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MORPHOLOGICAL INTEGRATION IN THE CARNIVORAN SKULL

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Abstract.—The correlated evolution of traits may be a principal factor in morphological evolution, but it is typically studied in genetic or developmental systems. Most studies examining phenotypic trait correlations, through analysis of morphological integration, consider only few taxa, with limited ability to test hypotheses of the influence of trait integration on morphological variation and diversity. The few comparative studies in less inclusive groups have yielded varying relationships of integration to the key factors of phylogeny and diet. In this paper, I present analyses of cranial morphological integration in 30 species from the mammalian order Carnivora, spanning eight extant families and a wide range of ecological and morphological diversity. Fifty-five cranial landmarks were captured through three-dimensional digitization of 15–22 specimens for each species. Using a node-based phylogenetic distance matrix, a significant correlation was found between similarity in patterns of integration and phylogenetic relatedness within Felidae (cats) and Canidae (dogs), but not within more inclusive clades, when size-related variation was removed. When size was included, significant correlations were found across all Caniformia, Musteloidea, Mustelidae, and Felidae. There was a significant correlation between phylogeny and morphological integration only within the higher-level clade Feliformia (cats, civets, mongooses, and hyaenas) when a branch-length-based phylogenetic distance matrix was analyzed, with and without size. In contrast, diet was significantly correlated with similarity in morphological integration in arctoid carnivorans (bears, raccoons, and weasels), but had no significant relationship with integration in feliforms or canids. These results support the proposition that evolutionary history is correlated with cranial integration across large clades, although in some smaller clades diet also exerts significant influence on the correlated evolution of traits.

Key words.—Carnivora, cranial evolution, diet, morphological integration, phylogeny.

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The idea that traits that are closely related through ontogeny or function have greater influence on each other than on more distantly associated traits has long been considered a significant factor in evolution (Olson and Miller 1958; Pigliucci and Preston 2004). Trait associations potentially influence evolutionary paths in many ways, from constraining the variability of individual traits to facilitating transformations of functional sets (Olson and Miller 1958; Vermeij 1973; Wagner 1996; Emerson and Hastings 1998; Bolker 2000). Despite this, trait correlations have been overlooked in most morphological analyses, with studies usually limited to a single functional group. Studies of morphological integration, however, can summarize broader patterns of trait correlations. Furthermore, recent studies have empirically or theoretically tied morphological integration to quantitative genetics, molecular pathways, novelty, life-history strategies, and macroevolutionary trends (Pigliucci and Preston 2004; Schlosser and Wagner 2004). Thus, empirical studies of morphological integration are well suited to promoting the inclusion of trait correlations into studies of morphological evolution.

Morphological integration is measured through statistical analysis of patterns of trait covariation or correlation, which reflect the tendency of characters to vary in a coordinated fashion. Cheverud (1996a) partitioned morphological integration into two aspects, genetic and evolutionary integration, to isolate their underlying biological roots. Genetic integration refers to the coinheritance of morphological traits, while evolutionary integration is the less-specific correlated evolution of morphological characters, whether due to genetics or selection. Nongenetic integration is further subdivided into developmental integration, caused by morphogenetic associations among traits, and functional integration, caused by a shared function among traits. Using these divisions of integration, specific mechanisms for the evolution of integration and modularity have been proposed and modeled. Stabilizing (Cheverud 1984) and directional (Wagner 1988, 1996) selection for functional integration could lead to genetic integration of traits that are functionally related, while decoupling traits that are related by pleiotropy. This combined change of genetic and functional integration of traits thus gives rise to new patterns of evolutionary integration for those traits (Cheverud 1984; Wagner 1988, 1996; Chernoff and Magwene 1999).

The relationships between observed patterns of morphological integration and the possible causes of integration (genetic, developmental, and functional) have inspired a broad array of studies. There is a wealth of microevolutionary studies of morphological integration, such as studies of insect wings (Klingenberg and Zaklan 2000; Klingenberg et al. 2001a), growth series of piranhas (Fink and Zelditch 1996; Zelditch et al. 2001), mammalian mandibles and dentition (Atchley et al. 1982; Atchley and Hall 1991; Cheverud et al. 1991, 1997, 2004; Atchley 1993; Badyaev and Foresman 2000, 2004; Klingenberg and Leamy 2001; Klingenberg et al. 2001b, 2003, 2004; Cheverud 2004; Polly 2005), and the mammalian skull (Cheverud 1982, 1988, 1989, 1995, 1996a,b; Cheverud et al. 1983; Zelditch 1988; Zelditch and Carmichael 1989a,b; Steppan 1997a,b; Ackermann and Cheverud 2000, 2004a,b; Marroig and Cheverud 2001, 2005; Marroig et al. 2004; Zelditch and Moscarella 2004). In particular,

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many studies have documented the relationship between genetic and phenotypic integration and have found some correlation between genetic and morphological integration (Cheverud 1982, 1996b, 2004; Cheverud et al. 1983, 1997, 2004; Atchley 1993), although there is not always a perfect correspondence between genetic integration and functional or developmental integration (Klingenberg and Leamy 2001; Klingenberg et al. 2001b, 2004). Still, phenotypic correlations generally are a good proxy for genetic correlations, and this relationship allows for application of genetic hypotheses to organisms for which only morphological data is available, such as fossils.

Many studies have also documented the relationship between development and phenotypic integration (Cheverud 1984, 1996a; Atchley and Hall 1991; Atchley 1993; Klingenberg and Nijhout 1999; Klingenberg and Zaklan 2000; Klingenberg et al. 2001a, 2003; Klingenberg 2002, 2004; Badyaev et al. 2005). A noteworthy series of studies of morphological integration in the rodent skull compared empirical observations of morphological integration with hypotheses of functional and developmental units, often incorporating ontogenetic series (Zelditch 1988; Zelditch and Carmichael 1989a,b; Zelditch and Moscarella 2004). Of particular note, great variability is discovered through ontogeny and between different regions of the skull, with the highest levels of integration found during puberty, and the neurocranial region showing greater variability than the orofacial region. While patterns of integration during early stages of ontogeny are highly correlated with those predicted from developmental models, patterns of integration in the crania of later embryological stages and juveniles show higher correlation with functional groups than with developmental groups, revealing a major shift in patterns and influences during growth (Zelditch and Carmichael 1989a,b).

Although several of these researchers stressed the need for broader studies of morphological integration (Chernoff and Magwene 1999; Eble 2004), few studies of integration involve comparisons above the genus level (Cheverud 1982, 1996a,b; Steppan 1997a,b; Ackermann and Cheverud 2000; Magwene 2001; Zelditch et al. 2001; but see Cheverud 1989; Marroig and Cheverud 2001, 2005; Ackermann and Cheverud 2004b; Marroig et al. 2004). This lack of comparative data hinders application of hypotheses of integration to large-scale evolutionary patterns (Eble 2004), because there is simply not enough diversity at the species or genus levels to assess the distributions of trait correlations or the potential developmental, ecological, or functional influences on them. The mammalian skull provides an excellent system for expanding studies of morphological integration to the macroevolutionary scale. The largest-scale, comparative studies ever conducted (Marroig and Cheverud 2001, 2005) were within the mammalian clade of platyrrhine primates, and several smaller-scale studies (generally within species or genera) provide data for comparison and a foundation for examination of morphological integration in the mammalian skull (Cheverud 1982, 1989, 1995, 1996a,b; Cheverud et al. 1983; Zelditch 1988; Zelditch and Carmichael 1989a,b; Steppan 1997a,b; Ackermann and Cheverud 2000, 2004b; Zelditch and Moscarella 2004). In this paper, I focus on two factors that are often considered in studies of integration as proxies for the potential correlation between cranial integration, evolutionary history, and function: phylogeny and diet.

Although the most obvious null hypothesis is that evolutionary history is correlated with similarity in patterns of morphological integration, previous studies have failed to support this hypothesis (Marroig and Cheverud 2001, 2005). Furthermore, studies of phylogenetic structure and similarity in integration at lower taxonomic scales for disparate taxa yield contradictory results. Some phylogenetic structure exists at the population and subspecies levels in a single species of rodent, but variation is very large. The same study showed that at the species level there is less among-group variation (Steppan 1997a,b). Ackermann and Cheverud (2000) found that phylogeny and integration are correlated within species of the platyrrhine genus *Saguinus*, whereas studies across all platyrrhine primates found no significant correlation between phylogeny and patterns of morphological integration (Marroig and Cheverud 2001, 2005). However, although differences in morphological integration do not correlate to phylogenetic distance, phenotypic modules are relatively conserved across platyrrhines.

Marroig and Cheverud's platyrrhine studies (2001, 2005) also found diet to be more strongly correlated with similar patterns of morphological integration than is phylogeny. Diet may strongly influence tooth size and shape and jaw musculature and thus overall skull morphology. Skulls must accommodate the functional demands of juvenile and adult food processing, and, if the functional integration of traits for mastication is reflected in morphological integration, then similarities in diet may be reflected in similarity in morphological integration.

These combined results suggest a complex relationship between phylogenetic relatedness, integration, and function in shaping the mammalian skull during evolution. In addition, as suggested by Steppan (1997b), disparate microevolutionary and macroevolutionary processes may manipulate morphological integration. While it is clear that evolutionary history is related to morphological integration to some extent, it is not understood how general this relationship is, nor how significant patterns of integration are in morphological evolution. This study addresses these questions in the largest clade yet studied, the order Carnivora, as an essential step toward understanding the complex relationships among morphological integration, phylogeny, and diet at a macroevolutionary scale.

The mammalian clade Carnivora has been chosen for this analysis for several reasons. Carnivora is the third most speciose order of mammals, with more than 270 extant species. Carnivorans (members of the order Carnivora, rather than any mammals with a carnivorous diet) display an extremely broad range of morphological and dietary diversity, from social insectivores to folivores to hypercarnivores (Nowak 1999; Myers 2000). Thus, their combination of taxonomic and ecological diversity surpasses that of any other mammalian clade. Finally, several morphological and molecular phylogenetic studies have been conducted for carnivorans in recent years, and these studies have provided robust resolution for most of the carnivoran tree. Using these attributes, one can rigorously examine morphological integration across

TABLE 1. Cranial landmarks, which are illustrated in Figure 1. The landmarks used to unify multiple orientations of individual specimens, as discussed in the Materials and Methods, are marked in bold.

Symbol	Landmark
MPR	**premaxilla–maxilla ventral suture**
PMA	premaxilla–maxilla anterior suture
NANT	nasal–anterior extreme
NP	nasal–premaxilla–anterior suture
CL	canine–lateral extreme
CM	canine–mesial extreme
M1L	anterior lateral M1
PML	posterior molar lateral
M1M	anterior mesial M1
PALM	**palatine–maxilla ventral suture**
JMV	jugal–maxilla ventral suture
JMD	jugal–maxilla dorsal suture
NF	nasal–frontal suture
JML	jugal–maxilla–lacrimal suture
LFM	lacrimal–frontal–maxilla suture
PORB	postorbital process
BA	bulla–anterior extreme
PTR	pterygoid tip
EPF	ethmoid–palatine–frontal suture
OAF	orbitosphenoid–alisphenoid–frontal suture
BPP	basisphenoid–presphenoid–pterygoid suture
PPP	presphenoid–pterygoid–palatine suture
JSV	**jugal–squamosal ventral suture**
BPL	bulla–posterior extreme
POC	paraoccipital process
OC	occipital condyle–extreme
BBB	**basioccipital–basisphenoid–bulla suture**
PF	**parietal–frontal suture**
PO	parietal–occipital suture
PSA	parietal–squamosal–alisphenoid suture
PFA	parietal–frontal–alisphenoid suture

a large clade and isolate several potential influences on patterns of cranial integration, including phylogeny and diet.

MATERIALS AND METHODS

Landmarks

Fifty-five landmarks were collected across the skull, emphasizing points of clear homology across taxa, such as tripartite sutures. To permit direct comparison with previous results, landmarks corresponding to those in earlier studies were used. Cranial landmarks were captured using an Immersion Microscribe (San Jose, CA) G2X three-dimensional digitizer. The G2X has a reported accuracy of 0.23 mm and uses optical sensors to measure three-dimensional coordinates, eliminating the problems of nonrandom error found in magnetic digitization systems. Use of the three-dimensional digitizer reduces data-collection time by approximately 80% over two-dimensional caliper methods, allowing for collection of 55 landmarks in less than 10 min. Landmarks are listed in Table 1 and illustrated in Figure 1 (symmetrical landmarks are displayed on one side only).

Specimens

A total of 511 specimens, representing 30 species (28 extant and two fossil) and all eight terrestrial families of carnivorans, were included in this analysis, with 15 to 22 specimens per species (Appendix 1; see Supplementary Material available online only at http://dx.doi.org/10.1554/05-110.1.s1). A series of rarefaction and bootstrap analyses was conducted to determine minimum sample sizes at which matrix correlation analysis and pairwise trait correlations were stable. Starting from a sample of 28 specimens for a single species (*Vulpes vulpes* in Fig. 2), specimen numbers were rarefied stepwise down to eight specimens, with 100 repetitions of each step. Trait correlation matrices were calculated for each rarefied matrix, which was then compared to the trait correlation matrix for the original 28-specimen matrix with matrix correlation analysis. The results show that matrix correlations do decrease with decreasing sample size. Means and confidence intervals for each step of the rarefaction analysis are shown in Figure 2. Matrix correlations between all carnivoran species average 0.66, with a variance of 0.04 (Fig. 2). Matrix correlations from rarefied single-species matrices cross the mean-between-species value at $n = 10$, with differences between matrices rarefied to 11 specimens statistically indistinguishable from between-species matrix correlations (ANOVA, $P > 0.01$). Examination of confidence intervals (Fig. 2) shows that the ranges of matrix correlations for rarefied single-species data and for observed between-species data begin to overlap at $n = 14$. Based on these two analyses, $n = 15$ was chosen as a practical and conservative minimum sample size. Because most matrix correlations between species are significantly lower than matrix correlations for the rarefied data even at lower samples sizes, this should not greatly influence any results. Furthermore, rarefaction analyses also show that matrix correlations between two species decrease with reduced sample size (Fig. 3). Therefore, the effect of lower sample sizes, if any, will be to reject real similarity in patterns of integration and to reduce the significance of results, rather than to create false similarity and increase significances.

As discussed above, only adult specimens were sampled in this study, and male and female specimens are equally or nearly equally represented in each species' dataset. Because error in the estimation of morphological integration for a single species, as determined by rarefaction analysis, is significantly lower than between-species variation (Fig. 2), and because this study focuses on patterns across larger clades, differences within species due to sexual variation and age variation should not affect the results of this study. Although larger samples sizes are preferable in studies of morphological integration, and though explicit control of sexual variation would be ideal, this study focuses on more distantly related taxa than previous studies, rendering these sample sizes sufficient for distinguishing among taxa and for observing general patterns across large clades.

In this study, fossil species were limited to Pleistocene taxa (*Smilodon fatalis* and *Canis dirus*), due to the availability of sufficient specimens without any distortion or crushing. Inclusion of these taxa increases the morphological breadth and within-family sampling for Canidae and Felidae. Because this study focuses on more inclusive clades, few congeneric species are included. The families Canidae, Felidae, and Mustelidae are better sampled than others, due to their taxonomic diversity and the availability of sufficient specimens in many

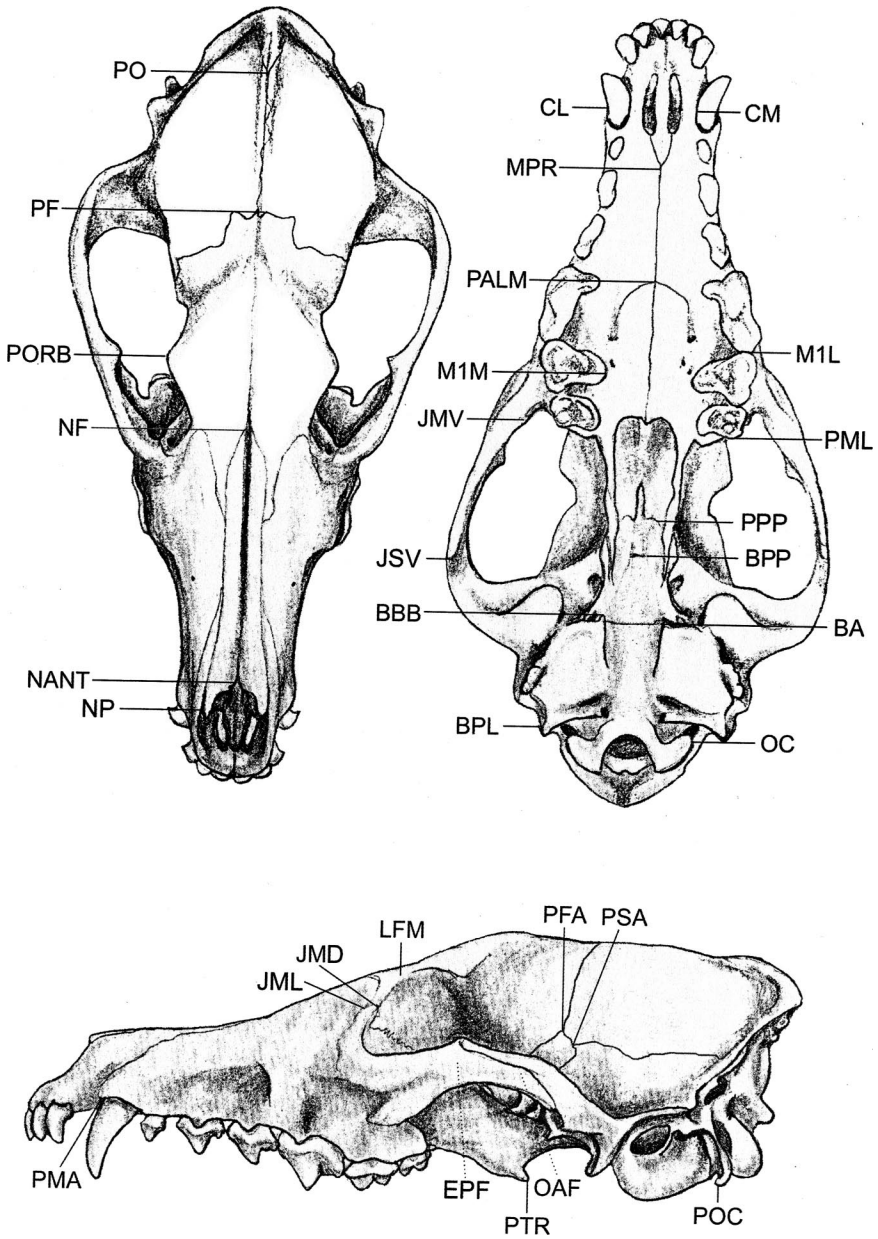

FIG. 1. Cranial landmarks used in analyses, shown on *Vulpes vulpes*. Symmetrical landmarks are shown on one side only.

museum collections; these will be used to examine patterns within families.

Data Analysis

Original three-dimensional data were subjected to a series of operations prior to analysis. Data were recorded in Microsoft (Redmond, WA) Excel format directly from the digitizer into a laptop computer. Larger specimens were digitized in two orientations and unified in Mathematica 5.0 (Wolfram Research, Inc., Champaign, IL) using a partial Procrustes algorithm. Seven midline and symmetrical landmarks were used to orient the two positions into a single frame (marked in bold on Table 1). A new Procrustes analysis script was written, due to the unavailability of an existing program that can treat specimens with missing data. The unifying program written for this analysis treated the data as follows. First, the seven primary orienting landmarks were used to compute a least-squares fit. If any of these were missing, they were excluded from the calculation. If more than four of the orienting landmarks were missing, unification was aborted. Second, the least-squares fit was applied to all of the landmarks in the second orientation, and missing datapoints remain as missing. The least-squares value (the sum of the squared distances between the seven orienting landmarks between the two positions) was used as a measure of unification error. Specimens with a high unification error ($>$0.25 mm per landmark, similar to the accuracy of digitization) were removed from the dataset.

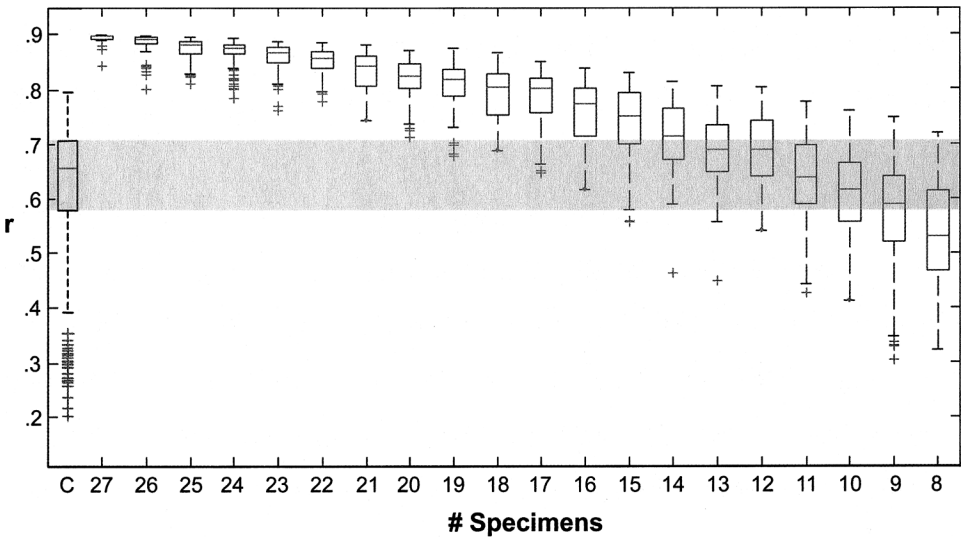

FIG. 2. Rarefaction analyses of *Vulpes vulpes*, showing matrix correlations of the original trait correlation matrix and matrices rarefied from 28 to eight specimens. Each rarefaction is repeated 100 times. The bar marked C (left) and the related shaded area shows the range of between-species matrix correlations in the study.

Following unification of individual specimens, reflection of symmetrical points was conducted to fill in missing data. Six midline traits were used to denote an axis of reflection for 48 symmetrical traits (one trait, antero-lingual M1, was captured only on the right side in this study). It should be noted that use of this algorithm masked fluctuating asymmetry, which constitutes a minor, though interesting, component of morphological variation, and thus was not considered in this study. As in the unification routine, the fit of the midline traits to a plane provided a measure of error. Specimens with high reflection mirror errors (i.e., the midline landmarks deviate more that 0.25 mm per landmark from the defined midline plane, either due to original measurement error or asymmetry in the specimen) were excluded from further analysis. In general, missing data comprised only a small part of the dataset, from two to five percent. However, these methods are useful for incorporating landmarks from delicate parts of the skull, such as the pterygoids or auditory bullae, and will prove useful in future studies of fossil taxa, which typically have much more missing data.

Following reflection, all specimens of a single taxon were oriented to the same position, as any differences in orientation would result in erroneous landmark covariances. A Procrustes algorithm, written in Mathematica 5.0, treats missing data by excluding individual missing datapoints from computation of the least-squares fit. In standard Procrustes algorithms that allow missing data, a missing datapoint necessitates the removal of entire landmarks or specimens from consideration, which would greatly reduce the final dataset. The new Procrustes algorithm rotates and translates each specimen to find

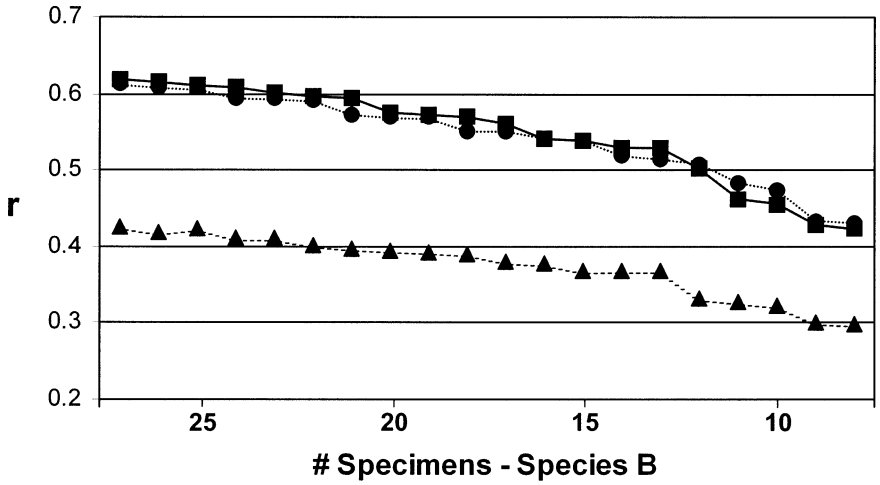

FIG. 3. Rarefaction analyses of matrix correlations between two species, showing the effect of small sample size on matrix correlation analysis. Species A is rarefied from 20 specimens (■) to 15 specimens (●) and 10 specimens (▲). Species B is rarefied from 28 to eight specimens. Each rarefaction is repeated 100 times, with mean matrix correlations displayed. The matrix correlation between the original datasets (A, 22 specimens; B, 28 specimens) is 0.619.

an optimal least-squares fit among the specimens. Scaling, a common Procrustes procedure, was not applied to specimens, to reduce the effect of inducing covariances through Procrustes fitting and because there was no clear a priori reason to do so.

For analysis, only landmarks from the midline (7) and right side of the skull (24) were used, as any variation due to asymmetry had already been confounded by implementation of the mirror algorithm described above. For each species, landmarks with excessive missing data (more than two missing values) were removed from further analysis. Comparisons across taxa used only landmarks found in all included taxa.

Pearson product-moment covariances were calculated for individual species in Mathematica 5.0. For some analyses, the first eigenvector, which mainly reflects size, was removed from the covariance matrix. Comparisons among results with and without the first eigenvector allow the estimation of the role of size in morphological integration. Trait variance-covariance matrices were converted to trait correlation matrices by dividing the covariances of traits a and b by the variances of these traits. These steps produced a simple 31×31 trait correlation matrix for each individual species, which were then used to determine similarity in morphological integration among all species.

Matrix correlation analysis was employed to assess similarity in patterns of morphological integration (Steppan 1997a, 2004). Pairwise comparisons of species-specific trait correlation matrices were conducted, using a common set of landmarks, with increasing numbers of common landmarks in less inclusive clades. Simply, the trait correlation matrix of each species was compared to that of every other species, using matrix correlation analysis. The matrix correlations between species were used to build the matrix of similarity of integration (MSI), which consists of pairwise matrix correlations (see Appendix 2 available online only at http://dx.doi.org/10.1554/05-110.1.s2). MSI was then used to assess the association of phylogenetic relatedness or dietary similarity with similarity in cranial integration. Analyses were conducted at several phylogenetic levels and were restricted to groups with more than five species sampled: order (Carnivora), suborder (Feliformia, Caniformia), parvorder (Arctoidea), superfamily (Musteloidea), and family (Felidae, Canidae, and Mustelidae) (for all, McKenna and Bell 1997).

Phylogeny

To test the relationship between morphological integration and phylogenetic relatedness, multiple phylogenetic distance matrices were constructed for all of the taxa examined, using recent published phylogenetic hypotheses (Wozencraft 1989; Decker and Wozencraft 1991; Hunt and Tedford 1993; Wyss and Flynn 1993; Zhang and Ryder 1993, 1994; Tedford et al. 1995; Flynn 1996; Dragoo and Honeycutt 1997; McKenna and Bell 1997; Flynn and Nedbal 1998; Bininda-Emonds et al. 1999; Flynn et al. 2000, 2005; Yoder et al. 2003; Flynn and Wesley-Hunt 2005). These phylogenetic hypotheses differed or were poorly resolved in two areas of the carnivoran tree, the relationships among the families with the suborder Feliformia and the relationships among the superfamily Musteloidea (Fig. 4). Due to these uncertainties, several competing phylogenetic hypotheses were tested. Phylogenetic hypotheses discussed below were limited to those involving the species included in this study. The following alternative hypotheses were used in these tests: within Feliformia: (A) Felidae branching first (Flynn et al. 2005); (B) Viverridae branching first (Flynn et al. 2005); within Musteloidea: (1) *Ailurus* (Mephitinae (Procyonidae + remaining Mustelidae)) (Dragoo and Honeycutt 1997; Flynn et al. 2000, 2005); (2) (*Ailurus* (Procyonidae + Mustelidae [including Mephitinae])) (Bininda-Emonds et al. 1999); (3) ((*Ailurus* + Mephitinae) (Procyonidae + remaining Mustelidae)) (Flynn et al. 2000); (4) ((*Ailurus* + Procyonidae) Mustelidae [including Mephitinae]) (Flynn et al. 2000; Zehr et al. 2001). These phylogenetic hypotheses were randomly ordered, with no weight given to any particular topology.

In the first metric, all branches were given an equal length of one. For this reason, this metric is referred to as a node-based phylogenetic distance metric and measured the patristic distance between each pair of species. However, because a similarity matrix was required for comparison, each distance value was subtracted from the maximum distance among species (those related only as carnivorans) +1, such that the most distantly related species had a value of 1.0 and sister species had the maximum value.

Branch lengths from a recent molecular phylogeny (Flynn et al. 2005) were also used to assess the relationship between phylogenetic distance and similarity in morphological integration (Fig. 4, A1). The sampled species differed between the two studies, so only 21 species were included in the comparison with branch lengths. Because only four felids and two canids overlapped between these two datasets, neither Felidae nor Canidae could be tested for correlation between similarity of morphological integration and branch lengths. Branch lengths were calculated to terminal branches, although four species (*Prionailurus bengalensis*, *Prionailurus viverrinus*, *Herpestes ichneumia*, and *Ursus americana*) were counted only to generic nodes, because studied taxa overlapped only to the generic level. A second analysis, limited to terminal nodes, was also conducted. Patristic distances were calculated and converted to a phylogenetic similarity matrix in a similar manner to that described above, but with molecular branch lengths. For this reason, this metric is referred to as the branch-length-based metric.

Matrix correlation analysis was used to test the correlation of various phylogenetic distance matrices with MSI. Mantel's test was used to determine the significance of the matrix correlation. Mantel's test randomly reorders the rows and columns of one of the two correlation matrices being compared and recalculates the matrix correlation between the two matrices (Manly 1997). This operation was repeated 10,000 times, providing a random distribution of matrix correlations with which to assess the significance of the observed matrix correlation.

An alternative analysis of phylogenetic relationship was also employed. Pairwise similarity of morphological-integration values were averaged for taxa related at various taxonomic levels (single pairs method; Steppan 2004). For example, the matrix correlations between all species pairs that are related at the genus level were averaged and compared to all pairs that are related at the family level but not at the

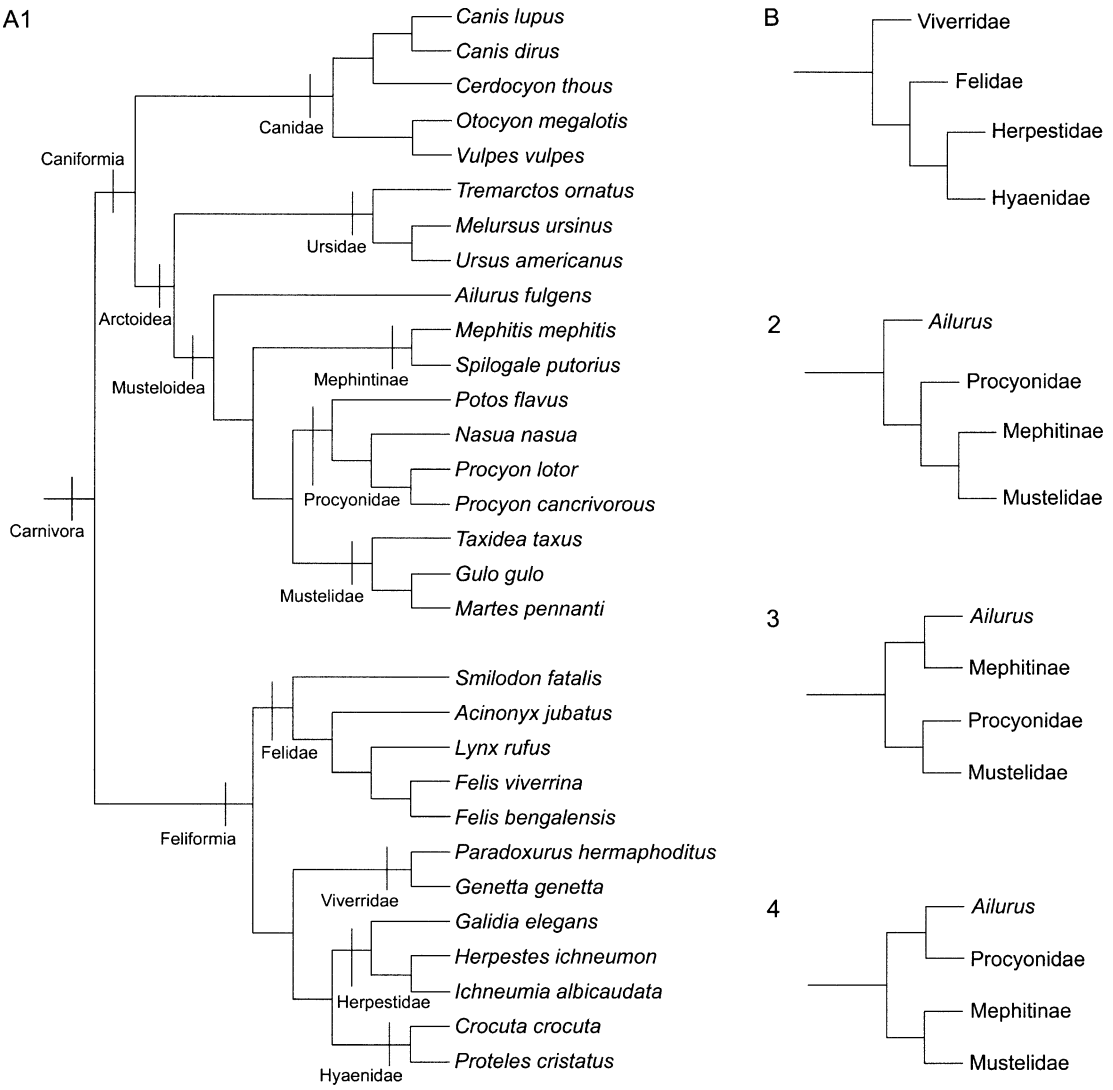

FIG. 4. Phylogenetic hypotheses for Carnivora. Branch-length data refers to topology A1.

genus level. If phylogenetic relatedness is correlated with similarity in morphological integration, it is expected that average pairwise matrix correlation will decrease from the generic to the ordinal levels. Matrix correlations for each taxonomic rank were bootstrapped 10,000 times and bootstrapped averages were plotted in histograms and box plots to examine possible trends in changes of similarity of morphological integration with taxonomic rank.

Diet

To test the correlation between morphological integration and similarity in diet, a dietary similarity matrix (DSM) was constructed among all taxa, based on the proportion of shared diet between species. This analysis followed the methodology of Marroig and Cheverud (2001) for quantifying similarity in diet based on the proportion of shared dietary types. Each species was categorized by the approximate percentage of vertebrates (*C*), invertebrates/insects (*I*), fruits (*F*), and leaves (*L*) in its diet (Appendix 1). Dietary information was taken from existing literature, using approximated contributions of each category to a species' total diet (Van Valkenburgh 1989; Nowak 1999; Myers 2000). Diet for generalist taxa was divided evenly among the four dietary groups. Although direct dietary information is not available for fossil taxa, the two extinct taxa included in this study (*Canis dirus* and *Smilodon fatalis*) are Pleistocene taxa with well-established probable diets from morphological and paleoecological studies (Van Valkenburgh 1989).

Dietary similarity between two species was calculated as a sum across the four categories. Each category had a value comprised of the square root of the product of each species' percentage for that particular dietary type. The dietary similarity of species A and species B was evaluated as follows:

$$(C_a \times C_b)^{1/2} + (I_a \times I_b)^{1/2} + (F_a \times F_b)^{1/2} + (L_a \times L_b)^{1/2}. \quad (1)$$

This process was repeated for each pair of taxa, resulting in a matrix of dietary similarity. DSM was then compared to MSI using matrix correlation analysis with Mantel's test for significance.

Phylogenetic relatedness may complicate the analysis of

TABLE 2. Results from matrix correlation analysis of phylogenetic distance matrix and matrix of similarity in morphological integration. Topology column refers to competing phylogenetic hypotheses listed in the Materials and Methods.

Group	Species	Topology	*r* with size	*r* without size
Carnivora	30	A1	0.17**	0.13
Carnivora	30	A2	0.17**	0.14
Carnivora	30	A3	0.17**	0.14
Carnivora	30	A4	0.16**	0.14
Carnivora	30	B1	0.17**	0.14
Carnivora	30	B2	0.17**	0.14
Carnivora	30	B3	0.17**	0.14
Carnivora	30	B4	0.16**	0.14
Feliformia	12	A	0.36	0.38
Feliformia	12	B	0.37	0.41
Felidae	5		0.84**	0.90*
Caniformia	18		0.33**	0.24
Canidae	5		0.58	0.78*
Arctoidea	13		0.33	0.34
Musteloidea	10	1	0.50**	0.50
Musteloidea	10	2	0.57*	0.62
Musteloidea	10	3	0.40	0.49
Musteloidea	10	4	0.46	0.56*
Mustelidae	5		0.83**	0.66

* $P < 0.10$; ** $P < 0.05$.

diet, due the possibility that more closely related taxa are more similar in diet because of common ancestry. To test for the possible influence of phylogeny, DSM was compared to the phylogenetic-distance matrix, using matrix correlation analysis with a Mantel's test for significance. Alternative phylogenetic hypotheses, listed above, yielded similar results. Correlations of DSM with each of the topologies were significant ($r = 0.22$–0.23, $P < 0.01$). As topology choice did not affect results, the following analyses and discussion refer solely to phylogenetic topology A1. Because diet is significantly correlated with phylogeny, DSM was regressed against the phylogenetic-distance matrix for topology A1. The dietary similarity residual matrix (DSRM) was compared to MSI, using matrix correlation analysis with Mantel's test for significance.

RESULTS

Phylogeny with Size

The results of the tests for the correlation of phylogeny with similarity in morphological integration are shown in Table 2 (node-based phylogenetic distance matrix), Table 3 (branch-length-based phylogenetic distance matrix), and Figure 5. All eight possible topologies for the entire order (node-based metric) showed significant correlations ($r = .17$) with similarity in morphological integration. The correlation between phylogeny and integration generally increased with less inclusive groups, although not all correlations within subgroups were significant. No significant correlation existed for either topology of the suborder Feliformia. The family Felidae, however, showed a very strong and significant correlation ($r = 0.84$) between phylogeny and integration. Within Caniformia, there was a significant correlation across the suborder, but not within the parvorder Arctoidea or family Canidae. Within the superfamily Musteloidea, topology 1 (paraphyletic Mustelidae) showed a significant correlation

TABLE 3. Results from matrix correlation analysis of branch lengths and matrix of similarity in morphological integration.

		Terminal branches		Terminal nodes	
Group	Species	*r* with size	*r* without size	*r* with size	*r* without size
Carnivora	21	0.17	0.16	0.20	0.16
Feliformia	9	0.50**	0.61**	0.54**	0.63**
Caniformia	12	0.19	0.22	0.03	0.07
Arctoidea	10	0.21	0.28	0.00	0.13
Musteloidea	8	0.32	0.35	0.10	0.19
Mustelidae	5	0.38	0.66	0.22	0.50

** $P < 0.05$.

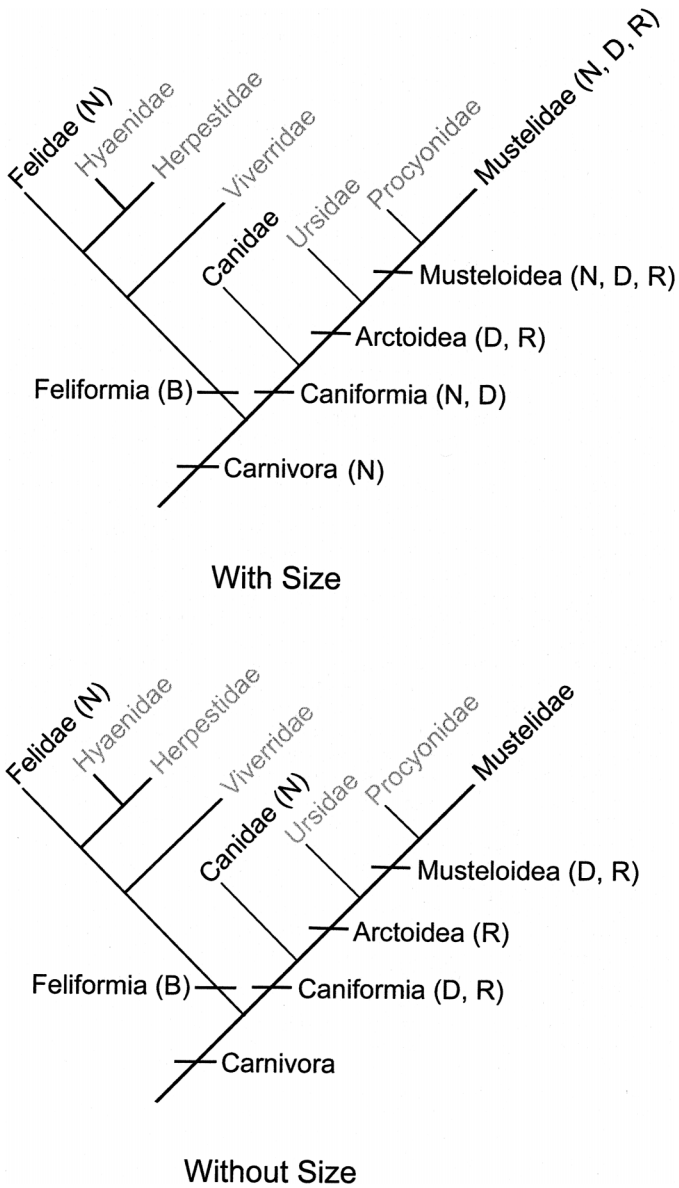

FIG. 5. One phylogenetic hypothesis for Carnivora (B2/4) showing taxa with significant or marginally significant correlations between similarity in morphological integration and phylogeny (N, node-based distances; B, branch-length-based distances), diet (D, DSM; R, DSRM), or neither. Taxa in gray type do not have enough species sampled in this study for statistical analysis.

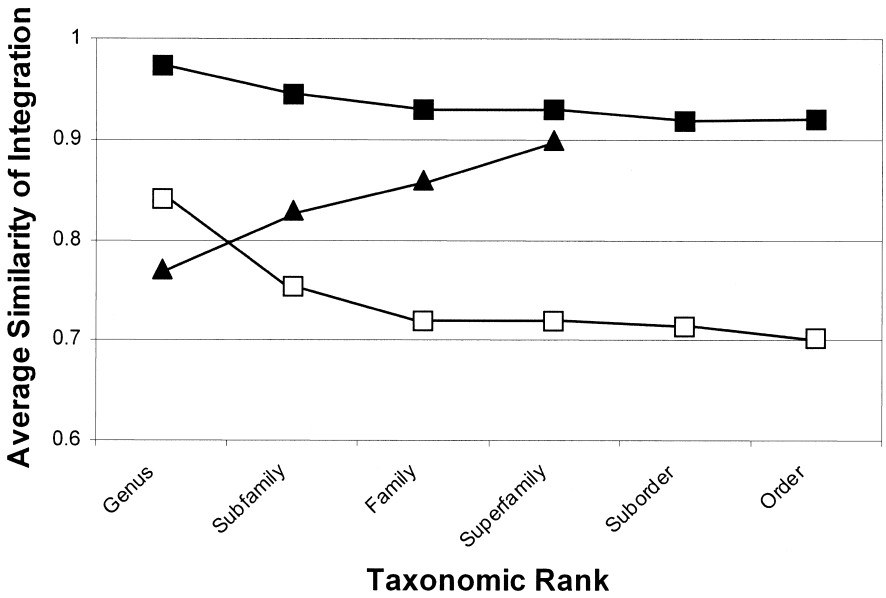

FIG. 6. Average matrix correlation between species related at increasingly disparate taxonomic levels for Carnivora (this study), with (■) and without (□) size, and platyrrhine primates (▲; Marroig and Cheverud 2001).

between phylogeny and integration, while topology 2 (monophyletic Mustelidae) showed a marginally significant correlation. Neither topology 3 nor topology 4 showed significant correlations between phylogeny and integration. The family Mustelidae showed a strong and significant correlation (r = 0.83) between phylogeny and integration.

The additional comparison of a branch-length-based metric and MSI was conducted for 21 species. In these analyses, the only significant correlation between phylogeny and integration was within the suborder Feliformia (Table 3). Both the terminal-nodes and the terminal-branches metrics recovered this significant correlation. Due to differences in taxon sampling, some less-inclusive clades, Felidae and Canidae, had fewer that five taxa in common between the molecular phylogenetic analysis used (Flynn et al. 2005) and those considered in this study.

Single-pairs analysis of matrix correlations between taxa grouped at various taxonomic levels (e.g., matrix correlations among congeneric species, confamilial genera) showed that average similarity in morphological integration slightly increased in less inclusive clades across Carnivora (Fig. 6), though the differences among taxonomic ranks were not significant (ANOVA, $F_{4,432} = 0.61$, $P > 0.05$). Data for platyrrhines (Marroig and Cheverud 2001) are presented for comparison in Figure 6. While ranges of bootstrapped data (not shown) for order, suborder, family, and subfamily comparisons of carnivorans were indistinguishable, genus-level values showed increases in overall similarity of integration. However, because there were only a few genus-level comparisons, these differences were not significant.

Phylogeny without Size

In node-based analyses without size, correlations and significance values again generally increased from higher to lower taxonomic rank, although only Felidae (r = 0.90) and Canidae (r = 0.78) showed marginally significant correlations (Table 2), in contrast to the analyses with size. An exception to this general increase was Mustelidae (r = 0.66), which did not exhibit even the marginally significant correlation between phylogeny and integration that is seen in the other families (Canidae and Felidae). Differences in tree topology did not affect results substantially, except in the case of Musteloidea, where topology 4 (monophyletic Mustelidae, r = 0.56) showed a marginally significant correlation (Table 2).

The branch-length metric showed a similar trend of increased correlation, although, again, only a few of these correlations were significant (Table 3). As in the analyses with size, the highest and only significant correlation was for the suborder Feliformia. The only groups with marginally significant correlations in the node-based phylogenetic distance analysis (Felidae and Canidae) were excluded due to low sample size (< five species).

Single-pairs analysis of matrix correlations, without size, between species related at various taxonomic levels again showed that average similarity in morphological integration within Carnivora increased with lower taxonomic rank (Fig. 6), although the differences among taxonomic ranks were still not significant (ANOVA, $F_{4,432} = 0.62$, $P > 0.05$). Order, suborder, and family values and ranges were indistinguishable, but both subfamily- and genus-level values increased in overall similarity of integration when size was removed. There was significant overlap of confidence intervals from bootstrap analysis, with the exception of the genus-level data, which overlapped only with the subfamily-level data.

Diet with Size

The results for the comparison of MSI with DSM and DSRM are displayed in Table 4. DSM was not significantly correlated with similarity in integration across the entire order, nor within Feliformia or Felidae. In contrast, this correlation was marginally significant within Caniformia (r =

TABLE 4. Results of matrix correlation analysis of dietary similarity matrix (DSM) and matrix of similarity in morphological integration (MSI), using phylogenetic hypothesis A1.

		DSM		DSRM	
Group	Species	r with size	r without size	r with size	r without size
Carnivora	30	0.09	0.12	0.05	0.04
Feliformia	12	0.06	−0.07	0.13	0.09
Felidae	5	0.01	0.18	0.48	0.28
Caniformia	18	0.27*	0.32**	0.19	0.31**
Canidae	5	0.18	0.45	0.01	0.19
Arctoidea	13	0.44**	0.33	0.40**	0.35*
Musteloidea	10	0.62**	0.49*	0.59**	0.58**
Mustelidae	5	0.74**	0.47	0.70**	0.51

* $P < 0.10$; ** $P < 0.05$.

0.27) and highly significant within the less inclusive clades Arctoidea ($r = 0.44$), Musteloidea ($r = 0.62$), and Mustelidae ($r = 0.74$). Among caniforms, only Canidae did not show a significant correlation between raw diet and integration. When the influence of phylogeny was removed, these values decreased in strength and significance, but the general pattern was similar. The correlation between DSRM and MSI was not significant across all carnivorans, within Feliformia, or within Felidae. The correlation between DSRM and MSI was not significant in Caniformia, although it was still highly significant in Arctoidea, Musteloidea, and Mustelidae. Canidae again showed no strong or significant correlation between dietary residuals and integration.

Diet without Size

Correlations between diet and integration were generally weaker and less significant when size was removed. DSM was not significantly correlated with MSI at the ordinal level, within Feliformia, or within Felidae. DSM and MSI were significantly correlated within the Caniformia ($r = 0.32$), and this correlation was marginally significant in Musteloidea ($r = 0.49$). They were not significantly correlated in Canidae, Arctoidea, or Mustelidae (Table 4).

DSRM was also not significantly correlated with MSI at the ordinal level. There was no significant increase in correlation or significance within Feliformia or Felidae. Within Caniformia, however, significant correlation with DSRM was evident (as for DSM). Correlation with DSRM again showed a variable pattern within Caniformia, increasing from Caniformia ($r = 0.31$) to Arctoidea ($r = 0.35$) to Musteloidea ($r = 0.58$). The correlations for Caniformia and Musteloidea were significant, and that for Artoidea was marginally significant. Canidae showed a very low value ($r = 0.19$), and Mustelidae showed a stronger correlation ($r = 0.51$), but none of the correlations within these less inclusive clades were significant.

DISCUSSION

Phylogeny

Previous studies of the relationship between patterns of morphological integration and phylogenetic relatedness produced mixed results. Studies at the population and subspecies levels showed little correlation with phylogeny (Steppan 1997b), while studies at the genus level (Ackermann and Cheverud 2000) showed a significant correlation with phylogeny. The single study of a higher taxonomic level, of a superfamily of neotropical platyrrhines, showed no significant correlation between phylogeny and similarity in morphological integration (Marroig and Cheverud 2001).

The current study of 30 carnivoran species, representing all terrestrial families of Carnivora, indicated that similarity in morphological integration was significantly correlated with phylogenetic relatedness within some larger clades of this order (Fig. 5; Tables 2, 3). When size-related correlation was included, several clades (Carnivora, Caniformia, Musteloidea, Mustelidae, and Felidae) displayed a significant correlation between phylogeny and integration. When size-related correlation was removed, only Felidae and Canidae displayed significant correlations among phylogeny and integration. Within clades, correlations generally increased from more-inclusive to less-inclusive subclades in both analyses, and, although many of these correlations were nonsignificant, a possible trend toward greater similarity in integration in less-inclusive clades was suggested across all carnivorans. When a branch-length-based metric was used to measure phylogeny, only Feliformia showed a strong and significant correlation, both with and without size, although it was not possible to analyze the less-inclusive clades Felidae and Canidae.

These differences between results including and removing size may reflect greater variation in body size among caniforms than feliforms. Caniforms define the full size spectrum for Carnivora (Gittleman and Purvis 1998), although, without the pinnipeds, the size ranges of the feliforms and caniforms in this study were comparable. However, caniforms may display a stronger phylogenetic signal in body size than feliforms do. Ursids and musteloids did not overlap at all in body size, with canids falling intermediate between the two. In contrast, all of the feliform families (Felidae, Viverridae, Herpestidae, and Hyaenidae) overlapped in body size. It may be hypothesized that these differences in body size distributions between feliforms and caniforms are reflected in differences between analyses with and without size. For example, if size is the dominant factor influencing trait correlations, and size is strongly coupled to phylogeny, then analyses including size will show strong correlations between phylogeny and integration. However, there was no significant correlation between similarity in morphological integration and similarity in body size (as estimated by skull length) across Carnivora or within Caniformia. Furthermore, some caniform clades showed increased correlations between phylogeny and integration when size was removed (Canidae and topology 3 of Musteloidea), which also suggests a decoupling of size and phylogeny or a decoupling of size and trait correlations. Therefore, there is not a simple relationship between size, phylogeny, and morphological integration in Carnivora, although the differences observed among Feliformia and Caniformia provide interesting avenues for future study.

Within Feliformia, only Felidae had enough species ($n = 5$) for statistical analysis. Felidae showed a strong correlation between similarity of morphological integration and phylogeny, both with and without size. As members of Felidae are

conservative in skull morphology and diet, relative to other carnivorans, this result may not be surprising. Within Caniformia, Canidae, the sister group to the remaining caniforms (Arctoidea), also showed a strong correlation between similarity of morphological integration and phylogenetic relatedness when size was removed. The canids analyzed in this study are more diverse morphologically and ecologically than the felids (Appendix 1), providing stronger additional evidence for the significance of phylogenetic relatedness to morphological integration in some clades.

Arctoidea, consisting of ursids, procyonids, and mustelids (as well as the aquatic carnivoran families Phocidae, Otariidae, and Odobenidae, which were not considered in this study) showed a low and nonsignificant correlation between phylogeny and similarity of morphological integration in analyses with and without size. Musteloidea showed a higher correlation of similarity of morphological integration with phylogeny, in all alternative phylogenetic topologies, although different topologies showed significant correlations between phylogeny and similarity of morphological integration in analyses with and without size. The most significant result without size was for topology 4 ($r = 0.56$, $P = 0.07$). It is interesting that, of the four examined topologies for Musteloidea, the two topologies with a monophyletic Mustelidae (topologies 2 and 4) were more highly significant in analyses without size than topologies hypothesizing a paraphyletic Mustelidae. In contrast, analyses with size showed significant correlations for topologies 1 and 2, which were similar in placing *Ailurus* outside of the rest of the musteloids, but differ in the monophyly of Mustelidae. Because all of these taxa overlapped in size, a simple size-based explanation is not sufficient to explain these differences in results.

The traditional family Mustelidae (including Mephitinae) is the only family within Musteloidea with a sample size sufficient for analysis ($n = 5$). Mustelidae did not show a significant correlation between phylogeny and similarity of morphological integration without size, but did show a significant correlation when size was included. This would suggest that size and phylogeny are correlated. However, skunks fall within the range of body size for other mustelids, although they comprise a much smaller range than all nonmephitine mustelids. Further analysis of additional musteloids is necessary to determine the relationship between phylogeny, body size, and integration in this clade.

Between the three families analyzed (Felidae, Canidae, and Mustelidae) three different results are obtained. Felidae showed significant correlations between phylogeny and similarity of morphological integration with and with size, Canidae showed significant correlations only without size, and Mustelidae showed significant correlations only with size. This suggests that integration and phylogeny is most strongly correlated in felids, while the relationships between phylogeny, body size, and integration are more complex in canids and musteloids. These results demonstrate that canids do display similarity in integration related to phylogenetic distance and that this phylogenetic signal is not due simply to size-related correlations. In contrast, the correlation between phylogeny and integration in mustelids might reflect phylogenetic structure in body-size distributions, but, as with Caniformia, there was not a significant correlation between similarity in body size and similarity in morphological integration within Musteloidea. Clearly, there was no single and universal relationship between phylogeny and integration. There was a possible general trend toward increasing similarity in integration with more closely related taxa, as shown by increasing correlations between phylogeny and integration in less-inclusive subclades within larger clades (e.g., Felidae vs. Feliformia, or Mustelidae vs. Musteloidea vs. Arctoidea), but it was not significant in this sample.

This general trend of increasing correlation between phylogeny and similarity of morphological integration in less-inclusive clades is also suggested by analysis of a branch-length-based phylogenetic-distance matrix (Table 3), although only Feliformia showed a significant correlation in these analyses. As all other comparisons at or below the subordinal level were within the Caniformia, this may suggest that a much stronger correlation between phylogeny and integration exists in Feliformia than in Caniformia. The exclusion of family-level analyses of Felidae and Canidae, due to small sample sizes, may have been a factor in this result, as these two families were the only groups showing a significant correlation in the node-based analyses without size. Examination of additional feliform taxa with branch-length data is necessary to determine if this correlation between phylogeny and patterns of integration is a general characteristic of the suborder.

Alternatively, the increased correlations in less-inclusive clades could simply be due to smaller sample sizes. To test this potential effect, random sets of species from the entire dataset were selected and analyzed. In all cases, these groupings did not produce correlations above that reported for the entire order ($r = 0.13$) and all results were nonsignificant. Overall, these differences suggest that phylogeny is generally correlated with morphological integration across all carnivorans, in that more closely related species are generally more similar in patterns of integration than more distantly related species are, although it does not fully explain similarity in patterns of morphological integration.

Single-pairs analysis also showed a tendency toward lower similarity across more inclusive clades, from an average of $r = 0.84$ for congeneric species to $r = 0.69$ for species related only at the ordinal level, without size, and $r = 0.97$ and 0.92, respectively, with size (Fig. 6). Although confidence intervals for all levels, except the genus level, overlapped (and thus are nonsignificant), average overall similarity generally increased in less-inclusive clades. Because this dataset focused on more-inclusive clades, there were only three pairs of congeneric species (*Canis*, *Procyon*, and *Prionailurus*), and so the result for the generic rank is tentative. Further analysis of congeneric species are necessary to determine if closely related carnivoran species are more similar in integration than more distantly related species, but there were no significant differences among more-inclusive clades. This result is consistent with the results described above in that only some clades showed a strong correlation between phylogeny and integration. Therefore, there may be no size-independent trend across all Carnivora, but only within subclades.

Figure 6 also displays similar measures from a study of neotropical platyrrhines (Marroig and Cheverud 2001). Although our studies differ in some of the landmark measures

used, it is unlikely that two similar studies using a large number of three-dimensional landmarks, evenly distributed across the cranium, would produce different results due to landmark choice alone. Neither study showed a significant increase in similarity of integration with less-inclusive clades, but the slope of the carnivoran line, from this study, does show an increase in average similarity of integration in less-inclusive clades, whereas the platyrrhine line shows a slight decrease in average similarity of integration in less-inclusive clades. Again, better sampling of congeneric data is necessary to determine whether carnivorans do show a significant increase in similarity of integration in less-inclusive clades, but these preliminary results suggest that there may be significant differences between these two large clades. It is likely that future analyses will support these results, because, in contrast to this study of carnivorans, Marroig and Cheverud (2001, 2005) did not find any significant correlations among phylogeny and integration in platyrrhine primates, but instead observed that similarity in morphological integration was a stronger reflection of similarity in diet.

Diet

Both DSM and DSRM returned similar results, differing mainly in the magnitude, not the general pattern, of correlations with similarity of morphological integration across Carnivora. When all carnivorans were compared, neither measure of dietary similarity was significantly correlated with similarity of morphological integration. The correlations remained low and nonsignificant within feliforms and felids. Initially, one might expect this result to simply reflect a lack of dietary diversity within the Feliformia. This reasoning may explain the result found within Felidae, as only *Prionailurus viverrinus* deviates from a strictly carnivorous diet. However, a great deal of dietary diversity exists within the other families of the Feliformia, including the frugivorous viverrid *Paradoxurus* and the insectivorous hyaenid *Proteles*. Therefore, these results clearly demonstrate that diet is not strongly correlated with morphological integration within carnivoran suborder Feliformia.

In contrast to this result, dietary similarity was significantly correlated with similarity of morphological integration in the Caniformia, with the exception of the DSRM with size analysis. When less-inclusive groups were analyzed separately, it was clear that this relationship was not consistent across the suborder. Within the Canidae, DSM and DSRM were not significantly correlated with MSI. Again, this result is probably not due solely to dietary diversity among canids, especially because the five species in this study include invertivores and omnivores, as well as more typical carnivores. Within the Arctoidea, the correlation between DSRM and MSI was marginally significant and moderately high without size and highly significant with size. The correlation between DSM and MSI was not significant without size but was highly significant with size. DSM and DSRM were both strongly correlated with MSI in the Musteloidea with and without size. Mustelidae showed a significant correlation between similarity of integration and both measures of dietary similarity, but only when size was included.

Overall, these results show that diet is strongly correlated with integration, but only within the arctoid subclade of caniform carnivorans. No significant correlation existed between diet and morphological integration for all Carnivora, Feliformia, Felidae, or Canidae. This is particularly interesting as Feliformia, Felidae, and Canidae all showed significant correlations with phylogeny in analyses without body size. In contrast, clades that did not show a strong correlation between similarity of morphological integration (without size) and phylogeny (Caniformia, Arctoidea, Musteloidea) did show a strong correlation between diet and integration. Mustelidae did not show a strong correlation between similarity of morphological integration (without size) and phylogeny or diet but did with both when size was included. The differences between results for Musteloidea and Mustelidae may be due to the general uncertainty in their interrelationships or to a strong correlation between dietary similarity and morphological integration within Procyonidae (untested). Dietary diversity should again be considered, as mustelids are less diverse in diet than are procyonids or ursids. However, mustelids are also less diverse in diet than feliforms and, arguably, than canids, and yet Mustelidae did not display a strong correlation between morphological integration and phylogeny. While including size in the analyses increased correlations and significances, it did not greatly change the results. Mustelidae was the only clade that only showed a significant correlation when size was included, in contrast to the influence of size inclusion on the analyses of phylogeny. As discussed above, diet is hypothesized to influence the functional integration of traits involved in mastication, which is reflected in patterns of morphological integration. However, it appears that this influence, while strong and significant in arctoids, is limited to smaller clades, without a more general correlation with patterns of morphological integration.

In conclusion, it is evident that both diet and phylogeny are important considerations for interpretation of evolutionary patterns of morphological integration. These two factors were significantly correlated with similarity of morphological integration, but mainly in different clades. Phylogeny had a more universal correlation with integration when size was included, possibly influenced by modern body size distributions, while the inclusion of size did not greatly affect the correlation between diet and integration. Without size, phylogeny was often more strongly correlated with integration patterns within Feliformia and Canidae, while the correlation with between integration and diet was significant only in the caniforms. The lack of a strong correlation between diet and integration within Canidae, and only when size was included in Mustelidae, suggests that this correlation may be driven by the inclusion of other arctoid taxa (bears and raccoons) in the analysis. Although these other arctoids are more ecologically diverse than most mustelids, canids, or felids, they are not more diverse than the feliform civets (Viverridae) and mongooses (Herpestidae) included in this study, precluding a simple solution based on differences in dietary diversity. Further study of additional taxa within Arctoidea and the feliform families Viverridae and Herpestidae will aid in isolating these and other potential factors related to the morphological integration of the skull.

From these analyses, it is clear that the results found for

platyrrhine primates or other mammalian taxa cannot simply be extended to all mammals. Furthermore, it appears that lower-taxonomic-scale analyses cannot be simply extended to higher taxonomic scales. These analyses revealed clear differences in morphological integration between large clades, most notably between the relationships among phylogeny, diet, and morphological integration in Feliformia and Caniformia. Of particular note is the marked difference between Feliformia and Caniformia, in that Feliformia showed a strong correlation between integration and phylogeny, while Caniformia showed a strong correlation between integration and diet. Many hypotheses have been proposed regarding the relationship of morphological integration and morphological variation (Olson and Miller 1958; Vermeij 1973; Wagner 1996; Emerson and Hastings 1998; Bolker 2000), which ultimately provide the raw material for morphological evolution. Thus, these observed differences in integration between Feliformia and Caniformia may be related to differences in morphological evolution between these two groups. Specifically, clades with significant correlations between morphological integration and ecology (diet) may show greater variation in patterns of integration, and subsequently greater morphological variation, than clades in which similarity in morphological integration simply reflects phylogeny. Future analyses will focus on determining the broader evolutionary significance of these different patterns and how they may relate to differences in the morphological evolution of the Feliformia and Caniformia. The analyses presented here represent the first comparisons of patterns of morphological integration across an order and display previously unrecognized complexity in cranial integration within Mammalia.

These results demonstrate that, while evolutionary history (phylogeny) is more universally correlated with cranial integration, diet is a significant influence on cranial integration in some less-inclusive clades. These differences across taxa provide an important foundation for further examination of variation in modularity and correlated trait evolution, as well as differences in microevolutionary and macroevolutionary patterns of cranial integration.

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APPENDIX 1.

Species list. Dietary categories used in the construction of the dietary similarity matrix are carnivore (*C*), invertivore (*I*), frugivore (*F*), and folivore (*L*).

Family	Species	Common name	Specimen number	Diet			
				C	*I*	*F*	*L*
Canidae	*Canis lupus*	wolf	18	1.00	0.00	0.00	0.00
	Canis dirus	dire wolf (extinct)	20	1.00	0.00	0.00	0.00
	Cerdocyon thous	crab-eating fox	18	0.40	0.60	0.00	0.00
	Otocyon megalotis	hoary zorro	16	0.00	1.00	0.00	0.00
	Vulpes vulpes	red fox	22	0.40	0.30	0.30	0.00
Ursidae	*Ursus americanus*	black bear	15	0.00	0.30	0.40	0.30
	Melursus ursinus	sloth bear	15	0.00	0.70	0.20	0.10
	Tremarctos ornatus	spectacled bear	15	0.00	0.10	0.70	0.20
Musteloidea	*Ailurus fulgens*	red panda	16	0.00	0.00	0.30	0.70
Procyonidae	*Procyon lotor*	raccoon	18	0.25	0.25	0.25	0.25
	Procyon cancrivorus	crab-eating raccoon	18	0.30	0.50	0.20	0.00
	Nasua nasua	coatimundi	15	0.00	0.70	0.30	0.00
	Potos flavus	kinkajou	20	0.00	0.00	1.00	0.00
Mephitinae	*Mephitis mephitis*	striped skunk	15	0.25	0.25	0.25	0.25
	Spilogale putorius	spotted skunk	17	0.40	0.40	0.20	0.00
Mustelidae	*Taxidea taxus*	badger	15	1.00	0.00	0.00	0.00
	Martes pennanti	fisher	15	0.90	0.00	0.10	0.00
	Gulo gulo	wolverine	16	1.00	0.00	0.00	0.00
Viverridae	*Paradoxurus hermaphoditus*	palm civet	19	0.10	0.10	0.80	0.00
	Genetta genetta	common genet	20	1.00	0.00	0.00	0.00
Felidae	*Smilodon fatalis*	sabre-toothed cat (extinct)	20	1.00	0.00	0.00	0.00
	Acinonyx jubatus	cheetah	15	1.00	0.00	0.00	0.00
	Lynx rufus	bobcat	16	1.00	0.00	0.00	0.00
	Prionailurus viverrinus	fishing cat	15	0.70	0.30	0.00	0.00
	Prionailurus bengalensis	bengal cat	18	1.00	0.00	0.00	0.00
Herpestidae	*Galidia elegans*	Malagasy ring-tailed mongoose	15	0.70	0.20	0.10	0.00
	Herpestes ichneumon	Egyptian mongoose	21	0.70	0.20	0.10	0.00
	Ichneumia albicauda	white-tailed mongoose	15	0.20	0.70	0.10	0.00
Hyaenidae	*Proteles cristatus*	aardwolf	15	0.00	1.00	0.00	0.00
	Crocuta crocuta	spotted hyaena	18	1.00	0.00	0.00	0.00