

## Dinosaur Brains

By Harry J Jerison

A dinosaur's "brain" is actually a cast molded by the cranial cavity. Most fossil endocasts are plaster casts made in the laboratory from well-preserved skulls that are carefully prepared and cleaned. There are a few hundred "natural" endocasts, mainly of fossil mammals and occasionally of other vertebrates, which have been collected and are available for study in the back rooms of a few museums of natural history. Endocasts provide a record of 450 million years of the evolution of the brain, beginning with fossil jawless fish related to living lampreys. Endocasts of birds and mammals are remarkably brain-like, whereas in reptiles and other vertebrates the brain incompletely fills the cranial cavity.

A natural fossil endocast is a rare object. Here is what had to happen to make one. An animal had to die under circumstances that allowed the soft tissue to be removed by scavengers without severe damage to the skull. The animal had to have died in a region where debris could enter and be packed tightly into the cranial cavity. The debris had to fossilize along with surrounding skull. Long after fossilization, the stratum in which the composite was deposited had to be exposed by erosion or earth movements. The fossil bone then had to erode, but its hard packing had to remain. The packing of the cranial cavity is then a natural endocast. A lucky fossil hunter might find the endocast, perhaps with a few fragments of fossil bone still attached. Such an endocast, that of *Bathysgenys reevesi*, a mammal that lived 35 million year ago, was illustrated in the article on "Brain Size." A natural endocast of the duckbill dinosaur, *Edmontosaurus*, is shown here in Figure 1.



**Figure 1. Natural endocast of *Edmontosaurus*, a Late Cretaceous duckbill dinosaur (about 70 million years old). Except for the anterior end, forebrain is accurately represented by the endocast. Pineal stalk and hypophyseal fossa also well represented. Midbrain, hindbrain, and foramen magnum (medulla) regions only vaguely suggested and still surrounded by rock matrix.**

*Edmontosaurus* was about 12 meters long and weighed about 6.2 metric tons. (Lower weights have been reported, based on statistical regression analysis in which body size is estimated from dimensions of the femur, but the estimation of 6.2 tons is based on a scale model and is probably more realistic.) The pictured endocast was found in Montana, where the animal died about 70 million years ago; only its fossilized bones and "brain" survive.

A few facts about the brain of this dinosaur can be determined directly from the endocast. The volume of the entire endocast was 374 ml, and the forebrain region was about 135 ml. Although there is

no evidence of a pineal eye (no hole in the frontal or parietal bones of the skull), the pineal stalk was evidently large. Similarly the pituitary fossa was appropriately large to hold a pituitary gland for an animal as large as *Edmontosaurus*. Perhaps most significantly, most of the forebrain region of the endocast is brain-like. The anterior tip where the olfactory bulbs or tract enter the cranial cavity is not brain-like. Hindbrain is less like a brain, though the cerebellar region can be distinguished. Brain does not fill the cranial cavity in vertebrates other than birds and mammals, and the brain-like forebrain region of the endocast is unusual for reptiles.

### Inferences from an endocast about the brain

The volume of the forebrain of *Edmontosaurus* suggests a total brain volume of about 200-ml. This makes it possible to compare *Edmontosaurus* to living reptiles and birds in which relative brain size has been analyzed. Figure 2 graphs all available information on living amniote vertebrates and on most dinosaurs. The datum on *Edmontosaurus* and on the earliest fossil bird, the late Jurassic (150 million years old) *Archaeopteryx*, are indicated by the letters E and A; data on the other dinosaurs are in the legend.

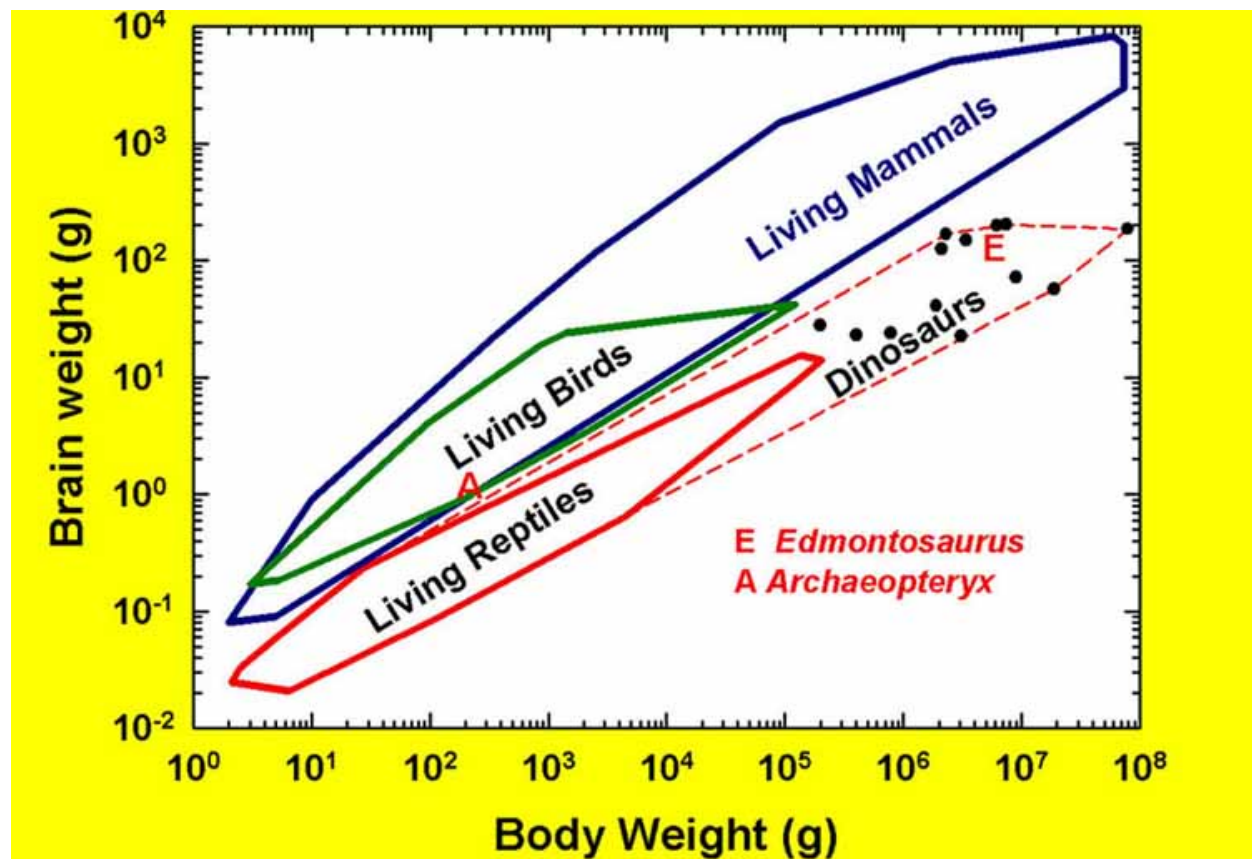


Figure 2. Minimum convex polygons containing presently available data on living amniotes (mammals, birds, and reptiles). Adding data on dinosaurs (red points) suggests an extended reptilian polygon (dashed lines). Earliest bird (*Archaeopteryx*) is at lower edge of living birds. Data on dinosaur genera (estimated body weights and brain weights): *Protoceratops* (200kg/28g); *Camptosaurus* (400kg/23g), *Kentrosaurus* (780kg/24g), *Euoplocephalus* (1,900kg/41g), *Iguanodon* (2,100kg/125g), *Allosaurus* (2,300kg/168g), *Stegosaurus* 3,100kg/22.5g, *Edmontosaurus* (6,200kg/200g), *Tyrannosaurus* (7,400kg/202g), *Triceratops* (9,000kg/72g); *Diplodocus* (19,000kg/57g), *Brachiosaurus* (78,300kg/186g).

Dinosaurs were ancestral to living birds, and many biologists now consider birds as miniaturized surviving dinosaurs with feathers. The comparison with *Archaeopteryx* is, therefore, of special interest. One immediate conclusion from the extended reptilian polygons is that dinosaurs were not unusually small-brained. Their brains were of a size appropriate for reptiles.

According to the graph, *Edmontosaurus* was a relatively large brained extinct reptile, near the upper border of the reptilian polygon. The other dinosaurs added to the graph to extend the reptilian polygon include *Tyrannosaurus rex*, located almost congruent to the *Edmontosaurus* point, also evidently large brained. The heaviest dinosaur added to the graph is *Brachiosaurus*. Its brain was smaller than that of *Edmontosaurus*.

It is instructive to compare dinosaurs with living species. The largest of the living reptiles included in Figure 2 was an alligator weighing 205 kg with a 14-gram brain. Living alley cats weigh about 3 or 4 kg, and their brains weigh about 30 grams, which is about average relative brain size (encephalization) in living mammals. Opossums, which weigh about as much as cats, have brains that weigh about 5 grams. Living opossums are similar in encephalization to the earliest known mammals, including those that were contemporaries of dinosaurs. Archaic fossil mammals (members of extinct orders) all lie at the lower edge of the mammalian polygon. The most encephalized of living birds are crows and parrots. A 1.2-kg raven may have a 15-g brain, and a 1.4-kg macaw has been reported with a 24-g brain. Pigeons, which rival rats as frequent subjects of experiments on conditioning and learning, are relatively small-brained birds. With bodies weighing about 300 grams, their brains typically weigh only about 2 grams. The *Archaeopteryx* point on the graph is an average of several reported sizes, indicating a body size of about 400 grams and brain size of about 1.5 grams. Analogously to archaic mammals, this early bird falls within the avian polygon but at its lower edge.

Data on dinosaur brains have been reexamined in recent years to suggest something about the behavioral capacities of these animals. The basic thrust has been that dinosaurs were more birdlike than reptile-like. There has also been an intriguing report of olfactory specialization in *Tyrannosaurus rex* based on evidence from its endocast. It is instructive to look more closely at these views, for insight into the analytic difficulties.

The new look for dinosaur-bird relations began in the 1970s and '80s, based on cladistic analyses. The method compares species on a large number of traits for judgments on similarities, to prepare likely phylogenetic trees. It has been this evidence that led systematic biologists to conclude that dinosaurs were closer to birds than to reptiles, in effect, that birds are surviving specialized dinosaurs. The new look for dinosaur brains came independently but at about the same time. It is in reports on two large-brained dinosaurs. The author of this article has reexamined the paleoneurological data on these, *Dromiceiomimus* and *Troodon*, which lived about 75 million years ago. The reexamination is presented here for the first time.

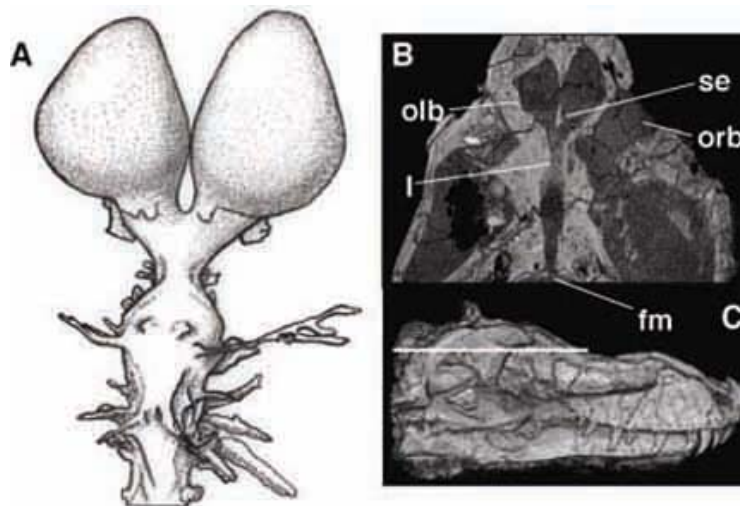
The first published reports on large-brained dinosaurs placed them within the polygons for living birds and mammals rather than reptiles. One can begin the reexamination with Figure 3, which shows the endocast of *Troodon* compared with that of two birds, an ostrich and the wandering albatross.

Ostriches usually weigh somewhat more than 100 kg, and the ostrich endocast shown in Figure 3 displaced 32 ml of water. The wandering albatross, one of the heaviest of flying birds, weighs about 12 kg, and its endocast in Figure 3 displaced 27 ml of water. The visible forebrain region of *Troodon* measured on a 3D-computer image is 15 cm<sup>2</sup>. The comparable measurements in the two birds were 17 cm<sup>2</sup> for albatross and 22 cm<sup>2</sup> for ostrich. Dimensionally, the whole *Troodon* endocast, scaled to correspond to the two birds, had a volume of about 20-ml. This is about half of that suggested in the early publications and repeated in many later statements about dinosaur brains. *Troodon*'s body size, reported at about 45 kg, coupled with a 20-ml brain, would place *Troodon* at the upper edge but within the same polygon as living reptiles, below the avian polygon. At this writing it has been impossible to redetermine the size of the brain in *Dromiceiomimus*, but from published illustrations of the endocast it appears to have been similar in size to that of *Troodon*. Its estimated body size of 150 kg would put it well within a reptilian polygon – the extended one that was drawn when dinosaur data were added. The issue remains open, however, pending the availability of more data.



**Figure 3.** Endocasts of ostrich, wandering albatross, and the “large-brained” dinosaur, *Troodon*. The dinosaur endocast is only of the dorsal surface, molded by the incomplete fossil remains of the skull. Visible on the dinosaur endocast are olfactory bulbs, olfactory tract, forebrain, and hindbrain. The gap between forebrain and hindbrain could represent the surface of the midbrain, but a lateral elevated bulge barely visible in this photograph may also represent the optic lobe (superior colliculus) of the right hemisphere. Brain size in *Troodon* is estimated by comparing visible forebrain surface area with that in birds to indicate expected total brain size from dimensional analysis.

The question of olfactory sensitivity in *Tyrannosaurus rex* is equally interesting for the interpretation of endocasts. The published data are summarized by Figure 4. All of the information about this skull, including the reconstruction of the endocast, is based on a CT (computerized tomography) scan of the skull.



**Figure 4.** Endocast and skull of *Tyrannosaurus rex*. A. Dorsal view of endocast. B. CT section: olb, olfactory bulb area; se, sphenethmoid bone; orb, orbit; I, olfactory tract; fm, foramen magnum. C. Reconstruction of skull from CT scans, showing level of CT section of B. (From Brochu, C. *Journal of Vertebrate Paleontology*, 20:1-6, 2000. By permission.)

If the olfactory bulbs filled the space available for them there is no question that they would have been enormous in *Tyrannosaurus rex*. They would, in fact have been uniquely large for an amniote. As

pictured in Figure 4, the olfactory bulbs would have had about four times the volume of the rest of the brain. No living bird or mammal has such massive olfactory bulbs. The kiwi, the bird most noted for olfactory sensitivity, has large olfactory bulbs, but these are less than 20 percent as large as the brain as a whole. The other famously olfactory bird, the turkey vulture, also has large olfactory bulbs, perhaps 10 percent of the volume of the brain as a whole.

It seems likely that although there was space available for very large olfactory bulbs in *Tyrannosaurus rex*, the space was filled mainly by non-neural tissue. This is not an unusual situation in vertebrates. The whole brain of the megamouth shark fills less than 20 percent of its cranial cavity. In the living coelacanth fish, *Latimeria*, the brain fills only about one percent of the cranial cavity.

One obviously has to be cautious in reasoning about brains from data on endocasts. Brain-body relations are instructive for interspecies comparisons, but data on brain size can validly be equated with those on endocast size only in birds and mammals. Even in these groups one must exercise caution, relying on endocasts to represent brains only when morphological evidence strongly supports the equivalence.

### **The Meaning of Brain Size**

This topic is discussed in some detail in the article on “Brain Size.” Applying the conclusions to fossil “brains” one should recognize that the relationship between brain size and information processing capacity has been elegantly demonstrated only in living mammals. Nevertheless, since the neurons in the brain as information processing units are probably packed efficiently we should anticipate a good relationship between brain size and processing capacity. It is this likely relationship that makes one interested in the evolution of brain size. The problem then is to relate processing capacity to the control of behavior.

We share a naive interest in brain size because we assume that braininess is more or less equivalent to intelligence. One can argue reasonably for such equivalence in some sense, but the argument requires a clear idea of what intelligence is. As arguments go, this is one of the more contentious. We do not appreciate how “intelligent” most animals are. Each species in its own habitat may display elaborate adaptive behaviors. Textbooks of ethology are filled with good examples. If we go to the laboratory for examples we should be prepared for some surprises. Honeybees, made famous for their dance that communicates information about where and how far away a good foraging area is from the hive, can surprise one even more by other adaptive capacities. Their learning abilities are indistinguishable from those of birds and mammals on tasks requiring learning new cues and reversing the significance of the cues. Pigeons are as good as or better than humans at identifying faces in photographs. Crows and monkeys are equally good at “learning sets,” that is, tests of ability to learn the rules governing choice of objects in a puzzle. This kind of evidence should warn us away from simple-minded views of animal intelligence.

We should be prepared to discover unusual behavioral capacities in other species, and we should not be surprised to find evidence of their presence in dinosaurs. We now have incontrovertible fossil evidence of group activity in dinosaurs that can be compared to living in herds as this occurs in living mammals. The evidence is also that dinosaurs nested the way living birds nest and that they cared for their eggs and hatchlings much as living birds do. Among smaller brained species, however, living alligators and crocodiles are as unusual as birds in their care of hatchlings. Many species of fish have elaborate behavior patterns related to courtship, egg laying, and care of the young. The point is that it does not necessarily take much brain to control very elaborate behavior.

At this time it is most acceptable to consider dinosaurs reptilian rather than avian with respect to brain size and shape. Their relationship to living birds is established on the basis of other morphological characters, not by the brain. On the other hand, the earliest evidence on bird brains, which is provided by *Archaeopteryx*, indicates that the brain’s expansion in the bird lineage had begun then, 75 million years before “large brained” dinosaurs appeared. (The evidence for “large brained” dinosaurs such as *Troodon* is, of course, uncertain as noted earlier.) If the relationship between birds and dinosaurs held true for the brain, the evidence has to come from a small dinosaur such as *Compsognathus*, which was a contemporary of *Archaeopteryx* and similar to it in body size. No endocasts of *Compsognathus* have

been recovered that could clarify this picture.

The endocast of *Archaeopteryx*, unlike the dinosaur endocasts, filled the brain case and shows clear differentiation of cerebellum, midbrain (optic lobes), and forebrain. It lacked one characteristic forebrain structure present in all living birds, namely the Wulst, which functions as a visual center.

One does not expect progressive evolutionary changes to be manifested in all traits that can be measured. Assuming that the current consensus relating birds to dinosaurs is correct, it is likely that the relationship would be evident in some, but not all, morphological features. Dinosaur brains as indicated by their endocasts were reptilian and could control a normal reptilian behavioral repertoire. One is nevertheless ignorant about the full range of behavioral demands that are met by the brains of birds that could not be met by a brain in the size range of reptiles. There is no reason to assume that the behavioral repertoire of dinosaurs was non-avian, merely on the evidence of the brain, especially in the light of its many features that appear to be similar to those of living birds.

### **Further Reading**

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