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Los Alisos, a new fossiliferous locality for Guanaco Formation (late Miocene) in Jujuy (Argentina), and a first approach of its paleoecological and biochronology implications

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Abstract

Very scarce information is available about the extinct Neogene communities of the Subandean valleys of Jujuy province, Northwestern Argentina. A new vertebrate fossiliferous locality (Los Alisos), and the first mammalian assemblage from Guanaco Formation, is described. The taxa recorded include mainly caviomorph rodents (Hystricognathi) represented by *Orthomyctera* sp., *Lagostomus* sp., and an Octodontoidea and cingulates (Xenarthra) represented by the armadillos aff. *Stenotatus*, *Dasypus* sp. nov., two Euphractinae, and a Glyptodontidae. A single remain of a turtle (Testudines) is also described. The composition of the faunistic record has similitude with Andalhuala, Chiquimil and Salicas formations, but some taxa differ from all other late Miocene Northwestern Argentina localities. The most outstanding feature of Los Alisos paleocommunity is the presence of *Dasypus*, which confirms the existence of the genus in times as old as the late Miocene. The presence of a tuff with known age (5.9 - 6.4 Ma) immediately below to the fossiliferous level gives a lower temporal constraint for the association, and this absolute age as well as the biochrons of the identified taxa are compatible with an Huayquerian stage. The integrative analysis of the mammals of Los Alisos allowed preliminary paleoecological and paleoenvironmental inferences for Guanaco Formation, indicating a landscape composed by open areas, whether extensive or arranged in patches, including grasslands, under warm and seasonal climatic conditions.

Keywords:

Jujuy province

Guanaco Formation

late Miocene

Xenarthra

Rodentia

Neogene paleoenvironments

1. Introduction

Los Alisos is a locality placed along Los Alisos ranges and the homonymous river, in the South of Jujuy province, Argentina, and it crossed by the Provincial Route N° 8 (Fig. 1). On both sides of this route, as well as at the ravines of the Los Alisos river, outcrops of sedimentary Neogene units of the Orán Group and Quaternary deposits are exposed (Gebhard et al., 1974; García et al., 2017).

Conversely to other fossiliferous localities of Northwestern Argentina (e.g., Reguero et al., 2007; Reguero and Candela, 2011; Esteban et al., 2014), relatively little is what is known about the fossil mammals of Neogene units of the Subandean valleys of Jujuy and Salta provinces. One of the main reasons of this is that the outcrops are immersed in forests and jungles environments that conform the Yungas and Montes ecoregions, as was previously stated by other researchers (e.g., Gebhard et al., 1974). For the case of Jujuy, it stands out the record of a very well-preserved Glyptodontidae *Cranithlastus xibiensis* ("Plohophorini"; Xenarthra), a species only known for this formation, and a mandibular fragment of an indeterminate Megatheriidae, both specimens found in the río Chico (= río Xibi-Xibi) ravine, nearby the city of San Salvador de Jujuy, and described by Arias et al. (1979). These records were originally considered as coming from Piquete Fm. (late Pliocene-Pleistocene), but posteriorly reinterpreted as coming from Guanaco Fm. (late Miocene; see Starck and Vergani, 1996; see also Starck and Anzótegui, 2001; Coira et al., 2018). Recently, Ercoli et al. (2017) presented the finding of a second specimen of a glyptodontid from the same locality, preliminarily assigned to the same taxon. Regarding to other fossil records of Guanaco Fm., it was mentioned the presence of fossilized trunks in the South of Salta province (Starck and Vergani, 1996; Starck and Anzótegui, 2001), and gastropods in Jujuy (Arias et al., 1979).

All these records represent isolate data about the extinct biodiversity of Guanaco Fm. In relation with this, it is of particular relevance the record of the multiple taxa coming from the same fossiliferous level. In this way, it allow assessing, for first time, the composition and structure of the late Miocene communities of Southern Jujuy, lesser known in comparison to Neogene Central and Northern units of Jujuy (i.e., Quebrada de Humahuaca and Puna; Castellanos, 1950; Reguero et al., 2007; Abello et al., 2015; Bonini et al., 2017; Zurita et al., 2017; Quiñones et al., 2018). The fossiliferous locality is particularly relevant because it contains a tuff level that gives it an absolute age for the paleocommunity and preserves several small to medium-sized xenarthran and rodent taxa, allowing paleoecological and paleoenvironmental inferences.

2. Geological setting

The fossiliferous ravine is located in the geological province of Subandean Ranges (Sierras Subandinas; Ramos, 1999; Ortega et al., 2003), a modern and active example of a thin-skinned fold and thrust belt in a retroarc, non-collisional setting (Echavarria et al., 2003) corresponding to the Andean Orogenic Cycle. This geological province is characterized by elongated anticlines with N-NE to S-SW trends, conforming a series of continuous and parallel ranges (Mingramm et al., 1979). Some of the continental Neogene deposits in NW Argentina foreland basin have been described as pertaining to the Orán Group (Russo, 1972; Russo and Serraiotto, 1979), which is composed by two main sedimentary sets. The base consists in the Metán Subgroup, characterized by sandy and pelitic sediments (Reynolds et al., 2001), constituted by Río Seco, Anta and Santa María formations (Russo, 1972; Gebhard et al., 1974). Overlies the Metán Subgroup a coarsening succession of

mainly sandstones and conglomerates that corresponds to the Jujuy Subgroup. This subgroup- includes Guanaco and Piquete formations (Gebhard et al., 1974).

In the study area, the fossiliferous ravine is part of Los Alisos Ranges, which have been interpreted as a fault-propagation fold with a west vergence (García et al., 2017). The central part of this structure corresponds to the brownish-red sandstones of Guanaco Fm., and the limbs are assigned to the coarser conglomerates deposits of Piquete Fm. (Russo and Serraiotto, 1978; Starck and Vergani, 1996; García et al., 2017), being the later unit absent in the study site.

Guanaco Formation has a special interest in this study because it comprises the fossiliferous levels here studied. This unit is characterized by the dominance of gray and brownish-red, moderately sorted, coarse to fine-grained sandstones, with levels of interleaved conglomerates, into a coarsening upward sequence. The Guanaco Fm. matrix-supported conglomerates beds are composed by rounded and well-selected clasts, with some abrupt transitions to pelitic levels (Gebhard et al., 1974; Russo and Serraiotto, 1979; González et al., 1996b; Reynolds et al., 2000). These sediments are mainly interpreted as deposited in high-energy fluvial environments, with facies that corresponds to a mega-alluvial fan, in warmer and wetter climatic conditions than those inferred for the Metán Subgroup (Starck and Vergani, 1996; Reynolds et al., 2000; Starck and Anzotegui, 2001; Hain et al., 2011). Furthermore, different tuffs levels have been identified into the Guanaco Formation, whose ages are between late Miocene and early Pleistocene (~10-5 Ma; Gebhard et al., 1974; González et al., 1996a; Reynolds et al., 2000; Hain et al., 2011; Coira et al., 2018). In the Jujuy and Salta outcrops of Guanaco Formation, there exist deposits of garnet-bearing tuffs that were correlated to the Corte Blanco Tuff resulted from the explosive magmatism of Ramadas Volcanic Center, located in the Puna of Salta province

(Viramonte et al., 1994; Coira et al., 2018; and cites therein). The specific mineralogical properties of the Corte Blanco Tuff allow considering it as a relevant stratigraphic and temporal marker. Dating of the garnet-bearing tuffs outcrops in several Salta and Jujuy localities (including the Río Chico, Jujuy) indicate that the most probable ages of these tuffs are between 5.9 - 6.4 Ma (Coira et al., 2018; see also Viramonte et al., 1994), corresponding to the Huayquerian stage (late Miocene; Arias et al., 1979; Coira et al., 2018; see also Cione et al., 2015). This tephra also outcrops in Los Alisos (Arias et al., 1979; González et al., 1996b; Coira et al., 2018), that is separated by 15 km from Río Chico. These two localities represent the only two vertebrate fossiliferous sites of the Guanaco known from Jujuy (Arias et al., 1979; Ercoli et al., 2017; this contribution).

2.1. Fossiliferous and studied area

The exhumed fossils come from a restricted level that outcrops in a ravine at the km. 4.5 of the RP8 (24° 15' 44.8"S, 65° 19' 32.1"W; Fig. 1). The fossiliferous level is composed of three sublevels or adjacent beds, corresponding to fine-grained deposits topped by associated conglomerate deposits. Relevant *in situ* fossil materials were collected only in the inferior, clay and silt composed, sublevel (Fig. 2). The overlying levels are coarse-grain and contain only minor indeterminable fragments poorly preserved. In consequence, all studied fossils come from the sublevel 1 (JUY-P-144, 146 and 149), or associated debris at the bottom of the ravine (remaining specimens described), always below the outcrop of the mentioned sublevel. Beyond the fact that fluvial systems could imply time-averaging in their deposits, the low-energy, fine-grained deposits of the fossiliferous sublevel 1 give confidence to be in presence of a local assemblage. The ravine has a thickness of 9 meters, and exclusively composed by Guanaco Fm. deposits (Fig. 2). Underlying the fossiliferous level, 1.5 meters below, it outcrops the garnet-bearing tuff corresponding to the pyroclastic

deposits of the "Corte Blanco Tuff", very well studied and used as a temporal guide level for Jujuy and Salta provinces. This exposed tuff deposit is the same as the one studied by Coira et al. (2018), and corresponds to the Ramadas Volcanic Center eruption occurred in the late Miocene (see Geological setting). The exhaustive revision of all beds that conform the ravine allowed postulating that the fossil collected in the debris should correspond to the same fossiliferous level. In one specific case (JUY-P-120), the material was collected *in situ* from the nearby Los Alisos river ravines, underlying few meters to the tuff and the described profile in Fig. 2.

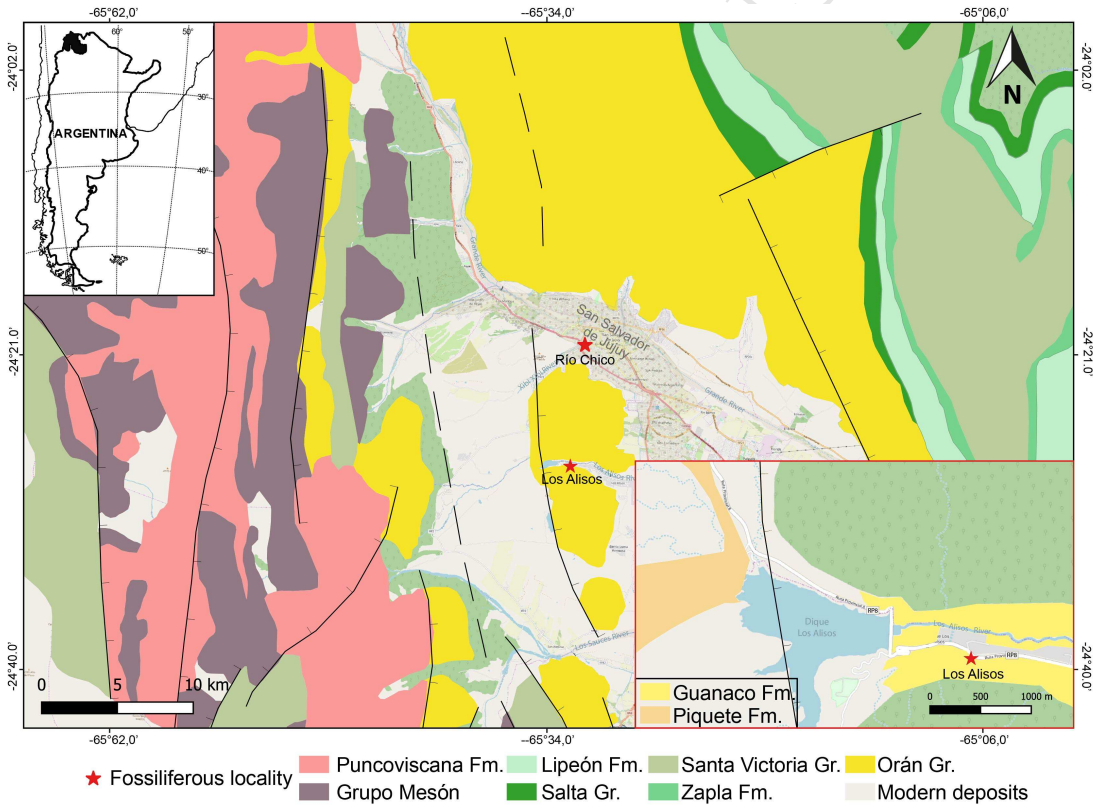

Fig. 1. Map indicating the geographic location of the fossiliferous localities (stars), including Los Alisos and Río Chico, in Jujuy province, Argentina. Main geological units are indicated. A detail of the Los Alisos locality is presented in the right bottom corner.

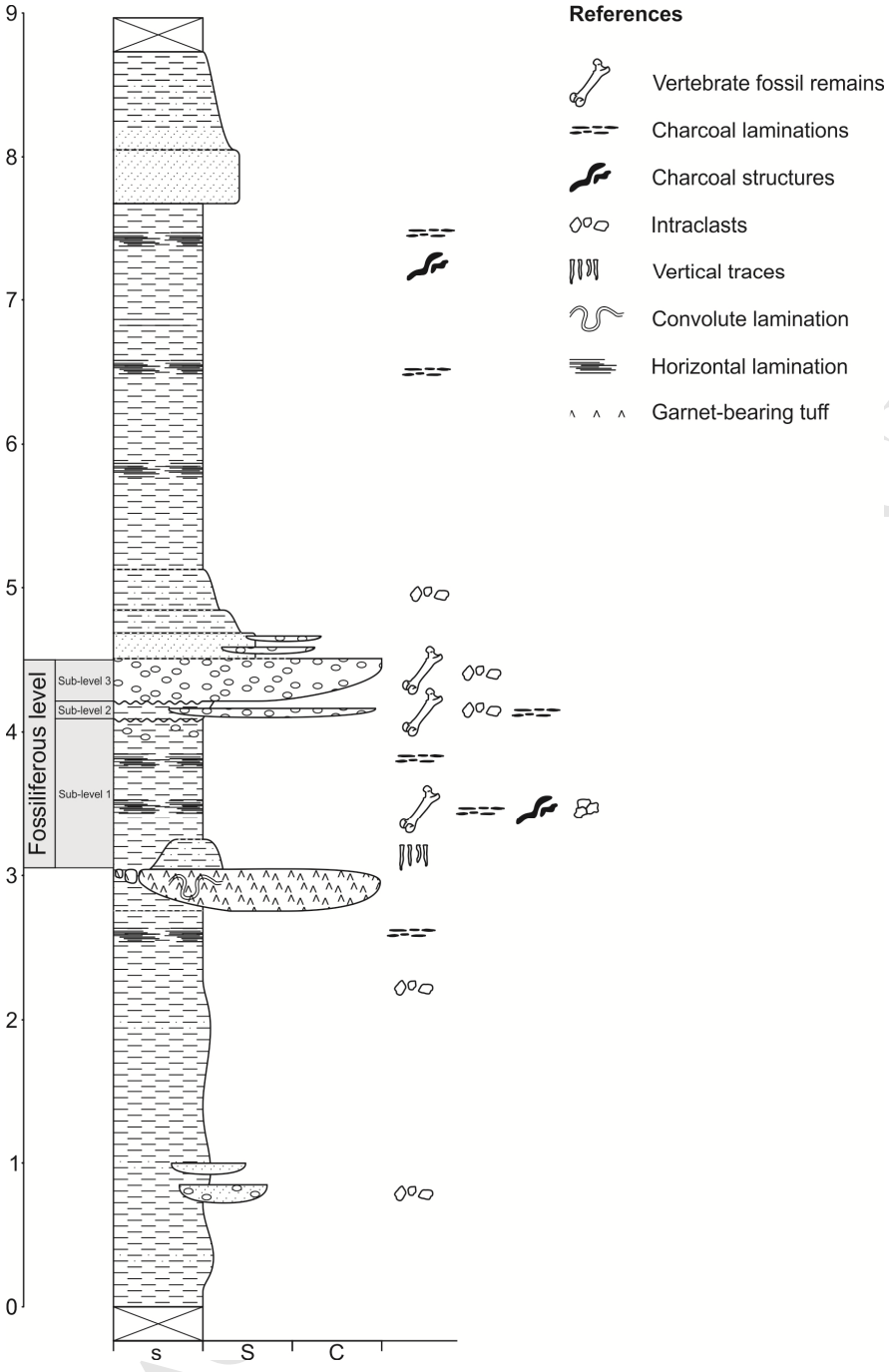

Fig. 2. Stratigraphic profile of the studied fossiliferous ravine. Granulometry: s, siltstones; S, sandstones; C, conglomerates. Scale in meters.

3. Materials and methods

3.1. Materials and anatomical abbreviations

The fossil specimens described in this study are housed in the paleontological collection of the Instituto de Geología y Minería, Universidad Nacional de Jujuy (IdGyM, UNJu), Jujuy province, Argentina.

Measurements were made on digital images through tpsDig software (Rohlf, 2010) or using a digital caliper in the largest specimens. Anatomical abbreviations mentioned throughout descriptions: L = Maximum length; W = Maximum width; H = Maximum height; al = anterior loph; pl = posterior loph; cf = central figure; ap = anterior portion; ac = acetabulum; l = left; r = right; * = measurement of a fragmentary remain.

4. Results

4.1. Systematic paleontology

Order Rodentia Bowdich, 1821

Suborder Hystricognathi Tullberg, 1899

Superfamily Cavioidea Fischer de Waldheim, 1817

Family Caviidae Fischer de Waldheim, 1817

Subfamily Dolichotinae Pocock, 1922

Orthomyctera sp.

(Fig. 3A-C)

Referred material- JUY-P-146, associated molarifoms including right P4, M1, left M1; and fragments of another molariform and one incisive.

Measurements- I: L, 2.69 mm, W, 2.52 mm; P4: L, 2.26 mm, Wal, 2.00 mm, Wpl*, 2.06 mm; M1(r): L, 2.24 mm, Wal,1.88 mm, Wpl, 1.90 mm; M1(l): L, 2.53 mm, Wal,2.06 mm, Wpl, 2.24 mm.

Description- Small molariforms composed by two similar-sized prisms with cordiform section, separated by a deep lingual hypoflexus filled with cementum and a shallow labial external flex. The hypoflexus of the P4 is shorter than those of molars. Particularly for both M1, the anterior margins of each lobe are more convex than the posterior ones, in relation to a slightly posterior tilting of the lobes. The lingual tips of the lobes are cramped nearly to their ends. In the occlusal view, the enamel is continuous along the lingual margins and particularly thick lingually, and on the labial external flex when preserved. A transverse dentine crest is present in the middle of each lobe.

Comparisons and comments- The general shape and the position of the external flex (at the level of the hypoflexus instead the posterior lobe such as occurs in Caviinae) allow the assignation to Dolichotinae (Ameghino, 1889; Pascual et al., 1966). The small size is compatible only with some Miocene *Orthomyctera* species, such as *O. rigens* and *O. andina* (Ameghino, 1889; Rovereto, 1914; Ubilla and Rinderknecht, 2003; Candela et al., 2012). Additionally, the hypoflexus of the P4 is not posteriorly deflected in its deepness aspect, differing from other dolichotines (e.g., Fields, 1957; Ubilla and Rinderknecht, 2003: fig. 4).

Superfamily Chinchilloidea Bennet, 1833

Chinchillidae Bennett, 1833

(Fig. 3H)

Referred material- JUY-P-144, a left coxal bone, with damages in the iliac wing and the posterior regions of pubis and ischium.

Measurements- L*, 41.98 mm; Lac, 7.16 mm, Hac, 7.04 mm.

Description- Circular and caudally tilted acetabulum, with a narrow acetabular notch; elongated and gracile ilium, with forward located and elongated rectus tuberosity, and triangular section of the iliac wing. On the medial surface of the neck of the ilium, a well-defined and sharp arcuate line is present. The preserved fragment of pubis shows a well developed iliopubic eminence that is markedly posteriorly tilted. The major axes of the ischium and ilium are aligned.

Comparisons and comments- The slender-shaped coxal bone, with the ilium and isquium aligned, is typically present in cursorial and saltatorial caviomorph rodents. A detailed comparison with other caviomorphs allows the assignment to Chinchillidae on the basis of the long neck of the ilium, open but narrow acetabular notch (present in small-sized chinchillids but not in *Lagostomus maximus*), the oval and anteroposteriorly elongated tuber for the m. rectus femoris, and the sharp and narrow arcuate line of the ilium.

Lagostominae Wiegmann, 1835

Lagostomus sp.

(Fig. 3D, E)

Referred materials- JUY-P-139, a right lower molar; JUY-P-138, batch of fragments of molariforms; JUY-P-128, distal epiphysis of a left femur.

Measurements- Molar: L, 1.72 mm, Wal, 3.92 mm, Wpl, 3.65 mm; Femur epiphysis: L, 6.44 mm, W, 6.53 mm.

Description- The molar JUY-P-139 is composed of two long and compressed lophs. The hypoflexid, which presents a layer of cementum, is anteriorly recurvated and the anterior loph surpasses labially the posterior one, which in turn allows the recognition of the element as a right lower molar. The enamel in contiguous but thin in the lingual margin, and absent in the anterior margin of the posterior loph. The remaining molariform fragments are too fragmentary and correspond mainly to enamel layers of lophs. The distal femoral element is a small non-fused epiphysis. The trochlea is narrow, symmetrical, with its margins parallel and well-defined. There are three marked scars for the lateral ligaments and muscles in the lateral epicondyle, and the lateral condyle is wider than the medial one.

Comparisons and comments- The described morphology of two compressed and long lophs is characteristic of the molars of all lagostomines. The assignment to *Lagostomus* corresponds to the presence of straight and long lophs and hypoflexid (Rasia, 2016; Rasia and Candela, 2016). It is worth noting that the features and size of the specimens here presented agree with those of late Miocene-Pliocene species of the previously considered valid genus or subgenus "*Lagostomopsis*", but this taxon was considered as a synonym of *Lagostomus* by Rasia (2016) and Rasia and Candela (2016). The record of isolated teeth does not contain sufficient features for a specific assignment. The femoral epiphysis presents a very similar configuration to that of small chinchillids, particularly fossil representatives of *Lagostomus* spp., with a shorter trochlea and relatively larger epicondyles than in caviids and *Lagostomus maximus*, but longer and much more defined trochlea than other generalized caviomorphs in particular, and small mammals in general.

Superfamily Octodontoidea Waterhouse, 1839

Gen. et sp. indet

(Fig. 3F, G)

Referred materials- JUY-P-133 and JUY-P-149, two fragmentary molariforms.

Measurements- JUY-P-133: L*, 3.27 mm; W*, 1.91 mm. JUY-P-149: L*, 2.25 mm; W*, 2.16 mm.

Description- Protohypsodont molariforms, with roots shorter than the estimated total height and width; each fragment preserves two lobes and one flexus between them. JUY-P-149 has two lobes that contact each other closing the flexus (Fig. 3F). Lobes of JUY-P-133 are triangular and the flexus is ample (Fig. 3G).

Comparisons and comments- The fragmentary materials do not allow the recognition of their position along the teeth row. The general morphology agrees with an Octodontoidea assignment given that is very similar to that present in Echimyidae or stem Octodontinae representatives, but very different to some morphologically modified octodontoids such as abrocomids (e.g., Verzi et al., 2016). The studied materials share some similitude with the morphology of young specimens of *Neophanomys* (see Verzi et al., 1999:fig. 2c), a taxon recorded from other Northwestern units of similar age (e.g., Salicas and Chiquimil formations; Tauber, 2005; Brandoni et al., 2012; Esteban et al., 2014; see Discussion).

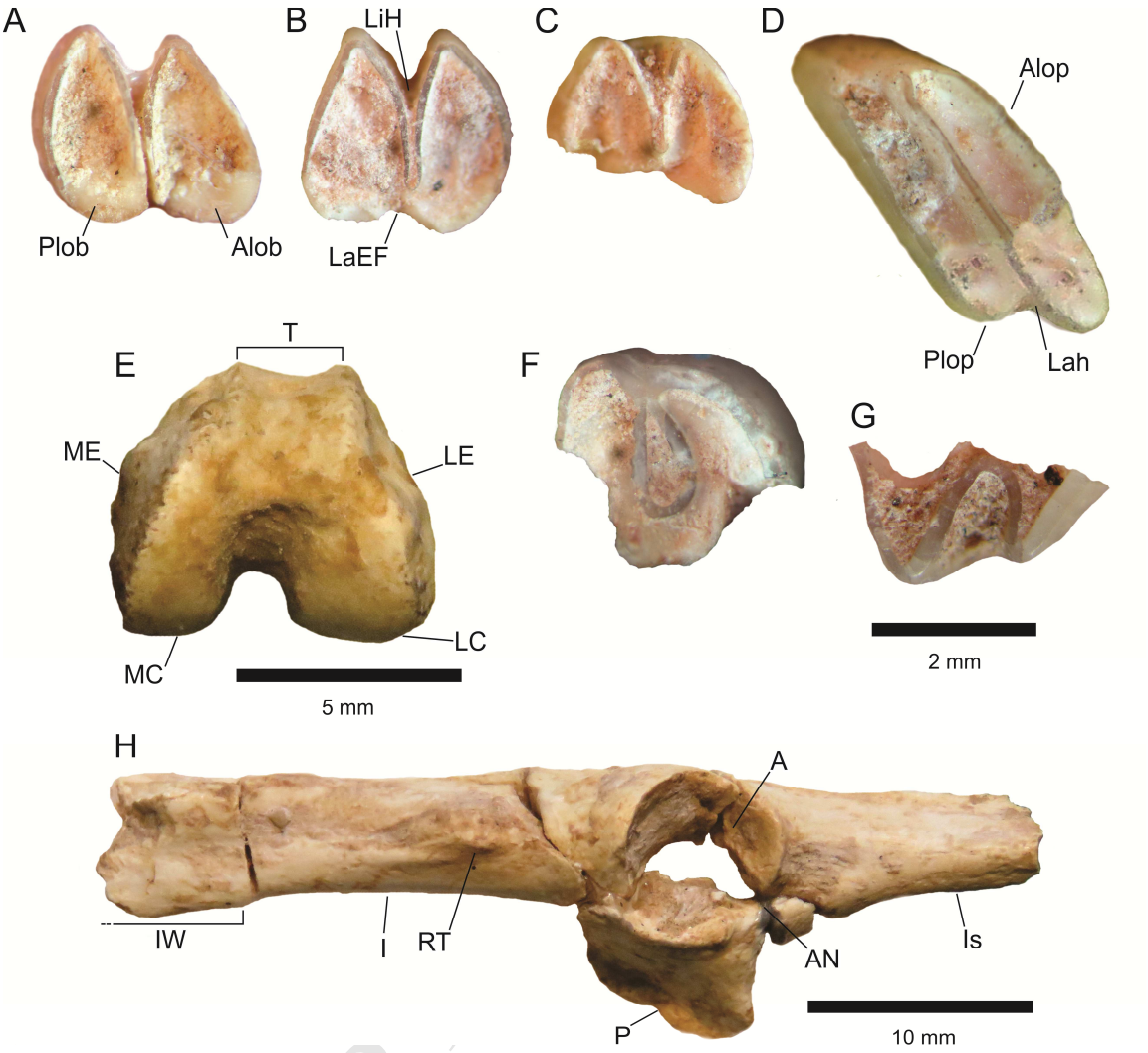

Fig 3. Fossil rodents of Los Alisos locality. **A, B, C.** *Orthomyctera* sp., JUY-P-146, associated molariforms including left M1 (**A**), right P4 (**B**), M1 (**C**); **D, E.** *Lagostomus* sp., JUY-P-139, right lower molar (**D**), JUY-P-128 distal epiphysis of left femur (**E**); **F, G.** Octodontoidea, gen. et sp. indet., JUY-P-133 (**F**), JUY-P-149 (**G**), two molariforms; **H.** Chinchillidae, JUY-P-144, left coxal bone. A-G have the same scale (2 mm). A = acetabulum, Alob = anterior lobe, ALop = anterior loph, AN = acetabular notch, I = ilium, Is = ischium, IW = iliac wing, LaEF = labial external flex, Lah = labial hypoflexid, LC = lateral condyle, LE = lateral epicondyle, LiH = lingual hypoflexus, MC = medial condyle,

ME = medial epicondyle, P = pubis, Plob = posterior lobe, PLop = posterior loph, RT = rectus tuberosity, T = throchlea.

Class Mammalia Linnaeus, 1758

Superoder Xenarthra Cope, 1889

Order Cingulata Illiger, 1811.

Family Glyptodontidae Gray, 1869.

Gen. et sp. indet.

(Fig. 4A)

Referred material- JUY-P-141, fragmentary isolate osteoderm of the dorsal carapace.

Measurements- L*, 22.51 mm; W*, 16.23 mm; Lcf, 14.56 mm; Wcf, 11.74 mm.

Description- The osteoderm remain does not preserve evident piliferous pits. The central figure is completely preserved; it has an oblong shape and is flat. An incomplete series of numerous polygonal peripheral figures are also present. Additional external figures are evident but not completely preserved.

Comparisons and comments- Although the state of preservation of the remain does not allow more preciseness, it is worth noting that the shape, the rossette pattern, and size of the osteoderm completely fit with some dorsal osteoderms of the single glyptodont species known for Guanaco Fm., the "Plohophorini" *Cranithlastus xibiensis* (see Arias et al., 1979). In consequence, it is highly probable that the isolate osteoderm corresponds to this species, beyond the discussion about the monophyly of the tribe (e.g., Fernicola, 2008), and the absence of systematic or phylogenetic studies analyzing the validity and affinities of the taxon since its recognition.

Family Dasypodidae Bonaparte, 1838.

Subfamily Euphractinae Pocock, 1924.

Gen. et sp. indet A

(Fig. 4B)

Referred material- JUY-P-130, an incomplete medium-sized movable osteoderm, preserving the anterior sector of the posterior portion.

Measurements- W, 7.25 mm.

Description- The osteoderm shows a central sub-triangular figure and two peripheral ones. These figures are separated by deep sulci that present triangular transverse sections and many small foramina. The central figure is flat to slightly convex in cross-section, and narrows toward the anterior region, due to the convergence of the sulci. The region anterior to the sculpted area is mainly smooth.

Gen. et sp. indet B

(Fig. 4C)

Referred material- JUY-P-125, an incomplete medium-sized movable osteoderm, preserving the anterior portion, and the anterior sector of the posterior one.

Measurements- W, 9.32 mm; Lap, 7.76 mm; Wap, 9.05 mm.

Description- The specimen is approximately 25% larger than any other dasypodid osteoderm of the locality. The anterior portion of a small central figure is preserved. It is delimited by two poorly-defined sulci that unite anteriorly, resulting in a rounded anterior end. Externally to these sulci there is a series of small foramina that surround the central figure on both sides and anteriorly. The preserved sectors of the peripheral figures are undivided and flat. The region between the anterior and posterior portions is very rugose.

The anterior region is approximately quadrangular, but narrows towards the anterior end. Small foramina are present in its posterior end and its anterior corners.

Tribe Euatini Bordas, 1933

aff. *Stenotatus*

(Fig. 4E-G)

Referred material- JUY-P-122, incomplete remains of two movable osteoderms; JUY-P-120, a complete isolated buckler osteoderm. One of the movable osteoderms preserves almost the entirety of the anterior portion and the anterior sector of the posterior portion, while the second movable osteoderm preserves the anterior sector of the posterior portion.

Measurements- larger movable osteoderm: W, 7.99; smaller movable osteoderm: L, 6.01, W, 7.90 mm; buckler osteoderm: L, 14.17 mm, W, 12.94 mm.

Description- The three elements are of medium to small size. The fragmentary movable osteoderms show the beginning of a main central figure and two peripheral ones conforming three longitudinal ridges, subequal in width. These figures are convex in cross-section and are separated by concave sulci, which present few small neurovascular foramina. The preserved regions of the external figures are undivided or eventually can be considered as poorly divided by very shallow transversal depression barely defined (Fig. 4E-F). The region between the anterior and posterior regions is somewhat rugose. The anterior region is wider than long.

The buckler osteoderm is small and mainly rectangular. The external surface presents little relief. The central figure is oblong and convex, delimited by a sulcus that disappears toward the posterior region. Five radiating sulci delimit six peripheral, polygonal figures of which four are well-delimited. Three of these figures reach the anterior

margin. Small and poorly defined piliferous foramina are present in the intersection of the radiating sulci and the central figure. Six large piliferous pits are present on the posterior region, organized in a single row. The deepness of the osteoderm increases progressively from the anterior end to the posterior one; furthermore, it decreases abruptly at the level of the piliferous pits and the posterior margin. The internal surface is smooth and presents some few foramina.

Comparisons and comments- The presence of a distal row of large piliferous pits, together with the absence of piliferous foramina on the external surface of movable osteoderms are diagnostical features of Eutatini (Scillato-Yané and Carlini, 1998; Croft, 2007). The combination of an antero-posteriorly narrowing condition of the piliferous pits, smooth relief in the external surface and the presence of an oblong central figure in buckler osteoderms, and the ornamentation characterized by three longitudinal ridges and a rugose surface separating the anterior and posterior portion of movable osteoderms, are diagnostical of *Stenotatus* (Croft, 2007; Scillato-Yané et al., 2010). Nevertheless, the three longitudinal ridges are pronounced in *Stenotatus* (Croft, 2007), while are shallow and poorly defined in the anterior region in the movable osteoderms of the specimens of Los Alisos. Beyond of this, some features, such as the mainly flat figure of the bucker osteoderm are shared by *S. planus* and the here described specimens, and considered a diagnostical feature of *S. planus* (Croft, 2007; Croft et al., 2009). Finally, the size of the movable plates of the aff. *Stenotatus* specimens of Los Alisos are slightly larger than the range of measurements presented for *Stenotatus planus* specimens recorded in Patagonia and Bolivia (Scillato-Yané and Carlini, 1998; Croft et al., 2009). In consequence, although the specimen shares many features with *Stenotatus*, and particularly with *S. planus*, we preferred to refer the here described material as aff. *Stenotatus*, considering the mentioned

differences. Quiñones et al. (2018) indicated the presence of *Stenotatus* sp. in Calahoyo locality, Jujuy, Argentina. Croft et al. (2016) suggested that record of *S. planus* in Cerdas locality, Bolivia, would be a new genus and species, but beyond this comment, they did not mentioned the morphological features that support this, neither give a formal description and diagnosis of this new taxon. In consequence, we could not compare our materials with this unpublished information.

Order Cingulata Illiger, 1811.

Family Dasypodidae Bonaparte, 1838.

Subfamily Dasypodinae Pocock, 1924.

Tribe Dasypodini Simpson, 1945.

Dasypus sp. nov.

(Fig. 4D)

Referred material- JUY-P-135, a fragment of the posterior region of a movable osteoderm.

Measurements- W, 5.14 mm.

Description- It shows a triangular central figure which presents two longitudinal rows of small neurovascular foramina surrounded by radial wrinkles. Some additional peripheral foramina are present in the posterior sector of the central figure. The central figure is delimited by relatively shallow sulci that reach the posterior margin, near the corners. These sulci are punctured by few, at least, three foramina. There are six posterior conspicuous piliferous foramina, five of them distributed in a single row on the posterior border, and the sixth foramen is immediately contiguous but on the right margin. A probable seventh, poorly defined, additional foramen is observed next to the latter in the right margin.

Comments and comparisons- The size and ornamentation of the osteoderm support a *Dasypus* assignment because other Dasypodini present larger sizes (*Propraopus*), different shape of the central figure (e.g., *Anadasypus*), and absence of principal sulci (*Cryptophractus*). A clear way to separate Dasypodini genera is the count of the piliferous foramina in the posterior border, being *Dasypus* the one with the largest number (1-2 in *Anadasypus*; 3 in *Pliodasypus*; 1-3 in *Propraopus*; 6-10 in *Cryptophractus*; 1-7 in *Dasypus*). Among *Dasypus* species, only the extinct ones present more than 4 posterior piliferous foramina (4-7 and typically 5 in *D. punctatus*, and 8 in *D. neogaeus*; Ameghino 1891; Castro 2014, 2015). In the here presented osteoderm and in *D. neogaeus*, some posterior piliferous foramina located just lateral to the posterior border, on the posterior end of the lateral border (Ameghino, 1891: fig. 69). Although the osteoderm here described is fragmentary, the ornamentation shows a distinctive pattern with not so well-marked figures and few foramina along the sulci that delimit de central figure. This is clearly different to *D. punctatus*, that presents an enormous number of piliferous foramina in the principal sulci (9 to 18), and to the single element known for *D. neogaeus* which present numerous foramina in each sulci (Ameghino, 1891; Scillato-Yané et al., 2013). Nevertheless, the availability of one single element discourages nominating a new species.

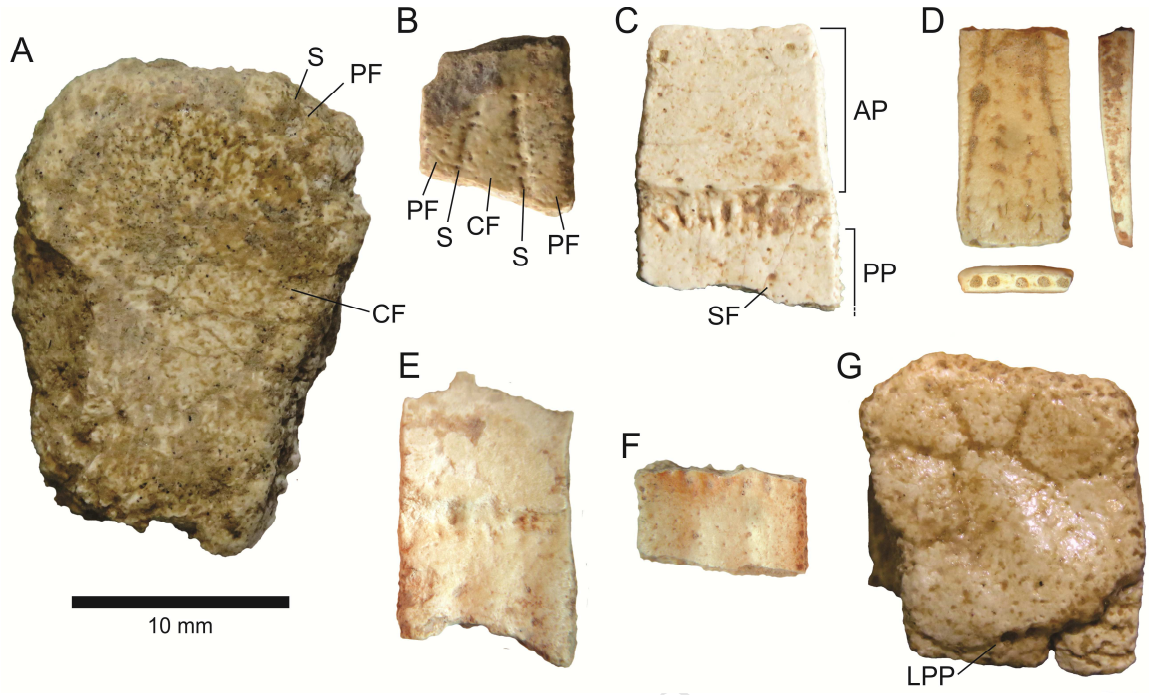

Fig. 4. Fossil xenarthrans of Los Alisos locality. **A.** Glyptodontidae, gen. et sp. indet., JUY-P-141, osteoderm; **B.** Dasypodidae, Euphractinae, gen et sp. indet. A, JUY-P-130, incomplete medium-sized movable osteoderm; **C.** Dasypodidae, Euphractinae, gen et sp. indet. B, JUY-P-125, incomplete medium-sized movable osteoderm; **D.** Dasypodidae, Dasypodinae, Dasypodini, *Dasypus* sp. nov., JUY-P-135, a fragment of movable osteoderm. **E, F, G.** Dasypodidae, Euphractinae, Euatini, aff. *Stenotatus*, JUY-P-120, JUY-P-122, incomplete remains of two movable osteoderms (**E**, **F**), complete buckler osteoderm (**G**). AP = anterior portion, CF = central figure, LLP = large piliferous pit, PF = peripherical figure, PP = posterior portion, S = sulcus, SF = small foramina.

Reptilia Laurenti, 1768

Order Testudines Batsch, 1788 *sensu* Joyce Parham and Gauthier, 2004

Gen. et sp. indet.

(Fig. 5)

Material- JUY-P-121, eroded complete entoplastron.

Measurements- L, 7.79 mm, W, 5.08 mm.

Description- Large triangular element with an external surface with sculpture pronounced, and internal surface smooth.

Comments and comparisons- The isolate plate does not allow a more precise assignment, but considering the fossil record of tortoises, it could be a representative of the families Testudinidae or Chelidae (de la Fuente, 1997), being Testudinidae the most probable candidate considering the large dimensions of the plate.

Fig. 5. Fossil turtle of Los Alisos locality. Testudines, gen. et sp. indet., JUY-P-121, complete entoplastron.

5. Discussion

Los Alisos locality represents the first vertebrate assemblage for Guanaco Fm. and constitutes the second fossiliferous locality for this formation. Also, the first small- and medium-sized mammals are described for Guanaco Fm., for which only two species of

large mammals were known, at Río Chico locality (Arias et al., 1979; Ercoli et al., 2017). This allows for the first time to have an outline of the composition of the communities of mammals that inhabited the southern region of Jujuy during the late Miocene and analyze their biostratigraphic and paleoenvironmental implications in comparison with other fossiliferous localities of similar age in Northwestern Argentina. In consequence, all taxa identified (maybe excepting the glyptodontid specimen), correspond to the first records of each one for the Guanaco Fm. Furthermore, *Orthomyctera*, *Lagostomus*, and *Dasypus* are the first records for Jujuy province.

5.1. Taxonomical diversity

Although our knowledge about the taxonomical diversity of Los Alisos is still limited and many specimens could not be assigned to genus or species level, some preliminary comparisons with other units can be performed. The record of Los Alisos is similar to that recorded in other late Miocene Northwestern Argentina localities, sharing five mammalian taxa with Andalhuala Fm. and Jarillal Mb. of the Chiquimil Fm., both units of Catamarca, and Salicas Fm. of La Rioja [i.e., Euphractinae, Glyptodontidae, *Lagostomus*, non abrocomid Octodontoidea, and *Orthomyctera*] (Marshall and Patterson, 1981; Tauber, 2005; Brandoni et al., 2012; Esteban et al., 2014). Palo Pintado Fm. represents the more geographically closer late Miocene fauna (Reguero et al., 2014; Zimicz et al., 2018), and shares only three of these taxa, without records of- *Orthomyctera* and non abrocomid octodontoids (Armella et al., 2016; Zimicz et al., 2018). Nevertheless, it is worth noting that both, Palo Pintado and Guanaco formations are mostly underexplored units, and more similitude would arise in future prospections. If Río Chico locality is considered, and *Cranithlastus xibiensis* and a megatheriid are added to the assemblage (Arias et al., 1979;

Ercoli et al., 2017), the similitude with Salicas Fm. would decrease considering the endemic nature of *C. xibiensis*, and the absence of megatheriids in the latter (present in Andalhuala and Chiquimil formations; Marshall and Patterson, 1981; Brandoni et al., 2012; Bonini, 2014; Esteban et al., 2014).

Beyond the scarce available information, the current knowledge of the paleontology of Guanaco Fm. reveals at least two taxa not recorded in the compared Northwestern Argentinean units: *Cranithlastus xibiensis* and *Dasypus*. Additionally, the record of specimens assigned to aff. *Stenotatus*, resemble Los Alisos to Puna localities (Croft, 2007; Croft et al., 2009; Quiñones et al., 2018). These three xenarthran taxa bring a particular imprint the paleocommunity of Los Alisos, and in the case of *Dasypus*, it has biochronological implications discussed below.

5.2. Biochronology

A strength of Los Alisos locality is the presence of a tuff of known age (5.9 - 6.4 Ma; Coira et al., 2018), which gives a chronological constraint. All the described fossils came from a level 1.5 mts below this temporal marker. This dating agrees with a Huayquerian age for Guanaco Fm., and in this way the previous scarce fossils known for this unit were considered by other researchers (Arias et al., 1978; Starck and Vergani, 1996). Thus, the description of the first vertebrate assemblage for Guanaco Fm. allowed us making a robust re-evaluation of the compatibility of the fossil association of Los Alisos with a Huayquerian assignation.

With regards to rodent records of Los Alisos, *Orthomyctera* and the smallest species of *Lagostomus* (considered by previous authors as "*Lagostomopsis*") biochrons span from late Miocene, Chasicoan to Pliocene, Chapadmalalan (Tauber, 2005; Rasia, 2016).

Specifically for *Orthomyctera*, small-sized species (similar to the specimen here presented) are only recorded from Chasicoan to Montehermosan (Candela et al., 2012; Bonini, 2014). Although not assigned at genus or species level, the occlusal morphology of the octodontoid molariforms corresponds to that of the present in octodontids from early late to late Miocene, i.e. Chasicoan or Huayquerian (Diego H. Verzi comm. pers.).

The only potential discrepancy with a late Miocene age for Los Alisos would be the record of aff. *Stenotatus*, in the case that these specimens would be considered as belonging to this genus (recorded from late Oligocene, Deseadan; to middle Miocene, Friasian/Colloncuran; Ameghino, 1897; Croft et al., 2009). *Stenotatus planus* is recorded in Cerdas, a middle Miocene Southern Bolivian locality (Croft et al., 2009), and Cerro Boleadoras, an early to middle Miocene locality of Argentinean Patagonia (Scillato-Yané and Carlini, 1998; Croft et al., 2009). *Stenotatus* sp. is known for Calahoyo, from levels that are likely to be middle or late Miocene ages (Quiñones et al., 2018). Nevertheless, Croft et al. (2016) postulated that the materials from Cerdas would represent a new genus and species, close related to *Stenotatus*, but no published comparisons or further information are available for these Bolivian materials.

The more remarkable record of Los Alisos is the presence of an isolated plate of *Dasypus*. The previous early record of *Dasypus* corresponds to an isolated movable plate collected by Ameghino in the late Miocene "conglomerado osífero" locality (Ituzaingó Fm., Entre Ríos province, Argentina; Ameghino, 1891; Scillato-Yané et al., 2013). On the basis of this specimen, Ameghino (1891) established the species *D. neogaeus*, which was diagnosed by the more numerous piliferous pits (8) present in its posterior border than other *Dasypus* species (Ameghino, 1891). Castro (2014, 2015) considered to *D. neogaeus* as *nomen dubium* considering that the material presents a morphology that does not fit with

that expected for an early *Dasypus* species, but highlighting that the record of this tropical and subtropical genus is poorly known (in relation to the poor fossiliferous potential of low latitude localities). Conversely, other authors considered that the species should be maintained as a Huayquerian valid taxon waiting for future studies or materials (Scillato-Yané et al., 2013:120). In this context, our material supports the presence of *Dasypus* in late Miocene. Furthermore, many morphological similitudes regarding some traits of its sculpture and the high number of piliferous pits (although variable as in all *Dasypus* species) are shared between the specimen of Los Alisos and *D. neogaeus*. Contrary to the Ituzaingó Formation record, the *Dasypus* remain of Guanaco Fm. has an exact geographical provenance and is associated to a late Miocene tuff, exposed in a profile in which no younger units outcrop, and pertains to a mammalian association compatible with a Huayquerian stage. Moreover, Delsuc et al. (2004) estimated that *Dasypus* species diverged at least during late Miocene, at 7 Ma (5-11 Ma), and that the genus should be found at late Miocene fossiliferous deposits, in agreement with the age of Guanaco Fm. In consequence this record is relevant for the evolutionary history of Dasypodini. In summary, all these records match with a Huayquerian age for Guanaco Fm. in general, and Los Alisos locality in particular.

5.3. Paleoenvironmental and paleoecological inferences

Following González et al. (1996b), the deposits of fine sediments of the analyzed profile of Guanaco Fm. could correspond to low-energy deposits probably linked to floodplains, with minor intercalations of medium-to-high energy deposits related to channels and bar complexes. These conglomeratic levels with relatively poor distribution into- fine-grained deposits indicate the domain of low energy in the system. In contrast to other sections of

Guanaco Fm., this particularity could help to the variability in faunistic composition and/or generated taphonomic bias towards the preservation of small fossils.

The overall rodent assemblage of Los Alisos is composed by taxa related to open and seasonal habitats, in particular, dolichotines and lagostomines which are cursorial and euhypsodont caviomorphs. Interestingly, there are no records of families typically adapted to wet or forested environments (e.g., erethizontids, neopiblemids, and dinomyids; Reguero et al., 2007; Zimicz et al., 2018). The only probable exception to this pattern could be represented by the octodontoid indet., but the scarce remains, in addition to the wide ecological diversity of octodontoids prevent further analyses. The late Miocene species of *Lagostomus* were described as a small lagostomine of open and seasonal environments, and specifically inhabiting grasslands during the late Miocene (Rasia 2016). Furthermore, Rasia (2016) indicated that the dental morphology of the late Miocene lagostomines suggests a diet based on leaves and grasses, similar to the living species *L. maximus* (Jackson et al., 1996). Although there no exist paleobiological studies of the dolichotine *Orthomyctera*, its remarkable morphological similitude with *Dolichotis* (except by size), and especially regarding its dentition, could suggest similar life habits. *Dolichotis* species are opportunistic herbivores of seasonal, and open or mostly open environments, which feed on the most abundant vegetal source of each season (grasses in the wet season and shrubs in the dry one; Puig et al., 2010; Furnari, 2011:113).

The relatively high abundance of remains of dasypodids and ground-dweller rodents in Los Alisos resembles that of other late Miocene localities of Central and Northwestern Argentina. Lagostomines and dasypodids, which are the more abundant taxa in Los Alisos, are specialized scratch-diggers (Scillato-Yané et al., 2013; Rasia, 2016). Fossoriality is linked to mainly non-flood environments, and typically related to the occupancy of open

and arid habitats, in relation to stable temperatures present in burrow systems, as well as avoiding predation in absence or less abundance of other kind of refuges (e.g., trees) (Nevo, 1979; Kinlaw, 1999; Ebensperger and Bozinovic, 2000; Hayes et al., 2007; Scillato-Yané et al., 2013).

The presence of glyptodontids, large herbivores typically interpreted as grazers (Fariña and Vizcaíno, 2001; McDonald, 2005; Scillato-Yané et al., 2013), supports the inference of large open areas such as grasslands suggested by the caviomorph assemblage. The abundant hair coverage of eutatines, has been interpreted as allowing its presence in colder climates in comparison to other dasypodids (Scillato-Yané et al., 2010), but this does not exclude their presence in subtropical and tropical communities, in which they have been recorded (Vizcaíno et al., 2012; Croft et al., 2016). In consequence, the record of eutatines is not easy to interpret from an environmental point of view. Finally, the *Dasypus* extinct representatives are morphologically similar to living ones, and considered as a versatile group of insectivore species that inhabited a wide range of ecoregions, but always in subtropical and tropical latitudes, avoiding cold environments in relation to its low hair density and physiology (Scillato-Yané et al., 2013; Castro, 2014, 2015; Serrano-Fochs et al., 2015). Because of this, the presence of *Dasypus* can be interpreted as a reliable proxy of relatively warm environments.

In summary, the integrative analysis of the fossil and geological record of Los Alisos allows the inference of a landscape composed by open areas, whether extensive or arranged in patches, including grasslands and the presence of water courses, under warm and seasonal climatic conditions (Fig. 6). The community and environment inferred from Los Alisos fossil record contrast with those observed today in South-Central Jujuy, occupied by the densely forested of Yungas. This study could contribute to understand a

part of the natural history of the communities of this regions and how and when Yungas was shaped. Palynological and macroscopic paleobotanical would allow to confirm the inferences of warm and seasonal environments as was proposed in other Northwestern Argentinean localities (Anzótegui et al., 2017; see also Reguero et al., 2014; Zimicz et al., 2018). This reconstruction should be considered as a preliminary proposal, waiting for more evidence to accomplish more accurate paleoenvironmental inferences.

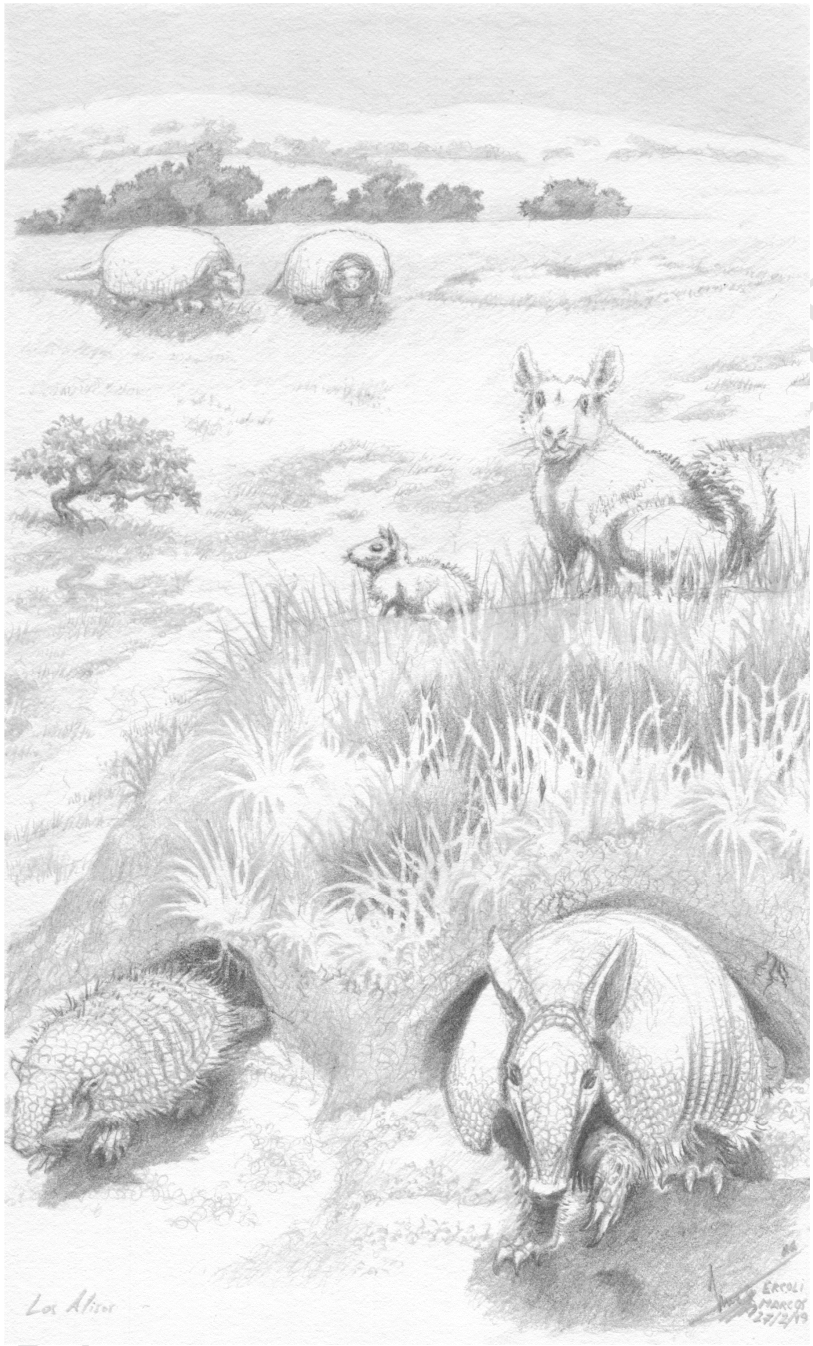

Fig. 6. Reconstruction of the late Miocene paleocommunity of Guanaco Fm. including taxa recorded in Los Alisos, Jujuy province, Argentina. In the foreground, the rodents *Orthomyctera* (left) and *Lagostomus* ("*Lagostomopsis*") (right) are standing on the top of a ravine, and a euphractine (left) and the dasypodini *Dasypus* (right) are coming out from their dens located at the bottom of the ravine. In the background, two glyptodonts *Cranithlastus xibiensis* are wandering through the open landscape.

6. Concluding remarks

1- The value of the new fossiliferous locality of Los Alisos is enhanced because it represents the first vertebrate assemblage from the Neogene of Southern Jujuy, the first record of many taxa for Jujuy, and also highlighted by the presence of an associate dated tuff.

2- The presence of *Dasypus*- in the paleocommunity of Los Alisos, support the existence of the genus in times as old as the late Miocene, but more specimens are needed.

3- The paleoecological analysis of the mammalian paleocommunity and the sedimentary record of Los Alisos indicate a landscape composed by open areas, including grasslands, under warm and seasonal climatic conditions.

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Figure legends

Fig. 1. Map indicating the geographic location of the fossiliferous localities (stars), including Los Alisos and Río Chico, in Jujuy province, Argentina. Main geological units are indicated. A detail of the Los Alisos locality is presented in the right bottom corner.

Fig. 2. Stratigraphic profile of the studied fossiliferous ravine. Granulometry: s, siltstones; S, sandstones; C, conglomerates. Scale in meters.

Fig 3. Fossil rodents of Los Alisos locality. **A, B, C.** *Orthomyctera* sp., JUY-P-146, associated molarifoms including left M1 (**A**), right P4 (**B**), M1 (**C**); **D, E.** *Lagostomus* sp., JUY-P-139, right lower molar (**D**), JUY-P-128 distal epiphysis of left femur (**E**); **F, G.** Octodontoidea, gen. et sp. indet., JUY-P-133 (**F**), JUY-P-149 (**G**), two molariforms; **H.** Chinchillidae, JUY-P-144, left coxal bone. A-G have the same scale (2 mm). A = acetabulum, Alob = anterior lobe, ALop = anterior loph, AN = acetabular notch, I = ilium, Is = ischium, IW = iliac wing, LaEF = labial external flex, Lah = labial hypoflexid, LC = lateral condyle, LE = lateral epicondyle, LiH = lingual hypoflexus, MC = medial condyle, ME = medial epicondyle, P = pubis, Plob = posterior lobe, PLop = posterior loph, RT = rectus tuberosity, T = throchlea.

Fig. 4. Fossil xenarthrans of Los Alisos locality. **A.** Glyptodontidae, gen. et sp. indet., JUY-P-141, osteoderm; **B.** Dasypodidae, Euphractinae, gen et sp. indet. A, JUY-P-130, incomplete medium-sized movable osteoderm; **C.** Dasypodidae, Euphractinae, gen et sp. indet. B, JUY-P-125, incomplete medium-sized movable osteoderm; **D.** Dasypodidae, Dasypodinae, Dasypodini, *Dasypus* sp. nov., JUY-P-135, a fragment of movable osteoderm. **E, F, G.** Dasypodidae, Euphractinae, Euatini, aff. *Stenotatus*, JUY-P-120, JUY-P-122, incomplete remains of two movable osteoderms (**E**, **F**), complete buckler osteoderm

(**G**). AP = anterior portion, CF = central figure, LLP = large piliferous pit, PF = peripherical figure, PP = posterior portion, S = sulcus, SF = small foramina.

Fig. 5. Fossil turtle of Los Alisos locality. Testudines, gen. et sp. indet., JUY-P-121, complete entoplastron.

Fig. 6. Reconstruction of the late Miocene paleocommunity of Guanaco Fm. including taxa recorded in Los Alisos, Jujuy province, Argentina. In the foreground, the rodents *Orthomyctera* (left) and *Lagostomus* ("*Lagostomopsis*") (right) are standing on the top of a ravine, and a euphractine (left) and the dasypodini *Dasypus* (right) are coming out from their dens located at the bottom of the ravine. In the background, two glyptodonts *Cranithlastus xibiensis* are wandering through the open landscape.

- The first vertebrate assemblage of Guanaco Fm., late Miocene, Argentina, is presented.

- A first approach to the composition of the paleocommunity is accomplish.

- Some of the described taxa are the first records for Jujuy province.

- We present the earliest record of *Dasypus* with precise provenance (late Miocene).

- The analysis suggests open areas, including grasslands, and warm and seasonal climate.