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Citation for published version:

McKeown, M, Brusatte, S, Williamson, T, Schwab, J, Carr, TD, Butler, I, Muir, A, Schroeder, K, Epsy, MA, Hunter, JF, Losko, AS, Nelson, RO, Gautier, DC & Vogel, SC 2020, 'Neurosensory and sinus evolution as tyrannosauroid dinosaurs developed giant size: insight from the endocranial anatomy of *Bistahieversor sealeyi*', *The Anatomical record*. <https://doi.org/10.1002/ar.24374>

Digital Object Identifier (DOI):

[10.1002/ar.24374](https://doi.org/10.1002/ar.24374)

Link:

[Link to publication record in Edinburgh Research Explorer](#)

Document Version:

Peer reviewed version

Published In:

The Anatomical record

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Neurosensory and sinus evolution as tyrannosauroid dinosaurs developed giant size: insight
from the endocranial anatomy of *Bistahieversor sealeyi*

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RUNNING TITLE: NEUROSENSORY ANATOMY OF TYRANNOSAUROID
DINOSAURS

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Grant sponsors: European Research Council (ERC) under the European Union's Horizon 2020 research and innovation programme (grant agreement No 756226, ERC Starting Grant: PalM); Leverhulme Trust Research Project Grant (RPG-2017-167), Marie Curie Career Integration Grant (EC 630652), Royal Society Research Grant (RG130018), and the New Mexico Consortium.

ABSTRACT: *Tyrannosaurus rex* and other tyrannosaurid dinosaurs were apex predators during the latest Cretaceous, which combined giant size and advanced neurosensory systems. Computed tomography (CT) data have shown that tyrannosaurids had a trademark system of a large brain, large olfactory bulbs, elongate cochlear ducts, and expansive endocranial sinuses surrounding the brain and sense organs. Older, smaller tyrannosauroid relatives of tyrannosaurids developed some, but not all, of these features, raising the hypothesis that tyrannosaurid-style brains evolved before the enlarged tyrannosaurid-style sinuses, which might have developed only with large body size. This has been difficult to test, however, because little is known about the brains and sinuses of the first large-bodied tyrannosauroids, which evolved prior to Tyrannosauridae. We here present the first CT data for one of these species, *Bistahieversor sealeyi* from New Mexico. *Bistahieversor* had a nearly identical brain and sinus system as tyrannosaurids like *Tyrannosaurus*, including a large brain, large olfactory bulbs, reduced cerebral hemispheres and optic lobes, a small tab-like flocculus, long and straight cochlear ducts, and voluminous sinuses that include a supraoccipital recess, subcondyral sinus, and an anterior tympanic recess that exits the braincase via a prootic fossa. When characters are plotted onto tyrannosauroid phylogeny, there is a two-stage sequence in which features of the tyrannosaurid-style brain evolved first (in smaller, non-tyrannosaurid species like *Timurlengia*), followed by features of the tyrannosaurid-style sinuses (in the first large-bodied non-tyrannosaurid tyrannosauroids like *Bistahieversor*). This suggests that the

signature tyrannosaurid sinus system evolved in concert with large size, whereas the brain did not.

Key words: dinosaur, tyrannosaur, *Bistahieversor sealeyi*, *Tyrannosaurus rex*, sensory evolution, neuroanatomy, CT scanning

The iconic dinosaur *Tyrannosaurus rex* was the apex predator in North America at the very end of the Cretaceous Period (ca. 67-66 million years ago), and is renowned for its colossal size, bone-crushing jaws, and rapid growth rates (see review in Brusatte et al., 2010). *T. rex* is a member of a more inclusive group of large-bodied predatory dinosaurs called Tyrannosauridae, which were the top predators across North America and Asia during the final ca. 15-20 million years of the Cretaceous. The tyrannosaurids, in turn, were part of an even more expansive clade called Tyrannosauroidae, which originated in the Middle Jurassic (ca. 170 million years ago) as human-sized hunters and persisted at small-to-medium body sizes for most of their history before their acquisition of large size and top predator status (Brusatte et al., 2010; Brusatte and Carr, 2016 and references therein).

Tyrannosaurus rex and other tyrannosaurids were remarkable predators, because they combined brawn with high intelligence and advanced senses (Witmer and Ridgely, 2009). They had large brains compared to many other dinosaurs, sharp senses of smell and hearing, and an expansive network of endocranial sinuses that may have been related to their sensory abilities and/or an adaptation for weight saving. This ‘tyrannosaurid-style’ neurosensory and sinus system has been documented in many members of the clade using x-ray computed tomography (CT) scanning, including *Alioramus* (Bever et al., 2011, 2013), *Gorgosaurus* (Witmer and Ridgely, 2009), and *Tyrannosaurus* (Brochu, 2000, 2003; Witmer and Ridgely, 2009; Hurlburt et al., 2013). Recent CT studies have also examined smaller and more basal

non-tyrannosaurid tyrannosauroids, showing that the very oldest and tiniest tyrannosauroids like *Dilong* had brains and sensory systems that were much more similar to other coelurosaurs than to giant tyrannosaurids (Kundrát et al., 2018). Somewhat larger species intermediate between the smallest and largest tyrannosauroids, like *Timurlengia*, had developed some, but not all, of the signature features of the tyrannosaurid-style brain, but lacked many of the features of the elaborated tyrannosaurid-style sinus system (Brusatte et al., 2016). This suggests that key features of the tyrannosaurid brain evolved before their sinuses expanded, and might indicate that the larger sinuses evolved in concert with large body size.

These hypotheses are difficult to test, however, because there is a gap in our understanding of tyrannosauroid neurosensory and sinus systems. In between the oldest, smallest tyrannosauroids and the largest, latest-surviving tyrannosaurids is a grade of large-bodied tyrannosauroids outside of the Tyrannosauridae clade, including *Appalachiosaurus* and *Bistahieversor* (Brusatte et al., 2010; Brusatte and Carr, 2016; Carr et al., 2017). These were the first tyrannosauroids to obtain enormous body sizes (ca. >1 tons; the basal, Early Cretaceous *Yutyranus* convergently evolved large size). Unfortunately, we know little about their brains, sensory systems, and sinuses, because the requisite braincase bones are not preserved in *Appalachiosaurus* (Carr et al., 2005), and because the more complete and better preserved *Bistahieversor* has been the subject of only very brief description (Carr and Williamson, 2010). The salient question is whether these first large-bodied, non-tyrannosaurid tyrannosauroids had brain and sinuses systems that were very similar to tyrannosaurids, or whether they had still not developed a complete tyrannosaurid-style system despite their large body sizes.

We here provide the first x-ray computed tomography data for *Bistahieversor*, which allow us to describe its brain, sensory systems, and endocranial sinuses in detail. Our new

datasets include CT scans for both the adult holotype of *Bistahieversor* (NMMNH P-27469), which is known from a nearly complete skull, and a subadult specimen (NMMNH P-25049) that is known from partial braincase material. The scans clearly show that *Bistahieversor* has a tyrannosaurid-style neurosensory and sinus system, which is nearly identical to that of tyrannosaurids like *Alioramus*, *Gorgosaurus*, and *Tyrannosaurus*. This supports the hypotheses that the tyrannosaurid-style brain evolved before the sinuses were elaborated, that the large sinuses developed alongside large body size, and that the tyrannosaurid-style bauplan was present before the evolutionary appearance of Tyrannosauridae.

MATERIALS AND METHODS

Fossil Specimens

This study is based on two specimens. The first is the holotype skull of *Bistahieversor sealeyi* (NMMNH P-27469), which is part of a semi-articulated partial skeleton collected from the upper Campanian (Upper Cretaceous) Hunter wash Member of the Kirtland Formation in the Bisti/De-na-zin Wilderness Area of northwestern New Mexico (Figs. 1-8). The specimen was briefly described by Carr and Williamson (2010). The skull is nearly complete and its bones are articulated. However, the right side is crushed dorsomedially and the occipital region is crushed mediolaterally, distortion that affects the resolution, symmetry, volume, and completeness of the digital endocasts presented here. The second is a subadult specimen (NMMNH P-25049) that includes disarticulated and articulated portions of the skull. The portion of the braincase that was scanned using x-ray CT includes most of the right lateral wall of the braincase, consisting of the articulated and fused prootic, basisphenoid, and exoccipital-opisthotic (Figs. 9-10).

Bistahieversor was originally described as a large-bodied, deep-snouted tyrannosauroid, phylogenetically positioned as one of the immediate outgroups to Tyrannosauridae (Carr and Williamson, 2010). This has been corroborated by comprehensive phylogenetic analyses of Tyrannosauroida (e.g., Brusatte et al., 2010; Brusatte and Carr, 2016; Carr et al., 2017). The analysis of Loewen et al. (2013), however, nested *Bistahieversor* within Tyrannosauridae, more closely related to *T. rex* than to other tyrannosaurids like *Albertosaurus* and *Gorgosaurus*. Brusatte and Carr (2016) argued that this placement might be an artefact, with the similar deep-snouted skull shapes of *Bistahieversor* and derived tyrannosaurids (like *T. rex*) causing them to artificially group together in the analysis. We here follow the phylogenetic hypothesis that places *Bistahieversor* outside Tyrannosauridae.

X-Ray Computed Tomography and Visualization

The adult skull (NMMNH P-27469) was scanned at the Microtron Facility at Los Alamos National Laboratory, using a Bremsstrahlung source (Scanditronix M22 medical therapy source, Microtron) with 10MeV x-rays with a 0.25mm lead filter (Svensson et al., 1977). The x-ray source spot size was ~ 0.8 mm. The source-part distance was 2.8 meters and the source-detector distance was 3.3 meters for a magnification of ~ 1.18. Images were captured on a Perkin Elmer XRD 1611 digital flat panel with a detection area of 41 cm X 41 cm. Because the specimen is large, the CT scan was collected in four slightly overlapping positions from the snout to the base of the skull. The skull was packed in a specially made drum with steel ball bearings as fiducials to aid image stitching. Because the skull exceeded the width of the detector, we used a modified “half-scan” method in which the center of rotation was always in the field of view; however, the part was not always completely within the field of view. The part rotated through a full 360 degrees with 4000 views and 10 averages per view to

reduce noise. The detector panel has a pixel size of 100 x 100 μm (4096 x 4096). However for all but position #2, the detector was binned 2x2 for 200 μm pixels. Each scan took \sim 3 hours.

Data were reconstructed using a Feldkamp method (Feldkamp et al., 1984) with the Los Alamos Recon software (Smith & Hunter, Los Alamos National Laboratory Report LA-UR-09-03501). To account for the rotation of the part outside the field of view, the resulting sinograms were zero-padded and filtered before reconstruction as described in Espy et al. (Espy M. et al., Los Alamos National Laboratory Report LA-UR-17-24813).

Complementary to the x-ray CT scan, a fast neutron scan (neutron energies above 0.1 MeV) was conducted at the 60R beam line (Nelson et al., 2018) at LANSCE (Lisowski and Schoenberg, 2006). Because neutrons interact with the nucleus rather than the electronic shell, they provide fundamentally different contrast mechanisms from x-rays. Consequently, count times of several minutes per radiograph required breaking the beam time into several periods with intermittent removal of the sample. Together with the smaller field of view, stitching of the images posed significant obstacles in producing a dataset suitable for CT reconstruction. Results from this dataset will be reported in a later contribution.

The subadult partial skull (NMMNH P-25049) was scanned at the School of GeoSciences, University of Edinburgh using an instrument constructed in-house. The scan was performed at 140 keV peak energy, with 25 W target power loading and a 2mm thick Cu energy filter. The scan comprised 2000 projections each of 2 seconds exposure acquired through a full 360° rotation of the specimen. Tomographic slices were reconstructed by filtered back projection using Octopus (v 8.9) software. The voxel size of the reconstructed volume is 104.7 μm .

For each specimen, the resulting dataset of TIFF image slices was imported into Mimics 19.0 and 20.0 (Materialize N.V. 2014) at the University of Edinburgh School of

GeoSciences, for segmentation and three-dimensional reconstruction. This work was carried out by MM, under the guidance of JAS and SLB.

Standard linear, angular, curvature, and volumetric measurements of the endocast, inner ear, and associated structures were made using the measuring tools in Mimics 19.0.

Comparative Material

In describing the endocranial anatomy of *Bistahieversor*, we make comparisons to other tyrannosauroids and close outgroups with well-preserved braincases, whose sinuses and endocasts have been studied using CT data. The most important comparison taxa are the small-bodied basal tyrannosauroid *Dilong paradoxus* (Kundrát et al., 2018), the mid-sized ‘intermediate’ taxon *Timurlengia euotica* (Brusatte et al., 2016), the long-snouted tyrannosaurid *Alioramus altai* (Bever et al., 2011, 2013), and the deep-skulled tyrannosaurids *Gorgosaurus libratus* (Witmer and Ridgely, 2009) and *Tyrannosaurus rex* (Brochu, 2000; Witmer and Ridgely, 2009; Hurlburt et al., 2013). Together, these taxa span tyrannosauroid phylogeny and document the evolution of the group from small-bodied minor predators to colossal apex predators.

DESCRIPTION

Our CT-based reconstruction of the cranial endocast and sinuses of the *Bistahieversor sealeyi* holotype (NMMNH P-27469) is shown in Figures 1-8. Our reconstruction of the inner ear (endosseous labyrinth) of the subadult specimen (NMMNH P-25049) is shown in Figures 9-10. As the braincase bones of derived tyrannosaurids have been described in detail (e.g., Brochu, 2003; Currie, 2003; Bever et al., 2013), and characters related to them have been

incorporated in many phylogenetic analyses (e.g., Brusatte et al., 2010; Loewen et al., 2013; Brusatte and Carr, 2016; Carr et al., 2017), we do not exhaustively describe osteology in this paper, other than to note particularly important or unusual features.

Cranial Endocast

The reconstructed endocast is nearly complete, and consists of both olfactory bulbs and cerebral hemispheres, along with the midbrain and hindbrain regions and the pituitary fossa (Figs. 1-6). Some dural sinuses are visible on the endocast, but cranial nerves and blood vessels were difficult to observe in the CT slices, and thus were not reconstructed. The endocranial cavity is minimally distorted, so the endocast is nearly symmetrical and its measurements should be accurate. As in most other dinosaurs, the endocast does not exactly reflect the morphology of the brain; this is because, in life, the brain would not have completely filled the endocranial cavity, which also included dural tissue. It is likely, however, that the anterior part of the endocast more faithfully records the shape of the forebrain than the middle and posterior parts reflect the shapes of the mid- and hindbrain (Sedlmayer, 2002; Witmer and Ridgely, 2009; Bever et al., 2013; Hurlburt et al., 2013). This is because there are extensive dural sinuses in the mid- and hindbrain regions, but these are absent or minimal in the forebrain.

The endocast measures 236.19 mm at its maximum length and 58.58 mm at its greatest width. Its narrowest width is 37.59 mm, where the endocast constricts posterior to the olfactory bulbs. The deepest point of the endocast is 106.26 mm, which includes the pituitary fossa. The volume of the endocast is 362.21 cm³.

The endocast is long, shallow, and tubular, with only a slight midbrain flexure (Fig. 5). This distinctive shape is also seen in large-bodied tyrannosaurids, including *Alioramus*

(Bever et al., 2011, 2013), *Gorgosaurus* (Witmer and Ridgely, 2009), *Tarbosaurus* (Saveliev and Alifanov, 2007), and *Tyrannosaurus* (Brochu 2000; Witmer and Ridgely, 2009). It is also present in the intermediate-sized *Timurlengia* (Brusatte et al., 2016). In contrast, the basal tyrannosauroid *Dilong* has an anteroposteriorly shorter, dorsoventrally deeper, and more S-shaped endocast, which is similar to the condition in outgroups, including close coelurosaurian relatives of tyrannosauroids (e.g., Balanoff et al., 2009, 2013; Norell et al., 2009) and more distantly related non-coelurosaurian theropods (e.g., Larsson, 2001; Brusatte and Sereno, 2007; Sampson and Witmer, 2007; Witmer and Ridgely, 2009).

The olfactory bulbs constitute the most anterior portion of the endocast (Figs. 5, 7, ofb). The left bulb is complete, but the right is missing a small portion anterolaterally. The large size of the olfactory bulbs is one of the most noticeable features of the endocast. At its maximum dimensions, an individual bulb measures 71.63 mm long anteroposteriorly, and 71.74 mm deep dorsoventrally, and the conjoined bulbs measure 90.2 mm wide mediolaterally. The conjoined bulbs have a volume of 90.55 cm³, which is ca. 25% of the volume of the entire endocast. The bulbs are broad, wide, and deep. In dorsal view, they are the widest region of the endocast, which is also the case in some specimens of *Tyrannosaurus rex* (Kundrát et al., 2018:fig. 5D). Other tyrannosaurid specimens have large olfactory bulbs that approach the width of the cerebrum, which is the widest region of these endocasts (Witmer and Ridgely, 2009:Fig. 3; Bever et al., 2011, 2013). In *Dilong*, by contrast, the reconstructed olfactory bulbs are considerably smaller (Zelenitsky et al., 2009; Kundrát et al., 2018), whereas in *Timurlengia* they are not preserved (Brusatte et al., 2016). Comparative studies have previously shown that the olfactory bulbs of tyrannosaurids are abnormally large among theropods (Zelenitsky et al., 2009, 2011), and this is the case in *Bistahieversor* as well.

The olfactory bulbs are bounded ventrally by the orbitosphenoid and sphenethmoid, and the left and right bulbs are separated on the midline by an ossified mesethmoid (Figs. 7-8, oms), as is the case in other large-bodied tyrannosauroids (Ali et al., 2008).

The olfactory bulbs are followed posteriorly by an anteroposteriorly short and mediolaterally narrow olfactory tract (Figs. 5, 7, oft), which joins the cerebrum. The cerebrum (Fig. 5, cer), which consists of left and right hemispheres, is wider than the midbrain and forebrain regions, and thus is the most laterally expanded portion of the endocast save for the olfactory bulbs. A slight midline peak projects dorsally from cerebrum in lateral view, similar to the condition in tyrannosaurids (Brochu, 2000; Saveliev and Alifanov, 2007; Witmer and Ridgely, 2009; Bever et al., 2011, 2013), but differing from the more broadly rounded dorsal margin of the cerebrum in *Dilong* (Kundrát et al., 2018). The latter morphology is likely related to the more enlarged cerebral hemispheres of *Dilong*, which are expanded posterolaterally compared to those of tyrannosaurids and *Bistahieversor* (Kundrát et al., 2018).

Ventral to the cerebrum, the pituitary fossa is an elongate, finger-like structure that extends posteroventrally (Figs. 5, 7, ptf). The carotid artery would have entered the fossa ventrally. The contrast in the CT slices is not clear enough to distinguish between the fossa itself and the artery; thus, the structure we reconstruct as the fossa may include a substantial part of the artery tract. A similarly elongate pituitary fossa is present in most tyrannosaurids (Brochu, 2000; Witmer and Ridgely, 2009), but is seemingly stouter and thicker in *Alioramus* (Bever et al., 2011, 2013). *Dilong*, however, may lack a well-defined pituitary fossa (Kundrát et al., 2018). In the *Bistahieversor* skull, the fossa is positioned slightly left of center of the sagittal axis of the endocast, likely due to slight distortion in this region of the skull.

The optic lobes of the midbrain are not apparent on the endocast. They almost certainly were present in life, but might not be observable due to the poor contrast of this part

of the scan and/or because they did not leave clear impressions on the surrounding endocranial bones. Alternatively, they may have been present, but not developed as discrete structures. There is considerable variability among this feature in tyrannosauroids. No large-bodied tyrannosaurids have particularly large and distinctive optic lobes, although some specimens have small swellings on the lateral wall of the endocast, posteroventral to the cerebral hemispheres (e.g., Osborn, 1912; Maleev, 1965; Witmer and Ridgely, 2009; Bever et al., 2011, 2013). Other tyrannosaurid specimens, however, exhibit no clear trace of optic lobes (e.g., Brochu, 2000; Witmer and Ridgely, 2009). There is extensive intraspecific variation—for example, some specimens of *Tyrannosaurus rex* possess clear lobes whereas others do not, and this may in part be related to ontogeny, with more discrete lobes in younger individuals (e.g., Witmer and Ridgely, 2009; Bever et al., 2011). *Dilong*, on the contrary, has enlarged optic lobes that project laterally as distinct bulges, posterior to the cerebral hemisphere (Kundrát et al., 2018). This is similar to the condition in many other coelurosaurs (e.g., Domínguez Alonso et al., 2004; Kundrát, 2007), and indeed, it has been noted that the optic lobes become progressively larger and positioned further laterally on the line to birds (e.g., Witmer and Ridgely, 2009; Bever et al., 2011; Balanoff et al., 2013).

Posterior to the cerebrum, the dorsal surface of the endocast (above the hindbrain) is marked by a pronounced midbrain dural peak (Fig. 5, dp), which is probably related to the transverse and longitudinal venous sinuses (Witmer and Ridgely, 2009; Bever et al., 2013). This is an often-noted feature of tyrannosaurids, first depicted in Osborn's (1912) description of the *Tyrannosaurus* brain, and subsequently noted in *Alioramus* (Bever et al., 2011), *Gorgosaurus* (Witmer and Ridgely, 2009); *Tarbosaurus* (Saveliev and Alifanov, 2007), and additional specimens of *Tyrannosaurus* (Brochu, 2000; Witmer and Ridgely, 2009). It was recently described in *Timurlengia* (Brusatte et al., 2016), but is absent in *Dilong* (Kundrát et al., 2018). This peak is the most prominent feature on the dorsal surface of the endocast in

Bistahieversor, and it is especially pronounced even when compared to other large-bodied tyrannosauroids. Posteriorly, a large posterior middle cerebral vein system (Figs., 5, 7, pmcv) extends posterodorsally from the dural peak, similar to the condition in *Alioramus* (Bever et al., 2011), *Gorgosaurus* (Witmer and Ridgely, 2009), and *Tyrannosaurus* (Brochu, 2000; Witmer and Ridgely, 2009).

Posterior to the midbrain and dural peak, the endocast narrows in the region of the hindbrain. The flocculus of the cerebellum is the most notable feature of this part of the endocast. It is tabular in morphology, extending from the lateral surface of the cerebellum as a small stump that would have barely, if at all, crossed the plane of the anterior semicircular canal. A similar condition is present in *Timurlengia* (Brusatte et al., 2016) and tyrannosaurids (*Alioramus*: Bever et al. 2011, 2013; *Gorgosaurus*: Witmer and Ridgely, 2009; *Tarbosaurus*: Saveliev and Alifanov, 2007; *Tyrannosaurus*: Witmer and Ridgely, 2009), along with noncoelurosaurian outgroups (Witmer and Ridgely, 2009). The flocculus of *Dilong* is remarkably different: it is a long stalk that projects far laterally from the endocast and extends as far posteriorly as the posterior semicircular canal (Kundrát et al., 2018). This morphology is similar to the larger, more tubular flocculi of most other coelurosaurs (Witmer and Ridgely, 2009). In making these comparisons, we acknowledge that what appears on the endocast is a cast of the floccular recess, and the actual flocculus of the brain may not have closely matched the shape of the recess.

Inner Ear

The inner ear (endosseous labyrinth) region of the adult holotype specimen of *Bistahieversor* (NMMNH P-27469) is not clearly visible in the CT slice data, and thus we were unable to reconstruct it. However, much of the left endosseous labyrinth of the subadult referred

specimen (NMMNH P-25049) is observable, including details of the vestibular system (semicircular canals and associated structures) and cochlear duct, and thus we base our description on this specimen (Figs. 9-10). Because the braincase is damaged, dorsal parts of the anterior and posterior semicircular canals (Fig. 10, asc, psc) are missing, as well as the majority of the crus commune. The lateral semicircular canal (Fig. 10, lsc) also has a crack running through its middle, and hence is not a closed structure. Otherwise, details of the inner ear are well preserved.

The endosseous labyrinth, in general, is similar to that in other large-bodied tyrannosauroids (Witmer and Ridgely, 2009). The anterior and posterior semicircular canals are slightly curved, thin, and elongated. The anterior canal seems to be the longest, like in theropods typically, and anteriorly expanded similar to other coelurosaurs (Witmer and Ridgely, 2009; Knoll et al., 2012; Brusatte et al., 2016). The posterior and lateral semicircular canals are relatively circular, and similar in size and shape to those of other large tyrannosauroids (Witmer and Ridgely, 2009). All of the semicircular canals are essentially perpendicular to each other. The canals are thin and delicate, like in tyrannosaurids (Witmer and Ridgely, 2009; Bever et al., 2011, 2013), but unlike the thickened, robust canals that are autapomorphic for the mid-sized tyrannosauroid *Timurlengia* (Brusatte et al., 2016).

The crus commune (Fig. 10, cc) exhibits similar characteristics to many other dinosaurs. As in other large-bodied tyrannosauroids, the common crus slightly twists (Witmer and Ridgely, 2009), which is similar to sauropod dinosaurs, in which it is slightly curved (Knoll et al., 2012). The vestibule (Fig. 10, ve) is dorsoventrally shallow and hence does not extend over the lateral canal, as is the general case in archosaurs (Witmer and Ridgely, 2009). The endolymphatic duct is not observable in the specimen; however, it most likely entered at the base of the common crus as in other tetrapods (Witmer and Ridgely, 2009).

The cochlear duct (lagena) extends from the vestibule in an anteroventral direction (Fig. 10, cd). It is long and slender, which indicates a long basilar membrane. A long duct is a notable characteristic of all tyrannosauroids whose inner ears have been studied, including the mid-sized *Timurlengia* (Brusatte et al., 2016), the long-snouted tyrannosaurid *Alioramus* (Bever et al., 2011, 2013), and deep-snouted, large-bodied tyrannosaurids like *Tyrannosaurus* (Witmer and Ridgely, 2009). This would have increased sensitivity to lower-frequency sounds in these dinosaurs (Manley, 1990; Walsh et al., 2009). Furthermore, the cochlear duct is straight. This is also the case in other tyrannosauroids, but differs from the curved morphology of some other coelurosaurs (Witmer and Ridgely, 2009; Bever et al., 2013; Brusatte et al., 2016). Unfortunately, the cochlear duct of the small-bodied basal tyrannosauroid *Dilong* is not observable in CT data (Kundrát et al., 2018), so it is unclear whether the smallest, earliest tyrannosauroids had the same autapomorphic long, straight cochlear duct as the later, larger-bodied taxa.

Both the fenestra vestibuli and the fenestra cochleae (and the canals leading from them) are not as clearly visible in the CT slices as in other tyrannosauroids (Witmer and Ridgely, 2009). Additionally, the columella and columellar canal are not preserved, or at least not visible, in this specimen.

It is unclear how the inner ear of the subadult would have compared to the inner ear of an adult *Bistahieversor*. Minor ontogenetic changes in labyrinth morphology have been described in some dinosaurs. In the early sauropodomorph *Massospondylus carinatus*, the labyrinth became larger during ontogeny, and its geometry changed slightly (mostly in the angle and position of the crus commune and the degree of curvature of the posterior canal) (Neenan et al., 2018). No significant changes in labyrinth morphology, however, occurred during ontogeny in the ornithischian *Dysalotosaurus lettowvorbecki* (Lautenschlager and Hübner, 2013).

Pneumatic Sinuses of the Braincase

The braincase bones of *Bistahieversor* are heavily pneumatized, with several air-filled sinuses surrounding the brain, ear, and other endocranial structures. It has long been recognized that an extensive sinus network extends through the braincase of large-bodied tyrannosauroids (e.g., Russell, 1970; Bakker et al., 1988; Molnar, 1991; Brochu, 2003; Currie, 2003; Bever et al., 2011, 2013), and this has been figured and described in meticulous detail for *Tyrannosaurus* (Witmer and Ridgely, 2009). We here follow the terminology of Witmer and Ridgely (2009), as the sinus network of *Bistahieversor* is very similar to that of *Tyrannosaurus*.

The sinuses of *Bistahieversor* are illustrated in Figures 1-4 and 6. Note that, in some cases, different sinuses communicate or merge with each other, making their boundaries difficult to trace in CT data. This is particularly true of the subcondylar recess (depicted in red in Fig. 2-4, 6). Although we illustrate an expansive subcondylar recess, some of this is likely part of the adjoining anterior tympanic recess. Similar issues with recognizing the boundaries between the sinuses in *Tyrannosaurus* were noted by Witmer and Ridgely (2009).

As in other large-bodied tyrannosauroids, there are three sinus ‘families’ in the endocranial region of *Bistahieversor*: 1) the tympanic system, which communicates with the middle ear; 2) the median pharyngeal system, which probably derives from the pharynx; and 3) the subcondylar system, whose source is unclear (Witmer and Ridgely, 2009).

The most extensive sinus ‘family’ is the tympanic system, which consists of anterior and posterior tympanic recesses (Figs. 1-4, 6, atr, ptr), along with a supraoccipital sinus that communicates with the posterior tympanic recess (Figs. 1-3, 6, sos). The dorsal tympanic recess is absent on the lateral surface of the prootic (Fig. 3), as is the case in tyrannosaurids

(Witmer and Ridgely, 2009; Bever et al., 2013; Brusatte, 2013). This sinus is present, however, in many coelurosaurian outgroups to tyrannosauroids (e.g., Witmer, 1997; Makovicky and Norell, 1998; Norell et al., 2004; Rauhut, 2004) and the small-bodied basal tyrannosauroid *Guanlong* (IVPP V14531; Bever et al., 2013; Brusatte, 2013). It is unclear if the small-bodied tyrannosauroid *Dilong* (Bever et al., 2013; Brusatte et al., 2014) or the mid-sized *Timurlengia* possessed this sinus (Brusatte et al., 2016).

The anterior tympanic recess invades much of the basisphenoid and prootic, and internally fills the notch between the pituitary fossa and the remainder of the brain endocast. It is delimited anteriorly and dorsally by the preotic pendant (Fig. 9, prp), a structure on the lateral surface of the braincase. Abutting the preotic pendant posteriorly is a large opening on the lateral surface of the prootic, called the prootic fossa (Fig. 3, 4, 9 pro fos), which leads into the anterior tympanic recess. The prootic fossa, which was described in detail by Bever et al. (2013), is a characteristic feature of large-bodied tyrannosauroids, as it is also known in *Albertosaurus*, *Alioramus*, *Daspletosaurus*, *Gorgosaurus*, *Tarbosaurus*, *Teratophoneus*, and *Tarbosaurus*. In the best-preserved specimens of these taxa, such as the *Alioramus* braincase described by Bever et al. (2013), branches of the trigeminal and facial nerves can also be seen passing through this fossa. As far as is known, the prootic fossa is not present in any non-tyrannosauroid theropods, and it is also absent in the mid-sized tyrannosauroid *Timurlengia* (Brusatte et al., 2016), which has various openings for the facial and trigeminal nerves and lacks any external pneumatic openings leading into the prootic (although it does have an anterior tympanic recess). The morphology of this region of the braincase is unclear, however, in the small-bodied basal tyrannosauroids *Dilong* and *Guanlong* (Bever et al., 2013).

The anterior tympanic recess (Figs. 1-4, 6, atr) is particularly small, but this is likely an artefact because the boundary between it and the adjoining subcondylar recess is difficult

to trace. The size and extent of the anterior tympanic recess is similar to that in *Tyrannosaurus* and most other tyrannosaurids (Witmer and Ridgely, 2009), but is smaller than the enlarged recess of *Alioramus* (Bever et al., 2011, 2013). The anterior tympanic recess of *Bistahieversor* is notably smaller than the posterior tympanic recess, and it appears to be asymmetrical, deeper on the right side of the skull than the left, although this may be in part due to deformation of the specimen. The left and right portions of the recess communicate on the midline, underneath the brain. The posterior region of the anterior tympanic recess communicates slightly with the posterior tympanic recess.

The posterior tympanic recess (Figs. 1-4, 6, ptr) is the largest sinus of the braincase, as in other large-bodied tyrannosauroids (Witmer and Ridgely, 2009). This recess fills much of the interior of the paroccipital processes of the exoccipital-opisthotic, and also appears to extend into the prootic, where it makes contact with the anterior tympanic recess (Fig. 4). In this portion of the braincase, the posterior tympanic recess envelops the posterior portion of the brain and the inner ear. The recess fills most of the paroccipital process, as in *Gorgosaurus* (Witmer and Ridgely, 2009), not only the dorsal portion of the process like in *Alioramus* (Bever et al., 2013) and *Tyrannosaurus* (Witmer and Ridgely, 2009). Although only the bases of the paroccipital processes are preserved in *Timurlengia*, these are completely hollowed out by the posterior tympanic recess, similar to the morphology in *Bistahieversor* and *Gorgosaurus* (Brusatte et al., 2016). In *Bistahieversor*, the proximal portion of the recess, at the base of the paroccipital process before the process extends laterally, seems to communicate with the subcondylar recess (Fig. 4). Similar communication has been noted in juvenile *Tyrannosaurus* (Witmer and Ridgely, 2009) and subadult *Alioramus* (Bever et al., 2013), but is not present in adult *Gorgosaurus* and *Tyrannosaurus* (Witmer and Ridgely, 2009). The recess opens externally onto the posterior surface of the

braincase through a foramen in the base of the paroccipital process (Fig. 3D), as in tyrannosaurids (Bever et al., 2013).

The left and right posterior tympanic recesses make contact with each other on the midline, above the posterior end of the brain. Here, they invade the supraoccipital, forming the supraoccipital sinus (Figs. 1-3, 6, sos). A pneumatized supraoccipital is present in tyrannosaurids, and has been well described in *Tyrannosaurus* (Brochu, 2003; Witmer and Ridgely, 2009) and *Alioramus* (Bever et al., 2013). It is absent, however, in *Timurlengia*, which has an internally solid supraoccipital, and thus separate left and right posterior tympanic recesses on each side of the brain (Brusatte et al., 2016). In *Bistahieversor*, the supraoccipital sinus (if described as if it is a single midline structure) fills most of the supraoccipital and is dorsoventrally ovoid in shape. It is angled, such that it follows the sloping contours of the posterior end of the brain endocast.

The second major sinus ‘family’, the median pharyngeal system, consists of the basisphenoid and subsellar recesses (Figs. 1-4, 6, bsr, ssr), both of which are single midline structures underneath the brain. The two recesses abut each other, with basisphenoid recess positioned posterior to the subsellar recess. They are separated, at most, by a thin lamina of bone (Fig. 3F, I).

The basisphenoid recess (Figs. 1-4, 6, bsr) fills the space between the basiptyergoid processes and basal tubera, and opens posteroventrally. The internal details of this recess are difficult to describe, because the CT slices have low contrast in this region. The external opening of the basisphenoid recess is ovoid in ventral view (Fig. 3C), like in tyrannosaurids, but unlike the more funnel-like opening of the basal tyrannosauroids *Guanlong* and *Proceratosaurus*, which expands in width posteriorly (Brusatte et al., 2010: character 160; Brusatte & Carr, 2016: character 160). *Bistahieversor* does not have the extreme condition of *Tarbosaurus*, *Teratophoneus*, and *Tyrannosaurus*, in which the basicranium is so

anteroposteriorly shortened that the basiptyergoid processes lie nearly underneath the basal tubera, thus reducing the size of the external opening of the basisphenoid recess and making it widely visible in posterior view (Brusatte et al., 2010: character 158; Carr and Williamson, 2010; Brusatte & Carr, 2016: character 158). Instead, the recess opens posteroventrally and is visible in both ventral and posterior views, as in other tyrannosaurids.

The subsellar recess (Figs. 1-4, 6, *ssr*) excavates the ventral surface of parasphenoid, including nearly all of the cultriform process (Fig. 4, *cp*). The condition in *Bistahieversor* is most similar to that of *Alioramus*, in that the recess extensively invades the cultriform process (Bever et al., 2013). The recess invades much, but not all, of the cultriform process in *Gorgosaurus* and juvenile *Tyrannosaurus*, but only the base of the process in adult *Tyrannosaurus* (Witmer and Ridgely, 2009).

The third and final sinus ‘family’ is the subcondylar recess (Figs. 1-4, 6, *scs*). This recess invades the basioccipital and part of the exoccipital-opisthotic, ventral and lateral to the occipital condyle. It appears to extend into part of the basisphenoid, where it is difficult to distinguish from the anterior tympanic recess (see above). In *Tyrannosaurus* the recess is divided into lateral and medial portions on each side of the foramen magnum (Witmer and Ridgely, 2009), but it is unclear if this is the case in *Bistahieversor*, because of the low resolution of the scan slices in this region. The recess communicates with the exterior of the braincase via apertures within a fossa on the basal tuber, below the occipital condyle (Fig. 3, *scr*). A similar system—with external apertures leading into a subcondylar recess—is present in tyrannosaurids, as has been described using CT data in *Alioramus* (Bever et al., 2011, 2013), *Gorgosaurus* (Witmer and Ridgely, 2009), and *Tyrannosaurus* (Witmer and Ridgely, 2009). Both external apertures and an internal recess are absent in *Timurlengia*, as confirmed by x-ray CT data (Brusatte et al., 2016).

The condition is less straightforward in other tyrannosauroids. The basal tyrannosauroids *Guanlong* (IVPP V14531), *Proceratosaurus* (Rauhut et al., 2010), *Dilong* (IVPP V14243), and *Xiongguanlong* (Li et al., 2010) have what appear to be small openings on their basal tubera, but whether these lead into a recess has yet to be corroborated with x-ray CT data. Because of this, the phylogenetic analyses of Brusatte et al. (2010: character 156) and Brusatte and Carr (2016: Character 156) recognize two conditions: an absent or shallow condition, which is present in basal tyrannosauroids and *Timurlengia*, and a deep, funnel-like condition which characterizes tyrannosaurids. *Bistahieversor* has this latter condition. A further caveat, however, is that the most derived tyrannosaurines (*Tarbosaurus* and *Tyrannosaurus*) have small openings within a shallow fossa, but have an enlarged internal recess within the basal tubera. Thus, the morphology of the subcondylar recess, and its external expression on the braincase, appears to be highly variable in tyrannosauroids (see discussion in Bever et al., 2013).

The subcondylar and anterior tympanic recesses are broadly confluent, which is why they are difficult to distinguish from each other. This is also the case in *Alioramus* (Bever et al., 2013) and juvenile *Tyrannosaurus* (Witmer and Ridgely, 2009), but not *Gorgosaurus* and adult *Tyrannosaurus* (Witmer and Ridgely, 2009). As described above, there is also communication between the subcondylar and posterior tympanic recesses in *Bistahieversor*; this is variable within other tyrannosauroids (Witmer and Ridgely, 2009; Bever et al., 2013).

DISCUSSION

The CT data for *Bistahieversor sealeyi* provide important new information on the brain, inner ear, and cranial sinuses of tyrannosauroid dinosaurs. As *Bistahieversor* is one of the phylogenetically most basal large-bodied, deep-skulled tyrannosauroids, it helps to clarify

how the neurosensory and sinus systems of these dinosaurs changed as they evolved from human-sized ancestors to colossal apex predators like *Tyrannosaurus rex* (Fig. 11).

Neurosensory and Sinus Evolution in Tyrannosauroids

The new x-ray CT data for *Bistahieversor* fill an important gap in our knowledge of tyrannosauroid brain, ear, and sinus evolution. Previous CT-based studies have revealed important details on the internal cranial anatomy of the largest, last-surviving tyrannosaurids like *Alioramus* (Bever et al., 2011, 2013), *Gorgosaurus* (Witmer and Ridgely, 2009), and *Tyrannosaurus* (Brochu 2000, 2003; Witmer and Ridgely, 2009; Hurlburt et al., 2013), along with smaller basal species like *Dilong* (Kundrát et al., 2018) and *Timurlengia* (Brusatte et al., 2016). What has been missing, however, is information on the first large-bodied tyrannosauroids, which fall in between the basal species and the tyrannosaurids.

Bistahieversor provides the first glimpse at the neurosensory and sinus systems of such a species: one of the first tyrannosauroids to develop enormous size. It thus slots into a phylogenetic sequence that illuminates the acquisition and modification of key brain, ear, and sinus characters in tyrannosauroids (Fig. 11).

The most striking finding of our study is this: the neurosensory and sinus systems of *Bistahieversor* are extremely similar to those of *Tyrannosaurus rex* and other tyrannosaurids. *Bistahieversor* has a tubular brain that has lost the deeper, S-shaped morphology of its ancestors, enormous olfactory bulbs, reduced cerebral hemispheres marked by a midline cerebral peak, reduced optic lobes, a small and tab-like flocculus, a prominent hindbrain dural peak, and a long and straight cochlear duct. Its sinus system has a supraoccipital sinus (formed by extensions of the posterior tympanic recess), a large subcondylar recess, and a prootic fossa on the lateral surface of the prootic that includes both pneumatic and vascular

openings, but does not have a dorsal tympanic recess on the lateral surface of the prootic. All of these features are seen in the largest, most-derived tyrannosaurids like *Alioramus*, *Gorgosaurus*, and *Tyrannosaurus*. Essentially, in every major aspect, *Bistahieversor* has a tyrannosaurid-style brain, ear, and sinus system even though it is phylogenetically placed outside of Tyrannosauridae. Thus, this tyrannosaurid-style neurosensory and sinus system was already in place before the origin of Tyrannosauridae.

Some features of the tyrannosaurid-style brain and sinus system are known to have evolved earlier, as they are present in the horse-sized ‘mid-grade’ tyrannosauroid *Timurlengia* (Brusatte et al., 2016). This observation led Brusatte et al. (2016) to propose that tyrannosauroids evolved greater intelligence and sensory abilities before large body size. There are some features of the tyrannosaurid-style system, however, that *Timurlengia* does not possess, like a supraoccipital sinus, subcondylar recess, and prootic fossa. *Bistahieversor* has these features, and thus has a more ‘tyrannosaurid-like’ system than *Timurlengia*.

When all of the aforementioned features are mapped onto tyrannosauroid phylogeny, an interesting pattern emerges (Fig. 11). Features of the tyrannosaurid-style system appear to have evolved in two stages. The first is on the lineage leading to *Timurlengia* and more derived tyrannosauroids, which developed a tubular endocast with a large dural peak but a reduced flocculus. Then, in tyrannosauroids more derived than *Timurlengia*—in other words, the clade including *Bistahieversor* and tyrannosaurids—the supraoccipital sinus, subcondylar recess, and prootic fossa appeared. It seems, therefore, that the signature features of the tyrannosaurid brain developed before the signature features of their sinus system. The brain changes were occurring in small-to-mid-sized tyrannosauroids, whereas the sinus changes were occurring in only the very largest tyrannosauroids.

This might suggest that the changes to the sinus system, which mostly involved the development of new and larger sinuses that communicate more readily with the external

braincase, were evolving in concert with large body size. Perhaps they provided weight reduction as tyrannosauroid skulls got larger, or in the case of the tympanic sinuses, helped tyrannosauroids maintain their keen hearing at larger body sizes. These hypotheses were proposed by Brusatte et al. (2016), based on the absence of the enlarged sinuses in *Timurlengia*, which otherwise had a tyrannosaurid-style brain and ear. Alternatively, enlarged sinuses in larger-bodied tyrannosauroids may have provided increased surface area for evaporative cooling, which would become more important as tyrannosauroids got larger (e.g., Witmer and Ridgely, 2009; Porter and Witmer, 2019), or opportunistically expanded inside the cranial bones as the skull got larger (e.g., Witmer, 1997a,b; Rae and Koppe, 2008; Zollikofer and Weissman, 2008). However, these types of hypotheses could not be adequately tested by Brusatte et al. (2016), because no large-bodied non-tyrannosaurid (filling the gap between basal tyrannosauroids and tyrannosaurids—see Fig. 11) had been studied using CT data. It remained unknown: did the first large-bodied tyrannosauroids outside of Tyrannosauridae have enlarged sinuses or not? *Bistahieversor* now answers that question, in the affirmative. Thus, based on our current understanding of tyrannosauroid phylogeny, the expansive sinuses appeared with the evolution of large body size, not at the Tyrannosauridae node.

The two-stage model of ‘brain before sinus’ evolution is dependent on our current understanding of tyrannosauroid phylogeny, and is based on the still-limited sample of tyrannosauroids subjected to CT scanning. Thus, it is liable to change with new discoveries, and it may be that the evolution of brain and sinus features was more gradual rather than pulsed. Additionally, there are several features of the tyrannosaurid-style brain and ear that clearly emerged at some point in tyrannosauroid evolution, but cannot be confidently optimized onto the phylogeny because of missing data in key taxa (particularly *Timurlengia*, which is known from partial braincase material) (Fig. 11). For example, enlarged olfactory

bulbs, reduced cerebral hemispheres, and reduced optic lobes characterize *Bistahieversor* and tyrannosaurids, whereas smaller olfactory bulbs and larger cerebral hemispheres and optic lobes are present in the basal tyrannosauroid *Dilong*. Because these features are unobservable in *Timurlengia*, it is not clear whether they evolved on the line to *Timurlengia* and more derived tyrannosauroids (with the other major features of the tyrannosaurid-style brain) or after *Timurlengia* had split (and thus after the tubular brain with a large dural peak and reduced flocculus developed). Furthermore, *Timurlengia*, *Bistahieversor*, and tyrannosaurids all share an elongate, straight cochlear duct. However, as the cochlear duct is not observable in *Dilong*, it is not clear whether the tyrannosaurid-style cochlear duct originated on the line to *Timurlengia* and more derived tyrannosauroids, or whether it actually characterizes all tyrannosauroids, even the smallest and most primitive species like *Dilong*. These questions can only be addressed through more fossil discoveries and by subjecting more tyrannosauroid skulls (particularly non-tyrannosaurid species like *Guanlong*, *Proceratosaurus*, *Xiongguanlong*, and *Yutyranus*) to CT scanning.

Ontogenetic Changes in Tyrannosauroid Neurosensory and Sinus Systems

The specimens we describe here represent different ontogenetic stages of *Bistahieversor*. Large-bodied tyrannosaurids underwent extensive changes in skull shape, proportions, and osteology as they matured (e.g., Carr, 1999; Carr and Williamson, 2004). Less is known, however, about how internal endocranial features changed during ontogeny (Witmer and Ridgely, 2009, 2010). Unfortunately our specimens do not provide much new evidence in this regard, as the braincase bones of the subadult *Bistahieversor* are limited.

We predict that the following differences will be seen in the endocranium between juvenile and adult *Bistahieversor*, based on the differences seen between juvenile (CMNH

7541) and adult (e.g., AMNH FARB 5117) specimens of *T. rex* that were documented by Witmer and Ridgely (2009). Note that we consider CMNH 7541 to represent a juvenile *T. rex*, following Carr (1999). In the adult, the cochlear duct would be short and wide (vs. long and thin), the lateral canal of the inner ear would extend a great distance laterally (vs. a short distance laterally), and pneumatization of the cultriform process would be limited (vs. extensive). In juvenile *Bistahieversor*, the optic lobes would be visible (vs. not visible), and the flocculus would be large (vs. small). Other ontogenetic differences will, we predict, include the presence of a prohypophyseal sinus in juveniles, which will be absent in adults; the presence of an ascending diverticulum of the anterior tympanic recess in juveniles and its absence from adults; presence of a connection between the posterior tympanic recess with the lateral subcondylar recess in juveniles, but absent from adults; and the invasive extent of the lateral subcondylar recess will be extensive in juveniles, but will barely extend into the tuberal crest in adults.

These predictions can hopefully be tested with future discoveries of better subadult skull material for *Bistahieversor*. If they hold true, then this would indicate that large-bodied tyrannosauroids outside of Tyrannosauridae exhibited similar ontogenetic trajectories in this region of the skull as tyrannosaurids.

Biology and Behavior of *Bistahieversor*

Our CT-based descriptions of the neurosensory and sinus systems help flesh out the biology of *Bistahieversor*. Based on this evidence, we can surmise that *Bistahieversor* was extremely similar to *T. rex* and other tyrannosaurids, at least in terms of intelligence and sensory abilities. Although we do not calculate an encephalization quotient (EQ) here because of difficulties in accurately estimating the body size of *Bistahieversor*, the size and shape of the

brain endocast are very similar to those of tyrannosaurids of similar body size. Thus, it is likely that *Bistahieversor* had an EQ in the same general range of those tyrannosaurids that have been studied—*Alioramus*, *Gorgosaurus*, and *Tyrannosaurus*—which measure between 1.2-2.5 depending on the equation used (Brusatte et al., 2009; Hurlburt et al., 2013). This is relatively large for a dinosaur and suggests that tyrannosaurids, generally, were intelligent animals for their time and place (see detailed discussion in Hurlburt et al., 2013). There is no evidence, however, that tyrannosaurids had mammal-like levels of intelligence, as reported in a popular account by one of us (Brusatte, 2018). This was an erroneous statement based on an improper comparison of reptile and mammalian EQ values. Because studies such as Hurlburt et al. (2013) have used reptilian equations to calculate the EQ of tyrannosaurids, whereas mammal scores are generated using different mammal-specific equations, it is not true that a similar EQ score for a tyrannosaurid and a mammal implies similar levels of intelligence (see discussion in Hurlburt et al., 2013).

Bistahieversor also shares key features with tyrannosaurids indicative of strong sensory systems. Its enlarged olfactory bulbs imply a strong sense of smell, as has been argued for *T. rex* and other tyrannosaurids (Zelenitsky et al., 2009, 2011; see also Brochu, 2000 and Witmer and Ridgely, 2009). Its long, straight cochlear duct would have imparted heightened ability to hear low frequency sounds (Manley, 1990; Walsh et al., 2009), as has been argued for tyrannosaurids (Witmer and Ridgely, 2009) and the smaller, more basal *Timurlengia* (Brusatte et al., 2016). Its elongate semicircular canals are suggestive of high agility and sophisticated gaze stabilization of the eyes during head movement, as in tyrannosaurids (Witmer and Ridgely, 2009), but perhaps not *Timurlengia*, which has peculiarly robust semicircular canals, which albeit are still quite elongated (Brusatte et al., 2016). The elongate semicircular canals of tyrannosaurids are consistent with other indicators of agility from the postcranial skeleton and musculature, described by Snively et al. (2014,

2019). The small optic lobes of *Bistahieversor* might seemingly indicate a poor sense of vision compared to other dinosaurs, but as reviewed by Witmer and Ridgely (2009), this is not a robust inference. Indeed, the partially forward facing eyes of the broad-skulled tyrannosaurids and *Bistahieversor* would have permitted some binocular vision (=overlapping visual fields from left and right eyes), which was not the case in many other predatory dinosaurs (Stevens, 2006).

In summary, *Bistahieversor* was probably similar to tyrannosaurids in many of the biological and behavioral attributes that are linked to the neurosensory systems. These animals were intelligent predators with keen hearing, olfaction, balance, and likely eyesight. Some of these sensory enhancements were established while tyrannosauroids were still small-to-mid-sized, middle-tier predators, as shown by their presence in *Timurlengia* (large brain, long cochlear duct). Others, however, may have developed later as these smaller tyrannosauroids grew to enormous sizes, and large-bodied species adapted to their new role as apex predators (e.g., large olfactory bulbs, improved agility and gaze stabilization). This is currently uncertain because of the paucity of CT data for smaller, basal tyrannosauroids. Obtaining these data should be a priority for future work.

ACKNOWLEDGEMENTS

This project stemmed from MM's MScR dissertation at the University of Edinburgh, supervised by SLB, with training provided by JAS. X-ray and neutron CT scanning of the specimens was supported by the New Mexico Consortium. SLB's CT processing lab was supported by funding from the European Research Council (ERC) under the European Union's Horizon 2020 research and innovation programme (grant agreement No 756226, ERC Starting Grant: PalM), a Leverhulme Trust Research Project Grant (RPG-2017-167,

which also supports JAS' studentship), a Marie Curie Career Integration Grant (EC 630652), a Royal Society Research Grant (RG130018), and the University of Edinburgh School of GeoSciences. This work was performed by the LANL collaborators under the auspices of the U.S. Department of Energy (DOE) under Contract No. DE-AC52-06NA25396. This work has benefitted from use of the LANSCE accelerator facility supported under DOE Contract No. DE-AC52-06NA25396. We thank Brandon Prince for assistance in preparation of NMMNH P-27469 for CT scanning. We thank Alexander Averianov, Amy Balanoff, Gabe Bever, Grant Hurlburt, Hans-Dieter Sues, and Lawrence Witmer for discussion on tyrannosauroid brains and sensory systems, and for previous collaborations that introduced SLB to the subject. We thank the US Bureau of Land Management and the Navajo Nation for permitting the excavation of the *Bistahieversor* fossils. We thank Eric Snively, an anonymous reviewer, and editor Tim Smith for their helpful comments on our manuscript.

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FIGURE CAPTIONS

Fig. 1. Right lateral views of the skull of the holotype of *Bistahieversor sealeyi* (NMMNH P-27469). A: photograph; B: CT slice displaying features of neuroanatomy; C: Three-dimensional CT-based model of the skull and inner neuroanatomy. Abbreviations: atr, anterior tympanic recess; bsr, basisphenoid recess; ec, brain endocast; ofb, olfactory bulbs; pmcv, posterior middle cerebral vein; ptr, posterior tympanic recess; scs, subcondylar recess; sos, supraoccipital sinus; ssr, subsellar recess. Scale bar represents 10 cm.

Fig. 2. Three-dimensional CT-based model of the holotype skull of *Bistahieversor sealeyi* (NMMNH P-27469), transparent with internal neurosensory and sinus structures, in: right lateral (A), left lateral (B), dorsal (C), ventral (D), posterior (E), and anterior views (F). Abbreviations: atr, anterior tympanic recess; bsr, basisphenoid recess; ec, brain endocast; pmcv, posterior middle cerebral vein; ptr, posterior tympanic recess; scs, subcondylar recess; sos, supraoccipital sinus; ssr, subsellar recess. Scale bar represents 10 cm.

Fig. 3. Three-dimensional CT-based model of the holotype skull of *Bistahieversor sealeyi* (NMMNH P-27469) in: posterior (A, D, G), right lateral oblique (B, E, H), and ventral (C, F, I) views. Each set of views includes a surface rendering (top), surface rendering with externally exposed neurosensory or sinus structures (middle), and transparent rendering with internal neurosensory and sinus structures (bottom). Abbreviations: atr, anterior tympanic recess; bsr, basisphenoid recess; cp, cultriform process; ec, brain endocast; ofb, olfactory bulb(s); or, otic recess; pmcv, posterior middle cerebral vein; pro foss, prootic fossa; prp, preotic pendant; ptf, pituitary fossa; ptr, posterior tympanic recess; ptra, aperture of the posterior tympanic recess; scr, external pneumatic openings for subcondylar recess; scs,

subcondylar recess; sos, supraoccipital sinus; ssr, subsellar recess. Scale bar represents 10 cm.

Fig. 4. Three-dimensional CT-based model of the holotype skull of *Bistahieversor sealeyi* (NMMNH P-27469) in right lateral/ventral oblique view. Surface rendering with externally exposed neurosensory or sinus structures (A), and transparent rendering with internal neurosensory and sinus structures (B). Abbreviations: atr, anterior tympanic recess; bsr, basisphenoid recess; ec, brain endocast; oc, occipital condyle; ofb, olfactory bulb(s); or, otic recess; pop, paroccipital process; pro foss, prootic fossa; ptf, pituitary fossa; ptr, posterior tympanic recess; ptra, aperture of the posterior tympanic recess; scr, subcondylar recesses; scs, subcondylar recess; ssr, subsellar recess. Scale bar represents 10 cm.

Fig. 5. Three-dimensional CT-based model of the brain endocast of the holotype skull of *Bistahieversor sealeyi* (NMMNH P-27469) in right lateral (A), left lateral (B), dorsal (C), ventral (D), anterior (E), and posterior (F) views. Abbreviations: cer, cerebrum; dp dural peak; fl, flocculus; ofb, olfactory bulb(s); oft, olfactory tract; pmcv, posterior middle cerebral vein; ptf, pituitary fossa. Scale bar represents 5 cm.

Fig. 6. Three-dimensional CT-based model of the brain endocast and endocranial sinuses of the holotype skull of *Bistahieversor sealeyi* (NMMNH P-27469) in right lateral (A), left lateral (B), ventral (C), dorsal (D), anterior (E), and posterior (F) views. Abbreviations: atr, anterior tympanic recess; bsr, basisphenoid recess; ec, brain endocast; pmcv, posterior middle cerebral vein; ptr, posterior tympanic recess; scs, subcondylar recess; sos, supraoccipital sinus; ssr, subsellar recess. Scale bar represents 10 cm.

Fig. 7. CT scan two-dimensional slices of the holotype skull of *Bistahieversor sealeyi* (NMMNH P-27469) in right lateral (A) and dorsal (B) views, illustrating key features of the

brain endocast. Abbreviations: ec, brain endocast; lob, left olfactory bulb; ofb, olfactory bulb(s); oft, olfactory tract; oms, ossified median septum; or, otic recess; pmcv, posterior middle cerebral vein; ptf, pituitary fossa; ptr, posterior tympanic recess; rob, right olfactory bulb; scs, subcondylar recess; sos, supraoccipital sinus. Scale bar represents 5 cm.

Fig. 8. CT scan two-dimensional slices of the holotype skull of *Bistahieversor sealeyi* (NMMNH P-27469), illustrating key features of the olfactory bulbs: coronal slice (A), dorsal view (B). Abbreviations: lob, left olfactory bulb; oms, ossified median septum; or, otic recess; rob, right olfactory bulb. Scale bar represents 1 cm.

Fig. 9. Three-dimensional CT-based model of the referred subadult skull of *Bistahieversor sealeyi* (NMMNH P-25049) in left lateral (external) (A, C, E) and medial (internal) (B, D, F) views. Each set of views includes a surface rendering (top), surface rendering with externally exposed inner ear structures (middle), and transparent rendering with internal inner ear structures (bottom). Abbreviations: asc, anterior semicircular canal; bsr, basisphenoid recess; cd, cochlear duct; lsc, lateral semicircular canal; oc, exoccipital-opisthotic contribution to occipital condyle; or, otic recess; pop, paroccipital process; pro foss, prootic fossa; prp, preotic pendant; psc, posterior semicircular canal; ptr, aperture of the posterior tympanic recess. Scale bar represents 1 cm.

Fig. 10. Three-dimensional CT-based model of the left inner ear of the referred subadult skull of *Bistahieversor sealeyi* (NMMNH P-25049) in lateral (A), medial (B), dorsal (C), posterior (D), and anterior (E) views. Abbreviations: asc, anterior semicircular canal; cc, crus commune; cd, cochlear duct; lsc, lateral semicircular canal; psc, posterior semicircular canal; ve, vestibule. Scale bar represents 1 cm.

Fig. 11. Neurosensory features optimized onto tyrannosauroid phylogeny, scaled against time. Tyrannosauroid taxa shown are those for which CT-based neurosensory data are available. Ovals next to taxon names depict temporal range, which in most cases is age uncertainty and not true range. Silhouettes next to taxon names indicate approximate relative body size. Gray box indicates the portion of the phylogeny for which neurosensory information was not available, prior to the current description of *Bistahieversor*. Features optimized onto the phylogeny are unambiguous optimizations. Features listed at bottom left are attributes of the ‘tyrannosaurid-style’ neurosensory system that cannot be unambiguously optimized because of missing data in at least one taxon. Enlarged olfactory bulbs, reduced cerebral hemispheres, cerebrum midline peak, and reduced optic lobes cannot yet be assessed for *Timurlengia*, so these may have appeared at either the *Timurlengia* + derived taxa or *Bistahieversor* + derived taxa nodes. Elongate, straight cochlear duct cannot yet be assessed for *Dilong*, so this may have appeared at either the *Dilong* + derived taxa or *Timurlengia* + derived taxa nodes. Loss of dorsal tympanic recess cannot yet be assessed for *Dilong* or *Timurlengia*, so it may have appeared at any of the nodes prior to the divergence of *Bistahieversor*. Endocasts next to taxon names are sourced from: *Dilong* (Kundrát et al., 2018), *Timurlengia* (original figure, similar to that in Brusatte et al., 2016), *Bistahieversor* (this paper), *Gorgosaurus* and *Tyrannosaurus* (Witmer and Ridgely, 2009), *Alioramus* (original figure, similar to that in Bever et al., 2011, 2013). Taxon silhouettes from phylopic.org (*Dilong*: FunkMonk; *Timurlengia*: *Eotyrannus* of S. Hartman; *Bistahieversor* and *Gorgosaurus*: *Albertosaurus* of C. Dylke; *Alioramus*: *Daspletosaurus* of S. O’Connor and T.M. Keesey; *Tyrannosaurus*: S. Hartman).