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Allometry of the bones of living and extinct armadillos (Xenarthra, Dasypoda)

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Abstract

This study examines the allometry of long bones in ten species of armadillo spanning the entire size range of the group, and including its five extant subfamilies. The fossil species *Propraopus grandis* (middle to late Pleistocene of South America) was included in order to assess its locomotory habits. Its mass was estimated to be about 47 kg, assuming a geometrical similarity to two species of *Dasypus*. It was concluded that the armadillos scale their humeri, ulna and partially their tibia like other digging mammals previously studied, i.e. ctenomyid rodents, but their femora as generalised mammals. The limb bone dimensions of *Propraopus grandis* are those expected for an armadillo of its size. *Priodontes maximus* was found to have a humerus stronger than expected from the general pattern of armadillos.

Introduction

Research on allometry of the leg bones has shed light on how those bones scale in relation to body mass in ungulates (McMahon 1975), bovids (Alexander 1977), mammals of varied size from shrews to elephant (Alexander et al. 1979; Biewener 1983), primates (Alexander 1985) and birds (Alexander 1983). However, the studies about mammals did not include diggers. More recently, this approach has been applied to small digging mammals, like insectivores and rodents (Bou et al. 1987) and ctemonyine rodents (Casinos et al. 1993). In those studies two hypotheses were tested and corroborated: 1) in digging mammals, the regression of the long bone length against diameter (the latter being the independent variable) involves a slope of less than 1; and 2) long bone length must scale to body mass with an exponent of less than 0.33, while the long bone diameter should do so with an exponent greater than 0.33.

Those authors mentioned the interest of undertaking this kind of study on other monophyletic groups of digging mammals. Armadillos seem to be a very suitable subject, because they are a monophyletic group of diggers, ranging in size from hundreds of grams to tens of kilograms. The fossil *Propraopus grandis* (Dasypodinae, Dasypodini), one of the giant armadillos from Middle and Late Pleistocene of South America, was included among the species considered here in order to infer its possible locomotor habits.

Material and methods

The species studied here broadly represent the systematic and size diversity of extant armadillos. They are listed below under their corresponding subfamily, following the classification proposed by Scillato-Yané (1980). Each name is followed by its collection location and number of the specimens examined. The initials MACN mean Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos

Aires, Argentina; MLP and MLP-DPV mean respectively the collections of fossils and of recent animals in the Departamento Científico de Paleontología de Vertebrados of the Museo de La Plata, Argentina; and AMNH means the American Museum of Natural History, New York, USA.
Euphrachtinae:
Chaetophractus vellerosus (MLP-DPV 74); *Chaetophractus villosus* (MLP-DPV 48); *Zaedyus pichiy* (MLP-DPV 35)
Dasypodinae:
Dasypus hybridus (MLP-DPV 65); *Dasypus novemcinctus* (MLP-DPV 80); *Dasypus kappleri* (AMNH 267011); *Propraopus grandis* (MACN 17989 and MLP 69-IX-9-9)
Tolypeutinae:
Tolypeutes matacus (MLP-DPV 13)
Priodontinae:
Priodontes maximus (MACN s/n)
Chlamyphorinae:
Chlamyphorus truncatus (MACN 471).

The masses of the specimens belonging to living species were obtained from the literature (Rood 1970; McNab 1980; Wetzel 1985).

The estimate of the mass of the fossil species *Propraopus grandis* was obtained by scaling up the specimens of *Dasypus hybridus* (MLP-DPV 65) and *Dasypus novemcinctus* (MLP-DPV s/n). These two species were chosen as models because of their close morphological and phylogenetical relationships with *Propraopus grandis* (Vizcaíno 1990).

The maximum lengths and anteroposterior diameters at or immediately below the midshaft of humeri, ulnae, tibiae and femora were measured using proper callipers in both limbs (when available) and averaged.

Using reduced major axis regression, the following regressions of log-transformed values were calculated: length against diameter, diameter against body mass, and length against body mass. The variable mentioned in the second place was in all cases the independent one.

The values of slopes for humeri and femora given by Alexander et al. (1979), who used least square regressions, were recalculated after the original data using the reduced major axis method. The other values, namely the slopes for ulna and tibia, as well as those given by Casinos et al. (1993), were directly taken from the respective paper.

Results and discussion

The masses of the studied species and the lengths and diameters of their humeri, ulna, femora and tibia are shown in table 1. The mass of *Propraopus grandis*, estimated after comparison with *Dasypus novemcinctus*, turned out to be 46.7 kg; and after *Dasypus hybridus*, 47.5 kg. Thus, we decided to use 47 kg, but our calculations or conclusions would not be altered by choosing other values within the cited range.

Table 1. Masses and long bone dimensions of the studied species of armadillos. Masses (*m*, in kg), lengths (*L*) and diameters (*D*) of humeri (*H*), ulna (*U*), femora (*F*) and tibia (*T*) in millimetres

Species	m	LH	DH	LF	DF	LC	DC	LT	DT
C. vellerosus	1.10	40.6	5.1	40.3	4.5	42.7	5.3	39.0	4.6
C. villosus	4.50	66.2	6.3	69.7	7.9	64.8	8.0	58.2	7.9
Z. pichiy	1.74	43.4	4.1	45.6	5.1	44.5	5.5	5.1	5.1
D. hybridus	2.04	48.1	4.4	69.1	7.2	53.9	6.3	53.2	7.7
D. novemcinctus	3.30	62.0	5.5	120.0	10.3	72.5	8.6	80.8	11.5
D. kappleri	10.60	80.5	14.0	17.5	12.7	94.5	11.4	91.5	16.8
P. grandis	47.00	128.0	22.0	215.0	24.9	133.0	24.3	133.8	34.8
T. matacus	1.53	41.8	4.3	62.9	5.8	51.0	6.1	57.4	4.9
P. maximus	45.19	125.0	31.5	180.0	22.3	138.3	21.0	147.8	24.5
C. truncatus	0.12	19.5	2.8	22.0	2.8	22.1	2.5	21.5	2.8

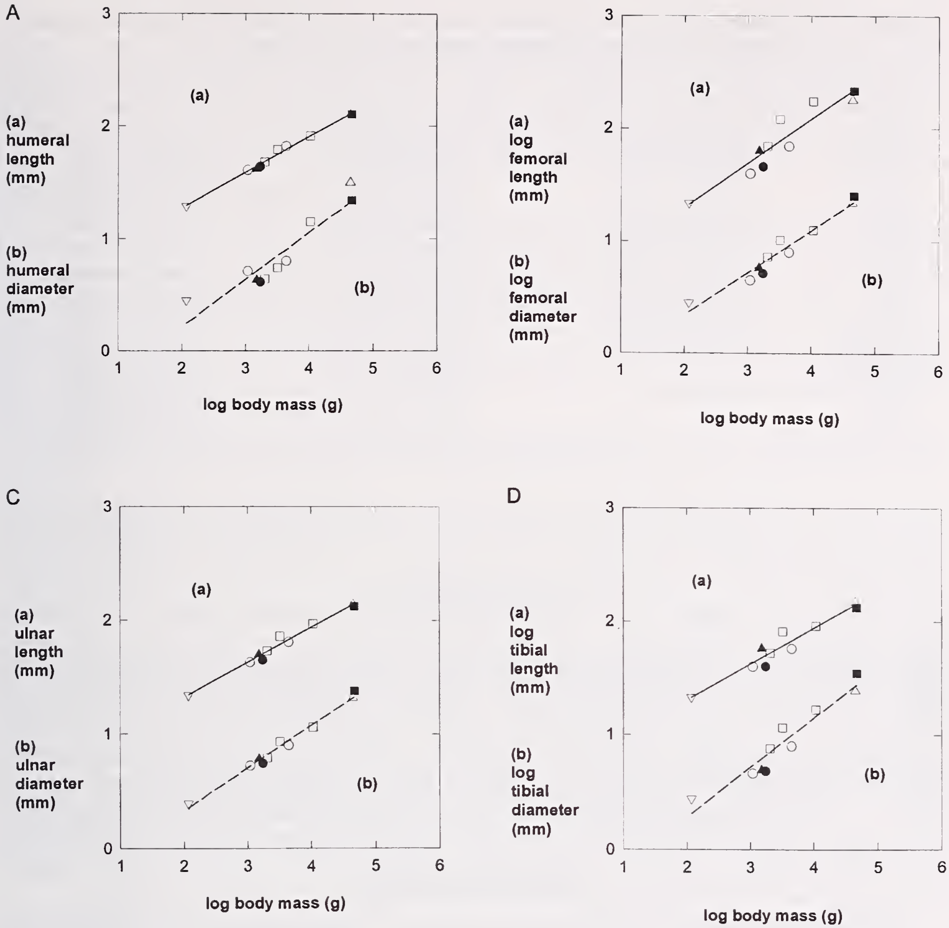

Fig. 1. Graphs on logarithmic coordinates of bone dimensions in armadillos. Linear dimensions are in millimetres and masses in grams. (A) humeral length (*a*) and diameter (*b*) against body mass; (B) ulnar length (*a*) and diameter (*b*) against body mass; (C) femur length (*a*) and diameter (*b*) against body mass; (D) tibia length (*a*) and diameter (*b*) against body mass.

Symbols:

Chaetophractus vellerosus	○	*Dasypus kappleri*	□
Chaetophractus villosus	○	*Propraopus grandis*	■
Zaedyus pichiy	●	*Tolypeutes matacus*	▲
Dasypus hybridus	□	*Priodontes maximus*	△
Dasypus novemcinctus	□	*Chlamyphorus truncatus*	▽

Our allometric curves (Fig. 1) are compared with the values recalculated after Alexander et al. (1979), and with those obtained by Casinos et al. (1993) in table 2. Since all the correlation coefficients of the calculated regressions were greater than 0.9, the differences in the values yielded by reduced major axis or least squares are very small (for further discussion, see Swartz and Biewener 1992).

In armadillos, the diameter of the humerus is related to its length by a slope of 0.70, i. e. lower than 1, as predicted by the hypothesis 1 of Bou et al. (1987). This figure is even

Table 2. Comparison of slopes of the allometric curves, after different authors. Confidence intervals shown between brackets. Abbreviations as in table 1

Slopes	Alexander et al. (1979)	Casinos et al. (1993)	this study
m/LH	0.36(0.35–0.38)	0.30(0.28–0.32)	0.32(0.31–0.33)
m/DH	0.38(0.37–0.39)	0.41(0.37–0.46)	0.45(0.39–0.51)
m/LU	0.37(0.35–0.38)	0.24(0.20–0.29)	0.31(0.30–0.33)
m/DU	0.36(0.34–0.37)	0.42(0.37–0.48)	0.38(0.36–0.39)
m/LF	0.37(0.35–0.38)	0.29(0.27–0.32)	0.41(0.36–0.46)
m/DF	0.37(0.36–0.38)	0.36(0.30–0.41)	0.39(0.36–0.42)
m/LT	0.33(0.31–0.34)	0.26(0.21–0.30)	0.33(0.30–0.36)
m/DT	0.37(0.35–0.39)	0.54(0.43–0.65)	0.45(0.41–0.50)
DH/LH	0.95(0.91–0.99)	0.75(0.67–0.84)	0.70(0.61–0.80)
DU/LU	–	0.68(0.58–0.79)	0.82(0.78–0.87)
DF/LF	0.99(0.95–1.04)	0.86(0.77–0.95)	1.07(0.98–1.16)
DT/LT	–	0.62(0.50–0.73)	0.72(0.65–0.80)

lower than the respective value obtained in ctenomyids, although the corresponding confidence intervals overlap. In the cases of the ulna and of the tibia that prediction is correct too. However, in the case of the femur the value rises to 1.07, much higher than the exponent predicted for diggers, and even higher than the recalculated figured we obtained after the data from Alexander et al. (1979). That seems to be valid also for the tibia, whose length scale in armadillos with an exponent of 0.33, the same as that yielded in the study of mammals in general, and higher than the exponent obtained in ctenomyids (0.26).

The diameters, on the other hand, scale with an exponent greater than 0.33, as predicted by the hypothesis 2 of Bou et al. (1987). Also, the humerus length behaves as predicted, i. e. with a slope of less than 0.33. However, femur length shows a slope of 0.41, much higher than the prediction of hypothesis 2 and also higher than the upper limit of the confidence interval in the results on ctenomyids of Casinos et al. (1993). This value is even higher than the average in Alexander et al. (1979) for mammals in general.

The linear dimensions of *Propraopus grandis* are approximately the expected for a generalised armadillo of its size, while *Priodontes maximus* show a thicker humerus than the average and near the prediction obtained by using the upper limit of the confidence interval of the slope.

Summing up, the humeri, ulnae and to some extent tibiae of armadillos scale in a similar way as those of digging mammals. On the other hand, their femora scale as generalised mammals and unlike the ctenomyids, the other group of digging mammals already studied. A possible explanation of this might be the wider size range of armadillos, although humeri did not seem to be affected by this factor. Another explanation might be related to the fact that, while all ctenomyids are fully subterranean, i. e. they spend most of their lives under the surface, almost all the dasypodids studied here are, to a great extent, of epigeous habits. This interpretation has the advantage of explaining the similar slope of the humeri among armadillos and ctenomyids, for in either case the excavation function of this bone is similar. Therefore, it can be stated that, from the point of view of the long bones scaling, armadillos have the forelimb of a digger and the hindlimb of a cursorial, generalised mammal.

Priodontes maximus shows much a higher value than expected for the diameter of the humerus. It must be emphasised that this is particularly important because of the fact that *Priodontes maximus* lies in the upper extreme of size range among the studied species, and, therefore, in that region of the graph the confidence limits for the regression are wider. At the same time, the rest of its bone dimensions are the expected for its size, including those of the femur. This result is paradoxical, because this species has well-known bipedal locomotor habits (Frechkop 1949, 1950). An explanation to this observation is related to the fact that their bipedal gait (a slow walk) is not strenuous at all. Therefore, it might not pose any risk of bone failure to the hind limb. On the other hand, the humerus is involved in the much harder activities of tearing down termite nests or of excavating large galleries in hard ground.

In regard to the studied variables, the behaviour of the bone dimensions of *Propraopus grandis* is very similar to that of *Dasypus* species, with the exception of the diameter of humerus. The two smaller species of *Dasypus* show lower values for this dimension than expected for armadillos of their size, while in *Propraopus grandis* and in *Dasypus kappleri* they are in the average and slightly above, respectively. This fact suggests that the fossil species invested more in digging than these living relatives do. Unfortunately, the biology of *Dasypus kappleri* is not enough known to bolster this hypothesis more properly (Szeplaki et al. 1988).

Therefore, it can be stated that *Propraopus grandis* kept the generalised habits of the subfamily Dasypodinae, although with a body mass near 50 kg. At the same time, the sole species of armadillos attaining this size in the recent is *Priodontes maximus*, and it does it in association with a high specialisation in its trophic niche.

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Zusammenfassung

Allometrische Beziehungen von Extremitätenknochen bei lebenden und fossilien Gürteltieren (Xenarthra, Dasypoda)

Die allometrischen Beziehungen von Maßen an Extremitäten wurden bei 10 Gürteltier-Arten untersucht, einschließlich Vertretern der fünf Unterfamilien mit lebenden Arten, und in Bezug auf das gesamte Größenspektrum der Gruppe. Die fossile Art *Propraopus grandis* (Mittel- bis Oberpleistozän Südamerikas) wurde mit einbezogen, um ihre Bewegungsmöglichkeiten zu ermitteln. Aufgrund der angenommenen geometrischen Ähnlichkeit mit 2 Arten von *Dasypus* wurde die Körpermasse von *Propraopus grandis* auf etwa 47 kg geschätzt. Daraus wurde der Schluß gezogen, daß Gürteltiere ihre Oberarmknochen, Ellen und teilweise auch ihre Schienbeine wie andere grabende Säugetiere (z.B. Ctenomyide Nagetiere) ausgebildet haben, ihre Schenkelknochen jedoch entsprechend der allgemeinen Säugetiere. Die Ausmaße dieser Knochen von *Propraopus grandis* entsprechen denen eines Gürteltieres der gleichen Größe. Der Oberarmknochen von *Priodontes maximus* ist stärker ausgebildet als der der übrigen Gürteltiere.

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