

Review of Digitized endocasts and brains: measurements and analyses of the evolution of 172 fossil and extant vertebrate specimens

Thank you so much for giving me the opportunity to review this manuscript. Thank you to the authors for this incredible amount of work of digitizing all of these natural endocasts as well as braincasts. I, myself used some of them as data point in my analyses but knowing that they are now available in 3D and not just as illustrations is unvaluable. Now, all of these specimens will be preserved forever and not suffer from the degradation of time. The manuscript is well-written, and the supporting document includes a lot of important details about each natural endocast or braincast. The statistic treatment of the data is simple but done appropriately. I commend the authors for all the work on measuring the size of different areas of brain on so many endocasts. Overall, this is a great addition to the field of Paleoneurology. Below are my comments to improve this manuscript. I recognize that it's quite long, I usually do quite detailed reviews and it's not specific to this paper. These are all suggestions that I believe could enhancing this paper.

I completely understand that the authors wanted to use the same methods as originally used for previous studies by the first author and this is a work compilation of many years. The analyses are statistically sound even if other more recent methods could be used. Other papers are indeed in the making with more advance methodologies and I understand that it is not the primary goal of this paper.

That being said, I would suggest the authors to cite the work using virtual endocasts that has been produced during the last decade. A lot of virtual endocasts have been produced for fossil rodents, primates, plesiadapiforms, artiodactyles, condylarthrs, elephants, bats, ect... and hypotheses about encephalization and neocorticalization have been proposed. The reader might wonder why they were not added to these analyses so you should explain why.

Some examples:

- Benoit J, Legendre LJ, Tabuce R, Obada T, Maraescul V, Manger P (2019) Brain evolution in Proboscidea (Mammalia, Afrotheria) across the Cenozoic. *Sci Rep*, 9, 9323.
- Bertrand OC, Amador-Mughal F, Lang MM, Silcox MT (2019) New Virtual Endocasts of Eocene Ischyromyidae and Their Relevance in Evaluating Neurological Changes Occurring Through Time in Rodentia. *J. Mamm. Evol.*, 26, 345-371.
- Bertrand OC, Shelley SL, Wible JR, et al. (2020) Virtual endocranial and inner ear endocasts of the Paleocene 'condylarth' *Chriacus*: new insight into the neurosensory system and evolution of early placental mammals. *J. Anat.*, 236, 21-49.
- Harrington AR, Silcox MT, Yapuncich GS, Boyer DM, Bloch JI (2016) First virtual endocasts of adapiform primates. *J Hum Evol*, 99, 52-78.
- Maugoust J, Orliac MJ (2021) Endocranial Cast Anatomy of the Extinct Hipposiderid Bats *Palaeophyllophora* and *Hipposideros (Pseudorhinolophus)* (Mammalia: Chiroptera). *J. Mamm. Evol.*
- Orliac MJ, Gilissen E (2012) Virtual endocranial cast of earliest Eocene *Diacodexis* (Artiodactyla, Mammalia) and morphological diversity of early artiodactyl brains. *Proc. R. Soc. B*, 279, 3670-3677.

Rowe TB, Macrini TE, Luo ZX (2011) Fossil evidence on origin of the mammalian brain. *Science*, **332**, 955-7.

Silcox MT, Benham AE, Bloch JI (2010) Endocasts of *Microsyops* (Microsyopidae, Primates) and the evolution of the brain in primitive primates. *J Hum Evol*, **58**, 505-21.

Recent papers also have look at relative brain size through time in mammals and in birds. These studies should be cited. Tsuboi et al. (2018) don't have any fossils but use them as calibration points.

Ksepka DT, Balanoff AM, Smith NA, et al. (2020) Tempo and Pattern of Avian Brain Size Evolution. *Current Biology*, **30**, 2026-2036.e3.

Smaers JB, Rothman RS, Hudson DR, et al. (2021) The evolution of mammalian brain size. *Science Advances*, **7**, eabe2101.

Tsuboi M, van der Bijl W, Kopperud BT, et al. (2018) Breakdown of brain-body allometry and the encephalization of birds and mammals. *Nat. Ecol. Evol.*, **2**, 1492-1500.

1) The introduction is nicely written; I particularly enjoyed the fact that Tilly Edinger is cited in the second sentence of the paper. I really appreciate the respect that the authors give her in their article. However, I would suggest making it a bit longer and include a bigger background about what has been done with virtual endocasts of mammals (see examples of citations above) and studies that have look at brain evolution through time. The analyses of the paper can stay the same, but you should acknowledge the work of others who have worked on brain evolution.

2) The study from Jerison (1973) is an amazing contribution to Paleoneurology and to Science in general in which many hypotheses about brain evolution still hold true today as this paper shows with the addition of new data. However, there has been work done since then and the original encephalization quotient did not include small mammals such as rodents and bats. There is a bias because of inadequate sampling and the intercept is too high for small mammals. Rodents are the most speciose mammal today, so making generalization about mammalian brain evolution without including this group is a bit of an issue but I understand if they cannot be added. However, the authors should say that this is a limitation of the study. Other studies have incorporated smaller mammals in their EQ equation (Eisenberg, 1981) but in this case the slope is too high, overestimating the EQ of small species. There is even an equation for rodents that was made by Pilleri (1984) showing that rodents have a different brain to body relationship compared to the rest of mammals. Burger et al. (2019) produced different EQ equations for many mammalian groups. These equations do not have to be used here but should be cited in the introduction or need to be mentioned in the discussion for the limitation of the study.

Burger JR, George MA, Jr., Leadbetter C, Shaikh F (2019) The allometry of brain size in mammals. *J. Mammal.*, **100**, 276-283.

Eisenberg JF (1981) *The mammalian radiations: an analysis of trends in evolution, adaptation, and behaviour*, University of Chicago Press, Chicago.

Pilleri G, Gahr M, Kraus C (1984) *Cephalization in rodents with particular reference to the Canadian beaver (Castor canadensis)*, Institute of Brain Anatomy, Berne.

3) The method incorporates a lot of details about the scanner that was used, and the statistical section is robust. However, I would suggest adding some details about how the neocortical and olfactory bulb surface area were obtained. Was it using the same software as the one used for obtaining the total endocranial surface? What tools were used? Also make sure that appropriate references for the method are cited.

4) I am impressed by the number of endocasts that was digitized for this study. I have noticed some small omissions. Maybe the authors were not aware of them, so I just wanted to suggest adding a sentence or two about their existence. One natural endocast of a fossil rodent from the Oligocene, Orellan, *Ischyromys typus*, AMNH 12252 has been digitized. There are also published natural endocasts of *Adelomys vaillanti*, also *Trechomys bonduelli* and *Trogontherium* all from France (Dechaseaux, 1958). Please add a note in the text that rodent natural endocasts exist but they have not been included here and say why.

Bertrand OC, Silcox MT (2016) First virtual endocasts of a fossil rodent: *Ischyromys typus* (Ischyromyidae, Oligocene) and brain evolution in rodents. *J. Vertebr. Paleontol.* 36.
Dechaseaux C (1958) Encéphales de Simplicidentés fossiles. In *Traité de paléontologie: L'origine des mammifères et les aspects fondamentaux de leur évolution*. 2. v (ed Piveteau J), pp. 819-821. Masson.

5) I appreciate the details in the supporting document on how the body mass was calculated and how the age was determined by specifying the locality where the specimens were found for some specimens. But for some, it is not clear how body mass and age were determined. Also, I have noticed that there is almost never a reference for the age in the supporting document. The geological time scale has been reviewed recently (2012). Did the authors check that the ages were accurate related to Gradstein et al. (2012)? Also, there is not systematically a reference for the body mass of each specimen. Was the same method to determine body mass used for all specimens? Please specify so the readers know specifically how they were obtained.

Gradstein FM, Ogg JG, Schmitz MD, Ogg GM (2012) *Geologic Time Scale 2012*, Elsevier Science.

6) I commend the authors for illustrating so many natural endocasts and braincasts. The quality of the images is good, and I appreciate that the authors have included a lateral and dorsal views for most of the specimens. However, the figures should be labelled or at least one specimen per figure. We should at least have the olfactory bulb, neocortex, paleocortex, cerebellum, braincase labelled. It would be good to have the delimitation of the neocortex for each specimen that is pictured. It can be hard for some of them to see when the delimitation would actually be. There is also no scale bar on any of the figures. Please add them so we know the size of the endocasts.

7) Some of the endocasts are only halves, which is of course completely fine, but it should be specified in the method how the endocranial volume/brain size and regions were obtained. I suppose that only the ones that have a half were doubled for the brain, neocortex, and olfactory bulb size but this should be specified.

8) The discussion is very interesting and raise very great points about brain evolution, but I would suggest adding more comparison with the work that has been published in last decades about brain evolution in mammals, birds and vertebrates in general.

9) Please be sure to provide access to all of these wonderful natural endocasts and braincasts that were digitized for this study. It is crucial for reproducibility.

Please check additional comments in the manuscript and supporting PDFs for additional suggestions.

Detailed comments:

Lines 16-25: The abstract is a bit short and more details about what was done would improve it. Could you also explicitly write that they are all natural endocasts and braincast?

Line 18: “were quantified” What exactly was quantified? The endocranial volume, the volume of the olfactory bulbs, the surface of the neocortex? Please specify

Lines 20-26: The encephalization was obtained for the sample but the results are not discussed in the abstract. Please add a few lines about the results from the study of how relative brain size vary in the sample.

Lines 29-30: “cranial endocasts ... plaster or latex” This statement is incomplete, please add the third type “virtual endocast” obtained after a skull has been CT scanned and the endocast has been virtually segmented in a 3D treatment software.

Line 42-46: “The cerebral cortex ... surface area.” This section needs at least one reference.

Line 51-53: “However... vertebrates” This sentence requires references.

Line 58-59: “endocast’s virtual image” and “three-dimensional (3D) images” Could the authors specify that they are referring to “natural endocasts” that have surface scanned/digitized to avoid confusion with virtual endocasts.

Line 66-67: Thank you to the authors for providing 2D images of these unpublished endocasts but the authors should also make the 3D models available in an online repository such as Morphosource. It’s especially important for the reproducibility of the different analyses presented in this paper.

Line 76-77: See comment above. Please make sure that these data are made available. Here the authors could had a comment saying that the digitized endocasts will be made available.

Line 81: “The majority of endocasts” please change to “The majority of natural and ?latex endocasts” so there is no confusion.

Line 108-110: Thank you to the authors for providing so many details about the digitization. Please add that this is “surface scanning” so it’s clear to the reader that there was not “CT scanning”.

Line 117-118: “Surface regions ... by hand” I’m not sure that I understand what the authors mean here by “annotated” Where these regions measured, quantified or just pointed out? Please add details about how the brain regions were estimated.

Lines 124-125: “The rhinal fissure ... ventrally” Please add a reference for this sentence.

Figure 1, part of Fig. 31 and Fig S3B: From what I can read, the authors are not allowed to publish the images from <http://neuroscielibrary.org/index.html>. Please make sure that you take them out.

From the website: “For users who are interested in using any of our images for educational or research purposes, you have our permission to use them. **But, they are not to be published and copyrighted since this would prohibit others from using the same images.** At any rate, we request that you identify them as from the University of Wisconsin and Michigan State Comparative Mammalian Brain Collections, as well as from those at the National Museum of Health and Medicine. Also, we request that you refer to the Web Site where you obtained them, as well as the fact that preparation of all these images and specimens have been funded by the National Science Foundation, as well as by the National Institutes of Health.”

Line 147-148: “For extant species ... size graphed” Did the authors applied a correction on brain size to make sure that the comparisons were consistent with endocranial volume? Please see Stephan et al (1981) who multiple endocranial volumes in cm³ by 1.036 to obtain the value in grams.

Stephan H, Frahm H, Baron G (1981) New and Revised Data on Volumes of Brain Structures in Insectivores and Primates. *Folia Primatologica*, 35, 1-29.

Figure 3B: The green line used to measure the length of the endocast does not appear to represent the maximum length of the of endocast (not at the tip of the olfactory bulbs and it ends at the level of the lateral lobes of the cerebellum instead of the vermis). Could you specify why this is considered the length of the endocast? Also, there is no “measurement marks” in Fig. 3C.

Figure 4D: There is a caption about it, but the photograph is not present in the figure. Please take the caption out or add the missing image.

Figure 6C: The lateral view of the endocast of *Barylambda* appears shorter than the dorsal view. It looks like a part is missing. Could you check the image and make sure that there is no error?

Figure 31: Please add letters to the caption of this figure that match the letters for each section of the figure.

Figure 37: Please change numbers to letters in the caption to match the letters in the figure.

Lines 251-254: I understand that La Brea specimens are fossils, but they are so close in time to the extant dataset. The difference between these fossils and the extant taxa is extremely small compared to specimens dated from the Oligocene (30 Ma) for instance. I would suggest taking the 0.01-0.03 Ma specimens out of the analysis that is supposed to test for biases. Right now, both graphs look identical. The rationale behind making two graphs should also be integrated in the text.

Lines 260-262: This needs a reference.

Figure 40: Graph (B) “155 scanned mammals” do those only include extant or also fossils? Please specify.

Lines 273-275: “Electric fish ... fish polygone” Is this observation can be seen in the graph presented in this paper? If not, please add a reference for this sentence.

Lines 357-359: How do your results compared to other studies such as Long et al. (2015)?

[Long A, Bloch JJ, Silcox MT \(2015\) Quantification of neocortical ratios in stem primates. *Amer J Phys Anthropol*, 157, 363-73.](#)

Line 363: Reference is needed for these sentences.

Lines 366-373: References are needed here or is this a conclusion from the present analysis?

Lines 374-375: For this sentence, please clarify that it's based on the analyses conducted in this paper and that's why you are able to make this statement.

Lines 385-388: References are needed here.

Lines 436-438: Reference here would be good.

Lines 460-461: That's correct but the last ten years studies using virtual endocasts have also been doing that and have to be acknowledged.

Table 1: *Leptictis* is not a rodent. What reference was used? The literature would not classify as a member of this group. To be fair, it's not clear where it belongs but it definitely lacks features present in all rodents.

Yours Sincerely,
Ornella Bertrand

Digitized endocasts and brains: measurements and analyses of the evolution of 172 fossil and extant vertebrate specimens (#61251)

1

First submission

Guidance from your Editor

Please submit by **28 Sep 2021** for the benefit of the authors (and your \$200 publishing discount) .



Structure and Criteria

Please read the 'Structure and Criteria' page for general guidance.



Raw data check

Review the raw data.



Image check

Check that figures and images have not been inappropriately manipulated.

Privacy reminder: If uploading an annotated PDF, remove identifiable information to remain anonymous.

Files

Download and review all files from the [materials page](#).

42 Figure file(s)

2 Table file(s)

1 Other file(s)



Structure and Criteria

Structure your review

The review form is divided into 5 sections. Please consider these when composing your review:

1. BASIC REPORTING
2. EXPERIMENTAL DESIGN
3. VALIDITY OF THE FINDINGS
4. General comments
5. Confidential notes to the editor

 You can also annotate this PDF and upload it as part of your review

When ready [submit online](#).

Editorial Criteria

Use these criteria points to structure your review. The full detailed editorial criteria is on your [guidance page](#).

BASIC REPORTING

-  Clear, unambiguous, professional English language used throughout.
-  Intro & background to show context. Literature well referenced & relevant.
-  Structure conforms to [PeerJ standards](#), discipline norm, or improved for clarity.
-  Figures are relevant, high quality, well labelled & described.
-  Raw data supplied (see [PeerJ policy](#)).

EXPERIMENTAL DESIGN

-  Original primary research within [Scope of the journal](#).
-  Research question well defined, relevant & meaningful. It is stated how the research fills an identified knowledge gap.
-  Rigorous investigation performed to a high technical & ethical standard.
-  Methods described with sufficient detail & information to replicate.

VALIDITY OF THE FINDINGS

-  Impact and novelty not assessed. *Meaningful* replication encouraged where rationale & benefit to literature is clearly stated.
-  All underlying data have been provided; they are robust, statistically sound, & controlled.
-  Conclusions are well stated, linked to original research question & limited to supporting results.



The best reviewers use these techniques

Tip

Example

Support criticisms with evidence from the text or from other sources

Smith et al (J of Methodology, 2005, V3, pp 123) have shown that the analysis you use in Lines 241-250 is not the most appropriate for this situation. Please explain why you used this method.

Give specific suggestions on how to improve the manuscript

Your introduction needs more detail. I suggest that you improve the description at lines 57- 86 to provide more justification for your study (specifically, you should expand upon the knowledge gap being filled).

Comment on language and grammar issues

The English language should be improved to ensure that an international audience can clearly understand your text. Some examples where the language could be improved include lines 23, 77, 121, 128 – the current phrasing makes comprehension difficult. I suggest you have a colleague who is proficient in English and familiar with the subject matter review your manuscript, or contact a professional editing service.

Organize by importance of the issues, and number your points

1. Your most important issue
2. The next most important item
3. ...
4. The least important points

Please provide constructive criticism, and avoid personal opinions

I thank you for providing the raw data, however your supplemental files need more descriptive metadata identifiers to be useful to future readers. Although your results are compelling, the data analysis should be improved in the following ways: AA, BB, CC

Comment on strengths (as well as weaknesses) of the manuscript

I commend the authors for their extensive data set, compiled over many years of detailed fieldwork. In addition, the manuscript is clearly written in professional, unambiguous language. If there is a weakness, it is in the statistical analysis (as I have noted above) which should be improved upon before Acceptance.

Digitized endocasts and brains: measurements and analyses of the evolution of 172 fossil and extant vertebrate specimens

Harry J. Jerison^{Corresp., 1}, Catherine M. Early², Andrew A Farke³, Ashley C. Morhardt^{Corresp. 4}

¹ Department of Psychiatry and Biobehavioral Sciences, University of California, Los Angeles, Los Angeles, California, United States of America

² Biology Department, Science Museum of Minnesota, Saint Paul, Minnesota, United States of America

³ Raymond M. Alf Museum of Paleontology, Claremont, California, United States of America

⁴ Department of Neuroscience, Washington University School of Medicine in St. Louis, St. Louis, Missouri, United States of America

Corresponding Authors: Harry J. Jerison, Ashley C. Morhardt
Email address: hjerison@ucla.edu, amorhardt@wustl.edu

This article records brain evolution in vertebrates using 172 digitized endocasts of extinct and extant species spanning 60 million years. Three-dimensional (3D) images of 126 fossil endocasts, including Cenozoic mammals, Bathygenys, and dinosaurs, were quantified and compared with the endocasts and brains of extant species. Encephalization quotients and neocorticalization were calculated from digitized endocasts. On average, mammals became increasingly neocorticalized over time, increasing at an average of about 5% additional neocortex per 10 million years. About 60 million years ago, mammalian neocorticalization averaged about 20%, increasing to a present average of 50%, and reaching a maximum of about 80% in primates within the past 10 million years. These data redefine the allometric boundary between mammals and reptiles and confirm that measurements on a single species adequately represent the brains of the entire species.

1 Digitized Endocasts and Brains: Measurements and 2 Analyses of the Evolution of 172 Fossil and Extant 3 Vertebrate Specimens

4 Harry J. Jerison¹, Catherine Early², Andrew A. Farke³, Ashley C. Morhardt⁴

5

6 ¹Department of Psychiatry and Biobehavioral Sciences, University of California
7 Los Angeles, Los Angeles, California, United States of America;

8 ²Biology Department, Science Museum of Minnesota, Saint Paul, Minnesota,
9 United States of America;

10 ³Raymond M. Alf Museum of Paleontology at The Webb Schools, Claremont,
11 California, United States of America;

12 ⁴Department of Neuroscience, Washington University School of Medicine in St.
13 Louis, St. Louis, Missouri, United States of America
14 **Corresponding author:** Harry J. Jerison; hjerison@ucla.edu

Abstract

This article records brain evolution in vertebrates using 172 digitized endocasts of extinct and extant species spanning 60 million years. Three-dimensional (3D) images of 126 fossil endocasts, including Cenozoic mammals, *Bathysenys*, and dinosaurs, were quantified and compared with the endocasts and brains of extant species. Encephalization quotients and neocorticalization were calculated from digitized endocasts. On average, mammals became increasingly neocorticalized over time, increasing at an average of about 5% additional neocortex per 10 million years. About 60 million years ago, mammalian neocorticalization averaged about 20%, increasing to a present average of 50%, and reaching a maximum of about 80% in primates within the past 10 million years. These data redefine the allometric boundary between mammals and reptiles and confirm that measurements on a single species adequately represent the brains of the entire species.

Introduction

Cranial endocasts are casts molded by the endocranial cavity of the skull, either naturally through fossilization of interred material or artificially with materials such as plaster or latex. Endocasts provide a powerful window into deep time for studying neuroanatomy and brain evolution. Tilly Edinger, the founder of paleoneurology, described endocasts as *fossilen Gehirne* (Edinger 1929), or “fossil brains,” and by the time of her death in 1967, she had compiled a then-comprehensive annotated bibliography of over a thousand vertebrate fossil genera and their cranial cavity endocasts (Edinger 2012).

Bird and mammal endocasts largely mirror brains in size and appearance, although the narrow space around a brain containing meninges, blood vessels, and cerebrospinal fluid add to the surface area and volume of an endocast compared to a brain. Yet, endocasts have been regularly shown to be generally faithful proxies for brain size, especially in extant, adult animal groups such as mammals (Haight and Nelson 1987; DeMiguel and Henneberg 2001) and birds (e.g., Iwaniuk and Nelson 2002, Watanabe et al. 2019).

The cerebral cortex is an outer layer of forebrain consisting of layers of nerve cells. This layered organization of cells is a unique feature of the brain in all living mammals and in no other living vertebrates. Neocorticalization, or the comparative increase in neocortex relative to other brain structures, is quantifiable as the increase in surface area of cerebral cortex dorsal to the rhinal fissure relative to the total cortical surface area. Encephalization, the evolutionary increase in brain complexity or relative size reflecting environmental adaptations, is a general phenomenon in many species of mammals and birds more or less independent of their phylogenetic details (Jerison 1973). Brain–body allometry has for over a century explained a large fraction of brain size variation across vertebrates (Snell 1892), a pattern typically explained by physiological scaling (Jerison 1973) and developmental constraints (Gould 1975). However, many birds and mammals have evolved a substantially larger brain for a given body size, or larger encephalization, compared to other vertebrates.

The measurement of neocorticalization evolution is an outstanding example of a quantitative analysis made possible by digitizing data. Endocast volumes were traditionally measured using Archimedes’ method, i.e., the loss of weight when endocasts were immersed in water, but this approach introduced error due to water uptake by the endocast plaster or matrix. Digital scanning and software analysis enable direct measurements from an endocast’s virtual image. This study exploited digitization technology to review 126 three-dimensional (3D) images of fossil endocasts and compare them with the endocasts and brains of 41 extant specimens. In

doing so, this study not only describes the evolution of neocorticalization over 60 million years but further refines interclass allometric boundaries.

Although components of the dataset have been presented in other venues (e.g., Long et al., 2015, using data provided by Jerison), this is the most comprehensive collection to date. Equally importantly, we provide figures for many of the endocasts, many of which have not been previously illustrated in the literature. It is hoped that these illustrations will be a useful resource for future work on endocranial anatomy.

Lastly, we are aware of relatively recent and wide-spread leaps in the statistical calculation and determination of evolutionary trends collectively known as phylogenetic comparative methods (PCM); e.g., Harmon 2019; Adams and Collyer 2019). We are also aware that many of these methods are appropriate for application to studies of brain (or brain region) vs. body size in vertebrates (e.g., see review in Striedter and Northcutt 2019). The use of these methods provides rich and potentially more nuanced and/or more accurate analysis of datasets such as the one presented in our paper. However, because this paper serves as the culmination of decades of work by our lead author, we have elected to present methods consistent with his previous studies for the sake of comparison. We eagerly anticipate that future work will incorporate all or parts of the dataset into more advanced and sophisticated analyses.

Materials and Methods

Endocast specimens

The majority of endocasts were obtained from the Radinsky Collection at the Field Museum of Natural History (FMNH) in Chicago, most of which were collected and prepared by the late Professor Len Radinsky and catalogued by Collections Manager William Simpson. Other

endocasts were scanned from specimens in the following collections: University of Adelaide (Adelaide), Victoria, Australia; American Museum of Natural History (AMNH), New York; American Museum of Natural History (AMNH FAM) - Frick Collection at AMNH; British Natural History Museum (NHMUK), London; Carnegie Museum of Natural History (CM), Pittsburgh, Pennsylvania; Comparative Mammalian Brain Collection (WISC), Madison, Wisconsin; Falk Collection (Falk), now deposited with Mammals at AMNH; Jura-Museums Eichstaett (JME), Germany; Los Angeles County Natural History Museum (LACM), California; The Museum of Comparative Zoology (MCZ) at Harvard University, Cambridge, Massachusetts; Muséum National d'Histoire Naturelle (MNHN), Paris; Museum of Paleontology at UC Berkeley (UCB), California; Museum of the Rockies (MOR), Bozeman, Montana; National Museum of Victoria (NMV), Melbourne, Australia; National Museums of Canada (NMC), Ottawa; Raymond M. Alf Museum of Paleontology at the Webb Schools (RAM), Claremont, California; Senckenberg Natural History Museum (SNHM), Frankfurt, Germany; Texas Memorial Museum (UT) and (TMM), Austin, Texas; United States National Museum (USNM), Washington, DC; University of the Witwatersrand (WITS), Johannesburg, South Africa; and Yale Peabody Museum (YPM), New Haven, Connecticut.

Most endocasts were from fossilized mammals, but some endocasts and braincasts were from living species and four were from dinosaurs for mammal-reptile boundary analysis. Non-fossilized endocasts were prepared using plaster or latex. All endocasts were molded by the cranial cavity, with little difference between endocasts prepared with plaster or latex from a cranial cavity or filled with fossilized matrix preserved when the skull eroded.

Digitization

Endocasts were digitized by the first author, scanning with a Cyberware Model 15 Scanner using headus 3D Tools software (<http://www.headus.com.au>), which creates endocast images as headus PLY files. headus rotates the base through 45° steps, scanning at each step, with a complete 360° rotation producing a full scan. After performing a first set of scans, the object was placed in a different orientation to expose areas previously hidden from the laser beam before acquiring a further set of scans. The final set of 16 scans was merged into a 3D digitized image.

headus outputs the following image measurements: volume in mm³, surface area in mm², and length in mm. Endocast lengths were measured from the anterior tip of the forebrain or olfactory bulbs to the posterior hindbrain at the end of the medulla. Surface regions of the endocast, such as olfactory bulbs or neocortex, were annotated by hand. Measurements were recorded in centimeter-gram-seconds (cgs) unless otherwise noted.

Neocorticalization

Unlike other gyri and sulci, endocast rhinal fissures are a reliable landmark of the ventral boundary of neocortex. Except in cetaceans, it is a superficial landmark that is visible on the brains of living mammals (Welker 1990). The rhinal fissure differentiates neocortex dorsally from paleocortex ventrally. Measurements of the surface area of forebrain dorsal to the rhinal fissure were defined as neocortex (see example, Fig. 1).

Brain-body allometry

Brain-body allometry relates endocast volume (representing brain size) to estimated body size. Brain-body allometry was conducted using head and body length as an independent variable and brain size as the dependent variable, as described previously (Jerison 1973; Jerison 1991; Jerison 2001; Jerison 2002). Briefly, the power function for the regression of body size relative to body length, which reflects a surface area (the skin) for mapping the brain, was as in (Jerison 1973):

$$P = 0.021 L^{3.03} \quad (1)$$

where P is body weight or volume, and L is body length in the cgs system. In a few species in which accurate models of the body were prepared, body volume was determined from 3D scans of the model.

Brain-body size relationships in different species measured logarithmically were then fitted by linear regression:

$$\log E = \alpha \log P + \log b \quad (2)$$

or the power function:

$$E = b P^\alpha \quad (2a)$$

where E is brain size (from the French, *encephale*); P is body size (from the French, *poids*); α is the regression line's slope, and $\log b$ is its y intercept. E and P were in the same units (ml and grams or liters and kilograms) in Eq. 2 for easy interpretation.

For extant species, the brains and bodies of species were weighed or the volumes determined and the data of log brain size as a function of log body size graphed. Bivariate statistical regression analysis of the log brain-body relationship for vertebrate classes can be used to estimate α empirically. The empirical encephalization quotient (EQ) in brain size in each species is its residual from the regression, but EQ can be different if the allometric factor is

determined by theoretical analysis rather than regression. Therefore, EQ was taken as the residual relative to Eq. 2 or 2a, with α a theoretical constant of exactly $2/3$. In this way, the allometric equation transforms the 3D information of the body into a 2D map created by the brain (Jerison 2001; Jerison 2002).

Results

Assessing neocorticalization and encephalization over 60 million years using endocasts

Complete summary data on the digitized scans of endocasts and brains are shown in **Table 1**. A complete description of endocast provenance, endocast features, and body size determinations are presented in the **Supplementary Results**. The digitized endocast images are presented below.

Edinger's Early Horses

To illustrate the use of endocasts in modeling neocorticalization and encephalization, the endocasts of Edinger's horses (Edinger 1948), photographs of which have frequently been used to illustrate progressive brain evolution (MacFadden 1994; Simpson 1951), are first presented. **Figure 2** shows scans of endocasts of five of Edinger's species and adds *Hyracotherium* (FMNH PM 59207=AMNH 55268; Edinger's "*Eohippus*" (YPM 11694) from (Radinsky 1976). The digitized models of the bodies presented in **Figs. 3 and 4** are scans of careful sculptures by Gidley (1927), from which the length, surface area, and volume were determined.

The endocast of *Mesohippus* (**Fig. 4A**) was larger, more encephalized, and much more convoluted than that of *Hyracotherium* (**Fig. 3A**). However, at its anterior border, the rhinal

fissure of *Hyracotherium* is a dark line in **Fig. 3A**, with the forebrain surface area dorsal to this line being neocortical. **Figure 5** shows the remainder of the endocasts of Edinger's equoid genera: three fossil genera and three recent genera, including a zebra and two domesticated horses (a pony and a draft horse, reflecting body size variations within the domesticated species).

Paleocene Fossils

The earliest digitized mammalian endocasts presented here are of the very large and heavy late Paleocene *Titanoides* and *Barylambda* and the smaller *Arctocyon*, with the Paleocene sampled, here defined as about 60 Ma to 56 Ma and the Paleocene-Eocene boundary being somewhat artificial; the *Phenacodus* specimen is an individual that had survived into the early Eocene, but which should be representative of Paleocene members of the genus. These species are shown in **Fig. 6**.

Early Eocene Fossils

The Early Eocene dates used here are from 56 Ma to 42 Ma, and the endocasts of *Coryphodon*, *Palaeosyops*, *Heptodon*, and *Isectolophus* are shown in **Fig. 7**; Edinger's Eocene "*Eohippus*" and *Hyracotherium* are shown in **Figs. 2 and 3**; *Hyrachyus*, *Orthocynodon* ("*Amyrnodon*"), *Amyrnodon*, and *Eomoropus* are shown in **Fig. 8**; *Mesatirhinus junius*, *Mesatirhinus petersoni*, *Pachyaena*, and *Mesonyx* are shown in **Fig. 9**; and *Smilodectes* and *Notharctus* are shown in **Fig. 10A and B**.

Later Eocene Fossils

Here, "Later Eocene" is 42 Ma to 34 Ma. The endocast images of *Necrolemur* and *Adapis* are shown in **Fig. 10**; *Uintatherium*, *Menodus* (*Titanotherium*), *Moeritherium*, and *Arsinotherium* in

Fig. 11; *Pterodon*, *Cynodictis*, *Cynohyaenodon*, and *Procynodictis* in **Fig. 12**; *Cebochoerus*,
Hylomeryx, *Mixtotherium*, and *Chadronia* in **Fig. 13**; and *Anoplotherium*, *Patriomanis*,
Poebrotherium, and *Bathygenys* in **Fig. 14**.

Oligocene Fossils

The “Oligocene” samples are dated from 34 Ma to 23 Ma. These dates anchor the analysis of
neocorticalization as changes with the passage of time. *Daphoenus*, *Dinictis*, *Eusmilus*, and
Hoplophoneus are shown in **Fig. 15**; *Merycoidodon*, *Meshippus*, *Promerycochoerus*, and
Hesperocyon in **Fig. 16**; *Leptictis* (*Ictops*), *Leptauchenia*, *Halitherium*, and *Hapalops* in **Fig. 17**;
Leontinia, *Rhynchippus*, *Archaeotherium*, and *Promartes* in **Fig. 18**; and *Mesocyon* in **Fig. 19A**.

Mio-Pliocene Fossils

This group is dated from 23 Ma to mid-Pliocene, about 3 Ma. Although the earliest hominins
could have been included here, they are reviewed with later Plio-Pleistocene and recent primates.
Mustelictis, *Leptocyon*, and *Eporeodon* are shown in **Fig. 19**; *Enaliarctos*, *Potamotherium*,
Plesiogale, and *Zodiolestes* in **Fig. 20**; *Desmathyus* (*Hesperhyus*), *Oxydactylus*,
Homalodotherium, and *Borhyaena* in **Fig. 21**; *Protypotherium*, *Proterotherium*, *Nesodon*, and
Merycochoerus in **Fig. 22**; *Adinotherium*, *Merychippus* (*Atavahippus*), *Plionictis*, and
Pseudaelurus in **Fig. 23**; *Paracynarctus*, *Ustatochoerus*, *Carpocyon* (“*Osteoborus*”), and
Pseudhipparion in **Fig. 24**; *Paratomarctus*, *Hemicyon*, *Pseudotypotherium*, and *Tyopotheriopsis*
in **Fig. 25**; and *Cormohipparion*, *Procamelus*, *Homotherium*, and *Myiodon* in **Fig. 26**.

Plio-Pleistocene and Recent Fossils

Glossotherium, *Arctodus*, *Canis dirus*, and *Megalonyx* are shown in **Fig. 27**; *Nothrotheriops*, *Panthera*, *Smilodon*, and *Urocyon* are shown in **Fig. 28**; *Platygonus*, *Sthenurus*, *Thylacoleo*, and *Archaeolemur* are shown in **Fig. 29**; *Pachylemur (Lemur) insignis*, and *Palaeopropithecus*, *Australopithecus robustus*, and *Australopithecus africanus* in **Fig. 30**.

Cetacean Fossils

As in the living cetacean brain, there is no rhinal fissure in these fossils and thus no indication of an olfactory bulb or tract; therefore, neocorticalization cannot be assessed. Scans of the three fossil whales are shown in the left panel of **Fig. 31**.

Living Non-Primate Mammals

Aonyx, *Ursus* (Black Bear), *Canis latrans*, and *Felis catus* are shown in **Fig. 32**; *Cerdocyon*, *Odocoileus*, *Ursus* (Kodiak), and *Lama* are shown in **Fig. 33**; *Lutra lutra*, *Lutra canadensis*, *Procyon endocast and braincast*, and *Nasua* are shown in **Fig. 34**; and *Phascolarctos*, *Macropus*, *Vombatus*, and *Taxidea* in **Fig. 35**.

Living Primates

Chiropotes, *Mandrill*, *Homo-Falk A*, and *Homo-Falk B* are shown in **Fig. 36**, and primate endocasts and braincasts (16 left hemisphere endocasts) are shown in **Fig. 37**.

Changes in neocorticalization over time

Fig. 38A shows neocorticalization as a function of time for all 155 mammalian endocasts, including those of 18 modern primates and 25 from other extant species, with the latter seen as a vertical column of points at zero Ma. Overall, neocorticalization increased in mammals over the sampled 60-million-year period at a rate of ~5% per 10 million years, similar to the smaller sample reported in Jerison (2012). The regression calculates a present average neocorticalization of 58% and an expected level of neocorticalization at 60 Ma of ~15%. From **Table 1**, we observe that the oldest Paleocene fossils, *Arctocyon* and *Titanoides*, are reasonably approximated by these regressions, neocorticalized at 22.5% and 14.1%, respectively.

The analysis of neocorticalization as a function of geological age was then limited to the 122 fossil samples to avoid bias from extant species (**Fig. 38B**). Although species at 0.01 Ma and 0.03 Ma aggregate at the right-hand side of the plot due to the number of La Brea fossil endocast sampled, the results remain similar to the full dataset. According to the regression equation, the average level of neocorticalization at 0.01 Ma was slightly over 51%, and neocorticalization increased over the past 60 million years from 21.3% to 51.3%.

Neocorticalization was next related to Encephalization Quotient (**Fig. 39**), which revealed plateauing of neocorticalization at a maximum of ~80%. This maximum was true for the largest endocasts in the series for which neocorticalization could be measured—two human endocasts (neocorticalization of 80.0% and 77.7% and EQ of 5.8 and 6.7, respectively). Although this upper limit may in part be dictated by the degree of neocorticalization measurable in endocasts, a genetically determined maximum may also be in play. Additionally, the incorporation of body size as a denominator in the calculation of EQ may also have an effect here. For example, modern human body sizes tend to be reduced relative to other closely related primates, which then results in a relatively larger EQ regardless of brain size.

266

267 Revisiting the mammalian-reptile boundary

268 Brain-body relationships in large numbers of living amniotes (mammals, $N = 647$; birds,
269 $N = 219$; and reptiles, $N = 59$) have been described historically using convex polygons to better
270 understand inter-class allometric relationships ((Jerison 2007) and **Fig. 40A**). Living birds and
271 mammals show similar encephalization (relative to body size), with birds forming a subset of the
272 mammalian polygon, and living reptiles being less encephalized. Most nonamniotes overlap the
273 reptile polygon (Jerison 2001). Electric fish, however, are within the mammalian range, and
274 cartilaginous fish overlap the reptilian and mammalian ranges. Agnathans form a small polygon
275 at the lower margin of the main fish polygon.

276 Re-examining these historical polygons in light of our new digitized endocast data, all of
277 the digitized data and their regression line were added to **Fig. 40B**, and only the fossil data and
278 their regression line were added to **Fig. 40C**. Unsurprisingly, only a few of the extinct mammals
279 fell below the lower boundary of the extant mammalian polygon, suggesting that there was likely
280 some encephalization as mammals evolved to reach the present lower limit.

281 However, the datum contributed by *Arctocyon primaevus* is surprising and represents a
282 mammalian point falling within the non-avian dinosaur polygon. This requires reconsideration of
283 previous conclusions about the allometric border between mammals and reptiles (Jerison 1973),
284 as non-avian dinosaurs (hereafter, “dinosaurs”) have hitherto been considered a natural extension
285 of the polygon of extant reptiles. The datum on *Arctocyon* is robust, with the endocast prepared
286 by Russell & Sigogneau-Russell (1965) quite brain-like and the measurements accurate.
287 Although the body size was originally uncertain, a reanalysis of the skeletal material by (Argot
288 2013) is definitive, making the body size estimate as good as it can be.

Therefore, the area of the polygon drawn for dinosaurs requires reconsideration. **Fig. 40D** summarizes a new view of mammal-dinosaur allometric relationships. The upper boundary of the reptile-dinosaur convex polygon has been redrawn, and instead of connecting foci of the living reptile polygon to a convex polygon that included speculations about dinosaur brain sizes, in **Fig. 40D** the living reptile polygon is extended (dotted line) to include larger body sizes. The earlier drawing assumed that dinosaur brains were half the volume of their endocasts, and the earlier boundary was drawn to cover their assumed brain sizes. The new extended boundary of the reptile polygon is a brain boundary (not a brain-endocast boundary) that assumes that living reptile brain sizes would best estimate dinosaur brain sizes, with a parallel lower boundary drawn through the smallest reptile brain sizes to complete the new convex polygon.

The new boundaries do not depend on prior estimates of brain-endocast relationships in dinosaurs. Rather, they assume that dinosaur brains would follow the same size rules as living reptile brains. The 59 data points (Platel 1979) of extant reptiles were added to its polygon as a reminder of how it is drawn. The maxima of the extant reptile polygon are a 134 kg crocodile and a 205 kg alligator; their brains, 15.6 g and 14.08 g, respectively.

Using these new boundaries, the lowest mammalian point, *Arctocyon primaevus*, now lies above the reptile polygon, still supporting the hypothesis that there is a distinct mammal-reptile boundary. A second issue concerns the dinosaur brains estimated by the new polygon. Scanning a handful of dinosaur endocasts (**Fig. 41**), the estimated body sizes for each were just under 10 metric tons. The new reptile-dinosaur polygon at that body size estimates a brain size (not endocast size) of about 150 ml. The four scans in **Fig. 41** are 570 ml, 228 ml, 348 ml, and 375 ml, respectively. A second look at *Tyrannosaurus rex* (**Fig. 41A**) suggested sectioning a brain portion of the endocast to remove the expanded regions associated with the olfactory bulb and tract and the “medulla” posterior to cranial nerve X. This reduced the *T. rex* endocast volume to 374 ml for the “brain” region of the endocast. Brain-endocast relationships for *T. rex* would be 150/374, or

about 40%, rather than the old estimate of 50%. This percentage is about the same for the other endocasts in **Fig. 41**. Jirak & Janacek (2017) recently examined brain-endocast relationships in crocodilians and found that the brain in mature crocodiles occupied 29% of the volume of the endocast. Their result confirms this approach to probable brain-endocast relationships in dinosaurs, namely that some adult dinosaur brains may have been less than 40% of the endocast volume (see Watanabe et al. 2019 for further data and discussion).

Surface-volume relationships

The data presented in **Table 1** enable us to take a closer look at the relationship between endocasts and brains with respect to convolutedness. Using log-transformed data, there was a very high correlation ($r = 0.991$) between endocast volume and surface area in the entire sample of 155 endocasts (**Fig. 42A**) and in brains of sampled extant mammalian species ($r = 0.996$; **Fig. 42B**), suggesting that the surface areas in brains and endocasts are almost deterministic of brain volume and that it is not necessary to measure the additional brain surface hidden within in sulci to then accurately predict brain volume. However, the exponents differed, with 0.91 in **Fig. 42B** reflecting increased convolutedness with brain size and the role of additional surface area of buried cortex, and the exponent of 0.67 (approximately $2/3$) in endocasts in **Fig. 42B** implying the conservation of shape as endocasts become larger. The idea that all mammal brains are similarly shaped may be counterintuitive, since different species show very distinct differences in brain shape. The basic brain shape must be something between a sphere in which the multiplier is 4.84 and a cube in which the multiplier is 6. The multiplier in **Fig. 42A** is 5.93, suggesting that the idea of a general brain shape in mammals is valid.

Within-species variation

A previous analog analysis of twenty natural endocasts collected at the Reeves Fossil Bed in the Big Bend area of Texas, Chadronian, end of the Eocene (Wilson 1971) and regarded as variants of a single species, *Bathysphenops reevesi*, revealed that endocast volumes were between 10 and 12 ml and normally distributed, with a coefficient of variation (CV) of about 10% (Jerison 1979). The same analysis showed that a CV of ~10% was also a good fit for the data of other extant and fossil brains and endocasts including house cats, chimpanzees, living and fossil equoids, and living and fossil hominins (Jerison 1979). Prior to the advent of digitization, variability in neocorticalization and surface area could not be analyzed.

CVs were calculated using data from eight *Bathysphenops* endocast specimens limited to those without olfactory bulbs for comparison with the general sample (**Table 2**). Using digitized endocast data, the CVs for endocast volume, surface area, neocortical area, and neocortical:surface area ratio were 10.6%, 9.9%, 7.8%, and 6.5%, respectively. This compares to a previous analysis of digitized CT images of 157 *Bathysphenops* samples, which showed higher CVs for the length of olfactory bulbs (CV = 15.8%), width of the hypophyseal endocast (CV = 16.3%), and cerebellum (13%) (Macrini 2009). Although higher, these CV values are similar enough to the current results to raise no important questions about the adequacy of measurements on a single species to represent its brain as the information-processing organ.

Discussion

To date, this is the largest analysis, with 172 cranial endocast specimens and incorporating 41 extant species, of broad patterns of relative brain size and neocorticalization across vertebrate evolution. Our analysis shows that, on average, mammals

became increasingly neocorticalized at about 5% additional neocortex per 10 million years. About 60 million years ago, mammalian neocorticalization averaged about 20%, increasing to a present average of 50%, with a maximum at about 80% in primates reached within the past 10 million years. Compared to results of previous bivariate analyses, these data redefine the observed boundary between mammals and reptiles and confirm that measurements on a single species adequately represent the brains of the entire species.

These analyses used the basic measurement of brain size determined from digitized endocast images, which generally estimates total neural information processing capacity in living mammals, as well as the size of many major structures in the brain identifiable by comparative neuroanatomy. Crude as it is, gross brain size serves as a metric (“statistic”) that estimates finer brain variables (“parameters”). Generally speaking, this relationship between “statistic” and “parameter” is likely to be especially true in birds and mammals because endocast volume is nearly equivalent to gross brain size and is, therefore, reliably measurable for evolutionary analysis.

As a between-species trait, brain size is determined primarily by body size, and that is its “allometric” factor. During evolution, bird and mammal brains were further enlarged beyond a basal vertebrate grade, or “encephalization,”. There are significant differences between species in encephalization within vertebrate classes, and there are variations in the roles of body size in all species consistent with their adaptations. Although between-species effects beyond their role in brain-body allometry were not analyzed here, differences in body size clearly involve a mosaic of genetic and epigenetic determinants (Damuth et al. 1990). Nevertheless, about 80% of the variance in brain size in living mammals is attributable to body size differences. The residual from the allometric “regression” of log brain size on log body size is the statistic that defines an encephalization quotient (*EQ*). Across species it describes the remaining 20% of the variance, and species do differ reliably in *EQ*.

The brain shows significant cortical and subcortical functional localization, but this is not usually measurable in endocasts. For example, specialized motor areas in living brains control body and limb movements, while specialized auditory, visual, tactile, kinesthetic, and olfactory regions analyze sensory information. Functional disuse results in reorganization of the cortical projections, resulting in important changes in the details of the brain maps (Qi et al. 2000). These aspects of brain function should be recognized in endocasts as constraints on their interpretation as brains.

The uniformitarian hypothesis (Simpson 1970), a principle of parsimony according to which present “laws of nature” have always been true, is fundamental both to the validity of our approach and to the confidence with which we can infer function in extinct taxa. The hypothesis states that the relationship between brain size and the “parameters” that it estimates in living species is comparable to the relationship between endocast volume and those parameters in fossils. There are important limitations to this hypothesis applied to brain structures. As uniquely specialized behavioral capacities evolved, their representation in brain structure evolved, which complicates the interpretation of quantitative effects.

Yet, despite anticipated anatomical and functional differences between and across the brains of vertebrate taxa, it appears that brain size remains a reliable between-species statistic in certain cases. In a number of analyses (Stephan et al. 2012; Stephan et al. 1981) of hedgehogs, shrews, tree shrews, lemurs, Old World and New World monkeys, apes, and a human brain, the weight or volume of living mammalian brains estimated the size of the hippocampus and cerebellum very well, with a correlation coefficient of 0.98 between hippocampus and brain size measurements. These values indicate a strongly concerted relationship between the sizes of the cerebellum and hippocampus, as well as potential for some overarching control by the same factors that determine the size of the whole brain in these living species (Jerison 1991). It is especially impressive that the size of the human hippocampus can be estimated with precision by

a regression equation determined from a large sample of living mammals. This tiny part of the brain in humans, less than 1% of total, is a major control center for short-term memory (Baddeley 2007; Brown et al. 2016; O'keefe & Nadel 1978). That gross brain size estimates the hippocampus size as well as it does partly supports the utility of brain size as a statistic. Neuroscientists have been surprised by these very high correlations due to the frequent emphasis of the uniqueness of human behavior, in particular of memory as a cognitive process (Deacon 1998). Nevertheless, the size of these components in humans is determined mainly by the large size of the human brain, which is true for the hippocampus, cerebellum, and many other parts of the brain (Jerison 1991). This result shows how the size of important human brain components may be determined by rules applicable in the living brains of all mammals.

Fossil evidence sometimes contests the uniformitarian hypothesis. For example, a 24 ml brain from a extant species has about a 3 ml cerebellum (Jerison 1991). The endocast volume of the Eocene *Hyracotherium* was 24 ml (**Table 1**), and the approximate volume of its cerebellum was estimated as at least 5 ml, almost twice as large as expected in living brains. However, the whole brain of this Eocene equoid was less encephalized than in most living species, but the size of its cerebellum was as appropriate as in living species for its body size for the control of cerebellar functions. The ratio of cerebellum (and/or occipital sinus) to total brain size in early species is greater than in extant species because the denominator in the ratio is smaller.

A third example of brain size as a statistic is also important for cladistic use of gyrencephaly or lissencephaly as a brain trait. **Fig. 42B** shows that the estimated parameter or dependent variable is the area of the cerebral cortex surface in a diverse sample of living mammals. We see first that if we wish to use the surface area as a trait to differentiate species, we might as well use absolute brain size; the measures are statistically equivalent. To two significant digits, the correlation between brain size and cortical surface area in this sample is 1.00, as if the relationship were deterministic rather than probabilistic.

A multiple regression analysis with body size as a dependent variable samples all factors. Head and body length represent only one spatial array of neural inputs to the brain. It is currently unclear why these may also be related to other spatial arrays, such as the retina of the eye or the distribution of nerve endings in the olfactory bulbs, as they appear to be. If one thinks of genetic systems as represented in the various factors, the relevant factors in brain-body allometry would not be identical with the full set of factors in the system.

This study used a 2/3rds exponent in theoretical allometry rather than an empirical value determined by regression analysis (Jerison 2001). Localization of function in the mammalian brain means that neural systems are mapped on different regions of the brain. Bats provide dramatic examples in their use of echolocation (Grinnell 1995; Ridley 1995). The platypus may be even more unusual in its use of electric information to guide its behavior (Scheich et al. 1986). Species vary, and their mappings vary and encumber different amounts of brain circuitry. The description and analysis of the perceptual worlds of birds and mammals is the foundation of ethology and its views on the evolution of behavior. Here they are translated into neurobiological terms for discussion of the brain's work-controlling behavior.

The empirical brain-body allometric exponent in mammals is about 3/4 (Martin 1990), which can be explained as due to the thickness of cerebral cortex in mammals. The cerebral cortex maps the body not onto a 2D sheet but onto a thin 3D sheet that varies in thickness in a fairly orderly way, with about the 1/6th power of brain size. Cortical thickness ranges from an average of about 0.7 mm in the half-gram mouse brain to an average of about 2.5 mm in the 1350 g human brain (Braitenberg & Schüz 2013). The net effect is to convert the allometric exponent as determined empirically into a compound dimensional statement about the map of the body on the brain, rather than as a dimensionless constant. The 2/3rds dimensionless component converts the volume of the body into the area of the map, and a small additional dimensional component of about 1/9th of a millimeter reflects the correlated thickness of the map.

In conclusion, this study draws on the long history of interpreting endocasts as brains in mammals but exploits their quantitative analysis using digitization technology. This updated and fairly direct analysis of brain evolution compares past allometric relationships and encephalization with those in living species and provides new information on brain evolutionary trajectories, interclass boundaries, and interspecies homogeneity.

Acknowledgments

Acknowledgments below are from the perspective of the first author, and we have maintained this perspective out of respect and admiration for his multiple decades of work on this study.

I acknowledge first Bob Martin, Bill Simpson, and the late Bill Turnbull and his widow Hedy, who made my frequent visits to FMNH a special pleasure. I was often joined by my late wife, Irene, before she succumbed to Alzheimer's. Hedy Turnbull and Anjali Goswami made my last visit especially memorable by spending much time with Irene. Special thanks to Anjali for photographing my specimens at FMNH.

The Hanse-Wissenschaftskolleg at Delmenhorst, Germany, where I was a Fellow in 1998, enabled me to buy my laser scanner, and institute members helped me learn to use it. Among other colleagues at museums and institutes at which I worked, I thank Susan Bell at AMNH, Robert Purdy and Mike Brett-Surman at USNM, and Chris Morris at YPM. John Harris at LACM helped with many specimens. My French colleagues Stéphane Peigné and Thierry Smith assisted with their specimens, and Mark Uhen and Phil Gingerich helped me with whale fossils. I thank Kris Carlson of Witwatersrand for a chimpanzee endocast, and Maria Teresa Dozo, John Flynn, and Denis Croft for help with Neotropical species. Phil Gingerich loaned me the *Pachyaena* endocast that I scanned, and Jack Johnson helped with dolphins and brains in general.

Gregg Gunnell checked my geological dating, and Dean Falk helped me with hominid evolution. Xiaming Wang of LACM, Ted Macrini at St. Mary's University, Texas, Blaire Van Valkenburgh of UCLA, and Michel Hofman of the Amsterdam Brain Institute all deserve thanks, along with Andy Farke, Marcus Eriksen, and Jack Horner who each let me scan their dinosaur endocasts for Fig 58. My daughter, Elizabeth Jerison Terry, helped in many ways in the preparation of the manuscript and tables, and Phil Dench of HEADUS Computing programmed my software and hardware, and helped me scan the *Tyrannosaurus rex* endocast. Finally, I must thank Liesl Erman who supported me through the difficult final editing of the entire manuscript, its figures and legends. All deserve special thanks. To the many colleagues who helped on specific emails and whose "personal communications" I cite, thank you all.

References

- Adams, DC and Collyer, ML.2019. Phylogenetic comparative methods and the evolution of multivariate phenotypes. *Annual Review of Ecology, Evolution, and Systematics*. 50:405-425. <https://doi.org/10.1146/annurev-ecolsys-110218-024555>
- Argot C. 2013. Postcranial analysis of a carnivoran-like archaic ungulate: the case of *Arctocyon primaevus* (Arctocyonidae, Mammalia) from the late Paleocene of France. *Journal of Mammalian Evolution* 20:83-114.
- Baddeley A. 2007. *Working memory, thought, and action*: OUP Oxford.
- Braitenberg V, and Schüz A. 2013. *Cortex: statistics and geometry of neuronal connectivity*. Berlin, Heidelberg, New York: Springer Science & Business Media.
- Brown TI, Carr VA, LaRocque KF, Favila SE, Gordon AM, Bowles B, Bailenson JN, and Wagner AD. 2016. Prospective representation of navigational goals in the human hippocampus. *Science* 352:1323-1326. [10.1126/science.aaf0784](https://doi.org/10.1126/science.aaf0784)

- 508 Damuth JD, Damuth J, MacFadden BJ, and John D. 1990. *Body size in mammalian*
509 *paleobiology: estimation and biological implications*. Cambridge and New York:
510 Cambridge University Press.
- 511 Deacon TW. 1998. *The symbolic species: The co-evolution of language and the brain*. New
512 York: WW Norton & Company.
- 513 De Miguel, C. and Henneberg, M., 2001. Variation in hominid brain size: how much is due to
514 method?. *Homo*, 52(1), pp.3-58.
- 515 Edinger T. 1929. Die Fossilen Gehirne. *Ergebnisse der Anatomie und Entwicklungsgeschichte*
516 28:1-249.
- 517 Edinger T. 1948. *Evolution of the horse brain*: Geological Society of America.
- 518 Edinger T. 2012. *Paleoneurology 1804–1966: an annotated bibliography*. Berlin: Springer
519 Science & Business Media.
- 520 Gidley JW. 1927. American Wild Horses. *The Scientific Monthly* 25:265-271.
- 521 Gould SJ. 1975. Allometry in primates, with emphasis on scaling and the evolution of the brain.
522 *Contributions to primatology* 5:244-292.
- 523 Grinnell AD. 1995. Hearing in bats: an overview. *Hearing by bats*. Heidelberg: Springer, 1-36.
- 524 Haight JR, Nelson JE. 1987. A brain that doesn't fit its skull: a comparative study of the brain
525 and endocranium of the koala, *Phascolarctos cinereus* (Marsupialia: Phascolarctidae).
526 *Possums and opossums: studies in evolution*. 1:331-52.
- 527 Harmon, LJ. 2019. Phylogenetic comparative methods. Independent,
- 528 Hopson J. 1979. Paleoneurology. *Biology of the Reptilia* 9:39-148.
- 529 Iwaniuk, AN and Nelson, JE. 2002. Can endocranial volume be used as an estimate of brain size
530 in birds?. *Canadian Journal of Zoology* 80:16-23.
- 531 Jerison HJ. 1973. *Evolution of the brain and intelligence*. New York: Academic Press.

- 532 Jerison HJ. 1979. The evolution of diversity in brain size. *Development and evolution of brain*
533 *size: behavioral implications*. New York: Academic Press, 29-57.
- 534 Jerison HJ. 1991. *Brain size and the evolution of mind (James Arthur lecture on the evolution of*
535 *the human brain, no. 59, 1989)*: American Museum of Natural History.
- 536 Jerison HJ. 2001. The study of primate brain evolution: where do we go from here. In: Falk D,
537 and Gibson K, eds. *Evolutionary anatomy of the primate cerebral cortex*. Cambridge,
538 England: Cambridge University Press, 305-337.
- 539 Jerison HJ. 2002. On theory in comparative psychology. *The evolution of intelligence*:251-288.
- 540 Jerison HJ. 2007. Fossils, brains, and behavior. In: Watanabe S, and Hofman M, eds. *Integration*
541 *of comparative neuroanatomy and cognition*. Tokyo: Keio University Press, 13-31.
- 542 Jerison HJ. 2012. Digitized fossil brains: neocorticalization. *Biolinguistics* 6:383-392.
- 543 Jirak D, and Janacek J. 2017. Volume of the crocodilian brain and endocast during ontogeny.
544 *PLoS One* 12:e0178491. 10.1371/journal.pone.0178491
- 545 Long A, Bloch JI, Silcox MT. 2015. Quantification of neocortical ratios in stem primates.
546 *American Journal of Physical Anthropology*. Jul;157(3):363-73.
- 547 MacFadden BJ. 1994. *Fossil horses: systematics, paleobiology, and evolution of the family*
548 *Equidae*. Cambridge, England: Cambridge University Press.
- 549 Macrini TE. 2009. Description of a digital cranial endocast of *Bathysphenops reevesi*
550 (Merycoidodontidae; Oreodontoidea) and implications for apomorphy-based diagnosis of
551 isolated, natural endocasts. *Journal of Vertebrate Paleontology* 29:1199-1211.
- 552 Martin RD. 1990. *Primate origins and evolution*. London: Chapman and Hall.
- 553 O'keefe J, and Nadel L. 1978. *The hippocampus as a cognitive map*: Oxford: Clarendon Press.
- 554 Platel R. 1979. Brain weight-body weight relationships. *Biology of the Reptilia* 9:147-171.

- 555 Qi HX, Stepniewska I, and Kaas JH. 2000. Reorganization of primary motor cortex in adult
556 macaque monkeys with long-standing amputations. *J Neurophysiol* 84:2133-2147.
557 10.1152/jn.2000.84.4.2133
- 558 Radinsky L. 1976. Oldest horse brains: more advanced than previously realized. *Science*
559 194:626-627.
- 560 Ridley M. 1995. *Animal behavior: an introduction to behavioral mechanisms, development, and*
561 *ecology*. Boston: Wiley-Blackwell Publications.
- 562 Russell DE, and Sigogneau-Russell D. 1965. Étude de moulages endocrâniens de mammifères
563 paléocènes. *Memoires du Muséum National D'Histoire Naturelle, Paris*:1-43.
- 564 Scheich H, Langner G, Tidemann C, Coles RB, and Guppy A. 1986. Electoreception and
565 electrolocation in platypus. *Nature* 319:401-402. 10.1038/319401a0
- 566 Simpson G. 1951. *Horses*. New York: Oxford University Press.
- 567 Simpson GG. 1970. Uniformitarianism. An inquiry into principle, theory, and method in
568 geohistory and biohistory. In: Hecht M, and Steere W, eds. *Essays in evolution and*
569 *genetics in honor of Theodosius Dobzhansky*. Amsterdam: North-Holland Publishing
570 Company, 43-96.
- 571 Snell O. 1892. Die Abhängigkeit des Hirngewichtes von dem Körpergewicht und den geistigen
572 Fähigkeiten. *Archiv für Psychiatrie und Nervenkrankheiten* 23:436-446.
- 573 Stephan H, Baron G, and Frahm HD. 2012. *Insectivora: with a stereotaxic atlas of the hedgehog*
574 *brain*. New York: Springer Science & Business Media.
- 575 Stephan H, Frahm H, and Baron G. 1981. New and revised data on volumes of brain structures in
576 insectivores and primates. *Folia Primatol (Basel)* 35:1-29. 10.1159/000155963
- 577 Striedter, G.F. and Northcutt, R.G., 2019. *Brains Through Time: A Natural History of*
578 *Vertebrates*. Oxford University Press.

579 Watanabe A, Gignac PM, Balanoff AM, Green TL, Kley NJ, Norell MA. Are endocasts good
 580 proxies for brain size and shape in archosaurs throughout ontogeny?. *J Anat.*
 581 2019;234(3):291-305. doi:10.1111/joa.12918

582 Welker W. 1990. Why does the cortex fissure and fold: a review of determinants of gyri and
 583 sulci. In: Jones E, and Peters A, eds. *Cerebral cortex: comparative structure and*
 584 *evolution of cerebral cortex*. New York: Plenum Press, 3-136.

585 Wilson JA. 1971. Early Tertiary vertebrate faunas, Vieja Group Trans-Pecos Texas:
 586 Agriochoeridae and Merycoidodontidae. Texas Memorial Museum, The University of
 587 Texas at Austin.

588

Figure 1

Armadillo rhinal fissure, on brain (*Dasypus novemcinctus*; University of Wisconsin Brain Collection, Specimen 40-465).

(A) Coronal section through the brain indicating the rhinal fissure, neocortex dorsal to the fissure, and paleocortex with dark lamina II ventral to the fissure. (B) Lateral views of the same brain, with (C) rhinal fissure indicated by white line.

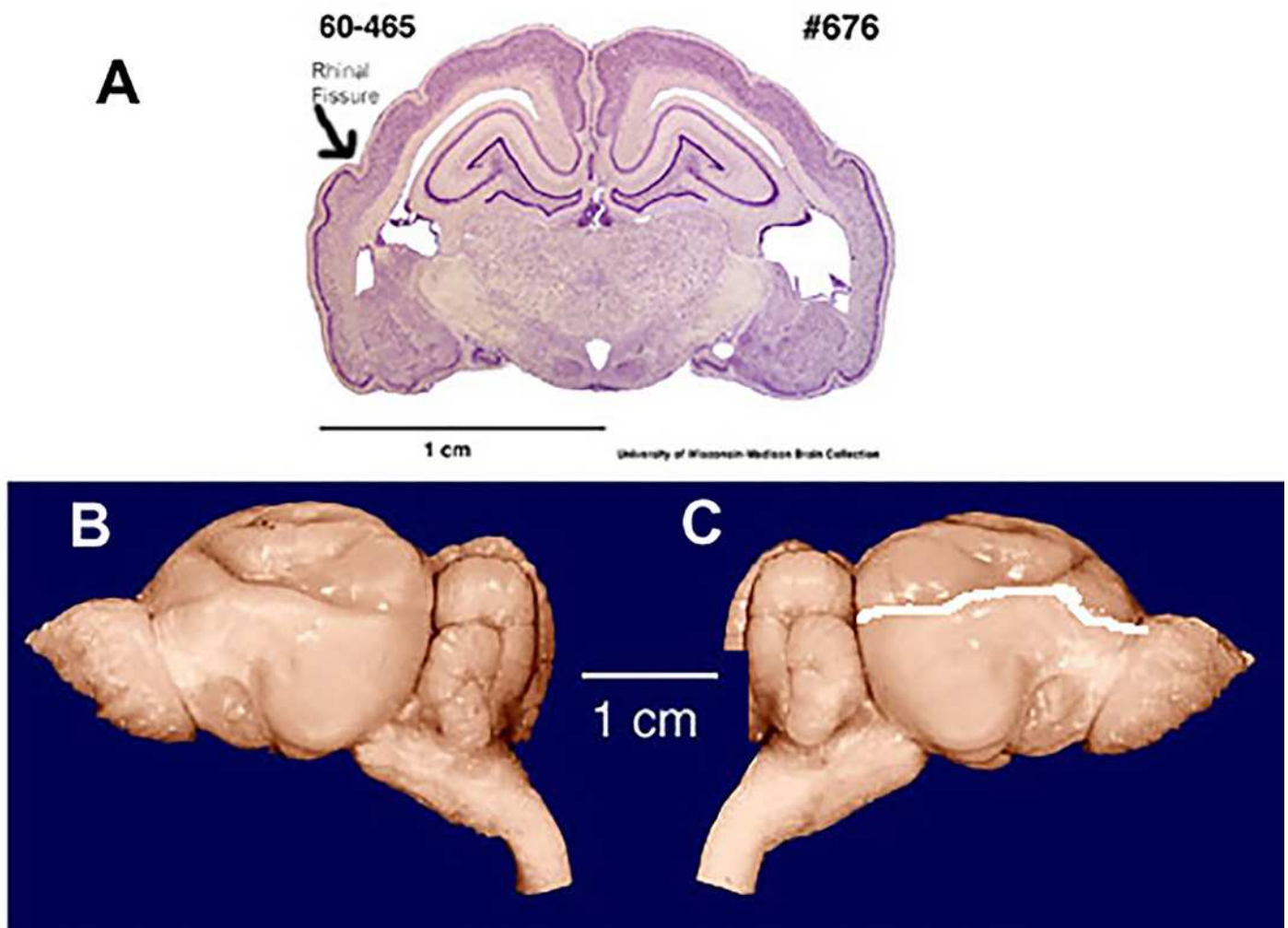


Figure 2

Five Edinger equoids plus one. Digitized images of six fossil endocasts sketched by Edinger (1948) and Radinsky (1976b).

(A) Edinger's Eocene "*Eohippus*" (YPM 11694). (B) Eocene "*Hyracotherium*" *tapirinum* (FMNH PM 59207 = AMNH 55268). (C) Oligocene *Mesohippus bairdi* (FMNH PM 59221 = AMNH 9814). (D) Miocene *Merychippus isonesus* (FMNH 59208 = AMNH FAM 71150). (E) Mio-Pliocene *Pliohippus* (FMNH P 15870). (F) Pleistocene La Brea Horse *Equus occidentalis* (LACM 3500-17).

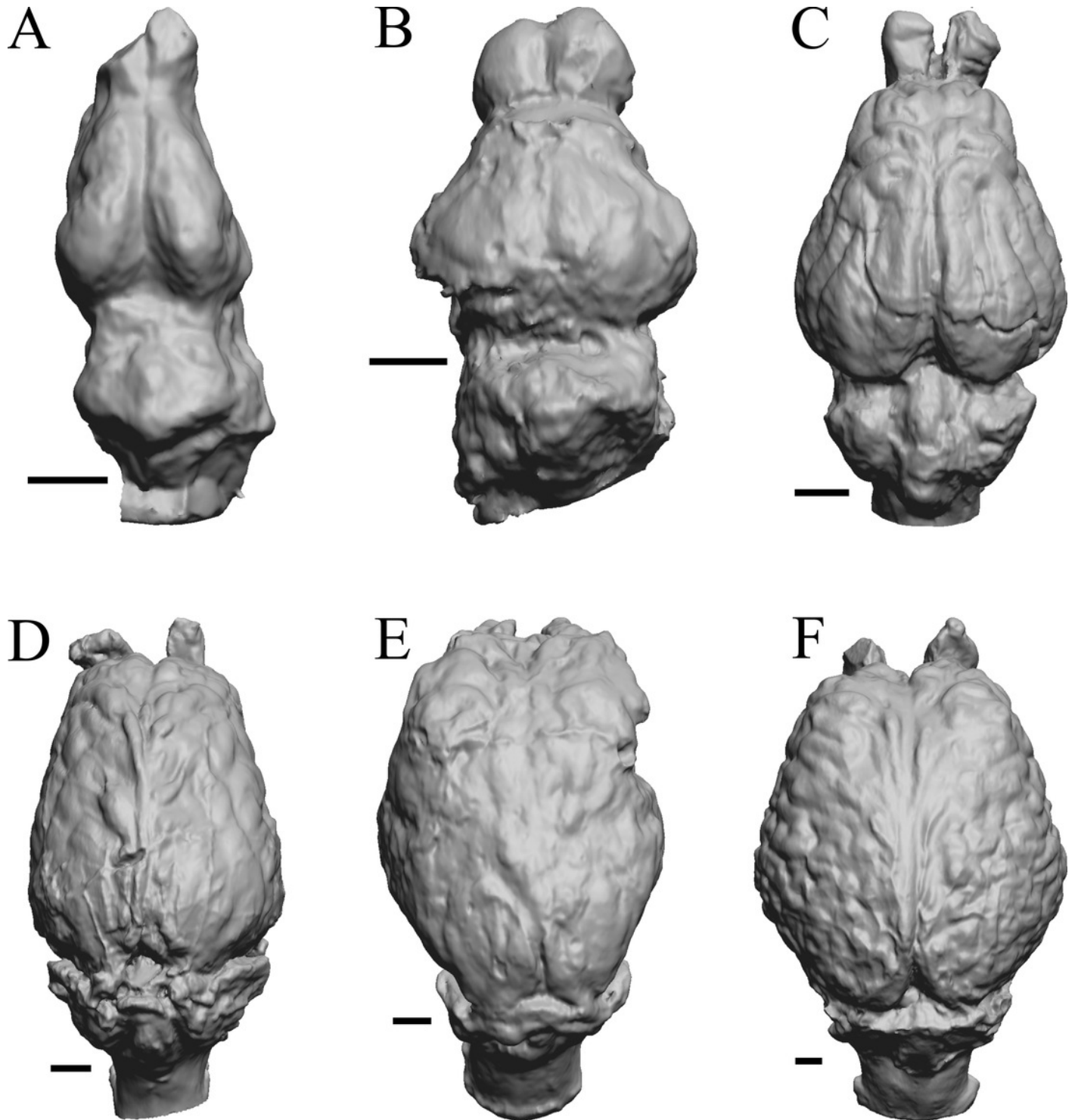


Figure 3

Hyracotherium endocast and body.

(A) 3D image of the *Hyracotherium* endocast (FMNH PM 59207, (Radinsky 1976)) rotated to a dorsolateral perspective; neocortex marked green in the left hemisphere. (B) Tessellated image of endocast prior to rendering; measured length (green line) marked by software. (C) Scan of model sculpted by Gidley (1927) with measurement marks added by the software.

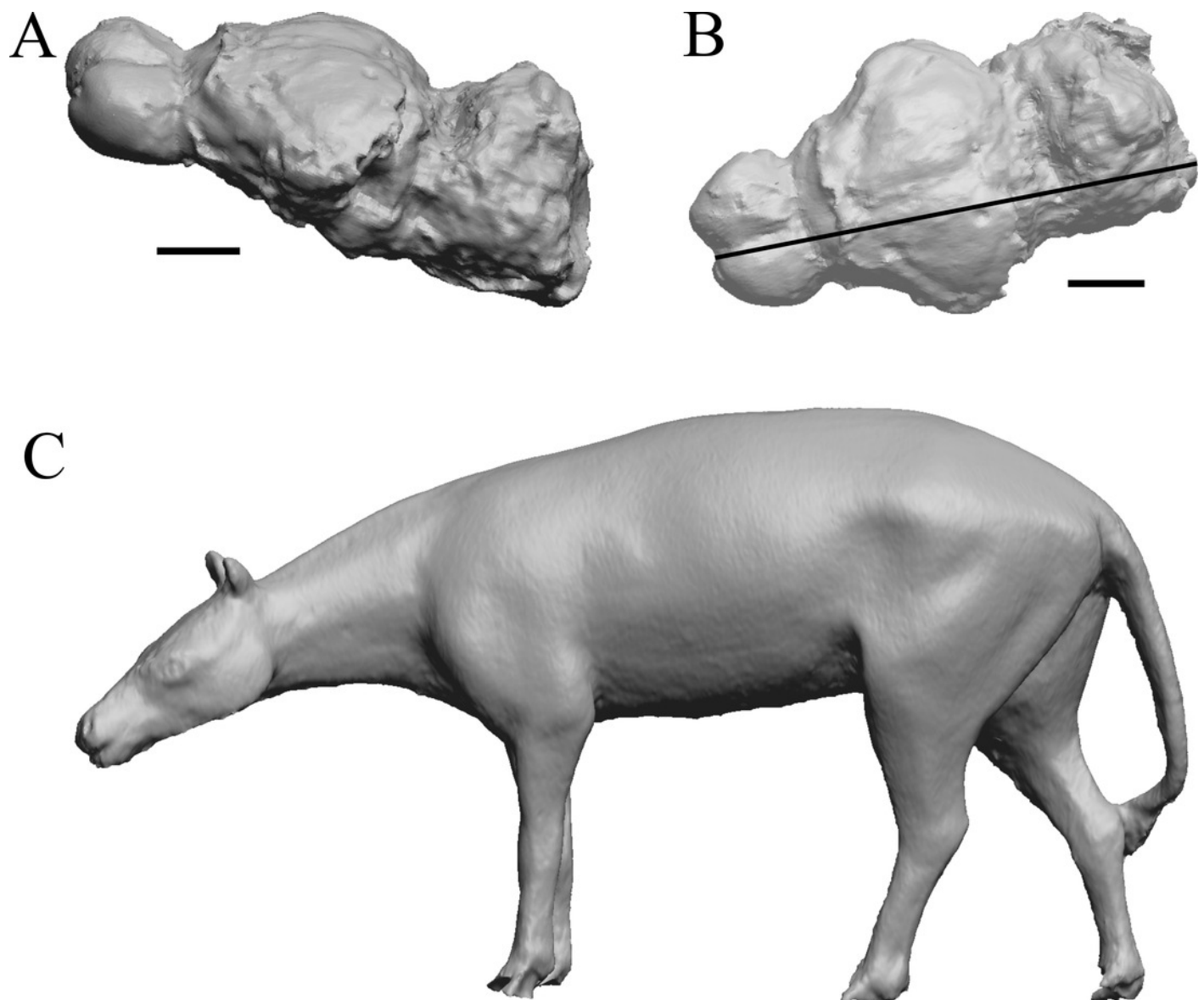


Figure 4

Meshippus endocast and body.

(A) *Meshippus bairdi* endocast (FMNH PM 59221 = AMNH 9814). (B) Tessellated image of the endocast, showing length line (C) digital image of the Gidley model, with length markings and author's notes. (D) Mounted skeleton of *Meshippus bairdi* (AMNH1477; photograph courtesy of Dr. Ted Macrini).

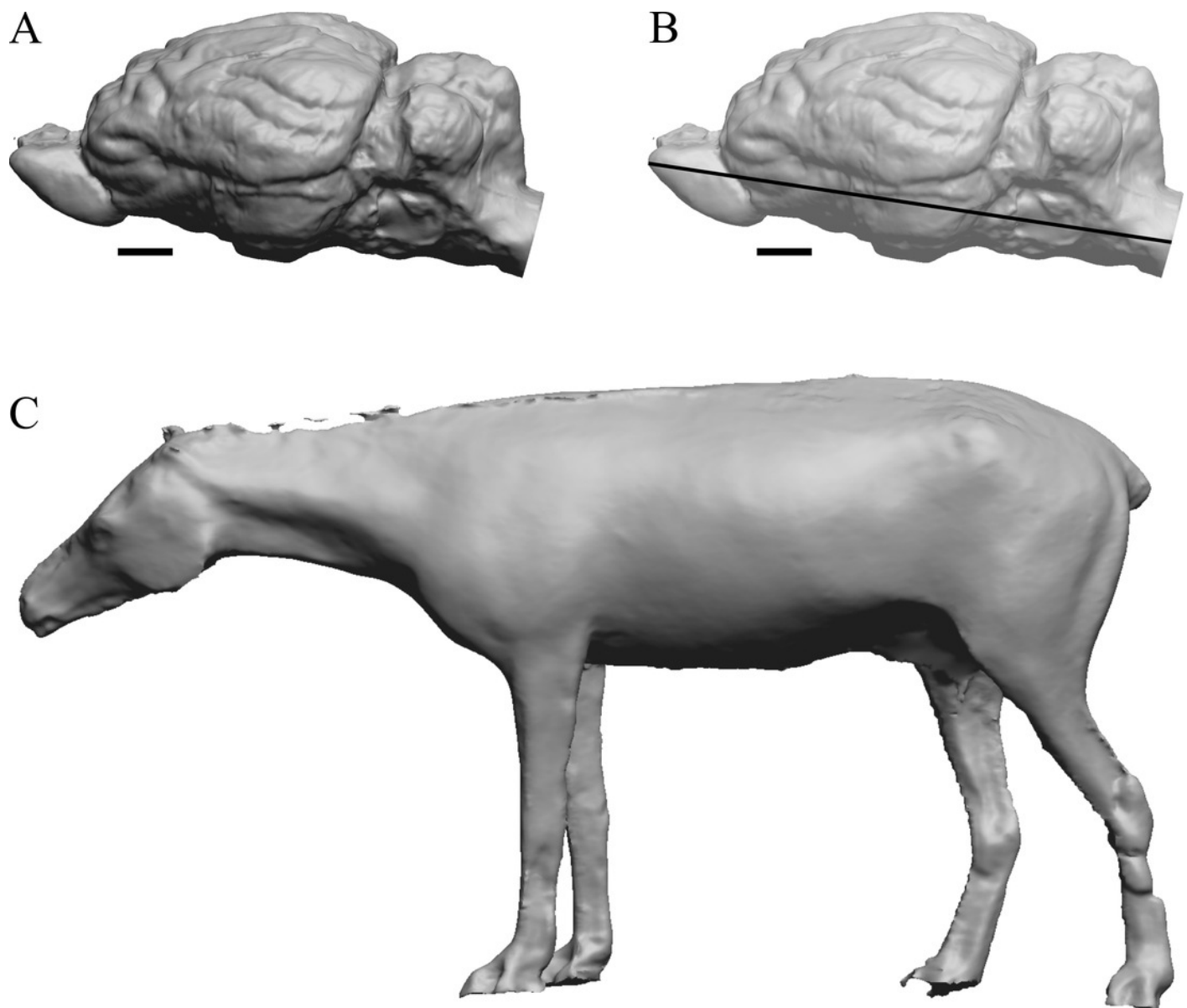


Figure 5

Six of Edinger's later horses; additional digitized Edinger endocasts.

(A) *Pseudhipparion* (FMNH PM59211= AMNH FAM 70025). (B) *Neohipparion* (FMNH P 15871). (C) *Cormohipparion* (FMNH PM 59220). (D) *Equus quagga* (Grant's zebra, LACM M548). (E) *Equus caballus* (Arabian horse, LACM). (F) *Equus caballus* (draft horse, LACM).

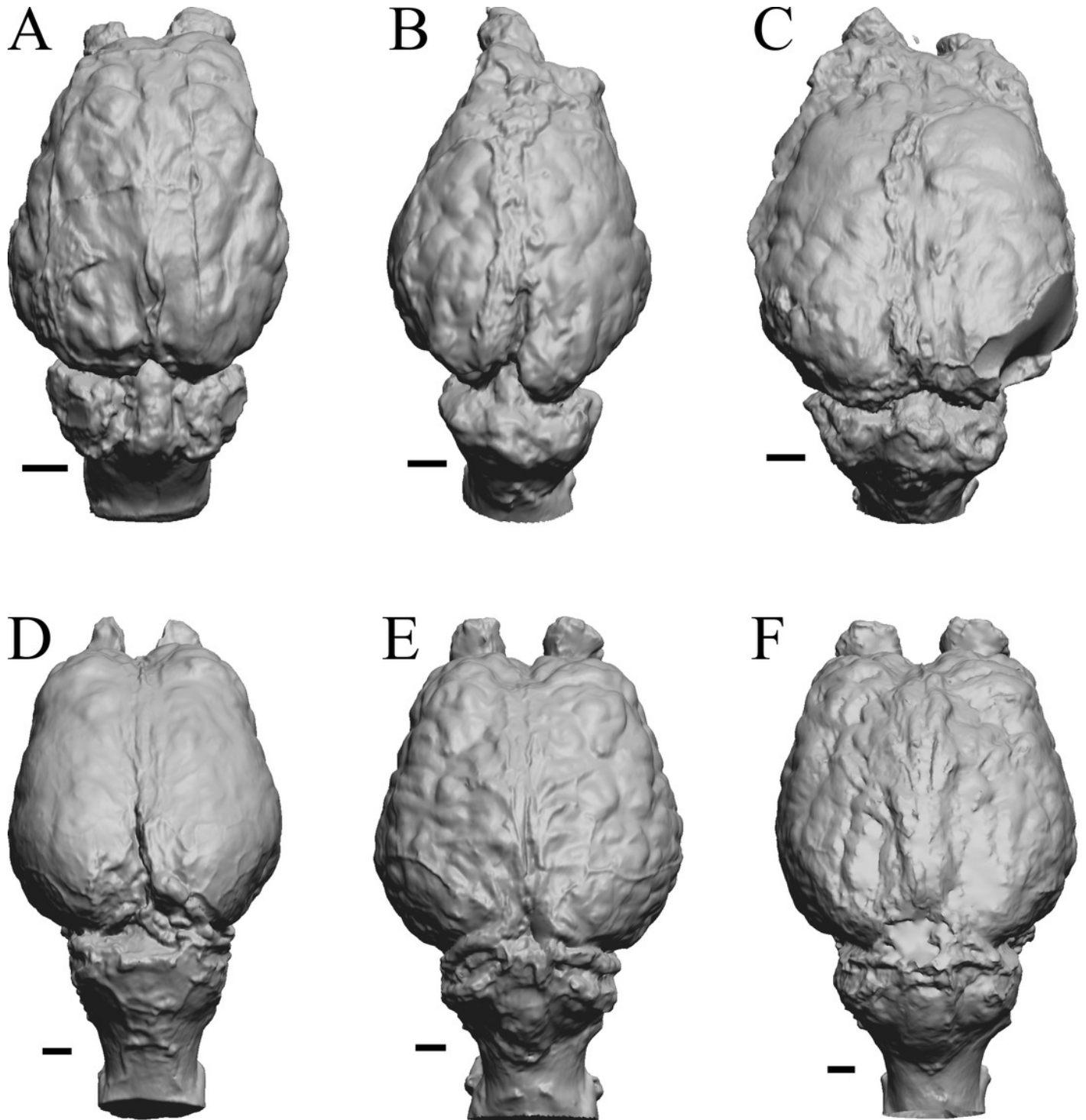


Figure 6

Titanoides, *Arctocyon*, *Barylambda*, *Phenacodus*.

Endocast views, dorsal and lateral. (A) *Titanoides primaevus* (FMNH PM 8655). (B) *Arctocyon primaevus* (MNHN CR 700). (C) *Barylambda schmidtii* (FMNH P 26075 and FMNH Pm 15573).

Evidence of neocortex on this endocast is marginal: two small anterior mounds on the frontal surface and a poorly marked olfactory tract; the expanded cerebellar representation in this specimen probably reflects fluid surrounding the cerebellum. (D) *Phenacodus primaevus* (FMNH PM 59042). The cast is unusually smooth for a cast prepared from a fossil skull and may have been smoothed to look more brain-like during preparation.

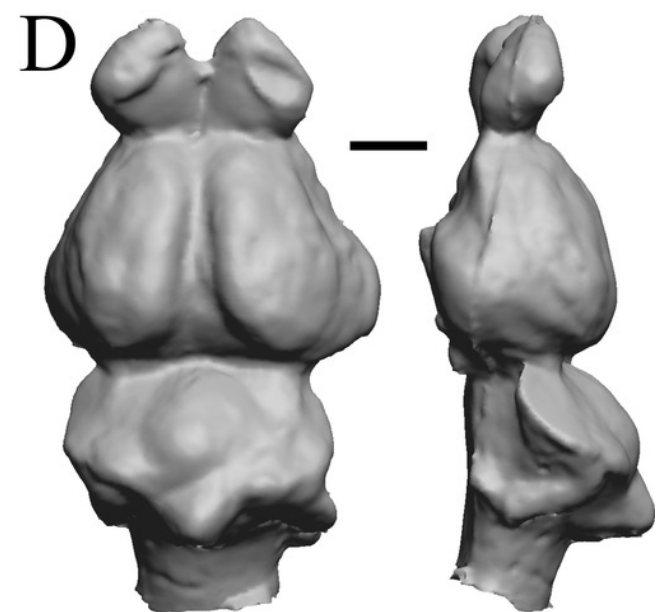
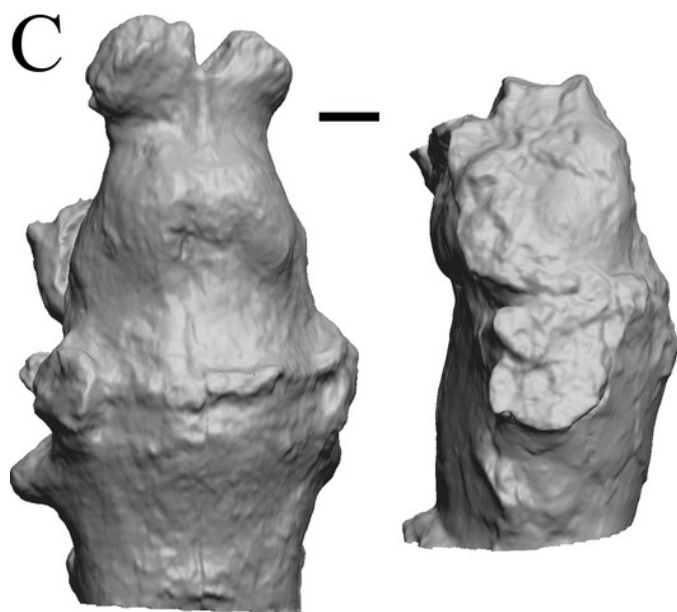
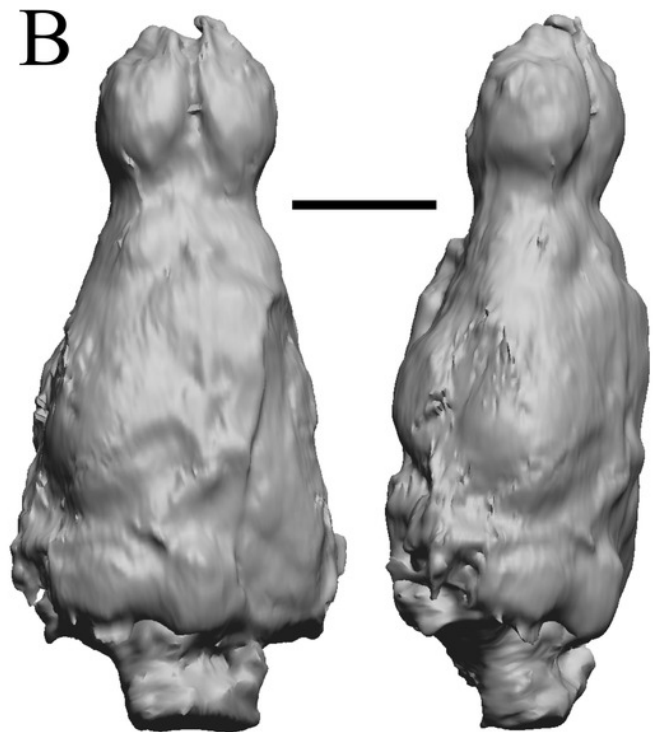
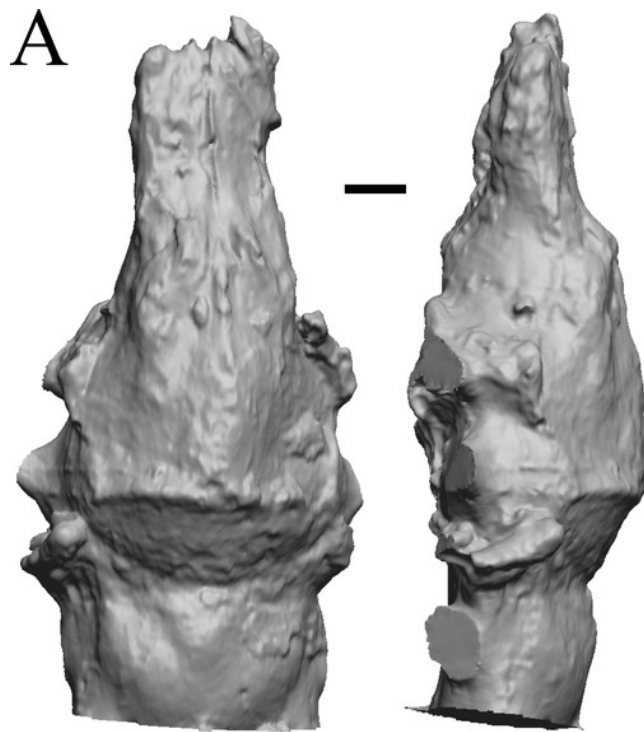


Figure 7

Cranial endocasts of *Coryphodon*, *Palaeosyops*, *Heptodon*, *Isectolophus*.

(A) Endocast of *Coryphodon hamatus* (FMNH PM 59241). (B) *Palaeosyops leidy* (FMNH PM 49198). (C) Three views of *Heptodon* sp. Vertically oriented endocast at left; photograph of specimen above center; horizontally oriented endocast below center. (D) *Isectolophus latidens* (FNMNH PM 59179). The odd preservation of its olfactory bulbs and tract are examples of the poor quality of olfactory bulb representation in endocasts, a reason for excluding them from endocast surface area estimates, along with the presence of non-neural tissue.

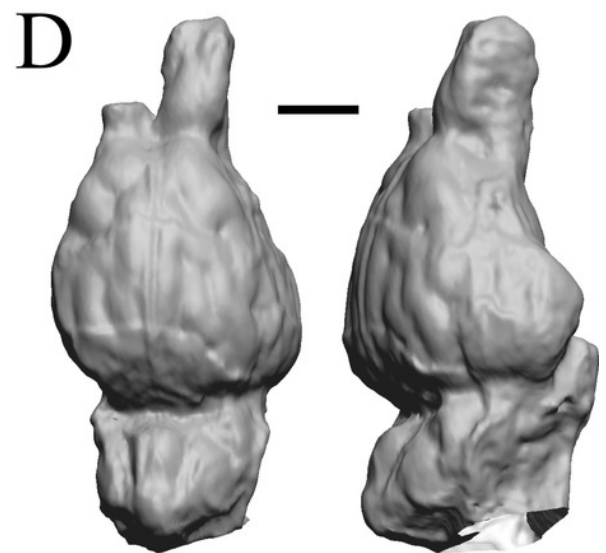
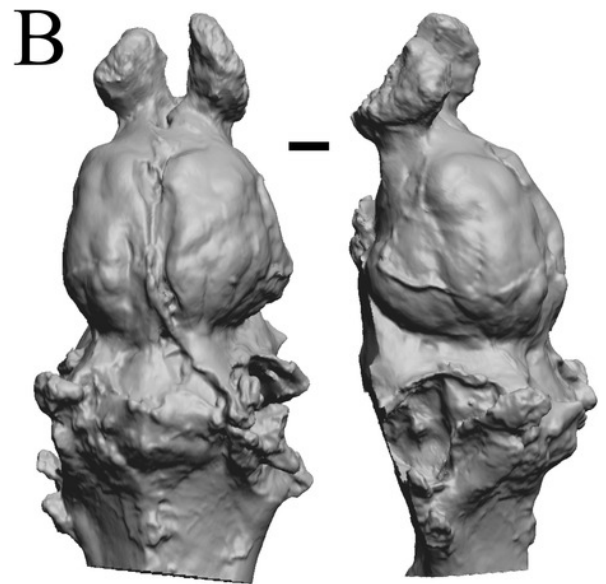
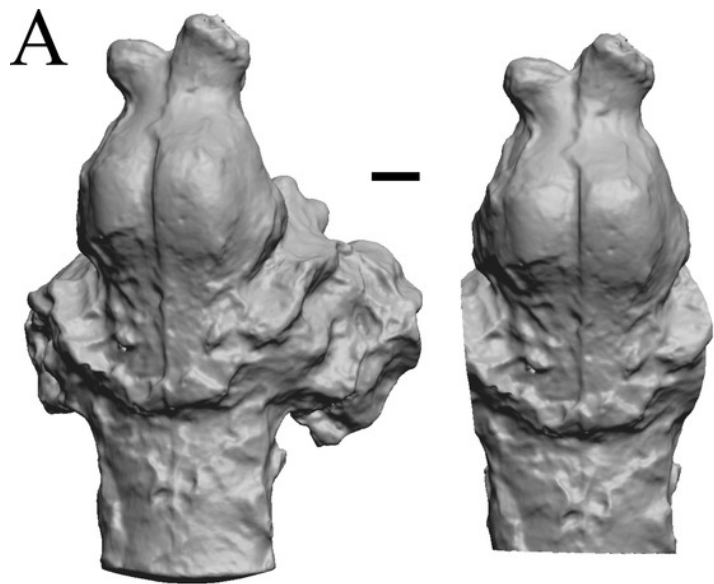


Figure 8

Hyrachyus, *Orthocynodon* ("Amynodon"), *Amynodon*, *Eomoropus*; dorsal and lateral views of endocasts.

(A) *Hyrachyus modestus* (FMNH PM 59240). (B) *Orthocynodon* sp. (FMNH PM 59177). (C) *Amynodon advenus* (FMNH PM 59231). (D) *Eomoropus amaorum* (FMNH PM 57168).

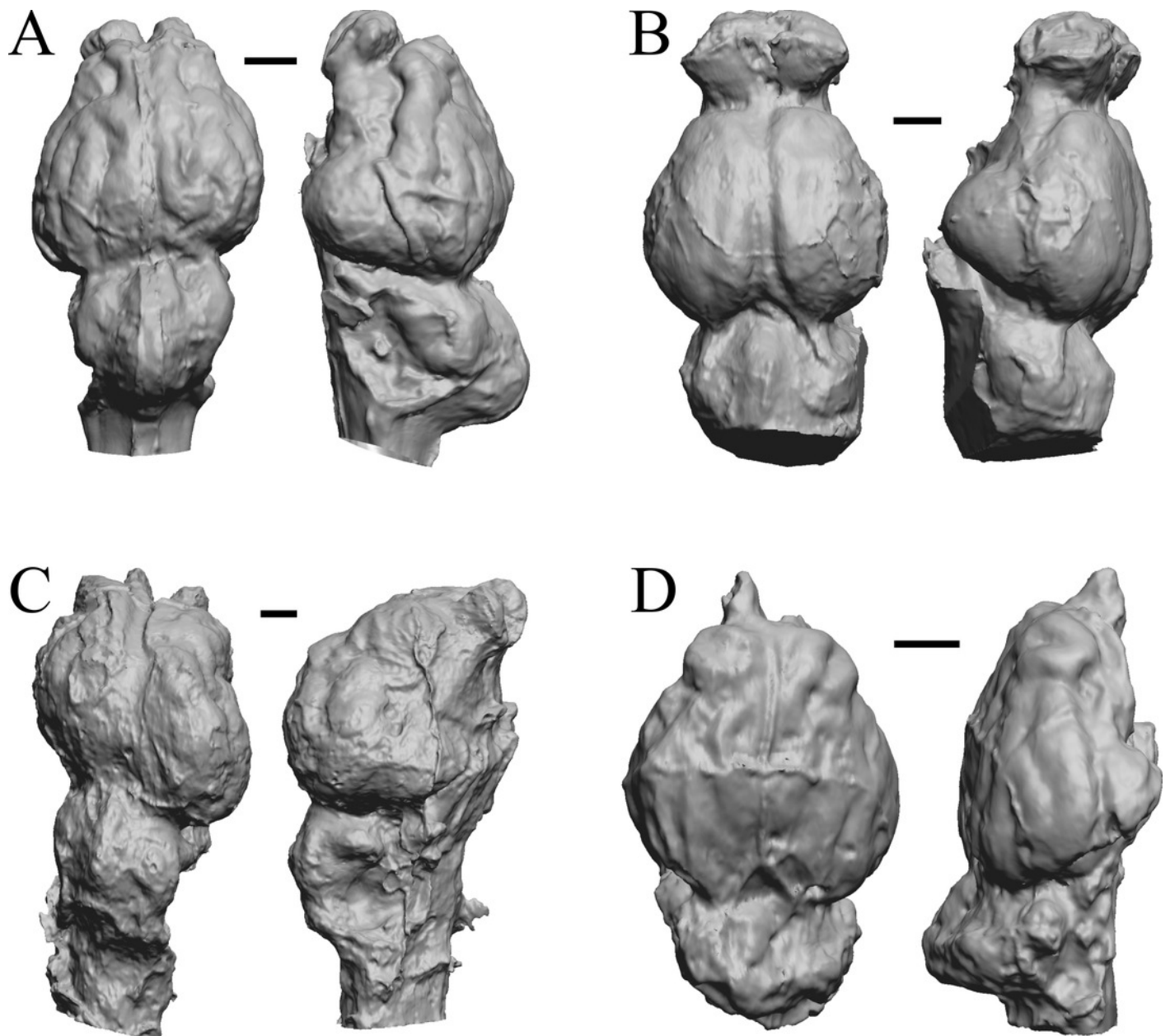


Figure 9

Mesatirhinus junius, *Mesatirhinus petersoni*, *Pachyaena*, *Mesonyx*; dorsal and lateral views of endocasts.

(A) *Mesatirhinus junius* (FMNH PM 59197); the lateral view on the right shows the rhinal fissure. (B) *Mesatirhinus petersoni* (FMNH PM 59196). (C) *Pachyaena ossifraga* (YPM 14708); the forebrain and hindbrain are linearly aligned, similar to many Eocene species. (D) *Mesonyx obtusidens* (FMNH PM 57139); about half of the brain and matrix was present, and excess matrix was removed when preparing the digital image.

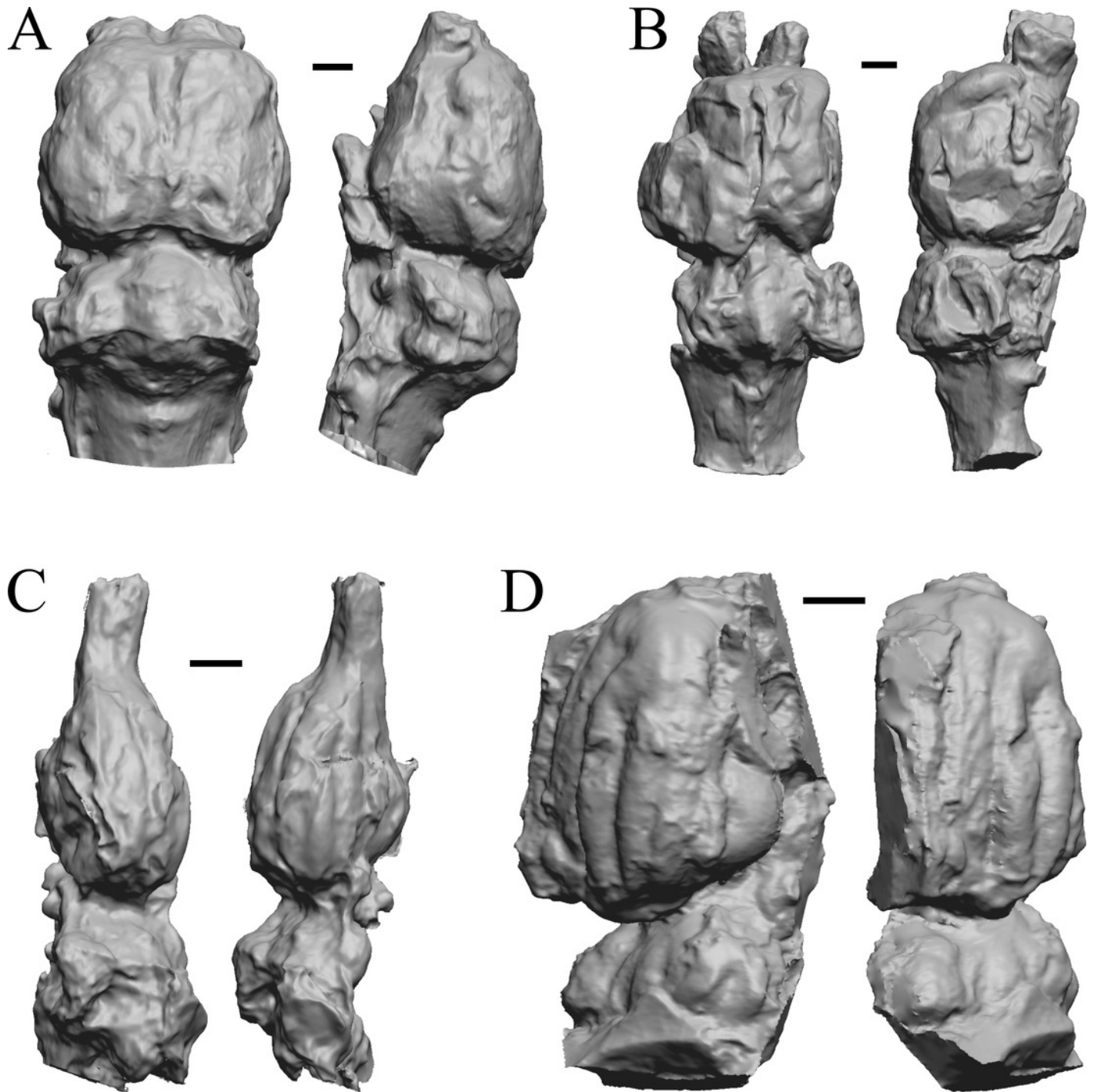


Figure 10

Smilodectes, *Notharctus*, *Necrolemur*, *Adapis*; dorsal and lateral views of endocasts.

(A) *Smilodectes gracilis* (FMNH PM 56263). (B) *Notharctus tenebrosus* (FMNH PM 59264); estimating neocorticalization was difficult because of the fragmented endocast, which was of approximately half the brain region and included posterior “brain” and matrix. (C) *Necrolemur antiquus*, (FMNH PM 59261). (D) *Adapis parisiensis* (FMNH 59259).

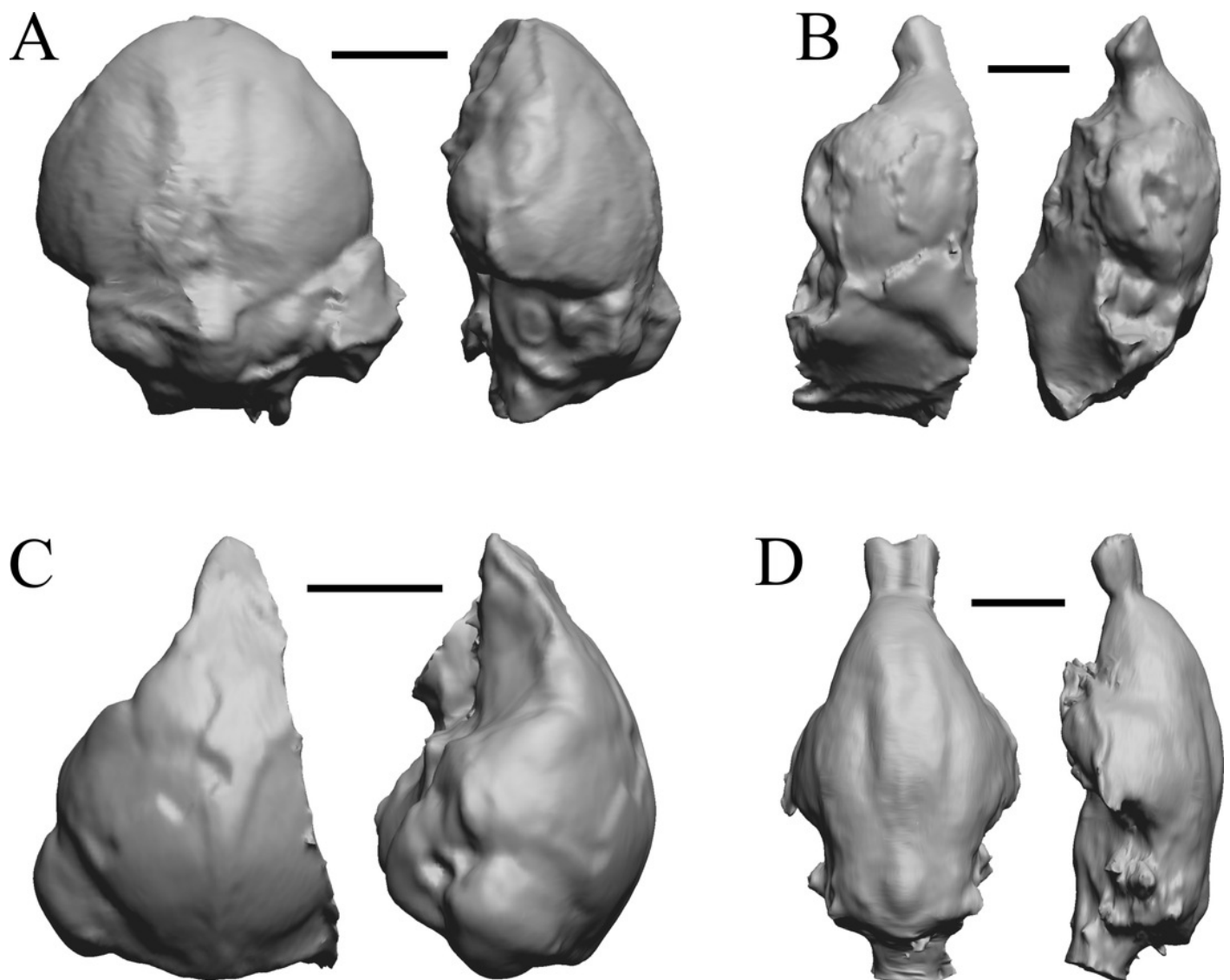


Figure 11

Uintatherium, *Menodus* (*Titanotherium*), *Moeritherium*, *Arsinotherium*; dorsal and lateral views of endocasts.

(A) *Uintatherium anceps* (YPM 11036); the anterior portion of the skull was almost certainly drilled out when the skull was prepared for the endocast, and the size of the endocast's "olfactory bulbs" are grossly overestimated. (B) *Menodus* (*Titanotherium*) *ingens* (FMNH PM 59199). (C) *Moeritherium* (NHMUK M.9176); the matrix forms a large mass of material at the ventral border of the olfactory bulbs. (D) *Arsinotherium zitelli* (NHMUK M.5539); there appears to be matrix added to the right cerebellar area in the region of the flocculus. Convolutions, presumably present in its brain, did not mold the cranial cavity and are not represented in the endocast. It is unique in the sample of land mammals in that the rhinal fissure is not visible, so neocorticalization could not be estimated.

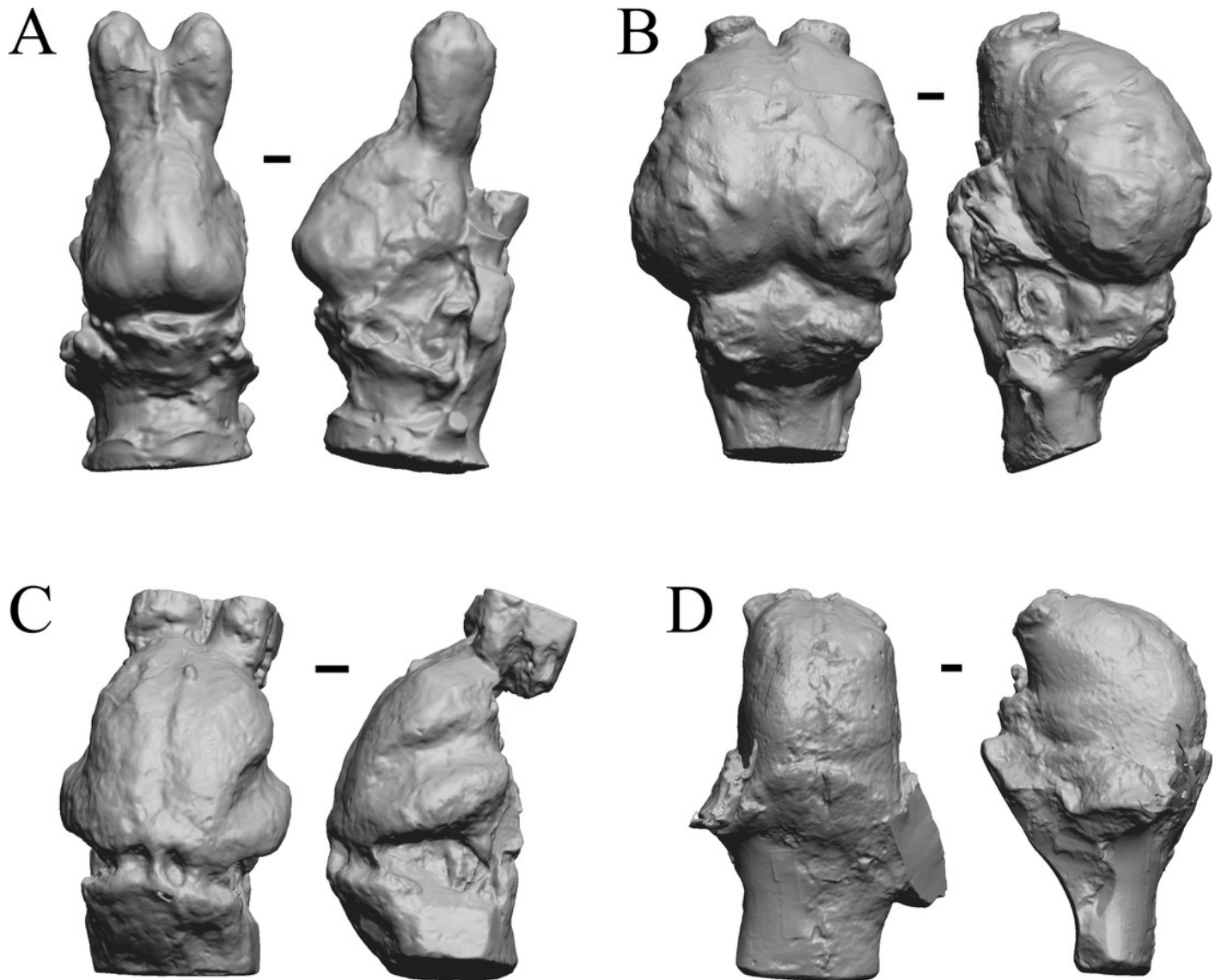


Figure 12

Pterodon, *Cynodictis*, *Cynohyaenodon*, *Procynodictis*; dorsal and lateral views of endocasts.

(A) *Pterodon dasyuroides* (NHMUK M. 25985); olfactory bulbs not preserved. (B) *Cynodictis cayluxi* (FMNH PM 59013). (C) *Cynohyaenodon cayluxi* (FMNH PM 57153); only its left half was preserved, and although the rhinal fissure was unclear in this image, it was clear enough to estimate neocorticalization. (D) *Procynodictis angustidens*, (FMNH PM 57168); in the lateral view, the rhinal fissure is faintly visible dorsal to the olfactory tract.

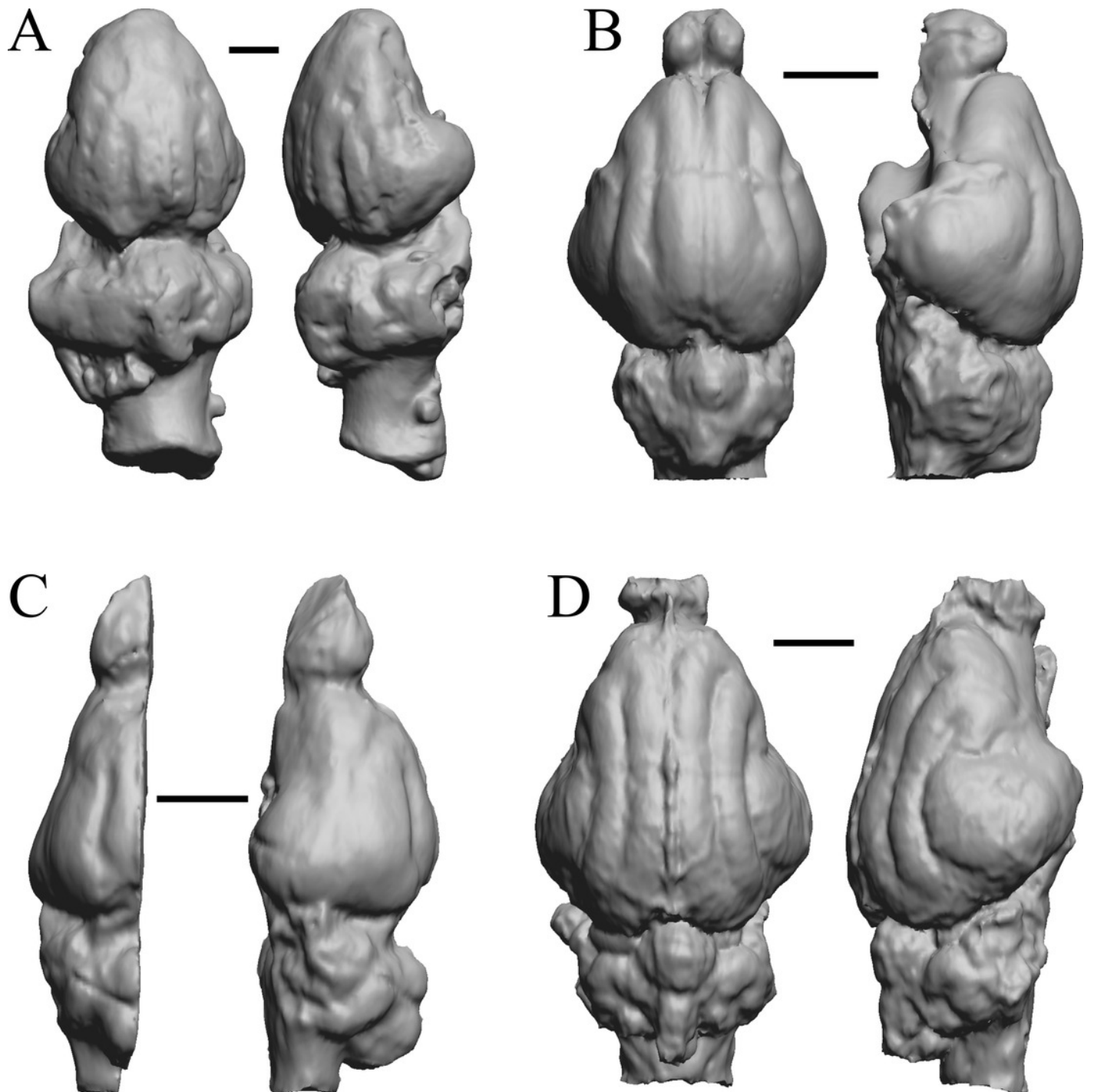


Figure 13

Cebochoerus, *Hylomeryx*, *Mixtotherium*, *Chadronia*; dorsal and lateral views of endocasts.

(A) *Cebochoerus lacustris* (FMNH PM 59051); only a partial endocast was available. (B) *Hylomeryx* (*Sphenomeryx*) *simplicides* (FMNH PM 59055); olfactory bulbs missing. (C) *Mixtotherium cuspidatum* (FMNH PM 59052); just over half of the endocast could be scanned, and the olfactory bulbs were preserved. (D) *Chadronia margaretae* (FMNH PM 57129); endocast is appropriately convoluted for a brain its size, comparable to capybara, and more convoluted than the surprisingly smooth-brained beaver.

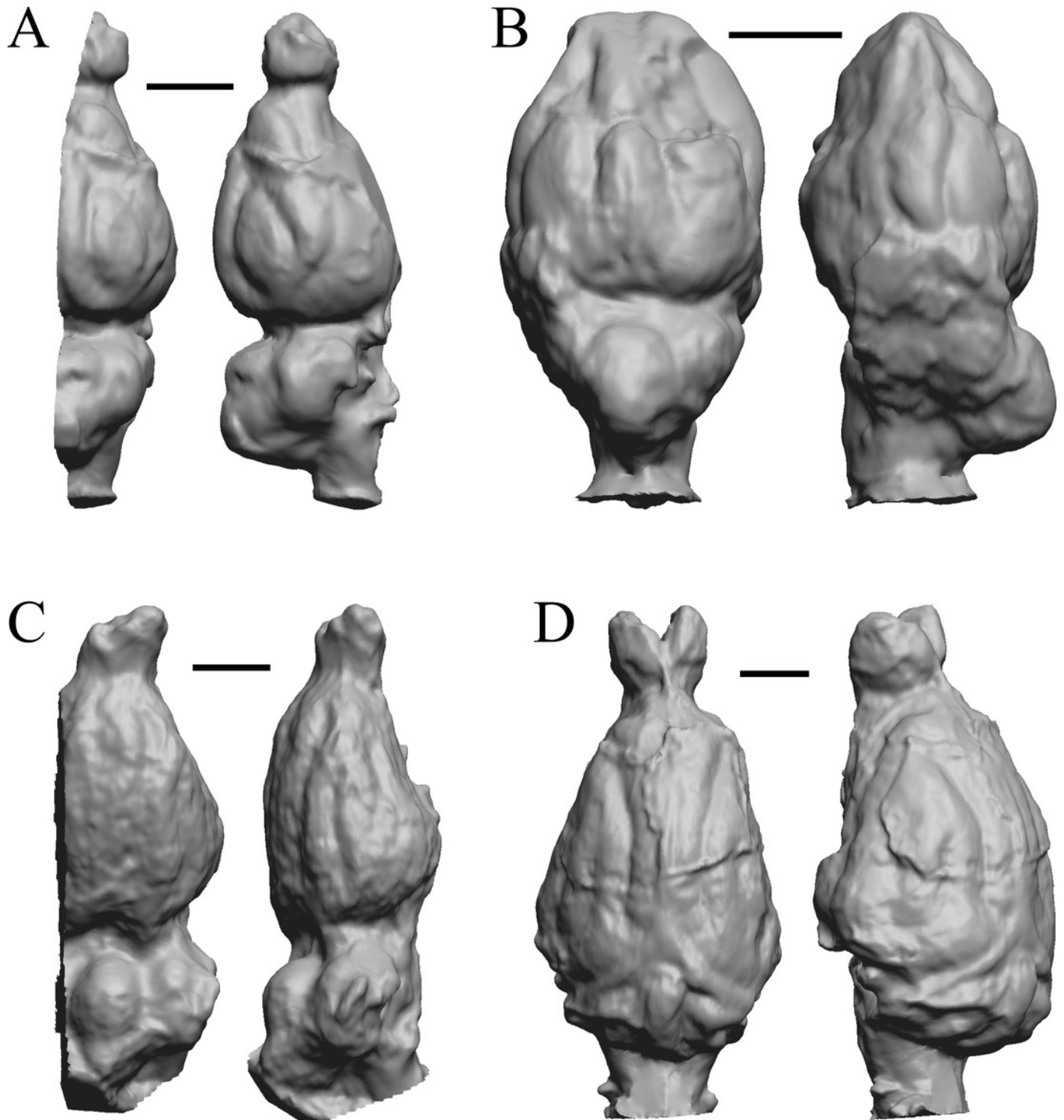


Figure 14

Anoplotherium, *Patriomanis*, *Poebrotherium*, *Bathygenys*; dorsal and lateral views of endocasts.

(A) *Anoplotherium commune* (NHMUK 3753); endocast edited to remove matrix artifacts from the base of the “medulla”. This endocast is an important example of the railroad-car appearance, elongated to distinguish cerebellum from forebrain as occurs in some Paleogene fossil endocasts. (B) *Patriomanis americana* (FMNH PM 57103). (C) *Poebrotherium* (PM 59167 FAM 31700). (D) *Bathygenys reevesi* (UT 40209-431); the olfactory tract abuts the anterior border of the rhinal fissure, but the fissure continues ventral to neocortex.

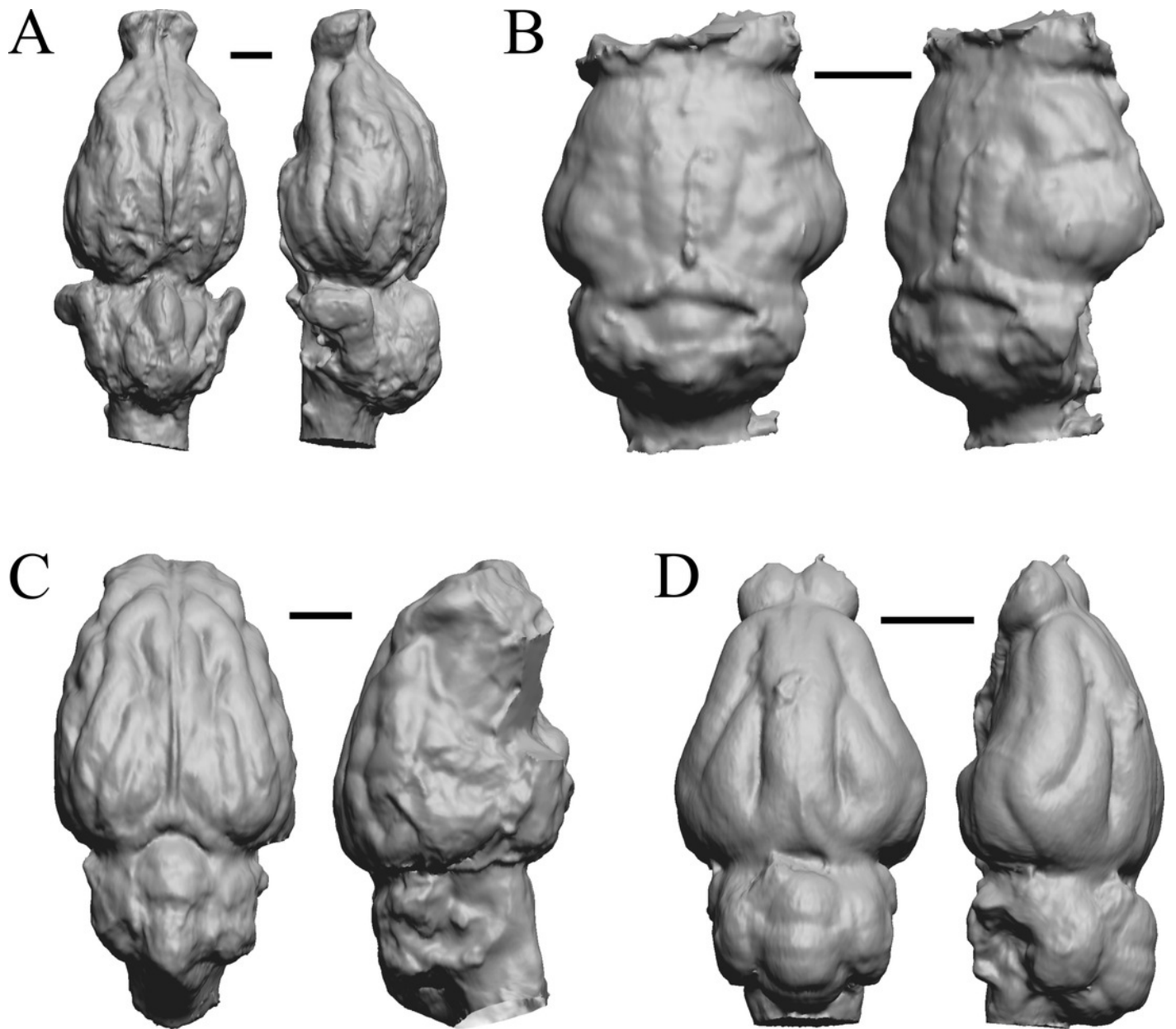


Figure 15

Daphoenus, *Dinictis*, *Eusmilus*, *Hoplophoneus*; dorsal and lateral views of endocasts.

(A) *Daphoenus vetus* (FMNH PM 59008a UM1); olfactory bulbs were not preserved in the specimen. (B) *Dinictis felina* (FMNH PM 58866). (C) *Eusmilus bidentatus* (FMNH PM 58871); only about half of the brain is present in the right hemisphere. (D) *Hoplophoneus primaevus* (USNM 22538); olfactory bulbs were not recovered.

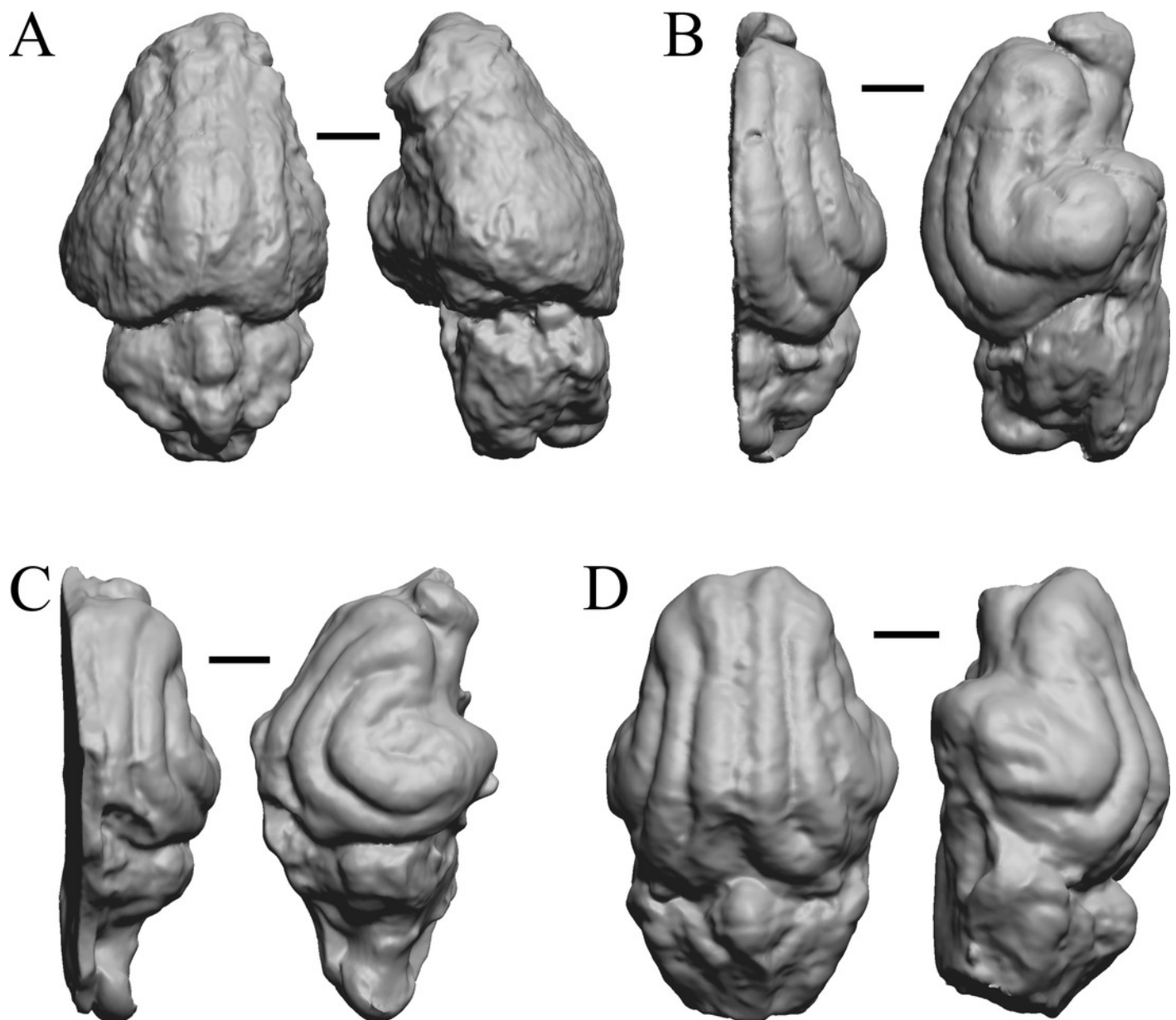
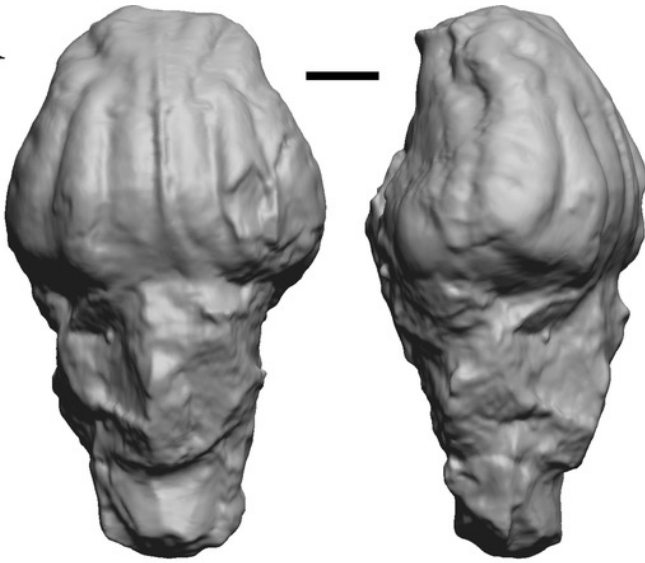


Figure 16

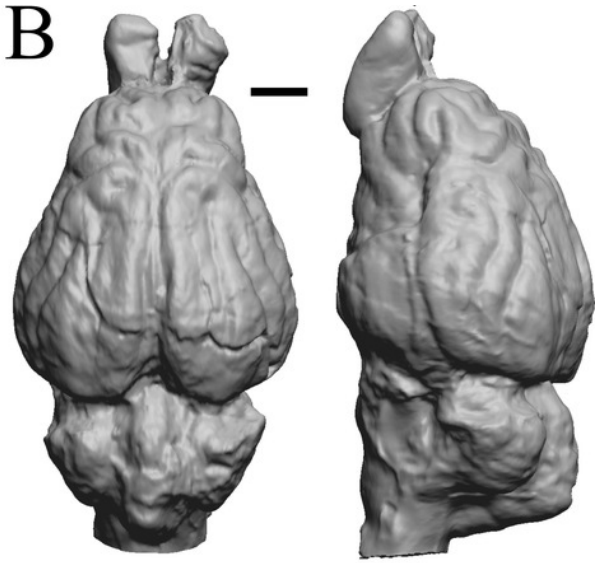
Merycoidodon, *Meshippus*, *Promerycochoerus*, *Hesperocyon*; dorsal and lateral views of endocasts.

(A) *Merycoidodon culbertsoni* (FMNH UM3); the scanned endocast did not include an olfactory bulb region. (B) *Meshippus bairdi* (FMNH-PM59221). (C) *Promerycochoerus superbus* (FMNH PM 59072). (D) *Hesperocyon gregarius* (FMNH PM 58989); sectioned at the midline and the data doubled from the measurements; errors incurred by having only a partial endocast available and, furthermore, the cast of the olfactory bulb and tract is unusually large, adding both to endocast volume and to its total surface area.

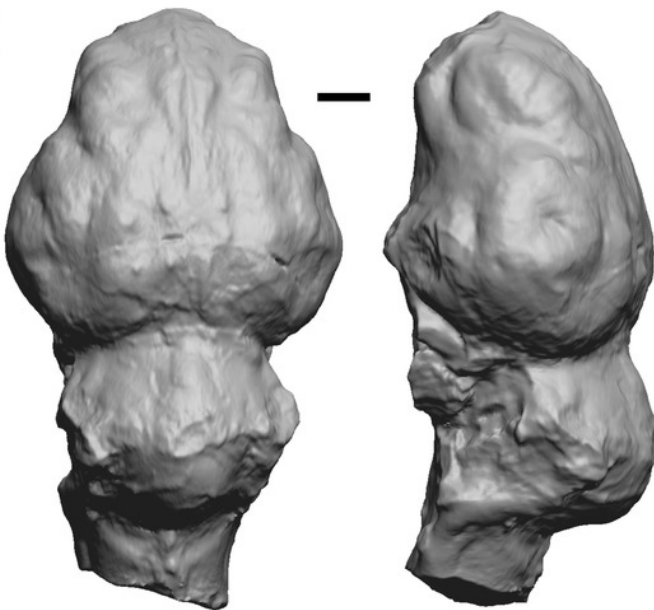
A



B



C



D

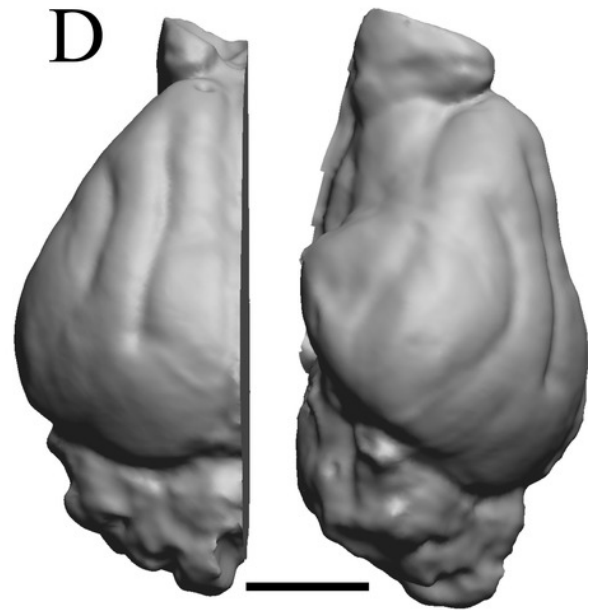
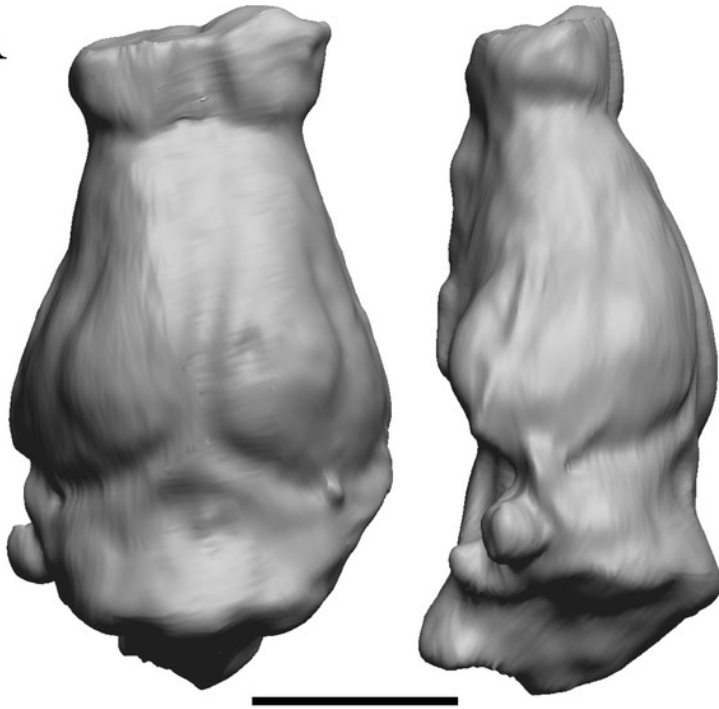


Figure 17

Leptictis (*Ictops*), *Leptauchenia*, *Halitherium*, *Hapalops*; dorsal and lateral views of endocasts.

(A) *Leptictis* (= *Ictops acutidens* Douglass). (B) *Leptauchenia decora* (FMNH PM 59074). (C) *Halitherium schinzi* (SNHM M. 3921); the endocast had a small postorbital extension which I removed. (D) *Hapalops* sp. (LACM).

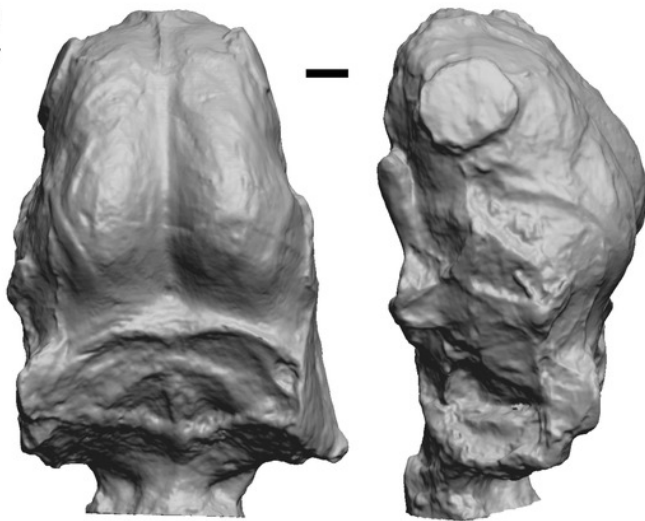
A



B



C



D

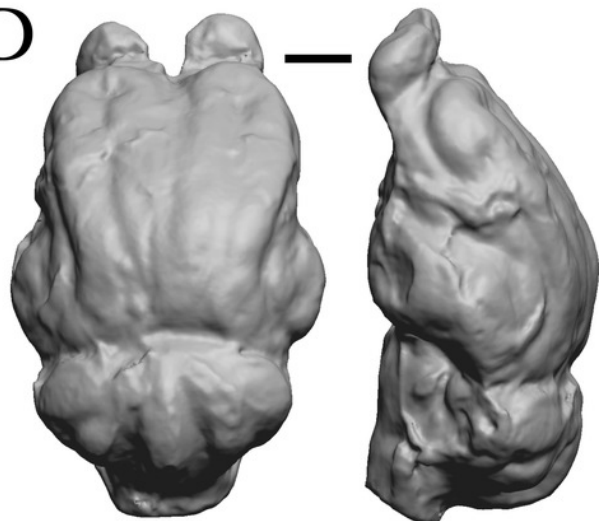


Figure 18

Leontinia, *Rhynchippus*, *Archaeotherium*, *Promartes*; dorsal and lateral views of endocasts.

(A) *Leontinia gaudryi* (FMNH P 13285). (B) *Rhynchippus equinus* (FMNH P 13410). (C) *Archaeotherium mortoni* (FMNH PM 59061). (D) *Promartes olcottii* (FMNH P 25233).

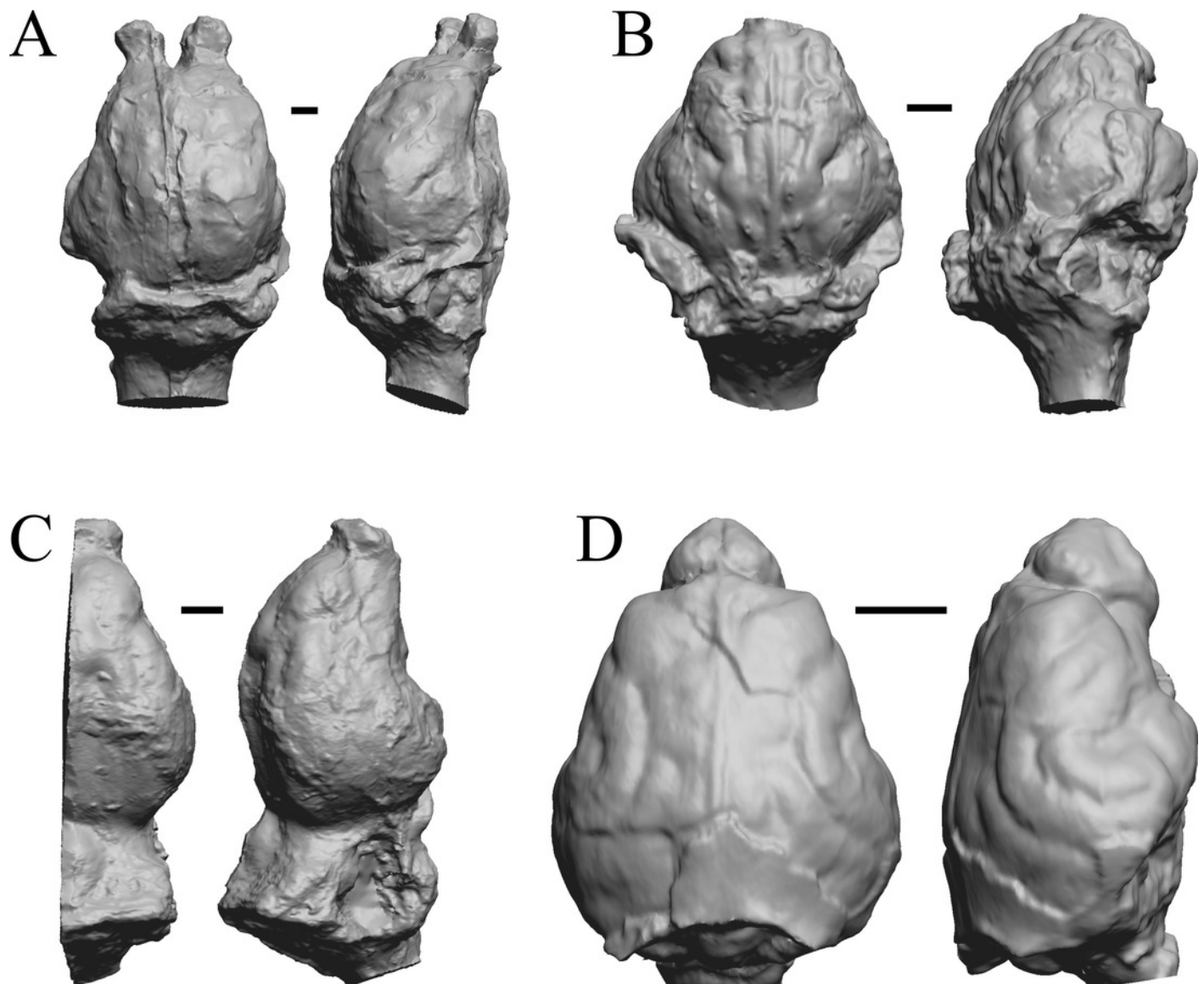


Figure 19

Mesocyon, *Mustelictis*, *Leptocyon*, *Eporeodon*; dorsal and lateral views of endocasts.

(A) *Mesocyon coryphaeus* (FMNH PM 58979). (B) *Mustelictis piveteaui* (FMNH PM 58907). (C) *Leptocyon* sp. (FMNH PM 58961). (D) *Eporeodon socialis* (FMNH PM 59076).

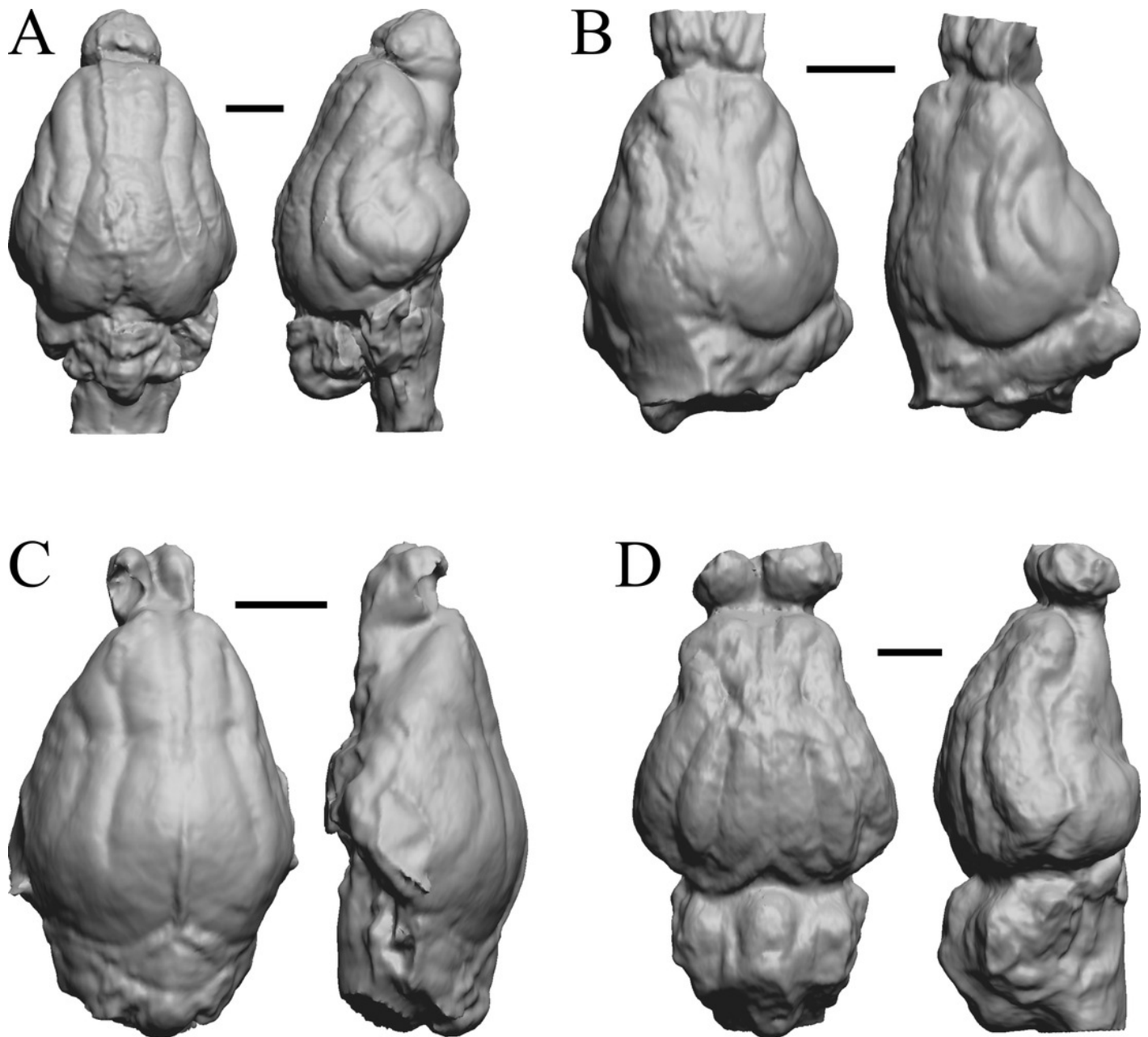


Figure 20

Enaliarctos, *Potamotherium*, *Plesiogale*, *Zodiolestes*; dorsal and lateral views of endocasts.

(A) *Enaliarctos* sp. (FMNH 57161); the well preserved endocast is primarily of forebrain, although the olfactory bulbs are missing, as are some hindbrain (cerebellar) extensions. (B) *Potamotherium valetoni* (FMNH PM 58906). (C) *Plesiogale paragale* (FMNH PM 58910). (D) *Zodiolestes daimonedlixensis* (FMNH P 12032).

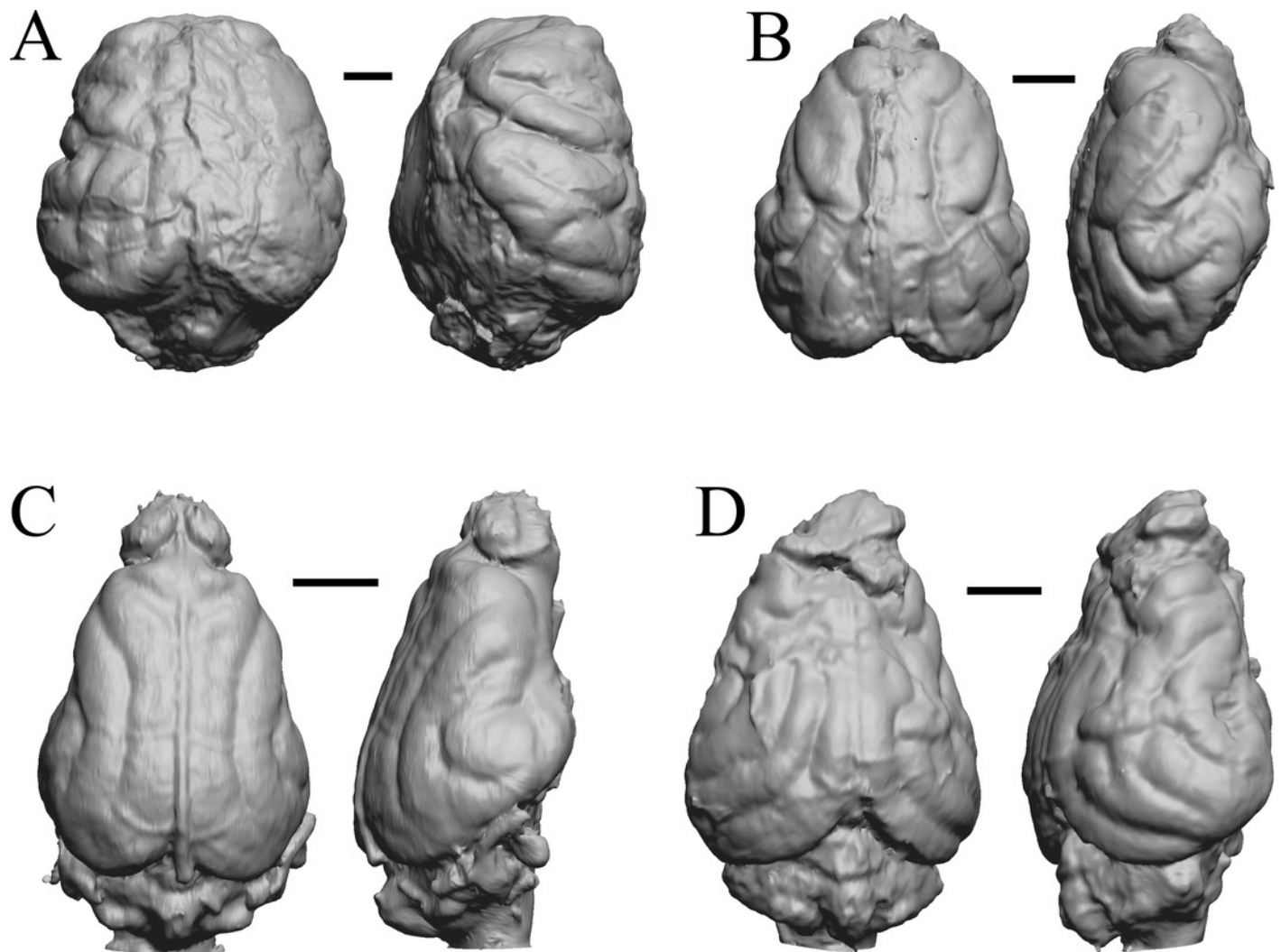


Figure 21

Desmathyus (*Hesperhyus*), *Oxydactylus*, *Homalodotherium*, *Borhyaena*; dorsal and lateral views of endocasts.

Dorsal and lateral views of endocasts. (A) *Desmathyus* sp. (*Hesperhyus*) (FMNH PM 59066). (B) *Oxydactylus longipes* (FMNH P 12117). (C) *Homalodotherium* sp. (FMNH PM 59291). (D) *Borhyaena tuberata* (FMNH P13266).

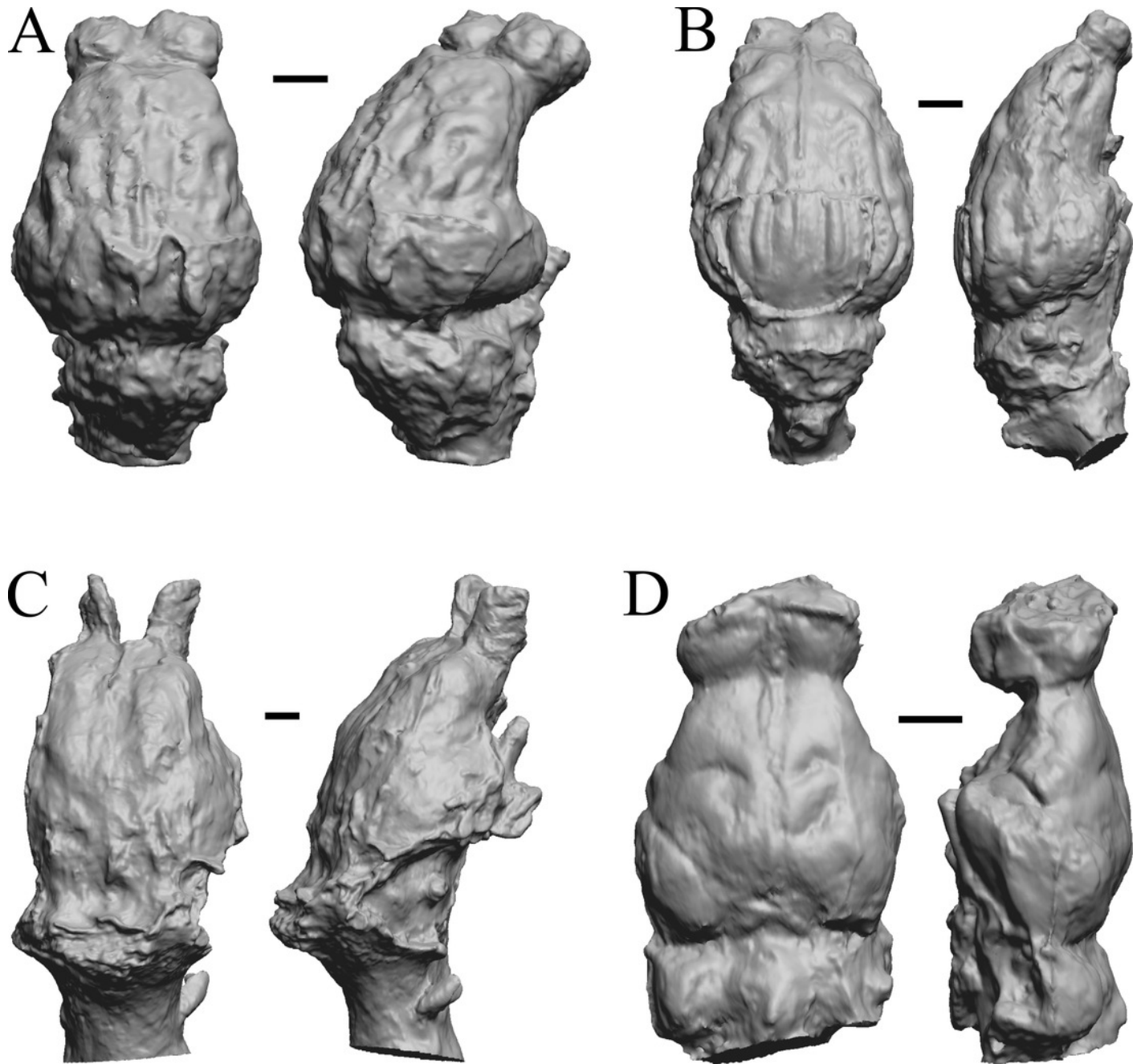


Figure 22

Protypotherium, *Proterotherium*, *Nesodon*, *Merycochoerus*; dorsal and lateral views of endocasts.

(A) *Protypotherium australe* (FMNH P 13046). (B) *Proterotherium cavum* (FMNH PM 59742).
(C) *Nesodon imbricatus* (FMNH P 13076). (D) *Merycochoerus proprius* (FMNH PM 59081).

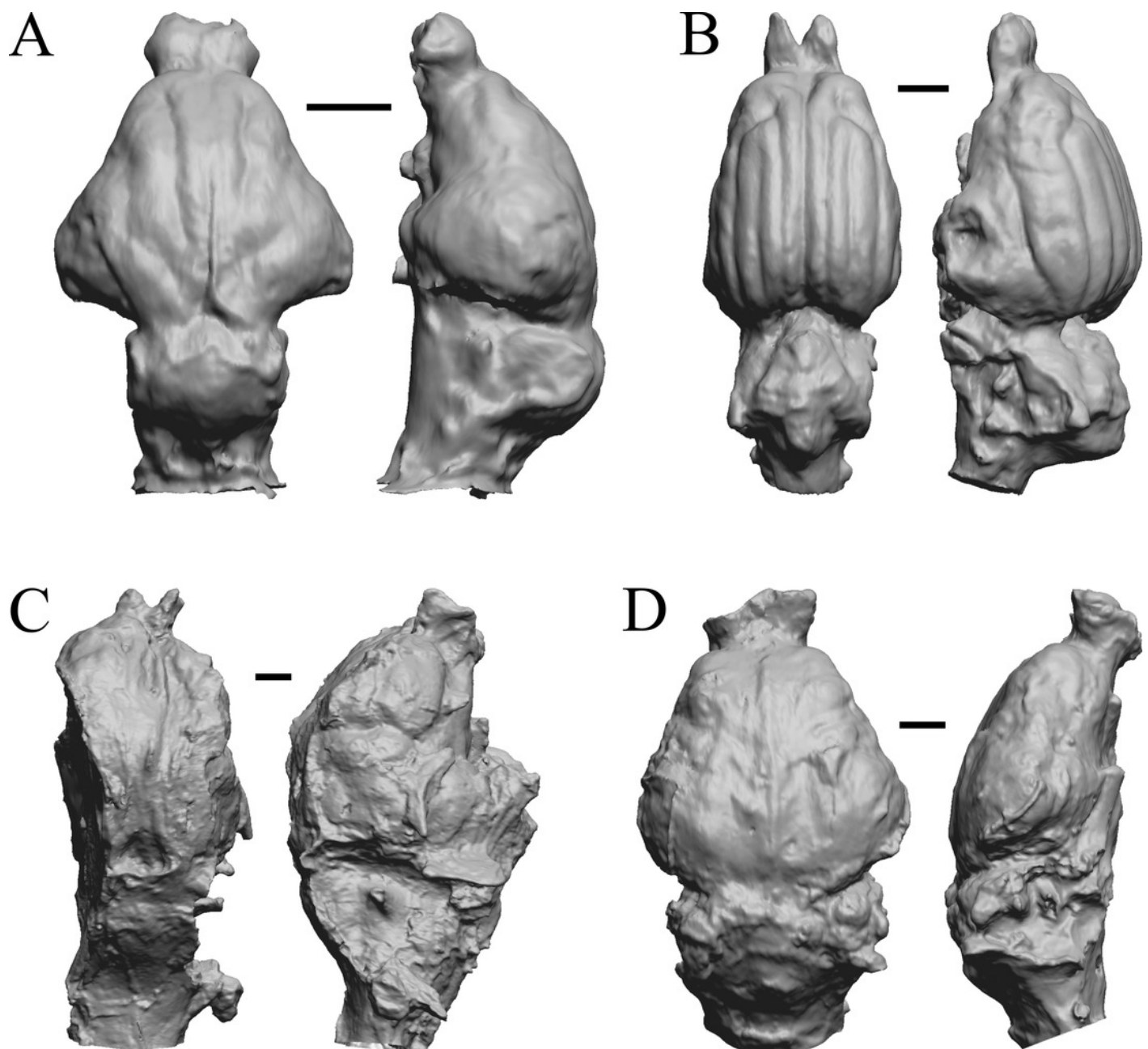


Figure 23

Adinotherium, *Merychippus* (*Atavahippus*), *Plionictis*, *Pseudaelurus*; dorsal and lateral views of endocasts.

(A) *Adinotherium ovinum* (FMNH P 13108I). (B) *Merychippus isonesus* (FMNH PM 59208). (C) *Plionictis* sp. (FMNH PM 58945). (D) *Pseudaelurus validus* (FMNH PM 58867); this species features unusually long olfactory tracts and consequently have enlarged representation of the olfactory system in their brain images.

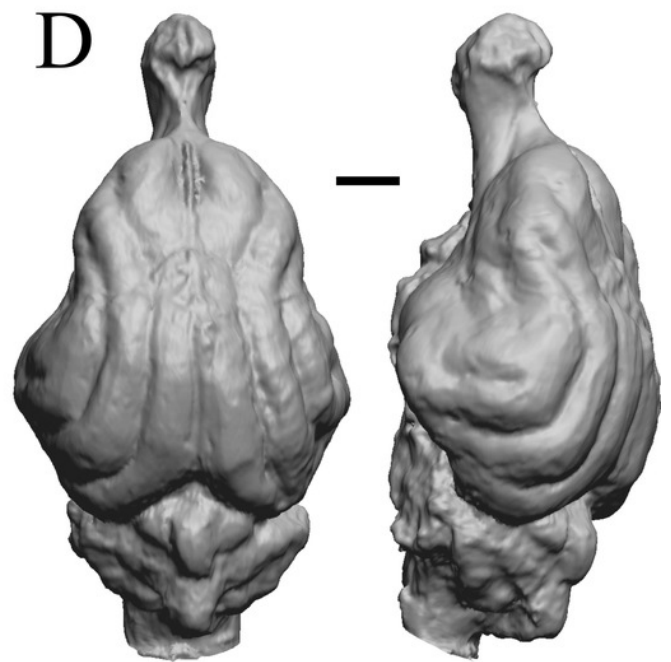
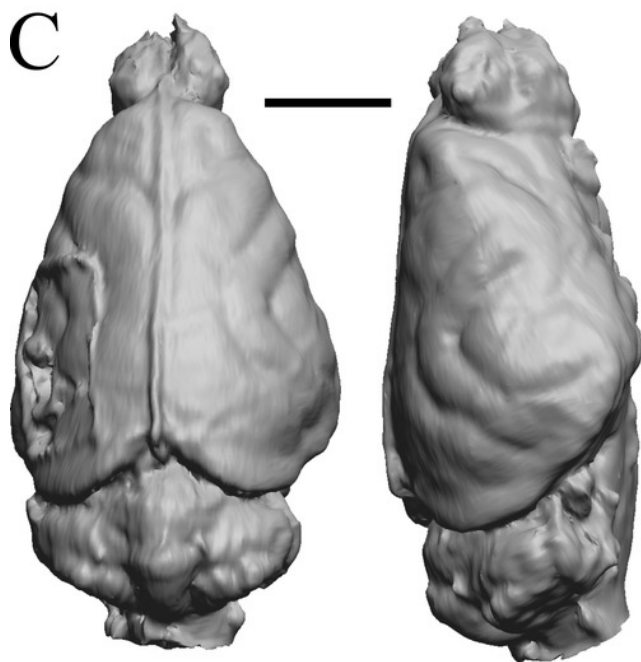
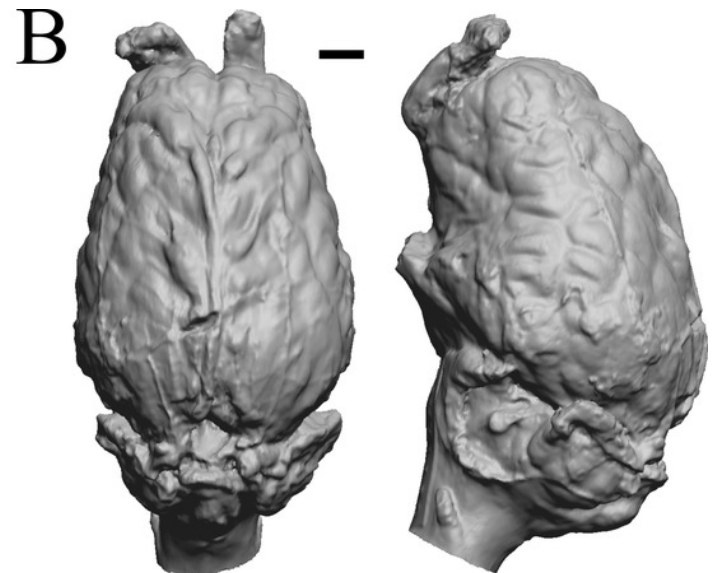
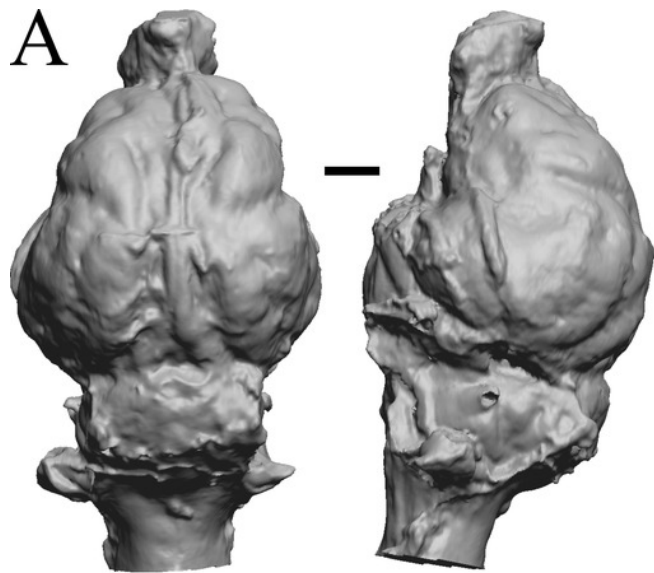


Figure 24

Paracynarctus, *Ustatochoerus*, *Carpocyon* ("Osteoborus"), *Pseudhipparion*.; dorsal and lateral views of endocasts.

(A) *Paracynarctus sinclairi* (FMNH PM 58973). (B) *Ustatochoerus profectus* (FMNH PM 59071); the endocast is enlarged in the cerebellar region, so in light of the likely significant overestimate of its endocast size, it is reasonable to conclude that it was comparable to living species in encephalization. (C) *Carpocyon webbi* (FMNH PM 58964). (D) *Pseudhipparion gratum* (FMNH PM59211).

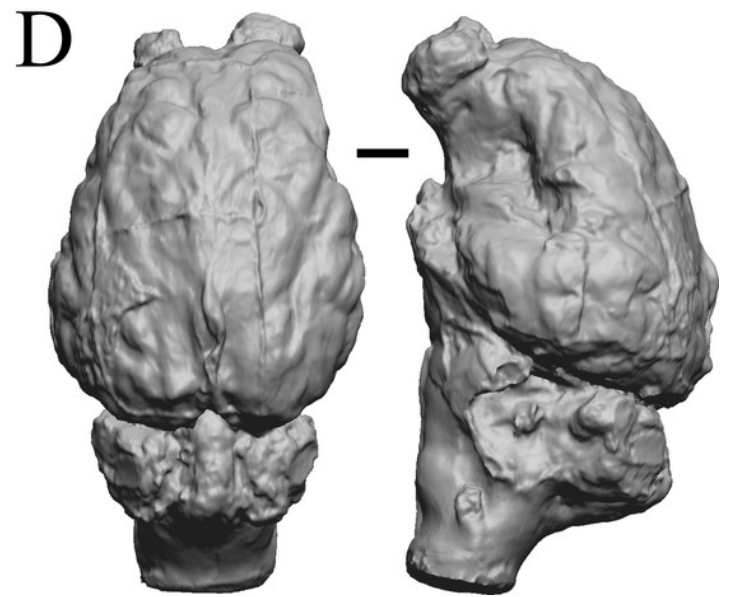
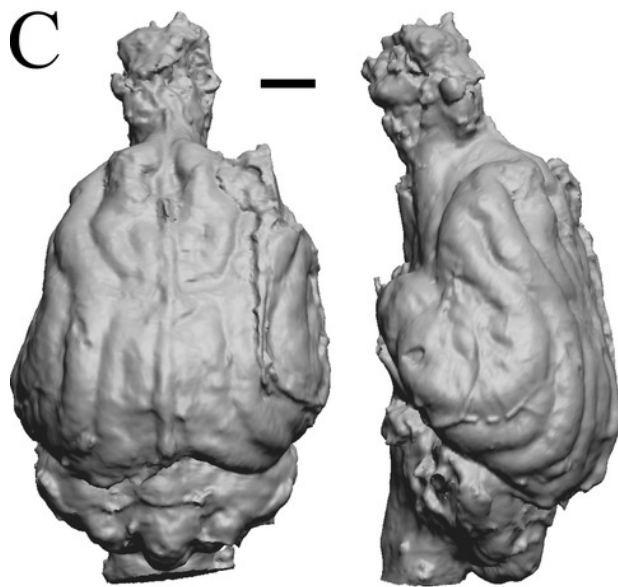
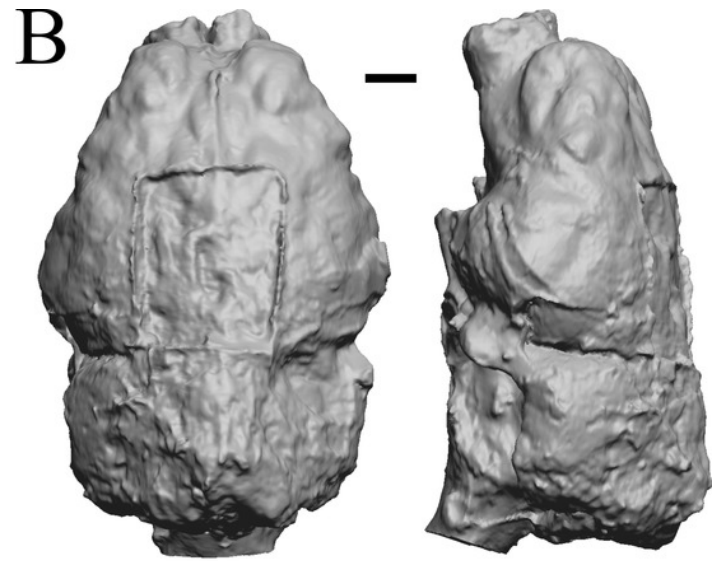
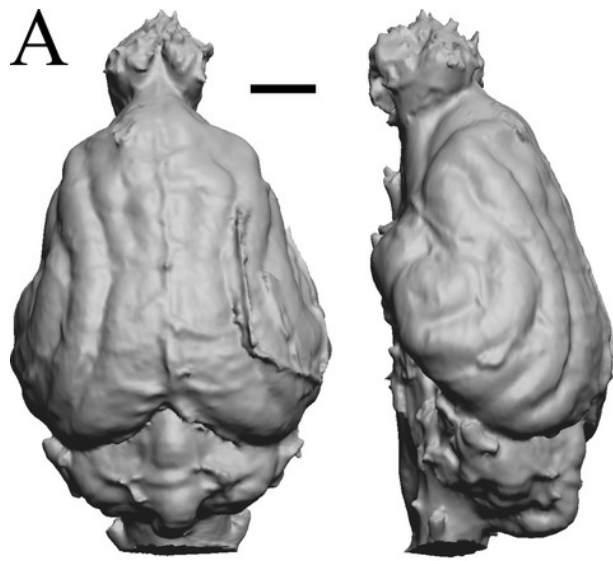


Figure 25

Paratomarctus, *Hemicyon*, *Pseudotypotherium*, *Tyopotheriopsis*; dorsal and lateral views of endocasts.

Dorsal and lateral views of endocasts. (A) *Paratomarctus euthos* (FMNH PM 58958). (B) *Hemicyon* cf. *barbouri* (FMNH PM 59030). (C) *Pseudotypotherium pseudopachygnathum* (FMNH PM59292). (D) *Tyopotheriopsis internum* (FMNH P 14420).

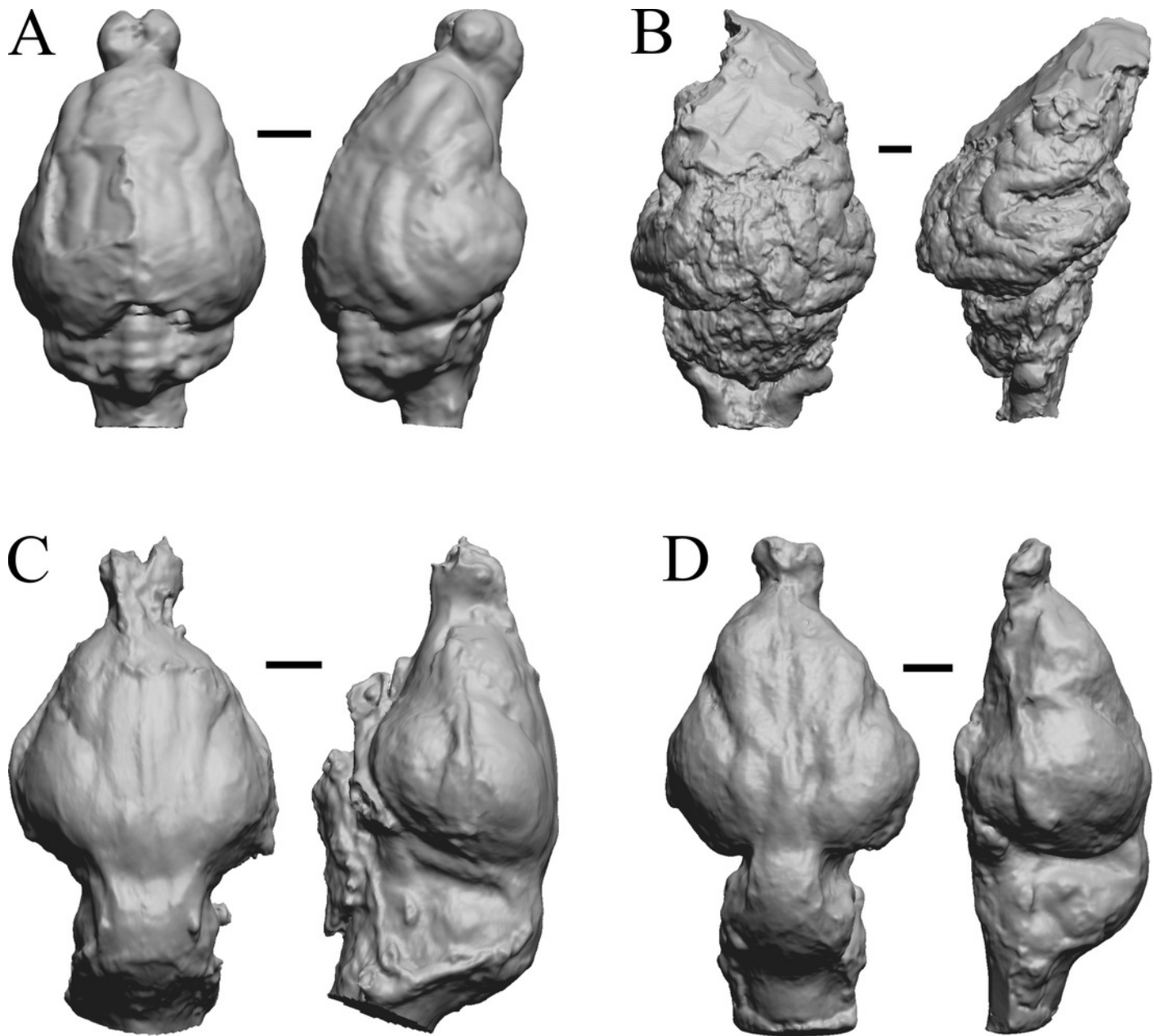


Figure 26

Cormohipparion, *Procamelus*, *Homotherium*, *Mylodon*; dorsal and lateral views of endocasts.

(A) *Cormohipparion occidentale* (FMNH PM 59220). (B) *Procamelus grandis* (FMNH PM 59160). (C) *Homotherium ischyrosmilus* (FMNH PM 58891). (D) *Mylodon* sp. Owen (1840) (LACM 157696).

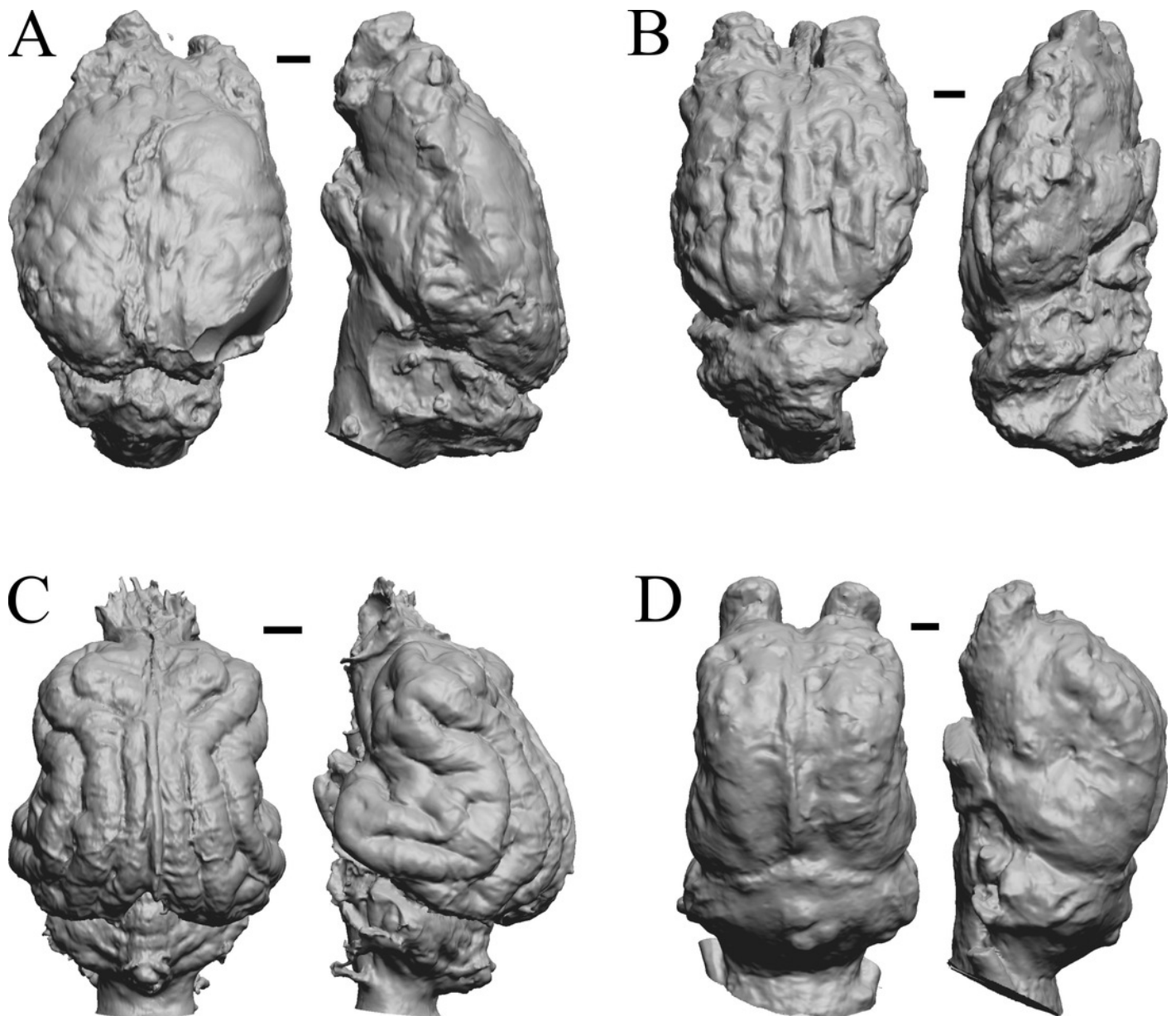


Figure 27

Glossotherium, *Arctodus*, *Canis dirus*, *Megalonyx*; dorsal and lateral views of endocasts.

(A) *Glossotherium harlani* (LACM 1717-33). (B) *Arctodus simus* (*Tremarctotherium*) (LACM).
(C) *Canis dirus* (LACM). (D) *Megalonyx jeffersoni* (LACM).

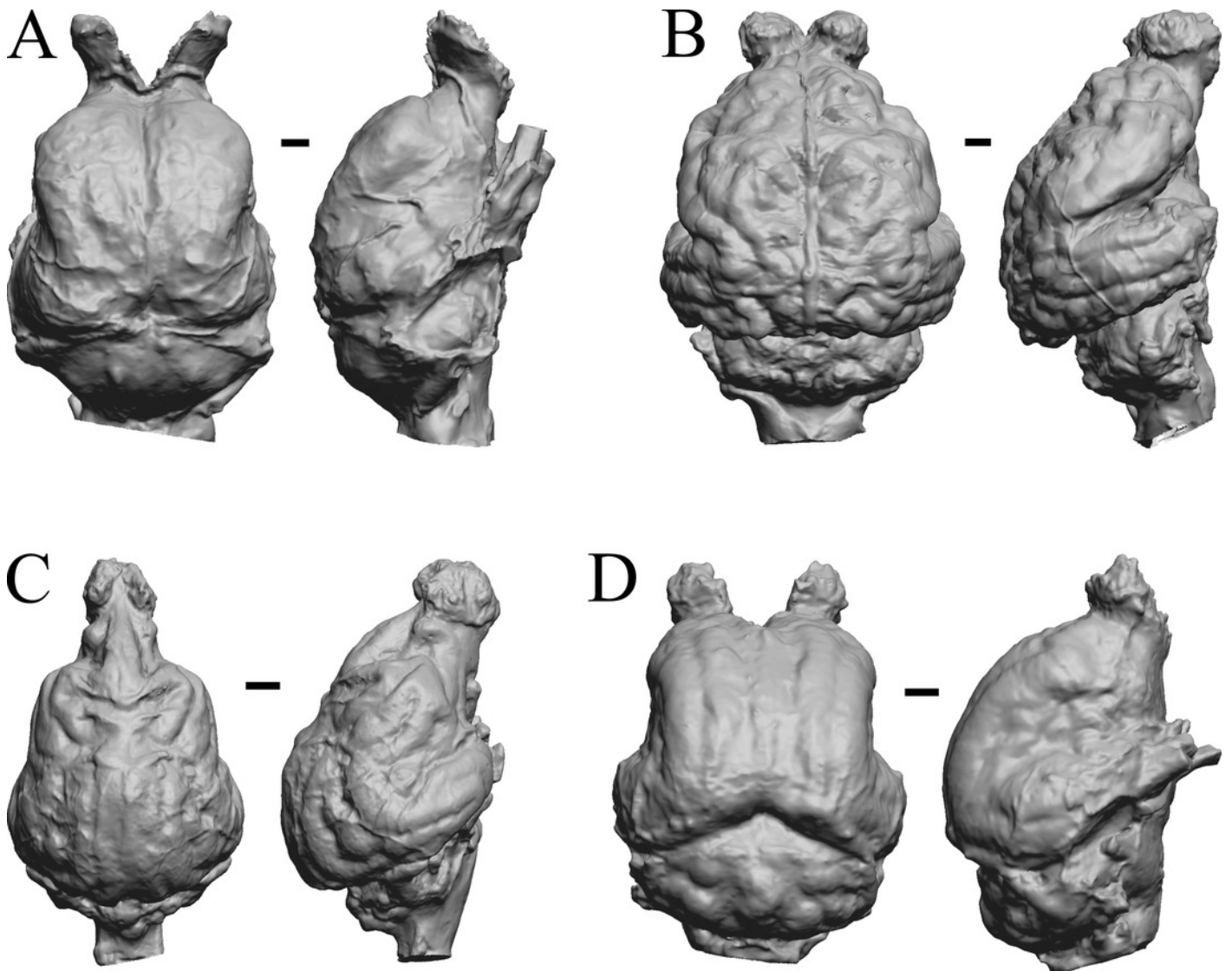


Figure 28

Nothrotheriops, *Panthera*, *Smilodon*, *Urocyon*; dorsal and lateral views of endocasts.

(A) *Nothrotheriops shastensis* (LACM C-3). (B) *Panthera leo atrox* (LACM). (C) *Smilodon fatalis* (LACM). (D) *Urocyon cinereoargenteus* (LACM).

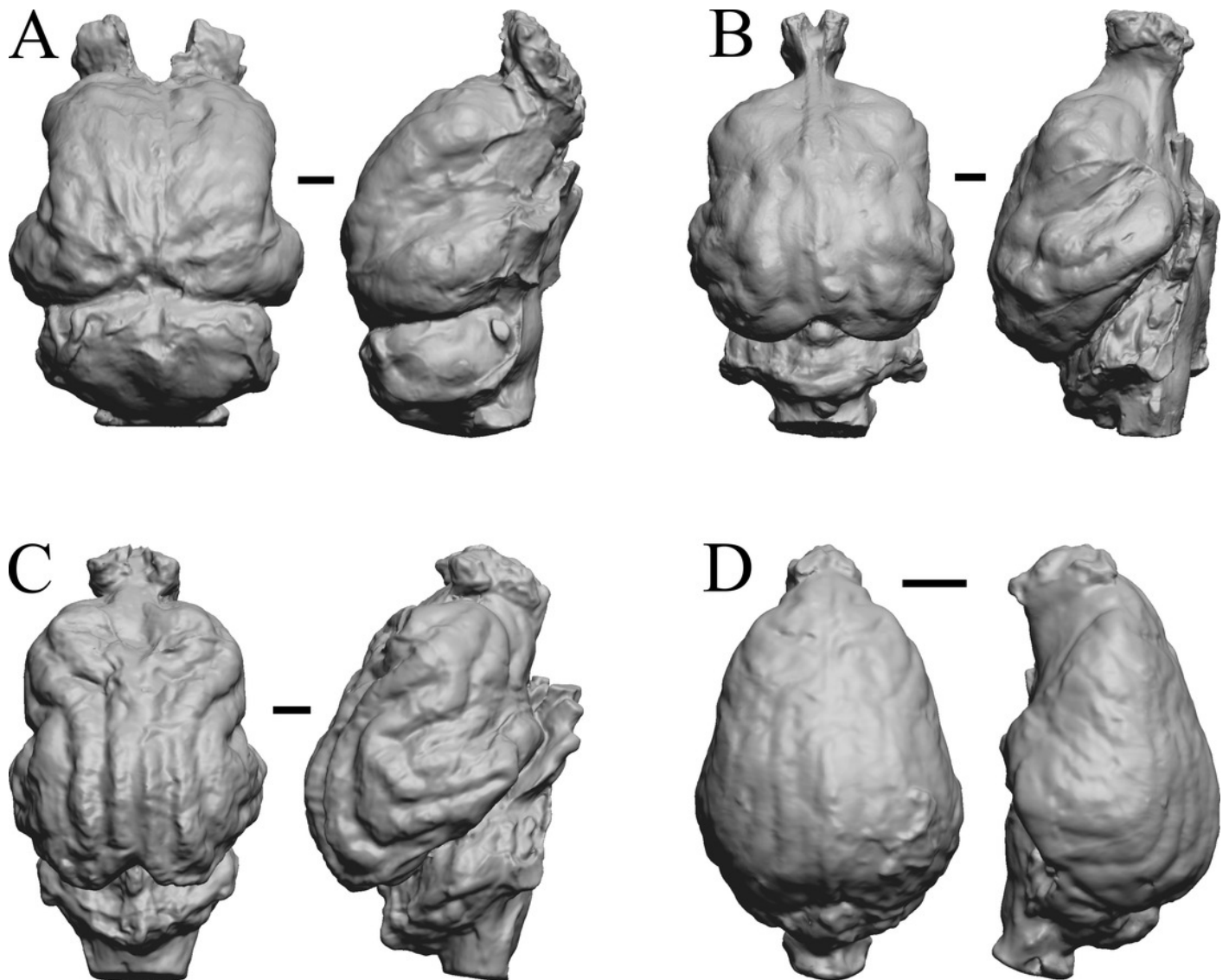


Figure 29

Platygonus, *Sthenurus*, *Thylacoleo*, *Archaeolemur*; dorsal and lateral views of endocasts.

(A) *Platygonus compressus*. (FMNH PM 59058); only half of the endocast was preserved, but it was a relatively clean half, easy to double to estimate its measurements. (B) *Sthenurus* cf. *S. orientalis* (FMNH PM 59245). (C) *Thylacoleo carnifex* (FMNH PM 59244); it is worth noting that the characteristic gyri of the felid and canid endocasts are not a feature of this marsupial carnivore. In felids and canids, the ectosylvian gyri are useful maps of the auditory cortex; they are not a feature in the marsupial. (D) *Archaeolemur majori* (FMNH PM 59258).

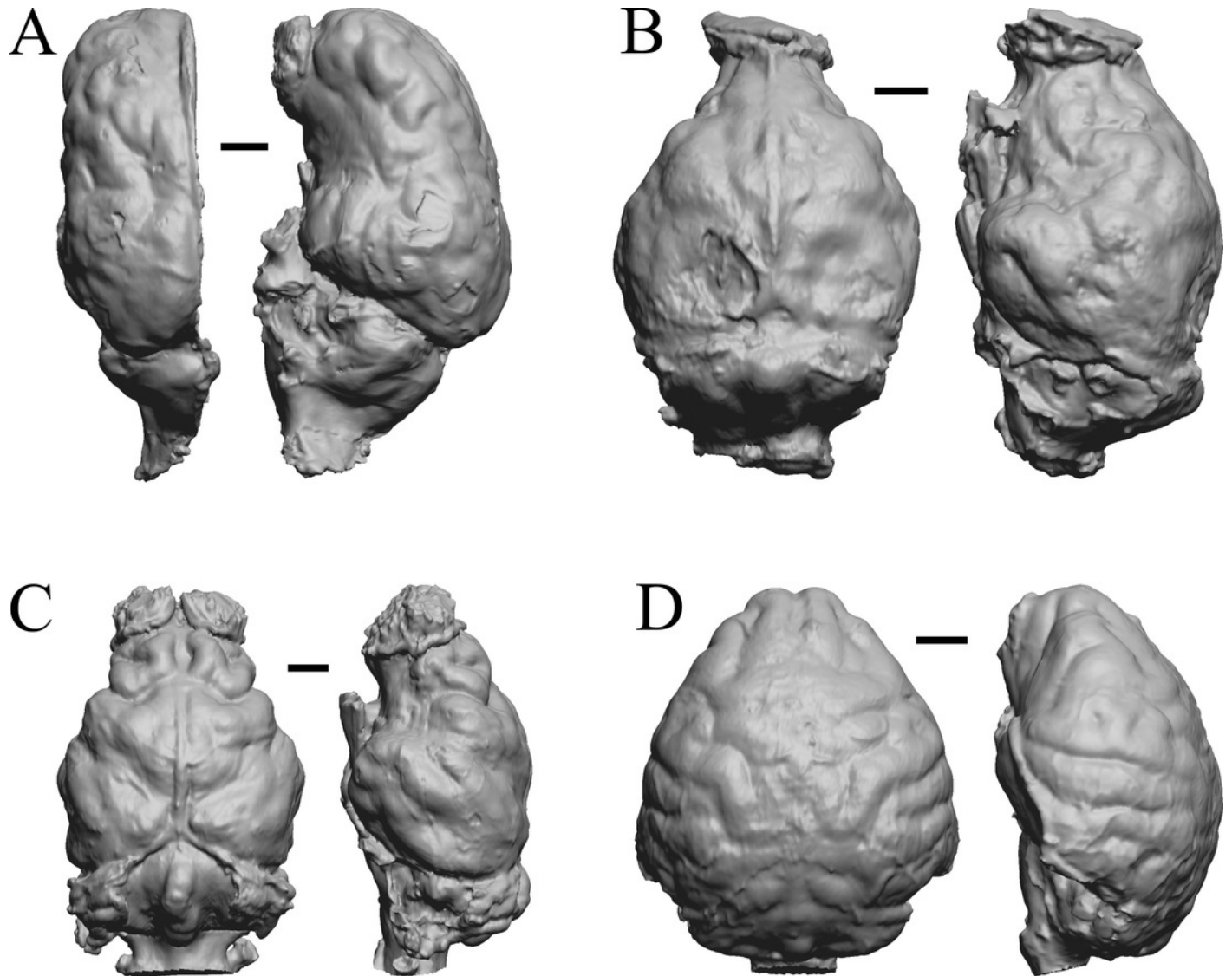


Figure 30

Pachylemur (Lemur) insignis, *Palaeopropithecus*, *Australopithecus robustus*, *Australopithecus africanus*; dorsal and lateral views of endocasts.

(A) *Pachylemur insignis* (FMNH PM 59253). (B) *Palaeopropithecus maximus* (FMNH PM 59250). (C) *Australopithecus robustus* (SK1585). (D) *Australopithecus africanus* Taung (left scan has frontal pole at bottom).

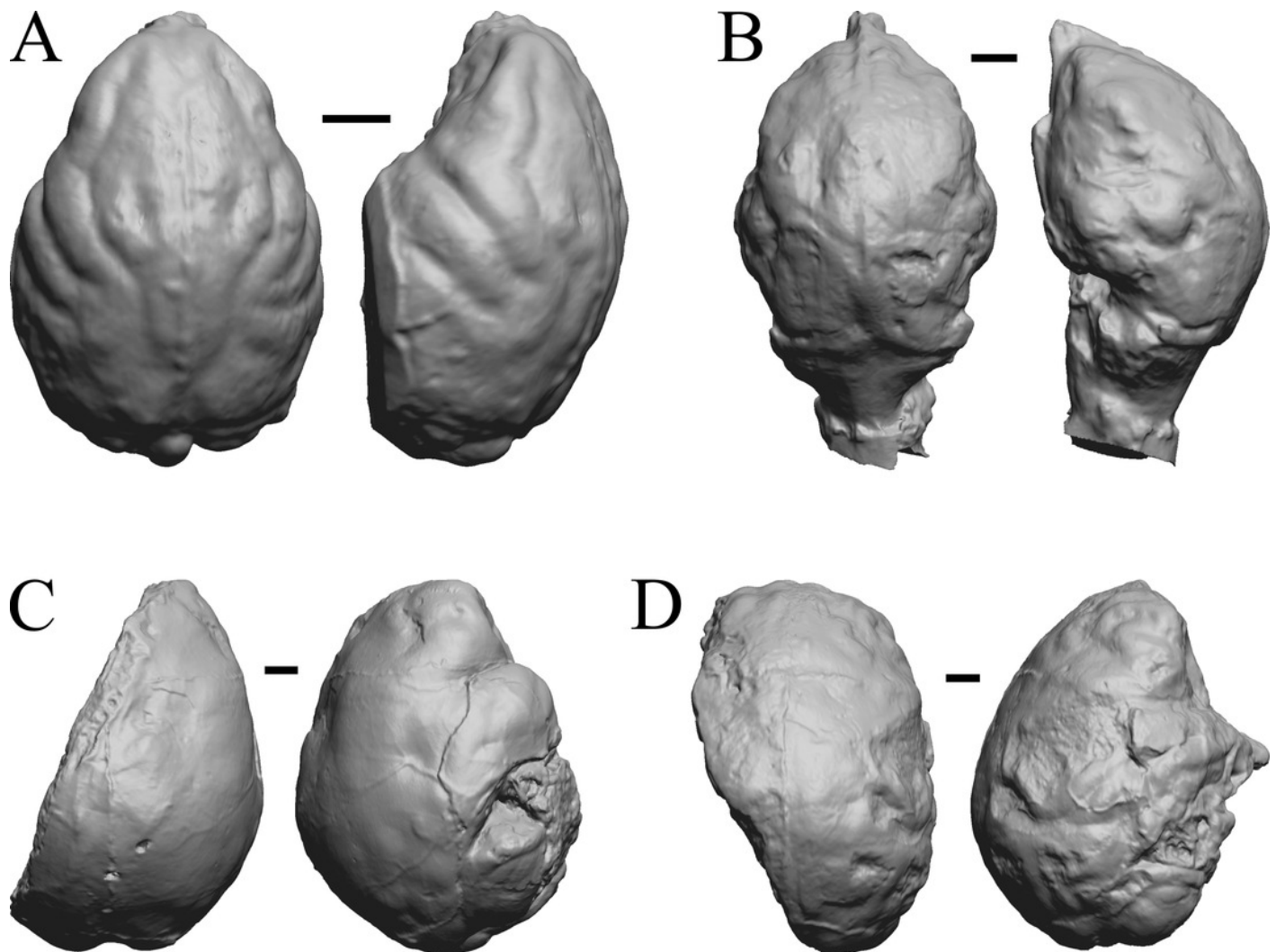


Figure 31

Dorudon, *Argyrocerus*, *Aulophyseter*, *Tursiops*; endocasts and brain.

(Left panel top) *Dorudon atrox* (NHMUK 10173); the endocast shows some non-neural material. (Left panel center) *Argyrocerus joaquinensis* (UCMP 99668). (Left panel bottom) *Aulophyseter morricei* (LACM 3161/131912). (Right panel) Three views of brain of *Tursiops truncatus* (WISC 66-130): top: lateral view; center: dorsal view; bottom: ventral view, anterior to right.

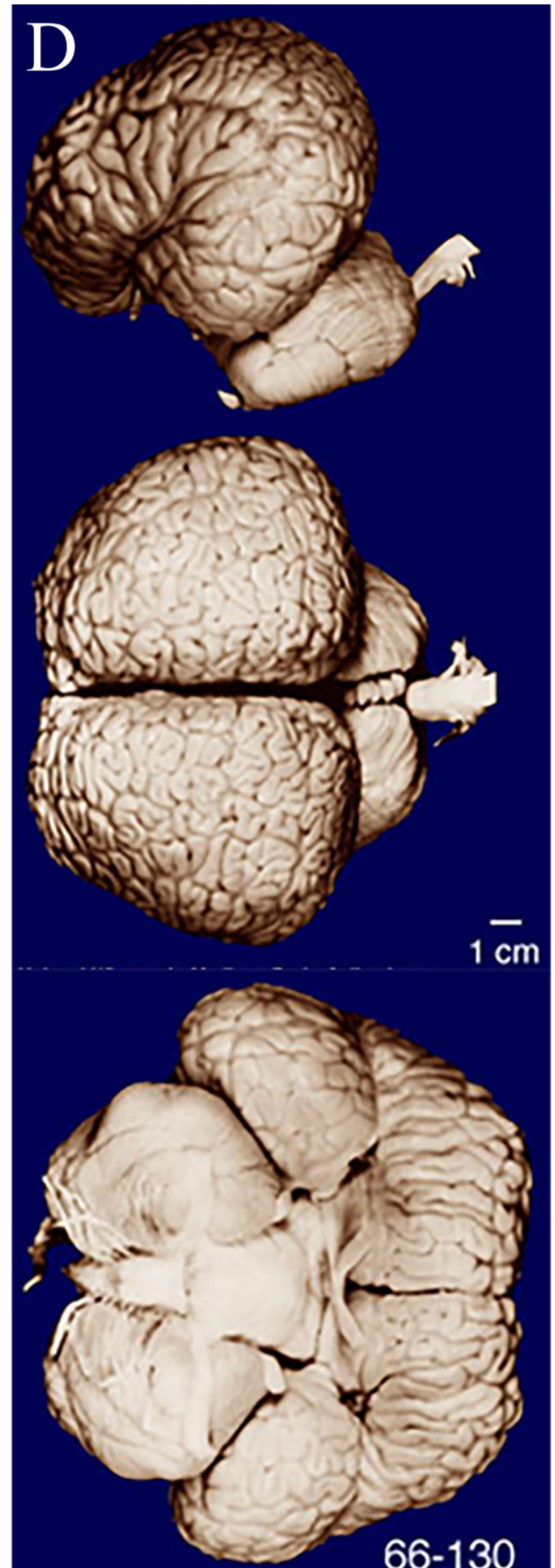
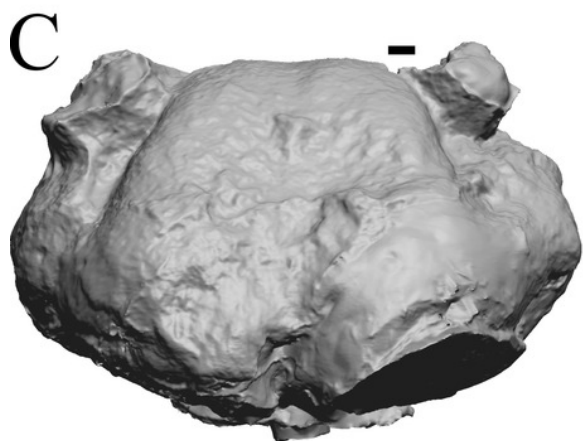
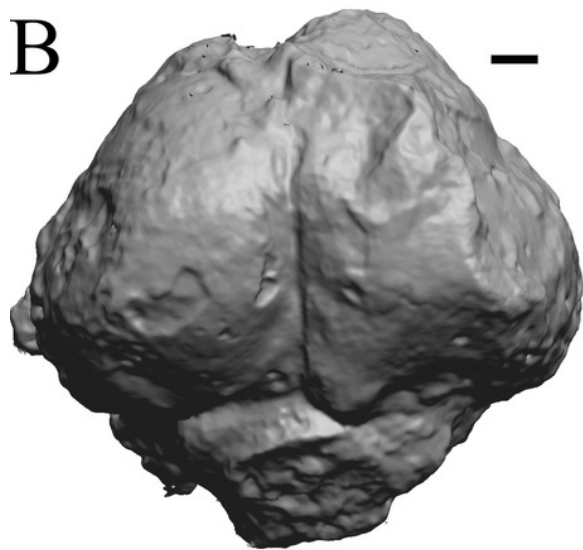
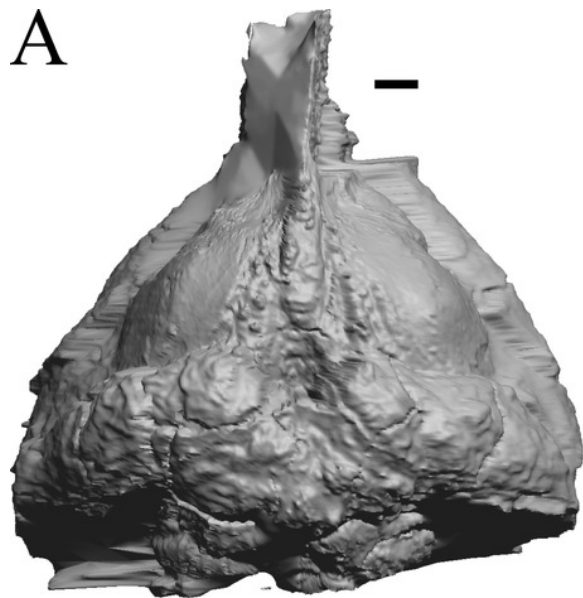


Figure 32

Aonyx, *Ursus* (Black Bear), *Canis latrans*, *Felis catus*; dorsal and lateral views of endocasts.

(A) *Aonyx* (*Amblyonyx*) *cineria* (Radinsky Specimen 358). (B) *Ursus americanus* (LACM). (C) *Canis latrans* (LACM 2007). (D) *Felis catus* (Radinsky Specimen 101).

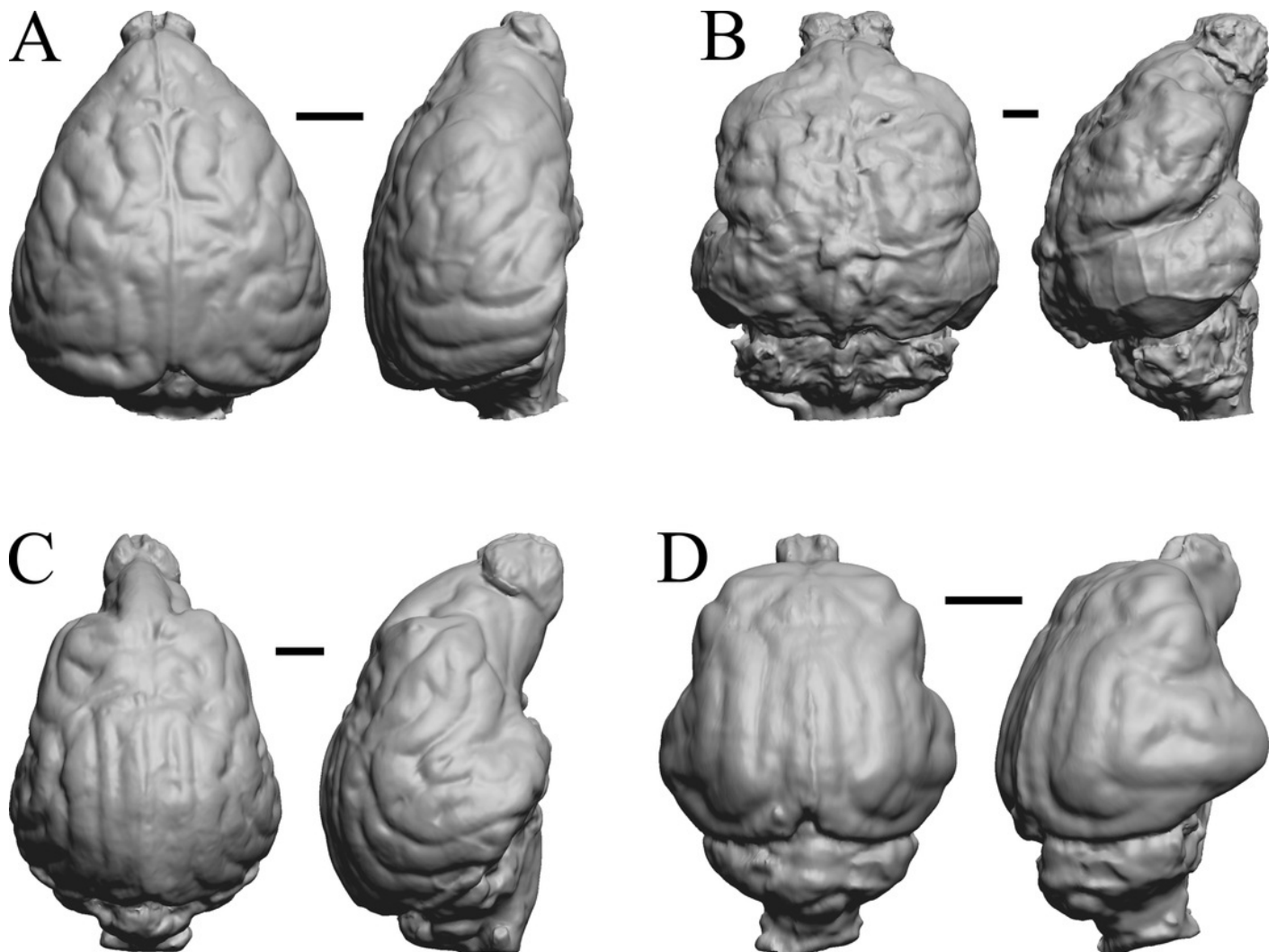


Figure 33

Cerdocyon, *Odocoileus*, *Ursus* (Kodiak), *Lama*; dorsal and lateral views of endocasts and braincasts.

(A) *Cerdocyon thous* endocast (Radinsky Specimen 294). (B) *Odocoileus virginianus* braincast (WISC 67-81); approximately half of the braincast was available. (C) *Ursus* endocast (Kodiak LACM). (D) *Lama glama* braincast (WISC 65-139); note how much more detail shows on a brain than on an endocast.

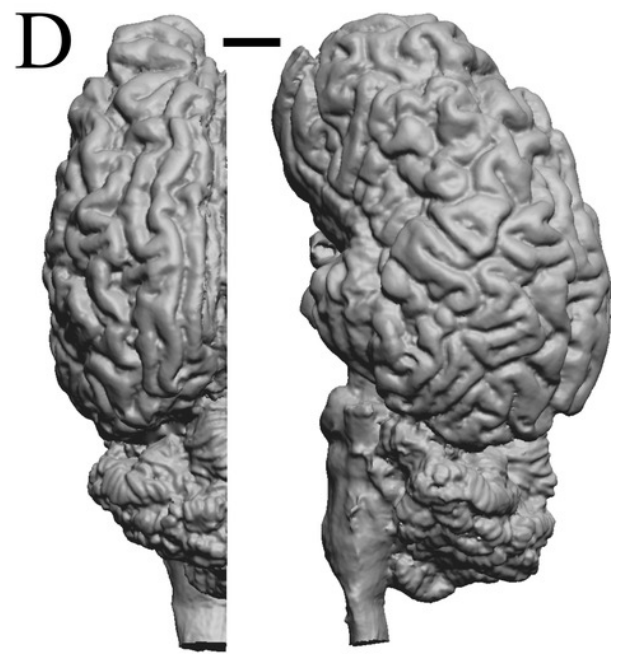
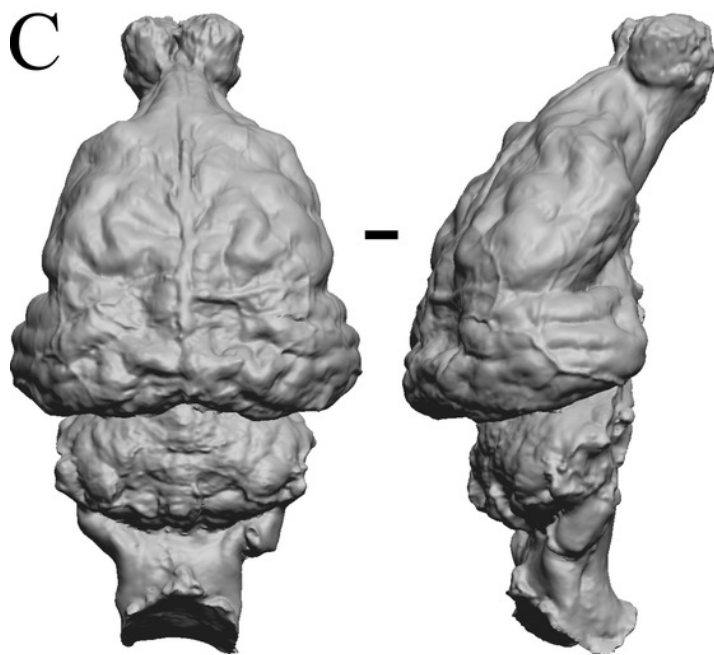
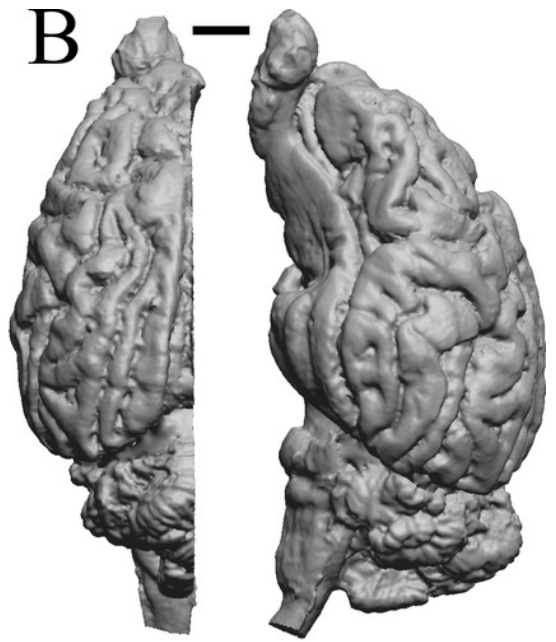
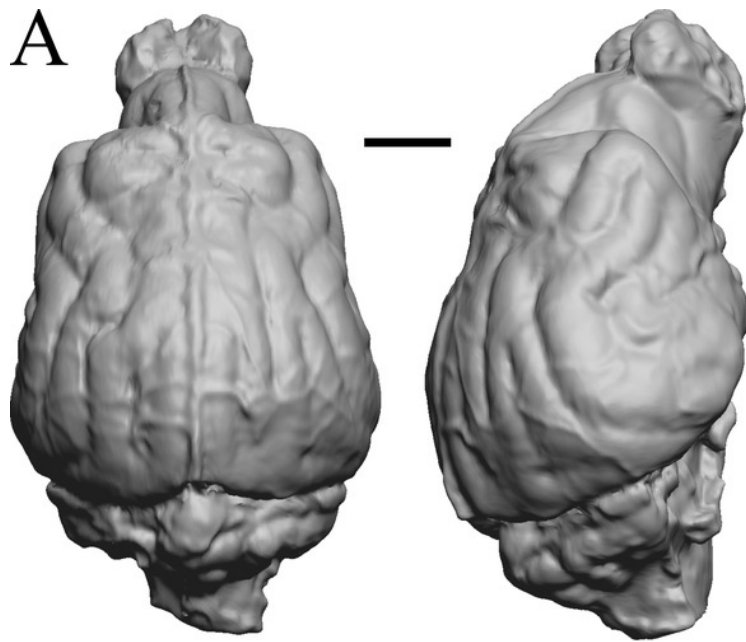


Figure 34

Lutra lutra, *Lutra canadensis*, *Procyon* endocast and braincast, *Nasua*; dorsal and lateral views of endocasts and braincasts.

(A) *Lutra lutra* endocast (Radinsky Specimen 366). (B) *Lutra canadensis* endocast (Radinsky Specimen 129). (C) *Procyon lotor* endocast (Radinsky Specimen 154). (D) *Procyon lotor* braincast (WISC 61-824). (E) *Nasua narica* braincast (WISC 62-404). D and E compare the scans of the raccoon (D) and coati (E) brains. These are not endocranial casts; they are of brains and show their external appearance vividly, although sulcal depths are obscured when casting whole brains. It is clear that although these brains are similar, they are not identical, and it is difficult to make localizations.

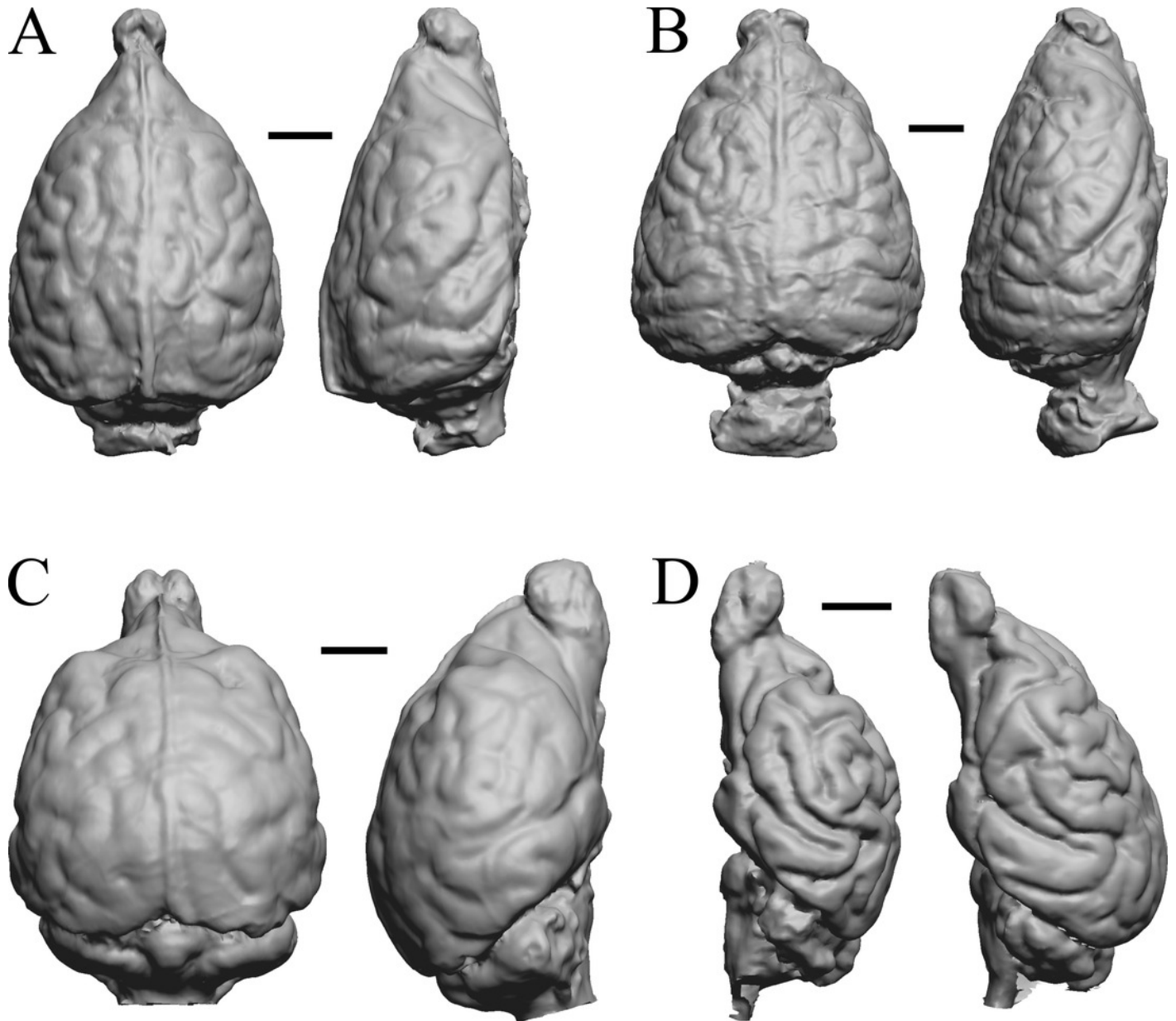


Figure 35

Phascolarctos, *Macropus*, *Vombatus*, *Taxidea*; dorsal and lateral views of endocasts and braincasts.

(A) *Phascolarctos cinereus* endocast (Adelaide; see also Figure 50). (B) *Macropus fuliginosus* braincast (MSU 64023); the braincast measurements are hardly comparable to those on the endocast because so much midbrain surface is measurable. (C) *Vombatus ursinus* endocast (NMA Specimen C7780); half endocast shown. (D) *Taxidea taxus* endocast (Radinsky Specimen 360).

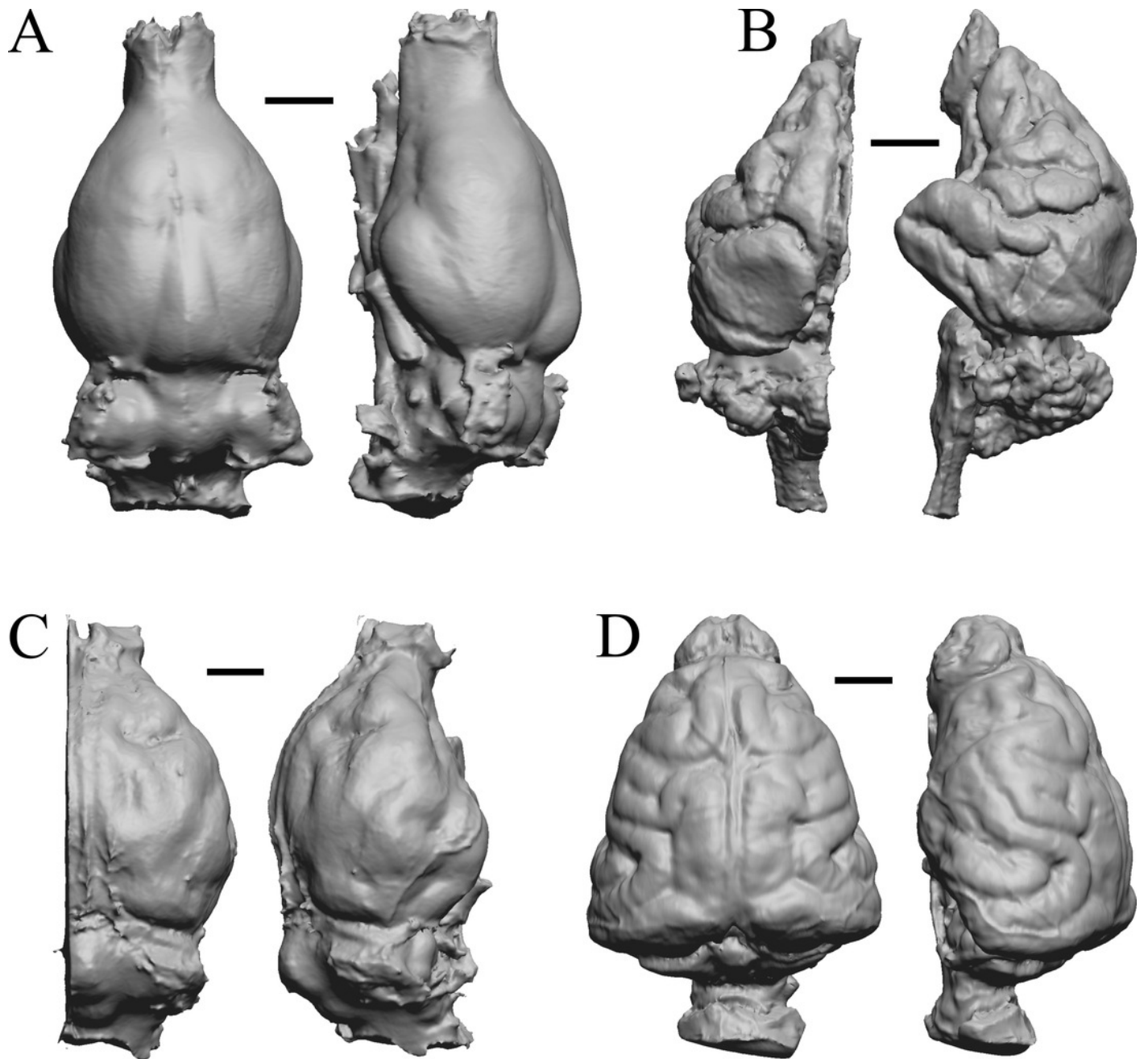


Figure 36

Chiropotes, Mandrill, *Homo*-Falk A, *Homo*-Falk B; endocasts.

(A) *Chiropotes albinansa* (FM 94927). (B) *Mandrillus sphinx* (AMNH AM 274). (C) *Homo sapiens* (Falk A). (D) *Homo sapiens* (Falk B). The ventrolateral view exposes more of the rhinal fissure, though it is not easy to trace it in this figure; the fissure is often hidden in more familiar lateral views in primates.

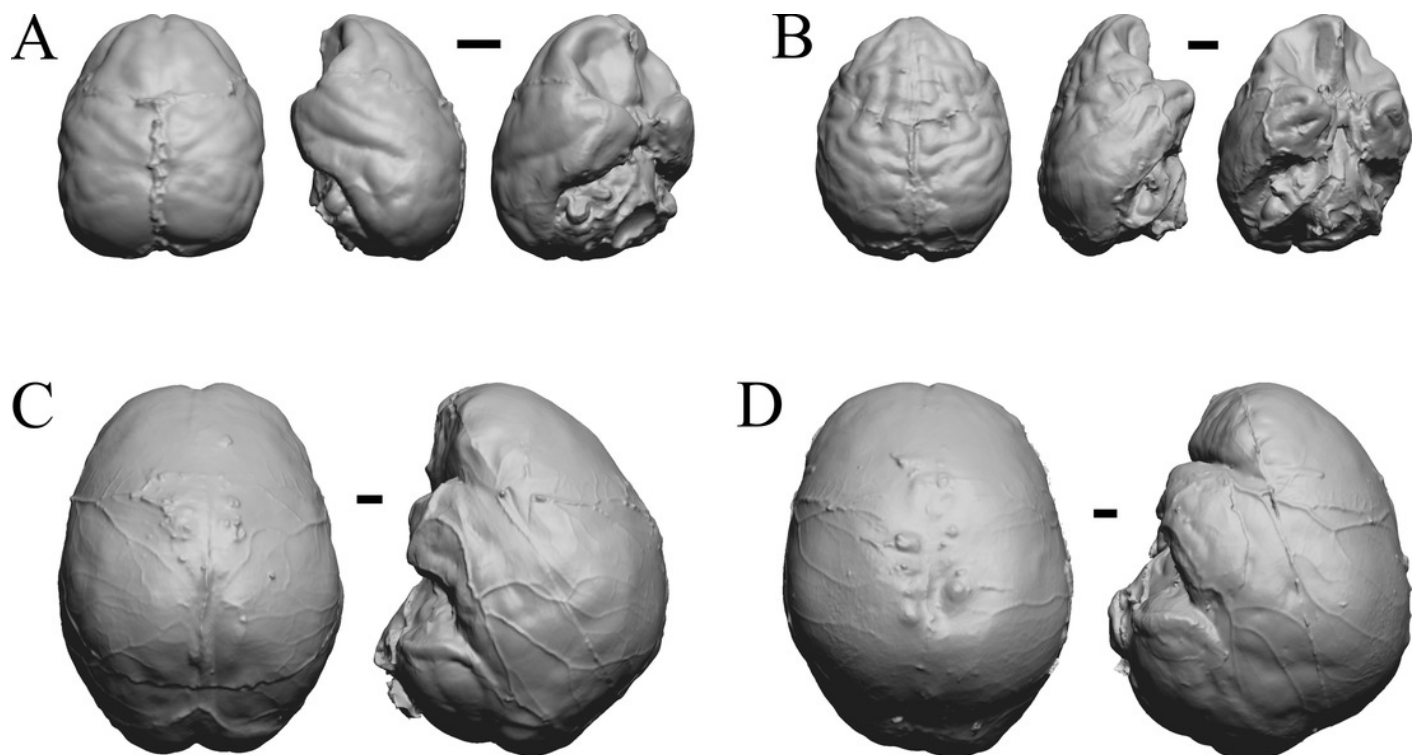


Figure 37

Sixteen primate endocasts and braincasts, lateral views, forebrain left.

1. *Homo sapiens* endocast 2. *Pan troglodytes* endocast 3. *Pan troglodytes* braincast 4. *Colobus guereza* endocast 5. *Erythrocebus patas* endocast 6. *Hylobates lar* endocast 7. *Macaca mulatta* braincast 8. *Nasalis larvatus* endocast 9. *Pithecia monachus* endocast 10. *Presbytis johnii* endocast 11. *Rhinopithecus (Pygathrix) avunculis* endocast 12. *Pygathrix nigripes* endocast 13. *Simias concolor* endocast 14. *Theropithecus gelada* endocast 15. *Cercocebus albigena* endocast 16. *Cercopithecus pygenthus* endocast. The brain images of chimpanzee and rhesus monkey are of somewhat shrunken specimens prepared from preserved brains used in electrophysiological studies on the right hemispheres. The olfactory bulb areas are small enough in all of these primate specimens to be disregarded.

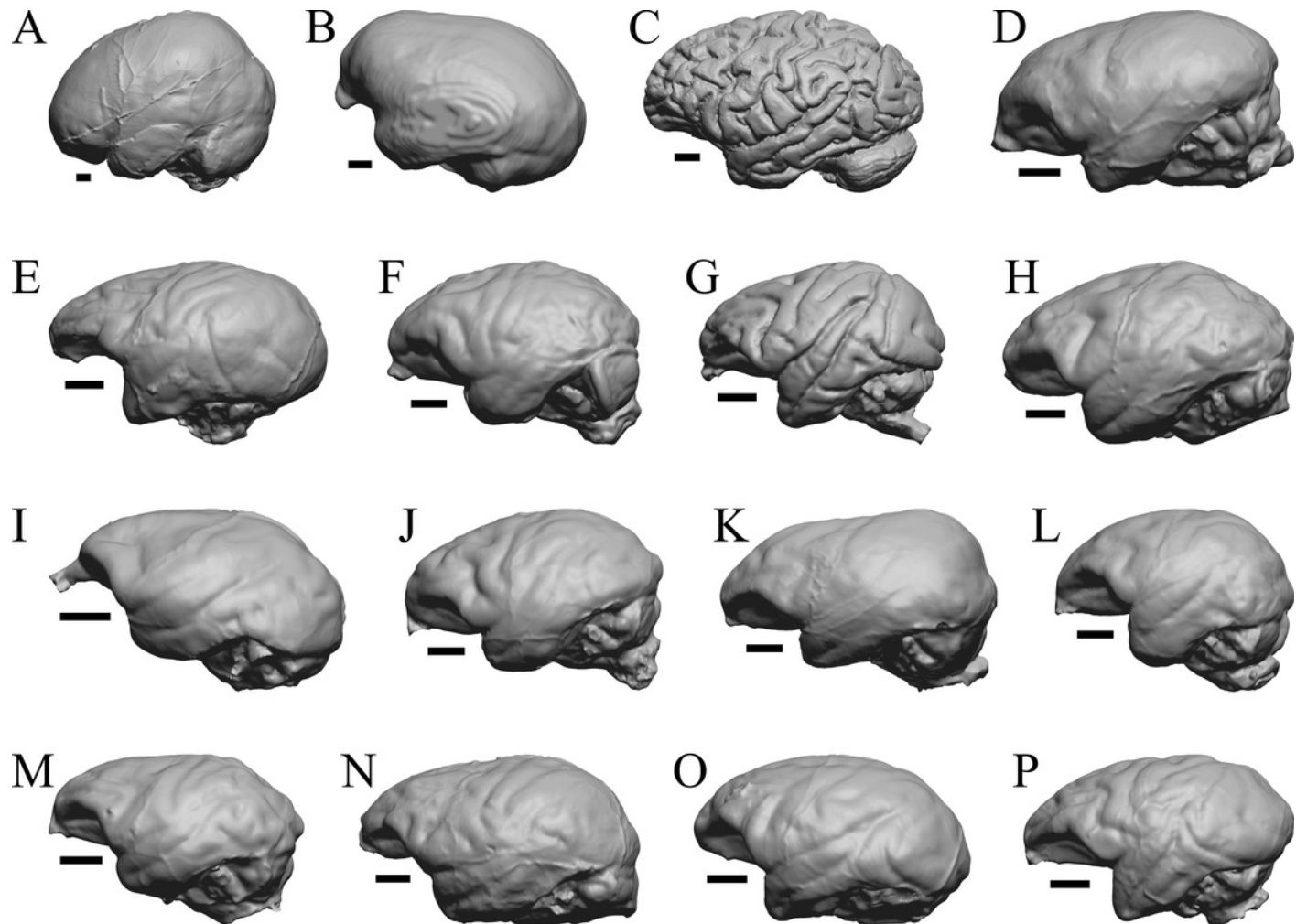


Figure 38

Neocorticalization and geological age.

(A) Neocorticalization as a function of geological age in 155 scanned specimens. (B)

Neocorticalization as a function of geological age in 122 scanned fossils.

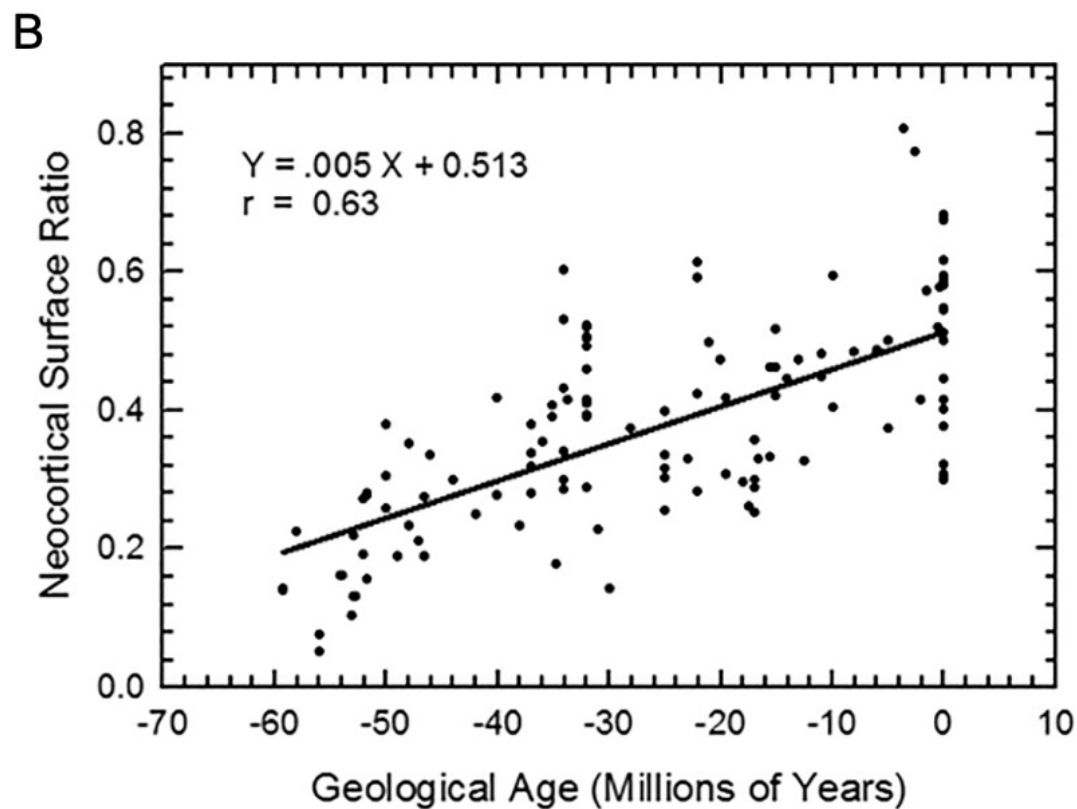
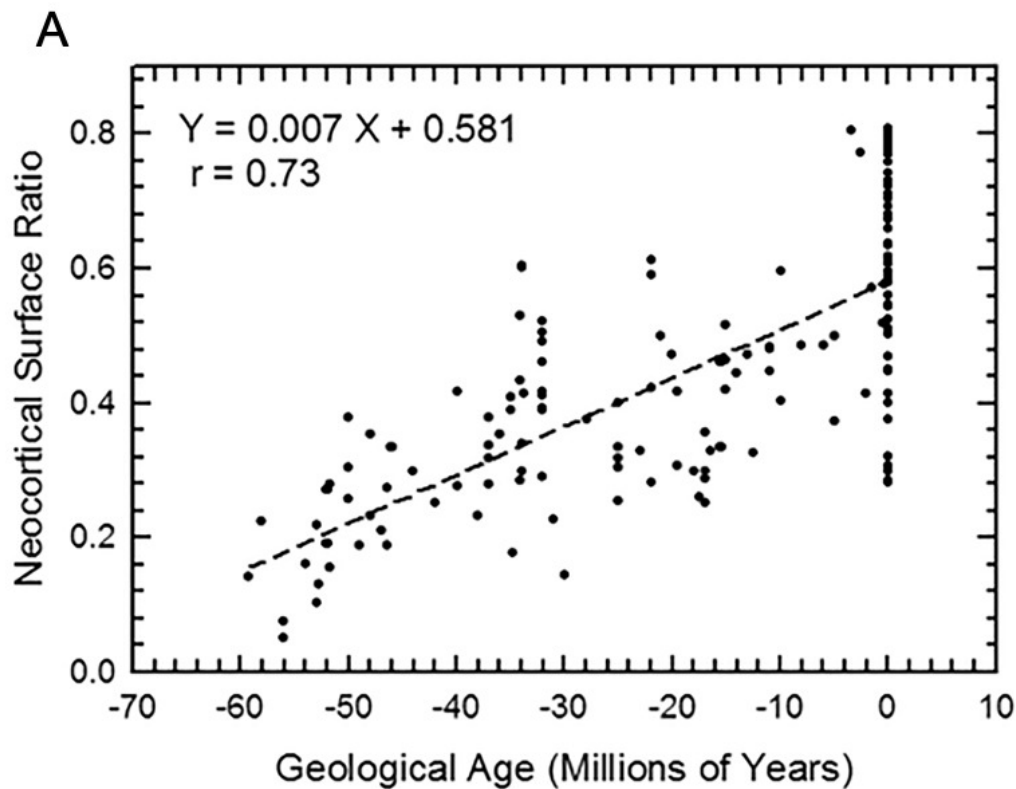


Figure 39

Neocorticalization and encephalization.

Neocorticalization as a function of encephalization; maximum about 81%.

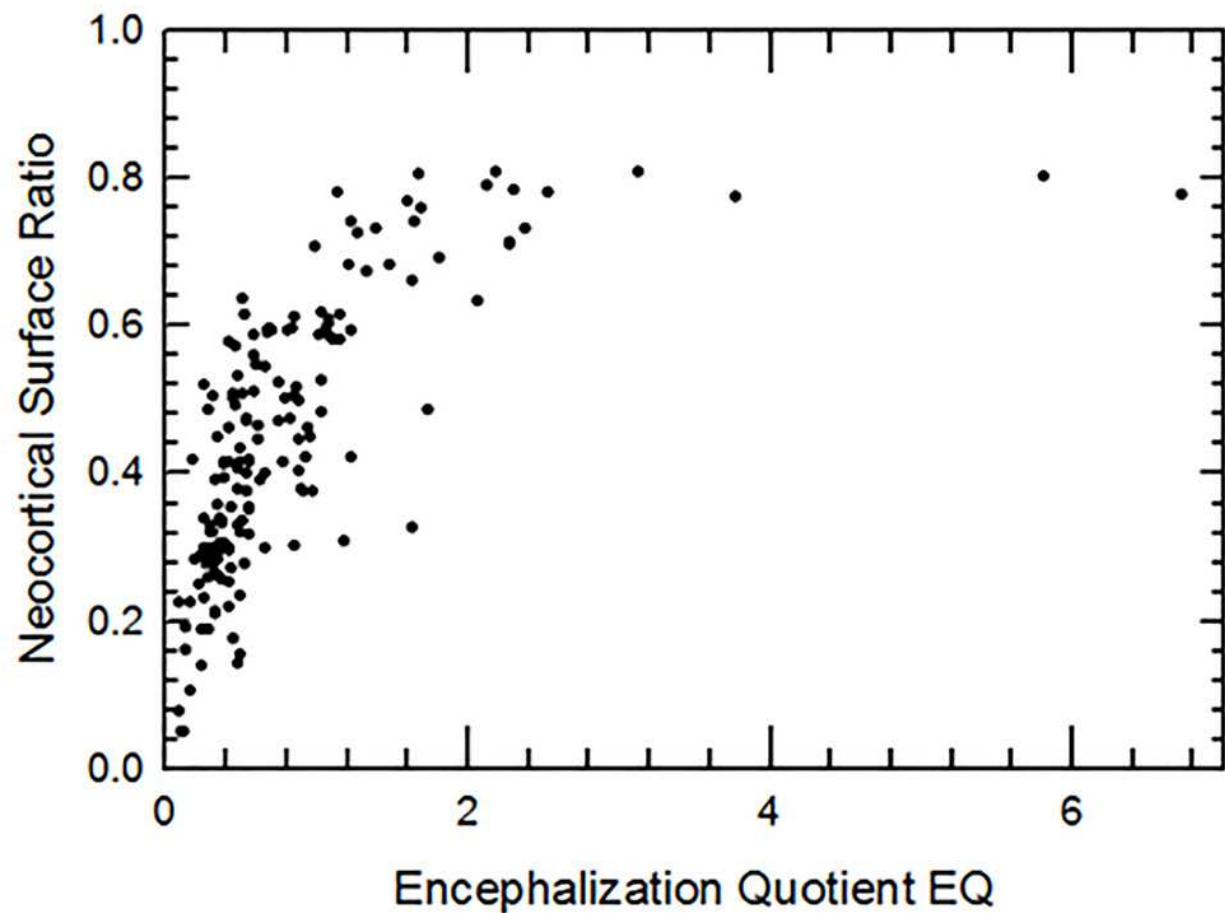


Figure 40

Amniote allometry.

(A) Brain-body relationships in amniotes. Convex polygons enclose data on living species: mammals (N = 647), birds (N = 219), and reptiles (N = 59). Additional data points for the late Jurassic bird (*Archaeopteryx lithographica*), living albatross (*Diomedea exultans*), living ostrich (*Struthio camelus*), and fifteen non-avian dinosaurs including struthiomimids, Late Cretaceous "ostrich-dinosaurs" (from (Jerison 2007), by permission). (B) Amniote brain-body polygons with data on 155 scanned mammals and polygons of reptiles, including dinosaurs (see (Hopson 1979)). (C) Encephalization in 122 fossil mammal species shown within allometry polygons. Amniote brain-body polygons with data on 122 fossil mammals. (D) New reptile polygon. Amniote brain-body polygons with fossil mammal and living reptile data; revised reptile polygon based only on brain size.

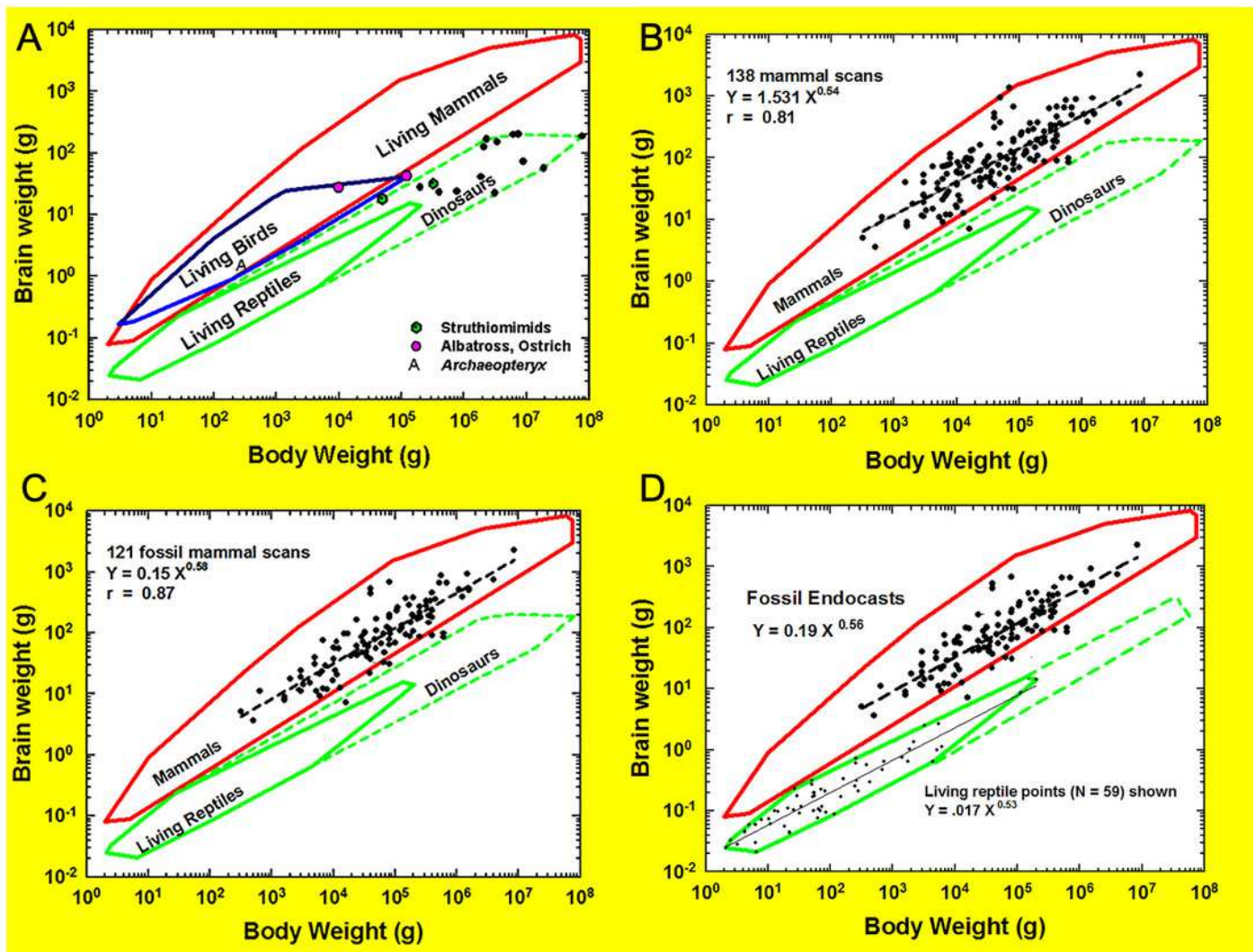


Figure 41

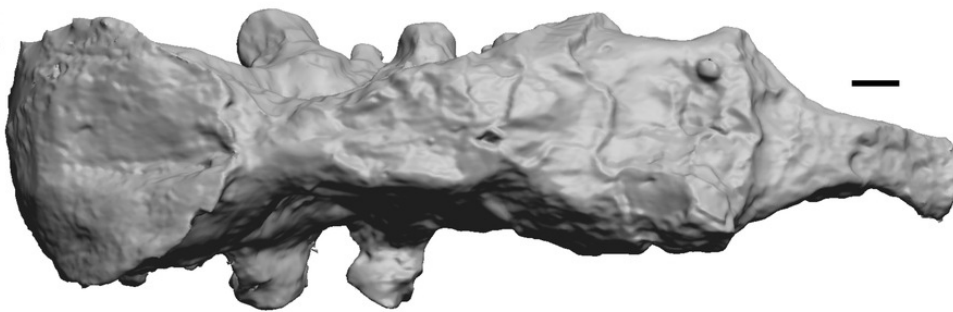
Endocasts of *Tyrannosaurus*, *Triceratops*, *Gryposaurus*, *Edmontosaurus*.

Endocast scans of four dinosaurs: (A) *Tyrannosaurus*, (B) *Triceratops*, (C) *Gryposaurus*, (D) *Edmontosaurus*.

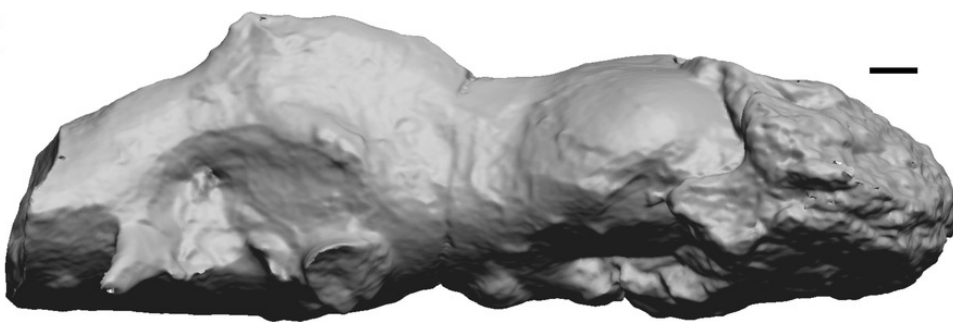
A



B



C



D

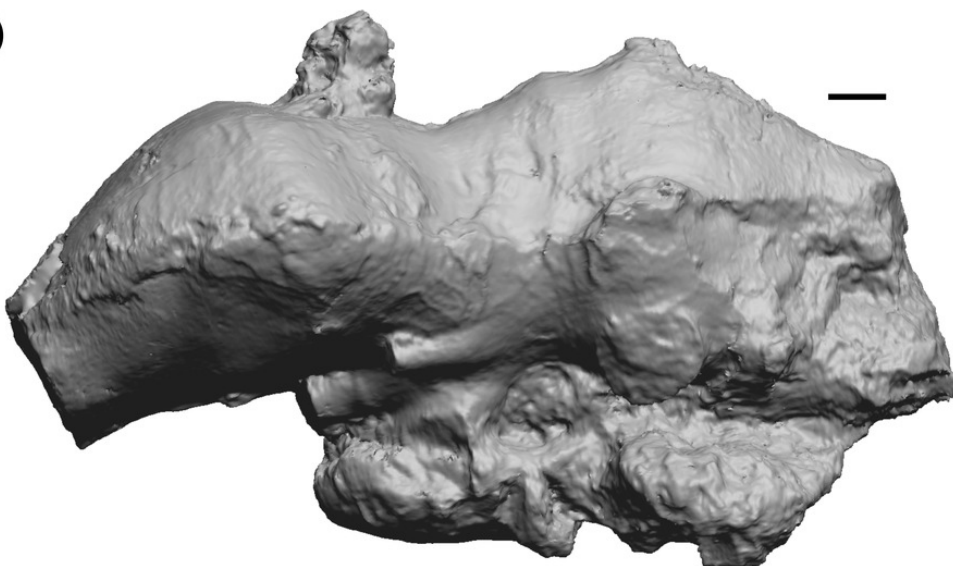


Figure 42

Surface area – volume relationship in endocasts and living mammals.

(A) Endocast surface area as a function of endocast volume. (B) Cortical surface area (including that buried within sulci and fissures) as a function of brain size in fifty species of living mammals. Correlation: $r = 0.996$. Bivariate regression: $Y = 3.75 X^{0.91}$. Labeled species indicate the sample diversity. Human and dolphin data are presented as minimum convex polygons enclosing 23 brains for humans and 13 brains for dolphins. (Graph from (Jerison 1991), by permission).

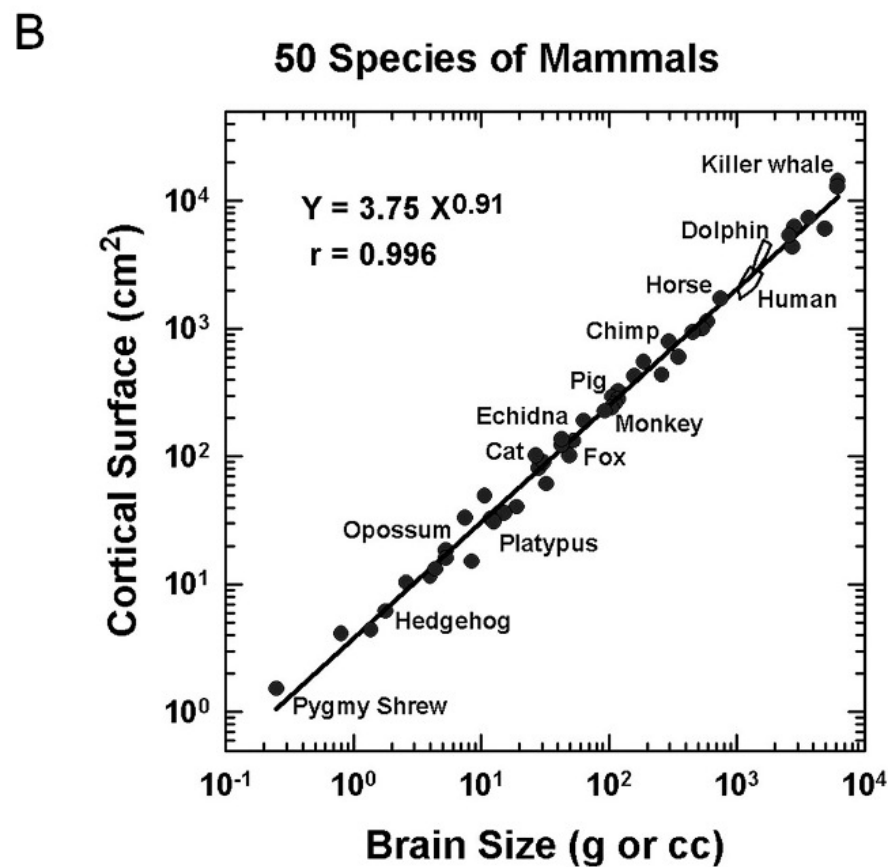
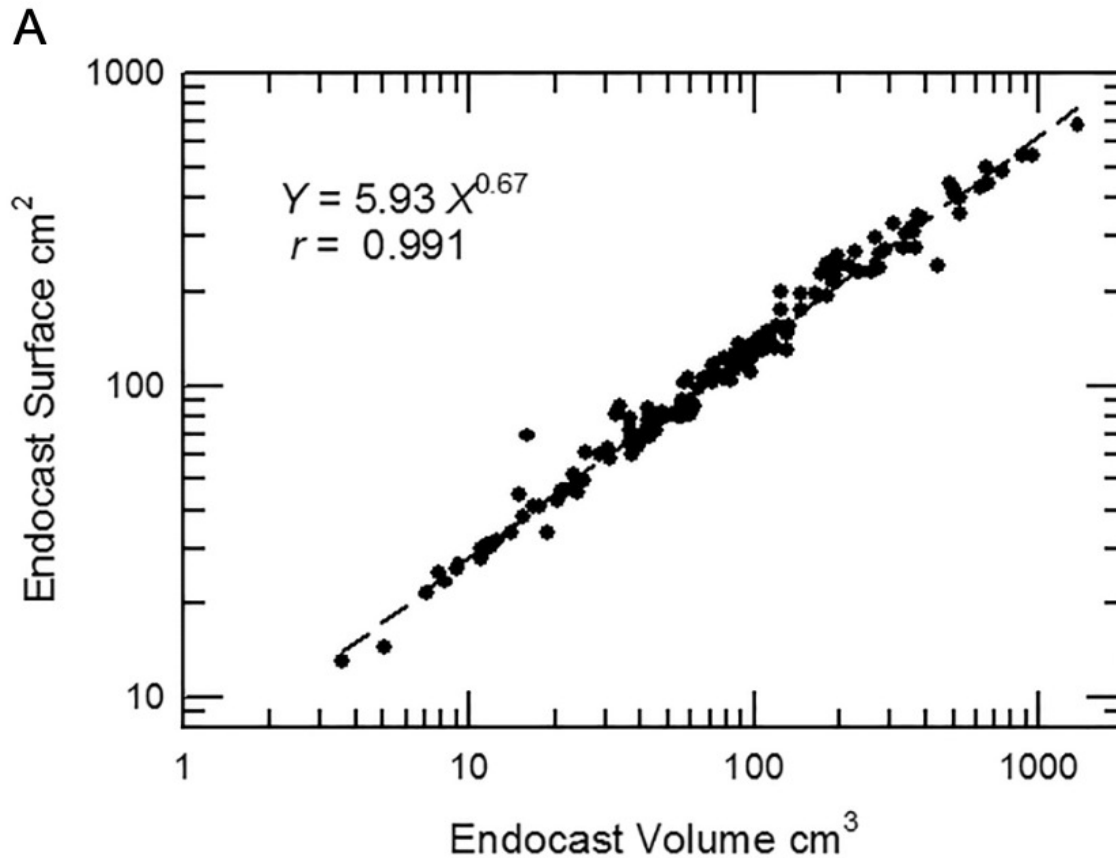


Table 1(on next page)

Measurements of endocasts and brains of fossils and living mammals.

S: surface area; OB: olfactory bulb area; S-OB: surface area excluding olfactory bulbs; NC: neocortex; L: length of specimen image; MYA: millions of years ago; E: volume of specimen; P: body size; %NC: neocorticalization; EQ: encephalization quotient re 2/3.

Species/Genera:	S cm ²	OB cm ²	S-OB cm ²	NC cm ²	L cm	MYA	E ml or g	P g	%NC	EQ	Taxon
118 FOSSIL SPECIMENS INCLUDING 7 PRIMATES											
<i>Adapis parisiensis</i> FMNH PM 59259 NHMUK M1340	24.95	1.42	23.53	10.17	4.7	-34.1	8.2	1600	43.23	0.5	Primates
<i>Adapis parisiensis</i> FMNH PM 59275 Le Gros Clark	26.52	1.55	24.97	13.25		-34.1	7.85	1600	53.06	0.48	Primates
<i>Adinotherium ovinum</i> FMNH P 13108	155.35	7.99	147.35	49.07	10.2	-15.5	111.04	120000	33.30	0.38	Notoungulata
<i>Amynodon advenus</i> FMNH PM59231 = YPM 11453	239.39	12.41	226.98	75.77		-46	180.99	263000	33.38	0.37	Perissodactyla
<i>Anoplotherium commune</i> BM3753	129.18	6.88	122.31	34.83	10.4	-34.1	78.37	82000	28.48	0.35	Artiodactyla
<i>Apterodon macrognathus</i> FMNH PM 57147	115.74	0	107.68	34.33		-37	77.54	47007.5	31.88	0.5	Carnivora
<i>Archaeolemur majori</i> FMNH PM 59258	121.19	1.88	119.3	76	7.6	-0.01	95.89	17000	63.70	1.21	Primates
<i>Archaeotherium mortoni</i> FMNH PM 59061	204	12	192	49	16.2	-32	168.74	230000	25.52	0.37	Artiodactyla
<i>Arctocyon primaevus</i> MNHN CR 700	25.89	4.29	21.6	4.86	4.9	-58	7.14	16144	22.49	0.09	Procreodi
<i>Arctodus simus</i> LACM short faced bear	542.37	44.34	498.03	296.05	16.8	-0.03	654.14	525763	59.45	0.84	Carnivora
<i>Argyrocetus joaquinensis</i> USNM 11996					13.3	-23	629.94	80100		3.01	Cete
<i>Arsinotherium zitelli</i> NHMUK M.5539					18.6	33	926.6	1500000		0.59	Embrithopoda
<i>Aulophyseter morricei</i> USNM 11230					16.7	-16	2246	8508540		0.45	Cete
<i>Australopithecus africanus</i> Taung	241.72		241.72	194.69	10.8	-3.5	440	40000	80.54	3.13	Primates
<i>Australopithecus robustus</i> SK1585	356.35		356.35	275.03	11.6	-2.5	530	40000	77.18	3.78	Primates
<i>Bathygenys reevesi</i> UT TMM 40209-431	33.46	2.35	31.11	8.71	5	-37	12.08	6795	28.00	0.28	Artiodactyla
<i>Borhyaena tuberata</i> FMNH P 13266	82.09	13.08	69.01	17.39	7.4	-17	43.05	24600	25.20	0.42	Marsupialia
<i>Canis dirus</i> LACM	207.83	15.12	192.71	114.41	11.7	-0.03	181	80000	59.37	0.81	Carnivora
<i>Canis latrans</i> endocast LACM 7-2007	117.79	7.79	110	73.97		0.03	97.85	15000	67.25	1.34	Carnivora
<i>Carpocyon webbi</i> ("Osteoborus") FMNH PM 58964	142.9	13.12	129.78	61.35	10.6	-13	100.04	32000	47.27	0.83	Carnivora
<i>Cebochoerus lacustris</i> FMNH PM 59051	34.1	3.84	30.26	7.01	5.6	-38	11.9	8000	23.17	0.25	Artiodactyla
<i>Chadronia margaretae</i> FMNH PM 57129	66.47	6.09	60.38	23.48	7.7	-35	28.86	7500	38.89	0.63	Cimolesta
<i>Cormohipparion occidentale</i> FMNH PM 59220	333.71	24.39	309.32	184	11.2	-10	363.94	151000	59.49	1.07	Perissodactyla
<i>Coryphodon hamatus</i> FMNH PM 59241	140.94	13.66	127.28	24.34	11.8	-52	90.6	394000	19.12	0.14	Cimolesta
<i>Cynodictis cayluxi</i> FMNH PM 57153	33.29	2.5	30.79	12.54		-34	11.6	2800	40.73	0.49	Carnivora

Species/Genera:	S cm ²	OB cm ²	S-OB cm ²	NC cm ²	L cm	MYA	E ml or g	P g	%NC	EQ	Taxon
-----------------	----------------------	-----------------------	-------------------------	-----------------------	---------	-----	-----------------	--------	-----	----	-------

<i>Cynohyaenodon cayluxi</i>											
FMNH PM 57153	32.46	4.58	27.88	8.32		-34	11.04	5392	29.83	0.3	Creodonta
<i>Daphoenus-vetus</i>											
FMNH PM 59008a			80.89	39.82		-32	46.87	24000	49.22	0.47	Carnivora
<i>Daphoenus-vetus</i>											
FMNH PM 59008b UM1			84.96	39.1		-32	42.61	24000	46.02	0.43	Carnivora
<i>Desmathyus (Hesperhyus)</i>											
FMNH PM 59066	122.43	13.59	108.84	33.38	8.3	-19.5	71.27	11291	30.67	1.18	Perissodactyla
<i>Dinictis felina</i>											
FMNH PM 58866	88.4	4.9	83.23	42.14	6.8	-32	60.1	37000	50.63	0.45	Carnivora
<i>Durodon atrox</i>											
NHMMUK 10173					13.1	-40	459.55	393540		0.71	Cete
<i>Enaliarctos sp.</i>											
FMNH PM 57161	132		132	80.64	7.2	-22	118	82000	61.00	0.52	Carnivora
<i>Eomoropus amarorum</i>											
FMNH PM 59182	80.41	1.76	78.66	23.46	6.8	-44	36.89	40000	29.83	0.26	Perissodactyla
<i>Eporeodon socialis</i>											
FMNH PM 59076	78.72	6.92	71.8	23.67	7.6	-23	41.79	19400	32.96	0.48	Artiodactyla
<i>Equus occidentalis</i>											
La Brea LACM	573.34	32.01	541.33	317.55		-0.03	869	550000	85.19	1.08	Perissodactyla
<i>Eusmilus bidentatus</i>											
FMNH PM 58871	70.19	4.87	65.32	32.92	7.2	-32	40.12	35000	50.40	0.31	Carnivora
<i>Glossotherium harlani</i>											
LACM 1717-33	469.74	46.57	423.17	129.54		-0.03	501.94	1100000	30.61	0.39	Xenarthra
<i>Halitherium schinzi</i>											
SNHM M.3921	298.77		298.77	94.59	12.2	-25	267	250000	31.66	0.56	Sirenia
<i>Hapalops sp.</i>											
LACM	91.8	7.29	84.51	30.12	7.8	-17	54.7	49000	35.64	0.34	Xenarthra
<i>Hemicyon cf. barbouri</i>											
FMNH PM 59030	251.22	8.25	242.97	97.95	12.6	-10	199.28	82000	40.31	0.88	Carnivora
<i>Heptodon sp.</i>											
FMNH PM 59193	89.03	11.42	77.6	20.96	9.2	-52	42.67	24000	27.00	0.43	Perissodactyla
<i>Hesperocyon gregarius</i>											
FMNH PM 58989	37.81	4.05	33.75	17.58	4.9	-32	18.8	3000	52.08	0.75	Carnivora
<i>Homalodotherium cunninghami</i>											
FMNH PM 59291	284.85	15.96	268.89	70.22	14.3	-17.5	227.3	400000	26.12	0.35	Notoungulata
<i>Homotherium ischyrosmilus</i>											
FMNH PM 58891	243.67	19.22	224.45	128.35	11.2	-1.5	192.5	200000	57.18	0.47	Carnivora
<i>Hoplophoneus primaevus</i>											
UM2 PF	73.11		73.11	28.48	6.7	-32	42.67	35000	38.96	0.33	Carnivora
<i>Hoplophoneus primaevus</i>											
USNM 22538	79.38		79.38	32.57	6.7	-32	49.47	35000	41.03	0.39	Carnivora
<i>Hyaenodon</i>											
FMNH P 12723	114.55	8.31	106.23	32.41		-50	67.37	60000	30.51	0.37	Carnivora
<i>Hylomeryx simplicidens</i>											
FMNH PM 59055	26.78	0	26.78	6.71	4.3	-42	9.14	6000	25.04	0.23	Artiodactyla
<i>Hyrachyus modestus</i>											
PM 59240 = YPM 11082	115.32	8.47	106.85	29.75	8.7	-51.7	68.95	100000	27.85	0.27	Perissodactyla
<i>Hyracotherium</i>											
PM 59207 AMNH 55268	57.33	8.53	48.8	10.66	6.6	-52.9	24.16	10700	21.84	0.41	Perissodactyla
<i>Isectolophus latidens</i>											
FMNH PM 59179	51.05	8.29	42.75	9.03	6.6	-47	20.37	11600	21.13	0.33	Perissodactyla
<i>Leontinia gaudryi</i>											
FMNH P 13285	346.9	28.2	318.7	106.48	15	-25	356.91	450000	33.41	0.51	Notoungulata
<i>Leptauchenia decora</i>											
FMNH PM 59074	50.78	5.02	45.76	10.35	6.3	-31	21.95	39300	22.61	0.16	Artiodactyla
<i>Leptictis (Ictops acutidens</i>											
Douglass)	15.11	2.08	13.03	1.87	3.2	-32	3.61	500	14.32	0.48	Rodentia

Species/Genera:	S cm ²	OB cm ²	S-OB cm ²	NC cm ²	L cm	MYA	E ml or g	P g	%NC	EQ	Taxon
-----------------	----------------------	-----------------------	-------------------------	-----------------------	---------	-----	-----------------	--------	-----	----	-------

<i>Leptocyon</i> sp. FMNH PM 58961	36.41	2.6	33.81	15.95	5.2	-20	14.14	3260	47.16	0.54	Carnivora
<i>Leptolambda schmidtii</i> FMNH PM 26075	143.3	17.77	125.52	6.46	8.7	-56	98.13	620000	5.15	0.11	Cimolesta
<i>Leptolambda</i> sp. FMNH PM 15573	126.79	0	126.79	9.71		-56	85.22	620000	7.66	0.1	Cimolesta
<i>Megalonyx jeffersoni</i> LACM	302.84	27.05	275.75	103.69	12.6	-0.03	332.78	370000	37.60	0.54	Xenarthra
<i>Meniscotherium robustum</i> USNM V 19509						-53	14.8	6500		0.35	Condylarthra
<i>Menodus ingens</i> FMNH PM 59199	521.47	36.62	484.85	164.37	17.1	-34	750	4000000	33.90	0.25	Perissodactyla
<i>Merychippus isonesus</i> (<i>Atavahippus</i>) FMNH PM 59208	248.43	18.23	230.2	119.03	12.4	-15	231.79	105700	51.71	0.86	Perissodactyla
<i>Merychippus severus</i> LACM 368	296.34	65.09	231.25	106.82	14.5	-15.5	258.77	110000	46.19	0.94	Perissodactyla
<i>Merycochoerus proprius</i> FMNH PM 59081	142.44	9.53	132.91	39.48	10.2	-18	95.74	122000	29.70	0.32	Artiodactyla
<i>Merycoidodon culbertsoni</i> FMNH UM3	78.05	0	78.05	22.57	7.2	-32	47.25	68000	28.92	0.24	Artiodactyla
<i>Mesatirhinus junius</i> (<i>Eobasileus</i>) FMNH PM 59197	227.32	14.56	212.76	58.23	12.3	-46.5	189.5	350000	27.37	0.32	Perissodactyla
<i>Mesatirhinus petersoni</i> PM 59196	221.06	24.68	196.38	37.17	13.2	-46.5	146.9	350000	18.93	0.25	Perissodactyla
<i>Mesocyon coryphaeus</i> FMNH PM 58979	71.01	4.99	66.02	26.37	7.2	-25	36.55	10000	39.94	0.66	Carnivora
<i>Mesohippus bairdi</i> FMNH PM 59221	127.48	9.86	117.62	48.89	9.6	-32	86.42	28500	41.56	0.77	Perissodactyla
<i>Mesonyx obtusidens</i> FMNH PM 57139 = YPM 13141	133	0	133	31	8.2	-48	96	65000	23.31	0.49	Cete
<i>Mixtotherium cusculatum</i> FMNH PM 59052	45.93	0	45.93	12.74	6.7	-40	21.04	6000	27.73	0.53	Artiodactyla
<i>Moeritherium lyonsi</i> NHMUK M.9176	265.93	34.58	231.35	78.26	11.6	-37	233.33	394000	33.83	0.36	Proboscidea
<i>Mustelictes piveteaui</i> FMNH PM 58907	35.32	3.25	32.07	9.04	4.4	-22	12.61	12973	28.20	0.19	Carnivora
<i>Mylodon</i> LACM 157696	420.76	21.67	399.1	119.19	15.8	-0.01	514.88	1100000	29.86	0.4	Xenarthra
<i>Glossotherium (Mylodon) harlani</i> LACM 1717-33	454.58	44.54	410.04	129.54	15.5	-0.05	501.94	1591000	31.59	0.31	Xenarthra
<i>Necrolemur antiquus</i> FMNH PM 59261	39.18	2.08	37.1	14.04		-37	5.05	320	37.84	0.9	Primates
<i>Nesodon umbricatus</i> FMNH P 13076	253.29	9.28	244.01	72.74	12.3	-17	180.06	250000	29.81	0.38	Notoungulata
<i>Notharctus</i> sp. FMNH PM 59264	40.57	2.32	38.25	10	5	-47	15.38	4200	26.14	0.48	Primates
<i>Nothrotheriops shastensis</i> LACM C-3	279.43	40.35	239.08	98.87	11.8	-0.03	277.12	320000	41.35	0.49	Xenarthra
<i>Orthocynodon (Aminodon)</i> sp. FMNH PM 59177	140.52	21.25	119.27	30.82	9	-50	93.99	150000	25.84	0.28	Perissodactyla
<i>Oxydactylus</i> sp. FMNH P 12117	131.44	9.24	122.2	51.01	10.3	-19.5	86.65	250000	41.74	0.18	Perissodactyla
<i>Pachyaena ossifraga</i> YPM PU 14708	88.51	7.95	80.56	8.4	9.2	-53	32.66	65000	10.43	0.17	Cete
<i>Pachylemur (Lemur) insignis</i> FMNH PM 59253	80.37	0	80.37	49.61	6.4	-0.01	57.38	10000	61.73	1.03	Primates
<i>Palaeopropithecus maximus</i> FMNH PM 59250	134.93	1.43	133.5	72.73		-0.01	108.33	50000	54.48	0.67	Primates

Species/Genera:	S cm ²	OB cm ²	S-OB cm ²	NC cm ²	L cm	MYA	E ml or g	P g	%NC	EQ	Taxon
-----------------	----------------------	-----------------------	-------------------------	-----------------------	---------	-----	-----------------	--------	-----	----	-------

<i>Palaeosyops</i> sp. FMNH PM 59198	288	28.24	259.76	40.2	14.2	-51.7	195.31	191000	15.48	0.49	Perissodactyla
<i>Panthera leo atrox</i> La Brea Lion LACM	326.92	21	305	166.65	13.8	-0.03	338.43	325000	54.64	0.6	Carnivora
<i>Paracynarctus sinclairi</i> (<i>Phlaocyon</i>) FMNH PM 58973	97.54	8.53	89.01	39.56	8.2	-15	55.93	12263	44.44	0.88	Carnivora
<i>Paratomarctus euthos</i> FMNH PM 58958	87.6	8	79.6	35.6	7.6	-11	56.3	10900	44.72	0.95	Carnivora
<i>Patriomanis americana</i> FAM 57103	33.86	4.21	29.65	5.23		-34.7	11.21	3000	17.65	0.45	Cimolesta
<i>Phenacodus primaevus</i> FMNH PM 59042 AMNH 4369	72.75	10.33	62.42	10.01	7.7	-54	30.82	82000	16.04	0.14	Condylarthra
<i>Plagiolophus minor</i> Remy	58.6	9.64	48.96	29.51		-34			60.27		Perissodactyla
<i>Platygonus compressus</i> FMNH PM 59058	138.82	9.52	129	74.44	9.7	-0.3	130	130000	57.71	0.42	Artiodactyla
<i>Plesiogale paragale</i> FMNH PM 58910	44.19	3.22	40.96	16.3		-22	17.76	2000	39.79	0.93	Carnivora
<i>Plihippus</i> sp. FMNH P 15870	291	21	270	135		-5	289	169700	50	0.79	Artiodactyla
<i>Plionictis</i> FMNH PM 58945	32.97	2.94	30.03	12.63	5.1	-15	10.99	640	42.07	1.23	Carnivora
<i>Poebrotherium</i> FMNH PM 59167	81.59	0	81.59	33.79	7.5	-33.7	47.82	29800	41.41	0.41	Artiodactyla
<i>Potamotherium valentoni</i> FMNH PM 58906	64.4	4.02	60.37	35.69	5.7	-22	37.3	10000	59.11	0.67	Carnivora
<i>Procamelus grandis</i> FMNH PM 59160	365.7	16	350	131.07	14.3	-11	374.21	200000	37.45	0.91	Artiodactyla
<i>Procyonodictis angustidens</i> FMNH PM 57168	53.09	1.32	51.77	21.56	6.3	-40	23.33	6571	41.64	0.55	Carnivora
<i>Promartes olcottii</i> FMNH P 25233	49.16	3.83	45.33	16.96	5.2	-28	24.12	3000	37.42	0.97	Carnivora
<i>Promerycochoerus superbus</i> FMNH PM 59072	174.4	0	174.4	68.59	10.8	-32	147.12	178000	39.33	0.39	Artiodactyla
<i>Proterotherium cavum</i> FMNH PM 59742	106.09	4.54	101.55	29.23	9.2	-17	57.35		28.79		Notoungulata
<i>Protypotherium</i> FMNH P 13046	43.62	2.61	41.01	13.53	5.7	-16.5	16.69	9683	32.98	0.31	Notoungulata
<i>Pseudaelurus validus</i> FMNH PM 58867	114.43	5.49	108.94	50.38	9.7	-15	71.72	30000	46.24	0.62	Carnivora
<i>Pseudhipparion (Griphippus)</i> gratum FMNH PM 59211	207.87	13.39	194.47	93.65	10.6	-11	168.43	50000	48.15	1.03	Perissodactyla
<i>Pseudotypotherium</i> <i>pseudopachygnathum</i> FMNH PM 59292	104.6	5.97	98.64	48	8.6	-6	63.71	80000	48.66	0.29	Notoungulata
<i>Pterodon dasyuroides</i> NHMUK M.25985	105.05	0	105.05	37.19	9.6	-36	58.51	37000	35.40	0.44	Creodonta
<i>Rhynchippus equinus</i> FMNH P 13410	158.13	15.85	142.28	43.14	8.9	-25	103.56	32000	30.32	0.86	Notoungulata
<i>Smilodectes gracilis</i> FMNH PM 56263	25.93	0	25.93	9.13	3.4	-48	9	1600	35.23	0.55	Primates
<i>Smilodon fatalis</i> LACM	256.51	16.45	240.06	120.3	11.7	-0.03	216	250000	50.11	0.45	Carnivora
<i>Sthenurus cf. orientalis</i> FMNH PM 59245	141.46	11.48	129.98	67.35	8.4	-0.5	107.05	200000	51.82	0.26	Marsupialia
<i>Thylacoleo carniflex</i> FMNH PM 59244	170.89	16.9	153.99	63.7	9.6	-2	120.01	130000	41.37	0.39	Marsupialia
Tillyhorse YPM 11694	49.52	4.83	44.69	5.84	6.4	-52.8	15		13.07		Condylarthra
Species/Genera:	S	OB	S-OB	NC	L	MYA	E	P	%NC	EQ	Taxon
	cm ²	cm ²	cm ²	cm ²	cm		ml or g	g			

<i>Titanoides primaevus</i> FHNH PM 8655	152.94	17.87	135.06	18.98	11.7	-59.2	88.35	172032	14.05	0.24	Cimolesta
<i>Typotheriopsis internum</i> FMNH P 14420	112.8	4.4	108.4	52.69	9.6	-8	75.1	6846	48.60	1.74	Notoungulata
<i>Uintatherium anceps</i> YPM 11036	391.2	76	343.2	64.37	17.2	-49	386	1250000	18.75	0.28	Dinocerata
<i>Urocyon cinereoargenteus</i> LACM gray fox	68.05	4.38	63.67	36.94	6.5	-0.03	38.95	5000	58.02	1.11	Carnivora
<i>Ustatchoerus profectus</i> FMNH PM 59071	209.04	11.81	197.23	64.2	10.6	-12.5	162.67	24000	32.55	1.63	Artiodactyla
<i>Zodiolestes daimonelixensis</i> FMNH PM 12032	61.59	3.32	58.26	29.03	6.1	-21	31.2	5000	49.83	0.89	Carnivora
22 LIVING NON-PRIMATES											
<i>Aonyx cinerea</i> (<i>Amblyonyx</i>) Rad 358	69.95	2.38	67.57	44.62	6	0	40.59	3000	66.04	1.63	Carnivora
<i>Canis latrans</i> brain WISC 62-301	125.27	8.22	117.05	82.44		0	72.67	15000	70.43	1	Carnivora
<i>Cerdocyon thous</i> Rad 294	78.5	6.93	71.57	43.89	7.1	0	45.67	6000	61.32	1.15	Carnivora
<i>Equus caballus</i> (Arabian)	487.14	42.71	444.43	232.74		0	669	400000	52.37	1.03	Perissodactyla
<i>Equus caballus</i> (draft horse)	595.08	54.18	540.9	273.23		0	881	800000	50.33	0.85	Perissodactyla
<i>Equus quagga</i> LACM M.548 Zebra	473.08	41.55	431.54	249.9		0	625	300000	57.91	1.16	Perissodactyla
<i>Felis catus</i> Rad 101 endocast	51.92	2.6	49.31	28.87	5.5	0	25.41	3000	58.54	1.02	Carnivora
<i>Lama glama</i> WISC 65-139 braincast	232.01	5.28	226.74	144.2	11	0	172.22	150000	63.60	0.51	Artiodactyla
<i>Lutra canadensis</i> Rad 129	91.94	2.31	89.63	54.43		0	59.87	10000	60.73	1.07	Carnivora
<i>Lutra lutra</i> Rad 366	70.54	1.96	68.58	40.6	6.6	0	39.22	10000	59.20	0.7	Carnivora
<i>Macropus fuliginosus</i> MSU 64023 braincast	89.85	3.8	86.05	38.38	7	0	33.83	23600	44.60	0.34	Marsupialia
<i>Nasua Narica</i> WISC 62-404 braincast			62.74				28				Carnivora
<i>Odocoileus virgianus</i> WISC 67-81 braincast	181	6.6	174.4	102.24		0	124.6	75000	58.62	0.58	Artiodactyla
<i>Odocoileus virgianus</i> WISC 67-81 braincast	206.58	6.6	199.98	102.24	11.2	0	124.6	75000	51.13	0.58	Artiodactyla
<i>Phascolarctos cinereus</i> Koala brain	71.57	2.46	69.11	19.57		0	15.93	10000	28.32	0.29	Marsupialia
<i>Phascolarctos cinereus</i> Koala endocast	78.01	6.52	71.49	21.32	7.2	0	36.5	10000	29.83	0.66	Marsupialia
<i>Procyon lotor</i> brain WISC 61-824			60.99	34.37		0	25.79	7000	56.35	0.59	Carnivora
<i>Procyon lotor</i> Rad 154	84.42	5.18	79.23	47.03	7	0	54.18	7000	59.36	1.23	Carnivora
<i>Taxidea taxus</i> Rad 360	87.11	6.83	80.28	48.3	7	0	60	10000	60.16	1.08	Carnivora
<i>Ursus americanus</i> LACM	281.56	19.26	262.3	160	11.8	0	276.67	140000	61.00	0.86	Carnivora
<i>Ursus arctos</i> Kodiak Bear LACM	479.97	38.33	441.64	224.44	18.5	0	488.55	700000	50.82	0.52	Carnivora
<i>Vombatus ursinus</i> NMV C7780			103.23	48.45	7	0	82.2	28000	46.93	0.74	Marsupialia

Species/Genera:	S cm ²	OB cm ²	S-OB cm ²	NC cm ²	L cm	MYA	E ml or g	P g	%NC	EQ	Taxon
-----------------	----------------------	-----------------------	-------------------------	-----------------------	---------	-----	-----------------	--------	-----	----	-------

19 LIVING PRIMATES

<i>Cercocebus albigena</i> female AMNH 52583	107.84	86.65	6.7	0	79.64	7900	80.35	1.67	Primates	
<i>Cercopithecus pygenthus</i> male AMNH AM 52468	101.93	79.91	6.8	0	71.86	4200	78.40	2.3	Primates	
<i>Chiropotes albinasa</i> female FM 94927	82.57	65.26	5.9	0	53	3000	79.03	2.12	Primates	
<i>Colobus guereza</i> AM 52217	112.01	76.33	7	0	85.27	10500	68.15	1.48	Primates	
<i>Erythrocebus patas</i> female infant AMNH 52574	116.93	91.23	7.1	0	90.06	17000	78.02	1.14	Primates	
<i>Homo sapiens</i> Falk A	540.59	432.55	14.3	0	945.7	50000	80.01	5.81	Primates	
<i>Homo sapiens</i> Falk B	682.38	530.32	16.3	0	1369.7 1	70000	77.72	6.72	Primates	
<i>Hylobates lar</i> Falk 386	123.4	78.11	7.1	0	99.32	8000	63.30	2.07	Primates	
<i>Macacca mulatta</i> brain WISC 69-307	114.72	79.45	6.2	0	71.61	6000	69.26	1.81	Primates	
<i>Mandrillus sphinx</i> AMNH AM 274	154.88	119.09	8.1	0	131.85	18000	76.89	1.6	Primates	
<i>Nasalis larvatus</i> male MCZ 37328	121.94	89.15	5.9	0	97	14000	73.11	1.39	Primates	
<i>Pan troglodytes</i> WISC braincast 63-397	331.52	267.73	10.1	0	307.39	40000	80.76	2.19	Primates	
<i>Pan troglodytes</i> Wits endocast	278.46	1.8	276.66	196.58	0	371.18	50000	71.05	2.28	Primates
<i>Pithecia monachus</i> female AMNH 75981	68.05	53.09	5.9	0	39.73	1500	78.02	2.52	Primates	
<i>Presbytis johnii</i> female AMNH 54644	114.26	82.62	7.2	0	85.85	13400	72.31	1.27	Primates	
<i>Pygathrix nigripes</i> male AMNH 69555	106.08	80.39	6.5	0	77.71	7500	75.78	1.69	Primates	
<i>Rhinopithecus avunculus</i> male MCZ 13681	136.64	99.75	7.4	0	114.21	8000	73.00	2.38	Primates	
<i>Simias concolor</i> male AMNH 103359	82.54	61.19	5.8	0	54	7000	74.13	1.23	Primates	
<i>Theropithecus gelada</i> male FMNH 8174	146.82	108.74	8.1	0	131.08	17000	74.06	1.65	Primates	

Table 2 (on next page)

Intra-species analysis of selected *Bathysgenys reevesi* specimens.

E: endocast volume; S: endocast surface area; nc: neocortex area; nc/S: neocortex re surface area; SD: standard deviation; M: mean; CV: statistical coefficient of variation. Specimens are from the Texas Natural History Museum, where each specimen number is preceded by "TMM" (e.g. TMM 443D is the specimen label at the museum).

I.D. #	E ml	S cm ²	nc cm ²	nc/S
443D	11.362	28.5	8.22	0.288421
443F	10.98	31.5	8.64	0.274286
443H	11.386	34	8.3	0.244118
443I	11.914	34.5	8.32	0.241159
443J	13.557	28.8	7.62	0.264583
I.D. #	E ml	S cm ²	nc cm ²	nc/S
443K	13.981	30.8	8.24	0.267532
443L	10.386	28.3	6.96	0.245936
443X	11.422	25.8	7.1	0.275194
Mean	11.8735	30.275	7.925	0.26265363
SD	1.253082	2.994161	0.62094	0.01719269
SD/M (CV)	0.105536	0.098899	0.07835	0.06545764
CV percentage	10.60%	9.90%	7.80%	6.50%

Supplementary Results

Digitized Endocasts and Brains: Measurements and Analyses of the Evolution of 172 Fossil and Extant Vertebrate Specimens

Edinger's Early Horses

Body size estimates

Evolution of the Horse Brain (Edinger 1948) was my introduction to paleoneurology (see Jerison, 2001a), and I use it to introduce these results. Edinger's photographs and drawings of horse species (Edinger 1948) have frequently been used to illustrate progressive brain evolution (MacFadden, 1992; Savage & Long, 1986; Simpson, 1951). **Fig. 2** shows scans of endocasts of five of Edinger's species and adds Radinsky's (1976b) *Hyracotherium* (FMNH PM 59207=AMNH 55268; Edinger's "*Eohippus*" (YPM 11694). The taxonomy of the American *Hyracotherium* is uncertain because the generic name was only correctly applied to the European species (Hooker, 1994). Secord et al. (2012) offered "*Sifrhippus*" as its new generic name; the species *tapirinum* remains its present identification at AMNH; here, the Radinsky terminology is used.

The digitized models of the bodies presented in **Figs. 3 and 4** are scans of Gidley's (1927) careful sculptures, which determined the length, surface area, and volume. To enable the data in **Fig. 2** to be used to analyze *Hyracotherium*, the mounted skeleton was measured and reported a head length of 137 mm and body length of 559 mm, a 69.6 cm head+body length (courtesy of Dr. John Harris, then Chief Curator of the George C. Page Museum (LACM)). The volume and length of the model were scaled up (volume = 90.8 ml, length =

14.2 cm) and the model's volume was multiplied by the cube of the ratio of the lengths ($69.6 \text{ cm}/14.2\text{cm})^3$ to estimate a body size of 10,692 ml ($\sim 10.7 \text{ kg}$), which compares to an estimated body size of 9 kg (Radinsky, 1976b) using a regression analysis of the skull size (Jerison, 1973). Similarly, the AMNH mounted specimen of *Mesohippus bairdi* was photographed and measured (Dr. Ted Macrini, formerly at AMNH (**Fig. 3D**)) and the Smithsonian mounted specimen, USNM 244183, was measured (Dr. Robert Purdy, USNM). USNM 244183 and AMNH 1477 had almost identical body lengths (108 cm vs. 109.2 cm). Therefore, the body weight for *Mesohippus* was estimated to be 28.5 kg, which compares to MacFadden's (1986) estimates of between 40 and 60 kg, which appeared to be high compared to the body-length ranges of living ungulates (Nowak, 1999).

Radinsky (1976b) judged Edinger's "*Eohippus*", found as a natural isolated endocast, to be a condylarth rather than an equoid, and it remains taxonomically unidentified.

Neocorticalization and encephalization

The endocast measurements and neocorticalization of Edinger's equoids, a zebra, and two domesticated horses (a pony and a draft horse, reflecting body size variations within the domesticated species) according to geological age are presented in **Table S1** and **Fig. S1**.

Table S1. Measurements of the endocasts of 12 of Edinger's equoids.

Species	E (ml)	S (cm ²)	NC (cm ²)	P (ml)	MYA
0. "Tillyhorse" YPM 11694	13.97	38.74	7.12	n/a	52.9
1. <i>Hyracotherium</i> PM59207	24.162	57.74	10.66	10700	52.9
2. <i>Mesohippus</i> PM59221	86.422	130.1	40.8	28500	32
3. <i>Merychippus</i> PM59208	231.794	229.9	40.8	110000	15
4. <i>Pseudhipparion</i> PM59211	168.437	1941.2	92.7	50000	13.6
5. <i>Pliohippus</i> P15870	288.762	270.2	134.6	169700	12
6. <i>Neohipparion</i> P15871	227.465	224.8	107.7	172100	12

7. <i>Cormohipparion</i> PM59220	363.956	309.3	175.7	151000	11
8. <i>Equus</i> (LaBrea) 3500-17	868.78	541.3	317.6	550000	0.5
9. <i>Equus quagga</i> (Zebra) M548	625.423	431.5	204.3	30000	0
<i>Equus caballus</i> (Arabian) LACM	669	444.4	232.7	400000	0
<i>Equus caballus</i> (Draft Horse) LACM	881	540.1	273.2	800000	0

E: specimen volume; S: surface area; NC: neocortex; P: body size; MYA: millions of years ago.

The Arabian and draft horse can be represented in Fig. 12 by Species 8 and 9.

Equid Work 1/23/2017

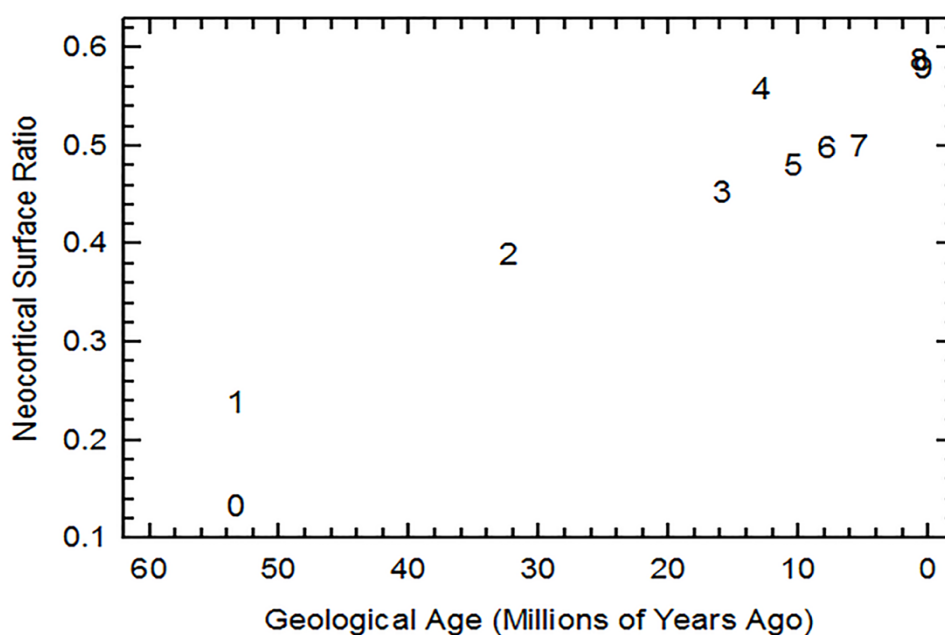


Figure S1. Neocorticalization in equoids. Neocorticalization in Edinger’s horses with the regression line determined on a smaller sample of fossils. Data relabeled in Table S1 with Edinger’s “*Eohippus*”, my Tillyhorse (Point 0), and Radinsky’s *Hyracotherium* (Point 1).

Like Edinger, Radinsky (1976b) discussed the presence of visible cortical sulci in *Hyracotherium*, which is likely to be a correlate of brain size (24.2 ml vs. 14 ml) and comparable to brains in this size range in living species. More unusual was the size of the *Hyracotherium* cerebellum, which was larger relative to the whole endocast than would be

expected according to the quantitative analysis of living brains (Stephan, Frahm & Baron, 1981; Jerison 1991). It is an interesting exception to the uniformitarian hypothesis and is explained by the small forebrain in early mammals. The cerebellum is probably a correct size for its neural control functions, but its ratio to the whole brain in this early Eocene equoid is high because early forebrains were relatively small.

The endocast of *Mesohippus* (**Fig. 4A**) was larger, more encephalized, and much more convoluted than that of *Hyracotherium* (**Fig. 3A**). Except at its anterior border, the rhinal fissure is a dark line in **Fig. 3A** with the forebrain surface area dorsal to this line being neocortical. Neocorticalization in *Mesohippus* is 38% (Point 2 in **Fig. S1**).

With the exception of the smaller *Pseudhipparion* (renamed from “*Griphippus*” in the FMNH catalogue), the Neogene equids are in the body size range of living equids, and MacFadden’s regression estimates of body size for the larger species are acceptable. Gidley (1927) prepared careful models of several of these (*Merychippus*, *Neohipparion*, and *Equus*), but these could not be digitized in order to measure their body sizes. *P. (Griphippus) gratum* FMNH PM 59211 was a small Miocene equid with an estimated body weight of 50 kg (pers. comm. and Hulbert, 1993). For *Merychippus* and larger fossils, rounded averages from MacFadden’s (1986) regressions, similar to previously published (Jerison, 1973), have been used.

Fig. 5 shows the remainder of the endocasts of Edinger’s equoid genera: three fossil genera and three recent genera, including a zebra and two domesticated horses (a pony and a draft horse, reflecting body size variations within the domesticated species). The encephalization of the equoid sample is plotted in **Fig. S2** using endocast sizes and body weights, with two living domesticated equids removed for clarity (centered around Point 9). The statistically determined regression equation at slope $3/4$ is similar to my preferred theoretical allometric “regression” at slope $2/3$.

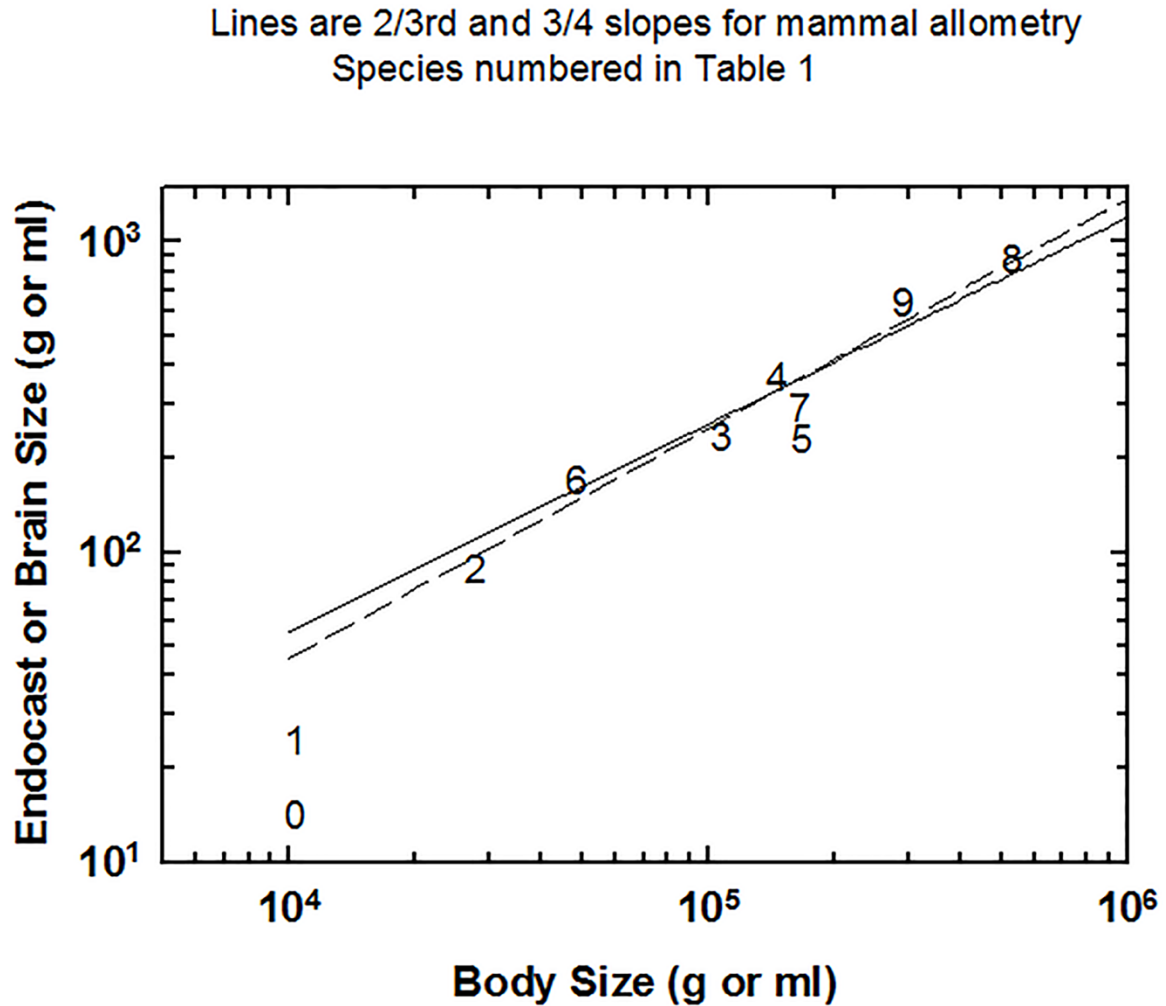


Fig. S2. Encephalization in equoids. Encephalization in Edinger’s horses numbered as in Table S1. Regression lines are of living mammals within the equoid body size range for log-log data. The least squares regression equation as a power function for living mammals (Martin, 1990) is $Y = 0.05 X^{0.74}$, and the “regression” through the mammalian centroid (Jerison, 1973, 2001a) is $Y = 0.12 X^{2/3}$. See also Fig. S1.

Given that encephalization in the early Eocene was at the grade of the equoid *Hyracotherium* and comparable to its Eocene contemporaries, it was below the encephalization relative to the allometry of later equids. With the appearance of *Mesohippus* in the late Eocene or early Oligocene at about 32 Ma (Species 2 in **Fig. S2**), encephalization

among equids reached the average grade of living mammals. The later equids, such as the La Brea horse (**Fig. 5** and Point 8 in **Fig. S2**) and the living horses and zebras are all at about the present average mammalian grade of encephalization.

Overall, the evolution of encephalization in many groups appears to have followed a relatively early increase to a particular grade followed by stasis at that grade. *Hyracotherium* was about half as encephalized as average extant mammals. *Mesohippus*, at a body size $P = 28.5$ kg and endocast volume $E = 86$ ml, was within the average range for living mammals. In living equids, the range is $0.75 < EQ < 1.11$ (cf. Count, 1947). In the Oligocene to Pleistocene equids, the range is $0.63 < EQ < 1.12$.

Reliable body size data for the early Eocene condylarth that Edinger called “*Eohippus*” is not available, but I previously estimated it as 13 kg (Jerison, 1973) and here modify it to 10.7 kg, the same size as *Hyracotherium* in **Table S1** and **Fig. S2**, due to a reduction in endocast volume from a previous measurement of 15 g the current 3D measurement of 14 g. These estimates lead to $EQ = 0.24$, a typical value for late Paleocene and early Eocene mammals, one-quarter to one-third as encephalized as extant species of similar body weights. It is worth adding that many living insectivores and didelphids have a similar low grade of encephalization; there are clearly many niches in which that grade of encephalization works.

Description of all the endocasts

Paleocene Fossils

TITANOIDES

The endocast of FMNH PM 8655 (**Fig. 6A**), probably *Titanoides primaevus*, was donated by Dr. William D. Turnbull to the FMNH collection in 1962. He collected it in the Tongue River Formation, Mercer County, Garrison Reservoir area, 2-3 miles north of Riverdale in North Dakota. According to dating of the area (Kihm & Hartman, 2004; Secord et al., 2006) *T. primaevus* lived 59.2 Ma. McKenna & Bell (1997) list this pantodont in the order Cimolesta, family Titanoideidae. From Savage & Long (1986), its body length was 160 cm and, from Eq. 2, this results in a body weight (heavy habitus) of 172 kg in the allometric analysis of encephalization. With respect to its endocast (**Fig. 6**), the length = 11.7 cm; $E = 88.35$ ml; $EQ = 0.24$; endocast surface area = 152.94 cm^2 ; total neocortical surface area (twice the marked surface) = 18.98 cm^2 ; and olfactory bulb surface area = 17.9 cm^2 . The neocorticalization ratio is 14.1%.

ARCTOCYON

On my first field trip to Europe in Paris at MNHN in 1964, I especially enjoyed working with this specimen of *Arctocyon primaevus*. Dr. Donald Russell showed me its skull, in which an endocast could be prepared by pouring molding compound into the cleaned cranial cavity. I already had a copy of an endocast that had been described in 1870 by Gervais, and I had recognized that an error must have been made in its preparation. Edinger (1964) illustrated and discussed the specimen, noting that Gervais had actually prepared a half endocast and combined it with a mirror image. I am uncertain how Gervais managed this, but **Fig. S3** shows my digital approach with a wombat skull, scanning the cranial cavity and inverting its digitized image.

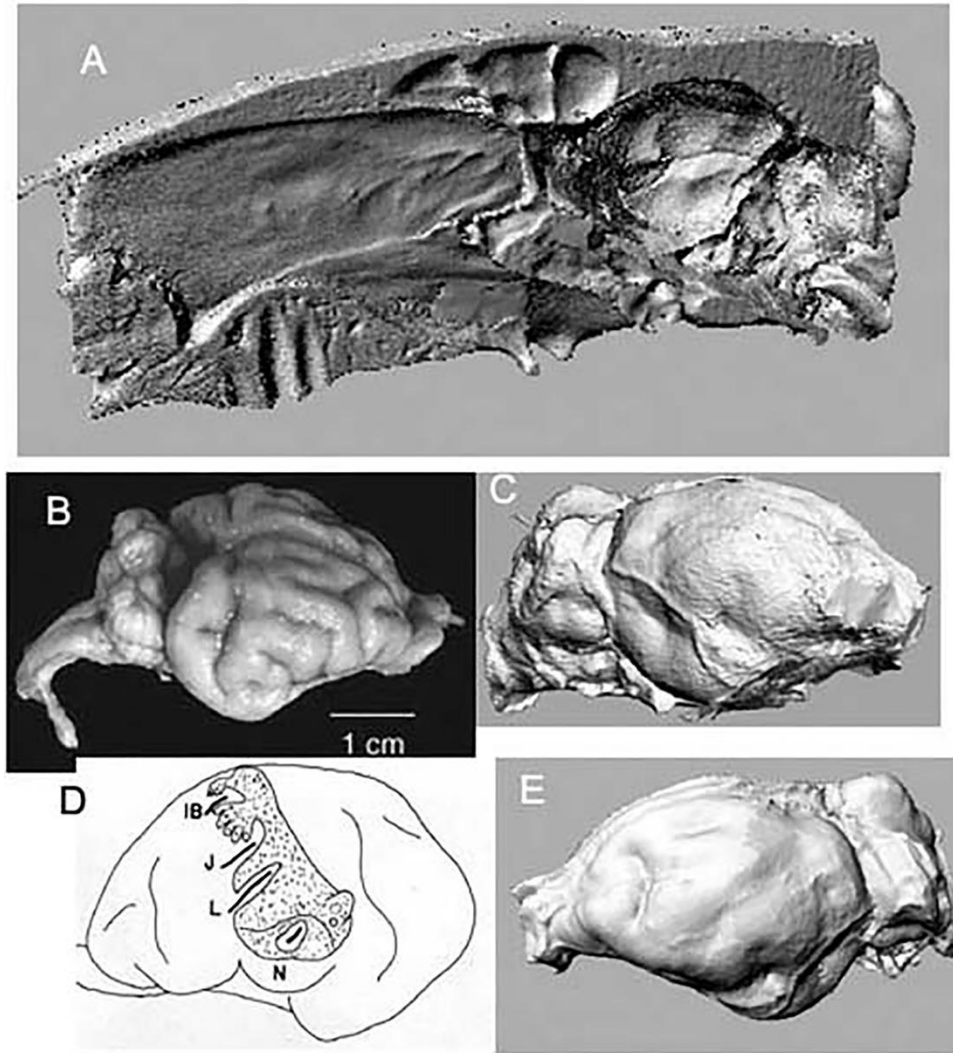


Fig. S3. Wombat brain and endocast. *Vombatus ursinus* (wombat) skull, brain, and endocast. (A) Skull (NMV Specimen C7780), anterior left. (B) Brain (WISC Specimen 64-11), anterior right, 55.4 g. (C) Endocast, anterior right, 73.7 ml. (D) Brain map, anterior left, showing somatosensory cortex as determined by Johnson (1980) from evoked potentials. (E) Silicone endocast, anterior left. Images of skull and endocasts prepared by the author.

While Edinger emphasized an error in the “cerebellum”, which lacked a vermis, I was even more impressed by the odd triangular shape of Gervais’s endocast. When we saw the new *Arctocyon* skull, I convinced Dr. Russell to allow me to prepare a new endocast from it. Sadly, my procedure involved a quick-fixing poisonous latex-like compound with which I

worked at the time. It produced an excellent endocast, clearly different from Gervais's, but I could not remove my entire mold successfully. Drs. Russell and Sigogneau were able to repair my damage and prepare a proper endocast, publishing it the following year (Russell & Sigogneau, 1965).

The scans in **Fig. 6B** are dorsal and lateral views of their endocast of *Arctocyon primaevus* (MNHN CR 700). The *Arctocyon*-specimen is from the late Paleocene in the Cernay-Berru (Marne) in France. Dr. Thierry Smith (pers.comm.) was studying the region and wrote to me that the area is “late Thanetian” and that my estimated age of 58 Ma was reasonable. Its endocast volume is $E = 7.1$ ml, with the length (top of olfactory bulb to bottom of medulla) = 4.9 cm. The endocast volume of 38 ml and body weight of 86 kg, published in Jerison (1973), are typographical errors. The species body length is estimated as 87 cm (Argot, 2013), leading to an estimated body weight of 16 kg ($EQ = 0.09$). When I examined the fossil it was a creodont, but it was later reclassified a condylarth and it is now classified in the archaic order Procreodi. Working on the present study, my small Paleocene procreodont forces me to modify some long-held ideas, as discussed in the main text. The neocortical measurements of *Arctocyon* are presented in **Table 1**.

BARYLAMBD

One specimen is listed as FMNH P 15573 and is shown on the right in **Fig. 6C**. The second specimen is listed as FMNH P 26075 and is shown on the left in **Fig. 6C**. Both specimens are now called *Leptolambda schmidt*. McKenna & Bell (1997) treated *Leptolambda* as a junior synonym for *Barylamba*, which is used here. These are the heaviest Paleocene pantodonts in my sample, order Cimolesta. At body lengths of just over 230 cm and heavy habitus, I estimated both of their weights to be 620 kg. Both specimens are from the DeBeque Formation in Colorado and dated as 56 Ma (**Table 1**). On specimen FMNH P

15573, I removed casts of cranial nerve roots by dissecting the digital ~~image~~ before determining the endocast volume to be 85.22 ml; surface area = 126.79 cm²; olfactory bulbs absent; neocortical surface area = 9.71 cm²; neocorticalization = 7.7%; and $EQ = 0.10$. Evidence of neocortex on this endocast is marginal: two small anterior mounds on the frontal surface and a poorly marked olfactory tract.

The forebrain of specimen FMNH P 26075 (**Fig. 6C**, left) is more brain-like. Expanded cerebellar representation in this specimen probably reflects fluid surrounding the cerebellum. Unlike the *Arctocyon* endocasts shown in **Fig. 6B**, it is not divided into vermis and lobules. The volume of the endocast of specimen P 26075 is $E = 98.13$ ml; endocast length (olfactory bulbs to medulla) = 8.7cm; total surface area = 143.30 cm²; olfactory bulb surface area = 17.77 cm²; remainder surface area = 125.52 cm²; neocortex = 6.46 cm²; and neocorticalization = 5.15%. The rhinal fissure is only marginally recognizable. These two *Barylambda* endocasts are among the least brain-like of the current specimen set, with both showing much-enlarged “medulla” in the posterior area, definite non-neural space in the foramen magnum for blood vessels, meninges, and sinuses.

PHENACODUS

The endocast of the condylarth *Phenacodus primaevus* (FMNH PM 59042) is the specimen described in Cope’s “Bible” (Cope, 1883, pp. 435-442). It was probably copied by Radinsky from specimen AMNH 4369, which is from the Big Horn Basin of Northern Wyoming, Wind River Region. It can be dated as Biochron zone Wa1 or Wa2, about 54 Ma (Dr. Gregg Gunnell, pers. comm.). The temporal range of the species is from late Paleocene to middle Eocene, and its endocast is also representative of the late Paleocene. The endocast was originally prepared by Cope or his staff in the 1870s and is shown in **Fig. 6D**. The cast itself was unusually smooth for a cast prepared from a fossil skull compared, for example,

with the equally complete endocast of *Arctocyon*. It may have been smoothed to look more brain-like when Cope prepared it. The *Phenacodus* head+body was about 150 cm long; body weight $P = 82$ kg; $E = 30.82$ ml; $EQ = 0.14$; endocast length (olfactory bulbs to medulla) = 7.7 cm; surface area = 72.75 cm^2 ; olfactory bulbs = 10.33 cm^2 ; remainder area = 62.42 cm^2 ; neocortex = 10.01 cm^2 ; and neocorticalization = 16%.

Early Eocene Fossils

The Early Eocene dates in this report are from 54 Ma to 42 Ma.

CORYPHODON

When I first saw the endocast of *Coryphodon hamatus* (FMNH PM 59241, copied from YPM 113310), its cerebellum struck me as not at all brain-like. The specimen came from the archaic Cimolesta located in the Wyoming Uinta County Evanston and dated to about 52 Ma (Woodburne, 2004). It was presumably prepared at the Yale Peabody Museum under O. C. Marsh's supervision over a century ago. That endocast alerted me to the occasional large errors in preparation. I thought at the time that my observation was original but then discovered that Edinger (1933) had also noted the likely error. Evidently, fossil petrosal bone had been drilled away, leaving massive lateral bubbles that enlarged the "cerebellum" cast. With the digitized image, I simply deleted the bubbles and measured the remaining endocast (**Fig. 7A**), which produced sufficient correction even in the absence of more cerebellar-like edges. *Coryphodon* was about 2 meters long with a heavy habitus, indicating a body weight of about 400 kg. The vertical length of *Coryphodon* endocast = 11.8 cm; endocast volume $E = 90.6$ ml; $EQ = 0.14$; endocast surface area = 140.94 cm^2 ; olfactory bulbs = 13.66 cm^2 ; remainder area = 127.28 cm^2 ; neocortex = 24.34 cm^2 ; and neocorticalization = 19.12%.

PALAEOSYOPS

The endocast FMNH PM 59198 is probably *Palaeosyops leidy*, a large brontothere (Perissodactyla), late Wasatchian, beginning of Bridgerian, and dated as 51.7 Ma for the neocorticalization analysis (**Fig. 7B**). From Osborn (1929), the body length is estimated as 198 cm, and from the appearance of the limbs in the mounted skeleton at AMNH, its habitus was normal (not heavy). This leads to a body weight estimate of 191 kg for allometric brain-body analysis; endocast vertical length = 14.2 cm; endocast surface area = 288.00 cm²; olfactory bulb area = 28.24 cm²; remainder = 259.76 cm²; neocortex = 40.20 cm²; and neocorticalization = 15.5%.

HEPTODON

The genus of this early tapiroid is known to date to 55 Ma to 49 Ma. Without any knowledge about when or where my specimen was collected, I dated it as 52 Ma for the neocorticalization analysis. The animal was about 100 cm long with a body weight $P = 24$ kg. For the encephalization analysis, the endocast volume $E = 43$ ml and $EQ = 0.43$. The specimen is FMNH PM 59193, marked “MCZ” without further identification, and has length = 9.2 cm (**Fig. 7C**). Based on body weight, I prefer my Eq. 1 based on body length but note that the evidence of tooth size suggests a smaller, 15.5 kg body (Mendoza, Janis, & Palmqvist, 2006). Endocast surface area = 89.03 cm²; olfactory bulbs = 11.42 cm²; remainder = 77.6 cm²; neocortex = 20.96 cm²; neocorticalization = 27.0%. **Fig. 7C** shows a photograph of the endocast and another view of the scan to its right.

ISECTOLOPHUS

Isectolophus latidens (FMNH PM 59179, copied from AMNH 12222) is a tapiroid from Bridger C-D and dated to 47 Ma (**Fig. 7D**). Its endocast volume $E = 20$ ml, including

the olfactory bulb region preserved in its right hemisphere; length (olfactory bulb to medulla) = 6.6 cm. Holbrook, Lukas & Emry (2004) recorded its skull as 15.5 cm long and, assuming a body length of 78 cm, its body weight was about 12 kg, resulting in an $EQ = 0.33$. Endocast surface area of *Isectolophus* = 51.05 cm²; olfactory bulbs = 8.3 cm²; remainder = 42.75 cm²; neocortex = 9.03 cm²; and neocorticalization = 21.1%.

TILLYHORSE

The identification of this endocast (YPM 11694; **Fig. 2**) as equoid was corrected by Radinsky (1976b). It was described by Edinger (1948) as “*Eohippus validus*” and continues to be described in some publications as an early equid brain. Edinger reported that it was from the upper Wasatchian, Almagré zone of Canyon Largo group, San Juan Basin, New Mexico. From Woodburne (2004), it appears to be Wa5 or Wa6, about 53 Ma. In Jerison (1973), it was described as *Hyracotherium*, with a 15 g endocast and a 13 kg body. While the brain size was a datum from the endocast, the body size was a complete guess. Nevertheless, neocorticalization could be determined because its total surface area, the surface area of its olfactory bulbs and the surface area of its neocortex, could be measured. Lacking an identification of its body, one cannot estimate body size for an allometric analysis of encephalization, although I graphed a new estimate of 10.7 kg (cf, Jerison, 1973). The endocast length = 6.4 cm, and neocorticalization data for the specimen were analyzed as follows: total endocast surface area = 49.52 cm²; olfactory bulb area = 4.83 cm²; remainder = 44.69 cm²; neocortex = 5.84 cm²; and neocorticalization = 13.07%.

HYRACOTHERIUM

This is the corrected “*Eohippus*” endocast that was prepared by Radinsky (1976b) from American *Hyracotherium* skulls in the Frick Collection (AMNH 55268 = FMNH PM

59207), where it is identified as *Hyracotherium tapirinum* (see also **Fig. 3**). The locality is Oak Creek, Castillo Pocket, Colorado, Horizon: Huerfano, and its geological age is 52.9 Ma. Its inclusion among the equids may be inappropriate, because *Hyracotherium* may be valid only for the European palaeothere species discussed by Owen (1841). Following a suggestion by Dr. Jerry Hooker (pers. comm. and Hooker, 1994) one can refer to it as an equoid, although the nomenclature is still debated. Its data are included in **Table S1** and **Table 1** and in the encephalization and neocorticalization plots in **Fig. S1 and S2**. *H. tapirinum* was somewhat larger than the skeleton at LACM. Its head+body length was about 88 cm (MacFadden, 1992, Fig. 12.9), leading to an estimated body size of 16 kg, one of the larger species of this early equoid. The endocast length (olfactory bulb to medulla) = 6.6 cm; volume $E = 24.16$ ml; surface area = 57.33 cm^2 ; olfactory bulbs = 8.53 cm^2 ; remainder = 48.8 cm^2 ; neocortex = 10.66 cm^2 ; and neocorticalization = 21.84%. I continue to use $P = 10.7$ kg, following my scale model and data derived from the LACM mounted skeleton.

MENISCOTHERIUM

Probably contemporaneous with and similar in brain size to the Tillyhorse, this specimen is *Meniscotherium robustum* (USNM V 19509), Early Wasatchian of Southern Wyoming. It has been described as about the size of a cocker spaniel, which on average weigh about 14 kg, but Gazin (1965) included pictures of the endocast and of a mounted *Meniscotherium* skeleton (not included here). Its head+body length was about 65 cm, leading to a body weight estimate of 6.5 kg, which is smaller than living adult cockers. This weight and a date of 53 Ma are used here. In a footnote to his review of *Hyracotherium*, Radinsky (1976b) suggested that the Tillyhorse was a specimen of *Meniscotherium*, which was common at that site. The narrow Tillyhorse forebrain proportions are significantly different, however, from the equally brain-like but differently proportioned *Meniscotherium* endocast

illustrated by Gazin. Tillyhorse, therefore, remains an unidentified species, probably a condylarth. *Meniscotherium*, like *Hyracotherium*, was a relatively large-brained species for its time. Its 14.8 ml endocast indicates an $EQ = 0.35$. My endocast only had its dorsal surface, which made all measurements uncertain, in particular measurements of neocorticalization, although the dorsal half included the rhinal fissure.

HYRACHYUS

Three Eocene specimens that I first saw listed as *Hyrachyus* were scanned. One was probably correctly described as *Hyrachyus modestus* (FMNH PM 59240 = YPM 11082), while a second had also been described as *Hyrachyus modestus* (YPM PU 10145) at YPM as well as “*Orthocynodon (Amynodon)*” at FMNH (PM 59177). The endocasts are similar but not identical. *Hyrachyus* were early rhinos or tapiroids. The second is described below as *Orthocynodon*, while the third specimen was much larger and discussed as *Amynodon*. The specimen numbers will keep them distinct, and I assume paleontologists expert in perissodactyl taxonomy, following Radinsky (1963, 1978), will review the specimens. I measured endocast volume of *H. modestus* (FMNH PM 59240) $E = 69$ ml and of *Orthocynodon* (FMNH PM 59177) $E = 94$ ml. My scan of the much larger *Amynodon* endocast (CMNH PM 59231, YPM 11453) was $E = 180.69$ ml.

Hyrachyus modestus (FMNH PM 59240 & YPM 11082; **Fig. 8A**) is from the Wyoming Bridger Formation, and from Woodburne (2004) I estimated its age as 51.7 Ma. Savage & Long (1986) provided a head+body length as 1.6 meters, and my weight-length formula gives it a body weight $P = 100$ kg; $E = 69$ ml; and $EQ = 0.27$. I disagree with Radinsky’s (1978) estimates of head and body length = 122 cm and do not know why he chose $P = 22$ kg. Radinsky also reported $E = 70$ ml, presumably by using Archimedes’ method, which is close to my scan measurement. My endocast length for *H. modestus* is 8.7

cm. Surface area = 115.32 cm²; olfactory bulbs = 8.47 cm²; remainder = 106.85 cm²; neocortex = 29.75 cm²; and neocorticalization = 27.85%.

ORTHOCYNODON

This specimen (FMNH PM 59177 = YPM PU 10145; **Fig 8B**) is still listed as *Hyrachyus modestus* in the YPM Catalogue, as it was reported by Radinsky (1963, 1978). It is from the Wyoming Bridger Formation, dated to 50 Ma. Radinsky (1978) had reported a body weight of about $P = 50$ kg, which was clearly too small; it was heavier than *H. modestus*, and I work with $P = 150$ kg. Endocast length = 9 cm; volume $E = 94$ ml; and $EQ = 0.28$, about the same as *H. modestus*. The surface area = 140.52 cm²; olfactory bulbs = 21.25 cm²; remainder = 119.27 cm²; neocortex = 30.82 cm²; and neocorticalization = 25.8%, again about the same as *H. modestus*.

AMYNODON

According to Wall (1998), *Amyrnodon* ranged from 46.7 Ma to 39.5 Ma. I scanned what were originally listed as two specimens in the FMNH catalogue, FMNH PM 59231 and FMNH PM 59177. The first of these, copied by Radinsky from YPM 11453 and listed at FMNH by Radinsky as *A. erectus*, is listed by YPM as *A. advenus*. The second specimen was listed as “*Orthocynodon (Amyrnodon)*” (sic) and is FMNH PM 59177, copied from YPM PU 10145, probably also prepared by Radinsky. His placing the species in parentheses must have reflected his uncertainty at that time about the name. The YPM describes it as *Hyrachyus modestus* in its catalogue, and Radinsky appears to have used the name. In view of these uncertainties, the specimen's measurements are listed under *Orthocynodon* above. With respect to the first specimen, the YPM catalogue lists FMNH PM 59231 (YPM 11435) as *Amyrnodon advenus* Marsh from Uintah County, Utah, and this can be dated to about 46 Ma.

The scans are shown in **Fig. 8C**. From Wall (1982, 1998), skull length = 45 cm; body length = 220 cm; $P = 263$ kg. For the encephalization analysis, its endocast volume $E = 181$ ml and $EQ = 0.37$. Endocast surface area = 239.39 cm^2 ; olfactory bulbs = 12.41 cm^2 ; remainder = 226.98 cm^2 ; neocortex = 75.77 cm^2 ; and neocorticalization = 33.4%.

EOMOROPUS

Scans of the endocast of this Eocene early chalicothere (Perissodactyla) are shown in **Fig. 8D**. I have seen only the skull and endocast. The skull was just under 30 cm long and suggested an animal about 120 cm in length; $P = 40$ kg. The endocast is of *Eomoropus amarorum* (FMNH PM 59182 copied from AMNH FM 5096); length = 6.8 cm; and volume $E = 37$ ml. It was recovered from the Washakie Formation with the suggested geological age of 44 Ma. The $EQ = 0.26$; endocast surface area = 80.41 cm^2 ; olfactory bulbs = 1.76 cm^2 ; remainder = 78.66 cm^2 ; neocortex = 23.46 cm^2 ; and neocorticalization = 29.8%.

MESATIRHINUS JUNIUS

My two scanned specimens of *Mesatirhinus* are FMNH PM 59196 (= AMNH 1509) and FMNH PM 59197 (= YPM 10041), both from the Bridger Eocene, about 46.5 Ma. The first is probably *M. petersoni* (AMNH 1509; **Fig. S9A**), and the second (YPM 10041; **Fig. S9B**) is probably *Mesatirhinus junius*; both are now identified as *Mesatirhinus junius* (Mihlbachler, 2008). YPM 10041 came from Sweetwater County, Wyoming. Their data are presented in **Table 1**.

There are ambiguities in the history of the nomenclature. FMNH PM 59197 was copied from Marsh's specimen YPM 10041. It is recorded in the Yale Peabody Museum catalogue as *M. junius*, family Brontotheriidae in Perissodactyla. According to the Yale

catalogue, both specimens were probably collected from the Bridger Formation and the Washakie Formation and are dated to approximately 46 Ma. This *M. junius* may have been somewhat larger than “*M. petersoni*”, but I take them both as $P = 350$ kg. The Yale Peabody Museum also records it as *Tetheopsis ingens* and *Eobasileus commutus*; that is, as uintatheres, but I treat it as a brontothere, Perissodactyla. *Mesatirhinus* is thus “progressive” rather than “archaic” with respect to survival and extinction. It is shown in **Fig. S9A**; the lateral view on the right shows the rhinal fissure. The endocast length is 12.3 cm; $E = 189.5$ ml; $EQ = 0.32$; endocast surface area = 227.32 cm^2 ; olfactory bulbs = 14.56 cm^2 ; remainder = 212.76 cm^2 ; neocortex = 58.23 cm^2 ; and neocorticalization = 27.37%.

MESATIRHINUS PETERSONI

My endocasts are shown in **Fig. S9B**. The endocast is of *M. petersoni* (FMNH PM 59196 copied from AMNH 1509). The length = 13.2 cm; $P = 350$ kg; $E = 146.90$ ml; $EQ = 0.25$; endocast surface area = 221.06 cm^2 ; olfactory bulbs = 24.68 cm^2 ; remainder = 196.38 cm^2 ; neocortex = 37.17 cm^2 ; and neocorticalization = 18.93%.

PACHYAENA AND MESONYX

Pachyaena ossifraga (YPM 14708) is a mesonychid collected in 1947 from the Willwood Formation in Wyoming, dated to about 53 Ma. Its body size was estimated as about 65 kg (Zhou, Sanders, & Gingerich, 1992). Its endocast is illustrated in **Fig. S9C**. The endocast of *Mesonyx obtusidens* (FMNH 57139) was copied by Radinsky from YPM 13141 (Radinsky, 1976a). Only about half of the brain+matrix was present, and I removed excess matrix when preparing its digital image (**Fig. S9D**). A dramatic evolutionary development in the brain of mesonychids is evident in comparing the *M. obtusidens* endocast with the earlier mesonychid, *Pachyaena ossifraga* (Zhou et al., 1992). The *Pachyaena* endocast length = 9.2

cm, while the *Mesonyx* endocast length = 8.2 cm. Note the poorly defined olfactory tracts and bulbs in the older specimen and their complete absence in the later one.

Mesonyx obtusidens is from Bridger B in Wyoming, dated to about 48 Ma. Savage & Long (1986) illustrated the animal and estimated its body length as 150 cm, which resulted in a body weight $P = 82$ kg. Radinsky had estimated its body weight from the skull length as about 50 kg. Here I use the middle value of 65 kg, the same as the estimated body weight suggested by Zhou et al. (1992) for *P. ossifraga*. The endocast volume of the earlier mesonychid *P. ossifraga* is $E = 32.66$ ml; $EQ = 0.17$. The allometric expected brain size in a 65 kg living species is 194 ml, which would be the denominator of EQ in both mesonychids. My *Mesonyx obtusidens* fragment is 48 ml. Assuming that the volume of the fragment of *Mesonyx* is half the total volume (disregarding the absence of olfactory bulbs), the total volume $E = 96$ ml and $EQ = 0.49$, more than twice as encephalized as the older mesonychid.

For a context of EQ s in living carnivoran species weighing about 65 kg, here are some numbers from Van Dongen's (1998) tables for living mammals. Zhou et al. measured the living hyena, *Hyaena crocutta*, for comparisons with *P. ossifraga*. The living hyena's reported body weight was 66 kg and its brain weight 161g; hence $EQ = 0.82$. The smaller living jaguar, *Panthera onca*, weighed 56 kg and had a 150 g brain, $EQ = 0.85$.

The forebrain and hindbrain in *Pachyaena ossifraga* are linearly aligned, similar to many Eocene species. The *M. obtusidens* endocast is bundled more spherically, comparable to that of *Eusmilus bidentatus* and *Felis catus* shown above. Its cerebellum, however, extends posteriorly beyond the forebrain. That my estimated total endocast was only half the volume of comparable living brains ($EQ = 0.49$) is of course part of the story of increasing encephalization in brain evolution.

The quantitative analysis of neocorticalization in the mesonychids is similar to their encephalization. The endocast surface area in *P. ossifraga* was 88.5 cm^2 , including olfactory

bulbs and tract, which measured 7.95 cm². The total neocortex surface area was 8.4 cm², hence a neocorticalization of 10%. The total endocast surface area of *M. obtusidens* was 133 cm², with neocortical surface area of 31 cm² and a neocorticalization percentage of 23%. Both endocasts contain a disproportionate amount of hindbrain. The denominator is high in both specimens, reflecting greater representation of hindbrain relative to forebrain.

SMILODECTES

The endocast of this Eocene lemuroid (shown in **Fig. 10A**) *Smilodectes gracilis* (FMNH PM 56263), was copied from YPM 12152. *S. gracilis* is from Uinta County, Wyoming. I was given a copy by C.L. Gazin (1958) but scanned the more carefully prepared endocast in the Radinsky Collection at FMNH, which originates from the Bridger Formation in Wyoming and is dated to 48 Ma. Radinsky and I differed in our views on its body size (Jerison, 1979, Radinsky, 1979). I judged it to be a 1.6 kg prosimian. The endocast scans (length = 3.4 cm) are shown in **Fig. 10A**. The endocast volume $E = 9$ ml; $EQ = 0.55$; endocast surface area (olfactory bulbs missing) = 25.93 cm²; neocortex surface area = 9.13 cm²; and neocorticalization = 35.23%. The endocast was compared with that of the Paleocene *Plesiadapis tricuspidens* by Orliac et al. (2014), who noted that EQ s in the later primates were higher, the endocasts more globular, and olfactory tract and bulbs were smaller.

NOTHARCTUS

This endocast, FMNH PM 59264 and identified only as “Tertiary: Eocene,” is shown in **Fig. 10B**. It is described in Gunnell et al. (2007). Fleagle (1999) estimated the body weight in four species as between 4200 g in *N. tenebrosus* to 6900 g in *N. robustus*, based on tooth measurements. The endocast length (olfactory bulb to medulla) = 5 cm. The lateral view emphasizes the rhinal fissure emerging from the olfactory bulb. The specimen was sketched

by Radinsky (1979). My measurements were of the left hemisphere but, despite its distorted form, a reasonable guess of its endocast volume is $E = 15.38$ ml. I used a 4200 g body weight and a 15 ml endocast volume for the analysis of encephalization in the specimen; $EQ = 0.48$. Estimating neocorticalization was difficult because of the fragmented endocast, which was of approximately half the brain region and included posterior “brain” and matrix. An estimate of its total brain surface area is 40.57 cm^2 ; half its neocortex area is about 5 cm^2 ; neocortex = 10 cm^2 ; olfactory bulbs = 2.32 cm^2 ; remainder = 38.25 cm^2 ; and neocorticalization = 26.14%. Its age is about 47 Ma.

Later Eocene Fossils

Here, “Later Eocene” is 42 Ma to 32 Ma.

NECROLEMUR

The scanned endocast is of *Necrolemur antiquus*, FMNH PM 59261 copied from YPM 18402. This small fossil primate is from the Quercy deposits, late Eocene, about 37 Ma. There are a number of body size estimates, all small. Working from tooth data, Fleagle (1999) calculated body size $P = 320$ g; endocast $E = 5.05$ ml; and $EQ = 0.90$. The endocast is remarkably clean, and somewhat more than half could be cast. The half volume was determined from the clear midline ridge. Its encephalization is the highest of the Eocene mammals. Its olfactory bulbs and tract as distinguished from the rest of the forebrain lead to a reasonable analysis of neocorticalization. The endocast surface area = 39.18 cm^2 ; olfactory bulbs = 2.08 cm^2 ; remainder = 37.10 cm^2 ; neocortex = 14.04 cm^2 ; and neocorticalization = 37.84%. The endocasts are shown in **Fig. 10C**; the lateral view of almost all of the left temporal lobe with some rhinal fissure is visible at its lower border. The almost hidden rhinal fissure in lateral views is typical of later primate brains.

ADAPIS

My scan of this Eocene lemuroid (FMNH 59259 = NHMUK M1340), *Adapis parisiensis*, is of Professor R. D. Martin's (1990) endocast, which has clearer surface features than earlier preparations (LeGros Clark, 1959; FMNH PM 59275). It is from a well-preserved Quercy skull and dates to 34.1 Ma; $E = 8.2$ ml; length (olfactory bulbs to medulla) = 4.7 cm. I estimated its body weight $P = 1600$ g (cf. Jerison, 1979; Radinsky, 1979). The $EQ = 0.50$; endocast surface area = 24.95 cm^2 ; olfactory bulbs = 1.42 cm^2 ; remainder = 23.53 cm^2 ; neocortex = 10.17 cm^2 ; and neocorticalization = 43.23%. It is similar in shape to the brains of living lemuroids. My FMNH 59259 is shown in **Fig. 10D**.

My other *Adapis* specimen, FMNH PM 59275, has $E = 7.85$ ml; $P = 1600$ g; $EQ = 0.48$, and is not illustrated. The specimen may occasionally have been referred to as *A. magnus*. The endocast surface area = 26.52 cm^2 ; olfactory bulbs = 1.55 cm^2 ; remainder = 24.97 cm^2 ; neocortex = 13.25 cm^2 ; neocorticalization = 53.06%. The data are quite similar for the two specimens; the difference is due to my error of measurement and some minor differences between the endocasts. Martin (1990) provided a detailed review of these specimens and of other fossil and living primate brains and endocasts, including consideration of sexual dimorphism.

UINTATHERIUM

I scanned the endocast of *Uintatherium anceps* (YPM 11036), prepared by O. C. Marsh, from material retrieved from the Bridger Formation in Uinta County, Wyoming (Marsh, 1886). One of the largest species of its time, it dates from about 49 Ma. My scanned endocasts are shown in **Fig. 11A**. Its body size was determined by scaling up a carefully prepared model (Jerison, 1973) to produce a body weight of about 1,250 kg. The entire

endocast measured 434 ml, but when the olfactory bulbs were removed it measured 386 ml. The anterior portion of the skull was almost certainly drilled out when the skull was prepared for the endocast, and the size of the endocast's "olfactory bulbs" are grossly overestimated. The endocast resembles an enlarged rat brain and reflects the error that enlarged olfactory bulbs are primitive traits, more represented in rats than in humans. As in all the specimens in the neocorticalization analysis, the surface area of these "olfactory bulbs" is subtracted from the area of the entire endocast when determining the neocortex-to-endocast area ratio. Taking $E = 386$ ml as the brain volume, the $EQ = 0.28$. The endocast length as illustrated (including olfactory bulbs) = 17.2 cm; surface area (including olfactory bulbs) = 391.2 cm^2 ; olfactory bulbs = 76 cm^2 ; remainder = 343.20 cm^2 ; neocortex = 64.37 cm^2 ; and neocorticalization = 18.75%.

MEGACEROPS COLORADENSIS

The endocast of this brontothere (**Fig. 11B**) was probably prepared from a skull from the White River Group. It is catalogued as FMNH PM 59199 and identified only as from the Radinsky Collection, but I think it was copied by Radinsky from YPM 12010. In the FMNH catalogue it is listed with a minor spelling error as *Titanotherium "inges" (Menodus)*. In the Yale catalogue it is referred to as *Menodus ingens*, and following Mhlbachler et al. (2004), it is likely synonymous with *Megacerops coloradensis*. It was described by O. C. Marsh (1874) as collected from Colorado, "Devendorf party (1873)" and called early Oligocene. I believe that it would now be dated Late Eocene 34 Ma. Described in various places as small-brained, its impressive endocast, $E = 750$ ml, is of an appropriate size for its time and body size. The $EQ = 0.25$ and length = 17.1 cm. It was a heavily built animal that measured about 4.3 meters in length and weighed about 4,000 kg. The endocast surface area = 521.47 cm^2 ; olfactory

bulbs = 36.62 cm²; remainder = 484.85 cm²; neocortex = 164.37 cm²; and neocorticalization = 33.9%.

MOERITHERIUM

This endocast (**Fig. 11C**) of the early Eocene proboscidian (NHMUK M. 9176) is from the Fayum in Egypt (Fayum Chron17, 37 Ma). The animal has been described as pig-sized or small hippopotamus-sized. Its skull as sketched in Savage & Long (1986) is 44 cm long, and I estimate its body length to be about 200 cm. My formula for a species of heavy habitus of that body length suggests body weight $P = 394$ kg, used here. Savage & Long indicated a lower body weight of 230 kg; I do not know their source. Its endocast $E = 233.33$ ml and $EQ = 0.36$. The reconstructions of the body have an interesting history. One was prepared for the 1851 London Crystal Palace Exposition, and I think it is presently in the entry court of MNHN. The endocast length = 11.6 cm; surface area = 265.93 cm²; olfactory bulbs = 34.58 cm²; remainder = 231.35 cm²; and neocorticalization = 33.8%. **Fig. 11C** shows that the matrix forms a large mass of material at the ventral border of the olfactory bulbs, which can be removed by digital editing.

ARSINOTHERIUM

A. zitelli (NHMUK M. 5539), suborder Embrithopoda, from the Fayum in Egypt about 33 Ma, was one of the heaviest species of its time. Its endocast is illustrated in **Fig. 11D**. There appears to be matrix added to the right cerebellar area in the region of the flocculus. The most recent description of the species is by Sanders et al. (2010), from which I estimated its heavily built body length as 330 cm. From my Eq. 2, this leads to $P = 1.51$ metric tons. After clipping a portion of its right “cerebellum”, its endocast volume measured 926.6 ml; $EQ = 0.59$; and endocast length = 18.6 cm. Convolutions, presumably present in its

brain, did not mold the cranial cavity and are not represented in the endocast. It is unique in my sample of land mammals in that the rhinal fissure is not visible, so neocorticalization could not be estimated.

PTERODON

This “creodont” hyaenodontid species, described by Piveteau (1961) as the size of a large wolf, is from the Quercy deposits that date from about 40 Ma to about 32 Ma. My endocasts are shown in **Fig. 12A**. It is one of the “Creodonta”, more specifically a hyainailourine hyaenodontan, that can be compared with the Carnivora illustrated here. This *Pterodon dasyuroides* endocast is NHMUK M. 25985; olfactory bulbs not preserved; length (forebrain to medulla) in the vertically oriented illustration 9.6 cm; and $E = 58.51$ ml. The olfactory bulbs were preserved in the specimen illustrated in Piveteau (1961, p. 809), and the skull illustrated in Piveteau (1961, p. 679) is 23 cm long. I thus estimated the body length to be about 115 cm. This results in a body weight of 37 kg, somewhat less than the 42 kg weight of the wolf recorded by Van Dongen (1998). I date it to 36 Ma. $EQ = 0.44$; endocast surface area = 105.05 cm^2 ; neocortex = 37.19 cm^2 ; and neocorticalization = 35.4%.

STENOPLESICTIS

Radinsky evidently copied this endocast (**Fig. 12B**) of the Eocene stenoplesictid feliform (FMNH PM 59013) from NHMUK M. 1381, which was a Quercy specimen, probably “*Cynodictis*” *cayluxi* (now *Stenoplesictis cayluxi*), figured in Piveteau (1961, p. 705 and p. 809). It was a small species of Carnivora, family Stenoplesictidae., with an age of about 34Ma for the scanned specimen. Its skull as pictured in Piveteau was 9.9 cm long, and its body length was about 49 cm, leading to body weight of $P = 2.8$ kg. The endocast volume

$E = 11.60$ ml; $EQ = 0.49$; endocast surface area = 33.29 cm^2 ; olfactory bulbs = 2.50 cm^2 ; remainder = 30.79 cm^2 ; neocortex = 12.54 cm^2 ; and neocorticalization = 40.73%.

CYNOHYAENODON

This small “creodont” hyaenodontid is specimen FMNH PM 57153, but there is no record of species or location recorded at FMNH. It is a Quercy locality specimen, about 34 Ma, probably *Cynohyaenodon cayluxi*. Only its left half was preserved and it is shown in **Fig. 12C**, to the left of its lateral view. Although the rhinal fissure was unclear in this image, it was clear enough to estimate neocorticalization. As with all Quercy specimens, Piveteau provided an overall description, and the natural endocast is described by Dechaseaux in Piveteau (1961 p.809, fig.189). Piveteau included information on skull and body size: skull length is given as 2/3 natural size, but from data on the endocast, the actual magnification of the text image was 0.61. I assumed a body length of 61 cm and body weight of $P = 5.4$ kg. My scan of its endocast indicated $E = 11.04$ ml; $EQ = 0.30$; endocast surface area = 32.46 cm^2 ; olfactory bulbs = 4.58 cm^2 ; remainder = 27.88 cm^2 ; neocortex = 8.32 cm^2 ; and neocorticalization = 29.83%.

QUERCYGALE

My specimen was originally identified as *Procynodictis angustidens*, FMNH PM 57168, and was copied from AMNH 95590, probably by Radinsky (1978). Its endocast volume $E = 23.33$ ml. According to the AMNH catalogue, it is *Quercygale angustidens* from the Quercy deposits in France. McKenna & Bell (1997) suggested that *Procynodictis* may be a *nomen nudum*, but Radinsky, who earlier examined the skull at MNHN, chose the listed name for the FMNH specimen. Piveteau (1961) evidently accepted the name. *Procynodictis* is listed among the Canidae in McKenna & Bell (1997), whereas *Quercygale* is listed among

the Viveridae, and later assigned to Miacidae (Wesley-Hunt and Werdelin, 2005), although there is still some uncertainty in its precise phylogenetic position within Carnivoraformes (e.g., Tomiya, 2011). The distinction may be appropriate for paleoneurologists who study the details of patterns of convolutions as Radinsky does, but I am skeptical about the emphasis on those convolutional details as firm signs of functional areas. The *Quercygale* endocast is shown in **Fig. 12D**; in the view of its lateral surface, the rhinal fissure is faintly visible dorsal to the olfactory tract. The endocast length = 6.3 cm. Radinsky (1978 p. 828) reported a body size of about 6 kg, which he “modeled after other carnivores”. I found no other estimates and used $P = 6571$ g. Radinsky suggested a geological age of about 40 Ma, the older extreme for Quercy; he may have used the probable age of the American species of *Procynodictis*. In any case, an age of 40 Ma is an acceptable estimate and it is used here. The $EQ = 0.55$, which may be high for the Eocene and suggests that the body size is underestimated. The endocast surface area = 53.09 cm^2 ; olfactory bulbs = 1.32 cm^2 ; remainder = 51.77 cm^2 ; neocortex = 21.56 cm^2 ; and neocorticalization = 41.64%, also a relatively high value for an Eocene species, in this instance uninfluenced by the estimate of body size.

CEBOCHOERUS

The skull of *Cebochoerus lacustris* illustrated by Piveteau (1961, p. 900. Fig. 14) was 16.4 cm long, indicating a body length of 70 cm. My weight-length equation resulted in a body weight estimate of $P = 8$ kg. My scanned endocast specimen FMNH PM 59051 has not been identified with respect to species or locality, but from Piveteau, *C. lacustris* is the likely name of the FMNH specimen. It is an early relative of the suids (family Cebochoeridae) from the Quercy deposits. Erfurt & Métais (2007) described the genus as from MP13 to MP19 and a geological age of 38 Ma. Only a partial endocast was available, illustrated in **Fig. 13A** and with length = 5.6 cm. Its half “brain” volume indicated a total $E = 11.9$ ml; $EQ = 0.25$;

endocast surface area = 34.1 cm²; olfactory bulbs = 3.84 cm²; remainder = 30.26 cm²; neocortex = 7.01 cm²; and neocorticalization = 23.17%.

HYLOMERYS

This artiodactyl endocast is FMNH PM 59055 and was copied from CM 2915, originally designated as a paratype for *Sphenomeryx quadricuspis* (Peterson, 1919). The taxon has since been included in *Hylomeryx* (Stucky, 1998). The endocast was from Uinta C, Member Myton, and its age ranges from 45.9 to 39.5 Ma. It is shown in **Fig. 13B**, olfactory bulbs missing; and length = 4.3 cm. For neocorticalization analysis, I date it to 42 Ma. I found the estimate $P = 6$ kg in my data sheet but do not know its source, and a literature search did not help. The endocast $E = 9$ ml. Assuming that the brain and body size are correct, $EQ = 0.23$; endocast surface area (olfactory bulbs absent) = 26.78 cm²; neocortex = 6.71 cm²; and neocorticalization = 25.04%.

MIXTOTHERIUM

The specimen is FMNH PM 59052, with no species or locality data. In his discussion of its 14 cm skull, Piveteau (1961, p. 901, Fig. 15) treated this small artiodactyl as similar to *Cebochoerus* and probably another Quercy species of about 40 Ma. Piveteau called it *Mixtotherium cuspidatum* and described it as another suid-like species, family Mixtotheriidae. It is shown in **Fig. 13C**. Just over half of the endocast could be scanned, and the olfactory bulbs were preserved; length = 6.7 cm; and $E = 21$ ml. Assuming a body length of 62 cm, it weighed $P = 6$ kg; $EQ = 0.53$; endocast surface area = 45.93 cm²; neocortex = 12.74 cm²; and neocorticalization = 27.73%.

CHADRONIA

The endocast of this species, FMNH PM 57129, is a good image of the brain, despite the shattered skull from which it was prepared. It is the species described by Cook (1954), *Chadronia margaretae*; the species name memorializes his wife, who found the skull. Endocast $E = 28.86$ ml. The skull length was 15.1 cm, indicating a body length of 68 cm and body weight $P = 7.5$ kg. It is late Eocene, about 35 Ma. The animal, according to McKenna & Bell (1997), was a cimolestid and among the Pantolestinae, and later removed to Pantolestidae outside of Pantolestinae (Gunnell et al., 2008). McKenna, amused, once showed it to me as an unusually large and modern looking fossil insectivore endocast, given the frequent view of living insectivores such as hedgehogs (*Erinaceus europeaus*) as having primitive brains. The *Chadronia* endocast is appropriately convoluted for a brain its size, comparable to capybara, and more convoluted than the surprisingly smooth-brained beaver. It had been considered a “creodont” and a mesonychid, and most recently a pantolestid. Regardless, its habits were probably those of a small carnivorous species. It is shown in **Fig. 13D**: length = 7.7 cm; $EQ = 0.63$; endocast surface area = 66.47 cm^2 ; olfactory bulbs = 6.09 cm^2 ; remainder = 60.38 cm^2 ; neocortex = 23.48 cm^2 ; and neocorticalization = 38.89%.

ANOPLOTHERIUM

This artiodactyl endocast was recognized by Edinger (1975) as a “first” in the history of paleoneurology. Well-articulated remains of the animal were found in the plaster of Paris gypsum beds of Montmartre. Georges Cuvier named it *Anoplotherium commune*. Part of the natural endocast was mentioned by Cuvier in his 1804 lecture (Cuvier, 1835), when he used this MNHN specimen to discuss fossils. His point was that these were petrified bones, not ordinary rocks that God had shaped like bones to tempt people to adopt views inconsistent with the book of Genesis. In a public demonstration, Cuvier, as organizer and director of the Muséum Nationale d'Histoire Naturelle (MNHN), exposed parts of the fossil and predicted

that additional preparation would reveal features evident in the skeletons of living species. With hammer and chisel he exposed previously hidden parts of the skeleton. Opening the cranium revealed part of a convoluted surface of the brain-like endocast. The specimen that I scanned, *Anoplotherium commune* (NHMUK 3753; my **Fig. 14A**), is from Quercy rather than Paris (Palmer, 1913) and is now dated to 34.1 Ma. In an earlier publication (Jerison, 1973), I estimated its endocast volume as 80 ml and its body size as 82 kg. Editing the endocast to remove matrix artifacts from the base of the “medulla”, I remeasured it as $E = 78.37$ ml; $EQ = 0.35$; and length = 10.4 cm. It was an early artiodactyl, family Anoplotheriidae. The endocast surface area = 129.18 cm^2 ; olfactory bulbs = 6.88 cm^2 ; remainder = 122.31 cm^2 ; neocortex = 34.83 cm^2 ; and neocorticalization = 28.48%. This endocast is an important example of the railroad-car appearance, elongated to distinguish cerebellum from forebrain as occurs in some Paleogene fossil endocasts.

PATRIOMANIS

This Eocene pangolin, *Patriomanis americana* (FMNH PM 57103 FAM 78999), is listed in the FMNH catalogue as Oligocene, from Bates Hole, Wyoming. Its skull (Emry, 2004) was about 10 cm long, and from Emry’s sketch of its body (Emry and Gaudin, pers. comm.), I determined its head+body length as about 50 cm. It is from the Ash 5 Layer and dates to about 34.7 Ma. My weight-length regression analysis resulted in a body weight of about 3 kg. The scans are shown in **Fig. 14B**. Its endocast $E = 11.21$ ml and $EQ = 0.45$. Interestingly, one living pangolin, *Manis javanica*, has been reported (Van Dongen, 1998) with a body weight of 3.5 kg and brain weight of 11 grams. Evidently there was no progress in relative brain sizes in pangolin species from the Eocene to the present. The endocast surface area = 33.86 cm^2 ; olfactory bulbs = 4.21 cm^2 ; remainder = 29.65 cm^2 ; neocortex = 5.23 cm^2 ; and neocorticalization = 17.65%.

POEBROTHERIUM

The endocast (PM 59167 FAM 31700) shown in **Fig. 14C** is from the Brule Formation, Wyoming. I found no definite dating, but from Woodburne (2004) it appears to be late Eocene, about 35 Ma. Multiple regression analysis (Mendoza et al., 2006) gave body weights ranging from 29.8 kg to 42.9 kg. Savage & Long (1986) reported a skull length of 17.5 cm, suggesting a body length of 88 cm. My length-weight equation suggested a much smaller body weight $P = 16$ kg, but I use Mendoza's lower body weight of 29.8 kg to assess its encephalization. Endocast $E = 47.82$ ml; $EQ = 0.41$; length (olfactory bulbs not preserved) = 7.5 cm; surface area = 81.59 cm^2 ; neocortex = 33.79 cm^2 ; and neocorticalization = 41.41%.

BATHYGENYS

I reviewed one specimen (UT TMM 40209-431, and Fig 46 Species 431) from a larger sample of *B. reevesi* described by Dr. Jack Wilson (Wilson, 1971) and more recently studied by Macrini (2009). Although originally dated to 34 Ma, they are Chadronian, about 37 Ma. My specimen's skull is about 9.4 cm long. If its body had been shaped like that of its larger later relatives (e.g., *Merycoidodon culbertsoni*), it would have been about 42 cm long, weighing about 2 kg for encephalization analysis. Mendoza et al. (2006) estimated its body size from a multiple regression analysis of tooth dimensions in four specimens, the results showing body sizes ranging between 6 and 8.5 kg, which also seem reasonable. I used 6795 g for my analysis. Its endocast volume $E = 12.08$ ml; length = 5 cm; and $EQ = 0.28$.

The sample of 20 endocasts that Dr. Wilson allowed me to measure provided the best available data at the time (Jerison, 1979) on within-species variability in fossil endocasts. I discuss these data and Macrini's (2009) analysis in "Within Species Variation" below. In my specimen UT 40209-431 shown in **Fig. 14D**, the olfactory tract abuts the anterior border of

the rhinal fissure, but the fissure continues ventral to neocortex. The endocast surface area = 33.46 cm²; olfactory bulbs = 2.35 cm²; remainder = 31.11 cm²; neocortex = 8.71 cm²; and neocorticalization = 28.0%.

Oligocene Fossils

The “Oligocene” samples in this monograph are dated from 32 Ma to 23 Ma. These dates anchor the analysis of neocorticalization as changes with the passage of time.

DAPHOENUS

Two endocasts were identified as *Daphoenus vetus*, FMNH PM 59008a UM1 and FMNH PM 59008b; only the former is shown in **Fig. 15A**. They are probably from the White River Badlands in South Dakota and date to 32 Ma. They are from the bear-like arctoid family Amphicyonidae, order Carnivora. Olfactory bulbs were not preserved in either specimen. The endocast volume of FMNH PM 59008a was $E = 46.87$ ml and FMNH PM 59008b was $E = 42.61$ ml. From tooth sizes, the body weight for the species has been estimated as 7.84 kg (Legendre & Roth, 1988). From the head and body length of about 1 meter, I estimated their body weights as much heavier, about 24 kg; $EQ = 0.47$ for 59008a and $EQ = 0.43$ for 59008b. For PM 59008a, the endocast surface area = 80.89 cm²; neocortex = 39.82 cm²; and neocorticalization = 49.22%. For 59008b, the surface area = 84.96 cm²; neocortex = 39.10 cm²; and neocorticalization = 46.02%. My two casts were almost indistinguishable.

DINICTIS

The scanned half endocast (**Fig. 15B**) of this early nimravid, *Dinictis felina*, order Carnivora, is FMNH PM 58866, copied by Radinsky from the South Dakota School of Mines Museum of Geology (SDSM) specimen 2431. It is Orellan, from the White River Badlands of South Dakota, 32 Ma. The half endocast displaced 30 ml, indicating $E = 60.1$ ml. Its head+body length was 115 cm leading to a body weight of $P = 37$ kg; $EQ = 0.45$; length = 6.8 cm; endocast surface area = 88.4 cm^2 ; neocortex = 42.14 cm^2 ; olfactory bulbs = 4.9 cm^2 ; remainder = 83.23 cm^2 ; and neocorticalization = 50.63%.

EUSMILUS

The endocast of this nimravid sabretooth, *Eusmilus bidentatus* (FMNH PM 58871), is shown in **Fig. 15C**, in which its ectosylvian complex is compared with that visible in the living cat's endocast and brain. In living cats, this complex represents most of the auditory neocortex (Johnson, 1990), and it is reasonable to assume that this was also true of their relatives of the late Eocene and early Oligocene. My original *Eusmilus* is a Quercy specimen at MNHN and is illustrated in Piveteau (1961, Fig. 202, p. 817). Dating is imprecise; I assumed that it is early Oligocene, partly because individuals from North America are early Oligocene and about 32 Ma. Only about half of the brain is present in the right hemisphere in **Fig. 15C**. The endocast length = 7.2 cm. The half volume was 20 ml, indicating a 40 ml endocast volume. Its 19 cm skull suggested a head+body length of about 90 cm and body weight $P = 18$ kg. Its tooth measurements suggested a much larger animal, perhaps 70 kg (Legendre & Roth, 1982). It has been described as the size of a small leopard (as was *Hoplophoneus*). I propose that *Eusmilus* was about the same size as *Hoplophoneus*, $P = 35$ kg; $EQ = 0.31$; endocast surface area = 70.19 cm^2 ; olfactory bulbs = 4.87 cm^2 ; remainder = 65.32 cm^2 ; neocortex = 32.92 cm^2 ; and neocorticalization = 50.4%.

HOPLOPHONEUS

My specimens are USNM 22538 (**Fig. 15D**) and UM2. In Jerison (1973), I reported two body weights for *Hoplophoneus*: one as *H. oreodontis* and the other as *H. primaevus*, which is shown here. I published a body weight of 20 kg for a 74 cm head+body length in *H. oreodontis*, and a body weight of 49 kg for *H. primaevus* with a 100 cm head+body length. I treated both as of “heavy” habitus. Reviewing skeletal reconstructions, I change these estimates here.

Hoplophoneus has been described as the size of a small leopard. Walker (Nowak, 1999) reported the head+body lengths of these living carnivores as 91 to 191 cm, and *H. primaevus* fits into that range. It is also described as heavily built, which may explain my treating its habitus as heavy, although the skeletal reconstructions do not suggest an unusually heavily built small carnivore. Body weights in living leopards are reported as ranging between 37 and 90 kg for males and 28 to 60 kg for females. Van Valkenburgh (1990) estimated body weights of 13 or 19 kg for *H. primeavus* and 66 or 69 kg for *H. occidentalis* using head+body length and skull length in her regression analysis. A reasonable estimate for body size is $P = 35$ kg. The forebrain-to-medulla length = 6.7 cm.

My *Hoplophoneus* specimens are from the South Dakota White River Badlands, early Oligocene, about 32 Ma. Olfactory bulbs have not been recovered. The endocast UM2 volume was $E = 42.67$ ml, hence $EQ = 0.33$. The volume of endocast USNM 22538 was $E = 49.47$ ml, hence $EQ = 0.39$. Endocast UM2 surface area = 73.11 cm^2 ; neocortex = 28.48 cm^2 ; and neocorticalization = 39.0%, while endocast USNM 22538 surface area = 79.38 cm^2 ; neocortex = 32.57 cm^2 ; and neocorticalization = 41%.

The differences between brain measurements in *Eusmilus* and *Hoplophoneus*, including EQ , are related to small differences in preservation of the *Hoplophoneus* endocasts and the incomplete endocast of *Eusmilus*, which had to be doubled to provide estimates. They

reflect underlying errors in measurements in the material due to the endocasts' conditions.

The errors in these carnivore endocasts were larger than those usually encountered when preparing and analyzing scans.

MERYCOIDODON

The endocast of *Merycoidodon culbertsoni* (FMNH UM3) is from the lower Brule Formation of South Dakota. This is no later than 32 Ma, a reasonable date for my specimen. Its head+body length of about 140 cm results in a $P = 68$ kg for its body weight. The scanned endocast did not include an olfactory bulb region. *M. culbertsoni* is one of the most frequently collected Oligocene artiodactyls in the South Dakota Badlands, an oreodont in the family Merycoidodontidae. It is shown in **Fig. 16A**: length (top to bottom) = 7.2 cm; endocast volume $E = 47.25$ ml; $EQ = 0.24$; surface area = 78.05 cm^2 ; neocortex = 22.57 cm^2 ; and neocorticalization = 28.9%.

MESOHIPPUS

This scanned specimen, *Mesohippus bairdi* (FMNH-PM59221) from the Brule of the South Dakota Badlands and dated as 32 Ma, was discussed at length and illustrated earlier. The body size determined from Gidley's accurate scale model was $P = 28.5$ kg. The endocast is shown in **Fig. 16B**; length (olfactory bulbs to medulla) = 9.6 cm; $E = 86.42$ ml; $EQ = 0.77$; surface area = 127.48 cm^2 ; olfactory bulbs = 9.86 cm^2 ; remainder = 117.62 cm^2 ; neocortex = 48.89 cm^2 ; and neocorticalization = 41.56%. Encephalization in this early Oligocene equid had reached the range of living horses and the evolution of this trait had reached its present grade.

PROMERYCOCHOERUS

My specimen of *Promerycochoerus superbus* (FMNH PM 59072 copied from YPM 11002; **Fig. 16C**) from the John Day Valley, Bridge Creek, dates to about 32 Ma (Woodburne, 2004, p. 330). According to my equation on this heavily built pig-like oreodont, the head+body length = 154 cm and $P = 178$ kg. Smaller body weights were recorded by Damuth & MacFadden (1990), who did not take body build into account. In my specimen, $E = 147$ ml; $EQ = 0.39$; lacking olfactory bulbs, remaining endocast length = 10.8 cm; surface area = 174.4 cm^2 ; neocortex = 68.59 cm^2 ; and neocorticalization = 39.33%.

HESPEROCYON

The species is *Hesperocyon gregarius* (FMNH PM 58989) from the Nebraska Brule, dated to about 32 Ma. I estimated its head+body length as 80 cm, indicating $P = 12$ kg. Savage & Long (1986) described it as 45 cm long, which would be only about 2 kg, while Janis (2008) had it as 50 cm. Here I treat it as 50 cm with $P = 3$ kg for encephalization analysis. The species is a member of Carnivora, family Canidae. My endocast in **Fig. 16D** is sectioned at the midline and the data doubled from the measurements; additional errors incurred by having only a partial endocast available and uncertainty about body size must therefore be considered. The measurements suggest a more modern brain than was probably the case; in particular, the cast of the olfactory bulb and tract is unusually large, adding both to endocast volume and to its total surface area. As a result, endocast length = 4.9 cm; volume $E = 18.8$ ml; $EQ = 0.75$; surface area = 37.8 cm^2 ; half olfactory bulb area = 2 cm^2 ; remainder = 33.75 cm^2 ; neocortex = 17.6 cm^2 ; and neocorticalization = 52%.

LEPTICTIS (“*ICTOPS*”)

This natural endocast was given to me a half century ago by Dr. James Dye Bump, then Director of the Paleontology Museum of the South Dakota School of Mines near the

Badlands of South Dakota. He described it as “*Ictops acutidens* Douglass”, and I assume it is from the Badlands Orellan. It had evidently been found as an isolated natural endocast, and it can be dated to about 32 Ma. My scans are shown in **Fig. 17A**. The genus has since been renamed *Leptictis* (Novacek, 1982). My endocast $E = 3.61$ ml and is about half the volume of the *Leptictis* described by Novacek. I estimated the body size of this small squirrel-sized species as $P = 500$ ml to estimate encephalization, $EQ = 0.48$, which is perhaps high. Endocast measurements for my specimen are length = 3.2 cm; surface area = 15.11 cm^2 ; olfactory bulbs = 2.08 cm^2 ; remainder = 13.03 cm^2 ; neocortex = 1.87 cm^2 ; and neocorticalization = 14.3%.

LEPTAUCHENIA

This oreodont is FMNH PM 59074 (**Fig. 17B**), copied by Radinsky from AMNH 627. It is *L. decora* from the Protoceras Beds, Poleside Member of the Brule Formation, White River South Dakota, Whitneyan (31 Ma). The estimated body size is $P = 39.3$ kg (source not traced; possibly from Bill Turnbull, pers. comm.). Measurements of the half endocast were doubled to give an estimated total endocast volume of $E = 21.95$ ml; $EQ = 0.16$; length = 6.3 cm; surface area = 50.78 cm^2 ; olfactory bulbs = 5.02 cm^2 ; remainder = 45.76 cm^2 ; neocortex = 10.35 cm^2 ; and neocorticalization = 22.6%.

HALITHERIUM

Several copies of the *Halitherium schinzi* plaster endocast were in Tilly Edinger's room at the Senckenberg when I visited Frankfurt in 1999, and one (SNHM M.3921) was given to me for my personal collection (**Fig. 17C**). This late Oligocene sea cow had been described by Edinger (1933). *Halitherium schinzi* is from the Egyptian deserts, probably the

Fayum, and for the analysis of neocorticalization it is dated to 25 Ma (Gunnell, pers. comm.). The endocast had a small postorbital extension which I removed. Its volume $E = 266.7$ ml; estimated body weight $P = 250$ kg; $EQ = 0.56$; endocast length = 12.2 cm; surface area = 298.77 cm^2 ; total neocortical surface area = 94.59 cm^2 ; olfactory bulbs not preserved; and neocorticalization = 31.66%.

HAPALOPS

My endocast of *Hapalops* (**Fig. 17D**) is from LACM, but I have no additional museum identification. I further recorded it by reference to Scott (1937) and Piveteau (1961). Another endocast was prepared and discussed by Dozo (1987). *Hapalops* was smaller than *Nothrotherium* but of similar shape. The estimated head+body length is 1 meter, excluding the tail. It was heavily built with a body volume $P = 49$ kg. Scott (1937) had *H. longiceps* and Dozo (1987) had *H. indifferens* as *Hapalops* sp. There is additional discussion in Piveteau (1958) on the species and by Dechasaux (1958) on the endocast. It is Santa Cruzian in age, 17 Ma, from Argentina. Endocast length = 7.8 cm; $E = 54.7$ ml; $EQ = 0.34$; endocast surface area = 91.80 cm^2 ; olfactory bulbs = 7.29 cm^2 ; remainder = 84.51 cm^2 ; neocortex = 30.12 cm^2 ; and neocorticalization = 35.6%.

LEONTINIA

Two of my Neotropical notoungulates from the South American Oligocene are shown in **Fig. 18**. One is the toxodon, *Leontinia gaudryi*, shown in **Fig. 18A**. It was a heavily built animal, with a 207 cm head+body length and estimated body weight of $P = 450$ kg. It is dated to 25 Ma, from the Deseado Formation, Pyrotherium beds in Chubut Province, Cabeza Blanca (Loomis loc. J), Rio Chico in Argentina. The endocast is FMNH P 13285; length = 15 cm; endocast $E = 356.91$ ml; $EQ = 0.51$; endocast surface area = 346.90 cm^2 ; olfactory bulbs

= 28.2 cm²; remainder = 318.70 cm²; neocortex = 106.48 cm²; and neocorticalization = 33.4%.

RHYNCHIPPUS

The second Neotropical notoungulate is *Rhynchippus equinus* (FMNH P 13410, see Martínez et al. and Dozo & Martínez, 2016), shown in **Fig. 18B**. It was a horse-like notoungulate that was described by Savage & Long (1986) as about 1 meter (head+body) long. Like *Leontinia*, it was from the Deseado of Argentina, about 25 Ma. Body size $P = 32$ kg; endocast volume $E = 103.56$ ml; $EQ = 0.86$; endocast length = 8.9 cm; surface area = 158.13 cm²; olfactory bulbs = 15.85 cm²; remainder = 142.28 cm²; neocortical surface area = 43.14 cm²; and neocorticalization = 30.3%.

ARCHAEOTHERIUM

The half endocast (FMNH PM 59061) was copied by Radinsky from PU 10908 (**Fig. 18C**). It is of *A. mortoni*, an entelodont from the White River beds of South Dakota. I measured the skeleton as 167 cm in head+body length, of heavy habitus, and determined $P = 230$ kg. It was probably from Whitneyan strata, about 32 Ma. Endocast length = 16.2 cm. Endocast doubled half measurements $E = 169$ ml; $EQ = 0.37$; surface area = 204 cm²; olfactory bulb surface = 12 cm²; neocortex = 49 cm²; and neocorticalization = 26%.

PROMARTES

The endocast of *Promartes* (**Fig. 18D**), probably *P. olcottii* (FMNH P 25233), was from Wounded Knee, Decker Canyon, South Dakota, Rosebud Formation, early Arikareean, Oligocene, about 28 Ma. Its volume $E = 24.1$ ml and skull length = 10 cm, suggesting head+body length = 50 cm and $P = 3$ kg, which are within the range of living martens. $EQ =$

0.97, about the average for living mammals. Endocast length = 5.2 cm; surface area = 49.16 cm²; olfactory bulbs = 3.83 cm²; remainder = 45.33 cm²; neocortex = 16.96 cm²; and neocorticalization = 37.4%.

MESOCYON

This early canid is *M. coryphaeus* (FMNH PM 58979 = AMNH 6946) from the John Day beds, unspecified stratum, but about 25 Ma (**Fig. 19A**). Radinsky measured its skull as 15 cm, indicating a body length of 75 cm. Tooth measurements by Legendre & Roth (1988) led to body sizes of 7.4 kg and 7.19 kg in two specimens. I used head+body length **x** and body size $P = 10$ kg for encephalization analysis. Endocast length = 7.2 cm; $E = 36.6$ ml; $EQ = 0.66$; endocast surface area = 71 cm²; olfactory bulbs = 4.99 cm²; remainder = 66.02 cm²; neocortex = 26.37 cm²; and neocorticalization = 40%. This specimen (as AMNH 6946) was also figured most recently by Lyras (2009; see also citations mentioned therein).

Mio-Pliocene Fossils

I dated this group from 23 Ma to mid-Pliocene, about 3 Ma. Although the earliest hominins could be included here, they are reviewed with later Plio-Pleistocene and recent primates.

MUSTELICTIS

The specimen (**Fig. 19B**) is labeled FMNH PM 58907, but there is uncertainty about it. Radinsky's label was misread as “*Mustelictis pireteauvi*”, clearly intending *Mustelictis piveteau*, recognizing the great French paleontologist, Jean Piveteau and matching a published name in the literature (Lange 1970). It may correspond to PVPH PVQ69–1, the

specimen indicated in Lange's work (1970). The specimen is also labeled as Quercy. Its stratum in the Quercy would have been relatively late, about 32 Ma. However, it is also labeled "Aquitainien de Saint-Gérard-le-Puy" (Piveteau, 1961). The FMNH label (probably Radinsky's) has it as "Aquitanian". Present American dating has the "Aquitanian" as "equivalent to the latest Arikareean - early Hemingfordian" (Prothero and Wang, pers. comm.), which is early Miocene, about 22 Ma. I therefore present my data on this early procyonid here rather than with my Oligocene cohort. McKenna and Bell (1997) included it in *Pseudobassaris*. Endocast length = 4.4 cm; $E = 12.61$ ml; $P = 13$ kg; $EQ = 0.19$; endocast surface area = 35.32 cm^2 ; olfactory bulbs = 3.25 cm^2 ; remainder = 32.07 cm^2 ; neocortex = 9.04 cm^2 ; and neocorticalization = 28.2%.

LEPTOCYON

The endocast of this Miocene canid (FMNH PM 58961, copied from P AMNH FAM 49063) is described as Late Arikareean, suggesting a date of about 20 Ma. The species name was not recorded. My scans are shown in **Fig. 19C**. It is about 35 cm long and its body weight was reported as $P = 3.26$ kg (Legendre & Roth, 1988). Endocast length = 5.2 cm; $E = 14$ ml; $EQ = 0.54$; surface area = 36.4 cm^2 ; olfactory bulbs = 2.6 cm^2 ; neocortex = 16 cm^2 ; and neocorticalization = 47%.

MERYCOIDODON BULLATUS

The endocast of this oreodont is of *E. socialis* (FMNH PM 59076 = YPM 13118A), now synonymized into *Merycoidodon bullatus* (Christopher Norris at Yale, pers. Comm.; Stevens and Stevens 1996). The fossil was described and its mounted skeleton illustrated in Thorpe (1921). It is from Scott's Bluff, Nebraska, Arikareean, dated 23 Ma. My scans are shown in **Fig. 19D**. The endocast length = 7.6 cm; $E = 41.79$ ml; total surface area = 78.72

cm²; olfactory bulbs = 6.92 cm²; remainder = 71.8 cm²; neocortex = 23.67 cm²; and neocorticalization = 32.97%. From Thorpe's mounted skeleton, the head+body length = 93 cm, which results in a $P = 19.4$ kg and $EQ = 0.48$.

ENALIARCTOS

The endocast of this early pinneped (FMNH 57161), *Enaliarctos* sp., is dated to approximately 22 Ma and is shown in **Fig. 20A**. The animal was 144-154 cm long. Taking 150 cm as its length, this gives a $P = 82$ kg, which is consistent with the regression estimate by Berta & Ray (1990). The well preserved endocast of *Enaliarctos* is primarily of forebrain, although the olfactory bulbs are missing, as are some hindbrain (cerebellar) extensions. Although details were not recorded, it may correspond to LACM (CIT) 5302, figured by Mitchell and Tedford (1973). Extant California seal (*Zalophus californianus*) females are approximately in the body size range of *Enaliarctos*, 150-200 cm long and 50-110 kg (Nowak, 1999). No brain-body data were available for this species, but records of brains of living seals in the body size range 39.6-150 kg are from 270-442 g (Van Dongen, 1998). Despite its modern appearance, the fraction of brain of *Enaliarctos* indicated by the endocast was $E = 118$ ml; $EQ = 0.52$; endocast length as pictured 7.2 cm; neocortex = 80 cm²; surface area = 132 cm²; and neocorticalization = 61%, larger than many living mammals. The denominator in the ratio (endocast surface area) was low because of incomplete preservation, so the surface area is very much underestimated in view of the incompletely represented total brain size.

POTAMOTHERIUM

This mustelid *Potamotherium valetoni* (FMNH PM 58906 = NHMUK M7694) was from the Montaigu-le-Bain deposits in France, dating to about 22 Ma. The specimen,

including endocast and entire body, were described by Savage (1957). The endocast was also illustrated by Dechaseaux in Piveteau (1961, T. VI vol. 1, p. 815, Fig. 199) and is an example of errors in using published data. It is described as “x 4/3.” My scan of the endocast (**Fig. 20B**) resulted in a length of 5.7 cm. The published photograph at the same position as my scan had a length of 8.5 cm, with a 4/3rds magnification suggesting a true length of 6.4 cm. If I accepted the published photograph’s measurement, my error would be an overestimation of about 10%, not a critical error for my measurements but pointless to retain when much better measurements are available from the digitized data. The endocast $E = 37.3$ ml, and Savage described its head+body length as 29 inches (73.4 cm), hence $P = 10$ kg; $EQ = 0.67$; endocast length = 5.7 cm; surface area = 64.4 cm^2 ; olfactory bulbs = 4.02 cm^2 ; remainder = 60.37 cm^2 ; neocortex = 35.69 cm^2 ; and neocorticalization = 59.1%.

PLESIOGALE

This mustelid, *Plesiogale paragale* (FMNH PM 58910 = UKNHM MA 4741) from the Montaigu-le-Bain in France, is dated to 22 Ma. My scans are shown in **Fig. 20C**. Endocast volume $E = 17.8$ ml; $P = 2$ kg; $EQ = 0.93$; endocast surface area = 44.2 cm^2 ; olfactory bulbs = 3.22 cm^2 ; remainder = 40.96 cm^2 ; neocortex = 16.3 cm^2 ; and neocorticalization = 39.8%.

ZODIOLESTES

This Miocene mustelid, *Zodiolestes daimonelixensis* (FMNH P 12032), is from the lower Harrison formation of Sioux County, Nebraska, at the Niobrara River. My scans are shown in **Fig. 20D**. The geology was discussed in Woodburne (2004 p. 211) as late Arikareean, about 21 Ma. Endocast volume $E = 31.2$ ml; $P = 5$ kg; $EQ = 0.89$; endocast

length = 6.1 cm; surface area = 61.59 cm²; olfactory bulbs = 3.32 cm²; remainder = 58.26 cm²; neocortex = 29.03 cm²; and neocorticalization = 49.85%.

DESMATHYUS (HESPERHYUS)

I scanned specimen FMNH M 59066 (= CM 1423), a tayassuid endocast from the Upper Harrison Formation of Nebraska, dated to 19.5 Ma. My scans are shown in **Fig. 21**. Endocast length = 8.3 cm; E = 71.27 ml; body weight P = 11.3 kg (source not found); EQ = 1.18; endocast surface area = 122.43 cm²; olfactory bulbs = 13.59 cm²; remainder = 108.84 cm²; neocortex = 33.38 cm²; and neocorticalization = 30.7%.

OXYDACTYLUS

This Miocene camelid endocast of *Oxydactylus longipes* (FMNH P 12117), shown in **Fig. 21B**, is from Agate Springs, Nebraska, and is dated to 19.5 Ma. Damuth (pers. comm.) suggested a body weight of about 250 kg. Endocast length = 10.3 cm; E = 86.65 ml; EQ = 0.18; surface area = 131.44 cm²; olfactory bulbs = 9.24 cm²; remainder = 122.20 cm²; neocortex = 51.01 cm²; and neocorticalization = 41.7%. Dr. Damuth expressed reservations about the body weight which, given the unusual neck and body proportions of the camelid, might be exaggerated, producing the very low EQ .

HOMALODOTHERIUM CUNNINGHAMI

This heavy South American notoungulate endocast (FMNH PM 59291), shown in **Fig. 21C**, was among those cited by Patterson (1937, see also Martínez & Dozo, 2016) and was from the Santacrucian of Patagonia, 17.5 Ma; P = about 400 kg. Endocast length = 14.3 cm; E = 227.3 ml; EQ = 0.35; surface area = 284.85 cm²; olfactory bulbs = 15.96 cm²; remainder = 268.89 cm²; neocortex = 70.22 cm²; and neocorticalization = 26.1%.

BORHYAENA

The endocast of this carnivorous marsupial, *B. tuberata* (FMNH P13266), shown in **Fig. 21D**, is from San Juan strata in Argentina and is dated to approximately 17 Ma. Argot (2003) reviewed the species in detail for postcranial data, deriving an estimated body weight of $P = 23$ kg based on published regression analyses of similarly built living mammals. From her illustration (Argot, 2003, text-fig. 22) and her tables of data on femoral length, I was able to make a similar estimate based on its head+body length (100.7 cm). My length-weight equation resulted in $P = 24.6$ kg, which I used for estimating encephalization. Endocast length = 7.4 cm; $E = 43.05$ ml; $EQ = 0.42$; surface area = 82.09 cm^2 ; olfactory bulbs = 13.08 cm^2 ; remainder = 69.0 cm^2 ; neocortex = 17.39 cm^2 ; and neocorticalization = 25.2%.

PROTYPOTHERIUM

This notoungulate endocast *Protypotherium austral* (FMNH P 13046), shown in **Fig. 22A**, was from the coastal San Juan of Argentina and is dated to 16.5 Ma. Its head+body length (Croft & Anderson, 2008) is 74 cm, leading to a $P = 9.7$ kg; endocast length = 5.7 cm; $E = 16.69$ ml; $EQ = 0.31$; endocast surface area = 43.6 cm^2 ; olfactory bulbs = 2.61 cm^2 ; remainder = 41.01 cm^2 ; neocortex = 13.53 cm^2 ; and neocorticalization = 32.98%.

PROTEROTHERIUM

The endocast is of *P. cavum* (FMNH PM 59742), shown in **Fig. 22B**. It is from the Rio Robles Santa Cruz region, dating to about 17 Ma (Simpson, 1933). Endocast length = 9.2 cm; $E = 57.35$ ml. The body weight was uncertain, hence encephalization was not determined. Endocast surface area = 106.1 cm^2 ; olfactory bulbs = 4.54 cm^2 ; remainder = 101.55 cm^2 ; neocortex = 29.23 cm^2 ; and neocorticalization = 28.8%.

NESODON

My endocast is of *Nesodon imbricatus* (FMNH P13076), shown in **Fig. 22C**, a toxodon from the Santa Cruz formation in Argentina, about 17 Ma. It was described in Patterson (1937). Cassini et al. (2012) reported its body weight as 550 kg, their largest of the Nesodontinae of the Santacrucian age. **Table 1** gives a size of $P = 250$ kg, which I used to estimate encephalization. Endocast length = 12.3 cm; $E = 180.06$ ml; $EQ = 0.38$; endocast surface area = 253.29 cm^2 ; olfactory bulbs = 9.28 cm^2 ; remainder = 244.01 cm^2 ; neocortex = 72.74 cm^2 ; and neocorticalization = 29.81%.

MERYCOCHOERUS

My scan of *Merycochoerus proprius* is shown in **Fig. 22D**. The endocast of this large pig-like oreodont, *Merycochoerus* (FMNH PM 59081 = AMNH FAM 43016), was from the Marsland Formation. “Marsland” is now treated as Anderson Ranch Formation and Running Water Formation (Woodburne 2004, p. 212R), Hemingfordian Formation, about 17 Ma. Thorpe (1937) presented measurements on all of the species that he identified, listing *M. proprius* as the smallest, with a skull length of 28.6 cm, and *M. magnus* the largest, with a skull length of 33.4 cm. He reported an endocast volume of 77 ml, though it is unclear which species he intended; he merely quoted Moodie (1922). I remeasured my endocast (*M. proprius*) and recorded a volume of $E = 95.74$ ml, presumably correcting Thorpe. The head+body length = 150 cm. The skeleton of *M. proprius* was illustrated by Scott (1962, Fig. 220, p. 359) and, from comparisons with skeletal structures illustrated elsewhere, my original index card showed a body length of 120 cm. Body weight $P = 122$ kg; endocast length = 10.2 cm; $EQ = 0.32$; endocast surface area = 142.44 cm^2 ; olfactory bulbs = 9.53 cm^2 ; remainder = 132.91 cm^2 ; neocortex = 39.48 cm^2 ; and neocorticalization = 29.7%.

ADINOTHERIUM

Another toxodon from the Santa Cruz shown in **Fig. 23A** is a smaller species described by Cassini et al. (2012) as weighing 120 kg. The endocast is FMNH P 13108, *Adinotherium ovinum*; $E = 111$ ml; $EQ = 0.38$. It lived about 15.5 Ma. Endocast length = 10.2 cm; surface area = 155.35 cm^2 ; olfactory bulbs = 7.99 cm^2 ; remainder = 147.35 cm^2 ; neocortex = 49.07 cm^2 ; and neocorticalization = 33.3%.

MERYCHIPPUS SEVERSUS

This endocast LACM 368 (**Fig. S4**). It is probably *Merychippus seversus*, age 15.5 Ma. Its “olfactory bulbs” are atypically large, reflecting destruction of the bony casing of the olfactory bulbs during fossilization. Endocast volume $E = 259$ ml; $P = 110$ kg; $EQ = 0.94$; endocast length = 14.5 cm; surface area = 296.34 cm^2 ; olfactory bulbs = 65.09 cm^2 ; remainder = 231.25 cm^2 ; neocortex = 106.82 cm^2 ; and neocorticalization = 46.2%.

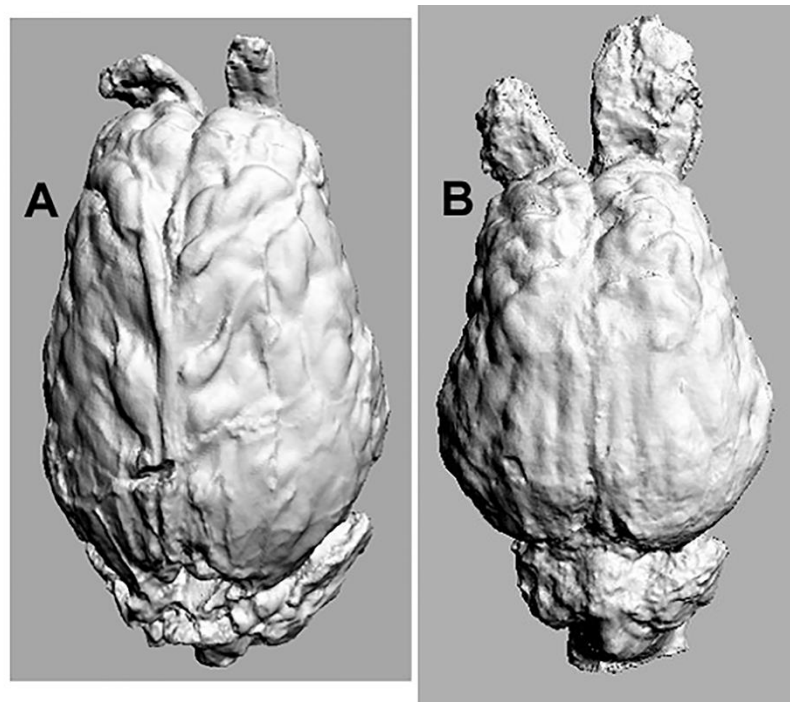


Figure S4. Olfactory bulbs in *Merychippus*. Endocasts of two specimens of *Merychippus*. Left-right diameter of each specimen about 25 cm. (A) *Merychippus isonesus* (FMNH PM 59208 = AMNH FAM 71150), 232 ml with typical olfactory bulbs. (B) *Merychippus severus* (LACM 368 = FMNH 26032), 282 ml with enlarged olfactory bulbs, probably resulting from removal of too much bone anteriorly, either naturally or by a preparator.

ACRITOHIPPUS ISONESUS (“*ATAVAHIPPIUS*”)

Labeled “*Atavahippus*” in the FMNH catalogue that I used (FMNH PM 59208), Radinsky had evidently copied it from AMNH FAM 71150. Unable to locate it in McKenna & Bell (1997), I queried Dr. Susan Bell. She explained, “the name ‘*Atavahippus*’ appears in an unpublished manuscript by Morris Skinner and was applied by him to the endocast in our collection. Because the name was never published, it is not valid -- that is why it does not appear in McKenna & Bell. You should ... identify the endocast as belonging to *Merychippus isonesus*”. In 1995, *Merychippus isonesus* was given its own genus, *Acritohippus* (Kelly, 1995). It is from the West Sand Quarry, Lower Snake Creek, Nebraska. It may still be described as *Atavahippus* in the FMNH catalogue.

My scans are shown in **Fig. 23B**. Measurements are endocast length = 12.4 cm; $E = 231.79$ ml; $P = 105.7$ kg; $EQ = 0.86$; surface area = 248.43 cm^2 ; olfactory bulbs = 18.23 cm^2 ; remainder = 230.20 cm^2 ; neocortex = 119.03 cm^2 ; and neocorticalization = 51.7%.

PLIONICTIS

This small early Miocene mustelid is FMNH PM 58945, described in the Radinsky Collection as Barstovian, 15 Ma. My scans are shown in **Fig. 23C**. The body size estimated from tooth data was $P = 640$ g (Legendre & Roth, 1988), an acceptable estimate comparable to living minks and ermines. The specimen was discussed by Loomis (1932). Endocast length

= 5.1 cm; E = 10.99 ml; P = 640 g; EQ = 1.23; endocast surface area = 32.97 cm²; olfactory bulbs = 2.94 cm²; neocortex = 12.63 cm²; remainder = 30.03 cm²; and neocorticalization = 42.1%.

PSEUDAEELURUS

Probably *P. validus*, my scan (**Fig. 23D**) is specimen FMNH PM 58867, one of three endocasts in the Radinsky collection of this genus. No species name was offered. My specimen was described as Early Barstovian, which suggests a geological age of 15 Ma. This endocast was copied from AMNH FAM 61835. Radinsky also copied AMNH FAM 61834, recorded as FMNH PM 58870. They are from the Lower Snake Creek Formation of Nebraska. Rothwell (2003) identified it as *P. validus*, and I believe all of the endocasts are of that species. They all feature unusually long olfactory tracts and consequently have enlarged representation of the olfactory system in their brain images. The whole endocast, including olfactory tract and bulbs, was 9.7 cm long and measured E = 73 ml. Radinsky had measured the endocast with Archimedes' method as 89 ml. After deleting the olfactory bulbs and tract, the measurement from my digitized scan was E = 71.72 ml. I found no record of body size but found P = 30 kg in one note, without a source, used here. EQ = 0.62; surface area = 114.43 cm²; neocortex = 50.38 cm²; and neocorticalization = 46.2%.

PARACYNARCTUS SINCLAIRI

Recorded in the FMNH catalogue as “*Phlaocyon*” (FMNH PM 58973), this canid (FAM 61009) is the holotype of *Paracynarctus sinclairi* in Wang, Tedford & Taylor (1999). It was only tentatively recorded by Radinsky as “*Phlaocyon*” when he prepared the endocast (Wang, pers. comm.). The fossil is from Quarry 2, Olcott Formation (Early Barstovian), Sioux County, Nebraska, dated 15.5 Ma, and is shown in **Fig. 24A**. Endocast length = 8.2

cm; $E = 55.93$ ml; $P = 12263$ g; $EQ = 0.88$; surface area = 97.54 cm^2 ; olfactory bulbs = 8.53 cm^2 ; neocortex = 39.56 cm^2 ; remainder = 89.01 cm^2 ; and neocorticalization = 44.4%.

USTATOCHOERUS

The endocast (FMNH PM 59071) of this oreodont was prepared by Prof. Len Radinsky from skull AMNH FAM 33617, which is recorded as *U. profectus* at the American Museum of Natural History. It was from the Deep Creek Quarry, Brown County, Nebraska, with a geological age of 12.5 Ma. The identification “cannot be shown to differ from *U. major*” (Stevens & Stevens, 2007), and from a sketch of the skull of *U. major*, its head+body length is approximately 100 cm, resulting in a $P = 24$ kg. The endocast, illustrated in **Fig. 24B**, is enlarged in the cerebellar region. I measured its total volume as $E = 162.67$ ml, leading to an $EQ = 1.63$, higher than average living species of its body size. In light of the likely significant overestimate of its endocast size, it is reasonable to conclude that it was comparable to living species in encephalization. Endocast length = 10.6 cm; surface area = 209 cm^2 ; olfactory bulbs = 11.81 cm^2 ; remainder = 197 cm^2 ; neocortex = 64.2 cm^2 ; and neocorticalization = 32.6%.

CARPOCYON (OSTEOBORUS)

The endocast of this canid, *Carpocyon webbi* (perhaps still labeled “*Osteoborus tagarctus*” in the Field Museum catalogue) is FMNH PM 58964 = AMNH FAM 61328, and was from the Midway Quarry, Burge Member, Valentine Formation, Cherry County, Nebraska (Wang, Tedford & Taylor, 1999). My scans are shown in **Fig. 24C**. Its geological date is about 13 Ma. Its 23 cm skull suggests a head+body length of about 110 cm. My Eq. 2 estimated its body weight as $P = 32$ kg; endocast length = 10.6 cm; $E = 100$ ml; $EQ = 0.83$;

endocast surface area = 142.9 cm²; olfactory bulbs = 13.1 cm²; remainder = 129.8 cm²; neocortex = 61.35 cm²; and neocorticalization = 47.3%.

PSEUDHIPPARION

This specimen is illustrated in **Fig. 24D**. It was listed elsewhere in my notes as *Griphippus* (a former name for the taxon) and is now identified more properly as *Pseudhipparion retrusum* (FMNH PM59211 = AMNH FAM 70025) from Nebraska, Cherry County, Burge Quarry. I date it at 11 Ma. Endocast length = 10.6 cm; *E* = 168.43 ml; *P* = 50 kg; *EQ* = 1.03; surface area = 207.87 cm²; olfactory bulbs = 13.39 cm²; remainder = 194.47 cm²; neocortex = 93.65 cm²; and neocorticalization = 48%.

PARATOMARCTUS

This Miocene canid, *P. euthos* (FMNH PM 58958 = AMNH FAM 61074) from Burge Quarry, Nebraska (Wang et al., 1999, p. 212), lived about 11 Ma. The genus had been named *Tomarctus* but is renamed in the Wang et al. monograph. I scanned several specimens, and the one illustrated here (**Fig. 25A**) *E* = 56.3 ml; length = 7.6 cm; head+body length = 85 cm; *P* = 10.9 kg; *EQ* = 0.95; surface area = 87.6 cm²; olfactory bulbs = 8 cm²; remainder = 79.6 cm²; neocortex = 35.6 cm²; and neocorticalization = 44.7%.

HEMICYON

The endocast shown in **Fig. 25B** is of the ursoid *Hemicyon cf. H. barbouri* (FMNH PM 59030 = AMNH FAM 25530). It was from Turtle Canyon, lower level, Sheridan County, Nebraska, and was treated as Clarendonian, about 10 Ma. Head+body length = 150 cm; *P* = 82 kg; endocast length = 12.6 cm; *E* = 199.28 ml. The allometric expected brain size at that body size was 226 g, hence an *EQ* = 0.88. For comparison, a 143 kg grizzly in my sample

had a 234 g brain; its allometric expected brain size was 318 g and $EQ = 0.74$, so *Hemicyon* was a bit brainier than its living relative. Surface area = 251.2 cm²; olfactory bulbs = 8.2 cm²; remainder = 244 cm²; neocortex = 98 cm²; and neocorticalization = 40.3%.

MESOTHERIUM

The endocast of this notoungulate from Argentina is FMNH PM 59292, copied by Radinsky (1981) from AMNH 14509. It has been referred previously to *Pseudotypotherium pseudopachygnathum*, and more recently as *Mesotherium pachygnathum* (MacPhee, 2014). The original fossil is from Monte Hermosa and, after consulting with Dr. Maria Teresa Dozo, I date it to 6 Ma. My scans are shown in **Fig. 25C**. Endocast length = 8.6 cm; $E = 63.7$ ml; $P = 80$ kg; $EQ = 0.29$; surface area = 104.6 cm²; olfactory bulbs = 5.97 cm²; remainder = 98.64 cm²; neocortex = 48 cm²; and neocorticalization = 48.66%.

TYPOTHERIOPSIS

My endocast of *T. internum* (FMNH P 14420) is from the Arroyo Chasico Formation, Huayquerian South American Land Mammal Age, Buenos Aires Province, Late Miocene (Dozo, pers. comm.), about 8 Ma. Dozo described it as a small digging herbivorous species. The endocast of this notoungulate, shown in **Fig. 25D**, is $E = 75$ ml; $P = 6.9$ kg; $EQ = 1.74$; endocast length = 9.6 cm; surface area = 112.8 cm²; olfactory bulbs = 4.4 cm²; remainder = 108.4 cm²; neocortex = 52.69 cm²; and neocorticalization = 48.4%.

The genus *Typotheriopsis* may have been misidentified for this specimen. I think of rodents as living small mammals, and the largest of these, capybara, has a 28 kg body weight and 52 g brain in my sample (Crile & Quiring, 1940); $EQ = 0.47$. Although not a digging rodent, capybara would qualify as a model for the notoungulate, and the much larger notoungulate brain of *Typotheriopsis* would not correspond to a 6.9 kg body. The shape of

the endocast is appropriate for related notoungulates such as *Pseudotypotherium*, or my sources on its body size may be wrong. Nevertheless, $EQ = 1.74$ may be ignored until this is clarified.

CORMOHIPPARION

My endocast of *C. occidentale* (FMNH PM 59220 = AMNH FAM 71866) was reported by Radinsky as from the Hans Johnson Quarry in Nebraska, medial Clarendonian in the Miocene, about 10 Ma. The endocast of this Miocene equid was $E = 364$ ml; $P = 151$ kg; $EQ = 1.07$. It is shown in **Fig. 26A**. Endocast length = 11.2 cm; surface area (minus olfactory bulbs) = 309 cm^2 ; neocortex = 184 cm^2 ; and neocorticalization = 59.5%.

PROCAMELUS

The specimen is from the Burge Quarry, estimated age 11 Ma, and is shown in **Fig. 26B**. The volume of the endocast of *P. grandis* (FMNH PM 59160 = AMNH FAM 40425) is $E = 374$ ml; $P = 200$ kg; $EQ = 0.91$; endocast length = 14.3 cm; surface area = 366 cm^2 ; olfactory bulbs = 16 cm^2 ; remainder = 350 cm^2 ; neocortex = 131 cm^2 ; and neocorticalization = 37.4%.

HOMOTHERIUM

The endocast of the sabretooth *H. crusafonti* (FMNH PM 58891 = AMNH 95297) measured 192.5 ml; I took its body size as $P = 200$ kg; $EQ = 0.47$. My scans are shown in **Fig. 26C**. It was early Pleistocene, about 1.5 Ma. Endocast length = 11.2 cm; surface area (minus olfactory bulbs) = 224 cm^2 ; neocortex 128 cm^2 ; neocorticalization = 57%.

MYLODON

I was given this *Myiodon* endocast during a visit to the Natural History Museum in London (NHMUK) decades ago, but the museum presently has no record either of the endocast or the gift. After many searches, Dr. Pip Brewer, Curator of Fossil Mammals at the museum, suggested checking Woodward (1900) for clues. Indeed, Woodward accurately drew the specimen when he described how and where it was found. My scan is shown in **Fig. 26D**, and the measurements are $E = 514.88$ ml; body weight estimated from a scale model of a similar specimen at LACM gave a $P = 1100$ kg (Jerison, 1973 p. 334); $EQ = 0.40$; endocast length = 15.8 cm; surface area (less olfactory bulbs) = 399.1 cm^2 ; neocortex = 119.19 cm^2 ; and neocorticalization = 29.86%.

Woodward (1900, p. 64) wrote, “Dr. Rudolph Hauthal, geologist at the La Plata Museum ... not only found another piece of skin, but also various broken bones of more than one individual ... in a remarkably fresh state of preservation.” The skull must have been lent to NHMUK, where it was “vertically bisected” (Woodward, 1900, p.69) to prepare the endocast. From the description of the cave where it was found, Woodward considered it a subfossil, no more than 0.01 Ma. The original endocast described by Woodward may have been sent to the La Plata Museum in Argentina. I have given my copy of the endocast to LACM, where it is now specimen LACM 157696. The species had been named by Owen (1841).

Plio-Pleistocene and Recent Fossils

GLOSSOTHERIUM

The volume of this endocast (LACM 1717-33) of *Glossotherium harlani* from La Brea Tar Pits in Los Angeles was $E = 502$ ml; from a scale model I estimated $P = 1100$ kg (Jerison, 1973); $EQ = 0.39$. It is shown in **Fig. 27A**. Endocast length = 15.5 cm; surface area

(less olfactory bulbs) = 423 cm²; neocortex = 129 cm²; neocorticalization = 30.61%. Its age is about 0.03 Ma. Like all La Brea material, it was reviewed and illustrated by Harris (1992).

ARCTODUS (TREMARCTOTHERIUM)

The endocast of this short faced bear *Arctodus simus (Tremarctotherium)* (LACM, Harris, 1992) was from La Brea Tar Pits in Los Angeles. It is shown in **Fig. 27B**. It dates to about 0.03 Ma. Endocast E = 654 ml; body size P = 526 kg (Christiansen, 1999); EQ = 0.84; endocast length = 16.8 cm; surface area (less olfactory bulbs) = 498 cm²; neocortex = 296 cm²; and neocorticalization = 59.45%.

CANIS DIRUS

The endocast of this dire wolf (LACM) was from La Brea Tar Pits in Los Angeles. It is shown in **Fig. 27C**, and it dates to about 0.03 Ma; E = 181 ml; P = 80 kg; EQ = 0.81; endocast length = 11.7 cm; surface area (less olfactory bulbs) = 193 cm²; neocortex = 114 cm²; and neocorticalization = 59.37%.

MEGALONYX

M. jeffersoni (LACM), from La Brea Tar pits, is historically interesting because a specimen of this ground sloth was among those named by Thomas Jefferson. It dates to about 0.03 Ma and is shown in **Fig. 27D**. My endocast E = 332.78 ml; P = 370 kg; EQ = 0.54; endocast length = 12.6 cm; surface area (less olfactory bulbs) = 275.75 cm²; neocortex = 103.69 cm²; and neocorticalization = 37.6%.

NOTHROTHERIOPS

LACM C-3 is the endocast of a La Brea ground sloth *N. shastensis* dating to about 0.03 Ma. It is shown in **Fig. 28A**. Endocast volume $E = 277$ ml; $P = 320$ kg; $EQ = 0.49$; endocast length = 11.8 cm; surface area (less olfactory bulbs) = 239 cm^2 ; neocortex = 99 cm^2 ; and neocorticalization = 41.4%.

PANTHERA ATROX

The endocast of *P. atrox*, the La Brea lion, is shown in **Fig. 28B** and is dated to about 0.03 Ma. Endocast volume $E = 338$ ml; $P = 325$ kg; $EQ = 0.60$; endocast length = 13.8 cm; surface area (less olfactory bulbs) = 305 cm^2 ; neocortex = 167 cm^2 ; and neocorticalization = 54.64%.

SMILODON FATALIS

The endocast is of *S. fatalis* (LACM, La Brea Tar Pits), the sabretooth “cat” that is the official fossil of California. It lived about 0.03 Ma and is shown in **Fig. 28C**. Endocast volume $E = 216$ ml; $P = 250$ kg; $EQ = 0.45$; endocast length = 11.7 cm; surface area (less olfactory bulbs) = 240 cm^2 ; neocortex = 120 cm^2 ; and neocorticalization = 50.11%.

UROCYON

The Pleistocene grey fox, *Urocyon cinereoargenteus*, from La Brea Tar Pits (LACM), lived about 0.03 Ma. It is survived by living individuals in Southern California and the Channel Islands. Its endocast is shown in **Fig. 28D**. Endocast length = 6.5 cm; $E = 39$ ml; $P = 5$ kg; $EQ = 1.11$; surface area (less olfactory bulbs) = 64 cm^2 ; neocortex = 37 cm^2 ; and neocorticalization = 58.02%.

PLATYGONUS

The endocast of this tayassuid *Platygonus compressus* (FMNH PM 59058) from La Brea dates to 0.03 Ma. Only half of the endocast was preserved, but it was a relatively clean half, easy to double to estimate its measurements. It is shown in **Fig. 29A**. $E = 130$ ml; $P = 130$ kg; $EQ = 0.42$; endocast length = 9.7 cm; surface area (less olfactory bulbs) = 129 cm^2 ; neocortex 74 cm^2 ; and neocorticalization = 57.71%.

STHENURUS

Professor Radinsky collected this endocast in Wellington Cave, New South Wales, and his widow, Dr. Sharon Emerson, donated it to the Radinsky Collection. It is *Sthenurus cf. orientalis*, specimen FMNH PM 59245, shown in **Fig. 29B**. My software measured its volume as $E = 107$ ml, and from Wells & Tedford (1995) I estimated the geological age as 0.5 Ma. The body size of this extinct large kangaroo was $P = 200$ kg; $EQ = 0.26$; endocast length = 8.4 cm; surface area (less olfactory bulbs) = 130 cm^2 ; neocortex = 67 cm^2 ; and neocorticalization = 51.82%.

THYLACOLEO

The endocast of *T. carniflex* (FMNH PM 59244) was copied by Prof. Radinsky from the South Australian Museum P18681; age estimated as 2 Ma. It is shown in **Fig. 29C**. Although I avoid discussing gyral features, in this case it is worth noting that the characteristic gyri of the felid and canid endocasts are not a feature of this marsupial carnivore. In felids and canids, the ectosylvian gyri are useful maps of the auditory cortex; they are not a feature in the marsupial. Endocast volume $E = 120$ ml; body weight of this marsupial sabretooth $P = 130$ kg (Wroe, 2004); $EQ = 0.39$; endocast length = 9.6 cm; surface area (less olfactory bulbs) = 154 cm^2 ; neocortex = 64 cm^2 ; and neocorticalization = 41.37%.

ARCHAEOLEMUR

The endocast of *Archaeolemur majori* (FMNH PM 59258 = AMNH 30007), copied by Radinsky from the AMNH specimen, is shown in **Fig. 29D**. It is a subfossil lemur from Madagascar and can be dated to 0.01 Ma. Endocast volume $E = 96$ ml; $P = 17$ kg; $EQ = 1.21$; endocast length = 7.6 cm; surface area = 122 cm^2 ; olfactory bulbs = 1.88 cm^2 ; remainder = 119.3 cm^2 ; neocortex = 76 cm^2 ; and neocorticalization = 63.7%.

PACHYLEMUR

This Madagascar lemur (FMNH PM 59253), probably copied from MNHN, is shown in **Fig. 30A**. It was listed as *Lemur insignis* by Radinsky and has been renamed *Pachylemur insignis*. It became extinct only a few thousand years ago, and the endocast may be dated to 0.01 Ma. Endocast volume $E = 57.4$ ml; $P = 10$ kg (Fleagle, 1999, table 4.2); $EQ = 1.03$; endocast length = 6.4 cm; surface area (less olfactory bulbs) = 80 cm^2 ; neocortex = 49.61 cm^2 ; and neocorticalization = 61.73%.

PALAEOPROPITHECUS

This endocast is of *P. maximus* (FMNH PM 59250). My scans are shown in **Fig. 30B**. I estimated the age of this Madagascar subfossil lemur as 0.01 Ma. Endocast volume $E = 108$ ml; $P = 50$ kg; $EQ = 0.67$; surface area (less olfactory bulbs) = 134 cm^2 ; neocortex = 73 cm^2 ; and neocorticalization = 54.48%.

AUSTRALOPITHECINES

My volume measurements on my australopiths are **from the literature**, not from my scans. Surface areas on my scans were measured from the fairly complete half-brain scans.

Lateral images of both australopiths show the essentially complete right half of each endocast.

PARANTHROPUS ROBUSTUS

The scans of *P. robustus* (SK1585) are shown in **Fig. 30C**. I estimated the geological age as 2.5 Ma. Midline positioned vertically, length = 11.6 cm; $E = 530$ ml (Holloway et al., 2004); $P = 40$ kg; $EQ = 3.78$, about 4 times that of average living mammals. Neocortex = 275 cm^2 ; endocast surface area (less olfactory bulbs) = 356 cm^2 ; and neocorticalization = 77.18%.

AUSTRALOPITHECUS AFRICANUS

This is the famous endocast of *A. africanus*, the specimen from Taung, discovered and described by Raymond Dart (1925). It brought human origins more than a million years earlier than “*Pithecanthropus erectus*” (*Homo erectus*), which had been discussed and described by Eugen Dubois (1895). Dart was criticized by other anatomists and paleontologists when he discussed the specimen, but his discovery was accepted within decades (Tobias, 1971; Falk, 2009). My endocast, **Fig. 30D**, was unlabeled in a drawer at FMNH, but I believe it was copied from Professor Phillip Tobias's collection which is described in several places, most usefully in Holloway et al. (2004). It is described as from a 3-year-old child.

The reconstructed endocast (including the missing fraction of left hemisphere) estimated an adult $E = 440$ ml; adult body size $P = 40$ kg; $EQ = 3.13$, about the same as living chimpanzees. Endocast length = 10.8 cm. The endocast fragment illustrated in **Fig. 30D** was 278 ml in volume, but for encephalization I took the accepted adult $E = 440$ ml. Surface area = 242 cm^2 ; neocortex = 195 cm^2 ; and neocorticalization = 80.54%. Although this specimen is

subadult, the neocorticalization probably accurately reflects the adult state. It is dated to about 3.5 Ma.

Cetacean Fossils

As in the living cetacean brain, there is no rhinal fissure in the fossils and thus no indication of an olfactory bulb or tract; therefore, neocorticalization cannot be assessed.

Scans of my three fossil whales are shown in the left panel of **Fig. 31**; forebrain at the top in each case. These are discussed at length in Jerison (1973, pp. 346-351), and two more recent publications (Gingerich, 2016; Uhen, 2004) extend that discussion. The right panel of **Fig. 31** shows photographs of a dolphin brain (University of Wisconsin specimen 66-130, *Tursius truncatus*) to compare with the fossils. The top and center dolphin brain photographs have the forebrain pointing left. The bottom dolphin brain is a ventral view with forebrain to the right. The optic chiasma is evident with unclear olfactory bulbs and tract.

DORUDON

Dorudon atrox, named *Basilosaurus* and *Zeuglodon* in earlier reports, is NHMUK 10173. It was from the Fayum in Egypt, about 40 Ma. My scan is shown in the top of the left panel of **Fig. 31**. In Jerison (1973), I guessed its weight as 20,000 kg, probably based on its long skeleton as mounted in Egypt, or perhaps from the discussion by **Breathnach (1955)**. Uhen (pers. comm.) indicated a more likely weight of $P = 394$ kg based on a model he had prepared from the Egyptian skeleton. $E = 460$ ml; length (forebrain to medulla) = 13.1 cm. The endocast has a good deal of non-neural material but, taking it all as “brain” and $P = 394$ kg, $EQ = 0.71$.

ARGYROCETUS

The endocast of *A. joaquinensis*, a Miocene dolphin (UCMP 99668), dates to about 17 Ma. My scan is shown as the center of the left panel in **Fig. 31**. The endocast was found by Dr. Larry Barnes of LACM, but no species name was available when he allowed me to photograph the endocast (Jerison, 1973, fig. 15.4). I wrote that *Argyrocetus* was much smaller than the living bottlenose dolphin (Jerison, 1973), although I had no good estimate of its body size. Uhen (pers. comm.) identified it as USNM 11996 and suggested a body weight of $P = 80.1$ kg, which I now use. I now use $EQ = 3.01$ for the fossil, comparable to living dolphins; length (forebrain to hindbrain) = 13.3 cm; $E = 630$ ml; neocorticalization not measurable.

AULOPHYSETER

I scanned my endocast of *Aulophyseter morricei* (LACM 3161/131912) and it is shown in the bottom of the left panel of **Fig. 31**; age 17 Ma. It was a small sperm whale. Endocast length (neural protuberance to hindbrain) = 16.7 cm; $E = 2246$ ml. Uhen identified it as USNM 11230 (which I now use to identify the specimen) and gave its body weight $P = 8509$ kg; $EQ = 0.45$.

Encephalization in whales is not really comparable to that in land mammals. Whales adapted to life in the water and had few gravitational constraints on their body size. Therefore, size relationships between brain and body do not equate to the relationships in land mammals, in which body size estimates the size of the map of the perceptual world created by the brain.

Living Non-Primate Mammals

AONYX

My endocast of the clawless otter, *A. (Amblyonyx) cineria*, is Specimen 358 given to me by Professor Len Radinsky. My scans are shown in **Fig. 32A**. The volume of the endocast $E = 41$ ml, and from Nowak (1999) I estimated its body size $P = 3$ kg; $EQ = 1.63$. Endocast length = 6 cm; surface area (less olfactory bulbs) = 67.57 cm^2 ; neocortex = 44.62 cm^2 ; and neocorticalization = 66.04%.

URSUS

I assumed that this black bear endocast from LACM was *U. americanus*, but I have no additional identification. My scans are shown in **Fig. 32B**. Endocast $E = 277$ ml; assume $P = 140$ kg; $EQ = 0.86$; length = 11.8 cm; surface area (less olfactory bulbs) = 262 cm^2 ; neocortex = 160 cm^2 ; and neocorticalization = 61%.

CANIS LATRANS

My scan of a fossil coyote endocast from La Brea Tar Pits (LACM7-2007) is shown in **Fig. 32C** but is not represented in Table 1. The age of this specimen is about 0.03 Ma. Endocast $E = 98$ ml; the body size was assumed to be the same as its living relatives, $P = 15$ kg; $EQ = 1.34$; length = 8.4 cm; surface area (less olfactory bulbs) = 110 cm^2 ; neocortex 74 cm^2 ; and neocorticalization = 67.3%.

My coyote brain from was from Wisconsin (WISC 62-301). Its data are in **Table 1**. Brain volume $E = 72.67$ ml; $P = 15$ kg; $EQ = 1.0$; surface area 125.27 cm^2 ; neocortex = 82.44 cm^2 ; olfactory bulbs = 8.22 cm^2 ; remainder = 117.05 cm^2 ; and neocorticalization = 70.43%.

FELIS CATUS

This endocast of *F. catus* was a gift from Professor Radinsky and is his specimen 101. My scans are shown in **Fig. 32D**. Endocast volume $E = 25.41$ ml; assuming a small domestic

cat weight, $P = 3$ kg; $EQ = 1.02$, average for living mammals; endocast length = 5.5 cm; surface area (less olfactory bulbs) = 49.31 cm^2 ; neocortex = 28.87 cm^2 ; and neocorticalization = 58.54%.

CERDOCYON THOUS

This is Prof Radinsky's Specimen 294. My scans of the endocast of this crab-eating fox *C. thous* are shown in **Fig. 33A**. Endocast volume $E = 45.67$ ml; assuming a body weight $P = 6$ kg, $EQ = 1.15$; length = 7.1 cm; surface area (less olfactory bulbs) = 71.57 cm^2 ; neocortex = 43.89 cm^2 ; and neocorticalization = 61.32%.

ODOCOILEUS

I scanned the braincast (not endocast) of the white-tailed deer, *O. virginianus* (University of Wisconsin Brain Collection 67-81), which provides significantly more detail. My scans are shown in **Fig. 33B**. Approximately half of the braincast was available, so doubling resulted in $E = 124.6$ ml. Assuming $P = 75$ kg; $EQ = 0.58$; brain length = 11.2 cm; surface area = 206.58 cm^2 ; olfactory bulbs = 6.6 cm^2 ; remainder = 199.98 cm^2 ; neocortex = 102.24 cm^2 ; and neocorticalization = 51.13%.

My record on this deer is uncertain; I made different measurements over several years which resulted in some small discrepancies between two sets of measurements on one specimen.

URSUS (KODIAK)

My endocasts of this Kodiak bear from LACM are shown in **Fig. 33C**. Endocast volume $E = 488.55$ ml; estimated body weight from Nowak (1999) $P = 700$ kg; $EQ = 0.52$;

length = 18.5 cm; surface area (less olfactory bulbs) = 441.64 cm²; neocortex = 224.44 cm²; and neocorticalization = 50.82%.

LAMA

I scanned the braincast (not endocast) of Specimen 65-139 (*Lama glama*) of the University of Wisconsin brain collection. My scans are shown in **Fig. 33D**. Endocast volume $E = 172.22$ ml; $P = 150$ kg. Again, note how much more detail shows on a brain than on an endocast. Brain length = 11 cm; surface area remainder = 226.74 cm²; neocortex = 144.2 cm²; and neocorticalization = 63.6%.

LUTRA LUTRA

My possibly erroneous record has this as the European species *L. lutra*. My scans of Radinsky's Specimen 366 are shown in **Fig. 34A**. Endocast volume $E = 39.22$ ml; $P = 10$ kg; $EQ = 0.70$; endocast length = 6.6 cm; surface area (less olfactory bulbs) = 68.58 cm²; neocortex = 40.6 cm²; and neocorticalization = 59.2%.

LUTRA CANADENSIS

My scans of Radinsky's otter Specimen 129, probably *L. Canadensis*, are shown in **Fig. 34B**. Endocast volume $E = 59.87$ ml; $P = 10$ kg; $EQ = 1.07$; endocast surface area (less olfactory bulbs) = 89.63 cm²; neocortex = 54.43 cm²; neocorticalization = 60.73%. This was probably the American species. Its endocast is impressively larger than my other *Lutra* species.

PROCYON LOTOR

Radinsky's endocast Specimen 154 is of the raccoon *P. lotor*. My scans are shown in **Fig. 34C**. Endocast volume $E = 54.18$ ml; $P = 7$ kg; $EQ = 1.23$; endocast length = 7 cm; surface area (less olfactory bulbs) = 79.23 cm^2 ; neocortex = 47.03 cm^2 ; and neocorticalization = 59.36%.

I scanned the left hemisphere of a raccoon brain from the Wisconsin Brain Collection (61-824) and show it in **Fig. 34D**. The raccoon brain measurements, no olfactory bulbs, are $E = 25.79$ ml (obviously low and probably shrunken); $P = 7$ kg; brain scan surface area = 60.99 cm^2 ; neocortex = 34.37 cm^2 ; and neocorticalization = 56.35%.

NASUA NARICA

Wally Welker, late Professor of Physiology at the University of Wisconsin, maintained the important brain collection (<http://www.brainmuseum.org/>) in his department with the cooperation of his associate, Professor John Johnson of Michigan State University. It is a facility I used frequently when comparing my endocasts with brains. Wally gave me casts of brains of over 200 species of mammals, including the raccoon (WISC 61-824) and the coati *Nasua narica* (WISC 58-360 and WISC 62-404). In **Fig. 34**, the scans of the raccoon (**Fig. 34**) and coati (**Fig. 34E**) brains are compared. These are not endocranial casts; they are of brains and show their external appearance vividly, although sulcal depths are obscured when casting whole brains. It is clear that although these brains are similar, they are not identical, and it is difficult to make localizations. Electrophysiological analysis provided a brain map of the coati rhinarium, showing that its nose sensing area was relatively enlarged, and a map of the forepaw area of the raccoon brain is also relatively enlarged. In these experiments, the nose and forepaw areas were stimulated, and electrical responses were recorded at the exposed brain. The electrophysiological maps (Welker, 1990, Fig. 53) show where evoked potentials were recorded on the brains. As mapped physiologically, the coati's

nose area and the raccoon's forepaw area are dramatically different, each enlarged appropriately, and reflect the animal's food foraging behavior.

PHASCOLARCTOS

In **Fig. 35A**, different orientations of the Koala endocast are shown. Both braincast and endocast were given to me by Dr. Maciej Henneberg, Professor of Anatomy, University of Adelaide, Australia, and they are deposited in the brain collection at the University of Adelaide. The endocast volume $E = 36.5$ ml; brain volume is 15.93 ml. Encephalization with respect to the endocast, $EQ = 0.66$; with respect to brain, $EQ = 0.29$. Endocast length = 7.2 cm; surface area (less olfactory bulbs) = 71.49 cm^2 ; neocortex = 21.32 cm^2 ; and neocorticalization = 29.83%. The braincast measurements are hardly comparable to those on the endocast because so much midbrain surface is measurable. Nevertheless, the brain measurements were surface area = 71.57 cm^2 ; olfactory bulbs = 2.46 cm^2 ; remainder = 69.11 cm^2 ; neocortex = 19.57 cm^2 ; and neocorticalization (brain) = 28.32%.

MACROPUS

Professor Jack Johnson of Michigan State University prepared my braincast, not endocast, of this kangaroo, as shown in **Fig. 35B**. He informed me that the animal was probably a juvenile. It is *Macropus fuliginosus*, Michigan State University Specimen MSU 64023. I doubled half measurements to estimate $E = 34$ ml. MSU has a recorded brain weight $E = 61.35$ g, which I did not use. Its weight may have been measured at dissection, whereas mine is based on a braincast from a shrunken brain. Brain length = 7 cm. Body weight $P = 23.6$ kg; $EQ = 0.34$. Brain surface area (less olfactory bulbs) = 86.05 cm^2 ; neocortex = 38.38 cm^2 ; and neocorticalization = 44.6%. The specimen should be compared with the large fossil kangaroo *Sthenurus* in **Fig. 29B**.

VOMBATUS

My data on the wombat (*Vombatus ursinus*) are from a skull donated by E. Allen and sent by Erica Moe of NMV, Specimen C7780. It was a male. My measurements were based on the half endocast shown in **Fig. 35C**, doubled as appropriate. Endocast length = 7 cm; $E = 82.2$ ml; $P = 28$ kg, based on Nowak (1999), which leads to $EQ = 0.74$. Endocast surface area (less olfactory bulbs) = 103.23 cm^2 ; neocortex = 48.45 cm^2 ; and neocorticalization = 46.93%.

TAXIDEA

The endocast of this badger, *T. taxus*, Professor Radinsky's Specimen 360, measures $E = 60$ ml, and from Nowak (1999) I assumed a body weight of $P = 10$ kg; $EQ = 1.08$. My scans are shown in **Fig. 35D**. Endocast length = 7 cm; surface area (less olfactory bulbs) = 80.28 cm^2 ; neocortex 48.3 cm^2 ; and neocorticalization = 60.16%.

Living Primates

Most of my specimens in this section are from Professor Dean Falk's collection of primate endocasts (Falk, 1992, 2012 and pers. comm.). She did not report body sizes, and for this section I take most from Van Dongen (1998) and Nowak (1999). At Falk's request, I gave her endocasts to Dr. John Fleagle at SUNY. His identifications and numbering are included in my description of each endocast. Dr. Sharon Bell at AMNH informed me that they had been deposited in the living mammal collection at AMNH (Bell, Fleagle, pers. comm.), and Fleagle's numbers refer to that collection. In the set as illustrated in **Fig. 36 and 37**, the brains were shrunken but the endocasts were not.

The endocast of the small South American grey saki *Chiropotes albinasa* is shown in **Fig. 36A**, and the endocast of the much larger African *Mandrillus sphinx* is shown in **Fig. 36B**. The ventrolateral view exposes more of the rhinal fissure, though it is not easy to trace it in this figure; the fissure is often hidden in more familiar lateral views in primates. The saki and mandrill endocasts are similar in shape but differ in the amount of gyrification, presumably related to their size difference; sakis weigh about 2 kg while male mandrills may weigh 20 kg or more. As similar as they are, they are from two distinct groups of primates, the New World Superfamily Callitrichoidea (=Platyrrhini) and the Old World Superfamily Cercopithecoidea (= Catarrhinae).

CHIROPOTES ALBINASA

The volume of the endocast (FM 94927) of this South American white-nosed bearded saki shown in **Fig. 36A** is $E = 53$ ml. I have no data on its body size, but from Nowak (1999) I took its weight as $P = 3$ kg; $EQ = 2.12$; endocast length = 5.9 cm; surface area = 82.57 cm^2 ; neocortex = 65.26 cm^2 ; and neocorticalization = 79.03%.

MANDRILLUS SPHINX

The endocast of *M. sphinx* AMNH AM 274 is shown in **Fig. 36B**. Body size $P = 18$ kg; endocast length = 8.1 cm; $E = 131.85$ ml; $EQ = 1.60$; surface area = 154.88 cm^2 ; neocortex = 119.09 cm^2 ; and neocorticalization = 76.89%.

HOMO SAPIENS

Fig. 36C shows the first of my two *H. sapiens* endocasts (Falk A) in this group from Dean Falk's collection. I have no museum number. This is an unusually small endocast, $E =$

945.7 ml. Assuming small body size, $P = 50$ kg; $EQ = 5.81$; endocast length = 14.3 cm; surface area = 540.59 cm^2 ; neocortex = 432.55 cm^2 ; and neocorticalization = 80.01%.

HOMO SAPIENS

This endocast shown in **Fig. 36D** is shown again as Specimen 1 in **Fig. 37**. It is Falk B, more like other humans in average size, $E = 1,369.7$ ml; and assuming $P = 70$ kg; $EQ = 6.72$. It is comparable to MRI data from the living humans. Endocast length = 16.3 cm; surface area = 682.38 cm^2 ; neocortex = 530.32 cm^2 ; and neocorticalization = 77.72%.

The Sylvian fissure is a prominent feature of lateral views of human brains, although it is almost never completely evident in endocasts. The endocasts in **Fig. 36C and D** emphasize the inadequate image of the Sylvian Fissure. The difference in volume of more than 300 g amounts to about two standard deviations in living human brains. The size of the smaller endocast is unusual, but its shape in the Sylvian region is like that of other human endocasts.

Only lateral images of primate endocasts are shown in **Fig. 37**. The size differences between them are indicated in the paragraph on each specimen, including left-to-right length and endocast or brain volume E ; grams and milliliters are equivalent. I note finally that the brain images of chimpanzee and rhesus monkey in **Fig. 37** are of somewhat shrunken specimens prepared from preserved brains used in electrophysiological studies on the right hemispheres. The olfactory bulb areas are small enough in all of these primate specimens to be disregarded, but when present they are included in the left-to-right length measurements.

I refer to the specimens in **Fig. 37** by number and with museum numbers if available. The two braincasts in **Fig. 37** are of the chimpanzee (Specimen 3) and of the rhesus monkey (Specimen 7). The other “brains” in **Fig. 37** are all endocasts, including the chimpanzee endocast (Specimen 2).

My chimpanzee brain scan was prepared from the University of Wisconsin brain collection (63-397), one of many sent to me by Professor Wally Welker. The chimpanzee endocast was prepared at the University of Witwatersrand and sent to me by Dr. Kristian Carlson, Institute for Human Evolution, University of Witwatersrand. I believe it was prepared for him at the Peabody Museum at Yale, a less adequate preparation from CT scans. Their problem was to combine successive 2D scans into a 3D image, and their program did not completely hide the rings of successive 2D scans. The program used here was more successful, as are other recent programs for rendering 2D scan images into 3D digitized images.

Specimen 7 of **Fig. 37** is the braincast (not endocast) of a rhesus monkey, *Macaca mulatta*, Specimen 62-133 of the Wisconsin brain collection. In contrast to the endocasts, the Sylvian fissure is prominent. Although some gyri and sulci are evident in all of the primate endocasts, they are less marked and certainly less complete than in the brains. One morphological feature in the human brain related to the localization of language is the bilateral asymmetry of the Sylvian, which is somewhat longer on average in the left hemisphere. This asymmetry is not measurable in endocasts.

PAN TROGLODYTES

On chimpanzee brain and body size I often use Bauchot & Stephan (1969) for data (e.g., in Jerison, 1979). For this monograph, I scanned the two specimens illustrated in **Fig. 37**. Specimen 2 is the Wits endocast mentioned earlier. Specimen 3 is the scan of a chimpanzee brain from the Wisconsin brain collection (63-397). This WISC braincast is from a presumably shrunken brain: $E = 307.39$ ml; length = 10.1 cm. Assuming a body size $P = 40$ kg; $EQ = 2.19$; surface area = 331.52 cm^2 ; neocortex = 267.73 cm^2 ; and neocorticalization =

80.76%. Crile & Quiring (1940) reported on a chimpanzee, body size $P = 52$ kg; brain size $E = 440$ g; $EQ = 2.70$. Van Dongen reported a 46 kg body and 405 g brain; $EQ = 2.63$.

For the Wits chimpanzee endocast: $E = 371.18$ ml; $P = 50$ kg; $EQ = 2.28$; surface area = 278.46 cm²; remainder (less olfactory bulbs) = 276.66 cm²; and neocorticalization = 71.05%.

COLOBUS GUEREZA

Colobus guereza (AM 52217, **Fig. 37** Specimen 4) is an African colobus monkey. The species was listed by Van Dongen (1998) as $P = 10.5$ kg; $E = 85.27$ ml; $EQ = 1.48$. I accept his colobus body weight for my Specimen 4, with the measured length = 7 cm; surface area = 112 cm²; neocortex = 76 cm²; and neocorticalization = 68.15%.

ERYTHROCEBUS PATAS

In this Ethiopian red guenon endocast (AMNH 52574, **Fig. 37** Specimen 5), $E = 90.06$ ml. Van Dongen reported a body size $P = 17$ kg; $EQ = 1.14$; endocast length = 7.1 cm; surface area = 116.93 cm²; neocortex = 91.23 cm²; and neocorticalization = 78.02%.

HYLOBATES LAR

I recorded the endocast as Number 386 from Falk (**Fig. 37** Specimen 6). In most instances, the number would refer to endocasts given to me by Professor Len Radinsky, but in this case my incomplete notes place it in the Falk collection. Professor Fleagle did not comment on it, nor did he give it a museum number. The measurements would be appropriate for the gibbons. Endocast $E = 99.32$ ml; length = 7.1 cm; P (after Nowak, 1999) = 8 kg; $EQ = 2.07$; surface area = 123.4 cm²; neocortex = 78.11 cm²; and neocorticalization = 63.3%.

MACACA MULATTA

I have only incomplete data on this rhesus monkey braincast that was given to me by Wally Welker. It is one of his braincasts prepared after neurophysiological experiments (WISC 69-307). It is shown in **Fig. 37** Specimen 7; $E = 71.61$ ml. Having worked with monkeys years ago, I recognized this as small for a laboratory rhesus monkey and guess that it shrank following laboratory fixation and preservation. I recorded 6 kg as its body size based on my experience with such specimens, but I have no additional record of its source. $EQ = 1.81$; length = 6.2 cm; surface area = 114.72 cm^2 ; neocortex = 79.45 cm^2 ; and neocorticalization = 69.26%.

NASALIS LARVATUS

This nasalis monkey (MCZ 37328, **Fig. 37** Specimen 8) was from Borneo. I take $E = 97$ ml; $P = 14$ kg; $EQ = 1.39$; length = 5.9 cm; surface area = 121.94 cm^2 ; neocortex = 89.15 cm^2 ; and neocorticalization = 73.11%.

PITHECIA MONACHUS

Endocast volume of this New World saki (AMNH 75981, **Fig. 37** Specimen 9) $E = 39.73$ ml; $P = 1.5$ kg; $EQ = 2.52$; length = 5.9 cm; surface area = 68.05 cm^2 ; neocortex = 53.09 cm^2 ; and neocorticalization = 78.02%.

PRESBYTIS JOHNNI

The volume of the endocast (AMNH 54644, **Fig. 37** Specimen 10) of this langur (leaf monkey) $E = 85.85$ ml; length = 7.2 cm; $P = 13.4$ kg; $EQ = 1.27$; surface area = 114.26 cm^2 ; neocortex = 82.62 cm^2 ; and neocorticalization = 72.31%.

RHINOPITHECUS (PYGATHRIX) AVUNCULIS

The endocast (MCZ 13681, **Fig. 37** Specimen 11) of this snub-nosed langur $E = 114.21$ ml; $P = 8$ kg; $EQ = 2.38$; length = 7.4 cm; surface area = 136.64 cm^2 ; neocortex = 99.75 cm^2 ; and neocorticalization = 73%.

PYGATHRIX NIGRIPES

The endocast (AMNH 69555, **Fig. 37** Specimen 12) of this douc langur $E = 77.71$ ml; $P = 7.5$ kg; $EQ = 1.69$; length = 6.5 cm; surface area = 106.08 cm^2 ; neocortex = 80.39 cm^2 ; and neocorticalization = 75.78%.

SIMIAS CONCOLOR

The endocast (AMNH 103359, **Fig. 37** Specimen 13) of this pig-tailed langur $E = 54$ ml; $P = 7$ kg; $EQ = 1.23$; length = 5.8 cm; surface area = 82.54 cm^2 ; neocortex = 61.19 cm^2 ; and neocorticalization = 74.13%.

THEROPITHECUS GELADA

The volume of the endocast (FMNH 8174, **Fig. 37** Specimen 14) of this gelada baboon was $E = 131.08$ ml; $P = 17$ kg; $EQ = 1.65$; length = 8.1 cm; surface area = 146.82 cm^2 ; neocortex = 108.74 cm^2 ; and neocorticalization = 74.06%.

CERCOCEBUS (LOPHOCEBUS) ALBIGENA

Endocast volume of this gray-cheeked langur (AMNH 52583, **Fig. 37** Specimen 15) $E = 79.64$ ml; $P = 7.9$ kg; $EQ = 1.67$; length = 6.7 cm; surface area = 107.84 cm^2 ; neocortex = 86.65 cm^2 ; and neocorticalization = 80.35%.

The endocast is **Fig. 37** Specimen 16 and is Fleagle's Male AM 52468 at AMNH. I assumed the body weight of this guenon to be $P = 4.2$ kg from Nowak (1999); $E = 71.86$ ml; $EQ = 2.3$; length = 6.8 cm; surface area = 101.93 cm^2 ; neocortex = 79.91 cm^2 ; and neocorticalization = 78.4%.

References

- Argot C. Functional adaptations of the postcranial skeleton of two Miocene boryaenoids (Mammalia, Metatheria), *Borhyaena* and *Prothylacinus*, from South America. *Paleontology*. 2003; 46: 213–267.
- Argot C. Postcranial analysis of a carnivoran-like archaic ungulate: The case of *Arctocyon primaevus* (Arctocyonidae, Mammalia) from the late Paleocene of France. *Journal of Mammalian Evolution*. 2013; 20: 83–114.
- Bauchot R, Stephan H. Encephalisation et niveau évolutif chez les Simiens. *Mammalia*. 1969; 33: 225–275.
- Berta A, Ray CE. Skeletal morphology and locomotor capabilities of the archaic pinniped *Enaliarctos mealsi*. *Journal of Vertebrate Paleontology*. 1990. 10:141–157.
- Cassini GH, Flores DA, Vizcaíno SF. Postnatal ontogenetic scaling of Nesodontine (Notoungulata, Toxodontidae) cranial morphology. *Acta Zoologica (Stockholm)*. 2012; 93: 249–259.
- Christiansen P. What size were *Arctodus simus* and *Ursus spelaeus* (Carnivora: Ursidae)? *Annales Zoologica Fenneci*. 1999; 36: 93–102.

Cook HJ. A remarkable new mammal from the lower Chadron of Nebraska. *American Midland Naturalist*. 1954; 52: 388–391.

Cope ED. The vertebrata of the tertiary formations of the west. Report of the United States Geological Survey of the Territories. Book 1. Washington DC: US Government Printing Office; 1883.

Crile GW, Quiring DP. A record of the body weight and certain organ weights of 3690 animals. *Ohio Journal of Science*. 1940; 40: 219–259.

Croft DA, Anderson LC. Locomotion in the Extinct Notoungulate *Protypotherium*. *Palaeontologia Electronica*. March 2008; 11.1.1A. Available from: https://palaeo-electronica.org/2008_1/toc.htm.

Cuvier G. *Recherches sur les Ossements Fossiles*, 4th ed. vol. 5 and atlas. Paris: D'Ocagne; 1835.

Damuth J, MacFadden BJ, editors. *Body Size in Mammalian Paleobiology: Estimation and Biological Implications*. Cambridge and New York: Cambridge University Press; 1990.

Dart RA. *Australopithecus africanus*: the man-ape of South Africa. *Nature*. 1925; 115: 195–199.

Dechaseaux C. Encéphales de Zénarthes fossils. In: Piveteau J. *Traité de paléontologie*, tome VI, vol. 2. Paris: Masson; 1958. pp. 636–640.

Dozo MT. The endocranial cast of an early miocene edentate *Hapalops indifferens* Ameghino (Mammalia, Edentata, Tardigrada, Megatheriidae). *Comparative Study with Brains of Recent Sloths*. *Journal für Hirnforschung*. 1987; 28(4): 397–406.

Dozo MT, Martínez G. First digital cranial endocasts of late oligocene Notohippidae (Notoungulata): implications for endemic South American ungulates brain evolution. *Journal of Mammalian Evolution*. 2016; 23: 1–16.

Dubois E. The brain-cast of *Pithecanthropus erectus*. Proceedings of the Fourth International Congress of Zoology; 1898. pp.79–96.

Edinger T. Über Gehirne tertiärer Sirenia Ägyptens und Mitteleuropas sowie der reznten Seekühe. Abhandlung bayerische Akademie Wissenschaften, Mathematische – naturwissenschaften. Abt. N.F. 1933; 20: 5–36.

Edinger T. 1948. *Evolution of the horse brain*: Geological Society of America.

Edinger T. Midbrain exposure and overlap in mammals. *American Zoologist*. 1964; 4: 5–19.

Edinger T. Paleoneurology 1804-1966: an annotated bibliography. *Advances in Anatomy, Embryology and Cell Biology*. Berlin: Springer-Verlag; 1975; 49: 12–258.

Emry RJ. The edenulous skull of the North American pangolin, *Patriomanis americanus*. *Bulletin of the American Museum of Natural History*. 2004; 285: 130-138.

Erfurt J, Métais G. Endemic European artiodactyls. In: Prothero DR, Foss SE, editors. *The evolution of the Artiodactyls*. Baltimore: Johns Hopkins University Press; 2007. pp. 59–84.

Falk D. The natural endocast of Taung (*Australopithecus africanus*): insights from the unpublished papers of Raymond Arthur Dart. *Yearbook of Physical Anthropology*. 2009; 52: 49–65.

Fleagle JG. *Primate adaptation and evolution*. New York: Academic Press; 1999.

Gazin CL. A review of the middle and upper Eocene primates of North America. *Smithsonian Miscellaneous Collections*. 1958; 136, no. 1.

Gazin CL. A study of the early Tertiary condylarthran mammal *Meniscotherium*. *Smithsonian Miscellaneous Collections*. 1965; 149, no. 2.

Gidley JW. American Wild Horses. *The Scientific Monthly* 1927; 25:265-271.

Gingerich PD. Body weight and relative brain size (encephalization) in Eocene Archaeoceti (Cetacea). *Journal of Mammal Evolution*. 2016; 23: 17–31.

Gunnell GF, Bown TM, Bloch JJ, Boyer DM, Janis CM. Proteutheria. *Evolution of Tertiary mammals of North America*, vol. 2: small mammals, xenarthrans and marine mammals. Cambridge University Press; 2007. pp. 63–81.

Gunnell GF, Rose KD, Rasmussen DT. Euprimates. In: Janis CM, Gunnell GF, Uhen MD, editors. *Evolution of Tertiary mammals of North America*, vol. 2: small mammals, xenarthrans and marine mammals. Cambridge University Press; 2007. pp. 239–262.

Holbrook LT, Lucas SG, Emry RJ. Skulls of the Eocene perissodactyls (Mammalia) *Homogalax* and *Isectolophus*. *Journal of Vertebrate Paleontology*. 2004; 24: 951–956.

Holloway RL, Broadfield DC, Yuan MS, Schwartz JH, Tattersall I. The human fossil record, vol. 3: brain endocasts—the paleoneurological evidence. New York: Wiley; 2004.

Hooker JJ. The beginning of the equoid radiation. *Zoological Journal of the Linnean Society*. 1994; 112: 29–63.

Hulbert RC Jr. Late Miocene *nannipus* (mammalia: perissodactyla) from Florida, with a description of the smallest hipparionine horse. *Journal of Vertebrate Paleontology*. 1993; 13: 350–366.

Hunt RM Jr. Small Oligocene amphicyonids from North America (*Paradaphoenus*, Mammalia, Carnivora). *American Museum Novitates*. 2001; No. 3331.

Jerison HJ. *Evolution of the brain and intelligence*. New York: Academic Press; 1973.

Jerison HJ. The evolution of diversity in brain size. In: Hahn ME, Jensen C, Dudek BC, editors. *Development and evolution of brain size: Behavioral implications*. New York: Academic Press; 1979. pp. 29–57.

- Jerison HJ. Brain size and the evolution of mind. The 59th James Arthur Lecture on the evolution of the human brain. New York: American Museum of Natural History; 1991.
- Jerison HJ. The study of primate brain evolution: Where do we go from here? In: Falk D, Gibson K, editors. Evolutionary anatomy of the primate cerebral cortex. Cambridge, England: Cambridge University Press; 2001a. pp. 305–337.
- Johnson JI. Comparative development of somatic sensory cortex. In: Jones EG, Peters A, editors. Cerebral Cortex, vol. 8B. New York: Plenum Press; 1990. pp. 335–449.
- Kelly TS. New Miocene horses from the Caliente Formation, Cuyama Valley Badlands, California. Contributions in Science, Natural History Museum of Los Angeles County. 1995; 455:1–33.
- Kihm AJ, Hartman JH. A Reevaluation of the Biochronology of the Brisbane and Judson Local Faunas (late Paleocene) of North Dakota. Bulletin of Carnegie Museum of Natural History. 2004, 36: 97–107.
- Lange B. *Mustelictis piveteaui*, mustélide nouveau des Phosphorites du Quercy. Masson; Annales de Paléontologie. 1970; 3–16.
- Legendre S, Roth C. Correlation of carnassial tooth size and body weight in recent carnivores (Mammalia). Historical Biology. 1988; 1: 85–98.
- LeGros Clark WE. The Antecedents of Man, 2nd ed. Chicago: Quadrangle Books; 1962.
- Loomis FB. The small carnivores of the Miocene. American Journal of Science. 1932; 24: 316–329.
- Lyras GA. The evolution of the brain in Canidae (Mammalia: Carnivora). Scripta Geologica. 2009; 139:1–39.

- MacFadden BJ. Fossil horses from "eohippus" (*Hyracotherium*) to *Equus*: scaling, Cope's Law, and the evolution of body size. *Paleobiology*. 1986; 12: 355–369.
- MacFadden BJ. Fossil horses: Systematics, paleobiology, and evolution of the family Equidae. Cambridge: Cambridge University Press; 1992.
- MacPhee RD. The serialis bone, interparietals, “X” elements, entotympanics, and the composition of the notoungulate caudal cranium. *Bulletin of the American Museum of Natural History*. 2014; 384:1–69.
- Macrini TE. Description of a digital cranial endocast of *Bathysphenys reevesi* (Merycoidodontidae; Oreodontoidea) and implications for apomorphy-based diagnosis of isolated, natural endocasts. *Journal of Vertebrate Paleontology*. 2009; 29: 1199-1211.
- Marsh OC. Small size of the brain in Tertiary mammals. *American Journal of Science and the Arts*. 1874; 8: 66–67.
- Marsh OC. Dinocerata: A monograph of an extinct order of gigantic mammals. Washington: U.S. Geological Survey vol. 10; 1886.
- Martin RD. Primate origins and evolution: A phylogenetic reconstruction. London: Chapman & Hall; 1990.
- Martínez G, Dozo MT, Gelfo JN, Marani H. Cranial morphology of the Late Oligocene Patagonian Notohippid *Rhynchippus equinus* Ameghino, 1897 (Mammalia, Notoungulata) with emphases in basicranial and auditory region. *PLoS ONE*. 2016;11(5): e0156558. Available from: <https://doi.org/10.1371/journal.pone.0156558>.
- McKenna MC, Bell SK. Classification of mammals above the species level. New York: Columbia University Press; 1997.
- Mendoza M, Janis C, Palmqvist P. Estimating body mass of extinct ungulates: a study on the use of multiple regression. *Journal of Zoology*. 2006; 270: 90–101.

Mihlbachler MC. Species taxonomy, phylogeny, and biogeography of the Brontotheriidae (Mammalia: Perissodactyla). *Bulletin of the American Museum of Natural History*. 2008; 311:1–475.

Mihlbachler MC, Lucas SG, Emry RJ. The holotype specimen of *Menodus giganteus*, and the “insoluble” problem of Chadronian brontothere taxonomy. *New Mexico Museum of Natural History and Science Bulletin*. 2004;26:129–35.

Mitchell E, Tedford RH. The Enaliarctinae: a new group of extinct aquatic Carnivora and a consideration of the origin of the Otariidae. *Bulletin of the American Museum of Natural History*. 1973; 151: 201–284.

Moodie RL. On the endocranial anatomy of some Oligocene and Pleistocene mammals. *Journal of Comparative Neurology*. 1922; 34: 343–370.

Nowak RM. Walker’s mammals of the world. 2 vols. Baltimore and London: Johns Hopkins University Press; 1999.

Owen R. Description of fossil remains of a mammal (*Hyracotherium leporinum*) and of a bird (*Lithornis vulturinus*) from the London Clay. *Transactions of the Geological Society London*. 1841; 6: 203–208.

Orliac MJ, Sandrine L, Gingerich PD, Lebrun R, Smith T. Endocranial morphology of Palaeocene *Plesiadapis tricuspidens* and evolution of the early primate brain. *Proceedings of the Royal Society B: Biological Sciences*. 2014; 281: 20132792.

Osborn HF. The Titanotheres of ancient Wyoming, Dakota, and Nebraska. Washington DC: U. S. Geological Survey, Monograph 55; 1929.

Palmer RW. The brain and brain-case of a fossil ungulate of the genus *Anoplotherium*. *Proceedings of the Zoological Society of London*. 1913; 83: 878–893.

Patterson B. Some notoungulate braincasts. Field Museum of Natural History Geological Series. 1937; 6: 273–301.

Peterson OA. Report upon the material discovered in the upper Eocene of the Uinta Basin by Earl Douglas in the years 1908-1909, and by OA Peterson in 1912. Annals of the Carnegie Museum. 1919; 12:40–168.

Piveteau J. Traité de paléontologie, tome VI, vol. 2. Paris: Masson; 1958.

Piveteau J. Traité de Paléontologie, tome VI, vol. 1. Paris: Masson; 1961.

Radinsky LB. Origin and early evolution of North American Tapiroidea. Yale University: Bulletin of the Peabody Museum of Natural History 17; 1963.

Radinsky LB. The brain of *Mesonyx*, a Middle Eocene mesonychid condylarth. Fieldiana: Geology. 1976a; 33: 323–337.

Radinsky L. Oldest horse brains: more advanced than previously realized. Science 1976b; 194:626-627.

Radinsky L. Evolution of brain size in carnivores and ungulates. American Naturalist. 1978; 112: 815–831.

Radinsky L. The Fossil Record of Primate Brain Evolution. The James Arthur Lecture. American Museum of Natural History, New York. 1979.

Radinsky L. Brain evolution in extinct South American ungulates. Brain, Behavior and Evolution. 1981; 18: 169–187.

Rothwell T. Phylogenetic systematics of North American *Pseudaelurus* (Carnivora: Felidae). American Museum Novitates. 2003; No. 3403.

Russell DE, Sigogneau D. Étude de moulages endocraniens de mammifères paléocènes. Memoires du Muséum National D'Histoire Naturelle, Paris. 1965; 16: 1–43.

- Sanders WJ, Rasmussen DT, Kappelman J. Embrithopoda. In: Werdelin L, Sanders WJ, editors. Cenozoic mammals of Africa. Berkeley: University of California Press; 2010.
- Savage RJG, Long MR. Mammal evolution: An illustrated guide. London: British Museum (Natural History); 1986.
- Scott WB. A History of Land Mammals in the Western Hemisphere (2nd edition). New York: Macmillan; 1937.
- Secord R, Gingerich PD, Smith ME, Clyde WC, Wilf P, Singer BS. Geochronology and mammalian biostratigraphy of middle and upper Paleocene continental strata, Bighorn Basin, Wyoming. *American Journal of Science*. 2006; 306: 211–245.
- Simpson GG. Horses. London and New York: Oxford University Press; 1951.
- Stevens MS, Stevens JB. Family Merycoidodontidae. In: Prothero DR, Foss SE, editors. The evolution of Artiodactyls. Baltimore: Johns Hopkins University Press; 2007. pp. 157–168.
- Stephan H, Frahm HD, Baron G. New and revised data on volumes of brain structures in insectivores and primates. *Folia Primatologica*. 1981; 35: 1–29.
- Stevens MS, Stevens JB. Merycoidodontinae and Miniochoerinae. The terrestrial Eocene-Oligocene transition in North America. Cambridge University Press, Cambridge. 1996:498–573.
- Stucky RR. Eocene bunodont and bunoselenodon Artiodactyla (“dichobunids”). In: Janis CM, Scott KM, Jacobs L, editors. Evolution of Tertiary mammals of North America. Cambridge: Cambridge University Press; 1998. pp. 358–374.
- Thorpe MR. John Day eporeodonts, with descriptions of new genera and species. *American Journal of Science, Series 5*. 1921; 6: 93–111.
- Thorpe MR. The Merycoidodontidae: An extinct group of ruminant mammals. New Haven: Memoirs of the Peabody Museum; Yale University Press; 1937.

- Tobias PV. The Brain in Hominid Evolution. New York: Columbia University Press; 1971.
- Tomiya S. A new basal caniform (Mammalia: Carnivora) from the middle Eocene of North America and remarks on the phylogeny of early carnivorans. PLOS ONE. 2011; 6:e24146.
- Uhen MD. Form, function, and anatomy of *Dorudon atrox* (Mammalia, Cetacea): An archaeocete from the Middle to Late Eocene of Egypt. University of Michigan Papers on Paleontology. 2004; 34: 1–222.
- Van Dongen PAM. Brain size in vertebrates. In: Nieuwenhuys R, ten Donkelaar HJ, Nicholson C, editors. The central nervous system of vertebrates, vol. 3. Berlin: Springer-Verlag; 1998. pp. 2099–2134.
- Wall WP. The genus *Amynodon* and its relationship to other members of the Amynodontidae (Perissodactyla, Rhinocerotidae). Journal of Paleontology. 1982; 56: 434–443.
- Wall WP. Amynodontidae. In: Janis C, Scott KM, Jacobs LL, editors. Evolution of Tertiary mammals of North America, vol.1: Terrestrial carnivores, ungulates, and ungulate like mammals. Cambridge University Press, Cambridge, England. 1998. pp. 583–588.
- Wang X, Tedford RH, Taylor BE. Phylogenetic systematics of the Borophaginae (Carnivora: Canidae). Bulletin 243. New York: American Museum of Natural History; 1999.
- Welker WI. Why does cerebral cortex fissure and fold? A review of determinants of gyri and sulci. In: Jones EG, Peters A, editors. Cerebral Cortex vol. 8B. New York: Plenum Press; 1990. pp. 1–132.
- Wells RT, Tedford RH. *Sthenurus* (Macropodidae, Marsupialidae) from the Pleistocene of Lake Callabonna, South Australia. New York: Bulletin of the American Museum of Natural History, No. 225; 1995.

Wesley-Hunt GD, Werdelin L. Basicranial morphology and phylogenetic position of the upper Eocene carnivoramorph *Quercygale*. *Acta Palaeontologica Polonica*. 2005;50:837–846.

Wilson JA. Early Tertiary vertebrate faunas, Vieja Group, Trans-Pecos Texas: Agriochoeridae and Merycoidodontidae. *Texas Memorial Museum Bulletin*. 1971; 18:1–83.

Woodburne MO, editor. Late Cretaceous and Cenozoic Mammals of North America. New York: Columbia University Press. 2004.

Woodward AS. On some remains of *Grypotherrium (Neomylodon) listai* and associated mammals from a cavern near Consuelo Cove, Last Hope Inlet, Patagonia. *Proceedings of the Zoological Society of London*. 1900: 64–79.

Zhou X, Sanders WJ, Gingerich PD. Functional and behavioral implications of vertebral structure in *Pachyaena ossifraga* (Mammalia, Mesonychia). *Contributions from the Museum of Paleontology, University of Michigan*. 1992; 28: 289–319.