A NEW PALEOCENE ARMADILLO (MAMMALIA, DASYPODOIDEA) FROM THE ITABORAÍ BASIN, BRAZIL

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ABSTRACT. Riostegotherium yanei is a new genus and species described on the basis of isolated osteoderms from Itaboraí Basin (Brazil) of Itaboraian land-mammal age (middle Paleocene). The osteoderms of this armadillo have unique features distinguishing it from members of the early Tertiary Patagonian Astegotheriini. Among these are the presence of a subcircular main field, many pits in the grooves around this field, a better-developed central keel, and the absence of foramina on the posterior border. It is difficult to precise the affinities of the astegotheriines among the Dasypodoidea. Astegotheriines differ from other dasypodoids in having a moderate number of pits in the grooves limiting the main field, pelvic osteoderms with straight anterior and posterior borders, smooth lateral borders (indicating little articulation between osteoderms), and reduced number of piliferous foramina. The occurrence of at least two families of dasypodoids in the Itaboraian of Brazil, together with the presence of Peltephilidae and Astegotheriini in the Riochican of Patagonia, suggests that cingulates (or xenarthrans) were present at least since the early Paleocene in South America.

INTRODUCTION

Cingulate xenarthran remains are frequent in Cenozoic South American mammal-bearing beds, especially in post-Paleocene deposits (Scillato-Yané, 1986). By contrast, in older deposits, xenarthrans are recorded only in the upper Paleocene of Patagonia (Riochican land-mammal age), and Itaboraí Basin, Brazil (middle Paleocene, Itaboraian land-mammal age). The relative scarcity of xenarthran remains in comparison to the well-represented ungulate and marsupial specimens in these deposits is remarkable.

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The discovery of osteoderms in the Itaboraí fauna was reported nearly 30 year ago (Paula Couto, 1949), but they were not described and illustrated until 1976 (Scillato-Yané). The description was based on two isolated osteoderms assigned to Prostegotherium aff. P. astrifer Ameghino, 1902. Later, Ciffeli (1983) referred two astragali to Dasypodidae and ?Glyptodontidae indet. Recently, the discovery of astragali and other postcranial elements, confirmed the presence of dasypodoids in Itaboraí (Bergqvist and Oliveira, 1995a). Reexamination of Cifelli’s (1983) glyptodontid specimen revealed that it was identified on presumed plesiomorphic characters for cingulates, and that it shares no derived characters with glyptodonts (Bergqvist and Oliveira, 1995b). Thus, the specimen was thought to be a dasypodoid.

The Itaboraian land mammal age was based on a faunal assemblage from the Itaboraí Basin, and from levels belows Riochican deposits in Patagonia. This
fauna represents an intermediate interval between the Riochican and older assemblages (Marshall, 1985). This scheme generated controversy as to the validity of this age and the time interval represented (see Pascual and Ortiz-Jauregui, 1991; Bonaparte et al., 1993). Recent advances in the knowledge of the Paleocene land mammal-bearing deposits of central Patagonia show that the Itaboraian interval corresponds to middle Paleocene (Bond et al., 1995).

Herein, we describe a new genus and species of armadillo and discuss the role of early Tertiary dasypodoids in the understanding of the early history of South American xenarthrans.

Abbreviations. MCN-PV, Museu de Ciências Naturais, Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre, RS, Brazil; MCT-M (ex-DGM), Museu de Ciências da Terra, Departamento Nacional de Produção Mineral, Rio de Janeiro, RJ, Brazil; MLP, Museu de La Plata, La Plata, Argentina; AP, maximum antero-posterior length; W, maximum width.

SYSTEMATICS

Superorder Xenarthra Cope, 1889
Order Cingulata Illiger, 1811
Superfamily Dasypodioidea Simpson, 1931
Tribe Astegotherini (Ameghino, 1902)

Riostegotherium gen. nov.

Riostegotherium yanei sp. nov.

Type species. Riostegotherium yanei sp. nov.

Etymology. Rio, of Rio de Janeiro, in reference to the state where the specimens were found; stego (Latin), meaning covering; therium (a latinized Greek word), meaning beast, a commonly-used suffix for mammalian genera.

Diagnosis. As for the type and only species.

Riostegotherium yanei sp. nov.

Figures 2A-H


Holotype. MCN-PV 1774, pelvic osteoderms.

Hypodigm. The type, and MCN-PV 1775: pelvic osteoderms; MCN-PV 1776, 1778, 1779, MCT 2081 M, MLP 75-XII-26-1 and MLP 75-XII-26-2: isolated moveable osteoderms; and MCN-PV 1777: caudal osteoderms.

Etymology. yanei, for Dr. Gustavo J. Scillato-Yané, from the Museo de La Plata, Argentina, in recognition of his contributions to knowledge of Itaborian cingulates and of xenarthran systematics and evolution.

Diagnosis. Differs from all known early Tertiary astegotheriins in having a better-developed central keel, subcircular main field, many pits in groove around field, ranging from seven to twelve in moveable osteoderms, and from eighteen to twenty-five in pelvic osteoderms; slightly wrinkled external surface, presence of at least two pits in groove surrounding anterolateral fields, and complete absence of piliferous foramina on posterior border.

Horizon and Locality. Itaboraí Formation, near Itaboraí, Rio de Janeiro (figure 1), Brazil (22° 44'51"S, 42° 51'21"W); Itaboraian land-mammal age; middle Paleocene (61.8 to 58.5 Ma, Pascual and Ortiz-Jauregui, 1991).

Measurements. MCN-PV 1774: AP = 12.1 mm, W = 9.7 mm; MCN-PV 1775: AP = 11.6 mm, W = 8.3 mm; MCN-PV 1776: AP = 11.6 mm, W = 8.2; MCN-PV 1778: AP = 10.1 mm, W = 5.5 mm; MCN-PV 1779: AP = 12.1 mm, W = 9.8 mm; MCN-PV 1777: AP = 10.3 mm, W = 7.1 mm; MCT 2081-M: AP = 10.7 mm, W = 5.4 mm.

Description. The material does not include any articulated osteoderms. The pelvic osteoderms are large and subrectangular in shape. In comparison with osteoderms of Dasypus hybrius, for example, those of Riostegotherium yanei are relatively more robust. The lateral borders of the osteoderms in the Itaboraian species are slightly concave and smooth. The anterior and posterior borders are irregular; the posterior border has a U-shaped concavity when viewed internally. The anterior border has a small, weakly defined articulation zone. The external surface is very punctate and bears fine irregularities; in combination with the presence of small depressions, these irregularities give the surface a slightly wrinkled appearance. The main field has an inverted U-shape, with a subcircular anterior outline and occupies almost the whole osteoderm surface. It is limited by a shallow groove with eighteen to twenty-five pits. Although the anterior shape of the main field varies slightly, it never is triangular or lageniform. Two to four small peripheral fields are present, limited by shallow radial grooves with at least two pits. A well-developed central keel is present on the external surface of the main field. 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 moveable osteoderms vary in shape, ranging from subquadrangular to subrectangular. The anterior articular surface is poorly developed, and the external surface resembles that of the pelvic osteoderms. The main field has a subcircular anterior outline, but with a very reduced number of pits (seven to twelve). The external surface bears a well-developed central keel. No foramina 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 (figure 2G) resembles caudal osteoderms of the extant dasypodid Dasypus. The most important differences in relation to the typical moveable osteoderms are as follows: articulation surface more developed laterally; smoother external surface; pits more widely spaced in the groove limiting the main field and a sharp posterior border.
DISCUSSION. Vizcaíno (1994) included all the oldest known armadillos in a taxon that he considered a tribe (Astegotheriini) of the Dasypodinae. However, some characters used to define this tribe are thought to be plesiomorphic (e.g., slender osteoderms, and presence of central keel). We propose that the most important derived characters supporting the assignment of *Riostegotherium yanei* to the astegotheriines are the following: moderate
number of pits in the grooves limiting the main field; pelvic osteoderm with straight posterior border; smooth lateral border indicating little articulation between osteoderms, and reduced number of piliferous foramina. Compared to the other taxa referred to Astegotheriinae: Prostegotherium, Astegotherium, P. seudostegotherium and Stegosimpsonia, Riostegotherium seems to be more related to Prostegotherium. However, Riostegotherium yanei differs from these Patagonian astegotheriines in having (1) a subcircular anterior outline of the main field, (2) more pits in the grooves limiting this field, (3) a better-developed central keel, (4) slightly wrinkled external surface, (5) presence of at least two pits in the groove surrounding anterolateral fields, and (6) absence of foramina on the posterior border.

It is difficult, in view of the present state of knowledge, to precise the affinities of astegotheriines within Dasypodoidea. Ameghino (1902, 1906) grouped

Figure 2. Osteoderms of <i>Riostegotherium yanei</i> gen. et sp. nov.; A: holotype/holotipo (MCN-PV 1774); B: pelvic osteoderm/osteodermo pélvico (MCN-PV 1775); C: moveable osteoderm/osteodermo móvil (MCN-PV 1776); D: moveable osteoderm/osteodermo móvil (MCN-PV 1778); E: moveable osteoderm/osteodermo móvil (MCN-PV 1779); F: moveable osteoderm/osteodermo móvil (MCN-PV 1777); G: caudal osteoderm/osteodermo caudal (MCN-PV 1777); H: moveable osteoderm/osteodermo móvil (MLP 75-XII-26-1).

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the oldest armadillos in the Stegototheriidae and Astegotheriidae, separated from the extant Dasypodidae (including Praopidae). Other authors arrangement group the early armadillos in the Stegototheriinae as a subfamily of Dasypodidae (Simpson, 1945; Hoffstetter, 1958; Paula Couto, 1979). A third scheme placed the armadillos in different tribes within the Dasypodinae (Patterson and Pascual, 1972; Scillato-Yané, 1980, 1986; Vizcaíno, 1994). As currently conceived, Dasypodidae comprises a numerous taxa placed in the subfamilies Dasypodinae, Euphractinae and Peltephilinae, with a records from the middle Paleocene to Recent (Simpson, 1945; Scillato-Yané, 1986; Vizcaíno, 1994), i.e. a temporal range of about 60 Ma. However, the inclusion of astegotherines in the family Dasypodidae is not clearly justified by characters in most works cited above. Vizcaíno (1994) considered the presence of epidermal scales covering two or three adjoining osteoderms to be a synapomorphy uniting Astegotheriini and Dasypodini within Dasypodinae. However, this synapomorphy should be viewed with caution. Carapaces of extant (e.g., Dasypus) or extinct (e.g., Proproopus Ameghino) dasypodids have well-articulated osteoderms (not necessarily a rigid articulation), with well-developed spicular sutures along the lateral borders. These sutures provide strong support for the delicate and complex epidermal scutes covering the osteoderms. Conversely, this kind of support is absent in astegotherines, because the osteoderms have almost smooth articular surfaces. In Stegototheriun and Astegotherium dichotomus, for example, the osteoderms were thought to have been joined by “cartilaginous” tissue in life (Ameghino, 1897, 1902). Even if the presence of anterolateral fields in the osteoderms of astegotherines indicates a complex arrangement of epidermal scales, this feature does not provide definitive support for Vizcaíno’s (1994) interpretation, because the presence of anterolateral fields in the osteoderms of the glyptodontid Glyptatelas Ameghino suggests that this character is widespread within the cingulates (see Ameghino, 1897).

COMMENTS ON THE OLDEST SOUTH AMERICAN TERTIARY XENARTHANS

Riostegotherium yanai is the oldest xenarthran known, as the Paleocene putative Xenarthra Sudamerica ameghinoi, (Scillato-Yané and Pascual, 1985), is now considered to be a derived multituberculate (Krause and Bonaparte, 1990). We concur with Rose and Emry (1993) that the presence of osteoderms is a derived xenarthran trait (not dasypodoid as suggested) as it is also a feature of some tardigrades. Osteoderms are not present in any other mammal or mammal-like reptiles.

Although very important in documenting the Paleocene diversification of dasypodoids, the remains described herein offer little to the understanding of the origin and relationships of the xenarthrans. However, despite the absence of important fossils, some hypotheses have been proposed concerning the origin of this enigmatic group. The concept of Paratheria involves an ancient Gondwanan group of mammals, with African (Pholidota) and South American (Edentata) derivatives of the original stock, and with West Gondwana as a possible area of origin (Scillato-Yané, 1986; Pascual et al., 1985). This proposition is in part supported by the record of a “true” Myrmecophagidae, Eurotamandua joresi Storch, from the middle Eocene of Europe (Storch, 1981; but see Rose and Emry, 1993) and other possible Eurasian “edentates” (Chow, 1963; Ding, 1987). The synapomorphies that support a close relationships between Xerarthra, Pholidota, and fossil “edentates” were interpreted by Rose and Emry (1993) as related to fossorial behavior and myrmecophagy. It is suggestive, however, that no South American or African Cretaceous or Tertiary fossils that support a close relationship of these groups have been recovered.

The absence of xenarthrans in the uppermost Cretaceous or lower Paleocene of Patagonia and Bolivia have been considered as suggestive (Pascual and Ortiz-Jaureguizar, 1991), but not conclusive (Carlini et al., 1994) evidence, against the origin or early diversification of the group in South America. However, we agree with the latter suggestion taking into account the presence of some xenarthran postcranial bones in the Itaboraí Basin (Bergqvist and Oliveira, 1995a, 1995b) and the comments of Scillato-Yané (1976, 1986) on the dasypodoids of the Paleocene of South America. According to Scillato-Yané (1976), the distinctive basic dasypodoid traits were already developed in the Itaboraian and Riochican armadillos and, therefore, their ancestors should be recorded in older horizons. The finding of new astragali in Itaboraí shows that two or three distinct dasypodoids (possibly two families) were already present in Itaboraian times; one Euphractinae-like morph and two other Peltephilidae-like morphs (Ciffeli, 1983; Bergqvist and Oliveira, 1995b). This, coupled with the presence of unpublished material of Peltephilidae and Astegotheriini from the Riochican of Patagonia (Scillato-Yané, 1986), argues in favor of an older history (early Paleocene at least) of the xenarthrans in South America. On this basis, the absence of xenarthrans in the early Paleocene of South America may be an artifact of the fossil record, despite the fact that already Patagonia was apparently a distinct biogeographical unit, closely related to East Gondwana (Pascual, in press). Furthermore, known latest Cretaceous and early Paleocene mammal-bearing beds in South America are almost entirely restricted to Argentina and Bolivia. The intertropical region of South America and Africa, obviously representing a large part of a still not well known West Gondwana, has not been sufficiently prospected yet, and it may contain clues on early xenarthra evolution.
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