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Geometric morphometric analysis of the second upper molar of the genus *Apodemus* (Muridae: Rodentia) in Northern Iran

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Wood mice of the genus *Apodemus* are widespread in temperate areas of the Palaearctic region. Dental shape variation and morphological differences among three species of *Apodemus* (*A. witherbyi, A. hyrcanicus, A. uralensis*) were investigated using outline-based geometric morphometrics of the second upper molar (M2/) and a morphological study of 92 museum specimens belonging to five populations of *Apodemus* in northern Iran (East Azerbaijan, Khorasan, Tehran, Golestan, and Noor) were analyzed and identified. All species were distinguishable by the shape of the second upper molar (M2/). The Noor population was identified as *A. hyrcanicus*, and the Khorasan, Tehran, East Azerbaijan populations overlap with specimens of *A. witherbyi* and are differentiated from *A. uralensis* and *A. hyrcanicus*. Two species (*A. hyrcanicus* and *A. witherbyi*) were detected in the population from Golestan. Morphological traits could not separate *A. uralensis* from *A. witherbyi*, and according to the results of canonical variate analysis (CVA), only *A. hyrcanicus* is separate from the other two studied species.

Key words: *Apodemus*, geometric morphometrics, morphology, Iran, molar

INTRODUCTION

Wood mice of the genus *Apodemus* Kaup, 1829 are widespread in temperate areas of the Palaearctic region (Filippucci et al., 2002). Twenty-one species have been recorded (Musser and Carleton, 2005; Darvish et al., 2006), 12 of which are ascribed to the subgenus *Sylvaemus*, distributed in the western Palaearctic region (Darvish et al., 2006; Filippucci et al., 1989; Filippucci et al., 1996; Michaux et al., 2002; Musser and Carleton, 1993; Musser et al., 1996; Vorontsov et al., 1992). All *Apodemus* taxa that have been described from Iran belong to *Sylvaemus* (Michaux et al., 2002).

The three species *A. hyrcanicus*, *A. flavicollis*, and *A. hermonensis* Filippucci, Simson, and Nevo, 1989 were reported in Iran by Macholan et al. (2001). The geographic distribution of *A. hyrcanicus* in Iran is restricted to the Hyrcanian forests along the southern coast of the Caspian Sea. *A. hermonensis* was first reported in Israel (Filippucci et al., 1989) and subsequently in Anatolian Turkey and North Iran using allozymic and morphological data (Filippucci et al., 1996; Macholán et al., 2001). Based on a genetic study, Macholan et al. (2001) confirmed the geographic distribution of *A. hermonensis* in eastern Turkey and Iran (Javidkar et al. 2005). *A. arianus* Blandford, 1881 was described in Iran as a synonym of both *chorassanicus* and *hermonensis* taxa by Mezhzherin (1997) and Zagorodnyuk et al. (1997) (Siahsarvie and Darvish, 2008). Krystufek (2002), on examining the holotype of the species *A. witherbyi*, noted that it might be identical to *A. hermonensis*.

Musser and Carleton (2005) used *A. witherbyi* as the oldest designation for both *A. arianus* and *A. hermonensis*, the name that is also used in this study. *A. witherbyi* is distributed in the Zagros and

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Albrouz steppic provinces including Azerbaijan and Kurdestan and in the Kopet-Dagh Mountains (Musser and Carleton, 2005). The species is syntopic with *A. uralensis* Palas, 1811 in NW Iran (Krystufek and Hutterer, 2006) and *A. flavicolis* in the Zagros Mountains (Macholan et al., 2001) and is altitudinally parapatric with *A. hyrcanicus* (Frynta et al., 2001; Macholan et al., 2001; Musser and Carleton, 2005). *Apodemus uralensis* was reported in Makidi in Arasbaran (NW Iran) by Krystufek and Hutterer (2006). Marchand and Denys (2003) indicated that the upper molars are more useful than the lower molars in differentiating three species of European wood mice (*A. sylvaticus, A. flavicollis,* and *A. alpicola*), documenting the importance of the upper molar for morphological studies.

The aim of this study was to determine whether the species of *Apodemus* in Iran are independent, using morphometric studies of specimens that were investigated in previous molecular studies. The results of these biosystematic studies were used to identify museum specimens as well. For this purpose, we used morphology and an outline-based geometric morphometrics method on the M2/. This is the first report of shape differences in molars of Iranian wood mice using outline-based geometric morphometrics.

MATERIAL AND METHODS

A total of 126 specimens of three species (*A. witherbyi*, *A. hyrcanicus*, *and A. uralensis*) of *Apodemus* were analyzed. Only adults with full maxillary molar eruption were included. The specimens were taken from 21 sites in northern Iran, pooled into five geographic groups, first according to taxonomic affiliation and then to geographic proximity. The specimens examined originated from the collection of the Zoology Museum of Ferdowsi University of Mashhad, Iran (ZMFUM).

The study was conducted in two parts. Part one was a geometric morphometric study of *Apodemus* specimens that were taxonomically identified in earlier studies, based on molecular and morphological analyses (Darvish et al., 2010; HosseinPour Feizi et al., 2009). Thirty-four specimens of *Apodemus* from northern Iran which were classified into three haplotypes using RFLP studies

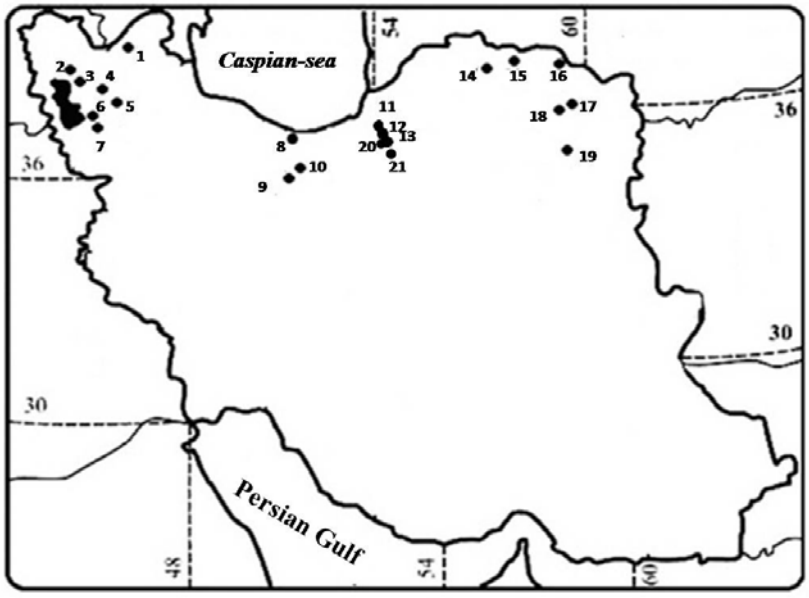

FIGURE 1. Sampling sites in northern Iran. East Azerbaijan Province (1- Makidi, 2- Marand, 3- Soufian, 4- Tabriz, 5- Lighvan, 6- Kandovan, 7- Sefidkhan); Mazandaran Province (8- Noor); Tehran Province (9- Sorkhehesar National Park, 10- Abnik); Golestan Province (11- Tuskahestan, 12- Garmabdasht, 13- Gachian, 20- Jahannama, 21- Chelcheli); Khorasan Province (14- Bojnord, 15- Shirvan, 16-Dargaz, 17- Mashhad, 18- Moghan village, 19- Torbate Heidarieh).

TABLE 1. Sampling localities of the studied species. Figure 1 shows collection sites.

Species	Locality	Collection site	Geographic coordinates	Number of specimens
	Garmabdasht	12	36° 41' N, 54° 35' E	1
A. hyrcanicus	Tuskestan	11	36° 42' N, 54° 34' E	3
	Gachian	13	36° 41' N, 54° 35' E	2
A. uralensis	Tuskestan	11	36° 42' N, 54° 34' E	6
	Gachian	13	36° 41' N, 54° 35' E	1
	Lighvan	5	37° 50' N, 46° 26' E	7
A. witherbyi	Kandovan	6	37° 48' N, 46° 14' E	2
	Makidi	1	38° 49' N, 46° 55' E	1
	Sefidkhan	7	37° 50' N, 46° 23' E	1
	Marand	2	38° 25' N, 45° 46' E	3
	Soufian	3	-	4
	Tabriz	4	38° 05' N, 46° 17' E	3

and identified as *A. witherbyi*, *A. hyrcanicus*, and *A. uralensis* using morphological analyses (Darvish et al., 2010) were morphometrically investigated. The specimens studied belong to three localities of Golestan Province and seven localities of East Azerbaijan Province (Table 1).

In the second part, the results of the first step were employed to identify the museum specimens (specimens on which no molecular study has been performed). Ninety-two unidentified museum specimens were included in the morphometric analyses and their affinity to one of the three species was examined (Table 2). These specimens belonged to 17 populations of *Apodemus* in northern Iran and were pooled into five geographic groups (East Azerbaijan, Khorasan, Tehran, Golestan and Noor).

In both parts of the study, morphological and geometric morphometric analyses were conducted on the specimens and the results were interpreted separately.

TABLE 2. Collecting locations for museum specimens.

Collection site	Locality	Geographic coordinates	Number of specimens
2	Marand	38° 25' N, 45° 46' E	2
3	Soufian	-	3
4	Tabriz	38° 05' N, 46° 17' E	3
5	Lighvan	37° 50' N, 46° 26' E	3
6	Kandovan	37° 48' N, 46° 14' E	2
7	Sefidkhan	37° 50' N, 46° 23' E	1
21	Chelcheli	36° 39' N, 54º 34' E	8
20	Jahannama	36° 40' N, 54º 33' E	4
14	Bojnord	37° 27' N, 57° 19' E	1
15	Shirvan	37° 36' N, 57° 55' E	1
16	Dargaz	37° 26' N, 59° 6' E	5
17	Mashahad	36° 17' N, 59° 35' E	4
18	Moghan	36° 07' N, 59° 22' E	12
19	Torbate Heidarieh	35° 37' N, 59° 18' E	2
10	Abnik	35° 58' N, 51° 42' E	12
9	Sorkhehesar	35° 41' N, 51° 38' E	20
8	Noor	36° 42' N, 52° 1' E	9
	Total		92

GEOMETRIC MORPHOMETRIC ANALYSES

The shape of the second upper molar (M2/) was digitized using an outline of its two-dimensional projection viewed from the occlusal surface. One hundred and fifty equally spaced points were sampled along the outline. Images were captured using a digital camera (DP71) connected to a stereoscope (Olympus SZH10) with magnification of 30x. The digitization was performed using TPSdig 2.12 software (Rohlf, 2008).

Elliptic Fourier Analysis (EFA) was primarily described by Kuhl and Giardinia (1982). The EFAWIN software (Rohlf and Ferson, 1992) was used to conduct an EFA. The program GMTP (Taravati, 2010) was used to adjust the TPSDig output file format directly opened in EFAWIN.

The first 12 harmonics were used to describe the shape variations of M2/. Each harmonic corresponded to four coefficients, A_n, B_n for x, and C_n, D_n for y, and defines an ellipse on the XY-plane (Hautier et al., 2009). The output file of EFAWIN includes these harmonic coefficients which can be employed as raw data for statistical analyses.

Harmonic coefficients were used as statistical variables in SPSS, version 16, and PAST, version 1.98 (Hammer et al., 2010). In the first phase, the centroid size was calculated for each individual. The difference among populations was tested by Analysis of Variance (ANOVA). For visualizing the size variation among groups, a 95% confidence interval error bar graph was plotted. Discriminant function analysis (DFA) was carried out to assess interspecific differences. Cluster analysis was performed on the Euclidean distances between the mean shapes of the taxa computed from DFA to investigate between group morphometric similarities.

In the second phase, we performed a discriminant function analysis of the three species using the specimens with a confirmed taxonomic affiliation. The populations for which no molecular study had been performed (East Azerbaijan, Khorasan, Tehran, Golestan, and Noor) were projected on the discriminant space to identify their specific attributes. The relationship between shape variables and centroid size was evaluated by multivariate regression analysis (Rolf and Marcus 1993), to investigate the allometric patterns associated with molar size.

MORPHOLOGICAL STUDIES

Thirteen dental and cranial characters were studied, and the frequency of each morphological trait was recorded. These characters are presented in Figure 2 and Table 3. Dental and cranial character states were adapted from Javidkar et al. (2007). The specimens studied belong to the same age group, as determined by tooth wear (Frynta and Zizkova, 1992).

RESULTS

GEOMETRIC MORPHOMETRICS

Morphometric analysis of the *Apodemus* specimens confirmed earlier results from molecular analyses. *A. hyrcanicus* possessed the largest centroid size for the M2/, while *A. uralensis* had the smallest and these differences were significant (Fig. 3, ANOVA $P < 0.01$). M2/ size in *A. uralensis* and *A. witherbyi* was similar and significantly smaller than in *A. hyrcanicus* (Tukey's test).

In discriminant function analysis, the two components were responsible for 76.2% and 23.8% of all variation. The Wilks' Lambda value confirmed the significance of these two functions ($P < 0.001$ and $P < 0.01$ respectively for DF1 and DF2). Projection of the specimens on the first two discriminant functions and the changes in shape associated with them are shown in Figure 4. *A. hyrcanicus*, with positive scores of DF1, was characterized by a broad molar while *A. uralensis*, with negative scores on DF1, presented a slender molar. The M2/ was particularly slender in *A. uralensis* and *A. witherbyi*, and the labial anteroconid (t3) and metacon (t9) cusps in A. *witherbyi* were prominent.

TABLE 3. Characters and character states used in the morphological analyses (see Javidkar et al., 2007).

Characters	Character states
1. Bulla	1 Massive and well-developed 2 Medium
2. Angular process of mandible	1 Well-developed and wide (A1) 2 Tender and blade shaped (A2)
3. Position of incisor	1 Orthodont (B1) 2 Semiorthodont (B2) 3 Opisthodont (B3)
4. Fronto-parietal suture	1 V shaped and angled 2 U shaped and curved
5. Posterior edge of the palatine	1 Curved (C1) 2 Rather straight (C2)
6. Connection between anterocone(t3) or anterostyle (t1) and protocone (t5) in upper M1/	1 t1 or t3 without any enamel horn towards t5 (D1) 2 t1 ort3 with a short enamel horn towards t5 (D2) 3 t1 ort3 with a long enamel horn towards t5 (D3) 4 t1 or t3 is connected to the side of t5 (D4)
7. Position of enterostyle (t4) to paracone (t6) in upper M1/	1 t4 and t6 are placed in the same alignment (E1) 2 t4 is placed anteriorly relative to t6 (E2) 3 t4 is placed posteriorly relative to t6 (E3)
8. Position of anteroconule (t1bis, t3bis) in upper M1/	1 absent (F1) 2 present (F2) 3 well developed and similar to a real cusp (F3)
9. Position of metacone (t9) in upper M1/	1 Massive and comparable with paracone. 2 Relatively small and tender.
10. Position of median anteroconid (tma) in lower M/1	1 Well developed and comparable with lower cusps (G1) 2 Medium size (G2) 3 Tiny (G3)
11. Number of cingulums in lower M/1	1 One cingulum (I1) 2 Two cingulums (I2) 3 Three cingulums (I3) 4 Four cingulums (I4)
12. Number of cingulums in lower M/2	1 Absent (J1) 2 One cingulum (J2) 3 Two cingulums (J3)
13. Size of cingulums in lower M/2	1 Massive (H1) 2 Tiny (H2) 3 Absent (H3)

Distinction of *A. hyrcanicus* from *A. uralernsis*, and *A. witherbyi* was achieved along DF1. On the other hand, *A. uralensis* was discriminated from *A. witherbyi* and *A. hyrcanicus* along DF2. Classification results were 100% correct for all species.

In cluster analysis, *A. hyrcanicus* occurred in a cluster distinct from *A. uralensis*, while *A. witherbyi* was grouped closely with the latter species (Fig. 5).

The regression between centroid size and shape variables was not significant (P_{reg} = 0.286). This demonstrated that differences in M2/ shape in the studied species were not due to allometry.

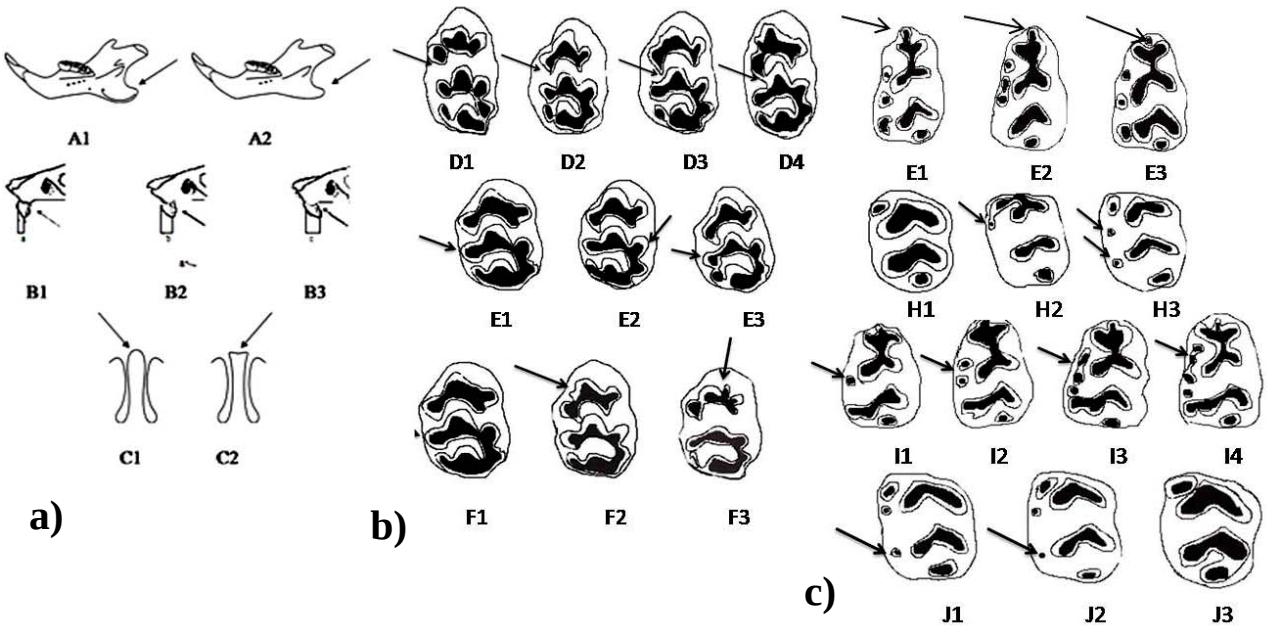

FIGURE 2. a: Morphological character states of mandible, incisor and skull (A-C). b: Morphological states of dental characteristics in M1/. c: Morphological states of dental characteristics in M/1 (G, I) and M/2 (J, H).

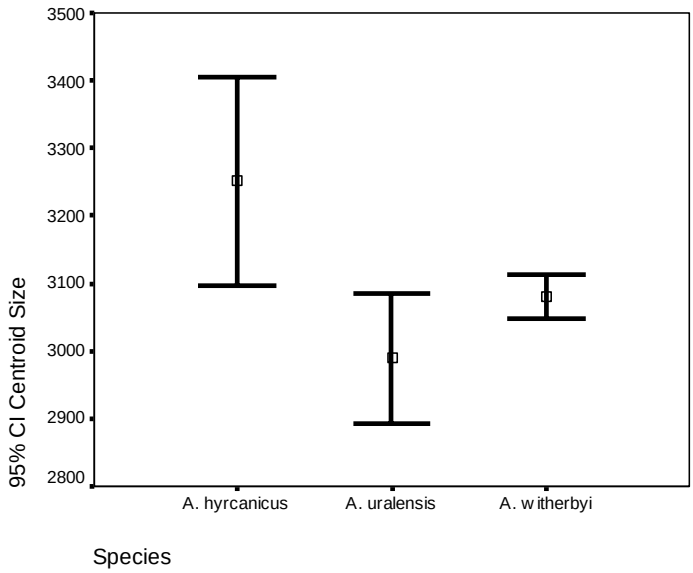

FIGURE 3. Error bar of centroid size of M2/ in three species of *Apodemus*. The rectangle on each line is the mean centroid size.

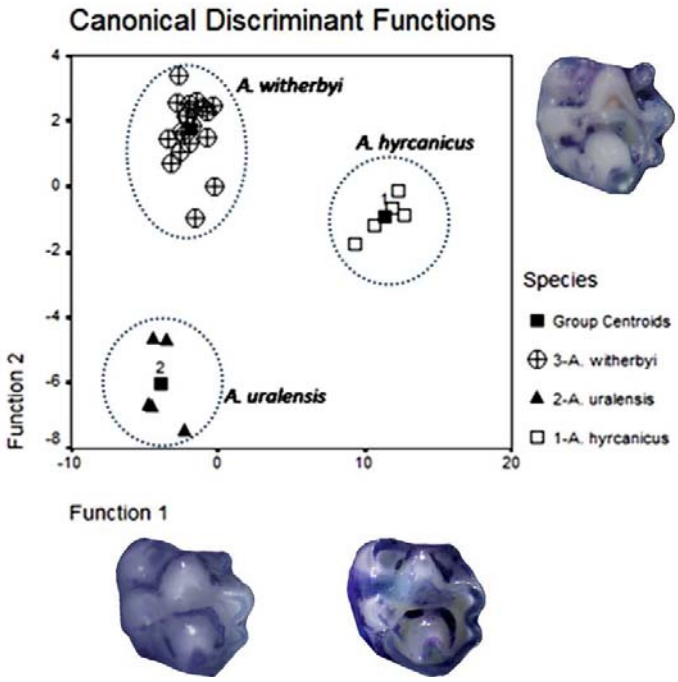

FIGURE 4. Discriminant function analysis (DFA) based on First (1) and Second (2) components. Shape differences on the extremities of each axis are presented.

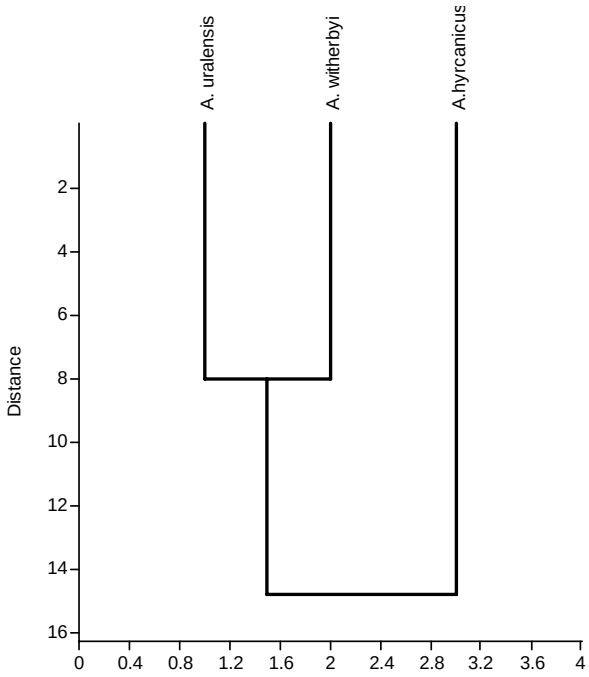

FIGURE 5. Dendogram resulting from cluster analysis based on Euclidean distances among the mean shapes of the species.

MORPHOMETRIC STUDIES OF MUSEUM SPECIMENS

The results of discriminant function analysis based on First (DF1) and Second (DF2) functions are shown in Figure 6. The Wilks' Lambda distribution confirmed the significance of these two functions ($P < 0.001$ and $P < 0.01$ respectively for the first and second functions).

Scatter plots show the populations of East Azerbaijan, Khorasan, Tehran and specimens of *A. witherbyi* overlap along both axes (Figs. 6a, b, c). The Noor populations and specimens of *A. hyrcanicus* are completely overlapped (Fig. 6d). Five specimens from the Golestan population and *A. hyrcanicus* specimens overlap while the remaining specimens from Golestan are integrated with *A. witherbyi* (Fig. 6e). For each case, the variance percent of the first and second functions is shown in Figure 6.

MORPHOLOGY

The frequencies of the morphological character states for all species are shown in Table 4. Character states related to each taxon were compared to explanatory character states for each species. *A. hyrcanicus* differed from the other species, while *A. witherbyi* showed character states similar to *A. uralensis*.

DISCUSSION

Considering the known distribution range of *A. witherbyi* and *A. hyrcanicus* (Karami et al., 2008; Musser and Carleton, 2005), the presence of *A. witherbyi* in NW Iran, the southern slopes of the Alborz Mountains**,** NE Iran, and Golestan Province as well as that of *A. hyrcanicus* in the northern foothills of the Elburz Mountains in Golestan Province, is not unexpected. Krystufek and Hutterer (2006) reported *A. uralensis* from Arasbaran forests, where it is sympatric with *A. witherbyi*. Currently, the Caucasus and eastern Elburz are the two extremities of the distribution range of *A. uralensis*, which occurs in sympatry with *A. hyrcanicus* in the Gorgan Mountains.

Based on a molecular study, Darvish et al. (2010) identified three haplotypes, corresponding to *A. cf. uralensis*, *A.* cf. *hyrcanicus*, and *A. witherbeyi*. While the two latter species have been previously reported from the study area, the discovery of *A.* cf. *uralensis* in the region extends the eastern border of this species' distribution. (Darvish et al. in Press).

Apodemus cf. *hyrcanicus* was identified from Asalem and Nokandeh in northern Iran by Macholan et al. (2001). Javidkar et al. (2005) reported new records of this species from the Hyrcanian forests of Noor in Mazandaran Province along the Caspian Sea in northern Iran. Macholan et al. (2001) showed geographic distribution of *A. witherbyi* into eastern Turkey and western Iran. Moreover, Krystufek and Hutterer (2006) reported *A.witherbyi* from Makidi in NW Iran

Based on the morphological analyses, the following traits were seen with high frequency in each of the species considered: *A. hyrcanicus*: V-shaped fronto-parietal suture, curved posterior edge of palatine, wide angular process of mandible, massive bulla, the position of t4 in the first upper molar placed superior to t6. *A. witherbyi*: U-shaped fronto-parietal suture, straight posterior edge of palatine and medium bulla, in the first upper molar t4 to t6 are placed in the same alignment. *A. uralensis*: V-shaped fronto-parietal suture, medium bulla, straight posterior edge of palatine and presence of one cingulum in the second lower molar.

Using landmark-based geometric morphometrics Siahsarvie and Darvish (2008) showed that three species of Iranian wood mice, *A. witherbyi*, *A. hyrcanicus*, and *A. avicenicus* are completely distinguishable by shape differences in the upper molars. Marchand and Denys (2003) indicated that upper molars, especially the second upper molar, are effective for discrimination of species of European wood mice (*A. sylvaticus, A. flavicollis, A. alpicola*). Our analyses confirm the importance of this structure for discrimination of Iranian wood mice.

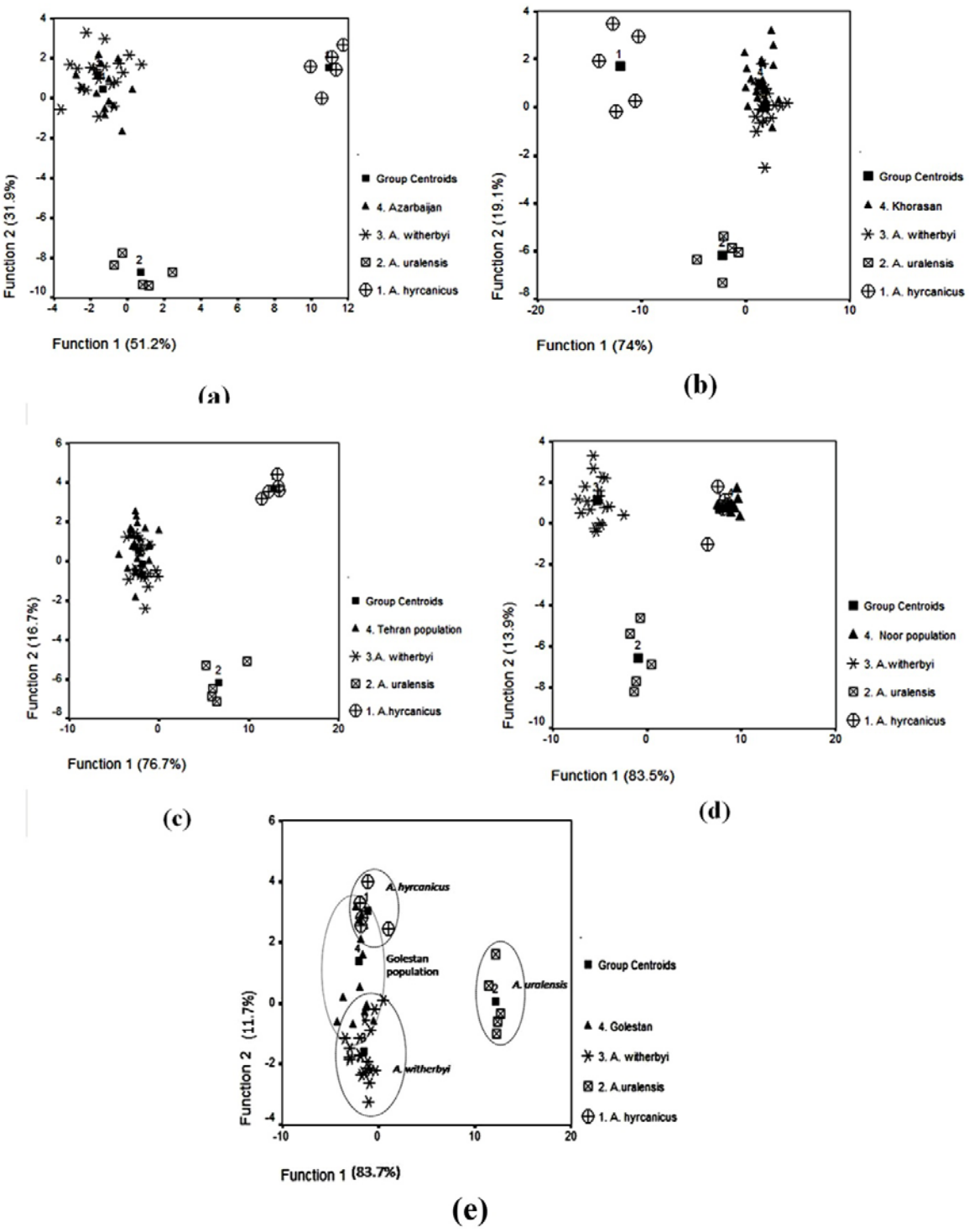

FIGURE 6. The results of discriminant function analysis using projections of museum specimens on the identified species space. Museum specimens belong to five geographic groups: (a) Azerbaijan, (b) Khorasan, (c) Tehran, (d) Noorand, and (e) Golestan.

TABLE 4. Frequencies (percent) of the character states for the species considered.

Species		*A. uralensis*	*A. hrcanicus*	*A. witherbyi*
Number of specimens		6	6	22
Characters	States			
Fronto-parietal suture	1	83	95	5
	2	17	5	91
Posterior edge of the palatine	1	34	79	9
	2	66	21	91
Bulla	1	34	89	5
	2	66	11	95
Angular process of mandible	1	44	86	49
	2	56	14	51
Incisor	1	31	71	37
	2	69	19	57
	3	0	10	6
Position of metacon	1	100	100	100
	2	0	0	0
Position of t4 to paracone t6 in upper M1/	1	0	78	5
	2	100	13	85
	3	0	9	10
Position of anteroconule in upper M1/	1	34	12	65
	2	16	85	16
	3	50	3	19
Position of tma in lower M/1	1	34	7	26
	2	16	88	41
	3	50	5	33
Number of cingulums in lower M/1	1	60	6	25
	2	20	79	18
	3	16	9	49
	4	3	6	8
Number of cingulums in lower M/2	1	83	81	20
	2	0	10	28
	3	17	9	52
Size of cingulums in lower M/2	1	21	4	13
	2	6	8	82
	3	73	88	5
Connection between t3 or t1 and t5 in upper M1/	1	50	77	14
	2	33	14	13
	3	16	6	34
	4	0	3	39

The Noor population was similar to specimens of *A. hyrcanicus*. Therefore, considering that the Noor population is located in the central areas of Asalem and Nokandeh and also in terms of habitats is similar to each other. On the other hand, Asalem and Nokandeh populations were taxonomically identified in earlier studies as *A. hyrcanicus* based on morphometric and morphological analyses (Frynta et al., 2001), and this study confirmed results of M2/ outline identifying the Noor population as *A. hyrcanicus*.

An earlier molecular study of the East Azerbaijan population demonstrated that they belong to *A. witherbyi* (HosseinPour Feizi et al., 2009). Siahsarvie and Darvish (2008), examining the upper molar and the mandible using landmark-based geometric morphometry, noted that wood mice of northeastern Iran are morphometrically similar to *A. witherbyi* of the Elborz Mountains and are

assumed to be the same species. Javidkar et al. (2005) report *A. hermonesis* from the uplands of the Elborz Mountains (Abnik) and Sorkhehesar National Park.
Results of the present study are in agreement with Darvish et al. (2010) who indicated the presence of two sympatric species in Golestan Province, *A. witherbyi* and *A. hyrcanicus*.
Analysis of shape variation of M2/ showed that the Khorasan, Tehran, East Azerbaijan, and Golestan (seven samples) populations and specimens of *A. witherbyi* overlap.
The results of geometric morphometric analysis and previous studies confirm that the Khorasan, Tehran, and East Azerbaijan populations, along with seven specimens from Golestan, belong to *A. witherbyi*. The results also determined that characteristics of five specimens of the Golestan and Noor populations and *A. hyrcanicus* are similar. These specimens are assumed to be the same species.
In conclusion, the present geometric morphometrics study based on M2/ shape allowed us to partially discriminate three morphological groups that are congruent with the three haplotypes suggested by molecular identification. The application of this technique provides a powerful tool for identification of *Apodemus* species.

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