

Endocranial Morphology of the Extinct North American Lion (*Panthera atrox*)

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Keywords

Fossil · Lion · Brain · Endosseous labyrinths · Encephalization

Abstract

The extinct North American lion (*Panthera atrox*) is one of the largest felids (Mammalia, Carnivora) to have ever lived, and it 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 its 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 showing 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 the expected brain mass for a given body mass) is also larger than that of extant lions but similar to that of the other pantherines. The advent of CT scans has allowed nondestructive sampling of anatomy that

cannot otherwise be studied in these extinct lions, leading to a more accurate reconstruction of endocranial morphology and its evolution.

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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 11 ka. The precise phylogenetic affinities of *P. atrox*, and even its status as a separate species, have 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*) [Goldfuss, 1810], several early 20th century comparative studies, as well as more recent morphometric studies, nested them closer to tigers [Groiss, 1996] or jaguars [Simpson, 1941; Christiansen, and Harris, 2009], though recently a study suggested that many of these morphological similarities arise from allometric changes [Benoit, 2010]. The rise in molecular phylogenetics, including techniques that allow extraction of genetic material from the fossil specimens, has brought new insight into this debate, with molecular data

Table 1. log₁₀-transformed data for the 17 felid species used in this study

Species	Specimen No.	Body mass	Minimum brain mass	Maximum brain mass
<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> ^a		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> ^a		1.09	-1.17	-1.17
<i>Caracal aurata</i>	AMNH 51996	1.05	-1.24	-1.21
<i>Leopardus pardalis</i> ^a		1.03	-1.20	-1.20
<i>Caracal serval</i> ^a		0.99	-1.22	-1.22
<i>Felis silvestris cf 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

Body masses for AMNH specimens are averages for species from Cuff et al. [2015] as no specimen-specific masses were available. LACMP, Natural History Museum of Los Angeles County; AMNH, American Museum of Natural History; NMS, National Museums of Scotland. ^a Data are from Finarelli and Flynn [2009].

nesting *P. atrox* as a sister to *P. spelaea*, and *P. atrox* + *P. spelaea* then being a sister clade to the ancestors of today's modern lion *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 body sizes larger than modern lion species, and possibly larger than any other felids [Cuff et al., 2015], with estimates of up to 420 kg [Sorkin, 2008], although more recently these have been revised down to 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 with the 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 has 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 focusing particularly on the size of the brain [Wroe and Milne, 2007]. The advent and increasing availability of CT scanning has resulted in a 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, providing great insight into brain and inner-ear structure, their evolution, and their relation to numerous ecological attributes [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.

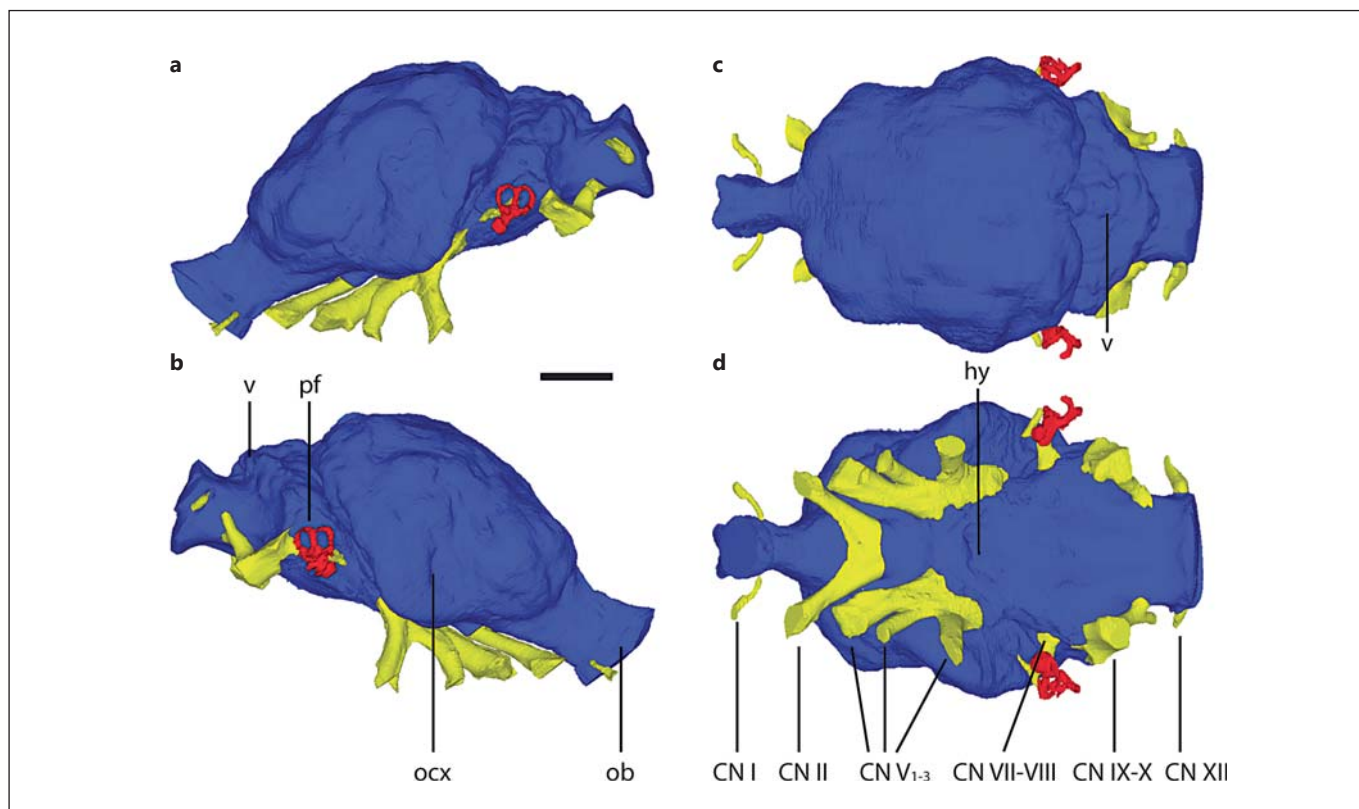


Fig. 1. Endocranial reconstruction of *P. atrox* in left lateral (**a**), right lateral (**b**), dorsal (**c**), and ventral (**d**) views. Anterior is toward the left in **a**, **c**, and **d** and toward the right in **b**. The endocranium is rendered in blue, the inner ear in red, and the cranial nerves in yellow. CN II, optic nerve; CN V₁₋₃, 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. The endocranial orientation in **a** and **b** is linked to the likely “alert” head posture.

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 using a GE Phoenix c/tome/x scanner (200 kV, 80 mA, 0.24 mm/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 semicircular 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 a resolution of 0.58 mm/pixel, 178 slices with a 5-mm slice thickness, 120 kV, 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 postmortem that involved removal of the brain via sawing through and removal of the dorsal region of the 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 employing condylobasal length (for pantherines [Mazák et al., 2011]) and femoral length [Anyonge, 1993]. The resulting masses of 195.2 and 219.5 kg, respectively, were averaged to give a mean body mass for LACMP23-555 of 207.4 kg, which is the mass used for the following analysis. Additionally, a convex hull model was constructed to calculate the body mass using the entire skeleton, which produced an average body mass estimate of 200 kg [Cuff et al., in review].

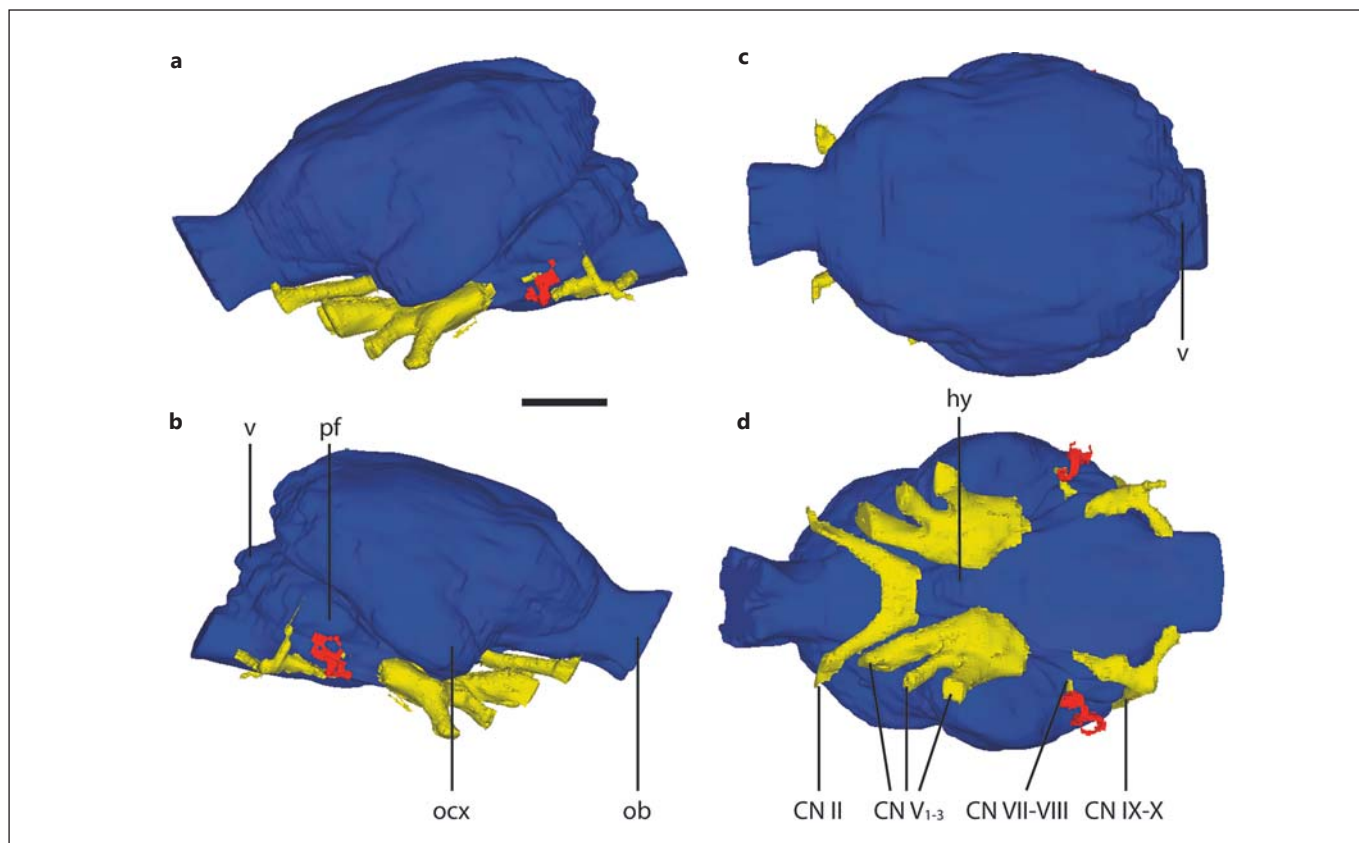


Fig. 2. Endocranial reconstruction of *P. leo persica* in left lateral (**a**), right lateral (**b**), dorsal (**c**), and ventral (**d**) views. Anterior is toward the left in **a**, **c**, and **d** and toward the right in **b**. The endocranium is rendered in blue, the inner ear in red, and the cranial nerves in yellow. CN II, optic nerve; CN V₁₋₃, 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. The endocranial orientation in **a** and **b** is linked to the likely “alert” head posture.

For a broad comparison of felid endocranial anatomy, braincases of *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), *P. pardus* (AMNH 113745), *P. tigris* (AMNH 45519), *Pardofelis marmorata* (AMNH 102844), *Prionailurus viverrinus* (AMNH 102691), and *Puma concolor* (AMNH 6677) were scanned at the Microscopy and Imaging Facility. 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 endocrania (aligned so that CN II was horizontal for each specimen) for the total length from the anteriormost cerebrum to the posteriormost cerebellum and the length of “exposed” cerebellum (the length posterior to the cerebrum) and calculating the 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/cm³ [Schröder, 1968] to 1,100 g/cm³ [Barber et al., 1970]), maximum and minimum estimates were used to generate a range for the estimated brain mass. These estimates were combined with data from the additional 11 extant endocrania and published data for an additional 4 felid brain sizes (*Leopardus pardalis*, *Leptailurus serval*, *Lynx lynx*, and *P. 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 standardized reduced major axis regression in the “smart” 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 phylogenetic correction using independent contrasts before repeating the standardized reduced major axis regression. Phylogenetically corrected analyses used the phylogeny from Piras et al. [2013] pruned to include only the taxa in this analysis.

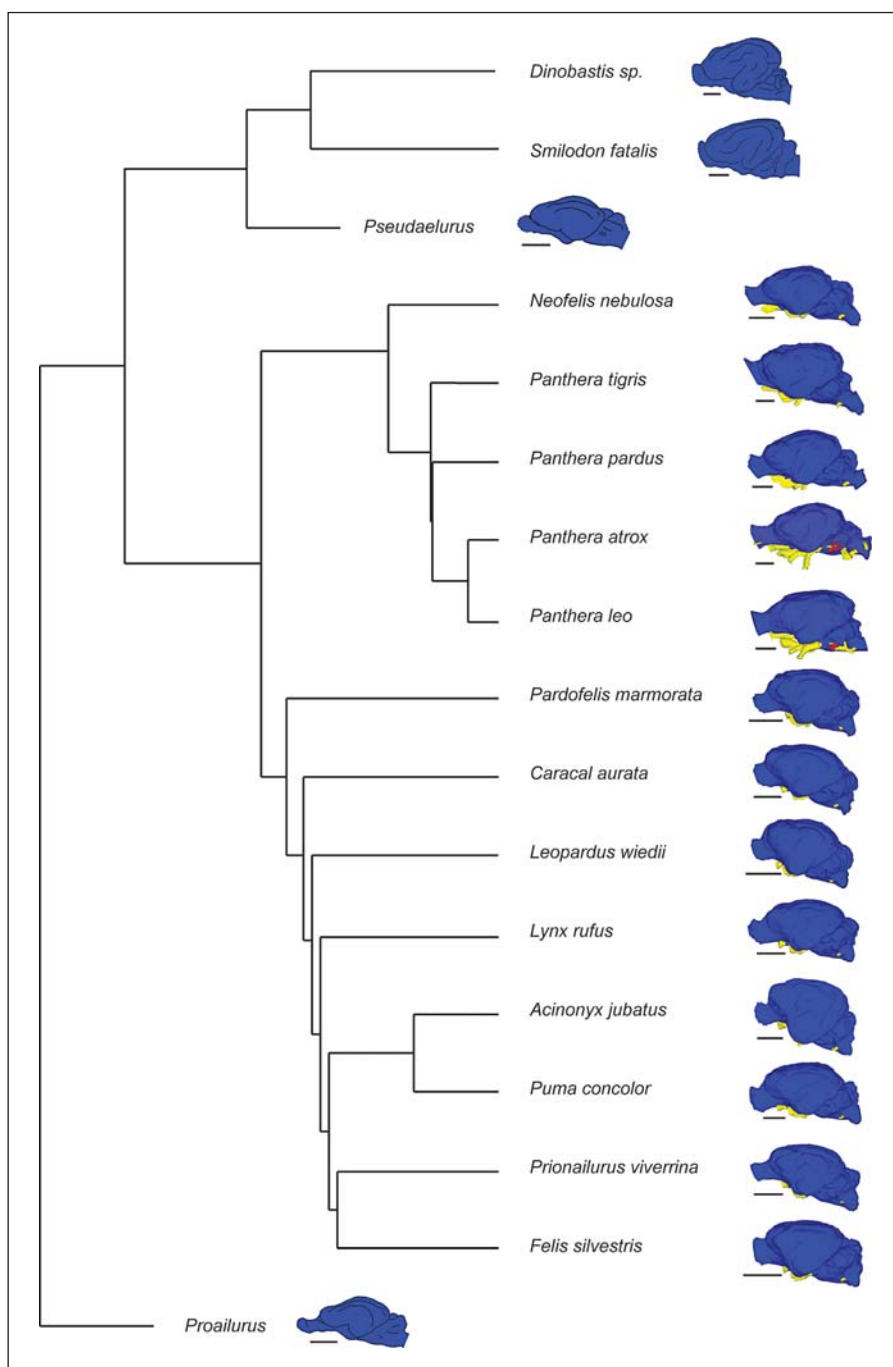


Fig. 3. Brain anatomy through Felidae. *Proailurus*, *Pseudaelurus*, *Dinobastis*, and *Smilodon* are all modified from Radinsky [1975]. Phylogeny is modified from Piras et al. [2013] (total length 27 Ma). All scale bars = 2 cm.

Results

Brain Anatomy

The endocranium of this *P. atrox* specimen is incredibly well preserved (Fig. 1), showing little to no evidence of taphonomic deformation in comparison to the recently deceased specimen of the extant *P. leo persica* (Fig. 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 (Fig. 3), but the brain volume of *P. atrox* (i.e., 323 cm³) corresponds to a brain mass of between 331 and 355 g, making it as large as the biggest extant tigers [Yamaguchi et al., 2009]. *P. atrox* has a relatively longer brain (dis-

Table 2. Measure of relative cephalic flexure across felids

Species	Cerebrum and cerebellum length ^b , m	“Exposed” cerebellum length ^c , m	Proportion “exposed”
<i>Dinobastis</i> sp. ^a	0.0979	0.0095	0.097
<i>Smilodon fatalis</i> ^a	0.0923	0.0124	0.134
<i>Pseudaelurus</i> ^a	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> ^a	0.0641	0.0141	0.220

^a From Radinsky [1975]. ^b Total lateral length of both. ^c Length of the cerebellum not overlapped by cerebrum.

tance from olfactory bulbs to the foramen magnum)-to-condylobasal length than that of an extant *P. leo persica* (42.4 vs. 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 (Fig. 3) [Radinsky, 1975], although there is no clear pattern with regard to relative levels of cephalic flexure across Felidae (Table 2). Within the Machairodontinae there is a high level of cephalic flexure, which is also seen independently within *P. leo* and *P. tigris* (Fig. 3). Among the extant, non-pantherine felids there are generally higher levels of cephalic flexure, but this may be the result of a rotation of the forebrain such that the olfactory bulbs emerge relatively lower (Fig. 3).

The majority of the cranial nerves can be located within the endocranium in positions similar to those in all other examined felids. CNs III (oculomotor), IV (trochlear), and VI (abducens) could not be located in the reconstruction, but they are likely to exit with CNs V₁ and V₂ through the cavum epiptericum, and the CN XI acces-

sory 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. 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% (Fig. 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 (Fig. 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 (Fig. 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 an alert head posture [Witmer and Ridgely, 2009]. For *P. atrox* this angle may be as high as 55°, 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 3). log brain mass scaled against log body mass slope varies between 0.51 and 0.52 (95% between 0.44 and 0.60) across felids before phylogenetic correction and between 0.895 and 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 (Fig. 4). The result is that the encephalization quotient for *P. atrox* is above 1.0, but when the 95% CI are accounted for this result may not always hold.

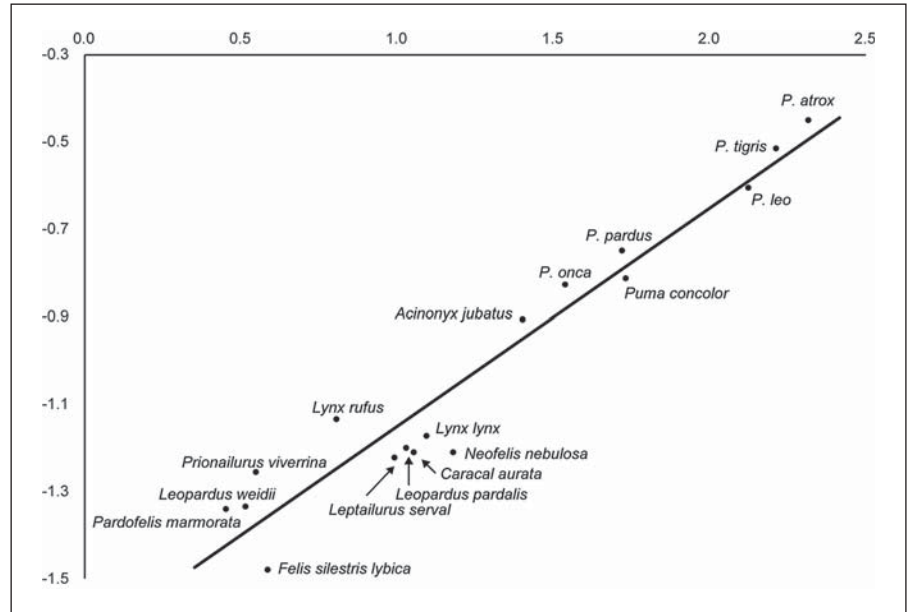
Discussion

We present here the first digital reconstruction of a *P. atrox* endocranium from CT scans, allowing a detailed visualization of its anatomy. 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 CT scans have allowed the addition of

Table 3. Results of reduced major axis analyses of log brain mass against log body mass

	Slope	95% CI	r^2	r^2p	Intercept
Minimum	0.517	0.448–0.596	0.932	0.000	–1.69
Minimum _{phylogenetic}	0.903	0.646–1.261	0.647	0.000	–0.045
Maximum	0.514	0.447–0.591	0.935	0.000	–1.67
Maximum _{phylogenetic}	0.896	0.642–1.249	0.650	0.000	–0.047

r^2p , statistical significance of the correlation between brain mass and body mass.

**Fig. 4.** Regression of log maximum brain mass against log body mass (both in kg) for Felidae.

inner-ear morphology. This specimen of *P. atrox* possesses one of the largest published felid brains to date (behind that estimated from an endocranial cast of another *P. atrox* specimen, i.e., LACM2900-1 [Merriam and Stock, 1932]), but it appears to have a larger endocranial volume than LACM2900-16, which is an individual with a larger skull [Merriam and Stock, 1932]. The endocast for LACM2900-16 is derived from a 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 whether 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 encephalization observed in smaller cats than in larger ones (up to about 90 kg of mass) when pooled with other carnivorans [Finarel-

li 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 that of 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 *P. atrox* towards the right in Figure 4.

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 it reduces 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 sex 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 provide 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 vary tremendously across not just the large felid species but also 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 the endocranial morphology, behavior, and posture of this extinct cat.

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Disclosure Statement

There are no conflicts of interests to declare.

Authors' Contributions

A.R.C. and C.S. segmented the CT scans, A.G. provided the data on extant felid brain masses, A.R.C. carried out the analyses, and A.R.C. and A.G. interpreted the results and wrote this paper.

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