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Original article

# The oldest record of *Hemiauchenia* Gervais and Ameghino (Mammalia, Cetartiodactyla) in South America: Comments about its paleobiogeographic and stratigraphic implications<sup>☆</sup>



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## ARTICLE INFO

### Article history:

Received 5 September 2016

Accepted 19 December 2016

Available online 6 January 2017

### Keywords:

Lamini

Camelidae

Fossil record

Great American Biotic Interchange

Late Pliocene

## ABSTRACT

The South American camelids belong to the Tribe Lamini; this Tribe originated in North America and arrived in South America during the “Great American Biotic Interchange”. The goals of this paper are: (i) to describe the specimen MAM-70, the oldest record of *Hemiauchenia* Gervais and Ameghino in South America; (ii) to analyze this specimen from a stratigraphic point of view; (iii) to update the distribution and stratigraphic ranges of Lamini in South America; and (iv) to discuss its dispersal pattern to South America. The finding of *Hemiauchenia* sp. in late Pliocene Chapadmalalan sediments cropping out at the city of Olavarría (Buenos Aires Province, Argentina) represents the oldest record of a Lamini taxon in South America. This finding refutes the hypotheses that consider the genus *Lama* as the first North American immigrant and those considering that *Hemiauchenia* and *Palaeolama* arrived in South America after the closure of the Central America land bridge, during the early–middle Pleistocene. In turn, this specimen corroborates the hypothesis of the dispersal of Lamini from North America to South America, which considered that *Palaeolama* dispersed after *Hemiauchenia*, in a later and isolated event. In addition, this finding suggests the possibility that a form closely related to the North American *Hemiauchenia macrocephala* could have dispersed to South America during the Pliocene, thus originating the South American forms of *Hemiauchenia* and *Lama*.

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## 1. Introduction

The Camelidae (Cetartiodactyla, Mammalia) has a Holarctic origin, with the oldest records known from the Eocene of North America (Honey et al., 1998). The South American camelids belong to the Tribe Lamini; that Tribe originated in the Great Plains of western North America ca. 11 m.y. ago (Harrison, 1985; Webb and Meachen, 2004). The Lamini spread to South America during the “Great American Biotic Interchange” (GABI), as occurred with other groups of Holarctic mammals (Webb, 1985; Woodburne, 2010). In South America, this Tribe became widely distributed and diversified during the Pleistocene; almost all taxa became extinct

at the end of this period and the beginning of the Holocene, when most of the megafauna species became also extinct (*Broken Zig Zag hypothesis*; Cione et al., 2003, 2009).

However, works dealing with the dispersal and distribution of South American Lamini are few, and many points of these events remain uncertain (Webb, 1974; Webb and Stehli, 1995; Woodburne, 2010; among others). Among these questions, the exact moment of the arrival of the Lamini in South America, the taxonomical identity of the fossil camelids involved in the GABI, and the phylogenetic relationships among South American taxa are still in need of revision. Several authors (Cione and Tonni, 1999, 2005; Cione et al., 2007; Woodburne, 2010) considered that the Lamini arrived in South America during the late Pliocene (ca. 3.3 Ma; early Marplatán Age, Barrancalobean substage), represented by the genus *Lama* Frisch, 1775. Then, in a second pulse, *Hemiauchenia* Gervais and Ameghino and *Palaeolama* Gervais

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would have arrived after the closure of the Central America land bridge (GABI 2 *sensu* Woodburne, 2010), during the early–middle Pleistocene (ca. 1.8 Ma; Ensenadan stage/age). However, Scherer (2013) considers that *Palaeolama* had dispersed to South America after *Hemiauchenia*, in a later and isolated event.

According to recent systematic studies, five genera of the tribe Lamini are recognized in South America (Scherer, 2009, 2013): *Hemiauchenia* Gervais and Ameghino, 1880, *Palaeolama* Gervais, 1867, *Eulamaops* Ameghino, 1889, *Lama* Cuvier, 1800, and *Vicugna* Gray, 1872. The extant forms include only two genera with two wild species, the guanaco, *Lama guanicoe* (Müller, 1776) and the vicuña, *Vicugna vicugna* Molina, 1782, and two domesticated species, the llama, *Lama glama* (Linnaeus, 1758) and the alpaca, *Vicugna pacos* (Linnaeus, 1758). In South America, fossil records of Lamini are the following:

- *Hemiauchenia* was recorded from the late Pliocene?–earliest Pleistocene to the late Pleistocene–earliest Holocene in Argentina, Brazil, Bolivia and Uruguay (Menegaz and Ortiz Jaureguizar, 1995; Cione and Tonni, 1999; Cione et al., 1999; Ubilla and Perea, 1999; Ubilla, 2004; Scherer et al., 2007; Scherer, 2013);
- *Palaeolama* was recorded during the late Pleistocene–earliest Holocene in Brazil, Argentina, Uruguay, Chile, Venezuela, Ecuador and Paraguay (Marshall et al., 1984; Cartelle, 1992; Scherer et al., 2007; Scherer, 2013), and in Bolivia and Peru with uncertain stratigraphic provenance (Marshall et al., 1984; MacFadden and Shockey, 1997; Salas et al., 2003);
- *Lama* was recorded from the late Pliocene to the late Pleistocene–earliest Holocene in Argentina, Bolivia, Brazil, Uruguay, Peru, and Chile (Kraglievich, 1946, 1952; Cartelle, 1994; Casamiquela, 1999; López et al., 2005a, b; Cione and Tonni, 2005; Ubilla, 2004; Deschamps, 2005; Labarca and López, 2006; Ferrero, 2006; Coltorti et al., 2007);
- *Eulamaops* was restricted to the late Pleistocene–earliest Holocene of Argentina (Menegaz and Ortiz Jaureguizar, 1995; Cione et al., 1999; Scherer, 2009);
- *Vicugna* was recorded from the middle to late Pleistocene in Argentina, Bolivia, Uruguay, and Brazil (McKenna and Bell, 1997; Ubilla, 2004; Scherer, 2009).

On that ground, the goals of this paper are:

- to describe the oldest record of *Hemiauchenia* in South America;
- to analyze this specimen from a stratigraphic point of view;
- to update the distribution and stratigraphic ranges of Lamini in South America;
- to discuss its dispersal pattern to South America.

**2. Location, geological setting and stratigraphic context**

The fossils studied here were exhumed from the Neogene sedimentary cover of the “Tandilia System” (Nágera, 1940), more precisely from the limestone quarry “Calera Avellaneda” (36°59'14" S, 60°14'14" W) located near the city of Olavarría, Buenos Aires Province, Argentina (Fig. 1). These sediments are unconformably overlying the limestones of the Neoproterozoic Loma Negra Fm. (Borrello, 1966), which is the upper unit of the Sierras Bayas Group (Dalla Salda and Iñiguez, 1979; Poiré, 1993). The Neogene sedimentary cover is composed of the following units (from bottom to top): La Alcancía Fm., El Polvorín Fm., La Esperanza Fm., and El Búho Fm. (Poiré et al., 2005, 2007; Prado et al., 2013; Fig. 2).

The Polvorín Fm. includes different lithological types, including conglomerates, sandstones, siltstones and clays, which show strong sedimentary processes and facies changes in an alluvial

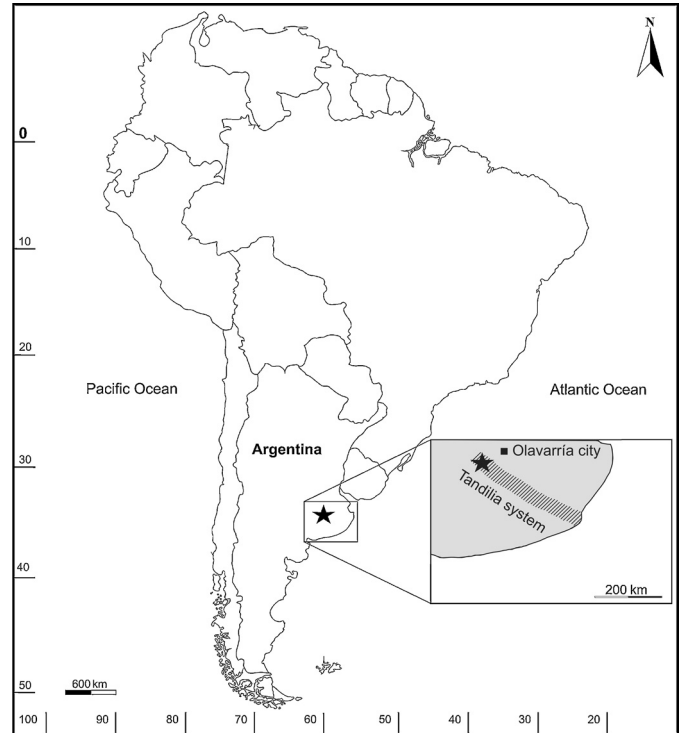


Fig. 1. Geographic location of the quarry “Calera Avellaneda” (36°59'14" S, 60°14'14" W), Olavarría, Buenos Aires Province, Argentina.

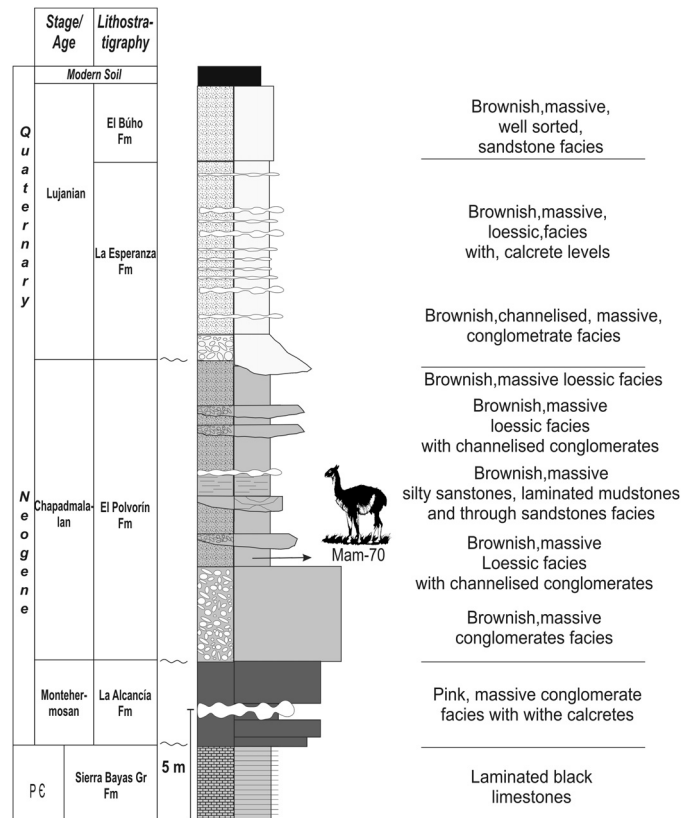


Fig. 2. Lithostratigraphical profile at the locality where the specimen of *Hemiauchenia* sp. (MAM-70) was found.

paleoenvironment (Poiré et al., 2005). One of its peculiar facies was named as “Facies Calera” (De Los Reyes et al., 2013), which is composed by lens-shaped sandstone bodies and massive mudstones with scarce, fine-grained conglomerate levels. The specimen MAM-70 comes from the “Body A” of this unit (De Los Reyes et al., 2013), which reaches up to 6 m in thickness and has a maximum width of 30 m. This level is composed of pink-brownish (dry 7.5YR7/4, humid 7.5YR4/4) well-sorted silty sandstone showing small-scale (20 × 50 cm on average) trough cross-bedding and bearing a high-frequency occurrence of fossil vertebrates. To the top, an isolated, 0–1 m thick, rounded hillock calcrete level was recognized (De Los Reyes et al., 2013; Fig. 2).

Several taxa were recorded in the “Calera Facies”, such as: *Eosclerocalyptus* cf. *E. lineatus* (Hoplophorinae), *Phugatherium novum* (Hydrochaeridae), *Microtragulus reigi* (Argyrolagidae), *Promacrauchenia* (Machraucheniiidae), *Eumysops* (Echimyidae), Cricetidae indet., *Paedotherium* cf. *P. typicum* (Hegetotheriidae), *Platygonus* sp. (Tayassuidae), *Thylacosmilus atrox* (Thylacosmilidae), and cf. *Eleutherocercus antiquus* (Glyptodontidae) (De Los Reyes et al., 2014). This paleofauna assemblage is characteristic of the Chapadmalalan Age (late Pliocene) (Deschamps et al., 2012; De Los Reyes et al., 2013, 2014; Zurita et al., 2014). Recently, a paleomagnetic profile was obtained for this facies, which showed a normal polarity assignable to the Gauss Chron (3.55–2.59 Ma; Gomez Samus et al., 2014).

### 3. Material and methods

Measurements were taken using Vernier callipers, with a 0.01 mm accuracy; all data are expressed in millimeters. We adopted the taxonomical arrangement proposed by Scherer (2009) because it is the current integrative review of the South American Lamini. Chronostratigraphic and geochronologic references correspond to the schemes of Cione and Tonni (1999, 2005).

The studied material was compared to the following North American Lamini genera: *Aepycamelus* Macdonald, 1956 (*A. procerus*), *Blancocamelus* Dalquest, 1975, *Alforjas* Harrison, 1979 (*A. taylori*), *Camelops* Leidy, 1854 (*C. hesternus*), and *Pleiolama* Webb and Meachen, 2004 (*P. mckennai* and *P. vera*). In turn, it was also compared with the South and North American genera

*Hemiauchenia* (South American species, such as *H. paradoxa*, and North American species, such as *H. macrocephala*, *H. blancoensis*, *H. edensis*, *H. “minima”*, and *H. gracilis*), *Palaeolama* (South American species, such as *P. major* and *P. weddelli*, and the North American species *P. mirifica*), and the extant genera *Lama* (*L. castelnaudi* and *L. guanicoe*) and *Vicugna* (*V. provicugna* and *V. vicugna*).

**Abbreviations.** **c**: lower canine; **C**: upper canine; **pm**: lower premolar; **m**: lower molar; **PM**: upper premolar; **M**: upper molar; **pm1**: first pm; **pm3**: third pm; **pm4**: fourth pm; **m1**: first m; **m2**: second m; **m3**: third m; **PM1**: first PM; **PM3**: third PM; **PM4**: fourth PM; **M1**: first M; **M2**: second M; **M3**: third M; **HD**: height on the diastema; **Hm3**: height of the horizontal mandible ramus at the level of m3; **Hm1**: height at the m1 level; **LDpm3-pm1**: length of the diastema from the mesial border of the alveolus of pm3 to the distal border of the alveolus of pm1; **LDC-pm1**: length of the diastema from the mesial border of the alveolus of pm1 to the distal border of the alveolus of c; **LDC-pm3**: length from the distal border of the alveolus of c to the mesial border of the alveolus of pm3; **LDC-i3**: length of the diastema from the mesial border of the alveolus of c to the distal border of the alveolus of i3; **Lpm3-m3**: length of pm3-m3 row, measured near the occlusal surface; **Lpm4-m3**: length of pm4-m3 row, measured near the occlusal surface; **Lpmx**: length of pmx; **Wpmx**: width of pmx; **Lmx**: length of mx; **Wmx**: width of mx; **LPMx**: length of PMx; **WPMx**: width of PMx; **LMx**: length of Mx; **WMx**: width of Mx.

### 4. Systematic paleontology

Order Cetartiodactyla Montgelard, Catzeflis and Douzery, 1997  
Suborder Tylopoda Illiger, 1811  
Family Camelidae Gray, 1821  
Subfamily Camelinae Zittel, 1893  
Tribe Lamini Webb, 1974  
Genus *Hemiauchenia* Gervais and Ameghino, 1880  
*Hemiauchenia* sp.  
Figs. 3–5

**Studied material:** MAM-70, including an almost complete mandible with both pm1-m3 series, complete left canine and portion of the crown and root of the right canine and third lower

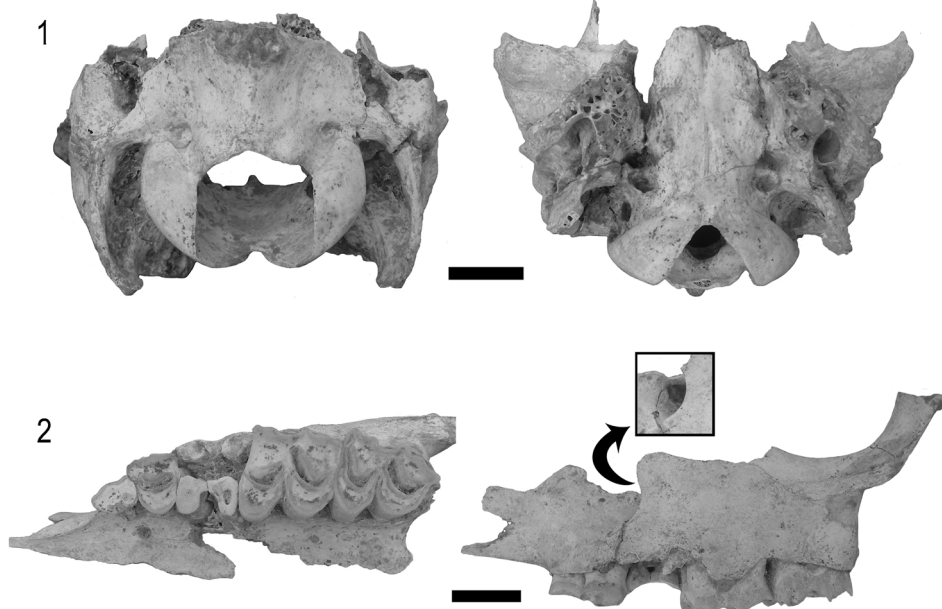
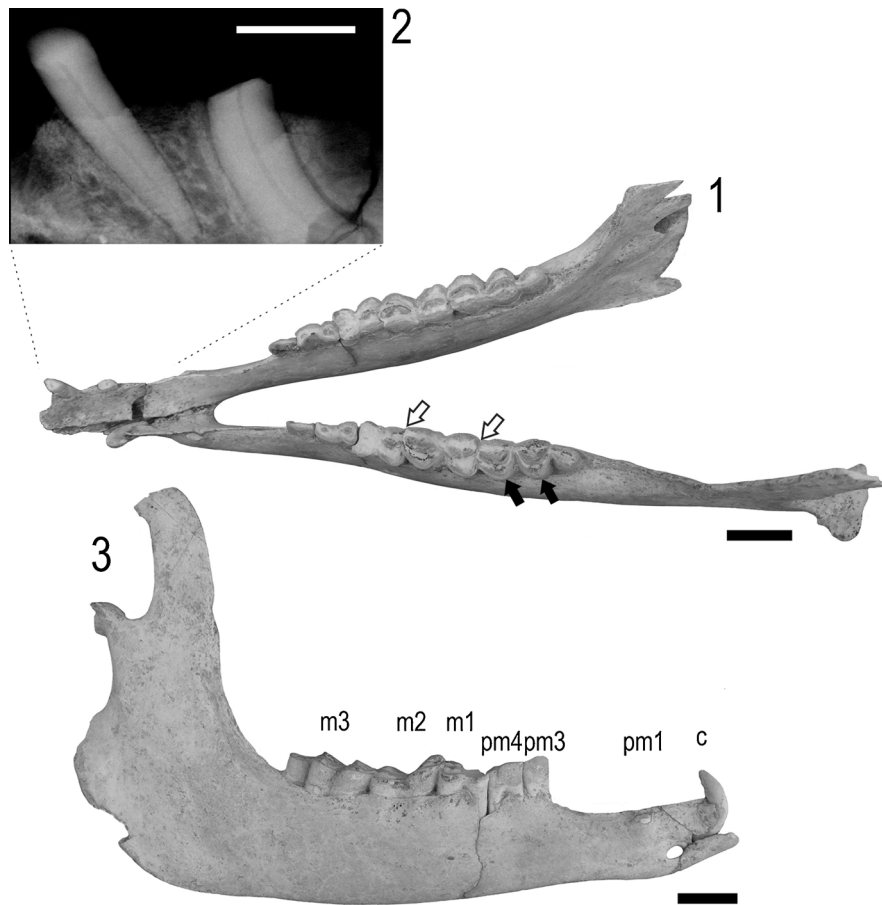


Fig. 3. *Hemiauchenia* sp., MAM-70. 1. Skull in occipital (left) and ventral (right) views. 2. Maxillary in occlusal (left) and labial (right) views. Scale bars: 10 mm.



**Fig. 4.** *Hemiauchenia* sp., MAM-70. 1. Mandible in occlusal view; black arrows indicate the U-shape of labial lophids and white arrows indicate the weak mesiolabial stylid. 2. X-ray photograph of right c1 and i3. 3. Right mandible in lateral view. Scale bars: 10 mm (1, 3), 5 mm (2).

right incise; a left maxillary fragment with complete PM4-M3 series; a basicranial portion; an almost complete pelvic girdle; and three vertebrae (2 cervical and 1 thoracic).

**Geographic and stratigraphic provenance:** “Calera Avellaneda” Quarry (36°59′14″ S, 60°14′14″ W), Olavarría, Buenos Aires Province, Argentina. “Body A” in “Facies Calera”.

**Age:** Chapadmalalan (late Pliocene). A paleomagnetic profile showed a normal polarity for this Facies, assignable to the Gauss Chron (3.55–2.59 Ma).

**Measurements:** See Tables 1 and 2.

**Description:**

**Skull** (Fig. 3(1)). The material corresponds to the occipital and temporal region. The auditory bullae are missing. The subcircular foramen magnum is surrounded laterally by the occipital condyles and dorsally by the supraoccipital. The paraoccipital processes are projected laterally from the occipital condyles. In the temporal region, the auditory meatus is observed laterally; it is broad with thick walls and oval outline. A small retroarticular foramen is developed forward to this meatus; it is oval and limited anteriorly by the retroarticular process. Above this structure, a thin temporal crest ends posteriorly in the fragmentary mastoid process. Two holes for the access to the temporal meatus are observed.

**Maxilla** (Fig. 3(2)). The anterior infraorbital foramen of the left maxillary is broad, subcircular and located above the mesial margin of M1. The PM3-M3 series is almost complete, although only the roots of M1 are preserved. The PM3 is small and simple, and transversely compressed. The PM4 has a square outline and develops a simple lobe with a lingual U-shaped loph. The M2 and M3 have two lobes, the mesial one being transversely larger than the distal one; the lingual lophs are U-shaped. The mesostyles,

endostyles, parastyles and metastyles are small; the prostyles are absent.

**Mandible** (Fig. 4). The mandible is gracile; the dorsal and ventral margins of the horizontal ramus are almost parallel to each other. The medial (lingual) surface of the horizontal ramus is flat and the lateral (labial) side is convex. The angular process is slightly marked and the condyle is convex and transversely wide. The mandibular notch is marked and has a circular outline. The coronoid process is broken at the bottom. The lingual mandibular foramen is located below the alveolar margin. The dorsal margin of the post-canine diastema is narrow and develops a crest. The mental foramen is oval and is located posteriorly to c, between c and pm1.

The left incise 3 has an enamel layer on both labial and lingual surfaces. The left c is complete, but only the neck and the root of the right c are preserved; both teeth have an elliptical section and are transversely compressed and posteriorly curved. An X-ray photograph shows that this tooth has a simple root (Fig. 4(2)). A long diastema is developed between pm1 and pm3, and there is a small diastema between c and pm1. The pm1 has an elliptical section and is transversely compressed. The pm3 is transversely compressed with little wear. The pm4 has a flexid on the labial and lingual sides forming a mesial, mesiodistally elongated lobe and a distal, transversely wide lobe. The molars have no protostylids and parastylids; their labial lophids are U-shaped, and their lingual stylids are small with no enamel folds. The m1 has a square outline with two lobes similar in size. The m2 has the mesial lobe larger than the distal one; the enamel folds of metaconid and entoconid are small; the metastylid is marked and the talonid and trigonid fossetids are semilunar in shape. The m3 has the typical characteristics of the third lobe without fossetid.

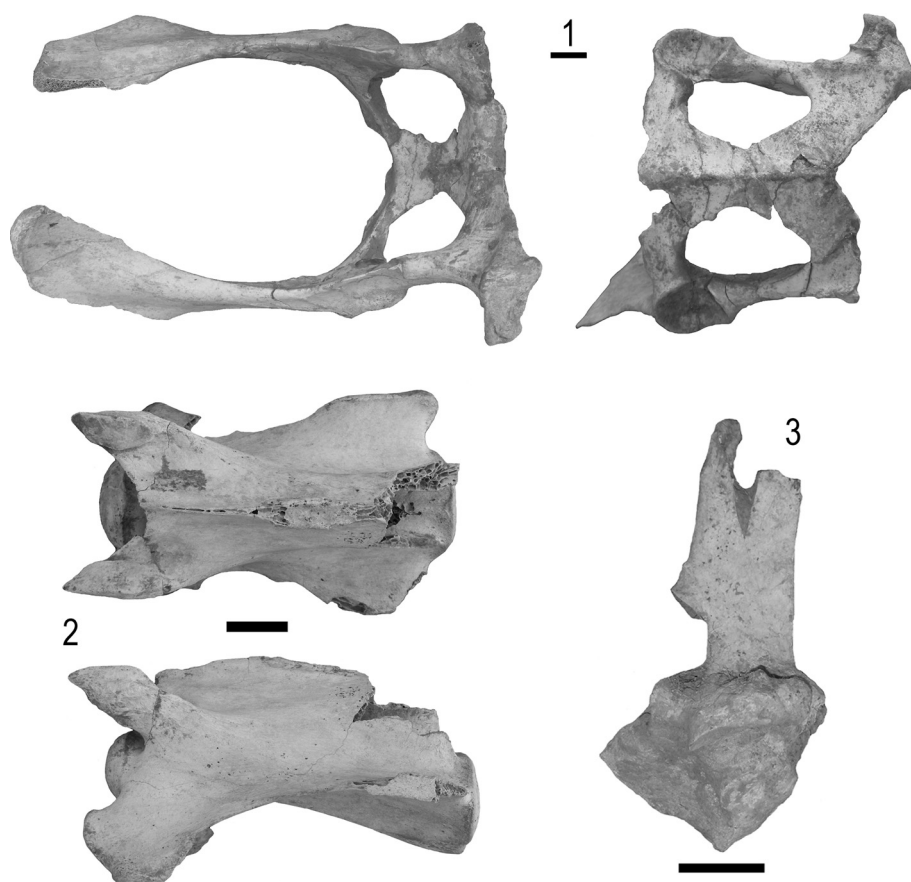


Fig. 5. *Hemiauchenia* sp., MAM-70. 1. Pelvic girdle. 2. Cervical vertebrae. 3. Thoracic vertebrae. Scale bars: 10 mm.

**Postcranial bones** (Fig. 5). The pelvic girdle is almost complete, lacking the right ischial tuberosity (Fig. 5(1)). The acetabulum is circular and communicates medially with the obturator foramen. The ischial arch is broad, forming an obtuse angle. The left ischial tuberosity is conspicuous. The right ilium preserved the sacral tuberosity and the left ilium is broken at the ala, lacking the sacral and coxal tuberosities. However, it can be seen that this bone is mediolaterally much flattened.

The cervical vertebrae are incomplete (Fig. 5(2)). One of these vertebrae corresponds to the first ones and the other to the last ones. Both of them have an anteroposteriorly elongated and dorsoventrally flattened vertebral body. The mesial side of the vertebral body is convex, and the posterior one is flat. The pre- and post-zygapophyses are markedly anteroposteriorly elongated with flat surface.

The thoracic vertebra is almost complete, lacking just the dorsal end of the neural spine (Fig. 5(3)). The vertebral body is mesiodistally short; the anterior face is convex and the posterior one is concave. The pre- and post-zygapophyses have flat surface on a median position. The transverse process is present, and the parapophysis and diapophysis are marked and have a concave surface.

## 5. Discussion

### 5.1. Morphological and morphometric comparisons with South and North American camelids

According to the latest systematic scheme for South American Camelidae Lamini (Scherer, 2009), the morphological and morphometric features that allow us to determine MAM-70 as *Hemiauchenia* sp. are: the U-shape of the labial lophids and lingual

lophs; the presence of a weak mesiolabial stylid; the presence of three premolars (pm1, pm3 and pm4); the position of pm1, slightly posterior to the mental foramen; the canine posteriorly curved and separated from the third lower incisor by a short diastema; and the teeth and mandible dimensions.

#### 5.1.1. Comments about the generic assignment of MAM-70

*Blancocamelus* is known from a few Blancan localities in North America (Honey et al., 1998). Because it is known only by limb bones, we could not compare the material under study with this genus.

*Aepycamelus* represents a giant Camelidae from North American Miocene deposits (Barstovian to Hemphillian; Harrison, 1985). Harrison (1985) mentioned this genus as a basal form of Camelidae, while Honey et al. (1998) and Scherer (2013) considered this taxon as a basal Lamini, because of the presence of arched nasals and the anterior limit of the choanae at the level of M2. *Aepycamelus* differs from MAM-70 in the following characters: larger size of mandible and teeth (Tables 1 and 2), quite brachydont teeth, and presence of pm2 (Matthew and Cook, 1909; Douglass, 1909; Harrison, 1985; Honey et al., 1998).

*Alforjas* and *Camelops* (both also considered as giant Camelidae) were placed within Lamini (Harrison, 1979, 1985; Honey et al., 1998; Scherer, 2013). *Alforjas* is recorded since the late Hemphillian to the late Clarendonian in North America (Harrison, 1979; Webb and Meachen, 2004). *Alforjas* differs from MAM-70 in the following characters: greater size of the mandible and teeth (Tables 1 and 2), much broadened symphysis, and lower incisors 1–3 usually spatulate (Harrison, 1979). *Camelops* is recorded in North American Pleistocene deposits (Webb, 1965; Honey et al., 1998). This genus differs from MAM-70 in the following characters: much larger size of mandible and teeth

**Table 1**  
Measurements (in mm) of the mandible of MAM-70 and other Camelidae.

	LD pm3-pm1	LD pm1-c	LD pm3-c	LD pm4-c	LD c-i3	L pm3-m3	L pm4-m3	HD	Hm3	Hm1
<b>MAM-70</b>										
Mean	27.8	19.4	52.2		7.7	91.3	82.6	23.3	40.7	37.8
Sample size	1	1	1		1	1	1	1	1	1
<b>Paleolama major</b>										
Min			49.0			91.0	77.0	18.2	38.3	26.4
Max			91.1			103.0	93.0	28.5	55.0	39.4
Mean			63.5		13.1	98.7	87.5	23.3	46.3	32.4
Sample size			9		1	13	17	15	22	20
<b>P. weddelli</b>										
Min			51.7		12.0	103.0	90.0	26.2	52.0	32.0
Max			82.0		20.0	107.0	94.0	32.2	54.3	37.0
Mean			66.9		16.0	104.7	91.6	29.2	53.3	34.2
Sample size			2		2	3	3	5	4	5
<b>P. mirifica</b>										
Min			29.7		16.0	85.2	73.2	15.5	40.4	21.0
Max			80.0		18.0	104.5	92.5	32.5	54.6	40.2
Mean			59.4		17.0	95.5	83.9	25.2	46.4	32.1
Sample size			12		2	34	34	27	38	46
<b>Hemiauchenia paradoxa</b>										
Min			58.0			97.5	84.0	23.6	52.7	31.0
Max			75.0			122.3	112.5	33.4	66.0	52.9
Mean			67.3			111.7	100.9	29.4	61.1	39.0
Sample size			11			15	16	17	23	25
<b>H. macrocephala</b>										
Min	31.3	15.0	75.3			101.2	90.2	19.0	47.5	30.0
Max	52.2	23.5	92.0			117.8	105.4	30.4	68.2	46.3
Mean	44.8	19.5	83.0			109.7	98.1	25.5	58.9	39.2
Sample size	13	7	5			13	15	20	12	21
<b>H. minima</b>										
Min										
Max										
Mean	33.0					78.5	69.2	17	38.4	26.4
Sample size	1					1	1	1	1	1
<b>H. edensis</b>										
Min						70.0	63.0			21.0
Max						72.0	65.0			23.6
Mean						71.0	64.0	16.0	37.0	22.2
Sample size						2	2	1	1	3
<b>H. blancoensis</b>										
Min	44.0					106.3	94.3	17.0	55.0	39.0
Max	46.0					118.0	105.7	26.8	60.7	44.5
Mean	45.0		75.6			112.2	100.0	21.9	57.8	41.8
Sample size	2		1			2	2	2	2	2
<b>H. gracilis</b>										
Min										
Max										
Mean								21.0	43.4	30.4
Sample size								1	1	1
<b>L. guanicoe</b>										
Min			36.0	35.5	7.7		72.8	19.7	42.7	24.0
Max			44.3	53.7	11.0		78.9	28.4	57.0	41.0
Mean			40.9	46.3	9.4		76.0	23.2	51.0	31.9
Sample size			7	5	2		7	12	10	12
<b>L. castelnaudi</b>										
Min				46.7			69.0	19.6	46.5	27.0
Max				54.5			91.5	25.0	53.8	33.7
Mean			52.4	50.8	12.4		80.2	22.4	49.6	30.8
Sample size			1	3	1		10	9	11	11
<b>Vicugna vicugna</b>										
Min				39.0	4.0		51.2	12.5	24.6	22.7
Max				48.0	7.3		69.0	23.0	48.0	28.0
Mean				42.0	5.6		59.4	19.3	38.8	24.2
Sample size				3	4		13	12	14	12
<b>Camelops hesternus<sup>a</sup></b>										
Min				92.0			154.0		73.0	53.0
Max				112.0			168.0		85.0	65.0
Mean				99.4			161.4		78.6	58.6
Sample size				5			3		5	5
<b>Pleiolama mckennai<sup>b</sup></b>										
Min	36.0	21.9	66.9		9.2	114.7		24.2	34.5	31.3
Max	37.9	22.7	69.9		10.9	119.1		25.6	38.8	33.8
Mean	37.0	22.3	68.4		10.1	116.8		24.9	36.6	32.6
Sample size	2	2	2		2	4		2	2	2
<b>Alforjas taylori<sup>c</sup></b>										
Min	28.6	11.9			4.1	124.6				
Max	42.4	20.5			8.9	132.9				

Table 1 (Continued)

	LD pm3-pm1	LD pm1-c	LD pm3-c	LD pm4-c	LD c-i3	L pm3-m3	L pm4-m3	HD	Hm3	Hm1
Mean	34.1	16.6			6.5	128.9		30.4	65.2	44.0
Sample size	6	4			3	6		1	1	1
<i>Aepycamelus procerus</i> <sup>d</sup>										
Mean	32.4	26.0	72.8		12.8	164.0				
Sample size	1	1	1		2	2				

<sup>a</sup> Measurements from Webb (1965).

<sup>b</sup> Measurements taken from figures of Webb and Meachen (2004).

<sup>c</sup> Measurements taken from figures of Harrison (1979).

<sup>d</sup> Measurements taken from figures of Matthew and Cook (1909).

(Tables 1 and 2), absence of pm1 and pm3, canine reduced, and broadened symphysis (Webb, 1965).

*Pleiolama* is considered the oldest Lamini (Webb and Meachen, 2004; Scherer, 2013). This genus is recorded from Clarendonian to Hemphillian ages in North America (Webb and Meachen, 2004). *Pleiolama* differs from MAM-70 in the following characteristics: it is smaller in size, it develops a much longer diastema (Table 1), and has a larger pm1 and pm3. In turn, the mesiolabial styliids are stronger and the pm2 can be present in some specimens of this genus. Taking into account the tooth size, molariforms of *Pleiolama* are larger than those of MAM-70 (Table 2). The ventral margin of the horizontal ramus of the mandible in *Pleiolama* is anteriorly convex and becomes concave at the region between the canine and pm1 (Webb and Meachen, 2004), whereas this ventral margin is nearly straight in MAM-70.

*Palaeolama* is recorded since the late Pliocene up to the late Pleistocene in the whole American continent (North, Central and South America; Ruez, 2005; Scherer, 2013). *Palaeolama* is markedly different from the studied material in the following characters: longer rostrum (Table 1), pm1 absent and development of V-shaped labial lophids. The angular process is marked in some specimens of *Palaeolama*, whereas it is not developed in MAM-70 (Scherer et al., 2006).

The extant genus *Lama* is considered one of the most derived Lamini (Scherer, 2013). It is different from MAM-70 because of the absence of pm1 and well-developed mesiolabial styliids. Besides, MAM-70 has larger teeth and mandible (Tables 1 and 2). The presence of pm3 in *Lama* is not constant, and when present it is markedly smaller (Menegaz et al., 1989). The other extant genus, *Vicugna*, differs from MAM-70 in its smaller size (Tables 1 and 2) and in the lower incisive shape, which crowns are cylindrical with trapezoidal section, chisel-shaped wear facets, and absence of enamel on the lingual side (Honey et al., 1998; Scherer, 2013).

### 5.1.2. Comparison of MAM-70 with *Hemiauchenia* species

*Hemiauchenia* is only represented in South America by *H. paradoxa* (Webb, 1974; Scherer et al., 2007). The specimen MAM-70 differs from this species in the weak development of mesiolabial styliids, in the presence of pm1, and in a slightly shorter rostrum. The remaining species of the genus listed below are recorded in the Pliocene–Pleistocene of North America. The systematics of these taxa is still controversial. In addition, the systematic assignment of MAM-70 among these North American species is complex, taking into account the fragmentary nature of this specimen.

*Hemiauchenia edensis* is recorded in late Hemphillian sediments (Webb et al., 2008). The diagnostic characters of this species are the small size (Table 1), the strong llama buttress and V-shaped labial lophids. None of these characters is developed in MAM-70.

"*H. minima*" is recorded from the late Clarendonian to Hemphillian (Webb et al., 1981); its taxonomic status is controversial (Bravo Cuevas et al., 2012). This taxon is smaller than MAM-70 (Tables 1 and 2) and its molars have V-shaped labial lophids whereas these structures are U-shaped in MAM-70.

*H. gracilis* is recorded in Blancan, Irvingtonian and Rancholabrean sediments (Meachen, 2005; White et al., 2010; Bravo Cuevas et al., 2012). This species differs from the specimen MAM-70 in the following characters: well-developed mesiolabial styliids, absence of pm1 and pm3, and smaller tooth size (Table 2).

*H. macrocephala* is recorded from the late Blancan to the Rancholabrean (Morgan and Hulbert, 1995; Bravo Cuevas et al., 2012). The holotype consists of a partial mandible, which has no pm1 and pm3 (Cope, 1893). However, some specimens assigned to this species by several authors have a caniniform pm1 and a pm3 (Hibbard and Dalquest, 1962; Webb, 1974; Breyer, 1977; Webb and Stehli, 1995).

*H. blancoensis* is recorded from the Blancan to the Irvingtonian (Jiménez Hidalgo and Carranza Castañeda, 2010; Bravo Cuevas et al., 2012). It is characterized by the presence of pm1 and pm3, besides a greater size and a shorter rostrum than *H. macrocephala*. However, its taxonomic position is controversial (Dalquest, 1992; Jiménez Hidalgo and Carranza Castañeda, 2010).

### 5.2. Comments about the distribution and stratigraphic ranges of Lamini in South America

In South America, fossil remains of Lamini were recorded in Argentina, Peru, Ecuador, Venezuela, Brazil, Paraguay, Uruguay, Bolivia, and Chile (Scherer, 2013; Fig. 6).

#### 5.2.1. Late Pliocene fossil record

The specimen studied here (MAM-70), assigned to *Hemiauchenia* sp. in Chapadmalalan sediments (late Pliocene), represents the oldest record of Lamini in South America. Much older than so far known, according to Cione et al. (2007), who reported that the first camelids that entered into South America (represented by the endemic genus *Lama*) were recorded in the Barrancalobian substage (early Marplatán, late Pliocene). *Palaeolama* was already known from the late Pliocene of Uruguay (Mones, 1988) and Argentina (Marshall et al., 1984). However, recent studies suggest that those remains probably correspond to *Hemiauchenia*, and the bearing sediments of the material from Uruguay would be much younger (early to middle Pleistocene; Ubilla and Perea, 1999; Cione et al., 1999).

In Argentina, there is a dubious record of *H. paradoxa* in late Pliocene–early Pleistocene of the Province of Jujuy (Scherer, 2013). All the other fossils of this age come from several localities of the southeastern coast of Buenos Aires Province: Cañada Chapar (*P. weddelli parodii* = *L. guanicoe* according to Scherer, 2009); Miramar (*P. weddelli* = *H. paradoxa* according to Scherer, 2009); Punta Vorohué (*Lama* sp. = *L. guanicoe* according to Scherer, 2009). These records were considered Chapadmalalan in age (middle Pliocene; Rusconi, 1933; Cabrera, 1935; Frenguelli, 1936; Kraglievich, 1946). However, according to Kraglievich (1959), the bearing sediments are not so old: in Cañada Chapar, there are Barrancalobian (late Pliocene) as well as Vorohuean and Ensenadan (early to middle Pleistocene) deposits; in Miramar, there are sediments assigned to Vorohuean, Ensenadan, and Bonaerian ages

**Table 2**  
Measurements (in mm) of upper and lower teeth of MAM-70 and other Camelidae.

Upper dentition	LPM3	WPM3	LPM4	WPM4	LM1	WM1	LM2	WM2	LM3	WM3
<b>MAM-70</b>	12.3	7.9	12.6	14.5	15.3		21.3	28.2	24.6	20.9
<i>Paleolama major</i>										
Min	13.1	8.3	15.0	12.0	18.0	11.7	21.3	12.4	22.0	14.5
Max	17.5	12.1	20.0	17.4	28.5	21.4	34.5	23.2	31.0	20.8
Mean	15.1	10.6	16.8	14.5	22.4	18.2	24.9	18.7	24.9	17.2
Sample size	10	6	10	7	30	22	29	22	19	14
<i>P. weddelli</i>										
Min			15.5	11.8	19.4	18.7	22.2	20.0	26.0	17.6
Max			19.1	17.4	27.4	23.6	26.4	25.5	30.0	22.3
Mean			17.4	13.7	22.9	21.6	24.9	23.0	27.2	19.1
Sample size			6	5	10	9	8	7	6	5
<i>P. mirifica</i>										
Min	12.3	8.0	14.0	11.5	16.0	15.2	18.0	15.0	20.4	13.5
Max	15.0	10.8	17.0	16.5	23.7	22.4	26.0	23.5	28.3	21.5
Mean	13.1	9.6	15.5	13.7	20.0	18.9	22.6	19.1	23.0	17.4
Sample size	16	16	25	25	45	45	42	42	36	36
<i>Hemiauchenia paradoxa</i>										
Min	11.5	5.0	12.0	11.0	16.7	20.0	22.5	18.8	21.3	15.0
Max	16.0	14.0	28.0	16.1	30.0	25.8	34.7	26.7	33.5	23.0
Mean	13.9	8.6	17.2	14.3	22.6	22.8	28.2	22.8	27.8	19.2
Sample size	11	11	17	18	21	19	30	30	26	26
<i>H. macrocephala</i>										
Min	13.8	7.6	13.4	12.5	19.0	13.5	20.0	12.0	20.3	13.7
Max	19.0	11.5	20.0	18.0	29.3	24.0	29.5	23.5	30.2	28.7
Mean	16.0	9.3	17.1	15.3	24.9	20.1	26.4	20.2	26.8	18.7
Sample size	8	8	14	14	25	24	24	24	25	24
<i>H. minima</i>										
Min	9.3	3.5	12.3	6.8	15.1	6.4	17.0	8.7	19.0	8.4
Max	11.5	8.0	12.9	10.8	18.0	15.1	20.5	17.0	25.3	14.9
Mean	10.4	5.7	12.6	9.1	16.6	10.9	18.6	12.0	21.2	11.2
Sample size	3	3	3	3	5	5	9	9	7	7
<i>H. blancoensis</i>										
Min									27.0	16.4
Max									30.5	22.5
Mean					29.0	21.0	33.2	19.0	28.5	18.6
Sample size					1	1	1	1	4	4
<i>H. gracilis</i>										
Min					17.8	12.7				
Max					21.8	14.3				
Mean			13.8	10.9	19.8	13.5	22.2	15.7		
Sample size			1	1	2	2				
<i>Lama guanicoe</i>										
Min	8.0	5.4	10.4	10.0	13.8	11.3	16.3	13.7	17.1	11.4
Max	9.6	7.7	14.7	13.5	24.6	21.3	26.8	25.0	30.0	24.3
Mean	8.9	6.4	12.6	11.7	19.2	16.8	23.1	18.0	23.6	16.6
Sample size	4	3	12	11	23	20	24	22	18	15
<i>Vicugna vicugna</i>										
Min	5.3	3.2	6.3	7.7	11.5	12.7	16.0	12.5	16.0	9.0
Max	8.4	4.5	10.8	10.6	18.6	16.7	22.6	17.0	19.8	14.0
Mean	6.8	3.8	8.5	8.9	14.3	14.7	18.7	14.6	18.4	11.8
Sample size	4	4	15	13	16	15	19	18	17	16
<i>Camelops hesternus</i> <sup>a</sup>										
Min	18.8	7.6	19.7	20.3	26.1	28.1	39.2	28.2	45.8	26.3
Max	22.6	11.1	30.4	23.8	44.0	33.6	54.5	32.8	48.5	30.3
Mean	20.6	9.3	26.3	22.3	36.0	30.5	47.4	30.1	47.5	27.9
Sample size	3	6	4	4	4	4	4	4	3	3
<i>Pleiolama mckennai</i> <sup>b</sup>										
Min	14.9	7.6	12.6	13.6	15.8	18	22.2	18.8	25.2	16.6
Max	16.8	13.4	16.7	14.9	26.8	19.6	30.5	19.4	30.5	18.7
Mean	16.0	11.4	15.2	14.0	23.1	18.7	27.5	19.0	28.4	17.8
Sample size	3	3	3	3	3	3	3	3	3	3
<i>Alforjas taylori</i> <sup>c</sup>										
Min	18.5	11.7	21.8	18.3	22.9	23.2	31.2	22.8	34.9	20.0
Max	19.1	13.2	23.7	20.1	37.8	30.8	40.3	28.6	41.4	25.1
Mean	18.9	12.3	22.7	19.4	30.0	26.4	36.3	25.1	37.8	22.0
Sample size	4	3	6	5	8	7	9	7	8	5
<i>Aepycamelus procerus</i> <sup>d</sup>										
Mean	20.0	12.0	20.0	19.0	23.0	22.0	33.0	28.5	34.0	27.0
Sample size	1	1	1	1	1	1	1	1	1	1
Lower dentition	Lpm3	Wpm3	Lpm4	Wpm4	Lm1	Wm1	Lm2	Wm2	Lm3	Wm3
<b>MAM-70</b>	9.3	4.6	13.4	8.0	17.2	13.5	23.4	14.5	31.9	13.9
<i>Paleolama major</i>										
Min	9.4	4.9	13.0	6.7	17.0	9.8	17.5	8.7	25.2	9.2
Max	13.0	6.0	17.0	13.7	24.0	22.0	32.0	21.6	38.5	16.3



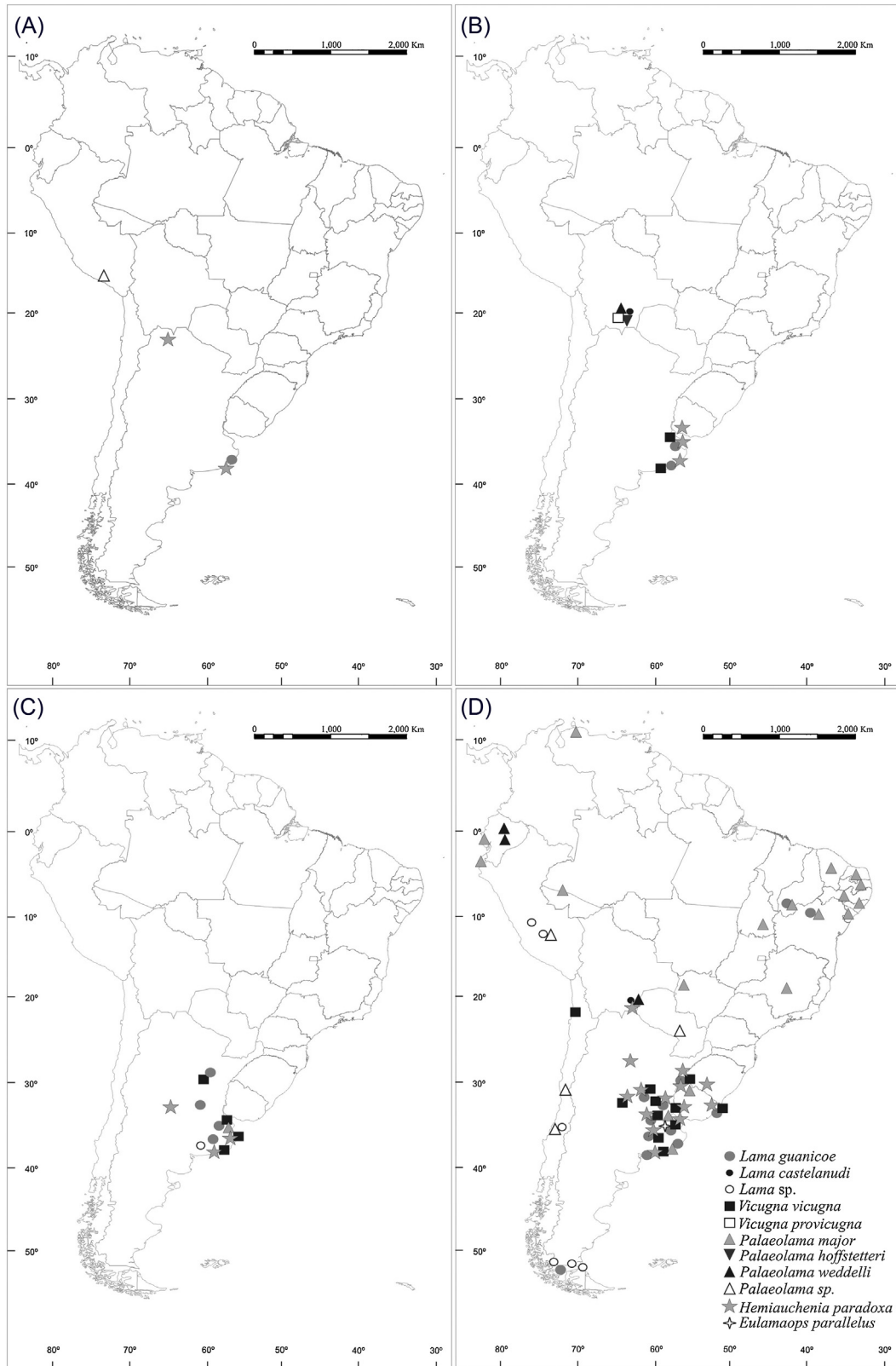
**Table 2** (Continued)

Lower dentition	Lpm3	Wpm3	Lpm4	Wpm4	Lm1	Wm1	Lm2	Wm2	Lm3	Wm3
Mean	10.7	5.5	15.2	9.2	20.0	13.6	22.5	14.0	28.9	13.0
Sample size	8	5	19	17	34	32	39	36	35	32
<b><i>P. weddelli</i></b>										
Min	10.5	4.8	13.4	9.0	19.5	11.8	18.3	12.3	29.3	12.0
Max	15.3	7.2	21.4	11.8	25.0	19.0	31.5	18.4	36.0	17.7
Mean	12.6	6.2	16.4	10.6	22.0	15.9	24.8	16.0	33.5	15.3
Sample size	4	4	6	6	9	9	14	14	10	11
<b><i>P. mirifica</i></b>										
Min	8.7	4.0	4.8	6.9	15.7	9.8	18.5	10.3	17.2	9.4
Max	12.0	6.0	16.5	13.8	27.6	16.0	24.4	21.1	33.0	16.7
Mean	10.9	4.9	14.9	8.5	19.2	12.9	21.9	14.1	29.0	13.2
Sample size	15	15	35	35	65	65	58	58	54	55
<b><i>Hemiauchenia paradoxa</i></b>										
Min	5.5	3.6	12.0	7.0	13.0	10.4	19.4	11.0	31.0	9.0
Max	14.5	5.6	19.0	17.1	28.0	17.8	35.0	19.0	42.5	16.8
Mean	10.2	5.0	14.7	8.8	21.2	14.8	27.5	15.2	35.0	13.6
Sample size	13	12	26	25	36	35	42	41	29	31
<b><i>H. macrocephala</i></b>										
Min	10.3	4.4	14.0	7.8	17.8	10.0	22.0	10.0	28.2	10.0
Max	12.5	6.1	19.6	14.3	27.7	15.2	29.6	16.4	36.8	15.6
Mean	11.5	5.4	16.9	9.0	22.5	13.7	25.7	14.3	32.5	13.2
Sample size	11	11	21	21	25	25	26	25	23	23
<b><i>H. minima</i></b>										
Min					17.7	7.1	18.2	9.6	21.5	9.0
Max					18.3	9.4	19.8	10.0	22.0	9.7
Mean					18.0	8.3	19.0	9.8	21.8	9.4
Sample size					2	2	2	2	2	2
<b><i>H. blancoensis</i></b>										
Min					19.6	12.2	23.0	12.2	32.5	12.0
Max					25.5	14.6	27.0	16.6	35.0	15.7
Mean	12.3	5.8	18.2	8.5	23.2	13.3	25.5	13.9	33.8	13.9
Sample size	1	1	1	1	3	3	3	3	2	2
<b><i>H. gracilis</i><sup>e</sup></b>										
Min									26.5	11.1
Max									26.5	11.1
Mean			9.5	5.6	13.9	9.9	19.9	12.1	28.0	11.5
Sample size			1	1	1	1	1	1	3	3
<b><i>Lama guanicoe</i></b>										
Min	7.2	3.5	9.4	5	13.0	8.0	17.6	8.5	20.0	8.5
Max	10.3	6.8	15.3	9.2	26.2	14.2	27.1	15.0	31.0	13.0
Mean	8.75	5.15	12.23	6.724	17.1	11.3	21.3	11.6	26.3	10.5
Sample size	2	2	28	25	38	31	45	35	27	23
<b><i>Vicugna vicugna</i></b>										
Min			7	3	10.6	8.5	15.2	7.9	18.8	6.0
Max			11	5.5	17.8	11.6	21.0	11.8	26.0	11.0
Mean			8.94	4.36	13.8	10.1	17.9	10.2	23.0	8.8
Sample size			10	10	18	18	22	22	21	19
<b><i>Camelops hesternus</i><sup>a</sup></b>										
Min			17.4	10.2	28.2	19.2	39.2	21.2	57.3	18.5
Max			27.5	14.7	43.7	22.3	50.5	22.3	58.4	22.3
Mean			24.4	13.4	35.0	20.8	44.4	21.7	58.0	20.8
Sample size			5	5	5	5	5	5	4	4
<b><i>Pleiolama mckennai</i><sup>b</sup></b>										
Min	12.0	6.2	16.0	9.0	21.5	15.1	26.8	16.1	35.5	15.4
Max	12.5	6.3	16.5	9.8	25.1	16.0	28.1	17.5	39.3	15.6
Mean	12.3	6.3	16.3	9.4	23.3	15.6	27.5	16.8	37.4	15.5
Sample size	2	2	2	2	2	2	2	2	2	2
<b><i>Alforjas taylori</i><sup>c</sup></b>										
Min	12.1	6.2	19.1	10.4	22.4	13.9	28.1	14.1	38.5	13.1
Max	14.4	7.5	21.2	12.4	33.1	17.1	39.2	19.6	46.5	18.9
Mean	12.9	7.0	20.3	11.5	26.9	15.7	33.4	17.2	41.5	16.2
Sample size	6	6	9	10	13	11	14	13	9	11
<b><i>Aepycamelus procerus</i><sup>d</sup></b>										
Mean	19.0	8.8	23.0	12.3	26.0	16.5	31.0	20.0	47.0	22.0
Sample size	1	1	1	1	1	1	1	1	1	1

<sup>a</sup> Measurements from Webb (1965).<sup>b</sup> Measurements taken from figures of Webb and Meachen (2004).<sup>c</sup> Measurements taken from figures of Harrison (1979).<sup>d</sup> Measurements taken from figures of Matthew and Cook (1909).<sup>e</sup> Meachen (2005).

(middle Pleistocene); and in Punta Vorohué, there are Vorohuean and Ensenadan sediments. Thus, their stratigraphic provenance is uncertain. In turn, other remains were also found in Marplatan sediments cropping out at Arroyo Las Brusquitas (*H. paradoxa* and *L. guanicoe*) and Baliza Chica (*L. guanicoe*). Remains assigned to

*Vicugna vicugna* were found in sediments tentatively considered Marplatan in age at Las Brusquitas and Chapadmalal streams; however, their stratigraphic provenance is dubious (Scherer, 2013). In the coastal region of Peru, fossil remains of *Palaeolama* were found in late Pliocene/Pleistocene sediments (Salas et al., 2003).



**Fig. 6.** Geographic and temporal distribution of Lamini. **A.** Marplatan (Salas et al., 2003; Scherer, 2009). **B.** Ensenadan (Ubilla and Perea, 1999; Scherer, 2009; MacFadden et al., 2013). **C.** Bonaerian (Deschamps, 2005; Scherer, 2009). **D.** Lujanian (Castellanos, 1944; Churcher, 1965; Marshall et al., 1984; Casamiquela, 1999; Tauber, 1999; López et al., 2005; Ferrero, 2006; Labarca and López, 2006; Socorro, 2006; Francia et al., 2013; Scherer, 2009). Modified from Scherer (2013).

### 5.2.2. Early–middle Pleistocene fossil record

During this period, the Lamini record became more abundant in South America. The genera *Hemiauchenia*, *Palaeolama*, *Lama*, and *Vicugna* are recorded mainly in Argentina and Bolivia. The species *Hemiauchenia paradoxa* and *Lama guanicoe* are recorded in several deposits of this age in the Pampean region of Argentina. Some of them show certain similarities with the species *Vicugna vicugna*; however, their fragmentary condition does not allow the confirmation of the record of *V. vicugna* during the Ensenadan Age.

In Bolivia, the species *P. weddelli*, *P. hoffstetteri*, *L. castelnaudi*, and *V. provicugna* are recorded. Their stratigraphic provenances are uncertain: Ensenadan Age (*sensu* Hoffstetter, 1952; Marshall et al., 1984; MacFadden et al., 1983; MacFadden, 2000) or Lujanian Age (Coltorti et al., 2007). Recently, MacFadden et al. (2013) considered the sediments of Tarija Valley as Ensenadan in age, more precisely middle Pleistocene ( $0.76 \pm 0.03$  Ma). In Uruguay, the species *H. paradoxa* is also recorded (Mones, 1988; Ubilla and Perea, 1999).

### 5.2.3. Middle Pleistocene fossil record

During this period, the camelid fossil record is restricted to the Pampean region of Argentina, with the species *H. paradoxa*, *L. guanicoe*, *V. vicugna*, and *Palaeolama major* (Scherer, 2013). Remains assigned to *Lama* sp. were also recorded in other localities of southern Buenos Aires Province (Deschamps, 2005).

### 5.2.4. Late Pleistocene–earliest Holocene fossil record

The greatest abundance and diversity of Lamini in South America is listed during this period (Argentina, Brazil, Uruguay, Ecuador, Bolivia, Perú, Chile, Paraguay, and Venezuela). Four genera (*Palaeolama*, *Hemiauchenia*, *Eulamaops*, and *Lama*) and at least seven species (*P. weddelli*, *P. major*, *H. paradoxa*, *E. parallelus*, *L. guanicoe*, *L. castelnaudi*, and *V. vicugna*) have been recorded so far.

*H. paradoxa*, *L. guanicoe*, and *V. vicugna* are recorded in Argentina (Pampean and Mesopotamian region), Uruguay, and southern Brazil (Castellanos, 1944; Tauber, 1999; Deraco et al., 2006; Ferrero, 2006; Scherer et al., 2007; Scherer, 2013; Francia et al., 2013). *P. major* is recorded in Argentina (Pampean region) and Uruguay through a few and isolated specimens, as well as *Eulamaops parallelus* in the case of Argentina (Scherer, 2009).

In Bolivia (Ñuapua locality), three species (*L. castelnaudi*, *P. weddelli*, and *H. paradoxa*) are recorded in sediments attributed to the late Pleistocene. In Brazil, more precisely in the northeastern region, *P. major* and *L. guanicoe* are recorded in late Pleistocene sediments. *P. major* is also recorded in northern, mid-western and southeastern regions of Brazil, and in the coastal region of Ecuador. The species *P. weddelli* is also recorded in the Andean region of Ecuador (Salles et al., 2006; Silva, 2009; Scherer, 2013; Rocha-dos-Santos et al., ongoing work).

In Chile, there are records of *L. guanicoe*, *Lama* sp., *V. vicugna*, and *Palaeolama* sp. for the late Pleistocene (Marshall et al., 1984; Casamiquela, 1999; López et al., 2005a, b; Labarca and López, 2006). In Perú, *Lama* sp. and *Palaeolama* sp. are recorded in sediments of the late Pleistocene; in Paraguay, *Palaeolama* sp. is also listed (Marshall et al., 1984). There are records of *P. major* for the late Pleistocene of northern Venezuela (Socorro, 2006) and possibly for the coastal region of northern Perú (Churcher, 1965).

Finally, during the late Pleistocene–early Holocene, like most of the Pleistocene megafauna, the large South American camelids became extinct, and the smaller species became restricted to drier and colder regions. Tonni and Politis (1980) and Menegaz et al. (1989) attributed this to the climatic changes that took place at this time, which increased the moisture availability in a great part of the continent, making these regions not favorable for camelids.

### 5.3. Comments about the dispersal of Lamini to South America

The dispersal and distribution of South American Lamini has been addressed in some research papers, but many aspects of these events remain unclear (Webb, 1974; Webb and Stehli, 1995; Scherer, 2013). Among the main problems is the knowledge and understanding of the oldest records of Camelidae in South America. There are a few records of Camelidae in Pliocene sediments, but all are considered dubious (Rusconi, 1933; Cabrera, 1935; Kraglievich, 1946). Other authors considered that the first camelids in South America (represented by the endemic genus *Lama*) are recorded in the Barrancalobian substage (early Marplatan, late Pliocene; Cione et al., 2007; Woodburne, 2010). However, Scherer (2013) considered their systematic assignment as dubious (*Lama* or *Hemiauchenia*), making obvious the lack of conclusive information on this aspect. The new data reported here shed light on this issue since we present the oldest unambiguous record of a Lamini form in South America assigned to *Hemiauchenia* sp., found in late Pliocene, Chapadmalalan sediments.

The material herein described corroborates the hypothesis of the dispersion of Lamini from North America to South America proposed by Webb and Stehli (1995) and Scherer (2013). Considering that the oldest record of *Hemiauchenia* occurred in the late Pliocene (Chapadmalalan Age), a species morphologically similar with the North American *H. macrocephala* could have dispersed to South America during the Pliocene. This is supported by the record of this genus in Central America during the early Pliocene (Dalquest and Mooser, 1980; Montellano, 1989; Ruez, 2005). *Hemiauchenia* arrived at the Pampean region of Argentina, where it could be related to the origin of *Lama*, which has its first record in the Vorohuean substage (middle Marplatan; late Pliocene–early Pleistocene) in this area (Scherer, 2013). Some representatives of *L. guanicoe* possibly dispersed afterwards to the Intertropical region, where they are recorded in the late Pleistocene from northeastern Brazil. In turn, *L. guanicoe* could be related to the origin of *V. vicugna*, which was first recorded probably in the Ensenadan of the Pampean region (Menegaz et al., 1989; Scherer, 2013). The related species recorded in Tarija, *L. castelnaudi* and *V. provicugna*, could have arisen from populations of *L. guanicoe* and *V. vicugna*, respectively, which could have dispersed to this region during the early to middle Pleistocene (*sensu* MacFadden et al., 2013). *Palaeolama* would have dispersed to South America in a later and isolated event. Its first record in this continent is dubious, from the late Pliocene–early Pleistocene of Peru or the early–middle Pleistocene of Bolivia, younger than the record of *Hemiauchenia* (Chapadmalalan, taking into account the new record mentioned here). *Palaeolama* then would have colonized the Intertropical region of South America (mainly Brazil, Ecuador, and Bolivia). This genus, although placed in a more basal position than *Hemiauchenia* in cladistic analyses, is younger in North America (late Pliocene–early Pleistocene) than *Hemiauchenia* (late Miocene?; Scherer, 2013). The gaps in these dispersion hypotheses could be solved through a full review of the North American taxa.

## 6. Conclusions

The finding of the specimen MAM-70 assigned to *Hemiauchenia* sp. in late Pliocene Chapadmalalan sediments cropping out near the city of Olavarría (Buenos Aires Province, Argentina) represents the oldest record of Lamini in South America. This fossil refutes the hypotheses that considered the genus *Lama* as the first North American immigrant, as well as those that considered that *Hemiauchenia* and *Palaeolama* arrived into South America after the closure of the Central America land bridge (GABI 2 *sensu* Woodburne, 2010), i.e., during the early–middle Pleistocene. In turn, this specimen corroborates the hypothesis of the dispersion

of Lamini from North America to South America as proposed by Webb and Stehli (1995) and Scherer (2013). In addition, this finding suggests that a species morphologically similar to the North American species *H. macrocephala* could have dispersed to South America during the Pliocene, giving birth to the South American species of *Hemiauchenia* and *Lama*. From that point of view, and according to Scherer (2013), *Palaeolama* migrated to South America after *Hemiauchenia*, in a later and isolated event.

### Acknowledgements

The authors thank the Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET) and the company Cementos Avellaneda S.A. We are grateful to the following curators and collection managers for the access to the collections under their care: Alejandro Kramarz (MACN), Marcelo Reguero, and Itatí Olivares (MLP). We thank Bruce MacFadden and two anonymous reviewers for valuable comments that improved a previous version of this paper. This work was partially funded by PICT 2010-0804 and PIP 0496.

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