# Fossils, Brains, and Behavior

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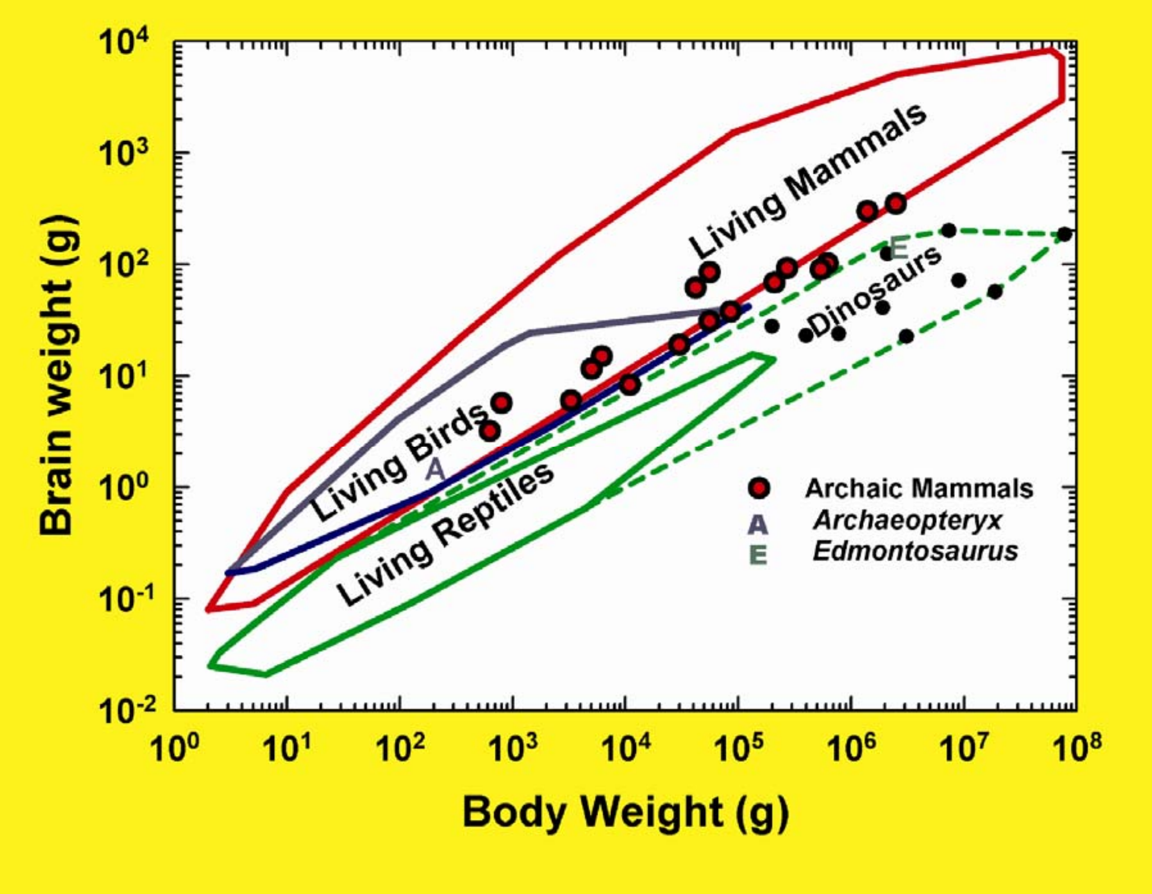

**Figure 1. Brain-body relations in amniotes. Convex polygons enclose data on living mammals (N=647), birds (N=219), and reptiles (N=59). Additional data points for 17 fossil archaic mammals, the late Jurassic bird, *Archaeopteryx*, and 13 dinosaurs including the Late Cretaceous duckbill, *Edmontosaurus*.**

Fossils tell a simple story about the evolution of the brain, much of which is summarized in Figure 1. This graph introduces my topic and summarizes many of my results. My data are morphological with only hints about behavior, but they show results on fossil species in the context of the present diversity of amniotes. The story of brain evolution is told by fossil "brains" (endocasts of the cranial cavity), comparing their size with those of living brains in living animals and judging the evidence of encephalization.

There is first the problem of scale as shown by the axes of the graph. The measurement of brains and bodies is first of all of size, and the proper scale is usually logarithmic. The centimeter-gram-second system is conventional for this analysis, and it is used here. Log scaling is correct for biological size in vertebrates, because their organs and bodies, including the brain, grow by cell division. The scale should feature the fact that successive changes in size reflect doublings in the number of cells, and the sequence of sizes might be 1,2,4,8,16 units, etc. Transformed to log-to-the-base 2, this sequence is 0,1,2,3,4, etc. Log transforms all work this way. Natural logarithms of the sequence to the base *e* are 0, 0.7, 1.4, 2.1, 2.8. etc. With log-to-the-base 10, as in the scaling in this report, that sequence is 0, 0.3, 0.6, 0.9, 1.2, etc. It is convenient to create log-transforms of linear measures by graphing one's data directly on log-log coordinate axes.

Linear and logarithmic scaling for the data on living reptiles is compared in Figure 2. The reptile data are the same as presented in Figure 1, which are from Platel (1979). They were chosen because the small but representative sample of 59 species makes for a simple graph. A regression line appropriate to this and other sets of data on vertebrate classes is linear on log-log coordinates:

$$\log E = \alpha \log P + \log k \qquad (1)$$

The parameters $\alpha$ and $\log k$, which are the slope and intercept of the regression line, are the exponent and multiplier of a power function, the brain-body *allometric* function for living vertebrates. That allometric function is

$$E = k\, P^{\alpha} \qquad (1a)$$

For the data in Figure 2, $k = 0.02$, $\alpha = 0.53$.

## Data Analysis

The initial analysis after collecting data on brain and body sizes is the simple description of the empirical relationship between brain and body size. The contrast between graphing on a linear versus a logarithmic scale is evident in Figure 2. A regression "curve" for the power function could be fitted to the upper graph, but adds little useful information for further analysis.

The convex polygon of the lower graph provides an adequate picture of the diversity of brain size in living reptiles. Most living reptile species are small; median body weight in the population of 59 species was 64 grams, and median brain weight was 0.17 grams. One can verify the median values by counting points and finding the coordinates of the median (29th) point. The information about allometry and diversity is adequately conveyed by the orientation and thickness of the convex polygon.

Perhaps the most useful thing about calculating the coefficients of the linear regression equation is to show the instability of this empirically determined allometric exponent for characterizing the amniotes. As we have seen, the allometric exponent in these reptiles is $\underline{\alpha} = 0.53$. For the 647 species of mammals in Figure 1, $\underline{\alpha} = 0.74$. Regression analysis of the data on 219 bird species showed $\underline{\alpha} = 0.59$.

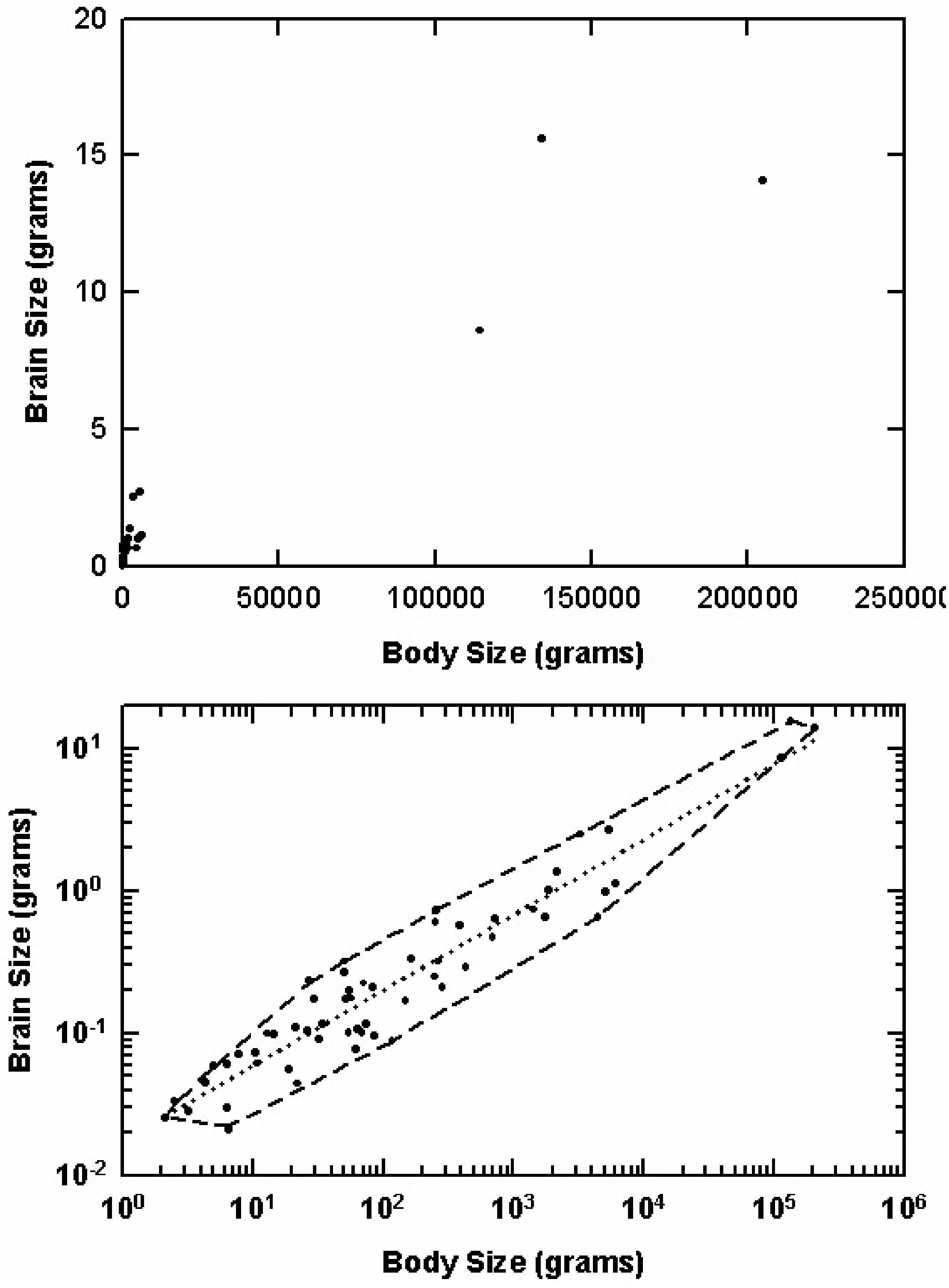

**Figure 2. Brain-body relations in living reptiles (Platel, 1979). Linear scaling above and logarithmic scaling below on the same data on 59 species. The convex polygon in the lower graph is the same as shown for living reptiles in Figure 1. The regression as a power function (Eq. 1a.) is $E = 0.02\ P^{0.53}$; correlation coefficient, $r = 0.95$.**

Theorizing about a "true" value of $\alpha$ in amniotes is problematic if one begins with regression equations. Convex polygons without parameters convey the basic information and do not require the misleading assumptions inherent in regression analysis. We learn that the orientation of the polygons is similar in these classes of amniotes. In addition the polygons indicate that living birds and mammals are similar in encephalization and more encephalized than reptiles. When fossils are added one can see how fossil species are related to their living relatives.

The brain and body weights in the living species represented in Figure 1 are from various sources that I have assembled over the years. Many of the data are also in Nieuwenhuys, ten Donkelaar, H.J. & Nicholson, C. (1998), Platel (1979), Quiring (1950), and Worthy & Hickie (1985). The data on reptiles (N=59) were shown in detail in Figure 2 to illustrate logarithmic as opposed to linear graphs and to contrast the regression analysis with analysis with minimum convex polygons. The convex polygons in Figure 1 enclose data on living mammals (N=647), birds (N=217), and the same reptiles as in Figure 2. Individual data points on living species are omitted for the sake of clarity. The fossils shown individually are archaic mammals from Jerison (1973), and the dinosaurs and *Archaeopteryx* from Hopson (1979) and Jerison (1973). The data point for the dinosaur *Edmontosaurus* is from Figures 3 and 4.

When the dinosaur points were added to Figure 1 it was clear that they could be placed most naturally within an enlarged reptile polygon rather than in an extended avian polygon. *Archaeopteryx* (Figure 5, below) was at the lower edge but within the avian polygon. Although it is evidence on only a single specimen it suggests that encephalization, that is, the enlargement of the brain, is an avian trait not shared by the 13 dinosaurs on the graph (see also Jerison, 2004). The 17 fossil "archaic" mammal points are from Jerison (1973) and are species that are members of orders of mammals that are now entirely extinct. They are more encephalized than either reptiles or dinosaurs but less encephalized than most living mammals. Their data are scattered about the lower edge of the mammalian polygon.

## The Fossils: Dinosaurs

Brain size in birds and mammals can be estimated directly from their endocasts, which are casts of the cranial cavity, because the endocasts are like brains in size and shape. They look like brains with dura intact. In reptiles and in nonavian dinosaurs, the brain fills only about half of the available space in the cranial cavity, hence brain size is conventionally assumed to be some fraction of the endocast volume. Perhaps one or two thousand fossil endocasts are available (Edinger, 1975). Most have been prepared by cleaning the skull and making plaster endocasts, but a fair number have been found as natural endocasts. These were prepared by nature. The *Edmontosaurus* endocast in Figure 3 is such a natural endocast.

The natural endocast of this hadrosaurian ("duckbill") dinosaur was probably made when the animal died near the end of the Cretaceous period 66 million years ago. Here is probably its story. Its cadaver lay in a stream or lake bed, and its soft tissue was removed by scavengers, but most of its skull was left intact. Its cranial cavity then had to be filled, packed hard by mud and other debris, and then buried under sediment and left to fossilize. Relatively recently the fossil had to be exposed and skull weathered away. The fossilized contents of the skull, were presumably more resistent to weathering and were exposed as a natural endocast. It was discovered by Rev. Ken Olson, working with Dr. Jack Horner of the Musuem of the Rockies in Montana.

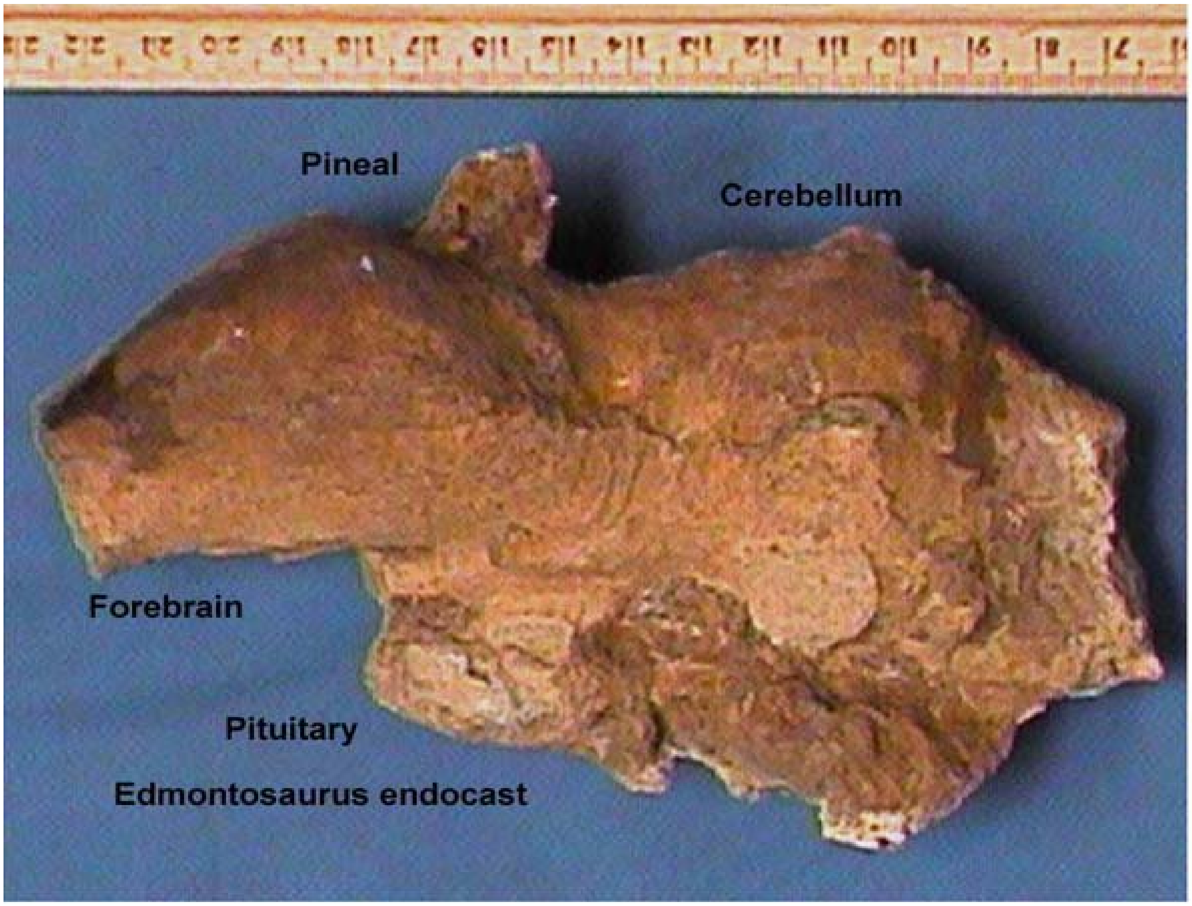

**Figure 3. Natural endocast of *Edmontosaurus*, a Late Cretaceous duckbill dinosaur from Montana. The cast preserved impressions of the pineal and pituitary regions and non-neural matrix about midbrain and hindbrain. Forebrain is probably correctly represented except in the anterior end, where the connection of olfactory bulbs and olfactory tract to forebrain is obliterated. Posterior to forebrain, the midbrain, cerebellar and medulla regions are not distinct, presumably masked by supporting tissue and fossilizd debris that had been cast as brain when the specimen fossilized. (Specimen MOR 639 from the Museum of the Rockies, photographed and reproduced by permission.)**

The whole *Edmontosaurus* endocast measured 374 ml in volume. Working from a digitized image it was possible to “dissect” and remove from this virtual endocast various portions that are not normally included in measurements of brain volume. These included the pineal protrusion, actually a cast of a hole in the skull through which the pineal sometimes extends to a cyclopean eye. It did not extend through the skull in *Edmontosaurus*, indicating that such an eye was absent. The hypophseal region, which would have contained the pituitary gland and stalk were also removed by virtual dissection as were other structures that were not part of the brain proper. The effect was to reduce probable brain size to 175 ml or 200 ml, a not unusual range of "error" for measuring dinosaur endocasts as brains.

Estimating body size can be more difficult. In mammals one is often reduced to estimates based either on whole body length or measurements estimated from the cross-sectional area of the femur or the foramen magnum (Alexander, 1997, cf. Jerison, 2001). The best approach is to work from model reconstructions and then to scale the measurements appropriately. I estimated the size of *Edmontosaurus* by scanning a model that Dr. Jack Horner of the Museum of the Rockies considered a reasonable reconstruction of the animal in life. The model is shown in Figure 4. Scaled up appropriately, it indicates that *Edmontosaurus* weighed about 6 tons, the weight of a heavy elephant. There was comparable precision in all of the dinosaur measurements. For more on dinosaur brain-body allometry see Jerison (1973) and Hopson (1979).

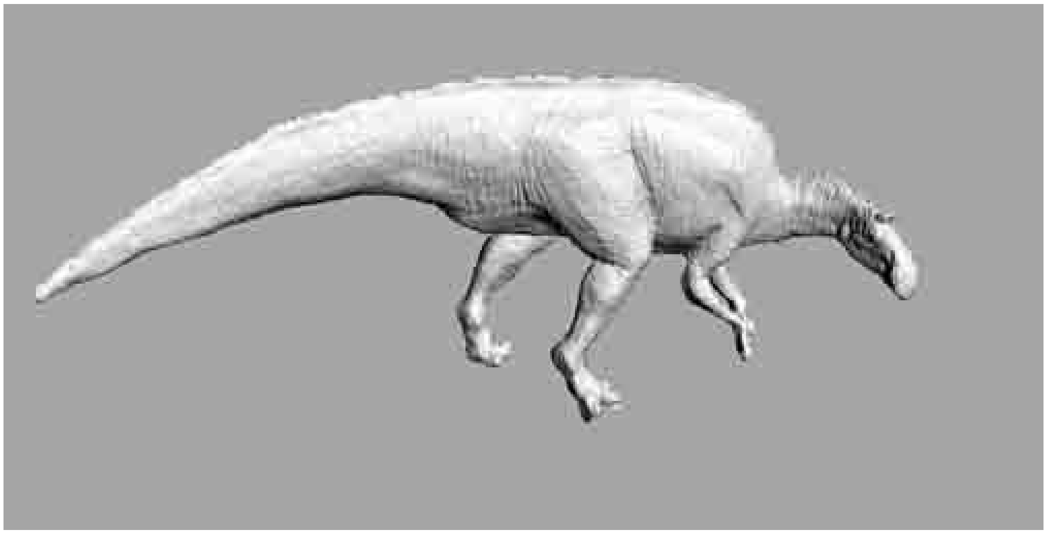

**Figure 4. Model hadrosaur for estimating the size of *Edmontosaurus*, which was about 10 meters long. The model as scanned was 22 cm long and had a volume of 66 ml. Scaling up to the size of *Edmontosaurus* = $(1000cm/22cm)^3$ x 66 ml = 94,000 x 66 = 6.2 metric tons.**

## The Fossils: Birds

The earliest bird, the Late Jurassic *Archaeopteryx* of about 150 mya (million years ago), is one of three fossil species in my sample. I also discuss an Eocene curlew (about 40 mya), *Numenius gypsorum*, and an as yet unnamed Miocene raptor (about 15 mya). The least encephalized of the fossil birds, *Archaeopteryx*, is avian in encephalization and lies within the living avian polygon of Figure 1, albeit at its lower margin. It was not possible to estimate body size in the other two fossil birds, but from comparisons with living species they are almost certainly avian in encephalization, above the minimal grade.

Birds as a class are presently viewed as small feathered dinosaurs that survived the great extinctions at the end of the Cretaceous 65 million years ago. The diagnosis is based on overall morphological features, which also distinguish dinosaurs from living reptiles (Farlow & Brett-Surman, 1997). The evidence of the brain is contrary to this consensus. With respect to brain size all birds are nonreptilian, whereas the nonavian dinosaurs are reptilian in this feature. It is commonplace in evolutionary thinking to recognize that distinctions are based on a mosaic of traits. The traits that distinguish birds and dinosaurs from reptiles are a mosaic of this kind, but relative brain size (encephalization) is not among them.

The evidence is that there was progressive evolution of the brain in birds, limited as it is to the small sample reported here. The evidence from the three species that provide measurable data is fairly convincing. The forebrain became relatively larger from the Mesozoic grade of *Archaeopteryx* to the Eocene grade of *Numenius*. There appears to have been additional encephalization in the transitions after the Eocene epoch. One can compare the endocasts of the Eocene fossil with a Recent relative, *Numenius tahitiensis*. The evidence is in the extent that the optic lobes (superior colliculi) are exposed. As the forebrain becomes enlarged the optic lobes are less visible on the surface of the endocast. There was relatively more forebrain in the Recent curlew than in its Eocene relative of 40 mya. The data are in Table 1 and illustrated in Figure 4.

## Table 1

## Optic Lobe Exposure in Birds

| Species | Endocast vol ml | Endocast surface mm$^2$ | Forebrain (fb) surface mm$^2$ | Optic Lobe (ol) mm$^2$ | ratio ol/fb |
|---|---|---|---|---|---|
| *Archaeopteryx* (150mya) | 1.5 | n/a | 137.4 | 72.0 | 0.52 |
| *Numenius gypsorum* (40 mya) | 2.7 | 1130.7 | 526.5 | 181.3 | 0.34 |
| *N. tahitiensis* (Recent) | 3.0 | 1272.4 | 776.6 | 126.1 | 0.16 |
| Miocene raptor (15mya) | 8.4 | 2380 | 1379.2 | 216.8 | 0.16 |
| Albatross (Recent) | 27.3 | 5820.1 | 2858.6 | 366.0 | 0.13 |
| Ostrich (Recent) | 31.0 | 6175.7 | 3314.9 | 548.9 | 0.17 |

Note.- The complete endocast was not exposed in *Archaeopteryx* and could not be measured.

The quantitative evidence is in the ratio of the visible surface area of the optic lobe to that of the forebrain, ol/fb in Table 1. The decrease in exposed optic lobe area indicates encephalization. The decrease is most dramatic in the comparison of *Archaeopteryx* with living birds, but it is also evident within the related curlews, the Eocene *Numenius gypsorum* compared with the living *Numenius tahitiensis*. I do not have a diagnosis or body size estimation on the Miocene raptor but could measure the endocast (J. Mlikovsky, personal communication). It was comparable to living raptors in brain size.

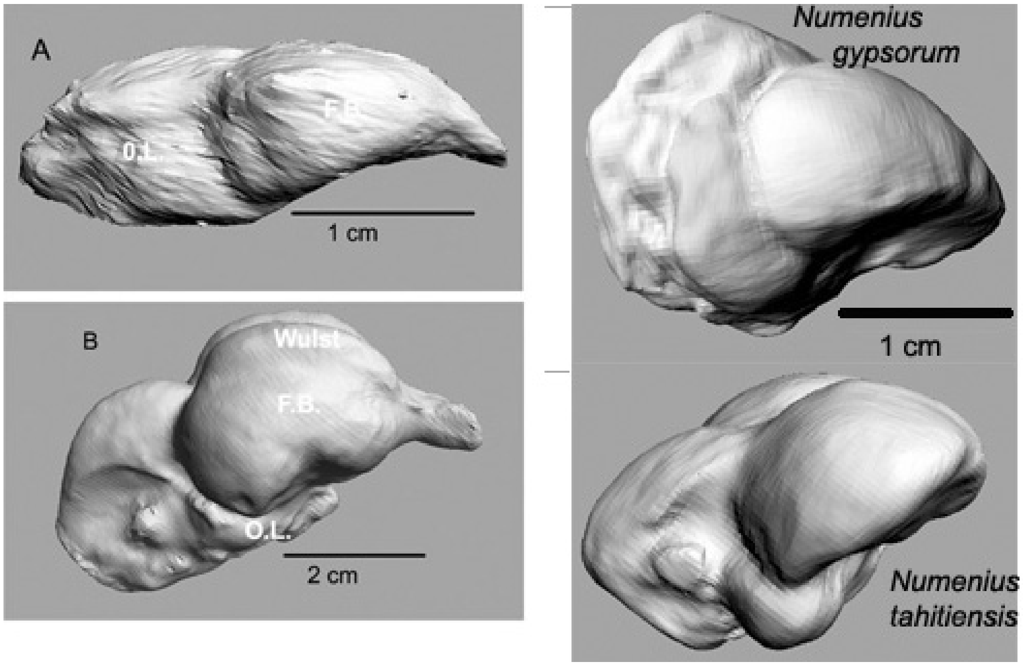

**Figure 5. Endocasts of four species: At left, (A) Archaeopteryx , Late Jurassic, about 150mya (B) Albatross, *Diomedea exulans*, Recent. Labels: forebrain (F.B.), optic lobe (O.L.), Wulst present only in Albatross. At above right, *Numenius gypsorum*, Late Eocene, about 45 mya. No Wulst is evident. Lower right, *Numenius tahitiensis*, Recent; Wulst is present but small and not well shown in photograph.**

Figure 5 shows digitized images of the endocasts of four of these birds. The Miocene raptor endocast resembled that of *N. tahitiensis*; the ostrich (*Struthio*) resembled that of the albatross (*Diomedea*). Optic lobes were easily distinguished from other structures on these endocasts. The measurements in Table 1 are all from digitized images prepared by a Cyberware laser scanner and analyzed with their software (http://www.cyberware.com). Despite their differences in absolute size, one can compare the dinosaur endocast in Figure 3 with that of the birds in Figure 5 to get a sense of the encephalization in birds.

One feature of the evolution of the bird brain is the evidence of the Wulst. This appears in endocasts as a dorsal enlargement, a bump, on the forebrain. Its size varies in living species, hardly evident at all in the endocast of *Numenius tahitiensis* but dramatically evident in the albatross endocast. It was evident in the Miocene raptor and is comparable in the ostrich to that of the albatross. It is not evident at all in the endocast either of the earliest bird, *Archaeopteryx* or of the Eocene curlew. In living birds Wulst is often thought of as visual brain, receiving projections from midbrain and diencephalic visual structures and homologous to mammalian visual neocortex. Its enlargement may reflect increased forebrain control of vision, though other functions are also represented there.

The forebrain enlargement as reflected in endocasts, which is specific to the Wulst is not presently understood. It is basically an issue in brain-endocast relations.

The question is: how is an enlarged Wulst in the brain reflected as “Wulst” on an endocast? In mammals the reflection of cortical sulci and gyri in endocasts, which are often impressively similar to their appearance on the brain, is a result of the growing brain pushing up the inner table of the cranial cavity. I have not been able to find appropriate analysis of skull-brain relations to indicate how this would occur in birds. In mammals it is basically an epigenetic phenomenon, and gyrification is, therefore, a questionable morphological trait for evolutionary analysis. It is known to be related to brain growth, which is genetically programmed (Chenn & Walsh, 2002). It is not known whether it is the growth of the brain that generates the configuration of the skull as opposed to independent genetic control of the growth of the skull and cranial cavity. If it is the growth of the brain, then details of the shape of a bird’s endocast are determined epigenetically, by the fact that the brain fills the cranial cavity.

## The Fossils: Mammals

I have scanned 106 mammalian endocasts for this report, including 84 fossil species. The fossils are all Cenozoic, beginning in the Paleocene, about 60 mya and ending with Plio-Pleistocene australopithecines. My data on 22 living (Recent) species are mainly on primates. A number of Mesozoic endocasts have been described (Kielan-Jaworowska, 1986), which are too small to be measured by my scanning system. The record on mammals is much more extensive than that of the 13 dinosaurs and six birds that I have reported, and it enables us to examine conclusive evidence of neocorticalization in addition to the evolution of encephalization within mammals. Most of the mammalian endocasts look like freshly dissected brains. A few are shown in Figure 6, which includes a sketch of the endocast of *Bathygenys reevesi* to indicate significant landmarks visible on most mammalian endocasts. The landmarks separate the indicated structures, for example, the rhinal fissure separates neocortex from paleocortex.

The endocast of *Bathygenys* is a natural one. The other two are snapshots of virtual images as scanned by my system. (I have a virtual endocast of *Bathygenys*, which I used for measurement but do not show its snapshot. The natural endocast is unusually well preserved, showing a few fragments of fossil skull.)

*Bathygenys* was an even-toed ungulate (Artiodactyla), a very small oreodont (about 5 kg estimated body weight) that lived at the end of the Eocene, 34.7 mya. Its fossil beds on the Rio Grande River are “Chadronian,” and date the end of the Eocene epoch of the Cenozoic period distinguishing it from the Oligocene. There were several dozen endocasts of *Bathygenys* in the fossil bed, each about 10 ml in volume. *Merycochoerus* was a very large (about 120 kg) Miocene oreodont that lived about 17.5 mya and had a 96 ml endocast. This is not an ancestor-descendant relationship, although the two species represent grades of encephalization and increases body size within the family of oreodonts, the Merycoidontindae. The evolutionary trend to enlarged body size has been called “Cope’s Law,” and has been recognized in many taxa, including the equids.

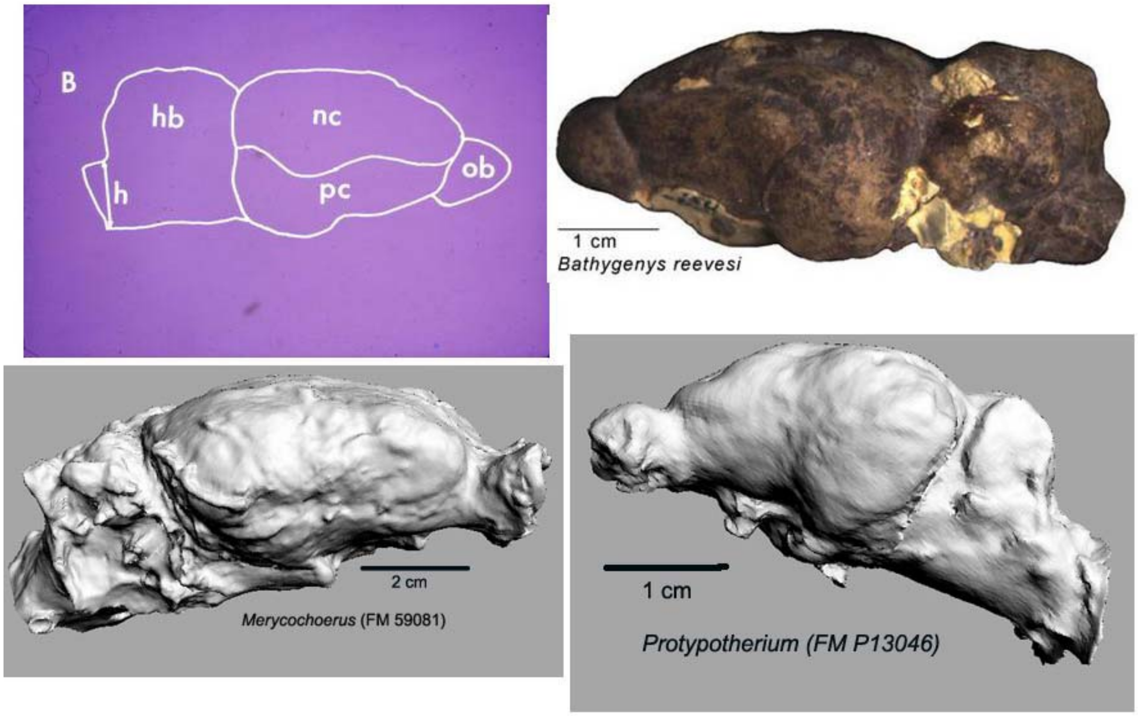

**Figure 6. Endocasts of three fossil mammals, *Bathygenys* (35 mya), *Merycochoerus* (17.5 mya), and *Protypotherium* (17.5 mya), with an outline sketch (B) of *Bathygenys* showing several brain regions. Areas are olfactory bulbs (ob), neocortex (nc), paleocortex (pc), and the height (h) of the foramen magnum, which is related to the height of the medulla.**

The third species in Figure 6, *Protypotherium*, is a Neotropical notoungulate, is about the same age as *Merycochoerus* (17.5 mya). Representative fossils of the order were among those found by Charles Darwin on the voyage of the Beagle (http://www.aboutdarwin.com/voyage/voyage04.html). The notoungulates are entirely extinct, and *Protypotherium* is, therefore, one of the “archaic” mammals graphed in Figure 1. “Archaic” and “progressive” are arbitrary categories, reflecting only the extinction of the major taxon towhich a species belonged.

We do not know why particular groups became extinct, but the usual view of the extinction of South American (“Neotropical”) mammals is that it resulted from the reestablishment of the isthmus of Panama in the Pliocene (3 - 4 mya). This permitted the migration of better adapted North American (“Holarctic”) species to South America, and many were better adapted than native species to the available niches. *Protypotherium* was fairly small, estimated as about 6 or 7 kg, and was probably rabbit-like or rodent-like in its adaptations. Although its endocast indicates a relatively small brain it was larger brained, more encephalized, than *Bathygenys*, which is a “progressive” species by our criterion, because many there are many surviving artiodactyls (sheep, cows, hogs, etc). The point is to recognize the arbitrariness of the categorization. We know that archaic species were, on the whole, less neocorticalized than progressive species in comparable niches (Jerison, 1990, 2006b).

In the three species illustrated in Figure 6, and in all the other mammal species that I scanned, gyri and sulci visible on the surface of the endocast were clear enough to show the rhinal fissure. This is a fissure that separates neocortex from paleocortex and is drawn on the sketch of *Bathygenys* (**B** in Figure 6). It does not show up as well as one would hope in the photograph of the endocast, but one can trace it at the dorsal margin of the olfactory bulb and tract as these enter the cerebrum proper. In any case, this fissure provides a clear boundary separating neocortex from paleocortex, and one can measure neocortical surface area of the endocast as dorsal to the fissure.

Measuring surface area is one of the capacities of software developed for analyzing laser scans of endocasts; one marks the area to be measured. What had been an extremely difficult, often impossible, exercise when working with irregular solids such as endocasts, has become a quick and easy job with the digitized image. My hardware and software for scanning is described on the internet at <http://www.cyberware.com>.

The idea of neocorticalization, that is, the increase in size of neocortex in some species, is essentially the idea that more of the brain is occupied by neocortex. It is, therefore, natural to measure neocorticalization by measuring the ratio of the surface area of neocortex to the whole surface area of the brain. Working with endocasts is easier than working with brains, because one measures only areas visible on the endocast. The results of the analysis of neocorticalization are shown in Figure 7.

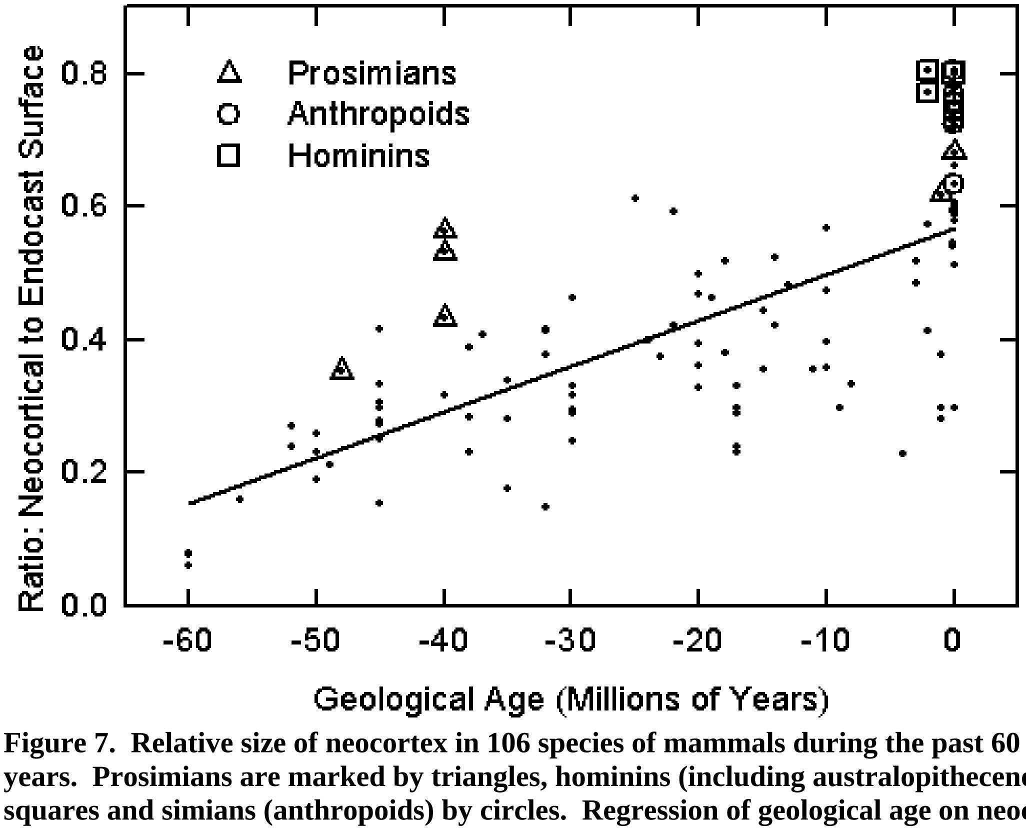

**Figure 7. Relative size of neocortex in 106 species of mammals during the past 60 million years. Prosimians are marked by triangles, hominins (including australopithecenes) by squares and simians (anthropoids) by circles. Regression of geological age on neocortical ratio: Y = .007 X + 0.57; r = 0.72.**

Because, as primates, we all have a special interest in primate brain evolution, I have marked data on the major primate taxa in Figure 7, to distinguish neocorticalization of prosimians, anthropoids, and humans from that in other mammals. Primate classification has become much more complex during the past decades (McKenna & Bell, 1997), but the basic interest is in the first appearance of differentiation of the major groups in geological time. The earliest primates were related to living prosimians, that is lemurs and tarsiers, and are known from the Paleocene. Their endocasts are known from throughout the Eocene (55 mya - 40 mya). Anthropoid primates appeared at the end of the Eocene, but the earliest endocast, of *Aegyptopithecus,* is Early Oligocene, about 30 mya. It is an oddity of the fossil record that *Aegyptopithecus* could be ancestral both to living monkeys and to living apes, but its endocast was more similar to that of prosimians than to anthropoids. In and case, the quantitative analysis of neocorticalization (Figure 7) shows that primates have been more neocorticalized than average mammals throughout their known history. It must have been encoded in our genome for at least the 55 million years of the known fossil history of the primate brain. A more complete analysis of the fossil evidence of the evolution of neocortex is in Jerison (2006a, 2006b).

Figure 7 shows that there has been an overall trend in all the mammals toward neocorticalization during the Cenozoic era. The evidence is the positive slope of the regression line in Figure 7, which indicates an average increase in neocorticalization of about 7 per cent per 10 million years. The relatively low correlation of neocorticalization with geological age and the scatter of data-points about the regression line is evidence that mammal species have been markedly diverse in this trait. Primates as a group have been more neocorticalized than other orders of mammals, with about 75 to 80 per cent of the surface of the endocast accounted for by neocortex. The most neocorticalized of the primates in my sample was a mangabey (*Cercocebus albigena*), which was slightly more neocorticalized than one of the humans at about 80.4 percent relative to 80.1 per cent. A second human had 77 per cent of its endocast identifiable as neocortex, about midway among my living anthropoid primate sample. Differences among living primate species in my sample were small, and we humans are not unique.

There are more details in two other reports (Jerison, 2006a, b). “Enlarged” olfactory bulbs, frequently treated as a primitive mammalian trait is not primitive. It is the mammalian norm. Unlike neocorticalization, which increased with geological age, there was stasis in the relative size of the olfactory bulbs in the mammals as a whole (Jerison, 1990). The odd trait is the reduction of olfactory bulbs that has occurred in primates. (It is perhaps even more odd that olfactory bulbs may have completely disappeared in some cetaceans.)

On neocorticalization, archaic species were less neocorticalized than progressive species. Marsupials are less neocorticalized than placentals. The least neocorticalized of the living species in my sample is marupial koala, with less than 30 per cent of its endocast and brain taken up by neocortex. This grade of neocorticalization is higher than that of the earliest mammals in which less than 20 per cent of the endocasts consisted of neocortex. There is an important lesson in the diversity of neocorticalization as an evolutionary trait, which should not be overlooked. In general the amount of neocortex in a species is more likely to be related to brain specializations appropriate to behavioral demands of a species rather than some broad idea of animal intelligence and its evolution.

## Fossils and Behavior

There is fossil evidence beyond the brain. Among the most interesting are fossil eggs of dinosaurs. Horner and Gorman (1988) describe their discoveries of some of these as do several chapters in Farlow and Brett-Surman (1997). It is very likely that at least some dinosaurs tended their eggs in the same ways as many living birds. The fossil eggs have been discovered in small clusters that suggest that they were cared for in ways similar to living birds.

The fossil evidence on behavioral specializations is usually assessed from skeletal information such as the configuration of some joints or the appearance of the teeth. These may be enough to indicate a capacity for arboreal living, grazing, browsing, or carnivory (see Butler & Hodos, 2005; Farlow & Brett-Surman, 1997). They do provide general insights but not into specific behavioral activities and capacities, such as hunting strategies or evasive strategies. They provide nothing like the insight into primate communication that has developed from careful observation of social behavior and foraging in chimpanzees (Goodall, 1986), language-like behavior (Rumbaugh & Washburn, 2003), and warning calls in vervets (Cheney & Seyfarth, 1990).

The most specific recent report relevant to fossil behavior was by Clarke & Tobias (1995) on an issue in human evolution: whether our australopithecine relatives could climb trees. The issue is important for understanding the niche invaded or occupied by the australopithecines, which is usually described as savannah, treeless semi-desert area. If some australopithecine speces were adapted for tree-climbing like living pongids they may not have been under selection pressure for life in the open. This limits the scenarios for selection in hominid, including human, phylogeny.

With such limitations it has nevertheless been possible to demonstrate with fair certainty two patterns of behavior in dinosaurs (Farlow & Brett-Surman, 1997). There is good evidence that some dinosaur species lived or moved in groups, comparably to the way birds and large mammalian herbivores do. Dinosaur tracks (see also <http://paleo.cc/paluxy/ovrdino.htm>) provide the evidence. The paleontological specialty dealing with remnants of behavior as evidence is called ichnology. Fossil eggs are fossils, but they can also be analyzed for evidence on behavior. It has been possible to identify brooding as part of the pattern of egg laying in some dinosaurs. These kinds of behaviors do not require noticeable brain specializations that might be identified in endocasts, and it would be fruitless to expect such insights. It is a matter of speculation, but it may be the case that social hunting in felids and canids can be identified with brain specialization, at least from the neocortical pattern of the coronal sulcus (Radinsky,1973, 1975).

It is problematic to find real insights into the evolution of behavior from the study of endocasts, or “fossil brains.” There are insights, but we should not be too disappointed by their limitations. They are comparable to the limitations on insight from the study of living brains. The great insights come from our ability to correlate what we learn about the brain with our observation of correlated living behavior. From the brain alone we can learn about size and shape. We can also learn about connections within the brain among various localized systems. But we could not understand frontal lobes function or executive functions of prefrontal cortex from morphology alone. That, for better or worse, is our situation with the fossil evidence, which is evidence about the brain but not about correlated behavior. There is speculation, of course.

We rely on the uniformitarian “hypothesis,” that laws of nature have been the same throughout time, to enable us to identify some functions. In cats we identify the region of the ectosylvian gyrus as auditory cortex (not illustrated in this report, but see Jones & Peters, 1990). This gyrus is visible pretty much the same way in Eocene and Oligocene sabretooths (*Eusmilus* and _*Hoplophoneus*, cf. Radinsky, 1975) as in living felids and canids, and we assume that it represents a localized auditory area. When we see a third frontal convolution in a Neandertal endocast (Jerison, 2006a) we assume that it probably represents a motor speech area as it does in living humans. Although we should appreciate their limitations, those are important insights available from the fossil record.

## Summary and Conclusions

Fossil “brains” are casts (endocasts) molded by the cranial cavity. In birds and mammals they are brainlike in size and shape, and they provide quantitative evidence of evolutionary enlargement (encephalization) of the neocortex and forebrain during the past several hundred million years. In other vertebrates the brain does not fill the cranial cavity, and the evidence is not good enough to document evolutionary changes. Among mammals, there has been an average trend toward neocorticalization, greatest in primates and least in marsupials. Olfaction, inferred from the size of the olfactory bulbs, has been reduced in primates (including humans) and cetaceans. There is more evidence not presented here (see Jerison, 2006a, 2006b) that binocular vision became emphasized in primates, which can be inferred from the position of the orbits of the eyes. The Wulst is evident in the endocasts of birds during much of the Tertiary period, the last 50 million years suggesting that vision (and perhaps bird song) became more prominent aspects of the adaptations of the various species. There is behavioral evidence of social behavior (from assemblages of fossils), of brooding behavior (from clusters of dinosaur eggs associated with adult fossils), and of locomotor capacities (from fossil appendages). These are overall trends, with many variations among fossil species just as living species vary. Although encephalization is undoubtedly related to the evolution of “intelligence,” one should keep in mind the remarkable performance of relatively small-brained living species, such as rats and pigeons, in thinking about intelligence as a behavioral capacity.

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