

The evolution of orbit orientation and encephalization in the Carnivora (Mammalia)

John A. Finarelli^{1,2} and Anjali Goswami³

¹Department of Geological Sciences, University of Michigan, Ann Arbor, MI, USA

²University of Michigan, Museum of Paleontology, Ann Arbor, MI, USA

³Department of Earth Sciences, University of Cambridge, Cambridge, UK

Abstract

Evolutionary change in encephalization within and across mammalian clades is well-studied, yet relatively few comparative analyses attempt to quantify the impact of evolutionary change in relative brain size on cranial morphology. Because of the proximity of the braincase to the orbits, and the inter-relationships among ecology, sensory systems and neuroanatomy, a relationship has been hypothesized between orbit orientation and encephalization for mammals. Here, we tested this hypothesis in 68 fossil and living species of the mammalian order Carnivora, comparing orbit orientation angles (convergence and frontation) to skull length and encephalization. No significant correlations were observed between skull length and orbit orientation when all taxa were analysed. Significant correlations were observed between encephalization and orbit orientation; however, these were restricted to the families Felidae and Canidae. Encephalization is positively correlated with frontation in both families and negatively correlated with convergence in canids. These results indicate that no universal relationship exists between encephalization and orbit orientation for Carnivora. Braincase expansion impacts orbit orientation in specific carnivoran clades, the nature of which is idiosyncratic to the clade itself.

Key words Carnivora; convergence angle; encephalization; frontation angle; Mammalia.

Introduction

The evolution of encephalization, or brain volume scaled to body mass, has long been of interest in mammalian evolutionary biology, due at least in part to the extreme increases in encephalization observed in mammals relative to several other amniote clades, particularly within the lineage leading to modern humans. There have been multiple, independent increases in encephalization through the evolutionary history of the mammalian order Carnivora (Finarelli & Flynn, 2007; Finarelli, 2008b). However, it is possible that evolutionary changes in the relative size of the braincase can impose corresponding structural changes on the morphology of other regions of the skull. Focusing on primates, Cartmill (1970) linked increased encephalization, particularly expansion of the frontal lobe, to increased verticality of the orbit, through forward displacement of the upper margin of the orbit.

Orbit orientation has been studied extensively within and among mammalian clades (Cox, 2008), and is of

particular interest because of its hypothesized relationship to such ecological factors as locomotory style and hunting/foraging behaviour (e.g. Cartmill, 1972, 1974; Ross, 1995; Noble et al. 2000; Heesy, 2005). Orbit orientation is most commonly described using the convergence angle (CA) (the degree to which the orbits face laterally) and frontation angle (FA) (the degree of verticality of the orbits) (Cartmill, 1970, 1972, 1974). Increased CA is related to greater stereoscopic vision and depth perception, and has been linked to arboreality and nocturnal visual predation in Primates (Cartmill, 1970, 1972). Noble et al. (2000) compared CA and FA for two carnivoran families, Felidae (cats) and Herpestidae (mongooses), as well as pteropodid bats, recovering significant positive correlations between FA and encephalization within the Felidae and between felids and herpestids (Noble et al. 2000). However, that analysis only examined two families within one of the two carnivoran suborders, Feliformia, and furthermore only considered extant species. Carnivorans exhibit a large morphological diversity outside those two families, especially within the suborder Caniformia (Wesley-Hunt, 2005). Moreover, including data from the fossil record has the potential to dramatically alter inferences of character evolution relative to analyses based solely on extant taxa (e.g. Finarelli & Flynn, 2006). Carnivora has both a well-resolved phylogeny (e.g. Flynn et al. 2005; Wesley-Hunt &

Correspondence

J. A. Finarelli, Department of Geological Sciences, University of Michigan, 2534 C.C. Little Building, 1100 North University Avenue, Ann Arbor, MI 48109, USA. E: john.finarelli@umich.edu

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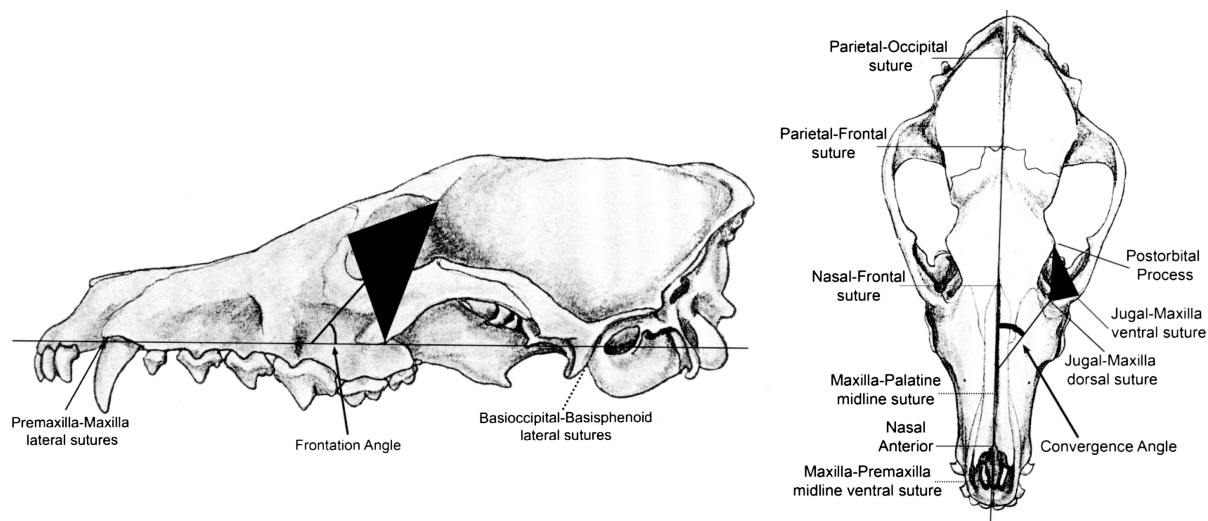


Fig. 1 Red fox (*Vulpes vulpes*) skull showing the landmarks used to define the orbital plane and the two reference planes (basal plane, left and mid-sagittal plane, right). The convergence and frontation angles were measured as the dihedral angles between the orbital reference planes.

Flynn, 2005) and an extensively sampled fossil record (e.g. Wesley-Hunt, 2005; Finarelli, 2008a), allowing us to study the interaction between change in orbit orientation and encephalization through carnivoran evolutionary history.

Materials and methods

Landmark measurements and encephalization data

We measured the CA and FA of the orbital plane (Cartmill, 1970, 1972, 1974) for 68 carnivoran taxa (37 extant and 31 fossil species), examining 442 specimens. To define the orbital plane we captured three-dimensional landmark data using a G2X three-dimensional digitizer (Immersion Microscribe, San Jose, CA, USA) (Goswami, 2006a,b). The orbital plane was defined using three landmarks: (1) the post-orbital process, (2) the dorsal suture of the jugal and maxilla, and (3) the ventral suture of the jugal and maxilla (Fig. 1). Although using the post-orbital process of the zygomatic would more closely correspond to the orbital plane, the zygomatic arch posterior to the jugal-maxilla suture is often incomplete or distorted in fossil specimens, which would severely restrict our ability to incorporate fossil taxa into our analysis. Because this plane does not directly correspond to the orbital plane, the angles measured in this study are not directly comparable to those in other data sets (e.g. Cartmill, 1970, 1972; Ross, 1995; Noble et al. 2000; Heesy, 2005). However, these data do distinguish more and less convergent or frontated orbits, and can be used to study the impact of changes in relative volume of the braincase on the orientation of the orbits. We also defined two reference planes in the skull: the mid-sagittal plane (defined using three to six landmarks, as some fossil specimens were missing some of the six mid-sagittal plane landmarks) and the basal plane (defined using four landmarks; Fig. 1) (Goswami, 2006a,b). Using routines written in Mathematica (Wolfram Research, Inc., Champaign, IL, USA), we calculated the measures of the dihedral angles between the orbital and reference planes; the angle between the orbital plane and the mid-sagittal plane of the skull measured the CA and the angle between the

orbital plane and the basal plane of the skull measured the FA. A larger CA indicates more anteriorly-oriented orbits, when viewed from above, whereas a larger FA indicates more vertically-oriented orbits, when viewed from the side.

We evaluated the relationship of orbit orientation angles to both skull length and encephalization. Skull length was used as a proxy for body size (Van Valkenburgh, 1990) and we estimated this using the chord length between the occipital condyle lateral margin and the premaxilla-maxilla anterior lateral suture (Goswami, 2006a,b), averaging over measurements of both the left and right sides. To calculate encephalization, we used an extensive database of adult body masses and endocranial volume estimates for living and fossil carnivorans (Finarelli, 2008a,b; Finarelli & Flynn, 2006, 2007), measuring the logarithm of the encephalization quotient ($\log_{10}EQ$) (e.g. Marino et al. 2004; Finarelli & Flynn, 2007), calculating the encephalization quotient relative to the brain volume/body mass allometry for extant Carnivora. We used the base-2 logarithm, such that $\log_2EQ = 1$ indicates a brain double the expected volume for a given body mass, whereas $\log_2EQ = -1$ indicates a volume half as large as expected. Body masses, brain volumes, skull lengths and orbit orientation angles are reported in Table 1.

Phylogeny of the carnivora and independent contrasts

Valid statistical analysis of comparative data in biological systems requires information on the phylogenetic relationships of the organisms being analysed to account for the statistical non-independence of character values observed for closely related taxa (Felsenstein, 1985; Garland et al. 1992, 1999; Garland & Ives, 2000). To account for this, we constructed a composite cladogram of the Carnivora, assembling evolutionary relationships among taxa from numerous molecular morphological and total evidence phylogenetic analyses that have recently been performed for this clade (see review in Flynn et al. in press). The cladogram depicting the relationships among the major Carnivoran clades is given in Fig. 2. Taxa included in this analysis span all of the extant families of terrestrial carnivorans, in addition to the extinct families Amphicyonidae and Nimravidae. The clade of marine carnivorans,

Table 1 Data for carnivoran taxa

Suborder	Family	Subfamily	Genus	Species	log ₂ EQ	CA	FA	Skull length
Caniformia	Amphicyonidae		<i>Daphoenodon</i>	<i>superbus</i>	-0.755	36.737	59.025	200.892
Caniformia	Amphicyonidae		<i>Daphoenus</i>	<i>hartshornianus</i>	-0.051	27.039	66.21	138.620
Caniformia	Amphicyonidae		<i>Daphoenus</i>	<i>vetus</i>	-0.171	21.349	70.168	179.704
Caniformia	Canidae	Borophaginae	<i>Aelurodon</i>	<i>ferox</i>	0.117	28.874	74.554	176.419
Caniformia	Canidae	Borophaginae	<i>Aelurodon</i>	<i>mcgrewi</i>	-0.757	26.946	74.692	179.021
Caniformia	Canidae	Borophaginae	<i>Aelurodon</i>	<i>taxoides</i>	0.089	32.753	72.216	220.284
Caniformia	Canidae	Borophaginae	<i>Borophagus</i>	<i>littoralis</i>	0.140	22.93	83.303	172.120
Caniformia	Canidae	Borophaginae	<i>Borophagus</i>	<i>secundus</i>	-0.030	22.271	73.851	157.511
Caniformia	Canidae	Borophaginae	<i>Carpocyon</i>	<i>webbi</i>	0.049	18.324	83.604	190.146
Caniformia	Canidae	Borophaginae	<i>Epicyon</i>	<i>saevus</i>	-0.341	21.257	74.063	187.444
Caniformia	Canidae	Borophaginae	<i>Microtomarctus</i>	<i>conferta</i>	-0.244	20.863	71.756	106.906
Caniformia	Canidae	Borophaginae	<i>Tomarctus</i>	<i>brevirostris</i>	-0.693	30.806	68.551	153.065
Caniformia	Canidae	Borophaginae	<i>Tomarctus</i>	<i>hippophaga</i>	0.026	26.462	68.531	145.706
Caniformia	Canidae	Caninae	<i>Canis</i>	<i>lupus</i>	0.187	18.122	75.619	198.859
Caniformia	Canidae	Caninae	<i>Canis</i>	<i>dirus</i>	-0.022	19.552	79.335	223.315
Caniformia	Canidae	Caninae	<i>Cerdocyon</i>	<i>thous</i>	0.249	18.49	80.232	110.083
Caniformia	Canidae	Caninae	<i>Otocyon</i>	<i>megalotis</i>	-0.169	19.029	81.256	98.888
Caniformia	Canidae	Caninae	<i>Vulpes</i>	<i>vulpes</i>	0.239	21.527	71.41	105.873
Caniformia	Canidae	Hesperocyoninae	<i>Enhydrocyon</i>	<i>pahinsintewakpa</i>	-0.583	36.505	59.309	146.455
Caniformia	Canidae	Hesperocyoninae	<i>Enhydrocyon</i>	<i>stenocephalus</i>	-0.327	32.614	65.535	148.812
Caniformia	Canidae	Hesperocyoninae	<i>Hesperocyon</i>	<i>gregarius</i>	-0.460	27.78	64.125	80.396
Caniformia	Canidae	Hesperocyoninae	<i>Mesocyon</i>	<i>brachyops</i>	-0.150	22.674	No data	119.707
Caniformia	Canidae	Hesperocyoninae	<i>Mesocyon</i>	<i>coryphaeus</i>	-0.196	24.916	70.134	135.245
Caniformia	Canidae	Hesperocyoninae	<i>Osbornodon</i>	<i>fricki</i>	-0.357	18.515	84.84	208.343
Caniformia	Ailuridae		<i>Ailurus</i>	<i>fulgens</i>	0.280	28.497	68.448	91.303
Caniformia	Mephitidae		<i>Mephitis</i>	<i>mephitis</i>	-0.903	22.895	71.825	65.095
Caniformia	Mephitidae		<i>Spilogale</i>	<i>putorius</i>	-0.229	23.617	72.205	46.684
Caniformia	Mustelidae	Basal group	<i>Leptarctus</i>	<i>primus</i>	-0.803	26.624	80.809	78.975
Caniformia	Mustelidae	Basal group	<i>Meles</i>	<i>meles</i>	-0.341	28.131	65.415	102.450
Caniformia	Mustelidae	Basal group	<i>Taxidea</i>	<i>taxus</i>	0.188	33.727	61.457	111.521
Caniformia	Mustelidae	Basal group	<i>Melogale</i>	<i>personata</i>	-0.283	22.056	73.446	66.340
Caniformia	Mustelidae	Lutrinae	<i>Enhydra</i>	<i>lutris</i>	0.412	33.824	60.593	117.395
Caniformia	Mustelidae	Martes group	<i>Gulo</i>	<i>gulo</i>	0.040	31.291	66.054	127.112
Caniformia	Mustelidae	Martes group	<i>Martes</i>	<i>pennanti</i>	0.111	26.94	67.183	97.503
Caniformia	Procyonidae	Potosinae	<i>Potos</i>	<i>flavus</i>	0.066	32.079	80.52	69.395
Caniformia	Procyonidae	Procyoninae	<i>Procyon</i>	<i>lotor</i>	0.137	25.075	69.938	95.517
Caniformia	Procyonidae	Procyoninae	<i>Procyon</i>	<i>cancrivorus</i>	0.490	26.11	68.892	109.064
Caniformia	Procyonidae	Procyoninae	<i>Nasua</i>	<i>narica</i>	0.055	22.243	73.128	101.707
Caniformia	Ursidae	Ailuropodinae	<i>Ailuropoda</i>	<i>melanoleuca</i>	-0.125	33.529	58.287	220.604
Caniformia	Ursidae	Ursinae	<i>Arctodus</i>	<i>simus</i>	0.595	18.885	83.276	349.314
Caniformia	Ursidae	Ursinae	<i>Tremarctos</i>	<i>ornatus</i>	-0.407	23.351	75.728	185.386
Caniformia	Ursidae	Ursinae	<i>Melursus</i>	<i>ursinus</i>	0.393	18.165	73.616	234.368
Caniformia	Ursidae	Ursinae	<i>Ursus</i>	<i>americanus</i>	0.096	25.583	78.855	236.004
Feliformia	Eupleridae	Euplerinae	<i>Cryptoprocta</i>	<i>ferox</i>	-0.693	25.402	70.656	109.353
Feliformia	Eupleridae	Euplerinae	<i>Eupleres</i>	<i>goudotii</i>	-0.525	22.485	70.062	74.604
Feliformia	Eupleridae	Euplerinae	<i>Fossa</i>	<i>fossana</i>	0.347	25.353	67.376	74.732
Feliformia	Eupleridae	Galidiinae	<i>Galidia</i>	<i>elegans</i>	0.062	21.687	71.633	58.678
Feliformia	Felidae		<i>Acinonyx</i>	<i>jubatus</i>	-0.475	32.761	67.122	137.928
Feliformia	Felidae		<i>Felis</i>	<i>silvestris</i>	0.036	33.161	79.028	No data
Feliformia	Felidae		<i>Homotherium</i>	<i>hadarensis</i>	-0.261	22.177	74.019	279.630
Feliformia	Felidae		<i>Lynx</i>	<i>rufus</i>	0.220	31.883	71.700	103.509
Feliformia	Felidae		<i>Panthera</i>	<i>atrox</i>	0.415	12.408	78.698	302.918
Feliformia	Felidae		<i>Prionailurus</i>	<i>bengalensis</i>	0.178	30.403	76.709	80.014
Feliformia	Felidae		<i>Smilodon</i>	<i>fatalis</i>	-0.262	21.423	76.558	248.126
Feliformia	Herpestidae		<i>Cynictis</i>	<i>penicillata</i>	-0.009	27.696	85.708	50.700
Feliformia	Herpestidae		<i>Ichneumia</i>	<i>albicauda</i>	-0.152	24.747	72.716	92.962
Feliformia	Hyaenidae		<i>Crocota</i>	<i>crocota</i>	-0.319	28.975	74.439	209.125
Feliformia	Hyaenidae		<i>Proteles</i>	<i>cristata</i>	-0.612	35.35	70.705	122.051

Table 1 Continued

Suborder	Family	Subfamily	Genus	Species	log ₂ EQ	CA	FA	Skull length
Feliformia	Nandiniidae		<i>Nandinia</i>	<i>biontata</i>	-0.113	25.728	70.634	88.973
Feliformia	Nimravidae		<i>Barbourofelis</i>	<i>morrissi</i>	-0.667	30.601	86.551	174.303
Feliformia	Nimravidae		<i>Dinictis</i>	<i>cyclops</i>	0.004	31.453	72.78	125.563
Feliformia	Nimravidae		<i>Dinictis</i>	<i>feline</i>	-0.312	32.687	66.869	141.283
Feliformia	Nimravidae		<i>Hoplophoneus</i>	<i>primaevus</i>	0.133	25.202	71.12	135.388
Feliformia	Nimravidae		<i>Nimravus</i>	<i>brachyops</i>	-0.387	32.386	68.402	160.492
Feliformia	Nimravidae		<i>Pogonodon</i>	<i>platycopis</i>	-0.390	22.914	75.049	186.115
Feliformia	Viverridae		<i>Civettictis</i>	<i>civetta</i>	-0.712	29.011	64.663	126.256
Feliformia	Viverridae		<i>Genetta</i>	<i>genetta</i>	-0.417	33.652	63.854	75.967
Feliformia	Viverridae		<i>Paradoxurus</i>	<i>hemaphroditus</i>	-0.447	41.574	59.446	84.479

Species are arranged by taxonomic groups. Log₂EQ, convergence angle (CA), frontation angle (FA) and skull length are given for each species, angles in degrees and skull length in mm. Log₂EQ is the base-2 logarithm of the encephalization quotient (Jerison, 1970, 1973; Radinsky, 1977). Missing values are shown as 'no data.' See text for further discussion.

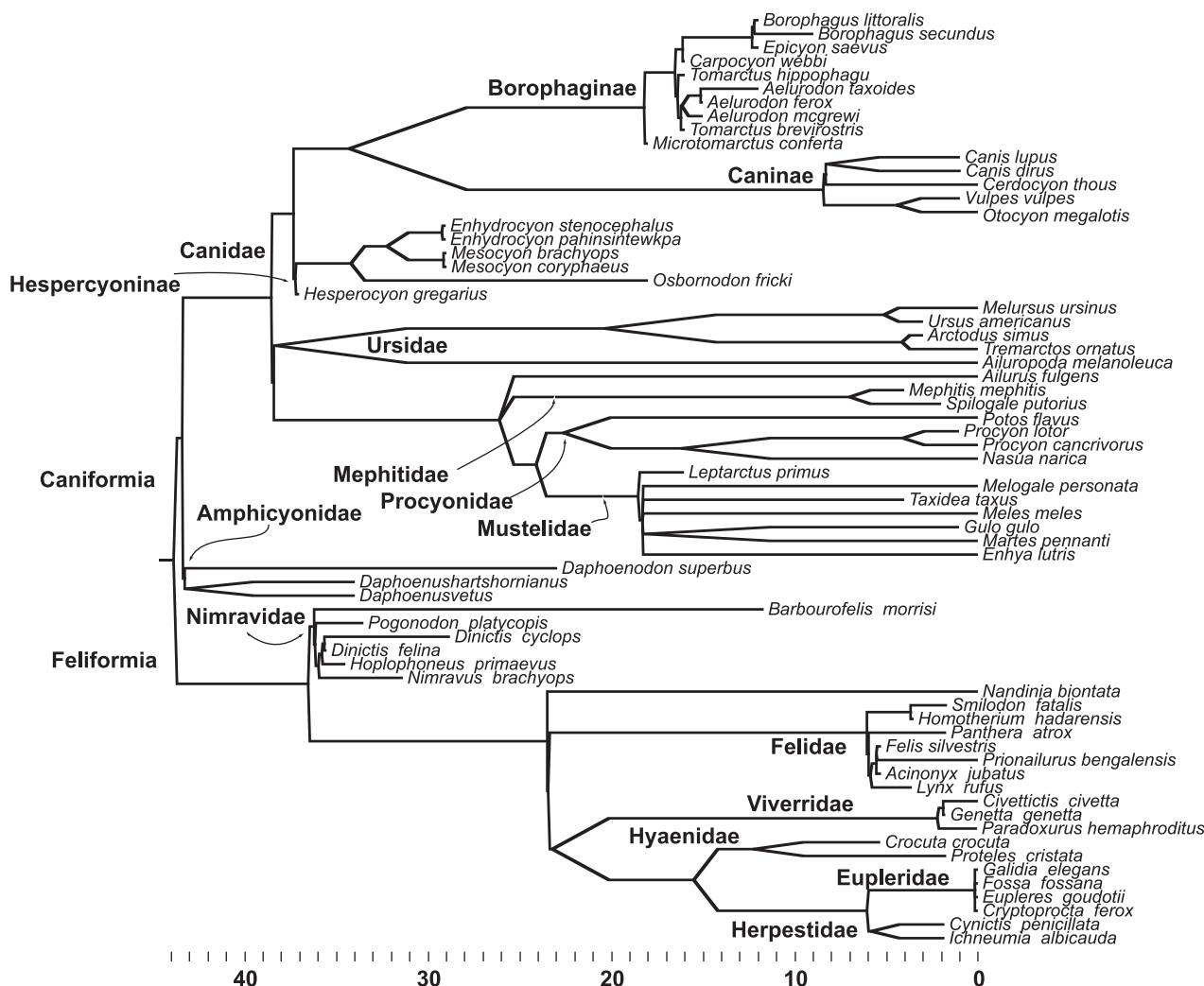


Fig. 2 Phylogeny of the Carnivora used in the analysis of independent contrasts of orbit orientation angles and encephalization. Branch lengths are calibrated using first appearance data from the fossil record and the units along the horizontal axis represent millions of years before present. The phylogenetic analyses supporting the nodes in the cladogram are summarized in a review by Flynn et al. (in press).

Pinnipedia, was not included, however, as brain volume/body mass scaling for this group is still poorly understood and no model for estimation of brain volumes for fossil taxa exists.

Using this composite cladogram, we calculated correlations for phylogenetically independent contrasts (Felsenstein, 1985) of CA and FA with both skull length and encephalization, with the PDAP (Midford et al. 2003) module for Mesquite (Maddison & Maddison, 2007). Independent contrasts are scaled relative to the distance (branch length) between the observation and the node estimate (Felsenstein, 1985; Garland et al. 1999; Garland & Ives, 2000). Incorporating branch length information can have a significant impact on reconstruction (Oakley & Cunningham, 2000; Webster & Purvis, 2002; Finarelli & Flynn, 2006) and we therefore calibrated branch lengths using first appearances in the fossil record (Finarelli & Flynn, 2007; Finarelli, 2008b).

Results

Fossil taxa have a large impact on the strength of correlations between orientation angles and both skull length and encephalization. CA is significantly and positively correlated with skull length in extant Carnivora although, when comparing Feliformia and Caniformia separately, this significant correlation appears confined to feliforms. However, when all available taxa are included in the analysis, no significant correlations are recovered for CA (Table 2). It should be noted that Felidae shows a strong negative correlation between CA and skull length, whereas its sister clade Viverridae + 'Herpestidae' + Hyaenidae shows an equally strong positive correlation. Although neither of these correlations differs significantly from zero, they are significantly different from one another ($P < 0.001$). Thus, Felidae shows a significantly different response in CA with respect to increasing encephalization than do other feliforms. No significant correlations are observed between FA and skull length, irrespective of whether or not fossils are included (Table 2). From this we conclude that no single relationship between skull size and orbit orientation characterizes Carnivora.

In contrast to skull length, no significant correlations exist between encephalization and orbit orientation among extant taxa. When fossil and extant taxa are included in the analysis, no relationships exist between encephalization and either orientation angle, arguing against Carnivora-wide structural relationships between orbit orientation and encephalization (Fig. 3). However, we do observe several significant correlations for analyses among carnivoran subclades when fossil and living taxa are analysed. FA is positively correlated with encephalization for Felidae (Noble et al. 2000) (Table 3), although in our data set this is due to the cheetah (*Acinonyx jubatus*), which stands out as an outlier (Fig. 4). Excluding the cheetah removes the significance ($r = 0.320$, $P = 0.588$); therefore this correlation must be viewed with caution until a larger sample is examined.

Within Caniformia encephalization is correlated positively with FA and negatively with CA (Table 3); larger relative brain size is associated with more vertically- and laterally-

Table 2 Correlations for independent contrasts of orientation angles and skull length

Clade	n	Convergence angle		Frontation angle	
		r	P	r	P
Extant taxa only					
Carnivora	38	0.506	0.001	-0.189	0.263
Caniformia	22	0.138	0.541	-0.236	0.290
Arctoidea	17	0.261	0.311	-0.403	0.110
Feliformia	16	0.546	0.035	-0.188	0.501
All taxa					
Carnivora	68	0.057	0.649	0.108	0.389
Caniformia	43	-0.122	0.437	0.296	0.057
Crown-clade Caniformia*	40	-0.126	0.439	0.306	0.058
Canidae	21	0.132	0.569	0.380	0.099
Arctoidea	19	-0.116	0.636	-0.039	0.900
Feliformia	25	0.151	0.480	0.013	0.951
Felidae	7	-0.783	0.065	0.031	0.544
Viverridae, Hyaenidae, 'Herpestidae'†	11	0.541	0.085	-0.131	0.701
'Herpestidae'†	6	0.728	0.101	-0.152	0.773

*Crown-clade Caniformia excludes the Amphicyonidae and is identical to 'Caniformia' in the extant-only analysis.

†'Herpestidae' includes true mongooses and Malagasy carnivorans, as previous analyses include some or all of these taxa in Herpestidae.

n, number of taxa; r, Pearson correlation coefficient; P, two-tailed significance. Significant correlations are highlighted in bold. Extant-only analyses are made for a smaller number of taxonomic groups, as sample size precluded finer partitioning.

oriented orbits. The significance in these correlations is driven solely by Canidae; both angles are significantly correlated for Canidae but its sister clade Arctoidea displays no significant correlations (Table 3). However, modern canids (subfamily Caninae) have a significantly higher degree of encephalization than the two extinct subfamilies Borophaginae and Hesperocyoninae (Finarelli, 2008a). It is possible that the increase in encephalization characterizing Caninae coincides with changes in CA and FA, rather than there being a true correlation linking encephalization with orbit orientation (Fig. 5). Calculating the values of \log_2EQ against two regressions fit specifically to the modern subfamily and the extinct canid subfamilies eliminates the offset in encephalization between living and extinct canids. When this is done, both correlations remain significant (FA: $r = 0.595$, $P = 0.006$; CA: $r = -0.482$, $P = 0.027$) and thus the significant correlations are not artefacts of the encephalization increase in modern Caninae.

Discussion

The impact of taxonomic breadth and inclusion of fossils in the sample on perceived correlations is remarkable. With

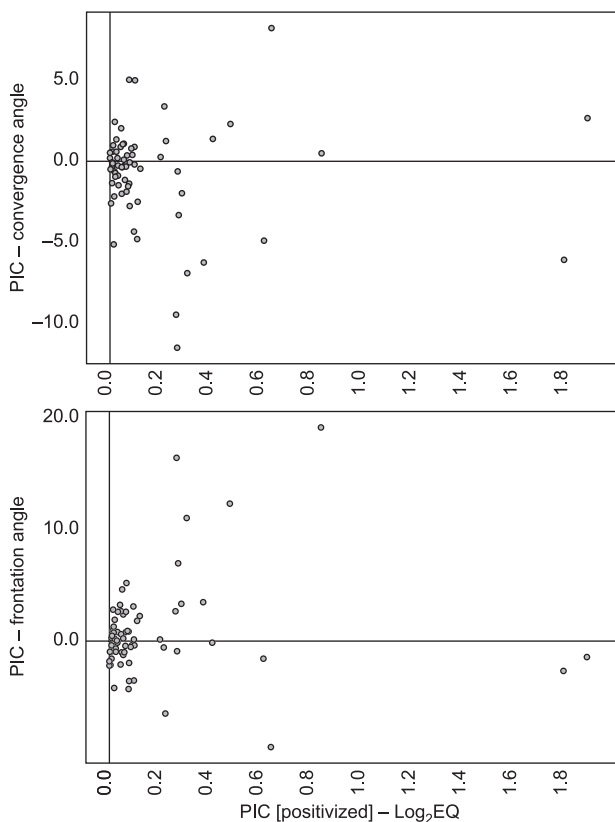


Fig. 3 Biplots of phylogenetically independent contrasts (PICs) for all taxa in the Carnivora. The PIC values for \log_2EQ have been ‘positivized’ along the x-axis (see Garland et al. 1992, 1997; Garland & Ives, 2000). PICs for orientation angles (convergence angle, top; frontation angle, bottom) are given on the y-axes. There is no systematic pattern across the Carnivora between either of the two orientation angles and relative brain volume. Rather, all significant correlations that we observe are restricted to the families Canidae and Felidae.

all taxa included, significant correlations are observed but are confined to two families, i.e. Felidae and Canidae. Felids show a positive correlation between FA and encephalization (Table 3), although we note that this may be a sampling artefact. Both angles are significantly correlated in the Canidae, positive for FA and negative for CA (Table 3). It should be noted that, in both cases where we observe a significant correlation between FA and encephalization, the correlation is positive and the corresponding correlation for both families’ sister clades is negative. Thus, it is not simply the strength of the relationship in these two clades that differs from closely related carnivorans but also the direction of the relationship.

Noble et al. (2000) also recovered a significant, positive correlation between FA and encephalization in Felidae. Following Cartmill (1970, 1972), they hypothesized a structural constraint on FA in response to an expanding braincase such that, for taxa with more convergent orbits, increased encephalization necessitates a forward rotation

Table 3 Correlations for independent contrasts of orientation angles and encephalization

Clade	n	Convergence angle		Frontation angle	
		r	P	r	P
Extant taxa only					
Carnivora	38	0.004	0.982	0.030	0.857
Caniformia	22	0.088	0.698	-0.318	0.151
Arctoidea	17	0.720	0.783	-0.221	0.395
Feliformia	16	0.001	0.998	0.041	0.880
All taxa					
Carnivora	68	-0.163	0.183	0.166	0.179
Caniformia	43	-0.442	0.002	0.466	0.002
Crown-clade Caniformia	40	-0.438	0.005	0.464	0.003
Canidae	21	-0.484	0.026	0.542	0.010
Arctoidea	19	-0.124	0.613	-0.191	0.434
Feliformia	25	-0.076	0.719	0.062	0.769
Felidae	7	-0.184	0.694	0.911	0.004
Viverridae, Hyaenidae, 'Herpestidae'	11	-0.005	0.989	-0.403	0.219
'Herpestidae'	6	-0.020	0.970	-0.428	0.397

Abbreviations as in Table 2.

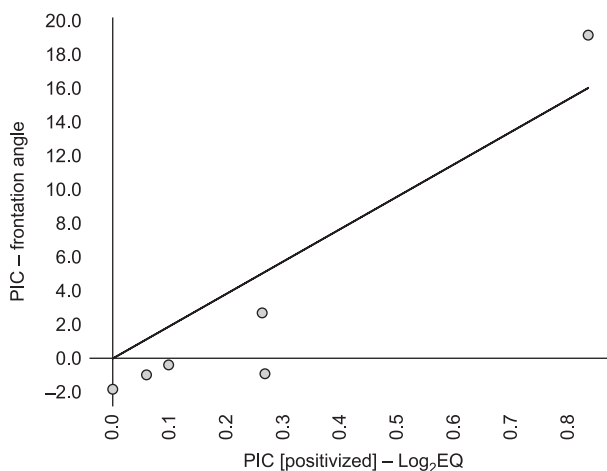


Fig. 4 Biplot of independent contrasts [\log_2EQ , x-axis; (FA), y-axis] for Felidae. Note that an outlier (*Acinonyx jubatus*, the cheetah) is responsible for drawing the correlation into significance. Although it is possible that a significant relationship between FA and encephalization among cats does indeed exist, this result must be considered speculative as yet. PIC, phylogenetically independent contrast.

of the upper orbit margin. They argued that failure to recover a significant correlation among their sample of Herpestidae could have resulted from uniformly lower CA, lower encephalization or both. However, even if we accept that the significant correlation between FA and encephalization observed in our data set for Felidae is not an artefact,

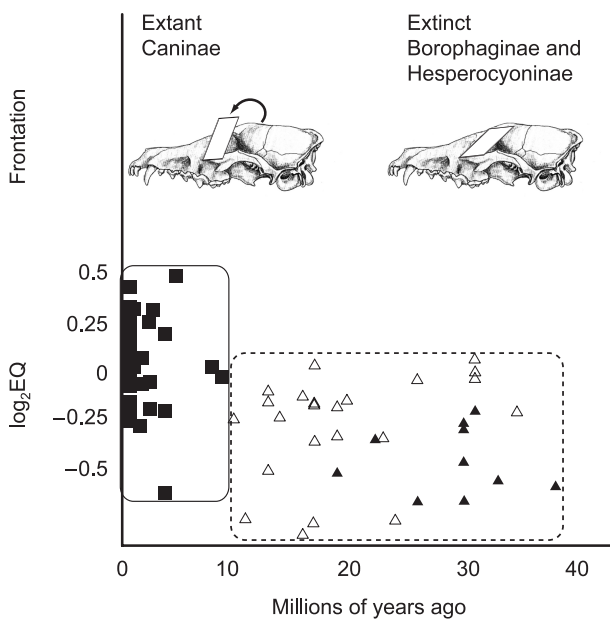


Fig. 5 A shift in canid encephalization could be responsible for a perceived relationship between relative brain volume and orientation angles. At the bottom, encephalization data for the Canidae from Finarelli (2008b) are plotted against first appearances in the fossil record. The extinct Borophaginae (open triangles) and Hesperocyoninae (closed triangles) exhibit a lower degree of encephalization than modern Caninae (squares). It is possible that the correlations are an artefact of this shift coinciding with a shift in orientation angle (e.g. frontation). This is not the case, as the correlations remain significant even after this offset in encephalization is removed with clade-specific regressions.

Felidae is not significantly more convergent than either all other feliform taxa (Mann-Whitney test, two-tailed, $P = 0.653$) or their sister clade ($P = 0.653$).

Moreover, among canids, encephalization is positively correlated with FA but negatively correlated with CA, i.e. we observe more vertically- and more laterally-oriented orbits in canids as encephalization increases. The model of Noble et al. (2000) for the positive relationship with FA in Felidae would predict the opposite of what we observe in Canidae, i.e. increasingly less convergent orbits as encephalization increases should not be simultaneously more frontated. As discussed above, Noble et al. (2000) explained the lack of this pattern in Herpestidae as potentially reflecting lower CA, and one could make a similar argument that canids have not surpassed some threshold convergence value that is needed to impart structural constraints. However, canids are not significantly less convergent than felids (Mann-Whitney test, two-tailed, $P = 0.337$) and, even if canids were, one would still need a separate model to explain the correlation with frontation in this clade. These results cast doubt on a single structural relationship between encephalization and orbit orientation across Carnivora and, by extension, across Mammalia. Rather, the correlations that we observe appear idiosyncratic

to individual carnivoran clades and structural relationships are probably equally distinct.

The carnivoran skull is composed of multiple phenotypic modules, characterized by relatively high within-module and low among-module correlations (Goswami, 2006a,b). This modularity is hypothesized to allow independent evolution among different cranial regions, while preserving necessary functional relationships within modules. Goswami (2006a) demonstrated that the braincase and orbit represent two independent modules that are conserved across therian mammals. The lack of a systematic relationship between encephalization and orbit orientation in carnivorans, observed here, is consistent with this model of module independence. It is noteworthy that the only clades that displayed significant correlations between phylogeny and degree of integration were Felidae and Canidae (Goswami, 2006b), the same two families that deviate from other carnivorans (and more importantly their immediate sister taxa) in this study. Most studies of carnivoran skull morphology, ontogeny and allometry have focused on Felidae and Canidae, and patterns within these two families are often generalized to their respective suborders, Feliformia and Caniformia (Sears et al. 2007). However, this study joins a growing body of work demonstrating that skull development, morphology and integration for Canidae and Felidae are probably atypical, rather than representing carnivoran exemplars.

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