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RAPID COMMUNICATION

THE ENDOCAST OF *EUPARKERIA* SHEDS LIGHT ON THE ANCESTRAL ARCHOSAUR NERVOUS SYSTEM

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Abstract: Understanding the evolution of the tetrapod brain is essential to trace the history of ecomorphological diversification of modern clades. While previous studies focused on the morphological transformation of the nervous system along the dinosaur–bird transition, little is known about the brain anatomy of archosauriformes and early archosaurs. Here, we describe the endocast of *Euparkeria capensis*, a small bodied, terrestrial archosauriform closely related to Archosauria, with the goal of resolving the current uncertainties surrounding the ancestral condition of the archosaurian nervous system. The endocast of *Euparkeria* is sigmoidal, with large olfactory bulbs, an expanded cerebral hemisphere and an elongated flocculus. We suggest that this pivotal taxon was an active predator with a remarkable olfactory acuity. Overall, the endocast of *Euparkeria* resembles the ones observed in phytosaurs, crocodilians and early dinosaurs, implying that modern crocodilians retain an archosaurian plesiomorphic brain morphology.

Key words: Archosauria, brain, ecomorphology, *Euparkeria*.

THE tempo and mode of evolution of the nervous system in tetrapods is a fundamental question in biology. The brain of Archosauria, the clade including Pseudosuchia and Avemetatarsalia, underwent major morphological rearrangement. Birds, the extant representatives of avemetatarsalians, possess a vertically organized brain, which is distinguished by reduced olfactory bulbs, an enlarged cerebrum, lateroventrally shifted optic lobes and an expanded cerebellum (Hopson 1977; Alonso *et al.* 2004; Balanoff *et al.* 2013; Fabbri *et al.* 2017; Beyrand *et al.* 2019). This condition strongly differs from the one found in pseudosuchians, the clade including modern crocodilians (Kley *et al.* 2010; Holloway *et al.* 2013; Stocker *et al.* 2016; Fabbri *et al.* 2017; Pierce *et al.* 2017; Baczko *et al.* 2018; Mastrantonio *et al.* 2019); although retaining a sigmoidal silhouette in lateral view, the nervous system of these taxa is horizontally arranged with large olfactory bulbs connected to the cerebrum via elongated olfactory tracts; the midbrain is medially positioned, in line with a relatively small cerebellum.

The evolution of the avian brain from their dinosaur ancestors has been the major focus of previous research. Because of its phylogenetic position as sister clade to Avemetatarsalia, the brain morphology of crocodilians (and Pseudosuchia in general) has usually been considered to be the archosaurian ancestral condition. However, it is unclear whether, rather than representing the plesiomorphic condition, the semi-aquatic ecological adaptation characterizing the more recent evolutionary history of this clade affected its brain morphology, leaving an important gap in our understanding of the evolution of the nervous system among archosaurs.

Parasuchidae is a clade composed of longirostrine, semi-aquatic archosauriforms, anatomically convergent with modern crocodiles. Although still debated, the clade is phylogenetically placed as the earliest diverging branch or sister taxon of Archosauria (Nesbitt 2011; Ezcurra 2016). Investigation of the brain endocast of multiple parasuchid taxa has shown a certain degree of similarity with the brain of modern crocodilians (Lautenschlager & Butler 2016; Lessner & Stocker 2017). It has previously been argued that such phenotypical similarity in the nervous system is the result of a shared aquatic ecomorphological convergence (e.g. Lessner & Stocker 2017), rather than representing the ancestral archosaur condition. Additional support of this hypothesis was found in the endocasts of earlier archosauriforms, such as *Proterosuchus* (Brown *et al.* 2020), *Prolacerta* (Stocker *et al.* 2016), and a few terrestrial Triassic pseudosuchians (Holloway *et al.* 2013), which show a more tubular arrangement of the brain regions, as in *Sphenodon* and other squamates (Fabbri *et al.* 2017; Macrì *et al.* 2019; Yohe *et al.* 2020). Based on this, the plesiomorphic condition in

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Archosauria remains unclear, affecting our understanding of evolutionary and developmental patterns that shaped the divergence of archosaurian clades.

Euparkeria capensis is a bipedal (Demuth *et al.* 2020), terrestrial (Botha-Brink & Smith 2011; Fabbri *et al.* 2022) archosauriform from the Triassic of South Africa (Gower 1997; Gower & Weber 1998; Sobral *et al.* 2016; Sookias *et al.* 2020). Although its phylogenetic affinities are not fully resolved, it is widely accepted to be closely related to Archosauria (Nesbitt 2011; Ezcurra 2016). Because of its phylogenetic position and its land-dwelling ecology, *Euparkeria* represents the ideal taxon to clarify the ancestral condition of the nervous system in Archosauria and to resolve the stepwise character acquisition marking the evolutionary morphogenetic rearrangement of the brain towards the origin of birds. Here, we qualitatively describe the endocast of *Euparkeria capensis* and discuss implications for its neurosensorial capabilities and the ancestral archosaur brain.

MATERIAL AND METHOD

The specimen under study is the holotype of *Euparkeria capensis*, SAM-PK 5867. Although the skull is partially deformed, the three-dimensional braincase remains remarkably well preserved, with the exception of the disarticulated laterosphenoids (Sobral *et al.* 2016; Fabbri *et al.* 2017; Sookias *et al.* 2020). The skull was CT-scanned at the University of the Witwatersrand Bernard Price Institute for Palaeontological Research (BPI) (Fabbri & Bhullar 2022). Scanning was conducted with an X Tek HMX ST 225 (Nikon Metrology Inc.), comprising 3000 projections, using a tungsten target with gain 4 and binning 0. Files were reconstructed using CT Pro 3D software (Nikon Metrology, Inc.) Scan settings were as follows: 70 kV, 140 μA, 1000 ms, 57.50 μm voxel size, 1.8 mm Al filter.

The scan was imported in VGStudio 3.4 Max for segmentation and isolation of the braincase elements, namely the frontals, parietals, occipital complex, parabasisphenoid and laterosphenoids. The laterosphenoids were segmented first and then rearticulated with the other braincase elements in VGStudio 3.4 Max (Fig. 1), following the methods in Fabbri *et al.* (2021). The correct re-articulation of the laterosphenoids was based on both the sutures of the surrounding skull elements and anatomical comparisons with *Proterosuchus* (Brown *et al.* 2020), *Gracilisuchus* (Fabbri *et al.* 2017) and modern crocodilians. The rearticulated braincase was exported as a mesh, then imported into VGStudio Max 3.4 as a new volume for manual segmentation of the endocast. Smoothing was applied to the resulting region of interest of the endocast in VGStudio Max 3.4 following Balanoff *et al.* (2016) to exclude artefacts deriving from segmentation; this was then extracted as a mesh for illustration of the endocast morphology in this study.

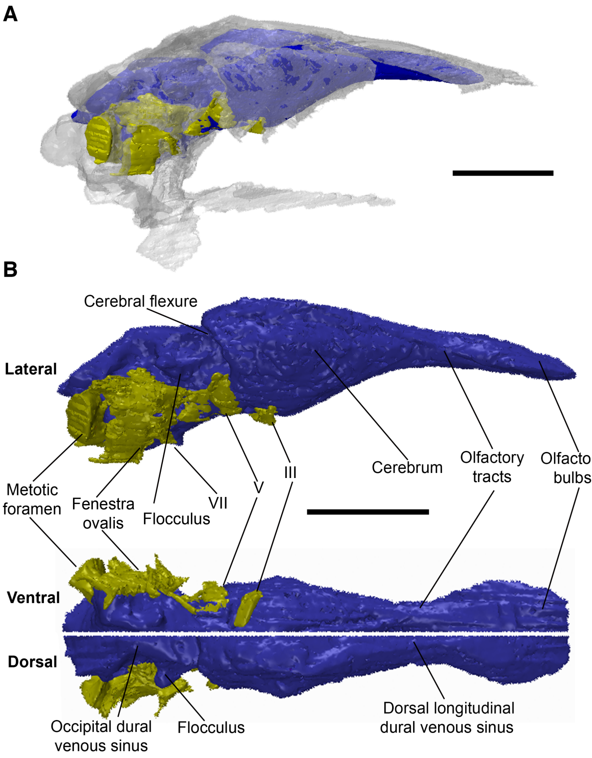

FIG. 1. Endocast of *Euparkeria capensis*. A, transparent mesh of the reconstructed braincase (blue) of *Euparkeria* with endocast (yellow) *in situ*. B, endocast of *Euparkeria* in lateral, ventral and dorsal views. Roman numbers (III, V and VII) refer to cranial nerves. Both scale bars represent 20 mm.

To estimate the sigmoidal shape of the endocast, we quantified the cephalic and pontine flexures following Lautenschlager & Hübner (2013). The relative size of the olfactory bulbs and the flocculus, previously used to respectively infer the sense of smell (e.g. Zelenitsky *et al.* 2011) and trends in agility (e.g. Stocker *et al.* 2016), were quantified in freely available software Fiji (https://imagej.net/software/fiji/downloads). The olfactory bulb ratio (ob) was calculated as the ratio between the longest diameter of the olfactory bulb and the cerebrum, regardless of the orientation, and multiplied by 100. The relative size of the flocculus (flocculus ratio, fe) was calculated as the ratio between the maximum length of the flocculus and the whole endocast, multiplied by 100. Measurements were taken for 13 additional extinct and extant archosaromorphs as a qualitative comparative framework (Table 1).

Institutional abbreviations. BSPG, Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany; CAPPA/UFSN, Centro de Apoio à Pesquisa Paleontológica da Quarta Colônia da Universidade Federal de Santa Maria, São João do Polêsine, Brazil; IGM, Instituto de Geología,

TABLE 1. Measurements of olfactory bulb and flocculus ratios among selected archosauromorphs.

Taxon	Specimen	References	ob	fe
Euparkeria capensis	SAM-PK-5867	This study; Fabbri *et al.* (2017)	58.9	5.1
Proterosuchus fergusi	RC 846	Brown *et al.* (2020) and Fabbri *et al.* (2017)	60	3.35
Parasuchus angustifrons	BSPG 1931 X 502	Lautenschlager & Butler (2016)	58.9	5.7
Pseudopalatus mccauleyi	USNM 15839	Holloway *et al.* (2013)	58.5	2.56
Triopticus primus	TMM 31100-1030	Stocker *et al.* (2016)	41.8	8.07
Gracilisuchus stipanicicorum	MCZ 4117	Fabbri *et al.* (2017)	53.3	5.41
Simosuchus clarki	UA 8679	Kley *et al.* (2010)	44.5	5.62
Alligator mississippiensis	Uncatalogued	Yohe *et al.* (2020) and Fabbri *et al.* (2017)	55.4	5.42
Herrerasaurus ischigualastensis	PVSJ 407	Fabbri *et al.* (2017)	48.56	5.15
Buriolestes schultzi	CAPPA/UFSM 0035	Müller *et al.* (2020)	49.3	5.35
Allosaurus fragilis	UUVP 5961	Fabbri *et al.* (2017)	51.6	10.96
Alioramus altai	IGM 100/1844	Bever *et al.* (2011)	65.9	8.38
Gallus gallus	Uncatalogued	Yohe *et al.* (2020) and Fabbri *et al.* (2017)	15.4	12.2

ob is defined as the ratio between the maximum linear measurement of the olfactory bulb and the cerebrum diameters; fe is calculated as the ratio between the maximum linear measurement of the flocculus and the total length of the endocast. Both ratios are given in percentages.

Universidad Nacional Autónoma de México, México; MCZ, Museum of Comparative Zoology, Harvard University, USA; PVSJ, División de Paleontología de Vertebrados del Museo de Ciencias Naturales y Universidad Nacional de San Juan, Argentina; RC, Rubidge Collection, Wellwood, Graaff-Reinet, South Africa; SAM, Iziko South African Museum, Cape Town, South Africa; TMM, Texas Memorial Museum, Austin, USA; UA, Universite d'Antananarivo, Antananarivo, Madagascar; USNM, National Museum of Natural History, Smithsonian Institution, Washington DC, USA; UUVP, University of Utah Natural History, Salt Lake City, USA.

RESULTS

The endocast is mediolaterally narrow (Fig. 1). It appears linearly organized and sigmoidal in lateral view, as in phytosaurs (Lautenschlager & Butler 2016; Lessner & Stocker 2017), pseudosuchians (Kley *et al.* 2010; Holloway *et al.* 2013; Stocker *et al.* 2016; Fabbri *et al.* 2017; Pierce *et al.* 2017; Baczko *et al.* 2018; Mastrantonio *et al.* 2019) and early dinosaurs (Sampson & Witmer 2007; Witmer *et al.* 2008; Bronzati *et al.* 2017; Fabbri *et al.* 2017; Müller *et al.* 2020) (Fig. 2). The volume of the endocast is 1.459 cm^3.

The olfactory fossae present in the frontals clearly delimit the extension of the olfactory bulbs, which appear to be relatively large and are only partially separated in their cranial most portion. The ob ratio is 58.8%, similar to that of other archosauriforms, parasuchids, pseudosuchians and early dinosaurs (Zelenitsky *et al.* 2011) (Table 1). Elongated olfactory tracts (21.5% of the total endocast length) connect the olfactory bulbs to the cerebrum. Because of the lack of ventral ossification of the braincase (Fig. 1), the delimitation of the olfactory bulbs and tracts is based on the lateral limitations of the laterosphenoids and the depth of the frontal fossa encasing the bulbs. Our endocast reconstruction of the olfactory complex should therefore be considered as a conservative estimate.

The cerebrum is piriform and expanded caudally. A median interhemispheric sulcus dividing the two hemispheres of the cerebrum is not visible, suggesting that the dural envelope in this region did not faithfully match the morphology of the brain. The visible dorsal longitudinal dural venous sinous overlaps with the olfactory tracts and the cranial portion of the cerebrum. A pineal–parapineal complex, a trait present in all extant reptiles (Quay 1979; Stocker *et al.* 2016) other than crocodilians, is not found, in agreement with the lack of a pineal foramen in the skull roof of *Euparkeria* (Sobral *et al.* 2016; Sookias *et al.* 2020).

Following the cerebral hemisphere, and coinciding with the widest region of the endocast, a marked cephalic flexure (134°) indicates the transition from the cerebrum to the midbrain (*sensu* Lautenschlager & Hübner 2013). If a dorsal division between midbrain and hindbrain (such as that observed in phytosaurs and earlier archosauriforms, e.g. *Proterosuchus* (Fig. 2)) is present, it is obscured by the occipital dural venous sinus. However, morphological features exemplifying lateralization of the optic lobes are absent, implying that, as in other archosauriforms, non-avian and non-pterosaurian archosaurs, the optic lobes were in contact along the midline of the brain. The pontine flexure (*sensu* Lautenschlager & Hübner 2013) is 110°. The only feature clearly recognizable for the hindbrain is the flocculus, which is better preserved on the right side. Contrary to previous interpretations, the

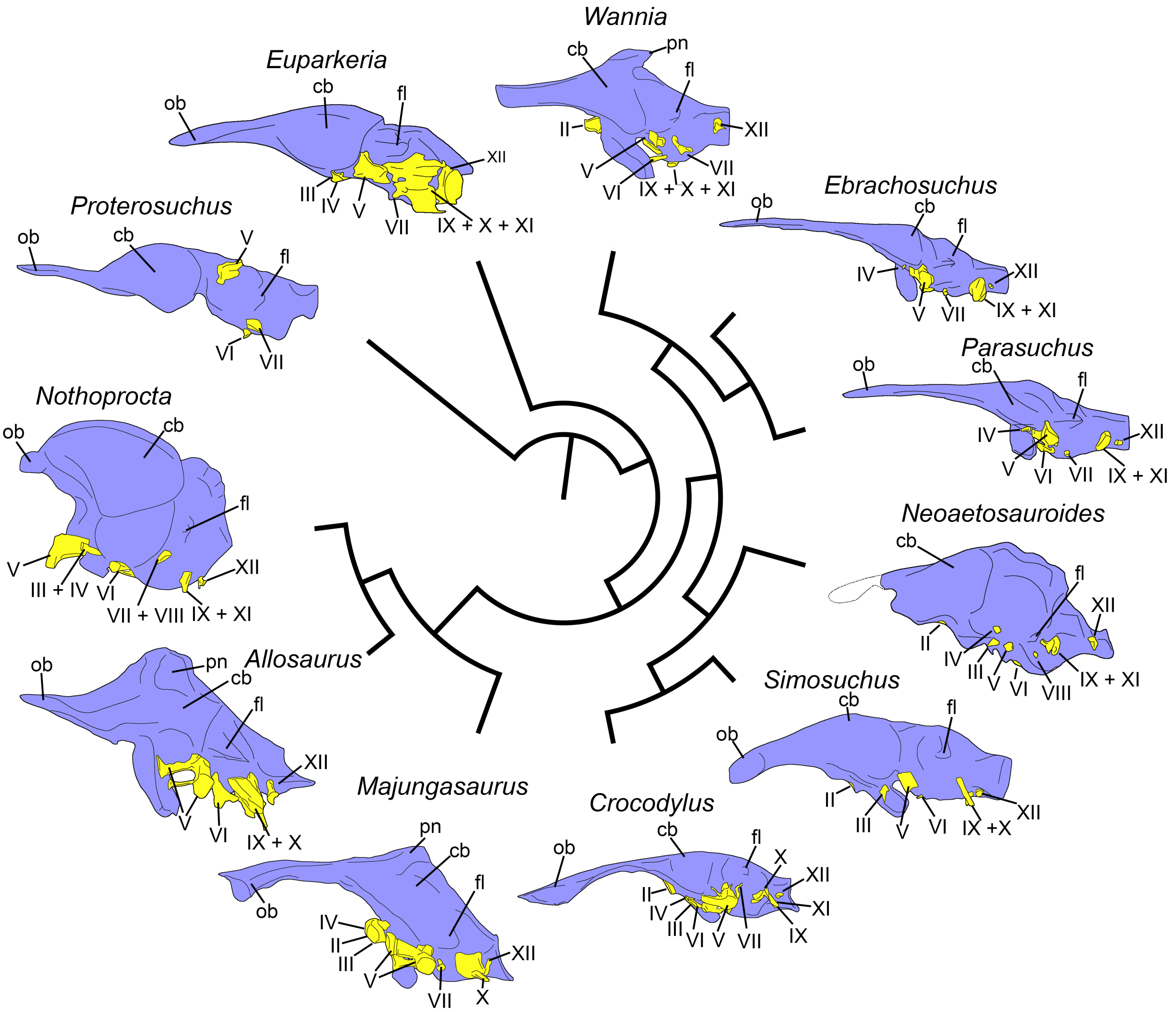

FIG. 2. Evolutionary comparative framework of endocranial anatomy among archosauromorphs. The informal phylogenetic tree is based on Ezcurra *et al.* (2020). Endocasts were redrawn from the literature: *Proterosuchus* from Brown *et al.* (2020), *Euparkeria* from this study, *Wannia* from Lessner & Stocker (2017), *Ebrachosuchus* and *Parasuchus* from Lautenschlager & Butler (2016), *Neoceratoides* from Baczko *et al.* (2018), *Simosuchus* from Kley *et al.* (2010), *Crocodylus*, *Majungasaurus* and *Allosaurus* from Witmer *et al.* (2008), and *Nothoprocta* from Torres & Clarke (2018). *Abbreviations*: cb, cerebrum; fl, flocculus; ob, olfactory bulbs; pn, pineal expansion; II–XII, cranial nerves.

floccular lobe appears to be relatively well developed and elongated (5.1% of the total endocast length) when compared to other archosauriforms, such as *Proterosuchus* and *Pseudopalatus* (Table 1). The relative size of the floccular lobe is similar to other phytosaurs, such as *Parasuchus*, the pseudosuchians *Gracilisuchus*, *Simosuchus* and *Alligator*, and early dinosaurs, such as *Herrerasaurus* and *Buriolestes* (Fig. 2, Table 1). On the other hand, it is not as developed as in the stem pseudosuchian *Triopticus* (8% of the total endocast length) and tetanuran dinosaurs (Table 1). Caudally, the width of the endocast increases towards the foramen magnum.

Although not all the exits of the cranial nerves (CN) could be reconstructed due to incompleteness of the braincase elements, the general arrangement of the observed cranial innervation is conserved and similar to modern crocodilians and phytosaurs (Fig. 2). Large oculomotor nerves (CN III, IV) are placed ventrally to the cerebrum at the suture of the laterosphenoids. CN V (trigeminal) is placed below the hindbrain and is relatively large in comparison to other archosauriforms, but not as large as in *Desmatosuchus* and other aetosaurs (Baczko *et al.* 2018, 2021). CN IX, X, and XI converge on the large fenestra ovalis, which connects to the ear system. The metotic foramen, a lateral opening enclosing the recessus scala tympani and cranial nerves such as the vagus, is relatively large in *Euparkeria*, suggesting a potential secondary reduction in phytosaurs and early stem archosaurs (Fig. 2).

DISCUSSION

Euparkeria shows major morphological innovation in comparison to earlier archosauriforms. Specifically, the expansion of the cerebral hemisphere causes the appearance of a sigmoidal brain shape, which differs from the tubular outline found of *Proterosuchus* (Brown *et al.* 2020), *Tropidosuchus* (Trotteyn & Paulina-Carabajal 2016) and earlier archosauromorphs. On the other hand, although a pineal process is absent, the overall anatomy of the endocast of *Euparkeria* is remarkably similar to the one observed in phytosaurs, pseudosuchians (including modern crocodilians) and non-paravian dinosaurs (Fig. 2). The morphological similarity between phytosaurs and crocodiles is therefore unlikely to be dictated by the independent acquisition of a semiaquatic ecology, but rather reflects the plesiomorphic condition of the archosaurian nervous system. Previous three-dimensional (Fabbri *et al.* 2017) and two-dimensional (Brown *et al.* 2020) quantification of brain morphology among reptiles by means of geometric morphometrics support a retained plesiomorphic condition among these basal groups, independently from ecomorphological adaptations characterizing their evolutionary diversification.

The study of endocasts of fossil taxa provides clues to their ecomorphological behaviour. The sensorial capabilities of *Euparkeria* can be extrapolated in a qualitative fashion from the endocast here described. The size of the olfactory bulbs was previously found to correlate with the quantity, and potentially diversity, of olfactory receptors, which are proteins responsible for olfactory detection (Steiger *et al.* 2009; Zelenitsky *et al.* 2011; Müller *et al.* 2018; Yohe *et al.* 2020). The size of the olfactory bulbs in *Euparkeria* is strikingly similar to that of earlier archosauriforms, phytosaurs, crocodiles and non-avian dinosaurs, implying similar olfactory adaptation in these animals (Fig. 2, Table 1). Additionally, the olfactory bulbs are larger than the optic lobes, a stereotypical condition in squamates, crocodilians, non-volant stem archosauriforms and non-avian theropod dinosaurs. We therefore suggest that *Euparkeria* was primarily driven by smell in its interaction with the surrounding environment.

The flocculus size has the important role in stabilizing gaze such as the vestibulo-ocular and vestibulocollic reflexes through coordination of the eyes, head and neck (Witmer *et al.* 2003; Voogd & Wylie 2004; Sereno *et al.* 2007; Cassone & Kumar 2014; Stocker *et al.* 2016). The relatively large flocculus suggests that *Euparkeria* was an active predator.

Finally, our results have important implications for evolutionary and developmental studies focused on archosaurs, and reptiles in general. The plesiomorphic condition of the archosaur brain found in *Euparkeria* and among early diverging stem archosaurs is remarkably similar to that of extant crocodilians, implying evolutionary conservatism of the plesiomorphic condition for the brain phenotype through time among non-avian archosaurs. Because of their plesiomorphic anatomy, our study confirms modern crocodilians as remarkably relevant organisms in the study of the nervous system in evolutionary developmental biology.

CONCLUSION

Because of the abundance of semiaquatic species characterizing the early divergence of archosaurs and the uncertainty on how this ecology affected the morphology of the nervous system, the inference of the plesiomorphic phenotype of the archosaur brain has been difficult to resolve. Based on the investigation of the endocast of the terrestrial archosauriform *Euparkeria*, our study shows that pseudosuchians and phytosaurs retain a sigmoidal and elongated brain characterized by large olfactory bulbs and long olfactory tracts, and a relatively small midbrain and hindbrain. This is here interpreted as the plesiomorphic condition for the archosaur nervous system.

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Author contributions. **Conceptualization** Matteo Fabbri (MF), Bhart-Anjan S. Bhullar (B-ASB); **Investigation** B-ASB (CT-scanning), MF (segmenting braincase elements, rearticulating braincase & segmenting endocast); **Supervision** B-ASB; **Writing – Original Draft Preparation** MF; **Writing – Review & Editing** MF.

DATA ARCHIVING STATEMENT

The .stl files of the *Euparkeria* endocast described herein, and the reconstructed braincase, are available in the Dryad Digital Repository: https://doi.org/10.5061/dryad.r4xgxd2gh

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