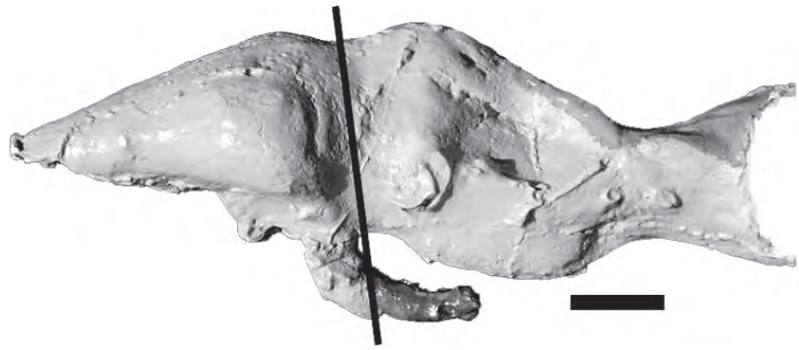**6.1.** Left lateral view of endo-cranial cast of wild *Alligator mississippiensis.* Skull length 34.3 cm, estimated body length, 2.6 m. Scale bar equals 1 cm.

Relative Size of Brain and Cerebrum in Tyrannosaurid Dinosaurs: An Analysis Using Brain-Endocast Quantitative Relationships in Extant Alligators

6

Grant R. Hurlburt, Ryan C. Ridgely, and Lawrence M. Witmer

Abstract

Brain and cerebrum mass are estimated from endocasts of three tyrannosaurid taxa (*Tyrannosaurus rex, Gorgosaurus,* and *Nanotyrannus*) using morphological and quantitative brain-endocast relations in a size series of sexually mature alligators (*Alligator mississippiensis*). The alligator size series (N = 12) ranged from the smallest sexually mature size to the largest size commonly encountered. Alligator brain mass (MBr) increased regularly with increasing body mass, while the ratio of brain mass to endocast volume (MBr:EV) declined regularly from 67 percent to 32 percent. The ratio of cerebrum mass to cerebrocast was 38 percent in the largest alligators and regularly exceeded the MBr:EV ratio by 5.6 percent. For estimates from endocasts of non-avian dinosaurs of unknown sex, a MBr:EV ratio of 37 percent was used, the mean of the ratio of the largest male and female alligators. A corresponding 42 percent ratio was used for the cerebrum-cerebrocast ratio.

Relative brain size was measured as Encephalization Quotients (EQs) based on brain-body relations in extant non-avian reptiles (REQs) and birds (BEQs). *Tyrannosaurus rex* has the relatively largest brain of all adult non-avian dinosaurs, excepting certain small maniraptoriforms (*Troodon, Bambiraptor,* and *Ornithomimus*), which are well within the extant bird relative brain size range. The relative brain size of *T. rex* is within the range of extant non-avian reptiles and, at most, 2 standard deviations (SDs) above the mean of non-avian reptile log REQs, which are normally distributed. *Gorgosaurus* REQs overlapped the lower end of the *T. rex.* Log BEQs of all theropods, excepting small maniraptoriforms, were well below the range of extant birds. *Nanotyrannus* log REQs were anomalously high for an adult, but the difference between *Nanotyrannus* log REQs and *T. rex* values paralleled the difference between log REQs of the smallest subadult and largest alligators. *Nanotyrannus* cerebrum:brain ratios were also consistent with those of an older juvenile or youngest subadult. Cerebrocast:endocast ratios of the three *T. rex* endocasts ranged from 41.1 to 43.5 percent, and cerebrum mass:brain mass (MCb:MBr) ratios range from 47.5 to 49.53 percent, more than the lowest ratios for extant birds (44.6 percent) but very close to ratios (45.9–47.9 percent) typical of the smallest sexually mature alligators. In

Carcharodontosaurus saharicus, these ratios were 37.1 percent and 42.1 percent, respectively, the latter essentially identical to actual MCb:MBr ratios (40.76–42.91 percent) of the two largest alligators. Although the relative brain size of *Carcharodontosaurus* (SGM-Din 1), was approximately two thirds that of *T. rex,* the MCb:MBr ratio of the former was only 5.5–7.5 percent less than that of *T. rex.*

Introduction

Endocasts (endocranial casts) are natural or artificial casts made from the endocranial (or brain or cranial) cavity of vertebrates, or they exist as virtual endocasts produced by laser or X-ray computed tomography (CT scans). The external morphology of an endocast corresponds to the external surface of the dura mater, of which the surface topography reflects contained sinuses and underlying blood vessels.

Excepting species in which the brain filled the cranial cavity, the endocasts of non-avian dinosaurs strongly resemble those of crocodilians in general proportions and specific anatomical features. Among non-avian dinosaurs, the brain apparently filled the cranial cavity in the following taxa: pachycephalosaurs, small theropods, *Archaeopteryx,* and the hypsilophodont *Leaellynasaura* (Russell 1972; Hopson 1979; Nicholls and Russell 1981; Rich and Vickers-Rich 1988; Currie and Zhao 1993; Osmólska 2004; Evans 2005). This is inferred because the skull surface, and thus the corresponding endocast, reproduces the contours of the gross brain divisions (cerebrum, midbrain, cerebellum) and, in some cases, the blood vessels of the brain surface, as in extant birds (Iwaniuk and Nelson 2002), pterosaurs (Hopson 1979; Witmer et al. 2003), and most mammals (Hurlburt 1982, and references cited therein). In most other dinosaurs, the endocranial surface does not bear impressions of brain divisions or the cerebral (vs. dural) blood vessels, indicating that the brain either did not fill the endocranial cavity or, at most, contacted the endocranial surface at the lateral poles of the cerebrum, as in hadrosaurs (Evans 2005). These endocasts resemble those of extant crocodilians, in which the brain does not fill the cranial cavity (Hopson 1979). In the largest alligators, the only brain parts that contact the endocranial walls are the lateral poles of the cerebrum (Hurlburt, unpublished results). This resemblance makes endocasts of crocodilians excellent models for the brain-endocast relationship in most dinosaurs.

Brain-Endocast Relations in Extant Non-avian Reptiles

Brain volume traditionally has been estimated for non-avian reptiles using a brain-mass:endocast volume ratio (MBr:EV) of 0.5; that is, the brain occupies 50 percent of the brain cavity. This ratio is based on an observation of the *Sphenodon* brain (Dendy 1910) and the MBr:EV ratio in one *Iguana* specimen (Jerison 1973). Although a very rough approximation (and one re-evaluated here), it provided a productive starting point (Hopson 1977, 1980). Larsson et al. (2000) made an important contribution in

analyzing relative size of the brain and cerebrum in several theropods and comparing them to non-avian reptiles and birds. Their approach made use of laser-scan data and analyzed brain and cerebrum size in a phylogenetic context. They tested, for the first time, the hypothesis of increasing size of the cerebrum relative to the rest of the brain in a phylogenetic context and also pioneered the study of brain division scaling in extinct taxa.

Relative Brain Size and Encephalization Quotients

Brain and body mass are highly correlated, as exemplified by the high correlation coefficients of equations in this paper. Relative brain size is the size of the brain compared to the size of the body, usually measured as body mass. It has been used to infer cognitive capacity and thermoregulatory mode in extinct vertebrates (Jerison 1973; Hopson 1977, 1980) and associated with complex cognitive behavior in birds and mammals (Lefebvre et al. 2002; Marino 2002). Because the specific gravity of the brain is approximately unity (Jerison 1973; Hurlburt 1982), brain size can be expressed as mass or volume. A commonly used measure of relative brain size is the Encephalization Quotient (EQ; Jerison 1973), which is the ratio of brain mass to a predicted brain mass, obtained from the brain-body equation of a reference group, such as non-avian reptiles or birds (Jerison 1973). Jerison (1973) was the first to state that dinosaurs had brains of the size expected for non-avian reptiles of their body mass. He supported this statement with graphical illustrations of brain-body relations in reptiles and dinosaurs, although four of his ten dinosaurs actually had LVEQs (Lower Vertebrate EQs; discussed below) less than those of the least encephalized reptile (Hurlburt 1996). His EQs were based on two equations, both with a slope (*b*) of 0.67, and with intercepts (*a*) of 0.007 and 0.07 for "lower" and "higher" vertebrates, respectively (Jerison 1973). He fitted the 0.67 slope "by eye" to the brain-body point scatter because it is the coefficient relating volume to surface area. He considered it a "theoretical" slope, but it is more properly termed a "hypothetical" slope. Hurlburt (1996) developed Reptile EQs (REQs), and Bird EQs (BEQs) using species-based brain-body equations. The reduced major axis regression (RMA) brain-body equation for non-avian reptiles by species (N = 62) is

$$\log MBr = -1.810 + (0.553 \times \log MBd), \tag{1}$$

where MBd is body mass, *r* = 0.9616, and the 95 percent confidence limits (CL) of *b* are 0.5150 and 0.5915. The RMA brain-body equation for birds by species (N = 174) is

$$\log MBr = -0.930 + (0.590 \times \log MBd), \tag{2}$$

where *r* = 0.9355 and the 95 percent CL of *b* are 0.5578 and 0.6213. These equations were based on much larger and more taxonomically comprehensive samples than those of Jerison (1973). The 95 percent confidence

limits (95 percent CL) of both equations exclude 0.67, constituting clear evidence that the 0.67 slope is inappropriate and falsifying Jerison's hypothesis. Moreover, the categories of birds (the monophyletic Aves) and the grade of non-avian reptiles are more appropriate than the categories of "lower vertebrates" (fish, amphibians, and reptiles) and "higher" vertebrates (birds and mammals) used by Jerison (1973). The bird slope is steeper than the reptile slope but within the 95 percent CL of the reptile slope. The bird intercept is approximately 10 times that of the non-avian reptile slope (Hurlburt 1996).

The corresponding EQ formulae (based on species-level equations) are

$$\text{REQ} = \text{MBr}/(0.0155 \times \text{MBd}0.553) \tag{3}$$

and

$$\text{BEQ} = \text{MBr}/(0.117 \times \text{MBd}0.590), \tag{4}$$

where antilog$_{10}$ −1.810 = 0.0155; antilog$_{10}$ −0.930 = 0.117. The RMA equation is appropriate for data with unequal variation in x and y variables, as is typical of brain and body data (Sokal and Rohlf 1981). From this point on, the term "non-avian reptiles" refers to extant non-avian reptiles.

The purposes of this study are (1) to determine three regression equations relating (*a*) log endocranial volume (EV), (*b*) log brain mass (MBd), and (*c*) REQ to TL (snout to tail-tip length) in a size series of alligators; (2) to determine ratios of brain-mass:endocast-volume (MBr:EV) and cerebrum mass:cerebrocast-volume (MCb:CbcV) in a size series of alligators; (3) to determine REQ and log REQ ranges of reptiles and BEQ and log BEQ ranges of birds; (4) to estimate endocranial and cerebrocast volume from actual or virtual endocasts of several large theropod dinosaurs and to estimate MBr and MCb from dinosaur endocasts using MBr:EV and MCb:CbcV ratios in alligators; (5) to compare relative brain size of dinosaurs with that of reptiles and birds, using REQs and BEQs; (6) to calculate ratios of cerebrum to total brain size in dinosaurs and compare these ratios to those of reptiles and birds; (7) to discuss methods of analyzing brain size, including methods of obtaining volumes from dinosaur endocasts; and (8) to test hypotheses regarding evolution of brain size.

Methods and Materials

The fossil specimens consisted of three taxa of the Late Cretaceous tyrannosaurids *Tyrannosaurus rex* (AMNH 5029, AMNH 5117, FMNH PR 2081), *Gorgosaurus libratus* (ROM 1247), and "*Nanotyrannus lancensis*" (CMNH 7541), as well as two allosauroids, the late Jurassic allosaurid *Allosaurus* (UUVP 294) and the late Cretaceous carcharodontosaurid *Carcharodontosaurus* (SGM-Din 1). In addition, EQs were calculated from endocast data for *Archaeopteryx* (BMNH 37001) and three small theropods: *Bambiraptor* (KUVP 129737), *Ornithomimus* (NMC 12228), and *Troodon* (RTMP 86.36.457 and RTMP 79.8.1). To provide a context for the theropod data, we also provide data for other dinosaur taxa. The relations of brain to

endocast and of cerebrum to cerebrocast were determined from a size series of 12 sexually mature alligators (*Alligator mississippiensis*), of which half were wild and half were pen-raised domestic animals.

Volumetric Relations between Brain and Endocast and between Cerebrum and Cerebrocast in *Alligator mississippiensis*

In the alligator sample, MBd ranged from 11.3 to 276.9 kg, TL ranged from 1.613 to 3.810 m, and MBr ranged from 4.47 to 10.51 g (Hurlburt and Waldorf 2002). Although alligators have been known to reach TL slightly exceeding 4 m, generally there is little growth after 3.5 m TL in males and 2.6 m TL in females. Alligators can be sexually mature at 1.60 cm (Woodward et al. 1991). Thus, the sample ranged from the smallest sexually mature individual – that is, the smallest subadult – to the largest commonly encountered size. It thus constitutes a useful comparison sample for studying relations between relative brain size and ontogenetic age in extinct, non-avian archosaurs.

Brains were removed immediately postmortem in the alligators and weighed within 10–30 minutes, following removal of the olfactory tracts. Brain weight included pia mater but excluded the pituitary gland, dura mater, arachnoid, grossly visible blood vessels, and any dried blood, which occurred between the meninges in some specimens. Brains were dissected into gross divisions (cerebrum, cerebellum, optic lobes [= tectum], and brain stem, including diencephalons), which were then weighed. The first three divisions were cut off from the brain stem in a horizontal plane. Divisions were fixed in 10 percent formalin. The skulls were cleaned, and endocasts were made by applying successive layers of latex to the skull and calvarium. Because the specific gravity of brain tissue approximates unity (one), brain volume and mass are used interchangeably. Volumes of alligator endocasts were determined by suspending endocasts from an electronic balance, once in air and once immersed in water. The difference in the two masses equals the mass (g) of water displaced by the volume of the cast. Because the specific gravity of water is one, this mass equaled the volume in milliliters (Alexander 1985).

Limits and landmarks on alligator and dinosaur endocasts were chosen to correspond to the brain portion of the endocast. The limits were anteriorly, the point where the cerebrum narrows to meet the olfactory tract, and posteriorly, the stump of the hypoglossal nerve (XII). Endocast portions beyond these limits were removed, as were foramen fillings corresponding to nerves and blood vessels. Cerebrocast volumes were determined by suspending the cast with the water line at the posterior cerebrocast boundary line and again subtracting the wet mass from the dry mass.

In alligators, the cerebrocast boundary line was somewhat oblique, from rostrodorsal to caudoventral (Fig. 6.1). The line always fell just at the posterior contact of the cast of the infundibulum connecting to the pituitary. The cerebrocast (endocast portion corresponding to the

forebrain) includes the cerebrum and also unavoidably includes the portions corresponding to the diencephalon, optic chiasma, and optic tracts because the cerebrum lies dorsal and lateral to these brain components. Alligator cerebrum-cerebrocast ratios are the ratio of the cerebrum alone to the cerebrocast.

The MBr:EV ratio was determined for 12 alligators, and least squares regression equations were calculated with EV and MBr as dependent variables and TL as the independent variable. Reptile Encephalization Quotients of a sample including four additional specimens (total N=16) were calculated to describe the ontogenetic pattern relative to TL. These four were included to increase sample size although cerebrum data were unavailable for these specimens. Total length was used because some alligators were pen-raised and heavier for their length than wild alligators.

Relative Brain Size in Extant Non-avian Reptiles and Birds

Both non-avian reptile log REQs and bird log BEQs were normally distributed, unlike either non-avian reptile REQs or bird BEQs (all logarithms are $\log_{10}$ in this paper). Accordingly, dinosaur log REQs and log BEQs were compared to ranges of these parameters in non-avian reptiles and birds and analyzed in terms of z-scores (SD units) as appropriate (Sokal and Rohlf 1981). Additionally, the relationship between log REQs and TL in alligators was calculated (Hurlburt, unpublished data) to describe the ontogeny of REQ in a modern group.

Estimating Body Mass, Brain Mass, and Relative Brain and Cerebrum Size in Dinosaurs

Except for those of *Nanotyrannus* and *Bambiraptor*, dinosaur body mass (MBd) estimates were taken from the literature. In most cases, two estimates were used to cover a range of reasonable possible masses because no robust mechanism for MBd estimation has been universally accepted for extinct vertebrates (Hurlburt, 1996, 1999). The MBd of *Nanotyrannus lancensis* (CMNH 7541) was calculated from estimated femoral circumference. Femoral length was calculated from premaxilla-quadrate skull length (572 mm; Gilmore 1946) using Currie's (2003) least squares regression equations for tyrannosaurids ($N = 26$, $r = 0.980$) and tyrannosaurines ($N = 14$, $r = 0.988$), giving femoral lengths of 589.33 and 563.06 mm, respectively. Femoral circumference was estimated from femoral length, using the "All Theropods" RMA regression equation ($n = 33$, $r = 0.9923$) of Christiansen (1999), giving femoral circumferences of 192.72 and 182.84 mm, respectively. Body mass was calculated using the equation

$$W = 0.16\,Cf2.73, \tag{5}$$

where W is mass (g), and Cf is minimum femur circumference (mm) (Anderson et al. 1985). Adult MBd of *Bambiraptor* was calculated from Cf of an adult femur cast provided by David Burnham, and of *Ornithomimus*

from *Cf* of ROM 852, an adult femur. Volumes of dinosaur endocasts and cerebrocasts were taken by one of three methods: (1) Double Graphic Integration (DGI; see Jerison 1973; Hurlburt 1999) of illustrations of endocasts of *Carcharodontosaurus saharicus* (SGM-Din 1; see Larsson 2001) and of *Tyrannosaurus rex* (AMNH 5029; see Hopson 1979), (2) volume calculation from virtual endocasts produced from three dimensional CT scans of the four tyrannosaurids, and (3) water displacement by the wet-dry method, as described above, of an endocast of *Allosaurus fragilis* (UUVP 294). Volumes derived from CT scans were generated using Amira 3.1.1 visualization software.

The posterior limit of the cerebrocast in dinosaurs was defined as a vertical line in the transverse plane just posterior to the bulge corresponding to the cerebrum. This line was usually just rostral to the rostral limit of the base of the cast of the trochlear nerve (IV) where apparent. Dinosaur MBr and MCb were obtained by applying the MBr:EV and MCb:CbcV ratios of the largest alligators and also by application of the widely used 50 percent ratio. The 50 percent ratio was used both for comparison to results of other studies and because it is the ratio of alligators halfway between the youngest and oldest sexually mature specimens. In addition, MBr and MCb values for *Nanotyrannus* were also obtained using MBr:EV and MCb:CbcV ratios typical of the youngest subadult alligators, owing to the hypothesis that it is a juvenile, as indicated by suture contacts, and as bone grain indicates juvenile status for *Nanotyrannus* (Carr 1999). No ratios are known for juvenile alligators. Calculated dinosaur log EQs were compared to ranges of log REQs of non-avian reptile species ($N = 62$) and of log BEQs of bird species ($N = 174$). Encephalization Quotients for other dinosaur species, including small theropods, were also used to provide a context for analysis of large theropods. Encephalization Quotients for small theropods and *Archaeopteryx* were calculated from endocast and MBd data in Russell (1972; see Nicholls and Russell 1981), Hopson (1977), Currie and Zhao (1993), Hurlburt (1996), Elzanowski (2002), Burnham (2004), and Dominguez Alonso et al. (2004) or as described in Methods. Encephalization Quotients were calculated for other dinosaurs (stegosaurs, ankylosaurs, ceratopsians, and sauropods), applying MBr:EV and MCb:CbcV ratios in alligators to EV. These data are from Hurlburt (1996) with two exceptions. The EV of *Stegosaurus* (64.18 ml) was obtained by DGI of the endocast of CM 106 figured in Galton (2001). The EV of *Iguanodon* was obtained by DGI of the brain cavity of BMNH R2501, an isolated endocranium (Andrews 1897; Norman 1986), after excluding an area corresponding to an extensive sinus complex (Norman and Weishampel 1990).

<div style="text-align:center">

**Brain:Endocast and Cerebrocast:Cerebrum
Ratios in *Alligator mississippiensis***

</div>

Results and Discussion

The MBr:EV (brain mass to endocast volume) ratio decreased from 68 percent in the smallest to 32 percent in the largest alligators. Among the
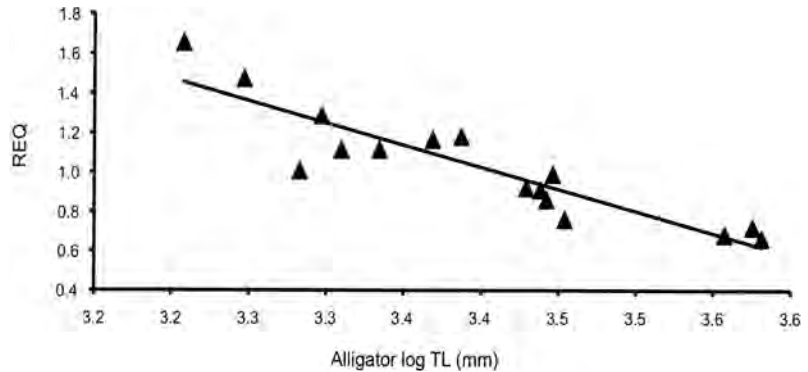
three largest males, the TL range was 3610–3840 mm, the MBr range was 9.82–10.71 g, and the MBr:EV ratio range was 31.09–34.82 percent with a mean of 32.6 percent. The largest female (TL 284.5 cm, MBr 8 g) had an MBr:EV ratio of 42.04 percent. Alligator REQs regularly declined from 1.648 (log value = 0.217) in the smallest alligator (TL = 1613 mm) to 0.667 (log value =−0.176) in the largest alligator (TL = 3810 mm), in a mixed sample of wild and domestic alligators ($N = 16$; see Fig. 6.2). The associated least squares regression equation, REQ = $8.558 + (−2.215 × \log$ TL), had 95 percent CL of (−2.804–1.627) enclosing the slope ($b = −2.2732$) of the smaller sample ($N = 12$).

Endocast volume increases faster than MBr relative to TL. In the least squares regression equation relating log EV (ml) to log TL (mm), the slope ($b = 1.811$; 95 percent CL 1.652, 1.978; $r = 0.992$) is statistically significantly larger than the slope of the equation relating log MBr (g) to TL (mm), where $b = 0.997$ (95 percent CL 0.890, 1.104; $r = 0.989$), although both variables increase with increasing body size (Hurlburt and Waldorf 2002). To take into account the pronounced sexual dimorphism of alligators, in which the greatest male size markedly exceeds that of females, MBr estimates from EV in mature dinosaurs and crocodilians should apply the largest male ratio (33 percent) for undoubted males, the male-female mean (37 percent) when specimen sex is unknown, and the largest female ratio (42 percent) for undoubted females when sexual dimorphism is known. The mean cerebrum:cerebrocast ratio of the largest males and females of 42 percent was applied to estimate cerebrum mass from dinosaur cerebrocasts.

Relative Brain Size in Extant Non-avian Reptiles and Birds

Reptile Encephalization Quotients of the 62 non-avian reptile species ranged from 0.402 to 2.404; the BEQs of 174 extant avian species ranged from 0.357 to 2.986. Figure 6.3 shows polygons that surround the non-avian reptile and bird brain-body data on which the EQ equations are based. Figure 6.4 shows the same polygons and unlabeled dinosaur brain-body data with the slopes for the Lower Vertebrate and Higher Vertebrate EQ (LVEQ and HVEQ) equations. The REQ slope, empirically
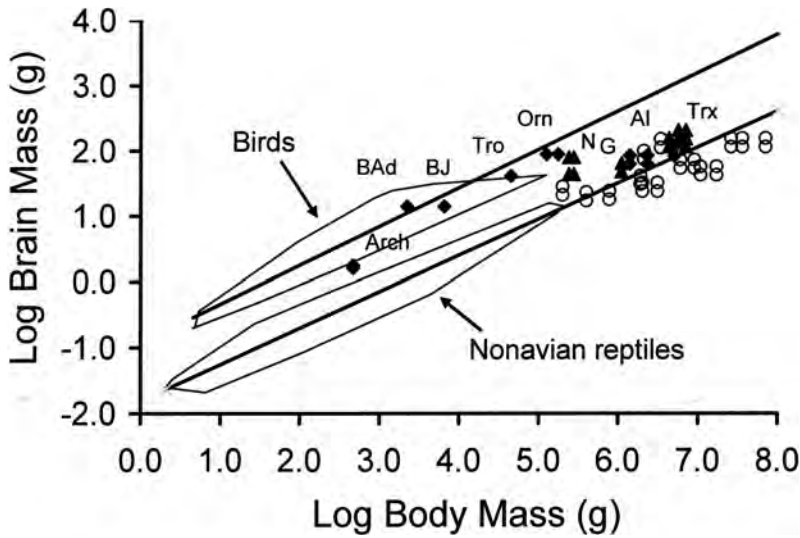
6.3. Log brain (MBr) and body mass (MBd) of dinosaurs, plotted with slopes of brain-body equations of non-avian reptile species (lower slope) and bird species (upper slope). Polygons surrounded brain-body point scatters of non-avian reptiles (*N* = 62) and birds (*N* = 174), as indicated. Legend: filled triangles, tyrannosaurids; filled diamonds, other theropods; hollow circles, other dinosaurs. Abbreviations: Al, *Allosaurus;* Arch, *Archaeopteryx,* BAd, *Bambiraptor,* estimated adult values; BJ, *Bambiraptor,* juvenile; G, *Gorgosaurus;* N, *Nanotyrannus;* Orn, *Ornithomimus;* Trx, *Tyrannosaurus rex;* Tro, *Troodon.*
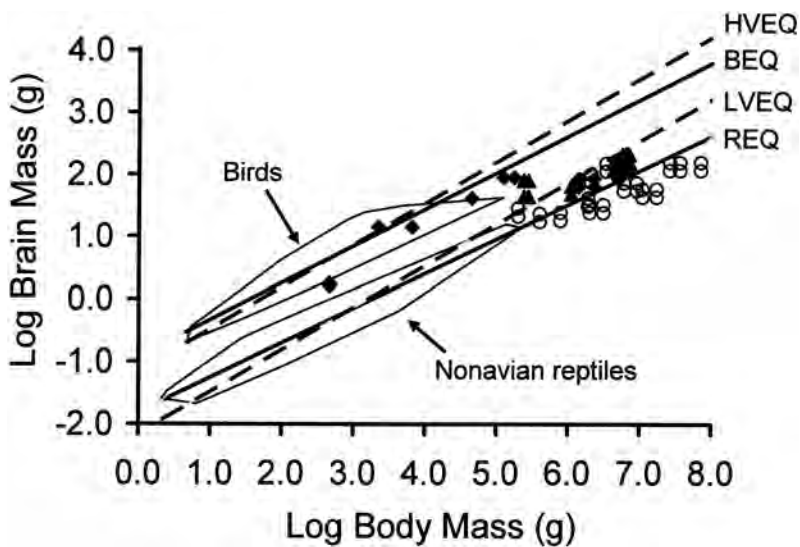

6.4. Comparison of slopes of Lower Vertebrate Encephalization Quotient (LVEQ), Higher Vertebrate Encephalization Quotient (HVEQ), Reptile Encephalization Quotient (REQ), and Bird Encephalization Quotient (BEQ) equations. Polygons and dinosaur data as in Figure 6.3. Jerison (1973) chose the 0.67 slope of both the LVEQ and HVEQ because it is the coefficient of the volume to surface area relationship and fitted the intercepts (0.007 and 0.07) "by eye" to the Lower and Upper Vertebrate brain-body point scatters. The LVEQ slope passes above most dinosaur data points, and four of Jerison's ten dinosaur genera had LVEQs less than those of the least-encephalized reptiles. The REQ slope passes through the middle of the dinosaur distribution. Both the REQ and BEQ equations were empirically derived. Lower Vertebrates: fish, amphibians, and reptiles; Higher Vertebrates: birds and mammals.

derived from reptile brain-body data, passes through the middle of the dinosaur brain-body distribution, whereas the LVEQ slope (dashed), passes above most dinosaur brain-body points, and results in lower LVEQs for several dinosaurs than for the least-encephalized reptiles (Hurlburt 1996). Neither non-avian reptile REQs nor bird BEQs were normally distributed (Hurlburt 1996), but both non-avian reptile log REQs (range: −0.396–0.381) and bird log BEQs (range: −0.447–0.475) were normally distributed. Accordingly, dinosaur log EQs were compared to statistics of distribution (mean and SD) of reptile log REQs and bird log BEQs. The reptile log REQ distribution has mean −0.0087 and SD 0.1968; the mean + 2 SDs is −0.402 and 0.385, respectively. The bird log BEQs distribution has mean 0.0002 and SD 0.1815; the mean ± 2 SDs is −0.363 and 0.363, respectively (see Tables 6.1 and 6.2; Figs. 6.5 and 6.6).

6.5. $\log_{10}$ REQs of dinosaurs and 62 non-avian reptile species. Vertical dashed lines indicate non-avian reptile mean log REQ and mean ± 2 SDs. Non-avian reptile log REQ range, −0.318–0.237; mean, −0.0087; SD, 0.1968; mean ± 2 SDs, −0.403– 0.385. Open bars, reptiles; cross-hatched bars, dinosaurs; filled bars, reptile and dinosaur bars of equal height. Abbreviations: A and B indicate two MBd estimates (two MBrs for Arch.); Ad, adult; Carch, *Carcharodontosaurus,* Gorg, *Gorgosaurus;* Juv, juvenile; Nan, *Nanotyrannus;* Trx 2081 & 5117, *Tyrannosaurus rex* FMNH PR 2081 and AMNH 5117. Other abbreviations as in Figure 6.3.
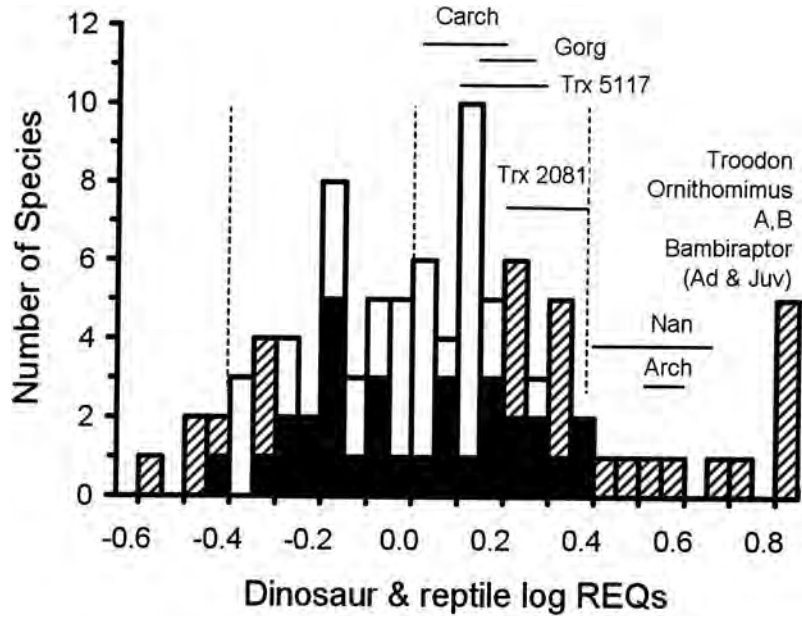
6.6. $\log_{10}$ BEQs of *Archaeopteryx,* dinosaurs, and 174 bird species. Bird log BEQ range, −0.447– 0.475; mean, 0.0002; SD, 0.1815; mean ± 2 SDs, −0.363–0.363. Extant bird species are underlined. Open bars, birds; cross-hatched bars, dinosaurs; filled bars, bird and dinosaur bars of same height. Dashed lines and abbreviations as in Figure 6.4.
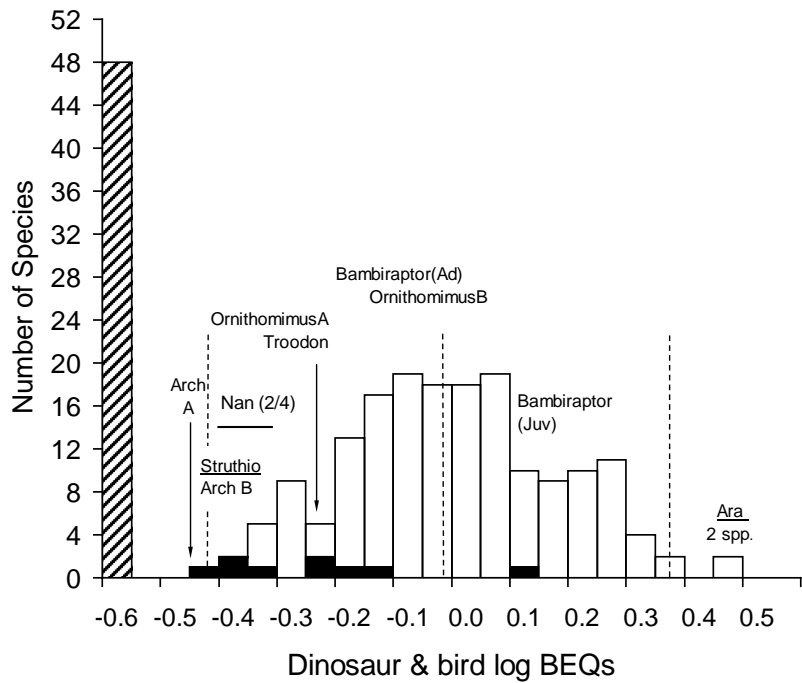
Body Mass, Endocast Volume, Brain Mass, and Cerebrum Mass in Dinosaurs

Tyrannosaurus is assigned a MBd range of 5000–7000 kg, from Holtz (1991) and Henderson (1999; modified from 7200 kg), respectively, unless other estimates for individual specimens were available. This MBd range encloses the estimates of 6250 kg for *T. rex* by Christiansen (1999),

of 6650.9 kg by Seebacher (2001), and estimates by all researchers cited by Seebacher (2001), except Anderson et al. (1985). The estimate by Anderson et al. (1985) was more than 2.8 SDs below the mean of estimates by six researchers using various methods, more than twice the next greatest deviation (analysis of data in Seebacher 2001). The large FMNH PR 2081 specimen of *T. rex* had an estimated ontogenetic age of 28.9 years (Erickson et al. 2004). The *Gorgosaurus* MBd estimate (1105 kg) is calculated from *Cf* (mm) of RTMP 94.12.602 by Erickson et al. (2004), who suggests it is likely an underestimate (Erickson, pers. comm., 2005). Estimates for individual *T. rex* specimens of 5634 kg for FMNH PR 2081 and 4312 kg for AMNH 5117 kg are from Erickson et al. (2004) and Erickson (pers. comm., May 2006) and are based on the equation of Anderson et al. (1985). Given the discrepancy between the results of Anderson et al. (1985) and those of other researchers for *T. rex,* these are probable underestimates but permit comparisons to the other *T. rex* specimens. Anderson et al. (1985) produced their equation for bipedal dinosaurs by fitting a regression line with a slope of 2.73 to the MBd: *Cf* data point for a model and femur of *Troodon.* Their *T. rex* and *Allosaurus* MBd estimates were two thirds of Colbert's (1962) estimates from scale models, and their *Anatosaurus* MBd estimate exceeded the estimate from Colbert's (1962) model. The 2.73 slope was the exponent of an equation predicting MBd from the sum of femur and humerus circumferences of 33 mammal species, of which 29 massed under 500 kg and only two exceeded 1500 kg (Anderson et al. 1985). This exponent may notably underestimate MBd in large terrestrial amniotes (>1500 kg) because leg bones of the smaller amniotes have smaller duty factors (Alexander et al. 1979) and experience greater compressive forces during locomotion (Hurlburt 1996). The method may be more accurate for smaller theropods near the mass of *Troodon* (45 kg), such as *Bambiraptor* and *Nanotyrannus.*

Body mass estimates for *Allosaurus* of 2300 and 1400 kg were obtained from Colbert (1962) and Anderson et al. (1985), respectively. Body masses of 5000 and 7000 kg were used for *Carcharodontosaurus,* assuming its MBd to be in the same range as *T. rex,* following Larsson et al. (2000).

Table 6.1 lists endocast volumes for theropods. The DGI endocast volume (404 ml) estimate for AMNH 5029 is about 106 percent of the presumably more accurate CT estimate (381.76 ml) and is not used in the following analyses of *T. rex.* The over-estimate of endocast volume by the DGI method is likely due to erroneous inclusion of volumes of the concave regions dorsal to the brainstem and lateral to the optic lobes and cerebellum, but it is accurate when the subject analyzed is convex (Hurlburt 1999). The EV produced by Larsson et al. (2000) for AMNH 5029 appears to be an underestimate caused by methodological limitations and is not used in the following analyses. Higher values were obtained in this study for the *Allosaurus* EV than by Larsson et al. (2000), although both used water displacement. The estimates calculated in this study are used here because there was more control, but EQs resulting from both sets of estimates are similar. Double Graphic Integration produced higher

Table 6.1. Body mass, endocast volumes, associated brain volumes, REQs and log REQs of large alligators (ROM R8328 and R8333) and large theropod dinosaurs

Specimen	Meth	EV (ml)	MBr 37% (ml)	MBr 50% (ml)	MBd (t)	REQ 37%	REQ 50%	log REQ 37%	log REQ 50%
T 5117 (4.3)	CT	313.64	116.05	156.8	4.312	1.604	2.168	0.205	0.336
T 5117 (7)	CT	313.64	116.05	156.8	7.00	1.227	1.659	0.089	0.220
T 5029 (5)	CT	381.76	141.25	190.9	5.00	1.799	2.432	0.255	0.386
T 5029 (7)	CT	381.76	141.25	190.9	7.00	1.494	2.019	0.174	0.305
T 2081 (5.65)	CT	414.19	153.25	207.1	5.654	1.824	2.465	0.261	0.392
T 2081 (7)	CT	414.19	153.25	207.1	7.00	1.621	2.190	0.210	0.340
T 5029 (5)	DGI	404.0	149.48	202.0	5.00	1.904	2.573	0.280	0.410
G 1247	CT	128.93	47.70	64.47	1.11	1.400	1.892	0.146	0.277
N 7541 (0.24)	CT	111.18	41.14	55.59	0.24	2.812	3.800	0.449	0.580
N 7541 (0.28)	CT	111.18	41.14	55.59	0.28	2.597	3.510	0.414	0.545
N 7541 (0.24)	CT	111.18	*67% = 74.491*		0.24	*67% = 5.092*		*67% = 0.707*	
N 7541 (0.28)	CT	111.18	*67% = 74.491*		0.28	*67% = 4.703*		*67% = 0.672*	
C Din 1 (5)	DGI	263.68	97.56	131.8	5.00	1.243	1.680	0.094	0.225
C Din 1 (7)	DGI	263.68	97.56	131.8	7.00	1.032	1.394	0.014	0.144
C Din 1 (5)	Lsr	224	82.88	112	5.00	1.056	1.427	0.024	0.154
A 294 (1.4)	WaH	187.9	69.52	93.95	1.40	1.791	2.420	0.253	0.384
A 294 (2.3)	WaH	187.9	69.52	93.95	2.30	1.361	1.839	0.134	0.265
A 294 (1.4)	WaL	169.0	62.53	84.5	1.40	1.610	2.176	0.207	0.338
ROM R8328	WaH	27.34	10.50	—	0.238	0.721	—	0.060	—
ROM R8333	WaH	32.94	10.51	—	0.277	0.663	—	0.055	—

Note: REQ = MBr/($0.0155 \times$ MBd$^{0.553}$), both MBr and MBd in grams. Non-avian reptile REQ range: 0.402–2.404. Nonavian reptile log REQ mean ± 2 SDs, −0.403–0.385. MBr, brain mass estimated from EV using alligator MBR:EV ratios. 37% or 50% indicates ratio used, but 67% used for *Nanotyrannus* (italicized in table). Two MBd estimates for most species (see Methods). Numbers in parentheses after specimens indicate MBd. Abbreviations: A 294, *Allosaurus* UUVP 294; ROM R8328 and R8333, data for ROM alligator specimens; C Din 1, *Carcharodontosaurus saharicus* SGM Din-1; CT, computed tomography scans; DGI, Double Graphic Integration; EV, endocast volume; G 1247, *Gorgosaurus* ROM 1247; Lsr, laser scan (Larsson et al. 2000); MBd, body mass; MBr, brain mass; Meth, method by which volumes were obtained from endocasts; MBd, body mass in metric tons; MBr, brain mass (% indicates ratio); N 7541, *Nanotyrannus lancensis* CMNH 7541; REQ, Reptile Encephalization Quotient; T 5117, *Tyrannosaurus rex* AMNH 5117; T 5029, *T. rex* AMNH 5029; T 2081, *T. rex* FMNH PR 2081; WaH, volumes by water displacement by Hurlbut; WaL, volumes by water displacement by Larsson.

values than the laser scan for *Carcharodontosaurus* and are perhaps less accurate for reasons given above, but EQs again are similar between values from laser scan and DGI methods.

Dinosaur MBr was estimated by the mean of the MBr:EV ratio of the largest males and female alligators (37 percent) because the sexes of individual dinosaur specimens is unknown. Similarly, dinosaur cerebrum mass was obtained by applying the mean ratio of the largest males and females (42 percent). The possibility that some dinosaur specimens were not full adults is dealt with by application of the 50 percent MBr:EV ratio. All dinosaurs were treated as adults, including *Allosaurus* UUVP 294, which J. Madsen (pers. comm., June 2005) considered to be an adult despite Rogers (1999) regarding it as a subadult. Brain mass was considered to equal EV in small theropods and *Archaeopteryx*.

Table 6.1 provides estimates of body mass (MBd), endocast volume (EV), estimated brain mass (MBr), and methods by which EV was obtained. Figure 6.3 plots brain body data of large theropods, small theropods and other dinosaurs (stegosaurs, ankylosaurs, ceratopsians, and

Table 6.2. BEQs and log BEQs of theropod dinosaurs

Specimen	Meth	EV (ml)	MBd (t)	BEQ (37%)	BEQ (50%)	log BEQ (37%)	log BEQ (50%)
T 5117 (4.3)	CT	313.64	4.312	0.121	0.163	−0.918	−0.787
T 5117 (7)	CT	313.64	7.00	0.091	0.123	−1.042	−0.911
T 2081 (5.65)	CT	414.19	5.654	0.136	0.184	−0.867	−0.736
T 2081 (7)	CT	414.19	7.00	0.120	0.162	−0.921	−0.791
T 5029 (5)	CT	381.76	5.00	0.135	0.182	−0.871	−0.740
T 5029 (7)	CT	381.76	7.00	0.110	0.149	−0.957	−0.826
T 5029 (5)	DGI	404.0	5.00	0.143	0.193	−0.846	−0.715
T 5029 (7)	DGI	404.0	7.00	0.117	0.158	−0.932	−0.801
G 1247	CT	128.93	1.11	0.111	0.150	−0.955	−0.824
N 7541 (0.24)	CT	118.18	0.24	0.236	0.318	−0.628	−0.497
N 7541 (0.28)	CT	118.18	0.28	0.216	0.292	−0.665	−0.534
N 7541 (0.24)	CT	118.18	0.24	67% = *0.427*		67% = *−0.370*	
N7541 (0.28)	CT	118.18	0.28	67% = *0.392*		67% = *−0.407*	
A 294 (1.4)	WaH	187.9	1.40	0.141	0.190	−0.852	−0.722
A 294 (2.3)	CT	"	2.30	0.105	0.142	−0.979	−0.849
C Din 1 (5)	DGI	263.68	5.00	0.093	0.126	−1.031	−0.901
C Din 1 (7)	DGI	"	7.00	0.076	0.103	−1.118	−0.987
ROM R8328	WaH	10.50	0.238	0.060	—	−1.219	—
ROM R8333	WaH	10.51	0.277	0.055	—	−1.258	—

Note: BEQ = MBr/(0.117 × MBd$^{0.590}$); both MBr and MBd in grams. Encephalization Quotients are estimated from MBd and estimated MBr in Table 6.1. Note smallest subadult ratio (67%) used for *Nanotyrannus* in 50% column (italicized in table). Bird BEQ range: 0.357–2.986. Bird log BEQ mean ± 2 SDs, −0.363–0.363. Abbreviations: BEQ, Bird Encephalization Quotient. Other abbreviations as in Table 6.1.

Species	MBd (g)	EV (ml)	REQ	BEQ	log REQ	log BEQ
Ornithomimus A	175000	87.9	7.145	0.606	0.854	−0.218
Ornithomimus B	125000	87.9	8.606	0.739	0.935	−0.132
Troodon	45000	41.0	7.067	0.630	0.849	−0.201
Bambiraptor Juv	2240	14.00	12.680	1.263	1.103	0.101
Bambiraptor Ad	6581.96	14.0	6.986	0.669	0.844	−0.175
Archaeopteryx A	468	1.60	3.445	0.363	0.537	−0.440
Archaeopteryx B	468	1.76	3.789	0.400	0.579	−0.398

Table 6.3. Body mass, endocast volume, EQs and log EQs for three Late Cretaceous small theropods and *Archaeopteryx*

Note: Endocast data from *Archaeopteryx* (BMNH 37001), *Bambiraptor* (KUVP 129737), *Ornithomimus* (NMC 12228), and *Troodon* (RTMP 86.36.457 and RTMP 79.8.1). Data from Hurlburt (1996), except for *Bambiraptor* and *Archaeopteryx* (see text). MBr = EV since the brain filled the cranial cavity. Abbreviations: Ad, adult; Juv, juvenile. Other abbreviations as in Tables 6.1 and 6.2.

sauropods) with slopes and polygons that surround brain-body data of reptile (N = 62) and bird (N = 174) species.

Relative Brain Size in Dinosaurs

Tables 6.1 and 6.2 provide REQs, BEQs, log REQs, and log BEQs for all large theropods analyzed, and Table 6.3 gives data for three Late Cretaceous small theropods and *Archaeopteryx*. Figures 6.5 and 6.6 are histograms of log REQs and log BEQs of large theropods, small theropods, and other dinosaurs. Encephalization Quotients based on 37 percent MBr:EV ratios are more consistent with the analytical method, but EQs from 50

percent ratios are provided for reasons given above. Comparisons among species are made using raw (i.e., not log-transformed) EQ data, which are more easily comprehended; comparisons to reptile and bird distributions are made with log EQs, which are normally distributed, unlike raw EQs.

TYRANNOSAURIDAE *Tyrannosaurus rex* has the largest relative brain size of any dinosaur, other than some small theropods. Reptile Encephalization Quotients of *T. rex* range from 1.2 to 1.82 (37 percent ratio) and 1.66 to 2.47 (50 percent ratio). The highest *T. rex* log REQ (50 percent ratio) is no more than 2 SDs above the mean of reptile REQs, with one exception, from a 50 percent MBr:EV ratio for FMNH PR 2081, an unlikely ratio because this is the ontogenetically oldest and most mature *T. rex* in the sample (Table 6.1; Fig. 6.5). A high log REQ from a 50 percent MBr:EV ratio for the DGI EV value is discounted because DGI probably overestimates total EV. Log BEQs of *T. rex* are almost 4 SDs below the mean bird log BEQ and well below the lowest bird log BEQ (−0.447; see Table 6.2 and Fig. 6.6). It appears that the body size sequence of *T. rex* specimens increases through AMNH 5117, AMNH 5029, and FMNH PR 2081, and the pattern of EV increasing with body size is typical of alligators, as is continuing increase in body size with ontogenetic age (Table 6.1).

Gorgosaurus (ROM 1247) is less encephalized than *T. rex*, and only the REQ (1.89) derived from a 50 percent MBr:EV ratio reaches the lower end (37 percent ratio) of the REQ range of *T. rex* (Table 6.2; Fig. 6.5), while a 67 percent MBr:EV ratio produces an REQ of 2.54. ROM 1247 is clearly a subadult (Carr 1999). If *Gorgosaurus* and *T. rex* follow a similar growth trajectory, these REQs are lower than would be expected of a subadult *T. rex* because ontogenetically younger alligators have larger relative brain sizes than adults.

Reptile Encephalization Quotients of *Nanotyrannus* (e.g., 2.812–2.597 for a 37 percent MBr:EV ratio) clearly exceed the REQ range of *Tyrannosaurus rex*, even for a 50 percent MBR:EV ratio for *T. rex* (Table 6.1). Log REQs (37 percent ratio: 0.414–0.449) are more than 2 SDs above the reptile log REQ mean (mean + 2 SDs = −0.403–0.385). Larger MBR:EV ratios produce even higher REQs for *Nanotyrannus* (Table 6.1). Expressed as SDs of reptile log REQs (*z*-scores), *Nanotyrannus* log REQs are 0.86 SDs above *T. rex* values whether comparing 37 percent or 50 percent MBr:EV ratios and are as much as 2.99 SDs above the reptile log REQ mean (Sokal and Rohlf 1981). When calculated from a 67 percent MBr:EV ratio, *Nanotyrannus* log REQs are 3.64–3.64 SDs above the reptile mean and about 1.5–2.0 SDs above the highest *T. rex* values (*z*-scores = 1.47 for 37 percent ratio, 2.13 for 50 percent ratio; see Table 6.1). If *Nanotyrannus* is a juvenile or young subadult of *T. rex* or a similar tyrannosaurid, the difference between its log REQs and those of an adult tyrannosaurid such as *T. rex* approximates the difference (2.0 SDs) between log REQs of the smallest subadult and largest adult alligators in the comparison sample (Tables 6.1, 6.2; Figs. 6.2, 6.3). *Nanotyrannus* log REQs are consistent with those of a young subadult or older juvenile

tyrannosaurid. Conversely, even the smallest *Nanotyrannus* MBr estimate produces REQs much larger than those of any adult dinosaur whose brain does not fill the cranial cavity; we consider this to be unlikely and therefore inconsistent with adult ontogenetic status. *Nanotyrannus* log BEQs are more than 2 SDs below the bird log BEQ mean, even with the large 67 percent MBR:EV ratio (Table 6.2; Fig. 6.6).

CARCHARODONTOSAURUS AND *ALLOSAURUS*   Data for the two allosauroids indicate that *Carcharodontosaurus* had an REQ range of 1.032–1.240, less than that of *Allosaurus* UUVP 294 (1.361–1.791) and about two thirds that of *Tyrannosaurus rex* (Table 6.1; Figs. 6.3, 6.5). Neither dinosaur enters the bird BEQ range (Table 6.2; Fig. 6.6). However, the spread of *Allosaurus* MBd estimates is wide, and REQs from the larger MBd estimate approximate those of *Carcharodontosaurus*.

SMALL THEROPODS AND *ARCHAEOPTERYX*   *Archaeopteryx* Brain mass ranged from 1.6 to 1.76 ml, exceeding an estimate of 1.47 ml from DGI of the figure of *Archaeopteryx* in Bühler (1985; also see Hurlburt 1996). Body mass was 468 g (Elzanowski 2002). The log REQ range (0.537–0.579) is more than 2.5 but slightly less than 3 SDs above the mean reptile log REQ, and its brain-body points overlapped the lower edge of the bird brain-body polygon (Figs. 6.3, 6.5). The log BEQs of *Archaeopteryx* (−0.365–−0.415) are within the bird log BEQ range, overlapping values for *Struthio* (Figs. 6.3, 6.6), although slightly more than 2 SDs below the bird log BEQ range. These results falsify the hypothesis that *Archaeopteryx* lies between the reptile and bird relative brain-body distributions (Larsson et al. 2000).

Cerebrocast:Endocast Volume and Cerebrum:Brain Mass Ratios in Theropod Dinosaurs

Larsson et al. (2000) suggested that relative cerebrum size increased in coelurosaurian dinosaurs, the lineage leading to and including birds, relative to allosauroids, a lineage including *Carcharodontosaurus*, a large theropod approximately equal in MBd to *Tyrannosaurus rex*. They compared the ratio of cerebrocast to EV, considering it equivalent to the MCb:MBr ratio. To test this hypothesis, we computed the same ratios using MCb estimates from applying the alligator MCb:CbcV ratio to CT scans of dinosaur endocasts. We also combine the result of a laser scan for EV with DGI of the cerebrocast of *Carcharodontosaurus* because DGI is fairly accurate for convex solids but less so for entire endocasts, as discussed above.

Cerebrocast volume:endocast volume ratios from CT scans of the three *Tyrannosaurus rex* and *Gorgosaurus* specimens ranged from 41.1 to 43.5 percent, and MCb:MBr ratios ranged from 47.5 to 49.53 percent (Tables 6.4 and 6.5). While MCb:MBr ratios estimated for *T. rex* enter the lower end of ratios typical of birds, they are very close to ratios (45.9–47.9 percent) typical of the smallest sexually mature alligators (Table 6.5).

Table 6.4. Endocast (EV) and cerebrocast (CbcV) volumes, associated brain and cerebrum mass (MCb), and associated CbcV:EV and MCb:MBr ratios of large alligators and theropod dinosaurs

Specimen	Meth	Brain part of EV (ml)	CbcV (ml)	EV less CbcV (ml)	MBr = 37% EV (ml)	MCb = 42% CbcV (ml)	CbcV: EV Ratio (%)	MBr: MCb Ratio (ml)
T 5117	CT	313.64	131.4	182.3	116.05	55.17	41.88	47.54
T 2081	CT	414.19	170.2	244.0	153.25	71.48	41.09	46.65
T 5029	CT	381.76	165.9	215.8	141.25	69.69	43.47	49.34
T 5029	DGI	404.0	147.8	256.2	149.48	62.07	36.58	41.53
T 5029	Lsr	343	111.8	231.2	126.91	46.96	32.59	37.00
G 1247	CT	128.93	56.0	72.9	47.70	23.52	43.43	49.30
N 7541 (Ad)	CT	111.18	64.73	46.45	41.14	27.19	58.22	66.09
N 7541 (Sub)	CT	111.18	64.73	46.45	74.49	46.61	58.22	62.57
C Din 1	DGI	263.68	83.1	180.6	97.56	34.90	31.51	35.77
C Din 1	Lsr,DGI	224	83.1	140.9	82.88	34.90	37.10	42.11
C Din 1	Lsr	224	53.7	170.3	—	—	23.97	24.00
A 294	WaH	187.9	101.7	86.2	69.52	42.71	54.12	61.44
A 294	WaL	169.0	46.7	122.3	—	—	27.63	27.63
ROM R8328 4	WaH	27.34	10.9	6.2	10.50	4.28	39.87	40.76
ROM R8333	WaH	32.94	11.3	6.0	10.51	4.51	34.15	42.91

Note: Theropod dinosaur volumes were calculated using MBr:EV (37%) and MCb:CbcV (42%) ratios of largest adult alligators. *Nanotyrannus* (N 7541) EV and CbcV were estimated using ratios from smallest subadult alligators, which were MBr:EV, 67%, and MCb:CbcV, 72%. Both Larsson et al. (2000) and the present study obtained *Allosaurus* volumes by water displacement. For *Carcharodontosaurus,* one CbcV:EV and one MCb:MBr ratio were obtained by combining CbcV from DGI with EV from a laser scan (Larsson et al. 2000). Abbreviations: Ad, adult; CbcV, cerebrocast volume; Sub, sub-adult. Other abbreviations as in Tables 6.1 and 6.2.

Table 6.5. Cerebrocast: endocast volume (CbcV:EV) and cerebrum:brain mass (MCb:MBr) ratios of dinosaurs, alligators, nonavian reptiles, and birds. *Ameiva* data from Platel (1979).

Specimen	Meth	CbcV:EV Ratio (%)	MCb:MbrRatio (%)
T. rex (N = 3)	CT scans	41.1–43.5	46.6–49.3
G 1247		43.3	49.3
N 7541 (Ad)		58.2	66.1
C Din 1 (5)	DGI	31.5	35.8
C Din 1 (7)	Lsr-DGI	37.1	42.1
A 294		54.1	61.4
Two smallest alligators		37.9–43.8	44.8–47.9
Two largest alligators		34.2–39.9	40.8–42.9
Reptiles: Mn ratio = 33.52. Actual range in column 3			23.57–43.56
Reptiles: Mn ratio ± 2 SDs			25.6–41.5
Ameiva and largest alligator *Alligator*			31.4, 40.8
Birds: Mn ratio = 63.7. Actual range in column 3			44.6–82.3
Birds: Mn ratio ± 2 SDs			47.4–80.0

Note: MCb:MBr ratios were calculated from cast volumes for all fossil specimens. Only MCb:MBr ratios are provided for extant species other than alligators. For the two smallest alligators, TL = 1613 mm and 1985 mm; for the two largest alligators, TL = 3759 mm and 3810 mm. Abbreviations: Mn, mean; Rep, Reptile; TL, snout to tail tip length. Other abbreviations as in Tables 6.1 and 6.2.

Because it cannot be determined whether a larger MCb:MBr ratio arises from a larger MCb or a decline in one or more of the other brain divisions, this result can be taken to indicate an avian-like condition, but tyrannosaurid MCb:MBr ratios are high. These ratios do not reflect the significant difference in brain size relative to body size between *T. rex* and birds, and thus that bird cerebrum size is relatively larger than in *T. rex*. The same applies to differences in relative cerebrum size between *Carcharodontosaurus* and *T. rex*. Ratios are useful in comparisons between related taxa of similar relative brain size.

Nanotyrannus has a CbcV:EV ratio of 58.2 percent. Its MCb:MBr ratios are 66.1 percent, using adult brain:endocast ratios, and 62.6 percent, using youngest subadult brain:cast ratios (Tables 6.4, 6.5). These CbcV:EV and MCb:MBr ratios are 15 percent or more higher than for other tyrannosaurids and than for alligators and other reptiles (Tables 6.4 and 6.5). While these ratios resemble those of the *Allosaurus* endocast, the endocasts are dissimilar in appearance, whereas the *Nanotyrannus* endocast resembles those of other tyrannosaurids. Because higher MCb:MBr ratios are typical of ontogenetically younger alligators, these data support the hypothesis that *Nanotyrannus* is a young subadult or juvenile, as do req data.

Larsson et al. (2000) proposed that cerebral volume is 100 percent greater in *T. rex* than in *Carcharodontosaurus*, accounting in part for the larger relative brain size of *T. rex*. Cerebrum mass:brain mass ratios of *Carcharodontosaurus* are as high as 42.1 percent when combining laser-scanned ev and dgi of CbcV, comfortably in the upper reptile range and only 5–7 percent less than those of *T. rex*. This rejects the hypothesis that cerebral volume is 100 percent greater in *T. rex* than in *Carcharodontosaurus* (Larsson et al. 2000). A quite high MCb:MBr ratio (61.4 percent) was obtained for *Allosaurus*. This may be due to experimental error or to relative size differences of other brain components.

Summary

The purpose of this study was assessment of the relative brain and relative cerebrum size of tyrannosaurid dinosaurs (*Tyrannosaurus rex*, *Gorgosaurus*, and *Nanotyrannus*) and comparison of these data to results for allosauroid dinosaurs (*Allosaurus* and *Carcharodontosaurus*). To measure relative brain size, EQs (Encephalization Quotients) were calculated using brain-body data for extant non-avian reptile species ($N = 62$) and extant bird species ($N = 174$). We compared dinosaur log EQs to the ranges of reptile log REQs and bird log BEQs because these samples were normally distributed, unlike either reptile REQs or bird BEQs. To estimate brain mass (MBr) from dinosaur endocast volume (ev), the MBr:EV ratio was determined in a size series, ranging from the smallest sexually mature to the largest commonly encountered size, of *Alligator mississippiensis*, an examplar of the extant archosaurian clade Crocodylia. The mean of MBr:EV ratios of the largest male and female was 37 percent, and the ratio was 67 percent in the smallest sexually mature

alligators. Dinosaur MBr and MCb (cerebrum mass) were estimated from virtual endocasts produced from CT scans and also from laser scans and double graphic integration. Brain mass was estimated from EV in dinosaurs using the adult ratio and in *Nanotyrannus*, a possible juvenile, also using the youngest subadult ratio. Estimates were also made using the traditional 50 percent MBr:EV ratio, for comparison to previous studies and because this is the MBr:EV ratio in midrange subadult alligators, appropriate for the *Gorgosaurus* specimen. Relative brain sizes of small theropods and a wide sample of other dinosaurs were also determined to provide a context for evaluation of these large theropods. The cerebrum mass:brain mass (MCb:MBr) range was compared among dinosaurs and between dinosaurs and each of reptiles and birds.

Conclusion

This is the first study to use empirically based brain:endocast (MBr:EV) and cerebrum:cerebrocast (MCb:CbcV) ratios, derived from extant alligators, to estimate dinosaur relative brain and relative cerebrum size. It is also the first to measure dinosaur relative brain size by Reptile Encephalization Quotients (REQs) and Bird Encephalization Quotients (BEQs). Both MBr and EV increase with body size in alligators, but the MBr rate is significantly less, so that the MBr:EV ratio in alligators declines with increasing body size, as does REQ. Other than small theropods, which are well within the relative brain size range of extant birds, *Tyrannosaurus rex* has the largest relative brain size of any dinosaur but is within the relative brain size of extant reptiles and within 2 SDs of the mean of reptile log REQs. It is well below the relative brain size range of extant birds. *Gorgosaurus* plots at the lower end of log REQs of *T. rex.* The log REQs of *Nanotyrannus lancensis* are anomalously high for an adult but consistent with a juvenile or very young subadult age. The difference between its log REQs and those of an adult *T. rex* paralleled the difference between the youngest subadult and the oldest adult alligators of the comparison sample, when measured as log reptile REQ SD units. *Nanotyrannus* MCb:MBr ratios were also consistent with an older juvenile or young subadult ontogenetic age. *Carcharodontosaurus* has an REQ about two thirds that of *T. rex* and showed no increase in relative brain size compared to the late Jurassic *Allosaurus*, supporting a hypothesis of a trend of larger relative brain size in coelurosaurian compared to allosauroid dinosaurs. All three late Cretaceous small theropods (*Bambiraptor*, *Troodon*, and *Ornithomimus*) plotted well within in the bird log BEQ range and well above the reptile log REQ range. The relative brain size range of *Archaeopteryx* overlapped the lower edge of the bird log BEQ range and exceeded the reptile REQ range. Both tyrannosaurids and allosauroids had cerebrum mass:brain mass (MCb:MBr) ratios in the high end of the reptile range, and *T. rex* entered the low end of the bird MCb:MBr range. These values were also similar to those of subadult alligators. The MCb:MBr ratio of *Carcharodontosaurus* was less than 7

percent below that of *T. rex*, falsifying a hypothesis that a larger cerebrum accounted for the larger brain of *T. rex.*

Acknowledgments

Literature Cited

Alexander, R. McN. 1985. Mechanics of posture and gait of some large dinosaurs. *Zoological Journal of the Linnean Society* 83:1–25.

Alexander, R. McN., G. M. O. Maloiy, B Hunter, A. S. Jayes, and J. Nturibi. 1979. Mechanical stresses in fast locomotion of buffalo (*Syncerus caffer*) and elephant (*Loxodonta africana*). *Journal of Zoology* 189:135–144.

Anderson, J. F., A. Hall-Martin, and D. A. Russell. 1985. Long-bone circumference and weight in mammals, birds, and dinosaurs. *Journal of Zoology,* London 207:53–61.

Andrews, C. W. 1897. Note on the cast of the brain of *Iguanodon. Annals and Magazine of Natural History.* 115:585–591.

Bühler, P. 1985. On the morphology of the skull of *Archaeopteryx;* pp. 135–140 in M. K. Hecht, J. H. Ostrom, G. Viohl, and P. Wellnhofer (eds.), *The Beginnings of Birds.* Freunde der Jura-Museums, Eichstatt.

Burnham, D. A. 2004. New information on *Bambiraptor feinbergi* (Theropoda: Dromaeosauridae) from the Late Cretaceous of Montana; pp. 67–111 in P. J. Currie, E. B. Koppelhus, M. A. Shugar, and J. L. Shugar (eds.), *Feathered Dragons: Studies on the Transition from Dinosaurs to Birds.* Indiana University Press, Bloomington.

Carr, T. D. 1999. Craniofacial ontogeny in Tyrannosauridae (Dinosauria, Theropoda). *Journal of Vertebrate Paleontology* 19:497–520.

Christiansen, P. 1999. Long bone scaling and limb posture in non-avian theropods: evidence for differential allometry. *Journal of Vertebrate Paleontology* 19:666–680.

Colbert, E. H. 1962.The weights of dinosaurs. *American Museum Novitates,* no. 2076.

Currie, P. J. 2003. Allometric growth in tyrannosaurids (Dinosauria, Theropoda) from the Upper Cretaceous of North America and Asia. *Canadian Journal of Earth Sciences* 40:651–665.

Currie, P., and X. Zhao. 1993. A new troodontid (Dinosauria, Theropoda) braincase from the Dinosaur Park Formation (Campanian) of Alberta. *Canadian Journal of Earth Sciences* 30:2231–2247.

Dendy, A. 1910. On the structure, development and morphological interpretation of pineal organs and adjacent parts of the brain in the Tuatara (*Sphenodon punctatus*). *Philosophical Transactions of the Royal Society,* ser. B, 201:227–331.

Dominguez Alonso, P. D., A. C. Milner, R. A. Ketcham, M.J. Cookson, and T. B. Rowe. 2004. The avian nature of the brain and inner ear of *Archaeopteryx. Nature* 430:666–669.

Elzanowski, A. 2002. Archaeopterygidae (Upper Jurassic of Germany); pp. 129–159 in I. Chiappe and L. M. Witmer (eds.), *Mesozoic Birds: Above the Heads of Dinosaurs* University of California Press, Berkeley.

Erickson, G. M., P. J. Makovicky, P. J. Currie, M. A. Norell, S. A. Yerby, and C. A. Brochu. 2004. Gigantism and comparative life-history parameters of tyrannosaurid dinosaurs. *Nature* 430:772–779.

Evans, D. C. 2005. New evidence on brain–endocranial cavity relationships in ornithischian dinosaurs. *Acta Palaeontologica Polonica* 50:617–622.

Galton, P. M. 2001. Endocranial casts of the plated dinosaur *Stegosaurus* (Upper Jurassic, Western USA): a complete undistorted cast and the original specimens of Othniel Charles Marsh; pp. 103–129 in K. Carpenter (ed.), *The Armored Dinosaurs.* Indiana University Press, Bloomington.

Gilmore, C. W. 1946. A new carnivorous dinosaur from the Lance Formation of Montana. *Smithsonian Miscellaneous Collections* 106:1–19.

Henderson, D. B. 1999. Estimating the masses and centers of mass of extinct animals by 3-D slicing. *Paleobiology* 25:88–106.

Holtz, T. R. 1991. Limb proportions and mass estimations in the Theropoda. *Journal of Vertebrate Paleontology* 11:35A.

Hopson, J.A. 1977. Relative brain size and behaviour in archosaurian reptiles. *Annual Review of Ecology and Systematics* 8:429–48.

Hopson, J. A. 1979. Paleoneurology; pp. 39–146 in C. Gans, R. G. Northcutt, and P. S. Ulinski (eds.), *Biology of the Reptilia,* vol. 9: *Neurology A.* Academic Press, New York.

Hopson, J. A. 1980. Relative brain size in dinosaurs: implications for dinosaurian endothermy; pp. 287–310 in R. D. K. Thomas and E. C. Olson (eds.), *A Cold Look at the Warm-Blooded Dinosaurs.* American Association for the Advancement of Science, Washington, D.C.

Hurlburt, G. R. 1982. Comparisons of brains and endocranial casts in the domestic dog *Canis familiaris* Linnaeus 1758. M.Sc. thesis, University of Toronto, Toronto, Ontario.

Hurlburt, G. R. 1996. Relative brain size in recent and fossil amniotes: determination and interpretation. Ph.D. dissertation, University of Toronto, Toronto, Ontario, 250 pp.

Hurlburt, G. R. 1999. Comparison of body mass estimation techniques, using recent reptiles and the pelycosaur *Edaphosaurus boanerges. Journal of Vertebrate Paleontology* 19:338–350.

Hurlburt, G. R., and L. Waldorf. 2002. Endocast volume and brain mass in a size series of alligators. *Journal of Vertebrate Paleontology* 23(3, suppl.):69A.

Iwaniuk, A. N., and J. E. Nelson. 2002. Can endocranial volume be used as an estimate of brain size in birds? *Canadian Journal of Zoology* 80:16–23.

Jerison, H. J. 1973. *Evolution of the Brain and Intelligence.* New York: Academic Press.

Larsson, H. C. E. 2001. Endocranial anatomy of *Carcharodontosaurus saharicus* (Theropoda: Allosauroidea) and its implications for theropod brain evolution; pp. 19–33 in D. H. Tanke and K. Carpenter (eds.), *Mesozoic Vertebrate Life.* Indiana University Press, Bloomington.

Larsson, H. C. E., P. C. Sereno, and J. A. Wilson. 2000. Forebrain enlargement among nonavian theropod dinosaurs. *Journal of Vertebrate Paleontology* 20:615–618.

Lefebvre, L., N. Nicolakakis, and D. Boire. 2002. Tools and brains in birds. *Behaviour* 139:939–973.

Marino, L. 2002. Convergence in complex cognitive abilities in cetaceans and primates. *Brain, Behavior and Evolution* 59:21–32.

Nicholls, E. L., and A. P. Russell 1981. A new specimen of *Struthiomimus altus* from Alberta, with comments on the classificatory characters of Upper Cretaceous ornithopods. *Canadian Journal of Earth Sciences* 18:518–526.

Norman, D. B. 1986. On the anatomy of *Iguanodon atherfieldensis* (Ornithischia: Ornithopoda). *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique* 56: 281–372.

Norman, D. B., and D. B. Weishampel. 1990. Iguanodontidae and related ornithopods; pp. 510–533, in D. B. Weishampel, P. Dodson, and H. Osmólska, eds, *The Dinosauria.* University of California Press, Berkeley.

Osmólska, H. 2004. Evidence on relation of brain to endocranial cavity in oviraptorid dinosaurs. *Acta Paleontologica Polonica* 49:321–324.

Platel, R. 1976. Analyse volumetrique comparee des principales subdivisions encephaliques chez les reptiles Sauriens [Lizards]. *Journal für Hirnforschung* 17:513–537.

Platel, R. 1979. Brain weight–body weight relationships; pp. 147–171 in C. Gans, R. G. Northcutt, and P. S. Ulinski (eds.), *Biology of the Reptilia,* vol. 9: *Neurology A.* Academic Press, New York.

Rich, T. H., and P. Vickers-Rich. 1988. A juvenile dinosaur brain from Australia. *National Geographic Research* 4:148.

Rogers, S. W. 1999. *Allosaurus,* crocodiles, and birds: evolutionary clues from spiral computed tomography of an endocast. *Anatomical Record* 257:162–173.

Russell, D. A. 1972. Ostrich dinosaurs from the late Cretaceous of Western Canada. *Canadian Journal of Earth Sciences* 9:375–402.

Seebacher, F. 2001. A new method to calculate allometric length-mass relationships of dinosaurs. *Journal of Vertebrate Paleontology* 21:51–60.

Sokal, R. B., and F. J. Rohlf. 1981. *Biometry.* W. H. Freeman, New York.

Witmer, L. M., S. Chatterjee, J. Franzosa, and T. Rowe. 2003. Neuroanatomy of flying reptiles and implications for flight, posture and behaviour. *Nature* 425:950–953.

Woodward, A., C. T. Moore, and M. F. Delaney. 1991. Experimental Alligator Harvest: Final Report. Study no. 7567. Bureau of Wildlife Research, Florida Game and Fresh Water Fish Commission, Tallahassee, 118pp.