

# A new *Dasypodini* armadillo (*Xenarthra*: *Cingulata*) from San Gregorio Formation, Pliocene of Venezuela: affinities and biogeographic interpretations

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**Abstract** We describe *Pliodasypus vergelianus* gen. et sp. nov., a *Dasypodini* armadillo from the middle Pliocene of Venezuela (Vergel Member, San Gregorio Formation). Although scarce, the remains are remarkable because of their geochronologic proximity to the main phase of Great American Biotic Interchange (GABI). The cladistic analysis conducted reveals that *Pliodasypus* groups with *Dasypus* and both are sister taxa of *Propraopus*, whereas *Anadasypus* is at a basal position. With respect to the records of tribe *Dasypodini*, after its oldest representative (*Anadasypus*, middle and late Miocene), the chronologically subsequent form is *Pl. vergelianus* (middle Pliocene), followed by *Dasypus bellus* in higher northern latitudes (late Pliocene), and then by

widespread occurrences in the Pleistocene of North America (*D. bellus*) and South America (*Propraopus*, *Dasypus punctatus*, and *Dasypus novemcinctus*). Thus, we infer that *Dasypus* differentiated in the late Pliocene at low latitudes in the northern South America. It leads to two alternative hypotheses of dispersal: (a) some early *Dasypus* remained cryptically in South America until the Pleistocene, whereas others dispersed to North America between 2.2 and 2.7 Ma, or (b) they dispersed to North America subsequently to the emersion of the Panamanian isthmus and *D. bellus* differentiated there; later, during the Pleistocene, *D. bellus* entered South America and experienced speciation. The same process of re-ingression has been proposed to other xenarthrans, breaking with the traditional assumption that the GABI was unidirectional.

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*Pliodasypus* · Pliocene · Venezuela

## Abbreviations

AMU-CURS	Colección de Paleontología de Vertebrados de la Alcaldía de Urumaco, Estado Falcón, Venezuela
GABI	Great American Biotic Interchange
NALMA	North American Land Mammal Age
SALMA	South American Land Mammal Age

## Introduction

The evolutionary history of dasypodid armadillos (*Xenarthra*, *Cingulata*) took place in America during most of the Cenozoic, with first records in the early Paleogene of Argentina (Ameghino 1902; Simpson 1948; Tejedor et al. 2009; Carlini et al. 2010) and Brazil (Scillato-Yané 1976; Oliveira and Bergqvist 1998; Bergqvist et al. 2004). The

Dasypodinae, well represented in warmer and more humid environments, comprise Astegotheriini (Itaboraian–Laventan South American Land Mammal Ages (SALMAs)), Stegotheriini (Casamayoran–Friasian SALMAs), and Dasypodini (Laventan SALMA–recent) and are one of the most basal lineages (Gaudin and Wible 2006; Delsuc et al. 2012). The synapomorphies of Dasypodini are the morphology of the peripheral figures of movable osteoderms (which suggests the presence of triangular epidermal scales with a posteriorly directed apex partially covering two adjacent osteoderms) and double line of osteoderms composing each ring of the caudal sheath (Vizcaíno 1990; Carlini et al. 1997). The group includes *Anadasypus* (*Anadasypus hondanus* Carlini et al., 1997 from the middle Miocene of Colombia and *Anadasypus aequatorianus* Carlini et al., 2013 from late Miocene of Ecuador), *Propraopus* Ameghino, 1881 (?Pliocene–early Holocene of South America), and the long-nosed armadillo *Dasypus* Linnaeus, 1758 (?late Miocene–recent).

Besides being the most diverse (Wilson and Reeder 2005) and widespread extant xenarthran, *Dasypus* is the only armadillo genus that occupied North America. The nine-banded armadillo *Dasypus novemcinctus* has its first records in recent times, reaching 40° N (Wetzel 1985; Aguiar and da Fonseca 2008) and rapidly spreading northward in USA (Taulman and Robbins 1996 and references therein). The current distribution of *D. novemcinctus* is mostly coincident with that of *Dasypus bellus*, which is recorded in the late Pliocene–late Pleistocene (Blancan–Rancholabrean North American Land Mammal Ages (NALMAs)) of the southeastern and mid-USA, up to 42° N (Klippel and Parmalee 1984; Voorhies 1987), and in the late Pleistocene of Mexico (Carbot-Chanona 2010). Although the external morphology of its osteoderms remained the same, this taxon experienced an increase in size through time, and a relatively complete specimen from the late Pleistocene suggests a total length of 1.2 m (Auffenberg 1957; Downing and White 1995; McDonald 2005; Morgan 2005).

The xenarthrans were probably the most successful South American mammals participating in the Great American Biotic Interchange (GABI), given that both Pilosa and Cingulata reached and even differentiated in North America (McDonald 2005; Carlini et al. 2008b). Previous to the formation of a stable Panamanian isthmus (estimated between 2.5 and 3.1 Ma; Coates and Obando 1996; but see Montes et al. 2012 and Bacon et al. 2013), chains of emerged lands linked both Americas. Although this condition certainly regulated the type and intensity of biotic migrations, several records indicate a diffuse vertebrate interchange beginning in the late Miocene, by at least 9 Ma (Webb 2006; Campbell et al. 2010; Head et al. 2012). Based on records of South American taxa at 4.7 to 3.6 Ma in Mexico, Carranza-Castañeda and Miller (2004) and Flynn et al. (2005) proposed that this land bridge originated earlier, but not necessarily was continuous in time. The major influx North American mammals to South America was recorded in sediments of the late

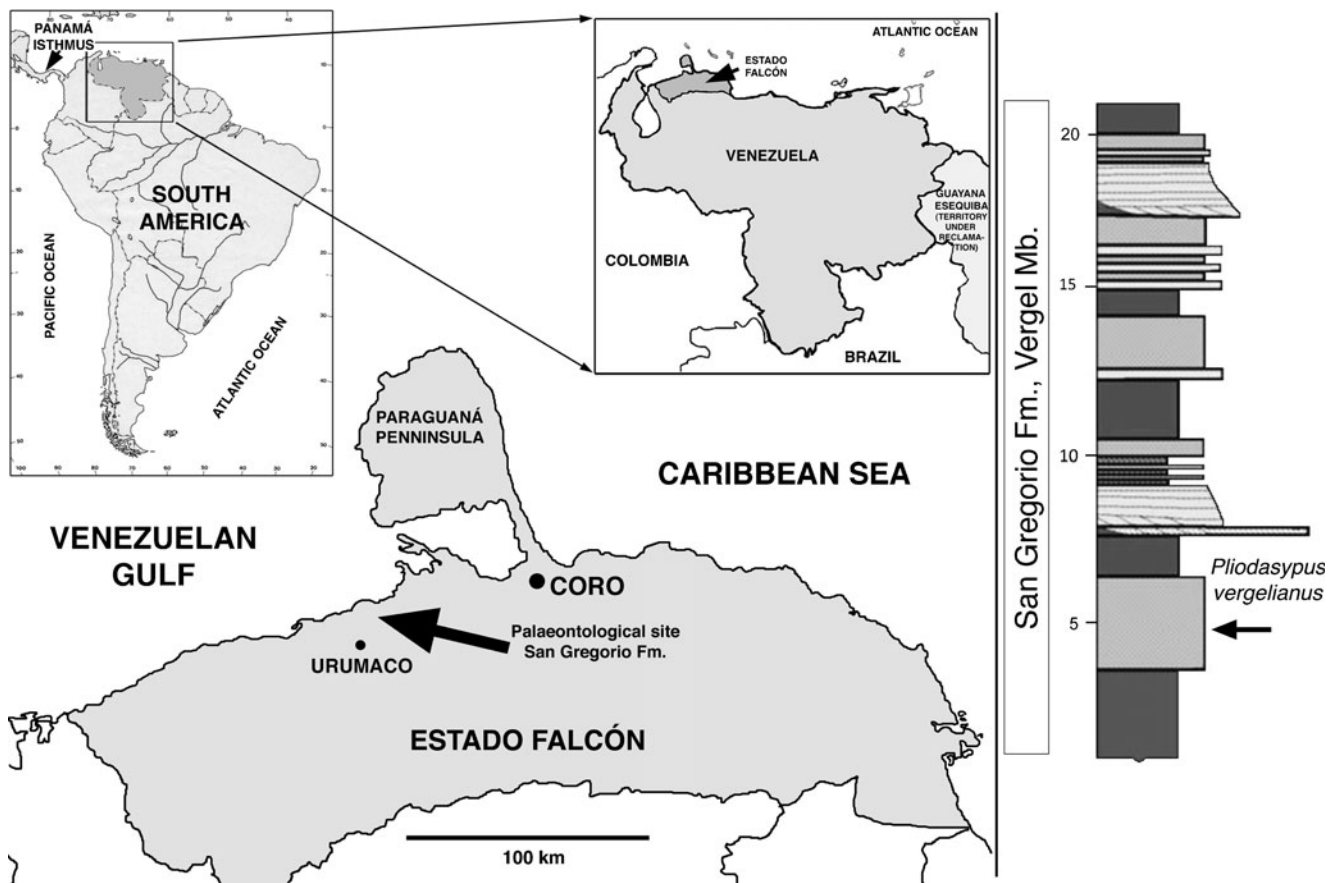
Chapadmalalan and the Uquian/Marplatan SALMAs (approximately between 3.4 and 2.5 Ma), slightly before or contemporaneous to the cohesive dispersal of South American immigrants to North America during the late Blancan NALMA (ca. 2.7 Ma) (Cione and Tonni 2001; Flynn et al. 2005; Woodburne 2010). Thus, we consider that the main phase (in terms of diversity and frequency of findings) of GABI began at 2.7 Ma, as it represents the oldest records of continuous bidirectional flux of land mammals without discretionary selectivity. *D. bellus* is one of the xenarthrans assumed to be involved in this phase of the GABI (Morgan 2005; Woodburne 2010), rapidly dispersing in USA during the late Blancan. Despite advances on glyptodonts and, in less extent, on pampatheres (Scillato-Yané et al. 2005; Carlini et al. 2008a, b; Carlini and Zurita 2010; Zurita et al. 2011), the role of dasypodids in the GABI is still poorly known.

Carlini and Zurita (2010, p. 240) reported remains of Dasypodinae in the San Gregorio Formation, Pliocene of Venezuela, provisionally related to *Propraopus*. The present contribution aims to describe these osteoderms and to compare them to related taxa. Their unique morphology serves to diagnose a new Dasypodini (*Pliodasypus vergelianus*).

## Material and methods

The three specimens were collected in the Urumaco area, Estado Falcón, Venezuela (11°17' N, 70°13' W; Fig. 1), in sediments of the Vergel Member, the 350-m-thick lower member of the San Gregorio Formation, below the Cucuiza Member and above the Algodones Member of the Codore Formation (Stainforth 1962; Scheyer et al. 2013). Rey (1990) established that the delimitation of its three members is only possible between the Urumaco or Codore rivers on the west and the Quebrada El Paují on the east. The depositional environment is interpreted as an alluvial plain, with braided rivers, under subhumid conditions (Rey 1990). The stratigraphic position, the absence of Holarctic taxa, and the fauna present in the unit indicate a middle Pliocene age, about 3.5 Ma, chronologically earlier than the main phase of the GABI (González de Juana et al. 1980; Rey 1997; Zurita et al. 2011).

The comparisons with related taxa were based on direct observation of specimens housed in several institutions (Figs. 2 and 3 and Appendix 1). The terminology adopted for the osteoderms corresponds to that of most recent publications on dasypodids (Hill 2006; Krmpotic et al. 2009; Ciancio et al. 2012; Castro et al. 2013a). In the case of *D. bellus*, as it shows an increment on size along its chronologic distribution (Blancan–Rancholabrean NALMAs; McDonald 2005), we focused our analysis on the older remains (Blancan). We assume that *Propraopus* has a single species, *Propraopus sulcatus*, which is synonymous to



**Fig. 1** Map showing the locality and stratigraphic log (modified from Scheyer et al. 2013) where the specimens of *Pliodasyptus vergelianus* gen. et sp. nov. were recovered

*Propraopus grandis*, *Propraopus magnus* is still to be addressed (see Castro et al. 2013b).

### Systematic paleontology

Xenarthra Cope, 1889

Cingulata Illiger, 1811

Dasypodidae Gray, 1821

Dasypodinae Gray, 1821

Dasypodini Gray, 1821

*Pl. vergelianus* gen. et sp. nov.

Etymology: “*Plio*,” from the Pliocene; “[*D*]asyptus,” type genus of the family; “*vergelianus*,” from the Vergel Member, San Gregorio Formation, Venezuela

Holotype: Colección de Paleontología de Vertebrados de la Alcaldía de Urumaco, Estado Falcón, Venezuela (AMU-CURS) 192A, a complete buckler osteoderm

Paratypes: AMU-CURS 192B and C, a buckler and a partial movable osteoderms, respectively. Type series not associated

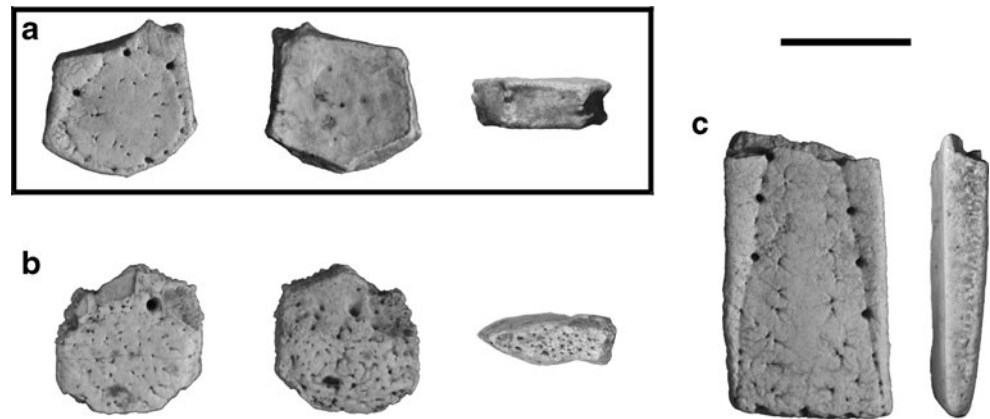
Type locality: Vergel Member, San Gregorio Formation, Estado Falcón, Venezuela (11°17' N, 70°13' W; Fig. 1)

Differential diagnosis: The osteoderms of *Pl. vergelianus* have the following unique combination of characters: in the buckler (i.e., immovable) osteoderm, the flatter and smoother surface of the main figure, the shallower and more external principal sulcus, the smaller foramina, and the absence of the radial sulci (Fig. 2).

### Comparative description

The complete buckler osteoderm is roughly pentagonal on internal view, whereas externally, it is rounded on the posterior border and on the left side of anterior border, where the preceding osteoderm articulated (Fig. 2a). The main figure is smooth and flat; it bears small circularly disposed neurovascular foramina, some of which are sided by fine wrinkles. The principal sulcus is shallow, displaced posteriorly almost until the margin, and it is more external than in other Dasypodini. Radial sulci are absent. The peripheral region is slightly elevated in the anterior and in the left side. There are three foramina in the anterior half of the principal sulcus, and a single one is the posterior half, besides several smaller ones all over the sulcus (Fig. 2a). The maximum measurements

**Fig. 2** *Pliodasypus vergelianus* gen. et sp. nov.: **a** buckler osteoderm, holotype; **b** posterior pelvic buckler osteoderm; **c** partial movable osteoderm

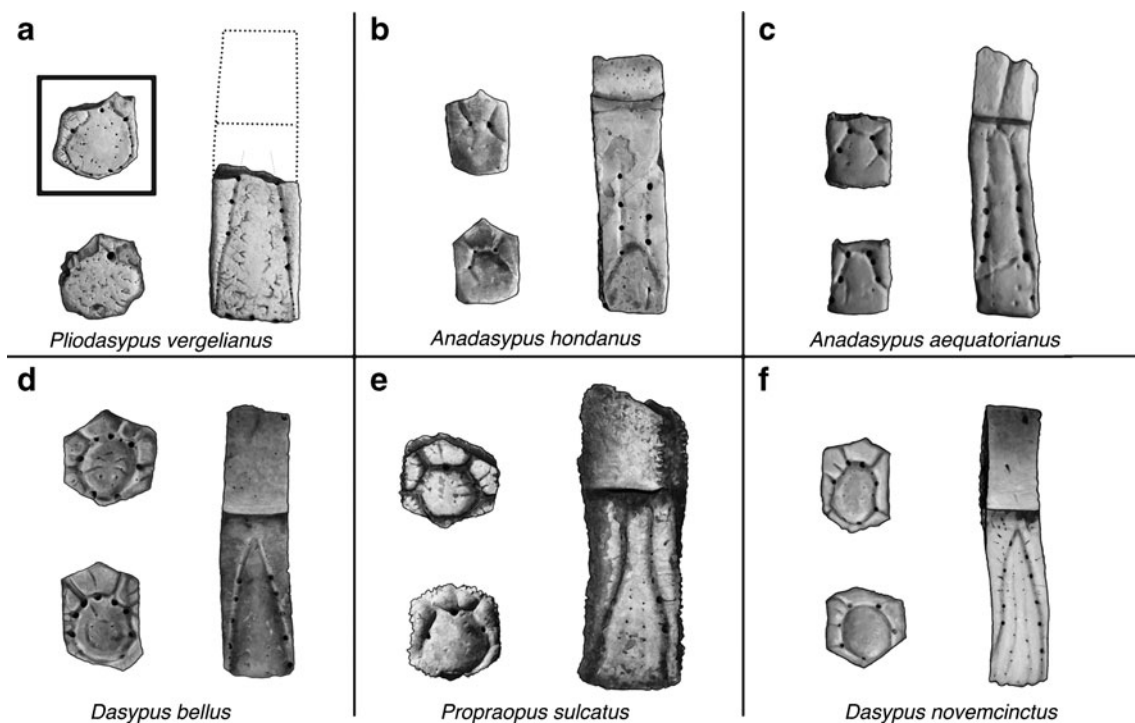


(millimeters) are 12.4 long, 12.2 wide, and 4.2 thick. It means that the size is in the range of *Pr. sulcatus* and *D. bellus*. The remarkable differences of *Pl. vergelianus* are the flatter and smoother surface of the main figure, the shallower and more external principal sulcus, the smaller foramina, and the absence of the radial sulci (Fig. 3).

The other buckler osteoderm (Fig. 2b) has a wedge-shaped posterior end and an articulation on the internal surface. This morphology is compatible with the elements of the posterior border of the pelvic buckler, which contact the caudal sheath, as can be observed in extant *Dasypus*. The principal sulcus is restricted to the lateral and anterior borders, running very close

to the formers; there is a single foramen anteriorly. The main figure has several small neurovascular foramina which are randomly distributed (Fig. 2b).

The movable osteoderm (Fig. 2c) lacks the entire non-ornamented portion and part of the ornamented portion. The posterior end is 12.7-mm wide. As in *Dasypus* and *Propraopus* (but not in *Anadasypus*; Fig. 3), the main figure is completely flat and bears two divergent sulci that end in the posterior corners; the difference of *Pl. vergelianus* is that the sulci are shallower (Fig. 3). It preserves three and four foramina on the left and right sulci, respectively. The presence of small neurovascular foramina in the main figure is also



**Fig. 3** Drawings of buckler and movable osteoderms of the main taxa considered in the comparisons (not to scale): **a** *Pliodasypus vergelianus* gen. et sp. nov., holotype inside the square; **b** *Anadasypus hondanus*; **c**

*Anadasypus aequatorianus*; **d** *Dasypus bellus*; **e** *Propraopus sulcatus*; **f** *Dasypus novemcinctus*

conspicuous in the Dasypodini, and in *Pl. vergelianus*, these are surrounded by fine radial wrinkles. The three piliferous foramina in the posterior border are concentrated in the central part (Fig. 2c). There is no foramen at or close to the posterior corners, whereas *D. bellus* and *Pr. sulcatus* usually have a foramen by the posterior end of at least one sulcus. The texture of the peripheral figure is completely smooth in *Pl. vergelianus*, but this feature is quite variable, as can be depicted from the osteoderms of *Pr. sulcatus* from the late Pleistocene of Venezuela (very wrinkled; Rincón et al. 2008) and of Brazil (smoother; Winge 1915, pl. V). The size is equivalent to that of *Pr. sulcatus* (see Castro et al. 2013b) and to the larger range of *D. bellus*. Table 1 compares *Pl. vergelianus* with the above-mentioned taxa.

### Affinities of *Pl. vergelianus*

In order to test the affinities of *Pl. vergelianus* within Dasypodini, we conducted a cladistic analysis, based on a previous data set (Castro et al. 2013a). In relation to that matrix, one character was excluded (#16 therein) and eight new characters (#18 to 25) and three new taxa were added, as well as information on the skull of *A. hondanus*. Fernicola and Porpino (2012) evaluated the use of exoskeletal characters (i.e., related to carapace and osteoderms) in cladistic studies of glyptodonts and concluded that they “bear levels of homoplasy similar to those of the endoskeleton and there is no reason to exclude them from the process of phylogenetic inference or to consider them as the sole source of reliable phylogenetic signal.” Thus, as most morphological phylogenies of Cingulata, our study adopts characters related to both endoskeleton and exoskeleton. Twenty-five characters, 10 related to the cranial anatomy and 15 to the osteoderms, were scored based on direct observation of specimens (Appendix 1) for 10 ingroup taxa. These are the extinct *Pl. vergelianus*, *A. hondanus*, *A. aequatorianus*, *Pr. sulcatus*, *Dasypus punctatus*, *D. bellus*, and the extant *Dasypus hybridus*,

*Dasypus kappleri*, *D. novemcinctus*, and *Dasypus septemcinctus* (Appendixes 2 and 3). The outgroup is represented by *Nanoastegotherium prostaticum*, from the middle Miocene of La Venta, Colombia; it was selected because it represents the last known record of Astegotheriini and shows similarities with the oldest Dasypodini (*A. hondanus*), which was also recorded from La Venta (Carlini et al. 1997). Although previous phylogenetic studies that do not include astegotherines found *Stegotherium* and *Dasypus* to be sister taxa (Engelmann 1985; Abrantes and Bergqvist 2006; Gaudin and Wible 2006), *Stegotherium* has an extremely derived carapace, precluding adequate comparisons with the ingroup (see Castro et al. 2013a).

Under a maximum parsimony criterion, an exact analysis was conducted with TNT 1.1 (Goloboff et al. 2008). Treating multistate characters as nonadditive, six most parsimonious trees (MPTs) were found (score 37); these differ on the relationships among the species of *Dasypus*. The strict consensus is given in Fig. 4, which also shows the estimated chronological distribution of taxa (black rectangles), the apomorphic characters (numbers assigned in Appendix 2), and the difference in frequency bootstrap values (GC, 1,000 replicates under implicit enumeration search); the GC (for “group present/contradicted”) measures the support as the difference in frequency between the group and its most frequent contradictory group in order to avoid problems in interpreting absolute group frequencies as a measure of support (see Goloboff et al. 2003).

The strict consensus tree reveals that *Pl. vergelianus* groups with *Dasypus* (supported by character 11[1]; GC 45); both genera are sister taxa of *Propaopus* (supported by characters 19[1], 20[1], 22[1]; GC 67), and *Anadasypus* is at a basal position in the tree (supported by character 21[1]; GC 67). Characters 24 [1] and 25[1] represent the autapomorphies of *Pl. vergelianus*. The relatively low bootstrap values (between 45 and 67) might be related to the great amount of missing entries in our analysis, a common problem of phylogenetic studies with incomplete taxa (Kearney and Clark 2003). With

**Table 1** Comparison of osteoderms of *Pliodasypus vergelianus* with other fossil Dasypodini

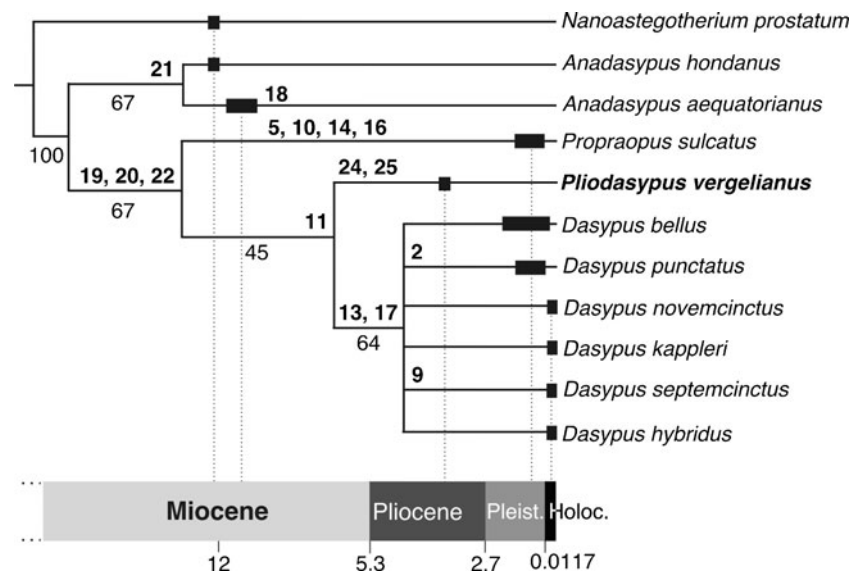
	Age	Foramina		Max. width	
		<i>B</i>	<i>M</i> (ps; pb)	<i>B</i>	<i>M</i>
<i>Pl. vergelianus</i>	Mid-Pliocene (~3.5–3.0 Ma)	4, all over	7 <sup>a</sup> ; 3	12.2	12.7
<i>D. bellus</i>	Late Pliocene–late Pleistocene (2.4 Ma–11 ka); Blanc–Ranch	3–6 (4), all over	5–18 (10); 1–4 (2)	11.1	10.1
<i>Pr. sulcatus</i>	Pleistocene–early Holocene; Ens–Luj	1–5 (3), anterior half	2–8 (4); 1–3 (2)	13.5	13.7
<i>A. hondanus</i>	Mid–late Miocene; Lav	2–5 (3), anterior half	5–7 (6); 0–2 (1)	6.5	7.0

Maximum width in millimeters

*B* buckler osteoderm, *Blanc* Blancan, *Ens* Ensenadan, *Lav* Laventan, *Luj* Lujanian, *M* movable osteoderm, *pb* posterior border, *ps* principal sulcus, *Ranch* RanchoLabrean

<sup>a</sup> Estimated

**Fig. 4** Strict consensus tree resulting from the cladistic analysis of Dasypodini: estimated chronological distribution of taxa represented by *black rectangles*; apomorphic characters (*boldface*, above the branches) are represented by the numbers assigned in Appendix 2; difference in frequencies bootstrap values (*GC* for group present/contradicted, below the branches; Goloboff et al. 2003) calculated with 1,000 replicates



multistate characters treated as additive, eight MPTs were found (score 39); the topology of their strict consensus tree differs from that presented on Fig. 4 by grouping *D. septemcinctus* and *D. hybridus*.

Despite the scarce remains, *Pl. vergelianus* shows a combination of characteristics not found in other Dasypodini that indicate it represents a new genus. This is corroborated by the phylogenetic analysis, as *Pl. vergelianus* is clustered within neither *Dasypus* nor *Anadasypus*, nor does it have a sister-taxon relationship with the monotypic *Pr. sulcatus*. *Pl. vergelianus* shares more similarities with *Dasypus* and *Propraopus* than with the basal *Anadasypus* and was grouped with the former in the cladistic analysis. With the *Dasypus* clade, *Pl. vergelianus* shares the presence of the foramina all over the principal sulcus of buckler osteoderms.

## Discussion

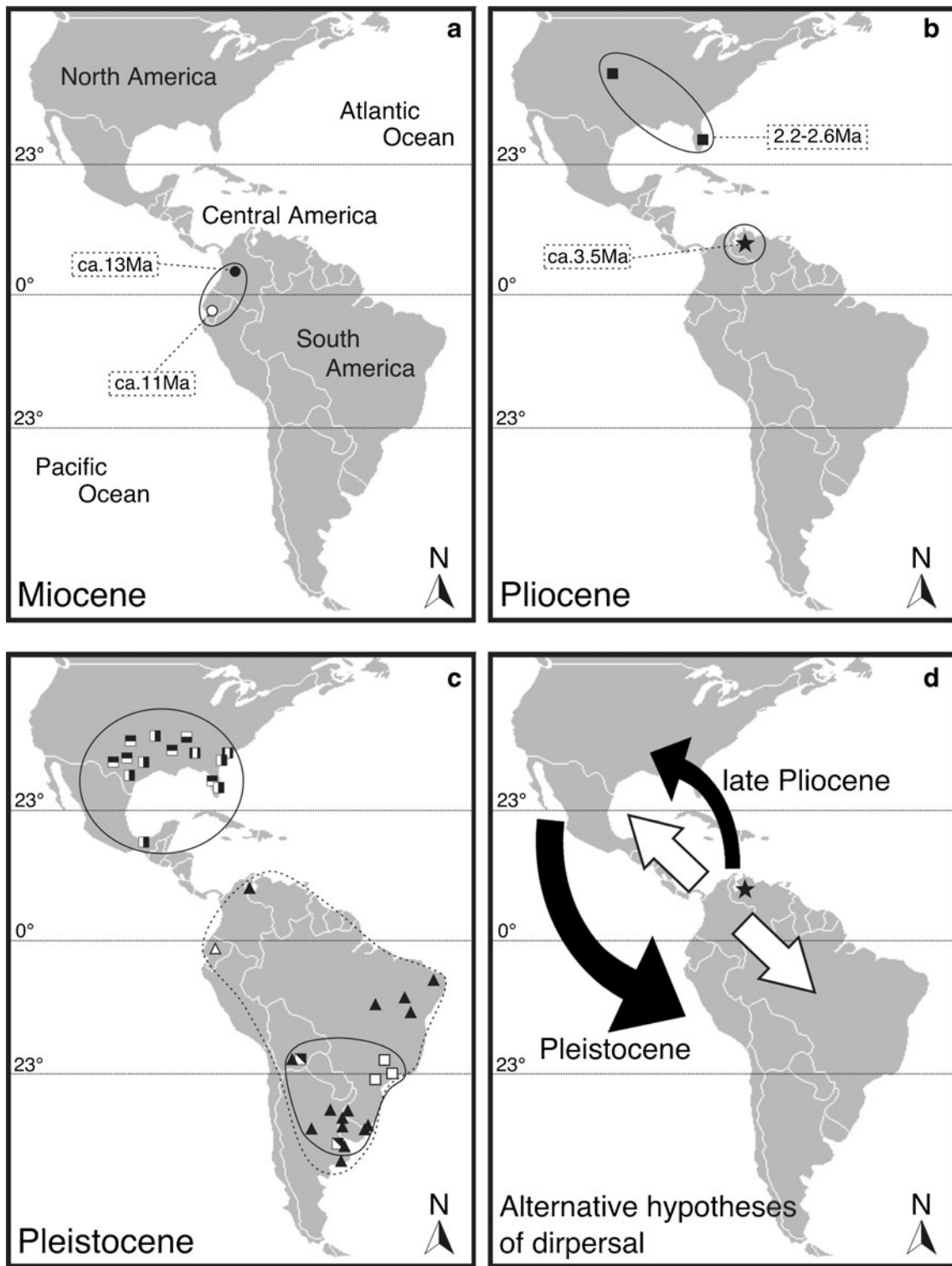
Although not numerous, the remains presented herein are especially relevant because of their geochronologic context (Fig. 5). The remarkably poor knowledge of Pliocene faunas of northern South America is due, in part, to the lack of fossils chronologically close to the first continuous connection between South and North America (Vucetich et al. 2010; Zurita et al. 2011).

Living dasypodids show greater diversity in intertropical forests and savannas (Wetzel 1985). Also, extant *Dasypus* has a temperature-limited distribution (McNab 1980). It led to the hypothesis that their major cladistic events, including the origin and diversification of Dasypodini, took place within tropical environments of South America (Scillato-Yané 1986; Vizcaíno 1990; Carlini et al. 2010; Ciancio et al. 2012). The location of the oldest members of the tribe (*A. hondanus* and

*A. aequatorianus*) and the discovery of *Pl. vergelianus* at low latitudes corroborate this hypothesis.

In relation to the species of *Dasypus*, *Pl. vergelianus* has more similarities with *D. bellus* (size, number of foramina in the osteoderms; Fig. 3 and Table 1), agreeing with their greater geographic and temporal proximity. It suggests that the lineage of Dasypodini that participated in the GABI was closely linked with the taxon described herein. The same relationship between the Pliocene taxon from northern South America (Venezuela) and the lineage that dispersed and diversified in North America was proposed for the Glyptodontinae (Zurita et al. 2011). Additionally, a rapid entrance and dispersion is assumed to this group, which reached as far north as 37° during the Blancan (ca. 2.6 Ma; Carlini et al. 2008a); it was probably also the case of *Dasypus*, based on the oldest records of *D. bellus*.

The oldest well-dated sites containing *D. bellus* are 2.2–2.6 Ma (late Blancan), in Florida and Nebraska, whereas the youngest records are about 8 ka (Robertson 1976; Voorhies 1987; Morgan 2005; Webb 2006). In South America, genus *Dasypus* has a record in the late Miocene of Argentina (*Dasypus neogaeus*, “Mesopotamian,” Huayqueriense SALMA; Scillato-Yané 1980; Scillato-Yané et al. 2013), but this is based on a single movable osteoderm (MACN A 8882) that may have come from upper (Pleistocene) deposits of the profile. Besides this dubious occurrence, the oldest records of the genus are *D. punctatus*, in the late Pleistocene of southeastern Brazil (Castro et al. 2013a), and *D. novemcinctus*, from the Pleistocene of Argentina and Bolivia, in “undetermined Pleistocene units” (Scillato-Yané 1980), probably Lujanian. In North America, the oldest record of *D. novemcinctus* is about 3 ka ago in the USA (Robertson 1976). With respect to genus *Propraopus*, its oldest certain record is in the middle Pleistocene of Argentina (Ensenadan SALMA), but it might occur in the Pliocene (Chapadmalalan; Scillato-Yané 1980).



**Fig. 5** Geochronological distribution of Dasypodini: **a** Miocene; **b** Pliocene; **c** Pleistocene; **d** alternative hypotheses of dispersal. Each genus is represented by a symbol and has the distribution contoured (discontinuous for *Dasypus* in the Pleistocene because of the wide geographic gap). ● for *Anadasypus hondanus*, ○ for *Anadasypus aequatorianus*, ★ for

*Pliodasypus vergelianus*; ▲ for *Propraopus sulcatus*, △ for *P. magnus*; ■ for Blancan *Dasypus bellus*, ■ for Irvingtonian *D. bellus*, ■ for Rancholabrean *D. bellus*, ■ for Pleistocene *D. bellus*, □ for *D. punctatus*, and ▣ for *D. novemcintus*

Therefore, after the oldest records of Dasypodini (*A. hondanus*, middle Miocene of Colombia, ca. 13 Ma;

*A. aequatorianus*, late Miocene of Ecuador, ca. 11 Ma; Fig. 5a), there is a time lapse of about 7 Ma without any

occurrence of the tribe, until the record of the taxon described herein (*Pl. vergelianus*, middle Pliocene, ca. 3.5 Ma). The subsequent record is *D. bellus* in higher northern latitudes (USA, late Pliocene, Blancan NALMA, ca. 2.4 Ma; Fig. 5b). The following records are widespread in the Pleistocene: *Propraopus* (Ensenadan to Lujanian SALMAs, ca. 1 Ma–8 ka), *D. punctatus* and *D. novemcinctus* (Lujanian SALMA; Ensenadan records are uncertain) in South America, and *D. bellus* in USA (Irvingtonian to Rancholabrean NALMA) and Mexico (Rancholabrean NALMA) (Fig. 5c).

Based on these records and on the cladogram presented on Fig. 4, we can infer that *Dasyopus* differentiated in the late Pliocene, ca. 3.5 Ma ago (the minimal age of the node encompassing *Dasyopus* and *Pliodasyopus*), at low latitudes in northern South America. Based on a  $11 \pm 2$ -Ma estimated divergence date between *D. novemcinctus* and *D. kappleri*, Delsuc et al. (2012) proposed that the origin of *Dasyopus* must have occurred in the late Miocene, soon after the appearance of *Anadasyopus* (*A. hondanus*), contrasting with the fossil evidence available. As *Dasyopus* is the only living representative of its tribe, and therefore the only Dasyopodini sampled by Delsuc et al. (2012) in their molecular timetree, we can interpret that in fact the divergence date presented by those authors represents the emergence of tribe Dasyopodini (and this adequately fits the known fossil record).

We offer two alternative hypotheses on how *Dasyopus* dispersed after its emergence in northern South America. In the first one, some early *Dasyopus* remained in South America, leaving no fossils until the Pleistocene, whereas others dispersed to North America between 2.7 Ma (which represents the beginning of the main phase of GABI) and 2.2 Ma (younger limit of the estimated age of the oldest records of *D. bellus*) (Fig. 5d, white arrows). In the other hypothesis of dispersal, it entered North America subsequently to the emersion of the Panama isthmus and *D. bellus* differentiated there; later, during the Pleistocene, *D. bellus* entered South America and experienced speciation then (Fig. 5d, black arrows). The same process of emigration from South America during the mid/late Pliocene, diversification in North America, and re-ingression into South America during the Pleistocene was proposed for pampatheres (Scillato-Yané et al. 2005), glyptodonts (Carlini et al. 2008a; Carlini and Zurita 2010; Zurita et al. 2011), and some pilosans (Carlini et al. 2006; Carlini et al. 2008c), breaking with the traditional assumption that the GABI for the xenarthrans was a unidirectional process in which they simply dispersed from South to North America. Without further fossil evidence and/or more resolution on the internal relationships of *Dasyopus*, a better evaluation of both hypotheses of dispersal is unfeasible, as they are equally parsimonious.

The ingression of the immigrant taxa in South America was a gradual process: their relative abundance and diversity is low in the 3.9–1.8-Ma interval (Chapadmalalan and Uquian/

Marplatan SALMAs) and increases in the earliest Pleistocene, about 1.7 Ma (Tonni et al. 1992; Cione and Tonni 2001). If *Dasyopus* entered South America in the early Pleistocene, the gap until its oldest records (late Pleistocene) is smaller. Additionally, the widespread distribution of *Dasyopus* and *Propraopus* in the South American Pleistocene must have been facilitated by the great latitudinal expansion of grasslands during glacial periods, probably forming a biogeographic corridor that ranged from northern South America to the current Argentinean Pampean region (Cione et al. 2003; Rabassa et al. 2005; Ortiz-Jaureguizar and Cladera 2006; Carlini and Zurita 2010). Certainly, future findings in Pliocene sediments of northern South America and Central America will greatly clarify the evolutionary history of Dasyopodini.

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