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ORIGINAL PAPER

Allometric and Group Differences in the Xenarthran Femur

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Abstract The aim of this study is to analyze shape variation in the xenarthran femur to gain insights into their behavior and locomotion. Specimens of both Cingulata (armadillos and glyptodonts) and Pilosa (anteaters and sloths) were studied and within each group body mass varies by several orders of magnitude. The main focus of the analysis was allometric variation in femoral shape in the three groups studied, armadillos, glyptodonts, and pilosans. Three dimensional coordinates were recorded for 40 homologous landmarks on each of 51 xenarthran femurs. The data were analyzed by geometric morphometric methods, and form space analysis was used to identify the allometric variation in each of the three groups. Across all groups, larger specimens tended to have larger articular surfaces, more robust femora generally, and the shape of the femoral condyles was more suited to extended postures. In addition, in larger specimens the medial condyle was much larger than the lateral condyle and the third trochanter was located more distally. The larger armadillo femora had a greater trochanter located considerably proximal to the femoral head and this is thought to improve femoral extension, but in glyptodonts and pilosans the larger specimens had a greater trochanter that was far lateral to the femoral head and this is interpreted as enhancing femoral rotation.

Keywords Femur · Allometry · Xenarthran · Geometric morphometrics

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Introduction

This study presents an analysis of variation in femoral shape among mainly terrestrial xenarthrans. We include specimens from extant armadillos and anteaters, as well as some fossil armadillos, glyptodonts, and ground sloths (see Fig. 1).

Two major clades within Xenarthra are recognized by most authors: Cingulata and Pilosa (see Gaudin and McDonald 2008 and references therein). The defining feature of cingulates is their armor, which is formed by dermal scutes lined with epidermal scales that protect the head and body, and includes a sheath for the tail. Living cingulates are represented only by armadillos, which constitute two-thirds of the diversity of all living xenarthrans (Aguiar and Fonseca 2008). Fossil cingulates include armadillos, glyptodonts, and pampatheres. Pilosa includes anteaters (Vermilingua, represented by only three living genera and with a very scarce fossil record) and sloths (Folivora, represented for two living arboreal genera, but with an extraordinarily rich fossil record).

Armadillo body masses range from 85 g (pink fairy armadillo *Chlamyphorus* Harlan, 1825, see Nowak 1999) to more than 30 kg (giant armadillo *Priodontes* F. Cuvier, 1825, see Nowak 1999), their armor is flexible, and they are mostly specialized digging animals with forelimbs well

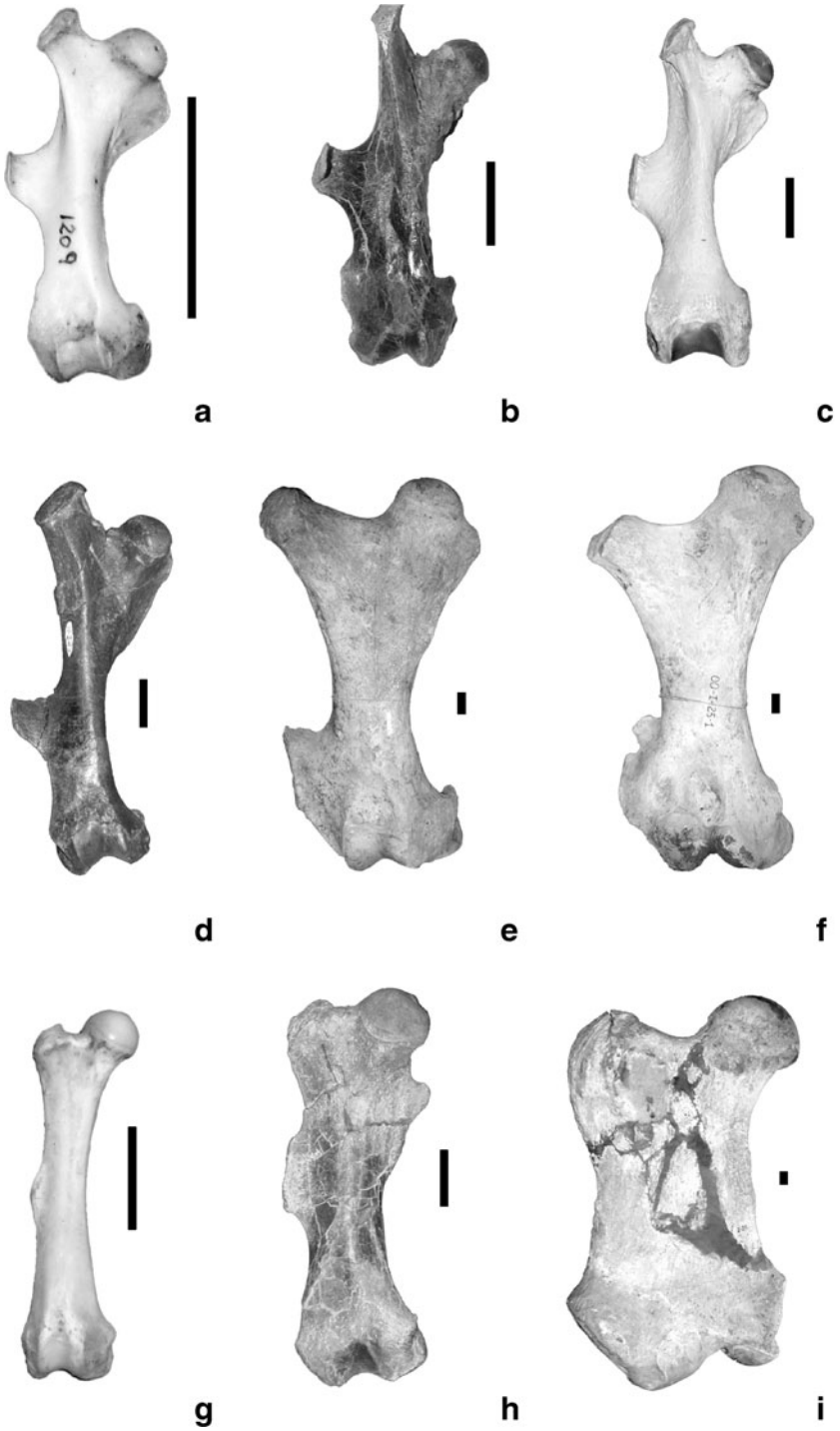

Fig. 1 Femora of taxa studied, in anterior view. **a** *Zaedyus pichiy,* MLP-1209; **b** *Proeutatus* sp., MPM-PV 3415; **c** *Priodontes maximus,* SFV s/n (left femur shown reversed in order to facilitate visual comparison); **d** *Propalaehoplophorus* sp., MLP-91-II-25-6; **e** *Glyptodon* sp., MLP-04-X-1-1(65); **f** *Doedicurus* sp., MLP-00-I-25-1; **g** *Tamandua tetradactyla,* MLP-s/n; **h** *Hapalops* sp., MPM-PV 3467; **i** *Megatherium* sp., MLP-229. Scale bar = 3 cm

designed for this activity. In a study of armadillo limb proportions, Vizcaíno and Milne (2002) showed that while the proportions of the forelimbs are related to digging behavior, the hind limb proportions correlate with body mass and seem to be more related to weight bearing. The hip moment index (HMI), which indicates the position of the third trochanter along the length of the femur, was shown to increase with body size, indicating that the third trochanter is closer to the knee in larger armadillos. In line with these observations concerning weight bearing in armadillo hind limbs, it has long been noted that many armadillos walk on the soles of their hind feet with only the tips of the manus claws touching the ground (Frechkop 1949; Nowak 1999).

Glyptodonts are considered to be functionally unsuited to digging, because their relatively rigid carapace is fused to the pelvic girdle, the thoracic and lumbar vertebrae are also fused forming a tube, and the other skull and limb

structures typical of fossorial mammals are absent (Kraglievich 1934; Quintana 1992). Early glyptodonts, the Miocene propalaehoplophorines, weighed less than 100 kg, while their Pleistocene counterparts reached body masses estimated at up to one ton (Vizcaíno et al. 2010). Studies of fossil glyptodonts, estimating body mass and strength indices of their long bones (Fariña 1995; Fariña et al. 1998; Vizcaíno et al. 2010), show that the center of glyptodont body mass is located posteriorly, and thus the hind limbs bear most of the body weight. Estimates of the proportion of mass supported by the glyptodont hind limbs range from 56 to 60% (Fariña 1995) up 100% in some species studied by Vizcaíno et al. (2010). The latter study examined the possibility that glyptodonts were capable of functional bipedality, a hypothesis first formulated by Fariña (1995).

Living anteaters comprise the terrestrial giant anteater *Myrmecophaga* Linnaeus, 1758, with an average bodymass of 30 kg (Nowak 1999), the scansorial *Tamandua* Gray, 1825 (around 4.5 kg, see Nowak 1999), and the small and fully arboreal silky anteater *Cyclopes* Gray, 1821 (average less than 300 g, see Nowak 1999). Living sloths are represented only by the tree sloths *Bradypus* Linnaeus, 1758 (the three-toed sloth) and *Choloepus* Illiger, 1811 (the two-toed sloth). Both of these animals are almost completely arboreal, and their limbs are slender and gracile.

The fossil record of sloths is extremely rich. Miocene forms ranged around 80 kg and it is proposed that they were semiarboreal (White 1993), while Pleistocene sloths were gigantic forms with body masses reaching several tons (Bargo et al. 2000) and hence considered to have been ground dwellers since the first description of *Megatherium* by Cuvier (1796). Among the ground sloths, the hind limbs also seem to bear most of the body weight. Although most ground sloths are considered as quadrupedal, there is still debate concerning whether *Megatherium* was bipedal or quadrupedal, but it is generally accepted that this genus was capable of adopting bipedal postures in order to free the forelimbs for food acquisition (Aramayo and Manera de Bianco 1996; Blanco and Czerwonogora 2003; Casinos 1996; Fariña and Blanco 1996; Toledo 1998).

To summarize, each of the xenarthran groups included in this study have a size range covering several orders of magnitude, and members of each group bear most of their body weight on their hind limbs. Our analysis comprises an examination of allometric variation in femoral shape to seek insights into how the femur adapts to increasing body size. Our expectation is that the differences in the allometric patterns among the groups will provide information about differences in locomotor styles and function. Contrary to Toledo (1998), we consider that all specimens studied bear a third trochanter (see "Discussion"), but its functional significance in locomotion is unknown.

Materials and Methods

Femurs from 51 xenarthran specimens, including 25 extant (23 armadillos and two anteaters (one *Tamandua* and one *Myrmecophaga*) and 26 fossil (eight armadillos, seven glyptodonts, and 11 ground sloths) were examined in this study. The specimens are housed in museums of natural sciences in Argentina (Museo de La Plata–MLP, and Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" – MACN). Details of fossil specimens are presented in the Appendix.

Forty 3-dimensional landmarks were digitized on each femur using a Microscribe G2L. The landmarks are defined in Table 1 and illustrated in Fig. 2, and were chosen to represent the shapes of articular surfaces and the positions of muscle attachment sites.

The data were analyzed by geometric morphometric methods using morphologika software (O'Higgins and Jones 1998). Generalized Procrustes analysis was first used to remove differences in size, position, and orientation among the sets of coordinates representing each specimen. For each femur, centroid size was calculated as the square root of the sum of the squared distance of each landmark to the centroid of that specimen's landmark configuration, and provided an unbiased measure of the specimen size (O'Higgins and Jones 1998). Principal components analysis (PCA) was then used to analyze shape variation among the specimens. Allometric differences were examined separately among armadillos, glyptodonts, and pilosans using Procrustes form space, where the log of the centroid size is included with the landmark coordinates submitted to PCA (Milne et al. 2009). This method forces all the shape variation associated with size into the first principal component (PC1).

Results

Figure 3 is a plot of PCs 1 and 2 from a shape space analysis that includes all 51 specimens in the study. Principal component 1 accounts for 48% and PC2 accounts for 12% of the total variation. As can be seen, PC1 separates the living armadillos, *Tamandua,* and *Myrmecophaga* from the large fossil xenarthrans (glyptodonts and ground sloths). There is a strong correlation between PC1 and centroid size (r=0.92 $p<$ 0.0001). The analysis shows that large femurs are relatively wider and have larger articular surfaces (femoral head, condyles, and patellar surface), the third trochanter is also situated more distally, and the medial condyle becomes larger than the lateral. A lateral view of these shapes (not shown) indicates the larger femora have condyles more suited to extended postures, and also confirms the difference in the size of the medial and lateral condyles. However, the allometric shape variation associated with PC1 is confounded by the

Table 1 Landmarks used in the analysis

Number	Definition of landmarks of the femur
1	Superior/lateral edge of the head
2	Posterior edge of the head
3	Inferior/medial edge of the head
4	Anterior edge of the head
5	Middle of the articular surface
6	Most proximal point of the head
7	Lower end of the trochanteric fossa
8	Lowest point on the upper surface of the neck
9	Most proximal (superior) point of the greater trochanter
10	Most anterior point of the greater trochanter
11	Lateral point of the greater trochanter
12	Posterior point of the greater trochanter
13	Lateral border just above the third trochanter
14	Top of the third trochanter
15	Bottom of the third trochanter
16	Lateral border/linea aspera midway between points 15 and 24
17	Apex of lesser trochanter
18	Midpoint of the crest of the lesser trochanter
19	Lowest point on the crest of the lesser trochanter
20	Anterior margin at level of 19
21	Medial epicondyle—hollow
22	Lateral epicondyle—hollow
23	Upper end of medial gastrocnemius
24	Upper end of lateral gastrocnemius/plantaris
25	Posterior end of the medial condyle
26	Posterior end of the lateral condyle
27	Medial edge of medial condyle (posterior point)
28	Lateral edge of medial condyle (posterior point)
29	Medial edge of lateral condyle (posterior point)
30	Lateral edge of lateral condyle (posterior point)
31	Medial edge of medial condyle (distal point)
32	Lateral edge of medial condyle (distal point)
33	Medial edge of lateral condyle (distal point)
34	Lateral edge of lateral condyle (distal point)
35	Anterior end of the medial condyle
36	Anterior end of the lateral condyle
37	Lower end of patella surface
38	Upper end of patella surface
39	Medial end of patella surface (at widest/deepest point)
40	Lateral end of patella surface (at widest/deepest point)

mixed nature of the sample and the fact that the smaller specimens are predominantly armadillos.

Principal component 2 has no correlation with centroid size, but separates the two main xenarthran groups with the pilosans having high scores and the cingulates, low scores. Specimens with low scores on this PC have very prominent greater and third trochanters. In the plot there is some overlap between the larger fossil armadillos (*Eutatus*) and the smaller glyptodonts (*Propalaehoplophorus*). One large glyptodont (*Doedicurus*) occupies shape space close to that of the ground sloths and this seems to be on the basis of its somewhat less pronounced third and greater trochanters.

Principal component 3 accounts for 10% of the variation and seems to be related to the overall robusticity of the femur, particularly the width of the distal epiphysis; however, there is no correlation ($r=-0.04$) between PC3 and centroid size.

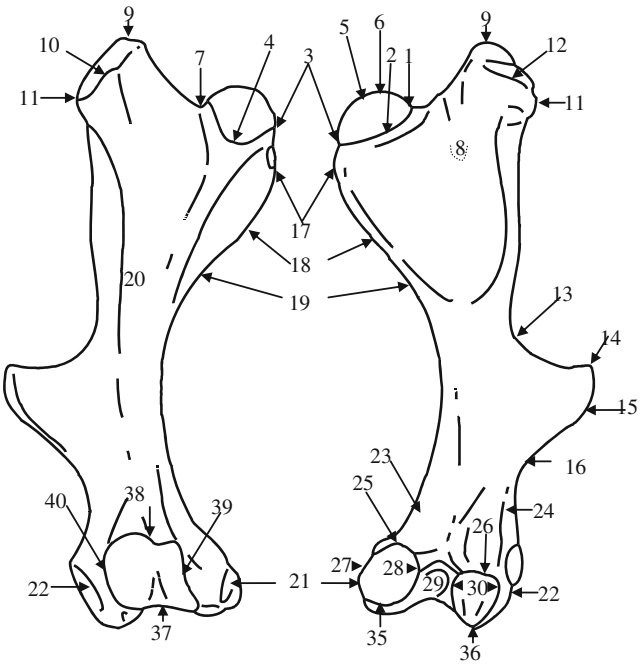

Fig. 2 Femoral landmarks. Left, anterior view. Right, posterior view. For landmark definitions see Table 1

None of the PCs in the analysis distinguish the two groups of ground sloths (mylodontids and megatheres).

Figure 4 is a plot of the first principal component in Procrustes form space (that accounts for 96.4% of the total variation) and centroid size (r=0.98) in an analysis that includes only the armadillos (extant and fossil). The wireframe diagrams to the left and right are the anteroposterior and mediolateral views of the wireframe diagrams representing the extremes of PC1. The anteroposterior views show that the larger armadillos have relatively larger articular surfaces, a greater trochanter that extends further beyond the femoral head, a diaphysis that is more curved on the medial side, and a third trochanter that is positioned somewhat lower on the shaft of the femur. The lateral views show that the femoral condyles of the larger specimens have less articular surface facing posterosuperiorly and so are somewhat less suited for flexed postures.

Figure 5 is a plot of the first principal component in Procrustes form space (that accounts for 94.6% of the total variation) and log centroid size (r=0.99) in an analysis that includes only the glyptodonts. The wireframe diagrams to the left and right are the anteroposterior and mediolateral views of the wireframe diagrams representing the extremes of PC1. The anteroposterior views show that larger glyptodonts have

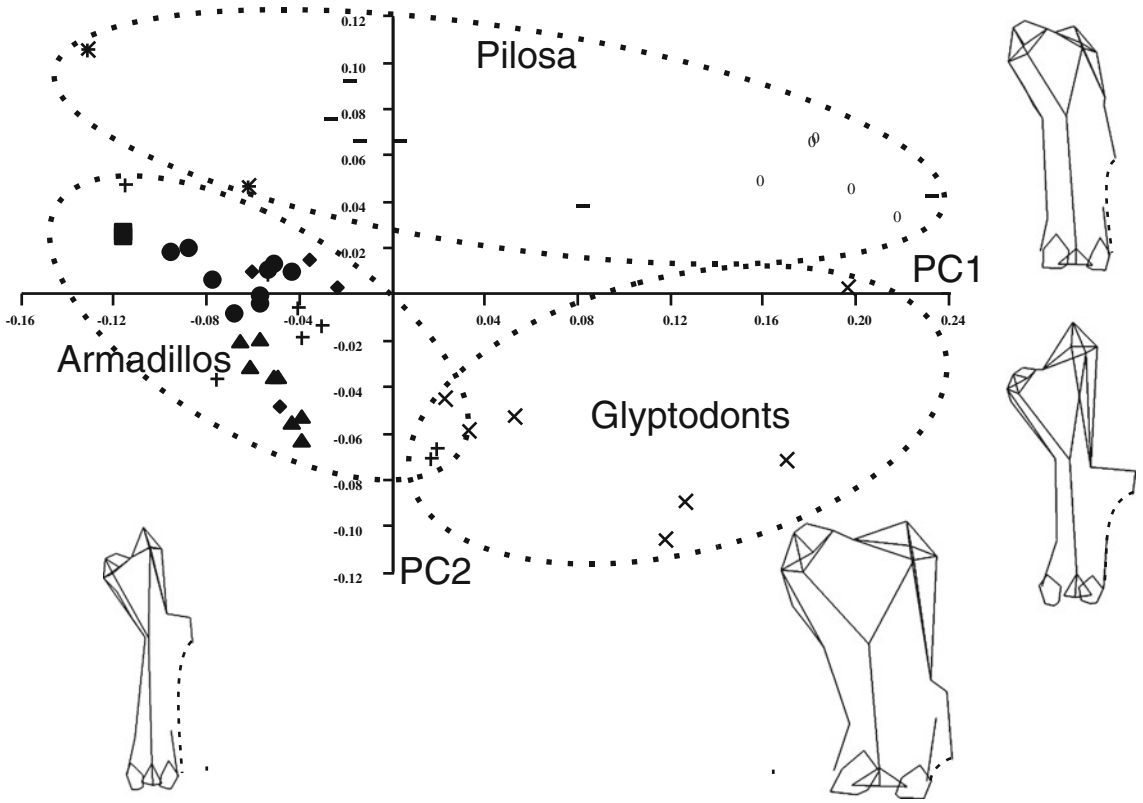

Fig. 3 Plot of PCs 1 and 2 from an analysis that includes all 51 specimens in the study. The shapes below the plot indicate the variation on PC1 and those to the right indicate the shape variation associated with PC2. The living armadillos are shown in solid shapes (Tolypeutini – squares, Dasypodini – triangles, Priodontini – diamonds, Euphactini - circles), fossil armadillos are crosses, glyptodonts are Xs, anteaters are stars, and the ground sloths are indicated with dashes (megatheres) and open circles (mylodontids)

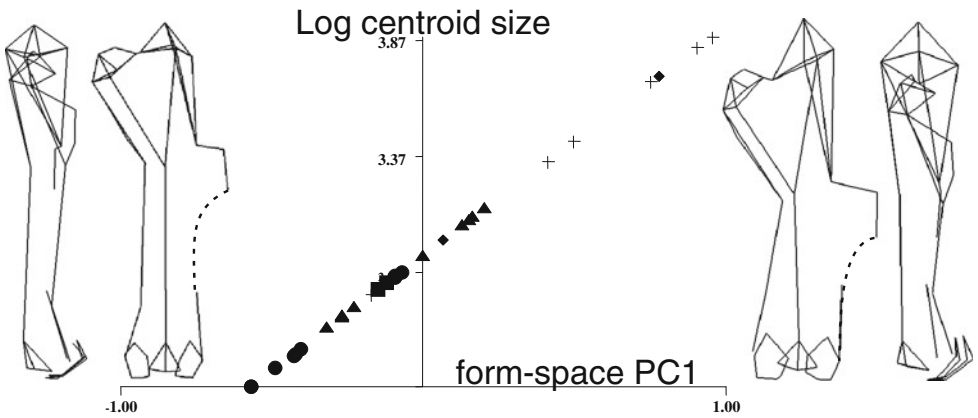

Fig. 4 Plot of PC1 from a Procrustes form space analysis of the armadillo specimens against the log centroid size. The diagrams to the left and right of the plot are anteroposterior and lateral views of the mean shape warped to the extremes of PC1

much more robust femora with relatively larger articular surfaces, an increasingly more laterally placed greater trochanter, a diaphysis that is more curved on the medial side, and a third trochanter that is situated close to the knee. The mediolateral views show that the larger glyptodonts have a medial femoral condyle that is much larger than the lateral (also evident in the anteroposterior views) and that both condyles are more suited for extended postures. The knee of larger specimens can be described as deeper, because the anteroposterior dimension of the distal epiphysis is larger relative to the length of the femur. The patella surface is also relatively wider in the larger glyptodonts.

Figure 6 is a plot of the first principal component in Procrustes form space (that accounts for 95.7% of the total variation) and centroid size (r=0.99) in an analysis that includes only the Pilosa. The wireframe diagrams to the left and right are the anteroposterior and mediolateral views of the wireframe diagrams representing the extremes of PC1. The anteroposterior views show a large increase in the transverse dimensions of the bones. The greater trochanter is larger and more prominent in the larger specimens, the medial side of the diaphysis is more curved, and the apex of the third trochanter is close to the knee and there is no indentation marking its upper limit. The mediolateral views show that the medial femoral condyle is much larger than the lateral in larger specimens and that both condyles are deeper anteroposteriorly, and less suited for flexed postures. The patella surface is also relatively shorter and wider in larger specimens. In the diagrams the diaphysis looks very thin in the anteroposterior direction, and this is because the lateral border is situated more anteriorly with respect to the epiphyses.

Discussion

In the initial analysis including all the specimens (Fig. 3), PC1 has a strong correlation with centroid size and shows features that vary with size in all the xenarthrans collectively. The relatively larger articular surfaces and features of the femoral condyles that suggest less flexed postures are features that are predicted by allometric principles (Schmidt-Nielsen 1984; Biewener 2000). However, the increasing relative size of the medial femoral condyle, the lateral expansion of the femur, and the increasingly distal position of the third trochanter, are features that seem to be unique to xenarthrans. Although Toledo (1998) considers that only early sloths possess a third trochanter, most authors (e.g., McDonald and De Iuliis 2008) consider the third trochanter to be one of the most conspicuous features of the xenarthran femur (see Fig. 1). In the late Pleistocene Megatheriidae and Mylodontidae, the third trochanter extends towards the lateral epicondyle (Pujos et al. 2007),

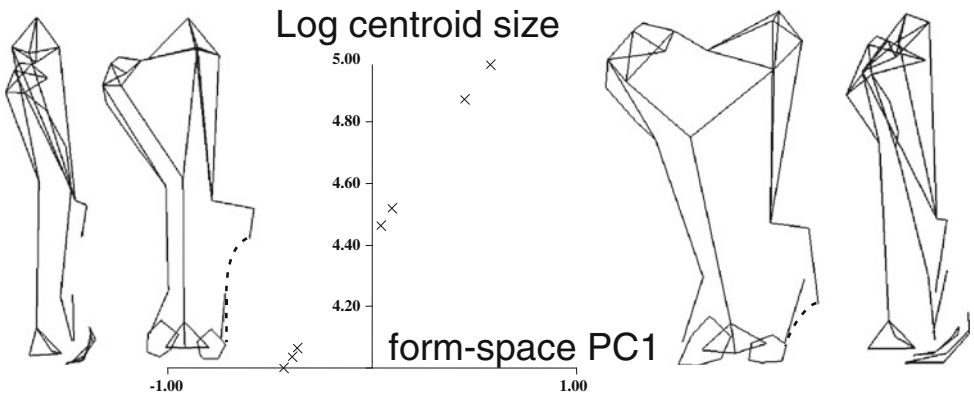

Fig. 5 Plot of PC1 from a Procrustes form space analysis of the glyptodont specimens against the log centroid size. The diagrams to the left and right of the plot are anteroposterior and lateral views of the mean shape warped to the extremes of PC1

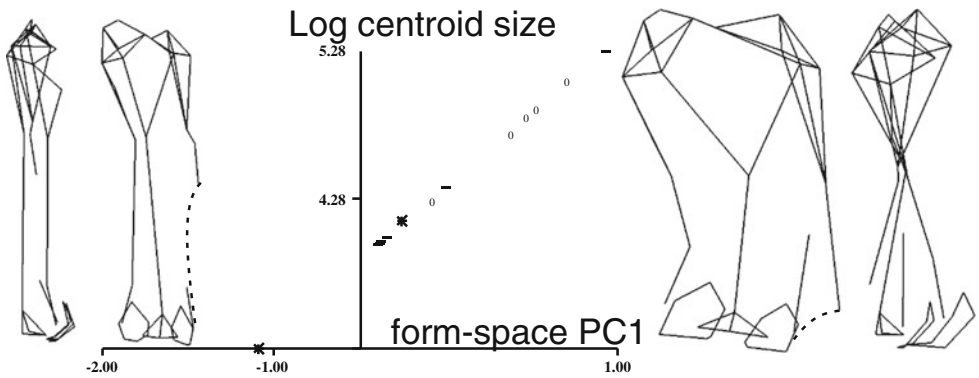

Fig. 6 Plot of PC1 from a Procrustes form space analysis of the pilosa specimens against the log centroid size. The diagrams to the left and right of the plot are anteroposterior and lateral views of the mean shape warped to the extremes of PC1

while the whole lateral border of the femur is expanded above that level.

When armadillos, glyptodonts, and pilosans are examined separately (Figs. 4–6), there are some features of the femur that vary with size in all three groups, and some features that are particular to armadillos, glyptodonts, and pilosans, respectively. The allometric features that the three groups have in common largely agree with those identified in the overall analysis. The larger specimens have femoral condyles that have more articular surface facing distally and/or less facing posteriorly, and this suggests that larger specimens have more extended postures (Biewener 2000; Argot 2002). In armadillos that are small and probably never fully extend their knees, there is no difference in the distal extent of the condyles, but in the large glyptodonts and sloths there is a clear increase in the distal extent of the condyles. The larger specimens also display relatively deeper knees, and wider and shorter patella surfaces suggesting better leverage for knee extension in larger specimens, but probably reduced range of motion (Sargis 2002; Argot 2002).

Other allometric features that are common to all groups are that the medial femoral condyle becomes larger than the lateral, the third trochanter becomes closer to the knee, and the medial border of the femur is more concave. The larger medial condyle in the larger armadillos (which are much smaller than the larger glyptodonts and pilosans) is subtle and only seen in the lateral view. The presence of a larger medial condyle suggests that, as size increases, more load is borne by the medial side of the knee, and thus it would appear that the primary force transmitted through the femur passes in a line from the femoral head to the medial femoral condyle (Toledo 1998; Argot 2002; Sargis 2002). This, together with the increased curvature of the medial border, would result in more bending stress in femurs of the larger xenarthrans, where the medial side may be under compression and the lateral border under tension. It seems likely that aspects of the lateral side of the femur may act to reduce this bending stress. In all groups the third trochanter on the lateral side of the femur becomes more distal as size increases. It may be that the muscles attaching to the third trochanter (tensor fasciae latae and gluteus maximus: Macalister 1869; Humphry 1869; "crête du grand fessier" Jouffroy 1971; Koneval 2003; Vizcaíno et al. 2003) pull proximally and compress the lateral side of the femur above the level of the third trochanter. This may function to reduce bending stresses in that part of the femur above the third trochanter, and in larger specimens this would involve most of the femoral shaft. Finite element analysis could be used to test this hypothesis.

There are some allometric features that are unique to armadillos (Fig. 4). The greater trochanter becomes more and more proximal to the level of the femoral head as size increases. The muscles attaching to the greater trochanter (gluteus medius and minimus) are commonly considered as extensors and abductors of the hip joint (Argot 2002; Candela and Picasso 2008). However, the high position of the greater trochanter reduces mobility of the hip in abduction (White 1993; Pujos et at. 2007), and considering the posture of armadillos the direction of pull of the lesser gluteals is in a cranial direction, so the greater elevation of the greater trochanter would mean that these muscles can contribute to powerful extension of the hip joint. In larger armadillos this would enhance this action and help to support and propel larger and heavier armadillos. Armadillos are also known to use extension of their hind himbs when inside their burrows to press their carapace against the roof of the tunnel. This action is used to secure themselves in the burrow in case of attack (Taber 1945; Talmage and Buchanan 1954), and perhaps also to compact the earth and thus maintain the integrity of their tunnel system.

Among glyptodonts (Fig. 5) the greater trochanter becomes more lateral with increasing size. The direction of pull of the lesser gluteal muscles (gluteus medius and minimus) in glyptodonts is similar to that in armadillos, but the lateral position of the greater trochanter would improve the action of the lesser gluteals as medial rotators of the hip. It is unclear how this would improve their locomotion. In animals that rotate their pelvis to increase stride length, the foot is placed on the ground with the hip in lateral rotation and medial rotators act during the stance phase to help swing the pelvis forward increasing stride length (Inman 1966). However, in glyptodonts that have a rigid vertebral column and carapace fixed to

the pelvis (Kraglievich 1934), it seems unlikely that they would employ this strategy as it would involve large excursions of the whole torso and carapace. Another possibility is that with such a large and rigid body, changing direction would be difficult and perhaps powerful medial rotation of the pelvis about the stance hind limb could be used to turn the body and alter course. This method could also be used to augment the action of the tail muscles when generating a powerful tail swing as used for defense or intraspecific fighting in a bipedal stance (Fariña 1995; Alexander et al. 1999; Blanco et al. 2009; Vizcaíno et al. 2010). Zurita and Aramayo (2006) have also described the predominance of the medial femoral condyle and the large fossa for the popliteus muscle, and these observations together suggest that glyptodonts were also capable of powerful axial rotations at the knee where the medial condyle acts as a pivot while the lateral condyle slides on its tibial plateau.

Among the Pilosa (Fig. 6) the larger specimens have an increasingly broad and rectangular femur where the whole lateral border is expanded while the bone is not particularly deep dorsoventrally. In other mammals, flattening of the femoral diaphysis provides extensive insertion site for thigh adductors and pectineus muscles (e.g., Candela and Picasso 2008 for caviomorph rodents). In addition, a mediolaterally expanded diaphysis could provide increased mechanical resistance to bending forces in the coronal plane, as suggested above for xenarthrans as a whole. It could also be related to an adaptation for axial rotation where, as in glyptodonts, the greater trochanter is positioned to enhance medial rotation at the hip. In the ground sloths there is also evidence that there is substantial rotation at the knee. The large hemispherical medial femoral condyle is thought to be the axis of knee rotation (Tardieu 1983; Salas et al. 2005), while the cylindrical lateral femoral condyle undergoes translation on the tibial plateau. The large scar for the popliteus muscle on the tibia together with a facet for a cyamo-flabella on the back of the lateral tibial plateau indicate that powerful knee rotation may be a feature of pilosan locomotion (Toledo 1998; Salas et al. 2005). The pedolateral ankle posture of ground sloths suggests that the ankle is also adapted for axial rotation (Salas et al. 2005; McDonald 2007).

The propensity for axial rotation at the knee and hip seen in both glyptodonts and ground sloths may be an aspect of xenarthran inheritance (phylogenetic constraint) that has been employed for different purposes. In glyptodonts where the tibia of the stance limb is fixed to the substrate and the torso is fixed by its rigidity and inertia, rotation of the femur at both the knee and hip may allow it to accommodate the rotation involved during forward movement. In ground sloths it is difficult to understand the functional significance of the broad, flat femur. It may be that the more flexible torso and pedolateral ankle posture may allow rotation of the hip, knee, and ankle to be a feature of their locomotion.

In the larger glyptodonts and ground sloth femora examined in this study, features of the distal epiphysis reflect the huge body weights that must be supported. The knees of the larger specimens are deeper, and this provides more mechanical advantage for the quadriceps muscle acting through the patella. The patella surface is broad and short, and this suggests that there is not a large range of flexion and extension at the knee. Further, in larger xenarthrans the femoral condyles face more distally and less posteriorly and this is in line with the more extended (although perhaps not necessarily fully extended) postures expected for such large animals.

This study found some allometric features of the xenarthran femur that are common to all groups (armadillos, glyptodonts, and pilosans). These include increased robusticity and relative sizes of articular surfaces and features that suggest more extended postures for larger specimens. There is also a tendency for larger specimens to have a more distal third trochanter and a more dominant medial femoral condyle. These features suggest that there are large mediolateral bending stresses in larger xenarthrans, and the position of the third trochanter may be involved in a mechanism that relieves this bending stress. Group differences in the allometric trends suggest that in glyptodonts and ground sloths the hind limb may be more adapted to accommodate femoral rotation as part of the locomotor repertoire.

In a revision on the masticatory apparatus, Vizcaíno (2009) claimed that xenarthrans are unique animals that depart from patterns developed in the other main clades of mammals. The preceding discussion suggests that this is also the case for the limbs. However, although a series of novel research initiatives undertaken since the mid-1990s have produced new insights on the diversity and their adaptive possibilities of the limbs of fossil xenarthrans (Vizcaíno et al. 2008 and references therein; Milne et al. 2009), field and lab studies on the correlation of form and function in extant xenarthrans are almost nonexistent. Perhaps the only exception are the very recent efforts by Nyakatura and Fischer (2010a, b) on the tree sloth *Choloepus*, but their results do not seem to be applied to most fossil sloths due to the obvious morphological features related to its unusual behavior. Much more work is needed to understand the natural history, ecomorphology, and physiology of extant and fossil xenarthra.

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Appendix

Table 2 Specimens included in the analysis

Taxon	Collection number
Priodontes maximus	SFV-s/n
Cabassous chacoensis	MLP-1183sa
Cabassous sp.	MLP-843
Dasypus novemcinctus	MLP-2-X-02-1
Dasypus novemcinctus	MLP-1-I-03-73
Dasypus novemcinctus	MLP-1-I-03-72
Dasypus novemcinctus	MLP-1-I-03-76
Dasypus novemcinctus	MLP-1-I-03-77
Dasypus hybridus	MLP-1-I-03-65
Dasypus hybridus	MLP-1-I-03-66
Dasypus hybridus	MLP-1-I-03-70
Dasypus septemcinctus	MLP 1-II-03-64
Chaetophractus vellerosus	MLP-16-V-00-7
Chaetophractus vellerosus	MLP-18-XI-99-9
Chaetophractus vellerosus	MLP-30-XII-02-41
Chaetophractus villosus	MLP-821
Chaetophractus villosus	MLP-15-X-98-3
Chaetophractus villosus	SFV-s/n
Zaedyus pichiy	MLP-9-XII-02-10
Zaedyus pichiy	MLP-1209
Zaedyus pichiy	MLP-1210
Tolypeutes matacus	MLP-15-VII-95-2
Tolypeutes matacus	MLP-12-17
Tamandua tetradactyla	MLP-s/n
Myrmecophaga tridactyla	MLP-1230
Stenotatus sp.	MACN Pv-sc406
Proeutatus sp.	MPM-PV 3415
Proeutatus lagena	MPM-PV 3413
Peltephilus nanus	MACN a-7958-59 (type)
Chorobates recens	MACN Pv-7943
Eutatus? sp.	MACN Pv-985
Eutatus? sp.	MACN Pv-2436
Kraglievichia sp.	MLP-69-IX-8-13a
Propalaehoplophorus sp.	MACN Pv-5134
Propalaehoplophorus sp.	MLP-91-II-25-6
Propalaehoplophorus sp.	MLP-16-15
Neosclerocalyptus sp.	MACN-Pv 18107
Neosclerocalyptus sp.	MLP-16-28
Doedicurus sp	MLP-00-I-25-1
Glyptodon sp.	MLP-04-X-1-1(65)
Elassotherium sp.	MLP-66-XII-13-5
Hapalops sp.	MPM-PV 3400
Hapalops sp.	MPM-PV 3467
Eucholoeops sp.	MPM-PV 3403
Folivora indet.	MPM-PV 3651
Glossotherium sp.	MLP-3-143
Lestodon sp.	MLP-3-767
Megatherium sp.	MLP-229
Prepotherium sp.	MLP-4-152
Scelidodon sp.	MLP-89-XII-6-5
Scelidotherium sp.	MLP-41-V-16-3

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