



Taxonomy/Taxinomie

Morphometric analysis of six *Gerbillus* species (Rodentia, Gerbillinae) from Tunisia

Analyse morphométrique de six espèces du genre Gerbillus (Rodentia, Gerbillinae) de la Tunisie

Awatef Abiadh^{a,*}, Paolo Colangelo^b, Ernesto Capanna^b, Tahar Lamine-Cheniti^a, M'barek Chetoui^a

^a Laboratoire d'écologie animale, faculté des sciences de Tunis, 1092 Tunis, Tunisia

^b Dipartimento di Biologia Animale e dell'Uomo, Università di Roma "La Sapienza", Via Borelli 50, 00161 Roma, Italy

ARTICLE INFO

Article history:

Received 16 March 2010

Accepted after revision 21 July 2010

Keywords:

Gerbillus

Geometric morphometric

Systematic

Taxonomy

ABSTRACT

Size and shape changes in the skull of the genus *Gerbillus* were investigated using geometric morphometrics. Six species from Tunisia were studied (*G. gerbillus*, *G. campestris*, *G. nanus*, *G. tarabuli*, *G. simoni* and *G. latastei*). Statistical analyses of shape variability allowed us to discriminate three morphological groups which are congruent with the three groups suggested by previous morphological and molecular studies. However, our results contrast with previous molecular investigations. In fact, according to results obtained by the use of principal component analysis, canonical variate analysis and UPGMA, we found a higher degree of divergence between the subgenus *Dipodillus* and the other two subgenera *Gerbillus* and *Hendecapleura*. This fact suggests that the morphometric differences observed among species within the genus *Gerbillus* are not mainly related to phylogeny. To reconcile the molecular and morphological approaches, we propose a hypothesis of differential rates of phenotypic evolution in the genus *Gerbillus*. In this view, the species belonging to the subgenus *Dipodillus* evolved apomorphic features of the skull likely related to a higher degree of habitat specialization. By contrast, the more generalist *Gerbillus* and *Hendecapleura* subgenera show less differentiated plesiomorphic morphology.

© 2010 Académie des sciences. Published by Elsevier Masson SAS. All rights reserved.

R É S U M É

La différenciation morphologique au sein du genre *Gerbillus* a été étudiée en utilisant la géométrie morphométrique. Six espèces provenant de la Tunisie (*G. gerbillus*, *G. campestris*, *G. nanus*, *G. tarabuli*, *G. simoni* et *G. latastei*) ont été examinées. Les analyses statistiques permettent la distinction de trois groupes morphologiques qui sont congruents avec les groupes morphologiques et moléculaires antérieurement établis. Cependant, nos résultats sont en partie contradictoires avec les analyses moléculaires. En effet, d'après les résultats obtenus par l'analyse en composant principal, l'analyse canonique des variables et l'UPGMA, on a trouvé une divergence entre le sous-genre *Dipodillus* et les deux autres sous-genres, *Gerbillus* et *Hendecapleura*. Cette divergence suggère que les différenciations observées entre les espèces ne sont pas reliées principalement à la phylogénie. Afin de

Mots clés :

Gerbillus

Géométrie morphométrique

Systématique

Taxinomie

* Corresponding author.

E-mail address: abiadhawatef@yahoo.fr (A. Abiadh).

réconcilier les approches moléculaires et morphologiques, on a proposé l'hypothèse de l'évolution phénotypique différentielle au sein du genre *Gerbillus*. Ainsi, les espèces du sous-genre *Dipodillus* possèdent des critères apomorphiques, probablement, permettant de se spécialiser dans leurs habitats. Par contre, les espèces des sous-genres *Gerbillus* et *Hendecapleura* montrent une morphologie plésiomorphe peu différenciée.

© 2010 Académie des sciences. Publié par Elsevier Masson SAS. Tous droits réservés.

1. Introduction

The genus *Gerbillus* Desmarest, 1804 is one of the most diversified groups of rodents inhabiting arid and semiarid areas. It is known for its morphological homogeneity [1–3] but high karyotype heterogeneity with a diploid number ranging from $2n = 34$ to $2n = 74$ [3–9]. *Gerbillus* has never been comprehensively revised [10] and its taxonomy is still holding a number of controversies. Among these, the genus *Gerbillus* is still a matter for discussion for taxonomists ([10] and reference herein). In fact, whether this genus is holding subgenera or good to split off into several genera is yet debated.

Since its early description, three different subgenera were created for the genus *Gerbillus* [11,12]. These are *Gerbillus*, *Dipodillus* and *Hendecapleura* and this on the basis of some morphological features.

The subgenus *Gerbillus* is characterized by the presence of well developed auditory bullae of which the posterior parts reach or even exceed the level of the occipital bone, a maximum number of five metatarsal tubercles, one carpal tubercle, and the presence of opposite cusps in the first upper molar and haired hind feet. The latter is bare in the species of the subgenus *Hendecapleura* which share some of the other characteristics of the subgenus *Gerbillus* (e.g. the well developed auditory bullae).

On the other hand, the subgenus *Dipodillus* shows a mediocre development of the auditory bullae, a higher number of metatarsal tubercles (six), a first upper molar with alternate cusps and hairless plantar surfaces. Even though these three taxa were mostly accepted by most of authors, there was no general agreement about the taxonomic rank to assign to them, in particular, regarding the *Dipodillus* species. In fact, during the last century, this taxon has been regarded as a subgenus [13–15] or as a genus [16–22]. However, Lay [23], studying the most important characters used to separate these subgenus, recognized only one genus “*Gerbillus*”.

To solve these controversial allocations, the genus *Gerbillus* was the subject of new molecular studies [24,25]. These investigations allowed an insight in the systematic, the taxonomy and the evolutionary pattern of *Gerbillus*. Particularly, the mitochondrial DNA analysis [25] confirmed the subdivision into three distinct taxa as previously identified on the basis of morphology [11,12] and revealed that the elevation of *Dipodillus* to a genus rank will make *Gerbillus* a paraphyletic genus. On the basis of this analysis, it was concluded that the three taxa *Dipodillus*, *Gerbillus* and *Hendecapleura* must be considered as three distinct subgenera belonging to a unique monophyletic genus [25].

In the present work, we adopted a taxonomic scheme emerging from the molecular investigation and, in order to provide a new insight into the *Gerbillus* systematics and taxonomy, we used a geometric morphometric approach to investigate the patterns of morphological differentiation among species and subgenera. In fact, the geometric morphometric approach has proved to be a useful technique to investigate morphological similarity due to ecological convergence and to solve taxonomic issues in small mammals, particularly in rodents [26–29]. In order to investigate the morphological differentiation among *Gerbillus* species and its implication in systematics, we studied skull size and shape differentiation among six species from Tunisia: *G. simoni* and *G. campestris* belonging to the subgenus *Dipodillus*, *G. gerbillus*, *G. tarabuli* and *G. latastei* belonging to the subgenus *Gerbillus*, and *G. nanus* belonging to the subgenus *Hendecapleura*.

2. Material and methods

A total of 148 specimens were analysed, representing six species of the genus *Gerbillus* from eight localities of Tunisia (Table 1). Samples were unambiguously identified by cytogenetic analysis. Only adult specimens were used in this study. Images of all dorsal and ventral sides of the skulls were digitized using a Nikon D100 camera. Successively, 28 landmarks were collected on the dorsal and 22 on the ventral side (Fig. 1) using the program Tps-Dig2 [30]. The obtained landmark configurations were successfully aligned using the generalized procrustes analysis (GPA) and analysed using the MorphoJ program [31].

Size was computed as the centroid size (CS, the square root of the sum of the square of the distance between landmark and the centroid [32]). Size differences among species were tested by Anova and visualized using a boxplot. The significance of the CS pairwise differences among species was tested through the Tukey HSD test.

Shape differences among species were investigated by a principal component analysis (PCA) and by a canonical variate analysis (CVA). A multivariate analyses of the variance (Manova), computed on principal component scores matrix, was used to test the significance of the observed shape differences. The percentages of correct classifications were calculated using the leave-one-out cross-validation procedure. A regression between shape variables and centroid size was computed in order to investigate the influence of size on shape.

The presence of a significant sexual dimorphism for size and shape was tested by Anova and Manova computed separately for each species. Finally, unweighted pair group method with average (UPGMA) were computed from the

Table 1

List of the specimens included in the analysis; collections are preserved in the laboratory of Animal Ecology "research unit: Ecology and Population Biodiversity"; Faculté des Sciences de Tunis, Tunisia.

Species	Locality	n	Coordinates
<i>G. campestris</i>	Bouhedma	9	34°48'N – 09°65' E
	chenini	4	32°54'N – 10°17'E
	Djebil	8	33°01'N – 09°03'E
	Kondar	10	35°55'N – 10°22'E
<i>G. latastei</i>	Sidi toui	11	32°44'N – 11°17'E
	Bouhedma	15	34°48'N – 09°65'E
	Faouar	8	33°16'N – 08°29'E
<i>G. tarabuli</i>	Dghoumes	12	34°04'N – 08°56'E
	Faouar	10	33°16'N – 08°29'E
<i>G. simoni</i>	Kerkennah	24	34°42'N – 11°11'E
<i>G. gerbillus</i>	Faouar	20	33°16'N – 08°29'E
<i>G. nanus</i>	Sidi toui	14	32°41'N – 11°44'E
	Dghoumes	4	34°04'N – 08°56'E
	Bouhedma	4	34°48'N – 09°65'E

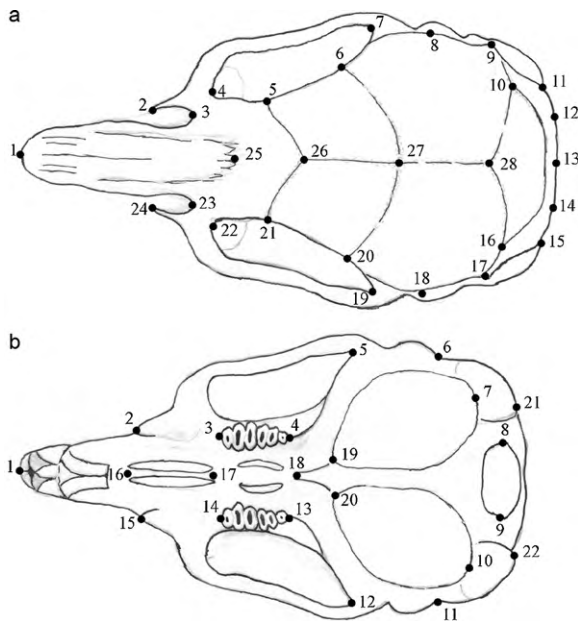


Fig. 1. Collected landmarks. Dorsal side (a): tip of the nasal (1), front of the zygomatic plate (2, 24), inferior base of the zygomatic plate (3, 23), posterior edge of the postorbital bar (4, 22), infraorbital constriction (5, 21), frontal-parietal structure (6, 20), back of the zygomatic notch (7, 19), squamosal structure (8, 9, 17, 18), junction of parietal and squamosal and occipital (10, 16), posterior limit of parietal structure (11, 15), limit foramina jugular on the posterior edge of auditory bulla (12, 14), occipital tip (13), parietal-temporal suture (28), diagonal intersection of frontal bone (26), frontal-parietal suture (27), nasal-frontal structure (25). Ventral side (b): tip of the nasal (1), inferior margin of infraorbital foramen (2, 15), anterior extremity of molar row (3, 14), posterior extremity of molar row (4, 13), back of zygomatic notch (5, 12), tympanic bulla at the posterior border of the external auditory meatus (6, 11), posterior extremity of tympanic bulla (7, 10), posterior limit of accessory bulla (21, 22), anterior extremity of foramen (16), posterior extremity of foramen (17), junction between tympanic bulla and pterygoid process (19, 20), anterior limit of mesopterygoid fossa (18), posterior intersection between foramen magnum and occipital condyle (8, 9).

interspecific Procrustes distances computed among reference configurations of the dorsal and ventral views. The UPGMA were computed using Mega 4.0 program [33].

All the statistical analyses were performed using the software R version 2.8.1 [34].

3. Results

3.1. Size

A significant size variation ($F_{\text{sex}} = 70.856$, $P < 0.001$) is found among species (Fig. 2). A significant sexual dimorphism is absent in all the species with the exception of *G. simoni*. However, the Anova suggests that sexual dimorphism found in this species did not influence the observed species differences ($F_{\text{sex} \times \text{species}} = 0.977$, $P = 0.43$).

The Tukey HSD test suggests that *G. nanus* and *G. simoni* are significantly smaller than all the other species ($P < 0.001$). *G. tarabuli* is the largest one ($P < 0.001$), while *G. latastei*, *G. gerbillus* and *G. campestris* exhibit an intermediate size value. Among these, *G. gerbillus* shows a significant difference with *G. campestris* ($P = 0.004$) while *G. latastei* exhibits an intermediate size without significant differences.

3.2. Shape

The Manova did not reveal the presence of sexual dimorphism both on dorsal and ventral configurations in all the species. The regression between shape and size shows that a significant component of the shape can be explained by the size both in ventral ($P < 0.0001$) and dorsal ($P < 0.0001$) configurations. However, the variation of the shape related to the size in ventral and dorsal views remains low (2.94% and 7.3%, respectively).

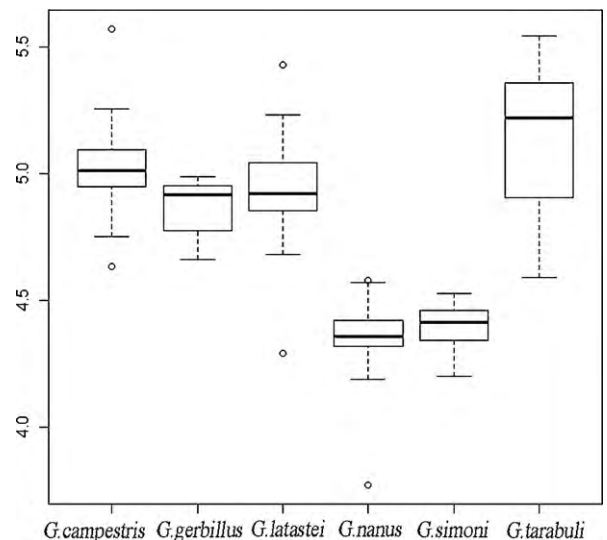


Fig. 2. Box plot showing the average of centroid size (based on dorsal configurations) of each species. The inner line represents the median. Box margins are at 25th and 75th percentiles, bars extend to 5th and 95th percentiles, circles represent outliers.

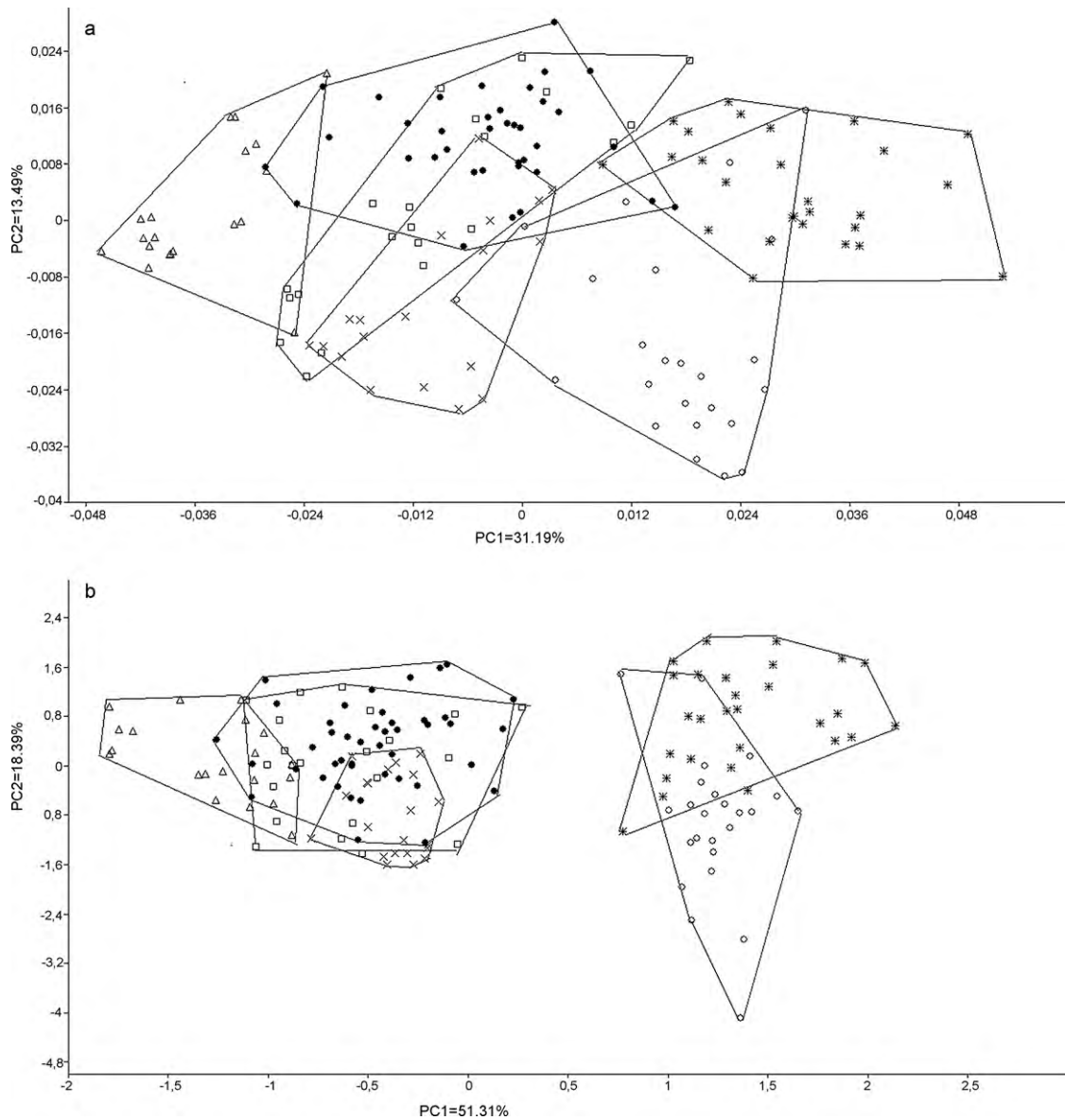


Fig. 3. Principal component analyses (PCA) of dorsal (a) and ventral (b) configurations. Symbols represent different species: *G. campestris* (star), *G. simoni* (white circle), *G. nanus* (white triangle), *G. gerbillus* (cross), *G. tarabuli* (white square), *G. latastei* (black circle).

The Manova performed on dorsal configuration suggests the presence of significant shape differences between species (Wilks' $\lambda = 0.001$, $P < 0.0001$). The scatter plot of the first two principal component axis (Fig. 3a) shows a good discrimination of *G. campestris*, *G. simoni* and *G. nanus*. These species are located on the two extreme points of the variation described by PC1 with *G. campestris* and *G. simoni* characterized by positive values of PC1 while *G. nanus* is characterized by negative values. By contrast, *G. latastei*, *G. tarabuli* and *G. gerbillus* show an intermediate position and are located in the same portion of the morphospace. The second PC axis allows only a partial discrimination between *G. campestris* and *G. simoni*. The CVA performed on the dorsal shape variables (Fig. 4a) shows a good discrimination of *G. campestris*, *G. simoni* and *G. nanus*.

Differently from PCA, *G. gerbillus* is also discriminated from other species but it still shows a partial overlap with *G. tarabuli* and *G. latastei*. By contrast, the two latter species are not discriminated by CVA analysis. These results are confirmed by the cross-validation (Table 2) which shows a high percentage of correct classification for all the species (> 95%) with the only exception of *G. tarabuli* and *G. latastei* who respectively show a 36.37% and 26.48% of misclassified specimens. Wireframes obtained for the dorsal view (Fig. 4a) show that *G. campestris* and *G. simoni* (positive values of CV1) are characterized by a restriction of the interparietal and of the occipital bones. On the other hand, the remaining species (negative values of CV1) show an opposite trend, with a tendency towards a lateral extension of the parietal bone that is particularly evident

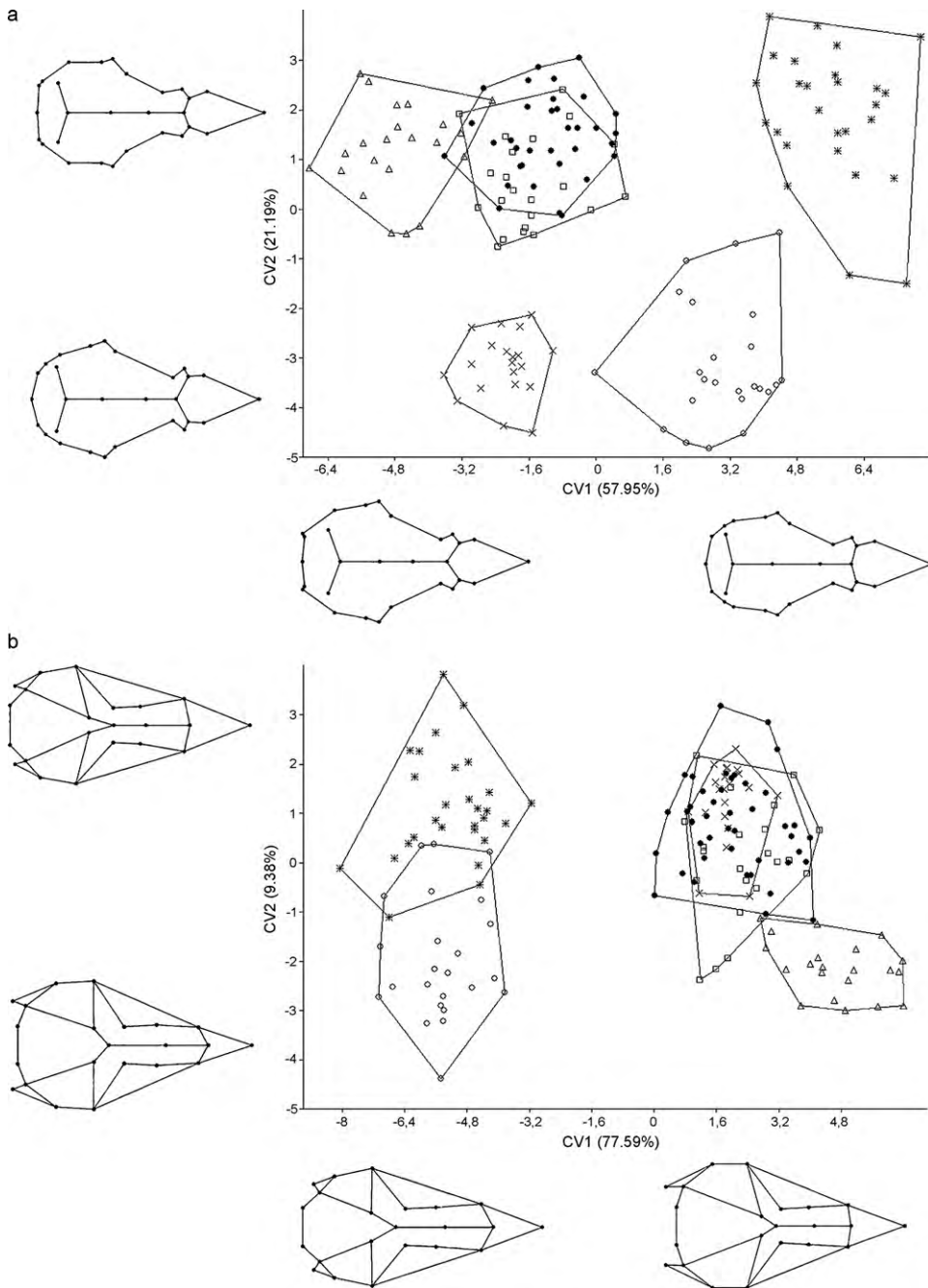


Fig. 4. Canonical variate analyses (CVA) of dorsal (a) and ventral (b) configurations. Symbols represent different species: *G. campestris* (star), *G. simoni* (white circle), *G. nanus* (white triangle), *G. gerbillus* (cross), *G. tarabuli* (white square), *G. latastei* (black circle). Shape differences along the CV1 and CV2.

in *G. nanus*. Wireframes associated to the CV2 (Fig. 4) suggest that *G. gerbillus* and *G. simoni* share a thinner rostrum while *G. campestris*, *G. tarabuli*, *G. latastei* and *G. nanus* have a larger and shorter rostrum.

Similarly to the dorsal configuration, the ventral one shows a significant shape difference between the species (Manova: Wilks' $\lambda=0.0027$, $F=12.1$, $P<0.0001$). However, both PCA and CVA analyses suggest that these shape differences observed within the same subgenus are of a

lower magnitude regarding the ventral configuration (Figs. 3 and 4). This is particularly evident for the species of the subgenus *Gerbillus*. Conversely, a higher phenetic divergence is observed between the subgenus *Dipodillus* and the subgenera *Gerbillus* and *Hendecapleura*. In fact, the PCA (Fig. 3b) performed on the ventral configurations shows that *G. campestris* and *G. simoni* are well discriminated from the other species while *G. nanus* partially overlaps with *G. latastei*, *G. tarabuli* and *G. gerbillus*. The

Table 2

Classification results of the discriminant analyses performed on the dorsal configuration according to the leave-one-out cross-validation procedure. In the diagonal there are the percentages of correct classification for each species.

	<i>G. campestris</i>	<i>G. gerbillus</i>	<i>G. latastei</i>	<i>G. nanus</i>	<i>G. simoni</i>	<i>G. tarabuli</i>
<i>G. campestris</i>	26 (96.29%)	0	0	0	1	0
<i>G. gerbillus</i>	0	20 (95.23%)	0	0	0	1
<i>G. latastei</i>	0	1	25 (73.52%)	2	0	6
<i>G. nanus</i>	0	0	1	21 (95.45%)	0	0
<i>G. simoni</i>	1	0	0	0	23 (95.83%)	0
<i>G. tarabuli</i>	0	1	7	0	0	14 (63.63%)

Table 3

Classification results of the discriminant analysis performed on ventral configuration according to the leave-one-out cross-validation procedure. In the diagonal there are the percentages of correct classification for each species.

	<i>G. campestris</i>	<i>G. gerbillus</i>	<i>G. latastei</i>	<i>G. nanus</i>	<i>G. simoni</i>	<i>G. tarabuli</i>
<i>G. campestris</i>	26 (96.29%)	0	0	0	1	0
<i>G. gerbillus</i>	0	18 (85.71%)	0	1	0	2
<i>G. latastei</i>	1	2	24 (68.57%)	3	1	4
<i>G. nanus</i>	0	0	1	18 (85.71%)	0	2
<i>G. simoni</i>	4	0	0	0	20 (83.33%)	0
<i>G. tarabuli</i>	0	2	8	0	0	12 (54.5%)

three latter species are completely overlapping. The CVA (Fig. 4b), explaining the 86.97% of the total shape variation, differently from the CVA obtained for the dorsal configuration, does not allow any discrimination between the three taxa. *G. nanus* is well discriminated by CVA but it is located close to the species belonging to the subgenus *Gerbillus*. The other two species belonging to the subgenus *Dipodillus*, i.e. *G. simoni* and *G. campestris*, are largely differentiated from the other species but show a higher degree of overlapping if compared to the results obtained from the CVA performed on the dorsal shape variables (Fig. 4a). Cross-validation (Table 3) shows a high percentage of correct classification for *G. campestris*. The other species show a higher number of misclassified specimens regarding the dorsal configuration with *G. tarabuli* which is nearly reaching 50% of misclassified individuals (Table 3). The wireframes obtained for the ventral view (Fig. 3b) suggest that the major deformations are associated to the shape of the tympanic bullae and the maxillary bone. The first CV axis describes clearly an opposite tendency in shape characterizing respectively the subgenera *Gerbillus* and *Hendecapleura* versus the subgenus *Dipodillus*. In *G. campestris* and *G. simoni*, the auditory bullae are of mediocre development while *G. nanus* shows a particularly hypertrophic tympanic bullae and a very well developed accessory bulla. The second CV axis describes shape difference in the position of the junction between tympanic bullae and pterygoid process (landmarks 19 and 20), more backward in both *G. simoni* and *G. campestris* comparing to the other species (Fig. 4). These two species, according to the wireframes described by CV2, show also a larger palate due to the enlargement of the posterior extremity of the molar row.

3.3. UPGMA

The UPGMA trees based on Procrustes distances (Fig. 5) show the same topology both for dorsal and ventral views highlighting the occurrence of two clusters reflecting the

subgeneric assignment of the species. One cluster includes *G. campestris* and *G. simoni* while the other includes the three species belonging to the subgenus *Gerbillus*, i.e. *G. gerbillus*, *G. tarabuli* and *G. latastei*. *G. nanus*, the sole species of the subgenus *Hendecapleura*, shows a phenotypic similarity with the subgenus *Gerbillus*. According to the PCA and CVA, the UPGMAs suggest that the subgenus *Dipodillus* has a higher phenetic distance from the other subgenera, particularly in the ventral configuration. On the other side, the Procrustes distances between species belonging to the same subgenus are lower in the ventral configuration with respect to the dorsal one.

4. Discussion

Although skull features were one of the main arguments used to assess the systematics and the taxonomy of the genus *Gerbillus*, most previous studies regarded only a limited data set of measures mainly related to the dental

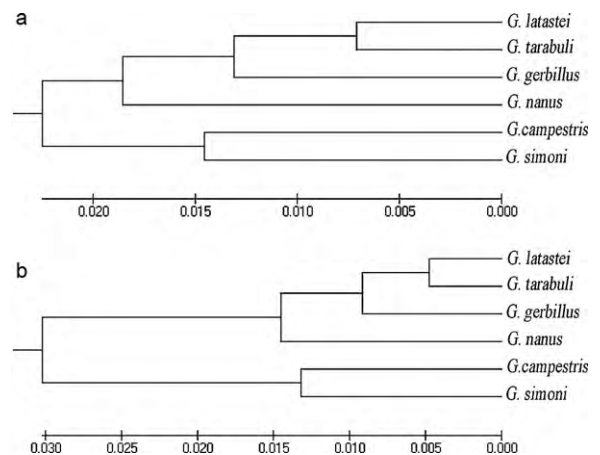


Fig. 5. UPGMA phenograms based on Procrustes distances for dorsal (a) and ventral (b) configurations of the skull.

and bullae morphology [9,20,35–37]. This is the first study which investigated the systematic relationships within the genus *Gerbillus* by a statistical quantification of the skull shape differences and suggests the study that the magnitude of differentiation among species and subgenera is different in ventral or dorsal configurations of the skull. The latter aspect should indeed be taken into account when morphology is used to assign a taxonomic rank to the different taxa.

Recent molecular data [25] proved that the subgenera *Dipodillus* and *Gerbillus* are actually sister taxa which comes across the view of two subgenera or even two different genera. However, according to our results and in particular those obtained for the ventral configuration (Figs. 3, 4 and 5), *G. campestris* and *G. simoni*, the two species belonging to the subgenus *Dipodillus*, appear as the most differentiated. Moreover, we found a close phenotypic similarity between the subgenus *Gerbillus* and *G. nanus* (subgenus *Hendecapleura*). These results contrast with the molecular systematics of *Gerbillus* [25] and agree with the previous morphological investigations that supported the separation of *Dipodillus* from the rest of the genus *Gerbillus*.

The differences observed between morphological and molecular data could be explained by a different rate of phenotypic evolution among subgenera. According to molecular data [25], *G. nanus*, which is phenotypically closely related to the subgenus *Gerbillus*, is the most basal species of the genus. This suggests that the subgenus *Gerbillus*, which is from a molecular point of view a sister taxon of *Dipodillus*, retained ancestral morphological features while *Dipodillus* has got a different phenotypic evolution and shows an apomorphic shape comparing to both the subgenera *Gerbillus* and *Hendecapleura*. It is worth mentioning that, even if the dorsal and the ventral configurations analyses have led to similar results, we observed a different degree of differentiation among subgenera when ventral or dorsal configurations are considered. In fact, our analyses suggest that the ventral side of the skull is more different in the subgenus *Dipodillus* compared to the subgenera *Gerbillus* and *Hendecapleura* (Figs. 3b and 4b) while a lower degree of differences in the ventral configuration were observed among species within the same subgenera. On the other hand, when the dorsal configuration is considered, we observed a higher degree of differentiation between species belonging to the same subgenus while, especially in the PCA (Fig. 3a), the subgenus *Dipodillus* appears less differentiated from the subgenus *Gerbillus*. These different degrees of interspecific differentiation observed when ventral and dorsal configurations are considered could suggest the action of different selective pressures or functional constraints in the morphological evolution of the skull of *Gerbillus* species. Notably, the phenotypic diversification observed between *Dipodillus* and *Gerbillus* subgenera appears mostly related to the ventral side of the skull and the nature of these modifications should be considered when a higher taxonomic rank for *Dipodillus* is claimed.

Shapes analyses clearly demonstrated that species belonging to the subgenus *Dipodillus* show modifications in the shape of the rostrum, in the zygomatic plate and

especially in the tympanic bullae and in the accessory bullae. In fact, the tympanic bullae in *G. campestris* and *G. simoni* show a mediocre development compared to other species and the posterior extremity of the accessory bullae is reduced. Moreover, a narrow zygomatic length which accentuates the angle between the anterior edge of posterior part of zygomatic arc and the dorsal root of squamosal, was observed in *G. campestris* and *G. simoni*. Some of these modifications were suggested to have an adaptive value related to auditory and feeding behaviour [28,37–39]. It has also been suggested that different degree of bullae hypertrophy in gerbils is inversely proportional to the population density [38,40] and that different degrees of hypertrophy could influence the efficiency of con-specific mate recognition [38] and the recognition of predators [40], especially in open habitat. The specimens involved in this study were all trapped in southern Tunisia, which is characterized by an arid bioclimate. In general, all species studied here are known to feed on seeds, insect larva and plants stems growing in the desert all over the year but with different proportionality [38,41,42]. Since all these species occur in similar habitats, the morphological features cannot be easily interpreted in the light of different pattern of trophic adaptations. However, with the exception of *G. latastei*, all of the subgenera *Gerbillus* and *Hendecapleura* have a wide distribution range while *G. campestris* and *G. simoni* (subgenus *Dipodillus*) are restricted to North Africa. Evolution of increased specialization in habitat or resources use occurred frequently in animals and it might be regarded as a trend where species with morphological adaptation to specialized habitat evolved from more generalist ancestors [43]. Thus, in the genus *Gerbillus*, this fact apparently favours a model of phenotypic evolution likely related to a higher habitat (and possibly trophic) specialization of *Dipodillus* species versus the *Gerbillus* and *Hendecapleura* species. In this view, differential selective pressures in the genus *Gerbillus* led to a peculiar (apomorphic) phenotype of *Dipodillus* species that can explain the observed incongruence between morphological and molecular data. Thus, phenetic difference could not be representative of the correct systematic relationships among the three subgenera.

In conclusion, the present geometric morphometrics study based on skull shape allowed to discriminate three morphological groups which are congruent with the three subgenera suggested by molecular analyses and by early morphological classification. Moreover, the skull structure, investigated by geometric morphometric study, may play an important role in taxonomy and could be of enough significance to be a valid identification criterion. Furthermore, we suggest that the integration of different techniques might provide a powerful tool to investigate phenotypic evolution and taxonomic issues in the genus *Gerbillus* and might help to solve systematic issues due to contrasting results from different sources.

Acknowledgments

This work was supported by a grant from the search unit “Biodiversity and Biology of Population”. We would

like to thank Professor Said Nouira, the director of the search unit, for his help and support. We are grateful to the team of “Anatomia Comparata Università la Sapienza, Roma”. We are also grateful to the people that helped to collect specimens, especially Lazar Hamdi the ranger of Bouhedma National Park.

References

- [1] J. Chibani, T.L. Cheniti, Étude caryologique des gerbilles (Genre *Gerbillus*) de Tunisie, Rev. Fac. Sc. Tunis 2 (1982) 147–153.
- [2] M. Chetoui, K. Said, M. Rezig, T.L. Cheniti, Analyse caryologique de quatre espèces de gerbilles (Rongeurs, *Gerbillinae*) de Tunisie, Bull. Soc. Zool. France 3 (2002) 211–221.
- [3] L. Granjon, V. Aniskin, V. Volobouev, B. Sicard, Sand-dwellers in rocky habitats: a new species of *Gerbillus* (Mammalia: Rodentia) from Mali, Zool. Soc. London 256 (2002) 181–190.
- [4] E. Capanna, M.S. Merani, Karyotypes of Somali rodent populations. 2. The chromosomes of *Gerbillus dunni* (Thomas, 1904), *Gerbillus pusillus* (Peters, 1878) and *Ammodillus imbelis* (De Winton, 1898), Mont. Zool. Ital. Suppl. 14 (1981) 199–226.
- [5] V. Volobouev, M. Lombard, M. Tranier, B. Dutrillaux, Chromosome-banding study in *Gerbillinae* (Rodentia). I. Comparative analysis of *Gerbillus poecilops*, *G. henleyi* and *G. nanus*, J. Zool. Syst. Evol. Res. 33 (1994) 54–61.
- [6] V. Volobouev, N. Vogt, E. Viegas-Péquignot, B. Malfoy, B. Dutrillaux, Characterization and chromosomal location of tow repeated DNAs in three *Gerbillus* species, Chromosoma 104 (1995) 252–259.
- [7] L. Granjon, H. Bonnet, W. Hamdine, V. Volobouev, Reevaluation of the taxonomic status of North African gerbils usually referred to as *Gerbillus pyramidum* (*Gerbillinae*, Rodentia) chromosomal and biometrical data, Z. Saugetierkunde 64 (1999) 298–307.
- [8] V. Aniskin, T. Benazzou, L. Biltueva, G. Dobigny, L. Granjon, V. Volobouev, Unusually extensive karyotype reorganization in four congeneric *Gerbillus* species (*Muridae*: *Gerbillinae*), Cytogenet. Gen. Res. 112 (2006) 131–140.
- [9] R.G. Jordan, L. Bruent, H. Baccar, Karyotypic and morphometric studies of Tunisian *Gerbillus*, Mammalia 38 (1974) 667–680.
- [10] G.C. Musser, M.D. Carleton, Superfamily *Muroidea*, in: D.E. Wilson, D.M. Reeder (Eds.), Third ed., Mammal species of the world: a taxonomic and geographic reference, Vol. 2, Johns Hopkins University Press, Baltimore, 2005, pp. 894–1531.
- [11] F. Lataste, Diagnoses de mammifères nouveaux d'Algérie. 3. *Gerbillus simoni* sp., Le Naturaliste 63 (1881) 497–500.
- [12] F. Lataste, Mammifères nouveaux d'Algérie, Le Naturaliste 16 (1982) 126–127.
- [13] J.R. Ellerman, The families and genera of living rodents, Br. Museum (Natural History) 2 (1941), pp. xii–690.
- [14] J.R. Ellermann, T.C.S. Morrison-Scott, Checklist of palearctic and Indian mammal, British Museum (Natural History) (1951) 1–810.
- [15] G.C. Musser, M.D. Carleton, Family *Muroidea*. A taxonomic and geographic reference, in: D.E. Wilson, D.M. Reeder (Eds.), Mammal species of the world, Second ed., Smithsonian Institution Press, Washington and London, 1993, pp. 501–755.
- [16] G.M. Allen, Checklist of African mammals, Bull. Museum Comparative Zool. Harvard 83 (1939) 1–763.
- [17] G.B. Corbet, The mammals of the Palearctic Region: a taxonomic review. British Museum (Natural History), London, 1978.
- [18] D.J. Osborn, I. Helmy, The contemporary land mammals of Egypt (including Sinai), Fieldiana Zool. New Ser. 5 (1980) 1–579.
- [19] I.J. Pavlinov, A.Y. Dubrovsky, E.G. Potabova, O.L. Rossolimo, Gerbillids of the wild world, Nauka. Publ., Moscow, 1990.
- [20] I.J. Pavlinov, Current concepts of Gerbillid phylogeny and classification, African small mammals, in: Proceedings of the 8th International Symposium on African Small Mammals, Paris, (2001), pp. 141–149.
- [21] F. Petter, Subfamily *Gerbillinae*, in: J. Meester and H.W. Setzer, (Eds.), The mammals of Africa: an identification manual Smithsonian Institution, Washington, DC, 1975, pp. 7–12.
- [22] M.B. Qumsiyeh, D.A. Schlitter, Cytogenetic data on the rodent family *Gerbillidae*, Occas. Papers Mus. Texas Tech. University 144 (1991) 1–20.
- [23] D.M. Lay, Taxonomy of the genus *Gerbillus* (Rodentia: *Gerbillinae*) with comments on the applications of generic and subgeneric names and an annotated list of species, Z. Saugetierkunde 48 (1983) 329–354.
- [24] P. Chevret, G. Dobigny, Systematic and evolution of the subfamily *Gerbillinae* (Mammalia, Rodentia, *Muridae*), Mol. Phylogenet. Evol. 35 (2005) 674–688.
- [25] A. Abiadh, M. Chetoui, T.L. Cheniti, E. Capanna, P. Colangelo, Molecular phylogenetics of the genus *Gerbillus* (Rodentia, *Gerbillinae*): implications for systematics, taxonomy and chromosomal evolution, Mol. Phylogenet. Evol. 56 (2010) 513–518.
- [26] G. Dobigny, M. Baylac, C. Denys, Geometric morphometric natural networks and diagnosis of sibling *Taterillus* species (Rodentia, *Gerbillinae*), Biol. J. Linn Soc. 77 (2002) 319–327.
- [27] A. Lalis, A. Evin, C. Denys, Morphological identification of sibling species: the case of West African *Mastomys* (Rodentia: *Muridae*) in sympatry, C. R. Biol. 332 (2008) 480–488.
- [28] P. Colangelo, R. Castiglia, P. Franchini, E. Solano, Pattern of shape variation in the eastern african gerbils of the genus *Gerbillus* (Rodentia, *Muridae*): environmental correlations and implication for taxonomy and systematic, Mammalian Biol. 75 (2010) 302–310.
- [29] F.J. Rohlf, A. Loy, M. Corti, Morphometric analysis of Old World *Talpidae* (Mammalia, *Insectivora*) using partial-warp scores, Syst. Biol. 45 (1996) 344–362.
- [30] F.J. Rohlf, a. Tps-Dig, Version 1.40. Department of Ecology and Evolution, State University of New York at Stony Brook, 2004.
- [31] C.P. Klingenberg, MorphoJ. Faculty of Life Sciences, University of Manchester, UK. http://www.flywings.org.uk/MorphoJ_page.htm, 2008.
- [32] F.L. Bookstein, Morphometric Tools for Landmark Data, Cambridge New York, 1991.
- [33] K. Tamura, J. Dudley, M. Nei, S. Kumar, MEGA4 Molecular Evolutionary Genetics Analysis (MEGA) Software Version 4.0, Mol. Biol. Evol. 24 (2007) 1596–1599.
- [34] R Development CoreTeam, A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN3-900051-07-0. <http://www.R-Project.orgS> (2008).
- [35] M. Chetoui, T.L. Cheniti, La gerbille de l'île Chargui (Archipel Kerkennah, Tunisie) *Dipodillus simoni* (Rongeurs, *Gerbillinae*), Bull. Soc. Zool. Fr. 130 (1) (2005) 107–117.
- [36] J. Bernard, Les mammifères de Tunisie et des régions voisines, Bul. Fac. Agronomie 8 (24–25) (1969) 47–171.
- [37] D.M. Lay, C.F. Nadler, A study of *Gerbillus* (Rodentia, *Muridae*) east of the Euphrates River, Mammalia 39 (3) (1975) 423–445.
- [38] F. Petter, Répartition géographique et écologie des rongeurs désertiques (du Sahara occidental à l'Iran oriental), Mammalia 25 (1961) 1–222.
- [39] C. Fadda, M. Corti, E. Verheyen, Molecular phylogeny of *Myomys/Stenocephalemys* complex and its relationships with related African genera, Biochem. Syst. Ecol. 29 (2001) 585–596.
- [40] D.M. Lay, The anatomy, physiology, functional, significance and evolution of specialized hearing organs of *Gerbillinae* rodents, J. Morph. 138 (1972) 41–120.
- [41] Y. Bar, Z. Abramsky, Y. Gutterman, Diet of gerbilline rodents in the Israeli Desert, J. Arid Env. 7 (1984) 371–376.
- [42] A. Zaime, J.Y. Gautier, Comparaison des régimes alimentaires de trois espèces sympatriques de *Gerbillidae* en milieu saharien au Maroc, Rev. Ecol. 44 (1989) 153–163.
- [43] D.J. Futuyma, G. Moreno, The evolution of ecological specialization, Annu. Rev. Ecol. Syst. 19 (1988) 207–233.