

ALLOZYME VARIATION AND SYSTEMATICS OF THE GENUS *APODEMUS* (RODENTIA: MURIDAE) IN ASIA MINOR AND IRAN

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Starch gel electrophoresis at 36 presumptive loci was used to study genetic variation and systematic status of 110 wood mice (genus *Apodemus*) from 19 sites scattered across Anatolia, Armenia, and Iran. Seventeen loci were monomorphic and fixed for the same allele among populations, whereas 19 loci were found to be polymorphic or discriminant among samples. The following species were determined in the material: *A. flavicollis*, *A. uralensis*, *A. hermonensis*, and a taxon provisionally called *Apodemus* cf. *hyrcanicus*. The study material was compared with previously analyzed samples from western Anatolia, increasing the total material to 245 specimens from 31 localities. In general, the pattern of variation and level of genetic differentiation within and among species were comparable between western and eastern samples. Intraspecific genetic distances were low, ranging from 0 to 0.051, but interspecific distances were an order of magnitude higher. Similarly, neighbor-joining trees showed negligible differentiation between populations of individual species and no sign of intraspecific structuring. *A. uralensis* seems to prefer humid sites, whereas *A. hermonensis* and *A. flavicollis* also occur in drier places. Individuals referred to *Apodemus* cf. *hyrcanicus* were limited to lowlands south of the Caspian Sea. Problems associated with the systematic relationships and taxonomy of *A. falzfeini-fulvipectus-hermonensis-arianus* and *A. cf. hyrcanicus* from northern Iran are briefly discussed.

Key words: *Apodemus*, Asia Minor, electrophoresis, Iran, systematics, wood mice

The systematics and biology of the genus *Apodemus* have received growing attention. During the last 25 years, efforts of numerous scientists have benefited from molecular methods (especially allozyme-based), which have led to major advances in our knowledge of the systematics of wood mice from Europe and some other parts of the Palearctic region. Among the most recent achievements have been a substantial re-analysis of the genetic differentiation and taxonomy of the entire genus within the former USSR (Mezhzherin 1987, 1990, 1991, 1996; Mezhzherin and Mikhailenko 1991;

Mezhzherin and Zagorodnyuk 1989; Mezhzherin and Zykov 1991; Mezhzherin et al. 1992; Vorontsov et al. 1989) and elucidation of the systematic identity of wood mice from Israel (Filippucci et al. 1989). In the former case, *A. sylvaticus uralensis* was shown to be a distinct species, conspecific with *A. microps* from Slovakia (Kratochvíl and Rosický 1952), with *uralensis* being the older synonym (Mezhzherin 1990). Several other taxa, previously thought to be subspecies of *A. sylvaticus* (*charkovenssis*, *mosquensis*, *ciscaucasicus*, and *tscherga*) also were placed within *A. uralensis* (Mezhzherin 1990; Mezhzherin and Mikhailenko 1991). Subsequently, occurrence of 4 spe-

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cies was reported for Caucasus and Transcaucasus: *A. uralensis*, *A. fulvipectus*, *A. ponticus*, and *A. hyrcanicus* (Mezhzherin et al. 1992; Vorontsov et al. 1992). In Israel, the presence of 3 species was demonstrated: *A. mystacinus*, *A. flavicollis*, and newly described *A. hermonensis* (Filippucci et al. 1989). On the other hand, *A. sylvaticus*, previously believed to inhabit the entire Middle East, has not been found in Israel (Filippucci 1992; Filippucci et al. 1989).

Despite recent progress in our knowledge of the systematics and zoogeography of wood mice, there are still geographic areas from which only incomplete or confused information is available. Among these areas are Asia Minor and Iran. Usually, occurrence of 6 species of *Apodemus* has been credited to this region: *A. mystacinus*, *A. flavicollis*, *A. sylvaticus*, *A. uralensis*, *A. ponticus*, and *A. fulvipectus* (Filippucci et al. 1996). However, information on the taxonomic status and geographic distribution of these taxa has been based mostly on fragmentary data. Moreover, *A. uralensis* has only been reported from Uludağ and the Rize region (Steiner 1978a, 1978b), whereas *A. ponticus* and *A. fulvipectus* have been thought to be restricted to areas adjacent to the Caucasus and northern Turkey, respectively (Musser and Carleton 1993).

Recently, Mezhzherin (1997), in his revision of *Apodemus* from northern Eurasia, reported *A. mystacinus*, *A. ponticus*, *A. uralensis*, and *A. hyrcanicus* for Asia Minor and Iran. All those taxa, except *hyrcanicus*, have been considered to be distributed throughout Asian Turkey and, in the case of *uralensis*, as far south as Israel. At the same time, results from a genetic and morphologic survey of mice from western Anatolia (Filippucci et al. 1996) demonstrated that the distribution of *A. sylvaticus* seemed to be limited to a small area in a northwestern Asia Minor on the southern coast of the Black Sea. *A. flavicollis*, *A. uralensis*, and *A. hermonensis* also were shown to be present in the area studied.

We present new genetic data for *Apode-*

mus from Asia Minor and Iran. Our aim was to uncover the systematic identity of animals under study, to compare genetic variation and intra- and interspecific differentiation of the studied samples with previously published data from western Turkey (Filippucci et al. 1996), and to discuss some of the taxonomic implications. *A. mystacinus*, although also found in the study area, was not considered.

MATERIALS AND METHODS

A total of 110 individuals of *Apodemus* wood mice were collected from 19 sites scattered across Anatolia, Armenia, and Iran (Fig. 1; Appendix I gives details on the collecting sites, sample sizes, and population codes). Voucher specimens were deposited as skulls and skins at the Department of Zoology, Charles University, Prague, Czech Republic (D. Frynta, in litt.).

Of the 19 sampling localities, 1 (Burdur) was located in western Anatolia, 1 (Seyfe) was located in the north-central Asian Turkey, 10 samples were taken from eastern Asia Minor, and the remaining 7 samples were collected from northern (3), southwestern (1), and southern Iran (3). Data were compared with and supplemented by data published in Filippucci et al. (1996), who reported on 20 populations of *A. sylvaticus*, *A. flavicollis*, *A. uralensis*, and *A. hermonensis* from Turkish Thrace and western Anatolia. Thus, the total number of sites was increased to 31 and the number of animals analyzed to 245.

Muscle and kidney tissue from each specimen were snap-frozen in liquid nitrogen and preserved at -80°C until processed. Homogenates for electrophoresis were obtained from tissue crushed in distilled water immediately before electrophoresis.

Standard horizontal starch gel electrophoresis (Harris and Hopkinson 1976) was carried out on the homogenates, and 24 enzymes coded for by 36 presumptive loci were analyzed (Appendix II). Details of the electrophoretic procedures were described by Filippucci et al. (1988). Samples of *A. uralensis*, *A. hermonensis*, *A. flavicollis*, and *A. sylvaticus* with known genotypes were used as standards and run alongside unknown samples. Isozymes were numbered in order of decreasing mobility from the most anodal one. Allozymes were numbered according to their mobility, relative to the most common al-

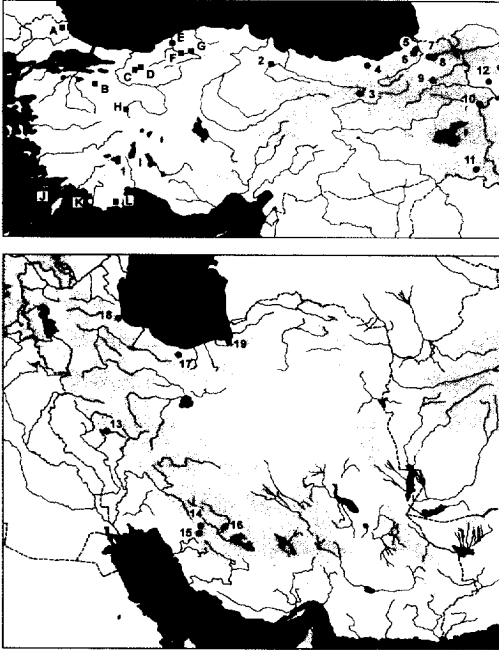


FIG. 1.—Map of Turkey (top) and Iran (bottom) with collecting sites, indicated with black circles (numbers are the same as in Table 1): 1, Burdur; 2, Seyfe; 3, Güzyurdu; 4, Sumelas; 5, Damar; 6, Kabaca; 7, Yalnızçam Pass; 8, Bağdaşan; 9, Sırbasan; 10, Doğubayazıt; 11, Hak-kâri; 12, Yerevan; 13, Gholaman; 14, Baba Hasan; 15, Abshar; 16, Sivand; 17, Vali Abad; 18, Asalem; 19, Now Kandeh (see Appendix I for more details). Localities indicated with black squares are those studied by Filippucci et al. (1996): A, Velika Köprüsü bridge, Demirköy (Kırklareli); B, Uludağ (Bursa); C, Hanyatak (Sakarya); D, Lake Abant Gölü (Bolu); E, Çaycuma (Zonguldak); F, Yenice (Zonguldak); G, Safranbolu (Zonguldak); H, Gökseyu River, 10 km SE Kütahya (Kütahya); I, Yılanlı, 11 km SE Eğirdir (Isparta); J, Datça, Marmaris (Muğla); K, Ölüdeniz, Fethiye (Muğla); L, Ciglikara (Antalya); see Filippucci et al. (1996) and Benda and Horáček (1998) for details on the latter sites. Shaded areas indicate mountainous areas.

lele (= 100) in the reference population of *A. sylvaticus* from Burano, Italy (Filippucci 1992).

Allozyme data were processed with BIOSYS-1 (Swofford and Selander 1981). Intrapopulation genetic variation was estimated using standard indices: the mean number of alleles per locus (A), the proportion of polymorphic loci under

1% ($P_{1\%}$) and 5% ($P_{5\%}$) criteria, mean observed heterozygosity (H_o), and mean "unbiased" expected heterozygosity (H_e) based on conditional expectations (Nei 1978).

The amount of genetic divergence between populations was estimated with Nei's (1978) unbiased genetic distance and the chord distance introduced by Cavalli-Sforza and Edwards (1967). Our rationale for using 2 indices was because they are based on different evolutionary models. Although Nei's indices of genetic distance have been the most frequently used measure used in electrophoretic studies, problems are inherent in these procedures (no matter if "standard" or "unbiased" indices are used) in cases of different levels of polymorphism among populations (cf. Hillis 1984). On the other hand, the chord and arc indices of Cavalli-Sforza and Edwards incorporate some realistic assumptions about the nature of evolutionary change in gene frequencies, thus avoiding the undesirable properties of the Nei's measures (Swofford et al. 1996). However, relative superiority of respective methods clearly depends on which underlying model is more evolutionarily appropriate within and among populations of wood mice, as well as within the genus *Apodemus* as a whole.

Neighbor-joining trees (Saitou and Nei 1987) were constructed from both Nei's and Cavalli-Sforza's indices; support for each node was examined with the bootstrap procedure (Felsenstein 1985) using 1,000 pseudoreplications. PHYLIP, version 3.5c (Felsenstein 1995) was used for these analyses, and TreeView, version 1.2 (Page 1996) was used to print resultant trees.

RESULTS

Pattern of genetic variation.—Seventeen of the 36 loci analyzed were monomorphic and fixed for the same allele among populations: SDH, LDH-1, MDH-1, MDH-2, IDH-2, G6PD, G3PD, SOD-2, GOT-2, HK-1, HK-2, AK, LAP, AP-3, ALDO, FUM, and GPI. Nineteen loci were polymorphic or discriminant among population samples, and their allele frequencies are shown in Table 1.

Comparisons with genetically known and determined specimens confirmed the presence of *A. uralensis*, *A. hermonensis*, and *A. flavicollis* in the samples. In the case of *A. hermonensis*, for the reasons given in Fi-

TABLE 1.—Allele frequencies at 19 polymorphic or discriminant loci in 26 population samples studied and values of intrapopulation genetic variation at 36 loci (see Appendix I for designations of the samples; numbers of animals analyzed are given in parentheses).

Loci	Allele	Population											
		USFE (7)	UGUZ (2)	USUM (5)	UDAM (16)	UKBC (6)	UYAL (4)	UBGD (3)	HBUR (1)	HSFE (1)	HGUZ (3)	HDAM (3)	HYAL (5)
GPD	102	—	—	0.10	0.06	—	—	—	1.00	1.00	1.00	1.00	1.00
	106	1.00	1.00	0.90	0.94	1.00	1.00	1.00	—	—	—	—	—
	93	—	—	—	—	—	—	—	—	—	—	—	—
LDH-2	100	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
	97	—	—	—	—	—	—	—	—	—	—	—	—
ME-1	100	1.00	1.00	0.50	0.57	0.75	1.00	1.00	—	1.00	1.00	1.00	0.88
	105	—	—	0.50	0.43	0.25	—	—	1.00	—	—	—	0.12
	93	—	—	—	—	—	—	—	—	—	—	—	—
ME-2	98	—	—	—	—	—	—	—	—	—	0.17	—	—
	94	1.00	1.00	1.00	1.00	1.00	0.88	1.00	1.00	1.00	0.83	1.00	1.00
	88	—	—	—	—	—	0.12	—	—	—	—	—	—
IDH-1	100	1.00	1.00	1.00	1.00	1.00	1.00	1.00	—	—	—	—	—
	108	—	—	—	—	—	—	—	1.00	1.00	1.00	1.00	1.00
	113	—	—	—	—	—	—	—	—	—	—	—	—
PGD	100	0.64	0.50	0.50	0.25	0.17	0.12	0.17	1.00	1.00	0.67	1.00	1.00
	108	0.36	0.50	0.50	0.75	0.83	0.88	0.83	—	—	0.33	—	—
	92	—	—	—	—	—	—	—	—	—	—	—	—
SOD-2	100	1.00	1.00	1.00	1.00	1.00	1.00	1.00	—	—	—	—	—
	97	—	—	—	—	—	—	—	1.00	1.00	1.00	1.00	1.00
NP	100	—	—	—	—	—	—	—	1.00	1.00	1.00	1.00	1.00
	95	1.00	1.00	1.00	1.00	1.00	1.00	1.00	—	—	—	—	—
	90	—	—	—	—	—	—	—	—	—	—	—	—
GOT-1	100	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
	106	—	—	—	—	—	—	—	—	—	—	—	—
CK	100	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
	95	—	—	—	—	—	—	—	—	—	—	—	—
PGM-1	100	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.90
	103	—	—	—	—	—	—	—	—	—	—	—	—
	95	—	—	—	—	—	—	—	—	—	—	—	0.10
PGM-2	100	1.00	1.00	1.00	1.00	1.00	1.00	0.83	1.00	1.00	1.00	1.00	1.00
	96	—	—	—	—	—	—	0.17	—	—	—	—	—
AP-1	100	—	—	—	—	—	—	—	1.00	1.00	1.00	1.00	1.00
	105	1.00	1.00	1.00	1.00	1.00	1.00	1.00	—	—	—	—	—
AP-2	94	—	—	—	—	—	—	—	—	—	—	—	—
	100	1.00	1.00	1.00	1.00	1.00	1.00	1.00	—	—	—	—	—
	90	—	—	—	—	—	—	—	1.00	1.00	1.00	1.00	1.00
ADA	100	0.93	1.00	1.00	0.78	0.83	1.00	1.00	1.00	1.00	0.75	0.83	0.80
	105	—	—	—	—	—	—	—	—	—	—	—	—
	108	0.07	—	—	0.09	0.08	—	—	—	—	0.25	0.17	—
	113	—	—	—	—	—	—	—	—	—	—	—	—
	115	—	—	—	—	—	—	—	—	—	—	—	0.20
GPI	85	—	—	—	0.13	0.08	—	—	—	—	—	—	—
	100	1.00	1.00	1.00	0.97	0.92	1.00	1.00	0.50	0.50	0.33	0.83	0.80
	96	—	—	—	0.03	0.08	—	—	0.50	0.50	0.67	0.17	0.20
ES-1	100	1.00	1.00	1.00	0.80	0.83	0.88	1.00	1.00	1.00	1.00	1.00	0.90
	103	—	—	—	0.10	0.17	—	—	—	—	—	—	0.10
	95	—	—	—	0.10	—	0.12	—	—	—	—	—	—
ES-2	100	—	—	—	—	—	—	—	1.00	1.00	—	0.75	0.90
	98	0.21	—	0.30	0.16	0.33	—	0.17	—	—	—	—	—
	95	0.79	1.00	0.70	0.84	0.67	1.00	0.83	—	—	1.00	0.25	0.10

TABLE 1.—Extended.

Population													
HSBS	HDOG	HHAK	HGHO	HBHS	HABS	HSIV	HVAL	FGUZ	FDAM	FYER	FGHO	ASLM	NOWK
(9)	(1)	(1)	(8)	(10)	(2)	(1)	(2)	(2)	(2)	(2)	(7)	(6)	(2)
0.89	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	—	—
—	—	—	—	—	—	—	—	—	—	—	—	1.00	1.00
0.11	—	—	—	—	—	—	—	—	—	—	—	—	—
1.00	1.00	1.00	0.75	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
—	—	—	0.25	—	—	—	—	—	—	—	—	—	—
1.00	1.00	1.00	0.64	0.40	1.00	0.50	1.00	1.00	0.75	1.00	0.58	0.17	0.25
—	—	—	0.36	0.60	—	0.50	—	—	0.25	—	0.42	—	—
—	—	—	—	—	—	—	—	—	—	—	—	0.83	0.75
—	—	—	0.06	0.15	—	—	—	—	—	—	—	—	—
1.00	1.00	1.00	0.94	0.85	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	1.00	1.00
1.00	1.00	1.00	1.00	0.95	1.00	1.00	1.00	1.00	1.00	1.00	1.00	—	—
—	—	—	—	0.05	—	—	—	—	—	—	—	—	—
1.00	1.00	1.00	0.75	0.50	0.75	1.00	0.50	1.00	1.00	1.00	0.86	1.00	1.00
—	—	—	0.25	0.50	0.25	—	0.50	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	0.14	—	—
—	—	—	—	—	—	—	—	1.00	1.00	1.00	1.00	1.00	1.00
1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	—	—	—	—	—	—
1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	—	—	—	—	—	—
—	—	—	—	—	—	—	—	1.00	1.00	1.00	1.00	—	—
—	—	—	—	—	—	—	—	—	—	—	—	1.00	1.00
1.00	1.00	1.00	0.56	0.70	0.75	1.00	1.00	1.00	1.00	1.00	0.93	1.00	1.00
—	—	—	0.44	0.30	0.25	—	—	—	—	—	0.07	—	—
1.00	1.00	1.00	1.00	0.95	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
—	—	—	—	0.05	—	—	—	—	—	—	—	—	—
1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.75	0.93	1.00	1.00
—	—	—	—	—	—	—	—	—	—	0.25	0.07	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—
1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
—	—	—	—	—	—	—	—	—	—	—	—	—	—
1.00	1.00	1.00	1.00	0.85	1.00	1.00	1.00	—	—	—	—	—	—
—	—	—	—	0.15	—	—	—	—	—	—	—	1.00	1.00
—	—	—	—	—	—	—	—	1.00	1.00	1.00	1.00	—	—
—	—	—	—	—	—	—	—	1.00	1.00	1.00	1.00	1.00	1.00
1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	—	—	—	—	—	—
1.00	1.00	1.00	0.50	0.70	1.00	1.00	1.00	0.75	0.75	1.00	0.92	—	—
—	—	—	—	—	—	—	—	—	—	—	—	0.83	0.75
—	—	—	0.50	0.30	—	—	—	0.25	0.25	—	0.08	—	—
—	—	—	—	—	—	—	—	—	—	—	—	0.17	0.25
—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—
0.61	0.50	—	0.69	0.70	0.50	—	1.00	0.50	1.00	1.00	1.00	1.00	1.00
0.39	0.50	1.00	0.31	0.30	0.50	1.00	—	0.50	—	—	—	—	—
1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—
0.89	1.00	1.00	1.00	0.95	1.00	1.00	0.50	0.75	1.00	1.00	1.00	1.00	1.00
—	—	—	—	—	—	—	—	—	—	—	—	—	—
0.11	—	—	—	0.05	—	—	0.50	0.25	—	—	—	—	—

TABLE 1.—Continued.

Loci	Allele	Population											
		USFE (7)	UGUZ (2)	USUM (5)	UDAM (16)	UKBC (6)	UYAL (4)	UBGD (3)	HBUR (1)	HSFE (1)	HGUZ (3)	HDAM (3)	HYAL (5)
ES-3	100	1.00	1.00	1.00	0.97	0.92	1.00	1.00	1.00	1.00	1.00	1.00	1.00
	105	—	—	—	—	—	—	—	—	—	—	—	—
	110	—	—	—	0.03	0.08	—	—	—	—	—	—	—
A		1.08	1.03	1.11	1.28	1.22	1.08	1.08	1.03	1.03	1.11	1.08	1.17
P _{1%}		0.083	0.028	0.111	0.222	0.194	0.083	0.083	0.028	0.028	0.111	0.083	0.167
P _{5%}		0.083	0.028	0.111	0.167	0.194	0.083	0.083	0.028	0.028	0.111	0.083	0.167
H _n		0.036	0.028	0.056	0.048	0.056	0.021	0.028	0.028	0.028	0.023	0.032	0.035
H _e		0.028	0.019	0.049	0.060	0.060	0.021	0.028	0.028	0.028	0.053	0.032	0.043

lippucci et al. (1996) and to avoid possible taxonomic confusion (Mezhzherin 1997; Zagorodnyuk et al. 1997), the name *hermonensis* is retained throughout this paper. The taxon from Asalem and Now Kandeh in northern Iran appeared distinct from all the species used as standards, as well as from *A. alpicola*, *A. mystacinus*, *A. epimelas*, *A. agrarius*, and *A. peninsulae* (M. G. Filippucci et al., in litt.), thus deserving specific status. Because of its external morphologic similarity with a species described by Vorontsov et al. (1992) and the close proximity of the type locality, northern Iranian samples were provisionally referred to *Apodemus cf. hyrcanicus*.

The level of genetic variation for the eastern Anatolian and Iranian group of populations (Tables 1 and 2) was compared with variation in western Anatolia (Filippucci et al. 1996). Samples from Burdur and Seyfe were excluded from the analysis because of their geographic location (western and central part of Asia Minor, respectively; cf. Fig. 1), and gene frequencies were then summed for the eastern group. In all but a single case, no marked differences were found between the 2 samples. The only exception was the low P_{1%} in *A. flavicollis* from the east (19.4%) relative to the western sample (41.7%); however, that difference probably was caused by generally small sample sizes from eastern Turkey and Armenia. Unfortunately, it was not possible to test differences between indices because

of the severe nonnormality of the data, but by far the lowest level of genetic variation appeared in *A. cf. hyrcanicus* (Table 2). Data from eastern and western parts (i.e., the present data and those of Filippucci et al. 1996) were then pooled.

Intra- and interspecific genetic differentiation.—Genetic differentiation among conspecific populations was assessed between samples within the eastern group of populations (Burdur and Seyfe excluded; Table 3). Genetic distances were then compared with those within the western group (Burdur included) and between western and eastern populations.

In *A. uralensis*, genetic distances (D) among eastern populations were exceptionally low, ranging from 0 to 0.011 (average D = 0.0040), and yet fully comparable with those within the western group (average 0.0061, range 0–0.013) and between western and eastern populations (0.0074; maximum D = 0.027 between Yenice and Yalnızçam Pass). The average of the total sample equaled that within the western group (D = 0.061).

Genetic distances between populations of *A. hermonensis* were 2–4 times higher than those in *uralensis* but still quite low: D = 0.0162 (0–0.051) within the eastern group and D = 0.0126 (0–0.014) within the western group; again, the divergence between western and eastern populations did not exceed the divergence within the 2 regions (D = 0.0154; maximum D = 0.061 between

TABLE 1.—Continued and Extended.

Population													
HSBS (9)	HDOG (1)	HHAK (1)	HGHO (8)	HBHS (10)	HABS (2)	HSIV (1)	HVAL (2)	FGUZ (2)	FDAM (2)	FYER (2)	FGHO (7)	ASLM (6)	NOWK (2)
0.94	1.00	1.00	0.94	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.83	1.00
0.06	—	—	0.06	—	—	—	—	—	—	—	—	0.17	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—
1.11	1.03	1.00	1.22	1.28	1.08	1.03	1.06	1.08	1.06	1.03	1.14	1.08	1.06
0.111	0.028	0.000	0.222	0.278	0.083	0.028	0.056	0.083	0.056	0.028	0.139	0.083	0.056
0.111	0.028	0.000	0.222	0.278	0.083	0.028	0.056	0.083	0.056	0.028	0.139	0.083	0.056
0.031	0.028	0.000	0.088	0.081	0.056	0.028	0.056	0.056	0.028	0.014	0.025	0.028	0.028
0.029	0.028	0.000	0.085	0.089	0.046	0.028	0.056	0.046	0.028	0.014	0.035	0.025	0.028

Burdur and Güzyurdu). The average genetic distance between all the populations of *A. hermonensis* in the total sample was $D = 0.0101$.

In *A. flavicollis*, the values of Nei's distances within the eastern group of populations were the lowest among the 3 species, ranging from zero to 0.008 ($D = 0.0018$), whereas between-population distances within the western part were an order of magnitude higher (0–0.035; $D = 0.0163$). However, west–east differentiation was similar to that within the western sample (0.0174, maximum $D = 0.039$ between Strandzha in the west and Yerevan and Güzyurdu in the east). The average value of D between populations within the total sample was 0.0141.

The highest genetic distances between populations of different species were 0.294 between *A. uralensis* from Yalnızçam Pass (northeastern Turkey) and *A. hermonensis* from Sivand (southern Iran), and 0.292 between *A. cf. hyrcanicus* from Asalem

(northern Iran) and *A. hermonensis* from Güzyurdu (northeastern Turkey).

Information on intra- and interspecific genetic relationships among the study populations (Table 3) was used for cluster analysis and construction of neighbor-joining trees. Four distinct groups, coincident with presumed species groups, appeared on the trees irrespective of the distance measure used (only 1 tree shown here; Fig. 2). Conversely, little differentiation and substructuring were found within individual species where the branching pattern was mostly random. That pattern was even more obvious when the pooled sample (i.e., including the western Anatolian populations) was considered (Fig. 3).

DISCUSSION

Systematic status of the eastern Anatolian and Iranian wood mice.—Four species, belonging to the subgenus *Sylvaemus* of the genus *Apodemus*, were demonstrated in the material analyzed. Three of those (*A. flav-*

TABLE 2.—Mean values of indices of genetic variability in *Apodemus* at 36 loci.

Species	Number of populations	\bar{N}^a	\bar{A}	$\bar{P}_{1\%}$	$\bar{P}_{5\%}$	\bar{H}_0	\bar{H}_c
		<i>A. uralensis</i>	7	6.09	1.175	0.151	0.131
<i>A. hermonensis</i>	13	3.52	1.147	0.159	0.159	0.052	0.056
<i>A. flavicollis</i>	4	3.23	1.102	0.101	0.101	0.029	0.032
<i>A. cf. hyrcanicus</i>	2	3.95	1.075	0.076	0.076	0.028	0.026

^a \bar{N} is mean sample size per locus.

TABLE 3.—Matrix of Nei (1978) unbiased genetic distances (below diagonal) and Cavalli-Sforza and Edwards (1967) chord distances (above diagonal), based on 36 loci from *Apodemus* (see Appendix I for the designation of population samples).

Popu- lation	Population												
	UGUZ	UYAL	UBGD	USFE	UDAM	UKBC	USUM	HGUZ	HYAL	HSFE	HDAM	HSBS	HHAK
UGUZ	—	0.070	0.074	0.060	0.121	0.120	0.107	0.387	0.407	0.413	0.396	0.403	0.432
UYAL	0.001	—	0.083	0.099	0.120	0.126	0.128	0.395	0.420	0.426	0.410	0.416	0.445
UBGD	0.000	0.000	—	0.075	0.119	0.106	0.107	0.396	0.418	0.424	0.408	0.414	0.442
USFE	0.000	0.008	0.004	—	0.113	0.105	0.094	0.387	0.406	0.412	0.393	0.402	0.431
UDAM	0.006	0.006	0.005	0.009	—	0.058	0.083	0.390	0.408	0.422	0.404	0.413	0.439
UKBC	0.005	0.003	0.000	0.006	0.000	—	0.096	0.396	0.415	0.426	0.411	0.418	0.441
USUM	0.005	0.011	0.007	0.005	0.001	0.002	—	0.391	0.400	0.413	0.398	0.404	0.432
HGUZ	0.200	0.211	0.211	0.202	0.214	0.215	0.209	—	0.182	0.179	0.144	0.164	0.189
HYAL	0.224	0.245	0.238	0.217	0.237	0.237	0.219	0.029	—	0.092	0.092	0.093	0.141
HSFE	0.235	0.256	0.248	0.228	0.253	0.250	0.233	0.030	0.003	—	0.080	0.058	0.081
HDAM	0.211	0.232	0.225	0.205	0.228	0.228	0.212	0.019	0.000	0.002	—	0.071	0.135
HSBS	0.221	0.243	0.235	0.215	0.240	0.238	0.221	0.026	0.000	0.000	0.000	—	0.108
HHAK	0.260	0.282	0.274	0.253	0.277	0.272	0.259	0.033	0.018	0.007	0.019	0.010	—
HDOG	0.235	0.256	0.248	0.228	0.253	0.250	0.233	0.030	0.003	0.000	0.002	0.000	0.007
HBUR	0.271	0.294	0.285	0.264	0.258	0.268	0.233	0.061	0.024	0.029	0.031	0.029	0.036
HGHO	0.252	0.267	0.260	0.244	0.249	0.251	0.238	0.040	0.013	0.018	0.012	0.017	0.031
HBHS	0.232	0.239	0.234	0.229	0.219	0.223	0.209	0.039	0.016	0.023	0.018	0.022	0.036
HABS	0.227	0.242	0.235	0.222	0.241	0.236	0.226	0.024	0.000	0.000	0.000	0.000	0.004
HSIV	0.271	0.294	0.285	0.264	0.273	0.275	0.252	0.040	0.022	0.014	0.026	0.018	0.007
HVAL	0.193	0.200	0.197	0.194	0.204	0.203	0.196	0.018	0.013	0.021	0.007	0.016	0.043
FGUZ	0.116	0.136	0.129	0.110	0.129	0.128	0.116	0.136	0.121	0.119	0.116	0.118	0.126
FDAM	0.126	0.145	0.138	0.118	0.131	0.134	0.115	0.168	0.120	0.128	0.119	0.126	0.152
FYER	0.125	0.144	0.137	0.118	0.140	0.139	0.122	0.171	0.122	0.128	0.121	0.125	0.151
FGHO	0.130	0.147	0.140	0.123	0.130	0.134	0.113	0.175	0.125	0.134	0.127	0.132	0.158
ASLM	0.111	0.130	0.123	0.102	0.111	0.112	0.101	0.292	0.235	0.250	0.237	0.243	0.275
NOWK	0.102	0.121	0.113	0.093	0.103	0.104	0.093	0.281	0.225	0.239	0.227	0.234	0.264

icollis, *A. hermonensis*, and *A. uralensis*) also were found in western Anatolia by Filippucci et al. (1996); our data thus enlarge our knowledge about the ranges of these species across a vast area of southwestern Asia. The specific status of the 4th taxon was proven in our analysis and it was provisionally called *A. cf. hyrcanicus*; it was found at only 2 sites south of the Caspian Sea and was reported in the fauna of Iran for the 1st time. Conversely, *A. uralensis* was not found in either Iranian locality investigated.

The absence of *A. sylvaticus* in our material is consistent with Filippucci et al. (1996), who found only 3 individuals of this species from only 2 adjacent sites south of the Black Sea. Thus, it can be concluded from analysis of our data (collected from

>30 Turkish and Iranian localities altogether and from several sites in Israel and Jordan—Benda and Sádlová 1999; Filippucci 1992), that *A. sylvaticus* is virtually absent from the entire area of the Middle East. Whether the minute inland isolate offshore of the Black Sea is a result of past human-mediated immigration, or rather a relict of a larger former range, is difficult to decide; however, the former hypothesis seems more plausible.

From analysis of our data and those of Filippucci et al. (1996), the range of *A. uralensis* seems to be restricted to a narrow belt of relatively humid habitat in the very north of Asia Minor, where this species lives in mountain chains at 850–2,800 m above mean sea level. Uludağ and Güyzurdu seem to be the southernmost known lo-

TABLE 3.—Extended.

Population												
HDOG	HBUR	HGHO	HBHS	HABS	HSIV	HVAL	FGUZ	FDAM	FYER	FGHO	ASLM	NOWK
0.413	0.440	0.428	0.407	0.410	0.440	0.376	0.308	0.320	0.316	0.325	0.299	0.292
0.426	0.452	0.437	0.413	0.419	0.452	0.383	0.325	0.337	0.332	0.341	0.317	0.310
0.424	0.449	0.435	0.412	0.416	0.449	0.383	0.324	0.334	0.329	0.338	0.313	0.307
0.412	0.438	0.423	0.405	0.410	0.438	0.380	0.303	0.313	0.314	0.321	0.295	0.289
0.422	0.425	0.416	0.390	0.416	0.433	0.387	0.315	0.318	0.332	0.321	0.316	0.311
0.426	0.436	0.424	0.399	0.419	0.439	0.394	0.323	0.330	0.340	0.333	0.318	0.312
0.413	0.413	0.415	0.389	0.409	0.424	0.379	0.310	0.305	0.315	0.306	0.305	0.300
0.179	0.233	0.197	0.185	0.176	0.206	0.146	0.328	0.362	0.366	0.370	0.459	0.455
0.092	0.147	0.161	0.162	0.120	0.142	0.132	0.317	0.318	0.320	0.322	0.423	0.419
0.000	0.150	0.157	0.167	0.078	0.115	0.141	0.310	0.320	0.316	0.326	0.424	0.419
0.080	0.170	0.150	0.157	0.112	0.158	0.106	0.303	0.313	0.316	0.322	0.422	0.417
0.058	0.161	0.162	0.170	0.097	0.135	0.125	0.309	0.323	0.318	0.328	0.421	0.419
0.081	0.171	0.185	0.194	0.112	0.081	0.189	0.320	0.344	0.340	0.350	0.442	0.437
—	0.150	0.157	0.167	0.078	0.115	0.141	0.310	0.320	0.316	0.326	0.424	0.419
0.029	—	0.171	0.157	0.169	0.115	0.206	0.344	0.333	0.350	0.330	0.434	0.432
0.018	0.027	—	0.098	0.128	0.173	0.180	0.334	0.329	0.348	0.330	0.435	0.434
0.023	0.017	0.003	—	0.136	0.172	0.166	0.336	0.330	0.350	0.329	0.429	0.426
0.000	0.026	0.006	0.009	—	0.139	0.130	0.320	0.330	0.325	0.330	0.431	0.426
0.014	0.014	0.028	0.026	0.012	—	0.206	0.331	0.341	0.350	0.342	0.445	0.441
0.021	0.051	0.028	0.023	0.012	0.051	—	0.327	0.331	0.326	0.335	0.431	0.427
0.119	0.152	0.137	0.140	0.118	0.135	0.136	—	0.112	0.125	0.137	0.371	0.365
0.128	0.145	0.134	0.134	0.128	0.153	0.138	0.001	—	0.095	0.065	0.359	0.354
0.128	0.160	0.147	0.147	0.127	0.160	0.137	0.005	0.000	—	0.097	0.362	0.356
0.134	0.140	0.138	0.132	0.132	0.153	0.141	0.008	0.000	0.004	—	0.365	0.360
0.250	0.256	0.246	0.240	0.251	0.271	0.261	0.171	0.157	0.171	0.164	—	0.047
0.239	0.248	0.237	0.231	0.241	0.262	0.250	0.161	0.148	0.161	0.155	0.000	—

calities for the species in the Middle East and include 1 of the southernmost findings of *A. uralensis* in the Palearctic region in general (Uludağ is also the westernmost limit of the species' range in Anatolia). Conversely, no such habitat preferences were found in *A. flavicollis* and *A. hermonensis*, and the species were found throughout most of the whole study area, although the distribution of *A. flavicollis* in Iran seems to be limited to the western edge of the Zagros Mountains (Gholaman, west of Khorram Abad). Finally, *A. cf. hyrcanicus* was found at only 2 sites near the southern coast of the Caspian Sea. This form thus seems to be limited to humid, lowland deciduous forests stretched from Talysh (southeastern Azerbaijan) in the west to the

foothills of Kopet Dag (southwestern Turkmenistan) in the east.

Genetic variation and differentiation.—No substantial differences were found in the level of genic variation between western and eastern Anatolian and Iranian populations of *A. uralensis*, *A. hermonensis*, and *A. flavicollis*. Lowered values for the proportion of polymorphic loci (P) and heterozygosity (H) of eastern populations of *A. flavicollis* were most probably caused by small sample sizes, as indicated by increased value of P = 14% in Gholaman, the only eastern sample containing >2 specimens of *A. flavicollis*. However, it is not clear if low variation in *A. cf. hyrcanicus* was genuine or related to limited sample sizes. Clearly, more extensive sampling of these species is needed.

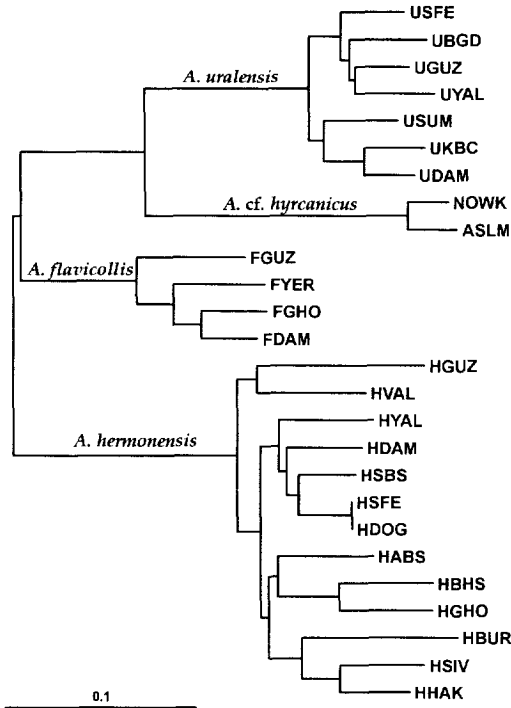


FIG. 2.—Neighbor-joining tree based on Cavalli-Sforza and Edwards (1967) chord distances, computed from 36 presumptive loci (basic branching pattern based on Nei's distances was the same). Population acronyms are as those listed in Appendix I. Note that although the tree is presented here as mid-rooted, it is an unrooted one. The scale represents evolutionary change expressed as the chord distance.

Analysis of our data suggests that only low differentiation exists between local populations, as is exemplified by low values of genetic distances and by the absence of any apparent structuring within individual species. As in the case of the level of genetic variation, no differences were found in values of genetic distances between western and eastern groups of populations. When intraspecific distances are compared between species, western and eastern populations of *A. uralensis* are less differentiated from each other than those of *A. hermonensis* and *A. flavicollis*, in which between-population distances are >2 times higher. This is probably due to the much

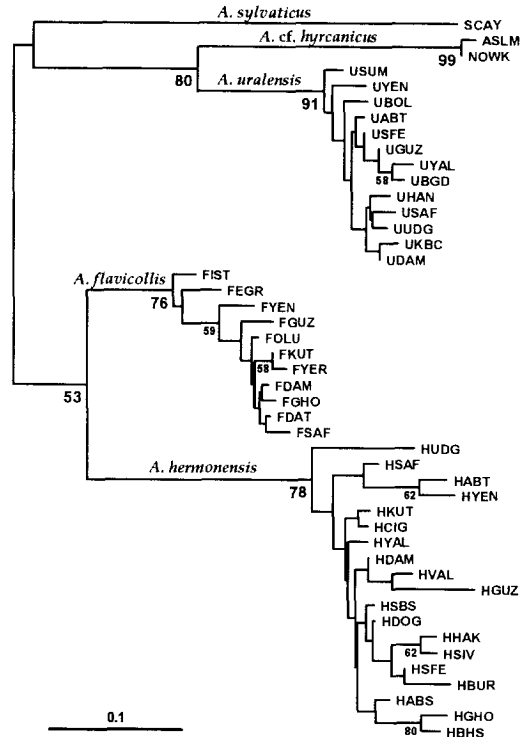


FIG. 3.—Neighbor-joining tree based on Cavalli-Sforza and Edwards (1967) chord distances, computed from 36 loci (basic branching pattern on Nei's distances was very similar), for 46 population samples from this study and Filipucci et al. (1996). Population acronyms are listed in Appendix I; for samples from Filipucci et al. (1996), acronyms are: *A. sylvaticus*: SCAY, Çaycuma; *A. uralensis*: UYEN, Yenice; UBOL, Bolu; UABT, Abant; UHAN, Hanyatak; USAF, Safranbolu; UUDG, Uludağ; *A. flavicollis*: FIST, Istranca (Strandzha) Mts.; FEGR, Eğirdir; FYEN, Yenice; FOLU, Ölüdeniz; FKUT, Kütahya; FDAT, Datça; FSAF, Safranbolu; *A. hermonensis*: HUDG, Uludağ; HSAF, Safranbolu; HABT, Abant; HYEN, Yenice; HKUT, Kütahya; HCIG, Çiğlikara. The numbers indicate how many times a node appeared in 1,000 pseudo-replicates (large numbers are for nodes representing specific clades and higher groupings, small numbers for intraspecific nodes). Bootstrap values >50 are shown. Note that although the tree is presented here as mid-rooted, it is an unrooted one. The scale shown is the chord distance.

larger ranges (and hence higher geographic distances between some populations) of the last 2 species.

Genetic relationships between species studied, as displayed by the phylogenetic trees (Figs. 2 and 3), are similar to those reported in earlier papers (Filippucci 1992; Filippucci et al. 1996). However, it should be noted that genetic relationships within the subgenus *Sylvaemus* are rather mosaic-like, probably due to rapid adaptive radiation of the group, so resolving branching order within the subgenus is rather difficult (M. G. Filippucci et al., in litt.).

Taxonomic remarks.—Although we provisionally have referred the unknown populations from Asalem and Now Kandeh to *Apodemus* cf. *hyrcanicus*, their affinity requires confirmation. *A. hyrcanicus* was characterized genetically by Vorontsov et al. (1989) on the basis of 4 loci, and later by Mezhzherin et al. (1992) and Vorontsov et al. (1992) using more comprehensive sets of loci. Unfortunately, it is not possible to compare our results with those by Mezhzherin and his colleagues. Of the loci discriminating *A. hyrcanicus* from other species (either separately or in combination with other loci), only IDH-1 revealed the same pattern in the present study. GPD was reported by Mezhzherin et al. (1992) to have the same allele as in *A. hermonensis* and *A. flavicollis*, whereas being different from *A. uralensis*. However, the opposite pattern was found in the present study. Finally, G6PD (Gpd-x in Mezhzherin et al. 1992) was monomorphic in our study, but alternative alleles were found by Mezhzherin and coworkers. Confusion also exists in the designation of esterase loci in the papers by Mezhzherin et al. (1992) and Vorontsov et al. (1992). Discrepancies between Mezhzherin's data and ours can probably be accounted for by different electrophoretic methods used (polyacrylamide versus starch gels, buffers, and so on). Hence, examination of our samples with those from the type locality of *A. hyrcanicus* on the same gel is needed.

Morphologically, all 8 specimens from Asalem and Now Kandeh that we analyzed genetically fall into the ranges given by Vorontsov et al. (1992) and Mezhzherin (1997); the mean body length was $96.11 \text{ mm} \pm 1.54 \text{ SE}$ and the length of hind foot averaged $22.66 \pm 0.25 \text{ mm}$. However, the tail ($99.86 \pm 1.52 \text{ mm}$) was distinctly longer than the body ($\text{tail/body} \times 100 = 104.02 \pm 1.83\%$, range = 98.5–111.5%), and the pectoral spot was only apparent in 2 animals ($n = 8$ for all measures). Yet, given the morphologic similarity and geographic location of the 2 sampling sites, conspecificity of the mice from Asalem and Now Kandeh with *A. hyrcanicus* from Talysh seems plausible. If this is so, then the latter locality extends the known range of the species by 700 km east of the type locality and represents the easternmost limit of its distribution.

Apodemus arianus was first described by Blanford (1875:311–312) as *Mus erythronotus* and later renamed *Mus arianus* (Blanford 1881). In the original paper, the animal is described as being similar to *Mus* (i.e., *Apodemus*) *sylvaticus*, having a tail (107 mm) longer than its body (102 mm) and a hind foot of $<23 \text{ mm}$; neither pectoral spot nor collar were mentioned. It may be hypothesized that *A. arianus* is either a distinct species, as suggested by Musser and Carleton (1993) and Musser et al. (1996), or it is conspecific with 1 of the following taxa: *flavicollis*, *ponticus*, *hyrcanicus*, *uralensis*, *fulvipectus*, or *wardi*.

Given the local distribution of *A. hyrcanicus* and the absence of *A. uralensis* in Iran, coupled with their ecologic preferences (avoiding areas with strictly continental climate), the 2 species may be dismissed. Moreover, *A. uralensis* is characterized by smaller overall size and a tail shorter than the body (Mezhzherin 1996; Vorontsov et al. 1992). Conversely, *A. flavicollis* is typical in having a body and hind feet much larger than those described for *A. arianus*, and by the presence of pectoral spot or, frequently, a collar. Furthermore, *A. ponticus*

is described as a large animal with a bold spot and as being genetically close to *A. flavicollis* (Mezhzherin 1991).

Darviche et al. (1979) report on a population of wood mice, genetically distinct from both *A. sylvaticus* and *A. flavicollis*, from Quazvin in northern Iran. Although no external measurements were given, they mention the absence of a pectoral spot. Recently, the taxon has been asserted as being identical with *A. arianus* by Mezhzherin (1997) and Zagorodnyuk et al. (1997). As far as it is possible to compare results by Darviche et al. (1979) with our own data, we cannot decide whether this form should be classified with *A. hermonensis* or *A. flavicollis* because, unfortunately, we did not score for albumin and we found no polymorphism in sorbitol dehydrogenase, as reported by Darviche et al. (1979). It should be noted that Darviche et al. (1979) compared only *A. sylvaticus* and *A. flavicollis* with the Quazvin population.

Taking into account genetic data and absence of the distinct pectoral spot, typical for *A. flavicollis* but frequently missing or very tiny in *A. fulvipectus*, we may draw a provisional conclusion that Iranian *A. arianus* is conspecific with *A. fulvipectus* (and *falzfeini*) as was suggested by Mezhzherin (1997) and Zagorodnyuk et al. (1997). It also seems plausible that this taxon may be conspecific with *A. hermonensis*, as suggested by Filippucci et al. (1996; cf. Mezhzherin 1997; Zagorodnyuk et al. 1997), although this conclusion still awaits genetic confirmation. Finally, data on *A. wardi* are very scarce. This species is said to occur in eastern Iran, Nepal, Kashmir, Pakistan, and Afghanistan (Musser and Carleton 1993). Whether this form genuinely represents a distinct species it is not clear, and its systematic relationships with other species of the subgenus *Sylvaemus* are unknown. Again, genetic studies of animals from the type locality of *A. arianus* (and *A. wardi*) and morphologic examination of the type specimens together with voucher specimens

seem to be necessary to solve this taxonomic problem.

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APPENDIX I

List of sampled species and populations, sampling sites, and numbers of animals investigated. Note that because of small sample sizes and close proximity of the sites, samples from Damar and Kabaca were pooled in *Apodemus hermonensis* (into HDAM) and *A. flavicollis* (into FDAM).

Species	Locali- ty	Locality	n	Sample code
<i>A. uralensis</i>	2	Seyfe, 35 km NNE of Amasya, Amasya Province, ca. 1,500 m, N Turkey	7	USFE
	3	Güzyurdu, 5 km S, Otlukbeli Mts., Gümüşhane Province, 2,300 m, E Turkey	2	UGUZ
	4	Sumelas, 35 km S of Trabzon, Trabzon Province, ca. 1,500 m, NE Turkey	5	USUM
	5	Damar, 4 km SE of Murgul, S of Borçka, Artvin Province, ca. 2,200 m, NE Turkey	16	UDAM
	6	Kabaca, 8 km S of Murgul, S of Borçka, Artvin Province, ca. 2,000 m, NE Turkey	6	UKBC
	7	Yalnızçam Pass, Artvin Province, 2,650 m, NE Turkey	4	UYAL
	8	Bağdaşan, Yalnızçam Mts., Kars Province, 2,800 m, NE Turkey	3	UBGD
	<i>A. hermonensis</i>	1	Burdur, Isparta Province, ca. 850 m, W Turkey	1
2		Seyfe, 35 km NNE of Amasya, Amasya Province, ca. 1,500 m	1	HSFE
3		Güzyurdu, Otlukbeli Mts., Gümüşhane Province, 2,300 m	3	HGUZ
5		Damar, 4 km SE of Murgul, S. of Borçka, Artvin Province, ca. 2,200 m	3	HDAM
7		Yalnızçam Pass, Artvin Province, 2,650 m	5	HYAL
9		Sırbasan, 5 km N, 25 km W of Sarıkamış, Güllü Mts., Kars Province, ca. 2,500 m, E Turkey	9	HSBS
10		Doğubayazıt, Ağrı Province, E Turkey	1	HDOG
11		Hakkâri, Hakkâri Province, SE Turkey	1	HHAK
13		Gholaman, 30 km W of Khorram Abad, Zagros Mts., Lorestan Province, 1,000 m, SW Iran	8	HGHO
14		Baba Hasan, 10 km N of Yasuj, Zagros Mts., Boyerahmadva-Kuhgiluyeh Province, 2,000 m, S Iran	10	HBHS
15		Abshar, Zagros Mts., Fars Province, 1,000 m, S Iran	2	HABS
16		Sivand, 10 km E, Zagros Mts., Fars Province, 1,700 m, S Iran	1	HSIV
17		Vali Abad, Alborz Mts., Mazandaran Province, 1,800–2,500 m, N Iran	2	HVAL
<i>A. flavicollis</i>		3	Güzyurdu, Otlukbeli Mts., Gümüşhane Province, 2,300 m	2
	4	Damar, 4 km SE of Murgul, S of Borçka, Artvin Province, ca. 2,200 m	2	FDAM
	12	Yerevan, 10 km W by road to Echmiadzin, Armenia	2	FYER
	13	Gholaman, 30 km W of Khorram Abad, Zagros Mts., Lorestan Province, 1,000 m, SW Iran	7	FGHO
<i>A. cf. hyrcanicus</i>	18	Asalem, 12 km W, Talesh Mts., Gilan Province, 280 m, N Iran	6	ASLM
	19	Now Kandeh, 10 km S, Mazandaran Province, 200 m, N Iran	2	NOWK

APPENDIX II

List of enzymes and loci investigated.

Enzyme	Locus	Enzyme Commission no.
α -Glycerophosphate dehydrogenase	GPD	E.C. 1.1.1.8
Sorbitol dehydrogenase	SDH	E.C. 1.1.1.14
Lactate dehydrogenase	LDH-1	E.C. 1.1.1.27
	LDH-2	
Malate dehydrogenase	MDH-1	E.C. 1.1.1.37
	MDH-2	
Malic enzyme	ME-1	E.C. 1.1.1.40
	ME-2	
Isocitrate dehydrogenase	IDH-1	E.C. 1.1.1.42
	IDH-2	
6-Phosphogluconate dehydrogenase	PGD	E.C. 1.1.1.44
Glucose-6-phosphate dehydrogenase	G6PD	E.C. 1.1.1.49
Glyceraldehyde-3-phosphate dehydrogenase	G3PD	E.C. 1.2.1.12
Superoxide dismutase	SOD-1	E.C. 1.15.1.1
	SOD-2	
Nucleoside phosphorylase	NP	E.C. 2.4.2.1
Glutamate-oxalacetate transaminase	GOT-1	E.C. 2.6.2.1
	GOT-2	
Hexokinase	HK-1	E.C. 2.7.1.1
	HK-2	
Creatine kinase	CK	E.C. 2.7.3.2
Adenylate kinase	AK	E.C. 2.7.4.3
Phosphoglucomutase	PGM-1	E.C. 2.5.7.1
	PGM-2	
Esterases	ES-1	E.C. 3.1.1.1
	ES-2	
	ES-3	
Leucyl aminopeptidase	LAP	E.C. 3.4.11
Aminopeptidases	AP-1	E.C. 3.4.11
	AP-2	
	AP-3	
Adenosine deaminase	ADA	E.C. 3.5.4.4
Aldolase	ALDO	E.C. 4.1.2.13
Fumarase	FUM	E.C. 4.2.1.2
Mannose phosphate isomerase	MPI	E.C. 5.3.1.8
Glucose phosphate isomerase	GPI	E.C. 5.3.1.9