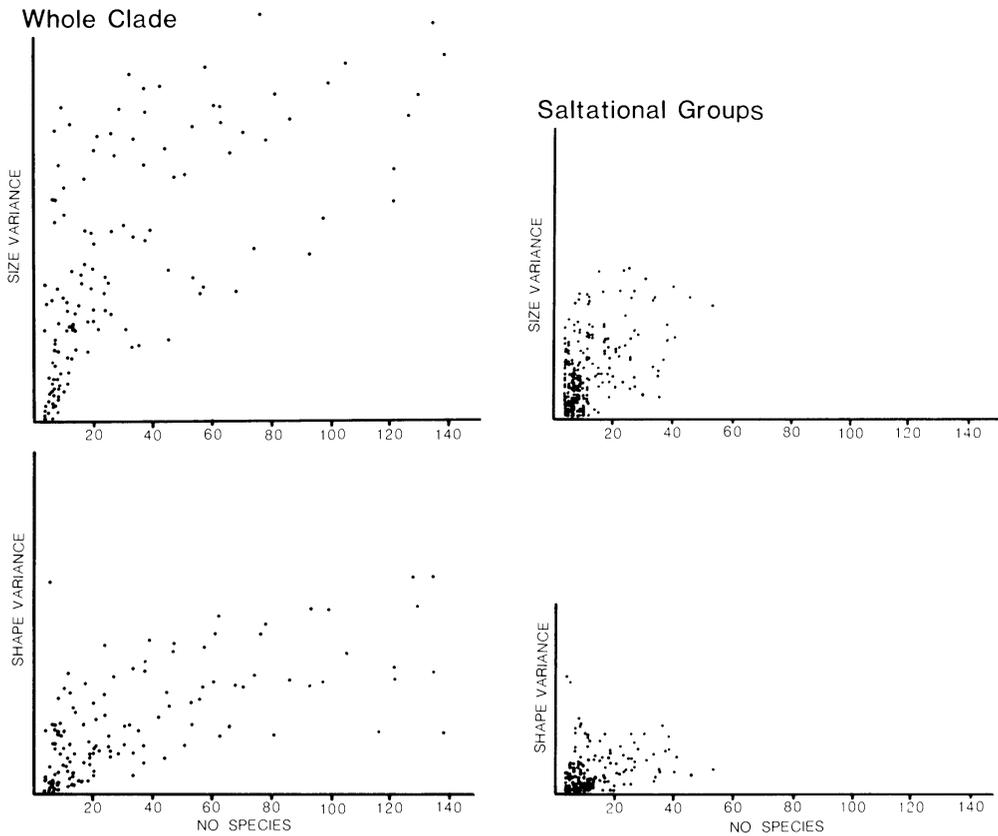
FIG. 10. This figure is similar to Figure 9 except that it represents the data from the saltational model. Note that the variances in both size and shape of the saltational groups are below the variances expected of whole clades with 100 or more species.

events only increase the number of species in a saltational group. Scattergrams of the variation in size and shape against the number of species in saltational groups are shown in Figure 10. Variance in shape behaves much as it did in the previous model, but now the variation in size is also low in the saltational groups. This happens because these groups are separated by saltational events (large changes in size *and* shape), while within saltational groups there are no such jumps. Therefore at the whole clade level there is more variation in size and shape than found in any one of the saltational groups. Because these saltational groups fail to have properties similar to real genera, we also subjected these data to shape anal-

ysis to form shape groups. The result of this analysis is shown in Figure 11. The saltational model produces shape groups that are shape and size conservative. Relative variance in size averages 13% and relative variance in shape averages 9% (relative size and shape variation are not statistically different, Mann-Whitney $U = 87$, $n_1 = n_2 = 13$, $P > .1$). None of the shape groups has a relative variance in shape over the 50% level and only one has a relative size variance over 50%.

DISCUSSION

In the three families of bats studied we consistently find that size differences explained most of the morphological variation of the characters we used. In the

phyllostomid data set the variance in size at the family level is 2.25 times greater than the variance in shape, but at the genus level variances in size average 15 times greater than variance in shape. Direct comparison cannot be made between the Phyllostomidae and the other two bat families, because of differences in the morphological measurements taken. However, comparisons can be made within the two families Emballonuridae and Molossidae where the same morphological characters are available. Such comparisons show that shape variation at the genus level is similar for the genera of both families (Fig. 5). These bat families do show differences in morphological structure. The largest difference is in the total shape variation found in each family. For the six characters available for comparison among all data sets, the variance in shape of the family Phyllostomidae is about three times as much as the variance in shape in the Molossidae or Emballonuridae. Also, the average correlation between the six characters in common among all data sets for the phyllostomids was .647 but averages .942 and .885 for the emballonurids and molossids, respectively. This difference in shape variation is consistent with the great ecological diversity of the Phyllostomidae. Within this one family are insectivores, frugivores, sanguinivores, nectarivores, and carnivores, while the Molossidae and Emballonuridae contain only insectivores. We might expect a correlation between family level shape diversity and family level ecological diversity (Findley, 1973; Ricklefs and Travis, 1980; Ricklefs et al., 1981).

Analyzing the variation in size and shape of the phyllostomids indicates that size variance of genera can closely approach that of the whole family, even though the genera contain 12 or fewer species and the family has 139 species. The variance in shape of the genus is far below that of the family. Thus, for some reason, size and shape behave differently in these genera. The molossid data generally support this finding from the phyl-
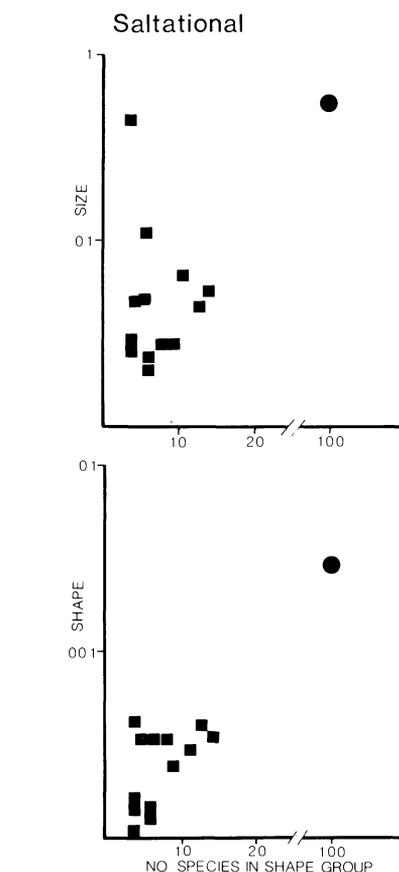

FIG. 11. These are the results of a shape analysis on the saltational model. Once again the squares represent shape groups and the circles, the whole clade. Note that all the shape groups have small relative variances in shape, and all but one group have small relative variances in size as well. The one group with a high size variance is the product of convergence.

lostomids. Once again genera are size variable (in one case with relative variance in size over 100%) and shape conservative.

The data collected on the Emballonuridae show a different pattern from the one found in the two other families. The basic difference is not in the variances in size and shape at the genus level, they are about the same as those found in the molossids (Fig. 5). The distinction is at the family level where the size variance for this family is 2.2 times that of the mo-

lossids and the shape variance is only .62 times as much. How significant this is to our models is a complex problem. First, the Emballonuridae is a small family. We used 39 species, and only four genera have more than four species in them. Our models are run using 100 or more species, so the predictions of the models may not apply to such a small family. Second, all of the models can allow for a situation where there is little shape diversification (especially when only a few species and genera are involved). As example, in the decoupled model if there are few decoupled events, and/or these events produce small changes in shape, there will be little diversity in shape in the clade. Perhaps all we can conclude from the emballonurid data is that they appear to show a different pattern in size and shape variation. At this time it is not known if other, larger families will tend to appear more like the emballonurids or the phyllostomids.

Ultimately, this paper was written to come to grips with a problem in macroevolution. What can genera tell us about the evolutionary process? The basis of our test is to study the morphological variation within and among genera and compare our findings to the predictions of the models we have constructed. Our analysis indicates that the uni-modal and the saltational models cannot produce groups that are size variable and shape conservative like the genera of the Phyllostomidae. The decoupled/adaptive zone model can produce such groups. Therefore, our results are consistent with the hypothesis that evolution proceeds as a two step process: one, diversification in size within one shape group, and two, decoupling of correlated characters to form new shape groups that may in turn diversify in size. The mechanism that produces this pattern is not known at this time, but reasonable hypotheses would include genetic/developmental constraints, ecological pressures or both.

One of the important points to understand is why the data from the uni-modal and saltational models failed to produce

patterns like the real data even when shape groups are used. This is critical because it seems plausible to assume that the reason genera are shape conservative is that shape has been used as a criterion in forming them. Our results contradict this common sense conclusion because we find genera are *too* shape conservative. Even if shape is the only criterion used, some models of evolution simply cannot produce species that can be put into such shape-conservative and size-variable groups. Understanding why this happens is our next topic.

As just mentioned, one of the most troublesome and perhaps the most obvious difficulty in modeling real genera as monophyletic groups is that real genera may be trimmed of aberrant (in shape) species in order to fit some taxonomic ideal of the genus in the mind of the systematist. Thus real genera may be actually formed phenetically on the basis of shape. This may or may not produce groups that are monophyletic. Under such a system, members of a genus might typically be members of a clade except when a species or group of species in the clade strays too far in shape from the genus average. These species would be split off to form new genera. Thus at the expense of forming new genera, shape diversity within genera could be reduced. The actual shape diversity of a genus would then be a matter of whittling down clades to the accepted norm set by the systematists of that group. The danger this possibility presents to this analysis is clear. We have just maintained that the genera of the Phyllostomidae are more conservative in shape than would be expected of clades under the uni-modal model of evolution. But "trimmed genera" (paraphyletic and polyphyletic groups) might reasonably be expected to be more shape conservative than monophyletic groups as well. The next issue is to determine the morphological properties of "trimmed genera" and find what size and shape relationships these kinds of groups can have.

Modeling "trimmed genera" is conceptually difficult because it should apply

the same trimming rules used by systematists. Trimming standards could be quite different in different taxonomic groups, and there might not be equivalence of the genus (or any other higher taxonomic level). The trimming rules, if they indeed exist, would probably entail what would be loosely called a feeling or intuition by a systematist for his group. Such things have escaped our quantification. However, one form of taxonomy is amenable to computer analysis, and that is numerical taxonomy. Using the methods of numerical taxonomy, we can analyze our artificial species and create groups in much the same way an analysis on real species might be run. For our artificial taxonomic simulation we used 16 characters and 100 species. Shape relationships among species were calculated using the sizeout method (Freeman, 1981; Lemen, 1983). An arbitrary level of similarity is set to form shape groups and the original clade can be broken into smaller groups using the UPGMA clustering technique. These shape groups have been created to be shape conservative, or in our previous terminology, they have been trimmed to contain no more than a certain amount of shape diversity. Because the level of similarity set will determine the average number of species in the shape groups, we investigated the properties of shape groups within the entire range of similarities that can produce groups with a similar distribution of species diversity to the actual numbers of species found in real genera of bats. Once the shape groups are defined they can be analyzed for variation in size and shape and compared to the diversity of the whole clade.

Two important factors affecting the results of a shape analysis are the number of characters used in the analysis and the way that the species are arranged in morphological space. The effect of the number of characters used in the shape analysis of the data from the uni-modal model with the rapidly increasing clade is shown in Figure 7. When only a few characters are used the shape groups have relatively low variances in shape as compared to the variation in shape of the whole clade. The shape groups become less shape conservative as more characters are entered into the analysis. Once 10–16 characters are used, the shape variance of the groups approaches that of the whole clade. This pattern is caused by interaction of convergence and hyperdimensionality. Shape groups formed on the basis of a few characters include species that are not closely related, but that have converged to the same shape on these few axes. The chance that species will be convergent on all axes decreases rapidly as more characters are used in the analysis. Therefore, convergence becomes unlikely if many characters are considered.

Convergence is only one way species can come to the same point in hyperspace. Another way is through common ancestry. In the uni-modal simulation species with a recent common ancestor will tend to be more similar to one another than they are to more distantly related forms. With this thought in mind we created the long-simulation uni-modal model. The idea is that if the simulation is run long enough, species have the time to wander far apart in morphospace and then, occasionally found new clades. These new clades can be widely separated in morphological space. But, because the members of these new clades will tend to look like their recent common ancestor, they will have relatively high within group similarities. Thus the long-running simulation will produce an arrangement in morphospace with more distinct subgroups than is produced by the simulation using a rapidly increasing clade. This conceptualization of the model is supported by the data from the long-simulation uni-modal model (Fig. 8). Shape-conservative groups can be formed even when 30 characters are used in the shape analysis. There are too many characters in the analysis for these shape-conservative groups to be the product of convergence alone. Instead, these groups reflect the fact that subclades within the whole clade can become more distinct in the long-running simulations. However,

for exactly the same reason that these groups are relatively shape conservative, they are also size conservative. Size and shape are both correlated with relatedness, and groups that are variable in size but conservative in shape (characteristic of real genera) cannot be formed except by convergence.

Of course, convergence can occur even in a many dimensional hyperspace. In Figure 11 the shape group with the highest variation in size is formed by two saltational groups that converged toward the same shape, but not the same size. This fusion does produce a group that is variable in size and conservative in shape. However, while convergence does take place in 16-space, it is not common enough to explain the high proportion of real genera that are conservative in shape and variable in size. Therefore if real species actually vary on at least 10–16 independent shape axes and real genera are shape conservative on at least 10–16 of these axes, then making groups based on shape will not help the uni-modal model (or the saltational model) make predictions more compatible with the real world. On the other hand, there may be processes that make convergence common at the genus level. If so, our conclusions are not valid because we have not taken such processes into account.

SUMMARY

Analysis of morphological data collected from microchiropterans indicates that genera are shape-conservative groups that often vary greatly in overall size. The patterns found in real data are compared to different models of evolution we developed. The uni-modal model and the saltational model cannot produce patterns consistent with real data, but the decoupled/adaptive zone model can.

Based on these findings, we conclude that size and shape do not diversify in the same manner. These two processes should be considered as fundamentally different evolutionary events. It is the interaction of the evolution of size and shape that produces the shape-conservative groups that can vary greatly in size.

The evidence for shape groups within families does not mean that the genus can now be precisely quantified as a certain amount of shape variation any more than species can be defined by intraspecific variation. Rather, the constraints on shape may vary from strong to weak, producing different levels of variation in shape that make the actual formation of genera difficult and perhaps a matter of art in science (Simpson, 1943; Mayr, 1943). Our analysis predicts certain properties of the genus. First, decoupled (or adaptive zone) groups will exist that differ internally in size along an allometric growth curve, and these groups may have been identified as genera by systematists. These groups will be shape conservative, but they will not always be monophyletic. This can be seen in Figure 1 where there are two decoupled groups. The group founded by species b is monophyletic, but the other group founded by A is paraphyletic. There do not have to be gaps between decoupled groups because gaps are a function of the magnitude of the decoupled jumps (or the nature of the adaptive zones). If decoupled events are always large, gaps will appear; if jumps vary from small to large, gaps may or may not exist between the shape groups (Lemen and Freeman, 1981). And last, the rates of coupled and decoupled events will determine the number of species in each genus and the shape diversity of the family.

In conclusion, genera are a product of the way groups evolve and how species diversify in morphology. The process of shape change produces groups that often show clear morphological discontinuities beyond those expected by the uni-modal model. We can speculate that the evolutionary mechanism that makes shape-conservative genera may work at higher taxonomic levels as well. This idea leaves us to wonder to what extent the typological concept of discrete hierarchical categories in systematics might have origi-

nally hinged on the shape groups produced by the interaction of two different processes, the evolution of size and the evolution of shape.

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