

Estimating the endocranial volume and body mass of *Anteosaurus*, *Jonkeria*, and *Moschops* (Dinocephalia, Therapsida) using 3D sculpting

Julien Benoit and A.J. Midzuk

ABSTRACT

Dinocephalians represent a highly successful early radiation of mid-Permian therapsids. Despite the abundance of their fossils, data on their paleoneurology is challenging to acquire and remain scarce. The current study proposes to overcome these challenges by using digital 3D sculpting. Based on previous works, realistic digital models of brain endocasts and live reconstructions of three taxa sampling the major families of Dinocephalia (*Anteosauridae*, *Titanosuchidae*, and *Tapinocephalidae*) were generated, their volumes measured, and endocranial volume and body mass were estimated. Encephalization quotients were calculated. The results suggest that the dinocephalians evolved a surprisingly high degree of encephalization for such early tetrapods. Some dinocephalians are hypothesized to have practiced head-butting, a complex social behavior, which would have favored the enlargement of the brain. Alternatively, the enlarged endocast may have been filled mostly by protective tissue to protect the central nervous system when the head was used as a weapon. This is supported by the apparent absence of direct imprints of the soft tissue of the brain on the endocast.

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INTRODUCTION

Dinocephalians were among the most conspicuous tetrapods in high latitude terrestrial ecosystems of the Guadalupian. They had a worldwide distribution, and their diversity encompassed large bone-crushing predators, small sectorial-toothed carnivores, and medium-sized to gigantic herbivores (Kammerer, 2011; Angielczyk and Kammerer, 2018). Alongside the pareiasaurs, they were among the first terrestrial vertebrates to come close to the 1000 kg threshold (Romano et al., 2021; Romano and Rubidge, 2021; Van den Brandt et al., 2024). This success and their abundance in the fossil record contrast sharply with the admittedly poor state of our knowledge about the evolution of their brain and behavior.

The paleoneurology of non-mammalian therapsids, particularly cynodonts, is a highly active field of research, with many dozens of endocasts described and measured, and many others being described each year (Jerison, 1973; Edinger, 1975; Rowe et al., 2011; de Simão-Oliveira et al., 2020; Kerber et al., 2021, 2023; Gigliotti et al., 2023; Benoit, 2023). In comparison, the literature on the behavior and paleoneurology of dinocephalians is scarce, most acutely when it comes to addressing their brain evolution using endocranial casts (Brink, 1958; Boonstra, 1968; Barghusen, 1975; Benoit et al., 2017a, b, 2021) as data is notoriously difficult to obtain.

Dinocephalian fossils are large, very heavy (due to pachyostosis), difficult to transport, and often preserved in compact sandstone that is difficult to prepare or X-ray scan. Well-preserved cranial material is rare, often broken, weathered, and unprepared. The dinocephalian braincase is often hidden beneath a thick pachyostosed skull that makes the endocast difficult to observe non-destructively. Moreover, dinocephalian paleoneurology has been the object of less research interest because, compared to cynodonts, they are less closely related to mammals (Hopson, 1979). So far, only two papers describe dinocephalian endocasts: Boonstra (1968) using sectioned and serially sectioned skulls, and Benoit et al. (2017a) using synchrotron scanning. The volume of the endocast has been estimated in only two species: *Moschognathus whaitsi* (AM 4950) and *Struthiocephalus whaitsi* (SAM-PK-12049), the former using the digitally segmented volume of the endocast and the second using graphic double integration on Boonstra's figure of SAM-PK-12049. The small sample size and fact that they both belong to the tapinocephalid family makes tracing general trends in

dinocephalian brain evolution impossible. Additionally, the endocranial volume of AM4950 is based on a subadult individual, and that of SAM-PK-12049 is based on an estimate made using graphic double integration, a technique whose accuracy has been criticized (Hurlburt, 1999; Hurlburt et al., 2013). More data is desperately needed to better understand dinocephalian evolution, their adaptation to head butting, and their possible gregariousness (Barghusen, 1975; Benoit et al., 2023a).

Similarly, body mass estimates, which are necessary to calculate the Encephalization Quotient (EQ) to compare brain size across taxa, are also difficult to obtain for dinocephalians. Equations based on individual limb elements fail to capture realistic body weight estimates in therapsids, in part because of their unusual body proportions (large head and relatively smaller body) and posture (Romano and Manucci, 2019; Romano and Rubidge, 2021). As a result, body mass estimates of dinocephalians are rare. Bakker (1975) proposed body weights that were rough visual estimates of taxa designated as *Anteosaurus*, moschopid, struthiocephalid, tapinocephalid, and *Titanosuchus*. Benoit et al (2017a, b) calculated the body mass of AM4950 and SAM-PK-12049 based on their skull length but admitted the equations used were not well-adapted to large specimens. Romano and Rubidge (2021) estimated the body mass of *Tapinocaninus pamela* based on a 3D life reconstruction and argued this is the most accurate way to approximate a realistic body weight. This last method requires that complete skeletal reconstructions are available. Body mass can strongly affect EQ results, so accurate estimates are essential to compare endocranial size across taxa. Over the last 10 years, many independent teams have shown that, to estimate body mass of extinct taxa, volumetric methods are experimentally better performing than classical regression formulas based on long bones or cranial dimensions, which have often given unlikely results in many tetrapod groups (Sellers et al., 2012; Bates et al., 2015; Brassey et al., 2015; Romano and Manucci, 2019; Romano et al., 2021, 2022; 2023).

Innovative and original approaches are necessary to cope with the issues presented above and enrich the therapsid dataset with more data on dinocephalian brain and body sizes. This study proposes to use Boonstra's (1968) figures to digitally recreate the endocasts of three dinocephalians in 3D: the Anteosauridae *Anteosaurus*, the Titanosuchidae *Jonkeria*, and the Tapinocephala-

lidae *Moschops*, thus expanding the phylogenetic coverage to two new families of dinocephalians (Figure 1). Following the method of Romano and Rubidge (2021), digital 3D sculpturing is used to provide accurate estimates of the body mass of these taxa. These data are then used to discuss the evolution of the EQ in dinocephalians.

MATERIAL AND METHODS

To be included in this study, dinocephalian taxa had to fulfil two conditions: firstly, a complete skeletal reconstruction of, at least, a very close relative had to be available in the scientific literature, and secondly the endocast had to be figured by Boonstra (1968). Only three genera matched this description, *Anteosaurus*, *Jonkeria*, and *Moschops*. Measurements of volume were made using Avizo (Thermo Fisher Scientific, Hillsborough, U.S.A.).

The life reconstructions of *Anteosaurus*, *Jonkeria*, and *Moschops* (Figure 2) were created in the open-source 3D software Blender (versions 3.8 and 4.8). Simple low-detail “base meshes” were generated from scratch in Blender’s Edit Mode and then converted into high detail models using a Multiresolution Modifier and Blender’s Sculpt Mode

Tools (Midzuk, 2020). The life reconstructions of *Moschops* and *Jonkeria* were based on complete skeletal reconstructions of *Moschops capensis* (Gregory, 1926) and *Jonkeria truculenta* (Broom, 1929; Boonstra, 1969) and digital cranial reconstructions (Midzuk, 2020). The reconstruction of *Anteosaurus* is based on the more complete post-cranial remains of the related taxon *Titanophoneus* (Orlov, 1958; Kemp, 2005) but incorporates a more robust torso, longer limbs and hypertrophied neck musculature needed to support the proportionally more robust and heavier skull. Life reconstructions based on figures in the existing literature is ultimately an interpretive process since i) different views of figured material do not always align perfectly, so slight proportional stretching is needed to reach realistic proportions and ii) these models represent the best interpretation of the data displayed by previous authors and not direct observation.

Body models were scaled to Boonstra’s specimens, and their volume measured. Body volumes were then converted into body weight by multiplying them with average body density (Table 1). For the alleged semi-aquatic taxa *Moschops* and *Jonkeria* (Bhat et al., 2022), the body density of

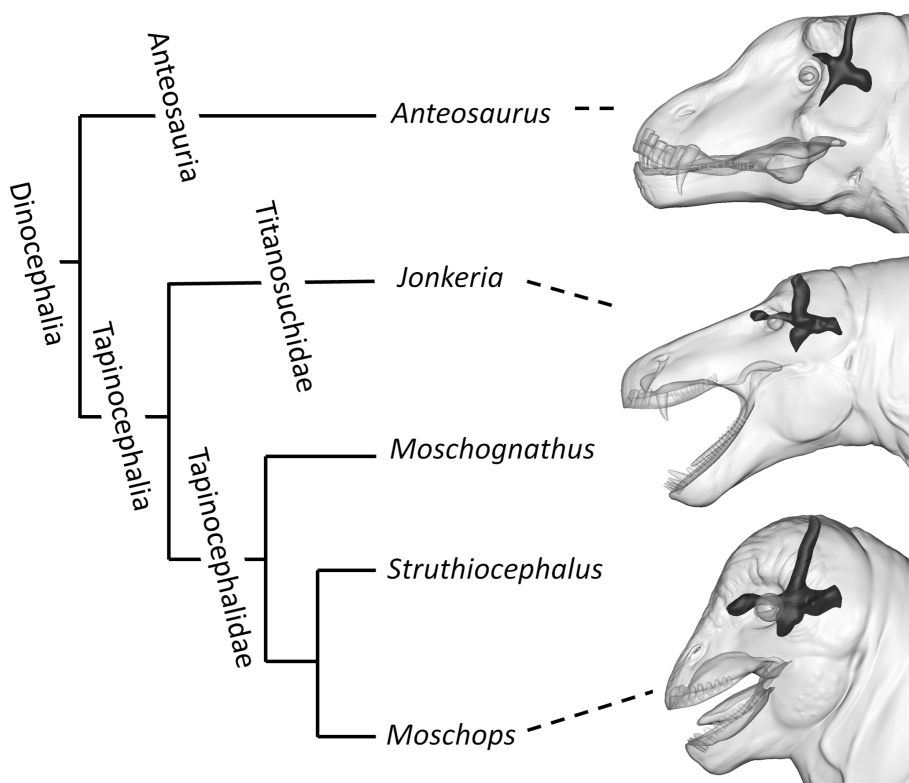
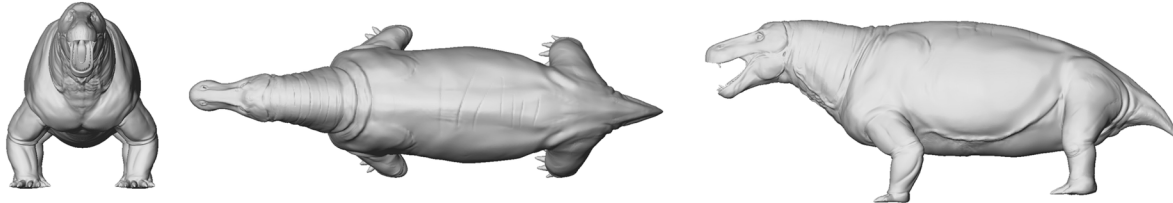


FIGURE 1. The phylogenetic sampling of dinocephalian taxa considered in this study. Pictures of endocast within transparent life reconstructions are not to scale. Phylogeny after Fraser-King et al. (2019) and Neumann (2020).

A. *Anteosaurus*



B. *Jonkeria*



C. *Moschops*

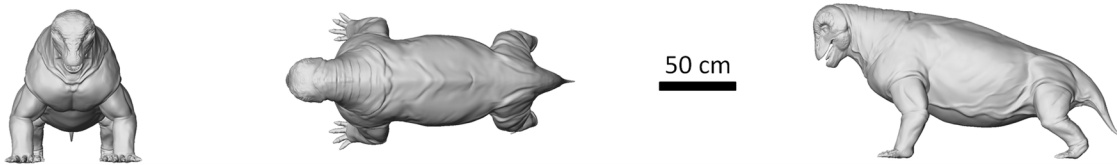


FIGURE 2. 3D digital life reconstructions of *Anteosaurus* (A), *Jonkeria* (B), and *Moschops* (C). Scale bar equals 50 cm.

aquatic mammals was preferred (i.e., 1.05; Larramendi, 2016; Larramendi et al., 2021). For *Anteosaurus*, a terrestrial predator (Benoit et al., 2021; Bhat et al., 2022), the average body density of terrestrial tetrapods was preferred (i.e., 1.00; Larramendi, 2016; Larramendi et al., 2021).

The endocast models (Figure 3) are based on the figured endocranial casts in Boonstra (1968). The 3D models of the endocranial casts of *Anteosaurus magnificus* (SAM-PK-12082), *Jonkeria truc-*

ulenta (SAM-PK-11574), and *Moschops* sp. (SAM-PK-11972) were digitally sculpted in Blender using blender’s sculpt mode and remeshing options. As a dorsal view of the endocranial cast of *Anteosaurus* is not supplied, so shape information in the coronal plane is inferred from the *Jonkeria* specimen. The olfactory cavities were included in the models, though these were not included in the volumetric analysis (see below). Blood vessels, the cochlea,

TABLE 1. Body and endocast measurements. All volumes in cm³, body mass in g. SEQ, synapsid encephalization quotient.

	Body Volume in cm ³	Body Mass (if terrestrial) in g	Body Mass (if semiaquatic) in g	Complete Endocast Volume (OB removed) in cm ³	Pineal Tube Volume in cm ³	Pituitary Fossa Volume in cm ³	Partial Endocast Volume (pituitary and pineal removed) in cm ³	SEQ (complete endocast)	SEQ (partial endocast)
<i>Anteosaurus magnificus</i> (SAM-PK-12082)	403587	403587	423766	163	26	21	116	1.91	1.36
<i>Jonkeria truculenta</i> (SAM-PK-11556)	942119	942119	989225	200	48	29	123	1.29	0.79
<i>Moschops</i> sp. (SAM-PK-11972)	405963	405963	426261	152	33	30	89	1.72	1.00

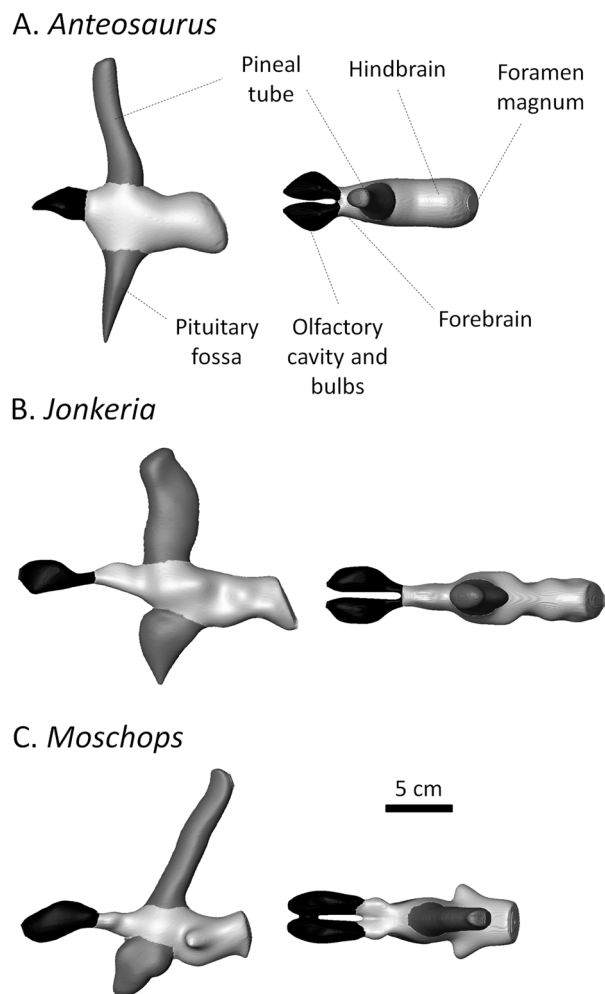


FIGURE 3. 3D digital reconstructions of the endocranial structures of *Anteosaurus* (A), *Jonkeria* (B), and *Moschops* (C). Scale bar equals 5 cm.

and other smaller structures were excluded from the sculpt.

The endocranial models were scaled to Boonstra's figures (Boonstra, 1968, figures 6, 7, 22, 24, 32, 37, 46, 49) in Avizo and their volume measured directly. The cast of the pineal tube and pituitary fossa are enlarged in dinocephalians, so measurements were made including and excluding these parts of the endocranium (Table 1). In Boonstra's endocranial drawings, part of the nasal chamber is mistakenly included with the olfactory bulbs (Benoit et al., 2017a). These are colored in black in Figure 3 and were not considered for measurements. Olfactory bulbs are usually removed from measurement of endocranial volumes in the literature (Jerison, 1973; Benoit et al. 2017a, b; Rodrigues et al., 2018) so this does not alter the interpretation of the results presented here. Rather than converting endocranial

volume into brain mass, raw endocranial volumes were used here to compute the EQ (see Discussion section).

As a validation step, a braincase model of the *Moschognathus* specimen AM4950 was digitally sculpted based on figure 3 in Benoit et al. (2017a) in order to compare its volume to that of the actual endocranium (Figure 4). The volume of the actual endocranium, excluding the pituitary fossa, is 61.1398 cm³ and that of the 3D sculpture is 60.9171 cm³, which indicates the volume measured from the sculpted model is 99.6% accurate. As such, it can be safely assumed that the volume of the 3D sculpted models provides a reasonable approximation for the volume of the corresponding original endocranium, likely because 3D sculpted models average deformation artifacts and reconstruction errors resulting in a similar volume.

Relative endocranial volumes were compared using the synapsid adjusted Encephalization Quotient (SEQ, Benoit et al., 2023a). It is expressed as follows: $SEQ = EV/10^{((0.669 \times \log BM) - 1.8188)}$, where EV is the endocranial volume and BM the body mass. An SEQ of one indicates an animal with an average relative endocranial size for a synapsid of the Paleozoic or Mesozoic. An SEQ above one indicates that the relative size of the endocranium is larger than expected for a synapsid of similar body mass, whereas an SEQ below one indicates that the relative endocranial size is smaller than expected. The resulting body mass, endocranial volumes, and encephalization quotients are summarized in Table 1.

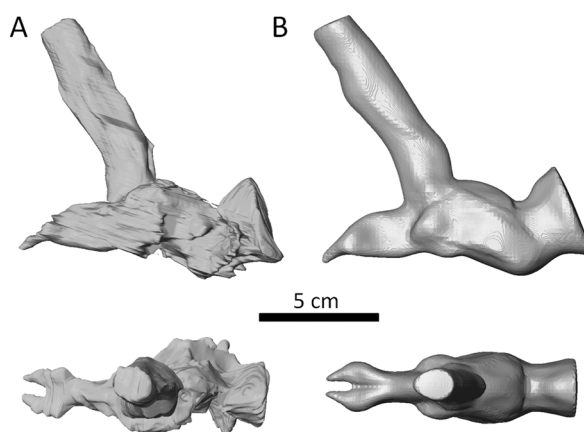


FIGURE 4. 3D digital reconstructions of the endocranium of *Moschognathus* specimen AM4950 in lateral (top) and dorsal (bottom) views, comparing the endocranium reconstructed by Benoit et al. (2017a) (A) to the 3D sculpted reconstruction made here for validation (B). Scale bar equals 5 cm.

Abbreviations. SAM-PK: Iziko Museum of Natural History, Cape Town, South Africa; AM: Albany Museum, Grahamstown (Makhanda), South Africa.

RESULTS

The body weight of the *Jonkeria* specimen approaches a ton (989 kg), which is close to the estimate given by Bakker (1975). The estimated body weights of *Anteosaurus* and *Moschops* are about 400 kg, which is below what Bakker (1975) estimated. The endocranial volumes are all comprised between 150 and 200 cm³, and between 80 and 130 cm³ when excluding the pineal tube and pituitary fossa (Table 1). The pineal tube in the dinocephalians studied here occupies 15% (*Anteosaurus*) to 25% (*Jonkeria*) of the volume of the braincase. The pituitary fossa occupies 13% of the endocranial volume in *Anteosaurus*, 15% in *Jonkeria*, and 20% in *Moschops* (Table 1). These are a lot more than measured in *Moschognathus* (less than 3%, Benoit et al., 2017a), although the latter is not a fully grown individual. That the tapinocephalids have proportionally larger pituitary fossa would support Nopcsa's (1926) and Boonstra's (1968) hypotheses that pachyostosis in this clade was linked to hyperpituitarism.

The SEQ (excluding the pineal tube and pituitary fossa) is slightly above one in *Anteosaurus* and equals one in *Moschops*; consistent with that previously calculated in *Moschognathus* (Benoit et al. 2017a). *Jonkeria* has the smallest SEQ. The SEQs calculated based on complete endocasts all exceed one (Figure 4). *Anteosaurus* even reaches a SEQ close to two (Table 1). Noticeably, Boonstra's figure of the endocast of *Anteosaurus* failed to capture the long and slender floccular fossa later described by Benoit et al. (2021). Although the volume difference may be close to negligible, an even higher EQ for this genus may be expected.

DISCUSSION

Previous attempts at calculating the EQ and SEQ in tapinocephalids (i.e., *Moschognathus* and *Struthiocephalus*) found that they were surprisingly encephalized for such large, Paleozoic animals (Benoit et al., 2017a, 2023). The data presented here bolster these previous results (Table 1). Dinocephalian SEQs approaching one supports that their brain was not small given their body size, except *Jonkeria*, which has an SEQ (excluding the pineal tube and pituitary fossa) well below one. The condition in *Jonkeria* is consistent with most non-theriodont synapsids (Figure 5) and may be the

ancestral condition for the clade. This would imply that anteosaurids and tapinocephalids independently evolved a larger endocast (Figure 5). Alternatively, an SEQ of one could be the ancestral condition, and the increase in body mass in titanosuchids would be responsible for the low SEQ in *Jonkeria*. Although the first hypothesis seems more likely given the current knowledge, the sampling of non-theriodont synapsids is still too small to properly address these hypotheses.

Whether the enlarged endocast of anteosaurids and tapinocephalids accommodated an equally large brain warrants some discussion. On the one hand, tapinocephalids most likely engaged in head-butting combat for mates and territory, a behavior that implies complex social interactions and hierarchy, which suggests they were likely gregarious tetrapods (Benoit et al., 2017a, 2023). A larger brain would have been advantageous to navigate this social space, which in turn would have favored brain enlargement (Dunbar, 2009). On the other hand, it must be noted that in cynodonts and early mammaliaforms, the enlarged olfactory bulbs, cerebellar vermis, and brain hemispheres leaves marks on the endocast (Kielan-Jaworowska, 2004; Rowe et al., 2011; Benoit et al., 2016). Similar observations were made on the endocast of the highly encephalized dicynodont *Kawingasaurus* (Laaß and Kaestner, 2017), which suggest that if the skull of dinocephalians was accommodating an enlarged brain, their braincase would likely have preserved imprints of the brain tissue like in their closest relatives. No such marks are present on the endocast of dinocephalians (Boonstra, 1968; Benoit et al., 2017a), which suggests that the central nervous system did not fill up the braincase, as in modern reptiles (Jerison, 1973).

When the complete endocast is considered (including the pineal tube and pituitary fossa), the SEQ of dinocephalians is much higher (Table 1, Figure 5). Reasoning on the principle that a hypothetical typical therapsid SEQ should be around one, the excess encephalization in dinocephalians could be interpreted as reflecting additional non-brain matter inside the endocast (Figure 5). It becomes possible to roughly estimate the relative amount of non-neural tissue in the endocast of dinocephalians. Some 48% of the endocast would be filled with non-neural tissue in *Anteosaurus*, 22% in *Jonkeria*, and 42% in *Moschops*. The same applies to the subadult *Moschognathus*, which, using published data (Benoit et al., 2017a), gives a value of 35%. These values are probably underes-

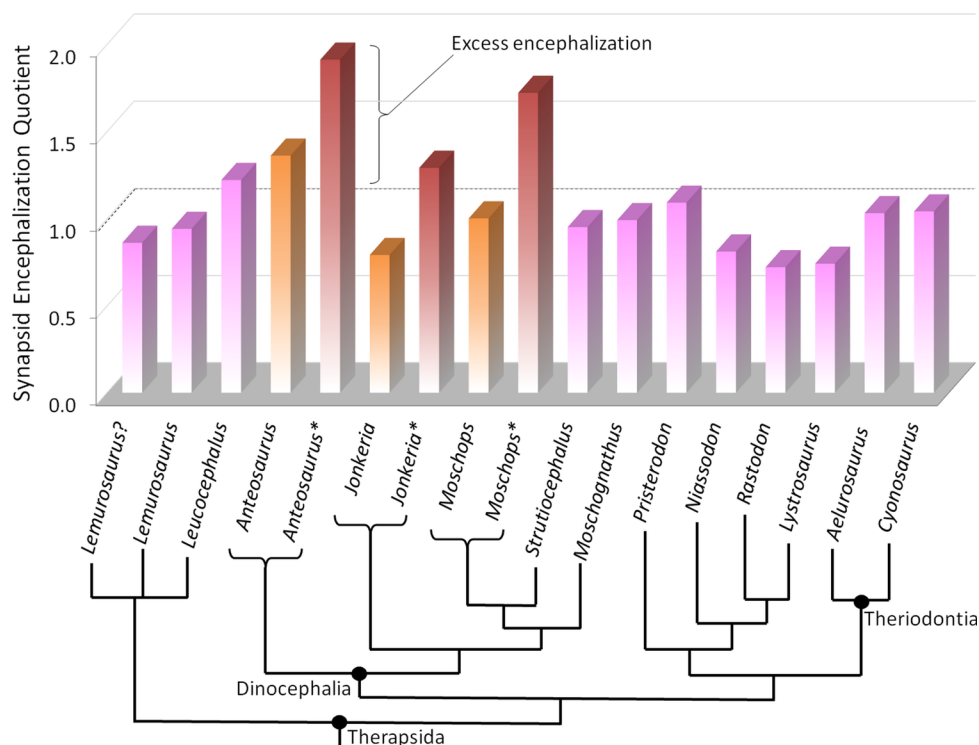


FIGURE 5. The synapsid Encephalization Quotient in non-theriodont therapsids. Data from Benoit et al. (2023a) and Table 1. Phylogeny after Fraser-King et al. (2019), Neumann (2020), and de Simão-Oliveira (2020). For *Anteosaur*, *Jonkeria*, and *Moschops*, measurements including (marked with an *) and excluding the pineal canal and pituitary fossa are provided.

timated given that i) in modern reptiles, non-neural tissue is classically considered to account for 50% of the volume of the endocranial cavity (Jerison, 1973; Hurlburt et al., 2013); and ii) it is not known how completely the brain would have filled the endocranial space in non-mammalian therapsids (Benoit et al., 2017b). This non-neural tissue could be a mix of meninges, blood vessels, and protective adnexa (Bauchot and Stephan, 1967), although the values presented above far exceed the amount of non-neural tissue measured in the endocast of modern mammals (which averages 11% according to Benoit, 2015). Noticeably, the taxa displaying the most pachyostosis (i.e., *Moschops*, *Moschognathus*, and *Anteosaur*) are also those that would have had the most non-neural tissue, which would be consistent with the use of the head as a weapon (Boonstra, 1968; Benoit et al., 2017a, but see Benoit et al., 2021 about *Anteosaur*). In modern mammals, meningeal thickness is directly proportional to absolute brain size (Benoit, 2015), but species that practice high-energy head-butting (e.g., bighorn sheep) have thicker meninges that cushion the part of their brain that is the most exposed to impacts (Ackermans et al., 2022).

Following the interpretation that the excess encephalization is the result of thickened intracranial protective tissue, it is remarkable that tapinocephalid dinocephalians would display all the most prominent adaptations to head-butting observed in modern high-energy head-butting animals, i.e. braincase re-orientation, enlarged absolute cranial size (to diffuse impact-induced stress), and thickened meninges (Ackermans et al., 2021; 2022). In modern bovids, complete protection against head-butting induced brain damage is rarely achieved as genes can be passed through to the next generation despite the accumulation of brain trauma (Ackermans et al., 2022). The more extreme adaptations observed in tapinocephalids, as exemplified by their grotesque cranial pachyostosis, suggest that they must have practiced intense head butting from a young age for these traits to be selected. Play-fighting in young tapinocephalids was recently supported by the description of an intracranial injury in the sub-adult specimen of *Moschognathus* and would imply complex intra-specific social communication to convey the idea of combat without aggression (Benoit et al., 2024). However, it must be reminded that besides paleoneurology, independent fossil evidence supporting

the “social tapinocephalids” hypothesis remains ambiguous. Although dinocephalian skeletons can be found in small groups, the rich record of footprints has failed to produce parallel trackways that would demonstrate gregariousness (Benoit et al., 2023 a, b).

CONCLUSIONS

The approach proposed here based on 3D sculpturing provides the first reasonably accurate body mass estimates for three dinocephalian taxa. The 3D sculpted endocasts compensate for the absence of more direct data on the dinocephalian brain. Their unexpectedly high volume is puzzling to interpret but remains consistent with adaptations to head-butting. It is more parsimonious to hypothesize that the endocast was filled with protective

tissues rather than by an enlarged brain, but with all the caveats possibly linked to correlating brain size with intelligence (Manger, 2006, 2013; Healy and Rowe, 2007; Manger et al., 2013), the possibility that dinocephalians were smarter than usually assumed nevertheless remains open. The future capabilities to CT and synchrotron study large and heavy dinocephalian skulls will hopefully enable to test the accuracy of the above-presented results and hypotheses and bring new data to compliment the current study.

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