




ORIGINAL ARTICLE

Estimating Endocranial Volume in the Domestic Cat (*Felis catus*) Using Computed Tomography

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ABSTRACT

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Changes in brain and endocranial volume size are observed in most mammals during domestication. However, while much attention has been paid to comparing domesticated species with their wild relatives, few studies have focused on the differences between domesticated breeds, especially in cats. In this study, we estimated the endocranial volume of two different domestic cat breeds (*Felis catus*) using virtual endocasts obtained from computed tomography (CT) images. Our analysis did not reveal any significant differences between the British Shorthair and the Scottish Fold domestic breeds in terms of endocranial volume. In addition, we found similar results with volumes previously obtained from domestic cats using bead methods. Although these results represent only a limited sample of the entire cat breed diversity, we hope they will contribute to our understanding of the macroevolutionary changes in brain volume during domestication.

Introduction

With more than 400 million animals estimated today (of which approximately 350 million are household pets), the cat represents a special case of domestication due to its importance in the history of human cultures and its influence on current biodiversity.¹⁻³ Genetic analyses indicate that the ancestor of the nowadays domestic cat is more likely to be sought from both the Near Eastern and Egyptian populations of wild cats, *Felis silvestris lybica*.⁴⁻⁶ But despite their rapid spread in almost all continents, domestic cats have a morphology that has remained very close to those of their wild ancestors, a phenomenon that can be partly explained by hybridization between wild and domestic/feral cats.^{7,8}

Most of the phenotypic variation, in domesticated animals, is the result of artificial selection to improve

the animals usefulness for specific tasks or behaviors. Phenotypic characteristics in cat breeds are selected for their aesthetic qualities based on, among other things, coat colors and patterns, texture and length of hair associated with other morphological traits such as the length of the legs, tail and ears.⁹ The number of recognized cat breeds vary depending on the organization: 73 (The International Cat Association, TICA) and 45 (Cat Fanciers' Association, CFA). However, unlike dog breeds, studies focusing on domestication processes within domestic cats are still limited, probably due to the less apparent morphological diversity of cat breeds and both taxonomic and sampling issues intrinsic to this species which have long plagued research on domestic cat evolution and diversity. Regarding the brain, both dogs and cats¹⁰ which are probably the most human-interacting

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domestic mammals,^{11,12} have been proven to show a significant reduction of the relative brain size compared to their wild counterparts. The first studies on the endocranial volume changes in domestic cats reported that the brain size of domestic individuals was significantly smaller than wild animals.¹³ Although the results are controversial because of the limited number of individuals sampled (7 domestic cats) and the model chosen (comparison between domestic animals and *Felis silvestris lybica* individuals, former *Felis maniculata*), more recent studies also find a similar trend of decreased brain size for domestic cats.^{14,15} More precisely, brain volume reduction between domestic cats and their ancestors/wild relatives was estimated as 23.9%¹⁵ and 23.4%¹⁶, depending on methods and sampling. It is also interesting to note that the authors found a lower reduction when considering the endocranial volume, and not the brain volume itself ($\approx 18\%$). Therefore, estimating the brain size change through endocranial volume induces a reasonable error of less than 6%.

The endocranial volume (i.e., the volume of the internal cavity of the neurocranium) is a useful proxy of the brain size, commonly used for estimating evolutionary changes between closely related species.¹⁷⁻¹⁹ In mammals, the endocranial volume not only shows variations within populations but also has an intricate relationship with brain size and structure.²⁰⁻²² Although the endocranial volume (EV) does not always give accurate indications for the volume and proportion of the different structures that compose the brain,²³⁻²⁵ this proxy remains today one of the most widely used measures to study brain evolution, especially regarding mammalian domestication.

The selection of an endocranial volume estimation method is critical, especially when comparing dry-skull and live-skull. Utilizing the same estimation technique, suitable for both live samples and fixed samples delivers more robust outcomes. Estimation of EV by filling the inside of the neurocranium with a matrix (most commonly beads), also referred to as the “beads method”, is frequently used and has the advantage of being easily implemented on a dry skull without an expensive cost. For example, a recent study using the beads method estimated the mean volume of the endocast of domestic cats at 30317 mm³.²⁶ Besides not being applicable to live animals, in some cases, this method can lead to the overestimation of the total endocranial volume.²⁷⁻²⁹ In addition, the tentorium (i.e., the bone plate that separates the cerebrum from the cerebellum) is strongly ossified in the taxonomic group of Carnivora, which can complicate and ultimately bias the calculations made with the beads. Although this method is still used in a variety of fields, past decades have seen the rise of new 3D imaging techniques which have become essential tools in our

understanding of the evolutionary mechanisms, particularly concerning brain size evolution.³⁰

Recently, neuroscientists and paleontologists heavily rely on structural imaging techniques such as computed tomography (CT).²⁷ CT scanners are indeed one of the most useful techniques for digitizing bone structures and performing morphometric measurements on both dry skulls and live animals.³¹⁻³⁵ For example, such methods have been very useful in studying with fine detail the sexual dimorphism of skull volume and proportions in the Van cat³⁵ and European Shorthair.³⁶ Moreover, internal volumes such as the neurocranial cavity area could easily be extracted from CT images and are proven to reflect accurately the overall size and external morphology of the brain and cerebral-associated structures, especially in mammalian taxa.^{27,37} Despite all these advantages, the use of CT scanner technologies for the study of endocranial volume within cats remains relatively rare.

This study aimed to compare the endocranial volume of two breeds of domestic cats, the British Shorthair and the Scottish Fold cats, using volume estimation of the virtual endocasts extracted from CT images. Both British Shorthair and Scottish Fold breeds shared a recent genetic history,³⁸⁻⁴⁰ however, different selective pressures had led to anatomical features and even specific breed-related diseases in the case of the Scottish Fold. Probably the oldest English breed of cat, the British Shorthair cats are extremely docile animals that often seek contact with humans.⁴¹ British Shorthairs cats are relatively powerful-looking animals with a broad chest and a short muzzle. Although this breed shares many of its physical characteristics with the Scottish folds, the latter is also characterized by cartilage abnormalities causing their typical “fold” ear shape and are particularly susceptible to painful musculoskeletal problems.⁴² Although very similar in their external appearance, fundamental differences exist between these breeds, and, to our knowledge, brain/endocranial volume size has never been studied for both the British Shorthair and the Scottish Fold cats.

Materials and Methods

Animal Data

No animals were sacrificed for this study and full consent was obtained from all owners for the authors to collect and use these data. We sampled a total of 13 adult individuals, 6 cats (2 males and 4 females) belonging to the British Shorthair breed, and 7 cats (3 males and 4 females) of the Scottish Fold breed. To include in our study only adult animals and without pathologies, we ensured the skeletal development was completed and that no traumatic or gross pathological structural osseous changes could be observed for any of the cats. We

sampled both healthy males and females. CT scanner data were obtained from the Department of Surgery, Faculty of Veterinary Medicine. Images were recorded during the clinical routine. The study was approved by the Local Ethics Committee of the Faculty of Veterinary Medicine.

Each cat head was scanned at 110 kV, 28 mA, and 0.6 mm section thickness using a Siemens (Somatom Scope vc30b) Multi-Detector Computed Tomography (MDCT). The images were recorded in the format of DICOM (Digital Imaging and Communications in Medicine) and were used for the calculation of the endocranial volume (Figure 1).

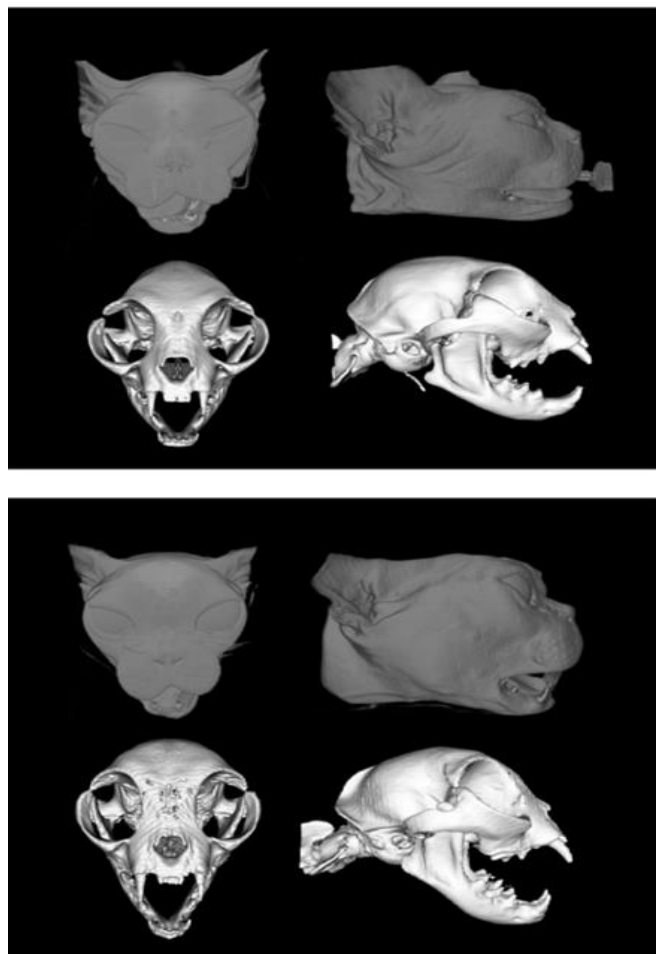


Figure 1. General morphology (public domain images) and head characteristics of the (Upper) British Shorthair (female) and (Lower) Scottish Fold (female) sampled in this study. The visualizations were obtained with AVIZO.

Estimation of Endocranial Volume and Statistical Analysis

Three-dimensional virtual endocasts were generated from CT scanner images following a threshold-based 2D segmentation procedure using AVIZO (v. 8.1.1). Segmentation was performed by the same operator. Openings in the skull (e.g., foramina, nerve canals, and foramen magnum) were closed manually under AVIZO software using straight lines to allow for the selection of the endocranial cavity only. The endocranial volume was then estimated from the virtual endocasts and measured as the volume enclosed by its 3D area (Figure 2).

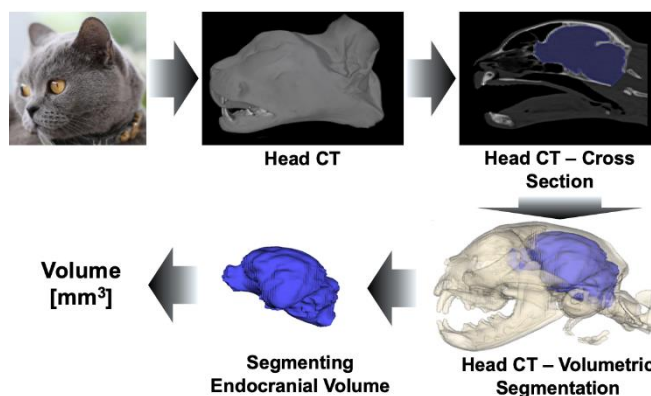


Figure 2. This is an illustration of how virtual endocast extraction was done for a female British Shorthair cat. The process involved obtaining a CT scan of the animal's head and rendering a 3D image of the tissues. The endocast segmentation was then done on a transverse axis, resulting in a clear view of the skeleton (in white) and the endocast (in blue) in 3D from which the endocranial volume was calculated.

All statistical analyses were conducted with R version 4.0.2. (R Core Team, 2020). We analyzed both the endocranial volume (EV) and relative endocranial volume (rEV). The latter was extracted from the regression between the total endocranial volume (EV) and the weight of the animal (built-in function in R). We used GLS analysis to test the correlation between EV and cat weight. Both EV and weight values were log10 transformed prior to the calculation of the regression slope.

First, EVs were tested for normality using Shapiro-Wilk normality tests and homogeneity of variances was assessed through Levene's test. Our analysis showed that the distribution of EV does not follow a normal distribution ($p = 0.016$), while the distribution of variance is homogeneous between breeds ($p = 0.27$) and sexes ($p = 0.10$). Therefore, the difference in endocranial volume (EV) and relative endocranial volume (rEV) between breeds (British Shorthair/Scottish Fold) and sex (females/males) was assessed using a Mann-Whitney test for nonparametric variables.⁴³

Results

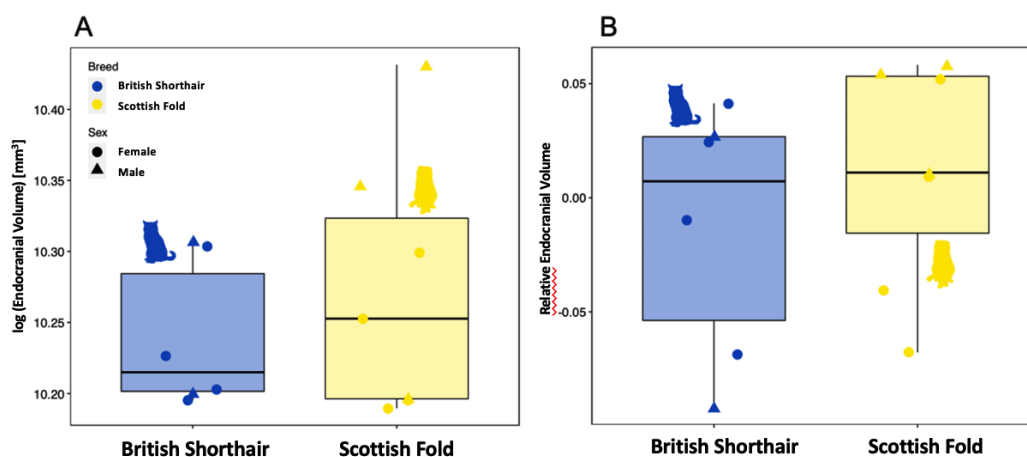
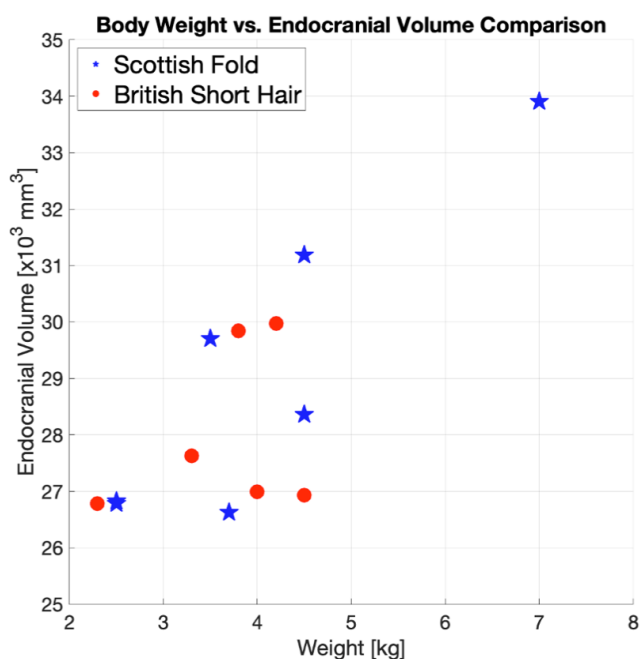
The endocranial volume of our sampling varied from 26626.0 mm³ to 33908.6 mm³, while the relative endocranial volume ranged from -0.092 to 0.058 (Table 1). No significant difference was found for endocranial volume difference and relative endocranial volume depicted in Figure 3.

It is expected to have a positive correlation between brain weight and body weight⁴⁴. While the comparison between the EV and weight yielded a positive correlation ($r = 0.8830$, $p < 0.05$); British shorthair did not show a strong correlation ($r = 0.31$, $p = 0.53$). Where the breed was not considered, the total population delivered a reasonable correlation ($r = 0.78$, $p < 0.05$) (Figure 4).

Our results showed that Scottish cats generally had a higher EV and rEV than British cats. In particular, the

Table 1. The endocranial volume estimated by the CT-scanner for each animal included in the analyses.

Breed	ID	Endocranial volume (mm ³)	Relative endocranial volume	Sex	Age (months)	Weight (kg)
British	1	26779.1	0.024	F	9	2.3
British	2	26931.3	-0.092	M	54	4.5
British	3	26989.1	-0.068	F	108	4
British	4	27631.0	-0.010	F	18	3.3
British	5	29839.6	0.041	F	24	3.8
British	6	29970.7	0.027	M	12	4.2
Scottish	1	26626.0	-0.068	F	60	3.7
Scottish	2	26778.7	0.009	F	36	2.5
Scottish	3	26828.0	0.011	M	9	2.5
Scottish	4	28359.9	-0.040	F	48	4.5
Scottish	5	29704.0	0.052	F	6	3.5
Scottish	6	31185.2	0.055	M	60	4.5
Scottish	7	33908.6	0.058	M	84	7

**Figure 3.** Boxplots represent differences in (A) the endocranial volume and (B) the relative endocranial volume of the British Shorthair and Scottish Fold cats.**Figure 4.** Correlation between the endocranial volume and the weight for the two cat breeds (Scottish fold as blue star, British short hair as red circle) are included in our analysis.

mean EV was estimated as 28023.46 mm³ for British Shorthair and 29055.77 mm³ for Scottish Fold cats. Likewise, the mean rEV was estimated as -0.013 for British Shorthair and 0.011 for Scottish Fold cats. However, our analysis demonstrated no significant differences for both the EV ($W = 21, p = 1$) and the rEV ($W = 10, p = 0.1709$) between the British Shorthair and Scottish Fold cats. Similarly, we could not highlight any difference related to sexual dimorphism regarding the EV ($W = 14, p = 0.366$) or the rEV ($W = 13, p = 0.3543$).

Discussion

To investigate differences between breeds for domestic species is crucial for our understanding of the mechanisms of domestication.²⁶ One of the structures, where this morphological change in mammals is paramount, is the volumetric change of the brain.⁴⁵⁻⁴⁷ This evolutionary change has been carefully studied in various taxa such as carnivorans,⁴⁸ pigs,⁴⁹ sheep,⁵⁰ and cattle.⁴⁶ But few studies have focused on the different breeds of cats. Moreover, many studies over the past decades have

demonstrated that the evolutionary process of brain size evolution is more complex than previously thought. Indeed, although the relative brain size is thought to increase for domesticated species and captive animals compared to their close relatives,^{46,51} a growing number of studies have highlighted unexpected evolutionary trends, with relative brain size remaining constant^{11,46,51-54} and even in some cases decrease over time. Therefore, the assessment of the differences in brain size between cat breeds is of major interest to draw a more accurate portrait of the evolutionary mechanisms of volumetric brain changes in domestic species.

In this study, the endocranial volume (EV) and the relative endocranial volume (rEV) were estimated in a sample including British Shorthair and Scottish Fold domestic cats (*Felis catus*) using virtual endocasts. Although Scottish Fold cats display larger endocranial size than the British Shorthair breed (both absolute and relative), our analysis did not reveal any significant statistical differences between the endocranial volume (absolute or relative) between these two breeds. Two reasons could explain these results.

First, the small sample size may have prevented to detection of statistical differences between these two groups accurately. Indeed, it has been proven that the sampling size had a non-negligible importance in the morphological delimitation between males and females within the same species.⁵⁵ This same statistical bias could apply to our study, which is based on only 13 individuals. This relatively small sample reflects the difficulty of finding domestic cats with a perfectly informed pedigree. The fact that our analysis did not find the influence of sexual dimorphism on endocranial size while this phenomenon is confirmed in other breeds for cranial measurements³⁵ could also tend to confirm this hypothesis.

Second, the absence of significant differences may be due to the strong morphological and genetic resemblance between the British Shorthair and Scottish Fold breeds.³⁸⁻⁴⁰ A study conducted by Schmidt *et al.* on Persian cats demonstrated that high grades of brachycephaly are related to significant differences in the endocranial volume between peke-face and doll-face Persians.⁵⁶ However, peke-face Persians are characterized by extreme deformations of the skull, with a very round neurocranium combined with an extremely short face strongly impacting the overall endocranial volume and cerebral-structures morphology. Such deformations are not observed in the British Shorthair or the Scottish Fold cats that share similar brachycephaly index, which could explain why there is no difference in the endocranial volume between these two breeds.

This study aimed to initiate the comparison with different morphological-varied breeds and contribute to

the rather scarce studies about endocranial/brain volume within domestic cats and hope that further studies can explore this hypothesis with more data.

The use of computed tomography imaging techniques is also an extremely promising avenue to highlight morphological differences between cat breeds. Compared with other whole-body imaging techniques (e.i. MRI), CT offers more cost-effective options. Especially for measuring hard tissue (such as bone), CT scanners remain to be the most accurate technique and thus for estimating intracranial cavity volumes.¹⁹ Moreover, CT applies to both dry skulls and live skulls while enabling a reliable comparison between the two sets of data. Although we did not find any differences regarding the endocranial volume, these two breeds may display significant differences in their brain morphologies (and by extension differences in their endocranial shape). These fine details of endocranial surface can be obtained by high-end CT scanners while this study was limited by the resolution of the CT scanner in the veterinary center dedicated to the care of live animals. The results presented here drove the curiosity of the researchers to explore the heterogeneity of endocranial shape between the British Shorthair and the Scottish Fold cats. It is hoped that these results would pave the way for new approaches on this subject and further research studies will help us understand the phenotypic diversity of cat breeds, establish and understand the differences between domesticated animals and their close ancestors/wild counterparts.

This study analyzed the endocranial volume (absolute and relative) of two breeds of domestic cats, the British Shorthair and the Scottish Fold cats, using computed tomography (CT scanners). We found no significant difference between breeds and sex of these animals, neither for the absolute nor the relative endocranial volume. To our knowledge, this study was the first study to present original data on the endocranial volume for the British Shorthair and the Scottish Fold breed that may provide an important baseline for further research in this field. We hope that this study could add a valuable contribution to scarce basic research data on the neurocranial anatomy of domestic cats.

Conflict of Interest

The authors have no conflicts of interest to declare. No funds, grants, or other support was received for conducting this study

References

1. Driscoll Carlos A, Clutton-Brock J, Kitchener AC, O'Brien SJ. The taming of the cat. Genetic and archaeological findings hint that wildcats became housecats earlier--and in a different place--than previously thought. *Scientific American*. 2009; 300(6): 68-75.

2. Trouwborst A, McCormack PC, Martínez Camacho E. 2020. Domestic cats and their impacts on biodiversity: A blind spot in the application of nature conservation law. *People and Nature*. 2020; 2(1): 235–250. doi: 10.1002/pan3.10073
3. Woolley LA, Murphy BP, Geyle HM, Legge SM, Palmer RA, Dickman CR, Doherty TS, Edwards GP, Riley J, Turpin JM, Woinarski JCZ. 2020. Introduced cats eating a continental fauna: Invertebrate consumption by feral cats (*Felis catus*) in Australia. *Wildlife Research*. 2020; 47(8): 610–623. doi: 10.1071/WR19197
4. Driscoll Carlos A, Macdonald DW, O'Brien SJ. An evolutionary view of domestication. *The Proceedings of the National Academy of Sciences*. 2009; 106: 9971–9978. doi: 10.1073/pnas.0901586106
5. Driscoll CA, Menotti-Raymond M, Roca AL, Hupe K, Johnson WE, Geffen E, Harley EH, Delibes M, Pontier D, Kitchener AC, Yamaguchi N, O'Brien SJ, Macdonald DW. The near eastern origin of cat domestication. *Science*. 2007; 317(5837): 519–523. doi: 10.1126/science.1139518
6. Ottoni C, Van Neer W, De Cupere B, Daligault J, Guimaraes S, Peters J, Spassov N, Prendergast ME, Boivin N, Morales-Muñiz A, Bălăşescu A, Becker C, Benecke N, Boroneant A, Buitenhuis H, Chahoud J, Crowther A, Llorente L, Manaseryan N, Monchot H, Onar V, Osypińska M, Putelat O, Quintana Morales EM, Studer J, Wierer U, Decorte R, Grange T, Geigl E-M. The palaeogenetics of cat dispersal in the ancient world. *Nature Ecology and Evolution*. 2017; 1: 0139. doi: 10.1038/s41559-017-0139
7. Clutton-Brock JA. Natural history of domesticated mammals, 2nd ed. Cambridge: Cambridge University Press. 1999.
8. Reig S, Daniels MJ, Macdonald DW. Craniometric differentiation within wild-living cats in Scotland using 3D morphometrics. *Journal of Zoology*. 2001; 253(01): 121–132. doi: 10.1017/S0952836901000115
9. Morris D. Cat world: A feline encyclopedia, 1st ed. Penguin Reference. 1997.
10. Röhrs M, Ebinger P. Die Beurteilung von Hirngrößenunterschieden zwischen Wild- und Haustieren. *Journal of Zoological Systematics and Evolutionary Research*. 2009; 16(1): 1–14. doi: 10.1111/j.1439-0469.1978.tb00916.x
11. Balcarcel AM, Geiger M, Clauss M, Sánchez-Villagra MR. The mammalian brain under domestication: Discovering patterns after a century of old and new analyses. *Journal of Experimental Zoology. Part B, Molecular and Developmental Evolution*. 2022; 338(8): 460–483. doi: 10.1002/jez.b.23105
12. Balcarcel AM, Sánchez-Villagra MR, Segura V, Evin A. Singular patterns of skull shape and brain size change in the domestication of South American camelids. *Journal of Mammalogy*. 2021; 102(1): 220–235. doi: 10.1093/jmammal/gyaa135
13. Klatt B. Über die Veränderung der schaedelkapazität in der domestikation. *Sitzungsbericht: Gesellschaft naturforschender Freunde*. 1912; 3: 153–179.
14. Rohrs M. Vergleichende untersuchungen an wild- und hauskatzen. *Zoologischer Anzeiger*. 1955; 155: 53–69.
15. Röhrs M, Ebinger P. Die Beurteilung von hirngrößenunterschieden zwischen wild- und haustieren. *Journal of Zoological Systematics and Evolutionary Research*. 1978; 16(1): 1–14. doi: 10.1111/j.1439-0469.1978.tb00916.x
16. Herre W, Röhrs M. Haustiere-zoologisch gesehen (Compendium of basic data). 1978.
17. Colby AE, Kimock CM, Higham JP. Endocranial volume is variable and heritable, but not related to fitness, in a free-ranging primate. *Scientific Reports*. 2021; 11(1): 1–11. doi: 10.1038/s41598-021-81265-w
18. Finarelli JA. Estimating endocranial volume from the outside of the skull in Artiodactyla. *Journal of Mammalogy*. 2011; 92(1): 200–212. doi: 10.1644/09-MAMM-A-391.1
19. Logan CJ, Clutton-Brock TH. Validating methods for estimating endocranial volume in individual red deer (*Cervus elaphus*). *Behavioural Processes*. 2013; 92: 143–146. doi: 10.1016/j.beproc.2012.10.015
20. Benson-Amram, S., Dantzer, B., Stricker, G., Swanson, E.M., Holekamp, K.E., 2016. Brain size predicts problem-solving ability in mammalian carnivores. *Proceedings of the National Academy of Sciences*. 2016; 113(9): 2532–2537. doi: 10.1073/pnas.1505913113
21. González-Lagos C, Sol D, Reader SM. Large-brained mammals live longer. *Journal of Evolutionary Biology*. 2010; 23(5): 1064–1074. doi: 10.1111/j.1420-9101.2010.01976.x
22. Sol D, Bacher S, Reader SM, Lefebvre L. Brain size predicts the success of mammal species introduced into novel environments. *American Naturalist*. 2008; 172: 63–71. doi: 10.1086/588304
23. Agnvall B, Béteky, J, Jensen P. Brain size is reduced by selection for tameness in Red Junglefowl-correlated effects in vital organs. *Scientific Reports*. 2017; 7(1): 3306. doi: 10.1038/s41598-017-03236-4
24. Finarelli JA. Estimation of endocranial volume through the use of external skull measures in the Carnivora (Mammalia). *Journal of Mammalogy*. 2006; 87(5): 1027–1036. doi: 10.1644/05-MAMM-A-430R1.1
25. Stuermer IW, Wetzel W. Early experience and domestication affect auditory discrimination learning, open field behaviour and brain size in wild Mongolian gerbils and domesticated laboratory gerbils (*Meriones unguiculatus forma domestica*). *Behavioural Brain Research*. 2006; 173(1): 11–21. doi: 10.1016/j.bbr.2006.05.025
26. Lesch R, Kitchener AC, Hantke G, Kotrschal K, Fitch WT. Cranial volume and palate length of cats, *Felis* spp., under domestication, hybridization and in wild populations. *Royal Society Open Science*. 2022; 9(1): 210477. doi: 10.1098/rsos.210477
27. Czeibert K, Sommese A, Petneházy O, Csörgő T, Kubinyi E. Digital endocasting in comparative canine brain morphology. *Frontiers in Veterinary Science*. 2020, 7: 1–13. doi: 10.3389/fvets.2020.565315
28. Falk D, Redmond JC, Guyer J, Conroy GC, Recheis W, Weber GW, Seidler H. Early hominid brain evolution: A new look at old endocasts. *Journal of Human Evolution*. 2000; 38(5): 695–717. doi: 10.1006/jhev.1999.0378
29. Kubo D, Kono RT, Saso A, Mizushima S, Suwa G. Accuracy and precision of CT-based endocranial capacity estimations: A comparison with the conventional millet seed method and application to the Minatogawa 1 skull. *Anthropological Science*. 2008; 116(1): 77–85. doi: 10.1537/ase.070502
30. Wu X, Schepartz LA. Application of computed tomography in paleoanthropological research. *Progress in Natural Science*. 2009; 19(8): 913–921. doi: 10.1016/j.pnsc.2008.10.009
31. Boistel R, Swoger J, Kržič Ů, Fernandez V, Gillet B, Reynaud EG. The future of three-dimensional microscopic imaging in marine biology. *Marine Ecology*. 2011; 32(4): 438–452. doi: 10.1111/j.1439-0485.2011.00442.x
32. Bruner E, Ogihara N, Tanabe HC. Digital endocasts. From skulls to brains, Replacement of Neanderthals by Modern Humans Series. 2018.

33. Carril J, Tambussi CP, Degrange FJ, Benitez Saldivar MJ, Picasso MJB. Comparative brain morphology of Neotropical parrots (Aves, Psittaciformes) inferred from virtual 3D endocasts. *Journal of Anatomy*. 2016; 229(2): 239–251. doi: 10.1111/joa.12325
34. Demircioğlu İ, Kocyigit A, Aydogdu S, Gezer İnce N, Yılmaz B. Calculation of the intracranial volume in gazelles (*Gazella subgutturosa*) by stereology and computed tomography. *Harran Üniversitesi Veteriner Fakültesi Dergisi*. 2021; 10(2): 178–183. doi: 10.31196/huvfd.1005996
35. Yılmaz O, Demircioğlu İ. Examination of the morphometric features and three-dimensional modelling of the skull in van cats by using computed tomographic images. *Ankara Üniversitesi Veteriner Fakültesi Dergisi*. 2021; 68(3): 213–222. doi: 10.33988/auvfd.775971
36. Ramos J, Viegas I, Pereira H, Requicha JF. Morphometrical study of the European shorthair cat skull using computed tomography. *Veterinary Sciences*. 2021; 8(8): 161. doi: 10.3390/vetsci8080161
37. Holloway RL. The Relevance of endocasts for studying primate brain evolution, In: Noback CR. Ed., *Sensory Systems of Primates*. Springer, New York, USA, 1978; 181–200.
38. Bertolini F, Gandolfi B, Kim ES, Haase B, Lyons LA, Rothschild MF. Evidence of selection signatures that shape the Persian cat breed. *Mammalian Genome*. 2016; 27(3-4): 144–155. doi: 10.1007/s00335-016-9623-1
39. Lipinski MJ, Froenicke L, Baysac KC, Billings NC, Leutenegger CM, Levy AM, Longeri M, Niini T, Ozpinar H, Slater MR, Pedersen NC, Lyons LA. The ascent of cat breeds: Genetic evaluations of breeds and worldwide random-bred populations. *Genomics*. 2008; 91(1): 12–21. doi: 10.1016/j.ygeno.2007.10.009
40. Menotti-Raymond M, David VA, Pflueger SM, Lindblad-Toh K, Wade CM, O'Brien SJ, Johnson WE. Patterns of molecular genetic variation among cat breeds. *Genomics*. 2008; 91(1): 1–11. doi: 10.1016/j.ygeno.2007.08.008
41. Salonen M, Vapalahti K, Tiira K, Mäki-Tanila A, Lohi H. Breed differences of heritable behaviour traits in cats. *Scientific Reports*. 2019; 9(1): 1–10. doi: 10.1038/s41598-019-44324-x
42. Gandolfi B, Alamri S, Darby WG, Adhikari B, Lattimer JC, Malik R, Wade CM, Lyons LA, Cheng J, Bateman JF, McIntyre P, Lamandé SR, Haase B. A dominant TRPV4 variant underlies osteochondrodysplasia in Scottish fold cats. *Osteoarthritis Cartilage*. 2016; 24(8): 1441–1450. doi: 10.1016/j.joca.2016.03.019
43. Sokal RR, Rohlf FJ. *Biometry: The principles and practice of statistic in biological research*. W.H. Freeman, New York, USA; 1995.
44. Dane S, Tan U. Relation of brain weight to body weight in cats to sex and paw preferences: Anomalous results in left-preferent cats. *International Journal of Neuroscience*. 1991; 62(1-2): 75–80. doi: 10.3109/00207459108999759
45. Balcarcel AM, Sánchez-Villagra MR, Segura V, Evin A. Singular patterns of skull shape and brain size change in the domestication of South American camelids. *Journal of Mammalogy*. 2021; 102(1): 220–235. doi: 10.1093/jmammal/gyaa135
46. Balcarcel AM, Veitschegger K, Clauss M, Sánchez-Villagra MR. Intensive human contact correlates with smaller brains: Differential brain size reduction in cattle types. *Proceedings of the Royal Society B: Biological Sciences*. 2021; 288(1952): 20210813. doi: 10.1098/rspb.2021.0813
47. Kruska D. Volumenvergleich optischer Hirnzentren bei Wild- und Hausschweinen. *Zeitschrift Fur Anatomie Und Entwicklungsgeschichte*. 2004; 138: 265–282.
48. Röhrs M, Ebinger P. Die beurteilung von hirngrößenunterschieden zwischen wild- und haustieren. *Journal of Zoological Systematics and Evolutionary Research*. 1978; 16(1): 1–14. doi: 10.1111/j.1439-0469.1978.tb00916.x
49. Kruska D. Vergleichend cytoarchitektonische untersuchungen an gehirnen von wild- und hausschweinen. *Anatomy and Embriology*. 1970; 131, 291–324.
50. Ebinger P. A cytoarchitectonic volumetric comparison of the area gigantopyramidalis in wild and domestic sheep. *Anatomy and Embryology*. 1975; 147(2): 167–175. doi: 10.1007/BF00306731
51. Yamaguchi N, Kitchener AC, Gilissen E, MacDonald DW. Brain size of the lion (*Panthera leo*) and the tiger (*P. tigris*): Implications for intrageneric phylogeny, intraspecific differences and the effects of captivity. *Biological Journal of the Linnean Society*. 2009; 98(1): 85–93. doi: 10.1111/j.1095-8312.2009.01249.x
52. Isler K, Christopher Kirk E, Miller JMA, Albrecht GA, Gelvin BR, Martin RD. Endocranial volumes of primate species: scaling analyses using a comprehensive and reliable data set. *Journal of Human Evolution*. 2008; 55(6): 967–978. doi: 10.1016/j.jhevol.2008.08.004
53. Turschwell MP, White CR. The effects of laboratory housing and spatial enrichment on brain size and metabolic rate in the eastern mosquitofish, *Gambusia Holbrooki*. *Biology Open*. 2016; 5(3):205-210. doi: 10.1242/bio.015024
54. Welniak-Kaminska M, Fiedorowicz M, Orzel J, Bogorodzki P, Modlinska K, Stryjek R, Chrzanowska A, Pisula W, Grieb P. Volumes of brain structures in captive wild-type and laboratory rats: 7T magnetic resonance *in vivo* automatic atlas-based study. *PLoS One*. 2019; 14(4): e0215348. doi: 10.1371/journal.pone.0215348
55. Cardini A, Elton S. Sample size and sampling error in geometric morphometric studies of size and shape. *Zoomorphology*. 2007; 126(2): 121–134. doi: 10.1007/s00435-007-0036-2
56. Schmidt MJ, Kampschulte M, Enderlein S, Gorgas D, Lang J, Ludewig E, Fischer A, Meyer-Lindenberg A, Schaubmar AR, Failing K, Ondreka N. The relationship between brachycephalic head features in modern Persian cats and dysmorphologies of the skull and internal hydrocephalus. *Journal of Veterinary Internal Medicine*. 2017; 31(5): 1487–1501. doi: 10.1111/jvim.1480