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Spectrum of Camel Evolution and its Impact on Ancient Human Migration

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Abstract

The Evolutionary history and domestication of Camels are largely unexplored because of the lack of well dated early archaeological records. However, limited records suggest that domestication of Camels likely happened in the late second millennium BCE. Over the time, camels have helped human for their basic needs like meat, milk, wool, dung to long routes transportation. This multifaceted animal has helped the mankind to connect through continents and in trade majorly through the Silk route. In India, both dromedary and Bactrian camels are found and their habitat is entirely different from each other, dromedaries inhabit in hot deserts and Bactrians are found mostly in cold places (Nubra Valley, Ladakh). Fewer studies on Indian dromedaries have been conducted but no such studies are done on Bactrian camels. It is needed to study the genetics of Bactrian camels to find out their genetic affinity and evolutionary history with other Bactrians found in different parts of the world. Furthermore, parallel studies on humans and Bactrian camel are required to understand the co-evolution and migration pattern of humans during their dispersal in different time periods.

Keywords: Bactrian camel, Last Glacial Maximum, Million Years Ago, Human migration

Milieu

Camels have survived and adapted to earth's most crucial changes and also played a pivotal role in human survival since ancient times as they facilitate trading as well as cultural exchange. Moreover, camels are considered as 'the most adaptable travelers' considering their time to time adaptations with the crucial changes in the climate. There are three extant species of the camel *viz*. one-humped dromedary (~94% of the total camel population), two-humped Bactrian camel (6% of the camel population) (Wu et al., 2014) and the Wild Bactrian camel which is considered as a separate species and has been included in the list of critically endangered species (Kaczensky et al., 2014). The most accepted classification of the family Camelidae is presented in the figure 1.

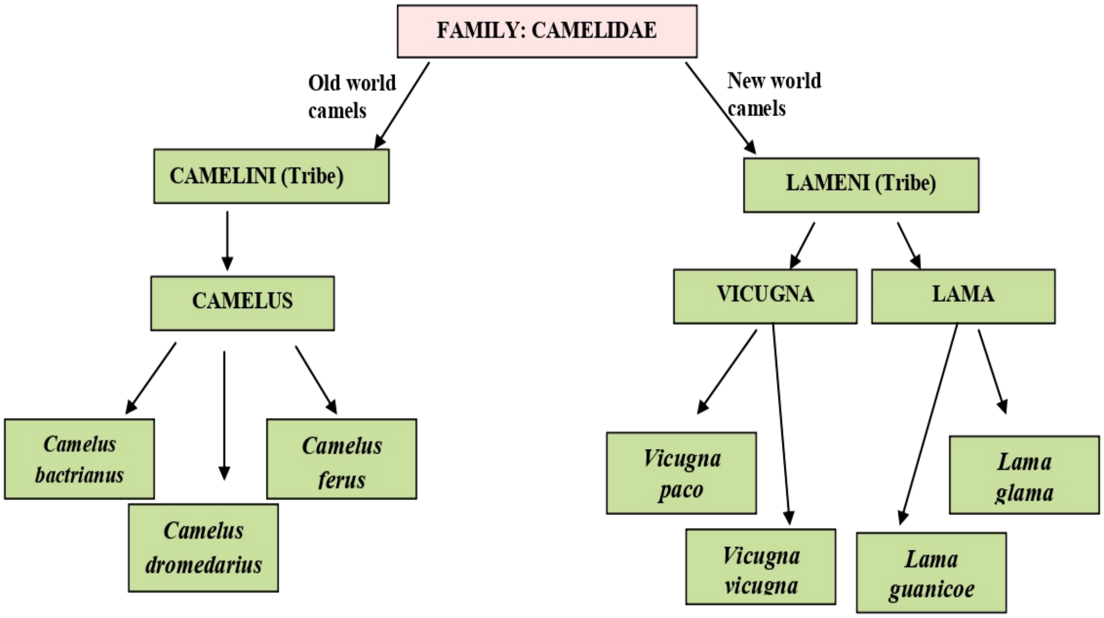

Figure 1: Classification of Camels; Source: (Wu et al., 2014)

In quest of camel as most adaptive life-form it becomes pertinent to understand the chronological evolution of camels that may also provide some insight towards the palaeo-geography and climate; their impact on phenotypes and migration pattern of other life form especially humans.

Adaptive Camel Evolution in Chronological Epoch

Origin of camels traces back to the Eocene period about 40-45 million years ago in North America (P. A. Burger, 2016). Of the entire Cenozoic, early Eocene epoch had the highest mean annual temperatures and high ice free precipitation. Protylopus, the most primitive camelid which occurred in the Eocene, having no hump and were of the size of a hare (Rybczynski et al., 2013). During this period, a significant plate boundary rearrangement occurred due to the tectonic shifts that resulted in major effects on atmospheric temperature. A major event of global cooling was observed during the middle Eocene due to the creation of circum Antarctic current created during separation of Antarctica and Australia (P. A. Burger, Ciani, & Faye, 2019). The end of Eocene was marked by lower temperatures and increased seasonality that resulted in alteration in the type of vegetation to savanna-like and increased body size of mammals. Further, camelids evolved and Proebotherium, a camelid found in the middle of Oligocene and Miocene around 35 million years ago, was about the size of a goat having long neck that would helped them in approaching comparatively higher vegetation with no hump like the previous ones. Further, evolution of camelids took place into procamelus which survived from Oligocene to Miocene. This was the period when cooling of the earth took place and has resulted in many changes like replacement of dry savannah vegetation to steppe.

Owing to these changes in the environment during the end of Miocene and the beginning of Pliocene, camelids evolved into much larger sized body with long neck than their predecessors. Around 25 million years ago, due to the bridging of North and South America, many camelids migrated. Those who migrated to the north and west (Tribe Camelini) through Bering Strait are evolved into extant Bactrian and Dromedary Camels where as those who drifted to the south (Lamini) via Panam’s Isthmus are ancestors to the new world camels (Llama, Vicuna, Guanaco, Alpaca) (Al-Swailem et al., 2010; P. A. Burger, 2016).

It is believed that the Paracamelus has evolved into the modern *Camelus* (Yam & Khomeiri, 2015). One-humped modern dromedary is supposed to be evolved from the two-humped bactrian species, *i.e., Camelus bactrianus* having thick coat that can withstand very low temperature. It has been reported that around 2 million years ago, Bactrian somewhat similar to modern bactrian, having a height of about 7 feet might had evolved from the Procamelus/ Paracamelus camelids that had moved into the arctic regions of Asia through the Bering Strait (P. A. Burger et al., 2019). The evidence of their movement can be evidences by fossils of giant camels *e.g.* Procamelus that have been reported from Asia (Flynn, 1997), North Africa (Peters & Driesch, 1997), Europe (Pickford, Morales, & Soria, 1995) and Arabian Peninsula (Martini, Costeur, Le Tensorer, & Schmid, 2015). Central Asian countries like Mongolia, China, Afghanistan, Kazakhstan, Russia, Uzbekistan occupies the major Bactrian population whereas few have also been reported in India, Northern Pakistan, Iran and Turkey (P. A. Burger et al., 2019).

Table 1: Evolution of Camels in Different Epoch

EOCENE	OLIGOCENE	MIOCENE	PLIOCENE	PLEISTOCENE
56-39 MYA (Warm to ice house climate)	**33.9-23 MYA** (Increased global cooling and ice cover)	**23.03-5.332 MYA** (Slower global cooling and moderately warm**)**	**5.332-2.558 MYA** (more cooler and arid over the course of time)	**2.558-11,700 YA** (Ice age)
Protylopus ***P. petersoni*** ***P. annectans*** ***P. pearsonensis*** ***P. robustus*** ***P. stocki*** Very small size, 2ft tall, Low crowned teeth, no hump				
	Probotherium ***P. wilsoni*** ***P. chadronensis*** ***P. eximium*** ***P. franki*** ***P. labratum*** Larger than Protylopus 3ft tall, Long neck Angled front teeth, no hump			
		Procamelus ***P. angustidens*** ***P. robustus*** ***P. occidentalis*** ***P. gracilis*** ***P. leptognathus*** Around 4.3 ft tall, pair of small incisor teeth among the other large teeth in the Upper jaw		
			Paracamelus ***P. agguirrei*** ***P. alexejevi*** ***P. gigas*** ***P. khersonensis*** Double the size of modern camel Wide flat feet and hump	
				Camelus ***C. bactarianus*** ***C. dromedaries*** ***C. gigas*** ***C. hesternus*** ***C. sivalensis*** ***C. moreli*** 6-7 ft tall, Widened toes, have hump

MYA- Million Years Ago

Source: ("Camels the most undervalued invaluable creature," 2014).

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Several studies have reported that the wild Bactrian species and the domesticated Bactrian population have different maternal origins where the divergence of the subspecies occurred around 0.7 million years ago (P. Burger, Charruau, & Enkhbileg, 2012). Members of the Lamini tribe (Llama, Vicuna, Guanaco, Alpaca) are indigenous population of South America of which Guanaco and Alpaca are wild which appeared about 10.4 and 6.4 million years ago respectively whereas Llama and Vicuna are the domesticated ones (Wu et al., 2014). Although, above stated studies impending towards the presence of camels in different epochs (summarized in table 1), their contemporary distribution of new and old word camels and their different species are listed in table 2. The presence of different species of camels in Pleistocene to present period and that too in different climatic conditions (table 1) evolving through natural selection (table 1) make camels an interesting life form, if studied with respect to evolutionary perspective, that may have implication on human migration.

Table 2: Global Distribution of Old World and New World Camels

	Species	**Present location**
Old world Camels	Bactrian Camel	Cold deserts of China (Taklamakan, Lop Nur Desert), Mongolia (Gobi Desert), India (Nubra Valley, Pratapur, Leh-Ladakh), Northern Pakistan, Russia, Kazakhstan, Uzbekistan
	Dromedary Camel	Africa-Ethiopia, Somalia, Sudan, Djibouti and Kenya, Australia
New world Camels	Llama	Native to South America (central Andes), Peru, northwestern Argentina, Bolivia, and northern Chile.
	Vicuna	

Source: ("Camels (extant/living species; Camelus spp.): Distribution & Habitat," 2009-2019; Lamo et al., 2020)

Presence of Camels, their domestication and putative impact on Human Migration

The most remarkable characteristic of the camels is their adaptation capability favored by natural selection, they have undergone deep historical events of climatic changes (glacial periods to their survival in arid conditions). Their unique physiological and morphological characters to provide the essential products like milk, meat, transportation and dung under extreme conditions made them ideal as military animals, incense roads and domestication (Bulliet, 1990; P. A. Burger, 2016). The domestication of Bactrian camel was estimated to be near the beginning of third millennium (Bulliet, 1990) whereas domestication of dromedaries were estimated in the late second millennium (Uerpmann & Uerpmann, 2002). The domestic camels were important being multi-purpose in civilizations of the old world and even today, evident by mitochondrial genetic profile of the camels that reflects their movements and extreme trade (P. A. Burger et al., 2019). However, the exact region for the domestication remains uncertain but with the advent of high throughput sequencing techniques, the researchers have been able to detangle the mystery by analyzing the data from the domesticated and wild Bactrian camels from Asia. The study supported that the origin of domestic Bactrian camels from Central Asia which later on migrated eastwardly to Mongolia (Ming et al., 2020). In same year, whole genome sequencing study with an objective to identify the genome-wide variations in Bactrian camels of Iran and also compare them with other domestic as well as wild Bactrian camels inhabited in different geographical locations has been reported. Around 4.9 million (Iranian), 4.4 million (Mongolian), and 4.7 million (Wild Bactrian) SNPs have been identified where as 0.3 million to 0.5 mllion INDEL (insertion-deletion) variations have been observed. Most SNPs are missense in zinc finger (98) and four fertility-related genes but lack information about geogrpahical distinct species (Hedayat-Evrigh, Khalkhali-Evrigh, & Bakhtiarizadeh, 2020).

Camels have special position in trade history through the famous Silk route, in cultural dialogue between three continents by connecting the Arabian Peninsula with the Sahara and the Levant to the Far-East and Asia, with northern Arabia at the crossroads and human migrations (Almathen et al., 2016). The movement of humans parallel to dromedaries have also been studied, highlighting effective migration patterns of the global dromedary population, also the paths of dispersal after domestication, mirrors the ancient caravan routes (Lado et al., 2020). The movement of dromedaries parallel to humans and genetic admixture detected in Asian and African populations strongly indicates anthropogenic influence. For the development of mankind domestic animals have always played an essential role. The cultural and genetic exchange through trade have influenced the gene flow, this highlights that it is necessary to extensively study ancient genome along with the existing camel species throughout the trade route and merging the study with the ancient and modern DNA of humans. Since this species existed much before humans and had been extensively used over millennia for trade and had opened corridors for gene flow which has shaped the genetic diversity in Bactrian and in dromedaries camels also other livestock species (Edwards, Baird, & MacHugh, 2007; Fages et al., 2019; Ming et al., 2020). Since no such study has been carried out on Indian Bactrian/dromedary camel, extensive sampling and genome wide analysis is needed to be conducted to fill the void in the literature. It will deepen our knowledge about the genetic diversity and genetic architecture of camels present in India.

Both Bactarian and Dromedary camels have been found in India but have occupied different habitats; where Bactarian species are found in cold desert, dromedaries are inhabitants of hot desert. The species of single hump dromedary camels are found in western desert of India (Rajasthan and Gujarat) are Bikaneri, Jaisalmeri, Kutchi and Mewari (Mehta, Mishra, & Sahani, 2006). Double humped Bactarian species of Camel is only found in cold arid region of Nubra valley of Ladakh. These species were the main mode of transport via silk route due to their adaptability to lowest temperatures, scarce feeding and water availability (Gazi, ul Nabi, & Ahmed, 2013) and it is believed that these belong to group of camels which left here in India due to the closure of Indian Tibet border due to the Chinese aggression (Banerjee, Joshi, Ganai, & Vijh, 2012). It has been reported that around 220 Bactarian camels are found in Ladakh which is quite a less number (Gazi et al., 2013). Extensive research has been performed on the Indian dromedaries like genetic characterization, nutrient utilization, hormonal patterns, reproductive features etc. which has led to their better breeding and management (Agarwal, Khanna, Agarwal, & Dwaraknath, 1986; Agarwal, Khanna, Agarwal, & Dwaraknath, 1987; Gautam, Mehta, Gahlot, & Gautam, 2004; Khanna, Tandon, & Rai, 1990; Mehta, 2013; Mehta et al., 2006; Nagpal & Patil, 2013; Nagpal, Rai, & Khanna, 1993). On the contrary, very few studies have been conducted on the Indian Bactrian camel when compared to the dromedaries. In order to observe the genetic diversity we tried to perceive the genetic data from different geographical locations of camels in different databases and observed that most of the studies are focused on whole mtDNA genome, very less on Y chromosome and recently researchers were able to generate whole genome data from limited locations. The phylogentic tree from whole mtDNA of camel from different geograhical was drawn. It has been observed that scant work has been carried out on Indian camels at molecular level. The study conducted on Indian Bactrian camel, based on microsatellite loci reported quite a good level of heterozygosity in them that could be exploited by implementation of strategies for conservation and by checking inbreeding (Banerjee et al., 2012). Moreover, other studies like morphometeric characterization, analysis on reproductive status, hematological, physio-biochemical analysis of Bactrians in India have also been done but needed to be explored for the proper camel husbandary as well as management of their health and also for the future research projects (Gazi et al., 2013; Lamo et al., 2020; Vyas et al., 2015).

As discussed earlier, it has been reported that the Bactrians in India are the left out population but there are no concrete evidences at the molecular level which could detangle and confirm the ancestory and evolutionary history of these double hump camelids found in India. By implying different genetic studies like exploring mitochondrial DNA, microsatellite markers, whole genome sequencing, we can determine their origin and genetic diversity which will help us in understanding the pattern of gene flow and phylogeography of the Indian double humps with that of the other Bactrians found in different geographical locations. Further, the genetic data for the different species of camels in India required to be analyzed and comparision with other populations of camels present in different geographical locations is essential to observe the diversity of Indian camels (both dormedry and bactrian) at different time scale. It will be interesting to explore the direction of selection of genes that aided this living being to survive in extreme conditions. Additionally, by comparing the migration pattern of camels along with humans can also aid in tracing the missing link of human gene flow especially the South Asian populations where these beings are believed to be exploited for migration due to their multiple charactertics and high endurance towards extreme conditions. This will also help in knowing the clearer relationship between camel and human, their domestication and migrating from Africa to other parts of the globe. Effective population size of Bactrian camels was reduced upto 70% around 100,000-20,000 Years Before Present (P. A. Burger, 2016), it is also been found that during the same time period a diverged population from modern humans, who have contributed to ancestoral human populations (Kuhlwilm et al., 2016) could have utilized these camels as source for survival. To have a deeper insight into this hypothesis, ancient DNA/fossil studies of double humped camels and humans along with the migration routes followed by the early humans migrating “out of Africa” is needed to be explored and studied extensively.

Humans have started domesticating animals about 13000 years ago (Diamond, 2002). Understanding human evolution in context to the human migration could not be possible without understanding the migration patterns of the domesticating animals, since domesticated animals and human share common migration patterns because of their interdependency. A study carried on mtDNA of 781 ancient and mordern *Sus* speciemens revealed, human mediated dispersal of Sulawesi warty pig (*Sus celebensis*) and domestic pig (*Sus scrofa*) through Southeast Asia into

Oceania (Larson et al., 2007). It because of the domestication of animals, that led humans to change from hunter-gatherer into sedentarty agriculture lifestyle and also led to the development of societies (Frantz, Bradley, Larson, & Orlando, 2020). Dispersal of dogs back 11,000 years ago was also supposed to have took place along with humans. Humans have domesticated dogs and took them to different parts of the world during migration (Callaway, 2020). These studies proved that humans and domestic aniamls have something common in their migration pattterns. Taking these hypothesis into consideration, it becomes pertinent to explore the dispersal of camel population which may help us in understanding the pattern of human migration to some extent.

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