



Journal of Vertebrate Paleontology

Publication details, including instructions for authors and subscription information:

<http://www.tandfonline.com/loi/ujvp20>

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Version of record first published: 03 May 2012.

To cite this article: Carlo Meloro & Graham J. Slater (2012): Covariation in the skull modules of cats: the challenge of growing saber-like canines, *Journal of Vertebrate Paleontology*, 32:3, 677-685

To link to this article: <http://dx.doi.org/10.1080/02724634.2012.649328>

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COVARIATION IN THE SKULL MODULES OF CATS: THE CHALLENGE OF GROWING SABER-LIKE CANINES

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ABSTRACT—Shape variation in the vertebrate skull is often studied by considering this bony structure as a single discrete unit, but it can also be interpreted exploring covariation among functionally and developmentally distinct regions, or modules. In this paper, we explore the evolution of skull shape in extant and fossil carnivorous cats by looking at covariation between two distinct modules: the rostrum (splanchnocranium) and braincase (neurocranium). Previous work suggests that the evolution of extreme skull shapes in sabertoothed cats may occur along developmental axes similar to the allometric trajectory observed for extant conical-toothed cats. Here, we reassess this hypothesis by using geometric morphometric data to test for covariation between rostral and braincase modules in sabertoothed and conical-toothed cats. Using partial least squares analysis, we detect a correlated pattern of evolution between rostrum and braincase shape in both forms. However, when we compare within-module integration between conical and sabertoothed cats, we find significant differences in vector trajectories for the rostrum but not the braincase. Both skull modules of conical-toothed cats are more influenced by allometry. For sabertoothed taxa, relative canine height drives shape in the rostrum, but both size and canine length affect braincase shape. We suggest that sabertoothed skull morphology is the result of genetic and developmental processes that were affected by the growth rate of the upper canines. The striking convergence between independent sabertooth radiations indicates that elongation of the canines influenced interspecific skull shape variation in different lineages but in a similar way.

INTRODUCTION

Interpreting morphological variation at macroevolutionary scales provides an important contribution to a comprehensive theory of evolution (Simpson, 1953; Gould, 2002). The evolution of the extreme cranial adaptations found in sabertoothed cats is a topic that has received particular attention in the paleobiological literature (e.g., Cope, 1880; Matthew, 1910; Simpson, 1941; Emerson and Radinsky, 1980; Akersten, 1985; Bryant, 1996; Antón et al., 2004; Christiansen, 2008; Slater and Van Valkenburgh, 2008). Elongate upper canines evolved at least four times in the history of carnivorous mammals (Emerson and Radinsky, 1980; Van Valkenburgh, 2007) and sabertooths were the top carnivorous predators in most terrestrial ecosystems from the Eocene until a few thousand years ago (e.g., the South American *Smilodon populator* has been dated to 9250 ± 150 years BP; Fiedel, 2009), when they were replaced by the extant conical-toothed true cats (Felinae). The most conspicuous feature of sabertoothed carnivores is the elongate, laterally compressed upper canine teeth, although considerable ecomorphological variation exists among them (Martin et al., 2000). In addition to possessing elongate upper canine teeth, sabertooths exhibit a suite of extreme cranial adaptations, such as a dorsally rotated palate, hypertrophied mastoid processes, ventrally displaced jaw joint, vertically inclined occiput, and short, deep temporal fossae. Several studies have analyzed the morphometric variation among sabertoothed species (e.g., Emerson and Radinsky, 1980; Christiansen, 2008; Slater and Van Valkenburgh, 2008), leading to a broad consensus on how these cats killed their prey. Sabertooth cranial adaptations were related to the need to bite at a wide gape angle in order to

clear the tips of the upper and lower canines. As a consequence of biting at wide gapes, bite force was probably less powerful than a similar sized conical-toothed cat (McHenry et al., 2007). However, whereas extant cats typically use a crushing bite to the throat or nape, sabertooths would have made shallow, high precision shearing bites into vulnerable body parts of the prey, such as the throat (Akersten, 1985; Salesa et al., 2005; Anderson et al., 2011). These bites would have been aided by the head-depressing musculature that inserted on the hypertrophied mastoid processes (Akersten, 1985; Antón et al., 2004; Salesa et al., 2005; Slater and Van Valkenburgh, 2008), and would have led to rapid death of prey from blood loss or shock.

Slater and Van Valkenburgh (2008) emphasized the role of relative canine length in explaining patterns of morphological variation in the skulls of sabertoothed cats. They contrasted this finding with the pattern observed in conical-toothed felines, where skull shape is better predicted by overall skull size (Werdelin, 1983; Slater and Van Valkenburgh, 2008). Slater and Van Valkenburgh (2008) also noted that sabertoothed and conical-toothed cat skull shapes appear to be primarily distributed along a common axis of variation, leading them to suggest that evolution of the extreme skull shapes of sabertoothed cats may have resulted from the extension or co-opting of an allometric trend present in extant cats. Their study considered the skull as a discrete functional structure, however, whereas many recent studies support the idea that the vertebrate skull is the complex result of developmental and functional integration of different subunits called modules that may or may not covary with one another (Goswami, 2006a,b, 2007). Although the concept of modularity is an old paradigm in evolutionary biology (Olson and Miller, 1958), it would represent a novel way of looking at the evolution of sabertooth skull shape.

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In this study, we explore the evolution of skull shape in both conical-toothed and sabertoothed cats by testing for covariation between two distinct regions of the skull: the rostrum (splanchnocranium) and the braincase (neurocranium). We opt to look at these two modules for two reasons: (1) they are developmentally independent, and (2) we are interested in linking patterns of interspecific variability with functional attributes—whereas the neurocranium houses the brain and its external shape reflects the arrangements of specific masticatory muscles, the splanchnocranium houses several sense organs and the upper jaw with teeth. Furthermore, these two regions have been shown to exhibit strong patterns of covariation in other groups of mammals (e.g., Mitteroecker and Bookstein, 2007). We explore covariation between the rostrum and braincase using a two-dimensional (2D) geometric morphometric data set for a sample of conical-toothed and sabertoothed cats (cf. Slater and Van Valkenburgh, 2008). We expect that the shapes of these two skull regions will exhibit significant patterns of covariation due to the need to maintain functional integration of the jaw adducting musculature and the jaws themselves. If sabertooths achieved their extreme morphologies by exploiting the allometric pattern of cranial shape variation found in conical-toothed cats (Slater and Van Valkenburgh, 2008), we would additionally expect to find indistinguishable patterns of integration within each module. In contrast, if the evolution of elongate canines and the associated demands on jaw mechanics resulted in dramatic reorganization of the entire skull, we would expect to find significant differences in patterns of integration within both the rostrum and braincase.

MATERIALS AND METHODS

We examined 292 skulls belonging to 54 species of cat-like Carnivora including extant and fossil members of Felidae (48 species)

and Nimravidae (six species). Our initial sample consisted of 2D digital pictures and some line drawings described in Slater and Van Valkenburgh (2008). We excluded from that sample several fossil nimravids (five species) for which skulls were incomplete. We subsequently incorporated more specimens ($N = 34$) belonging to extant and fossil Felidae collected by Meloro at the Natural History Museum London, Museum d'Histoire Naturelle (Paris), and Museo Nacional de Ciencias Naturales-CSIC (Madrid). The specimens belong to six species of extant conical-toothed cats (specimen number in parenthesis): *Felis nigripes* (2), *Felis manul* (3), *Felis margarita* (2), *Lynx pardinus* (2), *Lynx lynx* (7), and *Prionailurus bengalensis* (8); and six fossil taxa: *Acinonyx pardinensis* (1), *Homotherium crenatidens* (1), *Megantereon cultridens* (4, of which 2 are casts), *Dinofelis* sp. (2, of which 1 was cast), *Promegantereon ogygia* (1), and *Amphimachairodus giganteus* (1 cast). Some fossil specimens were redundant with the Slater and Van Valkenburgh (2008) data set but we included them to be sure that data were collected in the same way and that cast specimens were not affecting our sample.

Specimens were landmarked with 17 homologous points using TpsDig 2.09 (Rohlf, 2006a) to describe both the rostrum (landmarks 1–9 and 15–17) and the braincase (landmarks 10–14) regions (Fig. 1). A generalized Procrustes analysis (GPA) was computed to scale, rotate, and translate the original landmark x- and y-coordinates (Zelditch et al., 2004). This procedure was repeated for each species, as represented by multiple specimens, in order to obtain a mean consensus configuration that was used for the interspecific analyses (cf. Meloro et al., 2008). GPA was then repeated to align the 54 consensus configurations for rostrum and braincase areas separately.

We examined evolutionary covariation between rostrum and braincase shape using two-block partial least squares analysis (PLS; Rohlf and Corti, 2000) implemented in tpsPLS 1.18 (Rohlf, 2006b). PLS is similar to multivariate methods such as principal

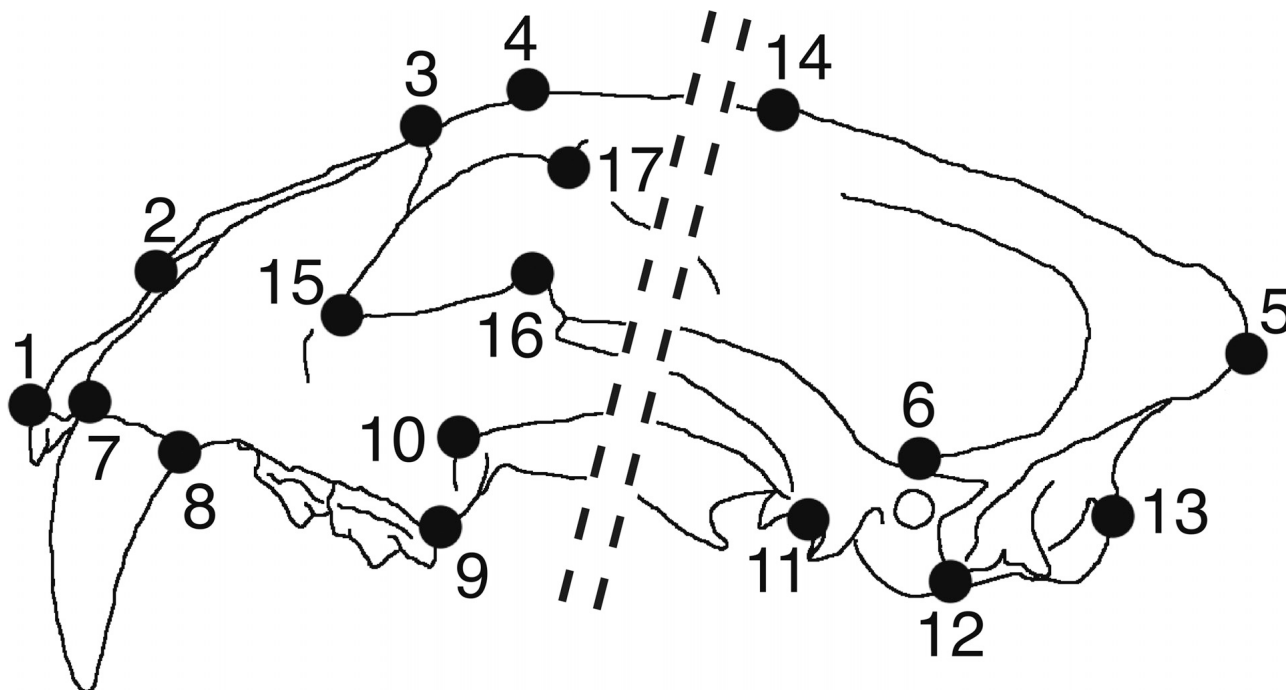


FIGURE 1. The position of landmarks to describe skull shape in cats. Landmarks record 17 homologous points that identify two distinct areas: 1–10 and 15–17, splanchnocranium; 10–14, neurocranium. Landmarks 1–9 and 12–13 are described in Slater and Van Valkenburgh (2008), landmark 10 is placed at the suture distinguishing maxillary from zygomaticus, landmark 11 is in the middle portion of the glenoid fossa, landmark 14 records the coronal suture, landmark 15 is the inferior tip of the lacrimal border, landmark 16 is the tip of the orbital border of the zygomatic arch, whereas landmark 17 records the tip of the frontal zygopophysis.

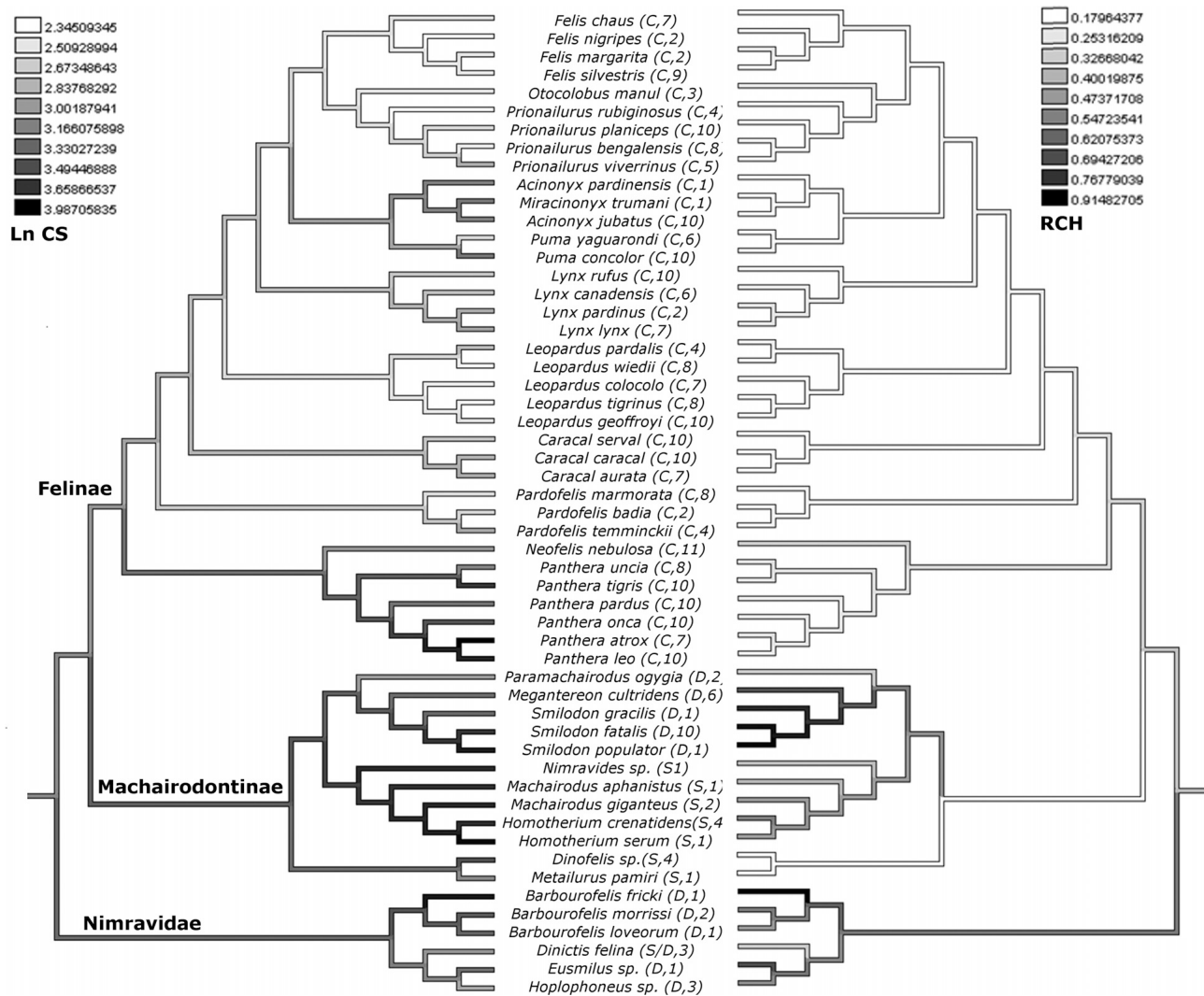


FIGURE 2. Composite phylogeny of 54 species of cat-like Carnivora. On the left, natural log transformed centroid size (Ln CS) is mapped using squared-change parsimony (Maddison and Maddison, 2009). On the right, the same method is employed to map relative canine height (RCH). Values in parentheses describe tooth type (C = conical, S = saber, D = dirk) and number of specimens.

component analysis (PCA) in that the original data are reduced to a set of orthogonal combinations of variables. However, PLS differs from PCA in that it produces pairs of correlated axes ordered by the amount of covariance explained between the two original blocks of data, rather than single axes explaining portions of the total amount of covariance within the data (Rohlf and Corti, 2000; Zelditch et al., 2004). PLS is therefore an ideal tool for testing patterns of correlated shape change between predefined morphological modules. To perform PLS analysis, we first compute partial warp (PW) and uniform components (Uni) as shape descriptors of both landmark configurations. Pearson product moment correlation scores are then calculated to generate a correlation matrix between the two blocks of variables (in this case PWs and Uni for each configuration). The correlation matrix is then decomposed using singular value decomposition to extract a pair of vectors (singular axes, SAs) that describe the correlation between the two blocks of variables. We repeated this procedure for the complete data set of 54 species, as well as in nested data sets of conical-toothed (36 species) or saber-toothed (18 species) cats to detect possible differences in covari-

ation patterns (Fig. 2). Significance for the correlations between pairs of singular axes was determined by randomizing the samples 999 times to generate a null distribution. We considered that the observed correlation coefficient, r , was higher than expected by chance if the correlation between a pair of SAs was significant at $P < 0.05$.

We used thin plate splines to visualize shape variation along pairs of SAs. Based on the findings of an earlier study of cat skull shape (Slater and Valkenburgh, 2008), we also wanted to test for the effects of two other factors on shape of the rostrum and braincase singular axes: the size of the skull, as described by natural log (ln)-transformed values of centroid size (Bookstein, 1989), and the relative canine height (canine crown height divided by the distance between postglenoid process of the jaw joint to the center of the canine; Slater and Van Valkenburgh, 2008). Non-parametric correlation tests were employed to detect covariation between skull size or relative canine height with significant singular axes.

Because of the bias introduced by phylogenetic relationship in interspecific data sets (Felsenstein, 1985; Garland et al., 2005),

TABLE 1. Correlation coefficient, r , between pair of the first singular axes together with centroid size (ln CS) and relative canine height as for the overall sample of 54 species.

	SA1 rostrum	SA1 braincase	ln CS	Relative canine
SA1 rostrum	—	0.366	0.647	0.509
SA1 braincase	0.876	—	0.489	0.597
ln CS	0.839	0.733	—	0.397
Relative canine	0.828	0.864	0.358	—

Values below the diagonal are based on raw data, values above diagonal are after PGLS. When correlation coefficients are reported, it implies significant association with $P < 0.05$.

we validated our results by employing Phylogenetic Generalized Least Squares (PGLS; Martins and Hansen, 1997; Rohlf, 2001, 2006c; Adams, 2008). PGLS employs a generalized least squares regression model while including the phylogenetic covariance matrix as an error term. We modified the topology presented in Slater and Van Valkenburgh (2008) to incorporate the newly sampled extant species based on Johnson et al. (2006) (Fig. 2). The fossil *Acinonyx pardinensis* was included as sister taxon of the extant cheetah (*A. jubatus*) following Christiansen and Mazak (2009). The tree was then ultrametricized, with all terminal branch lengths set to unity (Fig. 2) using Mesquite 2.72 (Maddison and Maddison, 2009). Tests of correlation between pairs of SAs were repeated using PGLS, arbitrarily using SAs for the rostrum as X (cf. Meloro et al., 2011). This approach is exactly equivalent to performing Ordinary Least Square (OLS) on independent contrasts of shape variables from both blocks and was preferred because PGLS does not alter original shape coordinates and does not require regression through the origin as well as data standardization (Rohlf, 2001, 2006c). PGLS was repeated also to validate association between significant SAs and size or relative canine height. PGLS analyses were conducted using the software NTSYS vs. 2.21c (Rohlf, 2006d).

We finally tested for differences in the patterns of evolutionary integration within the two cranial modules of conical-toothed and sabertoothed cats using the PLS Angle module within the IMP

software package (Sheets, 2002). For both rostrum and braincase, we computed the angle between significant singular axes for conical and sabertoothed cats. We then determined whether the observed value was greater than random expectation by bootstrapping the original sample 999 times (Zelditch et al., 2000, 2004).

RESULTS

Combined Sample

Eight singular axes were extracted by PLS. The first pair of axes (SA1 rostrum and braincase) explain most of the covariance among the two blocks (97.40%) and their positive correlation is significantly higher than expected by randomising the sample 999 times (one case on 999, $P = 0.001$). The linear correlation coefficient is also high ($r = 0.876$), confirming that shape change in the skulls of cats occurs in a coordinated fashion between rostrum and braincase (Table 1). Conical and sabertoothed cats occupy different regions of the singular axis morphospace, with sabertooths tending towards extreme positive scores (Fig. 3).

Coordinated shape changes can be visualized with deformation grids that represent shape changes in both regions along negative and positive singular axis scores (Fig. 4A). Positive scores are associated with an overall lengthening of the rostrum. This pattern is driven in particular by an enlargement of the canine area combined with elevation of the nasals and frontals, whereas the orbital area appears contracted relative to the other regions. The coordinated shape changes in the braincase are associated with anteroposterior shortening and dorsoventral deepening of the temporo-parietal region. In addition, the occipital area is more vertically inclined. Negative scores are associated with the opposite pattern. These skulls have short, tall rostra with large orbits. The braincases of these skulls are long, with small mastoid processes. These coordinated shape changes are not an artefact of phylogenetic relationships (Table 1). Skull size is highly correlated with SA1 of the rostrum, whereas the relative canine height is highly correlated to SA1 of braincase. This trend does not change after PGLS (Table 1).

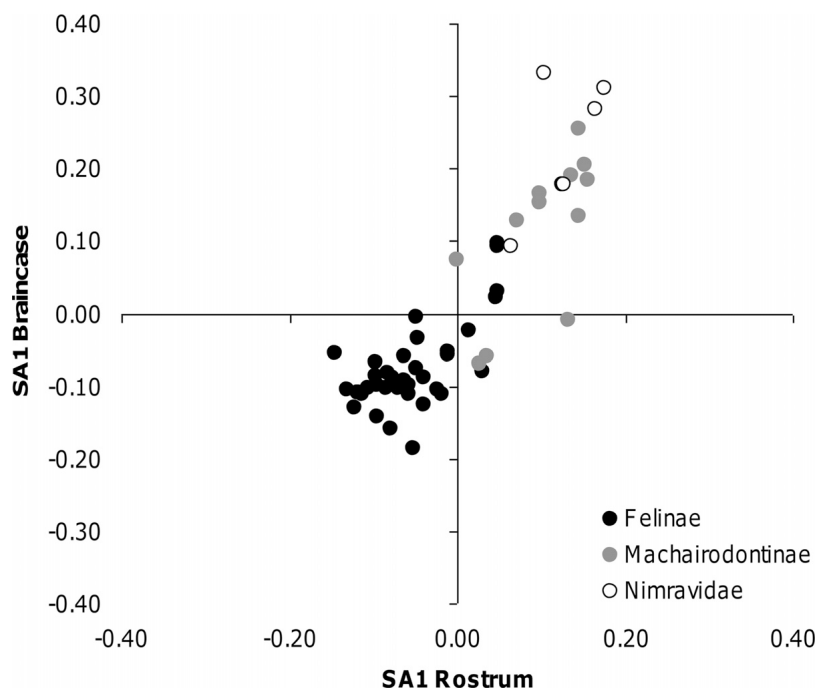


FIGURE 3. Scatter plot of singular axes for 54 skull cat data. Conical-toothed cats (black circles); sabertoothed cats, Machairodontinae (gray circles) and Nimravidae (white circles).

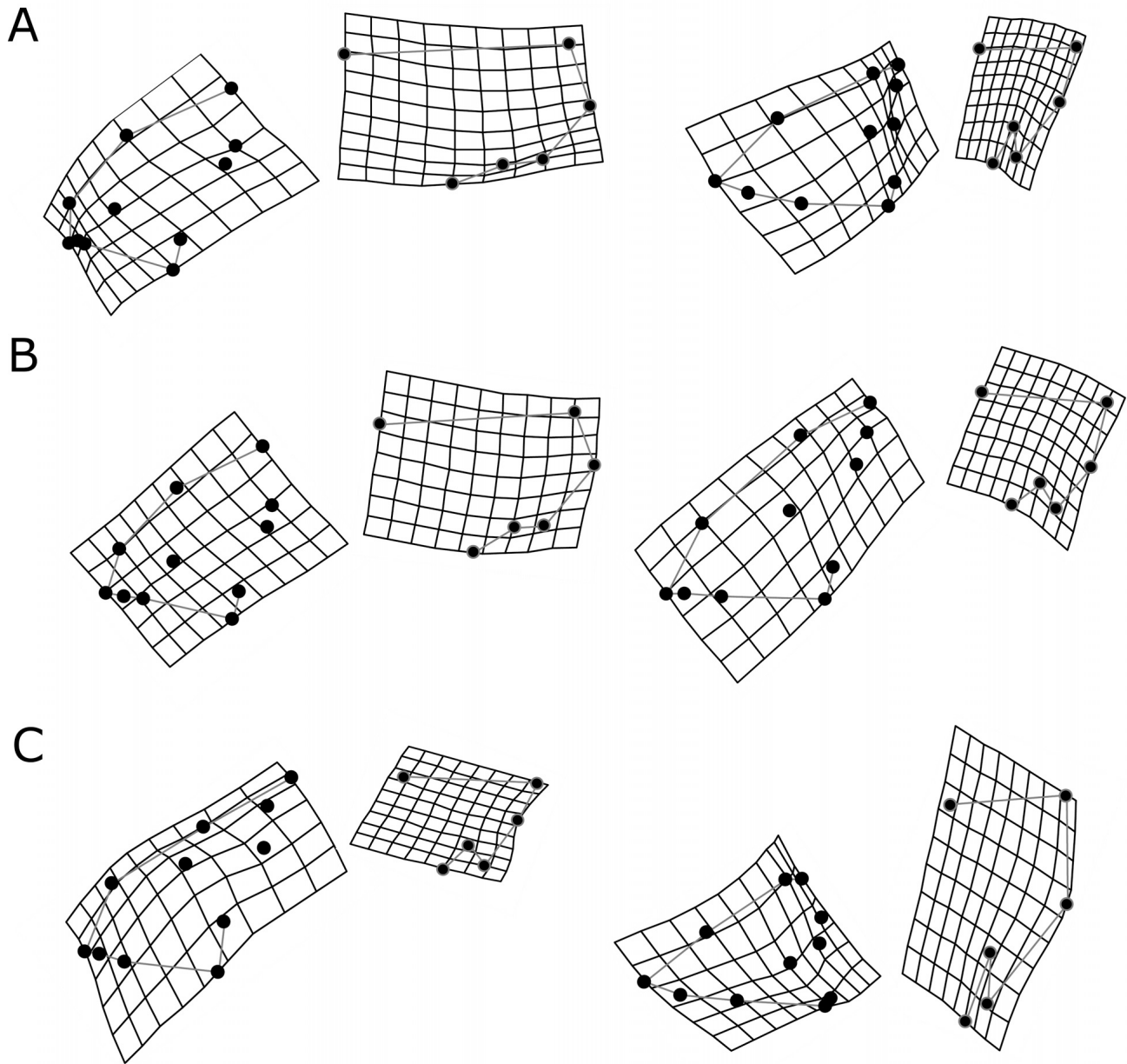


FIGURE 4. Shape changes of rostrum and braincase along negative (left) and positive (right) scores of SA1 in the overall sample of 54 species (A), and nested subsets of 36 conical toothed cats (B) and 18 sabertoothed cats (C). (A) Extreme negative scores are occupied by *F. margarita* and *F. nigripes*, whereas extreme positive scores are occupied by *B. fricki* and *Eusmilus*; (B) extreme negative scores are occupied by *P. bengalensis* and *L. tigrinus*, whereas positive scores are occupied by *P. leo* and *P. atrox*; (C) extreme negative scores are occupied by *Dinofelis* sp. and *P. ogygia*, whereas positive deformations are of *Eusmilus* and *B. fricki*.

Conical-Toothed Cats

When partial least square is performed on 36 species of conical-toothed cats, the first pair of singular axes again explains the highest portion of block covariance (89.59%, 38 out of 999 random cases with higher linear correlation, $P = 0.038$). The linear correlation coefficient is 0.841, similar to that obtained for the combined sample.

Inspection of deformation grids confirmed the general pattern of coordinated enlargement of rostrum relative to the shortening of the braincase (Fig. 4B). However, in the conical-toothed cat sample, shortening of the braincase was less extreme than observed in analysis of the combined data set and the orbit ap-

peared to be unaffected by changes in the rostrum. For positive SA scores, the canine area increased somewhat but the length of the palate region showed the greatest increase in size relative to other landmarks (Fig. 4B). Skull size and relative canine length were both significant predictors of rostrum and braincase shape, although correlation coefficients were larger for skull size for both modules (Table 2). When phylogeny is taken into account, the rostrum and braincase still covary significantly, but to a lesser degree than compared with the association between each SA1 and skull size (Table 2). Relative canine height no longer showed significant covariation with either the rostrum or the braincase (Table 2).

TABLE 2. Correlation coefficient, r , between pair of the first singular axes together with centroid size (ln CS) and relative canine height as for the sample of 36 conical toothed species.

	SA1 rostrum	SA1 braincase	ln CS	Relative canine
SA1 rostrum	—	0.516	0.937	ns
SA1 braincase	0.841	—	0.57	ns
ln CS	0.976	0.862	—	ns
Relative canine	0.436	0.363	0.404	—

Values below the diagonal are based on raw data, values above diagonal are after PGLS. When correlation coefficients are reported, it implies significant association with $P < 0.05$.

Sabertoothed Cats

Although the sample size of sabertoothed species is limited to 18 species, PLS analysis detects significant shape covariation between the rostrum and braincase. Again, the first singular axis is also the only significant one (89.51% of the covariance, 22 out of 999 random cases with higher linear correlation, $P = 0.022$). The linear correlation is $r = 0.809$, slightly lower but very similar to that obtained for conical-toothed and the combined sample (Table 3).

Inspection of deformation grids along the singular axis reveals dramatic patterns of shape change for sabertoothed cats compared with conical-toothed cats. The coordinated changes in the rostrum and braincase are dominated by an enlargement of the canine area relative to the other landmarks, combined with anteroposterior shortening and dorsoventral deepening of the temporo-parietal area, especially in the orbital region (Fig. 4C). Neither of the singular axes correlates with size, although a correlation between size and braincase SA1 is detected using PGLS (Table 3). Relative canine height is significantly correlated with both SA1 axes with or without incorporation the of phylogenetic error term (Table 3).

Integration within Modules

In order to evaluate the potential differences in integration within the rostrum and braincase of conical-toothed and sabertoothed cats, the observed angle of the first singular axis between these two groups can be compared with random expectation. The angle observed between conical and sabertoothed cats of the SA1 rostrum is 82.16° , with random expectation varying between 46.61° and 54.9° . This indicates that there is a significant difference in the covariation vector for the rostrum area between conical-toothed and sabertoothed cats and suggests that there are different patterns of integration in the two forms. We visualized these patterns by displaying the directions of PLS vectors for both conical-toothed and sabertoothed cats (Fig. 5). Major differences in vector directionality occur in the rostrum involving landmarks that describe the orbital and nasal areas. The angle observed between conical- and sabertoothed cats for the SA1 of the brain-

TABLE 3. Correlation coefficient, r , between pair of the first singular axes together with centroid size (ln CS) and relative canine height as for the sample of 18 sabertoothed species.

	SA1 rostrum	SA1 braincase	ln CS	Relative canine
SA1 rostrum	—	0.590	ns	0.847
SA1 braincase	0.809	—	0.612	0.809
ln CS	ns	ns	—	0.609
Relative canine	0.662	0.627	ns	—

Values below the diagonal are based on raw data, values above diagonal are after PGLS. When correlation coefficients are reported, it implies significant association with $P < 0.05$.

case is 45.38° , with a random range of values between 43.67° and 66.50° . As the angle observed falls within the range of possible values, we conclude that there are no differences in braincase covariation vector and that both groups share a common pattern of braincase integration. Visualization of shape changes in this region confirms that most of the vectors tend to overlap with the exception of slight differences in the mastoid and the occipital regions.

DISCUSSION

A complete understanding of macroevolutionary patterns of shape variation requires that functional adaptations be linked with evolutionary history and structural constraints (Gould, 2002). Traditionally, functional and morphometric studies have considered the skull as a single structure. However, several recent studies based on adult forms and ontogenetic series have identified distinct, covarying developmental modules in the mammalian skull (e.g., Goswami, 2006a,b, 2007; Cardini and Elton, 2008; Mitteroecker and Bookstein, 2008; Goswami and Polly, 2010a,b,c). Here, we demonstrate that integrated shape changes within and between modules can also be used to analyze and interpret evolutionary patterns within lineages over macroevolutionary scales. This approach allows us to consider interspecific variability within a methodological framework that is explicitly linkable to the theoretical background of modularity (Mitteroecker and Bookstein, 2007). The partial least squares approach (Rohlf and Corti, 2000) represents an ideal way of exploring interspecific variation by focusing on the evolutionary pathways of two functionally distinct anatomical areas (Mitteroecker and Bookstein, 2008; Meloro et al., 2011).

The evolution of the extreme cranial adaptations found in sabertooths has been of long standing interest in paleobiology (Cope, 1880; Matthew, 1910; Simpson, 1941; Emerson and Radinsky, 1980). Some authors have suggested that the evolution of elongate upper canines resulted in dramatic changes in the shape of the entire skull relative to conical-toothed cats (Christiansen, 2008), whereas others have suggested that the overall pattern of shape change might represent the extension or co-opting of an allometric pattern of shape variation observed in extant cats (Slater and Van Valkenburgh, 2008). Our results suggest that although the evolution of elongate canine teeth clearly impacted the evolution of skull shape in sabertooths, the way in which the canines impact covariation within and between cranial modules is more subtle. The variation observed at negative and positive extremes of the singular axes parallels that observed for the whole skull, with small felines occupying negative scores and the extreme morphotypes of large sabertooths, such as *Barbourofelis* or *Eusmilus*, located at the positive end (Christiansen, 2008; Slater and Van Valkenburgh, 2008). However, comparison of integration within the rostrum and braincase among extant and fossil cats reveals a more striking pattern. Macroevolutionary shape changes within the posterior skulls of conical and sabertoothed cats are broadly similar, whereas patterns of integration within the rostrum differ significantly between these two forms. Our results (Table 2) lend additional support to the hypothesis that skull shape in conical-toothed cats is primarily driven by allometry (Slater and Van Valkenburgh, 2008). For sabertooths, the pattern is more complicated; whereas shape change in the braincase is influenced by both size and relative canine length (although these two variables are correlated with each other), rostrum shape is influenced solely by the relative length of the canines. The evolution of elongate upper canines thus seems to result in a decoupling of the allometry-driven feline pattern of integration between the rostrum and braincase.

Accommodating enormous canine roots within the facial skeleton should impose significant constraint on the patterns of shape

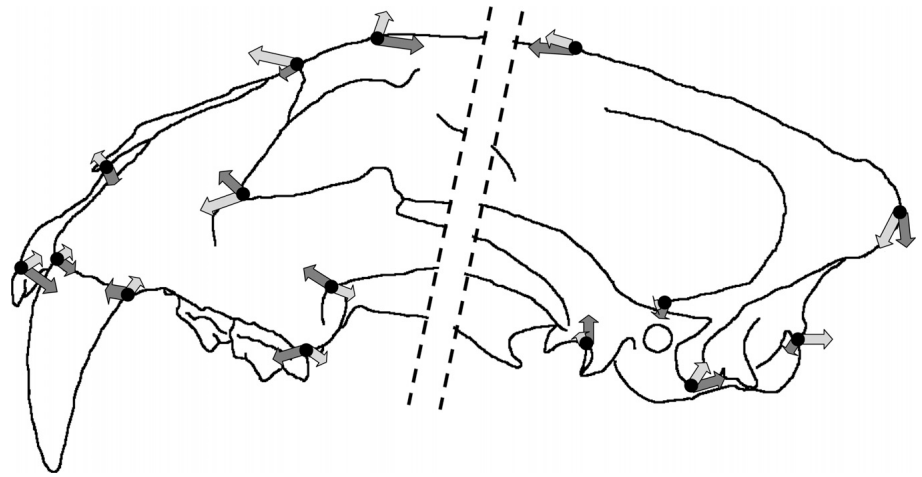


FIGURE 5. Coordinated shape changes along the pair of SA1 axes for rostrum and braincase areas described by vectors. Light gray identifies vectors related to variation in conical cats; dark gray is for the sabertoothed cats. Vector magnitudes have been amplified ($\times 2.5$) for clarity.

variation that can be realized in sabertoothed cats. Therefore, it is not surprising that the PLS vectors differentiating sabertooths from conical-toothed cats are associated with an overall enlargement of the rostrum in the canine root area and, to a lesser extent, dorsal rotation of the palate to increase jaw opening for a given gape angle (Figs. 4C, 5). In an earlier study aimed at identifying intra-cranial modules in mammals, Goswami (2006b) noted that most mammals showed a well-integrated oral-nasal module. However, in the sabertoothed felid *Smilodon fatalis*, this anterior region was dissociated into separate canine and facial modules. Our results converge with her findings because major differences between conical and sabertoothed carnivorans are limited to the rostral vector. Goswami (2006b) also noted, however, that this pattern was limited to the single sabertoothed felid in her sample, and did not appear in the two nimravids (*Dinictis* and *Hoplophoneus*) that she examined, suggesting that this pattern was not explicitly associated with elongation of the canines. It may be that the level at which shape variation was examined in this study was not sufficiently fine to tease apart fine-scale differences in patterns of cranial integration. A more detailed examination of cranial modularity and integration in a large sample of sabertoothed carnivorans would certainly be worthwhile.

Clearly, allometry with body size was not the main factor driving the evolution of rostrum shape in sabertoothed carnivores. In extant felids, rostrum shape is best predicted by size, consistent with our predictions (Slater and Van Valkenburgh, 2008). We found limited evidence for an association between relative canine length and cranial shape in extant felids. Significant but weak correlations were recovered between relative canine length and all other variables, but these disappeared when phylogenetic tests were employed. SA1 for the rostrum is strongly correlated with relative canine length in sabertoothed carnivorans, yet shows no association with skull size based on both phylogenetic and non-phylogenetic tests (Tables 1, 3). Although we initially found no evidence for a relationship between relative canine length and skull size in sabertooths, PGLS reveals that this non-significance is driven by phylogenetic relatedness (Table 3). Non-phylogenetic methods can fail to uncover patterns of correlated evolution when the traits evolve under different regimes in two or more lineages (cf. Meloro and Raia, 2010). In this case, our sabertooth samples contained two distinct ecomorphs, the long-toothed dirk-tooth cats, such as *Smilodon* and *Barbourofelis*, and the shorter-toothed scimitar-tooth cats, such as *Homotherium*, and *Machairodus* (Martin et al., 2000; Slater and Van Valkenburgh, 2008). It seems that differences in maximum relative canine height between these distinct ecomorphs may mask a

more general pattern of increasing canine length with increasing body size for sabertooths when non-phylogenetic methods are employed. Skull size variation among sabertoothed taxa is also limited and they are generally larger than conical cats ($\ln CS$; $\chi^2 = 20.210$, $df = 1$, $P < 0.0001$). Consequently, size explains much less variation in skull shape than canine height in these taxa.

Although patterns of integration in the rostrum are significantly different between conical-toothed and sabertoothed cats, this is not true for the braincase. In some respects, the similarity in braincase shape trajectories is perhaps to be expected due to a balancing effect that moulds the shape of the rostrum and braincase in all cat-like carnivorans. When the rostrum is enlarged, the braincase becomes shorter and vice versa. This trend was documented by Ewer (1973) in her early observations of skull morphology in Felidae and it is evident when considering our combined sample (Fig. 4A), but becomes truncated when only conical cats are analyzed (Fig. 4B). In large extant felids, the skull most notably compensates for the shortening of the neurocranium via the development of a sagittal crest, providing increased area for attachment of the temporalis muscle. Our finding that conical-toothed and sabertoothed felids do not differ in patterns of integration in the braincase suggests that if some rearrangement occurred in the jaw musculature of sabertooths, it was probably no different from that expected for a conical-toothed cat of similar skull size (see also Christiansen, 2011). However, other shape changes in the skulls of extant felids better predict the extreme adaptations found in sabertooth skulls. Large extant felids have enlarged mastoid processes and more ventrally displaced jaw joints compared with small felids (Fig. 4B), features that are typically associated with increased gapes (Herring, 1975). Although extant felids kill their prey in broadly different ways to that hypothesized for sabertooths (Andersson et al., 2011), large felids do similarly specialize on prey that are much larger than themselves. Large conical-toothed cats therefore face a similar feeding challenge in that the jaws must be opened wide enough to fit the throat of their prey between the canines. Slater and Van Valkenburgh (2009) used a simple mechanical model to demonstrate that the elongate rostra of extant big cats result in relatively greater clearance of the canine tips for a given gape angle. They also pointed out that canine clearance could be additionally enhanced by a lowered jaw joint, which would further facilitate access to even larger prey. Using finite element models, they found that large felids produce lower bite forces at the canines for a given muscle effort and gape angle, compared with small felids. In advanced sabertooths, the gape-related loss of mechanical advantage from the jaw

adducting musculature was probably compensated during prey killing by increased use of the head-depressing musculature inserting on the massive mastoid processes (Akersten, 1985; Antón et al., 2004; Salesa et al., 2005). Although they do not approach the morphologies seen in advanced sabertooths and clearly differ in prey-killing mode, the enlarged mastoid processes of large extant cats may similarly reflect increased use of head-depressing musculature in these species during predation as a gape-related adaptation. Indeed, it is well known that even small extant felids utilize dorsoventral motion of the atlanto-occipital joint when feeding (Gorniak and Gans, 1980). Patterns of integration within the sabertooth braincase may therefore represent use of the general feline pattern. We note that for felines, only skull size is a significant predictor of braincase shape, whereas both size and relative canine length predict shape for sabertooths. Although the general pattern of integration and functional drivers of shape evolution may be similar, a complicated interplay of size and canine length determine braincase shape in sabertooths.

The functional hypothesis regarding the evolution of sabertooths has been considered multiple times (summarized in Slater and Van Valkenburgh, 2008): highly competitive landscapes may have favored predators with long, blade-like canines that facilitated a faster mode of killing (Salesa et al., 2005). It is also clear from the repeated appearance of the sabertooth morphotype in the fossil record that this strategy was extremely successful. The results presented in this study indicate that the elongation of the canines resulted in a decoupling of a pattern of allometry-driven integration within the rostrum and the braincase. However, the fact that these unique features appeared multiple times in different branches of the carnivoran phylogeny suggests that the repeated development of sabertoothed morphologies may have occurred along similar genetic and developmental pathways. Several recent studies have aimed to identify quantitative trait loci associated with morphological variation in the domestic dog. For example, Fondon and Garner (2004) showed that variation in the ratio of glutamine/alanine residues in a tandem repeat within Runx-related transcription factor 2 (*Runx-2*), a regulator of osteoblast differentiation, was strongly correlated with a diverse array of morphological variation, such as facial length and facial angle (clinorhynch) in domestic dogs. The ratio of repeats in *Runx-2* has also been found to correlate with facial length more broadly across carnivorans (Sears et al., 2007). Much more work is clearly needed to fully understand the roles of putatively important genes in morphological development of integrated structures such as the mammalian skull. However, the extreme patterns of morphological variation found in sabertooths could similarly result from one or a few genes of large effect.

ACKNOWLEDGMENTS

We are grateful to museum curators and staff at the Natural History Museum of London, Muséum National d'Histoire Naturelle (Paris), and Museo Nacional de Ciencias Naturales-CSIC (Madrid) for allowing C. Meloro to expand data collection on extant and fossil Felidae. In particular, we would like to thank P. Jenkins, L. Tomsett, R. Portela-Miguez, A. Salvador, D. Hills, J. J. Hooker, P. Brewer, and A. Currant (Natural History Museum, London); B. Sanchez, J. Morales, J. Cabarga, and J. B. Rodríguez (Museo Nacional de Ciencias Naturales, Madrid); and D. Goujet, P. Tassy, and C. Signe (Muséum National d'Histoire Naturelle, Paris). We also thank A. Curtis, S. Price, and S. Santana for many helpful comments on previous versions of this paper. A. Goswami, P. D. Polly, and M. J. Salesa provided important insights to improve the quality of the manuscript. Visits at museums in Paris and Madrid were supported by Synthesys European grants ES-TAF 858 and FR-TAF 1680 awarded to C. Meloro for the project 'The evolution of feeding habits in extinct European carnivores.'

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Submitted August 23, 2011; revisions received December 4, 2011; accepted December 7, 2011.

Handling editor: Anjali Goswami.