

1.10 The Role of Endocasts in the Study of Brain Evolution

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1.10.1	Introduction	223
1.10.1.1	Crown, Stem, and the Heuristic Potential of Fossil Endocasts	224
1.10.2	Assessing the Anatomical Identity of Endocasts	225
1.10.2.1	Endocranial Cavity as Brain Proxy	226
1.10.2.2	What Anatomical Structures Share the Endocranial Cavity With the Brain and Thus Lower Brain-to-Endocranial Cavity Values?	226
1.10.2.3	Partial Endocasts	229
1.10.3	Endocast Contributions to Comparative Neuroscience	231
1.10.3.1	Comparative Morphology	232
1.10.3.2	Encephalization	233
1.10.3.3	Correlative Change	234
1.10.4	Concluding Remarks	236
References		237

Abstract

Endocasts are windows into deep history and as such provide modern neuroscience a more complete appreciation of: (1) the brain's evolutionary potential (by allowing sampling of extinct lineages) and (2) the origins of modern neurological disparity. Imaging technology has increased the number of endocasts and thus their integrative potential for informing broad patterns of brain evolution. Our goal is to facilitate this integration by explicating the inferential framework in which endocasts are studied, their anatomical identity, and the hypotheses they can and cannot address. Examples of endocasts' explanatory power and limitations are drawn largely from birds and their extinct relatives.

1.10.1 Introduction

The chordate brain began its remarkable evolutionary history when changes in an increasingly complex and genetically controlled developmental network produced an anterior expansion of the deuterostome dorsal hollow nerve cord. This initial neuroectodermal enlargement is most faithfully conserved among extant chordates in the lancelets (amphioxus) (Butler, 2000; Lacalli, 2008)—a lineage that diverged from our own ancestral line well over 500 million years ago (Yue et al., 2014). The antiquity of the chordate brain thus exceeds, and considerably so, the cranial skeleton that in the majority of chordate groups provides support and protection to the brain and related sensory organs. The precocious appearance of the brain relative to its supportive skeletal framework in evolutionary history is paralleled during chordate ontogeny. Here, the brain begins to emerge during secondary neurulation and then likely serves an underappreciated developmental role as an early signaling center and organizer of the neighboring head mesenchyme—directing cells that will eventually contribute to a wide diversity of adult cranial structures, including the skull (eg, Hu et al., 2015). This signaling relationship between brain and neighboring head mesenchyme certainly moves in both directions (see Creuzet, 2009a,b).

The spatial integration that occurs in ontogeny and phylogeny between the brain and head skeleton creates an interfacing surface, preserved in many vertebrate fossils, that can be estimated and studied as an endocast. The goal of this chapter is to explore the logical framework within which endocasts can be combined with data from modern neuroscience to provide a more complete evolutionary account of the vertebrate brain. We begin the exploration with an explicit description of the inferential model in which fossils inform macroevolutionary patterns and the phylogenetic terminology used to communicate these patterns. Inconsistent application of this terminology by neuroscientists and paleontologists alike is an unnecessary trend that creates confusion and impedes whatever understanding might be achieved through a clear integration of data from these seemingly disparate, but actually complementary, fields. We will then outline what an endocast does, and does not, represent anatomically and thus what lines of neuroanatomical investigation endocast data can potentially support. Examples will be drawn heavily from the reptile side of the amniote tree and especially from the long evolutionary stem lineage that produced modern birds. For reasons that hopefully will become clear during the course of this chapter, the deep history of the avian lineage represents well the challenges, opportunities, and potentialities that endocasts present to the greater neuroscience community.

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1.10.1.1 Crown, Stem, and the Heuristic Potential of Fossil Endocasts

Considered against the backdrop of Life's more than four billion year history (Bell et al., 2015), the extant biota provides us with a rather impoverished view of taxonomic, and probably, process diversity. At the same time, we rely heavily on living species both for our understanding of detailed biological functions and as a framework for establishing broad, macroevolutionary patterns. We tend to perceive extant forms as islands of either actuated or potential insight floating in a rather murky sea of extinction. These islands are not floating freely, of course, but are instead tethered to each other within the historical edifice of the evolutionary process. The logical framework provided by this edifice is what gives us hope that we may meaningfully clarify the deep biological history which extinction has muddled. The involved model of inference, and the beneficial role that fossils play within that model, is perhaps best demonstrated using an explicit crown-stem distinction (Fig. 1).

A crown clade is a monophyletic group whose definition is drawn from the ancestral divergence of two lineages, both of which retain at least some extant members (Hennig, 1966; Budd and Jensen, 2000; Gauthier and De Queiroz, 2001). The crown clade of mammals (Mammalia; Rowe, 1987), for example, is defined as the most recent common ancestor of monotremes and therians and all of that ancestor's descendants. The extant sister taxon to crown mammals is the crown clade of reptiles (Reptilia; Gauthier et al., 1988), which is defined based on the ancestral split between the lineages that would eventually produce the modern radiations of turtles, lepidosaurs (modern lizards, snakes, and tuatara), crocodylians, and birds. The most exclusive clade that includes both Mammalia and Reptilia is the crown clade of amniotes (Amniota; Gauthier et al., 1988). More inclusive crown clades in our own ancestral line as chordates include (Fig. 2; see also Rowe, 2004): Tetrapoda (Amniota + Amphibia), Choanata [Tetrapoda + Dipnoi (lungfish)], Sarcopterygii [Choanata + Actinistia (coelacanth)], Osteichthyes [Sarcopterygii + Actinopterygians (ray-finned fish)], Gnathostomata [Osteichthyes + Chondrichthyes (sharks and rays)], Vertebrata [Gnathostomata + Cyclostomata (lampreys and hagfish)], Euchordata [Vertebrata + Cephalochordata (lancelets or amphioxus)], and Chordata [Euchordata + Urochordata (tunicates or sea squirts)].

All crown clades, from the most inclusive to the most exclusive, are separated from each other by some expanse of evolutionary time, which is circumscribed by their collective stem lineages (Fig. 1). These stem lineages are somewhat of an evolutionary black box because, by definition, they lack any modern representatives (outside of the crown clade). Our understanding of the evolutionary transformations that populate these stems is based largely on a combination of: (1) the empirical observations that we make on the extant taxa within the associated crown clades—observations that we cannot make directly on stem taxa and (2) phylogenetically justified inferences (Farris, 1983; Bryant and Russell, 1992; De Queiroz and Gauthier, 1992; Witmer, 1995). This model is rich in explanatory power and forms the basis of all comparative biology, including all the biomedical research that is grounded in the study of model organisms. The problem is that as these phylogenetic stems come to represent more and more time and are inhabited by an increasing number of evolutionary transformations, the model itself grows less and less heuristically powerful. In other words, as the stems lengthen, the explanatory power of the inferential model tends to diminish.

Recognizing the inverse tendencies of this relationship is important, especially when we consider the incredible spans of evolutionary time represented by some stem lineages—including many of those attracting great interest from comparative neuroscientists. The phylogenetic stem of our own human crown clade, for example, is currently estimated at approximately 6 million years (Dos Reis et al., 2012; Benton et al., 2015), whereas that of crown Mammalia is approximately 150 million years

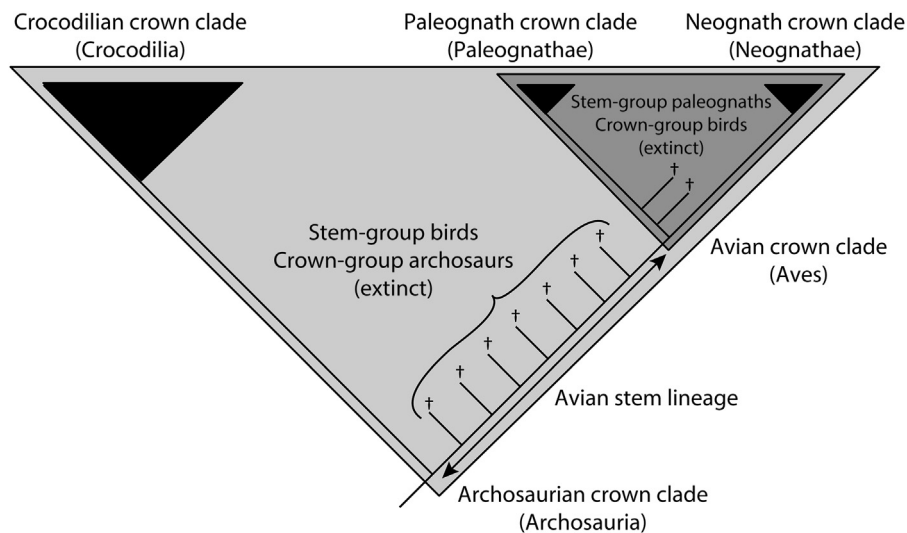


Figure 1 Tree depicting the phylogenetic concept of crown and stem as it applies to birds. The concept is critical because crown clades define the inferential framework lying at the heart of all comparative biology and within which fossils (including fossil endocasts) play a key role (see text). The extant sister taxon to the avian crown clade (Aves) is the crown clade Crocodylia, and together Crocodylia and Aves define crown-clade Archosauria. The avian stem lineage includes all those extinct forms (including pterosaurs and all nonavian dinosaurs) that are more closely related to Aves than Crocodylia. The crown-stem distinction is a nested concept, so that, for example, stem-group birds are also crown-clade archosaurs.

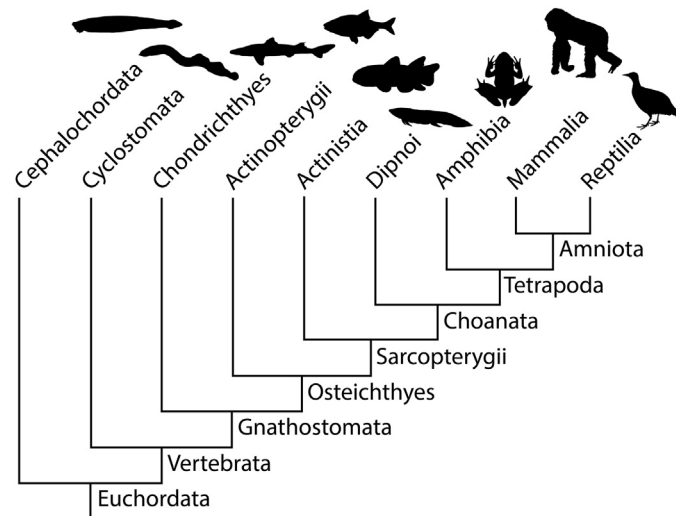


Figure 2 Phylogenetic relationships of the major euchordate crown clades discussed in this chapter. For an expanded discussion of the tree topology, see Rowe (2004) and Benton et al. (2015).

(O’Leary et al., 2013; Luo et al., 2015), and that of crown-group birds (Aves; Gauthier, 1986) exceeds 150 million years (Prum et al., 2015). The stems associated with the crown clades informing the earliest history of the vertebrate brain (ie, cephalochordates, cyclostomes, chondrichthyans) may exceed 200 million years (Kuraku and Kuratani, 2006; Chen et al., 2012; Hedges et al., 2015).

The inherent difficulty of inferring details across such long stem lineages can be eased through an effective utilization of the fossil record. Fossils, and only fossils, afford windows (in the form of semaphoronts; Hennig, 1966) into these otherwise empirically opaque histories. Fossils can enlighten, either directly or indirectly, the nature and timing of evolutionary transformations and thus help to “break up” long phylogenetic stems (Fig. 1). The most obvious beneficiary of integrating vertebrate fossils into comparative studies is our understanding of transformations within the more readily fossilized bony skeleton. The skeleton enjoys, however, at least some form of correlative relationship with most other anatomical systems, including the brain (see the following section). Establishing the strength of these correlations is critical to maximizing the explanatory potential of fossils for macroevolutionary patterns.

The crown-stem distinction is a nested concept wherein every individual fossil falls along a single phylogenetic stem, but at the same time, is nested within a series of more inclusive crown clades. *Ardipithecus* is a fossil form on the stem of the human crown clade (White et al., 2009) but one that is nested within the crown clades of Catarrhini, Primates, Placentalia, Theria, Mammalia, and so forth. *Archaeopteryx* is a stem bird that lies relatively near, but still outside, the radiation of crown-clade avians (Gauthier, 1986; Turner et al., 2012), but *Archaeopteryx* is a crown-clade archosaur, reptile, and amniote. Fossils, like extant forms, express a combination of primitive (plesiomorphic) and derived (apomorphic) morphologies, not all of which are going to reflect the ancestral phenotype of their most closely related crown clade. A well-supported understanding of a fossil’s phylogenetic position is crucial to maximizing its potential for informing the ancestral series of stem transformations (accrual of apomorphies along the stem), which make its associated crown clade unique compared to those of other lineages. Even when this position enjoys widespread consensus, however, the inferential role of the fossil can be confused when the employed terminology and taxonomy mean different things to different researchers.

Paleontologists and neuroscientists often employ “crown” and “stem” in ways that differ significantly from the usage advocated here. Paleontologists are known to apply these terms to wholly extinct groups, especially when these lineages include a subclade that is especially distinct morphologically (eg, crown and stem sauropterygians; Rieppel, 1994). Neuroscientists often describe extant groups lying outside some clade of interest as “stem.” For example, Corfield et al. (2015) recently referred to turtles as stem reptiles in a study whose focus was the neuroanatomy of crown-clade birds. It is not that these usages are incorrect—the meanings intended by their authors may be effectively conveyed, especially within their respective research communities. Different usages, however, do confuse the inferential roles of crown and stem and thus hinder meaningful integration of what are complementary datasets.

1.10.2 Assessing the Anatomical Identity of Endocasts

In the strictest anatomical sense, endocasts are representations (casts) of any enclosed, three-dimensional (3D) space. The term usually is reserved for those cavities defined by the cranial skeleton (eg, nasal capsule, semicircular canals and vestibule, bony sinuses, neurovascular canals) and especially the endocranial cavity housing the brain (Figs. 3 and 4). It is in this latter, most-restricted, sense that we will confine our usage in this chapter.

1.10.2.1 Endocranial Cavity as Brain Proxy

The brain is not isolated within the endocranial cavity but shares this space with a variable number of intimately associated structures (see the following section). This anatomical reality creates a differential relationship between the brain and cavity walls that varies widely between vertebrate lineages and has important implications for endocast studies. Although this variable relationship has long been recognized (Edinger, 1951; Hopson, 1979; Witmer et al., 2008), it was only recently named the brain-to-endocranial cavity (BEC) index (Balanoff et al., 2015a). High BEC values can be expected to produce an endocast that reflects brain volume and morphology with high fidelity, whereas low BEC values are associated with a more cylindrical endocast bearing less resemblance to the actual brain (Figs. 4 and 5).

A phylogenetically inclusive survey of empirical BEC values for vertebrates does not yet exist. The current absence of such a valuable contribution likely reflects, at least in part, the labor-intensive nature of assessing this relationship using traditional histological sections (Corfield et al., 2012). Modern visualization techniques and scanning technology are rapidly transcending these logistical issues, so we can expect to learn much of this pattern in the near future (Clement et al., 2015; Gignac and Kley, 2014). Based on qualitative evaluation of cross-sectional anatomy, we can predict that the ancestral crown-clade vertebrate had a low BEC index and that a relatively low value is broadly conserved even within tetrapods. For example, the extant coelacanth, *Latimeria chalumnae*, and the basking shark, *Cetorhinus maximus*, reportedly fill less than 1% of their endocranial cavities (Millot and Anthony, 1965; Kruska, 1988), although these exceedingly low numbers are likely due in part to desiccation of neural tissue in alcohol-preserved specimens. Within crown-group reptiles, an index of 0.33 is reported in the snapping turtle, *Chelydra serpentina* (Humphrey, 1894), whereas the BEC index of the tuatara, *Sphenodon punctatus* is 0.5 (Dendy, 1910). The brain of *Alligator mississippiensis* occupies from 32% to 68% of the endocranial cavity, with the lowest BEC values being found in the largest specimens (Hurlburt et al., 2013). A number of vertebrate lineages have independently acquired a high BEC index under a variety of evolutionary and morphological contexts (Coates, 1999; Northcutt, 2002; see Balanoff et al., 2015a). A brief discussion of the anatomical factors that influence BEC values should increase our understanding of endocasts and their neuroanatomical implications.

It is likely no surprise that encephalized taxa—those expressing a high ratio of brain volume to body mass—also tend to enjoy large BEC values. Mammalia, particularly our own branch of the primate tree, is one such taxon (Jerison, 1975; Northcutt, 2002; Isler et al., 2008). Birds are another lineage of highly encephalized amniotes, with encephalization values (see later discussion) rivaling those of most mammals (Figs. 3 and 4). The BEC values of birds may actually exceed those of mammals (Iwaniuk and Nelson, 2002), making birds a particularly attractive group for integrating endocasts with other forms of neuroscience data.

Moving outside of tetrapods, we find interesting relationships between BEC indices and encephalization. Chondrichthyans express a relatively high level of encephalization (Northcutt, 1977, 2002), exceeding that of most tetrapods, but retain a plesiomorphically low BEC index (Kruska, 1988). Actinopterygians, a hugely diverse radiation of osteichthyan fish include numerous lineages that express high BEC indices in the absence of significant encephalization (Bjerring, 1991; Northcutt, 2002; Giles and Friedman, 2014). These bony fish demonstrate that the two logical pathways of increasing the BEC index—enlarging the brain within the endocranial cavity or shrinking the endocranial cavity around the brain—are both represented in the evolutionary history of vertebrates.

1.10.2.2 What Anatomical Structures Share the Endocranial Cavity With the Brain and Thus Lower Brain-to-Endocranial Cavity Values?

The external surface of the brain and the deep surface of the bony and/or cartilaginous endocranial cavity are not in direct contact but rather are consistently buffered by meningeal tissue. These tissues appear to have a rather complicated evolutionary history of differentiation across chordates that is far from well understood. It does seem clear that the plesiomorphic condition is a single,

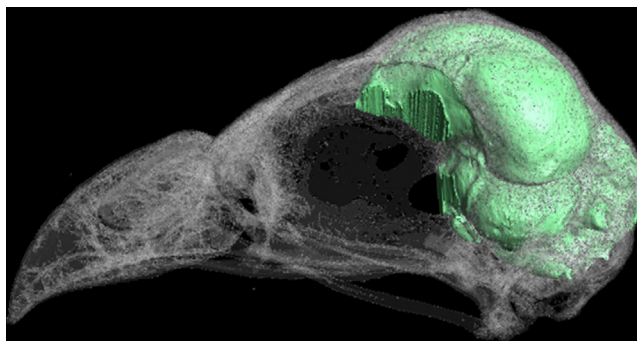


Figure 3 Digital skull and endocast of the extant red-crested turaco, *Tauraco erythrolophus* (AMNH 27414). The data are derived from a high-resolution X-ray computed tomography scan of specimen. The skull is rendered transparent to show the positional relationship of the endocranial cavity and its endocast to other cranial features. Crown-clade birds express an apomorphically high brain-to-endocranial cavity index, making them particularly conducive for studies that integrate endocasts with other forms of neurological data. AMNH, American Museum of Natural History, New York.

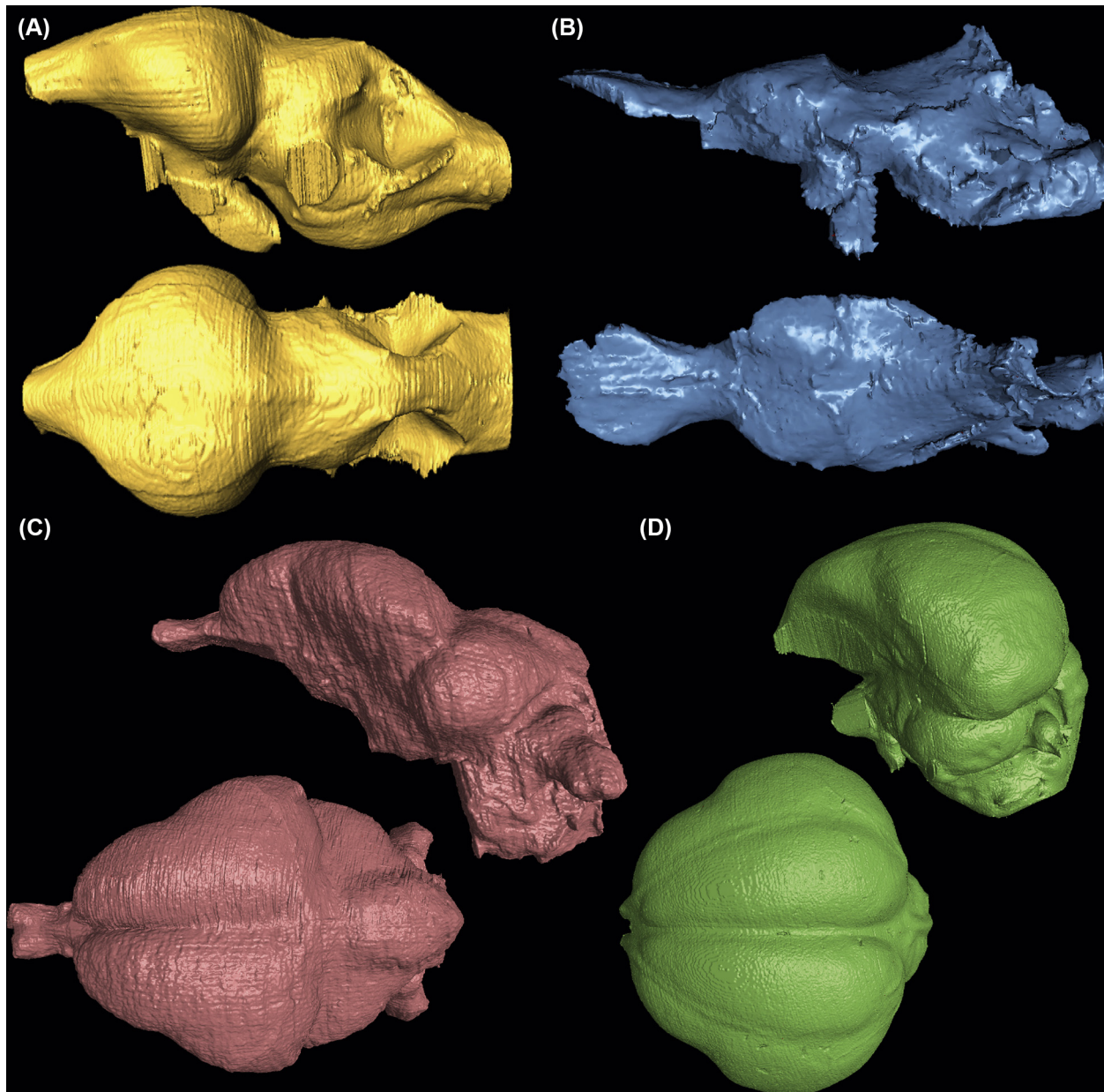


Figure 4 Digitally rendered endocasts from representative crown-clade archosaurs. (A) *Paleosuchus trigonatus* (AMNH 137175), extant crown-clade crocodilian; (B) *Alioramus altai* (IGM 100/1844), an extinct tyrannosaurid dinosaur (avian stem-group); (C) extinct unnamed troodontid (IGM 100/1126), paravian maniraptoran (avian stem-group); and (D) *Colius striatus* (AMNH 12378), extant crown-clade avian. AMNH, American Museum of Natural History, New York; IGM, Institute of Geology, Mongolian Academy of Sciences, Ulan Bator.

undifferentiated layer known as the primitive meninx (Bjerring, 1991; Coates, 1999; Butler and Hodson, 2005). This layer divided, probably somewhere along the tetrapod stem lineage, to form a secondary meninx (endomeninx) and a more superficial layer of dura mater (Brocklehurst, 1979; Butler and Hodson, 2005). The secondary meninx subsequently differentiated to form an internal pia and intermediate arachnoid layer, with cerebrospinal fluid filling the intervening, subarachnoid space. This differentiation is sometimes considered a convergently derived feature of crown-clade mammals and birds and possibly correlated with a homeothermic physiology (see Starck, 1979; Gauthier et al., 1988). At the same time, a third meningeal layer, often explicitly identified as the arachnoid layer, has been described for a diverse assemblage of tetrapods, including crocodilians (Hurlburt, 2014), turtles (Humphrey, 1894), and amphibians (Francis, 1934; Kuhlenbeck, 1973; Brocklehurst, 1979; Joven et al., 2013). It seems unlikely that if three layers are present across crown-clade Tetrapoda, these layers are not homologous (the null hypothesis is homology, with the burden of proof lying with a convergent origin; Hennig, 1966). Homology would not, however, negate the possibility that crown-clade mammals and birds do convergently share a derived transformation of some form, and this apomorphy is causally

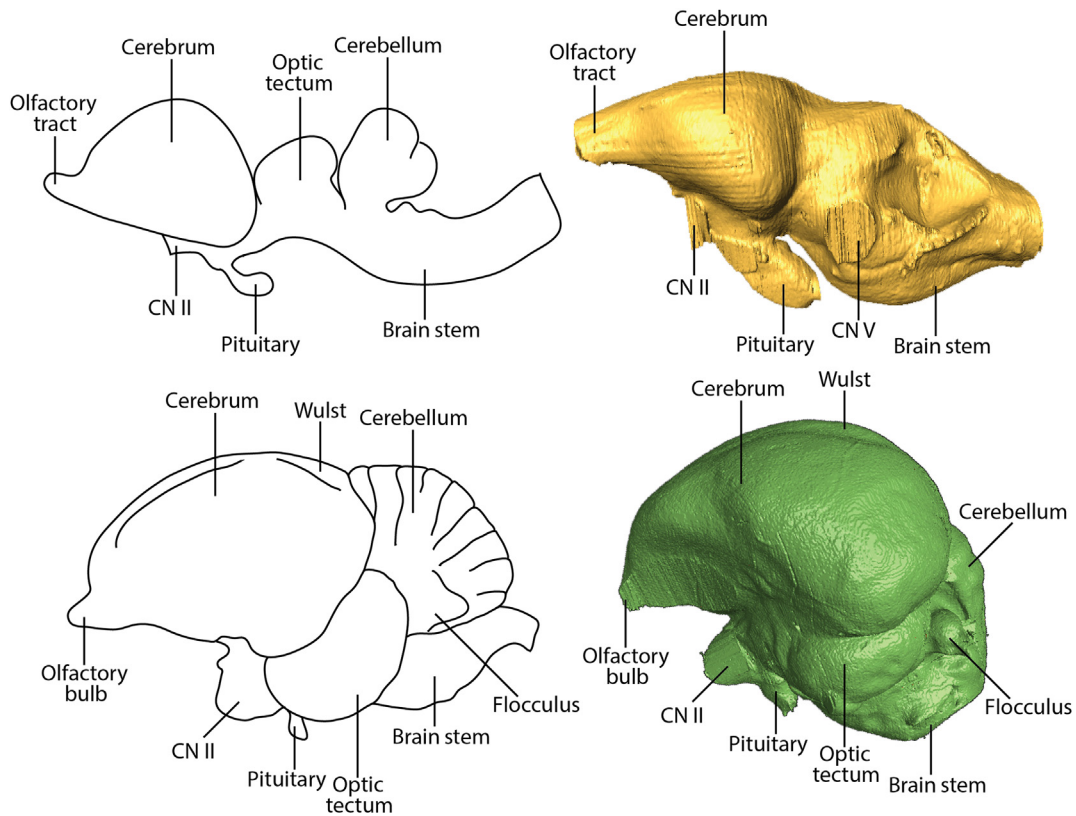


Figure 5 Comparison between the brain (*line drawing*) and endocast (*digital rendering*) for the crown-group crocodylian *Paleosuchus trigonatus* and the crown-clade bird *Colius striatus* (in left lateral view). Note the strong brain–endocast fidelity and marked cerebral expansion of the bird relative to the crocodylian. This expansion was the primary driver of encephalization along the avian stem-group and likely responsible for the conversion from a more linear, anterior–posterior arrangement of the neuroanatomical regions (as expressed in the crocodylian) to the more s-shaped neuro-architecture of crown-clade birds and their closest stem relatives. *CN*, cranial nerve.

related to the maintenance of an elevated body temperature. The general conclusion that the transformational history of these tissues across Chordata is in need of further study seems a safe one.

The homology of the individual meningeal layers is of less importance for the stated goals of this chapter than their collective thickness. A systematic survey of vertebrate meningeal thickness has not been attempted, but clade-level variation certainly does exist. Crown-clade birds, for example, possess exceptionally thin meninges relative to other vertebrates (Iwaniuk and Nelson, 2002), helping to explain why avian BEC values may even exceed those of mammals (see previously mentioned). The relatively thick meninges of mammals sometimes obscure surface features of the brain such as cerebral gyri and sulci.

Dural infolding creates a system of intracranial sinuses that help to drain the metabolically active brain of its large quantity of venous blood (Fig. 6). These volumetric requirements can translate to relatively large individual sinuses that significantly influence endocast morphology and thus reduce the size and shape correspondence between endocast and brain (lowering BEC values). The vertebrate occipital sinus, for example, extends posteriorly along the sagittal midline of the cerebellum, separating that region from the deep surface of the overlying neurocranial roof. In crown-clade birds, the occipital sinus is rather narrow mediolaterally—likely a derived condition, considering the broadened occipital sinus of crocodylians and other nonavian reptiles (Goodrich, 1930). The phylogenetic stem of birds is witness to an inflation of the occipital sinus that produced a prominent dural peak projecting posterodorsally over the hindbrain and the cerebellar region of the endocast (Fig. 4B). This peak has a somewhat complicated history along the avian stem. It probably reaches its greatest development in the tyrannosaurids (Fig. 4B) and is variably present in the crownward and more birdlike, deinonychosaurs (Norell et al., 2009; Witmer and Ridgely, 2009; Bever et al., 2011, 2013). The functional significance of the dural peak is unclear, but the structure is not present in any avialan, including *Archaeopteryx* and the entire diversity of the crown radiation.

The occipital sinus of crown-group avians also exhibits interesting variation. For example, diving birds, such as penguins and loons, have a distinctively wide occipital sinus that obscures the details of their cerebellar folia on an endocast (Ksepka et al., 2012; Tambussi et al., 2015). The functional driver of this correlation between diving behavior and a wide occipital sinus is unclear; but if such a correlation does exist, then endocasts could be used in combination with other skeletal signatures (apomorphically thick limb-bone cortices, reduced pneumaticity, reduced sternum; Ksepka et al., 2006; Hinić-Frlog and Motani, 2010; Smith and Clarke, 2013) to identify this behavioral ecology in fossils and thus trace it through deep time. In a similar fashion, the endocast

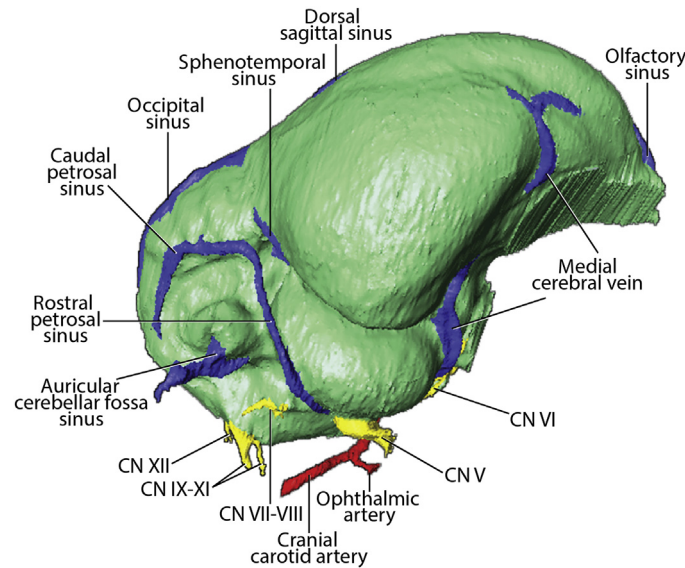


Figure 6 Digital endocast of the crown-group bird, *Tauraco erythrolophus*, this time showing selected sinuses of the dural venous system (blue), intracranial arteries (red), and cranial nerves (CN) (yellow). All intracranial structures that are not part of the brain proper effectively lower the brain-to-endocranial cavity index and decrease fidelity between brain and endocast. That stated, these “other” features often convey important neuroanatomical information.

signatures of the sphenotemporal and rostral petrosal sinuses (Fig. 6) conceal details of the midbrain in crown and stem avians but at the same time serve as landmarks that allow the optic tectum to be identified and traced in the fossil record (Sedlmayr, 2002; see later discussion). The use of vasculature and other overlying structures to inform our understanding of the size and shape of brain regions is an area of active research and will surely become increasingly refined (Morhardt et al., 2012).

Although their influence on the size and shape of an endocast is not typically large, certain cranial nerves and arteries do course through the endocranial cavity and thus diminish BEC values (Fig. 6). The trigeminal ganglion, for example, is an endocranial structure that resides within a subtle excavation of the neurocranial wall—an excavation that is visible on the resultant endocast (Fig. 6). The complex of intracranial arteries that extend through the endocranial cavity, such as the internal carotid canals, circle of Willis, basilar arteries (Midtgård, 1984; Baumel, 1993), do not lie within their own excavations of the endocranial wall and thus do not have a specific identity on the endocast; but because they are present and lie between the brain and floor of the neurocranium, they are collectively contributing in a small way to endocast volume and morphology.

Another important predictor of brain-endocast correspondence is the structural architecture of the braincase itself. In many vertebrate lineages, the endocranial cavity is poorly delineated in bone, often reflecting a failure of the orbital cartilages to ossify. This is generally not a large problem for either crown- or stem-group avians, where these anterior cartilages ossify extensively as the laterosphenoid and orbitosphenoid bones. These bones largely close the rostral end of the endocranial cavity, leaving only well-delineated paths for olfactory tracts, cranial nerves II–V, and their associated vasculature. In contrast, in many crown-clade turtles the orbital cartilages and the medial wall of the inner ear both fail to ossify. This is a derived condition within reptiles that does not extend across the entire turtle stem lineage (Gaffney, 1990; Bhullar and Bever, 2009; Bever et al., 2015), but it is certainly a structural plan that presents an obstacle to assessing brain evolution in turtles using endocasts (Gaffney, 1977; Carabajal et al., 2013).

1.10.2.3 Partial Endocasts

The BEC index, defined as the percentage of the endocranial cavity filled by the brain, is an important metric for assessing the explanatory potential of endocasts whose distribution across the vertebrate tree is not well understood. The index, however, does not take into account the anatomical reality that the spatial relationship between the brain and the endocranial wall is not uniform but may vary widely between neuroanatomical regions. The cerebrum of crocodylians and early dinosaurs, for example, appears to fill most of its portion of the endocranial cavity, whereas the hindbrain of these taxa remains poorly defined (Fig. 4; Osmólska, 2004; Evans, 2005). The olfactory bulbs comprise another region of the nonavian dinosaur brain that appears to enjoy a strong correspondence with its expression on the endocast when compared to that of other regions. The fidelity of the olfactory bulb and cavity has even been used to investigate the evolution of olfactory acuity among nonavian dinosaurs (Zelenitsky et al., 2009, 2011; Sales and Schultz, 2014).

An elegant demonstration of the variable relationships between brain and endocast is found in a description of the brain and endocranial cavity of the Australian lungfish, *Neoceratodus forsteri* (Clement et al., 2015). The study maps the distance between the brain and endocranial wall and communicates the observed variation using a color gradient (analogous to a heat map). Their data

demonstrate that the brain of this important lineage is a close fit with the endocast, except in the areas of the diencephalon and the hindbrain/anterior spinal cord. Such distances could easily be converted to 3D shape data and analyzed morphometrically to provide a clade-level perspective of these spatial relationships and their evolutionary history. The larger point here is that even if the overall BEC index of a taxon is relatively low, an endocast can still convey important morphological details for at least some brain regions.

Although endocasts are likely to reflect varying levels of neuroanatomical resolution for different brain regions, partial endocasts derived from specimens whose neurocranial anatomy is incomplete may serve important roles in constructing and testing evolutionary hypotheses. The vast majority of fossil endocast studies, not surprisingly, are based on well-preserved specimens whose braincases, and thus endocasts, are complete (or nearly so). Most fossils, however, are to varying degrees fragmentary. Simply excluding the majority of the fossil record from evolutionary analyses may leave significant phylogenetic gaps in our sampling, which can easily compromise the explanatory power of our results and interpretations (Heath et al., 2008).

Partial endocasts may be constructed from even a single bony element. The utility of such fragmentary endocasts is largely question dependent, but it is certainly governed by a combination of the neuroanatomical detail provided by that element and the phylogenetic resolution it provides. A fossil must be placed within a phylogenetic tree with some level of statistical support before the anatomical data provided by that fossil can meaningfully inform a tree-based evolutionary hypothesis (see Fig. 7). Considering that the number of phylogenetically informative features expressed by a specimen can be expected to decrease as a specimen becomes less and less complete, it must be recognized that fragmentary specimens are not likely to support a taxonomically exclusive identification (eg, to the species or "genus" level) (Bever, 2005; Bell et al., 2010; Bever et al., 2009). It should also be recognized that a fossil may meaningfully inform a macroevolutionary pattern without meeting the requirements of such refined taxonomic resolution. The question being pursued will generally dictate the required level of resolution. The most important thing is that both paleontologists and neuroscientists are aware of where on the tree a fossil endocast can be placed with some confidence and whether that position can support the hypothesis of interest.

Birds provide a helpful example of how partial endocasts might inform the evolutionary history of a profoundly interesting and important neuroanatomical structure. The avian Wulst is a thickening of the cerebral hyperpallium that functions as a processing center for a diverse array of sensory input (Medina and Reiner, 2000; Jarvis, 2009; Jarvis et al., 2013; Reiner et al., 2005; Butler et al., 2011). Anteriorly, the Wulst organizes somatosensory data from several regions, including the body feathers, beak, and feet (Wild, 1987; Funke, 1989; Wild et al., 2008; Cunningham et al., 2013). Visual input is processed largely in the structure's posterior aspect (Reiner et al., 2005). Because a Wulst has yet to be identified in any other extant reptile clade, we can infer that its evolutionary origin lies somewhere along the avian stem lineage.

Birds are an extant lineage of theropod dinosaurs (Ostrom, 1976; Gauthier, 1986). The realization that not all dinosaurs (Fig. 7) went extinct at the end of the Cretaceous sparked an exciting and fruitful reconsideration of the modern avian body plan (see Dingus and Rowe, 1997). Features we formerly associated exclusively with birds—feathers, wings, wishbones (furcula), pneumatization of the skeleton, egg-brooding behaviors, and almost undoubtedly a homeothermic

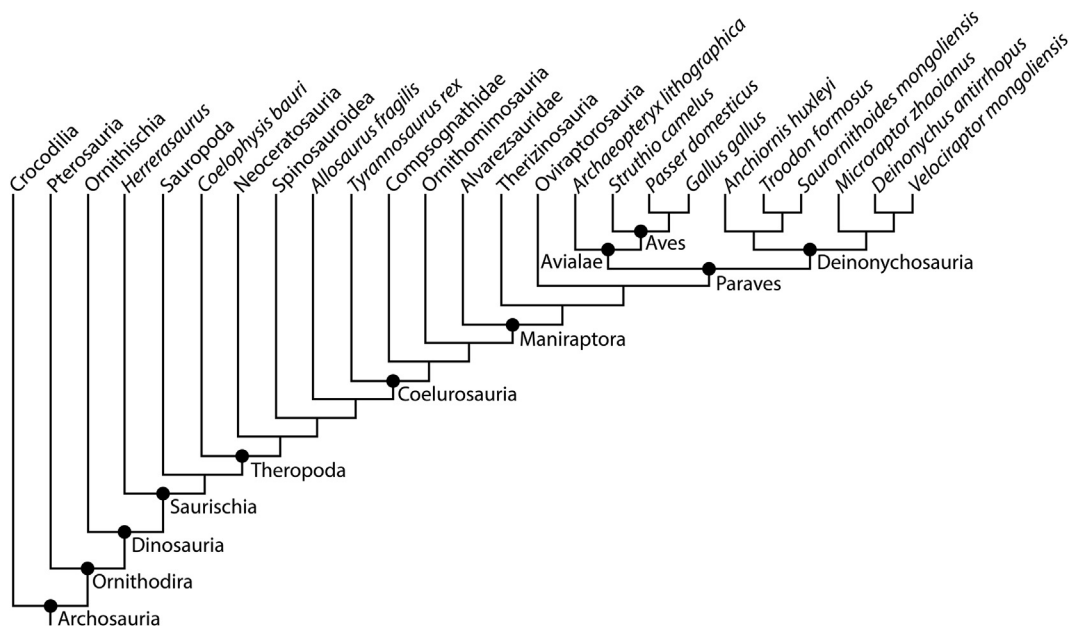


Figure 7 Phylogenetic tree of crown-clade Archosauria showing selected lineages of the hugely diverse phylogenetic stem of birds. The majority of this stem is nested within the Dinosauria, although the stem also includes nondinosaurian lineages such as the highly encephalized and volant pterosaurs. See Smith et al. (2007), Nesbitt (2011) and Turner et al. (2012) for details of tree topology.

physiology—now find their origins deep within nonavian dinosaurs (Ostrom, 1976; Norell et al., 1995; Dong and Currie, 1996; Xu and Norell, 2004; Norell and Xu, 2005; Turner et al., 2007; Nesbitt et al., 2009). Some form of functional bipedalism, a derived feature of birds among extant reptiles, may actually have originated along the archosaur stem lineage, with the obligatory quadrupedal gait of modern crocodylians being secondarily evolved (Hutchinson, 2006; Gauthier et al., 2011). Based on this pattern, we might well expect to find that the apomorphic thickening of the hyperpallium into a proper avian Wulst also occurred well outside of the crown-group radiation of birds.

The first century or so of endocast research, however, produced no records of a Wulst outside of the crown clade (Marsh, 1880; Edinger, 1951; Osborn, 1916; Milner and Walsh, 2009; Witmer and Ridgely, 2009; Balanoff et al., 2014; Walsh et al., 2015). This empirical absence suggests the Wulst evolved right at, or just before, the origin of the avian crown group, providing modern birds with a competitive advantage not enjoyed by their dinosaurian counterparts on the stem (Fig. 7). The Wulst presumably allowed crown birds to exploit the vast array of aerial and nonaerial ecologies and to achieve the impressive levels of taxonomic diversity that they currently exhibit (Milner and Walsh, 2009).

This hypothesis was challenged by the report of a Wulst-like structure in the endocast of a stem bird—the avialan *Archaeopteryx lithographica* (Fig. 7; Balanoff et al., 2013). The evidence consists of a rather subtle ridge running a short distance along the deep surface of the frontal bone in an area of the endocranial cavity that corresponds to the dorsolateral surface of the cerebrum. The identity of this structure as a cerebral thickening homologous to the crown-clade Wulst is both tentative (Balanoff et al., 2013) and controversial (Walsh et al., 2015). If this homology is established, it will force an important reconsideration of cerebral architecture and processing potential in nonavian dinosaurs.

Establishing homology between the aforementioned cerebral structure in *Archaeopteryx* and the avian Wulst requires demonstrating, to some reasonably acceptable level, a continuity of Wulst expression along the backbone of the avian stem lineage—between the ancestral crown-clade bird and that bird's most recent common ancestor with *Archaeopteryx*. Another, less direct, way of establishing a reasonable probability that the cerebral architecture of *Archaeopteryx* shares some sort of Wulst with the crown condition is to establish that a Wulst-like structure is more widespread among the nonavian, but extremely birdlike, coelurosaurian theropod dinosaurs (Fig. 7). Unfortunately, well-preserved braincases are not abundant in either area of the tree. Most avialan specimens, outside of the crown radiation, are either highly fragmentary or exhibit severe compressional distortion (O'Connor and Chiappe, 2011; Turner et al., 2012). The fossil record of nonavian coelurosaurs is more promising, but even here, most of the known braincases exhibit some significant level of damage (especially crownward of tyrannosaurs, Fig. 7; eg. Makovicky et al., 2003; Balanoff et al., 2009, 2014; Bever et al., 2011, 2013; Turner et al., 2012).

A specimen of the ornithomimosaur *Gallimimus bullatus* (IGM 100/133) provides a nice example of our intended point. The braincase of this specimen is poorly preserved overall, especially because its floor and lateral walls are broken and distorted. In contrast, the dermal roof of the endocranial cavity is nicely preserved and yields a partial digital endocast that appears to closely approximate the morphology of the brain's dorsal surface (Fig. 8). The cerebral portion of this surface bears no signature of the Wulst. Therefore, the controversial record of the Wulst-like structure in *Archaeopteryx* remains the only one outside of the crown clade, at least for now. The ability to identify the Wulst using a single bone (the frontal)—as opposed to an entire braincase—greatly increases the probability that the fossil record will inform the potentially complex evolutionary origin of this characteristic feature of avian neuroanatomy.

1.10.3 Endocast Contributions to Comparative Neuroscience

Endocasts are windows into the deep history of neuroanatomy and as such provide modern neuroscience a more complete appreciation of: (1) the brain's evolutionary potential (by allowing sampling of extinct lineages) and (2) the origins of modern neurological disparity. Endocast research, however, remains very much in its descriptive phase, with the vast majority of studies focused on the neuroanatomical details of a single fossil taxon (eg. Brochu, 2000; Franzosa and Rowe, 2005; Kunderát, 2007; Bever et al., 2011; Carabajal and Succar, 2013; Balanoff et al., 2014) or perhaps the evolutionary patterns within a taxonomically restricted clade (eg. Witmer and Ridgely, 2009; Balanoff et al., 2010; Ksepka et al., 2012; Carril et al., 2015). These descriptive studies are certainly advancing our general understanding of the brain's evolutionary potential as well as its constraints. For example, the huge hypophysial complex of sauropod dinosaurs informs the relationship between gigantism and the pituitary gland (Edinger, 1942; Balanoff et al., 2010).

In terms of modern neurological disparity, there have been exceedingly few attempts, outside of Harry Jerison's groundbreaking contributions, to generate and test endocast-based hypotheses that target the extensive stem lineages of major vertebrate crown clades and the origin of those clades' often highly derived neuroanatomical configurations. Perhaps the best example is Rowe et al. (2011). This study determined that the brain of crown-clade mammals is the product of at least three significant pulses of encephalization that are strongly tied to enhanced olfaction, tactile sensitivity, and neuromuscular coordination. In this section, we will explore the analytical role of endocasts in broad-based comparative neuroscience using our relatively scanty understanding of neuroanatomical evolution along the avian stem lineage as a general organizational tool. The origin of the highly encephalized, s-shaped brain of crown-clade birds is almost undoubtedly the product of numerous, but perhaps highly correlated, transformations (Figs. 4 and 5). While recognizing their probable nonindependence, we are going to divide and discuss these transformations under the individual headings of comparative morphology, encephalization, and correlative change.

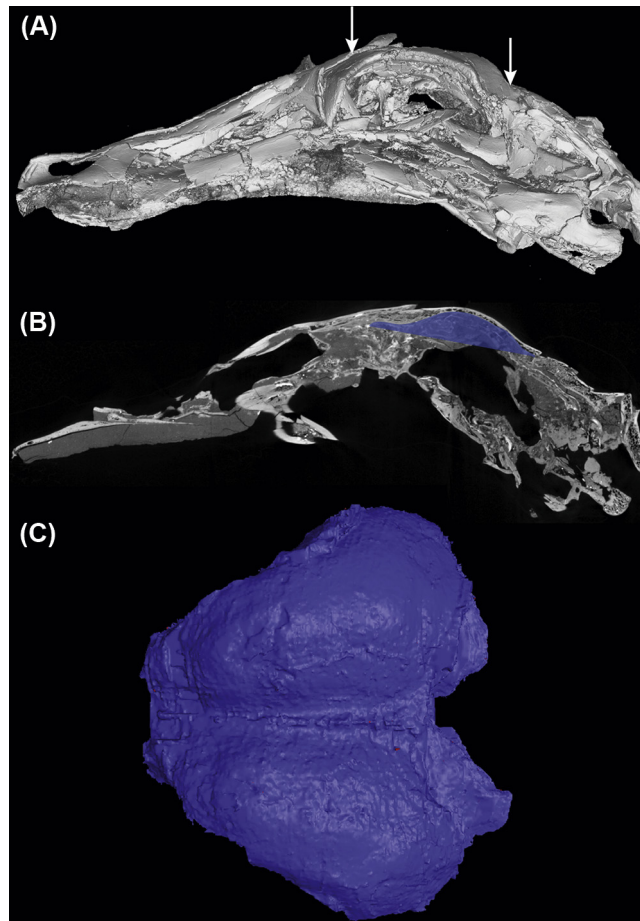


Figure 8 (A) Digital 3D rendering of the skull of the extinct ornithomimid dinosaur *Gallimimus bullatus* (IGM 100/1133) with arrows indicating the anterior and posterior limits of the endocast. (B) Sagittal CT slice revealing the position of a partial cerebral endocast (blue). (C) Partial endocast generated from the frontal and parietal bones showing the dorsal surface of the cerebrum. The rendering of this surface exhibits no trace of an avian-like Wulst. IGM, Institute of Geology, Mongolian Academy of Sciences, Ulan Bator.

1.10.3.1 Comparative Morphology

Descriptive neuroanatomy is perhaps the most intuitive use of endocasts, especially in reference to their potential for illuminating transformations otherwise concealed within stem lineages (eg. Alonso et al., 2004; Franzosa, 2004; Sampson and Witmer, 2007; Ashwell and Scofield, 2008; Witmer and Ridgely, 2009; Balanoff et al., 2010, 2013, 2014, 2015b; Bever et al., 2011, 2013; Lautenschlager et al., 2012; Ksepka et al., 2012; Kawabe et al., 2013a,b, 2015; Lautenschlager and Hübner, 2013) and/or inferring behavior in the fossil record (Hopson, 1977, 1979; Brochu, 2000; Witmer et al., 2003; Sereno et al., 2007; Witmer and Ridgely, 2009; Walsh and Milner, 2011; Walsh et al., 2013; Marek et al., 2015). Given the relatively strong correspondence between their brain and endocast (Fig. 5), it is perhaps not surprising that mammals, birds, and their respective stem lineages have enjoyed the majority of research attention from endocast workers (see Balanoff et al., 2015a for a more complete list). Attention to those vertebrate lineages lying phylogenetically outside of Amniota has steadily increased in recent years. Many of these anamniote data are concentrated in the chondrichthyan crown and stem (Schaeffer, 1981; Maisey, 2004, 2005, 2007, 2011; Pradel et al., 2009; Lane, 2010; Pradel, 2010), but endocast research on actinopterygians (Coates, 1999; Hamel and Poplin, 2008; Giles and Friedman, 2014; Giles et al., 2015a), dipnoan sarcopterygians (Säve-Söderbergh, 1952; Campbell and Barwick, 1982; Challands, 2015; Clément and Ahlberg, 2010; Clement and Ahlberg, 2014; Clement et al., 2015), and both stem (Romer, 1937; Stensiö, 1963; Jarvik, 1972; Chang, 1982; Johanson et al., 2003; Snitting, 2008; Lu et al., 2012; Holland, 2014) and crown tetrapods (eg. stem and crown amphibians; Romer and Edinger, 1942; Maddin et al., 2013) are all steadily increasing.

The comparative biology of early vertebrate fossils remains cryptic and contentious in many respects, including their phylogenetic relationships with extant lineages (Brazeau, 2009; Davis et al., 2012; Brazeau and Friedman, 2014; Giles et al., 2015b). That stated, this area of the tree has produced a surprising wealth of endocast data (eg. Stensiö, 1925; Janvier, 1981, 1985, 1996, 2008; Chen et al., 1999; Gai et al., 2011). These endocasts are often lacking in surface details, but they still provide important insights into the general shape and extent of individual neuroanatomical regions, as well as the size and distribution of cranial nerves and vessels

during what was a critical early history of endocranial evolution (Janvier, 2008). The most recent endocast data flowing from this part of tree are being facilitated by significant improvements to high-resolution CT and increased access to synchrotron X-ray tomographic data. Synchrotron data have proven especially helpful for delineating the lightly ossified and mineralized cartilaginous skeletons of important early vertebrate and gnathostome taxa from the highly indurated matrix in which they tend to be encased (Tafforeau et al., 2006; Sutton, 2008; Cunningham et al., 2014; Dupret et al., 2014; Rahman and Smith, 2014). Access to the endocranial details of these early lineages holds great promise for elucidating the basal transformations that continue to influence patterns of neuroanatomical evolution across the vertebrate tree.

Returning to the reptile side of the amniote radiation and the expansive evolutionary history of the avian stem lineage (Fig. 7), we find compelling transformations that help fill empirical gaps in our understanding of archosaur neuroanatomy and thus shed light on the highly derived structural organization characterizing the crown-avian brain. For example, the plesiomorphic condition for reptiles is an elongate brain whose major neuroanatomical regions are arranged in an almost linear, anterior–posterior fashion. This morphology is conserved across much of the reptile crown clade, including the extant sister taxon of birds—the crocodylians (Fig. 5; see Hopson, 1979; Butler and Hodos, 2005; George and Holliday, 2013; Ngwenya et al., 2013). Birds, in contrast, exhibit a derived neural architecture in which the expanded cerebrum and cerebellum are pushed into broad contact, obscuring the pineal gland and third ventricle from dorsal view and displacing the optic tectum into a more ventrolateral position (Cohen and Karten, 1974; Hopson, 1979). This major neuroanatomical rearrangement gives the modern bird brain a sinusoidal shape (characterized by two distinct flexure zones: the cephalic flexure between the fore- and midbrain and the pontine flexure within the brain stem between the mid- and hindbrain; Hopson, 1979) (Fig. 5). The rearrangement also creates a significant morphological gap between the conditions expressed in the avian and crocodylian crown clades. The origin of this disparity can be inferred to lie along the avian stem lineage, although the timing, tempo, and nature of those rearrangements will remain out-of-the-reach of comparative neuroscience unless the fossil record can help illuminate this deep history.

A linear arrangement of the major neuroanatomical regions is expressed in both ornithischian dinosaurs and the early divergences within Saurischia (sauropodomorphs and early theropods) suggesting that the basic, plesiomorphic architecture of the reptile brain is conserved along the backbone of the avian stem lineage (Galton, 1985, 1988; Giffin, 1989; Galton and Knoll, 2006; Zhou et al., 2007; Evans et al., 2009; Carabajal and Succar, 2013; Lauters et al., 2013; Cruzado-Caballero et al., 2015). There are derivations on this basic plan nested within the major extinct radiations of the avian stem (see Balanoff et al., 2010; Miyashita et al., 2011; Carabajal, 2012; Lautenschlager and Hübner, 2013). Perhaps the most dramatic example of an apomorphic rearrangement of this linear brain is found among the pterosaurs. Pterosaurs lie completely outside of Dinosauria phylogenetically, making them one of the earliest divergences along the avian stem lineage (Fig. 7; Nesbitt, 2011). Just as pterosaurs evolved the ability to perform powered flight independently of birds, they also evolved a highly derived neural architecture that includes a birdlike expansion of the cerebrum and overall s-shaped morphology (see Witmer et al., 2003). The independent acquisition of these avian features suggests a highly positive correlation, and possibly causative relationship, between the origin of archosaurian powered flight and the neural expansion and geometric rearrangement of the brain expressed in these two groups (but see later discussion).

The derived transformation responsible for the modern s-shaped brain does not appear in the dinosaurian fossil record until deep within the history of theropods, at the origin of Maniraptora (Figs. 4 and 7). The earliest history of the maniraptoran sinusoidal brain may be marked by a taxonomically sporadic (ie, homoplastic) pattern of expression (AM Balanoff, personal observation), but the variability in the system was apparently reduced by the origin of Paraves where the morphology is consistently expressed (Fig. 4C and D; Alonso et al., 2004; Balanoff et al., 2009, 2013, 2014; Norell et al., 2009; Witmer and Ridgely, 2009; Walsh et al., 2015). Although a relatively late acquisition, the s-shaped brain is still at least 160 million years old (ie, appearing 90 million years prior to the origin of the avian crown clade; Turner et al., 2012; Brusatte et al., 2014; Prum et al., 2015).

1.10.3.2 Encephalization

Endocasts provide a close approximation of volumetric brain size in groups with a high BEC index (Haight and Nelson, 1987; De Miguel and Henneberg, 1998; Iwaniuk and Nelson, 2002; Isler et al., 2008) and a maximum brain size in those with low BEC values. Endocranial volumes, including those from fossil taxa, have therefore been employed in numerous analyses to assess encephalization dynamics through time (eg, Jerison, 1969, 1973, 1977; Hopson, 1977, 1979; Larsson et al., 2000; Alonso et al., 2004; Franzosa, 2004; Ashwell and Scofield, 2008; Lautenschlager et al., 2012; Balanoff et al., 2013). Encephalization, in its most simplistic conceptualization, is brain size relative to body size (Jerison, 1977) and has been thought, with some amount of controversy, to correlate with cognitive ability or other measures of “intelligence” such as innovation rate—the rate at which novel behaviors or techniques are acquired (Jerison, 1977; see Healy and Rowe, 2007; Lefebvre and Sol, 2008; Overington et al., 2009; Lefebvre, 2013 for overviews).

The most commonly employed metric is the encephalization quotient (EQ). The EQ was first proposed by Jerison (1973) as the ratio between actual brain size (described as either a mass or volume estimate) and expected brain size and was designed to remove the allometric effects of body size on brain-size assessments. Body size remains an inherent factor in the index given that expected brain size reflects the correlative relationship between brain and body size for a given taxonomic group (Jerison, 1973). Expected brain-size estimations must therefore be calculated for individual clades without the expectation that this relationship will remain constant for any area of phylogenetic tree space. EQ is subject to the same general sources of variability and estimation error that underlie all evolvable traits, thus making its meaningful assessment in extinct taxa difficult

(see Hurlburt, 1996; Hurlburt et al., 2013). Perhaps the most daunting limitation of the EQ is the notorious difficulty of estimating body mass in fossils. Alleviating these difficulties is an active area of research, which is not surprising considering that body mass is an important variable for a wide assortment of morphological, physiological, and paleoecological considerations (eg, Christiansen and Fariña, 2004; Finarelli and Flynn, 2006; De Esteban-Trivigno et al., 2008; Campione and Evans, 2012; Field et al., 2013). An important step forward is the recognition that every skeletal measurement correlates with body mass at some level and can be used as long as the associated error is explicitly considered (Field et al., 2013).

Attempts have been made to refine the efficacy of using living taxa for estimating the expected brain size within extinct stem taxa. Hurlburt et al. (2013) used variation in the BEC index of extant crocodylians to predict EQ at the base of Dinosauria. These advances may be rendered moot as the utility of the EQ is now being seriously questioned. A myriad of other cognitive proxies, including residual brain size, residual cerebral size, and absolute brain size, may all outperform EQ—at least for certain taxonomic groups (Deaner et al., 2007; Lefebvre and Sol, 2008; Lefebvre, 2013). Each of these estimators can be derived from volumetric measurements thus increasing the explanatory potential of endocasts. Furthermore, digital technologies have facilitated the partitioning of endocasts into functional neuroanatomical regions (Walsh and Milner, 2011, 2013; Balanoff et al., 2013, 2015b; Kawabe et al., 2013b). Such partitioning allows us to pursue more specific questions and makes us less reliant on both total brain values and the vagaries of body size estimation. EQ is still used, but its days in the analytical sun may well be numbered (see Healy and Rowe, 2007; Deaner et al., 2007).

Our understanding of avian encephalization is still largely grounded in the seminal endocast studies of Jerison (1968, 1969, 1973) and Hopson (1977, 1979). These studies examined encephalization as the relationship between endocranial volume and body mass, and in doing so found distinct differences between birds and a paraphyletic reptile group. This reptile assemblage included crown-group turtles, lepidosaurs, and crocodylians, as well as a small series of ornithischian, sauropod, and nonavian theropod dinosaurs. *Archaeopteryx* was recovered as uniquely transitional between the “reptile” and avian morphospaces suggesting that a pulse of encephalization accompanied the origin of flight.

These studies assumed that “dinosaurs” conserved the relatively low BEC index of *Sphenodon* (0.5), which is undoubtedly not the case, especially as sampling moves progressively crownward (Osmólska, 2004; Evans, 2005; Hurlburt et al., 2013). Combine this point with the fact that these influential analyses could not consider the rich diversity of recently discovered fossils (Fig. 7), and one might suspect that the birdlike qualities of the *Archaeopteryx* brain may well characterize a wider array of dinosaurian forms (see Fig. 4C and D). If a larger, more avian-like brain is present in other theropods, then its relationship with the origin of flight becomes less clear.

The hypotheses of Professors Jerison and Hopson went uncontested for nearly a quarter century. This period of stagnation reflects the highly comprehensive nature of these early studies, even though the data available during this period were largely restricted to naturally occurring endocasts—a restriction that placed severe limitations on sampling and hypothesis testing. The appearance and rapid spread of nondestructive digital technologies for building and studying endocasts both loosened these sampling constraints and increased the rigor of endocast-based comparative analyses. Digital methods allow endocasts to be generated in a more standardized way (eg, with or without such structures as cranial neurovasculature) that increases the accuracy and precision of their shape and volumetric assessment (see Balanoff et al., 2015a).

The comparative studies emerging as part of the digital era of endocast research have, in many respects, confirmed the early hypothesis that crown-clade birds express apomorphically large brains and that *Archaeopteryx* is an important transitional form. Its degree of encephalization is intermediate between those of modern birds and most reptile clades—including most of the nonavian dinosaur groups (eg, Larsson et al., 2000; Alonso et al., 2004; but see Hurlburt et al., 2013, which found the EQ of *Archaeopteryx* to overlap with the lower range of encephalization expressed by crown-clade birds). The Larsson et al. study drew the important conclusion that encephalization along the avian stem was driven largely by cerebral expansion and that this expansion began deep within theropod history (at least by the time the tyrannosaurs diverged from the backbone of the avian stem lineage; Fig. 7). From this conclusion, they made the correlative prediction that more dinosaurs enjoyed encephalization levels comparable to that of *Archaeopteryx* (Fig. 9); unfortunately, they did not have the data to test their own hypothesis.

The crownward part of theropod history is just now beginning to be sampled with some density (eg, Lautenschlager et al., 2012; Balanoff et al., 2013, 2015b). The patterns emerging from these studies support the predictions of Larsson et al. (2000) (Fig. 9). The data of Balanoff et al. (2013) clearly indicate that cerebral expansion was the primary driver of increasing endocranial volume along the avian stem lineage. These data also suggest that this expansion was not continuous but appeared in pulses (Balanoff et al., 2013). More work is required to determine how much of this pattern reflects evolutionary reality as opposed to sampling artifact (Balanoff et al., 2015b). The limiting factor to testing such patterns is no longer access to the anatomy but rather the time and effort of researchers. This new reality bodes well for the future of encephalization studies that utilize the fossil record.

1.10.3.3 Correlative Change

One of the most important yet formidable tasks of the comparative neuroscientist is to address questions on how the evolution of the brain and its gross morphology relates to the historical patterns of other biological systems. For example, how does the size and shape of a particular brain region correspond to the functions that the region serves (eg, Iwaniuk et al., 1999, 2000)? How does encephalization impact the morphology and functional anatomy of other cranial modules (eg, Lieberman et al., 2008)? Does the brain play a significant role in patterning other cranial tissues during development through the production of signaling proteins,

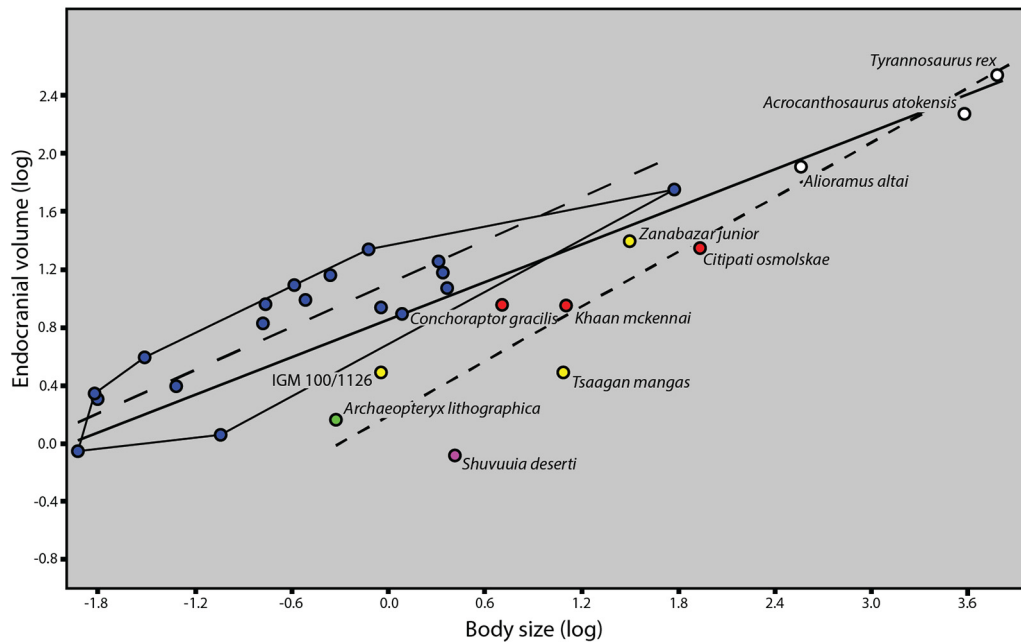


Figure 9 Bivariate plot of log-transformed body-mass data. Body mass (kg) plotted against total endocranial volume (cm³). Colors indicate crown-clade birds (blue), nonmaniraptoran theropods (white), *Shuvuuia deserti* (purple), oviraptorosaurs (red), deinonychosaurs (yellow), and *Archaeopteryx lithographica* (green). Reduced major-axis regression line for entire sample (solid line), crown birds (large dashes), and nonavian theropods (small dashes). Crown-clade birds display apomorphically high endocranial and cerebral volumes with respect to body size, but *Archaeopteryx* falls within the distribution of other nonavian maniraptoran dinosaurs. Balanoff, A.M., Bever, G.S., Rowe, T.B., Norell, M.A., 2013. Evolutionary origins of the avian brain. *Nature* (Nature Publishing Group) 501 (7465), 93–96. <http://dx.doi.org/10.1038/nature12424>.

and how has this developmental dynamic evolved to impact cranial diversity across the tree (eg, Marcucio et al., 2011)? How does the transformational history of the brain correspond to other macroevolutionary patterns of taxonomic diversity (eg, Flinn et al., 2005)?

Here the ability of fossil endocasts to serve as empirical windows into the history of a phylogenetic stem may be especially valuable. To take full advantage of the insights that endocasts can provide and to understand the broader implications of brain evolution, we have to move away from treating endocast data as abstract shapes and sizes. This integrative process is certainly underway, and there are many examples that we could provide to demonstrate this point. To explore a few of them, let us once again return to avian cerebral expansion.

Cerebral hyperinflation is the primary driver of encephalization in the deep history of birds and likely initiated the geometric conversion of the plesiomorphic linear brain to the apomorphic sinusoidal brain (Fig. 5; Balanoff et al., 2013, 2015b). Such a dramatic neuroanatomical reconfiguration did not evolve in an anatomical vacuum, but is correlated, at least in part, to an equally impressive transformation of cranial morphology as a whole. Expansion of the cranial vault and overlying dermal roof, enlargement and repositioning of the orbits, and shortening of the facial skeleton (Brusatte et al., 2012; Bhullar et al., 2012) are all stem transformations within maniraptoran dinosaurs that we now associate with the avian cranial form. This form is distinctive when compared to that of adult crocodylians and early dinosaurs, yet remarkably similar to the juveniles of those same taxa (Bever and Norell, 2009; Bhullar et al., 2012). It now appears likely that these birdlike features of the cranial skeleton are the products of multiple, global shifts in developmental timing (paedomorphosis) (Bhullar et al., 2012), at least some of which are temporally congruent with the neuroanatomical transformations that produced the avian s-shaped brain (Balanoff et al., 2013).

Phylogenetic congruence raises the question of whether the cranial and neuroanatomical transformations are linked in some deeper, perhaps causative manner. Among extant birds, variation in orbit size and shape is correlated with dramatic shifts in endocranial morphology, including a more globular brain and braincase (Kawabe et al., 2013b). A large endocranial volume relative to the length of the cranial base has also been associated with a more globular brain (Marugán-Lobón and Buscalioni, 2003). Whether these correlations reflect geometrically imposed constraints on morphospace or perhaps are the phenotypic products of some shared, deeply conserved linkage in their developmental pathways is as yet unclear. Certainly, these types of broadly integrative questions are of critical importance to the morphologist, paleontologist, and comparative neuroscientist and cannot be answered without input from each discipline (Rowe, 1996; Rowe et al., 2011; Werneburg et al., 2014).

Another correlative relationship that may be informed by the fossil record is the one uniting neuroanatomy and behavior. For example, the discovery that the brain of *Archaeopteryx* corresponds closely in both shape and size to that of at least some other nonavian theropod dinosaurs (Fig. 9; Balanoff et al., 2013) suggests that we may have to rethink the relationship between the origins of

avian encephalization and flight. If we accept that *Archaeopteryx* could fly in some capacity (Gatesy and Dial, 1996; Burgers and Chiappe, 1999; Wang et al., 2012), then we must also logically accept that the brain of *Archaeopteryx* had the processing power and cognitive range necessary to support that behavior in an amniote (these neural requirements may differ significantly from those that flight incurs, for example, in arthropods). If the brain of *Archaeopteryx* was “flight ready,” then volumetrically speaking, so were the brains of these other apparently nonvolant dinosaurs (Fig. 9). This point, in turn, supports the conclusion that avian encephalization was an exaptation for flight rather than an adaptation that coevolved with this highly successful avian locomotory and ecological strategy (Balanoff et al., 2013, 2015b). In fact, flight explains almost none of the observed variation in total endocranial volume for birds and their stem relatives (Balanoff et al., 2015b).

There is a theoretical basis for employing brain size (ie, the amount of neural tissue present), and the size of its constituent regions, as a proxy for processing power and behavioral potential. The hypothesis is formally termed the Principle of Proper Mass (Jerison, 1973), and it is often invoked in studies that attempt to use size measurements drawn from endocasts to support conclusions regarding activity of function and behavior in extinct taxa (Jerison, 1973; Witmer et al., 2003; Zelenitsky et al., 2009, 2011; Lautenschlager et al., 2012; Sales and Schultz, 2014). Even if we set aside for a moment the difficulties of measuring cognitive ability, the relationship between the size of a neural region and the intensity of its use is almost assuredly more nuanced than is apparent from our interpretations (see Healy and Rowe, 2007). The shape of a neural region, for example, appears to be an important arbiter of processing speed and thus should also be explicitly considered when attempting to relate endocasts to behavior. This point was demonstrated elegantly in primates whose globular-shaped brain serves to decrease average connection length. A shorter connection length in turn facilitates more efficient processing and faster communication (see Sepulcre et al., 2010; Smaers and Soligo, 2013). Neuronal density may outcompete both size and shape as a reflection of a region's intensity of use (see Olkowicz et al., 2016). Although such considerations may complicate our ability to use volumetric data from endocasts for inferring behavior in the fossil record, they also open new pathways for constructing and testing evolutionary and functional hypotheses—thus contributing to the integrative potential of endocast research.

1.10.4 Concluding Remarks

The study of endocasts was pioneered well over a century ago (eg, Marsh, 1880; Osborn, 1916; Edinger, 1925, 1951, 1975). For most of this history, it is difficult to argue that endocast data had more than a subtle influence on paleobiology or comparative neuroscience. The muted impact of such interesting data largely reflects the severe logistical constraints that once plagued the discipline. A reliance on the chance discoveries of natural endocasts, the suboptimal resolution of latex or other physically generated endocasts, and the destructive nature of traditional serial sectioning meant that the sampling benefits afforded the comparative biologist by the fossil record could not be fully realized for endocasts. These difficulties have now been largely overcome through digital technologies (Carlson et al., 2003; Witmer et al., 2008; Balanoff et al., 2015a). Endocasts are actively being constructed for the best specimens in all the major vertebrate clades. Including an endocast with the description of a newly discovered fossil skull is rapidly becoming the standard operating procedure.

The limiting factor in this golden age of endocast research is not whether the fossil record will produce the data we need to adequately document neuroanatomical transformations in deep time. What ultimately limits research is the degree to which we can correlate endocast morphology with the 3D complexity and modularity of the brain itself (Boire and Baron, 1994; Barton and Harvey, 2000; Iwaniuk et al., 2004; Iwaniuk and Hurd, 2005; Smaers and Soligo, 2013). Attempts to rigorously partition the endocast into neurologically meaningful volumetric regions are a step in the right direction. Although the quantitative relationship between the bony landmarks and the neuroanatomy require verification in a broader sample of lineages, the approach appears useful in tracing the modular nature of the brain in deep time (Balanoff et al., 2013, 2015b).

Volumes will continue to be an important aspect of comparative endocast and brain studies. There are compelling recent data, however, indicating that internal architectural rearrangements may be a more efficient mechanism for increasing processing efficacy and speed than simply increasing the volume of a neuroanatomical region (Sepulcre et al., 2010; Smaers and Soligo, 2013). If this is the case, then shape variation may be as important a predictor of that internal architecture and its neurophysiological implications as volume—a hypothesis that is especially intriguing given the remarkable level of shape variation that vertebrate endocasts appear to possess. The analytical potential of establishing these types of correlative relationships make the study of endocasts fertile ground for the increasingly sophisticated morphometric tools of shape analysis (Kawabe et al., 2013b; Klingenberg and Marugán-Lobón, 2013).

The structural and functional complexity of the brain is always going to exceed the volumes, shapes, and surface features available from an endocast. The point that we hope to convey here is that, just as every skeletal metric has some relationship with body size, each of the complex, 3D components of the brain bear some correlative relationship with the surface of the brain and with the morphology of the endocast. These correlations will not always be strong; certainly some of the brain's architectural and functional nuances will remain beyond the reach of the endocast. But, by gaining an understanding of where these strengths and weakness lie, we will comprehend the range and depth of questions that endocast data can and cannot support. We are willing to wager that this process of discovery will reveal that endocasts have a greater potential for broadly interesting, significant discoveries than most of us might currently conclude.

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