Bull. Inst. fr. études andines
2003, 32 (2): 347-359

THE PRESENCE OF PLIO-PLEISTOCENE *PALAEOLAMA* SP. (ARTIODACTYLA: CAMELIDAE) ON THE SOUTHERN COAST OF PERU

Rodolfo SALAS[*][**], Marcelo STUCCHI[**], Thomas J. DEVRIES[***]

Abstract

We report the oldest record of the genus *Palaeolama* in Peru; its constitutes one of the oldest records for the genus in South America. The shape and size of the fossil material is comparable to South American forms *P.* (*Hemiauchenia*) *paradoxa* and the smallest forms of *P.* (*Palaeolama*) *weddellii*. The bones were found within unnamed littoral marine deposits near Atiquipa, on the south coast of Peru. The occurrence of the extinct bivalve mollusk, *Chlamys vidali*, at the base of the section and coquinas of exclusively extant mollusks in the highest marine terrace capping the section indicates an age of about two million years. This age is slightly older or equal to the oldest records of *P.* (*Palaeolama*) in North America. The present report confirms that the Lamini were no strangers to Andean ecosystems prior to the Holocene.

Key words: *Mammalia, Camelidae, Palaeolama, Plio-Pleistoceno, Atiquipa, Perú.*

PRESENCIA DE *PALAEOLAMA* SP. (ARTIODACTYLA: CAMELIDAE) DEL PLIO-PLEISTOCENO EN LA COSTA SUR DEL PERÚ

Resumen

Se presenta el registro más antiguo del género *Palaeolama* en el territorio peruano y uno de los más antiguos de Sudamérica. La forma y tamaño del material conservado es comparable con las formas sudamericanas *P.* (*Hemiauchenia*) *paradoxa* y los especímenes más pequeños de *P.* (*Palaeolama*) *weddellii*. Procede de los depósitos marinos litorales innominados de Atiquipa, en la costa sur del Perú. La ocurrencia del molusco bivalvo extinto *Chlamys vidali* en la base de la sección y la coquina de moluscos actuales presentes en la terraza marina más alta que termina dicha sección, indicaría una edad aproximada de 2 millones de años. Esta edad es ligeramente mayor o igual a los registros más antiguos de *P.* (*Palaeolama*) en Norteamérica. El presente reporte confirma que los Lamini no fueron ajenos a los ecosistemas andinos antes del Holoceno.

Palabras claves: *Mammalia, Camelidae, Palaeolama, Plio-Pleistoceno, Atiquipa, Perú.*

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PRÉSENCE DU *PALAEOLAMA* SP. (ARTIODACTYLA: CAMELIDAE) DU PLIO-PÉISTOCÈNE SUR LA CÔTE SUD DU PÉROU

Résumé

Nous présentons un spécimen du genre *Palaeolama* qui correspond au registre le plus ancien du genre sur le territoire péruvien ainsi que l'un des plus anciens en Amérique du Sud. La morphologie et la taille des éléments découverts sont comparables aux formes sudaméricaines *P*. (*Hemiauchenia*) *paradoxa* ainsi qu'aux formes les plus petites de *P*. (*Palaeolama*) *weddellii*. Ce spécimen provient des dépôts marins littoraux d'Atiquipa (côte sud-péruvienne). La présence du mollusque bivalve *Chlamys vidali* à la base de la section ainsi que de faluns coquilliers actuels, présents au niveau des terrasses marines les plus hautes qui terminent la section, correspondrait à un âge de 2 millions d'années. Cette date est légèrement supérieure ou égale aux registres les plus anciens de *P*. (*Palaeolama*) en Amérique du Nord. Cette découverte confirme que les Lamini étaient présents dans les écosystèmes andins avant l'Holocène.

Mots clés : *Mammalia, Camelidae, Palaeolama, Plio-Pleistocène, Atiquipa, Pérou*.

INTRODUCTION

The evolution of camelids took place principally in North America. Their migration to South America probably occurred during the late Pliocene (Hoffstetter, 1952). The earliest material was assigned tentatively to the Plio-Pleistocene of Argentina (Cabrera, 1935; Kraglievich, 1946; Marshall *et al.*, 1984) and Uruguay (Mones, 1988).

Descriptions of the genera *Palaeolama* Gervais, 1867, and *Hemiauchenia* Gervais & Ameghino, 1880, were based on material collected from the Argentine Pampas. Cabrera (1935) and Hoffstetter (1952) agreed in considering *Hemiauchenia* as synonymous with *Palaeolama*. Webb (1974) distinguished *Hemiauchenia* from *Palaeolama* as a separate genus and tried both diagnosis. Most recently, Guérin & Faure (1999) designated *Hemiauchenia* as a subgenus of *Palaeolama*.

The best documented and oldest account of *P*. (*Palaeolama*) from South America comes from the Ensenadan of Tarija, Bolivia (Webb & Stehli, 1995). In contrast, *P*. (*Hemiauchenia*) was present in the upper Uquian, having immigrated during the second panamerican dispersal that occurred between 2,0 and 1,9 Ma (Marshall, 1985). In North America, *P*. (*Hemiauchenia*) is recognized from the Hemphillian (lower Pliocene), while *P*. (*Palaeolama*) is well represented in the Irvingtonian (lower Pleistocene) in shell banks from Leisey, Florida (Webb & Stehli, 1995).

There are only two reliable reports of *Palaeolama* from the coast of Peru, both upper Pleistocene. The first report describes material from deposits of La Brea, near Talara (Lemon & Churcher, 1961), which was assigned by Churcher (1965) and Webb (1974) to *P. aequatorialis* Hoffstetter, 1952. The second refers to material identified by Hoffstetter collected from the Pampa de los Fósiles, La Libertad (Marshall *et al.*, 1984).

The objective of this paper is to describe material of *Palaeolama* (*sensu* Guérin & Faure, 1999) from the Plio-Pleistocene of Peru and discuss its biostratigraphic and biogeographic implications.

The chronology of mammal ages for South America used in this study is that proposed by McKenna & Bell (1997).

Institutional abbreviations:

MUSM: Museo de Historia Natural – Universidad Nacional Mayor de San Marcos, Lima.

UF: Florida Museum of Natural History – University of Florida, Florida.

1. GEOLOGY AND AGE

The camelid bones were found in an outcrop of conglomerate and bioclastic sandstone exposed in a roadcut along the Panamerican Highway on the northwestern side of Quebrada Infiernillo (SITE 596, Fig. 1). The lower part of the section (6,6 meters), which rests upon a seaward-tilting igneous platform; consists of a prograding sequence that represents shallow subtidal, lower shoreface, upper shoreface, and fluvial/alluvial environments characteristic of a high-energy beach fronting an attenuated flood-prone alluvial fan.

The middle part of the section (7,0 meters) is a transgressive succession of laminated bioclastic gravel, lenticular bioclastic gravel, and several meters of massive, poorly sorted, coarse-grained bioclastic sandstone with dispersed, transported whole fossils of mollusks, barnacles, and the camelid bones. The massive sands may had been accumulated in a small embayment at the mouth of Quebrada Infiernillo that captured debris washed in from the Pacific Ocean and down from the Andean foothills.

The upper part of the section includes a regressive sequence of cross-bedded bioclastic cobbly gravel and sandstone (2,2 m) overlain by a transgressive and regressive cycle (>3,2 meters) with similar deposits. A coquina that caps the second regressive sequence also constitutes the surface of the most elevated marine terrace, which stands 250 meters above sea level.

The oldest mollusks from the Atiquipa outcrop, disarticulated valves of *Choromytilus chorus* (Molina, 1782) and *Chlamys vidali* (Philippi, 1887), are wedged between boulders at the base of the section. *C. vidali* is found in lower and upper Pliocene strata of Chile (Herm, 1969), lower Pliocene shoreface deposits near Sacaco (Muizon & DeVries, 1985), and on the surface of the oldest marine terraces of northern and southern Peru (DeVries, 1986). Absent from the base of the Atiquipa section are mollusks that signify a lower Pliocene age, *e.g.*, *Acanthina ‘triangularis’* DeVries, 1986; *Herminespina mirabilis* (Philippi, 1887); *H. saskiae* DeVries & Vermeij, 1997; *Concholepas kieneri* Hupe, 1859; and *C. nodosa* Moricke, 1896 (Devries & Vermeij, 1997; Devries, 2000).

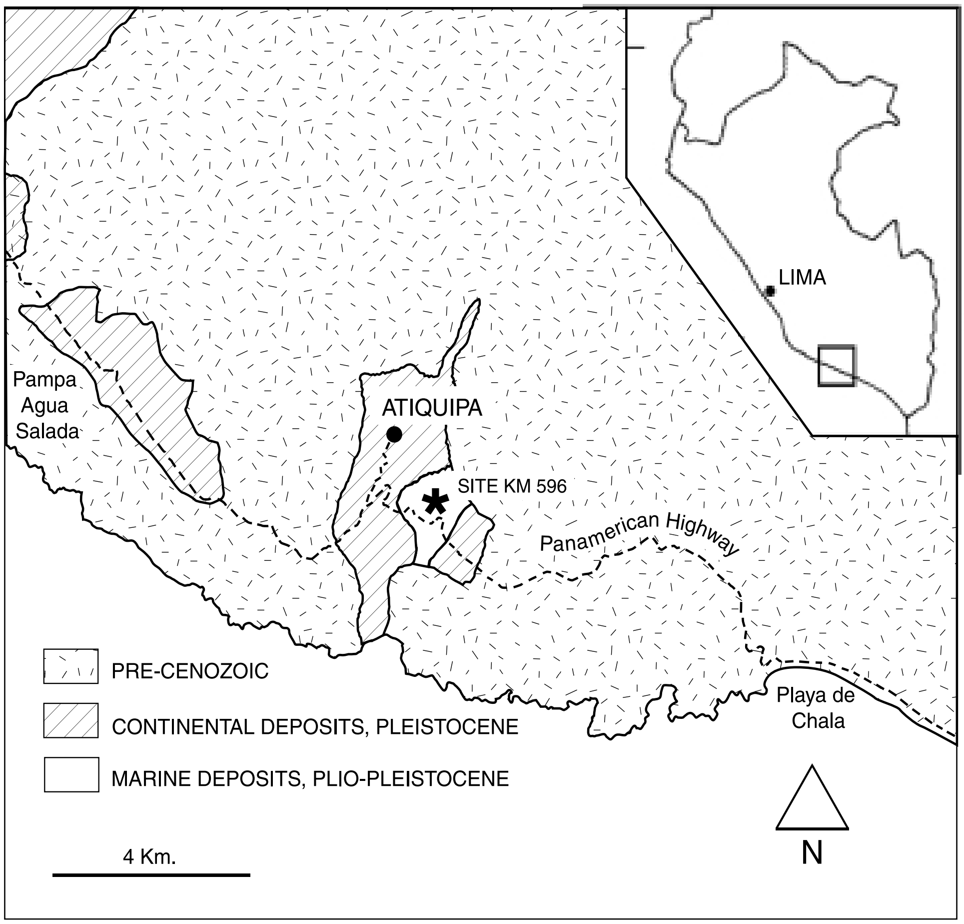


Fig. 1 - Map of the area of Atiquipa showing “SITE 596” where the camelid material was found.

The bone-bearing sandstones contain an assemblage of mollusks that includes *Concholepas camerata* DEVRIES, 2000, which indicates a latest Pliocene or early Pleistocene age. The coquina that caps the section at Atiquipa contains an assemblage of the extant mollusks *Glycymeris ovata* (BRODERIP, 1832), *Eurhomalea lenticularis* (SOWERBY, 1835), *Mulina edulis* (KING, 1831), and *Oliva peruviana* LAMARCK, 1811. Elsewhere along the coast between Chala and Camaná, these species occur in a comparable geological setting together with the extinct gastropod, *Chorus grandis* (PHILIPPI, 1887), suggesting a pre-Pleistocene age (Devries, 1997) (Fig. 2).

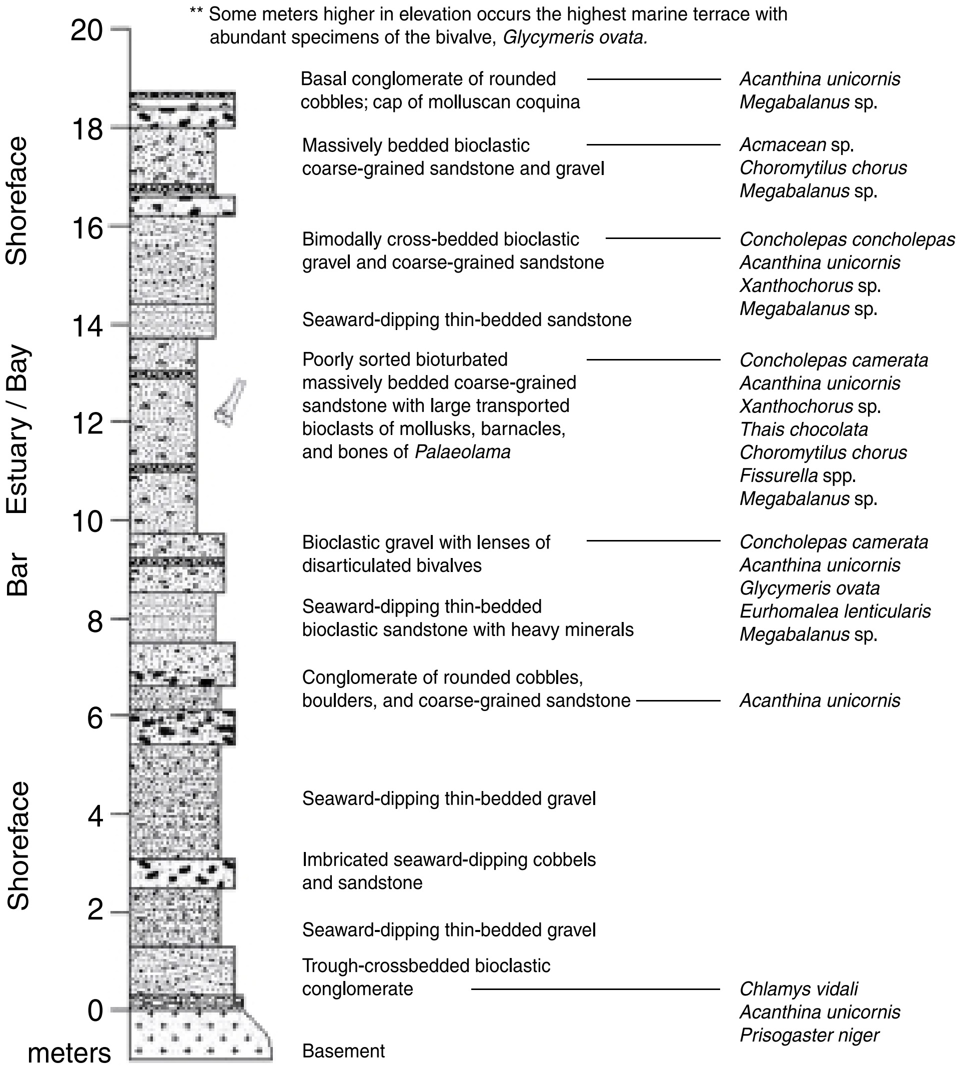


Fig. 2 - Stratigraphic column of the "SITE 596" section near Atiquipa.

2. SYSTEMATIC PALEONTOLOGY

Order ARTIODACTYLA Owen, 1848
Family CAMELIDAE Gray, 1821
Subfamily CAMELINAE Gray, 1821
Tribe LAMINI Webb, 1965

Palaeolama Gervais, 1867

Material – MUSM 51 **-** Departamento de Paleontología de Vertebrados, Museo de Historia Natural (UNMSM); associated distal portions of the left femur and right humerus without the proximal epiphysis. Collected by Thomas DeVries and Marcelo Stucchi.

Locality – 15º48’42"S, 74º21’25"W; SITE 596, Atiquipa (Panamerican Highway, km. 596 south), 200-250 meters above sea level, Arequipa Department, Peru.

Age – Late Pliocene to earliest Pleistocene (2,2 – 1,6 Ma).

2. 1. Description

Humerus – In the humerus MUSM 51 (Fig. 3 A, B), the lateral epicondyle is more robust than the medial epicondyle, in contrast to that of *Vicugna vicugna* Molina, 1782, where the two are subequal. From a cranial perspective, the articular trochlea is compressed proximodistally. The interlabial longitudinal distance-distal articular transversal distance index in MUSM 51 is 39; in *V. vicugna* it is 48. The axial throat is deep. In relation to the medial lip, the lateral lip extends proximally more than in *V. vicugna* and *P. weddellii*. The epiphyses of the lateral and medial epicondyles are partially fused.

The preserved part of the MUSM 51 humerus does not exhibit significant differences in shape or proportion from any of the *Palaeolama* species. Among the southamerican species, it is practically equal in size to the smallest forms of *P. weddellii* Gervais, 1855 of the Pleistocene of Ecuador (Hoffstetter, 1952) and the average of *P. paradoxa* (Gervais & Ameghino, 1880). *P. major* Lias, 1872 has only been able to be compared in one of its dimensions. The total length of the MUSM 51 humerus is estimated to be 270-300 mm (Table 1).

Femur – The distal epiphysis of the MUSM 51 femur is robust (Fig. 3 C). The femoral trochlea is symmetrical and perfectly parallel with the axial axis. Although the lateral condyle is only partially preserved, it can be seen to be larger than the medial condyle.

As mentioned for the humerus, the form and proportions of the femur are similar to those of *P. weddellii* from Ecuador (Hoffstetter, 1952) and *P. paradoxa* (Cabrera, 1935). Its estimated maximum transverse diameter is slightly less than the minimum value for *P. weddellii* (Table 2). The material of *P. major* of Winge (1906) has proven to be that of a juvenile individual (Hoffstetter, 1952). As evidenced by the dimensions of a femur of *P. major* from Brazil (Guérin & Faure, 1999), the distal epiphysis does not have the same proportions (Fig. 3).

Table 1 - Comparative dimensions of the humerus of *Palaeolama* sp. (MUSM 51). TL – total length; PTD – proximal transversal diameter; DTD – distal transversal diameter; DATD – distal articular transversal diameter; MTDD – maximum transversal diameter of the diaphysis (Dimensions in mm).

		TL-var	PDT-var	DTD-var	DATD-var	MTDD-var
***Palaeolama* sp.**	**MUSM 51**	**-**	**-**	**63,2**	**56**	**30,4**
P. (*Palaeolama*) *weddellii*	Hoffstetter, 1956	302-316	81-92	65,2-79	54-64,5	-
	Guérin & Faure, 1999	278	83,5	68,5	-	32,5
P. (*Hemiauchenia*) *paradoxa*	Cabrera, 1935	279-297	76-81	—	57-60	-
	Guérin & Faure, 1999	270	74	61,5	-	30
P. (*Hemiauchenia*) *major*	Winge, 1906	261	79	-	47-54,5	-
P. (*Hemiauchenia*) *niedae*	Guérin & Faure, 1999	325-348	79,5-93,5	70,5-82,5	-	36,5-43
P. (*Hemiauchenia*) *macrocephala* Inglis, Florida	UF 179748	329	~81	67	61	37
	UF 45478	326	83	66	61	36
	UF179744	-	-	62,5	56	33
	UF 45480	-	-	67	60	32
	UF 176912	-	-	66	60	35
Palaeolama sp.** Leisey Shell Pits, Florida	UF 65323	-	-	68	60	34
	UF 66487	307	-	65	61	36
	UF 66490	304	81	71	60	36
	UF 80400	-	-	65	55	31
	UF 80493	-	-	67	57	30
	UF 83661	301	84	64	61	33
	UF 85018	306	83	67	61	36

** The specimens may belong to either *P*. (*Palaeolama*) *mirifica* or *P*. (*Hemiauchenia*) *seymourensis*.

2. 2. Discussion

Abundant material assigned to *Palaeolama* and "*Auchenia*" from Miramar, Argentina, is referred to the Chapadmalalian by Cabrera (1935) and Kraglievich (1946). Nevertheless, Marshall *et* al. (1983) did not include the family Camelidae among mammals of Holarctic origin assigned to the Chapadmalalian of Argentina. Later, Marshall *et al.* (1984) characterized the Uquian (lower Pleistocene) by the presence of Camelidae, among other families. The occurrence of *Palaeolama* (*sensu* Guérin & Faure, 1999) in upper Pliocene-lower Pleistocene deposits of coastal southern Peru

Table 2 - Comparative dimensions of the femur of *Palaeolama* sp. (MUSM 51). ML – medial length; LL – lateral length; DTD – distal transversal diameter; PTD – proximal transversal diameter; DAPD – distal antero-posterior diameter (Dimensions in mm).

		ML-var	LL-var	PTD-var	DTD-var	DAPD-var
***Palaeolama* sp.**	**MUSM 51**	**-**	**-**	**-**	**~80**	**84**
P. (*Palaeolama*) *weddellii*	Hoffstetter, 1956	369-400,5	358-394	94,5-113	83-92,5	88,5
P. (*Hemiauchenia*) *paradoxa*	Cabrera, 1935	~370	-	90	79	-
P. (*Hemiauchenia*) *major*	Winge, 1906 Guérin & Faure, 1999	357 384*	- -	86-95 -	79 89	- 88
P. (*Hemiauchenia*) *niedae*	Guérin & Faure, 1999	443*	-	101-107	85-92	89,5-94
P. (*Hemiauchenia*) *macrocephala* Inglis, Florida	UF 179749 UF 179750 UF 45279	- - -	- - -	- - -	93 83 83	98 89 87
Palaeolama sp.** Leisey Shell Pits, Florida	UF 66500 UF 66602 UF 64331 UF 66601 UF 66603 UF 66604 UF 68884	377 - - 373 - - -	~375 - - 369 - - -	100 - - 101 - - -	82 82 ~81 85 ~86 82 86	87 83 90 89 95 86 87

* These measurements correspond to the maximum length of the bone.
** The specimens may belong to either *P.* (*Palaeolama*) *mirifica* or *P.* (*Hemiauchenia*) *seymourensis*.

confirms the presence of camelids, particularly of *Palaeolama*, in the Uquian, as was also noted by Mones (1988) based on evidence of associated fauna from Uruguay. Owing to these records, the Uquian Age (characterized by various first appearances of mammals in Argentina) can be extended, at least with respect to the Camelidae, to Peru and Uruguay. The Peruvian material has an age similar to that of the oldest occurrence of *P.* (*Palaeolama*) in North America, referred to the Irvingtonian of Leisey, Florida (Webb & Stehli, 1995). The existence of *P.* (*Hemiauchenia*) is pushed back to the Hemphillian (Webb & Stehli, 1995).

P. (*Palaeolama*) is distinguished from *P.* (*Hemiauchenia*) principally by the proportion and size of its limb bones (Webb, 1974; Webb & Stehli, 1985; Guérin & Faure, 1999). Nevertheless, a morphological analysis of the fossil material does not reveal a distinction within the genus**.** All *Palaeolama* species show important

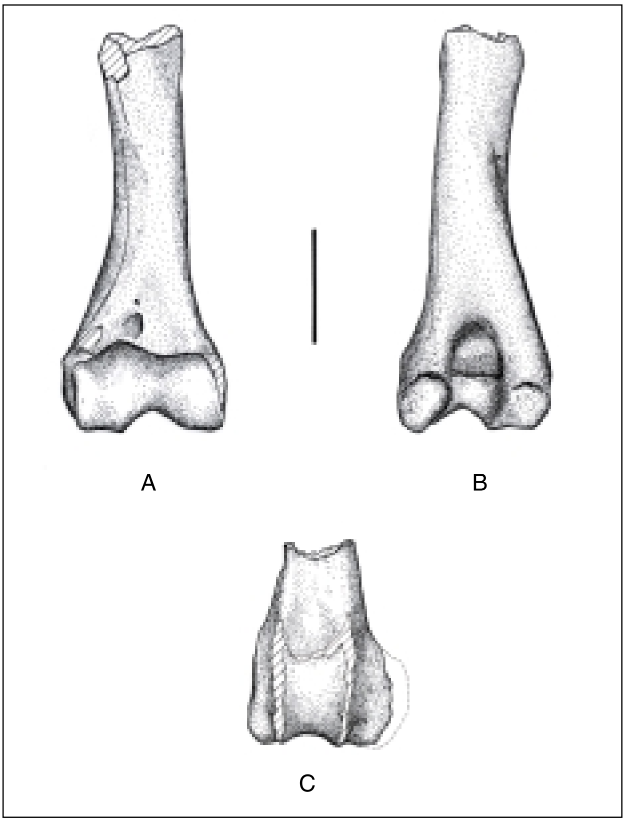
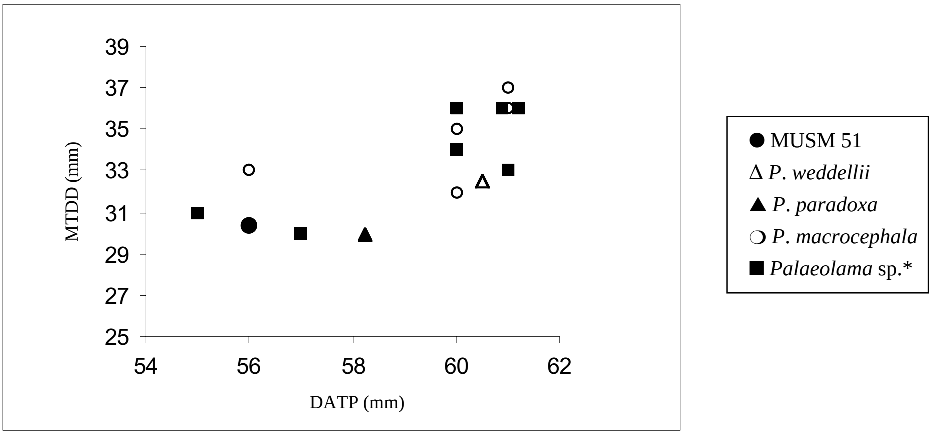


Fig. 3 - *Palaeolama* sp., MUSM 51. *A-B.* Right humerus: *A*, anterior view; *B*, posterior view. *C.* Left femur, anterior view (Scale 5 cm).

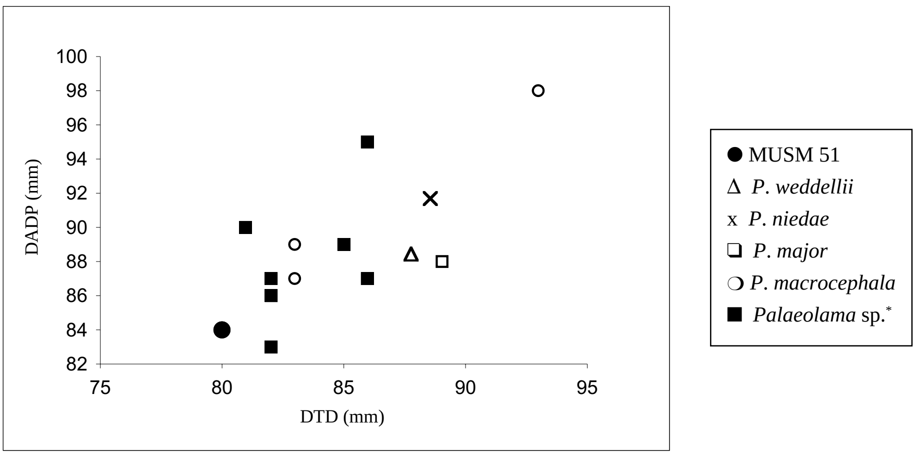
intraespecific variation in size and also are indistinguishable in humerus and femur proportions (Table 1 and 2, Figs. 4 and 5). In localities like Leisey Shell Pits, Florida, where *P*. (*Palaeolama*) and *P*. (*Hemiauchenia*) are present, complete humerus and femur could not be assigned to infra-generic level. However, a morphological analysis of humerus and femur remains from Peru indicate that they are comparable in proportion and size with southamerican *P*. (*Hemiauchenia*) *paradoxa* and the smallest forms of *P*. (*Palaeolama*) *weddellii*. Additionally, this can be extended to the smallest specimens of northamerican P. (*Palaeolama*) *mirifica*, *P*. (*Hemiauchenia*) *seymourensis* and *P*. (*Hemiauchenia*) *macrocephala*. Considering that the peruvian material might be from a young adult (see below), the measurements could be slightly less than those for a completely mature individual (Figs. 4 and Fig. 5).

Other points of distinction between *P*. (*Palaeolama*) and *P*. (*Hemiauchenia*) are habitat and diet. While *P*. (*Palaeolama*) was a browser with robust metapods that lived in montagne regions, *P*. (*Hemiauchenia*) had a mixed diet (browsing and grazing) and gracile metapods suitable to living on the open plains (Webb, 1974; Webb & Stehli,



* The specimens may belong to either P. (*Palaeolama*) *mirifica* or P. (*Hemiauchenia*) *seymourensis*; Loc. Leisey Shell Pits, Florida.

Fig. 4 - Scatter diagram in milimeters of MTDD (maximum transversal diameter of the diaphysis) versus DATD (distal articular transversal diameter) in humerus of MUSM 51 and species of *Palaeolama* from South and North America. In *P. weddellii* and *P. paradoxa* the dimension is an average.



* The specimens may belong to either P. (*Palaeolama*) *mirifica* or P. (*Hemiauchenia*) *seymourensis*; Loc. Leisey Shell Pits, Florida.

Fig. 5 - Scatter diagram in milimeters of DAPD (distal antero-posterior diameter) versus DTD (distal transversal diameter) in femur of MUSM 51 and species of *Palaeolama* from South and North America. In *P. weddellii* the dimension is an average.

1995). The fossil record of both subgenera, the rugged relief, and the desert character of the Peruvian coast since the middle Miocene (Sébrier *et* al., 1984; Alpers & Brimhall, 1988) suggest that the Lamini from Atiquipa was a *P.* (*Palaeolama*)-like camelid.

MUSM 51 (portions of femur and humerus) was found associated in the same section of the outcrop. Preceding statement and their relative size suggest that both belong to a single individual. However, the bone fusion secuence does not correspond. In modern camelids, the fusion of the epiphyses of the distal epicondyles of the humerus takes place between an age of 12 and 18 months (Wheeler, 1999). The epiphyses are not completely fused in sample MUSM 51, which suggests it belongs to a young individual. The distal epiphysis of the femur of MUSM 51, however, is completely fused, contradicting the aforementioned suggestion. In modern camelids, the fusion of epiphyses in the femur happens at an age of 42 to 44 months, when the animal is a young adult (Wheeler, 1999). According to Wheeler (personal communication, 2000), exceptional cases do occur in modern camelids in which the fusion of the epiphyses of the distal epicondyles in the humerus never occurs due to certain environmental conditions. In light of these comparisons, we consider MUSM 51 could belong to an individual older than a young adult.

The nearshore marine sediments which yielded MUSM 51 were deposited near the mouth of a canyon and a mountainous escarpment. We propose that the bones could have been transported by a river from the mountains to the coast. The fragmentary nature of the bones is consistent with high-energy transport. Thus, *Palaeolama* sp. might have inhabited both the Pacific coast and Andean mountains, as presently does the guanaco, *Lama guanicoe* (Muller, 1776) according to Wheeler (1999). Ochsenius (1995) contends that the Lamini did not truly exploit Andean ecosystems prior to the Holocene. The occurrence of MUSM 51 in Plio-Pleistocene strata, as well as recent discoveries of *Lama guanicoe* in upper Pleistocene levels from the Peruvian coast (Salas & Stucchi, 2002) challenges that claim. We propose that the rarity of Pleistocene camelid material in the region is due to a scarcity of outcrop, rather than a failure of camelids to exploit pre-Holocene Andean environments.

Acknowledgments.

The authors wish to thank Christian de Muizon (Muséum National d'Histoire Naturelle, Paris) for his critique revision of the manuscript and valuable suggestions; Jane Wheeler (Universidad Nacional Mayor de San Marcos, Lima) for her comments about the ontogeny of modern camelids; René Marocco (Institut de recherche pour le développement, Lima) and François Pujos (Instituto Francés de Estudios Andinos, Lima) for their helpful insights; Bruce MacFadden and Richard Hulbert of Florida Museum of Natural History for providing access to the vertebrate paleontology collection. We would like to thank A. Cisneros, J. Tejada and D. Omura. We also thank Jean Vacher (Director - Instituto Francés de Estudios Andinos, Lima) and Niels Valencia (Director - Museo de Historia Natural - UNMSM, Lima) for their continued support of this research.

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