

Investigation into the Paleobiology of *Dasyopus bellus* Using Geometric Morphometrics and Variation of the Calcaneus

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Abstract The extinct taxon *Dasyopus bellus* has long been considered identical to the extant *Dasyopus novemcinctus* osteologically when disregarding allometric differences. In this study, we undertake a preliminary investigation into this extinct taxon and an extant relative *D. novemcinctus*, by comparing the calcanea of these two dasypodids. Clear osteological differences are observed including a mediolaterally-reduced facet region, an anteriorly-shortened calcaneal head, a reduced peroneal process, and a curved and dorsoventrally-shortened calcaneal foot in *D. bellus*. Such characters are not allometric and likely correlate to distinct behavioral differences. Specifically, we suggest that *D. novemcinctus* maintains a more fossorial lifestyle, while the larger *D. bellus* was likely more terrestrial, with potentially little digging behavior. Such lifestyle differences could not only explain the osteological differences present, but also why fossils of *D. bellus* have been recovered farther north than the present range of *D. novemcinctus*. Fossils of *Dasyopus* may need to be re-evaluated to determine how these two taxa relate temporally and geographically, which may have further implications regarding some past interpretations

and provide new details on the behavior and potential relationships between these (and other) xenarthrans.

Keywords *Dasyopus* · Xenarthra · Geometric morphometrics · Calcaneus · Evolutionary morphology · Allometry

Introduction

Fossil records of *Dasyopus* first appear in North America during the late Pliocene (Blancan North American land mammal age) in the form of *D. bellus* Simpson, 1929, the beautiful armadillo, from Florida (Webb 1974; Robertson 1976) and questionably (*Dasyopus* cf. *D. bellus*) from Nebraska (Voorhies 1987). However, *D. bellus* remains become far more common in North America during the late Pleistocene (e.g., Klippel and Parmalee 1984; Hulbert and Pratt 1998; McDonald and Naples 2008). Overall, there are at least 50 localities with *D. bellus* remains within the contiguous United States (Fig. 1), and no other extinct dasypodids have been described from North America. In one of the more recent studies on *D. bellus*, beyond modest occurrence data, Schubert and Graham (2000) discussed some of the youngest *D. bellus* material known, reviewed the taxon based on current understanding, and discussed systematic problems surrounding it.

Today, *Dasyopus novemcinctus* Linnaeus, 1758, the nine-banded armadillo, is the only extant dasypodid in North America. This species has been steadily expanding its range throughout the southern and central United States over the last century (see Layne 2003; Loughry and McDonough 2013), and has been found as far north as southeastern Tennessee (Eichler and Gaudin 2011), central Missouri (Taulman and Robbins 1996), and Macon County in central Illinois (Van Deelen et al. 2002; Hofmann 2009), although there is no direct

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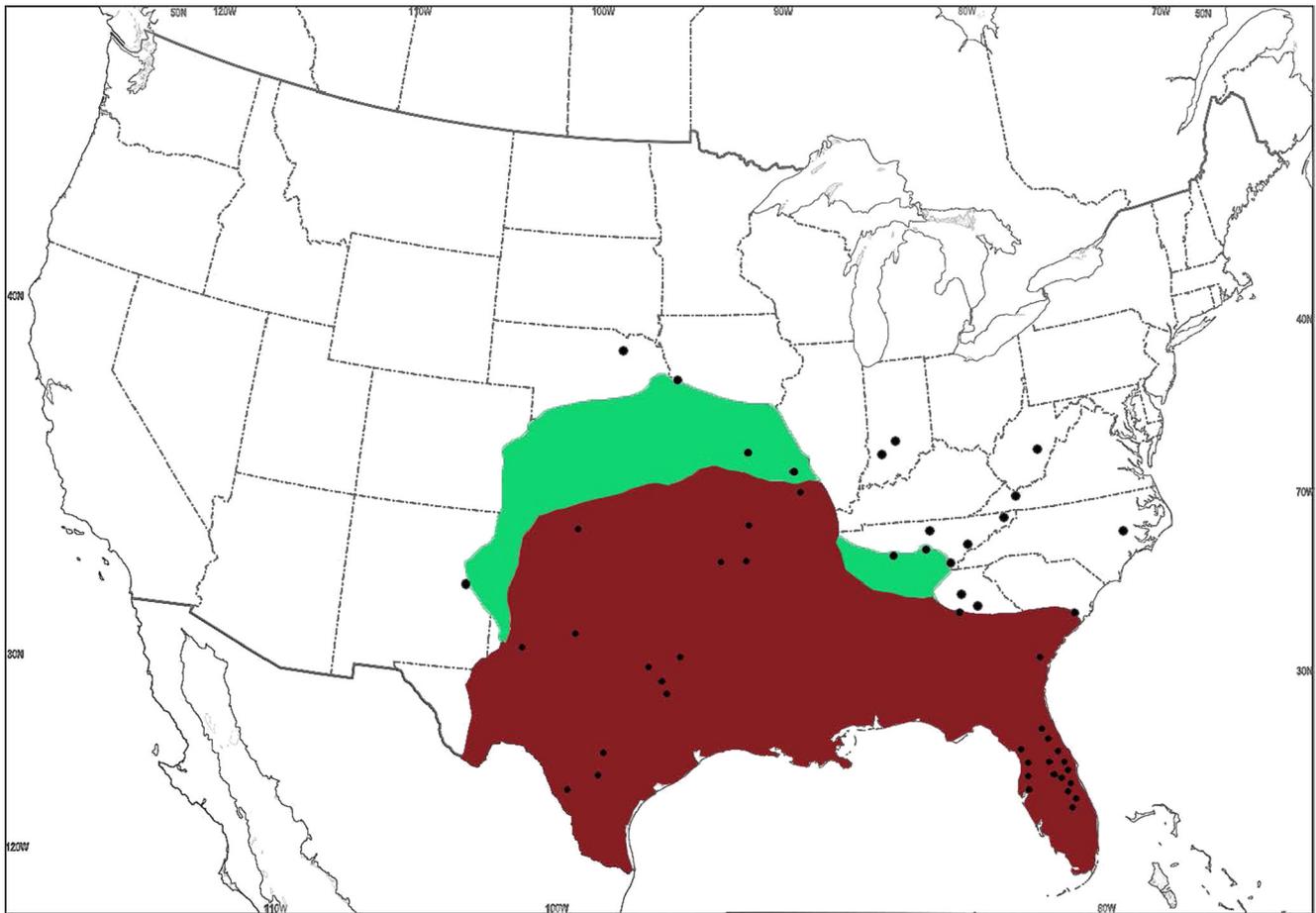


Fig. 1 Distribution of dasypodids in the United States. Normal ranges of *Dasybus novemcinctus* (darker shaded), extensions to the normal range of *D. novemcinctus* based on scattered individual occurrences (lighter

shaded), and sites where *D. bellus* have been found (black dots). Modified from Layne (2003), Klippel and Parmalee, (1984), Voorhies (1987), and Hulbert and Pratt (1998)

evidence of these individuals surviving over the winter season (Eichler and Gaudin 2011). Overall, *D. novemcinctus* has a south-southeastern range in the United States, although the range can be extended slightly farther north when individual sightings and occurrences are considered (Fig. 1). Unfortunately, there have been no definitive prehistoric remains of *D. novemcinctus* recovered in the United States (Schubert and Graham 2000). This is probably due to its recent invasion north into the United States in the mid 1800's (Audubon and Bachman 1854; Humphrey 1974; Klippel and Parmalee 1984; Schubert and Graham 2000; Layne 2003; Loughry and McDonough 2013).

Subsequently, the fossil record of *Dasybus* Linnaeus, 1758, in North America is currently comprised of a single taxon, *D. bellus*, commonly considered the fossil counterpart of *D. novemcinctus* (see McBee and Baker 1982; McDonald and Naples 2008). Size and temporal occurrence are the major characteristics used to differentiate *D. novemcinctus* from *D. bellus*. While numerous Pleistocene fossils of *Dasybus* have been discussed in the literature (see Klippel and Parmalee 1984; McDonald and Naples 2008), none have been identified,

at least confidently, as *D. novemcinctus*. In addition, the fact that *D. bellus* has not been identified outside of the United States also leads to further confusion to the differentiation of these taxa, although records of similar taxa have been documented farther south (e.g., Rincon et al. 2008). In a study of late Pleistocene cingulates from Venezuela, Rincon et al. (2008) compared *D. bellus* with *Propraopus* Ameghino, 1881, and *D. kappleri* Krauss, 1862, and suggested that, due to similarities between the carapace osteoderms, skull morphology, and carpal bones, *D. bellus* and *D. kappleri* were synonymous. Rincon et al. (2008) also stated that similarities between the carapace osteoderms supported the idea put forth by Hoffstetter (1958) that *D. bellus* belongs within *Propraopus*. Inclusion of *D. bellus* within *Propraopus* is beyond the scope of this study, but should be investigated further to clarify the systematic placement of this taxon. It is of note that some work, including that of Letts and Shapiro (2010, 2012), have found close affinities between the DNA of *D. bellus* and *D. novemcinctus*. In agreement with molecular data, numerous workers have noted that *D. bellus* is osteologically identical to *D. novemcinctus* except for the

greater size of the former, implying that the two could potentially be synonymous (e.g., Slaughter 1961). Direct osteological comparison between *D. bellus* and *D. novemcinctus* may shed light on (at least) specific, if not generic, placement of the former. Unfortunately, non-osteoderm remains of *D. bellus* are relatively rare, so little to no non-cranial research has been done. Therefore, a specimen of *D. bellus* with multiple non-osteoderm elements is important, and some elements, such as the calcaneus, with a more distinct morphology, may be useful to further investigate potential differences between *D. bellus* and other related dasypodids.

In investigating the osteology, Rincon et al. (2008) mentioned two distinctions between *D. bellus* and *D. novemcinctus* based on the cuneiform and unciform. In *D. bellus*, the unciform has five articular facets, but lacks a facet for the fifth metacarpal. In the cuneiform of *D. bellus*, there are two articular facets on the anterolateral surface, which Rincon et al. (2008) suggested articulate with the fifth metacarpal and another bone, potentially a sesamoid. Both of these states differ from those present in *D. novemcinctus*, where the unciform articulates with the fifth metacarpal and the cuneiform has a single articular facet on its lateral surface (Rincon et al. 2008).

The calcaneus was chosen for this study for several reasons, including: it is a robust and easily identified element, has a better chance of being preserved due to its robust nature, and is particularly important in hind limb usage. Additionally, the calcaneus often undergoes adaptations for animals to particular substrates, for habitat exploration and utilization, and social activities (e.g., Szalay 1994; Bassarova et al. 2009). It has also been shown that the morphology of the calcaneus can aid in determining an animal's posture, locomotor style, stance, and number of digits (e.g., Carrano 1997, 1998; Bassarova et al. 2009; Polly and MacLeod 2008), although the last two do not apply to this study. Specifically, the calcaneus acts as a lever arm for the gastrocnemius and soleus muscles, allowing stronger and more rapid foot retraction, while also being involved in the rotation, flexion/extension, and adduction/abduction movements of the foot (Polly and MacLeod 2008; Bassarova et al. 2009). It is noted that some authors (e.g., Vizcaíno and Fariña 1997; Vizcaíno et al. 1999, 2003, 2008; Vizcaíno and Milne 2002) have reported that the forelimb, its dimensions, and some of its elements, may have more association with fossoriality and digging habits than do the hind limbs. Vizcaíno and Milne (2002) stated that hind limb indices were related more to weight bearing. However, as the largest bone in the mammalian ankle, the calcaneus forms part of the primary ankle joint and is closely related to locomotor function (Polly and MacLeod 2008), so we feel that the hind limbs also factor into fossoriality/digging. Specifically, it factors in the added removal of substrate after initial digging by the forelimbs.

Consequently, landmark-based geometric morphometrics were used here to derive thin-plate splines and plot principal

component analyses of the calcanea of *D. bellus* and *D. novemcinctus*, which were then further analyzed with respect to behavior and potential taxonomic placement. If dissimilarity is found to be from allometry, then the hypothesis that *D. bellus* is simply a larger version of *D. novemcinctus* cannot be disproven through this study. If, on the other hand, differences are found that cannot be attributed to allometry, then these two taxa are more distinct from each other and further details can potentially be assessed.

Institutional Abbreviations

ETVP, East Tennessee State University Vertebrate Paleontology Laboratory, Johnson City, TN, USA; **RMM**, Red Mountain Museum (collections now housed in the McWane Science Center), Birmingham, AL, USA.

Materials and Methods

Terminology

Herein the portion of the calcaneus anterior to (and including) the astragalar facet region is referred to as the calcaneal head, whereas the portion posterior to the astragalar facet region is the calcaneal foot (= calcaneal heel of some authors, see Carrano 1997). Various facets of the calcaneus, along with the groove for the tendo calcaneus, also known as the Achilles tendon, are also shown in Fig. 2 to illustrate the calcaneal features discussed below, and to better demonstrate the size difference between *D. bellus* and *D. novemcinctus*.

Specimens Used

Only complete adult *Dasypus* calcanea were used in this study (seven *D. novemcinctus* and one *D. bellus*). A specimen from ACb-3 Cave, Colbert County, Alabama, with multiple elements (RMM 6356) was utilized because it preserved the only complete and well-preserved adult calcaneus of *D. bellus* available. Specimens of *D. novemcinctus* utilized herein are housed at East Tennessee State University, Johnson City, Tennessee, while that of *D. bellus* was on loan from the McWane Science Center, Birmingham, Alabama. Six of the *D. novemcinctus* specimens studied (ETVP 229, 397, 398, 400, 401, and 7032) were right calcanea. The lone left calcaneus studied (ETVP 399) was mirrored. *Dasypus novemcinctus* specimens all represented the subspecies *D. novemcinctus mexicanus* Peters, 1864, but were collected throughout its current distribution, and so are believed to be representative of the modern species as a whole. The single *D. bellus* specimen (RMM 6356) was also a right calcaneus, allowing direct comparison.

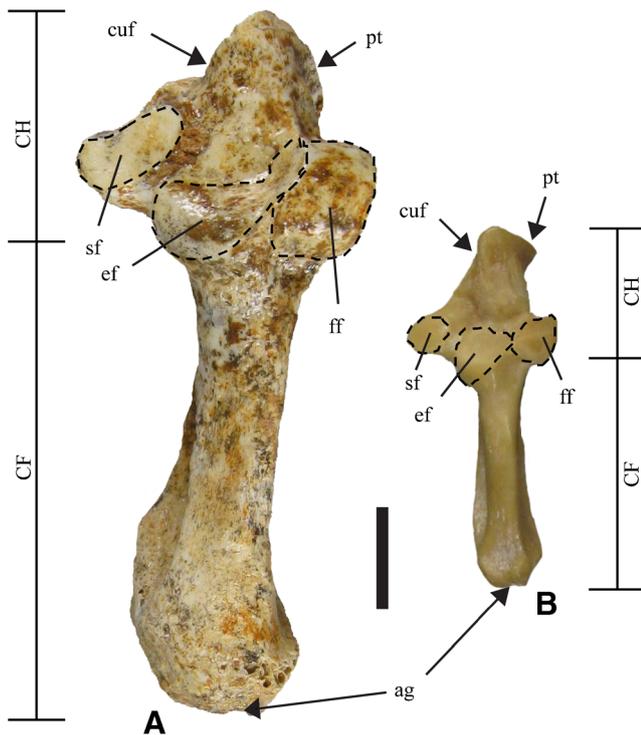


Fig. 2 Right calcaneus of (A) *Dasyypus bellus*, RMM 6356, and (B) *D. novemcinctus*, ETVP 401, in dorsal view. Abbreviations: **ag**, groove for tendo calcaneus (= Achilles tendon); **CH**, region of calcaneal head; **CF**, region of calcaneal foot (= calcaneal heel of some authors); **cuf**, cuboid facet; **ef**, ectal facet; **ff**, fibular facet; **pt**, peroneal tubercle (with peroneal process); **sf**, sustentacular facet. Note *arrow* pointing to the general region of the cuboid facet because the facet is just out of view, but is visible in anterior view. An *arrow* also points to the groove for the tendo calcaneus because only a small posterodorsal portion of the groove can be seen in dorsal view. Scale bar equals 1 cm

Geometric Morphometrics

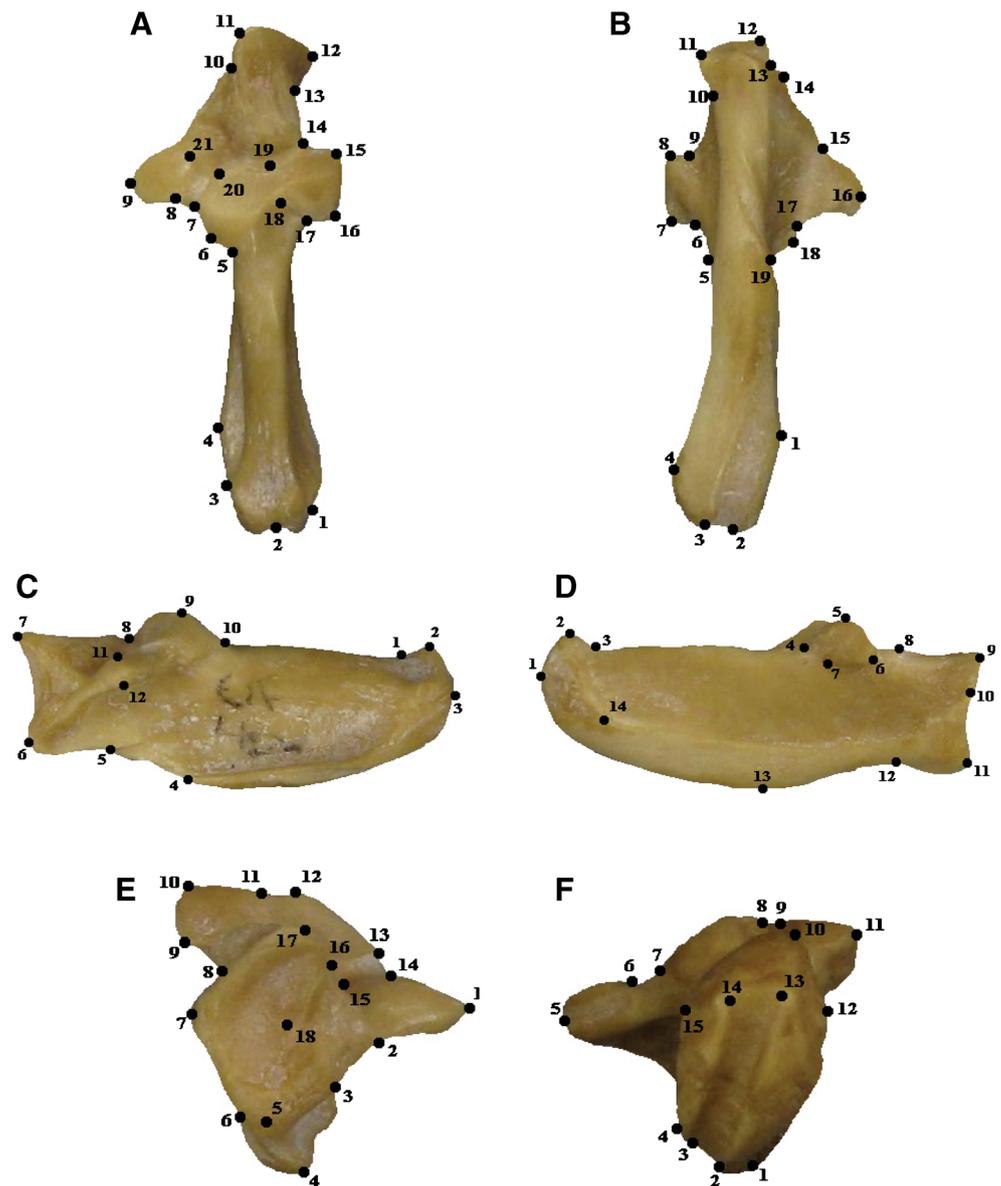
High-resolution photographs of dorsal, ventral, lateral, medial, anterior, and posterior views of each calcaneus were taken using a digital camera (Canon PowerShot A590, resolution 8.0 megapixels). Commonly, a maximum dimension, or dimensions, was used to help orient the specimens, along with orientation vertical or horizontal to the camera lens. For dorsal view, specimens were positioned with the major portion of the dorsoventral axis vertical (in line with camera lens) and the maximum anteroposterior length possible visible. Twenty-one landmarks (mainly type 2 and type 3, following Bookstein 1991) were recorded, with the majority positioned near the facets (Fig. 3A, Table 2 in supplementary data). In ventral view, specimens were positioned with the major portion of the dorsoventral axis vertical and the maximum anteroposterior length possible visible as well. Nineteen landmarks were recorded with most on the anterior half of the calcaneus (Fig. 3B, Table 3 in supplementary data). For lateral view, specimens were positioned with the dorsoventral axis horizontal and the maximum anteroposterior length possible visible.

Twelve landmarks were recorded with the majority on the perimeter of the calcaneus, except for two located near the sustentacular facet (Fig. 3C, Table 4 in supplementary data). In medial view, specimens were positioned with the dorsoventral axis horizontal and the maximum anteroposterior length possible visible. Fourteen landmarks were recorded, with the majority around the perimeter of the calcaneus (Fig. 3D, Table 5 in supplementary data). For anterior view, specimens were positioned with their long axis vertical and the major facet region as horizontal as possible. Eighteen landmarks were recorded, with most around the perimeter and several around the anterior-most end and cuboid facet (Fig. 3E, Table 6 in supplementary data). In posterior view, specimens were positioned with their long axis vertically and the major facets visible dorsal to the posterior-most end. Fifteen landmarks were recorded with several around the groove for the Achilles tendon (Fig. 3F, Table 7 in supplementary data). At least ten photographs were taken of each specimen for each view on separate occasions. Each photograph was analyzed and the one with the maximum dimensions was selected for landmark placement in each view.

Using tpsDig2 (Rohlf 2010a), landmarks were digitized onto the calcaneus in all six views. Following this, tpsUtil (Rohlf 2010b) was used to build combined tps format files. These tps format files were then aligned using tpsSuper (Rohlf 2004b), where all specimens were superimposed and a consensus was created. In this case, a consensus of all *Dasyypus novemcinctus* specimens was created for easier comparisons with *D. bellus*. Finally, tpsSpln (Rohlf 2004a) was used to create thin-plate splines comparing *D. novemcinctus* to *D. bellus*. In all six views, the *D. bellus* landmarks were warped to the consensus of *D. novemcinctus* to visualize the differences in shape. Superimpositions removed potential size-dependent differences by scaling the specimens equally. *Dasyypus bellus* was warped to *D. novemcinctus* to investigate the hypothesis that the former was simply a larger version (or subspecies) of the latter. Consequently, in the results, *D. bellus* is the one commonly being referred to, unless otherwise noted.

MorphoJ was utilized for comparisons with the effects of allometry removed and for each principal component analysis (following van Heteren et al. 2009, 2012). Using MorphoJ, raw 2D coordinates were scaled, rotated, and translated by Procrustes superimposition. Since allometry would still factor into these data, the effects of allometry were removed by performing a pooled regression within species of the Procrustes coordinates onto the log centroid size (following Bookstein 1991; van Heteren et al. 2009, 2012). Such an analysis operates on the assumption that slope of the allometry of both species would be the same, but have different intercepts; an idea that has been shown to give reliable results (e.g., Cardini and O’Higgins 2004). Following this, a principal component analysis (PCA) was conducted on the regression

Fig. 3 Landmarks of the *Dasypus* spp. calcanea in (A) dorsal, (B) ventral, (C) lateral, (D) medial, (E) anterior, and (F) posterior views. Details of landmarks in supplementary data, Table 2 for (A), Table 3 for (B), Table 4 for (C), Table 5 for (D), Table 6 for (E), and Table 7 for (F)



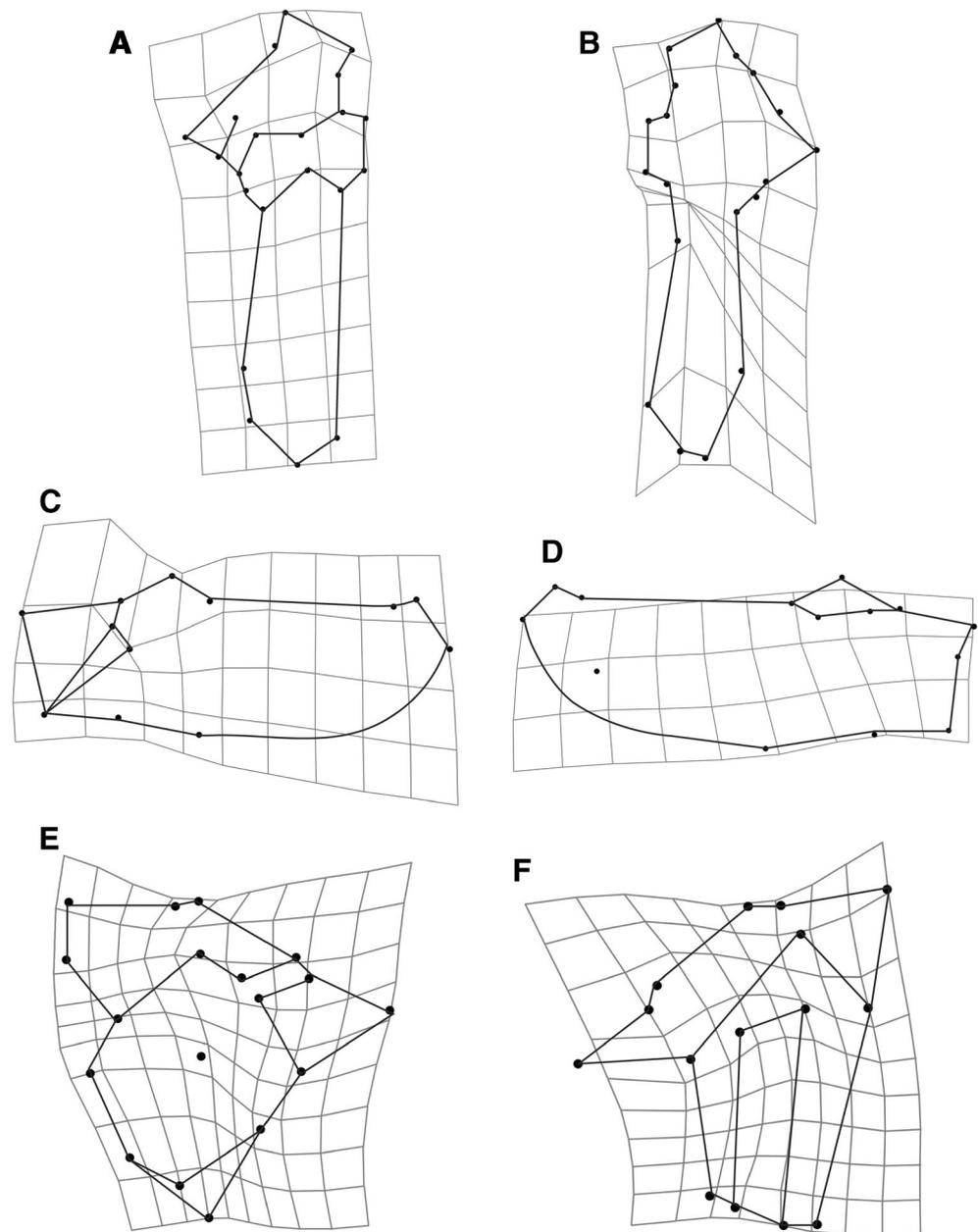
residuals instead of the Procrustes shape variables for each of the six views. Results are the morphological differences between the species with allometry removed and focus on size-independent shape change.

Results

Thin-Plate Splines Six different views of *D. bellus* and a consensus of *D. novemcinctus* were compared, with the former warped to the latter. In the thin-plate spline showing dorsal view (Fig. 4A), the calcaneal foot showed little deformation between the two dasypodids. Around the facets and the calcaneal head, *D. bellus* is slightly narrower mediolaterally and reduced anteriorly compared to *D. novemcinctus*. The

anterior-most portion of the calcaneal head around the cuboid facet and the fibular facet is slightly compact in *D. bellus*, unlike the rest of the anterior portion of the calcaneus. In ventral view (Fig. 4B), similar to what is seen in dorsal view, the mediolateral width is still relatively narrower in *D. bellus*. However, the lateral border of the calcaneal foot is elongated posteriorly in *D. bellus* compared to *D. novemcinctus*. On the medial edge around the fibular facet in *D. bellus*, there is significant deformation, with the posterior portion exhibiting significant “pinching,” or compression, between landmarks 5 and 6; by far the most warping seen in ventral view for the extinct taxon. Landmarks 4 and 5 show a significant amount of elongation. Conversely, the remaining deformation in *D. bellus* is minor, with some elongation and constriction around the facets and calcaneal head.

Fig. 4 Thin-plate spline showing deformation from *Dasyopus bellus* to *D. novemcinctus* in (A) dorsal, (B) ventral, (C) lateral, (D) medial, (E) anterior, and (F) posterior views. Orientation and order are the same as in Fig. 2. Further details of exact landmarks can be found through direct comparison with Fig. 2 and from supplementary data Table 2 for (A), Table 3 for (B), Table 4 for (C), Table 5 for (D), Table 6 for (E), and Table 7 for (F)



In lateral view, there are several key areas of deformation in the thin-plate spline (Fig. 4C). Near the posterior calcaneal foot, *D. bellus* shows a shorter height dorsoventrally. Conversely, the remainder of the calcaneus is quite similar between *D. bellus* and *D. novemcinctus*. There is significant shortening dorsally on the anterior portion of the calcaneus in *D. bellus*. Around the ectal facet, there is distinct warping, with the surface rotated slightly more posteriorly. The sustentacular facet is more ventral, leading to constriction around its ventral side, but more elongation dorsally. Slight rotation is present about the calcaneal head as well. The calcanea of the two dasypodids appear most similar in medial view (Fig. 4D). Although the medial side of the fibular facet is

present, there is little warping in the ventral region of *D. bellus*. Deformation was relatively minor near the dorsal surface. Only a slight elongation around the anterodorsal portion of the calcaneus of *D. bellus* and some minor constriction on the anteroventral portion between landmarks 11 and 12 are evident.

Significant warping occurred in the thin-plate spline showing anterior view (Fig. 4E). Mediolaterally, *D. bellus* is shortened along the fibular and sustentacular facets, while dorsoventrally it is slightly elongate compared to *D. novemcinctus*. There is slight constriction in *D. bellus* near the ventral half, while the dorsal half shows elongation mediolaterally. In *D. bellus*, the groove between the fibular facet and the ectal facet

(landmarks 11 and 12) also shows slight warping laterally. In posterior view (Fig. 4F), some of the same changes are evident as seen in anterior view. A dorsoventral constriction is still present and is significant in *D. bellus*. Near the calcaneal foot, the most prominent feature is the groove for the Achilles tendon, and significant warping is seen in this feature for the extinct armadillo. Specifically, there is distortion with the dorsal- and ventral-most portions of the Achilles tendon groove, which appear bowed laterally. In fact, there is some lateral bowing present throughout the entire laterodorsal portion in posterior view. Similarly, this bowing in *D. bellus* is present when comparing the posterior-most surface with the facets present on the anterior half of the calcaneus.

Principal Component Analyses Dorsally, principal component 1 (PC1, 58.171 % of variance, see Table 1) was best able to separate the species (Fig. 5). Moving toward more negative values and toward *D. bellus*, the calcaneal head becomes more compact and less elongate. However, the sustentacular facet becomes more elongate. In addition, the ectal facet becomes shorter anteroposteriorly, while the fibular facet gets longer, particularly anteromedially, and the calcaneal foot becomes more robust. Ventrally, PC1 (96.901 %, see Table 1) again serves as the key component to separate the two dasypodids (Fig. 6). Moving toward more positive PC1 values, the posterior end of the calcaneal foot, particularly around its medial portion, undergoes a great deal of change. Landmark 5 in ventral view (see Fig. 3B and Table 3 in supplementary data) shifts posteriorly, while landmark 4

moves medially. The anterolateral curve of the calcaneal head shifts lateroposteriorly. In fact, most of the calcaneal head appears to shift posteriorly as values get more positive on PC1. The medial projection that is part of the fibular facet shifts slightly anteromedially.

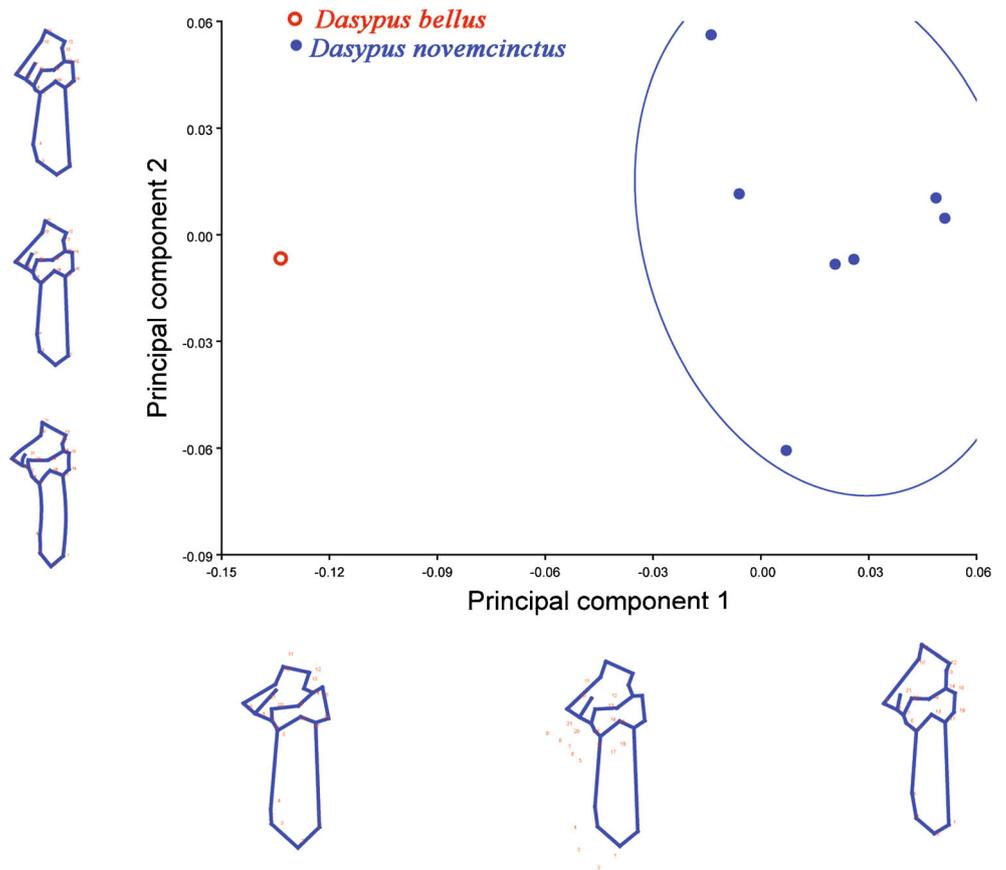
Principal component 1 (Fig. 7) best separates the species in lateral view (54.744 %, see Table 1). As *D. bellus* is found toward more negative PC1 values, one of the main features that changes is the calcaneal foot, which gets thinner dorsoventrally. While little change is observed in the calcaneal head, the sustentacular facet has shifted dorsally, rotated, and laterally is somewhat thinner and more gracile. In medial view (Fig. 8), PC1 (54.810 %, see Table 1) again shows a thinner and more gracile calcaneal foot moving toward more negative values (and toward *D. bellus*). Though slight, the fibular facet is higher (dorsally), shorter (anteroposteriorly), and its highest point (landmark 5 in Table 5 in supplementary data) more posterior.

In anterior view, PC1 (55.555 %, see Table 1) is again the main species distinguisher, with *D. bellus* positioned toward more positive values (Fig. 9). Moving toward more positive PC1 values, the fibular facet again appears to be getting smaller and is shifting medially. Landmark 4 (see Fig. 3E and Table 6 in supplementary data) shows the calcaneal foot shifting medially and not projecting as far laterally. The cuboid facet is becoming more constricted, less sub-circular, and more ovular. Constriction of the cuboid facet implies that the cuboid is located relatively more medial in *D. novemcinctus*. Finally, posteriorly PC3 is the optimal component to show

Table 1 Percent variance and eigenvalues describing first six principal components conducted on regression residuals for each of the six views of the calcanea

View		PC1	PC2	PC3	PC4	PC5	PC6
Dorsal	% variance	58.171	17.452	12.746	5.372	3.616	2.643
	Cumulative %	58.171	75.623	88.369	93.741	97.357	100
	Eigenvalue	0.0034568	0.0010371	0.0007574	0.0003192	0.0002149	0.0001571
Ventral	% variance	96.901	1.064	0.715	0.601	0.503	0.216
	Cumulative %	96.601	97.965	98.681	99.282	99.784	100
	Eigenvalue	0.0453995	0.0004986	0.0003351	0.0002816	0.0002355	0.0001011
Lateral	% variance	54.744	21.054	12.885	4.978	3.747	2.593
	Cumulative %	54.744	75.798	88.682	93.661	97.407	100
	Eigenvalue	0.0028017	0.0010775	0.0006594	0.0002548	0.0001917	0.0001327
Medial	% variance	54.81	15.727	12.835	7.727	6.073	2.83
	Cumulative %	54.81	70.536	83.371	91.098	97.17	100
	Eigenvalue	0.0022019	0.0006318	0.0005156	0.0003104	0.000244	0.0001137
Anterior	% variance	55.555	18.453	11.929	6.309	5.481	2.184
	Cumulative %	55.555	74.097	86.027	92.335	97.816	100
	Eigenvalue	0.0090498	0.0030205	0.0019432	0.0010277	0.0008928	0.0003558
Posterior	% variance	54.047	28.766	10.472	3.51	1.802	1.403
	Cumulative %	54.047	82.813	93.285	96.795	98.597	100
	Eigenvalue	0.012241	0.0065152	0.0023718	0.0007951	0.0004082	0.0003177

Fig. 5 Principal component analysis of the dorsal view of the calcanea of *Dasyopus bellus* and *D. novemcinctus* comparing principal component 1 (horizontal axis) with principal component 2 (vertical axis). Wireframe images for principal component 1, from left to right, are at -0.13, -0.04, and 0.05, respectively. Wireframe images for principal component 2, from top to bottom, are at 0.05, 0, and -0.07, respectively. A 90 % confidence ellipse encompasses *D. novemcinctus*



differences between the species (Fig. 10), although it only accounts for 10.472 % of the total variance (see Table 1).

Still, it shows that the sustentacular facet is becoming thinner and shifts more medial toward more negative values. The

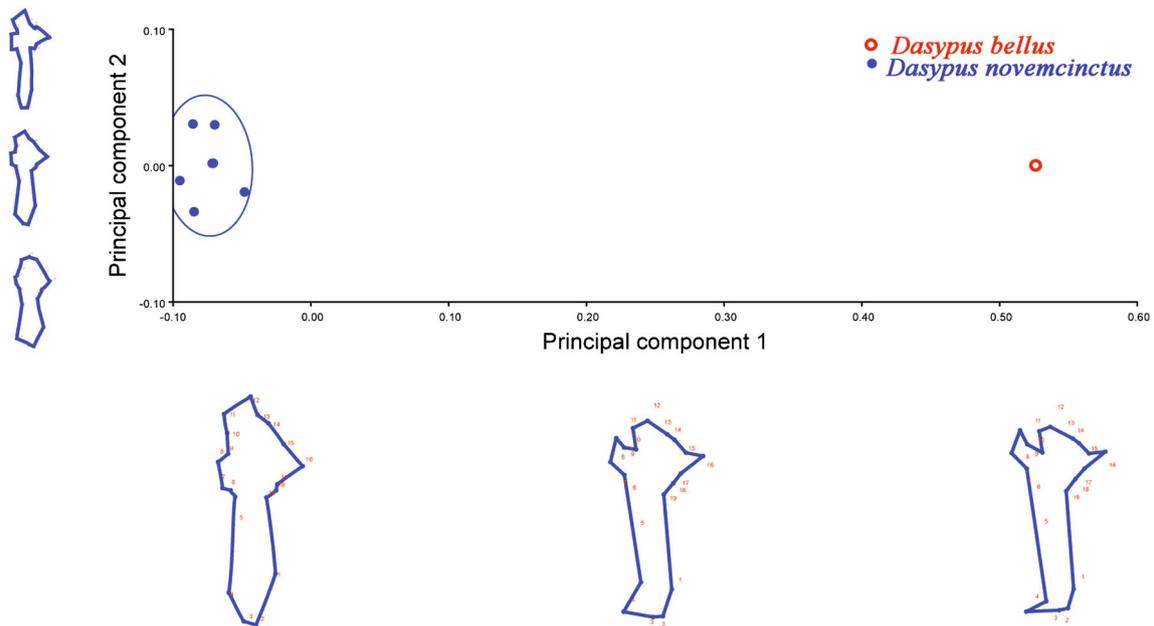


Fig. 6 Principal component analysis of the ventral view of the calcanea of *Dasyopus bellus* and *D. novemcinctus* comparing principal component 1 (horizontal axis) with principal component 2 (vertical axis). Wireframe images for principal component 1, from left to right, are at -0.1, 0.25, and

0.52, respectively. Wireframe images for principal component 2, from top to bottom, are at 0.1, 0, and -0.1, respectively. A 90 % confidence ellipse encompasses *D. novemcinctus*

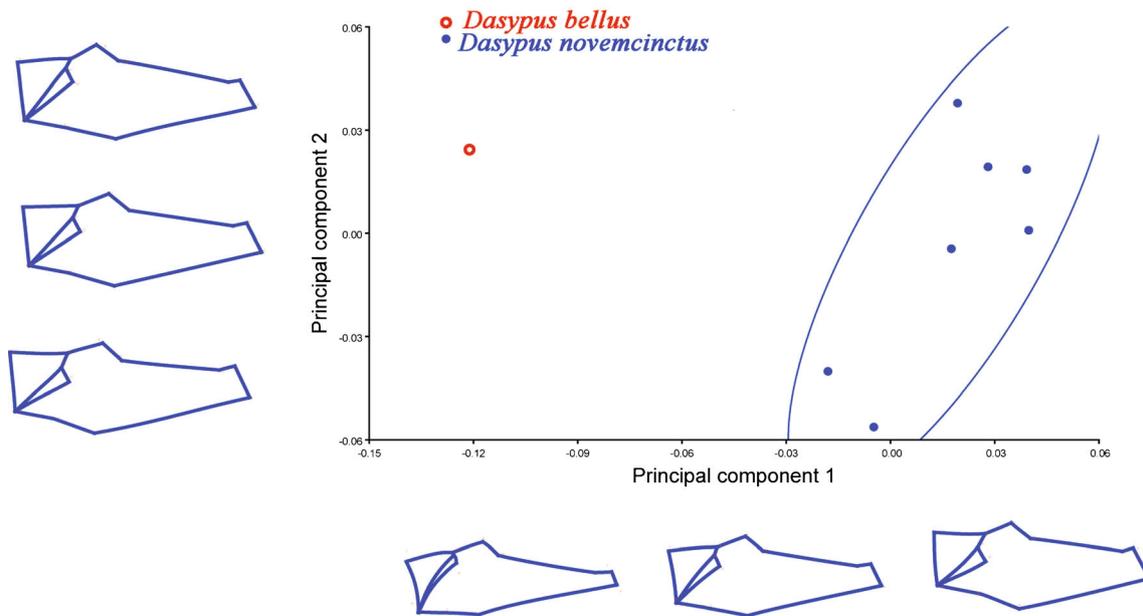


Fig. 7 Principal component analysis of the lateral view of the calcanea of *Dasypus bellus* and *D. novemcinctus* comparing principal component 1 (horizontal axis) with principal component 2 (vertical axis). Wireframe images for principal component 1, from left to right, are at -0.12, -0.04,

and 0.04, respectively. Wireframe images for principal component 2, from top to bottom, are at 0.05, 0, and -0.05, respectively. A 90 % confidence ellipse encompasses *D. novemcinctus*

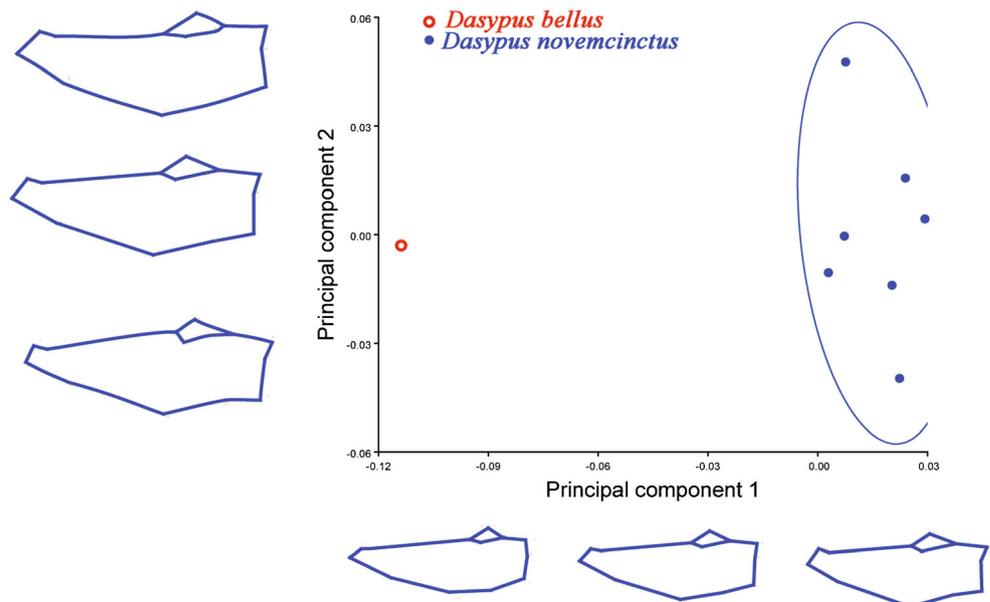
fibular facet is becoming smaller and shifts ventrally. The more ventrally-positioned portion of the Achilles tendon groove becomes further squared off and less angled as well.

Discussion

Allometric studies have aided in investigating taxonomic issues (e.g., Dodson 1975; Currie 2003; Campione and Evans

2011), and have commonly been used as a means to suggest synonymies. Conversely, they can also be used to show important differences, potentially refuting synonymies and identifying distinct features. Needless to say, allometry is an important consideration when comparing *D. bellus* to *D. novemcinctus*. If there are differences present that are not caused by larger overall mass, body size, and/or areas for larger muscles to attach (Christiansen 1999, 2002), then the dissimilarities may be due to distinct taxonomic differences. If *D. bellus* really is simply a larger version of *D. novemcinctus*,

Fig. 8 Principal component analysis of the medial view of the calcanea of *Dasypus bellus* and *D. novemcinctus* comparing principal component 1 (horizontal axis) with principal component 2 (vertical axis). Wireframe images for principal component 1, from left to right, are at -0.11, -0.04, and 0.03, respectively. Wireframe images for principal component 2, from top to bottom, are at 0.05, 0, and -0.05, respectively. A 90 % confidence ellipse encompasses *D. novemcinctus*



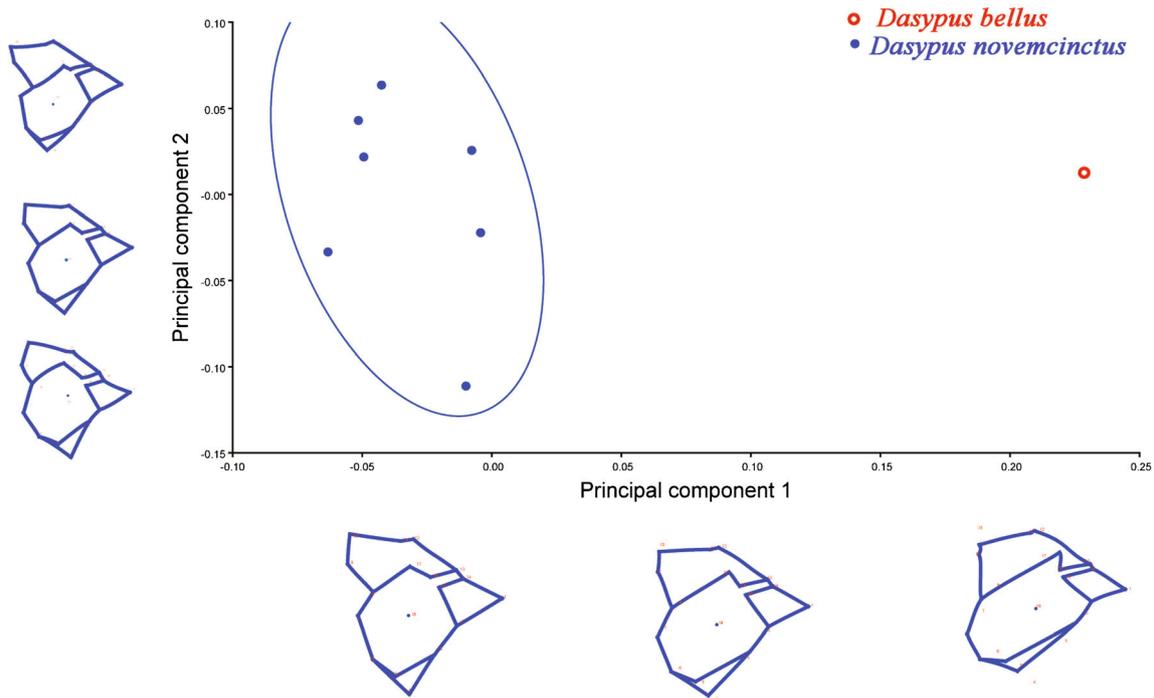
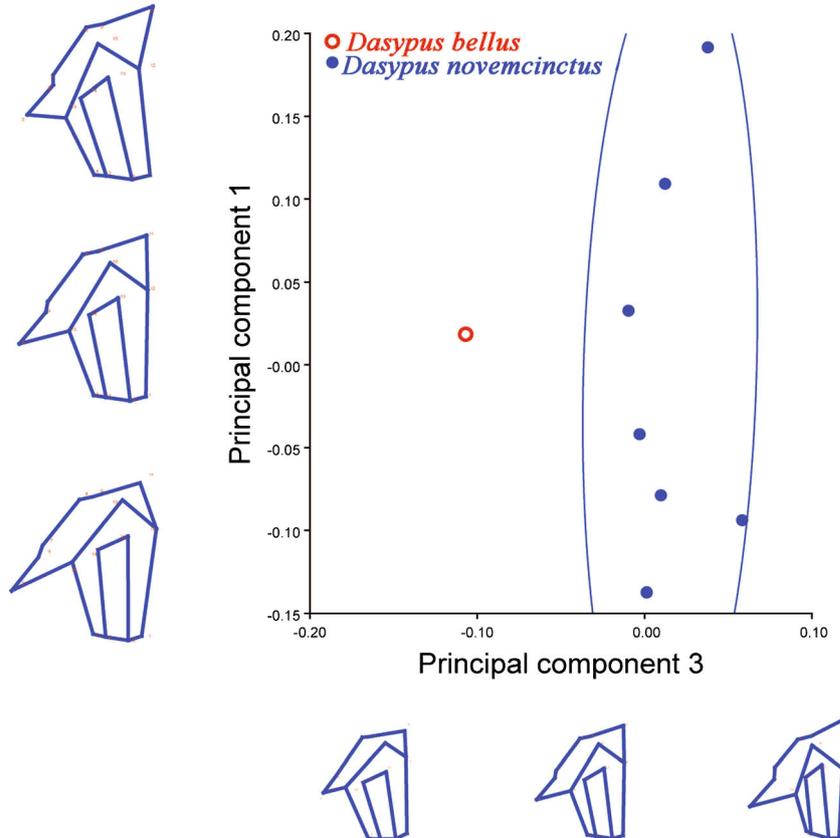


Fig. 9 Principal component analysis of the anterior view of the calcanea of *Dasyopus bellus* and *D. novemcinctus* comparing principal component 1 (horizontal axis) with principal component 2 (vertical axis). Wireframe images for principal component 1, from left to right, are at -0.05, 0.08,

and 0.23, respectively. Wireframe images for principal component 2, from top to bottom, are at 0.1, 0, and -0.12, respectively. A 90 % confidence ellipse encompasses *D. novemcinctus*

Fig. 10 Principal component analysis of the posterior view of the calcanea of *Dasyopus bellus* and *D. novemcinctus* comparing principal component 3 (horizontal axis) with principal component 1 (vertical axis). These principal components showed the greatest separation between the species, particularly PC3. Wireframe images for principal component 3, from left to right, are at -0.1, 0, and 0.15, respectively. Wireframe images for principal component 1, from top to bottom, are at 0.12, 0, and -0.12, respectively. A 90 % confidence ellipse encompasses *D. novemcinctus*



then the thin-plate splines and PCAs should only show differences based on larger muscle attachments areas and muscle scars (size-dependent differences). Moreover, the overall shapes should be quite similar if synonymous, with the only modifications being related to allometry. However, this study focused on size-independent differences and several identified suggest something other than allometry. Since allometry is at least partially ruled out, differences in behaviors or ecological needs can be evaluated as potential alternative explanations.

Allometric differences are often more complicated than merely scaling up size and proportions and enlarging areas for muscle scars and muscle attachments. Indeed, body size can commonly affect the shape of joints due to biomechanical scaling pressures. A common way to maintain similar stress levels with mammals of different sizes is to alter limb posture (Biewener 1989, 1990, 2005). Biewener (1990) mentioned that larger mammals tend to have a more upright posture to counteract increased stresses. He also stated that mammals at greater sizes have increased skeletal allometry and decreased locomotor performance, while those at smaller sizes may have increased skeletal stiffness. While it is shown that *D. bellus* could have a more upright posture, this may be either from allometric scaling as noted immediately above, or from a difference in locomotor function. In reality it is probably some of both.

The most common geometric morphometrics methods place landmarks on 2D images or 3D objects and compare the landmarks in various ways (see summaries in Bookstein 1991; Elewa 2004). Thin-plate splines can be used to help visualize the deformation between landmarks. Principal component analyses derived from regression residuals help portray morphological differences without allometry as a factor. In dorsal view (Figs. 4A and 5), distinctiveness in these two dasypodids with the facet region can be interpreted as a feature derived for the relative area on the calcaneus needed for facets rather than due to size differences. The non-allometric enlargement of the fibular and sustentacular facets from the PCA (Fig. 5) would enable the lower leg to have a wider range of motion in *D. novemcinctus*. Ventral view portrays the greatest deal of warping between the two taxa (Figs. 4B and 6), with the PCA showing portions of the calcaneal head becoming more compact and beginning to undergo more drastic changes toward more positive values on PC1 and in *D. bellus* (Fig. 6). With the facet region shifting, less leverage can be gained through the calcaneus. Laterally, a shifting of the lateral projection, along with tilting of the ectal and fibular facets somewhat posteriorly, is probably not due to muscle attachment areas or size differences, but instead is more likely the result of different morphologies of the astragalus to deal with these differently-angled facets. As evidenced in lateral view, rotation of the sustentacular facet allows the calcaneus of *D. bellus* to be held more vertically when articulated. Medially, constriction near the anterior end in *D. bellus* may

be due to allometric differences since little deformation is seen otherwise. In anterior view, mediolateral elongation of *D. novemcinctus* provides more area for the facets to contact and potentially stronger articulations. The more compact nature of *D. novemcinctus*, as evidenced by constrictions seen in anterior view, could hypothetically lead to more leverage in its hind feet. For posterior view, a wider facet area may imply that this region is more important to *D. novemcinctus*, or just that the two taxa are behaving differently. A constriction around the Achilles tendon groove may be for a stronger or larger contact between the Achilles tendon and the calcaneus.

Throughout all six views it seems that *D. bellus* may have had a more restricted lower hind limb with less range of motion. Regardless, there is more interspecific variation between *D. bellus* and *D. novemcinctus* than there is intraspecific variation within the latter. All six PCA figures (Figs. 5, 6, 7, 8, 9 and 10) show that *D. bellus* varies based mainly on one principal component, but never on a second. Since all specimens were from adult individuals, it is currently unknown how variation would relate, both inter- and intraspecifically, throughout ontogeny. Since focus was placed on comparing these two species, others, including *D. kappleri* and *Propraopus*, were not investigated in this study.

As stated above, while some authors feel that forelimbs are more strongly associated with fossorial behavior (e.g., Vizcaíno et al. 1999; Vizcaíno and Milne 2002), others have shown hind limb morphology to be related as well. Polly and MacLeod (2008) discussed differences in calcanea due to locomotor function. In particular, they discussed differences between those of semifossorial and terrestrial taxa. While semifossorial taxa tend to have a more straight distal end (= calcaneal foot) and a larger peroneal process (and peroneal tubercle), more terrestrial (and digitigrade) taxa tend to have slimmer sustentacular facets placed less distally than arboreal (and plantigrade) taxa (Polly and MacLeod 2008). As is visible in the PCA of lateral view (Fig. 7), the sustentacular facet has been rotated and allows the calcaneus of *D. bellus* to be held more vertically when articulated, implying more terrestrial movement for the extinct taxon. Indeed, *D. novemcinctus* has a straighter calcaneal foot, and the peroneal process is larger and projects further medially, as evidenced in Fig. 4A. This supports the idea that *D. novemcinctus* is semifossorial (see Loughry and McDonough 2013 and references therein), or at least more fossorial than *D. bellus*.

While not all views gave the same results, differences between these two dasypodids tend to follow a general trend. *Dasyopus bellus*, while being larger and temporally older, has relatively smaller facet and articulation surfaces. It also has a wider and more robust groove for the Achilles tendon, with the calcaneal foot being more robust mediolaterally and more gracile dorsoventrally. The smaller articulation and facet surfaces may mean a smaller range of motion, potentially with the ability to gain more leverage. While appearing very similar

and closely related, these two taxa, undoubtedly, were behaving differently.

Implications *Dasyopus novemcinctus* has stout limbs that are well adapted for digging and maintains a fossorial to semi-fossorial lifestyle (see Loughry and McDonough 2013 and references therein). It has been assumed that *D. bellus* lived in much the same way as the extant species, leading to the assumption that *D. bellus* was also at least semi-fossorial (e.g., Slaughter 1961; Kurtén and Anderson 1980; Klippel and Parmalee 1984). Being a larger taxon, this activity may not have been as important to *D. bellus* though. *Dasyopus bellus* has been found farther north than *D. novemcinctus* and, while the two distributions are similar toward the west and north-central areas of the ranges, *D. bellus* does range a fair distance farther to the northeast (see Fig. 1). However, differences in the ranges of the two taxa are less pronounced than previously interpreted (e.g., Schubert and Graham 2000). Even so, the range difference could be the result of various factors, including the fact that *D. bellus* may have been able to retain more body heat in colder environments and travel more quickly due to its larger body size compared to *D. novemcinctus*, assuming colder temperatures were present to the northeast and away from the Mississippi River. Blackburn et al. (1999) and Meiri and Dayan (2003) discussed Bergmann's Rule and how it can be used to help explain larger body size in mammals at higher latitudes. Meiri (2011), on the other hand, discussed how Bergmann's Rule was intended to be utilized at the intra-specific level, rather than with closely related species. As a result, while closely related, the ecological requirements of *D. bellus* and *D. novemcinctus* cannot be as closely compared, at least in relation to Bergmann's Rule.

In addition, paleoclimates at the time of *D. bellus* may have been milder or more subdued, with less severe winters within its former range (Slaughter 1961; Guilday et al. 1978). However, *D. bellus* potentially could have exhibited a hibernative lifestyle, "waiting out" the winter and/or colder months, although *D. novemcinctus* does not hibernate and cannot survive freezing temperatures today (McNab 1980; Loughry and McDonough 2013). This potential hibernative lifestyle may help explain why a number of the fossil localities containing *D. bellus* specimens are from cave sites. Whether *D. bellus* did or did not hibernate, it still seems to have traveled farther north than *D. novemcinctus* does today. If less time is spent maintaining a fossorial lifestyle and a specific home range around a burrow, *D. bellus* may have had more opportunities to travel. Current distributions suggest that *D. novemcinctus* has less tolerance to lower temperatures and, coupled with the need for certain temperatures to maintain its dietary habits (insects), cannot survive in colder temperatures (Slaughter 1961). *Dasyopus novemcinctus* is known to travel farther north over the summer and remain there with milder winters and temperatures as well (see Van Deelen et al. 2002;

Eichler and Gaudin 2011). Slaughter (1961) also mentioned the increase in range of *D. novemcinctus* when a string of milder winters occur, only to have their range reduced when a colder or more severe winter would occur. With warmer temperatures, or a string of milder winters, *D. bellus* could have potentially traveled farther than *D. novemcinctus* before colder temperatures and winters pushed their ranges farther south again. On the other hand, *D. novemcinctus* may eventually inhabit the entire former range of *D. bellus* once its range has stabilized, considering its recent invasion of the lower 48 states and recent more northern expansion (see Layne 2003; Loughry and McDonough 2013).

Alternatively, *D. bellus* and *D. novemcinctus* may not compare as closely ecologically as previously thought (Schubert and Graham 2000). The two taxa may also be less similar physiologically than previously thought (contra Slaughter 1961). Fossils of *D. bellus* have been recovered with those of boreal rodents from the Craigmile local fauna in Iowa, where Rhodes (1984) stated the "occurrence of *D. bellus* in southwestern Iowa casts doubt on the strict limits previously interpreted for this taxon. Its association with taxa from colder regions, in the Craigmile and other local faunas, suggests that *D. bellus* must have been better adapted for survival in cold, even subfreezing, weather than the modern *D. novemcinctus*". Voorhies (1987) agreed with this assessment and also suggested that *D. bellus* may have been more cold adapted than its extant relative, *D. novemcinctus*. Additionally, *D. bellus* may have had different dietary habits such as feeding on different insects, or a lower percentage of them and having a larger portion of its diet made up of carrion and eggs, which *D. novemcinctus* still feeds on today, albeit less often (see Loughry and McDonough 2013). If so, then the possible paleoclimate and paleoenvironmental implications are still somewhat open, and more data are needed.

Considering that *D. bellus* is the only extinct dasypodid described from North America, it may be possible that the taxon is a waste-basket for all North American fossil *Dasyopus* or dasypodid material, regardless of any other possible osteological differences. While allometry would account for differences between the two taxa based on their body sizes, and may account for some of the differences presented in this study, such as a potentially more upright posture in *D. bellus*, other morphological differences may reveal possible dissimilarities in their lifestyles and, potentially, the environmental requirements of *D. bellus*. Therefore, differences found in the calcanea of these two dasypodids have implications for their taxonomy and the interpretations of each, particularly *D. bellus*. With morphological differences present, it may be that the two taxa overlapped in time and biogeography. Consequently, numerous fossils of *Dasyopus* may need to be re-evaluated to test the potential differences between the taxa and find how they relate to each other. This change may result in further adjustments to interpretations based on their presence

and absence and how they lived. It has already been suggested that *D. bellus* may be closely related to, and perhaps even belong within, the genus *Propraopus* (Hoffstetter 1958; Rincon et al. 2008); however, additional distinctions between both *D. bellus* and *D. novemcinctus*, along with *Propraopus*, may have further implications for how these taxa are studied and interpreted.

Summary and Conclusions

Specimens identified as *D. bellus* make up the entirety of the fossil dasypodid record from North America. Consequently, *D. bellus* may have become a garbage taxon, specifically if the only or main criteria for assignment within the taxon are that the remains represent a fossil *Dasypus* species larger than those of a “normal”-sized *D. novemcinctus*. However, by comparing the calcanea of these two dasypodids, clear osteological differences and trends were found and are interpreted here to be the result of behavioral variations. Based on differences present between the calcanea of *D. bellus* and *D. novemcinctus*, the latter taxon has a distinctive calcaneus that is here interpreted as an adaptation for digging. Thus, *D. novemcinctus*, the smaller taxon, is thought to have maintained a more fossorial lifestyle than its fossil relative, whereas the larger *D. bellus* would not have been as well adapted for digging. In other words, the pes of *D. bellus* was better adapted for a terrestrial lifestyle, and potentially walking longer distances. Lifestyle differences would not only explain the osteological differences seen when investigating size-independent variables, but also may explain why fossils of *D. bellus* have been found farther north and northeast than the present range of *D. novemcinctus*. However, the fact that the distribution of *D. novemcinctus* is still stabilizing, coupled with changing temperatures and climates, may lead to *D. novemcinctus* inhabiting more of the range of the fossil taxon as well. Morphological differences may result in the re-interpretation of various fossils of *D. bellus* to evaluate if some are actually fossils of *D. novemcinctus*. If they are found to be the latter taxon, then various interpretations based on that taxonomy may have to be re-visited. Phylogenetically this study shows differences between the taxa, but does not show the two are more closely or distantly related than any other dasypodids, including *D. kappleri* and *Propraopus*.

This preliminary study helps provide insight into calcaneal differences within dasypodids, although investigation of more calcanea is needed to confirm or deny these findings. In addition, an in-depth look at the astragali of these two taxa would be an important next step, especially to determine if the expanded facet area seen in the calcaneus of *D. novemcinctus* translates to its astragalus. A full osteological description of *D. bellus* is also long overdue. Nevertheless, even the investigation into a

single element shows that there are more differences between *D. novemcinctus* and *D. bellus* than previously thought. Additional comparisons and information about these and other cingulates could have further paleoclimate and paleoenvironmental implications, although caution should be adhered to when using the extant *D. novemcinctus* as an ecological and physiological equivalent animal to *D. bellus*.

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