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South American camelids - past, present and future

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Abstract

This paper provides a review of South American camelid origins, evolution, classification, present status and future trends.

Keywords: guanaco, vicuña, llama, alpaca, conservation

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Introduction

The South American camelids are classified together with the Old World camels in the order Artiodactyla, suborder Tylopoda, and family Camelidae, but subdivided into Lamini and Camelini at the tribe level. Two New World genera, *Lama* and *Vicugna*, and one Old World genus, *Camelus*, are recognized. Ruminant digestion in the Tylopoda evolved independently of, and parallel to, ruminant digestion in the suborder Pecora (Bohlken, 1960). The Camelidae are distinguished by: absence of horns or antlers, presence of true canines separated from the premolars by a diastema in both the upper and lower jaws, position of the vertebral artery confluent to the neural canal in the cervical vertebrae, anatomy of the rear limbs which permits the animal to bend its legs beneath the body and rest on its stomach, and the presence of a nail covered digital pad rather than a hoof.

In 1758, Linnaeus described the two domestic New World camelids as *Camelus lama* "Camelus peruvianus Glama dictus" (llama) and *Camelus pacos* "Camelus peruvianus laniger Pacos dictus" (alpaca), placing them together in a single genus with the Old World dromedary and bactrian camels, *Camelus dromedarius* and *Camelus bactrianus*. The two remaining New World species, the wild guanaco and vicuña, were subsequently designated *Camelus guanicoe* by Müller in 1776 and *Camelus vicuña* by Molina in 1782. As early as 1775, Frisch proposed that the four New World species be placed in the genus *Lama*, but this work is not accepted by the International Commission on Zoological Nomenclature (Hemming, 1985a), and authorship of *Lama* is credited to Cuvier, 1800 (Hemming, 1958b). According to the accepted nomenclature as listed in Cabrera (1961), the vicuña was assigned to a separate genus, *Vicugna*, in 1872 by Gray. Nonetheless, the citation of Gray, 1872 is in error as this author described the vicuña as *Llama vicugna* (1872:101). The earliest reference to *Vicugna* is by Miller, who in 1924 proposed the generic separation based upon the vicuña's unique hypselodont incisors. Analysis of both mitochondrial and nuclear DNA (Stanley *et al.*, 1994; Kadwell *et al.*, 2001) confirm classification in two genera. Four species of New World camelids survive today: the domestic llama, *L. glama* (Linnaeus, 1758) and alpaca *V. pacos* (Linnaeus, 1758); and their wild ancestors the guanaco *L. guanicoe* (Müller, 1776) and vicuna *Vicugna vicugna* (Molina, 1782) respectively (Table 1); together with the Old World domestic dromedary *Camelus dromedarius* Linnaeus, 1758, the domestic Bactrian camel *C. bactrianus* Linnaeus, 1758 and the surviving, undomesticated, wild *C. ferus* (Silbermayr *et al.* 2009).

The tribe Lamini, represented by fossils of the genus *Pleiolama* (Webb and Meachan, 2004, previously *Pliauchenia* Cope 1875), originated in the Great Plains of western North America between 13.6 and 11 million years ago (Myr)(Harrison, 1985; Webb and Meachan, 2004) (Table 2). Two genera, *Alforjas* (10-4.5 Myr) (Harrison, 1979) and *Hemiauchenia* (10-0.1 Myr) (Webb, 1965, 1974) evolved from *Pleiolama* at approximately 10 Myr. The first of these, *Alforjas*, and its descendant *Camelops* (4.5-0.1 Myr) remained in North America (Harrison, 1979; Webb, 1965, 1974), while some species of *Hemiauchenia* migrated to South America during the Pliocene/Pleistocene transition approximately 3.3 Myr (Woodburne, 2010). It is apparently from the latter genus that *Lama* and *Vicugna* evolved in South America approximately 2 Myr (López Aranguren, 1930; Cabrera, 1932; Webb, 1972; Harrison, 1985). A second genus, *Palaeolama,* was also present from ca 2.0-0.1 Myr. Webb (1974). Only *Lama* and *Vicugna* survived the end of the Pleistocene period some 10,000 years ago.

Table 1. Systematic classification of the extant South American Camelidae

Order	Artiodactyla Owen, 1848
Suborder	Tylopoda Illiger, 1811
Family	Camelidae Gray, 1821
Subfamily	Camelinae Gray, 1821
Genus	***Lama* Cuvier, 1800**
	***Lama glama* (Linnaeus, 1758) – domestic llama**
	***Lama guanicoe* (Müller, 1776) – wild guanaco**
	Invalid Names
	Camelus Linnaeus, 1758
	Lama Frisch, 1775 (rejected, ICZN Opinion 258)
	Lacma Tiedemann, 1804 (unused senior synonym)
	Auchenia Illiger, 1811 (previously utilized by Thunberg, 1789)
	Lama Lesson, 1827
	Llama Gray, 1872
Genus	***Vicugna* Miller, 1924**
	***Vicugna vicugna* (Molina, 1782) – wild vicuña**
	***Vicugna pacos* (Linneaus, 1758) – domestic alpaca**
	Invalid Names
	Camelus Molina, 1782
	Lacma Tiedemann, 1804 (unused senior synonym)
	Auchenia Illiger, 1811 (previously utilized byThunberg, 1789)
	Lama Lesson, 1827
	Llama Gray, 1872

Table 2. Systematic classification of the fossil South American Camelidae, after Harrison, 1979, 1985

Order	Artiodactyla Owen, 1848
Suborder	Tylopoda Illiger, 1811
Family	Camelidae Gray, 1821
Subfamily	Camelinae Gray, 1821
Tribe	**Lamini Webb, 1965 - South American camelids**
Subtribe	**Lamina Harrison, 1979**
	Pleiolama Webb and Meachen 2004 (13.6-9 my) (previously *Pliauchenia* Cope 1875)
	Hemiauchenia H. Gervais and Ameghino, 1880 (10-0.1 my) (classified as a subgenus of *Palaeolama* by Guérin and Faure 1999)
	Palaeolama P. Gervais, 1867 (3/2-0.1 my)
	Lama Cuvier, 1800 (originated 2 my, survives today) [May include late Pleistocene *Lama (Vicugna) gracilis* H. Gervais and Ameghino, 1880 which is said by Menegaz and Ortiz-Jaureguizar 1995 and Guérin and Faure 1999 to be intermediate between vicuña and guanaco, although south Chilean specimens have been classified as *Vicugna* based on aDNA by Weinstock *et al.* 2010.
	Vicugna Miller, 1924 (originated 2 my, survives today)
Subtribe	**Camelopina Harrison, 1979**
	Alforjas Harrison, 1979 (10-4.5 my)
	Camelops Leidy, 1854 (4.5-0.1 my)

The wild South American camelidae: past and present

1. The guanaco, *Lama guanicoe* (Müller, 1776)

The guanaco is the largest wild artiodactyl in South America. Fossil remains of *L. guanicoe* are found in Argentine Pleistocene deposits (López Aranguren, 1930; Cabrera, 1932; Menegaz *et al.*, 1989) that probably date to some 2 Myr (Webb, 1974). They are also present at Tarija, Bolivia (Hoffstetter, 1986) in strata dated 97-73,000 years BP (before present) by magnetic polarity (MacFadden *et al.,* 1983), but more recently placed at 44,000 to 21,000 radiocarbon years BP (Coltori *et al.*, 2007). To date there are no reports of the presence of guanacos in the high Andean puna ecosystem prior to the end of the Pleistocene 12,000 to 9,000 years ago (Hoffstetter, 1986). Before European contact, guanacos were found along the Pacific shore and into the high Andes from approximately 8° South latitude to Tierra del Fuego, as well as east into the Paraguayan Chaco and across the pampas to the Province of Buenos Aires (Torres, 1985; Tonni and Politis, 1980). Neither fossil nor recent guanaco remains have been found in Ecuador or Colombia to date. Raedeke (1979) has estimated the prehispanic guanaco population at 30 to 50 million based on carrying capacity of the territory they occupied. These numbers rapidly declined during the European conquest, and during the nineteenth century the impact of indiscriminate hunting and commercial sheep rearing reduced the guanaco population to 7 million. In 1954, Dennler de la Tour (1954) called attention to the impending disappearance of the Patagonian guanaco if the hunting of yearling *chulengos* was not controlled and protected reserves

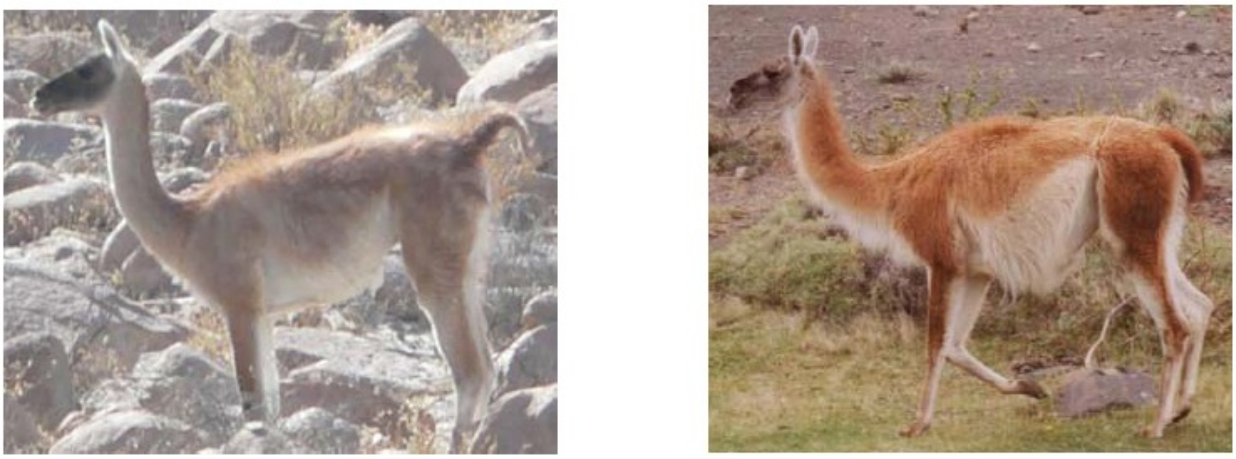

Figure 1. a) *Lama guanicoe cacsilensis* 8°-18°30'S **b)** *Lama guanicoe guanicoe* 22°-55°50'S

established. In 1969, Grimwood found that the Peruvian guanaco population was on the edge of extinction, and in 1971 the government responded by declaring it an endangered species. At present, according to the IUCN Red List of Threatened Species, 2008 (www.iucnredlist.org), between 535,750 and 589,750 survive, with fewer than 3,000 *Lama guanicoe cacsilensis* in Peru (Wheeler *et al.*, 2006).

All guanacos exhibit similar pelage coloration varying from dark reddish brown in the southern populations (*L.g. guanicoe*) (Figure 1b) to lighter brown with ocher yellow tones in the northern variety (*L.g. cacsilensis*) (Figure 1a). The chest, belly and internal portion of the legs are more or less pure white, the head grey to black with white around the lips, eyes and borders of the ears. Fiber diameter varies from 16.5 μm to 24 μm and contains from 5 to 20% hair (Verscheure and Garcia, 1980). Sexual dimorphism is absent except for the presence of large canines in the male. Withers height of adult animals varies from 110 to 120 cm for *L.g. guanicoe* from Patagonia and Tierra del Fuego (Cabrera and Yepes, 1960; Franklin, 1982; Herre, 1952; Raedeke, 1979; MacDonagh, 1949), compared to 100 cm for the small northern guanaco *L.g. cacsilensis* (Herre, 1952). Reported body length, from the tip of the nose to the base of the tail, varies from 167 (MacDonagh, 1949), 185 (Cabrera and Yepes, 1960), 191 (Raedeke, 1979) and 210 cm (Dennler de la Tour, 1954) for *L.g. guanicoe* and 90-100 cm for *L.g. cacsilensis* from Calipuy, Peru (Kostritsky and Vilchez, 1974). Live weight for adult *L.g. guanicoe* varies from 120 to 130 kg (Raedeke, 1979; Miller *et al.*, 1973), compared to 96 kg for *L.g. cacsilensis* (Kostritsky and Vilchez, 1974).

Historically four poorly defined subspecies of guanaco have been described based on distribution, size and coloration (González *et al.,* 2006): the first, *Lama guaunicoe guanicoe* (Müller, 1776), in Patagonia, Tierra del Fuego and Argentina south of 35° S latitude; the second, *L.g. huanacus* (Molina, 1782), on the western slope of the Chilean Andes between 22° and 38° S (Cunazza 1992); the third, *L.g. cacsilensis* Lönnberg, 1913, found from the Pacific coast to high altitude along the western slope of the Andes from 8° to 18° 30' S in Peru (Hoces, 1992) and northern Chile (Torres 1992) ; and the fourth, *L.g. voglii* Krumbiegel, 1944, on the eastern slope of the Argentine Andes, in southeastern Bolivia (Villalba 1992) and northwestern Paraguay (Torres 1992) between approximately 21° and 32° S latitude. The characteristics that set each subspecies apart are not fully detailed in these early works, and little information on zoogeographic variations in guanaco morphology is available. The most extensively studied populations are located at the southernmost limits of guanaco distribution, and it is clear that these larger, darker animals (*L.g. guanicoe*) contrast markedly with the smaller, lighter colored specimens (*L.g. cacsilensis*) found at the northern boundary.

Recent analysis of the complete cytochrome-*b* and partial control region mitochondrial DNA sequences from representatives of all four proposed subspecies (Marín *et al*., 2008) separates the northern *L.g. cacsilensis* from the remaining guanacos (*L.g. guanicoe*). The southernmost populations (*L.g. guanicoe* and *L.g. huanacus*) are characterized by reduced genetic variability suggesting that they have suffered a severe bottle neck or extinction event with subsequent recolonization in the past, while in contrast, the high levels of genetic diversity in the northern *L.g. cacsilensis* populations suggests they were stable over long periods of time allowing accumulation of the relatively high levels of genetic diversity.

2. The vicuña, *Vicugna vicugna* (Molina, 1782)

At present vicuña distribution is limited to areas of extreme elevation between 9° 30' and 29° S latitude in the Andes. None the less, paleontological remains suggest that the genus *Vicugna* originated further east on the Argentine plains as early as two million years ago (López Aranguren, 1930; Cabrera, 1932; Webb, 1974; Harrison, 1985), although Menegaz *et al.,* (1989), conclude that the vicuña evolved from the guanaco at the beginning of the Holocene on the Argentine plains. Nonetheless, mtDNA sequence data support a divergence of at least two million years between vicuña and guanaco (Stanley *et al.,* 1994), and fossils from Tarija, Bolivia include vicuña remains (Hoffstetter, 1986) dated to between 97 and 73,000 years ago (MacFadden *et al.,* 1983) indicating that their range had expanded westward towards the Andes by that date. The oldest reported vicuña remains from high altitude have been dated to 22,220 ± 130 B.P. at Cueva Rosselló, Peru (3,875 masl) (Shockey *et al.,* 2009), but data from analysis of mitochondrial DNA (Marín *et al.,* 2007) indicates that current population distribution appears to be the result of a recent demographic expansion associated with the last major glacial event of the Pleistocene 14-12,000 years ago. Vicuña remains have not been found in either paleontological deposits (Hoffstetter, 1986) or archaeological sites (Miller and Gill, 1990) in Ecuador and Columbia.

Remains of another small vicuña-like genus, *Lama (Vicugna) gracilis* (Gervais and Ameghino, 1880) are found in late Pleistocene and early Holocene deposits in both the Patagonian and eastern Pampean region of Argentina (Buenos Aires Province) and Urugay, Argentine and Chilean Patagonia, as well as on the north Chilean coast at Calama (Cartajena *et al.*, 2010). They appear to represent a separate genus and became extinct at the Pleistocene/Holocene transition (Cajal *et al.,* 2010).

The Precolumbian Peruvian vicuña population has been estimated at 2 million (Brack, 1980), and may have been far greater on an Andean scale. Prior to the conquest, vicuña were considered (together with the guanaco) to be the herds of the *Apus* or mountain gods. Hunting was prohibited and only the Inca royalty could use garments made from vicuña fiber that was obtained through live shearing and release at *Chaku* or roundup events. After contact, these sustainable utilization practices disappeared and by 1957, Koford calculated the total Andean vicuña population to be at most 400,000, including 250,000 in Peru. Twelve years later Grimwood (1969) reported only 10,000 in Peru, and in 1971 Jungius estimated a total of between 5,000 and 10,000 in Peru, with another 2,000 living in Bolivia, Argentina and Chile. According to the IUCN (2010) the present Andean population is 347,273.

Two subspecies of vicuña have been described, separated mainly on the basis of size difference. The first, larger, *Vicugna vicugna vicugna* Molina, 1782 (Figure 2b) is found between 18º and 29º S latitude, while the second, smaller, *V.v. mensalis* Thomas, 1917 (Figure 2a) is reported between 9º 30' and 18º S latitude. A third purported subspecies, *V.v. elfridae* Krumbiegel, 1944 has been described based on specimens found in German zoos.

The most studied vicuña, the northern *V.v. mensalis,* is distinguished primarily by the long growth of hair on the chest. The head, neck, back, sides and dorsal surface of the tail are a dark cinnamon color, with white covering the lower portion of the face, the chest, belly, interior surface of the legs and ventral surface of the tail. The eyes and edges of the ears are outlined in white. Average coat length is 3.28 cm in adult animals and the long chest hairs reach 18 to 20 cm (Hofmann *et al.,* 1983). Fleece fiber diameter is 12.52 ± 1.52 µm (Carpio and Solari, 1982a) and the average fleece fiber length is 3.2 cm in adult males (Carpio and Santana, 1982).

Figure 2. a) *Vicugna vicugna mensalis* 9º30'-18ºS **b)** *Vicugna vicugna vicugna* 18º-29ºS

Follicle density averages 78.65 per mm2 (Carpio and Solari, 1982b) and the frequency of primary hair in the fleece is 2% (Carpio and Solari, 1982b). In contrast, *V.v. vicugna* lacks the long chest hairs, and has a lighter beige pelage coloration with white covering a greater portion of the body, rising halfway up the sides to mid-rib height and all the way to the ileum crest, as well as covering the anterior portion of the rear legs.

Although Sarno and collaborators have come to a differing conclusion (2004), validation of the two proposed subspecies has come from the study of both nuclear (Wheeler *et al.,* 2001, 2003; Dodd *et al.*, 2006; Wheeler and Laker 2008) and mitochondrial (Marín *et al.,* 2007) DNA. In the latter study, analysis of 261 individuals from 29 populations across Peru, Chile, and Argentina, suggests that *V.v. mensalis* and *V.v. vicugna* comprise separate mitochondrial lineages, with current population distribution apparently resulting from a recent demographic expansion associated with the last major glacial event of the Pleistocene in the northern dry Andes (18 to 22ºS) at 14 to 12,000 years ago and the establishment of an extremely arid belt known as the "Dry Diagonal" to 29ºS. Within the Dry Diagonal, small populations of *V.v.vicugna* appear to have survived showing the genetic signature of demographic isolation, whereas to the north *V.v. mensalis* populations underwent a rapid demographic expansion before recent major anthropogenic impacts.

The domestic South American camelidae: past and present

1. The llama, *Lama glama* (Linnaeus, 1758)

The llama is the largest of the domestic South American camelids and resembles its ancestor, *Lama guanicoe cacsilensis*, in almost all aspects of morphology and behavior (Kadwell *et al.*, 2001). Like the guanaco, the llama has adapted to a wide range of environments. It plays a key role in the economy, providing meat, fiber, dung and service as pack animal, and culture of the native high Andean populations.

Both archeozoological and DNA (Wheeler *et al.*, 2006; Kadwell *et al.,* 2001) evidence have made it increasingly clear that llama domestication took place in several Andean locations. In N.W. Argentina and northern Chile, the concerted efforts of archaeologists and archeozoologists have produced evidence that llama domestication took place between 5,000 and 3,800 B.P. in the dry *puna* at elevations of 3,200 meters and above (Mengoni-Goñalons and Yacobaccio, 2006; Cartajena, 2009; Cartajena *et al.*, 2007, Benavente, 1985; Olivera and Grant, 2009; Yacobaccio, 2004), based on both changes in size of the animals (llamas are larger than guanacos) and human settlement patterns. A second center of domestication was probably located in the Central Andes of Peru at 4,000 meters elevation, around 4,000 BP (Mengoni-Goñalons and Yacobaccio, 2006; Moore, 1988; Kent, 1982) again based on the larger size of the llama remains.

After domestication at high elevation in the puna, the llama was moved to lower interAndean valleys (Wing, 1986), and by 1,400 years ago they were being bred on the north coast of Peru (Shimada and Shimada, 1985) and in Ecuador (Wing, 1986; Stahl, 1988; Miller and Gill, 1990). By 1,250 BP, herding was central to the Chiribaya economy at El Yaral, located at 1,000 meters elevation in the dry Osmore drainage of south coastal Peru (Wheeler, 1995; Lozada *et al.,* 2009), and shortly thereafter at 900-1,000 BP, llamas were also being reared at sites in the cloud forest on the eastern slope of the central Andes (Wheeler, 1995). Under Inca rule (1470-1532) llama distribution reached its furthermost expansion as pack trains accompanied the royal armies to southern Colombia and central Chile. It is impossible to estimate the size of this preconquest llama population, but it clearly must have exceeded present numbers since early Spanish administrative documents record the virtual disappearance of these animals within a century of contact (Flores Ochoa, 1977).

Because Andean civilization was nonliterate, knowledge of pre-Spanish llama (and alpaca) herding practices must be reconstructed from archaeological remains. The discovery of 900-1000 year old naturally desiccated llamas and alpacas at El Yaral, an archaeological site in the Moquegua valley of southern Peru (Rice, 1993), has provided a first view of what may have been preconquest breeds (Wheeler *et al.,* 1995; Lozada *et al.,* 2009). Associated with the pre-Inca Chiribaya culture, these animals had been sacrificed by a blow between the ears and immediately buried beneath house floors where they became naturally mummified due to the extreme aridity of the environment.

Research on the physical appearance and fiber quality of the El Yaral llamas, has revealed the possible existence of both a fine fiber and a coarse fiber breed (Wheeler *et al.*, 1995; Lozada *et al.,* 2009). Average fleece diameter of the former was found to be 22.2 with a between sample standard deviation of 1.8 μm, compared to 32.7 (sd ± 4.2) μm for the latter. The reduction of both fiber diameter and variation in the fine fiber llama fleece was certainly produced by selective breeding for a single-coat through modification of the primary hair to resemble secondary undercoat fiber. The uniform coloration and fineness, as well as the absence of visible hairs in the El Yaral fine llama fleeces are ideally suited for textile production, and contrast markedly with the multi-colored double-coat of the coarse fiber breed.

Prior to discovery of the El Yaral mummies, our most detailed data on preconquest camelid breeding practices came from written documents of the colonial period. These records describe the use of llamas as pack animals for the Inca army, but make no mention of fine fiber producing llamas. This may be due to the general failure of the early Spanish writers to distinguish between llamas (and alpacas), as well as their special interest in pack animals for use in transporting ore. Despite their European perspective, these documents do provide details about Inca husbandry. Expansive state and shrine herds were managed by the *llama camayoc*, members of a hereditary caste of herding specialists, and emphasis was placed on breeding pure brown, black and white animals for sacrifice to specific deities, as well as on quality fiber production for the state controlled textile industry (Murra, 1965, 1975, 1978; Brotherston, 1989). Detailed data on size and color of flocks were kept utilizing the *quipu,* a memory assistance device made of knotted camelid fiber cords. Communally and individually owned herds also existed.

a) *Lama glama*, Q'ara or Ccara type

b) *Lama glama*, Ch'aku type

c) *Lama glama*, Suri type, mummy from El Yaral, 900-1,000 AP

d) *Lama glama*, Suri type

e) *Lama glama*, Llamicho type

Figure 3. The different breeds of llama

Native Andean stockrearing was largely destroyed by the arrival of the Spanish. Within little more than a century of the conquest in 1532, administrative documents record the disappearance of approximately 90% of the domestic camelids (Flores Ochoa, 1982), as well as 80% of the human population (Wachtel, 1977). Coastal and highland valley herds were the first to disappear, as their grazing lands were usurped for the production of sheep, goats, cattle and pigs. In the *puna* this process was somewhat slower because both the Spanish and their livestock found the harsh climate and extreme elevation inhospitable. This region became a refuge for the native livestock and herders, and their descendants continue to inhabit the same marginal lands today. The prolonged Spanish civil wars and heavy tribute levies, paid either in domestic camelids or in money obtained from their sale, resulted in depletion of the herds. By 1651, llamas (and alpacas) had practically disappeared even in the Lake Titicaca basin (Flores Ochoa, 1982), the former heartland of their distribution (Murra, 1975). The impact of such catastrophic mortality upon camelid genetic diversity and breeding practices has yet to be fully explored. Today, the total llama population is estimated to be 3,776,793 (Wheeler, 1995). Small groups are found near Pasto, Colombia (1° N latitude) and Riobamba, Ecuador (2° S latitude). To the south they extend to 27° in central Chile, but the most important production zone is located between 11° and 21° S latitude at elevations of 3,800-5,000 meters above sea level.

The name, “llama”, comes from Quechua (Flores Ochoa, 1988), and it is known as *qawra* by Aymara speakers (Dransart, 1991). Although specific llama breeds do not exist, at least four varieties of llama exist: k'ara (Figure 3a), chaku (Figure 3b), suri (Figures 3c,d) and llamingo (Figure 3e). Most llamas in Peru, Bolivia and northern Chile are of the "nonwoolly" k'ara variety characterized by sparse fiber growth on the body and the very short fiber on the face and legs. To the south, especially in Argentina where seven distinct fiber types have been described (Frank and Wehbe, 1994), the "woolly" chaku llama variety is more common and has a greater density of fiber on the body that extends forward between the ears and grows from inside the ears, but is absent on the legs. The woolly type is known as *chaku* in Quechua (Flores Ochoa, 1988) and *t'awrani* in Aymara (Dransart, 1991), while the nonwoolly variety is called *k'ara* in both languages (ibid.). In both areas llamas with intermediate phenotypes are also recognized. The *suri* llama variety is characterized by long straight fibers, organized in waves that fall to each side of the body in much the same manner as Lincoln sheep. As in the case of suri alpacas, they represent a small percentage of llamas, but have existed since preInca times (Wheeler *et al.* 1995, 2012). In Ecuador, the *llamingo*, a markedly smaller, genetically distinct "nonwoolly" variety, has been present for the past 2,000 years (Wheeler et al., 2012; Miller and Gill, 1990).

The vast majority of llamas are held by traditional Andean pastoralists who utilize elaborate classification hierarchies based on color, fiber and conformation characteristics to describe their animals. The existence of these systems among both Quechua (Flores Ochoa, 1988) and Aymara (Dransart, 1991) speaking herders suggests that earlier management strategies may have been directed at producing animals with specific fiber types, but it is not clear to what extent selection is made for these characteristics today. Contemporary llamas lack the phenotypic uniformity associated with true breeds, and Flores Ochoa (1988) indicates that the primary breeding criteria used by Quechua speaking herders in southern Peru is to divide llamas into "*allin millmayuq*" and "*mana allin millmayuq*" or fine and coarse fiber animals. Pelage coloration varies from white to black and brown passing through all intermediate shades with a tendency to spots and irregular color patterns, and llamas with wild guanaco coloration occur. Fleece quality is uneven, with wide variation in fiber diameter and a strong tendency to hairiness, ranging from 32.5± 17.9 µm (female) to 35.5 ± 17.8 14 µm (male) for coarse "nonwoolly" *k'aras*, 30.5 ± 18.5 µm (female) to30.5 ± 17.9 µm (male) for intermediates, and 27.0 ± 15.6 µm (female) to 29.1 ± 12.7 µm (male) for "woolly" *chakus* (Vidal, 1967). The variability of present day llama fiber is related to an increase in hairs and general coarsening of the fleece, which probably began at the time of the Spanish conquest. Increased hairiness is produced by lack of controlled breeding, and crossing between the two preSpanish llama breeds from El Yaral could account for the entire range of fleece variation observed in today's animals. Analysis of mitochondrial and nuclear DNA from a large sample of Andean llamas has also shown that approximately 40% of the population is hybridized with alpacas (Kadwell *et al*., 2001).

2. The alpaca, *Vicugna pacos* (Linnaeus, 1758)

The alpaca is smaller than the llama and resembles its ancestor, *Vicugna vicugna mensalis*, the vicuña, in many aspects of morphology and social organization (Kadwell *et al*., 2001). It plays a key role in both the economy, producing fiber for industry and export, as well as meat for human consumption and dung for fuel, and the culture of the native Andean populations.

Domestication of the alpaca is independent of, and possibly earlier than, that of the llama. Excavations at Telarmachay Rockshelter in the central Peruvian puna have placed its origins around 6,000 years ago (Wheeler, 1984, 1986, 1999), and it was from this region that the alpaca was subsequently moved to lower elevation interandean valleys 3,800 years ago (Wing, 1972; Shimada, 1985). Evidence of alpaca rearing at coastal sites in southern Peru dates from 900 to 1,000 years ago (Wheeler *et al.,* 1995; Lozada *et al.*, 2009). No reliable evidence for the presence of alpacas has been found in the faunal materials from precolumbian sites in Argentina (Olivera and Grant 2009), Chile (Cartajena *et al.*, 2007; Cartajena, 2009) or Ecuador (Miller and Gill, 1990), although they have been recently introduced to these regions today. It is impossible to estimate the number of preconquest alpacas. Spanish documents record their rapid decimation and displacement to remote, extreme high elevation regions of the Andes (Flores Ochoa, 1977). Over the last four decades alpaca numbers have fallen significantly in Peru, from 3,290,000 in 1967 to 2,510,912 in 1986, and in 1991 the total Andean alpaca population was estimated to be 2,811,612 (Wheeler, 1995). More recent census data is not available.

Figure 4. a) *Vicugna pacos*, Huacaya type

b) *Vicugna pacos*, Suri type

Although the European concept of a breed (stud book, registry etc.) is not truly applicable to the South American camelids, representatives of two possible preconquest alpaca breeds have been found among the 900-1,000 year old El Yaral mummies. Fine fiber and extra fine fiber alpacas were distinguished based on physical appearance and average fiber diameter. The former have fleeces averaging 23.6 ± 1.9 14 µm, while the latter fleeces average 17.9 ± 1.0 µm (Wheeler *et al.*, 1995). Both groups had lustrous fiber ranging from wavy to crimped and dense to very dense. Hairs were not significantly coarser than the undercoat fibers and fiber diameter variation both within and across the fleece was remarkably low, suggesting that rigorous breeding selection for fine quality fiber was being practiced.

The Spanish conquest had a disastrous effect on both llama and alpaca populations. Massive mortality accompanied the displacement of alpaca herds from the coast, interandean valleys and most of the puna, as introduced stockrearing practices pushed the survivors into the marginal, extreme high elevation pastures where they are found today (Flores Ochoa, 1982). At present, alpaca distribution extends from approximately 8º S latitude, where they have been recently reintroduced in Cajamarca, to 20º S latitude, in the vicinity of Lake Poopo, Bolivia, with small populations located further to the south in northern Chile and northwestern Argentina, and to the north in southern Ecuador.

In Peru, 75% of all alpacas, *paqocha* in Quechua (Flores Ochoa, 1988) and *allpachu* in Aymara (Dransart, 1991), are held by traditional herders (Novoa, 1989). Two alpaca phenotypes, known in the literature by their Quechua names as *huacaya* or *wakaya* (Figure 4a) and *suri* (Figure 4b), and are recognized but these do not breed true. The *suri* variety has long straight fibers, organized in waves which fall to each side of the body in much the same manner as a Lincoln sheep, while the huacaya variety has shorter, crimped fibers which give it a spongy appearance similar to that of a Corriedale sheep. Occasionally animals with intermediate fiber characteristics are seen, and these have been named *chili* by Cardozo (1954). Crosses between *huacaya* and *huacaya* produce a certain percentage of suri offspring, and crosses of *suri* with *suri* produce some *huacaya* offspring. Although no artificial selection is made, an estimated 90 percent of all alpacas are *huacayas* (Novoa, 1989). The *suri* is not known among the Aymara herders of Chile who refer to their *huacayas* simply as *allpachu* or alpacas (Dransart, 1991). The fleece of both phenotypes varies from white to black and brown, passing through all intermediate shades, with a greater tendency to uniform coloration than in the llama. Alpacas with wild vicuña coloration occur.

In comparison to the preconquest El Yaral alpacas, contemporary Andean *huacaya* and *suri* fleeces average 31.2 ± 3.8 µm (Carpio, 1991) and 26.8 ± 6.0 µm (Von Bergen, 1963) respectively, are coarser, may have a tendency to hairiness, and are of uneven quality. Some coats containing up to 40% hair have been reported for both living varieties, and considerable variation is reported in published statistics on fiber diameter. The most probable cause of coarsening and hairiness in both *huacayas* and *suris* would be through hybridization with the coarser fibered llama, and this has been documented through analysis of both mitochondrial and nuclear DNA (Kadwell *et al.*, 2001).

Hybridization

In 2001, Kadwell *et al.* utilized both mitochondrial DNA sequencing and nuclear microsatellite markers to examine the origins of the domestic South American camelids using an extensive data set of guanaco, vicuña, llama and alpaca samples taken throughout their geographic range. The results of this study: 1. confirmed the generic separation of *Lama* and *Vicugna* approximately two to three million years ago, 2. determined that the guanaco and vicuña are the ancestors of the llama and the alpaca respectively, and 3. documented extensive hybridization between llama and alpaca. The results show that 40% of llamas and 80% of alpacas are hybridized, a far greater percentage than had been imagined. Subsequent research has shown that hybridization of alpacas may exceed 90% (Wheeler, 2005), indicating that the original alpaca genome is in danger of disappearing.

Traditional herders recognize the existence of llama and alpaca crosses. These are referred to by the generic terms *wari* in Quechua (Flores Ochoa, 1988) and *wik'uña* in Aymara (Dransart, 1991). These hybrids are classified as *llamawari* or llama-like and *paqowari* or alpaca-like by Quechua speakers (Flores Ochoa, 1977). Aymara speaking herders use *waritu* and *wayki* for llama and alpaca phenotype hybrids, as well as the generic term *wakayu* for any llama x alpaca offspring (Dransart, 1991). Although first generation crosses are easily recognized, but given the extent of hybridization DNA testing is required for absolute identification.

Crosses between the wild and domestic South American camelids produce fertile offspring, but do not normally occur in nature. The pacovicuña, or alpaca x vicuña hybrid, has received considerable attention for its potential as a fine fiber producer. Based on a very limited sample size (n=5), Carpio *et al.* (1990) report fiber diameters ranging from 13.3 to 17.3 μm for first generation crosses, but this is said to rapidly increase in subsequent generations. The pacovicuña phenotype may closely resemble that of the vicuña, depending on the characteristics of the alpaca half. It is slightly larger and less gracile than its wild progenitor. Scientific research on the fixation of phenotypic traits from generation to generation of alpaca x vicuña hybrids is lacking, and much remains to be done before its potential as a fine fiber producer can be evaluated. Unfortunately, massive indiscriminate crossing of alpacas and vicuñas, has been promoted by the Peruvian government over the past five years, without taking into account the potential negative impact that this could have on the genome of both species (see below).

The possibility that feral llamas and alpacas exist and might have crossed with wild camelids has not been fully explored. According to Murra (1978), Xerez observed in 1534 that domestic llamas were sometimes so numerous some escaped to the wild, while in 1555 Zarate wrote that once each year some llamas were released into the wild as an offering to the gods. It is unclear, however, if feral populations existed at that time. The current consensus of opinion in the central Andean region is that no such populations exist today. Even so, MacDonagh (1940) has described a group of guanaco and llama hybrids living in a feral state in the Province of Cordoba, Argentina. These animals were the product of natural crosses, and generally exhibited the guanaco phenotype, although some had white blotches on the head and upper part of the neck, and others are almost entirely white. No observations on changes in body size and fiber quality were recorded. The behavior of these feral hybrids was considered to be virtually identical with that of the guanaco, and they lived and reproduced without problem.

DNA, conservation and the future

Since the discovery of the structure of DNA by Watson and Crick in 1953 gave origin to the science of molecular genetics, the rapidity of technological advance has brought us to the present routine sequencing of entire genomes. The information thus obtained permits reconstruction of the evolutionary history of species, information that in most cases is otherwise inaccessible, and in the South American camelids absolutely essential for conservation planning given the history of major population size reductions in all four forms.

In the case of the vicuña, analysis of the current Andean populations (Wheeler *et al.,* 2001, 2003; Dodd *et al.,* 2006; Marín *et al.,* 2007; Wheeler and Laker 2008) has documented the impact of their brush with extinction in both reduced genetic diversity and fragmentation into five genetically and geographically distinct groups. Although numbers have now recovered sufficiently so that the species is currently classified in the category of Least Concern by the IUCN, (2010), and sale of the extremely fine fiber taken from live-shorn animals generates important income for those communities located in vicuña territory (Wheeler and Hoces 1997; Lichtenstein and Vilá 2003). Separate conservation measures and DNA monitoring are required for each of the five groups (Wheeler *et al.*, 2001; Marín *et al.,* 2007; Wheeler and Laker 2008) in order to prevent further loss of diversity.

In the case of the guanaco, analysis of the current Andean populations (Marín *et al.*, 2008) has shown a different situation than that of the vicuña, with considerable genetic diversity extant in both subspecies (Casey *et al.,* in revision). Because this finding validates the strategy of moving individuals to repopulate adjacent areas, it can, together with further genetic research, facilitate conservation measures, especially for the endangered northern subspecies *L.g. cacsilensis* (Wheeler *et al.,* 2006).

In the case of the domestic llama and alpaca, analysis of both nuclear and mitochondrial DNA has documented the existence of extensive bidirectional hybridization affecting at least 80% of alpacas and 40% of llamas (Kadwell *et al.,* 2001; Wheeler *et al.,* 2006). The extent of hybridization, especially in the case of the alpaca, is of great concern as the crossing alpacas and llamas to produce a greater volume and weight of fiber for sale, regardless of the negative impact on fiber fineness, has been common practice over the past 30 years, and may even have begun inadvertently in the chaos produced by the Spanish conquest. With genetic tests available to detect hybrid alpacas and llamas, they should be applied to establish reserve herds in order to conserve the original genome of both the alpaca and llama. These herds should form the basis for breeding of improved quality stock, aided by the future discovery of genetic markers for economically desirable traits such as fiber fineness.

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