The Xenarthra (Mammalia) of São José de Itaboraí Basin (upper Paleocene, Itaboraian), Rio de Janeiro, Brazil

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KEY WORDS
Mammalia,
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Riostegotherium,
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armadillo,
osteoderm,
appendicular skeleton.

ABSTRACT

Here we present new information on the oldest Xenarthra remains. We conducted a comparative morphological analysis of the osteoderms and postcranial bones from the Itaboraian (upper Paleocene) of Brazil. Several osteoderms and isolated humeri, astragali, and an ulna, belonging to at least two species, compose the assemblage. The bone osteoderms were assigned to *Riostegotherium yanei* Oliveira & Bergqvist, 1998, for which a revised diagnosis is presented. The appendicular bones share features with some "edentate" taxa. Many of these characters may be ambiguous, however, and comparison with early Tertiary Palaeanodonta reveals several detailed, derived resemblances in limb anatomy. This suggests that in appendicular morphology, one of the Itaboraí Xenarthra may be the sister-taxon or part of the ancestral stock of Palaeanodonta.

RÉSUMÉ

Les Xenarthra (Mammalia) du bassin de São José de Itaboraí (Paléocène supérieur, âge itaboraiense), Rio de Janeiro, Brésil.

Nous présentons ici de nouvelles données anatomiques sur les plus anciens restes de Xenarthra. L'essentiel de ce travail porte sur des analyses morphologiques comparées entre les plaques osseuses et les os postcrâniens trouvés à Itaboraí (Paléocène supérieur, Brésil). L'ensemble du matériel se compose de plusieurs plaques osseuses, d'humérus, d'astragales isolés et d'un ulna qui appartiennent à au moins deux espèces. Les plaques osseuses sont attribuées à *Riostegotherium yanei* Oliveira & Bergqvist, 1998, pour lequel une diagnose révisée est proposée. Les os des ceintures partagent des caractères communs à ceux de quelques taxons d'édentés. Pourtant beaucoup de ces caractères sont ambigus et la comparaison avec les Palaeanodonta du début du Tertiaire souligne des ressemblances dans l'anatomie du membre. Ainsi le Xenarthra d'Itaboraí pourrait être le groupe-frère de tout ou partie des Palaeanodonta.

MOTS CLÉS
Mammalia,
Xenarthra,
Cingulata,
Riostegotherium,
Astegotheriini,
Palaeanodonta,
tatou,
ostéoderme,
squelette appendiculaire.

INTRODUCTION

The discovery of osteoderms in Itaboraí was first reported 50 years ago (Paula-Couto 1949), but they were only studied in the mid-1970s by Scillato-Yané (1976), who described two isolated osteoderms, assigning them to *Prostegotherium* aff. *P. astrifer* Ameghino, 1902 a dasypodid from the Casamayoran of Argentina. These osteoderms, together with new material, were later studied by Oliveira & Bergqvist (1998), who considered them distinct from *P. astrifer* as well as from any early Tertiary Patagonian Astegotheriini Vizcaíno, 1994. They proposed a new taxon for this material, *Riostegotherium yanei*, the oldest known cingulate.

Cifelli (1983) described two different tarsals of Itaboraí cingulates, assigning one to a dasypodid and the other to a glyptodontid(?); the latest assignment was questioned by Bergqvist & Oliveira (1998). New xenarthran remains (humeri and ulna), allocated by Bergqvist & Oliveira (1995) to cingulates, were only briefly described by the authors.

In this paper we gather all available information on Itaboraí Xenarthra, providing a broad description and illustrations of the forelimb bones mentioned above, and review the material already described. As the bones and osteoderms were collected separately, and there is no confident information from where they were recovered, no direct association could be made among the bones themselves and between them and the osteoderms. Each bone is thus discussed separately.

The São José de Itaboraí Basin, located in the County of Itaboraí, Rio de Janeiro State, is the oldest (Itaboraian, upper Paleocene) and smallest basin of the Continental Rift of Southern Brazil. The sediments that filled this basin are grouped in two sequences: the lower sequence (S1) is basically composed of interbedded clastic and chemical carbonates that are originated from debris flows in a tectonic lake with hydrothermal fonts. Fossil mollusks are abundant in this sequence. The upper sequence (S2) comprises fissure fill deposits with marls and collapse breccias where abundant fossil vertebrates (specially mammals) were recovered (Medeiros & Bergqvist 1999a). An updated list of the fossils recovered from Itaboraí Basin is provided in Medeiros & Bergqvist (1999b).

ABBREVIATIONS

DNPM LE	Departamento Nacional da Produção Mineral, Lote de Entrada ("entrance lot" – a temporary number sometimes given to a group of fossils before they are cataloged);

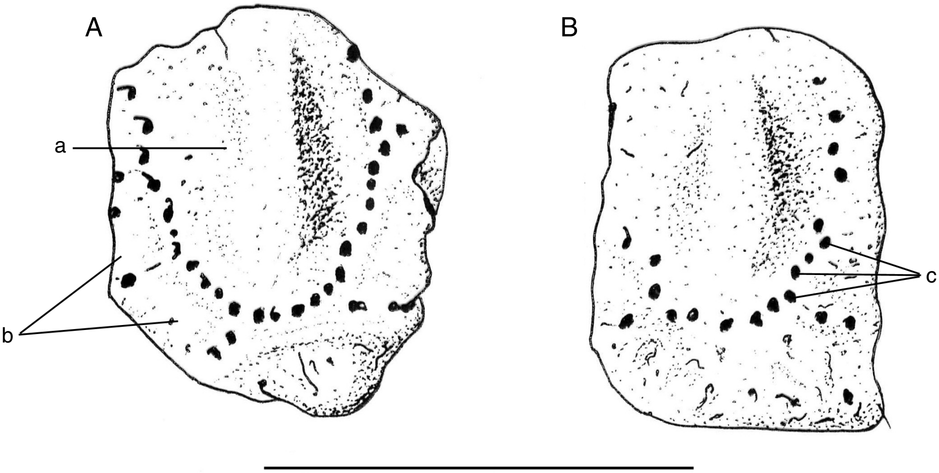

FIG. 1. — *Riostegotherium yanei* Oliveira & Bergqvist, 1998, dorsal view of buckler osteoderms; **A**, holotype (MCN-PV 1774); **B**, MCN-PV 1775; **a**, main figure; **b**, peripheral figures; **c**, pits. Modified from Oliveira & Bergqvist 1998. Scale bar: 1 cm.

MCN-PV	Museu de Ciências Naturais, Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre, RS;
MCT-M (ex-DGM)	Museu de Ciências da Terra, Departamento Nacional de Produção Mineral, Rio de Janeiro, RJ;
MLP	Museo de La Plata, La Plata;
UFRJ-DG-M	Departamento de Geologia, Universidade Federal do Rio de Janeiro, RJ.

SYSTEMATICS

XENARTHRA Cope, 1889
CINGULATA Illiger, 1811
Family DASYPODIDAE Gray, 1821
Tribe ASTEGOTHERIINI Vizcaíno, 1994

Riostegotherium yanei
Oliveira & Bergqvist, 1998

REFERRED MATERIAL. — Buckler osteoderms (MCN-PV 1774 [holotype], 1775); movable osteoderms (MCN-PV 1776, 1778, 1779, MCT 2081-M, MLP 75-XII-26-1, MLP 75-XII-26-2, UFRJ-DG 317-M); caudal osteoderm (MCN-PV 1777).

DIAGNOSIS (emended from Oliveira & Bergqvist 1998). — Differs from all known early Tertiary astegotheriines in having more than 10 pits in the groove around the main figure on buckler osteoderms (25 pits on the holotype, MCN-PV 1774; and 16 pits on MCN-PV 1775).

DESCRIPTION

The former description of the osteoderms (Oliveira & Bergqvist 1998) is partly repeated here, with additions and comments. No articulated osteoderms were preserved. The buckler osteoderms are larger than the movable ones, sub-rectangular in shape and bear more than 10 pits in the groove around the main figure (Fig. 1). In comparison with buckler osteoderms of other astegotheriines, *Riostegotherium yanei* has the largest number of foramina for the tribe. The lateral and medial borders are slightly concave and smooth. The anterior and posterior borders are irregular; the posterior has a U shaped concavity when viewed internally. The anterior border has a small, weakly defined articulation zone. The external surface is very punctated and bears fine irregularities; in combination with the presence of small depressions, these irregularities give the surface a slightly wrinkled appearance, as in *Prostegotherium* Ameghino, 1902 and *Stegosimpsonia* Vizcaíno, 1994. The main figure has an inverted U-shape, with a subcircular anterior

FIG. 2. — *Riostegotherium yanei* Oliveira & Bergqvist, 1998, dorsal view of a movable osteoderm (UFRJ-DG 317-M). Scale bar: 1 cm.

outline, and covers almost the whole osteoderm surface, a very characteristic feature of some genera of the tribe (*Prostegotherium*, *Astegotherium* Ameghino, 1902, *Stegosimpsonia* and *Nanoastegotherium* Carlini, Vizcaíno & Scillato-Yané, 1997). It is limited by a shallow groove with 16 to 25 pits. Although the anterior outline of the main figure varies slightly, it is never triangular as in some Astegotheriini. Its U-shape is very similar to the osteoderms of *Prostegotherium* and *Nanoastegotherium*. Two to four small peripheral figures are present, limited by shallow radial grooves with at least two pits, as in *Prostegotherium*. A well developed central keel is present on the external surface of the main figure, noted by Vizcaíno (1994) as one of the synapomorphies of Astegotheriini. The internal surface of the osteoderms is smooth and slightly concave. No foramina of the piliferous system are observed in the posterior border.

The typical movable osteoderms vary in shape, ranging from sub-quadrangular to sub-rectangular (Fig. 2), which is characteristic of Dasypodidae. The anterior articular surface is poorly developed, and the external surface resembles that of the buckler osteoderms. The main figure has a subcircular anterior outline, but with a reduced number of pits (seven to 12) which is similar to *Prostegotherium* and *Stegosimpsonia*. The external surface also bears a well developed central keel. No foramina are present on the posterior border. The internal side of the posterior border is moderately inclined toward the edge of the osteoderm.

The shape of the osteoderm MCN-PV 1777 resembles caudal osteoderms of the extant dasypodid *Dasypus*. It differs from typical movable osteoderms in: articular surface more developed laterally, smoother external surface, pits more widely spaced in the groove limiting the main figure, and a sharp posterior border.

XENARTHRA *incertae sedis*

REFERRED MATERIAL. — Humeri (MCN-PV 1780, 1781, MCT 2396-M, 2397-M); ulna (MCN-PV 3606); astragali (MCN-PV 1340, 1380, MCT 2394-M, 2395-M).

DESCRIPTION

Humeri (MCN-PV 1780, 1781, MCT 2396-M, 2397-M)

The humeri can be separated into two morphotypes, slightly distinct in shape but clearly distinct in size.

The larger humeri (MCT 2396-M, 2397-M – HUM-morph 1) are powerfully built (Figs 3; 4). The head has an elliptical outline and is more posteriorly directed than dasypodids, in a way similar to *Manis pentadactyla* Linnaeus, 1758. The articular area for the scapular acromion, a very characteristic feature of fossorial armadillos, is shallow. As in other xenarthrans, the shaft is flat and wider than deep in its proximal half. The greater tuberosity is higher than the lesser (but not projected above the head), but less transversely expanded. There are well marked impressions for the *infraspinatus* and *subscapularis* muscles on the greater and lesser tuberosities, respectively. The tubercle for insertion of the *teres major* and *latissimus dorsi* muscles is more prominent than in any known Xenarthra, although less than in *Metacheiromys* Wortman, 1903, and is placed at the level of the deltoid tuberosity, as in this genus. These two muscles are frequently well developed and fused in burrowers, in which they have an important digging function (Reed 1951 *apud* MacPhee 1994; MacPhee 1994). The bicipital groove differs from that of any known "edentate" in being wide, shallow and well defined in the proximal third of the shaft. A similar condition is present in most pilosans and some derived cingulates, but the groove is not as defined in the shaft as in the Itaboraí humeri. The deltopectoral crest, as in *Eurotamandua* Storch, 1981, *Palaeanodon* Matthew, 1918 and *Metacheiromys* is broad, shelf-like and extends more than halfway down the shaft, unlike the condition in most dasypodids. In *Priodontes* and *Cabassous* McMurtrie, 1831, the deltopectoral crest is quite longer but not as robust as in the Itaboraí humeri. However, they form a derived monophyletic group (Priodontina *sensu* Abrantes 2002), and this feature may represent a new acquisition compared to the pattern observed in other cingulates. The shelf is proximodistally concave, but transversely concave only on the distal half; its outline is very close to that of *Palaeanodon ignavus* Matthew, 1918 (Rose 1999: figs 2, 3). Unlike Dasypodidae, the medial (pectoral) border of the crest overhangs the shaft. This is a distinctive feature of palaeanodonts, even though the pectoral tuberosity is more marked. It is distal to the deltoid tuberosity, which is also well marked, but more distally located on the lateral border than in *Eurotamandua* and palaeanodonts. As in palaeanodonts, manids and *Eurotamandua*, but unlike xenarthrans, the deltopectoral shelf is anteromedially oriented.

The distal extremity is incomplete in both specimens, but its preserved portion suggests that the distal end was very broad transversely, more than in most Xenarthra currently known, with the possible exception of *Priodontes*. The entepicondyle is prominent, a typical feature of "edentates" (Rose 1999). A small portion of the supinator crest is preserved in specimen MCT 2397-M, showing that it was very prominent, probably like *Eurotamandua* and palaeanodonts. Its shape recalls *Palaeonodon ignavus* (Rose 1999) in having a straight border parallel to the shaft. However, its proximal end forms an angle of almost 90° with the proximodistal axis of the shaft, and is straighter than in *P. ignavus*. *Tamandua* Gray, 1825 also presents a straight supinator crest, but it is considered here a parallelism, as this genus is a derived Myrmecophagidae, which is a derived group within Xenarthra (Gaudin & Branham 1998).

The other humeri (MCN-PV 1780, 1781 – HUM-morph 2) are shorter than HUM-morph 1 (Fig. 5). They are very similar to morphotype 1, except in having the tuberosities more equally developed and transversely expanded, and the tuberosity of the *teres major* muscle less prominent. Compared to morphotype 1, the deltoid tuberosity is more proximal, less projected, more rounded and rougher.

Ulna (MCN-PV 3606)

The ulna, like the smaller humerus, is gracile (Fig. 6). Only the proximal portion is preserved. The olecranon process, like that of *Dasypus* Linnaeus, 1758, is straight and long, with a broad and medially inflected epiphysis, in the same way as in some Dasypodidae. The enlargement and inflection of the olecranon is associated with great enlargement of the triceps muscles, and perhaps also the digital flexor (K. Rose pers. comm.), which powerfully extend the forearm during the power stroke of digging (Puttick & Jarvis 1977 *apud* Rose & Emry 1983). The medial surface of the olecranon is concave and the lateral is flat, but from the trochlear notch to the distal preserved portion, it bears a deep and narrow concavity. The trochlear notch is shallow and very similar in orientation to that of *Proeutatus* Ameghino, 1891. The anconeal process is little

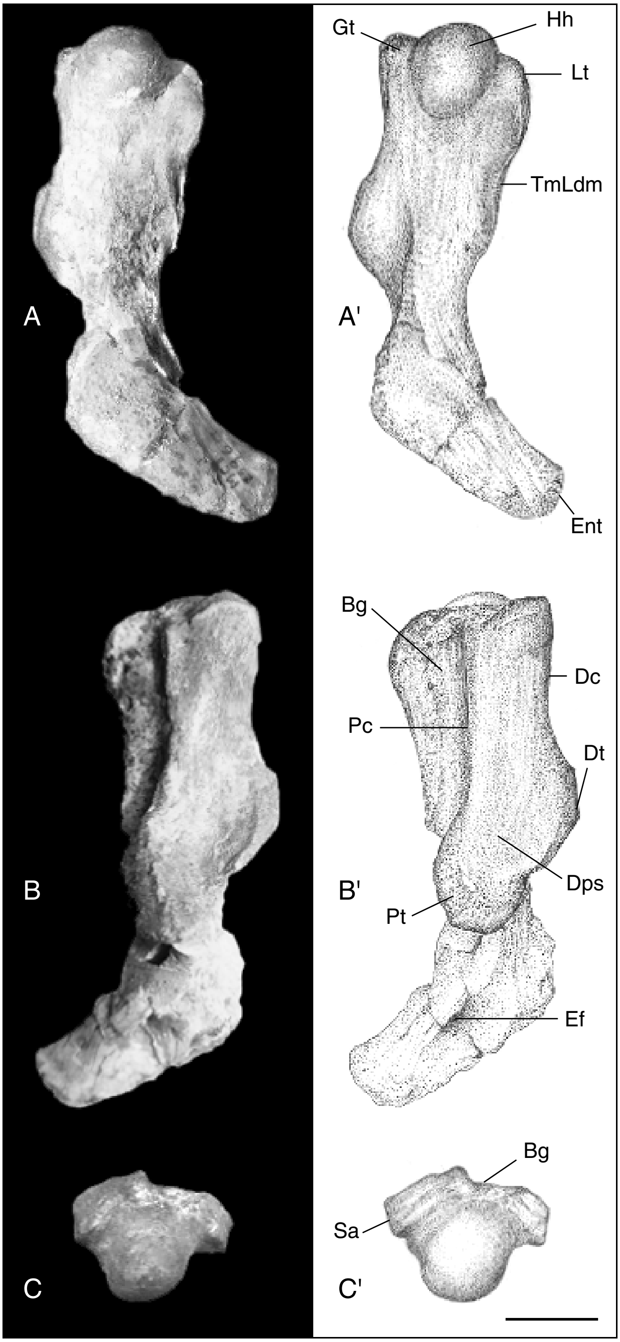

FIG. 3. — Xenarthra *incertae sedis*, left humerus (MCT 2396-M); **A**, caudal view; **B**, cranial view; **C**, proximal view; **A'**, **B'** and **C'**, interpretive drawings of the specimen. Abbreviations: **Bg**, bicipital groove; **Dc**, deltoid crest; **Dps**, deltopectoral shelf; **Dt**, deltoid tuberosity; **Ef**, entepicondylar foramen; **Ent**, entepicondyle; **Gt**, greater tuberosity; **Hh**, humeral head; **Lt**, lesser tuberosity; **Pc**, pectoral crest; **Pt**, pectoral tuberosity; **Sa**, scapular acromion articulation surface; **TmLdm**, *teres major-latissimus dorsi* muscles. Scale bar: 1 cm.

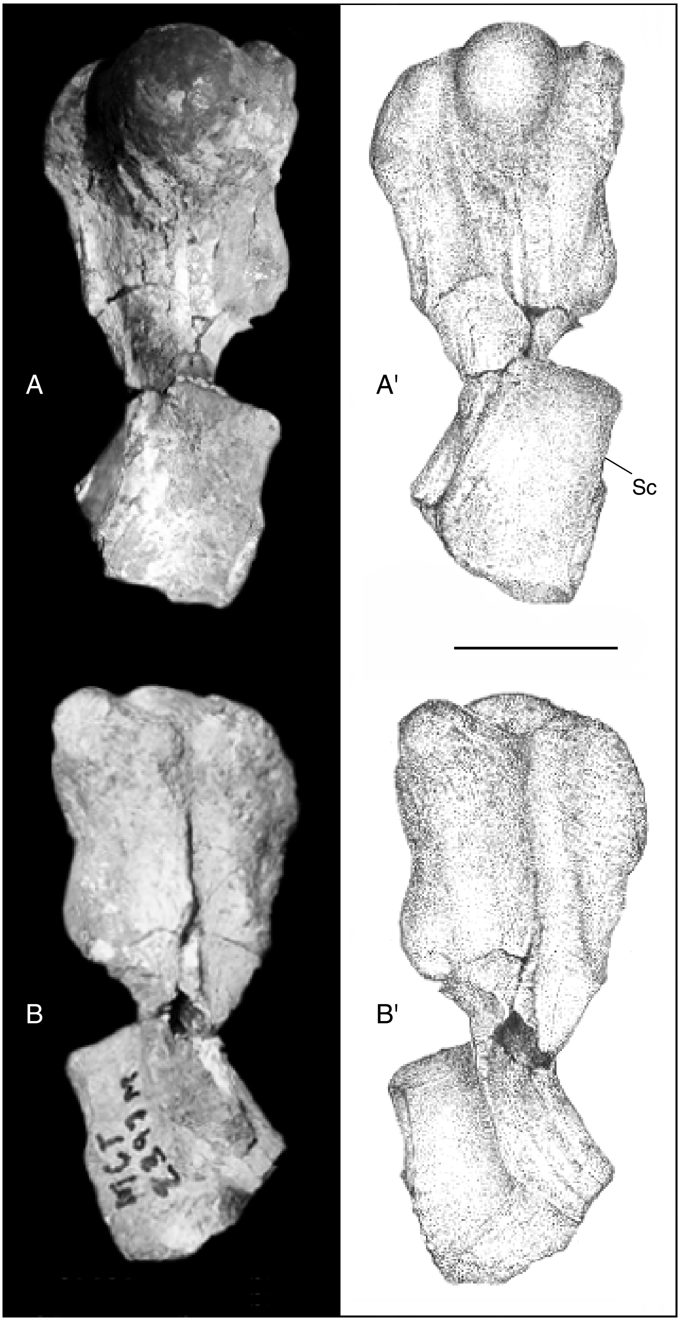

FIG. 4. — Xenarthra *incertae sedis*, right humerus (MCT 2397-M); **A**, cranial view; **B**, caudal view; **A'** and **B'**, interpretive drawings of the specimen. Abbreviation: **Sc**, supinator crest. Scale bar: 1 cm.

projected. The radial facet is comparable to *Tolypeutes*, but with its lateral portion in a more distal position than in this taxon. As in other “edentates”, the ulnar shaft is deeper than wide.

Astragali (MCN-PV 1340, 1380, MCT 2394-M, 2395-M)

There are two different patterns and sizes of astragali (Fig. 7). The larger (MCN-PV 1340, MCT 2395-M – AST-morph 1) is morphologically similar to *Utaetus* Ameghino, 1902. The smaller (MCN-PV 1380, MCT 2394-M – AST-morph 2) in some ways (especially in the shape of trochlea) resembles *Peltephilus* Ameghino, 1887. They were first described by Cifelli (1983), whose description is partially transcribed here with additions provided by two new specimens not seen by this author.

The body of AST-morph 1 is low, transversely broad and anteroposteriorly shortened, as in several cingulates. The trochlea is moderately deep, with the medial crest shorter and less defined than the lateral one, as seen in *Utaetus*. A rugose fossa, possibly a remnant of the superior astragalar foramen, is present posterolaterally on the trochlea. The lateral wall of the astragalar body is vertical, and a small fibular shelf protrudes from the anteroinferior angle of the lateral wall, a very common feature of dasypodids, but less so in other “edentates”. The medial wall bears a discrete protuberance for the medial collateral ligament. Both ectal and sustentacular facets are posterolaterally-anteromedially aligned. The alignment of ectal and sustentacular facets on the same axis of rotation was proposed by Szalay & Schrenk (1998) as a synapomorphy of Xenarthra and Palaeanodonta. The sustentacular facet extends from the poorly defined groove for the digital flexor tendons, which is more distinct from the trochlea in the specimen MCN-PV 1340. Distally, the sustentacular facet touches the navicular facet by a medial prolongation. The ectal facet has the typical triangular shape and concavity of cingulates. It is separated from the sustentacular facet by a developed sulcus tali.

As in other cingulates, but differently from palaeanodonts and pholidotans, the neck is relatively wide, short, shallow and markedly oblique to the anteroposterior axis of the trochlea. A well defined crest occupies the dorsodistal extremity of the neck, which, as in living dasypodids, would have given rise to the astragalonavicular ligament. The head is transversely narrow, as in other dasypodids, and extends posteriorly medially, almost reaching the groove for the digital flexor tendons, as in *Utaetus*, for example.

The AST-morph 2, like morphotype 1, lacks the superior astragalar foramen. The trochlea is deeper than in the AST-morph 1 and strongly constricted, as in *Peltephilus*, *Propraopus* Ameghino, 1881 and most Glyptodontidae, as well as *Myrmecophaga* Linnaeus, 1758. Its lateral border is condyloid and does not extend anteriorly beyond the middle of the astragalus. Both medial and lateral walls of the body are vertical, and the protuberance for the medial collateral ligament is poorly developed in specimen MCT 2394-M. Compared to AST-morph 1, the fibular shelf is more prominent. The ectal and sustentacular facets are placed the same way as in other astragali. The latter facet is rounded and does not contact either the navicular facet or the trochlea (the digital flexor groove is not distinct from the posteroinferior margin of the trochlea). The ectal facet is narrower than morphotype 1 and more concave.

DISCUSSION

The monophyly of Edentata has been subject of discussion since the 18th century. However, from the 20th century on, for most authors Edentata comprises Xenarthra, Pholidota, and Palaeanodonta (e.g., Novacek & Wyss 1986; Patterson *et al.* 1992; Gaudin & Wible 1999). Morphological studies have suggested alternative relationships within Edentata: Palaeanodonta closer to Pholidota (e.g., Emry 1970; Shoshani *et al.* 1997) and Palaeanodonta closer to Xenarthra (e.g., Simpson 1931; Patterson *et al.* 1992; Gaudin & Wible 1999). The clade Xenarthra-Pholidota is an old idea, resurrected by Novacek & Wyss (1986), contrary to Simpson’s (1931,

1945) conclusions that it lacks any definite paleontological support.

Recent molecular cladistic analyses (Waddell *et al.* 1999; Delsuc *et al.* 2001) also failed to support a Xenarthra-Pholidota clade, but proposed different phylogenetic relationships for Pholidota: closer to Carnivora, and included in a higher-taxon called Ferae (DeJong 1982; Waddell *et al.* 1999), and sister-group of Cetartiodactyla (Cetacea + Artiodactyla; Delsuc *et al.* 2001). A detailed taxonomic history of Edentata can be found in Szalay & Schrenk (1998).

The record of mammalian osteoderms in Itaboraí Basin is a clear indication of the presence of Xenarthra-Cingulata, as these bones are exclusive to the group (the osteoderms of some Tardigrada are isolated bony nodules without articular surfaces). Cingulata is considered the most primitive Xenarthra (e.g., Patterson *et al.* 1992), with the Astegotheriini as its oldest member (Vizcaíno 1994; Oliveira & Bergqvist 1998). Until the first recovered cingulates from Itaboraí Basin (Itaboraian), the oldest record of astegotheriines was from the Casamayoran of Argentina, approximately 5 My younger (Scillato-Yané 1976).

The forelimb bones indicate that their owners were proficient diggers. The prominent tubercle for the *teres major* and *latissimus dorsi* muscles and their insertion marks on the humeral shaft suggest that these muscles were well developed and fused (Reed 1951; MacPhee 1994), which corroborates the first argument. Moreover, these humeral features and the well developed olecranon of the ulna reinforce the proposition of well adapted burrowers in the Itaboraí fossil record.

The allocation of the forelimb bones to the Xenarthra would be easy, as they present an expected xenarthran general morphology, and no other "edentates" than Xenarthra are found in South America. These bones show closer similarities with Priodontini (*sensu* McKenna & Bell 1997), but this group is a very derived dasypodid lineage (Engelmann 1985; Abrantes 2002) that appeared recently in the fossil record (middle Pleistocene; McKenna & Bell 1997). So, the similarities observed between the Itaboraí Xenarthra and Priodontini humeri are assumed here as parallelism, as the probability of homoplasy increases with time since divergence from a common ancestor (Simmons & Geisler 1998).

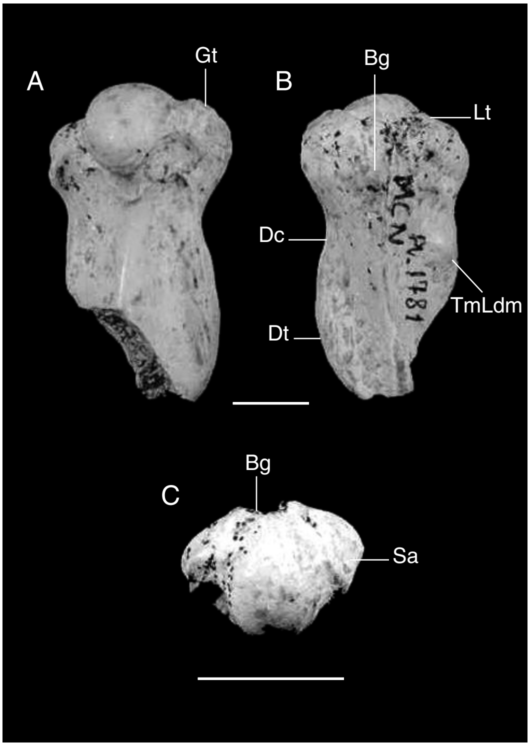

FIG. 5. — Xenarthra *incertae sedis*, right humerus (MCN-PV 1781); **A**, cranial view; **B**, caudal view; **C** proximal view. Abbreviations: **Bg**, bicipital groove; **Dc**, deltoid crest; **Dt**, deltoid tuberosity; **Gt**, greater tuberosity; **Lt**, lesser tuberosity; **Sa**, scapular acromion articulation surface; **TmLdm**, *teres major-latissimus dorsi* muscles. Scale bar: 1 cm.

On the other hand, several features of the Itaboraí forelimb bones are derived attributes shared by other "edentates", mainly Palaeanodonta. This similarity hinges on the medially turned elongation of the pectoral crest (Szalay & Schrenk 1998) and the very prominent supinator crest (Rose & Emry 1993; Rose 1999). This latter feature was indicated as diagnostic for *Metacheiromys* (Palaeanodonta) by Simpson (1931: 342) and it was used to relate *Eurotamandua* and Palaeanodonta (Rose 1999). So we pose the classic question: do these similarities indicate convergences or phylogenetical signals? For Hennig (1966), in cases that it is impossible

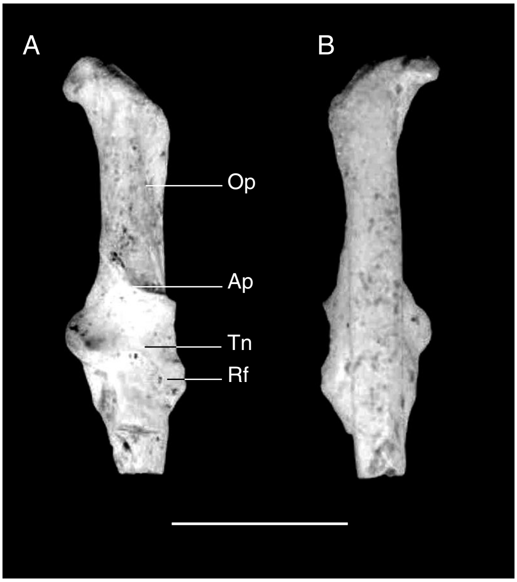

FIG. 6. — Xenarthra *incertae sedis*, left ulna (MCN-PV 3606); **A**, cranial view; **B**, caudal view. Abbreviations: **Ap**, anconeal process; **Op**, olecranon process; **Rf**, radial facet; **Tn**, trochlear notch. Scale bar: 1 cm.

to decide whether the common character is a synapomorphy, parallelism, homology or even a convergence, kinship must be assumed *a priori* (auxiliary principle).

A same problem was raised by Rose (1999) when he analyzed forelimb bones of *Eurotamandua*. In spite of the biogeographical problem, this "edentate" from the lower Eocene of Germany has always been viewed as related to the Xenarthra (Rose & Emry 1993; Storch 1981; Storch & Habersetzer 1991). However, after Shoshani *et al.* (1997), who argued that *Eurotamandua* is a pholidotan and not a xenarthran, several studies were conducted in order to place *Eurotamandua* within Eutheria (Gaudin & Branham 1998; Szalay & Schrenk 1998; Rose 1999). In fact, only Shoshani *et al.* (1997) related *Eurotamandua* to Pholidota. What appears to be a consensus since Rose (1999) is that *Eurotamandua* shows many more detailed similarities to primitive Palaeanodonta than to South American anteaters or any other xenarthrans. Moreover, T. Gaudin & K. Rose (pers. comm.) suggested that *Eurotamandua* belongs or is related to the Palaeanodonta, based on the homology of the features of forelimb elements (including humeri and ulna).

Except for the shallow articular area for the scapular acromion, the Itaboraí humeri do not share other "exclusive" similarity to Xenarthra. Additionally, the ulnar morphology appears to be much more informative on a functional perspective (see Vizcaíno *et al.* 1999), and as noted by MacPhee (1994), all fossorial mammals have similar ulnae (with well developed olecranon). Thus, these humeri from the Paleocene of Itaboraí share several similarities with primitive palaeanodonts than to South American anteaters or any other xenarthrans.

It should be emphasized that the resemblances observed here between the humeri from the Paleocene of Itaboraí and those of palaeanodonts are suggestive of a closer affinity between xenarthrans and paleonodonts. This hypothesis meets the conclusion of several authors that had recently suggested that palaeanodonts are more closely related to xenarthrans than to pholidotans (Storch & Habersetzer 1991; Patterson *et al.* 1992; Szalay & Schrenk 1994, 1998; Gaudin & Branham 1998; Gaudin & Wible 1999). Additionally, the humeri described here from the Itaboraian of Brazil are, together with the osteoderms of *Riostegotherium*, one of the most ancient records of South American "edentates".

The value of the astragalus in mammalian taxonomy has long been recognized (at least since Matthew [1909]). Simpson (1931) noticed the difficulty of designating a general xenarthran type of astragalus, for in the ground sloths and tree-sloths this bone has extreme divergent specializations. Szalay & Schrenk (1998), reviewing *Eurotamandua* and Edentata, presented the following features as tentative apomorphies of the tarsus of the higher clade Xenarthra: transversely broad astragalar body with greater arc laterally, and calcaneal facets aligned virtually on the same axis of rotation. Both characters are present in the Itaboraí astragali, supporting their placement is this clade, but their assignment to one of the xenarthran higher taxa was made on a tentative basis.

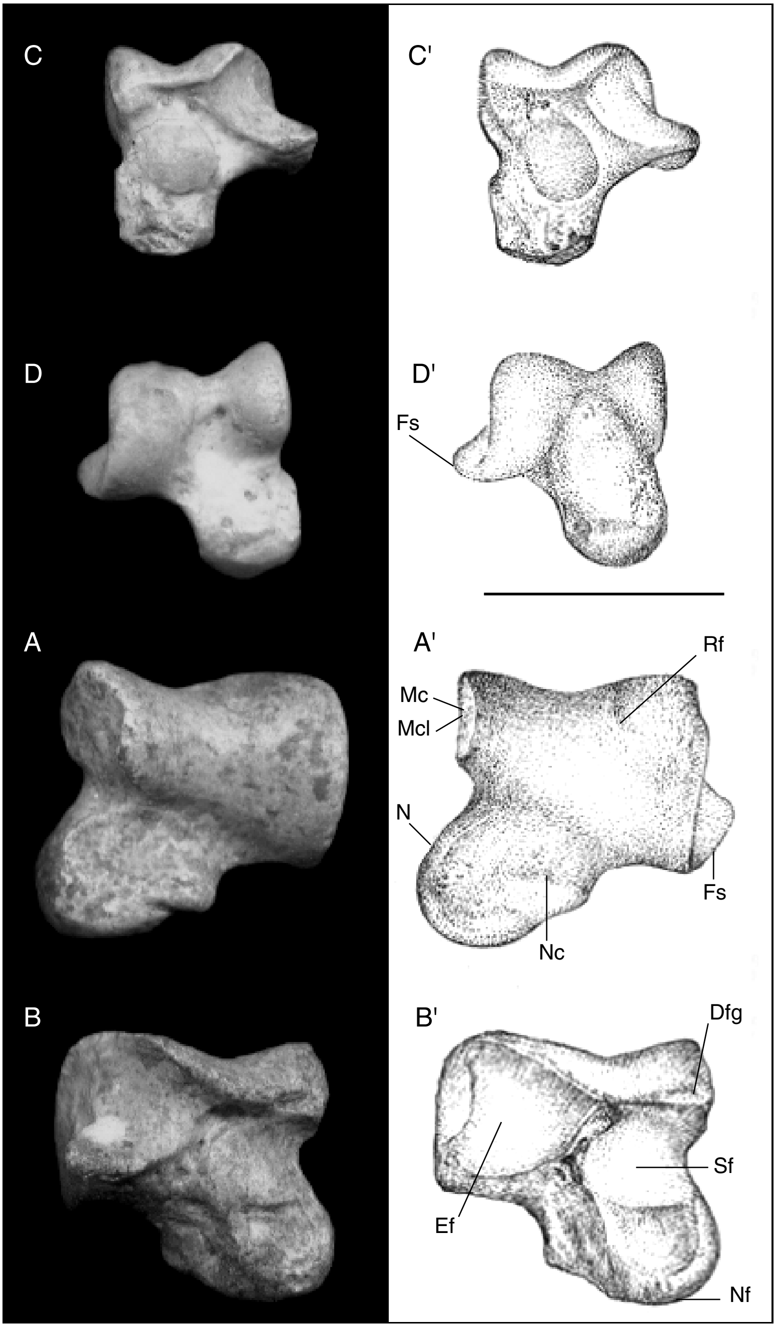

FIG. 7. — Xenarthra *incertae sedis*, rigth and left astragali; **A**, **B**, MCT 2395-M; **A**, dorsal view; **B**, plantar view; **A'** and **B'**, interpretive drawings of the specimen; **C**, **D**, MCT 2394-M; **C**, dorsal view; **D**, plantar view; **C'** and **D'**, interpretive drawings of the specimen. Abbreviations: **Dfg**, digital flexor tendon groove; **Ef**, ectal facet; **Fs**, fibular shelf; **Mc**, medial crest; **Mcl**, protuberance for the medial collateral ligament; **N**, neck; **Nc**; neck crest; **Nf**, navicular facet; **Rf**, rugose fossa; **Sf**, sustentacular facet. Scale bar: 1 cm.

The two astragali previously studied by Cifelli (1983) (DNPM LE 449A and 449B – now MCT 2394-M and 2395-M, respectively) were assigned to the Cingulata based on the absence of derived pilosan characters rather than on the presence of distinctively cingulate features. The author assigned the smaller astragalus to the family Glyptodontidae, despite of the absence of two distinctive and derived features of the glyptodont astragalus – a flattened sustentacular facet and a shorter neck. His assumption was supported by the presence of an anterior constriction of the trochlea and the morphology of its medial crest-condyloid and shorter than half of the astragalar length. Bergqvist & Oliveira (1998) pointed out that the crests of the tibial trochlea of *Hoplophorus*, which is the most condyloid among glyptodonts, are less condyloid than the specimens MCN-PV 1340 and MCT 2394-M (AST-morph 2), and the other features, although present in the glyptodontid *Propaleohoplophorus* Ameghino, 1891, are also seen in the dasypodid *Propraopus* and *Cabassous*. The anterior constriction of the tibial trochlea is also shared by *Hapalops* Ameghino, 1887 and *Myrmecophaga* (though not well developed), showing that this feature is widespread among the Xenarthra, and cannot be used as distinctive for Glyptodontidae.

The absence of a diagnostic glyptodont astragalar feature in AST-morph 2, and of glyptodont osteoderms at Itaboraí, weakens their assignment to the family Glyptodontidae. The presence of dasypodid osteoderms in the basin and astragalar features shared by members of the families Dasypodidae and Peltephilidae (Bergqvist & Oliveira 1998) is suggestive of a Dasypodoidea affinity, but no conclusive placement can be made until the derived features of the astragalus of Dasypodoidea are defined to the exclusion of Glyptodontoidea and vice-versa. A phylogenetic analysis within Cingulata is urged.

The larger astragali possess most of the characters listed by Simpson (1931) as the primitive type of xenarthran astragalus: 1) body relatively broad and short; 2) groove of trochlea broad, deep, oblique; its lowest part relatively medial; 3) lateral crest higher, sharper and longer; 4) malleolar facets nearly vertical; 5) neck distinct, constricted, but short; and 6) articular surface of head convex from side to side and extending up almost to the body of the astragalus medially. The only exception is the presence of a superior astragalar foramen, in a vestigial stage, as in *Priodontes maximus* F. Cuvier, 1827.

Simpson (1931) and Cifelli (1983) mentioned that dasypodid ankle morphology shows the primitive pattern of Cingulata. The body of AST-morph 2 is narrower and longer than in Dasypodidae, the trochlea is less oblique and the neck longer and more slender, resembling the pattern seen in *Palaeanodon*, which Simpson (1931) considered more primitive and closer to the most generalized insectivore type. In some ways, it also resembles the pattern seen in *Protoungulatum*, which would be predicted for a primitive eutherian morphotype (Cifelli 1983). As mentioned above, the astragali also present features broadly distributed among xenarthrans and probably primitive for the group. Even if the primitive pattern cannot be confidently recognized without a phylogenetic analysis, the morphology of the smaller astragali seems to be the primitive pattern for Xenarthra, despite of the absence of a vestige of the astragalar foramen. Although not discussed here, the rugose fossa present in the trochlea of AST-morph 1 is laterally placed, and might be related to ligaments, rather than the superior opening of the astragalar channel. Ameghino (1905, 1906) observed that in *Priodontes maximus* the superior astragalar foramen is medially placed, in a plantar tendinous groove, as is also seen in Itaboraí ungulates (Cifelli 1983; Bergqvist 1996). The lateral fossae present in several armadillos may be related to ligaments, not to the foramen. If this is true, then both morphotypes may be considered derived with respect to the superior astragalar foramen.

Cifelli (1983) noted the near absence of osteoderms in the Itaboraí Basin compared to the number of postcranial remains, to the good preservation of the bones and to the abundance of herpetofauna. Although more osteoderms have been recovered since then, they are still very few compared to the common ratio of osteoderms/

bones in other sites (e.g., Bergqvist 1989). The senior author of this paper has thoroughly examined all vertebrate fossil specimens collected in Itaboraí, numbered or non-numbered, and only the osteoderms listed here were found. We agree with Cifelli (1983) that it is unlikely that this small number is an artifact of collecting, and that is likely that these primitive cingulates possessed fewer osteoderms than later cingulates.

AST-morph 2 is the size of the astragalus of *Tolypeutes* Illiger, 1811 whose osteoderms are about the size of the osteoderms recovered in the Itaboraí Basin. The astragalus of *Stegotherium* Ameghino, 1887 as described by Scott (1903), resembles the AST-morph 2. The size and resemblance suggest that AST-morph 2 might belong to *Riostegotherium*. However, no confident association can be supposed until a detailed evaluation of the correlation between size of the osteoderms and astragalus among armadillos is done or an associated skeleton is discovered.

Rose & Emry (1993) proposed that Xenarthra was a relatively ancient eutherian group, long isolated in South America and with no obvious close relationship to any other eutherian. However, the evidence presented here by the limb bones suggests the possibility that the Itaboraí Basin cingulates might represent part of an ancestral stock of a monophyletic group uniting Xenarthra and Palaeanodonta (including *Eurotamandua*). Despite of the lack of geological evidence, the idea of a landbridge connection during the Late Cretaceous/early Paleocene between Gondwana and Laurasia cannot be discounted, as biogeographical patterns presented by some terrestrial vertebrates (see Schoch & Lucas 1985; Muizon & Marshall 1992; Salgado & Calvo 1997) and plants (see Wang 1978; Hay *et al.* 1999) support the presence of such a connection.

CONCLUSION

The validity of *Riostegotherium* as the oldest cingulate is confirmed.

The morphology of forelimb bones and their muscle scars indicate that well adapted burrowers were part of the mammalian biota of the Itaboraian SALMA of Brazil.

The mosaic of derived features presented by the appendicular bones prevents us from assigning them to any particular known Xenarthra, principally to Astegotheriini. However, their shared similarities to palaeanodonts add support to the proposal that Palaeanodonta may have been ancestral to, or is the sister-taxon of Xenarthra.

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