LETTER

Evolutionary origins of the avian brain

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Features that were once considered exclusive to modern birds, such as feathers and a furcula, are now known to have first appeared in non-avian dinosaurs[1]. However, relatively little is known of the early evolutionary history of the hyperinflated brain that distinguishes birds from other living reptiles and provides the important neuro-logical capablities required by flight[2]. Here we use high-resolution computed tomography to estimate and compare cranial volumes of extant birds, the early avialan *Archaeopteryx lithographica,* and a number of non-avian maniraptoran dinosaurs that are phylogeneti-cally close to the origins of both Avialae and avian flight. Previous work established that avian cerebral expansion began early in theropod history and that the cranial cavity of *Archaeopteryx* was volumetrically intermediate between these early forms and modern birds[3,4]. Our new data indicate that the relative size of the cranial cavity of *Archaeopteryx* is reflective of a more generalized maniraptoran volumetric signa-ture and in several instances is actually smaller than that of other non-avian dinosaurs. Thus, bird-like encephalization indices evolved multiple times, supporting the conclusion that if *Archaeopteryx* had the neurological capabilities required of flight, so did at least some other non-avian maniraptorans. This is congruent with recent findings that avialans were not unique among maniraptorans in their ability to fly in some form[5,6].

Birds are distinct among living reptiles in the degree to which their brains, particularly their forebrains, are expanded relative to body size.
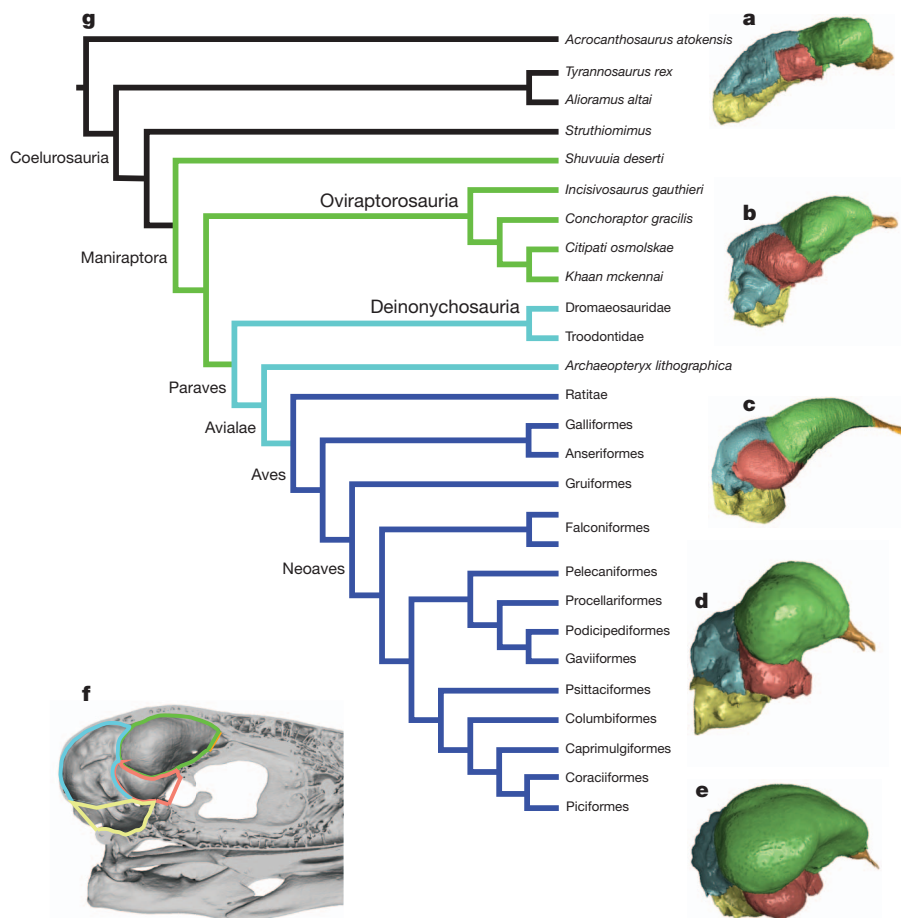

Figure 1 | Coelurosaur phylogeny and partitioned endocranial casts.
a–e, Endocasts of *Citipati osmolskae* (IGM 100/978) (**a**), unnamed troodontid (IGM 100/1126) (**b**), *Archaeopteryx lithographica* (BMNH 37001) (**c**), *Struthio camelus* (ostrich) (**d**), and *Melanerpes aurifrons* (woodpecker) (**e**) divided into neuroanatomical partitions based on homologous osteological landmarks using computed tomography data. Partitions roughly correlate to the olfactory bulbs (orange), cerebrum (green), optic lobes (pink), cerebellum (blue) and brain stem (yellow). Endocasts are not scaled to size. **f,** Sagittally sectioned skull of *Phaethon rubricauda* with osteological landmarks highlighted to correspond to the regions shown in the endocasts. **g,** Phylogeny of included taxa. Proposed episodes of encephalization are indicated by changes in colour. Phylogeny adapted from ref. 30.

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This index of encephalization ranges from six to eleven times higher in birds than other groups[7–9], and comparably large indices are known only among mammals[10–12]. The hyperinflated forebrains of birds and mammals evolved independently[11,13], possibly in response to different sensory cues; derived olfactory capabilities versus enhanced visual acuity[14,15]. Details of this neuroanatomical elaboration were recently explicated for the mammalian side of the tree based largely on fossil evidence from the latter portion of the stem and the early history of the crown[16]. No correspondingly comprehensive study exists for birds, despite broad interest in the relationship between brain size and structure, cognitive ability, and the origin of avian flight[2].

The volumetric expansion of the avian endocranium began relatively early in theropod evolution[4,17–19], and the early avialan *Archaeopteryx lithographica* is volumetrically intermediate between those of more basal theropods (for example, tyrannosaurs) and crown birds[3,4]. What remains unclear is whether the *Archaeopteryx* endocranium will continue to occupy a uniquely intermediate space between non-avialan theropods and crown birds once additional endocranial features, some with neurological implications for flight, are sampled from a wider range of bird-like, non-avian theropods. This is particularly relevant considering that recent studies argued, first, that avialans are not unique among maniraptorans in their ability to fly in some form[20], and second, that *Archaeopteryx* is more closely related to dromaeosaurs and troodontids than to modern birds[21].

We tested the relative position of *Archaeopteryx* in the evolution of avian endocranial space using comparative volumetric analyses. Volumes were obtained from digital endocasts constructed from computed tomography data sets for a diversity of crown and stem avians (Supplementary Table 1). Our study differs from previous efforts in that we sampled those theropod lineages most closely related to Avialae; Troodontidae, Dromaeosauridae, Oviraptorosauria and Alvarezsauridae (Fig. 1). In addition to considering the relationship between total endocranial volume and body size, we also divided the endocasts into volumetric partitions that estimate the major neuroanatomical regions, including the olfactory bulbs, cerebrum, optic lobes, cerebellum and brain stem (Fig. 1; Supplementary Table 2). This partitioning, accomplished using homologous osteological landmarks, enabled us to examine how the volumetric signature of different endocranial regions evolved in relation to total body size, total endocranial volume, and to one another. This approach allows detection of previously unrecognizable evolutionary complexity.

Our analysis of total endocranial volume relative to body size (estimated based on femur length[22]), recovered the apomorphically high volumetric signature for the avian crown (Fig. 2; Supplementary Tables 2 and 3)[3,4,10,23], but failed to recover *Archaeopteryx* in a uniquely transitional position between non-avialan maniraptorans and crown birds. Several oviraptorosaurs and the troodontids *Zanabazar junior* and IGM 100/1126, all have relative endocranial volumes that fall between the values of *Archaeopteryx* and crown birds (Fig. 2). The same basic pattern was recovered when cerebral volume was compared to body size. Thus, the total endocranial and cerebral volumes of *Archaeopteryx* relative to body size are not uniquely avian but reflect plesiomorphic values expected of a non-avian maniraptoran. Even the uniquely derived signature of crown birds is lost when volumes of other partitions are examined relative to body size (Supplementary Fig. 1). For each of these indices, there is direct overlap between the avian crown and one or more non-avian maniraptorans. The only partition in which *Archaeopteryx* plots within the range of crown birds is that of the olfactory bulbs, and it is not unique in this overlap. Optic lobes, cerebellum and brain-stem partitions of *Archaeopteryx* all fall outside the volumetric area defined by crown birds, *Zanabazar*, and at least some oviraptorosaurs.

Linear regressions of partitions against total endocranial volume reveal a different pattern (Fig. 3 and Supplementary Fig. 2). The strong correlation between cerebral and total volume is expected if cerebral expansion is the primary driver of general endocranial expansion along the
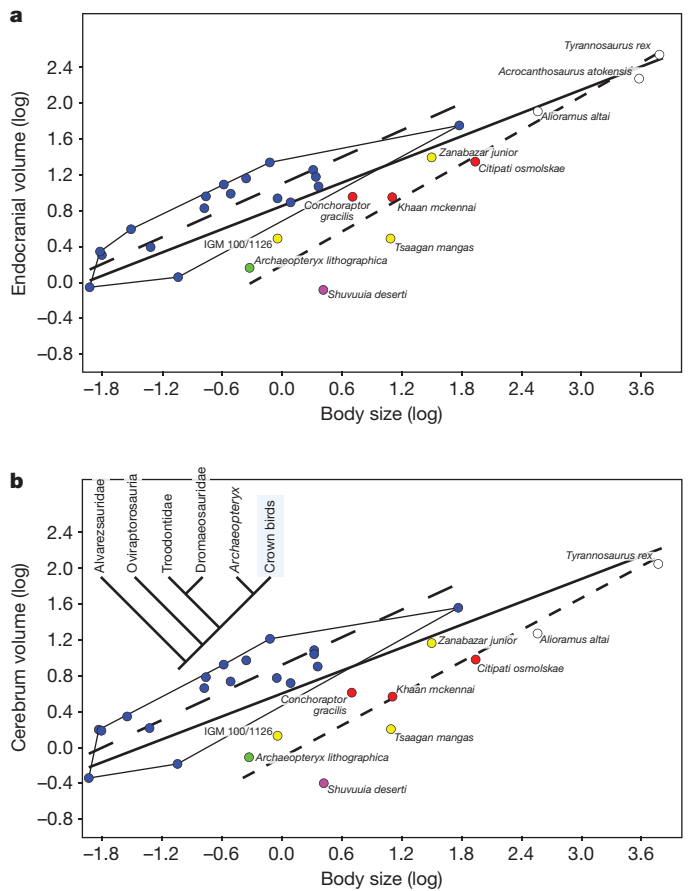

Figure 2 | Bivariate plots of log-transformed body-mass data. a, **b**, Body mass (kg) plotted against total endocranial volume (cm³) (**a**) and cerebral volume (**b**). Crown birds display apomorphically high endocranial and cerebral volumes with respect to body size. Colours indicate crown birds (blue), non-maniraptoran theropods (white), *Shuvuuia deserti* (purple), oviraptorosaurs (red), deinonychosaurs (yellow), *Archaeopteryx lithographica* (green). Reduced major-axis regression line for entire sample (solid line), crown birds (large dashes), and non-avian theropods (small dashes). Regression statistics given in Supplementary Table 3.

avian stem[4,9]. The relatively high correlations between total volume and partitioned volumes (Fig. 3 and Supplementary Fig. 2) indicate that each region, with the exception of the olfactory bulbs, expanded along the avian stem. This suggests no notable structural constraint on total endocranial volume. If such a constraint were in place, then selection-driven cerebral expansion would be expected to occur at the volumetric expense of one or more of the other regions. The fact that these regions are expanding together attests to the high responsive potential of the surrounding skeleton to the tissues they envelop[24].

Principal components analysis of the five partitions divided by total endocranial volume reveals complete volumetric separation between Paraves and Oviraptorosauria (Fig. 4). Principal component I accounts for approximately 82% of total sample variance (Supplementary Table 5) and is defined largely by the cerebral expansion described above. Principal component II describes approximately 11% of total sample variance and is defined largely by the inverse relationship between the relative volumes of the optic lobes and cerebellum. The relatively large cerebral volume of the troodontid, *Zanabazar*, pulls this taxon within the volumetric space defined by crown birds, so that again the crown clade is not volumetrically unique. *Archaeopteryx* plots well outside crown birds along principal component I, and even outside the alvarezsaurid *Shuvuuia deserti*, helping to define a more generalized maniraptoran space.

For volumetric indices in which *Archaeopteryx* and crown birds overlap or nearly overlap (that is, cerebellum, cerebrum and optic lobes
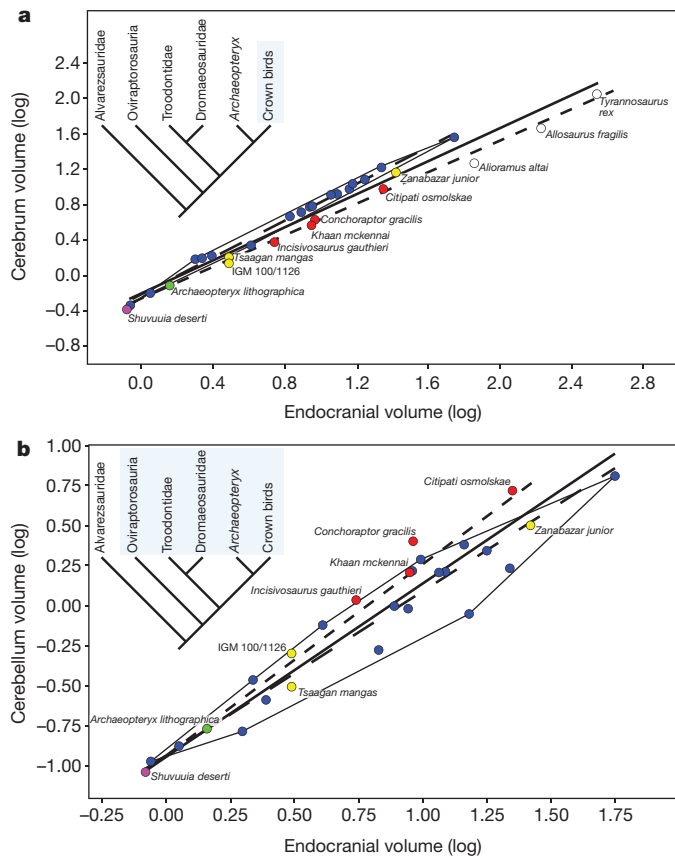
Figure 3 | Bivariate plots of log-transformed total-endocranial-volume data. a, b, Total endocranial volume (cm³) plotted against cerebral (**a**) and cerebellar (**b**) volumes. Colours are the same as in Fig. 2. Highlighting on the tree indicates those groups that share crown-like volumes. These can be interpreted as being either homologous (synapomorphic for a more inclusive group including crown birds) or convergent (appears in crown birds and more distantly related groups). Regression statistics are given in Supplementary Table 4.
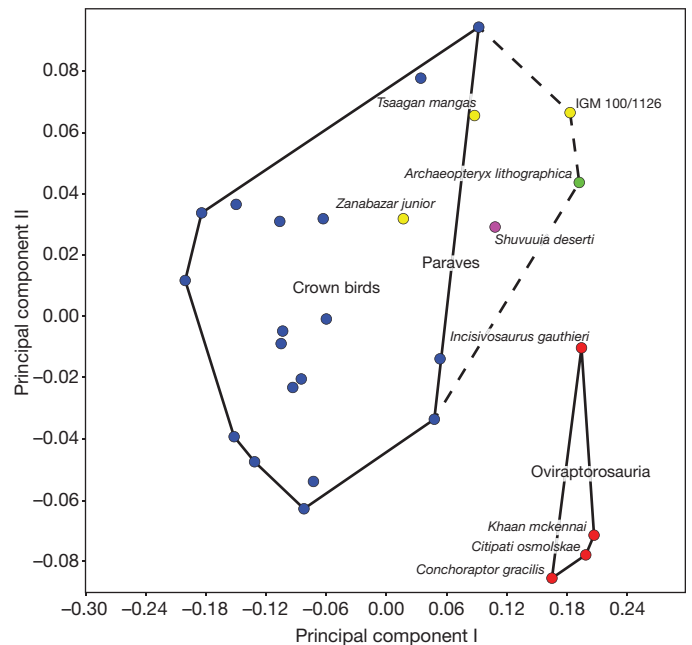

Figure 4 | Principal components analysis plot of neuroanatomical region volumes. Colours are the same as in Fig. 2. Complete volumetric isolation is indicated for Oviraptorosauria. A paravian (see Fig. 1) group is recovered in the principal components analysis (PCA) plot, but not an avialan (*Archaeopteryx* plus crown birds) volumetric grouping. PCA loadings are provided in Supplementary Table 5.

versus total endocranium; olfactory bulbs versus body size), crown-like values are also expressed in at least some non-avialan taxa. For the remaining indices, *Archaeopteryx* plots further from the crown than some other non-avialan taxa. Thus, regardless of whether *Archaeopteryx* is an early avialan or the sister to deinonychosaurs, there is no unique volumetric signature diagnosing the avialan endocranial cavity for the entirety of its evolutionary history (since Avialae diverged from Deinonychosauria).

The evolutionary history of those volumetric expansions that makes the endocranial space of modern birds so distinctive depends largely on how we interpret *Archaeopteryx*. For example, we recover at least three episodes of coelurosaur cerebral expansion relative to total endocranial volume. If the volumetric signature of the *Archaeopteryx* cerebrum reflects the ancestral avialan condition, then these three expansions optimize respectively at the base of Maniraptora, within Deinonychosauria, and somewhere within Avialae after the divergence of *Archaeopteryx* (Fig. 1). This would make the high cerebral indexes of crown birds and deinonychosaurs non-homologous, and the relatively low cerebral index of *Archaeopteryx*, a conserved condition, plesiomorphic for Paraves. Alternatively, if the relative cerebral volume of *Archaeopteryx* is autapomorphically small, then the high cerebral index expressed in deinonychosaurs and crown birds is homologous, and the three coelurosaurian expansions optimize respectively at the bases of Maniraptora, Paraves and within Avialae—again, after the divergence of *Archaeopteryx* but before the origin of the crown (Fig. 1). A cerebral expansion at Paraves corresponds roughly with an inferred paedomorphic event for the skull[25] and may be either a cause or effect of that event.

Studying cerebral expansion with regard to only body size limits the explanatory value of the results because high encephalization may be acquired through gross expansion of the neural tissue, gross reduction of body size, or a combination thereof[26]. The maintenance of relatively small body size along the lineage uniting non-avian maniraptorans with the avian crown[27] indicates that the cerebral expansions we recover cannot be explained solely as body size decreasing around a conserved endocranial volume. Gross neurological expansion was the primary driver in producing these bird-like indices.

The brain of *Archaeopteryx* is not volumetrically avian but conforms to the expectation of a generalized paravian. Thus, if *Archaeopteryx* has a 'flight-ready' brain[3], which is almost certainly the case given its postcranial morphology, then so did other paravians. The hypothesis that dromaeosaurs and troodontids had the neurological capabilities required of powered flight, gliding, or some intermediate condition is congruent with the discovery of the 'four-winged' deinonychosaurs, *Microraptor zhaoianus*[20] and *Anchiornis huxleyi*[5,6].

Endocranial volumes alone, of course, do not tell the whole story. Even volumetrically identical spaces can differ in their shape and structural arrangement with important functional and systematic implications. For example, the wulst is a neurological structure unique to crown birds used in information processing and motor control with two primary inputs: somatosensory and visual[28]. Our re-examination of *Archaeopteryx* revealed a cerebral indentation within the area occupied by the variably positioned wulst of modern birds (Supplementary Fig. 3). If homologous, the wulst appeared before the significant cerebral expansion marking the latter part of the avian stem with which the wulst is typically associated[28,29]. The behavioural implications of this structure's absence in the volumetrically expanded cerebra of *Zanabazar* and *Tsaagan* are unclear, but until evidence of the wulst is recovered from other deinonychosaurs, its homologous presence in *Archaeopteryx* would be an unambiguous synapomorphy shared with crown birds.

METHODS SUMMARY

All computed tomography scanning parameters and volumetric measurements are available in the Supplementary Information. Original computed tomography

scans performed at the University of Texas High-Resolution X-Ray Computed Tomography Facility (UTCT) and Ohio University. Endocranial cast reconstruction and segmentation were performed in VGStudioMAX and detailed in the Supplementary Information. It is important to note that these regions are casts and may contain more neurological tissues than implied by the descriptors used in the text. Bivariate and multivariate statistics performed in PAST (see Supplementary Information for full details).

Full Methods and any associated references are available in the online version of the paper.

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METHODS

Scanning parameters and endocast construction. Digital endocasts were extracted using computed tomography data from the cranial cavity of examined specimens (Supplementary Table 1). The endocranial casts were reconstructed using original two-dimensional imagery, either tiff or DICOM images, in the volumetric rendering program VGStudioMax 2.0.1. The reconstructions were made by adjusting grayscale contrast in the images until bone and matrix were distinguishable from one another. The cranial cavity was selected using the segmentation tools available in that program. Measurements taken from the endocast (including volume) were acquired using this same version of VGStudioMax. Endocast volume measurements were obtained by calculating the volume of negative space of the cranial cavity. For ease of description, features of the endocranial casts are referred to by the names of the soft tissues of the brain that they reflect (for example, cerebrum rather than cast of cerebrum). It is important to note that what is actually preserved is a cast of the endocranial space, which may reflect structures other than the brain, such as meninges and vascular sinuses. The endocast does help to determine relative size and shape of features of the brain as well as recognizing the branching points of the cranial nerves[23].

Osteological markers used to partition endocranium. Homologous osteological markers of the endocranium were used during the segmentation of the endocasts to distinguish five separate anatomical regions of the brain based on gross anatomical descriptions. Divisions along tissue boundaries are of course not possible when segmenting the endocranial space into separate regions. It is important to note that these regions are casts and may contain more neurological tissues than are implied by the descriptors that are used in the text. As far as preservation allowed, these regions were isolated from each endocast so that their volumes could be measured independently (Fig. 1 and Supplementary Table 2). The five segments included in this analysis comprise the olfactory bulbs and cerebrum (forebrain); the optic lobes (midbrain); and the cerebellum and brain stem (hindbrain)[7]. The pituitary body volume was also segmented but not included in the final analysis because of its sporadic preservation in the fossil taxa. The osteological landmarks used to define the regions were identified in the two-dimensional, coronal computed tomography slices (except the olfactory bulbs, which were identified in the sagittal slices) and delineated from each other using the computer program VGStudioMax 2.0.1. Standard segmentation tools from this program were used in the isolation of anatomical regions.

In this analysis, the region defined as the olfactory bulb is delineated from the rest of the forebrain anteriorly by the anterior-most constriction of the endocranial space before it opens into the nasal cavity and posteriorly by the crista that lies between the olfactory bulb fossa and the anterior cerebral cavity (Fig. 1).

The cerebral region is defined anteriorly by the same crista that delineates the posterior margin of the olfactory bulbs, dorsally by the roof of the cranial cavity formed by the frontals and parietals, posterodorsally by the crista between the cerebral and the cerebellar fossae, and ventrally by the crista between the optic lobe fossa and the cerebral fossa (Fig. 1). There is no clear posterior border of the cerebral fossa in the cranial space, so a straight line was drawn dorsally between the paired cristae that lie at the junction of the cerebral and cerebellar fossae and ventrally between the paired cristae lying at the junction of the cerebral and optic lobe fossae. These were followed posteriorly until they converged, simulating the folding of the cerebellum over the cerebrum.

The cast of the optic lobes is the only anatomical structure from the midbrain that is isolated on the endocasts. These are easily identified dorsally by drawing a line between the crista lying between the cerebral and optic lobe fossae to their opposite on the other side of the braincase. Ventrally, the border of the optic lobe cast is defined as the crista between these structures and the pituitary fossa until the fossa closes posteriorly. Posterior to the pituitary fossa a line is drawn along the crista between the fossa for the brain stem and the optic lobe fossa. The posterior border is formed as the dorsal line and ventral line converge towards the midpoint of the endocranial space (Fig. 1). The optic nerve cast is included in the midbrain and terminates anteriorly at the level of the optic foramen.

The two isolated regions of the hindbrain include the casts of the cerebellum and brain stem (Fig. 1). The cerebellar cast at its anterior margin can overlie or lie just posterior to the posterior margin of the cerebral fossa. In life, the cerebellum resides in a distinctive fossa on the roof of the cranial cavity, delineated by a surrounding crista, crista marginalis (Fig. 1). The fossa for the brain stem underlies both those of the optic lobes and the cerebellum. Again, a distinctive crista is present at the dorsal border of the brain stem fossa and traverses both of these sections (Fig. 1). The posterior margin of this region is determined by the opening of the foramen magnum (Fig. 1).

Regressions and principal components analysis. This analysis segments the endocranial cast into five separate regions that correspond closely with neuroanatomical partitions of the brain. Although previous studies of fossil taxa have partitioned the endocast (that is, cerebral cast and everything else[4]), those analyses were not able to observe changes in the various neuroanatomical divisions with respect to each other, body size, or total endocranial volume.

Several different analyses were run on the volumetric data gained from the digital endocasts of both avian and non-avian theropods. The initial analysis was a simple regression run between body mass and total endocranial volume, similar to the analyses reported by previous papers[3,4,10,17,23] but with an expanded taxonomic sampling. In addition, body mass was plotted against each of the endocranial regions. Endocast volumes were obtained from the volume of negative space as calculated by VGStudioMax 2.0.1. Endocranial volumes in crown birds were found to be an accurate measure of brain volume; and it is assumed that this also holds for non-avian theropods given that impressions of the brain on the cranial cavity indicate that the brain was sufficiently expanded so as to fill the space. Cranial nerves were cut off as close to the 'brain' as possible to minimize their influence on the total volume. Body masses for both avian and non-avian theropods were calculated using femur length (Supplementary Table 2)[22]. All volumetric and body mass data were log transformed to accommodate them onto a single chart and to facilitate ease of pattern recognition. Best-fit lines were mapped onto the data using reduced major axis regression. These lines were fit to the coelurosaurian and crown bird datapoints. A best-fit line also was drawn for the paraphyletic group 'non-avian theropods' to approximate the ancestral condition in the data (Supplementary Table 3).

The Phenotypic Diversity Analysis Program (PDAP) was used subsequently on bivariate data to test for non-independence of variables due to phylogenetic influence, and a second set of regressions was run using independent contrasts (Supplementary Table 4). As the inclusion of fossils required the use of strictly morphological trees, branch lengths within the crown were set at one. Branch lengths for fossil taxa were set according to their distribution in the fossil record. Dates were set at the midpoint of ranges.

A PCA was run on the volumes of all of the five regions of the endocranium that were isolated in this analysis (olfactory bulbs, cerebrum, optic lobes, cerebellum and brain stem). Rather than running the PCA on the absolute values of the volumes, each region was divided by the overall endocranial volume both for consistency with previous analyses performed on crown birds and mammals and to minimize errors that may be associated with shape and distortion. Minimal polygons were drawn around the taxa belonging to the clades Oviraptorosauria, Aves, and Paraves for ease of comparisons (Supplementary Table 5).