Systematics and Phylogenetics
Research Article

ACTA ZOOLOGICA BULGARICA
Acta zool. bulg., 65 (3), 2013: 299-306

Allozyme Variations in the Genus *Meriones* (Gerbilinae: Rodentia) from Turkey

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Abstract: Allozymic variability of 24 loci was compared in the genus *Meriones* representing 5 species in Turkey. The phylogenetic relationship of these *Meriones* species was established according to the variations of twelve polymorphic loci (*Ald*, *Ldh*, α-*Gpdh*, *Ca-1*, *Ca-2*, *Gpi*, *Me*, *Mpi*, *G6pdh*, *Ldh-1*, *Sod*, *Ak*). According to the patterns of allozyme variation, the percentage of polymorphic loci was found to be 12.5 in *Meriones crassus*, 16.7 in *Meriones persicus*, 12.5 in *Meriones tristrami*, 18.7 in *Meriones vinogradovi* and 8.3 in *Meriones dahli*. Interspecific genetic distances were found to be high, ranging from 0.032 to 0.332. Neighbor-joining and UPGMA dendrograms showed that *M. tristrami* and *M. crassus* have a high genetic similarity. The most diverged one was appeared to be *M. vinogradovi*. It was also concluded that the genus *Meriones* is not monophyletic since *M. persicus*, which belongs to a different subgenus, was placed between the clades of *M. tristrami*, *M. crassus* and *M. vinogradovi*.

Key words: Allozyme, *Meriones*, Turkey

Introduction

The genus *Meriones* representing five species (*Meriones crassus* Sundevall, 1842*, Meriones persicus* Blanford, 1875*, Meriones tristrami* Thomas, 1892*, Meriones vinogradovi* Heptner, 1931 and *Meriones dahli* Shidlovsky, 1962) in the Asiatic part of Turkey has adapted to the semi-arid steppe of the Palearctic region (Harrison & Bates 1991, Yiğit *et al*. 1997, Musser & Carleton 2005). Of these taxa, only *M. tristrami* has the wide range in Asiatic Turkey, which extends from the Iranian border to the westernmost border around İzmir, whereas the distribution of the other four species is confined to certain marginal areas: *M. persicus* and *M. dahli* in the eastern part of Turkey, *M. crassus* in southeastern Turkey, and *M. vinogradovi* in eastern and southeastern Turkey (Misonne 1957, Yiğit *et al*. 1997). Apart from these five species, *Meriones libycus* was reported in southeastern Turkey (Misonne 1957), but not recorded in this area later. The morphological identification of these taxa is somehow difficult due to very poor intraspecific variations. The research on this genus was mainly focused on morphology and karyology, which were performed on Turkish species by Yiğit *et al*. (1997), Yiğit & Çolak (1998, 1999), Yiğit *et al*. (1998) and on Iranian species by Darvish (2009). These karyological studies showed that the diploid numbers of chromosomes are distinctive among taxa: *M. crassus* (2n=60)*, M. persicus* (2n=42)*, M. tristrami* (2n=72) *M. vinogradovi* (2n=44) and *M. dahli* (2n=50). The genetic research for establishing the phylogenetic relationship of species is very scarce and mostly achieved on *Meriones ungiuculatus*, which is used as laboratory animal (Chevret & Dobigny, 2005; Naseri *et al*., 2006;

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Du *et al*., 2010; Ito *et al*., 2010). Ito *et al*. (2010) suggested using Cyt*b* and COII genes and that the genus *Meriones* is not monophyletic. In supporting this suggestion, the subgenera *Parameriones* (*Meriones rex*) and *Pallasiomys* (*M. unguiculatus*, *M. libycus*, *M. crassus* and *Meriones meridianus*) were reported not to be monophyletic by Chevret & Dobigny (2005). All this phylogenetic research was based on samples with only a few species and was very far from establishing the phylogenetic relationship of certain species. The allozyme analysis of the genus *Meriones* was first performed using nine enzyme systems by Benazzou *et al*. (1984), which also showed the informative polymorphism at several loci and even used a low sample size. In this context, the aim of the present study is to determine the allozyme variations and provide an informative database for establishing the phylogenetic relationship of five *Meriones* spp. from Turkey.

Material and Methods

A total of 90 specimens from five species of the genus *Meriones* were studied at nine localities in Turkey (Fig. 1); *M. crassus*: (N=10): Şanlıurfa (N=10), *M. persicus* (N=17): D.Beyazıt - Ağrı (N=13) + Hakkari (N=1) + Erzurum (N=3), *Meriones tristrami lycaon* (N=10): Karadağ - Karaman (N=10), *Meriones tristrami blackleri* (N=12): Turgutlu - Manisa (N=12), *M. vinogradovi1* (N=17): D.Beyazıt –Ağrı (N=17), *M. vinogradovi2* (N=8): Ceylanpınar – Urfa (N=8), *M. dahli* (N=16): Aralık - Iğdır (N=16). Specimens were caught with Sherman live traps, transferred to the laboratory, and were then sacrificed under anaesthesia. The muscles were removed and stored at 70°C until homogenisation. Identification was performed according to cranial and karyological criteria in Yiğit *et al*. (1997). Voucher specimens and tissues were deposited at Prof. Dr. N. Yiğit and Prof. Dr. E. Çolak's collection (Ankara University, Faculty of Science and Department of Biology).

Protein electrophoresis was performed in a horizontal block of starch gel. The preparation of gels, electrophoresis and staining of proteins followed standard protocols described in detail in numerous manuals (Harris & Hopkinson 1976, Pasteur *et al*., 1988). Protein extractions from tissues (muscle) were used as samples. The extractions were made by grinding small tissue fragments in distilled water. Isozymes (genetically determined multiple variants of an enzyme with similar substrate specificities found in the same animal) were designated by numbers in the order of decreasing anode mobility. Multiple forms of structural and transport proteins lacking enzymatic activity and, hence, substrate specificity were distinguished on the basis of the visible electrophoretic characteristics, such as the density, shapes, and sizes of the bands. When describing the heterogeneity of the proteins having a quaternary structure, the "hybrid" protein forms resulting from the interaction between different allelic variants or products of different gene loci were not taken into account.

The gel percentage was 12% and samples were run at 120 V for a period of 4-6 hours. Different buffer systems were used in accordance with the enzyme systems used during different parts of the procedure (gel preparation, sample running, and staining). Genetic variation was assessed using conventional horizontal starch gel electrophoresis and 20 enzymes coded for 24 presumptive loci were analysed. The name of the enzyme systems were as follows (the abbreviation and EC numbers were provided within parenthesis): Aconitase (*Aco*, E.C. 4.2.1.3), Glucose-6-phosphate dehydrogenase (*G6pdh*, E.C. 1.1.1.49), Glucose-6-phosphate isomerase (*Gpi*, E.C. 5.3.1.9), α-Glycerophophate dehydrogenase (α-*Gpdh*, E.C. 1.1.1.8), Isocitrate dehydrogenase (*Idh*, E.C. 1.1.1.42), Malate dehydrogenase (*Mdh*, E.C. 1.1.1.37), Malic enzyme (*Me*, E.C. 1.1.1.40), Phosphoglucomutase (*Pgm*, E.C. 5.4.2.2), Superoxide dismutase (*Sod*, E.C. 1.15.1.1), Fumaraz (*Fum*, E.C. 4.2.1.2), Phosphogluconate dehydrogenase (*Pgd*, E.C. 1.1.1.44), Adenosine deaminase (*Ada*, E.C. 3.5.4.4), Hexokinase (*Hk*, E.C. 2.7.1.1), Lactate dehydrogenase (*Ldh*, E.C. 1.1.1.27), Aldolase (*Ald*, E.C.4.1.2.13), Carbonic anhydrase (*Ca*, E.C.4.2.1.1), Glyceraldehyde-3-phosphate dehydrogenase (*G3pdh*, E.C.1.2.1.12), Glutamic oxaloacetic transaminase (*Got*, E.C.2.6.1.1), Mannosephosphate isomerase (*Mpi*, E.C.5.3.1.8), Adenylate kinase (*Ak*, E.C.2.7.4.3). Band profiles were considered, based on their flow speeds on the gel, as A, B and C after staining.

Allozymic data were analysed as allele frequencies with BIOSYS-2 (Black 1997, the original version BIOSYS-1 v.1.7 programme of Swofford & Selander 1981). Genetic variation between populations was estimated as mean heterozygosity per locus (*Ho* = observed and *He* = expected and frequencies

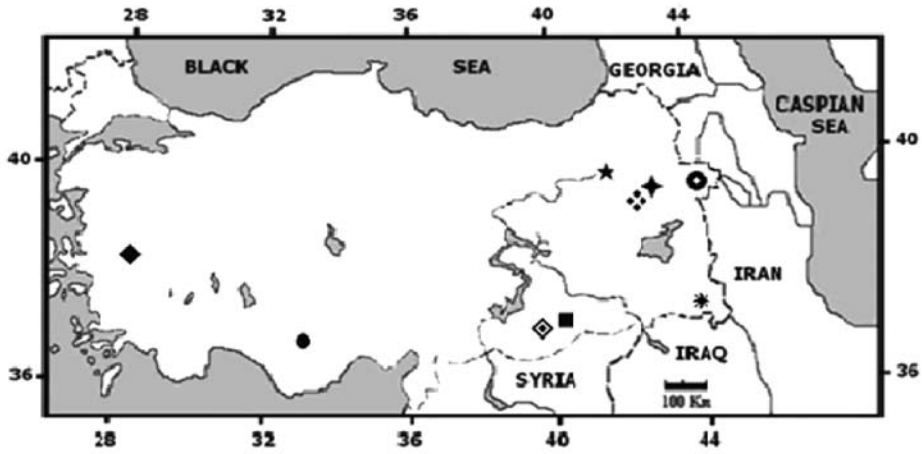

Fig. 1. The collecting sites of *Meriones* specimens in Turkey. ■: Şanlıurfa (*M.crassus*), ✦: D.beyazıt - Ağrı (*M.persicus*), ★: Hakkari (*M.persicus*), ✷: Erzurum (*M.persicus*), ◆: Karadağ – Karaman (*M.t. lycaon)*, ●: Turgutlu - Manisa (*M.t.blackleri*), ❖: D.Beyazıt–Ağrı (*M.vinogradovi*1), ◈: Ceylanpınar–Urfa (*M.vinogradovi*2), ✪: Aralık - Iğdır (*M.dahli*)

of heterozygotes under the Hardy-Weinberg equilibrium) (Nei 1978), proportion of polymorphic loci in the population (a locus was considered polymorphic if the frequency of the common allele was ≤ 0.95), and mean number of alleles per locus. The amount of genetic divergence between populations 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 similarity between the populations was constructed using the unweighted pair group method with arithmetic mean UPGMA (Sneath & Sokal 1973, Rohlf 2000).

Results and Discussion

Allozymic patterns and genetic variation. According to the allozyme electrophoresis, 12 of the 24 loci were polymorphic in five species of the genus *Meriones*; the others were monomorphic and fixed for the same allele. The frequencies of polymorphic loci are summarised in Table 1.

In *M. crassus,* 10 specimens from only one location (Şanlıurfa province in south eastern Turkey) were analyzed and three markers (*Ca-1*, *Gpi*, *Mpi*) were found to be polymorphic and other alleles were fixed at the same alleles. *M. persicus* was captured from three different locations in eastern Turkey. Four of twenty-four loci (α-*Gpdh*, *Ca-1, Ca-2*, *Me*) were polymorphic in this species. *M. tristrami* is represented by at least five subspecies in Turkey. In our analysis, only two topotype specimens of *M. t. blackleri* and *M. t. lycaon* were used for electrophoretic analysis. *Ca-1* and *Ca-2* were similarly found to be polymorphic in both subspecies, but α-*Gpdh* and *G3pdh* only appeared to be polymorphic in the specimens of *M. t. lycaon*. The specimens of *M. vinogradovi* were captured from two different locations; eastern Turkey (Mv1) and south-eastern (Mv2) Turkey. Seven loci (*Ald*, *Ldh,* α-*Gpdh*, *Ca-1*, *Ca-2*, *Gpi* and *Me*) were found to be polymorphic in Mv1 but only two (*Ca2* and *Gpi*) in Mv2. *M. dahli* only inhabits sandy ground around the north of the Ağrı Mountain in eastern Turkey. Sixteen specimens of this species were analyzed and two loci (*Ca1, Ca2*) were found to be polymorphic. *Sod* was found to be distinctive among taxa fixing the B allele only in *M. persicus*. The B allele of *Ak* was found to be specific to *M. tristrami*. The other four species had the A allele for this allozyme. Apart from these, the D allele of *Ca-2* only appeared in the specimens of *M. dahli*.

Genetic variation was explained by three statistics: A (average number of alleles per locus), p (proportion of polymorphic loci) and *H* (average number of heterozygosity). Values of A varied from 1.08 to 1.38 among the populations and the highest values were found in Mv1. The values p in all populations ranged from 8.33 to 29.17; the highest value consistently appeared in *M. vinogradovi1*. The values p were also found to be significantly different between two subspecies of *M. tristrami*. *M. t. blackleri*, where p=8.3, occupies the coastal part of western Turkey, whereas *M. t. lycaon* lives in the central Anatolia where more severe climatic conditions prevail than the coastal area (Table 2). Karyological differences

Table 1. Allele frequencies of 12 polymorphic loci in populations of *Meriones spp.* - *M. crassus* (Mc), *M. persicus (*Mp), *M. t. lycaon* (Mtl), *M. t. blackleri* (Mtb), *M. vinogradovi1* (Mv1), *M. vinogradovi2* (Mv2), *M. dahli* (Md)

Populations N Loci	Mc (10)	Mp (17)	Mtl (10)	Mtb (12)	Mv1 (17)	Mv2 (8)	Md (16)
Ald							
A	1.000	1.000	1.000	1.000	0.059	1.000	1.000
B	-	-	-	-	0.941	-	-
Ldh							
A	1.000	-	-	-	0.882	1.000	1.000
B	-	1.000	1.000	1.000	0.118	-	-
C	-	-	-	-	-	-	-
α-Gpdh							
A	1.000	0.882	0.800	1.000	0.059	-	1.000
B	-	0.118	0.200	-	0.941	1.000	-
Ca-1							
A	0.050	0.235	0.600	0.333	0.029	-	0.875
B	0.950	0.706	0.400	0.667	0.029	1.000	0.125
C	-	0.059	-	-	0.941	-	-
Ca-2							
A	-	0.794	0.600	0.833	0.088	-	0.125
B	1.000	0.206	0.400	0.167	0.735	0.875	0.188
C	-	-	-	-	0.176	0.125	0.656
D	-	-	-	-	-	-	0.031
Gpi							
A	0.900	-	1.000	1.000	0.941	0.125	-
B	0.100	1.000	-	-	0.059	0.875	1.000
Me							
A	1.000	0.824	1.000	1.000	0.647	1.000	-
B	-	0.176	-	-	0.353	-	1.000
Mpi							
A	0.500	1.000	1.000	1.000	1.000	1.000	1.000
B	0.500	-	-	-	-	-	-
G3pdh							
A	1.000	1.000	0.850	1.000	-	-	1.000
B	-	-	0.150	-	1.000	1.000	-
Idh-1							
A	1.000	-	1.000	1.000	-	-	1.000
B	-	1.000	-	-	1.000	1.000	-
Sod							
A	1.000	-	1.000	1.000	1.000	1.000	1.000
B	-	1.000	-	-	-	-	-
Ak							
A	1.000	1.000	-	-	1.000	1.000	1.000
B	-	-	1.000	1.000	-	-	-

in these subspecies were also reported in the number of chromosomal arms by Yiğit *et al*. (1998). The difference in p values also appeared between the subpopulations of *M. vinogradovi.*

The mean heterozygosity of polymorphic loci (*Ho* and *He* values) in all subpopulations and species showed significant deviations from the Hardy-Weinberg equilibrium. Considering the overall loci for species, the lowest mean *Ho* value was found to be *Ho* = 0.000 in *M. t. blackleri* and *M. vinogradovi2* and the highest *Ho*= 0.046 in *M. crassus* (Table 2). Apart from these, two loci in *M. crassus* (*Gpi, Mpi*), four in *M. persicus* (*α-Gpdh*, *Ca-1*, *Ca-2*, *Me*), two in *M. tristrami* (*Ca-1*, *Ca-2*), seven in *M. vinogra-*

Table 2. Levels of genetic variation based on 24 loci in all *Meriones* populations. Standard errors in parentheses. * A locus is considered polymorphic if the frequency of the most common allele does not exceed 0.95; ** Unbiased estimate (Nei 1978)

Populations	N	Mean number of alleles per locus (A)	Percentage of polymorphic loci (p)*	Mean heterozygosity (*Ho*)	Mean heterozygosity (*He*)**
M. crassus	10	1.13 (0.07)	12.50	0.046 (0.042)	0.034 (0.023)
M. persicus	17	1.21 (0.10)	16.67	0.002 (0.002)	0.054 (0.026)
M. t .lyacon	10	1.17 (0.08)	16.67	0.029 (0.020)	0.067 (0.033)
M. t. blackleri	12	1.08 (0.06)	8.33	0.00 (0.00)	0.031 (0.022)
M. vinogradovi1	17	1.38 (0.13)	29.17	0.005 (0.003)	0.066 (0.027)
M. vinogradovi2	8	1.08 (0.06)	8.33	0.000 (0.000)	0.019 (0.013)
M. dahli	16	1.17 (0.13)	8.33	0.003 (0.003)	0.032 (0.024)

Table 3. Nei's unbiased genetic identity "I" (above) and distance "D" (below) values (Nei 1978) between *Meriones* populations - *M. crassus* (Mc), *M. persicus (*Mp), *M. t. lycaon* (Mtl), *M. t. blackleri* (Mtb), *M. vinogradovi1* (Mv1), *M. vinogradovi2* (Mv2), *M. dahli* (Md)

I D	Mc	Mp	Mtl	Mtb	Mv1	Mv2	Md
Mc		0.800	0.098	0.102	0.223	0.134	0.881
Mp	0.200		0.216	0.164	0.277	0.175	0.807
Mtl	0.902	0.784		0.968	0.708	0.724	0.847
Mtb	0.898	0.836	0.032		0.668	0.719	0.801
Mv1	0.777	0.723	0.292	0.332		0.932	0.735
Mv2	0.866	0.825	0.276	0.281	0.068		0.789
Md	0.119	0.193	0.153	0.199	0.265	0.211	

dovi (*Ald*, *Ldh*, *α-Gpdh*, *Ca-1*, *Ca-2*, *Gpi*, *Me*) and *M. dahli* (*Ca-1*, *Ca-2*) were found to be deviated from this equilibrium. Benazzou *et al*. (1984) first conducted similar research on this genus with a low sample size and reported that the two loci *Pgd* and *Got* were polymorphic. Contrary to these findings, no polymorphism for these loci was detected in Turkish specimens.

Genetic distance. Nei's genetic distances (Nei 1978) were computed among the populations of *Meriones* for all pair-wise comparisons from the allele frequencies of the 24 loci and were found to be high among species ranging from 0.032 to 0.332 (Table 3). The lowest value of interspecific genetic distance was found to be D=0.032 between *M. t. lycaon* and *M. t. blackleri*, and the highest between *M. vinogradovi*1 and *M. t. blackleri* (D=0.332). The UPGMA and Neigbour joining dendrograms summarize the genetic relationships between the *Meriones* populations (Figs 2-3). *M. t. blackleri* and *M. t. lycaon* established the first sub-cluster with the value of D=0.032. According to the dendrograms generated from the matrix in Table 3, *M. tristrami* and *M. crassus* had a high genetic similarity and *M. dahli* and *M. persicus* were also connected to this sub-cluster, respectively. The most diverged one was *M. vinogradovi*.

Our results show that the overall mean percentage of polymorphic loci in the Turkish *Meriones* was p = 14.3. However, the p value was very low in Mtb, Mv2 and Md (p=8.3), moderate in Mtl (p=16.7), Mc (p=12.5), Mp (p=16.7) and high in Mv1 (p=29.2). The mean value of polymorphic loci in Turkish *Meriones* species was almost similar to the black rat

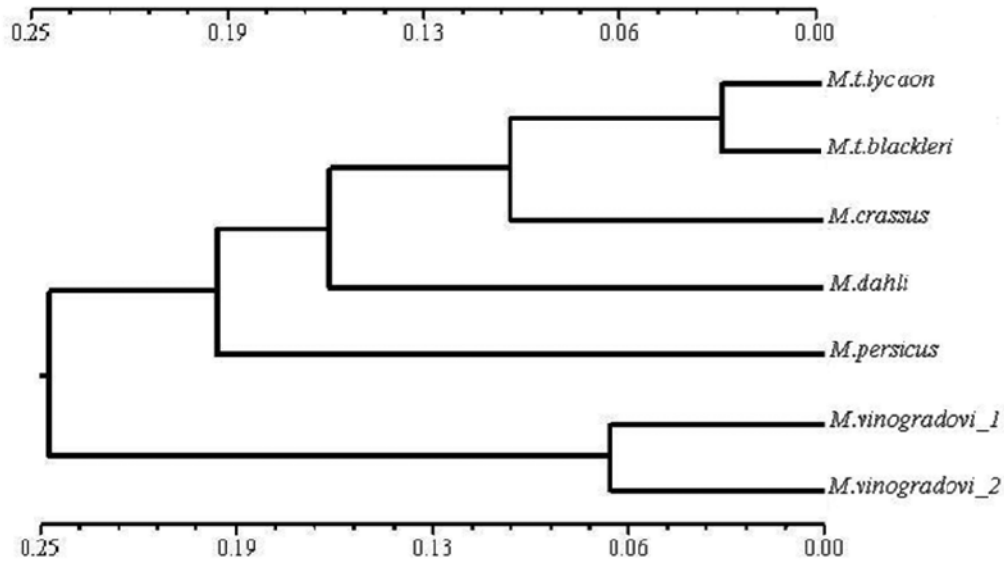

Fig. 2. UPGMA dendrogram summarizing the genetic relationships among the *Meriones* populations studied. D = Nei's (1978) unbiased genetic distance, based on 24 enzyme loci

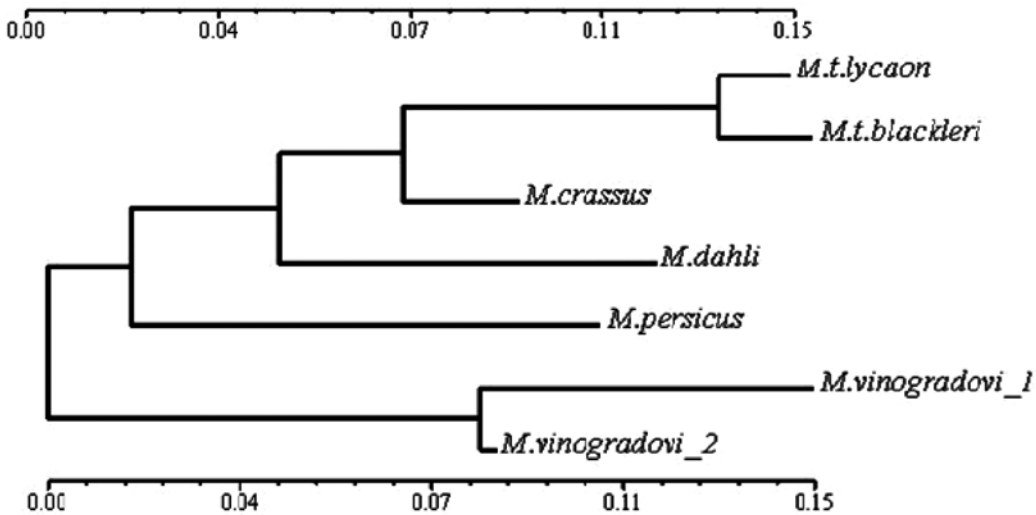

Fig. 3. Neigbour joining dendrogram summarizing the genetic relationships among the *Meriones* populations studied (Nei 1978)

subpopulations in Turkey with p=15.1 (Yiğit *et al*. 2008) and also p=18.1 (Yiğit *et al*., 2010), it was less than those reported in *Mus musculus domesticus*, p=25 (Britton-Davidian 1990) and *Mesocricetus brandti*, p=29.4 (Yiğit *et al*. 2007), and higher than in the subgenus *Sylvaemus* (p=13.7) in western Anatolia (Macholan *et al*. 2001) and in *Mesocricetus auratus* (p=5.9) (Yiğit *et al*. 2007). The overall mean heterozygosity (*He*: 0.043) of Turkish *Meriones* species was found to be relatively higher than those reported for different species of rodents; in *Rattus*, it was reported to be *He*: 0.044 (in Turkey), *He*: 0.025 (western Mediterranean), *He*: 0.03 (Galapagos Archipelago), *He*: 0.01 (Southeast Asian subpopulations) (Patton *et al*. 1975, Baverstock *et al*. 1983, 1986, Cheylan *et al*. 1998, Yiğit *et al*. 2008). This value was reported to be *He*: 0.098 and *He*: 0.024 in *M. brandti* and *M. auratus,* respectively (Yiğit *et al*. 2007).

Nevo (1978) estimated the mean heterozygosity value for 44 small rodents to be 0.038, with values ranging from 0 to 0.106. In this study, the heterozygosity values (*He*) for Turkish *Meriones* were consistently found to be in the range of small rodents, varying from 0.019 to 0.067. Chevret & Dobigny (2005) studied the systematic and evolution of Gerbillinae based on the genetic markers, such

as Cyt*b* and 12S rRNA. They suggested that subgenera of the genus *Meriones* are not monophyletic since *Meriones rex* and *M. crassus* which belong to different subgenera appear to be sister species in the Maximum likelihood tree. Ito *et al*. (2010) supported this finding using Cyt*b* and COII markers, and suggested that *Meriones tamaracinus* be placed as the sister group to a clade comprising *Brachiones*, *Psammomys*, *Rhombomys* and other *Meriones* species.

Turkish *Meriones* were placed into two subgenera; *Pallasiomys* (*M. crassus, M. tristrami, M. vinogradovi* and *M. dahli,*) and *Parameriones* (*M. persicus*). The UPGMA tree, produced from the matrix given in Table 3, showed that *M. persicus* was placed between the clades of *M. vinogradovi* and *M. tristrami, M. crassus, M. dahli* (Figs 2-3). In this respect, this finding supports the assumption that *Meriones* is not monophyletic and is consistent with those of Chevret and Dobigny (2005) and Ito *et al*. (2010). Because of this, it can be said that establishing the phylogenetic relationships and determining the level of intraspecific variation of these species requires further research with a large sample size and more genetic markers.

Acknowledgements: This work was supported by the Ankara University-BAP (09H4240003) and TUBITAK-TBAG (107T324), Turkey.

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Received: 08.06.2012
Accepted: 05.02.2013