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Phylogenetic analysis of the five-toed Jerboa (Rodentia) from the Iranian Plateau based on mtDNA and morphometric data

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The genus *Allactaga* is a group of rodents with five morphospecies distributed in the Iranian plateau. In order to conduct a taxonomic revision at the species level, 27 individuals were collected in the Iranian plateau from localities typical of each species. Phylogenetic relationships within species were analyzed using cytochrome oxidase subunit I and morphometric data. Maximum parsimony, maximum likelihood and Bayesian analysis demonstrated that Hotson´s Jerboa and the Iranian Jerboa are identical, with very low molecular divergence. This was confirmed by biometrical analyses of cranial and dental characteristics. Both molecular and morphometric analyses separated the small five-toed Jerboa from the other species. In the phylogenetic tree and haplotype network, the taxonomic situation of the Toussi Jerboa as a new species is prominent, as had been concluded by morphometric data.

Key words: Cytochrome oxidase subunit I, taxonomy, morphometry, *Allactaga*

INTRODUCTION

The five-toad Jerboa of the genus *Allactaga* include 12 morphospecies, defined by morphometric and morphologic characteristics, reported to inhabit arid and semiarid areas of North Africa, the Iranian plateau, and Central Asia and Mongolia (Lay, 1967; Etemad, 1978; Darvish et al., 2006).

This genus can be identified by its large ears and tufted tail. Extensor knee muscles and hind tarsals indicate compatibility with jumping on hind feet (Jouffroy et al., 2003; Krystufek and Vohralik, 2005). First and second upper and lower molars are considerably larger than the third molars (Shahin, 1999).

Five morphospecies of this genus are distributed in the Iranian plateau, including the small five-toed Jerboa, *A. elater* Lichtenstein, 1825; the Toussi Jerboa, *A. toussi,* Darvish et al. 2008*;* the Iranian Jerboa, *A. firouzi,* Womochel, 1978; Hotson´s Jerboa, *A. hotsoni* Thomas, 1920; and Williams´ Jerboa, *A. williamsi,* Thomas, 1897. The small five-toed Jerboa Lichtenstein, 1825 is distributed throughout most of the desert and semi-desert regions of Iran with the exception of the northern slope of the Alborz Mountain forest (Misson, 2001). The Toussi Jerboa was recently described by Darvish et al. (2008) from the Cheshme Gilas area in NW Mashhad. The Iranian Jerboa is described by Womochel (1978) as an endemic species of the highland regions of Shahreza in Esfahan Province, a flat plain

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with a gravel substrate and sparse mountainous and steppe vegetation at 2/253 m elevation. Hotson´s Jerboa was reported by Thomas (1920) in Baluchistan and subsequently in Kavir National Park (Brown, 1980) and Kalmand in the south of Yazd Province (Darvish et al., 2006). The habitat of this species is flat gravel or rocky open plains with sparse vegetation (Hassinger, 1973; Brown, 1980). Williams´ Jerboa has been reported from rocky hills at elevations from 1000 to over 2500 m in western and northwestern Iran (Lay, 1967; Colak et al., 1998).

Most studies of *Allactaga* systematics have been based on morphological and morphometrical characteristics (Darvish et al., 2006; 2008; Shenbrot, 2009). In a recent study based on morphometric data, Shenbrot (2009) demonstrated that the Iranian Jerboa is identical with Hotson´s Jerboa (Shenbrot, 2009). However, the Iranian Jerboa is distinguished from Hotson´s Jerboa by characteristics such as a longer tail, larger ears and feet, darker coloration, a larger skull and smaller premolars (Shenbrot, 2009).

This study confirmed that biological species is not synonymous with morphospecies, and new concepts and methods should be used to descriminate morphospecies.

To shed light on the taxonomic situation among the five-toed Jerboas in the Iranian plateau to delimitate morphospecies and revise the taxonomic determination of each biospecies, we used a total of 638_bp of mitochondrial protein-coding gene, cytochrome oxidase subunit I (*Cox1*) along with morphometric characters. For these, *Cox1* gene sequences were obtained from individuals of 5 recognized species of *Allactaga* to examine the conspecifity of Hotson´s Jerboa and the Iranian Jerboa, and to clarify the status of the Toussi Jerboa relative to the small five-toed Jerboa. The combination of molecular markers and morphometrical characters should yield a robust phylogenetic resolution (Aliabadian et al., 2009; Forschler et al., 2010).

MATERIAL AND METHODS

Sampling design

Tissue samples of 27 individuals were collected from the five nominal species of *Allactaga* distributed in the Iranian plateau. *Pygeretmus pumilio* was used as out group to root the phylogenetic tree. Classification and taxonomy followed Wilson and Reeder (2005).

Following Shenbrot (2009), we measured 24 cranial and dental morphometric variables of 140 samples using digital calipers and a Nikon measuring microscope MM-40, to the nearest 0.01 mm and 0.001 mm, respectively (Tables 2, 3). The specimens are stored in the collection of the Zoological Museum of Ferdowsi University of Mashhad (ZMFUM). Voucher numbers of samples and locality information are shown in Table 1.

Morphometric analyses

Comparison of means was carried out using multiple and single analysis of variance. We conducted ANOVAs for comparison of each of the 24 parameters (Table 2). To normalize distribution, we log-transformed all measurements. Discriminant analyses were conducted using SPSS 16.0. The aim of this procedure was to maximize the variance among groups relative to that within groups.

DNA extraction and sequencing

The whole genomic DNA was extracted from frozen and preserved (90% Ethanol) tissues (liver or muscle) using salt methods (Bruford et al., 1992). The entire *Cox1* gene was PCR amplified using primers VF1d 5´-TTC TCA ACC AAC CAC AAR GAY ATY GG-3´ and VR1d 5´-TAG ACT TCT GGG TGG CCR AAR AAY CA-3´ (Ivanova et al., 2006). The entire gene was sequenced (Aliabadian et al., 2007).

Alignment was performed by BioEdit (Hall, 1999). *Cox1* as a protein-coding gene also controlled for the presence of stop codons or insertion/deletion events that would have disturbed the reading frame. The final aligned dataset included 638 bp for each taxon.

TABLE 1. Tissue samples, numbers and location.

Species	Sample ID Number ZMFUM	Location
A. williamsi	61	Zanjan-Amirabad-Iran
A. williamsi	62	Zanjan-Amirabad-Iran
A. williamsi	44	Hamedan-Karafs-Iran
A. williamsi	45	Hamedan-Karafs-Iran
A. williamsi	36	Chaharmahalobakhtiari-Dashte marjan-Iran
A. williamsi	37	Chaharmahalobakhtiari-dashte marjan-Iran
A. williamsi	2125	Ardabil-Iran
A. williamsi	2138	Ardabil-Iran
A.williamsi	2139	Ardabil-Iran
A. elater	2128	Kaashmar-Iran
A. elater	55	Tehran-Eshtehard-Iran
A. elater	56	Tehran-Eshtehard-Iran
A. elater	15	Golestan-Iran
A. elater	9	Golestan-Iran
A. toussi	78	Mashhad-Cheshme Gilas-Iran
A. toussi	79	Mashhad-Cheshme Gilas-Iran
A. toussi	72	Mashhad-Cheshme Gilas-Iran
A. toussi	1415	Mashhad-Cheshme Gilas-Iran
A. toussi	2130	Sarakhs-Iran
A. firouzi	8	Esfahan-Peykaan-Iran
A. firouzi	26	Esfahan-Peykaan-Iran
A. firouzi	32	Esfahan-Aminabad-Iran
A. firouzi	33	Esfahan-Aminabad-Iran
A. firouzi	20	Esfahan-Pookande mirabad-Iran
A. hotsoni	1277	Yazd-Iran
A. hotsoni	1533	Yazd-Iran
A. hotsoni	1521	Yazd-Mehriz-Iran
Pygeretmus pumilio	1815	Golestan-Gonbade kaavoos-Iran

SEQUENCE ANALYSES

Maximum likelihood (ML), maximum parsimony (MP) and Bayesian phylogenetic analysis were carried out. ML and MP phylogenetic analyses were performed using PAUP* 4.0b10 (Swofford, 2002). To test the robustness of the nodes we ran 500 and 2000 bootstrap replicates under ML and MP, respectively, with a single random addition sequence replicate per bootstrap replicate. Bayesian analysis, using the Markov Chain Monte Carlo method, was conducted with MrBayes 3.1.1 (Huelsenbeck and Ronquist, 2001).

A minimum spanning network was constructed for *Cox1* using the TCS software package (Clement et al., 2000), which employs the method of probability of parsimony according to Templeton et al. (1992). It calculates the number of mutational steps by which pairwise haplotypes differ and computes the probability of parsimony for pairwise differences until the probability exceeds 0.95 (Templeton et al., 1992). The number of mutational differences associated with the probability just before the 0.95 cut-off is then the maximum number of mutational connections between pairs of

TABLE 2. Morphometric variables

Cranial measurements		Dental measurements	
LCB	Condylo-basal length	PM	Diameter of premolar
LR	Rostrum length	ML1	Length of first molar (upper)
LZ	Zygomatic length	MW1	Width of first molar (upper)
BM	Mastoid breadth	ML2	Length of second molar (upper)
BZ	Zygomatic breadth	MW2	Width of second molar (upper)
BB	Braincase breadth	ML3	Length of third molar (upper)
BI	Inter-orbital breadth	MW3	Width of third molar (upper)
BR	Rostrum base breadth	M1L	Length of first molar (lower)
HB	Braincase height	M1W	Width of first molar (lower)
WB	Tympanic bulla width	M2L	Length of second molar (lower)
UR	Upper tooth row length	M2W	Width of second molar (lower)
		M3L	Length of third molar (lower)
		M3W	Width of third molar (lower)

sequences justified by the parsimony criterion, and these justified connections are applied in a haplotype network (Clement et al., 2000).

RESULTS

MORPHOMETIC ANALYSES

Standard descriptive statistics including the mean and standard deviation for 24 cranial and dental measurements of Allactaga are given in Table 4. This table shows that Williams´ Jerboa is significantly larger than the other species. ANOVAs analyses showed significant differences among the species of Allactaga. All species differed significantly from one another in all variables ($P < 0.05$) (Table 4), but Iranian Jerboa and Hotson´s Jerboa are not significantly different in any variable (Tukey´s test). The small five-toed Jerboa and the Toussi Jerboa are significantly different in all cranial characters except WB, and different in ML2, M2L, M3L and M3W. We conducted a discriminant analysis on all variables (Fig. 1). Discriminant functions (DF) 1 and 2 together explained 98.3% of the variance, with DF1 having an eigenvalue of 41.68 (89.9% of variance) and DF2 an eigenvalue of 3.91 (8.4% of variance). Two species, the Iranian Jerboa and Hotson´s Jerboa were more separated from the small five-toed Jerboa, the Toussi Jerboa, and Williams´ Jerboa by DF2, while Williams´ Jerboa was well separated from Hotson´s Jerboa and the Iranian Jerboa and two species the small five-toed Jerboa, the Toussi Jerboa by DF1 (Fig. 1). The morphometric characters LCB, LR, UR, BB, M2L, BM, LZ, M1L, BZ, M3L, ML2, ML1, ML3, M1W and MW1 have the greatest effect on formation of function 1 and WB and PM have the most effect on formation of function 2. The structure matrix is shown in Appendix.

GENETIC ANALYSES

We sequenced 638 bp for the Cox1 gene. The data file comprising 28 individuals, showed 180 parsimony-informative characters (441 characters were constant, 17 variable characters were parsimony-uninformative). A strict consensus tree indicates that the Iranian Jerboa is clustered with Hotson´s Jerboa. Furthermore, it supports the separation of Williams´ Jerboa from the two other complex species, Hotson´s Jerboa/Iranian Jerboa and the Toussi Jerboa/small five-toed Jerboa.

TABLE 3. Specimens of *Allactaga* spp. for morphometric study

Species	Locality	Specimens (n)
Allactaga elater	Kashmar	44
A. elater	Torbat jam	7
A. elater	Bardeskan	5
A. elater	Shirvan	3
A. elater	Nehbandan	9
A. elater	Tehran-Eshtehard	4
A. elater	Golestan	9
A. toussi	Sarakhs	1
A. toussi	Cheshmeh gilas	15
A. firouzi	Esfahan-Shahreza	13
A. hotsoni	Yazd	4
A. williamsi	Zanjan-Amirabad	8
A. williamsi	Ardabil	3
A. williamsi	Chaharmahalo bakhtiari-Dashte marjan	7
A. williamsi	Hamedan-Karafs	9

TABLE 4. Comparison of 24 morphometric variables among all species of *Allactaga* using ANOVA means with standard error (SE) and significance.

Variables	*A. elater* (n=81) Mean± S.D	*A. toussi* (n=16) Mean± S.D	*A. firouzi* (n=12) Mean± S.D	*A. hotsoni* (n=4) Mean± S.D	*A. williamsi* (n=27) Mean± S.D	*P*
LCB	25.45±0.968	26.70±1.04	28.38±0.536	27.93±0.931	32.51±0.805	.000
LR	8.56±0.393	9.20±0.446	9.68±0.253	9.41±0.586	11.20±0.321	.000
LZ	13.20±0.611	14.00±0.681	13.64±0.382	13.77±0.513	16.47±0.512	.000
BM	16.02±0.495	16.53±0.725	17.75±0.449	17.42±0.277	19.07±0.582	.000
BZ	19.74±0.828	20.50±0.958	20.44±0.418	20.74±1.07	23.90±0.648	.000
BB	15.22±0.329	15.69±0.476	15.89±0.294	15.93±0.529	17.83±0.554	.000
BI	8.89±0.364	9.30±0.386	8.77±0.300	8.76±0.362	8.96±0.335	.000
BR	4.83±0.277	5.15±0.230	4.88±0.197	4.85±0.403	5.79±0.275	.000
HB	9.84±0.753	10.95±0.766	11.51±0.270	10.81±0.847	13.59±0.823	.000
WB	4.93±0.284	5.01±0.299	6.18±0.273	5.80±0.165	6.03±0.269	.000
UR	5.07±0.317	5.37±0.225	5.24±0.200	5.45±0.264	6.79±0.220	.000
PM	0.38±0.104	0.438±0.844	0.33±0.049	0.33±0.099	0.54±0.118	.000
M1L	1.91±0.125	1.98±0.084	1.99±0.109	1.96±0.086	2.49±0.089	.000
M2L	1.63±0.092	1.70±0.073	1.69±0.081	1.70±0.025	2.13±0.085	.000
M3L	0.771±0.105	0.861±0.083	0.83±0.094	0.84±0.027	1.19±0.066	.000
M1W	1.32±0.189	1.42±0.182	1.38±0.100	1.37±0.170	1.77±0.202	.000
M2W	1.31±0.165	1.42±0.198	1.38±0.076	1.34±0.201	1.72±0.187	.000
M3W	0.98±0.122	1.10±0.133	1.05±0.072	0.97±0.130	1.48±0.128	.000
ML1	1.91±0.141	1.99±0.156	2.02±0.108	2.06±0.169	2.48±0.176	.000
ML2	1.82±0.121	1.90±0.076	1.95±0.059	1.97±0.047	2.31±0.104	.000
ML3	1.15±0.150	1.26±0.169	1.20±0.121	1.26±0.098	1.69±0.141	.000
MW1	1.31±0.156	1.36±0.163	1.48±0.089	1.49±0.269	1.63±0.199	.000
MW2	1.28±0.166	1.31±0.209	1.41±0.094	1.41±0.218	1.65±0.176	.000
MW3	1.04±0.118	1.08±0.163	1.10±0.050	1.07±0.157	1.38±0.122	.000

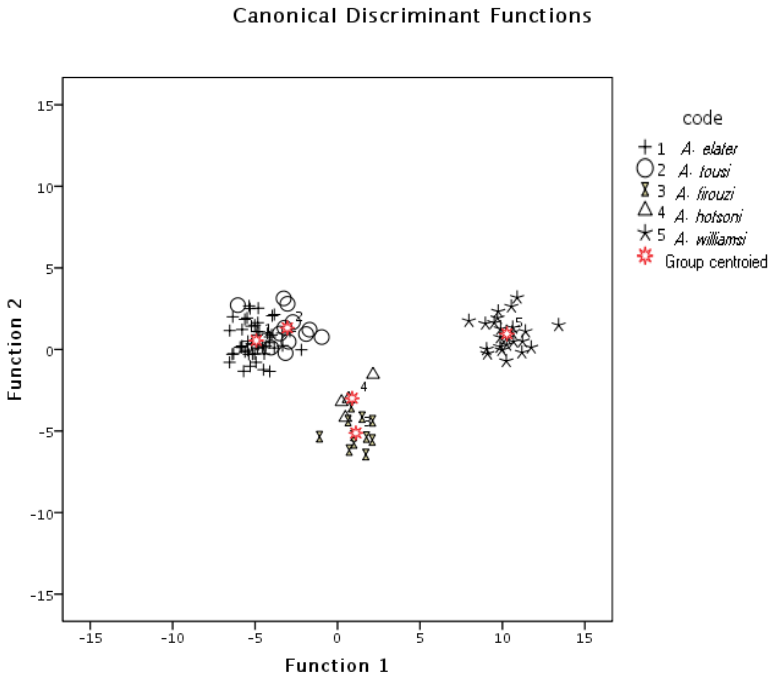

FIG. 1. Scatter plot of a stepwise discriminant analysis, based on all morphometric variables of *Allactaga*.

TABLE 5. Kimura-2-parameter genetic distance interspecies and intraspecies (Bold numbers)

Species	*A. elater*	*A. toussi*	*A. firouzi*	*A. hotsoni*	*A. williamsi*
A. elater	**0.054**				
A. toussi	0.119	**0.003**			
A. firouzi	0.224	0.223	**0.008**		
A. hotsoni	0.228	0.227	0.009	**0.008**	
A. williamsi	0.196	0.184	0.215	0.215	**0.020**

Maximum likelihood analyses yielded a single tree (—ln L = 2623.0479), which agreed largely with the MP consensus tree (Fig. 2). Kimura-2-parameter genetic distance also showed a high genetic distance between Hotson´s Jerboa and the small five-toed Jerboa (0.228%) and a low distance between the Iranian Jerboa and Hotson´s Jerboa (0.009%) (Table 5).

Using TCS, 24 haplotype networks were recovered based on Cox1 sequences of 27 individuals (Fig. 3). The Iranian Jerboa and Hotson´s Jerboa were consigned to one network, and all samples of the Toussi Jerboa were grouped in a single network. The small five-toed Jerboa presents a more complicated picture with 2 samples from Golestan province representing a separate haplotype, one sample from Kashmar making a single haplotype, and two samples from Tehran constituting a distinct haplotype (samples from Tehran are connected with a mutation). Two samples of Williams´ Jerboa show a distinct network.

DISCUSSION

At least five morphospecies of the genus *Allactaga* have been identified in Iran, determined by morphological and morphometric studies. Most are reported based on a low number of specimens. Application of the biological species concept and utilization of molecular data as an indicator of taxonomic separation between species provides the ability to revise the morphospecies taxonomy

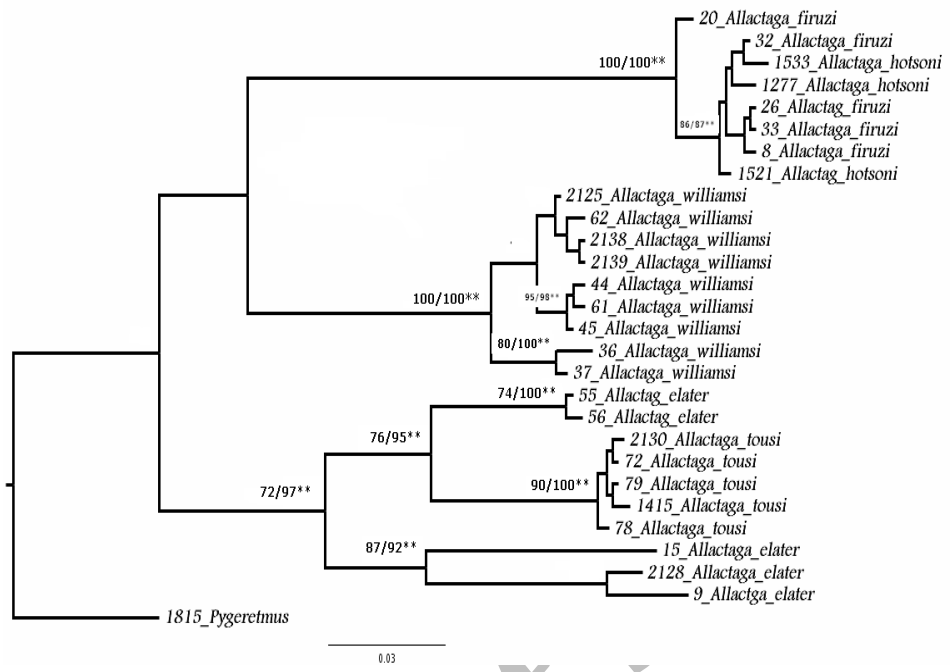

FIG. 2. Ninety-percent majority-rule consensus tree sampled from the posterior distribution of the most-partitioned analysis. Posterior probability values from the Bayesian analysis are indicated at the >99% (**) >95% (*) significance levels. Numbers represent ML and MP bootstrap values (500/5000 replicates; given only if >50%).

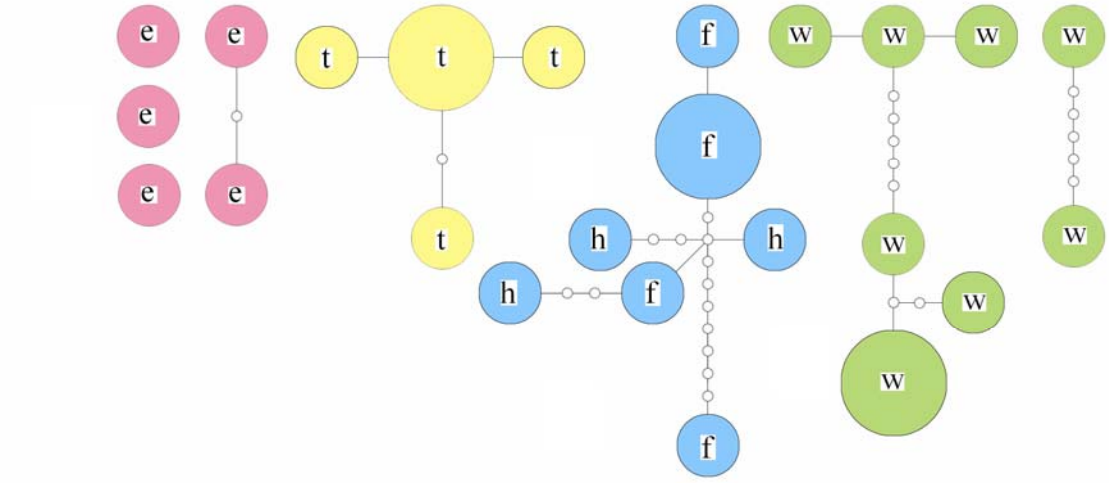

FIG. 3. Haplotype networks of *Allactaga* spp. (27 individuals), based on 616 bp of the cytochrome oxidase subunit I gene (*Cox1*). Networks were not joined if haplotypes were separated by more than 9 mutations. Each circle represents one haplotype. (pink circles (e): *A. elater*, yellow circles (t): *A. toussi*, blue circles (h, f): *A. hotsoni* and *A. firouzi*, green circles (w): *A. williamsi*).

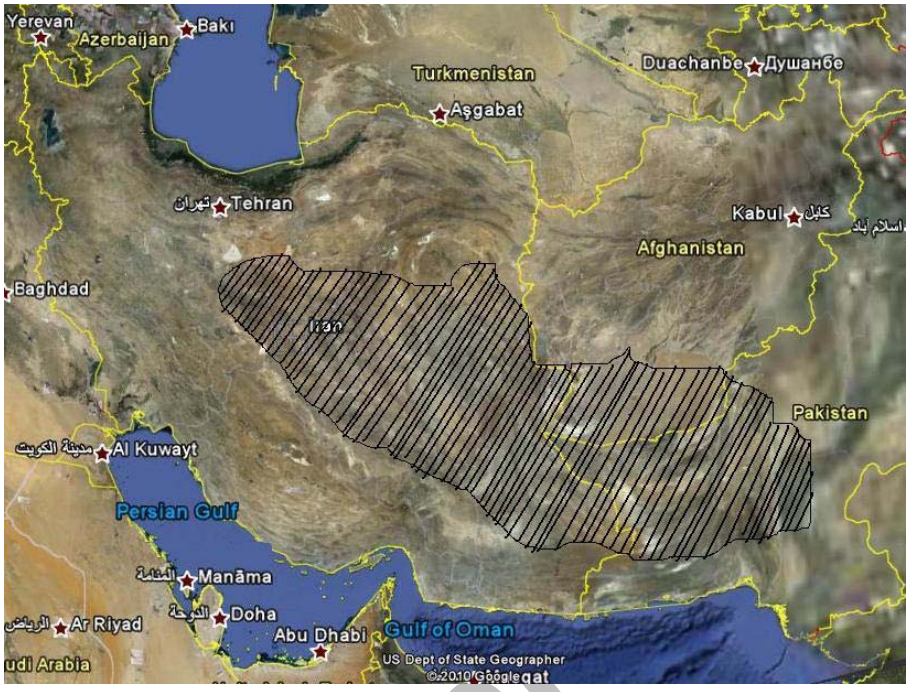

FIG. 4. New map of *A. hotsoni* distribution.

using a low number of specimens, species density is low in Iran due to a hot and arid climate, and it is essential to minimize the number of captured specimens. Utilizing the *COXI* gene to describe the specimen at the specific level confirmed four species of *Allactaga* in Iran. Williams´ Jerboa, the Toussi Jerboa, the small five-toed Jerboa and the conspecific Iranian Jerboa/Hotson´s Jerboa.

The morphospecies Iranian Jerboa and Hotson´s Jerboa, with morphometric differences reported by previous authors, are similar at the molecular level, which confirms the study of Shenbrot (2009).

The distribution range of Hotson´s Jerboa, which was first reported by Thomas (1920), has expanded from the east of Iranian Baluchestan to the west of the Zagros Mountains via central Kavir Garmsaar (Brown, 1980 and Darvish et al., 2006). The present study suggests that the range of this species is much larger than has been previously reported. This species may be a polytypic with two subspecies, *A. hotsoni hotsoni* (Thomas, 1920) and *A. hotsoni firouzi* (Womochel, 1978). This study confirmed that Hotson´s Jerboa may have passed through the highlands of Esfahan and penetrated Shahreza (Fig. 4).

The Toussi Jerboa is separated from the parapatric species, the small five-toed Jerboa, and the other two species evaluated in this study by size, morphometrics and geographical distribution. The findings are reinforced by molecular studies. The Toussi Jerboa and the small five-toed Jerboa are molecularly the most homogenous and heterogenous species, respectively, which suggests further investigation of the status of populations of small five-toed Jerboa in the Central Iranian Plain. Morphometric studies confirmed the separation described by Darvish et al. (2008) based on morphological data. The small five-toed Jerboa has been separated from the others by morphometric methods in the present study.

Williams´ Jerboa can be clearly distinguished morphometrically from the other three species, by size and shape and can be regarded as a biologically distinct species morphometrically and morphologically.

Based on the haplotype network results, we suggest further molecular studies to clarify populations of small five-toed Jerboa. The haplotype pattern for the small five-toed Jerboa is apparently related to the distribution of its subspecies in Iran. A sample from Kashmar was identified as *A. elater indica* (Gray, 1842), whereas samples from Golestan were *A. elater turkmeni* (Goodwin, 1940) and samples from Tehran were *A. sp.*

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Appendix

Correlations within groups among discriminant variables and standardized canonical discriminant functions in *Allactaga*. Variables are ordered by the absolute value of correlation within the function. (*) signifies the highest absolute correlation between a variable and the discriminant function.

Discriminant Function				
	1	2	3	4
Eigenvalue	41.686	3.918	0.458	0.330
% variance	89.9	8.4	1.0	0.7
Canonical correlation	0.988	0.893	0.561	0.498
Lcb	.502*	-.003	.164	.023
Lr	.432*	.010	.366	-.080
Ur	.420*	.338	-.015	-.007
Bb	.402*	.166	.110	-.034
m2l	.383*	.284	.035	.182
Bm	.372*	-.161	.124	.008
Lz	.344*	.261	.155	-.011
m1l	.337*	.230	.070	.267
Bz	.333*	.211	.036	-.036
m3l	.300*	.250	.021	.145
ml2	.294*	.100	.020	-.010
ml1	.254*	.125	-.088	.055
ml3	.224*	.207	-.004	-.018
m1w	.169*	.103	-.006	.145
Mw1	.133*	-.059	-.069	.005
Wb	.296	-.560*	.025	.226
Pm	.100	.203*	.050	.125
Bi	-.003	.095	.432*	-.257
Hb	.294	.027	.377*	-.007
Br	.210	.238	.286*	-.037
m3w	.256	.199	.134	.328*