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Palaeoneurology and palaeobiology of the dinocephalian therapsid *Anteosaurus magnificus*

JULIEN BENOIT, ASHLEY KRUGER, SIFELANI JIRAH, VINCENT FERNANDEZ, and BRUCE S. RUBIDGE

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Dinocephalians (Therapsida), some of the earliest amniotes to have evolved large body size, include the carnivorous Anteosauria and mostly herbivorous Tapinocephalia. Whilst the palaeoneurology of the Tapinocephalia has been investigated in *Moschognathus whaitsi*, that of the Anteosauria remains completely unknown. Here we used X-ray micro-Computed Tomography to study, for the first time, the palaeoneurology of *Anteosaurus magnificus*. Compared to *Moschognathus*, we reconstruct *Anteosaurus* as an agile terrestrial predator based on the enlarged fossa for the floccular lobe of the cerebellum and semicircular canals of the inner ear. A major difference between the two genera resides in the orientation of the braincase, as indicated by the angle between the long axis of the skull and the plane of the lateral semicircular canal. This angle is 25° in *Anteosaurus*, whereas it is 65° in *Moschognathus*, which suggests that the braincase of the latter was remodelled as an adaptation to head-butting. This is consistent with less cranial pachyostosis and the retention of a large canine in Anteosauria, which suggests that dentition may have been used for intraspecific fighting and display in addition to trophic interactions. The evolution of a thick skull, horns, and bosses in tapinocephalids parallels the evolutionary reduction of the canine, which lead to a shift of the agonistic function from the mouth to the skull roof, as observed in extant social ungulates. Similarly, tapinocephalians may have developed complex social behaviour.

Key words: Therapsida, Dinocephalia, head-butting, carnivory, trigeminal nerve, bony labyrinth.

Julien Benoit [julien.benoit@wits.ac.za; ORCID: https://orcid.org/0000-0001-5378-3940], Sifelani Jirah [sifelani.jirah@wits.ac.za; ORCID: https://orcid.org/0000-0002-6747-4388, and Bruce S. Rubidge [bruce.rubidge@wits.ac.za; ORCID: https://orcid.org/0000-0003-2477-1873], Evolutionary Studies Institute (ESI); School of Geosciences, University of the Witwatersrand, PO WITS, 2050, Johannesburg, South Africa.
Ashley Kruger[ashleykruger@gmail.com; ORCID: https://orcid.org/0000-0003-1196-8693], Department of Palaeobiology, Swedish Museum of Natural History, Post Office Box 50007, SE-104 05 Stockholm, Sweden.
Vincent Fernandez [v.fernandez@nhm.ac.uk; ORCID: https://orcid.org/0000-0002-8315-1458], European Synchrotron Radiation Facility, 71 Avenue des Martyrs, 38000 Grenoble, France; Imaging and Analysis Centre, Natural History Museum, Cromwell Road, SW7 5BD, London, UK.

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Introduction

Head-butting (wrestling and ramming) is a widespread behaviour among modern ungulate mammals. Taxa that regularly engage in this behaviour are usually characterised by a suite of specialized anatomical traits that protect the brain (e.g., extensive pachyostosis or pneumatization) and conspicuous cranial ornamentation such as bosses and horns that are often sexually dimorphic (Geist 1966; Emlen 2008). Combat is usually associated with complex behavioural traits such as sexual display, territoriality, and hierarchical social behaviour (Geist 1966; Schaffer and Reed 1972; Emlen 2008; Cabrera and Stankowich 2018), and intraspecific contests are undertaken to secure mating partners and territory (Geist 1966). Accordingly, the suggestion of intraspecific fighting in extinct species implies a certain degree of behavioural complexity.

Dinocephalians were a diverse and abundant group of mostly large-bodied therapsids that are restricted to the middle Permian (265–260 Ma) (Rubidge and Sidor 2001; Kemp 2005; Angielczyk and Kammerer 2018). They are classified in the carnivorous Anteosauria and the primarily herbivorous Tapinocephalia, including the family Tapinocephalidae (Angielczyk and Kammerer 2018;

Fraser-King et al. 2019). Tapinocephalid dinocephalians are characterised by extensive pachyostosis of their skull roof, remodelling of their braincase (complete ossification of the ventral aspect of the braincase and mesethmoid, anterior shift of the occipital condyle, and posterior tilting of the braincase) and the presence of often grotesque cranial adornments (horns and bosses), which have been interpreted as adaptations to use the head as a weapon (Brink 1958; Barghusen 1975; Benoit et al. 2016b, 2017c). In contrast, the Anteosauria and other non-tapinocephalid dinocephalians display a lesser degree of cranial pachyostosis (Kammerer 2011) and the bones of their braincase are thinner (Boonstra 1968). In addition, the vertical orientation of the occiput in *Anteosaurus* indicates that the cranial roof did not align with the neck during head-butting, in contrast to the situation in tapinocephalids, which increased the risk of injuries to the skull, neck articulation, and spinal cord while fighting (Barghusen 1975). This suggests that non-tapinocephalid dinocephalians either did not engage in head-butting or practiced a low energy version of it, such as flank-butting (Barghusen 1975). Among anteosaurs in particular, if intraspecific agonistic behaviours occurred (combat and display), they would likely have involved the oversized canines, as in modern sabre-toothed ungulates (Geist 1966; Emlen 2008; Cabrera and Stankowich 2018). Pachyostosis of the cranial roof and circum-orbital regions in *Anteosaurus* and *Titanophoneus* could have evolved to absorb the load generated by the powerful external adductor musculature during bites, rather than as an adaptation for head-butting (Kammerer 2011).

Although head-butting behaviour is well supported for tapinocephalids (Barghusen 1975; Benoit et al. 2016b, 2017c; Angielczyk and Kammerer 2018), relatively little research on this subject has been undertaken on non-tapinocephalids and understanding the polarity of the tapinocephalid palaeoneurological features proves challenging as no other dinocephalian nervous system has yet been studied. The current study utilises X-ray micro Computed Tomography (XμCT) to elucidate the paleoneurology of the anteosaurian *Anteosaurus magnificus* Watson, 1921, the best known and most abundant carnivorous dinocephalian from the South African Karoo (Kammerer 2011; Kruger et al. 2018). Comparison with the internal neurological structures of a non-head-butting dinocephalian with that of a head-butting tapinocephalid will improve our understanding of cranial adaptations for head-to-head combat in the tapinocephalid lineage and its implications for the palaeobiology of all dinocephalians.

Institutional abbreviations.—AM, Albany Museum (Grahamstown, South Africa); BP, Evolutionary Studies Insitute (formerly Bernard Price Institute, Johannesburg, South Africa); MB.R, Museum für Naturkunde, Fossil Reptile Collection (Berlin, Germany); PIN, Paleontological Institute of Moscow (Russia).

Material and methods

The disarticulated skull (BP/1/7074) of a juvenile *Anteosaurus magnificus* from the middle Permian of the South African Karoo (from mudstone L of the Moordenaars Member of the Abrahamskraal Formation, farm Bullekraal, Beaufort West district (Jirah and Rubidge 2014; Day and Rubidge 2014, 2020) was XμCT scanned to be digitally re-articulated some years ago (Kruger et al. 2018) but, due to the presence of numerous metallic inclusions, the contrast was not sufficient to distinguish internal structures well, particularly the delicate maxillary canal for the trigeminal nerve and the osseous capsule of the inner ear (bony labyrinth). As a result, the left maxilla and complete occiput were scanned again at the Evolutionary Studies Institute (ESI) using Nikon Metrology XTH 225/320 LC with a 225 kV reflection target, to obtain workable resolution and contrast. The following parameters were used: 140 kV, 150 μA, and an isotropic voxel size of 0.089 mm for the occiput, and 120 kV, 150 μA, and an isotropic voxel size of 0.102 mm for the maxilla. Both scans were performed with a 2.5 mm copper filter.

The recently scanned maxilla and occiput were digitally re-positioned onto the 3D model of the complete skull compiled by Kruger et al. (2018). The 3D reconstruction of BP/1/7074 was accomplished using VSG's Avizo® Fire (FEI VSG, Hillsboro OR, USA). Each element was exported as a PLY file and was read into memory as a surface file. The surface files were combined as separate elements manually by rotation, translation, and alignment. The skull reconstruction was accomplished by reconstructing the separate areas of the skull roof, palate, and occiput. Once the translation and rotation of the individual elements were as close to real-life as possible, translation was applied. A total of 22 elements that were missing or damaged were replaced by mirroring the opposing complete element and then added to the reconstruction. Much of the right side of specimen BP/1/7074 was reconstructed from the left.

The left maxillary canal, bony labyrinths, and brain endocast were segmented manually using Avizo® 9 (FEI VSG, Hillsboro OR, USA). The maxillary canal was segmented following the method described by Benoit et al. (2016a) as the canal running through the maxilla that carries the maxillary branch of the trigeminal nerve in modern amniotes. It extends from the maxillary sinus posteriorly and internally to the "nutrient" foramina of the snout anteriorly and externally. The branches of the maxillary canal in *Anteosaurus* were identified and named after the corresponding branches of the trigeminal nerve in modern mammals, as their homology in non-mammalian therapsids and modern mammals is now well supported (Benoit et al. 2016a, b, 2017c, d, 2019; Laaß and Kaestner 2017; Wallace et al. 2019; Pusch et al. 2019, 2020). It should be noted that in extant species the maxillary canal also carries blood vessels and some segments of the facial nerve (Watkinson 1906; Bellairs 1949; Abdel-Kader et al. 2011).

Table 1. Measurements of the bony labyrinth of *Anteosaurus magnificus* Watson, 1921 (BP/1/7074) and *Moschognathus whaitsi* Broom, 1914 (AM4950, from Benoit et al. 2017b, d).

Measurement	*Anteosaurus*	*Moschognathus*
Skull length (mm)	280	340
Body mass (g)	71031	327367
Length bony labyrinth (mm)	38	36
Vestibule length (mm)	21	22
Anterior semicircular canal radius (mm)	6.16	5.73
Anterior semicircular canal length (mm)	20.01	20.28
Anterior semicircular canal eccentricity	0.42	0.52
Anterior semicircular canal lumen diameter (mm)	1.63	1.58
Lateral semicircular canal radius (mm)	4.41	4.27
Lateral semicircular canal length (mm)	13.64	12.08
Lateral semicircular canal eccentricity	0.44	0.02
Lateral semicircular canal lumen diameter (mm)	1.96	3.09
Posterior semicircular canal radius (mm)	4.89	4.06
Posterior semicircular canal length (mm)	18.56	12.30
Posterior semicircular canal eccentricity	0.36	0.58
Posterior semicircular canal lumen diameter (mm)	1.54	1.31
Average semicircular canal radius (mm)	5.15	4.69
Coefficient of agility (Spoor et al. 2007)	5	4
Angle between the anterior and lateral semicircular canals (°)	78	90
Angle between the posterior and lateral semicircular canals (°)	93	74
Angle between the anterior and posterior semicircular canals (°)	73	76
Angle between the long axis of the skull and the plane of the lateral semicircular canal (°)	25	65

The bony labyrinths were segmented out from the occiput fragment. As the right bony labyrinth is better preserved, the description and measurements are mostly based on the morphology of this side. Measurements of the bony labyrinth (Table 1) were taken digitally using Avizo® 9 and following the protocol of Benoit et al. (2017b) (see SOM, Supplementary Online Information available at http://app.pan.pl/SOM/app66-Benoit_etal_SOM.pdf). Semicircular canal eccentricity and lumen diameter were measured following Araújo et al. (2018). The values in Table 1 were averaged from the measurements taken on the right and left bony labyrinths, except for the semicircular canal radii and eccentricity, which could be measured only on the right side. The angle between the main axis of the skull and the plane of the lateral semicircular canal could only be measured on the right side as the prootic and opisthotic are displaced on the left side of the occiput. The coefficient of agility was calculated using the equation of Spoor et al. (2007) and Silcox et al. (2009) using the average semicircular canal radius and an estimation of the body mass of BP/1/7074 (Table 1). The body mass of BP/1/7074 was estimated using Benoit et al's (2017a) equations based on a cranial length of 280 mm (Kruger et al. 2018).

The brain endocast was reconstructed using the Scan Surface to Volume function of Avizo® 9 on the digitally re-articulated skull of BP/1/7074. This enabled the conversion of the 3D model into a series of stacked images on which manual segmentation could be performed. It should be noted that even though BP/1/7074 is an almost complete skull, it lacks the orbitosphenoids and the digitally articulated bones do not fit perfectly onto each other (Kruger et al. 2018). As such, the so-obtained endocast only gives a rough idea of the outlines of the endocast and no description or measure of the endocast volume could be safely performed. However, this reconstruction shows the orientation of the braincase inside the skull, which is an important character while discussing adaptations to head-butting in dinocephalians (Boonstra 1968; Benoit et al. 2017c).

Specimen BP/1/7074 is here compared to AM4950 (erroneously referred to as AM6556 in Benoit et al. 2016b), a sub-adult tapinocephalid skull (skull length 340 mm, see Table 1), whose palaeoneurology has been thoroughly studied using synchrotron radiation micro-computed tomography (Benoit et al. 2016b, 2017a, c). This specimen was previously identified as *Moschops capensis*, but was recently tentatively re-assigned to *Moschognathus whaitsi* Broom, 1914 (Neumann 2020). Specimen AM4950 was scanned in two parts at the European Synchrotron Radiation Facility (Grenoble France) on the ID17 beamline: first the snout in 2007, and then the braincase in 2015 (see Benoit et al. 2016b, 2017c for more detail). The temporary export of the material for synchrotron scanning was enabled by the South African Heritage Resources Agency (cases 8090 and 8560).

Results

Bony labyrinth.—The bony labyrinth of *Anteosaurus* specimen BP/1/7074 is a cavity within the occiput fragment that molds the shape of the membranous inner ear. It is divided

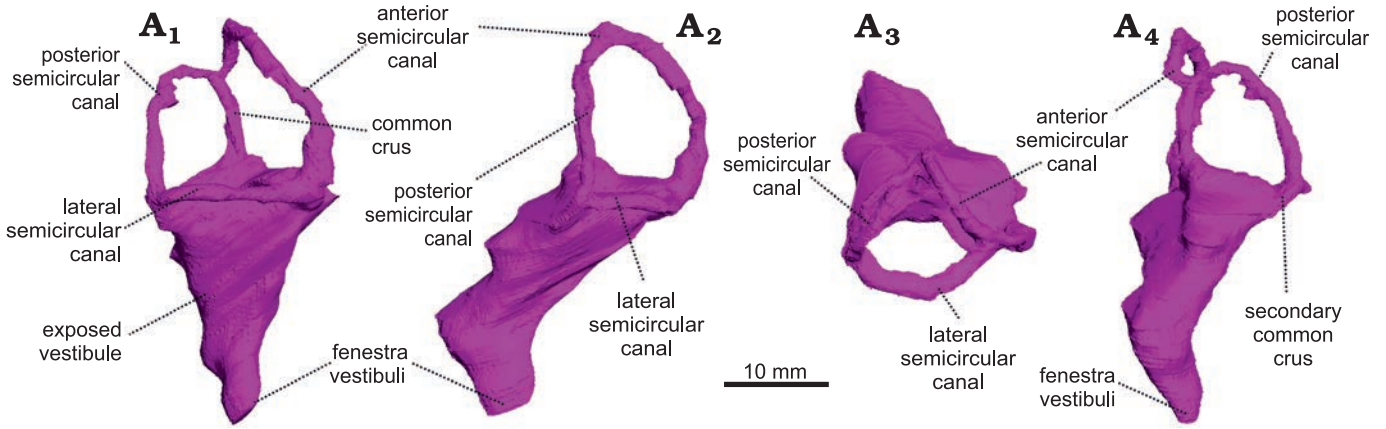

Fig. 1. The right bony labyrinth of *Anteosaurus magnificus* Watson, 1921 (BP/1/7074) from the middle Permian of farm Bullekraal, South Africa. In lateral view (A_1), posterolateral view parallel to the plane of the anterior semicircular canal (A_2), dorsal view (A_3), posterior view perpendicular to the plane of the anterior semicircular canal (A_4).

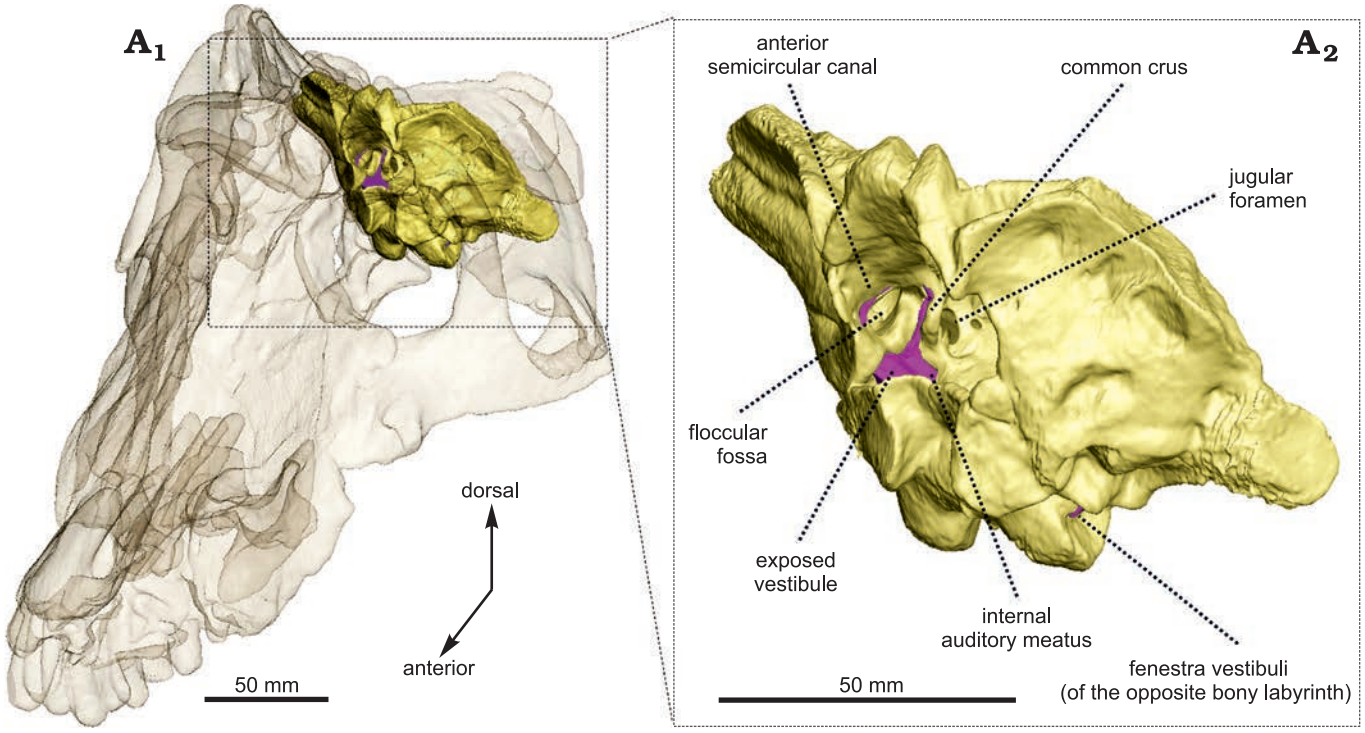

Fig. 2. Occiput fragment of *Anteosaurus magnificus* Watson, 1921 (BP/1/7074) from the middle Permian of farm Bullekraal, South Africa. Internal view showing the exposure of the bony labyrinth (purple) in the braincase (A_1), enlarged view (A_2).

between a ventral vestibular part (the auditory organ) and the semicircular canals dorsally (the balance organ) (Graf and Klam 2006; Ekdale 2016). The total length of the bony labyrinth from the fenestra vestibuli to the dorsalmost end of the anterior semicircular canal is 38 mm, which is 1.5 mm longer than that of *Moschognathus* (Benoit et al. 2017b, c). This suggests the two specimens are comparable in terms of bony labyrinth development stages, despite the skull of BP/1/7074 being about 20% smaller than that of AM4950, and only one-third the maximum size for *Anteosaurus* (Kruger et al. 2018). The total volume of the labyrinth is 1.27 cm^3.

The vestibule is bordered by the basisphenoid medially, the prootic anteriorly, and the opisthotic posteriorly. As in *Moschognathus*, the vestibule looks like a long cone in lateral view that tapers ventrally towards the fenestra vestibuli (Fig. $1A_1$). In posterior and posterolateral views, the vestibule bends ventrolaterally at its midlength (Fig. $1A_2$, A_4) as in gorgonopsians and some dicynodonts (Sigogneau 1974; Araújo et al. 2017; Bendel et al. 2018; Araújo et al. 2018; Benoit et al. 2017b), whereas the vestibule of *Moschognathus* is straight (Benoit et al. 2017b, c). No cochlear canal is present. The vestibule is 21 mm long, 13 mm (right side) to 14 mm (left side) large, and its maximum mediolateral thickness is 6 mm (Table 1). The stapedial ratio (length-to-width ratio of the fenestra vestibuli) is 1.1 on the right side and 1.0 on the left side, which indicates a rounded fenestra

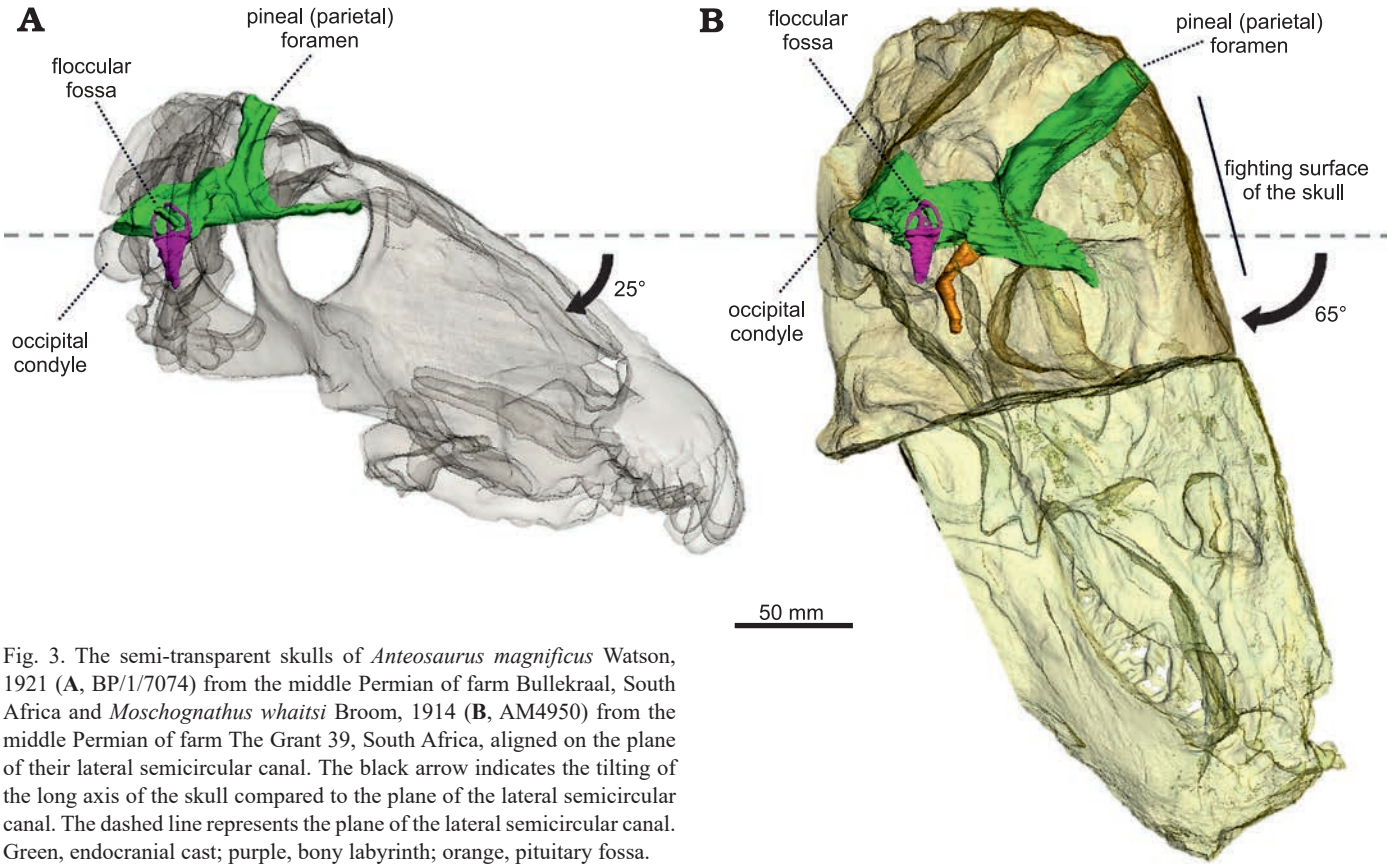

Fig. 3. The semi-transparent skulls of *Anteosaurus magnificus* Watson, 1921 (**A**, BP/1/7074) from the middle Permian of farm Bullekraal, South Africa and *Moschognathus whaitsi* Broom, 1914 (**B**, AM4950) from the middle Permian of farm The Grant 39, South Africa, aligned on the plane of their lateral semicircular canal. The black arrow indicates the tilting of the long axis of the skull compared to the plane of the lateral semicircular canal. The dashed line represents the plane of the lateral semicircular canal. Green, endocranial cast; purple, bony labyrinth; orange, pituitary fossa.

vestibuli. As in *Moschognathus* (AM4950) and *Syodon* (PIN 2505/1 and PIN 157/1047; Ivakhnenko 2008), the dorsalmost part of the vestibule of *Anteosaurus* is exposed medially in the brain cavity (Fig. 2). The vestibule and jugular foramen are located in two distinct recesses inside the brain cavity (Fig. 2) as in gorgonopsians and other dinocephalians (Boonstra 1968; Kemp and Parrington 1969; Sigogneau 1974; Ivakhnenko 2008).

The semicircular canals are bordered by the prootic (anterior semicircular canal and ampullar limb of the lateral semicircular canal) and opisthotic (posterior semicircular canal and posterior limb of the lateral semicircular canal). The anterior canal may contact the supraoccipital dorsally, although the suture is obscured by the iron-rich matrix in XμCT data. Medially, the anterior semicircular canal and the common crus are exposed in the braincase (Fig. 2). In *Syodon* the ampullae of all three semicircular canals are largely exposed in the braincase, but the anterior semicircular canal is completely enclosed in an osseous tube (Ivakhnenko 2008). Unlike in *Moschognathus* (Benoit et al. 2017c), the space delineated by the anterior semicircular canal is pierced by a deep and broad floccular fossa in *Anteosaurus*. Among non-mammalian therapsids, such a deep floccular fossa is also present in *Syodon*, gorgonopsians, and cynodonts (Sigogneau 1974; Hopson 1979; Ivakhnenko 2008; Araújo et al. 2017; Benoit et al. 2017b; Pusch et al. 2019). All three semicircular canals have a roughly oval outline (Fig. 1) and are more slender than in *Moschognathus* (Benoit et al. 2017b, c). As in *Moschognathus* (Benoit et al. 2017b, c), the ampullae are inconspicuous (Fig. 1). The anterior canal has the largest radius of curvature and is the longest of all three canals, whereas the lateral one is the smallest and shortest (Table 1), as is usual in therapsids, including mammals (Ivakhnenko 2008; Ekdale 2013; Castanhinha et al. 2013; Benoit et al. 2017b; Araújo et al. 2017, 2018; Pusch et al. 2019). The anterior canal is also taller than the posterior one as it reaches higher dorsally (Fig. $1A_1$). Even though the skull of BP/1/7074 is smaller than that of AM4950, the radius of curvature of all three semicircular canals is larger in BP/1/7074 than in AM4950, and the average radius of curvature is 0.47 mm larger in BP/1/7074 than in AM4950 (Table 1). BP/1/7074 also has longer posterior and lateral semicircular canals than AM4950, whereas their anterior canals are equivalent in length (Table 1). BP/1/7074 and AM4950 also differ by the angle between the plane of the lateral semicircular canal and the main axis of the skull. This angle is about 25° in BP/1/7074, whereas it is much larger (about 65°) in AM4950 (Fig. 3). The angles between the anterior and lateral semicircular canals and between the anterior and posterior semicircular canals are smaller in *Anteosaurus* than in *Moschognathus*. In contrast, the angle between the posterior and lateral semicircular canals is larger in *Anteosaurus* (Table 1). The posterior and lateral semicircular canals are fused into a secondary common crus (Fig. $1A_4$), as is usual in non-mammalian therapsids and early mammals (Ekdale 2013; Benoit et al. 2017b). Unlike in biarmosuchians (Benoit

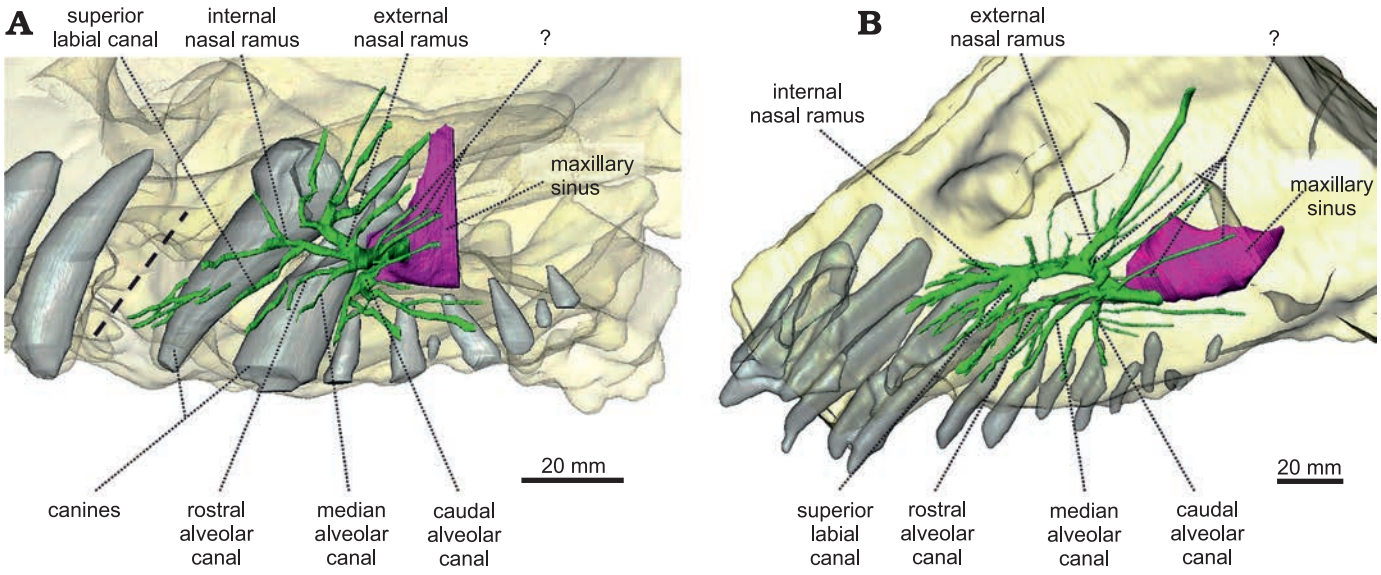

Fig. 4. The maxillary canal system of *Anteosaurus magnificus* Watson, 1921 (**A**, BP/1/7074) from the middle Permian of farm Bullekraal, South Africa and *Moschognathus whaitsi* Broom, 1914 (**B**, AM4950) from the middle Permian of farm The Grant 39, South Africa. The dashed line indicates the position of a crack in BP/1/7074. Green, maxillary canal; purple, maxillary sinus; light grey, teeth.

et al. 2017b), the posterior canal does not project ventrally below the level of the plane of the lateral semicircular canal, although it is evident that the posterior canal enters the vestibule slightly below the plane of the lateral semicircular canal (Fig. 1A$_4$).

Maxillary canal.—The maxillary canal appears to be a morphologically conservative structure in dinocephalians, judging by its similarity in the two genera documented so far, *Anteosaurus* and *Moscognathus*. Compared to that of other non-prozostrodontian synapsids (Benoit et al. 2016a, b, 2017d, 2018, 2019; Laaß and Kaestner 2017; Wallace et al. 2019; Pusch et al. 2019, 2020) the maxillary canal of *Anteosaurus* is relatively short anteroposteriorly, as in *Moschognathus* (Fig. 4). Caudally, the maxillary canal of *Anteosaurus* emerges from the maxillary sinus above the level of the second postcanine tooth. The maxillary sinus could not be completely reconstructed digitally because of the fragmentary nature of the maxilla of BP/1/7074. Between the level of the first and second postcanines, almost immediately after leaving the maxillary sinus, the caudal alveolar canal branches off the maxillary canal ventrally (Fig. 4A). As in *Moschognathus*, it ramifies further distally into two branches oriented ventrally and three branches oriented posteriorly (Fig. 4A). Three branches of unknown identification are located immediately dorsally to the alveolar canal and are positioned dorsolaterally (Fig. 4A). Similar branches are present in *Moschognathus* (Fig. 4B) as well as in the therocephalians *Bauria* and *Olivierosuchus* (Benoit et al. 2017d) and in the anomodont *Patranomodon* (Benoit et al. 2018), in which they were identified as belonging to the external nasal branch of the maxillary canal. We prefer to remain cautious about the identity of these rami as they do not stem from the same trunk as the external nasal branch (Fig. 4). Anterior to the caudal alveolar branch, the rostral and medial alveolar branches diverge anteroventrally from a common trunk, as in *Moschognathus* (Fig. 4). They remain simple in *Anteosaurus*, although an isolated branch may belong to either the rostral alveolar or the superior labial branches (Fig. 4A). In contrast, the rostral alveolar branch is extremely ramified (as is the superior labial branch) in *Moschognathus*, most likely to innervate and supply the soft tissue associated with the elaborate rostral dentition in this tapinocephalid (Fig. 4B) (Benoit et al. 2017a). The external nasal ramus is the most ramified branch of the maxillary nerve in *Anteosaurus*. It branches off the maxillary canal at the level of the functional canine (Fig. 4A) and comprises five branches directed dorsally and slightly caudally. This departs from the condition in *Moschognathus* in which the external nasal ramus is dominated by one long and thick branch oriented dorsocaudally (Fig. 4B). A similar condition is encountered in the therocephalian *Lycosuchus* (Pusch et al. 2020) and the anomodont *Patranomodon* (Benoit et al. 2018). The condition in *Anteosaurus* looks more similar to that in other non-prozostrodontian therapsids (Benoit et al. 2016a, b, 2017d, 2018, 2019; Laaß and Kaestner 2017; Pusch et al. 2019). Even more rostrally in *Anteosaurus*, at the level of the replacement canine, the maxillary canal divides into two branches oriented rostrally (Fig. 4A). The dorsalmost branch is the internal nasal ramus, which is itself divided into a dorsal and ventral branch. The ventralmost branch is the superior labial ramus, which appears to bear no ramification. Three isolated canals oriented anteroposteriorly might belong to one of the superior labial or internal nasal branches, or may represent purely vascular, "nutrient" canals (Fig. 4A).

Discussion

Adaptations to carnivory.—Because of its recurved canines, bone-crushing dentition, prominent pterygoid processes, and enlarged temporal fenestrae that provide large points of insertion for powerful jaw adductor musculature, *Anteosaurus* has been unquestionably interpreted as a carnivorous animal (Boonstra 1954b; Kammerer 2011). These adaptations to carnivory are expected to be reflected in the nervous system as well (Witmer and Ridgely 2009; Grohé et al. 2018; King et al. 2020). The bony labyrinth of *Anteosaurus* is remarkable for its large semicircular canals compared to those of *Moschognathus*, both in terms of length and radii of curvature (Table 1), even though the *Anteosaurus* skull studied here (BP/1/7074) is 20% smaller than that of AM4950. The average radius of curvature of all three semicircular canals is 5.15 mm in BP/1/7074, which is greater than that of all non-mammalian therapsids studied so far (Castanhinha et al. 2013; Rodrigues et al. 2013; Benoit et al. 2017b; Araújo et al. 2017, 2018; Pusch et al. 2019, 2020). Few non-mammalian therapsids are large enough to be compared to *Anteosaurus*, but Pusch et al. (2020) reported an average semicircular canal radius of 3.44 mm in the contemporaneous carnivorous therocephalian *Lycosuchus* (specimen MB.R.995) with similar skull length (estimated to 260 mm). As *Anteosaurus* has semicircular canals larger than both *Moschognathus* and *Lycosuchus*, it is safe to conclude that its semicircular canals are larger than expected for a middle Permian therapsid of this size. This is supported by the agility score calculated for BP/1/7074, which is five (given an estimated body mass of 71 kg for this individual, Table 1). This corresponds to a medium-to-fast-moving animal and is equivalent to that of a mountain lion (*Felis concolor*) among modern carnivores (Spoor et al. 2007). In comparison, the agility score of *Moschognathus* and *Lycosuchus* is four (using body masses estimated from skull lengths using the equation of Benoit et al. 2017b) which corresponds to less agile animals (Spoor et al. 2007). As the semicircular canals are involved in synchronizing eye, head, and neck movements, larger semicircular canals compared to body size are usually associated with enhanced tracking abilities, agility, and fast locomotion in carnivores (Spoor et al. 2007; Silcox et al. 2009; Witmer and Ridgely 2009; Ryan et al. 2012; Grohé et al. 2018; King et al. 2020). The skull of BP/1/7074, which is a juvenile, is only one third the maximum size for *Anteosaurus magnificus* (Kruger et al. 2018) and it is not yet known whether the proportions of the semicircular canals would be conserved in adulthood. Current data on the ontogeny of the bony labyrinth in non-mammalian therapsids are scarce, and it is difficult to assess if their bony labyrinth reached their adult morphology early in ontogeny as in mammals (e.g., in primates [MacPhee 1981; Daniel et al. 1982; Jeffery and Spoor 2004], rodents and rabbits [Hoyte 1961; Lindenlaub and Burda 1993], carnivorans [Curthoys et al. 1982], afrotherians [Klaauw 1931; Fischer 1989], artiodactyls [Mennecart and Costeur 2016], and marsupials [Ekdale 2010]), or whether it continued growing throughout ontogeny as is plesiomorphic for amniotes (Bullar et al. 2019; Neenan et al. 2019). In the dataset published by Benoit et al. (2017b), the bony labyrinths of two specimens of the cynodont *Cynosaurus suppostus* of very different skull lengths were measured. The smallest skull measures 49.70 mm, slightly less than half the size of the adult one, which measures 115.83 mm. The bony labyrinths of the two specimens are 6.22 mm and 12.58 mm long, respectively. Although this is not enough data to suggest an isometric scaling of the bony labyrinth to cranial size, it nevertheless indicates that preservation of size proportions of the semicircular canals relative to skull length during ontogeny cannot be excluded in Permian therapsids.

The hypothesized enhanced locomotory and tracking abilities in *Anteosaurus* are also supported by the presence of a deep and broad floccular fossa compared to a very shallow one in *Moschognathus* (Fig. 3). The contrasting dimensions of the fossa in the closely related *Anteosaurus* and *Moschognathus* support the notion that this trait is not constrained by phylogeny in dinocephalians. Moreover, in mammals and non-mammalian therapsids, a deep floccular fossa is more typically encountered in small taxa (Hopson 1979; Gannon et al. 1988; Schmitt and Gheerbrant 2016), whereas *Anteosaurus* is one of the largest Anteosauria, which suggests that its deep floccular fossa was functionally significant. This structure housed the floccular lobe of the cerebellum, a region of the brain that monitors the vestibuloocular and vestibulocollic reflexes during motion, and enhances gaze stability while tracking moving prey (Sánchez-Villagra 2002; King et al. 2020). Sight stabilization would have been particularly important if anteosaurids were not hunting in broad daylight as suggested for *Titanophoneus* by using the dimensions of the sclerotic ring (Angielczyk and Schmitz 2014). Although the dimensions of the floccular fossa do not perfectly reflect the volume of the floccular lobe (Walsh et al. 2013), it is expected that agile, active terrestrial predators would have an enlarged floccular fossa (Hopson 1979; Witmer and Ridgely 2009; King et al. 2020; Schade et al. 2020; but see Ferreira-Cardoso et al. 2017 for a critical reappraisal of this hypothesis). Even though enlarged semicircular canals or floccular fossa alone are weak indicators of agility (David et al. 2016; Ferreira-Cardoso et al. 2017), taken together, the presence of both features in *Anteosaurus* gives a consistent signal supporting the idea that the latter was likely more agile than its herbivorous close relative *Moschognathus*. Overall, the palaeoneurology of *Anteosaurus* thus corresponds to that of a more agile and rapidly moving predator than previously considered based on its postcranial anatomy (Boonstra 1955), and far removed from the sluggish amphibious lifestyle that has been proposed for anteosaurids by some authors (Olson 1962; King 1988; Ivakhnenko 2008).

Re-organisation of the braincase and head-butting in tapinocephalids.—*Anteosaurus* and *Moschognathus* dif-

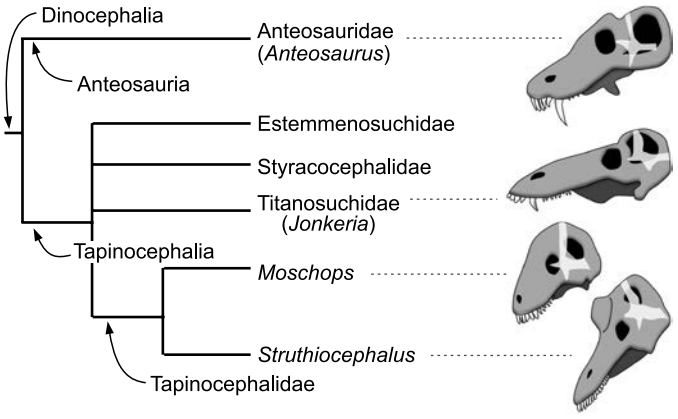

Fig. 5. Phylogeny of the Dinocephalia (after Fraser-King et al. 2019). Skulls and braincase (transparent white) redrawn after Boonstra (1968). The skulls are positioned so that their braincases are oriented the same way.

fer greatly in the orientation of the braincase compared to the rest of the skull (Fig. 3). In *Anteosaurus*, the long axis of the braincase and the skull are almost parallel, as in the other non-tapinocephalid dinocephalians *Syodon* and *Jonkeria* (Boonstra 1968; Ivakhnenko 2008), which illustrates that their braincase retains the plesiomorphic orientation for therapsids. In contrast, in *Moschognathus* the snout points distinctly downward when the braincase is horizontal (Benoit et al. 2017c). The same downward tilting of the snout is also observed when aligning the braincase to the horizontal in the tapinocephalids *Mormosaurus*, *Moschops*, *Keratocephalus*, and *Struthiocephalus* (Brink 1958; Boonstra 1968; Fig. 5). This orientation of the braincase can be quantified by measuring the orientation of the plane of the lateral semicircular canal compared to the long axis of the skull. This angle is 25° in *Anteosaurus*, whereas it is 65° in *Moschognathus* (Benoit et al. 2017c; Fig. 3). This demonstrates a dramatic re-organisation of the braincase in tapinocephalid dinocephalians (Brink 1958; Benoit et al. 2017c) which was probably driven by an adaptation to using the head as a weapon in this lineage as hypothesized by Barghusen (1975) and Benoit et al. (2017c) (Fig. 5).

Such misalignment of the braincase and snout is termed klinorhynchy or cyptocephaly in modern mammals and is usually interpreted as an adaptation to grazing or head butting in ungulates, or as a consequence of the enlargement of the braincase in Great Apes (Schaffer and Reed 1972; Lieberman et al. 2000; Solounias 2007). As the braincase of tapinocephalid dinocephalians is relatively small (Benoit et al. 2017a), the last hypothesis is unlikely. The downward pitching of the snout relative to the braincase could be an adaptation to feed on low vegetation (Solounias 2007), as hypothesized for the dinosaur *Nigersaurus* (Sereno et al. 2007) and modern Rhinocerotidae (Schellhorn 2018). However, this hypothesis is not supported by the data published by Benoit et al. (2017b), who documented the angle between the long axis of the skull and the plane of the lateral semicircular canal in 29 non-mammalian therapsids and found no difference between herbivores and carnivores. Diet is thus unlikely to account for the cyptocephaly of the tapinocephalid skull and adaptation to head-butting seems more likely.

Most authors accept that tapinocephalids were head-butting taxa (Geist 1972; Barghusen 1975; Rubidge and Sidor 2001; Kemp 2005; Emlen 2008; Benoit et al. 2016b, 2017c). Tapinocephalid skulls have numerous traits (such as ossified braincase, inner ear, and cranial architecture) that are interpreted as adaptations for head-butting and are absent or less pronounced in other dinocephalian taxa (Barghusen 1975; Benoit et al. 2016b, 2017c). The skull roof of tapinocephalids, as indicated in *Moschognathus* AM4950*,* comprises two histologically distinct layers (Benoit et al. 2016b, 2017c). The outer bony layer (15–20 mm thick) has dense, osteosclerotic cortical bone that covers a 40 mm thick layer of trabeculated, spongy bone. In some tapinocephalids cranial thickness can reach up to 310 mm around the pineal foramen (Boonstra 1954a; Day et al. 2015). These bone layers were likely covered by an external keratinous sheath since blood vessels supplied the surface of the hypothesized fighting surface in *Moschognathus* (Barghusen 1975; Benoit et al. 2016b, 2017c). The thickened and histologically differentiated cranial vault of tapinocephalids presumably aided in absorbing shocks and dissipating stresses as in pachycephalosaurid dinosaurs (Snively and Cox 2008; Snively and Theodor 2011). In addition, the ossified braincase in tapinocephalids was also an important adaptation to head-butting as the braincase walls comprise thick trabeculated bone that, coupled with thick meninges, would have protected the central nervous system against mechanical stress (Boonstra 1968; Benoit et al. 2016b, 2017c). The re-orientation of the braincase is also consistent with head-butting behaviour as it results in the posterior shifting of the parietal foramen in tapinocephalids compared to that of *Anteosaurus* (Fig. 5). This served to remove the delicate pineal eye from the top of the skull where it would have been directly exposed to blows (Benoit et al. 2017c) and to align the fighting surface, braincase, and occipital condyle with the neck, which enhanced the transmission and dissipation of energy to the body (Barghusen 1975; Benoit et al. 2017c) This cyptocephalic reorganisation of the braincase is similar to that of modern high energy head-butting mammals (Schaffer and Reed 1972).

Trends in dinocephalian behavioural evolution.—Among dinocephalians, the Anteosauria are distinguished from derived Tapinocephalia by their very large upper canines and their relatively small cranial adornments (Kammerer 2011; Angielczyk and Kammerer 2018; Kruger et al. 2018). The presence of a large canine and limited cranial pachyostosis is likely plesiomorphic for dinocephalians (Kammerer 2011; Fraser-King et al. 2019). The oversized canine was likely used as a weapon and/or a display tool during intraspecific contests for mates and territory to impress and stab rivals, as in the walrus and modern saber-toothed ruminants (Geist 1966, 1972; Emlen 2008). A low energy form of agonistic behaviour too cannot be excluded for *Anteosaurus* given the pachyostosis of its skull (Barghusen 1975; Benoit et al.

2016b), although the pachyostosis of the circum-orbital region may have enabled the skull to withstand the action of the powerful adductor musculature (Kammerer 2011) and the nasal ridge may have strengthened the snout against a large struggling prey. As such, head-butting is not a necessary condition to account for cranial pachyostosis in *Anteosaurus*. Tapinocephalia, on the other hand, show a transition from basal taxa that have both enlarged canines and pachyostotic cranial bosses and horns, such as the Titanosuchidae, Estemmenosuchidae, and Styracocephalidae, to the derived Tapinocephalidae that have a reduced or no visible caniniform but conspicuous cranial adornments and horns (Geist 1972; Angielczyk and Kammerer 2018; Fraser-King et al. 2019; Fig. 5). Such a displacement of the display/combat function from the mouth to the skull roof occurred numerous times in ruminants (e.g., cervids, giraffids) (Geist 1966; Cabrera and Stankowich 2018), rhinocerotids (Heissig 1973), and perhaps pachycephalosaurs (Dieudonné et al. 2020) and correlates significantly with a shift from solitary to social behaviour in ungulates (Cabrera and Stankowich 2018). Agonistic behaviour involving stabbing by canines is mostly found in solitary taxa as it would be counter-selected in gregarious species since individuals with open wounds would attract predators, thus threatening the security of the herd (Cabrera and Stankowich 2018). Also, living in herds would increase the probability of agonistic intraspecific encounters and thus the risk of individuals being fatally wounded (Geist 1966). In gregarious species, it is expected that an evolutionary shift toward more dissuasive and less harmful cranial adornments, such as the massive yet blunt cranial roof of tapinocephalids, would lead to more ritualized and less dangerous combat (Geist 1966, 1972; Emlen 2008; Cabrera and Stankowich 2018). Head-butting results in a ranking of individuals and implies social bonds and a hierarchical structure of the group that are two complex behavioural traits (Geist 1966; Schaffer and Reed 1972; Emlen 2008; Cabrera and Stankowich 2018). There is no direct evidence for gregariousness in tapinocephalids (i.e., parallel trackways), but group death assemblages comprising 5–12 individuals have been anecdotally reported (Gregory 1926; Boonstra 1955; Rubidge et al. 2019; Neumann 2020), which would support the hypothesis that tapinocephalids might have lived in small groups, at least intermittently.

Additionally (or alternatively), the evolutionary change from an omnivorous diet in basal tapinocephalians toward a more specialized herbivorous diet in tapinocephalids imposed a strong selection toward homodonty (i.e., the talon and heel morphology of tapinocephalid dentition) (Rubidge and Sidor 2001; Angielczyk and Kammerer 2018). This selected against the presence of a caniniform tooth, hence facilitating the displacement of the display/combat function to the cranial roof. A combination of a shift from carnivory to herbivory, and from biting contest to head-butting could well account for the re-organisation of the braincase in tapinocephalid dinocephalians (Fig. 5).

Conclusions

The study of the bony labyrinth, braincase, and maxillary canal of *Anteosaurus magnificus* enables, for the first time, comparison between the tapinocephalids and their non-head-butting relatives. The maxillary canals of *Anteosaurus* and *Moschognathus* are very similar, suggesting that the morphology of the trigeminal nerve was conservative in dinocephalians. The bony labyrinth of the two genera differs mostly in the larger dimensions of the semicircular canals in *Anteosaurus*, which, along with the presence of an enlarged floccular fossa, suggests that *Anteosaurus* was a comparatively more agile predator than hitherto envisioned. Comparisons of the orientation of the braincase and lateral semicircular canal between tapinocephalid and non-tapinocephalid dinocephalians confirm that the former were cyptocephalic, probably as a result of adaptations to withstand head-butting. Anteosaurids likely used their canines for display and face biting during agonistic intraspecific behaviours, whereas tapinocephalids were using their thickened, pachyostotic skulls for display and fighting. Accordingly, we hypothesize a displacement of the display/combat function during the evolutionary history of dinocephalians. This could be further tested by a systematic survey of fighting injuries and bite punctures on well-preserved skulls of dinocephalians, an approach that has already proven fruitful for many other taxonomic groups (Boucot 1990; Boucot and Poinar 2011; Peterson and Vittore 2012).

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