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Geographic pattern of cranial differentiation in the Asian Midday Jird *Meriones meridianus* (Rodentia: Muridae: Gerbillinae) and its taxonomic implications

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Abstract

The existence of cryptic species in the midday jird (*Meriones meridianus*) has been suggested in literature, although based on little empirical data to support this hypothesis. In this study, a two-dimensional landmark-based geometric morphometric approach was used to investigate whether patterns in intraspecific variation in skull shape and size exist, using 110 skull specimens from more than 20 different localities along the distribution range of *M. meridianus*. This is the first study of morphological differences on such a big sample size and geographical range, and it tries to find whether skull shape variation in this species is best described as being clinal or rather reflecting cryptic diversity. The latter seems to be the case, as a dimorphic skull phenotype was found, reflecting a geographic disparity between the Middle East and the Far East specimens both in shape and in size. Distinct cranial differences were found in the overall cranial size and, also at the level of the inflation of the bulla, the elongation of the nasal, the length of the teeth row and the incisive foramen, as well as the distance in between the latter two. It thus seems that *M. meridianus* from Middle East is morphologically distinct from that of the Far East. Furthermore, our results also demonstrate that clinal variation could explain variation within Middle East populations, whereas a more heterogenous pattern is found for those of the Far East. The hypothesis that the observed phenotypic variation may reflect cryptic species is discussed, with the recommendation for a thorough taxonomical revision of the genus in the region.

Key words: Central Asia – geometric morphometrics – Iran – Muridae – skull morphology

Introduction

The midday jird (*Meriones meridianus* Pallas, 1773) is a rodent species distributed from the Northern Caucasus and eastern Iran [central desert of Kerman (Darvish 2009)] to Northern Afghanistan, Mongolia and Northern China (Lay 1967; Hassinger 1973; Sheng et al. 1999; Denys et al. 2001; Musser and Carleton 2005). Substantial intraspecific variation in morphological (external) characters, such as coat colour, body size and bone structure in populations coming from different geographical locations has been shown (Chaworth-Musters and Ellerman 1947; Wang and Yang 1983; Zhang 1997; Ito et al. 2010), leading to the description of many subspecies. Seven subspecies have been recognized from the Xinjiang of China (Ito et al. 2010), as well as a separate species (*Meriones dahlia*; Musser and Carleton 2005), whereas other species have been considered synonymous [e.g. *Meriones chengi* by Pavlinov et al. (1990, 1995) and Ito et al. (2010)]. In most keys and revisions on the genus *Meriones*, diagnostic features generally are ambiguous (Allen 1940; Chaworth-Musters and Ellerman 1947). Most of the studies on *M. meridianus* mainly provided external diagnostic features, rather than cranial characters, and are often based on local samples without covering the species' distribution range (e.g. Allen 1940). Especially in the arid habitat of the Iranian regions (especially the Iranian plateau), this species has remained poorly studied (Misonne 1975). As the midday jirds from the Iranian plateau are geographically most distinct from the Far East specimens, morphological differences resulting from clinal variation can be expected. To what degree *M. meridianus* intraspecific variation reflects a continuous range of clinal variation requires comprehensive analyses of characters that allow a quantification of even subtle levels of phenotypic variation. Considering the taxonomic ambiguities related to this species, emerging patterns in this phenotypic variation may also reflect cryptic species diversity.

To test this hypothesis on clinal variation versus variation suggesting cryptic species diversity, *M. meridianus* from the Middle East are compared with those of the Far East (Fig. 1), by performing a landmark-based geometric morphometric analysis on the skull. Cranial differences, such as a cranial size difference between the specimens from Turkestan (Uzbekistan and Kazakhestan) and those from China (Far East populations), have already been reported in the past by Chaworth-Musters and Ellerman (1947). Specimens originate from the localities spanning the species distribution range, including specimens collected from the type localities, as for example, the topotype of *M. chengi* (Musser and Carleton 2005). Using the cranium is especially relevant for studying phenotypic variation, as it is both genetically and functionally relevant and hence subjected to a substantial amount of selective pressure (Caumul and Polly 2005; Cordeiro-Estrela et al. 2008).

As such, the aims of this study are to (1) reveal the patterns of intraspecific skull shape and size variation in *M. meridianus* along its distribution range; (2) test the hypothesis whether continuous clinal variation rather than cryptic phenotypic differentiation explains the observed patterns; and (3) find potential diagnostic cranial characters allowing further taxonomical clarification of this species. For the second aim, the congruence of shape variation in specimens from Iran with that of the Middle East is evaluated, where in the case of clinal variation, a more similar phenotype is expected with Middle East specimens that are geographically closest.

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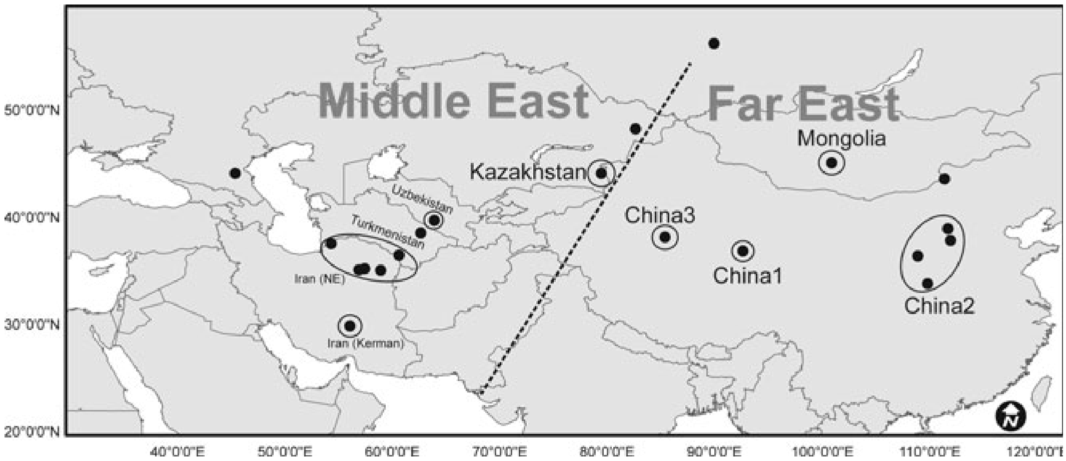

Fig. 1. Map showing sampling localities of the *Meriones meridianus* (closed circles) and groups of sampling locality (ovals) used in this study. The dashed line separates the Middle East from the Far East groups

Material and Methods

Specimens analysed

In total, 110 skull specimens of *M. meridianus* (Pallas, 1773) from 21 localities, originating from Iran to Mongolia and China, were used. 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. The only available type specimens [*Meriones auceps* (BMNH 8.8.4.30 male) and paratype of *Gerbillus psammophilus* (1867N°138 MNHN)] were broken and thus not be included in the analyses.

The specimens were obtained from the collections of the Smithsonian Natural Museum of Natural History, Washington, DC, USA (USNM), the Field Museum of Natural History, Chicago, CA, USA (FMNH), the British Museum of Natural History, London, UK (BMNH), and the Musée national d'Histoire naturelle, Paris, France (MNHN). The list of studied specimens with catalogue numbers is available in the appendix.

Specimens were plotted according to the geographical coordinates of the sample location, using ARCGIS, ARCMAP 9.2 (Fig. 1). Latitude and longitude were assigned based on the field notes of the collectors, the collections catalogue of the museums or the climate-database of the Food and Agriculture Organization of the United Nations (FAO, 2007; Table S1).

To perform robust canonical variate analyses, localities represented by only a few specimens were pooled according to their geographic proximity into eight analytical groups. Considering their use in statistical analyses, samples far from other localities and having too few specimens were not included in this analysis (Table S1).

Geometric morphometric data collection

The use of landmark data to describe variation in both skull size and shape in mammals has been proven to be sufficiently powerful in the past to resolve issues where only subtle variation is at hand (Rohlf and Marcus 1993; Fadda and Corti 2000; Barèiová and Macholán 2006; Cardini et al. 2007; Macholàn et al. 2008). Landmark data were obtained from photographs taken with a Nikon D70 digital reflex camera using a Sigma 105-mm macro lens (Sigma Aldrich, Bornem, Belgium) 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. Left–right symmetry on the ventral and dorsal sides and perfect overlap at the level of bullae, teeth rows and the optic canals on the lateral side were the most important criteria used to position the skulls in a standardized way. The ventral, dorsal and lateral sides of the skull specimens were photographed. Millimetre paper was included in the images to allow the acquisition of a scaling factor afterwards.

Shape models based on the three sides of the skulls were digitized using the software TPSDIG 2.12 (Rohlf 2004). Only one side (left side) of the skulls was used so that specimens that were broken on one side could still be included (Elewa 2004). In case, the right side was used (left side was broken), the landmark set was mirrored (following the assumption that left–right asymmetry was smaller than the level of intra- and interspecific variation that was the subject of this study). On the ventral, dorsal and lateral sides of cranium, respectively 20, 19 and 21 two-dimensional (2D) landmarks, were chosen on the basis that they include all relevant features of the cranium (Fig. 2). The landmarks were defined for each view of the cranium based upon the terminology used by Popesko et al. (2002) and Tong (1989; Table S2).

Data analysis

Shape analysis

A generalized procrustes analysis was performed using PAST (PAlaeontologica STatistics) ver. 1.74 (Hammer et al. 2001), to standardize the non-shape related variation in landmark coordinates. As such, landmark configurations were aligned by Procrustes superimposition, with removing differences in rotation and translation and by scaling to unit centroid size (Gower 1975; Bookstein et al. 1985; Rohlf and Slice 1990; Rohlf and Marcus 1993). Both uniform and non-uniform partial warps were calculated in PAST. Principal component analyses (PCA), using PAST, and Canonical variate analysis (CVA), using STATISTICA (StatSoft, version 7.0, www.statsoft.com, StatSoft, Inc., Tulsa, USA) were performed on partial warp scores of each data set separately for the dorsal, ventral and lateral data, to investigate the intraspecific variation and morphological differences among the operational taxonomic units (OTU's), respectively. The scatter plots demonstrating the results of the canonical variate analysis were generated in STATISTICA to visualize how specimen groups are distributed in morphospace. Visualization of shape changes explained by the canonical variates (CV) was carried out using MORPHOJ ver. 1.02c (Klingenberg 2011), by generating deformed outline drawings with the average shape as a reference. The pairwise testing for sexual dimorphism and differences between groups was carried out by applying a Monte Carlo randomization using POPTOOLS ver. 3.2.3 (Hood 2010) run under Microsoft Office Excel 2007. This test showed that no sexual dimorphism could be observed in the skull shape ($p > 0.5$). Consequently, the specimens of both sexes could be pooled for further analyses.

To evaluate the overall pattern of morphometric similarities between all the *M. meridianus* group means, a UPGMA cluster analysis was performed on the matrix of shape distances (Euclidean Distances) between the group means using PAST. Partial warp scores of each view were pooled to calculate the mean for each group. The corresponding matrix of Euclidean distances was calculated with POPTOOLS. The branch support was estimated by performing a bootstrapping of 10 000 randomizations using PAST.

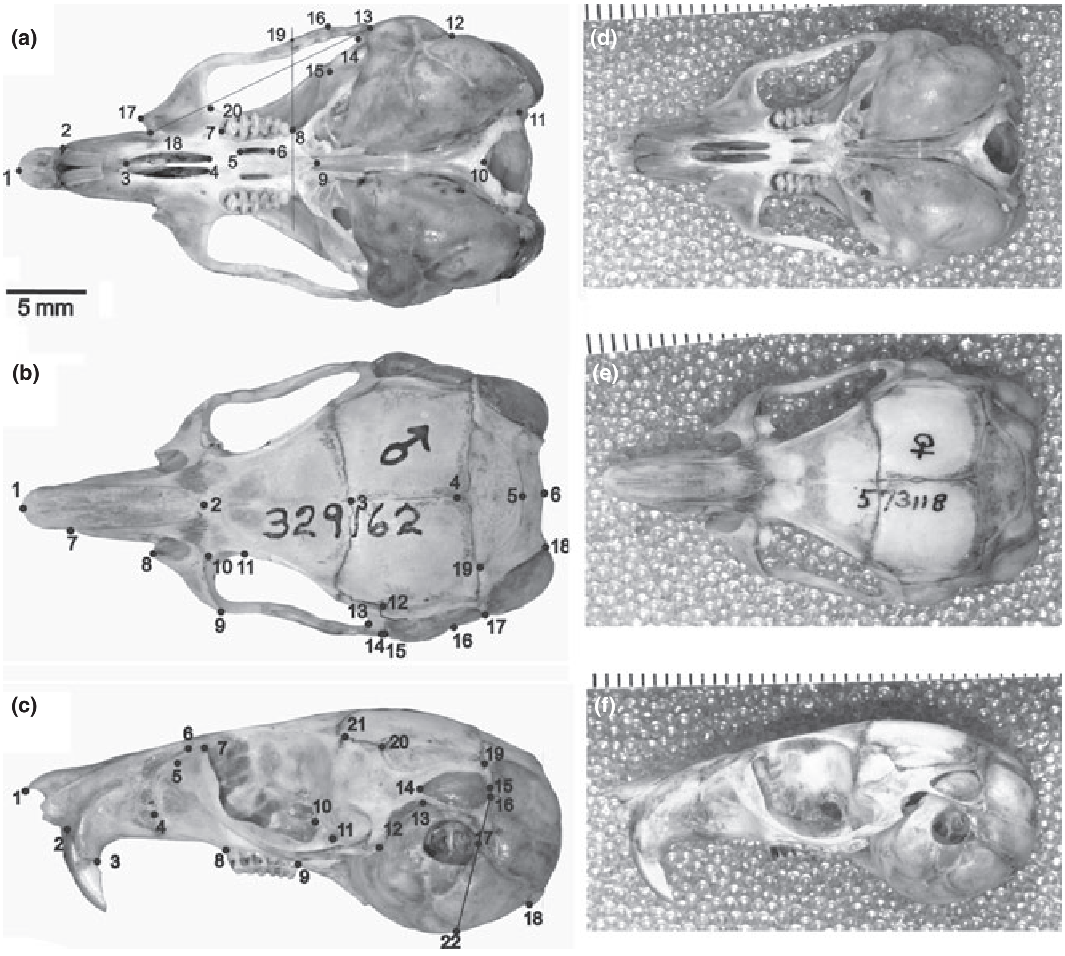

Fig. 2. Landmarks positioned on the cranium of *Meriones meridianus* shown in (a) ventral, (b) dorsal and (c) lateral view of the specimen from Kerman, Iran (USNM 329162). (d–f) Same views of a Far East specimen from Xinjiang, China, (USNM #573118) including millimetre-scale

Size analysis

The size analysis was performed at different levels, with data obtained from scaled pictures: centroid size (CS) of ventral cranium, length and relative length of tooth row and incisive foramen, and distance between tooth row and incisive foramen based on the landmarks on the ventral cranium. Centroid size (Bookstein 1991) of the cranium was calculated using PAST. Relative length of the incisive foramen was calculated as the distance between landmarks 3 and 4 on the ventral cranium, divided by the distance between landmarks 1 and 10 (proxy for ventral cranium length; Fig. 2). Relative length of the tooth row was calculated as the distance between landmarks 7 and 8 on the ventral cranium divided by the distance between landmarks 1 and 10. The landmark distances were calculated in PAST, and the relative lengths of the incisive foramen and tooth row (in percentage) were calculated using Microsoft Office Excel 2007. An overview of size variation for these absolute length variables for each group is given in Table S4. The distance between tooth row and incisive foramen (between landmarks 4 and 7) was calculated based on distances between the Procrustes x-coordinates of landmarks 4 and 7, obtained in PAST after Procrustes fitting was carried out to align the specimens. Size differences in the whole skull, as well as in other skull and tooth variables between the OTU's, were tested using a Monte-Carlo randomization (10 000 times resampling; confidence limit of 95% probability was maintained). The sexual size dimorphism in the skull was tested through a Monte Carlo randomization using POPTOOLS ver. 3.2.3 run under Microsoft Office Excel 2007. As this test showed no sexual size difference in the skull ($p = 0.33$), also for the size analyses, the specimens could be pooled.

Results

Intergroup shape differences

Although shape variation within the studied groups (Fig. 1) was considerable and the groups largely overlap along the first two PC's (not shown), they were arranged in two major clusters in the PCA-plot: one representing the Middle East groups, the other those from the Far East. First two PC's explained more than 40% of the variation for all three data sets individually (ventral, dorsal and lateral views). The morphological variation explained by PC1 (ca. 25% of variance), involved the relative size of the tympanic bulla, convexity of the zygomatic arch, nasal length, width of the interparietal and occiput and opening of the suprameatal triangle. However, despite the overlap in the PCA plots, the canonical variate analysis demonstrates the distinctness of the cranial phenotypes that characterize the groups (Fig. 3). The first canonical vector (CV1) of each plot (explaining more than 40% of total among-group variance relative to within-group variance) even emphasizes the distinctiveness of the Middle East groups (Iran, Uzbekistan and Kazakhstan) versus the Far East groups (China and Mongolia), the former being characterized by an inflated bulla (most striking in a dorsal view). From scatter plots in Fig. 3, it can be derived that the most important shape differences (explained by CV1 and CV2) do not represent gradual clinal variation. For example, of all Far

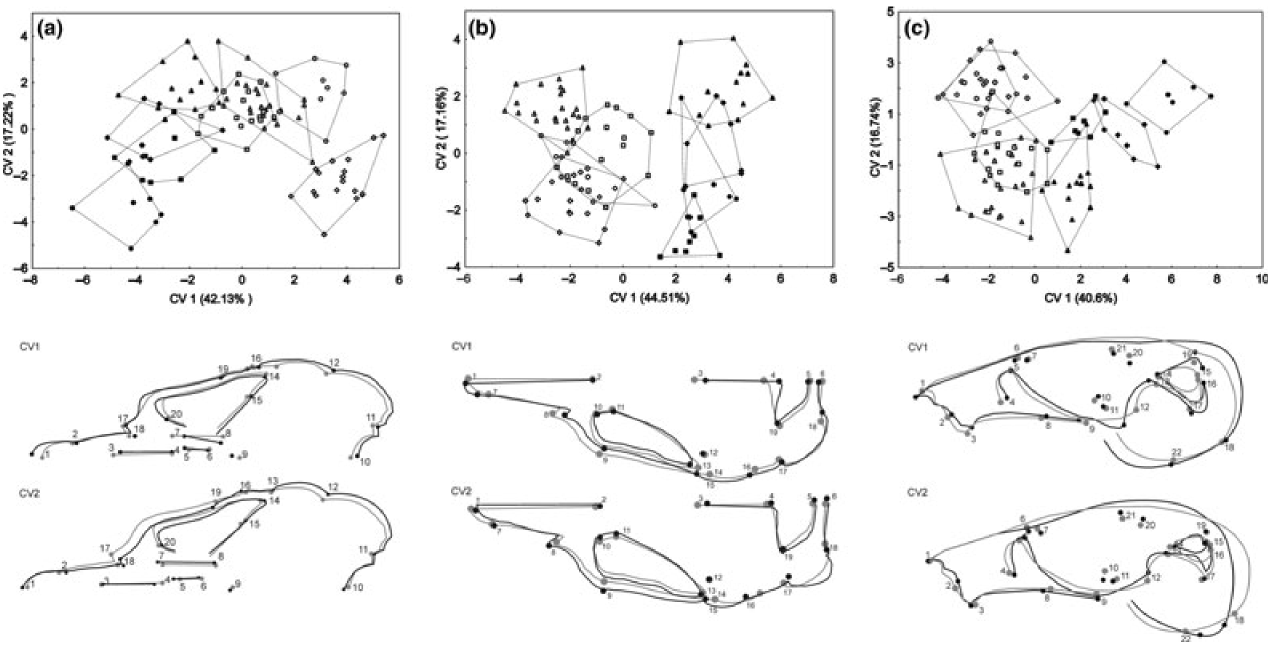

Fig. 3. Canonical variate analysis (CVA) scatter plot (axes 1 and 2) on shape variables of the (a) ventral, (b) dorsal and (c) lateral side of specimens. Symbols of the groups are the following: ◇ China 1, △ China 2, ○ China 3, ■ Iran (Kerman), • NE Iran, ▲ Kazakhstan, □ Mongolia, ♦ Uzbekistan. Deformed outline drawings (3× magnified for better visibility) show the shape changes from the overall mean (in grey) associated with each CV axis to the shape of Middle East specimens along CV1 and to the Iranian specimens along the CV2 (in black; in positive direction for the dorsal and lateral sides and negative direction for the ventral side)

East groups, Mongolian specimens are most similar to those of the Middle East, whereas the Far East specimens geographically closest to the Middle East are most distinct from the latter (China 1 and 3). For the Middle East cluster, a pattern of clinal variation seems to be more supported, as reflected along CV2.

This variation along CV2 (ca. 17% of variance) is mainly related to the zygomatic plate and the shape of the bulla and reflects differences between the Middle East and Far East clusters. The apparent dimorphic pattern in skull shape variation between the Middle East and Far East clusters can be characterized as follows (Fig. 3): Middle East specimens show a nasal elongation; an inflated tympanic bulla (landmarks 12 and 13) resulting in the zygomatic arch being positioned more rostrally (landmark 16 shifts rostrally); a narrower zygomatic plate (landmarks 17 and 18 shift caudally); the front of the upper jaw tooth row positioned more caudally (landmark 7 shifts caudally and towards landmark 8; Fig. 3a); narrower interparietal (landmark 4 shifts caudally); narrower zygomatic plate (landmarks 8 and 9 shift towards the midline and slightly caudally; Fig. 3b); and the suprameatal triangle becoming substantially wider with posterior processes more separated (landmarks 15 and 16 shift away from each other; Fig. 3c). The Euclidian distances between the *M. meridianus* group means (for all three views of skull) are shown in Table S3. The morphological distances are mostly similar; however, some groups proved to be significantly different.

The cluster analysis, based on the pooled data set of all three skull views, confirms the dimorphic nature of the skull shape: (1) a Middle East cluster, comprising the consensus configurations from Iran, Uzbekistan and Kazakhstan; and (2) a Far East cluster, with the consensus configuration from China and Mongolia (Fig. 4). Although all three Chinese groups cluster together, the bootstrap support for this is low. Within the Middle East cluster, the Iranian groups are not most similar to each other, again with low bootstrap support, but as indicated by Cardini and Elton (2009), nodes with low bootstrap could be strongly affected by sampling error.

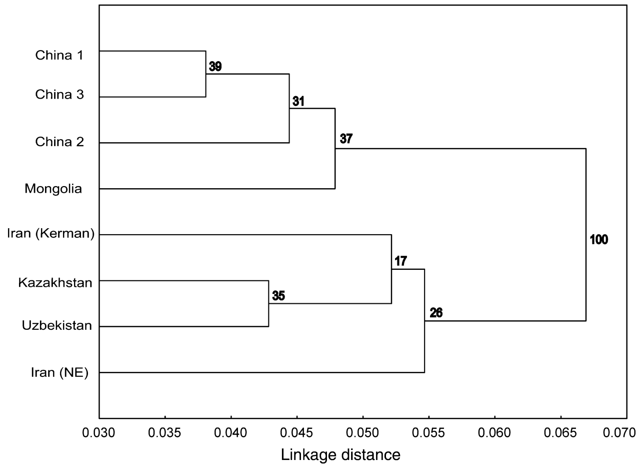

Fig. 4. Dendrogram obtained from the UPGMA on combined data set (shape information from dorsal, ventral and lateral view), using Euclidean distances between group means (branch bootstrap support shown as percentage at the nodes, 10 000 replicates)

Size variation among the *Meriones meridianus* groups

Cranium

The Middle East *M. meridianus* on average have a smaller cranium than those from the Far East, although not significantly different for all pairwise comparisons ($p > 0.05$). The randomization test on the centroid size data shows significant differences ($p < 0.05$) between the *M. meridianus* groups of the Middle East and the Mongolian one, with the latter having a bigger cranium (Fig. 5a). There was also no significant difference between the two Iranian groups nor between these and the Chinese groups ($p > 0.05$), although the latter on average have a bigger cranium. Within the Middle East cluster, the Iranian specimens appear to have the largest cranium. Only for the specimens of Kerman, this difference is significant compared to those from Uzbekistan ($p = 0.03$). Among the Middle East groups, only the Uzbekistan group had a significantly smaller cranial size compared to all groups from the Far East ($p < 0.005$).

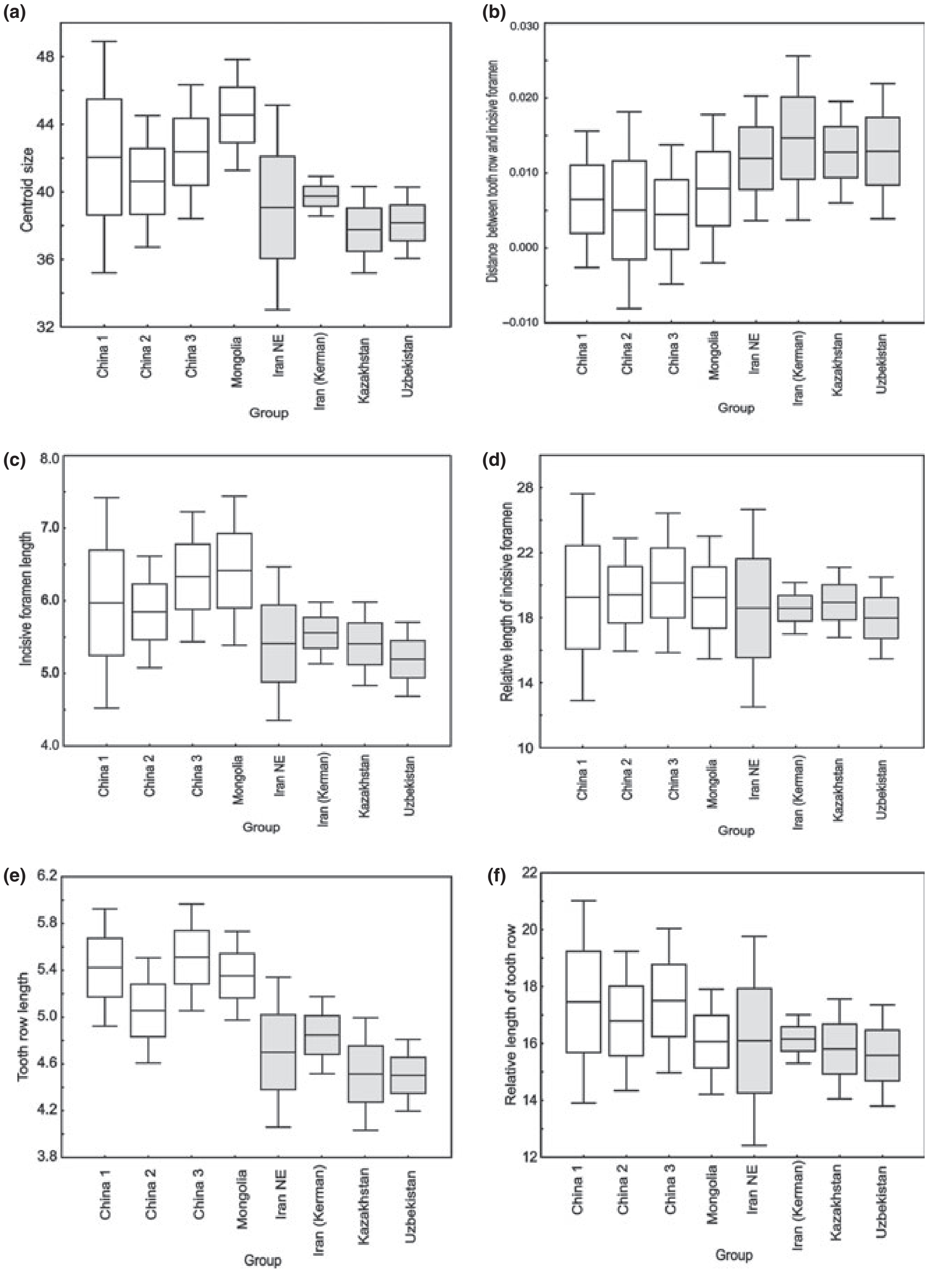

Fig. 5. Box-and-whisker plots of centroid size of the ventral cranium (a), the distance between the tooth row and incisive foramen in millimetres (b), incisive foramen length in millimetres (c) and the relative length of incisive foramen (d), tooth row length in millimetres (e) and the relative length of tooth row (f). Box represents mean ± SD and whiskers represent mean ± 2 SD. For better visibility and comparison between the Middle East and the Far East clusters, the Middle East cluster is shown in grey

Incisive foramen and tooth row

On average, the Far East *M. meridianus* specimens revealed a significantly longer incisive foramen than those from the Middle East ($p < 0.05$), where no significant differences were found among the Middle East groups nor among the Far East groups, except for China 2 (compared with China 3 and Mongolia, $p < 0.05$). Pairwise comparisons between all groups showed that only the specimens of the China 2 are not significantly different from those of Iran ($p > 0.2$). These results are mainly similar with what was observed in the cranial size differences among the groups. A post hoc test on the relative length of the incisive foramen showed that the apparent longer incisive foramen in Mongolian specimens was the result of the larger overall skull size, as no significant difference in relative foramen size was observed (Fig. 5d). The general pattern is, though, that all the Far East groups have an overall longer foramen than those of the Middle East (Table S4 and Fig. 5d).

With respect to tooth row length, the Far East groups (with the exception of China 2) have a significantly longer tooth row compared with the Middle East groups ($p < 0.05$).The pairwise comparisons did not reveal a difference among any of the Middle East groups, where the average length ranged between 4.5 and 4.8 mm for the Uzbekistan and Iranian (Kerman) specimens, respectively (Table S4). On the contrary, there is a significant difference between all Middle East groups and the Far East groups, with averages in the latter ranging between 5.1 and 5.5 mm for China 2 and China 3, respectively (Table S4 and Fig. 5e). Within the Middle East groups, the specimens from Iran (NE Iran and Kerman) on average have a longer tooth row than those from Kazakhstan and Uzbekistan, although not significant ($p > 0.07$). The pairwise comparisons on relative tooth row size did not show any significant difference neither within the Middle East groups nor within the Chinese groups ($p > 0.09$). The Mongolian group has a relatively smaller tooth row than the Iranian groups but longer than the other Middle East groups, although both differences being not significant ($p > 0.90$ and $p > 0.40$, respectively; Table S4 and Fig. 5f).

With respect to the distance between the anterior border of the tooth row and the posterior tip of the incisive foramen, the Far East groups are not significantly different from each other ($p > 0.19$). All the Middle East groups, having a larger average distance than those from the Far East, also are not different from each other ($p > 0.37$). A significant difference was found between the Iran NE group and each of the Far East groups ($p < 0.04$), except for Mongolia ($p = 0.10$), as well as between the Kerman, Kazakhstan and Uzbekistan groups and each of the Far East groups ($p < 0.04$) (Fig. 5b).

Discussion

Clinal variation versus cryptic differentiation in the skull phenotype in *Meriones meridianus*

One of the aims was to reveal to what degree the observed phenotypic variation in the skull of *M. meridianus* reflects a rather continuous variation along its distribution range or rather that a more patchy pattern emerges that could indicate cryptic differences between local populations. The results revealed a pattern supporting the hypothesis on cryptic diversity, as skull shape clearly is dimorphic when comparing specimens from the Middle East with those from the Far East. Far East specimens are characterized by a more swollen tympanic bulla and consequently wider suprameatal triangle with more widely spread posterior processes, a less wide zygomatic plate, an elongated nasal and a narrower interparietal. This duality is also reflected in the skull size, as Middle East specimens on average have a smaller cranium and a significantly shorter tooth row (in absolute terms; Fig. 5e). These results confirm the observations by Chaworth-Musters and Ellerman (1947) with respect to the cranial size, more specifically that specimens from Turkestan (i.e. Bukhara and Djarkent) on average have smaller skulls than those from China. These differences are apparent when looking at absolute sizes, but analyses showed that this was due to overall size differences in the skull (Fig. 5f). This was not the case for the relative distance between the tooth row and the incisive foramen, which is longer in Middle East specimens (Fig. 5b). As such, this character may prove to be very useful to discriminate between both geographical groups. This character was also used by Allen (1940) to distinguish *Meriones unguiculatus* from *M. meridianus psammophilus* from Mongolia.

When looking within the two clusters (Middle East versus Far East), clinal variation only seems to be supported in the Middle East (but see below). For the Far East, Mongolian specimens are more similar to more distant groups, such as those from the Middle East, as well as skulls of Chinese specimens geographically closest to those from the Middle East differ more from them. As discussed below, there is currently no indication from literature that this discrepancy reflects increased species diversity in the Far East compared with the Middle East.

Phenotypic variation in *Meriones meridianus* from the Middle East

Within the Middle East group, most cranial shape differences between the groups involve the posterior part of the bulla, which is more inflated in the Iranian *M. meridianus* specimens than in the specimens from the Middle East, especially (and significantly) those from Kazakhstan. The other differences (bigger cranium, longer upper molar teeth row, slightly longer incisive foramen, and longer relative length of the teeth row in the Iranian specimens) are not statistically significant and support the relative homogeneity within the Middle East group.

Rodent species living in xeric environments are known to have a relatively large tympanic bulla, which is believed to sharpen the hearing for a particular sound frequency range (Harrison 1972; Vaughan et al. 2000). This relation between bulla size and dry habitats seems to be corroborated by this study, where a more inflated bulla especially found in *M. meridianus* from Iran, living in extremely dry and harsh climatic conditions (Firouz 2005). In case an increased bulla size does indeed allow an increased hearing performance, the data presented may reflect patterns of adaptive morphometric variation along different environmental variables. However, this requires further testing of correspondences between variation in bulla morphology and specific climatological condition.

Taxonomical issues related to this study

What is clear from previous literature is that the taxonomy of the genus *Meriones* is highly debated (Chevret and Dobigny

2005; Darvish 2009) and that its phylogenetic relationships with other gerbilline taxa, such as *Psammomys* and *Rhombomys*, are still ambiguous and poorly resolved (Chevret and Dobigny 2005; Ito et al. 2010). This is largely due to the fact that the range of inter- and intraspecific variation is not clearly known for each of the *Meriones* species (Misonne 1975; Darvish 2009; Ito et al. 2010). In addition to demonstrating levels and patterns of intraspecific variation, this study provides strong support for even more cryptic diversity, with two different skull phenotypes found in the Middle East and Far East populations. The observation and the description of a slightly smaller skull in *M. meridianus* (*M. meridianus meridianus*) from Turkestan compared with the Chinese *M. meridianus psammophilus* in the past (Chaworth-Musters and Ellerman 1947), as well as the apparent range of variation in the bulla size seen by the previous authors (Allen 1940), are now supported based on a larger sample size.

Previous studies that could not integrate this level of variation nevertheless lead to new taxonomical demarcations of what are considered natural groups in *Meriones*, as well as an extensive list of synonyms that have been proposed (19 junior synonyms were listed by Musser and Carleton 2005). Although this study documents a phenotypic substructure within the nominal species *M. meridianus*, the validity of known subspecies and associated subspecies recognition has largely been based upon external characters. With respect to the extensive list of subspecies (see Musser and Carleton 2005), our observations do allow some consideration with respect to designating the geographical morphotypes to potential species. Considering the type locality of *M. meridianus* Pallas, 1773 in Kazakhstan, the introduction of *M. meridianus* from the Turkestan fauna into Iran (Misonne 1959), the affinity of the Iranian specimens to those from Uzbekistan and Kazakhstan, and the phenotypical differences between the Middle East and Far East specimens enable us to conclude that the *M. meridianus* groups from Iran, Kazakhstan and Uzbekistan most likely correspond to the subspecies *M. meridianus meridianus*, which is phenotypically clearly distinct from the Chinese and Mongolian *M. meridianus psammophilus* (synonym of *M. meridianus auceps*; Allen 1940; Ellerman 1947). The Far East specimens included in this study (China and Mongolia) cannot be assigned to *M. unguiculatus*, as it is easily distinguishable from the other *Meriones* species occurring in this region, such as *M. meridianus* (Thomas 1908; Allen 1940; Ito et al. 2010), as well as *M. chengi* (only reported from China, North Xinjiang, Turfan). Wel et al. (1995, in Ito et al. 2010) documented *M. chengi* and *M. meridianus* from the Xinjiang-Uygur region (Western China) producing viable offspring when crossed, and Ito et al. (2010) reported a close similarity in cranial morphology and molecular phylogeny between *M. chengi* and *M. meridianus* from that same region. This supports a synonymy between *M. chengi* and the Far East populations of *M. meridianus* (especially those from China 1 and 3, which originated from a locality close to where *M. chengi* is known from). As such, it can be concluded that there is supportive evidence that these *M. meridianus* (from Far East) and *M. chengi* actually represent the same species. This hypothesis has been already suggested previously by Pavlinov et al. (1990, 1995) and Ito et al. (2010) based on morphological and molecular affinities, respectively.

Although this study can develop biogeographic insights and provide a solid framework for inventorying taxonomic and nomenclatural details, a systematical revision combined with an analysis of geographical variation in genetic traits is recommended to investigate to what degree the observed cryptic phenotypic diversity does reflect reproductive isolation and hence currently unknown species diversity in these jirds.

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Résumé

Divergence géographique du phénotype crânien des Mériones *de midi d'Asie (*Meriones meridianus*, Rodentia, Gerbillinae)*

L'existence d'espèces cryptiques dans le mérione de midi (*Meriones meridianus*) a été suggérée dans la littérature, cependant basée sur des données empiriques limitées pour confirmer cette hypothèse. Dans cette étude, une analyse de morphométrie géométrique, basée sur des landmarks en 2D, a été réalisée afin d'examiner si des tendances dans la variation intraspécifique de la forme et la taille du crâne existent, en utilisant 110 spécimens de crânes venant de plus de 20 endroits différents le long de la zone de distribution de *M. meridianus.* Cette étude est la première à étudier les différences morphologiques sur une aussi grande base de données et étendue géographique, et qui essaye de trouver si la variation de la forme crânienne de cette espèce est la mieux décrite en tant que clinale ou plutôt en réfléchissant la diversité cryptique. Cette dernière semble être le cas, puisque un phénotype crânien dimorphe au niveau de la forme et de la taille a été trouvé, ce qui reflète une disparité géographique entre les spécimens du Moyen-Orient et de l'Extrême-Orient. Des différences crâniennes distinctes ont été trouvées dans la taille globale du crâne, et aussi au niveau de l'inflation de la bulle, de l'allongement de la nasale, la longueur de la rangée des dents et de la fosse incisive, ainsi que la distance entre ces deux derniers. Il semble donc que *M. meridianus* du Moyen-Orient est morphologiquement différent de celui de l'Extrême-Orient. En outre, nos résultats démontrent que la variation clinale pourrait expliquer la variation dans les populations du Moyen-Orient, alors qu'une tendance plus hétérogène a été trouvée pour ceux de l'Extrême-Orient. L'hypothèse que la variation phénotypique observée peut refléter des espèces cryptiques est discutée, avec la recommendation d'une révision taxonomique approfondie du genre dans la région.

References

Allen GM (1940) The Mammals of China and Mongolia, Vol. 2. American Museum of Natural History, New York, pp 621–1350.

Barèiová L, Macholán M (2006) Morphometric study of two species of wood mice *Apodemus sylvaticus* and *A. flavicollis* (Rodentia: Muridae): traditional and geometric morphometric approach. Acta Theriol **51:**15–27.

Bookstein FL (1991) Morphometric Tools for Landmark Data: Geometry and Biology. Cambridge U Press, Cambridge, UK, pp 1–435.

Bookstein FL, Chernoff B, Elde RL, Humphries JM, Smith GR, Strauss RE (1985). Morphometrics in evolutionary biology, the geometry of size and shape change with examples from fishes. Acad Nat Sci Philadelphia Spec Pub **15**, pp 1–277.

Cardini A, Elton S (2009) The radiation of red colobus monkeys (Primates, Colobinae): morphological evolution in a clade of endangered African primates. Zool J Linn Soc Lond **157:**197–224.

Cardini A, Jansson A-U, Elton S (2007) Ecomorphology of vervet monkeys: a geometric morphometric approach to the study of clinal variation. J Biogeogr **34:**1663–1678.

Caumul R, Polly PD (2005) Phylogenetic and environmental components of morphological variation: skull, mandible, and molar shape in marmots (Marmota, Rodentia). Evolution **59:**2460–2472.

Chaworth-Musters JL, Ellerman JR (1947) A revision of the genus *Meriones*. Proc Zool Soc Lond **117:**478–504.

Chevret P, Dobigny G (2005) Systematics and evolution of the subfamily Gerbillinae (Mammalia, Rodentia, Muridae). Mol Phyl Evol **35:**674–688.

Cordeiro-Estrela P, Baylac M, Denys C, Polop J (2008) Combining geometric morphometrics and pattern recognition to identify interspecific patterns of skull variation: case study in sympatric Argentinian species of the genus *Calomys* (Rodentia: Cricetidae: Sigmodontinae). Biol J Linn Soc **94:**365–378.

Darvish J (2009) Morphometric comparison of fourteen species of the genus *Meriones* Illiger, 1811 (Gerbillinae, Rodentia) from Asia and North Africa. Iran J Anim Biosyst **5:**59–77.

Denys C, Granjon L, Poulet A (Scientific Editors) (2001) African small Mammals, Petits mammiferes africains. Proceedings of the 8th International Symposium on African Small Mammals, Paris, July 1999, Institut de Recherche pour le Développement, Paris (collection Colloques et Séminaires), pp 151–160.

Elewa AMT (ed) (2004) Morphometrics: Applications in Biology and Paleontology. Springer, Berlin. ISBN 3-540-21429-1.

Ellerman JR (1947) Notes on some Asiatic Rodents in the British Museum. Proc Zool Soc Lond **117:**256–271.

Fadda C, Corti M (2000) Three-dimensional geometric morphometrics of *Arvicanthis*: implications for systematics and taxonomy. J Zool Syst Evol Res, **39:**235–245.

FAO (2007) FAO World Climate Data. Available at http://freegeographytools.com/2007/fao-world-climate-data.

Firouz S (2005) The Complete Fauna of Iran. I B Tauris Publishers, London, pp 1–322.

Gower JC (1975) Generalized Procrustes analysis. Psychometrika **2:**241–248.

Hammer Ø, Harper DAT, Ryan PD (2001) PAST: Paleontological Statistics Software Package for Education and Data Analysis. Palaeontol Electron **4:**1–9.

Harrison DL (1972) The Mammals of Arabia, Vol. 3. Lagomorpha, Rodentia. Ernest Been Ltd, London. pp 559–593.

Hassinger JD (1973) A study of the mammals of Afghanistan, resulting from the 1965 Street Expedition (excluding Bats). Fieldiana Zool **60:**1–189.

Hood GM (2010) PopTools version 3.2.3. Available on the internet. URL http://www.Poptools.org.

Ito M, Jiang W, Sato JJ, Zhen Q, Jiao W, Goto K, Sato H, Ishiwata K, Oku Y, Chai J-J, Kamiya H (2010) Molecular phylogeny of the subfamily Gerbillinae (Muridae, Rodentia) with emphasis on species living in the Xinjiang-Uygur autonomous region of China and based on the mitochondrial cytochrome *b* and cytochrome *c* oxidase subunit II genes. Zool Sci **27:**269–278.

Klingenberg CP (2011) MorphoJ: an integrated software package for geometric morphometrics. Mol Ecol Resour **11:**353–357.

Lay DM (1967) A study of the mammals of Iran, resulting from the Street Expedition of 1962–63. Fieldiana Zool **54:**1–282.

Macholàn M, Mikula O, Vohralik V (2008) Geographic phenetic variation of two eastern-Mediterranean non-commensal mouse species, *Mus macedonicus* and *M. cypriacus* (Rodentia: Muridae) based on traditional and geometric approaches to morphometrics. Zool Anz **247:**67–80.

Misonne X (1959) Analyse Zoogéographique des mammifères de l'Iran. Bruxelles Mem Inst Roy Sci Nat Belgique, 2nd Ser **59:**1–157.

Misonne X (1975) The rodents of the Iranian deserts. In: Prakash I, Ghosh PK (ed.), Rodents in Desert Environments. Junk W, The Hague, pp 47–58.

Musser GG, Carleton MD (2005) Superfamily Muroidea. In: Wilson DE, Reeder DM (eds), Mammal Species of the World: A Taxonomic and Geographic Reference, 3rd edn. Johns Hopkins University Press, Baltimore, MD, pp 894–1531.

Pavlinov IY (2008) A Review of Phylogeny and Classification of Gerbillinae (Mammalia : Rodentia). Moscow Univ Publ, Moscow, pp 1–68.

Pavlinov IY, Dubrovskiy YA, Rossolimo OL, Potapova EG (1990) Gerbils of the World Fauna. Nauka, Moscow, pp 1–364. [In Russian]

Pavlinov IY, Yakuhontov EL, Agadzhanyan AK (1995) Mammals of Eurasia. I. Rodentia. A taxonomic and geographic reference. Archives of the Zoological Museum, Moscow State University, Moscow, pp 1–240. [In Russian]

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

Popesko P, Rajtovà V, Horàk J (2002) Colour Atlas of the Anatomy of Small Laboratory Animals. Vol. 2, Rat, Mouse and Golden Hamster. Wolfe Publishing, Bratislava, pp 1–253.

Rohlf FJ (2004) TPSDig: Thin Plate Spline Digitise. Stony Brook, New York, Department of Ecology and Evolution, State University of New York. Available at http://life.bio.sunysb.edu/morph/.

Rohlf FJ, Marcus LF (1993) A revolution in morphometrics. Trends Ecol Evol **8:**129–132.

Rohlf FJ, Slice DE (1990) Extensions of the Procrustes method for the optimal superimposition of landmarks. Syst Zool **39:**40–59.

Sheng HL, Ohtaishi N, Lu HJ (1999) The Mammals of China. China Forestry Publishing House, China, pp 1–298.

Tong H (1989) Origine et évolution des Gerbillidae (Mammalia, Rodentia) en Afrique du Nord. Mem Soc Geol France, NS, Paris, **155:**1–120.

Vaughan TA, Ryan JM, Czaplewski NJ (2000) Mammalogy. Fourth Edi. Saunders College Publishers, Orland, FL, pp 1–565.

Wang S, Yang G (1983) Rodent Fauna of Xinjiang. Xinjiang People's Publishing House, Urumqi, China, pp 1–223. [In Chinese]

Zhang Y (1997) Distribution of Mammalian Species in China. Forestry Publishing House, Beijing, China, pp 1–98.

Supporting Information

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

Table S1. Overview of the grouped sampling localities of *Meriones meridianus* considered in this study (*type locality of *M. m. auceps*).

Table S2. Definition and numbering of the landmarks used for the skull morph analyses.

Table S3. Euclidean distances between the *M. meridianus* groups means and the p-levels obtained from the Monte-Carlo randomization test (*p < 0.01, **p < 0.001).

Table S4. Variation in size variables per geographical group (for group numbers, see Table S1) (measurements in mm).

Table S5. List of specimens studied in this study and their voucher numbers.