

**The endocranial morphology of the extinct North American lion (*Panthera atrox*)**

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Four figures, two tables.

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## Abstract

The extinct North American lion (*Panthera atrox*) is one of the largest felids (Mammalia, Carnivora) to have ever lived, and is known from a plethora of incredibly well preserved remains. Despite this abundance of material, there has been little research into its endocranial anatomy. CT scans of a skull of *P. atrox* from the Pleistocene La Brea Tar pits were used to generate the first virtual endocranium for this species and to elucidate previously unknown details of its brain size and gross structure, cranial nerves, and inner ear morphology. Results show that the gross brain anatomy is broadly similar to that of other pantherines, although *P. atrox* displays less cephalic flexure than either extant lions or tigers, instead displaying a brain shape that is reminiscent of earlier felids. Despite this unusual reduction in flexure, the estimated, absolute brain size for this specimen is one of the largest reported for any felid, living or extinct. Its encephalization quotient (brain size as a fraction of expected brain mass for a given body mass) is also larger than that of extant lions, but similar to the other pantherines. The advent of CT scans allows for non-destructive sampling of anatomy that cannot otherwise be studied in these extinct lions, leading to more accurate reconstruction of endocranial morphology and its evolution.

Key words: Fossil lion, brain, endosseous labyrinths, encephalisation

## Introduction

*Panthera atrox* [Leidy, 1853] was a large felid that lived in North America during the Pleistocene epoch from approximately 340 thousand years ago (ka) before going extinct at the end of the last ice age, approximately 11ka. The precise phylogenetic affinities of *P. atrox*, and even its status as a separate species, has been heavily debated for decades. Although the earliest work aligned them with the extant lion (*P. leo*) [Merriam, and Stock, 1932] and the extinct Eurasian cave lion (*P. spelaea*), several early 20<sup>th</sup> century comparative studies, as well as more recent morphometric studies, nesting them closer to tigers [Groiss, 1996] or jaguars [Simpson, 1941; Christiansen, and Harris, 2009] although recently a study suggested many of these morphological similarities arise from allometric changes [Benoit, 2010]. The rise of molecular phylogenetics, including techniques that allow for extraction of genetic material from the fossil specimens, has brought new insight into this debate, with molecular data nest *P. atrox* as sister to *P. spelaea*, with *P. atrox* + *P. spelaea* then being a sister clade to the ancestors of today's modern lions, *P. leo* [Barnett et al., 2009]. If that latter relationship is correct, it suggests that *P. atrox* was derived from a Beringian population.

The excellent fossil record of *P. atrox* shows that they attained sizes larger body sizes than modern lion species, and possibly larger than any other felids [Cuff et al., 2015] with estimates up to 420kgs [Sorkin, 2008], although more recently these have been revised down to give size ranges only slightly larger than the maximum recorded for modern lions and tigers [Christiansen, and Harris, 2009]. *P. atrox* has been found across the southern reaches of North America and into Central America [Montellano-Ballesteros, and Carbot-Chanona, 2009] (with some uncertainty over whether they crossed into South America)[Barnett et al., 2009; Yamaguchi et al., 2004]. As one of the largest predators in the area (larger than the sympatric *Smilodon fatalis*) it has been suggested that *P. atrox* was feeding on most of the mega-herbivorous fauna that existed in North America at that time [Van Valkenburgh, and Hertel, 1993]. Modern lions live in pride systems (particularly where there is a high density of prey [Schaller, 1972]), and it has been suggested that this may also be the case for *P. atrox*, which show similar levels of sexual dimorphism in canine size to their extant relatives [Yamaguchi et al., 2004]. However, the rarity of *P. atrox* at La Brea relative to *S. fatalis* [Marcus, 1960], and the observation that the leopard shares canine size dimorphism to that of modern *P. leo* [Van Valkenburgh, and Sacco, 2002], means that the evidence for group living in *P. atrox* is still ambiguous.

Most studies of *P. atrox* have focused on external morphology, particularly cranial proportions, in an attempt to clarify its phylogenetic position and species status (e.g., [Benoit, 2010]). The only description of the endocranial anatomy have relied on sectioned skulls and casts made from them [Merriam, and Stock, 1932]. Since then the endocranial anatomy of *P. atrox* has been generally overlooked with published data focussing particularly on the size of the brain (e.g., [Wroe, and Milne, 2007]). The advent and increasing availability of CT scanning has brought new ability to reconstruct the internal morphology of fossil taxa with precision and without destructive sampling. Endocranial anatomy has been heavily studied in recent years using CT technology, bringing great insights into brain and inner ear structure, their evolution, and their relationship to numerous ecological attributes (e.g., [Macrini et al., 2006; Arsznov, and Sakai, 2012]). Here, we present the first high-resolution reconstruction of the endocranium of *P. atrox* including cranial nerve and inner ear morphology.

## Methods

Page Museum specimen LACMP23-555 is a remarkably well-preserved skull and skeleton of *P. atrox* from the La Brea Tar Pits (Project 23-1), dating to approximately 35 ka [Fuller et al., 2014]. The skull was microCT scanned at The Aerospace Corporation in four sections, with a GE Phoenix c/tome/x

scanner (200kV, 80mA, 0.24mm/pixel). One of the CT scan sections contained the entirety of the braincase which was segmented using Mimics 16.0 (Materialise Corp, Belgium) to isolate the endocranium. This involved manually isolating the endocranial space (which is a combination of matrix and air in the *P. atrox* specimen) from the foramen magnum at the posterior towards the cribriform plate at the anterior. In this specimen of *P. atrox* the cribriform plate is not preserved due to the thin bones being destroyed so the anterior margins are estimated. Nerves were identified by the canals leading from the endocranium, with the semi-circular canals identifying the inner ear morphology. For anatomical comparisons the skull of an Asian Lion (*P. leo persica*) was scanned at the Royal Veterinary College (helical scan resulting in resolution of 0.58mm/pixel, 178 slices with 5mm slice thickness, 120kV, Lightspeed Pro 16 CT scanner, GE Medical Systems) and the resulting scans were segmented in Avizo 8.1 (VSG SAS, Bordeaux, France). As the *P. leo persica* specimen was a captive specimen at a local zoo that died unexpectedly, it was subjected to a post-mortem that involved removal of the brain via sawing through and removing the dorsal region of braincase. This piece was digitally replaced onto the skull in Avizo 8.1 by rotating the skull piece into position to provide the original dorsal margins of the braincase. During segmentation, each of the anatomical structures (nerves, inner ear and brain) was isolated for individual study and comparison between *P. atrox* and *P. leo persica*.

The body mass for LACMP23-555 was estimated using published regressions using condylobasal length (for pantherines [Mazák et al., 2011]) and femoral length [Anyonge, 1993]. The resulting masses of 195.2kg and 219.5kg, respectively, were averaged to give the mean body mass for LACMP23-555 of 207.4kg, which is the mass used for the following analysis. Additionally, a convex hull model was constructed for calculating the body mass using the entire skeleton which produced an average body mass estimate of 200kg (Cuff et al., in review).

For a broad comparison of felid endocranial anatomy, braincases of a *Acinonyx jubatus* (AMNH VP CA2502), *Caracal aurata* (AMNH 51996), *Felis silvestris* (AMNH 81233), *Leopardus wiedii* (AMNH 95085), *Lynx rufus* (AMNH 24225), *Neofelis nebulosi* (AMNH 22919), *Panthera pardus* (AMNH 113745), *Panthera tigris* (AMNH 45519), *Pardofelis marmorata* (AMNH 102844), *Prionailurus viverrinus* (AMNH 102691) and *Puma concolor* (AMNH 6677) were scanned at the Microscopy and Imaging Facility (MIF). All endocrania were segmented using Avizo 8.1 and volumes were measured using the “surface statistics” function. Additionally a comparative measure for relative cephalic flexure across the felids was carried out. This involved measuring the lateral aspects of the endocasts (aligned so that CN II was horizontal for each specimen) for total length from anteriormost cerebrum

to posteriormost cerebellum and the length of “exposed” cerebellum (the length posterior to the cerebrum) and calculating a percentage of “exposed” cerebellum to total cerebrum and cerebellum lengths.

### Brain scaling

The mass of the brain of *P. atrox* was estimated from the full endocranial volume and multiplied by the density of brain tissue. Due to the variability in published densities (from 1.027 g/cm<sup>3</sup> [Schröder, 1968] to 1.100 g/cm<sup>3</sup> [Barber et al., 1970]) maximum and minimum estimates were used to generate a range for estimated brain mass. These estimates were combined with data from the additional 11 extant endocasts and published data for an additional four felid brain sizes (*Leopardus pardalis*, *Leptailurus serval*, *Lynx lynx*, *Panthera onca* [Weisbecker, and Goswami, 2010]) before both brain and body masses were log-transformed (Table 1). Log brain mass was then regressed against log body mass using Standardised Reduced Major Axis (SMA) regression in the ‘smatr’ package [Warton et al., 2012] in R 3.1.0 (R Core Team, 2014). Because relative brain size has been previously shown to be strongly influenced by phylogenetic relatedness [Weisbecker, and Goswami, 2010], we further conducted a phylogenetically-correction using independent contrasts, before repeating the SMA regression. Phylogenetically-corrected analyses used the phylogeny from Piras et al. (2013) pruned to include only the taxa in this analysis.

## **Results**

### Brain anatomy

The endocranium of this *P. atrox* specimen is incredibly well preserved (Figure 1), showing little to no evidence of taphonomic deformation in comparison to the recently deceased specimen of the extant *P. leo persica* (Figure 2). Overall, the gross morphology (particularly the size and relative positions of the cerebrum and cerebellum, see below) resembles that of the leopard more than the Asian lion (Figure 3), but the brain volume of *P. atrox* (323cm<sup>3</sup>) corresponds to a brain mass of between 331g - 355g making it as large as the biggest extant tigers [Yamaguchi et al., 2009]. *P. atrox* has a relatively longer brain (distance from olfactory bulbs to foramen magnum) to condylobasal length than that of an extant *P. leo persica* (42.4% against 40% respectively). This measure would likely be even longer if the anteriormost margins of the olfactory bulbs could be accurately defined, discussed below. Most of this difference in brain length can be ascribed to differences in the cephalic flexure of the brain, with the cerebrum extending less over the cerebellum in *P. atrox* than in *P. leo*. This more extended condition in *P. atrox* resembles that observed in the most basal felids (Figure 3)[Radinsky, 1975] although there is no clear pattern in regards to relative levels of cephalic flexure

across Felidae (Table 3). Within the Machairodontinae there is high levels of cephalic flexure, which is also seen independently within *P. leo* and *P. tigris* (Figure 3). Of the extant, non-pantherine felids, there are generally higher levels of cephalic flexure, but this may be a result of a rotation of the forebrain such that the olfactory bulbs emerge relatively lower (Figure 3).

The majority of the cranial nerves can be located within the endocranium in similar positions to those in all other examined felids. CNs III (oculomotor), IV (trochlear), and VI (abducens) could not be located in the reconstruction, but are likely to exit with CNs V<sub>1</sub> and V<sub>2</sub> through the cavum epiptericum, and the CN XI accessory nerve, which also was not visible, likely exits with CNs IX-X.

The anterior margins of the olfactory bulb are poorly defined. This endocranial region is normally demarcated by soft tissue and turbinates which do not preserve readily, even in Lagerstätten like La Brea. Even still the posterior olfactory bulbs appear relatively small particularly compared to the cerebral cortex. For example, in *P. atrox* the narrowest region of the olfactory bulbs is 15% the maximal width of the cerebral cortex, whilst in *P. leo* this number is 26% (Figure 1-2).

The structures of the inner ear were well generally well preserved, although the horizontal canal on the left hand side appeared to be incomplete (Figure 1). The overall morphology of the semicircular canals appear similar in most aspects to other felids, such as *P. leo* but the scan quality for the specimen here proved too low to get detailed morphological comparisons (Figure 2). The angle of the lateral semicircular canal is of particular interest, as previous studies have identified that the lateral semicircular canal is horizontal in alert head posture [Witmer, and Ridgely, 2009]. For *P. atrox* this angle may be as high as 55 degrees, which is comparable and possibly even exceeds that of extant lions.

#### Brain scaling

As in all mammals [Weisbecker, and Goswami, 2010], felids display a significant correlation between brain mass and body mass, with or without phylogenetic correction (Table 2). The log brain mass scaled against log body mass slope varies between 0.51- 0.52 (95% between 0.44 and 0.60) across felids before phylogenetic correction and 0.895-0.905 (95% between 0.64 and 1.261) after phylogenetic correction, depending on the metric used. The *P. atrox* specimen falls above the regression line for all felids whilst the closest relative, *P. leo*, falls below (Figure 4). The result is that

the EQ for *P. atrox* is above 1.0, but when the 95% confidence intervals are accounted for this result may not always hold.

## Discussion

We present here the first digital reconstruction of a *P. atrox* endocranium from CT scans, allowing detailed visualisation of its anatomy. When compared to the two published endocrania for *P. atrox* that were described from casts [Merriam, and Stock, 1932], the gross brain morphology and the location and relative sizes of nerves are very similar, but the CT scans have allowed the addition of inner ear morphology. This specimen of *P. atrox* possesses the one of the largest published felid brains to date (behind that estimated from an endocranial cast of another *P. atrox* specimen, LACM2900-1 [Merriam, and Stock, 1932]), but appears to have a larger endocranial volume than that of LACM2900-16 which is an individual with a larger skull [Merriam, and Stock, 1932]. The endocast for LACM2900-16 is derived from an cast, a method which is known to be less accurate than CT scans for estimating endocranial volumes [Macrini et al., 2006] although it is uncertain if this volumetric difference is a result of methodology or intraspecific variance.

Previous work has suggested that tigers have relatively larger brains than any of the other extant large cats [Yamaguchi et al., 2009], but felids in general scale differently to other carnivorans, with greater encephalisation observed in smaller cats than in larger ones (up to about 90kg mass) when pooled with other carnivorans [Finarelli, and Flynn, 2009]. Although this one specimen of *P. atrox* follows this larger pattern, its brain is not only greater in raw size than found in most of the extant felids (which is expected given its larger body size), but it also is greater than expected for its body size, with a positive residual from the regression of brain and body mass across felids. There is the caveat that this is a single specimen, but at only half the estimated mass of some of the largest individuals of the species [Sorkin, 2008], *P. atrox* likely had the largest average raw brain size across Felidae. It should be noted that if the ontogenetic scaling of the *P. atrox* endocranium is like most felids (and Carnivora as a whole), larger individuals of the species will have relatively smaller endocranial volumes [Kruska, 2005], which will shift the position of the *P. atrox* towards the right of Figure 3.

Within felids, sociality – group living – is important for helping to maintain territories and reducing infant mortality through territorial conflict [Mosser, and Packer, 2009], and in certain locations reduce kleptoparasitism from other species [Cooper, 1991]. However, there is little support for a correlation between overall brain size and sociality [Yamaguchi et al., 2009], but there may be a

correlation between anterior cerebrum volume and group living (at least for female African lions vs male lions or any gender of *Puma*) [Arsznov, and Sakai, 2012]. Unfortunately, we do not know the sex of the *P. atrox* specimen under study so the question of whether *P. atrox* practiced pride living cannot be easily assessed here.

The use of CT scans allows a greater understanding of complex endocranial anatomy that cannot be obtained otherwise without using destructive techniques. Here we provided the first digital models of the inner cranial morphology of *P. atrox* demonstrating that this individual had a relatively large brain compared to other pantherines and possesses a cephalic flexure pattern more like that of early felids. The cephalic flexure patterns and the effect on overall morphology varies tremendously across not just the large felid species, but across Felidae as a whole. This work, and other future work on additional specimens, provides a foundation for more in depth studies of the evolution of endocranial morphology, behaviour, and posture of this extinct cat.

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## Author contributions

ARC and CS segmented the CT scans, AG provided the data for extant felid brain masses, ARC carried out the analyses, ARC and AG interpreted the results and wrote the paper.

## Competing financial interests

There are no conflicts of interests to declare.

## References

- Anyonge W (1993): Body mass in large extant and extinct carnivores. *J Zool* 231: 339–350.
- Arsznov BM, Sakai ST (2012): Pride diaries: sex, brain size and sociality in the African lion (*Panthera leo*) and cougar (*Puma concolor*). *Brain Behav Evol* 79: 275–289.



253 Barber TEDW, Brockway JA, Higgins LS (1970): The density of tissues in and about the. *Acta Neurol*  
254 *Scand* 46: 85–92.

255 Benoit MH (2010): What’s the difference? A multiphasic allometric analysis of fossil and living lions;  
256 in Goswami A, Friscia A (eds): *Carnivoran Evolution*. Cambridge, Cambridge University Press,  
257 pp 165–188.

258 Barnett R, Shapiro B, Barnes I, Ho SY, Burger J, Yamaguchi N, et al. (2009): Phylogeography of lions  
259 (*Panthera leo* ssp.) reveals three distinct taxa and a late Pleistocene reduction in genetic  
260 diversity. *Mol Ecol* Apr;18:1668–1677.

261 Christiansen P, Harris J (2009): Craniomandibular morphology and phylogenetic affinities of *Panthera*  
262 *atrox*: implications for the evolution and paleobiology of the lion lineage. *J Vertebr*  
263 *Paleontology* 29:934–945.

264 Cooper SM (1991): Optimal hunting group size: the need for lions to defend their kills against loss to  
265 spotted hyaenas. *Afr J Ecol* 29: 130–136.

266 Cuff AR, Randau M, Head J, Hutchinson JR, Pierce SE, Goswami A (2015): Big cat, small cat:  
267 reconstructing body size evolution in living and extinct Felidae. *J Evol Biol* 28:1516–1525.

268 Finarelli JA, Flynn JJ (2009): Brain-size evolution and sociality in Carnivora. *Proc Natl Acad Sci USA*  
269 106:9345–9349.

270 Fuller BT, Fahrni SM, Harris JM, Farrell AB, Coltrain JB, Gerhart LM, et al. (2014): Ultrafiltration for  
271 asphalt removal from bone collagen for radiocarbon dating and isotopic analysis of  
272 Pleistocene fauna at the tar pits of Rancho La Brea, Los Angeles, California. *Quat Geochronol*  
273 22: 85–98.

274 Goldfuss GA (1810): *Die Umgebungen von Muggendorf*. Ein Taschenbuch für Freunde der Natur und  
275 Altertumskunde.

276 Groiss JT (1996): Der höhlentiger *Panthera tigris spelaea* (Goldfuss). *Neues Jahrbuch für Geologie*  
277 *und Paläontologie* 7:399–414.

278 Kruska DC (2005): On the evolutionary significance of encephalization in some eutherian mammals:  
279 effects of adaptive radiation, domestication, and feralization. *Brain Behav Evol* 65: 73–108.

280 Leidy J (1853): Description of an extinct species of American lion: *Felis atrox*. *T Am Philol Assoc* 10:  
281 319–321.

282 Macrini TE, Rowe T, Archer M (2006): Description of a cranial endocast from a fossil platypus,  
283 *Obdurodon dicksoni* (Monotremata, Ornithorhynchidae), and the relevance of endocranial  
284 characters to monotreme monophyly. *J Morphol* 267:1000–1015.

285 Marcus LF (1960): A census of the abundant large Pleistocene mammals from Rancho La Brea.  
286 *Museum of Natural History of Los Angeles County, Contributions to Science* 35:1–11.

287 Mazák JH, Christiansen P, Kitchener AC (2011): Oldest known pantherine skull and evolution of the  
288 tiger. *PLoS ONE* 6:e25483.

289 Merriam JC, Stock C (1932): *The Felidae of Rancho La Brea*. Washington, Carnegie Institute of  
290 Washington.

291 Montellano-Ballesteros M, Carbot-Chanona G (2009): *Panthera leo atrox* (Mammalia: Carnivora:  
292 Felidae) in Chiapas, Mexico. *Southwest Nat* 54:217–222.

293 Mosser A, Packer C (2009): Group territoriality and the benefits of sociality in the African lion,  
294 *Panthera leo*. *Animal Behaviour* 78: 359–370.

295 Piras P, Maiorino L, Teresi L, Meloro C, Lucci F, Kotsakis T, et al. (2013): Bite of the cats: relationships  
296 between functional integration and mechanical performance as revealed by mandible  
297 geometry. *Syst Biol* 62: 878–900.

298 Radinsky L (1975): Evolution of the felid brain. *Brain Behav Evol* 11:214–254.

299 Schaller GB (1972): *The Serengeti Lion: A Study of Predator-Prey Relations*. Chicago, University of  
300 Chicago Press.

301 Schröder R (1968): Über das spezifische Gewicht des Hirngewebes in der Nachbarschaft von  
302 Tumoren. Aus dem Max-Planck-Institut für Hirnforschung, Abteilung für Tumorforschung  
303 und experimentelle Pathologie, und der Neurochirurgischen Universitätsklinik, Köln.

304 Simpson GG: Large Pleistocene felines of North America. *American Museum Novitates* 1941;1136:1–  
305 27.

306 Sorkin B (2008): A biomechanical constraint on body mass in terrestrial mammalian predators.  
307 *Lethaia* 41:333–347.

308 Van Valkenburgh B, Hertel F (1993): Tough times at La Brea: tooth breakage in large carnivores of  
309 the late pleistocene. *Science* 261:456–459.

310 Van Valkenburgh B, Sacco T (2002): Sexual Dimorphism, Social Behavior, and Intrasexual  
311 Competition in Large Pleistocene Carnivorans. *J Vertebr Paleontology* 22:164–169.

312 Warton DI, Duursma RA, Falster DS, Taskinen S (2012): smatr 3- an R package for estimation and  
313 inference about allometric lines. *Methods in Ecology and Evolution*: 257–259.

314 Weisbecker V, Goswami A (2010): Brain size, life history, and metabolism at the marsupial/placental  
315 dichotomy. *Proc Natl Acad Sci USA* 107: 16216–16221.

316 Witmer LM, Ridgely RC (2009): New insights into the brain, braincase, and ear region of tyrannosaurs  
317 (Dinosauria, Theropoda), with implications for sensory organization and behavior. *Anat Rec*  
318 292:1266–1296.

319 Wroe S, Milne N (2007): Convergence and remarkably consistent constraint in the evolution of  
320 carnivore skull shape. *Evolution* 61: 1251–1260.

321 Yamaguchi N, Cooper A, Werdelin L, Macdonald DW (2004): Evolution of the mane and group-living  
322 in the lion (*Panthera leo*): a review. *J Zool* 263:329–342.

323 Yamaguchi N, Kitchener A, Gilissen E, Macdonald D (2009): Brain size of the lion (*Panthera leo*) and  
324 the tiger (*P. tigris*): implications for intrageneric phylogeny, intraspecific differences and the  
325 effects of captivity. *Biol J Linn Soc* 98: 85–93.

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Table 1. Log<sub>10</sub> transformed data for the 17 felid species used in this study. <sup>1</sup> denotes data from Finarelli and Flynn [2009]. LACMP: Natural History Museum of Los Angeles County, AMNH: American Museum of Natural History, NMS: National Museums of Scotland. Body masses for AMNH specimens are average for species from Cuff et al. [2015] as no specimen specific masses were available.

Species	Specimen no.	Body mass	Brain mass min.	Brain mass max.
<i>Panthera atrox</i>	LACMP23-555	2.32	-0.480	-0.450
<i>Panthera tigris</i>	AMNH 45519	2.21	-0.544	-0.514
<i>Panthera leo</i>	NMS.Z.2015.128	2.12	-0.635	-0.605
<i>Puma concolor</i>	AMNH 6677	1.73	-0.842	-0.812
<i>Panthera pardus</i>	AMNH 113745	1.72	-0.779	-0.749
<i>Panthera onca</i> <sup>1</sup>		1.54	-0.827	-0.827
<i>Acinonyx jubatus</i>	AMNH VPCA 2502	1.40	-0.936	-0.906
<i>Neofelis nebulosa</i>	AMNH 22919	1.18	-1.24	-1.21
<i>Lynx lynx</i> <sup>1</sup>		1.09	-1.17	-1.17
<i>Caracal aurata</i>	AMNH 51996	1.05	-1.24	-1.21
<i>Leopardus pardalis</i> <sup>1</sup>		1.03	-1.20	-1.20
<i>Caracal serval</i> <sup>1</sup>		0.99	-1.22	-1.22
<i>Felis silvestris</i> cf <i>lybica</i>	AMNH 81233	0.59	-1.51	-1.48
<i>Lynx rufus</i>	AMNH 24225	0.81	-1.16	-1.13
<i>Prionailurus viverrinus</i>	AMNH 102691	0.55	-1.29	-1.26
<i>Leopardus wiedii</i>	AMNH 95085	0.51	-1.36	-1.33
<i>Pardofelis marmorata</i>	AMNH 102844	0.45	-1.37	-1.34

Table 2. Results of Reduced Major Axis analyses of log brain mass against log body mass. Upper and lower limits represent 95% confidence intervals, whilst the “r<sup>2</sup> p” shows the statistical significance of the correlation between brain mass and body mass.

	Slope	lower limit	upper limit	r <sup>2</sup>	r <sup>2</sup> p	intercept
Minimum	0.517	0.448	0.596	0.932	0.000	-1.6937
Minimum <sub>phylogenetic</sub>	0.903	0.646	1.261	0.647	0.000	-0.045
Maximum	0.514	0.447	0.591	0.935	0.000	-1.6738
Maximum <sub>phylogenetic</sub>	0.896	0.642	1.249	0.650	0.000	-0.047

Table 3. Measure of relative cephalic flexure across felids. Cerebrum and cerebellum lengths correspond to total lateral length of both, “exposed” cerebellum length is the length of the cerebellum not overlapped by cerebrum. All lengths in m. Species marked with an asterisk (\*) are from [Radinsky, 1975].

Species	Cerebrum and cerebellum length	“Exposed” cerebellum length	Proportion “exposed”
<i>Dinobastis</i> sp.*	0.0979	0.0095	0.097
<i>Smilodon fatalis</i> *	0.0923	0.0124	0.134
<i>Pseudaelurus</i> *	0.0677	0.0165	0.243
<i>Neofelis nebulosi</i>	0.0717	0.0168	0.235
<i>Panthera tigris</i>	0.0999	0.0104	0.104
<i>Panthera pardus</i>	0.0918	0.0160	0.175
<i>Panthera atrox</i>	0.0984	0.0183	0.186
<i>Panthera leo</i>	0.0905	0.0053	0.059
<i>Pardofelis marmorata</i>	0.0550	0.0078	0.142
<i>Carcal aurata</i>	0.0671	0.0093	0.139
<i>Leopardus wiedii</i>	0.0517	0.0065	0.125
<i>Lynx rufus</i>	0.0655	0.0106	0.163
<i>Acinonyx jubatus</i>	0.0697	0.0080	0.115
<i>Puma concolor</i>	0.0855	0.0131	0.154
<i>Prionailurus viverrina</i>	0.0623	0.0108	0.174
<i>Felis silvestris</i>	0.0499	0.0100	0.200
<i>Proailurus</i> *	0.0641	0.0141	0.220

Figure 1. Endocranial reconstruction of *P. atrox* in A, left lateral; B, right lateral; C, dorsal; and D, ventral views. Anterior is toward the left in A, C, D and toward the right in B. The endocast is rendered in blue, the inner ear in red, and the cranial nerves in yellow.; CN II optic nerve; CN V<sub>1-3</sub>, trigeminal nerve (ophthalmic, maxillary and mandibular branches); CN VII facial nerve; CN VIII vestibulocochlear nerve; CN IX, glossopharyngeal nerve; CN X, vagus nerve; CN XII, hypoglossal nerve; hy, hypophysis/pituitary; ob, olfactory bulb; ocx, olfactory cortex; pf, paraflocculus; v, vermis. Scale bar = 20 mm. Endocranial orientation in A and B linked to the likely “alert” head posture.

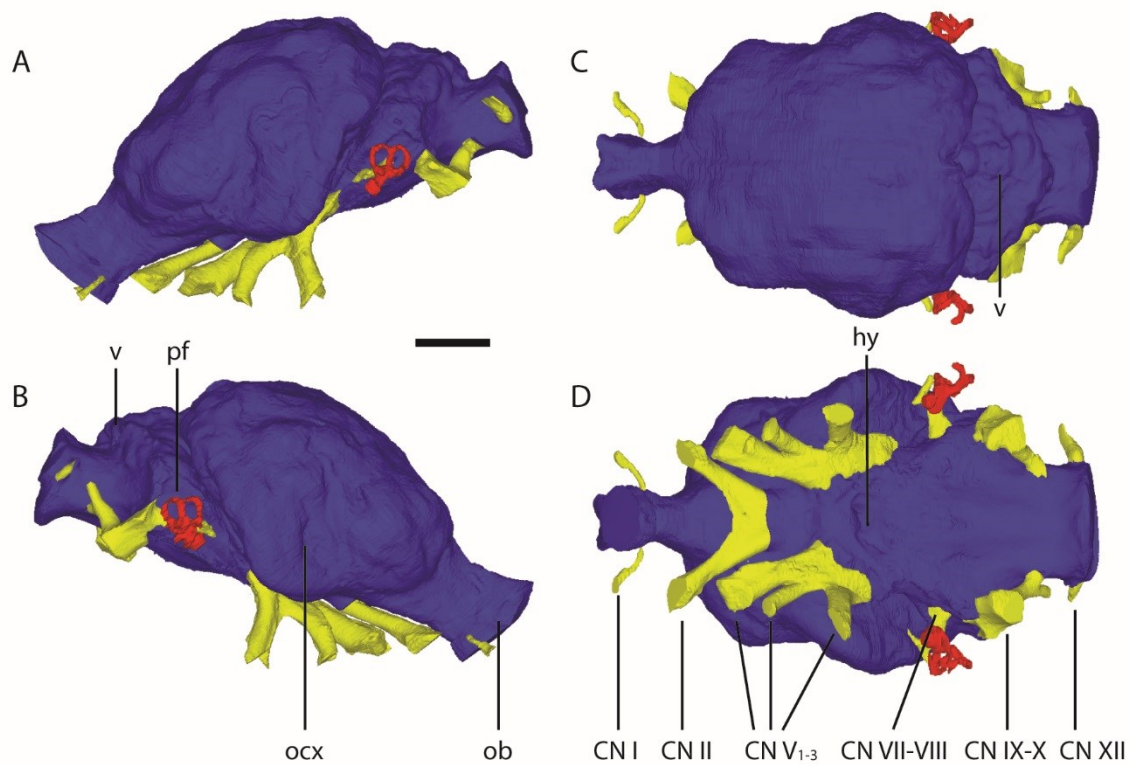


Figure 2. Endocranial reconstruction of *P. leo persica* in A, left lateral; B, right lateral; C, dorsal; and D, ventral views. Anterior is toward the left in A, C, D and toward the right in B. The endocast is rendered in blue, the inner ear in red, and the cranial nerves in yellow.; CN II optic nerve; CN V<sub>1-3</sub>, trigeminal nerve (ophthalmic, maxillary and mandibular branches); CN VII facial nerve; CN VIII vestibulocochlear nerve; CN IX, glossopharyngeal nerve; CN X, vagus nerve; CN XII, hypoglossal nerve; hy, hypophysis/pituitary; ob, olfactory bulb; ocx, olfactory cortex; pf, paraflocculus; v, vermis. Scale bar = 20 mm. Endocranial orientation in A and B linked to the likely “alert” head posture.

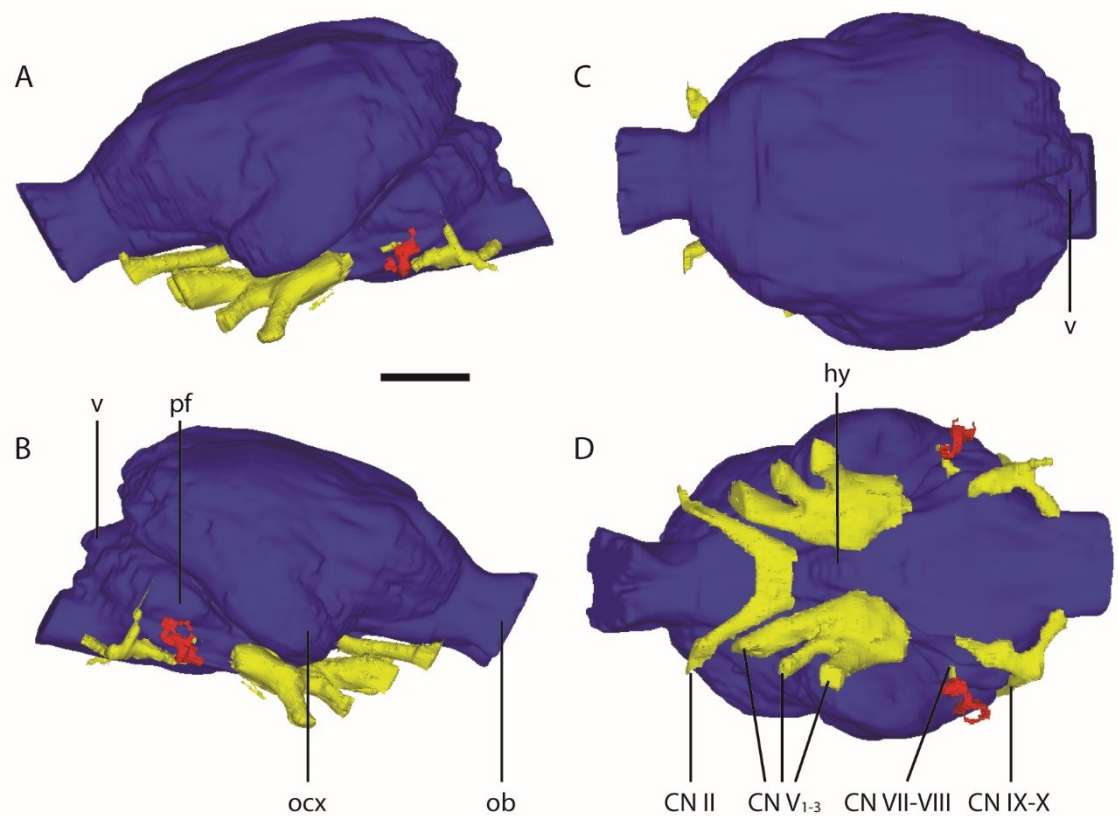
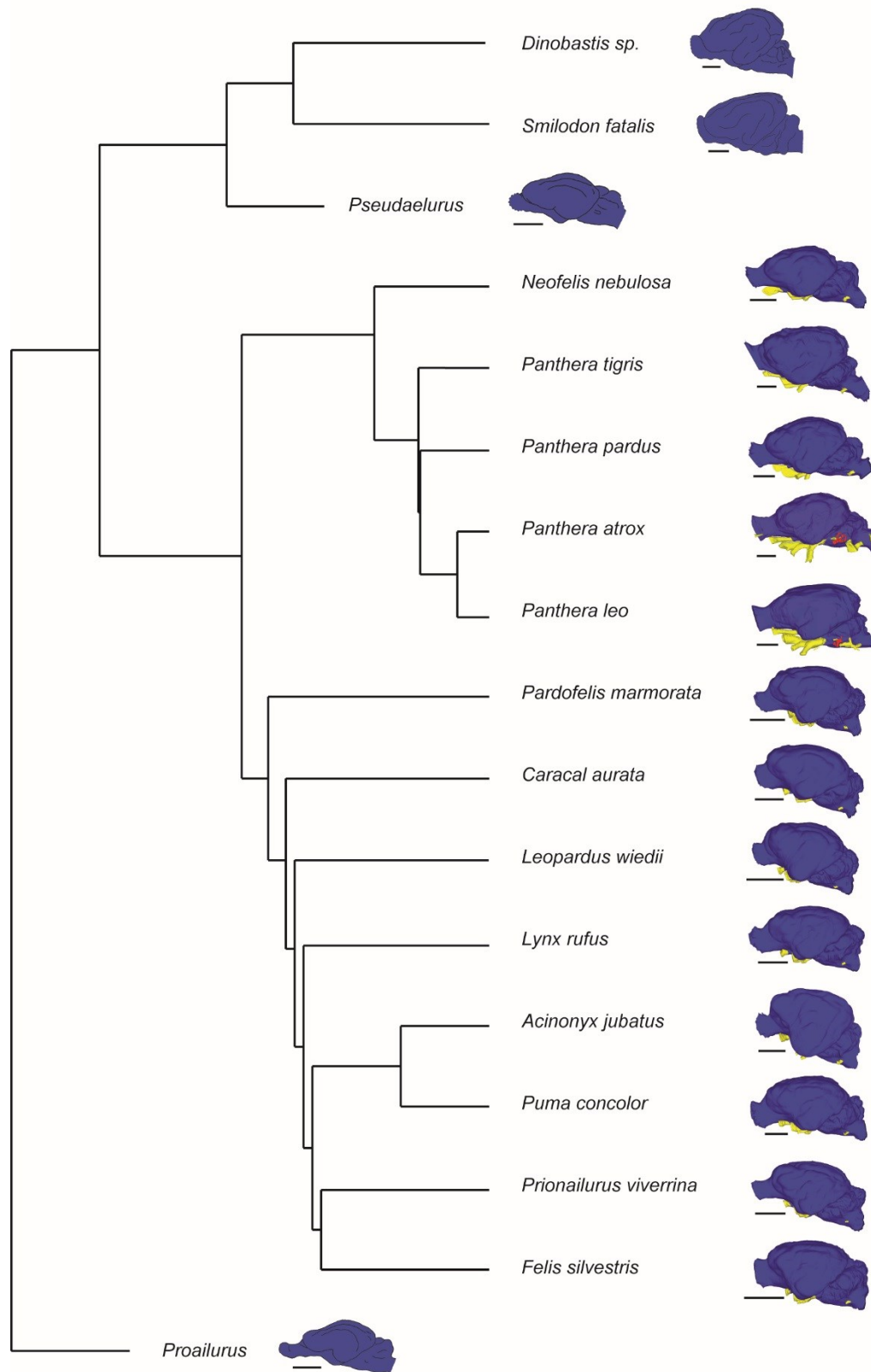


Figure 3. Brain anatomy through Felidae. *Proailurus*, *Pseudaelurus*, *Dinobastis* and *Smilodon* are all modified from Radinsky[1975]. Phylogeny modified from Piras et al.[2013], total length 27Ma. All scale bars = 2cm.



369 Figure 4. Regression of log maximum brain mass against log body mass (both in kilograms) for  
 370 Felidae.

