

# KIRTLANDIA

The Cleveland Museum of Natural History

November 2010

Number 57:61–81

## THE CLEVELAND TYRANNOSAUR SKULL (*NANOTYRANNUS* OR *TYRANNOSAURUS*): NEW FINDINGS BASED ON CT SCANNING, WITH SPECIAL REFERENCE TO THE BRAINCASE

LAWRENCE M. WITMER AND RYAN C. RIDGELY

Department of Biomedical Sciences, College of Osteopathic Medicine  
Ohio University, Athens, Ohio 45701  
witmerL@ohio.edu

### ABSTRACT

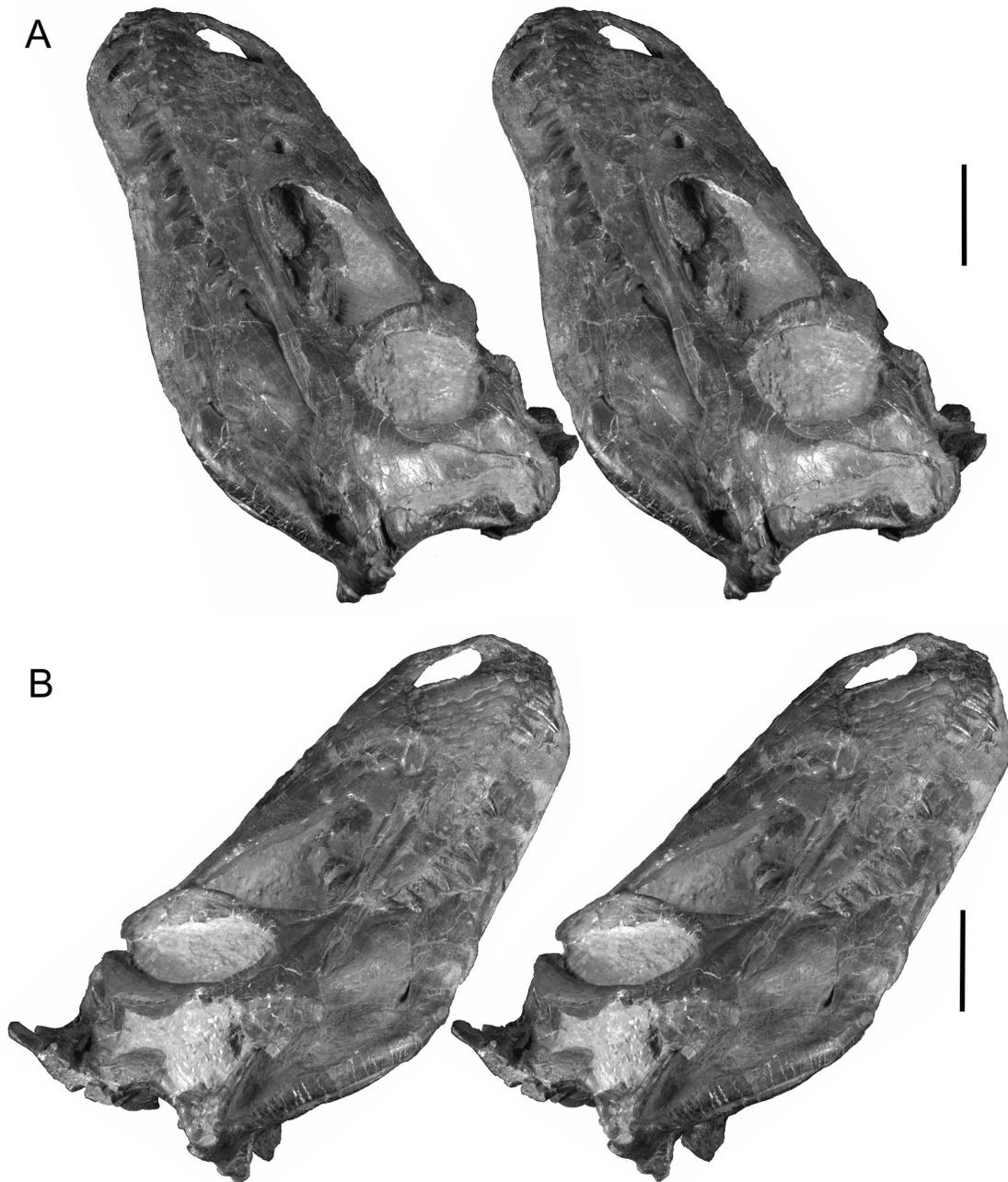
The Cleveland Museum of Natural History's skull of a small tyrannosaurid theropod dinosaur (CMNH 7541) collected from the Hell Creek Formation has sparked controversy, with competing hypotheses suggesting that it represents a separate taxon of dwarf tyrannosaurid (*Nanotyrannus lancensis*), a juvenile specimen of *Tyrannosaurus rex* (the only other acknowledged Hell Creek tyrannosaurid), or a compromise position (a juvenile *Nanotyrannus*). Beyond this controversy, CMNH 7541 holds importance because of the anatomical information that such a well preserved skull can provide, and it is in this context that we have sought to probe the structure of the braincase region (e.g., pneumatic sinuses, cranial nerve foramina), as well as other regions of the skull. We subjected the skull to computed x-ray tomography (CT scanning), followed by computer analysis and 3D visualization. The braincase and a number of other bones (e.g., vomer, quadrate, quadratojugal, palatine, mandible) were digitally "extracted" from the CT datasets. Although the new findings strongly confirm the long-held view that CMNH 7541 pertains to a tyrannosaurid, the mosaic of characters it presents makes finer taxonomic assignment difficult. For example, some characters support affinities with *T. rex*, yet other characters argue for a much more basal position. The key question that awaits resolution is whether the differences observed can be attributed to juvenility, and such resolution will require information from new, as yet unpublished specimens. Nevertheless, some of the differences seen in CMNH 7541 (e.g., the pattern of pneumatic foramina in the basicranium) are highly divergent and are harder to attribute to ontogeny. Among other findings, we report here thin, laminar structures within the main nasal airway that are interpretable as being respiratory turbinates, which have potential implications for metabolic physiology.

### Introduction

The Cleveland Museum of Natural History (CMNH), in a 1942 expedition led by David H. Dunkle, collected an isolated skull of a tyrannosaurid theropod dinosaur from the Hell Creek Formation (Late Maastrichtian, Cretaceous) of southeastern Montana. This skull (CMNH 7541) was described by Gilmore (1946) as a new species of *Gorgosaurus*, *G. lancensis*. Since its discovery, CMNH 7541 has attracted considerable attention, primarily because of its small size. With a length of only about 570 mm, it was—and remains—one of the smallest skulls known for definitive tyrannosaurids; for comparison, the skulls of adult *Tyrannosaurus rex* can exceed 1300 mm. Given its small size, some workers (e.g., Rozhdestvensky, 1965) suggested that CMNH 7541 might pertain to a juvenile of a known species, presumably *T. rex*, the only other definitively known Hell Creek tyrannosaurid. Russell (1970), however, later supported Gilmore's assignment of adult status to the skull, as well as its referral to *Gorgosaurus* (a

name that Russell regarded as a junior synonym of *Albertosaurus*).

In 1988, the results of a collaborative project by R. T. Bakker, the late Cleveland Museum of Natural History curator Michael Williams (to whom this issue of *Kirtlandia* is dedicated), and P. J. Currie were published (Bakker et al., 1988). This article suggested that not only was CMNH 7541 an adult skull, but also the skull of a new genus and species of dwarfed tyrannosaur that was only very distantly related to *Tyrannosaurus rex*. Thus, *Nanotyrannus lancensis* and "pygmy tyrants" entered the lexicon of dinosaurs. Nevertheless, doubts lingered and others suggested that CMNH 7541 might be in fact a juvenile *T. rex* (Carpenter, 1992). In 1999, T. D. Carr published a major article documenting the juvenile features of CMNH 7541 and identifying a number of derived features that suggested that CMNH 7541 pertains to a young *T. rex* (Carr, 1999; see also Carr and Williamson, 2004; Carr et al., 2005). Carr's work has been very influential, such that many

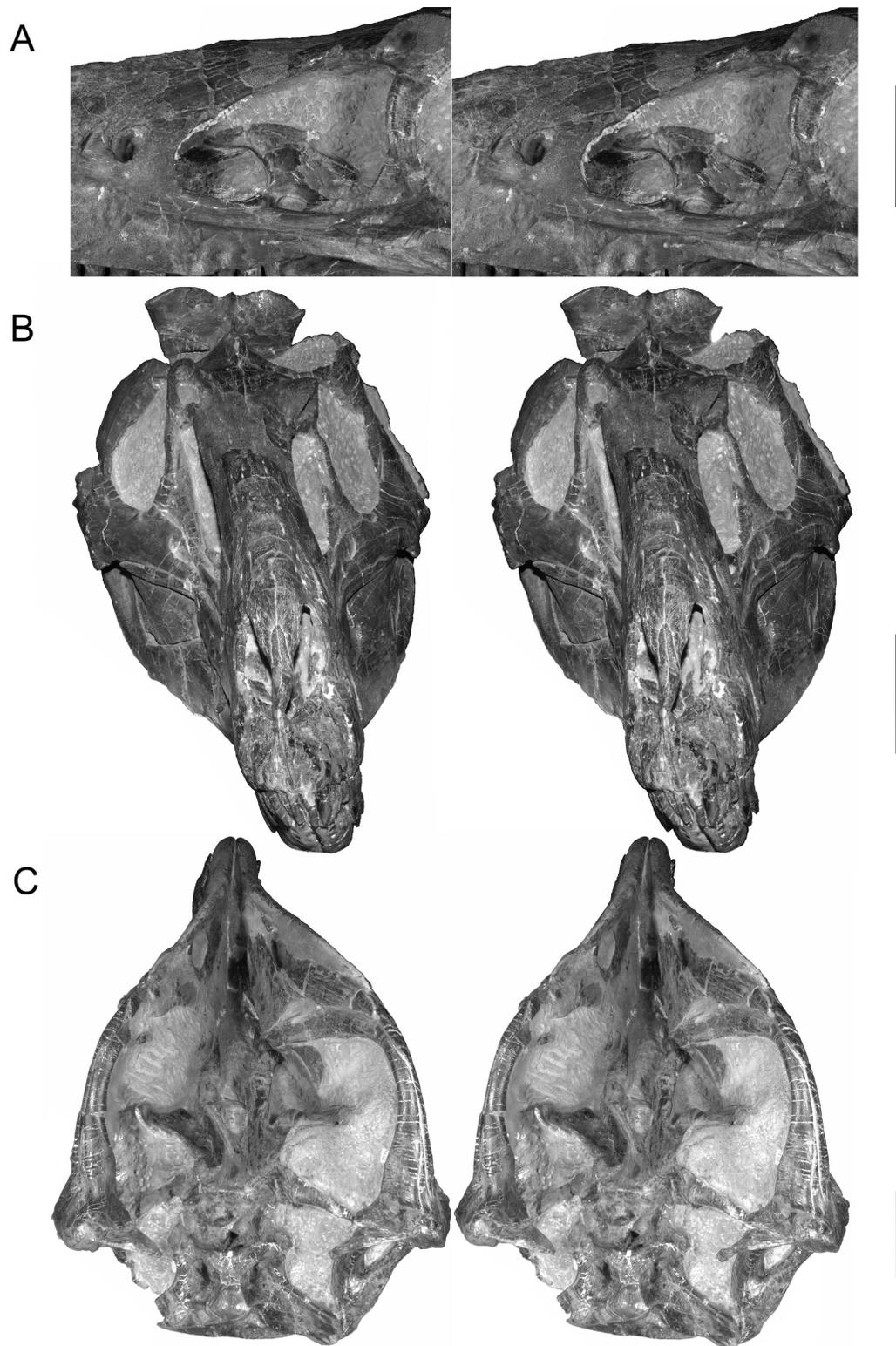


**Figure 1.** Cleveland tyrannosaur skull, CMNH 7541. Stereophotographs of skull in A, left lateral view; B, right lateral view. Orientations reflect posture with lateral semicircular canal horizontal. Scale bars equal 10 cm.

workers regard CMNH 7541 as a juvenile *T. rex* (Holtz, 2001, 2004; Brochu, 2003; Paul, 2008; Brusatte et al., 2009). However, although he accepted the juvenile status of the skull, Currie (2003a, b; Currie et al., 2003) regarded *Nanotyrannus lancensis* as a valid taxon, albeit very closely related to *T. rex*. Recently, P. Larson (2008) has emerged as a vocal advocate for the validity of *N. lancensis*, even referring several other specimens to this species.

Thus, the Cleveland Museum tyrannosaur skull has had a somewhat tortured systematic history, starting out as a gorgosaur (Gilmore, 1946; Russell, 1970), then becoming its own genus (*Nanotyrannus*) that was placed as the most basal tyrannosaurid (Bakker et al., 1988), then becoming a juvenile *T. rex* (Carr, 1999;

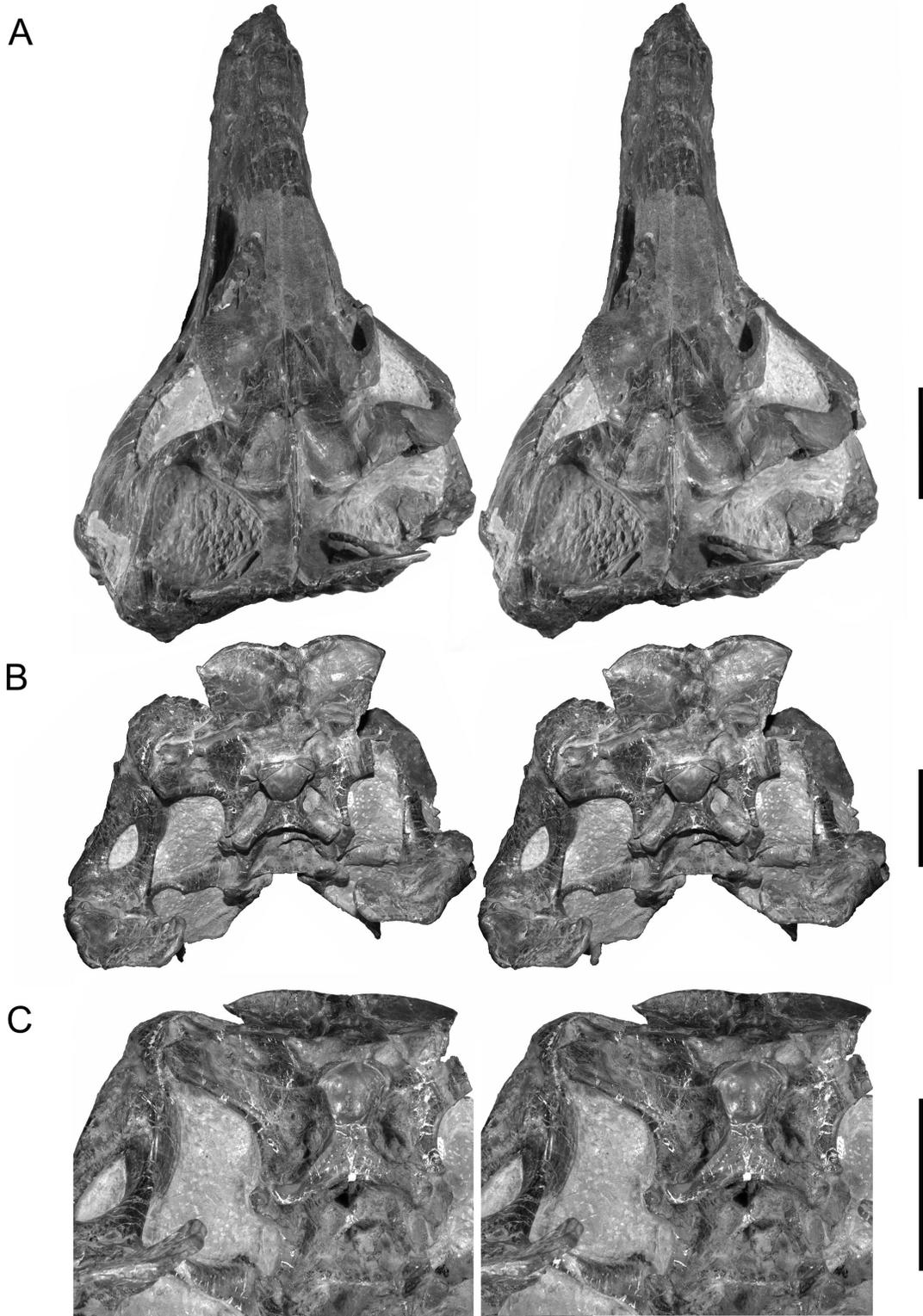
Holtz, 2001, 2004; Brochu, 2003; Carr and Williamson, 2004; Carr et al., 2005; Brusatte et al., 2009), and then becoming a juvenile that grew up into a distinct *Nanotyrannus*, yet placed as the sister-group to *T. rex* (Currie 2003a, b; Currie et al., 2003). Resolution of this issue is important because, on the one hand, if CMNH 7541 is a juvenile *T. rex*, then there may remain just a single Late Maastrichtian tyrannosaur species in western North America. Moreover, it would mean that ontogenetic studies of *T. rex* would be on a much sounder footing, because most other juvenile or subadult *T. rex* skulls are less complete than CMNH 7541 (Carr and Williamson, 2004). On the other hand, if *Nanotyrannus* is valid, then we have a greater diversity of tyrannosaurs, but less information about ontogeny.



**Figure 2.** Cleveland tyrannosaur skull, CMNH 7541. Stereophotographs of A, close-up of left antorbital region; B, skull in rostral view; C, skull in ventral view. Orientations reflect posture with lateral semicircular canal horizontal. Scale bars equal 10 cm.

Our interest in the Cleveland skull, however, did not arise from this interesting and important systematic controversy. Our studies of CMNH 7541 are part of a larger study of the evolution of the brain and ear regions of dinosaurs and other archosaurs (Witmer

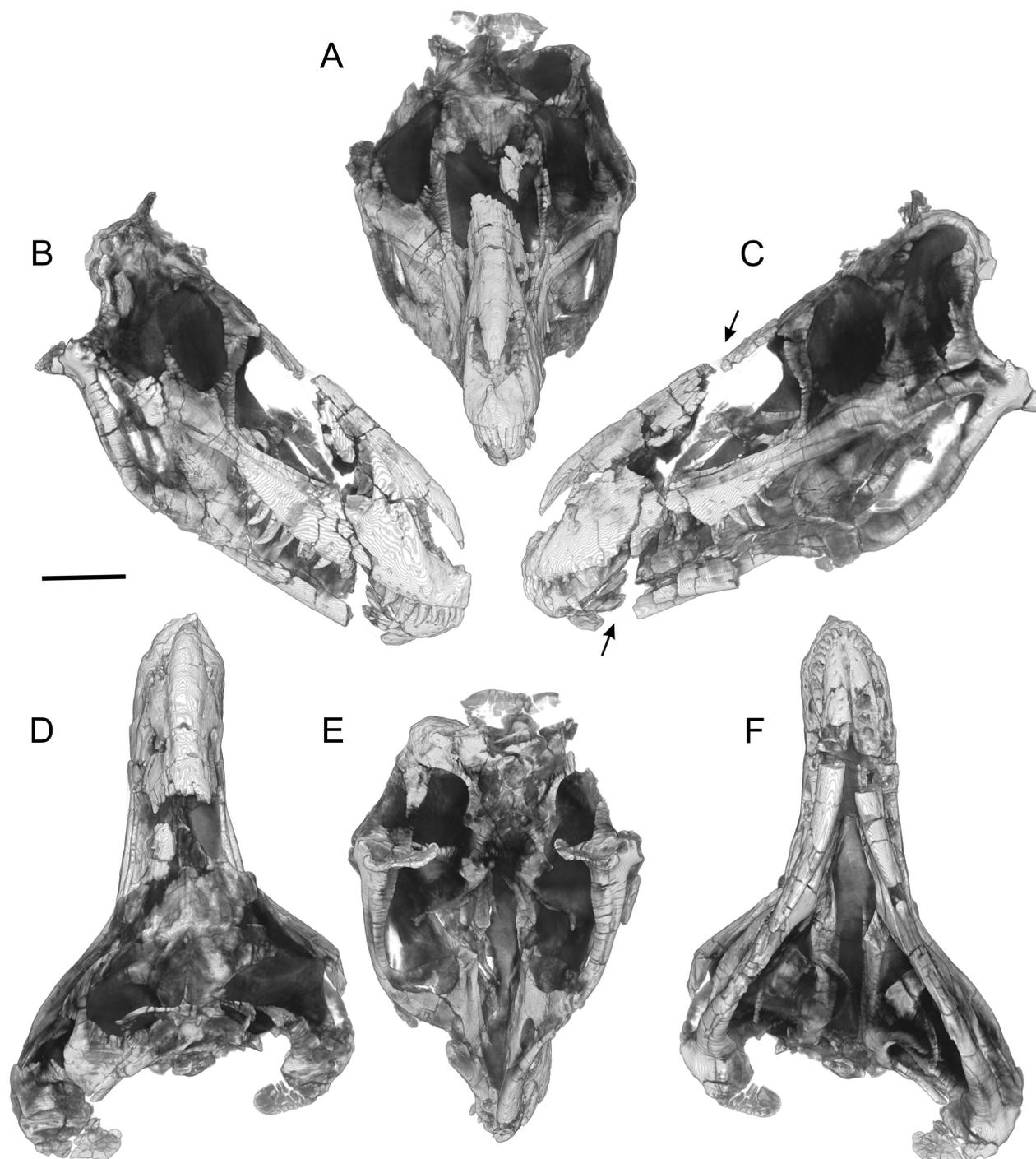
et al., 2003; Sampson and Witmer, 2007; Sereno et al., 2007; Witmer and Ridgely, 2008a, b, 2009; Witmer et al., 2008). Tyrannosaurs are often regarded (particularly in public venues) as having expanded brains and heightened sensory apparatuses



**Figure 3.** Cleveland tyrannosaur skull, CMNH 7541. Stereophotographs of A, skull in dorsal view; B, skull in caudal view; C, close-up of cranial base in ventral view. Orientations reflect posture with lateral semicircular canal horizontal. Scale bars equal 10 cm.

(Bakker et al., 1988; Horner and Lessem, 1993; Brochu, 2000, 2003; Witmer et al., 2008; Witmer and Ridgely, 2009; Zelenitsky et al., 2009). Study of CMNH 7541 has helped shaped this perception, with early computed x-ray tomographic (CT) scans suggesting that the animal “combined the eyes and brain of an

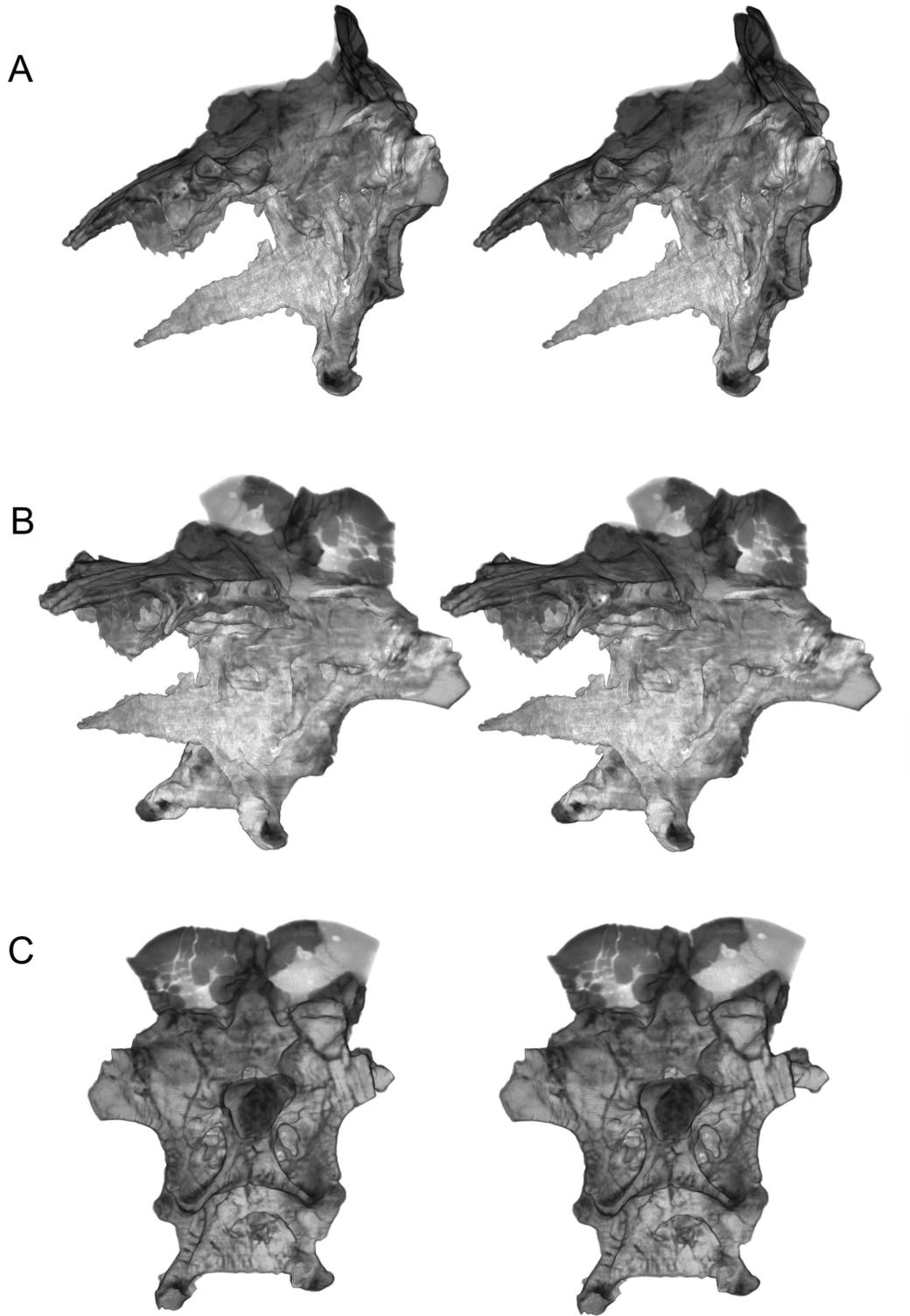
eagle with the snout and hearing of a wolf” (Bakker, 1992, p. 60). The goal of our project was to probe braincase structure of the Cleveland skull using CT data and to reconstruct the brain cavity (cerebral endocast), inner and middle ear anatomy, and general patterns of cranial blood flow, and compare these findings with



**Figure 4.** Cleveland tyrannosaur skull, CMNH 7541. Volume renderings of the skull derived from the CT data in A, rostral view; B, right lateral view; C, left lateral view; D, dorsal view; E, caudal view; F, ventral view. Densities corresponding to plaster have been excluded, revealing the extent of plaster restoration. Arrows in C indicate the transverse oblique plane of fracture that the specimen experienced prior to restoration. Scale bar equals 10 cm.

similar findings from other tyrannosaurs and other theropods in general. Michael Williams was to be a collaborator on the project, but passed away before the work began. Some of the results of the project are presented here and others (e.g., a comparative analysis of the brain endocast) are presented in a companion article (Witmer and Ridgely, 2009).

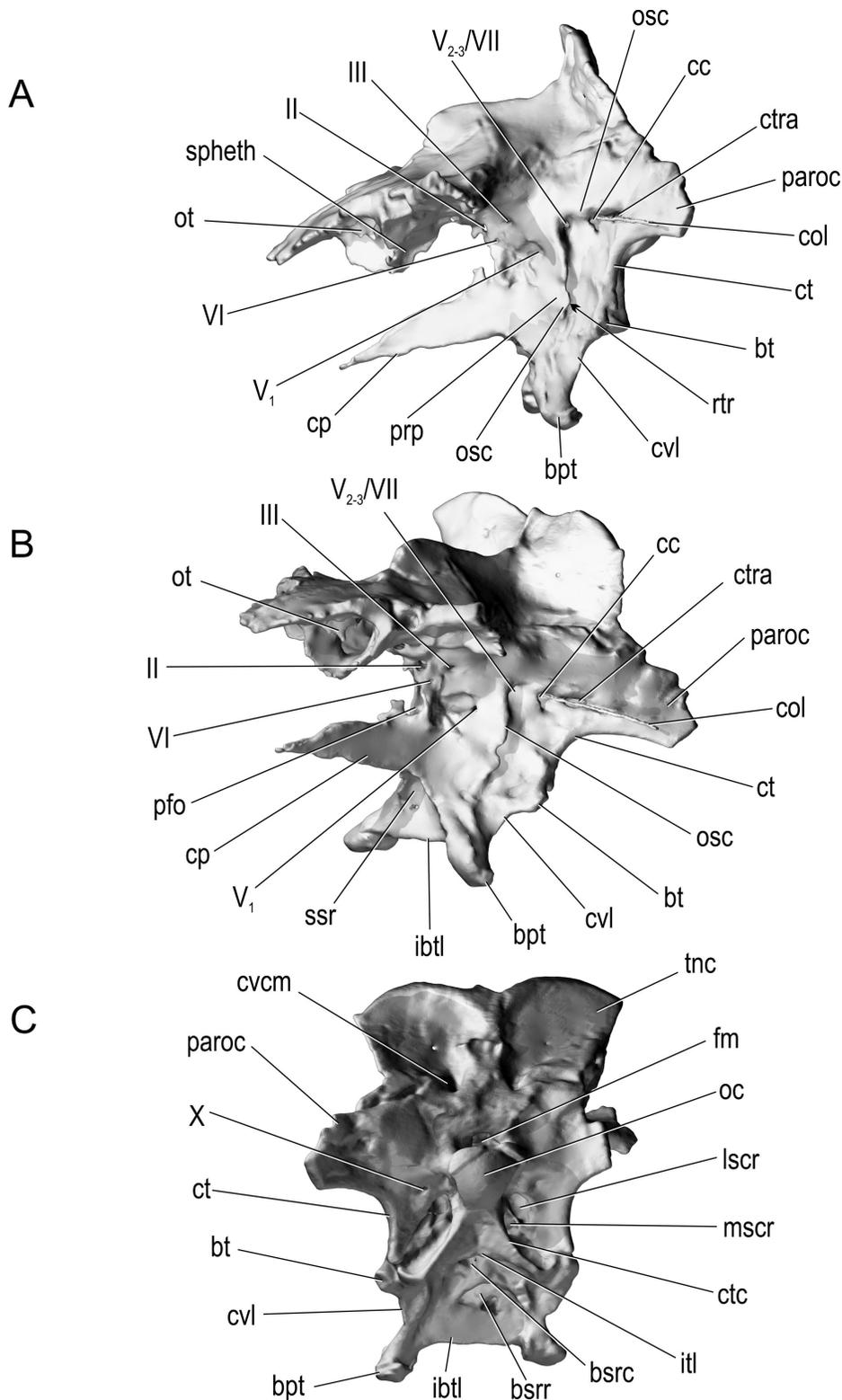
The present article, in particular, presents some details on braincase structure and patterns of paratympanic pneumaticity in CMNH 7541. We also will present some findings on other areas of the skull that might have bearing on the systematic issues raised above, because we recognize that resolution of the controversy impacts any conclusions (e.g., intraspecific/ontogenetic versus



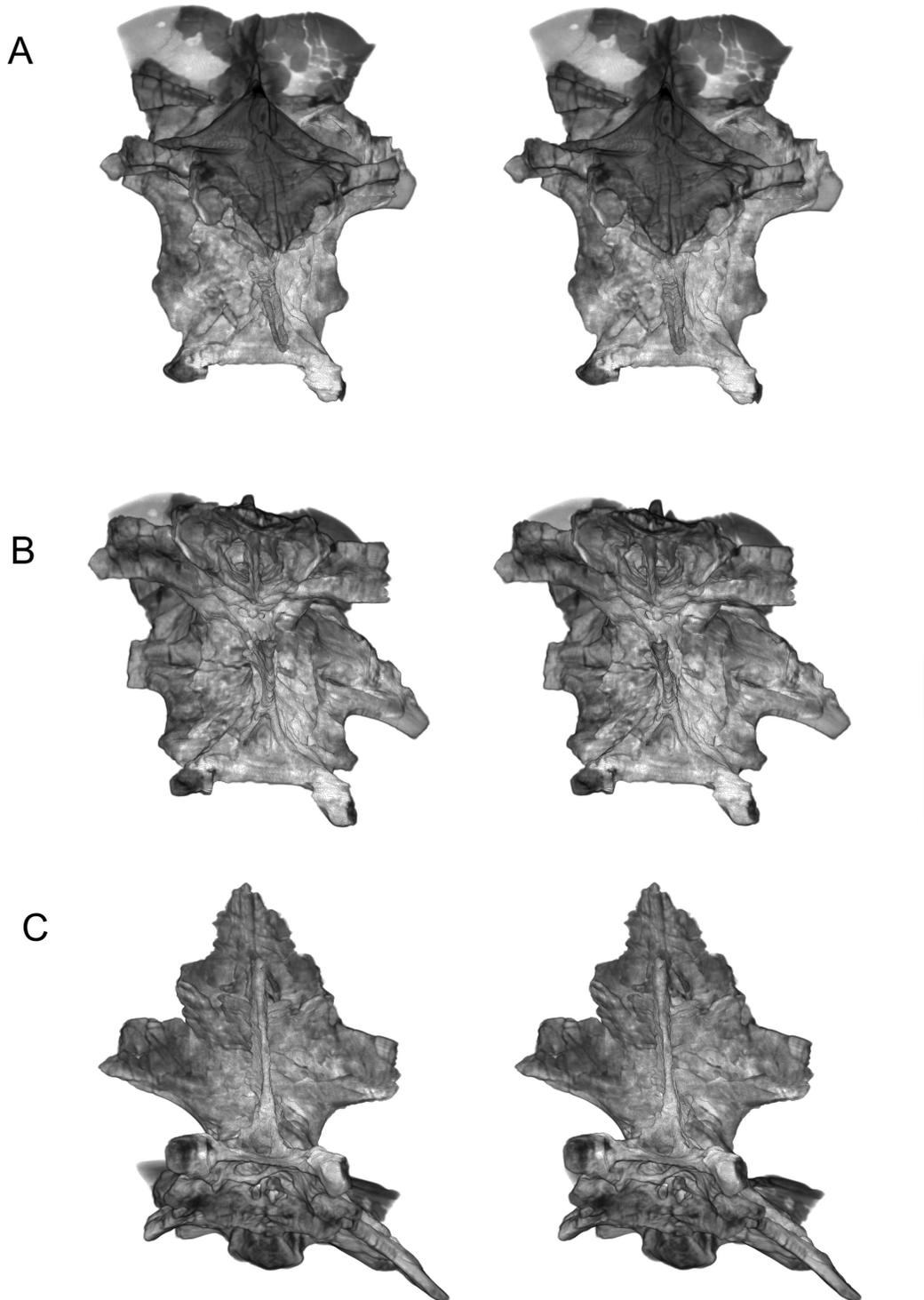
**Figure 5.** Cleveland tyrannosaur skull, CMNH 7541. Volume renderings (stereopairs) of digitally extracted braincase derived from CT data in A, left lateral; B, left rostroventrolateral; C, caudal views. Figure 6A–C provides corresponding labeled views. Scale bar equals 10 cm.

interspecific/taxonomic variation). Some of these issues are explored in the Discussion. We also take the opportunity to provide some high quality stereophotographs of the specimen with the hope that they will help other workers sort out the critical

systematic issues. A critical new find that has bearing on the interpretation and taxonomic status of the Cleveland skull was the discovery in 2001 of a relatively complete skeleton of a tyrannosaurid by the Burpee Museum of Natural History (BMR



**Figure 6.** Cleveland tyrannosaur skull, CMNH 7541. Surface renderings of digitally extracted braincase derived from CT data in A, left lateral; B, left rostroventrolateral; C, caudal views. Figure 5A–C shows corresponding stereopairs of volume renderings. Scale bar equals 10 cm. See Appendix for abbreviations.

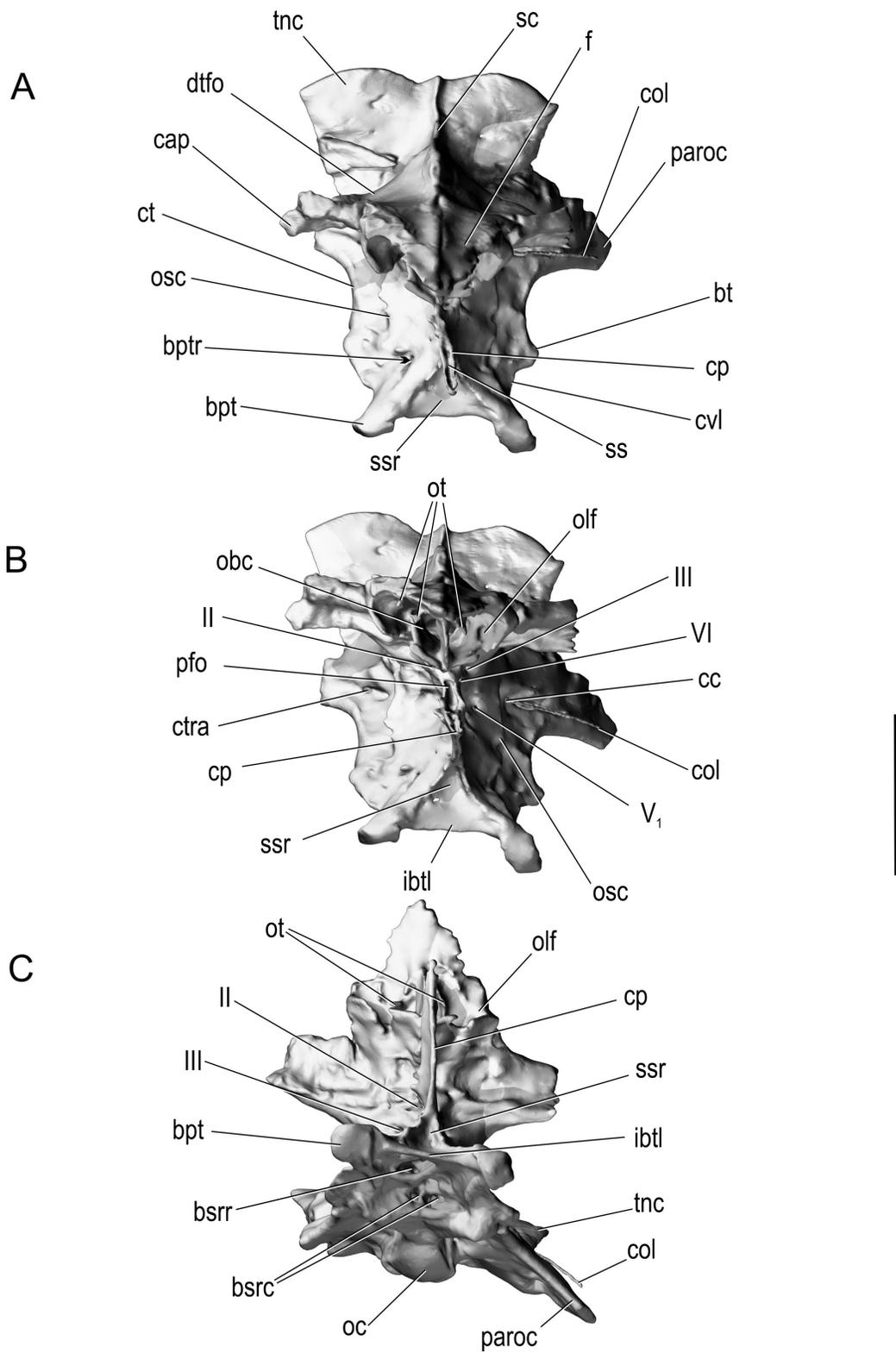


**Figure 7.** Cleveland tyrannosaur skull, CMNH 7541. Volume renderings (stereopairs) of digitally extracted braincase derived from CT data in A, rostral; B, rostroventral; C, ventral views. Figure 8A–C provides corresponding labeled views. Scale bar equals 10 cm.

P2002.4.1) that closely resembles CMNH 7541 in many ways (Henderson and Harrison, 2008) and which is generally thought to represent a similar ontogenetic age of the same species (P. Larson, 2008). Remarkably, this otherwise very complete specimen lacks the braincase, and so the Cleveland skull remains critical in this regard, but comparisons to BMR P2002.4.1 are made here where relevant.

#### Materials and Methods

The primary specimen used in this study was CMNH 7541, a nearly complete skull of a probably juvenile tyrannosaurid, collected from the Hell Creek Formation of Carter County, Montana (see Gilmore, 1946, for collection details and geological setting). A variety of other tyrannosaurid specimens were studied in connection with this project (for a full listing,



**Figure 8.** Cleveland tyrannosaur skull, CMNH 7541. Surface renderings of digitally extracted braincase derived from CT data in A, rostral; B, rostroventral; C, ventral views. Figure 7A–C shows corresponding stereopairs of volume renderings. Scale bar equals 10 cm. See Appendix for abbreviations.

see Witmer and Ridgely, 2009). In addition to general observation, the major tool used in this study was CT scanning (computed x-ray tomography), followed by 3D analysis and visualization. CMNH 7541 has been CT scanned no fewer than three times.

The first scans were done in 1990 on a medical scanner at a Toronto hospital, in the presence of Michael Williams, Andrew Leitch, and Robert T. Bakker (Bakker, 1992). Scanning details have not been published, but results were presented in a popular article by Bakker (1992), who reconstructed the brain cavity and, within the nasal cavity, an elongate turbinate. The same CT data were used later by J. A. Ruben to refute the finding of respiratory turbinates in this skull (Ruben, 1996; Ruben et al., 1996, 1997).

The Cleveland skull was scanned for the second time in 1998 at the Boeing Rocketdyne CT Lab in California under the auspices of the Cleveland Museum of Natural History with funding from the Field Museum of Natural History. The skull was scanned at a slice thickness of 1 mm with slices in the horizontal plane, yielding 300 slices; voxel sizes were  $0.4042 \times 0.4042 \times 1.0$  mm. As part of the collaboration with M. Williams, the Cleveland Museum of Natural History provided Witmer with the full 16-bit dataset from these scans.

In hopes of revealing aspects of anatomy that are unclear in the Boeing dataset, the skull was scanned for the third time in 2005 at O'Bleness Memorial Hospital, Athens, Ohio, on a General Electric LightSpeed Ultra MultiSlice CT scanner equipped with the Extended Hounsfield option, which enhances the ability to resolve details from dense objects such as fossils. Because the Boeing dataset was derived from scans of the skull in the horizontal plane, the x-rays had to pass through the full length of the skull, which can produce artifacts. Thus, we scanned the skull axially, which minimized the amount of material the x-rays had to penetrate. The full skull was scanned helically with a slice thickness of 1.25 mm at 140 kV and 300 mA, yielding 483 slices and voxel sizes of  $0.082 \times 0.082 \times 1.25$  mm. The skull was then scanned again, this time focusing on the braincase, tightening the field of view and extending from the caudal end of the skull through the orbits and ending rostrally just in front of the lacrimals' jugal processes; slice thickness was 625 microns (0.625 mm) at 140 kV and 170 mA, yielding 385 slices and voxel sizes of  $0.049 \times 0.049 \times 0.625$  mm. No CT scan is free from artifact, and both the Boeing and Athens datasets have their advantages and disadvantages. Ultimately, much of the work presented here is based on a composite "super-dataset" created by registering and combining the Boeing and multiple Athens datasets.

Viewing, analysis, and visualization of the scan data were done using Amira 3.1.1 and 4.2 (Mercury-TGS, Chelmsford, MA) on 32- and 64-bit Windows XP PCs equipped with nVidia Quadro FX graphics cards and 2–8 GB of RAM. Structures of interest were highlighted (segmented) using Amira's segmentation tools and visualized either in isolation or combined with other structures or the whole skull. Both surfaces and volumes were generated, and these served as the basis for most of the illustrations in this article. Additional information, such as interactive movies and 3D PDFs, are available on the authors' website: [www.ohio.edu/witmerlab](http://www.ohio.edu/witmerlab).

Museum abbreviations used in this paper are: AMNH, American Museum of Natural History, New York City, New York; BMR, Burpee Museum of Natural History, Rockford, Illinois; CMNH, Cleveland Museum of Natural History, Cleveland, Ohio; FMNH, Field Museum of Natural History, Chicago, Illinois; MOR, Museum of the Rockies, Bozeman, Montana; OMNH, Oklahoma

Museum of Natural History, Norman, Oklahoma; ROM, Royal Ontario Museum, Toronto, Ontario; and TMP, Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta.

## Results

CMNH 7541 has been the subject of at least three major anatomical studies (Gilmore, 1946; Bakker et al., 1988; Carr, 1999), and thus there is no need for in-depth anatomical description here. Instead, our intent is to focus on a few areas that have not been adequately discussed in print and that are revealed by the CT scan data. It is also our intent to capitalize on the new-found visualization capabilities provided by the new imaging technologies and software, and so we emphasize illustration over text (in the spirit of the old adage of a picture being worth a thousand words).

### General attributes

Figures 1–3 provide stereophotographs of the skull in several views, showing not just bony structure but also the amount of matrix remaining in the skull and, to a certain extent, the amount of plaster restoration. Plaster is relatively low density and homogenous and is easily identified and removed in volume renderings of the CT data. Figure 4 presents views of the skull with the plaster (and some regions of thin matrix) dropped out. Examination of Figure 4 reveals that the snout had been fractured along an oblique transverse plane running caudodorsally to rostroventrally (arrows in Figure 4C) such that, when repaired and restored in plaster (quite expertly, it may be said), much of the central parts of the nasal and antorbital cavities wound up being largely plaster.

### Braincase

The braincase of CMNH 7541 is visible in dorsal, caudal, and ventral views in the actual (physical) specimen (Figures 2D–E, 3A–C), but the other surfaces are obscured by matrix and other bones. To more easily compare the braincase to those of other theropods, the braincase of CMNH 7541 was digitally "disarticulated" along sutures and then extracted so that it could be viewed in isolation (Figures 5–8). The general conformation of the braincase is fairly similar to those of other tyrannosaurs in having a well developed otosphenoidal crest (= crista prootica) running from the otoccipital bone caudally and arching rostrally and then ventrally on the prootic, laterosphenoid, and basisphenoid bones (Figure 6B). Tucked ventrally or caudoventrally below the margin of the otosphenoidal crest, from caudal to rostral, are the caudal tympanic recess aperture, columellar recess (with the columella [= stapes] in place in the fenestra vestibuli), the maxillomandibular and facial foramina (for CN  $V_{2-3}$  and CN VII, respectively), the rostral tympanic recess, and cerebral carotid foramen. As in other tyrannosaurids, the facial foramen opens so close to the maxillomandibular foramen that the two essentially share an aperture laterally (Witmer et al., 2008; Witmer and Ridgely, 2009; Brusatte et al., 2009).

As in other tyrannosaurids, perhaps all coelurosaurs, and many tetanurans (Sampson and Witmer, 2007; Witmer and Ridgely, 2009), the ophthalmic nerve (CN  $V_1$ ) exits the laterosphenoid rostrally via its own foramen. Another attribute shared with other tyrannosaurids is the almost complete ossification of the front of the braincase, with orbitosphenoid and sphenethmoid ossifications contacting their fellows in the midline and enclosing foramina for the olfactory bulbs and tracts, optic nerves (CN

II), oculomotor nerves (CN III), and abducens nerves (CN VI) (Figures 6, 8). The sphenethmoid is particularly significant because it preserves details relating to the olfactory apparatus. The sphenethmoid itself is divided by a midline osseous septum (mesethmoid), which in life would have separated the rostral terminations of the olfactory tracts (i.e., the olfactory bulbs), as described for other theropods (Sampson and Witmer, 2007; Ali et al., 2008; Witmer and Ridgely, 2009). Lateral to the region of the olfactory bulbs are a series of thin bony laminae descending from the roof of the sphenethmoid and possibly also the frontal (Figures 6A, B; 7B, C; 8). These laminae are external to the neural domain and would be within the nasal cavity, and thus these laminae are best interpreted as olfactory turbinates that would have supported the sensory olfactory epithelium, as observed in extant taxa. The olfactory apparatus indeed seems well developed in CMNH 7541, which is consistent with its large olfactory bulbs, as well as with the large bulbs and expansive nasal olfactory regions seen in other tyrannosaurs (Witmer et al., 2008; Witmer and Ridgely, 2009).

CMNH 7541 shares with other tyrannosauroids modestly-sized but widely-spaced basal tubera (Bakker et al., 1988; Carr, 1999; Currie et al., 2003; Li et al., 2010), yet it retains strong basiptyergoid processes. Likewise, all tyrannosaurids, including CMNH 7541, share extensive pneumaticity associated with the middle ear and pharynx (rostral and caudal tympanic recesses, basisphenoid recesses, subcondylar recess, subsellar recess; Witmer, 1997b; Witmer and Ridgely, 2009; see below).

Despite the similarities with other tyrannosaurids noted above, CMNH 7541 displays a number of noteworthy differences. For example, the cultriform process (parasphenoid rostrum) is relatively low and straight (Figures 5A, 6A), rather than, as in most other tyrannosaurids (Russell, 1970; Carr, 1999; Brochu, 2003; Currie, 2003b), having a strongly arched ventral margin that sweeps dorsally before leveling off parallel to the frontals. This may relate to CMNH 7541 having a relatively smaller subsellar recess (a ventral pneumatic chamber in the base of the cultriform process; Figures 6B, 9) relative to other tyrannosaurids. Among tyrannosaurids, the conformation of the cultriform process and subsellar recess is most similar to that of *Gorgosaurus* (Witmer and Ridgely, 2009) and *Alioramus* (Brusatte et al., 2009). Another difference is that CMNH 7541 has a much less projecting preotic pendant (Figure 6A), whereas in other tyrannosaurids it is a large and rugose structure associated with the otosphenoidal crest (Holliday and Witmer, 2008; Witmer and Ridgely, 2009); its weak development in CMNH 7541 may relate to the small size of the animal.

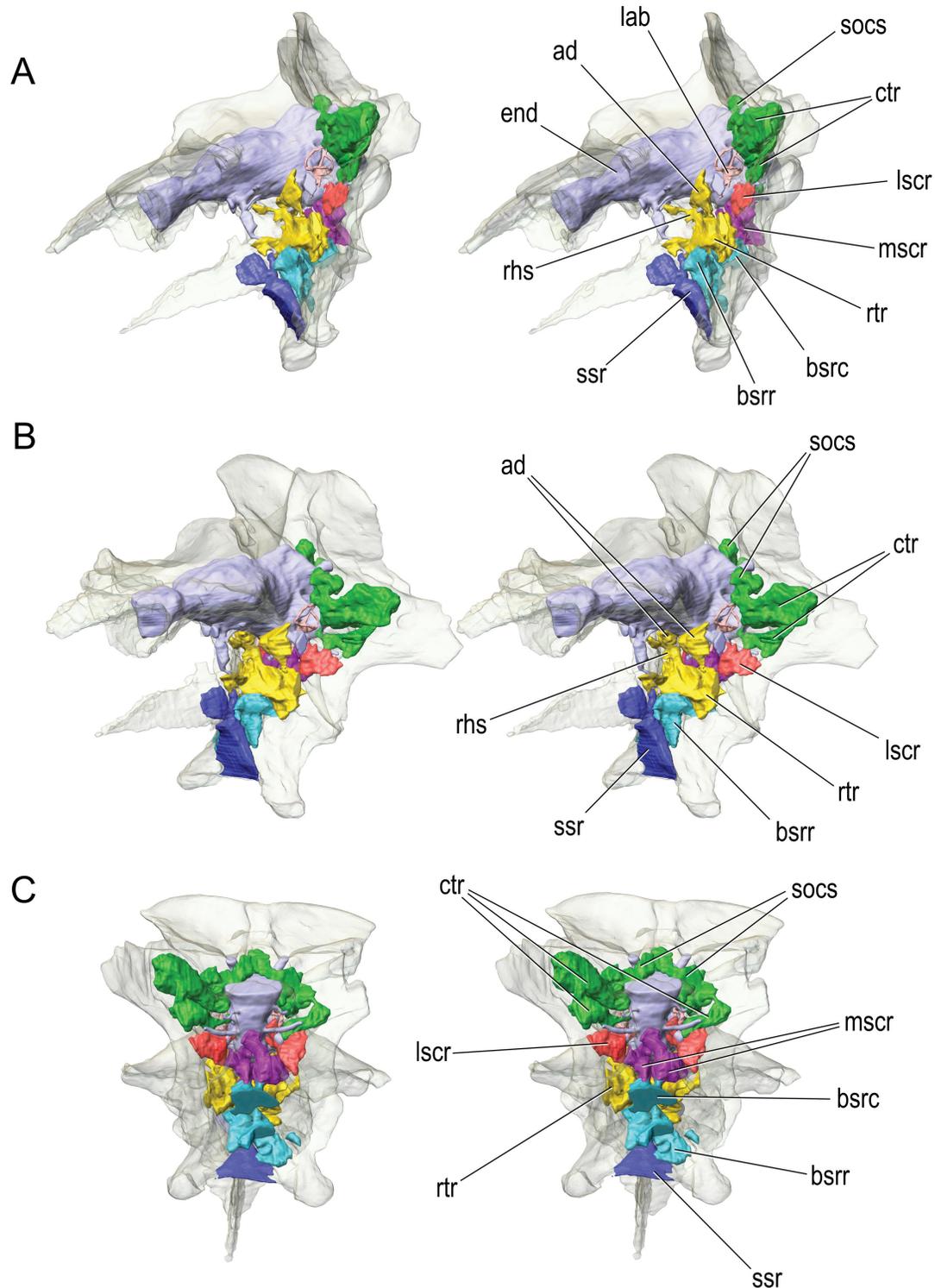
Other differences relate to the location of the vagus foramen (CN X) on the occiput and to the structure of the subcondylar recesses of the basicranium. In most other tyrannosaurids (certainly *T. rex*), the vagus foramen (CN X) is located medially in the caudal surface of the otoccipital within a paracondylar pocket or recess adjacent to the occipital condyle. In CMNH 7541, however, the vagus foramen is located more laterally (Figure 6C), in a position more typical of other coelurosaurs.

Ornithomimids, all tyrannosaurids (although apparently not the tyrannosauroid *Xiongguanlong*; Li et al., 2010), and potentially even some non-coelurosaurs (Sampson and Witmer, 2007) have subcondylar recesses (lateral and medial), which are pneumatic recesses located ventral to the occipital condyle and which excavate the basioccipital and otoccipital in the region above the basal tubera. Furthermore, in most tyrannosaurids,

there are pneumatic apertures in the floor of the recess leading into chambers within the basioccipital and otoccipital (Currie, 2003b; Witmer and Ridgely, 2009). The subcondylar recesses of CMNH 7541 differ from those of *T. rex*. In the former, the recesses as a whole are deeper and the basioccipital and otoccipital pneumatic apertures (leading into the medial and lateral subcondylar sinuses, respectively) are much closer together (essentially adjacent to each other and within a shared fossa; see Figures 5C, 6C, 9). Related to this difference is that the ventromedial wall of the subcondylar recess (the condylotuberal crest; Figures 5C, 6C, 9) is much stronger in CMNH 7541 than in specimens of *T. rex*. Taken together, the subcondylar region of CMNH 7541 is more primitive than that of *T. rex* and is intermediate between the latter and more basal tyrannosaurids (e.g., *Gorgosaurus*, ROM 1247; *Daspletosaurus*, FMNH PR308; see Witmer and Ridgely, 2009) and even more basal theropods (e.g., *Acrocanthosaurus*, OMNH 10146).

Other workers (e.g., Gilmore, 1946; Bakker et al., 1988) have pointed out the divergent nature of the apertures within the basisphenoid pneumatic recess of CMNH 7541, but 3D visualization of the pneumatic sinuses helps clarify the situation in comparison to other tyrannosaurids. In general, the basisphenoid recess of CMNH 7541 more closely resembles that of *Gorgosaurus* and *Daspletosaurus* in having a longer rostrocaudal distance between the intertuberal and interbasiptyergoid laminae (= basituberal and basiptyergoid webs, respectively, of Bakker et al., 1988; see Figures 5–8), whereas in *T. rex* these two laminae are quite closely appressed (Witmer and Ridgely, 2009). However, what makes CMNH 7541 so divergent is the pattern of apertures within the basisphenoid recess. As preserved (Figures 3C, 6C), there are three asymmetrical apertures, unlike any other known theropod. When traced dorsally into the pneumatic sinuses using the CT data, the caudal two apertures can be seen to represent a pair (even if they are not fully bilaterally symmetrical) because they expand into paired (i.e., left and right) sinuses (the caudal basisphenoid sinuses; Figures 8C, 9) that lead into the basioccipital and communicate on either side of the occiput with the medial subcondylar recesses. Expansion of the basisphenoid recess into sinuses within the basioccipital is fairly common in theropods generally, although the pattern of apertures in CMNH 7541 is unique.

The third and most rostral aperture within the basisphenoid recess has been difficult to interpret. Other tyrannosaurids have a rostral pair of foramina (left and right) in the interbasiptyergoid lamina that lead into pneumatic chambers within the basisphenoid (Russell, 1970; Bakker et al., 1988; Witmer, 1997b; Currie, 2003b; Witmer and Ridgely, 2009). Tracing the seemingly single aperture in CMNH 7541 in the CT data reveals that the aperture branches dorsally into essentially left and right sinuses (the rostral basisphenoid sinuses) that expand within the basisphenoid and eventually communicate with the rostral tympanic recesses on their respective sides (Figures 7C, 8C, 9). As a result, it would seem that the pair of foramina in the interbasiptyergoid lamina of other tyrannosaurids is present in CMNH 7541, but that the two apertures share a common fossa that is diverted towards the right side somewhat. Thus in sum, we are proposing that the basisphenoid pneumatic sinuses are fundamentally similar to those of other tyrannosaurids, albeit highly modified. Gilmore (1946, p. 10) explained this unusual and asymmetric morphology as representing “an unhealthy condition of the bone,” but there is no overt sign of pathology in this region.



**Figure 9.** Cleveland tyrannosaur skull, CMNH 7541. Surface renderings of digitally extracted braincase derived from CT data, made partially transparent to reveal brain endocast (light blue) and internal pneumatic sinuses, in A, left lateral; B, left rostroventrolateral; C, caudoventral views. Scale bar equals 10 cm. See Appendix for abbreviations.

### Pneumatic sinuses of the braincase

The pneumatic recesses of CMNH 7541 have been touched on above, but they will receive fuller treatment here in that they have been reconstructed in three dimensions using the CT-scan data (Figure 9). As noted, there is a clear aperture leading into the

caudal tympanic recess, and, as in most other coelurosaurs (Witmer, 1997b), the aperture is located in the base of the paroccipital process adjacent to the columellar recess and bounded by the prootic and opisthotic. In CMNH 7541, the caudal tympanic recess expands within the paroccipital process,

giving off two diverticula, one ventrally and the other dorsally. The ventral diverticulum enters the crista tuberalis (= basioccipital wing of the otoccipital, descending ventral root of the paroccipital process of Bakker et al., 1988) where it is broadly confluent with the lateral subcondylar recess. Despite this confluence, the cavity within the crista tuberalis of CMNH 7541 clearly derives as a primary diverticulum of the lateral subcondylar recess, because, in other tyrannosaurids (e.g., *T. rex*, *Gorgosaurus*), the communication between the two pneumatic spaces is slight to nonexistent, and it is the lateral subcondylar sinus that occupies the crista tuberalis (Witmer and Ridgely, 2009). The dorsal diverticulum certainly derives as an outgrowth of the caudal tympanic recess and forms a series of interconnecting chambers medially within the otoccipital and supraoccipital and laterally within the paroccipital process (Figure 9), as in other tyrannosaurids and indeed most other coelurosaurs (Witmer, 1997b; Witmer and Ridgely, 2009). There may be a tenuous communication between contralateral recesses within the supraoccipital but not the broad communication observed in *T. rex* and *Gorgosaurus*.

The rostral tympanic recess is located, again fairly typically, in the region where the cerebral carotid artery enters the braincase under shelter of the otosphenoidal crest, that is, in the area where the basisphenoid, prootic, and laterosphenoid contact each other (Figure 9). The rostral tympanic recess expands within the basisphenoid where it communicates with both the rostral and caudal basisphenoid sinuses, but more broadly with the rostral basisphenoid sinus. The rostral tympanic recess has a major dorsal diverticulum (the ascending diverticulum; Figure 9A, B) that leads into the substance of the laterosphenoid bone, occupying the region between the canals for the ophthalmic nerve (CN V<sub>1</sub>) rostrally and maxillomandibular nerve (CN V<sub>2-3</sub>) caudally. The connection between the ascending diverticulum and the rostral tympanic recess is very narrow. The ascending diverticulum is present in *Gorgosaurus* but is usually absent (or very rudimentary) in adult *T. rex* and *Dapletosaurus* (Witmer and Ridgely, 2009), which could be a legitimate, systematically informative difference. However, a newly discovered, very young skull of *Tarbosaurus* (just 29 cm total skull length; Tsuihiji et al., 2007, in review) displays a well developed ascending diverticulum of the rostral tympanic recess; although we lack comparable CT data for adult *Tarbosaurus*, if we assume that *Tarbosaurus* resembled adult *T. rex*, ontogenetic loss of the ascending diverticulum in tyrannosaurines remains a possibility.

The rostral tympanic recess has another, more medial, diverticulum (the retrohypophyseal sinus, Figure 9A, B) that extends dorsomedially within the clivus of the basisphenoid just caudal to the hypophyseal (pituitary) fossa. This sinus represents a contralateral communication of the left and right rostral tympanic recesses, and has been found in all the tyrannosaurids studied here (Witmer and Ridgely, 2009). In CMNH 7541, the retrohypophyseal sinus itself sends a small median diverticulum between the paired abducens (CN VI) canals.

The sinuses associated with the basisphenoid recess have been mentioned above in connection with their external apertures. Given the asymmetry of their bony apertures, it is not surprising that the sinuses themselves are quite asymmetrical, much more so than the caudal and rostral tympanic recesses and their associated diverticula. The caudal basisphenoid sinuses expand dorsally and somewhat caudally, passing through the basioccipital, as noted above, to become broadly confluent with the medial subcondylar recess on the occiput (Figure 9). The caudal basisphenoid sinus has

some communication with the rostral tympanic recess (more so on the left side). The rostral basisphenoid sinuses expand dorsally and rostrally within the basisphenoid. Interestingly, although the shared aperture of the two rostral basisphenoid sinuses within the recess is shifted to the right side, the left sinus is larger and more broadly communicates with the rostral tympanic recess (Figure 9). This asymmetry could be natural but some small amount of postmortem crushing cannot be ruled out, as the right side of the braincase is generally not as well preserved as is the left side.

The subsellar recess is located rostral to the interbasipterygoid lamina at the ventral base of the cultriform process (Figure 9). The subsellar recess is relatively small in comparison to that of *T. rex* and *Daspletosaurus* but is similar in size to that of some juvenile *Gorgosaurus* specimens (e.g., ROM 1247). There are no pneumatic foramina within the subsellar recess on CMNH 7541.

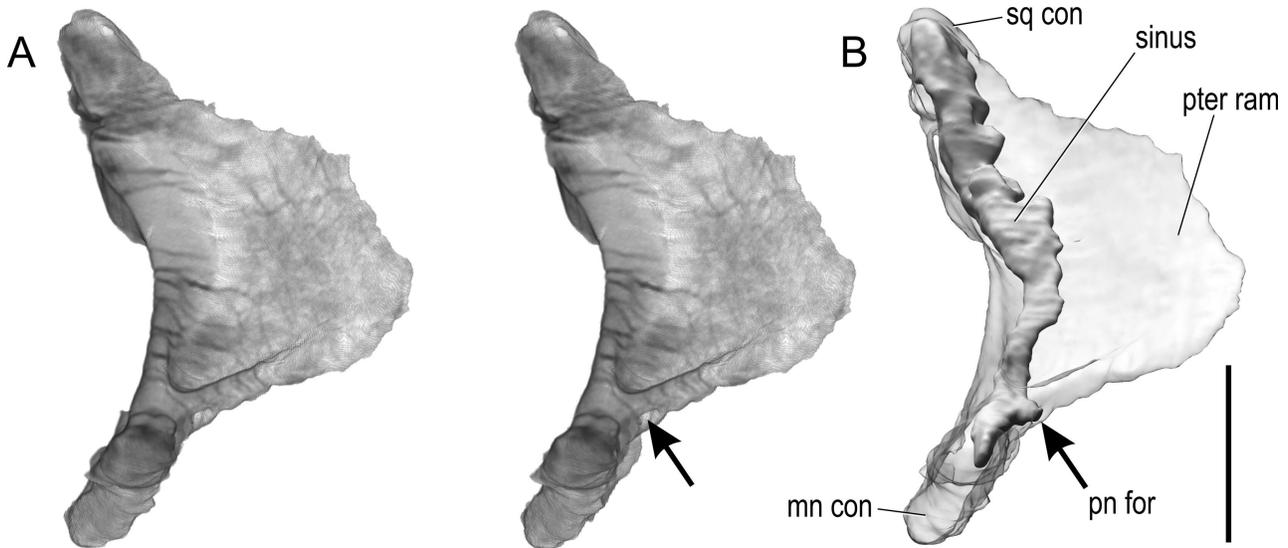
On the right side of CMNH 7541, but not the left, there is an aperture in the basisphenoid bone just dorsal to the base of the basiptyergoid process. The aperture is surrounded by a shallow fossa, and these features can be regarded as a basiptyergoid recess (Chure and Madsen, 1996; Witmer, 1997b). The aperture leads into a sinus (the basiptyergoid sinus) that ascends dorsally within the basisphenoid. Its communications with other sinuses in the basisphenoid are slight to nonexistent, although it does appear to breach the interbasipterygoid lamina within the basisphenoid recess, where, if so, it would then communicate with the air sinus located there. The basiptyergoid process itself is not pneumatized.

Finally, the subcondylar recesses open into a pneumatic fossa on the occiput below the occipital condyle (Witmer, 1997b) and have been mentioned above in connection with pneumatic apertures located in the otoccipital and basioccipital within the fossa (Figure 9C). Carr (1999) and Currie (2003b) both regarded the fossa for the subcondylar recesses of CMNH 7541 as shallow, but to our eyes it seems intermediate between the deep recess of young *Gorgosaurus* specimens (ROM 1247) and the very shallow recess of mature specimens of *T. rex* (e.g., AMNH 5027, AMNH 5117, FMNH PR2081; see Witmer and Ridgely, 2009). As noted above, the otoccipital aperture of the lateral subcondylar recess expands into a sinus within the crista tuberalis (where it communicates with the caudal tympanic recess), whereas the basioccipital aperture leads to the medial subcondylar sinus that communicates with the caudal basisphenoid sinus. The medial subcondylar sinus does not pneumatize the occipital condyle but just the very base of the neck, as Osborn (1912) showed for *T. rex* (AMNH 5029; see also Witmer and Ridgely, 2009).

Thus in summary, CMNH 7541 has an extensively pneumatized braincase, with clearly identifiable rostral and caudal tympanic recesses, a series of basisphenoid sinuses arising rostrally and caudally from the basisphenoid recess, medial and lateral subcondylar recesses, a small subsellar recess, and, on one side only, a basiptyergoid recess. Virtually all of these sinuses communicate broadly with adjacent sinuses. The two tympanic recesses are clearly derived from the middle ear sac (as their names imply), but the basisphenoid and subsellar recesses may derive from a separate median pharyngeal system (Witmer, 1997b). Likewise, although the subcondylar recesses could be tympanic in origin, it is not possible to rule out pneumatization via a cervical pulmonary diverticulum (Witmer, 1997b; Witmer and Ridgely, 2009).

### Columella (= stapes)

The columella is clearly preserved in natural position on the left side (Figure 6A, B; 8A, B). It is a very delicate element, extending from the fenestra vestibuli within the columellar recess,



**Figure 10.** Cleveland tyrannosaur skull, CMNH 7541. Volume (A) and surface (B) renderings of digitally extracted left quadrate derived from CT data in medial view. Volume renderings (A) are stereopairs; arrow points to the pneumatic foramen. Surface rendering (B) is partially transparent to reveal the internal pneumatic sinus. Scale bar equals 5 cm. See Appendix for abbreviations.

passing along the paroccipital process below the otosphenoidal crest, to end laterally just caudomedial to the dorsal head of the quadrate. The columella is only about 1.4 mm in diameter, yet is 71.7 mm in length. The length is probably an underestimate in that the lateral tip is exposed in the actual fossil, and it is unknown how much was lost in collection, preparation, etc. The fact that the columella is preserved in situ and is straight suggests that the braincase region as a whole has not undergone significant deformation.

#### Quadrate and its pneumaticity

The left quadrate was digitally extracted from the full CT dataset to examine and illustrate the position of its pneumatic aperture (Figure 10). Although a taxonomic difference in position of this foramen has not been noted previously, the quadrate pneumatic foramen of albertosaurines (*Gorgosaurus*: AMNH 5363; *Albertosaurus*: TMP 81.10.1; see also Currie, 2003b, p. 200) is in a slightly different position than in *Daspletosaurus* (FMNH PR 308) and *Tyrannosaurus* (FMNH PR2081). In the former, the pneumatic foramen is directed more medially, whereas in the latter group the crest of bone above the foramen on the quadrate's pterygoid ramus is much stronger and diverts the pneumatic foramen to a more rostral position such that it no longer directly faces the tympanic cavity. In CMNH 7541, the quadrate pneumatic foramen again has more of an intermediate position (Figure 10). The foramen itself is relatively small in CMNH 7541. BMR P2002.4.1 is very similar in these regards. The quadrate pneumatic sinus in CMNH 7541 is somewhat better preserved on the right side (not illustrated in Figure 10), but on both sides the sinus extends essentially the full height of the element (Figure 10B).

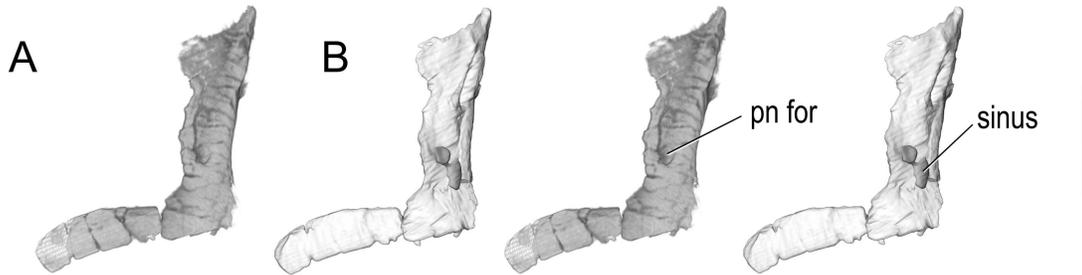
#### Quadratojugal and its pneumaticity

The quadratojugal is preserved on only the left side of CMNH 7541, and even here the bone is fractured and displaced such that its jugal process remains in articulation with the jugal, whereas its

squamosal process has been shifted dorsally and rostrally. The most significant attribute of the quadratojugal is the peculiar foramen in its lateral surface within the ventral apex of the lateral fossa. BMR P2002.4.1 shows a virtually identical foramen, but such a foramen is absent in adult *T. rex* and has not been reported in other tyrannosaurids, other than a small foramen in a specimen of *Gorgosaurus* sp. reported by P. Larson (2008). Although only rarely noted in print (e.g., P. Larson, 2008), some tyrannosaur workers have wondered if this difference supports the validity of the taxon *Nanotyrannus lancensis*. To clarify the anatomy, we examined this foramen in the CT dataset and digitally extracted the bone for visualization (Figure 11). The foramen is almost certainly a pneumatic foramen, expanding into a blind cavity within the substance of the bone. The cavity has no medial outlets, only the lateral aperture. This also would tend to indicate that the lateral quadratojugal fossa is a pneumatic fossa, most likely associated with the middle ear. Although it remains possible that presence of this quadratojugal pneumatic foramen is a juvenile feature of *T. rex* that was lost later in ontogeny, the very young skull of *Tarbosaurus* described by Tsuihiji et al. (2007; in review) lacks such a foramen, as do adult *Tarbosaurus* quadratojugals, suggesting that presence and then loss of the pneumatic foramen was not a general ontogenetic sequence of tyrannosaurines.

#### Palatine bone and its pneumaticity

The left palatine bone of CMNH 7541 also was digitally extracted (Figure 12). The bone is a fairly typical tyrannosaurid palatine. The bone is pneumatic as in other tyrannosaurids and some other theropods (Witmer, 1997a, b; Witmer and Ridgely, 2008b) with two pneumatic foramina plainly visible on the actual skull (Figure 2A). When examined with CT, however, it can be seen that the two pneumatic sinuses within the bone do not communicate but instead form separate chambers. Although the vomeropterygoid process is fully pneumatized (Figure 12B), the bone is not strongly inflated, as seen in many *T. rex* specimens (e.g.,



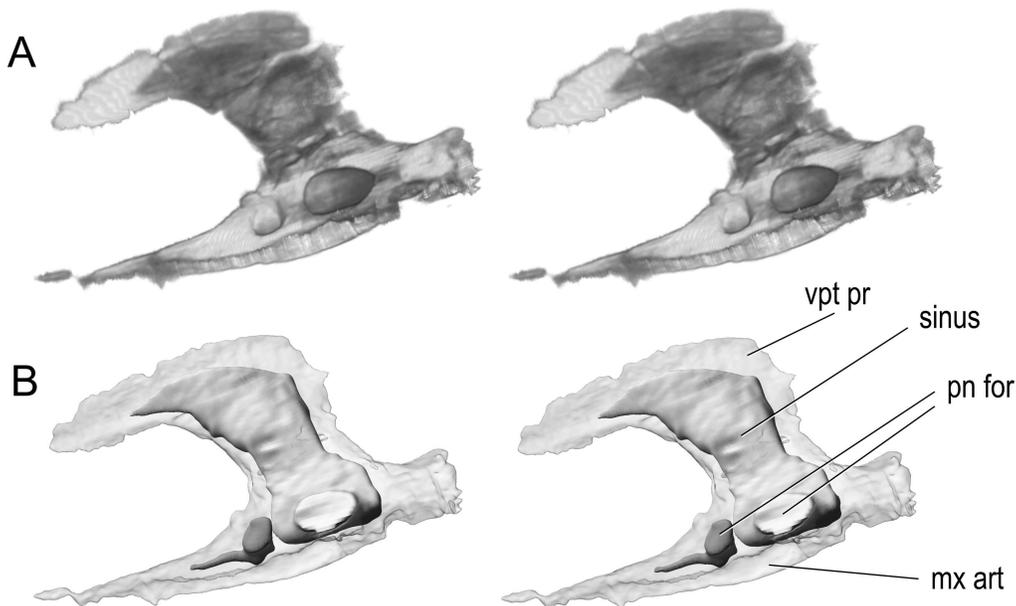
**Figure 11.** Cleveland tyrannosaur skull, CMNH 7541. Volume (A) and surface (B) renderings of digitally extracted left quadratojugal derived from CT data in lateral view. Both sets are stereopairs. Surface rendering (B) is partially transparent to reveal the internal pneumatic sinus. In the actual specimen, the jugal process was displaced relative to the rest of the bone, but has been digitally reattached here. Scale bar equals 5 cm. See Appendix for abbreviations.

FMNH PR2081, MOR 008). In general, the palatine of BMR P2002.4.1 has a similar conformation with a large pneumatic aperture caudally, but, unlike CMNH 7541, the rostral pneumatic feature does not breach the bone and so is a fossa, not a foramen.

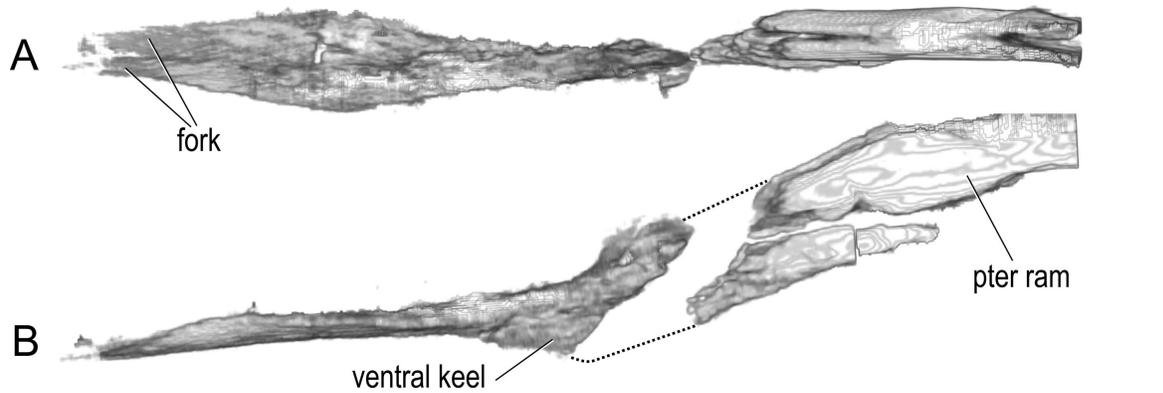
### Vomer

The shape of the rostral end of the vomer is an important character in tyrannosaurid systematics, with basal tyrannosauroids and albertosaurines (*Gorgosaurus* and *Albertosaurus*) retaining the primitive condition of a narrow, “lanceolate” vomer and tyrannosaurines (*Daspletosaurus*, *Tarbosaurus*, *Tyrannosaurus*) having a derived, laterally expanded, diamond-shaped vomer (Holtz, 2001, 2004; Currie et al., 2003; Li et al., 2010). The vomer of CMNH 7541 is almost completely enclosed in matrix, with just the caudalmost portion exposed within the antorbital cavity (Figures 1A, 2A). So, to shed light on the systematically important end of the bone, we digitally extracted the vomer for visualization (Figure 13). The vomer of CMNH 7541 has the

primitive condition, with a narrow rostral end. In fact, the rostralmost tip has the further primitive attribute of forking to contact the palatal processes of the maxilla and premaxilla. Overall, the vomer is a fairly typical non-tyrannosaurine theropod vomer with a dorsal sulcus and a ventral keel. The vomer of BMR P2002.4.1 is again almost identical to that of CMNH 7541. A valid question is whether this morphology is truly primitive or just reflective of an early ontogenetic stage that would transform later in life to the definitive adult tyrannosaurine condition (i.e., *T. rex*). In this context, the very young *Tarbosaurus* specimen described by Tsuihiji et al. (2007; in review) is significant in having a rostrally narrow vomer similar to those of CMNH 7541 and BMR P2002.4.1, suggesting that indeed a lanceolate vomer can ontogenetically transform into a diamond-shaped vomer. That said, if CMNH 7541 pertains to a juvenile *T. rex*, then the rate of transformation would have had to have been markedly different in *T. rex* and *Tarbosaurus* in that an unnumbered juvenile *Tarbosaurus* skull (only about 27% larger than CMNH 7541) already has a diamond-shaped vomer.



**Figure 12.** Cleveland tyrannosaur skull, CMNH 7541. Volume (A) and surface (B) renderings of digitally extracted left palatine derived from CT data in lateral view. Both sets are stereopairs. Surface rendering (B) is partially transparent to reveal the internal pneumatic sinuses; note that the two sinuses do not communicate. Scale bar equals 2 cm. See Appendix for abbreviations.



**Figure 13.** Cleveland tyrannosaur skull, CMNH 7541. Volume renderings of digitallly extracted vomer derived from CT data in A, dorsal; B, left lateral views. Note that rostral portion of the bone is primitive in being lanceolate and forked. Dotted lines represent restored portions in the area corresponding to the transverse oblique plane of fracture (see Figure 4C). Scale bar equals 5 cm. See Appendix for abbreviations.

### Possible respiratory turbinates

Respiratory turbinates in amniotes have received a great deal of attention because of their potential role in debates on dinosaur metabolic status (Bakker, 1992; Ruben, 1996; Ruben et al., 1996, 1997). The idea promoted by J. A. Ruben (1995) is that respiratory turbinates may be mandatory in endothermic animals to help mitigate the effects of respiratory evaporative water loss that would result from the high lung-ventilation rates characteristic of endotherms. As mentioned above, CT scanning of CMNH 7541 has been a major player in this debate. Bakker (1992) reconstructed a large scrolled turbinate within the snout of this animal, but, given that the reconstruction was published in a popular magazine (*Discover*), no details were given. Later Ruben and his team (1996, 1997) argued (using the same scan data) that no turbinates were present, and that, moreover, the airway was too small to house turbinates.

Unfortunately, CMNH 7541 is not the best specimen on which to base a debate, because so much of the snout is damaged and reconstructed with plaster. As noted above, clear *olfactory* turbinates are present far caudally (Figures 5–8); they are immediately adjacent to the olfactory bulb fossa and could not have functioned as respiratory turbinates because they are well out of the main nasal airstream (see Witmer and Ridgely, 2008b, 2009). Rostral to the olfactory turbinates is a large segment of matrix in which no ossified or calcified (i.e., fossilized) turbinate-like structures can be seen, and rostral to this is a large plaster-reconstructed area (in association with the oblique transverse fracture mentioned earlier; see Figure 4B, C). Ironically, this large region is the area in which Bakker (1992, p. 61) reconstructed his turbinates.

Our new scanning of CMNH 7541, however, has identified structures within the rostral portion of the snout—in front of the region where Bakker (1992) reconstructed a turbinate and behind the region where Ruben et al. (1996) showed turbinates to be lacking—that may be interpreted as being respiratory turbinates (Figure 14). The structures in question are located in the main nasal airway above the maxillary antra (which themselves are largely reconstructed in plaster). These structures form a series of thin, but moderately dense laminae visible within undistorted matrix that are associated with both the nasal and the maxilla and project into the nasal airway. There are some regions of

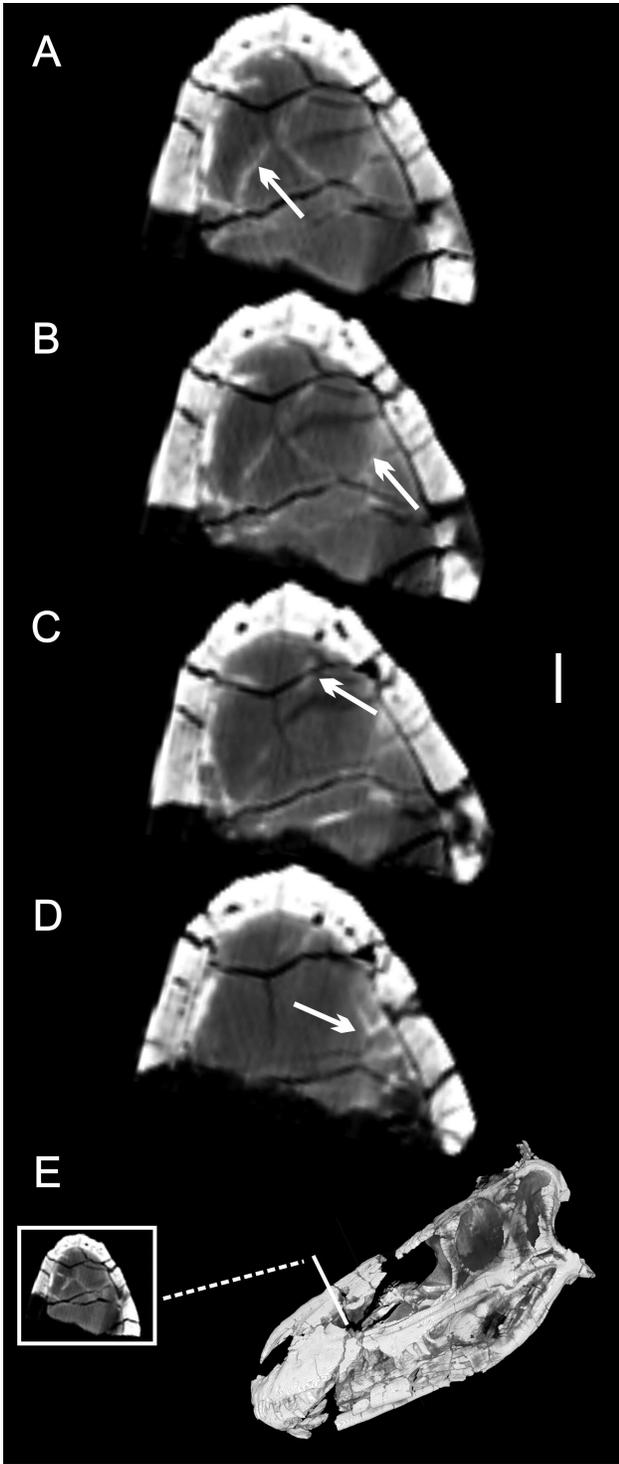
symmetry, and some elements that can even be tentatively regarded as “scrolls” (Figure 14). The density of these putative turbinates is less than the adjacent nasal and maxilla but more than the surrounding matrix. Whether or not these moderate density values reflect calcification of cartilaginous structures or just very thin bone is difficult to determine. Certainly, they are positioned appropriately to be turbinates with a respiratory function in that they are within the portion of the main nasal airway between the naris and choana.

### Mandible

The two mandibles are preserved in full occlusion with the skull, and so, although many details of the mandible can be seen (Figures 1–3), details of the tooth-bearing portions are not easily observed. Thus, obtaining information on the common comparative metric of number of tooth positions had been impossible for CMNH 7541. To remedy this situation, we digitallly extracted the right mandible because the dental region is better preserved (Figure 15). CMNH 7541 has at least 16 relatively clear tooth positions, which is similar to BMR P2002.4.1, which has 16 or 17 (P. Larson, 2008). For comparison, Holtz (2004, p. 119) provided a range among tyrannosaurids of 18 in *Alectrosaurus* and 11 in *T. rex*. Hurum and Sabath (2003, p. 187) reported 12–14 dentary tooth positions in *T. rex* and 14–15 in *Tarbosaurus*. Russell (1970) reported 15–16 for *Daspletosaurus*. Thus, CMNH 7541 is fully within the range of Tyrannosauridae, but does not overlap *T. rex*. Significantly, Tsuihiji et al. (2007; in review) reported the exact same range of dentary tooth positions (14–15) in a very young specimen of *Tarbosaurus* as Hurum and Sabath (2003) reported for adult *Tarbosaurus*, suggesting no ontogenetic change in tooth counts in this species that is so closely related to *T. rex*, and thus diminishing the case for CMNH 7541 being a young *T. rex*.

### Discussion

The preceding sections have sought to provide anatomical details of the Cleveland tyrannosaur skull (CMNH 7541) that have not been previously widely available (or available at all). CT scanning—and, more significantly, 3D visualization of the CT scan data—has yielded a new look at this famous fossil. For many workers, the systematic question is paramount, but it is obvious that the ontogenetic question is inextricably linked to any

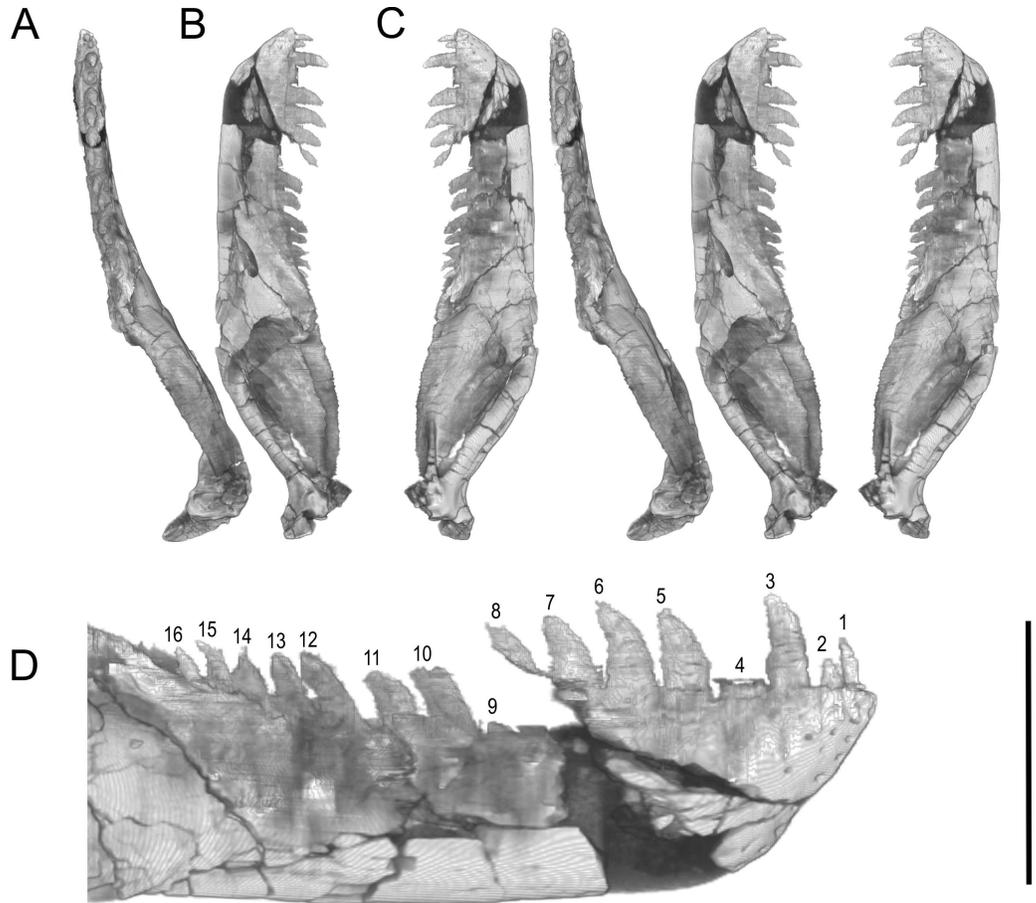


**Figure 14.** Cleveland tyrannosaur skull, CMNH 7541. A–D, progressively more caudal CT slices through the snout at the position shown in E, showing structures interpretable as respiratory turbinates (arrows). Note that some symmetry is preserved in A and B. In C, a structure (arrow) can be seen to cross a crack. D shows a series of structures associated with the maxilla. Scale bar equals 1 cm.

systematic outcome. That is, are the differences observed in CMNH 7541 attributable to its apparent young age or to it being a different taxon or both? Some of the different ideas were presented in the Introduction, and no firm resolution is offered here, in part because other data pertinent to this debate have yet to be published. Most significant is the discovery of a skull and associated partial postcranium (BMR P2002.4.1) of an animal that is very similar to CMNH 7541 and which will be critical in providing information from the postcranial skeleton that could be relevant to the systematic question. Moreover, there are other, still unpublished skulls of young and juvenile tyrannosaurids (Tsuihiji et al., 2007; in review; N. Larson, 2008; Carr and Williamson, 2010) that can shed light on patterns of ontogenetic transformation and help with discrimination of primitive versus juvenile characters. Other unpublished, clearly adult specimens have raised the prospect of there being species of tyrannosaurids in the Hell Creek other than *T. rex* (N. Larson, 2008; P. Larson, 2008). The question in this case would be, do these specimens display attributes of CMNH 7541 that might indicate that they are adult *Nanotyrannus lancensis*? Until these new specimens are analyzed and published, the status of CMNH 7541 must remain uncertain.

Having said that, the foregoing discussions have revealed an interesting suite of apparently derived attributes observed in CMNH 7541 that might suggest that it represents a taxon separate from *T. rex*. For example, the patterns of pneumatic sinuses and their bony apertures in the braincase are quite distinct from other tyrannosaurids. Although pneumatic sinuses certainly can change ontogenetically (Witmer, 1990, 1997a, b; Witmer and Ridgely, 2008b; and references therein), most of the changes in later ontogeny of most taxa pertain to expansion, contraction, and/or communication of sinuses and not to the basic pattern of bony apertures. For example, *Gorgosaurus* and *Tyrannosaurus* are more similar to each other in their patterns of basicranial pneumatic foramina than either is to the highly asymmetrical apertures of CMNH 7541, and there is no evidence to suggest that either of the two named taxa went through an ontogenetic stage resembling CMNH 7541. Likewise, the broad communication of the caudal tympanic recess and lateral subcondylar recess in CMNH 7541 is unique among tyrannosaurs sampled thus far. To these apparent apomorphies can be added the findings from the brain endocast of CMNH 7541 (Witmer and Ridgely, 2009), such as the rostrally offset pituitary fossa and orbital cranial nerve canals, as well as the strongly downturned endocast and skull as a whole, as indicated by the orientation of the lateral semicircular canal of the inner ear.

Although many workers have been struck by the *T. rex*-like temporal expansion of CMNH 7541, this derived character is coupled with a series of primitive attributes, such as the narrow and lanceolate vomer, the uncompressed basisphenoid recess, the pattern of pneumatic apertures in the subcondylar recess, the strength of the condylotubular crest, the low cultriform process and small subsellar recess, the laterally positioned vagus foramen, and the high number of dentary tooth positions. Although the possibility cannot be ruled out, it seems hard to believe that the animal pertaining to CMNH 7541 would have ontogenetically transformed all of these attributes (both primitive and derived) and grown up to be a typical member of *Tyrannosaurus rex*. CMNH 7541 does not pertain to a hatchling, but rather a fairly mature (“teenage”) animal, though perhaps not yet in the exponential stage of growth (in the sense of Erickson et al., 2004), and thus it is hard to envision such major morphological



**Figure 15.** Cleveland tyrannosaur skull, CMNH 7541. Volume renderings of digitally extracted right mandible derived from CT data in A, dorsal; B, medial; C, lateral views. A–C are stereopairs. D, close-up of mandible in lateral view; numbers correspond to tooth positions, of which there are 16. Scale bars equal 10 cm.

changes. Certainly, significant morphological changes can take place in animals at nearly adult age, as Sampson (1999, 2001; see also Sampson et al., 1997) showed for ceratopsids in which many of the attributes relating to sexual display develop at essentially adult body sizes (see also Horner and Goodwin, 2006, 2009). Obviously, few if any of the features listed above for CMNH 7541 are of the type that would either be recruited for sexual display or are even remotely related to secondary sexual characteristics. We (Witmer and Ridgely, 2009) previously evaluated in some detail other means of explaining our findings, such as diagenetic distortion or pathology, but neither explanation is compelling. That said, we recognize that some aspects of CMNH 7541 are unusual enough that its being simply aberrant may always remain possible, which is why we have never stated definitively that it is not a juvenile *T. rex*. Ultimately, until the known but unpublished specimens are fully analyzed, we regard the taxonomic status of CMNH 7541 to be an open question, being either a separate taxon (*Nanotyrannus lancensis*) or a juvenile *Tyrannosaurus rex*.

Finally, given the finding here of structures interpretable as respiratory turbinates, it is tempting to make broader claims about metabolic physiology and endothermy. We hesitate to do so, because the skull has only a small area well enough preserved to make such assessments, and we would prefer to be able to sample more widely within the nasal cavity. Nevertheless, taking

our data at face value, it is difficult to explain the laminar structures within the nasal airway as anything else. They are not artifacts of the CT scanning process, nor are they sedimentary structures. In fact, such structures are found nowhere else in the entire dataset. Assuming that they are indeed real structures projecting into the nasal airway and covered with moist mucosal respiratory epithelium, it is hard to imagine how they would *not* function as counter-current heat exchangers, precisely as postulated by Ruben and colleagues (1996, 1997). Whether or not these structures are indeed causally associated osteological correlates of endothermy or whether these supposed turbinates are extensive enough to have the effect posited by Ruben et al. (1996) is harder to say, but certainly it now seems unreasonable to argue that such structures are absent in dinosaurs.

#### Acknowledgments

We give posthumous thanks to Michael Williams for agreeing to the studies conducted here and regret that his passing did not allow him to participate. We thank the Cleveland Museum of Natural History and B. Latimer, M. Ryan, B. Redmond, and G. Jackson for loan of CMNH 7541 and for allowing it to be CT scanned yet again. We are grateful to H. Rockhold and O'Bleness Memorial Hospital in Athens, Ohio, for providing access to their top-notch scanning services which provided us with an excellent

new dataset. We thank the Cleveland Museum for providing access to the existing Boeing CT dataset. We thank M. Henderson for sharing unpublished information on the Burpee Museum of Natural History tyrannosaur specimen. We thank T. Tsuihiji and M. Watabe for allowing us to participate in the CT scanning and analysis of the juvenile *Tarbosaurus* skull. For fruitful discussion, we thank J. Bourke, C. Brochu, S. Brusatte, T. Carr, P. Currie, J. Daniel, D. Dufeu, M. Henderson, T. Hieronymus, C. Holliday, J. Horner, T. Holtz, G. Hurlburt, J. Hurum, M. Lamanna, P. Larson, P. Makovicky, P. Manning, A. Martiny, R. Molnar, W. Porter, O. Rauhut, M. Ryan, S. Sampson, P. Sereno, E. Snively, K. Stevens, F. Therrien, T. Tsuihiji, and D. Zelenitsky among many others. We thank M. Ryan and J. Hannibal for comments that greatly improved the manuscript. We thank the Ohio Supercomputer Center for their support. Funding was provided by the National Science Foundation (IBN-0343744 and IOB-0517257) and the Ohio University College of Osteopathic Medicine.

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## Appendix. Key to abbreviations.

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II	foramen for optic nerve (cranial nerve II)	ibtl	interbasipterygoidal lamina of basisphenoid, running between basipterygoid processes
III	foramen for oculomotor nerve (cranial nerve III)	itl	intertuberal lamina of basisphenoid/basioccipital, running between basal tubera
V <sub>1</sub>	foramen for ophthalmic nerve (cranial nerve V <sub>1</sub> )	lab	endosseous labyrinth
V <sub>2-3</sub> /VII	common external opening in braincase for maxillomandibular and facial nerve canals	lscr	lateral subcondylar recess
VI	foramen for abducens nerve (cranial nerve VI)	mn con	mandibular condyle of quadrate
X	foramen for vagus nerve (cranial nerve X)	mx art	maxillary articular surface of palatine
ad	ascending diverticulum of rostral tympanic recess	mser	medial subcondylar recess
bpt	basipterygoid process of basisphenoid	obc	olfactory bulb cavity
bptr	basipterygoid process pneumatic recess	oc	occipital condyle of basioccipital
bsrc	basisphenoid recess, caudal	olf	olfactory chamber of frontal
bsrr	basisphenoid recess, rostral	osc	otosphenoidal crest
bt	basal tuber	ot	olfactory turbinates within olfactory chamber
cap	capitate process of laterosphenoid	paroc	paroccipital process of otoccipital (fused exoccipital + opisthotic)
cc	columellar recess	pfo	pituitary (hypophyseal) fossa
col	columella auris (= stapes)	pn for	pneumatic foramen
cp	cultriform process (= parasphenoid rostum)	prp	preotic pendant
ctc	rista tuberalis of otoccipital	pter ram	pterygoid ramus of quadrate or vomer
ctc	crista condylotuberalis of basioccipital, running between occipital condylar neck and basal tuber	rhs	retrohypophyseal pneumatic sinus
ctr	caudal tympanic recess	rtr	rostral tympanic recess
ctra	caudal tympanic recess, aperture	sc	sagittal crest
cvcm	caudal middle cerebral vein foramen	socs	sinus in supraoccipital from caudal tympanic recess
cvl	crista ventrolateralis of basisphenoid, running between basal tuber and basipterygoid process	spheth	sphenethmoid ossification
dtfo	dorsotemporal fossa	sq con	squamosal condyle of quadrate
end	brain endocast	ss	sulcus septalis on cultriform process (for cartilaginous septum)
f	frontal bone	ssr	subsellar recess
fm	foramen magnum	tnc	transverse nuchal crest on parietal
		vpt pr	vomeroterygoid process of palatine

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