Exploring Dinosaur Neuropaleobiology: Computed Tomography Scanning and Analysis of an *Allosaurus fragilis* Endocast

Viewpoint

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Summary

The unique opportunity to examine an exceptionally well-preserved natural endocranial cast (endocast) from a carnivorous dinosaur of the late Jurassic period, *Allosaurus fragilis*, was afforded this neurobiologist. The endocast exhibits numerous surface features including the complete vestibular apparatus. Spiral computed tomography scanning revealed multiple internal features including putative blood vessels, connective tissue-like arrays, and a prominent symmetrical density consistent with the putative brain or its cast. The evidence suggests that this organism's neurobiology resembled closely that of modern crocodylian species and should be included for consideration when examining ideas of *Allosaurus* evolution, behavior, and eventual extinction.

Allosaurus fragilis (*A. fragilis*) was the dominant carnivorous theropod dinosaur of Western North America in the late Jurassic period of the Mesozoic era (about 140 million years ago). This is a particularly well-characterized dinosaur due to abundant skeletal remains amassed from a presumed predator trap now known as the Cleveland-Lloyd quarry (Madsen, 1976; Stokes, 1985). Although fossilized bones provide information about dinosaur ancestry, physiology, and behavior, a glimpse of a dinosaur brain would be most useful in adding a neurobiological perspective into how *A. fragilis* approached its environment. Of course, the brain is a soft-tissue structure that is sensitive to rapid necrosis upon death, and it is generally assumed to be lost prior to fossilization. There is, however, growing evidence that occasionally soft tissues, or their imprints, are retained. For example, the Jurassic *Archaeopteryx* and other fossilized birds exhibit feathers, strongly suggesting an evolutionary link between certain dinosaur linages and modern birds (Carroll, 1988; Chatterjee, 1997; Forster et al., 1998). Fossilized lung structures (Ruben et al., 1997), abdominal structures, muscles (Sasso and Signore, 1998) and other soft tissues including blood vessels have also been identified (Kellner, 1996), as well as the elucidation by computed tomography (CT) scanning of embryonic cartilage concealed within dinosaur eggs (e.g., Hirsch et al., 1989). Even amino acid composition from proteins over 100 million years old have been obtained (e.g., Gurley et al., 1991; Muyezer et al., 1993). As for the brain,

descriptions of natural or prepared dinosaur endocasts are not new (reviewed by Hopson, 1979; Russell, 1997). However, their application to comparative neuroanatomy has been limited by both their infrequency and the inability to visualize their contents through noninvasive methods. Housed in the paleontology collections at the University of Utah museum of natural history is one such remarkably complete, and well-preserved, natural *A. fragilis* endocranial cast obtained from the Cleveland-Lloyd quarry (sample UUVP 294; Madsen, 1976). In this paper, I present the exceptionally well-preserved surface features of this endocast and an analysis using spiral CT imaging. These data offer the opportunity to consider what the neurobiology of *A. fragilis* was like through comparisons with modern relatives such as crocodiles and birds and in turn speculate on issues of behavior and adaptive responses to its environment.

The complete natural endocast from *A. fragilis* is shown in Figure 1. The endocast is ~16 cm tall and ~16 cm long and strikingly narrow, since its broadest point is ~4 cm in the cerebrum. During original preparation (Madsen, 1976), a hole was drilled into the endocast to facilitate positioning a metal rod for mounting, and yellow paint was used to highlight surface features resembling articulations. From the dorsal and posterior perspectives, the medulla–brain stem is slightly displaced to the left side relative to the cerebrum and olfactory processes (Figures 1D and 1E). A partial list of key endocast surface features are labeled in Figure 1B (see also Hopson, 1979, for a brief description). These include conspicuous olfactory processes that extend directly anterior from the endocast cerebrum before narrowing into the olfactory peduncles and reexpanding into the olfactory bulbs. Amorphous rock matrix composes almost half of the ventral side of the olfactory processes (Figure 1C). The cerebral region of the endocast is somewhat oval but constricts dorsally where it is capped by amorphous matrix. Posterior to the cerebrum center, the endocast tapers sharply in the cerebellar region, and a tight constriction occurs just anterior to the medulla–brain stem. At the cerebellar base are bilaterally well-preserved vestibular structures including the semicircular canals through which the flocculus projects. Immediately anterior and slightly ventral to the semicircular canals are the ophthalmic and maxillary–mandibular branches of the trigeminal nerves. Proceeding anteriorly toward the ventral base of the cerebrum, the optic nerve and oculomotor and/or trochlear nerve are readily identified.

How does the *A. fragilis* endocast compare with endocasts and brains of modern species? In Figure 2, the *A. fragilis* endocast is compared with an endocast of *Caiman crocodilus* (Hopson, 1979) and the brains of *Alligator mississippiensis* (Crosby, 1916; Kruger and Berkowitz, 1960), a Kiwi (*Apteryx australis*; Craigie, 1930), and a pigeon (genus *Columba*, see Butler and Hodos, 1996). These organisms were selected for comparison because they are living decendants of species related to *A. fragilis* (Chatterjee, 1997; Parrish, 1997). Also, the Kiwi is of interest because it relies strongly on
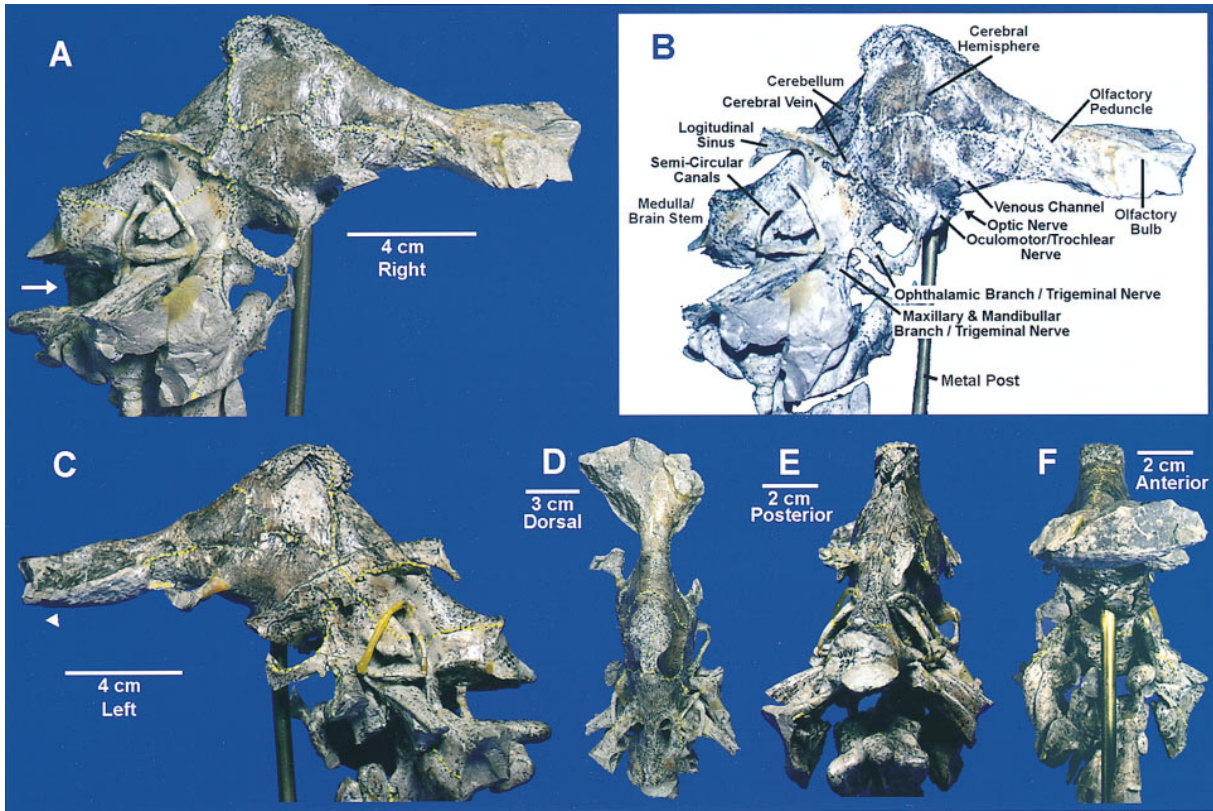
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Figure 1. Surface Features of the *Allosaurus fragilis* Endocast (UUVP 294)

(A) Right lateral view. The yellow paint was applied to delineate natural articulations (Madsen, 1976), and endocast structures studied are dorsal to the arrow.

(B) Identification of surface features. The metal post inserted at the time of original endocast preparation is noted.

(C) Left lateral view. The arrowhead points to lighter colored rock matrix material that underlies the olfactory processes. The yellow material comprising the anterior semicircular canal is epoxy that was used to reconstruct this feature on this side (see text).

(D) Dorsal view. Note the slight displacement of the medulla–brain stem to the left side.

(E) Posterior view.

(F) Anterior view.

olfaction for feeding, it is bipedal and flightless, and mammals were not significant predators until relatively recently in New Zealand. The Kiwi has also been suggested to be a "primitive" bird due to its rudimentary neurobiology (Craigie, 1930). Finally, the pigeon is included as a representative of more specialized birds that exhibit flight and well-developed visual acuity. The *Caiman* endocast and alligator brain exhibit a notable similarity with the *A. fragilis* endocast. For example, the olfactory processes of *A. fragilis* embody ∼25% of its length (olfactory bulbs to cerebellum), which is similar to the alligator brain (∼35%) and endocasts from *Caiman crocodilus* (34%) and *Crocodylus niloticus* (33%; Hopson, 1979). The Kiwi brain has relatively large ovoid olfactory bulbs (Figure 2), and they reside ventral to the cerebrum where they project only a short distance
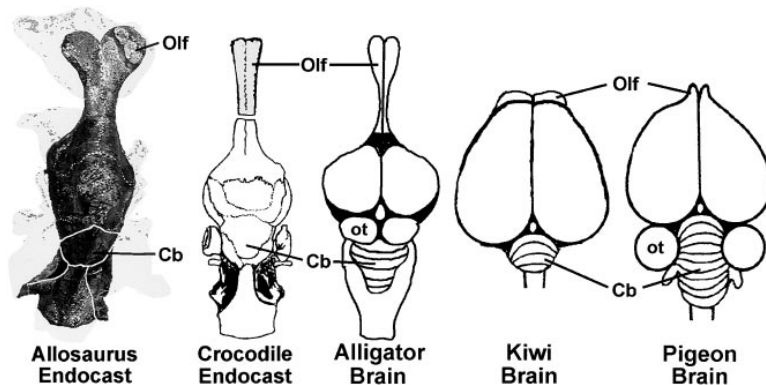

Figure 2. Comparison of *A. fragilis* Endocast Morphology with that of a Crocodile Endocast and Alligator and Bird Brains

The *A. fragilis* endocast with surrounding rock matrix recolored in light gray is compared with an endocast made from a crocodile (*Caiman crocodilus*) and the brains of an alligator, a Kiwi, and a pigeon (see text for references and details). The crocodile endocast olfactory projections (in darker gray) are reconstructed for this illustration (see Hopson, 1979). Olfactory structures (Olf), the cerebellum (Cb), and the optic tectum (ot) are noted, and outlines for comparison were added to the *Allosaurus* endocast.
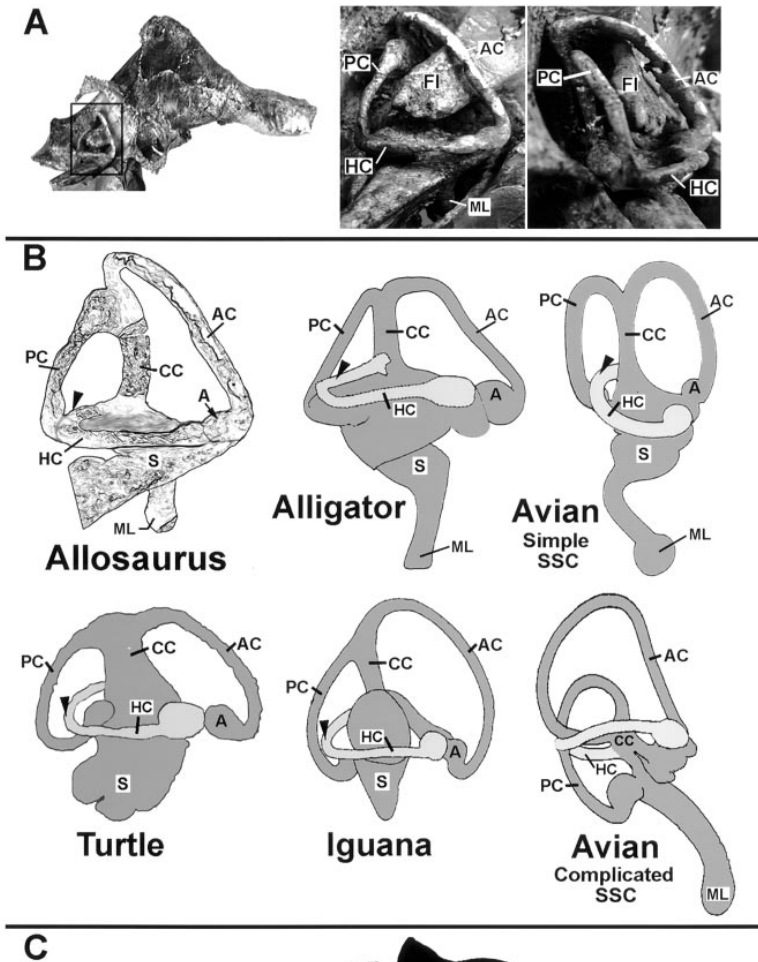
Figure 3. Comparative Morphology of the *A. fragilis* Vestibular Apparatus

(A) The well-preserved vestibular apparatus from the right side of the *A. fragilis* endocast (boxed) is enlarged to show the right lateral view (middle) and posterior view (right). Notable structures are the flocculus (FI), the anterior canal (AC), the posterior canal (PC), the horizontal canal (HC), and the structure projecting ventrally from the saccule (S) housing the macula lagenae (ML). The width of the semicircular canal complex is ~3.5 cm and its height is ~3 cm.

(B) The *A. fragilis* vestibular complex is compared with similar complexes (redrawn from references within the text) from an alligator, a turtle, an iguana, and birds, which can exhibit semicircular canal relationships that are relatively simple (simple SSC) or more complex (complicated SSC). Additional structures are the crus commune (CC) and the anterior canal ampule (A). The horizontal canals are shown in light gray and the arrowhead points to the sharp turn of the horizontal canal discussed in the text.

(C) The *A. fragilis* endocast profile is placed within a shadow drawing of an *A. fragilis* skull to which two vertebrae have been added. The endocast is oriented as in the text, and the vestibular apparatus is highlighted as in (B).

beyond the cerebrum (~6% as measured above). Both Kiwi and pigeon exhibit a proportionately wider forebrain (posterior telencephalic region) relative to the alligator brain or the *Caiman* or *Allosaurus* endocasts. These general features suggest a distinct similarity between the endocast of *A. fragilis* with similar neurological and endocast features of crocodylian species.

Retained on the *A. fragilis* endocast are the well-defined structures of the vestibular sense organs (Figures 1 and 3), including semicircular canals and a ventral projection consistent with the housing of the papilla basilaris (cochlear duct) and macula lagenae (Wersäll and Bagger-Sjöbäck, 1974; Wever, 1978). The semicircular canals on the right side are complete (Figure 3A), but the anterior semicircular canal on the left side was reconstructed during original endocast preparation (Figures 1C and 3; Madsen, 1976). The posterior and anterior

canal both arise from the dorsal aspect of the crus commune and radiate to produce a "triangular" shape. The anterior canal ends ventrally in a prominent ampule that is juxtaposed with the anterior-most progression of the horizontal canal that enlarges at its termination. The horizontal canal proceeds from the crus commune in a generally posterior direction until it encounters the ventral end of the posterior canal, where it turns sharply and proceeds forward. The horizontal canal is almost parallel with the endocast cerebral surface, and it ends in a slight enlargement adjacent to the anterior canal ampule (Figure 3B).

In Figure 3B, a drawing of the *A. fragilis* endocast vestibular structure is compared that of a turtle (*Chrysemys scripta*; Wever, 1978), an iguana (*Iguana tuberculata*; Wever, 1978), an alligator (*Alligator mississipiensis*; Wever, 1978), and two generalized birds (simple and
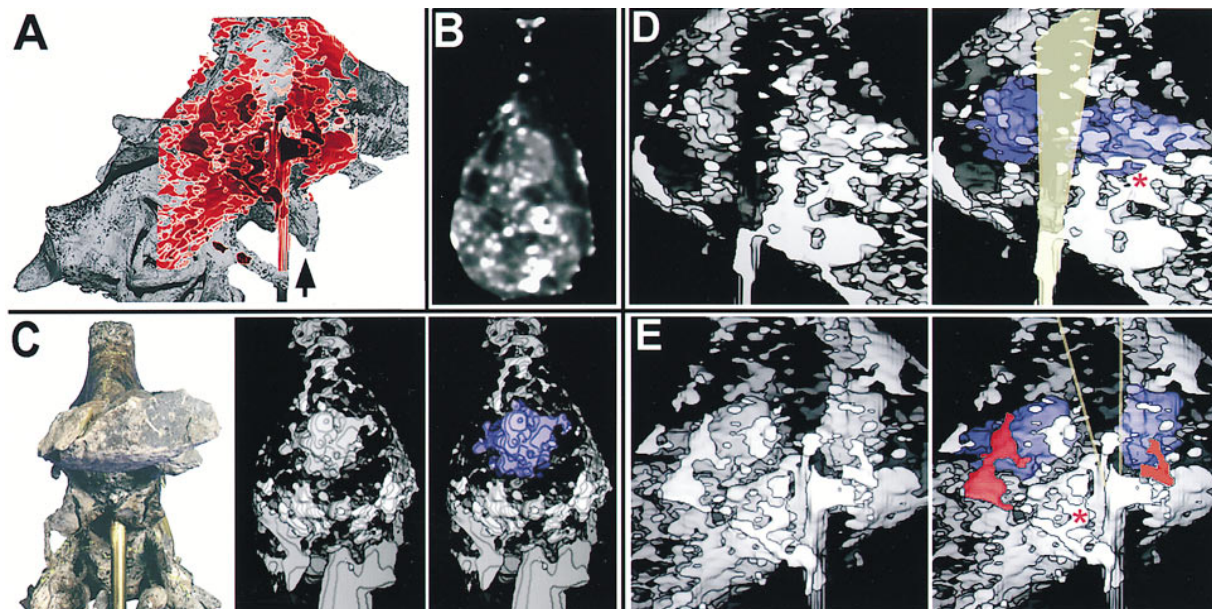
Figure 4. Spiral Computed Tomography (CT) Analysis of the *A. fragilis* Endocast

(A) Region of the *A. fragilis* endocast examined by spiral CT analysis (highlighted in red).

(B) An example of a spiral CT coronal cross-sectional image collected at approximately the level indicated by the arrow in (A). Regions of high attenuation are observed as an ovoid body roughly in the center of the endocast and an array of images seen predominantly ventral to this body.

(C) Coronal view of the endocast (far left) is compared with the three-dimensional shaded spiral CT surface rendering. For this image, the endocast superficial material is mostly removed to reveal the computer assigned internal structure segmentation of high intensity volumes. The large body protruding ventrally from the endocast is the metal mounting rod. This three-dimensional reconstructed image can be compared with the unprocessed image shown in (B). Note the location and symmetry of the prominent internal ovoid feature (highlighted in blue, far right).

(D and E) Sagittal views (left side [D] and right side [E]) of the CT surface rendering of the *A. fragilis* endocast. The prominent ovoid body that is consistent with the putative brain structure or its cast is in blue. Two putative blood vessels, which were identified based upon the criteria of shape and continuity with identified endocast surface vessels (see Figure 1B), are highlighted in (E) in red. The internal structures that were destroyed by drilling of the endocast during its original preparation (Madsen, 1976) are delineated by yellow shading (D) or yellow lines (E). The additional mesh-like array of material in the ventral posterior region (red asterisks) is discussed in the text.

complex semicircular canal geometry; Lowenstein, 1974; Wersäll and Bagger-Sjöbäck, 1974). The alligator, iguana, and turtle posterior and anterior semicircular canals are at distinct angles relative to each other (approximate range of 45°–55°). This resembles closely the ∼50° relationship between these canals and the general triangular geometry of *A. fragilis*. In contrast, the homologous semicircular canals in birds suggest a more "rectangular" shape and reside at relative angels of ∼15°–20°. As with the horizontal canals of alligators, iguanas, and turtles, there is a sharp turn by the horizontal canal of *A. fragilis* that is distinctly different from the more gradual bend or arc seen in birds (see Figure 3B). Also, the ventral projection from the saccule of the *A. fragilis* vestibular structure exhibits no curvature or ventral expansion as is often associated with birds (Figure 3A; Wersäll and Bagger-Sjöbäck, 1974). Since this ventral projection is prominent in alligators but poorly represented in iguanas and turtles (Figure 3B), it can be concluded that there are distinct similarities between the vestibular apparatus of *A. fragilis* and alligators that are not shared with turtles, iguanas, or birds. Of course, there is the possibility that this geometry changed over evolutionary time or was distorted upon fossilization. Both of these possibilities seem unlikely since semicircular canal geometry and size are remarkably similar

between related organisms (Jones, 1974), and the close resemblance to modern alligator semicircular canals would seem conspicuously coincidental if distortion during fossilization was responsible. In fact, the fossilized vestibular apparatus from an upper Triassic crocodylian ancestor, *Leptosuchus* (Case, 1928), retains a close similarity to its extant relative, further suggesting that this fossilized structure is faithfully preserved.

The orientation of the vestibular apparatus is critical to balance and is associated with how an organism holds its head (Wever, 1978; Henn, 1988; Dickman, 1996). Consequently, the *A. fragilis* vestibular complex offers an opportunity to consider how this animal held its head. To examine this, the *A. fragilis* endocast was placed into an *A. fragilis* skull (University of Utah Museum of Natural History). The final orientation of the endocast (Figure 3C) was based upon inner cranial surface anatomical and stearic considerations, alignment of the medulla–brain stem relative to vertebral column attachment, location of the olfactory processes within the skull, and correspondence of the vestibular apparatus and optic nerve with appropriate cranial openings. This configuration suggests that the head would have been held level or slightly inclined (≤10°) to the horizontal plane.
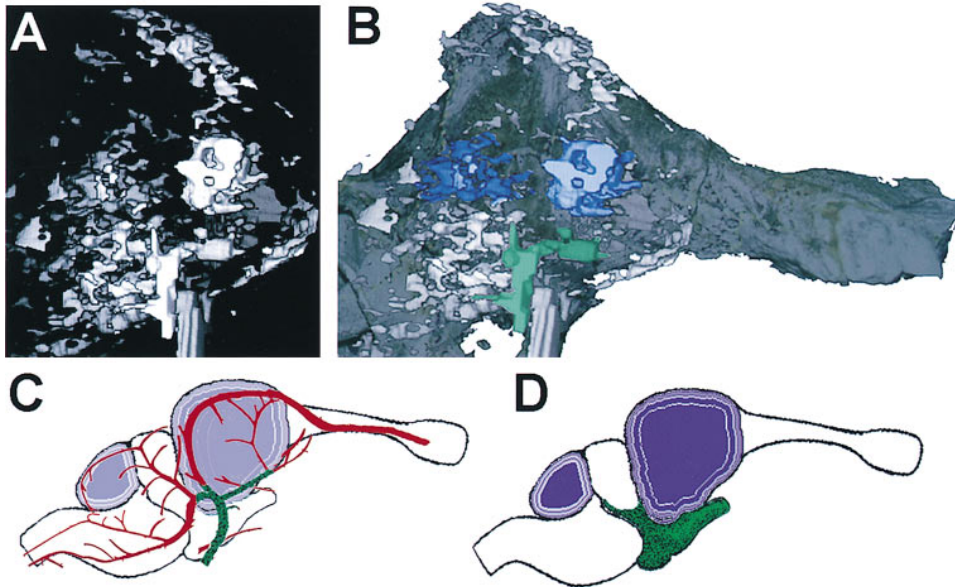
Spiral CT scanning (Fishman and Jeffrey, 1995) was

Figure 5. Additional Internal Structure of the *A. fragilis* Endocast Revealed by Spiral CT Scanning

(A and B) This endocast view (A) similar to Figure 4E is rotated slightly clockwise and sectioned further toward the center to reveal another prominent endocast internal feature that is highlighted in green in (B). The putative brain image is highlighted in blue. This perspective also highlights the extensive internal network seen in the lower posterior of the endocast. Two possibilities for the identity of this structure are suggested.

(C) First, this structure exhibits a strong similarity to a portion of the internal carotid artery (highlighted in green) of the alligator brain blood supply (in red). The alligator cerebral hemisphere and cerebellum are colored in blue to approximately match the images highlighted in the same color on the spiral CT scanning image in (B). In this depiction, the site of the optic tectum would be absent due to its location within the site of drilling (see Figure 4 and text).

(D) This image depicts the optic tract for the alligator brain (green), which is also coincident with the location and shape of this CT image endocast internal structure. The hypothesis that this structure reflects the internal carotid artery as presented in (C) is favored for reasons discussed in the text.

performed to explore the possibility that internal features of the endocast were preserved with similar fidelity as surface features. The endocast was positioned in a Picker PQ5000 spiral CT scanner, and images were collected from just posterior to the olfactory processes to the medulla–brain stem region (Figure 4A). Volumetric data collected primarily from regions of high attenuation and thresholds (Figure 4B) were combined to produce a three-dimensional shaded surface rendering using the Voxel-Q software system. Upon removal of the endocast superficial material, the presence of prominent internal features was revealed (Figures 4C–4E), including a pronounced collection of high intensity material that forms a conspicuous ovoid body (Figure 4C, blue). This body resides within the site of cerebral expansion and immediately posterior to the location of olfactory process input. In sagittal views, this density persists posteriorly until it is disrupted by the drill hole. It again appears (but with less density) before tapering symmetrically into a cone-like shape at its posterior termination within the confines of the endocast cerebellar region. The possibility that this ovoid density reflects a preserved brain structure or a cast of this body is discussed below.

Spiral CT scanning also reveals abundant vesicular-like structures that form a complex internal maze that surrounds the putative brain structure (Figures 4D and 4E). If not CT artifact, these structures may reflect a mixture of blood vessels and connective tissue. Some of these tubular structures are likely to be blood vessels, since there is well-defined continuity with blood vessels found on the endocast surface (see Figures 1B and 4E). For example, the venous channel can be followed into the endocast where it widens before bifurcating into two branches that persist to the dorsal and anterior, respectively. A similar continuity is seen between the cerebral vein and a tubular feature that bifurcates in the ventral anterior endocast region. Other possible blood vessels are seen (Figure 4D), but, due to a lack of continuity with surface features, they cannot be unambiguously distinguished from this complex internal framework of interconnected tubules surrounding the putative brain structure (Figure 4E).

Another feature revealed by spiral CT scanning is a long tubular structure on the right side (Figure 5) that begins immediately posterior to the optic nerve. Two possibilities are presented for its identity. First, it resembles closely the internal carotid artery of the alligator (Burda, 1969; Figure 5C), and its anterior-most extension is consistent with the foramen through which this artery emerges from the cranial cavity in crocodiles (Hopson, 1979). Branches from this structure progress ventrally, but they blend into the complex internal maze described above. Also, although the anterior expansion of this structure is consistent with the site of bifurcation into the middle cerebral artery, no structure was identified that transverses dorsally from this point. A second, but

less likely, possibility is that it is an optic tract (Figure 5D). The location of the anterior-most progression is coincident with the entrance of the optic nerve in the alligator brain (Crosby, 1916), and the posterior aspect parallels the drilling void, which is where the optic tectum would be located. However, the ventral aspect continues to its point of termination, which is somewhat too far to favor this interpretation.

Clearly, the interpretation of soft-tissue structures visualized by spiral CT scanning within the endocast must be approached with caution. However, if CT artifact, the close agreement of shape, size, and location of both external and internal features with homologous structures in modern organisms would be extraordinarily fortuitous. If indeed the CT densities reflect soft-tissue structures, particularly the cerebral image, is this the native shape and configuration? For example, these internal structures may have originally filled the entire endocranial case but "shrank" subsequent to death. If true, however, necrosis of the brain proceeds rapidly (particularly grey matter) and would be expected to produce distortions consistent with shrinkage or collapse in the general direction of gravity. This is difficult to reconcile with objects that are roughly symmetrical and suspended evenly both within the plane of the endocast and within the expansion of the endocast cerebral region (Figure 4). Also, unlike birds or mammals, the brain of crocodylian species fills only ~50% of the endocranial space and is surrounded by a connective tissue array similar to that seen for the A. fragillis endocast (Case, 1921; Jerison, 1973; Hopson, 1979). Nevertheless, in the context of preservation, not all structures are obviously bilateral, which could be due to several factors. First, some bilateral structures may have been destroyed unilaterally due to drilling (particularly on the left-hand side). Second, the ability to distinguish between blood vessels and other internal mesh-like arrays is not straightforward and may obscure relevant bilateral features. Third, the right-hand side of the endocast is somewhat better preserved, and the brain stem is distorted toward the left (Figure 1). This relatively small distortion on the surface may be responsible for the "well-spread" CT images on the right side but more "compressed" images on the left side (Figure 4). Finally, perhaps complete bilateral preservation of such unique soft-tissue structures simply did not occur. However, taken collectively, the available data are remarkably consistent with living extant crocodylian relatives, which suggests that the internal structures imaged were not generated simply from decay or a random collection of sediment.

The proposed crocodylian-like neurobiology of A. fragilis has several implications. For example, is there a close ancestry of Allosaurus, and its later relative Tyrannosaurus, with those of avian species (e.g., Bakker, 1986; Reid, 1997)? One position might be that there is no need for A. fragilis to be a neurological close relative of birds since avian-like neuroanatomy was already present in contemporary organisms. For example, endocast reconstructions of the Archaeopteryx forebrain resembles that of the Kiwi (Edinger, 1926), and other feathered avian ancestors resemble modern birds (Chatterjee, 1997). Consequently, avian-like neurobiology may well have evolved in some theropod dinosaurs with evolutionary connections to modern birds as well as possibly independently in organisms that did not give rise to birds, such as pterosaurs (Carroll, 1988). The neurobiology of A. fragilis, and possibly its later Cretaceous relatives such as Tyrannosaurus whose endocast shape is even more tubular than that of A. fragilis (Case, 1921), does not resemble that of birds. Consequently, the better fit of A. fragilis with crocodylian-like neurobiology and the existence of avian-like neurology in "bird-like" and other contemporaries suggest that theropods distinct from A. fragilis are perhaps better candidates as avian ancestors.

In addition to illuminating potential evolutionary relationships, the structure of the endocast of A. fragilis endocast also provides a framework for speculating about the behavior of this extinct theropod. For instance, the enlarged olfactory apparatus of Allosaurus suggests a significant dependence upon its sense of smell. Because the vertebrate brain has been largely conserved in evolution (Jerison, 1973; Butler and Hodos, 1996), additional very general speculations regarding Allosaurus behavior can be proposed based upon comparisons with modern day relatives. For example, birds display substantial elaboration of the cerebrum (Figure 2) relative to crocodylian species (and A. fragilis). The increased elaboration of the forebrain imparts greater neuronal complexity (e.g., somatosensory processing; Northcutt, 1981; Karten and Shimizu, 1989; Butler and Hodos, 1996), which enhances the ability of these organisms to extend foraging ranges, explore and succeed in novel environments, and develop behaviors such as discriminatory feeding. In contrast, alligators or crocodiles, with the substantially lower energy needs of ectothermic (cold-blooded) metabolism, readily sustain their feeding requirements by swallowing most anything that comes near enough to snatch. This basic difference in metabolism and brain structure (and therefore behavior) contributes to the ability of birds to radiate into their many diverse environmental niches, while crocodylian species are confined to more restricted environments. Are these considerations relevant to Allosaurus? Before speculating, key caveats must be considered. First, Allosaurus must have been very well adapted since its kind existed for several millions of years. Nevertheless, Allosaurus is extinct, whereas other thecodonts (crocodiles, alligators, and birds) succeeded in adapting and flourishing. This alone suggests that the neurobiological–behavioral–physiological–environmental relationships of modern ancestors must differ in fundamental ways from Allosaurus. Second, evolutionary pressures act upon the whole organism, and many key issues about Allosaurus, including metabolic state, remain unclear (see Bakker, 1986; Reid, 1997). Consequently, direct neurobiology–behavior comparisons between Allosaurus and crocodylian species (or birds) can at best provide a provocative platform for speculation. In this context, given the indication of a poorly elaborated Allosaurus brain, even if Allosaurus had acquired complex behaviors, these behaviors would have been highly structured and not particularly plastic. For example, if the foraging–hunting response of Allosaurus was refined toward an almost exclusive recognition of the great plant-eating sauropod dinosaurs, the extinction of this group around the close of the Jurassic period (Cifelli et al., 1997) may have

presented an insurmountable challenge for the neurobiology of *Allosaurus* to overcome.

The present study suggests that modern imaging methods may provide insight into heretofore perplexing questions regarding soft-tissue structures such as the brains of extinct species. Certainly, this application alone will provide substantial opportunities and novel lines of investigation toward understanding how the interaction between complex environmental, physiological, and neurological variables contributed both to the success of *Allosaurus* and also to its ultimate extinction.

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