New Insights Into the Brain, Braincase, and Ear Region of Tyrannosaurs (Dinosauria, Theropoda), with Implications for Sensory Organization and Behavior

LAWRENCE M. WITMER* AND RYAN C. RIDGELY
Department of Biomedical Sciences, College of Osteopathic Medicine, Ohio University, Athens, Ohio

ABSTRACT

The braincase region of tyrannosaurs was investigated to provide insights on anatomical attributes relevant to inferences of sensory biology and behavior. CT scanning focused on three specimens of *Tyrannosaurus rex*, a juvenile *Gorgosaurus*, and the controversial Cleveland skull (CMNH 7541). Analysis shows that the cerebral hemispheres were enlarged, but conflicting information on the optic lobes suggests that brain conformation was not fully avian. Previous estimates of olfactory bulb size for *T. rex* were much too large, but even the corrected sizes are relatively larger than other theropods, suggesting that odor detection was indeed of particular importance to tyrannosaurs. The inner ears show a number of coelurosaurian traits, such as elongate and rounded and rostral, lateral semicircular canals, and incipient twisting of the common crus, which we interpret to be related to enhanced reflexes coordinating rapid eye and head movements. The cochlea is elongate, which, coupled with the finding of extensive tympanic pneumaticity, supports the inference of behavioral emphasis of low-frequency sounds. Three main groups of sinuses pneumatized the braincase, and there are a number of perhaps systematically relevant differences. Orientation of the endosseous labyrinth reveals that alert head postures of *T. rex* and *Gorgosaurus* were somewhat depressed below the horizontal, but the Cleveland skull had a very strongly down-turned posture. It is concluded that tyrannosaur sensory biology is consistent with their predatory coelurosaurian heritage, with emphasis on relatively quick, coordinated eye and head movements, and probably sensitive low-frequency hearing; tyrannosaurs apomorphically enhanced their olfactory apparatus. The taxonomic status of the Cleveland skull remains unresolved. Anat Rec, 292:1266–1296, 2009. © 2009 Wiley-Liss, Inc.

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The braincase region of the skull is biologically important for a variety of reasons. It houses the brain and cranial nerves, and it partially or completely encloses some cephalic sense organs (e.g., inner ear, eyeball, olfactory region). Moreover, the braincase provides area of attachment for the musculature of the jaw and neck, as well as the bony articulation for the neck itself. The braincase may even sport bony scaffolding for display or agonistic structures, and thus may play a direct behavioral role. Despite these fundamental and far-reaching functions, Currie (1997, p 81) was correct in regarding the braincase as "generally one of the most poorly understood regions of the dinosaur skeleton." Indeed, its morphological complexity and fragility have made interpretation of braincase structure challenging. Moreover, braincases tend to be embedded within the skull, which itself may be filled with rock matrix. But even isolated, well-prepared, well-preserved braincases often keep some secrets locked away, such as the structure of the brain cavity or inner ear. Fortunately, the advent of X-ray computed tomography—i.e., CT scanning—has revolutionized the study of braincases by allowing us to peer inside and visualize these structures in 3D (Rogers, 1998, 1999, 2005; Brochu 2000, 2003; Witmer et al., 2003; Domínguez Alonso et al., 2004; Franzosa, 2004; Franzosa and Rowe, 2005; Kundrát, 2007; Sampson and Witmer, 2007; Sereno et al., 2007; Zhou et al., 2007; Witmer and Ridgely, 2008a,b, in press; Witmer et al., 2008). We present here the results of a CT-based study of the braincases of tyrannosaurs and other dinosaurs, in which we reconstruct and analyze the cranial endocast, inner ear, and pneumatic sinuses, and from which we draw inferences about tyrannosaur behavior and sensory capabilities.

The study of the braincases of tyrannosaurs dates back almost a century to Osborn's (1912) seminal paper in which he described three specimens of *Tyrannosaurus rex* (AMNH FR 5027, AMNH FR 5029, and AMNH FR 5117). Osborn sagittally sectioned AMNH FR 5029 and generated a cranial endocast, providing our first glimpse into the brain of a tyrannosaur (Osborn, 1912). Osborn's (1912) *T. rex* endocast was very influential, both anatomically (Hopson, 1979) and in studies of relative brain size (Jerison, 1973; Hopson, 1977, 1980; Hurlburt, 1996; Larsson et al., 2000). Brochu's (2000, 2003) CT-based work on FMNH PR2081 represented the first new data on tyrannosaur endocasts since Osborn. Saveliev and Alifanov (2007) presented a reanalysis of the endocast of *Tarbosaurus* based on the same sagittally sectioned braincase described by Maleev (1965). We present here new cranial endocasts of *T. rex* based on both AMNH FR 5029 and FMNH PR2081, as well as another, better specimen (AMNH FR 5117), and compare these to other tyrannosaurs and other theropods. Russell (1970) was perhaps the first to recognize that the large sinuses within the basicranium of tyrannosaurs were air-filled in life (i.e., pneumatic), and we present here a new analysis of braincase pneumaticity in *T. rex* and *Gorgosaurus*, integrating it with our work elsewhere (Witmer and Ridgely, in press) on the Cleveland tyrannosaur skull (CMNH 7541, holotype of *Nanotyrannus*).

This last taxon, *Nanotyrannus lancensis*, was named by Bakker et al. (1988) for the enigmatic Cleveland skull (CMNH 7541). Almost since its discovery, the Cleveland skull has been controversial. Gilmore (1946) first described it as a species of *Gorgosaurus* and regarded it as an adult. Rozhdestvensky (1965) considered it to be juvenile, but Russell (1970) considered it to be adult. Bakker et al. (1988) also regarded it as an adult, but as an adult of a new genus, *Nanotyrannus*. Carpenter (1992) suggested that it might pertain to a juvenile *T. rex*. Carr (1999; see also Carr and Williamson, 2004) subsequently presented compelling evidence for its juvenile status, likewise suggesting that it pertains to *T. rex*, which has been followed by Holtz (2001, 2004), Brochu (2003), and Paul (2008). Finally, Currie (2003a,b; Currie et al., 2003) agreed that CMNH 7541 was a juvenile, but disputed its referral to *T. rex*, instead retaining *N. lancensis*. Likewise, Larson (2008) argued strongly for *Nanotyrannus* being distinct from *Tyrannosaurus*, and, moreover, referred a new specimen (BMR P2002.4.1; Henderson and Harrison, 2008) that is very similar to CMNH 7541 to *N. lancensis*. We present here new data on the cranial endocast and inner ear of the Cleveland skull, complementing our work (Witmer and Ridgely, in press) on other aspects of the braincase and skull as a whole. CMNH 7541 continues to be problematic, and, although internal braincase structures shed important new light, resolution of the systematic issues remains elusive.

Despite literally dozens of known tyrannosaur skulls, there are very few anatomical descriptions of the bony braincase in the literature. The work of Bakker et al. (1988) remains among the most detailed and taxonomically diverse in scope. Other important papers include Currie (2003b) on *Albertosaurus* and *Daspletosaurus*, Maleev (1965, 1974) and Hurum and Sabath (2003) on *Tarbosaurus*, Osborn (1912), Molnar (1991), Brochu (2003) on *Tyrannosaurus*, and Carr (1999) and Carr and Williamson (2004) on a diversity of tyrannosaurs. It is not our intention to redescribe the bony braincase in detail. Rather, we focus on the structures housed within the braincase (e.g., endocast, labyrinth, sinuses) and their relationships to the surrounding bones. New insights into bony structure, however, result from visualizing these "virtual casts" of soft-tissue structures together with the bone in 3D computer-generated models, allowing greater clarity regarding identification of various foramina and spaces.

MATERIALS AND METHODS

Institutional abbreviations are listed in Table 1, and anatomical abbreviations are listed in Table 2.

The reconstructions of soft-tissue structures, sensory capabilities, and behaviors presented here are grounded in comparative approaches that draw extensively on observations made in the extant realm, in particular the extant outgroups of tyrannosaurs (birds and crocodilians; Witmer, 1995b). As a result, first hand knowledge of not only the bony braincase but also the relevant soft-tissue systems (e.g., brain, cranial nerves, vasculature, cephalic air sacs, jaw and cervical muscles) provides critical information on how these systems interact with the bone to produce interpretable osteological correlates. This tyrannosaur study is part of a much larger, phylogenetically controlled project in our laboratory looking at the evolution of all of these systems in archosaurs as a whole. We drew on this broader perspective when making identifications of structures and assigning names.

TABLE 1. Institutional abbreviations

Abbreviation	Institution	Location
AMNH	American Museum of Natural History	New York City, New York
BHI	Black Hills Institute	Hill City, South Dakota
BMNH	Natural History Museum	London, United Kingdom
BMR	Burpee Museum of Natural History	Rockford, Illinois
CM	Carnegie Museum of Natural History	Pittsburgh, Pennsylvania
CMN	Canadian Museum of Nature	Ottawa, Ontario, Canada
CMNH	Cleveland Museum of Natural History	Cleveland, Ohio
FMNH	Field Museum of Natural History	Chicago, Illinois
IGM	Institute of Geology, Mongolian Academy of Sciences	Ulan Bataar, Mongolia
MOR	Museum of the Rockies, Montana State University	Bozeman, Montana
MWC	Museum of Western Colorado	Grand Junction, Colorado
MCZ	Museum of Comparative Zoology, Harvard University	Cambridge, Massachusetts
OMNH	Oklahoma Museum of Natural History, Oklahoma University	Norman, Oklahoma
PIN	Paleontological Institute, Russian Academy of Sciences	Moscow, Russia
ROM	Royal Ontario Museum	Toronto, Ontario, Canada
SDSM	South Dakota School of Mines and Technology	Rapid City, South Dakota
TMP	Royal Tyrrell Museum of Palaeontology	Drumheller, Alberta, Canada
UMNH	University of Utah Museum of Natural History	Salt Lake City, Utah
ZPAL	Institute of Paleobiology of the Polish Academy of Sciences	Warsaw, Poland

Although a number of specimens were subjected to CT scanning (see below), the total sample includes specimens studied more traditionally via observation, and this latter category was critical for establishing basic anatomy and assessing variability. Specification of a museum catalog number throughout this article indicates that the original material was studied, whereas observations from casts or the literature are indicated as such. The primary specimens of *Tyrannosaurus rex* used in this study were as follows: (1) AMNH FR 5117 (virtually complete and undistorted braincase), (2) AMNH FR 5029 (sagittally sectioned braincase), and (3) FMNH PR2081 (complete skull). Other *T. rex* specimens studied include AMNH FR 5027, CM 79057, TMP 81.6.1, BHI 3033, SDSM 12047, MOR 008, MOR 555, MOR 1125, and MOR 557. It should be noted that there is some debate about the alpha taxonomy of these specimens (Carr and Williamson, 2004; Larson, 2008), but until any new species are formally named, we regard them all as pertaining to *T. rex*. The primary specimen of *Gorgosaurus libratus* was ROM 1247 (nearly complete, somewhat laterally compressed braincase). Other specimens of *G. libratus* studied include ROM 1422, TMP 91.36.500, TMP 94.12.602, AMNH FR 5336, and AMNH FR 5664. Specimens of *Daspletosaurus* studied include CMN 8506, FMNH PR308, TMP 94.143.1, TMP 2001.36.1, and MOR 590. The Cleveland skull (CMNH 7541) was studied in detail (see Witmer and Ridgely, in press). Despite lacking the braincase, original and cast material of BMR P2002.4.1 were also examined. The braincase of *Tarbosaurus* was studied via a cast of a sagittally sectioned specimen (PIN 553-3/1; Maleev, 1965, 1974; Saveliev and Alifanov, 2007) and CT data of ZPAL MgD-I/4 provided by J. H. Hurum; these data are currently under study by the authors in collaboration with D. L. Dufeau and J. H. Hurum. Also, a newly discovered skull of a very young *Tarbosaurus* collected by the Hayashibara Museum and Mongolian Paleontological Center was studied by the authors in connection with a project led by T. Tsuihiji (Tsuihiji et al., 2007). The grouping of these taxa more or less corresponds to traditional definitions of Tyrannosauridae (e.g., Holtz, 2004), but revisions currently being undertaken by a number of researchers may change the definitions. Consequently, we use the term "tyrannosaur" in a relatively general sense to include the above taxa.

AMNH FR 5117, AMNH FR 5029, ROM 1247, CMNH 7541, and some elements of CM 79057 were scanned at O'Bleness Memorial Hospital (OBMH) in Athens, Ohio, using a General Electric (GE) LightSpeed Ultra Multislice CT scanner equipped with the Extended Hounsfield option, which improves resolvability of detail from dense objects such as fossils by extending the dynamic range of images as much 16-fold. Specimens were scanned helically at a slice thickness of 625 μm, 120 kV, and usually 200–300 mA. Additional scans of some specimens were done with somewhat different parameters (e.g., 1.25 mm slice thickness, 140 kV), and an additional scan of larger specimens was done with a narrower field of view (e.g., the central region encompassing the brain cavity and labyrinth) so that a bow-tie filter could be used to decrease beam-hardening artifacts. The raw scan data were reconstructed using a bone algorithm. Data were output from the scanner in DICOM format and then imported into Amira 3.1.1 or 4.1.2 (Mercury-TGS, Chelmsford, MA) for viewing, analysis, and visualization. Datasets deriving from different scans of the same specimen were subsequently registered in Amira, and thus the benefits of the different scan parameters could be combined in a single analysis. In contrast to the above, we used the "industrial" CT dataset for FMNH PR2081 published by Brochu (2003), and that paper may be consulted for scan details. It should be noted, however, that the CT metrics (e.g., voxel size) used by Brochu (2000, 2003) to produce the cranial endocast were in error, and thus the proportions of his illustrated digital renderings are somewhat foreshortened along the z or long axis; likewise, the dataset from which he worked was mirrored such that left and right are reversed. Prior to our scanning of CMNH 7541 noted above, the Cleveland skull had been scanned at the Boeing Rocketdyne CT Lab in California at a slice thickness of 1 mm with slices in the horizontal plane (voxel sizes were 0.4042 mm × 0.4042 mm × 1.0 mm); the results presented here

TABLE 2. Anatomical abbreviations

Abbreviation	Meaning of abbreviation
ad	ascending diverticulum of rostral tympanic recess
aoc	antotic crest
aw	main airway through the nasal cavity
bsr	basisphenoid recess (es)
bt	basal tubera
car	cerebral carotid artery canal
c	cochlear duct (= lagena)
cc	columellar canal
cer	cerebral hemisphere
col	columella (= stapes)
crc	crus communis
csc	caudal (posterior vertical) semicircular canal
csca	ampulla of caudal semicircular canal
ct	crista tuberalis, running between paroccipital process and basal tuber
ctc	condylotuberal crest, running between occipital condylar neck and basal tuber
ctr	caudal tympanic recess
ctra	bony aperture of caudal tympanic recess
cvcm	caudal middle cerebral vein
dp	dural peak
dv	diploic vein draining bone tissue
ed	endolymphatic duct canal
epif	articular facet for epipterygoid bone
fc	fenestra cochleae (= round window)
fl	flocculus (= cerebellar auricle)
fm	foramen magnum
fv	fenestra vestibuli (= oval window)
gps	glossopharyngeal sulcus
ibtl	interbasipterygoidal lamina, running between basipterygoid processes
itl	intertuberal lamina, running between basal tubera
lab	endosseous labyrinth
lsc	lateral (horizontal) semicircular canal
lsca	ampulla of lateral semicircular canal
lscr	lateral subcondylar recess
mes	mesethmoid ossification
mscr	medial subcondylar recess
ob	olfactory bulb
oevc	orbital emissary vein canal
olf	olfactory region of nasal cavity
ons	sulcus (or sulci) for olfactory nerve branches and associated vessels
opt	optic lobe (= tectum)
ot	olfactory turbinates
otc	olfactory tract cavity
ovc	orbital venous canal, running from olfactory region of nasal cavity into the orbit
pfo	pituitary (= hypophyseal) fossa
pin	pineal peak
prp	preotic pendant
prpn	prootic pneumatic fossa
rhs	retrohypophyseal pneumatic sinus
rsc	rostral (anterior vertical) semicircular canal
rsca	ampulla of rostral semicircular canal
rtr	rostral tympanic recess
rvcm	rostral middle cerebral vein
sin	blind dural venous sinus of hindbrain
socs	supraoccipital pneumatic sinuses
ssr	subsellar recess
ts	transverse sinus
vcd	dorsal head vein
ve	vestibule of inner ear
vg	fine vascular grooves on endocranial surface
II	optic nerve canal
III	oculomotor nerve canal
IV	trochlear nerve canal
V_1	ophthalmic nerve canal
V_{2-3}	maxillomandibular nerve canal
V_{2-3}/VII	common external opening in braincase for maxillomandibular and facial nerve canals
VI	abducens nerve canal
VII	facial nerve canal
VII_{pal}	canal for palatine branch of facial nerve
VIII	vestibulocochlear nerve canals
IX	glossopharyngeal nerve canal
IX–XI	shared canal for glossopharyngeal, vagus, and accessory nerves and accompanying vessels
X	vagus nerve canal
XII	hypoglossal nerve canal
?	canal found in some *T. rex*, may be an accessory hypoglossal canal or a venous canal

derive from a composite dataset generated by registering and combining five separate CT datasets (four OBMH datasets plus the Boeing dataset). All CT data, regardless of source, were analyzed on 32- and 64-bit PC workstations with 4 GB of RAM and nVidia Quadro FX 3000 or 4500 video cards and running Microsoft Windows XP Professional, Windows XP Professional ×64, or Linux 2.6.18 (Debian 4.0 distribution). In all cases, structures of interest (e.g., endocast, sinuses) were highlighted and digitally extracted using Amira's segmentation tools for quantification and visualization. Both surfaces and volumes were generated and were used to illustrate this article. To facilitate discussion, we will refer to the digital casts of structures as if they were the structures themselves (e.g., "rostral middle cerebral vein" versus "digital cast of rostral middle cerebral vein").

The research presented here is part of our larger project on the evolution of the brain cavity and ear regions in archosaurs, and thus we have data comparable to those presented here for a range of outgroup taxa. From this larger sample, we selected a few for comparison and illustration. Outgroup coelurosaur taxa include *Struthiomimus altus* (TMP 90.26.1, AMNH FR 5355), *Deinonychus antirrhopus* (MOR 747, frontal, parietal, and laterosphenoids; OMNH 50268, occiput and prootic; ventral endocast restored based on *Tsaagan mangas*, IGM 100/1015), *Troodon formosus* (TMP 86.36.457, braincase lacking skull roof; TMP 79.8.1, skull roof), and *Archaeopteryx lithographica* (BMNH 37001). Noncoelurosaurian outgroups include *Allosaurus fragilis* (UMNH VP 18050 [formerly UUVP 3304]) and *Majungasaurus crenatissimus* (FMNH PR2100; see also Sampson and Witmer, 2007; Witmer and Ridgely, 2008b). All of the above represent *de novo* endocasts based on new scanning, with the exception of *Archaeopteryx* from which we generated an endocast *de novo* from the scan data used by Domínguez Alonso et al. (2004). The *Allosaurus* and *Majungasaurus* braincases were scanned at OBMH using parameters similar to those listed above. *Struthiomimus* was scanned at the high-resolution X-ray CT Facility at the University of Texas at Austin at a slice thickness of 312 μm. The *Deinonychus, Tsaagan*, and *Troodon* specimens were scanned at the Ohio University MicroCT Scanning Facility (OUμCT) on a GE eXplore Locus MicroCT Scanner at slice thicknesses of 92 and 45 μm, 80 kV, and 500 μA.

An endocast was generated photographically from the sagittally sectioned braincase (AMNH FR 5029; Fig. 7B) by taking standard stereophotographs and swapping the images left for right. Swapping the images changes the perspective from being a cavity (a negative) to being a volume (a positive). Although perhaps an unorthodox way of viewing the fossil specimen, it provides better comparability to the digital endocasts otherwise presented here.

RESULTS

The following presentation of results begins with the cranial endocast, followed by the endosseous labyrinth, and pneumatic sinuses. Along the way, some details of the bony braincase will be clarified. The intent of these sections is not to present exhaustive written descriptions, but rather to focus on comparisons and issues of interest, allowing our illustrations to carry the burden of presenting the morphology.

Cranial Endocast

As noted above, there are published *T. rex* endocasts for AMNH FR 5029 (Osborn, 1912; Hopson, 1979) and FMNH PR2081 (Brochu, 2000, 2003). We generated new endocasts for both of these to provide an independent assessment, and Brochu's (2000) and Hopson's (1979) identifications are largely in accord with ours. For FMNH PR2081, we used the same data as Brochu (see above for caveats regarding Brochu's illustrations). For AMNH FR 5029, however, although Osborn (1912) extracted a physical endocast from one side, we CT scanned both halves of AMNH FR 5029 and assembled the first complete endocast of this specimen. We also generated an endocast for CM 79057, but the scan data are not sufficient to reveal much more than that it was generally similar to other *T. rex* endocasts. The best CT data come from AMNH FR 5117, which is better preserved than AMNH FR 5029 and was scanned at a higher resolution than FMNH PR2081. As a result, we present AMNH FR 5117 in more detail as our main example (Figs. 1, 2). All endocasts are oriented with the lateral semicircular canal horizontal, corresponding to the typical tetrapod "alert" head posture (see Discussion).

All of the endocasts of *T. rex* are very similar and are generally long and narrow (Fig. 3A–I). As is typically the case in more basal theropods, the forebrain and hindbrain are more or less horizontal, with the midbrain angled between them. But whereas the midbrain angulation in outgroups is stronger (about 45- to 60-degree angle, Fig. 4; Hopson, 1979; Larsson, 2001; Franzosa and Rowe, 2005; Sampson and Witmer, 2007), the *T. rex* endocasts are more drawn out and the angulation is shallower. The other tyrannosaur endocasts presented here, *Gorgosaurus* (Fig. 3J–L) and CMNH 7541 (Fig. 3M–O), likewise show a shallow midbrain angulation. Precise measurement of these angles is problematic because many details of brain structure are not recorded in the cranial endocast, which ultimately is a cast of the dural envelope. Despite being coelurosaurs, adult tyrannosaurs reflect the primitive noncoelurosaurian sauropsid condition, in which the relatively small brain is suspended within the larger endocranial cavity by dural venous sinuses, cerebrospinal fluid, and other tissues (Hopson, 1979; Hurlburt, 1996; Rogers, 2005). Most other coelurosaurs resemble mammals, birds, and pterosaurs in having relatively large brains that mostly fill the cavity such that an endocast is a better representation of gross brain structure (Jerison, 1973; Witmer et al., 2003; Franzosa, 2004). The endocast of the new, very young *Tarbosaurus* suggests that young tyrannosaurs resembled other coelurosaurs in this attribute.

The endocasts of tyrannosaurs are dominated by large dural venous sinuses that covered much of the brain structure, especially dorsally. As in modern archosaurs (Sedlmayr, 2002), the dorsal longitudinal (sagittal) sinus is well developed and expanded caudally into a large occipital sinus overlying much of the hindbrain. A prominent feature of AMNH FR 5029 is a very tall median dural peak (Fig. 3D); CT scans confirm that the peak is indeed blind. Although this peak has been a familiar

feature since Osborn's (1912) paper, none of the other tyrannosaur specimens has such a tall dural prolongation, in most cases being simply the apex of the dorsal longitudinal sinus (Fig. 3). Saveliev and Alifanov (2007) suggested that the same peak in *Tarbosaurus* was occupied by the cerebellum, but the available evidence suggests that cerebellum was located more ventrally. Alternatively, Sampson and Witmer (2007) argued that a similar dural peak in noncoelurosaurian theropods corresponds well to the position (i.e., just caudal to the cerebrum) of a pineal apparatus (Fig. 4A,B), but the peak in tyrannosaurs and indeed other coelurosaurs (Fig. 4C–E) is too caudally situated to be pineal in origin. Moreover, the presence of both rostral (pineal) and caudal dural peaks in *Struthiomimus* (Fig. 4D) suggests that the peak in tyrannosaurs is not homologous with the pineal peak of more basal theropods. It is not presently possible to suggest a precise function for the tyrannosaur dural peak other than as housing a dural venous sinus. Likewise, why the peak is so tall in AMNH FR 5029 is
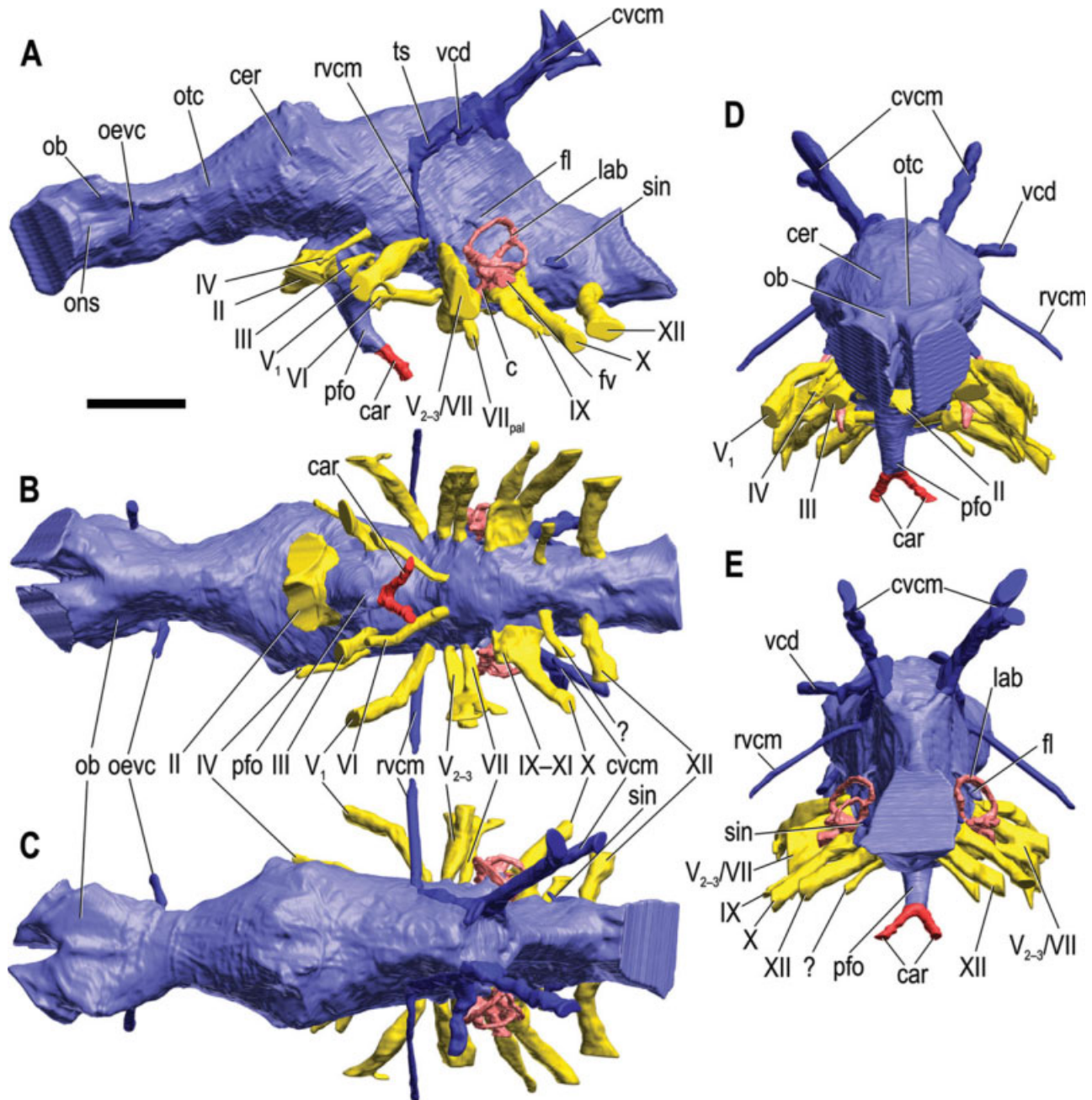
Fig. 1. Cranial endocast of *Tyrannosaurus rex* (AMNH FR 5117) reconstructed from CT scans. Some vascular elements and the endosseous labyrinth are depicted. Labeled illustrations in **A**, left lateral; **B**, ventral; **C**, dorsal; **D**, rostral; and **E**, caudal views.

obscure. The dural peak is very close to the transverse sinus system (Fig. 3) and so is likely to be a hypertrophied confluence of sinuses (=torcular Herophili). Indeed, some sauropods also exhibit a dural expansion associated with the confluence of sinuses (Witmer et al., 2008), and even some ceratopsians have a median dural peak associated with the confluence (Witmer and Ridgely, 2008a).
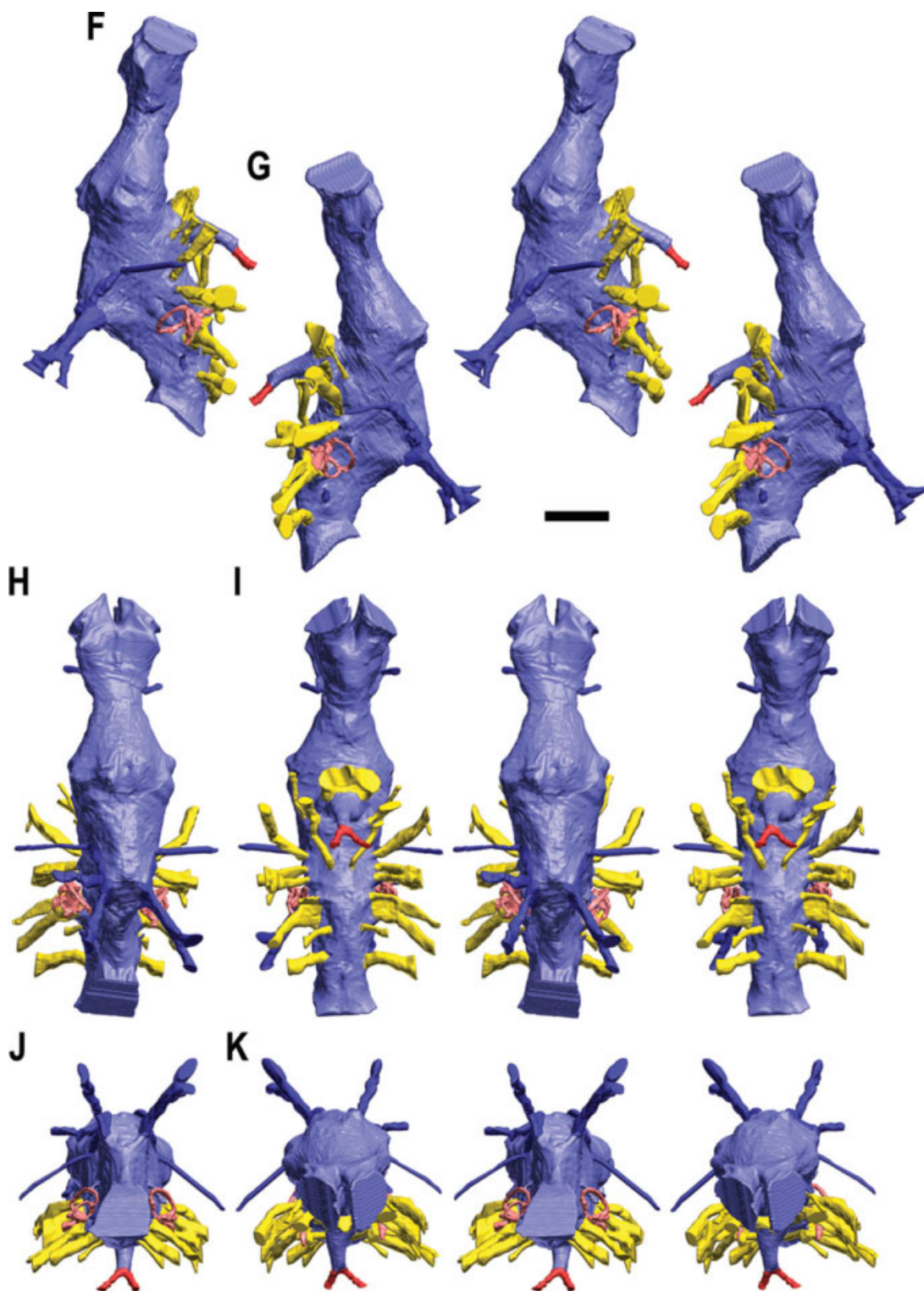

Fig. 1. Stereopairs in **F**, right lateral; **G**, left lateral; **H**, dorsal; **I**, ventral; **J**, caudal; and **K**, rostral views. Scale bars = 4 cm.
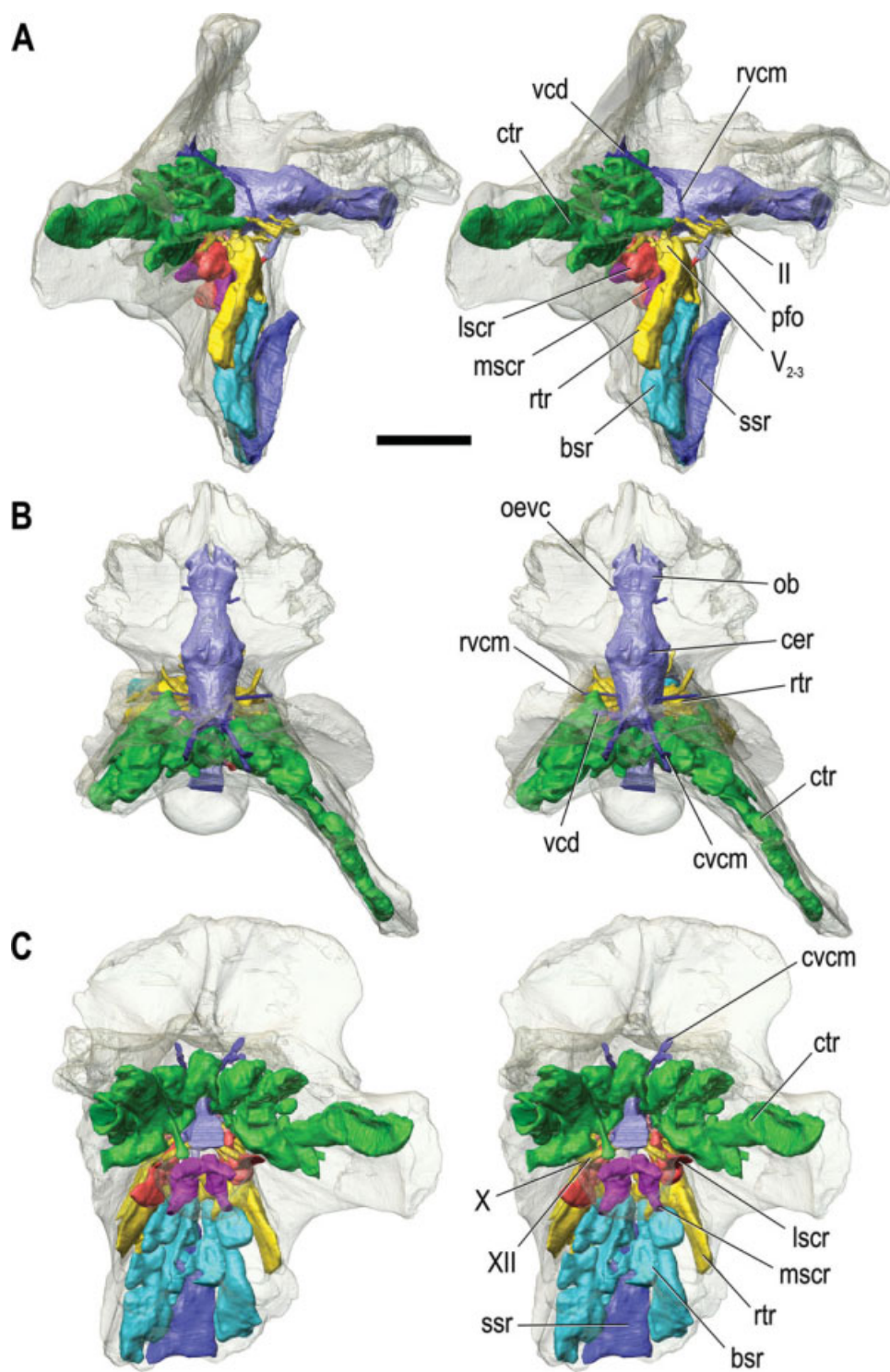
Fig. 2. Stereopairs of articulated braincase of *Tyrannosaurus rex* (AMNH FR 5117) derived from reconstructed CT scans and shown in the following views: **A**, right lateral; **B**, dorsal; **C**, caudal.
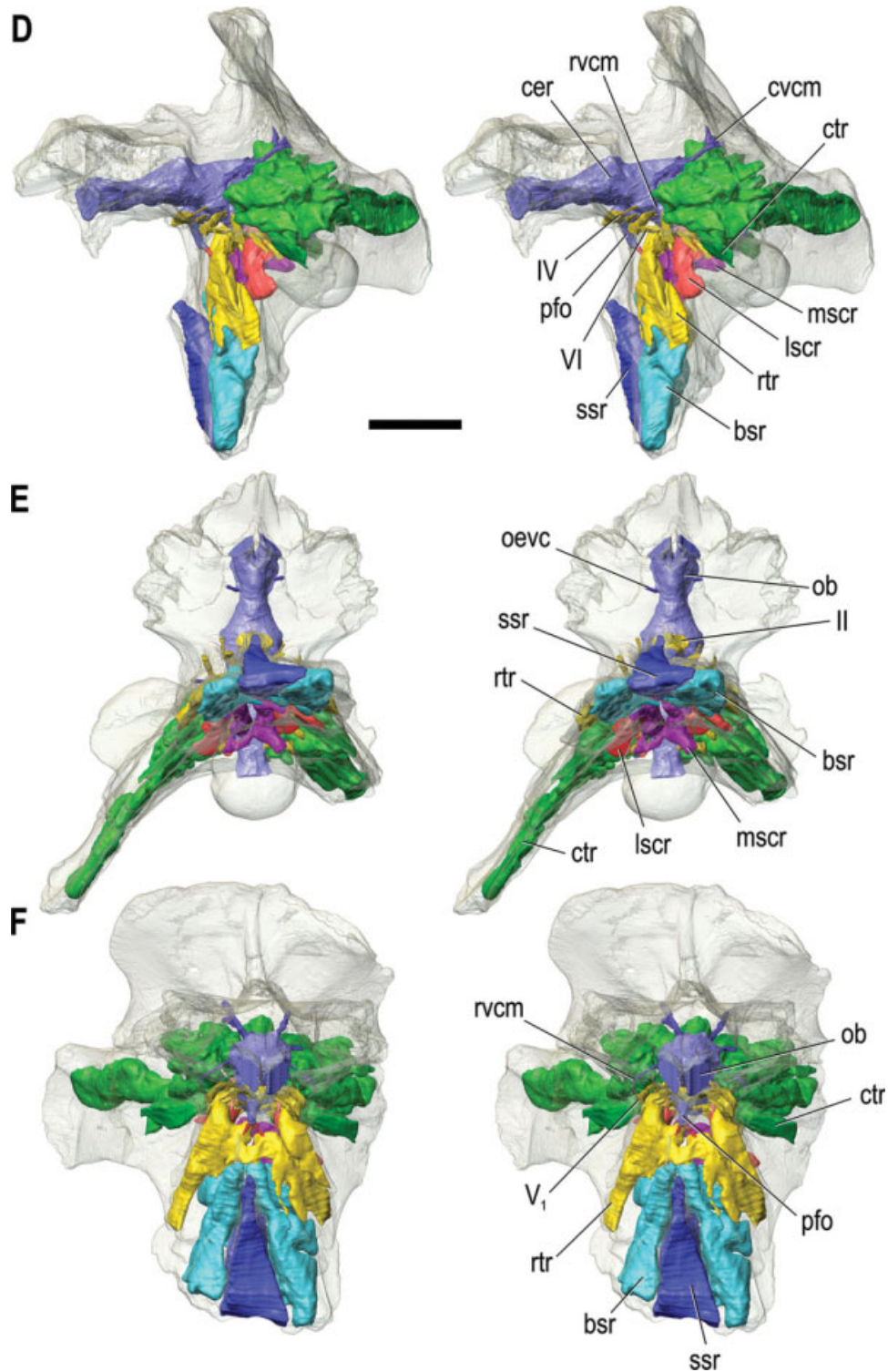
Fig. 2.   **D,** left lateral; **E**, ventral; **F**, rostral. Bone is rendered semitransparent, revealing pneumatic recesses, cranial endocast, vascular elements, and the endosseous labyrinth. For detailed labeling of the cranial endocast, bony braincase, and endosseous labyrinth, see Figs. 1, 5, and 8, respectively. Scale bars = 10 cm.

The transverse dural sinus is well marked on all of the tyrannosaur endocasts, being a raised ridge curving between veins diverging from the endocast rostrally and caudally. Unfortunately, both of these veins have been referred to as the middle cerebral vein, and we will not revise that terminology here, but rather differentiate the veins as rostral or caudal. The rostral middle cerebral vein takes a long course through the laterosphenoid to
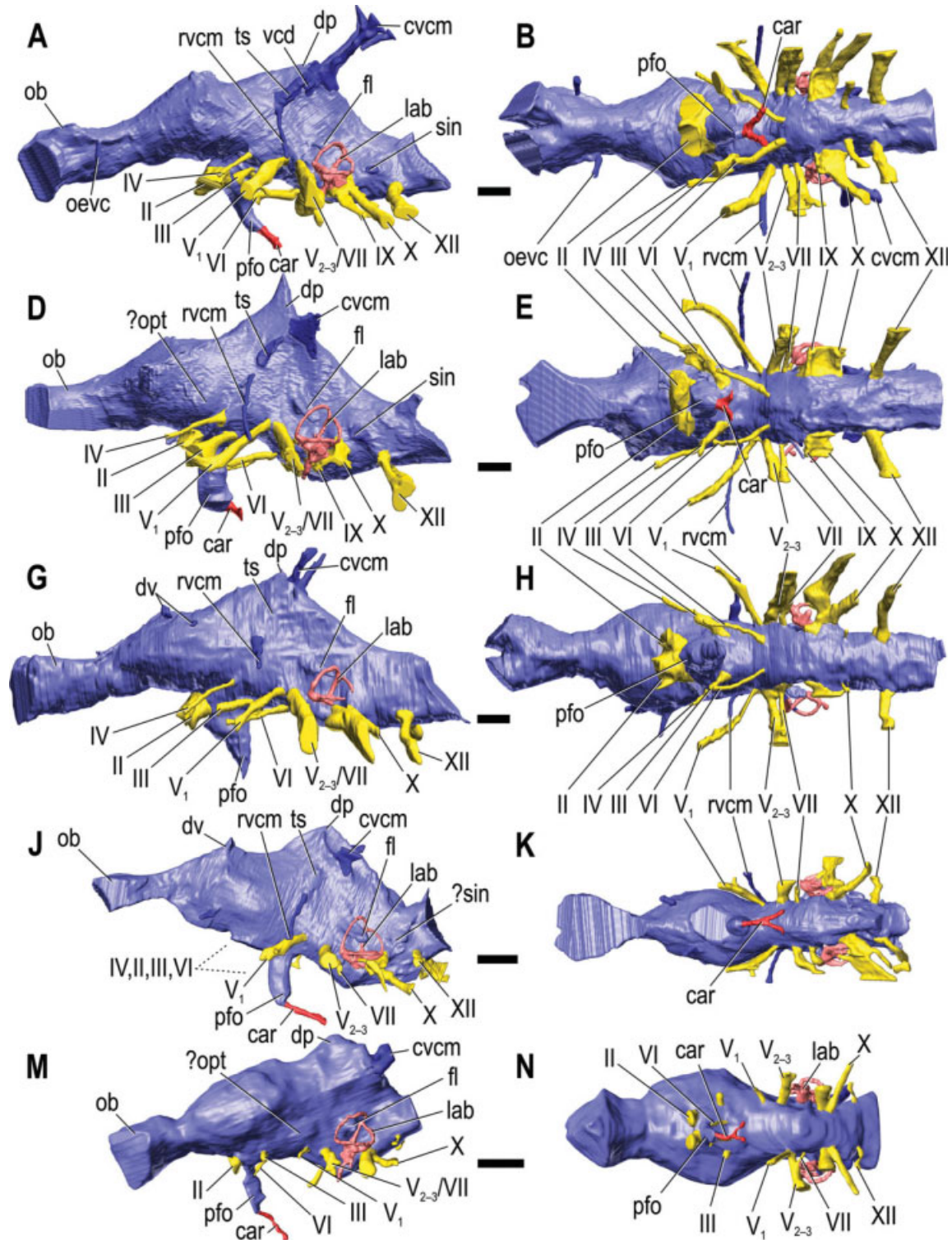
Fig. 3. Cranial endocasts reconstructed from CT scans in left lateral view (left column, this page), ventral view (right column, this page), and dorsal view (left column, facing page). **A–C**, *Tyrannosaurus rex* (AMNH FR 5117); **D–F**, *T. rex* (AMNH FR 5029); **G–I**, *T. rex* (FMNH PR2081); **J–L**, *Gorgosaurus libratus* (ROM 1247); **M–O**, Cleveland skull (CMNH 7541; reversed). Some vascular elements are depicted, as well as the endosseous labyrinth. Scale bars = 2 cm.
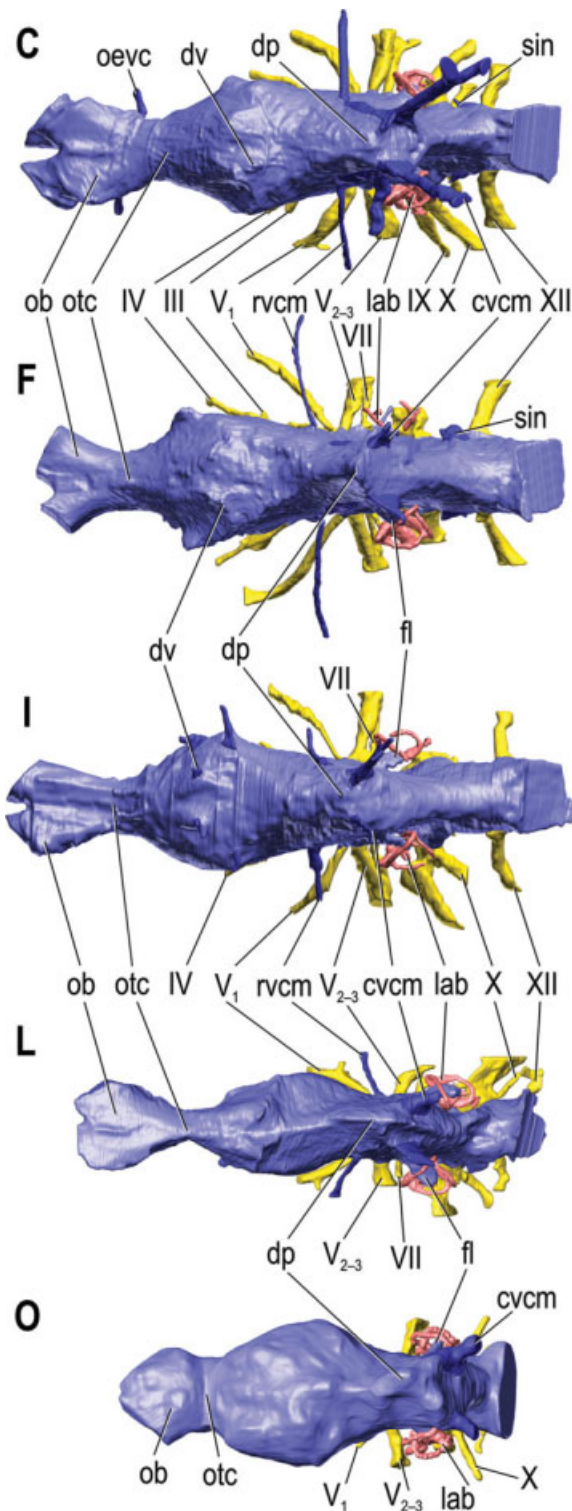
Fig. 3. (cont.)

and Witmer, 2007). It should be noted that Saveliev and Alifanov (2007) misidentified the canal for the rostral middle cerebral vein in *Tarbosaurus* as being for the trochlear nerve. The caudal middle cerebral vein (=caudal petrosal sinus, external occipital vein) passes between bones to emerge on the occiput between the supraoccipital, otoccipital, and parietal (Fig. 2). Linked with the transverse sinus and caudal middle cerebral vein is the dorsal head vein (Fig. 1), which extends laterally to emerge at a foramen within the adductor chamber between laterosphenoid, parietal, and prootic (Fig. 5). In some of the tyrannosaur specimens, the bony lateral head vein canal is discontinuous as it passes through or just borders the pneumatic chamber within the prootic (Fig. 2). The external foramina of both the dorsal head vein and caudal middle cerebral vein each lead to grooves that ultimately unite at the posttemporal foramen, suggesting that the same intra- and extracranial anastomotic loops identified in *Majungasaurus* (Sampson and Witmer, 2007) are found in tyrannosaurs.

Within the forebrain regions of the tyrannosaur endocasts, there are a variable series of venous canals that exit the endocast dorsally and laterally (Figs. 1–3). Many of the dorsal canals end blindly and may be regarded as diploic veins draining the bone, whereas the lateral canals open into the orbit and may be regarded as emissary veins. Some of these emissary canals open into a prominent vascular groove that runs within the roof of the orbit between the frontal and the unit comprised of the laterosphenoid, orbitosphenoid, and sphenethmoid (Fig. 5). These emissary vein canals would have provided a route of venous anastomosis between the orbit and endocranial cavity. A similar arrangement of emissary canals opening into a frontosphenoidal groove in the orbital roof has been found in *Majungasaurus* (Sampson and Witmer, 2007) and other dinosaurs (including ornithischians), and may be a conserved system.

Although the brain did not fill the endocranial cavity in adults, some portions are fairly faithfully recorded in the endocast. The cerebrum is most clearly distinguished and, as in most theropods, its lateral contours and breadth are readily apparent (Fig. 1). However, unlike most theropods, the dorsal cerebral contour is apparent (because of the absence of the pineal peak of more basal theropods), as is the ventral contour (because of well-ossified sphenoid elements). As noted for *T. rex* by Larsson et al. (2000) and Hurlburt et al. (in press), the cerebrum is enlarged in all of our *T. rex* endocasts, and the same is true of the Cleveland skull (Fig. 3M–O), *Daspletosaurus*, and *Gorgosaurus* (Fig. 3J–L). The olfactory tracts, particularly in *T. rex*, are relatively short and thick in comparison to most other theropods and clearly are much broader than was necessary to house the paired olfactory tracts and encephalic vessels. The transverse breadth could be an allometric consequence of large body size, but the similarly sized *Carcharodontosaurus* (Larsson, 2001) has the plesiomorphic longer, narrower olfactory tract. Moreover, the tracts are relatively short and broad in the smaller sized tyrannosaur represented by the Cleveland skull. Instead, the olfactory tracts being short and broad in *T. rex* may relate more to overall braincase shape, which likewise is apomorphically broad and relatively shortened fore-aft, which is also somewhat true of CMNH 7541.

open very near or within the epipterygoid facet (Fig. 5). Its external foramen is distinct from the maxillomandibular and ophthalmic (trigeminal) foramina, which is the derived saurischian condition (Rauhut, 2003; Sampson
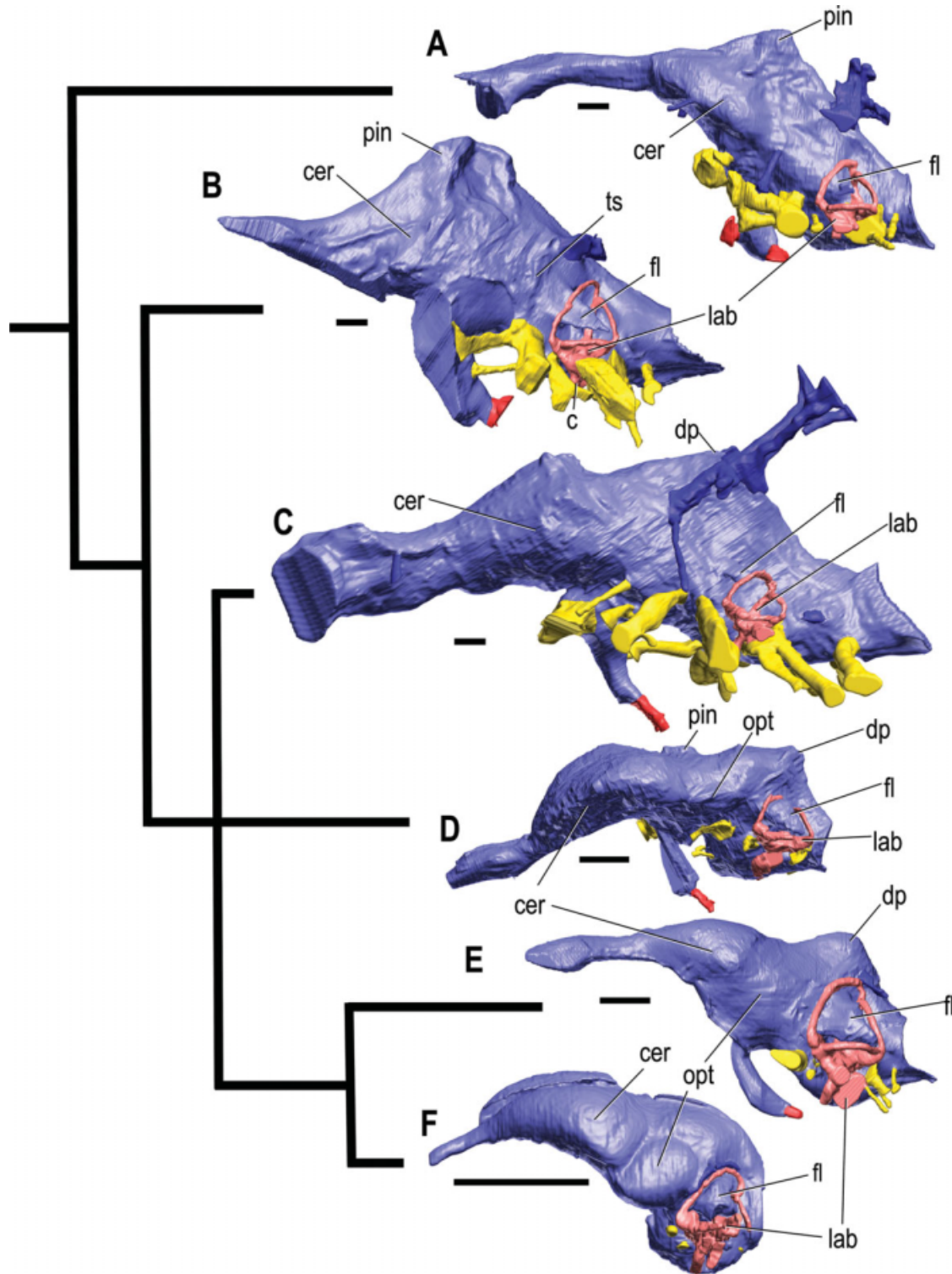
Fig. 4. Cranial endocasts reconstructed from CT scans in left lateral view, arranged in a cladogram. **A**, *Majungasaurus crenatissimus* (FMNH PR2100; modified from Sampson and Witmer, 2007); **B**, *Allosaurus fragilis* (UMNH VP 18050); **C**, *Tyrannosaurus rex* (AMNH FR 5117); **D**, *Struthiomimus altus* (TMP 90.26.1); **E**, *Deinonychus antirrho-pus* (composite of MOR 747 and OMNH 50268); and **F**, *Archaeopteryx lithographica* (BMNH 37001). **C, D**, and **E+F** are arranged in a polytomy to reflect uncertain relationships near the base of Coelurosauria, which impacts the optimization of some attributes (e.g., position of optic lobe). Scale bars = 1 cm.
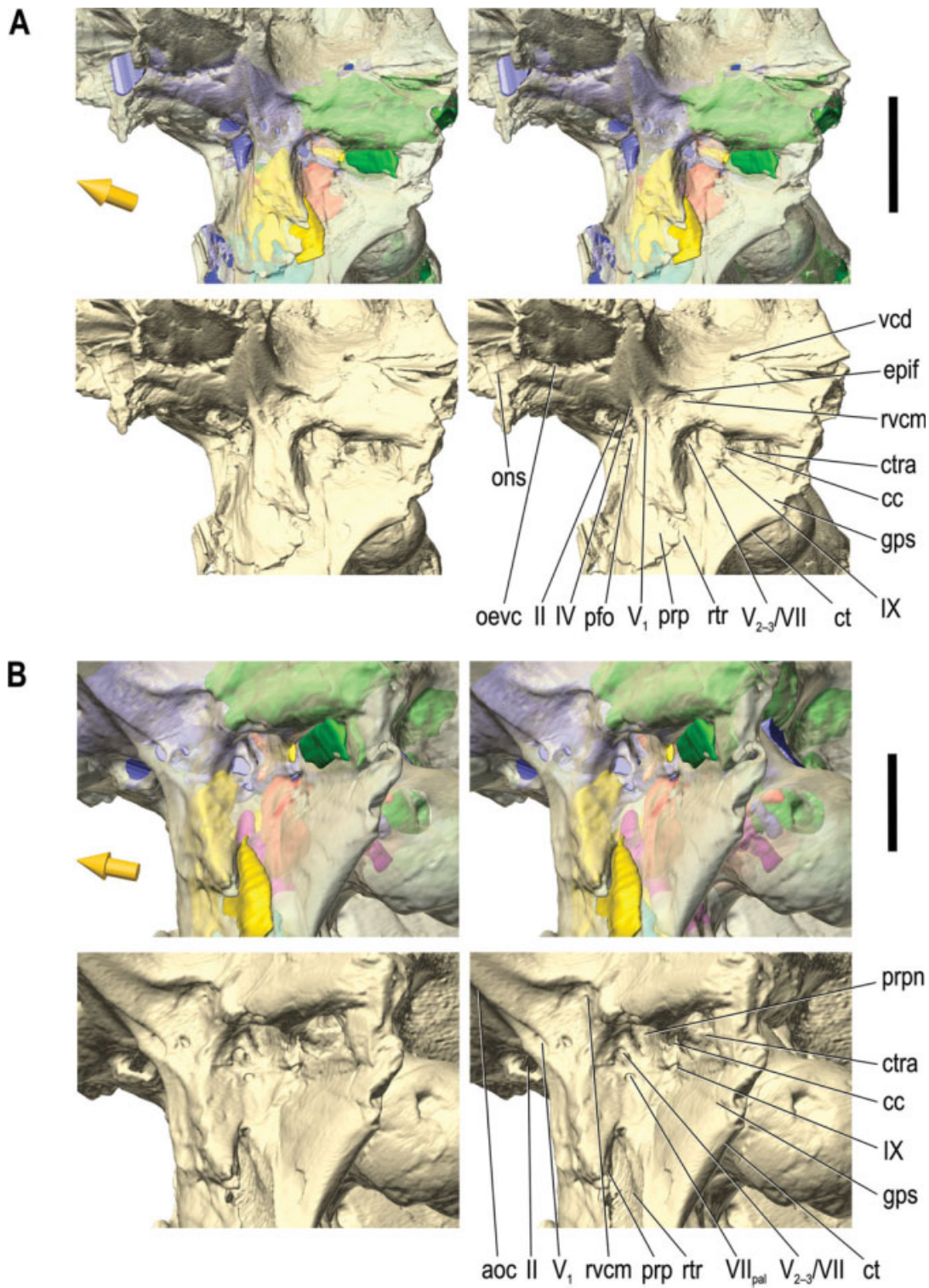
Fig. 5. Stereopairs of a braincase of *Tyrannosaurus rex* (AMNH FR 5117) reconstructed from CT scans in various views to show the osteological correlates (e.g., foramina, fossae, crests) of many of the soft-tissue structures discussed in the text. Each view consists of a set of stereopairs (above) showing a semitransparent braincase revealing enclosed soft-tissue structures, coupled with a set of stereopairs (below) in the same view showing the bony braincase and labeled structures. **A**, left lateral view; **B**, left lateral view, close-up.
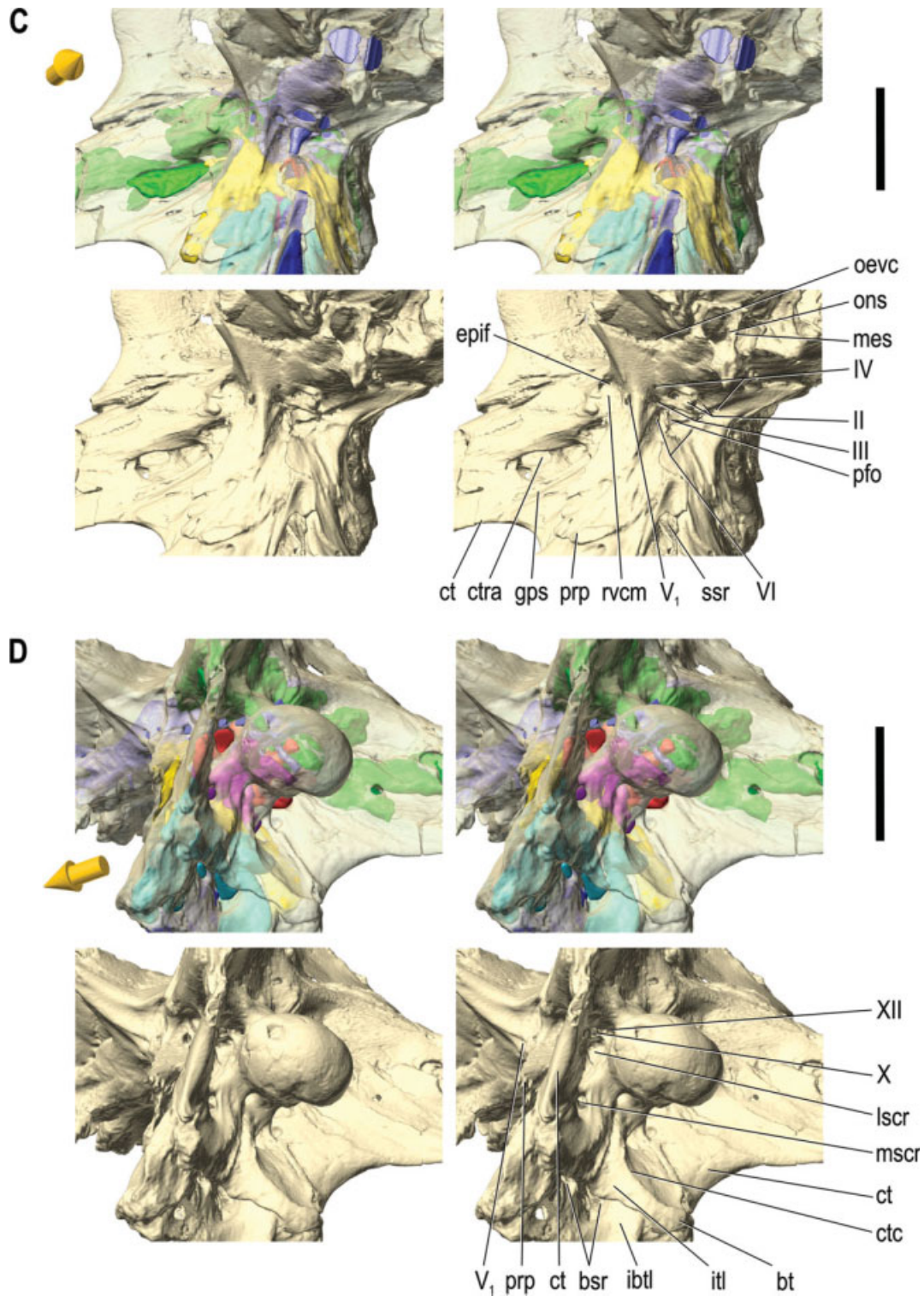
Fig. 5. **C**, right rostroventrolateral view; and **D**, left caudoventrolateral view. Arrows point rostrally. Scale bars = 10 cm, except in **B** where scale bar = 5 cm.

The olfactory bulbs of *T. rex* have received a lot of attention since Brochu's (2000) paper on FMNH PR2081 in which he reconstructed bulbs so enormous (Fig. 6A) that they seemingly were larger than the rest of the brain itself. This dramatic finding, implying that *T. rex* had remarkable olfactory capabilities, played into the existing debate on whether *T. rex* was primarily a predator or scavenger (Horner and Lessem, 1993; Horner,
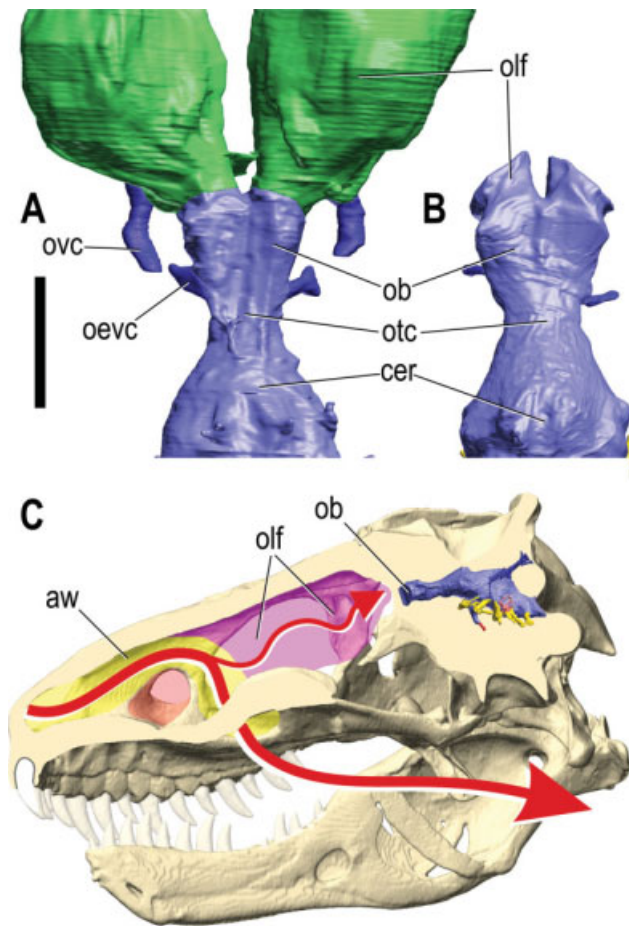
Fig. 6. Olfactory structures in *Tyrannosaurus rex*. **A**, FMNH PR2081; **B**, AMNH FR 5117; dorsal views of the cranial endocast. Green structures in A are the caudal portions of the olfactory region of the nasal cavity, which correspond to what Brochu (2000, 2003) regarded as olfactory bulbs. The true limits of the olfactory bulb cast are indicated in blue of the cranial endocast. **C**, sagittal section of a *T. rex* skull, showing the cranial endocast in place (generated by registering AMNH FR 5117 to a one-third scale restored sculpture of FMNH PR2081). The large arrow shows the course of the respiratory airway (yellow) through the rostral portion of the nasal cavity, choana, and pharynx. The small, wavy arrow shows the low-velocity path of odorant molecules through the large olfactory region of the nasal cavity (reddish). Scale bar for **A–B** = 5 cm.

1994), and quickly found its way into both dinosaur texts (Fastovsky and Weishampel, 2005) and neuroanatomy texts (Striedter, 2005). Unfortunately, almost all of what Brochu (2000) regarded as olfactory bulb is actually the caudal portion of the olfactory region of the nasal cavity, that is, the site of the sensory epithelium (i.e., mucous membrane) onto which odorant molecules would have diffused (Fig. 6C, small arrow head).

The true olfactory bulbs are very well demarcated (Witmer et al., 2008). They are roofed for the most part by the frontal and otherwise lodged within the mesethmoid and sphenethmoid (Fig. 5). The rostrodorsal limit of the bulb is marked by the juncture of the frontal with the ethmoid ring, forming a clear rostral ridge in the endocast (Fig. 6A,B). There are clear grooves within the walls of the ethmoid ring, both laterally on the sphe-

nethmoid and on its median septum (mesethmoid; Fig. 5A,C), that conducted olfactory nerve bundles, as well as blood vessels, as noted for tyrannosaurs by Ali et al. (2008) and for lambeosaurs by Evans (2006). These olfactory nerve bundles joined with the bulb and are thus outside of it. It is likely that the olfactory bulb itself protruded somewhat into the sphenethmoid ring. Although quantitative assessments are beyond the scope of this article, the corrected size of the olfactory bulbs remains moderately large and are relatively larger than in coelurosaurian outgroups and large bodied basal theropods (Larsson, 2001; Franzosa and Rowe, 2005; Witmer et al., 2008; Zelenitsky et al., 2009). The olfactory bubs of CMNH 7541 are relatively even larger than in *T. rex*, and here the presence of preserved olfactory turbinates (Witmer and Ridgely, in press) provides very clear demarcation between neural and nasal domains. The olfactory bulb region of the PIN 553-3/1 specimen of *Tarbosaurus* is very similar to that of other tyrannosaurs, but Saveliev and Alifanov (2007, p 283) interpreted it housing not only the definitive olfactory bulb ventrally but also a "vomeronasal bulb" dorsally. We regard such a division as unwarranted in that the supposed line of separation represents a suture (between frontal and sphenethmoid), not a ridge separating neural domains. Moreover, extant archosaurs lack vomeronasal organs (Witmer, 1995a), and there is no reason to believe that extinct archosaurs had them either (Senter, 2002), including tyrannosaurs. Thus, we regard the entire rostralmost extent of the forebrain to pertain to the olfactory bulbs.

Whether or not the optic lobes (midbrain tectum) are visible in tyrannosaur endocasts is controversial. Osborn (1912) identified an optic lobe in *T. rex* (AMNH FR 5029), and Maleev (1965) did the same for *Tarbosaurus*, but Brochu (2000) did not identify it in FMNH PR2081. We can confirm their observations in that distinct swellings are visible in AMNH FR 5029 (Fig. 3D) and PIN 553-3/1 and absent in FMNH PR2081 (Fig. 3). To these we can add that clear swellings for optic lobes are absent in AMNH FR 5117 (*T. rex*) and ROM 1247 (*Gorgosaurus*), but may be present in CMNH 7541 (Fig. 3). Maleev's (1965) identification of an optic lobe in *Tarbosaurus* (PIN 553-3/1) was not affirmed by Saveliev and Alifanov (2007), who assumed a much more dorsal position for the optic lobe. The interpretation of optic lobes in AMNH FR 5029 was accepted by Jerison (1973) and Wharton (2002), but Hopson (1979, p 96) suggested that the swelling "more likely represents the posterolateral part of the cerebrum." The significance here is that laterally positioned and visible optic lobes would be a derived trait reflecting a more avian organization of the brain, with enlarged cerebrum and cerebellum pushing the lobes ventrolaterally, rather than the primitive reptilian condition of having modest-sized brain parts arranged rostrocaudally in a row. Our data on coelurosaurs other than tyrannosaurs clearly show a trend for greater visibility and more lateral positions of the optic lobes on the phylogenetic line to birds (Fig. 4), and both Wharton (2002) and Franzosa (2004) found the same trend with their smaller samples.

Indeed, the available endocast data on tyrannosaur optic lobes are equivocal, and we caution against making too much of subtle bulges. Phylogenetics can play a key role here in that character optimization can guide

morphological interpretation. According to Norell et al. (2001), Rauhut (2003), Holtz (2004), Xu et al. (2006), and Benson (2008), Tyrannosauroidea is the most basal coelurosaur clade for which reliable endocast data are available, and thus absence of visible, laterally positioned optic lobes (as in AMNH FR 5117, FMNH PR3081, and ROM 1247) might be expected. However, some tyrannosaur specimens might have laterally positioned optic lobes (e.g., AMNH FR 5029, CMNH 7541, and PIN 553-3/1). This equivocal situation may well legitimately reflect natural variation as adults or even ontogeny in that both CMNH 7541 and PIN 553-3/1 are small and presumably subadult individuals. In this context, it is significant that the newly discovered very young *Tarbosaurus* also seems to display more visible, ventrolaterally positioned optic lobes. Moreover, this equivocal situation could reflect a transitional state. For example, the optic lobes of ornithomimids (another fairly basal coelurosaurian clade) are not as clearly visible as are those of some taxa closer to the crown (Fig. 4; Hopson, 1979; Wharton, 2002; Franzosa, 2004; Maxwell and Larsson, 2005). It is conceivable that a transitional or incipient condition likewise may be present in tyrannosaurs such that a brain with the beginnings of a birdlike organization may be concealed within the large dural envelope of adults, perhaps for allometric reasons relating to their large body sizes.

Controversies regarding optic lobe bulges notwithstanding, some clues about relative positions of brain parts, based on consistent relationships among extant sauropsids, are provided by other features on the endocast (Ridgely and Witmer, 2007, 2008). For example, the transverse sinus and the rostral middle cerebral vein roughly mark the boundary between the optic lobe in front and cerebellum behind (Fig. 1). The trochlear nerve canal always passes behind and then ventral to the optic lobe in extant taxa. In tyrannosaurs, the course of the trochlear canal is consistent with the putative optic lobe swellings hypothesized above, although the dural envelope is "sloppy" enough that the canal is not decisive in differentiating the optic lobe from the cerebellum. Another marker for cerebellar position is the position of the endosseous labyrinths, which sandwich the cerebellum between them. Again, other than gross position, little about the cerebellum can be discerned, with one exception, its floccular lobe (cerebellar auricle).

The flocculus is relatively small in all of the adult *T. rex* specimens examined here, but is relatively larger in CMNH 7541 and the subadult *Gorgosaurus* specimen (ROM 1247; Figs. 1, 3). The flocculus is generally among the easiest features to see in CT, and so we regard these results as real. Saveliev and Alifanov (2007) referred to the flocculus in *Tarbosaurus* (PIN 553-3/1) as the being the trunk of the vestibulocochlear nerve (CN VIII), but the nerve foramina are clearly identifiable more ventrally. In the adult *T. rex* specimens, the flocculus generally has the tabular shape (i.e., flat in section) observed in noncoelurosaurian theropods (e.g., *Herrerasaurus*, MCZ 7063; *Ceratosaurus*, MWC 1.1; *Allosaurus*, UMNH VP 18050; *Acrocanthosaurus*, OMNH 10146; Fig. 4), whereas the flocculus in coelurosaurs tends to be relatively larger, rounder at its base, and often has a distal swelling (e.g., *Troodon*, TMP 86.36.457; *Struthiomimus*, TMP 90.26.1, AMNH FR 5355; *Dromaeosaurus*, AMNH FR 5356; *Chirostenotes*, ROM 43250; Fig. 4). A signifi-

cant difference between *T. rex* and other theropods is that the floccular cast is relatively so small that it barely crosses the plane of the rostral semicircular canal, which is in stark contrast to theropods generally in which the flocculus extends far beyond the rostral semicircular canal to be largely surrounded by the three semicircular canals (Fig. 4). *Gorgosaurus* (ROM 1247) is closer to the typical condition, as is the very young *Tarbosaurus*. CMNH 7541, however, is more like adult *T. rex* in that the flocculus barely breaks the plane of the rostral semicircular canal. The adult *T. rex* condition may relate simply to its larger size (the condition in CMNH 7541 notwithstanding; see below), but also may reflect a real difference in brain structure. The cerebellum (of which the flocculus is an appendage) was apparently located more rostrodorsally in *T. rex* (as indicated by the position of the transverse sinus), whereas the labyrinth was constrained to remain nearer the base of the brainstem adjacent to its innervation from the eighth cranial nerve. Thus, the flocculus in *T. rex* may simply not have reached the labyrinth. However, not only are there potential differences in brain structure (cerebellar position), but also the flocculus on the endocast is truly apomorphically small-and not only relative to body mass but also absolutely in that the floccular dimensions of all three adult *T. rex* specimens are smaller than those in smaller-bodied theropods, such as *Acrocanthosaurus* and *Allosaurus*. In Fig. 4, *Allosaurus* and *T. rex* are reproduced at the same scale, and the flocculus is clearly larger in the former; note also that, based on transverse sinus position, the cerebellum of *Allosaurus* has the more typical caudoventral position.

The cranial nerve trunks are clearly identifiable on the endocasts, and they generally conform to a pattern that is highly conserved among dinosaurs (Hopson, 1979). Thus, we will not describe all the trunks in detail (see Figs. 1–4). The cranial nerves were probably accompanied by veins (as in extant archosaurs; Sedlmayr, 2002), and the size of the canals may not be fully indicative of the enclosed nerve. For example, the oculomotor canal is quite large in all of the *T. rex* endocasts, suggesting that substantial orbital veins accompanied cranial nerve III. It should be noted that Saveliev and Alifanov's (2007) criticisms of Brochu's (2000) cranial nerve identifications are almost entirely in error, and our findings largely support those of Brochu (2000). Tyrannosaurs differ from other theropods in a number of features. One feature found in all of the tyrannosaurs in our study but, thus far, nowhere else is the lateral union of the facial (CN VII) and maxillomandibular (CN V_{2-3}) canals (Figs. 1, 3) such that they open in a common bony aperture on the external surface of the braincase (Fig. 5) rather than separately as in other theropods.

As other workers have noted (e.g., Bakker et al., 1988; Brochu, 2000; Currie, 2003b), tyrannosaurs have a separate bony foramen for the ophthalmic branch of the trigeminal nerve (CN V_1; Fig. 5), and a separate ophthalmic foramen is common among tetanurans although not universal (e.g., *Allosaurus* has a separate foramen, but not most carcharodontosaurids [Larsson, 2001; Coria and Currie, 2002; but see Brusatte and Sereno, 2007]). However, tyrannosaurids are different in that the ophthalmic and maxillomandibular canals branch separately off of the endocast (Figs. 1, 3, 4C) rather than being united by a short trunk before diverging, as in

Allosaurus (UMNH VP 18050, UMNH VP 18055; Fig. 4B), *Struthiomimus* (TMP 90.26.1; Fig. 4D), *Troodon* (TMP 86.36.457; Fig. 4E), and *Dromaeosaurus* (AMNH FR 5356), among others. *Gorgosaurus* (ROM 1247; Fig. 3) takes this even further by having the two canals widely separated. As noted by Witmer et al. (2008), the fact that the ophthalmic and maxillomandibular canals of tyrannosaurs and many other tetanurans arise separately from the endocast indicates that the trigeminal ganglion (the collection of nerve cell bodies proximal to the trigeminal branches) must have been located internally within the endocranial cavity. Having an intracranial position of the trigeminal ganglion is a derived feature found in extant birds, whereas the ganglion of extant crocodilians and many extinct clades such as sauropods had an extracranial position (Witmer et al., 2008).

Another difference pertains to the region of the pituitary fossa. For *Majungasaurus*, Sampson and Witmer (2007) described a cavernous-sinus-like morphology in which, as in extant archosaurs (Sedlmayr, 2002) and mammals, the abducens and oculomotor canals (again, containing veins as well as nerves) join with the cerebral carotid canal in the pituitary fossa or infundibular region (where the pituitary fossa joins the main cranial cavity). A cavernous sinus involving the abducens and/or oculomotor canals characterizes many archosaurs and basal theropods (e.g., *Herrerasaurus* MCZ 7063; *Allosaurus*, UMNH VP 18055; *Acrocanthosaurus*, OMNH 10146; *Carcharodontosaurus* [Larsson, 2001]). Most coelurosaurs (e.g., *Troodon*, TMP 86.36.457; *Dromaeosaurus*, AMNH FR 5356), however, show a derived condition in which the abducens and oculomotor canals tend to open into the endocranial cavity separate from the pituitary/infundibular region such that there is, strictly speaking, no cavernous sinus. All three *T. rex* endocasts clearly display the derived coelurosaurian condition (Figs. 1–5). The relevant area of ROM 1247 (*Gorgosaurus*) is missing (drilled out for a mounting rod). The area is preserved in CMNH 7541, however, and is very different from the three definitive *T. rex*. The abducens canals in CMNH 7541 almost intersects the pituitary fossa (Fig. 3) rather than, as in *T. rex*, strongly diverging lateral to it. It is tempting to score CMNH 7541 with the primitive condition, but its diencephalic region is either highly apomorphic (being shifted relatively forward, again unlike *T. rex*) or is distorted because of postmortem factors (see below). Thus, we regard the condition in the Cleveland skull as either a transformation from the derived coelurosaur condition or an artifact of preservation.

The vagal (or jugular) canal, transmitting cranial nerves X and XI and probably a small posterior cerebral (jugular) vein, clearly passes caudal to the crista tuberalis (the web of otoccipital connecting the paroccipital process to the basal tuber; Kurzanov, 1976; Sampson and Witmer, 2007) to open on the occiput (Figs. 1, 2, 5). This condition was recently identified in abelisaurids (Sampson and Witmer, 2007), and thus is not as advanced a feature as once thought (Chatterjee, 1993; see also Rauhut, 2003). In *Gorgosaurus* and adult *T. rex* specimens, the vagal canal opens caudally within the paracondylar fossa adjacent to the hypoglossal canal (Fig. 3), just as in *Allosaurus* and *Majungasaurus* (Sampson and Witmer, 2007). In CMNH 7541, however, the vagal canal

extends strongly laterally to open not next to the hypoglossal but relatively far lateral to it (Fig. 3); this difference is real and cannot be attributed to postmortem deformation. The glossopharyngeal nerve did not run through the vagal canal in potentially any of the tyrannosaurs under study here, but rather passed rostral to the crista tuberalis, running through a separate canal rostral to the vagal canal and ventral to the columellar canal (Fig. 1). The lateral course of the nerve is indicated by a well-marked sulcus on the rostral surface of the crista tuberalis just ventral to the aperture of the caudal tympanic recess (CTR) (Fig. 5). Kurzanov (1976) and Sampson and Witmer (2007) reported similar glossopharyngeal grooves for *Itemirus* and *Majungasaurus*, respectively, and the same is found in *Allosaurus* and may be more widely distributed.

One underappreciated benefit of CT-based endocasts is that the full lengths of nerve and vascular canals can be traced all the way to their foramina on the external surface of the braincase. Identifying braincase foramina can be daunting because of the high variability of the surface of the braincase. However, based on our broader studies, the internal (endocranial) ends of these canals are highly conserved across archosaurs and are easily identified. Thus, visualizing the full lengths of the endocast canals simultaneously with the bony braincase makes identifying external braincase foramina a trivial matter (Fig. 5). In this light, we would note that many of the foramina are incorrectly labeled by previous workers (e.g., Osborn, 1912; Brochu, 2003). For example, many of Osborn's (1912) identifications are painted directly on AMNH FR 5117, a photograph of which is shown in figure 7 in Osborn (1912). Almost all of these are incorrect: e.g., (1) "fen. ov." (fenestra ovalis, = f. vestibuli) is the aperture of the CTR, (2) "VII" is the columellar canal, (3) "$V_{2,3}$" is the prootic pneumatic recess, (4) "V_1" is the common opening of CN $V_{2–3}$ and CN VII, and (5) "IV" is CN V_1. Brochu's braincase illustration (Brochu, 2003: Fig. 30) corrects some of Osborn's errors, but a few still remain: (1) "$V_{2,3}$" is the common opening of CN $V_{2–3}$ and CN VII, (2) "VII" is probably either the columellar recess or the glossopharyngeal foramen, (3) "car" (carotid foramen) is unknown because the carotid foramen is tucked up deep to the preotic pendant within the rostral tympanic recess (RTR), (4) "eor" (external otic recess) is also unknown because none of the specimens has an aperture in that position, (5) "III" is CN IV (trochlear canal), and (6) "IV" is CN III (oculomotor canal). In contrast with the external openings, Osborn's (1912) identifications painted on the endocranial surface of AMNH FR 5029 are virtually all correct (Fig. 7), highlighting the difficulty of correlating conservative endocranial morphology with variable external morphology without the aid of CT scanning.

Despite the benefits of digital endocasts, CT scanning currently cannot adequately resolve very fine features, such as the faint bony grooves produced by meningeal blood vessels. First illustrated by Russell (1969, 1972) for troodontids and ornithomimosaurs, the presence of such vascular grooves has been used as evidence that the brain so filled the endocranial cavity that grooves were etched in the bone (Hopson, 1979). The presence of fine vascular grooves has since been reported in oviraptorosaurs (Osmólska, 2004) and even some ornithischians (hadrosaurs and pachycephalosaurs; Evans,
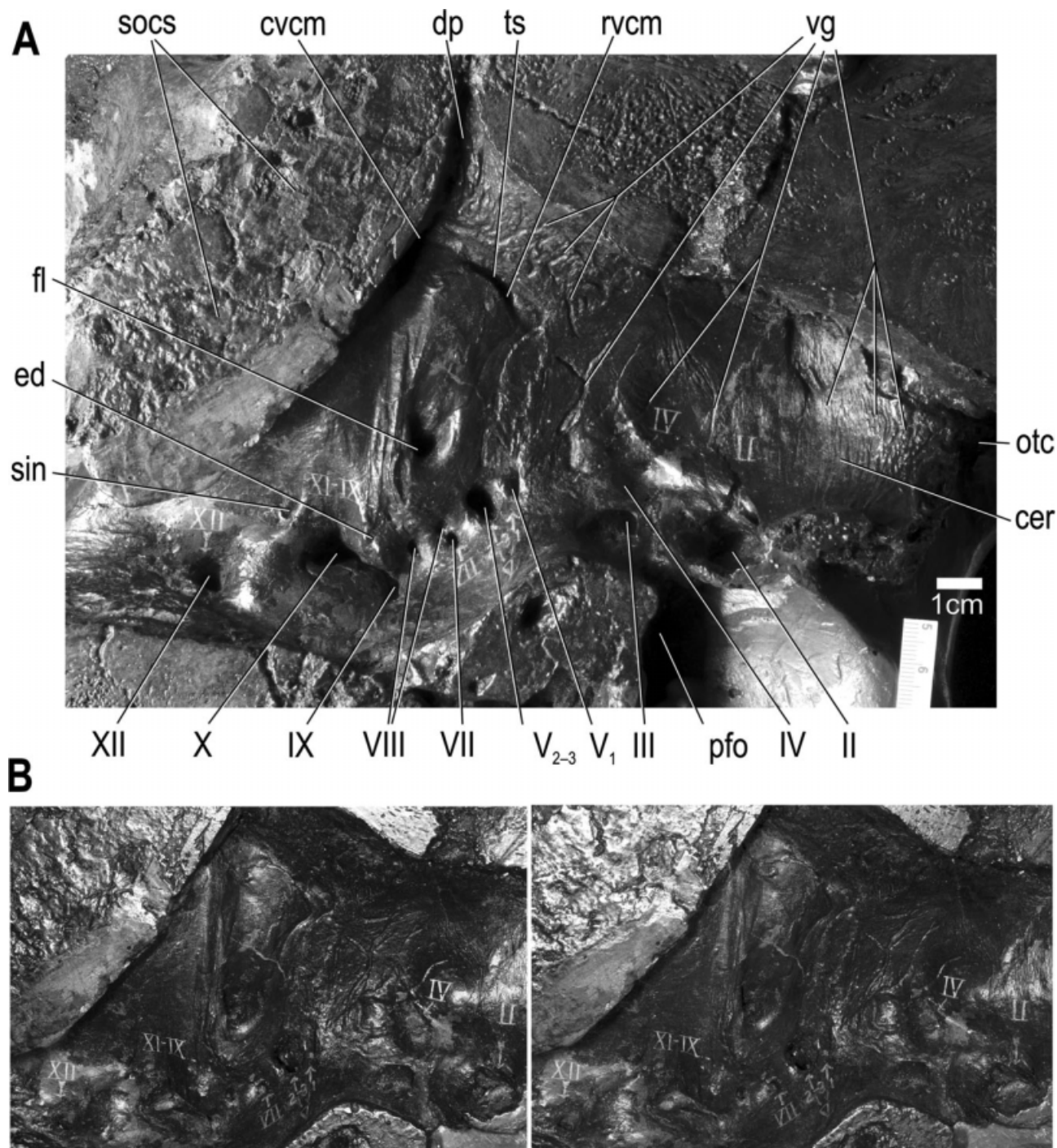
Fig. 7. Endocranial region of *Tyrannosaurus rex* (actual fossil specimen of AMNH FR 5029, sagittally sectioned) in left medial view to show the fine vascular grooves on the endocranial surface. **A**, Labeled view showing the whole endocranial cavity. **B**, Close-up view with reversed stereopairs such that the endocranial cavity looks "filled," making the view more comparable to the digital endocasts illustrated elsewhere in this article.

2005), again carrying the implication that at least parts of the brain closely fit the endocranial surface. We report here similar grooves in *T. rex* based on direct observation of the endocranial surface of AMNH FR 5029 (Fig. 7). There are very clearly a series of multiply branching grooves on the internal surface of the laterosphenoid,

perhaps extending onto the adjacent prootic and basisphenoid. Moreover, our cast of PIN 553-3/1 (*Tarbosaurus*) shows similar fine grooves in the same general positions. We agree with other workers (Osborn, 1912; Hopson, 1979; Brochu, 2003) that the brain generally did not fill its cavity, but these grooves suggest that,

using the same argumentation as other workers, some parts of the brain were closely appressed to the bone. Although in all the other reported cases the best grooves were in cerebral regions, the clearest grooves in AMNH FR 5029 are not in the cerebrum but rather just behind it. Another alternative is that fine vascular grooving may not always indicate a close fit between brain and endocranium, in which case caution should be exerted when interpreting such grooves.

Inner Ear

Casts of the endosseous labyrinths were digitally extracted from all of the tyrannosaurs in the sample here, as well as numerous outgroups. Complete labyrinths are available for *T. rex* and *Gorgosaurus*, and a partial labyrinth for CMNH 7541 (Fig. 8). Brochu (2000, 2003) illustrated some fragments of the labyrinth of FMNH PR2081; we were able to extract the semicircular canals completely (Fig. 3), and they resemble those of the better preserved *T. rex* specimens. All of the tyrannosaur labyrinths are generally similar to each other and resemble those of other theropods in being somewhat triangular in lateral view (Rogers, 1998, 1999; Larsson, 2001; Franzosa and Rowe, 2005; Sampson and Witmer, 2007). The semicircular canals are generally thin, elongate, and roughly mutually orthogonal. The only canal that deviates from planarity is the caudal semicircular canal, which is somewhat rostrally bowed dorsally, but not as markedly as in most other coelurosaurs. This departure from planarity of the caudal canal results from the caudodorsal expansion of the rostral semicircular canal beyond the common crus, which has the effect of "twisting" the common crus such that the caudal canal joins the common crus rostrolaterally, imparting a slight rostral bowing of the caudal canal. Although this twisting of the common crus in tyrannosaurs is not as prominent as in other coelurosaurs (e.g., *Struthiomimus* [Fig. 8Q–T], *Troodon*, *Deinonychus, Chirostenotes*), it still represents a more derived state than that observed in more basal theropods (e.g., *Allosaurus*, *Majungasaurus*; Sampson and Witmer, 2007).

The rostral canal of tyrannosaurs resembles that of other theropods in being the longest, but it is like that of other coelurosaurs in being expanded rostrally as well as caudodorsally (Fig. 8A), rather than being more strongly elliptical as in noncoelurosaurian theropods (Fig. 8U). The caudal and lateral semicircular canals are very similar in size and shape, and both are relatively circular. The more circular shape of the lateral canal (Fig. 8B) contrasts with the shape reported by Rogers (1998, 1999, 2005, p 352) for *Allosaurus*, in which the lateral canal is "hooked" caudally such that it makes a sharp bend. Our *Allosaurus* labyrinth shows the same "hook" (Fig. 8V), but the tyrannosaurs all more closely resemble *Struthiomimus* (Fig. 8R) and other coelurosaurs (including birds) in that the lateral canal sweeps laterally in a broader arc. The differences in this attribute can be subtle and variable. For example, AMNH FR 5029 (Fig. 8B) and FMNH PR2081 (not figured) more closely resemble *Struthiomimus* than does AMNH FR 5117 (Fig. 8F), which is more similar to *Gorgosaurus* (Fig. 8J) and CMNH 7541 (Fig. 8N). This variability may relate to true biological variation or slight diagenetic deformation, but it ultimately speaks to the subtlety of some differences in canal

structure. The caudal canal extends just slightly ventral to the lateral canal such that the two are indistinct caudally (Fig. 8). This condition characterizes tyrannosaurs, basal theropods (Sampson and Witmer, 2007), and many coelurosaurs, although some advanced maniraptorans (e.g., *Chirostenotes* but not *Archaeopteryx*) show the beginnings of the derived avian condition of having the lateral and caudal canals distinct throughout.

The vestibule of the inner ear has the typical archosaurian condition of not extending dorsally beyond the level of the lateral canal. The endolymphatic canal enters the vestibule near the base of the common crus (Fig. 8), which is the condition in theropods as diverse as *Ceratosaurus* (MWC 1.1), *Dromaeosaurus* (AMNH FR 5356), and *Chirostenotes* (ROM 43250). The cochlear duct (lagena) projects rostroventrally and slightly medially from the vestibule (Fig. 8). It is long and slender in *T. rex*, but may be somewhat shorter in *Gorgosaurus* (ROM 1247 is not well enough preserved to be certain). The cochlea of CMNH 7541 is relatively very long and thin, even more so than in *T. rex*. It is very straight in all the tyrannosaurs and not medially curved as in *Struthiomimus* and *Troodon*. The cochlea varies in length and orientation in theropods, and it may emerge that a long, slender, straight lagena is a tyrannosaur apomorphy. The site where the footplate of the columella contacted the vestibule is very clear and corresponds to the bony fenestra vestibuli (Fig. 8). Directly caudoventral to the latter is the cast of the fenestra cochleae, marking the position of the perilymphatic duct and secondary tympanic membrane, which is clearly distinct from the vagal canal located caudal to it (Figs. 1, 8, 9B). Unlike most theropods, the fenestra vestibuli is not located on the braincase surface, but rather is recessed far medially such that the columella must pass through a tube, the columellar canal, to reach the fenestra vestibuli (Fig. 9B). In AMNH FR 5117, the columellar canal is more than 40 mm in length, sandwiched between the otoccipital and a superficial lamina of prootic (Fig. 5). In CMNH 7541 (Fig. 9A), FMNH PR2081 (*T. rex*), and FMNH PR308 (*Daspletosaurus*), the columellae are preserved in place passing through the tubular recess.

Pneumatic Sinuses of the Braincase

A complex series of air-filled (pneumatic) sinuses permeate the braincases of tyrannosaurs (Fig. 2), as has been discussed by Russell (1970), Bakker et al. (1988), Molnar (1991), Brochu (2003), and Currie (2003b), among others. We will base the discussion here largely on our previous attempts to homologize and codify theropod pneumatic sinuses (Witmer, 1997; Sampson and Witmer, 2007; Witmer and Ridgely, 2008b, in press; Witmer et al., 2008). Figure 2 presents the basic pattern of sinuses in *T. rex* based on AMNH FR 5117, but the other specimens (AMNH FR 5029 and FMNH PR2081) are very similar. The different colors in Fig. 2 reflect our assessments of the individual sinuses; given that some of the sinuses communicate broadly, some distinctions, although founded in anatomy and occasionally subtle differences in X-ray attenuation in the rock matrix, have an arbitrary component. Figure 10 compares the sinuses in *T. rex* with those in *Gorgosaurus* (ROM 1247) and in CMNH 7541, using the same color scheme.
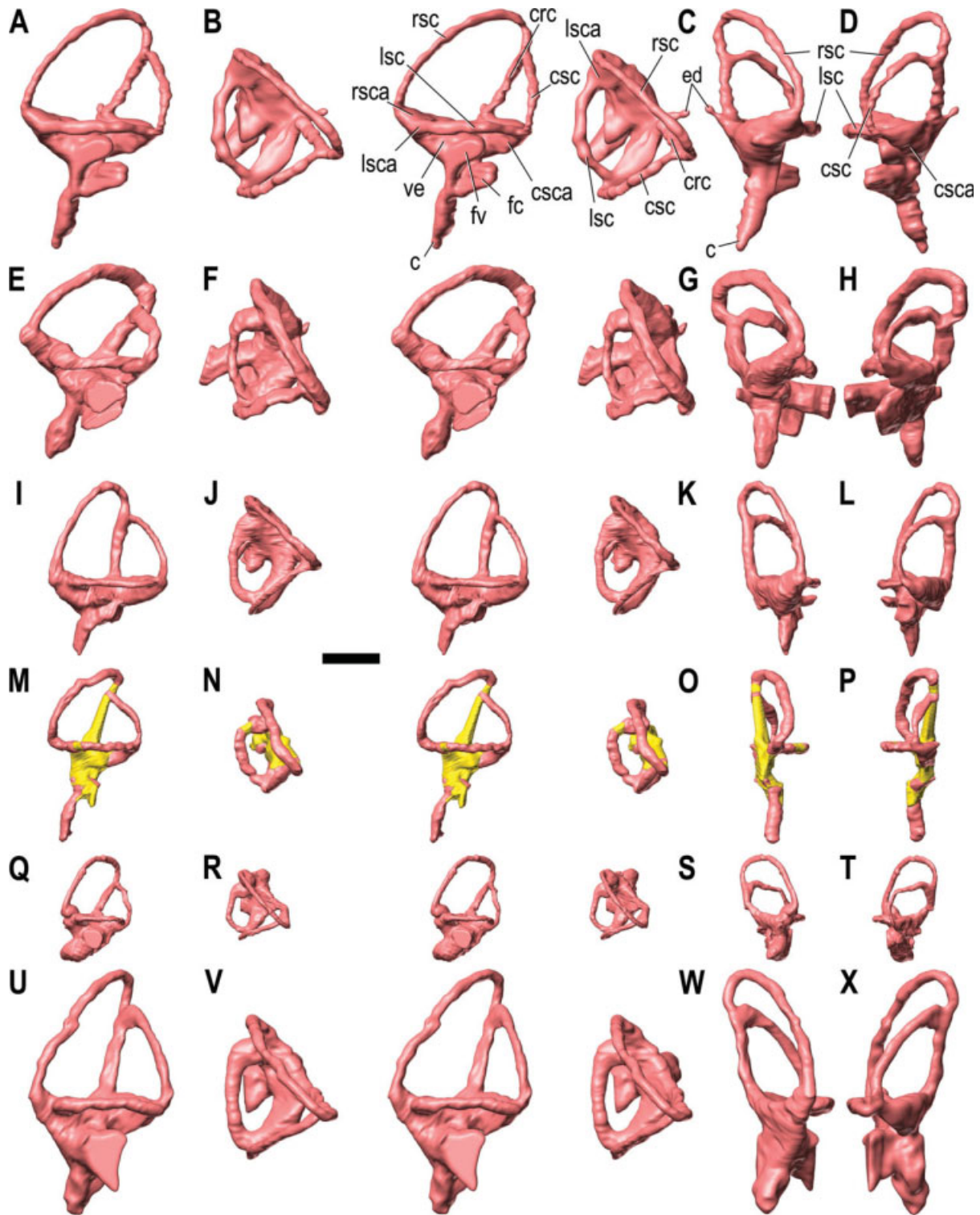
Fig. 8. Endosseous labyrinths (left sides). Left four columns are stereopairs of left lateral and dorsal views. Right two columns are rostral and caudal views, respectively. **A–D**, *Tyrannosaurus rex* (AMNH FR 5029); **E–H**, *T. rex* (AMNH FR 5117); **I–L**, *Gorgosaurus libratus* (ROM 1247, composite of both sides); **M–P**, Cleveland skull (CMNH 7541, composite of both sides, restored parts in yellow); **Q–T**, *Struthiomimus altus* (AMNH FR 5355); and **U–X**, *Allosaurus fragilis* (UMNH VP 18050, right side reversed). All are to the same scale (Scale bar = 1 cm).
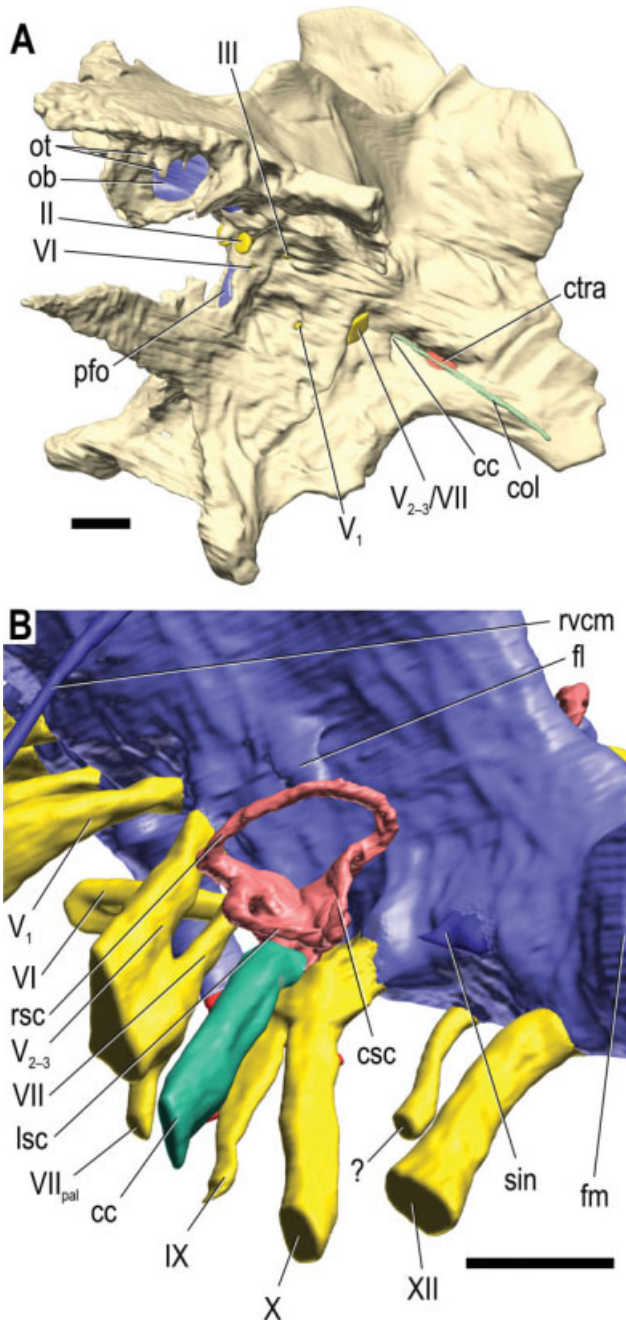
Fig. 9.   Columella and columellar region. **A**, braincase of the Cleveland skull (CMNH 7541, extracted from the full CT dataset) in left rostroventrolateral view, showing the left columella preserved in place. **B**, Cranial endocast and labyrinth of *Tyrannosaurus rex* (AMNH FR 5117) reconstructed from CT scans in left caudodorsolateral view, with the columellar canal (highlighted in teal) leading toward the fenestra vestibuli of the endosseous labyrinth. Scale bars = 2 cm.

Six main sinus systems can be identified in all of the tyrannosaur braincases. It is useful heuristically to group these into three "families," which is an appropriate metaphor in that some sinuses within a family may well be "offspring" (i.e., diverticula) of others: (1) the tympanic or middle ear system, (2) the median pharyn-

geal system, and (3) the subcondylar system. The tympanic family derives from pneumatic diverticula of the middle ear sac. Tyrannosaurs clearly have rostral and caudal tympanic recesses, but the dorsal tympanic recess, which is present variably in other coelurosaurs (Witmer, 1997; Makovicky and Norell, 1998; Norell et al., 2004; Rauhut, 2004), is apparently absent. Pneumaticity of the quadrate and articular bones also belongs to this family (Witmer, 1990), and, despite their being well developed in tyrannosaurs (Molnar, 1991; Witmer, 1997; Brochu, 2003; Witmer and Ridgely, 2008b, in press), we ignore them here to focus on the braincase. The RTR arises in the region of the cerebral carotid foramen, invading the basisphenoid deep to the otosphenoidal crest and preotic pendant, typically extending caudally somewhat within the basicranium as well as dorsally into the laterosphenoid and/or prootic (Figs. 2, 5). There is contralateral communication of left and right RTRs within the basisphenoid caudoventral to the pituitary fossa (retrohypophyseal sinus; Witmer and Ridgely, in press). *Gorgosaurus* and CMNH 7541 have another RTR extension rostral to the pituitary fossa that is absent in *T. rex* (prohypophyseal sinus; Fig. 10). *Gorgosaurus* and CMNH 7541 also share a well-developed ascending diverticulum of the RTR that extends dorsally into the laterosphenoid between the ophthalmic and maxillomandibular nerves (Fig. 10), whereas *T. rex* has at best (AMNH FR 5029) a rudimentary ascending diverticulum, and it usually is absent (AMNH FR 5117, FMNH PR2081); it is also absent in the *Daspletosaurus* in our sample (TMP 2001.36.1). As noted above, *T. rex* typically has a blind pneumatic fossa within the prootic just caudal to the maxillomandibular-facial foramen (Fig. 5B; Brochu, 2003). This prootic recess seems to have little direct relationship with the main part of the RTR.

The caudal tympanic recess and its extensions comprise volumetrically the largest braincase sinus in tyrannosaurs. The CTR aperture is in the typical location just ventral to the otosphenoidal crest, bounded mostly by the otoccipital and roofed by the prootic. The aperture is very large in AMNH FR 5117 (Figs. 2, 5) but smaller in other specimens. The position of the columellar canal shows that the columella would traverse the CTR aperture in *T. rex* and *Gorgosaurus*, and the *in situ* columella of CMNH 7541 confirms this relationship (Fig. 9A). In all the tyrannosaurs studied here, the CTR expands dorsally in the paroccipital process, and then extends laterally within the process and also dorsomedially into the supraoccipital. The contralateral supraoccipital sinuses are confluent above the hindbrain, and the caudal middle cerebral veins partially separate cells of the supraoccipital sinus (Figs. 2, 10). In AMNH FR 5029 and FMNH PR2081, the supraoccipital and paroccipital sinuses communicate via relatively narrow pneumatic tubes, whereas they are more broadly confluent in AMNH FR 5117. The exact patterns, sizes, and shapes of the pneumatic "bubbles" vary from specimen to specimen and even from side to side, which is characteristic of pneumatic systems, yet the basic patterns are consistent. All of the *T. rex* CTRs lack any significant extension ventrally into the crista tuberalis from the main CTR aperture, such that there is little to no communication between the CTR and the lateral subcondylar recess. The same is generally true of *Gorgosaurus* (ROM 1247), but CMNH 7541 has relatively broad communication between the CTR and lateral
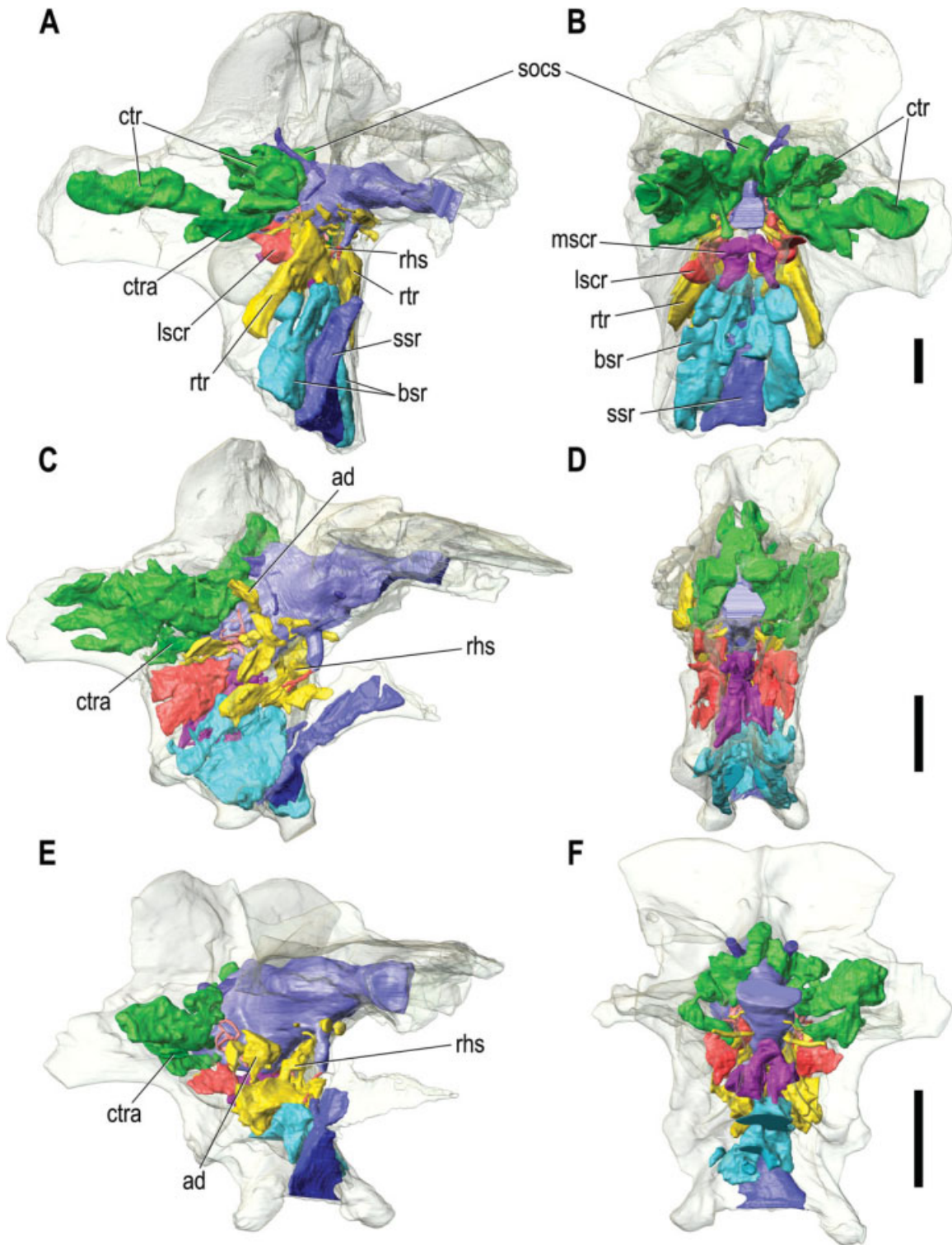
Fig. 10. Pneumatic sinuses in the braincase of tyrannosaurs in right rostroventrolateral view (left column) and caudal view (right column). Bone is rendered semitransparent, revealing pneumatic recesses, cranial endocast, vascular elements, and the endosseous labyrinth. **A**, *Tyrannosaurus rex* (AMNH FR 5117); **B**, *Gorgosaurus libratus* (ROM 1247); and **C**, the Cleveland skull (CMNH 7541). Scale bars = 5 cm.
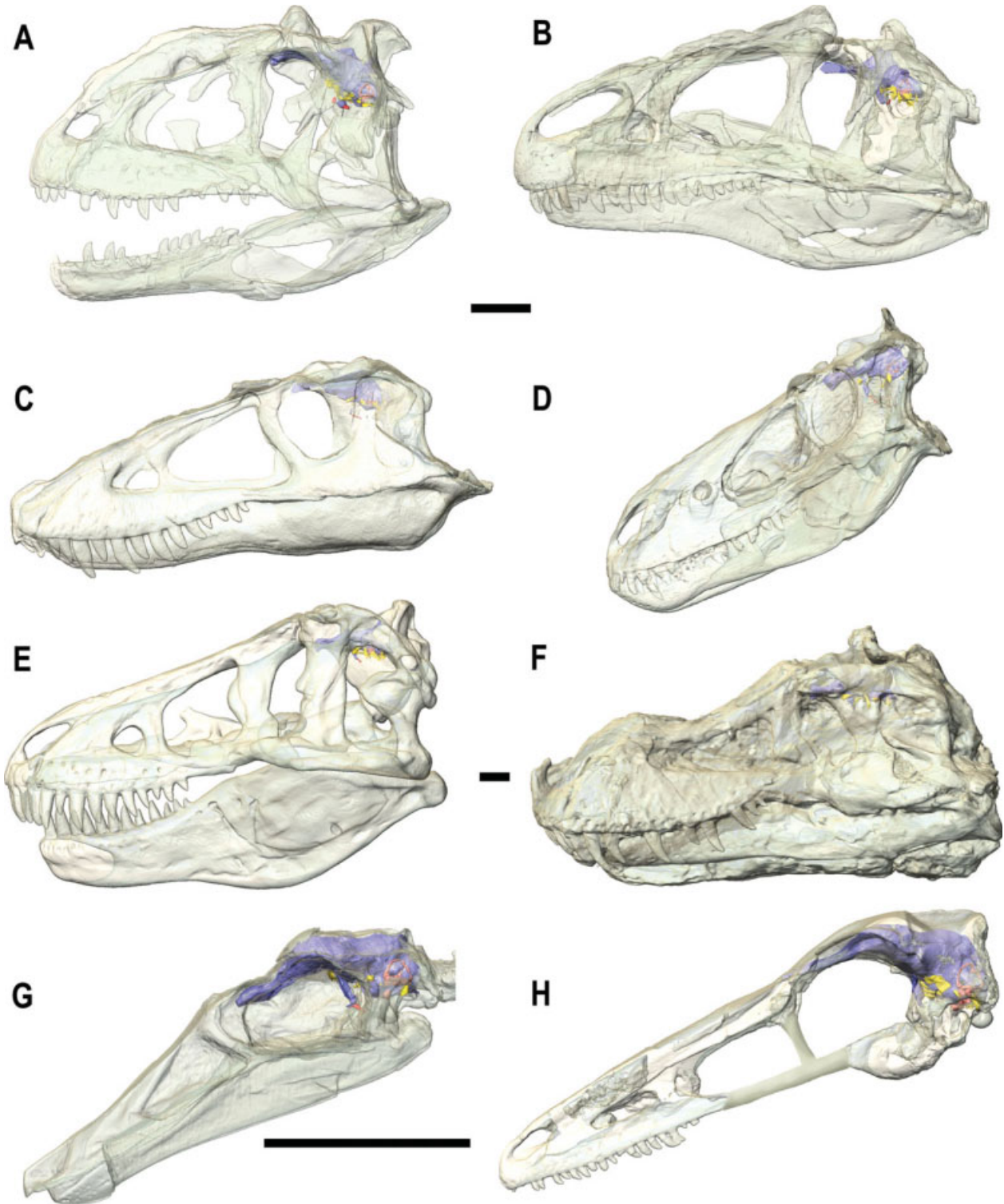
Fig. 11. "Alert" head postures based on orienting the skull such that the lateral semicircular canal is horizontal. **A**, *Majungasaurus crenatissimus* (FMNH PR2100; modified from Sampson and Witmer, 2007); **B**, *Allosaurus fragilis* (UMNH VP 18050, registered to MOR 693); **C**, *Gorgosaurus libratus* (ROM 1247, registered to a cast of AMNH FR 5664); **D**, the Cleveland skull (CMNH 7541); **E**, *Tyrannosaurus rex* (AMNH FR 5117, registered to a model of a *T. rex* skull); **F**, *T. rex* (FMNH PR2081); **G**, *Struthiomimus altus* (TMP 90.26.1); and **H**, *Troodon formosus* (composite of TMP 86.36.457 and TMP 79.8.1, registered to the skull of *Saurornithoides junior*, IGM 100/1). Scale bars pertain to **A–D** (top bar), **E–F** (middle bar), and **G–H** (lower bar). Scale bars = 10 cm.

subcondylar recess within the crista tuberalis (Fig. 10; Witmer and Ridgely, in press).

The median pharyngeal family probably derives from a diverticulum of the pharynx separate from the middle ear sac (Witmer, 1997; Chure and Madsen, 1998), producing two typical sinuses, the subsellar and basisphenoid recesses. These recesses are separated only by a thin lamina of bone, yet in some respects they seem to pertain to different anatomical domains, with the subsellar sinus being linked more to the orbital and palatal domains, whereas the basisphenoid sinus is connected more to the cervical and middle ear domains. Despite these differences, both pneumatic sinuses are grouped together in the same "family" because they are both median in position and direct pneumatization from the pharynx seems most likely. The subsellar recess in tyrannosaurs is well developed, occupying the triangular fossa rostral to the interbasipterygoid lamina and ventral to the pituitary fossa (Figs. 2, 5). In CMNH 7541 and especially *Gorgosaurus*, the subsellar recess has pneumatic extensions into the thin cultriform process (Fig. 10). In *T. rex*, the subsellar recess extends into at least the base of the cultriform process, and, in AMNH FR 5117, there is a large pneumatic foramen (on the left side only) leading from the subsellar recess into the basipterygoid process. The pattern of basisphenoid sinuses is complex in theropods generally and more so in tyrannosaurs. In general, the basisphenoid sinuses occupy the median space bounded by the basipterygoid processes in front and basal tubera behind. Primitively, there is a single pyramidal cavity, which may split caudodorsally into two recesses separated by a median septum (Chure and Madsen, 1998; Norell et al., 2004; Rauhut, 2004; Sampson and Witmer, 2007). Most tyrannosaurs have this system plus, in some taxa, another pair of often large apertures located more rostrally within the interbasipterygoid lamina, ventrolaterally near the basipterygoid processes (e.g., *Gorgosaurus*, *Daspletosaurus*; Russell, 1970; Bakker et al., 1988; Carr, 1999; Currie, 2003b).

In *Gorgosaurus* (ROM 1247), the rostral basisphenoid apertures open into large pneumatic chambers that fill the basipterygoid processes and basisphenoid, but remain separate from the subsellar recess and RTR; the caudal basisphenoid sinus system ramifies dorsally, but it cannot be determined (due to crushing) whether there is a median septum. *T. rex* is apomorphic in that the basisphenoid sinus is highly compressed fore-aft by apposition of the interbasipterygoid and intertuberal laminae (Bakker et al., 1988). As a result of this compression, the primitive caudal basisphenoid sinus system was reduced or lost, but the rostral system was retained, as indicated by the retention of the large apertures in the interbasipterygoid lamina (Figs. 2, 5, 10). As in *Gorgosaurus*, the basipterygoid processes and basisphenoid are highly pneumatized via these apertures. CMNH 7541 is highly divergent with regard to its basisphenoid sinuses (Bakker et al., 1988; Carr, 1999). They are not compressed to the extent seen in *T. rex* and seemingly present a distorted, asymmetrical pattern of apertures. As elaborated elsewhere (Witmer and Ridgely, in press), CT scanning shows that CMNH 7541 ultimately displays the primitive condition (albeit with an apomorphic transformation; Fig. 10). That is, the single rostral aperture in the interbasipterygoid lamina diverges dorsally into roughly paired sinuses, and likewise, the caudal aperture splits dorsally into paired sinuses. These sinuses, although perhaps now reconcilable with other basal tyrannosaurs (e.g., *Gorgosaurus*), exhibit numerous unique attributes, such as only weak pneumatization of the basipterygoid processes and unusual communications with other pneumatic sinuses. Although the braincase region indeed exhibits some postmortem deformation, we regard that deformation as not being significant enough to account for the disparity in basisphenoid sinuses exhibited by the Cleveland skull.

The final "family" of braincase sinuses consists of the subcondylar recesses (lateral and medial) that comprise apertures located within a fossa on the occiput and most intimately involve the basioccipital and otoccipital (Witmer, 1997). Subcondylar recesses are found in a wide range of theropods (Makovicky and Norell, 1998; Rauhut, 2004; Sampson and Witmer, 2007), although the precise source of the pneumatic diverticulum (i.e., tympanic vs. pulmonary vs. pharyngeal) is not entirely clear. For tyrannosaurs, a pulmonary or tympanic source is more likely. The subcondylar fossa of *T. rex* is relatively very shallow, bounded medially and ventrally by the condylotuberal crest (running between the neck of the occipital condyle and the basal tuber; Witmer and Ridgely, in press). The condylotuberal crest is relatively low and subtle in *T. rex* (Fig. 5), but it is much more pronounced and sharper in *Gorgosaurus* (ROM 1247, TMP 94.12.602), *Daspletosaurus* (CMN 8506, MOR 590, FMNH PR308), and CMNH 7541. Thus, the subcondylar fossa is much deeper in these other tyrannosaurs than in *T. rex*. Within the subcondylar fossa, there is typically a pneumatic aperture within the basioccipital and another within the otoccipital, leading to the medial and lateral subcondylar recesses, respectively. *Gorgosaurus* and CMNH 7541 both display the primitive condition of having the apertures located close together, near and on either side of the basioccipital-otoccipital suture, whereas in definitive *T. rex* the apertures are relatively widely separated. The medial subcondylar recess in all the tyrannosaurs studied here pneumatizes the basioccipital and extends into the condylar neck. The lateral subcondylar recess occupies the otoccipital and extends into the crista tuberalis in CMNH 7541 and especially *Gorgosaurus*, whereas it barely extends at all into the crista tuberalis in *T. rex* (Figs. 2, 5, 10). The communications of the subcondylar recesses with other braincase sinuses are variable, but one perhaps significant difference is that the lateral subcondylar recess communicates broadly with the CTR in CMNH 7541 but not at all in definitive *T. rex* or *Gorgosaurus* (Fig. 10).

DISCUSSION
Inferences on Sensory Function and Behavior

Much has been written on the sensory capabilities of tyrannosaurs, which is justified given that tyrannosaurs have perhaps the best fossil record of any predatory dinosaur group. However, there are severe limits on what inferences can be made, because we lack critical information on central neural connectivity as well as peripheral responses and sensitivities. Thus, it is important not to try to paint with too fine a brush. Keeping such caveats in mind, a comparative approach, coupled

with application of well-understood biophysical principles, can shed light on general sensory attributes.

Olfaction. We would expect there to be significant differences in olfactory capabilities based on the reconstructed olfactory bulbs of *T. rex* presented by Brochu (2000, 2003; Fig. 6A) and by us (Fig. 6A,B). Had Brochu's hypothesis been corroborated it would indeed have justified—even demanded—inferences of extraordinary olfactory capabilities (Larson and Donnan, 2002) and perhaps supported the notion of special adaptations for scavenging (Barsbold, 1983; Horner, 1994; Horner and Dobb, 1997). Our new findings (see also Witmer et al., 2008; Zelenitsky et al., 2009) argue for moderation in inferring tyrannosaur olfactory capabilities, but even these findings suggest that tyrannosaurs devoted an unusually large amount of neural tissue to the olfactory apparatus. *T. rex* and especially CMNH 7541 had relatively large olfactory lobes in comparison to other theropods (our data for *Gorgosaurus* are inconclusive because the sphenethmoid is not preserved in ROM 1247). Qualitative assessments of olfactory acuity will be quantitatively tested elsewhere using volumetric data, but the recent quantitative study using linear measurements presented by Zelenitsky et al. (2009) fully supports these findings.

Additional information on olfaction can be obtained by consideration of the nasal cavity. Witmer and Ridgely (2008b) recently reconstructed the cephalic air spaces in *T. rex*, revealing the basic structure and relative sizes of various parts of the nasal cavity. As shown in Fig. 6C here, the nasal cavity of *T. rex* was very long, extending from the rostroventrally positioned nostril (Witmer, 2001) to the front of the braincase medial to the orbits. The front portion of the nasal cavity is largely devoted to respiration, and the large arrow shows the respiratory airway from nostril to pharynx. The caudal portion, however, corresponds to the olfactory region in modern vertebrates (Witmer, 1995a) and represents the cul-de-sac found in virtually all tetrapods (Negus, 1958) where reduced airflow rates (Fig. 6C, small arrow) allow odorant molecules to diffuse to their receptors on the olfactory epithelium (Simmen et al., 1999; Settles, 2005; Craven et al., 2007). We have no way of knowing how much of this huge olfactory chamber in tyrannosaurs was actually cloaked in the sensory olfactory epithelium. In extant archosaurs, the vast majority of the equivalent epithelial region is, in fact, histologically olfactory (Witmer, 1995a), and this would be a very large territory in tyrannosaurs. Indeed, some tyrannosaur specimens preserve olfactory turbinates (e.g., CMNH 7541; Fig. 9A; Witmer and Ridgely, in press), suggesting that increasing olfactory epithelial surface area was important. Thus, it is perhaps not unreasonable to suggest that much of the observed olfactory region was indeed sensory. The large size of the olfactory chamber in tyrannosaurs would produce a caudally decreasing gradient in airflow rates. Given that the ability of odorant molecules to adsorb to the epithelial mucosa varies in a complex manner with airflow rate (Dawes, 1952; Sobel et al., 1999; see also Mainland and Sobel, 2006), the large airflow-rate gradient in tyrannosaurs might have provided a refined mechanism for discriminating odors. Moreover, Craven et al. (2007) showed that surface area require-

ments for olfaction are much greater than for the respiratory function, because odorant receptors tend to have regional specificity requiring adequate surface area to accommodate the numerous receptor types. Thus, again, the large area devoted to the olfactory region in tyrannosaurs may indicate a discriminating sense of smell, particularly given the new findings from genomics (Steiger et al., 2008) and ethology (e.g., Nevitt, 2008; Roth et al., 2008) that extant theropods (birds) may rely much more on olfactory cues than previously thought. The importance of scaling of these phenomena is completely unknown, but such a determination will become tractable as data of the kind presented here and elsewhere (Witmer and Ridgely, 2008b; Zelenitsky et al., 2009) become available for more taxa.

Hearing. Information on the sense of hearing comes from two sources in the braincase, the cochlear portion of the inner ear and the pneumatic sinuses of the middle ear. As noted above, tyrannosaurs have a relatively very elongate cochlear duct, and such is not universally the case in theropods. The length of the cochlea is causally related to the length of the neuroepithelium of the basilar papilla and has been correlated with rough measures of auditory capability or at least the behavioral importance of hearing (Baird, 1970; Wever, 1978; Manley, 1990; Gleich and Manley, 2000). Thus, by this measure, hearing was particularly important to tyrannosaurs. Gleich et al. (2005) also showed in extant taxa an allometric relationship between body mass and length of the basilar papilla, and also an inverse relationship between these two parameters and an animal's most sensitive ("best") frequency; that is, larger animals tend to have relatively longer basilar papillae and are more sensitive to low-frequency sounds. Gleich et al. (2005) had no tyrannosaurs in their sample of fossil archosaurs (only *Brachiosaurus*, *Allosaurus*, and *Archaeopteryx*), but applying their findings to our data would suggest that tyrannosaurs, in particular, emphasized low frequencies. These results agree with the acoustic consequences of extensive tympanic pneumaticity in tyrannosaurs in that a larger volume impacts the impedance-matching function of the middle ear by reducing stiffness at low frequencies as well as contributing to frequency-dependent amplification of sounds (Henson, 1974; Wever, 1978; Pickles, 1988; Manley, 1990; Dooling et al., 2000; Witmer and Ridgely, 2008b; Witmer et al., 2008). The columella and tympanum obviously also bear on hearing, and these are under comparative study by the authors, but, even absent analysis of these, all indications are that hearing in tyrannosaurs was important and low-frequency sounds were behaviorally the most relevant.

Equilibrium. The sense of balance is governed by the vestibular portion of the inner ear (otolith organs, semicircular canals), as well as central processing of these inputs in the brain. The otolith organs of the utricle, saccule, and lagena sense linear acceleration due to translational head movements. These structures are hidden within the bony labyrinth, and we have little direct information on these in tyrannosaurs. The tyrannosaur labyrinths, however, do preserve the bony semicircular canals that, in life, housed the membranous ducts that responded to angular acceleration due to rotational head

movements (Fig. 8). The interpretation of behavior based on the structure of the semicircular canals has been controversial because of lingering uncertainties (both theoretical and experimental) about the biophysical attributes of the canals, as well as apparent conflicting information from empirical comparative studies (see Graf and Klam, 2006; Hullar, 2006; Sipla and Spoor, 2008). It is well beyond our scope to review these controversies here. Ultimately, the question comes down to the functional significance of apomorphic canals. For example, Clarke (2005) interpreted the elongate rostral semicircular canal of *Brachiosaurus* as enhancing sensitivity so as to modulate slow, stately, pitching movement of the head. This notion agrees with Jones and Spells (1963, p 405) who found that larger animals tend to have more elongate (and hence "more responsive") canals, suggesting to them that "it seems plausible that larger animals...[have] in general, more sluggish head movements." On the other hand, this seems to contradict a wealth of empirical data linking expanded canal sizes in birds (Tanturri, 1933; Turkewitsch, 1934; Hadziselimovic and Savkovic, 1964; Money et al. 1974) and primates (Spoor and Zonneveld, 1998; Spoor, 2003; Spoor et al., 2007) with the quick head and body movements that characterize the more highly agile and acrobatic or aerobatic species within these clades.

This latter interpretation seems to better match the widely held inference of high levels of agility, quickness, and activity in nonavian coelurosaurs. Viewed in this light, and keeping all caveats surrounding semicircular canal biophysics in mind, the elongate canals of tyrannosaurs would be consistent with their active and agile coelurosaurian heritage. Tyrannosaur canal dimensions cannot be attributed solely to scaling phenomena, because their canal shapes and sizes (adjusted for body mass) resemble those of *Struthiomimus* (Fig. 8Q–T), *Troodon*, *Deinonychus* (Fig. 4E), *Archaeopteryx* (Fig. 4F), and the other small-bodied coelurosaurs in our broader sample more so than canal shape in large-bodied, more basal theropods, such as *Allosaurus* (Fig. 8U–X), *Acrocanthosaurus*, *Ceratosaurus*, and *Majungasaurus* (Sampson and Witmer, 2007). Tyrannosaurs do resemble other theropods in general in having the rostral canal the longest of the three, which may well be associated with bipedality. A link between rostral canal elongation and bipedality was proposed by Spoor et al. (1994, 1996) for hominids and by Sipla et al. (2004) for dinosaurs, and our large sample generally supports that association. However, further elongation of the rostral canal and, additionally, the lateral canal in tyrannosaurs and other coelurosaurs cannot be explained solely by bipedality and may relate, at least in part, to gaze stabilization mechanisms (see below).

Vision. Our data provide little information on the sense of sight, at least with regard to such parameters as acuity and sensitivity. The controversy surrounding the positions of the optic lobes—whether they are laterally displaced as in birds or medially located as in reptiles—probably has little bearing on assessing vision in that it generally has been thought that the lateral position of the optic lobes in birds and pterosaurs has more to do with the relative sizes of the cerebrum and cerebellum than the optic lobe itself (Jerison, 1973; Hopson,

1979; Witmer et al., 2003). Stevens (2006) discussed tyrannosaur vision in detail, and our findings again do not relate closely to many of the attributes he analyzed, with the exception of head posture, which is discussed below. Our findings on the inner ear, however, do relate to the behavioral importance of vision in that there is a tight functional relationship between the semicircular canals and eye muscles associated with the vestibulo-ocular reflex (VOR; Schwarz and Tomlinson, 1994; Cohen and Raphan, 2004; Graf and Klam, 2006). The VOR ensures that as the head turns (sensed by the semicircular canals) the eye muscles make coordinated and compensatory movements to maintain an image focused on the retina. In species for which tracking movements of the eyes are important, including aerial/arboreal specialists and visually oriented predators, the semicircular canal system tends to be well developed (Spoor and Zonneveld, 1998; Witmer et al., 2003; Spoor et al., 2007). Conversely, reduction of ocular musculature and diminished VOR in cetaceans has been linked to their reduced canal systems (Spoor and Zonneveld, 1998). To our knowledge, there are no broad quantitative studies specifically relating VOR performance with degree of canal elongation, but the two no doubt are linked. As noted above, rostral canal and especially lateral canal elongation in tyrannosaurs and other coelurosaurs cannot be fully explained by either scaling phenomena or bipedality. Instead, we propose that these changes may be adaptations for gaze stabilization, most likely related to predatory habits. The lateral canal is particularly elongate in *T. rex*, suggesting that mediolateral movements of the eyes and head were behaviorally important. This suggestion is consistent with Snively and Russell's (2007a,b) findings that tyrannosaur neck morphology emphasized quick and powerful lateroflexion. These inferences regarding the importance of rapid eye, head, and neck movements based on semicircular canal morphology might seem to be at odds with the apparently small flocculus observed in definitive adult *T. rex*, given that the flocculus in extant birds is associated with the vestibular system and VOR (see Witmer et al., 2003 and references therein). However, as noted above, it is very possible that the floccular endocast in fully adult tyrannosaurs is not a fair proxy for the size of the neural structure in life, in that there is good evidence that the endocranial cavity continues to grow after the cessation of brain growth. Thus, it is possible (perhaps likely) that a relatively large flocculus was present but failed to extend deeply into the otic region of the braincase.

Head posture. Although Hullar (2006) was critical about many aspects of basing behavioral inferences on semicircular canal structure, he fully supported the evidence linking orientation of the lateral semicircular canal with head posture. Indeed, there is a strong empirical relationship extending across amniotes between the planar elevation of the lateral canal and the stereotyped "alert" posture adopted by an animal, such that the head is typically oriented with the lateral canal roughly horizontal or perhaps slightly elevated (Lebedkin, 1924; de Beer, 1947; Duijm, 1951; Blanks et al., 1972; Vidal et al., 1986; Erichsen et al, 1989; Witmer et al., 2003, 2008; Graf and Klam, 2006; Hullar, 2006). Recently, Taylor et al. (2009) questioned the relationship between lateral

canal orientation and head posture (largely in the context of debates on sauropod neck postures), arguing that "although it has been claimed that HSCCs [horizontal semicircular canals, a synonym for lateral semicircular canals] are *habitually* held horizontally" (p 216, emphasis added), the behavioral data show considerable variation in canal orientation. We note that our work (Witmer et al., 2003, 2008; Sampson and Witmer, 2007) has referred to *alert* not *habitual* postures, recognizing that animals obviously orient their heads in many different postures depending on momentary behavioral requirements. Duijm (1951), for example, indeed recorded a range of postures for birds, but, as acknowledged by Taylor et al. (2009), the mean avian alert posture was with the lateral canal basically held horizontally. Likewise, Vidal et al. (1986, p 549) noted considerable variation in lateral canal orientation during different behaviors, but "at other times, presumably when the vigilance level increased [i.e., when alert], the horizontal canals were brought into the earth horizontal plane." In truth, many of the older studies need to be replicated using more modern imaging and analytical methods, but we remain comfortable using labyrinth orientation when animals are alert as a biologically meaningful and consistent comparative approach.

Figure 11 presents a number of theropods in their alert head postures as determined by orienting the skull with the lateral canal roughly horizontal. Assuming alert postures seek to optimize the cephalic sensory systems (hence aligning the labyrinth more or less with earth-horizontal), it is reasonable to assume that these would be similar to postures maximizing the binocular field of view (Witmer et al., 2003; Stevens, 2006). As noted by Sampson and Witmer (2007) and Rogers (1998, 1999), *Majungasaurus* (Fig. 11A) and *Allosaurus* (Fig. 11B), respectively, have an essentially horizontal head posture. The *Allosaurus* findings agree with those of Stevens (2006), and Samson and Witmer (2007) likewise suggested that in *Majungasaurus* the posture elevates the lacrimal rugosities such that they minimize obstruction of the binocular field of view. Among the coelurosaurian outgroups of tyrannosaurs, both *Struthiomimus* (Fig. 11G) and *Troodon* (Fig. 11H) have a fairly strongly down-turned alert posture, similar to what Stevens (2006) predicted for *Troodon*. Labyrinths from all three *T. rex* specimens indicate similar alert postures (Fig. 11D,E), with the head somewhat depressed (5- to 10-degree angle), actually slightly more than what Stevens (2006) found. *Gorgosaurus* (as measured by registering ROM 1247 to a cast of AMNH FR 5664; Fig. 11C) is fairly similar to *T. rex* in having a somewhat down-turned head posture.

The outlier is CMNH 7541, which has a more strongly depressed head posture (25- to 30-degree angle) than almost any of the other theropods in our sample (although still much less down-turned than in diplodocid sauropods; Sereno et al., 2007; Witmer et al., 2008). It is fair to wonder whether postmortem distortion can account for its head posture, in that, indeed, there are some signs of very slight displacements of some of the braincase bones. If one were to assume that the head posture of the animal represented by the Cleveland skull matched that of definitive adult *T. rex*, one would have to argue for postmortem deformation of CMNH 7541 producing *selective* rostrodorsal rotation of the braincase

relative to the rest of the skull, and we have found none of the significant displacements or disarticulations that would require. For example, the upper part of the braincase that encloses the labyrinth (the orientation of which again provides the signal for reconstructing alert postures) does not show nearly enough displacement between bones to account for the reconstructed head posture. Likewise, the preserved columellae traverse this region and are completely straight, undistorted, and in place (Fig. 9A), as are the epipterygoids that pass from the palate to the braincase. Moreover, the cultriform process of CMNH 7541 is not directed rostrodorsally, as would be expected if the braincase was selectively distorted and rotated; on the contrary, the cultriform process is lower and straighter than in most other tyrannosaurs (Witmer and Ridgely, in press). Significantly, Stevens (2006) found almost the same degree of head depression for CMNH 7541. The fact that our data are internally consistent, as well as consistent with Stevens' (2006) very different dataset, suggests that these findings are robust and reflect real behavioral similarities (e.g., between *T. rex* and *Gorgosaurus*) and differences (e.g., between CMNH 7541 and other tyrannosaurs). It also may be pointed out that the reconstructed head postures for the tyrannosaurs presented here (including CMNH 7541) result in very similar and comparable orientations of the occiput and cranial base relative to the neck, and thus similar attachments and actions of the cervical musculature.

Implications of tyrannosaur sensory systems.

On the basis of the above inferences regarding the sensory biology of tyrannosaurs, we can make some assessments as to the broader behavioral implications of these findings. The overall picture that emerges is that the brain and sensory structures were consistent with an active predatory mode of life. Although the debate has often focused on whether one species, *T. rex*, was a scavenger or a predator (see Holtz [2008] for an excellent recent review), the findings presented here show that that this one species was much like the other tyrannosaurids in our sample (e.g., *Gorgosaurus*, *Daspletosaurus*, *Tarbosaurus*, CMNH 7541) with regard to its brain and sensory structures. And likewise, tyrannosaurs generally have the attributes we might expect given their phylogenetic position between more basal theropods and more advanced coelurosaurs. For example, their cerebral hemispheres are moderately expanded, and it seems likely that their optic lobes were in an intermediate position—not the "reptilian position" inferred for more basal theropods (Sampson and Witmer, 2007), but not quite the fully "avian position" observed in more advanced coelurosaurs (Fig. 4). The visual systems of tyrannosaurs were those of a predator in that, based on the structure of the endosseous labyrinth, they had the capability to engage in rapid tracking movements of the eyes, head, and neck. Their cochleae were elongate, suggesting that the reception of air-borne sounds was important, and the length of the cochlea and the extensive pneumatic chambers further suggests that low-frequency sounds were emphasized. Low frequencies are transmitted with relatively little attenuation over long distances and through dense or closed habitats (Garstang, 2004), and thus enhanced low-frequency hearing could have been important for tracking prey movements, as well as for

other behavioral reasons, such as breeding or territoriality. One remarkable apomorphy of tyrannosaurs is the expansion of the olfactory apparatus, both the neural processing component (the olfactory bulb; see also Ali et al., 2008; Zelenitsky et al., 2009) and the olfactory region of the nasal cavity. This enhanced sense of smell was one of the key elements in the argument for scavenging (e.g., to locate carcasses), but, of course, many behaviors often use odors (e.g., maintenance of a territory), including predation (e.g., locating and tracking prey). Indeed, the finding of enlarged olfactory bulbs in herbivorous dinosaurs (sauropods; Witmer et al., 2008) reveals that prey, as well as predator and scavenger, can benefit from an enhanced sense of smell. Thus, tyrannosaurs had the sensorineural tools of a predator, but, as with virtually all extant predators today, almost certainly were willing to scavenge a carcass when available.

The Status of the Cleveland Skull, CMNH 7541

As noted at the outset, controversy has followed CMNH 7541, resting in recent years on the question of whether it represents a juvenile *T. rex* or a separate taxon (*Nanotyrannus lancensis*). We explored this question elsewhere (Witmer and Ridgely, in press) and found there to be no clear resolution, a position we take here as well. We identified a series of primitive characters in CMNH 7541 that are absent in *T. rex* but are found more basally (e.g., in *Gorgosaurus*), such as a narrow lanceolate vomer (rather than broad and diamond shaped), adjacent medial and lateral subcondylar recess foramina (rather than widely spaced), a strong condylotuberal crest (rather than subtle), a low cultriform process (rather than strongly vaulted), a relatively small subsellar recess (rather than large), a laterally positioned vagus foramen (rather medially positioned), a high number of dentary tooth positions (rather than a low number), among others (Witmer and Ridgely, in press). To this list can be added the presence of two paired sets of basisphenoid sinus apertures (rather than a single set) and having an extensive medial subcondylar recess (rather than a more moderate one). An ascending diverticulum of the RTR is found within the laterosphenoids of CMNH 7541 and *Gorgosaurus* but none of the *T. rex* (nor the sole *Daspletosaurus* in our sample), but we do not yet know if this similarity is primitive or derived. Nevertheless, a few features may be added to those listed by others (e.g., Carr, 1999) in favor of referral of CMNH 7541 to *T. rex*. For example, both have a highly elongate lagena, potentially a laterally positioned optic lobe, and a highly enlarged olfactory bulb, although none of these characters is without problems. Indeed, perhaps the most remarkable attribute of the braincase of CMNH 7541 is simply how different it is, and not just from *T. rex*, but also from other tyrannosaurs. As just noted, the entire skull and endocast are unique among tyrannosaurs in being very strongly down-turned. Aspects of the cranial endocast are very unusual, such as the rostrally offset pituitary fossa and orbital cranial nerves. The broad communication between the CTR and lateral subcondylar recess was not found in any of the other tyrannosaurs, nor were the highly asymmetrical basisphenoid sinus apertures. The pneumatic foramen in the quadratojugal of CMNH 7541

(Witmer and Ridgely, in press) has been reported in no other tyrannosaur other than BMR P2002.4.1.

We have evaluated explanations for the divergent nature of the braincase of CMNH 7541. For example, we cannot ascribe the differences to diagenetic factors such as crushing or plastic deformation. It is true that the skull has suffered postmortem damage, most markedly to the snout and laterotemporal fossa regions, and, as noted above, there are some subtle displacements between some of the bones of the braincase. As is typically the case with fossils, there are various cracks and defects. However, the braincase as a whole is basically symmetrical, as are the endocast and labyrinths. There are no large fractures or faults passing through the braincase that have disrupted relationships. Again, both of the delicate columellae are preserved in place and are undistorted (Fig. 9A). Other than the minor displacements noted, the skull remains remarkably well articulated, including the palate and such delicate elements as the epipterygoids. Indeed, there is postmortem distortion and breakage which no doubt has had some impact on the soft-tissue reconstructions presented here, but we have been unable to find significant enough evidence for distortion to explain away our basic findings as artifacts of preservation.

Pathology also seems an unlikely explanation, again given the overall symmetry and absence of obvious pathological signs (e.g., tumor growth). Gilmore (1946, p 10) suggested that the asymmetric basisphenoid sinus apertures represented "an unhealthy condition of the bone," but none of the other major workers on this specimen (e.g., Bakker et al., 1988; Carr, 1999; Currie, 2003b; Larson, 2008) invoked pathology to explain the strange basisphenoid sinuses. The last credible alternative is perhaps the most obvious: ontogeny. However, the differences are so striking that it is simply difficult for us to accept so much ontogenetic change (Witmer and Ridgely, in press), particularly in systems as fundamental and conservative as the brain cavity and inner ear. CMNH 7541 was not a particularly young individual, and, given the widespread ontogenetic precociousness of the brain and ear (Jeffery and Spoor, 2004; Butler and Hodos, 2005; Striedter, 2005), it may be unreasonable to believe that these structures transformed into something like those of definitive *T. rex*. Indeed, the endocast and labyrinth of ROM 1247 (i.e., juvenile *Gorgosaurus*) are more generally similar to adult *T. rex* than are those of CMNH 7541.

It is indeed frustrating that one of the only skeletal elements that is missing from the beautifully preserved BMR P2002.4.1 is, in fact, the braincase. Given the obvious closeness of CMNH 7541 and BMR P2002.4.1, it would likely have been taxonomically decisive. Our data on CMNH 7541 may be taken as evidence for the validity of *N. lancensis* on the grounds that it is "too different" from *T. rex*. However, we are hesitant to argue that the debate over its status is settled for the simple reason of sample size. CMNH 7541 presents one specimen—one highly divergent specimen. Although we see no clear signs of distortion or pathology in the braincase, its divergent nature concerns us, and we maintain that the possibility remains that future discoveries will show CMNH 7541 to be aberrant. For that reason, we urge caution and continue to regard the specimen's status as open.

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