



Research Article

Sexual dimorphism, allometry, and interspecific variation in the cranial morphology of seven *Meriones* species (Gerbillinae, Rodentia)

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Abstract

Jirds (*Meriones*) are a mostly desert-adapted genus of gerbils, with a wide geographic range, through which it encounters various climatic conditions, which may influence their morphology. In this study, we quantified cranial morphometric variation both within and among seven jird species (*M. meridianus*, *M. hurrianae*, *M. crassus*, *M. tristrami*, *M. persicus*, *M. libycus* and *M. vinogradovi*), based on a two-dimensional landmark-based geometric morphometric analysis of 972 specimens, covering their entire geographic distribution. The aforementioned analysis was used to compare sexual dimorphism in size and shape within each species, as well as the relationship between size and shape (i.e. allometry) for each species. Despite greatly overlapping in morphospace (when examined visually), statistical analysis indicates significant differences in both size and shape among the seven examined jird species. UPGMA and CVA both show two main species clusters. Deformation grids indicate that these two clusters differ mostly in the relative size of the tympanic bulla, along with differences in the extent of nasal elongation, and the broadness of the zygomatic arch. Allometric changes in shape were analyzed in all species that show an allometric relationship. Sexual dimorphism in shape and size was detected in only three of the seven jird species. A visual inspection of the data indicates high overlap in shape space, and that male skulls are significantly larger than female skulls. When specimens were divided by sex, we found significant allometry in six of the seven species (for both sexes). A factorial multivariate analysis of covariance (MANCOVA) indicated that even when taking size variation into account, the residual shape variation was also significantly different among the sexes of the examined species. The outcome of this study confirms the presence of cranial variation in the examined jirds, and that the patterns of sexual dimorphism and allometry vary considerably among jird species.

Introduction

The genus *Meriones* Illiger, 1811 (Gerbillinae, Rodentia), or jirds, is a diverse murid rodent group that includes 17 recognized species with a geographic range that includes both North Africa and Asian countries (Musser and Carleton, 2005). Jirds generally favor semi-desert regions and steppes of mountains, as well as alluvial plains, cultivated valleys, and arid saline flats (Pavlinov, 2008; Darvish, 2011). Although most jirds are true desert specialists (e.g. the Sundevall's jirds and midday jirds) (Nowak, 1999), this group also includes non-desert rodents such as the Indian jird (Tabatabaei Yazdi, 2017).

Various processes could explain the intraspecific morphological variation in the crania of jirds. At the intraspecific level, climate could be a major driver of morphological variation in jirds, where climatic variation has been shown to be associated with the variation in the cranial morphology in a clinal fashion, which may reflect phenotypic plasticity (Tabatabaei Yazdi, 2011; Tabatabaei Yazdi et al., 2014a). Similarly, at the interspecific level, cranial variation has been shown to be associated with climate in the gerbil genus *Gerbillus* (Alhajeri, 2017), a close relative of jirds, as well as in the subfamily Gerbillinae (Alhajeri et al., 2015), to which jirds belong.

The cranial morphology of jirds may also be influenced by selective pressures on the sexes. Sexual dimorphism occurs when males and females of the same species exhibit differences in characteristics bey-

ond that of their sexual organs (e.g. size, shape, color, or even behavior); these differences, which may range from subtle to extreme, may arise as a consequence of sexual selection (Benítez et al., 2013). Sexual dimorphism in body size is often accompanied by shape dimorphism; both of which have been observed in various taxa as the consequence of environmental pressures (Benítez et al., 2013). Thus, dimorphism in shape may either arise as a consequence of natural or sexual selection for shape differences, or selection for size differences (and thus shape differences may arise as a byproduct of selection for the former) (Schwarzkopf, 2005; Raia et al., 2015). Sexual dimorphism in the skull has been studied in various animals—including primates (Uyterschaut, 1986; Cardini and Elton, 2008), carnivores (De Marinis et al., 1990; López-Martín et al., 2006), lizards (Sanger et al., 2013; Kelly, 2015), and rodents (Xia and Millar, 1987; Xiong and Zhang, 2007; Čanádý and Mošanský, 2017). Using traditional (distance-based) morphometric approaches, Darvish (2009) found no evidence of cranial sexual dimorphism in jirds. Similarly, Tabatabaei Yazdi et al. (2012) found no sexual dimorphism in the skull size of the midday jird (*M. meridianus*), by using the geometric morphometric approach (Bookstein, 1991; Zelditch et al., 2012; Cardini, 2016).

Jird cranial shape may also covary with size (i.e. allometry), which may in turn show different patterns between males and females. The allometric relationship between skull size and shape has been investigated in various taxa, including, crab-eating fox (De Moura Bubadué et al., 2016), *Gerbillus* (Alhajeri, 2017), Hymenoptera (Benítez et

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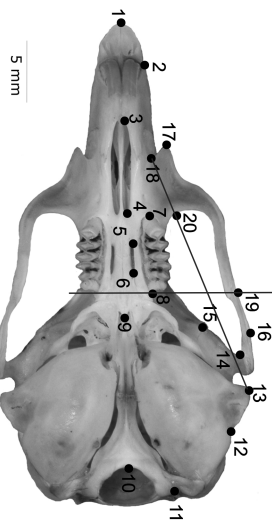


Figure 1 – Position of landmarks used in the study, shown on the ventral view of the Persian jird (*M. persicus*). Landmarks are described in Tab. S2.

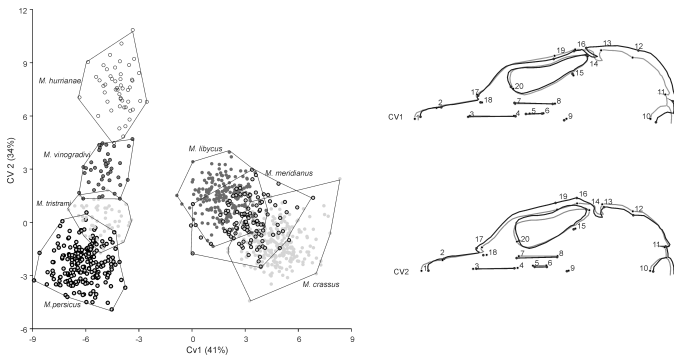


Figure 2 – Scatter plot of the outcome of the canonical variate analysis (CVA) performed on the shape variables of the ventral view of the crania. The outlines represent the shape differences between the overall mean (in grey) and the configurations corresponding to the highest positive values of each CV axis (in black). The percentage of explained variance by each CV are indicated in parentheses.

al., 2013), common geckos (Kelly, 2015), snakes (Shine, 1991) and macaques (Simons and Frost, 2016).

In this study, we examine intra- and interspecific variation in jird crania using the geometric morphometric approach, a technique that allows for the investigation of the morphology of complex structures, such as mammalian skulls (Monteiro et al., 1999; Reis et al., 2002a,b; Cardini and Elton, 2008; Tabatabaei Yazdi, 2011; Cardini, 2016). We sample intact adult specimens, belonging to seven jird species from the genus *Meriones*, for two objectives. The first is to examine the differences in cranial size and shape, and the differences in the relationship between cranial size and shape (i.e. allometry) among the sexes (i.e. sexual dimorphism) of each of *M. crassus*, *M. hurrianae*, *M. libycus*, *M. meridianus*, *M. persicus*, *M. tristrami*, and *M. vinogradovi*. Although morphological differences between some of the aforementioned species have already been investigated using geometric morphometrics (Tabatabaei Yazdi, 2011; Tabatabaei Yazdi and Adriaens, 2013; Tabatabaei Yazdi et al., 2014a), this is the first time that all seven of these *Meriones* species have been used to investigate intersexual size and shape variation. The second objective is to examine interspecific variation in cranial size and shape, as well as the variation in allometric patterns among (i.e. across) the aforementioned seven *Meriones* species.

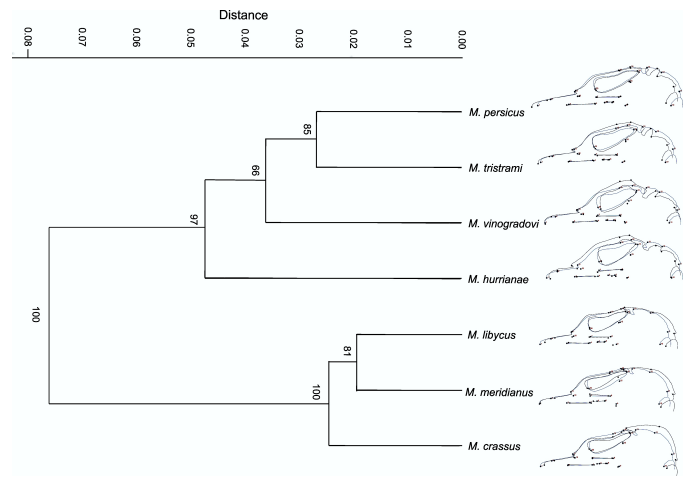


Figure 3 – UPGMA phenogram showing overall similarity in the skull shape among the species. The nodes show the branch bootstrap support based on 10,000 replicates, as a percentage. The outlines represent the shape differences among the consensus configuration for each species (in black) when compared with the mean shape of all the species pooled together (in grey).

Methods

Data acquisition and morphometric processing

We examined a total of 972 museum skull specimens of seven jird species (272 of *M. crassus*, 110 of *M. meridianus*, 53 of *M. tristrami*, 222 of *M. persicus*, 221 of *M. libycus*, 51 of *M. hurrianae*, and 43 of *M. vinogradovi*) for this study (see Tab. S1 for voucher numbers). The specimens were obtained from the collections of the Smithsonian National Museum of Natural History (Washington D.C., USA), the Field Museum of Natural History (Chicago, USA), the British Museum of Natural History (London, UK), Musée national d'Histoire naturelle (Paris, France), the Natural History Museum of Ferdowsi University (Mashhad, Iran), and the Royal Belgian Institute of Natural Sciences (Brussels, Belgium). The specimens were sampled from throughout the geographic range of each species. Specimens were divided into species based on the identification keys of jirds (Chaworth-Musters and Ellerman, 1947; Darvish, 2011). We identified juvenile specimens based on the degree of eruption of their third molars, following Petter (1959), Tong (1989), and Pavlinov (2008), which were subsequently excluded from all analyses. All type specimens available in the visited museums were included in the analyses.

For all specimens, photographs of the ventral view of the skull were taken with a Nikon D70 digital reflex camera, using a Sigma 105 mm macro lens, at five megapixels. Photographs were taken in a standardized manner; the camera was placed on a tripod with the camera lens parallel to the ground, while the skulls were placed on a box filled with glass pearls. The skulls were positioned in such a way as their frontal plane being parallel to both the camera lens. A scale bar was included in all the photographs in order facilitate the extraction of a scaling factor, which can be used to estimate the centroid size (see below).

Table 1 – Summary of the multivariate linear regression analysis, of ventral cranial shape data (retained PCs based on the interspecific Procrustes coordinates, PCI-12=66.2% variation) on log centroid size of the seven *Meriones* species (sexes pooled). Significant *p*-values are indicated in bold.

Species	F-statistic	R ²	<i>p</i> -value
<i>Meriones crassus</i>	6.267	0.023	0.0129
<i>Meriones hurrianae</i>	4.875	0.090	0.0320
<i>Meriones libycus</i>	2.320	0.010	0.1290
<i>Meriones meridianus</i>	0.686	0.006	0.4090
<i>Meriones persicus</i>	5.398	0.024	0.0211
<i>Meriones tristrami</i>	1.202	0.024	0.2780
<i>Meriones vinogradovi</i>	7.395	0.156	0.0096

Table 2 – Summary of the MANOVA analysis conducted on the shape variables represented by the retained PCs (based on the intraspecific Procrustes coordinates) testing for shape differences among males and females in the seven species. The percentage of shape variation explained by the retained PCs for each species are indicated in the table. Significant *p*-values are indicated in bold.

Species	F-statistic	<i>p</i> -value
<i>Meriones crassus</i> (PC1–3=44.5% variation)	5.7371	0.0008
<i>Meriones hurrianæ</i> (PC1–10=78.5% variation)	1.4417	0.1989
<i>Merione libycus</i> (PC1–2=33.3% variation)	0.6471	0.5249
<i>Meriones meridianus</i> (PC1–6 = 61.9% variation)	1.373	0.233
<i>Meriones persicus</i> (PC1–3=49.4% variation)	2.6435	0.0505
<i>Meriones tristrami</i> (PC1–3=48.6% variation)	2.8416	0.0483
<i>Meriones vinogradovi</i> (PC1–6=66.0% of variation)	4.3809	0.0024

In each photograph, 20 two-dimensional (2D) landmarks, covering all important aspects of the ventral view of the cranium, were chosen to represent the cranial morphology (Fig. 1). The digitized landmarks are described in Tab. S2. Landmarks were digitized using tpsDig (Rohlf, 2010, 2015a).

A generalized Procrustes analysis (GPA; Rohlf and Slice, 1990) was conducted separately for each species using PAST (PALaeontological Statistics) ver. 3.14 (Hammer et al., 2001) in order to obtain Procrustes coordinates (shape variables) and centroid sizes. These shape variables (henceforth, referred to as intraspecific Procrustes coordinates), along with the centroid sizes, were used for intraspecific comparisons (i.e. sexual dimorphism).

For interspecific comparisons, the intraspecific Procrustes coordinates were first re-aligned using a second GPA in order to obtain new

re-aligned Procrustes coordinates (henceforth, referred to as interspecific Procrustes coordinates). The interspecific Procrustes coordinates along with the centroid sizes obtained from the first GPA were used for interspecific comparisons. The second GPA was conducted in the Geomorph library (Adams and Otárola-Castillo, 2013) in R (R Development Core Team, 2016).

Prior to conducting the statistical analyses described below, a principal component analysis (PCA) was performed on both the intraspecific and the interspecific Procrustes coordinates in order to reduce the number of shape variables analyzed in subsequent steps (required for most analyses).

Statistical analyses

PCA, using singular value decomposition, was conducted in the pcaMethods library (Stacklies et al., 2007) in R. Only the PCs that had eigenvalues greater than the values generated by the broken stick model (Legendre and Legendre, 1998) as implemented in the Vegan library (Oksanen et al., 2015) in R were retained for subsequent analyses (see below).

For the PCA conducted on the intraspecific Procrustes coordinates, the retained PCs for each species were: *M. crassus* (PC1–3=44.5% variation), *M. hurrianæ* (PC1–10=78.5% variation), *M. libycus* (PC1–2=33.3% variation), *M. meridianus* (PC1–6=61.9% variation), *M. persicus* (PC1–3=49.4% variation), *M. tristrami* (PC1–3=48.6% variation), and *M. vinogradovi* (PC1–6=66.0% of variation). Because none of the PCs satisfied the broken stick rule for the interspecific Procrustes coordinates dataset, the less conservative Kaiser’s eigenvalue-greater-than-one rule (Kaiser, 1960) was used instead, which led to the retention of PC1–12 (=66.2% variation).

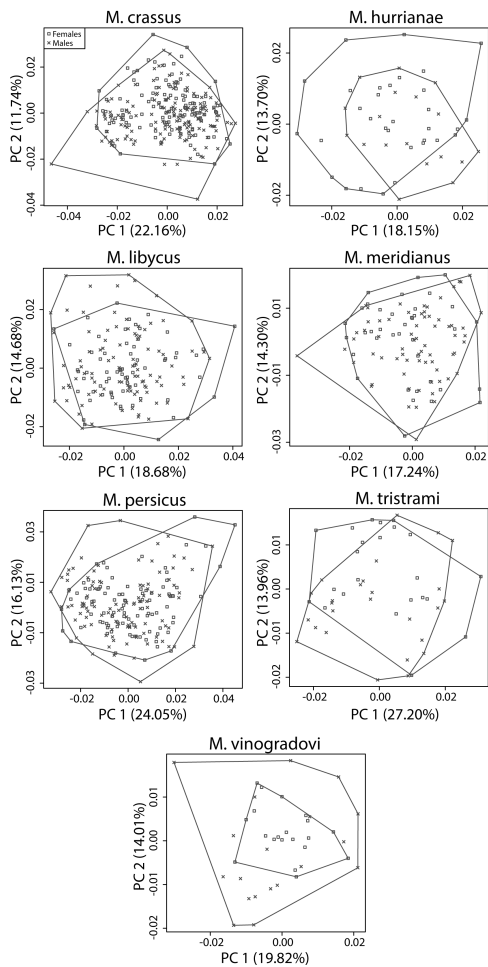


Figure 4 – Morphospace represented by the first two principal components (of intraspecific procrustes coordinates) occupied by each sex for each species. Symbols representing each sex are indicated in the first panel. The percentage of explained variance by each PC are indicated in parentheses.

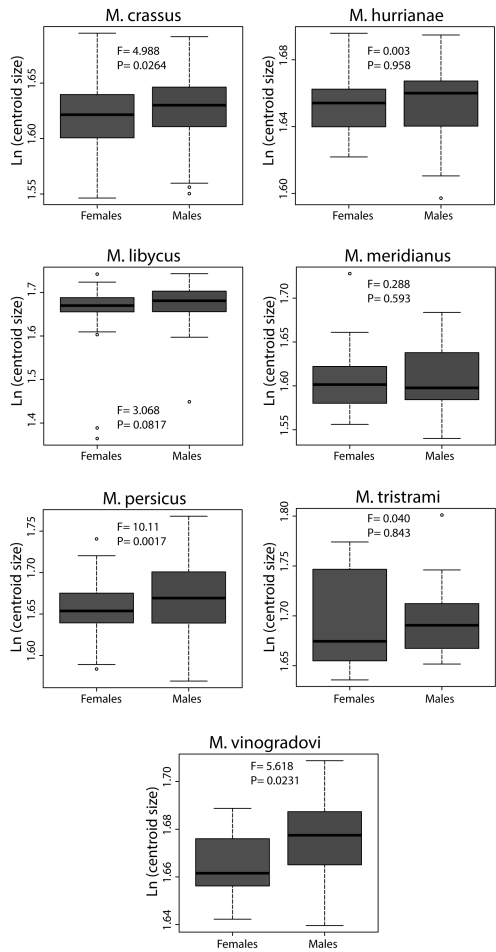


Figure 5 – Differences in the log transformed centroid sizes among males and females of the seven *Meriones* species, based on the ventral cranial landmarks. Inner boxplot lines are median values, box margins are 25th and the 75th percentiles, whiskers are 5th and 95th percentiles, and points beyond the whiskers are outliers. Results of the ANOVA analyses are also shown (as in Tab. 3).

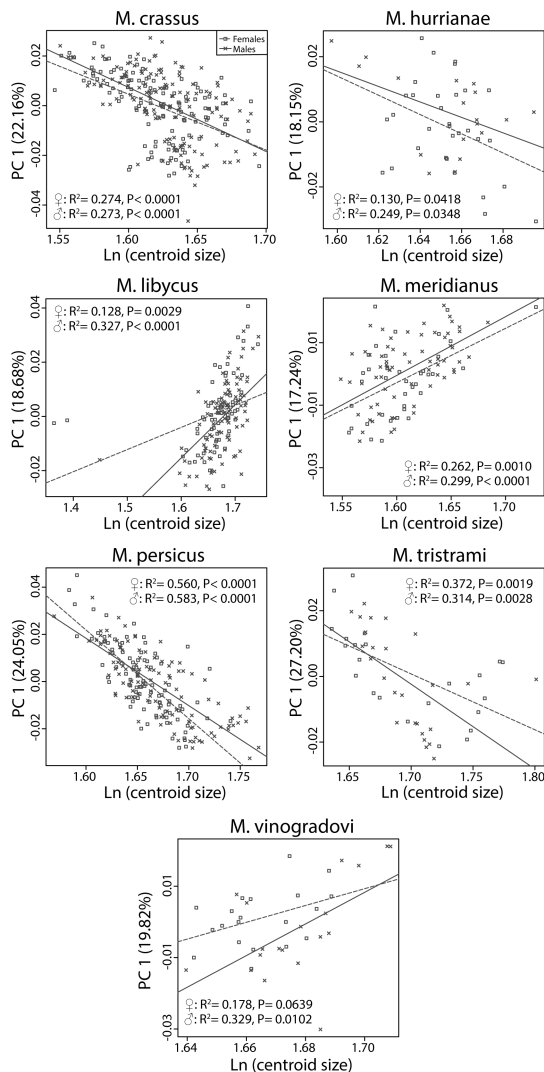


Figure 6 – Scatterplot showing the outcome of a univariate linear regression of PC1 of cranial shape being regressed onto log centroid size for females (statistics represented by the Venus symbol ♀) and males (statistics represented by the Mars symbol ♂) of the seven examined *Meriones* species. Separate best fit lines are shown for females and males. The percentage of explained variance by PC1 of each species is indicated in parentheses.

The significance of cranial shape differences among the species was assessed via a MANOVA on the retained shape PCs of the interspecific Procrustes coordinates and visualized using a scatterplot of the first two PCs, with the data points coded by species. A canonical variate analysis (CVA), was also performed in MorphoJ to assess the distribution of the specimens belonging to each species in morphospace. The distribution of the specimens of each species in morphospace based on both PC1–2 (see above) and CV1–2 (separately) were visualized using scatterplots.

In order to determine the overall shape differences and the clustering patterns among the species, an unweighted pair-group method with arithmetic mean (UPGMA) cluster analysis (based on Euclidean distance), was conducted on the consensus configuration for each species using PAST. Branch support was estimated by performing 10,000 bootstrap randomizations. The consensus landmark configuration of each species (mean shape), as well as the consensus for the whole samples (all species) were calculated using tpsSmall 1.33 (Rohlf, 2015a). The shape differences between the consensus of each species and the consensus of the whole sample were visualized using thin-plate spline deformation grids, as implemented in MorphoJ 1.06 (Klingenberg, 2011).

Cranial size differences among the species were assessed via an ANOVA on the log transformed centroid sizes and visualized using boxplots. Significance of pairwise differences in centroid size means among the species were determined via a post-hoc Tukey honest significant difference (HSD) test.

Sexual dimorphism in cranial shape within each species (separately) was investigated using a multivariate analysis of variance (MANOVA) on the retained shape PCs of the intraspecific Procrustes coordinates. Sexual dimorphism in cranial shape of each species was also visualized using scatterplots of the first two PCs, with the data points coded by sex.

Also, in a similar fashion, variation in cranial size among the sexes for each species was determined using an analysis of variance (ANOVA) on the log transformed centroid size—these differences were visualized using boxplots.

Differences in allometric patterns between species were determined, as in above, using a multivariate linear regression of the retained shape PCs of the interspecific Procrustes coordinates (PC1–12) onto the log centroid size, and visualized using a scatterplot of PC1 of shape vs. log centroid size separated by species. As in above, the best fit lines (and the values represented on the plots) were based on univariate regressions (i.e. PC1 of shape regressed onto log centroid size). ANOVA (including Tukey's HSD test), MANOVA and multivariate and univariate linear regression were all performed in the R base package.

Sexual dimorphism in allometry within each species was determined using a multivariate linear regression of the retained shape PCs of the intraspecific Procrustes coordinates onto the log centroid sizes. The aforementioned sexually dimorphic allometric patterns were visualized using a scatterplot of PC1 of shape vs. log centroid size separated by sex; the best fit lines (and the values represented on the plots) were based on univariate regressions (i.e. PC1 of shape regressed onto log centroid size). A factorial MANCOVA was conducted on the PC1–32 of the shape variables (explaining >99.1% of the shape variation), with both sex and species as fixed factors, and centroid size as a covariate, as implemented in the Jmv library (Selker et al., 2018) in R. This analysis was conducted to test for both sexual dimorphism and interspecific variation, as well as their interaction, after accounting for allometric shape variation (i.e. “allometry-free” shape variation).

Results

Interspecific variation

Although a visual inspection of the scatterplots indicates that the seven species greatly overlap in the shape space represented by PC1–2 (Fig. S3), MANOVA indicates a significant difference in shape among the seven *Meriones* species (when sexes are pooled) ($F=20.35$, $p<0.0001$). On the other hand, the species overlap much less in the shape space represented by CV1–2 (Fig. 2). *M. tristrami* + *M. vinogradovi* + *M. hurrianae* + *M. persicus* are clearly separated from *M. meridianus* + *M. crassus* + *M. libycus* along CV1; while *M. hurrianae* is separated from all other species along CV2 (Fig. 2). Specimens with low CV1 scores have less inflated tympanic bullae and closer supra-meatal triangle (landmarks 12 and 13), and relatively longer nasals (landmark 1) than those with higher scores (Fig. 2). When specimens with lower CV2 scores were compared to those with higher scores, the former has longer nasals, more convex and laterally positioned zygomatic arches (landmarks 16 and 19), and broader zygomatic plates (landmark 17) (Fig. 2).

Based on the UPGMA dendrogram, the species were arranged in two main clusters (with the nodes being supported by high bootstrap scores): (1) *M. tristrami* + *M. vinogradovi* + *M. hurrianae* + *M. persicus*, and (2) *M. meridianus* + *M. crassus* + *M. libycus* (Fig. 3). The species in the first cluster show relatively smaller tympanic bullae compared to the consensus (Fig. 3). While *M. tristrami* and *M. persicus* are characterized by longer nasals, *M. vinogradovi* and *M. hurrianae* are characterized by a relatively more convex zygomatic arch (Fig. 3). On the other hand, species in the latter cluster have relatively shorter nasals and wider zygomatic plates when compared to the consensus (Fig. 3). *M. meridianus*, *M. crassus*, and *M. libycus* are all characterized by more inflated bullae and open suprametral triangles, while *M. crassus* is characterized by a considerably inflated bulla, and a less convex zygomatic arch (Fig. 3).

ANOVA indicates significant differences in log centroid size among the seven *Meriones* species (when sexes are pooled) ($F=88.45$, $p<0.0001$). Tukey's HSD test indicates that all pairwise compar-

Table 3 – Summary of the ANOVA conducted on the log-transformed centroid sizes among males and females of the seven *Meriones* species, based on the ventral cranial landmarks. Significant *p*-values are indicated in bold.

Species	F-statistic	<i>p</i> -value
<i>Meriones crassus</i>	4.988	0.0264
<i>Meriones hurrianae</i>	0.003	0.958
<i>Merione libycus</i>	3.068	0.0817
<i>Meriones meridianus</i>	0.288	0.593
<i>Meriones persicus</i>	10.11	0.0017
<i>Meriones tristrami</i>	0.04	0.843
<i>Meriones vinogradovi</i>	5.618	0.0231

Table 4 – Tab. 4 Summary of the multivariate linear regression analysis, of ventral cranial shape data (retained PCs based on the intraspecific Procrustes coordinates) vs. log centroid size, separated for males and females, in the seven *Meriones* species. The percentage of shape variation explained by the retained PCs for each species are indicated in the table. Significant *p*-values are indicated in bold.

Species	Sex	F-statistic	R ²	<i>p</i> -value
<i>Meriones crassus</i>	Females	0.320	0.003	0.5730
(PC1–3=44.5% variation)	Males	0.079	0.001	0.7800
<i>Merione hurrianae</i>	Females	5.637	0.158	0.0242
(PC1–10=78.5% variation)	Males	1.627	0.036	0.2200
<i>Meriones libycus</i>	Females	12.500	0.161	0.0008
(PC1–2=33.3% variation)	Males	57.960	0.379	<0.0001
<i>Meriones meridianus</i>	Females	16.250	0.311	0.0003
(PC1–6=61.9% variation)	Males	18.900	0.223	<0.0001
<i>Meriones persicus</i>	Females	25.460	0.213	<0.0001
(PC1–3=49.4% variation)	Males	7.799	0.071	0.0062
<i>Meriones tristrami</i>	Females	0.089	0.004	0.7680
(PC1–3=48.6% variation)	Males	2.551	0.096	0.1230
<i>Meriones vinogradovi</i>	Females	2.204	0.109	0.1550
(PC1–6=66.0% of variation)	Males	5.195	0.234	0.0358

ons were significant, even after the *p*-values were adjusted for multiple comparisons (all *p*<0.0217), except for those between *M. hurrianae* – *M. persicus*, *M. hurrianae* – *M. vinogradovi*, *M. libycus* – *M. persicus*, *M. libycus* – *M. vinogradovi*, and between *M. vinogradovi* – *M. persicus* (all *p*>0.1113; Fig. S4).

According to the multivariate linear regression analysis, when the sexes were pooled together, log centroid size was significantly associated with the shape variables (retained PCs), in *M. crassus*, *M. hurrianae*, *M. persicus*, and *M. vinogradovi* ($R^2=0.02–0.15$, all *p*<0.0320), but not in *M. libycus*, *M. meridianus*, nor in *M. tristrami* (all *p*>0.1290; Tab. 1). Similar results were observed when PC1 of shape was regressed onto log centroid size (i.e. univariate regression)—log centroid size was significantly correlated to PC1 of shape for *M. crassus*, *M. libycus*, and *M. persicus* ($R^2=0.07–0.21$, all *p*<0.0001), but not for *M. hurrianae*, *M. meridianus*, *M. tristrami*, nor for *M. vinogradovi* (all *p*>0.0906; Fig. S5). Taken together with the results of the multivariate linear regression analysis, this result indicates that shape variation can be explained by size variation (i.e. allometry) in only 3–4 of the seven studied *Meriones* species.

Sexual dimorphism

MANOVA indicates a significant difference in shape among the sexes in *M. crassus*, *M. tristrami*, and *M. vinogradovi* ($F=2.84–5.73$, all *p*<0.0483), but not in *M. hurrianae*, *M. libycus*, *M. meridianus*, nor *M. persicus* (*p*>0.0504 for all; Tab. 2). A visual inspection of the scatterplots indicates that males and females highly overlap in the shape space represented by PC1–2 in all species (Fig. 4).

ANOVA indicates significant differences in log centroid size among the sexes in *M. crassus*, *M. persicus*, and *M. vinogradovi* ($F=4.98–10.11$, all *p*<0.0264), but not in *M. hurrianae*, *M. libycus*, *M. meridianus*, nor in *M. tristrami* (*p*>0.0817 for all; Tab. 3; Fig. 5). In *M. crassus*, *M. persicus*, and *M. vinogradovi*, male skulls are significantly larger than female skulls (Fig. 5).

According to the multivariate linear regression, when the dataset was divided by sex, log centroid size was significantly related to the shape variables (retained PCs), in *Meriones hurrianae* (females), *Meriones libycus* (both sexes), *Meriones meridianus* (both sexes), *Meriones persicus* (both sexes), and *Meriones vinogradovi* (males) ($R^2=0.07–0.37$, all *p*<0.0358; Tab. 4). Other contrasts were not significant (*p*>0.1230; Tab. 4). Similar results were observed when PC1 of shape was regressed onto log centroid size (i.e. univariate regression)—log centroid size was significantly related to PC1 of shape for all the species (both sexes) ($R^2=0.12–0.58$, all *p*<0.0418), except for *M. vinogradovi*, where the female regression was not significant (*p*=0.0639), but the male regression was ($R^2=0.32$, *p*=0.0102; Fig. 6).

The factorial MANCOVA indicate that even when taking size variation into account, both the species (Wilks' lambda=0.117, *F*-value=12.34; *p*<0.001) and the sexes (Wilks' lambda=0.801, *F*-value=2.19; *p*<0.001) had significantly different cranial shape (i.e. they were different in allometry-free shape). The MANCOVA also show a significant interaction effect among the fixed factors (species*sex) (Wilks' lambda=0.507, *F*-value=1.83; *p*<0.001), which indicates that species identity and sex have a combined effect on allometry-free cranial shape differences. In other words, the difference in allometry-free cranial shape among the species depends on sex, or that the nature of sexual dimorphism in allometry-free cranial shape differs among the species.

Discussion

Species belonging to the genus *Meriones* are broadly distributed throughout Palearctic desert regions, occupying habitats that range in environmental conditions from being extremely arid to mesic (Musser and Carleton, 2005). As is the case for broadly distributed taxa, they exhibit extensive morphological diversity, which is brought about by adapting to different environmental conditions. Previous studies show that intraspecific morphological variation seem to be correlated with various environment factors, including annual rainfall and altitude, which argues for extensive morphological plasticity in jirds (Tabatabaei Yazdi and Adriaens, 2011; Tabatabaei Yazdi et al., 2014b). In the present study, based on a considerable sample of specimens from seven *Meriones* species, we found clear size and shape differences between the examined species; we also found evidence for significant sexual dimorphism and allometry in most of the examined species.

Our results indicate that despite having similar overall cranial morphology (as indicated by occupying a similar region in cranial morphospace), close relatives (e.g. *M. crassus* and *M. libycus*), can vary considerably in allometric trajectories of cranial shape.

Cranial sexual dimorphism is common in mammals (e.g. Johnson et al., 1989; O'Higgins et al., 1990). While only little sexual size dimorphism within the small mammals has been observed (Lu et al., 2014), and previous studies that use traditional, distance-based morphometric approaches, found no evidence of cranial sexual dimorphism in jirds (e.g. Darvish, 2009; Tabatabaei Yazdi et al., 2012), we do find such a pattern (in both size and shape) when we apply the geometric morphometric approach. We found different degrees of sexual dimorphism in the sampled jirds—some of the species had significant cranial sexual dimorphism (*M. crassus* and *M. vinogradovi*), while others did not (e.g. *M. libycus*). While significant sexual size dimorphism is often accompanied by significant shape dimorphism—this was not the case some of the investigated jirds. A similar result (sexes differ in head size, but not head shape) has been documented before in lizards (Huyghe et al., 2009; Kelly, 2015).

Of all the species that we examined, all the ones that had significant size dimorphism had males larger than females (*M. crassus*, *M. persicus*, and *M. vinogradovi*, Fig. 5). Rensch's rule states that in species where males are larger than females, size dimorphism increases with increasing body size (while it decreases with increasing body size in species where females are larger than males) (Schutz et al., 2009). While we do not directly test the applicability of Rensch's rule to jirds, of the three species that showed significant sexual size dimorphism: *M. vinogradovi*, which is larger than both *M. crassus* and *M. persicus*, also

showed the most amount of sexual dimorphism in cranial size (Fig. 5), lending some support to this rule in jirds. Moreover, we found that even though species that live in similar habitats might have similar cranial morphology (e.g. the desert rodents: *M. crassus*, *M. libycus*, *M. meridianus*, are similar in having more inflated bullae, and cluster together in the UPGMA dendrogram), this does not necessarily arise from a similar pattern of allometry. Further comparisons need to be conducted in other species in order to determine if the pattern observed in jirds can be generalized to other jirds and gerbils. ☞

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Supplemental information

Additional Supplemental Information may be found in the online version of this article:

- Supplemental Table S1** Museum voucher numbers of examined specimens.
- Supplemental Table S2** Description of cranial landmarks used in this study.
- Supplemental Table S3** Morphospace represented by the first two principal components occupied by each of the seven *Meriones* species.
- Supplemental Figure S4** Differences in the log transformed centroid sizes among seven *Meriones* species when males and females were pooled together.
- Supplemental Figure S5** Scatterplot showing the outcome of a univariate linear regression of PC1 of cranial shape.