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Geometric morphometric comparison of mandible and skull of five species of genus *Allactaga* (Rodentia: Dipodidae) from Iran

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The genus *Allactaga* is distributed in North Africa, Iran, Afghanistan, southwestern Syria, North Turkemenistan, the Middle East, Central Asia, and Mongolia. Six morphospecies have been reported from regions of Iran. Morphological differences among 41 specimens of *A. elater, A. williamsi, A. hotsoni, A. firouzi*, and *A. toussi* were investigated using landmark-based geometric morphometrics of the dorsal aspect of the skull and ventral aspect of the mandible. Results of canonical variate analysis (CVA) indicated that all species are distinguishable by skull shape. Canonical variate analysis showed that most studied species of *Allactaga* were separated along CV1. Cluster analysis indicated a high morphometric distance between *A. toussi* and *A. elater*, confirming the division of *A. toussi* and *A. elater* into different species. The species *Allactaga williamsi* exhibited the greatest morphometric distance from other studied species. Based on mandible shape, *A. williamsi* is similar to *A. elater* and *A. toussi*. *Allactaga firouzi* clustered with *A. hotsoni*, in comparison with the results obtained from skull shape variation, the morphometric distance between these two species is higher than other species.

Key words: *Allactaga toussi, A. firouzi,* geometric morphometrics, Iran, landmark, mandible, skull.

INTRODUCTION

The genus *Allactaga* is distributed in the Middle East in North Africa, Iran, Afghanistan, southwestern Syria, and North Turkamanistan, and in Central Asia and Mongolia. Six morphospecies are reported from regions of Iran (Darvish et al., 2008; Lay, 1967), including *A. elater* Gray, 1824 (small five-toed jerboa), *A. williamsi* Thomas, 1907 (Williams jerboa), *A. euphratica* Thomas, 1881 (Euphrates jerboa), *A. hotsoni* Thomas, 1920 (Hotson's jerboa), *A. firouzi* Womchel, 1978 (Firouz jerboa), and *A. toussi* Darvish, 2008 (Toussi jerboa).

Allactaga williamsi has been reported in western and northwestern Iran (Wilson and Reeder, 2005). *Allactaga elater* is distributed in most desert and semi-desert regions of Iran except the northern slope of the Alburz Mountain forest (Darvish et al., 2008). *Allactaga hotsoni* is described from Baluchistan of Iran by Thomas (1920) and is distributed in Baluchistan (Lay, 1967; Corbet and Hill, 1991), Kavir National Park of Varamin (Brown, 1980), Khorasan and Yazd Province (Darvish et al., 2006). Womochel (1978) reported *A. firouzi* as an endemic species of Shahreza of Isfahan Province (Ziaee 1996, Wilson and Reeder, 2005; Naderi et al., 2009). *Allactaga hotsoni* is distinguished from *A. firouzi* by a shorter tail, smaller ears and feet, a smaller skull, larger premolars, and narrower incisors and palate (Womochel, 1978). Darvish et al. (2008) reported *A. toussi* for the first time from the Cheshmeh Gilas area of northeast Iran. This species is distinguished from *A. elater*, and other Iranian

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five-toed jerboas, by differences in cranial and molar morphological and morphometric characteristics (Darvish et al., 2008).

The number of species of *Allactaga* is controversial, and the genus has been the subject of many systematic studies in recent decades (e.g. Shenbrot et al. 1995; Darvish et al., 2006, 2008; Miljutin 2008; Naderi et al., 2009). In this study, we investigated the shape variation of the skull and mandible to re-examine the taxonomic status of species of *Allactaga* in Iran using landmark- based geometric morphometrics of the skull and mandible.

MATERIAL AND METHODS

Forty-one specimens of five species of *Allactaga* were analyzed: 1. *A. elater* (9 specimens from Golestan Province, Eshtehard of Tehran Province, Sarakhs, and Kashmar of Khorasan Razavi Province); 2. *A. firouzi* (10 specimens from Esfahan Province); 3. *A. hotsoni* (4 specimens from Yazd); 4. *A. tousi* (6 specimens from Cheshmeh Gilas of Khorasan Razavi Province); 5. *A. williamsi* (12 specimens from Zanjan, Ilam, Dashte marjan of Chaharmahal-o-Bakhtiari Province, Ardabil, and Karafs of Hamedan Province). The localities of populations studied and their numbers are shown in the Table 1 and Fig. 1. Only adult specimens were examined.

Geometric and morphometric analyses were performed separately using two-dimensional projection of the skull and mandible. Nineteen landmarks were collected from the skull in dorsal view and 11 landmarks on the left mandible in lateral view using TPSdig 2.12 software (Rolf, 2008) (Fig. 2). Images were captured using digital camera (DP71) connected to stereoscope (Olympus SZH10). Landmarks on the dorsal aspect of the skull are as follows (mostly based on Lalis et al., 2009): 1 tip of the nasal; 2, 3 anterior points at suture between nasals and premaxilla; 4, 5 front of the zygomatic plate; 6, back of zygomatic plate; 8, 9, 17 frontal-parietal suture; 10, 11 back of zygomatic notch; 12, 13 lateral points of parietal; 14, 15 intersection of parietal-interparietal and supraoccipital sutures; 16 midpoint of nasal-frontal suture; 18 midpoint of parietal interparital suture; 19 posterior point of supraoccipital. Landmarks on the lateral aspect of the mandible are as follows [mostly based on Siahsarvie et al., (2008) and Cardini (2003)]: 1 upper extreme anterior part of the incisor alveolus; 2 anterior extremity of the maxillary toothrow; 3 tip of the coronoid process; 4 ventral most point on the curve of the coronoid process; 5 anterior edge of condylar process; 6 posterior edge of condylar process; 7 anterior most point on the curve of the posterior boundary of the mandible; 8 tip of the angular process; 9 dorsal most point on the ventral border of horizontal ramus; 10 ventral most point of incisive alveolus; 11 antero-ventral border of incisive alveolus.

The size was computed as the centroid size, which corresponds to the sum of the squared distances from the landmarks to the centroid of configuration (Bookstein, 1991). The centroid size was calculated for each individual and the size difference among species was tested by analysis of variance (ANOVA). For visualizing the size variation among groups, a 95% confidence interval error bar graph was plotted using SPSS 16. The coordinates were superimposed on an average shape created with Procrustes generalized least squares, to remove difference in shape due to scaling, rotation, or translation (Drvden and Mardia, 1998; Rolf et al., 2006), and the consensus configuration as well as thin-plate spline parameters were computed (Bookstein, 1991, 1996; Rohlf, 1993). Multivariate analysis (MANOVA) was performed on the partial warp scores combined with uniform components to test the significance of differences among species. Patterns of interspecific variation in total shape space were examined by canonical variate analysis (CVA) of the partial warp scores matrix and two uniform components, U1 and U2. Shape changes associated with the canonical variate axes were depicted as deformation grids generated by regression of the partial-warp scores onto canonical axis (Rohlf et al., 1996). A UPGMA cluster analysis was conducted of group centroid of squared of Euclidean distances computed from partial warp scores to investigate between group morphometric similarities.

TABLE 1. The geographic locations and the number of specimens examined.

Collecting Site ID	Location	Geographic coordinates	Specimens
1	Ardebil	37º 56.132´ N 46º 58.954´ E	1
2	Zanjan	36º 32.97´ N 47º 51.16´ E	6
3	Hamedan province, Karafs	35º 22.973´ N 49º 19.3´ E	2
4	Ilam	32º 20.508´ N 47º 34.33´ E	1
5	Tehran province-Eshtehard	35º 42.839´ N 50º 33.431´ E	3
6	Golestan	37º 28.6´ N 56º 18.2´ E	4
7	Cheshme Gilas	36º 38.6´ N 59º 20.6´ E	6
8	Sarakhs	36º 30.21´ N 61 7.10´ E	1
9	Kashmar	35º 13.56´ N 58º 27.29´ E	1
10	Esfahan	32º 39.5´ N 51 40.45´ E	10
11	Chaharmahal-o- Bakhtiari province, Dashte marjan	32º 02.05´ N 51º 19.496´ E	2
12	Yazd	31 53.47´ N 54 21.38´ E	4
	Total		41

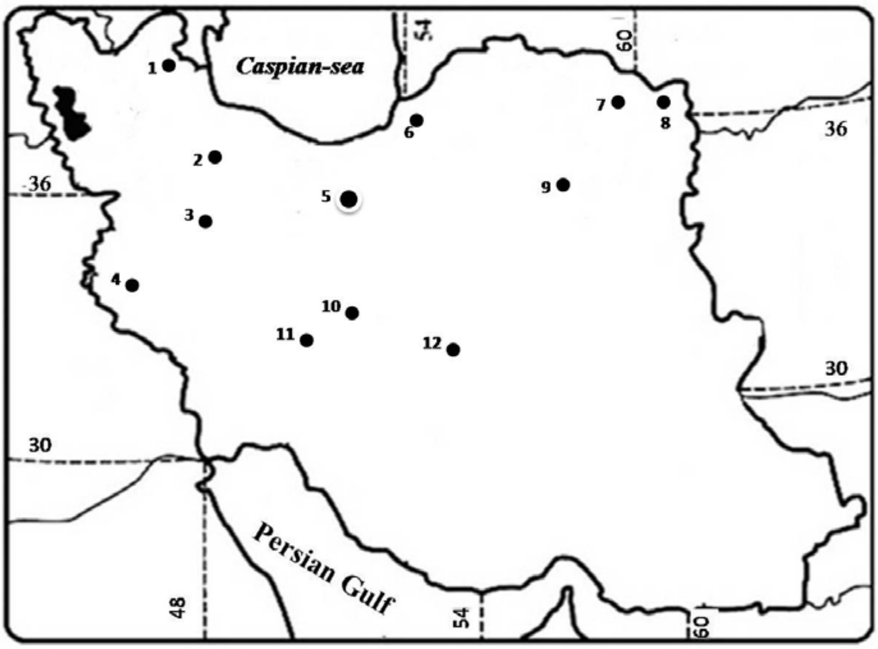

FIG. 1. Collection sites of *Allactaga* in Iran. 1 Ardabil, 2 Zanjan, 3 Hamedan, 4 Ilam, 5 Tehran, 6 Golestan Province, 7 Cheshmeh Gilas, 8 Sarakhs, 9 Kashmar, 10 Esfahan, 11 Chaharmahal-o-Bakhtiari, 12 Yazd.

The relationship between partial warps and centroid size was evaluated by multivariate regression analysis (Rolf and Marcus, 1993) to investigate the allometric patterns associated with skull size.
Procrustean superimposition, partial warps, and deformation grids were generated using tpsRelw program v.1.42 (Rohlf, 2005). Multivariate regression analysis, canonical variate analysis, and clustering were conducted using PAST v. 2.02 (Hammer et al., 2010), except for graphing the error bars, for which the SPSS program, v.16 was used.

RESULTS

SKULL

ANOVA of centroid size was significant among species (P < 0.005). An error bar graph of species centroid size is given in Fig. 3. *Allactaga williamsi* has the largest skull, while *A. elater* has the smallest. Skull size in *A. firouzi* and *A. hotsoni* are statistically similar.
The link between centroid size and shape was not significant ($P_{(reg)}$ = 0.624). This showed that the differences of M/2 shape in the studied species of *Allactaga* are not due to allometry.
MANOVA results revealed highly significant differences between species of *Allactaga* (P < 0.01, Wilk's λ). The first two axes of the CVA explained 52.73% and 30.8% of the shape variance, respectively. The corresponding scatter plot is shown in Fig. 4. Almost all species of *Allactaga* are separated along CV1. First axis sharply separated *A. elater* from *A. tousi*. *Allactaga firouzi* and *A. hotsoni* are separated from each other, while CV2 clearly separated *A. williamsi* from other species.
Shape differences associated with the CV1 and CV2 are shown as deformation in skull shape in Fig. 4. *Allactaga firouzi*, with positive scores on CV1, has a narrower and longer nasal, narrow braincase and a slightly more slender parietal than specimens with negative scores for CV1. *Allactaga tousi*, with negative scores of CV1, has a short and wider nasal and wider braincase.
In cluster analysis, *A. williamsi* occurs in a distance cluster from other species. *Allactaga hotsoni* clustered with *A. firouzi* and connected to *A. elater*, and this cluster connected with *A. toussi* with a high distance (Fig. 5).

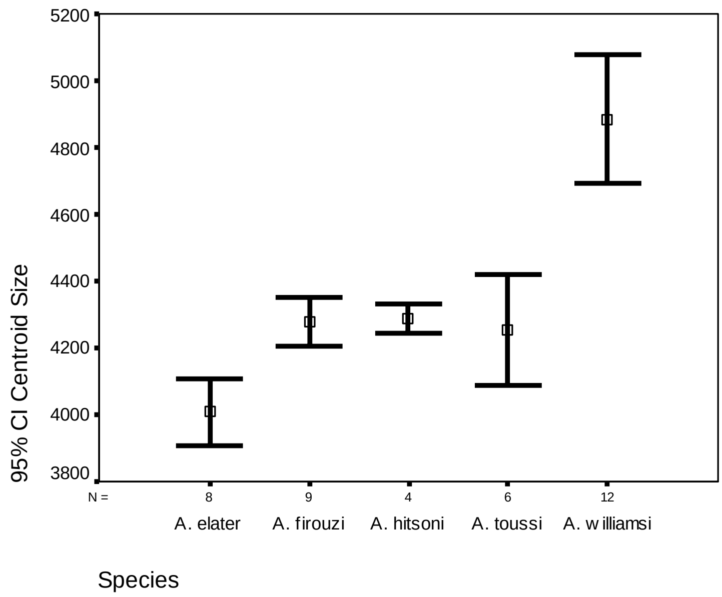

FIG. 3. Error bar for centroid size of dorsal aspect of the skull in *Allactaga* spp. The middle square indicates the mean

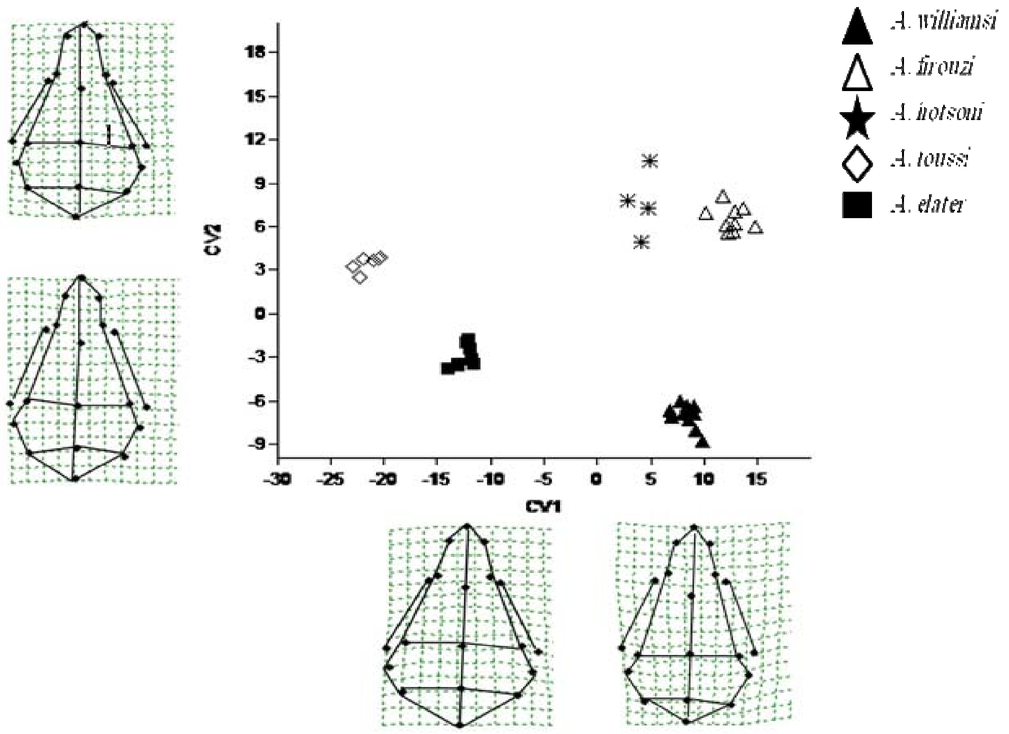

FIG. 4. Scatterplots of the first two canonical variate scores based on the total shape matrix of the skull. Deformation grids for the extreme points of each axis are shown

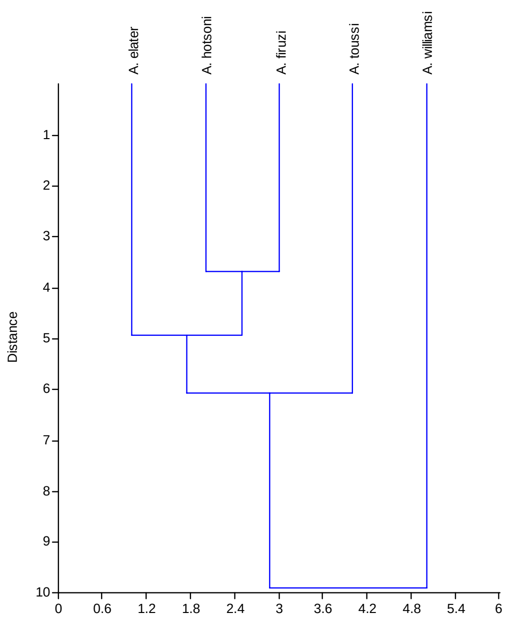

FIG. 5. Dendogram resulting from cluster analysis based on Euclidean distance.

MANDIBLE

ANOVA of centroid size was significant among species (P < 0.005). An error bar graph of species centroid size showed that *A. williamsi* has the largest mandible, while *A. elater* has the smallest (Fig. 6).The link between centroid size and shape is significant ($P_{(reg)}$ = 0.01); therefore we removed allometries from shape of mandible using a multivariate regression. MANOVA analysis of total shape space indicated a significant difference in all investigated species of *Allactaga* (P < 0.001, Wilk's λ). In canonical variate analysis (CVA), the two components are responsible for 66.18% and 24.1% of all variation, respectively. Projection of the specimens onto these axes is shown in Fig. 7. Deformation grids for specimens at the extremes of each axis are used in Fig. 7 to describe shape differences in mandibles of species of *Allactaga.*

Figure 7 shows that *A. williamsi*, *A. firouzi*, and *A. hotsoni* are separated by the first axis, whereas *A. elater* and *A. tousi* overlap on CV1. Distinction between *A. elater* and *A. tousi* is achieved along the second axis. *A. williamsi*, with a positive score on CV1, has short coronoid and angular processes, and a more expanded condylar process, whereas *A. firouzi*, with negative scores on CV1, shows the opposite situation. *Allactaga hotsoni*, *A. tousi*, and *A. elater* exhibit an intermediate configuration. *Allactaga elater*, with negative scores on CV2, has a longer coronoid process and a slightly more contracted carpus region than does *A. williamsi*. *Allactaga hotsoni* clustered with *A. firouzi*, and *A. tousi* clustered with *A. elater* and connected to *A. williamsi* with a high distance (Fig. 8).

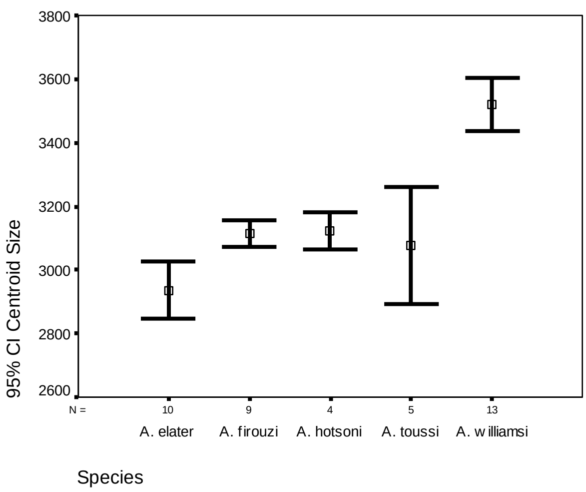

FIG. 6. Error bar for mandible centroid size in *Allactaga* spp. The middle square indicates the mean

DISCUSSION

Analysis of the centroid size shows that *A. williamsi* has a significantly larger mandible and skull than other species, while *A. elater* possesses the smallest.

Results of CVA indicated that all species are recognizable by shape. The five species are significantly different with respect to mandible and skull size.

CVA of the skulls showed that most species of *Allactaga* are separated along CV1, and cluster analysis indicated a high morphometric distance among *A. toussi* and *A. elater*, confirming the division of *A. toussi* and *A. elater* into separate species. Based on the multivariate analysis, Darvish et al. (2008) also demonstrated the separation of *A. williamsi*, *A. tousi*, *A.* hotson,i and *A. elater* and showed that *A. toussi* and *A. elater* are significantly different in morphometric characters. *Allactaga williamsi* shows high morphometric distance from other species studied. This is in agreement with the results obtained from analysis of the centroid size.

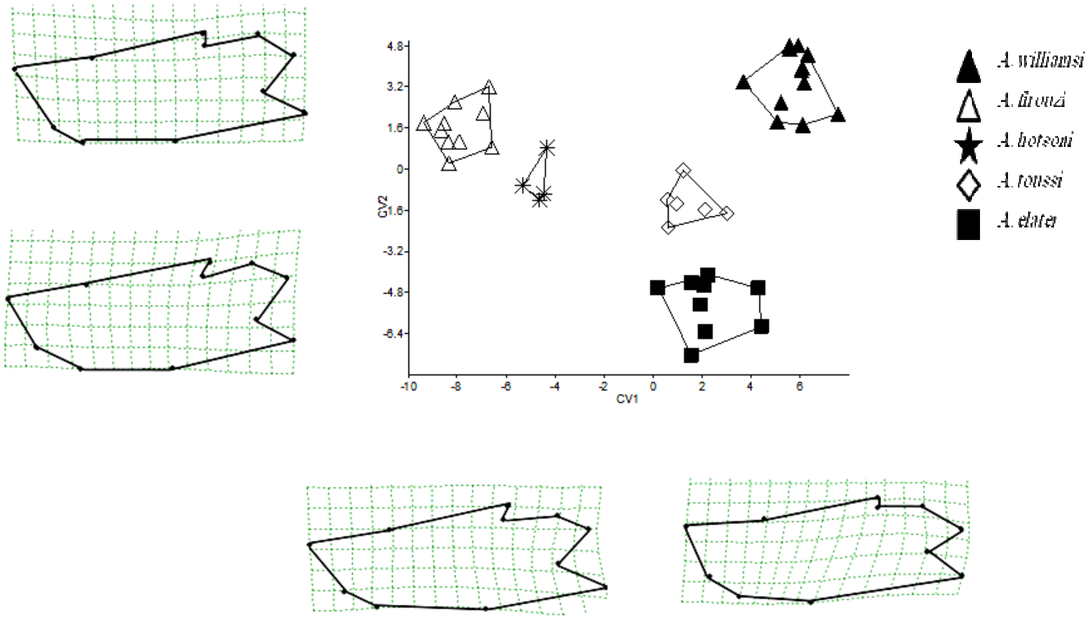

FIG. 7. Scatterplots of the first two canonical variate scores based on the total shape matrix of the mandible. Deformation grids for the extreme points of each axis are shown.

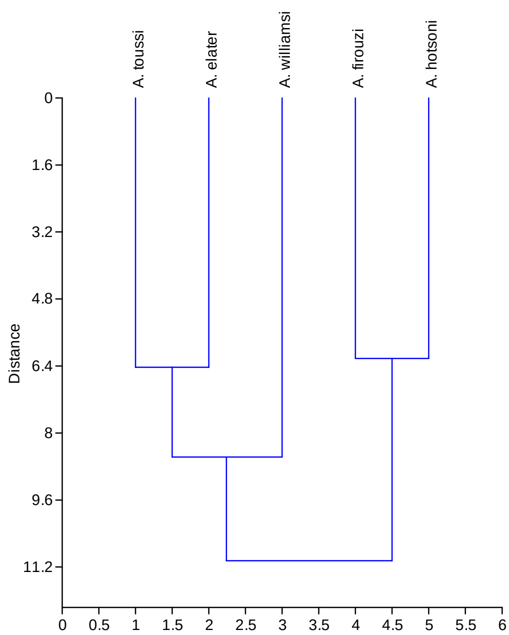

FIG. 8. The dendogram resulting from cluster analysis based on Euclidean distance

Skull shape differences between *A. toussi* and *A. elater* are high and allow distinction between the two taxa, but, based on mandible shape, these two species are grouped together as are *A. firouzi* and *A. hotsoni*. Compared with results obtained from skull shape variation, the morphometric distance between these two species is higher.

The mandible shape of *A. williamsi* is similar to that of *A. elater* and *A. toussi*, although the former is completely recognizable by larger size. In our opinion, geographic speciation may be a cause of the distribution of the species of the genus. For example, *A. williamsi* is limited to the northwestern mountains of Alburz and Zagros. *Allactaga firouzi* is limited to semiarid lands of Esfahan. Womochel (1978) reported that *A. hotsoni* is present at elevations below 100 m in clay-loess deserts, whereas *A. elater* occupies salty semiarid areas (Darvish et al., 2006)

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