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Patterns of Size and Shape Skull Variability in Tunisian Populations of *Jaculus jaculus* (Rodentia: Dipodidae)

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Abstract: This paper describes the patterns of size and shape skull variability in Tunisian populations of *Jaculus jaculus*, for 147 specimens as a function of their geographical origin, using univariate and multivariate statistics with traditional morphometrics. We examined also the distribution of the foramen number groups (1versus 2) among specimens. Size and shape patterns of the skulls were analyzed by using the Log shape ratio approach (LSR), and then allometries were figured out. In addition, we tested the influence of age, sex, geography and some habitat variables (such as precipitation and vegetation) on the size and shape of the skull. The plot of the two mandibular foramen number groups, based upon the Log PCA, did not indicate a distinction between them. The canonical variable analysis (CVA) of Log and Log shape ratio reached 92% of correctly classified specimens for the mandibular foramen number criterion. The results showed that habitat and vegetation have significant effects on the skull size and shape, while altitude is not significantly effective. Nevertheless, precipitation was significantly correlated with isometric size and Log shape ratios of the skull.

Key words: *allometry, Jaculus jaculus, geographic variation, isometric size, Log Shape Ratio, traditional morphometrics, Tunisia.*

Introduction

The jerboas belonging to the genus *Jaculus* (E rxleben 1777) are widely distributed in desert and semi-arid regions across the Palearctic (Holden, Musser, 2005). Among them, *Jaculus jaculus* (Linnaeus, 1758) is especially common in Egypt, from where it gets its common name (the lesser Egyptian jerboa), but it is also found in the Middle East, Arabia, and North Africa (Holden, Musser, 2005, Wilson, Reeder, 2005, AMORI *et al.* 2008). On the basis of morphological data, a number of subspecies have been described in North Africa (Heim De Balsac, 1936, Corbet 1978; Ranck 1968, Osborn, Helmy 1980).

According to Ranck (1968), the two different colour forms observed represent two sympatric species occurring in Libya: *Jaculus jaculus* (Linnaeus 1758) and *Jaculus deserti* (Loche 1867). The latter can be distinguished from *J. jaculus* by the following characters: (1) darker hair on dorsum, side, and sole of feet; (2) smaller and more compact skulls; (3) more inflated auditory bulla, and (4) two distinct foramina of equal or unequal size in the angular process of the mandible as opposed to a single foramen. However, Harrison (1972), by reviewing the material of *Jaculus* from the Arabian peninsula, has al-

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ready thrown doubt on the validity of these "sibling species" stating "I am quite unable to distinguish two small species of *Jaculus* in the extensive and random in the Arabian jerboas that the definitions of two species on this basis appears quite impossible." In addition, Corbet (1978) summarized Ranck's (1968) and Harrison's (1972) conclusions and agreed that the two forms are conspecific. Furthermore, in Egypt and Arabia, traits of colour and mandibular foramina were "quite uncorrelated." Additionally, Cockrum, Setzer (1976) examined the type specimens of *J. deserti* and concluded that the colour (dorsum, sides and soles of hind feet) and the number of mandibular foramina did not always coincide.

In Tunisia, the situation is still confusing due to the presence of the two distinct groups according to Gharaibeh (1997), based upon colour and other characters. The first group has pale organish dorsum with roots of hair grey mixed with white, while the second group has dark brownish cinnamon dorsum and roots of hair grey. The angular process on the mandible in the first group is pierced by a single foramen versus two foramina in the second group (Gharaibeh 1997). However, the validity of the mandibular foramen numbers has never been investigated properly. Recently, two distant sympatric lineages were described in Tunisia, based on morphometric, allozymic and molecular data, which may correspond to two cryptic species: *J. jaculus* and *J. deserti* (Ben Faleh *et al*. 2010a, Ben Faleh *et al.* 2010b).

The aims of this study were to answer to the following questions: **1)** Is the foramen number a diagnostic character between the two mandibular foramen number groups among specimens 2) What is the level of allometric variability in the Tunisian *J. jaculus* populations.

Materials and Methods

Sampling

Adult individuals of the lesser jerboa *J. jaculus* were collected in Tunisia between September 2007 and March 2008 from all currently known localities of their distribution as described by GHARAIBEH (1997). A total of 147 specimens from 11 localities were captured by hand, as jerboas do not readily enter traps according to the ethical proceedings in Tunisia. The sampled populations covered the steppes of central part of Tunisia, with littoral populations of Gabes, Mareth, Mednine to more southern ones of Remada, Tataouine. The Nefta, Douz, Hamma, Remada localities were situated in the Sahara zone. Two populations (Sbeitla, Matmata) were also collected from higher altitudes. The littoral populations always receive more than 160 mm of annual rainfall per year, while in the South the rainfall amount is relatively less (Fig. 1; Table S1).

The skull samples were preserved in formol in the field immediately after capturing. The collected whole animals were prepared and stored in freezers at the Biotechnology Institute of Monastir.

Classical morphometrics

Thirteen cranial and dental measurements were taken on the 147 skulls using digital callipers (RUPAC, Italy) and values were rounded to the nearest 0.01mm. Age classes were defined based upon molar wear stages and defined as below (Figure 2):

Stage C0: No upper M3 is erupted (not figured here).

Stage C1: Upper M3 erupted but not worn (not figured here).

Stage C2: Cusps still visible on all molars and link between first and second lobe of the upper M3 is very narrow (Fig. 2).

Stage C3: The longitudinal link between first and second lobe of upper M3 is larger and, in general, wider on the upper M12 (Fig. 2).

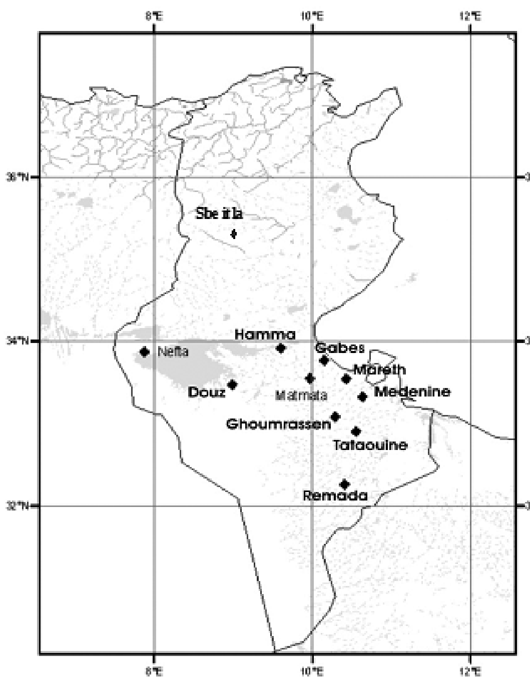

Fig.1. Map of Tunisia showing the geographical localities from which the populations of *Jaculus jaculus* were collected.

Fig.2. Different age classes (left to right) corresponding to C2, C3, C4 and C5, respectively.

Table S1. Localities and samples sizes (n) from *J. jaculus* populations collected in Tunisia.

Samples locality	Latitude	Longitude	Altitude (m)	Habitat	Precipitation Mean per year in mm	Vegetation	n
Gabes	33°56’31”N	9°43’15”E	4	steppe	190	Palm	30
Ghoumrassen	33°53’23”N	10°20’14”E	352	steppe	145	Shrubs	5
Mareth	33°35’51”N	10°13’17”E	39	steppe	230	Wheat field	6
Mednine	33°21’ 45”N	10°30’19”E	93	steppe	175	Wheat field	2
Tataouine	32°55’14”N	10°27’08”E	246	Mountain	157	Savane	8
Matmata	33°32’ 41”N	9°58’ 03”E	600	Mountain	180	Shrubs	30
Remada	32°19’ 24”N	10°24’10”E	300	Sahara	25	Savane	15
Nefta	33°52’32”N	7°52’ 49”E	58	Sahara	15	Savane	14
Hamma	33°53’56”N	9° 47’ 27”E	58	Sahara	150	Palm	20
Sbeitla	35°13’60”N	9° 08’ 05”E	525	Mountain	335	Alfa plant	1
Douz	33°27’42”N	9° 01’ 45”E	58	Sahara	90	Savane	16

Stage C4: The upper M3 displays nearly the total fusion of the first and second lobe of the longitudinal link that is very wide but it remains visible on the other molar cusps (Fig. 2).

Stage C5: No more cusps were visible and the longitudinal link is so wide that lobes appeared fused on all the molars (Fig. 2).

The skull distances were defined as follows and chosen for their high repeatability that include: greatest length of skull (LonC), length of palatal foramen (LaF), smallest interorbital width (LaC), length of maxillary toothrow (Las), greatest breadth of nasals (LaN), greatest length of nasals (LoN), length of mandibular toothrow (Lai), length of auditory bulla (Lob), greatest breadth of braincase (Lab), mandible height (at angular process, Lai 1), Postpalatal width (LaP), lower jaw length (Loi) and zygomatic breadth on the zygomatic process of the squamosal (Lac).

Morphometric and statistical analyses were performed using R version 2.5.1 (2007) and the specialized library for morphometrics, R morph (Baylac 2007). First, we realized analyses of variance (ANOVAs) and multiple analyses of variance (MANOVAs) to test the influence of sexual dimorphism, age, mandibular foramen number and geographical variables (habitat and vegetation) on both size and shape of the skull. Regressions were used to explore the correlations between isometric size, Log data and shape ratio, latitude, longitude, altitude, and precipitation. First, we performed different set of analyses by using principal component analysis (PCA) for the Log-transformed data of variance-covariance matrix for the whole set of individuals in order to globally visualize the data set trends. Depending upon the PCA graphs, we mapped either the number of mandibular foramens in relation to populations to see the trends of individual distribution. Additionally, we test the validity of the foramen number of *J. jaculus* by the canonical analyses (CVA) between the two mandibular foramen number groups (Gharaibeh 1997, Ranck 1968 hypotheses). Afterwards, we used Log shape ratio method (Mosimann 1970) in order to check the allometric patterns by distinguishing shape and size variability (Slater *et al.* 2009, Wilson *et al.* 2010, Suzuki *et al.* 2011). Isometric size (the individual mean of all variable Log data for each specimen) was retrieved to each Log data. The residuals were the Log shape

Table 1. ANOVAs and MANOVAs performed on different skull size and shape parameters.

Factors	Isometric size	Log data	Log Shape Ratio
Mandibular Foramen number groups	5,618e-09 ***	2,2e-16 ***	2,2e-16 ***
Populations	2,151e-05 ***	2,05e-14 ***	4,12e-13 ***
Age	0,3473 NS	0,623 NS	0,6898 NS
Sex	0,9221 NS	0,8619 NS	0,8046 NS
Habitat	2,921e-05 ***	6,596e-07 ***	3,773 e-06 ***
Vegetation	0,0488 *	0,0006212 ***	0,000563 ***

*** P<0.001; * P<0.05, NS: Not significant

Table 2. Regressions of the different skull size and shape parameters with environmental factors.

Factors	Isometric size	Log data	Log Shape Ratio
Latitude	0.4184 NS	5,619e-11 ***	2,721e-11 ***
Longitude	0,001869 ***	0.002937 ***	0,002996 ***
Altitude	0,1459 NS	0,09548 NS	0,0885 NS
Precipitation	0,03526 *	8,328e-05 ***	0,0005083 ***

*** P<0.001; * P<0.05, NS: Not significant

ratios that represent shape. The relationship between isometric size and LSR that usually shows allometry was represented in the form of a scatter plot (Packard, Boardman 2008, Packard 2009). A multivariate regression between size and shape gives us the percentage of allometry in the data set.

Results

Statistical tests on distance measurements for different variability factors

ANOVAs and MANOVAs

Our data sample does not present any significant relationship between the size and shape of the skull versus age or sex of the individuals (Table 1). Due to the absence of sexual dimorphism and of age structuration, we continued to treat the whole data set pooled. These first statistical tests displayed, however, significant differences between populations, habitats, vegetation and mandibular foramen number groups. The check of the relation between the numbers of mandibular foramens clearly provided non-significant result and indicated that this character vary independently from each other.

Regressions

Regressions were performed on Log data, isometric size and Log shape versus latitude, longitude, altitude and precipitation. All of the skull size and shape parameters varied significantly with longitude and precipitation (Table 2), while only Log data and LSR differed significantly with latitude. None of the size and shape parameters varied significantly with altitude.

PCA (Log-transformed data) on foramen groups

General trends of craniodental characters variation among samples of *J. jaculus* were surveyed by using principal component analysis (PCA) of the 13 skull Log-transformed distances of 147 individuals. In this case, differences were not shown between the foramens groups (Fig. 3). Specimens with one foramen distributed along axis 2 must have smaller values of each of the greatest breadth of nasals (LaN), length of mandibular toothrow (Lai) and length of maxillary toothrow (Las), while those along axis 1 must have large values of each of the greatest length of nasals (LoN), greatest breadth of braincase (Lab) and smallest interorbital width (LaC).

CVA on foramen groups

For better characterization of the two different

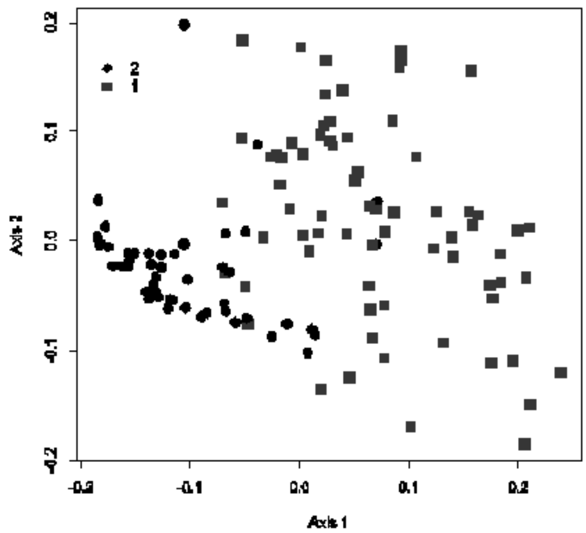

Fig. 3. Mapping of the mandibular foramen number on the PCA graph of the Log-transformed data (Axes 1 and 2). Circles refer to two foramens on the mandible, while the squares refer to the one foramen.

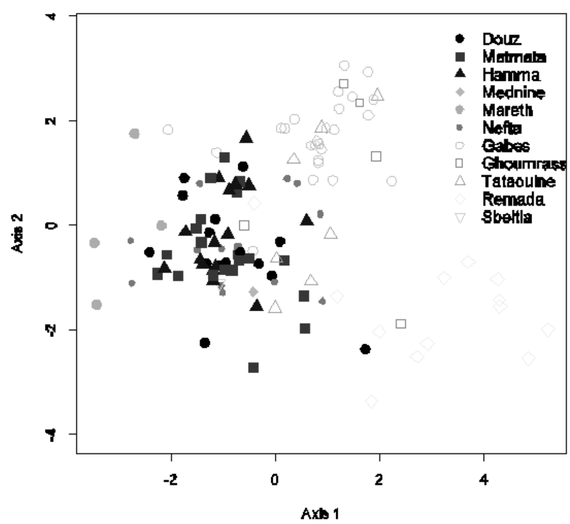

Fig. 4. CVA of the eleven populations sampled in this study (Plot of the Axes 1 and 2 represents 62.11% of variability).

Table 3. Specimens distribution in function of the mandibular foramen number groups and age classes.

Age class	1 Foramen	2 Foramens
CC2: N = 46	27	19
CC3: N = 73	38	35
CC4: N = 25	11	14
CC5:N = 3	1	2

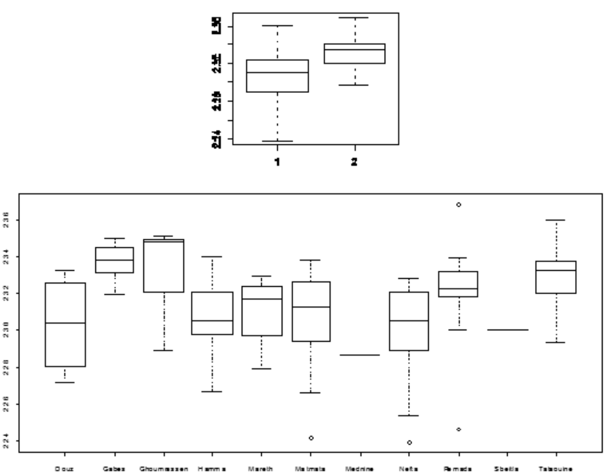

Fig. 5. Isometric size variability. Upper box-plots number of mandibular foramens and lower box-plots localities (limits are the 95 confidence intervals).

foramen number groups, different canonical analyses were performed on the Log-transformed data and Log shape ratios by defining the mandibular foramen number groups. For them, the discrimination was obtained with Log shape ratios (92%) against 90% for the Log (including isometric size).

Geographic structuration of the variability

We performed CVA on Log-transformed data of the 11 geographic localities. As shown in Fig. 4, quite differentiation was observed along axis 1 for Remada locality or along axis 2 for Gabes and Ghoumrassen localities. In addition, a wide variability was apparent for the localities Tataouine, Matmata, Nefta and Hamma. Therefore, there was no obvious separation between the two groups corresponding to the mandible foramen number groups. Axes 1 and 2 expressed 62.11% of the total variability, of which axis 1 explained 41.38% compared to only 20.73% for axis 2. Specimens of Remada locality were isolated in the extreme part of axis1, while some of those of Gabes (a locality from the littoral zone) were isolated in extreme part of axis 2. The most western localities of Nefta and Douz together with the other central Tunisia localities did not display any differences. This, the result was consistent with the significant correlation underlined by regression analyses, which already showed the importance of the latitude, longitude, and precipitation of our data set as defining geographic variables among geographic localities. However, this relation is not clear and does not seem to correspond to any longitudinal or latitudinal gradient.

Investigation of the allometry component

Isometric size

The extraction of the isometric size provided an interesting diagram where isometric size box-plots displayed some significant statistical differences between the mandibular foramen number groups (Fig. 5). In addition, some isometric size differences occurred between the populations, where the largest representatives were those of the Ghoumrassen and Gabes localities, while the smallest ones came from the Mednine and Sbeitla localities.

Discussion

Our approach describes the size and shape of skull variability in *J. Jaculus* populations in Tunisia. The patterns of variability were consistent from one analysis to another and both the size and shape varied strongly in the populations examined. The observed variability among these populations was not related to age, although the present samples did not present skulls with initial age class stages C0 and C1. The absence of sexual dimorphism was also clearly established. The sex ratio was quite equilibrated (77 females versus 70 males). Recently, it has been shown that some rodents sometimes can harbour sexual dimorphism (Lalis *et al.* 2009; Abdel-Rahman *et al.* 2008), but this remained the exception herein.

On the other hand, a discrimination rate (92%) was apparent amongst the mandibular foramen number groups by using CVA. Unfortunately, following Harrison (1978), Cockrum (1976) and Corbet (1978), the mandibular foramen number is variable in *J. jaculus* populations and cannot be considered as a diagnostic character. Nonetheless, when we compared the age classes of individuals with the number of mandible foramens, we did not find a significant pattern (Table 3). Our results are consistent with the recent publication of Ben Faleh *et al.*(2010a) who confirmed that the foramen number is randomly distributed among *J. jaculus* specimens.

The Log shape ratio approach is one of the means to define the allometry level and discuss the reason of skull size and shape differences (Mossiman 1970). It represented the most important variable in the present data set analyses. At least there were some factors, which influenced the skull size and shape relationship in the *J. jaculus* populations examined. For example, the existence of sympatry in the specimens from the two groups of mandibular foramen number displayed difficulty to separate them. Once again, this leads to the conclusion that some environmental factors may influence the intra-population morphological variability in this taxon. As clearly shown, coastal populations live in the subdesert steppe at low altitude (less than 100 m a.s.l, while Remada population comes from the continental subdesert steppe at 300 m a.s.l.). Both zones receive nearly from 25 to 200 mm of annual rainfall per year.

In conclusion, the foramen number in Tunisian *J. jaculus* populations is a matter of random individual variation differing in the two mandibles of an individual. The concept of two sibling species within the *J. jaculus* populations on the basis of this character proposed by Ranck (1968) is rejected. Our results revealed an extensive variability of skull size and shape among populations of this species collected from 11 localities in Tunisia, which could be explained in view of environmental variation.

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