A 3D geometric morphometric analysis of digging ability in the extant and fossil cingulate humerus

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Abstract

Digging ability in armadillos has been shown to be closely related to the relative length of the olecranon process of the ulna. This study uses geometric morphometrics to examine the relationship between humeral shape, digging ability and size in a range of living and fossil cingulates. The extant species in the sample include representatives of 11 species of armadillo, while the fossil specimens include three species of fossil armadillos (*Peltephilus*, *Proeutatus* and *Eutatus*) and three Glyptodonts (*Propalaeohoplophorus*, *Glyptodon* and *Neosclerocalyptus*). The results show that in general, living species with good digging ability have larger sites for muscle attachment, particularly the proximal tubercles and the crests descending therefrom, and the epicondylar region at the distal end of the humerus. Some differences were found in the smallest armadillo (*Chlamyphorus truncatus*), which seems to have a different method of digging. The proportions of the olecranon process would indicate good digging ability in some glyptodonts, but humeral features do not fit with this interpretation and the differences may be related to large size. The relationship between cingulate phylogeny and humeral morphology is also examined, and it seems that while cingulates are to some extent constrained by their phylogeny, many of the humeral features are directly related to digging.

Introduction

Cingulates (armadillos, pampatheres and glyptodonts) are grouped together with anteaters, ground and tree sloths as Xenarthra, one of the four major clades of placental mammals that evolved in South America (see Delsuc & Douzery, 2008; Gaudin & McDonald, 2008 and references therein). The most conspicuous feature of cingulates is armour, constituted by dermal scutes covered with epidermal scales and divided in shields that protect the head and body, with a sheath for the tail. Cingulate diversity shows variation in the development and mobility between scutes, ranging from thin and relatively loose articulation in the pygmy armadillo (*Chlamyphorus truncatus* Harlan), to thick and more rigid articulation in armadillos and glyptodonts.

Living cingulates are represented only by armadillos, which constitute two-thirds of the diversity of living xenarthrans (Wetzel, 1985; Aguiar & Fonseca, 2008). Wetzel (1985) subdivided them into five tribes: Dasypodini, which includes seven species in the genus *Dasypus* (Vizcaíno, 1995); Tolypeutini, with two species in the genus *Tolypeutes* Illiger; Chlamyphorini, with one species each in the genera *Chlamyphorus* Harlan and *Burmeisteria* Gray; Priodontini,

with five species in the genera *Priodontes* F. Cuvier and *Cabassous* McMurtrie; and Euphractini, with five species distributed among the genera *Euphractus* Wagler, *Chaetophractus* Fitzinger and *Zaedyus* Ameghino. A phylogenetic analysis by Gaudin & Wible (2006) based on craniodental morphology including living and fossil cingulates suggest that the last two tribes are paraphyletic. From their cladogram *Chlamyphorus* groups among living euphractines (Fig. 1a). The most recent molecular phylogeny (Möller-Krull *et al.*, 2007) supports the paraphyly of priodontines, grouping them with *Tolypeutes* in a clade called Tolypeutinae, *Tolypeutes* being the sister taxon to *Cabassous*, and *Chlamyphorus* the sister taxon to Tolypeutinae. The work by Möller-Krull *et al.* (2007) supports the monophyly of living euphractines, and places them as a sister group of Tolypeutinae and *Chlamyphorus* (Fig. 1b).

Armadillos usually have flexible armour, and are mostly specialized digging animals. Their limbs are well designed for that activity, with big claws, tibia and fibula fused proximally and distally, large tuberosities for strong muscular insertions (e.g. the deltoid tuberosity of the humerus and the third trochanter of the femur), and long lever arms for the line of action of the principal muscles (e.g. the long
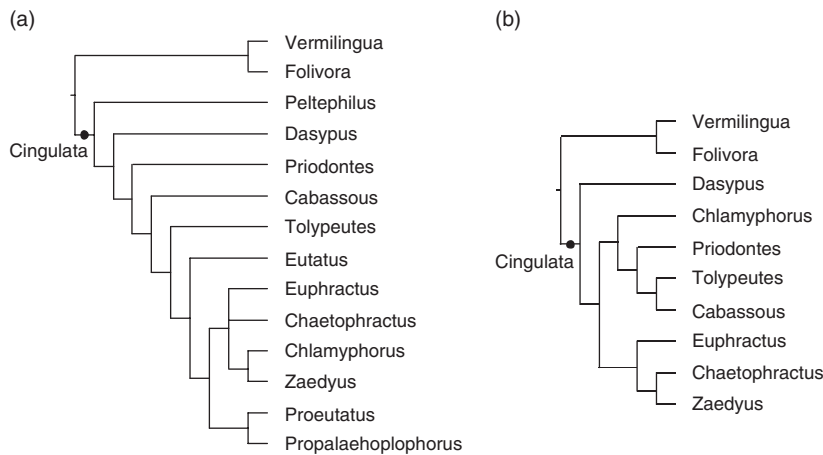
Figure 1 Cladograms based on morphological (a) and molecular data (b), taken from Gaudin & Wible (2006) and Möller-Krull *et al.* (2007), respectively.

olecranon process for the triceps – see Vizcaíno, Fariña & Mazzetta, 1999).

Vizcaíno *et al.* (1999) divided the fossorial habits of living armadillos into three categories that we have now modified in the following manner, after taking into consideration some recent behavioural information: (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, Udrizar Sauthier & Vizcaíno, 2005); (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* (Desmarest), which is the most cursorial within the family; Nowak (1991) observes that this species does not seem to dig burrows. Generalized diggers belong to the Dasypodini and Euphractini. All these species for which habits are known have the typical fossorial habits expected for the members of the group. Specialized diggers include the naked-tailed armadillo *Cabassous* spp. and the pygmy armadillo *C. truncatus*, both of which have extreme fossorial habits (Nowak, 1991), and the giant armadillo *Priodontes maximus* (Kerr), which is considered a powerful and rapid digger, that shelters in burrows of its own construction (Nowak, 1991) and is capable of destroying large termitaria (Redford, 1985).

Digging ability in armadillos has been previously shown to be well characterized by the relative length of the olecranon of the ulna [index of fossorial ability (IFA), Vizcaíno *et al.*, 1999]. IFA separated the five tribes and reflected their fossorial ability, with the Chlamyphorini having the greatest values followed, in decreasing order of fossorial ability, by the Priodontini, Euphractini, Dasypodini and the Tolypeutini. A study by Vizcaíno & Milne (2002) demonstrated that other proportions of the forelimb represented by indices [brachial index (BI) and shoulder moment index] 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 seem to be influenced more by body size. They also found that the correlations among the forelimb indices are quite strong and positive, while correlations between forelimb and hindlimb indices are very low or negative.

With over 100 genera named (McKenna & Bell, 1997), fossil cingulates attained a much greater diversity than their living representatives and were common elements of South American Cenozoic. Following McKenna & Bell (1997), they comprise typical armadillos (Dasypodidae), including fossil and living forms, some of which reached sizes of about 50 kg; the peltephilines (Peltephilidae), horned armadillos that ranged from about 2 kg to more than 100 kg; the pampatheres (Pampatheriidae), giant armadillos that may have reached 200 kg; and the glyptodonts (Glyptodontidae), whose terminal Pleistocene forms reached body masses varying between 1 and 2 tonnes (Fariña, 1995; Fariña, Vizcaíno & Bargo, 1998). According to Gaudin & Wible (2006), peltephilids are the sister group of the remaining cingulates, dasypodids are paraphyletic, and within them the Eutatini tribe of McKenna & Bell (1997) (represented in this work by *Eutatus* and *Proeutatus*; see below) is not monophyletic. Pampatheres and glyptodonts constitute a monophyletic group. The monophyly and internal relationships of glyptodonts were recently tested by Fernicola (2008), who supports a basal dichotomy between the propalaeohoplophorines and the remaining glyptodonts (see below and Fig. 1a).

Pampatheres are much larger than dasypodid armadillos and probably less fossorial than the dasypodids. Edmund (1985) described limbs of pampatheres as being intermediate in proportions and specialization between those of glyptodonts and the living armadillos, including graviportal adaptations for the hind limb. The three central fingers of the manus are equally developed, and no especially developed claws are present. The relative length of the olecranon process is considerably less than in the fossorial armadillos. Kraglievich (1934) considered that glyptodonts were not functionally suited to dig. Although there is no specific study on the matter, Quintana (1992) concurs with Kraglievich,

arguing that the carapace is relatively rigid (in comparison with armadillos) and fused to the pelvic girdle, the dorsal and lumbar vertebrae are fused forming a tube, and other structures in the skull and limbs typical of burrowing mammals are not present. Analysing 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 fights (see also Alexander, Fariña & Vizcaíno, 1999).

While the characteristics of the ulna indicative of digging ability seem to be fairly simple and well understood (Vizcaíno et al., 1999), little work has been done to analyse the humerus for features relating to digging. In a previous study (Vizcaíno & Milne, 2002), the relative length of the delto-pectoral crest of the humerus (SMI) was shown to correlate well with digging ability for all living armadillos except the most cursorial (Tolypeutes). However, there are other features of the humerus that may also be related to digging ability, including the proximal tubercles and the epicondyles at the elbow. This study aims to fully examine humeral shape to further identify aspects related to digging ability. Further, today the cingulates are only represented by small-to medium-sized species, the largest being P. maximus (30 kg in Wetzel, 1985; up to 60 kg in Nowak, 1991). Many of the fossil cingulates were very much larger, and the effect of these large body sizes on humeral morphology is poorly understood. To this end, geometric morphometrics is used to analyse shape variation in the humerus of living and fossil cingulates with respect to IFA and humeral size. The diversity of living and fossil cingulates provides the opportunity to examine the variation in humeral shape in a much wider context and, perhaps, to provide insights into the behaviour of fossil forms.

Materials and methods

The material for this study includes humeri and ulnae from 30 extant armadillos (Table 1). These comprise: 11 dasypodines including three species (*Dasypus novemcinctus*, *Dasypus hybridus* and *Dasypus septemcinctus*), 11 euphractines including four species (*Euphractus sexcintus*, *Chaetophractus villosus*, *Chaetophractus vellerosus* and *Zaedyus pichiy*), four *T. matacus*, two *P. maximus*, a *Cabassous chacoensis* and one specimen from *C. truncatus*. In addition, there are six fossil specimens: three armadillos (*Proeutatus* sp., *Eutatus seguini* and *Peltephilus nanus*), and three glyptodonts (*Propalaeohoplophorus australis*, *Neosclerocalyptus* sp. and *Glyptodon* sp.). These specimens are all housed in the Museo de La Plata and the Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia'.

The length of the olecranon and the functional length of the ulna (from the middle of the trochlea to the distal end) were measured and used to calculate the IFA (being the olecranon length divided by the functional length of the ulna – see Vizcaíno, Farina & Mazzetta, 1999). Further, the humeral length and functional length of the ulna were used to calculate the BI (being the functional length of the ulna

Table 1 Specimens used in the study

Species	Number	IFA	Museum	Fossil museum numbers
Dasypus novemcinctus	6	0.68	MLP	
Dasypus hybridus	4	0.74	MLP	
Dasypus septemcinctus	1	0.51	MLP	
Chaetophractus villosus	7	0.69	MLP	
Chaetophactus vellerosus	1	0.63	MLP	
Zaedyus pichiy	2	0.74	MLP	
Euphractus sexinctus	1	0.60	MLP	
Tolypeutes matacus	4	0.62	MLP	
Priodontes maximus	2	0.93	MLP	
Cabassous chacoensis	1	0.87	MLP	
Chlamyphorus truncatus	1	1.07	MLP	
Eutatus seguini	1	0.67	MLP	MLP 00-VIII-5-1
Proeutatus sp.	1	0.56	MACN-A	MLP 69-IX-8-11
Peltephilus sp.	1	0.64	MACN-A	7940
Propalaeohoplophorus australis	1	0.67	MLP	MLP 16-15
Glyptodo sp.	1	1.06	MLP	MLP 16-41
Neosclerocalyptus sp.	1	0.57	MACN-Pv	18 107

The museum numbers of extant specimens are given in Supporting Information Appendix S1.
MLP, Museo de La Plata; MACN, Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia'.

divided by the length of the humerus – Vizcaíno & Milne, 2002 and also Howell, 1944).

Twenty 3D landmarks were taken from the humerus of each specimen (see Table 2 and Fig. 2) using a Microscribe digitiser (Microscribe 3DX; http://www.immersion.com). The landmarks were chosen to define articular surfaces and sites of muscle attachment. The landmark data were analysed by the methods of geometric morphometrics, using morphologika software (http://www.york.ac.uk/res/fme). These methods are now well established in the literature (Kendall, 1984; Goodall, 1991; Dryden & Mardia, 1998; Milne & O'Higgins, 2002; Wroe & Milne, 2007) and will not be described in detail here. Procrustes analysis was first used to scale and register the landmark data so that only shape differences remained. An estimate of the size of each specimen was retained (centroid size). The Procrustes registered data were then submitted to principal components analysis (PCA) to examine the variation in shape.

Initially, the principal components (PCs) were examined separately to show the shape changes associated with each, and their correlations with independent variables of biological interest (centroid size, IFA and BI). To identify all the shape changes associated with increasing size, an analysis was conducted in 'size and shape space', where the log of centroid size was included with the Procrustes registered landmark data that was submitted to PCA. This has the effect of forcing all size-related shape variation into PC1.
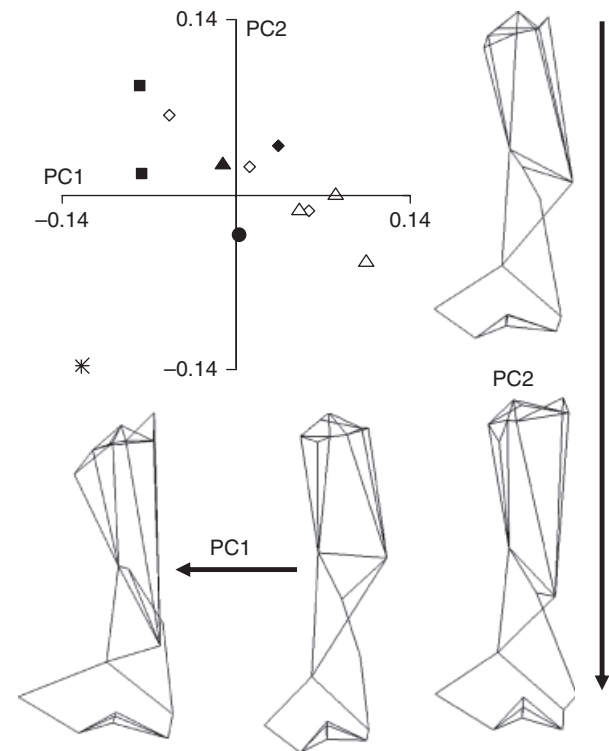
To identify all the shape changes associated with digging ability, a multivariate regression was conducted in

Table 2 Landmark descriptions

Number	Definition of landmarks of the humerus
1	Head at posterior end of greater tubercle
2	Head at top of bicipital groove – greater tubercle side
3	Head at top of bicipital groove – lesser tubercle side
4	Head at medial end of lesser tubercle
5	Head at middle of free surface
6	Proximal point of head
7	Apex of greater tubercle proximally
8	Apex of lesser tubercle anterolaterally
9	Distal end of the deltoid tuberosity
10	Distal end of lat dorsi/teres major insertion
11	Superior point of the epicondylar foramen
12	Tip of medial epicondyle
13	Medial end of trochlea distally
14	Concavity of trochlea distally
15	Anterior edge of trochlea concavity
16	Posterior point of the trochlea concavity (opposite 15)
17	Lateral end of distal articular surface
18	Lateral epicondyle (pit)
19	Apex of the lateral supracondylar line
20	Upper limit of lateral supracondylar line
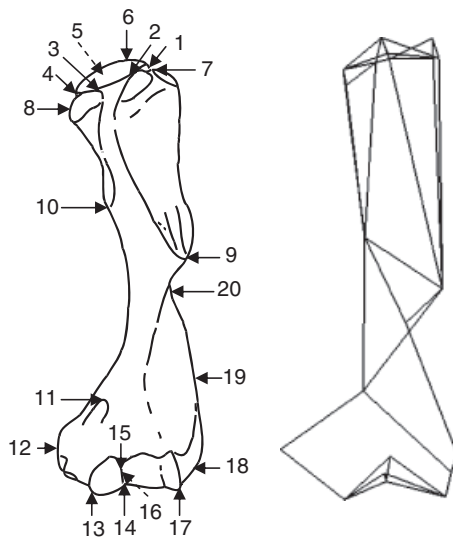
Figure 2 Landmarks on the humerus. The left hand diagram shows the landmarks on the humerus, while the diagram on the right is a wireframe representation of the digitized humerus.

Figure 3 A plot of principal components (PCs) 1 and 2. The wireframe diagrams below the plot indicate the shape changes associated with PC1, and those to the right of the plot show the shape changes associated with PC2. Key to symbols: ♦, dasypodines; ▲, euphractines; ●, *Tolypuetes*; ■, *Priodontes* and *Cabassous*; ✳, *Chlamyphorus*; ◇, fossil armadillos (from above down *Eutatus segunii*, *Proeutatus* sp. and *Peltephilus* sp.); ▽, glyptodonts (*Glyptodon* is separated from *Propalaehoplophorus australis* and *Neosclerocalyptus* sp.).

morphologika, where the PCs representing 81% of the total variation (PCs 1–8 = dependent variables) were regressed against IFA. The IFA was used in these analyses as a morphological proxy for digging ability (ref). This approach does not introduce circularity into the analyses because IFA is derived from ulnar, rather than humeral, measurements. The mean shape was then warped along all eight PCs according to the slope of their regression with IFA. Owing to the fact that *C. truncatus* is the smallest and most fossorial specimen in the sample, there was a concern that it might have biased the analyses; thus, it was removed from the sample and the above analyses were repeated and compared with previous results. The data were also analysed using all 36 specimens, but the results presented here are based on an analysis of the mean shapes calculated above. Both analyses yield essentially the same results.

Results

The first two PCs from an analysis of the mean shapes are plotted in Fig. 3. The first PC accounts for 38.8% and has a correlation of −0.39 (NS) with IFA. *Glyptodon* is an outlier, and if it is removed the correlation rises to −0.86 ($P < 0.0001$). Generally, features associated with low scores on PC1 (and high IFA) are large sites for muscle attachments, both proximally and distally. The deltopectoral crest is very long and lies on the anterior aspect of the humerus. The greater and lesser tubercles are relatively large, and the crest descending from the lesser tubercle (for attachment of *m. latissimus dorsi* and *m. teres major*) is also longer. At the distal end of the humerus, the medial epicondyle is very large and the supinator crest (lateral supracondylar line) is also larger. The distal articular surface, too, is relatively bigger and is orientated more medially (see Fig. 3). These features
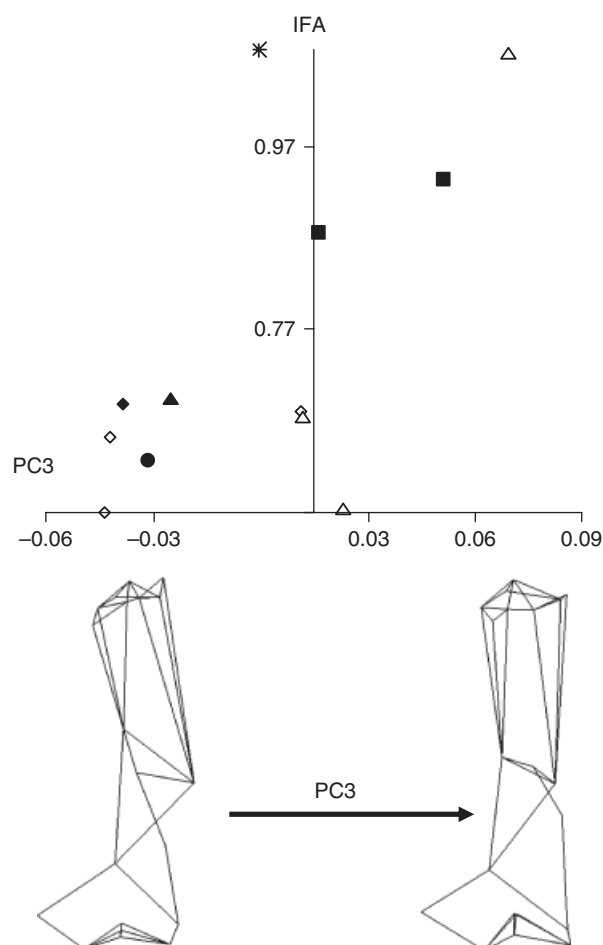
Figure 4 A plot of principal component (PC) 3 and index of fossorial ability (IFA). The wireframe diagrams below the plot indicate the shape changes associated with PC3. Key to symbols: ◆, dasypodines; ▲, euphractines; *Tolypeutes*; ■, *Priodontes* and *Cabassous*; ✳, *Chlamyphorus*; ◇, fossil armadillos (*Eutatus segunii*, *Proeutatus* sp. and *Peltephilus* sp.); △, glyptodonts (*Glyptodon* is separated from *Propalaehoplophorus australis* and *Neosclerocalyptus* sp.).

Figure 5 Wireframe diagrams of the humerus derived from a multivariate regression of index of fossorial ability (IFA) on principal components (PCs) 1–8.

distinguish Type 3, specialized diggers (*Chlamyphorus*, *Cabassous* and *Priodontes*) from the other species.

The second PC accounts for 26.8% of the total variation and has a correlation of -0.43 (NS) with IFA. It seems mainly to separate *C. truncatus* and, to some extent, *Tolypeutes* and *Glyptodon* from the other specimens because of their more deeply notched trochlea and supinator crest, which reaches its maximum close to the lateral epicondyle (see Fig. 3).

PC3 (10.9% of the variation) has a correlation with centroid size ($R = 0.68$, $P < 0.01$). It is also correlated with IFA (see Fig. 4. $R = 0.64$, $P = 0.02$) and BI ($R = -0.54$, $P = 0.05$). *Chlamyphorus truncatus* is an outlier in the correlation between PC3 and IFA, having a large IFA and a small PC3 score. If it is removed, the correlation improves ($R = -0.76$, $P = 0.01$). Larger specimens have relatively
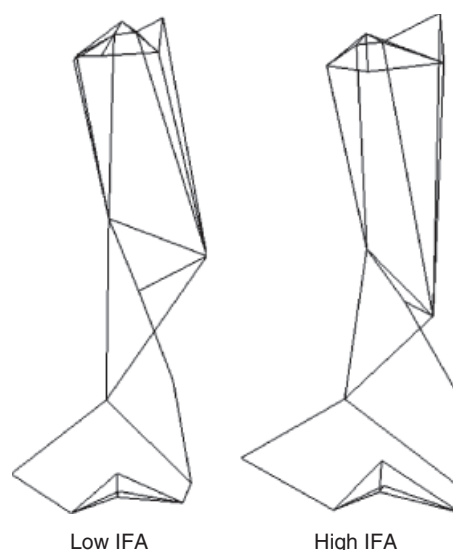
smaller tubercles proximally, and a somewhat less prominent deltopectoral crest, but the crest descending from the lesser tubercle is much longer (see Fig. 4). The relative sizes of the joint surfaces are similar, but the distal articular surface is more deeply notched and directed more laterally in the larger specimens.

A multivariate regression of all 11 PCs with IFA as the independent variable shows that only PC3 has a significant regression with IFA. Figure 5 shows the humeral shape associated with low and high IFA on a combination of the PCs. A large IFA is associated with a larger greater tubercle and deltopectoral crest that is more anteriorly positioned. The crest descending from the lesser tubercle is larger, but the lesser tubercle itself is not. The medial epicondyle and supinator crest are much more prominent, and the articular surfaces are slightly larger.

A size and shape analysis was carried out; the correlation between PC1 and log centroid size is 1 ($R = 0.9999$). The shape changes associated with PC1 are shown in Fig. 6. Generally, large specimens have relatively smaller tubercles and crests for muscle attachment. In particular, the greater tubercle and the deltopectoral crest are much smaller, but so too are the medial epicondyle and supinator crest. The exception to this is in larger specimens, which have a longer crest descending from the lesser tubercle. The articular surfaces are not relatively larger in bigger specimens, but the distal articular surface (trochlea) is more deeply notched and directed more laterally.

The possibility that the smallest and most fossorial specimen (*C. truncatus*) is biasing the analysis was tested by removing it from the sample and repeating the multivariate regression on IFA, and size and shape analyses. The results obtained were very similar to those reported above.
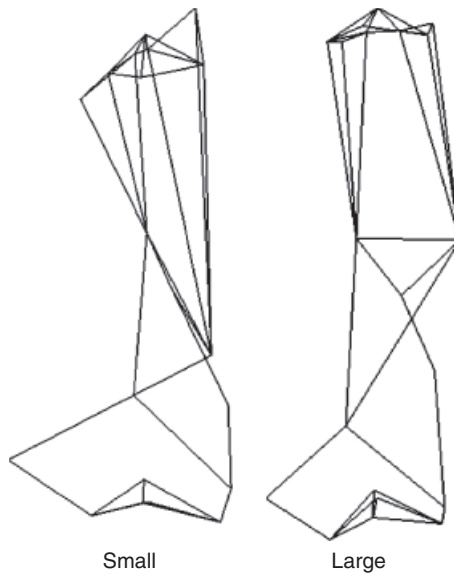
Figure 6 Wireframe diagrams of the humerus at the extremes of principal component (PC) 1 from a size and shape analysis (PC1 = centroid size).

Discussion

This study has revealed two main factors influencing the shape of the humerus in cingulates. Both digging ability and size have their effects, and this study has attempted to separate out these influences. Our discussion will first examine the relation between digging ability and the characteristics of *Chlamyphorus*, the smallest living cingulate that uses a distinctive digging style. We will then consider allometry and the insights that can be gained about the behaviour of glyptodonts, the largest cingulates for which we can only infer behaviour because they have no living representatives. Finally we will attempt to untangle the influences of function and phylogeny on humeral form.

Digging ability

Humeri of specimens with high IFA have: a larger supinator crest above the lateral epicondyle, a more deeply concave trochlea surface, a more massive medial epicondyle and a longer crest descending from the lesser tubercle. The deltopectoral crest, however, is only moderately enlarged (see Figs 4 and 5). Adaptations to digging ability seem to be mostly related to a more secure elbow joint and more powerful muscles that control the forearm and hand. All these features align with Hildebrand's (1985a) description of the adaptations of scratch diggers in which the forelimb operates in the sagittal plane, and the carpal and digital flexors, elbow extensors, humeral retractors and shoulder stabilizers are well developed and powerful. It is not immediately clear why the supinator crest is so large in good diggers. Observations from dissections of armadillos shows that there is no humeral component to the supinator muscle,

but that the posterior surface of the supinator crest (lateral supracondylar line) gives attachment to part of the triceps muscle (Windle & Parsons, 1899).

The longer crest descending from the lesser tubercle might be related to more powerful shoulder extension, adduction and medial rotation required in digging, but it should be acknowledged that larger specimens also have the same feature (Fig. 6 and see discussion below).

Chlamyphorus is clearly distinct from other cingulates as seen in Figs 3 and 4. It has exaggerated features that characterize digging ability in other armadillos, such as relatively large articular surfaces and extremely large tubercles and crests proximally. In particular, the deltoid crest lies on the anterior surface and extends almost to the elbow. In addition, the medial epicondyle is relatively larger than any other specimen (these features are best seen in PC1, Fig. 3). As well as those exaggerated features shared by other species, *Chlamyphorus* has a supinator crest that has its apex very close to the lateral epicondyle as can be seen on PC2 in Fig. 3. This feature, shared only with *Tolypeutes*, may be attributable to the muscles that typically attach on the supinator crest (*brachioradialis and extensor carpi radialis*) being relatively less important than those that attach to the crest more distally, such as *extensor digitorum* and *extensor carpi ulnaris* (of course, this suggestion is speculative, as it was not possible to obtain a specimen of *Chlamyphorus* to dissect). The PC3 correlates strongly with digging ability in the living armadillos, except *Chlamyphorus* (see Fig. 4). This seems to be due to its relatively smaller supinator crest, lesser tubercle and crest descending from the lesser tubercle. Macalister (1875) notes that the *subscapularis* muscle is very thick in *Chlamyphorus* compared with other armadillos. This suggests that medial rotation of the humerus is important in *Chlamyphorus*, and supports the idea that it may use a rotary rather than scratch-digging style as in other armadillos (Hildebrand, 1985a; Merrit, 1985; Nowak, 1991; Vizcaíno & Milne, 2002). Further, Hildebrand (1985a) states that a characteristic of rotary diggers is a large teres major muscle inserting on a tubercle on the humerus that is placed quite distally. Macalister (1875) describes the teres major of *Chlamyphorus* as 'large' and reports that its humerus has a tubercle at the end of the crest descending from the lesser tubercle, not present in other armadillos. These features help to distinguish *Chlamyphorus* from other armadillos and seem likely to be involved in the medial rotation of the humerus characteristics of rotary diggers.

Allometry

Bigger specimens have relatively larger proximal but not distal joint surfaces, relatively smaller tubercles at the proximal end, and the deltopectoral crest is shorter and positioned more towards the lateral side of the humerus. However, the crest descending from the lesser tubercle is relatively longer. The medial epicondyle is somewhat less developed, but the supinator crest is more prominent. The trochlea surface is more deeply notched and laterally directed (see Figs 4 and 6).

The longer crest descending from the lesser tubercle is apparent in both good diggers and larger specimens, but this feature seems more pronounced in larger specimens (see Figs 5 and 6). This could be related to the need for eccentric action of the teres major to control lateral rotation and abduction of the humerus in larger animals.

The fact that larger specimens in this study do not appear to have relatively larger distal joint surfaces and to have generally less well developed tubercles and crests for muscle attachment can be explained by allometric principles. The surface area of a bone increases in proportion to the square of the length increase; which would provide greatly increased area for muscle attachment. Similarly, joint surfaces also increase proportionally to the square of the length increase, but they have to support an increased load that is proportional to the cube of the length increase, so they are expected to be relatively larger. To compensate for this, larger animals tend to reduce the loads on their bones by adopting less flexed postures and less athletic behaviours (Schmidt-Nielsen, 1984; Hildebrand, 1985*b*; McGowan, 1994).

Glyptodonts

Many of the humeral features of glyptodonts seem to be related to their large body size. Figure 4 shows the relationship between PC3 and IFA, but PC3 correlates more strongly with size. There are also some clear distinctions between *Glyptodon* on the one hand, and *Neosclerocalyptus* and *Propalaeohoplophorus* on the other. *Glyptodon* has a high IFA and humeral features that accord with digging ability in other cingulates, while *Neosclerocalyptus* and *Propalaeohoplophorus*, which have a relatively low IFA, are outliers in Fig. 4. A simple consideration of IFA values in

glyptodonts would lead to the proposition that *Glyptodon* is a specialized digger, while *Propalaehoplophorus* is more generalized and *Neosclerocalyptus* had more cursorial habits. However, although *Glyptodon* has a very large IFA, it is doubtful that such a large animal could have foraged or sheltered in burrows of its own making (Kraglievich, 1934; Quintana, 1992). The fossorial features of *Glyptodon*'s forelimb may be directed towards tearing at the surface of the substrate in search of food, although the hands are not as specialized for that purpose as those of armadillos (Gillette & Ray, 1981). Alternatively, they may have developed an extremely long olecranon process (IFA) for other reasons, such as supporting and manoeuvring its huge body mass on flexed elbows, or rising to a bipedal position and returning to a quadrupedal stance. Adopting a bipedal stance is not uncommon among living armadillos, including *Priodontes* (Frechkop, 1950), and it has been suggested that this may be necessary in using its armoured tail in defence (Fariña, 1995; Alexander *et al.*, 1999).

Function and phylogeny

The main difference between the morphological (Gaudin & Wible, 2006) and molecular (Möller-Krull *et al.*, 2007) approaches lies in the position of *Chlamyphorus* and the consideration of the monophyly of the Tolypeutinae (see Fig. 1). Figure 7 shows the distribution in the cladograms of the fossorial habit types described in the introduction for the living armadillos and assigned to the fossils according to their IFA values. Figure 7a is the morphological hypothesis and Fig. 7b is a composite of the molecular hypotheses, with the fossils considered in this work included according to Gaudin & Wible's (2006) and Fernicola's (2008) cladograms.
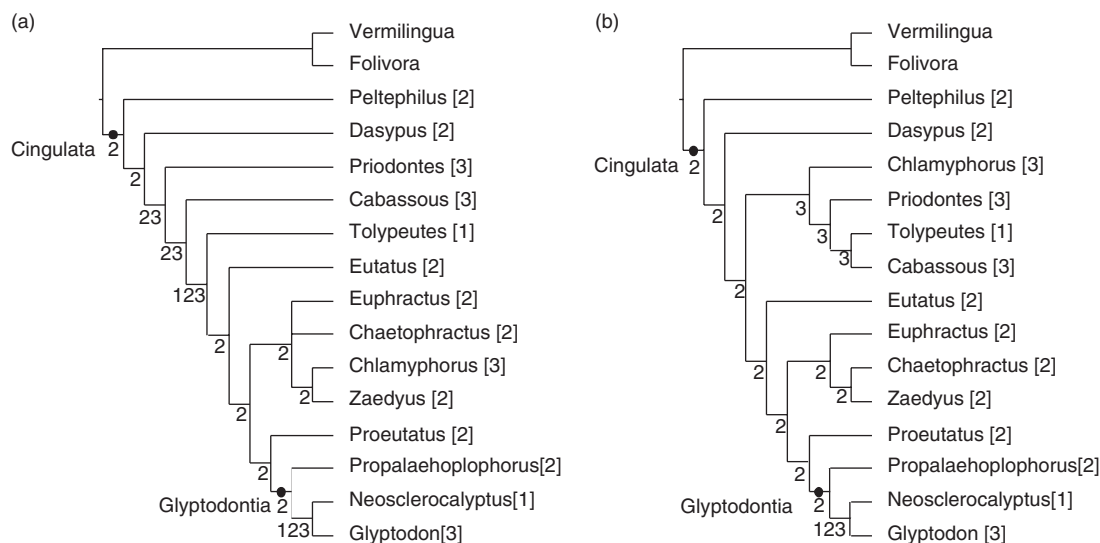

Figure 7 Combined (a) morphological and (b) molecular phylogenies. These dendrograms use information from Fernicola (2008) to include the fossil specimens used in the present study. The numbers after the genus names indicate the digging habits based on their index of fossorial ability.

Both phylogenies support the interpretation of the generalized digging habits (Type 2: species that dig short burrows for protection or in search of food and that also feed on the surface or just below it by making 'food probes') as ancestral for all cingulates, and that the cursorial habits of *Tolypeutes* derive from specialized digging ancestors in the molecular phylogeny, while in the morphological phylogeny it may derive either from digging or specialized digging ancestors. Excluding glyptodonts, which will be discussed below, the main difference between both phylogenies refers to the appearance of the specialized habits in armadillos. The morphological phylolgeny (Fig. 7a) suggests that the specialized digging habits (Type 3: species that are burrowers or that feed on termites or ants) appeared at least twice, and that this humeral morphology has resulted from evolutionary processes that have adapted the humeri to their function. In the molecular hypothesis (Fig. 7b) the appearance of such habits would be a single event correlated with the differentiation of the clade Chlamyphorinae + Tolypeutinae, suggesting that their similarities in humeral form are related to their common phylogeny. Independent of the assessment of the digging abilities of glyptodonts considering the morphological limitations mentioned above, the fore limb morphology of *Propalaeohoplophorus* seems consistent with its basal position within glyptodonts derived from generalized digging armadillos, and the derived condition, albeit in different directions, of *Glyptodon* and *Neosclerocalyptus*.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Museum numbers of extant armadillos specimens used in this study.

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