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Diversity of cingulate xenarthrans in the middle–late Eocene of Northwestern Argentina

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The study of Paleogene mammals of intermediate and low latitudes has increased in the last decades and has been clearly demonstrated their importance in the comprehension of the evolution and faunistic changes outside Patagonia. The study of these faunas permits establishing new comparisons among contemporaneous faunistic associations, completing the distributional patterns, and evaluating evolutionary changes in the lineages in relation to climatic conditions prevailing in each of the different regions. In this work we study the diversity of Dasypodidae recovered from the Geste Formation (Northwestern Argentina). Bearing levels of Geste Formation were referred alternatively to a Barrancan subage of Casamayoran SALMA (middle Eocene, Lutetian–Bartonian) or a Mustersan SALMA (middle–late Eocene, Bartonian–Priabonian) on faunistic comparations with their equivalent in Patagonia, although absolute isotopic data indicates ca. 37–35 Ma (late Eocene, Priabonian). We described the following taxa of Dasypodidae: (i) Dasypodinae Astegotheriini: cf. *Astegotherium* sp., ?*Prostegotherium* sp., *Parastegosimpsonia* cf. *P. peruana*; (ii) Dasypodinae indet.; (iii) Euphractinae Euphractini: *Parutaetus punaensis* sp. nov.; (iv) Dasypodidae incertae sedis: *Pucatherium parvum*, *Punatherium catamarcensis* gen. et sp. nov. In comparison with other beds bearing Eocene cingulate faunas from Northwestern Argentina, Geste Formation presents the greatest diversity of dasypodids. This association is consistent with a late Eocene age and shows a taxonomic and biogeographic relevant features given by a unique specific composition: (i) it differs from that known for contemporaneous faunas from Southern latitudes and younger associations from more tropical areas; (ii) it includes genera with close affinities to those distant areas; (iii) it presents unique taxa typical from Eocene units exposed at Northwestern Argentina. This highlights the evolutionary and biogeographic meaning of the cingulate of the Geste Formation and supports the idea that the faunistic regionalization probably obeyed to latitudinal than to temporal factors.

Key words: Mammalia, Cingulata, Dasypodidae, Palaeogene, Eocene, South America, Central Andean Puna.

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Introduction

Even though the most ancient cingulates come from the early Eocene outcrops of Itaboraí (Brazil, Itaboraian SALMA) (Oliveira and Berqvist 1998; Berqvist et al. 2004; Woodburne et al. 2014), the group is well-known from Riochican (early Eocene; Simpson 1948; Gelfo et al. 2010; Goin et al. in press) deposits exposed in the Southern Cone of South America (Patagonia, Argentina). Since then, the group was persistently recorded in almost all the Cenozoic South American faunistic associations (Carlini et al. 2010; Ciancio et al. 2013a).

In recent decades, the interest in the study of Paleogene mammals of intermediate and low latitudes has increased continuously because the significance in the comprehension of the evolution and faunistic changes outside Patagonia, has been clearly demonstrated (Carlini et al. 1997; Shockey

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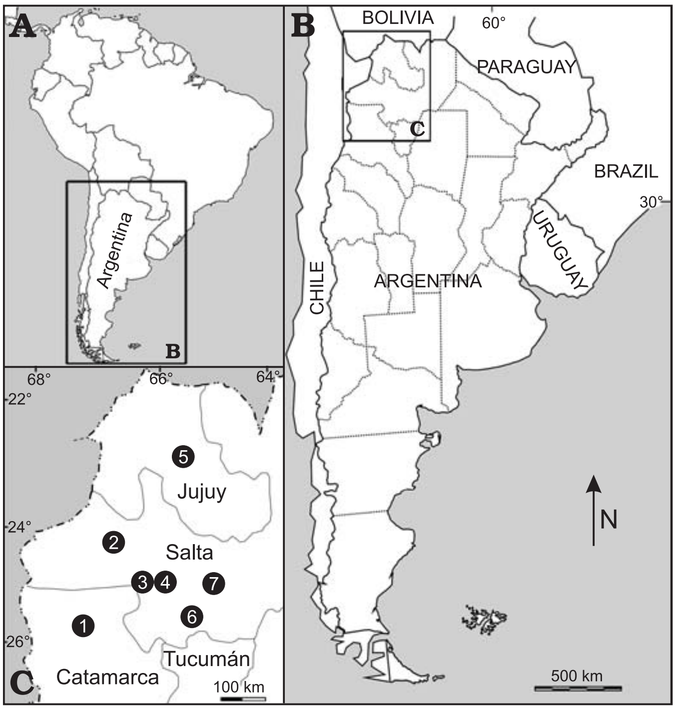

Fig. 1. **A**, **B**. Location of the studied area in South America. **C**. Map of Northwestern Argentina showing the main middle and middle–late Eocene fossil-bearing localities: 1, Antofagasta de la Sierra; 2, Quebrada El Paso; 3, Luracatao valley; 4, Cerro Tin Tin; 5, El Aguilar; 6, Estancia Pampa Grande—El Simbolar; 7, Juramento River.

et al. 2004; Reguero et al. 2008; García-López and Powell 2011; Antoine et al. 2012; Ciancio et al. 2013b; García-López and Babot 2015). The study of these faunas permits establishing new comparisons among contemporaneous faunistic associations, completing the distributional patterns, and evaluating evolutionary changes in the lineages in relation to the climatic conditions prevailing in each of the different regions (Carlini et al. 1997, 2006; Ciancio et al. 2013a).

In Northwestern Argentina the fossil mammal-bearing Paleogene units are widely distributed, mainly in Salta, Jujuy, and Catamarca provinces. The geologic units most extensively prospected and richest in terms of the fossil content are those formed during the Eocene (56.0–33.6 Ma, Ypresian–Priabonian; Cohen et al. 2013) (Powell et al. 2011 and references therein).

Up to now, the Paleogene xenarthran record in this region is restricted to the following Eocene geologic units: (i) Geste Formation exposed at Antofagasta de la Sierra (Catamarca Province) and Quebrada El Paso, near Pozuelos salt flat (Salta Province); (ii) Quebrada de los Colorados Formation exposed at Luracatao valley and Cerro Tin Tin (Salta Province); (iii) Casa Grande Formation exposed at Sierra Aguilar (Jujuy Province); and (iv) Lumbrera Formation exposed at Pampa Grande and Juramento River (Salta Province) (Fig. 1).

Among these units, one of the most interesting is the Geste Formation, mainly by the diversity and abundance of small to medium-size fossil vertebrate, especially mammals. The age of the fossil-bearing levels was recently isotopically dated and assigned to the late Eocene, although also has been proposed a middle Eocene age based on biochronological data (see Discussion). Initially the faunal associations were partially studied, being the most significant works those referred to the entire vertebrate assemblage (López 1997), and other restricted to particular groups, such as metatherians (Goin et al. 1998) and notoungulates (Bond and López 1995; López and Bond 1995; Reguero et al. 2008). In the last years, new paleontological prospections at the Geste Formation resulted in the discovery of new notoungulates (García-López and Babot 2015) and metatherians (Babot and García-López 2014). However, to date, no specific and detailed work on the diversity of xenarthrans were performed in this region.

In the Geste Formation, xenarthrans include only dasypodids, which are mainly represented by isolated osteoderms, although a petrosal assigned to Dasypodinae was recently described (Babot et al. 2012). Most taxa previously recognized were assigned to Astegotheriini (Dasypodinae); among them, cf. *Astegotherium* sp. and *Prostegotherium* sp. (Alonso et al. 1988), a new species assigned doubtfully to Astegotheriini (not formally described; Vizcaíno 1994), Astegotheriini indet. (Lopez 1997), and *Prostegotherium notostylopianum*, *Prostegotherium* sp., and *Astegotherium* sp. (Powell et al. 2011; Herrera 2013). Powell et al. (2011) mentioned the presence of cf. *Utaetus* (Euphractinae), and recently Herrera et al. (2012) described *Pucatherium parvum*, an indeterminate Dasypodidae.

In this work we study the diversity of Dasypodidae recovered from the Geste Formation levels exposed in Antofagasta de la Sierra (Catamarca Province) and Quebrada El Paso (vicinities of Pozuelos salt flat, Salta Province) (Fig. 1). In addition, we compare this association with that known for other South American Paleogene faunas and discuss its relevance in the resolution of the age of the Geste Formation. We also provide additional geological data of this unit, including a detailed stratigraphic profile of the fossil vertebrate-bearing horizons exposed at Antofagasta de la Sierra, and the geographical distribution of the formation in Catamarca and Salta Provinces.

Institutional abbreviations.—MHAS, Museo del Hombre de Antofagasta de la Sierra, Antofagasta de la Sierra, Catamarca, Argentina; MLP, Museo de La Plata, Facultad de Ciencias Naturales y Museo de La Plata, Universidad Nacional de La Plata, Buenos Aires, Argentina; PVL, Colección de Paleontología de Vertebrados Lillo, Tucumán, Argentina.

Other abbreviations.—SALMA, South American Land Mammal Age.

Geological setting

Turner (1960) recognized the Pastos Grandes Group as a lithostratigraphic unit including Geste, Pozuelos, and Sijes formations. The Geste Formation is broadly distributed in different basins of the NW Argentina (Fig. 2) as the Salar de Pastos Grandes (Blasco et al. 1996; DeCelles et al. 2007), Salar de Arizaro (Zappettini and Blasco 2001; Jordan and Mpodozis 2006), Salar de Antofalla (Kraemer et al. 1999; Carrapa et al. 2005; Seggiaro 2007), Salar del Hombre Muerto (Hongn and Seggiaro 2001) and in the surrounding areas of Antofagasta de la Sierra (Jordan and Alonso 1987). The distribution of this formation is mainly along NS areas close to the Eastern margin of the Puna Plateau, coinciding with the predominant Andean direction (e.g., Cumbres del Macón and Cordones del Gallego and Pozuelos ranges, Salta; Carachipampa and Incahuasi valleys and Sierra de Filo Colorado, Catamarca).

The Geste Formation type section of Pastos Grandes basin (Turner 1961, 1964) comprises mainly coarsening upward sandstone, conglomerate and subordinate shale deposited on a fluvial and alluvial fan environment. This unit covers unconformable different Paleozoic basements along the spatially separated basins where it outcrops: Copalayo or Coquena Formation in Pastos Grandes basin (Upper Ordovician; Alonso 1992; Blasco and Zappettini 1996), Falda Ciénaga Formation in Antofagasta de la Sierra and Cordón del Gallego (Ordovician; Aceñolaza et al. 1976; Hongn and Seggiaro 2001), Coquena Formation in Sierra de Calalaste (Upper Ordovician; Blasco and Zappettini 1996), and Patquía de la Cuesta Formation (Permian; Seggiaro 2007) in surrounding areas of the Antofalla volcano.

In the Pastos Grandes basin, in outcrops located on the eastern flank of the Sierra de Copalayo (Salta), the Geste Formation was divided by Alonso (1992) in three members: lower, middle, and upper. The fossil-bearing level was restricted to the middle member which differed from the others by its typical reddish colour and the lithology (mainly composed by sandstone and mudstone, with low participation of conglomerate sets). This author also proposed a stratigraphic correlation between the Geste Formation fossiliferous level exposed at Sierra de Copalayo and those of Antofagasta de la Sierra (Catamarca), based on the geological (lithology and fossil content) and physical (colour) similarity. DeCelles et al. (2007) and Carrapa and DeCelles (2008) used the same division, and proposed radiometric Paleogene depositional ages for the Geste Formation in the Pastos Grandes basin.

In Antofagasta de la Sierra the fossil-bearing level (Fig. 1, 2) is outcropping in the northern and southeastern areas of the town (Alonso 1992; Goin et al. 1998). The base of this member is not exposed and the top is unconformable covered by Pliocene ignimbrite from the Cerro Galán volcanic complex. Fine to medium micaceous reddish sandstone are intercalated with coarse conglomerate-sandstone matrix and subordinate mudstone. The succession thickness is approximately 600 m and has a coarsening upward trend (Fig. 3). The sandstone beds have primary structures developed as low-angle trough cross-stratification at the base, the conglomerates are present in lenticular beds with planar cross-bedding, and the mudstone have a diffuse interne bedding structure. Sedimentological features indicate that this member was deposited in a braided fluvial environment with minor floodplains that is geologically comparable with the middle member exposed at the the Salar de Pastos Grandes (Alonso 1992). Based on the high content of psamitic material, and the high degree of fragmentation and disarticulation of the fossil material we infer a high-energy fluvial environment.

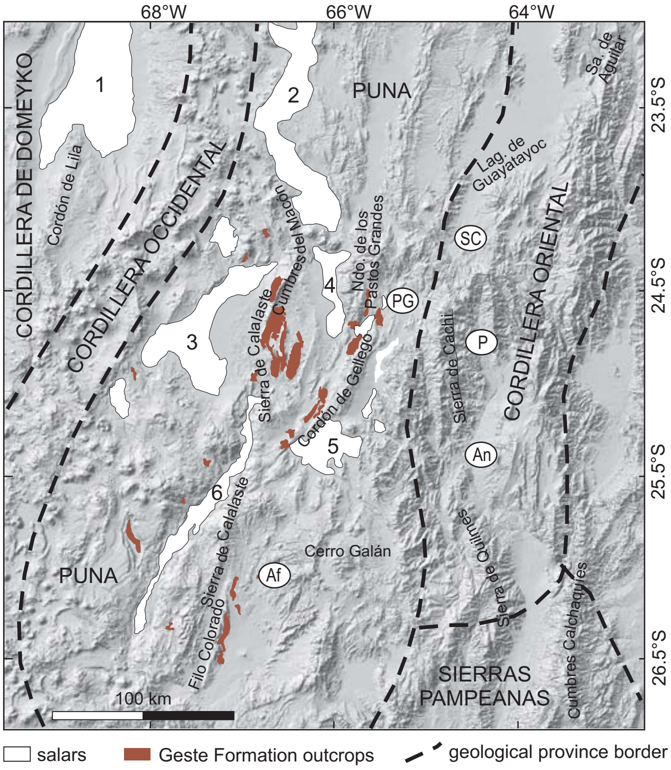

Fig. 2. Distribution of Geste Formation in different basins of the Northwestern Argentina. The distribution of this formation is mainly along N-S areas close to the Eastern margin of the Puna Plateau, coinciding with the predominant Andean direction. 1, Salar de Atacama; 2, Salar del Rincón; 3, Salar de Arizaro; 4, Salar de Pocitos; 5, Salar del Hombre Muerto; 6, Salar de Antofalla; SC, San Antonio de los Cobres; PG, Santa Rosa de los Pastos Grandes; P, La Poma; An, Angasto; Af, Antofagasta de la Sierra.

Material and methods

The materials here studied include isolated osteoderms which were recovered at Antofagasta de la Sierra (Catamarca Province, Argentina; 26°03’43” S, 67°24’27” W) and Quebrada El Paso, near the Salar of Pozuelos (Salta Province; 24°39’16.08” S, 66°45’4.83” W). This collection is composed by pieces gathered during paleontological prospections conducted between 1980 and 1993 (MLP) and recent fieldworks carried out since 2007 (MHAS).

The dasypodid osteoderms are elements frequently preserved in the fossil record; since the discovery of the earliest known records of the group, these pieces were consistently collected in almost all the South American fossil mam-

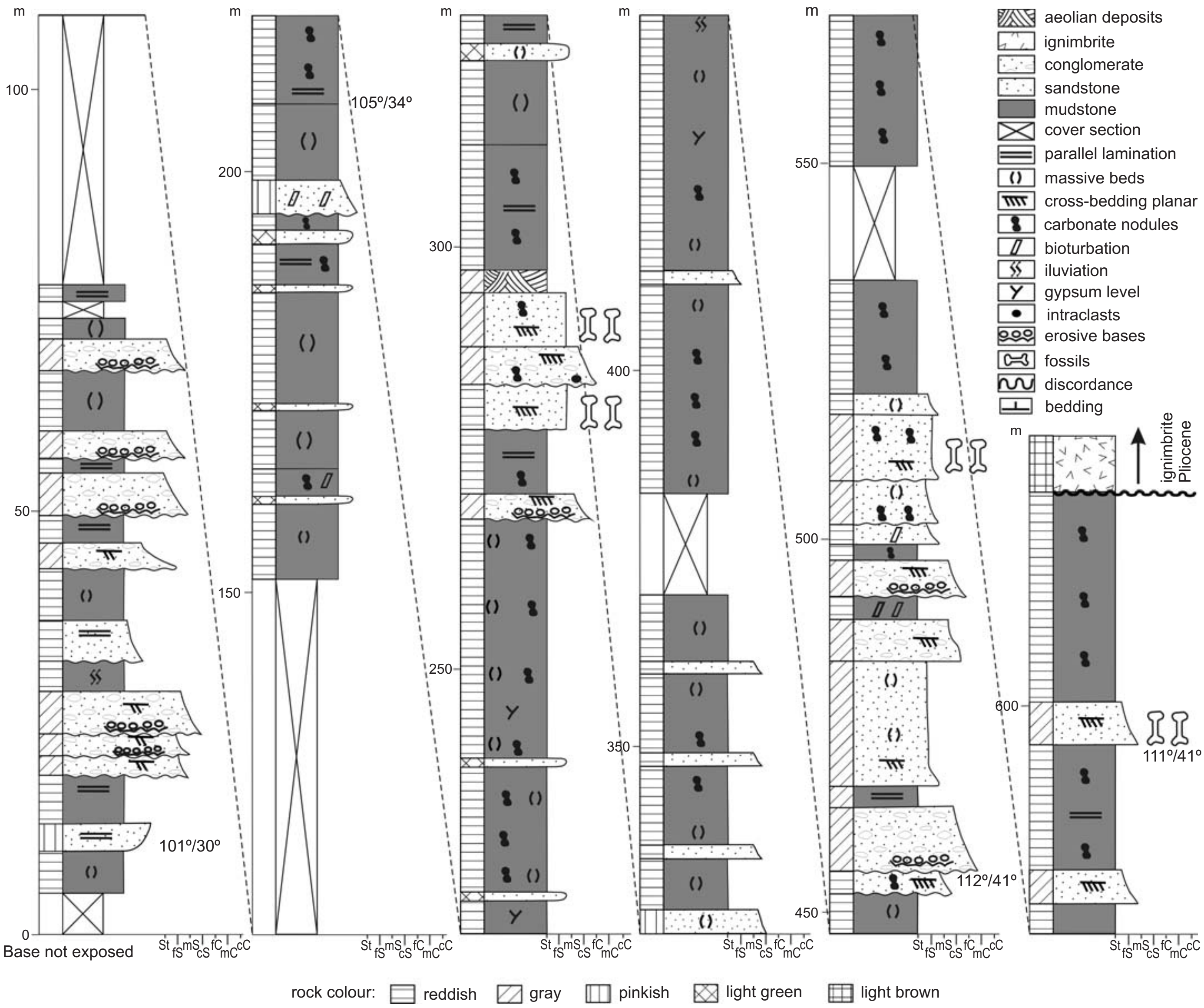

Fig. 3. Generalized lithostratigraphic profile of the Geste Formation exposed at Antofagasta de la Sierra, Catamarca, Argentina. Numbers indicate the bedding: strike/dip. Abbreviations: St, siltstone; S, sandstone; C, conglomerate; f, fine; m, medium; c, coarse.

mal faunas. The morphology of the osteoderms has a high diagnostic value for taxonomic determinations (Scillato-Yané 1982; Vizcaíno 1994; Carlini and Scillato-Yané 1996; Fernicola and Vizcaíno 2008; Carlini et al. 2010). However, this value is subject to the comparison of the elements corresponding to homologous regions of the carapace. Therefore, it is necessary to identify the intra and interspecific variability in the morphologic pattern of the osteoderms at the different portions of the carapace. In order to minimize misinterpretations, we examined this variation on the carapace or associated groups of osteoderms of some extinct and extant armadillo taxa.

Measurements of these and other specimens were taken using manual calipers. Osteoderms terminology follows Krmpotic et al. (2009), Ciancio et al. (2013a), and Francia and Ciancio (2013).

Systematic paleontology

Order Cingulata Illiger, 1811

Family Dasypodidae Gray, 1821

Subfamily Dasypodinae Gray, 1821

Tribe Astegotheriini Ameghino, 1906

Genus *Astegotherium* Ameghino, 1902

Type species: *Astegotherium dichotomus* Ameghino, 1902; Patagonia Argentina, middle Eocene.

cf. *Astegotherium* sp.

Fig. 4A.

Material.—MHAS 067, fixed osteoderm from Quebrada El Paso, near the Pozuelos salt flat, Los Andes Department,

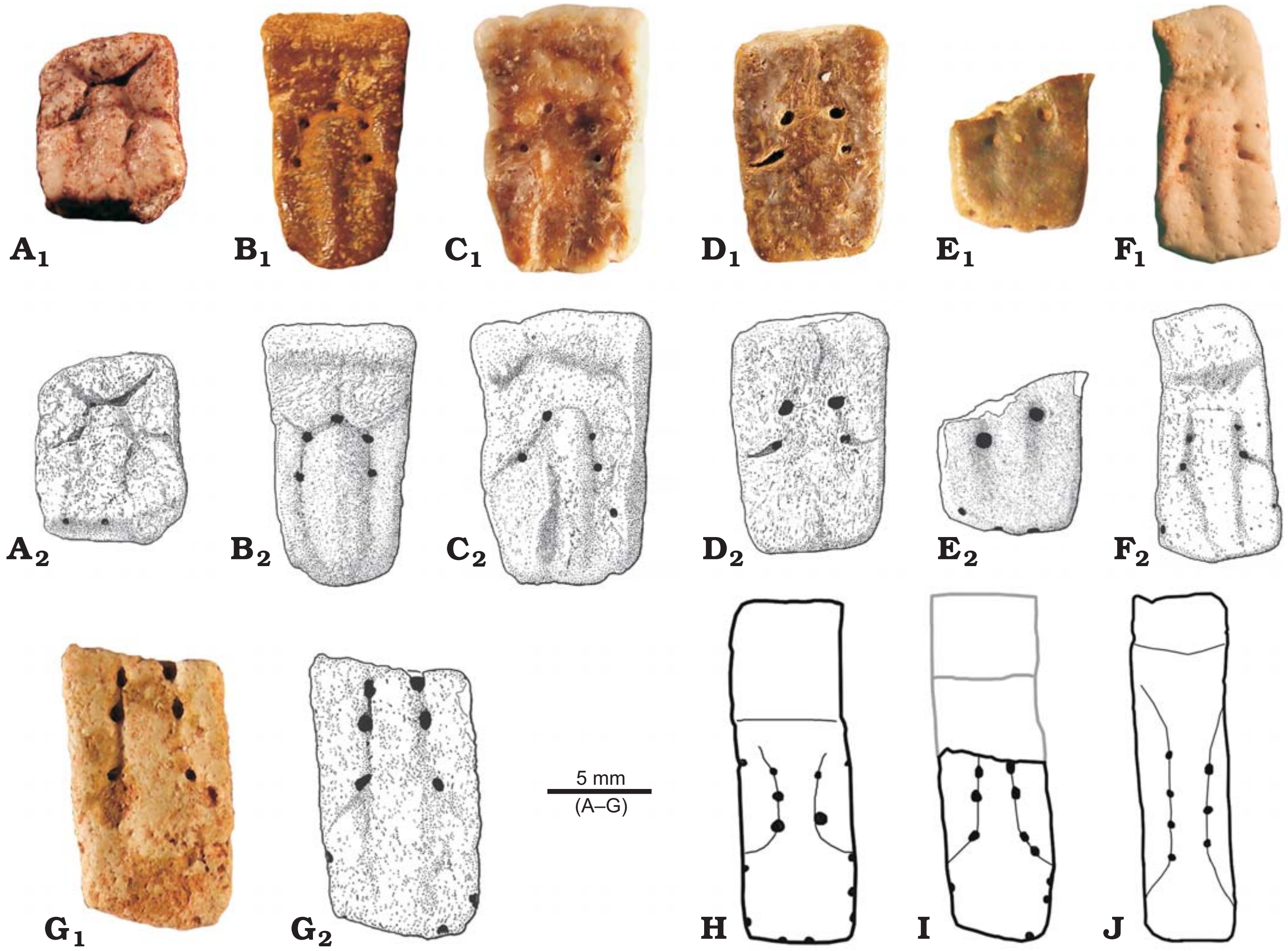

Fig. 4. Dasypodines from the middle member of the Geste Formation, middle–late Eocene, Northwestern Argentina. **A**. cf. *Astegotherium* sp., fixed osteoderm, MHAS 067; Quebrada El Paso, near the Pozuelos salt flat, Los Andes Department, Salta Province. **B**, **C**.?*Prostegotherium* sp., movable osteoderms, MHAS 024 (**B**) and PVL 6567 (**C**); Antofagasta de la Sierra, Catamarca Province. **D**–**F**. *Parastegosimpsonia* cf. *P. peruana*, fixed osteoderms, PVL 6569 (**D**) and MLP 88-V-10-19A (**E**, broken); movable osteoderm, PVL 6409 (**F**); Antofagasta de la Sierra, Catamarca Province. **G**. Dasypodinae indet., movable osteoderm, MLP 88-V-10-19; Antofagasta de la Sierra, Catamarca Province. **H**–**J**. Movable osteoderms of *Stegosimpsonia* (**H**), Dasypodinae indet. (**I**) and *Anadasypus* (**J**). Photographs (A_1–G_1), line drawings (A_2–G_2, H–J). H–J, not to scale.

Salta Province, Argentina; middle member of the Geste Formation (sensu Alonso 1992); middle–late Eocene.

Description.—This small osteoderm is similar in size to those of the living *Dasypus hybridus* or *D. septencinctus*. The osteoderm has a smooth surface and a lageniform principal figure with an elevated medial keel. There are an anterior and two anterolateral peripheral figures. The lateral border is smooth and slightly concave. On the posterior edge, there are two small piliferous foramina. Unlike other astegotheriins, *Astegotherium* have very few (or no) foramina surrounding the central figure. The differences of the osteoderm here described with those of the only species formally described for this genus, *Astegotherium dichotomus*, are the sulcus delimiting the principal and peripheral figures well defined, the posterior border straight (not bevel-shaped), the relative thickness, and the smaller size of the osteoderm.

Measurements.—6.8 mm long, 5.8 mm wide, and 3 mm thick.

Remarks.—*Astegotherium* represents a taxon frequently recorded in Eocene beds of Patagonia. The only species formally described is *Astegotherium dichotomus* Ameghino, 1902 from the early Casamayoran (Vacan subage of the Casamayoran SALMA, middle Eocene; Ciancio et al. 2013a, 2014), although a probably new species was mentioned from early–middle Eocene levels exposed at Laguna Fría (Tejedor et al. 2009).

Genus *Prostegotherium* Ameghino, 1902

Type species: *Prostegotherium notostylopianum* Ameghino, 1902; Patagonia Argentina, early–middle Eocene.

?*Prostegotherium* sp.

Fig. 4B, C.

Material.—MHAS 024 and PVL 6567, two movable osteoderms from Antofagasta de la Sierra, Catamarca Province,

Table 1. Comparative chart of cingulates from Eocene age in South America. ECAS, early Casamayoran SALMA (Vacan subage), middle Eocene; LCAS, late Casamayoran SALMA (Barrancan subage), middle Eocene; MUS, Mustersan SALMA, middle–late Eocene; TIN, Tinguiririican SALMA, late Eocene; GF, fauna of Geste Formation; PP, Eocene faunas from the Paleogene of Peru (Santa Rosa and Contamana); ×, presence; ?, doubtful assignation. From Carlini et al. (2010), Ciancio and Carlini (2008), Ciancio et al. (2013a), and Woodburne et al. (2014).

	ECAS	LCAS	MUS	TIN	GF	PP
DASYPODIDAE Dasypodinae, Astegotheriini						
Prostegotherium	×				×	
Parastegosimpsonia					×	×
?*Parastegosimpsonia*						×
cf. *Astegotherium*					×	
Astegotherium	×					
Stegosimpsonia	×	×				
Stegotheriini		?	×			
Dasypodinae indet.					×	
Euphractinae, “Utaetini”						
Utaetus		×				
Euphractini						
Parutaetus			×	×	×	
Anteutatus			×			
Mazzoniphractus			×			
Pseudeutatus			×			
Isutaetus			×			
Pachyzaedyus			×			
Eutatini						
Barrancatatus			?	×		
Sadypus			×	×		
Meteutatus			×	×		
DASYPODIDAE indet.						
Pucatherium					×	
Punatherium					×	
GLIPTODONTIDAE, Glyptatelinae						
Glyptatelus			×			
PALAEOPELTIDAE						
Palaeopeltis			×			
CINGULATA incertae sedis						
Machlydotherium		×	×	×		
Yuruatherium tropicalis						×
Yuruatherium intortum			×			

Argentina; middle member of the Geste Formation (sensu Alonso 1992); middle–late Eocene.

Description.—Medium size osteoderms, probably intermediate to the extant species *Dasypus hybrids* and *Dasypus novemcinctus*. The exposed surface is smooth, with numerous small pits. The lateral surface is straight and slightly smooth. The principal figure is lageniform with a wide neck and a conspicuous longitudinal keel occupying the entire central region of the osteoderm. At least five to seven foramina occur at the sulcus that encircles the neck of the lageniform main figure. The presence of a row of foramina in the external surface of the osteoderms forming a semicircle is characteristic of *Prostegotherium* and *Riostegotherium* (Astegotheriini), but *Riostegotherium* lacks figures and has more foramina. Peripheral figures are defined by a shallow sulcus. The lateral figures are markedly smaller than the anterior ones. The piliferous system is represented by two to five small foramina on the posterior margin.

Measurements.—10.6–11.3 mm long, 5.2–6.7 mm wide, and 1.9–2.4 mm thick.

Remarks.—The characteristics of the osteoderms are a combination of those of the known species of *Prostegotherium* (see Vizcaíno 1994) and probably they would represent a new species of this genus. The presence of a sharp medial keel, rugose surface and five small piliferous pits are characteristic of *P. astrifer*; but the size and the presence of 4–5 foramina in the external surface of the osteoderm forming an inverted U (not with triangular shape, as *P. astrifer*), resembles *P. notostylopianum*. More and better preserved remains could help a more accurate assignment. *Prostegotherium* is well represented in early–middle Eocene localities of Patagonia, Argentina (Carlini et al. 2002, 2010; Tejedor et al. 2009; Gelfo et al. 2010; Ciancio et al. 2013a; SOM: Supplementary Online Material available at http://app.pan.pl/SOM/app61-Ciancio_etal_SOM.pdf). In Northwestern Argentina, this genus was recovered at Casa Grande and Quebrada de los Colorados formations (Herrera and Powell 2009; Herrera et al. 2012; Herrera 2013; see Table 1). The temporal distribution of *Prostegotherium* provides further evidence to reinforce the interpretation of an Eocene age for Geste Formation (Powell et al. 2011; Herrera 2013).

Genus *Parastegosimpsonia* Ciancio, Carlini, Campbell, and Scillato-Yané, 2013

Type species: *Parastegosimpsonia peruana* Ciancio, Carlini, Campbell and Scillato-Yané, 2013; Yurúa River, Peru; Paleogene (Eocene?).

Parastegosimpsonia cf. *P. peruana* Ciancio, Carlini, Campbell, and Scillato-Yané, 2013

Fig. 4D–F.

Material.—PVL 6569 and MLP 88-V-10-19A, fixed osteoderms; PVL 6409, movable osteoderm; from Antofagasta de la Sierra, Catamarca Province, Argentina; middle member of the Geste Formation (sensu Alonso 1992); middle–late Eocene.

Description.—Small osteoderms similar in size to the extant *Dasypus hybridus*. The osteoderms are relatively thick, like *Stegosimpsonia* and *Parastegosimpsonia peruana*, but thicker than in other Astegotheriini (Ciancio et al. 2013a). The fixed osteoderm is subrectangular. The lateral surfaces are straight and smooth, with few isolated pits. The external surface is smoother than in *Parastegosimpsonia peruana* and exhibits a principal figure, and two anterior and two anterolateral ones. The principal figure is lageniform and flat (without keel) with a short neck, similar to that observed in

Parastegosimpsonia peruana. It is limited from the peripheral figures by an almost imperceptible sulcus housing four large foramina symmetrically arranged on each side of the neck of the principal figure, as in *Parastegosimpsonia*. The anterolateral figures are less evident; they are bounded by superficial grooves. The lateral margins lack foramina, unlike *Stegosimpsonia* and *Parastegosimpsonia*. In PVL 6569 no piliferous foramina are observed, but in MLP 88-V-10-19A, there are three in the posterior margin. The movable osteoderm has a main lageniform figure with a short neck and a medial keel occupying the whole length of the osteoderm. As the fixed osteoderm, it has four foramina in the anterior portion of the sulcus that defines the main figure, and two foramina on the posterolateral surfaces, similar to those present in fixed osteoderms of *Parastegosimpsonia peruana*. The peripheral figures are represented by two anterolateral figures. The transition area separating the overlapping portion of the osteoderm from the exposed portion is poorly developed and smooth, but exhibits some striations. The piliferous system is poorly developed; it includes two small foramina on the posterior margin.

Measurements.—Fixed osteoderm (PVL 6569): 9.7 mm long, 6.2 mm wide, and 2.4 mm thick, approximately 20% larger than those *Parastegosimpsonia peruana*. Movable osteoderm: 10.3 mm long, 5.0 mm wide, and 1.5 mm thick.

Remarks.—Ciancio et al. (2013a) described *Parastegosimpsonia peruana,* based on a fixed osteoderm from Santa Rosa, Peru. The age of the fossiliferous deposits of the Santa Rosa locality is still controversial, but the cingulates suggest an age between the late Eocene–early Oligocene. We consider the Antofagasta remains as similar to this species but there are some differences in the fixed osteoderm (larger size, absence of a keel on the main figure, absence of foramina on the lateral margin). The scarcity of remains of this species (only one fixed osteoderm constitutes the holotype) difficults to test the morphological variation of the osteoderms, hence we cannot confirm the formal assignation of these osteoderms to the Peruvian Astegotheriini. Additionally, we assign a movable osteoderm to *P. peruana*, based on the following features: the main figure is lageniform with a short neck and a medial keel occupying the whole length of the osteoderm, and the presence of a pair of large foramina on the lateral margin. New and more complete materials would help us to confirm this preliminary assignation.

Subfamily Dasypodinae Gray, 1821

Dasypodinae gen. et sp. indet.

Fig. 4G.

Material.—MLP 88-V-10-19, posterior portion of a movable osteoderm from Antofagasta de la Sierra, Catamarca Province, Argentina; middle member of the Geste Formation (sensu Alonso 1992); middle–late Eocene.

Description.—This broken osteoderm has some peculiar features that indicate that it could represent a new taxon. The osteoderm is larger than those of the others Dasypodinae from Geste levels, and similar in size to the extant species *Dasypus kappleri*. The main figure is lageniform, with a long neck that widens and reaches the lateral edges on the posterior third of the osteoderm. The morphology of the main figure is an intermediate condition between *Stegosimpsonia* (Astegotheriini; Fig. 4H) and *Anadasypus* (Dasypodini; Fig. 4J). In the former, the main figure opens on the middle portion of the osteoderm (see Vizcaíno 1994: fig. 2), and in *Anadasypus* this occurs more posteriorly (see Carlini et al. 2013: fig. 4). Both sides of the main figure are bounded by lateral figures. There are many foramina (10 or more) on the external surface that open in the sulci delimiting the main figure, and continue on the posterolateral margins. The posterior margin lacks foramina. *Stegosimpsonia* has up to 20 foramina surrounding the entire main figure, including the posterior border (Vizcaíno 1994; Carlini et al. 2010). *Anadasypus* has fewer foramina (9) but they are absent at the posterior edge (Carlini et al. 2014; Fig. 4H–J).

Measurements.—>14 mm long (anterior portion is broken; the total length could be around 25 mm), 7.5 mm wide, and 3 mm thick.

Remarks.—The material shares morphological characteristics with astegotheriins and *Anadasypus*, a primitive Dasypodini (see Carlini et al. 2013; Castro et al. 2014); hence, it could be considered as a primitive Dasypodini or a derived Astegotheriini. Previously, Babot et al. (2012) described an isolated petrosal bone of a Dasypodinae from Geste Formation at Antofagasta de la Sierra, which has a morphology more similar to *Dasypus* (Dasypodini) than to other Dasypodinae. However, taking into account the temporal range of Geste formation, and the lack of cranial remains of Astegotheriini to compare, it is difficult a more accurate assignation. The presence of a Dasypodini in Geste Formation might indicate an earlier origin of the group, up to 25 Ma earlier than it is known. Unfortunately, the few remains of this taxon prevent us to adjust the determination and clarify these speculations; probably, best preserved remains could provide new evidence in this regard.

Subfamily Euphractinae Winge, 1923

Tribe Euphractini Winge, 1923

Genus *Parutaetus* Ameghino, 1902b

Type species: *Parutaetus chicoensis* Ameghino, 1902 (= *P. signatus* Ameghino, 1902); Gran Barranca, Lake Colhue-Huapi, Chubut Province, Argentina; Sarmiento Formation; middle–late Eocene.

Parutaetus punaensis sp. nov.

Fig. 5.

Etymology: In reference to the Puna, the South American ecoregion where the type locality is located.

Holotype: MLP 83-XI-3-2 (Fig. 5A), two fixed osteoderms, one movable osteoderm, and several fragments. All these pieces are associated and included in the same lot.

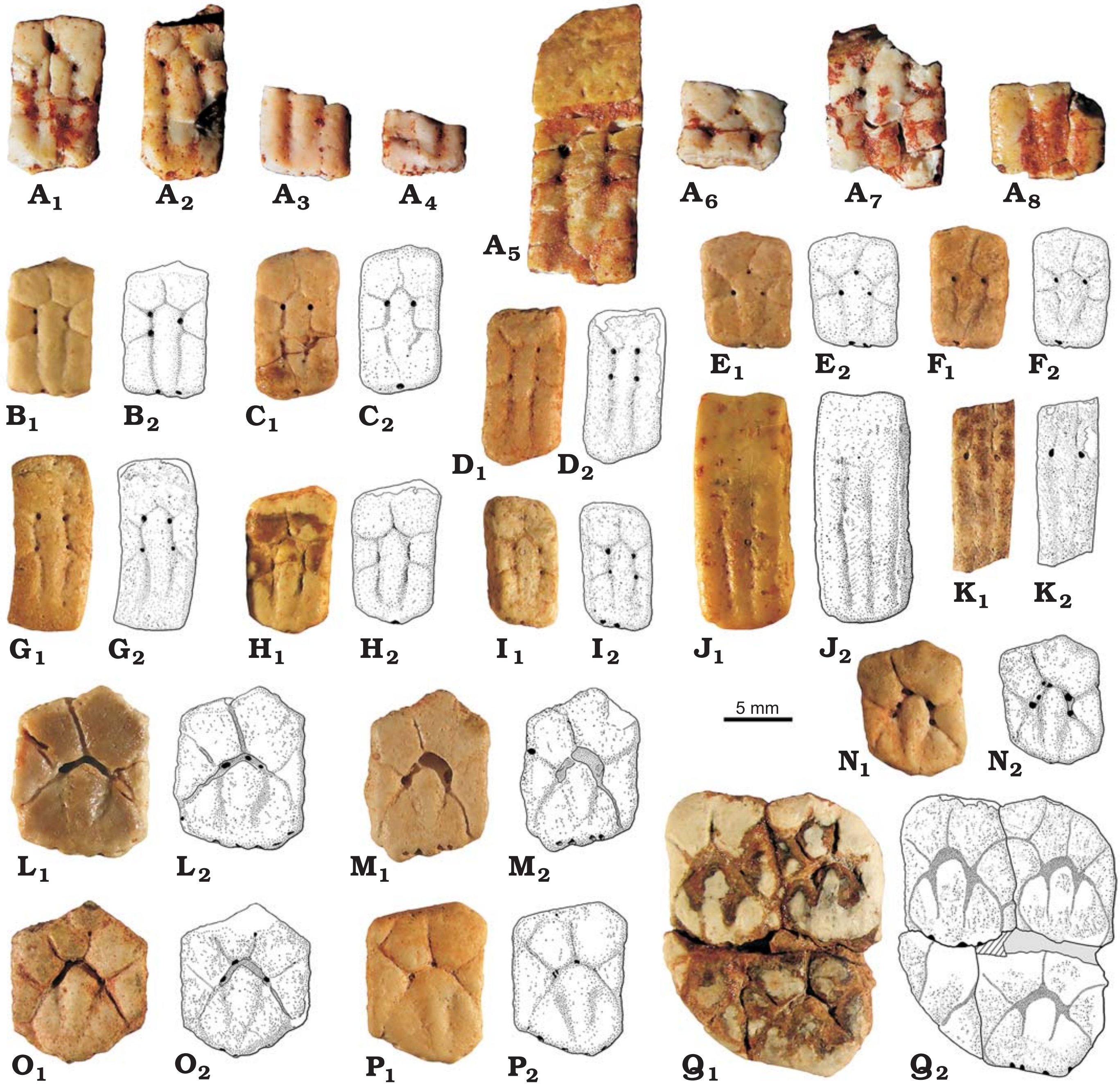

Fig. 5. Osteoderms of euphractin *Parutaetus punaensis* sp. nov. from the middle member of the Geste Formation, middle–late Eocene, Northwestern Argentina. **A**. Holotype, MLP 83-XI-3-2; Quebrada El Paso, near the Pozuelos salt flat, Los Andes Department, Salta Province. **B–E**. Fixed osteoderms from Antofagasta de la Sierra, Catamarca Province; morphotype assigned to the lateral zones of the pelvic buckler, MLP 93-VI-1-17 (**B**, **D**), MLP 86-V-6-25 (**C**, **E**, **F–I**), and movable osteoderms, MLP 86-V-10-19 (**J**), MLP 93-VI-1-18 (**K**). **L–Q**. Fixed osteoderms from Antofagasta de la Sierra, Catamarca Province; morphotype assigned to the medial zone of the pelvic buckler, MLP 88-V-10-18 (**L**), MLP 86-V-6-24 (**M–P**), MLP 86-V-6-25 (**Q**). Photographs (A, B_1–Q_1), line drawings (B_2–Q_2).

Type locality: Quebrada El Paso, near Pozuelos salt flat, Los Andes Department, Salta Province, Argentina.

Type horizon: Middle member of the Geste Formation (sensu Alonso 1992); middle–late Eocene.

Material.—MHAS 017–020, 029, PVL 6416, 6575, 6403, 6413–6415, 6407, 6417, 6568, MLP 86-V-6-24, 86-V-6-25, 93-IV-1-17, 93-IV-1-18, fixed and movable osteoderms of the dorsal shield. All specimens from Antofagasta de la Sierra, Catamarca Province, Argentina; middle section of the Geste Formation (sensu Alonso 1992); middle–late Eocene.

Diagnosis.—Osteoderms larger than those of other species of the genus, external surface of osteoderms smooth but with numerous small pits. The central figure of the fixed osteoderms is long but does not reach the posterior margin. This figure widens gradually toward the anterior border, differing from other *Parutaetus* species where the shape changes sharply. The anterior figures are polygonal and well developed as in *P. chicoensis* and *P. chilensis*. The anterolateral figures are triangular to subtrapezoidal and smaller than the long posterolateral figures. The anterior portion of the main figure bears two to five well-developed foramina in the intersection of the sulci that delimit the anterior figures from the central one. The piliferous system is restricted to the posterior margin and is poorly developed; it consists of two to five small, well-separated foramina; this trait differs from *P. chilensis* that exhibit two foramina. The movable osteoderms bear two longitudinal grooves dividing the surface into three low ridges. The central one, the principal figure, is wider anteriorly and thins gradually toward the posterior border. The lateral figures are divided by two shallow transverse sulci in the anterior half of the osteoderm, resulting in two anterolateral figures that are substantially shorter than the posterolateral ones. This pattern differs from *P. chilensis* which bears only one division and hence only one anterolateral figure, and from *P. chicoensis*, wherein the transverse sulci are absent. There are two piliferous foramina in each posterior corner.

Measurements.—MLP 83-XI-3-2, holotype, fixed osteoderms: 12.5 mm length, 6.4–7 mm width, and 3.3 mm thick; movable osteoderms: 21.6 mm length, 8 mm width, and 3 mm thick. Measurements of fixed osteoderms (referred material): 9–12 mm long, 5.5–9 mm wide, and 3–4.5 mm thick.

Description.—Small size, similar to extant *Chaetophractus villosus*. The osteoderms are smooth, with the contact areas between adjacent osteoderms smooth, concave in section, and with scattered small denticular projections. The fixed osteoderms range from pentagonal at the medial region, to rectangular or cuadrangular towards the lateral portion of the carapace. The figures are convex and well defined by narrow furrows. The main figure is wide at the anterior third and narrower backwards; it extends close to but does not contact the posterior margin. This figure is surrounded by a pair of anterior polygonal figures, two triangular to trapezoidal anterolateral, and two posterolateral ones. The anterolateral figures form a complex rhomboidal figure with those of the adjacent osteoderms. This condition is interpreted as an area covered by a single horny scale, feature present in some basal fossil Dasypodidae. Despite this general description, we identify two different morphotypes of fixed osteoderms, based in the variation of the osteoderm morphology observed in some primitive euphractins, such as *Utaetus buccatus*, *Parutaetus chilensis*, *Amblytatus*, *Isutaetus* (see Ciancio and Carlini 2008; Carlini et al. 2009, 2010). One group, probably from the lateral zones of the pelvic buckler (Fig. 5A–I), are rectangular (those defined in the diagnosis); and the other, interpreted as part of the central region of the pelvic buckler, includes pentagonal and almost as long as wide osteoderms. The second group of osteoderms (Fig. 5L–Q) is defined characteristics by the development of a semicircular sulcus (instead of singular foramina) in the anterior portion of the main figure. It is common to find this structure in some osteoderms of the central medial zone of the pelvic buckler of euphractins, generally associated to hypertrophied glands. Besides, the main figure is shortened and incorporates the posterolateral figures, acquiring a bell-shaped, and the anterolateral figures are triangular in shape (with the base directed laterally) and generally reach the posterior border. There are small accessory peripheral figures that do not contact with the principal ones in the anterior border of some osteoderms. The triangular lateral figures form a complex rhomboidal figure with that of the adjacent osteoderm. This condition is interpreted as an area covered by a single horny scale, and this characteristic occurs in some basal Dasypodidae.

The movable osteoderms (Fig. 5J, K) have a well-defined overlapping portion. In the external surface of the main portion of the osteoderm, there are two longitudinal furrows that define three elongated figures, one central and two laterals. Lateral figures are divided by two transverse furrows on the anterior third, which define two anterolateral figures and a longer posterior one. There are two pairs of foramina on the surface, at the intersection of the furrows that limit the figures. The piliferous system is poorly developed, with two foramina on the posterior corner of the osteoderm.

Remarks.—In previous works, some of the isolated osteoderms described here were identified as *Utaetus* (PVL 6403), a genus restricted to the Barrancan Subage (Casamayoran SALMA) of Patagonia, *Prostegotherium notostylopianum* (PVL 6407), *Prostegotherium* (MLP 86-V-6-24, 86-V-6-25, PVL 6413-6420), and *Astegotherium* (PVL 6412) (Powell et al. 2011; López 1997).

This is the first record of *Parutaetus* in Northwestern Argentina. This genus is known in post Casamayoran–pre Deseadan faunas (middle–late Eocene to early Oligocene) from Patagonia (Ciancio and Carlini 2008; Carlini et al. 2010) and Central Chile (Tinguiririca; Carlini et al. 2009).

Stratigraphic and geographic range.—Quebrada El Paso, near Pozuelos salt flat, Los Andes Department, Salta Province and Antofagasta de la Sierra, Catamarca Province, Argentina; middle section of the Geste Formation (sensu Alonso 1992); middle–late Eocene.

Familia Dasypodidae Gray, 1821

Dasypodidae incertae sedis

Genus *Pucatherium* Herrera, Powell, and del Papa, 2012

Type species: *Pucatherium parvus* Herrera, Powell, and del Papa, 2012; SE de Sierra Aguilar, 23°16'8.51" S 65°33'21.66" W, Humahuaca Department, Jujuy Province, Argentina; Casa Grande Formation (middle Eocene?).

Pucatherium parvum Herrera, Powell, and del Papa, 2012 (justified emendation, see below)

Fig. 6A–O.

Nomenclatural comment: The original spelling of the epithet of this species (*parvus*) is incorrect and should be emended into *parvum*, in accordance with Article 32.5 of the

International Code of Zoological Nomenclature. Thus a "justified emendation" (Article 33.2.2) is introduced in this work.

Material.—Osteoderms of the dorsal shield: MHAS 068–072, PVL 6424, 6400, 6401, MLP 86-V-6-24, 86-V-6-25, 88-V-10-19, and 93-IV-1-17, from Antofagasta de la Sierra, Catamarca Province, middle member of Geste Formation (sensu Alonso 1992); MLP 81-XI-15-3, from Quebrada El Paso, near Pozuelos salt flat, Los Andes Department, Salta Province, Argentina; middle member of Geste Formation (sensu Alonso 1992); PVL 6398, from Vicinities of Laguna and Casa Grande rivers, SE of Sierra Aguilar, Jujuy Province, Argentina; Casa Grande Formation.

Description.—Dasypodidae defined by the unique combination of the following characters: from the evidence until now, the dorsal shield was constituted only of movable osteoderms with different degrees of superposition. Osteoderms very small, anterior articular external surface with three, or less frequently two, well-developed longitudinal crests, separated by deep grooves; free posterior external area of movable osteoderms irregular and slightly wrinkled, showing a roughly rectangular main central figure with rounded anterior and posterior portions, reaching the posterior edge of the osteoderm. Lateral grooves of central figure not well-developed with five to seven small perforations each; scarce and small foramina on the lateral and posterior edges of movable osteoderms. Posterior edge of the internal face of the osteoderm with or without short longitudinal elevations and grooves.

Remarks.—*Pucatherium parvum* is a basal Dasypodidae (Herrera 2013) collected in several Paleogene localities from Northwestern Argentina (see SOM). This wide stratigraphic distribution allowed the correlation of these sedimentary units and the assignation of these levels to a Barrancan subage (Casamayoran SALMA; middle Eocene), based on a U/Pb dating of 39.9 Ma obtained from the top of Lumbrera Formation (del Papa et al. 2010; Powell et al. 2011). However, this faunistic correlation based only in one taxon should be contrasted with additional information derived from stratigraphical and evolutionary data of other mammalian taxa and other sources of information.

Stratigraphic and geographic range.—Middle–late Eocene of Argentina. Antofagasta de la Sierra, Catamarca Province and Quebrada El Paso, near Pozuelos salt flat, Los Andes Department, Salta Province; middle member of Geste Formation (sensu Alonso 1992). Juramento River, La Viña Department, Salta Province; upper section of Lumbrera Formation. Cerro Tin Tin, Cachi Department, Salta Province; Quebrada de los Colorados Formation. Vicinities of Laguna and Casa Grande rivers, south of Aguilar, Jujuy Province; Casa Grande Formation (see Powell et al. 2011 and Herrera et al. 2012).

Genus *Punatherium* nov.

Type species: *Punatherium catamarcensis* gen. et sp. nov., monotypic, see below.

Etymology: In reference to the Puna, the South American ecoregion, where the type locality is located; and from the Latin *therion*, beast; a common generic suffix for xenarthran taxa.

Diagnosis.—As for the type species by monotypy.

Punatherium catamarcensis sp. nov.

Fig. 6P, Q.

Etymology: In reference to the Catamarca Province (Argentina), where the type locality is located.

Type material: Holotype: MLP 93-VI-1-18, fixed osteoderm. Paratype: MLP 86-V-6-24, semimovable osteoderm.

Type locality: Antofagasta de la Sierra, Catamarca Province, Argentina.

Type horizon: Middle member of Geste Formation (sensu Alonso 1992); middle–late Eocene.

Diagnosis.—Dorsal shield osteoderms with rugose surface, with circular foramina in the sulci between figures, and in the lateral and posterior margins. Osteoderms ornamentation with a lageniform principal figure with keeled boss that is rounded and high, and anterior and anterolateral peripheral figures. Fixed osteoderms with large principal lageniform figure that occupies the entire posterior half of the osteoderm and becomes narrower anteriorly, surrounded by three anterior and a pair of anterolateral figures. Semimovable osteoderms also with large lageniform principal figure occupying the posterior two thirds of the dorsal surface, the sulcus surrounding the anterior portion of the principal figure with a row of large circular perforations. At both sides of the narrower part of the main figure there are two pairs of anterolateral figures.

Description.—Medium size armadillo, like the extant *Chaetophractus villosus*, according to the size of the osteoderms. Fixed osteoderms, probably from the pelvic buckler, with the principal figure anteriorly circumscribed by three conspicuous foramina. In addition, there are similar foramina located at the lateral and posterior margins, arranged in one pair at the left border, one single foramen at the right margin, and one pair in the posterior border. There are four peripheral figures on the anterior portion of the main figure. Anterior and lateral contact margins between osteoderms are covered by numerous, low and blunt protuberances. The external surface of the semimovable osteoderm shows a lageniform principal figure, also bordered by a series of large perforations in number of six. As in the case of the fixed osteoderm, there are large perforations in the posterior half of the lateral borders of the osteoderms (two on the left and three on the right). On the posterior border there is not any foramen. Proximally, this osteoderm shows two pairs of peripheral figures at both sides of the narrowest portion of the lageniform figure. The anterior margin of the osteoderm is broken, but it preserves a portion of the cranial overlapping region; the transition zone between the overlapping and main region is smooth and poorly developed.

Measurements.—Fixed osteoderm: 13 mm long, 7 mm width, and 3.5 mm thick. Semimovable osteoderm: ca. 16 mm long

Fig. 6. Osteoderms of Dasypodidae incertae sedis from the middle member of the Geste Formation, middle–late Eocene, Antofagasta de la Sierra, Catamarca Province, Argentina. **A–O**. *Pucatherium parvum* MLP 93-VI-1-17 (**A–F**), MLP 88-V-10-19 (**G–O**). **P**, **Q**. *Punatherium catamarquensis* gen. et sp. nov., holotype, fixed osteoderm, MLP 93-VI-1-18 (**P**) and paratype, semimovable osteoderm, MLP 86-V-6-24 (**Q**). Photographs (A_1–Q_1), line drawings (A_2–Q_2).

(the anterior portion is broken, total length could be 20 mm or a bit more), 8 mm width, and 4 mm thick.

Remarks.—This new taxon exhibits some particularities, which prevent its correct suprageneric assignation. The lateral contact surfaces (covered by numerous, low, and blunt protuberances), the presence of well-defined figures, and the thickness of the osteoderms are typical of euphractins. The presence of a lageniform main figure is typical of astegotheriins, but it is also present in primitive euphractins (e.g., *Archaeutaetus*, see Ciancio and Carlini 2008). On the other hand, the presence of foramina around a principal figure (with a well-developed central keel) and the roughness of the external surface resembles *Yuruatherium*, a peculiar cingulate from the Paleogene of Peru.

Stratigraphic and geographic range.—Type locality and horizon only.

Discussion

Diversity of cingulates in the Geste Formation.—According to the xenarthran record known up to date, the only clade represented in Paleocene and Eocene units from Northwestern Argentina is the cingulate family Dasypodidae. There are neither remains of Pilosa (Tardigrada and Mirmecophaga) nor other groups of cingulates (e.g., Peltephilidae, Pampatheriidae, Glyptodontoidea).

This taxonomic distribution is in general accordance with that recorded in other South American Eocene sediments. Except some remains of Glyptodontoidea (e.g., *Glyptatelus*, *Palaeopeltis*) and Pilosa (a partial jaw referred to *Pseudoglyptodon*, McKenna et al. 2006) from Patagonia Argentina, almost exclusively armadillos are recorded from the late Eocene. These features in the diversity of Xenarthra are documented mainly in Patagonian areas; however, in more northern regions, such as Paleogene strata of tropical latitudes (Contamana and Santa Rosa localities in Peru, Itaboraí in Brazil) this pattern is also present (Oliveira and Berqgvist 1995; Carlini et al. 2010; Antoine et al. 2012; Ciancio et al. 2013a; Gaudin and Croft 2015).

The diversity of dasypodids from the fossiliferous levels of the Geste Formation is represented by astegotheriins (Dasypodinae), euphractins (Euphractinae), and some peculiar taxa, which are difficult to assign to a suprageneric ranges. This association exhibits taxonomic and biogeographic relevant features given by a unique specific composition: (i) the presence of taxa related to Patagonian faunas (*Parutaetus*, *Prostegotherium*); (ii) peculiar genera only recovered in Argentinean Northwestern units (*Pucatherium* and *Punatherium*); (iii) a taxon akin to those described for the Paleogene of Peru (*Parastegosimpsonia*); and (iv) the absence of dasypodids frequently present in Patagonian faunas (e.g., Stegotheriini, Dasypodinae; Eutatini, Euphractinae).

In comparison with other beds bearing Eocene cingulate faunas from Northwestern Argentina, the Geste Formation present the greatest diversity of dasypodids (see SOM). Even if these data could indicate a chronological difference, as had been proposed for other mammalian groups (e.g., notoungulates; see García-López and Babot 2015), taphonomic causes should not be ruled out. The sedimentological analysis suggests that the fossiliferous member of Geste Formation was deposited in a high-energy fluvial environment; in this depositional context the skeletal elements of the vertebrates were postmortem disarticulated and scattered. In the case of the cingulates, this fragmentation and disarticulation caused the dispersion of the carapace osteoderms facilitating the posterior finding of the fossil pieces. In the Lumbrera Formation, different depositional conditions led to a rapid burial of the skeletons which remained articulated and hence concentrated in a more restricted area. This fact could be a limiting factor to located fossil pieces of cingulates in the exposed levels.

In relation with the evolutionary history of the cingulates, the Eocene was characterized by the differentiation, diversification, and extinction of several lineages, highly influenced by the climatic changes that distinguished this period (Carlini et al. 2005, 2009, 2010; Krmpotic et al. 2009; Ciancio 2010; Ciancio et al. 2013a; Woodburne et al. 2014). However, these processes fluctuated among faunas that evolved in different latitudes (e.g., southern South America vs. northern South America), probably as a consequence of regional differences in the climatic conditions. In particular, the presence in Northwestern Argentina of some endemic taxa and other allied with low latitude forms (e.g., Peru), would indicate that some cladogenetic events occurred in subtropical/tropical areas, regardless the contemporaneous changing sequences known for Patagonia (Ciancio et al. 2013a).

Eocene deposits with continental mammals in northern South America (NSA) are very poor (Marshall et al. 1983), and cingulates were recorded only in three of these localities with very scarce specimens and a low diversity: Itaboraí (Brazil), and Santa Rosa and Contamana (Perú). Conversely, in the Oligocene in low latitudes cingulates are more diverse and better represented, mainly in Bolivia (Salla and Lacayani) and Brasil (Taubaté) (Hoffstetter 1968; Hoffstetter et al. 1971; Oliveira et al. 1997). The pattern of taxonomic composition in Oligocene localities from NSA, is different compared to registered in the same areas during the Eocene. Although, it is interesting the fact of the presence of some taxa that are related with the Patagonian fauna, and the presence of own taxa exclusive of these regions.

In this context, the Geste Formation (located at intermediate latitude between northern and southern South America) exhibits a particular fauna that evolved in an evolutionary scenario characterized by an early cladogenesis of the xenarthrans. The presence of peculiar taxa displaying features that do not match those that define already known suprageneric categories (e.g., *Pucatherium*), could be crucial to identify the origin of those events and the evolution of some lineages (Herrera 2013).

The age of the Geste Formation.—The first chronological assignation proposed to the Geste Formation derived from the work of Turner (1960) where he suggested a Miocene age for this unit. In later decades fossil mammal findings coming from beds exposed near the Pozuelos salt flat (Salta Province), restricted tentatively the age of Geste Formation to the Paleogene, particularly to the Eocene (Pascual 1983). Although this fossiliferous levels were initially interpreted as the base of the Pozuelos Formation (Pascual 1983), posterior studies performed at Antofagasta de la Sierra (Catamarca Province) concluded that the mammal bearing levels pertained to the middle member of Geste Formation (Alonso and Fielding 1986; Alonso 1992). Subsequent paleontological works, based on the mammal "evolutionary degree" supported the former chronological assignation of Pascual (1983), although restricted the relative age to the Mustersan SALMA (Alonso et al. 1988; López and Bond 1995; López 1997; Goin et al. 1998; Reguero et al. 2008), now considered as middle–late Eocene, ca. 38–35 Ma (see Kay et al. 1999; Bond and Deschamps 2010; Dunn et al. 2013).

The assignation of the middle member of Geste Formation (at Antofagasta de la Sierra and near Pozuelos salt flat) to the Mustersan SALMA, was initially established on the basis of biochronological data derived from the comparison of the evolutionary state of the Northwestern Argentina mammalian associations with the well-known Patagonian mammalian fauna. These studies were mainly based on metatherians and ungulates. According to Goin et al. (1998) the first group suggested a late Eocene age based on the presence of taxa with more derived characters (*Punadolops alonsoi* and *Bonapartherium serrensis*) than those recovered from the Lumbrera Formation interpreted as middle Eocene (Pascual et al. 1981, Vucetich and Bond 1982; Bond and Vucetich 1983; Bond and López 1993; Babot et al. 2002). Among the native ungulates recovered at the Geste Formation the presence of notostylopids similar to their Mustersan Patagonian representatives (López 1997), more "advanced" Archaeohyracidae than the Casamayoran species (Reguero et al. 2008; García-López and Babot 2015), the absence of hypsodont notoungulates, and the alleged presence of *Propyrotherium* (López 1997; but see Reguero et al. 2008 and García-López and Babot 2015) also suggested a pre-Tinguirirican (late Eocene–early Oligocene) age for the Geste Formation mammal-bearing levels. This hypothesis was additionally supported by other data which proposed a biostratigraphic correlation between Geste and Casa Grande formations (Alonso and Fielding 1986; Bond and López 1995). The taxonomic evidence, although poorly supported, was based on the presence of an isotemnid notoungulate recovered from both units and evolutionarily similar to Mustersan taxa (Bond and López 1995; but see García-López and Babot 2015).

More recent data proposed a relative Barrancan subage (Casamayoran SALMA; middle Eocene, ca. 41.7–39.0 Ma after Dunn et al. 2012) for the fossil-bearing levels of the Geste Formation based on the presence of the particular cingulate *Pucatherium parvum* also found in Quebrada de los Colorados, Casa Grande, and Lumbrera formations (Powell et al. 2011; Herrera 2012). An isotopic dating revealed 39.9 ± 0.4 Ma at the top of this last unit (del Papa et al. 2010). This result reinforced previous ideas which proposed partial correlations among these units (see previous paragraph and also Hongn et al. 2007 for a correlation between Quebrada de los Colorados and Casa Grande formations).

However, this last assumption that suggests an older age for the Geste Formation contrasts with other studies which established a correlation between the Geste Formation and the Campo Negro member (lower member) of the Quinoas Formation (Voss 2002) dated at ca. 37.6 Ma (Kraemer et al. 1999) and Loma Amarilla Formation exposed in Salar de Atacama and dated at the base in 39.9 ± 3 Ma (Ramírez and Gardeweg 1982; Mpodozis et al. 2005; Arriagada et al. 2006).

In agreement with this evidence, absolute isotopic data indicate between 37.3–35.4 Ma for the fossiliferous middle member of Geste Formation outcropping on Pastos Grandes basin (DeCelles et al. 2007; Carrapa and DeCelles 2008); i.e., a middle–late Eocene age, partially equivalent to the Patagonian Mustersan SALMA. Although there are no detailed sedimentological studies, the mammal bearing levels of Geste Formation exposed at Salta Province are considered equivalent to those exposed at Antofagasta de la Sierra. This is consistent with the first biochronological hypothesis founded in the evolutionary degree of the metatherian and ungulate assemblage mentioned above.

Regarding the cingulate fauna recovered at the Geste Formation, it is difficult to evaluate the chronological relations with other Eocene xenarthran associations because of the peculiarity of the Punean assemblage. The first temporal interpretations were only based on the presence of Astegotheriini in common with the Patagonian assemblages for which a Casamayoran age had been proposed (see Table 1). However, the currently known armadillo diversity here presented opens other interpretations. The Punean diversity includes distinctive genera from the early–middle Eocene of Patagonia (*Astegotherium*, *Prostegotherium*), while typical Barrancan genera, such as *Utaetus*, *Stegosimpsonia*, or those common at the Mustersan levels (*Pseudeutatus*, *Pachyzaedyus*, *Anteutatus*; Ciancio and Carlini 2008; Carlini et al. 2010) are absent. By other hand, the presence at the Geste Formation of *Parutaetus*, a frequent genus from middle–late Eocene to early Oligocene levels exposed at Patagonia and Tinquiririca (Chile; Carlini et al. 2009), is consistent with the isotopic age established by DeCelles et al. (2007). The finding of *Parastegosimpsonia* in the fossiliferous levels of the Geste Formation could also indicate an equivalent age to the Mustersan or a bit earlier of Patagonia (Ciancio et al. 2013a). Summarizing, the taxonomic particularities of the Geste cingulate assemblage prevent us from determining biochronologically the age of these levels and precise equivalence with other South American Eocene units. This also exposes the importance of the Northwestern mammalian fossil association in the context of the study of the diversity and distributional patterns of the South American Paleogene faunas.

Conclusions

The species composition of armadillos recovered at the Geste Formation exhibits particular features. It differs from that known for contemporaneous faunas that evolved at Southern latitudes (i.e., Patagonia and central Chile) and younger associations from more tropical areas (i.e., Peru; late Eocene–early Oligocene), although it includes genera with close affinities to those distant areas. In addition, this unit presents unique taxa typical from other Eocene units exposed at Northwestern Argentina. This highlight the evolutionary and biogeographic meaning of the cingulate of the Geste Formation and supports the idea that the faunistic regionalization probably obeyed to latitudinal than to temporal factors.

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