

The role of phylogeny in quantitative paleobiological data analysis

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Abstract.—Phylogenies provide a rich source of information that should be exploited in designing quantitative hypothesis tests in paleobiological contexts. Viewing such problems with data analysis through the prism of phylogenetically-structured comparisons can help add realism and depth to paleobiological data-analysis strategies. Two examples of the importance of adopting a phylogenetic perspective are discussed. In the first example a phylogenetic-comparative approach is used to test correlations between ecological, morphological, and biological characteristics of planktonic foraminifera. Results suggest that the presence of spines and photosynthetic symbionts in Neogene–Recent species are not adaptations to living in shallow-intermediate planktonic depth habitats. In the second, a phylogenetic-comparative approach is used to reveal the presence of morphological correlations with locomotor function in a mammalian carnivore data set. Paleontologists can play an active role in improving phylogenetically-comparative data analyses by (1) helping to develop improved phylogenies, especially those that provide better estimates of branch lengths, and (2) helping to resolve a number of outstanding issues surround the question of ancestral character state specification.

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Introduction

The popular terms “evolutionary paleontology” and “evolutionary paleobiology” suggest a dominantly phylogenetic focus within these research programs. However, the use of phylogenetic information in paleontological data analysis is often the exception rather than the rule. Such studies are typically concerned with comparing data gathered from a cross-species sample for the purpose of discovering trends, similarities, or differences. These observations are then used to test or otherwise comment on various cause-effect models. While this generalized approach has been used to address a very wide range of paleontological topics, explicit consideration of the phylogenetic context within which such comparisons reside has been—and remains—relatively rare. In some instances, this tendency can be explained by a lack of access to detailed phylogenies for many fossil clades (see Foote 1996). To a much greater extent though, this phylogeny-free approach stems from (1) a traditional focus on narrative (as opposed to analytic) styles of argument, (2) a lack of understanding of the importance of taking the concept of ancestry with descent into consideration when making comparisons between data derived from biological/paleontological entities (see Felsenstein 1985, 1988), and (3) a lack of familiarity with the methods available to implement phylogenetically-informed comparisons. Since detailed phylogenetic hypotheses are rapidly becoming available for most organismal groups, it is important for paleontologists to incorpo-

rate phylogenetic information into their quantitative hypothesis tests whenever appropriate.

At the outset, it should be recognized that statistical hypothesis-testing strategies that incorporate phylogenetic information are available for the analysis of discrete and continuous data. In both instances the analytic problem posed by phylogeny is the same. Traditional comparisons between cross-species data assume that the observations represent a random sample drawn from the population in question. A fundamental part of the statistical concept of randomness is notion of independence—that observations made on individuals drawn from the population not be influenced by the presence of other individuals in the sample and that summary statistics not be influenced by the composition of the sample. If structured, nonrandom relationships among individuals are known to exist within a sample that is to be subjected to statistical testing, these must be compensated for during the analysis. The existence of phylogenetic relationships among individuals within cross-species samples—like genetic relationships among individuals within single-species samples—represents a serious violation of this independence concept. The effect of these structured relationships is to induce a correlation between variables that is solely attributable to the pattern of phylogeny rather than being the result of any interaction between the study variables themselves.

Failure to recognize this source of constraint on variation within biological systems can lead to incorrect interpretations, especially the conclusion that significant relationships between variables exist

when in fact they do not. This is a variant of the classic Type I error where the apparent relationship is due to the operation of an extraneous variable (phylogeny) on the observed variables (see Harvey and Pagel 1991 and references therein). Moreover, the behavior of single variables (e.g., ecology, geographic distribution, behavior) often shows a significant pattern of covariation with phylogeny that cannot be understood (or adequately demonstrated) unless explicit phylogenetically-informed tests are undertaken.

There are many data analytic strategies available to examine the relation between phylogeny and continuous/discontinuous variables measured on paleontological samples. No single strategy is adequate to deal with all data analysis problems of this type. In many instances it may be the case that phylogeny does not exert a significant influence on particular systems of observations or measurements. Regardless, the possibility that phylogeny may not be an important factor in understanding a biological problem does not excuse data analysts from determining whether this is indeed the case. The fact that paleontologists know their data to be nonindependent owing to the existence of phylogenetic relationships should be sufficient to require them to eliminate this obvious source of causal explanations before considering higher-order explanations. The following two phylogeny-based data analyses are offered as examples of the methods available, the type of insight to be gained, and the necessity for integrating this approach to data analysis into the tradition of quantitative paleobiology.

Phylogeny, Ecology, and Adaptation in the Study of Planktonic Foraminifera

While the twin themes of extinction and radiation together account for the major features of the fossil record, much paleontological research over the last two decades has focused on the analysis of extinctions, especially the study of “mass extinction” events. More recently, though, attention has begun to turn to the nature of controls on the ensuing taxic radiations and the role phylogeny plays in the analysis of those radiations (e.g., Cooper and Fortey 1998). A perennial issue often embedded within such studies has to do with the functional interpretation of morphological characteristics.

Gould and Vrba (1982) drew useful distinctions between two classes of adaptational explanations. One class used historical arguments to identify adaptations as features constructed through the process of natural selection in response to a particular selective pressure (or sets of selective pressures). An example of adaptation in this sense would be the enlargement of the avian sternum to accommodate and serve as an attachment surface for the enlarged wing muscles necessary for aerobic flight. The other

class of adaptive explanations focused only on the use of a feature at a fixed point in time—typically the present for modern lineages. An example of this ahistorical usage of adaptation as a “current” utility would be the arrays of contour-shaped feathers on bird wings. Although these feathers perform an aerodynamic function for flying birds, it is doubtful that such feather arrays originated for the aerodynamic roles they now fulfill (Regal 1975; Ostrom 1979; Bakker 1986; Paul 1988; Perle et al. 1994; Padian and Chiappe 1998, but see Feduccia 1996 for counter arguments). Gould and Vrba (1982) proposed that the term adaptation be retained for the original-use concept, but that this be distinguished from the co-opted or current-use concept by applying the term exaptation to the latter. It is important to note that historical data are necessary for the correct identification of both adaptations and exaptations because the exaptive uses for a feature are defined explicitly as differing from original (adaptive) uses.

The most ready source of historical data relevant to the question of distinguishing between adaptations and exaptations resides in phylogenies. The basic principles and procedures involved in the historical analysis of adaptation can be illustrated by considering the morphology and ecology of modern planktonic foraminifera. The Neogene–Recent planktonic foraminiferal fauna is typically described as being composed of two main morphological groups: the spinose forms (e.g., *Globigerina bulloides*, *Globigerinoides sacculifer*) and the nonspinose forms (e.g., *Globorotalia truncatulinoides*, *Neoglobobiquadrina dutertrei*). This morphological distinction is used to parse species at the superfamily level in the current foraminiferal taxonomy (Loeblich and Tappan 1988) and has recently received formal phylogenetic confirmation from molecular studies (de Vargas et al 1997).

Spinose globigerinid species are further distinguished from the nonspinose globorotalids by the fact that they typically occupy shallow (mixed layer and intermediate, 0–100 m) planktonic depth habitats (see Fairbanks 1980; Fairbanks et al. 1982) and harbor algal symbionts within their cytoplasm (see Boltovskoy and Wright 1976; Lipps 1979; Bé 1982; Hemleben et al. 1988; Murray 1991). Most works on planktonic foraminiferal biology discuss the correlation between these three morphological, ecological, and biological variables in terms of functional morphology and adaptation.

For example, Lipps (1979; p. 74) stated that spines “can be interpreted as adaptations for modifying sinking by changing form resistance or density but there is little experimental evidence to show it. Nevertheless, oxygen isotope data suggest that morphology may be related to the depth habitats of species in a general way (Douglas and Savin 1978)”. Similarly, Bé (1982) linked the presence of spines as a method of maintaining control over depth habitat to the physiological role of globigerinid algal symbi-

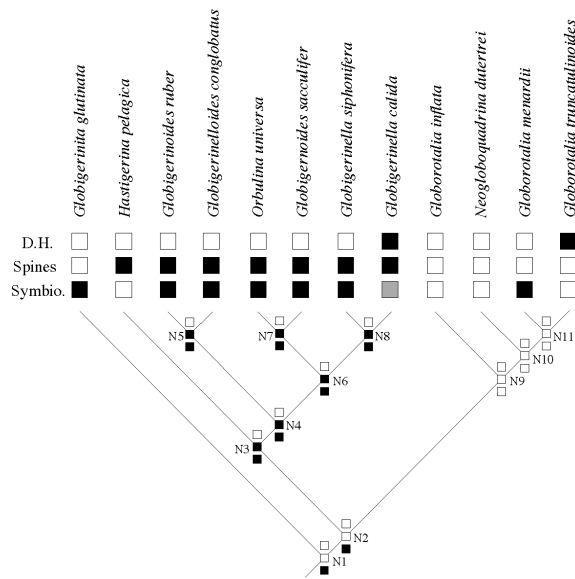


Figure 1. Neighbor-joining, maximum parsimony tree for 12 Recent planktonic foraminiferal species based on SSU rDNA sequences (from de Vargas et al. 1997) with depth habitat (D.H.), spines, and photosynthetic symbiont (Symbio.) character states for terminal species and internal nodes mapped onto the tree. Character states as follows. Depth habitat: white box = mixed layer and intermediate planktonic depth habitat (0-100 m); black box = subthermocline planktonic depth habitat. Spines: white box = absent; black box = present. Symbionts: white box = absent; black box = present. Character state data from Fairbanks et al. (1980, 1982), Bé (1982), Hemleben et al. (1988), Murray (1991). Note relatively small number of character state transitions and relatively independent patterns of association between character states changes implied by this mapping.

onts. While there is no question that the marine mixed-layer and intermediate planktonic depth habitats are populated by a greater proportion of spinose, symbiont-bearing species than are subthermocline habitats, this observation does not address the question of whether spines and the ability to harbor photosynthetic symbionts within the cytoplasm are adaptations to shallow planktonic depth habitats. In order to examine this hypothesis, historical data—in the form of phylogenies—must be included in the analysis.

Figure 1 shows a molecular phylogeny for all modern planktonic foraminiferal species for which the necessary ecological, morphological, and biological data are available. For this analysis the characters depth habitat, ability to harbor algal symbionts, and spines are all treated as binary characters as follows: depth habitat: shallow (super-thermocline), deep (thermocline and below); ability to harbor algal symbionts: present, absent; spines (present, absent). Invariably this coding simplifies a number of complexities. The planktonic foraminiferal species calcify the majority of their tests at a variety of water depths (Fairbanks et al. 1980, 1982; Bé 1982). Nevertheless, the distinction between shallow and deep-dwelling species is typically drawn at the thermo-

cline and this oceanic boundary has been used to parse the Cenozoic fauna into two ecologically-distinct groups in many previous studies (e.g., Berger, 1969; Bé 1977, 1982; Stanley et al. 1988). Similarly, planktonic foraminifera can harbor a variety of algal symbiont types, including diatoms and chrysophycophytid algae of uncertain origin (Bé 1977; Hemleben et al. 1988). Because of the limited amount of information available on the systematics of these algae, it is presently impossible to evaluate patterns of taxonomic distribution for individual symbiont species. However, the planktonic foraminiferal literature is replete descriptions of species as being symbiont-bearing or non-symbiont-bearing (e.g., Lipps 1979; Bé 1977, 1982; Hemleben et al. 1988), sometimes even using indirect and non-unique isotopic methods in attempts to assess the assessment of symbiont association back into the fossil record (e.g., D'Hondt and Zachos 1993; D'Hondt et al. 1994; Norris 1996). Accordingly, the character evaluated here is the nonspecific ability to harbor algal symbionts. Different spine morphologies (e.g., the round spines of *Orbulina universa*, the triradial spines of *Hastigerina pelagica*) are also subsumed into the spines:present character state, but, as mentioned above, the lumping of these organisms into spinose and nonspinose classes is very well established in systematic and ecological studies of the group (e.g., Bé 1977, 1982; Hemleben et al. 1988).

Parsimony-based character states for the tree's internal nodes are inferred (Maddison 1994) with uncertain character state assignments being represented a grey box (Fig. 1). While other methods for inferring ancestral character states are available, these often require information other than that contained in the simple tree topology (e.g., accurate estimates of branch lengths) or assume specific, non-null models of evolutionary change (e.g., rates of character change, [see Omland 1999]). The widely-recognized, general association between shallow and intermediate planktonic depth habitats, the presence of spines, and the presence of photosynthetic symbionts are all reflected among these species. However, once the distribution of these character states is mapped onto the independently-inferred cladogram, several problems arise in the interpretation of this character-state association as an adaptive response to change in depth habitat change.

First, the tree is characterized by relatively few character-state changes. This suggests that most species in this data set received their particular combination of character states via unaltered transfer from their ancestor. As a result, it is inappropriate to use the raw number of shallow-habitat, spine-bearing, symbiont-bearing species as evidence for the active association of these states within an adaptive system. The actual number of adaptive events involving these characters within this species group is much lower than the number of species present in the sample.

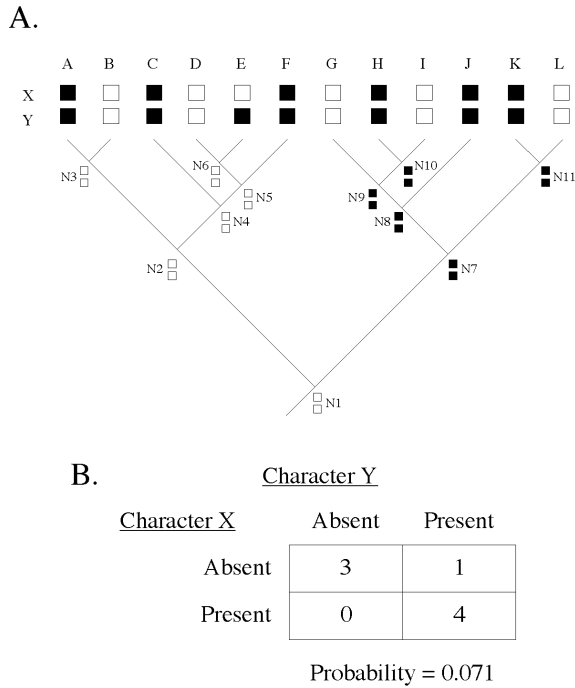


Figure 2. Ridley test of character state association for a hypothetical example. A, Cladogram of 12 hypothetical taxa showing character state distributions for two hypothetical characters and maximum parsimony reconstructions of ancestral character states. Symbol conventions as in Figure 1. B, Summary of character state changes shown on A arranged into a 2 X 2 contingency table. Note strong level of association between characters. Probability value represents result of a Fisher's Exact test for this contingency table. See text for discussion.

Second, there does not appear to be a close association between state changes among the three characters in question. In other words, a change in the state of one character cannot be used to predict changes in the states of the other characters with any great degree of certainty. This lack of correlation suggests that factors other than the three represented here must have been acting to influence the timing of state changes. Since state changes in the depth habitat, acquisition of spines, and acquisition of photosynthetic symbionts are distributed over the cladogram in patterns that are more or less independent of one another, the expected cause-effect signature of adaptation (Fig. 1) does not appear to be present.

Because the association between character state changes—the *sine qua non* of adaptive hypotheses—can be assessed over the entire structure of the cladogram, statistical tests can be devised to evaluate the null hypothesis of no association in a manner that explicitly incorporates the historical structure of these data. Previous authors (e.g., Lipps 1979; Bé 1982; Hemleben et al. 1988) have used simple counts to summarize the pattern of association between these characteristics. However, such arguments assume that each species represents an independent entity within which the characters under

study can adopt any state (see Felsenstein 1988; Harvey and Pagel 1991).

One of the simplest tests that can be used to examine the pattern of association between discrete character-state changes across a cladogram is that of Ridley (1983). This test was devised to assess patterns of association between pairs of binary characters by tabulating the character state transitions across all internal nodes within the cladogram as well as between the terminal taxa and the inferred states for their immediate hypothetical ancestors. The result is expressed as a 2 X 2 contingency table in which the cells represent sets of positive and negative associations between character state changes. For example, the hypothetical cladogram in Figure 2A shows two types of co-ordinated character state between the characters: three instances of the present condition changing to absent in both characters and four instances of the absent condition changing to present in both characters. The fact that a state change in one character is always accompanied by a state change in the other character provides evidence that the characters are linked. However, in one instance—the transition between node 6 and taxon E—a change in the state of one character occurs, but not the other. This provides evidence that the characters may not be linked. These observations are summarized on the contingency table (Fig. 2B) and their significance evaluated by Fisher's Exact test. (Note: Fisher's Exact test is preferable for this type of analysis because it is relatively more accurate at small sample sizes than other tests [e.g., χ^2].) In this instance the observed level of positive association between the characters would be expected to occur with a probability of only 0.071 under a null model of no intercharacter association. This result falls between the traditionally-accepted values of 0.100 (90%) and 0.050 (95%) for statistical significance and suggests that, despite the single example of nonlinkage, there is substantial evidence that the characters are deterministically linked. If one of these characters were a morphological character and the other were an ecological or behavioral character this would constitute evidence for direct adaptation.

Applying Ridley's test to the planktonic foraminiferal data of Figure 1 results in three different contingency tables (Fig. 3) representing all pairwise combinations of the characters. Even given the alternative ranges of character state change geometries allowed under equivalent parsimony solutions and by the uncertain status of symbionts in *Globigerinella calida*, probabilities of obtaining the observed character change distributions are well within the range allowable under a null model of no deterministic linkage. These results are inconsistent with the hypothesis of a deterministic linkage between any of these characters.

Third, the pattern of inferred ancestral character states among ancestral tree nodes suggests a far more complex history for these characters than had been

A.

<u>Depth Habitat</u>	<u>Spines</u>	
	Absent	Present
Shallow-Intermediate	0	1
Deep	1	1

Probability = 0.667

B.

<u>Depth Habitat</u>	<u>Symbionts</u>	
	Absent	Present
Shallow-Intermediate	1	1
Deep	2(1)	0(1)

Probability Range = 0.500 - 0.667

C.

<u>Spines</u>	<u>Symbionts</u>	
	Absent	Present
Absent	1	1
Present	1	1

Probability = 0.667

Figure 3. Ridley test contingency tables and associated Fisher's Exact test probabilities for patterns of pairwise character state changes shown in Figure 1. A, Depth habitat vs. spines. B, Depth habitat vs. ability to harbor algal symbionts. C, Spines vs. ability to harbor algal symbionts. Parentheses delimiters in B and C specify alternative contingency tables based on uncertainties in the character states of terminal and/or ancestral. These results suggest that the greater proportion of spinose, symbiont-bearing species in mixed layer and intermediate depth habitats is a passive by-product of speciation within the globigerinid clade. Consequently, tabulations of the raw numbers of spinose, symbiont-bearing species in this habitat yield a misleading picture of the association of these character state changes with species-specific changes in depth habitat. Statistical analysis of the Ridley test contingency tables fails to reject the null hypotheses that the observed level of association between all pairs of character state changes could be the result of a random process. (Note: a complete and highly accessible description of the construction of Ridley test contingency tables is available in Harvey and Pagel 1991:83–85).

suspected previously. For example, a shallow preferred depth habitat appears to be the primitive condition for Recent planktonic foraminifera in general. Species that have colonized deeper-water habitats (e.g., *G. truncatulinoides*) appear to have done so in an infrequent and presumably opportunistic manner. There are also no morphological characters that are consistently associated with either shallow or deep foraminiferal depth habitats. This suggests that adaptations specifically tied to depth habitat (if any) probably reside in the soft part and/or behavioral phenotype. It is interesting to note that these results are consistent with those obtained for the only other

planktonic foraminiferal lineage to be studied in this manner (MacLeod 1993). However, the extent that this result can be generalized across other planktonic foraminiferal lineages remains to be seen.

The spines of globigerinid foraminifera probably do function to help the organism resist sinking through the water column (Hutchinson 1967; Lipps 1979). But they do so in an exaptive rather than an adaptive manner. Since there are a number of non-spinose planktonic foraminiferal species that occupy shallow–intermediate planktonic habitats (see Fig. 1), and since the physical problems a small organism must overcome to maintain its position in the water column do not differ between shallow and deep planktonic habitats, the presence of absence or spines cannot be the sole determining factor. An alternative hypothesis for the function of spines is that they may provide the organism with a metabolically inexpensive means to increase greatly the area of its pseudopodial network and, in so doing, increase the opportunity for that network to come into contact with food items (Murray 1991). There is some anecdotal evidence for this in the observation that certain globigerinid species are more selective feeders than globorotalid species. However, it must be stressed that such a hypothesis must be evaluated in terms of a historical pattern of association between spine acquisition and selective feeding—as inferred by phylogenetic analysis—before it can be accepted.

In some ways the algal symbiont character map is the most interesting of the three analyzed here. Most previous summaries of planktonic foraminiferal biology have tacitly assumed that the ability to host photosynthetic symbionts was acquired independently and relatively late in the evolutionary histories of symbiont-bearing lineages. However, these phylogenetic-ecological data suggest that the harboring of photosynthetic symbionts is likely an ancestral condition for Recent planktonic foraminifera.

Additional investigations will be needed to determine when photosynthetic symbionts first became associated with modern planktonic foraminiferal lineages. As the systematics of the algal symbionts improves it will be possible to develop test more specific hypotheses regarding symbiont acquisition by particular planktonic foraminiferal lineages. In addition, as more information becomes available about Recent planktonic foraminiferal depth habitats it will be possible to repeat this analysis with a larger cohort of species to determine whether these results are representative of the modern fauna as a whole. Nevertheless, these data and results do serve to underscore the importance of adopting an explicitly phylogenetic approach to foraminiferal systematics and paleoecology as well as the types of reevaluations such studies might entail.

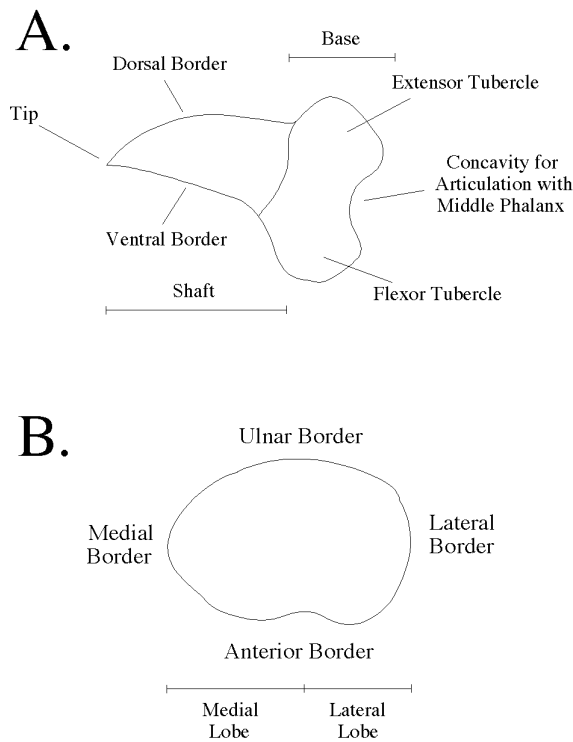


Figure 4. Line drawings of the ungual phalanx (A) and proximal radial head (B) of *Nasua narica* illustrating basic morphological features.

Phylogeny, Morphology, and Function in the Study of Mammalian Canivores

MacLeod and Rose (1993) employed a very different approach to comparative analysis in an attempt to infer the probable locomotor mode of a variety of Paleogene mammals on the basis of patterns of phenetic similarity among modern mammalian locomotor guilds. Two skeletal character complexes thought to be correlated with locomotor function in modern and ancient mammals were selected for analysis: the outlines of the distal phalanx and the proximal radial head (Fig. 4). This attempt to achieve an interpretable shape ordination for these skeletal character complexes within the modern fauna met with differing levels of success. Whereas a clear shape separation between arboreal-scansorial, cursorial, and fossorial taxa was achieved on the first two shape dissimilarity axes for the distal phalanx data (Fig. 5A), a comparable analysis for the proximal radial head data set (Fig. 5B) failed to achieve an adequate result.

These somewhat disappointing radial head results was described in the original MacLeod and Rose (1993) report. However, subsequent to that report, additional—and up to now unpublished—tests were undertaken to determine whether this result could have been due to phylogenetic covariation obscuring a subordinate functional signal. Under this model the fact that each of the four locomotor guilds was represented by species drawn from several different

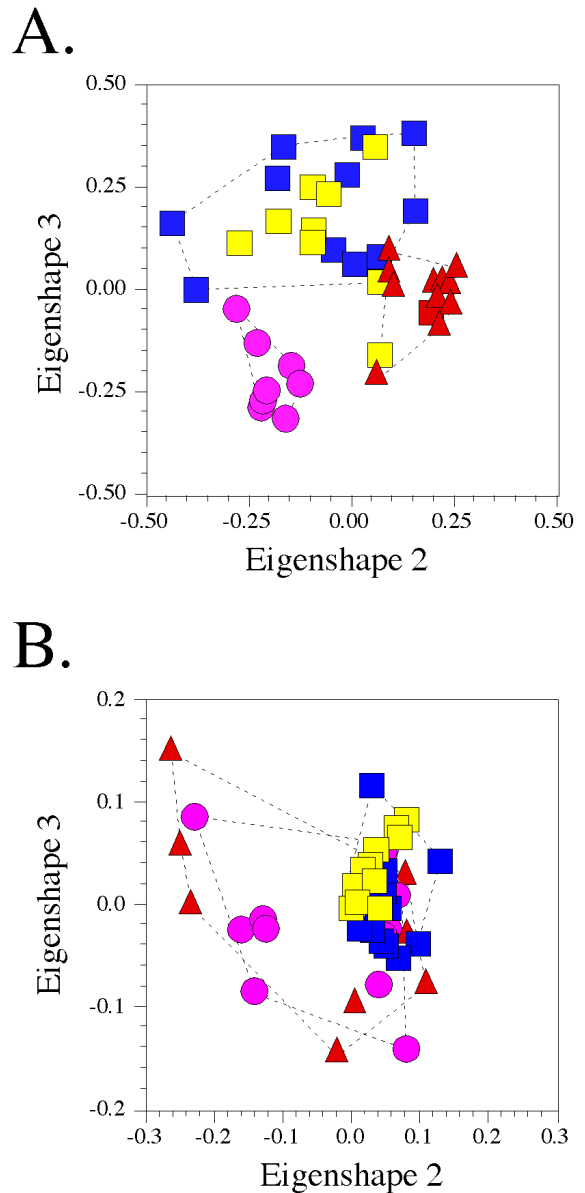


Figure 5. Results of MacLeod and Rose's (1993) shape analysis of modern mammalian distal phalanx (A) and proximal radial head (B) data. Symbols as follows: solid square = arboreal species, open squares = scansorial species, solid triangles = fossorial species, solid circles = cursorial species (see MacLeod and Rose 1993 Appendix 1 for species lists). Note that the ordination of species on the two most important distal phalanx shape-dissimilarity axes (eigenshape axes 2 and 3) separate the data set into three locomotor groups (with a small number of intergroup outliers) whereas the group separation in the proximal radial head analysis is much less pronounced. Since each locomotor group contains species from different mammalian clades, a functional signal may be overwhelmed by the phylogenetic signal in the latter analysis

resented by species drawn from several different mammalian clades might introduce a clade-specific morphological overprint to the geometric system. This overprint might interfere with a relatively weaker consistency between the shapes of radial heads that are performing the same range of functions, irrespective of their phylogenetic origins. Since the overall range of morphological variation

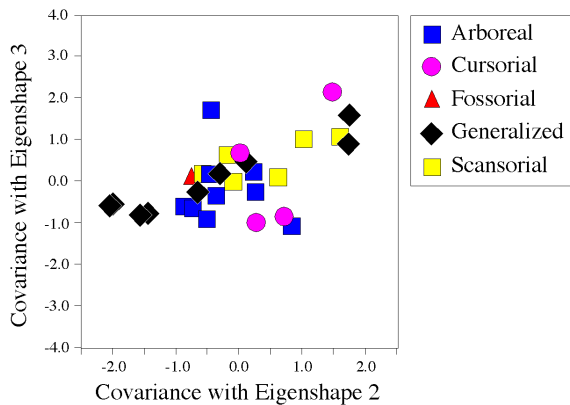


Figure 6. Results of a separate analysis of modern carnivore radial head shape. As in Figure 6, shape ordinations based on the first two shape-dissimilarity axes (Eigenshape 2 and Eigenshape 3) fail to separate locomotor groups.

was much less in the radial head data set than in the distal phalanx data set—presumably owing to the relative lack of freedom to accommodate radically different shapes enjoyed by the former—there is reason to suspect that phylogenetic covariation might play a more influential role in channeling patterns of morphological variation in the latter.

These analytic problems are exemplified by examining the plot of radial head-based outline shape ordinations for modern mammalian carnivores (Fig. 6). A scatter plot of carnivoran radial head outline shape on the two most significant linear shape-difference axes (Eigenshape 2 vs. Eigenshape 3 [see Lohmann and Schweitzer 1990; MacLeod and Rose 1993; MacLeod 1999]) shows no consistent differentiation between species belonging to different locomotor guilds.

To test the hypothesis that the lack of functionally-significant differentiation is due to a phylogenetic overprint (= observed patterns of differentiation largely reflect phylogenetic groupings), some method of statistically testing the eigenshape data for covariance with phylogenetic patterns is needed. If this hypothesis is confirmed then (ideally) some method of normalizing the raw shape data for phylogenetic covariance should be available so that the phylogenetic overprint might be stripped away. Tests for functional patterning within these residual data might be carried out to confirm or refute the original null hypothesis. This analytic design is further complicated by the fact that patterning can arise from multiple levels within the phylogenetic hierarchy.

Figure 7 shows the carnivore phylogeny used in this study (Wyss and Flynn 1993; Flynn 1996). Only the carnivore groups represented in the original MacLeod and Rose (1993) data set are shown on this cladogram. Alternative cladograms are available for this group (e.g., Wozenkraft 1996), but the Wyss and Flynn (1993) cladogram was preferred because it is one of the few that incorporates data from modern taxa and fossils (see also Flynn 1996), and its to-

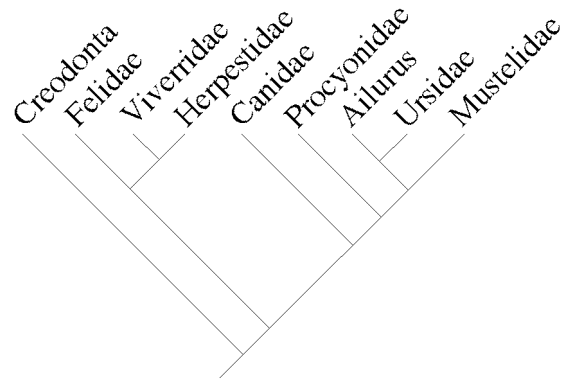


Figure 7. Carnivore phylogeny used in the phylogenetic autocorrelation analysis (after Wyss and Flynn (1993). Tree length = 83; consistency index = 0.699, retention index = 0.706.

pology agrees with molecular and biochemical data (e.g., Wayne et al. 1996).

There are several methods whereby continuous-variable data can be corrected for the effects of phylogenetic patterning: phylogenetic autocorrelation (Gittleman and Kot 1990), independent contrasts (Felsenstein 1988; Pagel 1991) and phylogenetic regression (Grafen 1989). Each method makes different assumptions about the data and each is sensitive to different types of deviations from those assumptions (see Purvis et al. 1994 and Grafen and Ridley 1996 for discussions). For the present analysis phylogenetic autocorrelation was chosen as the most appropriate method because it (1) does not assume a particular diversification mode (e.g., punctuational/gradualist), (2) does not require estimation of ancestral character states, and (3) exhibits greater robustness in the face of uncertainty about branch lengths. Although Martins (1996; see also Martins and Hansen 1996) expressed concern over phylogenetic autocorrelation's ability to detect statistically significant autocorrelations in small samples (≤ 10), the carnivore dataset analysed here (32 species) is sufficiently large to rule out sample-size effects. This is not to say that phylogenetic correlation is in all instances superior to independent contrasts, phylogenetic regression, or phylogenetic generalized least-squares for every analytic case, only that it proved a better match for these data.

Phylogenetic autocorrelation begins with the raw data and attempts to partition them into two parts:

$$y = \rho W y + \varepsilon \quad (1)$$

Where:

y = column vector of standardized trait values.

ρ = autocorrelation coefficient.

W = connectivity matrix.

ε = residual error (= phylogeny-free component value).

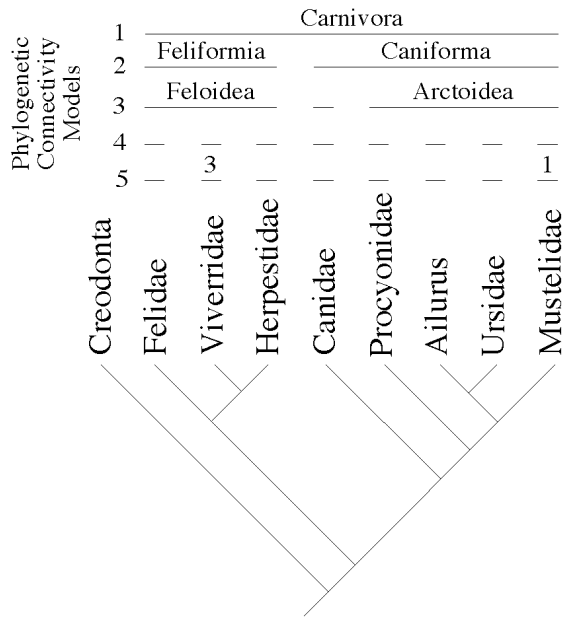


Figure 8. Phylogenetic connectivity models used to evaluate the hypothesis that the eigenshape covariance scores shown in Figure 6 exhibit a statistically-significant autocorrelation with phylogeny. All five models correspond to traditional carnivore taxonomic groupings. Level 5 represents the generic level of taxonomic/phylogenetic differentiation.

The (ρW_y) term represents that component of the original measurement values that is consistent with a phylogenetic autocorrelation model. The (ϵ) term represents that component of the original measurement values that is independent of phylogeny. If statistically-significant levels of phylogenetic autocorrelation are found in the data, equation (1) can be used to normalize the raw data into phylogeny-dependent and phylogeny-independent partitions with the resulting (in this case functional) analysis being directed at the phylogeny-independent partition.

To apply a statistical test for phylogenetic autocorrelation, a series of “connectivity models” (W) must first be specified. These models predict similarity relations between various taxic subgroups and serve as the predication templates against which the observed data are evaluated. Figure 8 shows five connectivity models based on the Wyss and Flynn (1993) phylogeny that were used to examine the carnivore radial head shape data for phylogenetic patterning.

Moran’s I statistic was used to test the hypothesis that no significant patterning consistent with the phylogenetic connectivity is present within the data (see Gittleman and Kot 1990 for an explanation of this test). Results of these tests are shown graphically in the form of phylogenetic correlograms (Fig. 9). These diagrams indicate which connectivity models yielded Moran’s I -values greater than expected under the null hypothesis of no significant phylogenetic autocorrelation ($\rho = 0.05$). On the basis

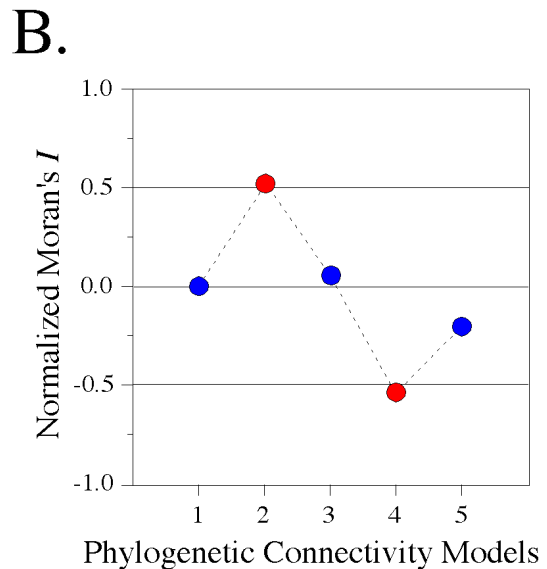
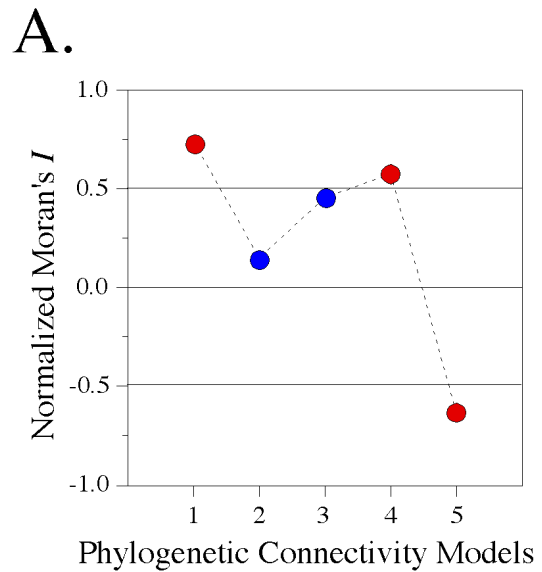


Figure 9. Correlograms illustrating the value of Moran’s I statistic for each of the phylogenetic connectivity models (see Fig. 8) A, Covariance with Eigenshape 2 data set. B, Covariance with Eigenshape 3 data set. Values of Moran’s I that exceed the critical value ($\alpha = 0.05$) indicate phylogenetic pattern models for which the data values exhibit a nonrandom correspondence.

of this analytic design, the modern mammalian carnivore data appear to be significantly autocorrelated with several different levels of phylogenetic similarity and to differ in the patterning of these correlations between the modes of radial head shape variation represented on the Eigenshape 2 and Eigenshape 3 axes. The latter result is consistent with the fact that these eigenshape axes are oriented orthogonal to each other (see MacLeod and Rose 1993; MacLeod 1999).

Once the data have been evaluated relative to the various connectivity models and significant autocorrelations identified, the normalization phase of the analysis may be undertaken. This involves using a

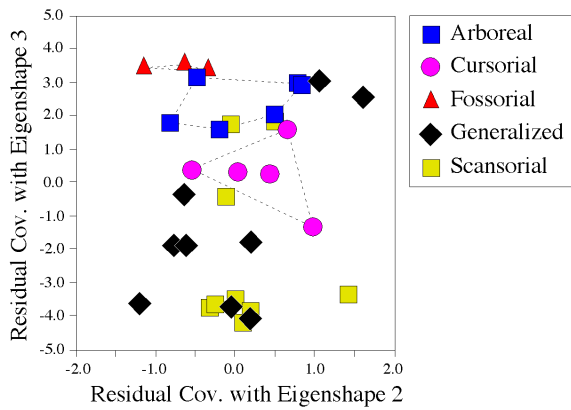


Figure 10. Scatterplot of residual covariance values obtained by normalizing the raw Eigenshape 2 and Eigenshape 3 data (Fig. 7) for the connectivity models found to be significantly autocorrelated with these data (see text for discussion). Note that once the portion of covariation associated with phylogeny is removed, the resultant shape-dissimilarity ordination exhibits a strong locomotor signal directed along Eigenshape 3.

maximum likelihood approach to estimation of the autoregression coefficient (term ρ of equation 1, see Gittleman and Kot 1990). After this result has been obtained it is an easy matter to normalize each variable for the significant phylogenetic connectivity models and achieve a “phylogeny-free” representation of residual patterns of (in this case) shape variation (Fig. 10).

Obviously, removal of the confounding effects of multiple, interfering levels of phylogenetic autocorrelation did reveal a previously-hidden, strong functional signal in these morphometric data, predominantly along the phylogeny-normalized residual Eigenshape 3 axis. Fossorial, cursorial, and arboreal species’ radial head morphologies are clearly distinguished from each other. Most of the scansorial radial heads also plot in a field of their own. Of the three scansorial outliers, two species appear to have residual radial head morphologies similar to those of arboreal forms, while the placement of the third suggests stronger residual-shape affinities with modern carnivorous cursorial species. None of these scansorial outliers are inconsistent with expectations of a scansorial life mode. Generalized mammals plot in a variety of locations within the plane through this empirical morphospace, as befits expectations for this life mode.

As a final step in the functional analysis of these data we can ask the question of whether the observed distribution of taxa along these phylogeny-free, residual-shape axes have a statistically-significant correlation with a priori-defined functional guilds. Once again, there are many ways to approach such a test. However, in order to re-illustrate the power of the autocorrelation technique it is worth noting that the same method just used to test for phylogenetic patterning can also be used to test for functional patterning within these data. This power derives from the fact that autocorrelation—unlike Pagel’s (1991)

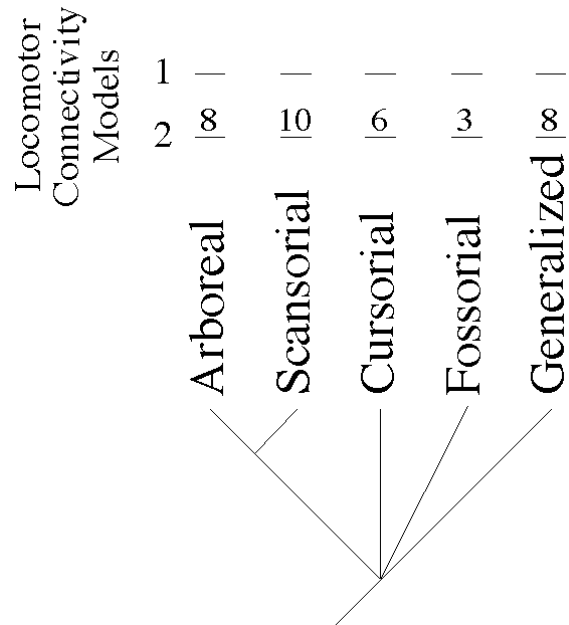


Figure 11. Locomotor group connectivity models used to analyze the association between the phylogeny-normalized residual shape-dissimilarity distributions and locomotor groupings.

independent-contrasts method or Grafen’s (1989) phylogenetic-regression procedure—is a generalized data analysis technique that can be employed in a wide range of contexts. All that is required is a model predicting the pattern of associations and a set of data to be tested.

In the functional context, the connectivity models (Fig. 11) identify species that belong to different functional groups. Moran’s I statistic is calculated in exactly the same manner with the results showing whether the test variable values covary in a manner inconsistent with (= null hypothesis) or consistent with (= alternative hypothesis) the patterning model. For the Eigenshape 3 data, the correlogram (Fig. 12) shows evidence of strong and statistically-significant functional patterning along this axis. Moreover, because Moran’s I is a nonparametric method, tests based on it are not subject to the requirement that test variable data conform to particular distributional assumptions.

Judging from these results, MacLeod and Rose’s (1993) initial working hypothesis—of a consistent functional signal residing within modern mammalian radial head outlines—is corroborated, but, qualified in that this functional signal is subordinated to a much stronger phylogenetic signal. Regardless, the equation of the residual Eigenshape 3 axis could be used to project fossil radial head outlines into the space of Figure 10 so that they could be compared with the functional component of shape variation in modern carnivore radial heads and assigned to probable locomotor categories according to the results of those comparisons (see MacLeod and Rose 1993).

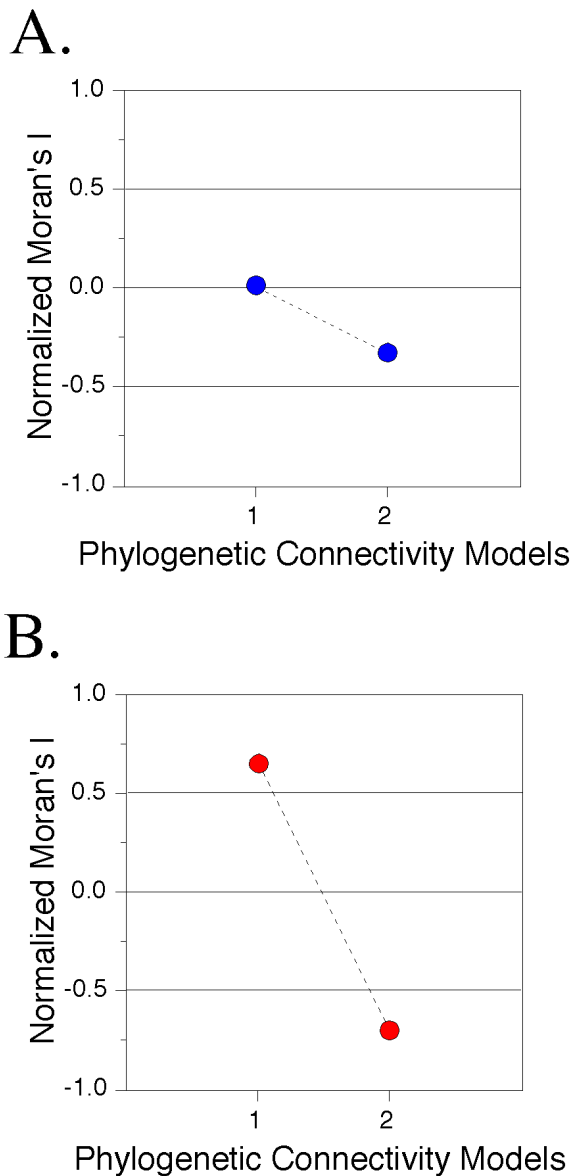


Figure 8. Correlograms illustrating the value of Moran's I statistic for each of the locomotor connectivity models (see Fig. 8) A, Phylogeny-normalized residual covariance with Eigenshape 2 data set. B, Phylogeny-normalized residual Eigenshape 3 data set. Values of Moran's I that exceed the critical value ($\alpha = 0.05$) indicate locomotor pattern models for which the data values exhibit a nonrandom correspondence. Note the lack of significant levels of locomotor group association for the residual Eigenshape 2 data set and the excellent correspondence between the predicted locomotor group pattern and the residual Eigenshape 3 data set (compare with Fig. 10).

Discussion

In 1974, at the end of a distinguished career in evolutionary biology during which he witnessed and made many substantive contributions to the “modern synthesis” of genetics, systematics, and darwinian natural selection theory, Theodosius Dobzhansky summed up the biological Zeitgeist of his times by noting that “Nothing in biology makes sense except in the light of evolution” (Dobzhansky 1974) Two decades later Gareth Nelson (1994) updated

Dobzhansky's summation for a post-cladistic generation of systematists as “Nothing in biology makes sense except in the light of phylogeny.” While these statements came toward the ends of conceptual revolutions in evolutionary theory (Dobzhansky) and systematic practice (Nelson), the implications of placing evolution/phylogeny at the heart of our understanding of life are still engendering revolutions in many biological subdisciplines.

Despite clear and well-documented arguments demonstrating the conceptual and theoretical links between phylogeny and statistical sampling theory, the current crop of canonical biometry texts are virtually silent on the issue of phylogenetic patterning in biological data. Moreover, (paleo)biometric articles routinely appear in paleontological and biological journals in which this aspect of comparative analysis is ignored. This unsatisfactory state of affairs is the result of biometric tradition which has regarded the analysis of biological data to be fundamentally similar to the analysis of physiochemical data. It is certainly true that in many experimental cases phylogeny is irrelevant to the system being studied. However, in historical sciences like paleontology/paleobiology such situations are comparatively rare.

There are also at least two general areas of phylogenetic analysis that need elaboration in order to better support quantitative data analysis. The first is branch lengths. These represent estimates of the relative amount of evolutionary diversification that has taken place subsequent to a cladogenetic event or (depending on the validity of the molecular-clock hypothesis) an estimate of the total amount of time a lineage has existed as an independent evolutionary entity. The performance of all methods in assessing the strength of a phylogenetic signal within a data set is greatly enhanced when accurate branch length estimates are available (Grafen 1989; Gittleman and Luh 1994; Purvis et al. 1994; Gittleman et al. 1996).

The second important area for development lies in the specification of ancestral character states. There are two parts to this issue: (1) the development of models for evolutionary change that support the inference of ancestral character states and (2) the testing of these models against systematic data to determine whether—or under what conditions—the assumptions that lies at the heart of these models are valid. The idea of inferring ancestral character states is uncontroversial in those instances where all descendant taxa share the same states. However, when states differ within a descendant clade the assignment of the ancestral state becomes a problem in probabilistic estimation. Maximum parsimony (MP, Swofford and Maddison 1992; Maddison 1994; Omland 1999) assumes, among other things, (1) that changes on all branches are equally likely, (2) that rates of evolution are relatively slow, and (3) that transformation probabilities are symmetric. A variety of evidence suggests that these assumptions are not

met by a large number of lineages, ancient and modern (Omland 1999).

In response to the limitations of MP, a number of investigators have recently developed alternative approaches to the estimation of ancestral character states, many based on a maximum likelihood approach (ML, e.g., Pagel 1994, 1997, 1999; Schuller 1995; Schuller et al. 1997). These methods can combine the information present in branch lengths with unequal transformation probabilities (e.g., state losses occur more frequently than gains) to provide more robust estimates of ancestor character states. At least, that's the theory. However, the larger number of parameters that must be estimated under the ML compromises the estimation accuracy of every parameter unless the estimations are based on very large data sets. Mooers and Schuller (1999) found that out of 28 example data sets, only 2 significantly improved their fit to the original data under a two-rate model. They concluded that few morphological data sets, as presently collected, contain enough detail to support a two-rate ML approach. This problem can be overcome to some extent by specifying the rate difference a priori (e.g., evaluating the hypothesis that backward change rates are twice as high as forward change rates), but such hypotheses must be generated with external data.

The lack of an external standard against which to calibrate expectations or compare estimates of ancestral character states represents by far the largest problem in this area. While it is depressingly easy to formulate alternative evolutionary models and evolutionary rate difference schemes, the only way to determine directly how well such models and schemes reflect reality is to compare the results with real ancestors. Unfortunately, the recent systematic literature contains very few morphometric examples of ancestor recognition (Prothero and Lazarus 1980; Theriot 1992), and attempts to recognise ancestors within cladistic data sets (e.g., Wagner 1998) remain controversial. The challenge for both paleontologists and neontologists then, is to come to grips with the issue of ancestors and what they tell us about evolutionary processes. Ideally, we might be able to recognize a sufficient number of ancestors to generate some expectations concerning the appropriate models to use in inferring probable ancestral characteristics from fully-resolved cladograms with accurate branch-length estimates. If this proves impossible—if ancestors really are as rare as Eldredge and Cracraft's (1980) autapomorphy criterion suggests, or if intra-lineage evolutionary rates vary widely and in nonstructured ways—comparative analytic strategies will need to switch to the development of methods that do not rely on the specification of ancestral character states (e.g., phylogenetic autocorrelation, pairwise comparison tests, [Felsenstein 1985; Maddison 2000]). However, as shown by simulation studies, such methods will almost certainly be suboptimal relative to the sorts of results that might

be produced by methods that take advantage of the information provided by accurate ancestral character states (Grafen 1989; Purvis et al. 1994; Grafen and Ridley 1996).

Summary

Quantitative analysis of paleobiological data must be about understanding the biological system from which the observations are obtained. In virtually all nonexperimental contexts, phylogeny is always an important part of that system. From a statistical point of view it is especially important to recognize, quantify, and, if possible, remove the phylogenetic component of variation in multispecies data sets. Failure to do so results in an overestimation of the degrees of freedom that characterize the data set, which, in turn heightens the possibility of committing Type 1 statistical errors.

Two examples of situations and strategies for using phylogenetic patterning in paleobiological data in hypothesis-testing situations were presented. Both are derived from published studies, but both present new results that evaluate and extend the arguments previously presented. In the first example the patterns of discontinuous morphological, ecological, and biological variables were compared with a species-level phylogeny of twelve Neogene–Recent planktonic foraminifera to examine the (previous) identification of globigerinid spines and photosynthetic symbionts as adaptations to life in shallow and intermediate planktonic depth habitats. Quantitative analysis (Ridley test) was used to examine the statistical significance of the association of character state change patterns on an independently-justified cladogram. Results suggest that neither the acquisition of neither spines nor the ability to harbor algal symbionts can be regarded as an adaptive correlate of a shift in depth habitat. Spines were acquired by the globigerinid lineage well after the transition to a shallow–intermediate depth habitat had been made by ancestral species. Similarly, the lack of photosynthetic symbionts among certain globorotalid species appears to be an example of secondary loss. While neither of these character states meets the expectations of adaptations to relatively shallow depth habitats, both probably function exaptively (Gould and Vrba 1982) within such habitats for the species that possess them.

The second example used patterns of morphometrically-quantified outline shape variation on the first two latent shape-dissimilarity (= eigen-shape) axes for a set of proximal radial head morphologies from modern carnivores. These patterns were compared with a phylogeny for this group to determine whether the lack of discrimination between locomotor guilds on the shape dissimilarity axes was the result of phylogenetic patterning within the raw data. A Moran's *I*-test of these data detected

significant association between the phylogenetic and morphometric data sets which, when removed by phylogenetic autocorrelation analysis, revealed the expected pattern of ecological differentiation. These results suggest that it is possible to improve the functional interpretation of fossil vertebrates by using morphometrics to quantify geometric comparisons between modern (= control group) and fossil (= test group) species and that such comparisons will be greatly enhanced if phylogenetic information is taken into explicit consideration.

In both instances recourse to phylogenetic data clarified the hypotheses being tested and resulted in a more nuanced and information-rich understanding of the biological systems under consideration. These examples illustrate the needed to take phylogenies into account whenever multispecies comparative data analyses are being designed to test (paleo)biological hypotheses. In addition, a phylogenetically-informed approach to biometry provides a practical rationale for the further development of phylogenetic systematic methods and results, especially in the areas of branch-length estimation and specification-identification of ancestral morphologies. If paleobiologists heed the words of Dobzhansky and Nelson—that nothing in biology can be understood except in the light of evolution-phylogeny—and use phylogenetic information to inform and improve their statistical hypothesis tests, our understanding of life's past, present, and perhaps its future can be brought into sharper focus.

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