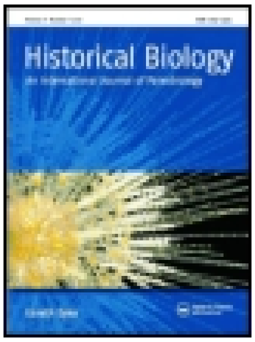

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ARTICLE

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Endocranial morphology of *Auroraceratops* sp. (Dinosauria: Ceratopsia) from the Early Cretaceous of Gansu Province, China

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ABSTRACT
Fossils of *Auroraceratops* are abundant and found in high concentrations within the Mazongshan area of northwestern China. As small basal Neoceratopsia discovered from the Lower Cretaceous, its general anatomy is well known; however, the endocranial morphology of this genus has never been formally described before. Here, we selected a well-preserved skull which belongs to *Auroraceratops* sp. and used a high-resolution CT scan to reconstruct its three-dimensional, virtual endocast in order to illustrate the endocranial structures in detail. Our study provides the first description of the endocranial anatomy of *Auroraceratops* and compares it with other relevant ceratopsian taxa. Our result shows that for a basal Neoceratopsia, the endocranial morphology of *Auroraceratops* is closer to that of non-neoceratopsian ceratopsian *Psittacosaurus* than the more derived neoceratopsians, such as *Pachyrhinosaurus*, which provides new insight into the endocranial characters of basal Neoceratopsia.

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Auroraceratops; cranial endocast; computed tomography scan; endocranial morphology; three-dimensional reconstruction

Introduction

Most of globally known basal neoceratopsian dinosaurs were found in China. The Lower Cretaceous in the Mazongshan Area of Gansu province in northwestern China has yielded four species within two genera of basal Neoceratopsia, which includes *Archaeoceratops oshimai* (Dong and Azuma 1997), *Archaeoceratops yujingziensis* (You et al. 2010), and *Auroraceratops rugosus* (You et al. 2005), *Auroraceratops* sp. (You et al. 2012). *Auroraceratops*, a small neoceratopsian, was recovered from the upper red beds of the Lower Cretaceous Zhonggou Formation, and the fossil beds exposed were interpreted as Albian age of the Early Cretaceous (Tang et al. 2001; Li 2008; Peng 2013). The Mazongshan Area of northwestern China yields a wide range of dinosaur taxa, including members of Theropoda, Sauropoda, Ankylosauridae, Euornithopoda, and Ceratopsia (You and Luo 2008). This group belongs to the Mazongshan dinosaur assemblage which has several unique characteristics in both lithology and fauna (Zhang et al. 2015), and the area is a significant source of dinosaur fossils from the Early Cretaceous of northern China.

Previous researches of neoceratopsian have been limited to descriptions of the external morphology of their skeletons while endocranial structures are rarely published. The endocranial morphology of ceratopsian dinosaurs remains poorly understood with only *Psittacosaurus* (Zhou et al. 2007) and *Pachyrhinosaurus* (Witmer and Ridgely 2008) being formally described. Here we describe a digital endocast of a well-preserved *Auroraceratops* sp. skull created by high-resolution X-ray computed tomography scanning. Additionally, we provide the first reconstruction of endocranial structures of *Auroraceratops* and compare it to ceratopsian endocrania previously produced.

Institutional abbreviations

AMNH: American Museum of Natural History; CAS: Chinese Academy of Science; GSGM: Gansu Geological Museum; PKUP: Peking University Paleontological Collections; TMP: Royal Tyrrell Museum of Palaeontology.

Anatomical abbreviations

ac: anterior semicircular canal; bo: basioccipital; bt: basal tubera; cbl: cerebellum; cc: crus commune; cer: cerebrum; ec: ectopterygoid; ej: epijugal; exo: exoccipital; fm: foramen magnum; ic: internal carotid artery; j: jugal; jh: jugal horn; l: lacrimal; lc: lateral semicircular canal; m: maxilla; mo: medulla oblongata; ob: olfactory bulb; oc: occipital condyle; ot, olfactory tract; p, parietal; pc, posterior semicircular canal; pit, pituitary fossa; pl: palatine; pm: premaxilla; pop: paroccipital process; pt: pterygoid; q: quadrate; qj: quadratojugal; qpt: pterygoid ramus of the quadrate; sq: squamosal; so: supraoccipital.

Material and method

Fossil specimen

The *Auroraceratops* sp. specimen (GSGM-FV-00500) used in this study was first described by You et al. (2012). The specimen

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is a partially articulated skeleton which includes the skull and lower jaw, and it was collected from a site located in northern Yujingzi Basin (Figure 1), northwest Gansu Province.

CT scanning and 3D reconstruction of endocast

High resolution X-ray CT scanning of the skull was carried out by using the 450 kV industrial-computerized tomography (450 ICT, developed by the Institute of High Energy Physics, Chinese Academy of Sciences) at the Key Laboratory of Vertebrate Evolution and Human Origins, CAS. The specimen was scanned with beam energy of 420 kV and a flux of 1.5 mA at a detector resolution of 160 μm per pixel. The skull of GSGM-FV-00500 was completely scanned with 360° rotation, a step size of 0.25°, and an unfiltered aluminum reflection target. A total of 1440 transmission images were made in a 2,048 × 2,048 matrix of 2048 slices using an unnamed two-dimensional reconstruction software developed by the Institute of High Energy Physics, CAS.

The braincase of GSGM-FV-00500 is well fossilized and three-dimensionally preserved, so the bone structures distinctly differ in density from the homogeneous surrounding matrix. Due to the high density differences between bones and matrix, the elements that make up the braincase were easily distinguishable. The three-dimensional images of the endocasts were assembled using the volume analysis software VGStudio Max 2.1 (Volume Graphics, Germany). Digital shearing and editing of the specific images of the endocranial cavity were conducted using Mimics 16.0 (Materialise, Belgium).

Results

Braincase morphology

Neoceratopsian braincases are generally narrow anteriorly and gradually widen posteriorly like a pyramid. Each side of the braincase is comprised of at least one distinguishable bone, with the exception of the dorsal and occipital views where direct observation of the bones are obscured by overlapping bones. Individual bones are difficult to distinguish since bones closely concrescence in adult ceratopsians (Kirkland and Deblieux 2010). Similarly, it is difficult to distinguish bones of *Auroraceratops* through observation or CT scans.

The skull of GSGM-FV-00500 is mostly preserved with fractured bones, and indeterminate suture lines (Figure 2). Dorsally, the roof of the braincase is slightly undulated and comprised of the frontal and parietal, with the former covering the top of the forebrain and the latter constituting the dorsal surface of the midbrain and the hindbrain. The occipital consists of the supraoccipital, exoccipital and basioccipital from top to bottom (Figure 2(a)), and the margin of the supraoccipital is faint, so it is difficult to determine whether or not the supraoccipital constitutes the dorsal margin of the foramen magnum. Both exoccipitals interconnect under the foramen magnum and exclude the basioccipital, and the spherical occipital condyle protrudes posteriorly. The prootic, opisthotic and laterosphenoid together constitute the lateral wall of the braincase; however, all of them are fused together and cannot be singly distinguished in GSGM-FV-00500. The left posterior portion of the braincase is roughly exposed because of the broken squamosal, quadrate and jugal. The base of the braincase is comprised of the parasphenoid, basisphenoid and basal tubera (Figure 2(b)), but they can hardly be identified, for the pterygoids cover the ventral surface of the braincase, as in other basal neoceratopsian (Dodson et al. 2010). The foramen magnum is similar to an isosceles triangle. Its width is about 11 mm, and the height is about 15 mm. The diameter of the occipital condyle is slightly larger than that of the foramen magnum, which is approximately 13 mm high. The maximum transverse width of basioccipital is about twice as that of the occipital condyle in posterior view.

Endocranial morphology

Although the cranial endocast is easily constructed by CT scanning, a few structures cannot be clearly distinguished in the current state due to the fractured nature of the braincase and the high degree of articulation of the bones.

The reconstructed endocast of GSGM-FV-00500 indicates that the forebrain is poorly preserved with the anterior end missing and the midbrain is difficult to distinguish; however, the hindbrain is well preserved, and part of the inner ear structure can be identified. Some major features such as the olfactory bulbs, medulla regions and pituitary body are also partially preserved. Based on measurements for the coronal, axial and sagittal maximum section, the cranial endocast is about 67 mm in length, about 38 mm in width and 32 mm in height.

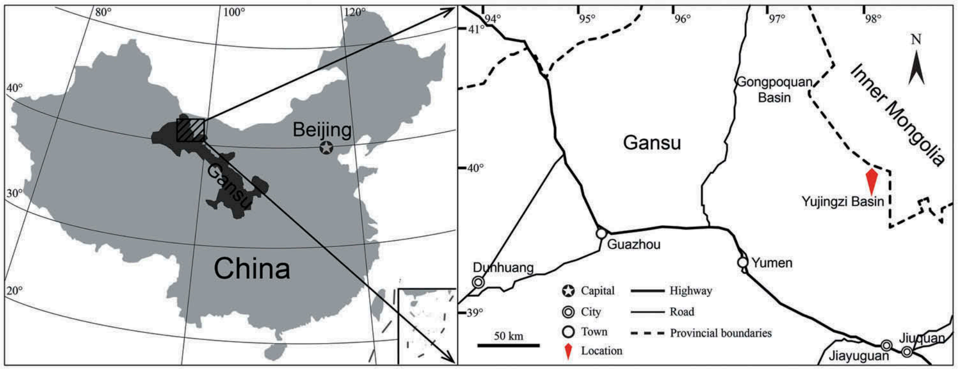

Figure 1. Fossil locality in the Yujingzi Basin of the Mazongshan Area.

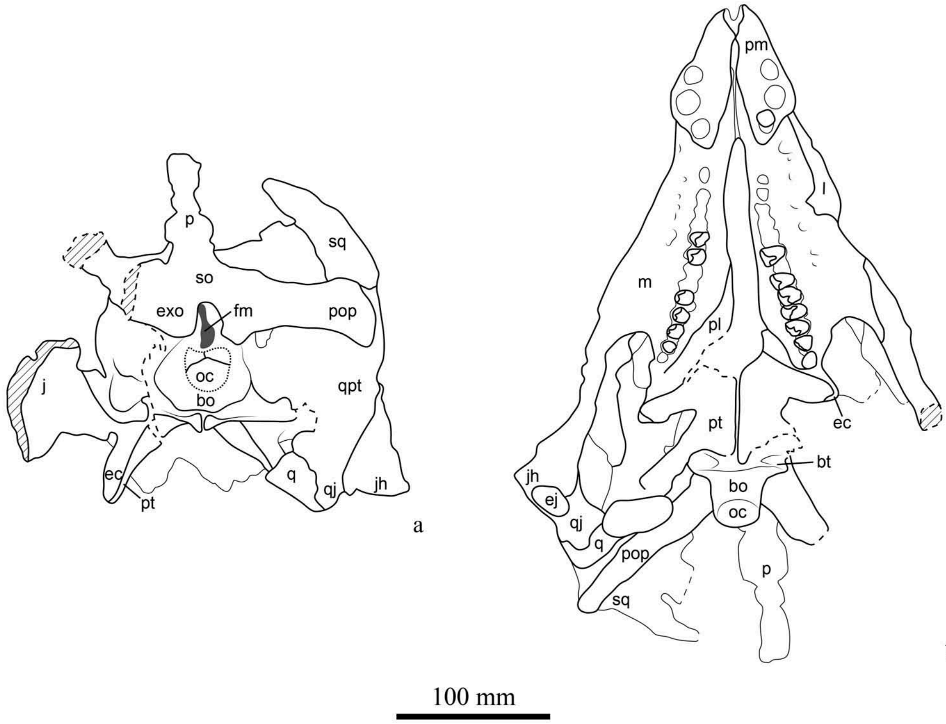

Figure 2. Posterior (a) and ventral (b) views of the skull of GSGM-FV-00500.

In lateral view (Figure 3(a,b)), the endocranial cast consists of three regions. The anterior-most protruding region, identified as the olfactory bulbs, is clearly expanded anterolaterally in dorsal view. A shallow median depression separates the dorsal surface of the olfactory bulb, but it cannot be ventrally reconstructed since it was not preserved along the ventral portion of the braincase (Figure 3(e,f)). The olfactory bulbs meld with the short olfactory tract, and its posterior margin widens and connects to the anterior of the cerebrum (Figure 3(e,f)). In dorsal view, the cerebrum expands laterally at the midpoint of the endocast and is relatively broad with smooth rounded lateral sides. In anterior view (Figure 3(c)), the pituitary fossa (an irregular globular structure) projects below the posterior region of the cerebrum and is accompanied by the paired canals of the internal carotid arteries. The connection point between the pituitary fossa and the brain is indistinct. The cerebellum originates from the posterior region of the cerebrum, slightly expands dorsally, and its lower part descends to the medulla oblongata by a steep pontine flexure at 50°in lateral view (Figure 3(a,b)). In dorsal and ventral views (Figure 3(e,f)), the medullary region is easily identified behind the steep posterior margin of the cerebellum. The medulla region is nearly parallel to the dorsal margin of the endocast – much like the primitive archosaurian state (Giffin 1989). The medulla is relatively narrow especially at the position of the otic capsules (Figure 3(a,b)), as in other dinosaurs (Hopson 1979). Anteriorly, the medulla widens to the ellipsoidal foramen. Cranial nerves in this specimen cannot be reconstructed because the canal pathways are not preserved in this specimen.

In lateral and dorsal views (Figure 3(a,b,e)), the posterolateral to the cerebellum are the prominent semicircular canals, but the inner ear structures are fragmentary because of the broken and compressed bones. The anterior and posterior semicircular canals are both long, thin, and ascend from the dorsal side of the crus commune. Part of the posterior canals form a high vertical arc that is located near the foramen magnum. The lateral semicircular canal has an almost horizontal orientation but no further description is possible from the incomplete canals.

Endocast volume

The presence of vascular impressions in ornithischian dinosaurs has been interpreted as evidence for a close brain-to-braincase volume (Evans 2005). However, we did not find any vascular impressions on the endocast of GSGM-FV-00500 which indicate that the endocranium represents that volume of the brain. The surface features show other preserved characters, and the positional relationship between endocast and skull is shown in reconstructions below (Figure 4), which helps us to acquire the endocast volume. Because of the incomplete preservation of this braincase, the endocast was calculated to be at least 8.9 ml (if integrated olfactory bulbs are included in our measurement, the endocast volume exceeds 10 ml) by using Mimics 16.0 in order to make relevant measurements based on the digital three-dimensional model. Unfortunately, the body mass could not be estimated since the femora were not completely preserved, otherwise the Encephalization Quotient (Jerison 1973) would have been calculated.

Discussion

Research on the endocrania of ceratopsians can be divided into two categories: one is based on real casts of endocrania such as those preserved in *Protoceratops* (Brown and Schlaikjer 1940), *Anchiceratops*, and *Triceratops* (Hopson 1979); and the other

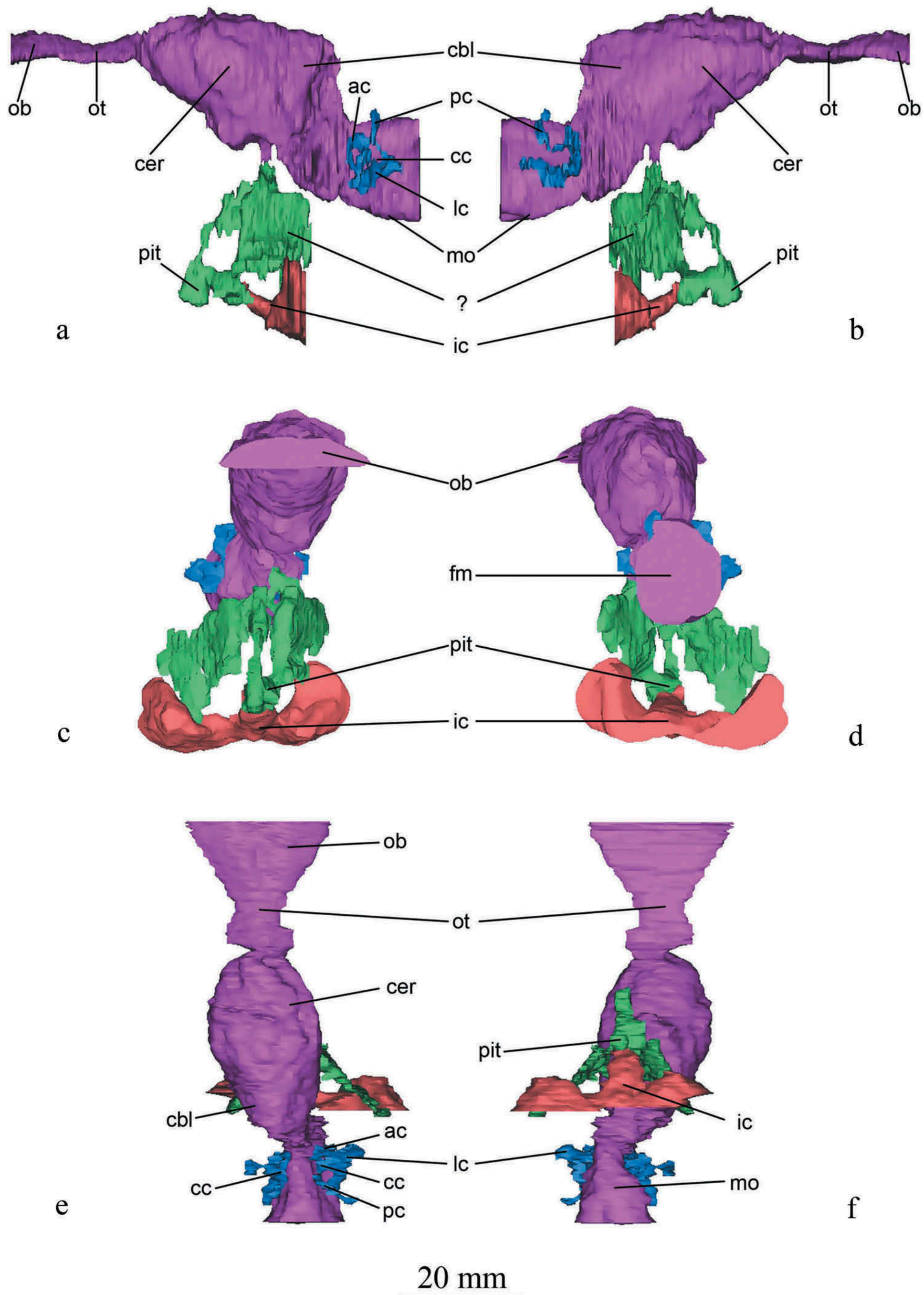

Figure 3. Left and right lateral (a,b), anterior and posterior (c,d), dorsal and ventral (e,f) views of the endocast of GSGM-FV-00500.

utilizes digital endocasts created by CT scans of *Psittacosaurus* (Zhou et al. 2007) and *Pachyrhinosaurus* (Witmer and Ridgely 2008). This study belongs to the latter. Comparisons can be easily made between *Psittacosaurus* (PKUP 1053, 1054 and 1060), *Pachyrhinosaurus* (TMP 1989.55.1243), *Protoceratops* (AMNH 6646), and *Auroraceratops*. *Psittacosaurus* and *Protoceratops* have a close phylogenetic relationship with *Auroraceratops* and make for comparative study.

The specimen described here is a subadult individual based on the fusion degree of the postcranial bones, and the intact, 3D endocast of its braincase. The partial olfactory bulbs of *Auroraceratops* are proportionally larger than those found in *Pachyrhinosaurus*; however, the wide, flat shape of the olfactory bulbs is more similar to *Psittacosaurus*, a basal ceratopsian. This is indicative that *Auroraceratops* had a well-developed sense of smell when compared to the more derived centrosaurine ceratopsian *Pachyrhinosaurus*. GSGM-FV-00500 does not preserve an optical lobe along any portion of the endocast. Although the orbit of *Auroraceratops* is comparatively large, a recognizable optical lobe was not found in GSGM-FV-00500 – a trait that is shared by all ceratopsians except *Psittacosaurus* (Zhou et al. 2007). As described above, the distinct cerebrum was significantly larger and more rounded than others mentioned above, but the unseparated cerebral hemispheres and the steep pontine flexure are most similar to *Psittacosaurus*. The cerebellum is moderately projecting posteriorly and notably larger than that

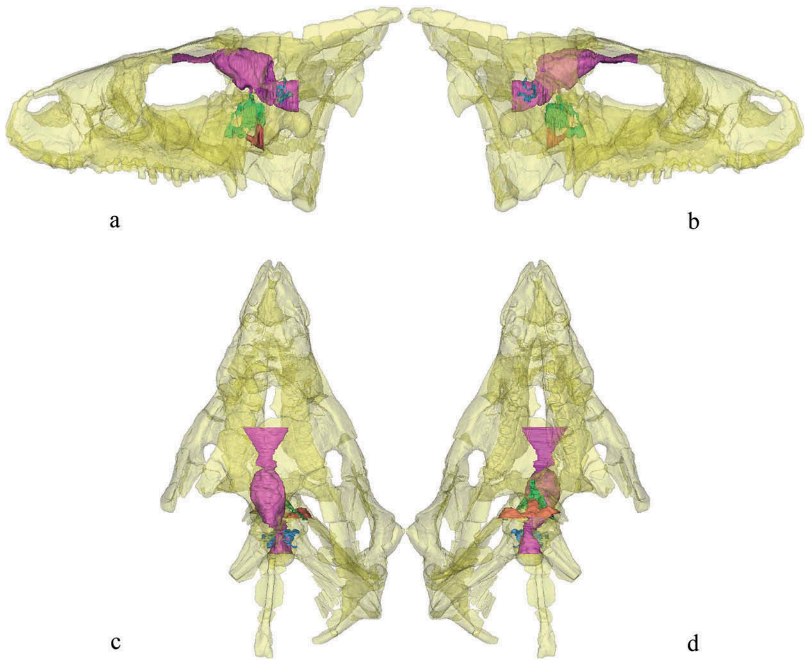

Figure 4. Left and right lateral (a,b), dorsal and ventral (c,d) views of the digital skull and endocast of GSGM-FV-00500.

of *Pachyrhinosaurus* (Witmer and Ridgely 2008). The proximity of the inner ear to the foramen magnum and the length of the medulla oblongata is comparable to those found in *Psittacosaurus* and *Protoceratops* (Brown and Schlaikjer 1940; Zhou et al. 2007). This is different in more derived ceratopsians such as *Pachyrhinosaurus, Anchiceratops* and *Triceratops*, where the inner ear is more anteriorly located, and the medulla oblongata is relatively long (Hopson 1979; Witmer and Ridgely 2008). The semicircular canals of *Auroraceratops* are slender and apparently curved, which are very similar to the morphology of *Psittacosaurus* (Zhou et al. 2007). In contrast, *Protoceratops* and *Pachyrhinosaurus* have shorter semicircular canals than *Auroraceratops*, and *Anchiceratops* has rather short and thick ones (Brown and Schlaikjer 1940; Hopson 1979; Witmer and Ridgely 2008). The lateral semicircular canal is typically the shortest of the three semicircular canals, especially in the *Pachyrhinosaurus* (Witmer and Ridgely 2008), but the lateral semicircular canal is longer than expected in *Auroraceratops* based on the extension of anterior and posterior canals. The pituitary is variable in its morphology, position, and orientation among ceratopsians (Hopson 1979). Both GSGM-FV-00500 and *Psittacosaurus* are posteroventrally directed; however, the pituitary in *Psittacosaurus* occupies a high position dorsal to the ventral margin of the medulla (Zhou et al. 2007). *Auroraceratops*, much like *Protoceratops*, has a pituitary fossa that occupies a low position and is far below the medulla oblongata. Other detailed information needs further study.

In summary, although *Auroraceratops* belongs to basal Neoceratopsia, its endocranial morphology is closer to that of *Psittacosaurus* than the more derived *Pachyrhinosaurus*. This is only a primary study on the endocranial morphology of basal Neoceratopsia, and the results are also primary. Future samplings of *Auroraceratops* skulls will help to expand our knowledge of endocranial relationships between poorly sampled neoceratopsians.

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Disclosure statement

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