The Origin and Evolution of the South American Camelids

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Introduction

The *Camelidae* family originated in North America during the Eocene period around 40 to 45 million years ago (Stanley *et al*. 1994). The most primitive camelid was *Protylopus petersoni*. This species was approximately 30 cm tall and its skeleton was similar to the actual camelid, with a slightly rounder body shape. An early descendant of this animal was *Poebrotherium wilsoni,* which lived during the middle Oligocene period around 25 to 30 million years ago, similar to the guanaco (*Llama guanicoe*). The main characteristic of this species were spaces between incisors, canines and premolars which were adapted for trituration of hard vegetation, and two fingers on each foot. During the late Miocene period, around 5 to 10 million years ago, the genus *Pliauchenia* evolved with similar characteristics to llamas (*Llama glama*) and alpacas (*Llama pacos*). Later the genus *Paracamelus* migrated to the east via the Bering Strait originating two species: the Bactrian camel and the Dromedary camel. In the early Pliocene the genus *Hemiauchenia* differentiated into two different genuses: *Peleolama* and *Lama* then migrated to South America, where the first genus become extinct while the second one subdivided into the genuses *Lama* and *Vicugna* which originated the South American camelids (Huanca 1993).

At present, four South American camelids (SAC) are recognized; two wild species - the guanaco (*Lama guanicoe*) and the vicuña (*Vicugna vicugna*) -

and two domestic forms - the alpaca (*Lama pacos*) and the llama (*Lama glama*) - whose evolutionary origins are debated (Wheeler et al. 1995). Interestingly, the four species of SAC and the two species of camels have the same number of chromosomes - 37 pairs (Taylor, et al. 1968) - and interspecies crossbreeding generates fertile hybrids (Gray 1954; Skidmore et al. 2001). Examples are the “pacovicuña” (alpaca + vicuña) and “huarizo” (llama + alpaca). The first generations of crossbred animals are easy to recognise by their phenotypic characteristics, but are impossible to recognise later on, as hybridisation has been an ongoing process. In this matter, DNA studies have confirmed the hybridisation process in several llama and alpaca populations (Stanley et al. 1994).

This article discusses the archaeozoological findings and the molecular research conducted to elucidate the origin of South American domestic camelids, and also the possible implications for the alpaca industry in the future.

Archaeological Findings

The earliest evidence of camelid domestication comes from archaeological sites located in the Puna ecosystem of the Peruvian Andes between 4,000 and 4,900 m above sea level. The guanaco (*Lama guanicoe*), the vicuña (*Vicugna vicugna*) and the huemul deer (*Hippocamelus bisulcus*) have inhabited this area for approximately 12,000 years (Wheeler 2003). An Archaeozoological remains from Telarmachay - situated 170 km northeast of

Lima, Peru at 4,420 m above sea level - has proved the domestication of the camelids. Climate conditions are very extreme in this location with an average annual temperature around 4.8°C, oscillating ± 20°C, frost 330 nights a year, poor precipitation from 500 to 1,000 mm restricted to the period November to March and extended periods of drought that make agricultural activities impossible. In these difficult environmental conditions, the SAC are bred due to their ability to convert the dry ligneous Puna grasses, characterized by a high concentration of tannins - a natural anti-herbivore mechanism - into a source of stored protein that can be utilized for human consumption and fibre, skin and manure production. It is also used as a fertilizer and fuel source.

An important discovery of well preserved naturally mummified llamas and alpacas between 900 and 1,000 years old at El Yaral, in the Moquegua valley on the south coast of Peru has been valuable in providing an opportunity to examine the physical appearance of the camelids prior to the arrival of the conquistadors. El Yaral is located 50 km from the Pacific coast at 1,000 meters above sea level. This area is extremely dry and condensations of winter fog provide most of the annual precipitation of around 15 to 20 mm from May through August. Average temperatures are 8°C in winter and 28°C in summer. Agriculture is not possible in this area without irrigation systems.

The excellent state of preservation of the llama and alpaca mummies has made possible a systematic analysis of the fibre to obtain information about fleece composition. Surprisingly, 5 samples of 6 llamas were found to belong to an apparently extinct fine-fibre breed, their fleeces averaging 22.4 ± 2.3 u

(Wheeler et al. 1992), in comparison with llamas today which have fleeces averaging 28.0 ± 14.0 u (Vidal 1967). Additionally their fleeces were very uniform in comparison with the animals bred today. This characteristic is linked to the presence of hair. The more hair, the less uniform the fleeces are, and it has been postulated that increased hairiness is produced by the lack of controlled breeding (Carpio 1991).

In the case of the alpaca, two probable breeds were distinguished in the El Yaral mummies based on the fineness of the fibre; fine and extra-fine fibre animals were distinguished, with readings of 23.6 ± 1.6 u and 18.0 ± 1.1 u respectively. Both groups exhibited uniform single-coats. In comparison, contemporary Huacaya and Suri fleece fibres are 31.2 ± 3.8 u and 26.8 ± 6.0 u respectively (Carpio 1991).

Based on a detailed study of teeth and bones found in those places, it has been postulated that the alpaca is a domestic form of the vicuña. Investigations have proven that the temporary and permanent incisors of the alpaca have the same morphology as those of the vicuña, which exhibit incipient roots and parallel borders, with enamel covering the superior lip surface, and are clearly different from those of the guanaco and llama (Wheeler et al. 1992). Nevertheless, other researchers studying morphological and behaviour variations between contemporary animals reached different conclusions. While it is postulated that the llama comes from the guanaco, the alpaca has been associated with a guanaco descendant, a vicuña, or a hybrid of llama and vicuña (Hemmer, 1990). Studies of cranial morphology concluded that the guanaco was the common ancestor of the llama and alpaca, and postulated that the vicuña was never domesticated (Herre 1952; Herre 1953). Additionally, studies in ethology concluded that the alpaca is the domesticated form of the vicuña (Steinbacher 1953).

In summary, studies based on archaeozoological samples are contradictory, but one of the most accepted hypotheses is that the guanaco is the ancestor of the llama and the alpaca, and that the vicuña was never domesticated (Fallet 1961; Kleinschmidt et al. 1986; Piccinini et al. 1990). All of these findings can be tested today with the study of molecular genetics like mitochondrial DNA and microsatellites (Harrison, 1991).

Molecular Studies

Molecular genetics uses methods such as mitochondrial DNA (mtDNA) sequencing and microsatellite and Y-chromosome analysis, has recently been used in order to examine the origins of modern domestic livestock, and makes possible the determination of genetic drift, selection and/or hybridization (Bradley et al. 1996; MacHugh et al. 1997; Hiendleder et al. 1998; Luikart et al. 2001; Vila et al. 2001; Gongora et al. 2004). The principle of the mtDNA technology is that it represents a small fraction of the total DNA in the cell and is only maternally inherited, while the remaining DNA is known as nuclear DNA and is inherited from both parents. Mitochondrial DNA analysis is widely used as a powerful tool to illustrate the evolution of species and to detect diagnostic markers which can discriminate between closely related species and populations (Kadwell et al. 2001). Microsatellite analysis measures the length of the alleles at a particular locus for each individual. Alleles are alternative forms of a gene, and every individual has two alleles at a specific locus, since one is inherited from each parent. If the alleles are identical, then the individual is homozygous for that locus, while the heterozygous individual would have different alleles at a specific locus. Allelic diversity represents how many different alleles are present throughout the population for each locus and, together with genetic heterozygosity, can provide a direct measure of genetic variability.

A recent study conducted by Kadwell *et al*., (2001), using mtDNA and microsatellite techniques supported the proposition that the alpaca is descended from the vicuña and suggested it be reclassified as *Vicugna pacos* instead of *Lama pacos*. This suggestion has been accepted by the scientific community. This important finding gives good perspectives on vicuña utilization, remembering that this species produces the finest fibre in the world - around 10 to 12.5 u in diameter, 3.2 to 4.0 cm long and with fleece weight of around 200 g shorn every 1-2 years. Recently, with its introduction to the international fibre market, an average price of US$ 850/kg is being paid, and thus represents a very attractive industry for Peru. One of the main problems in the past was that the vicuña was an endangered species due to over-hunting, but at the moment the current population in Peru is around 160,000 animals, which inhabit the Andes from 4,000 to 5,200 meters above sea level, corresponding to the Puna ecosystem (Ministry of Agriculture of Peru, 2004). In 1965 the population of vicuñas went down to between 5,000 and 10,000, and this was one of the reasons that the Peruvian government developed a project for conservation of the species in Pampa Galeras. In 1994 the estimated population grew to 65,000 animals. Today the vicuña population has been stabilised. The Pampa Galeras National Reserve in Ayacucho, Peru constitutes one of the largest reserves of vicuñas in the world which are being used rationally, and has been in operation for the last 10 years.

It is important to mention that the vicuña is being utilised by Andean people as it was in the time of the Incas. Every year in June the nearby community captures the vicuñas in a festive ceremony called “El Chaco” or “Chakku”, and carefully removes their fleeces and then releases them to the mountains. In the past hundreds of people participated in this activity, but today fences are used to make capture easier. The Peruvian government implemented this activity again 10 years ago and it has been operating ever since. The production of vicuña fibre in 2002 was 4.1 tons and it was exported without any processing. It has been reported that a scarf made with vicuña fibre cost around US$ 2,000 in one of the most exclusive boutiques in London (El Comercio, 2005). There is scope for entrepreneurs to invest in the processing of vicuña fibre in Peru into high quality clothes for the international market, thereby adding more value to the export and benefiting the communities that have vicuñas .

Another important fact is that molecular genetics studies have confirmed the occurrence of extensive hybridisation between llamas and alpacas, probably beginning at the time of conquest and continuing to the present day. A result of this is the degeneration of quality and value in present-day fibre, and probably also poor reproductive performance. It is well known that alpaca semen is poor in concentration and motility, and exhibits high viscosity in comparison with other domestic species like cattle and sheep. This could be related to extensive hybridisation with llama and the high degree of inbreeding. It is also possibly a natural characteristic of inducer ovulators. In the female alpaca the stimuli of copulation initialise the LH surge 15 minutes later, and ovulation occurs 30 h later. The semen then has more chance to reaching the oocyte than in species that are spontaneous ovulators. This may be evolutionary adaptation. It might be interesting to sample different animal populations to determine semen characteristics, making comparisons between herds that have been exposed to a selection process and those which have been hybridised, to elucidate if sperm quality can be affected.

There are two types of hybrids that have been described above. The first is the result of breeding a male llama with a female alpaca, and is known as “Huarizo”. The second is less frequent and results from the crossbreeding of a female llama and a male alpaca and is known as “Misti”. This crossbreeding is a reflection of socio-economic factors, as in the last 25 years the Peruvian textile industry has paid herders not by the fineness of the fleece but by its weight. The heavier the fleece, the better the price. This is a powerful reason why alpaca producers in the Andes hybridise their alpacas with llamas. This way they obtain a heavy fleece, and thereby increase their low income, but this has been catastrophic for the fibre quality. Today this tendency is changing and the most important textile industries are starting to pay for fleece by its fineness.

DNA technology is a valuable technique for identifying and eliminating hybrid animals from the breeding pool, since the antiquity of the ongoing hybridization process makes it impossible to accurately identify all hybrids on the basis of phenotypic characteristics. Hybrid animals can still be useful as receptors in embryo transfer programs. Another application of the DNA technology is to certify the purity of the breeders to be assigned to artificial insemination programs. To that end Dr. Wheels has been working at the San Marcos University in Lima, Peru on a test to determine purity, but the current price of the test is a limitation. The cost is currently around US$200, but in the future they are expecting to reduce this cost to US$50.

Now that we know that alpacas derive from the vicuña, a very interesting and promising approach could be to crossbreed a female alpaca with a male vicuña, producing the “pacovicuña” that produces fibre as fine as the vicuña but with a higher yield. There are no studies evaluating productive and reproductive performance of these crossbreeds, but it seems a promising idea in order to improve fleece finenesses and quality in the alpaca. On the other hand, these crossbreeds could be useful to rescue the genes that the alpaca has lost through hybridization with the llama, but techniques would have to be developed to collect semen/ eggs from vicuña donors and to facilitate *in vitro* production of embryos. While there are possibilities here, there is still a lot of basic research to be done on alpaca reproduction, especially on semen collection and preservation, time of ovulation and artificial insemination. This could prove in the future to be a viable tool of genetic gain.

Implications for the Alpacas Industry

In summary, the knowledge that the alpaca is descended from the vicuña through the analysis of the archaeozoological samples and the development of DNA techniques to determine whether the animals are pure or hybrids allows us to conclude that there are great opportunities for the alpaca industry to improve fibre quality through an efficient selection system. Work on vicuña may also yield techniques to recover the genes that have been lost in the hybridisation process. It will be necessary to develop DNA tests of purity of alpacas, maybe via a joint venture between private industry and universities/ research centres, and to use DNA tests to select males as breeders, in order to disseminate the right genes through the herd. Another characteristic that could be used as a selection criterion for sires would be semen quality. This could be determined by recently developed collection techniques (Vaughan 2003), and by taking into account fibre diameter and conformation as well. It could be possible to develop a fecundity test at the laboratory using alpaca semen in an *in vitro* production system. It will also be necessary to use DNA tests for designating female alpacas as donors for superovulation and embryo transfer programs.

Further studies need to be conducted to determine how hybridization has affected productive and reproductive parameters in alpacas, and also to evaluate the possibility of putting back fibre-fineness genes into the alpaca herd through crossbreeding with vicuñas.

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