

# The internal cranial morphology of an armoured dinosaur *Euoplocephalus* corroborated by X-ray computed tomographic reconstruction

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## Abstract

Internal cranial anatomy is a challenging area to study in fossilized skulls because of small sample sizes and varied post-mortem preservational alterations. This difficulty has led to the lack of correspondence between results obtained from direct osteological observation and from more indirect reconstruction methods. This paper presents corroborating evidence from direct osteological observation and from reconstruction based on computed X-ray tomography (CT) on the internal cranial anatomy of the ankylosaurid dinosaur *Euoplocephalus tutus*. A remarkable specimen of *Euoplocephalus* preserves rarely observed internal cranial structures such as vascular impressions in the nasal cavity, olfactory turbinates and possible impressions of conchae. Comparison with fossils and CT models of other taxa and other *Euoplocephalus* specimens adds osteological evidence for the previously reconstructed nasal cavity in this dinosaur and revises the previously described braincase morphology. A new interpretation of the ethmoidal homology identifies a mesethmoid, sphenethmoid and ectethmoid. These ethmoidal ossifications are continuous with the mineralized walls of the nasal cavity. The location of the olfactory fenestra provides further evidence that the olfactory regions of the nasal cavity are pushed to the sides of the main airway. This implies that the function of the vascular impressions in the nasal cavity and the looping of the cavity are not related to olfaction. A byproduct of the elongate, looping airway is a dramatic increase in surface area of the nasal respiratory mucosa, which in extant species has been linked to heat and water balance. A role in vocalization as a resonating chamber is another possible function of the looping and elongation of the nasal cavity. Olfaction remains as a possible function for the enlarged olfactory region, suggesting that multiple functions account for different parts of the ankylosaurid nasal cavity that underwent substantial modification. Cranial endocasts show negligible variation within *Euoplocephalus*, which lends some confidence to interspecific comparisons of endocranial morphology.

**Key words:** Ankylosauridae; braincase; Dinosaur Park Formation; nasal cavity.

## Introduction

Ankylosaurs are a clade of ornithischian dinosaurs commonly called 'armoured dinosaurs'. Due to their highly modified skulls, detailed description of the cranial anatomy is particularly important in identification of both basal and derived conditions within the clade. However, the skulls are extensively ossified and little is known about the internal cranial morphology of ankylosaurs. Cranial elements are rarely preserved individually and it is unusual to find a skull

that shows the internal morphology without the aid of X-ray computed tomography (CT). Several papers describe ankylosaur braincases and cranial endocasts (Maryańska, 1977; Coombs, 1978a; Kurzanov & Tumanova, 1978; Carpenter et al. 2001; Averianov, 2002; Vickaryous & Russell, 2003; Hayakawa et al. 2005; Witmer & Ridgely, 2008; Parsons & Parsons, 2009). However, these authors provided different identifications of the foramina perforating the braincases and this makes comparison difficult. Only a handful of papers deal with other regions inside ankylosaur skulls, such as the nasal cavity. Sections of a few skulls (e.g. *Euoplocephalus* AMNH 5403) led to reconstruction of the ankylosaur nasal cavity as a sagittal S-shaped airway (Maryańska, 1977; Coombs, 1978b; Witmer, 1997). Results from two-dimensional CT slices supported this view (Vickaryous & Russell, 2003; Vickaryous, 2006). A three-dimensional digital reconstruction of a CT scan of the skull

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of the ankylosaurid *Euoplocephalus* recently overturned the reconstruction of a simple S-shaped airway in this genus (Witmer & Ridgely, 2008). According to the new reconstruction, the nasal cavity of *Euoplocephalus* follows a complex path of twists and turns that create a series of loops of the airway (Fig. 1). The nasal cavity of the nodosaurid ankylosaur *Panoplosaurus* also has the anterior and posterior loops, although the path of the airway is less complicated than in *Euoplocephalus* (Witmer & Ridgely, 2008). The complex pathways of the ankylosaur nasal cavities in Witmer & Ridgely (2008) also revealed that the internal space within the skulls previously identified as paranasal sinuses (Witmer, 1997; Vickaryous & Russell, 2003; Vickaryous, 2006) are actually part of the looping airway, although this was not readily evident in two-dimensional CT slices.

Witmer & Ridgely (2008) radically transformed the previous view of a straight airway in ankylosaurs because their reconstruction was possible through sophisticated CT methodology. For instance, Witmer & Ridgely (2008) note that the nodosaurid ankylosaurs *Edmontonia* (AMNH 3076) and *Panoplosaurus* (ROM 1215) are likely to differ from each other in the degree of mineralization within the nasal cavity. Whereas their reconstruction showed a looping airway for *Panoplosaurus* (Witmer & Ridgely, 2008), a simple, straight airway was previously reconstructed for *Edmontonia* due to the lack of apparent subdivision within the nasal cavity (Vickaryous, 2006). Witmer & Ridgely (2008) observed thin mineralized laminae as well as heterogeneities in the matrix within the nasal cavity of the same specimen of *Edmontonia* (AMNH 3076), which highlights the sensitivity of data obtained via CT scanning. For these reasons, corroborative evidence from direct observation of the skull mor-

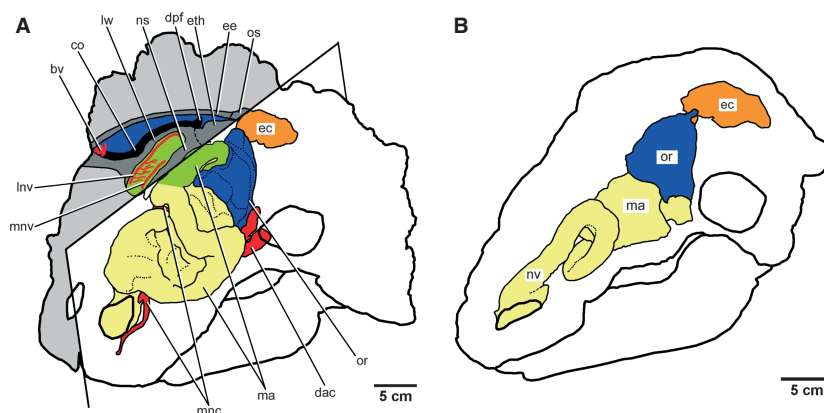
phology is important. In addition, the ankylosaur literature dealing with internal cranial anatomy rarely deals with comparative aspects of the braincase and nasal cavities.

Several specimens of the ankylosaurid *Euoplocephalus* from the Campanian (Late Cretaceous) of southern Alberta, Canada fill this gap. Two of the specimens (AMNH 5238 and UALVP 47977) reveal osteological correlates of the soft tissues within the skull, whereas the others (AMNH 5405 and UALVP 31) offer new data on braincase anatomy through three-dimensional reconstructions based on CT scanning. Cranial endocasts of these specimens establish correspondence between the cranial nerves and the foramina perforating the braincase wall in UALVP 47977.

Institutional abbreviations: AMNH (American Museum of Natural History, New York, NY, USA); MPC (Mongolian Paleontological Center, Ulanbaatar, Mongolia); followed by the collector's initials and field number; PIN (Paleontological Institute, Moscow, Russia); ROM (Royal Ontario Museum, Toronto, Canada); TMP (Royal Tyrrell Museum of Palaeontology, Drumheller, AB, Canada); UALVP (University of Alberta Laboratory for Vertebrate Paleontology, Edmonton, AB, Canada); and ZPAL (Institute of Palaeobiology of the Polish Academy of Sciences, Warsaw, Poland).

## Materials and methods

A partial ankylosaurid skull roof (UALVP 47977) was collected from the Dinosaur Park Formation in Dinosaur Provincial Park in 1971. The precise location and stratigraphic level of the site was not recorded, but the site is near Happy Jack's on the north side of Red Deer River (A.L. Lindoe, personal communication, 2007). Due to erosion of the skull before field collection, the nasal cavity, the orbital region and the upper half of the braincase are



**Fig. 1** Schematic reconstructions of the nasal cavity morphology of two ankylosaur skulls. (A) The ankylosaurid *Euoplocephalus tutus* (AMNH 5405). The left half of the skull is derived from the reconstruction published by Witmer & Ridgely (2008), whereas the right half represents new information based on the osteological correlates of the soft tissues within and around the nasal cavity in UALVP 47977. The specimen (UALVP 47977) preserves parts of the main airway (in green), the olfactory region (in blue), and the endocranial cavity (in orange). (B) The nodosaurid *Panoplosaurus mirus* (ROM 1215) after Witmer & Ridgely (2008) for comparison. The nasal passage of *Euoplocephalus* is looped in more complex ways than that of *Panoplosaurus*, and the olfactory region of *Euoplocephalus* is pushed to the side of the main airway. bv, blood vessel trace; co, groove that possibly housed the concha; dac, dorsal alveolar canal; dpf, descending process fused to the ventral surface of the frontal; olfactory turbinate; ec, endocranial cavity; ee, ectethmoid; eth, ethmoidal complex; Inv, lateral nasal vessels; lw, lateral wall of the main airway; ma, main airway; mnv, medial nasal vessels; mnc, medial nasal canal; ns, nasal septum; nv, nasal vestibule; or, olfactory region; os, orbitosphenoid.

exposed ventrally. Two ankylosaurid ankylosaurs are currently recognized from the Dinosaur Park Formation: *Dyoplosaurus*, known from a single specimen recovered from the lower part of the formation, and *Euoplocephalus*, known from numerous specimens throughout the formation and the overlying Horseshoe Canyon Formation (Parks, 1924; Arbour et al. 2009). The holotype specimen of *Dyoplosaurus* preserves the posterior part of the skull roof. The skull (along with most of the skeleton) is affixed to a panel and so the ventral side cannot be observed. At present, there are no cranial characters that separate *Dyoplosaurus* from *Euoplocephalus*; the features that distinguish *Dyoplosaurus* from *Euoplocephalus* are restricted to the pelvis and pes. As such, it is possible that isolated skulls (or skulls associated with skeletons that do not preserve the pelvis or pes) currently referred to *Euoplocephalus* may instead be referable to *Dyoplosaurus*. UALVP 47977 preserves distinct flat, polygonal osteoderms on the dorsal surface of the skull similar to those in *Euoplocephalus*. These osteoderms are not preserved in *Dyoplosaurus*, which may reflect either a taphonomic or a true diagnostic difference. As such, UALVP 47977 more closely resembles *Euoplocephalus* than *Dyoplosaurus*. For the purposes of this paper, UALVP 47977 is tentatively referred to *Euoplocephalus* to facilitate comparison with other skulls referred to this genus and pending a revision of the genus by V.M.A.

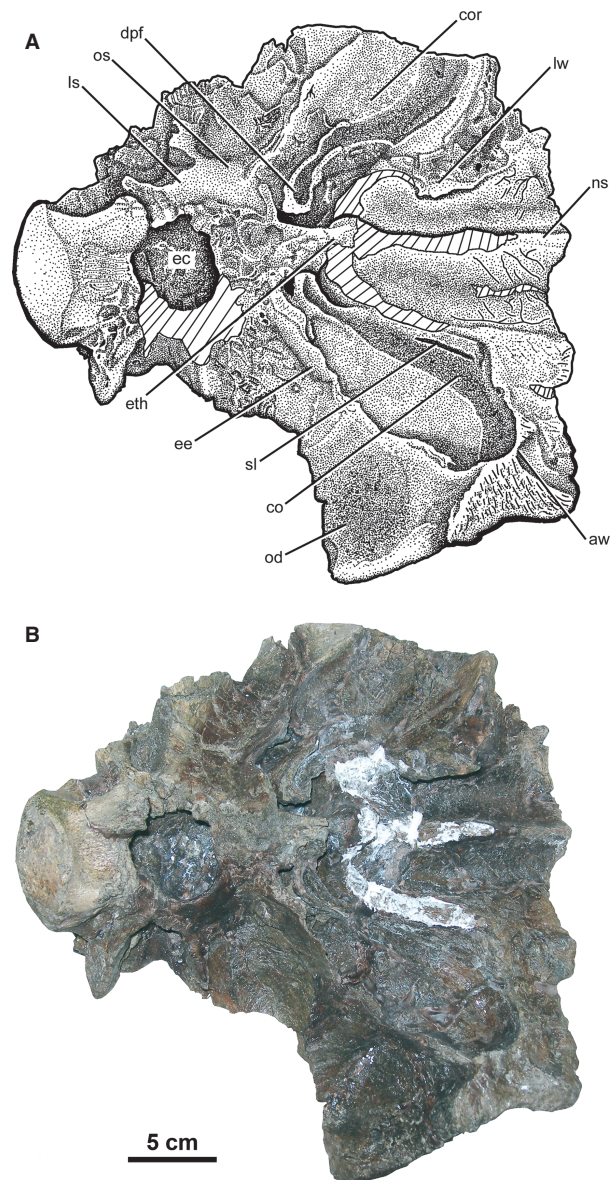
Computed tomography scans of two additional skulls of *Euoplocephalus* were available for this study. AMNH 5405 and UALVP 31 were both collected from the Steepleville locality in Dinosaur Provincial Park, Alberta, Canada. CT data of AMNH 5405 used by Witmer & Ridgely (2008) was made publicly available on a website (<http://www.oucom.ohiou.edu/dbms-witmer/3D-Visualization.htm>) and their article may be consulted for technical details of the scanning. UALVP 31 was scanned at the University of Alberta ABACUS CT scanner, in 1-mm increments. Both skulls were digitally reconstructed using the thresholding and segmentation tools in the software program MIMICS Version 14 (Materialise Inc., Leuven, Belgium). Digital cranial endocasts were created for each skull and internal structures were viewed both as two-dimensional slices and as three-dimensional reconstructions. As an independent check on Witmer & Ridgely's (2008) findings on the nasal cavity, V.M.A. performed *de novo* segmentation of the nasal cavity of AMNH 5405. Three-dimensional models cropped to resemble the broken surfaces of UALVP 47977 were also created to compare internal structures of the different specimens. A latex cranial endocast was prepared for UALVP 47977.

## Results

This description focuses primarily on UALVP 47977, as it best presents new information. This paper largely follows Witmer (1995, 1997), Evans (2006) and Witmer & Ridgely (2008) for homologies in the antorbital region (Figs 1 and 2). The nasal cavity refers to a respiratory and olfactory passage that extends between the external naris and the choana, and is equivalent to the respiratory tract, the respiratory passage and the airway in other papers.

### Skull roof

In UALVP 47977, the dorsal surface of the skull is moderately weathered. The specimen preserves the top and



**Fig. 2** Illustration (A) and photograph (B) of the ventral view of an ankylosaurid skull roof (UALVP 47977, *Euoplocephalus*) from the Dinosaur Park Formation (Campanian, Upper Cretaceous), southern Alberta. Hatched lines indicate parts reconstructed with plaster. Impressions of the soft tissues, including the main airway, nasal arteries, and possible turbinates, are well defined. The ethmoidal elements are well ossified and separate regions of the nasal cavity from each other. No sutures are visible. aw, anterior wall of the cavity for the olfactory region; cor, cavity for the olfactory region; ls, laterosphenoid; od, orbital depression; sl, sulcus associated with the groove in the olfactory region. For other abbreviations, see Fig. 1.

lateral parts of the nasal cavity, which represent both the non-olfactory and olfactory regions of the nasal cavity (Fig. 2; Witmer & Ridgely, 2008). As in most ankylosaurs, but unlike *Cedarpelta* (Carpenter et al. 2001) and *Pinacosaurus* (Maryańska, 1977), no sutures can be observed. The non-olfactory dorsomedial passage of the nasal cavity

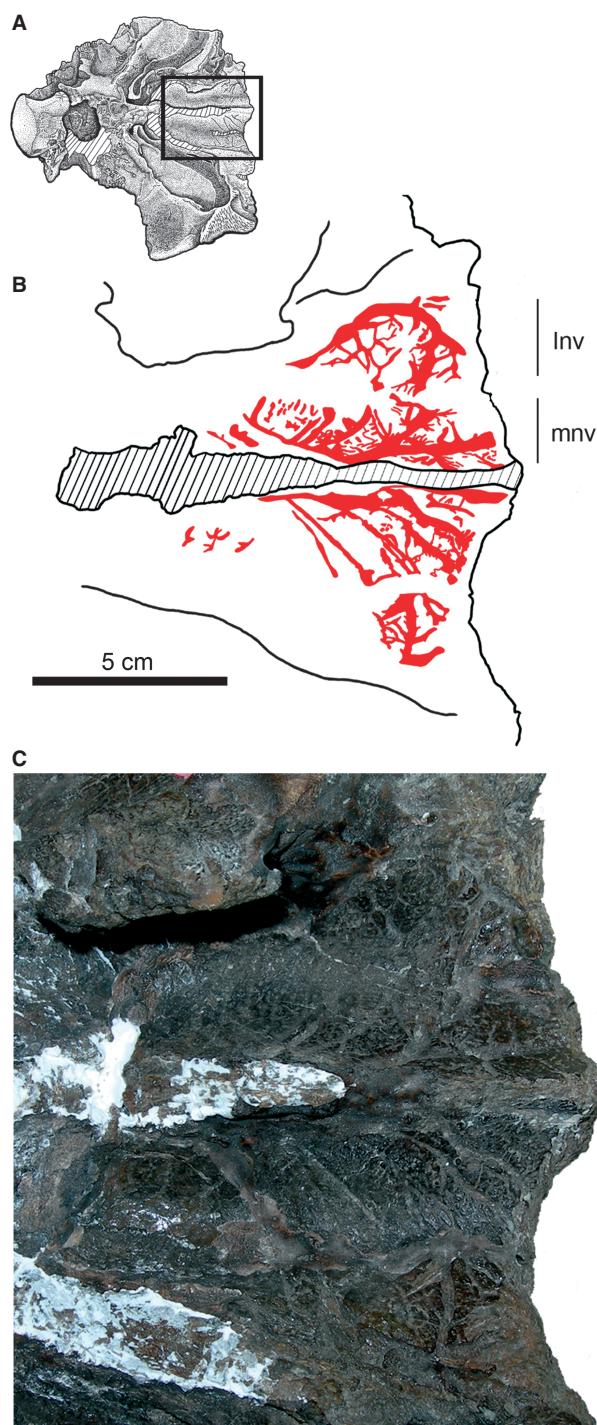
under the frontals extends posteriorly behind the orbits, just anterior to the braincase. The olfactory region of the nasal cavity occupies the large cavity on both sides of the non-olfactory dorsomedial passage. A well developed bony wall separates the dorsomedial passage from the olfactory region for all its preserved length.

The dorsomedial passage of the nasal cavity (main airway) is divided into right and left passages by the nasal septum. There is no evidence for a median common chamber as reconstructed for lambeosaurine ornithomorphs (Evans et al. 2009). On both the lateral and medial walls of the nasal cavity proper in UALVP 47977, deep grooves extend anteroposteriorly and lead to the extensive vascular impressions in the roof of the nasal cavity (Fig. 3). The impressions branch and extend posteromedially toward the nasal septum and this pattern is bilaterally consistent. The vascular impressions are conspicuous in the anterior half of the preserved length of the main airway but are absent in the posterior half. Vascular impressions are also preserved in this region in AMNH 5238. Vascular impressions could not be reconstructed from the CT scans of AMNH 5405 and UALVP 31, but this is because of inadequate resolution of the CT scans.

The cavity that housed the olfactory region of the nasal cavity occupies a large volume to the side of the dorsomedial part of the main airway. The cavity is surrounded by a thin sheet of bone (ectethmoid) laterally and by thick bony walls medially and anteriorly, and is connected posteriorly with the endocranial cavity through the olfactory fenestra. The olfactory bulb sat within this fenestra through which the olfactory nerves [cranial nerve (CN) I], ethmoidal vessels and their branches passed. This fenestra was previously identified as an olfactory tract in *Talarurus* (Carpenter, 2004) but the olfactory tract was located more posteriorly, well within the endocranial cavity.

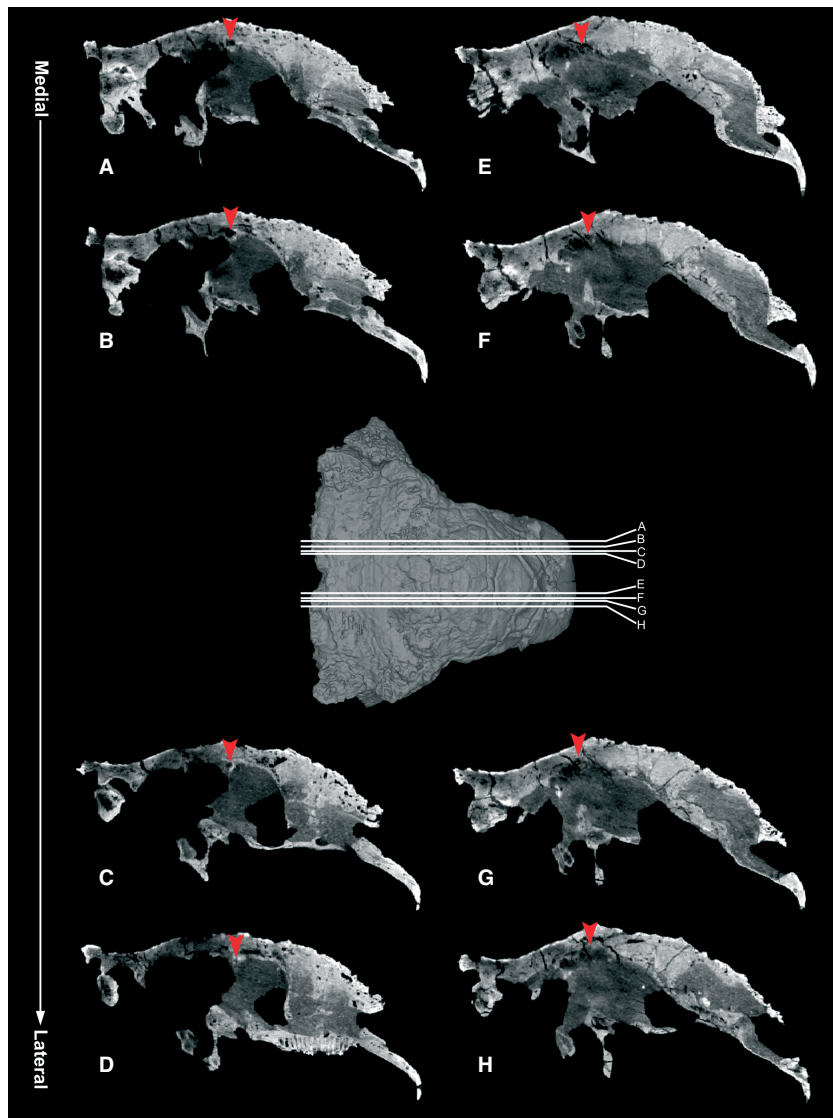
In UALVP 47977, a conspicuous descending process fused to the ventral surface of the frontal develops at the front of the olfactory fenestra. The descending process accommodates a deep, spacious groove that originates from the anterior margin of the orbit. Its anterolateral site of origin is associated with vascular impressions on the medial surface of the lacrimal. The groove extends medially along the anterior wall of the olfactory region and then posteriorly along the lateral wall of the main airway, and finally ventrally along the descending process. A deep sulcus parallels the groove medially along the lateral wall of the main airway. The soft tissue that filled this groove was extensively vascularized because of the vascular impressions at the anterolateral end of the groove and because of the sulcus associated with the groove along the lateral wall of the main airway.

In another skull of *Euoplocephalus* (AMNH 5405), a tunnel extends anterolaterally within the roof of the olfactory region (Fig. 4) and presumably opens into the descending process. Witmer & Ridgely (2008) did not reconstruct this



**Fig. 3** Vascular impressions in the dorsomedial part of the nasal cavity proper of UALVP 47977. (A) Drawing of skull showing region of enlargement in diagram (B) and photograph (C). These ethmoidal vessels are likely to be part of the median nasal canal system. Hatched area in B represents broken nasal septum (mesethmoid). Anterior is to the right. For abbreviations, see Fig. 1.

tunnel in AMNH 5405, but it is present on both sides in their CT data. A re-examination of the CT slices revealed that the tunnel branches laterally. Although UALVP 47977 does not



**Fig. 4** Sagittal sections of a *Euoplocephalus* skull (AMNH 5405) from CT data of Witmer & Ridgely (2008) show a tunnel within the frontal bone, laterally positioned and passing medially and slightly posteriorly on both sides. The most lateral sagittal section for each side is where the canal disappears into the bone. Arrowhead indicates the tunnel within the frontal, and letters A–H indicate the levels of the CT slices on the skull. Anterior is to the right in all CT slices and in the 3D model of the skull. CT data are available from the website (<http://www.oucom.ohiou.edu/dbms-witmer/3D-Visualization.htm>).

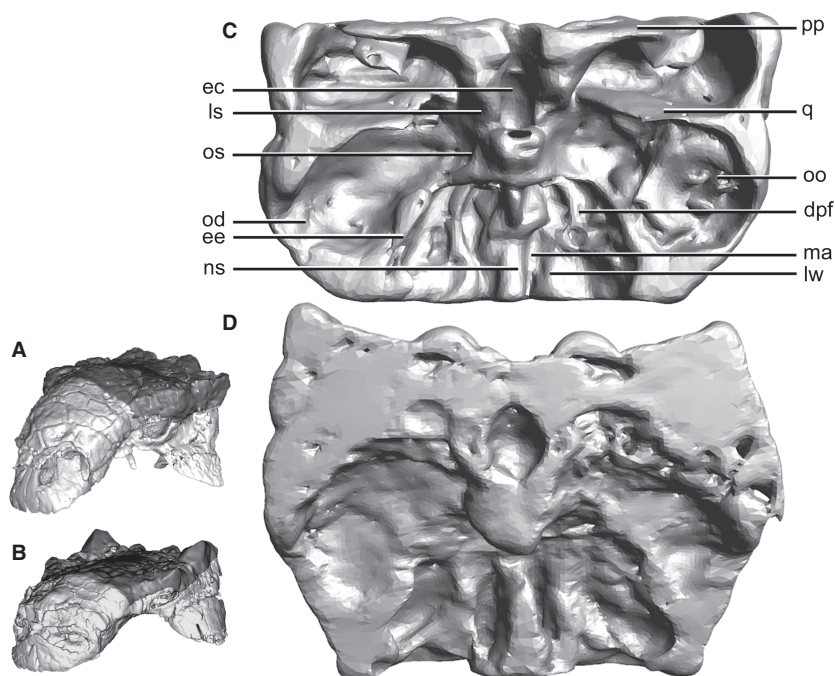
have the tunnel, the vascular impression associated with the groove in the olfactory region suggests that at least the vascular component of the tissue filling the groove may correspond to the tissue filling the tunnel in AMNH 5405. The descending process and the groove could not be reconstructed from the CT scan of UALVP 31 (Fig. 5). UALVP 47977 has cracks that show the cross-sections of the frontal and the nasal. None of these cross-sections indicate pneumatization within the bones.

### Ethmoidal region

UALVP 47977 preserves the mesethmoid, the sphenethmoid and the ectethmoid, all of which are fully mineralized (Figs 2 and 7). The mesethmoid is a septum on the midline that separated the olfactory bulbs and is continuous anteriorly with the mineralized nasal septum. The sphenethmoid is the lateral element of the ethmoidal complex (generally referred to as a presphenoid in ornithischians: Horner,

1992; Evans, 2005, 2006) that enveloped the olfactory bulb ventrally and laterally. The sphenethmoid is continuous with the lateral wall of the main airway. The mineralized median septum of the olfactory bulbs has been described for a variety of non-avian theropods (Brochu, 2002; Coria & Currie, 2002; Sampson & Witmer, 2007; Ali et al. 2008) and is considered a homologue of the mesethmoid in birds (Ali et al. 2008). Following this position, the ossified median septum of the ethmoidal complex in UALVP 47977 is identified as the mesethmoid. It is not possible to distinguish the boundary between the mesethmoid and the sphenethmoid in UALVP 47977 and these two elements probably fused to each other early in ontogeny.

The ectethmoid forms a thin lateral wall of the olfactory region, separating it from the orbital depression laterally. It contacts the orbitosphenoid posteriorly and the lacrimal anteriorly, although the sutures are not visible at either end. Because of the skull width and the relatively more anterior placement of the orbit, the ectethmoid is elongate



**Fig. 5** CT-based reconstruction corroborates direct osteological observation. CT renderings of the skull roofs of two *Euoplocephalus* specimens, AMNH 5405 (A,C) and UALVP 31 (B,D). A and B show in dark grey the portion of the skull represented in C and D in relation to the entire skull, in oblique right anterior view. C and D are sliced to mimic the areas preserved in UALVP 47977, and show internal features of the skull in ventral view that correspond to those of UALVP 47977 (Fig. 2), with anterior towards the bottom of the page. oo, ocular osteoderm; pp, paroccipital process; q, quadrate. For other abbreviations, see Figs 1 and 2.

and oriented anterolaterally rather than transversely. The ectethmoid forms a small, medially overhanging shelf near the base of the descending process. A small foramen that pierces the ectethmoid on the left side of the skull from the orbital depression to the olfactory region may represent the orbitonasal foramen.

Anteriorly to the ethmoidal complex, the nasal septum and the lateral walls of the main airway are mineralized (Figs 2 and 3). There is no suture that distinguishes the mineralized septum and walls of the main airway from any of the cranial elements, including the ethmoidal complex, nasal, frontal and lacrimal, which they contact. The nasal septum and the lateral walls converge at the midline anterior to the ethmoidal complex. There is no opening that connects the dorsomedial passage of the main airway with the endocranial cavity. The skull roof is damaged and does not preserve the ventral part of the main airway. On the right side of the skull, however, the preserved part of the lateral wall extends ventromedially. This suggests that the mineralized wall wrapped around the dorsomedial passage of the main airway ventrally as well as laterally and medially. The anterior wall of the olfactory region extends lateromedially between the lateral wall of the main airway and the lacrimal. The anterior wall separates the olfactory region and the groove filled with the vascularized tissue from the cavity that housed the posterior loop of the main airway anteriorly (Witmer & Ridgely, 2008).

### Sphenoidal region

The orbitosphenoid contacts the ectethmoid anterolaterally and the ethmoidal complex (sphenethmoid + mesethmoid)

anteriorly (Figs 2 and 7). The olfactory fenestra opens between these two contacts. The olfactory nerves (CN I) would have diffused from this fenestra to both lateral and medial sides of the descending process. The orbitosphenoid contacts the laterosphenoid posteriorly and the parasphenoid ventrally. The laterosphenoid is short anteroposteriorly, but has a long, laterally oriented postorbital process that is approximately half the width of the transversely expanded ankylosaurid skull. The element is firmly fused to the skull roof. Two other sets of foramina pierce the orbitosphenoid. The foramen for the optic nerve (CN II) is larger than all other foramina for the cranial nerves except the olfactory fenestra and consists of a single exit (Fig. 7). The shared foramen for the oculomotor (CN III) and trochlear (CN IV) nerves opens posterior to the optic foramen. The foramen for the abducens nerve (CN VI) opens directly ventral to the oculomotor/trochlear foramen, which is consistent with these foramina transmitting motor nerves to the extraocular muscles.

In the laterosphenoid, the foramen for the trigeminal nerve (CN V) is posterior to the oculomotor/trochlear foramen. Just dorsal to the trigeminal foramen is an aperture for the anterior middle cerebral vein. The trigeminal foramen is anteroventral with respect to the lateral wing of the braincase (pila antotica) that contacts the postorbital laterally. In addition, the trigeminal nerve is associated with the prootic in sauropsids. Although no suture can be observed between the laterosphenoid and prootic, the topographical relationships of the trigeminal foramen with other braincase landmarks suggest that the foramen was mainly within the laterosphenoid with contribution from the prootic posteriorly. This implies that the prootic extended anteriorly

below the lateral wing of the laterosphenoid. This interpretation is supported by the location of the foramen for the facial nerve (CN VII), which is located completely within the prootic in sauropsids and is just posteroventral to the trigeminal foramen.

### Occipital region

Most of the elements of the occipital region are highly ossified and fused to each other. The squamosal and parietal form a roof over a chamber for *M. adductor mandibulae posterior* (Holliday & Witmer, 2007). The otic region is anteroposteriorly short, and the prootic and the opisthotic are indistinguishably fused together. The well developed crista interfenestralis separates the fenestra vestibularis anteriorly and the jugular foramen posteriorly (Fig. 7). The posterior foramen for the hypoglossal nerve (CN XII) opens laterally at the base of the occipital condyle, whereas the anterior foramen for the hypoglossal nerve is merged to the posteroventral corner of the jugular foramen. In *Amtosaurus*, there are three foramina for the hypoglossal nerve (Averianov, 2002). In occipital view, the osteoderms overhang from the skull roof elements (Fig. 6). The foramen magnum is taller than it is wide and the margin is inflated into a rim. The crescentic occipital condyle is oriented posteroventrally.

### Cranial endocast

The description of the cranial endocasts focuses on AMNH 5405, which has the best preserved braincase amongst the specimens used in this study. The newly prepared cranial endocasts (AMNH 5405, UALVP 31 and UALVP 47977; Fig. 7) compare well with the published description of the cranial endocast of AMNH 5337 (Coombs, 1978a). In all specimens, the brains were anteroposteriorly short but relatively straight. The cranial endocast of UALVP 31 has a blockier, more robust appearance than that of AMNH 5405, because of the lower resolution of the CT data for UALVP 31. The endocast is also more strongly bowed dorsoventrally compared to the other specimens, but this is probably a result of taphonomic distortion of the skull. The anteroposterior shortening of the olfactory stalk partly accounts for the short anteroposterior length of the cranial endocasts of *Euoplocephalus*. The anteroposterior distance between the olfactory fenestra and the root of the optic nerve is less than a quarter the entire anteroposterior length of the cranial endocast in *Euoplocephalus*, whereas the distance is typically more than a third the length of the cranial endocast in other dinosaurs (based on figures in Hopson, 1979; Brochu, 2002; Sampson & Witmer, 2007; Witmer et al. 2008).

The olfactory bulbs diverge immediately anterior to the cerebrum at an angle of 80–100° and lead to the olfactory fenestra opening at the posteromedial end of the olfactory region. A general condition for ornithischian dinosaurs is

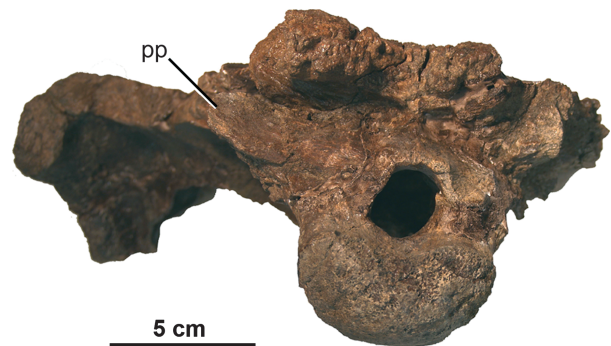
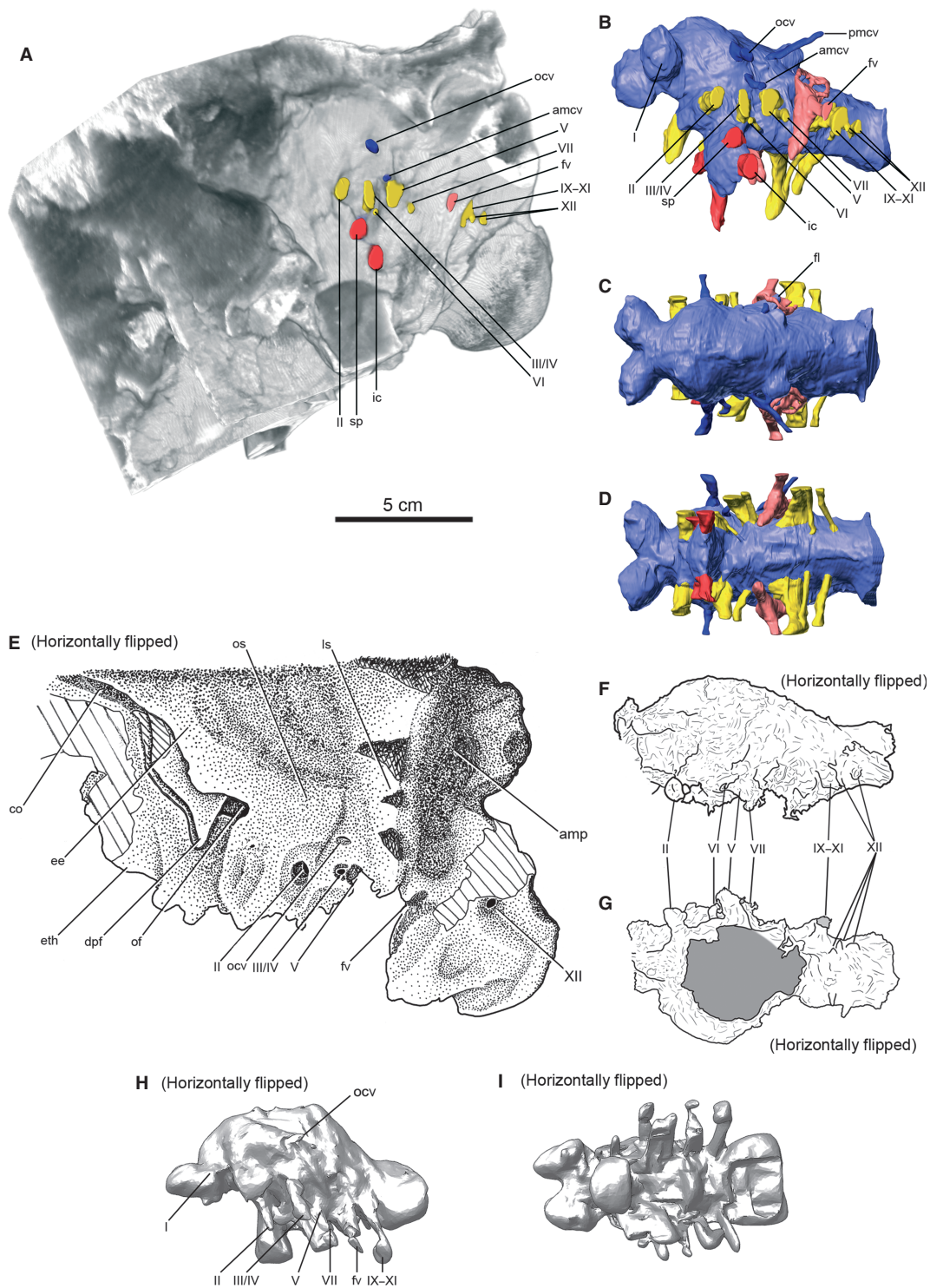


Fig. 6 UALVP 47977 (*Euoplocephalus*) in occipital view. For abbreviations, see Fig. 5.

that the olfactory tracts did not diverge as strongly anterolaterally as in *Euoplocephalus* (Hopson, 1979; Galton, 1983, 1988, 1989, 1997, 2001; Evans et al. 2009). The cerebral hemispheres are fairly discrete on the endocast, forming a rounded swelling immediately posterior to the olfactory tract. As is often the case in non-coelurosaurian dinosaurs (Witmer & Ridgely, 2009), however, other major neural structures such as the optics lobes and cerebellum are largely obscured by the dural envelope. An important exception is the flocculus (cerebellar auricle). The flocculus on the endocast of AMNH 5405 extends posterolaterally as a substantial, finger-like projection into the region of the inner ear and breaks the plane of the anterior semicircular canal. The presence of a flocculus in AMNH 5405 clears up the discrepancy in the reports on AMNH 5337 between Coombs (1978a: no flocculus) and Hopson (1979: large flocculus) in favor of the latter interpretation. The structure interpreted as an epiphysis cerebri (= pineal gland) projecting from the diencephalon noted in AMNH 5337 by Coombs (1978a) is also present in the endocasts of UALVP 31 and AMNH 5405, but is not visible in the endocast of UALVP 47977. Although being small, this structure is in the position to be the epiphysis. Epiphyses are present in extant birds and have been reconstructed in some dinosaurs (e.g. some theropods; Witmer & Ridgely, 2009). The lack of the epiphysis in UALVP 47977 is probably due to the presence of plaster infilling, which was used to strengthen the cracks during preparation of this specimen.

As already noted in the braincase description, the optic nerves in the endocast project almost directly laterally, such that the optic chiasm is oriented transversely rather than anterolaterally as in other archosaurs. The shared exit for the oculomotor and trochlear nerves is a large trunk directly posterior to the optic nerve. Both Coombs (1978a) and Hopson (1979) interpreted the smaller twig dorsal to the definitive oculomotor nerve canal as the trochlear nerve. This interpretation was widely accepted in the subsequent ankylosaur literature and the corresponding foramen was identified as that for the trochlear nerve in *Amtosaurus* (Averianov, 2002), *Saichania* (Maryańska, 1977), *Sauropelta*



**Fig. 7** Comparison of cranial endocasts and that of braincases reveals minor variation amongst specimens referred to as *Euoplocephalus*. The braincase of AMNH 5405 in left lateral view (A), the cranial endocast of the same specimen in left lateral (B), dorsal (C) and ventral (D) views, the braincase of UALVP 47977 in right lateral view (E), the cranial endocast of the same specimen in right lateral (F) and ventral (G) views, and the cranial endocast of UALVP 31 in right lateral (H) and ventral (I) views. The images E–I were all inverted horizontally to show the right sides in the same orientation with the left side of AMNH 5405 for the purpose of comparison. In both UALVP 47977 and UALVP 31, the right side is better preserved. UALVP 47977 is represented by a line drawing of a latex cast, and AMNH 5405 and UALVP 31 are 3D models based on CT data. Roman numerals refer to either the foramen for, or the trunk of, the cranial nerve. amcv, anterior middle cerebral vein; amp, insertion site for *M. adductor mandibulae posterior*; *sensu* Holliday & Witmer, 2007; fl, flocculus; fv, fenestra vestibularis; ic, internal carotid artery; ocv, orbitocerebral vein; of, olfactory fenestra; pmcv, posterior middle cerebral vein; sp, sinus of pituitary. For other abbreviations, see Figs 1 and 2.



and *Tatankacephalus* (Parsons & Parsons, 2009). We instead regard their putative trochlear nerve as an orbitocerebral vein. In the endocast of AMNH 5405, the 'trochlear nerve' of Coombs (1978a) and Hopson (1979) is comparable to the orbitocerebral vein canals of sauropods (Serenio et al. 2007; Witmer et al. 2008), theropods (Sampson & Witmer, 2007; Witmer & Ridgely, 2009) and other dinosaurs. This feature in AMNH 5405 emerges from the lateral pole of the cerebral region and opens into the orbit well dorsal to the canals for the other nerves supplying the extraocular muscles.

The trunk of the oculomotor nerve in this study was identified by Coombs (1978a) as being associated with the pituitary vein. Indeed, this canal shared by the trochlear and oculomotor nerves seems too large to have transmitted only these two small nerves. It is likely that veins also traversed this canal. However, the term 'pituitary vein' is not appropriate because the venous drainage of the pituitary was almost certainly within the pituitary fossa itself and the cavernous sinus within (see Sampson & Witmer, 2007). The trunk of the abducens nerve originates from the ventral side of the brain below the trigeminal nerve and passes anterolaterally below the oculomotor and trochlear nerves.

The fossa for the pituitary gland projects more or less straight ventrally in all the specimens as a bulbous structure. In AMNH 5405, the bulbous structure is twice as wide transversely as long anteroposteriorly. Ventral to the pituitary, the endocast of the internal carotid artery is oriented ventrolaterally, whereas the artery extended anterodorsally in the cranial endocasts of other dinosaurs (Hopson, 1979; Witmer et al. 2008). The pituitary in UALVP 31 expands posteriorly, but this is most likely a result of damage to the ventral portions of the braincase. The pituitary fossa of AMNH 5405 also preserves large paired apertures dorsal to the carotid canals, which almost certainly transmitted the sphenoid branch of the carotid artery into the floor of the orbit as well as receiving ophthalmic veins.

The single trunk of the trigeminal nerve indicates that the branches diverged outside the endocranial cavity. The endocast of this nerve is dorsoventrally taller than anteroposteriorly long, suggesting that the canal housed the ganglion, as in most dinosaurs except for tyrannosaurids and birds (Witmer et al. 2008). The anterior middle cerebral vein is preserved above the trigeminal nerve in the cranial endocast of AMNH 5405 (Fig. 7C). The trunk of the facial nerve originated from the shallow recess shared with that of the vestibulocochlear nerve (CN VIII). The course of the facial nerve closely parallels that of the trigeminal nerve anteriorly and laterally, and diverges away from that of the vestibulocochlear nerve. The trunk of the vestibulocochlear nerve has two branches that separate from each other immediately outside the endocranial cavity. The dorsal branch is directed laterally toward the vestibule and the ventral one toward the cochlear ventrally. The trunks of the glossopharyngeal, vagus and accessory nerves (CNs IX–XI)

exit the endocranial cavity through the jugular foramen. The jugular foramen is directly anterior to the foramen for the posterior branch of the hypoglossal nerve. AMNH 5405 has two trunks for the hypoglossal nerve, although there are possibly three trunks for this nerve in AMNH 5337 (Coombs, 1978a) and UALVP 47977 (Fig. 7). Even in the case of three trunks, the proximity and directions of the two smaller anterior trunks suggest that they likely joined to emerge from a single external foramen. In AMNH 5405, the foramen for the anterior trunk of the hypoglossal nerve is merged to the posteroventral corner of the jugular foramen. The foramen for the larger posterior trunk opens directly posterior to the jugular foramen on the lateral surface of the base of the occipital condyle.

The labyrinth of the inner ear is reasonably well preserved on the left side of AMNH 5405 and is generally similar to the one illustrated for AMNH 5337 by Hopson (1979). The lateral semicircular canal is extremely reduced, more so than in perhaps any dinosaur described to date. The anterior canal may seem somewhat elongate but this may result more from the constraint that the anterior canal must pass around the flocculus (Witmer et al. 2003). The cochlea is remarkably elongate in AMNH 5405, as illustrated also for AMNH 5337 by Hopson (1979). The elongate cochlea suggests that hearing was an important sense in *Euoplocephalus*.

## Discussion

A combination of direct visual observation of several partial specimens (in particular AMNH 5238 and UALVP 47977) and CT-based digital reconstructions (AMNH 5405, ROM 1215, UALVP 31) makes the data gained through either technique interchangeable. The osteological data from UALVP 47977 agree with the reconstruction by Witmer & Ridgely (2008) and complement it by adding fine-scale details (such as the vascular impressions in the dorsomedial part of the nasal cavity) that cannot be imaged using most medical CT scanners. Coupled with the previous observation of large vascular canals in an ankylosaurid nasal cavity based on CT data (Witmer & Ridgely, 2008), the vascular impressions (Fig. 3) provide further evidence of extensive vascularization in the nasal cavities of ankylosaurids. The medial neurovascular canal near the nasal septum is consistent with the medial nasal vessels and nerves, which extend along the nasal septum under the skull roof in both crocodylians and birds (Sedlmayr, 2002; Witmer & Ridgely, 2008). Similarly, the lateral canal presumably represents the lateral nasal vessels and nerves. Tumanova (1987) identified a groove that extends anteroposteriorly along the dorsolateral part of the nasal septum in *Talarurus* as the olfactory nerve impression. The groove does not represent the olfactory nerve because the dorsomedial passage of the nasal cavity is not olfactory. The current evidence suggests that the groove in *Talarurus* is a channel of the medial nasal vessels and nerve. The

presence of the vascular impressions on the dorsal roof of the nasal cavity proper indicates the mucosa of the cavity was appressed to the surfaces of the osseous walls. This makes it more certain that the shape and volume of the nasal cavity can be estimated from the osseous walls.

### Osteological correlates in the olfactory region

Substantial evidence has now accumulated for the presence of the olfactory region in the cavity lateral to the dorsomedial passage of the main airway (Witmer & Ridgely, 2008; this paper). Based mainly on UALVP 47977, the cavity for the olfactory region can be divided into three main parts: (i) the hollow descending process; (ii) the groove along the lateral wall of the main airway associated with a sulcus along its medial margin and vascular impressions at the anterolateral end; and (iii) the space characterized by the smooth surface on the ventral side of the frontal and bound by the groove and the ectethmoid laterally. Miyashita & Arbour (2007) initially hypothesized that the descending process and the groove were occupied by the nasolacrimal canal. If the process and the groove represented an impression of the nasolacrimal canal, the canal must have extended posteriorly, which would be a novel pathway amongst vertebrates. Embryologically, the nasolacrimal canal passes anteriorly between the frontonasal process and maxillary eminence along the developing nasal cavity (Parsons, 1959; Romanoff, 1960; Witmer, 1995). This is not the case for the tissue filling the descending process and the groove within the cavity for the olfactory region. Therefore, it is unlikely that the nasolacrimal canal filled the process and the groove. Another possible explanation is that this groove housed a salt gland, such as those found anterior to the orbits in crocodylians. However, the salt gland hypothesis is also unlikely because in crocodylians this structure is typically large, teardrop-shaped and composed of many smaller lobules (Fernandez & Gasparini, 2008).

Alternatively, the descending process in UALVP 47977 may represent a mineralized posterior wall of the olfactory turbinate, and the groove associated with the process may be an impression of the mucosal concha. The position of the descending process immediately lateral to the olfactory fenestra supports this hypothesis. Witmer & Ridgely (2008) also note scroll-like olfactory turbinates in this region in both *Euoplocephalus* and *Panoplosaurus*. The olfactory nerves would have innervated the concha from both lateral and medial sides. The turbinate hypothesis is also consistent with the vascular impressions at the anterolateral end of the groove. It is uncertain whether tissues other than the concha (and its turbinate) also participated in filling in this groove. The posterior conchae of birds are likely a homologue of the conchae of crocodylians, whereas the postconchae of crocodylians are probably a neomorph (Witmer, 1995). Therefore, it is equally plausible that the descending process housed the posterior concha homologous with

those of birds or the postconcha homologous with those of crocodylians.

The observed branching strongly suggests that the tunnel in AMNH 5405 (Fig. 4) was filled by blood vessels. It is likely that the same vessels were associated with the groove in the olfactory region of UALVP 47977, as the vascular impression at the anterolateral end of the groove implies. Perhaps the tunnel in AMNH 5405 is the groove in the olfactory region partly enclosed within the skull roof. If this were the case, the groove would not be an impression of the concha. Instead, the most likely candidate for filling the groove would be a venous sinus. However, the sheer size of the groove precludes the possibility that the groove was entirely an impression of the venous sinus. Furthermore, the descending process indicates that the tissue filling the groove extended ventrally, a morphology not seen in the venous system in the olfactory regions of living archosaurs. Although morphological variation in the olfactory region of *Euoplocephalus* and small sample size allow different interpretations, it is proposed here that the groove associated with vascular impressions in the olfactory region of UALVP 47977 represents the concha, olfactory turbinate and its associated blood vessels. There is no impression in the smooth dorsal surface along the ectethmoid that indicates tissues adjacent to the bone.

The area of the dorsal surface of the olfactory cavity in UALVP 47977 indicates that the olfactory region probably occupied a volume larger than the endocranial cavity. It is tempting to link this large volume of the cavity with increased olfactory acuity. Indeed, the olfactory bulbs of *Euoplocephalus* seem somewhat enlarged relative to the cerebral hemispheres but have not been subjected to the kind of quantitative analysis that has been done for theropods (Zelenitsky et al. 2009, 2011). The olfactory bulb in each of the cranial endocasts of *Euoplocephalus* is medio-laterally wide and dorsoventrally tall. Taken together, these findings suggest that olfaction was an important sense for *Euoplocephalus*, but we regard this as provisional until we can put these data in a broader comparative context.

### Functional implications of the looping nasal cavity

In addition to the large cavity for the olfactory region, the looping main airways reconstructed for ankylosaurs (Witmer & Ridgely, 2008) call for functional explanations. The olfactory nerves do not exit into the dorsomedial passage of the main airway, but extend into the cavity lateral to the main airway. Therefore, the olfactory region was outside the looping pathway of the main airway (Witmer & Ridgely, 2008). This suggests that increased olfactory acuity was not the primary selective pressure for the unusual looping of the main airway of *Euoplocephalus*.

The looping main airway in *Euoplocephalus* may have evolved to increase the surface area within the nasal

cavity for other functions, including thermoregulation or osmoregulation. It has previously been hypothesized that an antelope bovid (*Saiga tatarica*) uses its unusually large nose as a counter-current heat exchanger (Frey & Hofmann, 1997). However, Clifford & Witmer (2004) instead supported an alternate hypothesis that the nose acts as a filter for particulate matter. This is unlikely to be the function of the looping nasal passage of ankylosaurids because the small narial opening in *Saiga* opens into a large chamber that slows the velocity of inhaled dust particles, a morphology not seen in *Euoplocephalus*. Most fundamentally, the looping nasal passage of ankylosaurs results in a dramatic increase in the surface area of the respiratory mucous membrane (Witmer & Ridgely, 2008). Extant mammals and birds expand the mucosal surface area by the development of variously branched and scrolled conchal structures, which have been shown in numerous studies to act as intermittent counter-current heat exchangers, playing a key role in heat and water balance (e.g. Schmidt-Nielsen et al. 1969, 1970; Ruben, 1996; Geist, 2000; Van Valkenburgh et al. 2011), although the situation is clearly complex (Tieleman et al. 1999; Van Valkenburgh et al. 2004; Nelson et al. 2007). Thus, it is reasonable to suggest that the increased surface area conferred by the elongate ankylosaur nasal passage may have been an alternate morphological solution with comparable physiological functions, which is consistent with the evidence for extensive nasal blood supply. UALVP 47977 shows extensive vascularization in the nasal cavity, although the vascular impressions are found in the narrow, posterior part of the airway medial to the olfactory region. The looping part of the nasal cavity was also extensively irrigated in other specimens of *Euoplocephalus* and in *Panoplosaurus* (Witmer & Ridgely, 2008). With the evidence of extensive vascularity, nasal mechanisms for regulating heat and water balance remain possible selective forces for the looping main airway of *Euoplocephalus*. Indeed, regardless of whether nasal elongation evolved specifically for these physiological reasons, it is hard to imagine how such an extensive, moist surface with air passing over it would not be participating in these physiological functions.

Witmer & Ridgely (2008) also suggested that the looping nasal passages may have played a role in vocal resonance. In addition to using their unusual noses for removing inhaled dust, rutting males of *Saiga tatarica* tense and elongate the nasal vestibulum anteriorly to lengthen the vocal tract for nasal roaring and thereby produce a lower call (Frey et al. 2007). Many birds, such as cranes and swans, have looping tracheas that achieve the same effect, which exaggerates the body size of the caller in intraspecific display during mating (Fitch, 1999). The lengthening and looping of the nasal passages while retaining relatively small olfactory areas have been used to support an acoustic function in the cranial crests of lambeosaurine hadrosaurid dinosaurs (Weishampel, 1981; Evans, 2006; Evans et al. 2009). Simi-

larly, the complexity of the ankylosaur nasal passage may have lowered the frequency of nasal roars. Moreover, the finding here of an elongate cochlea in AMNH 5405 is consistent with this vocalization hypothesis, as argued as well for lambeosaurines (Evans et al. 2009).

In comparison with other ornithischians, the skull in ankylosaurids is shorter, but the looping of the nasal cavity more than compensated for the short skull length (Witmer & Ridgely, 2008). This strongly suggests that there is a functional advantage in maintaining or increasing high volume and surface area of the nasal cavity in ankylosaurids. This inverse correlation between skull length and nasal cavity complexity may be interpreted partly as a response to the reduction in the skull length to width ratio in ankylosaurids. The net result of the change in ratio is profound in the morphology of the ankylosaurid skull. The braincase is reduced in anteroposterior length relative to its width (Coombs, 1978a; Hopson, 1979); the trunks of the cranial nerves are oriented predominantly lateroventrally; the maxilla houses a large cavity (Coombs, 1978b; Maryańska, 1978; Witmer, 1997) for the loops of the main airway (Witmer & Ridgely, 2008); the olfactory region sits in a large cavity lateral to the dorsomedial part of the airway (Witmer & Ridgely, 2008); and the orbital depression is anteroposteriorly elongate, with the orbit in an anterior position in the skull (relative to positions in other ornithischians), whereas its medial end shifts posteriorly to align with the exit of the optic nerve from the anteroposteriorly shortened braincase. In contrast, lambeosaurine hadrosaurids achieved elongation of the main airway partly by developing a prominent crest over the skull roof (Weishampel, 1981; Evans, 2006; Evans et al. 2009). The development of different arrangements in ankylosaurids and lambeosaurines suggests widespread benefits of looping nasal passages amongst ornithischian dinosaurs.

### Identification of the ethmoidal elements

The ethmoidal elements of ankylosaurids are extensively ossified. The mesethmoid and the sphenethmoid form the ethmoidal complex (Fig. 2). The ectethmoid separates the orbital depression from the olfactory region. There is no direct evidence that the ethmoidal complex consists of two mineralized elements rather than a single one. Only the sphenethmoid (generally referred to as presphenoid in ornithischians) is mineralized and forms the lateral and ventral walls of the olfactory bulbs in hadrosaurids (Evans, 2006), which lack the ossified median septum between the olfactory bulbs (= mesethmoid). A mineralized sphenethmoid and a cartilaginous median septum seem to have also been present in pachycephalosaurids (pachycephalosaurid skull caps in TMP and UALVP; e.g. TMP 84.5.1; TMP 92.88.1). Based on these observations, it is highly likely that there are two distinct centres of mineralization (a mesethmoid and a sphenethmoid) in the cartilaginous capsule enveloping the

olfactory bulbs in ornithischians. Therefore, the midline ethmoidal ossification in UALVP 47977 is treated as a complex of the mesethmoid and the sphenethmoid.

The ectethmoid is part of the interorbitalis of Vickaryous & Russell (2003), the sphenethmoid of Vickaryous et al. (2004) or the anterior orbital wall of Carpenter (2004). A large part of the interorbitalis of Vickaryous & Russell (2003, Fig. 5A), however, clearly represents the orbitosphenoid, which renders the term interorbitalis redundant. In birds, an ectethmoid divides the antorbital cavity and the orbit, forming the posterior wall of the olfactory region (Witmer, 1995; Ali et al. 2008). Amongst dinosaurs, pachycephalosaurids (observed in UALVP 2, *Stegoceras* and UALVP casts of *Prenocephale* and *Homalocephale* holotype skulls) have ossified ectethmoids in the same position as the thin sheet of bone that forms the anteromedial wall of the orbit in UALVP 47977. The olfactory nerve passes through neither the ectethmoid nor the orbitosphenoid (both under the name 'interorbitalis') as Vickaryous & Russell (2003) suggested; it penetrates the sphenethmoid medial to the ectethmoid. In pachycephalosaurids (TMP 84.5.1; UALVP 2), the ectethmoid seems to contact the sphenethmoid posteriorly, but not the orbitosphenoid. Sanders & Smith (2005) used the term ectethmoid to describe an ossified element enveloping the olfactory tract in the ethmoidal region of the theropod *Ceratosaurus magnicornis* but this element is a sphenethmoid based on its position.

In the dorsomedial part of the anterior part of the main airway, it has been the general assumption that the ossified nasal septum in ankylosaurs is an extension of the nasal (Tumanova, 1987; Vickaryous & Russell, 2003; Vickaryous, 2006) with contributions from the premaxilla and vomer (Maryńska, 1977; Hill et al. 2003). In mammals, however, the nasal septum is largely mineralized anteriorly from the junction of the septoethmoid and septopresphenoid (Wealthall & Herring, 2006). Where mineralization occurs in tetrapods, the nasal septum is always endochondral. In birds, the nasal septum (confluent with the interorbital septum) develops from the trabecula communis (Zusi, 1993; Witmer, 1995). In crocodiles, the cartilaginous nasal septum represents a ventral part of the tectum nasi and an anterior and medial part of the planum supraseptales, within the homologue of which the mesethmoid of birds develops (Bellairs & Kamal, 1981; Klembara, 1991; Ali et al. 2008). Comparison with extant taxa suggests that the mineralized ankylosaurid nasal septum is largely the endochondral element. However, the endochondral nature of the entire nasal septum is incompatible with the observation that at least the premaxilla (a dermal bone) forms the anterior part of the nasal septum in ankylosaurids (Maryńska, 1977; Hill et al. 2003).

### Comparative morphology of ankylosaurid crania

The ankylosaurids with skulls showing internal structures include: *Euoplocephalus* (Vickaryous & Russell, 2003; Wit-

mer et al. 2008) from the Late Cretaceous of western North America; *Pinacosaurus* (Maryńska, 1971; Hill et al. 2003), *Saichania* (Maryńska, 1977), *Talarurus* (Tumanova, 1987) and an unidentified ankylosaurid (MPC PJC 2000.24), all from the Late Cretaceous of Mongolia; *Gobisaurus* (Vickaryous et al. 2001) from the Early Cretaceous of Asia; and *Cedarapelta* (Carpenter et al. 2001) and *Takantacephalus* (Parsons & Parsons, 2009) from the Early Cretaceous of North America. Overall, the skull is internally better ossified in UALVP 47977 (*Euoplocephalus*) than in the other ankylosaurid skulls. The characters discussed in this section seem to be independent of body size as some of the skulls compared here (e.g. MPC PJC 2000.14) are larger than UALVP 47977.

*Talarurus* has a relatively narrower skull than that of UALVP 47977. This is evident from the fact that the cavity for the olfactory region is more anterior in position than the orbital depression. In UALVP 47977, the orbital depression extends anterolaterally and separates the cavity for the olfactory region medially from the facial elements. The cavity for the main airway extends posteriorly to the orbit in UALVP 47977, whereas it is anterior to the orbit in *Talarurus*. The nasal septum is well developed in all the ankylosaurids that have been compared in this study. On the other hand, the lateral wall of the dorsomedial passage of the main airway is only defined by a low ridge in *Saichania* (Fig. 9 in Maryńska, 1977), *Pinacosaurus* (Pl. 27 in Maryńska, 1977) and MPC PJC 2000.14. In contrast, the thickly ossified walls separate the main airway from the olfactory region in UALVP 47977 and *Talarurus*. The fully mineralized lateral wall of the dorsomedial passage of the main airway is probably a universal condition in *Euoplocephalus* because Coombs (1978b) notes this wall and because CT images show a thick bony structure in each of the corresponding regions of TMP 1997.32.1 (Vickaryous & Russell, 2003), AMNH 5405 and UALVP 31. The variable degrees of development of the septa and walls amongst these taxa suggest that the septum mineralized independently from the lateral and posterior walls and that the mineralization of the lateral and posterior walls was regulated separately.

The descending process is less robust in an unidentified ankylosaurid from Mongolia (MPC PJC 2000.14) than in UALVP 47977. It merely amounts to a fold of a thin sheet of bone in this ankylosaurid. This is also the case for *Saichania* (Fig. 9 in Maryńska, 1977; labeled as 'ethmoid'). In *Talarurus* (PIN 3780/1), Tumanova (1987) illustrated and described a lamina, which extends from the anterior margin of the olfactory region along the lateral wall of the dorsomedial passage of the main airway. This lamina was labeled as the anterior transverse lamina by Tumanova (1987, Fig. 5) and is also visible in a photograph of the same specimen (Carpenter, 2004; Fig. 3). The location and orientation suggests that it represents the same groove in the olfactory region as in UALVP 47977. *Pinacosaurus grangeri* (ZPAL MgD II/1) differs

significantly from UALVP 47977 in this region. It lacks a descending process but possesses concave ridges that Maryńska (1971) interpreted as possible turbinates. The tunnel within the skull roof of *Euoplocephalus* (AMNH 5405) might have been present in other ankylosaurids that lack an anterolateral groove on the ventral surface of the skull roof in the olfactory region, if the groove or the tunnel is functionally associated with the descending process. However, no exits for the tunnel have been described or can be seen in illustrations of *Cedarpelta*, *Pinacosaurus*, *Saichania* or MPC PJC 2000.14, which suggests that the tissue filling the groove in UALVP 47977 was separate from the skull roof in each of these taxa.

Potential intraspecific variation occurs in the olfactory region of *Euoplocephalus*. The tunnel in AMNH 5405 (Fig. 4) cannot be identified in UALVP 47977. This suggests that a tunnel like that in AMNH 5405 may have formed as a result of partial enclosure of the groove found in the olfactory region of UALVP 47977. On the other hand, the descending process is conspicuous in UALVP 47977, whereas the process is smaller in AMNH 5405. It is uncertain if the differences were due to individual, ontogenetic, taxonomic or taphonomic variation. Although UALVP 47977 is currently best referred to *Euoplocephalus*, it could also be *Dyoplosaurus*, another ankylosaurid from the Dinosaur Park Formation (Arbour et al. 2009).

Intraspecific variation in cranial endocasts has been documented in the opossum *Monodelphis domestica* (Macrini et al. 2007) and oreodonts (Macrini, 2009). The proportions of cranial endocasts can vary among individuals and as a result of ontogeny (Macrini et al. 2007). Witmer et al. (2008) also showed that the morphology of the dural expansion varies in *Diplodocus*. The dural expansion is not conspicuous in the cranial endocasts of *Euoplocephalus* (Fig. 7). The variation in *Euoplocephalus* cranial endocasts results primarily from taphonomic distortion and limited resolution of CT scanning. None of the variations in the *Euoplocephalus* cranial endocasts described here are likely to be taxonomically informative. This does not entirely reject an influence of ontogeny on morphology of the endocranial cavity in *Euoplocephalus*, because the cranial endocasts compared here do not differ substantially in size. Nonetheless, the fact that the adult-sized cranial endocasts do not substantially vary in morphology implies that a single cranial endocast of an adult is likely sufficiently to represent a general condition for the taxon, provided that the endocranial cavity has not been taphonomically distorted.

## Conclusions

A combination of direct osteological observation and CT-based reconstruction provides corroborating, complementary evidence for the nasal and endocranial soft tissues and braincase morphology of the ankylosaurid dinosaur

*Euoplocephalus*. A partial skull roof (UALVP 47977) reveals vascular impressions in the nasal cavity, an unusual descending process (likely representing a turbinate) and deep groove possibly associated with the concha and the olfactory fenestra. The fenestra demonstrates that the cavity beside the dorsomedial passage of the main airway housed the olfactory region, which is directly anterior to the endocranial cavity in non-ankylosaur dinosaurs. The ethmoidal region preserves the ethmoidal complex (mesethmoid + sphenethmoid), the ectethmoid and mineralized walls of the nasal cavity. The neurovascular foramina of the braincase were re-interpreted. CT-based reconstructions of other specimens of *Euoplocephalus* show that many conspicuous osteological correlates are present in these specimens. Manually and digitally prepared cranial endocasts show minor variation within the taxon. Therefore, a single cranial endocast is likely to represent a general condition for a taxon. Two parts of the nasal cavity are unusual in ankylosaurids: the looping main airway and the large cavity for the olfactory region. The elongate, looping nasal cavity in ankylosaurid dinosaurs is not an adaptation for enhanced olfaction, but likely had thermo- and osmoregulatory benefits. An acoustic function is also possible. It is likely that the improved olfactory acuity is correlated with the increased volume of the cavity for the olfactory region in ankylosaurids, which is consistent with the size of the olfactory bulb, although the olfactory hypothesis requires corroborative evidence. These hypothesized functions suggest that multiple functional drivers may explain morphology in different parts of the ankylosaurid nasal cavity. The nasal osteological correlates are expressed or preserved differently in other ankylosaurid dinosaurs, which invites extensive interspecific comparison.

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## Author contributions

T.M., V.M.A. and L.M.W. are responsible for study design, data acquisition and analysis. All authors contributed to drafting of the manuscript. T.M. drew Figs 1, 2, 4 and 7E, V.M.A. prepared Figs 3, 5 and 7F–I, and L.M.W. contributed Fig. 7A–D.

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