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Allozyme Variations and Genetic Differentiation in *Mesocricetus brandti* Nehring, 1898 and *Mesocricetus auratus* (Waterhouse, 1839) (Mammalia: Rodentia)

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Abstract: Allozyme variations were investigated by the electrophoretic analysis of 20 gene loci in 5 populations of *Mesocricetus brandti* and *Mesocricetus auratus* from Anatolia and Iran. Of the 20 loci analysed, 11 were monomorphic and fixed for the same allele in all 5 populations, 9 loci were polymorphic, and 1 locus differed between *M. auratus* and *M. brandti* populations. The overall mean of polymorphic loci for all the populations was 24.7% (range: 5.9%-41.2%). The mean fixation index value was F_{ST} = 0.0748, indicating a 7% genetic variation in the *M. brandti* populations. The obtained F_{ST} values indicated that there are moderate genetic differences between the populations of *M. brandti*. The finding that the number of migrants (Nm) was 3.09 also suggests effective gene flow across populations. The overall mean heterozygosity (Ho = direct count) for all populations (*M. brandti* and *M. auratus*) was 0.069 (range: 0.029-0.118 at different locations). The mean heterozygosity of *M. brandti* and *M. auratus* was Ho = 0.080 and Ho = 0,029, respectively. Nei's measure of genetic distance varied from D = 0.006 to D = 0.026 between populations of *M. brandti*. Nei's distances varied from D = 0.102 to D = 0.122 between *M. auratus* and *M. brandti* populations.

Key Words: *Mesocricetus* spp., allozyme, variation, Turkey

Mesocricetus brandti Nehring, 1898 ve *Mesocricetus auratus* (Waterhouse, 1839) (Mammalia: Rodentia)'da Allozim Varyasyonları ve Genetik Farklılıklar

Özet: Anadolu ve İran'da yayılış gösteren *Mesocricetus brandti* ve *Mesocricetus auratus* türlerinin 5 populasyonunun allozim varyasyonu 20 gen lokusunun elektroforetik analiziyle incelenmiştir. Analiz edilen 20 gen lokusundan 11'i monomorfiktir ve bütün populasyonlarda aynı allelde fikse olmuştur. 9 lokus polimorfiktir ve tek bir lokus *M. auratus* ve *M. brandti* populasyonları arasında değişkenlik göstermiştir. Bütün populasyonlar için ortalama polimorfik lokus yüzdesi 24,7 ve 5,9 ile 41,2 arasında değişmektedir. Fiksasyon indeksinin ortalama değeri F_{ST} = 0,0748 olup *M. brandti* populasyonlarında % 7 genetik farklılık göstermektedir. Bu F_{ST} değeri orta derece genetik farklılığı göstermektedir. F_{ST}'den hesaplanan göç sayısı (Nm = 3,09) değeri etkili gen akışının olduğunu önermektedir. Bütün populasyonlar için (*M. brandti* ve *M. auratus*) ortalama heterozigotluk (gözlenen= Ho) 0,069'dır ve 0,029 ile 0,118 arasında değişmektedir. *M. brandti*'i ve *M. auratus*'un ortalama Ho değerleri sırasıyla Ho = 0,080 ve Ho = 0,029 olarak saptanmıştır. *M. brandti* populasyonları arasında Nei'nin genetik mesafesi D = 0,006 den D = 0,026'ya kadar değişmektedir. Nei'nin genetik mesafesi iki tür arasınada D = 0,102'den 0,122'e kadar değişkenlik göstermektedir.

Anahtar Sözcükler: *Mesocricetus* spp., allozim, varyasyon, Türkiye

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Introduction

Species of the genus *Mesocricetus* are distributed throughout the Palaearctic region (Wilson and Reeder, 1993). The genus *Mesocricetus* was first recorded in eastern Turkey by Nehring (1898). Subsequently, species of the genus *Mesocricetus* were reported from various localities in Anatolia by Neuhäuser (1936), Osborn (1965), Steiner and Vauk (1966), Spitzenberger (1972), Doğramacı et al. (1994), and Yigit et al. (1997, 2000). According to recent literature, 4 *Mesocricetus* species have been accepted to date: *M. raddei*, *M. newtoni*, *M. brandti*, and *M. auratus* (Wilson and Reeder, 1993; Neumann et al., 2006). *M. brandti* and *M. auratus* were also considered separate taxa by Doğramacı et al. (1994) and Yiğit et al. (2000). The 2 species were morphologically separated from each other by the shape of the end of the palate (Yiğit et al., 2000). The patterns of blood serum proteins of *M. brandti* and *M. auratus* in Turkey were compared by SDS-PAGE and did not show sufficient diagnostic characteristics to distinguish *M. auratus* from *M. brandti* (Verimli et al., 2000). Although research on the taxonomical, karyological, and reproductive biology of *M. brandti* and *M. auratus* are available, there are only a few studies on the allozyme variation or genetic relationships of these taxa (Csaikl, 1984; Kartavtsev et al., 1984; Neumann et al., 2006). Csaikl (1984) performed an electrophoretic comparison of Syrian and Chinese hamster species, and Kartavtsev et al. (1984) investigated the level of heterozygosity of 5 species of Palaearctic hamsters. Apart from these, Neumann et al. (2006) more recently provided valuable genetic data on the phylogenetic relationship of the Cricetinae subfamily, based on both mitochondrial and nuclear vWF genes. According to their findings, *M. auratus* nested with *M. raddei* in the same clade, which is well separated from another one corresponding to *M. brandti* and *M. newtoni*. Within this framework the present investigation aimed to estimate the electrophoretically detectable genetic variation and genetic distances in 2 species of hamsters.

Materials and Methods

The study included 44 specimens of *Mesocricetus* collected from 5 localities in Turkey and one locality in Iran and Syria (*M. brandti*: 1 = Ardahan, n = 16; 2 = Central Anatolia, n = 13; 3 = Van, n = 4; 4 = Zanjan (north-west Iran), n = 5. *M. auratus*: 5 = Kilis, n = 4, 5 = Aleppo (Syria), n = 2) (Figure 1). The samples from Central Anatolia were collected from 4 locations (Ankara (n = 4), Konya (n = 5), Kırşehir (n = 3), and Kayseri (n = 1)). Specimens were caught with Sherman live traps, transferred to the laboratory, and were then sacrificed. The liver, heart, kidney, and muscles were removed, immediately frozen, and stored at –70 ºC until homogenisation. With our modified method, the samples were homogenised in approximately 450 ml of distilled water with a glass homogeniser. The electrophoretic procedures were carried out as described by Shaw and Prasad (1970), and Harris and Hopkinson (1976); the gel percentage was 12 and the running of samples was performed for 4-6 h with 120 v. Different buffers for gel, and running and dying times were used in accordance with enzyme systems.

Genetic variation was assessed using standard horizontal gel electrophoresis and 16 enzymes' coding for 20 presumptive loci were analysed. Homogenates obtained from muscle were processed for the following enzymatic proteins: *α-glycerophosphate dehydrogenase* (E.C. 1.1.1.8; *α-Gpdh-1* and *α-Gpdh-2*), *lactate dehydrogenase* (E.C. 1.1.1.27; *Ldh*), *malate dehydrogenase* (E.C. 1.1.1.37; *Mdh*), *malic enzyme* (E.C. 1.1.1.40; *Me-1*), *isocitrate dehydrogenase* (E.C. 1.1.1.42; *Idh-1* and *Idh-2*), *phosphogluconate dehydrogenase* (E.C. 1.1.1.44; *Pgd*), *glucose-6-phosphate dehydrogenase* (E.C. 1.1.1.49; *G6pdh*), *xanthine dehydrogenase* (E.C. 1.1.1.204; *Xd*), *glyceraldehyde-3-phosphate dehydrogenase* (E.C. 1.2.1.12; *G3pdh*), *superoxide dismutase* (E.C. 1.15.1.1; *Sod-1* and *Sod-2*), *adenylate kinase* (E.C. 2.7.4.3; *Adk*), *phosphoglucomutase* (E.C. 2.5.7.1; *Pgm-1*), *aldolase* (E.C. 4.1.2.13; *Ald*), *fumarase* (E.C. 4.2.1.2, *Fum*), *mannose phosphate isomerase* (E.C. 5.3.1.8; *Mpi*), and *glucose phosphate isomerase* (E.C. 5.3.1.9; *Gpi-1* and *Gpi-2*).

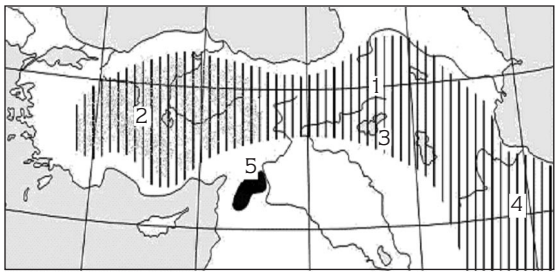

Figure 1. The study areas and recent distributions of *Mesocricetus* spp. in Turkey, Iran, and Syria. *M. brandti* (1 = Ardahan, 2 = Central Anatolia, 3 = Van, 4 = Zanjan (Iran)), *M. auratus* (5 = Kilis and Aleppo (Syria)).

The obtained electrophoretic band patterns were analysed according to the method reported by Harris and Hopkinson (1976). Presumptive alleles were designated alphabetically by their relative mobility, with the allele variant migrating farthest towards the anode denoted as A.

Allozymic data were analysed as allele frequencies with BIOSYS-2 (Black, 1997; original version BIOSYS-1 v.1.7 program of Swofford and Selander, 1989, and modifications to HDYWBG and FSTAT by William C. Black, IV). Genetic variation between intra-specific populations was estimated as the mean heterozygosity per locus (Ho = observed (direct count) and He = expected frequencies of heterozygotes under Hardy-Weinberg equilibrium (Nei, 1978)), the proportion of polymorphic loci in the population (a locus is considered polymorphic if the frequency of the common allele is ≤ 0.95), and the mean number of alleles per locus. The departure from Hardy-Weinberg equilibrium was tested by 3 methods: the chi-square for goodness of fit, an exact probability test (Haldane, 1954), and, because our samples were sometimes small, we also used a chi-square test with Levene (1949) correction for small sample sizes. The FSTAT program was used to calculate overall and population-specific Wright's F-statistics estimators of F_{ST}, F_{IT}, and F_{IS}. Fixation indices (F-statistics; Wright, 1951, 1965) were used to summarise the distribution of genetic variation within and between populations. Confidence limits for the estimates of F-statistics were established by jack-knifing over loci, as recommended by Weir and Cockerham (1984). We also employed a relatively conservative experiment-wise error rate (α = 0.005). According to the Nei and Chesser (1983) correction, negative values were considered zero. Estimates of overall gene flow between populations (Nm) were derived from the approximation $F_{ST} = 1/(1 + 4Nm)$, as recommended by Slatkin and Barton (1989). The amount of genetic divergence between species was estimated with the indices of standard genetic identity (I) and distance (D, Nei unbiased distance) proposed by Nei (1978). A dendrogram of the genetic relationships among the species was constructed using the unweighted pair-group method with arithmetic mean UPGMA (Sokal and Sneath, 1963; Rohlf, 2000).

Results and Discussion

Pattern of variation

Of the 20 loci analysed, 11 were monomorphic and fixed for one of the alleles in all the populations studied: *Idh-1*, *Idh-2*, *Ldh*, *Ald*, *Sod-1*, *Sod-2*, *α-Gpdh-1*, *α-Gpdh-2*, *G3pdh*, *Fum*, and *Ac*. Among the 5 populations, 9 loci were polymorphic and/or discriminant (Table 1). Only one locus (*Gpi-1*) was polymorphic in *M. auratus*, and just one locus (*Pgd*) was found to vary between *M. brandti* and *M. auratus*. In all of the populations studied, 9 loci were polymorphic (*Pgm*, *Mdh*, *Me*, *Pgd*, *G6pdh*, *Xd*, *Gpi-1*, *Gpi-2*, and *Mpi*) and fixed for the different alleles. In a previous report, Kartavtsev et al. (1984) analysed 18 enzyme systems for *M. auratus*, and reported that all loci were monomorphic.

Departures from Hardy-Weinberg equilibrium

Most departures from Hardy-Weinberg equilibrium were detected after the Levene (1949) correction for small sample sizes was applied to the chi-square tests. Within this framework all polymorphic loci-populations were analysed by the chi-square test for goodness of fit and the exact probability test. According to our results, 3 out of 8 loci violated Hardy-Weinberg equilibrium in the 5 populations. All departures were the result of heterozygote deficiencies at loci *Gpi-2*, *Me*, and *Xd*. These 3 polymorphic loci deviated from Hardy-Weinberg equilibrium in the Ardahan specimens, but *Me* deviated only in the specimens of Central Anatolia and *Gpi-2* in Iranian specimens (Table 2).

Genetic variation

Levels of genetic variation within each population are shown in Table 3. The expected frequency of heterozygotes (He) under Hardy-Weinberg equilibrium for all populations of the 2 species was 0.083, and ranged from 0.024 (Kilis and Aleppo) to 0.144 (Central Anatolia). However, Ho of heterozygotes varied from Ho = 0.035 to Ho = 0.118 in *M. brandti*, and was Ho = 0.029 in *M. auratus*. The observed values of genetic variation are within the range reported for other rodents (Nevo, 1978). In a review of the genetic variation in natural populations, Nevo (1978) estimated an Ho value for 44 small rodents to be 0.038, with values ranging from 0.0 to 0.106. However, the value of 0.104 for the Kilis and Aleppo populations of *M. auratus* and 0.144 for the Central Anatolian population of *M. brandti* are higher than those observed in natural populations by Nevo (1978).

Table 1. Allele frequencies of the 20 loci analysed in populations of *Mesocricetus* spp. from 5 localities (n = number of individuals).

Locus	Alleles	1 *M. brandti* (Ardahan) n = 16	2 *M. brandti* (Central Anatolia) n = 13	3 *M. brandti* (Van) n = 4	4 *M. brandti* (Zanjan) n = 5	5 *M. auratus* (Kilis & Aleppo) n = 6
Pgm	A:	0.719	0.885	1.000	1.000	1.000
	B:	0.281	0.115	-	-	-
Mdh	A:	0.906	0.846	1.000	1.000	1.000
	B:	0.094	0.154	-	-	-
Idh-1	A:	1.000	1.000	1.000	1.000	1.000
Idh-2	A:	1.000	1.000	1.000	1.000	1.000
Pgd	A:	1.000	1.000	1.000	1.000	-
	B:	-	-	-	-	1.000
Me	A:	0.938	0.538	1.000	1.000	1.000
	B:	0.062	0.462	-	-	-
Ldh	A:	1.000	1.000	1.000	1.000	1.000
Ald	A:	1.000	1.000	1.000	1.000	1.000
Sod-1	A:	1.000	1.000	1.000	1.000	1.000
Sod-2	A:	1.000	1.000	1.000	1.000	1.000
α-Gpdh-1	A:	1.000	1.000	1.000	1.000	1.000
α-Gpdh-2	A:	1.000	1.000	1.000	1.000	1.000
G6pdh	A:	0.938	0.885	0.750	0.900	1.000
	B:	0.062	0.115	0.250	0.100	-
Xd	A:	0.938	1.000	1.000	1.000	1.000
	B:	0.062	-	-	-	-
G3pdh	A:	1.000	1.000	1.000	1.000	1.000
Fum	A:	1.000	1.000	1.000	1.000	1.000
Adk	A:	1.000	1.000	1.000	1.000	1.000
Gpi-1	A:	1.000	0.885	1.000	1.000	0.250
	B:	-	-	-	-	0.750
	C:	-	0.115	-	-	-
Gpi-2	A:	0.813	0.577	0.750	0.800	1.000
	B:	0.188	0.423	0.250	0.200	-
Mpi	A:	0.406	0.615	0.500	0.200	1.000
	B:	0.594	0.346	0.375	0.800	-
	C:	-	0.038	0.125	-	-

The overall mean percentage of polymorphic loci for the 2 populations was 24.7 (range: 5.9%-41.2%). The overall mean number of alleles per locus was 1.28 (range: 1.2-1.5) (Table 3). As seen in Table 3, these values for *M. brandti* were the highest in the specimens from Ardahan and Central Anatolia (41.2), and the lowest in Van and Iranian specimens (17.6). The percentage of polymorphic loci of *M. auratus* (5.9) was also lower than Turkish hamster's. The genetic variations at 18-20 loci were previously investigated by Kartavtsev et al. (1984) for *Cricetus cricetus*, *Cricetulus barabensis*, *Tscherskia triton*, *Phodopus campbelli*, and *Mesocricetus auratus*. They found that the mean heterozygosity of these species varied from 3.5% to 6%. According to a laboratory strain of *M. auratus* brought from Syria in 1922, the mean heterozygosity in *M. auratus* was estimated to be 1.7%. This value is lower than our estimate for this species, but was not unexpected because it was obtained

Table 2. Results of chi-square test for deviation from Hardy-Weinberg equilibrium and significance test using exact probabilities. *A locus shows deviation from Hardy-Weinberg equilibrium.

Population	Locus	Allele	Observed frequency	Expected frequency	χ^2	DF	P	Exact test P
Ardahan	Mpi	AA	2	2.516	0.288	1	0.592	1.000
		AB	9	7.968				
		BB	5	5.516	1.113	1	0.291	0.530
	Pgm	AA	9	8.161				
		AB	5	6.667				
		BB	2	1.161	6.797*	1	0.009	0.048
	Gpi-2	AA	12	10.484				
		AB	2	5.032				
		BB	2	0.484	0.111	1	0.739	1.000
	Mdh	AA	13	13.097				
		AB	3	2.806				
		BB	0	0.097	31.034*	1	0.00	0.032
	Me	AA	15	14.032				
		AB	0	1.935				
		BB	1	0.032	31.034*	1	0.00	0.032
	Xd	AA	15	14.032				
		AB	0	1.935				
		BB	1	0.032	0.034	1	0.853	1.000
	G6pdh	AA	14	14.032				
		AB	2	1.935				
		BB	0	0.032				
Central Anatolia	Mpi	AA	5	4.800	0.889	1	0.828	1.000
		AB	5	5.760				
		AC	1	0.640				
		BB	2	1.440				
		BC	0	0.360				
		CC	0	0.000				
	Pgm	AA	10	10.120	0.142	1	0.706	1.000
		AB	3	2.760				
		BB	0	0.120				
	Gpi-1	AA	10	10.120	0.142	1	0.706	1.000
		AC	3	2.760				
		CC	0	0.120				
	Gpi-2	AA	4	4.200	0.052	1	0.82	1.000
		AB	7	6.600				
		BB	2	2.200				
	Mdh	AA	9	9.240	0.312	1	0.577	1.000
		AB	4	3.520				
		BB	0	0.240				
	Me	AA	7	3.640	14.098*	1	0.00	0.00
		AB	0	6.720				
		BB	6	2.640				
	G6pdh	AA	10	10.120	0.142	1	0.706	1.000
		AB	3	2.760				
		BB	0	0.120				

Table 2. (Contunued).

Van	Mpi	AA	1	0.857	1.833	1	0.608	1.000
		AB	1	1.714				
		AC	1	0.571				
		BB	1	0.429				
		BC	0	0.429				
		CC	0	0.000				
	Gpi-2	AA	2	2.143	0.200	1	0.655	1.000
		AB	2	1.714				
		BB	0	0.143				
	G6pdh	AA	2	2.143	0.200	1	0.655	1.000
		AB	2	1.714				
		BB	0	0.143				
Iran	Mpi	AA	0	0.111	0.143	1	0.705	1.000
		AB	2	1.778				
		BB	3	3.111				
	Gpi-2	AA	4	3.111	9.143*	1	0.002	0.111
		AB	0	1.778				
		BB	1	0.111				
	G6pdh	AA	4	4.000	0.000	1	1.000	1.000
		AB	1	1.000				
		BB	0	0.000				
Kilis	Gpi-1	AA	0	0.273	0.417	1	0.519	1.000
		AB	3	2.455				
		B	3	3.723				

Table 3. Levels of genetic variation based on 20 loci in all populations, (*M. brandti* 1, 2, 3, 4, *M. auratus* 5) (standard errors in parentheses).

Population	Mean sample size per locus	Mean number of alleles per locus	Percentage of polymorphic loci*	Mean heterozygosity	
				Direct count (Ho) -	HydWbg Expected (He)**
1. Ardahan	16	1.4	41.2	0.077	0.104
		(0 .1)		(0.037)	(0.039)
2. Central Anatolia	13	1.5	41.2	0.118	0.144
		(0.2)		(0.044)	(0.049)
3. Van	4	1.2	17.6	0.088	0.090
		(0.1)		(0.048)	(0.050)
4. Iran	5	1.2	17.6	0.035	0.054
		(0.1)		(0.026)	(0.030)
5. Kilis & Aleppo	6	1.1	5.9	0.029	0.024
		(0.1)		(0.029)	(0.024)

* A locus is considered polymorphic if the frequency of the most common allele is ≤ 0.95.

** Unbiased estimate (see Nei, 1978)

from a highly inbred laboratory strain. The overall allozyme diversity of *Mesocricetus* was comparable to the values obtained in previous investigations of Syrian (*M. auratus*) and Chinese hamsters (*M. griseus*) (Csaikl, 1984). It was found that *M. auratus* is polymorphic at 30% of the loci that were examined and *M. griseus* is polymorphic at 26% of the loci investigated (Csaikl, 1984). However, these values are higher than those observed in natural rodent populations by Nevo (1978). The *F*-statistics values reported by Wright (1965) were useful in estimating the amount of genetic differentiation between the species. Estimates of *F*-statistics for the 8 polymorphic loci among the *M. brandti* populations are given in Table 4. The values of F_{IS}, indicating the effect of inbreeding of an individual within samples, were moderately high (mean: 0.2242) and negative for 3 of the 8 loci, although negative F_{IS} values were not excessive. The values of F_{IS} ranged from –0.754 to 1.0 in the 8 loci. Of these loci, *Me* and *Xd* showed the highest F_{IS} value, indicating the inbreeding effect.

The F_{IT} values, indicating the effect of inbreeding among intra-specific populations (among the groups established for *M. brandti*), were also moderately high with a mean value of 0.2822 and were negative for 3 of the 8 loci. *Me and Xd* showed the highest F_{IT} values, as for F_{IS} (Table 4). Wright (1978) used the following groupings for the evaluation of F_{ST} values: the range 0.0-0.05 is considered to reflect little genetic differentiation, 0.05-0.15 is indicative of moderate differentiation, 0.15-0.25 indicates high genetic differentiation, and values > 0.25 reflect very high genetic differentiation. The mean value of the fixation index was F_{ST} = 0.0748, indicating that 7% of the genetic variation in the species *M. brandti* is considered to reflect moderate genetic differentiation. All loci with F_{ST} values other than zero for *M. brandti* were significant. According to the Nei and Chesser (1983) correction, all negative values are considered zero. The F_{ST} value (0.271) of the *Me* locus was significantly higher than other loci in the populations of *M. brandti*. The *Pgm* and *Mdh* loci were similar to *Me* with respect to the B allele, but their F_{ST} values were significantly lower than that of the *Me* locus. The values of F_{IS}, F_{IT}, and F_{ST} were very similar to the mean values of the jack-knife estimates (Table 4). According to the jack-knife estimates of *M. brandti* loci, the groups established for *M. brandti* did not show a clear subdivision, and it can be said that the F_{IS}, F_{IT}, and F_{ST} of the groups did not reflect differentiation at the subspecific level.

Table 4. F-statistics of variable loci in the populations of *M. brandti* calculated using the method of Wright (1965) and jack-knifing over loci, as recommended by Weir and Cockerham (1984).

Locus	FIS	FIT	FST	Nm
Pgm	0.1774	0.2387	0.0746	3.101
Mdh	–0.0921	–0.0866	0.0051	48.76
Me	1.000	1.000	0.2713	0.671
G6pdh	–0.099	–0.1065	–0.0060	-
Xd	1.000	1.000	–0.0702	-
Gpi-1	–0.0754	–0.0082	0.0625	3.75
Gpi-2	0.2838	0.2905	0.0093	26.63
Mpi	0.0113	0.0783	0.0678	3.43
Mean	0.2242	0.2822	0.0748	3.09
Jack-Knife Estimates over Loci				
Mean	0.2153	0.2792	0.0757	
S.D.(X)	0.1453	0.1633	0.0420	

Table 5. Values of Nei's (1978) unbiased genetic identity (I: below the diagonal) and distance (D: above the diagonal) between the *Mesocricetus* populations.

Populations	1	2	3	4	5
1. Ardahan	*****	0.0159	0.007	0.006	0.112
2. Central Anatolia	0.984	*****	0.015	0.025	0.114
3. Van	0.992	0.984	*****	0.008	0.102
4. Iran	0.993	0.974	0.992	*****	0.122
5. Kilis & Aleppo	0.887	0.885	0.897	0.877	*****

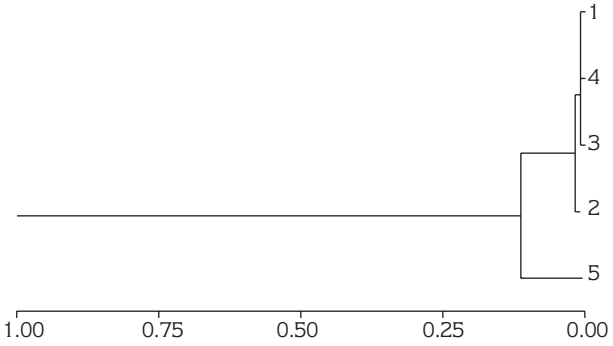

Figure 2. UPGMA dendrogram summarising the genetic relationships among the *Mesocricetus* populations studied (D = Nei's (1978) unbiased genetic distance based on 20 enzyme loci). The coefficient of cophenetic correlation is 1.00 (*M. brandti*; 1 = Ardahan, 2 = Central Anatolia, 3 = Van, 4 = Zanjan (Iran). *M. auratus*; 5 = Kilis and Aleppo (Syria)).

The number of migrants exchanged between our hamster population samples (Nm, Table 4) also suggested effective gene flow (average Nm = 3.09). The values of Nm_{Mdh} and $Nm_{Gpi\text{-}2}$ were much higher than those of other loci.

Genetic distance

The values of Nei's (1978) unbiased genetic identity (I) and distance (D) were calculated for all pair-wise population comparisons (Table 5). An UPGMA dendrogram summarising the genetic relationships among the populations is given in Figure 2. The observed values of genetic distance were low among the populations of *M. brandti* (Ardahan, Van, Iran). These values between populations of *M. brandti* varied from D = 0.006 to D = 0.026. The highest value of genetic distance was found between the Central Anatolian and Iranian specimens (D = 0.025), and the lowest was between Ardahan and Iranian specimens (D = 0.006) (Table 5). According to this, the specimens of *M. brandti* from Ardahan and Iran were genetically very close to one another (D = 0.006), and Van specimens were connected to this group with a distance of D = 0.007 (Figure 2). The specimens from Central Anatolia were the most divergent among intrapopulations of *M. brandti*. Apart from this, higher values of genetic distance were found between the Kilis population of *M. auratus* and *M. brandti* populations, with values ranging from D = 0.102 (Kilis and Van) to D = 0.122 (Kilis and Iran).

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