

FOREBRAIN ENLARGEMENT AMONG NONAVIAN THEROPOD DINOSAURS

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The gross size and shape of the brain is often preserved in extinct vertebrates with well-ossified braincases, such as dinosaurs. The volume within the braincase, termed the endocast, is the space occupied by the brain, cerebrospinal fluid, and surrounding tissues. Endocasts of most nonavian dinosaurs differ little in size and shape from those of living reptiles (Jerison, 1969, 1973; Hopson, 1977, 1979). Birds, in contrast, have dramatically increased the volume of the brain relative to body mass and enlarged the cerebrum (forebrain) relative to total brain volume, as seen in a partial endocast of the early fossil avian *Archaeopteryx* (Jerison, 1973; Bühler, 1985). The enlargement of the avian brain and, in particular, the cerebrum is believed to have begun among small-bodied nonavian theropods, such as dromaeosaurids (Sues, 1978; Currie, 1995) and troodontids (Russell, 1969; Currie, 1985). Reconstructing the evolutionary sequence that led to forebrain expansion in birds has been difficult because complete endocasts are not available for many of the closest relatives of birds (i.e., oviraptorosaurs, dromaeosaurids, troodontids). Furthermore, scaling ambiguities hamper such comparisons, because the body size of theropods closest to birds is at least one order of magnitude greater than that of the earliest avians.

We present here an alternative means of assessing brain and forebrain expansion among nonavian theropods. We use *Carcharodontosaurus* (Sereno et al., 1996) and *Tyrannosaurus* (Osborn, 1912), two large Late Cretaceous theropod dinosaurs that have similar adult body mass but differ in phylogenetic proximity to Aves (Holtz, 1994; Sereno, 1997). *Carcharodontosaurus* and other allosauroids were large-bodied predators that diverged from coelurosaurian theropods by the Early Jurassic (Fig. 1). Tyrannosaurids, including *Tyrannosaurus*, are large-bodied coelurosaurs that diverged from the lineage leading to avians by the Late Jurassic. The similar adult body mass of *Carcharodontosaurus* and *Tyrannosaurus* permits direct comparison of their brain volumes.

An endocast was made from a complete and undistorted braincase of an adult individual of *Carcharodontosaurus* (Fig. 2A, C). A *Tyrannosaurus* endocast (Fig. 2B, D) was made from a sagittally-sectioned adult braincase and checked against a partial unsectioned endocast from a second adult individual (see Materials and Methods for details).

Abbreviations

Institutional—AMNH, American Museum of Natural History, New York; MMS, Minnesota Museum of Science; SGM, Ministère de l'Énergie et des Mines, Rabat, Morocco; UUV, University of Utah.

Anatomical—cl, cavum labyrinthicum; h, hypophysis; pf, pontine flexure; ss, sagittal sinus; vcd, vena capitis dorsalis; I, olfactory nerve; II, optic nerve; V, trigeminal nerve; XII, hypoglossal nerve.

MATERIALS AND METHODS

Terminology

We use “Aves” for the clade that includes *Archaeopteryx*, extant birds (Neornithes), their common ancestor, and all descendants; “Ornithurae” refers to the clade that includes all avians closer to Neornithes than to *Archaeopteryx* (Sereno, 1998, 1999).

Three-dimensional Reconstruction of Fossil Endocasts

The endocast of *Carcharodontosaurus* was generated from a complete braincase of an adult individual (SGM-Din 1). The braincase was

axially scanned in 1 mm sections, with a bone algorithm of 120 kilovolts on a CT/iTM scanner at General Electric, Pewaukee, Wisconsin. The scan data was translated to an IGES format using Mimics from Materialise. The internal surface of the braincase was isolated by editing the point cloud using Surfacer from Imageware (version 8.1). The digital endocast was rapid-prototyped using a Helixys LOM machine at Baxter Health Care's Advanced Engineering Design Center.

A half endocast of *Tyrannosaurus rex* was made from one side of an adult braincase (AMNH 5029) that had been sagittally-sectioned and cleaned of matrix (Osborn, 1912). This cast was laser-scanned at Baxter Health Care's Advanced Engineering Design Center using their Laser Design scanner, formatted as an IGES point cloud, digitally-edited, and mirrored along the parasagittal plane to create the opposite side. A narrow sagittal slice was added between each half endocast to approximate the original width of the space within the braincase prior to sectioning. The resulting endocast was rapid-prototyped using a Stratsys FDM system. The corrected width of this computer-generated endocast was confirmed by a partial endocast preserving the entire cerebrum from another adult individual referred to *Tyrannosaurus rex* (MMS 51-2004).

Fossil Brain Volume Estimation

Endocast shape approximates brain shape in extant reptiles, including birds (Hopson, 1979). Because the relative volume of the endocast occupied by the brain varies in extant reptiles and birds, we apply a range of values encompassing the variance (50–100%) in this measure (Fig. 3).

Following previous studies (Osborn, 1912), the endocast volume was delimited as the region bounded anteriorly by the narrowest transverse constriction of the olfactory tracts and posteriorly by the exit of the hypoglossal nerve. Endocast volumes for *Carcharodontosaurus* and *Tyrannosaurus* were calculated from the digital three-dimensional data using Surfacer from Imageware (version 8.1). Endocast volume for *Allosaurus fragilis* was measured by water displacement of a copy of a natural endocast (UUV 294). Endocast volume for *Archaeopteryx* was estimated using a modified “graphic double integration” technique (Jerison, 1973). Endocast illustrations from Jerison (1973) were divided equally into 30 sections normal to their sagittal axis. An endocast volume of 1.12 ml was determined by summing the volumes of these 30 elliptical slices (calculated from the width, height, and thickness of each section). This value falls between previous estimates of 0.92 ml and 1.76 ml from Jerison (1973) and Hopson (1977), respectively.

Cerebral Volume

The cerebrum, cranial nerves, olfactory bulbs, and optic lobes can all be reliably identified from endocasts. We have limited our comparisons to the most recognizable feature, the cerebrum, which fills the braincase in living reptiles more completely than other parts of the brain (Hopson, 1977). Cerebral volumes were estimated by superimposing the largest possible pair of ellipsoids on the cerebrum. Measurements for *Archaeopteryx* were taken from the illustrations in Jerison (1973). Total brain and cerebral masses were obtained from published data for extant nonavian reptiles (Platel, 1976; Gans, 1980) and extant birds (Ebinger and Löhmer, 1984, 1987; Rehkämper et al., 1988; Rehkämper et al., 1991). Measurements of all domesticated birds were excluded.

Assuming ratios of the thickness of the dural coverings to the volume of the brain in cross-sectional slices throughout the endocast are similar

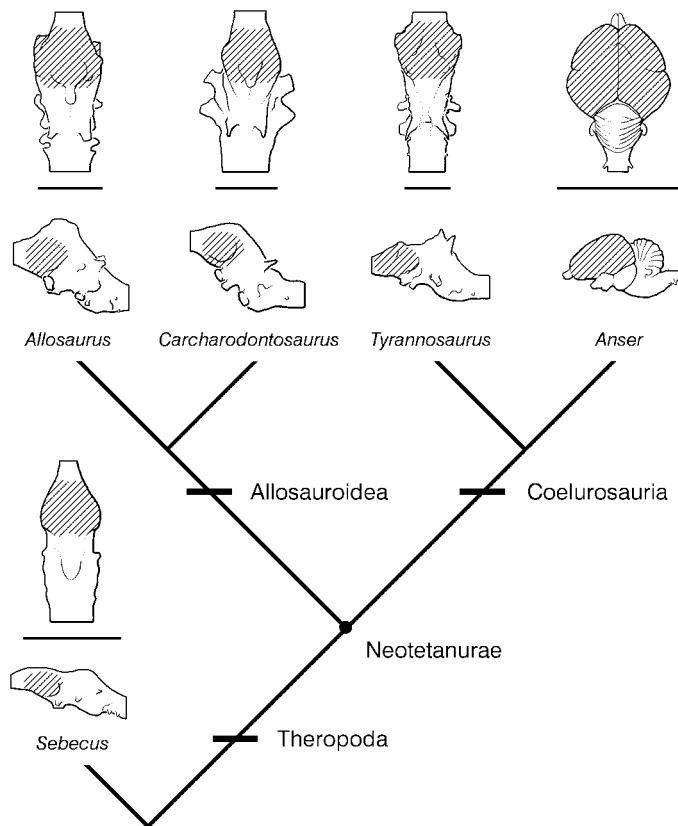


FIGURE 1. Phylogenetic diagram showing the relationships between five archosaurs, with illustrations of their endocasts (or brains) in left lateral (below) and dorsal (above) views. Illustrations of *Allosaurus*, *Carcharodontosaurus*, and *Tyrannosaurus* are based on specimens cited herein; those of the crocodylian *Sebecus* and the avian *Anser* are modified from Hopson (1979) and Romer (1955), respectively. Cerebral regions are cross-hatched. Scale bars equal 5 cm for the dorsal views, lateral views not to scale.

amongst the different specimens, a ratio of cerebral volume to brain volume derived from the endocast will approximate that of the formerly enclosed brain. Cerebral and total brain masses were plotted as log-transformations, and power regressions of $y = 0.332x^{0.95}$ ($R^2 = 0.993$) and $y = 0.484x^{1.12}$ ($R^2 = 0.982$) were calculated for the nonavian reptile and bird data, respectively. The nonavian reptile and bird regressions were extrapolated to the range occupied by *Allosaurus*, *Carcharodontosaurus*, and *Tyrannosaurus*, assuming a specific gravity of 1 g/ml for the fossil data (Jerison, 1973; Hopson, 1977). The respective positions of the fossil taxa were calculated as a percentage of the least squares residuals between the two regressions. This approach fixes the x-values at the total endocast mass to constrain the ratio relationships. Although the regressions have been greatly extrapolated, this remains the only available technique to compare the fossil and extant data. The high R^2 values suggest that extrapolations of the regressions are reasonably accurate.

COMPARISONS

The endocast of *Carcharodontosaurus* (Fig. 2A) closely resembles that of *Allosaurus* (Hopson, 1979), an earlier (Late Jurassic) allosauroid (Fig. 1). Both endocasts resemble extant archosaurs (crocodylians and birds) in that the pontine flexure is approximately 40° and the roof of the cerebrum is elevated above the cerebellum (Hopson, 1979; Giffin, 1989). *Tyrannosaurus*, in contrast, has the apex of the endocast positioned over the cerebellum, reflecting the general elevation of the cerebellum, sagittal sinus, and venae capitis dorsalis (Fig. 2B). It is not yet known whether this condition also characterizes nonavian maniraptorans, the small-bodied theropods most closely related to birds.

Endocast volumes for *Carcharodontosaurus* and *Tyrannosaurus* are

TABLE 1. Estimates of endocast volume, cerebral volume, and their proportion in relevant theropods. Volumes are given in milliliters (ml). *Allosaurus fragilis*, UUV 294; *Carcharodontosaurus saharicus*, SGM-Din 1; *Tyrannosaurus rex*, AMNH 5029; and *Archaeopteryx lithographica*. Estimates are based on published data and original calculations. For details, see Materials and Methods.

Taxon	Total endocranial volume (ml)	Estimated cerebral volume (ml)	% of brain composed of cerebrum	% toward bird regression from reptile regression using least squares residuals
<i>Allosaurus</i>	169.0	46.7	27.9%	2.6%
<i>Carcharodontosaurus</i>	224.0	53.7	24.0%	-2.4%
<i>Tyrannosaurus</i>	343.0	111.8	32.6%	10.2%
<i>Archaeopteryx</i>	1.1	0.5	44.6%	72.6%

strikingly different. Despite similar body size, endocast volume in *Tyrannosaurus* is approximately 50% greater than in *Carcharodontosaurus* (Table 1). Cerebral volume is approximately 100% greater in *Tyrannosaurus* than in *Carcharodontosaurus* (Table 1), as is particularly apparent in dorsal view (Fig. 2C, D). Consequently, the percentage of total endocast volume occupied by the cerebrum is greater in *Tyrannosaurus* (32.6%) than in *Carcharodontosaurus* (24.0%). Increase in total brain volume (relative to body mass) and in the volume of the cerebrum (relative to brain volume) also characterizes *Archaeopteryx* (Table 1; Fig. 3), living birds, and probably also small-bodied theropods closely related to birds (Russell, 1969; Sues, 1978; Currie, 1985, 1995).

Brain and body mass scale differently in nonavian reptiles and birds (Jerison, 1973; Hopson, 1977) (Fig. 3). Although total brain mass scales with similar negative allometry to body mass in both groups, birds generally have larger brains for a given body mass than nonavian reptiles (Fig. 3). However, when the regressions are extrapolated to the body masses of *Allosaurus*, *Carcharodontosaurus*, and *Tyrannosaurus*, their 95% confidence limits begin to overlap and place these three taxa within both regressions. The basal avian *Archaeopteryx* plots between the two regressions.

The proportion of brain mass composed of cerebral mass also scales differently in living nonavian reptiles and birds (Jerison, 1973; Hopson, 1977) (see Materials and Methods for details). In nonavian reptiles, cerebral mass scales with slight negative allometry relative to total brain mass. In contrast, avian cerebral mass scales with positive allometry, such that larger birds have relatively more cerebral mass than smaller birds. Relative cerebral volume in *Carcharodontosaurus* and *Allosaurus* plot near the nonavian reptilian regression, whereas the same measure for *Tyrannosaurus* plots significantly above that regression (closer to it than to the avian regression) (Table 1). *Tyrannosaurus* and *Archaeopteryx* are approximately 10% and 70% closer to the avian regression than to the reptile regression, respectively.

CONCLUSIONS

These data suggest the following conclusions. First, relative cerebral and total brain volumes in *Carcharodontosaurus* (and presumably more basal theropods) are similar to those of extant nonavian reptiles. An increase of perhaps 50% of total endocast volume (relative to body size) characterizes Coelurosauria. A disproportionate amount of this increase occurred within the cerebrum, which doubled in volume. This initial stage of relative brain and cerebral enlargement must have occurred after the divergence of coelurosaurians sometime in the Middle Jurassic (ca. 180–160 Ma) (Serenio, 1997).

Second, estimated total brain volume and relative cerebral volume in *Archaeopteryx* are intermediate between those in *Tyrannosaurus* and extant avians. This intermediate stage of brain and cerebral enlargement must have occurred by the Late Jurassic (ca. 150 Ma) and probably characterized small-bodied maniraptorans closely related to birds, such as *Troodon* and possibly *Caudipteryx* (Ji et al., 1998).

Third, additional brain enlargement occurred among ornithurine avians, because relative brain size and the proportion devoted to the cerebrum in *Archaeopteryx* are less than those in any extant avian. This

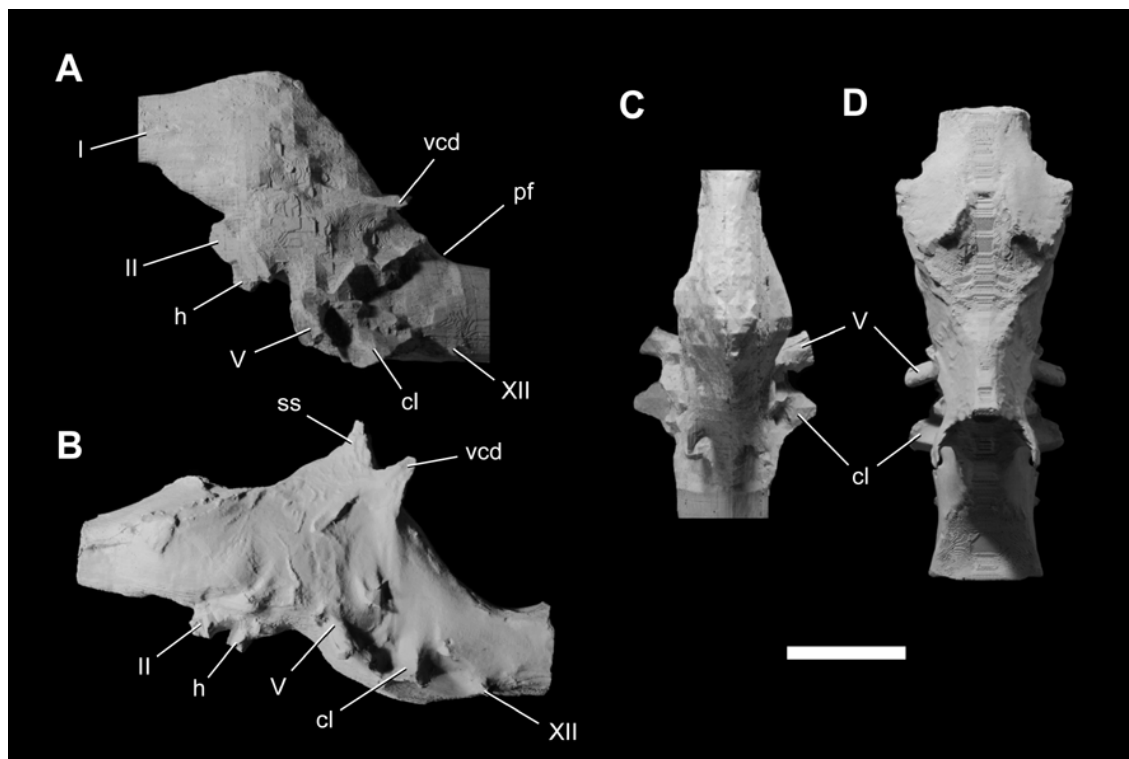


FIGURE 2. Endocasts of *Carcharodontosaurus saharicus* (A, C) and *Tyrannosaurus rex* (B, D) in lateral (A, B) and dorsal (C, D) views. Scale bar equals 5 cm. See Introduction for abbreviations.

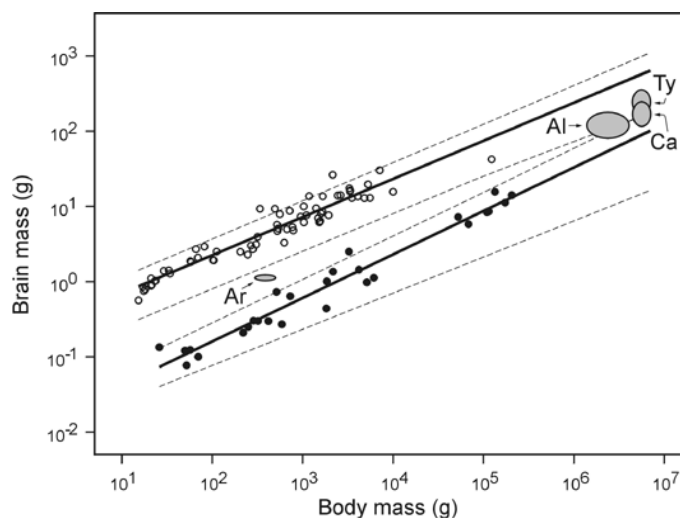


FIGURE 3. Log-log plot of brain and body masses among extant non-avian reptiles (closed circles), extant birds (open circles), and five extinct theropods (shaded ellipses). Extant data is from Crile and Quiring (1940). Data from domesticated birds and a hatchling alligator are excluded. Extinct theropod brain mass ranges reflect the assumption that the brain may occupy 50–100% endocast volume (specific gravity is assumed to equal 1.0 g/ml). Extinct theropod body mass ranges are from Jerison (1973), Hopson (1979), Anderson et al. (1985), and Peczkis (1994). **Abbreviations:** Al-, *Allosaurus*; Ar, *Archaeopteryx*; Ca, *Carcharodontosaurus*; Ty, *Tyrannosaurus*. The non-avian reptile and bird data are fitted with separate regressions of $y = 0.011x^{0.578}$ ($R^2 = 0.958$) and $y = 0.214x^{0.507}$ ($R^2 = 0.905$), respectively. Dashed lines indicate the 95% confidence limits of each regression.

most recent stage of brain and cerebral enlargement appears to have occurred at the base of Ornithurae by the earliest Cretaceous (ca. 140 Ma), judging from inspection of cranial remains of *Confuciusornis*. Brain enlargement from primitive reptilian proportions to that in living Aves, thus, would have taken place in less than 40 million years.

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