

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

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9 Short title: Endocranial anatomy of *Panthera atrox*.

10 Four figures, two tables.

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16

17 **Abstract**

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

32

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

34

35 **Introduction**

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

49

50 The excellent fossil record of *P. atrox* shows that they attained sizes larger body sizes than modern
51 lion species, and possibly larger than any other felids [Cuff et al., 2015] with estimates up to 420kgs
52 [Sorkin, 2008], although more recently these have been revised down to give size ranges only slightly
53 larger than the maximum recorded for modern lions and tigers [Christiansen, and Harris, 2009]. *P.*
54 *atrox* has been found across the southern reaches of North America and into Central America
55 [Montellano-Ballesteros, and Carbot-Chanona, 2009] (with some uncertainty over whether they
56 crossed into South America)[Barnett et al., 2009; Yamaguchi et al., 2004]. As one of the largest
57 predators in the area (larger than the sympatric *Smilodon fatalis*) it has been suggested that *P. atrox*
58 was feeding on most of the mega-herbivorous fauna that existed in North America at that time [Van
59 Valkenburgh, and Hertel, 1993]. Modern lions live in pride systems (particularly where there is a high
60 density of prey [Schaller, 1972]), and it has been suggested that this may also be the case for *P.*
61 *atrox*, which show similar levels of sexual dimorphism in canine size to their extant relatives
62 [Yamaguchi et al., 2004]. However, the rarity of *P. atrox* at La Brea relative to *S. fatalis* [Marcus,
63 1960], and the observation that the leopard shares canine size dimorphism to that of modern *P. leo*
64 [Van Valkenburgh, and Sacco, 2002], means that the evidence for group living in *P. atrox* is still
65 ambiguous.

66

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

79

80 **Methods**

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

84 scanner (200kV, 80mA, 0.24mm/pixel). One of the CT scan sections contained the entirety of the
85 braincase which was segmented using Mimics 16.0 (Materialise Corp, Belgium) to isolate the
86 endocranium. This involved manually isolating the endocranial space (which is a combination of
87 matrix and air in the *P. atrox* specimen) from the foramen magnum at the posterior towards the
88 cribriform plate at the anterior. In this specimen of *P. atrox* the cribriform plate is not preserved due
89 to the thin bones being destroyed so the anterior margins are estimated. Nerves were identified by
90 the canals leading from the endocranium, with the semi-circular canals identifying the inner ear
91 morphology. For anatomical comparisons the skull of an Asian Lion (*P. leo persica*) was scanned at
92 the Royal Veterinary College (helical scan resulting in resolution of 0.58mm/pixel, 178 slices with
93 5mm slice thickness, 120kV, Lightspeed Pro 16 CT scanner, GE Medical Systems) and the resulting
94 scans were segmented in Avizo 8.1 (VSG SAS, Bordeaux, France). As the *P. leo persica* specimen was
95 a captive specimen at a local zoo that died unexpectedly, it was subjected to a post-mortem that
96 involved removal of the brain via sawing through and removing the dorsal region of braincase. This
97 piece was digitally replaced onto the skull in Avizo 8.1 by rotating the skull piece into position to
98 provide the original dorsal margins of the braincase. During segmentation, each of the anatomical
99 structures (nerves, inner ear and brain) was isolated for individual study and comparison between *P.*
100 *atrox* and *P. leo persica*.

101

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

108

109 For a broad comparison of felid endocranial anatomy, braincases of a *Acinonyx jubatus* (AMNH VP
110 CA2502), *Caracal aurata* (AMNH 51996), *Felis silvestris* (AMNH 81233), *Leopardus wiedii* (AMNH
111 95085), *Lynx rufus* (AMNH 24225), *Neofelis nebulosi* (AMNH 22919), *Panthera pardus* (AMNH
112 113745), *Panthera tigris* (AMNH 45519), *Pardofelis marmorata* (AMNH 102844), *Prionailurus*
113 *viverrinus* (AMNH 102691) and *Puma concolor* (AMNH 6677) were scanned at the Microscopy and
114 Imaging Facility (MIF). All endocrania were segmented using Avizo 8.1 and volumes were measured
115 using the “surface statistics” function. Additionally a comparative measure for relative cephalic
116 flexure across the felids was carried out. This involved measuring the lateral aspects of the endocasts
117 (aligned so that CN II was horizontal for each specimen) for total length from anteriormost cerebrum

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

121

122 Brain scaling

123 The mass of the brain of *P. atrox* was estimated from the full endocranial volume and multiplied by
124 the density of brain tissue. Due to the variability in published densities (from 1.027 g/cm³ [Schröder,
125 1968] to 1.100 g/cm³ [Barber et al., 1970]) maximum and minimum estimates were used to generate
126 a range for estimated brain mass. These estimates were combined with data from the additional 11
127 extant endocasts and published data for an additional four felid brain sizes (*Leopardus pardalis*,
128 *Leptailurus serval*, *Lynx lynx*, *Panthera onca* [Weisbecker, and Goswami, 2010]) before both brain
129 and body masses were log-transformed (Table 1). Log brain mass was then regressed against log body
130 mass using Standardised Reduced Major Axis (SMA) regression in the ‘smatr’ package package
131 [Warton et al., 2012] in R 3.1.0 (R Core Team, 2014). Because relative brain size has been previously
132 shown to be strongly influenced by phylogenetic relatedness [Weisbecker, and Goswami, 2010], we
133 further conducted a phylogenetically-correction using independent contrasts, before repeating the
134 SMA regression. Phylogenetically-corrected analyses used the phylogeny from Piras et al. (2013)
135 pruned to include only the taxa in this analysis.

136

137 **Results**

138 Brain anatomy

139 The endocranium of this *P. atrox* specimen is incredibly well preserved (Figure 1), showing little to
140 no evidence of taphonomic deformation in comparison to the recently deceased specimen of the
141 extant *P. leo persica* (Figure 2). Overall, the gross morphology (particularly the size and relative
142 positions of the cerebrum and cerebellum, see below) resembles that of the leopard more than the
143 Asian lion (Figure 3), but the brain volume of *P. atrox* (323cm³) corresponds to a brain mass of
144 between 331g - 355g making it as large as the biggest extant tigers [Yamaguchi et al., 2009]. *P. atrox*
145 has a relatively longer brain (distance from olfactory bulbs to foramen magnum) to condylobasal
146 length than that of an extant *P. leo persica* (42.4% against 40% respectively). This measure would
147 likely be even longer if the anteriormost margins of the olfactory bulbs could be accurately defined,
148 discussed below. Most of this difference in brain length can be ascribed to differences in the cephalic
149 flexure of the brain, with the cerebrum extending less over the cerebellum in *P. atrox* than in *P. leo*.
150 This more extended condition in *P. atrox* resembles that observed in the most basal felids (Figure
151 3)[Radinsky, 1975] although there is no clear pattern in regards to relative levels of cephalic flexure

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

156

157 The majority of the cranial nerves can be located within the endocranium in similar positions to
158 those in all other examined felids. CNs III (oculomotor), IV (trochlear), and VI (abducens) could not
159 be located in the reconstruction, but are likely to exit with CNs V₁ and V₂ through the cavum
160 epiptericum, and the CN XI accessory nerve, which also was not visible, likely exits with CNs IX-X.

161

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

167

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

176

177 Brain scaling

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

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

186

187 **Discussion**

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

199

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

213

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

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

222

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

231

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239 Flynn JJ for providing the scans of the other species.

240

241 **Author contributions**

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

244

245 **Competing financial interests**

246 There are no conflicts of interests to declare.

247

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326

327

328 Table 1. Log₁₀ transformed data for the 17 felid species used in this study. ¹ denotes data from
 329 Finarelli and Flynn [2009]. LACMP: Natural History Museum of Los Angeles County, AMNH: American
 330 Museum of Natural History, NMS: National Museums of Scotland. Body masses for AMNH specimens
 331 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> ¹		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> ¹		1.09	-1.17	-1.17
<i>Caracal aurata</i>	AMNH 51996	1.05	-1.24	-1.21
<i>Leopardus pardalis</i> ¹		1.03	-1.20	-1.20
<i>Caracal serval</i> ¹		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

332

333 Table 2. Results of Reduced Major Axis analyses of log brain mass against log body mass. Upper and
 334 lower limits represent 95% confidence intervals, whilst the “r² p” shows the statistical significance of
 335 the correlation between brain mass and body mass.

	Slope	lower limit	upper limit	r ²	r ² p	336 intercept
Minimum	0.517	0.448	0.596	0.932	0.000	-1.69 ³³⁷
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	-1.67 ³³⁸
Maximum _{phylogenetic}	0.896	0.642	1.249	0.650	0.000	-0.047

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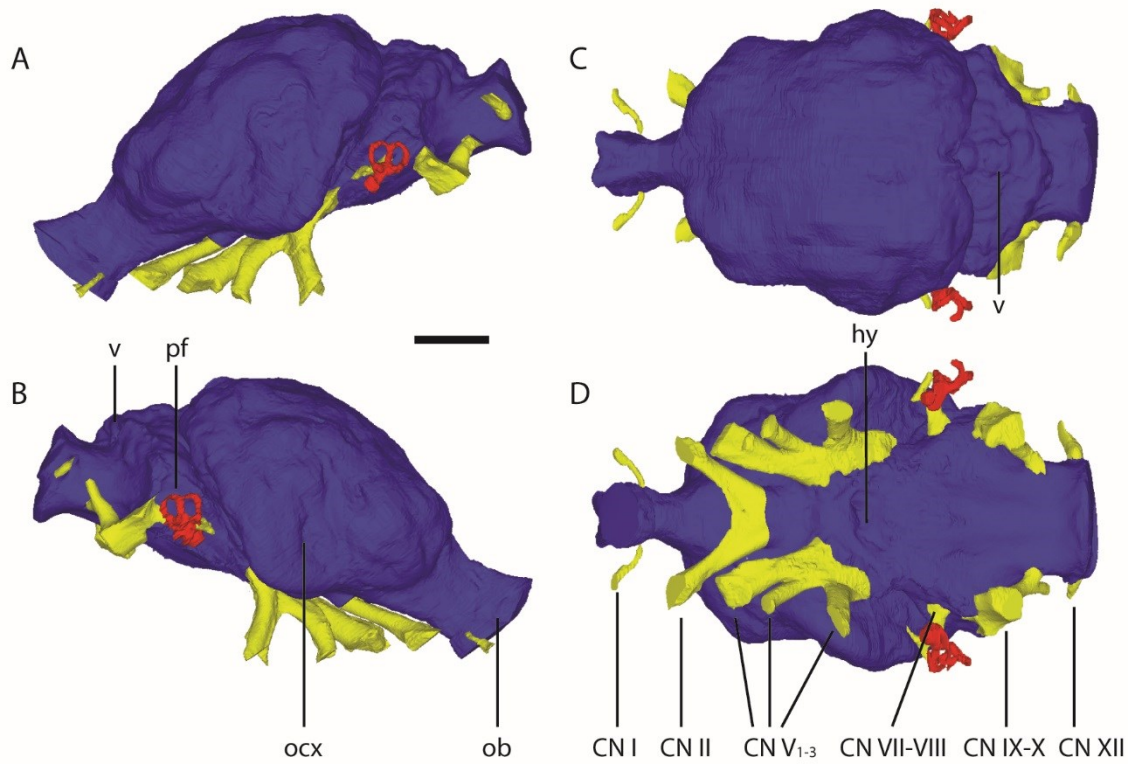
341 Table 3. Measure of relative cephalic flexure across felids. Cerebrum and cerebellum lengths
 342 correspond to total lateral length of both, “exposed” cerebellum length is the length of the
 343 cerebellum not overlapped by cerebrum. All lengths in m. Species marked with an asterisk (*) are
 344 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>Carcacal 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

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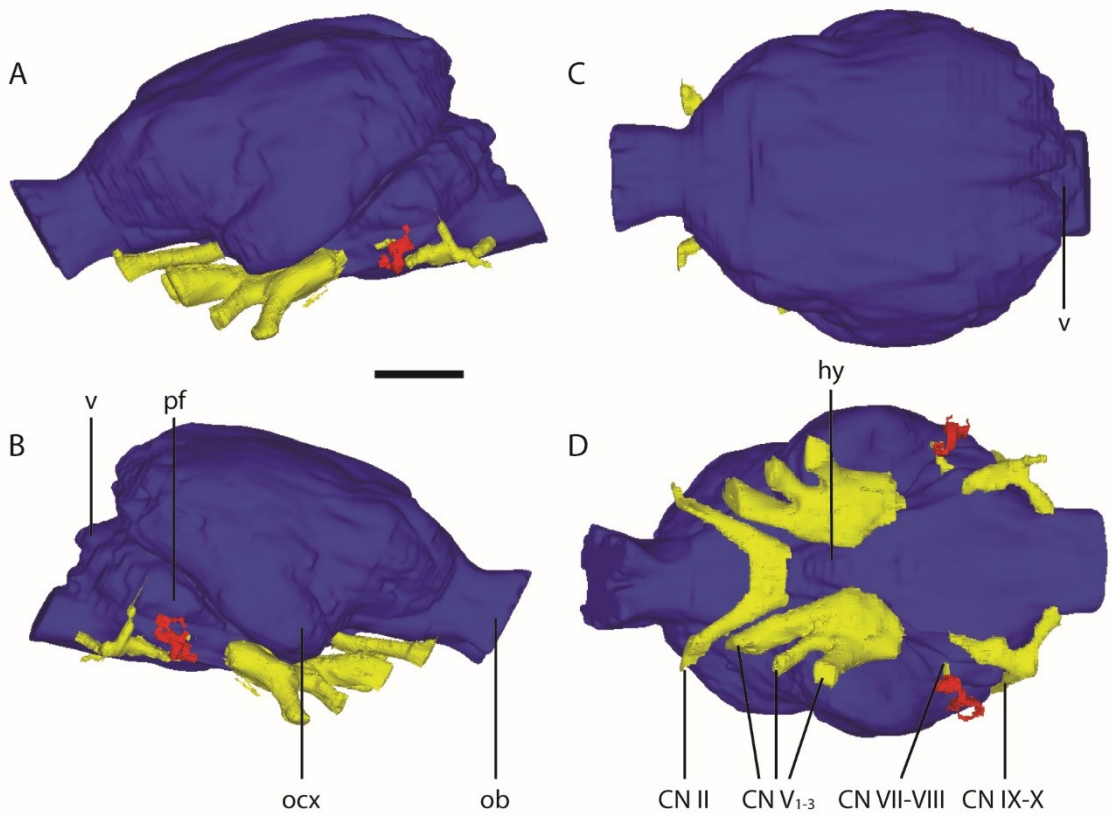
347 Figure 1. Endocranial reconstruction of *P. atrox* in A, left lateral; B, right lateral; C, dorsal; and D,
 348 ventral views. Anterior is toward the left in A, C, D and toward the right in B. The endocast is
 349 rendered in blue, the inner ear in red, and the cranial nerves in yellow.; CN II optic nerve; CN V₁₋₃,
 350 trigeminal nerve (ophthalmic, maxillary and mandibular branches); CN VII facial nerve; CN VIII
 351 vestibulocochlear nerve; CN IX, glossopharyngeal nerve; CN X, vagus nerve; CN XII, hypoglossal
 352 nerve; hy, hypophysis/pituitary; ob, olfactory bulb; ocx, olfactory cortex; pf, paraflocculus; v, vermis.
 353 Scale bar = 20 mm. Endocranial orientation in A and B linked to the likely “alert” head posture.



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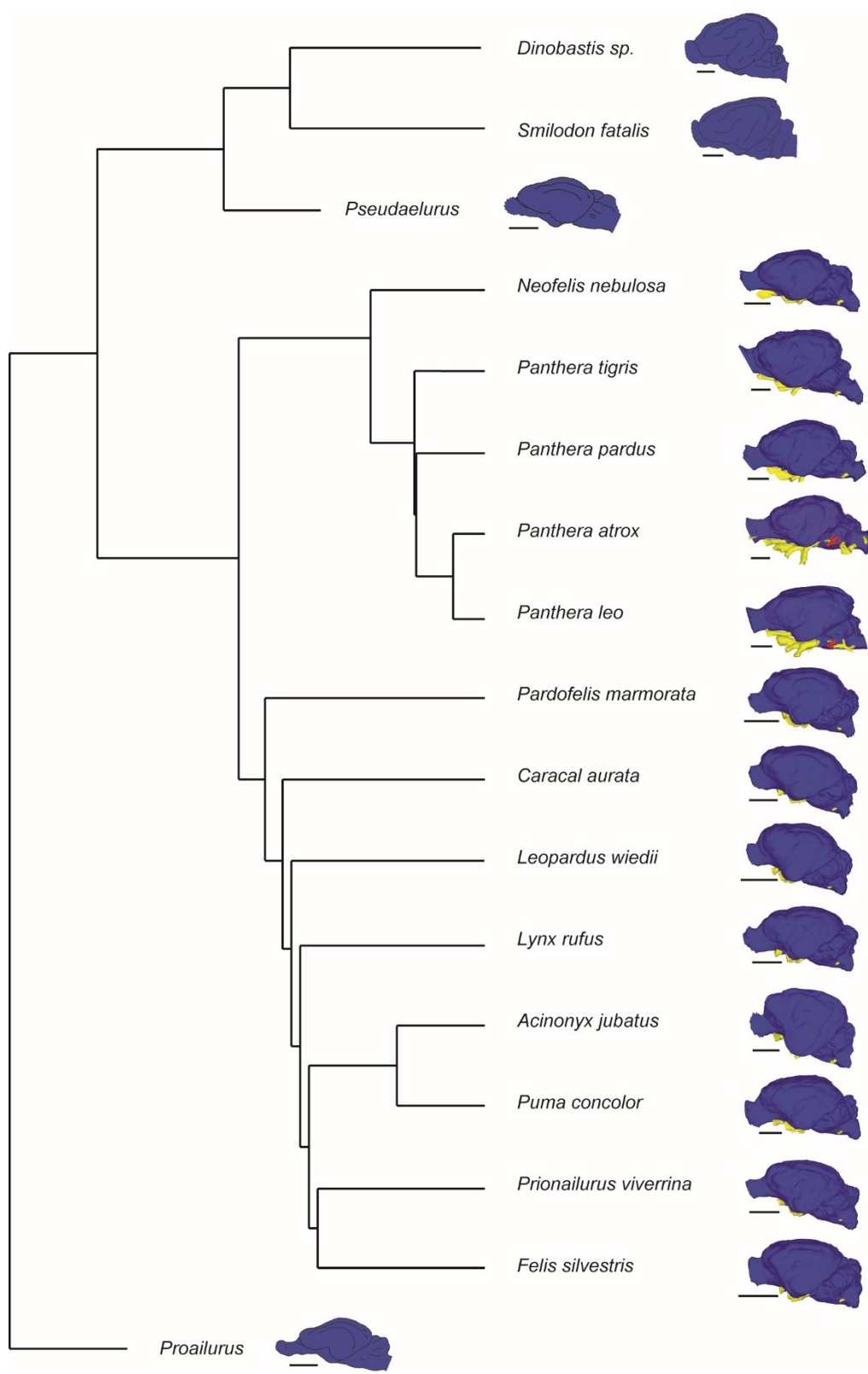
356 Figure 2. Endocranial reconstruction of *P. leo persica* in A, left lateral; B, right lateral; C, dorsal;
 357 and D, ventral views. Anterior is toward the left in A, C, D and toward the right in B. The endocast is
 358 rendered in blue, the inner ear in red, and the cranial nerves in yellow.; CN II optic nerve; CN V₁₋₃,
 359 trigeminal nerve (ophthalmic, maxillary and mandibular branches); CN VII facial nerve; CN VIII
 360 vestibulocochlear nerve; CN IX, glossopharyngeal nerve; CN X, vagus nerve; CN XII, hypoglossal
 361 nerve; hy, hypophysis/pituitary; ob, olfactory bulb; ocx, olfactory cortex; pf, paraflocculus; v, vermis.
 362 Scale bar = 20 mm. Endocranial orientation in A and B linked to the likely “alert” head posture.



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



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

