Endocranial Anatomy of Lambeosaurine Hadrosaurids (Dinosauria: Ornithischia): A Sensorineural Perspective on Cranial Crest Function

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ABSTRACT

Brain and nasal cavity endocasts of four corythosaurian lambeosaurines (Dinosauria: Ornithischia) were investigated to test hypotheses of cranial crest function related to sensorineural systems. Endocasts were generated through computed tomography and three-dimensional rendering and visualization software. The sample comprises a range of ontogenetic stages from the taxa *Lambeosaurus*, *Corythosaurus*, and *Hypacrosaurus*. Results show that the morphology of brain endocasts differs little from that of hadrosaurines. The strikingly convoluted nasal vestibule of *Hypacrosaurus altispinus*, when interpreted in the context of lambeosaurine phylogeny, suggests selective pressure for nasal cavity function independent from changes in the external shape of the crest and associated visual display function. The plesiomorphically small olfactory bulbs and apparently small olfactory region of the nasal cavity argues against the hypothesis that increased olfactory acuity played a causal role in crest evolution. The elongate cochlea of the inner ear reveals that hearing in lambeosaurines emphasized low frequencies consistent with the hypothesized low-frequency calls made by the crests under the resonation model of crest function. The brain is relatively large in lambeosaurines compared with many other large dinosaurs, and the cerebrum is relatively larger than that of all non-hadrosaurian ornithischians and large theropods, but compares favorably with hadrosaurine hadrosaurids as well as some maniraptoran theropods. It is concluded that the large brains of lambeosaurines are consistent with the range of social behaviors inferred when the crest is interpreted as an intraspecific signaling structure. Anat Rec, 292:1315–1337, 2009.   © 2009 Wiley-Liss, Inc.

Key words: archosaur; dinosaur; brain; Lambeosaurinae; Hadrosauridae; nasal cavity; inner ear; functional morphology

Lambeosaurine dinosaurs have undergone appreciable study due to questions concerning the function of their bizarre cranial crests and the associated evolutionary hypertrophy of their nasal cavities (Ostrom, 1962; Hopson, 1975; Weishampel, 1981 a,b, 1997; Evans, 2006). Despite this considerable attention and an abundance of fossil material, many aspects of lambeosaurine anatomy pertinent to cranial crest function, and lambeosaurine paleobiology in general, remain incompletely known. Of particular consequence is the lack of data on the morphology of the brain and the inner ear (Evans, 2006). Cranial endocasts, the three-dimensional casts of the cavity that encapsulated the brain and associated tissues, provide a wealth of information on the shape of the brain and the relative size of the brain parts (Jerison, 1973; Hopson, 1979; Witmer et al., 2008). With regard to testing hypotheses of cranial crest function in lambeosaurines, brain endocasts provides critical new information on brain structures associated with olfaction, and likewise casts of the endosseous labyrinth of the inner ear provide key information on hearing sensitivity that can be related to vocal resonation of the crest.

Among hadrosaurids, brain cavity endocasts have been described for several hadrosaurine taxa including *Edmontosaurus regalis* (Lambe, 1920; Ostrom, 1961), *E. annectens* (Lull and Wright, 1942), and *Gryposaurus notabilis* (Ostrom, 1961; Hopson, 1979). Lambeosaurine endocasts are considerably more poorly documented. Lull and Wright (1942) erroneously listed *Lambeosaurus* as having a described endocast; Gilmore (1924) described the braincase foramina of the holotype of *Lambeosaurus lambei* and commented on the shape of the cerebrum in a specimen now referred to *Parasaurolophus* sp. (Evans et al., in press), but a three-dimensional endocast was not figured or described. Young (1958) figured the endocast of *Tsintaosaurus spinorhinus* and on it labeled five cranial nerves (V, IX, X, XI, and XII), the cerebellum, pituitary, and optic lobe (Young, 1958). *Tsintaosaurus* is putatively a basal lambeosaurine (Buffetaut and Tong-Buffetaut, 1993; Godefroit et al., 2004a; Horner et al., 2004; Evans and Reisz, 2007), but this position is not followed by all workers (Wu, 2008, personal communication; Weishampel, 1981b). Regardless of its status, *Tsintaosaurus* does not seem to have the same degree of nasal cavity hypertrophy seen in other lambeosaurines. Although Ostrom (1961, 1962) reconstructed the brain and associated vasculature in *Corythosaurus* and other lambeosaurines based on braincase osteology, and Evans (2006) described a forebrain endocast for an indeterminate corythosaur, previous studies of lambeosaurine crest function have not presented evidence from a complete brain cavity endocast.

Lambeosaurines tightly enclose most of the nasal cavity within the premaxilla and nasal bones, which become allometrically elaborated through ontogeny into a cranial crest with species-specific external and internal morphologies (Dodson, 1975). The morphology and ontogeny of the crest cavities are still incompletely known in virtually all lambeosaurine taxa. Published reconstructions of the crest cavities in most lambeosaurines have been based on a few fortuitously broken specimens or even destructive "dissection" (*Parasaurolophus walkeri*, *P. cyrtocristatus*) of the crest (Ostrom, 1963;

Weishampel, 1981b). Notable exceptions are the reconstruction of the nasal passages of *Parasaurolophus tubicen* by Sullivan and Williamson (1999) and unpublished investigations of *Hypacrosaurus stebingeri* (Horner, 1995; Horner et al., 2001), which were accomplished nondestructively using computed tomographic (CT) scanning and visualization software. These pioneering studies demonstrated the considerable advantages of using CT scanning to reveal the internal anatomy of the lambeosaurine crest. This method can be used to visualize endocasts of all intraosseous cavities, including the brain cavity, nasal cavity, inner ear, vasculature, and air sinuses (Clark and Morrison, 1994; Ketcham and Carlson, 2001; Witmer and Ridgely, 2008b; Witmer et al., 2008), and is ideally suited for illuminating complex internal cranial anatomy of lambeosaurines. In this article, we present the first digital reconstructions of brain and nasal cavity endocasts for three species of fan-crested lambeosaurines: *Hypacrosaurus altispinus*, *Corythosaurus* sp., and *Lambeosaurus* sp. These endocasts of the brain cavity and endosseous labyrinth are the first complete endocasts for lambeosaurine hadrosaurids. The nasal cavity reconstructions provide new data on nasal cavity ontogeny and evolution and, together with the brain cavity endocasts, permit the most complete sensorineural evaluation of crest functional hypotheses to date.

MATERIALS AND METHODS
Materials

The specimens included in this study were chosen as representatives of the three most common genera of North American lambeosaurines, and the sample consists of four specimens from three species of fan-crested corythosaurian lambeosaurines: *Hypacrosaurus altispinus* (Fig. 1, Table 1), *Lambeosaurus* sp. (Fig. 2), and *Corythosaurus* sp. (Figs. 3, 4). The specimens differ with respect to their overall size and corresponding degree of cranial crest development, and were selected to cover most of the preserved ontogenetic stages of cranial crest development in the corythosaur clade. However, there are gaps in the ontogenetic representation of each genus at this time. This study is part of a larger project on comparative hadrosaurid cranial ontogeny, and we intend to scan more specimens to complete these ontogenetic series that will be presented in future publications.

The taxonomic identification and provenance of the specimens are as follows:

1. *Hypacrosaurus altispinus* (Royal Ontario Museum, Toronto, ROM 702): ROM 702 (Fig. 1) is a largely complete but disarticulated skull (skull length = ~700 mm) and associated partial tibia from a large individual with a fully developed cranial crest. This specimen has yet to be formally described, but can be referred to *Hypacrosaurus altispinus* on the basis of a foreshortened caudolateral premaxillary process that contributes to a helmet-shaped crest and a constricted external naris (Russell and Chamney, 1967; Evans, in press). The specimen was collected from the lower Maastrichtian part of the Horseshoe Canyon Formation, Alberta, within the series of strata that have yielded all of the known *H. altispinus* material (Russell and Chamney, 1967; Eberth, 2004; Evans, 2007).
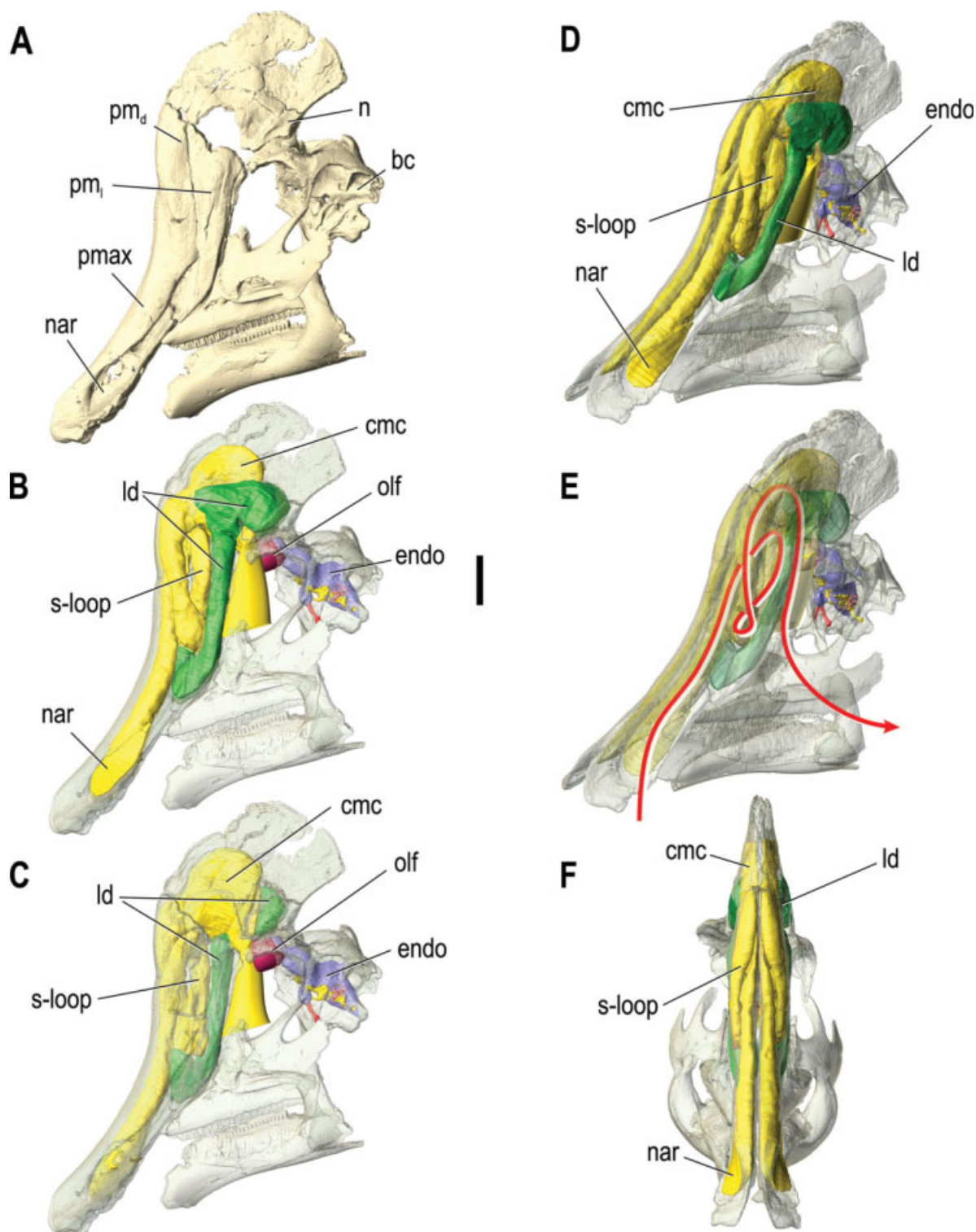
Fig. 1. Nasal cavity and other cephalic components of *Hypacrosaurus altispinus* (ROM 702). Left premaxilla and nasal airway have been mirrored from the right side. Labeled illustrations in (**A**) left lateral view; (**B**) left lateral view with transparent bone showing nasal airway; (**C**) left lateral view with transparent bone with nasal structures sagittally sectioned showing medial side of right nasal airway; (**D**) left rostrodorsolateral oblique view; (**E**) left rostrodorsolateral oblique view with transparent nasal airway to show the convoluted course of inspired air; and (**F**) rostral view with transparent bone showing nasal airway. Anatomical abbreviations are provided in Table 1. Scale bar = 20 cm.

TABLE 1. Anatomical abbreviations

Abbreviation	Meaning of abbreviation
bc	Braincase
car	Cerebral carotid artery canal
c	Cochlear duct (= lagena)
cer	Cerebral hemisphere
cmc	Common medial chamber of nasal airway
crc	Crus communis
csc	Caudal (posterior vertical) semicircular canal
csca	Ampulla of caudal semicircular canal
cvcm	Caudal middle cerebral vein
ed	Endolymphatic duct canal
endo	Cranial endocast
fp	Foramen perilymphaticum (= round window)
fv	Fenestra vestibuli (= oval window)
lab	Endosseous labyrinth
ld	Lateral diverticulum of nasal cavity
lsc	Lateral (horizontal) semicircular canal
lsca	Ampulla of lateral semicircular canal
n	Nasal
nar	External naris
ob	Olfactory bulb
olf	Olfactory region of nasal cavity
orb	Orbit
pfo	Pituitary (= hypophyseal) fossa
pmax	Premaxilla
pm_d	Caudodorsal process of premaxilla
pm_l	Caudolateral process of premaxilla
pnf	Premaxilla-nasal fontanelle
rsc	Rostral (anterior vertical) semicircular canal
rsca	Ampulla of rostral semicircular canal
s-loop	s-Loop in nasal airway
vcd	Dorsal head vein
ve	Vestibule of inner ear
II	Optic nerve canal
III	Oculomotor nerve canal
IV	Trochlear nerve canal
V	Trigeminal canal
V_1	Ophthalmic nerve canal
V_{2-3}	Maxillomandibular nerve canal
VI	Abducens nerve canal
VII	Facial nerve canal
VIII	Vestibulocochlear nerve canals
IX	Glossopharyngeal nerve canal (= jugular foramen)
X	Vagus nerve canal, also likely transmitting the accessory nerve (CN XI)
XII	Hypoglossal nerve canal

2. *Lambeosaurus* (ROM 758): ROM 758 (Fig. 2) is the smallest skull in the sample (skull length = 372 mm). It was originally designated the holotype of a distinct, small-bodied lambeosaurine species, *Tetragonosaurus praeceps* (Parks, 1931), but has more recently been interpreted as a juvenile *Lambeosaurus* by Dodson (1975) and Evans et al. (2005). This specimen was collected from the Campanian-aged strata of the Dinosaur Park Formation (76.5–74.8 Ma) at Dinosaur Provincial Park, Alberta.

3. *Corythosaurus* (ROM 759, Canadian Museum of Nature, Ottawa, CMN 34825): ROM 759 (Fig. 4) was originally designated the holotype of a small-bodied lambeosaurine species, *Tetragonosaurus erectofrons* (Parks, 1931), but was reidentified as a juvenile *Cory-thosaurus* by Dodson (1975) and Evans et al. (2005). This skull is only slightly larger than ROM 758, and it is incomplete in a number of areas, including the rostral end of the premaxillae and most of the right side of the face (Evans et al., 2005). Both of these specimens were collected from the Campanian-aged strata of the Dinosaur Park Formation (76.5–74.8 Ma) at Dinosaur Provincial Park, Alberta. CMN 34825 (Fig. 3) includes a complete skull (skull length = 465 mm) that is crushed on the left side. It is larger than ROM 759 and has a relatively larger cranial crest.

CT Scanning and 3D Visualization

All of the specimens were CT scanned at O'Bleness Memorial Hospital, Athens, Ohio, using a General Electric (GE) LightSpeed Ultra Multislice CT scanner equipped with the Extended Hounsfield option (which greatly improves resolvability of detail from dense objects such as fossils by extending the dynamic range of images as much as 16-fold) and a bow-tie filter (which decreases beam-hardening artifacts). All specimens were scanned helically at a slice thickness of 625 μm (except for the crest of ROM 702, for which, given its large size and simpler anatomy, a coarser slice thickness of 1.25 mm was used), 120–140 kV and 200–300 mA. The raw scan data were reconstructed using a bone algorithm. Data were output from the scanner in DICOM format, and then imported into Amira 4.1.2 and Amira 5.1 (Mercury-TGS, Chelmsford, MA) for viewing, analysis, and visualization. All scan 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). Anatomical features of interest (e.g., nasal cavity, cranial endocast, endosseous labyrinth, etc.) were highlighted and digitally extracted using Amira's segmentation tools for quantification and visualization.

The juvenile lambeosaurine specimens ROM 758 and 759 were more difficult to scan because metal mounting hardware could not be removed before scanning without risking damage to the specimens. Likewise, CMN 34825 and its supporting jacket were too large to traverse the scanner's gantry in a single pass. These specimens required multiple scans with different orientations and additional data processing to minimize the adverse effects of the scanning artifacts and, in the case of CMN 34825, digital assembly of the different datasets in Amira. Because of missing portions and historic plaster reconstruction, the dataset generated for ROM 702 presented some ambiguities that were difficult to interpret. Parts of our reconstruction of this specimen are therefore tentative, but represent testable hypotheses grounded in the context of the other corythosaurs and will be refined in future studies. Because only one side of the skull is preserved in ROM 702 and ROM 759, our reconstructions include the necessary mirroring of elements to provide a full picture of the skull.

Supplemental visualizations and native CT data for some of the specimens are available on the website www.ohio.edu/witmerlab.
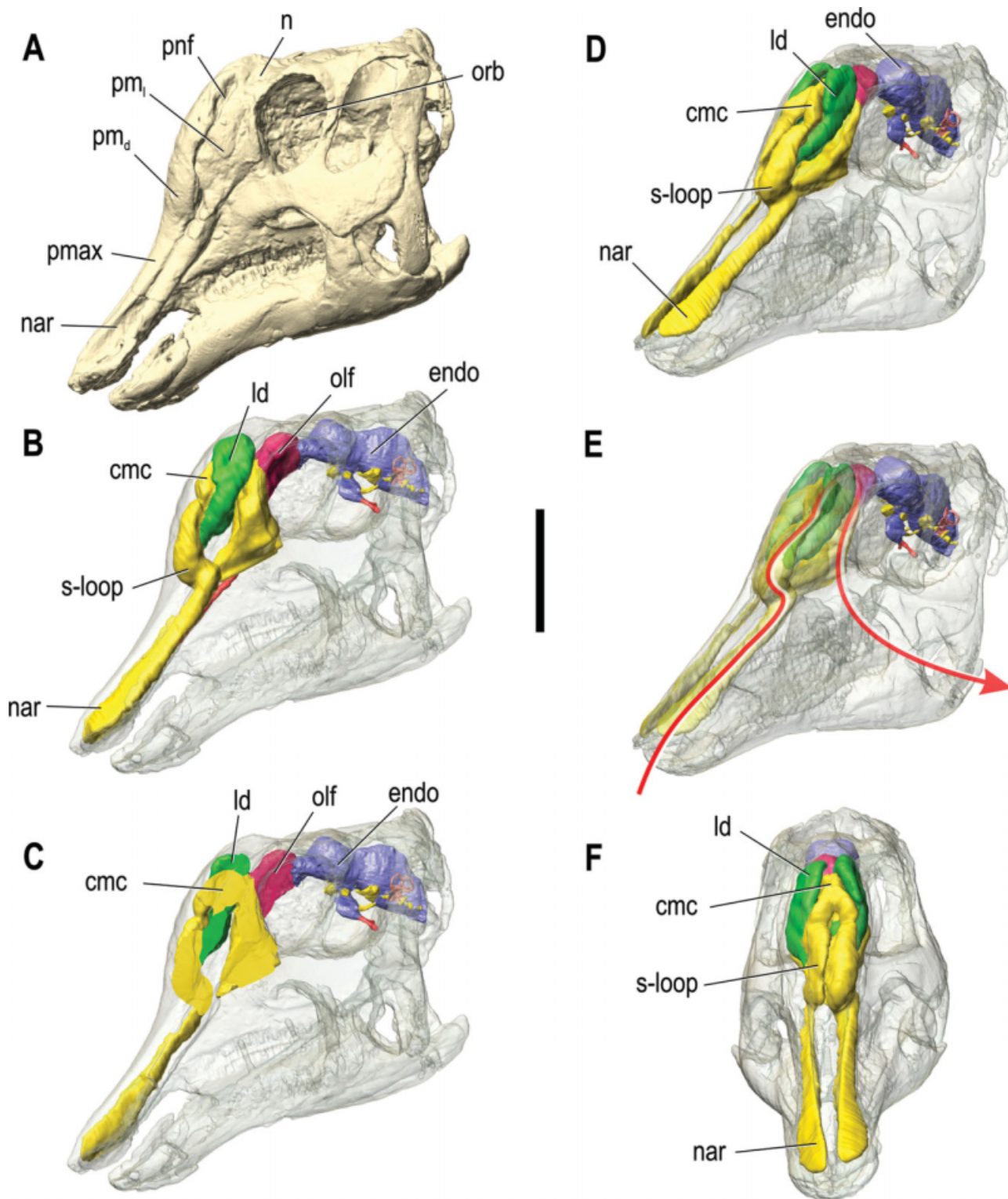
Fig. 2. Nasal cavity and other cephalic components of a juvenile *Lambeosaurus* sp. (ROM 758). Labeled illustrations in (**A**) left lateral view; (**B**) left lateral view with transparent bone showing nasal airway; (**C**) left lateral view with transparent bone with nasal structures sagittally sectioned showing medial side of right nasal airway; (**D**) left ros- trodorsolateral oblique view with transparent bone showing nasal airway; (**E**) left rostrodorsolateral oblique view with transparent nasal airway to show the convoluted course of inspired air; and (**F**) rostral view with transparent bone showing nasal airway. Scale bar = 10 cm.
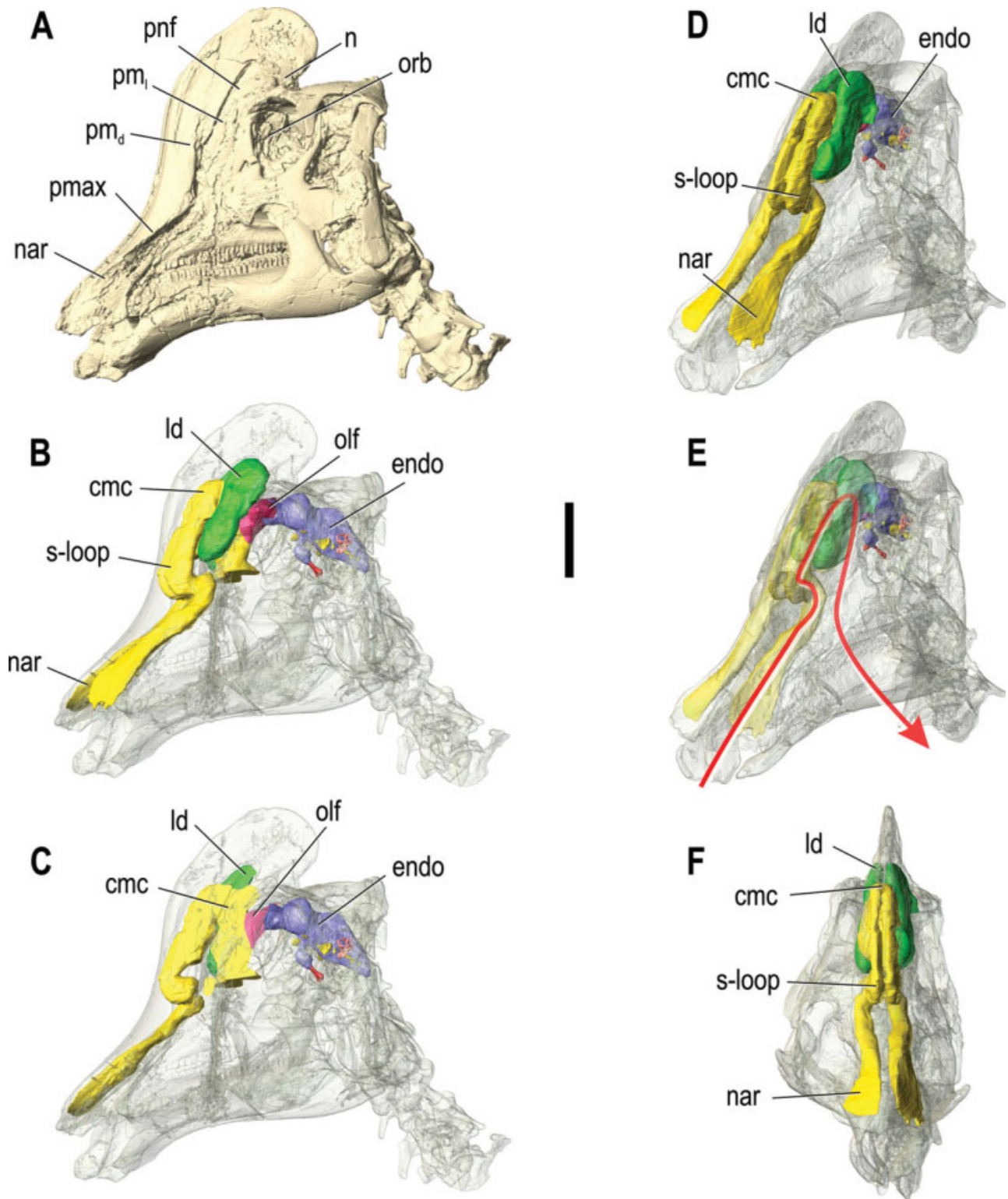
Fig. 3. Nasal cavity and other cephalic components of subadult *Corythosaurus* sp. (CMN 34825). Labeled illustrations in (**A**) left lateral view; (**B**) left lateral view with transparent bone showing nasal airway; (**C**) left lateral view with transparent bone with nasal structures sagittally sectioned showing medial side of right nasal airway; (**D**) left rostrodorsolateral oblique view; (**E**) left rostrodorsolateral oblique view with transparent nasal airway to show the convoluted course of inspired air; and (**F**) rostral view with transparent bone showing nasal airway. All images have been mirrored to illustrate the better side. Scale bar = 10 cm.
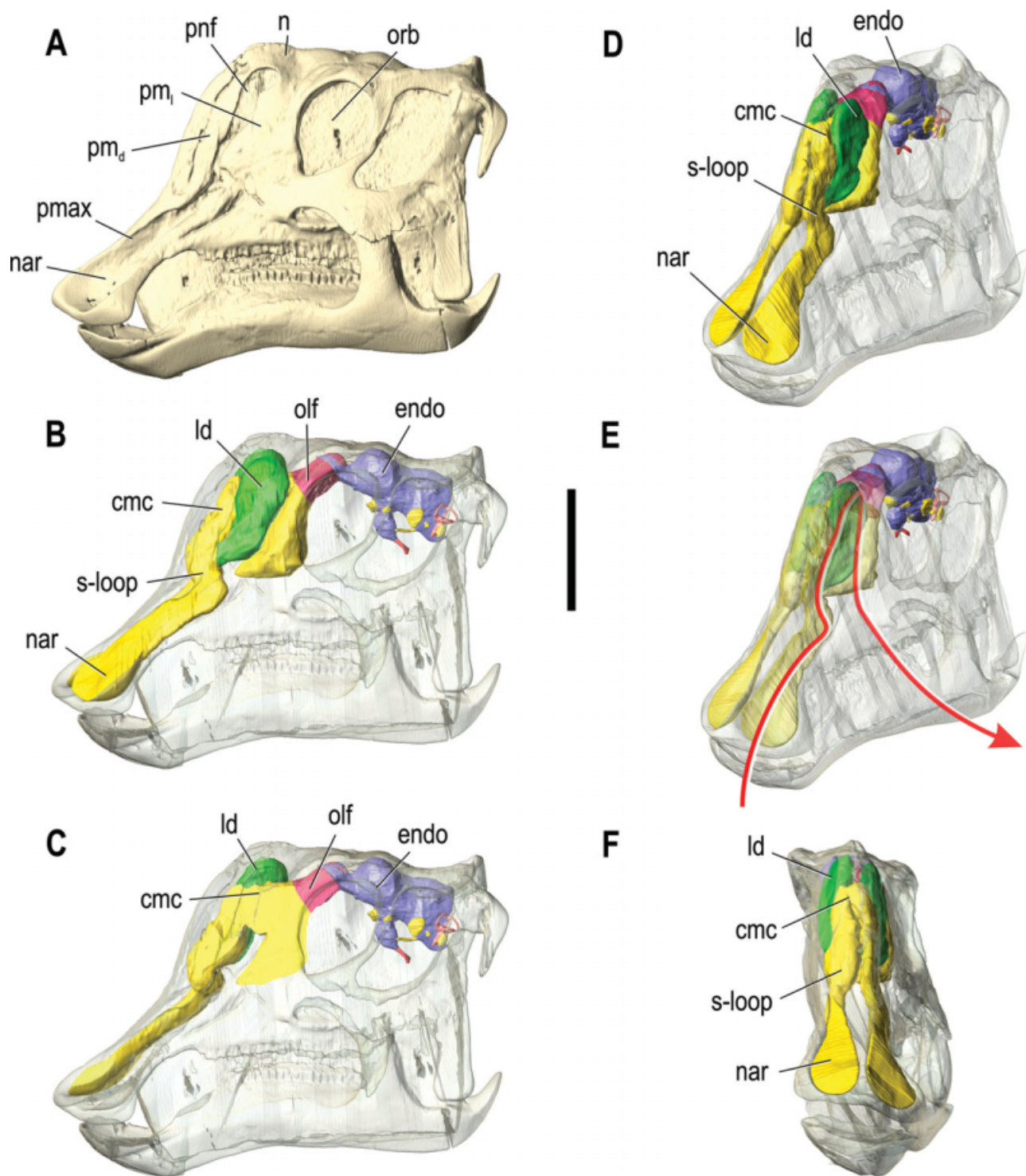
Fig. 4. Nasal cavity and other cephalic components of a juvenile *Corythosaurus* sp. (ROM 759). Labeled illustrations in (**A**) left lateral view; (**B**) left lateral view with transparent bone showing nasal airway; (**C**) left lateral view with transparent bone with nasal structures sagittally sectioned showing medial side of right nasal airway; (**D**) left ros-trodorsolateral oblique view; (**E**) left rostrodorsolateral oblique view with transparent nasal airway to show the convoluted course of inspired air; and (**F**) rostral view with transparent bone showing nasal airway. Scale bar = 10 cm.

TABLE 2. The volumes of complete brain cavity endocasts and the various brain regions, calculated from the digital endocasts using digital segmentation in the Amira program

Specimen no.	Taxon	Skull length (mm)	Endocast, length (mm)	Cerebrum, max. width (mm)	Endocast volume, incl. olfactory system (cm^3)	Cerebrum volume (cm^3)	Olfactory system volume (cm^3)
ROM 758	*Lambeosaurus* sp. (juvenile)	384	113.2	43.0	94.1	35.1	2.9
ROM 759	*Corythosaurus* sp. (juvenile)	–	110.1 (incomplete)	46.5	97.9	41.6	6.2
CMN 34825	*Corythosaurus* sp. (subadult)	470	142.0	44.7	145.4	51.1	11.2
ROM 702	*Hypacrosaurus altispinus* (adult)	~700	204.0	63.2	289.9	117.5	14.0

RESULTS

Nasal Cavity

Lambeosaurus and Corythosaurus. The nasal passages of the smallest skulls, ROM 758 and ROM 759, are virtually identical (Figs. 2, 4). The nasal cavity ascends caudodorsally within the premaxilla from the naris at the rostrum to the region directly rostral to the dorsal process of the maxilla. Here, the nasal cavity turns rostrodorsally and then caudodorsally to form an s-shaped loop within the premaxilla. The nasal passage then divides into the lateral diverticulum and a more medial passage that coalesces with its complement to form the common undivided camber within the nasals, deep to the lateral diverticula. The lateral diverticulum is enclosed laterally by the caudolateral process of the premaxilla and is exposed externally via the premaxilla-nasal fontanelle. These lateral chambers extend dorsal to the common chamber, are not inflated relative to the rest of the crest, and do not seem to communicate with the common median chamber or their counterparts caudal to it. The bony passage between the basal aperture of the lateral diverticulum and the rostral end of the common chamber occurs between the premaxilla and nasal bones and represents the homologue of the external naris in hadrosaurines and other non-lambeosaurine ornithischians. The common chamber is defined predominantly by the nasals dorsally and laterally and by the premaxillae rostroventrally, and occurs medial to the large lateral diverticula. An aperture occurs between the common chamber and each lateral diverticulum. The common median chamber extends ventrally beyond the crest proper into the antorbital cavity, deep to the prefrontal. Ventral to the crest, a small but significant portion of the nasal cavity occurs caudal to the main airway, between the main airway and the rostral end of the olfactory bulbs. This portion would house the olfactory region of the nasal cavity caudally, as well as that portion of the respiratory region located below the crest.

This general pattern also occurs in CMN 34825, a subadult *Corythosaurus* (Fig. 3). The small crest of CMN 34825, which extends dorsal to the orbits and overhangs the skull roof, is relatively larger than in ROM 759, but remains less developed compared with large individuals of this genus (Dodson, 1975). The nasal passage remains paired for a considerable distance caudal to the divergence of the lateral diverticula, and the lateral diverticula are notably large compared with the small common chamber. There is an aperture between each lateral di-

verticulum and the common chamber, but this is less clear between the diverticulum and the main airway rostrally. Consistent with its ontogenetic stage, the common chamber and lateral diverticula are more supraorbitally positioned than in the smaller ROM 759, but not as well developed as in large adults (Weishampel, 1981b).

Hypacrosaurus altispinus. The nasal cavity of *Hypacrosaurus altispinus* (Fig. 1) seems to be considerably more complex compared with the *Corythosaurus* and *Lambeosaurus* specimens described above, as well as to previous reconstructions for this taxon (Weishampel, 1981b). From the constricted external narial aperture at the rostrum, the nasal cavity extends caudodorsally as a narrow tube within the premaxilla to the level of the prefrontal at the rostroventral region of the crest. This passage then loops laterally and rostrally, and extends rostroventrally to the level of dorsal process of the maxilla. In this region, the main airway approaches the lateral diverticulum, which extends caudodorsally in parallel to the main airway toward the common median chamber of the crest. The lateral diverticulum deepens dorsally to reach its maximum depth on the lateral region of the crest such that the shape of the lateral diverticulum in lateral view mimics the general shape of the caudodorsal process of the premaxilla that encloses it laterally. The thin sheet of the nasal bone that divides the common chamber from the lateral diverticulum is broken in ROM 702, and it is uncertain whether or not there was a fenestra between these chambers.

Brain Cavity Endocasts

The digital endocasts of the four specimens show considerable detail (Figs. 5–7). Traditionally, non-avian dinosaurs have been regarded as "reptilian" in that their brains were thought to have filled only a relatively small portion of the endocranial cavity in contrast with the conditions in mammals and birds (Jerison, 1969, 1973; Hopson, 1977, 1979; Rogers, 1999; Larsson et al., 2000). In crocodilians, as in squamates, the brain typically fills <50% of the endocranium by volume. The remainder of the endocranial space consists of cerebrospinal fluid between the meninges and/or venous sinuses within the dura (Hopson, 1979). Lambeosaurines have recently been shown to have dense vascular grooves that are essentially continuous across the lateral regions of the

endocranium rostral to CN VII (Evans, 2005). This suggests that much of the rostral and ventral regions of the brain were closely associated with the endocranial wall, and that the endocast generally reflects the shape of the brain in this region (Evans, 2005). The largely undefined dorsal region of the endocast caudal to the cerebrum indicates the presence of a large longitudinal venous sinus, as in crocodilians, and a major ventrolateral division of the longitudinal sinus (the lateral head vein) is clearly present on the endocasts (Hopson, 1979). The amorphous nature of the endocast in the postcerebral

region suggests that much of the hindbrain of hadrosaurids was not in close relationship to the endocranial wall (Evans, 2005).

The endocast of ROM 702 is the largest in the sample (Table 2), and presumably represents that of a fully grown individual of *Hypacrosaurus altispinus*. The brain endocast measures 162.5 mm from the rostral margin of the cerebrum to the caudal branch of the hypoglossal, and has a total volume of 276 cm^3 (not including the olfactory system). The other specimens almost certainly represent immature individuals (Dodson, 1975; Evans et
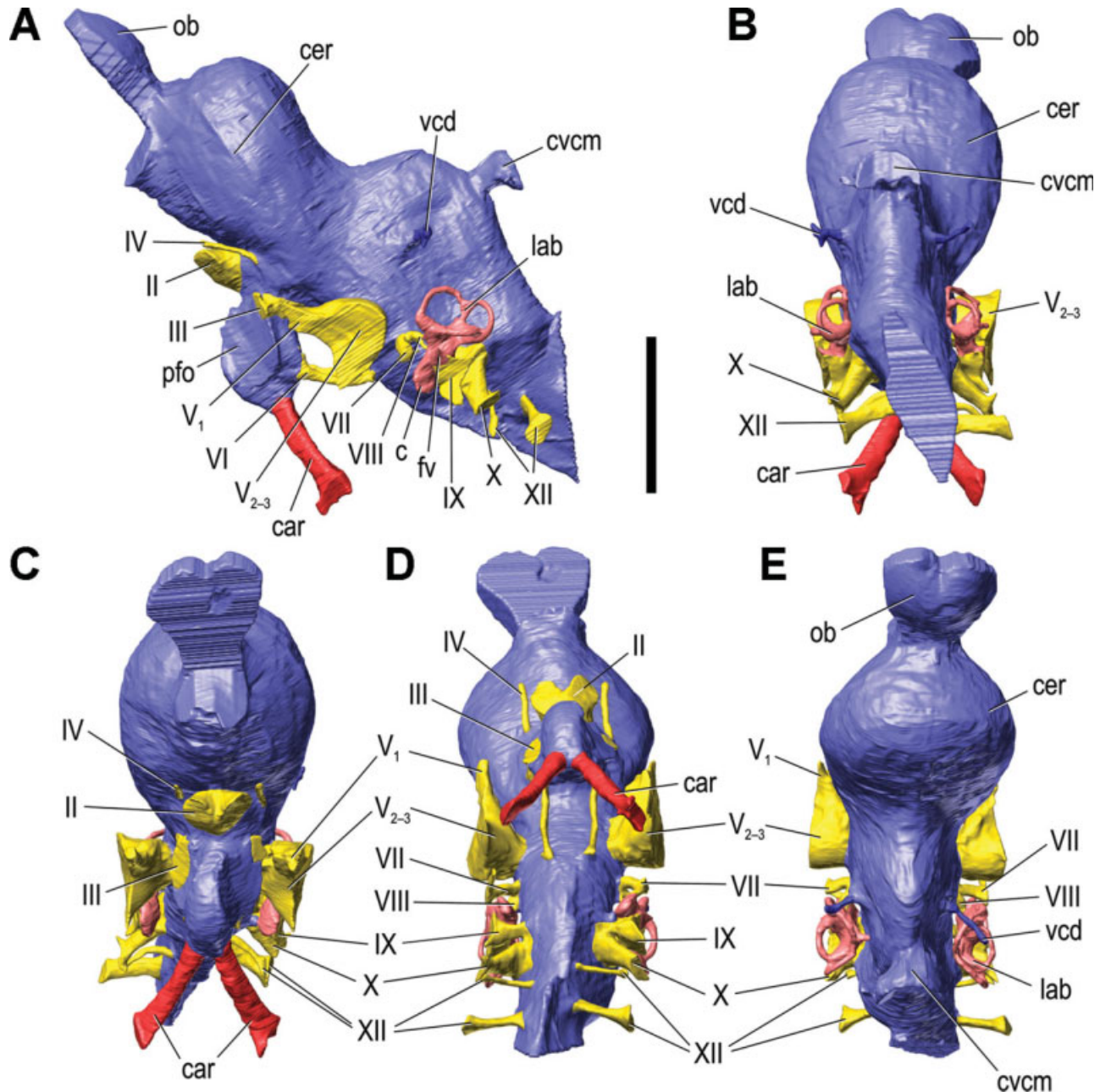

Fig. 5. Cranial endocast of *Hypacrosaurus altispinus* (ROM 702) reconstructed from CT scans. Some vascular elements are depicted, as well as the endosseous labyrinth. Labeled illustrations in (**A**) left lateral; (**B**) caudal; (**C**) rostral; (**D**) ventral; and (**E**) dorsal views.

al., 2005). The brain endocast of ROM 758 (Fig. 6), the smallest skull in the sample, is 113.6 mm in length, 43 mm in maximal width, and only 32% of the volume of ROM 702. Although the angle of flexure between the cerebellum and cerebrum is slightly greater in the adult specimen than in the juveniles, the general morphology of all four endocasts closely resemble each other and merit only one general description to accompany the
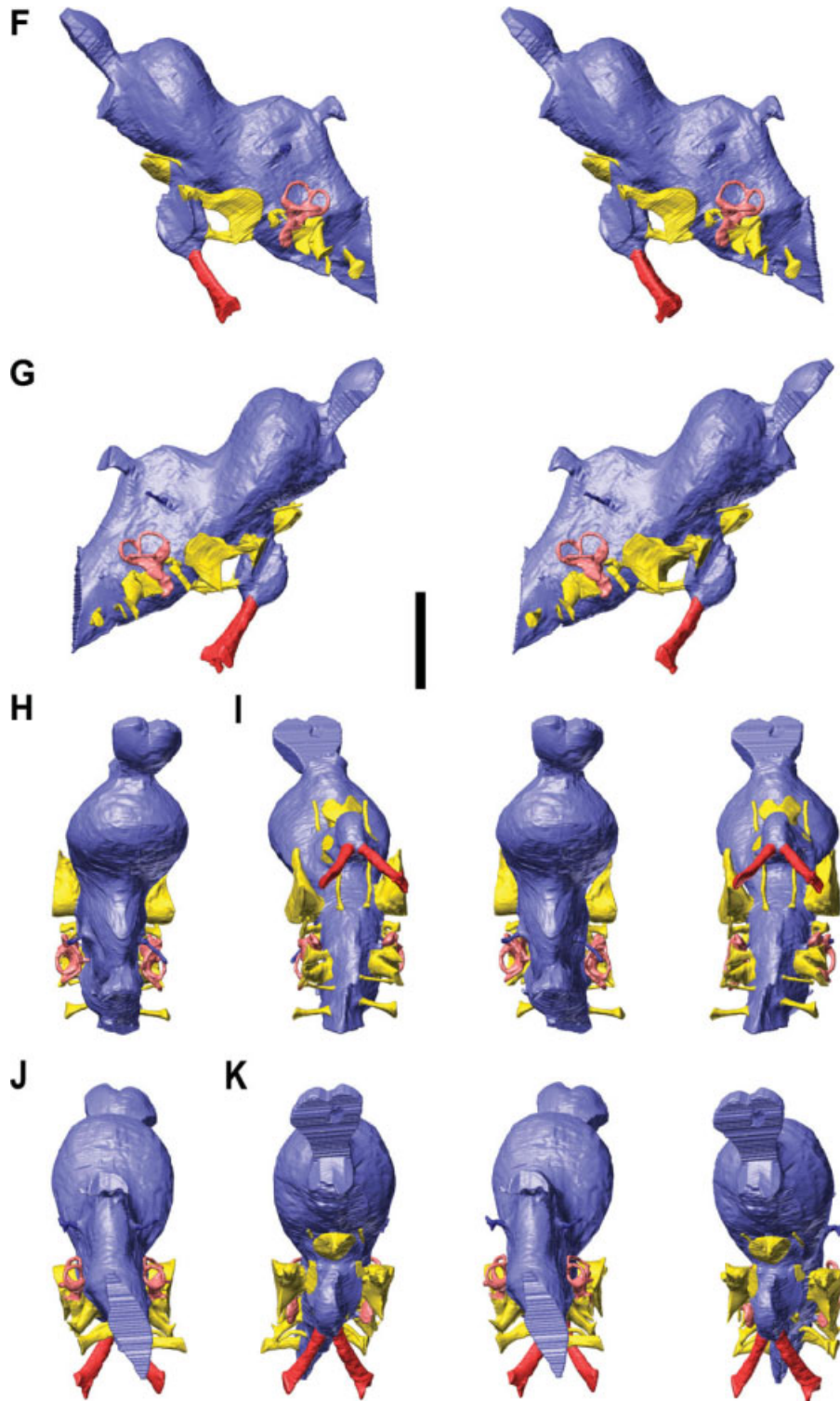

Fig. 5.   (cont.) Stereopairs in (**F**) right lateral; (**G**) left lateral; (**H**) dorsal; (**I**) ventral; (**J**) caudal; and (**K**) rostral views. Scale bar = 5 cm.

figures of all of the endocasts (Fig. 7). Because the endocast of the adult *Hypacrosaurus* (ROM 702) is the most detailed, we therefore focus our endocast description on this specimen (the external features of the braincase will be described elsewhere, Evans, in press) and supplement it with data from other specimens as appropriate (Figs. 5–7).

The endocast of ROM 702 reaches its maximum width of 63.2 mm across the broad cerebrum, and it constricts considerably at the level of the midbrain and maintains a constant width through the medulla. The shared cavity for the paired olfactory tracts is very short, and extends rostrally from the cerebral region in the area of

the skull bounded by the frontal and presphenoid. The olfactory bulbs are discernible in ROM 702 and ROM 758 (but less so in the other specimens), forming a pair of relatively small swellings visible on the dorsal surface of the endocast. The ventral and especially rostral margins of the olfactory bulb are difficult to discern, which is typical for dinosaurs (Witmer and Ridgely, 2008a,b; Witmer et al., 2008; Witmer and Ridgely, in press), but the position of the presphenoid (which is incomplete in ROM 702) gives some reliable measure of their rostroventral extent (Evans, 2006).

The cerebral hemispheres are very broad and moderately flattened dorsoventrally. The form of the cerebrum
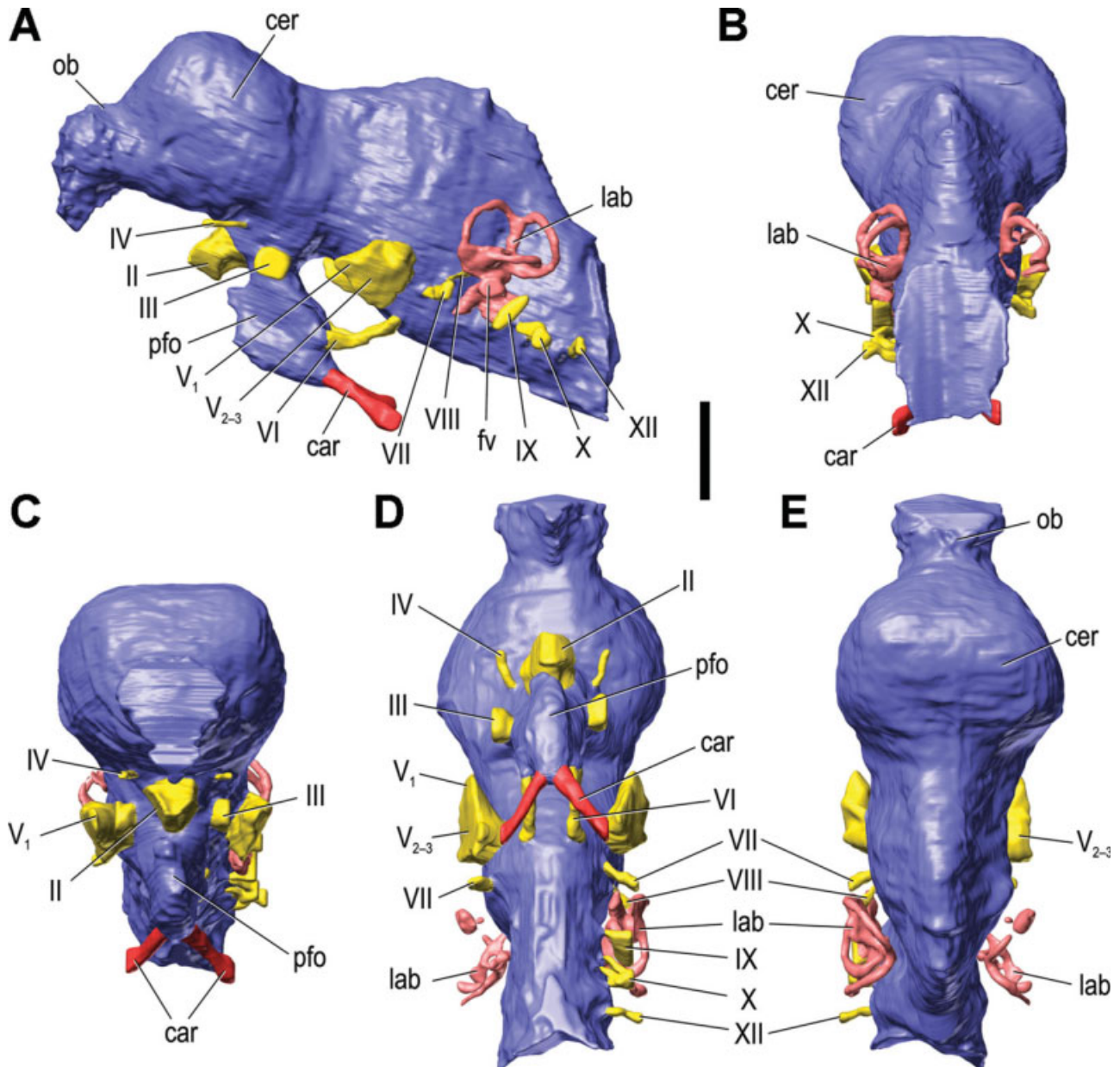

Fig. 6. Cranial endocast of a juvenile *Lambeosaurus* sp. (ROM 758) reconstructed from CT scans. Some vascular elements are depicted, as well as the endosseous labyrinth. Labeled illustrations in (**A**) left lateral; (**B**) caudal; (**C**) rostral; (**D**) ventral; and (**E**) dorsal views.
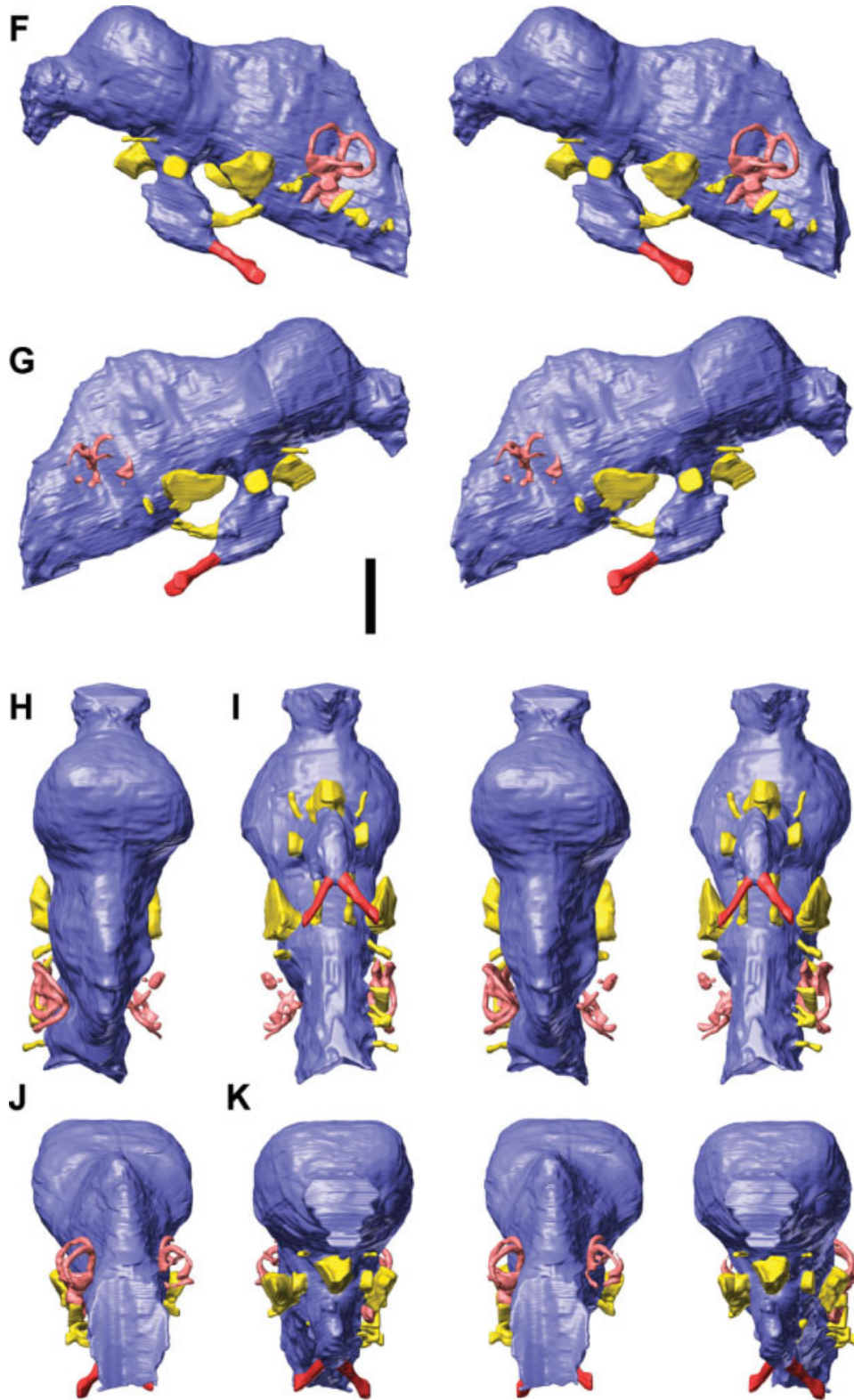
Fig. 6. (cont.) Stereopairs in (**F**) right lateral; (**G**) left lateral; (**H**) dorsal; (**I**) ventral; (**J**) caudal; and (**K**) rostral views. Scale bar = 2 cm.
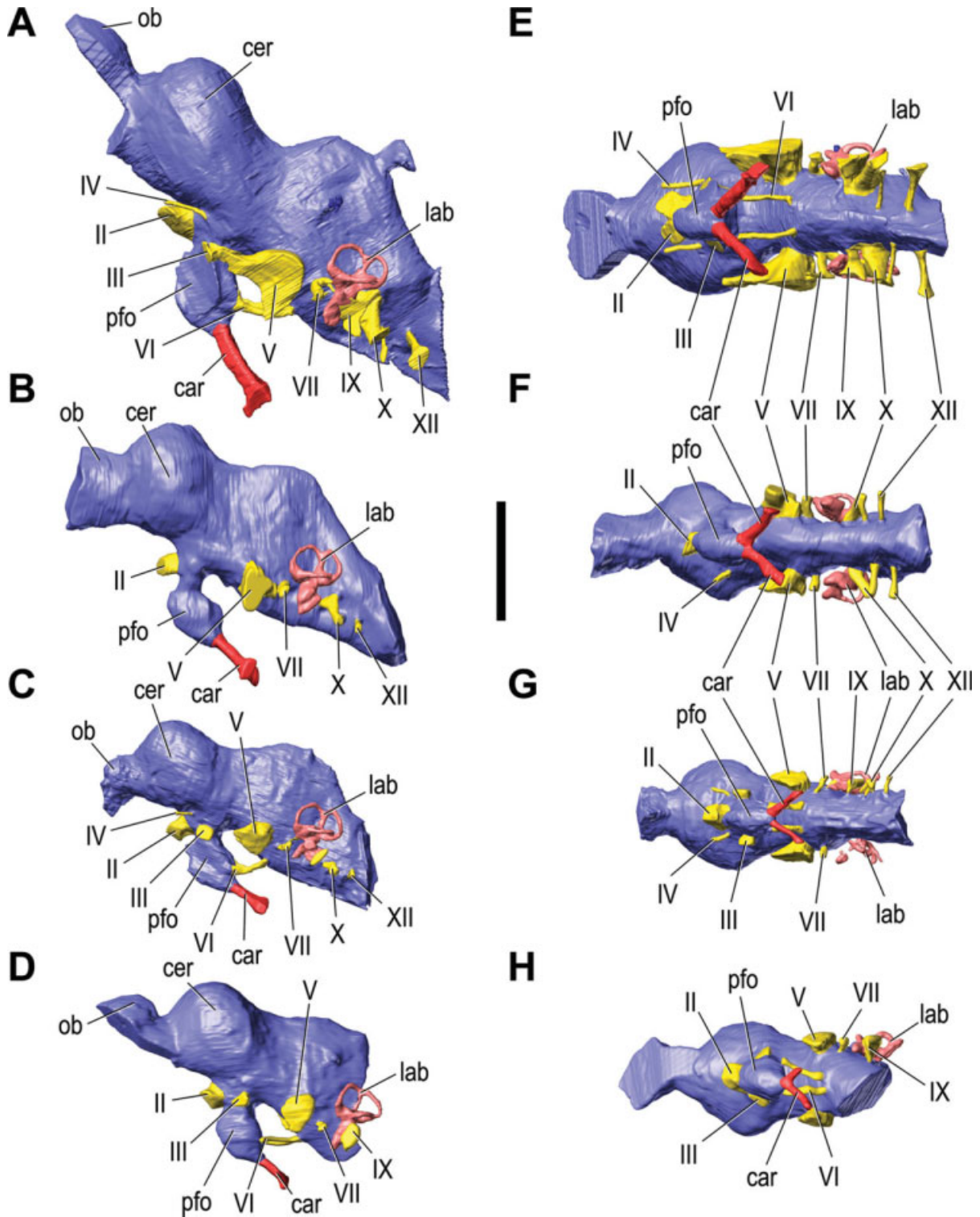
Fig. 7. Comparative illustration of lambeosaurine endocasts in left lateral (**A–D**), ventral (**E–H**), and dorsal (**I–L**) views. (A, E, I) *Hypacrosaurus altispinus* (ROM 702); (B, F, J) subadult *Corythosaurus* sp. (CMN 34825); (C, G, K) juvenile *Lambeosaurus* sp. (ROM 758); (D, H, L) juvenile *Corythosaurus* sp. (ROM 759). Scale bar = 5 cm.
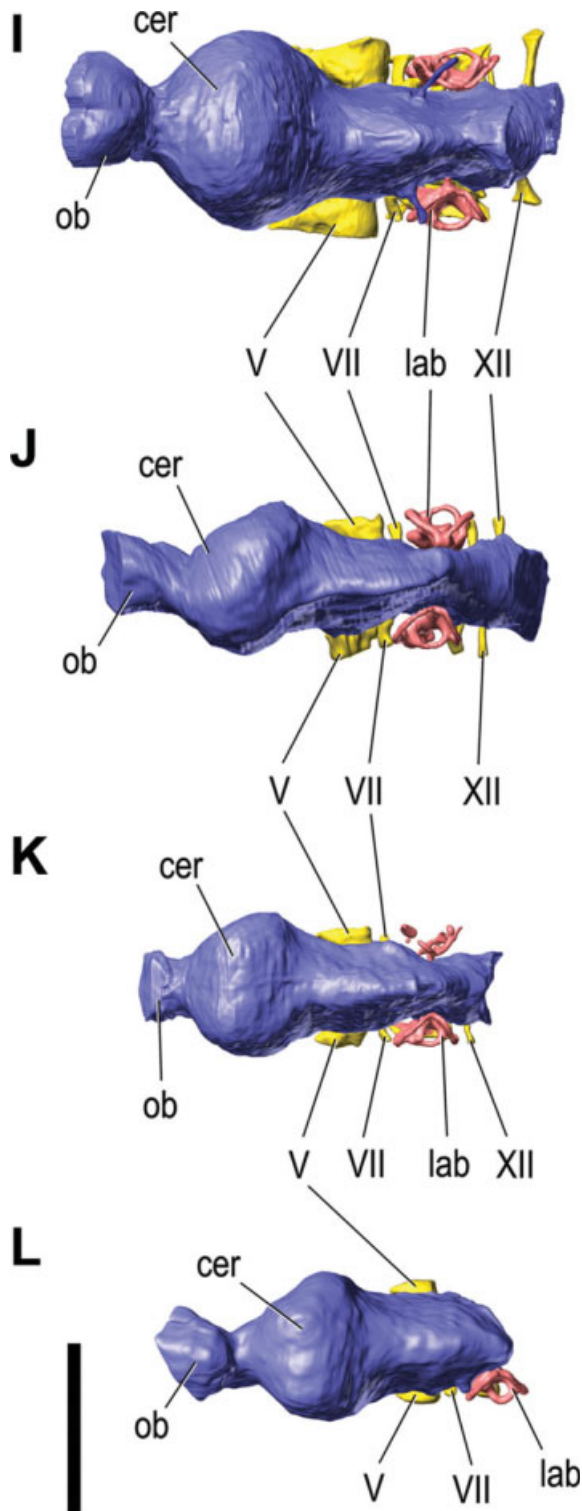
Fig. 7. (continued)

in ROM 758, ROM 759, CMN 34825, and ROM 702 is similar to that of an indeterminate lambeosaurine (cf. *Corythosaurus*, Ostrom, 1961) described by Evans (2006), and an incomplete natural endocast of *Hypacrosaurus altispi-*

nus (American Museum of Natural History, New York, AMNH 5248, not figured; Fig. 7). The hemispheres form a relatively large proportion of the overall size of the endocast, accounting for 39% of the total endocranial volume (not including the olfactory bulbs) in the smallest (ROM 758) and 43% of the endocranial volume in the largest (ROM 702) skull in our sample. Despite their large size, a longitudinal cerebral fissure is not present in any of the reconstructed endocasts. Caudal to the cerebrum, the endocast considerably narrows, and the midbrain and hindbrain regions are largely undifferentiated; there is no clear indication of the optic lobes or cerebellum.

Several vascular elements are also clearly indicated in the endocasts (Figs. 5–7). As previously mentioned, the poorly differentiated dorsal region above the medulla suggests the presence of a large dorsal venous sinus over the cerebellum. From the dorsal sinus, a prominent caudodorsally oriented canal extends along the upper surface of the inclined supraoccipital bone to emerge on the occiput. This canal presumably transmitted veins corresponding to the caudal middle cerebral veins of other archosaurs (Witmer et al., 2008; Witmer and Ridgely, in press). A canal extends caudolaterally from the lateral surface of the endocast above CN VII to emerge on the lateral wall of the braincase through a small foramen at the confluence of the laterosphenoid, prootic, and parietal. Godefroit et al. (2004b) identify this prominent vascular element in the lambeosaurine hadrosaurid *Amurosaurus* as the vena parietalis, but it is in precisely the same position as the dorsal head vein (vena capitis dorsalis), as documented for both theropods and sauropods (Sampson and Witmer, 2007; Witmer et al., 2008; Witmer and Ridgely, in press), although it is even more widely distributed in archosaurs. The large cerebral carotid arteries are represented by large dorsomedially and rostrally oriented canals that enter the pituitary fossa caudoventrally.

The cranial nerves are well represented in the digital endocasts, and their interpretation is rather straightforward, as described below:

The olfactory system, as noted above, is not completely preserved in ROM 702. The septate rostral flanges of the presphenoids observed in some specimens (Evans, 2006) are broken off and not preserved in ROM 702. Likewise, discrete sulci on the presphenoid for the olfactory nerve bundles were not identifiable in the other specimens described here, but in these cases the explanation may have more to do with their being immature and simply less ossified in this region.

The optic nerve (CN II) exits the braincase via a large foramen in the orbitosphenoid alongside the ventral midline of the braincase immediately rostral to the oculomotor foramen. The proximal section of the optic nerve extends rostrolaterally from the midline at an angle of ~45°, and descends slightly in lateral view. The optic chiasm of the diencephalon, rarely found in fossil endocasts (Hopson, 1979), is represented by a low, rounded protrusion dorsal to the pituitary and immediately caudal to the confluence of the left and right optic nerves.

The oculomotor nerve (CN III) innervates four of the six extraocular muscles of the vertebrate eye. This nerve exited the oculomotor foramen directly dorsal to the pituitary fossa and caudal to the optic nerve. The circular oculomotor foramen, formed by the orbitosphenoid in front and the laterosphenoid behind, is immediately

dorsomedial to, and possibly continuous with, the fenestra on the lateral side of the pituitary fossa for the abducens nerve (CN VI).

The small trochlear nerve (CN IV) passes rostrally from the metencephalon via a long canal in the orbitosphenoid bone on its path to the superior oblique extraocular muscle. The trochlear nerve exits the braincase via a dedicated foramen, as in extant *Caiman* and most other dinosaurs (Hopson, 1979), that is located immediately dorsal to the optic nerve foramen.

The trigeminal nerve (CN V) is located at the rostral end of the medulla, between CN III and CN VII. It extends laterally via a characteristically large, laterally expanding, funnel shaped foramen, a distinctive landmark on the lateral wall of the braincase. The large diameter of the external trigeminal foramen, 15 mm in ROM 702, suggests that it housed the trigeminal ganglion (Ostrom, 1961), from which the ophthalmic branch (CN V_1) extends rostrally via a horizontal sulcus on the laterosphenoid, and the combined maxillary and mandibular branches (CN V_{2-3}) extend ventrally at a right angle to the ophthalmic branch. Distally, the maxillary branch diverges from the mandibular branch rostral to the alar process on the lateral surface of the basisphenoid.

The abducens nerve (CN VI) passes rostroventrally from the endocranial floor at the rostral end of the medulla, through the basisphenoid, to emerge in the pituitary fossa through a small foramen on the caudal wall of the dorsum sellae. The abducens then passes into the orbit via a large fenestra in the lateral side of the pituitary fossa.

The facial nerve (CN VII) exits the endocranial cavity through the prootic bone between the trigeminal foramen and the fenestra vestibuli (= ovalis). The branches of the facial nerve diverge near the lateral surface of the prootic. The hyomandibular branch passes caudodorsally on its path above the fenestra vestibuli, and the palatine branch extends ventrally within a sulcus on the lateral surface of the prootic.

The morphology of the vestibulocochlear nerve (CN VIII) is particularly well preserved on the left side of the ROM 702 endocast. It exits the endocranial cavity together with the facial nerve, but before reaching the lateral wall of the prootic, curves caudally to enter the vestibular apparatus. Two distinct branches are present; one is directed dorsally to reach the otic vestibule, while another, the cochlear portion of the vestibulocochlear nerve, extends to the dorsal base of the cochlea at the level of the fenestra vestibuli.

The glossopharyngeal nerve (CN IX) exits the braincase through the metotic foramen immediately caudal to the fenestra vestibuli, and rostral to the vagus foramen opposite the metotic strut (Langston, 1960). The large root of the vagus nerve (CN X) extends caudolaterally from the region of the metotic fissure on the lateral side of the medulla oblongata to emerge via a large, oval foramen in the exoccipital caudal to the metotic strut. Identification of the accessory nerve (CN XI) on endocasts is difficult, as it is generally small in tetrapods. The accessory nerve most likely exited the braincase along with the vagus (CN X), but may have exited with the glossopharyngeal nerve (CN IX) through the metotic foramen. A small foramen ventral to the vagus foramen on the lateral wall of the exoccipital has recently been suggested as the exit of the accessory nerve (Godefroit et al., 2004b). On the lateral wall of the braincase this foramen is <2 mm in diameter in ROM 702. Like ROM 702, endocasts of hadrosaurines (e.g., Hopson, 1979) and disarticulated bones of other lambeosaurines (ROM 1940) reveal that the canal originates from the ventral region of the medulla, and not dorsolaterally on the medulla or in the region of the metotic fissure. Therefore, this canal more likely represents a small rostral branch of the hypoglossal (Hopson, 1979) or possibly a vessel.

The hypoglossal nerve (CN XII) is represented by two relatively large branches on the endocast of ROM 702. The more caudal branch passes caudolaterally through the base of the exoccipital near the occipital condyle, whereas the smaller branch extends rostrally from the ventral surface of the medulla to a point immediately caudal to the vagus on the lateral wall of the braincase. In lambeosaurines, the most caudal foramen for the hypoglossal nerve is invariably the largest. The hadrosaurine *Gryposaurus notabilis* and the ceratopsids *Triceratops*, *Pachyrhinosaurus*, and *Anchiceratops* have three hypoglossal foramina (Hopson, 1979; Forster, 1996; Witmer and Ridgely, 2008a).

Endosseous labyrinth

The digitally reconstructed vestibular apparatus is complete on at least one side of all four specimens in our sample, and is particularly well preserved on the left side of ROM 702 and in ROM 758 (Fig. 8). It closely resembles that of other hadrosaurids, and in general form also bears a distinct resemblance to the condition in extant crocodilians (Brown, 1914; Langston, 1960; Ostrom, 1961; Witmer et al., 2008). The three semicircular canals are oriented in approximately the three planes of space, as in all tetrapods. The rostral semicircular canal is slightly longer than the caudal semicircular canal, and the lateral (horizontal) semicircular canal is the shortest of the three. Of their corresponding ampullae, the rostral ampulla is the largest, followed by the lateral ampulla. The endolymphatic duct is represented by a short, funnel-shaped process that extends dorsomedially from the caudal wall of the vestibule at the base of the common crus. The otic vestibule is difficult to differentiate into the utriculus and sacculus. The fenestra vestibuli faces laterally and is located at the base of the cochlea, whereas the fenestra perilymphaticum opens caudally into the metotic fissure. The prominent, finger-like cochlea extends rostroventrally from the vestibule.

DISCUSSION

These new data provide the first complete picture of the brain endocast in lambeosaurine hadrosaurids at three different ontogenetic stages (Fig. 7). The overall shape of the endocast in corythosaurian lambeosaurines is somewhat different from the well-described condition in hadrosaurine hadrosaurids such as *Gryposaurus* and *Edmontosaurus* (Lambe, 1920; Lull and Wright, 1942; Ostrom, 1961; Hopson, 1979; Jerison, 2004). We confirm that the olfactory tracts that connect the olfactory bulbs to the rest of the brain are very short such that the bulbs are located immediately rostral to the cerebral hemispheres (Evans, 2006). The broad cerebral
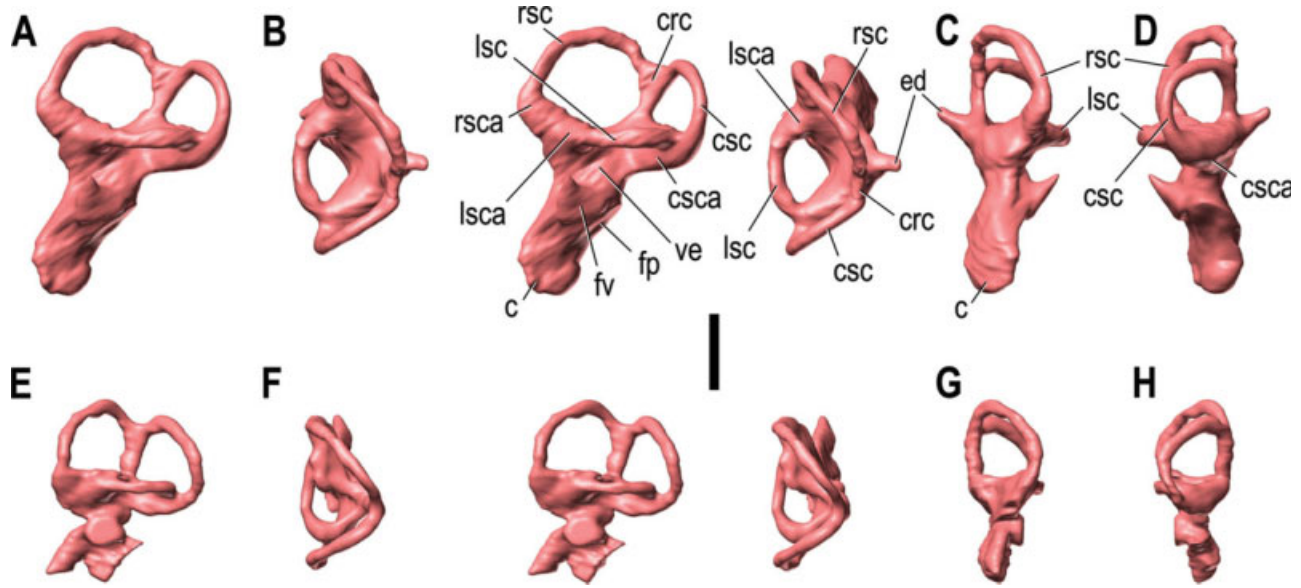
Fig. 8. Endosseous labyrinths of the left inner ear. Left four columns are stereopairs of left lateral and dorsal views. Right two columns are rostral and caudal views, respectively. (**A–D**) *Hypacrosaurus altispinus* (ROM 702) (**E–H**) a juvenile *Lambeosaurus* sp. (ROM 758). Scale bar = 1 cm, which is life size.

hemispheres rise above the level of the olfactory tracts, and reach their dorsal extent significantly higher than the dorsal venous sinus and underlying cerebellar region. The brain cavity seems to be rostrocaudally shorter than that of hadrosaurines, as observed by Gilmore (1924). The major axis of the cerebrum in the lambeosaurine endocasts is oriented ~45° to the horizontal (as seen in lateral view), as opposed to the more horizontal orientation observed in hadrosaurines and other ornithopods (Hopson, 1979). The foreshortening of the endocranial cavity and the rotation of the cerebrum is almost certainly related to the caudodorsal expansion of the nasal cavity and crest in the evolution of lambeosaurines.

Brain endocasts from juveniles (ROM 758, ROM 759) are similar in relative dimensions to that of the representative adult ROM 702. Juvenile endocasts are no more "brain-like" than the adult specimen, and give no indication that the brain filled the endocranial cavity to any greater degree than in the adult (Fig. 7). This observation is contrary to the trend in extant crocodilians noted by Hopson (1979), where the brain occupies a progressively decreasing proportion of the endocranial cavity with increasing size and apparently positive allometry of the dorsal venous sinus. It is likely that lambeosaurines exhibited a comparable ontogenetic relationship, but it is not recorded in our sample, which includes juvenile but not very young individuals. The angle of flexure between the cerebellum and cerebrum is noticeably smaller in ROM 702 than in the representative juvenile endocasts, which more closely resemble the hadrosaurine condition in this respect (Fig. 7). Although we do not have a complete ontogenetic series for each individual taxon, the composite ontogenetic series suggests a possible ontogenetic rotation of the cerebral hemispheres relative to the medullary axis that may be concomitant with the caudodorsal expansion of the nasal cavity through ontogeny. In this light, ontogenetic

change in crest shape provides a causal mechanism to explain conformational changes in the brain, and may provide insight into the evolution of the unique, foreshortened lambeosaurine neurocranium. However, the braincase of *Hypacrosaurus altispinus* is relatively shorter compared with other closely related corythosaurs, including *Corythosaurus* and *Lambeosaurus* (Evans, in press), and this difference in endocast morphology between the juveniles and adult in this sample may be phylogenetic rather than ontogenetic.

The CT data and crest cavity reconstructions of the juvenile lambeosaurines, together with previous reconstructions of mature corythosaurs from the Dinosaur Park Formation by Weishampel (1981b), permit the first detailed assessment of the ontogenetic development of the nasal cavity in a lambeosaurine. The juvenile skulls of *Lambeosaurus* (ROM 758) and *Corythosaurus* (ROM 759) are virtually identical in terms of their gross morphology (Evans et al., 2005). The nasal cavity reconstructions are also remarkably similar, and both digital reconstructions presented here seem relatively consistent with the reconstructions of the nasal passages in adult skulls (Ostrom, 1962; Weishampel, 1981b). In *Corythosaurus*, the development of both the nasal cavity and crest in CMN 34825 is intermediate between ROM 759 and that seen in adult *Corythosaurus* specimens (Weishampel, 1981b). The main airway is tubular from the naris to the common chamber of the crest, and the s-loop is present and relatively unmodified through ontogeny. Immediately caudal to the s-loop, the lateral diverticulum branches off from the main airway, and extends lateral to and in parallel with the main airway to the level of the common chamber. Concomitant with the caudodorsal development of the crest, the common chamber and the lateral diverticula migrate from an antorbital to a supraorbital position, and expand allometrically through ontogeny (Dodson, 1975). Although the common chamber does increase in size with growth, the major

allometric components of the nasal cavity expansion are clearly within the vestibule, both in terms of the relative elongation of the snout as well as the relative elongation of the lateral diverticula. The vestibule forms the largest part of the nasal cavity, and the main olfactory region is closely associated with the olfactory bulbs and is, at least in part, outside of the main airway (Evans, 2006).

The new CT data allow us to correct some aspects of the crest cavity reconstructions of corythosaurs in previous studies (Ostrom, 1962; Weishampel, 1981b). Weishampel (1981b) suggested that the nasal passage passed from the lateral diverticula into the common median chamber of the crest and that the lateral diverticula were thus part of the main airway in *Corythosaurus*, *Lambeosaurus*, and *Hypacrosaurus*. CT scans of the complete juvenile specimens suggest that the lateral diverticula were blind chambers of the nasal cavity (i.e., nasal vestibule) that were not involved in the direct conduction of air from the naris to the lungs (Figs. 1–4). The "portals" that Weishampel (1981b) identified in specimens of *Corythosaurus* (AMNH 5340, CMN 8676, ROM 1933) and *Hypacrosaurus* (ROM 702) are likely due to the failure to completely ossify this region and/or to breakage of the exceedingly thin sheet of bone (derived from the nasal) within the crest that separates the diverticulum chamber from the common chamber (such is certainly the case in ROM 702).

Weishampel (1981b) also suggested that juveniles of *Corythosaurus* and *Lambeosaurus* lacked lateral diverticula altogether and that these structures develop and enlarge with increasing size, and that the common chamber filled the incipient crests of ROM 758 and ROM 759. CT data show conclusively that juveniles of these taxa have well-developed lateral diverticula, and that they extend dorsally above the small common chamber to fill the incipient crests at this stage (Figs. 2, 4). The lateral diverticula only become prominent externally in subadults with allometric growth of the crest and the development of the non-narial bony "cocks comb" (Dodson, 1975). Even in CMN 34825, the lateral diverticula are not obvious on external examination of the crest, and they seem to become prominent only at larger size (Fig. 3). Weishampel (1981b) also suggested that the lateral diverticula of *Lambeosaurus* occur only rostral to the common chamber. However, the lateral diverticula, at least in ROM 758, extend along the lateral side of the common chamber (Fig. 2). Although this relationship may have changed with ontogeny, the extent of the lateral diverticula correspond in large part to the extent of the caudolateral processes of the premaxilla (Figs. 1–4), and the lateral diverticula likely extended both rostral and lateral to the common chamber in fully adult *Lambeosaurus*.

More major changes to the previous model of the nasal cavity are required for *Hypacrosaurus altispinus*. Weishampel (1981b), the only author to attempt a reconstruction of *H. altispinus*, suggested that it lacked an s-loop and reconstructed the nasal cavity as a simple, essentially straight tube extending from the naris to the common chamber of the crest. CT scans of ROM 702 reveal that the nasal vestibule is strikingly elongated and convoluted in *H. altispinus* compared with all other corythosaurs (Fig. 1). An s-loop seems to be present in the main airway in a position consistent with that of *Corythosaurus* and *Lambeosaurus*, but the ventral (more rostral) loop is twisted, elongated, and extends within the premaxilla adjacent to the long lateral diverticulum to the level of the prefrontal. If *H. altispinus* is phylogenetically nested deeply within corythosaurs, as suggested by Evans and Reisz (2007), this remarkable elongation of the nasal cavity (nasal vestibule) is a derived trait of *H. altispinus*, in contrast with the relatively short, plesiomorphic s-loop morphology of *Corythosaurus* and *Lambeosaurus* (Weishampel, 1981b). Within the least inclusive clade that includes *Corythosaurus* and *Hypacrosaurus*, the helmet-shaped external morphology of the crest is relatively consistent (Evans and Reisz, 2007).

Cranial Crest Function: A Sensorineural Perspective

The function of the enlarged nasal cavity within the cranial crests of lambeosaurines has been the subject of considerable speculation and debate (Ostrom, 1962; Hopson, 1975; Weishampel, 1981a,b, 1997; Evans, 2006). Although hypotheses that involve underwater feeding have been rejected (Ostrom, 1961, 1962), those that pertain to enhancement of physiological (olfaction, thermoregulation) functions (Ostrom, 1961, 1962; Horner, 1995) of the nasal cavity have been more difficult to assess, but are generally thought to have played a minor role compared with behavioral interpretations of the crest (Dodson, 1975; Hopson, 1975; Weishampel, 1997; Sullivan and Williamson, 1999; Ruben et al., 2003; Horner et al., 2004; Evans, 2006). In addition to visual display, the acoustic resonance model of crest function is undoubtedly the most widely cited hypothesis (Farlow et al., 1995; Weishampel, 1997; Horner, 2000; Horner et al., 2004; Emlen, 2008). Despite its apparent widespread acceptance, this hypothesis is not favored universally. Sullivan (in Sullivan and Williamson, 1999) argued for a predominant visual display function for the crest, and suggested that resonance properties were simply incidental and not a significant target of selection.

The new data presented here, however, when interpreted in the context of lambeosaurine phylogeny (Evans and Reisz, 2007), suggest significant evolutionary modification of the nasal cavity in the lineage leading to *Hypacrosaurus altispinus* that was largely independent of the external appearance of the crest. *H. altispinus* and *Corythosaurus* plesiomorphically share a helmet-shaped crest, whereas the elongation of the lower part of the vestibular s-loop in *H. altispinus* is derived compared with the plesiomorphic s-loop morphology exhibited by *Corythosaurus* and *Lambeosaurus*. The striking evolutionary elongation of the rostral portion of the nasal cavity in *Hypacrosaurus altispinus* seems to be coupled with minimal change to the external morphology of the crest, and suggests a selective pressure for nasal cavity function that operated independently from changes associated with the visual display properties of the crest. Significant internal differences between the crests suggest that these modifications were selection-driven, and imply functions for the enlarged nasal cavity in lambeosaurines in addition to the visual display functions the crests no doubt served. This also highlights that the crest and related nasal cavity in lambeosaurines had several functions and a complex evolutionary history involving multiple, potentially divergent selection pressures within the clade (Hopson, 1975; Evans, 2006). In

this context, it is clear that hypothesized physiological and resonance functions of the nasal cavity need further detailed testing.

The new data on the relative size and morphology of the brain and brain divisions derived from the virtual endocasts allow independent assessment of two crest function hypotheses: olfactory enhancement and vocal resonation. Endocasts also provide more generalized insight into the behavioral scope inferred under hypotheses of crest function related to social display and intraspecific communication. Additionally, the morphology and ontogeny of the nasal cavity also provide new perspectives on olfactory and thermoregulation hypotheses.

Olfaction. Ostrom (1961, 1962) hypothesized that the expansion of the nasal cavity and related cranial crests were related to an increase in surface area for olfactory epithelium and increased olfactory acuity in lambeosaurines relative to other herbivorous dinosaurs. Evans (2006) corrected the previous reconstruction of this system by Ostrom (1961, 1962) and showed that the olfactory system of lambeosaurines did not change dramatically from the plesiomorphic condition, thereby ruling out Ostrom's hypothesis that an important function of the crest was to increase olfactory acuity via enlargement of the olfactory region of the nasal cavity.

As noted by Evans (2006), the relative size of the olfactory bulbs compared with the size of the brain and body mass in lambeosaurines compared with other dinosaurs remained unknown at the time of that study. The new CT scan data presented here allow the first estimates of olfactory bulb size relative to other measures of total brain and body size. Impressions of the olfactory bulbs are discernible dorsally in ROM 702 and ROM 758, but these are not apparent in the other digital endocasts. The ventral and especially rostral margins of the bulbs can be estimated based on the position of the presphenoid (which is incomplete in ROM 702), but the greatly shortened olfactory tracts are difficult to distinguish from the bulbs proper. The olfactory system as a whole is easily differentiated at the rostral end of the cerebral hemispheres, and it is thus possible to estimate volumes of the olfactory system (i.e., bulbs plus tracts) and put an upper limit on the amount of neural tissue devoted to olfaction in lambeosaurines. Volumetrically, the olfactory system of the lambeosaurines analyzed here forms between 2.9% (ROM 758) and 7.7% (CMN 34825) of the total endocast volume. In ROM 702, the adult in our sample, the bulbs formed <5% of the total endocast volume. The relative size of the olfactory system in ROM 702 is comparable with that of the hadrosaurine hadrosaurids *Edmontosaurus* (CMN 2289, ROM 1794) and *Gryposaurus* (AMNH 5350) in which the bulbs form ∼5% of the total endocast volume (values obtained by graphic double integration from published endocast illustrations of CMN 2289 and AMNH 5350, respectively). The bulbs of lambeosaurines and other hadrosaurids are relatively smaller than in most other dinosaurs (Hopson, 1979), including the ceratopsians *Psittacosaurus* (Zhou et al., 2007) and *Pachyrhinosaurus* (Witmer and Ridgely, 2008a), and virtually all theropods (Hopson, 1979; Zelenitsky et al., 2008). Similarly, small olfactory bulbs in *Nigersaurus*, a small sauropod in which the volume of the bulbs is ∼5% of the total endocranial volume, have been used to suggest that olfaction

was less important behaviorally than other senses in this taxon (Sereno et al., 2007). The similarity in the relative size of the olfactory bulbs in lambeosaurines relative to representatives of their crestless sister group Hadrosaurinae, suggests strongly that increased olfactory acuity did not play a causal role in the evolutionary hypertrophy of the lambeosaurine nasal cavity and crest.

The morphology of the nasal cavity provides additional insight into the potential importance of olfaction in lambeosaurine crest evolution and behavior. A number of previous studies have attempted to determine the homologies of the different chambers within the crest (Ostrom, 1962; Hopson, 1975; Weishampel, 1981b; Evans, 2006). Originally, Ostrom (1961, 1962) hypothesized that the combined lateral diverticula and common chamber represented an enlarged olfactory region in lambeosaurines. Subsequent work has shown that the lateral diverticula as well as the rostral tubular region of the nasal cavity contained within the premaxilla, probably represent the nasal vestibule, and were likely lined with respiratory, not olfactory, epithelial tissues (Evans, 2006).

The olfactory epithelium is typically found within the nasal cavity proper in extant archosaurs (Witmer, 1995; Evans, 2006; Witmer and Ridgely, in press). The common chamber of the crest in lambeosaurines represents the rostral region of the nasal cavity proper (Evans, 2006). Although olfactory epithelium may have extended into the common chamber of the crest, the primary olfactory region was probably located in its plesiomorphic position outside of the crest cavities proper (Evans, 2006). This region represents the caudal portion of the nasal cavity that corresponds to the olfactory region in extant tetrapods (Witmer, 1995). Here, the small region outside of the main airway and directly rostral to the olfactory bulbs seems to represent the cul-de-sac found in virtually all tetrapods, in which reduced airflow rates promote diffusion of odorant molecules to their receptors on the olfactory epithelium (Negus, 1958; Simmen et al., 1999; Craven et al., 2007; Witmer and Ridgely, in press). In comparison with tyrannosaurs, for example, which have a large caudal cul-de-sac and are generally thought to have had a keen sense of smell compared with other dinosaurs (Saveliev and Alifanov, 2007; Zelenitsky et al., 2008; Witmer and Ridgely, in press), the relatively very small size of the olfactory cul-de-sac in lambeosaurines is striking. The olfactory cul-de-sac of lambeosaurines is also much smaller than that of both nodosaurid and ankylosaurid ankylosaurs, the only other ornithischian groups in which this region has been reconstructed in detail (Witmer and Ridgely, 2008b).

It is unknown whether the length of the vestibule decreased air flow rates sufficiently to promote efficient reception of odorant molecules across olfactory epithelium housed within the common chamber. However, the apparently plesiomorphically sized olfactory bulbs and the location and relative size of the olfactory region of the nasal cavity provide further justification to reject the hypothesis that increasing olfactory acuity drove the evolution of the lambeosaurine crest.

Hearing in lambeosaurines. The hypothesis that the crest was used in vocal communication is relatively old, but it did not gain significant attention until several

TABLE 3. The maximum length of the digital cochlea casts determined using the Amira program, and calculations of the corresponding hearing capabilities of lambeosaurines using the equations from Gleich et al. (2005)

Specimen no.	Taxon	Length of cochlea	Best frequency of hearing (Hz)	High frequency hearing limit (Hz)
ROM 758	*Lambeosaurus* sp. (juvenile)	9.2 mm	579	2,110
ROM 759	*Corythosaurus* sp. (juvenile)	11.9 mm	295	1,586
CMN 34825	*Corythosaurus* sp. (subadult)	12.3 mm (averaged)	267	1,534
ROM 702	*Hypacrosaurus altispinus* (adult)	16.7 mm (averaged 16.6 and 16.8)	80	1,190

decades after it was first argued in detail by Wiman (1931). Since the work of Hopson (1975) and Weishampel (1981a,b, 1997), the hypothesis that the hypertrophied nasal cavities of lambeosaurines varied in resonant properties and enhanced intraspecific vocal communication has become the most widely cited hypothesis of crest function, both scientifically and popularly (Heaton, 1972; Hopson, 1975; Weishampel, 1981a; Farlow et al., 1995; Weishampel, 1997; Sullivan and Williamson, 1999; Horner, 2000; Horner et al., 2004; Evans, 2006).

Using relatively simple physical models, Weishampel (1981b) predicted the resonant frequencies of the elongate nasal cavities of *Parasaurolophus walkeri* and *P. cyrtocristatus* at between 50 and 375 Hz. Using a more complicated digital 3D model derived from CT scans of *P. tubicen*, Diegert and Williamson (1998) also predicted low-frequency resonance, as low as 30 Hz. The resonant frequency of a tubular structure is related to its length. As such, taxa with shorter nasal cavities than *Parasaurolophus*, such as the corythosaurs in this study, would likely have produced calls at somewhat higher frequencies than *Parasaurolophus*. By the same reasoning, juvenile lambeosaurines of a given taxon would have produced relatively higher frequency calls than adults, and the frequency of their calls would deepen with nasal cavity growth through ontogeny (Weishampel, 1981a). The lateral diverticula of corythosaurs could have "muted out" certain frequencies and/or resonated as blind chambers at higher frequencies, and the complexity of their nasal cavities makes assessment of resonance so difficult that precise predictions have never been attempted (Weishampel, 1981a). Regardless, it is fairly certain that the fully developed crests of the large corythosaurs in this study (*Lambeosaurus*, *Corythosaurus*, and *Hypacrosaurus*) would have resonated in the low-frequency range, probably well below 1000 Hz.

A fundamental prediction of the vocal resonance hypothesis is that the lambeosaurines had the ability to detect the noises made by the crest (Hopson, 1975; Weishampel, 1981a, 1997). The length of the cochlea is related to the length of the basilar membrane neuroepithelium of the basilar papilla, and therefore provides insight into auditory capabilities, or at least the behavioral importance of hearing, in reptiles (Baird, 1970; Wever, 1978; Manley, 1990; Gleich and Manley, 2000; Gleich et al., 2005). Hopson (1975) and Weishampel (1981a, 1997) argued that lambeosaurines had hearing sensitivity similar to that of extant crocodilians due to the similarity of their inner ear morphology, and that they were capable of sensing the low-frequency calls hypothesized to have been made by the crests. Unfortunately, none of these studies were based on data derived from lambeosaurines, but rather used information on inner ear morphology from non-lambeosaurine hadrosauroids (hadrosaurines, *Bactrosaurus*) under the implicit assumption that these structures would be similar in lambeosaurines. The casts of the endosseous labyrinths described here reveal the detailed structure of the lambeosaurine inner ear for the first time, and allow us to test the hypothesis that lambeosaurines were capable of detecting low frequency sounds. The elongate cochlea in the adult of *Hypacrosaurus altispinus* measures 16.7 mm in length, and is similar in shape and relative proportions to that described for hadrosaurine hadrosaurids (Brown, 1914; Langston, 1960; Ostrom, 1961). The overall similarity of the auditory apparatus and elongate cochlea of lambeosaurines and hadrosaurines confirms this key assumption in previous studies of crest function in the group (Hopson, 1975; Weishampel, 1997).

Gleich et al. (2005) demonstrated in extant archosaurs a highly correlated inverse relationship between the length of the basilar papilla and an animal's most sensitive "best" frequency of hearing, as well as a positive relationship between basilar papilla length and the high frequency upper limit of hearing. Applying their findings to our data confirms that lambeosaurines and other hadrosaurids emphasized low frequencies, as in other large dinosaurs (Table 3). Although the lambeosaurines in this sample, particularly ROM 702, lie outside of the range of extant data points from which the equations of Gleich et al. (2005) were derived, the equations nonetheless allow us to put testable constraints on estimates of auditory sensitivity in large dinosaurs, including *Hypacrosaurus*, which are tied directly to observational data in extant archosaurs.

Using the length of the cochlear cast to estimate basilar membrane length, the lambeosaurines described here have an estimated best frequency of hearing ranging from 579 Hz in the smallest specimen (ROM 758, juvenile *Lambeosaurus*) to 80 Hz in the largest (ROM 702, adult *Hypacrosaurus altispinus*), with corresponding high frequency hearing limits of 2.1 and 1.2 kHz, respectively (Table 3). In the case of ROM 702, the calculated best frequency of hearing falls within the range of resonance frequencies (48–375 Hz) predicted for *Parasaurolophus* by Weishampel (1981a).

Weishampel (1981a) suggested that the lambeosaurine crests may have been important for communication between adults and juveniles. Neonatal lambeosaurine

skulls identified as *Hypacrosaurus stebingeri* from the Two Medicine Formation of Montana (Horner and Currie, 1994) permit estimation of the resonant properties of the crests of the smallest juvenile lambeosaurines. If modeled as a tube ~15 cm in length (admittedly a very simple model), the nasal cavity of a *Hypacrosaurus* hatchling would resonate at ~1.1 kHz using the calculations outlined in Weishampel (1981a). This approaches the upper limit of hearing of an adult *Hypacrosaurus*, as predicted from ROM 702, but it is likely to be within its audible range. Generally, resonant frequencies would decrease with increasing size of the nasal cavity through ontogeny, and progressively approach the rather low best frequency of hearing we predict in adults. This is consistent with the hypothesis that vocal communication between adults and juveniles, even the smallest individuals, may have been important to lambeosaurines (Weishampel, 1981a).

Relative brain size and behavior. Relative brain size is typically measured with an encephalization quotient (EQ), which represents an individual's actual brain size (in volume or mass) divided by the expected brain size for its particular body size calculated using an allometric relationship derived from a large extant sample (Jerison, 1973; Hopson, 1977; Hurlburt, 1996). In extinct taxa, both brain and body size of an individual must be estimated. These uncertainties make the EQ method problematic for fossil taxa (Larsson et al., 2000), but it is nonetheless a useful, although coarse, comparative metric. Evans (2005) estimated an EQ of ~2.8 for lambeosaurines, based on similarities in braincase size/morphology and body size between adult lambeosaurines and hadrosaurines. We can test this hypothesis here by calculating the relative size of the brain for the first time in an adult lambeosaurine, *Hypacrosaurus altispinus*, based on the endocast of ROM 702 and a similarly sized complete skeleton of this taxon.

ROM 702 is essentially an isolated skull, and as such, we estimated its body mass with reference to a complete, similarly sized skeleton of *H. altispinus*, CMN 8501. CMN 8501 is <7% larger than ROM 702 in linear measurements of the skull and braincase, and as such will provide a relatively accurate estimate of mass while at the same time will provide an EQ estimate that errs on the side of "conservatism" in that it will slightly underestimate the value. The body mass of CMN 8501 was calculated in two ways: (1) using a 1372 ml, 1/12 scale model based on CMN 8501 reported by Russell and Beland (1976) and the formula of Colbert (1962) and (2) using both the bipedal (femur circumference = 400 mm) and the quadrupedal mammal (humerus circumference = 225 mm) regression formulae of Anderson et al. (1985), because hadrosaurids are generally thought to be facultatively bipedal rather than true bipeds (Forster, 1997; Horner et al., 2004). These calculations resulted in mass estimates of 2,000 and 3,300 kg for the bipedal and quadrupedal formulae, respectively, with the scale model estimate of 2,134 kg falling between the two.

Given the problems with EQs of extinct taxa associated with uncertainty in brain and body mass estimation, we calculated a range of EQ values for *Hypacrosaurus* using both the 50% dinosaurian convention (Jerison, 1973) and the 60% estimate suggested by

Evans (2005) for hadrosaurids for brain size estimation, both the minimum and maximum estimated body masses for *H. altispinus*. EQs were calculated using the nonavian reptile dataset of Hurlburt (1996). Our EQ estimates for *H. altispinus* range from 2.3 to 3.7. The only previous EQ estimate for lambeosaurines (Evans, 2005) falls within this range. The average of the three mass estimates (2,478 kg) and the 50% convention for dinosaurs results in an EQ estimate of 2.7 for *Hypacrosaurus*. This value is comparable with that of other large ornithopods (hadrosaurines, 2.8; *Iguanodon*, 2.6; Evans, 2005) and the large coelurosaurian theropod *Tyrannosaurus rex* (2.7; Witmer et al., 2008). The lowest of our EQ estimates for *Hypacrosaurus* (2.3), is marginally higher than most extant nonavian reptiles (Hurlburt, 1996), allosauroid theropods (*Allosaurus*, 1.6), sauropods (*Diplodocus*, 0.4; *Nigersaurus*, 0.4–0.8), and ceratopsians (*Psittacosaurus*, 1.7; *Protoceratops*, 2.1; *Triceratops*, 0.7), but significantly less that that of maniraptoriform theropods (>4) (Hurlburt, 1996; Evans, 2005; Zhou et al., 2007; Witmer et al., 2008). The estimates of brain volume for *Hypacrosaurus* plot near the upper 95% confidence limit of a log–log regression of brain volume and estimated body mass in non-avian reptiles (Larsson et al., 2000).

The most striking aspect of the brain endocasts of lambeosaurines is the relatively large cerebral hemispheres. The hemispheres form ~43% of the total endocranial volume (without olfactory bulbs) in ROM 702, and a similar, but slightly smaller relative size in the juvenile specimens. Although similar to hadrosaurine hadrosaurids (the cerebrum is ~45% of the total endocranial volume in *Edmontosaurus* and *Gryposaurus*), the cerebrum is considerably larger than that of other non-hadrosauriform ornithischians, as well as large theropods such as *Carcharodontosaurus* (24%) and *Tyrannosaurus rex* (33%), but compares favorably with the maniraptoran theropod *Conchoraptor* (43%) and even the basal bird *Archaeopteryx* (45%) of considerably smaller body size (Larsson et al., 2000; Kundrat, 2007).

An enlarged brain relative to body size has been equated with expanded behavioral repertoires and/or increased behavioral complexity in vertebrates (Jerison, 1969, 1973; Hopson, 1977; Hurlburt, 1996). The relatively large size of the brain and cerebral hemispheres in lambeosaurines is consistent with the range and complexity of social behaviors inferred when the crest is hypothesized to be an intraspecific signaling structure for visual and vocal communication (but see Witmer and Ridgely, 2008a). The relatively large size of the brain and the cerebrum may even suggest that lambeosaurines had higher cognitive abilities not present in most other herbivorous dinosaurs (Witmer and Ridgely, 2008a). However, there is an increase in the relative size of the brain, and the cerebrum in particular, in Hadrosauriformes compared with their ornithischian outgroups (Hopson, 1977, 1979), and an enlarged brain and cerebrum, together with any inferred capacity for complex behaviors, appears to have been plesiomorphic for lambeosaurines.

Nasal Cavity and Thermoregulation

Ostrom (1961) noted the potential of the enlarged nasal cavity to function in the conditioning of respired air. However, he discounted the idea that the crests

were adaptations for thermoregulatory and water conservation functions on the grounds that the habitats in which lambeosaurines lived were probably warm and humid. This rationale is probably too simplistic and a number of authors have suggested thermoregulation as a possible function of convergently enlarged nasal vestibules of large ornithischian dinosaurs, including lambeosaurines (Sullivan and Williamson, 1999; Witmer, 2001; Evans, 2006; Witmer and Ridgely, 2008b).

The relatively small diameter of the nasal cavity in lambeosaurines has been used to argue that they do not show modifications associated with respiratory turbinates and associated thermoregulatory functions and that they were not endothermic (Ruben et al., 1996; Ruben et al., 1998, 2003). Moreover, CT scans conducted for this study revealed no evidence of turbinate-like structures within the vestibular tubes in any of the scanned specimens. If turbinate structures were present within the premaxillary tubes, as has been reported in the s-loop region of a juvenile specimen of *Hypacrosaurus stebingeri* (Horner, 1995), our data suggest that they did not typically ossify.

Although we cannot confirm turbinate-like structures, our data do allow us to reconstruct a major vascular pathway associated with supplying the nasal vestibule. A large neurovascular bundle would have passed rostrally through the body of the maxilla to emerge on the dorsal surface of the premaxillary shelf via a large foramen. From here, the neurovascular element passed laterally between the maxilla and the premaxilla, and then dorsally along a prominent sulcus on the premaxilla to enter the crest in the region of the s-loop through a gap between the dorsal and lateral premaxillary processes (Fig. 1). The sulcus that conducted this vascular element is typically over 10 mm in width in adult corythosaurs (e.g., ROM 1933, ROM 1218, Royal Tyrrell Museum of Palaeontology, Drumheller, TMP 81.37.01), suggesting significant blood flow into the nasal vestibule that is consistent with at least a minor thermoregulatory function for the nasal cavity. Similarly, the new data neither support nor reject Wheeler's (1978) hypothesis that the enlarged nasal cavity was related to brain cooling. The thermoregulatory potential of the enlarged nasal cavity in lambeosaurines and its role in the evolution of the crest still requires further detailed examination. Most hadrosaurine hadrosaurids have enlarged narial regions, suggesting that thermoregulation may have factored in the early evolution of the crest (Evans, 2006).

Relative growth patterns of the nasal cavity also provide insights into the relative significance of its functional divisions in lambeosaurines. In lieu of a more complete volumetric analysis, preliminary data for *Corythosaurus* and *Lambeosaurus* suggest that the most significant allometric components of the nasal cavity expansion through ontogeny are within the vestibule, in terms of both the relative elongation of the snout and the lateral diverticula, when compared with the common chamber. This finding reinforces the notion that functions associated with the nasal vestibule (e.g., vocalization, thermoregulation), and not the nasal cavity proper (e.g., olfaction), were functionally more important in the evolution of the lambeosaurine crest (Evans, 2006).

It was once thought that the complex, hypertrophied nasal cavity was a unique characteristic of lambeosaurines directly associated with the development of the crest. New data from nodosaurid and ankylosaurid ankylosaurs reveals analogous nasal cavity hypertrophy that evolved independently in this group (Witmer and Ridgely, 2008b). Here, nasal cavity evolution can clearly be distanced from a visual display function because ankylosaurs lack any crests or adornments associated with the nasal cavity, as in lambeosaurines. The bizarre nasal cavities of ankylosaurs present a functional problem that parallels that of the lambeosaurine crest, and which can be approached in a similar way.

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