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ARTICLE



First 3D reconstruction and volumetric body mass estimate of the tapinocephalid dinocephalian *Tapinocaninus pamela* (Synapsida: Therapsida)

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ABSTRACT

Dinocephalians were the earliest large terrestrial tetrapods from Gondwana, making this group crucial in understanding body mass (BM) evolution in basal synapsids, but no detailed weight determinations are available for the clade. Here we present the first BM estimate for a dinocephalian on the basis of the remarkably well preserved and complete skeleton of the basal tapinocephalid *Tapinocaninus pamela* from the lowermost Beaufort Group of South Africa. We reconstructed three 3D models of *Tapinocaninus* using mounted skeletons of the dinocephalians *Moschops* and *Ulemosaurus* to reconstruct the missing elements. Applying a density range between 0.9 and 1.15 Kg/1000 cm³ for living tissue to the model we reconstructed an average BM of 892.63 Kg for the taxon. Classic regression formulae, based on humerus and femur circumference, provide higher values of 1694.5 Kg and 2015.8 Kg, with an overestimation of 90% and 126% respectively. The study confirms that volumetric BM estimates are more precise, and are recommended if relatively complete skeletons are available. The 'intermediate' posture recognized for *Tapinocaninus*, more upright with respect to the sprawling condition characterizing spenacodontid 'pelycosaurs', could represent a response to a large BM, which, for the first time in synapsids, reaches weights close to a tonne.

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Introduction

Dinocephalian therapsids were a major component of Guadalupian tetrapod faunas, and are best known from South Africa, Cisuralian Russia, Tanzania, Zimbabwe, Zambia, China and Brazil (Boonstra 1946; Tchudinov 1983; King 1988; Rubidge 1993; Cheng and Ji 1996; Langer 2000; Munyikwa 2001; Simon et al. 2010; Cisneros et al. 2012; Sidor et al. 2014; Rubidge et al. 2019). Four dinocephalian families are recognized from the South African Karoo Supergroup, namely Anteosauridae (the most basal dinocephalian clade), Styracocephalidae, Tapinocephalidae and Titanosuchidae (Boonstra 1969; King 1988; Kammerer 2011).

Recently Rubidge et al. (2019) described the postcranial skeleton of the tapinocephalid dinocephalian *Tapinocaninus pamela*. Tapinocephalids are considered the most derived dinocephalian family, with *Tapinocaninus* representing the most basal genus of the clade (Kammerer 2011). This skeleton (holotype NMQR 2987) from deposits of the lowermost Beaufort Group of South Africa allows, for the first time, a precise vertebral count for a dinocephalian in the different axial regions (Rubidge et al. 2019) and description of the appendicular skeleton for the taxon. The cervical region of the axial skeleton is characterized by peculiar, primitive, laterally facing deep fossae, characterizing the area below the neural spines on all cervical vertebrae. *Tapinocaninus* long bones are autapomorphic in being relatively slender (especially the femur) for a tapinocephalid (Rubidge et al. 2019). Rubidge et al. (2019) consider the general morphology and articular surfaces of

stylopods (humerus and femur) in *Tapinocaninus* to indicate an 'intermediate' general posture between a primitive sprawling and erect stance (more upright than the condition characterizing spenacodonts but more sprawled than in theriodont therapsids), possibly representing a structural response of the appendicular skeleton to huge body size.

In addition to being the largest therapsids from the Guadalupian, dinocephalians also represent the first occurrence of huge terrestrial tetrapods in Gondwana (Rubidge 1995, 2005). The overall body dimensions of *Tapinocaninus* show that the very large body size and mass of tapinocephalids was already established in the most basal member of the family. Despite its significance for tetrapod body-size evolution, no detailed body mass estimates are yet available for dinocephalians. Here we provide a volumetric body mass estimate for *Tapinocaninus pamela* based on a 3D photogrammetric model of the almost complete holotype skeleton. To test the two different approaches, the results obtained from the volumetric model are compared with body masses derived using classic regression formulae based on stylopodial circumference. In addition, we also provide the first 3D reconstruction for *Tapinocaninus pamela*, to demonstrate the possible appearance of the animal in a reconstructed Guadalupian terrestrial setting.

Material and methods

The reconstruction and body mass estimate of *Tapinocaninus* is based on the holotype NMQR 2987, which is an almost

complete articulated skeleton lacking some propodial and autopodial elements (see Rubidge et al. 2019). The holotype was found on Modderdrift farm (Prince Albert district, Western Cape, South Africa) in 1985 by John Nyaphuli of the National Museum, Bloemfontein. The fossil was preserved in a fine grained sandstone bed of the lower Beaufort Group (Abrahamskraal Formation, *Eodicynodon* Assemblage Zone), alongside a second, slightly smaller, specimen (NMQR 2986).

To compare the volumetric method with the body mass estimate based on classic regression formulae, we calculated the weight using the formulas provided by Anderson et al. (1985) and Campione and Evans (2012). On the basis of a huge mammal dataset from the Kruger National Park and the Mountain Zebra National Park of South Africa, Anderson et al. (1985) provide a regression formula based on humerus and femur circumferences: $W = 0.078 \cdot C_{H+F}^{2.73}$, where C_{H+F} is the sum of the humerus and femur circumferences.

Campione and Evans (2012), on the basis of a large dataset of osteological measurements for mammals (200) and non-avian reptiles (47), proposed the following universal formula to estimate body mass corrected for phylogenetic correlation/covariance between observations: $\log BM = 2.754 \cdot \log C_{H+F} - 1.097$, where C_{H+F} similarly represents the sum of the humerus and femur circumferences.

Humerus and femur measurements were taken directly on the specimen using a digital caliper; a flexible tape was used to measure humerus and femur circumferences.

The first step to obtain a 3D model of *Tapinocaninus* required the reconstruction of a 3D photogrammetric model of the articulated skeleton NMQR 2987 (Figure 1). The model data was captured by taking 168 photographs around the specimen with a 24 Megapixel Canon EOS 750D (18 mm focal length) and calculated using the software Agisoft PhotoScan Standard Edition, version 1.4.0 (Educational License). This software enables automatic generation of point clouds, polygonal models, textured, georeferenced true orthomosaics, and DSMs/DTMs from still images. High-resolution Digital Photogrammetry is based on Structure from Motion (SfM) (Ullman 1979) and Multi View Stereo (MVS; Seitz et al. 2006) algorithms, with an accuracy for close-range photography of up to 1 mm in the obtained models. Over the last decade this has become a powerful

tool in vertebrate paleontology and ichnology (e.g. Castanera et al. 2013; Cifton et al. 2015, 2017, 2018, 2019; McCrea et al. 2015; Romano and Cifton 2016; Petti et al. 2018; Romano et al. 2018a, 2018b, 2019).

The photogrammetric model obtained from the Agisoft PhotoScan was exported as 'Ply' files, and modelled in the software for digital sculpting and painting ZBrush. This software enables separation of individual bones and body portions and to digitally modify and arrange the posture of the skeleton (see Romano et al. 2019) to perfectly fit the skeletal reconstruction of Rubidge et al. (2019, figure 10). With the software we modelled and sculptured the soft parts around the 3D photogrammetric model of the skeleton (Figure 2). To provide a possible range of values, we reconstructed three different models, adding different amounts of fleshy masses: a 'slim model', where the model essentially follows the outline of the skeleton, an 'average model' representing in our opinion the reconstruction closest to the natural condition (thus excluding starving or obese conditions), and a 'fat model' adding an excess of soft tissue mass around the digitally reconstructed skeleton (Figure 2).

The surface area and the volume were calculated using the software 3D Studio Max (see Romano et al. 2019). A range of putative body mass estimates for *Tapinocaninus* were calculated by applying several specific density values for living tissue to the three obtained volumes. A value of 1 Kg/1000 cm³ has been used in several studies to calculate vertebrate body mass (e.g. Alexander 1985, 1989; Henderson 1999; Hutchinson et al. 2007; Bates et al. 2009, 2015; Romano et al. 2019). A specific average body gravity of between 0.99 to 1.01 has been proposed by Larramendi (2016) for extinct proboscideans. The highest density of 1.15 Kg/1000 cm³ for land mammals has been determined in rhinoceros (Bellmann et al. 2005 in Gunga et al. 2007). In the present contribution we provide a range of possible body mass by applying the three densities of 0.99, 1 and 1.15 Kg/1000 cm³ to the volume.

Results

The new 3D models of *Tapinocaninus* are shown in Figure 2. Following the description provided by Rubidge et al. (2019) we reconstructed a 3D model with an 'intermediate' posture, between a classic sprawler posture characterizing sphenacodontid

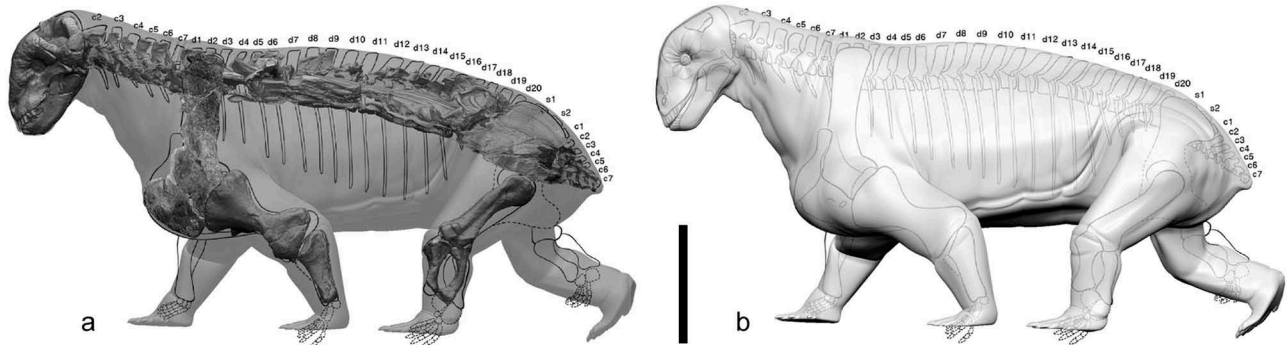


Figure 1. a) 3D digital model of *Tapinocaninus pamalae* obtained starting from a 3D photogrammetric model of the holotype skeleton (Rubidge et al. 2019) and scaled on the base of skeletal graph provided by Rubidge et al. (2019, fig. 10); a) 3D photogrammetric model superimposed to the skeletal graph provided by Rubidge et al. (2019, fig. 10), with 3D solid model of *Tapinocaninus* body in transparency; b) 3D 'average' solid model of *Tapinocaninus* in transparency superimposed on the skeletal graph provided by Rubidge et al. (2019, fig. 10).

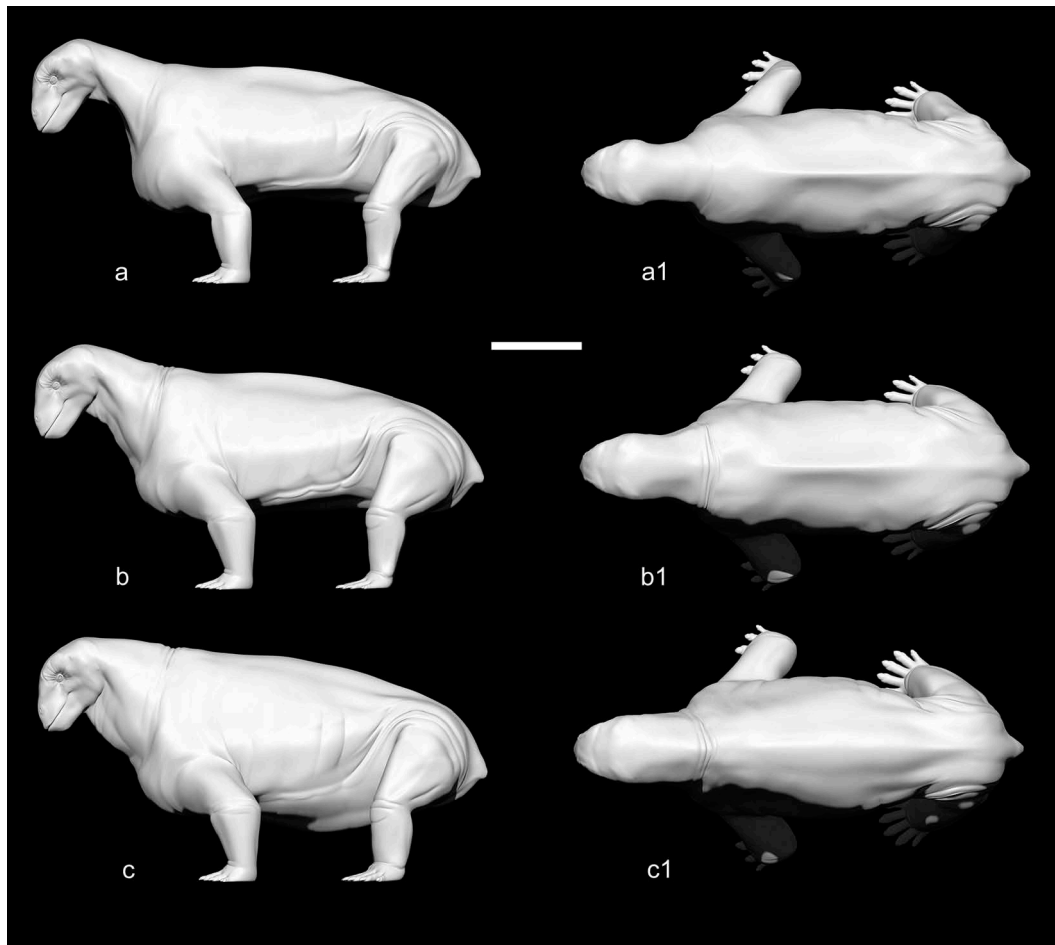


Figure 2. 3D solid models of *Tapinocaninus*. A-A1, 'Slim model' in lateral and dorsal views; B-B1, 'Average model' in lateral and dorsal views; C-C1, 'Fat model' in lateral and dorsal views. Scale bar equal to 50 cm.

'pelycosaurs' and an upright one characterizing biarmosuchians, gorgonopsians, therocephalians and cynodonts (Jenkins 1971; Kemp 1982; Sigogneau Russell 1989; Fourie and Rubidge 2009). In particular, the humerus and glenoid indicate a more upright posture for the front limb with respect to sphenacodonts but still quite sprawled: a condition similar to that characterizing dicynodonts (Rubidge et al. 2019). Conversely, the inflected head of the femur and the slight sloping articulation of the tibia with the femur indicates a more upright posture for the hindlimbs. The proximal heads of the dorsal ribs suggest a barrel-shaped rib cage (Figure 1–3), which is consistent with the reconstruction of the tapinocephalid *Moschops* (Gregory 1926).

Application of the formula of Anderson et al. (1985) to the stylopod circumferences of *Tapinocaninus* (250 mm for the humerus, 237 mm for the femur) provides a body mass of 1694.5 Kg. The formula of Campione and Evans (2012) returned a greater weight estimate of 2015.8 Kg for *Tapinocaninus*. Considering the 25% error discussed by Campione and Evans (2012) the reconstructed body mass using regression formulae varies from a minimum of 1511.05 Kg to a maximum of 2519.75 kg.

The 3D digital restoration of *Tapinocaninus*, reconstructed around the photogrammetric model of the holotype skeleton, enables estimation of a total body length (from the snout to point of the tail) of about 2.5 m, a total maximum height (at

the head) of about 1.4 m, and a shoulder height of about 1.3 m (Figure 1, 2, 4).

The 'slim' volumetric model (Figure 2A, A1) returned a total surface area of 7.2 m² and a total volume of 0.771 m³. By applying the densities of 0.9, 1, and 1.15 Kg/1000 cm³ to the reconstructed volume we obtained body masses respectively of 693.9 Kg, 771 Kg, 886.65 Kg, and an average body mass equal to 783.85 Kg.

The 'average' volumetric model (Figure 2B, B1) returned a total surface area of 7.62 m² and is characterized by a volume of 0.879 m³. By applying the densities of 0.9, 1, and 1.15 Kg/1000 cm³ to the obtained volume the reconstructed body masses are respectively of 791.1 Kg, 879 Kg, 1010.85 Kg, and an average body mass equal to 893.62 Kg.

The 'fat' volumetric model (Figure 2C, C1) is characterized by a total surface area of 8.13 m² and returned a total volume of 0.984 m³. By applying the densities of 0.9, 1, and 1.15 Kg/1000 cm³ to the obtained volume the reconstructed body masses are respectively of 885.6 Kg, 984 Kg, 1131.6 Kg, and an average body mass equal to 1000.4 Kg.

Thus, the average body mass for *Tapinocaninus pamela* based on the volumetric approach is 892.63 Kg. Considering volumetric body mass as more accurate with respect to an estimate based on linear regression (see Sellers et al. 2012; Brassey et al. 2015; Bates et al. 2015; Brassey 2016; Romano

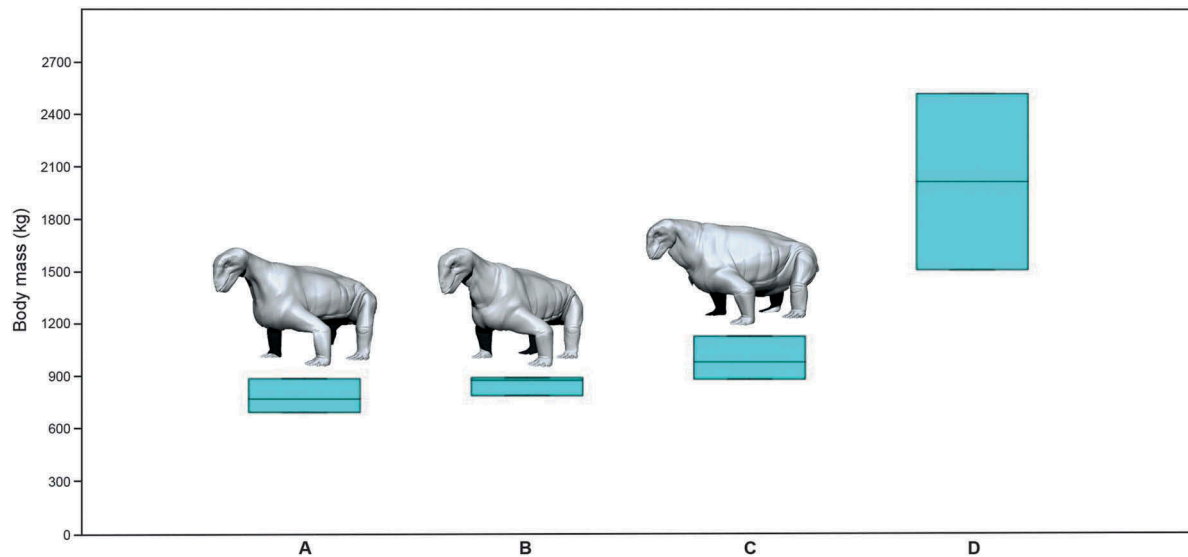


Figure 3. Range of body mass estimate in the ‘Slim model’ (a), ‘Average model’ (b) and ‘Fat model’ (c), in comparison with the range of weight calculated with the formula by Campione and Evans (2012) (D).

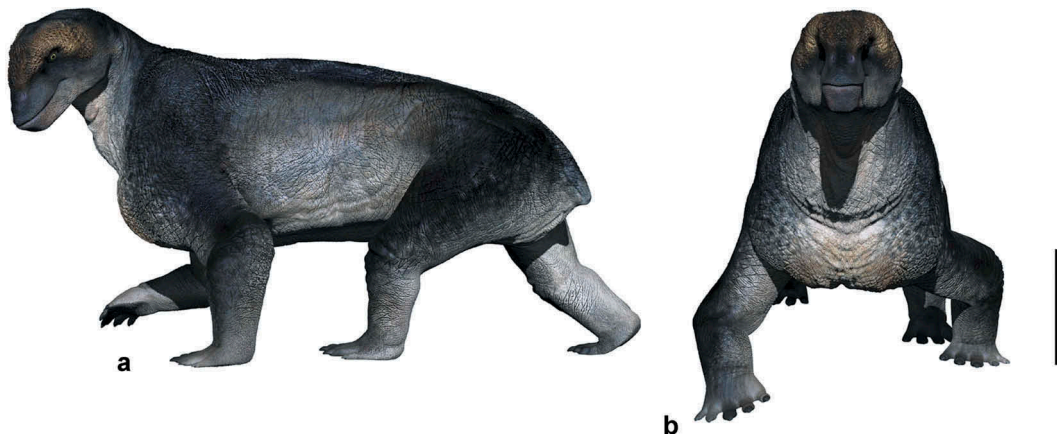


Figure 4. Artistic reconstruction of *Tapinocaninus* based on the 3D solid ‘Average model’ in lateral (a) and frontal views (b). Scale bar equal to 50 cm. Artwork by Fabio Manucci.

et al. 2019), we can use the new average estimate as a reference to analyze the results obtained with the classic regression formula (Figure 3). In particular, the formula provided by Anderson et al. (1985) results in a weight 802 Kg greater than the volumetric one, thus overestimating the body mass for *Tapinocaninus* by approximately 90%. An even greater overestimation is obtained when using the formula of Campione and Evans (2012), with a body mass about 1123 Kg more than the one calculated in this contribution based on the 3D model, an overestimation of about 126% (see Figure 3).

Discussion

In this short contribution we provide the first 3D reconstruction and body mass estimate for the tapinocephalid dinocephalian *Tapinocaninus pamela* from the lowermost Beaufort Group of the South African Karoo Supergroup. We present 3D models with an ‘intermediate posture’ between the primitive sprawling posture of sphenacodontid ‘pelycosaurs’ and the more erect limb posture of more derived therapsids (e.g.

biarmosuchians, gorgonopsians, therocephalians and cynodonts). The 3D models enable reconstruction of an animal with quite a large barrel-shaped rib cage, and an overall body size and body mass comparable to that of an adult black rhino. Using the volumes determined from the three different models (‘slim’, ‘average’ and ‘fat’) and the three densities for the living tissue of 0.9, 1, and 1.15 Kg/1000 cm³, we obtained a conservative average body mass of 892.63 Kg. In the literature lower density values ranging from 0.8 to 0.85 Kg/1000 cm³ have been obtained for some dinosaur clades with extensive postcranial skeletal pneumaticity (essentially prosauropods and sauropods), and used to calculate a putative body mass (e.g. Wedel 2003, 2005; Gunga et al. 2008). Since no pneumaticity characterizes the postcranial skeleton in dinocephalians, such low values were not considered in the present contribution. Even providing three different reconstructions based on different amount of fleshy mass, we consider the ‘average’ model to most likely resemble the animal in life and so we have chosen to use this model for our restoration of *Tapinocaninus* (Figure 4, 5).



Figure 5. Artistic reconstruction of a group of *Tapinocaninus* in a classic Guadalupian terrestrial setting. Artwork by Fabio Manucci.

As already empirically determined in other publications (e.g. Bates et al. 2015; Brassey et al. 2015; Romano et al. 2019), the use of classic regression formulae based on stylopod circumferences led to a consistent overestimation of body mass in *Tapinocaninus*. In particular, the methods proposed by Anderson et al. (1985) and Campione and Evans (2012) led to an overestimation of the body mass by 90% and 126% respectively. If we use the volume of our favoured ‘average’ model for *Tapinocaninus*, to achieve the body mass obtained by using regression formulae would require a tissue density of $1.93 \text{ kg}/1000 \text{ cm}^3$ and $2.3 \text{ kg}/1000 \text{ cm}^3$, respectively. These values are incongruent with existing data for terrestrial vertebrates (e.g. Alexander 1985, 1989; Henderson 1999; Bellmann et al. 2005; Gunga et al. 2007; Hutchinson et al. 2007; Bates et al. 2009; Campione and Evans 2012; Larramendi 2016).

Similar results to those of *Tapinocaninus* have been obtained recently by estimating body mass in the dwarf elephant *Palaeoloxodon* ex gr. *P. falconeri* from Sicily (Romano et al. 2019), and the large Late Triassic dicynodont *Lisowicia bojani* from Poland (Romano and Manucci 2019). In the case of the dwarf elephants, Romano et al. (2019) compared the volumetric estimate determined for four specimens (referable to three ontogenetic states) with values obtained from regression formulae and demonstrated that the formula of Campione and Evans (2012) overestimates BM by between 25% and 104%. The largest overestimate was obtained when applying the formula proposed by Christiansen (2004) (based on humerus and femur circumferences of a newborn male dog), which returns a BM of 40 kg for a newborn puppy dog of small adult size. When applying this body weight to the reconstructed volume, Romano et al. (2019) find a density for the living tissue of $4.97 \text{ kg}/1000 \text{ cm}^3$, which is greater than the density of titanium ($4.506 \text{ Kg}/1000 \text{ cm}^3$)! The consistent discrepancies between the results obtained by volumetric methods with those from the regression formulas have been brought into perspective because of the peculiar long bone structure of dwarf elephants (Romano et al. 2019), which have different proportions to those of

extant elephants (see Herridge 2010). In particular, limb bones in *P.* ex gr. *P. falconeri* are characterized by modifications (such as the fusion of both fore and hind zeugopodia as well as some peculiarities of the foot bones), which are more pronounced than in other insular Elephantini species, such as *Mammuthus lamarmorai* and *P.* ex gr. *P. mnaidriensis* and *P. tilensis*. Such modifications, linked with locomotory adaptations to the rocky island environments (Ambrosetti 1968; Sondaar 1977; Palombo 2003; Ferretti 2008; Palombo et al. 2012; Larramendi 2016; Scarborough et al. 2016), are most likely the reason for the consistent overestimation obtained by applying the regression formula based on extant taxa to such modified stylopodial bones (see Romano et al. 2019).

In the case of the huge dicynodont *Lisowicia bojani*, Romano and Manucci (2019) propose three different models (‘slim’, ‘average’ and ‘fat’) following the same procedure applied here for *Tapinocaninus*, and obtained an average BM of 5.88 tons. This value is 3.45 tons less than the average value obtained by Sulej and Niedźwiedzki (2019) who used the formula of Campione and Evans (2012). Also in this case, Romano and Manucci (2019) stressed how the discrepancy between the two methods is likely linked to the particularly robust long bones of *Lisowicia*, which are characterized by very massive and stout shafts when compared to the bone length.

These empirical tests, including the present *Tapinocaninus* study, have stressed the problem of uncritically applying universal regression formulas to taxa characterized by peculiar long bones (‘single bone’ problem, see Sellers et al. 2012). In several cases very robust long bones with stout shafts are not linearly correlated to body size but rather to specific behaviours, such as digging. For example, Romano (2017a) pointed out how the very robust and ‘overbuilt’ long bones of some small-sized basal caseids, are likely linked to the digging behaviour inferred for these taxa (see Stovall et al. 1966; Olson 1968; Hotton et al. 1997; Maddin and Reisz 2007). These previously adapted robust long bones were most probably exapted for the most derived taxa to achieve very large body sizes (Romano 2017a).

Differently captorhinids, which had a sprawling posture and reached quite large body sizes in the course of evolution, have long bones which scale very close to isometry (Romano and Rubidge 2019). These results demonstrate that for this clade, bones of large-bodied taxa do not show elastic deformation to accommodate the large BM. It follows that the elastic similarity, predicted by McMahon (1973, 1975) to maintain similar levels of peak stress with an increase in size, does not appear to be applicable to captorhinid long bones. These examples show how correlating the robustness and circumference of long bones to body mass can be misleading, especially when applied to primitively sprawling taxa which are phylogenetically distant from the extant clades used to derive regression formulas.

Overall, the major shortcoming of the 'universal' regression formulae based on stylopodial circumferences is that the database derived from extant taxa does not include large sprawler vertebrates with a weight close to, or greater than, a ton. All extant vertebrates with greater weight have sagittal posture and columnar graviportal limbs (posture that minimizes torsional stresses, and therefore leads to proportionally slimmer limb shafts). Thus, the lack of analogous examples in the reference datasets limits the application of universal formulas to extinct clades. Conversely, volumetric methods are based on total body volume which is independent of the robustness of long bones or other peculiar structures. Moreover, as demonstrated empirically for *Lisowicia* and *Tapinocaninus*, consistently modifying the volume with 'slim', 'average' and 'fat' models, results in a BM range which is always narrower than that derived from regression formulas and is closer to anticipated weights for tetrapods of that size.

Regarding body size, dinocephalians are the largest Guadalupian therapsids and *Tapinocaninus* represents the earliest occurrence of huge terrestrial synapsids in Gondwana (Rubidge 1995, 2005). Amongst basal synapsids, large body size had already evolved in the 'pelycosaurs' during the late Early Permian and the early Middle Permian, especially amongst the large herbivorous members of the Family Caseidae (Olson 1968; Reisz 1986). The largest were the North American genus *Cotylorhynchus* (especially *C. hanckocki*), and the huge Italian Permian caseid from Sardinia *Alierasaurus ronchii* (Ronchi et al. 2011; Romano and Nicosia 2014; Romano et al. 2017), with an estimated body length of 6.5–7 m. The independent evolution of large body size amongst basal synapsids at different geological periods is linked to a complex combination of physiological and ecological factors. In particular, large body size improves metabolic efficiency (Gould 1966), extends the longevity of an individual by maximizing the period of reproductive activity (Hotton et al. 1997), is a deterrent for predator attack (Pianka 1995), reduces annual mortality (Stanley 1973); because of increased heat retention, as a result of a relatively small surface area to volume ratio, large animals have greater independence from the external environment for body temperature regulation (Newell 1949).

The evolution of large body size is also linked to the acquisition of a herbivorous diet as plant-eating organisms require bacterial populations in an enlarged gut to digest celluloses and hemicelluloses (e.g., Hong et al. 2011; Romano 2017b) through hydrolysis and fermentation of otherwise indigestible plant polymers (Lombardo 2008). As

a result herbivorous tetrapods are generally characterized by larger body size with a wide trunk region to accommodate long digestive tracts (Hotton et al. 1997; Sues and Reisz 1998). Accordingly the evolution of a large body size is predictable for herbivorous caseids and dinocephalians such as titanosaurs and tapinocephalids, which includes *Tapinocaninus pamela* that reached a BM of close to a tonne. At the same time, large body size in *Tapinocaninus*, and other large herbivorous tapinocephalids, may have worked as a deterrent against predator attack.

Conclusions

This contribution provides the first volumetric body mass estimate of the tapinocephalid dinocephalian, *Tapinocaninus pamela* from the lowermost Beaufort Group of South Africa, and the first reconstruction of the taxon in a typical Guadalupian terrestrial setting.

The study shows that a body mass of close to 1 ton was already attained by the Middle Permian in basal dinocephalian synapsids, with the evolution of large body size probably triggered by several ecological and physiological factors. Amongst these is the evolution of huge torso to accommodate a large gut for fibre fermentation, and as a deterrent against faunivorous therapsids. The more upright posture of *Tapinocaninus* (especially in the hind limbs) discussed by Rubidge et al. (2019), could represent a structural response to huge body size reached by the taxon.

The present study corroborates the hypothesis that volumetric methods are more accurate for estimating body mass than regression formulae based on single bones, especially in extinct tetrapod clades with intermediate posture. We advocate that the volumetric method for body mass determination should rather be applied in cases where sufficiently complete skeletons are available.

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Disclosure statement

No potential conflict of interest was reported by the authors.

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