Vol.7, No.2, 129-142, 2011

ISSN: 1735-434X

Patterns of skull shape variation in *Meriones* persicus (Rodentia: Muridae) in relation to geoclimatical conditions

Tabatabaei Yazdi, F.a, Adriaens, D.b

This study investigates skull variation in Persian jird, *Meriones persicus* (Blanford, 1875) in relation to the geoclimatical conditions across its distribution range. The pattern of correlations between geoclimatical variables and geometric shape descriptors for 221 ventral crania was studied by landmark-based geometric morphometric techniques. The covariation between shape and geoclimatical variables was explored using the Two-Block Partial Least-Squares (2B-PLS) method. The studied geoclimatical variables are: altitude, temperature (mean annual, monthly maximum and monthly minimum), annual rainfall and seasonal variation in rainfall represented by the Shannon rainfall diversity index. The phenotypes of this species reflect a particular pattern of correlated shape variation to the geoclimatical variation. The Persian jirds from the Southern populations living in lower, warmer and drier localities are characterized by bulla hypertrophy, less convex zygomatic arch, narrower zygomatic plate, longer incisive foramen and slightly a shorter nasal. The studied populations which belong to different subspecies differ from each other through a smooth variation in cranial characters.

Key words: geoclimatical variation, geometric morphometrics, two-block partial least squares

INTRODUCTION

Phenotypic variation across a geographic space is an omnipresent phenomenon in most organisms. Therefore, the detection and description of patterns of variation and the inference of processes underlying the observed patterns are a fundamental task for evolutionary and systematic biology (Monteiro et al., 2003). Dealing with morphological variation among populations linked to environmental condition of their habitats and investigation of association between the morphological variation and geoclimatical condition using a geometric morphometric approach have already produced a large amount of literature (e.g. Reis et al., 2002a, b; Monteiro et al., 2003; Rychlik et al., 2006; Colangelo et al., 2010).

Of two major components of morph i.e. size and shape, the latter is multi-dimensional and is thought to have a high information content regarding the ecological and evolutionary processes responsible for the observed diversity (Thorpe, 1976; Atchley and Hall, 1991; Atchley et al., 1992; Monteiro et al., 2003). In this context, the geographic shape variation in relation to geoclimatical

^a Rodentology Research Department, Ferdowsi University of Mashhad, Mashhad, Iran

^b Evolutionary Morphology of Vertebrates, K.L. Ledeganckstraat 35, 9000 Gent, Belgium

variation provides valuable information for the description of patterns in shape differences and for testing hypothesis using geometric morphometric approaches (Bookstein, 1991; Rohlf, 1996; Rohlf and Corti, 2000). The genus *Meriones* is very interesting taxa for the study of morphological variation, as well as the mechanisms of speciation and adaptation (Darvish, 2009). *Meriones persicus* (Blanford, 1875) lives on the slopes of mountain areas and is distributed from Transcaucasia and Turkey to the eastern part of the Iranian Plateau (Fig. 1). From this distribution range, six subspecies have been already reported (Musser and Carleton, 2005). The definitions of the subspecies have been stated without a consideration of the morphological variation occurring in full distribution range of them. These subspecies were defined mainly based on the external diagnostic features (e.g. fur colour) which are not reliable comparing with cranial characters that are more robust criteria for taxonomic implication.

Considering (1) divers habitats along the geographical range it span, thereby covering a wide variety of ecogeographical niches and (2) morphological variation observed in this species, a study regarding the patterns of intraspecific morphological differences allows testing the phenotypic skull variation in this jird species in association with the geoclimatical variation and the cranial variation was investigated in order to test to what degree the geographical differences were reflected in the cranial morphology. Since the ventral skull is genetically and functionally divers structure, geometric descriptors are derived to describe this skull view. Moreover, in this study we have dealt with the taxonomic issues in this species as well.

MATERIAL AND METHODS Sample and data collection

In total 221 specimens were obtained from the collections of the Smithsonian Natural Museum of Natural History (Washington D.C. USA), the Field Museum of Natural History (Chicago, USA), the British Museum of Natural History (London, UK), the Musée national d'Histoire naturelle of Paris (Paris, France), the Zoological Museum of Ferdowsi University of Mashhad (Mashhad, Iran) and the Royal Belgian Institute of Natural Sciences (Brussels, Belgium). Specimens originate from the localities spanning the species distribution range, including specimens collected from the type localities (the topotypes of *M. p. baptistae, M. p. ambriousus, M. p. gurganensis* and *M. p. persicus*). The sampling localities (including the abbreviations which were used in the plots) are listed in Appendix 1. The sampling localities are depicted on Figure 1. A list of specimens with catalogue number is available in Appendix 2. The available type specimens that were intact [*M. p. ambrosius* (Thomas, 1919) originated from South West of Iran and *M. p. baptistae* (Thomas, 1920) originated from Baluchistan (Pakistan)] were included in the analyses. The cotype of *M. p. persicus* (Blanford, 18675) was available, but was not included in the analyses because the skull was broken.

Landmark data were obtained from photographs taken with a Nikon D70 digital reflex camera using a Sigma 105mm macro lens at five megapixels in a standardized manner. The camera was placed on a tripod parallel to the ground plane. The intact and cleaned skulls were mounted in a box with glass pearls and their ventral sides were photographed. Since the ventral cranium has even been suggested as a genetically and functionally the most diverse structure compared to the lateral and dorsal views and contains a larger number of evolutionary independent components of variation (Caumul and Polly, 2005), only this side of the skulls was studied.

Twenty landmarks (Fig. 2, described in Table1) on the ventral view of a total of 221 specimens were digitized using TpsDig 2.10 (Rohlf, 2006a) software. Juvenile specimens, identified based on the eruption and amount of wear on the molars (M2) (Petter, 1959; Tong, 1989; Pavlinov, 2008) were excluded from the analyses.

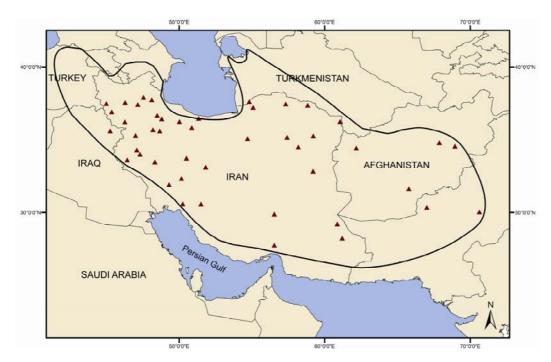


FIGURE 1. Map showing the sampling localities of the *Meriones persicus* (triangles). The polygon shows the distribution range of the species.

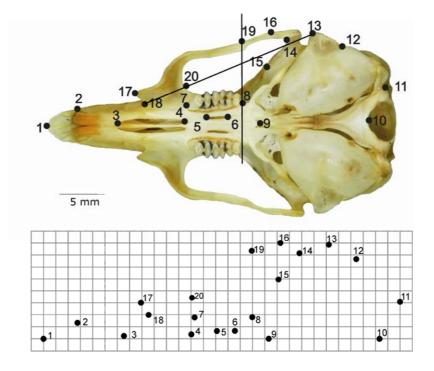


FIGURE 2. Landmarks positioned on the ventral view of a *Meriones persicus* skull specimen was originated from Baluchistan (Pakistan) from the collection of the Smithsonian Natural Museum of Natural History (cat. # 411093). Grid corresponds to the consensus shape configuration.

TABLE 1- Definition and numbering of the landmarks digitized on the ventral view of *Meriones persicus* skulls.

Landmark	Definition
1	rostral tip of internasal suture
2	most lateral junction point of incisive alveolus and body of premaxillary bone
3	most rostral point of incisive foramen
4	most caudal point of incisive foramen
5	most rostral point of palatine foramen
6	most caudal point of palatine foramen
7	most rostral point on the alveolus of the first molar
8	most caudal point on the alveolus of the third molar
9	most caudal point of median suture of palatine bone
10	most rostral point of foramen magnum
11	most lateral point of occipital condyle
12	most caudal point of acoustic tympanic bulla
13	rostral curvature point at level of the meatus
14	most caudal point of zygomatic process concavity formed by temporal bone
15	intersection between frontal squama, wing of presphenoid bone and wing of basisphenoid bone
16	most lateral point of zygomatic arch at maximum width of skull
17	rostral point of zygomatic plate
18	maximum curvature of zygomatic plate in infraorbital foramen
19	intersection of zygomatic arch and vertical line passing through most caudal point of third molar
20	intersection of the zygomatic plate and line connecting the landmarks 13 and 18

Geoclimatical variables

For each population the following geoclimatological data were taken from published records of the Iran Meteorological Organization and also from climate-database of the Food and Agriculture Organization of the United Nations (FAO) 2007: latitude, longitude, altitude (m), temperature (°C) (mean annual, monthly maximum and monthly minimum), annual rainfall (mm) and the seasonal variation in rainfall represented by the Shannon rainfall diversity index that is calculated based on the differences in mean monthly rainfall. Localities with less seasonal variation in rainfall have higher Shannon rainfall diversity index values (Hill and Dunbar 2002; Cardini et al. 2010). This index (*D*) was calculated as follows (Bronikowski and Webb 1996):

$$D = -\sum (p_i \ln (p_i) / \ln (12)$$

 p_i = proportion of rainfall per month

These variables were standardized to avoid that the variables with larger variances be more heavily weighted in the analyses (Rohlf, 2006b; Klingenberg, 2011). The standardization was done using this formula:

Z= standardised variable

 $Z=(x-\mu)/\sigma$

x is a raw score to be standardized;

 μ is the mean of the variable;

 μ is the standard deviation of the variable

TABLE 2- The correlations between shape and geoclimate singular vectors. Percent covariation explained by each singular vector and significance of these correlations (*p<0.05). The weighting of each variable on the PLS vector (1 and 2) is reported with the singular value.

	PLS		
Variable	1	2	
Elevation	-0.214	-0.270	
Rainfall	-0.338	0.605	
Mean T	0.482	0.290	
Max T	0.498	0.037	
Min T	0.439	0.456	
Shannon Rainfall Index	-0.409	0.517	
Singular value	0.014	0.004	
% Cov explained	88.015*	6.341*	
Correlation	0.6058*	0.337	

Data analysis

Two dimensional shape coordinates of landmarks were superimposed by Generalized Procrustes Analysis (GPA, Rohlf and Slice, 1990) using TpsPLS 1.18 (Rohlf, 2006b) and MorphoJ 1.02d (Klingenberg, 2008). This procedure removes the variation unrelated to shape (variation of landmark configurations due to scaling, position and orientation) and extracts shape variables. Two-Block Partial Least Square (2B-PLS) analysis (Rohlf and Corti, 2000) was carried out to analyse the covariation between two sets of variables, in our case shape variables represented by principal components and geoclimatical variables or in other words, to see how the shape differences are related to geoclimatical variation. 2B-PLS method extracts pairs of singular vectors (PLS vectors), one for shape (Shape singular vector) and one for geoclimate (Geoclimate singular vector) that maximize the covariation between the shape and geoclimatical variable blocks. The first pair of singular vectors (PLS1 vector) explains the highest percentage of the total covariance between the two blocks, and subsequent PLS vectors account for successively less amount of the total covariation. As an overall measure of covariation between the two set of variables (shape and geoclimatical variables) we used the RV coefficient (Escoufier, 1973). The significance of the RV coefficient was evaluated using permutation test (with 10,000 runs) under the null hypothesis of complete independence between the two blocks. The Geoclimate and Shape singular vectors scores were plotted against each other and shape differences between the consensus configuration and configuration shifted up or down along the respective Shape singular vector (PLS axis) were visualized with the thin plate spline deformation grids. 2B-PLS analysis was done in MorphoJ1.02d, while the variable profile plots for the geoclimatical variables associated with Geoclimate singular vectors were drawn using TpsPLS 1.18. The variable profile plots allow us to demonstrate environmental gradient associated with the Geoclimate singular vectors. The sign and magnitude of correlation coefficients are depicted by the position and size of bars, respectively.

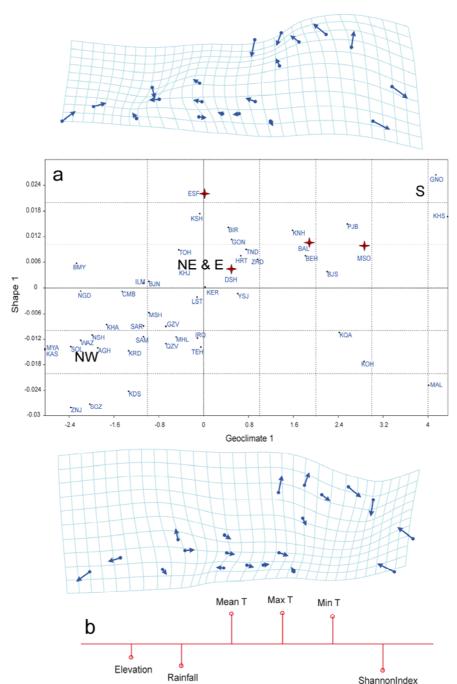


FIGURE 3. graphical representation of 2B-PLS results, based on the first paired vectors of shape and geoclimatical data (a) scatter plot showing the projections of the *M. persicus* populations onto the first shape and geoclimatical vectors; Grids: TPS deformations to the negative (bellow) and positive directions (above) respect to the consensus configuration. (b) variable profile plot for the geoclimatical variables. The orientation of the population from North Eastern Iran (NE), from Eastern Iran (E), from North Western Iran (NW) and from Southern Iran (S) is shown on the scatter plot. The type localities and the localities where the topotypes were collected from are shown by stars.

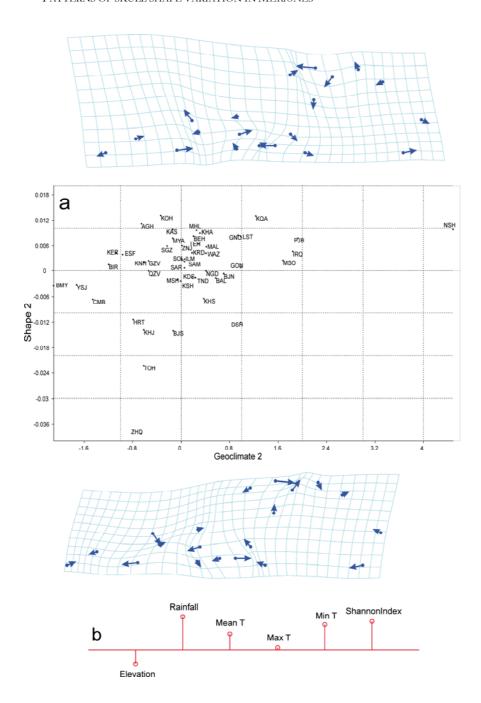


FIGURE 4. graphical representation of 2B-PLS results, based on the second paired vectors of shape and geoclimatical data (a) scatter plot showing the projections of the *M. persicus* populations onto the second shape and geoclimatical vectors; Grids: TPS deformations to the negative (bellow) and positive directions (above) with respect to the consensus configuration. (b) variable profile plot for the geoclimatical variables (variable profile plot shows the structure of the environmental gradient associated with the Geoclimate singular vector 2. The sign and magnitude of correlation coefficients are depicted by the position and size of bars, respectively.)

RESULTS

The results of the 2B-PLS analysis reveal that shape of ventral crania significantly covaries with geoclimatical conditions. RV coefficient of 0.1932 (p<0.0001) indicates a general pattern of covariation that exists between the geoclimatical variables and skull shape variables in this species. The first two pairs of singular vectors (PLS1 and PLS2) explain 94.36% (88.02% and 6.34%, respectively) of total covariance between the shape and geoclimatical variable blocks. The correlation between the first pair of singular vectors (shape vs. geoclimate) was 0.606 (p<0.05), whereas the correlation between the second pair was 0.337, but it was not statistically significant (p=0.292) (Table 2).

The 2B-PLS Geoclimate singular vector 1 represents an axis of warm and dry climate. Thus, the shape changes along the Shape singular vector 1 (PLS1 axis) reflect covariation with Max and Mean T (Table 2, Fig. 3) and mainly involve the tympanic bulla, the zygomatic arch and the zygomatic plate. The specimens of the Southern populations, from lower, warmer and drier areas, with positive PLS1 scores, are characterized by more inflated bulla (landmarks 11-13), less convex zygomatic arch (landmarks 16 and 19), shorter nasal and narrower zygomatic plate (Fig. 3, upper grid). The specimens of the North Western populations, associated with negative PLS1 scores, have a relatively less inflated bulla, a more convex zygomatic arch and the wider zygomatic plate (Fig. 3, lower grid). The 2B-PLS Geoclimate singular vector 2 represents an axis of humid climate and less seasonal variation in rainfall. Therefore, the shape changes explained by PLS2 vector, covary mainly with rainfall and seasonality of rainfall (Table 2, Fig. 4) and encompass the zygomatic plate, incisive and palatine foramens and the tooth row. More specifically, the zygomatic plate was narrower, incisive and palatine foramens and the tooth row was longer for specimens having negative PLS2-scores (Fig. 4, lower grid). These specimens are mostly from drier localities.

DISCUSSION

Pattern of shape variation

The partial least-square analysis showed a relationship between the ventral crania shape and the geoclimatical variables suggesting that morphometric variation in this species to some degree could be explained by an adaptation to local geoclimatical conditions.

The cranium in the Persian jirds, as well as in the external characters (Firouz, 2005) shows a variation reflecting the different environments spread over the range. Although the Persian jirds are mostly restricted to the Iranian Plateau and occur in arid rocky hillsides, and favoring dry stone embankment in highlands of this region, they inhabit different geoclimatical conditions and reveal morphological patterns in relation to the geoclimatical condition of their habitats. For instance, in this species the pattern of association between shape variables and geoclimate was as following: the specimens of Southern populations from drier localities are characterized by a relatively larger bulla, a longer incisive foramen and a narrower zygomatic plate of the maxilla (positioned toward the midline) and the specimens from higher and colder areas in the North Western localities (e.g. Zagros Mountain range, Iran) have a relatively broader zygomatic plate and a more convex zygomatic arch. This convexity in the zygomatic arch provides more space for the upper masticatory muscles that might functionally be associated with feeding behaviour of these animals and their feeding upon the seeds and vegetation cover of these areas.

Since prediction of diet from a morphological analysis is not easy and often unreliable, further ecological investigation and study of evolutionary morphological differentiation of the species would allow us to answer the questions concerning the behavioural and ecological limits imposed by morphological variability.

The observation of a relatively smaller bulla in the specimens from North Western localities (higher rainfall) and in contrast, existence of relatively larger tympanic present in the populations from

localities with lower rainfall in a jird species were not unexpected, because the latter pattern has similarly been observed in the past by previous authors such as Vaughan et al. (2000) and Monteiro et al. (2003) for the punaré rat (Rodentia: Echimyidae) and the rodent species from xeric environments. Since the bulla hypertrophy is claimed to increase the auditory sensitivity and offer a selective advantage for desert species against predation, especially in open habitats (Lay, 1972; Pavlinov, 1979, 1980, 2001, 2008; Webster, 1962, 1966; Oaks, 1967; Lay, 1972; Liao et al., 2007), the observed bulla hypertrophy in the studied specimens might functionally be a possible adaptation to the geoclimatical condition of their habitats. The Geno (GNO, Fig. 3) population from the South of Iran (warm and lowland region), in comparison with the other studied populations, in agreement with Momtazi et al. (2008), showed the most bulla inflation. Based on this character, the specimens from the latter locality reveal an affinity to *M. libycus* specimens, but the level of these shape differences at inter and intraspecific levels still has not been tested.

Exploration of the geoclimatical associations in other jird species and also comparison of the shape changes patterns depicted from different skull views and the mandible might provide complementary information for a better investigation of geographical shape variation in the jird species.

Taxonomic issues

The big problem in the definition of a subspecies is the delimitation of the geographic subdivisions and numerous forms can be recognized from a continuous variation (Monroe, 1982; O'Neill, 1982). Previous authors such as Monroe (1982) have stated that the subspecies category loses its potential usefulness if applied to situations of such continuous variations. Therefore, the subspecies category should not be used to describe populations differing from each other only through continuous variation (i.e. with all characters grading into each other along the clines). Numerous subspecies have been described within some of the Meriones species (e.g. at least six M. tristrami subspecies which have been reported from Turkey) without considering such continuous variation. Our observations of this study, being the continuous cranial variation observed among the studied M. persicus populations along a continuous geographical variation, also included the available topotypes of four subspecies, namely: M. p. baptistae (Thomas, 1920), M. p. ambrosius (Thomas, 1919), M. p. gurganensis (Goodwin, 1938) and M. p. persicus (Blanford, 1875), [of six subspecies that have been reported (Ellerman and Morrison-Scott, 1966; Musser and Carleton, 2005). But, as was demonstrated in the results, those populations were different from each other only through a continuous range among the cranial characters. Thus, this species still requires a considerable taxonomic revision with considering the morphological variation occurring in full distribution range of this species.

ACKNOWLEDGMENTS

We are very grateful to M.D. Carleton (USNM), L. R. Heaney (FMNH), J. Cuisin (MNHN), P. Jenkin and R. Portela Miguez (BMNH), A. Aalam (ZMFUM) who provided us with access to the collections. Thanks to the anonymous referees of earlier drafts of this manuscript for their valuable comments.

Appendix 1. Sampling localities of the examined specimens.

Country	Province	specific locality	Abbreviation	Lat.	Lon.	Sample size
Iran	Chahar mahal & Bakhtiari	Kuh rang, Lordegan	CMB	32.351 N	50.156 E	3
	East Azarbaijan	Miyaneh	MYA	37.433 N	47.155 E	4
	East Azarbaijan	Sarab	SAR	37.926 N	47.548 E	1
	East Azarbaijan	Kouhak (Kohak Darrehsī?)	KOH	37.578 N	46.284 E	1
	Esfahan	Sarvestan	ESF	33.133 N	51.818 E	1
	Kohgiluyeh and Boyer-Ahma	d Yasuj	YSJ	30.595 N	51.500 E	14
	Golestan	Dasht,Dashliboroon,Torkman sahra	DSH	37.633 N	54.817 E	2
	Golestan	Gonbad-e-Kavus	GON	37.233 N	55.083 E	1
	Hamedan	Hamedan	KHA	35.700 N	48.200 E	3
	Hormozgan	Geno	GNO	27.417 N	56.183 E	11
	llam	Ilam	ILM	33.638 N	46.431 E	19
	Kerman	Kerman	KER	29.900 N	56.533 E	3
	Kermanshah	Asadabad	KAS	37.766 N	48.116 E	2
	Kermanshah	Qhasr e shirin	KQA	34.318 N	47.087 E	1
	Kermanshah	Sameleh	SAM	34.021 N	47.307 E	5
	South Khorasan	Birjand	BIR	32.867 N	59.200 E	3
	North Khorasan	Bojnord	BJN	37.467 N	57.317 E	3
	Razavi Khorasan	Khajar	KHJ	35.100 N	54.700 E	11
	Razavi Khorasan	Kashmar, Duruna, Bardaskan (kavir-e-Namak)	KSH	35.183 N	57.415 E	1
	Razavi Khorasan	Mashhad	MSH	36.267 N	61.050 E	1
	Razavi Khorasan	Tandureh	TND	37.383 N	58.833 E	6
	Razavi Khorasan	Torbat-e-heidariyeh, Rushkar, Sangun=Sangan, Jangal, Isfadeh, Maehneh		35.283 N	59.217 E	7
	Razavi Khorasan	Bajestan	BJS	34.517 N	58.183 E	1
	Khuzestan	Behbahan	BEH	30.598 N	50.245 E	4
	Khuzestan	Masjed soleyman	MSO	31.933 N	49.300 E	8
	Kordestan	Aghbulagh Morshed	AGH	35.620 N	48.660 E	2
	Kordestan	Sanandaj, Bijar, Marivan	KDS (KRD)	35.310 N	46.999 E	6
	Kordestan	Saghez	SGZ	36.241 N	46.268 E	1
	Lorestan	Khorram abad	LST	33.491 N	48.333 E	7
	Markazi	Mahallat	MHL	33.750 N	50.500 E	2
	Mazandaran	Noshahr (Sama)	NSH	36.480 N	51.338 E	5
	Qazvin	Qazvin		36.267 N	50.017 E	5 19
		·	QZV (GZV)			3
	Sistan va Baluchestan	Khash	KHS	28.250 N	61.200 E	
	Sistan va Baluchestan	Zahedan	ZHD	29.217 N	60.867 E	1
	Tehran	Tehran	TEH	35.850 N	50.867 E	8
	West Azarbaijan	Naghadeh	NGD	36.933 N	45.367 E	3
	West Azarbaijan	Rezaeieh,Makoo	WAZ	37.491 N	44.992 E	10
	Zanjan	Soltanieh	SOL	36.454 N	48.799 E	1
	Zanjan	Zanjan	ZNJ	36.683 N	48.487 E	1
Afghanistan	•	Bamyan	BMY	34.817 N	67.879 E	5
	Herat	Herat, 8 mi N	HRT	34.449 N	62.167 E	6
	Kabol	Paghman	BMY	34.583 N	68.950 E	3
	Kandahar	Kandahar, 4 mi N	KNH	31.658 N	65.783 E	5
Pakistan	Baluchistan	Quetta Division, Urak Valley	BAL	30.360 N	67.020 E	14
	Punjab	Dera Ghazi Khan Division	PJB	30.050 N	70.633 E	1
Iraq	Sulaymaniyah	Penjwin	IRQ	35.617 N	45.000 E	2

Appendix 2. List of specimens analyzed in the present study and their catalogue numbers.

Smithsonian Natural Museum of Natural History (Washington D.C. USA)

```
354661, 350558, 350559, 350572, 354647, 354649, 354650, 354652, 354653, 354664, 354665, 326875, 326876, 326877, 326879, 326880, 326881, 326882, 326884, 326885, 326886, 326887, 326890, 326892, 326894, 326895, 326896, 326897, 326898, 326903, 341248, 350560, 350562, 350563, 350564, 350565, 350566, 350568, 350570, 350571, 341249, 341251, 354654, 354655, 354656, 354657, 354658, 354659, 328336, 328337, 328338, 329181, 353657, 353658, 353660, 353684, 353695, 353696, 353697, 353698, 411090, 411091, 411093, 411094, 413607, 413608, 411087.
```

Field Museum of Natural History (Chicago, USA)

97295, 97290, 97314, 57896, 57899, 57289, 57290, 57295, 57298, 97300, 97303, 97304, 97305, 97309, 97313, 97314, 97342, 97343, 97347, 97349, 84508, 111801, 111940, 111944, 111945, 111951, 111953, 111964, 111998, 112003, 112034, 112035, 103500, 103503, 103505, 103507, 103508, 103397, 103398, 103399, 103402, 103403, 103404, 103405, 103485, 103486, 103487, 103523, 103524, 103525, 103526, 103527, 84464,97358, 97360, 111968, 111982, 111986, 111989, 111992, 111979, 11980, 11982, 112021, 112023.

British Museum of Natural History (London, UK)

77.3052, 20.5.20.3, 20.2.9.21, 19.11.8.42, 19.11.7.72, 71.1581, 16.11.7.68, 19.11.7.71, 70.20.24, 70.20.23, Type of *Meriones persicus baptistae* (cat. #19.11.7.69), Type of *M. p. ambrosias* (cat. #5.10.4.35).

Zoological Museum of Ferdowsi University of Mashhad (Mashhad, Iran)

1399, 10, 14, 1396, 6, 1394, 28, 1395, 22, 24, 1397, 11, 27, 18, 8, 498, 135, 18, 333, 1392, 655, M-18, 566, 114, 320, 321, 315, M-15, 317, M-1111, M-1116, M-1113, M-1115, M-1110, M-110, 1571, M-1114, 1112, M560, 1398.

Musée National d'Histoire Naturelle (Paris, France)

1947.846, 1947.848, 1950.419, 1950.420, 1950.421, 1950.430, 1950.431, 1957.978, 1957.993, 1985.1628, 1991.241, 1957-290, 1957-203, 1957-257, 1957-200, 1957-221, 1957-285, 1957-245, 1957-215, 1957-226, 1957-234, 1957-273, 1957-186, 1957-983, 1957-209, 1957-272, 1957-210, 1957-283, 1957-229, 1957-223, 1957-246, 1957-227, 1957-231, 1957-232, 1957-190.

Royal Belgian Institute of Natural Sciences (Brussels, Belgium)

10498, 10369, 10072, 10363, 10051, 10427, 10365, 10034, 10043, 10370, 10038, 10425, 10026, 10366, 10041, 10039, 10361, 10368, 10025, 10042, 10044, 9884, 10377, 10364, 10379, 10032, 10074, 10064, 10373, 10031.

LITERATURE CITED

Atchley, W.R., Hall, B.K., 1991. A model for development and evolution of complex morphological structures. *Biological Reviews* 66, 101–157.

Atchley, W.R., Cowley, D.E., Vogl, C., Mclellan, T., 1992. Evolutionary divergence, shape change, and genetic correlation structure in the rodent mandible. *Systematic Biology* 41, 196–221.

Bookstein, F.L., 1991. Morphometric tools for landmark data: geometry and biology. Cambridge U Press, Cambridge, UK 435 pp.

Cardini, A., Diniz Filho, J.A.F., Polly, P.D., Elton, S., 2010. Biogeographic analysis using geometric morphometrics: clines in skull size and shape in a widespread African arboreal monkey. A. M. T. Elewa (Ed.), Morphometrics for Nonmorphometricians, Lecture Notes in Earth Sciences 124, Springer-Verlag Publishers, Heidelberg, Germany.

Caumul, R., Polly, P.D., 2005. Phylogenetic and environmental components of morphological variation: skull, mandible, and molar shape in marmots (Marmota, Rodentia). *Evolution* 59, 2460-72.

Colangelo, P., Castiglia, R., Franchini, P., Solano, E., 2010. Pattern of shape variation in the eastern african gerbils of the genus *Gerbilliscus* (Rodentia, *Muridae*): environmental correlations and implication for taxonomy and systematic, *Mammalian Biololgy* 75, 302-310.

Darvish, J., 2009. Morphmetric comparison of fourteen species of the genus *Meriones Illiger*, 1811 (Gerbillinae, Rodentia) from Asia and North Africa. *Iranian Journal of Animal Biosystematics* 5(1), 59-77.

Ellerman, J.R., Morrison-Scott, T.C.S., 1966. Checklist of Palearctic and Indian Mammals 1758 to 1946. British Museum (N H), London 810 pp.

Escoufier, Y., 1973, Le traitement des variables vectorielles. Biometrics 29, 751-760.

Firouz S (2005) The Complete Fauna of Iran. I B Tauris Publishers, London, 322 pp.

Hill, R.A., Dunbar, R.I.M., 2002. Climatic determinants of diets and foraging behaviour in baboons. *Evolutionary Ecology* 16, 579-593.

Klingenberg, C.P., 2011, MorphoJ: an integrated software package for geometric morphometrics. *Molecular Ecology Resources* 11, 353-357.

Lay, D.M., 1972, The anatomy, physiology, functional significance and evolution of specialized hearing organs of gerbilline rodents. *Journal of Morphology* 138, 41-120.

Liao, J., Zhang, Z., Liu, N., 2007. Effects of altitudinal change on the auditory bulla in Ochotona daurica (Mammalia, Lagomorpha). Journal of Zoological Systematics and Evolutionary Research 45(2), 151-154.

Momtazi, F., Darvish, J., Ghassemzadeh, F., Moghimi, A., 2008. Elliptic Fourier analysis on the tympanic bullae in three *Meriones* species (Rodentia, Mammalia): its application in biosystematics. *Acta zoologica cracoviensia* 51A(1-2), 49-58.

Monroe, J.R. B.L., 1982. A modern concept of the subspecies. Auk 99 (3), 608-609.

Monteiro, L.R., Duarte, L.C., dos Reis S.F., 2003. Environmental correlates of geographical variation in skull and mandible shape of *Thrichomys apereoides* (Rodentia: Echimyidae). *Journal of Zoology* 261, 47-57.

Musser, G.G., Carleton, M.D., 2005. Superfamily Muroidea. In: Wilson DE and Reeder DM (eds.) Mammal species of the world: a taxonomic and geographic reference (3rd ed.). Johns Hopkins University Press, Baltimore, MD 894-1531.

Oaks, E., 1967. Structure and function of inflated middle ears of rodents. Ph. D. thesis (Yale University, New Haven).

O'Neill, J.P., 1982. The subspecies concept in the 1980's. Auk 99(3), 609-612

Pavlinov, I.J., 1979. Morphology and taxonomic significance of the middle ear ossicles in the jirds of the genus *Meriones* (Rodentia: Cricetidae). *Zoological Journal* (Russ.) 58 (11), 1703-1712. In Russian, with English summary

Pavlinov, I.J., 1980. Evolution and taxonomic significance of the middle ear in the subfamily Gerbillinae (Rodentia: Cricetidae). *Bulletin of the Moscow Society for Natural Research (biology)* 85 (4), 20-33. In Russian, with English summary

Pavlinov, I.J., 2001. Current concepts of Gerbillid phylogeny and classification, African small mammals, in: Proceedings of the 8th International Symposium on African Small Mammals, Paris. pp. 141–149.

Pavlinov, I.Y., 2008. A review of phylogeny and classification of Gerbillinae (Mammalia: Rodentia). Moscow Univ Publ, Moscow, 67pp.

Petter, F., 1959. Evolution du dessin de la surface d'usure des molaires des *Gerbillidés*. *Mammalia*, 23(2), 304-315.

Reis, S.F., Duarte, L.C., Monteiro, L.R., Von Zuben, F.J., 2002a. Geographic variation in cranial morphology in *Thrichomys apereoides* (Rodentia: Echimyidae): I. Geometric descriptors of shape and multivariate analysis of geographic variation in shape. *Journal of Mammalogy* 83, 333-344.

Reis, S.F., Duarte, L.C., Monteiro, L.R., Von Zuben, F.J., 2002b. Geographic variation in cranial morphology in *Thrichomys apereoides* (Rodentia: Echimyidae): II. Geographic units, morphological discontinuities, and sampling gaps. *Journal of Mammalogy* 83, 345-353.

Rohlf, F.J., 1996. Morphometric spaces, shape components and the effect of linear transformations. In *Advances in morphometrics*: 117-130 in Marcus LF, Corti M, Loy A, Naylor G, Slice DE (Eds). New York: Plenum.

Rohlf, F.J., Slice, D., 1990. Extensions of the Procrustes method for the optimal superimposition of landmarks. *Systematic Zoology* 39, 40-59.

Rohlf, F.J., Corti, M., 2000. Use of two-block partial least squares to study covariation in shape. *Systematic Biology* 49, 740-753.

Rohlf, F.J., 2006a <u>TPSDig: Thin-plate spline digitize v2.10</u>. Department of Ecology and Evolution, State University of New York at Stony Brook (http://life.bio.sunysb.edu/morph/).

Rohlf, F.J., 2006b. TpsPLS: Partial Least-Squares, Version 1.18. Department of Ecology and Evolution, State University of New York at Stony Brook (http://life.bio.sunysb.edu/morph/).

Rychlik, L., Ramalhinho, M.G., Polly, D., 2006. Response to competition and environmental factors: skull, mandible, and tooth shape in Polish Water shrews (*Neomys*, Soricidae, Mammalia). *Journal of Zoological Systematics and Evolutionary Research* 44(4), 339-351.

Thorpe, R.S., 1976. Biometric analysis of geographic variation and racial affinities. *Biology Revolution* 51, 407–452.

Tong, H., 1989. Origine et évolution des Gerbillidae (Mammalia, Rodentia) en Afrique du Nord. *Mémoires Soc Géol France, NS, Paris*, 155, 1-120.

Vaughan, T.A., Ryan, J.M., Czaplewski, N.J., 2000. Mammalogy. Fourth Edition. New York: Harcourt College Publishers.

Webster, D.B., 1962. A function of the enlarged middle ear cavities of the kangaroo rat, *Dipodomys. Physiological Zoology* 35, 248-255.

Webster, D.B., 1966, Ear structure and function in modern mammals. American Zoologist 6, 451-466.