Journal of Comparative Neurology

WILEY

JCN RESEARCH IN SYSTEMS NEUROSCIENCE THE JOURNAL OF COMPARATIVE NEUROLOGY

RESEARCH ARTICLE OPEN ACCESS

Ontogenetic Changes in Endocranial Anatomy in *Gorgosaurus libratus* (Theropoda: Tyrannosauridae) Provide Insight Into the Evolution of the Tyrannosauroid Endocranium

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Received: 21 August 2024 | **Revised:** 11 March 2025 | **Accepted:** 7 April 2025

Funding: This study was funded in part by an Eyes High Doctoral Recruitment Scholarship (to JTV), an Izaak Walton Killam Memorial Scholarship (to JTV), a Dinosaur Research Institute Student Research Grant (to JTV), a Roger Soderstrom Memorial Scholarship (to JTV), a Natural Sciences and Engineering Research Council (NSERC) Discovery Grant (RGPIN 04854 to DKZ), the Royal Tyrrell Museum of Palaeontology (to FT), U.S. National Science Foundation grants (NSF IOB-0517257, IOS-1050154, IOS-1456503), and the Swedish Research Council (2021-02973) (to LMW and RCR).

Keywords: endocast | Eutyrannosauria | *Gorgosaurus* | ontogeny | paleoneurology | RRID:SCR_007353 | Tyrannosauroidea

ABSTRACT

Over the past two decades, increased accessibility to computed tomography (CT) scanners has greatly facilitated documentation of the endocranium in numerous extinct theropod taxa. However, most of these studies have focused on the morphology of mature individuals, thus changes or variation through ontogeny of the endocranium in theropods remains largely unknown. The current study sheds light on the endocranial anatomy of the eutyrannosaurian tyrannosauroid, *Gorgosaurus libratus*, in both an ontogenetic and evolutionary context. Based on CT scans of six *Gorgosaurus* braincases, including those of two recently discovered juvenile individuals, we virtually reconstruct and describe the endocranial morphology for a growth series of *G. libratus*. Despite considerable changes in skull architecture, relatively few ontogenetic changes occurred in the endocranium of *Gorgosaurus*. These changes include a subtle increase in the length of the hindbrain region of the endocast and increased inflation of the tympanic sinus diverticula in adults relative to juveniles. Among the most significant ontogenetic changes is a decrease in the distinctiveness of the brain morphology in endocasts as *Gorgosaurus* mature. The endocasts of juvenile *Gorgosaurus* exhibit better defined cerebral hemispheres, optic lobes, and cerebella than those of larger and more mature individuals. This suggests a closer correspondence between the endocast and the brain in juvenile tyrannosaurids, indicating the endocast of juvenile individuals provides a more accurate representation of the structure of the brain and its regions relative to the endocast of more mature individuals. The brain of *Gorgosaurus* displays a mix of basal archosaurian traits and more derived coelurosaurian traits. More primitive archosaurian features of the *Gorgosaurus* brain include large olfactory bulbs and tracts, a posteroventrally oriented long axis of the cerebrum, and posteriorly positioned optic lobes, whereas derived features include prominent hindbrain flexure, a somewhat enlarged cerebrum, and a cerebellum that at least partially separates the left and right optic lobes. An understanding of the evolutionary acquisition of such derived features leading to the avian brain may be further elucidated via the study of

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the endocasts of juvenile individuals (more reflective of the structure/organization of various brain regions) of earlier-diverging theropods (e.g., Allosauroidea, Megalosauroidea, and Coelophysoidea).

1 | Introduction

The field of paleoneurology (i.e., the study of brain shape and size in extinct animals) has long relied on the study of natural or artificial endocasts (e.g., Osborn 1912; Edinger 1929; Hopson 1979) but the increasing ease of access to computed tomography (CT scanning) over the past 25 years has led to a dramatic explosion of studies covering a myriad of extinct vertebrates. Dinosaurs are perhaps the one group that has benefitted the most from the application of CT technology to study paleoneurology, permitting the reconstruction of virtual brain endocasts (e.g., Rogers 1998, 1999, 2005; Brochu 2000, 2003; Alonso et al. 2004; Franzosa and Rowe 2005; Witmer et al. 2008; Paulina-Carabajal et al. 2023), cranial sinuses (e.g., Witmer and Ridgely 2008), and various sensory organs (e.g., pertaining to balance, hearing, olfaction: Witmer and Ridgely 2009; Zelenitsky et al. 2009, 2011) for countless species without the risk of damaging rare (sometimes unique) fossils. In a phylogenetic context, the evolution of the endocrania of theropod dinosaurs in particular has received considerable attention in recent years, with numerous studies focusing on the morphological and sensory changes that occurred during the transition from non-avian theropods to birds (e.g., Franzosa 2004; Zelenitsky et al. 2011; Balanoff et al. 2013; Ksepka et al. 2020). Several morphological trends have been identified in the theropod ancestry of birds, including a progressive increase in brain encephalization and enlargement of the forebrain (Larsson et al. 2000; Balanoff et al. 2013, Balanoff et al. 2014), the lateral displacement of the optic lobes (Balanoff et al. 2009, Balanoff et al. 2014; Witmer and Ridgely 2009; Paulina-Carabajal et al. 2023; Osvath et al. 2024), progressive flexure of the brain bringing the forebrain to rest above the midbrain (Franzosa 2004; Hu et al. 2021; King et al. 2024), and the progenetic retention of the embryonic sauropsid brain configuration (Beyrand et al. 2019). Many of these trends appear to have originated near the base of Coelurosauria (Larsson et al. 2000; Bever et al. 2011, Bever et al. 2013; Balanoff et al. 2013, Balanoff et al. 2014; Paulina-Carabajal and Currie 2017; Paulina-Carabajal et al. 2023), a clade of derived theropods that includes all species more closely related to birds than to *Allosaurus*, indicating that study of the endocast of early-diverging coelurosaurians may improve our understanding of the evolutionary origins of the avian brain.

Given their early-diverging position within Coelurosauria, Tyrannosauroidea ("tyrannosaurs" sensu lato) offers one of the best opportunities for documenting the transition from the ancestral theropod endocranium exemplified by early-diverging neotheropods (Xing et al. 2014; Paulina-Carabajal et al. 2019), ceratosaurians (Sampson and Witmer 2007; Paulina-Carabajal and Succar 2013; Paulina-Carabajal and Filippi 2018; Cerroni and Paulina-Carabajal 2019; Gianechini et al. 2020), and allosauroids (Franzosa and Rowe 2005; Brusatte and Sereno 2007; Paulina-Carabajal and Currie 2012; Paulina-Carabajal and Nieto 2019) to the more derived features of later-diverging coelurosaurs, including birds (Alonso et al. 2004; Kundrát 2007; Balanoff et al. 2009, Balanoff et al. 2013, Balanoff et al. 2014, Balanoff et al. 2018; Witmer and Ridgely 2009; Lautenschlager et al. 2012). However, despite an abundance of literature describing the endocranial morphology of tyrannosauroids (Osborn 1912; Hopson 1979; Brochu 2000, 2003; Saveliev and Alifanov 2007; Witmer and Ridgely 2009, 2010; Bever et al. 2011, Bever et al. 2013; Hurlburt et al. 2013; Kundrát et al. 2020; Paulina-Carabajal et al. 2021), as well as the recent focus on *Tyrannosaurus rex* in high-profile debates about the cognitive abilities of *T. rex* and other dinosaurs (Herculano-Houzel 2023; Caspar et al. 2024), most of these studies have focused on the endocranial morphology of mature individuals of derived large-bodied taxa, primarily tyrannosaurids. Endocasts of tyrannosaurids are noted for preserving little detail of the underlying brain structure due to the fact that, unlike in birds and mammals, the brain was much smaller than the brain cavity and, consequently, was generally not in close contact with the brain cavity walls (Hopson 1979; Witmer and Ridgely 2009; Hurlburt et al. 2013). However, recent studies of the endocasts of extant archosaurs have noted an ontogenetic reduction in correspondence between brain and endocast volume such that the endocasts of immature individuals more closely reflect the morphology of the brain (Jirak and Janacek 2017; Watanabe et al. 2019; Hu et al. 2021). Application of this observation to the fossil record suggests that more details of the brain anatomy of tyrannosaurids could be gleaned from the examination of immature tyrannosauroid specimens.

Recently, nearly complete skeletons of two juvenile individuals of the tyrannosaurid *Gorgosaurus libratus* were discovered, both preserving exceptionally complete skulls (Voris et al. 2022). Study of the endocranium of these immature specimens and comparison with those of *Gorgosaurus* individuals from later growth stages and of other tyrannosauroid species allows us to assess the anatomy and ontogeny of the *Gorgosaurus* endocranium, document ontogenetic trends within the tyrannosauroid endocranium, and potentially improve our understanding of the acquisition of avian brain traits over the course of theropod evolution.

2 | Materials and Methods

Six well-preserved braincases of *G. libratus*, representing four different ontogenetic stages (juvenile: TMP 2009.012.0014, TMP 2016.014.0001; subadult: TMP 1991.036.0500, TMP 1994.143.0001; young adult: ROM 1247: adult: TMP 1994.012.0602; taxonomic identification and ontogenetic stages based on Voris et al. 2022), were studied via X-ray CT. The specimens were CT scanned following the protocol of Ridgely and Witmer (2006: 120 kV, at between 200 and 300 mA, slice thickness of 0.625 mm, except for TMP 2009.012.0014 with a slice thickness of 0.5 mm) at the University of Calgary (Calgary, Alberta), OhioHealth O'Bleness Memorial Hospital (Athens, OH), Calgary Diagnostics Centre (Calgary, Alberta), and Mayfair Diagnostics (Calgary, Alberta).

DICOM files were imported into the three-dimensional data visualization software Amira v. 5.3.3. Three-dimensional digital models of the brain and inner ear cavities were digitally segmented from the skull using the label field function for the *Gorgosaurus* specimens examined. Paratympanic (braincase) sinuses were segmented only for TMP 2009.012.0014, TMP 1994.143.0001, ROM 1247, and TMP 1994.012.0602 as the sinuses of the other specimens were too poorly preserved. Volume, surface area, and linear dimensions of endocranial features were recorded using Amira's onboard measuring tools. Virtual brain endocasts were also compared to latex peels of the cerebral and olfactory bulb fossae from isolated *Gorgosaurus* frontals, including TMP 1986.036.0269 and TMP 2010.012.0061, which represent the smallest (and probably youngest) *Gorgosaurus* specimens examined in this study. All virtual endocast reconstructions were oriented so the lateral semicircular canal is oriented horizontally to allow for comparison of endocranial angulation and orientation with previously published theropod taxa (Witmer and Ridgely 2009, 2010). Due to the large amount of void space in *Gorgosaurus* braincases, postburial deformation can affect the apparent morphology of endocranial structures. To avoid misinterpreting taphonomically modified features as true anatomical structures, most of the features described herein were observed on both the left and right sides of the endocasts or were visible in multiple specimens.

The *Gorgosaurus* endocasts were compared with the endocranial virtual renderings of previously described tyrannosauroids, including *Albertosaurus sarcophagus*, *Alioramus altai*, *Bistahieversor sealyi*, *Daspletosaurus* spp., *Timurlengia euotica*, and *T. rex* based on re-segmentation of published CT scans by one of us (JTV) (see Supporting Information).

CT scan data of the *Gorgosaurus* braincases are accessible online via https://doi.org/10.5061/dryad.fxpnvx12j.

2.1 | Taxonomic Definitions

Tyrannosauroidea—Branch-based clade containing all taxa more closely related to *Tyrannosaurus rex* than to *Gallus domesticus*.

Eutyrannosauria—Node-based clade containing the most recent common ancestor of *T. rex* and *Dryptosaurus aquilunguis* and all its descendants (sensu Delcourt and Grillo 2018).

Tyrannosauridae—Node-based clade containing the most recent common ancestor of *T. rex* and *Albertosaurus sarcophagus* and all its descendants (sensu Sereno et al. 2005).

2.2 | Institutional Abbreviations

AMNH, American Museum of Natural History, New York; CMNH, Cleveland Museum of Natural History, Cleveland, Ohio; FMNH, Field Museum of Natural History, Chicago, Illinois; NMMNH, New Mexico Museum of Natural History, Albuquerque, New Mexico; RAM, Royal Alberta Museum, Edmonton, Alberta; ROM, Royal Ontario Museum, Toronto, Ontario; TLG, Todd L. Green Research Collection, Denver, Colorado; TMP, Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta.

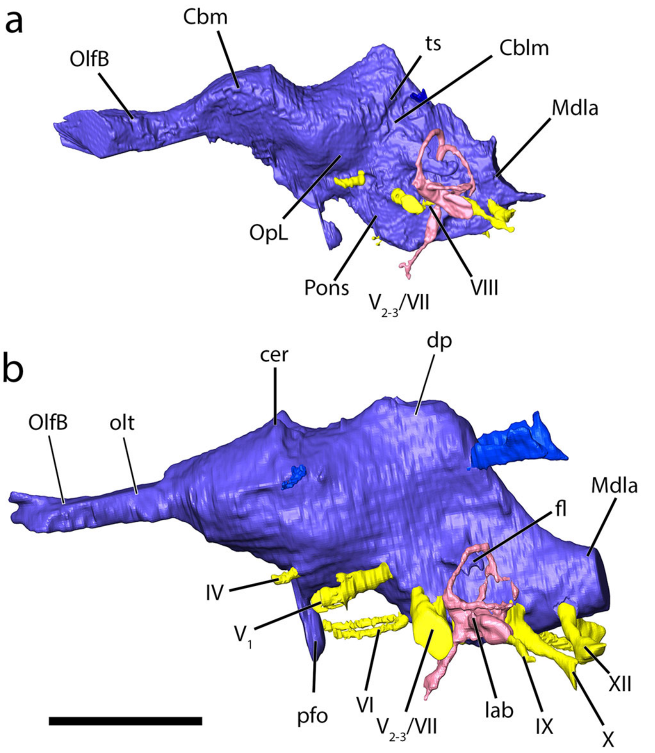

FIGURE 1 | Digital endocasts of juvenile *Gorgosaurus* TMP 2009.012.0014 (top) and adult *Gorgosaurus* TMP 1994.012.0602 (bottom) in lateral view with structures described in this manuscript labeled. Abbreviations: Cbm, cerebrum/cerebral hemispheres; Cblm, cerebellum; cer, cerebral region of endocast; dp, dural (cerebellar) peak; fl, floccular lobe of cerebellum; lab, endosseous labyrinth; OlfB, olfactory bulb; olt, olfactory tract; OpL, optic lobe; pfo, pituitary fossa; ts, transverse sinus; IV, trochlear nerve canal; V_1, ophthalmic nerve canal of the trigeminal ganglion; $V_{2-3/}$VII, common external canal for maxillomandibular and facial nerves; VI, abducens nerve canal; IX, glossopharyngeal nerve canal; X, vagus nerve canal; XII, hypoglossal nerve canal. Scale bar equals 5 cm.

3 | Results

3.1 | Endocranial Morphology

The endocast of *Gorgosaurus* is S-shaped in lateral view and exhibits prominent cephalic and pontine flexures in specimens of all growth stages. The dorsal margin of the endocast is raised in two locations corresponding to the cerebral and dural (cerebellar) peaks (Figure 1). This "dual-peaked" morphology is typical of coelurosaurs and of the megaraptoran *Murusraptor* (Paulina-Carabajal and Currie 2017) but contrasts with non-coelurosaurian neotheropods in which a singular pineal peak overlies the posterodorsal margin of the cerebrum (Witmer and Ridgely 2009).

The hindbrain region of the *Gorgosaurus* endocast is anteroposteriorly short relative to the combined fore- and midbrain regions and is slightly shorter in juvenile individuals than in larger adults (Figure 2). Despite the slight difference in hindbrain length between growth stages, the pontine flexure remains at an angle of ~120° in all *Gorgosaurus* specimens. Comparison with the endocasts of other tyrannosauroids reveals taxonomic

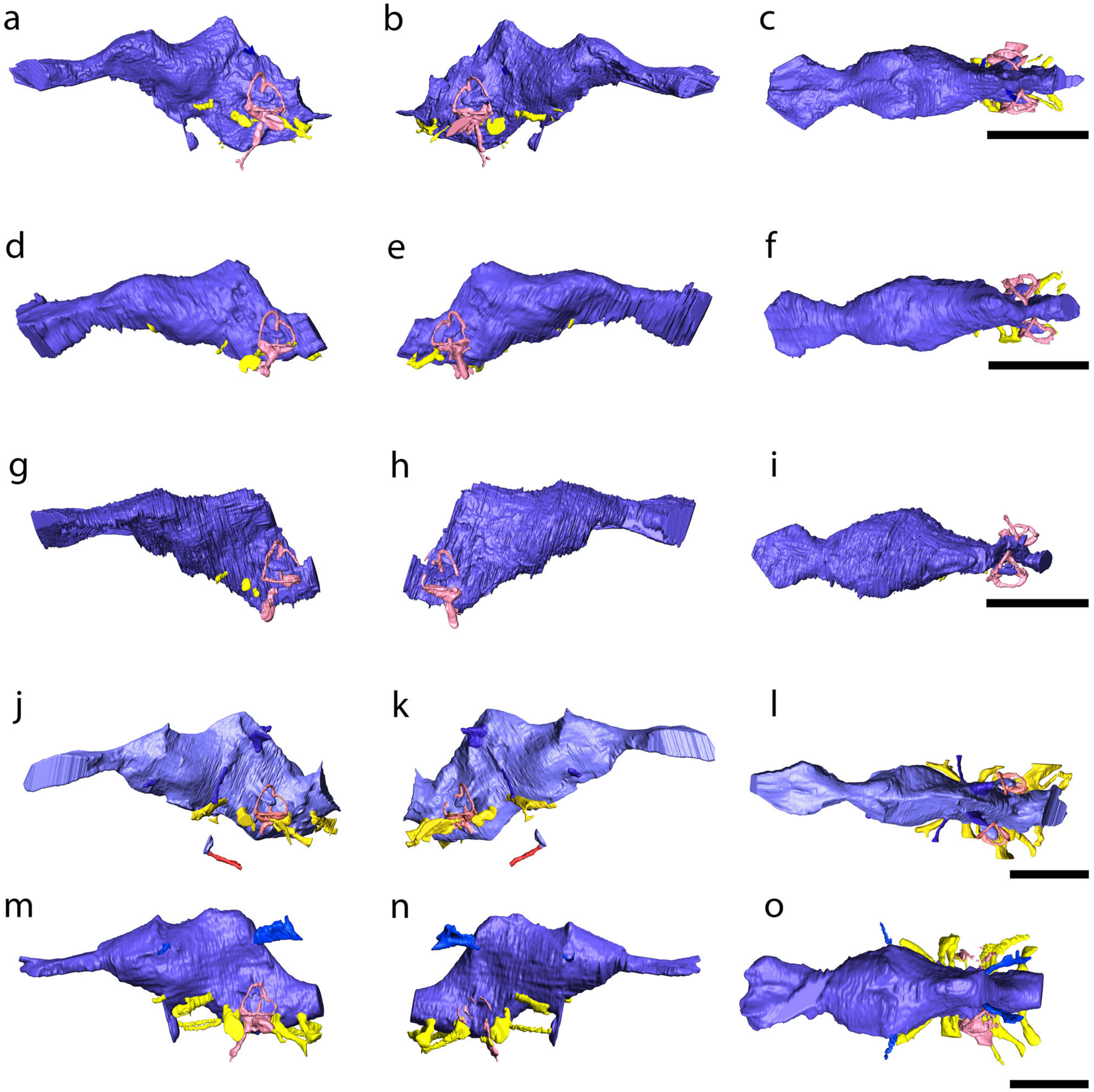

FIGURE 2 | Growth series of *Gorgosaurus* endocasts in left lateral view (a, d, g, j, m), right lateral view (b, e, h, k, n), and dorsal view (c, f, i, l, o). Specimens as follows: juvenile TMP 2009.012.0014 (a–c); juvenile TMP 2016.014.0001 (d–f); subadult TMP 1991.036.0500 (g–i); young adult ROM 1247 (j–l); adult TMP 1994.012.0602 (m–o). All scale bars equal 5 cm.

variation in comparable dimensions of the hindbrain. Dimensions of the hindbrain region are similar between *Gorgosaurus* and *Bistahieversor* in that they are both anteroposteriorly short and have a pontine flexure angle of 120°. In *Daspletosaurus*, the hindbrain region is anteroposteriorly longer and exhibits a shallower pontine flexure of ~130° (TMP 2001.36.1; see Paulina-Carabajal et al. 2021). In *Tyrannosaurus*, the hindbrain of juvenile individuals (CMNH 7541) is anteroposteriorly short with a steep pontine flexure angle of ~120°, whereas adults have a relatively long hindbrain with a shallow pontine flexure angle of ~140° (e.g., AMNH 5117, see Witmer and Ridgely (2009). Early-diverging tyrannosauroids, such as *Dilong paradoxus* and early-diverging maniraptorans possess a very short hindbrain region and a steep pontine flexure angle of ~90° (Balanoff et al. 2009; Kundrát et al. 2020).

3.1.1 Forebrain

The olfactory tract and bulbs are large in *Gorgosaurus*, together forming roughly half the length of the entire forebrain. The combined width of the two olfactory bulbs is nearly equal to the width of the cerebral region of the endocast. The original shape and size of the olfactory bulbs are most apparent in the two smallest juvenile *Gorgosaurus* specimens studied (TMP 1986.036.0269 and TMP 2010.012.0061) due to the presence of a small bony crest on the ventral surface of the frontals that marks the anterolateral edge of the olfactory bulb fossa; this crest is absent in larger specimens. Otherwise, the morphology and proportions of the olfactory bulbs and tracts are similar in all ontogenetic stages of *Gorgosaurus* and consistent with those observed in all eutyrannosaurians studied (Ali et al. 2008; Zelenitsky et al. 2009, 2011).

The details of the cerebral region of the endocast differ between juvenile and adult *Gorgosaurus* individuals. In juveniles, a closer correspondence between the braincase and the brain itself likely resulted in an endocast reflecting more closely the original brain shape (Figures 2 and 3). Features of the cerebrum are well-defined in juvenile *Gorgosaurus* specimens (TMP 2009.012.0014 and TMP 2016.014.0001), with individual cerebral hemispheres observable as distinctly lobate structures separated by an interhemispheric sulcus, whereas the individual cerebral hemispheres are indistinguishable in large adult *Gorgosaurus* specimens similar to other mature tyrannosaurid individuals (Figures 2a–f and 3a,b; Witmer and Ridgely 2009; McKeown et al. 2020; Paulina-Carabajal et al. 2021). In subadult and more mature *Gorgosaurus* individuals, the dorsolateral surface of the cerebral hemispheres is flat between the ridge-like eminences that mark the location of the frontoparietal and frontolaterosphenoid sutures; the posterior end of this flat region is raised into a pair of tall diploic peaks (Figures 2g–o and 3c–e).

The distinctiveness of the cerebral hemispheres in juvenile *Gorgosaurus* specimens provides novel information as to the morphology of the cerebrum in eutyrannosaurians. The size of the cerebrum in these specimens corresponds to more than 40% of the total volume of the endocast, making their relative size more consistent with derived coelurosaurs than with that reported for earlier-diverging theropods (see Larsson et al. 2000). The anterior margin of the cerebral hemispheres are clearly distinguishable from the olfactory tract in dorsal view by an abrupt medial curve, as seen in ornithomimids and oviraptorids (Balanoff et al. 2009), but unlike those of derived maniraptorans (e.g., troodontids and dromaeosaurids), in which the cerebral hemispheres are pyriform and gradually taper into the olfactory tract (Balanoff et al. 2014). The long axis of the cerebrum is oriented posteroventrally, which is consistent with other early-diverging theropods, such as abelisaurids (Sampson and Witmer 2007), but differs from the more horizontal long-axis orientation of maniraptorans. The posteroventral margin of the cerebrum is more clearly visible in TMP 2009.012.0014 than in other known eutyrannosaurians, being situated ventral to the saddle formed between the cerebral and dural peaks and corresponding to the widest portion of the endocast (Figures 1a and 2a–c).

3.1.2 Midbrain

The junction of the fore- and midbrain is generally concealed in the endocasts of large theropods, including Eutyrannosauria (Franzosa and Rowe 2005; Sampson and Witmer 2007; Paulina-Carabajal and Currie 2017; Paulina-Carabajal and Filippi 2018; Paulina-Carabajal et al. 2019; Gianechini et al. 2020; McKeown et al. 2020). As a result, the morphology of the optic lobes is poorly known in these taxa. While it is similarly not possible to distinguish between the cerebrum and the optic lobe in the larger *Gorgosaurus* specimens examined in this study, one juvenile specimen, TMP 2009.012.0014, clearly demonstrates the location

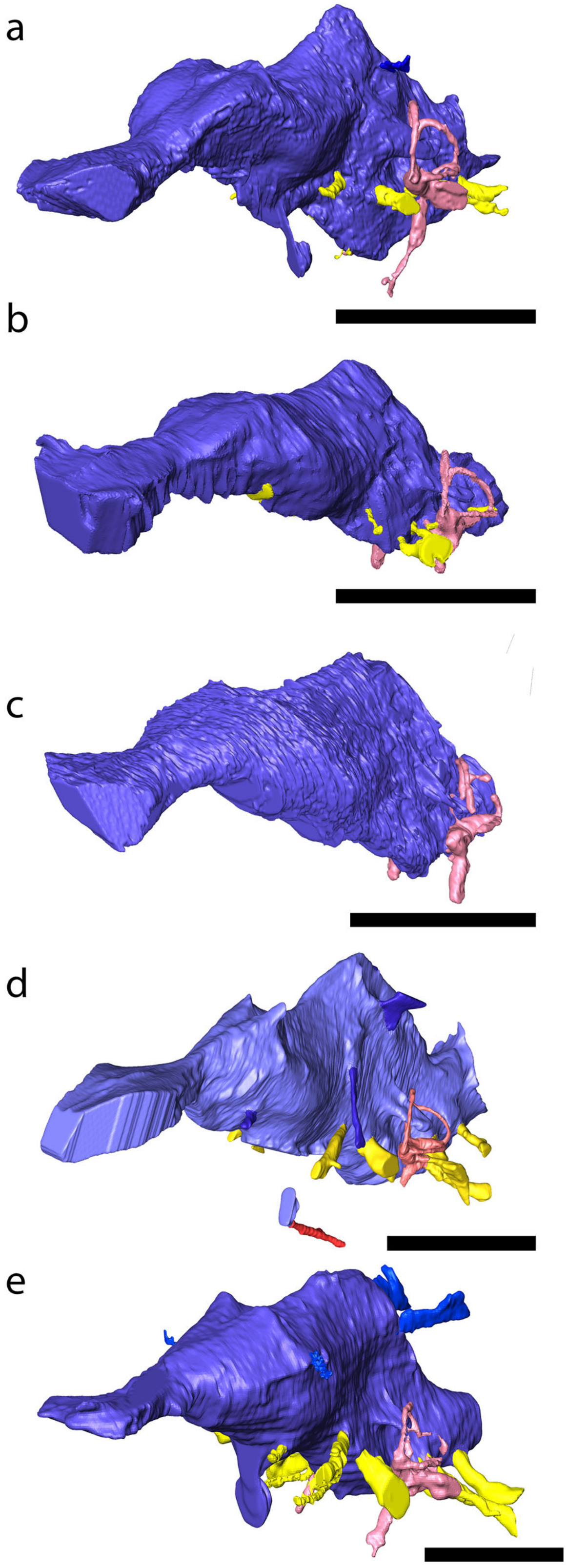

FIGURE 3 | Growth series of *Gorgosaurus* endocasts in anterodorsolateral view. Specimens as follows: juvenile TMP 2009.012.0014 (a); juvenile TMP 2016.014.0001 (b); subadult TMP 1991.036.0500 (c); young adult ROM 1247 (d); adult TMP 1994.012.0602 (e). All scale bars equal 5 cm.

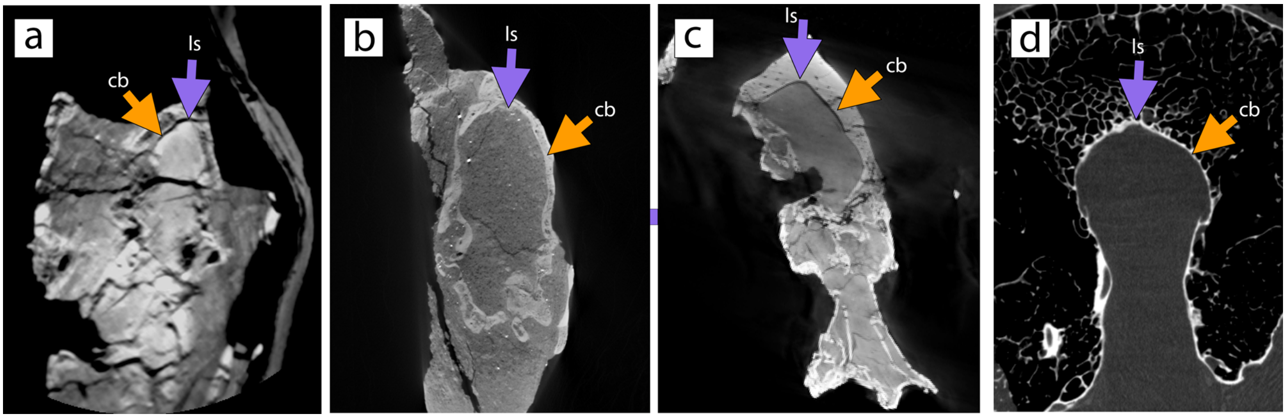

FIGURE 4 | Transverse CT slice through the posterior end of the endocranial cavity of juvenile *Gorgosaurus libratus* TMP 2016.014.0001(a), juvenile ornithomimid *Ornithomimus edmontonicus* TMP 2009.110.0001 (b), troodontid *Stenonychosaurus inequalis* TMP 1982.019.0023 (c), and ostrich *Struthio camelus* TLG SC080 (d; image data from Plateau et al. 2024) demonstrating a comparable cerebellar position in eutyrannosaurians (*Gorgosaurus*) and more derived coelurosaurs. Abbreviations: cb, cerebellar bulge; ls, longitudinal (occipital) sinus groove.

and form of these structures in this taxon. The optic lobes of TMP 2009.012.0014 are represented by smaller bulges located posteroventral to the cerebrum on both sides of the endocast (Figures 1a:OpL and 2a–c:OpL). These bulges are located immediately anterior to the transverse sinus and transversotrigeminal vein (anterior middle cerebral vein of Witmer and Ridgely 2009) and dorsal to the ophthalmic branch of the trigeminal nerve (CN V_1), supporting the identification of these bulges as the optic lobes (Witmer and Ridgely 2009). The locations of these bulges are broadly separated from the anteroventral margin of the endocast and, consequently, far from the location of the optic nerve. The form and position of the optic lobes in *Gorgosaurus* (and presumably other eutyrannosaurians) would, therefore, be intermediate between that of earlier-diverging sauropsids (i.e., directly posterior to the cerebrum, contacting each other in the midline, and broadly separated from the optic nerve root) and that of more derived coelurosaurs, including birds (i.e., displaced ventral to the cerebrum by midline contact of the cerebrum and cerebellum and adjacent to the optic nerve root).

3.1.3 Hindbrain

The endocasts of juvenile *Gorgosaurus* specimens (TMP 2009.012.0014 and TMP 2016.014.0001) preserve details of the cerebellum not visible in the endocasts of the larger *Gorgosaurus* specimens examined. In both juvenile specimens, the lateral surface of the hindbrain region exhibits a faint semicircular bulge located ventral to the dural peak (Figure 2:Cblm). This bulge extends dorsally from the base of the cerebellar floccular lobe then arcs anterodorsally to intersect the transverse sinus and continues anteriorly before fading near the posterodorsal edge of the cerebrum (Figure 2). The margin of this bulge extends anterior to the posterior margin of the optic lobe bulges. Endocasts of later-diverging coelurosaurs (e.g., oviraptorosaur; Balanoff et al. 2014; ornithomimids [TMP 2009.110.0001], and troodontids [TMP 1982.019.0023]) also have a similar bulge along the lateral surface of the hindbrain region, which corresponds to the dorsolateral margin of a more clearly defined cerebellum (Figure 4). Accordingly, the bulge observed in juvenile *Gorgosaurus* endocasts is interpreted as similarly demarcating the dorsolateral margin of the cerebellum, which is bounded dorsally and posterodorsally by a narrower region that likely corresponds to the longitudinal dural venous sinus (Figure 4). Relative to earlier-diverging sauropsids (e.g., crocodilians), this would indicate *Gorgosaurus* had a moderately enlarged cerebellum. Among larger *Gorgosaurus* specimens and mature individuals of other eutyrannosaurians (Witmer and Ridgely 2009; Paulina-Carabajal et al. 2021), this bulge is not visible and the margin of the cerebellum is almost completely indistinguishable.

The floccular lobe (flocculus) is the only structure of the cerebellum that can be readily identified in the *Gorgosaurus* endocast at all ontogenetic stages. In juvenile *Gorgosaurus*, the flocculus is bulbous and long, extending posterior to the level of the common crus of the endosseous labyrinth (nearly reaching the posterior semicircular canal in TMP 2009.012.0014), a condition identical to that of the early-diverging tyrannosauroid *Dilong* and the immature holotype specimen of the tyrannosaurine *Alioramus altai* (Bever et al. 2013; Kundrát et al. 2020). In larger *Gorgosaurus* and mature individuals of other eutyrannosaurians, the flocculus is tabular in shape and short, terminating anterior to the level of the common crus (Witmer and Ridgely 2009; Bever et al. 2013).

The pons is located anteroventral to the cerebellum and is easily identified by the roots of cranial nerves V–VIII. In all *Gorgosaurus* individuals examined, the pons extends posteroventrally from the cephalic flexure between the mid- and hindbrain to the pontine flexure, which marks the transition from the pons to the medulla oblongata.

Reconstruction of the individual cranial nerves emerging from the pons was met with varied levels of success in the *Gorgosaurus* specimens studied but they generally appear consistent in position and form between the different ontogenetic stages. The ophthalmic (CN V_1) and maxillomandibular branches (CN $V_{2\text{-}3}$) of the trigeminal ganglion (CN V) emerge from the pons portion of the endocast as separate roots, in both mature and immature individuals. This condition is also observed in other eutyrannosaurians and in the early-diverging tyrannosauroid *Dilong* (Kundrát et al. 2020) but not in *Timurlengia* or other theropods, in which all trigeminal nerve branches emerge together from the endocast and diverge distally (Brusatte et al. 2016). Even though the ophthalmic and maxillomandibular nerve branches are separated in juvenile *Gorgosaurus* specimens, the region of the endocast between their respective bases is slightly raised. This swelling could indicate that the separation of the ophthalmic and maxillomandibular nerves from the trigeminal ganglion occurred outside of the brain but within the endocranial cavity in *Gorgosaurus*, i.e., the trigeminal ganglion was intracranial as in birds (and most other tetanuran clades) rather than extracranial as in earlier-diverging theropods and other dinosaurs (Sampson and Witmer 2007; Witmer et al. 2008; Witmer and Ridgely 2009). An ontogenetic increase in the volume of the encasing dural venous sinus could obscure the point of separation between these nerve branches in larger, more mature individuals, such that they appear as distinct nerve roots. The canal for the abducens nerve (CN VI) is extremely narrow and could only be identified in the largest specimen, TMP 1994.012.0602. It is the only pons-derived cranial nerve that does not emerge from the lateral surface of the pons, instead emerging from its anteroventral surface. The facial nerve (CN VII) emerges from the endocast immediately posteroventral to the maxillomandibular branch of the trigeminal nerve. The facial nerve canal is nearly of the same diameter as the maxillomandibular branch of the trigeminal nerve in all *Gorgosaurus* endocasts examined regardless of ontogenetic stage. This condition, shared with other eutyrannosaurians (see Witmer and Ridgely 2009; Bever et al. 2013; McKeown et al. 2020; Paulina-Carabajal et al. 2021), is unlike that of other non-avian theropods, in which the facial nerve canal is much narrower than the canal of the trigeminal nerve (e.g., abelisaurids—Sampson and Witmer 2007, fig. 18; Paulina-Carabajal and Filippi 2018, fig. 4; allosaurids—Paulina-Carabajal and Nieto 2019; and *Stenonychosaurus*—Currie and Zhao 1993). The maxillomandibular and facial nerve foramina become distally united within a tube-like prootic fossa in all eutyrannosaurians (Witmer and Ridgely 2009; Bever et al. 2013; McKeown et al. 2020). However, the orientation of this fossa changes through ontogeny in *Gorgosaurus*, where it is directed laterally in juvenile individuals and oriented posteroventrolaterally in more mature individuals (Voris et al. 2022). The change in orientation is likely the result of the ontogenetic inflation of the anteriorly and dorsally bounding tympanic recesses within the prootic (Voris et al. 2022). The canal for the vestibulocochlear nerve (CN VIII) is narrow and located immediately posterior to and at the same dorsoventral level as the facial nerve canal. The vestibulocochlear nerve canal extends for only a short distance from the endocast before intersecting the endosseous labyrinth at the anterior junction of the vestibule and cochlear duct.

Despite the volume of the dural venous sinus around the hindbrain, the dorsal and lateral margins of the medulla are well-defined relative to the rest of the hindbrain in all *Gorgosaurus* specimens examined. This reveals that the medulla was narrow and shallow anteriorly and thickened posteriorly closer to the foramen magnum. The long axis of the medulla is inclined slightly anteroventrally at ~20° from horizontal. The medulla gives rise to cranial nerves CN IX–XII, which are morphologically consistent in all ontogenetic stages of *Gorgosaurus* studied. The glossopharyngeal (CN IX) and vagus (CN X) nerves are united upon emergence from the endocast and extend laterally toward the posterior margin of the endosseous labyrinth. The glossopharyngeal nerve subsequently separates from the vagus nerve and extends laterally, running parallel to the columella bone through the otic recess. In contrast, the vagus nerve arcs posteroventrally and exits the posterior surface of the braincase through the neck of the occipital condyle. The hypoglossal nerve (CN XII) emerges from the endocast and runs through its own canal parallel to the vagus nerve, extending posteroventrally and exiting the posterior surface of the braincase through the neck of the occipital condyle dorsomedial to the vagus nerve foramen.

3.2 | Inner Ear

The semicircular canals show little difference in size and shape among all *Gorgosaurus* specimens examined, regardless of ontogenetic stage (Figure 5). The anterior and posterior semicircular canals are dorsoventrally taller than anteroposteriorly long, and the lateral semicircular canal is anteroposteriorly longer than mediolaterally wide (Figure 5). Although the anterior semicircular canal is taller than the posterior semicircular canal, they are of nearly equal length. The common crus intersects the vestibule nearly perpendicular to the axis of the lateral semicircular canal. This configuration of the endosseous labyrinth is consistent with that of most eutyrannosaurians, including: *Albertosaurus* (TMP 1981.010.0001), *Bistahieversor* (JTV pers. obs. of NMMNH P-27469) (McKeown et al. 2020), *Alioramus* (Bever et al. 2013), and *Daspletosaurus* (Paulina-Carabajal et al. 2021), as well as the non-eutyrannosaurian tyrannosauroid *Timurlengia* (Brusatte et al. 2016). However, it differs from the configuration of *T. rex*, in which the anterior and posterior semicircular canals are nearly as long as they are tall, the anterior semicircular canal is longer than the posterior semicircular canal, and the common crus intersects the vestibule anteroventrally (Witmer and Ridgely 2009).

The cochlear duct (lagena) is a long, straight, and narrow canal in all *Gorgosaurus* specimens studied (Figure 5), as is the case in other eutyrannosaurians. Interestingly, the juvenile *Gorgosaurus* specimen TMP 2009.012.0014 has a second canal that is much narrower than the cochlear duct itself (Figure 5:sc). This canal extends anteroventrally from the ventral end of the cochlear duct for 9 mm before splitting into two branches that open into a sinus cavity that communicates with the anterior tympanic and basisphenoid recesses. A similar canal is potentially present in the adult *Gorgosaurus* specimen TMP 1994.012.0602 but is difficult to ascertain due to CT scan resolution. While we are unsure of the exact function of this canal, possibilities include the perilymphatic duct or connections with pharyngeal sinuses. The cochlear duct of larger, more mature *Gorgosaurus* specimens is slightly longer than those of smaller juvenile specimens.

3.3 | Paratympanic Sinuses

As in other coelurosaurs, the braincase of *Gorgosaurus* is highly pneumatized, possessing several paratympanic sinuses (Figure 6; see also Witmer and Ridgely 2009). These sinuses can be divided into three systems: the tympanic, median pharyngeal, and pulmonary sinus systems. The tympanic sinus system, which includes the anterior and posterior tympanic recesses in eutyrannosaurians, develops as evaginations of the middle ear sac (Witmer 1997a). The median pharyngeal sinus system, which

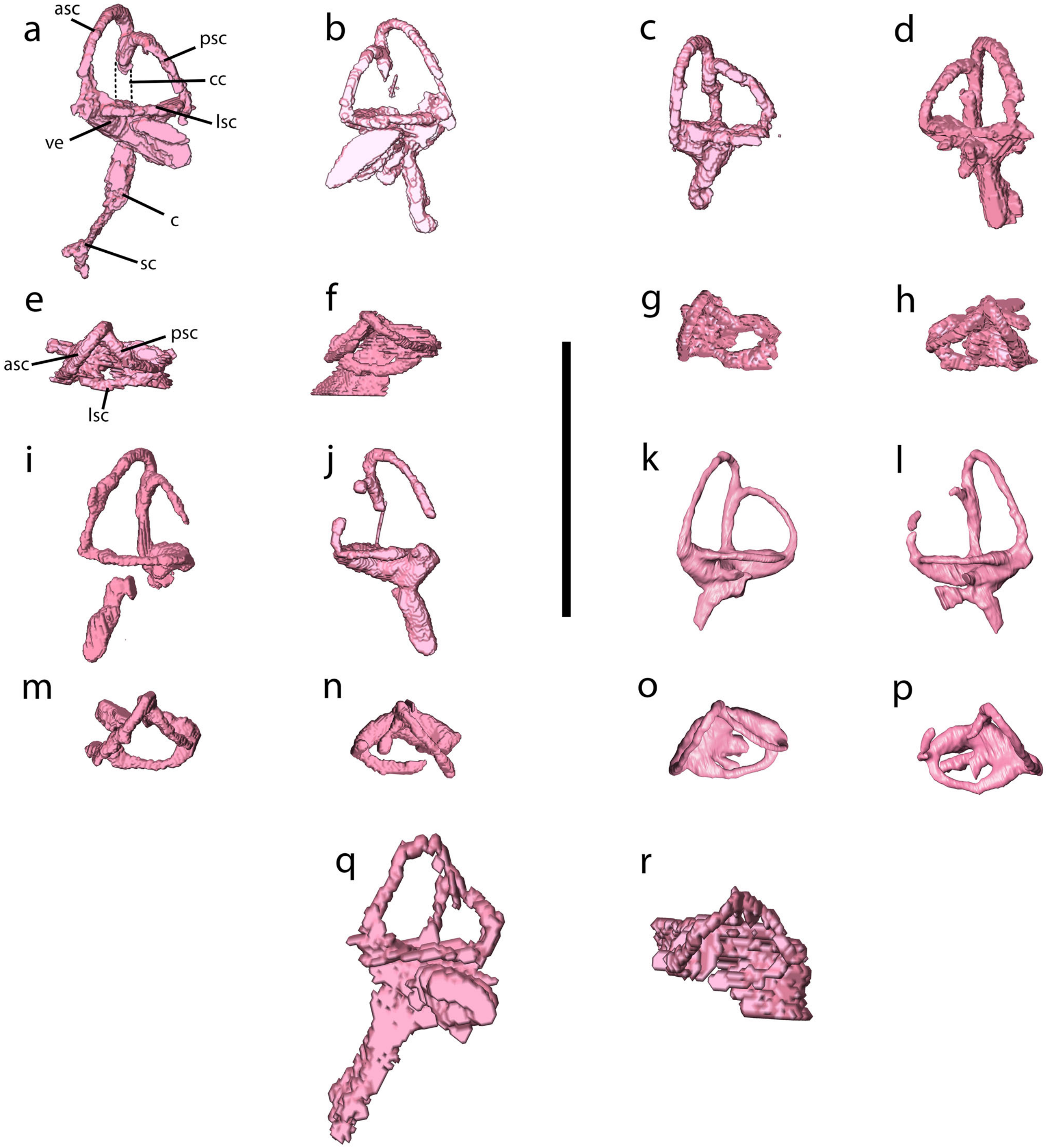

FIGURE 5 | Growth series of *Gorgosaurus* endosseous labyrinths in lateral view (a-d, i-l, q) and dorsal view (e-h, m-p, r). Specimens as follows: juvenile TMP 2009.012.0014 (a, b, e, f); juvenile TMP 2016.014.0001 (c, d, g, h); subadult TMP 1991.036.0500 (i, j, m, n); young adult ROM 1247 (k, l, o, p); adult TMP 1994.012.0602 (q, r). Note: both left and right endosseous labyrinths are presented for all specimens except TMP 1994.012.0602 (q, r) for which only the left could be reconstructed due to poor preservation of the right side. Abbreviations: asc, anterior semicircular canal; c, cochlear duct; cc, common crus; lsc, lateral semicircular canal; psc, posterior semicircular canal; sc, unidentified secondary canal; ve, vestibule. Scale bar equals 5 cm.

includes the basisphenoidal and subsellar recesses, probably develops as diverticula of the pharynx (Witmer 1997b; Witmer and Ridgely 2009; Dufeau 2011). Finally, the pulmonary sinus system could manifest in the skull as the medial subcondylar recess, which may develop as an evagination from the air sacs of the cervical vertebrae in eutyrannosaurians (Witmer 1997a; but also see Rauhut 2004).

3.3.1 Anterior Tympanic Recess

Compared to non-eutyrannosaurian theropods, the anterior tympanic recess of *Gorgosaurus* is large, extending dorsally from its foramen behind the ala basisphenoidalis as the retrohypophyseal diverticulum, before arcing posteriorly toward the posterior process of the prootic as the prootic diverticulum

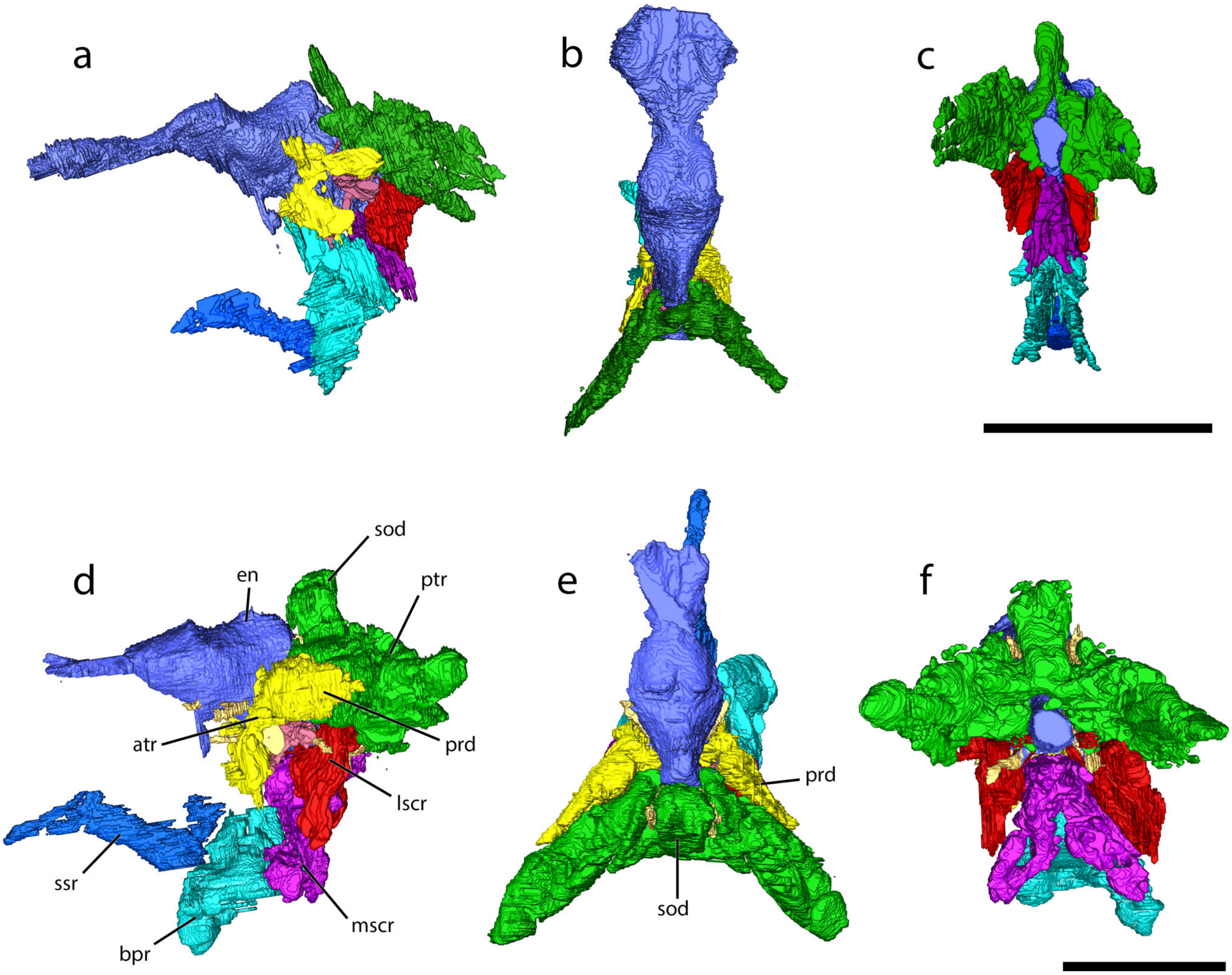

FIGURE 6 | Paratympanic (braincase) sinuses of juvenile TMP 2009.012.0014 (a–c) and adult TMP 1994.012.0602 (d–f) *Gorgosaurus* in lateral (a,d), dorsal (b,e), and posterior views (c–f). Abbreviations: atr, anterior tympanic recess (yellow); bpr, basipterygoid/basisphenoid recess (cyan); en, endocast (dull blue); lscr, lateral subcondylar recess (red); mscr, medial subcondylar recess (purple); prd, prootic diverticulum of the anterior tympanic recess; ptr, posterior tympanic recess (green); sod, supraoccipital diverticulum of posterior tympanic recess; ssr, subsellar recess (brighter blue). Scale bar equals 10 cm.

(Figure 6:atr). These two diverticula change in size during ontogeny: the retrohypophyseal diverticulum is relatively large and the prootic diverticulum is small in juvenile individuals (TMP 2009.012.0014), while the opposite is true in adult individuals (TMP 1994.012.0602). In addition to its overall increased size, the prootic diverticulum of larger *Gorgosaurus* individuals is inflated to the extent that the lateral surface of the prootic bulges outward (Voris et al. 2022). Contralateral retrohypophyseal diverticula appear to be separated in the juvenile *Gorgosaurus* TMP 2009.012.0014 but connected in TMP 1994.012.0602. This could suggest some contralateral communication of sinuses occurs through ontogeny.

In all *Gorgosaurus* specimens examined, the prootic diverticulum clearly communicates with the retrohypophyseal diverticulum of the anterior tympanic recess through a narrow, tubular channel that likely corresponds to the ascending diverticulum of Witmer and Ridgely (2009). In contrast, little, if any, communication occurs between the prootic diverticulum and the posterior tympanic recess, a condition that also occurs in *Albertosaurus* (TMP 1981.010.0001) and *Alioramus* (Bever et al. 2013). Although the prootic diverticulum was previously considered to be part of the posterior tympanic recess in *Daspletosaurus* (Paulina-Carabajal et al. 2021), *Bistahieversor* (McKeown et al. 2020), and *Tyrannosaurus* (Witmer and Ridgely 2009, 2010), our re-examination of their CT data confirms that it is actually part of the anterior tympanic recess in *Bistahieversor* and in one *Daspletosaurus* specimen (TMP 2001.036.0001), as we observed in *Gorgosaurus*. However, the prootic diverticulum is clearly part of the posterior tympanic recess in all examined *Tyrannosaurus* specimens (CMNH 7541, AMNH 5117, FMNH PR 2081) and is illustrated as such in the holotype of *Daspletosaurus torosus* (CMN 8506; see Paulina-Carabajal et al. 2021), with a large non-pneumatized region (presumably of the prootic) occurring between the anterior and posterior tympanic sinuses.

3.3.2 Posterior Tympanic Recess

The posterior tympanic recess is the most voluminous of the three paratympanic sinus systems in *Gorgosaurus*. It expands through nearly the entire otoccipital and supraoccipital bones regardless of ontogenetic stage (Figure 6), although it is more inflated and voluminous in adult *Gorgosaurus* (e.g., TMP 1994.012.0602) than in immature individuals, to the extent that the outer surface of the paroccipital processes and supraoccipital is bulging (Voris et al. 2022). The extent of the posterior tympanic recess within the otoccipital in *Gorgosaurus* is similar to that of most other eutyrannosaurians (including *Bistahieversor*, *Albertosaurus*, *Alioramus*, and *Daspletosaurus*) but differs from the condition seen in *Tyrannosaurus*, where the posterior tympanic recess is more restricted, occupying proportionally less of the bone's total volume (Witmer and Ridgely 2009). The latter condition is likely associated with the unique supraoccipital morphology seen in *Tyrannosaurus* and, if so, would also be expected in *Tarbosaurus* (see Brusatte and Carr 2016).

Eutyrannosaurians are unique among coelurosaurs in having contralaterally confluent posterior tympanic recesses within the supraoccipital, called the supraoccipital diverticulum (Brochu 2003; Witmer and Ridgely 2009; Bever et al. 2013; Brusatte et al. 2016). In *Gorgosaurus*, the supraoccipital diverticulum is tall, extending well above the dorsal-most point of the brain endocast (Figure 6:sod), as also seen in *Albertosaurus* and *Alioramus* (Bever et al. 2013). This condition exceeds that seen in other eutyrannosaurians, where the supraoccipital diverticulum is slightly taller than in *Bistahieversor* and much taller than in *Daspletosaurus* and *Tyrannosaurus*.

Previous studies of tyrannosaurid braincases have often included the lateral subcondylar recess as part of the median pharyngeal sinus system along with the medial subcondylar recess. However, our observations in *Gorgosaurus* support the identification of the lateral subcondylar recess as a diverticulum of the posterior tympanic recess, as previously suggested by Paulina-Carabajal et al. (2021), given that only minimal (if any) communication occurs between the lateral and medial subcondylar recesses across the otoccipital-basioccipital suture (Figure 6:lscr). Furthermore, our re-examination of CT data for other eutyrannosaurians (including *Alioramus* MPC-D 100/1844, *Bistahieversor* NMMNH P-27469, *Daspletosaurus* TMP 2001.036.0001, *Tyrannosaurus* FMNH PR 2081) supports our interpretation and suggests this condition occurs throughout the Eutyrannosauria clade.

3.3.3 Basisphenoid-Basipterygoid Recess

The ventral surface of the braincase in *Gorgosaurus* is excavated by a deep, funnel-like basisphenoid recess located within a rectangular area defined by the basipterygoid processes and basal tubera as in most nonavialan theropods except for troodontids (Norell et al. 2009; Rauhut 2014; Yin et al. 2018). This recess extends anteriorly into the parabasisphenoid via a pair of oval pneumatopores located on the posterior surface of the interbasipterygoid lamina to form the basipterygoid recess. This condition is shared with most eutyrannosaurians (except for *Daspletosaurus* and *Teratophoneus*) and with the non-eutyrannosaurian tyrannosauroid *Xiongguanlong* (Li et al. 2010; Bever et al. 2013; Paulina-Carabajal et al. 2021) but not with the non-eutyrannosaurian tyrannosauroids *Dilong* and *Timurlengia*. In *Daspletosaurus*, the paired pneumatopores are located further posterolaterally within the basisphenoid recess, along the medial surface of the basipterygoid-basituberal lamina (Paulina-Carabajal et al. 2021). In *Teratophoneus*, the pneumatopores are present in immature individuals but are absent in larger individuals (Carr et al. 2011). Finally, in *Dilong* and *Timurlengia*, the interbasipterygoid lamina is pierced by a single, large foramen on the anterior midline rather than smaller, paired pneumatopores (see Li et al. 2010).

In *Gorgosaurus* and other eutyrannosaurians, the basipterygoid recess is vast, extending throughout most of the parabasisphenoid bone anterior to the basisphenoid recess. The morphology of the basipterygoid recess is similar in immature and mature *Gorgosaurus* specimens. Immature individuals (e.g., TMP 2009.012.0014, TMP 1994.143.0001, TMP 1991.036.0500) and young adults (ROM 1247) possess a second dorsoventrally elongate pneumatopore located ventral to the ala basisphenoidalis and dorsal to the basipterygoid process, whereas such a feature is absent in adults. A similarly positioned pneumatopore is also observed in the immature holotype of *Alioramus altai* (fenestra A: Bever et al. 2013]) and in juvenile *T. rex* (CMNH 7541) (Witmer and Ridgely 2010) but not in adult specimens. The absence of this second pneumatopore in mature eutyrannosaurians (including adult *Gorgosaurus*) suggests it closed through ontogeny.

3.3.4 Subsellar Recess

The subsellar recess, with its pneumatopore located on the posteroventral surface of the cultriform process of the basisphenoid, extends throughout the entire length of the cultriform process in all *Gorgosaurus* specimens examined (Witmer and Ridgely 2009; Dufeau 2011). This condition is also seen in *Albertosaurus*, *Bistahieversor*, and *Alioramus* but contrasts with the condition in *Tyrannosaurus*, in which the recess is anteroposteriorly short and seems to be restricted to the base of the cultriform process (Witmer and Ridgely 2009; Bever et al. 2013; McKeown et al. 2020). Separation of the subsellar and basisphenoid recesses is maintained by the interbasipterygoid lamina in *Gorgosaurus* as in other tyrannosauroids and most theropods (Witmer and Ridgely 2009). The extent of the subsellar recess is unknown in other tyrannosaurids as the delicate cultriform process is rarely preserved.

3.4 | Pulmonary Sinus System

3.4.1 Medial Subcondylar Recess

The medial subcondylar recess of *Gorgosaurus* and other eutyrannosaurians is morphologically distinct from other braincase sinuses, as it is characterized by narrow, tubular canals that are widely separated from each other rather than being large, vacuous chambers separated by thin bony laminae as for the other paratympanic sinuses (Figure 6:bpr). In *Gorgosaurus*, the medial subcondylar recess is an anteroposteriorly short sinus that is largely restricted to the basioccipital bone, although small diverticula extend a short distance into the posteroventral corner of the parabasiphenoid in the largest specimen (TMP 1994.012.0602). Unlike *Alioramus* (Bever et al. 2013), there is no extension of the medial subcondylar recess into the otoccipital. The medial subcondylar recess is ventrally extensive within the basioccipital in all *Gorgosaurus* specimens examined, such that it nearly reaches the basal tubera. This condition is shared with *Bistahieversor* (McKeown et al. 2020), *Alioramus* (Bever et al.

2013), and *Daspletosaurus* (Paulina-Carabajal et al. 2021) but differs from that of both juvenile and adult *Tyrannosaurus*, in which the medial subcondylar recess is restricted to the dorsal half of the bone, not extending much farther than the level of the ventral margin of the occipital condyle (Witmer and Ridgely 2009). The presence of a medial subcondylar recess is variable within Tyrannosauroidea, being present in proceratosaurids (Rauhut et al. 2010; Bever et al. 2013), early-diverging tyrannosauroids (i.e., *Dilong* and a braincase tentatively identified as *Stokesosaurus*; Chure and Madsen 1998; Xu et al. 2004), and eutyrannosaurians but absent in "mid-grade" tyrannosauroids (i.e., *Xiongguanlong* and *Timurlengia;* Li et al. 2010; Brusatte et al. 2016).

4 | Discussion

4.1 | Ontogeny of the Eutyrannosaurian Endocranium

Ontogenetic changes in endocast morphology in eutyrannosaurians are poorly understood due to the scarcity of well-preserved braincases for juvenile individuals. Fortunately, skulls representing different growth stages of the tyrannosaurid *Gorgosaurus libratus*, including two recently discovered skulls from small juvenile individuals, offer a unique opportunity to investigate how brain endocasts change over the course of the lifespan in this theropod. Our study reveals that endocasts of juvenile *Gorgosaurus* individuals exhibit better definition of neural structures than those of more mature individuals, indicating a closer correspondence between endocast and brain morphology in younger individuals. This close brain-endocast correspondence in juvenile *Gorgosaurus* is most apparent in the fore- and midbrain regions, where the cerebral hemispheres appear as separate, ovoid lobes, and where the optic lobes are represented by distinct bulges located posteroventral to the cerebral hemispheres. The endocast of a juvenile *T. rex* (CMNH 7541) also reveals a closer correspondence between endocast and brain morphology, as the cerebral hemispheres are better defined than in mature individuals (see Witmer and Ridgely 2009, fig. 3) and bulges that likely represent the optic lobes are visible in the juvenile but not in adults. These observations indicate that an overall reduction of neural details visible in endocasts occurs during ontogeny in eutyrannosaurians. Thus, we suggest the endocast of juvenile or immature individuals is more representative of the true brain morphology than that of adults in eutyrannosaurians (and perhaps also in other earlier-diverging theropods), potentially due to a higher growth rate in the volume of the endocranial cavity relative to the brain itself, as also occurs in extant crocodylians (Witmer and Ridgely 2009; Hurlburt et al. 2013; Jirak and Janacek 2017; Hu et al. 2021). However, the timing of this ontogenetic change is not well constrained. The endocasts of young adult and adult eutyrannosaurians show little detail of the underlying brain structures, but it is unclear how much brain detail can be discerned in the endocasts of smaller subadult individuals due to CT scan artifacts. It is also possible that the endocasts of eutyrannosaurian specimens smaller/younger than those examined here (i.e., TMP 2009.012.0014 and TMP 2016.014.0001) will display more details of the brain morphology.

Although the adult eutyrannosaurian endocast tends to lack neuroanatomical detail (Hopson 1979; Witmer and Ridgely 2009), it still approximates the overall shape of the brain (Romer 1956; Jerison 1973; Hopson 1979; Balanoff et al. 2010) and thus allows an ontogenetic assessment of overall brain shape. In *Gorgosaurus*, both juvenile and adult individuals have a moderately elongate endocast with an anteroposteriorly short hindbrain and steeply angled pontine flexure. Although there appears to be a slight increase in hindbrain length relative to the combined lengths of the fore- and midbrain through ontogeny, overall endocast shape changes little between the juvenile to adult *Gorgosaurus* growth stages. In contrast, overall endocast morphology changes significantly during ontogeny in *T. rex* (Witmer and Ridgely 2009) in that juvenile individuals (CMNH 7541) had a much shorter and more steeply angled hindbrain, superficially similar to the *Gorgosaurus* endocast at any growth stage, whereas mature individuals had an elongate and relatively shallowly angled hindbrain, resulting in a more "tubular" endocast (see Brochu 2000). This difference suggests that *Tyrannosaurus* (and potentially other derived tyrannosaurines) experienced greater hindbrain elongation through ontogeny than did *Gorgosaurus* and possibly other early-diverging eutyrannosaurians (given the similar endocast morphology of adult *Gorgosaurus* and *Bistahieversor*).

Our study also provides some information related to ontogenetic changes in the endosseous labyrinth of eutyrannosaurians. Notably, there is little difference in either size or shape of the semicircular canals between juvenile and adult individuals of *Gorgosaurus* despite a 1.75-fold increase in skull length. In contrast, a slight ontogenetic size increase occurs in the endosseous labyrinth of *Tyrannosaurus* (see Witmer and Ridgely 2009). It is possible that the change in endosseous labyrinth size through ontogeny in *Tyrannosaurus* relates to an extended period of development of the endocranium, as occurs in other parts of the skull (Voris et al. 2022). It is also possible that the change in endosseous labyrinth size could simply be related to a greater increase in body size/age between juvenile and adult *Tyrannosaurus* specimens than in *Gorgosaurus* (> 2-fold difference in linear skull length in *Tyrannosaurus* vs. 1.75-fold increase in *Gorgosaurus*). Indeed, while the juvenile *Tyrannosaurus* CMNH 7541 is more immature but comparable in size to the two juvenile *Gorgosaurus* studied (TMP 2009.012.0014 or TMP 2016.014.0001), the adult *Tyrannosaurus* individuals (Witmer and Ridgely 2009) are nearly as mature as but much larger than the largest *Gorgosaurus* individuals studied (TMP 1994.012.0602; Carr 2020; Voris et al. 2022). Since growth of sensory organs is typified by strong negative allometry in other archosaurs (Lautenschlager and Hübner 2013; Neenan et al. 2019; Schwab et al. 2022), it is perhaps unsurprising that less disparately sized juvenile and adult *Gorgosaurus* individuals have more similarly sized endosseous labyrinths than do the more disparately sized juvenile and adult *Tyrannosaurus* individuals. If *Gorgosaurus* follows a similar pattern of endosseous labyrinth size change through ontogeny as *Tyrannosaurus*, then we would expect to find smaller endosseous labyrinths in *Gorgosaurus* individuals smaller and younger than those of TMP 2009.012.0014 and TMP 2016.014.0001.

The small difference in the overall length of the cochlear duct between the juvenile and adult *Gorgosaurus* may suggest a subtle change in the overall hearing capabilities through ontogeny. Using the regressions of Gleich et al. (2005), we find the hearing estimates of juvenile *Gorgosaurus* (TMP 2009.012.0014: mean best hearing = 218 Hz) are slightly higher than those for the largest adult specimen (TMP 1994.012.0602: mean best hearing = 15 Hz). The regressions of Walsh et al. (2009), however, produce similar hearing ranges regardless of ontogenetic stage (TMP 2009.012.0014: mean best hearing = 1808 Hz; TMP 1994.012.0602: mean best hearing = 1745 Hz). Regardless, both regressions show that both juvenile and adult *Gorgosaurus* were susceptible to sound frequencies at the lower threshold among terrestrial sauropsids. In fact, the estimates are considerably lower than those estimated for the southern cassowary, *Casuarius casuarius*, based on the same regressions (based on virtual model derived from CT scans of RAM 279.114.754: mean best hearing = 2117 Hz—Walsh et al. 2009; 1353 Hz—Gleich et al. 2005: see measurements in Supporting Information), a bird species known to communicate via sound frequencies as low as 23 Hz (Mack and Jones 2003). This could mean that *Gorgosaurus*, and probably Eutyrannosauria generally, were capable of perceiving infrasonic (< 20 Hz) or near-infrasonic frequencies. The largely consistent measurements of hearing capabilities among growth stages indicate minimal change in hearing capabilities through ontogeny in *Gorgosaurus*, suggesting that both juvenile and adult animals were capable of detecting the same frequencies, as has also been suggested for other dinosaurs (Lautenschlager and Hübner 2013).

The morphology of the various diverticula of the paratympanic sinuses shows little change through ontogeny in *Gorgosaurus*. However, there is an ontogenetic volume increase in some diverticula so that parts of the braincase appear inflated (Voris et al. 2022). This ontogenetic inflation affected mostly the diverticula of the tympanic sinus system and occurred late in ontogeny, as it is only apparent in adult specimens (Voris et al. 2022). A similar pattern is observed in *T. rex*, where juvenile and adult individuals possess morphologically similar paratympanic diverticula (see also Witmer and Ridgely 2009, 2010) but sinuses are more inflated in adults. These findings are not surprising given that paratympanic sinuses generally develop during embryonic stages among extant archosaurs whereas inflation, and in some cases reduction, of sinus volume occurs in later ontogenetic stages (Dufeau 2011).

4.2 | Trends in Tyrannosauroid Endocranial Evolution

Based on comparisons of the endocranial morphology of other tyrannosauroids, several in-group character transformations appear to have occurred within Tyrannosauroidea independently of those that occurred along the theropod lineage leading to birds. Identifying these transformations is crucial to disentangle Tyrannosauroidea-specific trends from those that characterize Theropoda evolution as a whole. Interspecific differences in endocast morphology within Tyrannosauroidea seem to reflect a sequence of character transformations from early-diverging tyrannosauroids to eutyrannosaurians, largely relating to variations in hindbrain length and depth. The endocast form of the early-diverging tyrannosauroid, *Dilong paradoxus*, is most similar to that of other coelurosaurs (e.g., ornithomimids, some oviraptorids, troodontids) in that the hindbrain is very short and the pontine flexure is very steep (~90°; Balanoff et al. 2018; Kundrát et al. 2020). The endocast of more derived non-eutyrannosaurian tyrannosauroids, exemplified by *Timurlengia*, exhibits a slightly more elongate and tubular hindbrain but a much shallower pontine flexure (~135°). Early-diverging eutyrannosaurians, such as *Gorgosaurus* and *Bistahieversor*, exhibit a moderately elongate hindbrain morphology similar to *Timurlengia* but are dorsoventrally deeper, resulting in a slightly steeper pontine flexure (~120°). Late diverging tyrannosaurines possess an endocast that is overall similar to those of early-diverging eutyrannosaurians but have an even more elongate hindbrain with a shallower pontine flexure (~140°).

The morphology of the semicircular canals of the endosseous labyrinth was largely consistent through tyrannosauroid evolution (also see Witmer and Ridgely 2009; Brusatte et al. 2016). With the exception of some differences previously noted among the labyrinths of non-eutyrannosaurian tyrannosauroids (e.g., *Timurlengia*) and eutyrannosaurians (Brusatte et al. 2016), the greatest divergence from the typical tyrannosauroid labyrinth morphology occurs in *Tyrannosaurus*, in which the common crus is anteroventrally inclined rather than vertical and the anterior semicircular canal is proportionally larger (relative to the size of the posterior semicircular canal) than in other tyrannosauroids. Given the known connections between gaze stabilization and semicircular canal morphology (Cohen and Raphan 2004; Schwarz and Tomlinson 2005; Graf and Klam 2006; Witmer and Ridgely 2009), one possible explanation for this divergence may relate to the autapomorphically wide morphology of the post-orbital region of the skull of *Tyrannosaurus*, which provided a wider binocular field of vision and greater stereopsis than in other eutyrannosaurians (Stevens 2006; Carr 2020).

The evolution of the paratympanic sinuses in tyrannosauroids generally reflects a sequence of increasing braincase pneumaticity from earlier-diverging taxa, like *Dilong* and "mid-grade" tyrannosauroids (e.g., *Xiongguanlong* and *Timurlengia*), to later diverging eutyrannosaurians, like *Gorgosaurus* and *Tyrannosaurus*. Early-diverging tyrannosauroids had a rudimentary paratympanic sinus system with small tympanic sinuses that were locally restricted within the otoccipital and prootic bones (Brusatte et al. 2016). Although they retained the rudimentary paratympanic system of early-diverging tyrannosauroids, "mid-grade" tyrannosauroids seemingly lack the subcondylar recess of the basioccipital present in early-diverging tyrannosauroids and proceratosaurids (Xu et al. 2004; Rauhut et al. 2010; Bever et al. 2013) and in various other theropods (Sampson and Witmer 2007). One of the more notable evolutionary shifts in the paratympanic sinus system occurred prior to the most recent common ancestor of the *Bistahieversor*+Tyrannosauridae clade. These eutyrannosaurians possessed an almost entirely pneumatized braincase with greatly inflated and expansive tympanic recesses (including a large prootic diverticulum of the anterior tympanic recess and confluence of the contralateral posterior tympanic recesses within the supraoccipital) and a potentially secondarily re-evolved medial subcondylar recess that pneumatizes the basioccipital. A potential reversal in paratympanic sinus expansion occurs in the most derived tyrannosaurines, such as *Tyrannosaurus* and one specimen of *Daspletosaurus* (*D. torosus* holotype, CMN 8506; see Paulina-Carabajal et al. 2021), in which the tympanic sinuses are more restricted within the braincase than in other eutyrannosaurians.

4.3 | Insights Into the Evolution of the Coelurosaurian Brain

The juvenile *Gorgosaurus* endocasts described herein reveal better defined neural structures than the endocasts of larger *Gorgosaurus* specimens and thus provide the most accurate picture of the morphology of the eutyrannosaurian brain (Figure 7). Consequently, we are able to more accurately estimate the size and shape of the cerebrum in eutyrannosaurians. The cerebrum represents roughly 44.7% of the total endocast volume in TMP 2009.012.0014 and 41.6% in TMP 2016.014.0001 (excluding the olfactory bulbs and tract), both of which are higher than reported for other tyrannosaurids but well within the range expected for other non-avian coelurosaurs (Larsson et al. 2000; Balanoff et al. 2014). This suggests that the characteristic forebrain expansion that occurred over the course of theropod evolution began prior to the origin of Tyrannosauroidea, as had been hypothesized previously (see Larsson et al. 2000). Although a large cerebrum is observed among more derived coelurosaurians, the steep posteroventral inclination of the cerebrum in *Gorgosaurus* is plesiomorphic among theropods (Sampson and Witmer 2007), where more derived theropods (e.g., birds) are characterized by a horizontal cerebrum. This suggests that forebrain expansion would have preceded the evolution of other more derived features of the cerebrum and other parts of the brain (e.g., horizontal long axis of the cerebrum) in theropod evolution.

The fact that the bulges for the optic lobes are located posteroventral to the cerebrum indicates that *Gorgosaurus* possessed a relatively large cerebrum and relatively small optic lobes. The position of the cerebellar bulge dorsal to the optic lobe bulges suggests that the cerebellum at least partly separated the two optic lobes in *Gorgosaurus*, and probably in other tyrannosauroids, as discussed by Witmer and Ridgely (2009), Bever et al. (2011), and Kundrát et al. (2020). This reflects a more derived condition than the plesiomorphic sauropsid condition wherein contralateral optic lobes are adjacent to one another. At the same time, the position of the optic lobe posterior to the cerebrum and well separated from the optic nerve root are characteristics shared with early-diverging sauropsids (e.g., crocodylians and squamates). As such, the brain morphology of *Gorgosaurus* and other eutyrannosaurians was intermediate between that of derived coelurosaurs and earlier-diverging sauropsids. This combination of derived and plesiomorphic traits would suggest a multiphasic evolution of the coelurosaurian brain (Figure 8), with lateral displacement of the optic lobes preceding the migration of the optic lobes to the more anteroventral position seen in derived coelurosaurs (e.g., oviraptorosaurs; Balanoff et al. 2014). Unfortunately, the combination of an expanded forebrain and separation of the optic lobes by the cerebellum in *Gorgosaurus* precludes clear identification of a single driver for the displacement of the optic lobes among coelurosaurs. This architecture could have been the result of: (1) cerebral expansion forcing the posterior displacement of the optic lobes to either side of the cerebellum, (2) expansion of the cerebellum causing separation of the contralateral optic lobes, (3) the interplay between both cerebral and cerebellar expansion causing the lateral displacement of the optic lobes, or (4) the migration of the optic lobes themselves may have facilitated cerebral and/or cerebellar expansion.

Our understanding of the evolution of brain morphology in theropods has largely been consigned to studies of later-diverging maniraptoran theropods. Endocasts of these taxa exhibit greater detail of brain structures, even in more mature specimens. This study illustrates the usefulness of ontogenetically immature specimens of earlier-diverging theropods lineages, like tyrannosauroids, for establishing brain morphology. Future studies utilizing this method in earlier-diverging theropod groups than tyrannosauroids will likely uncover more data about the evolution of the theropod brain and the sequence of character transformations that culminated in the unique brain morphology of birds.

4.4 | Conclusion

Several ontogenetic trends are noted within the endocranium of the eutyrannosaurian tyrannosauroid *Gorgosaurus libratus*. The endocasts of juvenile *Gorgosaurus* individuals show greater details of various neuroanatomical structures, specifically the cerebrum, optic lobe, and cerebellum, than those of adult individuals. Reduced detail of these structures in adult *Gorgosaurus* and other eutyrannosaurian endocasts suggests a reduction in the brain-endocast correspondence through ontogeny, perhaps due to faster growth of the brain cavity than of the brain itself, as seen in most archosaurs. Similarly, poor resolution of neuroanatomical structures in the endocasts of more early-diverging theropods (e.g., allosauroids, abelisaurids, and early-diverging neotheropods) could indicate they followed similar ontogenetic patterns. We propose, therefore, that the study of endocasts of small and/or immature theropod individuals may be more informative about true brain anatomy than endocasts of adult individuals.

Ontogeny of the braincase sinuses in *Gorgosaurus* is largely associated with inflation of existing sinus chambers rather than the invasion of new space within the braincase. Similar ontogenetic consistency in paratympanic sinus morphology is also observed in other eutyrannosaurian taxa (e.g., *T. rex*) and supports the usefulness of such features as taxonomic or phylogenetic characters among eutyrannosaurians and perhaps Tyrannosauroidea as a whole.

Details of brain anatomy in *Gorgosaurus*, particularly from juvenile individuals, also provide new information on the evolution of the coelurosaurian brain. We find that juvenile *Gorgosaurus* display a mixture of derived theropod and ancestral sauropsid characteristics in brain morphology. Derived characteristics include a flexed brain, somewhat enlarged cerebrum, and a cerebellum that at least partially separates the left and right optic lobes, whereas ancestral characteristics include large olfactory bulbs and tracts, a posteroventrally inclined cerebrum, posteroventral position of the optic lobes, and a long hindbrain. The identification of more derived theropod traits in a tyrannosauroid suggests that many of the characteristics thought to be unique to maniraptorans may have deeper origins within Theropoda.

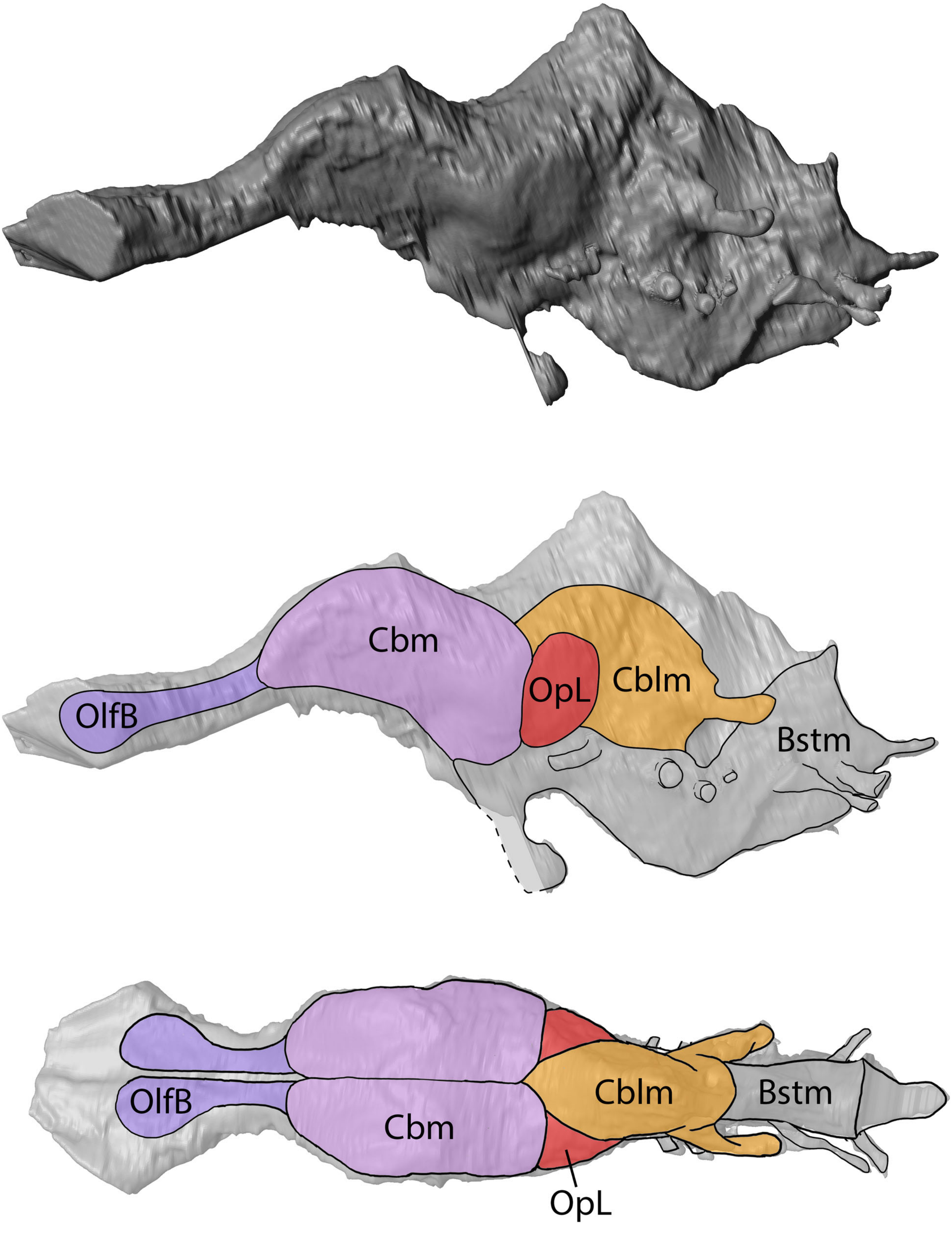

FIGURE 7 | Reconstructed brain morphology of *Gorgosaurus* based on observable structures in the endocasts of juvenile specimens TMP 2009.012.0014 and TMP 2016.014.0001. Abbreviations: Bstm, brainstem; Cbm, cerebrum/ cerebral hemisphere; Cblm, cerebellum; OlfB, olfactory bulb; OpL, optic lobe.

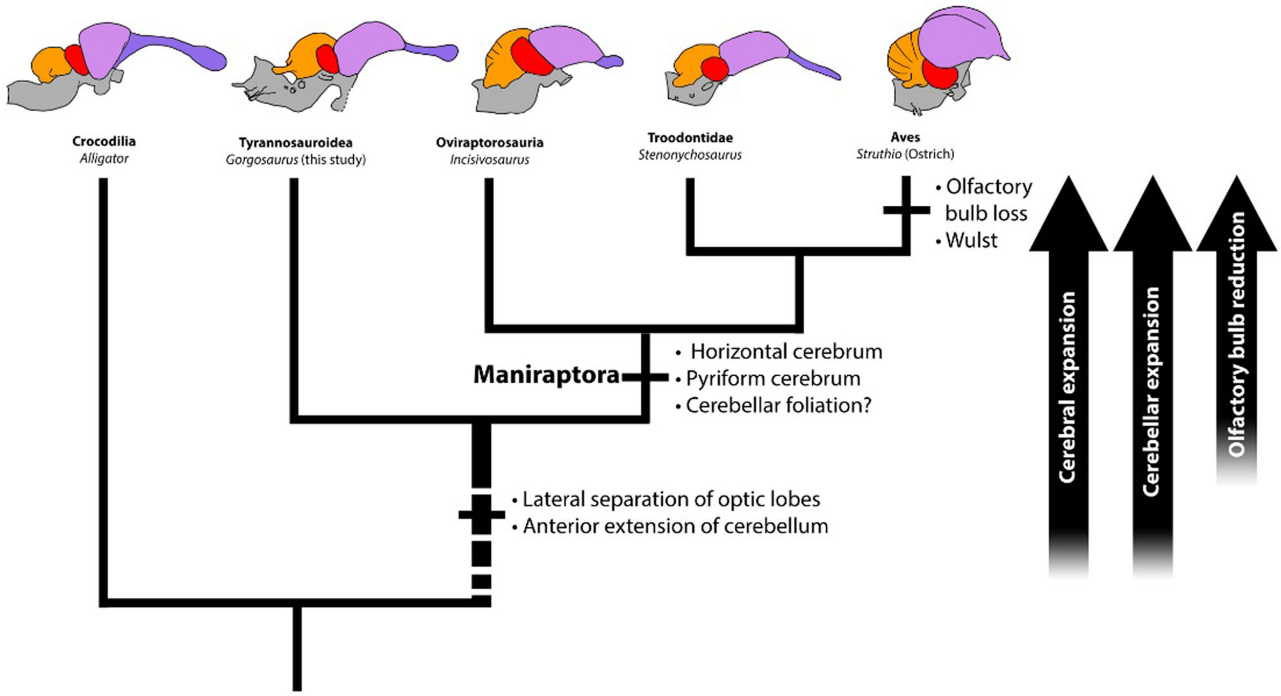

FIGURE 8 | Simplified cladogram with indicated hypothesized character transformations among theropods on the line toward birds relative to earlier-diverging archosaurs (e.g., Crocodilia) following the new information provided by *Gorgosaurus*.

Future studies should seek to reconstruct endocasts of juvenile individuals, particularly tyrannosauroids and early-diverging theropods, as they may provide valuable information about the ancestral theropod brain condition. From these, it will be possible to clarify the nature and timing of changes in brain morphology that occurred in the among theropods and that led to the evolution of the avian brain.

Author Contributions

Jared T. Voris conceived and designed the study, compiled data, conducted digital segmentation, wrote initial manuscript drafts, and proofed and edited manuscript drafts. **François Therrien** conceived and designed the study, compiled data, conducted segmentation, and scheduled CT scans. **Ryan C. Ridgely** conceived and designed the study, compiled data, conducted digital segmentation, scheduled CT scans, and edited manuscript drafts. **Lawrence M. Witmer** compiled data, conducted digital segmentation, scheduled CT scans, and edited manuscript drafts. **Darla K. Zelenitsky** conceived and designed the study, scheduled CT scans, and edited manuscript drafts.

Acknowledgments

We thank the CT scan technicians at the University of Calgary (Calgary, Alberta), OhioHealth O'Bleness Memorial Hospital (Athens, Ohio), Calgary Diagnostics Centre (Calgary, Alberta), and Mayfair Diagnostics (Calgary, Alberta) for their assistance over the course of this study. We thank B. Strilisky, B. Sanchez, T. Courtenay, R. Russell, J. Richards, and S. Haupt (RTMP) for access to specimens and transport of specimens to CT scan facilities. We also thank K. Bazzana-Adams, S. Lautenschlager, an anonymous third reviewer, and the editor for their constructive comments on a previous version of the manuscript.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The authors declare that all data needed to reproduce our results accompany this manuscript at https://doi.org/10.5061/dryad.fxpnvx12j and are on file at the repository institutions housing the fossil subjects.

Peer Review

The peer review history for this article is available at https://publons.com/publon/10.1002/cne.70056

References

Ali, F., D. K. Zelenitsky, F. Therrien, and D. B. Weishampel. 2008. "Homology of the "Ethmoid Complex" of Tyrannosaurids and its Implications for the Reconstruction of the Olfactory Apparatus of Non-Avian Theropods." *Journal of Vertebrate Paleontology* 28: 123–133.

Alonso, P. D., A. C. Milner, R. A. Ketcham, M. J. Cookson, and T. B. Rowe. 2004. "The Avian Nature of the Brain and Inner Ear of Archaeopteryx." *Nature* 430: 666–669.

Balanoff, A. M., G. S. Bever, and T. Ikejiri. 2010. "The Braincase of *Apatosaurus* (Dinosauria: Sauropoda) Based on Computed Tomography of a New Specimen With Comments on Variation and Evolution in Sauropod Neuroanatomy." *American Museum Novitates* 3677: 1–32.

Balanoff, A. M., G. S. Bever, and M. A. Norell. 2014. "Reconsidering the Avian Nature of the Oviraptorosaur Brain (Dinosauria: Theropoda)." *PLoS ONE* 9: e113559.

Balanoff, A. M., G. S. Bever, T. B. Rowe, and M. A. Norell. 2013. "Evolutionary Origins of the Avian Brain." *Nature* 501: 93–96.

Balanoff, A. M., M. A. Norell, A. V. C. Hogan, and G. S. Bever. 2018. "The endocranial cavity of oviraptorosaur dinosaurs and the increasingly complex, deep History of the avian brain." *Brain Behavior and Evolution* 91: 125–135.

Balanoff, A. M., X. Xu, Y. Kobayashi, and M. A. Norell. 2009. "Cranial Osteology of the Theropod Dinosaur *Incisivosaurus gauthieri* (Theropoda: Oviraptorosauria)." *American Museum Novitates* 3651: 1–35.

Bever, G. S., S. L. Brusatte, A. M. Balanoff, and M. A. Norell. 2011. "Variation, Variability, and the Origin of the Avian Endocranium: Insights From the Anatomy of *Alioramus altai* (Theropoda: Tyrannosauroidea)." *PLoS ONE* 6: e23393.

Bever, G. S., S. L. Brusatte, T. D. Carr, X. Xu, A. M. Balanoff, and M. A. Norell. 2013. "The Braincase Anatomy of the Late Cretaceous Dinosaur *Alioramus* (Theropoda: Tyrannosauroidea)." *Bulletin of the American Museum of Natural History* 376: 1–72.

Beyrand, V., D. Voeten, S. Bureš, et al. 2019. "Multiphase Progenetic Development Shaped the Brain of Flying Archosaurs." *Scientific Reports* 9: 10807.

Brochu, C. A 2000. "A Digitally-Rendered Endocast for *Tyrannosaurus rex*." *Journal of Vertebrate Paleontology* 20: 1–6.

Brochu, C. A 2003. "Osteology of *Tyrannosaurus Rex*: Insights From a Nearly Complete Skeleton and High-Resolution Computed Tomographic Analysis of the Skull." *Journal of Vertebrate Paleontology* 22: 1–138.

Brusatte, S. L., A. Averianov, H.-D. Sues, A. Muir, and I. B. Butler. 2016. "New Tyrannosaur From the Mid-Cretaceous of Uzbekistan Clarifies Evolution of Giant Body Sizes and Advanced Senses in Tyrant Dinosaurs." *PNAS* 113: 3447–3452.

Brusatte, S. L., and P. C. Sereno. 2007. "A New Species of *Carcharodontosaurus* (Dinosauria: Theropoda) From the Cenomanian of Niger and a Revision of the Genus." *Journal of Vertebrate Paleontology* 27: 902–916.

Carr, T. D 2020. "A High-Resolution Growth Series of *Tyrannosaurus rex* Obtained From Multiple Lines of Evidence." *PeerJ* 8: e9192.

Carr, T. D., T. E. Williamson, B. B. Britt, and K. Stadtman. 2011. "Evidence for High Taxonomic and Morphologic Tyrannosauroid Diversity in the Late Cretaceous (Late Campanian) of the American Southwest and a New Short-Skulled Tyrannosaurid From the Kaiparowits Formation of Utah." *Die Naturwissenschaften* 98: 241–246.

Caspar, K. R., C. Gutiérrez-Ibáñez, O. C. Bertrand, et al. 2024. "How Smart Was *T. rex*? Testing Claims of Exceptional Cognition in Dinosaurs and the Application of Neuron Count Estimates in Palaeontological Research." *Anatomical Record* 307: 3685–3716.

Cerroni, M. A., and A. Paulina-Carabajal. 2019. "Novel Information on the Endocranial Morphology of the Abelisaurid Theropod *Carnotaurus sastrei*." *Comptes Rendus Palevol* 18: 985–995.

Chure, D. J., and J. H. Madsen. 1998. "An Unusual Braincase (? *Stokesosaurus clevelandi*) From the Cleveland-Lloyd Dinosaur Quarry, Utah (Morrison Formation; Late Jurassic)." *Journal of Vertebrate Paleontology* 18: 115–125.

Cohen, B., and T. Raphan. 2004. "The Physiology of the Vestibuloocular Reflex (VOR)." In *The Vestibular System. Springer Handbook of Auditory Research*, edited by S. M. Highstein, R. R. Fay, and A. N. Popper, 235–285. Springer. https://doi.org/10.1007/0-387-21567-0_6.

Currie, P. J., and X.-J. Zhao. 1993. "A New Troodontid (Dinosauria, Theropoda) Braincase From the Dinosaur Park Formation (Campanian) of Alberta." *Canadian Journal of Earth Sciences* 30: 2231–2247.

Delcourt, R., and O. N. Grillo. 2018. "Tyrannosauroids From the Southern Hemisphere: Implications for Biogeography, Evolution, and Taxonomy." *Palaeogeography, Palaeoclimatology, Palaeoecology* 511: 379–387.

Dufeau, D. L 2011. "The Evolution of Cranial Pneumaticity in Archosauria: Patterns of Paratympanic Sinus Development." PhD diss., College of Arts and Sciences of Ohio University. https://www.proquest.com/docview/902729803/abstract/E4D3F777B1ED4239PQ/1.

Edinger, T 1929. "Die fossilen Gehirne." *Ergeb Anat Entwicklungsgeschichte* 28: 1–249.

Franzosa, J., and T. Rowe. 2005. "Cranial Endocast of the Cretaceous Theropod Dinosaur *Acrocanthosaurus atokensis*." *Journal of Vertebrate Paleontology* 25: 859–864.

Franzosa, J. W 2004. "Evolution of the Brain in Theropoda (Dinosauria)." PhD diss., University of Texas at Austin. https://www.proquest.com/docview/305128296/abstract/99CD34B5DEEB4921PQ/1.

Gianechini, F. A., A. H. Méndez, L. S. Filippi, A. Paulina-Carabajal, R. D. Juárez-Valieri, and A. C. Garrido. 2020. "A New Furileusaurian Abelisaurid From La Invernada (Upper Cretaceous, Santonian, Bajo de la Carpa Formation), Northern Patagonia, Argentina." *Journal of Vertebrate Paleontology* 40: e1877151.

Gleich, O., R. J. Dooling, and G. A. Manley. 2005. "Audiogram, Body Mass, and Basilar Papilla Length: Correlations in Birds and Predictions for Extinct Archosaurs." *Die Naturwissenschaften* 92: 595–598.

Graf, W., and F. Klam. 2006. "Le système vestibulaire: Anatomie fonctionnelle et comparée, évolution et développement." *Comptes Rendus Palevol* 5: 637–655.

Herculano-Houzel, S 2023. "Theropod Dinosaurs Had Primate-Like Numbers of Telencephalic Neurons." *Journal of Comparative Neurology* 531: 962–974.

Hopson, J. A 1979. "Paleoneurology." In *Biology of the Reptilia. Vol. Vol. IX: Neurology A*, edited by C. Gans, 39–146. New York Academic Press.

Hu, K., J. L. King, C. A. Romick, et al. 2021. "Ontogenetic Endocranial Shape Change in Alligators and Ostriches and Implications for the Development of the Non-Avian Dinosaur Endocranium." *Anatomical Record* 304: 1759–1775.

Hurlburt, G. R., R. C. Ridgely, and L. M. Witmer. 2013. "Relative Size of Brain and Cerebrum in Tyrannosaurid Dinosaurs: An Analysis Using Brain-Endocast Quantitative Relationships in Extant Alligators." In *Tyrannosaurid Paleobiology*, edited by J. M. Parrish, R. E. Molnar, P. J. Currie, and E. B. Koppelhus, 134–154. Indiana University Press.

Jerison, H 1973. *Evolution of the Brain and Intelligence*. Academic Press.

Jirak, D., and J. Janacek. 2017. "Volume of the Crocodilian Brain and Endocast During Ontogeny." *PLoS ONE* 12: e0178491.

King, L., Q. Zhao, D. L. Dufeau, et al. 2024. "Endocranial Development in Non-Avian Dinosaurs Reveals an Ontogenetic Brain Trajectory Distinct From Extant Archosaurs." *Nature Communications* 15: 7415.

Ksepka, D. T., A. M. Balanoff, N. A. Smith, et al. 2020. "Tempo and Pattern of Avian Brain Size Evolution." *Current Biology* 30: 2026–2036.e3.

Kundrát, M 2007. "Avian-Like Attributes of a Virtual Brain Model of the Oviraptorid Theropod *Conchoraptor gracilis*." *Die Naturwissenschaften* 94: 499–504.

Kundrát, M., X. Xu, M. Hančová, A. Gajdoš, Y. Guo, and D. Chen. 2020. "Evolutionary Disparity in the Endoneurocranial Configuration Between Small and Gigantic Tyrannosauroids." *Historical Biology* 32: 620–634.

Larsson, H. C. E., P. C. Sereno, and J. A. Wilson. 2000. "Forebrain Enlargement Among Nonavian Theropod Dinosaurs." *Journal of Vertebrate Paleontology* 20: 615–618.

Lautenschlager, S., and T. Hübner. 2013. "Ontogenetic Trajectories in the Ornithischian Endocranium." *Journal of Evolutionary Biology* 26: 2044–2050.

Lautenschlager, S., E. J. Rayfield, P. Altangerel, L. E. Zanno, and L. M. Witmer. 2012. "The Endocranial Anatomy of Therizinosauria and Its Implications for Sensory and Cognitive Function." *PLoS ONE* 7: e52289.

Li, D., M. A. Norell, K.-Q. Gao, N. D. Smith, and P. J. Makovicky. 2010. "A Longirostrine Tyrannosauroid From the Early Cretaceous of China." *Proceedings of the Royal Society B: Biological Sciences* 277: 183–190.

Mack, A. L., and J. Jones. 2003. "Low-Frequency Vocalizations by Cassowaries (*Casuarius* Spp.)." *Auk* 120: 1062–1068.

McKeown, M., S. L. Brusatte, T. E. Williamson, et al. 2020. "Neurosensory and Sinus Evolution as Tyrannosauroid Dinosaurs Developed Giant

Size: Insight From the Endocranial Anatomy of *Bistahieversor sealeyi*." *Anatomical Record* 303: 1043–1059.

Neenan, J. M., K. E. J. Chapelle, V. Fernandez, and J. N. Choiniere. 2019. "Ontogeny of the Massospondylus Labyrinth: Implications for Locomotory Shifts in a Basal Sauropodomorph Dinosaur." *Palaeontology* 62: 255–265.

Norell, M. A., P. J. Makovicky, G. S. Bever, et al. 2009. "A Review of the Mongolian Cretaceous Dinosaur *Saurornithoides* (Troodontidae: Theropoda)." *American Museum Novitates* 3654: 1–63.

Osborn, H. F 1912. "Crania of *Tyrannosaurus* and *Allosaurus*." *Memoirs of the American Museum of Natural History* 1: 1–30.

Osvath, M., P. Němec, S. L. Brusatte, and L. M. Witmer. 2024. "Thought for Food: The Endothermic Brain Hypothesis." *Trends in Cognitive Sciences* 28: 998–1010.

Paulina-Carabajal, A., M. Bronzati, and P. Cruzado-Caballero. 2023. "Paleoneurology of Non-Avian Dinosaurs: An Overview." In *Paleoneurology of Amniotes: New Directions in the Study of Fossil Endocasts*, edited by M. T. Dozo, A. Paulina-Carabajal, T. E. Macrini, and S. Walsh, 267–332. Springer International Publishing. https://doi.org/10.1007/978-3-031-13983-3_8.

Paulina-Carabajal, A., and P. J. Currie. 2012. "New Information on the Braincase of *Sinraptor dongi* (Theropoda: Allosauroidea): Ethmoidal Region, Endocranial Anatomy, and Pneumaticity." *Vertebrata PalAsiatica* 50: 85–101.

Paulina-Carabajal, A., and P. J. Currie. 2017. "The Braincase of the Theropod Dinosaur Murusraptor: Osteology, Neuroanatomy and Comments on the Paleobiological Implications of Certain Endocranial Features." *Ameghiniana* 54: 617.

Paulina-Carabajal, A., P. J. Currie, T. W. Dudgeon, H. C. E. Larsson, and T. Miyashita. 2021. "Two Braincases of *Daspletosaurus* (Theropoda: Tyrannosauridae): Anatomy and Comparison." *Canadian Journal of Earth Sciences* 58: 885–910.

Paulina-Carabajal, A., M. D. Ezcurra, and F. E Novas. 2019. "New Information on the Braincase and Endocranial Morphology of the Late Triassic Neotheropod *Zupaysaurus rougieri* Using Computed Tomography Data." *Journal of Vertebrate Paleontology* 39: e1630421.

Paulina-Carabajal, A., and L. Filippi. 2018. "Neuroanatomy of the Abelisaurid Theropod *Viavenator*: The Most Complete Reconstruction of a Cranial Endocast and Inner Ear for a South American Representative of the Clade." *Cretaceous Research* 83: 84–94.

Paulina-Carabajal, A., and M. N. Nieto. 2019. "Brief Comment on the Brain and Inner Ear of *Giganotosaurus carolinii* (Dinosauria: Theropoda) Based on CT Scans." *Ameghiniana* 57: 58.

Paulina-Carabajal, A., and C. Succar. 2013. "The Endocranial Morphology and Inner Ear of the Abelisaurid Theropod *Aucasaurus garridoi*." *Acta Palaeontologica Polonica* 60, no. 1: 2015: 141–144. http://www.app.pan.pl/article/item/app20130037.html.

Plateau, O., T. L. Green, P. M. Gignac, and C. Foth. 2024. "Comparative Digital Reconstruction of *Pica pica* and *Struthio camelus* and Their Cranial Suture Ontogenies." *Anatomical Record* 307: 5–48.

Rauhut, O. W. M. 2004. "Braincase Structure of the Middle Jurassic Theropod Dinosaur *Piatnitzkysaurus*." *Canadian Journal of Earth Sciences* 41: 1109–1122.

Rauhut, O. W. M 2014. "New Observations on the Skull of *Archaeopteryx*." *Paläontologische Zeitschrift* 88: 211–221.

Rauhut, O. W. M., A. C. Milner, and S. Moore-Fay. 2010. "Cranial Osteology and Phylogenetic Position of the Theropod Dinosaur *Proceratosaurus bradleyi* (Woodward, 1910) From the Middle Jurassic of England." *Zoological Journal of the Linnean Society* 158: 155–195.

Ridgely, R. C., and L. M. Witmer. 2006. "Dead on Arrival: Optimizing CT Data Acquisition of Fossils Using Modern Hospital CT Scanners." *Journal of Vertebrate Paleontology* 26: 115A.

Rogers, S. W 1998. "Exploring Dinosaur Neuropaleobiology: Computed Tomography Scanning and Analysis of an *Allosaurus fragilis* Endocast." *Neuron* 21: 673–679.

Rogers, S. W 1999. "*Allosaurus*, Crocodiles, and Birds: Evolutionary Clues From Spiral Computed Tomography of an Endocast." *Anatomical Record* 257: 162–173.

Rogers, S. W 2005. "Reconstructing the Behaviors of Extinct Species: An Excursion Into Comparative Paleoneurology." *American Journal of Medical Genetics. Part A* 134A: 349–356.

Romer, A. S 1956. *Osteology of the Reptiles*. University of Chicago Press.

Sampson, S. D., and L. M. Witmer. 2007. "Craniofacial Anatomy of *Majungasaurus crenatissimus* (Theropoda: Abelisauridae) From the Late Cretaceous of Madagascar." *Journal of Vertebrate Paleontology* 27: 32–104.

Saveliev, S. V., and V. R. Alifanov. 2007. "A New Study of the Brain of the Predatory Dinosaur *Tarbosaurus bataar* (Theropoda, Tyrannosauridae)." *Paleontology Journal* 41: 281–289.

Schwab, J. A., M. T. Young, S. A. Walsh, et al. 2022. "Ontogenetic Variation in the Crocodylian Vestibular System." *Journal of Anatomy* 240: 821–832.

Schwarz, D. W. F., and R. D. Tomlinson. 2005. "Physiology of the Vestibular System." In *Neurotology*, edited by T. K. Jackler and D. E. Brackmann, 91–121. Elsevier.

Sereno, P. C., S. McAllister, and S. L. Brusatte. 2005. "TaxonSearch: A Relational Database for Documenting Taxa and Their Phylogenetic Definitions." *Phyloinformatics* 8: 1–21.

Stevens, K. A 2006. "Binocular Vision in Theropod Dinosaurs." *Journal of Vertebrate Paleontology* 26: 321–330.

Voris, J. T., D. K. Zelenitsky, F. Therrien, R. C. Ridgely, P. J. Currie, and L. M. Witmer. 2022. "Two Exceptionally Preserved Juvenile Specimens of *Gorgosaurus libratus* (Tyrannosauridae, Albertosaurinae) Provide New Insight Into the Timing of Ontogenetic Changes in Tyrannosaurids." *Journal of Vertebrate Paleontology* 41: e2041651.

Walsh, S. A., P. M. Barrett, A. C. Milner, G. Manley, and L. M. Witmer. 2009. "Inner Ear Anatomy is a Proxy for Deducing Auditory Capability and Behaviour in Reptiles and Birds." *Proceedings of the Royal Society B: Biological Sciences* 276: 1355–1360.

Watanabe, A., P. M. Gignac, A. M. Balanoff, T. L. Green, N. J. Kley, and M. A. Norell. 2019. "Are Endocasts Good Proxies for Brain Size and Shape in Archosaurs Throughout Ontogeny?" *Journal of Anatomy* 234: 291–305.

Witmer, L. M 1997a. "Craniofacial Air Sinus Systems." In *The Encyclopedia of Dinosaurs*, edited by P. J. Currie and K. Padian, 151–159. Academic Press.

Witmer, L. M 1997b. "The Evolution of the Antorbital Cavity of Archosaurs: A Study in Soft-Tissue Reconstruction in the Fossil Record With an Analysis of the Function of Pneumaticity." *Journal of Vertebrate Paleontology* 17: 1–76.

Witmer, L. M., and R. C. Ridgely. 2008. "The Paranasal Air Sinuses of Predatory and Armored Dinosaurs (Archosauria: Theropoda and Ankylosauria) and Their Contribution to Cephalic Structure." *Anatomical Record* 291: 1362–1388.

Witmer, L. M., and R. C. Ridgely. 2009. "New Insights Into the Brain, Braincase, and Ear Region of Tyrannosaurs (Dinosauria, Theropoda), With Implications for Sensory Organization and Behavior." *Anatomical Record* 292: 1266–1296.

Witmer, L. M., and R. C. Ridgely. 2010. "The Cleveland Tyrannosaur Skull (*Nanotyrannus* or *Tyrannosaurus*): New Findings Based on CT Scanning, With Special Reference to the Braincase." *Kirtlandia* 57: 61–81.

Witmer, L. M., R. C. Ridgely, D. L. Dufeau, and M. C. Semones. 2008. "Using CT to Peer Into the Past: 3D Visualization of the Brain and Ear Regions of Birds, Crocodiles, and Nonavian Dinosaurs." In *Anatomical Imaging*, edited by H. Endo and R. Frey, 67–87. Springer. http://link.springer.com/10.1007/978-4-431-76933-0_6.

Xing, L., A. Paulina-Carabajal, P. J. Currie, et al. 2014. “Braincase Anatomy of the Basal Theropod *Sinosaurus* From the Early Jurassic of China.” *Acta Geologica Sinica—English Edition* 88: 1653–1664.

Xu, X., M. A. Norell, X. Kuang, X. Wang, Q. Zhao, and C. Jia. 2004. “Basal Tyrannosauroids From China and Evidence for Protofeathers in Tyrannosauroids.” *Nature* 431: 680–684.

Yin, Y.-L., R. Pei, and C.-F. Zhou. 2018. “Cranial Morphology of *Sinovenator changii* (Theropoda: Troodontidae) on the New Material From the Yixian Formation of Western Liaoning, China.” *PeerJ* 6: e4977.

Zelenitsky, D. K., F. Therrien, and Y. Kobayashi. 2009. “Olfactory Acuity in Theropods: Palaeobiological and Evolutionary Implications.” *Proceedings of the Royal Society B: Biological Sciences* 276: 667–673.

Zelenitsky, D. K., F. Therrien, R. C. Ridgely, A. R. McGee, and L. M. Witmer. 2011. “Evolution of Olfaction in Non-Avian Theropod Dinosaurs and Birds.” *Proceedings of the Royal Society B: Biological Sciences* 278: 3625–3634.

Brusatte, S., T. Carr. 2016. The phylogeny and Evolutionary History of Tyrannosauroid Dinosaurs. Scientific Reports 6: 20252.

Supporting Information

Additional supporting information can be found online in the Supporting Information section.