What Fossils Tell Us about the Evolution of the Neocortex

Harry J Jerison

The story of the brain's evolution is told by casts of the cranial cavities of extinct species. These endocasts document much of the evolution of the mammalian brain during the past 65 million years, the Cenozoic era. A single late Jurassic fossil (Simpson, 1927; Jerison, 1973) had extended the known evidence to about 150 million years ago (mya), and other explorations (Hu et al., 2005; Kielan-Jaworowska et al., 2004; Novacek, 1996) fill gaps in our knowledge of the Cretaceous period (65-145 mya). Mammals first appeared during the Triassic period of the Mesozoic, and it may one day be possible to trace the history of the mammalian brain almost to its beginnings, perhaps 225 mya.

Encephalization is the increase in relative size of the brain as a whole over geological time. Its history was reviewed in depth in Jerison (1973; cf. Falk & Gibson, 2001). Other recent evolutionary analysis emphasizes methodological innovations in cladistic analysis, with major revisions of mammalian phylogeny (McKenna & Bell, 1997; cf. Simpson, 1945). This chapter is consistent with those revisions.

Our central topic is neocorticalization, the increase of the relative amount of neocortex in the brain of mammals. Identifiable neocortex is a feature of the external morphology only of mammalian brains, but neural structures with similar functional significance have also evolved in birds and reptiles (Butler & Hodos, 2005; Karten, 1997; Reiner, Yamamoto & Karten, 2005). Avian and reptilian brain structures homologous with mammalian neocortex must first have appeared in the common amniote ancestor of these classes of vertebrates, but fossils are unlikely to be helpful in identifying these earlier ancestral connections. The question for this chapter is whether there was a change in neocorticalization within the mammals as they evolved during the past 225 million years. Like the avian Wulst, which is absent in endocasts of the earliest birds, evidence of neocortex may have been absent in endocasts of the earliest mammals. We don't yet know, but I review what we do know in this chapter.

We know that the neocortex, like the brain as a whole, became relatively larger in some but not all mammalian lineages (Jerison, 1990). Neocortex is present in all living mammals. Fossils tell its history, and it is reassuring that their evidence is consistent with inferences from the comparative neuroanatomy of living species (Butler & Hodos, 2005; Johnson, 1990; Shimizu, 2001). Opossums and hedgehogs (*Didelphis virginianus* and *Erinaceus europaeus*) can still be viewed as "primitive," and cats and dogs and monkeys may be thought of as "advanced," although one recognizes that this is an arbitrary dichotomy. From the fossils we learn approximately when some identifiable changes in the brain occurred and how they differed in different lineages. They are the real proof of what is otherwise conjecture, that in most mammal species the brain evolved to relatively larger size and that this encephalization was usually accompanied by increased neocorticalization. Surprisingly, there appears to have been no comparable change in the olfactory bulbs other than their reduction in primates evident since the Miocene (about 20 mya) and their complete disappearance in at least some cetaceans even longer ago.

All of the neural adaptations recognizable in the fossils are ancient, many occurring tens of millions of years ago. The most recent changes have been within the hominins, the human lineage, in which the most recent measurable increases in encephalization appeared about 250,000

years ago in the Neandertal and sapient species (*Homo neanderthalensis* and *Homo sapiens*)[1]. The evolutionary evidence is at the generic and species level. I review a few within-species differences (Figures 3 and 4, below), but these are small compared to between-species effects.

Fossil Brains

Molded by the cranial cavity, endocasts such as those reviewed here have been called fossil "brains" (Edinger, 1929; see Kohring & Kreft, 2003). The brain, as soft tissue does not fossilize, of course, but endocasts in birds and mammals resemble brains with dura intact, and they often show the superficial pattern of sulci and gyri in remarkable detail. Further analysis relies on relationships of external structures to the functional and microscopic anatomy of brains in living animals. In this chapter, brains and endocasts are treated as equivalent to one another. For most purposes one can ignore the small differences between them in size and shape and use the same terminology for parts of an endocast as for comparable parts of the brain.

Neocortex can be distinguished from other structures visible on the surface of an endocast in mammals by using the rhinal fissure as the landmark. The evidence is exemplified by the brain of the living armadillo shown in Figure 1A. Rhinal fissure can be traced backward from the dorsal margin of the olfactory tract, and the fissure visible on the brain is also visible on endocasts. Figure 1B is a coronal section to show how the rhinal fissure serves as the boundary between neocortex and paleocortex, with paleocortex identified by the darkly stained layer of neurons in Lamina II. Neocortex is taken as dorsal to the rhinal fissure on brains and endocasts.

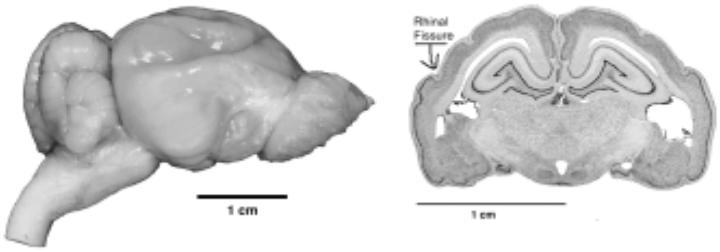

Figure 1. Left: Brain of armadillo, *Dasypus novemcinctus*; rhinal fissure faintly visible dorsal to olfactory tract then prominent further posteriorly. **Right:** Coronal section of armadillo brain showing Lamina II (dark stained layer) at border of rhinal fissure. Specimen WISC 60-465, see footnote 1.

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[1]Spellings and orthography in this chapter follow the rules of taxonomic nomenclature. Genus and species are italicized, genus capitalized and species in lower case. References in the text to Neandertal follow the current German spelling and capitalization of nouns. The Neandertals were named for the Neander Valley in which the first specimen was found in 1856. German is famous as a language that combines words and elongates them rather than keeping them as short phrases, thus, the Neander Valley (capitalized in English as a place name) was the "Neanderthal" before the German spelling reform of 1908, when it became "Neandertal." The rules of taxonomic nomenclature preserve the first published name of *Homo neanderthalensis*. The initial capital letter for the German was dropped in the species name in deference to taxonomic usage of lower case for species. The genus "*Homo*" is as named by Linnaeus in 1758. Specimens shown here are as catalogued in AMNH (American Museum of Natural History, New York), BMNH (Natural History Museum of London, British Museum), FMNH (Field Museum of Natural History, Chicago), WISC (University of Wisconsin: <http://brainmuseum.org/Specimens/index.html>), and UT (University of Texas, Department of Paleontology).

Endocasts can be made from the cranial cavity of any skull. Those made from fossils are of special interest, because they are a physical record of the actual evolution of the brain. Figure 2, for example, presents snapshots of 3D scans of endocasts of two Eocene fossil mammals that lived about 40 mya, a prosimian primate *Adapis parisiensis* and an even-toed ungulate (artiodactyl), *Anoplotherium commune*. Their endocasts may be compared with the brains of the living bushbaby (*Galago senegalensis)* and the living llama (*Lama glama*), a camelid distantly related to *Anoplotherium*. An endocast of another Eocene fossil artiodacyl, *Bathygenys reevesi*, is shown below in Figure 5 and that of an archaic Paleocene herbivore (*Phenacodus primaevus*, order Condylarthra, 58 mya) is shown in Figure 9.

The olfactory tract and rhinal fissure are easily distinguishable on the lateral surface of the endocasts of *Anoplotherium* and *Bathygenys*; they are less clear but also identifiable in *Phenacodus*. We identify and measure neocortical surface area as dorsal to the fissure. The rhinal fissure in *Adapis* follows a course very much like that in the living bushbaby, partly hidden by the temporal lobe. To be able to see the rhinal fissure in this endocast, it has to be rotated a bit to display more of the ventral surface. One objective of 3D analysis reported here was to rotate virtual endocasts in primates to expose neocortex and include primate measurements in the analysis of mammalian data. Neocorticalization is the increase of neocortex relative to the rest of the brain, and it can be measured as a ratio of surface areas on an endocast.

This chapter is primarily on a quantitative analysis, but there is one interesting qualitative feature evident in Figure 2 that may be important. Comparing the Eocene fossils and their living relatives there is an obvious difference in the flexure of the brain, more marked in the ungulates than the primates but evident in both, In the fossils, olfactory bulbs, forebrain, hindbrain and medulla are more or less in a line like railroad cars. The brains of their living relatives are bunched up and more globular. The difference probably results from the patterns of relative growth of the skull and skeleton compared to the growth of the brain, and is at least partly an epigenetic effect of squeezing a brain into the confines of the cranial cavity.

When an overall trend in skeletal growth resulted in enlargement of the cranial cavity, the brain can grow to fill, and to an extent shape, the cranial cavity. When trends toward encephalization became more prominent the pressure was to maximize the amount of brain that could be packed into a given space. Later brains became more globular, primarily as an accommodation to maximize their volume relative to the space available for their growth. The change in shape as an evolutionary event would have been one of the changes that occurred at the *Grande Coupure*, the extinction of many species at the end of the Eocene and the beginning of the Oligocene about 33 mya (Hooker, Collinson & Sille, 2004).

The Specimens and their Measurement

The 78 ml plaster endocast of *Anoplotherium* in Figure 2 was prepared from the carefully cleaned cranial cavity of the fossil's skull (Palmer, 1913). This animal probably weighed about 80 kg, a weight comparable to that of the living llama in which the brain's volume is about 230 ml. *Bathygenys* (Figure 5, below) was a small artiodactyl that lived at the end of the Eocene, 35 mya. It was about the size of the living chevrotain weighing about 5 kg. Its 12 ml natural endocast shown in Figure 5 is actually a piece of rock, but it unmistakably pictures the brain. One chevrotain (*Tragulus javanicus*) has been reported as weighing of 4 kg with a 19 gram brain

(Nieuwenhuys et al., 1998). The area of neocortex in both *Anoplotherium* and *Bathygenys* was 28% of the entire surface area of the endocast. In Oligocene species that lived about 30 mya, such as the fossil horse *Mesohippus*, typical ratios are about 40 % or more.

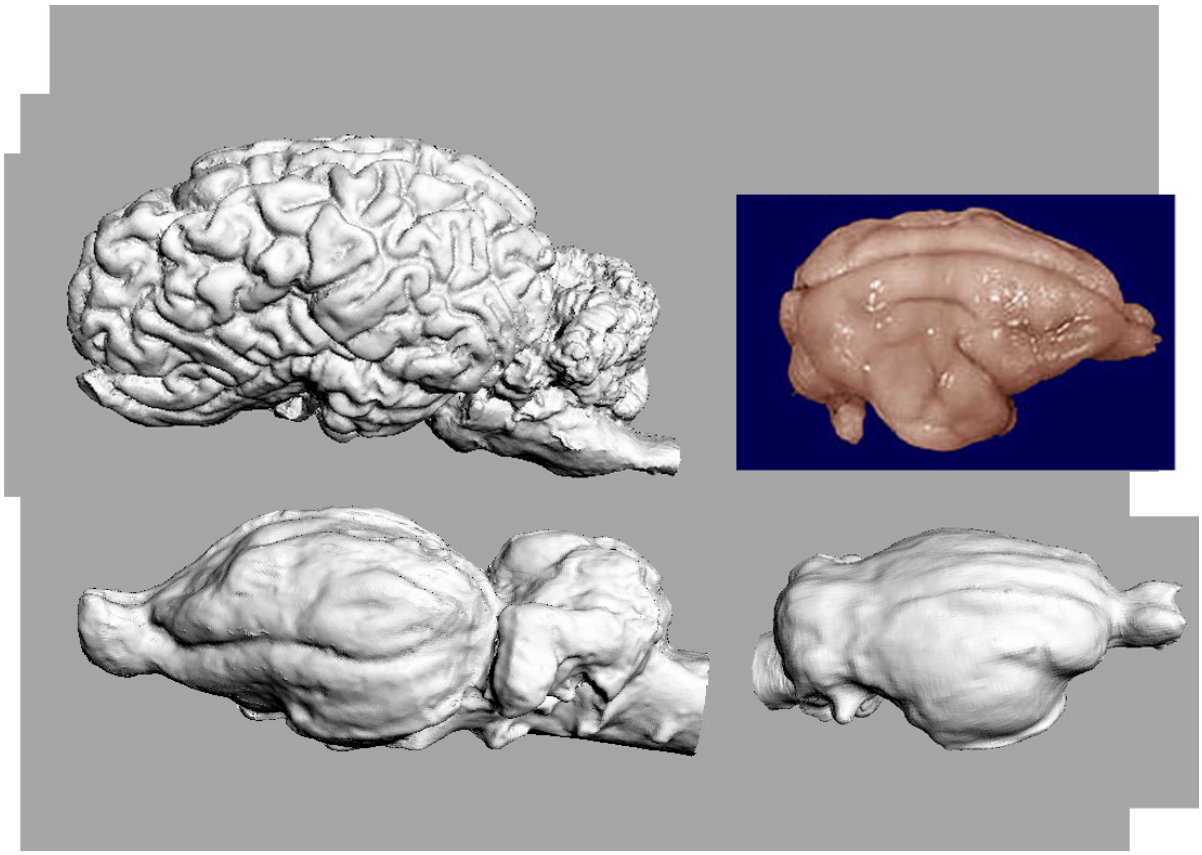

Figure 2. Brain (upper left) and endocast (lower left) in two artiodactyls, the living llama (*Lama glama*, WISC 65-139) and a 40 million year old camelid, *Anoplotherium commune*, BMNH 3753. Brain (upper right) of the living bushbaby (*Galago senegalensis*, WISC 61-686) and endocast (lower right) of a 40 million year old prosimian, *Adapis parisiensis*, FMNH 59259/BMNH 1340. See footnote 1. [*to be replaced with b&w fig+scales*]

The volume of the endocast of *Phenacodus* (Figure 9, below) is 31ml, and 16% of its surface area is neocortex. Its rhinal fissure is less marked than in the other endocasts illustrated here, but adequate for a measurement of the area of its neocortex. It was illustrated by Cope (1883). The endocast scanned for this analysis is a copy of the one made by Cope. Reconstructions of *Phenacodus* in life (Savage & Long, 1986) show it as living in a small herd of sheep-like five-toed animals. The weight of the fossil, estimated as 56 kg, is also appropriate for living sheep (*Ovis aries*) in which a brain weight of 130 g has been recorded.

Adapis, a prosimian primate that was a contemporary of *Anoplotherium*, weighed about 1.5 kg, and its endocast's volume was 8 ml. From skeletal features it has been reconstructed

as a tree-dwelling lemuroid. The brain of the living galago, the bushbaby, is shown for the comparison in Figure 2 because it is about the same size and shape as that of *Adapis*, but galago is a much smaller animal, weighing only about 250 grams. A living lemur (*Lemur fulvus*) has been recorded with a body weight of 1.4 kg and had a 23 g brain.

The differences between the fossil and living brain sizes at comparable body sizes are examples of encephalization. Brains in most Eocene species averaged a quarter to half the size of living species in comparable niches and their relative size might be reported as "encephalization quotients, *EQ*": $0.25 < EQ < 0.50$ for Eocene fossils. Brain and body weight data on living species for comparisons are now available in many places. Some of the published data collections on living mammal species that I have seen have been in Count (1947), in Quiring (1950), and in Nieuwenhuys et al. (1998). I have published estimates on many fossil mammals (Jerison, 1973, 1990), and Holloway (2004) has more recent data on primates in the human lineage.

Encephalization quotients are not ratios of brain size to body size. They are ratios of measured brain or endocast size relative to expected size, and expected size is determined from the allometric relationship between brain and body size. That relationship is nonlinear and is usually described by the power function:

$$E = kP^{\alpha} \qquad (1)$$

E is brain size and P is body size in the same metric units (e.g., grams or ml). There is some debate on correct values for the parameters k and α (see Jerison, 2001b), but empirically the values $\underline{k} = 0.06$ and $\underline{\alpha} = 0.75$ are good approximate values as determined on large samples of living mammal species. When the equation is transformed logarithmically it is

$$\text{Log } E = \alpha \log P + \log k \qquad (1a)$$

Graphed on logarithmic coordinates α is the slope and log k is the Y-intercept of the best-fitting straight line. An encephalization quotient is the residual from that regression. For theoretical reasons (Jerison, 2001b) I prefer $\alpha = 2/3$, in which case one must use $k = 0.12$ for computations. For a given set of parameters, it is an elementary exercise to compute an encephalization quotient.

To return to the specimens, the *Bathygenys* endocast in Figure 5, below, was made naturally. When this animal died, perhaps at a lakeside, its soft tissue decayed but its skull must have remained relatively undamaged. Sand and other debris could then pack the cranial cavity and could be covered and protected by layers of sediment. When the waters subsided the skull and its contents eventually fossilized. Many millions of years later the fossil was uncovered, presumably by erosion or earth movements. The fossilized skull must then have eroded, leaving only its hardened rock contents, the natural endocast. A lucky fossil hunter could find the specimen. Professor Jack Wilson of the University of Texas found the *Bathygenys* fossil, which he recognized as a natural endocast (Wilson, 1971), collected it for his Paleontology Department, and made it available for this report.

The plaster endocast of *Anoplotherium commune* shown in Figure 2 is part of the history of anatomy and paleontology. A largely intact fossil skeleton of the whole animal was found in gypsum quarries in Montmartre, now part of Paris, and was named in 1804 by Baron

Georges Cuvier. He noted that the fossil's canine teeth seemed short and ineffective as weapons; "anoplos" is from the Greek for "unarmed" and "therium" for beast, hence *Anoplotherium*. Serving under the Emperor Napoleon, Cuvier was director of the Muséum National d'Histoire Naturelle in Paris two centuries ago, and he undertook to demonstrate that fossils are evidence of the history of life.

At the time, fossils were sometimes considered to be mineral accretions that merely resembled living things. Cuvier accepted what we now recognize as the "uniformitarian hypothesis," namely, that the present laws of nature have always been valid (Simpson, 1970). That he named the fossil according to his judgment of its teeth is a uniformitarian view that is natural for us. We share the judgment that they are not merely rocks that happened to look like teeth but were once teeth and had fossilized. The story is that in a public exhibition, Cuvier "dissected" his *Anoplotherium*, in which some of the fossilized vertebral column was exposed. The dissection was with hammer and chisel, and Cuvier pointed out that if what looked like the vertebral column had been the vertebral column of an animal that once lived, further exposure would reveal pelvic bones. It did. This was his way of proving that he had been working on the remains of an animal that was comparable anatomically to living animals.

Among the other endocasts and brains illustrated in this chapter, *Phenacodus* was collected and named by Edward Drinker Cope as mentioned earlier, and it was one of the bones of contention in the fossil feud of the late nineteenth century about discoveries in the American West (Wallace, 1999). The adapid endocast is from a skull presently at the Natural History Museum of London and was from the phosphorites of Quercy in Southwest France, a late Eocene site in which the fossils are about 40 million years old. Its endocast was first prepared a century ago under the direction of Sir Grafton Eliot Smith (1903) and has had a prominent place in discussions of the evolution of the primate brain (LeGros Clark, 1962). This chapter's scan is from a later preparation for Professor Robert D. Martin, then at the Anthropology Department of University College, London (Martin, 1990). The brain of galago with which it is compared in Figure 2 is from the University of Wisconsin brain collection, a collection that I consulted for comparisons with almost all of the fossils analyzed for this chapter. At this writing the Wisconsin collection can be viewed on the internet at <http://www.neurophys.wisc.edu/>; one follows the link to "Brain Collection." Like the galago brain, the llama brain and the armadillo brain of Figure 1 are also in the Wisconsin collection. Some of that collection has been moved to Washington, D.C., and is now part of the National Museum of Health and Medicine of the Armed Forces Institute of Pathology.

Hundreds of fossil "brains" have been collected throughout the world, either as natural endocasts or as latex or plaster casts made from fossil crania (Edinger, 1975), and they are available for study in the back rooms of many museums. The quality of an endocast as a model of the brain differs in different taxa. In fish, amphibians, and reptiles the model is usually poor because when they mature their brains do not fill the cranial cavity. Semicircular canals and other auditory and vestibular structures are occasionally well preserved in many vertebrates (Rowe, 1996; Dominguez et al., 2004). In mammals and birds, endocasts often provide accurate and detailed pictures of the external surface of the brain as in Figures 2, 5, and 9. Comparisons between brains and endocasts in living mammals indicate that only minor errors occur in treating endocasts as undissected brains.

Measurement of surface area in endocasts was essentially impossible until

recently, when technologies were developed that enable us to scan and digitize irregular solids for computer analysis. The endocasts used for the 3D analysis in this chapter were digitized with a laser scanner system and its associated software. After scanning, the surface areas were measured with that software to provide the data for Figures 7 and 8. At this writing more details about the system are available on the internet at <http://cyberware.com> and <http://brainmuseum.org/Evolution/paleo/index.html>.

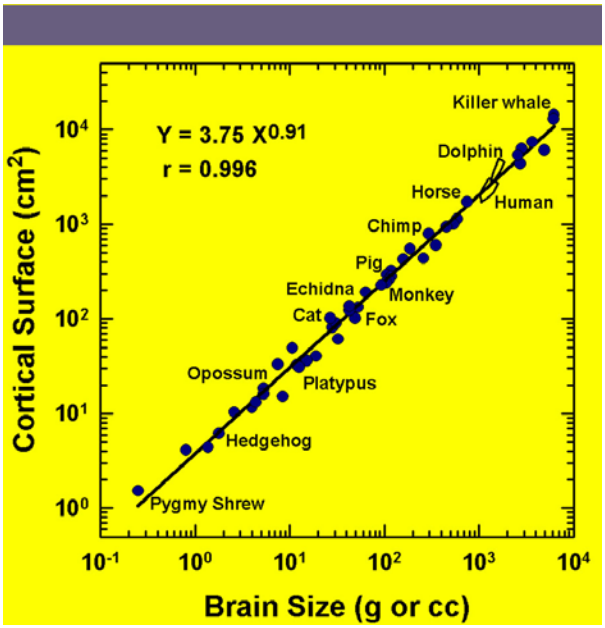

Figure 3. Total cortical surface area (including "buried" cortex) as a function of brain size in fifty species of living mammals. Correlation: r = 0.996; regression: $Y = 3.75\ X^{0.91}$. A few of the species are labeled to suggest the diversity of the sample. Human and dolphin data are presented as minimum convex polygons enclosing 23 points for humans and 13 points for dolphins to suggest within-species diversity. (Data from Brodmann, 1913: Elias & Schwartz, 1971; Ridgway, 1981, and Ridgway & Brownson, 1984. From Jerison, 1991, by permission.)

Brains and Endocasts

Why should we be concerned with simple-minded measurements of gross brain size? One obvious reason is that these are reliable measures that can be taken on fossils, and they enable us to quantify the evolution of the brain. Less appreciated is their utility for an understanding of the brain's work in living species, because gross brain size, either surface area or brain weight or volume, may estimate the total information-processing capacity of brains in living mammals. That relationship is inferred from Figure 3, which graphs surface area of living brains as a function of brain size. The number of neurons underneath a specific amount of surface appears to be constant in many species (Rockel, Hiorns and Powell, 1980, but see also Haug, 1987; Hofman, 1985, 1988). Since the total processing capacity of a neural system is related to the number of neurons in the system, total surface area must estimate the total number of information processing units in a brain. Analogously, the surface area of neocortex as a part of the brain measures the contribution of neocortex to the total amount of information processed

by the brain. The surface-volume relationship as shown in Figure 3 is almost perfect with a product-moment correlation coefficient r = 0.99. Uniformitarianism suggests that this almost deterministic relationship was as true for fossil endocasts as it is for living brains, although there are questions raised at the end of this chapter among the "caveats."

Figure 3 also provides information about within-species variability compared to that between species. In two of the species, *Homo sapiens* and *Tursiops truncatus*, it was possible to show the full range of individual data by enclosing those data in convex polygons that incorporate the complete samples. It is evident that the polygons are only slightly larger than the individual points graphed for the other species, each of which is a single datum for the species.

How good is an endocast as a representation of a brain? The obvious answer is in the endocasts and brains illustrated in this chapter. The relationship has been quantified for gross size in the human species and is shown in Figure 4. Although partly obscured by the well known variability in human brain size, there is a strong relationship between brain and endocast (cranial capacity) as indicated by the high correlation coefficients. Endocasts and brains are equivalent to one another for information on size, with a small difference (about 7 %) due to the fluids and meninges that surround the brain. The regression lines are parallel to one another, showing that the difference between endocast and brain follows the same rule for women and for men. This chapter is not concerned with the sex differences in human brain size, but that difference is also shown to complete the graphic summary of the data as published by Davis & Wright (1977).

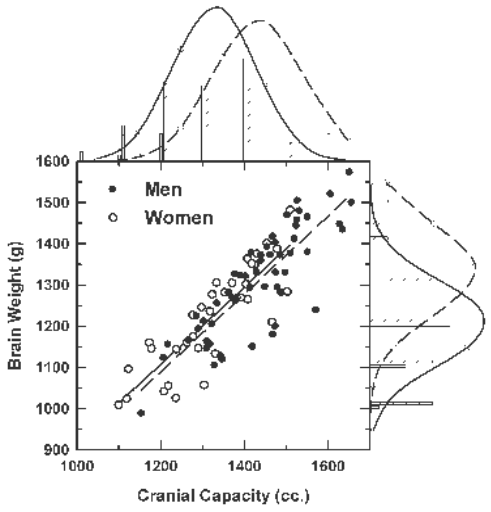

Figure 4. Relationship between brain size and cranial capacity (endocast volume) in 54 human male and 33 female cadavers. Mean brain size, Male = 1,308 g; Female = 1,221 g. Mean cranial capacity (endocast volume), Male = 1,431 ml; Female = 1,322 ml. Correlation coeffecients, r = 0.84 for men; r = 0.85 for women. Regression equations: Male: Y = 0.94 X - 44; Female: Y = 0.94X - 16. (Data from Davis & Wright, 1977)

Two-dimensional Analysis of Neocorticalization

The first quantitative analysis of neocorticalization presented measurements of the areas of neocortex and olfactory bulbs in two-dimensional lateral projections in a sample of 35 fossil and 24 living species of carnivores and ungulates (Jerison, 1990). It was based on profiles of the endocasts in which rhinal fissures were visible, and the measure was the area of neocortex dorsal to the fissure. The 2D analysis was also performed on the areas of the olfactory bulbs. Data for the analysis are illustrated in Figure 5A on the endocast of *Bathygenys reevesi*, discussed earlier; Figure 5B sketches the the areas that were measured.

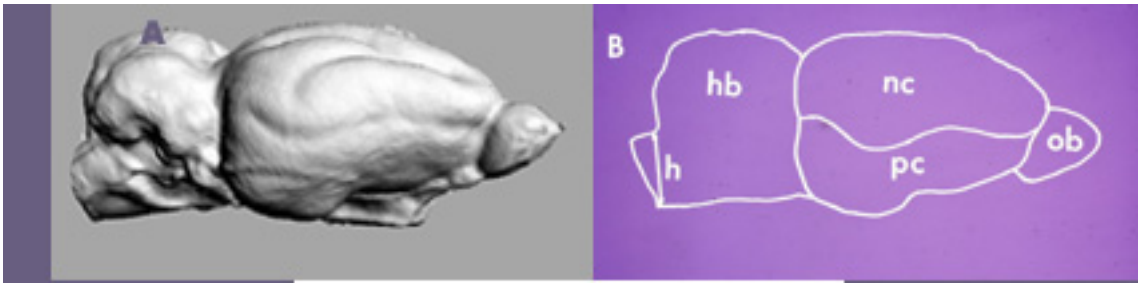

Figure 5. **A**. Scan of natural endocast of *Bathygenys reevesi* (UT 40209- 431). **B**. Profile of endocast, showing areas measured for Figure 6. **nc**, neocortex; **ob**, olfactory bulbs, **h**, height of foramen magnum. Not measured: **pc**, visible paleocortex; **hb**, visible hindbrain, including cerebellum.

The 2D results are graphed in Figure 6 and show how the neocortical and olfactory bulb quotients in this sample changed with geological age during the Cenozoic era. The quotients are ratios of measured brain areas relative to their expected areas, with the latter determined by the regression of brain areas on the height of the foramen magnum (medulla). The measure on the foramen magnum followed a suggestion by Radinsky (1967) to use the foramen measure to control for body-size differences in different species. The quantitative analysis was limited to neocortex and olfactory bulbs. Paleocortex and hindbrain were not analyzed because the curvature of the brain hides much of the paleocortex and because hindbrain regions such as the cerebellum are partly hidden under overlying neocortex. (Regression analysis such as this is often referred to as allometric analysis, the analysis of the measures of two organ-sizes relative to one another.)

The results of the 2D analysis as discussed in the original report (Jerison, 1990) were, first, that neocorticalization occurred, which is shown by the significantly positive slope of the regression of the neocortical quotient on geological age. Second, the olfactory bulbs did not change in relative size in these species during the Cenozoic. Taken together, these two results validated the method in that it could discriminate between change and the absence of change. A third result was that the "archaic" fossil species, that is, species from orders of mammals that are now entirely extinct, were significantly below average in neocorticalization, falling below the regression line determined for the entire sample. This suggests positive selection for neocorticalization, that it improved fitness in an evolutionary sense.

Two-dimensional data on brain size are flawed because they are limited to profiles of the brain and do not measure the actual areas of the curved surfaces of the endocasts. They are also limited to species in which rhinal fissure is visible on the lateral surface, and this excluded primates from the analysis. When the 2D analysis was published it was not possible to perform an

equivalent 3D analysis with the technology available at that time. Such a technology has since been developed, and the analysis of 3D images of endocasts is published here for the first time.

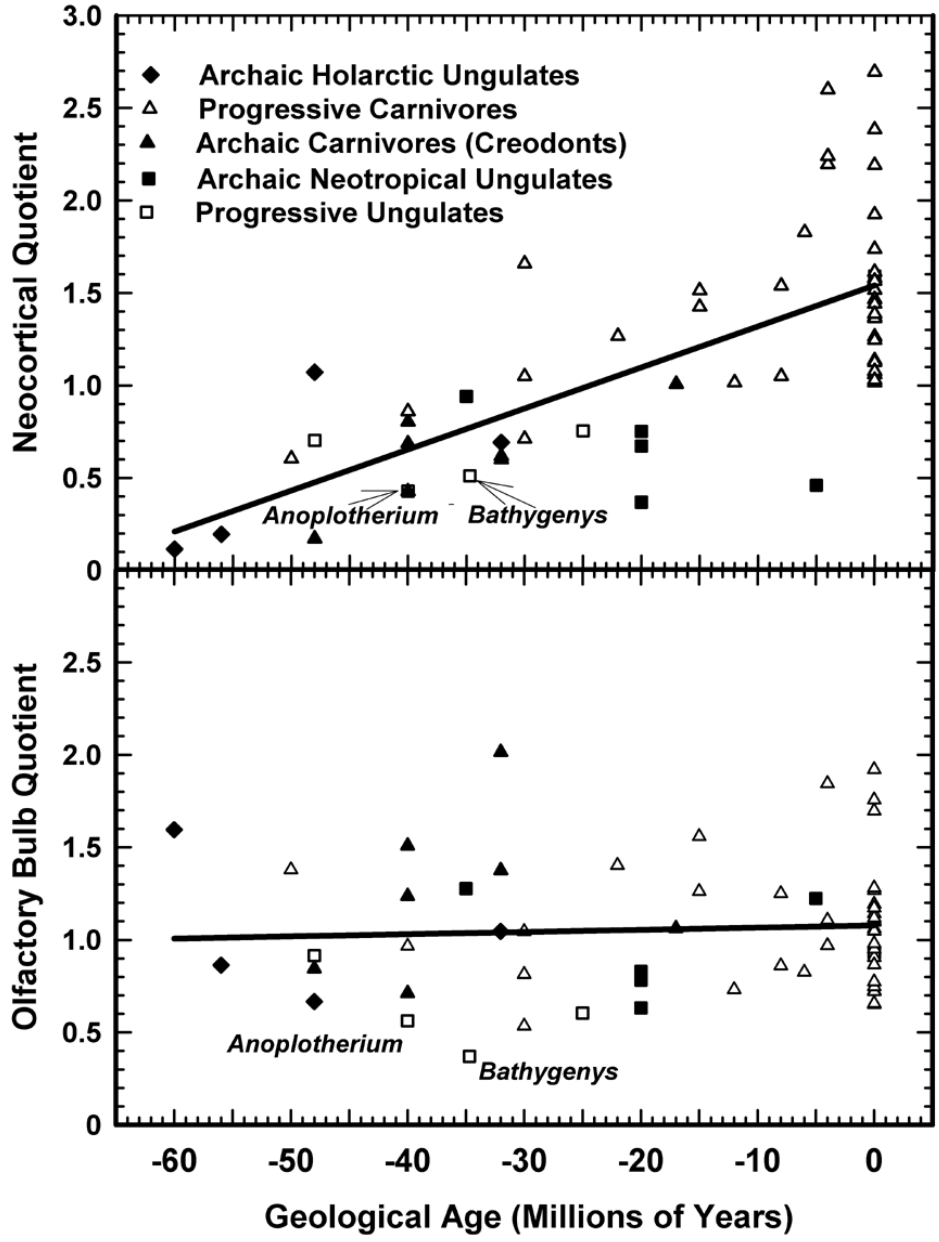

Figure 6. Two-dimensional analysis showing increased relative neocortical surface area (top) and stasis in olfactory bulbs (bottom) during the past 60 million years; see Figure 5. Quotients are residuals from regression of neocortex area and olfactory bulb area on foramen magnum height. They are interpreted as ratios of measured areas relative to expected areas on the basis of body size in this sample. "Progressive" neocortical change noted here (positive slope of regression line; r = 0.75) demonstrates neocorticalization over time. Each point is a species. Archaic carnivores are from the order Creodonta. Other groups are discussed in the text. (Redrawn from Jerison, 1990.)

Three Dimensional Analysis: Neocortex

The analysis of newly acquired 3D data on a larger sample of fossil and living mammals, which includes primates (Figure 7), confirms that there was progressive neocorticalization in mammals during the Cenozoic. The positive slope of the regression (Figure 7) is similar to that found in the 2D analysis. The sample of 106 mammals included 84 fossil species and 22 living species. There were seven fossil primates: two hominins and five prosimians, including the *Adapis parisiensis* shown in Figure 2. The hominins were two Plio-Pleistocene australopithecenes, *Australopithecus africanus* (the Taung specimen discovered by Raymond Dart in 1923) and *Australopithecus robustus* (SK 1585) from South Africa (see Tobias, 1971; Holloway, 2004). There are partial endocasts for Oligocene and Miocene anthropoids (*Aegyptopithecus*, *Libypithecus*, and *Proconsul*; see Radinsky, 1979), which were sufficient to indicate that frontal and temporal lobes were in a primate-like configuration (Jerison, in press), but they were too incomplete otherwise for this quantification. The 22 living mammal species included eight anthropoids (simians) and two humans. Primates have evidently always been above average in neocorticalization, that is, their data lay above the regression line determined for the entire sample as shown in Figure 7. Living and fossil hominins are typical primates on these measures. The highest ratio of neocortex to endocast surface area was a langur's (*Cercocebus albigena*) at 80.4% followed by one living human at 80.0%. A second living human endocast measured 77.7% and was topped by two other monkeys.

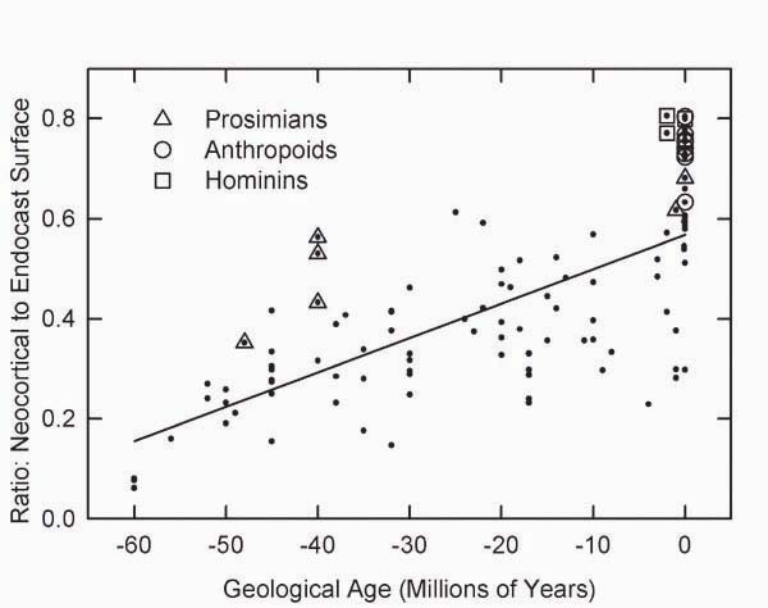

Figure 7. Relative size of neocortex measured in 3D analysis of the endocasts of 106 species of mammals during the past 60 million years. Prosimians are marked by triangles, hominins (including australopithecines) by squares and anthropoids by circles. Regression of neocortical ratio on geological age: $Y = .007 X + 0.57$; $r = 0.72$. In living mammals 57% of the endocast surface area is devoted to neocortex; the increase was about 7% per 10 million years. In living monkeys and living and fossil hominins the ratio averages about 75%.

As in the 2D analysis it was possible to compare species from archaic orders with those from "progressive" orders, and the data showing the difference are presented in Figure 8.

The species in which endocasts were illustrated earlier in Figures 2 and 5 were progressive in that there are even-toed ungulates (Order Artiodactyla) and primates (Order Primates) living today.

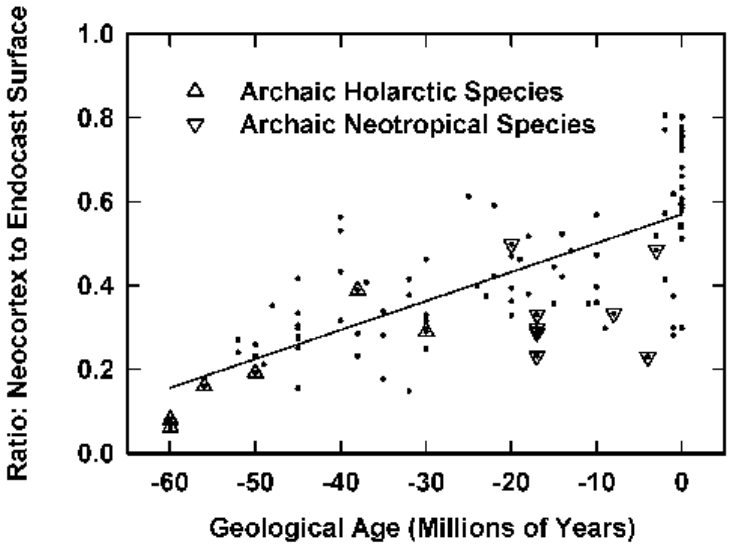

Figure 8. The same mammal species as in Figure 7, marked to distinguish "archaic" from "progressive" species, that is, species that are members of presently extinct orders or suborders of mammals from those that are members of surviving groups. Upright triangles for holarctic species, inverted triangles for neotropical species. Regression line is for the entire sample, and is the same as in Figure 7. Archaic species on average fall below the regression line.

Several orders of Miocene and Pliocene South American mammals, originally discovered as fossils by Charles Darwin in the 1830's on the voyage of the Beagle, are "archaic," having no surviving species. Their data are included in Figure 8 and marked with inverted triangles. Erect triangles mark holarctic species from Europe and North America, also from extinct orders. Thirteen of the 15 archaic species fell below the regression line. The probability that this was a random departure from "average" is less than 0.05 (chi-square test). The 3D analysis thus supports the conclusion that neocorticalization contributes to fitness, that is, that there was positive selection for neocorticalization.

Endocasts of archaic species are not superficially unusual. That of *Phenacodus primaevus* discussed earlier is shown in Figure 9. It might be distinguished from the other fossil endocasts because of slight differences in appearance, but it is also different quantitatively. At the animal's estimated body weight (56 kg), its expected endocast volume is 176 ml according to my preferred parameters of Eq. 1. The measured volume of the endocast at 31 ml results in an encephalization quotient of 0.18. Its ratio of neocortical area to total endocast area is 0.16, one of the lowest in the sample, and it is an example of the grade of encephalization and neocorticalization in most Paleocene mammals.

Three Dimensional Analysis: Olfactory Bulbs

The three-dimensional quantitative analysis of neocorticalization reported here supplements but does not entirely replace the 2D analysis. It omits the olfactory lobes, which could

not be measured reliably on too many of the fossil endocasts. There were obvious artifacts in many of them in the representation of olfactory bulbs. In preparing plaster endocasts from a skull the

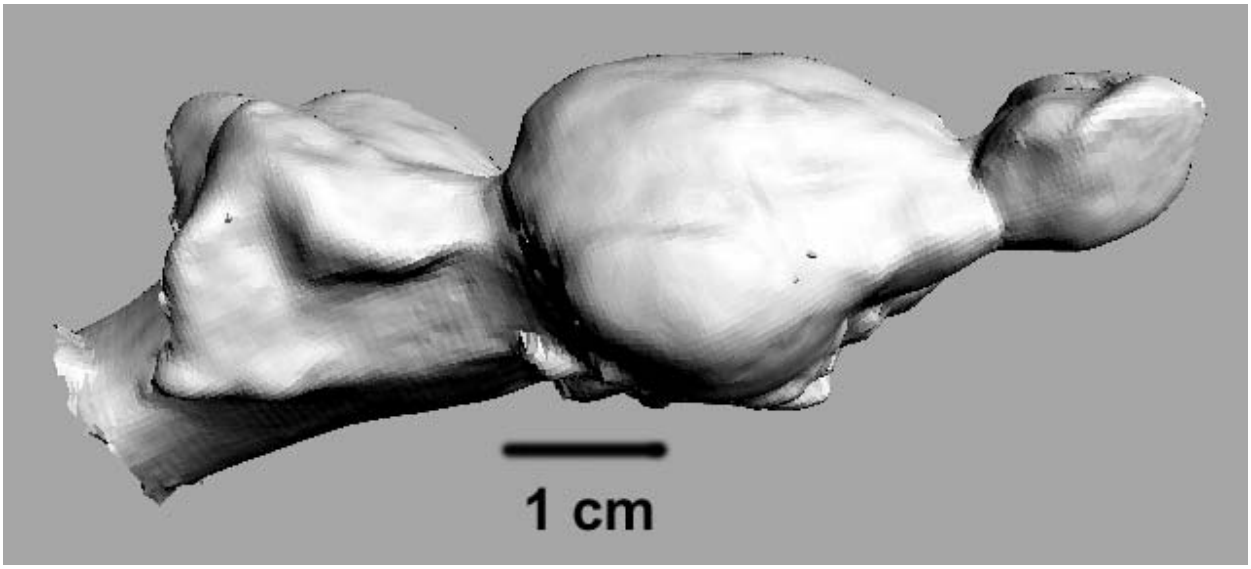

Figure 9. Endocast of *Phenacodus primaevus* (FMNH 59042/AMNH 4369), a late Paleocene archaic holarctic species (58mya).

region of the olfactory bulbs is cleaned out, and it is easy to make mistakes. The cribiform plate and the region of the turbinals is sometimes been excavated, resulting in artificially enlarged bulbs. In others, the olfactory bulbs may be incompletely excavated in preparing latex endocasts. Many natural endocasts, unlike the *Bathygenys* endocast illustrated in Figure 5, are also obviously distorted in the region of the olfactory bulbs. There were enough uncertainties in the sample of endocasts that were scanned for this chapter to make it inappropriate to present 3D data on the olfactory bulbs without further study. Olfactory bulbs in the 2D analysis were all sketched by neurobiologists familiar with normal living brains, who used that information in their reconstructions (see Jerison, 1990)**.** The sketches were all published prior to the later quantitative analysis, and the areas in the 2D analysis were measured independently of the sketching. The result that showed no change in the relative size of the olfactory bulbs was unexpected and unanticipated. Clearly unbiased, the conclusion of the 2D analysis can be accepted at least provisionally, namely that the relative size of the olfactory bulbs remained more or lessy unchanged during the Cenozoic.

The evidence of the reduction of olfactory bulbs in primates and cetaceans is from comparative anatomy. The fossils suggest that their reduction in primates occurred after the Oligocene, when *Aegyptopithecus* lived; Radinsky's (1979) sketches indicate olfactory bulbs in *Aegyptopithecus* that were comparable to those in fossil prosimians (Cf. *Adapis* in Figure 2) and relatively larger than in later anthropoid species. In Miocene and Pliocene anthropoids the olfactory bulbs appear as reduced as in living species, and australopithecine olfactory bulbs are reduced comparably to those of living chimpanzees and humans. Fossil data on cetaceans were reviewed in Jerison (1973) and indicate either reduced or completely absent olfactory bulbs.

Caveats and Conclusions

Neocorticalization occurred in many lineages, and there appeared to be some increase in all mammal species after the Paleocene epoch. The overall increase is evident in the positive slope of the regression lines of the neocortical ratio on geological age. The increase was most dramatic in primates, where it is evident in the earliest record of their brains in the Eocene epoch, but even in "primitive" living marsupials such as the koala (*Phascolarctos cinereus*) neocorticalization to the extent of 30% of the endocast surface is in advance of the Paleocene grade of the archaic *Phenacodus*.

The second conclusion is about the diversity of neocorticalization. The range between 30% in the living marsupial koala and 80% in living humans and langurs suggests the variety of niches for which neocorticalization could be selected. When I published the 2D data fifteen years ago I thought that the correlation of 0.7 between geological age and neocorticalization and the scattered points in its graph (Figure 6) might be due to inadequacies of 2D measurements. The better method for determining and measuring surface area, and the larger sample for the measures in Figures 7 and 8, indicate that the variability is real and reflects the true diversity of adapations for neocorticalization in mammals.

The third conclusion which also verified the 2D analysis indicated that neocorticalization contributed to fitness. The evidence is in the fates of archaic species, which were on the average less neocorticalized than progressive species. This kind of conclusion may seem obvious and hardly worth special mention, but it is difficult to find reasonable evidence for the fitness of quantifiable traits that evolved to different extents in different taxa. The unusual history of the olfactory bulbs in mammals is as instructive as that of the neocortex. On this trait living anthropoid primates (including *Homo sapiens*) are a "degenerate" order, and one can interpret the reduction in their olfactory bulbs as evidence of the relative unimportance of olfactory information in their lives. Stasis in the evolution of the olfactory bulbs is presumably the norm, and if primates had been included in the 2D analysis their degeneracy might have been clearer. But humans write the histories, and in our accounts of the history of the brain, large olfactory bulbs have erroneously been taken as a sign of primitiveness rather than normality. Olfactory bulbs, large or small, are adaptive to specialized niches.

The final caveat is to be wary of conclusions based on endocasts rather than brains and to be wary of conclusions based on externals rather than on the fundamental structure and function of the brain. On the other hand, conclusions based only on the fundamentals have to follow a cladistic analysis of data on living species, comparing apparently homologous traits and taking into account their differentiation in different living species. Johnson (1990) has reviewed cladistic analyses of neural evolution, and there have been several other important publications on phylogeny, which were cited in the opening paragraphs of the chapter. The conclusions based on endocasts and limited to externals, provide a time dimension for the brain's evolution and broadly date the events.

I have emphasized the place of endocasts as providing direct evidence on the evolution of the brain and that the relevance of the evidence comes partly from relationships between superficial data such as brain size and more fundamental measures of the brain's structure and function. Figure 3, showing the relationship between the gross size of the brain and the extent of its cortical surface area, is a good example of the approach, illustrating a likely relationship

between the gross measure of the brain itself and neural information processing capacity. In that graph the dependent variable was total cortical surface, including surfaces buried in the fissures. For a closer look, consider Figure 10, which graphs the measured surface area of endocasts rather than brains as a function of their volume. Although the relationship is equally strong for brain measures and endocast measures in which cortex buried in the fissures is not measured, the difference between the slopes on logarithmic coordinates (the allometric exponent) is instructive.

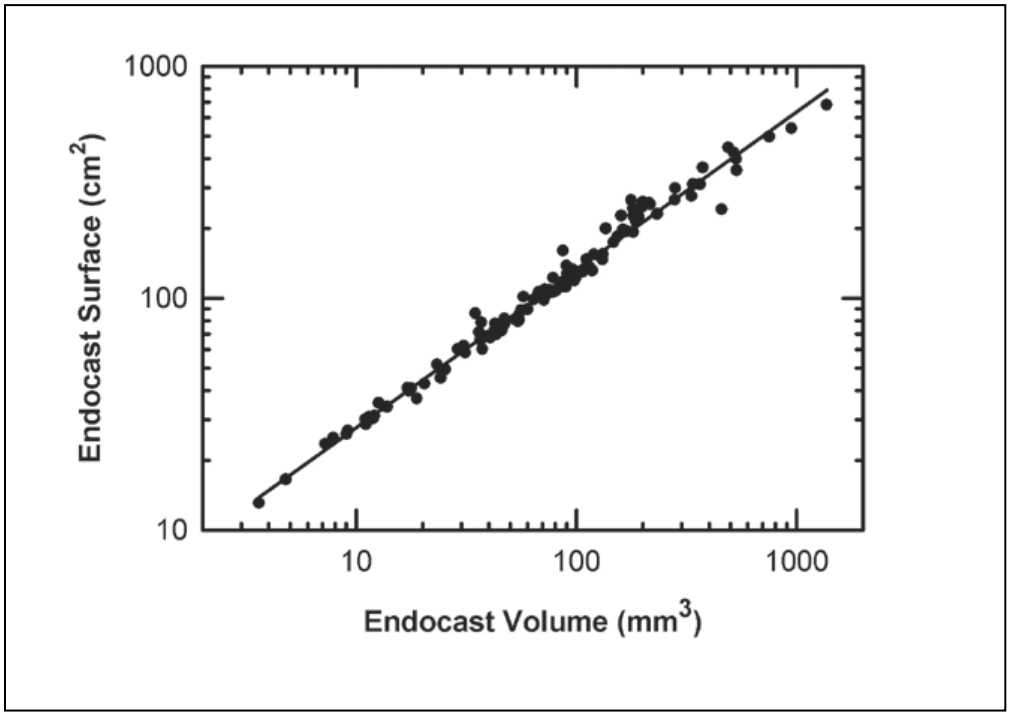

Figure 10. Surface-volume relations in endocasts as measured in the sample of 106 species used in the 3D analysis. Product-moment correlation, r = 0.992; regression, $Y = 5.8\ X^{0.68}$.

In the endocasts (Figure 10) the slope is about 2/3rds, which is the expected relationship among similar solids of different size. For example, in graphs of the surface-volume relationship in spheres of different size the slope is exactly 2/3rds, as it is in cubes or any other solid object of any shape if shape is conserved as size changes. In an equation like Eq. 1, $\underline{\alpha} = 2/3$ for a given solid, and the differences among solids are in the parameter $\underline{k}$. Regardless of their sizes, for all spheres, $\underline{k} = 4.84$; for all cubes, $\underline{k} = 6$. Figure 10 tells us that our endocasts were more alike in shape than we might have guessed at least with respect to this aspect of their geometry. Figure 3, on the other hand, tells us that had we been able to work with the brains of these fossils rather than their endocasts we should have expected convolutedness to increase as volume increased, that is, that convolutedness would be greater in larger brains. The change in convolutedness is reflected by the exponent $0.91 > 2/3$. That information is lost in working with endocasts. The high correlation coefficients save the day for a uniformitatian view. They indicate that the surface areas of portions of the neocortex buried in the sulci and fissures are also related in an orderly way to brain or endocast size. It is, therefore, likely that like actual brain surface area, the surface area of endocasts also estimates information processing capacity.

Acknowledgment

Assembling and interpreting the data presented in the chapter and reviewing the relevant literature was possible only with the help of too many friends and colleagues to list, but I have to name some of them while absolving them from blame for errors and misintepretations that may be present in this chapter. On the fossil materials I must thank Bill Simpson and Bill and Hedy Turnbull for more help than I can easily describe when I scanned many of the endocasts in the Radinsky Collection at the Field Museum of Natural History (FMNH) in Chicago. Dean Falk of Florida State University, María Teresa Dozo of CONICET in Argentina, Eric Delson of the American Museum of Natural History (AMNH), and Bob Martin of FMNH provided important endocasts for the analysis. I had help on systematics from Susan Bell and Tom Rothwell of AMNH; the UNITAXON computer program of Douglas McKenna of Mathemaesthetics in Colorado made checking taxonomic matters easy. On the neurobiology in this chapter I thank Bill Hodos of the University of Maryland, Jack Johnson of Michigan State University, Harvey Karten of the University of California at San Diego, Robert Miller of the University of Otago in New Zealand, Almut Schuez of the Tuebingen Max Planck Institute in Germany, and Wally Welker of the University of Wisconsin. I also thank Phil Dench of Headus/Metamorphosis in Australia and Gene Sexton of Cyberware, Inc. in California for their help with the hardware and software used in the 3D analysis. The research reported here was begun on a Fellowship at the Hanse-Wissenschaftskolleg (Institute for Advanced Study) in Delmenhorst, Germany, and I am grateful to that Institute for the support. I learned to use the 3D scanner there. The list is not complete, because I communicated with many colleagues via the internet, and that marvelous modern technology for fascilitating worldwide communication must also be acknowledged.

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