New camelid (Artiodactyla: Camelidae) record from the late Pleistocene of Calama (Second Region, Chile): a morphological and morphometric discussion

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ABSTRACT

A description of fossil remains belonging to camelids from the Kamac Mayu site (Second Region, Chile) is presented. This record was recovered from deposits of gravel and sand on karstic formations eroded by rivers during the late Pleistocene. In addition to the remains of camelids, diverse fossil material composed of Hippidion saldiasi (Mammalia, Equidae), Macrauchenia patachonica (Mammalia, Litopterna), undetermined xenarthrans (Mammalia, Xenarhra) and birds (Aves, Rheidae), were recovered, along with specimens of Planorbidae, Hydrobiidaee and Sphaeriidae (Mollusca) from deposits formed by the drainage of the Chiu Chiu-Calama basin. The comparative anatomical study of the fossil material enabled the taxonomic assignment of the camelid remains to Lama gracilis (Gervais and Ameghino 1880), constituting an unprecedented finding for this region of the country.

Key words: South American camelids, Lama gracilis, late Pleistocene, Northern Chile.

RESUMEN

En el presente trabajo se describe el material correspondiente a restos fósiles de camélidos del sitio Kamac Mayu (II Región, Chile). Este registro, fue recobrado a partir de excavaciones sistemáticas en depósitos de grava arenosa y arena dispuestos sobre una formación kárstica, erosionadas por cursos fluviales durante el Pleistoceno tardío. Además de los restos de camélidos se recobró material fósil diverso compuesto por Hippidion saldiasi (Mammalia, Equidae), Macrauchenia patachonica (Mammalia, Litopterna), xenarthros indeterminados (Mammalia, Xenarhra) y aves (Aves, Rheidae), junto a especímenes de Planorbidae, Hydrobiidaee and Sphaeriidae (Mollusca) dentro de depósitos formados por el desagüe de la antigua cuenca Chiu Chiu-Calama. El estudio anatómico comparado de los restos fósiles permitió la asignación taxonómica a Lama gracilis (Gervais y Ameghino 1880), constituyéndose en un hallazgo inédito para esta región del país.

Palabras clave: camélidos sudamericanos, Lama gracilis, Pleistoceno tardío, Norte de Chile.

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INTRODUCTION

Studies undertaken on the present-day species of camelids, both wild and domesticated, in the Southern Cone of America, distributed in various regions of Peru, Bolivia, Argentina and Chile, have emphasised diverse aspects related to their taxonomy, geographical distribution, ecology conservation and economic use (Cardozo, 1974; Franklin, 1983; Torres, 1992; Lichteinstein and Vilá, 2002; Marín *et al.*, 2007; Bonacic, 2008; among others). It should be noted that a large number of these issues have been addressed on archaeological reports of camelid remains (Wheeler, 1984; Mengoni-Goñalons and Yacobaccio, 2006; Cartajena *et al.*, 2007). Also, fossil records of Camelidae have been widely treated in the South American literature (Ferrero, 2005, 2006; Menegaz, 2000; Menegaz *et al.*, 1989, Menegaz and Ortiz Jaureguizar, 1995, Noriega y Ferrero, 2007; Ribeiro *et al.*, 2007; Scherer *et al.*, 2007; Ubilla, 2004; Ubilla *et al.*, 2004, 2007). However, they have been relatively scarce in the case of Chile (López *et al.*, 2005).

The first fossil remains belonging to South American Camelidae correspond to findings of deposits from the Late Pliocene (Marplatan Stage/Age, Barrancalobian Subage). Once the isthmus of Panama was formed, some Lamini forms (llamas) migrated to South America, where they radiated (Cione and Tonni, 1995; Menegaz and Ortiz Jaureguizar, 1995; Webb, 2006; Woodburne *et al.*, 2006). The greatest diversity of South American genera was produced in the late Pleistocene, including taxa with different morphological traits, distribution, and marked differences in size, from large species of *Hemiauchenia* Gervais and Ameghino, 1880 and *Palaeolama* Gervais, 1867, to smaller species within the genus *Lama* such as *Lama gracilis* (Gervais and Ameghino, 1880). Recent paleontological studies based on material from the northeast of Brazil (Guérin y Faure, 1999), from Córdoba Province (Tauber, 1999), from Entre Ríos Province (Ferrero, 2005; Scherer *et al.*, 2007), and from the of Pampa Bonaerense (Menegaz and Ortiz-Jaureguizar, 1995; Menegaz, 2000) have aimed to systematize an extensive list of camelid findings, in order to amend former classifications and identify new species. Menegaz' work (Menegaz, 2000; Menegaz *et al.*, 1989; Menegaz and Ortiz-Jaureguizar, 1995) is particularly interesting as he subordinates the genus *Vicugna* Lesson, 1842 as a subgenus of the *Lama* Cuvier, 1800, which would be represented by the *Lama (Vicugna) vicugna* (Molina, 1782) and the *Lama (Vicugna) gracilis* (Gervais and Ameghino, 1880). The latter corresponds to a species whose size and cranial characters (incisors) locate it between the vicuña and the guanaco (Menegaz and Ortiz-Jaureguizar, 1995; Guérin and Faure, 1999). The gracile camelid remains were recovered from Bolivia to the Tierra del Fuego deposits of middle to late Pleistocene and early Holocene age, and the majority of the material was collected from different archaeological sites (Menegaz and Ortiz-Jaureguizar, 1995; Menegaz, 2000). Recent DNA molecular analysis of dental pieces from chilean patagonian

remains show however that these remains previously classified as *Lama gracilis* corresponds to *Vicugna vicugna*. Therefore, this evidence suggests that these remains do not belong to an extinct species but rather to a large vicuña with a wider geographical distribution as known before (Weinstock *et al.*, 2009).

In the present study we describe material corresponding to fossil remains of camelids from the Kamac Mayu site (Second Region, Chile). The record was obtained by systematic excavations in deposits of gravel and sand set out on a karst formation eroded by river courses during the late Pleistocene (Figures 1a, 1b, 1c, 1d). As well as the Camelidae record, diverse fossil material was recovered, including *Hippidion saldiasi* Roth, 1899 (Mammalia, Equidae), *Macrauchenia patachonica* Owen, 1838 (Mammalia, Litopterna), undetermined xenarhrans (Xenarhra, Mammal), and birds (Aves, Rheidae) (Alberdi *et al.*, 2007; Gelfo *et al.*, 2008), as well as specimens of Planorbidae, Hydrobiidaee and Sphaeriidae (Mollusca) within deposits formed during the draining of the former basin in Chiu Chiu, Calama (May *et al.*, 2005). The morphological and osteometric analyses of cranial and postcranial elements enabled the taxonomic assignment of the remains to *Lama gracilis*, not seen before in this region of the country.

GEOLOGICAL SETTING

The paleontological site of Kamac Mayu (68° 54' 40'' W, 22° 26' 30'' S) is located in the city of Calama (2250 m a. s. l.), in a fluvial basin containing sandy gravel and sand deposits, 100–300 m away from the Loa river. According to Chong-Díaz and Jensen (2004), four stages of deposition can be distinguished at the Kamac Mayu site:

Lacustrine stage. Represented by a stratified unit of disintegrated marl with diatomite lenses from the Pliocene-Pleistocene age. Due to its lithology, this lacustrine unit can be assigned to the Chiu Chiu Formation from the Pliocene-Pleistocene age, defined by Naranjo and Paskoff (1981).

Karstic stage. Represented by an eroded surface formed by dissolution cavities. In the area under study, the walls of these cavities have a hard covering that is 1 to 3 mm thick and whose origin stems from calcium carbonate precipitation. This contrasts with the yellow marl, whose aspect is pulverulant and brittle. A fluvial system, characterized by clastic sediments, occurred after this event.

Fluvial stage. A third stage of fluvial origin represented by sandy gravel and sand deposits that fill multiple channels formed above the karstic horizon. The stratigraphic distribution comprises fine sequences of centimetric magnitude with crossed concave stratification. The fluvial stage was formed prior to the formation of the Loa River canyon and corresponds to the interval in which the fossil remains were deposited. The deposits with fossil remains reach a maximum depth of approximately 1.80 m.
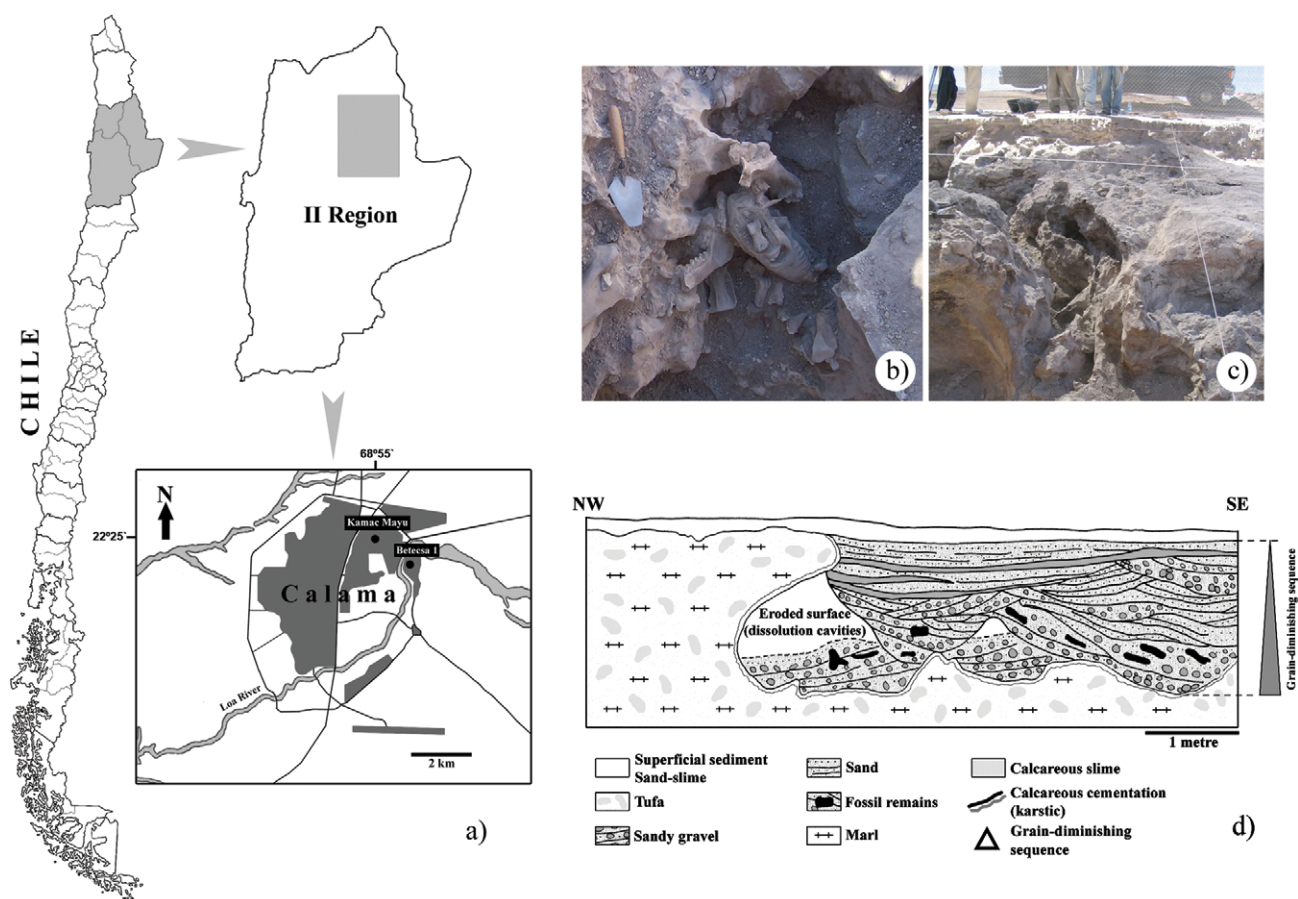
Figure 1. a: Localization of the Kamac Mayu site, b: *Macrauchenia patachonica* fossil remains *in situ*, c: eroded surface formed by dissolution cavities, d: the stratigraphy of Kamac Mayu deposits.

Calcareous cementation stage. After the gravel sedimentation, the meteoric waters, saturated in calcium carbonate, percolated through the gravel that fills the channels. This process enabled the precipitation of calcite in intergranular spaces leading to the cementation of clasts.

The presence of fossil remains belonging to *Macrauchenia patachonica* and *Hippidion saldiasi* suggests a late Pleistocene age for the deposits (Alberdi and Prado, 2004; Alberdi *et al.*, 2007). Two bone samples from the gracile camelids were sent to be dated. Unfortunately, they did not contain enough organic material. However, the remains of *Hippidion saldiasi* from the neighboring site Betecsa-1 (68º 54' 44'' W, 22º 26' 30'' S) were dated; the dating carried out on the right M^3 layer showed a ^{14}C age of $21,070 \pm 100$ B. P. (not calibrated. GrA-29389, Centrum voor Isotopen Onderzoek, Holland). In addition, the dating of a basicranium fragment belonging to the same *Hippidion saldiasi* showed an age of $21,380 \pm 100$ B. P. (not calibrated. GrA-29388, Centrum voor Isotopen Onderzoek, Holland) (Alberdi *et al.*, 2007). The faunistic and sedimentolgical affinities between the Betecsa-1 and Kamac Mayu suggest a similar age for both sites, equivalent to Lujanian stage of the South American Land Mammal Ages (SALMA).

MATERIAL AND METHODS

Morphometric analysis was performed in order to study the change and variation of the fossil sample. Size was studied by using osteometric methods and comparing measurements with fossil and modern camelid samples. Measures were taken following criteria presented in von den Driesch (1999) and Menegaz (2000). Multivariate analysis is commonly employed for morphometric studies, specially Principal Components (Menegaz *et al.*, 1989). However, in this case the number of observations is too small for the use of parametric statistics. Instead, we used bivariate scaterplots in order to compare the samples. In addition, a comparative anatomical study focused on the identification and description of diagnostic landmarks or characters was performed. For the morphological description of the material we use the criteria defined by Menegaz (2000), and Scherer *et al.* (2007) for the dental nomenclature.

For the identification and comparison of the sample considered in this study, we used camelid fossil remains from the Colección División Paleontológica de Vertebrados housed at the Museo de La Plata (Argentina) and the Collection of Mammifères fossils, Muséum National d'Histoire Naturelle

(Francia). In the same way, we also used as reference present-day collections and measurements of *Lama guanicoe* and *Vicugna vicugna* from Staatssammlung für Anthropologie und Paläoanatomie, Munich (Germany), Zoologische Staatssammlung, Munich (Germany), Zoologisches Museum, Berlin (Germany), Natural History Museum, London (England) and Departamento de Antropología Universidad de Chile, Santiago (Cartajena 2003).

Abbreviations

Institutional abreviations.

KM, Kamac Mayu; MLP, Museo de La Plata; MNHNP-TAR, Musee d'Histoire Naturelle Paris,fossil remains recovered from Tarija locality (Bolivia).

Anatomical abbreviations

DP, Deciduous premolar teeth; M, Molars; I, Incisors; DI, Deciduous incisors.

SYSTEMATIC PALEONTOLOGY

Order Artiodactyla Owen, 1848
Family Camelidae Gray, 1821
Subfamily Camelinae Gray, 1821
Genus *Lama* Cuvier, 1800

Lama gracilis (Gervais and Ameghino, 1880)
Figures 2-6

Auchenia gracilis Gervais y Ameghino, 1880, p. 115.
Auchenia frontosa Gervais y Ameghino, 1880, p. 117.
Auchenia lujanensis Ameghino, 1889, p. 586, fig. 8.
Hemiauchenia pristina Ameghino, 1891, p. 138, fig. 30
Palaeolama crequii var. *provicugna* Boule and Thevenin, 1920, p. 180. plate 20, fig. 1.
Lama gracilis López-Aranguren, 1930, p. 113, fig. 16, left.
Vicugna vicugna Cabrera, 1932, p. 116.
Lama (Vicugna) gracilis Menegaz, Goin y Ortiz-Jaureguizar 1989, p. 161, plate 1, figs. 1-4.

Diagnosis. The size of metapodials is smaller than the *Lama guanicoe* and slightly larger than the *Vicugna vicugna*, and the metapodials are comparatively more gracile than in these species. The lower incisors are slightly imbricated; with a thick layer of enamel on the labial face which becomes much thinner towards the lingual face of the tooth layer, especially in the I_1. The incisors show bicelated wear facets at their distal extremes. In vicuñas this feature is similar but much developed since the wear facet covers a wider surface at the lingual face of the tooth. On the other hand, in guanacos wear facets are much less developed and over the incisors borders, the dentine is exposed as a fine band on the lingual and labial enamel (Menegaz *et al.* 1989, p. 160). The wearing down of the inferior incisors is located in the sub quadrangular section, unlike the *Vicugna vicugna* where this section is enlarged, with a sub rectangular and sub elliptical section.

Materials. KM/SC/SA/1, right metatarsal; KM/SC/SA/2, right metacarpal; KM/SC/SA/3, incomplete metapodial; KM/SC/SA/4, left metacarpal; KM/SC/SA/5, incomplete metapodial; KM/SC/SA/6, incomplete metapodial; KM/SC/SA/7, incomplete left tibia; KM/SC/SA/8, incomplete metapodial; KM/SC/SA/13, incomplete metapodial, KM/SC/SA/17, right metacarpal; KM/SC/SA/62, fourth tarsal; KM/SC/SA/22, incomplete right femur; KM/SC/SA/23, incomplete radius; KM/SC/SA/24, incomplete right femur; KM/SC/SA/25, incomplete right radius; KM/SC/SA/26, incomplete right humerus; KM/SC/SA/27, incomplete right humerus; KM/SC/SA/28, incomplete left humerus; KM/SC/SA/30, incomplete cervical vertebrae; KM/SC/SA/31, incomplete left humerus; KM/SC/SA/33, incomplete right calcaneus; KM/SC/SA/35, incomplete cervical vertebrae; KM/SC/SA/36, caudal vertebrae; KM/SC/SA/37, incomplete first phalanx; KM/SC/SA/38, incomplete rib; KM/SC/SA/39, incomplete rib; KM/SC/SA/40, incomplete rib; KM/SC/SA/41, incomplete rib; KM/SC/SA/42, incomplete rib; KM/SC/SA/43, incomplete rib; KM/SC/SA/44, incomplete left humerus; KM/SC/SA/45, incomplete right tibia; KM/SC/SA/46, caudal vertebrae; KM/SC/SA/47, thoracic vertebrae; KM/SC/SA/48, incomplete right metatarsal; KM/SC/SA/53, incomplete right humerus; KM/SC/SA/56, sacrum; KM/SC/SA/62, scapula; KM/SC/SA/63, incomplete first phalanx; KM/SC/SA/64, incomplete first phalanx; KM/SC/SA/65, second phalanx; KM/SC/SA/66, incomplete rib; KM/SC/SA/67, second phalanx; KM/SC/SA/68, incomplete rib; KM/SC/SA/69, incomplete cervical vertebrae; KM/SC/SA/70, incomplete thoracic vertebrae; KM/SC/SA/71, incomplete thoracic vertebrae; KM/SC/SA/72, incomplete thoracic vertebrae; KM/SC/SA/73, skull; KM/SC/SA/74, incomplete right mandible; KM/SC/SA/75, incomplete left mandible; KM/SC/SA/76, incomplete left femur; KM/SC/SA/77; incomplete left maxilla; KM/SC/SA/78, incomplete left maxilla; KM/SC/SA/79, incomplete metapodial; KM/SC/SA/80, incomplete rib; KM/SC/SA/81, incomplete rib; KM/SC/SA/82, incomplete rib; KM/SC/SA/83, incomplete cervical vertebrae; KM/SC/SA/84, incomplete lumbar vertebrae; KM/SC/SA/85, incomplete lumbar vertebrae; KM/SC/SA/86, incomplete thoracic vertebrae; KM/SC/SA/87, incomplete thoracic vertebrae; KM/SC/SA/88, incomplete second phalanx; KM/SC/SA/89, incomplete rib; KM/SC/SA/90, incomplete rib; KM/SC/SA/91, incomplete rib; KM/SC/SA/92, incomplete rib; KM/SC/SA/93, incomplete mandible; KM/ B3/C3/RP15, complete left femur; KM/ B3/C3/RP16, complete right radius-ulna; KM/C3/B4/RP29, complete left metatarsal; KM/A4/C3/RP32, incomplete thoracic vertebrae; KM/A3/C1/SRP, second phalanx; KM/ B3/C3/SRP, patella; KM/B4/C3/SRP, incomplete right maxilla.
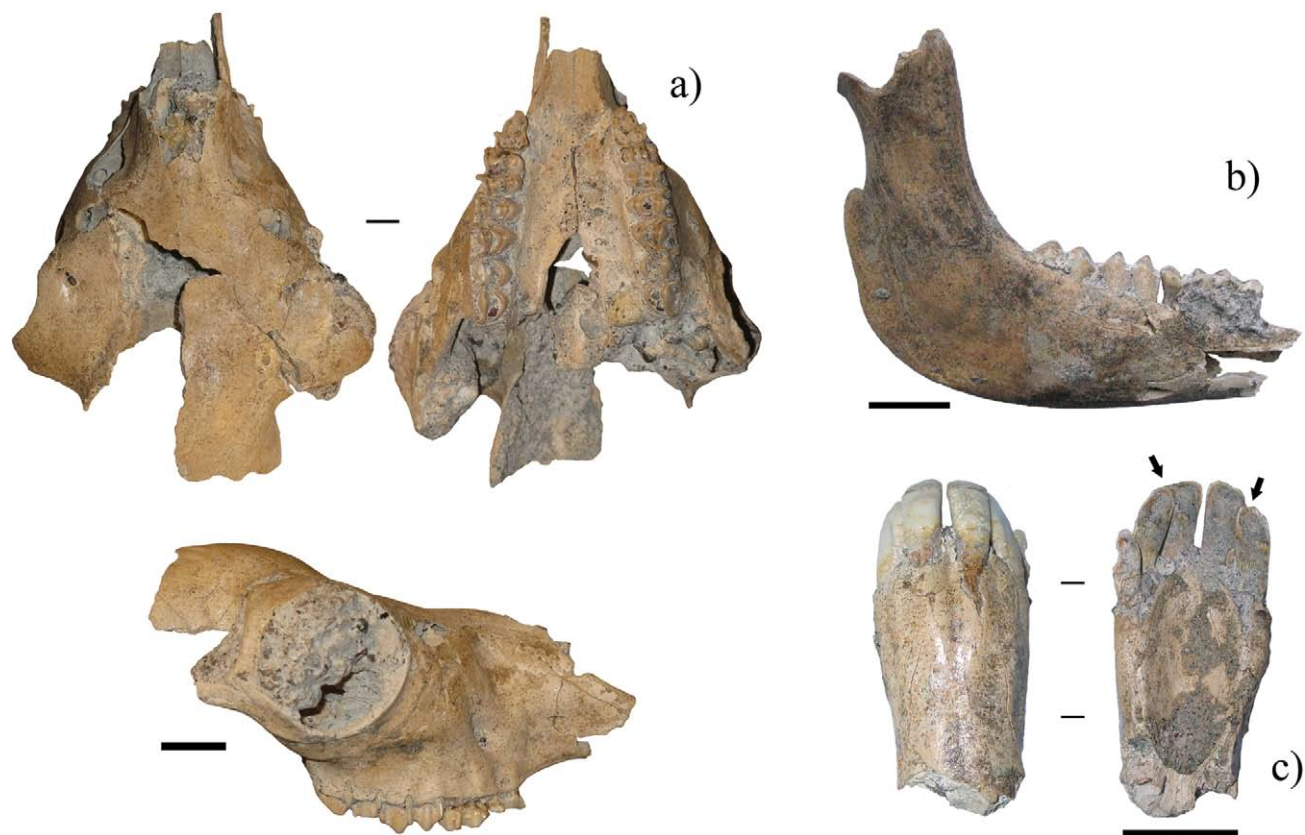
Figure 2. a: *Lama gracilis* skull (KM/SC/SA/73), b: right mandible (KM/SC/SA/74), c: Deciduous incisors (KM/SC/SA/93). The arrows mark the imbrication of the teeth. Scale bar 3 cm.

Preservation. The fossil record pertaining to camelids is composed of 37 specimens, including axial and appendicular elements, which showed a regular state of conservation due to fissures produced by the pressure of sediments and adhesion of salt crystals typical of this zone (López and Labarca, 2005). Taphonomic alterations such as weathering or damage produced by other natural agents such as carnivores were not observed.

DESCRIPTION AND DISCUSSION

Skull, mandible, and dentition

Skull

Four fragments of craniums have been recovered. Three of these specimens correspond to fragments of maxillaries, whereas one of the samples is a relatively complete cranium of a young individual. In the case of the maxillaries, the specimen KM/SC/SA/77 shows the DP^3, DP^4 and M^1 which suggests an age of 4 to 7 months (de la Torre, 1981). In the specimen KM/SC/SA/78 only the M^1 and M^2 are conserved, indicating an age of between 14 to 20 months. On the other hand, the fragment of maxillary KM/B4/C3/SRP is covered with an extremely hard calcare-

ous sediment, nevertheless, the presence of DP^3, DP^4 and M^1 suggests a similar age to that proposed for the specimen KM/SC/SA/77.

The cranium (KM/SC/SA/73) consists of both maxillaries, a part of the two frontals, a fragment of the right parietal (with a total absence of left one), both lacrimals, a part of the nasals, the temporal, the right zygomatic and part of the left one, as well as both supermaxillaries and the palatine, although there is a total absence of the premaxillaries. Both dental series are in a good state of conservation and are represented by the DP^3 whose occlusal surface exhibits an advanced tooth wear, the DP^4 shows intermediate wear, the M^1 does not show much wear. As the M^2 is still in the process of eruption, the age of this individual has been defined around 14-20 months (de la Torre, 1981). The relation between the molariform series is relatively convergent and there is a deep, well defined palatine notch (Table 1, Figure 2a).

One remarkable trait of the cranium (KM/SC/SA/73) recovered from the Kamac Mayu site, is the great development of the *Foramen ethmoidale*. Herre (1952) proposes that this feature is evident in guanacos, whereas it is poorly developed or absent in vicuñas. However, this feature cannot be considered as diagnostic, given that it has been observed in some recent camelids (Cartajena, 2003).

Mandible

The sample includes two fragments of mandibles (left and right) of the same individual and a mandibular symphysis with a complete dental series of another individual. The right mandible (KM/SC/SA/74, Figures 2b and 3b) shows a better state of preservation; the molar series DP_3, DP_4, M_1 and M_2 have been conserved, which suggests an age between 14 to 20 months (de la Torre, 1981); in this specimen the coronoid process and the mandibular symphysis are broken. The masseteric fossa is marked and deep and the mandibular condyle is low, with a triangular section and shows ample facets with well marked boarders (Menegaz, 2000). In the fragment of the left mandible (KM/SC/SA/75) part of the molar series DP_4, M_1 and M_2 can be observed (the DP_3 is broken at the root) the mandibular angular, the mandibular condyle, the coronoid process and the mandibular symphysis are broken.

In the case of mandibular symphysis (KM/SC/SA/93, Figure 2c), the development and damage of the lower deciduous incisors indicate an individual age of less than 15 months (de la Torre 1981). Measurements in Table 2.

Dentition

Upper deciduous dentition. The DP^3 and DP^4 from the specimens KM/SC/SA/77, KM/B4/C3/SRP, and KM/SC/SA/73 are moraliform, with two distinct, clearly defined U-shaped lobes. The mesostyle is projected towards the labial surface more than the parastyle and metastyle. In the DP^3 of the maxillary KM/SC/SA/77 the occlusal surface can be observed with greater clarity, whereas in KM/SC/SA/73 it is completely worn down and in the KM/B4/C3/SRP it is covered by calcareous sediment. In the DP^3 the trigon fossa is elongated and less curved than the talon fossa; at the same time the protocone is not touching the hypocone; the latter is barely visible; it disappears completely into the cranium due to the advanced state of tooth wear. On the other hand, the DP^4 is characterized by the even more marked prolongation of the mesostyle towards the labial surface. The trigon fossa and the talon fossa are also curved and unfolded; both lobes are U-shaped and subequal in size. The protocone
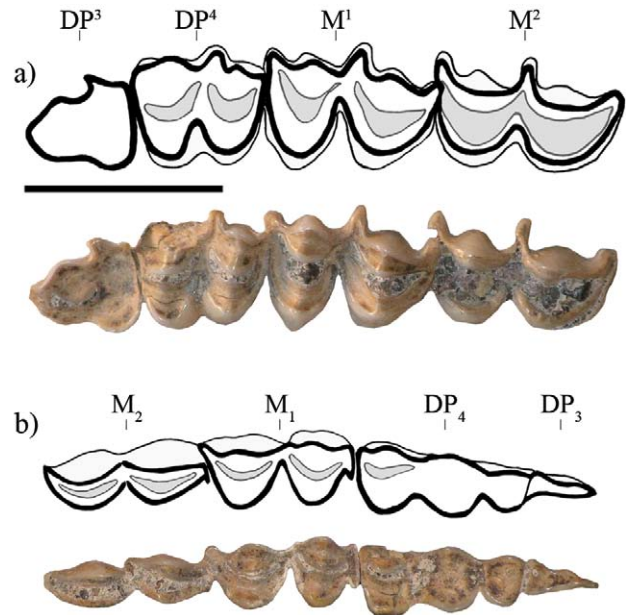

Figure 3. a: Occlusal view of the upper dentition from the *Lama gracilis* skull (KM/SC/SA/73), b: occlusal view of the lower dentition from the *Lama gracilis* right mandible (KM/SC/SA/74). Scale bar 3 cm.

and hypocone are united across the narrow valley. In the piece KM/SC/SA/73, the metastyle is practically absent due the damage to the DP^4, whereas the parastyle takes on a quadrangular form.

Upper permanent dentition. Various stages of wear can be observed in the four samples studied. In the cranium (KM/SC/SA/73) M^1 has also almost totally erupted, whereas the M^2 is in the initial stage of eruption (Figure 3a). In the fragment of the maxillary KM/SC/SA/78 a similar situation can be seen, although the M^2 is located further into the alveolar cavity. Lastly, in the specimens KM/SC/SA/77 and KM/BB5/C3/SRP the M^1 is in the process of eruption, as is the M^2, although the latter is more contained. In the M^1 the medial lobe is larger than the distal lobe. Like the deciduous premolars, the mesostyle is extended towards the lingual surface, surpassing the parastyle and the metastyle. In the specimen KM/SC/SA/77 both lobes tend to be V-shaped, although this condition is due to the slight wear of this molar as this is not observed in the rest of the material in which U-shaped lobes predominates; this feature is comparable to that observed in a fragment of a left maxillary (MLP. 9. 473) referable to the *Lama gracilis* from the Vitel Lagoon (Pampean Formation), Argentina. In the M^1 of the KM/SC/SA/77, the trigon fossa is narrow and curved, unlike the talon fossa, which does not show such a sharp convexity. In the same way, the protocone shows a greater labial-lingual length than the hypocone. In the rest of the M^1 these differences cannot be seen as both the fossas and the cones are very similar. On the other hand, all the M^2 studied are in the process of eruption and significant differences between them are not present.

Table 1. Measurements (mm) of *Lama gracilis* skull. 13[a]: Length of the cheek tooth row, DP^3-M^2 (measured along the alveoli); 14: length of the molar row (measured along the alveoli on the buccal side); 15: length of the premolar row, DP^3-DP^4 (measured along the alveoli); 16: greatest inner length of the orbit: Entorbitale-Entorbitale; 17: greatest inner height of the orbit; 26: least breadth between the orbits: Entorbitale- Entorbitale; 27: facial breadth between the infraorbital foramina (least distance); 29: greatest palatal breadth: measured across the outer borders of the alveoli; 31: height of the horizontal part of the maxilla: from the front border of the alveoli of DP^3 at right angles to the most dorsal point of the maxilla on one side.

Abbreviation	13[a]*	14*	15*	16*	17*	26*	27*	29*	31*
KM/SC/SA/73	60.6	48.9	11.9	41.2	39.7	82.3	49.9	40.9	54

*Measurements *sensu* von den Driesch (1999) taking as reference the cranium of the *Camelus*.

Table 2. Measurements (mm) of *Lama gracilis* mandibles. 1: Height of the mandibular condyle; 2: height of the angular process; 3: height of the horizontal part of the mandible: from the front border of the alveoli of M_2; 4: height of the horizontal part of the mandible: from the front border of the alveoli of DP_3; 5: length of the cheektooth row, DP_3-M_2 (measured along the alveoli).

Abbreviation	1*	2*	3*	4*	5*
KM/SC/SA/74	89	62.1	39.5	20.4	59.5
KM/SC/SA/75	-	-	39.5	-	-

*Measurements *sensu* Menegaz *et al.* (1988).

Lower deciduous dentition. The sample of the lower deciduous dentition is scarce and comprises of pieces of KM/SC/SA/74, *i.e.* the DP_3 and the right DP_4 and the DP_4 from the left mandible from the same individual (KM/SC/SA/75) (Figure 3b). The DP_3 consists of only one lobe that has been transversely compressed and shows significant wear on the occlusal surface. The molariform DP_4 shows two lobes with intermediate wear; the talonid fossa is absent, whereas the trigonid fossa is hardly visible, unfolded and curved. Due to the wear, the metastylid and the entostylid are absent and the parastylid can hardly be seen. The proto-conid and the hypoconid are united, whereas the size of the hypoconulid is equivalent to 2/3 of both main lobes.

In the mandibular symphysis (KM/SC/SA/93) the deciduous incisors show a slight imbrication, with signs of wear in the case of the DI_2 in the elliptical section and in the case of the DI_3 of a sub rectangular type. Based on the analyses carried out through the use of X-rays taken from these samples, it was possible to ascertain that the enamel tended to be thicker on the labial face, reducing to a thin layer on the lingual face (Figure 4a and 4b).

Lower permanent dentition. As in the last case, the only samples of lower molars correspond to the two mandibles recovered (KM/SC/SA74 and KM/SC/SA/75). In both cases the M_1 shows slight tooth wear whereas the M_2 is in the process of eruption. The M_1 has two lobes similar in size, with the metastylid and the parastylid barely visible, unlike the entostylid which sticks out towards the labial surface. The trigonid fossa and the talonid fossa show similar characteristics due to their size and to the slightly pronounced curve. In the labial surface both lobes are U-shaped and have a well defined and projected protostylid. In the case of the M_2 the very scarce degree of the eruption of the tooth does not allow for a detailed description. The mesial lobe is more developed than the distal lobe; the parastylid and the entostylid are scarcely developed; only the metastylid can be observed.

Axial skeleton

Scapula

The only scapula recovered from Kamac Mayu is very fragmented and only the neck of scapula and part of

the spine of scapula can be seen; the acromion process is absent. On the other hand, in the caudal border in the area of the neck of scapula, a ridged surface can be observed, situated on the border of a slightly marked tuberosity. Due to the state of conservation, only one measurement was obtained (Table 3).

Humerus

All the humeri from the Kamac Mayu site correspond to young individuals from which metric data was not ob-
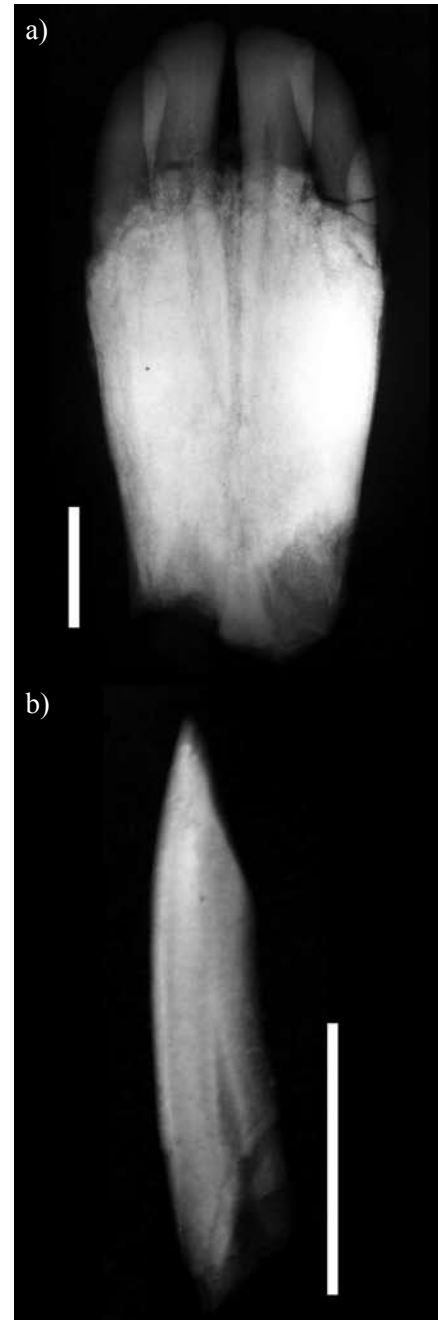

Figure 4. a: X-ray of the *Lama gracilis* mandible (KM/SC/SA/93) from the Kamac Mayu site, b: X-ray of a *Lama gracilis* incisor belonging to a fragment of the mandible (KM/SC/SA/93). Scale bar 1 cm.

tained. From the five samples recovered, three correspond to distal diaphyses (KM/SC/SA/44; KM/SC/SA/53; KM/SC/SA/27) all of them not presenting the humerus condyle although the olecranon fossa is deep and marked. The piece KM/SC/SA/27 possesses the majority of the diaphyses and here the helical torsion is less pronounced than in comparison with adult camelidae humerus (Cartajena, 2003). The proximal fragments (KM/SC/SA/26; KM/SC/SA/31) do not have the greater tubercle or the lesser tubercle fusion and in the best conserved piece KM/SC/SA/26, the deltoid tuberosity is hardly visible.

Radius-ulna

Among the bones that correspond to individual adults there is a radius-ulna (KM/B3/C3/RP16) in a very bad state of conservation due to fractures caused by sediment pressure (Figures 5a and 5b). Likewise, within the sample, two unfused radial diaphyses from young individuals were counted (KM/SC/SA/23; KM/SC/SA/25). Regarding the complete piece, the olecranon is long and tall, but compressed in the lateral-medial section. Both proximal articular facies are wide and deep with a shallow depression on the extremity of the head of the radius, whereas the lateral

Table 3. Measurements (mm) of *Lama gracilis* scapula. SLC: Smallest length of the *Collum scapulae* (neck of the scapula).

Abbreviation	SLC*
KM/SC/SA/67	31.7

*Measurements *sensu* von den Driesch (1999).

tuberosity and the lateral coronoid process are extremely pronounced. The distal articular surface is made up of three facies of the carpi: radial, intermediate, and ulnar; they have similar dimensions.

The width of the radius-ulna (KM/B3/C3/RP16) is comparable to that observed in specimens belonging to vicuña. However, the specimens from the Kamac Mayu site and also from the MLP are classified in the 'extremely high' range of the established size of present-day vicuñas (Table 4). This would suggest that the differences between the gracile camelid (*Lama gracilis*) and the vicuña radius-ulna are associated with the length of the bones. Nevertheless, the muscular insertion zone in the specimens from the Kamac Mayu site are much more pronounced in relation to present-day vicuñas.
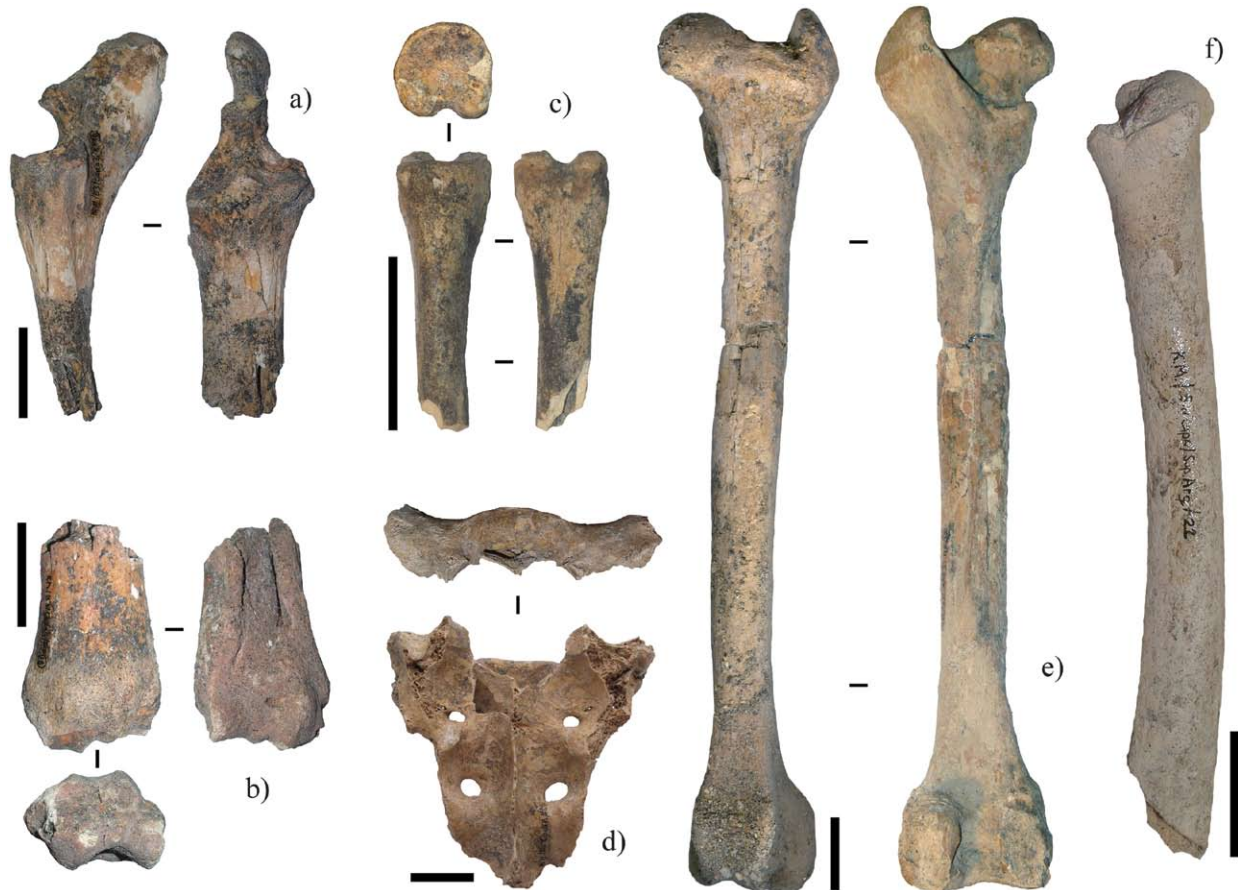

Figure 5. Bones of the axial skeleton. a: proximal right radius-ulna (KM/B3/C3/RP16), b. distal radius (KM/B3/C3/RP16), c: first phalanx (KM/SC/SA/63), d: sacrum (KM/SC/SA/56), e: (KM/B3/C3/RP15), femur, f: right femur (KM(SC/SA/22). Scale bar 3 cm.

Table 4. Measurements (mm) of *Lama gracilis* radius-ulna. Bp: Greatest breadth of the proximal end; BFp: greatest breadth of the *Facies articularis proximalis*; BFd: greatest breadth of the *Facies articularis distalis*; Bd: greatest breadth of the distal end; LO: length of the olecranon; SDO: smallest depth of the *olecranon*; DPA: depth across the *Processus anconaeus*; BPC: greatest breadth across the coronoid process.

Abbreviation	Bp*	BFp*	BFd*	Bd*	LO*	SDO*	DPA*	BPC*
KM/B3/C3/RP16	39	37.3	30.3	37.9	46.9	32.1	37.7	36.7

*Measurements *sensu* von den Driesch (1999).

Table 5. Measurements (mm) of *Lama gracilis* metacarpals. Dp: Depth of the proximal end; Bp: greatest breadth of the proximal end; DOFAI: oblique diameter of the internal articular facet; DOFAE: oblique diameter of the external articular facet.

Abbreviation	Dp*	Bp*	DOFAI**	DOFAE**
KM/SC/SA/17	22.63	30.10	21.20	19.21

*Measurements *sensu* von den Driesch (1999), **Measurements *sensu* Menegaz *et al.* (1988).

Metacarpals

Three metacarpals were recovered: a proximal fragment of a right metacarpal (KM/SC/SA/2), a diaphysis and a distal epiphysis from a left metacarpal from an adult animal (KM/SC/SA/4) and a right proximal fragment (KM/SC/SA/17). The specimen KM/SC/SA/2 shows a smooth articular facet for the fourth carpal, with rounded edges that show that the bone is not well developed and therefore corresponds to a young individual. Furthermore, the absence of a division between the articular facets for the second carpal and third carpal can be seen. On the other hand, the articular facets in the specimen KM/SC/SA/17 shows well marked borders with concave surfaces; the result of development and which correspond to an adult animal. As in the case of the radius-ulna, in terms of size the measurements from the proximal diaphysis of the adult individual show a similarity with the largest vicuñas (Table 5).

First phalanges

The first phalanges correspond to a proximal fragment (KM/SC/SA/63) and to a distal extreme (KM/SC/SA/64), both from the anterior member of adult animals, as well as a proximal fragment with an unfused articular surface (Table 6, Figure 5c). In the extreme proximal of the adult individual (KM/SC/SA/63), specifically on the palmar surface, the flexor tuberosity is long and it is distally extended. Furthermore, the articular surface on this specimen is quadrangular, whereas the diaphysis has a pronounced triangular section and tends to be more elongated and gracile compared to the vicuña and guanaco. In the extreme distal the axial distal trochlear lobe and the abaxial lobe are absent, due to fracture, therefore it is not possible to carry out a detailed description of this specimen.

Sacrum

The only recovered sacrum (KM/SC/SA/56) has a complete fusion of the first, second and third vertebra; due to a postdepositional fracture the fourth and fifth vertebra are absent (Table 7, Figure 5d). This is also the case for a large part of the sagital crest, the articular processes and part of the articular facies of the ilium which are posteroventrally extended. Between this articular facies and the cranial articular process there is a notch that is less marked in present-day wild Camelidae (Cartajena, 2003). This trait was observed in the specimen MLP. 71 .XI. 1-1 kept in the

MLP, although in this case it is much more pronounced. All the sacral foramen are ovoidal with a distribution that tends to be more horizontal, whereas the opening of the sacrum is triangular, although the vertebral arch is less elevated than in the case of the vicuña and the guanaco.

Femur

The femur sample is one of the most complete and informative as it comprises a complete piece (KM/B3/C3/RP15) and a distal diaphysis (KM/SC/SA/76) from two adult individuals, two unfused distal diaphysis (KM/SC/SA/24 and KM/SC/SA/28), and a diaphysis with the proximal epiphysis (KM/SC/SA/22) from a young animal.

Based on discreet morphological characteristics, some differences among wild camelids have been discussed (Cartajena, 2003). In the case of specimen KM/B3/C3/RP15 the fovea of the femoral head is deep and well marked, similar to the guanaco but different to the majority of the present-day vicuñas used as a comparison, in which the fovea of the femoral head is not pronounced. The trochanteric fossa is more similar to the guanaco than the vicuña as it is smaller and deeper. The rough line of the *Lama gracilis* shows a smooth, regular shape which is very similar to that of the vicuña, given that in the case of guanacos it is much more irregular and has a rigid surface. The *Linea aspera* in the Kamac Mayu specimen is distinct and has quite a prominent edge, similar to that of the vicuña.

In the distal diaphysis (KM/B3/C3/RP15), the edges of the trochlea are high and concave and extend towards the suprapatellar fossa. The fossa poplitea is deep, like in the case of the guanaco. The metric data taken from the Kamac Mayu sample show that the specimen is of medium size,

Table 6. Measurements (mm) of *Lama gracilis* first phalanges. Bd: Greatest breadth of the distal end; SD: smallest breadth of diaphysis; DAPD: anteroposterior diameter of the diaphysis; Bp: greatest breadth of the proximal end; BFp: greatest breadth of the *Facies articularis proximalis*; Dp: depth of the proximal end; DFp: depth of the proximal articular surface; DOEP: greatest breadth (oblique) of proximal end.

Abbreviation	Bd*	SD*	DAPD**	Bp*	BFp*	Dp*	DFp*	DOEP**
KM/SC/SA/63	-	8.64	12.3	16.8	16.7	17.1	15.9	18.5
KM/SC/SA/64	14.4	-	-	-	-	-	-	-

*Measurements *sensu* von den Driesch (1999), **Measurements *sensu* Menegaz *et al.* (1988).

Table 7. Measurements (mm) of *Lama gracilis* sacrum. BFcr: Greatest breadth of the *Facies terminalis cranialis*; HFcr: greatest height of the *Facies terminalis cranialis*; GB: greatest breadth.

Abbreviation	BFcr*	HFcr*	GB*
KM/SC/SA/56	30.1	14.7	93.3

*Measurements *sensu* von den Driesch (1999).

Table 9. Measurements (mm) of *Lama gracilis* patella. GL: Greatest length; GB: greatest breadth.

Abbreviation	GL*	GB*
KM/B3/C3/SRP	39.4	21.3

*Measurements *sensu* von den Driesch (1999).

between the guanaco and the vicuña, although it is more similar to the latter species (Table 8, Figures 5e and 5f).

Tibia

The remains of the tibias are scarce and in both cases they correspond to remains from young animals; one corresponds to an unfused distal diaphysis from a right tibia (KM/SC/SA/45) and the other corresponds to a reassembled distal epiphysis and diaphysis in a bad state of conservation from a left tibia (KM/SC/SA/7). In the surface diaphysis of piece KM/SC/SA/45 the notches for astragalus show long, deep, oval, facets parallel to the anteroposterior axis.

Patella

The anterior and posterior surfaces of the patella are oval shaped. Furthermore, on this surface the development of a convexity that appears in alpacas, llamas and in some vicuñas and guanacos is not transversally observed (Cartajena, 2003). Measurements in Table 9.

Calcaneus

Only one calcaneus was recovered from Kamac Mayu site. This piece corresponds to a right calcaneus from a young individual (KM/SC/SA/33) whose distal extreme is absent due to a postdepositional fracture; the calcaneal tuberosity is unfused.

Metatarsals

The sample from Kamac Mayu comprises two almost complete metatarsals (KM/SC/SA/1; KM/C3/B4/RP29) with the distal epiphyses unfused. In addition, there is a proximal fragment (KM/SC/SA/48) from a right metatarsal that is a slightly eroded, thus it was not possible to collect metric data from it (Table 10). In all specimens the proximal surface is characterised by two articular facets, one medial for the articulation with the third tarsal (triangle shaped) and a second lateral facet for the fourth tarsal (oval shaped). In

the plantar surface there is quite a deep, open groove that extends along almost the entire bone extension, with the exception of the distal quarter. As in the case of the metacarpals, the metatarsals are diagnostic anatomical units for the identification of the *Lama gracilis* (Figure 6a, 6b and 6c). This is due to their characteristically gracile metapodials and their intermediate length, which is between the guanaco and the vicuña. One interesting aspect is that the angle formed in the union between both facets tends to be more open than in vicuñas and guanacos and in the bones analysed it protrudes between 85° and 95° (Figure 7).

Despite the fact that all the specimens correspond to young individuals, some metric traits have been compared in order to obtain a general panorama of the dimensions of the metatarsals from Kamac Mayu with the samples from Tarija (Bolivia), Argentina (Table 11) and from the present-day vicuñas and guanacos (Figures 8a and 8b).

The specimens from Kamac Mayu are of different size in comparison to the specimens of present-day vicuñas in terms of length, despite the fact that they are unfused, which brings them closer to the Tarija specimens. The difference in the breadth of the diaphysis and the proximal epiphysis is less than in the present-day vicuñas.

Considering the ratio between the GL (Greatest length) and Bp (Greatest breadth of the proximal end), the metatarsals from Kamac Mayu are characteristically longer than those of the vicuña (Figure 8). In this respect, Menegaz (2000) states that the gracility index (Bp:GL) is 0,14 for the *Lama gracilis*. However, according to the IG obtained for the specimens from Kamac Mayu (IG 0.13), it can be seen that these are within the range of gracile individuals (IG 0.12-IG 0,14. See Table 12). Nevertheless, it should be noted that the specimens from Kamac Mayu are not fused; therefore the index is closer to the values obtained for the *Lama graclis* by Menegaz (2000, p. 45). We also compared the value of a non fused guanaco metatarsal in a similar ontogenic stage (IG 0.16), which differs considerably from those of Kamac Mayu, *Lama gracilis* and present day vicuñas suggesting that that fossil remains do not belong to adult nor juvenile *L. guanicoe* (see Table 12).

Fourth tarsal

The only tarsal bone corresponds to a very well preserved fourth tarsal (KM/SC/SA/62). Measurements in Table 13.

Second phalanges

Among the second phalanges four specimens were

Table 8. Measurements (mm) of *Lama gracilis* femur. GLC: Greatest length from *Caput*; SD: smallest breadth of diaphysis; Bp: greatest breadth of the proximal end; DC: greatest depth of the *Caput femoris*; Bd: greatest breadth of the proximal end.

Abbreviation	GL*	GLC*	SD*	Bp*	DC*	Bd*
KM/B3/C3/RP15	288.5	289.1	20.17	62.1	26.8	48.8
KM/SC/SA/76	-	-	-	-	-	46.3

*Measurements *sensu* von den Driesch (1999).

Table 10. Measurements (mm) of *Lama gracilis* metatarsals. SD: Smallest breadth of diaphysis; Bp: greatest breadth of the proximal end; Dp: depth of the proximal end; DAPD: diaphyseal anteroposterior diameter DTD: transversal diameter of the diaphysis; DAPEP: anteroposterior diameter of the proximal extremity; DOI: greatest breadth (oblique) of the articular facet for the third tarsal; DOE: greatest breadth (oblique) of the articular facet for the fourth tarsal; DTC: transversal diameter of the neck of the distal epiphysis (posterior point of bifurcation of the metatarsals); DAPC: anteroposterior diameter of the neck of the distal epiphysis.

Abbreviation	SD*	Bp*	Dp*	DAPD**	DTD**	DAPEP**	DOI**	DOE**	DTC**	DAPC**	DAPC:DTC**
KM/C3/B4/RP29	16.05	28.8	26.71	17.18	16.12	26.76	14.57	23.52	19.08	10.92	0.57
KM/SC/SA/1	14.87	29.08	26.79	17.83	15.99	27.06	14.68	22.77	18.63	11.00	0.59

*Measurements *sensu* von den Driesch (1999), **Measurements *sensu* Menegaz (1988).

recovered, three of which correspond to adult animals and one belongs to a young individual due to the absence of fusion of the proximal articular surface. The specimen KM/SC/SA/88 is extremely eroded therefore it was not considered for obtaining metric data (Table 14). In the case of the phalanges KM/SC/SA/65 and KM/SC/SA/67, these correspond to the posterior member. In both specimens the distal articular surface shows an inclination towards the axial and a very marked line of separation between the abaxial and the axial portion of the articular surface can be observed. As is shown in the graph of the Figure 8e, one of the specimens is within the lower range established for present-day guanacos, and as with the metatarsals, there is an extremely elongated tendency in the case of the inferior extremities.

CONCLUSIONS

Through a comparative anatomical study we managed to identify some diagnostic traits that enabled us to assign the studied fossil material to *Lama gracilis*; one of these traits is the morphology of the incisors, specifically the distribution of the enamel and the imbrication of the incisors. In addition, by means of osteometric comparison is it possible to observe that the size of the remains from the Kamac
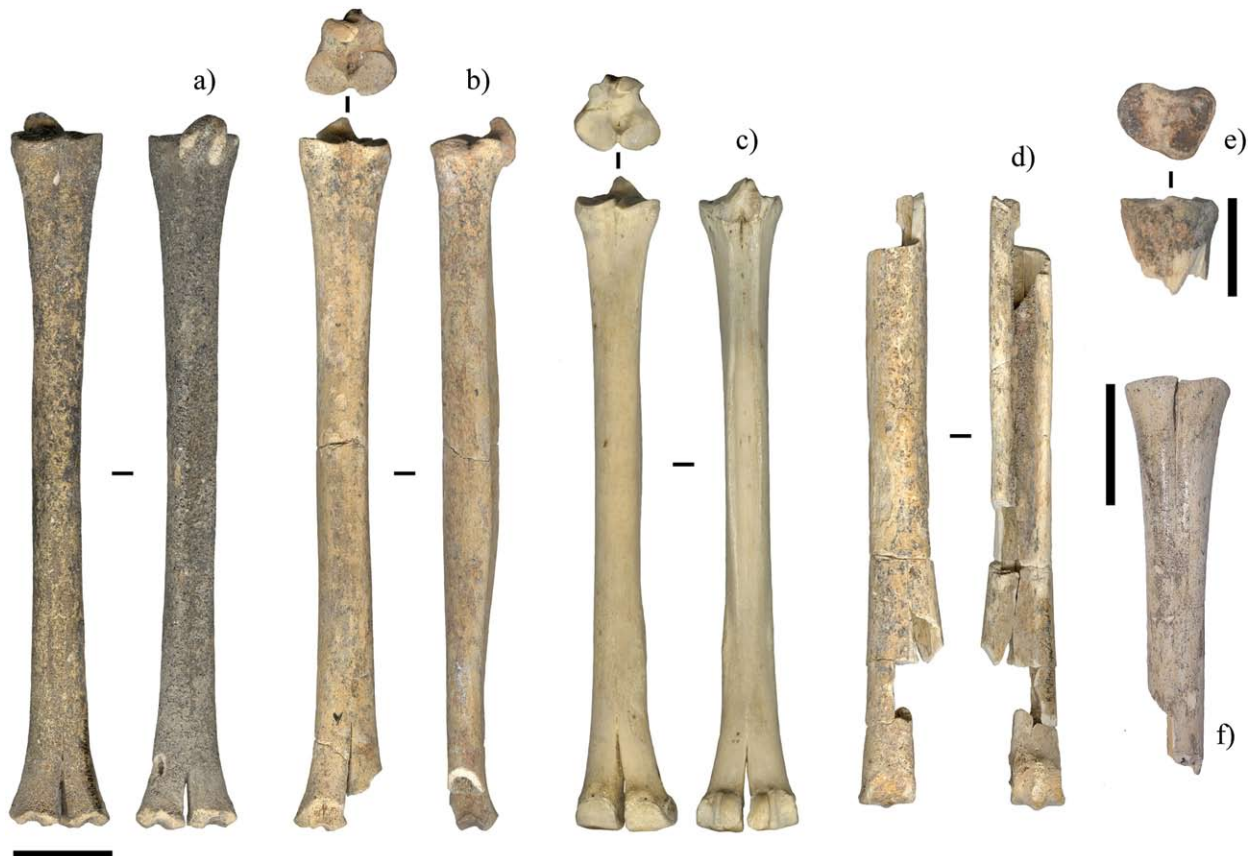

Figure 6. a and b: metatarsals of *Lama gracilis* from the Kamac Mayu site (KM/C3/B4/RP29-KM/SC/SA/1), c: metatarsals compared with *Vicugna vicugna*, d: metacarpal (KM/SC/SA/48), e: proximal metacarpal KM/SC/SA/17), f: proximal metacarpal KM/SC/SA/2). Scale bar 3 cm.

Lama gracilis   *Vicugna vicugna*   *Lama guanicoe*
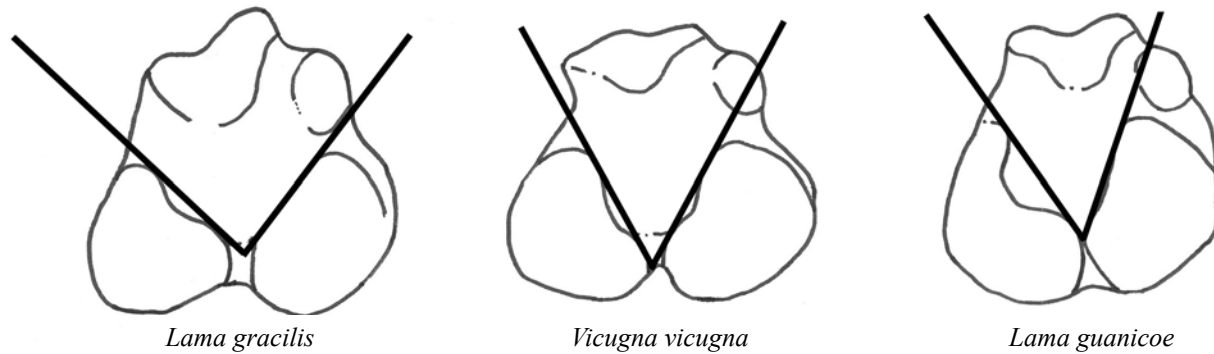
Figure 7. Comparison between *Lama gracilis*, *Vicugna vicugna* and *Lama guanicoe* metatarsals proximal surfaces. Images not to scale.

Mayu site is above the established size-range for present-day vicuñas. They are closer to samples of camelid fossils belonging to the *Lama gracilis* (MLP) and the *Palaeolama crequii provicugna* (NMNHP) and much lower than the collection of present-day guanacos (Cartajena, 2003).

One of the diagnostic traits of the *Lama gracilis* is associated with the length and gracility of the metapodials. As mentioned in above, although the metapodials registered belong to young individuals whose distal epiphyses are not fused, their length is greater than the specimens of present-day adult vicuñas and also juvenile (non fused) modern guanacos used as reference. However, with the non fussed guanaco the most notable differences are related to the breadth. Despite the fact that we measure young animals, we used them as comparison parameters. They show the gracile character of the specimens; the gracility index is similar to that of the vicuña. In the case of the long bones that were recovered belonging to adult animals, they are also intermediate sized, between the present-day vicuña and guanaco. However, it is noteworthy that the muscular insertions are marked in both the long and flat bones.

The remains of the *Lama gracilis* from the Kamac

Mayu site are similar morphologically to the remains located in strata from the middle and late Pleistocene from the Province of Buenos Aires (Menegaz *et al.*, 1989). In Chile, the records of this species are scarce and are limited to a few findings in sites in continental Patagonia dated from around the late Pleistocene (Prieto and Canto, 1997; Massone and Prieto, 2004), that have not been described in detail. According to Menegaz and Ortiz-Jaureguizar (1995, p. 323), the *Lama gracilis* was a herbivorous form with grazing habits, found linked to peneplain pasturelands. The presence of this species in deposits from the late Pleistocene associated with the *Hippidion saldiasi* and *Macrauchenia patachonica* suggests open environments with abundant pasture land and foraging material. In this respect, isotopic analysis carried out on the bone and teeth of an individual of *Hippidion saldiasi* from the Betecsa 1 site show typical values of animals that only feed on C3 grass (Alberdi *et al.*, 2007), which could be due to the altitude where the site is located (2250 m a. s. l.).

During the Finipleistocene and the Early Holocene the distribution of the *Lama gracilis* covered the Pampean Region, Patagonia Argentina, and the north of Uruguay

Table 11. Measurements (mm) of the comparative fossil samples from the División Paleontológica de Vertebrados housed in the Museo de La Plata, Argentina (MPL) and the Collection of Mammifères fossils, Muséum National d'Histoire Naturelle, France (fossil remains of the Tarija locality TAR). GL: Greatest length; Bp: greatest breadth of the proximal end; SD: smallest breadth of diaphysis; BFd: greatest breadth of the *Facies articularis distalis*; Bd: greatest breadth of the distal end.

Abbreviation	Anatomical unit	GL*	Bp*	SD*	BFd*	Bd*
MLP 71-XI-1-1	Metatarsal	210.50	26.90	15.70		
TAR 176	Metatarsal	212.75	27.15	16.97		
TAR 177	Metatarsal	229.99	29.63	17.65		
TAR 165	Metatarsal	229.07	29.50	17.82		
MLP 9-314	Metatarsal		27.20	15.00		
MLP 9-132	Metatarsal		27.70	17.00		
MLP 80-VIII-13-6	Metatarsal		29.30	16.40		
MLP 9-127	Femur	252.90				47.00
MLP 80-VIII-13-64	Radius-ulna		33.00		29.10	
TAR 206	Radius-ulna		36.44		30.74	
MLP 71-XI-1-1	Second phalanx	30.10	13.70			

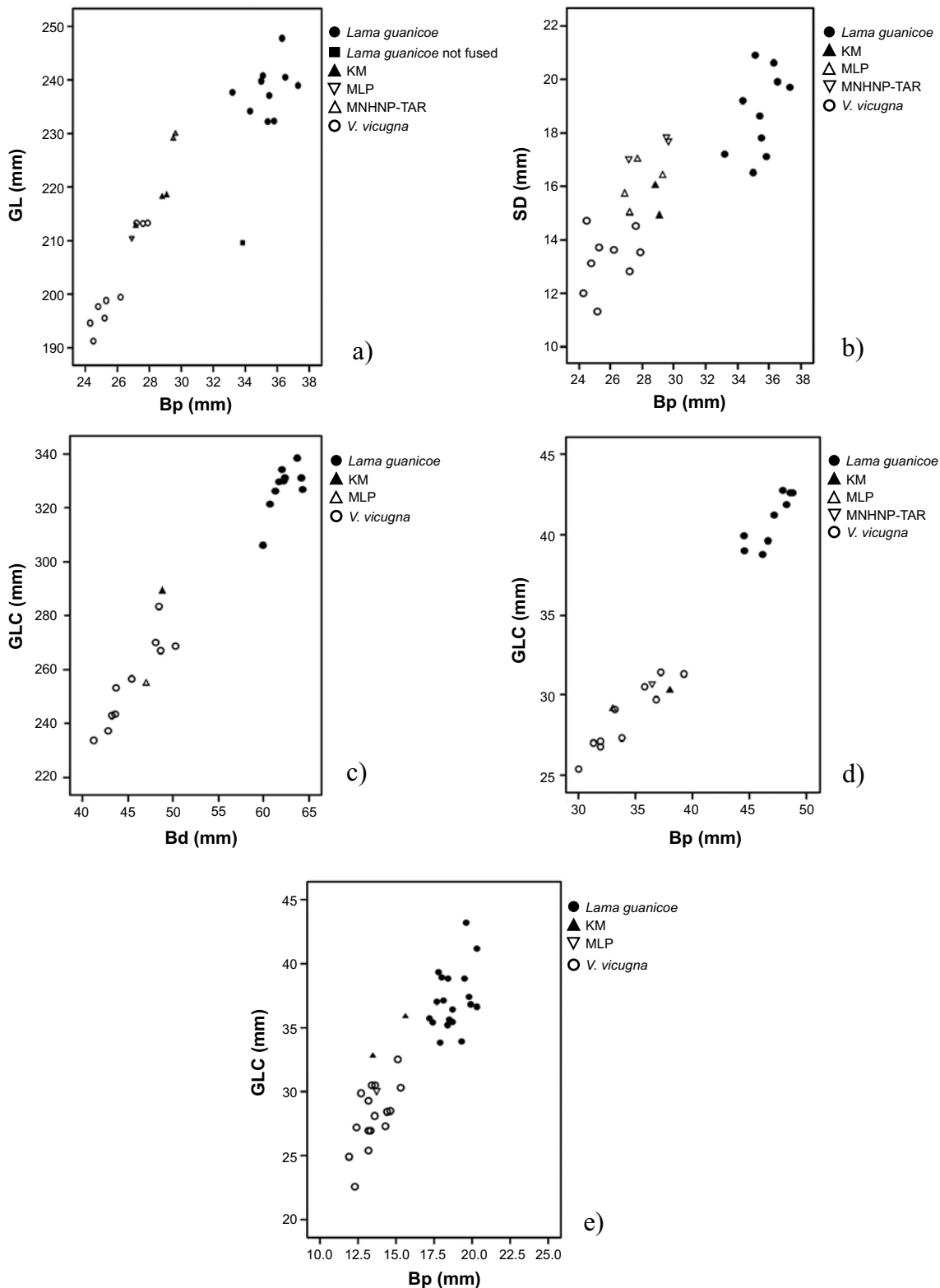*Measurements *sensu* von den Driesch (1999).

Figure 8. Metric comparison of osseous elements from the axial skeleton from the Kamac Mayu site with samples from Tarija, Bolivia (MNHNP-TAR), Argentina (MLP), present-day samples of *Vicugna vicugna* and *Lama guanicoe*. a: Dispersion of metatarsal measurements considering the GL (Greatest Length) and the Bp (Greatest breadth of the proximal end), the distal epiphyses from the specimens from Kamac Mayu are unfused. b: Dispersion of metatarsal measurements considering the SD (smallest breadth of diaphysis) and Bp (greatest breadth of the proximal end). c: Dispersion of the femur measurements, considering GLC (greatest length from the head of femur) and Bd (greatest breath of the distal end). d: Dispersion of the radius-ulna, considering the BFd (greatest breadth of the distal articulari facies) and the Bp (greatest breadth of the proximal end). e: Dispersion of second phalanges measurements considering the GL (greatest length) and the Bp (greatest breadth of the proximal end).

Table 12. Quotient of gracility for the metatarsal.

Metatarsal	Gracility index (IG)*
KM**	0.13
KM**	0.13
*Lama gracilis***	0.14
Present-day Vicuña	0.13
Present-day Guanaco	0.15
Present-day Guanaco not fused	0.16

* Gracility index *sensu* Menegaz (2001); ** Unfused distal epiphysis; *** Gracility Index for the metatarsal of the *Lama gracilicis* (Menegaz 2001, p. 45).

(Ubilla, 2004). Nevertheless, considering that their distribution probably also reached the north of Chile we can suggest that the specimens from Tarija (TAR 165, 176, 177 and 206 used as a comparison in this work), could correspond to a more septentrional distribution of *L. gracilis*. Although these latter remains should be studied in detail, the metric ranges of the specimens assigned to *Paleolama crequii provicugna* (Mones, 1986) are closer to those observed for the *L. gracilis*. In this context, the present study suggests a wider geographic spatial distribution of gracile llamas during the Pleistocene, and the use of not only the low plains but also the high plains, as in the case of Kamac Mayu.

These results contribute to the discussion of new molecular evidence regarding the assignation of fossil records from Patagonia to *Vicugna vicugna* instead of *Lama gracilis* (Weinstock *et al.*, 2009). In our study, morphological and osteometrical comparisons of cranial and postcranial anatomical units allow us to identify the presence of a gracil camelid with similar characteristics of a *Lama gracilis* (Menegaz *et al.*, 1989). The morphological and size differences observed between the *Lama gracilis* with present day vicuñas, raises the question of whether it is related to an extinct specie or they correspond to a late Pleistocene and early Holocene vicuña.

ACKNOWLEDGMENTS

Table 13. Measurements (mm) of *Lama gracilis* fourth tarsal. GD: Greatest depth; GB: greatest breadth; GH: greatest height.

Abbreviation	GD*	GB*	GH*
KM/SC/SA/18	25.5	15.6	18.4

*Measurements *sensu* Cartajena (2003).

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Table 14. Measurements (mm) of *Lama gracilis* second phalanges. GL: Greatest length; Bd: greatest breadth of the distal end; DAPD: diaphyseal anteroposterior diameter; Dd: greatest depth of the distal end; SD: smallest breadth of diaphysis; Bp: greatest breadth of the proximal end; BFp: greatest breadth of the *Facies articularis proximalis*; Dp: depth of the proximal end; DFp: depth of the proximal articular surface.

Abbreviation	GL*	Bd*	Dd*	SD*	DAPD**	Bp*	BFp*	Dp*	DFp*
KM/SC/SA/65	(35.8)	13.8	-	11.9	8.7	15.6	14.4	12.7	-
KM/SC/SA/67	32.8	11.7	(9.8)	-	-	13.5	12.8	10.4	10.1

*Measurements *sensu* von den Driesch (1999); **Measurements *sensu* Menegaz *et al.* (1988).

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