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Article

BODY MASS ESTIMATION FOR *NEOGLYPTATELUS URUGUAYENSIS* FERNICOLA *ET AL*., 2017 (MAMMALIA, CINGULATA, PACHYARMATHERIIDAE)

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ABSTRACT – This study presents the first body mass estimation for a member of the Pachyarmatheriidae, a distinctive group of cingulates that includes species with two rigid armours covering most of the body, unlike armadillos, which have mobile bands, or glyptodonts, characterized by a single continuous armour plate. Specifically, we estimate the body mass of *Neoglyptatelus uruguayensis*, a late Miocene member of the family Pachyarmatheriidae. Body mass estimations were performed using allometric equations based on extant cingulates and through a geometrical model of its armour. The results ranged from 16 kg to 28 kg, with the most reliable approximation suggesting a body mass of approximately 17 kg. We also estimated the position of the centre of mass and made some paleobiological suggestions based on our results.

Keywords: body mass estimation, allometry, geometrical model, *Neoglyptatelus uruguayensis*, Pachyarmatheriidae, Cingulata.

INTRODUCTION

The order Cingulata is a particular clade of armoured placental mammals that traditionally includes two structural designs: taxa with rigid armour that covers most of the body (glyptodonts) and those that have armour with scapular and pelvic shields between which mediate mobile bands (armadillos and pampatheres). This structural (not phylogenetic) division remained so until Fernicola *et al*. (2017) described an exceptional fossil from the late Miocene of Uruguay, which added a third category to this structural diversity. This new category consists of cingulates protected by two shields, scapular and pelvic, which articulate with each other without mobile bands between them. Based on this and other characteristics, the family Pachyarmatheriidae was proposed (Fernicola *et al*., 2017), which also includes the genus *Pachyarmatherium* from which its name is derived (Downing & White, 1995). The species *Neoglyptatelus uruguayensis* was described as the only family member with a nearly complete, preserved armour.

According to Delsuc *et al*. (2016), modern armadillos are classified into Dasypodidae (only *Dasypus*) and Chlamyphoridae (all other living genera), so in this study, we use the term "armadillos" in an inclusive sense.

In this article, we present the first estimate of body mass for *Neoglyptatelus uruguayensis*, based on its holotype, and one of the few for a member of the Pachyarmatheriidae, following recent estimations for *Pachyarmatherium* (Barbosa *et al*., 2024; Dantas, 2019). This estimation provides a reference for understanding the paleobiology of this recently recognized and peculiar group of cingulates and sheds light on their ecological roles and evolutionary adaptations. Body size is a highly relevant biological parameter for analyzing an animal's interaction with its environment (Peters, 1983). By establishing a reliable body mass estimation, we contribute to understanding the functional morphology, energy requirements, and ecological interactions of these cingulates. Therefore, the body mass estimation could provide insights into the role of *N. uruguayensis* within Miocene ecosystems. It could also be a basis for investigating the evolutionary dynamics and environmental adaptations of the Pachyarmatheriidae.

In the present work, we estimated the body mass of *Neoglyptatelus uruguayensis* using two methods: from allometric equations and through a geometrical reconstruction of the specimen. From the geometrical reconstruction, we estimated the position of the centre of mass of *N. uruguayensis*, which is relevant information for several biomechanical analyses. Based on our results, we also made some paleobiological considerations.

MATERIAL AND METHODS

Allometric estimation of body mass

The present work is based on the type-material MNHN 1642 of the *Neoglyptatelus uruguayensis*, stored in the collection of the Museo Nacional de Historia Natural de Uruguay (Fernicola *et al.*, 2017). The holotype consists of a partial skeleton, including a nearly complete pectoral armour, the right portion of the pelvic armour, a tail armour with associated vertebrae, three fused thoracic vertebrae, a complete right hindlimb, and the proximal half of the left femur. The left femur is fractured, providing an opportunity to obtain internal measurements (see Figure 1). All measurements were taken with an analogical gauge.

We used eleven allometric equations to estimate the body mass of the *Neoglyptatelus uruguayensis* specimen. Nine of these equations were derived from the body mass and femoral parameters of extant armadillos, as Biknevicius (1999) reported, who analyzed six species of armadillos based on field-recorded body masses. The other two equations were derived from a study of ten extant armadillo species and a body mass estimation of the fossil species *Propraopus grandis* Ameghino, 1881, which was estimated at 47 kg assuming geometric similarity with two species of *Dasypus* according to Fariña & Vizcaíno (1997). Of the nine equations of Biknevicius (1999), five are univariate equations (Table 1), and four are multivariate (Table 2). These equations have been previously used to estimate the body mass of extinct cingulates (see, for example, Perea *et al.*, 2019).

The variables used were the total length of the femur (*FL*), anteroposterior (*AP*) and mediolateral (*ML*) external (periosteal) diameters of the femoral diaphysis, internal anteroposterior and mediolateral diameters of the femoral diaphysis (*ap* and *ml* respectively), the cortical cross-sectional area of the diaphysis (*CA*) and the mean moment of area (*J/2*), where *J* is a measure of the mean torsional and flexion rigidity.

The femur's measurements were taken in millimeters (mm). As shown in Table 3, they have an error of 0.1 mm.

The measurements of *AP*, *ap*, *ML*, and *ml* were taken at 31% of the total femur length rather than at the 35% site stipulated by Biknevicius (1999) due to a fracture present at this location (see Figure 1). This adjustment was necessary to ensure accurate measurements despite the damage; however, this minimal difference does not significantly affect the calculations.

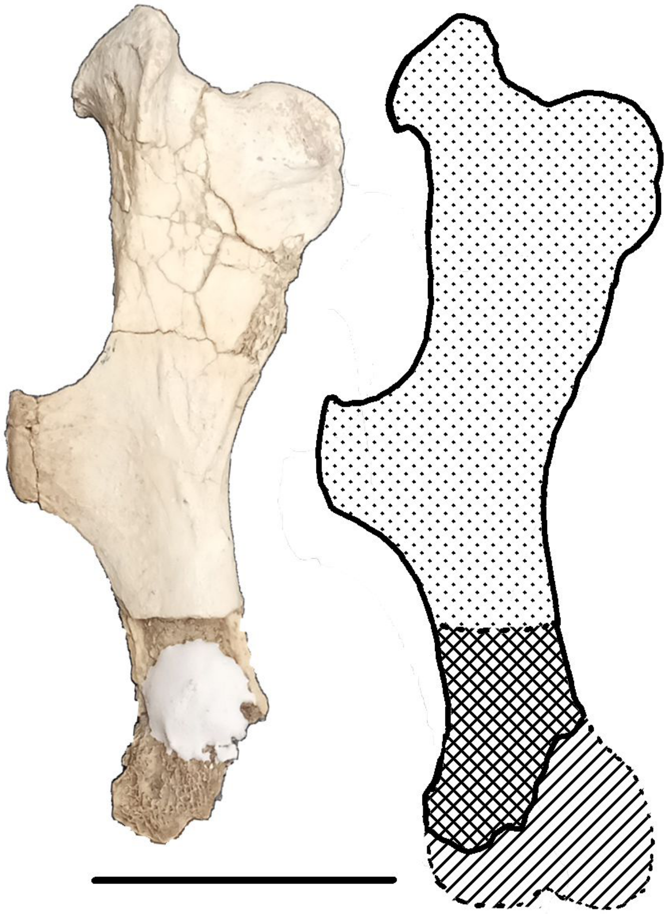

Figure 1. Left femur of *Neoglyptatelus uruguayensis* (MHNN 1642). Scale bar = 50 mm.

Table 1. Univariate predictive equations used for body mass estimates (Biknevicius, 1999).

Equation	r^2	%PE
$\log MB = 2.483(\log AP)-1.689$	0.940	17.84
$\log MB = 1.915(\log ML)-1.499$	0.942	18.52
$\log MB = 1.198(\log CA)-1.354$	0.985	8.39
$\log MB = 0.578(\log J/2)-0.911$	0.988	7.54
$\log MB = 2.955(\log FL)-4.905$	0.847	27.19

Table 2. Multivariate predictive equations used for body mass estimates (Biknevicius, 1999).

Equation	r^2	%PE
$\log MB = 3.235(\log AP)-0.974(\log FL)-0.572$	0.946	14.98
$\log MB = 1.317(\log ML)+1.165(\log FL)-2.998$	0.981	10.41
$\log MB = 1.280(\log CA)-0.232(\log FL)-1.057$	0.993	9.05
$\log MB = 0.551(\log J/2) + 0.161(\log FL)-1.140$	0.988	7.47

Table 3. Femur measurements (in mm).

Morphological variable	Measurement (mm)
FL	146.0
AP	14.4
ap	9.4
ML	21.8
ml	14.9

The second moment of area ($Ix-x$ and $Iy-y$) represents magnitudes related to bending force, while the cross-sectional area (*CA*) is associated with tensile and compressive forces, as studied by Anyonge (1993) and Egi (2001). The variables *CA* and *J/2* were calculated using the methodology described by Biknevicius (1999). The equations used to compute these variables from the measured parameters are detailed in Equations 1 to 4.

$$CA = \pi\left(\left(ML \times AP\right) - \left(ml \times ap\right)\right) / 4 \tag{1}$$

$$I_{x-x} = \pi\left(\left(ML \times AP^3\right) - \left(ml \times ap^3\right)\right) / 64 \tag{2}$$

$$I_{y-y} = \pi\left(\left(AP \times ML^3\right) - \left(ap \times ml^3\right)\right) / 64 \tag{3}$$

$$J / 2 = \left(I_{x-x} + I_{y-y}\right) / 2 \tag{4}$$

Geometrical estimation of body mass

For our geometrical model of *Neoglyptatelus uruguayensis* we used measurements from the armour and tail of the studied specimen. The lengths *H*, *R* and *h* (see Figure 2 for the definition) were taken from the scapular and caudal shields. All measurements were taken with an analogical gauge. The fossil remains of the armour are not preserved in their original shape, as the armour is transversally flattened. It is reasonable to assume that in the living form, each section had the shape shown in Figure 2B. The contour of the armour *H* was measured from one lateral edge to the sagittal midline for each slice cross-section, as illustrated in Figure 2B. This procedure was applied to both the scapular and pelvic armour at regular intervals of 2 cm.

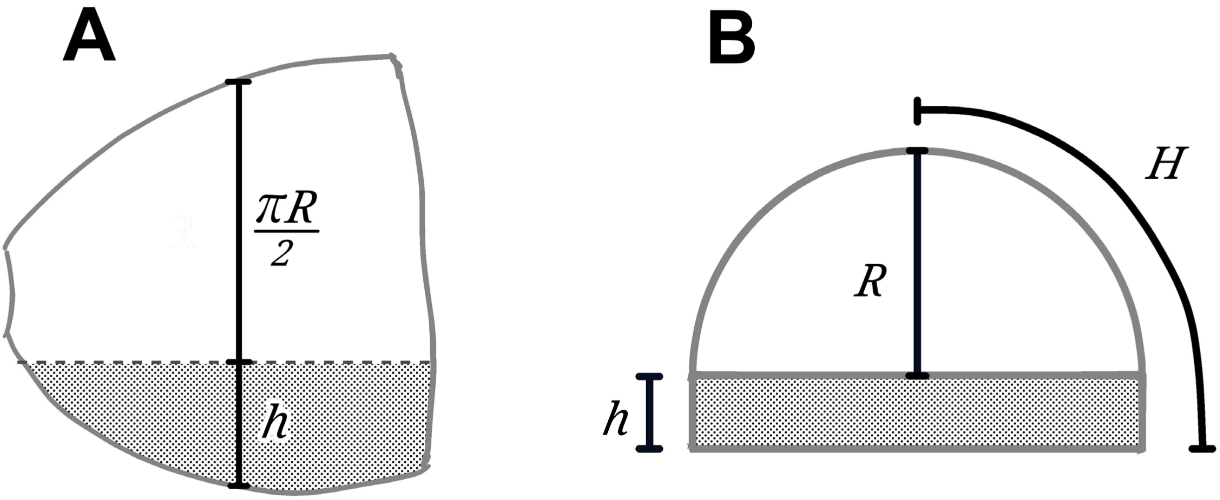

Figure 2. Schematic representation of the armour morphology and cross-sectional measurements. **A**, lateral view of a simplified representation of the armour based on Figure 2 of Fernicola *et al*. (2017), illustrating the total height and the segmented lower portion (*h*) that could be free of soft tissues. **B**, cross-section of a slice of the armour in caudal view, showing the geometric parameters used in the volumetric estimations. The shaded region represents the abdominal portion of the armour, where soft tissues may or may not be present.

The armour of extant armadillos has soft tissues distributed deep inside it. Also, it presents an abdominal region where they are not present (see Figure 2). In geometric reconstruction, two extreme values were considered to account for the uncertainties in the distribution of soft tissues. The maximum value of body mass from the geometrical model was defined by the total volume enclosed within the armour, calculated using the variables R and h, assuming it to be entirely occupied by soft tissues. In contrast, the minimum value of body mass from the geometrical model was determined by excluding the inferior region of the volume, calculated using only R, as this region was devoid of soft tissues (Figure 2). This geometrical method of estimate volume is an adaptation of methodology used previously in Bargo *et al.* (2000) and Vizcaíno *et al.* (2011).

From the geometrical assumption we made in Figure 2, the relation between the parameters is $H = h + \pi R/2$. From this relation, we can calculate the volume associated with each H value (corresponding to a slice of the model).

For the minimum value of body mass from the geometrical model, we modelized each H only considering the upper region with soft tissues as a half-disk with radius R and depth $d = 2$cm.

$$V_{min} = \frac{d \times \pi R^2}{2} \qquad (5)$$

For the maximum value of body mass from the geometrical model, we considered the volume of the half-disk added to that of the lower region.

$$V_{max} = \frac{d \times \pi R^2}{2} + d \times 2R \times h \qquad (6)$$

The body masses corresponding to the geometrical models were estimated from the total volume considering an average density of 1000 kg m^{-3} (Bargo *et al*., 2000; Vizcaíno *et al*., 2011).

RESULTS

Estimated body masses based on extant armadillos, whose mass ranges from 0.8 kg to 6.6 kg, are shown in Table 4.

We obtained two body mass estimations from equations from a study of extant and fossil armadillos (Fariña & Vizcaíno, 1997) (see Table 5).

Body mass estimations of *Neoglyptatelus uruguayensis* from the geometrical models are 16.0 kg (iterating Equation 5) and 28.3 kg (iterating Equation 6). The position of the centre of mass is 32 mm caudally displaced from the midpoint of the armour.

Table 4. Body mass of *Neoglyptatelus uruguayensis* values based on femur variables (Biknevicius, 1999).

Morphological variable	Measurement (mm)	Body mass (kg)
AP	14.4	15.4
ML	21.8	11.6
CA	137.3^2	16.1
J/2	4209.^4	15.3
FL	146.0	30.9
FL & *AP*	146.0 and 14.4	11.7
FL & *ML*	146.0 and 21.8	19.3
FL & *CA*	146.0 and 137.3^2	15.0
FL & *J*/2	146.0 and 4209.6 ^4	20.1

Table 5. Body mass of *N. uruguayensis* based on femur variables (Fariña & Vizcaíno, 1997).

Morphological variable	Measurement (mm)	Body mass (kg)
FL	146.0	16.2
AP	14.4	14.8

DISCUSSION

The mean value of the estimations obtained from allometric equations is 17 kg. This value is very close to the mean of the estimations obtained using only the four equations with the lowest error percentage of Biknevicius (1999) (16.6 kg). The body mass values obtained by both methods are between 13 kg and 28 kg. The allometric equations in Tables 1 and 2 were created from data from dasypodid, the closest living phylogenetic group to *Neoglyptatelus uruguayensis.* Living armadillos used for the allometric equations have a body mass range of 0.8 kg to 6.6 kg. Since *N. uruguayensis* body mass estimations are larger, we can have extrapolation uncertainties.

The mean value of the body mass estimations based on the geometrical models (22 kg) is larger than that obtained from the allometric equations (17 kg). This can be related to the uncertainties of the geometrical model. The volumetric estimation would have given us smaller estimations if the half-discs (see Figure 2) were changed to half-ellipses. We must remember that the state of preservation of the scapular and pelvic shields allows us to know their dimensions, but not the precise geometrical shape. Moreover, because the armour has a peculiarity not seen in extant animals, as there are no mobile bands between the pelvic and scapular shields, it is risky to assume the same shape as in *Dasypus hybridus* (Desmarest, 1804), which was used for scaling due to its overall similarity.

Body mass estimations have also been proposed for *Pachyarmatherium Brasiliense* Porpino, Fernicola & Bergqvist, 2009, a Quaternary representative of the family Pachyarmatheriidae, with values ranging from approximately 90 to 150 kg depending on the method applied (Barbosa *et al*., 2024). Although *Neoglyptatelus uruguayensis* is markedly smaller, this comparison highlights the morphological and possibly ecological disparity among known members of the family.

It would be interesting to find a living analogue with the same body mass to explore the paleobiological implications of our results. In the extant armadillos, the range of masses runs from the tiny *Chlamyphorus truncatus* Harlan, 1825 (0.120 kg)

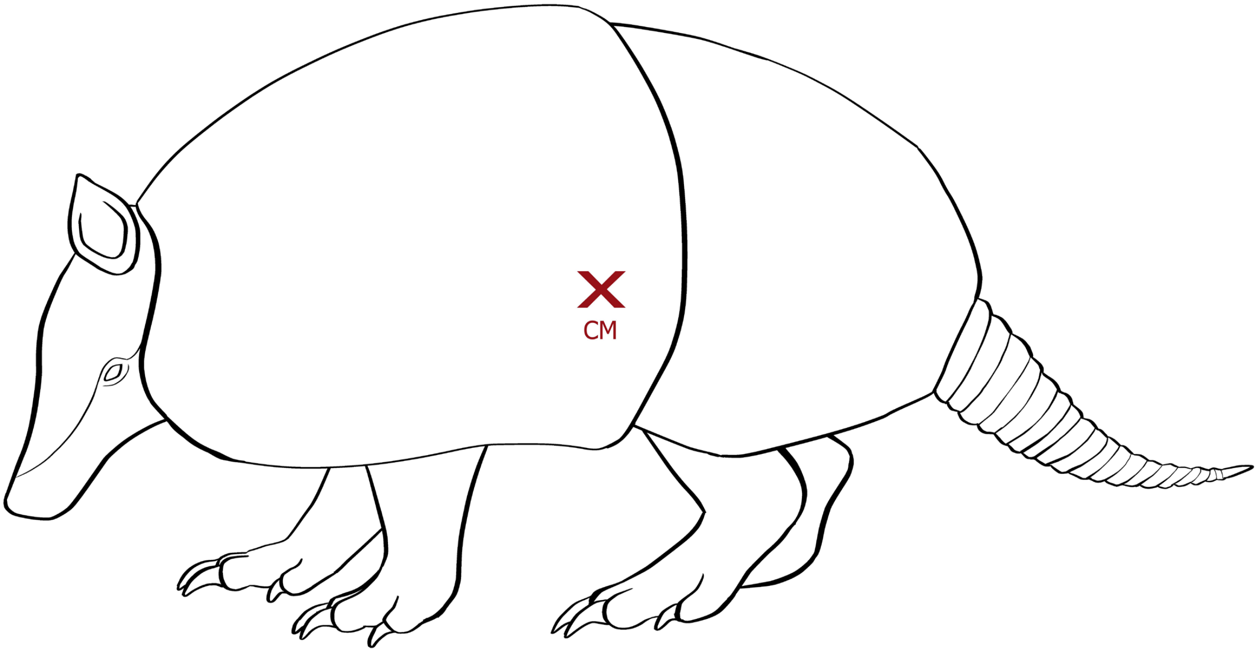

Figure 3. Representation of *Neoglyptatelus uruguayensis*. The position of the centre of mass is shown.

(Borghi *et al.*, 2011) to the large *Priodontes maximus* Kerr, 1792 (40 kg). However, in the range of masses of our estimation, there are no living armadillos to make some paleobiological hypothesis based on it.

Even so, it is possible to infer some paleobiological characteristics of *Neoglyptatelus uruguayensis*, which would be shared with the largest armadillos of today, such as *Priodontes maximus*, *Cabassous unicinctus* Linnaeus, 1758 and *Euphractus sexcinctus* Linnaeus, 1758, described in Hayssen (2014), Carter *et al*. (2016), and Redford & Wetzel (1985). From these species, we can deduce that *N. uruguayensis* probably dug small burrows, which could have served not only to protect its soft parts and possibly its young, but also for other purposes such as thermoregulation, avoiding predators, or creating microhabitats, as observed in extant armadillos (Desbiez & Kluyber, 2013). Furthermore, we can conclude that their offspring would have had a mass in the 100 g − 140 g range, as this attribute does not vary in the armadillos mentioned above. Based on gestation and maturation times observed in large extant armadillos of comparable body size, such as *P. maximus* (gestation 120 days, maturity at 9–12 months; Hayssen, 2014; Redford & Wetzel, 1985) and smaller but related species like *E. sexcinctus* and *C. unicinctus* (gestations 60–70 days, maturity at 6–9 months; Hayssen, 2014; Carter *et al*., 2016), we estimate that *N. uruguayensis* likely had a gestation period between 80 and 110 days and reached sexual maturity around 8–11 months. These values fall within the range established by extant armadillos with both lower and higher body masses than our estimates for *N. uruguayensis*, supporting the plausibility of these projections. We can also speculate that they would be solitary like the large extant armadillos.

The position of the centre of mass does not change with the estimations based on the two geometrical models (Equations 5 and 6) and is very close to the hindlimbs (Figure 3). In addition, the lungs' low density, which we do not consider in our calculations, would move the centre of mass even more caudally.

The position of the centre of mass located on the posterior limbs suggests the possibility for seesaw bipedalism-type locomotion, as well as a reduction in weight-bearing on the forelimbs (Milne *et al*., 2009; Vizcaíno *et al*., 2011). This biomechanical arrangement supports the hypothesis that *Neoglyptatelus uruguayensis* may have had good digging ability, either for foraging or for constructing burrows, behaviors commonly observed in extant dasypodid and consistent with the ecological adaptations inferred for this group.

CONCLUSIONS

The body mass of *Neoglyptatelus uruguayensis* was estimated using two complementary approaches: allometric equations derived from extant armadillos and a geometrical reconstruction of its armour. Both methods yielded consistent results within a range of 13 to 28 kg, with the most reliable mean value around 17 kg from the allometric equations. The geometrical model produced slightly higher mean estimates (22 kg), likely due to uncertainties in the armour's original shape and soft tissue distribution. The estimated centre of mass was located close to the hindlimbs, suggesting a biomechanical arrangement that may have facilitated digging behaviour and potentially supported occasional bipedal postures. These results provide a quantitative assessment of body mass for a member of the Pachyarmatheriidae, contributing to the understanding of the paleobiology of this peculiar group. They also highlight the morphological and ecological diversity within the family and open perspectives for future studies aimed at refining functional and ecological interpretations through the discovery of additional material.

DATA AVAILABILITY STATEMENT

The authors confirm that the data supporting the findings of this study are available within the article.

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AUTHOR CONTRIBUTIONS

Ezequiel García: writing – original draft, editing, visualization, investigation, formal analysis, software. Rudemar Ernesto Blanco: writing – review, conceptualization, resources. Andrés Rinderknecht: editing, visualization, investigation, formal analysis, data curation. All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

DECLARATION OF AI USE

We have not used AI-assisted technologies to create, review, or any part of this article.

ETHICS

This work did not require ethical approval, collecting licenses, or previous authorizations.

CONFLICT OF INTEREST

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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