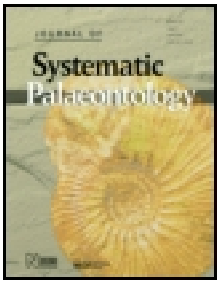

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New Palaeogene cingulates (Mammalia, Xenarthra) from Santa Rosa, Perú and their importance in the context of South American faunas

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New Palaeogene cingulates (Mammalia, Xenarthra) from Santa Rosa, Perú and their importance in the context of South American faunas

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The record of Palaeogene cingulate xenarthrans in low latitudes is very poor. The cingulate fauna from the Yurúa River near Santa Rosa in eastern Perú is important because it is one of the oldest known from the Palaeogene of Perú and because of its tropical latitudinal position. Although remains are scarce, we recognize three new taxa: two species of Astegotheriini (Dasypodidae); *Parastegosimpsonia peruana* gen. et sp. nov., of small size, related to Eocene species from Patagonia; and another new species, ?*Parastegosimpsonia* sp. nov., which consists of an incomplete osteoderm representing the largest species of this tribe. A third species, *Yuruatherium tropicalis* gen. et sp. nov., of indeterminate suprageneric rank, shares features with *Machlydotherium* Ameghino (Casamayoran-Tinguiririca SALMA – middle Eocene-early Oligocene of Patagonia) and is similar to *Eocoleophorus* Oliveira *et al.* (Deseadan SALMA – late Oligocene of Brazil). We assign ?*Machlydotherium intortum* Ameghino (from the late Eocene of Patagonia) to *Yuruatherium.* Sediments bearing these cingulates also yielded rodents, marsupials and notoungulates, among the most frequent mammals. The absolute age of the sediments is unknown but an estimated age is inferred from studies of the mammalian assemblages. The age of the Santa Rosa local fauna is still controversial and given the groups taken into account, could be from Early Eocene to Late Oligocene. According to sequences of southern cingulate faunas (especially those of Dasypodidae), the cingulates from Santa Rosa also suggest an age between the Late Eocene and Early Oligocene. Nevertheless, the very low latitude of the Santa Rosa local fauna should be taken into account because in lower latitudes it is not uncommon to find taxa with a more generalized set of characters than those present in contemporary taxa from higher latitudes.

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Keywords: Cingulata; Palaeogene; Astegotheriini; low latitudes; diversity; Perú, Amazonia

Introduction

Among the major groups of Xenarthra (Cingulata, Tardigrada and Vermilingua), the Cingulata, or ‘armored edentates’, are the first to appear in the fossil record. The oldest known representatives come from the Late Palaeocene of Itaboraí, Brazil (Scillato-Yané 1976; Oliveira & Bergqvist 1998; Bergqvist *et al.* 2004), the type locality of the Itaboraian South American Land Mammal Age (SALMA). They have been reported from the Early Eocene in the Riochican SALMA of Patagonia (Gelfo *et al.* 2009; Tejedor *et al.* 2009) on the basis of a few osteoderms attributed to the Peltephilidae? and to one species of Astegotheriini (Scillato-Yané 1986; Carlini *et al.* 2002a). It is only in the Casamayoran SALMA that Cingulata become more abundant and diverse, especially Dasypodoidea (Carlini *et al.* 2002b, c), whereas the remaining Cingulata are known only from one genus of disputed affinities, *Machlydotherium* Ameghino, 1902a.

Phylogenetic relationships among the groups that comprise Cingulata are controversial and the numerous hypotheses that have been advanced are often at odds with one another (e.g. Hoffstetter 1958, 1969, 1982; Patterson & Pascual 1972; Engelmann 1985; Scillato-Yané 1986; Carlini & Scillato-Yané 1993; Abrantes & Bergqvist 2006; Gaudin & Wibble 2006; Fernícola 2008; Porpino *et al*. 2009). The issue of possible centers of dispersal of the group is at the centre of a similar debate, made more difficult by both the scarcity of early Palaeogene deposits located in intratropical areas and the lack of certainty about the identity of the group of mammals from which xenarthrans might have evolved.

Fossil material from Palaeogene sediments of the Yahuarango Formation, in central eastern Perú (Fig. 1) (see

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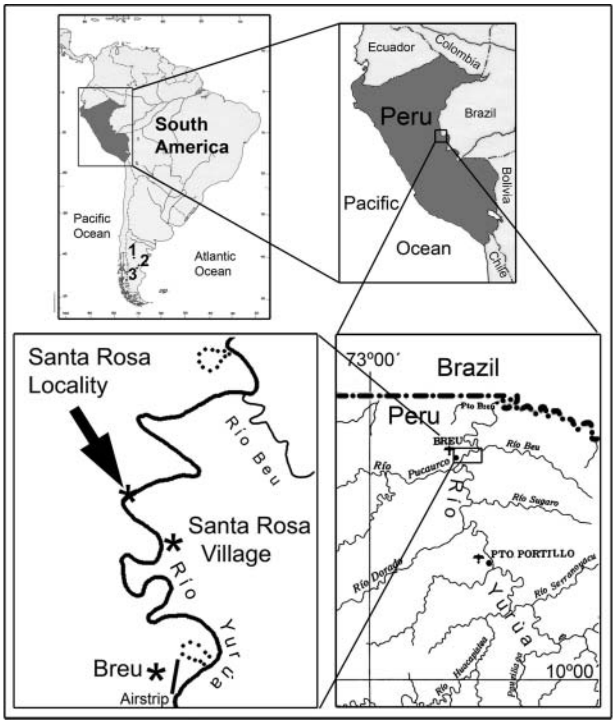

Figure 1. Map showing the location of the Santa Rosa fossil locality in eastern Peru and the Patagonian localities mentioned in the text. Inset. Lower left: map showing the Santa Rosa locality on a detailed outline of the Río Yuruá river channel in Perú. Inset. Upper right: map of Perú, showing location of lower map (modified from Campbell *et al.* 2004). **1**, Paso del Sapo; **2**, Cañadon Vaca; **3**, Gran Barranca.

Campbell *et al*. 2004), provides data relevant to these two issues. From this site, which produced the Santa Rosa local fauna, three new species of Cingulata are recognized: (1) a member of the family Dasypodidae, tribe Astegotheriini that is small in size and similar to an Eocene species from Patagonia; (2) a second member of the family Dasypodidae, tribe Astegotheriini, represented by a large, incomplete osteoderm that could conceivably correspond to one of the largest known species for the tribe; and (3) a species of Cingulata with affinities to the genera *Machlydotherium* and *Eocoleophorus* Oliveira, Ribeiro & Bergqvist, 1997.

Until the middle of the twentieth century, knowledge of Palaeogene cingulates was mostly linked to the work of the Ameghino brothers, first discovered by Carlos Ameghino during his numerous journeys in Patagonia and described by Florentino Ameghino (1897, 1902a). These early descriptions were brief, almost never accompanied by illustrations and probably overestimated the taxonomic significance of small morphological details of the osteoderms, which we now know display intraspecific variability (Ciancio & Carlini 2008a; Carlini *et al.* 2010). This resulted in the recognition of a large number of genera and species, frequently with little support. Simpson (1948) attempted to reduce this excessive number of Palaeogene species and designated lectotypes among what had been considered syntypes. Still, in a few cases, Simpson did not have enough material for adequate descriptions; thus he maintained the validity of some taxa that currently appear to be invalid and conversely considered as synonyms some taxa that are now seemingly valid (Ciancio & Carlini 2008a; Carlini *et al.* 2010; Ciancio 2010). Later, several authors (Hoffstetter 1958; Scillato-Yané 1977; Vizcaíno 1994) proposed taxonomic modifications and revisions of fossil cingulates.

Numerous collections have been made since 1995 from Eocene and Oligocene sediments of Patagonia, Argentina. Strict stratigraphical, palaeomagnetic and geochronological controls were maintained during collection. Fieldwork was particularly focused on micromammals and the successive faunas collected were placed within a geological scheme developed in parallel with the palaeontological collecting (Carlini *et al.* 1997, 1999, 2002a, b, c, 2004, 2005a, b, 2010; Kay *et al.* 1999, 2001; Madden *et al.* 2003a, b, 2005, 2010). At present it is possible to recognize a sequence of successive cingulate faunas from the high latitudes of Patagonia that are well defined both stratigraphically and geochronologically, as presented below. In this paper, following the description of the new material from the Santa Rosa local fauna, we use the Patagonian sequence to infer and discuss the possible age of the Santa Rosa local fauna of Perú.

Eocene sequence of Patagonian cingulates

Until now, Patagonian cingulates have been represented by species of the families Dasypodidae, Glyptodontidae, Pampatheriidae and Peltephilidae, as well as a group of taxa whose relationships to any of the former are uncertain (i.e. Palaeopeltidae; *Pseudorophodon* Hoffstetter, 1954 and *Machlydotherium* Ameghino, 1902).

Fauna from Laguna Fría and La Barda, Paso del Sapo, Chubut (Early-Middle Eocene)

Collections from the area of Laguna Fría and La Barda (Paso del Sapo, Chubut, approximately 42°45′S 69°51′W, Fig. 1) have provided vertebrate remains from continental sediments that are equivalent to the lowest levels of the Sarmiento Formation (Volkheimer & Lage 1981; Lage 1982; Aragón & Mazzoni 1997). These faunas are positioned stratigraphically between two ignimbrite levels, the isotopic dates (K –Ar dates) of which suggest an age of *c.* 49.5 Ma for the Laguna Fría fauna and 47–45 Ma for the La Barda fauna (see Wilf *et al.* 2003; Tejedor *et al.* 2009).

The best preserved osteoderms allow recognition of the following taxa, all belonging to the family Dasypodidae, subfamily Dasypodinae, tribe Astegotheriini: (1) a new species of *Riostegotherium* Oliveira & Bergqvist, 1998; (2) a new species of *Astegotherium* Ameghino, 1902a; (3) *Prostegotherium* sp. cf. *P. astrifer* Ameghino, 1902a; and (4) a new species of *Stegosimpsonia* Vizcaíno, 1994

(Tejedor *et al*. 2009). Given that these fossils were collected from more than one locality, it is highly probable that they represent a large number of individuals. This assemblage of species corresponds entirely to the tribe Astegotheriini, which comprises the oldest and probably most primitive dasypodids. In addition, there is a notable absence of Euphractinae (Dasypodidae), especially species of *Utaetus*, which are otherwise abundant in sediments frequently referred to the Barrancan sub-age of Casamayoran SALMA (Middle Eocene) of Chubut. There are also faunal differences with regard to the other Casamayoran sub-age (i.e. the Vacan, Middle Eocene), which has a lower diversity of Astegotheriini, with more advanced taxa. These differences from Casamayoran faunas (Carlini *et al.* 2002b, c, 2005a, b, 2010), together with the presence of a new species of *Riostegotherium*, a genus thus far only known from the Itaboraian SALMA (Late Palaeocene of Brazil) (Oliveira & Bergqvist 1998; Bergqvist *et al.* 2004), suggests an older age than that of the Casamayoran (i.e. Early? Eocene to Middle? Eocene) for the deposits from Laguna Fría and La Barda. From a palaeoenvironmental perspective, the absence of euphractine species (in which the numerous posterior osteodermal foramina are most probably indicators of greater pilosity; see Krmpotic *et al*. 2009) and the diversity of Astegotheriini suggest higher temperatures than those that prevailed during the deposition of Casamayoran sediments. This warm period probably correlates with the Early Eocene Climate Optimum (EECO) recorded in sea-surface temperatures (SST) at around 48 to 53 Ma (Zachos *et al.* 1994, 2001; Carlini *et al.* 2005b).

Vacan fauna, early Casamayoran SALMA (Middle Eocene)

Prior to recent collections from outcrops of the Sarmiento Formation at the Cañadón Vaca locality (45°12′ S, 68°05′ W, Fig. 1), about 50 km to the east-northeast of the southern cliff of Lake Colhué Huapi, only two species of dasypodids were known from this locality. Both species belong to the tribe Astegotheriini: *Prostegotherium* sp. and *Astegotherium dichotomus* Ameghino, 1902a (*sic* Simpson 1948; Cifelli 1985). In new collections from the same locality and levels, the following taxa are recognized: (1) *Astegotherium dichotomus*; (2) a new species of *Stegosimpsonia*, based on osteoderms different from those of *Stegosimpsonia* sp. nov. from Eocene sediments of Laguna Fría, Paso del Sapo and those of *S. chubutana* (Ameghino 1902a) from the Barrancan sub-age of the Casamayoran SALMA fauna of Lake Colhué Huapi; and (3) a ?Stegotheriini that would correspond to the oldest known representative of this tribe (Carlini *et al.* 2002b, 2004a, 2010). The dasypodid assemblage from Cañadón Vaca is considered more advanced than that from Paso del Sapo because no species of *Riostegotherium* are present. Instead, a new, more derived species of *Stegosimpsonia* has been discovered. The Vacan fauna is assumed to be older than that of the Barrancan because there is an absence of species of Euphractinae and a greater diversity of species of the tribe Astegotheriini. The Vacan fauna is assigned a Middle Eocene age based on ^{40}Ar/^{39}Ar isotopic dates that give an approximate age of 45 Ma for ash-bearing sediments (unpublished data, see Gelfo *et al.* 2009).

Barrancan fauna, late Casamayoran SALMA (Middle Eocene)

Numerous collections in the Barrancan levels of Gran Barranca (Chubut, Fig. 1) have allowed the specific record of the dasypodid assemblage to be updated. From the important stratigraphical column corresponding to the Sarmiento Formation that crops out in the South Cliff (Barranca Sur) of Lake Colhué Huapi (Madden *et al.* 2003a, 2005, 2010; Re *et al.* 2010), we recognize (after refining pre-existing lists) the following species of dasypodids from levels referable to the Barrancan sub-age of Casamayoran SALMA (*c*. 40 Ma): (1) Astegotheriini, *Stegosimpsonia chubutana*; (2) 'Utaetini' (Euphractinae), *Utaetus buccatus* Ameghino, 1902a (Carlini *et al.* 2010); and (3) ?Stegotheriini, a species that is perhaps related to that recorded in at the Cañadón Vaca locality (see Carlini *et al.* 2010).

At these levels, species of Euphractinae are already well established. They possess osteoderms with numerous perforations on the lateral and posterior margins, which indicates a greater development of the piliferous system than species of Dasypodinae. This greater pilosity could be linked to a decrease in temperature (also coincident with a variation in SST, see Zachos *et al*. 1994, 2001), which would explain the lower frequency of species of Dasypodinae compared to older faunas (e.g. dasypodid faunas from Cañadón Vaca or Laguna Fría and La Barda). This change in the composition of the dasypodid faunas, which had been progressively taking place since the earliest Eocene in Patagonia, agrees with the inferred changes that affected many mammalian faunas (both taxonomically and structurally) during the Eocene-Oligocene transition (Pascual *et al.* 1996; Flynn *et al.* 2003; Carlini *et al*. 2009, 2010; Goin *et al.* 2010). In addition, a definite dominance of Euphractinae species starts to become apparent, at least in southern South America.

The oldest record of *Machlydotherium* corresponds to the Barrancan sub-age of the Casamayoran SALMA (Ameghino 1902a; Simpson 1948) and was assigned by Ameghino (1902a) and Castellanos (1937) to 'Chlamydotheriidae' (= Pampatheriidae, according to current taxonomy; see Scillato-Yané *et al.* 2005). This genus is not well known and its affinities are debated.

Related cingulatan faunas in younger units

Cingulates from groups related to those recorded in Santa Rosa, Perú display diverse phylogenetic histories in younger faunas. To date, Astegotheriini are not represented in stratigraphical units belonging to the Mustersan, Tinguirirican or Deseadan SALMAs of Patagonia. The faunas found in this period (Late Eocene-Late Oligocene) in Patagonia are characterized not only by the absence of astegotherines but also by an increase in the diversity of euphractines (Carlini *et al.* 2010).

For the Colhuehuapian SALMA, the only record is *Pseudostegotherium glangeaudi* Ameghino, 1902b, an enigmatic taxon that shares characters with both Astegotheriini and Stegotheriini. Another peculiar dasypodid, *Nanostegotherium prostatum* Carlini *et al.*, 1997, the last known representative referred to this tribe, occurs in the Laventan SALMA (Middle Miocene) of Colombia (Carlini *et al.* 1997, 2010). Additionally, a probable new species (not yet formally named) of Dasypodidae has been described recently from the Deseadan levels of the Moquegua Formation, southern Perú, dated to *c*. 26 Ma. The specimen is a movable band osteoderm assigned to cf. Dasypodinae by Shockey *et al*. (2009).

With respect to *Machlydotherium*, its latest record is in the 'La Cancha' levels of Gran Barranca (Tinguiririca n SALMA, Early Oligocene) in Patagonia (Carlini *et al*. 2005a, 2010; Re *et al.* 2010). Although this taxon has been mentioned as occurring in the Fray Bentos Formation (Deseadan SALMA, Oligocene) of northeastern Argentina (Corrientes River, Corrientes Province) (Bond *et al.* 1998), its presence there seems highly improbable because the fragmentary osteoderm attributed to this taxon seems to represent an indeterminate species of Peltephilidae (Carlini *et al.* 2007).

Geographical and stratigraphical context

The Santa Rosa locality occurs on the left bank of the Yurúa River, at 9°29′39″ S, 72°45′48″ W (Fig. 1), Atalaya Province, Ucayali Departament, Perú. The site is approximately 4.0 km due north of the army post of Breu and approximately 9.2 km south of the Perú-Brazil border. The fossiliferous deposits were interpreted as coarse, conglomeratic bed-load deposits by Campbell *et al*. (2004) and occur within a thick body of red clay. The fossiliferous deposits form thin horizons, or lenses, of variable length that slope gently from left to right across the face of the outcrop (see Campbell *et al.* 2004, figs 3, 4). A number of these horizons were sampled in 1998 and all seemed to be fossiliferous. However, it was not possible to determine in the field which horizon was the most productive because the most significant array of fossils consist of minute specimens.

The fossiliferous deposits of the Santa Rosa locality were referred by Campbell *et al.* (2004) to the Eocene-Oligocene Yahuarango Formation, although these authors acknowledged that the stratigraphy in this region is still too poorly known to have complete confidence in this assignment. Given that the Santa Rosa local fauna is known only from a single river bank, and because it is currently the only Palaeogene fauna known from Amazonia, biocorrelation with other sites is impossible. The host formation for the fossiliferous horizons comprises massive red clays that are devoid of marker beds and, because there can be considerable distances between cut banks on the Río Yurúa, it is impossible to assess its precise level within the formation. The only geological marker in the region is the Ucayali Unconformity which separates the Yahuarango Formation from the overlying Madre de Dios Formation. For a complete discussion of the stratigraphy and possible geologic relationships of the red beds of the Río Yurúa assigned to the Yahuarango Formation, see Campbell *et al.* (2004).

A recent paper describing a new mammalian fauna from the Yahuarango Formation in Contamana, Peruvian Amazonia, found an age of *c*. 43 Ma (^{40}Ar/^{39}Ar) for tuffaceous silt placed 47 m above the fossiliferous level at the top of the Yahuarango Formation. It was inferred to have a Barrancan-Mustersan (Middle-Late Eocene) biochronological range based on the mammalian assemblage and Middle Eocene to Early Oligocene range according to the palynoflora (Antoine *et al.* 2011). This new information gave us new insights on the discussions of the probable age of Santa Rosa fauna.

Systematic palaeontology

Anatomical nomenclature. In describing the general morphology of osteoderms and carapace, researchers have used different terms to indicate specific structures. In order to avoid confusion in the descriptions, we present schematic drawings summarizing the terminology used here (Fig. 2).

Order **Cingulata** Illiger, 1811
Family ***incertae sedis***
Genus ***Yuruatherium*** gen. nov.

Type species. *Yuruatherium tropicalis* gen. et sp. nov.

Included species. The type species and ?*Machlydotherium intortum* Ameghino, 1902a.

Diagnosis. Dorsal shield osteoderms with rugose surface, large perforations in the sulci between figures, or in these sulci and the lateral and posterior margins. Semimovable osteoderms with large principal figure that occupies the entire posterior half of the osteoderm and becomes narrower anteriorly, delimiting at least one pair of anterolateral figures. Movable osteoderms with large principal figure occupying posterior two thirds of dorsal surface. Sigmoid sulcus surrounding anterior portion of principal figure with a row of large circular perforations.

Etymology. '*Yurua',* from the Yurúa River of Perú, the banks of which produced the Santa Rosa local fauna,

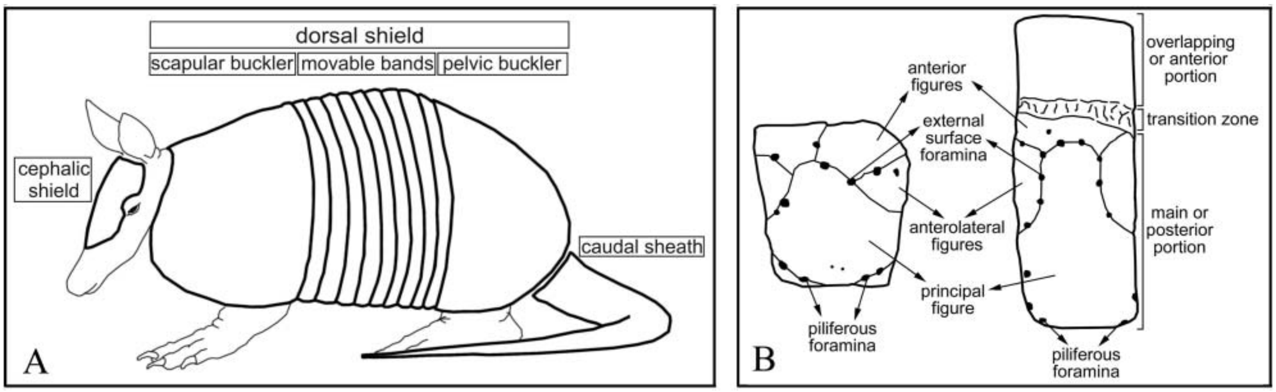

Figure 2. **A**, line drawing of generalized Dasypodinae showing the different parts of the carapace; **B**, line drawing of fixed (left) and movable (right) osteoderms of *Yuruatherium* gen. nov. from the dorsal shield showing external structures mentioned in the text. The anterior portion of the movable osteoderm is reconstructed.

+ '*therium*' from the Latin *therion*, 'beast', a common generic suffix for mammalian taxa.

Occurrence. Late Eocene (Mustersan SALMA), Patagonia, Argentina; Palaeogene (?Eocene), Río Yurúa, Perú.

Remarks. *Yuruatherium* is somewhat larger than *Priodontes giganteus*, the largest living dasypodid. When Ameghino (1902a) described *Machlydotherium*, he mentioned its affinity with *Chlamydotherium* (= *Pampatherium*) based on its large size and the presence of a bilobed tooth that he associated with one of its species (*Machlydotherium asperum*). In the same paper he described three additional species: *M. ater*, ?*M. intortum* and ?*M. sparsus*. However, his original assignment of the last two species to *Machlydotherium* was tentative. In fact, in the case of ?*M. intortum*, the presence of several circular perforations arranged in an inverted 'U' shape, as well as the absence of the two to four large proximal foramina, contrast with the pattern seen in *Machlydotherium*.

The dorsal shield osteoderms of *Yuruatherium* have a rugose surface caused by a large number of small perforations, mostly corresponding to the openings and pathways of blood vessels and nerves located below the epithelium that generated and maintained the horny scales. The known osteoderms indicate that the carapace seems to have been formed by a scapular buckler, a region of movable bands, and a pelvic buckler, although the number of rows in each region is unknown. According to the preserved areas of lateral contact between osteoderms, the junction between osteoderms must not have been very rigid because they present only a few tooth-like projections that are low and blunt.

Yuruatherium tropicalis gen. et sp. nov.
(Figs 3A–E, 4A–E)

Diagnosis. Semimovable osteoderms with principal figure displaced to posterior portion and surrounded anteriorly by triangular or prismatic peripheral figures, normally convex. Numerous large perforations on external surface, opening in the sulci delimiting figures, even anteriorly. Perforations on posterior and lateral margins. Principal figure with keeled boss that is sharp and high posteriorly.

Holotype. LACM 150606.

Hypodigm. The holotype and LACM 150604, LACM 150607, LACM 150610, LACM 150611.

Etymology. '*tropicalis*', in reference to the low-latitude location of Santa Rosa local fauna.

Occurrence. Palaeogene (?Eocene), Yurúa River, Perú.

Measurements. Holotype, semimovable osteoderm (LACM 150606): 17 mm long, 15 mm wide, 5 mm thick. Hypodigm, movable osteoderm (LACM 150607): ~22 mm long (broken), 10.5 mm wide, 4 mm thick. Fixed osteoderms (LACM 150604, LACM 150610, LACM 150611): 10–12 mm long, 8–10 mm wide, 3–4.5 mm thick.

Description. The holotype is a semimovable osteoderm, probably from the scapular buckler, with its principal figure proximally circumscribed by several large perforations arranged in a wide, parabolic curve with the concavity directed posteriorly. Large perforations also surround the principal figure on the posterior margin, arranged in two pairs at each angle and a group of three smaller perforations at the end of the keeled boss and extending across it. On the proximal third of the osteoderm are four irregular, non-symmetrical, peripheral figures, which are also surrounded by large foramina. Anterior and lateral contact margins between osteoderms are covered by numerous low and blunt protuberances.

The external surface of the osteoderm interpreted as part of a movable band (LACM 150607) has been eroded, so its

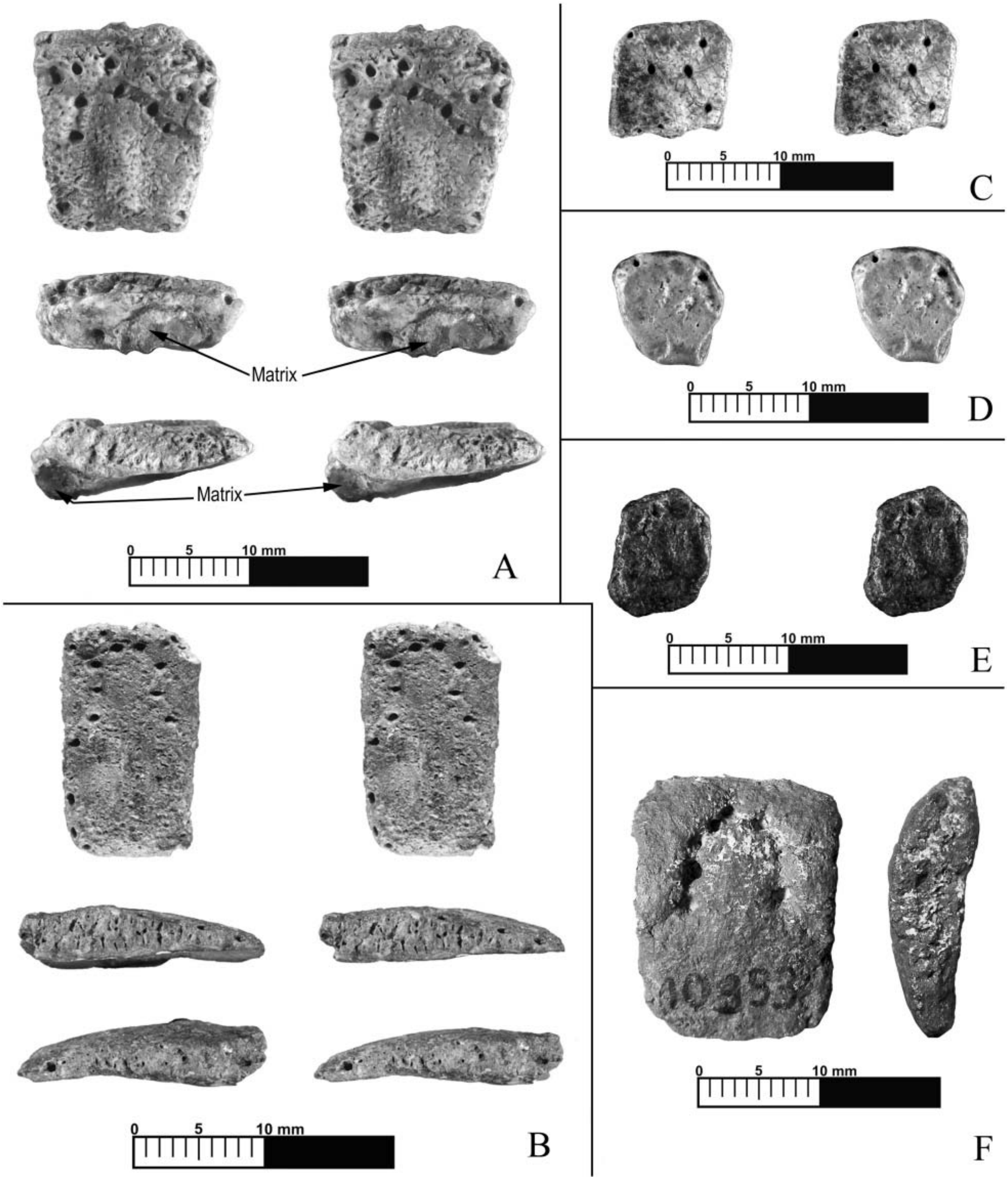

Figure 3. **A–E,** stereopairs of *Yuruatherium tropicalis* gen. et sp. nov.; **A**, holotype, LACM 150606, semimovable osteoderm; **B**, LACM 150607, movable osteoderm; **C**, LACM 150604, buckler osteoderm; **D**, LACM 150611, buckler osteoderm; **E,** LACM 150610, buckler osteoderm. **F**, *Yuruatherium intortum* new comb. (Ameghino, 1902a), holotype, MACN A-10953a.

outer bone layer is probably lost. Despite this, it shows a defined principal figure, also bordered by a series of large perforations that define a somewhat lageniform area, which is traversed by a keeled boss that reaches the posterior margin of the osteoderm but does not surpass it. As in the case of the semimovable osteoderm, the posterior angles of this element present a pair of large perforations and three smaller ones located at the end of the keel. Proximally, this

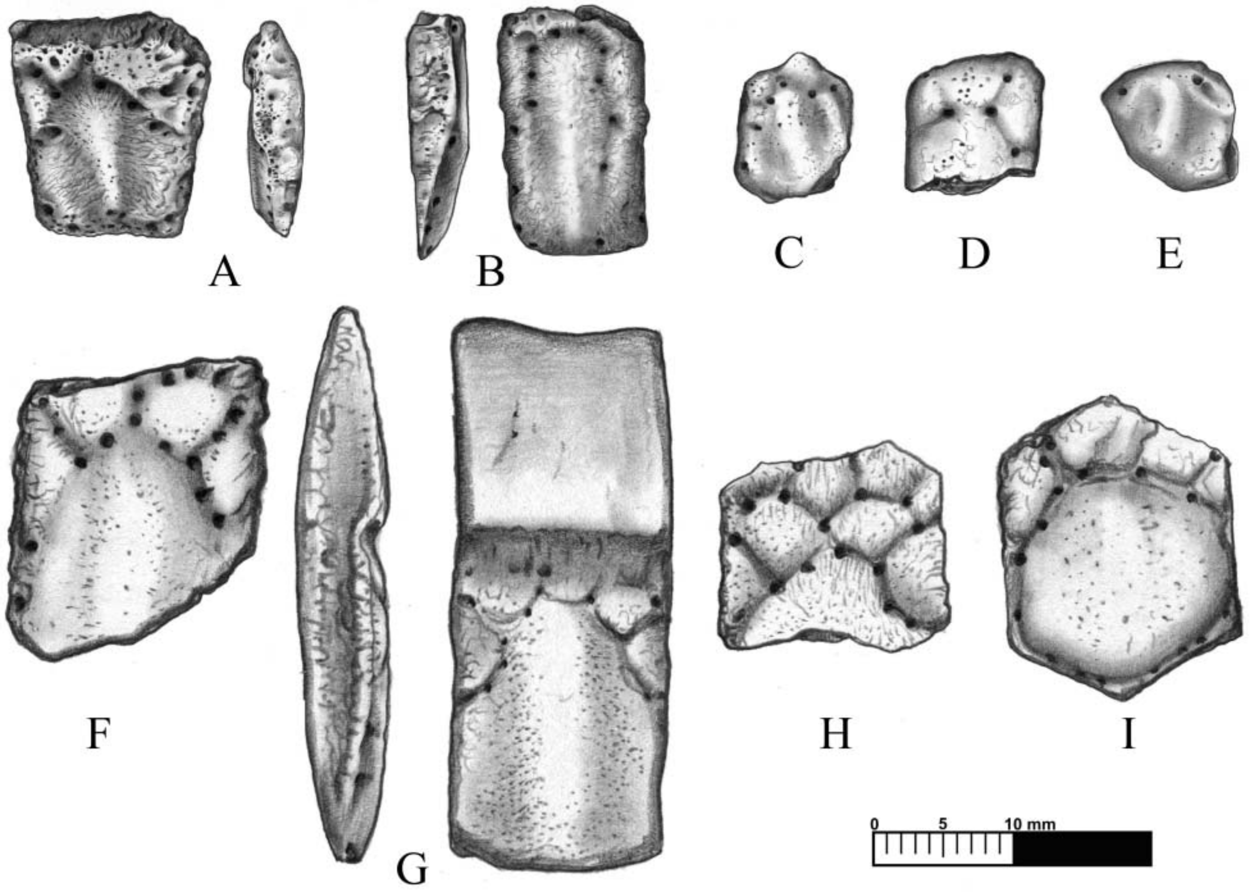

Figure 4. Osteoderms of *Yuruatherium tropicalis* gen. et sp. nov. (**A–E)** and *Eocoleophorus glyptodontoides* Oliveira, Ribeiro & Berqvist, 1997. **(F–I). A**, holotype, LACM 150606, semimovable osteoderm; **B**, LACM 150607, movable osteoderm; **C**, LACM 150610, buckler osteoderm; **D**, LACM 150604, buckler osteoderm; **E**, LACM 150611, buckler osteoderm. **F**, MNRJ 4598V, semimovable? osteoderm; **G**, MNRJ 4594V, movable osteoderm; **H**, MNRJ 4611V, buckler osteoderm; **I**, MNRJ 4607V, buckler osteoderm.

osteoderm shows three peripheral figures with a convex surface, delimited by perforations arranged in sulci. The anterior margin of the osteoderm is broken but it is inferred that it continued to form the anterior overlapping portion.

The remaining known osteoderms (LACM 150604, 150610 and 150611) that we assign to this new species are quite eroded. However, they maintain both the arrangement and type of proximal and lateral foramina defining an ornamentation pattern that is compatible with the above description, as well as a very similar surface in terms of rugosity. All of these osteoderms are unmovable elements and could correspond to the pelvic buckler, from either the central area (LACM 150604, Fig. 3C), part of the lateral region (LACM 150610, Fig. 3E), or even the shield margin (LACM 150611, Fig. 3D).

Yuruatherium intortum new comb. (Ameghino, 1902a) (Fig. 3F)

Machlydotherium intortum Amegino 1902a: 53.

Emended diagnosis. Semimovable osteoderm, with principal figure slightly convex and without medial keeled boss. Anterior portion of principal figure surrounded by two elongated anterolateral figures. Foramina on external surface restricted to anterior section of sulcus encircling principal figure. No foramina on lateral or posterior margins.

Holotype. MACN A-10953a.

Hypodigm. The holotype and MACN A-10953b.

Occurrence. Late Eocene (Mustersan SALMA), Patagonia, Argentina.

Measurements. Holotype, semimovable osteoderm: 22 mm long, 17 mm wide, 5 mm thick.

Remarks. According to Ameghino's (1902a, pp. 53–54) original description, only one of the three osteoderms deposited in the Ameghino Collection of the MACN (MACN A-10953) corresponds to the type material of *?Machlydotherium intortum*. Although there are no indications that these three specimens were ever associated, the other two partial movable osteoderms (MACN A-10953b) could belong to the same taxon. In one of these two, no perforations can be observed on the posterior margin and paired perforations on the anterior portion of the principal figure, behind the fracture, are similar in appearance to those in the type material of *Yuruatherium intortum* (= *?Machlydotherium intortum*).

On the other hand, because of their highly rugose surface and an apparently imperfect union between osteoderms, some of the osteoderms assigned to *Yuruatherium* resemble specimens referred to the enigmatic genus *Machlydotherium* (Middle-Late Eocene, Casamayoran-Mustersan SALMA).

Machlydotherium has been interpreted as related to Pampatheriidae (Ameghino 1902a; Castellanos 1937), as a primitive Glyptodontoidea (Carlini & Scillato-Yané 1993), or as sister group to the rest of the cingulates, forming a distinct clade with *Peltephilus* (Ciancio 2010). Unfortunately, only a few osteoderms are known for this taxon and there are almost no skeletal remains, either postcranial or craniodental, referred to this taxon with any degree of certainty. An exception is a fragmentary tooth which is bilobed and worn such that it presents a central ridge separating two asymmetrical diverging planes. This tooth is the strongest argument for assigning *Machlydotherium* to Pampatheriidae, given that the dentition of the oldest and undoubted pampatheriids (*Scirrotherium hondaensis* Edmund & Theodor, 1997) consists of bilobed elements. However, there is no evidence that this tooth was ever associated with the osteoderms.

Yuruatherium gen. nov. also shows some similarities with *Eocoleophorus* Oliveira *et al*., 1997 from the Oligocene of Taubaté, Tremembé, Brazil, and Salla, Bolivia (compare Fig. 4A with 4F, Fig. 4B with 4G, Fig. 4C with 4I, and Fig. 4D with 4H). The material from Santa Rosa could represent a structural stage prior to that of *Eocoleophorus* from the Oligocene of Brazil and Bolivia, as evidenced by the definition and symmetry of peripheral figures, which are fewer in number; a greater rugosity; and a more extended narrow portion of the principal figure. The polygonal principal figure in the unmovable osteoderms of the new genus, limited by straight sulci (see Figs 3C, 4D), is a primitive character within the Cingulata.

Family **Dasypodidae** Gray, 1821
Subfamily **Dasypodinae** Gray, 1821
Tribe **Astegotheriini** Ameghino, 1906
Parastegosimpsonia gen. nov.

Type and only species. *Parastegosimpsonia peruana* gen. et sp. nov.

Diagnosis. Osteoderms thick, with less rugose surface than those of *Stegosimpsonia*. As in the species of *Stegosimpsonia* from Laguna Fría and La Barda (Fig. 6C), and in contrast to *S. chubutana* (Fig. 6E) and *Stegosimpsonia* sp. from Cañadón Vaca (Fig. 6D), the osteoderms of this taxon have only a few foramina on the surface, which are arranged symmetrically around the principal figure; a pair of large foramina on the lateral margins, one at each side, behind the intersection of the proximal sulci with external osteoderm margin; and three smaller foramina on the posterior margin. A central keeled boss is elevated from the exposed surface; it is well defined, rounded in cross section and laterally circumscribed by a series of small foramina.

Etymology. ‘*Para*’ from greek παρά- ‘at or to one side of’, and ‘*stegosimpsonia*’ because of the similarity with this taxon.

Occurrence. Palaeogene (?Eocene), Yurúa River, Perú.

Remarks. The osteoderms referred to this genus are those of small dasypodids similar in size to *Dasypus hybridus* and *D. septemcinctus*. The osteoderms of euphractines can be clearly differentiated from those of dasypodines by several characteristics (e.g. greater thickness, strong union between osteoderms and absence of shared horny scales). However, these differences are not as evident in the more primitive taxa, closer to the time of divergence of the groups (see Ciancio & Carlini 2008b; Carlini *et al.* 2009; Ciancio 2010). The presence of denticular projections on the lateral contact surfaces between osteoderms and their thickness, as well as their ornamentation, suggest some affinity with basal euphractines. However, the sulci delimiting the narrower portion of the principal figure does not continue at the sides of the central keel, as in basal euphractines. The piliferous foramina of the osteoderms of *Parastegosimpsonia* are very small and there are large foramina surrounding the principal figure. Because of these characters, we reject the possibility that this taxon corresponds to a primitive euphractinae such as, for instance, *Parutaetus* Ameghino, 1902a (see Carlini *et al.* 2009).

Parastegosimpsonia peruana sp. nov.
(Fig. 5A)

Diagnosis. As for the genus.

Holotype. LACM 150608.

Etymology. ‘*peruana*’ from Perú, the country of origin.

Occurrence. Palaeogene (?Eocene), Río Yurúa, Perú.

Measurements. Anteroposterior length 8 mm, width 4.8 mm, thickness 2.2 mm.

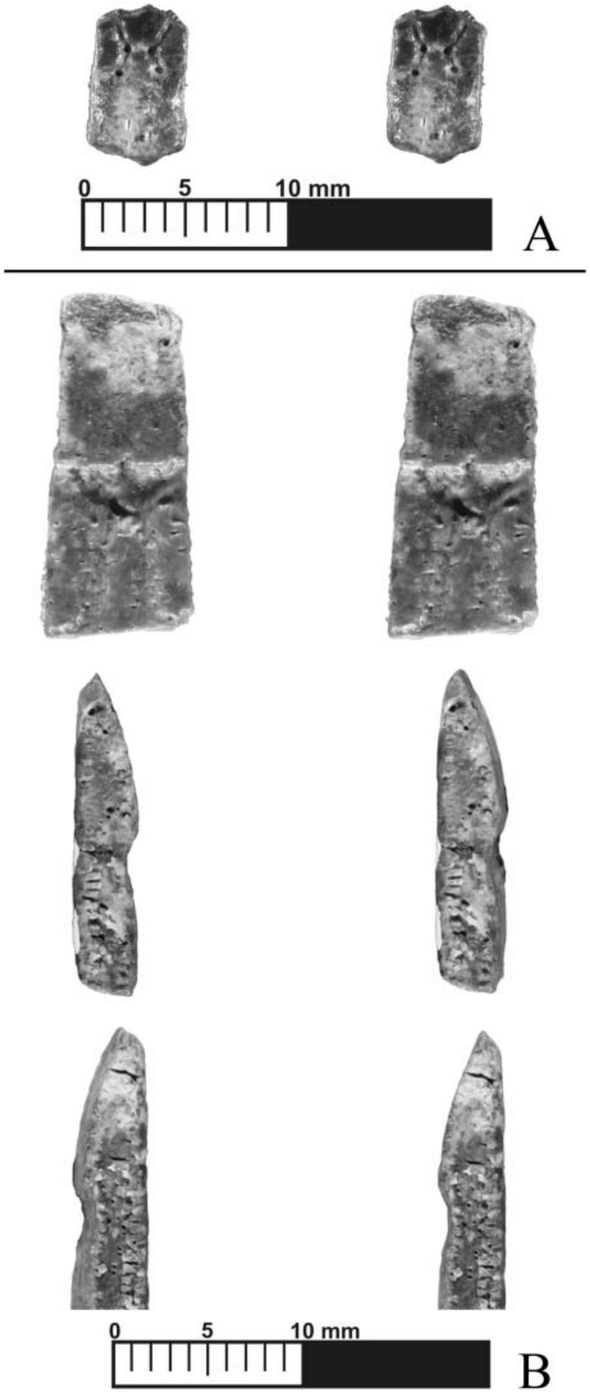

Figure 5. A, *Parastegosimpsonia peruana* gen. et sp. nov., holotype, LACM 150608, buckler osteoderm, stereopairs; **B**, ?*Parastegosimpsonia* sp. nov., movable osteoderm, LACM 150609, stereopairs.

Description. The buckler osteoderms of this species are relatively thick, like those of *Stegosimpsonia* (Fig. 6) and thicker than in the remaining Astegotheriini. Lageniform principal figure with short neck and surrounded by an anterior figure and a pair of anterolateral ones. Principal figure with well-defined medial keeled boss, rounded in cross section and flanked by series of small foramina. A pair of large foramina is arranged symmetrically at both sides of narrowest portion of the principal figure. A pair of large foramina also occurs on the lateral margins, one on each side, behind the intersection of the proximal sulci with the external margin of the osteoderm. This differs from the condition in the species of *Stegosimpsonia* that possess several foramina on the lateral margins. The posterior margin bears three small piliferous foramina.

Remarks. Shockey *et al*. (2009) reported the discovery of Deseadan fossils in the Moquegua Formation, southern Perú. Among these fossils, they described a movable osteoderm questionably assigned to Dasypodinae, based mainly on the assumption of the presence of overlapping scales covering lateral areas of two adjacent scutes (secondary horny scales), among other characteristics (e.g. small size, lateral margin smooth). However, the external morphology of the osteoderm from Moquegua suggests that it is from a species of Euphractinae (probably Euphractini). The characteristics considered diagnostic for assignment to a species of Euphractinae are: (1) the presence of three parallel figures, one central and two peripheral, separated by straight sulci that reach the posterior margin; and (2) the partition of the lateral figures into three figures by two shallow transverse sulci. There is no evidence for the presence of shared horny scales; indeed, the external morphology suggests the absence of such scales. Although the osteoderm is very small, similar in size to *Parastegosimpsonia* and other dasypodines, some Euphractines are also very small, such as *Prozaedyus* and *Parutaetus*.

Additionally, in the recently described fauna from Contamana, the presence of an Astegotheriini close to *Prostegotherium notostylopianum* was mentioned (Antoine *et al.* 2011). One of us (MC) analysed these remains (two osteoderms) and identified characters (e.g. lageniform principal figure with short neck and a pair of large foramina symmetrically arranged at both sides of the narrowest portion of the principal figure) that suggest these are closer to *Parastegosimpsonia*.

?*Parastegosimpsonia* sp. nov.
(Fig. 5B)

Material. LACM 150609, partial movable osteoderm.

Description. A middle-sized dasypodid with osteoderms similar in size to those of *Dasypus kappleri*. The osteoderms are from movable bands with a lageniform principal figure and a few very small perforations within the wide sulci that bound the principal figure, which does not reach anteriorly the transition zone of the osteoderm. Principal figure and lateral figures are very convex, with a well-defined cephalic

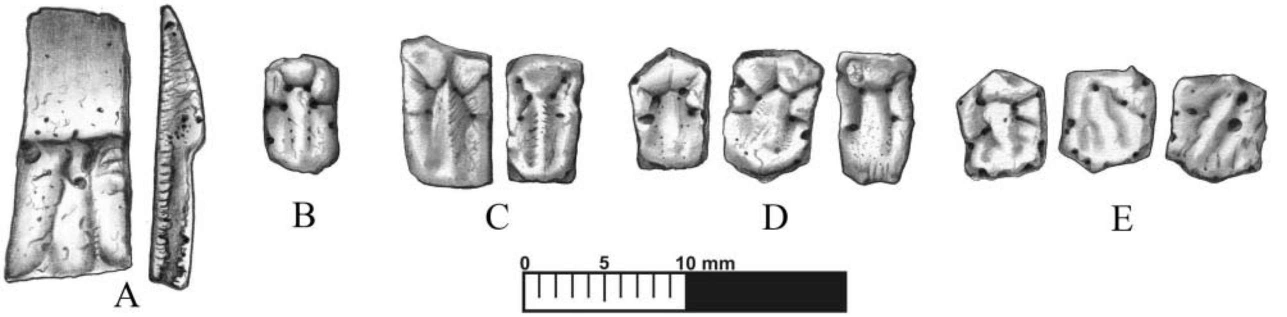

Figure 6. **A**, ?*Parastegosimpsonia* sp. nov., movable osteoderm, LACM 150609; **B**, *Parastegosimpsonia peruana* gen. et sp. nov., holotype, LACM 150608, buckler osteoderm; **C**, *Stegosimpsonia* sp. nov. from the Paso del Sapo fauna; **D**, *Stegosimpsonia* sp. nov. from Cañadón Vaca (Vacan sub-age of Casamayoran SALMA); **E**, *Stegosimpsonia chubutana* (Ameghino, 1902a) from Gran Barranca (Barrancan sub-age of Casamayoran SALMA).

imbricating portion. Contact areas between osteoderms are weakly dentate, with central area concave and smooth, but more dentate than in the remaining Astegotheriini.

Remarks. We tentatively assign this specimen to *Parastegosimpsonia* because some characters (e.g. lageniform principal figure, smooth and concave surfaces of contact areas) identify it as an Astegotheriini.

Discussion

The cingulate fauna of Santa Rosa, Perú cannot be placed within a known biostratigraphical sequence because no other cingulates from this latitude are known. Consequently, any biochronological information will be limited to comparisons with much better-known faunas from higher latitudes (e.g. Patagonia). Regarding the taxonomy of the Santa Rosa specimens, all undoubtedly represent new species. Their discovery and description open new and positive perspectives for hypotheses regarding the evolution of cingulates because they allow the evaluation of the biochronological importance of southern sequences, the identification of cladogenetic events and speculation on palaeobiogeographical aspects of xenarthrans during the Palaeogene.

The study of the taxonomic associations represented in the Eocene-Oligocene sediments of Patagonia and their relative diversity provides a broad perspective on the way these faunas changed in this palaeoenvironmental and palaeoclimatic setting. The relative diversity of the groups recorded as part of the different faunas represented in Patagonia suggest a close correlation with climatic changes (Carlini *et al.* 2009, 2010; Ciancio 2010). Climates during the Palaeogene in southern South America (SSA) were affected by a number of factors, such as tectonic movements, volcanism, sea-level changes, marine palaeotemperatures and glaciations (Ortiz-Jaureguizar & Cladera 2006). Changes in marine temperatures occurring in the South Atlantic Ocean (Fig. 7) were directly or indirectly reflected in inland environments, especially in SSA because of the 'peninsular' nature of Patagonia (Carlini *et al.* 2009, 2010; Ciancio 2010).

During the early Middle Eocene–Oligocene, a series of changes occurred in Patagonia regarding the composition of the cingulate fauna. The early Middle Eocene (Paso del Sapo Fauna) corresponds to the time of greatest diversity within Astegotheriini (Tejedor *et al*. 2009) and sea temperatures during this period indicate high values in what is known as the 'Early Eocene Climatic Optimum' (Pascual *et al.* 1996; Zachos *et al.* 1994, 2001).

During the Middle Eocene (Casamayoran SALMA), the diversity within Astegotheriini progressively decreased, in contrast to the appearance and increasing diversification within Euphractinae, frequently in areas with a temperate climate (see Krmpotic *et al*. 2009). In addition, the first species of Glyptodontoidea (Palaeopeltidae) is recorded. This could be linked to the gradual decrease of sea temperature (Carlini *et al.* 2009, 2010). Sea temperatures began a long term decline in the Middle Eocene, which continued into the Late Eocene, decreasing by nearly 8° to 9°C, with an additional 2°C of cooling by the Early Oligocene in high latitudes (Zachos *et al.* 1994). The cooling event at the Eocene-Oligocene transition, which is correlated with changes in sea circulation and the appearence of the first icesheets in Antarctica (Oi-Glaciation, see Zachos *et al.* 2001, fig. 7), caused a faunal turnover in marine and continental biotas. Regional examples among land-mammal faunas of such turnovers include the 'Grand Coupure' (Sthelin 1909), the 'Terminal Eocene Event' (Wolf 1978) and the 'Patagonian Hinge' (Goin *et al*. 2010). At the time of these turnovers, the Patagonian cingulate faunas record the disappearance of Astegotheriini from the fossil record (missing after the Casamayoran SALMA) and diversification within Euphractinae. The latter is marked by the

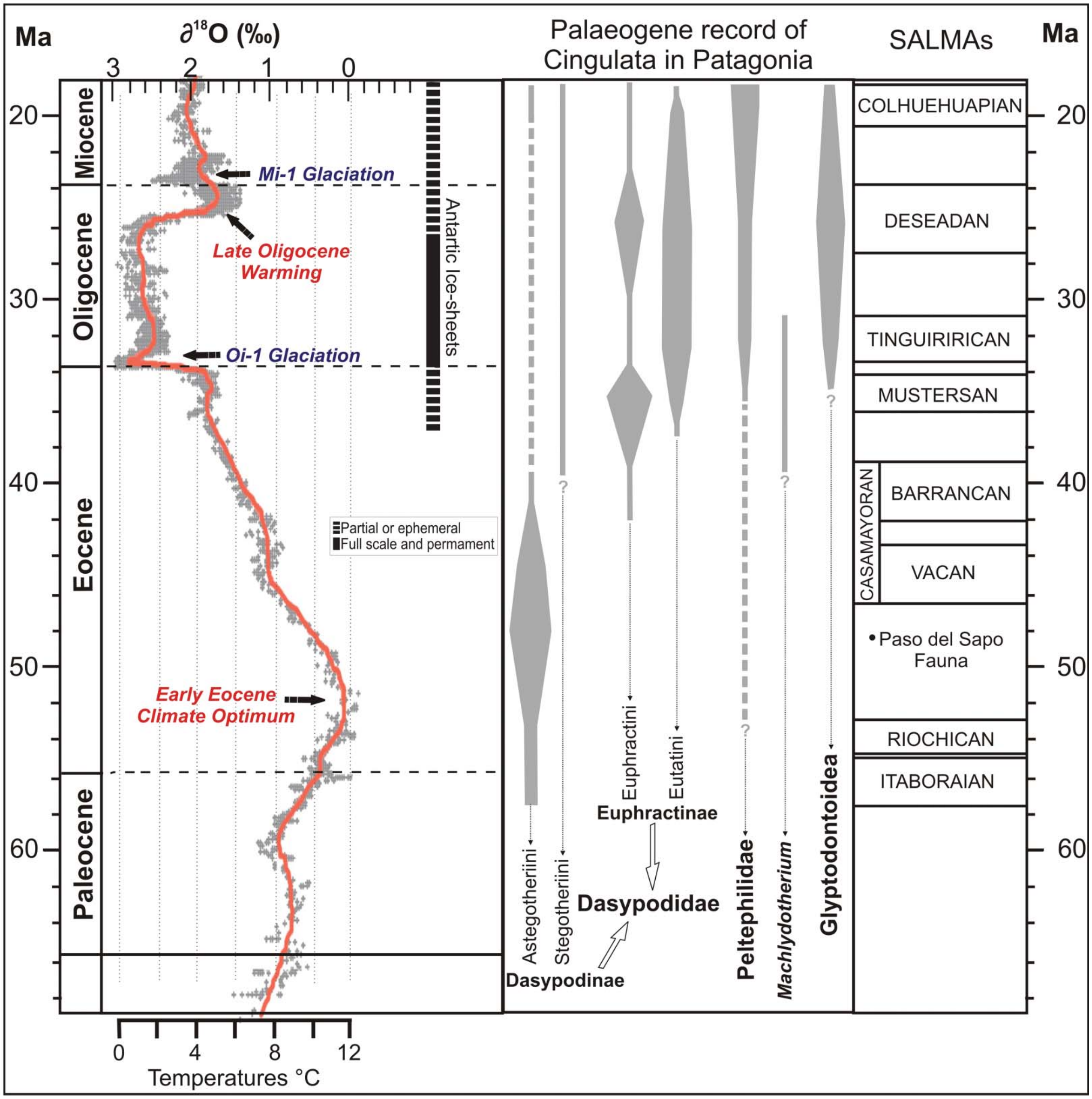

Figure 7. Approximate temporal placement of Cenozoic dasypodid-containing faunas discussed in the text, in relation to the main Cenozoic climatic events; the δ^{18}O temperature scale was computed for an ice-free ocean (see Zachos *et al*. 2001) (figure modified from Carlini *et al.* 2005a, 2010). In 'Palaeogene record of Cingulata in Patagonia', the thicknesses of the bars corresponding to the taxa are schematic and they do not strictly express taxon numbers.

early diversification of Euphractini and the evolution of medium-sized to large forms with greatly developed pilosity (Eutatini), which is associated with the change to temperate and cold climates that prevailed during the Oligocene (Ciancio & Carlini 2007). This period also coincides with the appearance of other large-sized cingulates such as *Machlydotherium* and Glyptatelinae. The latter taxa have been associated with herbivorous diets and open environments (Carlini *et al*. 2009, 2010).

The record of Cingulata in low latitude fossil beds is poor, especially in Palaeogene deposits, therefore the cingulates from Santa Rosa are particularly relevant to our understanding of the evolution of this group of xenarthrans in South America from both palaeobiogeographical and temporal perspectives. Using the evolutionary hypotheses proposed on the basis of studies of mammalian faunas (e.g. rodents, marsupials, notoungulates) from Patagonia as the reference for a strict biochronological context, the sediments bearing the Santa Rosa fauna are comparable to those deposited during the Late Eocene-Early Oligocene of Patagonia. From the studies of Marsupialia, Goin & Candela (2004) considered the Santa Rosa fauna to be Middle to Late Eocene in age but they suggested that there remained a possibility that it was Early Oligocene. For notoungulates, a Tinguiririان (Early Oligocene) to Deseadan (Late Oligocene) SALMA age was estimated based on comparisons with notoungulates of known age and on the degree of hypsodonty (Shockey *et al.* 2004). Based on the stage of evolution of their teeth, the Santa Rosan rodents are more primitive than those known from Oligocene deposits (from the Tinguiririان and Deseadan SALMAs) (Frailey & Campbell 2004). Based on these combined interpretations, a Mustersan age to be inferred for this fauna (Campbell 2004).

In the case of Cingulata, by comparing the fauna from Santa Rosa with the sequence of Eocene-Oligocene faunas in Patagonia, we estimate its maximum age as Middle Eocene. However, the latitudinal location of the fossil site (9°S, more than 35° north of the Patagonian faunas) must be taken into account because it is common to find taxa at lower latitudes with more primitive characteristics than in taxonomically related contemporary groups in higher latitudes (Carlini *et al*. 1997, 2008; Ciancio *et al.* 2005, 2008). Examples of such instances include those from La Venta (Middle Miocene, Colombia): *Megalodus, Prothoatherium* and *Prolicaphrium* (Litopterna, Proterotheriidae) (McKenna 1956; Ciffelli & Guerrero 1997), *Pachybiotherium* (Microbiotheria, Microbiotheriidae) (Goin 1997), *Nanostegotherium* (Dasypodidae, Astegotheriini) (Carlini *et al.* 1997); and from Venezuela: *Bounodus* (Litopterna, Proterotheriidae) (Carlini *et al.* 2006) from Urumaco deposits (Upper Miocene), and *Cardiatherium* (Rodentia, Cavioidea) and *Neoepiblema* (Rodentia, Chinchilloidea) (Vucetich *et al.* 2010) from the San Gregorio (Pliocene) deposits. All of these taxa were found in younger sediments than would be expected according to their evolutionary state with respect to the biostratigraphical sequences known from higher latitudes. Thus, we suggest that the Santa Rosa palaeofauna could prove to be somewhat younger than could be inferred directly from the context of the Patagonian palaeofaunas.

In the case of *Yuruatherium tropicalis*, we might consider that this species is more derived than the Late Eocene *Y. intortum*, given that it shows a more marked division of the anterior peripheral figures and piliferous foramina on the posterior and lateral margins, but that it is less derived than the Late Oligocene *Eocoleophorus glyptodontoides* because the division between figures never reaches the symmetry or the number present in the latter genus. This would suggest a latest Eocene to Early Oligocene age.

Regarding *Parastegosimpsonia peruana*, although the available material is extremely sparse, the thickness of its osteoderms is as great as in most species of *Stegosimpsonia* but the pattern of its surface is as primitive as that of the Casamayoran SALMA (Middle Eocene) species. In addition, as in the latter species, only a few foramina surround the principal figure. Thus we suggest that *Parastegosimpsonia* might be an example of a primitive taxon occurring at low latitudes.

Summing up these inferences and taking into account the new information from Contamana (Peruvian Amazonia), the Santa Rosa fauna may be older than the Tinguiririان SALMA and consequently closer to Late Eocene in age.

Conclusions

The Palaeogene Cingulata from southern South America (SSA) are quite well-known and it is possible to see evolutionary changes and changes in diversity occurring through the Palaeogene. However, it is not feasible to discern comparable changes in northern South America (NSA) because of the scarcity of Palaeogene sediments containing cingulates. That is why these new records from Santa Rosa are important keys for improving our understanding of the history of cingulates in NSA.

The presence of Astegotheriini (Dasypodinae) in the late Palaeogene of Perú gives us relevant data for inferring the palaeoclimates of that period in these latitudes. During the period estimated as the age of the Santa Rosa fauna (Late Eocene-Early Oligocene), an important faunal change was registered in Patagonia, most probably in response to the global climatic deterioration that began in the Middle Eocene and culminated at the Eocene-Oligocene transition. This change is reflected in cingulate diversity, primarily in the loss of Astegotheriini (Dasypodinae) and the diversification of Euphractinae (Euphractini and Eutatini), a group that is not recorded both in the Santa Rosa fauna and in Contamana (Peruvian Amazonia). This might indicate that the significant climatic changes that occurred in the Late Eocene and Early Oligocene in SSA did not occur in the same way in NSA, where climatic changes might have been more moderate.

As originally described, *Eocoleophorus* was an enigmatic cingulatan with uncertain affinities found exclusively in Oligocene sediments of NSA (Bolivia and Brazil; Ciancio 2010; Ciancio & Carlini 2011). The recognition of the new genus *Yuruatherium* allows us to postulate a new hypothesis about *Eocoleophorus* and its relationships. That is, *Yuruatherium* could be the sister group of *Eocoleophorus*, and the lineage *Yuruatherium-Eocoleophorus* might have evolved in areas with intertropical environmental conditions that were restricted to lower latitudes after the Eocene-Oligocene transition.

Finally, the Santa Rosan cingulate fauna does not correspond to any Patagonian Palaeogene fauna and it represents a case in which the use of a Patagonian 'biochronologic standard' is not accurate for estimating a relative age outside Patagonia. In this instance, the use of 'Patagonian standards' would not be appropriate because NSA and SSA apparently did not have the same palaeoecological history during the Palaeogene.

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