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The influence of character correlations on phylogenetic analyses: a case study of the carnivoran cranium

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Introduction

Character independence is a major assumption in many morphology-based phylogenetic analyses (Felsenstein, 1973; Emerson and Hastings, 1998). However, the fact that most studies of modularity and morphological integration have found significant correlations among many phenotypic traits worryingly calls into question the validity of this assumption. Because gathering data on character correlations for every character in every taxon of interest is unrealistic, studies of modularity are more tractable for assessing the impact of character non-independence on phylogenetic analyses in a real system because modules summarise broad patterns of trait correlations. In this study, we use empirically derived data on cranial modularity and morphological integration in the carnivoran skull to assess the impact of trait correlations on phylogenetic analyses of Carnivora.

Carnivorans are a speciose clade of over 270 living species, with an extremely broad range of morphological and dietary diversity, from social insectivores to folivores to hypercarnivores (Nowak, 1999; Myers, 2000). This diversity offers many opportunities to isolate various potential influences on morphology, and, in this case, to study the effects of trait correlations on cranial morphology. Carnivorans also have an excellent fossil record, providing the opportunity to examine morphologies not represented in extant species, such as in the sabre-toothed cat *Smilodon*. Perhaps most importantly, several recent molecular and morphological studies of carnivoran phylogeny (Hunt and Tedford, 1993; Wyss and Flynn, 1993; Tedford *et al.*, 1995; Flynn and Nedbal, 1998; Flynn *et al.*, 2000, 2005; Flynn and Wesley-Hunt, 2005; Wesley-Hunt and Flynn, 2005; Flynn *et al.*, this volume) provide the necessary resolution to assess the influence of character correlations on morphology-based phylogenetic analyses.

Carnivoran Evolution: New Views on Phylogeny, Form, and Function, ed. A. Goswami and A. Friscia. Published by Cambridge University Press.

Here, we present morphometric analyses of 47 species (38 extant and 9 fossil), representing 44% of extant genera, and 15% of extant species, and including all extant terrestrial families and the extinct families Nimravidae and Amphicyonidae. Using both simulations and empirically derived data, we test the following specific questions: (1) Do individual modules differ in the relationship between shape and phylogenetic relatedness? (2) Do individual modules differ in the relationship between similarity of pattern of integration and phylogenetic relatedness? (3) Do highly correlated characters show significantly more coordinated shifts in discrete character states than do uncorrelated characters? (4) Have correlated characters significantly misled previous phylogenetic analyses of Carnivora based on morphology?

Integration and modularity

The idea that the skull is composed of a series of autonomous 'functional components' dates to van der Klaauw (1948–1952) and has since become an important framework for examining the evolution of cranial morphology in mammals (Moss and Young, 1960; Schwenk, 2001). The concept of independent evolutionary units, however, has appeared in many forms before and since then. Developmental studies in the early twentieth century focused on morphogenetic fields and their evolutionary importance as 'discrete units of embryonic development', an idea contested at the time by geneticists who argued that the gene is the primary unit of evolutionary significance (Gilbert *et al.*, 1996). Decades later, and with the emergence of evolutionary developmental biology, it is clear that aspects of both positions may be valid. Structures and processes as diverse as signalling pathways and colonial individuals have been reasonably described as independent units of evolutionary change (Schlosser and Wagner, 2004). Yet, despite the early recognition of evolutionary 'parts' in genetic, developmental, and morphological systems, it is only in recent years that these fields have begun exploring the relationships among these different scales. The study of modules, autonomous subsets of highly correlated traits within larger systems of any type, and its application to understanding diverse biological systems (Schlosser and Wagner, 2004), thus may herald a new, more inclusive synthesis of evolutionary theory.

For morphologists and paleontologists, this emergence of modularity is particularly important, because the quantitative methods used to identify modularity can be applied equally to living, extinct, or rare taxa. Perhaps the first quantitative examination of phenotypic trait relationships can be attributed to Olson and Miller (1951), expounded in their book *Morphological Integration* (1958). Their argument was a simple one: many trait changes that occur during

the course of evolution do not occur independently of each other. More specifically, traits that are related by proximity in development or function have greater influence on each other than on more distant traits.

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; Atchley and Hall, 1991; Cheverud, 1996b; Wagner, 1996; Wagner and Altenberg, 1996; Emerson and Hastings, 1998; Bolker, 2000; Polly, 2005; Goswami and Polly, 2010). Thus, integration and modularity have been tied to some of the most fundamental and interesting questions in morphological evolution, including evolvability and constraints on morphological variation, the generation of novelties, and the production of morphological diversity (Vermeij, 1973; Wagner, 1995; Cheverud, 1996b; Wagner, 1996; Wagner and Altenberg, 1996; Chernoff and Magwene, 1999; Polly *et al.*, 2001; Eble, 2004; Shubin and Davis, 2004).

Integration involves linked interactions among traits, whereas modularity emphasises the autonomy of units. In a sense, integration and modularity can be taken as antagonistic forces, because, when applied to the same structure or process, they describe the opposite relationships among characters. However, both integration and modularity are structured in a hierarchical framework. Modules are autonomous from other modules, but the elements that compose them are highly integrated within themselves. Likewise, integration of genetically, developmentally, or functionally related traits implies autonomy from unrelated traits. Units that are modular or autonomous may, and in most cases must, interact with other units within the larger system. This implicit inverse relationship between the effects of integration and modularity is central to their potential importance to the evolutionary process.

Total independence among traits would allow each trait to vary independently and to respond to selection pressures in an optimal way. Correlations among traits may limit the variation of any individual trait by necessitating a coordinated response from several traits, perhaps preventing any one trait from responding optimally to selection. Conversely, functional or developmental units that require coordination among traits would suffer from complete independence among traits (in a sense, all traits independently have the same selective optimum).

Wagner and Altenberg (1996) proposed an evolutionary mechanism for modifying the relationships among traits: new modes of integration arise to link traits involved in new functional or developmental interactions, while new modularity (parcellation or fragmentation) decouples previously restrictive relationships (Figure 5.1). Some researchers have also hypothesised that modularity has generally increased during the course of evolution to circumvent

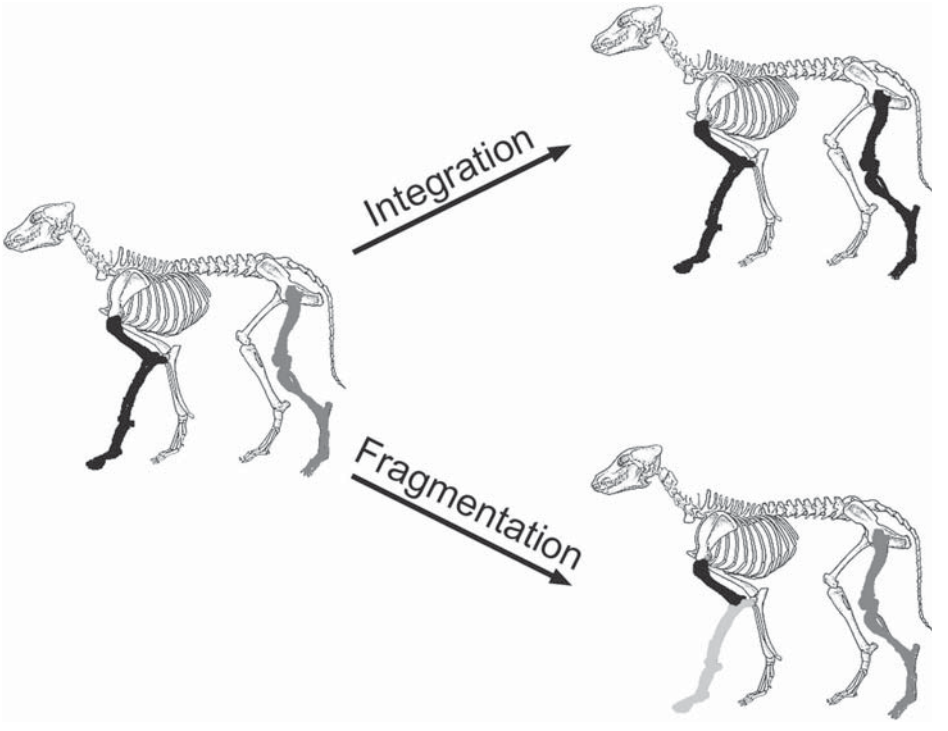

Figure 5.1 For colour version, see Plate 6. The two paths by which modules may evolve: integration, where ancestrally independent modules evolve strong correlations; or fragmentation, where ancestrally correlated traits become independent of each other, shown in the postcranial skeleton of a dog. Elements shaded with the same colour are integrated.

canalisation, the evolution of developmental constraints as systems become more complex, and its genetic counterpart, pleiotropy (Vermeij, 1973; Wagner and Altenberg, 1996). Because fragmentation of parts increases the scope for each part to vary and respond to selection, many have considered fragmentation to increase the 'adaptability' or 'evolvability' of organisms.

The breadth of studies of morphological integration has extended greatly since the publication of Olson and Miller's (1958) book, and the diversity of research in integration is apparent from contents of recent published collections (Pigliucci and Preston, 2004; Schlosser and Wagner, 2004). In recent years, morphological integration has been empirically or theoretically tied to quantitative genetics, molecular pathways, novelty, life-history strategies, and macroevolutionary trends (for recent reviews, see Pigliucci and Preston, 2004; Schlosser and Wagner, 2004).

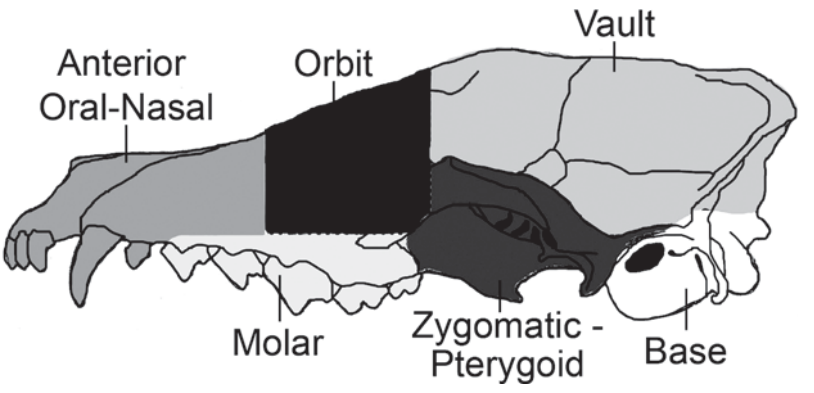

Figure 5.2 For colour version, see Plate 7. The six morphometrically derived cranial modules (Goswami, 2006a) upon which analyses of discrete character evolution are based.

The skull is a particularly good system to test for morphological integration and modularity, as it is a unified structure, yet is also both functionally and developmentally complex. The skull serves several functions (Moss and Young, 1960; Schwenk, 2001), from feeding and respiration, to housing the sensory organs and protecting the brain. Developmentally, in mammals it arises from two major tissues, the neural crest and the paraxial mesoderm, and is composed of both dermal and endochondral bones (Thorogood, 1993). The complexity of the skull thus provides many potential functionally or developmentally integrated units for assessing morphological integration, modularity, and their evolutionary significance (Atchley *et al.*, 1982; Cheverud, 1982, 1988, 1989, 1995, 1996a,b; Zelditch, 1988; Zelditch and Carmichael, 1989a, 1989b; Steppan, 1997; Ackermann and Cheverud, 2000, 2004; Badyaev and Foresman, 2000, 2004; Marroig and Cheverud, 2001; Zelditch *et al.*, 2001; Marroig *et al.*, 2004; Goswami, 2006a, 2006b, 2007a, 2007b).

Several recent studies have focused on modularity and integration in the carnivoran cranium (Goswami, 2006a, 2006b; Goswami and Polly, 2010). One study demonstrated that patterns of phenotypic modularity are strongly conserved in the cranium of carnivorans (Goswami, 2006a). Morphometric analyses of 3D cranial landmarks identified six sets of traits that were consistently recovered in the examined species (Figure 5.2): anterior oral–nasal; molar; orbit; zygomatic–pterygoid; vault; and basicranium. Correlations among traits that were not in the same cluster were consistently zero or not significantly different from zero. While all of the six groups of traits fulfilled the practical definition of phenotypic modularity, having significantly stronger correlations

within the module than across modules in at least some taxa. However, only three modules (anterior oral–nasal, molar, and basicranial) were significantly integrated in most taxa. In contrast, the orbit, zygomatic–pterygoid region, and cranial vault were not integrated in most taxa.

Correlated characters and phylogeny analysis

Modularity and integration have important consequences. They describe the correlated evolution of characters, and character independence is a well-known requirement of phylogenetic analysis (Kluge and Farris, 1969; Felsenstein, 1973, 1985; Kluge, 1989; Kluge and Wolf, 1993; Kangas *et al.*, 2004). Correlated characters cheat the parsimony algorithm by causing the same underlying evolutionary change to be counted more than once, spuriously increasing the signal-to-noise ratio. If character correlations are pervasive, treating characters as independent may mislead interpretations of phylogenetic relationships among taxa. However, determining when two discrete characters are correlated can be difficult because the limited number of character states combined with the fairly small number of taxon observations in most data sets leave very little statistical power to detect a correlation.

Because of the great potential of correlated character evolution to skew phylogenetic analyses, many studies have focused on estimating the effects of correlated characters on tree topologies, tree lengths, and tree support (Wagner, 1998; Huelsenbeck and Nielsen, 1999; Sadleir and Makovicky, 2008) and on identifying correlated characters from character distributions or character matrices (Read and Nee, 1995; Maddison, 2000; O'Keefe and Wagner, 2001). One of the most conservative methods considers characters that have identical state distributions (Harris *et al.*, 2003). Perfectly correlated characters are qualitatively evaluated for anatomical, developmental, or functional links suggesting that the correlation is due to biological interaction, in which case one of the characters is dropped or the two are recoded as a single composite character. While this method is unlikely to mistakenly conflate two uncorrelated characters, it will miss characters with an underlying and more subtle biological correlation, as can be ascertained qualitatively or with statistical analysis of continuous quantitative data, but whose discrete character states are not identical. A less conservative method uses principal coordinates analysis (PCO) to confirm correlations between characters that do not have identical state distributions (Naylor and Adams, 2001). Like the method of Harris *et al.* (2003), potentially correlated characters are first identified on the basis of anatomical, developmental, or functional criteria and then quantitatively assessed for whether they group in PCO space. The multivariate PCO space is derived

from a pairwise character distance matrix such that characters whose states are distributed similarly across taxa will cluster together. A close clustering is interpreted as supporting the hypothesis that the characters are correlated, whereas a significantly more distant clustering is interpreted as falsifying that hypothesis.

A consistent drawback in most existing studies examining the effect of correlated characters on phylogenetic analyses is that they do not use an independent measure of character correlations, or rigorously identify correlated characters a priori. Here, we used the observed differences in the cranial modules of the carnivoran skull and the quantitatively derived correlations among cranial traits, described above, to address whether correlated characters influence phylogenetic analyses of Carnivora. First, we examined whether there are differences among the modules in the relationship between phylogeny and module shape, thereby testing whether some cranial modules better reflect phylogenetic relationships among carnivorans. We also expanded the previous studies of modularity and integration in the carnivoran skull, combining the topics discussed above to establish whether the six cranial modules differ in the relationship between phylogenetic relatedness and within-module similarity in morphological integration. We used both methods described above to assess the effects of empirically derived trait correlations on the distribution of discrete character states in Carnivora, first assessing the power of the two methods using Monte Carlo simulations. Lastly, we examined previous morphology-based phylogenetic analyses of Carnivora to assess whether the focus on basicranial and molar traits is justified or has consistently misled interpretations of the relationships among carnivorans.

Methods

Phylogenetic signal in module shape and integration

Specimens

Three-dimensional landmark data were gathered with an Immersion Microscribe G2X 3-D digitiser. Fifty-one landmarks were gathered from across the skull (Figure 5.3) from a total of 744 specimens, representing 47 species (9 extinct, 38 extant; Table 5.1). Landmarks were distributed across the skull and are assigned to one of the six modules based on previous study of correlations (Goswami, 2006a).

Module shape

To test if modules differ in their relationship to phylogeny, each module was oriented across all 47 taxa with Generalised Procrustes Analysis, and partial

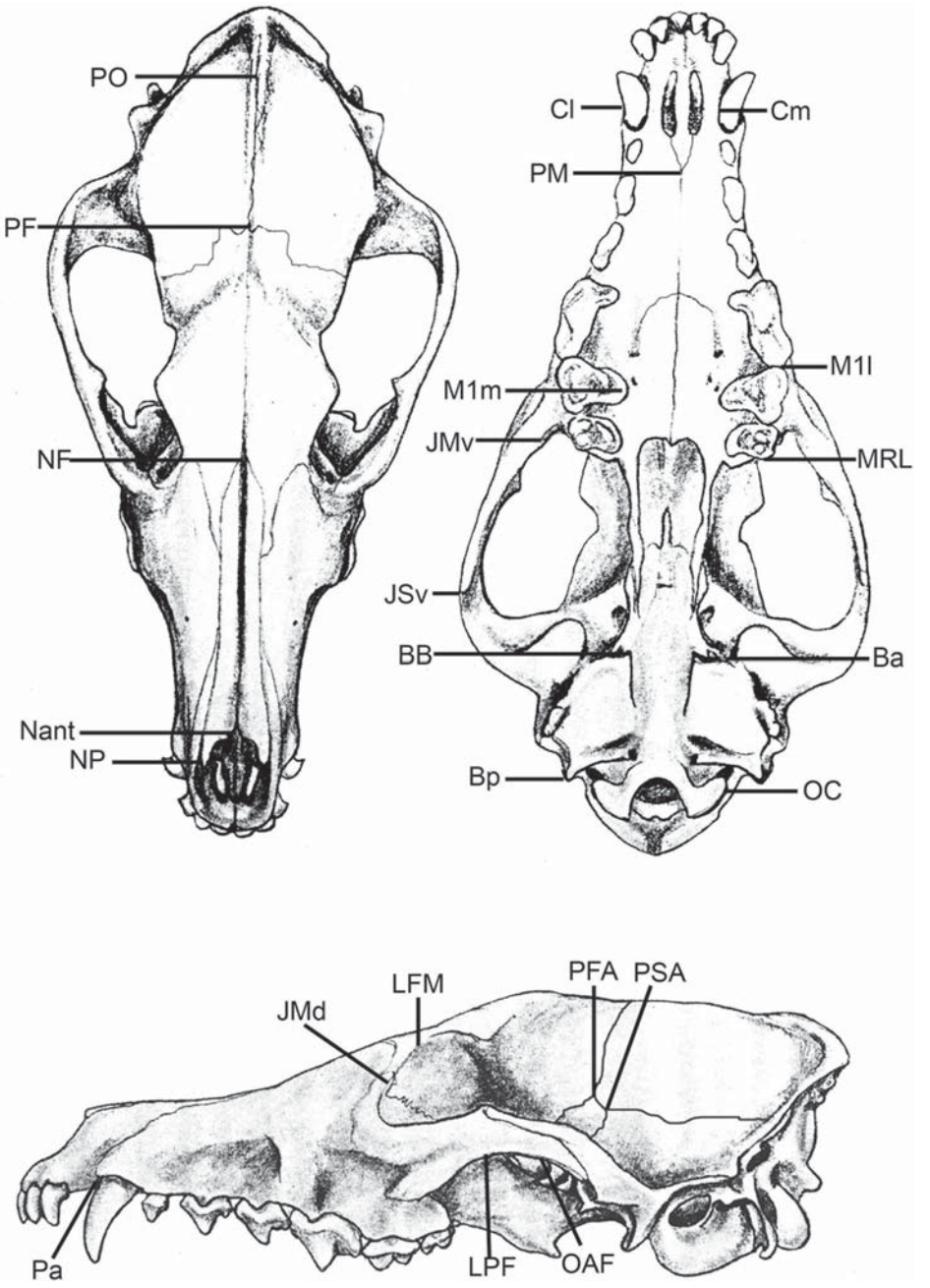

Figure 5.3 The 51 3D landmarks used in the analyses of shape disparity and integration. Symmetrical landmarks are represented by two numbers and shown on one side only.

Table 5.1 List of species and numbers of specimens used in analyses.

Suborder	Family	Species
Caniformia	Amphicyonidae	*Daphoenus* sp.* 11
	Canidae	*Hesperocyon* sp.* 13
		Mesocyon sp.* 12
		Canis lupus 18
		*Canis dirus** 20
		Cerdocyon thous 18
		Otocyon megalotis 16
		Vulpes vulpes 22
	Ursidae	*Ursus americanus* 14
		Melursus ursinus 15
		Tremarctos ornatus 15
		Ailuropoda melanoleuca 15
	Ailuridae	*Ailurus fulgens* 16
	Mephitidae	*Mephitis mephitis* 15
		Spilogale putorius 17
	Procyonidae	*Procyon lotor* 18
		Procyon cancrivorous 18
		Potos flavus 20
		Nasua nasua 15
	Mustelidae	*Melogale personata* 15
		Meles meles 15
		Enhydra lutris 15
		Martes pennanti 15
		Taxidea taxus 15
		Gulo gulo 16
Feliformia	Nimravidae	*Hoplophoneus* sp.* 19
		Dinictis sp.* 19
	Nandiniidae	*Nandinia binotata* 16
	Felidae	*Acinonyx jubatus* 15
		Lynx rufus 16
		Felis viverrina 15
		Felis bengalensis 18
		*Panthera atrox** 11
		*Smilodon fatalis** 20
	Viverridae	*Paradoxurus hermaphroditus* 19
		Civettictis civetta 15
		Genetta genetta 20
	Eupleridae	*Eupleres goudotii* 12
		Cryptoprocta ferox 13
		Fossa fossana 15
		Galidia elegans 15

Table 5.1 (*cont.*)

Suborder	Family	Species
	Herpestidae	*Cynictis penicillinatus* 15
		Herpestes ichneumon 21
		Ichneumia albicauda 15
	Hyaenidae	*Proteles cristatus* 15
		Crocuta crocuta 18
		Thalassictis sp.* 13

Note: *Indicates extinct species.

Procrustes distance was calculated for each pair of species. This quantification was repeated for each of the six cranial modules (Figure 5.2), resulting in six matrices of module distance across all 47 taxa. A patristic distance matrix was constructed using recent phylogenetic analyses (Figure 5.4), primarily based on molecular data for Recent taxa (Flynn *et al.*, 2005; Wesley-Hunt and Flynn, 2005). The six matrices of module distance were each compared to the patristic distance matrix using matrix correlation analysis with Mantel's test (10,000 repetitions) for significance.

Module integration

To test if the patterns of integration within modules differ in their relationship to phylogeny, correlation matrices were generated for each of the six modules (Figure 5.2) for each species. A matrix of similarity of integration (MSI) for each module was generated by pairwise matrix correlation analysis of species-specific correlation matrices. The six module MSIs were then compared to the patristic distance matrix using matrix correlation analysis with Mantel's test for significance.

Monte Carlo simulations

We assessed the power of existing methods for identifying correlation in character matrices using Monte Carlo simulations. We simulated character state evolution using a threshold model in which the state would change depending on the change in an underlying continuous variable (Otto and Day, 2007). A state change was triggered when the underlying continuous change was greater than a threshold value. Continuous changes were drawn from normal distributions, each with a mean of 0.0 and standard deviation of 1.0. The probability of state changes per step was controlled by setting the threshold to the appropriate number of standard deviations above or below 0.0.

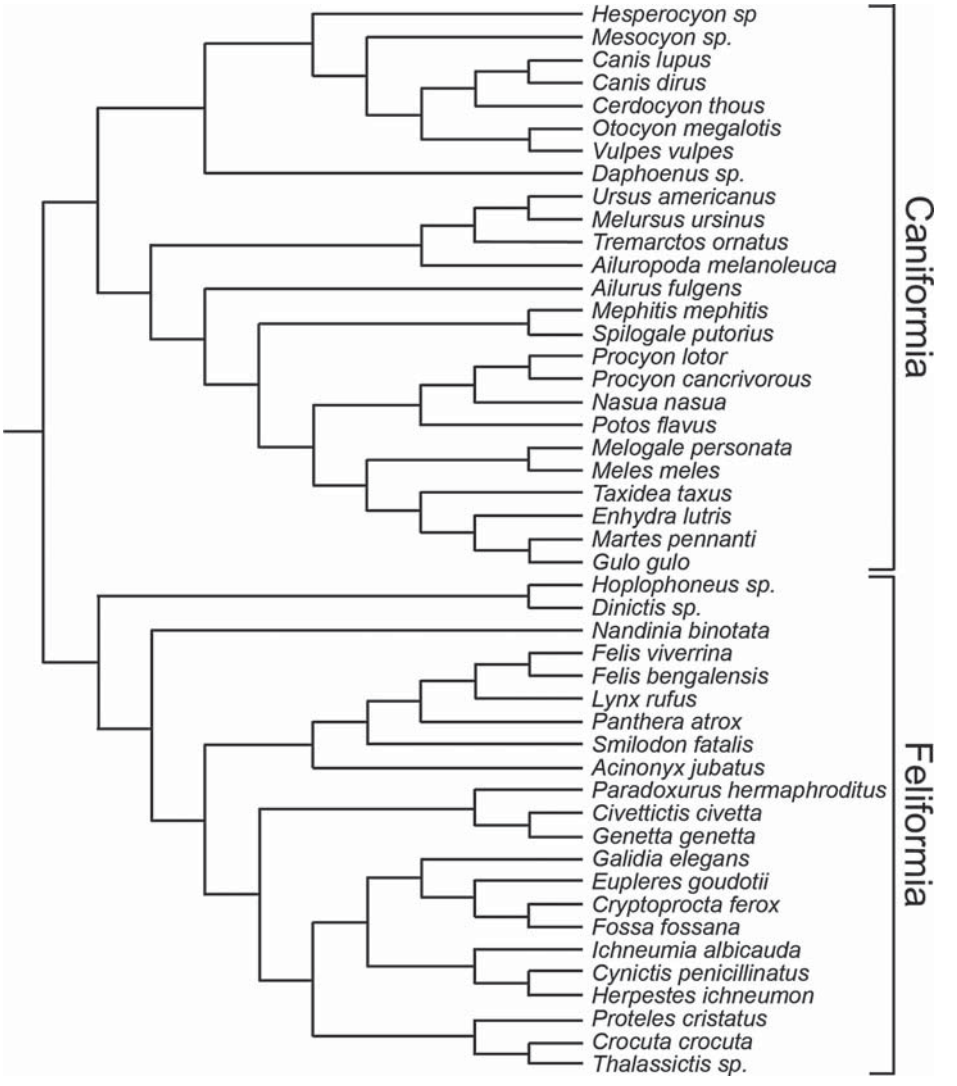

Figure 5.4 The phylogenetic tree for Carnivora (Flynn *et al.*, 2005; Flynn and Wesley-Hunt, 2005) that provided the model for the Monte Carlo simulations of discrete character evolution.

One random number was selected per character per step, yielding a k length vector $\mathbf{r}$ of random changes at each step, where k is the number of characters.

Correlations were introduced by dividing characters into blocks associated with the six cranial modules described above and imposing the corresponding module correlation onto the underlying continuous random variables for each block. The module correlations were empirically derived from the same

carnivoran taxa as used in this study (Goswami, 2006a). The following mean correlations were used for each module: Anterior Oral–Nasal, 6 characters, $r = 0.73$; Molar, 5 characters, $r = 0.47$; Orbit, 5 characters, $r = 0.37$; Zygomatic–Pterygoid, 8 characters, $r = 0.40$; Cranial Vault, 4 characters, $r = 0.40$; Basicranium, 4 characters, $r = 0.64$ (Figure 5.2). Correlations between traits from different modules were all set at 0.

To impose the empirical character correlations onto the continuous random variables, the Cholesky decomposition **G** of a $k \times k$ matrix of pairwise correlation coefficients (where k is the number of characters being simulated) was multiplied by the k length vector **r** of random changes in the continuous traits as follows to give the k length vector **r*** of correlated random changes: $\mathbf{r}^* = \mathbf{r} \cdot \mathbf{G}$. Character state changes were assessed by applying the threshold criterion to **r***. Note that even strong correlation in the underlying continuous variables does not necessarily result in perfect correlation among discrete character state changes (Figure 5.5a).

Character evolution was simulated on a tree with 47 tips (Figure 5.4), corresponding to taxa in which character correlations were studied in previous analyses (Goswami, 2006a), and the same topology as recent phylogenetic analyses of Carnivora (Flynn *et al.*, 2005; Flynn and Wesley-Hunt, 2005). Each simulation started at the base of the tree with all characters in the ancestral state 0 (Figure 5.5b). The simulation proceeded along each branch of the tree with character states changing randomly as determined by the threshold and character correlations. The simulations were run using a punctuational and anagenetic model of evolution. In the punctuational model, there was only one chance for character state change along each branch; in the anagenetic model, there were 100 chances for change. Two consequences of the anagenetic model are that reversals can erase character transformations that occur along a single branch and there is a higher probability of independent changes in characters that are correlated.

In addition to varying the number of opportunities for characters to change, we varied the probability of change, from equal (branching probability $b = 0.5$), high ($b = 0.9$), and low ($p = 0.1$), for a total of six simulations. Each simulation was repeated 200 times.

The effect of the underlying correlations on the character state matrix in the simulations was measured with three statistics. The first statistic was the proportion of correlated characters with identical character state distributions across the tip taxa. This metric is related to the Harris *et al.* (2003) method, which used identical distributions of states as confirmation of underlying character correlation.

The second statistic was the mean pairwise distance between correlated and uncorrelated characters. Even without a perfect correlation in character state

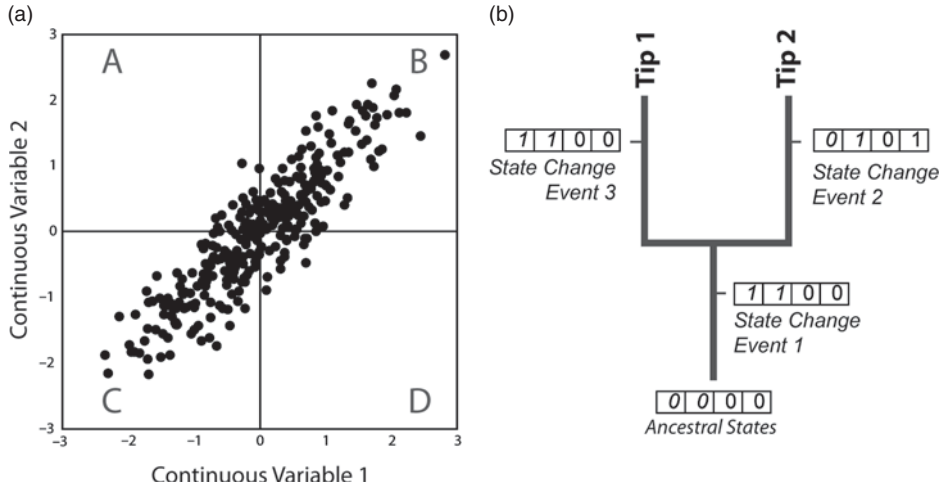

Figure 5.5 (a) Diagram showing relationship between the underlying continuous change and state change for a pair of characters when the underlying correlation is 0.9 and the threshold for state change is 50%. One hundred random changes in two correlated continuous variables are shown as points on the graph. Perfectly correlated character state distributions occur when the continuous points lie in quadrant C (no change in either character) or B (change in both characters). Seemingly uncorrelated character state changes occur when the continuous points lie in quadrant A (change in character 2, but not character 1) or D (change in character 1, but not character 2). (b) Diagram of how character state evolution was simulated, shown here with four characters and two tip taxa. The first pair of characters in this diagram has an underlying correlation and the second pair does not. Each simulation starts with all character states in the ancestral condition of 0. At each state change event (one per branch for punctuated simulations, 100 per branch for anagenetic simulations) a random change in the underlying triggers changes in the character states if the continuous change exceeds the threshold.

changes, it can be expected that correlated characters will be more similar to one another than are uncorrelated characters.

The third statistic was the mean distance of correlated and uncorrelated characters in PCO space. This metric was used by Naylor and Adams (2001) to assess whether potentially correlated characters are truly correlated. To calculate the mean PCO distances, characters were projected into PCO space by calculating a $k \times k$ pairwise squared distance matrix, where k is the number of characters, converting it to a similarity matrix by multiplying the squared distances by -0.5, double-centring it by subtracting the mean column and mean row values and adding the matrix mean, and calculating eigenvectors from the double-centred matrix using singular value decomposition (Gower,

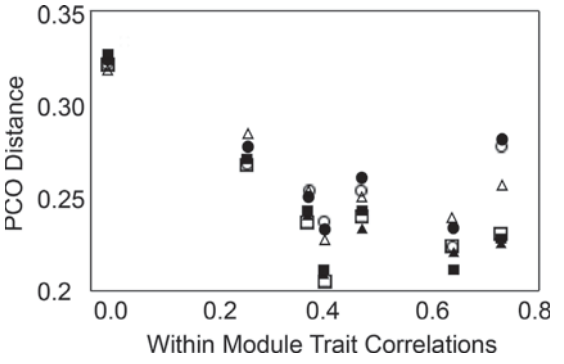

Figure 5.6 PCO distance plotted against mean within-module character correlations for the six Monte Carlo simulations: open symbols, anagenetic; closed symbols, punctuated; circles, equal probability of change; squares, high probability; triangles, low probability.

1966). Because PCO is a *Q*-mode analysis, the elements of the eigenvectors are the scores of the characters in PCO space. Mean pairwise distances on the first two axes between correlated and uncorrelated characters in the space were calculated. Mean and standard deviations from the 200 repetitions of each of the 6 simulations are reported for each measure.

We used these statistics to determine whether module correlations are likely to have an adverse effect on the character state matrix: when the proportion of identical state distributions was, on balance, higher in correlated than uncorrelated characters, when the mean pairwise character distance was, on balance, smaller in correlated than uncorrelated characters, and when the mean PCO distance was, on balance, smaller in correlated than uncorrelated characters.

Character distributions in previous phylogenetic analyses

In order to assess whether character correlations may actively have had an effect on previous phylogenetic analyses of Carnivora, we classified clades as valid or invalid and determined whether characters supporting invalid clades are predominantly correlated in modules. We first tabulated the characters supporting each clade for the most extensive recent phylogenetic analysis based solely on morphological characters (Wyss and Flynn, 1993). We compared the clades identified in that study with more recent studies (Flynn and Nedbal, 1998; Yoder *et al.*, 2003; Flynn *et al.*, 2005; Wesley-Hunt and Flynn, 2005), including several molecular studies using up to six mitochondrial and nuclear genes. We presumed that the later studies are more correct than the earlier morphological study, and the Wyss and Flynn (1993) clades (hereafter WF) were classified as valid if

Table 5.2 Correlation between similarity in shape, similarity in integration, and phylogenetic relatedness. $^{*}p < 0.05$, $^{**}p < 0.01$.

	Carnivora		Caniformia		Feliformia	
Module	Shape	Integration	Shape	Integration	Shape	Integration
Ant. Oral–Nasal	0.28^{**}	0.16	0.54^{*}	0.17	0.40	0.24
Molar	0.43^{**}	0.10	0.57^{*}	0.18	0.42	0.16
Orbit	0.38^{**}	0.13	0.40	0.17	0.57^{**}	0.19
Zyg–Pter	0.24^{**}	0.23^{*}	0.56^{**}	0.29	0.52^{*}	0.35
Vault	0.37^{**}	0.11	0.46^{*}	0.22	0.45	0.14
Base	0.53^{**}	0.24^{**}	0.69^{**}	0.36^{**}	0.53^{*}	0.37
All	0.46^{**}	0.17^{**}	0.69^{**}	0.36	0.55^{*}	0.33^{**}

upheld by more recent studies, or invalid if no longer considered to be a monophyletic group. We tabulated the characters supporting each clade and binned them into one of the six cranial modules described above. If character correlations have significantly misled this morphological phylogenetic analysis, then characters supporting an invalid clade are expected to represent fewer modules than those supporting valid clades. We calculated total character support and module range (the number of modules represented by characters) for each clade and compared these measures between valid and invalid clades.

Results

Phylogenetic signal in module shape

When module shape distance and patristic distance were compared across all carnivorans, all six modules showed significant correlations at the $p = 0.01$ level (Table 5.2). Total cranial shape (incorporating all 6 modules) was also significantly correlated with phylogenetic relatedness ($p < 0.01$). When analyses were conducted within Caniformia, all but the orbit module were significantly correlated with patristic distance at the $p = 0.05$ level, but only the zygomatic–pterygoid and basicranium were significant at the $p = 0.01$ level. Conversely, within Feliformia only the orbit was significantly correlated with patristic distance at the $p = 0.01$ level, while the zygomatic–pterygoid and basicranium were significantly correlated at the $p = 0.05$ level. Overall, caniforms showed stronger correspondence between cranial shape and phylogenetic relationship than do feliforms, and the zygomatic–pterygoid and basicranium were the only modules significantly correlated with patristic distance in both Feliformia and Caniformia.

Phylogenetic signal in module integration

It has previously been demonstrated that similarity in the pattern of integration across the whole skull is significantly correlated with phylogenetic relatedness in Carnivora ($p < 0.05$) and Feliformia ($p < 0.01$), but not in Caniformia (Table 5.2). When individual modules are considered separately, only the basicranium showed a significant correlation between similarity in pattern of integration and phylogenetic relatedness across Carnivora ($p < 0.01$) and within Caniformia ($p < 0.01$), but not within Feliformia.

Monte Carlo simulations

Identical character state scores

In only 3 of the 36 analyses were there any cases of identical character state scores for highly correlated characters. All of these cases were in the highly integrated anterior oral–nasal module, with a punctuational model and high probability of change (3.33% of 200 runs), a punctuational model and low probability of change (10%), and an anagenetic model and high probability of change (6.67%). All of the other modules failed to produce even a single instance of identical character state scores.

Mean pairwise character distance

In none of the 36 simulations was mean pairwise character distance significantly different between correlated characters within the six modules than between uncorrelated characters spanning the modules.

PCO distance

In all 36 cases, the mean PCO distance between uncorrelated characters was significantly greater than between correlated characters (Table 5.3). However, there were not significant differences among the modules, despite a large range of magnitude of mean within-module correlations (Figure 5.2).

Character distributions in previous phylogenetic analyses

Out of 31 clades within Carnivora that were identified in Wyss and Flynn (1993), 9 are not supported in more recent analyses (Miacinae, Viverravinae + Carnivora, Felidae + Hyaenidae, Viverride, Procyonidae + Ursdia + Ailurus, Ailurus + Ursida, Ursida, Mustelidae, Mephitidae + Lutrinae). Fifty-one characters used in Wyss and Flynn (1993) can be assigned to one of the 6 cranial modules. Because of homoplasy and multistate characters, the 31 clades were supported by a total of 129 apparent synapomorphies. Forty-four of these

Table 5.3. Mean PCO distances and standard deviations (s.d.) for each module and for uncorrelated traits for the six Monte Carlo simulations. *b*, probability of character changing, ranging from low (0.1) to high (0.9).

	Punctuation					
Module	$b = 0.5$	s.d.	$b = 0.9$	s.d.	$b = 0.1$	s.d.
Ant. Oral–Nasal	0.279	0.052	0.227	0.065	0.225	0.067
Molar	0.257	0.055	0.240	0.059	0.233	0.062
Orbit	0.250	0.049	0.242	0.056	0.240	0.061
Zyg.–Pterygoid	0.279	0.040	0.270	0.046	0.271	0.047
Vault	0.231	0.057	0.210	0.063	0.208	0.072
Basicranium	0.234	0.058	0.210	0.064	0.221	0.066
Uncorrelated	0.325	0.013	0.326	0.014	0.326	0.013
	Anagenesis					
	$b = 0.5$	s.d.	$b = 0.9$	s.d.	$b = 0.1$	s.d.
Ant. Oral–Nasal	0.277	0.053	0.230	0.063	0.257	0.054
Molar	0.254	0.050	0.239	0.054	0.252	0.057
Orbit	0.254	0.052	0.238	0.064	0.253	0.058
Zyg.–Pterygoid	0.279	0.039	0.266	0.043	0.284	0.039
Vault	0.236	0.059	0.202	0.070	0.229	0.066
Basicranium	0.238	0.059	0.224	0.062	0.239	0.061
Uncorrelated	0.323	0.011	0.326	0.015	0.324	0.013

supported invalid clades, and 105 supported valid clades. Characters were very unevenly distributed across the skull. Of the character support, 59.7% was derived from the molar region, and 28.7% was basicranial. The remaining characters were divided between the orbit (4.7%), zygomatic–pterygoid (5.4%), and anterior oral–nasal (1.6%). There were no characters from the cranial vault. Of the 31 clades, 2 were not supported by any cranial characters (only postcranial), 9 were supported by characters from a single module (ranging from 1 to 5 total character support), 13 were supported by 2 modules (2 to 8 total character support), 8 were supported by 3 modules (4 to 11 total character support), and 1 clade, Phocoidea, was supported by 7 characters from 5 modules. Module representation for invalid clades ranged from one to three, with character support ranging from one to seven. Module representation for valid clades ranged from 1 to 5, with total character support ranging from 1 to 11. Although the clades with the most character support and broadest module representation were supported by more recent molecular phylogenetic analyses, there were no significant differences between invalid and valid clades in module representation or total character support.

Discussion

It appears that character correlations may well have affected morphological phylogenetic analyses of Carnivora. Our simulations of correlated character evolution, using empirically derived character correlations (Goswami, 2006a) suggest that simply identifying characters with identical character state scores across taxa will underestimate the number of correlated characters. However, PCO distances were significantly greater among uncorrelated than correlated characters, demonstrating that character correlations are affecting character state changes across complex phylogenies and a range of evolutionary models. Even the most weakly integrated modules, with relatively low, but non-zero, correlations among traits, were significantly closer than were uncorrelated characters.

Tabulating character distributions in a large-scale morphological analysis of carnivoran phylogeny demonstrated that cranial characters are overwhelmingly concentrated in the molar and basicranial regions. Of course, this is not a new observation, and has been well appreciated in many previous studies (Flynn and Wesley-Hunt, 2005). However, from the analyses presented here, there is no evidence that this concentration on only a few regions of highly correlated characters has significantly misled phylogenetic analyses. Clades supported by characters from several modules were found to be invalidated by recent molecular analyses as often as clades only supported by characters from a single module. Furthermore, our analysis of phylogenetic signal in cranial module shape demonstrated that the basicranium and the zygomatic–pterygoid, which includes some of the anterior basicranium, have the strongest phylogenetic signal. As the phylogenies used for these analyses are predominantly based on molecular data, this does not simply reflect the fact that the major divisions within Carnivora are based on basicranial morphology. Feliformia and Caniformia are identified by their distinct bullar morphologies, which is included in the basicranial module. Understandably, recent and ongoing studies of the stem carnivoran groups Viverravidae and 'Miacoidea' also focus on basicranial morphology to untangle the relationships of these enigmatic taxa. The strong phylogenetic signals of basicranial and zygomatic–pterygoid shape shown in this study support the reliance on basicranial characters in morphological analyses of carnivoran phylogeny. However, the potential for correlated characters to display coordinated character state changes urges caution in basing phylogenetic analyses on characters from only a single module.

A relevant debate on the selection and atomisation of character has been occurring among phylogenetic systematists for decades (Rieppel and Kearney, 2002), alongside related debates on the selection pressures and lability

of certain types of characters and levels of homoplasy in different systems (Sanchez-Villagra and Williams, 1998; Williams, 2007). As Rieppel and Kearney (2002) note, many morphological phylogenetic analyses focus on increasing the quantity of characters, rather than on increasing the quality of characters. In fact, more complex suites of characters may serve as better representatives of discretely evolving traits (Strait, 2001; Gonzáles-José *et al.*, 2008), but it is difficult to determine the boundaries of such biological units. Because modules may well be stable across large clades (Goswami, 2006a), they can provide a more practical way to assess whether over-emphasis of a cranial region or atomisation of a module does negatively influence phylogenetic analyses, particularly in studies involving large amounts of fragmentary fossil material or in clades, such as Carnivora, where great emphasis is placed on a few anatomical regions.

While shape is the most obvious aspect of a module to consider, the relationships among traits within a module are flexible and may well change over evolutionary time, even if the actual composition of the module is stable (Goswami, 2006a, 2006b, 2007a). The basicranium was the only module to show any phylogenetic signal in its patterns of integration, and only when compared across all Carnivora and within Caniformia. Feliformia, which showed the strongest phylogenetic signal in whole-cranium integration (Goswami, 2006b) did not show significant phylogenetic signal in the patterns of integration for any individual module. This result again justifies the attention paid to the basicranium in phylogenetic analyses of Carnivora.

It is difficult to make a conclusive statement on the effect of character correlations on phylogenetic analyses of Carnivora. On the one hand, simulated character evolution shows unquestionably that correlated characters do shift in a coordinated matter on evolutionary time scales, reflected in their significantly lesser distances in PCO analyses. Perhaps even more surprisingly, these coordinated shifts are apparent even in the most weakly integrated of modules, and little difference is seen among any modules in PCO distance. This suggests that any correlation, however weak, has the potential to affect character state changes and, in turn, phylogenetic analyses based on morphological characters. This result on its own would suggest that workers should use extreme caution when focusing on a single cranial region, such as molars or the basicranium, when building a character matrix, or when interpreting the results of such an analysis.

On the other hand, the region that dominates our understanding of carnivoran phylogeny and provides the morphological support for the most fundamental divisions within Carnivora, the basicranium, shows the strongest phylogenetic signal in its shape when compared to molecular phylogenies. It also shows the strongest phylogenetic signal in its pattern of morphological integration. Furthermore, there is no evidence from examination of the

broadest morphological analysis of carnivoran phylogeny that the reliance on the molar and basicranial regions has in fact consistently and significantly misled analyses. There are no significant differences between valid and invalid clades in the modular distribution of their character support. Quite possibly, this result simply reflects the paucity of characters from other regions – only ~11% of characters come from modules other than the molar and basicranium. None the less, five of the eight clades supported by characters from only a single module are still considered monophyletic in recent molecular studies, and two of the nine clades supported by characters from three or more modules have been invalidated, leading to the conclusion that sampling across multiple modules does not necessarily translate in better phylogenetic analyses.

Thus, for the workhorse of carnivoran morphological phylogenetics, the basicranium, there is good support that its morphology strongly tracks phylogenetic relationships, as determined by molecular analysis. Perhaps more interestingly, the concordance between basicranial integration and phylogeny suggests that the changing relationships among basicranial traits retains a strong signal of their evolutionary history. However, in an ideal world, characters would be better distributed across the organism, and our simulations of character evolution do suggest that even the more weakly correlated characters display some coordination of state changes, which has the often discussed but little acted upon potential to mislead phylogenetic analyses based on morphological characters from a single anatomical region.

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6

What's the difference? A multiphasic allometric analysis of fossil and living lions

MATTHEW H. BENOIT

Introduction

Differentiating between various species in the fossil record is one of the most vital tasks in paleontology. As such, evaluating the morphological features that we use to make these taxonomic distinctions is critical. Without any confirmation from molecular lines of evidence, morphological analyses are the only option for such studies. Determining the validity and independence of character changes is a major part of that evaluation. Compounding this limitation to morphological analyses is the fact that assembling a significant sample size of fossil specimens for a single taxon is frequently very difficult, if not impossible. Often, paleontologists compare a single fossil specimen with a single specimen of a closely related extant taxon or representatives of several such taxa. Analyses of this nature, while valuable first glimpses, do not account for variation within populations (of either the fossil or the extant groups), and therefore may result in inaccurate conclusions regarding the relationships of the organisms in question. In this chapter, I present an example of a species–status conflict within the pantherine felids and use allometric analyses to evaluate some of the morphological characteristics that have been used as evidence to support arguments in this conflict.

Since its first official use by Pocock (1930), the generic designation of *Panthera* for the clade consisting of the lion (*P. leo*), tiger (*P. tigris*), leopard (*P. pardus*), jaguar (*P. onca*), and now the snow leopard (*P. uncia*) has reached standard usage. However, the attribution of species or subspecies status below the rank of genus has not been so readily settled, especially for fossil groups that seem to show a relationship to one of the extant pantherine cats. One of these fossil groups is the 'American lion' (*Panthera leo* cf. *atrox*). There has been some argument regarding the nature of the relationship of *P. atrox* and *P. spelea* (the 'cave lion') within *Panthera*, and several authors have maintained a *P. tigris* or

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