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Paleoneurology of the iguanodontian *Fostoria dhimbangunmal* from the mid-Cretaceous of Australia

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Abstract

Insights into the paleoneurology and endocranial anatomy of ornithopod dinosaurs come largely from Northern Hemisphere taxa. The recently described non-hadrosaurid iguanodontian *Fostoria dhimbangunmal* from the Cenomanian of eastern Australia includes a partial skull that offers novel insights into its endocranial anatomy (i.e., the cavity housing the brain). Here, we describe the paleoneurology of *F. dhimbangunmal* based on a digital cranial endocast obtained from computed tomography. The endocast is mostly complete; however, it is diagenetically dorsoventrally compressed and its ventral limits are not preserved. The endocranial anatomy of *F. dhimbangunmal* is generally consistent with that of other non-hadrosaurid iguanodontians, including a well-developed olfactory apparatus, suggesting a good sense of smell. In contrast to hadrosaurids and some non-hadrosaurid iguanodontians, *F. dhimbangunmal* possesses the ancestral flexure condition, in which cranial and pontine flexure angles are subequal. The cerebrum makes up a significant portion of the endocast volume; however, the cerebral hemispheres are not as enlarged or bulbous as seen in hadrosaurids. The forebrain of *F. dhimbangunmal* did not fill the braincase to the same extent as in hadrosaurids. A distinct vacuity in the supraoccipital of *F. dhimbangunmal* may represent a new autapomorphy. This study provides the first insights into the neuroanatomy of an Australian iguanodontian dinosaur.

Non-technical Summary

The size and shape of a dinosaur's brain can be estimated from the space in the skull that once held this organ. We used medical computed tomography (CT) scans of the skull to reconstruct the brain of *Fostoria dhimbangunmal*, a type of bipedal, herbivorous dinosaur known as an iguanodontian from the Cretaceous (approx. 100 million years ago) of Australia. We find that the brain of *Fostoria* was generally similar to its iguanodontian counterparts from the northern hemisphere, including features suggesting a good sense of smell. Other features, however, indicate that *Fostoria* and an Australian small, non-iguanodontian species of ornithopod may have evolved brains different to their northern counterparts to help them cope with their high-latitude setting.

Introduction

Paleoneurology is the study of the nervous system in extinct taxa, such as non-avian dinosaurs (hereafter 'dinosaurs') (Jerison, 1976). Because the soft tissues of the nervous system do not readily fossilize, paleoneurological studies utilize endocasts, particularly cranial endocasts, to infer brain features. Endocasts rarely occur naturally (i.e., in-filled with matrix) and are otherwise artificially created by physically or virtually casting the braincase; the latter via computed tomography (CT) (Walsh and Knoll, 2011, and references therein). In reptiles, including non-avian dinosaurs, cranial endocasts are not exact replicas of the brain; they include meninges and venous sinuses, and the brain typically does not fill the entire braincase. Nonetheless, they provide important insights into the relative shapes and sizes of the brain and its features, and are therefore critical for understanding comparative dinosaur neuroanatomy (Balanoff et al., 2016; Watanabe et al., 2019).

Among dinosaurs, the endocast of the non-hadrosaurid iguanodontian ornithopod *Iguanodon bernissartensis* was among the first dinosaur "brains" described (Andrews, 1897). Subsequent paleoneurological work on ornithopods has focused largely on hadrosaurids (Hopson, 1979; Evans, 2005, 2006; Evans et al., 2009; Godefroit et al., 2012; Saveliev et al., 2012; Lauters et al., 2013; Cruzado-Caballero et al., 2015; Becerra et al., 2018). In recent years, non-hadrosaurid iguanodontians have gained increasing attention. Iguanodontian endocast descriptions include: *Dryosaurus altus* Marsh, 1894 (Galton, 1989), *Dysalotosaurus lettowvorbecki* Virchow, 1919 (Galton, 1989; Sobral et al., 2012; Lautenschlager and Hübner, 2013),

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Iguanodon bernissartensis Boulenger, 1881 (Andrews, 1897; Lauters et al., 2012), *Lurdusaurus arenatus* Taquet and Russell, 1999 (Lauters et al., 2012), *Mantellisaurus atherfieldensis* (Hooley, 1925) (Lauters et al., 2012; Brasier et al., 2017), *Proa valdearinnensis* McDonald et al., 2012 (Knoll et al., 2021), and *Tenontosaurus tilletti* Ostrom, 1970 (Galton, 1989; Thomas, 2015). Notably, most non-hadrosaurid iguanodontian endocast descriptions are from the Northern Hemisphere, with fewer studies addressing their Gondwanan counterparts (e.g., *Dysalotosaurus* [Galton, 1989], *Lurdusaurus* [Lauters et al., 2012]).

In Australia, there are only two named non-hadrosaurid iguanodontian species, neither of which is known from their neuroanatomy: *Muttaburrasaurus langdoni* Bartholomai and Molnar, 1981 (Bartholomai and Molnar, 1981; Molnar, 1996) from the upper Albian Mackunda and Allaru formations in Queensland and *Fostoria dhimbangunmal* Bell et al., 2019a (Bell et al., 2019a) from the Cenomanian Griman Creek Formation in New South Wales. We investigated the paleoneurology of *F. dhimbangunmal* based on computed tomographic (CT) scans of the holotype partial skull (Lightning Ridge Fossil [LRF] 3050.A, Australian Opal Centre, Lightning Ridge, New South Wales, Australia). The aim of this study is to describe the cranial endocast of *F. dhimbangunmal* and compare it to other iguanodontians (including hadrosaurids), thereby providing an additional perspective on Gondwanan iguanodontian endocranial anatomy. In doing so, this study also provides novel insights into the neurosensory capabilities of *F. dhimbangunmal*, adding to our understanding of global brain evolution in Ornithomimidae.

Materials and methods

This study utilized CT scans of the braincase of *Fostoria dhimbangunmal* (LRF 3050.A) originally acquired by Bell et al. (2019a) using a Siemens Syngo CT2012B (120 kV; slice thickness = 0.74 mm) at I-MED Radiology Armidale (formerly Armidale Radiology) (Armidale, New South Wales, Australia). The braincase and cranial endocast were volume rendered in ORS Dragonfly (version 2020.1, Comet Technologies Canada Inc., Montreal, Canada; accessed under a free academic license; <https://www.theobjects.com/dragonfly>). Each image in the stack was upscaled by a factor of five to increase the resolution. All linear measurements were taken in Dragonfly five times and then averaged to reduce human error. The regions of interest were manually segmented using the 3D paint tools. The thresholding function was not employed due to the inability to clearly distinguish margins between the equally attenuated opalized bone and matrix in many places. Thus, volume rendering required a degree of operator interpretation. The volume renders were exported as STL files. The meshes were repaired (to remove minor artifacts), smoothed, colorized, and organized in Meshmixer (version 3.5.474) and ZBrush (version 2022.0.2). No attempt to retrodeform the endocast was made. Figures were created using Adobe Photoshop (version 23.1.1) and Adobe Illustrator (version 26.0.3). Endocast (excluding the olfactory apparatus) and cerebrum volumes were determined by importing the meshes (repaired in Meshmixer) into the program Chitubox (version 1.9.3). Measurements taken on the cranial endocast are shown in Figure 1.

Repository and institutional abbreviation

The holotype skull of *Fostoria dhimbangunmal* (LRF 3050.A) is deposited at the Australian Opal Centre (LRF = 'Lightning Ridge fossil'), Lightning Ridge, New South Wales, Australia.

Results

Preservation

The preserved braincase of *Fostoria dhimbangunmal* includes the frontals, parietal, supraoccipital, partial basisphenoid, and right paroccipital processes, as well as the incomplete left laterosphenoid and prootic (Fig. 2). The basioccipital, opisthotics, and ventral part of the right prootic are not preserved. The braincase is entirely opalized and crushed dorsoventrally, resulting in loss of details to the lateral and ventral margins of the braincase and obliteration of sutures between many of the cranial bones. This description will focus on the incomplete cranial endocast as it is preserved within the braincase (Figs. 2, 3); thus, we caution that some descriptions reflect taphonomic deformation of the endocast, including significant dorsoventral compression. Where apparent, we draw attention to these features in the description and following discussion. A detailed description of the braincase can be found in Bell et al. (2019a).

Neurocranial endocast

The dorsal aspect of the endocast is in good condition; however, the anterior, posterior, and ventral limits of the endocast, apart from the tentatively identified region of the pituitary, are incomplete. Few cranial nerves are preserved. The endocast has a maximum anteroposterior length (including the olfactory peduncles) of 75.8 mm, width of 54.0 mm, and dorsoventral height of 32.1 mm. The anteroposterior length of the endocast excluding the olfactory tracts is 63.1 mm. As preserved, the volume of the endocast is 26.3 cm³ and 25.4 cm³, with and without the olfactory apparatus, respectively. The endocast is roughly horizontally positioned within the skull, subparallel to the skull roof, which, based on the well-preserved frontals and parietals (Bell et al., 2019a), appears to be a real (not diagenetic) feature.

The regions of the brain represented by the endocast include the telencephalon and diencephalon of the forebrain (prosencephalon) and the posterodorsal region of the metencephalon of the hindbrain (rhombencephalon). The region of the infundibulum of the forebrain and pituitary are provisionally identified. The olfactory tracts and a posterior portion of the olfactory bulbs are preserved. The midbrain (mesencephalon), positioned between the infundibular and pituitary ventrally and hindbrain dorsally, is poorly preserved and difficult to interpret from the scans. The myelencephalon and ventral region of the metencephalon of the hindbrain are not preserved. The medulla oblongata is not preserved as a result of missing elements.

Although the endocast is dorsoventrally compressed, flexure of the brain axis is indicated. As preserved, a cranial flexure of 134° is estimated and pontine flexure of 135° is provisionally estimated, noting that the medulla oblongata is absent as a result of the missing basioccipital. In the original form, the angles of cranial and pontine flexure would have been more acute than measured. A well-developed recess is preserved posterior to the endocast within the supraoccipital and is here identified as a supraoccipital vacuity (Fig. 2). At the scan resolution available, the supraoccipital vacuity is fully enclosed in the supraoccipital and does not appear to communicate with the endocast, nor to other openings in or to the outside of the skull. It is dorsoventrally tall and anteroventrally–posterodorsally oriented, with a T-shaped profile in posterior view (Fig. 2.8, 2.10, 2.12).

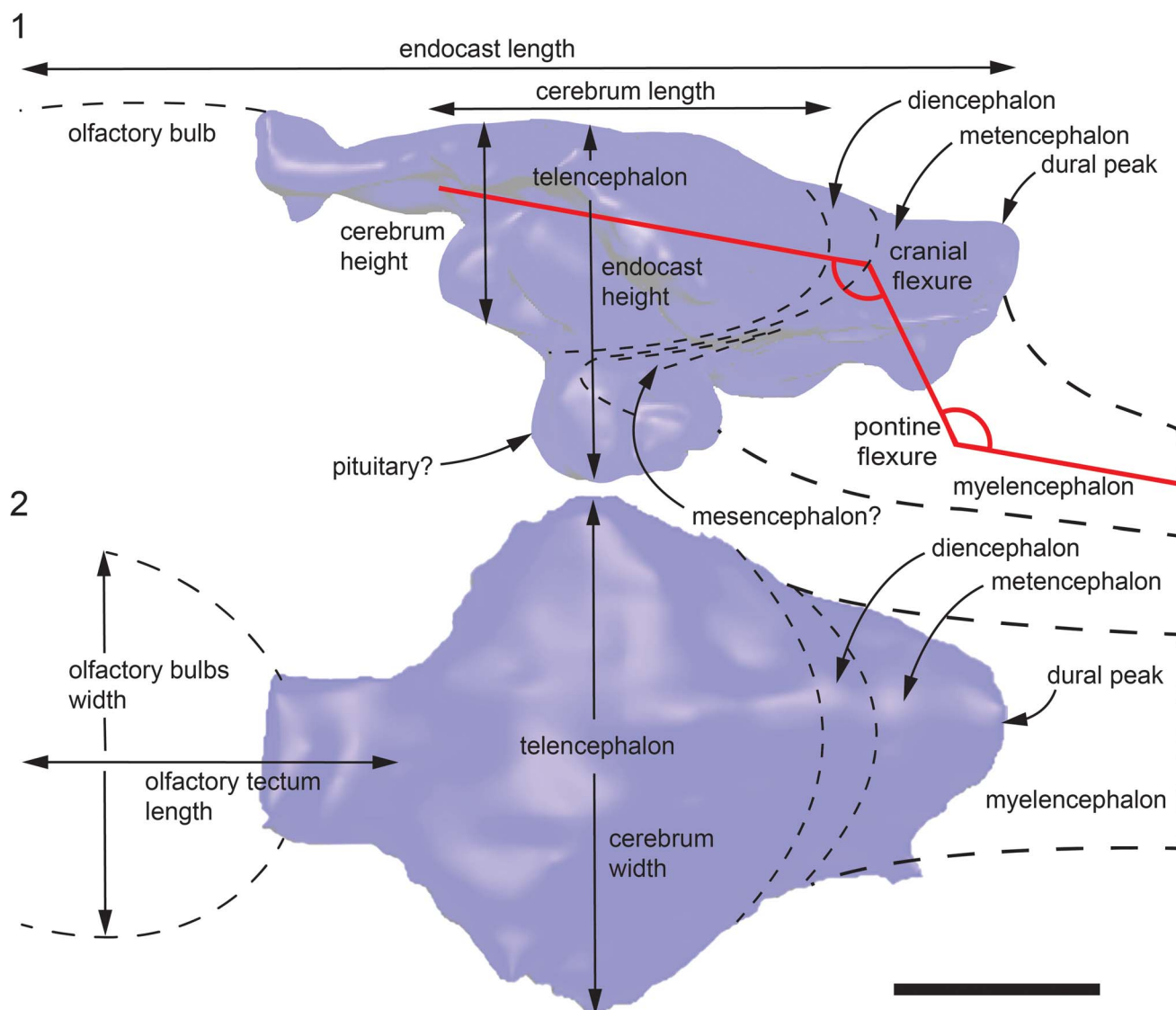


Figure 1. Volume-rendered cranial endocast of *Fostoria dhimbangunmal* in (1) lateral and (2) dorsal views. Locations of endocast measurements as indicated. Heavy dashed line indicates missing region of the hindbrain. Scale bar = 2 cm.

The olfactory apparatus in *F. dhimbangunmal* is well developed (Fig. 3). The olfactory tracts form a single element that projects horizontally from the dorsal surface of the cerebrum and are surrounded by the frontals dorsally and the presphenoid ventrally and laterally (Figs. 2.4, 3.1, 3.2). The olfactory tract does not broaden in width anteriorly.

Anterior to the presphenoid, impressions of the olfactory bulbs are delineated by the divergent crista cranii on the ventral surface of the frontals, indicating that they widened and extended farther anteriorly than is suggested by the endocast alone (dashed lines in Fig. 2.4). Based on the volume-rendered endocast, the olfactory tract has a preserved anteroposterior length of 12.9 mm; however, including the anterior impressions on the frontals, the olfactory apparatus is minimally 29.3 mm in length. The maximum preserved width of the bulbs, from their anterior impressions on the underside of the frontals, is 30.7 mm.

The cerebrum is broad (Table 1) with a volume of 19.2 cm³ and makes up the largest portion of the total endocast volume, as preserved. No valliculae—endocranial vascular impressions—

are preserved on the dorsal surface of the endocast, as seen in some hadrosaurids (Evans, 2005; Lauters et al., 2013). However, their absence may simply be due to poor preservation/scan quality. There is no bulging or notable separation between the cerebral hemispheres. Preservation of the infundibulum and pituitary body is uncertain, but a somewhat hemispherical midline protuberance is present in the expected location of the pituitary, forming the ventral-most portion of the endocast (e.g., Galton, 1989) (Fig. 3.3, 3.4). A dorsal protuberance is present in the region of the diencephalon at the posterior end of the forebrain, interpreted as the location of the pineal. Posteriorly from the diencephalon, the dorsal surface of the hindbrain is depressed ventrally relative to the forebrain. The width of the hindbrain narrows posteriorly. The dural peak is identified in the posterodorsal part of the hindbrain housed in the supraoccipital fossa. The midbrain, within which the optic tectum is located, is poorly preserved. The region of the myelencephalon, including the floccular fossae and lobes, is not preserved. Hence, the osseous labyrinths and cranial nerves CN VII to CN XII are not preserved.

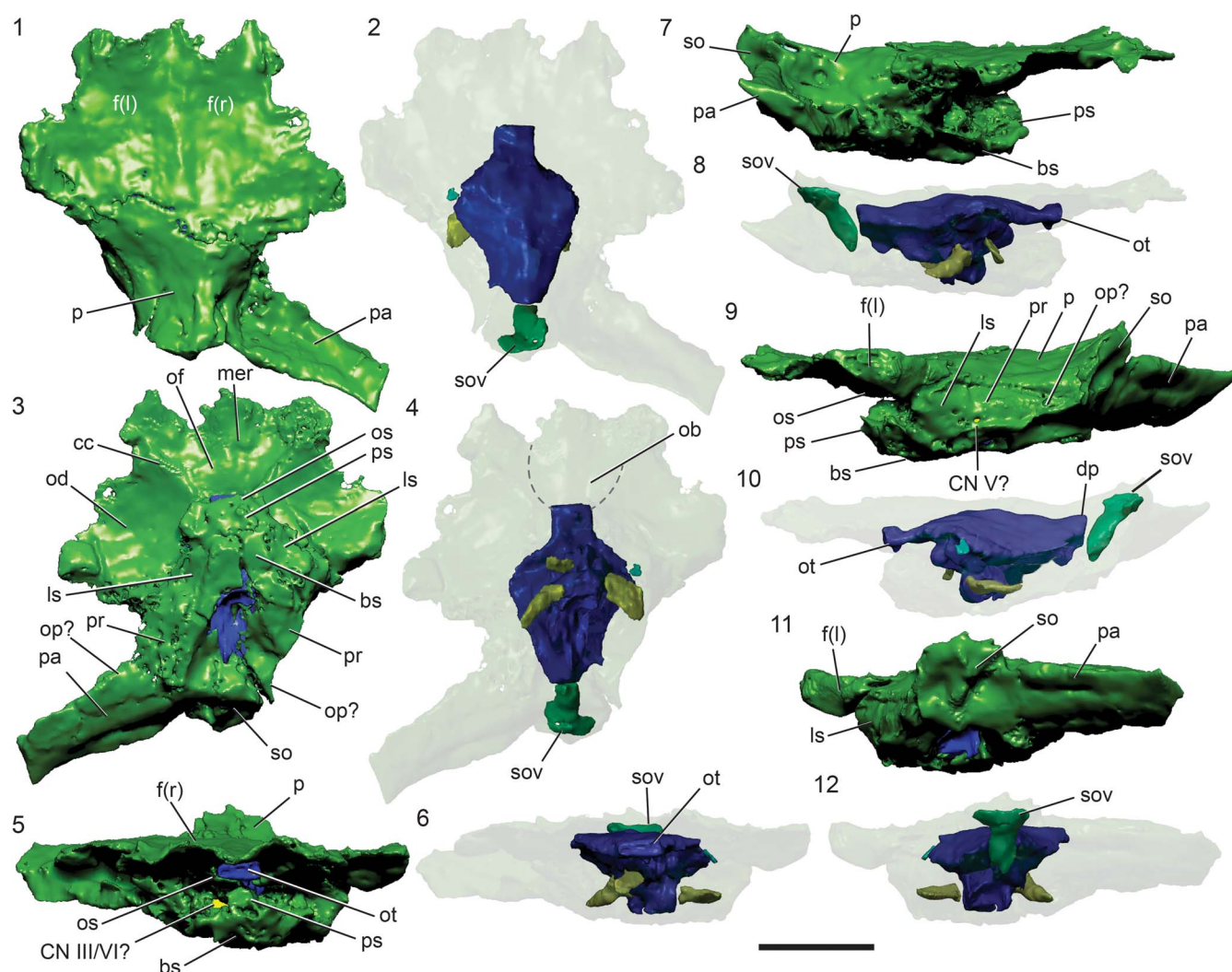


Figure 2. *Fostoria dhimbangunmal* braincase (green), cranial endocast (dark blue), and cranial nerves (yellow) in (1, 2) dorsal, (3, 4) ventral, (5, 6) anterior, (7, 8) right lateral, (9, 10) left lateral, and (11, 12) posterior views. Dashed lines in (2) and (4) represent olfactory bulb impressions on the underside of the frontals. bs = basisphenoid; cc = crista cranii; CN = cranial nerve; dp = dural peak; f (l, r) = frontal (left, right); ls = laterosphenoid region; mer = median ridge for nasal septum; ob = olfactory bulbs; od = orbital depression; of = olfactory fossa; op? = opisthotic region; os = orbitosphenoid; ot = olfactory tract; p = parietal; pa = paraoccipital process; pr = prootic region; ps = parasphenoid; so = supraoccipital; sov = supraoccipital vacuity. Scale bar = 5 cm.

Cranial nerves

Interpretations of the cranial nerves are challenging due to incomplete preservation of the canals in the braincase. Apart from the olfactory tracts (CN I), the largest reconstructed extension from the endocast is interpreted as the canal for the trigeminal nerve (CN V), although it is possible that these projections represent the carotid arteries. Assuming they represent the canals for CN V, the canals project posterolaterally and are visible on both sides of the endocast (Fig. 3). The three branches of the trigeminal nerve are not distinguishable, suggesting that the nerve may have split into individual branches outside the braincase, as seen in *Dysalotosaurus lettowvorbecki* (Lautenschlager and Hübner, 2013). However, such interpretations are tenuous owing to the incomplete and poor preservation of the braincase. A lateroventrally projecting canal on the right side of the endocast may have served the oculomotor (CN III) or trochlear (CN IV) nerve. Canals for the optic (CN II), abducens (CN VI), facial (CN VII), vestibulocochlear (CN VIII), glossopharyngeal (CN IX), vagus (CN X), accessory (CN XI), and hypoglossal (CN

XII) nerves are not preserved, again as a result of diagenetic crushing and/or missing elements.

Discussion

The results of this study provide insights into the neuroanatomy of *Fostoria dhimbangunmal* and permit additional and much-needed comparative analysis between a Gondwanan iguanodontian and those known from Laurasia. Overall morphology of the endocast is similar to Laurasian non-hadrosaurid iguanodontians, including a well-developed olfactory apparatus and a large cerebrum (the broadest part of the endocast). Additionally, details of the midbrain and much of the hindbrain were missing, as is the case in most other non-hadrosaurid iguanodontians (Galton, 1989; Lauters et al., 2012; Sobral et al., 2012; Lautenschlager and Hübner, 2013; Brasier et al., 2017; Knoll et al., 2021). Notably, ventral depression of the dorsal margin of the hindbrain metencephalon (i.e., between the diencephalon and the dural peak), relative to the forebrain, is comparable to the condition in the iguanodontians *Tenontosaurus*

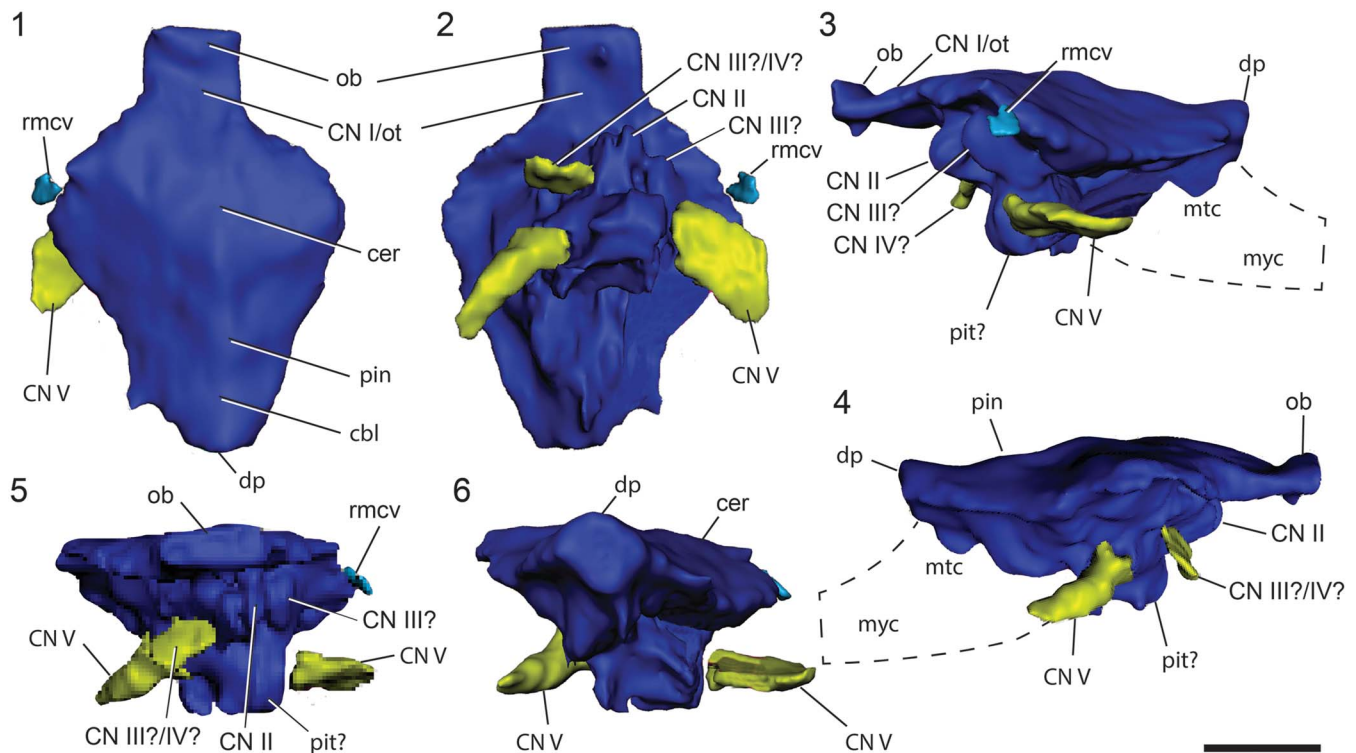


Figure 3. *Fostoria dhimbangunmal* volume-rendered neurocranial endocast (dark blue), inferred cranial nerves (yellow), and veins (light blue) in (1) dorsal, (2) ventral, (3) left lateral, (4) right lateral, (5) anterior, and (6) posterior views. The passage for cranial nerve I (the olfactory tract) is shown in dark blue. Abbreviations: cbl = cerebellum; cer = cerebrum; CN ? = possible cranial nerve; CN I/ot = cranial nerve I/olfactory tract; CN II = optic nerve; CN III? = region of the facial and vestibulo-cochlear nerve canals; CN III/CN IV? = region of the oculomotor and trochlear nerve canals; CN V = potential trigeminal nerve canal; dp = dural peak; mtc = metencephalon; myc = myelencephalon; ob = olfactory bulb; ot = olfactory tracts; pin = region of pineal; pit? = region of the pituitary; rmcv = rostral middle cerebral vein. Scale bar = 2 cm.

tilletti (Galton, 1989; Thomas, 2015), *Dryosaurus altus* (Galton, 1989), and hadrosaurids (Evans et al., 2009; Lauters et al., 2013; Cruzado-Caballero et al., 2015). Ventral depression of the dorsal metencephalic margin is minimal in the 'basal' ornithomorph *Hypsilophodon foxii* Huxley, 1870 (Galton, 1989) and the non-ornithomorph neornithischian *Thescelosaurus neglectus* Gilmore, 1913 (Galton, 1989; Button and Zanno, 2023). In addition, the metencephalon of *Fostoria dhimbangunmal* is anteroposteriorly extended, as in derived ornithomorphs such as *Tenontosaurus tilletti* (Galton, 1989; Thomas, 2015), *Dryosaurus altus* (Galton, 1989), and hadrosaurids (Evans et al., 2009). The anteroposterior length of the metencephalon is comparatively reduced in *Hypsilophodon foxii*, the 'basal' ceratopsian *Protoceratops andrewsi* Granger and Gregory, 1923 (Brown and Schlaikjer, 1940), and the basal neornithischian *Thescelosaurus neglectus* (Galton, 1989; Button and Zanno, 2023). Elongation of the metencephalon could be a phylogenetically useful character in the future; however, more detailed cranial endocast descriptions will be required across Ornithischia.

Degree of brain-fill

The degree to which the brain fills the endocranial cavity in dinosaurs remains unresolved. Initial paleoneurological studies assumed that dinosaur brains were similar to those of non-avian reptiles in that they filled approximately 50% of the endocranial cavity (Jerison, 1969; Hopson, 1977). However, subsequent works have demonstrated that brain-fill within the endocranium is phylogenetically dependent among non-avian dinosaurs, but

can also vary with ontogeny, adult body size, and between regions of the endocast (Osmólska, 2004; Evans, 2006; Hurlbert et al., 2013; Lauters et al., 2023; Paulina-Carabajal et al., 2023). Hadrosaurids are now commonly thought to have possessed a high degree of brain-fill based on the presence of valliculae on the internal surfaces of the braincase, and because the cerebral hemispheres are usually expanded, bulbous, and make up a considerable portion of the endocast volume (Evans, 2005; Evans et al., 2009; Godefroit et al., 2012; Lauters et al., 2023).

The amount to which the brain filled the endocast in *F. dhimbangunmal* is tentatively interpreted here, owing to the preservational state of the holotype specimen. However, like other non-hadrosaurid iguanodontians, it does not appear to possess the same degree of brain-fill within the endocranium as hadrosaurids. For instance, valliculae are not discernable on the endocast and the cerebral hemispheres are less bulbous (Evans et al., 2009; Cruzado-Caballero et al., 2015; see below), although suboptimal preservation/crushing and/or low-resolution scans could account for these differences. Further, owing to incomplete preservation of the endocast, we cannot determine whether the degree of brain-fill in *F. dhimbangunmal* varied across the different regions of the endocast (Evans, 2005; Evans et al., 2009; Lauters et al., 2012; Brasier et al., 2017).

Cerebrum

As preserved, the cerebrum of *F. dhimbangunmal* is relatively large compared to the total endocast. The encephalization

Table 1. Comparative table of iguanodontian cerebral and endocast measurements and proportions.

Taxon	Cerebrum		Endocast		Proportions		References
	Width (cm)	Volume (cm ³)	Length (cm)	Volume (cm ³)	Width/length (%)	CRV (%)	
Non-hadrosaurid Iguanodontia							
<i>Fostoria dhimbangunmal</i>	5.4	19.2	6.3	25.38	85.7	76	This work
<i>Batyrosaurus rozhdestvenskyi</i> Godefroit et al., 2012	4.6	—	10.5	27	43.8	—	Godefroit et al., 2012; Lauters et al., 2012
<i>Iguanodon bernissartensis</i>	11	68	18.3	357	60.1	19	Lauters et al., 2012
<i>Mantellisaurus atherfieldensis</i>	8.9	—	14.1	—	63.1	—	Lauters et al., 2012
<i>Lurdusaurus arenatus</i>	—	32	—	167	—	19	Lauters et al., 2012
<i>Proa valdearinnensis</i>	10.3*	129	18.9	325	54.5*	40	Knoll et al., 2021
Hadrosauridae							
<i>Amurosaurus riabinini</i> Bolotsky and Kurzanov, 1991 (AENM 1/123)	7.2	88	23	290	31.3	30	Lauters et al., 2012; Cruzado-Caballero et al., 2015
<i>Amurosaurus riabinini</i> (IRSNB R 279)	6.9	87	15.4	290	44.8	30	Lauters et al., 2013
<i>Arenysaurus ardevoli</i> Pereda-Suberbiola et al., 2009	4.8	65.4	11.7	122.8	41	53	Cruzado-Caballero et al., 2015
<i>Corythosaurus</i> sp. (ROM 759)	—	41.6	—	91.7	—	45	Evans et al., 2009
<i>Corthosaurus</i> sp. (CMN 34825)	—	51.1	—	134.2	—	38	Evans et al., 2009
<i>Hypacrosaurus altispinus</i> Brown, 1913	6.3	117.5	16.3	276	38.7	43	Evans et al., 2009
<i>Lambeosaurus</i> sp. (ROM 758)	—	35.1	—	91.2		38	Evans et al., 2009

CRV = cerebrum volume/endocast volume; endocast volumes exclude the olfactory apparatus. *Values are tentative, calculated using the figures in Knoll et al. (2021).

quotient, which measures the relative size of the brain (or endocast) given a particular body mass (Jerison, 1969) and adapted to reptiles (Hurlburt, 1996), could not be determined for *F. dhimbangunmal* due to the incomplete cranial endocast; its body mass is also unknown. However, cerebrum-to-endocast length and volume proportions could be obtained, providing a comparative basis (Table 1). Such values provide an estimate of relative cerebrum size, which has been linked to behavioral complexity and cognitive ability (Jerison, 1969; Hopson, 1977). *Fostoria dhimbangunmal* has notably high cerebral proportions, ~86% width-to-length (excluding the olfactory apparatus) and ~76% of the volume. These proportions are exaggerated due to the incomplete mid- and hindbrain regions, but they nonetheless suggest that a significant portion of the endocast was dedicated to the cerebrum. The cerebral hemispheres in *F. dhimbangunmal* are dorsoventrally flattened compared to the more bulbous hemispheres in other iguanodontians (e.g., *Dysalotosaurus lettowvorbecki* and *Proa valdearinnoensis*; Lautenschlager and Hübner, 2013; Knoll et al., 2021), including hadrosaurids (Evans et al., 2009; Godefroit et al., 2012; Cruzado-Caballero et al., 2015; Becerra et al., 2018), but this is almost certainly the result of crushing/preservation, which is an unmistakable taphonomic feature of the *Fostoria dhimbangunmal* holotype.

Brain flexures

Fostoria dhimbangunmal does not possess the derived flexure pattern seen in hadrosaurids and some non-hadrosaurid

iguanodontians where cranial and pontine flexures are significantly reduced or eliminated, making the endocast axis straight (Hopson, 1979; Giffin, 1989; Lauters et al., 2023). Reduced flexures (i.e., straight endocasts) are normally associated with large body size, although flexures also reduce ontogenetically in non-avian dinosaurs and crocodilians (Lautenschlager and Hübner, 2013; Hu et al., 2021). Shallow angles of flexure can also result from a rapid braincase growth rate compared to the brain (Lauters et al., 2023). In *F. dhimbangunmal*, both cranial and pontine flexures are subequal (~135°), as preserved; noting that diagenetic crushing has influenced the apparent flexure angles in the *F. dhimbangunmal* endocast and the angles would have been more acute in life. The angles of flexure are similar to those of *Dysalotosaurus lettowvorbecki*, which is the ancestral flexure condition observed in most dinosaur cranial endocasts (Hopson, 1979; Giffin, 1989; Lautenschlager and Hübner, 2013; Button and Zanno, 2023). In the ancestral condition, where cranial and pontine flexures are subequal, the subparallel cerebral and medullary regions are separated by an oblique mid- and hindbrain region (Giffin, 1989). This condition also is observed in *F. dhimbangunmal* (Fig. 1).

Supraoccipital vacuity

A large posterior vacuity, restricted to the supraoccipital, was identified in *F. dhimbangunmal*. This vacuity is entirely enclosed within the supraoccipital with no clear evidence that it communicated with the endocranial space, and no other pneumatic features

were observed in the skull (Fig. 2.2, 2.3, 2.10, 2.12). Although scan resolution and/or diagenetic crushing may have influenced these relationships, it nevertheless differs from the dorsal sagittal sinus in *Tenontosaurus tilletti*, which lies on the anterior surface of the supraoccipital (not within it) and forms the dorsal roof over the posterior part of the endocranium (Thomas, 2015). A similar vacuity within the supraoccipital (= supraoccipital sinus) is consistently present in tyrannosaurids, although this feature is pneumatic and communicates with other cranial sinuses (Witmer and Ridgely, 2009; McKeown *et al.*, 2020; Carabajal *et al.*, 2021). No such features have been observed in any other ornithomimid, suggesting a new autapomorphy for *F. dhimbangunmal*. Given the relatively limited number of ornithomimid skulls that have been CT scanned compared to theropods (e.g., Lauters *et al.*, 2023), it is possible that a supraoccipital vacuity may be found in additional taxa as more specimens are investigated.

Sensory capabilities

Based on the crista cranii and the reconstructed part of the olfactory bulbs, *Fostoria dhimbangunmal* possessed a relatively broad olfactory apparatus (potentially as broad as the cerebral hemispheres) compared to other non-hadrosaurid iguanodontians, such as *Dysalotosaurus lettowvorbecki*, *Iguanodon bernissartensis*, *Mantellisaurus atherfieldensis*, and *Proa valdearnhoensis* (Lauters *et al.*, 2012; Lautenschlager and Hübner, 2013; Knoll *et al.*, 2021), also differing from most hadrosaurids, except *Amurosaurus riabinini* Bolotsky and Kurzanov, 1991 (Lauters *et al.*, 2013), which had a relatively reduced olfactory apparatus compared to the cerebral hemispheres (Evans *et al.*, 2009; Becerra *et al.*, 2018). The olfactory tract is relatively shorter in *F. dhimbangunmal* compared to *D. lettowvorbecki* (Lautenschlager and Hübner, 2013) and, as preserved, the dorsal margin of the cerebrum is close to the level of the olfactory bulbs, unlike in *D. lettowvorbecki*, *P. valdearnhoensis*, and some hadrosaurids where the cerebrum exceeds the height of the olfactory bulbs (Evans *et al.*, 2009; Lautenschlager and Hübner, 2013), although we acknowledge this may have been affected by crushing in *F. dhimbangunmal*. Based on the relative proportions of the olfactory apparatus, *F. dhimbangunmal* likely possessed a strong sense of smell, assuming the olfactory apparatus is a proxy for olfaction capabilities (Zelenitsky *et al.*, 2008; Lauters *et al.*, 2012; Sakagami and Kawabe, 2020; Knoll *et al.*, 2021; Paulina-Carabajal *et al.*, 2023).

The midbrain, or optic tectum, was not visible in the cranial endocranium of *F. dhimbangunmal*; however, its absence is expected given that such structures are not typically observed in ornithomimid endocrania (Evans *et al.*, 2009; Lauters *et al.*, 2012; Lautenschlager and Hübner, 2013; Thomas, 2015; Brasier *et al.*, 2017). Even broadly among dinosaur cranial endocrania, the midbrain is indistinguishable from other regions and obscured by the cerebellum and/or thick venous sinus(es) (Hopson, 1979; Thomas, 2015). A notable exception is in small coelurosaurian dinosaurs, in which optic lobes can be readily observed and are linked to greater visual acuity (Hopson, 1979; Kundrát, 2007; Balanoff *et al.*, 2014). In non-iguanodontian ornithomimids, similar hypotheses have been made for the cranial fragment (NMV P185990) referred to *Leaellynasaura amicagraphica* Rich and Vickers-Rich, 1989, from the Eumeralla Formation (upper Aptian–lower Albian) in Victoria (Rich and Vickers-Rich, 1989), noting that this referral has also been questioned based on taphonomic arguments (Herne *et al.*, 2016). Nevertheless, the optic tectum is distinguishable in this small-bodied

ornithomimid, suggesting comparatively strong visual capabilities, which was a possible adaptation to the prolonged dark winter months of its polar environment (Galton, 1989; Rich and Vickers-Rich, 1989; Kundrát, 2007; Rich *et al.*, 2010; Buchholtz, 2012). However, *F. dhimbangunmal* may have been less dependent on its visual capabilities because its type locality (the Griman Creek Formation) was at a lower paleolatitude (~60°S) than the Eumeralla Formation (70–85°S) and likely experienced milder winter conditions (Rich and Vickers-Rich, 1989; Poropat *et al.*, 2018; Bell *et al.*, 2019a, b; Kitchener *et al.*, 2019). In either case, the primitive, indistinguishable optic lobes observed in *F. dhimbangunmal* highlight the unique condition seen in '*L. amicagraphica*' (NMV P185990), supporting previous visual adaptation and lifestyle hypotheses (Rich and Vickers-Rich, 1989), although a juvenile condition of the brain could alternatively account for exposure of the optic lobes, which may have become more embedded in the midbrain at a later ontogenetic stage (Agnolin *et al.*, 2010). These findings further demonstrate potentially diverse evolutionary paleoneurological trajectories between penecontemporaneous Australian ornithomimids and highlight the need for future endocranial reconstructions of other Gondwanan taxa.

Conclusion

This study provides the first description of the neuroanatomy of the Australian non-hadrosaurid iguanodontian, *Fostoria dhimbangunmal*. The braincase of *F. dhimbangunmal*, from which the cranial endocranium was derived, is crushed dorsoventrally and only a partial cranial endocranium was recovered, missing its anterior, posterior, and ventral limits. The overall morphology of the endocranium is similar in some regards to other large-bodied non-hadrosaurid iguanodontians (e.g., a relatively enlarged cerebrum, anteroposteriorly extended hindbrain). However, the olfactory apparatus is well developed, possibly indicative of strong olfactory capabilities (Lauters *et al.*, 2012; Lautenschlager and Hübner, 2013; Knoll *et al.*, 2021). The endocranium of *F. dhimbangunmal* also differs from most hadrosaurids in its ancestral flexure pattern and less developed cerebral hemispheres, although we cannot rule out diagenetic crushing as a major influence on the observed morphology in *F. dhimbangunmal*. A unique vacuity within the supraoccipital may represent a new autapomorphic feature of *Fostoria dhimbangunmal*. The endocranium of *F. dhimbangunmal* also differs from the only other Australian ornithomimid known to have an endocranium, NMV P185990 ('*Leaellynasaura amicagraphica*'), highlighting the unique development of the optic lobes in the latter. We recommend that future research should investigate Gondwanan non-hadrosaurid iguanodontian paleoneurology to improve our global understanding of ornithomimid behavior and brain evolution more generally.

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