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PHYLOGENETIC ANALYSIS OF COVARIANCE BY COMPUTER SIMULATION

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Abstract.—Biologists often compare average phenotypes of groups of species defined cladistically or on behavioral, ecological, or physiological criteria (e.g., carnivores vs. herbivores, social vs. nonsocial species, endotherms vs. ectotherms). Hypothesis testing typically is accomplished via analysis of variance (ANOVA) or covariance (ANCOVA; often with body size as a covariate). Because of the hierarchical nature of phylogenetic descent, however, species may not represent statistically independent data points, degrees of freedom may be inflated, and significance levels derived from conventional tests cannot be trusted. As one solution to this degrees of freedom problem, we propose using empirically scaled computer simulation models of continuous traits evolving along "known" phylogenetic trees to obtain null distributions of *F* statistics for ANCOVA of comparative data sets. These empirical null distributions allow one to set critical values for hypothesis testing that account for nonindependence due to specified phylogenetic topology, branch lengths, and model of character change. Computer programs that perform simulations under a variety of evolutionary models (gradual and speciational Brownian motion, Ornstein-Uhlenbeck, punctuated equilibrium; starting values, trends, and limits to phenotypic evolution can also be specified) and that will analyze simulated data by ANCOVA are available from the authors on request. We apply the proposed procedures to the analysis of differences in home-range area between two clades of mammals, Carnivora and ungulates, that differ in diet. We also apply the phylogenetic autocorrelation approach and show how phylogenetically independent contrasts can be used to test for clade differences. All three phylogenetic analyses lead to the same surprising conclusion: for our sample of 49 species, members of the Carnivora do not have significantly larger home ranges than do ungulates. The power of such tests can be increased by sampling species so as to reduce the correlation between phylogeny and the independent variable (e.g., diet), thus increasing the number of independent evolutionary transitions available for study. [Allometry; behavioral ecology; body size; branch lengths; comparative method; computer simulation; home range; physiological ecology; statistics.]

The comparative method in evolutionary biology can be used to denote any and all uses of interspecific comparisons to draw evolutionary inferences (e.g., Ridley, 1983; Cheverud et al., 1985; Felsenstein, 1985; Grafen, 1989, 1992; Gittleman and Kot, 1990; Brooks and McLennan, 1991; Harvey and Pagel, 1991; Lynch, 1991; Martins and Garland, 1991; Carpenter, 1992b; Gittleman and Luh, 1992; Pagel, 1992; Pagel and Harvey, 1992; Losos and Miles, 1994). Because species usually will not represent independent data points in the statistical sense, conventional parametric and nonparametric methods are inappropriate for hypothesis testing with interspecific data. Several explicitly phylogenetic statistical methods have therefore been developed. In addition to solving purely statistical problems, the incorporation of phylogenetic information (topology, branch lengths) into analyses of patterns seen among living (and/or extinct) species (e.g., phenotypic variation and covariation) sometimes allows inferences to be made concerning evolutionary processes (e.g., [co]adaptation, constraints, trade-offs, rates of evolution) (e.g., Huey and Bennett, 1987; Coddington, 1988; Lauder and Liem, 1989; Losos, 1990; Baum and Larson, 1991; Garland et al., 1991; Garland, 1992; Miles and Dunham, 1992).

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Most of the phylogenetically based "comparative methods" have focused on testing for character correlations, often with continuous traits such as body size, limb proportions, metabolic rate, or home-range area (Felsenstein, 1985, 1988; Grafen, 1989, 1992; Lynch, 1991; Martins and Garland, 1991; Garland et al., 1992; Gittleman and Luh, 1992; Pagel, 1992; and reviewed in Harvey and Pagel, 1991: chap. 5). In addition to testing for character correlations, however, biologists often wish to compare mean phenotypes among groups of organisms defined on the basis of phylogenetic affinity or on behavioral, ecological, or physiological criteria. In comparative physiology, for example, analyses of variance (ANOVAs) and analyses of covariance (ANCOVAs) (e.g., Tanner, 1949; Sokal and Rohlf, 1981; Packard and Boardman, 1988) are used routinely to compare metabolic rates among taxa (e.g., field metabolic rates of birds and mammals [Nagy, 1987]). Comparative biochemists have compared in vitro enzyme activities of fishes that differ in feeding strategies and locomotor habits (e.g., Hochachka and Somero, 1984). At the chromosomal level, Burton et al. (1989) compared the nuclear DNA content of four families of bats. Many other examples can be found in behavioral ecology, including Barclay and Brigham's (1991) comparison by ANCOVA of frequency of echolocation calls of bats that differ in foraging mode and comparisons of phenotypes of animals with different diets, social systems, geographic distributions, or habits (e.g., Milton and May, 1976; Garland, 1983; Garland et al., 1988; Harvey and Pagel, 1991; Janis, in press). Sometimes such comparisons will fall strictly along phylogenetic lines. For the species listed in Figure 1, for example, the carnivores (Canidae, Hyaenidae, Felidae) and omnivores (Ursidae, Procyonidae, Mustelidae, Viverridae) fall within a lineage (order Carnivora) that separated about 70 million years ago from herbivores in the orders Perissodactyla and Artiodactyla (together with Proboscidea, Hyracoidea, Sirenia, and [cladistically speaking] Cetacea, the "ungulates"). Other comparisons might cut across clades.

Unless all of the species being compared radiated more-or-less instantaneously from a common ancestor (a star phylogeny, e.g., Felsenstein, 1985: fig. 2; Martins and Garland, 1991: fig. 3a), their phenotypes probably are not statistically independent. Harvey and Pagel (1991:38–48) reviewed three biological reasons for lack of independence, which they termed time lags, phylogenetic niche conservatism, and phenotype-dependent responses to selection (see also discussions in Ridley, 1983; Cheverud et al., 1985; Felsenstein, 1985, 1988; Coddington, 1988; Grafen, 1989; Gittleman and Kot, 1990; Lynch, 1991). The time-lag reason is perhaps most intuitive. Once speciation has occurred, it simply takes time for divergence to occur either as a result of random genetic drift or in response to natural selection for new phenotypes (i.e., adaptation) (cf. McKinney, 1990b:106). The statistical consequences of nonindependent data points can include inflation of Type I error rates (due to overestimated degrees of freedom) when testing hypotheses, lowered power to detect significant relationships, and inefficient estimates of evolutionary parameters (e.g., Felsenstein, 1985, 1988; Grafen, 1989; Lynch, 1991; Martins and Garland, 1991).

Conventional ANOVAs and ANCOVAs use F statistics for hypothesis testing. Critical values for F statistics are determined by reference to standard tabular values (e.g., Rohlf and Sokal, 1981: table 16), with degrees of freedom determined by the number of groups being compared and the total number of observations (e.g., species) in the data set. Unfortunately, the hierarchical phylogenetic relationships of species within most comparative data sets make it difficult to know how many degrees of freedom actually obtain.

We therefore propose the use of empirically scaled computer simulations of characters evolving along "known" phylogenetic trees to obtain empirical F distributions for hypothesis testing. These null distributions are different from those that would ordinarily be obtained from such techniques as jackknifing and bootstrapping or from randomization tests (Sokal and Rohlf, 1981; Crowley, 1992). A typical application of such resampling

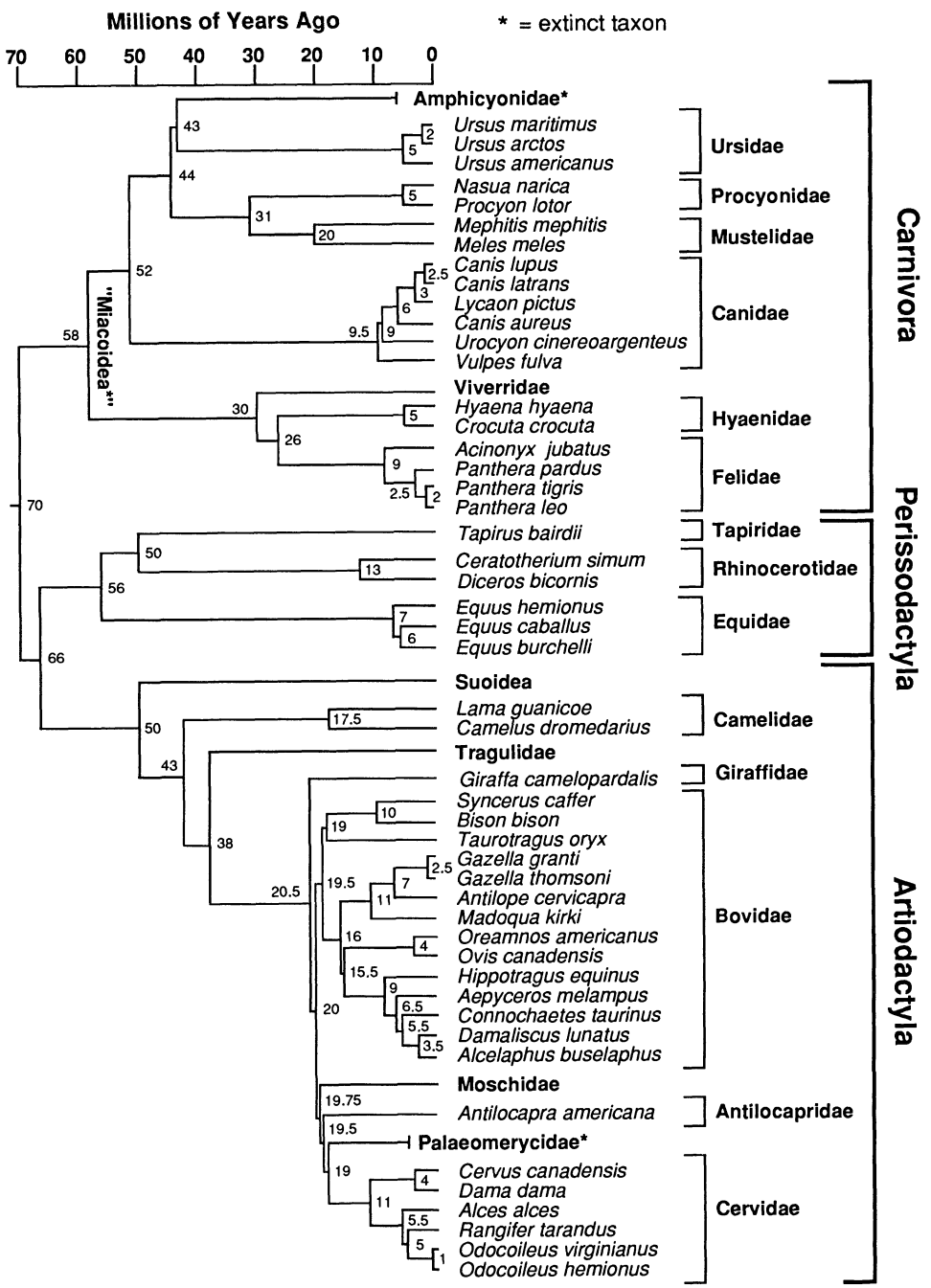

FIGURE 1. Hypothesis of phylogenetic relationships for 19 species of Carnivora and 30 species of ungulates (modified from Garland and Janis, 1993). This "best current compromise" cladogram, with branch lengths in units of estimated divergence times, is a composite derived from a variety of published and in-press sources (see Appendix). Most branch lengths are taken from first fossil appearances, supplemented with molecular clock estimates. As with any phylogeny, this is a "work in progress," to be updated as new information becomes available.

methods would sample or reshuffle across the tips of a phylogeny, ignoring cladistic structure (cf. Maddison and Slatkin, 1991; Carpenter, 1992a); thus, it would not fully account for the phylogenetic hierarchy (Harvey and Pagel [1991:152–155] discussed randomization tests that can be appropriately applied to phylogenetically independent contrasts). Perhaps some sort of hierarchical resampling scheme could be devised, but computer simulation methods would seem to allow greater flexibility for exploring alternative models of evolutionary change. In principle, the computer simulation (or Monte Carlo) approach can be applied to hypothesis testing with any type of statistical test; Martins and Garland (1991) originally developed it for testing correlated evolution.

We illustrate the simulation approach with an analysis of differences in home-range area between two clades of mammals, the Carnivora (primarily carnivores but including some omnivores) and ungulates (exclusively herbivores in the present subset of species) (Fig. 1). Differences in home range between trophic categories (e.g., Fig. 2) are of long-standing interest to behavioral and physiological ecologists. For mammals, herbivores tend to have smaller home ranges than do carnivores (Milton and May, 1976; Harestad and Bunnell, 1979; Garland, 1983; Calder, 1984; Harvey and Pagel, 1991:30–31, 122; Dunstone and Gorman, 1993; and refs. therein). In simple (and adaptive) terms, this difference has been explained by the higher trophic level occupied by carnivores, which means that their food (herbivores) is more widely dispersed and offers fewer joules per unit home-range area than does the food of herbivores (plants). The data for the 49 species that we analyzed are part of a larger study (Garland, 1992; Garland et al., 1992; Garland and Janis, 1993; Janis, in press) and are used here primarily for heuristic purposes. The generality of our results should be tempered by the knowledge that only a sparse sample of the diversity of living carnivores and herbivores is included. However, these 49 species do appear to represent an unbiased sample, with respect to home-range area, of Carnivora and ungulates. Moreover, the same conclusion—that home-range area does not differ significantly between Carnivora and ungulates—is reached when the data are analyzed by the proposed simulation methods, by phylogenetic autocorrelation procedures, and by an independent-contrasts approach. Our sample data also help point out the limitations of comparative analyses in which phylogeny is perfectly confounded with the independent variable (diet, in the present case).

Methods

Specification of Phylogeny

All of the tests proposed herein require specification of the phylogenetic topology and branch lengths for the species under study. This requirement is consistent with those for phylogenetically based methods for estimating and testing evolutionary correlations (Felsenstein, 1985, 1988; Grafen, 1989, 1992; Harvey and Pagel, 1991; Lynch, 1991; Martins and Garland, 1991; Garland et al., 1992). To avoid circularity (but see de Queiroz, 1989: appendix 4), the phylogenetic information should be based on data other than and independent of the phenotypic characters to be studied (Felsenstein, 1985, 1988; Brooks and McLennan, 1991; Harvey and Pagel, 1991; Martins and Garland, 1991; Sillen-Tullberg and Moller, 1993). The composite phylogeny used here is depicted in Figure 1; its evidential support is presented in the Appendix.

Specification and Implementation of the Model of Evolutionary Change

The simplest model for the evolution of continuous traits is Brownian motion, in which the successive changes of a character are independent of each other (uncorrelated) and of the character's starting value and are equally likely to be positive or negative. Brownian motion is a good model for purely random genetic drift, with no selection; it may also be a reasonable model for some forms of selection (Felsenstein, 1985, 1988; Charlesworth, 1990; and

refs. therein). Because it is a random process with no constraints, Brownian motion change can sometimes yield periods of rapid (almost punctuational) change as well as apparent trends over time (Lande, 1986; Bookstein, 1988: fig. 2).

In the context of phylogenetic simulations, Brownian motion can be implemented by drawing one random change for each branch segment from a normal distribution and rescaling the variance of the normal distribution in proportion to each branch segment. If branch lengths in units of time (or some other metric that varies among segments) are used, then a Brownian motion simulation is conventionally termed "gradual," to indicate that characters usually experience greater changes along longer branches. If, however, all branch segments are set at 1, then the simulation can be termed "speciational" (Rohlf et al., 1990). The concept behind a speciational model is that all change occurs in association with speciation events; setting all branch segments equal to 1 is simply a convenient way to simulate this process under Brownian motion. Martins and Garland (1991) termed such simulations "punctuational," but speciational is a preferable term because punctuational usually implies change occurring in only one daughter. Huey and Bennett's (1987) original implementation of a minimum-evolution (=squared-change parsimony of Maddison, 1991) algorithm for studying correlated evolution assumed speciational change. Martins and Garland (1991) and Maddison (1991; his weighted squared-change parsimony) generalized the Huey/Bennett algorithm for nonequal branch lengths (i.e., gradual Brownian motion evolution) (see also Garland et al., 1991).

Brownian motion evolution can be simulated with our PC-based PDSIMUL computer program, which is similar to but more flexible than the CMSIMUL program of Martins and Garland (1991). The means, variances, and correlation of the bivariate distribution from which random changes are drawn (input distribution of Martins and Garland [1991]) can be user specified. By default, PDSIMUL and CMSIMUL set variances of the input distribution such that simulated data sets (i.e., the phenotypes of the species at the tips of the phylogeny) will, on average, have variances equal to those of the real data set (see Martins and Garland, 1991). Because ANOVAs are based on relative amounts of variation within versus among groups, this scaling of variance is immaterial for the analysis of data sets simulated under Brownian motion. (The same is true for analyses of correlations [Martins and Garland, 1991], although estimation of regression slopes does depend on the actual proportionality of variances of different characters.)

As many workers have emphasized, both the inference of phylogenetic trees themselves and inferences about how other characters have evolved along given trees depend crucially on the model of change assumed (e.g., Felsenstein, 1985, 1988; Friday, 1987; Rohlf et al., 1990; Harvey and Pagel, 1991; Maddison, 1991; Maddison and Slatkin, 1991; Martins and Garland, 1991). Although Brownian motion models of character change lead to relatively simple analyses, many other models are possible, at least some of which are probably more biologically realistic (Felsenstein, 1985, 1988; Martins and Garland, 1991). The evolutionary relevance of P values derived from simulated data depends on the realism of the simulation conditions (cf. Stanley et al., 1981; Carpenter, 1992a, 1992b). Accordingly, we have also developed several other simulation models (available in PDSIMUL), all of which allow some parameters to be empirically scaled.

One model is the Ornstein–Uhlenbeck (OU) process, which has been described by Felsenstein (1988:464):

> Uhlenbeck & Ornstein defined a diffusion process that has a linear [force] returning [a particle] to a central point. At any instant the expected change is toward that point, at a rate proportional to the particle's distance from the point. The change varies around this in a way otherwise typical of Brownian motion.

According to Felsenstein (1988), the OU process is a good model for the motion of a population wandering back and forth on a selective peak under the influence of ge-

netic drift, with natural selection acting as an elastic band. The OU process "could also serve as the model for the wanderings of an adaptive peak in the phenotypic space, where the optimum remains within a relatively confined region" (Felsenstein, 1988: 464–465). An important feature of an OU model of character change "is that it gradually 'forgets' past history" (Felsenstein, 1988:465). The stronger the force tending to return species' phenotypes to their starting point, the more rapidly a set of species will become statistically independent—the more rapidly history will be "forgotten."

PDSIMUL implements the OU process as follows. Beginning at the bottom of the specified tree, a bivariate change is drawn for each branch segment. This random movement of the trait, similar to Brownian motion, occurs in conjunction with a tendency for the trait to be "pulled" towards a user-specified adaptive peak. At any time, the strength of this pulling is proportional to (1) the distance between the trait and the peak and (2) the decay constant, also user specified. A decay constant of zero would be equivalent to simple Brownian motion. An infinitely large decay constant would mean that a lineage's phenotype would decay back to the adaptive peak along each branch segment.

If the adaptive peak is specified to be the same as the starting values of the traits (at the root of the phylogeny), then stabilizing selection is being modeled by the OU decay constants. If the position of the adaptive peak is specified to be different from the starting values of the traits, then the phenotypic peak will move to this new position, either monotonically or stochastically, as specified in PDSIMUL; here, both directional and stabilizing selection are being modeled. Under gradual OU evolution, both the random movement of the trait and its movement due to the pull of the adaptive peak are modeled to take place continuously in time (or whatever the units of branch length) along each branch segment. In speciational OU evolution, the random movement is modeled to take place instantaneously at speciation events and then to decay back towards the specified adaptive peak along branch segments of unit length. (Mathematical details are in the PDSIMUL documentation.)

Another evolutionary model is punctuated equilibrium, in which character change is allowed only at speciation events and only in one of the two daughter lineages. This model agrees with the original descriptions of punctuated equilibrium, in which genetic and phenotypic change is postulated to occur only in small peripheral populations that bud off from a large "parent" species (Eldredge and Gould, 1972; Gould and Eldredge, 1977). Simulation algorithms by Raup and Gould (1974) and by Colwell and Winkler (1984) have followed this model.

None of the models described above provide for any explicit limits on how large or small a character can evolve to be. In many cases, however, one may be willing to specify limits to the realistic range of character values (see also discussions in Friday, 1987). For example, the smallest mammal has probably never been less than 1–2 g. The largest known terrestrial mammal is the fossil *Baluchitherium* (also known as *Indricotherium* or *Paraceratherium*), which probably weighed no more than about 15,000 kg (mean adult mass about 11,000 kg, M. Fortelius and J. Kappelman, pers. comm.; but see Economos, 1981; Alexander, 1989). Various explanations for such patterns are possible, such as "reflection inside the borders of a fitness range" that is "suggestive of . . . boundaries of a more or less fixed ecological niche" (Bookstein, 1988:381, 389) (see also McKinney, 1990a, 1990b). More generally, limits to phenotypic evolution may be attributable to any type of biomechanical, developmental, physiological, or genetic "constraint" (e.g., Rose et al., 1987; Werdelin, 1987; Garland, 1988; Pease and Bull, 1988; Lauder and Liem, 1989; Vrba, 1989; Charlesworth, 1990; McKinney, 1990b; Weber, 1990; Zelditch et al., 1990; Janson, 1992; Losos and Miles, 1994; also, Schmidt-Nielsen [1984] and Alexander [1989] discuss possible physical limits on *Baluchitherium*).

Many options for implementing limits are possible (see the PDSIMUL documen-

tation), and we have chosen one of the simplest for purposes of illustration (termed "Replace" in PDSIMUL). If a change to be drawn would exceed the specified limits, it was replaced with a new change.

Use of the foregoing limits procedure, as with our implementation of the OU model, will lead to variances for the tip data that may be smaller than those for the real data. It is not the differences in variances per se that affect ensuing F distributions, but rather the nature and interactions of the algorithms implementing the OU process and/or the limits to how far traits can evolve. Even with limits imposed, however, the variances of simulated data can generally be made to match those of real data by increasing the parameter for expected variances at the tips in the PDSIMUL program.

We have used limits of 0.03 and 15,000 kg for body mass (see Fig. 2). The former is the lower end of the size range of the least weasel, *Mustela rixosa*, the smallest living member of the Carnivora; the latter is the approximate upper size of *Baluchitherium*, the largest fossil ungulate (M. Fortelius and J. Kappelman, pers. comm.). We used limits of 0.001 and 2,000 km^2 for (nonmigratory) home-range area, based on inspection of values presented in Harestad and Bunnell (1979) and Goszczynski (1986) (e.g., the largest reported home range for a member of the Carnivora is for the wolverine, *Gulo gulo*, about 1,000–1,500 km^2). All simulations were done on a $\log_{10}$ scale; thus, specified limits were -1.5229 and 4.1761 for body mass and -3.0 and 3.3010 for home range. We used starting values of -0.3010 ($\log_{10}$ of 0.5 kg) for body mass and -1.8036 (on the $\log_{10}$ scale) for home-range area. This body mass is the approximate size of the last common ancestor of Carnivora and ungulates, assuming *Protungulatum* to be representative (see Appendix). The home-range value was estimated by a least-squares linear regression through the origin fitted to standardized independent contrasts (Felsenstein, 1985; Garland et al., 1992), yielding a slope of 1.2616 ($r = 0.7212$). This line was positioned through the point (2.0051, 1.1057), which represents the independent contrasts estimates for the root node, and extrapolated to -0.3010 (=$\log_{10}$ of 0.5 kg). Forcing through the values estimated for the root node is appropriate because these values are also estimates of the overall group means, weighted by phylogeny; in the present case, they are quite similar to means calculated in the conventional way (1.9037 and 1.1666, respectively). Maddison (1991) showed analytically that the independent contrasts estimates for the basal node are also identical to the squared-change parsimony or minimum evolution (Huey and Bennett, 1987; Martins and Garland, 1991) estimates (both are computed by the CMSINGLE program of Martins and Garland [1991]). These starting values are outside the range exhibited in the real data set for living species—such a pattern is not uncommon for mammals (e.g., MacFadden, 1986: fig. 4 on horses).

Creating Empirical Null Distributions for Hypothesis Testing

Once the phylogenetic topology, branch lengths, and model of evolutionary change have been specified, then a large number of computer simulations are run, typically 1,000. For each set of simulated tip data, various statistics (e.g., mean, variance, sums of squares, correlation) can be computed for each group specified a priori. These empirically scaled null distributions form the basis for hypothesis testing.

We have written computer programs to read in sets of simulated tip data, calculate various statistics, and output the results to standard ASCII files. These ASCII files can then be analyzed with conventional statistical packages.

For example, to compare the mean body mass of two clades, 1,000 simulated data sets would be produced. For each of these, PDANOVA would be used to compute the within- and between-group sums of squares, mean squares, and corresponding F ratio, as in a conventional ANOVA. A statistical package is then used to read in the ASCII file of F ratios and compute the 95th percentile of this distribution. If the

F ratio for the real data set (which can be obtained from PDSINGLE or from a conventional statistical package) exceeded the upper 95th percentile of the empirical null distribution, we would conclude that the two clades differed significantly in mean body mass. Conventional statistics were done with SPSS/PC+ version 3.1.

Available Programs

All of the programs discussed herein (named "PD__" as an acronym for "Phenotypic Diversity") are available from the authors on request.

PDTREE graphically displays trees and allows editing, including transforms of both branch lengths (see Garland et al., 1992) and phenotypic data. It will translate file format between that compatible with the Martins and Garland (1991) programs (__.INP) and that used with PDSINGLE and PDANOVA (__.PDI).

PDSIMUL simulates gradual and speciational Brownian motion, Ornstein–Uhlenbeck, or punctuated equilibrium evolution of two continuous characters (with specified correlation) along a specified phylogeny. It also allows specification of limits to how far phenotypes can evolve. It can be used with trees that contain multifurcating nodes (except with punctuated equilibrium).

PDSINGLE analyzes a single set of real data for two continuous characters and computes descriptive statistics (means, medians, variances, correlation), ANOVA, ANCOVA with one variable as covariate, and Levene's test for relative variation (Schultz, 1985).

PDANOVA analyzes multiple sets of simulated data, as produced by PDSIMUL or CMSIMUL. It performs the same computations as in PDSINGLE and writes a series of ASCII files as output, which can then be entered into conventional statistical packages for computation of empirical null distributions of F statistics, etc.

RESULTS

To illustrate the proposed method, we consider data on home-range area in relation to body mass for 49 species of mammals. The current working phylogeny for these species is shown in Figure 1 and described in the Appendix; phenotypic data are listed in Table 1.

Hypothesis Testing with Computer-Simulated Null Distributions

Figure 2 shows a scattergram of home-range area versus body mass (data presented in Table 1), suggesting that carnivores and omnivores as a group ($n = 19$; all in the order Carnivora) have larger home ranges than do herbivores ($n = 30$ ungulates in the orders Artiodactyla and Perissodactyla). A conventional ANCOVA (Table 2) of the log-transformed data yields an F statistic for the diet (=clade) effect of 23.97, which is highly significant with the nominal 1 and 46 degrees of freedom and a critical value of 4.049 for $\alpha = 0.05$. The pooled within-groups slope from the ANCOVA is 0.997, which is also highly significant ($F = 47.40$, df = 1,46, $P < 0.001$). Because omnivores do not appear distinct with respect to home range, we have lumped them with carnivores for simplicity.

The nominal critical value of 4.049 (Table 2; from harmonic interpolation, Rohlf and Sokal, 1980: table 16) for testing the main effect and covariate is most likely invalid for hypothesis testing because the species data points are probably not statistically independent, leading to overestimation of degrees of freedom (nominally 1 and 46). Table 2 also shows the critical value for $\alpha = 0.05$ (95th percentile) for 1,000 data sets simulated in five different ways. Under a gradual Brownian motion model with zero correlation between the two characters (as used by Martins and Garland, 1991), the critical value ($\alpha = 0.05$) for hypothesis testing of the clade (=diet) effect is approximately 68.07, yielding $P = 0.229$ for the real data set. Under a model of speciational change (punctuational of Martins and Garland, 1991), also with zero correlation, the critical value for hypothesis testing is approximately 52.61 and $P = 0.186$. Therefore, if these two traits have evolved in accord with either model, then we must conclude that home-range area,

TABLE 1. Body mass and home-range areas for 19 species of Carnivora and 30 ungulates. These are the same 49 species analyzed by Garland and Janis (1993) for correlations between maximal running speed and limb proportions.

Species	Body mass (kg)	Home range (km^2)	Reference
Ursus maritimus	265.0	115.6	DeMaster and Stirling, 1981; Schweinsburg and Lee, 1982
Ursus arctos	251.3	82.8	Janis, in press
Ursus americanus	93.4	56.8	Janis, in press
Nasua narica	4.4	1.05	Kaufmann, 1962; Kaufmann et al., 1976
Procyon lotor	7.0	1.14	Harestad and Bunnell, 1979
Mephitis mephitis	2.5	2.5	Harestad and Bunnell, 1979; Bjorge et al., 1981
Meles meles	11.6	0.87	Janis, in press
Canis lupus	35.3	202.8	Harestad and Bunnell, 1979
Canis latrans	13.3	45.0	Janis, in press
Lycaon pictus	20.0	160.0	Janis, in press
Canis aureus	8.8	9.1	Janis, in press
Urocyon cinereoargenteus	3.7	1.1	Janis, in press
Vulpes fulva	4.8	3.87	Harestad and Bunnell, 1979
Hyaena hyaena	26.8	152.8	Janis, in press
Crocuta crocuta	52.0	25.0	Janis, in press
Acinonyx jubatus	58.8	62.1	Janis, in press
Panthera pardus	52.4	23.2	Janis, in press
Panthera tigris	161.0	69.6	Janis, in press
Panthera leo	155.8	236.0	Janis, in press
Tapirus bairdii	250.0	2.0	Eisenberg et al., 1990 (estimate from density)
Ceratotherium simum	2,000.0	6.65	Janis, in press
Diceros bicornis	1,200.0	15.6	Janis, in press
Equus hemionus	200.0	35.0	Janis, in press
Equus caballus	350.0	22.5	Janis, in press
Equus burchelli	235.0	165.0	Janis, in press
Lama guanicoe	95.0	0.5	Franklin, 1982; Cajal, 1991 (estimate from territory size and densities)
Camelus dromedarius	550.0	100.0	Kohler-Rollefson, 1991
Giraffa camelopardalis	1,075.0	84.6	Janis, in press
Syncerus caffer	620.0	138.0	Janis, in press
Bison bison	865.0	133.0	Janis, in press
Taurotragus oryx	511.0	87.5	Janis, in press
Gazella granti	62.5	20.0	Janis, in press
Gazella thomsonii	20.5	5.3	Janis, in press
Antilope cervicapra	37.5	6.5	Janis, in press
Madoqua kirki	5.0	0.043	Janis, in press
Oreamnos americanus	113.5	22.75	Janis, in press
Ovis canadensis nelsoni	85.0	14.33	Harestad and Bunnell, 1979
Hippotragus equinus	226.5	80.0	Janis, in press
Aepyceros melampus	53.25	3.8	Janis, in press
Connochaetes taurinus	216.0	75.0	Janis, in press
Damaliscus lunatus	130.0	2.2	Janis, in press
Alcelaphus buselaphus	136.0	5.0	Janis, in press
Antilocapra americana	50.0	10.0	Harestad and Bunnell, 1979; Janis, in press
Cervus canadensis	300.0	12.93	Harestad and Bunnell, 1979
Dama dama	55.0	1.3	Putnam, 1988
Alces alces	384.0	16.1	Harestad and Bunnell, 1979
Rangifer tarandus	100.0	30.0	Janis, in press
Odocoileus virginianus	57.0	1.96	Harestad and Bunnell, 1979
Odocoileus hemionus	74.0	2.85	Harestad and Bunnell, 1979

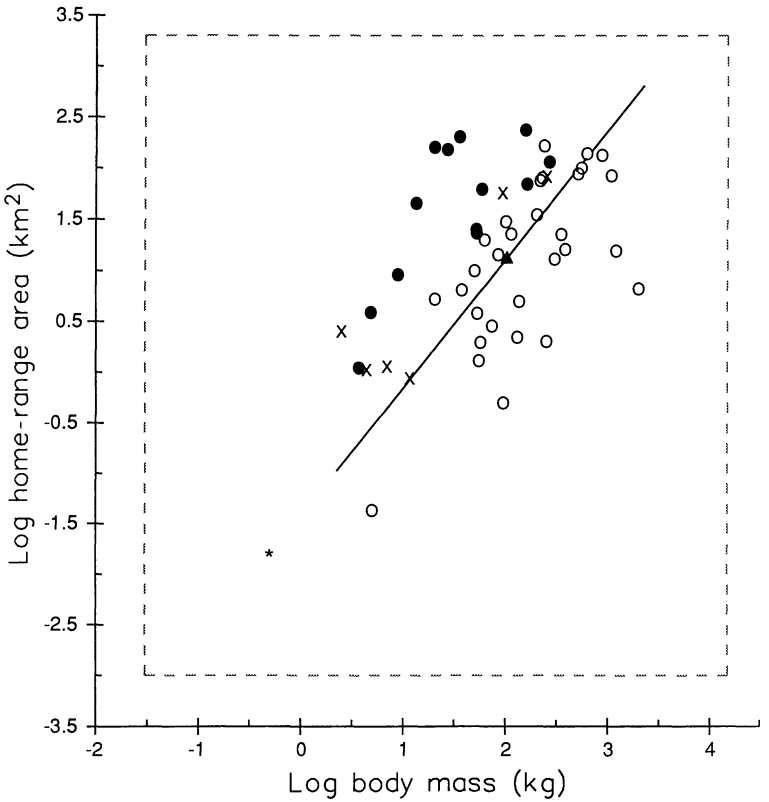

FIGURE 2. Log-log relationship between home-range area and body mass in 30 species of ungulates (○) and 19 species of Carnivora (● = carnivores; X = omnivores [*Ursus arctos, Ursus americanus, Nasua narica, Procyon lotor, Mephitis mephitis, Meles meles*]) (data from Table 1). The solid line is a least-squares linear regression fitted to standardized independent contrasts and positioned through the bivariate mean (▲) estimated by independent contrasts. For simulations, the asterisk (*) represents the ancestral starting value (−0.3010 for $\log_{10}$ body mass, −1.8036 for $\log_{10}$ home-range area) and the dashed line represents the specified limits to evolution (30 g and 15,000 kg for body mass, 0.001 and 2,000 km² for home range).

adjusted for body size, does not differ significantly between clades. Our conclusion about a possible group difference is thus different when phylogenetic nonindependence is incorporated through computer simulation techniques. However, the correlation between home-range area and body mass is highly significant under either model of change (Table 2; critical values were 17.02 and 15.20 for gradual and speciational change, respectively, with F = 47.40 for the real data).

Gradual and speciational Brownian motion models are among the simplest that can be employed for simulating correlated evolution of continuous characters, but they are not necessarily the most realistic. Lack of realism can be shown in a number of ways. For example, of the 1,000 data sets simulated under the gradual model, the largest $\log_{10}$ body mass value obtained was 5.056, or 113,763 kg, which is about an order of magnitude larger than any known extant or extinct terrestrial mammal (although blue whales may exceed 100,000 kg, and some sauropod dinosaurs may have approached or exceeded 40,000–50,000 kg [Alexander, 1989]). The smallest value obtained was −1.232, or 0.0586 kg, which is greater than the limit of 0.03 kg proposed above for Carnivora but below the size of the smallest fossil ungulate (e.g., the primitive artiodactyl *Diacodexis*, which was probably about 0.8 kg, based on measure-

TABLE 2. Analysis of covariance comparing $\log_{10}$ home-range areas of members of the Carnivora (including both carnivores and omnivores) with those of ungulates (all herbivores), with $\log_{10}$ body mass as the covariate. Critical values for F statistics and associated significance levels are presented for conventional tabular values (from harmonic interpolation, Rohlf and Sokal, 1981: table 16), which would be strictly appropriate only if all species radiated instantaneously from a common ancestor (a star phylogeny), and based on analyses of data simulated along the phylogeny shown in Figure 1 under different models of character change. For all five simulations, the starting phenotypic values (at the root of the phylogeny) were 0.5 kg for body mass and 0.031623 km^2 for home-range area, and limits on character evolution were set as 0.03–15,000 kg for body mass and 0.01–1,000 km^2 for home-range area. Values for covariate and explained are not relevant for the group difference hypothesis being tested. Last three simulations were done with a correlation of 0.7212, as indicated by an independent contrasts analysis of the real data (so the F for real data is exceedingly unlikely to be judged "different" at $P <$ 0.05).

					Conventional tabular		Brownian motion				Gradual with limits and trend[c]		Ornstein–Uhlenbeck[d]		Punctuated equilibrium[e]	
							Gradual[a]		Speciational[b]							
Source of variation	Sum of squares	df	Mean square	F	Critical value	P	Critical value	P	Critical value	P	Critical value	P	Critical value	P	Critical value	P
Main effect	8.48	1	8.48	23.97	4.049	<0.001	68.07	0.229	52.61	0.186	76.19	0.215	47.22	0.147	56.62	0.192
Covariate	16.77	1	16.77	47.40	4.049	<0.001	17.02	0.004	15.20	0.001	177.28	0.552	151.71	0.545	561.69	0.998
Explained	17.40	2	8.70	24.58	3.199	<0.001	43.60	0.153	31.93	0.104	158.07	0.742	113.79	0.707	359.31	0.999
Error	16.28	46	0.35													
Total	33.67	48	0.70													

[a] Mean means (±2 SE) were 1.900 ± 0.024 and 1.162 ± 0.030 for $\log_{10}$ body mass and $\log_{10}$ home-range area, respectively; mean variances were 0.502 ± 0.018 and 0.709 ± 0.024; mean Pearson correlation was −0.008 ± 0.020. Pseudorandom number seed was 2.

[b] Mean means were 1.908 ± 0.030 and 1.149 ± 0.038, respectively; mean variances were 0.501 ± 0.016 and 0.701 ± 0.022; mean correlation was 0.016 ± 0.018. Seed was 3. Speciational evolution (Rohlf et al., 1990) was referred to as punctuational by Martins and Garland (1991); this model allows equal probability of change in both daughter species rather than only in one daughter, as was originally specified for punctuated equilibrium. It is mathematically equivalent to gradual change along a phylogeny with all branch lengths set to be equal.

[c] Mean means were 1.886 ± 0.026 and 1.145 ± 0.030, respectively; mean variances were 0.489 ± 0.016 and 0.681 ± 0.022; mean correlation was 0.695 ± 0.012. Seed was 6.

[d] Mean means were 1.881 ± 0.020 and 1.134 ± 0.024, respectively; mean variances were 0.395 ± 0.010 and 0.575 ± 0.016; mean correlation was 0.703 ± 0.010. Seed was 4.

[e] Mean means were 1.898 ± 0.022 and 1.167 ± 0.024, respectively; mean variances were 1.216 ± 0.022 and 1.947 ± 0.024; mean correlation was 0.904 ± 0.004. Seed was 5.

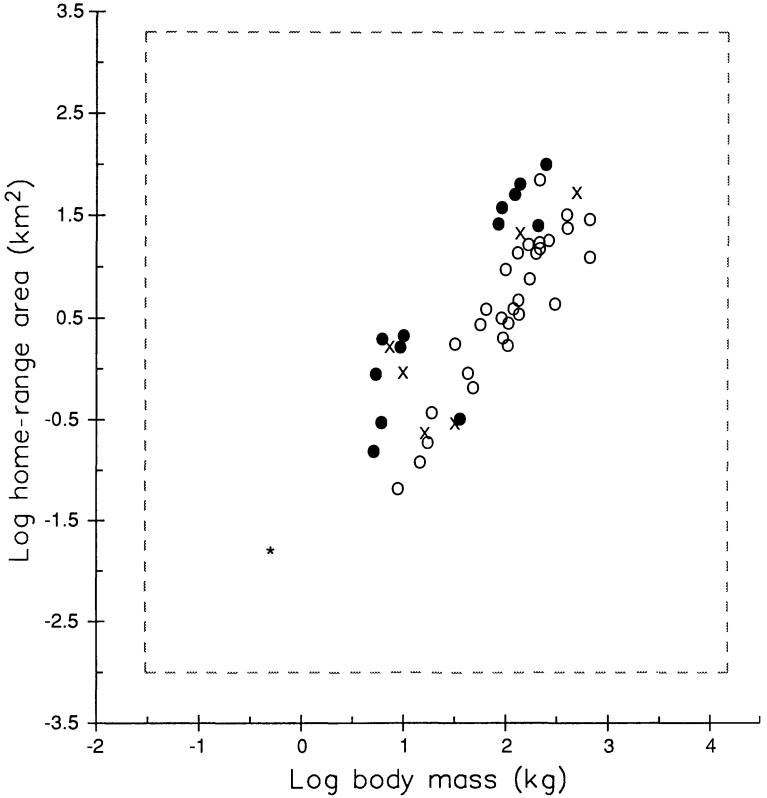

FIGURE 3. Example of computer-simulated home range and body mass data (from "Gradual with limits and trend" column in Table 2). The distribution from which changes were drawn was scaled so as to yield, on average, simulated tip data with variances similar to those of the real data (as listed in Table 1). The correlation of the distribution was set to be 0.7212, as indicated by analysis of standardized independent contrasts. Starting point for simulations is indicated by the asterisk (*) (see text and Fig. 2 caption). Limits to how far the characters could evolve (dashed lines; see text and Fig. 2 caption) were set using the "Replace" option of the PDSIMUL program. Other symbols are as in Figure 2. For this data set, the *F* statistics from the ANCOVA are 139.05 for body mass and 22.88 for diet (carnivores plus omnivores vs. herbivores).

ments of lower second lower molar lengths and using equations in Janis [1990]). For the 1,000 simulated speciational data sets, the maximum and minimum $\log_{10}$ body mass values were 5.697 (497,737 kg) and −2.523 (0.003 kg). Clearly, realistic limits can be exceeded even though variances of the simulated data are, on average, the same as those of the real data (the default in both PDSIMUL and CMSIMUL); similarity of variances does not guarantee similarity of minima or maxima. Moreover, starting simulations at the mean $\log_{10}$ body mass of the values exhibited by the extant species in the data (1.9037 = 80.1 kg) is very unrealistic for mammals living 70 million years ago. We therefore also simulated data under more complicated and, presumably, more realistic models.

The third model in Table 2 is like the first, gradual Brownian motion, but with parameters in PDSIMUL set to yield three differences (see Methods for reasons for choosing the particular values): (1) the correlation of the evolutionary changes to be drawn was set at 0.7212, as indicated by an independent contrasts analysis of the real data; (2) limits to phenotypic evolution ("Upper Bounds" and "Lower Bounds" in PDSIMUL) were set, as described in the Methods and Figure 2 caption; and (3) an algorithm was used gradually and mono-

tonically to shift (see documentation accompanying PDSIMUL, which also allows stochastic trends) the mean of the character distributions from the specified starting values (see Fig. 2) to the mean of the real tip data. The third of these conditions simulates a gradual trend for increasing body mass (cf. McKinney, 1990b) and home-range size. Such a model has been termed "diffusion with drift" by Berg (1983), where drift refers to the force pulling the particles (species) in a particular direction (see McKinney, 1990b:84–87). Figure 3 shows one example of data simulated under this model. Under this model, the critical value for the group effect was 76.19, yielding $P = 0.215$.

The fourth model in Table 2 uses the Ornstein–Uhlenbeck process (see Felsenstein, 1988). The following parameters were used in PDSIMUL: (1) the correlation was set at 0.7212; (2) the same limits to phenotypic evolution were set; (3) the position of the adaptive peak, initially at the starting values, was increased monotonically ("Final Means" in PDSIMUL) to yield tip data with means similar to those of the real data; and (4) "Decay Constants" (the strength of the "spring" mimicking stabilizing selection in the OU process) were set to 1.0×10^{-8} for both traits. Here, the critical value for $\alpha = 0.05$ is lower, $F = 47.22$, but still too high to indicate a significant difference in Carnivora and ungulate home ranges ($P = 0.147$).

The final model in Table 2 is punctuated equilibrium, in which change occurs only at speciation events and only in one daughter, chosen randomly by PDSIMUL. The same starting values and limits to evolution were used, and the correlation of evolutionary changes was again set to 0.7212. Final Means were set to 4.45 and 4.65 for $\log_{10}$ body mass and $\log_{10}$ home-range area, respectively, which were the values determined by trial and error to yield realistic tip means (see Table 2 footnotes). This model yielded a critical value of $F = 56.62$ and an insignificant $P = 0.192$.

Regardless of the simulation model employed, we cannot reject the null hypothesis of no significant difference in home-range area between Carnivora and ungulates for our sample of 49 species. The apparent difference in Figure 2—and commonly accorded ecological and evolutionary significance—is not very unusual when judged against a null model that includes both chance (as in conventional statistics) and phylogeny.

Phylogenetic Autocorrelation

Gittleman and Kot's (1990; Gittleman and Luh, 1992) phylogenetic autocorrelation programs were applied by H.-K. Luh to the data of Table 1. The transformation exponent for branch lengths, α, was estimated as 3.550 for $\log_{10}$ body mass and 4.006 for $\log_{10}$ home-range area; autocorrelation coefficients were estimated as 0.65 and 0.32, and the proportions of variance explained by phylogeny (true R^2) were 0.607 and 0.148, respectively. These parameter estimates were used in producing putatively phylogeny-free residuals. Figure 4 presents a scatterplot of these residuals: the ANCOVA yielded F statistics of 47.41 for body mass ($df = 1,44$, $P < 0.001$) and 0.58 for the clade effect ($df = 1,44$, $P = 0.46$) (two degrees of freedom are lost for estimating the α's used to transform branch lengths). Again, omnivores do not form a distinct group (cf. Fig. 2).

Phylogenetically Independent Contrasts

Felsenstein's (1985; Garland et al., 1992) independent contrasts approach can also be modified to compare means of different clades or ecological groups, at least in some cases. In the independent contrasts approach, each tip species or inferred node is compared with its closest relative in the data set. If two sister clades are compared, then the single basal contrast contains all of the information concerning possible clade differences; all other independent contrasts are within one clade or the other. Thus, we can compare the value of the standardized basal contrast to the distribution for all other standardized contrasts, which should be normal if appropriate standardization has been achieved (see Garland et al., 1992). Sokal and Rohlf (1981:

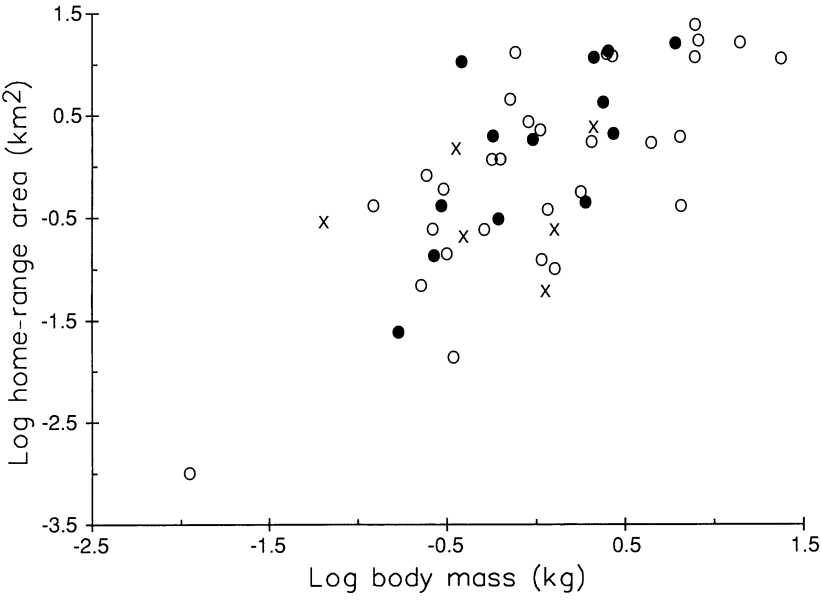

FIGURE 4. Putatively phylogeny-free residuals of $\log_{10}$ home-range area and $\log_{10}$ body mass (phylogeny from Fig. 1, data from Table 1) from a phylogenetic autocorrelation analysis (Gittleman and Kot, 1990). The ANCOVA of these residuals indicates no significant difference in mass-corrected home-range areas between herbivores (○) and carnivores (●) plus omnivores (X) ($P = 0.46$).

231) described an appropriate two-tailed test (modified for the present context):

$$t_s = \frac{\text{value of single observation} - \bar{x} \text{ of test distribution}}{\text{SD of test distribution} \cdot [(n + 1)/n]^{0.5}},$$

where the test distribution is the distribution of all standardized contrasts except the basal contrast and n is the number of contrasts in the test distribution ($n = 47$ here). Because the direction of subtraction of contrasts is arbitrary, the mean of the test distribution is zero and the sign of the basal contrast is irrelevant. Also, the variance of contrasts is computed as the simple sum of the squared contrasts, divided by $n - 1$ (see Garland et al., 1992: appendix 3). Applying this test to contrasts for our data on $\log_{10}$ body mass (from Table 1), we obtain

$$t_s = \frac{0.000170098}{0.000122639 \cdot [(47 + 1)/47]^{0.5}} = 1.372,$$

with degrees of freedom $n - 1 = 46$. The critical value for a t distribution with df = 46 is 2.0125 for $\alpha = 0.05$. We therefore conclude that the basal contrast is not unusual and hence that the two clades do not differ in mean body mass ($P > 0.16$).

To apply independent contrasts to clade differences in home-range area, we must allow for differences in body mass (Fig. 2). Figure 5 shows a bivariate scatterplot of standardized independent contrasts in $\log_{10}$ home-range area versus $\log_{10}$ body mass; the linear regression through the origin (formulas in Garland et al., 1992) serves as an estimate of the expected home-range contrast for a given body-mass contrast, using only the 47 nonbasal contrasts. In our sample, ungulates tend to be larger than members of the Carnivora (although not significantly so), and based on previous studies, we also expect them to have smaller home ranges. So, we expect the basal contrast to fall below the regression line (a one-tailed test). Figure 5 shows that it does, but not quite enough to be considered significant as compared with a one-tailed 95% prediction interval (dashed line). This prediction interval is computed following Equation 5.21 of Neter et al. (1989: 168), using all except the basal contrast (n

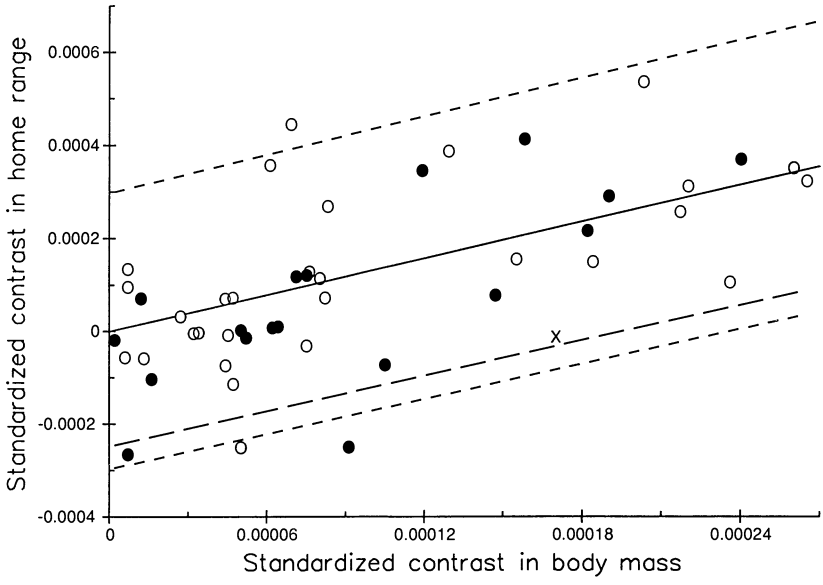

FIGURE 5. Bivariate scatterplot of 48 standardized independent contrasts in $\log_{10}$ home-range area and $\log_{10}$ body mass (redrawn from Garland et al., 1992: fig. 5a). Contrasts within Carnivora (●) and the ungulates (○) are shown, along with the basal contrast (X). In this figure, body mass contrasts have been "positivized" (Garland et al., 1992), and the signs of home-range contrasts changed accordingly. Solid line is least-squares linear regression through the origin for the 47 nonbasal contrasts (slope = 1.3171, $r^2 = 0.544$, $F = 54.90$, $P < 0.0001$). Short dashed lines are the two-tailed 95% prediction interval; long-dashed line is the one-tailed 95% prediction interval (although not immediately obvious from this graph, these prediction intervals become wider farther away from the origin) (formulas from Neter et al., 1989:167–170). The basal contrast falls within these intervals, which indicates no significant difference in home-range area between Carnivora and ungulates.

= 47). As illustrated in Garland et al. (1992: fig. 4) for a 43-species data set, branch lengths for home-range area provide more even standardization if they are log transformed. A reanalysis of Figure 5 with log-transformed branch lengths for home-range area (not shown) yields a qualitatively identical conclusion.

DISCUSSION

Analysis of variance and covariance, including multiple regression with dummy variables (Sokal and Rohlf, 1981; Neter et al., 1989), are often applied in comparative analyses of cross-species data (e.g., Schoener, 1968; Turner et al., 1969; Milton and May, 1976; Harestad and Bunnell, 1979; Harvey and Clutton-Brock, 1981; Garland, 1983; Christian and Waldschmidt, 1984; Goszczynski, 1986; Nagy, 1987; Garland et al., 1988; Burton et al., 1989; Bunnell and Harestad, 1990; Barclay and Brigham, 1991; Harvey and Pagel, 1991; Janis, in press). Such methods are powerful and general and are available in most statistics packages. However, the F statistics obtained from the ANOVA/ANCOVA of comparative data cannot properly be judged for significance against conventional tabular values (e.g., Rohlf and Sokal, 1981: table 16) because species' phenotypes generally are not statistically independent, which leads to overestimation of degrees of freedom. We have therefore proposed the use of empirically scaled, computer-simulated data to obtain "phylogenetically correct" or "PC" distributions of F statistics for testing hypotheses of differences between clades or other groups.

Conclusions about Home-Range Area and Diet

To illustrate the methods for phylogenetic ANCOVA, we compared home-range

areas of 19 members of the Carnivora (carnivores plus omnivores) with those of 30 ungulates, all of which are herbivores. Three different phylogenetically based tests agree: when judged by statistical tests that include both chance and phylogeny as part of the null hypothesis, ungulates do not have significantly smaller home ranges than do members of the Carnivora. What might explain this surprising result?

First, home-range area may actually be unrelated to diet, which is conceivable if, for example, carnivores have higher digestive efficiencies or perhaps higher foraging efficiencies than do herbivores (cf. Harestad and Bunnell, 1979; Garland, 1983; Calder, 1984; Goszczynski, 1986; Bunnell and Harestad, 1990; Harvey and Pagel, 1991:30–31, 122; Dunstone and Gorman, 1993). However, (nonphylogenetic) studies of other groups of mammals and of other vertebrates have generally indicated significant covariation between diet and home range (Schoener, 1968; Turner et al., 1969; Milton and May, 1976; Harestad and Bunnell, 1979; Harvey and Clutton-Brock, 1981; Christian and Waldschmidt, 1984; Gompper and Gittleman, 1991; and refs. therein). We suspect that a broader data base might indicate that herbivorous mammals have significantly smaller home ranges.

Second, our test may have inadequate power to detect a significant difference. In the present data set, diet is perfectly confounded with phylogeny (see Fig. 1 and Table 1); the two dietary groups fall on either side of the root. In a maximum-parsimony reconstruction of diet evolution in this group of mammals, irrespective of the true ancestral state, only one dietary transition has occurred—at the base of the tree. Intuitively, this confounding may yield low statistical power.

Statistical power can be increased in several ways, including increasing sample size. It may be more efficient to add data from other clades of mammals, rather than just increase sample sizes within Carnivora and ungulates, thus increasing the number of independent dietary transitions available for a study. Power could also be increased by obtaining diet information on a continuous scale, such as percent meat in diet. This would allow (multiple) correlation or regression tests for an association between diet and home-range size (e.g., using independent contrasts). Reduction in biological "noise" in the data through the use of additional covariates other than body mass, such as latitude, group size, or habitat type (cf. Milton and May, 1976; Gompper and Gittleman, 1991; Janis, in press), could also increase power. Finally, more powerful statistical methods might be possible. In future studies, we plan to use computer simulation (cf. Martins and Garland, 1991) to compare the power of the three approaches applied here plus that of Lynch (1991), modified for ANOVA.

Assumptions, Limitations, and Potential of the Simulation Approach

As with any method that uses phylogenies, the accuracy of topological and branch-length information will affect whether the null distributions derived from computer simulations along "known" phylogenies lead to accurate significance tests. Because all phylogenies are hypotheses subject to modification, statistical analyses that incorporate them should be redone as improved phylogenies become available. It is thus crucial for comparative biologists to publish the topologies and branch lengths they use in analyses (e.g., Fig. 1, Appendix); only then will readers know when reanalysis is in order. Methods that explicitly incorporate uncertainty about phylogeny into hypothesis testing have yet to be developed, although Felsenstein (1985) offered some suggestions for using maximum-likelihood techniques.

Many available phylogenies include unresolved polytomies. Polytomies can be dealt with in a variety of ways in comparative analyses (for discussions pertaining to independent contrasts approaches, see Felsenstein, 1985; Grafen, 1989, 1992; Harvey and Pagel, 1991; Pagel, 1992; Pagel and Harvey, 1992; Purvis and Garland, 1993; for discussions pertaining to autocorrelation approaches, see Gittleman and Kot, 1990; Gittleman and Luh, 1992). If available phylogenetic information includes unresolved polytomies, then simulations can reflect this (cf. Grafen, 1989; Gittleman

and Luh, 1992). Our PDSIMUL program can simulate data along unresolved trees by initially entering an arbitrarily resolved tree structure into PDTREE and then setting some internode branch lengths equal to zero.

Although unresolved nodes are easily incorporated into simulations, the relative lengths of the branches above and below a polytomy will affect the critical values obtained. If branches between a polytomous node and its descendants are set to be relatively short, then critical values will be conservative because the descendants are being treated as close relatives, expected to be relatively similar phenotypically (as if degrees of freedom were reduced). Conversely, if branches between a polytomous node and its descendants are set to be relatively long, descendants will be treated as relatively statistically independent, yielding liberal critical values. These effects should be kept in mind when using arbitrary branch lengths. Other ways to deal with polytomies include simply omitting species whose relationships are uncertain or performing the analysis with several alternative topologies (see also Grafen, 1992; Pagel, 1992; Sillen-Tullberg and Moller, 1993; Losos and Miles, 1994).

In the limit, we may have a completely unresolved tree—a star phylogeny sensu Martins and Garland (1991)—with all species derived from a single explosive radiation (cf. Felsenstein, 1985: fig. 2). Some groups of living species may actually derive from such a quick radiation, as has been suggested for African cichlid fishes (Mayden, 1986). If the group under study is accurately represented as a star phylogeny—a "hard" polytomy in Maddison's (1989) terminology—then conventional tabular F statistics can be used for the ANOVAs/ANCOVAs. It might also be possible to choose for study only taxa whose phylogenetic relationships are almost starlike (e.g., one species from each of the deep branches of a phylogeny or several populations of a single species [cf. Garland et al., 1992:26-27]).

A hypothetical star phylogeny can also be used to test whether our simulation methods yield the correct Type I error rates. We used PDTREE to "unresolve" the phylogeny of Figure 1 into a star and then used PDSIMUL to simulate gradual Brownian motion evolution of two characters with zero correlation 1,000 times. These data were then analyzed with PDANOVA, and the numbers of F statistics exceeding the nominal critical values for $\alpha = 0.05$ (from harmonic interpolation of Rohlf and Sokal, 1980: table 16) were counted. The Type I error rates were 0.048, 0.039, and 0.045 for the main effect, covariate, and explained, respectively (cf. Table 2). In a second trial, using a different random number seed (10 instead of 1), Type I error rates were 0.057, 0.044, and 0.046, respectively. Thus, our simulation and analysis procedures yielded acceptable Type I error rates.

In our example, estimates of branch lengths in units of absolute time were available (relative time would be computationally equivalent for our purposes). But temporal branch lengths are only appropriate if the characters being studied evolve as by pure gradual Brownian motion, with evolutionary rates stochastically equal over time and across lineages. What is really needed is branch lengths in units of expected variance of change (Felsenstein, 1985; Martins and Garland, 1991). Branch lengths can be obtained in a variety of ways (Grafen, 1989; Harvey and Pagel, 1991; Martins and Garland, 1991; Pagel, 1992; Walton, 1993; Martins, in press), and Garland et al. (1992; also Garland, 1992) discussed tests to check the statistical adequacy of branch lengths as well as ways to transform them to improve their statistical properties (see also Grafen, 1989). If transformation of branch lengths is indicated, then simulations could be done with the transformed branch lengths. Our current programs allow only bivariate simulations along a single set of branches. Nonetheless, the ability to set variances, limits, peak shifts, etc., separately for each trait (in PDSIMUL) allows, in effect, different branch lengths to be imposed during simulations.

The present version of PDANOVA allows only one main effect and one covariate to be tested. More complicated ANOVA or multivariate ANOVA designs could

be handled by using batch files to read simulated data sets into commercial statistics packages, such as SAS, SPSS, or SYSTAT. Multiple range comparisons with ordered predictions should also be possible (cf. Gaines and Rice, 1990). Comparisons of variances of groups of species are possible using Levene's test (e.g., Schultz, 1985), which is an ANOVA performed on absolute deviations of individual species' values from their within-group means or medians (Garland and Dickerman, in prep.). The simulation approach can be applied to any statistical test so long as one analyzes both the real and simulated data in an identical fashion.

Alternative Models of Character Evolution

The utility of *P* values derived from computer simulation depends on the realism of the simulation model (e.g., Stanley et al., 1981). We therefore used several different models, some with parameters set empirically, based on the data being analyzed and/or the fossil record. If scaling parameters are derived from the data being analyzed, as in our use of an independent contrasts regression to estimate a starting value for home range (see Methods and Fig. 2), then the resulting *P* values may be slightly liberal.

A gradual Brownian motion model of character change is reasonable under the neutral theory of phenotypic evolution and for some types of selection (Felsenstein, 1985, 1988; Charlesworth, 1990; Lynch, 1990; and refs. therein), but many other options are possible (see Felsenstein, 1988; Rohlf et al., 1990; Martins and Garland, 1991; and refs. in Slowinski and Guyer, 1989a, 1989b). PDSIMUL also allows speciational change, the Ornstein-Uhlenbeck process, punctuated equilibrium, trends, and limits to phenotypic evolution. Models that incorporate species selection or sorting (Vrba, 1989; Gould, 1990) would be of interest; they would require coincident simulation of both the tree and the characters evolving along it (cf. Rohlf et al., 1990; Vida et al., 1990; Vogl and Wagner, 1990; Maddison and Slatkin, 1991). Until we know more about micro- and macroevolutionary processes (Endler and McLellan, 1988; Felsenstein, 1988; Vrba, 1989; Gould, 1990), it is prudent to simulate character evolution under several models (cf. Rohlf et al., 1990; Martins and Garland, 1991)—a type of sensitivity analysis—and check for consistency in final results (cf. Losos, 1990; Garland et al., 1991; Sillen-Tullberg and Moller, 1993; Walton, 1993; Martins, in press).

Our implementation of punctuated equilibrium has some interesting properties. Because the tree topology is fixed and no extinction is allowed, the starting values at the root node will always be present at the tips in the simulated data. In fact, the phenotypes at every node will be represented at the tips. Thus, in our example, although we could obtain simulated data with realistic means (see Table 2), both distributions of means were left skewed because at least one tip species was always "anchored" at the root value, leading to variances that were too high, even with upper limits to evolution also imposed. Moreover, the Pearson correlation of tip data was higher than desired (Table 2 footnotes). Perhaps it would be more appropriate to model punctuated equilibrium by simulating the phylogeny simultaneously.

Application of both speciational (cf. Martins and Garland, 1991; Garland et al., 1992) and punctuated equilibrium models assumes that all branching points within the clade under study have been sampled, or at least that they have been sampled randomly or proportionately along all branches; otherwise, simulation along the phylogeny for only the species being compared (e.g., the present 49 species) may be misleading. Notwithstanding this and other indications of apparently unrealistic assumptions in some of our simulations, the conclusion regarding statistical significance is robust (Table 2).

Alternative Approaches for Phylogenetic ANCOVA

Three other existing comparative methods can be applied to perform ANOVAs and ANCOVAs in a fully phylogenetic

fashion. First, Lynch (1991) derived from quantitative genetics (treating phylogeny as analogous to a pedigree) a maximum likelihood-based method for estimating evolutionary correlations and phylogenetic "heritabilities." In principle, this method could be extended to estimate mean differences among clades or among ecologically defined groups. Computer programs to do so are not yet available (M. Lynch, pers. comm.).

Second, Gittleman and Kot's (1990) application of Cheverud et al.'s (1985; see also Gittleman, 1991; Miles and Dunham, 1992) phylogenetic autocorrelation method can produce residuals that are putatively free from phylogenetic effects. Harvey and Pagel (1991:137) questioned the logic of phylogenetic autocorrelation methods, because they discard a portion of the total variation observed among species: "potentially the majority of the variation is assigned to phylogenetic components and is ... not ... used to test questions about function and adaptation." Philosophical reservations aside, our use of putatively phylogeny-free residuals in a conventional ANCOVA (Fig. 4) yielded qualitatively the same result as did the computer simulation and independent contrasts methods.

Third, Felsenstein's (1985) method of standardized independent contrasts can be applied to comparisons of group means (see also Grafen, 1989, 1992; Martins, in press). Standardized independent contrasts are phenotypic differences between sister species or nodes divided by the square root of the patristic distance between them: they indicate "rates" of change in subclades of a tree (Garland, 1992). Thus, our application to the comparison of phenotypic means of two sister clades actually tests for a significantly higher "rate" of evolution at the point when the two clades diverged than at any time during evolutionary change within either. However, because the basal contrasts are entirely inferred from values for living species, the ultimate inference must be about the weighted mean values of the two samples of species; that is, an extreme basal standardized contrast is interpretable as a difference in weighted mean phenotype for the two clades (see Fig. 5).

For comparison of two clades for a single trait (contra Fig. 5), such as body mass, a basic nonparametric approach is possible. After ranking the absolute values of all standardized independent contrasts, one can compute the simple probability of the basal contrast being as extreme as observed. For example, the probability of the basal contrast being the most extreme of 48 contrasts (derived from 49 species) would be $1/48 = 0.020833$; the probability of its being one of the three most extreme contrasts would be $1/48 + 1/48 + 1/48 = 0.0625$. For the data in Table 1, the basal body mass contrast is the 11th greatest; the probability of a ranking this extreme is 0.22917. We could also rank the residual home-range contrasts, computed from a regression fitted to all 48 contrasts (as opposed to a line fitted to just 47 contrasts as shown in Fig. 5). If we do so, the basal contrast is the fourth smallest ($P = 0.08333$).

Another strategy would be to regress the absolute values of independent contrasts (not standardized) on their standard deviations (square roots of sums of branch lengths), omitting the one contrast of interest, and compute a one-tailed 95% confidence interval for a new value for the regression (probably constrained through the origin; see Garland, 1992). If the basal contrast fell outside the confidence interval, this could be interpreted as indicating a significant difference in clade means.

Independent contrasts can also be applied to compare group means when members of the groups are scattered across a phylogeny rather than separated on opposite sides of the root as in our example (Grafen, 1989, 1992). For example, standardized independent contrasts for a continuous dependent variable can be regressed on those for a two-category independent variable, a procedure equivalent to a two-sample t-test (e.g., Moller, 1991; Martins, in press). For a multistate categorical variable (e.g., diet categorized as nectarivore, frugivore, folivore, insectivore, carnivore, sanguinovore), a series

of 0/1 dummy variables could be used (e.g., Sokal and Rohlf, 1981; Neter et al., 1989). From a strict (multiple) regression perspective, only the residuals need to be checked carefully for normality, homoscedasticity, etc. (Grafen, 1989, 1992; Garland et al., 1992). The statistical properties of contrasts for categorical or ordered variables may, however, differ between those involving two tips (e.g., where all differences are either zero or unity) and those involving interior nodes, where differences get "smeared" across multiple contrasts (M. D. Pagel, pers. comm.). If categorical variables are employed with multivariate techniques such as principal components analysis, it is especially important to verify that branch lengths yield adequate standardization (Garland et al., 1992) and/or that the standardized contrasts are multivariate normal. In principle, categorical variables might even be used as dependent variables in regressions, but residuals often will behave poorly and Type I error rates may be compromised (e.g., Wu, 1986). Methods such as logistic regression are more appropriate (A. Grafen, pers. comm.).

Often, categorical variables represent coarse information about what is actually an underlying continuous variable (e.g., Moller, 1991:885). A carnivore–herbivore dichotomization, for example, can be viewed as a crude substitute for percent meat in diet. For our example data set, we can rescore diet as a three-category ordered variable (herbivores = 0, omnivores = 1, carnivores = 2), compute standardized contrasts, and perform a multiple regression of home-range contrasts on both body mass and diet contrasts. This procedure yields only six non-zero diet contrasts, although all 48 are properly analyzed (cf. Garland et al., 1992), and the partial F statistic for diet contrasts (controlling for body mass) is insignificant ($F = 0.696$, df = 1,46, $P = 0.4086$) (residuals from the multiple regression appear to behave adequately).

Independent contrasts can also be used to compare a single species to a group of other species. Ecological physiologists, for example, often study species living in "extreme" environments in the hope of finding particularly clear examples of adaptation (Bartholomew, 1987; Garland and Adolph, 1991). Often, the "exemplar" species is compared with the "norm" shown by a set of other species. A classic and frequent example of this approach (e.g., McNab, 1992) is to compare the metabolic rate of a single species with a 95% confidence interval for a nonphylogenetic regression of metabolic rate on body mass. To be phylogenetically correct, such analyses could be done with independent contrasts, similar to our comparison of the basal contrast to all other within-clade contrasts (Fig. 5).

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APPENDIX

The manner in which molecular, morphological, and paleontological information were integrated to generate the hypothesis of phylogenetic relationships shown in Figure 1 is discussed in detail below. The recent proliferation of cladograms generated from biochemical and molecular data has often led nonmorphological neontologists to see these methods as superior, more scientific means of obtaining phylogenies than are more traditional methods (e.g., Graur et al., 1991). However, molecular phylogenies may disagree with those generated from morphology and with each other. Great care must therefore be taken in evaluating such differences when determining the "best" currently available phylogeny for any particular group (see, for example, Wyss et al., 1987; Novacek, 1990). The cladogram that we have used represents a "consensus" not from any algorithmic method, but from a consideration of conflicting information and a best judgment as befits our current state of knowledge. This appendix documents the compromises and judgment calls made in generating the phylogeny, provides a review of the available literature, and discusses several nodes that are problematic in terms of topology and/or divergence times. We hope this discourse will help others to provide better composite cladograms in the future. Most of the fossil record data for divergence times can be found in Savage and Russell (1983), although more detailed studies are listed in most instances. For those readers not familiar with the names of the higher taxonomic categories, the discussion below reads more-or-less top to bottom along the cladogram of Figure 1.

Information Used and Carnivore/Ungulate Divergence

The carnivore phylogeny and divergence times are based both on fossil record data and on biochemical and molecular data from Wayne et al. (1989) and references cited therein. The ungulate phylogeny and divergence times are based primarily on fossil data. Some molecular data exist for certain portions of the ungulate phylogenetic tree (Georgiadis et al., 1990; Miyamoto et al., 1990; Cronin, 1991; Allard et al., 1992), and these have been incorporated where appropriate.

The carnivore/ungulate divergence time is placed at 70 million years ago (MYA) because of the possible occurrence of the "condylarth" ungulate *Protungulatum* in the latest Cretaceous (Lancian) (the Cretaceous/Tertiary boundary is currently placed at 66.4 MYA). *Protungulatum* may actually be confined to the Paleocene (J. D. Archibald, in press, pers. comm.), which would move this node upward a few million years. The carnivores ("miacoids") made their first appearance in the early Tertiary (Paleocene) at around 66.5 MYA (Flynn, in press). Thus, both carnivores and ungulates are very ancient clades.

Feliforma/Caniforma Divergence

The first main split in the carnivore phylogeny at 58 MYA is based on a study by Wayne et al. (1989). However, fossil record evidence might push this node back a little further. Flynn and Galiano (1982) showed that the "Miacoidea" is a paraphyletic assemblage, with most members assignable to either the feliform or the caniform lineage. The earliest viverravines (feliform "musteloids") first appeared around 65 MYA, although the earliest miacines (caniform "musteloids") did not appear until 58 MYA (Flynn, in press).

Arctoid Carnivores

Wayne et al. (1989) presented a phylogeny based on DNA hybridization data that shows a trichotomy among ursids, procynoids, and mustelids at 39 MYA and that additionally renders the Mustelidae paraphyletic (Mephitines [skunks] are placed as the sister taxon to all other extant arctoids). Wayne et al.'s phylogeny differs rather drastically from those of workers using morphological and/or fossil record evidence. Flynn et al. (1988), Wozencraft (1989), and Baskin (in press) all have supported the notion that procyonids and mustelids are sister groups, together forming a "Musteloidea." Although 39 MYA accords fairly well with fossil evidence for a Late Eocene appearance of the first arctoid carnivores represented by extant families, extinct families may present a problem with this date. If the Amphicyonidae ("bear dogs") are in fact the sister taxon to the Ursidae (rather than to the Canidae as originally thought [Hunt, 1977]), then their first fossil appearance at 43 MYA would push back the divergence of the ursids and musteloids to at least this date. Alternatively, amphicyonids might be the sister taxon to all other arctoids (Flynn et al., 1988), which would not affect the ursid/musteloid divergence time of Wayne et al. We have sided with the

fossil record evidence in placing the ursid/muteloid divergence at 44 MYA and the mustelid/procyonid split at the time of the first appearance of identifiable mustelids, 31 MYA (Baskin, in press).

The divergence between *Meles* and *Mephitis* within the mustelids (20 MYA) follows Baskin (in press), recording the first appearance of the "neomustelids" at 20 MYA. The earliest appearance in the fossil record of a definitive skunk is *Proputorius* at 15 MYA (Baskin, in press), despite the molecular evidence from Wayne et al. (1989) that skunks may have diverged from other mustelids as early as 30 MYA. The divergence at 5 MYA for the procyonids *Procyon* and *Nasua* is from fossil data of Baskin (1982, in press). The divergence of *Ursus americanus* at 5 MYA from the other bears is from Wayne et al. (1989) and seems to accord with fossil evidence. The divergence of *Ursus arctos* and *Ursus maritimus* at 2 MYA is based on fossil evidence in Kurtén (1964).

Canoid Carnivores

The canoid/arctoid divergence at 52 MYA is based on Wayne et al. (1989). The interrelationships and divergence times of the species within the Canidae are also from Wayne et al., based on isozyme genetic distances (0.1 genetic distance unit = 3.5 MYA), with a consensus phenogram of distance via Wagner trees and UPGMA. This divergence estimate appears to generally agree with the fossil record. We have followed Wayne et al.'s placement of the hunting dog *Lycaon* but note that this renders the genus *Canis* paraphyletic. This situation should be investigated more thoroughly in future studies.

Feliform Carnivores

Interrelationships and divergence times within the families Felidae and Hyaenidae are from Wayne et al. (1989), based on UPGMA for isozyme genetic distance data. The divergence times within the Felidae do not conflict with fossil record data, although the *Acinonyx*/*Panthera* split might be a little younger than 9 MYA: the earliest record of *Panthera* is about 2 MYA (Kurtén and Anderson, 1980), and the earliest record of the *Puma*/*Acinonyx* lineage is around 3 MYA (Van Valkenburgh et al., 1990). Within the Hyaenidae, fossil evidence (Werdelin and Solunias, 1991) suggests that the *Hyaena*/*Crocuta* split might be younger than proposed by Wayne et al., around 5 MYA rather than at 10 MYA, and 5 MYA is used here.

The feloid allozyme data give a felid/hyaenid divergence time of 20 MYA, whereas the overall carnivore tree in Wayne et al. (1989), based on thermal stability of DNA hybrids analyzed with the Fitch–Margoliash algorithm, gives a divergence time of 40 MYA. Neither of these dates accords well with fossil evidence. If hyaenids and felids are sister taxa (Martin, 1989; Wozencraft, 1989; Werdelin and Solunias, 1991), then the fossil record (appearance of first true felid) puts the date at 26 MYA. If, however, viverrids are actually the sister taxon to either the felids or the hyaenids (as in various earlier hypotheses), the divergence would have to be dated at the appearance of the first viverrid, around 30 MYA. Flynn et al. (1988) showed the felid/hyaenid/viverrid node as an unresolved trichotomy. We have placed the felid/hyaenid divergence at 26 MYA but note that hyaenids do not appear in the fossil record until 20 MYA.

Perissodactyl/Artiodactyl Divergence

This divergence time of 66 MYA (start of the Paleocene) is based on the phylogeny of Prothero et al. (1988), in which artiodactyls represent an earlier divergence than arctocyonid "condylarths," which first appear in the Early Paleocene. (The Late Cretaceous "condylarth," *Protungulatum*, is traditionally referred to the arctocyonids, but its phylogenetic position is in dispute [Prothero et al., 1988; Archibald, in press].) This divergence is earlier than the traditional one of around 55 MYA, based on the first appearance in the fossil record of the earliest members of both orders in the Early Eocene.

Ceratomorphs

The equid/ceratomorph divergence time of 56 MYA is based on fossil record evidence of the appearance of both undisputed equoids and tapiroids at the start of the Eocene (Prothero and Schoch, 1989). The rhino/tapir divergence time of 50 MYA is based on the appearance of the fisrt rhinocerotoid, *Hyrachyus*, in the Middle Eocene (Prothero and Schoch, 1989). The divergence time of *Diceros* and *Ceratotherium* at 13 MYA is based on the first fossil appearance of *Diceros* (Hooijer, 1978).

Equids

The interrelationships of the three species of *Equus* considered here are based on cladistic analysis of morphology by Bennett (1980), and the divergence times are based on both this paper and Churcher and Richardson (1978) (no disagreements), which provide the first fossil record appearance of each species.

Camels

The divergence between the suoids and other artiodactyls can be dated back to the early Middle Eocene of 50 MYA, based on the first appearance of artiodactyls more closely related to the camelid/ruminant lineage, such as oreodonts (Lander, in press). The divergence of the Camelidae from the Ruminantia (43 MYA) is based on fossil evidence in Honey et al. (in press). (The earliest camelids and ruminants both appeared in the Late Eocene.) The divergence time (17.5 MYA) between *Camelus* (Old World camelids) and *Lama* (New World camelids) is also based on Honey et al. and is earlier than more traditional estimates. The first species of both *Camelus* and *Lama* were Pleistocene, and it is usually assumed that the divergence was no earlier than 5 MYA. However, Honey et al. provided the first comprehensive cladistic analysis of the range of fossil and living camelids and showed that the two living genera have considerably more ancient origins within the family Camelidae.

Ruminantia Divergence Data

The divergence of higher ruminants from tragulids at 38 MYA is based on cladistic analysis and fossil record evidence from Webb and Taylor (1980). The

basal divergence of the ruminant families is placed at 20.5 MYA based on fossil record appearance for the first members of the Bovidae (cattle and antelope), Cervidae (deer), and Giraffidae (see Janis and Scott, 1987) and also accords with mitochondrial DNA data (Miyamoto et al., 1990). However, some problems remain in the consideration of the taxonomic assignments of certain extinct ruminant taxa. If *Dremotherium* is truly a member of the Moschidae (Webb and Taylor, 1980), and *Amphitragulus* is truly a member of the Palaeomerycidae (Janis and Scott, 1987), and these families actually belong within the Cervoidea (Leinders and Heintz, 1980; Janis and Scott, 1987), then this date would be pushed back to the first fossil record appearance of these taxa in the mid-Oligocene, around 30–32 MYA.

A critical taxon missing from current molecular studies is the Tibetan musk deer, *Moschus*. *Moschus* has been placed within Cervidae (traditional), in its own family Moschidae as the sister taxon to Antilocapridae plus Cervidae (Leinders and Heintz, 1980; Janis and Scott, 1987), or in its own family as the sister group to all other ruminants (Webb and Taylor, 1980). Information from this taxon would provide important data for molecular studies on ruminant interrelationships and divergence times: if moschids really are the sister taxon to other ruminants (and *Dremotherium* and *Amphitragulus* can both be placed within the Moschidae [as per Webb and Taylor, 1980]), then this does not influence the divergence time of the ruminant families considered here. If, however, *Moschus* is contained within the Cervidae or Cervoidea and the Oligocene taxa are shown to be moschids or some other type of cervoid, this means that the divergence time must be at least 30–32 MYA. Kraus and Miyamoto (1991) supported an earliest divergence of the horned ruminant families of 28 MYA (based on mitochondrial DNA [mtDNA] data) and suggested that Webb and Taylor (1980) were correct in placing the moschids (including *Dremotherium*) as the sister taxon to extant horned ruminants. Miyamoto et al. (1993) considered *Eumeryx* from the Late Oligocene of Asia to be a probable moschid, but Janis and Scott (1987) placed this taxon as the sister taxon to moschids, antilocaprids, and cervids.

Ruminantia Interrelationships

The interrelationships within the Ruminantia are based on the cladistic morphological analysis of Janis and Scott (1987). This analysis differs from the cladistic analysis by Gentry and Hooker (1988), but Scott and Janis (1993) provided a rebuttal to their use of characters within a PAUP matrix. A critical problem here is the placement of the Giraffidae. Janis and Scott believed this family to be the sister taxon to the other ruminant families, based on an apparent soft anatomy synapomorphy of the Bovidae plus Cervidae (the position of the entrance of the esophagus to the rumen). However, the state of this character has not been fully investigated throughout a range of ruminants and is unknown for *Moschus*, *Antilocapra*, and *Okapia*. However, Janis and Scott believed *Giraffa* to possess the primitive state because it resembles that of the more primitive mouse deer, *Tragulus*. Data from mtDNA (Kraus and Miyamoto, 1991; Miyamoto et al., 1993) have provided single most-parsimonious trees that place the Giraffidae as the sister taxon to either the Bovidae or the Cervidae. This lability in positioning indicates that mtDNA data do not at this time refute the hypothesis that Giraffidae is the sister taxon to both cervids and bovids. The traditional placement of *Antilocapra* (the pronghorn "antelope") is as the sister taxon of the Bovidae (with the Giraffidae then placed as the sister taxon of the Bovidae plus Antilocapridae) (O'Gara and Matson, 1975; Gentry and Hooker, 1988). However, we believe that nonhomoplastic morphological characters more strongly support Antilocapridae as the sister taxon of the Cervidae (Leinders and Heintz, 1980; Janis and Scott, 1987; Scott and Janis, 1993). The divergence times of the major higher ruminant families are based on fossil record evidence.

Bovids

Bovid interrelationships are based mainly on fossil data from Gentry (1990; see also Gentry, 1992). We treat the Bovidae as a monophyletic assemblage in this paper, but the evidence for monophyly is weak based on both morphological (Janis and Scott, 1987) and molecular data. Data from mtDNA suggest possible separation of the bovine and caprine lineages of bovids (Kraus and Miyamoto, 1991; Miyamoto et al., 1993), which would not be at variance with the fossil record evidence of virtually simultaneous appearance of the caprine and bovine-related boselaphine bovid lineages (Gentry, 1990, 1992). The divergence of *Ovis* and *Oreamnos* at 4 MYA is based on fossil data from Geist (1987). Georgiadis et al. (1990) provided a phenogram of African bovids based on 40 allozyme loci and derived using Nei's genetic distance and UPGMA. This phenogram gives a divergence time for the Bovidae of 45 MYA, which they (and we) considered unrealistic. In contrast, their divergence times at lower taxonomic levels almost uniformly underestimated those provided by the fossil record (e.g., 1 MYA for the divergence of *Alcelaphus* and *Damaliscus* vs. 3.5 MYA from fossil evidence [Gentry, 1990]). We thus based the divergence times in Figure 1 on the fossil record.

The main difference between the phenogram of Georgiadis et al. (1990) and the topology that we have used is their position of *Aepyceros* as the sister taxon of all African bovids (vs. the sister taxon of the Alcelaphini [*Connochaetes*, *Damaliscus*, and *Alcelaphus*] in our tree; Vrba, 1979) and their position of *Taurotragus* (and other tragelaphines) as the sister taxon of the remainder of the African bovids (vs. the sister taxon of the Bovini; Gentry, 1990). One result of Georgiadis et al. (1990) that we incorporated into the cladogam was the placement of *Hippotragus* as the sister taxon of the Alcelaphini (plus Aepycerotini in our scheme). Gentry (1990) tentatively allied hippotragines with the bovines but admitted that they might instead be related to the alcelaphines. Gentry (1992) aligned hippotragines plus reduncines (reedbuck, waterbuck, etc.; not included in Fig. 1) as the sister group to alcelaphines (including the impala) plus caprines (including *Ovis* and *Oreamnos*). Both fossil and molecular data

are in accordance here at placing a hippotragine/alcelaphine plus aepycerotine divergence at 9 MYA.

One problem with the analysis of Georgiadis et al. (1990) is that they only examined African bovids. The study of mtDNA by Allard et al. (1992) included the nilgai, an Indian bosealphine; bosealphines represent the most primitive of the bovid tribes (Gentry, 1990, 1992). Allard et al. provided two trees for the bovids that they examined, one using all variable and informative data and the other using transversions only. Neither tree supported an immediate sister group relationship of *Aepyceros* with the alcelaphines, although both supported the grouping of *Taurotragus* with the bovines (*Synceros* and *Bison* in our cladogram) (contra Georgiadis et al., 1990) and of *Hippotragus* with the alcelaphines. Allard et al.'s first tree, which in general is in better agreement with the morphological data, supported a sister grouping of *Aepyceros* plus caprines (*Ovis* and *Oreamnos* in our cladogram), which in turn is the sister group to *Hippotragus* plus the alcelaphines.

Cervids

Cervids appear to be a good monophyletic group, based on both morphological (Janis and Scott, 1987) and molecular (Kraus and Miyamoto, 1991; Miyamoto et al., 1993) data. The phylogeny of the Cervidae is based on morphological data from Groves and Grubb (1987). Because muntiacines appear to be the sister taxon of the Cervinae (see also data from mtDNA from Miyamoto et al., 1990), the first appearance of fossil muntjaks at 17 MYA should herald the cervine (Old World deer)/odocoileine (New World deer) divergence time. However, Miyamoto et al. (1990) suggested that these fossil taxa were not in fact true muntiacines (because the apparent similarity of antler morphology is merely the primitive cervid condition) and suggested a more recent divergence time of 11 MYA based on both molecular and fossil data on the appearance of deer similar to living species.

The divergence time of *Cervus* (red deer and others) and *Dama* (fallow deer) is based on fossil data from Kurtén and Anderson (1980) and Lister (1987). Although the odocoileine taxa *Rangifer* and *Alces* did not appear until 2 MYA in the Pleistocene (Kurtén and Anderson, 1980; Lister, 1987), the first *Odocoileus* appeared at 5 MYA (Tedford et al., 1987). Thus, the divergence of *Rangifer* and *Alces* from the odocoileine lineage must have occurred prior to this date but before 8 MYA because this marks the first appearance of *Capreolus* (roe deer, an odocoileine despite its Old World distribution), the sister taxon to the other odocoileines (Lister, 1987). We have estimated the *Rangifer* divergence time at 5 MYA and the *Alces* divergence time at 5.5 MYA (using the earliest "possible" times in deference to their late appearance in the fossil record).

In a study based on mtDNA, Cronin (1991) suggested that *Rangifer* is in fact the sister group to the other odocoileines (thus switching the positions of *Rangifer* and *Alces* on our cladogram) (Cronin does not estimate divergence times). However, we do not have much confidence in this phylogeny, because the results of his study also place the mule deer (*Odocoileus hemionus hemionus*) in a different clade than the black-tailed deer (*Odocoileus hemionus columbianus* or *O. h. sitkensis*).