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# Genetic relationship among camels of India based on microsatellite data

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## ABSTRACT

The microsatellite data on 4 breeds of dromedarian camel, viz. Bikaneri, Jaisalmeri, Kutchi and Mewari were analysed using Bactrian camel as an out-group. The genetic distances estimated included the distances based on allele frequency, purely geometric and arithmetic distances as well as genetic distances based on allele size (number of repeats). The genetic distances were utilized for construction of the phylogenetic trees using UPGMA and NJ algorithms. The genetic distances revealed very little differentiation among the 3 camel breeds, viz. Bikaneri, Jaisalmeri and Kutchi. The Mewari breed of camel was distinctive and the differences in allele frequency of this breed with other 3 dromedary breeds was attributed to small population size, inbreeding, drift and decreased gene flow.

**Key words**: Bactrian camel, Dromedarian camel, Genetic distance, Microsatellites, Phylogenetic tree

India possesses nearly 3.3% of the total camel population of the world with approximately 0.63 million camel. The camels of India are dromedarian (*Camelus dromedarius*) or single humped. However approximately 100–120 double humped camels (*Camelus bactrianus*) are also present in the Nubra valley and are feral. Bactrian camels are the remnants of the old silk route. The Bactrian is quite different from its single-humped counterpart. The camels of India are primarily categorised in 4 breeds: Bikaneri, Jaisalmeri, Mewari and Kutchi (Vijh and Sahai 2000). Generally, the approach to determine the relationships among breeds consists of estimating genetic distances from the allele frequency data and construction of trees depicting their relationships. There are very few reports of relationship among different dromedarian camels (Vijh *et al.* 2007). A detailed analysis of the genetic distances among different dromedarian and Bactrian camel of India is lacking.

### MATERIALS AND METHODS

The samples of 4 major breeds of dromedarian camel of India, viz. Bikaneri, Jaisalmeri, Kutchi and Mewari, were collected at random from their respective breeding tracts. The samples were collected in heparinised vacutainer tubes and transported to lab at 0–5°C. The samples from 10 Bactrian camel were collected from the Nubra valley of Jammu and Kashmir.

DNA was extracted from whole blood using standard

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protocol (Sambrook *et al.*1989). The quality of DNA was checked on 0.6% agarose gel prepared in TAE buffer. In this paper the data on 27 microsatellite loci, viz. CMS121, CMS13, CMS58, LCA18, LCA63, VOLP08, CMS50, CVRL04, CVRL05, LCA90, VOLP10, YWLL44, CMS16, CVRL01, CVRL06, LCA66, VOLP67, YWLL09, CVRL02, CVRL07, CVRL08, YWLL08, YWLL38, VOLP03, VOLP32, LCA37, LCA77 generated for 4 dromedarian breeds/populations comprising 148 camels and 10 bactrian camels were utilized to estimate the genetic distances among various breeds. The genetic distances were estimated based on geometrical and arithmetic considerations as well as genetic distances based on Infinite Allele model and Stepwise Mutation Model of microsatellite evolution. The loci were amplifiable in camel.

The PCR amplification was carried out in 25 μl reaction volume consisting of 50 ng genomic DNA, 1.5 mM $MgCl_2$, 200 μM dNTPs, 5 p mol of each primer, and 0.5U of Taq. The PCR reaction was carried out in GeneAmp 9700. The thermocycling conditions utilized were initial denaturation at 94ºC for 4 min, followed by 30 cycles of 60 s at 94ºC, 45 s at annealing temperature, and 60s at 72ºC. The final extension at 72ºC was prolonged for 10 min. The samples were analyzed using automated DNA Sequencer with Liz 400 as internal lane standard. The data was collected and analyzed using GeneScan and Genotyper software of ABI Prism, automated DNA sequencer.

*Statistical analysis*

Some of the genetic distances depend solely on

multidimensional geometric considerations without reference to a particular evolutionary model (IAM or SMM). These distances however perform well for reconstruction of phylogenies when the populations are of the same species or taxa and are very closely related. Amongst the distances are Cavalli-Sforza and Edward's (1967) Chord distance, Nei's *et al.* (1983) distance $D_A$ and Stephen's *et al.* (1992) allele sharing distance, $D_{AS}$. These genetic distances make use of the product of allele frequencies shared between the populations and have been shown to reconstruct closely related phylogenies better than SMM based genetic distances (Goldstein, *et al.* 1995a,b, Takezaki and Nei 1996). Their accuracy at short distances stem from their use of information available in the degree of overlap of allele frequency.

The allele frequency data were subjected to analysis for the estimation of genetic distances. We utilised several genetic distances based on the Infinite allele model and Stepwise Mutation Model of microsatellite evolution. We also utilised the genetic distances based on the geometrical and mathematical models. We estimated a large number of genetic distances as the appropriateness of each of the genetic distances shall be based on the data utilised and the most appropriate genetic distance is not easily discernible.

Let $ij$ $p$ and $ij$ $q$ be the frequencies of $i$ th allele at the $j$ th locus in populations $X$ and $Y$ respectively, while $j$ $a$ is the number of alleles at the $j$ th locus, and $m$ is the number of loci examined. Geometric distances are not negative, symmetric and satisfy the triangle inequality. The common distance is the Euclidean distance, defined as:

$$D_{EU} = \frac{1}{m} \sum_{j}^{m} \sqrt{\sum_{i}^{a_j} (p_{ij} - q_{ij})^2}.$$

Rogers's (1972) distance is a scaled Euclidian distance:

$$D_R = \frac{1}{m} \sum_{j}^{m} \sqrt{\frac{1}{2} \sum_{i}^{a_j} (p_{ij} - q_{ij})^2}$$

Prevosti *et al.*'s (1975) distance has statistical properties similar to those of $D$ $R$ and is defined as:

$$C_p = \frac{1}{2m} \sum_{j}^{m} \sum_{i}^{a_j} | p_{ij} - q_{ij} |.$$

Cavalli-Sforza and Edwards' (1967) distance gives the chord distance between the 2 populations if we represent 2 populations on the surface of a multidimensional hypersphere using allele frequencies at the $j$ th locus:

$$D_C = \frac{2}{\pi m} \sum_{j=1}^{m} \sqrt{2(1 - \sum_{i=1}^{a_j} \sqrt{p_{ij} q_{ij}})}.$$

Bhattacharyya (1946) and Nei (1987) recommended that the distance between the 2 populations be measured by

$$\theta^2 = \frac{1}{m} \sum_{j=1}^{m} (\arccos \sum_{i=1}^{a_j} \sqrt{p_{ij} q_{ij}})^2.$$

The Sanghvi distance (Sanghvi 1953) was derived from chi-square goodness-of-fit statistics, and the distance is defined as:

$$X^2 = \frac{2}{m} \sum_{j=1}^{m} \sum_{i=1}^{a_j} \frac{(p_{ij} - q_{ij})^2}{(p_{ii} + q_{ii})}.$$

Nei *et al.*'s (1983) *D A* distance:

None of the geometric distances described above involve any evolutionary models. Assuming that there is no mutation, and that all gene frequency changes are by genetic drift alone, the following two quantities are expected to rise linearly with amount of genetic drift.

Cavalli-Sforza's chord distance (1969) is given by:

$$f_v = 2 \sqrt{\frac{\sum_{j=1}^{m} \left(1 - \sum_{i=1}^{a_j} \sqrt{(p_{ij} - q_{ij})^2}\right)}{\sum_{j=1}^{m} (a_j - 1)}}.$$

Reynolds, Weir, and Cockerham's (1983) genetic distance (ignoring the terms involving sample size $n$) is (Reynold's

$$J_X = \sum_{j=1}^{m} \sum_{i=1}^{a_j} p_{ij}^2 / m, J_Y = \sum_{j=1}^{m} \sum_{i=1}^{a_j} q_{ij}^2 / m, J_{XY} = \sum_{j=1}^{m} \sum_{i=1}^{a_j} p_{ij} q_{ij} / m$$

$$2 \sum_{j=1}^{m} (1 - \sum_{i=1}^{a_j} p_{ij} q_{ij})$$

Nei's (1972) standard distance has an expected value linearly related to the time since divergence, assuming that all loci have the same rate of neutral mutation, and that the genetic variation is maintained by the equilibrium between infinite-alleles mutation and genetic drift, with the effective population size of each population remaining constant.

The quantity is defined as:

$$D_S = -\ln(J_{XY} / \sqrt{J_X J_Y}),$$

where,

Nei's (1973) minimum genetic distance ($D_m$), Latter's (1972) $\varphi$ * distance, and Latter's (1973) $D_L$ distance are all defined similarly:

$$D_m = (J_X + J_Y)/2 - J_{XY}$$

$$\phi^* = \frac{(J_X + J_Y) - J_{XY}}{1 - J_{XY}}$$

With the step-wise mutation model (SMM) assumption, Goldstein *et al.* (1995[a,b]) proposed several genetic distance for microsatellite loci

where,

$$\mu_{X_j} (= \sum_k k p_{kj}) \text{ and } \mu_{Y_j} (= \sum_k k q_{kj})$$

are the average numbers of repeats found,

and $kj\ p$ and $kj\ q$ are the frequencies of the allele with $k$ repeats at the $j$ th locus in population $X$ and population $Y$, respectively.

A distance measure closely related to $(\frac{1}{4})^2$ is the average square distance (*ASD*, Slatkin 1995), which is given by

Another related distance measure utilised in the present study is of Shriver *et al.* (1995) distance, defined as

where,

$$W_{XY} = \frac{1}{m} \sum_{j=1}^{m} \sum_{u,v} |u - v| p_{uj} q_{vj}$$

where, $P_{Uj}$ and $P_{Vj}$ are the ith and jth alleles at a locus in population U and V.

Another commonly used distance, the shared allele distance $D\ SA$ (Chakraborty and Jin 1993), is defined as:

The measure $D_{LS} = -\ln(1 - D_{SA})$ (usually referred as log shared allele distance) was also applied on microsatellite data on camels.

The dendrograms were prepared using distance matrix and using Unweighted Pair Group Method with Arithmetic mean (UPGMA) and Neighbour Joining (NJ) algorithm. The dendrograms were prepared for all the distance methods taking populations and individuals as units. Bootstrapping was used to generate increased confidence in the tree constructed from the original data. This procedure was used

as suggested by Felsenstein (1985) for use of bootstrap sampling for parsimony analysis. Multiple new datasets were generated by re-sampling with replacement over loci, where each locus is assumed to provide an independent estimate of the evolutionary history of the camel breed/population under study. The information about the tree defined by each new data set was then compared to the tree defined by the original data.

## RESULTS AND DISCUSSION

The present study included 148 dromedarian camels and 10 bactrian camels, which also acted as an out-group. The camels were genotyped for 27 microsatellite loci. Out of 27 microsatellite one microsatellite loci LCA77 was monomorphic in both Bactrian and dromedarian camel while one locus CVRL07 was found to be monomorphic in Bactrian camel. The locus LCA77 was polymorphic in African camel (Nolte *et al.* 2005). We utilized 15 genetic distance measures in the present study, which can be classified into 2 main groups: the distances based on allele distributions of frequencies – Euclidean and angular distances and the genetic distances based on allele size distributions (number of repeats).

The genetic distance developed by Cavalli-Sforza and Edwards (1967) conceptualises the populations as existing as points in a m-dimensional Euclidean space, which are specified by m allele frequencies (i.e. m equals the total number of alleles in both populations). The genetic distances obtained have been given in the Table 1. The UPGMA tree constructed using the bootstrapping over loci joins the 3 breeds of Bikaneri, Kutchi, and Jaisalmeri together but the nodes are poorly supported with bootstrap values of 37 (Fig. 1). Mewari breed joined the 3 breeds with a bootstrap value of 100 showing it to be clearly distinctive. The Bactrian camel is an out-group. When individuals were taken as a unit and the neighbour joining tree is constructed the double humped camel comes out as an out-group while the dromedary camels cluster together (Fig. 2). The Roger's distance (Table 1) and subsequently the tree constructed joined Jaisalmeri and Kutchi at the first node followed by Bikaneri and Mewari (Fig. 3). The bootstrap values in this case were significant.

The genetic distances estimated using Reynold's procedure and Latter's distance which are based on small populations size and differentiation among the populations occurring due to actions like drift are given in Table 1. The UPGMA trees for Reynold's distance (Fig. 4) and Latter's
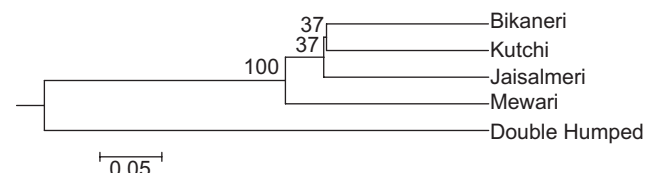


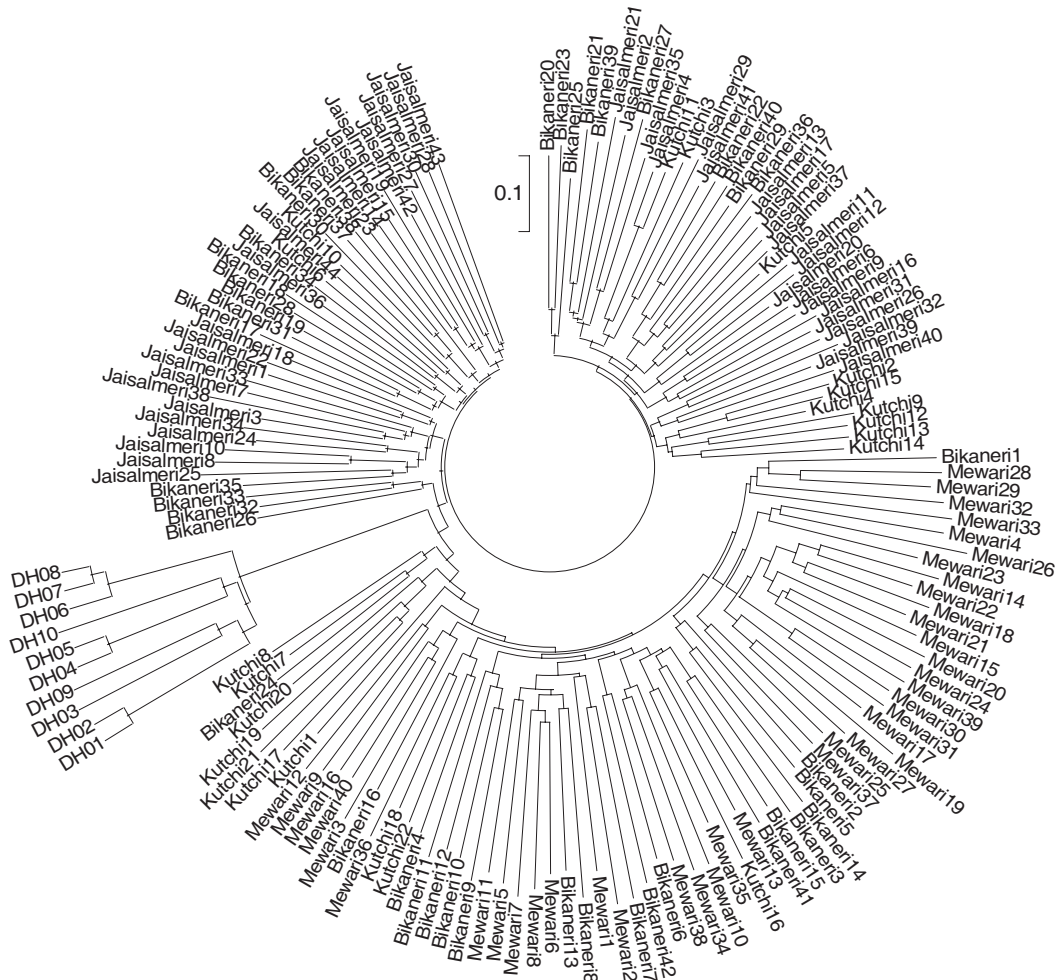Fig. 1. UPGMA tree based on chord distance.

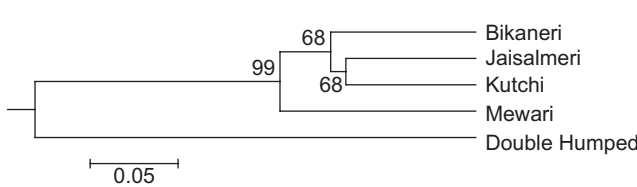Fig. 2. Circle tree constructed using NJ algorithm on the basis of chord inter-individual genetic distances



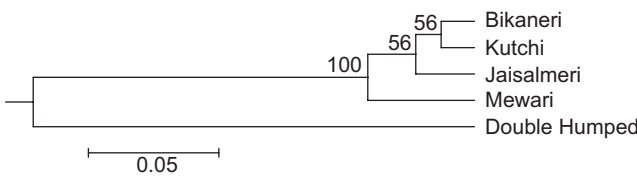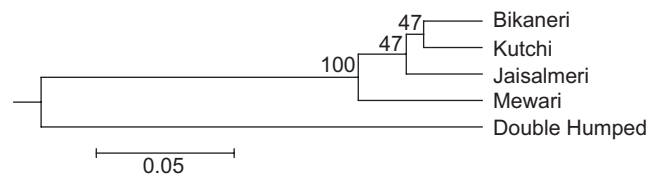Fig. 3. UPGMA tree with 1000 bootstrap over loci and using Roger's genetic distance.



Fig. 5. UPGMA tree with 1000 bootstrap over loci and using latter's genetic distance.

$F_{ST}$ (Fig. 5) are presented. In both the genetic distances Bikaneri and Kutchi join in the first node followed by Jaisalmeri camel. Both nodes have a bootstrap value of 56 (Reynold's distance) and 47 (Latter's distance). The values are nonsignificant in Latter's $F_{ST}$ and just significant for Reynolds distance. Mewari camel is distinctive in both the cases with a bootstrap value of 100%. The dendrogram obtained utilising Prevosti's distance (Table 1) were also similar (Fig. 6).

One of the simplest methods of estimation of genetic distance is based on the proportions of shared alleles (Bowcock *et al.* 1994). The distance was estimated between
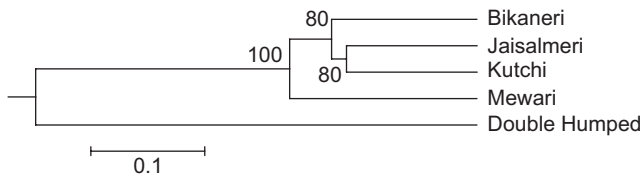


Fig. 4. UPGMA tree with 1000 bootstrap over loci and using Reynold distance.

Fig. 6. UPGMA tree with 1000 bootstrap over loci and using Prevosti 's genetic distance.
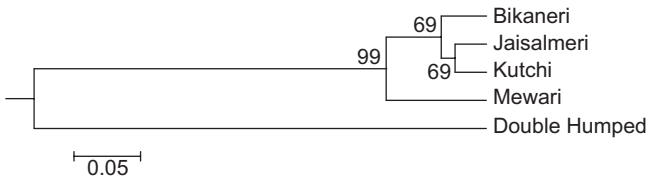


Fig. 7. UPGMA tree with 1000 bootstrap over loci and using allele sharing distance.

individuals as well as between the populations (Chakraborty and Jin 1993). For the individual pair-wise comparison the proportion of shared alleles was estimated and the distance is calculated utilizing (1–proportion of shared alleles). The inter-population distance estimated utilizing this genetic measure DSA. The values are given in Table 1. The genetic distance between the Bactrian camel and all the 4 breeds of dromedarian camel were the highest. Similar results were also obtained for log shared allele distances. Among the dromedary breeds the highest genetic distance was estimated between Mewari and rest of the 3 breeds. An UPGMA tree constructed (Fig. 7) with 1000 bootstrap over loci revealed the bactrian camel as an out-group. The inter-individual distances estimated on the basis of shared alleles and construction of a radiation tree exhibit the bactrian camel as an out-group and all the dromedarian individuals clustered together. The dromedarian camel formed 2 distinctive groups with 1 group having most of the camels belonging to Mewari and some Bikaneri camel. The radiation tree constructed
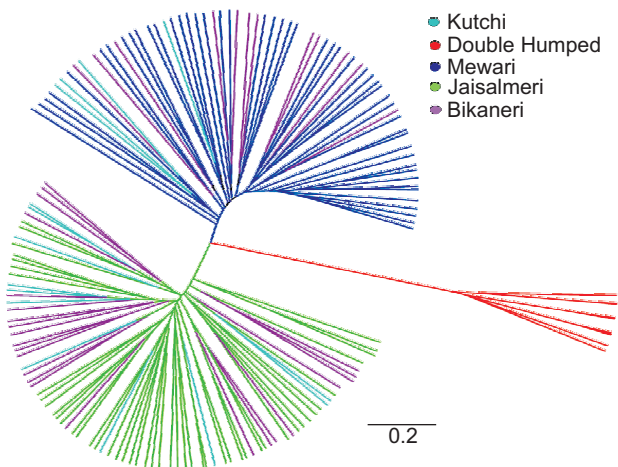


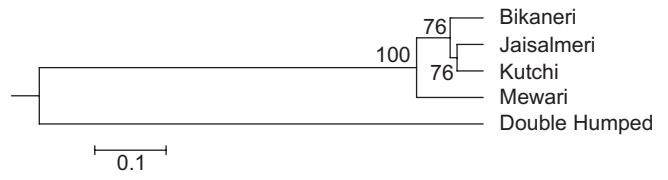Fig. 8. Radiation tree constructed using allele sharing distance and Neighbour Joining algorithm.



Fig. 9. UPGMA tree with 1000 bootstrap over loci and using Nei's Standard Genetic distance $D_S$

using the Neighbour Joining algorithm is presented in Fig. 8. The Mewari camels form a separate group with few camels of Bikaneri and Kutchi joining them. The rest of the 3 dromedarian breeds form a separate cluster.

The estimates of three Nei's genetic distances, viz. Standard ($D_S$), minimum (Dm) and $D_A$ are presented in Table 1 for the camel population and the dendrogram are presented as Figs. 9–10 and 11 respectively. Laval *et al.* (2002) compared the various genetic distances given by Nei and concluded that Dm and $D_S$ also depend on unknown parameters like founder frequencies. These distances cannot separate the effect of genetic drift occurring in each population and the ancient history of founder population. This fact can also disturb the phylogeny reconstruction mainly when migration or admixture does occur between the founder populations of these breeds. In these three genetic distances Mewari is distinctive and it is likely that it is the offshoot from the initial founder population which primarily consisted of the Bikaneri population.

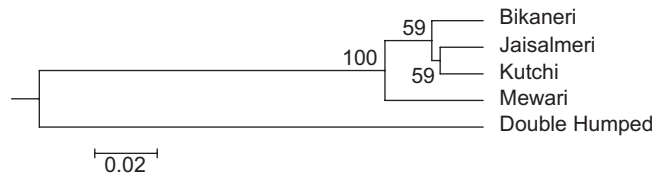The estimates of genetic distances based on the allele sizes



Fig. 10. UPGMA tree with 1000 bootstrap over loci and using Nei's minimum Genetic distance $D_{M.}$



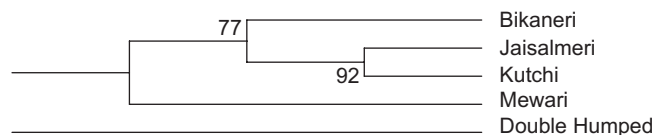Fig. 11. UPGMA tree with 1000 bootstrap over loci and using Nei's $D_A$ distance.

(number of repeats) are also given the Table 1 while the dendrograms are presented as Figs12–13, 14 for Goldstein, Shrivers' and Slatkin genetic distances. It is evident that the nodes among the 3 breeds of dromedarian camel, viz. Bikaneri, Jaisalmeri and Kutchi camel are poorly supported with poor bootstrap values of in the vicinity of 50% or less,
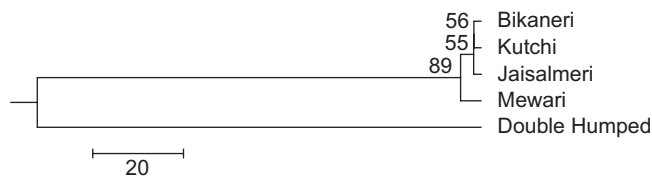
56 ┌ Bikaneri
55 └ Kutchi
89 └ Jaisalmeri
└ Mewari
└ Double Humped

20

Fig. 12. UPGMA tree with 1000 bootstrap over loci and using Goldstein's genetic distance (äì)$^{2.}$

53 ┌ Bikaneri
48 │ Jaisalmeri
94 │ Kutchi
│ Mewari
└ Double Humped
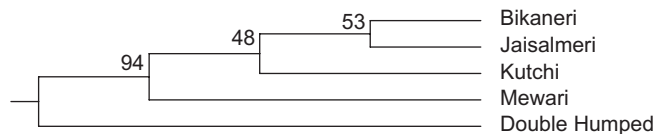
Fig. 13. Topology of camel based on Shriver's Genetic distance.

34 ┌ Bikaneri
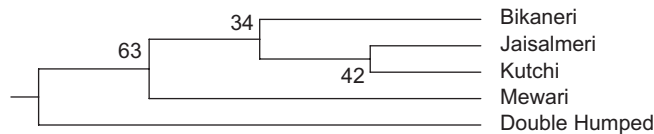63 │ Jaisalmeri
42 │ Kutchi
│ Mewari
└ Double Humped

Fig. 14. Topology of camel based on Slatkin's Genetic distance.

which gives credence to the similarity of the 3 camel breeds in terms of their allelic sizes (number of repeats). This can be attributable to free gene flow among different breeds and lack of population structure and also the geographical contiguity. Mewari has significant population differentiation with the other 3 dromedarian breeds. The differentiation can be due to their inhabiting hilly terrain and partial reproductive isolation due to their smaller body size. Laval *et al.* (2002) inferred that when drift is assumed the Latters' and Reynolds distances have to be privileged whatever the polymorphism of markers is used and the distance shall depend on the inbreeding coefficient of each breed. Similar can be the explanation for the Mewari camel.

Nei *et al.* (1983) suggested that the different distance measures should be used for constructing the topology of estimating the branch lengths. In general $D_A$ and $D_C$ are superior to other distance measures in topology construction and $D_S$ (Nei's standard distance) and $(dm)^2$ were better than other in branch length estimation (Takezaki and Nei 1996). Therefore it seems to be preferable to use $D_A$ and $D_C$ for constructing the topology and then using Ds for estimating branch lengths (Nei 1995). Takezaki *et al.* (1995) reported that the linear relationship with time was better for $D_A$ than for Chord distance $D_C$. Therefore a tree constructed for $D_A$ may be sufficient for many purposes unless the evolutionary time considered is very long. In the present case of 4 camel populations, belong to the dromedarian species, the evolutionary time cannot be long and thus $D_A$ genetic distance seems to be appropriate. In the present study on camel breeds which are very closely related the number of mutations cannot

explain the observed genetic variation even when highly mutable DNA sequences are used. The genetic drift allows genetic distances computed with allele frequencies to be strongly dependent on the number of generations since divergence and on the value of the effective sizes of breeds.

All the 4 genetic distance, viz. Nei's DA, Allele Sharing, Roger's distance, Prevosti's and Chord distance revealed similar pattern in terms of construction of tree and topology. The populations which have a contiguity of breeding tract (Bikaneri, Jaisalmeri and Kutchi) have low genetic distance compared with the genetic distance obtained for Mewari breed (Table 1). Goldstein *et al.* (1995a) using computer simulation compared the linearity of various genetic distance methods. The genetic distances $D_{AS}$ and Ds begin to asymptote in about 1000 generations. A log transformation of $D_{AS}$ was reported to improve the linearity only slightly. Takezaki and Nei (1996) have shown that Nei's $D_A$ is more efficient than Roger's distance and Chord distance in obtaining the correct topology. In this present study the NJ and UPGMA trees were constructed by using various genetic distance measures. The bootstrap values obtained in all the genetic distance were very high and close to 100% for the out-group and Mewari camels. This reveals that phylogenetic trees obtained in present case utilizing 26 polymorphic loci are reliable. Takezaki and Nei (1996) reported that the extent of sampling error is an important factor for determining the efficiency of a distance measure in phylogenetic reconstruction along with the linearity of time.

Indeed the location on the tree of the most recent common ancestor cannot be exactly determined when evolution rates vary between lineages. In order to infer the true history of these camel populations, it is necessary to root the tree using an *out-group*. The Bactrian camel in the present study is an out-group and it is known that the 2 species of camel hybridise among themselves and produce fertile offspring. More so the topology obtained was same in all the genetic distance measure utilized in the present study. The distances utilized were based on arithmetical and geometrical considerations utilising allele frequency data. The reliability of the tree was ensured by 100% bootstrap values for the out-group, which provided a measure of internal consistency of the dataset, and the number of loci (26) utilized in the study were sufficiently high to derive inferences in the relationship among the populations.

The inferences drawn in the present study have a definite impact on the conservation studies for the Indian camel, while it is evident that the selection of the camels for riding and carting purposes have been mostly on the basis of phenotypes and do not have any bearing on the genetic architecture. This can be due to lack of specialised breeding for production attributes as the owners have bred camels for multi-purposes especially when the environment in which the camels are reared have been uniformly harsh (Wilson 1997). In case of Mewari camel there is definitive change in the allele

frequencies which is attributed to drift, inbreeding and limited gene flow with dromedarians inhabiting the plains.

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