

3. Structure of the brain cavity and inner ear of the centrosaurine ceratopsid dinosaur *Pachyrhinosaurus* based on CT scanning and 3D visualization

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Abstract

Information on the structure of the brain, cranial nerves, encephalic vasculature, and inner ear of the centrosaurine ceratopsid dinosaur *Pachyrhinosaurus lakustai* (Upper Cretaceous, Wapiti Formation, Alberta, Canada) is presented based on computed tomographic scanning of an isolated braincase followed by 3D visualization. The resulting digital cranial endocast and endosseous labyrinth are the most complete for any ceratopsid, to date, and are compared with physical and digital endocasts of other ceratopsians. In general, the structure of the brain of *P. lakustai*, as inferred from the endocast, was relatively primitive and much more like extant nonavian diapsid endocasts than like endocasts of archosaur groups with derived brains, such as pterosaurs, hadrosaurs, or coelurosaurs (including extant birds). Total brain size is relatively small, and none of the externally discernable brain regions (e.g., olfactory bulbs, cerebrum, cerebellum, optic lobes) are expanded. Currently, there are insufficient data to determine whether the simple structure and small size of the brain of *P. lakustai* are truly plesiomorphic or represent apomorphic reduction (evolutionary

Note: An animation of the 3D visualization of the digital endocast is available on NRC Research Press' Web site at <http://pubs.nrc-cnrc.gc.ca/eng/books/books/9780660198194.html>.

reversal). The endosseous labyrinth reveals a short cochlea, suggesting that airborne sounds were not particularly important behaviorally. The semicircular canals of the labyrinth are actually somewhat more elongate compared with what little is known of other neoceratopsian labyrinths. The fossil specimen is slightly compressed transversely, and this plastic deformation was subsequently ameliorated by a simple digital retrodeformation that provides a realistic view of brain size and shape. The most significant biological result of the project is that, even accounting for any deformation, the sensorineural and cognitive capabilities of *Pachyrhinosaurus* were modest, certainly in comparison with some other dinosaur clades, such as hadrosaurids and coelurosaurian theropods.

Key words: Dinosauria, Ceratopsia, *Pachyrhinosaurus*, brain, behavior, endocast, CT scanning.

Résumé

Cette étude présente des données sur la structure du cerveau, des nerfs crâniens, du système vasculaire crânien et de l'oreille interne du dinosaure *Pachyrhinosaurus lakustai* (centrosaure cératopsien – Crétacé supérieur, Wapiti Formation, Alberta, Canada), obtenues par tomodensitométrie d'une boîte crânienne. Une analyse par visualisation en trois dimensions est également offerte. Les contre-empreintes (moulage) numériques du crâne et du labyrinthe endo-osseux de ce cératopsien, qui sont les plus détaillées à ce jour, sont comparées aux données physiques et numériques d'autres cératopsiens. En général, la structure du cerveau de *P. lakustai* est relativement primitive et s'apparente davantage aux contre-empreintes des reptiles diapsides existants plutôt qu'à celles du cerveau dérivé d'archosauriens (ptérosaures, hadrosaures, coelurosauriens, y compris les oiseaux actuels). Le cerveau est relativement petit et aucune de ses régions externes (bulbes olfactifs, cerveau, cervelet, lobes optiques) n'est élargie. Par ailleurs, les données sont actuellement insuffisantes pour établir si la structure simplifiée et la petite taille du cerveau de *P. lakustai* sont véritablement plésiomorphiques ou représentent plutôt une réduction apomorphique (renversement évolutif). L'examen du labyrinthe endo-osseux révèle une cochlée réduite, ce qui suggère que les sons aériens jouaient un rôle accessoire sur le plan comportemental. Les canaux semi-circulaires du labyrinthe sont en fait relativement plus allongés par rapport aux autres labyrinthes néocératopsiens, bien qu'encore peu connus. Le spécimen fossile est légèrement comprimé dans l'axe transversal, et cette déformation plastique a été subséquemment améliorée par une simple rétrodéformation numérique offrant ainsi une image réaliste de la taille et de la forme du cerveau. Sur le plan biologique, le résultat le plus important du projet est que, même en tenant compte de toute déformation éventuelle, les capacités cognitives et neurosensorielles de *Pachyrhinosaurus* étaient rudimentaires, surtout par rapport à d'autres clades de dinosaures comme les hadrosauridés et les thérapodes coelurosauriens.

Mots-clés : Dinosauria, Ceratopsia, *Pachyrhinosaurus*, cerveau, comportement, contre-empreinte, moulage, tomographie par ordinateur.

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Introduction

Computed tomographic (CT) scanning has revolutionized the study of brain evolution in extinct archosaurs, such as dinosaurs, its X rays digitally slicing through bone and stone to allow access to the endocranial cavity. CT has provided new insights into the brain structure of pterosaurs (Witmer et al. 2003), ankylosaurians (Witmer and Ridgely 2008), sauropods (Serenó et al. 2007; Witmer et al. 2008), and theropods (Rogers 1998, 1999, 2005; Brochu 2000, 2003; Larsson 2001; Franzosa 2004; Franzosa and Rowe 2005; Sampson and Witmer 2007; Kundrát 2007), including birds (Domínguez Alonso et al. 2004; Kurochkin et al. 2006, 2007). With the exception of a CT-based study of the basal ceratopsian *Psittacosaurus* (Zhou et al. 2007), the study of the brain structure of horned dinosaurs has not made the jump into the digital age, probably in part because the braincase tends to be attached to skulls that are simply too large to fit through most CT scanners. Here we report on the first CT-based study of ceratopsid endocranial structure, producing the most complete view to date for any ceratopsian. The disarticulated braincase of the centrosaurine *Pachyrhinosaurus lakustai*, derived from the Pipestone Creek bone bed (Grande Prairie, Alberta; see Currie et al. 2008), forms the basis of this study.

Some previous studies of ceratopsid endocranial structure have drawn on observations of broken specimens, whereas others have made latex or plaster casts of the endocranial surface from specimens from which the rock matrix had been removed (known as brain casts or cranial endocasts). The endocranial morphology of only a few neoceratopsian taxa has been reported in the literature (see Hopson (1979) for an excellent review): *Protoceratops* (Brown and Schlaikjer 1940); the chasmosaurine ceratopsids *Anchiceratops* (Brown 1914) and *Triceratops* (Burckhardt 1892; Marsh 1896; Hay 1909; Gilmore 1919; Forster 1996); and of significance for this paper, the centrosaurine ceratopsid *Pachyrhinosaurus canadensis* (Langston 1975). Of these reports, only Marsh (1896), Brown (1914), Brown and Schlaikjer (1940), and Forster (1996) provided data based on cranial endocasts. Thus, the findings presented here will be not only the first CT-based study but also the first presentation of a centrosaurine endocast and inner ear (Figs. 1–3).

Beyond simply affording “a look inside,” CT scanning provides a number of advantages for studying the endocranial region. For example, because CT scanning transfers the specimen into the digital realm, it provides new opportunities for visualization and analysis. Structures such as the brain endocast, cranial nerve trunks, vascular canals, and endosseous labyrinth can be digitally extracted (a process

often termed “segmentation”) and viewed in isolation or even in situ within the surrounding bone, which can be rendered transparent. This latter attribute can be useful for clarifying the identity of various apertures on the external surface of the braincase in that, whereas the external surface can be highly variable in form (due to the variable functional constraints to which this surface must respond), the internal surface of the braincase is evolutionarily conservative between even distantly related taxa. The ability to unambiguously trace canals through the bony walls of the braincase permits us to correct some previous identifications made on the basis of only external morphology. The jump into the digital realm also makes quantification a trivial matter, allowing the rapid and accurate determination of parameters such as endocast volume, etc. Moreover, the data can be digitally manipulated to ameliorate the effects of postmortem distortion. For example, Currie et al. (2008) reported that the *P. lakustai* braincase at hand is somewhat laterally compressed; we used a simple digital transformation to address the distortion and arrive at a more realistic representation of the braincase and endocast, as well as perhaps more accurate metrics.

Institutional abbreviations: AMNH, American Museum of Natural History, New York, USA; IGM, Mongolian Institute of Geology, Ulaan Bataar, Mongolia; TMP, Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada; USNM, United States National Museum of Natural History, The Smithsonian Institution, Washington, DC.

Materials and Methods

A single isolated braincase of *Pachyrhinosaurus lakustai* (TMP 1989.55.1243) was available for CT scanning. This specimen derives from the Pipestone Creek bone bed in west-central Alberta, in Upper Cretaceous (Upper Campanian to Maastrichtian) rocks of the Wapiti Formation (Currie et al. 2008). Based on comparison with braincases of other specimens from the bone bed, Currie et al. (2008) regarded this somewhat compressed transversely specimen as coming from a relatively small individual. Indeed, the degree of fusion of the sutures between bones suggests that the individual was mature but relatively young. Although the results will not be presented here, we have drawn on comparative analysis of CT scan data, digital endocasts, and endosseous labyrinths generated as part of a larger project. Relevant ceratopsian specimens in this larger sample include a *Psittacosaurus* skull (IGM 100/1132), an unnumbered IGM “protoceratopsian” skull, and an unnumbered TMP braincase of *Centrosaurus*. Moreover, the AMNH collection of physical endocasts

was studied, including the *Protoceratops* endocast (AMNH 6466) published by Brown and Schlaikjer (1940) and Hopson (1979), the *Anchiceratops* endocast (AMNH 5259) published by Brown (1914) and Hopson (1979), and the *Triceratops* endocast (USNM 4286) published by Hay (1909).

TMP 1989.55.1243 was scanned on 7 April 2005 at Canada Diagnostic Centre in Calgary, Alberta, on a General Electric LightSpeed Ultra Multislice CT scanner. It was scanned helically at a slice thickness of 1.3 mm, 140 kV, and 300 mA, and was reconstructed using both standard and bone algorithms. Data were output from the scanner in DICOM format and then imported into Amira 4.1.2 (Mercury-TGS, Chelmsford, Massachusetts) for viewing, analysis, and visualization 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 and Windows XP Professional x64. Anatomical features of interest (e.g., cranial endocast, labyrinth, blood vessels, etc.) 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 paper. To facilitate discussion, we will refer to the digital casts of structures as if they were the structures themselves (e.g., "carotid canal" versus "digital cast of carotid canal"). Thus, bony structures and the equivalent structures on the cranial endocast will be referred to by the same name, despite topologically having the relationship of glove to hand. Movies and interactive animations of the digital endocast and braincase are available on the authors' website (www.ohio.edu/witmerlab).

Although quantitative metrics of various structures (e.g., volumes, areas, lengths) are easily generated by the software, we choose not to report those numbers here (with the exception of endocast volume, which is reported in the Discussion in the heuristic context of retrodeformation). Instead, we use relative, more qualitative, characterizations of dimensions. The reason for this decision stems mostly from the fact that the braincase at hand is a disarticulated specimen for which a body mass or other general size metric is unavailable (setting aside the problems associated with reliably estimating body mass in extinct animals). Also, the specimen is sufficiently distorted that the precise values may not be trustworthy, although the general proportions likely are. Finally, different researchers use different measurement schemes, and thus, we hesitate to introduce values into a literature already cluttered with metrics of doubtful comparability. That being said, all metric data are available on request from the authors, as are the digital models from which new measurements can be made.

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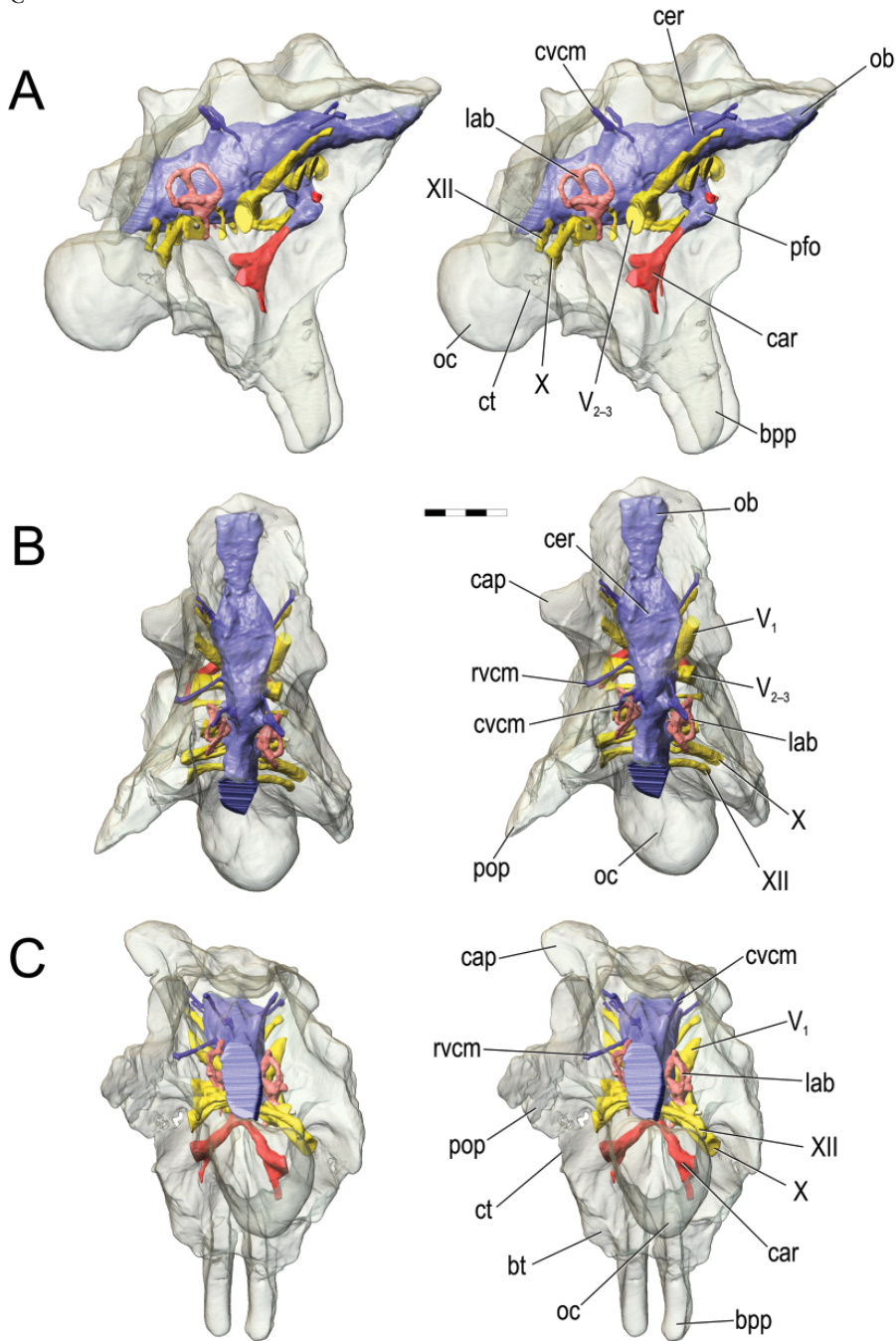
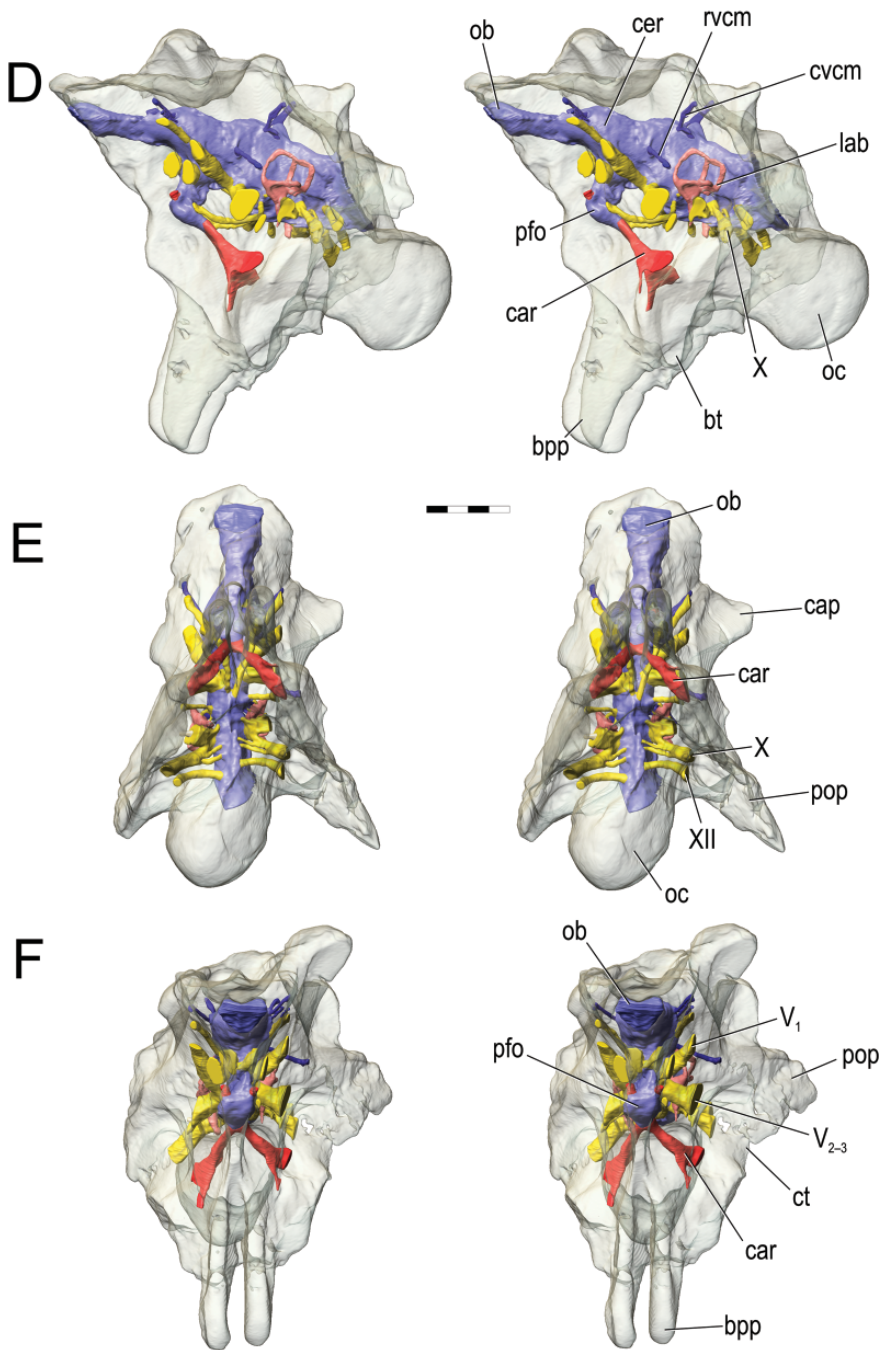


Fig. 1. Stereopairs of articulated braincase of *Pachyrhinosaurus lakustai* (TMP 1989.55.1243) derived from reconstructed computed tomographic (CT) scans and shown in the following views: (A) right lateral, (B) dorsal, (C) caudal, (D) left lateral, (E) ventral, and (F) rostral. Bone is rendered semitransparent, revealing cranial endocast in blue, endosseous labyrinth in pink, nerve canals (most of which also transmit veins) in yellow, smaller venous canals in dark blue, and arterial canals in red. Scale bar = 4 cm. Abbreviations: bpp, basiptyergoid process; bt, basal tuber; cap, capitata process of laterosphenoid; car, cerebral carotid artery canal; cer, cerebral hemisphere; ct, crista tuberalis; cvcm, caudal middle cerebral vein; lab, endosseous labyrinth; ob, olfactory bulb; oc, occipital condyle; pfo, pituitary (= hypophyseal) fossa; pop, paroccipital process; rvcm, rostral middle cerebral vein; V₁, ophthalmic nerve canal; V₂₋₃, maxillomandibular nerve canal; X, shared canal for vagus and accessory nerves and accompanying vessels; XII, hypoglossal nerve canal.

Figs. 1D–F



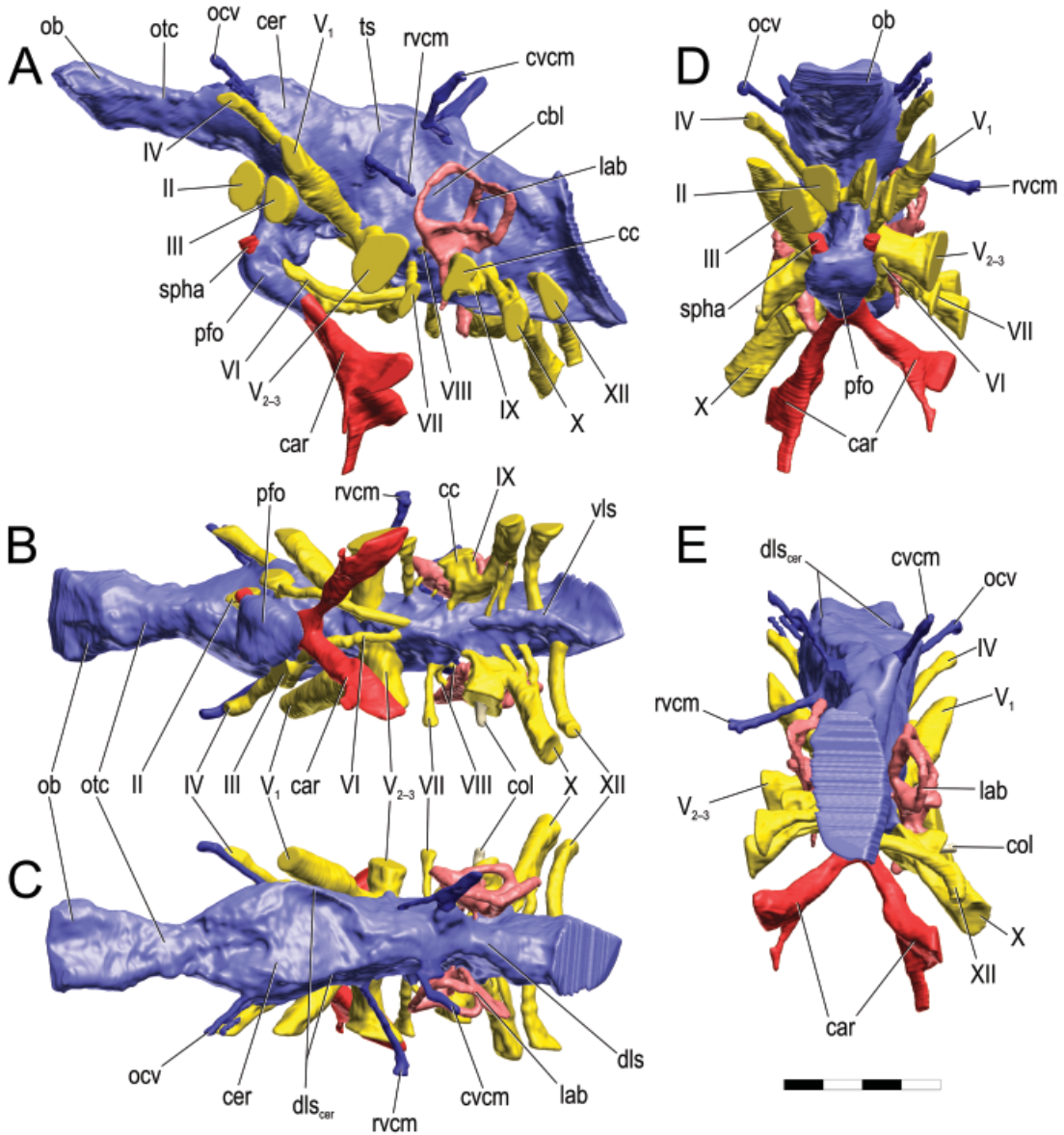


Fig. 2. Cranial endocast of *Pachyrhinosaurus lakustai* (TMP 1989.55.1243) reconstructed from computed tomographic (CT) scans and shown in the following views: (A) left lateral, (B) ventral, (C) dorsal, (D) rostral, and (E) caudal. Stereopairs are in the following views: (F) left lateral, (G) right lateral, (H) dorsal, (I) ventral, (J) caudal, and (K) rostral. Color scheme: cranial endocast, blue; endosseous labyrinth, pink; nerve canals (most of which also transmit veins), yellow; smaller venous canals, dark blue; arterial canals, red. Scale bar = 4 cm. Abbreviations: car, cerebral carotid artery canal; cbl, cerebellum; cc, columellar canal; cer, cerebral hemisphere; cvcm, caudal middle cerebral vein; col, columella (= stapes); dls, dorsal longitudinal sinus (a dural venous sinus); dls_{cer}, cerebral branch of dorsal longitudinal sinus; lab, endosseous labyrinth; ob, olfactory bulb; ocv, orbitocerebral vein canal; otc, olfactory tract cavity; pfo, pituitary (= hypophyseal) fossa; rvcm, rostral middle cerebral vein; spha, sphenoid artery canal; ts, transverse sinus; vls, ventral longitudinal sinus (a dural venous sinus); II, optic nerve canal; III, oculomotor nerve canal; IV, trochlear nerve canal; V₁, ophthalmic nerve canal; V₂₋₃, maxillomandibular nerve canal; VI, abducens nerve canal; VII, facial nerve canal; VIII, vestibulocochlear nerve canal; IX, glossopharyngeal nerve canal (part of columellar canal); X, shared canal for vagus and accessory nerves and accompanying vessels; XII, hypoglossal nerve canal.

Figs. 2F–K

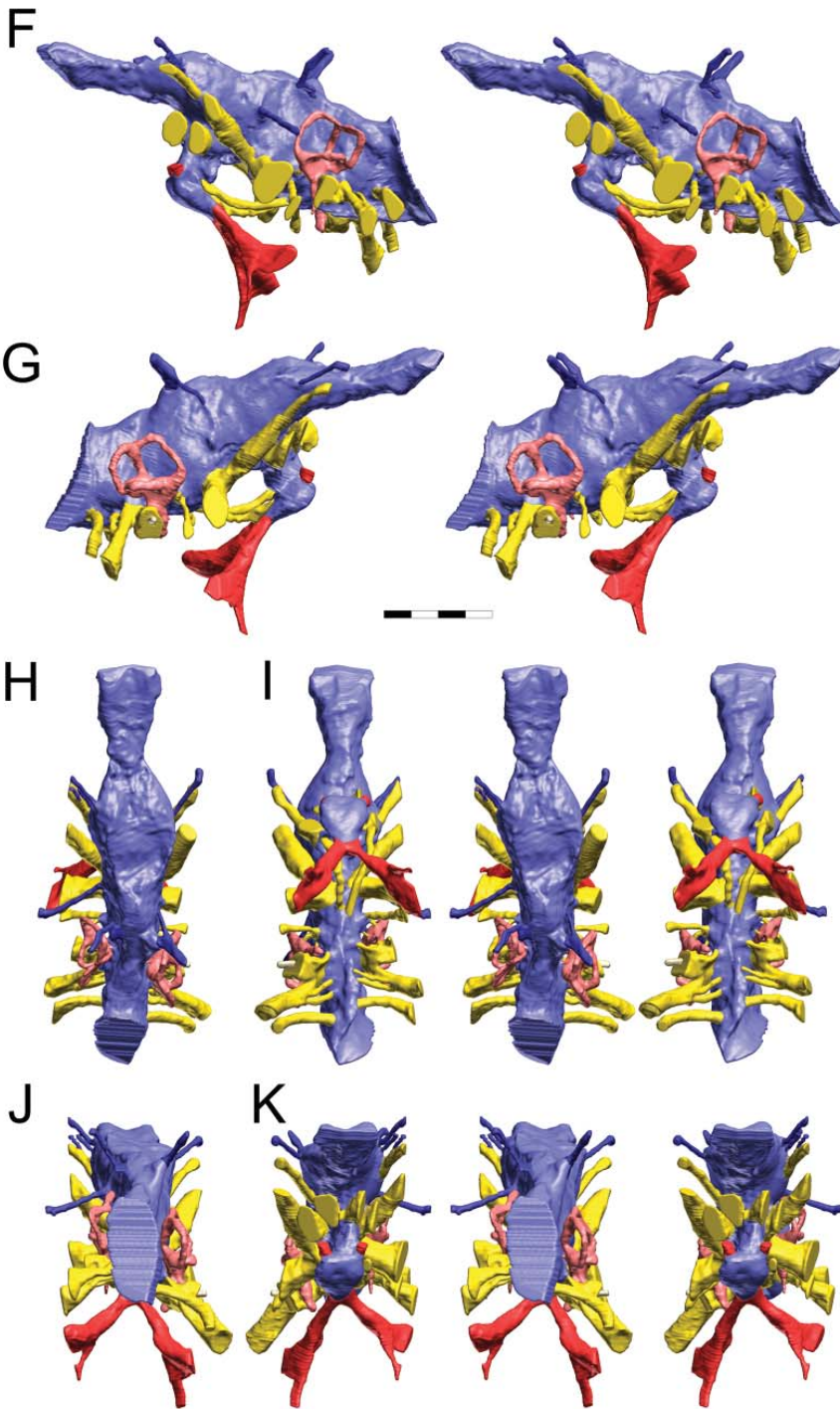


Fig. 3. Endosseous labyrinth of the left inner ear of *Pachyrhinosaurus lakustai* (TMP 1989.55.1243) reconstructed from computed tomographic (CT) scans. Stereopairs are in the following views: (A) lateral, (B) caudal, and (C) dorsal. Orientations were determined based on orientation of the labyrinth within the skull and with the lateral semicircular canal placed horizontally. Scale bar = 4 cm. Abbreviations: *c*, cochlea (= lagena); *crc*, crus communis; *csc*, caudal (posterior vertical) semicircular canal; *ed*, endolymphatic duct; *fp*, fenestra perilymphaticum (= round window); *fv*, fenestra vestibuli (= oval window); *lsc*, lateral (horizontal) semicircular canal; *lsca*, ampulla of lateral semicircular canal; *rsc*, rostral (anterior vertical) semicircular canal; *rsca*, ampulla of rostral semicircular canal; *ve*, vestibule of inner ear.

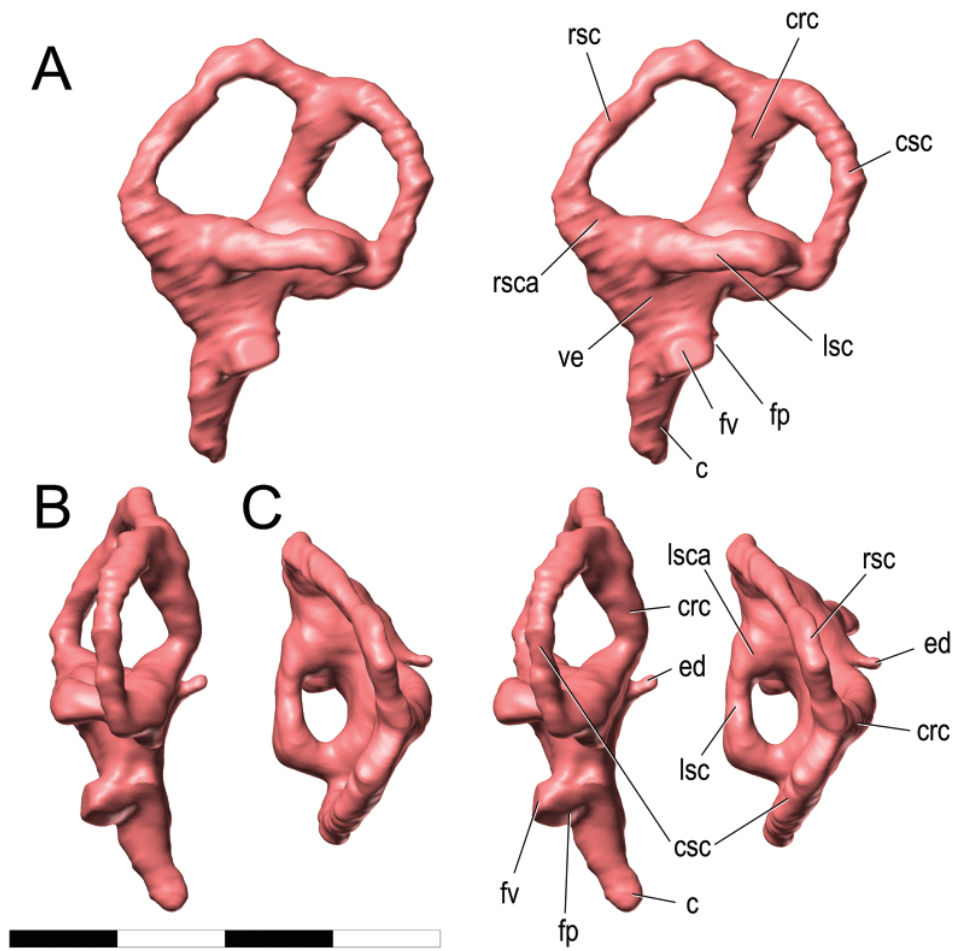


Fig. 4A

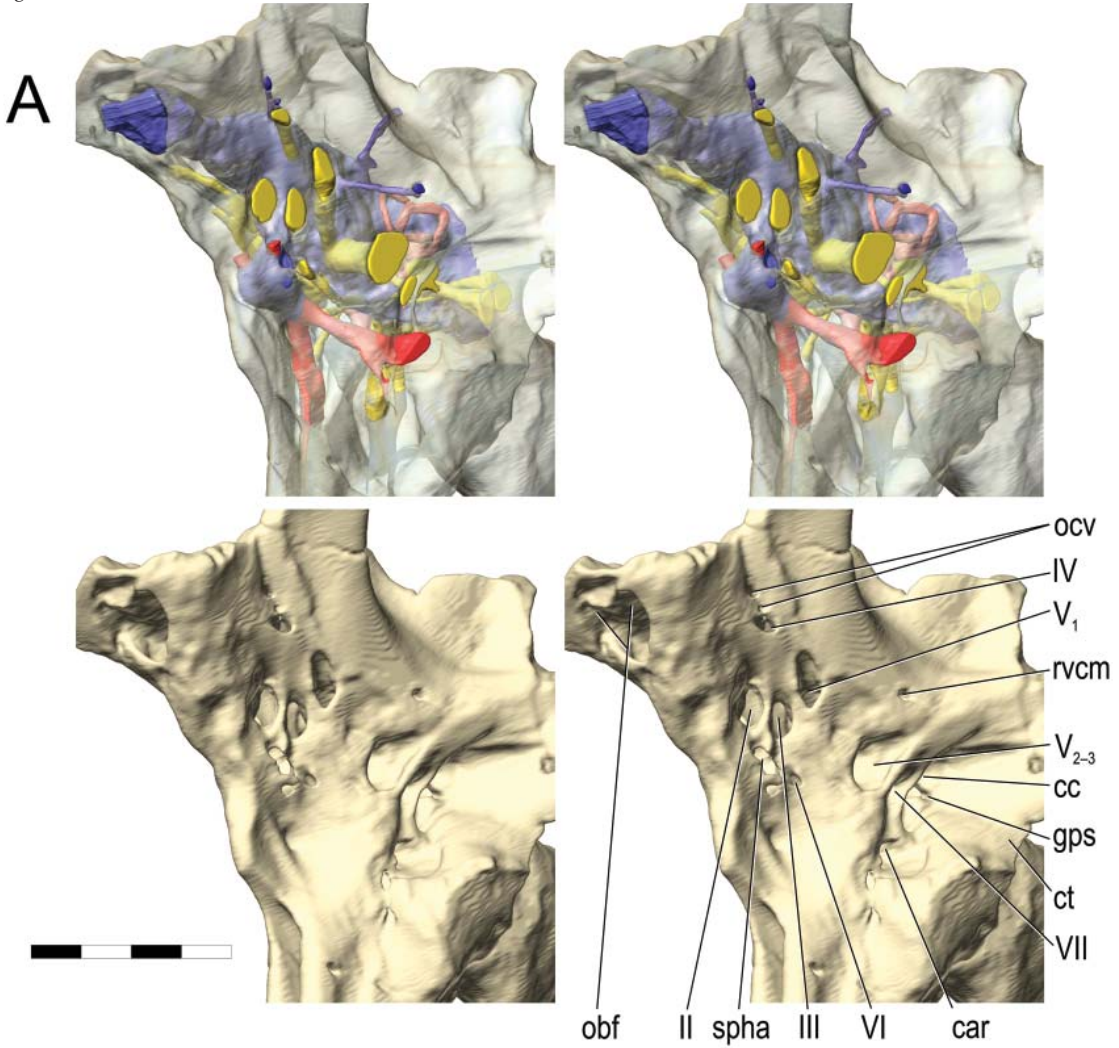
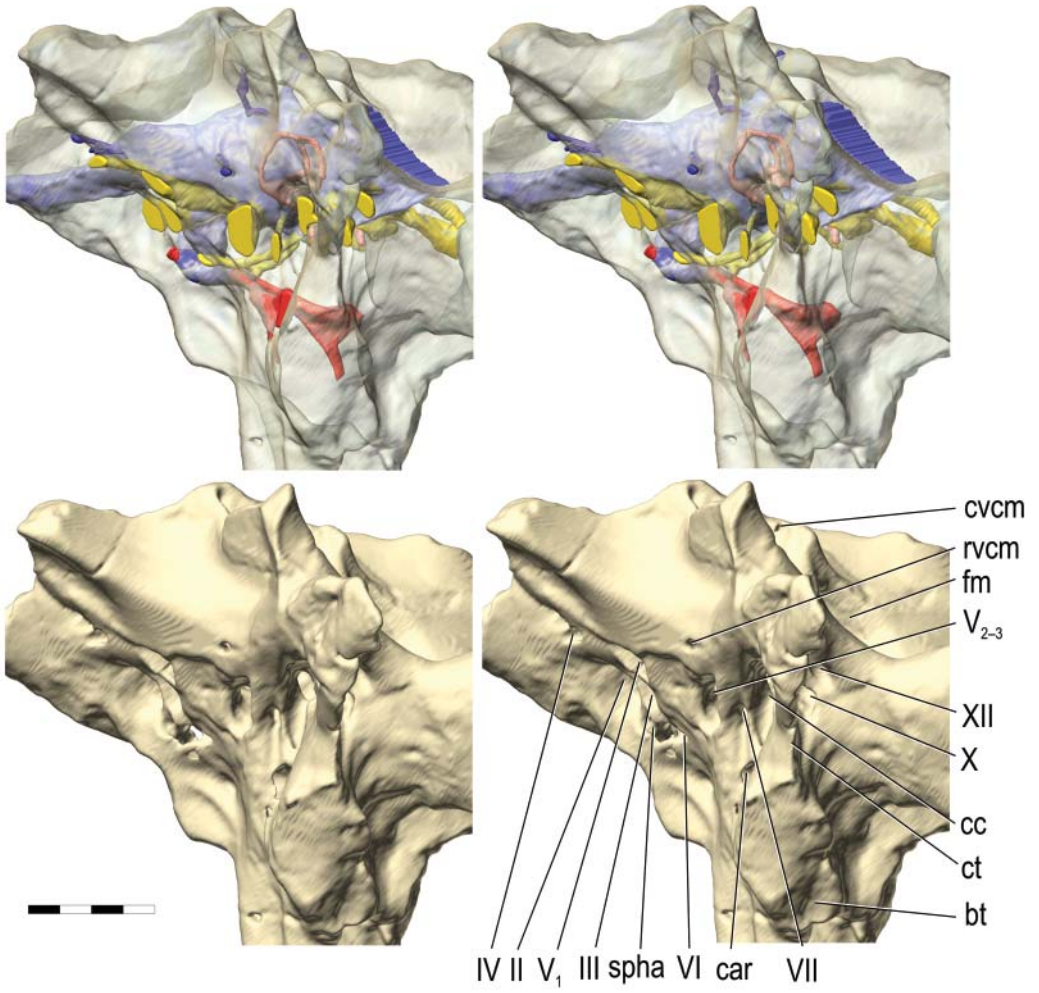


Fig. 4. Stereopairs of a braincase of *Pachyrhinosaurus lakustai* (TMP 1989.55.1243) reconstructed from computed tomographic (CT) scans in the (A) left rostroventrolateral view and (B) left caudolateral view to show the osteological correlates (e.g., foramina, fossae, crests) of many of the soft-tissue 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. Color scheme: cranial endocast, blue; endosseous labyrinth, pink; nerve canals (most of which also transmit veins), yellow; smaller venous canals, dark blue; arterial canals, red. Scale bar = 4 cm. Abbreviations: bt, basal tuber; car, cerebral carotid artery canal; cc, columellar canal; ct, crista tuberalis; cvcm, caudal middle cerebral vein; fm, foramen magnum; gps, glossopharyngeal sulcus; obf, olfactory bulb fossa; ocv, orbitocerebral vein canal; rvcm, rostral middle cerebral vein; spha, sphenoid artery canal; II, optic nerve canal; III, oculomotor nerve canal; IV, trochlear nerve canal; V₁, ophthalmic nerve canal; V₂₋₃, maxillomandibular nerve canal; VI, abducens nerve canal; VII, facial nerve canal; X, shared canal for vagus and accessory nerves and accompanying vessels; XII, hypoglossal canal.

Fig. 4B

B



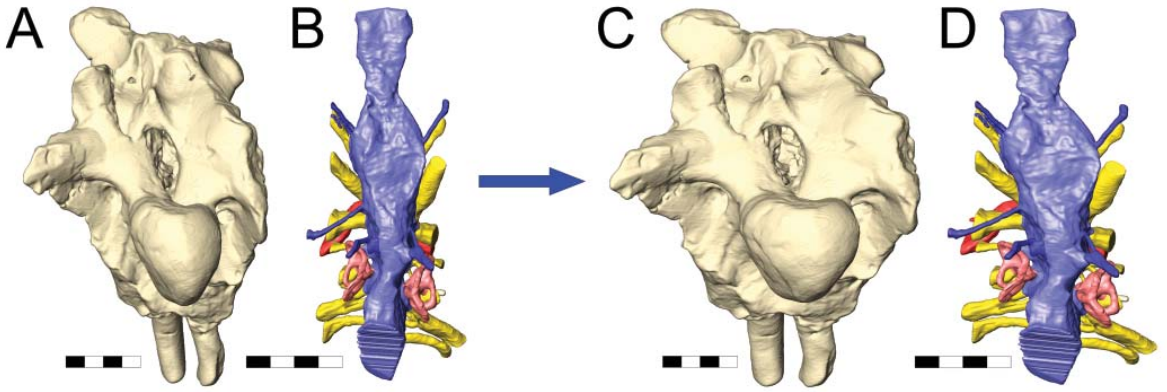


Fig. 5. Simple retrodeformation of a braincase and cranial endocast of *Pachyrhinosaurus lakustai* (TMP 1989.55.1243) reconstructed from computed tomographic (CT) scans. (A, C) Braincase in caudal view. (B, D) Cranial endocast in dorsal view. Scale bar = 4 cm. In A and B, the structures are shown as preserved prior to retrodeformation. In C and D, the structures have been transformed by simply stretching the dataset transversely so that the width of the occipital condyle equals its height (the condition observed in undeformed specimens). Even this simple retrodeformation restores a more natural shape to the braincase and endocast and increases endocast volume by 35%.

Results

The CT scan data for TMP 1989.55.1243 were excellent, allowing clear discrimination of fossil bone, rock matrix, and the plaster used to reconstruct the missing portions (e.g., left basiptyergoid process). Currie et al. (2008) provided a complete osteological description and illustration of this specimen, and thus this paper will focus on the cranial endocast, endosseous labyrinth, and endocranial vasculature. Nevertheless, some aspects of the bony braincase will be discussed, as they pertain to the reconstructed soft tissues, and the position of these soft-tissue systems are illustrated in place within the semitransparent braincase in Figure 1. Rather than provide a lengthy description of the structures, we will allow the illustrations to convey information on general form and relationships and instead focus on comparisons and significance.

Cranial endocast

The term “cranial endocast” (or just “endocast”) is generally used for a replica (whether virtual or physical) of the internal surface of the brain cavity. As discussed by many other workers (e.g., Jerison 1973; Hopson 1979), an endocast does not always faithfully record the shape of the underlying brain because the brain may not sufficiently fill the endocranium. In that case, the endocast constitutes a replica of the envelope of the dura mater (Osborn 1912). In some archosaurs, such as pterosaurs (Witmer et al. 2003), derived coelurosaurs (Currie 1985, 1995; Currie and Zhao 1993; Osmólska 2004; Kundrát 2007), and perhaps some ornithischians (Evans 2005), the brain resembled that of extant birds in that it largely filled the endocranium to the extent that an endocast fairly represents the general brain structure (Iwaniuk and Nelson 2002). However, the endocast of *P. lakustai* (Figs. 1, 2) is more like that of extant reptiles (and indeed most fossil archosaurs; Hopson 1979; Witmer et al. 2008) in that the endocast is not particularly brain-like in form, suggesting that the brain itself was perhaps markedly smaller than the endocast. Again, the endocast is somewhat distorted due to plastic deformation of the braincase (see above), but the transverse compression has not grossly altered its morphological features.

As is typically the case in archosaurs, the telencephalic portions of the brain are the most interpretable, presumably due to there having been less intervening tissue between the brain and bone. Thus, the cerebral hemispheres are clearly visible as rounded swellings in the forebrain region. Likewise, the paired olfactory bulbs are observable rostrally as they diverge from the median cavity for the olfactory tracts (Fig. 2C). Viewed in place (Fig. 1), the olfactory tract cavity can be seen to run through the dorsomedial roof of the orbit such that the olfactory bulbs are situated at the back of the nasal cavity. The pituitary region is also clearly visible (Figs. 2A, 2B), but the cast of the bony pituitary fossa does not provide a reliable measure of the

size and shape of the hypophysis itself because the fossa houses a number of other structures as well, such as the cerebral carotid artery and cavernous venous sinus. Nevertheless, the pituitary bears a well-marked infundibular constriction below the base of the oculomotor nerve trunk, and the structure generally resembles that illustrated for the endocasts of *Triceratops* (Marsh 1896; Hay 1909; Forster 1996) and *Anchiceratops* (Brown 1914; Hopson 1979). The cerebellum also is represented in the endocast as a low swelling (Fig. 2A). In extant diapsids, the cerebellum is typically located caudal to the transverse sinus system (including the rostral and caudal middle cerebral veins), between the paired rostral semicircular canals, and dorsal to the proximal trunk of the trigeminal nerve (Sampson and Witmer 2007; Ridgely and Witmer 2007). The swelling on the endocast of *P. lakustai* is in precisely this location, and a similar cerebellar swelling is present in the *Centrosaurus* endocast. Based on the size of the swelling, and even accounting for postmortem deformation, the cerebellum must have been relatively small in size. There is no indication in the endocast that the cerebellum had a floccular lobe (cerebellar auricle).

Unlike the brain components just noted, the position of the optic tectum (lobe) is not clearly visible. Hay (1909) and Forster (1996) identified low swellings on their endocasts of *Triceratops* as pertaining to the optic tectum, although Hopson (1979) regarded the tecta as not being visible in his ceratopsid endocasts, and the latter is likewise true for *P. lakustai*. Based on comparisons with extant diapsids (Ridgely and Witmer 2007), the optic tectum should be located in the region just caudal to the cerebral swelling and just rostral to the transverse sinus system, but there is no discernable swelling in this location in the endocast of TMP 1989.55.1243. This situation suggests that the optic tectum was relatively small, although the influence of postmortem deformation cannot be completely excluded. It moreover suggests that brain organization in *P. lakustai* resembled extant crocodylians and other reptiles in having an “in-line” brain with the cerebral hemispheres, optic tecta, and cerebellum in a rostrocaudal sequence and the contralateral optic tecta contacting each other. On the other hand, in more encephalized archosaurs, such as pterosaurs and many advanced theropods (especially birds), the optic tecta were displaced ventrolaterally and did not contact each other dorsally (Currie and Zhao 1993; Witmer et al. 2003; Kundrát 2007).

The cranial endocast preserves a number of vascular elements, and although these vessel traces obscure some of the underlying neural components, they also provide evidence for the gross limits of some of the brain parts. For example, the transverse sinus system was discussed in the context of providing a rough boundary between the optic tectum and cerebellum. The transverse sinus (a dural venous sinus) is visible on the endocast as a low curving ridge (Fig. 2A). It is continued laterally and caudodorsally as the rostral and caudal middle cerebral veins, respectively, the lateral branch opening in the skull just dorsal

to the maxillomandibular foramen and the caudal branch opening on the occiput (Figs. 1, 4). Another dural sinus that is clearly visible is the ventral longitudinal sinus. Identified earlier in the theropod *Majungasaurus* (Sampson and Witmer 2007), the ventral longitudinal sinus is a common feature of archosaur endocasts, forming a median ridge, which is long in *P. lakustai*, extending the length of the brainstem (Fig. 2B). The upper “shoulders” of the ventral longitudinal sinus represent the ventral margin of the medulla. The occipital dural venous sinus obscures the dorsal margin of the medulla and grades rostrally into the dorsal longitudinal sinus (Figs. 2A, 2C).

The dorsal longitudinal sinus extends rostr dorsally to the region directly above the cerebellum where it joins with the transverse sinus system. At this point, it splits and diverges, passing rostrally as a ridge along the dorsolateral edge of each cerebral hemisphere. These cerebral branches of the dorsal longitudinal sinus may correspond to the paired “dorsal venous sinuses” identified in *Triceratops* by Forster (1996). Interestingly, this branched dorsal longitudinal sinus is not present in the endocast of *Centrosaurus* but does appear to be present in the physical endocast of *Protoceratops* (AMNH 6466) and the digital endocast of *Psittacosaurus* (IGM 100/1132). In *Psittacosaurus*, the endocast ridges above the cerebral hemispheres are clearly coincident with sutures (e.g., frontal-laterosphenoid), perhaps suggesting that these features are architectural rather than vascular. However, dural venous sinuses positioned within bony sutures are common in archosaurs (Sampson and Witmer 2007; Witmer et al. 2008). Moreover, in *Pachyrhinosaurus lakustai* the ridges do not run entirely within sutures, and in both *Pachyrhinosaurus* and *Psittacosaurus* the endocast ridges are continuous with other, clearly vascular, features. In *Pachyrhinosaurus lakustai*, the cerebral branches of the dorsal longitudinal sinus drain into the orbit via the orbitocerebral vein canals (Figs. 2, 4). As in many other dinosaurs (see Witmer et al. 2008), the orbitocerebral vein(s) provided an important anastomotic connection between orbital veins and the endocranium.

The cerebral carotid artery passed through the typical canal in the basisphenoid on its way to the hypophyseal (pituitary) fossa, each side opening separately into the caudoventrolateral corner of the fossa (Currie et al. 2008; Figs. 1, 2, 4). Emerging from the rostr dorsally aspect of the hypophyseal fossa was a branch of the carotid artery that supplied the orbital contents and dorsum of the palate. Although this same vessel has been called the ophthalmic artery in other ceratopsids (Hay 1909; Brown 1914; Hopson 1979; Forster 1996), we regard this as the sphenoidal or sphenopalatine artery (Sampson and Witmer 2007; Fig. 2), a term from avian anatomy that recognizes the fact that in many birds, the true ophthalmic artery ontogenetically regresses to be replaced by the sphenoidal artery.

The pattern of the cranial nerve trunks is illustrated in Fig. 2 and their emergence externally on the braincase is in Fig. 4. In general, the nerve canals that enter the orbit are relatively large,

seemingly much larger than necessary to perform their neural functions (e.g., innervating extraocular muscles). In extant archosaurs, the cranial nerve canals and foramina—particularly the rostral ones (CN II–V)—transmit not only nerves but also veins from the orbit and nasal cavity into the endocranial cavity (Sedlmayr 2002). Thus, it seems likely that *P. lakustai* was like some other dinosaurs (e.g., sauropods; Witmer et al. 2008) in not only having the extant condition but also elaborating it further by expanding the venous component. The basic pattern of the nerves (Fig. 2) largely agrees with that presented by previous workers (e.g., Brown 1914; Hopson 1979; Forster 1996), and indeed the pattern is conservative across major clades (Witmer et al. 2008). Brown's (1914) study of *Anchiceratops* is the only comparable study that treated the cranial nerve canals throughout their entire length. One notable difference between *Pachyrhinosaurus* and *Anchiceratops* is the trigeminal nerve. In both taxa (as in ceratopsians generally; Langston 1975), the ophthalmic branch (CN V₁) and the maxillomandibular branch (CN V₂₋₃) took separate courses through the braincase to emerge at separate foramina (Figs. 1, 2, 4). However, whereas in *Anchiceratops* the two branches share a long common trunk coming off the endocast prior to their distal split, in *P. lakustai* the two trunks come off the main endocast almost separately. *Centrosaurus* shares the *P. lakustai* condition. It is not known whether this condition characterizes just centrosaurines, and it is possible that the *Anchiceratops* condition is a preservational artifact. Current work by the authors on the digital endocast of *Triceratops* should shed light on the chasmosaurine condition.

The facial and vestibulocochlear nerve canals (CN VII and CN VIII, respectively) share the typical common origin within the internal acoustic fossa. The facial nerve is unremarkable, but separate vestibular and cochlear branches of CN VIII were traceable on both sides (Fig. 2B). The caudalmost nerve trunks likewise display a relatively typical pattern. The vagus (CN X) and accessory (CN XI) nerve trunks were more or less indistinguishably joined within the vagal canal, and the glossopharyngeal nerve (CN IX) may well have joined them (but see subsequent discussion). As discussed by Sampson and Witmer (2007), numerous terms have been used for the common canal for these nerves (e.g., vagal, jugular, metotic), and the terminology is further complicated by the proximity of the perilymphatic system rostrally such that another set of terms (e.g., fenestra cochleae, fenestra pseudorotunda) is in play. The vagal canal passes caudal to the crista tuberalis (the bony crest that runs from the paroccipital process to the basal tuber; see Sampson and Witmer 2007) to open on the occiput (Figs. 1, 2, 4). The vagal canal receives the two rostral-most nerve canals of the three hypoglossal nerve canals, leaving the caudal-most—and by far the largest—hypoglossal trunk to open externally by way of its own foramen (Figs. 2, 4). Having three hypoglossal canals with the rostral two joining the vagal canal was reported previously for *Pachyrhinosaurus* (and *Chasmosaurus*) by Langston (1975)

and for *Triceratops* by Forster (1996), yet the digital endocast of *Centrosaurus* bears only two hypoglossal canals, the rostral one of which enters the vagal canal.

Whereas the vagal canal passes caudal to the crista tuberalis, it is continuous rostrally with a space (a projection on the endocast) that extends rostral to the crista. We have labeled this structure the columellar canal in Figs. 2 and 4 because it clearly houses the columella (= stapes), which is preserved more or less in place on the right side of TMP 1989.55.1243 (Figs. 2B, 2C, 2E). However, it also may have transmitted the glossopharyngeal nerve (CN IX) caudally given that there is a notch in the rostral margin of the crista tuberalis in this area (labeled glossopharyngeal sulcus in Fig. 4A; see also Fig. 2). The course of the glossopharyngeal nerve is variable in archosaurs and depends largely on whether the metotic fissure is divided or not, which it is in Ceratopsia. The structure on the endocast that we call the columellar canal may also contain some venous components but certainly contains portions of the perilymphatic system, which will be mentioned briefly in the next section on the inner ear.

As correctly noted by Langston (1975, p. 1588), the external foramina in the braincase can be difficult to identify because the nerve and vascular canals branch and “sometimes coalesce within the thickened ceratopsian cranial walls.” Fortunately, CT scanning and 3D visualization can resolve almost all such uncertainties, and Fig. 4 compares illustrations of the endocast and neurovascular trunks in situ with the isolated braincase so that the foramina can be identified. This approach allows correction of some published accounts that did not have the benefit of CT-based visualization. For example, in the braincase illustration of *Centrosaurus* presented by Dodson et al. (2004, p. 501), the foramen labeled “c.n. VI” should be the ophthalmic branch of the trigeminal nerve (CN V₁). These same authors also illustrate a grouping of three foramina, one of which is labeled “c.n. IV;” actually, the ventralmost opening is the trochlear foramen (CN IV) and the upper two openings are orbitocerebral vein foramina.

Endosseous labyrinth of the inner ear

The labyrinth of the inner ear is well preserved on both sides of TMP 1989.55.1243 (Fig. 3) and provides the best information to date on the inner ear of a ceratopsian (although we now have comparable data for *Psittacosaurus*, *Centrosaurus*, and *Triceratops*, which will be published elsewhere). Physical representations of the inner ears of *Protoceratops* (Brown and Schlaikjer 1940) and *Anchiceratops* (Brown 1914) have been published, having been made along with the cranial endocast. These are informative, but we assume that there must have been some measure of reconstruction involved given that they somehow were physically removed from the fossils. Zhou et al. (2007) presented CT-based data on the inner ear of their specimens

of *Psittacosaurus*. Our digital representation of the inner ear (Fig. 3) corresponds to neither the membranous (endolymphatic) labyrinth (which, being soft tissue, is not preserved) nor the osseous (bony) labyrinth but rather corresponds to the inside of the osseous labyrinth. Thus, although it is typically referred to as a digital “osseous labyrinth” (e.g., Sampson and Witmer 2007), we have adopted the more apt term “endosseous labyrinth” (Witmer et al. 2008; see also Sereno et al. 2007).

The endosseous labyrinth of *Pachyrhinosaurus lakustai* (Figs. 2, 3) is of a relatively generalized form. The upper part of the inner ear (the vestibule and semicircular canals) is associated with the sense of balance and equilibrium with important links to eye movements (see Discussion). The semicircular canals of *P. lakustai* are not as thin and elongate as in the labyrinths of *Psittacosaurus* (IGM 100/1132) but are not quite as stocky as those of *Anchiceratops* (AMNH 5259). The rostral semicircular canal is the longest of the three in *Pachyrhinosaurus lakustai* and actually ascends above the level of the common crus. This situation is different from that observed in *Anchiceratops* where the rostral and caudal canals are more similar in length. Likewise, in *Protoceratops* (AMNH 6466) and *Anchiceratops* (AMNH 5259), the rostral canals are lower and descend from the common crus. Still, the vestibular portion of the labyrinth of *Pachyrhinosaurus lakustai* more closely resembles that of these neoceratopsians than it does the gracile, theropod-like ear of *Psittacosaurus*. In particular, the lateral canal of *Pachyrhinosaurus lakustai* is relatively short (Fig. 3C), although not as short as that in sauropods (Witmer et al. 2008).

The lower part of the inner ear, the cochlea, comprises the hearing organ. We regard the cochlea as being that portion distal to the position of the fenestra vestibuli (= fenestra ovalis), which is where the footplate of the columella is seated. The cochlea of *P. lakustai* is relatively short, certainly in comparison to *Psittacosaurus* (IGM 100/1132) in which it is quite long. The form of the cochlea is not clear on the physical endocasts of *Protoceratops* (AMNH 6466) and *Anchiceratops* (AMNH 5259) but probably is comparable to that of *Pachyrhinosaurus lakustai*.

The form of the perilymphatic system is not entirely clear. As noted, the embryonic metotic fissure is divided in ceratopsians, and the portion rostral to the crista tuberalis was partially occupied by the perilymphatic duct. In some archosaurs with divided metotic fissures (e.g., crocodyliforms, advanced theropods), the perilymphatic duct extended caudally where it abutted bony elements to form a secondary tympanic membrane (e.g., fenestra cochleae or fenestra pseudorotunda; see Sampson and Witmer 2007, and references therein). We are not sufficiently certain that these perilymphatic modifications were fully present in *P. lakustai*, and so our labeling in Fig. 3 uses terms more consistent with a primitive state, that is, a fenestra perilymphaticum on the caudal surface of the labyrinth. Further analysis of other specimens will shed light on this issue and may ultimately argue for yet another independent evolution of a fenestra cochleae.

Discussion

Brain size and behavior

The relationship between endocast volume and body mass has attracted a great deal of attention because it allows a proper assessment of relative brain size (Jerison 1973; Hopson 1977; Hurlburt 1996). Although we can calculate endocranial volume easily and precisely in the digital realm, reliable body masses for extinct animals remain problematic in most cases. This problem is particularly acute in the present case because the specimen from which we have generated a digital endocast (TMP 1989.55.1243) is a disarticulated braincase found in a large bone bed and cannot be reliably associated with any postcranial elements (Currie et al. 2008). Thus, the traditional means of generating a body mass estimate are not available for TMP 1989.55.1243, and we cannot assess relative brain size at the present time. That is, we cannot calculate the encephalization quotient (EQ—Jerison 1973; or its reptilian extension, REQ—Hurlburt 1996), which provides a useful (although somewhat statistically problematic) comparative metric. It may ultimately be possible to establish a rough body mass estimate to accompany a braincase of this size, but until such time, we choose not to introduce poorly constrained estimates into the literature.

Nevertheless, it does not take complicated statistical models to justify the observation that the brain of *P. lakustai* must have been relatively very small in size and basically rudimentary in structure. As noted, the general brain structure was reptilian in that there is no evidence for any of the morphological apomorphies seen in derived theropods and birds. The cerebrum, cerebellum, and optic lobes were not at all expanded. That said, other attributes of *P. lakustai* suggest considerable behavioral sophistication. Its elaborate cranial ornamentations indicate the importance of intraspecific (and maybe also interspecific) behavioral communication and display (Sampson et al. 1997; Sampson 2001). Likewise, the evidence for herding and potentially even migration (Currie 1992) suggests some measure of behavioral complexity. These findings suggest that fairly elaborate behavioral repertoires are consistent with modest to small brain sizes. Moreover, they also put in perspective the relatively expanded brains of such dinosaurs as hadrosaurids, a group whose radiation and behavioral range is often compared with that of ceratopsids. The large brains of many hadrosaurids (Ostrom 1961; Hopson 1979; Evans 2005) may reflect cognitive capabilities lacking in ceratopsids such as *Pachyrhinosaurus*.

The effects of retrodeformation on brain size and form

As discussed, the *P. lakustai* braincase at hand (TMP 1989.55.1243) is somewhat deformed, being laterally compressed. Given that CT scanning digitizes the specimen, the possibility presents itself to address or even correct the fossil's deformation, a process called retrodeformation. A number of different approaches to retrodeformation have been proposed (e.g., Motani 1997; Srivastava and Shah 2006; Angielczyk and Sheets 2007), all of which have their advantages and disadvantages, and all of which require assumptions that we cannot adequately test for TMP 1989.55.1243. Consequently, pending a more formal treatment, we performed a simple transformation in an attempt to improve the cranial endocast to a first approximation. The assumption underlying the transformation is derived from the assessment of this specimen presented by Currie et al. (2008) that the occipital condyle should be about as wide as high. Thus, using Amira's Transform Editor module, we uniformly stretched the transverse dimension until the x dimension of the condyle equaled the y dimension. Thus, we only addressed plastic deformation and ignored brittle deformation (i.e., fractures). Although certainly overly simplistic, this approach to retrodeformation has the advantages of making fewer initial assumptions and being "quick and dirty."

The results returned are generally satisfying (Fig. 5). The braincase itself compares more favorably with less distorted specimens. Moreover, the endocast is credible, agreeing in general proportions with the physical endocasts of *Anchiceratops* (AMNH 5259; Brown 1914) and *Triceratops* (Forster 1996) and our digital endocast of *Centrosaurus*. The retrodeformation has a considerable impact on endocast metrics. The volume of the endocast as preserved (i.e., prior to transformation) is 63.0 cm³, whereas the retrodeformed volume is 85.4 cm³, a 35% increase. Even though we have no reliable body mass to accompany these endocranial values, the retrodeformed value would be more appropriate to use in studies of relative brain size. That said, we have chosen to illustrate the nonretrodeformed braincase, endocast, and labyrinth in Figs. 1–4 because these represent the unadulterated documents as preserved in the fossil record.

Sensorineural functional inferences

The dural envelope of *P. lakustai* (as represented by the cranial endocast) was sufficiently “loose-fitting” to the brain, as it was in most non-coelurosaurian dinosaurs, that fine details of brain structure are not recoverable. Nevertheless, based on what is preserved and also the structure of the endosseous labyrinth, some light may be shed on the sensorineural attributes and capabilities of this ceratopsid. Jerison’s (1973) “principle of proper mass” (see also Butler and Hodos 2005) affirms that the size of a brain region (e.g., the optic tectum) relates to the biological importance of the function of that region (e.g., processing visual information). Thus, the fact that the olfactory bulbs, cerebrum, optic tecta, and cerebellum are so small (regardless of any retrodeformation) suggests that precise sensory integration and control were not at a premium for *P. lakustai*. Given that some of these regions are enlarged in other dinosaurs (e.g., enlarged olfactory bulbs in sauropods, enlarged cerebrum in hadrosaurids, enlarged optic tecta in many coelurosaurs; Witmer et al. 2008), their small size in *P. lakustai* indicates their lower level of function. One remarkable attribute is the large size of the trigeminal nerve canals. Although some portion of each canal was no doubt occupied by veins, it is reasonable to suggest that the nerves themselves were also enlarged. Nevertheless, it is difficult to know whether tactile sensation (e.g., mechanoreception) was particularly heightened or whether the large size of the nerves simply reflects the enormous head, in that considerable trigeminal innervation would be required for general somatic sensation, as well as for motor supply to the large jaw musculature.

The structure of the inner ear shows that hearing was apparently not a particularly important sensory modality because the cochlea is quite short. The length of the cochlea is directly related to the length of the sensory epithelium (i.e., the basilar membrane; Manley 1990), and cochlear length has long been employed as a measure of hearing capabilities (Wever 1978; Gleich and Manley 2000; Gleich et al. 2004, 2005). The vestibular apparatus, on the other hand, was perhaps a little better developed than in some other neoceratopsians, in that the semicircular canals are somewhat more elongate. This elongation could be linked to a more general sense of balance and equilibrium, but recent research has shown that the semicircular canals have important neural links coordinating eye movements and head turning (Spoor et al. 2007, and references therein; see also Witmer et al. 2008). Thus, *P. lakustai* may have had somewhat better gaze stabilization mechanisms than some other neoceratopsians. We currently have insufficient data to assess whether the slight elongation would be statistically significant, but it is fair to suggest that it would be of doubtful biological significance.

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Philip J. Currie, Wann Langston, Jr., & Darren H. Tanke

A New Horned Dinosaur From an Upper Cretaceous Bone Bed in Alberta

with contributions from Patricia E. Ralrick, Ryan C. Ridgely, and
Lawrence M. Witmer

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