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Proportions and function of the limbs of glyptodonts

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This study examines the limb bone proportions and strength of glyptodonts (Xenarthra, Cingulata). Two methods are used to estimate the body mass and location of the centre of gravity of the articulated specimens. These estimates, together with measurements of the femur and humerus, are used to calculate strength indicators (SI). The other long bones of the limbs are used to calculate limb proportion indices that give an indication of digging ability, speed, and limb dominance in armadillos, the glyptodonts' living closest relatives. The results show that regardless of how the body mass and centre of gravity are calculated, the majority of the glyptodont's weight is borne by the hindlimbs. The SI calculations show that femora are sturdy enough to bear these loads. The fact that the femora have higher SI than the humerii indicates that sometimes the hindlimbs are required to bear an even greater proportion of the body weight, possibly when rising to a bipedal posture or pivoting on their hindlimbs to deliver a blow with their armoured tail. The analysis of limb proportions indicates that both the hindlimb and the forelimb have proportions that correlate strongly with body mass. This outcome supports the other results, but also shows that forelimbs must be also involved in manoeuvring the glyptodont body. ☐ *Glyptodonts, Mammalia, Xenarthra, limbs, strength indicators.*

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Glyptodonts (Glyptodontidae) constitute one of the most characteristic groups of fossil mammals in South America, although they are also found in Central and North America. They are classified together with living and extinct armadillos (Dasypodidae and Pampatheriidae) as Cingulata, a suborder of Xenarthra, the South American major clade of placental mammals (see Delsuc *et al.* 2004; Prasad *et al.* 2008). The oldest glyptodont remains include only isolated scutes from the middle Eocene of Patagonia, Argentina (*Glyptatelus*; McKenna & Bell 1997). The first complete specimens come from the Early Miocene of Patagonia (see Scott 1903–05; for complete descriptions and wonderful reconstructions) (Fig. 1A). These herbivorous animals reached gigantic sizes during the terminal Pleistocene, with forms that varied between 1 and 2 tonnes of body mass (Fig. 1B–F). With their essentially immobile dorsal carapace, different numbers of trilobate teeth, elephantine hindlimbs, and a masticatory apparatus telescoped well below the cranium (Hoffstetter 1958; Fariña & Vizcaíno 2001), the glyptodonts represent one of the most bizarre groups of mammals ever to have evolved. Although more or less refined hypotheses on the habits of many fossil mammals can be generally proposed by comparisons with appropriate extant relatives or analogues, this is clearly not the case of fossil xenarthrans like glyptodonts and the ground sloths (Tardigrada – related to the living tree sloths but many of them with body masses of several thousand kilograms). The uniqueness of these creatures forces researchers on the palaeobiology of these animals to apply different and innovative approaches (see Vizcaíno *et al.* 2008). In the case of glyptodonts, the palaeobiology has attracted some attention in the last 15 years, promoting sometimes peculiar proposals on their locomotion and intraspecific fighting behaviour (Fariña 1995; Alexander *et al.* 1999; Blanco *et al.* 2009).

In a study that examined humeral shape to identify aspects related to digging ability in armadillos and glyptodonts, Milne *et al.* (2009) found that many of the humeral features of glyptodonts appear to be related to their large body size and clear distinctions between the Pleistocene *Glyptodon* on the one hand, and the Pleistocene *Neosclerocalyptus* and the Early Miocene *Propalaehoplophorus* on the other (but see the

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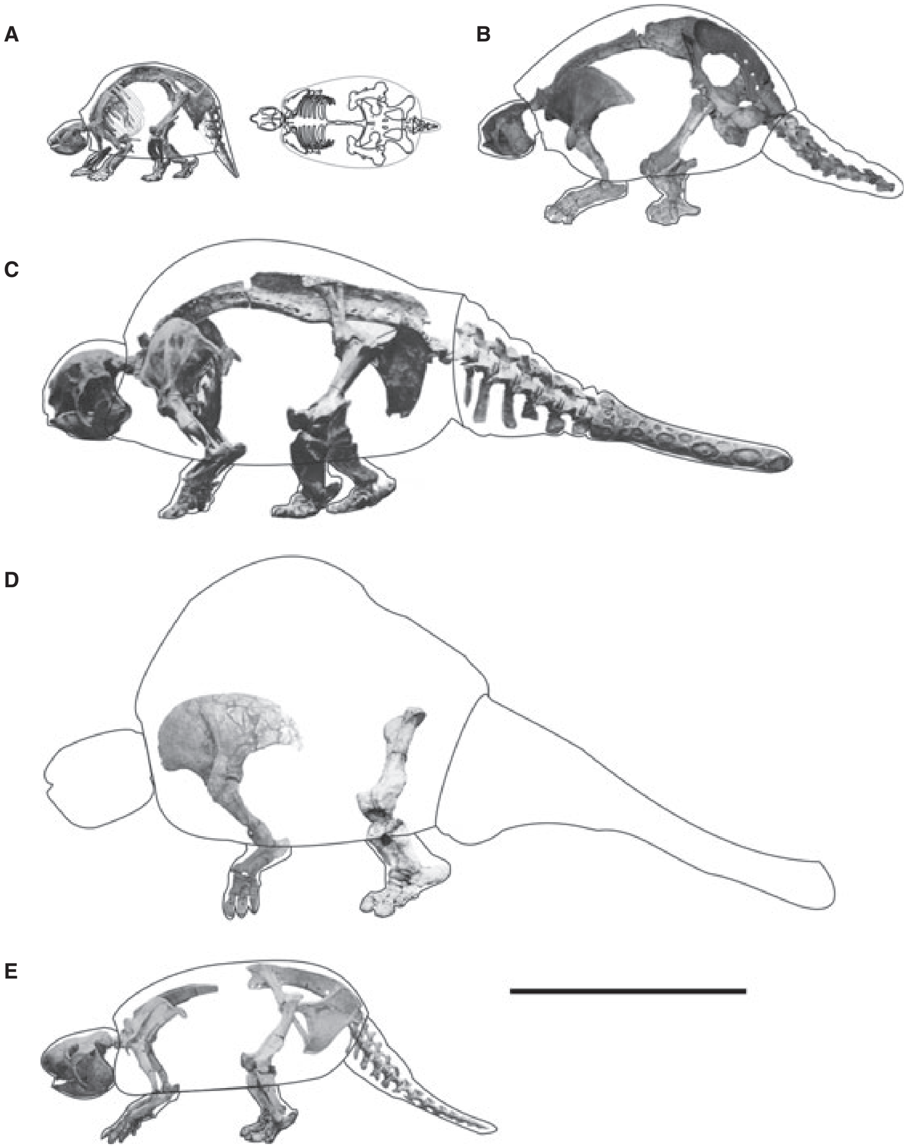

Fig. 1. Reconstruction of glyptodont specimens. A, *Propalaehoplophorus australis*, the first complete specimens come from the Early Miocene of Patagonia (Scott 1903–05). B–E, Pleistocene glyptodonts. B, *Glyptodon reticulatus*. C, *Panochthus tuberculatus*. D, *Doedicurus clavicaudatus*. E, *Neosclerocalyptus ornatus*. Scale bar 1 m.

discussion section). For instance, the ulnar proportions and humeral features of *Glyptodon* accord with digging ability in armadillos, while *Neosclerocalyptus* and *Propalaehoplophorus* do not fit this pattern. Milne *et al.* (2009) proposed that the fossorial features of *Glyptodon*'s forelimb may be directed towards tearing at the surface of the substrate in search of food, although another study has noted that the hands are not as specialized for that purpose as those of armadillos (Gillette & Ray 1981). An alternative explanation considered by Milne *et al.* (2009) is that glyptodonts may have developed an extremely long olecranon process for other reasons, such as supporting and manoeuvring their huge body mass on flexed elbows, rising to a bipedal position and returning to a quadrupedal stance. Adopting a bipedal stance is not uncommon among living armadillos, including *Priodontes* (Frechkop 1949) and it has been suggested that this may be necessary if it is to use its armoured tail in defence (Fariña 1995; Alexander *et al.* 1999).

The aim of this contribution is to analyse in more detail the function of the limbs of glyptodonts, particularly regarding their locomotory abilities and use of substrate. In doing so, we mimic part of the procedure applied to the study of the same functions in ground sloths by Bargo *et al.* (2000) who analysed limb proportions and resistance to bending forces.

Materials and methods

Materials

Six specimens consisting of complete mounted skeletons, all housed at the Museo de La Plata (MLP), Argentina, were selected for this study:

1. *Propalaehoplophorus australis* (Moreno), MLP 16-15. Locality: Santa Cruz Province, Argentina. Stratigraphy: Santa Cruz Formation (Santacrucian), Early Miocene.
2. *Neosclerocalyptus ornatus* (Owen), MLP 16-28. Locality: Mar del Plata, Buenos Aires Province, Argentina. Stratigraphy: Miramar Formation (Ensenadan), Early Pleistocene.
3. *Glyptodon* cf. *reticulatus* Owen, MLP 16-41. Locality: unknown, Argentina. Stratigraphy: Pampean Formation, Pleistocene.
4. *Glyptodon clavipes* Owen, MLP 16-40. Locality: unknown, Argentina. Stratigraphy: Pampean Formation, Pleistocene. Carapace.
5. *Panochthus tuberculatus* Owen, MLP 16-29. Locality: Tapalqué, Buenos Aires province, Argentina. Stratigraphy: Pampean Formation, Pleistocene.
6. *Doedicurus clavicaudatus* (Owen), MLP 16-24. Locality: Salto, Buenos Aires province, Argentina. Stratigraphy: Pampean Formation, Pleistocene.

Methods

Estimation of body mass. – Body masses were estimated using scale and computer-generated geometric models and compared with the results obtained from scale models by Fariña (1995) and from allometric equations by Fariña *et al.* (1998).

Scale plastic models were made by one of us (JBB). Reconstruction of the general shape of the animal is relatively simpler than for other mammals due to the existence of the bony carapace and caudal sheet covering most of the body, which impose precise limits to the contours of the body. Volumes for the scale models were obtained from water displacement (Archimedes' Principle) and then scaled up to obtain the volumes for fossil taxa.

Body masses were also calculated using computer-generated geometric models as was used by Bargo *et al.* (2000) for ground sloths. The transverse and dorsoventral diameters of the body were estimated at regular intervals (10–20 cm) along the endoskeleton or the carapace, from the snout to the tip of the tail. Each pair of measurements was assumed to represent the major and minor axis of an ellipse, and successive margins of the ellipses were joined and smoothed to yield a continuous body contour. The limbs were measured and treated as cylinders, and an overall density of 1000 kg/m^3 was used for the calculations.

In both cases, plastic and geometric models, masses were calculated on the assumption that the overall density of glyptodonts was the same as water (1000 kg/m^3) as is the case for most living tetrapods (Alexander 1983). It was also assumed that the bony armour does not affect body mass distribution because it is more or less equally dispersed all over the body of the animal. This last concept will be further discussed below.

Limb bone strengths. – It is accepted that limb bones are particularly vulnerable to forces that impose bending moments (Rubin & Lanyon 1982). When a bone has to withstand a force exerted at its distal end perpendicular to its long axis, its strength is directly related to its section modulus for bending in a parasagittal plane (Z). This value is obtained from second moment of area of the cross-section of the bone (Alexander 1983) and is inversely related to the bone's length and to the force exerted. This force is proportional to the fraction (a) of the weight (mg) of the animal that is supported by the corresponding pair of limbs. Thus, a strength indicator (SI) was formulated by Alexander (1983, 1985) that gives an indication of the strength of a bone in relation to its expected loading. This is calculated as $Z/amgx$ where x is the distance from the distal end to where the section is taken (at midshaft or near it when a large process for muscle attachment lies at this position), and the fraction (a) is inversely proportional to the distance of the respective pair of limbs to the projection of the centre of mass on the ground. To determine the centre of mass, we used two procedures. The plastic models were suspended, first from one, and then from another point in the sagittal plane, and the lines of the thread were extrapolated until they crossed each other (Alexander 1983, 1985). For the computer-generated models, the position of the centre of mass was estimated from the calculated mass of each slice (m_i) and its distance (x_i) from the snout (see for example Alexander 1983). The distance from the snout to the centre of mass is given by the equation $x_{cm} = (\Sigma m_i x_i)/\Sigma m_i$.

Cross-sections of femora and humeri were measured directly with the aid of a profile gauge at as close midshaft as practicable. Bones were assumed to have an internal structure typical of tetrapods, so that comparisons with available data on living species could be made directly (Alexander 1985; Alexander & Pond 1992; Fariña 1995; Casinos 1996; Fariña *et al.* 2005).

Limb indices. – The following indices (Fig. 2) were calculated from measurements of the long bones as in

Vizcaíno & Milne (2002). These authors evaluated the correlation of some limb proportions, locomotion and use of the substrate in living armadillos. All indices were multiplied by 100.

Index of fossorial ability (IFA): the length of the olecranon process divided by the functional forearm length (difference between ulnar length and the olecranon length) (OL/(UL-OL)). This index, originally defined by Vizcaíno *et al.* (1999), gives a measurement of the mechanical advantage of the triceps muscle in elbow extension.

Shoulder moment index (SMI): the proximal humeral length (humeral head to deltoid tuberosity) divided by the humeral length (PH/HL). This index provides an indication of the mechanical advantage of the deltoid muscle acting across the shoulder joint.

Brachial index (BI): the functional forearm length divided by the humerus length ((UL-OL)/HL), and provides an indication of the extent to which the forelimb is adapted for fast movement.

Leg robusticity index (LRI): the mid-leg width divided by the leg length (LW/LL), gives a rough indication of the strength of the fused tibia and fibula, as well as the relative width available for the origin of the muscles acting across the ankle.

Hip moment index (HMI): the proximal femoral length (from the head to the lower point on the third trochanter) divided by the functional femur length (PF/FL). This index is thought to give a measure of the mechanical advantage of the gluteus maximus muscle in hip extension.

Crural index (CI): the leg length divided by the functional femur length (LL/FL), and indicates the extent to which the hindlimb is built for speed.

Intermembral index (IMI): the forelimb length divided by the hindlimb length (HL+UL-OL)/(FL+LL), and gives an indication of forelimb or hindlimb dominance in locomotion.

Results

Measurements of the humerus, ulna, femur and tibia-fibula of the different specimens are provided in Table 1. The body mass estimates are shown in Table 2, together with comparative values obtained by other authors. The results are spread across three orders of magnitude, ranging from 67 kg for the Early Miocene *P. australis* to the 2 tonne Late Pleistocene *G. clavipes*. Although the estimations obtained with both scale and computer-generated models are rather consistent, there are some differences. The most conspicuous are the estimates for *D. clavicaudatus*: 1760 kg from scale model, and 1060 from computer-generated model. For this taxon, intermediate estimates were obtained previously by Fariña (1995) and Fariña *et al.* (1998): 1400 kg and 1468 kg respectively.

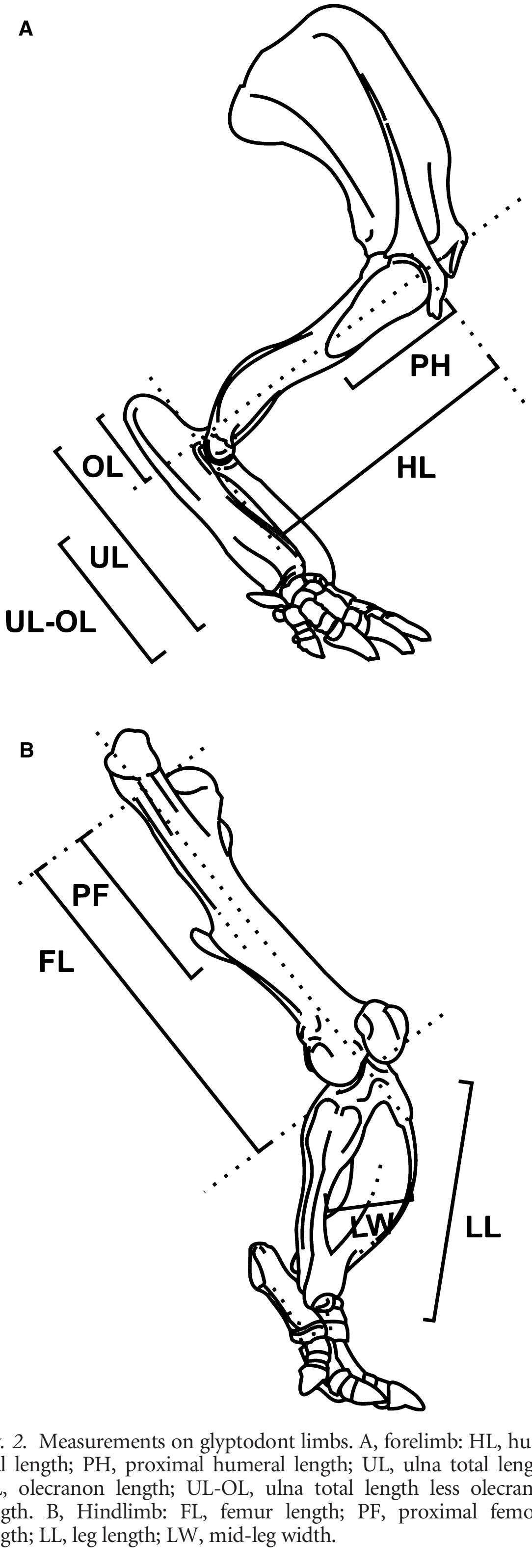

Fig. 2. Measurements on glyptodont limbs. A, forelimb: HL, humeral length; PH, proximal humeral length; UL, ulna total length; OL, olecranon length; UL-OL, ulna total length less olecranon length. B, Hindlimb: FL, femur length; PF, proximal femoral length; LL, leg length; LW, mid-leg width.

Table 1. Limb bone measurements for the five glyptodonts. (taken as in Vizcaíno & Milne 2002).

Specimens	HL	PH	UL	OL	FL	PF	LL	LW
Propalaehoplophorus australis	165	80	135	55	215	110	115	50
Neosclerocalyptus ornatus	250	125	205	85	300	240	190	85
Panochthus tuberculatus	375	190	275	115	475	455	245	130
Doedicurus clavicaudatus	340	200	250	105	530	490	230	155
Glyptodon reticulatus	305	140	250	105	425	365	195	125

HL, humeral length; PH, proximal humeral length; UL, ulna length; OL, olecranon length; FL, femur length; PF, proximal femoral length; LL, leg length; LW, mid-leg width.

Table 2. Body masses (M) in kilograms, and the percentage (a) of body weight supported by hindlimbs, as calculated by the two methods used in this study. Fariña's (1995) and Fariña's *et al.* (1998) estimates are provided for comparison. In the case of Fariña *et al.* (1998) we provide the arithmetic means.

Specimens	Scale Model M (a)	Computer-generated model M (a)	Fariña 1995	Fariña *et al.* 1998
Propalaehoplophorus australis	85 (56%)	67 (74%)	50	–
Neosclerocalyptus ornatus	320 (60%)	260 (100%)	280 (56%)	–
Panochthus tuberculatus	1330 (77%)	1040 (94%)	1100 (56%)	1061
Doedicurus clavicaudatus	1760 (71%)	1060 (70%)	1400 (57%)	1468
Glyptodon clavipes	2000 (66%)	1460 (77%)	2000 (60%)	–
Glyptodon reticulatus	411 (85%)	350 (100%)	–	862

Our body mass estimation for *Glyptodon reticulatus* is more similar to the geometric (403 kg) than the arithmetic mean (862 kg) provided by Fariña *et al.* (1998) for a different specimen.

The percentages of body mass supported by hindlimbs obtained with computer-generated models are, in general, higher than those obtained by scale models. Despite the fact that these calculations are sensitive to slight changes in limb position, it is clear that in all cases the percentage of body mass supported by the hindlimbs is much higher than that of the forelimbs.

The SI (Table 3) are higher for the femur than for the humerus in all genera except *Glyptodon.* Regardless of whether scale or computer models are used, the femur has an SI nearly two times that of the humerus. For *G. reticulatus*, the scale model shows SI values of 49 GPa^{-1} and 75 GPa^{-1} for femur and humerus respectively. We don't have skeleton of *G. clavipes* to calculate SI. The limb bones SI shown in Table 3 were calculated using the percentage of body weight supported by hindlimbs obtained from the scale models. These values are closer to those previously obtained by Fariña (1995), so were selected as a conservative estimate.

In the computer-generated models almost 100% of the body mass is calculated to be supported by the hindlimbs (Table 3). Consequently the femur SI is 42 GPa^{-1}, but the humerus indicator is virtually infinite. The values obtained for *Panochthus* and *Neosclerocalyptus* from the scale models also indicate femoral SI greater than those of the humerus, but the computer-generated model provided different results. In *Panochthus*, the percentage of body mass supported by the hindlimbs is calculated as 94% and the femur

Table 3. The strength indicators (SI) of the femur and humerus, and the ratio comparing the limbs. The estimates of body mass, and percentage of body mass supported by the hindlimbs (a) used in the calculations are also provided.

Specimens	Body mass (kg)	(a)	SI Femur Gpa^{-1}	SI Humerus Gpa^{-1}	SI ratio Femur/Humerus
Propalaehoplophorus australis (quadrupedal)	85	56%	50.00	31.12	1.60
Propalaehoplophorus australis (bipedal)	85	100%	28.00	–	–
Neosclerocalyptus ornatus (quadrupedal)	320	60%	42.68	21.38	1.99
Neosclerocalyptus ornatus (bipedal)	320	100%	25.60	–	–
Panochthus tuberculatus (quadrupedal)	1330	77%	25.57	16.61	1.54
Panochthus tuberculatus (bipedal)	1330	100%	19.68	–	–
Doedicurus clavicaudatus (quadrupedal)	1760	71%	26.11	13.96	1.87
Doedicurus clavicaudatus (bipedal)	1760	100%	18.54	–	–
Glyptodon reticulatus (quadrupedal)	411	85%	48.92	74.63	0.65
Glyptodon reticulatus (bipedal)	411	100%	41.58	–	–

Table 4. The limb proportion indices for the glyptodonts studied.

Specimens	IFA	SMI	BI	LRI	HMI	CI	IMI
Propalaehoplophorus australis	68.75	48.48	48.48	43.47	51.16	53.48	74.24
Neosclerocalyptus ornatus	70.83	50.00	48.00	44.73	80.00	63.33	75.51
Panochthus tuberculatus	71.87	54.16	44.44	53.06	95.78	51.57	74.3
Doedicurus clavicaudatus	72.41	58.82	42.64	67.39	92.45	43.39	72.22
Glyptodon reticulatus	72.41	45.9	47.54	64.10	85.88	45.88	72.58

IFA, index of fossorial ability; SMI, shoulder moment index; BI, brachial index; LRI, leg robusticity index; HMI, hip moment index; CI, crural index; IMI, intermembral index.

has an SI that is half those of the humerus. In *Neosclerocalyptus* the percentage of body mass supported by hindlimbs is almost 100% and so the femur appears to be very much weaker than the humerus.

The limb indices given in Table 4 show that for the forelimb there are strong relationships with body mass. The largest specimen has the largest IFA and SMI and the smallest BI. The correlation between log body mass and SMI ($r = 0.766$), BI ($r = -0.912$) and IFA ($r = 0.862$) are all significant, even with a sample size of five. For the hindlimb, the HMI and LRI both have positive correlations ($r = 0.939$ and $r = 0.694$ respectively) and CI ($r = -0.472$) has a negative correlation with body mass. However, only the correlation of HMI reaches significance ($P < 0.005$). The correlation of IMI with log body size (−0.708, ns) shows that larger specimens tend to have relatively smaller forelimbs compared to the hindlimbs.

Discussion

As mentioned above, the body mass estimations for glyptodonts are spread across three orders of magnitude, ranging from 67 kg for the *Propalaehoplophorus* to the 2 tonne *Glyptodon*. This values are fairly congruent with estimates obtained by other authors, and confirm the tendency for an increase in body size of the clade since the Early Miocene until its extinction by the Late Pleistocene–Early Holocene (Vizcaíno *et al.* in press).

Our results regarding the percentage of body mass supported by the hindlimbs show certain discrepancies between the values obtained from the two models, the computer-generated being generally higher than those from the scale model. Also, our values are higher than those obtained by Fariña (1995), except for *Propalaehoplophorus*. As mentioned above, SI calculations are sensitive to slight changes in limb position and this could explain the uncertainties associated with these values. Furthermore, although virtually all of the body is covered by bony armour, different parts may be comprised of denser tissues and this may affect the calculation of the proportion of the body mass supported by the hindlimbs. Certainly, the tail does not contain large body cavities, and is completely surrounded by a bony sheet constituted by scutes, often thicker than the average of those of the dorsal carapace. If we consider the caudal density greater than 1000 kg/m^3 due to its very important contribution of bone with a density close to 2000 kg/m^3 (Currey 1984), the proportion of body mass on the hindlimbs would deviate even more from that given in Fariña (1995). This consideration would be more important for *Doedicurus* and *Panochthus* than for *Glyptodon* or *Propalaehoplophorus* because, in the former two the tail has a great proportion of compact bone. In all cases, taking account of this effect (which only can be done easily in the computer-generated model), the percentage of body mass supported by the hindlimbs would be above 80% and, in some cases, close to 100%. Thus, it is clear that in all cases the proportion of body mass supported by the hindlimbs is much larger than the forelimbs. This is not the usual pattern for extant large mammals which show the opposite condition (Fariña *et al.* 2005 and references therein), but is similar to the situation in other extinct xenarthrans such as the ground sloths (Bargo *et al.* 2000; Vizcaíno *et al.* 2001). From a functional point of view, this means that a slight caudal displacement of the centre of mass would result in the animal being virtually bipedal, although not necessarily in an erect posture (Elissamburu & Vizcaíno 2003), liberating the forelimbs from the function of supporting body weight. This condition has been related to the ability to adopt complete bipedal postures as proposed for ground sloths (Bargo *et al.* 2000; and references therein) or a not fully erect bipedal posture as seen in modern armadillos and manids during digging (Heath 1992; Biknevicius 1999; Bargo *et al.* 2000; Vizcaíno *et al.* 2001). A good analogue may be the highly specialized armadillo *Priodontes maximus,* which essentially walks on its hindlimbs while maintaining its backbone roughly parallel to the ground (Frechkop 1949). A bipedal posture is commonly adopted for defence, observation and (often for) feeding in living representatives of the three main lineages of xenarthrans (anteaters, sloths, and armadillos; Wetzel 1982).

The fact that the SI using scale models are larger for the femora than the humeri is consistent with the results of Fariña (1995), and also indicates that the estimations of the location of the centre of gravity are reasonable. Indeed it supports the suggestion that glyptodonts could adopt bipedal postures during intraspecific fighting, defence, feeding or observation. An alternative, although not exclusive, interpretation is that as a consequence of bipedalism, forelimbs are liberated from their function of supporting body weight and are able to act on the substrate for digging. Digging is a common behaviour in living armadillos that correlates with morphological features of the limb bones (Vizcaíno *et al.* 1999; Vizcaíno & Milne 2002; and references therein), and these features have been used to infer the digging behaviour in fossil xenarthrans (Vizcaíno & Fariña 1997; Vizcaíno *et al.* 2006; Vizcaíno 2009). Vizcaíno *et al.* (1999) divided the fossorial habits of living armadillos into three categories that were subsequently modified by Milne *et al.* (2009) who took into consideration some recent behavioural information (Abba *et al.* 2005).

1. Non-diggers, species that are mainly cursorial (Jenkins 1971; Stein & Casinos 1997);
2. Generalized diggers, species that dig short burrows for protection or in search of food and that feed on the surface or just below it by making ‘food probes’ (Abba *et al.* 2005); and
3. Specialized diggers, species that are either burrowers or those that feed on termites or ants.

Non-diggers are represented by the three-banded armadillo *Tolypeutes matacus*, which is the most cursorial within the family, and according to Nowak (1991) this species does not seem to dig burrows. Generalized diggers belong to the Dasypodini and Euphractini (considered as monophyletic group by Möller-Krull *et al.* 2007 but paraphyletic by Gaudin & Wible 2006), and all these species, for which habits are known, have the typical fossorial behaviours associated with this group. Specialized diggers include the naked tailed armadillo *Cabassous* spp. and the pygmy armadillo *Chlamyphorus truncatus*, both of which demonstrate extreme fossorial habits (Nowak 1991). Specialized diggers also includes the giant armadillo *P. maximus* which is considered to be a powerful and rapid digger, that shelters in burrows of its own construction (Nowak 1991) and is capable of destroying large termitaria (Redford 1985). Both the morphological and molecular phylogenies support the interpretation that generalized digging habits (Type 2) are ancestral for all cingulates, and that the cursorial habits of *Tolypeutes* derive from digging ancestors.

Digging ability in armadillos has previously been shown to be well characterized by the relative length of the olecranon of the ulna (IFA, Vizcaíno *et al.* 1999). IFA served to separate out the five tribes of armadillos and reflected their fossorial ability, with the Chlamyphorini having the greatest values followed by, in decreasing order of fossorial ability, *Priodontes* and *Cabbassous* (formerly joined in a tribe Priodontini now considered paraphyletic; Gaudin & Wible 2006; Möller-Krull *et al.* 2007), the Euphractini, the Dasypodini and the Tolypeutini. Later, Vizcaíno & Milne (2002) demonstrated that other proportions of the forelimb represented by indices (BI and SMI) correlate well with digging habits, but also revealed some interesting exceptions, particularly in the most fossorial (*Chlamyphorus*) and most cursorial (*Tolypeutes*) forms. On the other hand, hindlimb proportions apparently do not correlate with digging habits, but instead appear to be more influenced by body size. The authors also found that while the correlations among the forelimb indices are quite strong and positive, the correlations between the forelimb and hindlimb indices are either very low or negative.

Kraglievich (1934) pointed that glyptodonts were not functionally suited for digging. Although there is no specific study on the matter, Quintana (1992) concurs with Kraglievich, on the basis that the carapace is relatively rigid (compared to armadillos) and fused to the pelvic girdle, the dorsal and lumbar vertebrae are fused forming a tube, and that glyptodonts lack other structures in the skull and limbs typical of burrowing mammals. Analysing the limb bone strength and locomotor habits in some glyptodonts, Fariña (1995) proposed that they were able to adopt bipedal postures to perform strenuous activities, such as intraspecific fighting (see also Alexander *et al.* 1999).

Comparing the limb proportion indices of the glyptodonts in the present study, with those of the living armadillos studied by Vizcaíno & Milne (2002), it appears that the glyptodonts have IFA and SMI values similar to the living Dasypodini and Euphractini (generalized diggers). The value that placed *Glyptodon* among the specialized diggers (Milne *et al.* 2009) should be considered with caution. The specimen, which was misidentified (MLP 16-41 instead of the actual MLP 16-114), seems to be an unusually mature individual, consisting only of the right forelimb and not associated with carapace remains that would allow an accurate specific identification.

Regarding other proportions glyptodonts have brachial and crural indices that are much lower than living armadillos, and seem to be more related to their larger body masses. Similarly, the hindlimb indices HMI and LRI of the glyptodonts are much higher than living armadillos, and this also seems to be related to their larger body masses and the fact that glyptodonts carry most of their body weight on their hindlimbs.

It is noteworthy that the forelimb indices correlate strongly with log body mass among glyptodonts, but not for living armadillos (Vizcaíno & Milne 2002), where IFA is strongly related to digging behaviour. This finding raises the possibility that the structure of the forelimb in glyptodonts is directly related to body support and movement, and not to digging behaviour. It also supports the proposal of Milne *et al.* (2009) that large glyptodonts may have an extremely long olecranon process (IFA) for reasons other than digging, such as supporting and manoeuvring its huge body mass on flexed elbows, rising to a bipedal position and returning to a quadruped stance. It may also be that powerful forelimbs are needed to initiate body rotation in order to accelerate the tail club. Whether this is related to the use of the armoured tail for defensive purposes or for intraspecific competition, is not able to be confirmed at this stage.

The hypothesis that hind limb bone strength values can be related to fighting behaviour, and the necessity of maintaining body posture against huge external loads imposed by tail blows, was explored in Alexander *et al.* (1999). While the energy of the blow is too small to explain strong leg bones in the victim, the aggressor's hindlimb bones would require great strength: not only would they need to provide attachments for powerful muscles required to accelerate the tail-club, they would also have to withstand large torsional loading to maintain posture, and control whole-body rotation, during the action of the tail blow.

In summary, regardless of the method of estimation, the centre of gravity of glyptodonts is displaced posteriorly compared with living large mammals; that is, located much closer to the hindlimbs than the forelimbs. Glyptodont femora generally have much greater SI than the humerii, and this supports the centre of gravity estimates, and suggests that glyptodonts were capable of adopting bipedal stances. Many of the limb proportion indices for both fore and hindlimbs correlate with body mass, and this indicates that although glyptodonts could adopt bipedal stances, they also relied on their forelimbs for locomotion and for manoeuvring their large body masses.

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