

CONVERGENCE AND REMARKABLY CONSISTENT CONSTRAINT IN THE EVOLUTION OF CARNIVORE SKULL SHAPE

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Received June 14, 2006

Accepted January 3, 2007

Phenotypic similarities between distantly related marsupials and placentals are commonly presented as examples of convergence and support for the role of adaptive evolution in shaping morphological and ecological diversity. Here we compare skull shape in a wide range of carnivorous placentals (Carnivora) and nonherbivorous marsupials using a three-dimensional (3-D) geometric morphometric approach. Morphological and ecological diversity among extant carnivores is considerably greater than is evident in the marsupial order Dasyuromorphia with which they have most commonly been compared. To examine convergence across a wider, but broadly comparable range of feeding ecologies, a dataset inclusive of nondasyuromorphian marsupials and extinct taxa representing morphotypes no longer present was assembled. We found support for the adaptive paradigm, with correlations between morphology, feeding behavior, and bite force, although skull shape better predicted feeding ecology in the phylogenetically diverse marsupial sample than in carnivores. However, we also show that remarkably consistent but differing constraints have influenced the evolution of cranial shape in both groups. These differences between carnivores and marsupials, which correlate with brain size and bite force, are maintained across the full gamut of morphologies and feeding categories, from small insectivores and omnivores to large meat-specialists.

KEY WORDS: Carnivora, convergence, feeding ecology, geometric morphometrics, marsupial.

The study of phenotypic and genotypic convergence and parallelism in mammals has provided key elements in the corroboration of evolutionary theory (Madsen et al. 2001; Nevo 2001; Winter and Oxnard 2001). Carnivorous marsupials and members of the placental order Carnivora exemplify some of the better-known instances, as reflected in the common names of various marsupial species, including marsupial “wolf” (*Thylacinus cynocephalus*), Pleistocene marsupial “lion” (*Thylacoleo carnifex*), and native “cats” (*Dasyurus* spp.).

Although functionally meaningful similarities between the morphologies of marsupial carnivores and those of placental carnivores adapted to comparable ecological roles have been found, quantifiable convergence has been less marked than previously

supposed (Werdelin 1986). Previous comparisons with carnivores (Werdelin 1986; Jones 2003) have focused largely on three marsupial genera, that is, *Dasyurus*, *Sarcophilus*, and *Thylacinus*, representing two families, Dasyuridae and Thylacinidae. Included species are mostly or wholly carnivorous taxa ranging in size from around 0.6 to 30 kg in body mass. Carnivora contains around 270 species, from 0.15 to 800 kg in body mass and includes not only carnivores, but also many species specialized toward more omnivorous or purely insectivorous diets (Nowak 1991). The term “marsupial carnivore” can also be somewhat misleading insofar as many smaller species are insectivorous. Moreover, taxa traditionally categorized as marsupial carnivores form a phylogenetically very diverse and paraphyletic clade, which includes

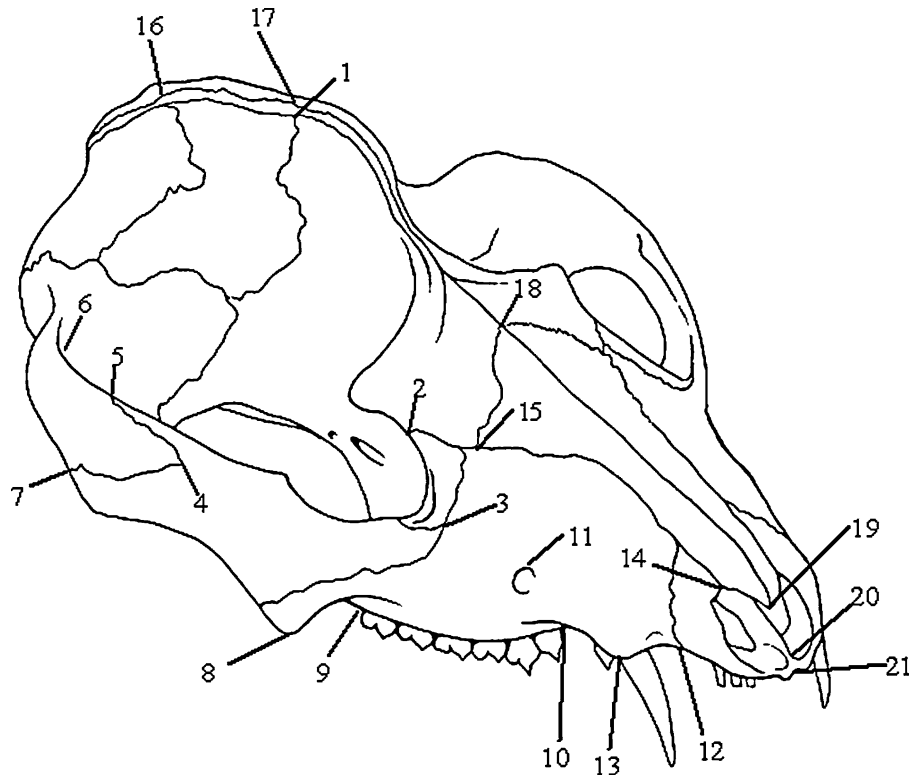


Figure 1. Landmarks (also see Table 1). *Didelphis virginiana* cranium showing the landmarks on the right side and midline. Points 1–15 are mirrored on the left hand side. Point 9 lies on the alveolar margin at the back of the molar teeth.

American didelphids and borhyaenoids, as well as Australian dasyuromorphians and some diprotodontians (Aplin and Archer 1987; Cardillo et al. 2004).

Here, applying multivariate techniques to three-dimensional (3-D) landmark coordinate data from crania (Fig. 1, Table 1) we examine the hypothesis that adaptive evolution has produced similar skull shape in nonherbivorous marsupials and carnivorans using a broad range of extant taxa supplemented by fossil species representing extinct ecomorphs.

Materials and Methods

Our sample comprised 89 crania representing 43 species (Table 2). For Carnivora there were 28 extant and two fossil taxa from seven families. It is thought that the now ecologically diverse Carnivora are descended from a generalized, viverrid-like ancestor not markedly specialized toward either a carnivorous or herbivorous diet (Martin 1989). Our sample comprised large and small hypercarnivores (e.g., *Panthera leo* [Lion], *Panthera atrox* [the extinct American lion], *Felis catus* [Domestic Cat]), bone-crackers (e.g., *Crocota crocuta* [Spotted Hyaena]), large and small omnivores (e.g., some ursid, canid, mustelid, and viverrid species), and largely or wholly insectivorous species (e.g., *Otocyon megalotis* [Bat-eared Fox] and *Proteles cristatus*

[Aardwolf]).

To amass a marsupial dataset that exhibited broadly comparable variation with respect to feeding ecology and morphology, we included a much greater proportion of extinct taxa than for carnivorans (i.e., five of the 13). Our objective was to examine convergence between nonherbivorous marsupials and placentals that had descended from relatively unspecialized taxa. To include marsupials that spanned as many feeding ecologies as possible, we also incorporated marsupials from outside the order most commonly considered (Dasyuromorphia).

Living marsupial species included larger carnivorous members of the two dasyuromorphian families, noted above, that have been included in previous treatments. For each of these species, vertebrate prey is, or almost certainly was, primary (Wroe et al. 2004). Among these carnivorous dasyuromorphians, broad comparisons have been made between species of *Dasyurus* and cats, between *Sarcophilus harrisii* (Tasmanian Devil) and hyaenas, and between *Thylacinus cynocephalus* and *Canis lupus* (gray wolf). We also included the sole representative of the third dasyuromorphian family, Myrmecobiidae. This species, the Numbat (*Myrmecobius fasciatus*), is a highly specialized insectivore, which, like *Proteles cristatus*, possesses a greatly hypotrophied cheektooth row. Generalist feeders were represented by bandicoots (Peramelemorphia). Fossil species comprised two

Table 1. Landmarks used in analysis (and see Fig. 1). Numbers 22–36 represent mirrored landmarks on opposing side of skull

Number	Definition of landmark
1 and 22	Fronto-parietal suture at the intersection of the temporal crest
2 and 23	Fronto-lacrimal suture at the medial orbital margin
3 and 24	Zygomatico-maxillary-lacrimal junction.
4 and 25	Anterior point of the zygomatic process of the temporal bone
5 and 26	Zygomatico-temporal suture on the upper edge of the zygomatic arch
6 and 27	Superior root of the zygoma (on the temporal bone)
7 and 28	Posterior end of the zygomatico-temporal suture
8 and 29	Lowest point on the anterior end of the zygomatic arch
9 and 30	Alveolar margin at the posterior aspect of the last molar
10 and 31	Alveolar margin at the anterior aspect of the first postdiastemal cheektooth
11 and 32	Infraorbital foramen
12 and 33	Maxillary-premaxillary suture at the alveolar margin
13 and 34	Alveolar margin at the posterior aspect of the canine
14 and 35	Naso-premaxillary suture at the margin of the nasal aperture
15 and 36	Fronto-naso-maxillary junction
16	Lambda
17	Bregma
18	Naso-frontal suture in the midline
19	Tip of the nasal bones in the midline
20	Interpremaxillary suture at the inferior margin of the nasal aperture
21	Interpremaxillary suture at the alveolar margin

additional dasyuromorphians, the Miocene *Nimbacinus dicksoni* (Thylacinidae) and the most morphologically conservative dasyurid (Wroe 1999), the Miocene *Barinya wangala*. Also included was the marsupial most likely to represent a large hypercarnivorous ecomorph comparable to that of large felids, the Pleistocene marsupial lion (*T. carnifex*). Largest of Australia's mammalian carnivores with a highly carnassialized cheektooth dentition and particularly powerful jaw adductors for its size (Wroe et al. 2005), recent analysis suggests that postcranial proportions in *T. carnifex* were most similar to those of dirk-toothed machairodont felids (Wroe et al., in press). In total 13 marsupial species representing seven families and four orders were included (Table 2).

From each specimen, data were collected in the form of 36 3-D landmarks (Table 1) using a Microscribe (3D \times , Immersion, San Jose, CA) digitizer. We used mean values for species

represented by more than one individual. These data were analyzed using the software package *morphologika* (available from www.york.ac.uk/res/fme) to perform generalized Procrustes and Principal Components (PCs) analyses (O'Higgins and Jones 1998; Milne and O'Higgins 2002; Chen et al. 2005). Procrustes analysis registers the specimens and scales them to the same size. This program allows the visualization of shape changes represented by PCs through "warping" mean shapes along PCs of interest, by adding the product of the eigenvectors (for the PC of interest) and score on that PC to the mean coordinates. This visualization obviates the necessity to examine the eigenvectors to appreciate the shape changes represented by each PC.

Coordinate geometry was used to rotate PCs 1 and 2 by the slope of the lines representing the two mammalian groups. This enabled the calculation of new axes (W–X Y–Z) perpendicular and parallel to the mammalian and placental lines.

Additional data collected for each species comprised centroid size, bite force, and endocranial volume or ECV (Table 2). Centroid size is the square root of the sum of squared Euclidean distances from each landmark to the centroid (Milne and O'Higgins 2002). Thus, although Procrustes scales all specimens, centroid size retains a measure of the original dimensions and can be used as a proxy for size. Raw values for bite force and ECV were normalized for body mass using the residuals of regression (Wroe et al. 2005) and both raw and transformed data were considered in analyses. Bite force was determined using the dry-skull method (Thomason 1991; Wroe et al. 2005; Christiansen and Wroe, 2007), using predictions of cross-sectional area of primary jaw adductors to estimate force. Most body masses were determined on the basis of skull length (Van Valkenburgh 1990; Myers 2001); however, for *T. carnifex*, which exhibits highly atypical skull shape, body mass was determined on the basis of endocranial volume and proximal limb bone circumference data (Wroe 2002; Wroe et al. 2003). All extant species were allocated to one of the four broad feeding categories (Table 2).

Results

The results of PC analysis on Procrustes registered landmark data for PC's one and two are plotted in Figure 2. The significance of analysis of variance calculations for feeding category are given in Table 3, as are correlations and their significance values for the relationship between the variables considered with respect to PCs and rotated axes.

Carnivoran and marsupial species form two distributions, which are approximately linear and parallel ($r^2 = 0.52$ and 0.78 , respectively) with PC2-intercepts that are significantly different ($F_{1,42} = 58.6384$, $P < 0.0000$). PC one accounts for 43% of the total variation. In dorsal view, shape changes along PC1 (–0.20 to 0.24) comprise a suite of transformations that include lengthening

Table 2. Taxa and variables considered in the analysis. FC, feeding category (●, omnivores and insectivores; ■, carnivores, small prey [up to 20% of predator body mass]; ▲, carnivores, medium-sized prey [up to the predator body mass]; ◆, carnivores, large prey [> predator body mass]); ◇, extinct (Stirling 1993; Sunquist and Sunquist 2002; Wroe et al. 2004; Wroe et al. 2005; Christiansen and Wroe, 2007). BoM, body mass in kilograms calculated on the basis of skull length (Myers 2001; Van Valkenburgh 1990); C, centroid; CBs, predicted bite force at the canines in Newtons (Thomason 1991); BFQ, bite force quotient (Wroe et al. 2005); ECV, endocranial volume in millilitres; EQ, encephalisation quotient (calculated on the basis of EQ for mammals (Jerison 1973)).*, extinct.

Symbol	Species (no. of individuals)	Common name	Family	FC	BoM	Centroid	CBs	BFQ	ECV	EQ
1	<i>Felis caracal</i> (6)	Caracal	Felidae	▲	11.6	25.6	129.5	95.1	57.7	93.9
2	<i>Acinonyx jubatus</i> (12)	Cheetah	Felidae	▲	58.6	36.5	338.8	108.1	118.4	65.5
3	<i>Panthera tigris</i> (4)	Tiger	Felidae	◆	159.2	55.1	1059.9	107.9	297.3	84.4
4	<i>Panthera pardus</i> (7)	Leopard	Felidae	◆	51.0	34.1	212.0	116.0	125.3	76.0
5	<i>Panthera onca</i> (1)	Jaguar	Felidae	◆	85.6	47.5	1108.8	121.2	200.4	86.0
6	<i>Panthera leo</i> (6)	Lion	Felidae	◆	176.0	58.9	1314.7	104.6	246.5	65.5
7	<i>Panthera atrox</i> * (1)	American Lion	Felidae	◇	382.0	71.3	1643.0	99.0	340.0	53.9
A	<i>Hyaena brunnea</i> (1)	Brown Hyaena	Hyaenidae	▲	43.4	45.7	560.1	104.7	117.7	79.5
B	<i>Crocuta crocuta</i> (1)	Spotted Hyaena	Hyaenidae	◆	51.9	48.2	565.7	90.8	173.7	104.1
C	<i>Proteles cristatus</i> (1)	Aardwolf	Hyaenidae	•	8.3	24.4	121.2	63.9	44.9	91.3
D	<i>Paradoxurus hermaphroditus</i> (1)	Palm Civet	Viverridae	■	3.0	18.3	167.9	95.8	17.5	70.1
E	<i>Arctictis binturong</i> (1)	Binturong	Viverridae	•	11.0	21.3	351.2	105.0	34.0	57.3
F	<i>Viverricula indica</i> (1)	Lesser Indian Civet	Viverridae	■	3.0	15.2	101.1	83.4	15.0	60.1
G	<i>Ursus arctos</i> (1)	Brown Bear	Ursidae	•	298.0	57.0	1894.9	88.5	382.9	71.6
H	<i>Ursus americanus</i> (1)	American Black Bear	Ursidae	•	111.0	45.1	1003.6	73.9	283.1	102.2
I	<i>Thalarcos maritimus</i> (1)	Polar Bear	Ursidae	▲	342.5	58.6	2349.6	106.6	526.5	89.7
J	<i>Ursus thibetanus</i> (1)	Asiatic Black Bear	Ursidae	•	100.5	42.7	1086.5	76.6	274.6	105.9
K	<i>Aonyx capensis</i> (1)	Cape Clawless Otter	Mustelidae	■	18.9	26.3	348.0	113.4	105.5	124.0
L	<i>Mellivora capensis</i> (1)	Honey Badger	Mustelidae	▲	8.1	25.1	317.7	96.9	78.3	161.9
M	<i>Meles meles</i> (1)	Eurasian Badger	Mustelidae	•	11.6	24.7	282.2	84.4	55.9	91.0
N	<i>Gulo gulo</i> (1)	Wolverine	Mustelidae	◆	11.6	21.3	348.5	97.5	81.5	132.6
O	<i>Procyon lotor</i> (1)	Northern Raccoon	Procyonidae	•	4.0	21.6	176.7	100.0	37.0	122.4
P	<i>Otocyon megalotis</i> (1)	Bat-eared Fox	Canidae	•	3.9	19.4	111.3	70.7	33.7	113.4
Q	<i>Lycaon pictus</i> (1)	Cape Hunting Dog	Canidae	◆	22.0	39.3	536.8	138.4	138.3	146.9
R	<i>Canis mesomelas</i> (2)	Black-backed Jackal	Canidae	•	7.7	31.7	187.5	85.2	55.4	118.5
S	<i>Canis lupus</i> (1)	Grey Wolf	Canidae	◆	30.0	39.8	753.9	125.2	143.9	124.3
T	<i>Canis adjustus</i> (1)	Side-striped Jackal	Canidae	■	11.2	28.1	233.2	82.4	55.4	92.3
U	<i>Canis laterans</i> (1)	Coyote	Canidae	■	10.6	33.2	289.6	85.7	88.2	152.4
V	<i>Vulpes chama</i> (1)	Cape Fox	Canidae	•	4.0	21.0	134.0	93.7	38.5	127.4
W	<i>Canis dirus</i> * (1)	Dire Wolf	Canidae	◇	50.0	50.0	893.0	163.0	190.0	116.7
a	<i>Didelphis virginiana</i> (1)	Virginia Opossum	Didelphidae	■	4.0	26.2	127.6	110.0	5.1	16.9
b	<i>Thylacinus cynocephalus</i> * (1)	Thylacine	Thylacinidae	◇	29.0	41.6	808.1	166.0	50.7	44.8
c	<i>Nimbicinus dixonii</i> * (1)	Dixon's Thylacine	Thylacinidae	◇	5.0	24.8	267.0	189.0	–	–
d	<i>Sarcophilus harrisii</i> (4)	Tasmanian Devil	Dasyuridae	◆	7.0	24.7	417.9	181.0	15.4	35.1
e	<i>Dasyurus viverrinus</i> (1)	Eastern Quoll	Dasyuridae	▲	1.4	13.7	65.4	137.0	5.0	60.6
f	<i>Dasyurus maculatus</i> (1)	Spotted-tailed Quoll	Dasyuridae	◆	2.5	19.1	179.8	179.0	5.4	24.4
g	<i>Dasyurus geoffroii</i> (4)	Western Quoll	Dasyuridae	▲	.5	16.0	43.6	122.0	9.1	66.2
h	<i>Isodon obesulus</i> (3)	Brown Bandicoot	Peremalidae	•	1.2	14.1	27.6	48.0	4.2	31.0
i	<i>Macrotis lagotis</i> (1)	Bilby	Thylacomyidae	•	1.0	18.6	45.1	41.0	6.1	50.9
j	<i>Myrmecobius fasciatus</i> (1)	Numbat	Myrmecobiidae	•	.4	11.4	24.1	92.0	3.5	58.8
k	<i>Thylacoleo carnifex</i> * (1)	Pleistocene Marsupial Lion	Thylacoleonidae	◇	104.0	49.3	1691.6	194.0	119.2	45.0
l	<i>Wakaleo vanderleurei</i> * (1)	Vanderleur's Marsupial Lion	Thylacoleonidae	◇	41.4	35.3	672.9	139.0	–	–
m	<i>Barinya wangala</i> * (1)	Miocene Dasyure	Dasyuridae	◇	.8	12.7	37.8	81.0	2.7	25.3

of the rostrum, nasals that increase posteriorly in width and extend further anteriorly relative to the premaxilla, as well as more posterior positioning of the temporomandibular-joint (TMJ) relative to the lambda. Observed laterally, the cranium becomes less flexed with the lambda higher and snout extending further forward. PC one correlates with bite force ($r = -0.44$, $P < 0.01$), body mass ($r = 0.41$, $P < 0.01$), endocranial volume ($r = -0.52$, $P < 0.001$), and centroid size ($r = -0.54$, $P < 0.001$ and see Table 3). In broad terms, variation along this axis might be described as from short snouted (brachycephalic) and cat like, to long snouted (dolichocephalic) and dog like. Although there is a tendency for species with low scores on this PC to predate larger prey, one-way analysis of variance does not show significance when the dataset inclusive of all taxa is considered.

PC two accounts for 11% of the variation and represents shape change (from -0.16 to 0.1) wherein the zygomatic arches become shorter, narrower, and more gracile, and the TMJ becomes more anteriorly positioned relative to the lambda (Fig. 2). The nasal bones also become shorter relative to the anterior dentition and narrower posteriorly, reducing the width of the face at the orbits. PC2 correlates negatively with bite force normalized for body mass (BFQ) ($r = -0.59$, $P < 0.001$), and positively with endocranial volume ($r = 0.34$, $P < 0.05$) and encephalization quotient ($r = 0.56$, $P < 0.001$).

The most notable shape change seen with increasing PC3 scores (8% of variance) is that the nasal bones increase in length posteriorly at the expense of the frontal bones. There is some correlation between PC3 and body mass ($r = 0.34$, $P < 0.05$). The viverrids have low and the fossil species have high scores on PC3. Subsequent PCs account for 5% or less of the variance and do not show clear functional or phylogenetic trends.

When our marsupial and carnivoran samples are considered independently, the marsupials show correlation between all variables with respect to PCs 1 and 2, excepting encephalization quotient and analysis of variance shows PC1 to be strongly related to feeding category ($P < 0.02$). This is not so for carnivorans where there are no significant correlations of any of the variables with PCs one or two, nor does ANOVA reveal a significant relationship with feeding category. However within Carnivora, PC1 shows significant correlation with body mass, ECV and centroid size for Felidae ($r = 0.78$, $P < 0.02$; $r = 0.78$, $P < 0.02$; $r = 0.78$, $P < 0.02$) and with bite force, BFQ, body mass, ECV, and centroid size in Canidae ($r = 0.72$, $P < 0.02$; $r = 0.81$, $P < 0.01$; $r = 0.67$, $P < 0.05$; $r = 0.72$, $P < 0.02$; $r = 0.66$, $P < 0.05$). Analysis of variance shows a significant relationship between PC1 and feeding category between both Felidae and Canidae ($P < 0.01$ and $P < 0.05$), as well as between feeding category and BFQ (ANOVA, $P < 0.001$).

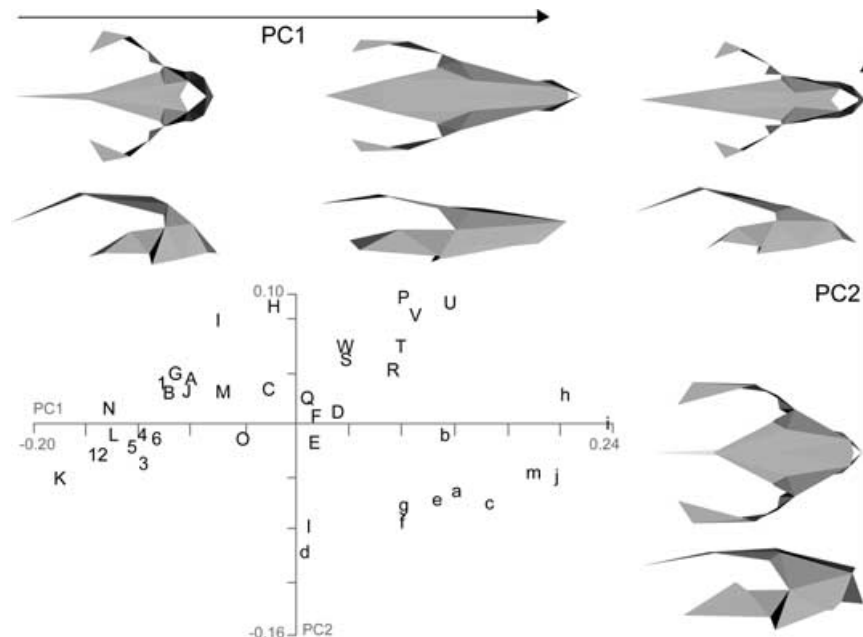


Figure 2. Principal components one and two. Plot of the first two PCs. The shape changes along PC1 and 2 are shown above and to the right of the plot, respectively. Key to symbols (and see Table 2 for complete binomials and family level classification): 1, *F. caracal*; 2, *A. jubatus*; 3, *P. tigris*; 4, *P. pardus*; 5, *P. onca*; 6, *P. leo*; 7, *P. atrox*(†); A, *H. brunnea*; B, *C. crocuta*; C, *P. cristatus*; D, *P. hermaphroditus*; E, *A. binturong*; F, *V. indica*; G, *U. arctos*; H, *U. americanus*; I, *T. maritimus*; J, *U. thibetanus*; K, *A. capensis*; L, *M. capensis*; M, *M. meles*; N, *G. gulo*; O, *P. lotor*; P, *O. megalotis*; Q, *L. pictus*; R, *C. mesomelas*; S, *C. lupus*; T, *C. adjustus*; U, *C. laterans*; V, *V. chama*; W, *C. dirus*; a, *D. virginiana*; b, *T. cynocephalus*(†); c, *N. dixonii*(†); d, *S. harrisi*; e, *D. viverrinus*; f, *D. maculatus*; g, *D. geoffroi*; h, *I. obsesulus*; i, *M. lagotis*; j, *M. fasciatus*; k, *T. carnifex*(†); l, *W. vanderleurei*(†); m, *B. wangala*(†). Extinct taxa denoted by †.

Table 3. The significance of analysis of variance calculations for feeding category, and correlations and their significance values for the relationship between the variables considered in the analysis, the first two principal components, and the rotated axes. For analyses of feeding behavior, only extant taxa were considered

All (<i>n</i> = 43)	PC1	PC2	Y–Z axis	X–W axis
Feeding category	<i>P</i> = 0.067	<i>P</i> = 0.150	<i>P</i> = 0.023	<i>P</i> = 0.973
Bite force (raw)	–0.443 <i>P</i> <0.01	0.105	–0.409 <i>P</i> <0.02	0.381 <i>P</i> <0.02
BFQ	–0.045	–0.589 <i>P</i> <0.001	–0.174	–0.397 <i>P</i> <0.01
Body mass	–0.413 <i>P</i> <0.01	0.191	–0.357 <i>P</i> <0.05	0.426 <i>P</i> <0.01
Centroid size	–0.537 <i>P</i> <0.001	0.214	–0.476 <i>P</i> <0.01	0.524 <i>P</i> <0.001
Endocranial volume	–0.524 <i>P</i> <0.001	0.340 <i>P</i> <0.05	–0.434 <i>P</i> <0.01	0.621 <i>P</i> <0.001
Encephalisation Q	–0.356 <i>P</i> <0.05	0.558 <i>P</i> <0.001	–0.225	0.662 <i>P</i> <0.001
Marsupials (<i>n</i> = 13)				
Feeding category	<i>P</i> = 0.016	<i>P</i> = 0.077	<i>P</i> = 0.016	<i>P</i> = 0.995
Bite force (raw)	–0.738 <i>P</i> <0.01	–0.635 <i>P</i> <0.01	–0.732 <i>P</i> <0.01	0.033
BFQ	–0.775 <i>P</i> <0.01	–0.736 <i>P</i> <0.01	–0.782 <i>P</i> <0.001	–0.149
Body mass	–0.688 <i>P</i> <0.01	–0.632 <i>P</i> <0.02	–0.690 <i>P</i> <0.01	–0.084
Centroid size	–0.681 <i>P</i> <0.01	–0.496	–0.657 <i>P</i> <0.01	0.222
Endocranial volume	–0.670 <i>P</i> <0.01	–0.591 <i>P</i> <0.05	–0.665 <i>P</i> <0.01	–0.074
Encephalisation Q	0.008	–0.039	0.002	–0.104
Carnivorans (<i>n</i> = 30)				
Feeding category	<i>P</i> = 0.069	<i>P</i> = 0.299	<i>P</i> = 0.027	<i>P</i> = 0.124
Bite force (raw)	–0.279	0.153	–0.212	0.566 <i>P</i> <0.001
BFQ	–0.152	–0.252	–0.177	–0.160
Body mass	–0.315	0.110	–0.251	0.557 <i>P</i> <0.001
Centroid size	–0.314	0.094	–0.253	0.535 <i>P</i> <0.01
Endocranial volume	–0.328	0.161	–0.253	0.641 <i>P</i> <0.001
Encephalisation Q	0.227	0.276	0.246	0.063
Canidae (<i>n</i> = 8)				
Feeding category	<i>P</i> = 0.029	<i>P</i> = 0.298	<i>P</i> = 0.054	<i>P</i> = 0.838
Bite force (raw)	–0.722 <i>P</i> <0.02	–0.447	–0.679 <i>P</i> <0.05	–0.001
BFQ	–0.809 <i>P</i> <0.01	–0.540	–0.771 <i>P</i> <0.01	–0.061
Body mass	–0.673 <i>P</i> <0.05	–0.381	–0.623	0.056
Centroid size	–0.657 <i>P</i> <0.05	–0.554	–0.656 <i>P</i> <0.05	–0.233
Endocranial volume	–0.723 <i>P</i> <0.02	–0.474	–0.687 <i>P</i> <0.05	–0.042
Encephalisation Q	–0.053	–0.054	–0.056	–0.034
Felidae (<i>n</i> = 6)				
Feeding category	<i>P</i> = 0.003	<i>P</i> = 0.581	<i>P</i> = 0.005	<i>P</i> = 0.192
Bite force (raw)	0.703	–0.150	0.628	–0.756 <i>P</i> <0.02
BFQ	0.447	0.305	0.470	–0.160
Body mass	0.784 <i>P</i> <0.02	–0.174	0.699	–0.848 <i>P</i> <0.01
Centroid size	0.783 <i>P</i> <0.02	–0.156	0.701	–0.832 <i>P</i> <0.01
Endocranial volume	0.783 <i>P</i> <0.02	–0.302	0.676	–0.949 <i>P</i> <0.001
Encephalisation Q	–0.282	–0.349	–0.327	–0.024

Although PC2 more clearly distinguishes morphological differences between our marsupial and carnivoran datasets than does PC1, there is overlap. For example, both PCs evidence changes in the relative position of the lambda/TMJ, length of the nasal bones and snout length. To more clearly differentiate between functional and phylogenetic differences separating the two groups, we rotated data from the original PC1–2 plot to generate an axis (W–X) along which there is no overlap. This highlights differences between the

two groups (Fig. 3). Shapes at the ends of the W–X axis represent carnivoran–marsupial differences, where the nasals become longer and wider posteriorly, the TMJ is situated more posteriorly and the zygomatic arches are correspondingly longer and more robust as the marsupial configuration is approached (from X to W). The marsupial crania are also flatter and less flexed. There are significant positive correlations with bite force, ECV, encephalization quotient, and centroid size, but a negative correlation with

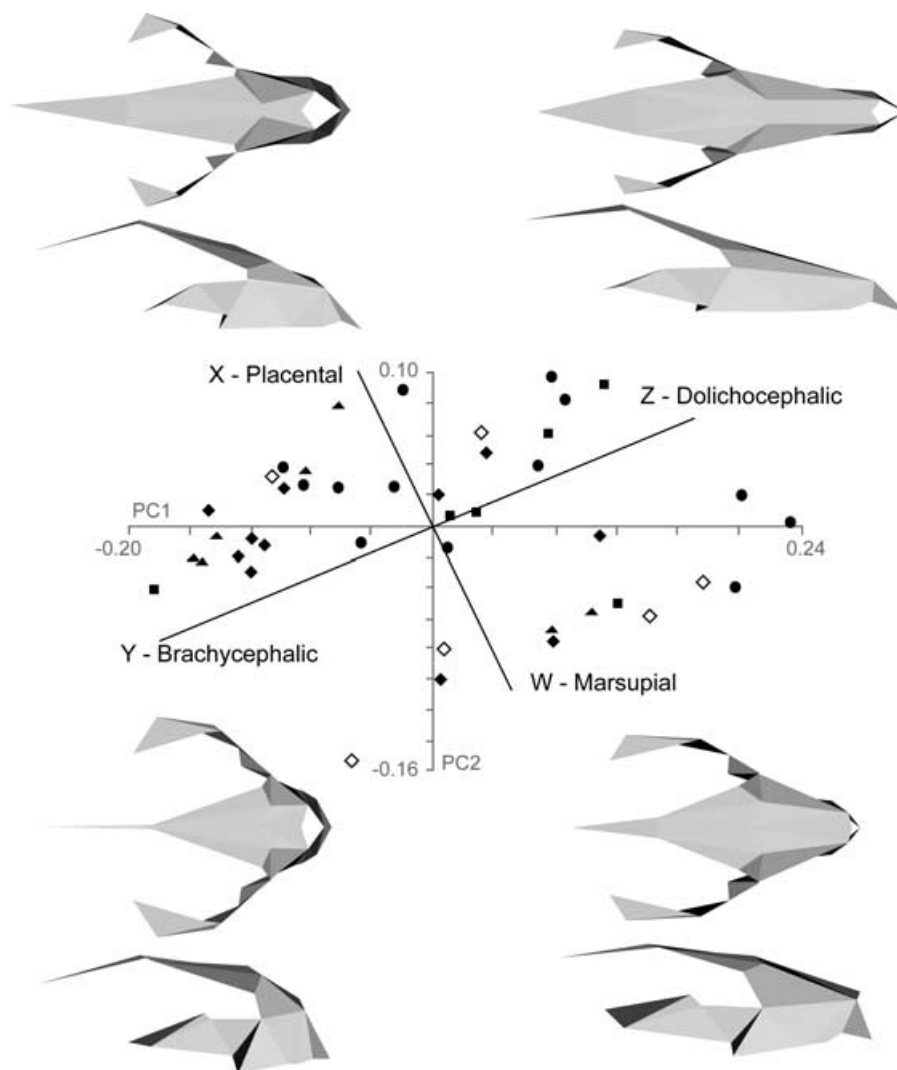


Figure 3. Shape changes along rotated axes (symbols as in Fig. 2, Table 2). FC = feeding category (●, omnivores and insectivores; ■, carnivores, small prey [up to 20% of predator body mass]; ▲, carnivores, medium-sized prey [up to the predator body mass]; ◆, carnivores, large prey [$>$ predator body mass]); ◇, extinct (Stirling 1993; Sunquist and Sunquist 2002; Wroe et al. 2004; Wroe et al. 2005; Christiansen and Wroe, 2007).

BFQ (Table 3). These shape differences between marsupials and carnivorans are maintained across all body masses and feeding categories (Fig. 3) as indicated by significantly different W–X intercepts ($F_{1,42} = 100.9588$, $P < 0.0000$).

Terminal shapes for the Y–Z axis (Fig. 3) show changes common to carnivorans and marsupials with increasing snout length. Areas available for the attachment of masticatory muscles diminish as the temporal region, sagittal crest, and zygomatic arches become smaller and less robust and the space under the arches is also reduced. There is no change in the position of the TMJ relative to the lambda or in apparent flexion of the cranium. In contrast to the findings for the X–W axis, ANOVA shows a significant relationship between scores on the Y–Z axis and feeding category for the entire sample ($P < 0.05$), as well as for clades within (e.g., marsupials $P < 0.02$; carnivorans $P < 0.05$) and Felidae

$P < 0.005$). There are also significant correlations with bite force, ECV, and centroid size for marsupials and canids (Table 3). These trends are likely to influence feeding ecology through their effects on force and mechanical advantage imparted to the jaw closing apparatus. Leverage diminishes with increasing snout length and potential force is reduced with reduction in available attachment area for jaw adductors.

Discussion

Our results provide some support for the contention of convergence between nonherbivorous marsupials and carnivorans across a broad spectrum of feeding ecologies. A number of variables correlating with PC1 and PC2 are thought to be functionally meaningful and have been forwarded as predictors of feeding ecology.

Shortening of the snout and skull, as well evidenced in decreasing PC1 values (Fig. 2), is accompanied by mechanical advantage through reduced outlever lengths for the jaws, as well as increased resistance to the torsional loadings that might be expected in close quarter encounters with large, struggling prey (Radinsky 1981a). Bite force normalized for body mass (BFQ) is also an indicator of relative prey size (Wroe et al. 2005; Christiansen and Wroe, 2007).

It is clear that the rotated axes more clearly characterize and demonstrate the differences between carnivorans and marsupials (X–W axis) and the differences associated with feeding category (Y–Z axis) than does either PC1 or PC2. The association with feeding category in the whole sample and also for the carnivorans improves when the Y–Z axis is examined. Similarly, among the whole sample, the associations with BFQ, body mass, centroid size, ECV, and EQ are stronger with the X–W axis. This improved clarity is also evident in the shape changes associated with the rotated axes, where the differences in TMJ position, cranial flexion, nasal bone length, and shape, snout length are only seen in either the W–X or Y–Z axes.

Although previous work has indicated that skull shape offers insights into function and ecology among a number of carnivoran families (Radinsky 1981a), overall relationships between form and diet have been shown to weaken when a more complete selection of taxa is considered (Radinsky 1981b). Mustelidae in particular show notable intrafamilial variation with respect to cranial morphology and poor correlation between skull shape and diet (Radinsky 1981b; Andersson 2005). Similarly, *contra* overall trends, we find that typically omnivorous bears are more brachycephalic than hypercarnivorous canids, with correspondingly lower scores on PC 1 (Fig. 2). Recent analysis has found that morphological integration in the crania of Carnivora is strongly influenced by phylogeny and that significant correlation with diet is restricted to subsets of taxa within the order (Goswami 2006) and our results are in broad agreement on each of these points. Thus, we find only weak correlation between PC1 and feeding ecology for this placental order, but stronger correlations for some constituent families, notably Felidae and Canidae.

Our results suggest that skull shape is a more reliable predictor of feeding ecology for nonherbivorous marsupials. The placement of marsupials along PC1 and the Y–Z axis is far more consistent with the inferred relationships between feeding category and brachycephalization–dolichocephalization. Without exception, insectivorous and omnivorous marsupials, for example, bandicoots and the numbat, have higher scores on PC1 than more carnivorous species and among carnivorous marsupials scores diminish with increasing relative prey size. The marsupial lion, indisputably a hypercarnivore and a probable large game specialist has the lowest PC1 score among marsupials.

The apparent reliability of skull shape as a predictor of diet for our marsupial sample is particularly striking given the very wide phylogenetic spread of taxa included in our analysis. These findings may be related to apparent constraints on behavioral plasticity. Killing behavior in living marsupials appears to be less specific and directed than in comparable carnivorans (Ewer 1969). Moreover, social hunting, unknown in marsupials, allows some dolichocephalic canid species to regularly take prey exceeding their own body masses. When pack-hunting extant canid species (*Lycaon pictus* [Cape Hunting Dog] and *Canis lupus*) are excluded from the dataset inclusive of marsupials and carnivorans, the relationship with feeding category improves for both PC1 and adjusted values on the rotated Y–Z axes (ANOVA $P = 0.045$ and $P = 0.011$, respectively). Results are internally consistent at the family level, however, in that within Canidae a tendency to take large prey is still reflected in relatively short snouts and lower scores on PC1 for these pack-hunting species relative to canids that take smaller prey (*Canis mesomelas* [Black-backed Jackal], *C. adjustus* [Side-striped Jackal], *C. laterans* [Coyote], *Vulpes chama* [Cape Fox], *Otocyon megalotis* [bat-eared fox]).

Consequently, with respect to the prediction of behavior in extinct carnivorans, geomorphometric analyses such as ours require strong and appropriate allowance for phylogenetic influences. While the influence of phylogeny certainly cannot be discounted for marsupials it appears less limiting, suggesting that geometric morphometric treatments will be of more use in the prediction of fossil marsupial feeding behavior.

Although we find some correlation between skull shape and feeding ecology and evidence for convergence, differences in skull shape between marsupials and carnivorans are remarkably consistent. These are most explicitly revealed in transformations along the “marsupial–placental” axis (X–W) and are maintained irrespective of body mass or feeding category. Phylogenetic constraint is very strongly implicated with respect to the four “marsupial” features identified here, that is, longer and wider nasals posteriorly, more posterior placement of the TMJ, longer, more robust zygomatic arches and flatter, less flexed crania overall.

Our results suggest that at least some of these constraints may be related to differences in masticatory musculature and brain size. The larger and more robust zygomatic arch suggests more powerful masseter muscles in marsupials. Our findings here are in keeping with previous assertions that the masseteric muscles may play a greater role in jaw adduction relative to those of the temporalis system for marsupials (Wells et al. 1982) and that bite force adjusted for body mass is higher (Wroe et al. 2005).

Endocranial volume is typically lower in marsupials, being around 40% that of same-sized carnivorans (Wroe et al. 2003). Certainly higher values for bite force normalized for body mass in marsupials (Wroe et al. 2005) and correlation between bite force and ECV ($r = 0.88$, $P < 0.0001$) in the present analysis

are consistent with the proposition that interrelated differences regarding bite force, muscle organization and/or brain size contribute to these dissimilarities in skull shape. This contention is reinforced by significant correlations between bite force and endocranial volume regarding the marsupial–placental axis, that is, when the PC1 and 2 axes are rotated to more fully differentiate between the two groups. It seems likely that smaller brain size allows more room for primary jaw adductors, and vice versa, inviting consideration of the intriguing possibility that carnivorans have sacrificed bite force for greater encephalization (Wroe et al. 2005). A similar thesis has been advanced with respect to hominid evolution, wherein the evolution of *Homo* is marked by significant reductions in masticatory muscle masses and corresponding increases in endocranial volume (Stedman et al. 2004).

However, one of the features identified as characteristic of our marsupial sample, posterior placement of the TMJ, does not obviously lend biomechanical advantage with respect to bite force. Theoretically, this should reduce bite force through extension of the jaw's outlever. It may be that this effect is countered by corresponding advantage lent to the jaw's inlever. Analyses incorporating mandibular material will be needed to examine this further.

Broader sampling is also required to more fully investigate to what extent differences in brain size might explain the differences in skull shape identified here. Among living taxa, applying a similar approach to herbivorous marsupial and placental clades may yield informative results. With respect to studies incorporating fossil taxa, if brain size does largely explain shape variation then we would predict that differences should diminish in comparisons between marsupials and smaller brained placental taxa such as Creodonta.

ACKNOWLEDGMENTS

This work has been supported by a Queen Elizabeth II Research Fellowship and Project Grant from the Australian Research Council and by a University of New South Wales Strategic Initiatives Grant (to S. Wroe). We thank P. Christiansen (Zoological Museum, University of Copenhagen), C. Shaw (Page Museum), S. Ingelby and T. Ennis (Australian Museum), J. McNamara (South Australian Museum), N. Cooper and J. Long (Western Australian Museum), and D. Hamerton (Cape Town Museum).

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Associate Editor: C. Janis

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