

Comparative mandible geometric morphometrics of two African rodents, *Thryonomys swinderianus* and *Cricetomys gambianus* (Rodentia: Thryonomyidae and Nesomyidae)

Samuel, O.M.*¹, Parés-Casanova, P.M.², Olopade, J.O.³

1. Department of Veterinary Anatomy, Federal University of Agriculture Makurdi Benue State, Nigeria, walesamuel10@gmail.com
2. Department of Animal Productions, University of Lleida, Catalonia, Spain
3. Department of Veterinary Anatomy, University of Ibadan Oyo State, Nigeria

Received 30-V-2016 • Corrected 16-VI-2016 • Accepted 15-VII-2016

ABSTRACT: The African giant pouched rat (*Cricetomys gambianus*) and greater cane rat or African cane rat (*Thryonomys swinderianus*) both have similar body conformation and share similar ecological biome. This study aimed to compare mandibular parameters in adults of both species. For this purpose, 9 lateral mandibular landmarks in male *T. swinderianus* (n=11) and *C. gambianus* (n=12) were analyzed by geometric morphometrics. *T. swinderianus* presented a coronoid process equivalent to condyle and a more caudally displaced angular process, whereas cheek teeth was less prominent and shorter in *C. gambianus*. This study may be useful in solving phylogenetic ambiguities, wildlife surveillance and age-population control, ration formulation in captive species, and eco-migration. This is the first time to our knowledge that geometric morphometric comparison of mandibles in these African rodents has enabled an inference of ecological preferences in diet based on mandible shape.

Key words: craniofacial, comparative morphometry, osteometry, comparative zoometry.

RESUMEN: Comparación de la morfología geométrica de la mandíbula de dos roedores africanos, *Thryonomys swinderianus* y *Cricetomys gambianus* (Rodentia: Thryonomyidae y Nesomyidae).

La rata gigante africana (*Cricetomys gambianus*) y la rata de caña africana (*Thryonomys swinderianus*) tienen conformación corporal similar y biomas similares. Este estudio tuvo como objetivo comparar los parámetros mandibulares en adultos de ambas especies. Para ello usamos 9 puntos de referencia mandibulares laterales en machos de *T. swinderianus* (n = 11) y *C. gambianus* (n = 12) analizándolos mediante morfometría geométrica. *T. swinderianus* presentó un coronoides equivalente al cóndilo y un proceso angular desplazado más caudal, mientras que los dientes de mejilla son menos prominentes y más cortos en *C. gambianus*. Este estudio puede ser útil para resolver ambigüedades filogenéticas, vigilancia de fauna y control con la edad de la población, formulación de raciones de especies en cautiverio, y eco- migración. Creemos que esta es la primera vez en que la comparación mandibular de estos roedores permite inferir preferencias ecológicas en la dieta con base en la forma de la mandíbula.

Palabras clave: craneofacial, morfometría comparativa, osteometría, zoometría comparativa.

The African giant pouched rat (*Cricetomys gambianus*) and the greater cane rat or African cane rat (*Thryonomys swinderianus*) are separated along family lines (*Nesomyidae* and *Thryonomyidae*, respectively) despite a similar morphology. These rodents inhabit Liberian coasts in the west to east African countries such as Kenya, Tanzania, and Gabon, and have been reported in the South African enclave (Ajayi, 1977; Hammond et al., 1999). Both rodents share ecological biome, habitat, diet, certain aspects of prehension and mastication, although body weight differ; (adult *T. swinderianus* / *C. gambianus* weight between 5-8 kg / 3-5.8 kg respectively irrespective of gender bias) (Onyeanusi et al., 2009). Pelage

identification might be misleading except for the white patch on posterior third of the tail length in *C. gambianus* (Olude et al., 2011).

A rapidly extending geographic distribution of the two species has been observed in areas otherwise not reported especially islands and landlocked enclaves (Hendry et al., 2006; Wright et al., 2006; Pergams & Lawler, 2009). Ecological separation and home range overlaps exist between them as they share and interact in conflict or competitively but not necessarily exploitatively within territory limits (Ajayi et al., 1978; Happolds, 1987). Occasional interaction between colonies of both in drought periods has increased in frequency due to

human and natural agents of change (Pergams & Lawler, 2009). A colony comprise of a male and about five females (Onyeanus et al., 2009;) making seasonal availability or scarcity of food, high temperature deviations, flooding and moonlight the limiting or promoting factors of interactions (Happolds, 1987).

Literary information on head morphology of the *T. swinderianus* and *C. gambianus* is rare despite an abundance of similar works in other small mammals, such as mole rat (Vinogradov & Argirnopulo, 1941), mink (Dursun & Tirpirdamaz, 1989), rabbit (De Abreu et al., 2006; Samuels, 2009), African giant pouched rat (Olude et al., 2011) and jirds, among others. This paucity justifies the necessity for this investigation. The objective of the study was to compare certain inter-species dimorphic variations in the macro anatomy of mandible morphology of both species. This study is performed using geometric morphometrics technique, which has a unique ability to measure displacements, deformations and rotations of objects, and as well graphically visualize these variations. This method enables a better representation of shape than traditional linear and angle measurements, allows visualization of shape differences within and between group means in specimen space, and can quantify such traits described qualitatively.

Some studies have pointed out the existence of a close relationship between feeding habits and skulls or mandibles morphology using classical and geometric morphometric tools for quantification of shapes (Michaux et al., 2007; Renaud et al., 2007; Samuels, 2009; Cox et al., 2012; Hautier et al., 2012). As the masticatory behaviors

are important in evaluating biomechanical properties, we predicted that aspects of mandibular shape, as revealed in the principal components analysis, would separate *C. gambianus* and *T. swinderianus*. Relevant data obtained will be useful in bridging knowledge gap in the comparative mandibular-macro morphology between *C. gambianus* and *T. swinderianus* as well in solving taxonomic challenges.

MATERIALS AND METHODS

Two initial mandibular samplings of *T. swinderianus* (n=11) and *C. gambianus* (n=12) were used. Each comprised animals collected from a village locality in South-western Nigeria between January to March and between July to October of year. Age was determined by dental eruptions and body length (Ajayi, 1977; Olude et al., 2011). Skull maceration of decapitated heads was done immediately after acquisition using procedures described by Onar and Parvant (2001). Mandibles were posteriorly disarticulated and two hemi-mandibles separated.

Photography: Pictures of right hemi-mandibles (on their lateral aspect) were taken using a digital camera Canon EOS1200D, (Canon Inc. Tokyo Japan) equipped with EFS 18-58mm telephoto and Hama® tripod with stabilizer. Images were taken at a DIN of 25cm, a focal axis of 5.6, a speed of 200 and sensitivity of 1/500 for all pictures taken. The landmarks assessed on each digital picture were 9 in number (Figure 1 and Table 1). Landmarks used



Fig 1. Right lateral mandible view of *Thryonomys swinderianus* and *Cricetomys gambianus* (left to right) with 9 landmark points. Numbers correspond to definitions in Table 1.

TABLE 1

Nine landmarks studied on lateral view of each mandible

Landmark No.	Right lateral view of mandible
1	Lateral point of first incisor teeth in the alveolus
2	Ventral point of first incisor alveolus
3	Direct ventral point of mental foramen on mandible body
4	Caudal angle point of mandible
5	Point on mandible condyle
6	Point on coronoid process
7	Point on last cheek tooth alveolus
8	Dorsal point of mental foramen
9	Point on alveolus of first premolar

in this study were primarily chosen to describe major mandibular regions, and points of particular morpho-functional interest. The x and y co-ordinates of all landmarks for the photographed views were then obtained using TPSDig 2.16 software (Rohlf, 2010) and processed with MorphoJ 1.06c (Klingenberg, 2011).

For the smallest shape variation around the point of tangency, the best point of tangency is the sample mean form. TpsSmall, v.1.20 software (Rohlf, 2014) was used to assess this correlation between the 2D Procrustes distances to the Euclidean distances in that tangent space. The correlation was very close to linear for all of the data ($r=0.998$; slope, $b=0.945$), suggesting that tangent space was an adequate approximation to Kendall and that no specimens deviated appreciably from the linear regression line. Thus, although the lateral view of the mandible is not a flat object, authors considered that two-dimensional approach implies a limited loss of information, and we proceeded with the morphometric analyses.

Landmark coordinates were then superimposed using generalized Procrustes analysis (GPA). Multivariate analyses based on Procrustes-aligned specimens were found to have higher statistical power than alternative geometric morphometric approaches (Rohlf, 2006). GPA superimposes specimen landmark configurations by translating them to a common origin, scaling them to unit centroid size (the square root of the sum of squared distances of all landmarks to the centroid of the object; the measure of size used here), and rotating them according to a best-fit criterion. This procedure eliminates “size” as a factor (although size-related shape differences may remain). “Shape” can therefore be analyzed separately from “size”. A Principal Component Analysis (PCA) from covariance matrix was used for analysis. PCA is a data-reduction exploratory technique, which summarizes the

total variance in a data set by rotating it so that the principal components explain progressively smaller amounts of the total variance (Lestrel, 2000). Principal component axes function as shape variables, the first of which represents the major axis of variation among the objects. A discriminant analysis was finally used to determine how well the principal components classified both species.

Ethics statement: The investigation did not involve endangered or protected species. All protocols according to the Veterinary decree 1962, animal welfare, game hunting and handling edict of the Federal Republic of Nigeria (1978) were strictly observed.

RESULTS

For both species, significant shape differences ($p<0,001$) seems to exist. Average shape data for each species is shown in Table 2. First two Principal Components in PCA explained a 84.81% of the total observed variance ($PC1+PC2=63,11+21,69\%$) represented in Table 3. Coefficients of PCA appear in Table 4. *C. gambianus* specimens were scattered along axis 1 and 2, with mostly negative scores. There were no overlaps with *T. swinderianus* (Figure 2). The first principal component of the PCA (63,11% of the total variance) described the functional mandibular shape, including the shape of the ramus, with low scores corresponding to short and low mandibles, and high scores reflecting long and high mandibles (Figure 2). *C. gambianus* had low scores and *T. swinderianus* had higher and positive scores. Correct classification for each species was 100%.

TABLE 2
Average shape (axis 1 (x) and 2 (y) for males in *Thryonomys swinderianus* (n=11) and *Cricetomys gambianus* with 9 landmarks (lmk)

lmk	<i>Cricetomys gambianus</i>		<i>Thryonomys swinderianus</i>	
	Axis 1 (x)	Axis 2 (y)	Axis 1 (x)	Axis 2 (y)
1	0,36	0,11	0,34	0,08
2	0,39	-0,01	0,35	-0,07
3	0,20	-0,15	0,13	-0,23
4	-0,38	-0,25	-0,49	-0,24
5	-0,46	0,06	-0,40	0,16
6	-0,33	0,20	-0,22	0,17
7	-0,05	0,03	-0,07	0,05
8	0,15	-0,02	0,13	0,009
9	0,11	0,01	0,21	0,06

TABLE 3
Principal component analysis for male mandibles.
The first two components (PC) represent most of
the variation in the data set

PC	Eigenvalues	% Variance	Cumulative Variance %
1	0,012	63,11	63,11
2	0,004	21,69	84,81
3	0,001	7,03	91,84
4	0,0005	2,89	94,74
5	0,0004	2,04	96,78
6	0,0002	1,35	98,14
7	0,0001	0,83	98,97
8	0,0001	0,51	99,49
9	3,93E-05	0,19	99,68
10	2,34E-05	0,11	99,80
11	1,69E-05	0,08	99,88
12	1,11E-05	0,055	99,93
13	8,09E-06	0,040	99,97
14	4,28E-06	0,021	100

Total variance: 0,02030138.

Variance of the eigenvalues: 0,0000112009608.

Eigenvalue variance scaled by total variance: 0,02718.

Eigenvalue variance scaled by total variance and number of variables:
0,40975.

TABLE 4
Principal Component Coefficients for Principal Component 1
(PC1) and 2 (PC2) (84.81%) between male mandibles

	PC1	PC2
x1	-0,14	-0,01
y1	0,09	-0,09
x2	-0,18	0,06
y2	-0,12	0,15
x3	-0,07	-0,02
y3	-0,09	0,08
x4	-0,32	0,003
y4	-0,33	0,08
x5	0,20	0,02
y5	0,19	-0,02
x6	0,35	-0,07
y6	-0,29	0,08
x7	-0,24	0,01
y7	0,08	-0,05
x8	0,17	0,48
y8	-0,006	-0,58
x9	0,25	-0,47
y9	0,47	0,35

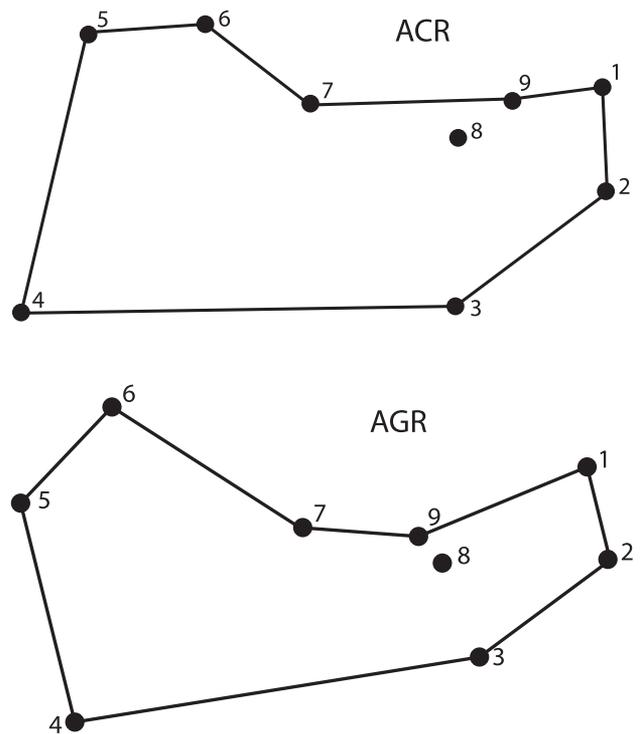


Fig. 2. Plotting for each species (*Thyronomys swinderianus* (ACR) above, *Cricetomys gambianus* (AGR) below).

T. swinderianus presented a coronoid process equivalent to condyle and a more displaced caudally angular process, whereas cheek teeth was less prominent and shorter in *C. gambianus*. Set of lines connecting the digitized points on a shape do not represent data, but are used to aid in visualization (Figure 2).

DISCUSSION

As predicted, mandibular shape was a valid distinguishing means for separating African giant pouched rat (*Cricetomys gambianus*) and greater cane rat or African cane rat (*Thyronomys swinderianus*). The latter presented a coronoid process equivalent in height to condyle, both processes getting closer, and the angular process being elongated (posteriorly displaced), whereas, cheek teeth was less prominent and shorter in *C. gambianus*, while the angular process enlarged (caudo-ventral expansion). *T. swinderianus* presented also a remarkable uplift of the tooth-row, a mental foramen further backward with a more rostral shift of coronoid process.

Comparatively, higher cheek teeth (above the alveola) and surface for *M. pterygoideus lateralis* muscle in *T. swinderianus* is a discriminant factor of diet adaptation

which favours fibrous diet type during the drier seasons compared to the reverse in *C. gambianus* mandibles. A more dorsally placed and posteriorly oriented coronoid process relative to the articular condyle in *C. gambianus* is similar to ruminant's mandible (Olopade, 2006) located well above the level of the cheek tooth row in contrast to *T. swinderianus* whose coronoid and condyle are placed at the same level with the tooth rows; a trait synonymous with primitive carnivoran condition (Figueirido et al., 2008) in some members of *Heteromyidae* (Pergams & Lawler, 2009) perhaps for mechanical advantage in prey/food summarization.

In comparing diet in these rodents, other authors (Ajayi, 1977; Ali et al., 2011) reported that the African Giant rat survives more on domestic waste and less fiber diet, this is perhaps corroborated by its curved and longer mandibular architecture (longer buccinators muscle attachment), for food stowaway in cheeks, while *T. swinderianus* utilizes high roughage and fiber content plant food such as *Austrophia species* (spear grass), *Pennisetum purpureum* (elephant grass) and *Saccharum species* (sugar cane). This fact is postulated to contribute to the characteristics of some mandible anatomic parameters and becomes important in formulation of captive animal diet. The plant species becomes scarce between the months of September-April being the drier periods of the year (Happolds, 1987; Tong, 1989) serving as a substrate in home range extension with probable overlap in spatial use and competitive interactions. Artificial ration formulation for species preservation especially in colonies and parks might be necessitated to avoid encroachments into other territories and exposure to raptors. The dental space length in *T. swinderianus* was found shortened compared to the *C. gambianus* and may be an adaptation for diversity in method of prehension, mastication and deglutition (Tong, 1989; Hammond et al., 1999). *T. swinderianus*; possess a more robust mandible architecture which supports vigorous horizontal snapping movements of the head; thus resulting in differing specific alterations in morphological proportions of the jaw. Fatalities resulting from brief occasional interactions between and within both species favour cane rats often by means of such differences. Numerical increases in the presence of such adults are precursors of new colonies and relocation of *C. gambianus* species (Matina et al., 2010; Ali et al., 2011).

Comparative studies on mandible typology of both rodents are relevant in phylogenetic investigations, domestication, and population surveillance and as well in diet research. New introductions of similar sized rodents may be identified by this means. In prolonged drought young *C. gambianus* species becomes exposed to risks

of raptors and contribute to economic losses in homes and farms, whereas the *T. swinderianus* relies more on adipose reserves, it selectively roams in late evenings with comparatively less dietary challenges (Ajayi, 1977; Hammond et al., 1999; Pergams & Lawler, 2009) body weight therefore remains relatively constant. Knowledge of mandibular relationship of these species as presented in the present study may be valuable in rodent taxonomic ambiguity (Tong, 1989; Yigit, 1999; Olopade, 2006), construction of head restraint tools and localization. Sustained temperature deviations in weather events are also postulated to trigger deadly and population threatening interactions (Serrat et al., 2008).

Abundance or lack of favourable ecological conditions is often an index of species population density but might be determined by inter-specific contacts more probable in food scarcity (Happolds, 1987; Pergams & Lawler, 2009; Samuel, 2009).

Conflict of interest statement

No conflicts of interests nor financial obligations/commitment to any institution exists

ACKNOWLEDGEMENTS

This investigation was collaborative in nature, carried out by departments of Veterinary Anatomy of three institutions mentioned above. We therefore acknowledge the effort of Professor Onwuka S.K, head of Anatomy University of Ibadan who authorized the use of facilities employed for this work Prof. Olopade J.O edited tirelessly the manuscript to the present extent, while Dr. Akpan M.O assisted in the acquisition of African Cane rat mandibles.

REFERENCES

- Ajayi, S. (1977). Field observations on the African giant rat *C. gambianus* in southern Nigeria. *East African Wildlife J.*, 15(3), 191-198.
- Ajayi, S., Tewe, O. Faturoti, E. (1978). Behavioral changes in African Giant rat (*C. gambianus* waterhouse) under domestication. *East African Wildlife J.*, 16(2), 137-143.
- Ali, M.N., Onyeanus, B.I., Ayo, J.O., Ojo, S.A., Salami, S.O., Nzalok, J.O., Byanet, O. (2011). Effects of season on the reproductive organs of Female African Giant rat (*C. gambianus*). *Int. J. Morphol.*, 29(3), 841-844.
- Cox, P.G., Rayfield, E.J., Fagan, M.J., Herrel, A., Pataky, T.C. et al. (2012). Functional Evolution of the Feeding System in Rodents. *PLoS ONE* 7, e36299

- De Abreu, A.T., Veeck, E.B., da Costa, N.P. (2006). Morphometric methods to evaluate cranio-facial growth- study in rabbits. *Dento maxillofac Radiol.*, 35(2), 83-87.
- Dursun, N.S., Tipirdamaz, N. (1989). Etudes macro anatomique- ment sur les os du squelette du vison (*Mustela vison*) *J. Fac. Vet. Med. Univ Selçuk*, 5, 13-27.
- Figueirido, B., Palmqvist, P. Pérez-Claros, J. A. (2009). Ecomorphological correlates of craniodental variation in bears and paleobiological implications for extinct taxa: an approach based on geometric morphometrics. *J. Zool.*, 277, 70-80.
- Hammond, K.A., Roth, J. Janes, D.N., Dohm, M.I. (1999). Morphological and physiological responses to altitude in deer mice (*Peromyscus maniculatus*). *Phys. Biochem. Zool.*, 73, 613-622.
- Happolds, D.C.D. (ed.) 1987. *The Mammals of Nigeria*. Clarendon Press. Oxford, pp., 180-189.
- Hautier, L., Lebrun, R., Cox, P.G. (2012). Patterns of covariation in the masticatory apparatus of hystricognathous rodents: Implications for evolution and diversification. *J. Morphol.* 273, 1319-1337.
- Hendry, A.P., Gant, P.I., Grant, B.R., Ford, H.A., Brewer, M.J. (2006). Possible human impact on adaptive radiation: beak size bimodality in Darwin's finches. *Proc. Roy. Soc. B*, 273, 1887-1894.
- Klingenberg, C. P., 2011. *MorphoJ v. 1.06c*. Faculty of Life Sciences. University of Manchester. Available at http://www.flywings.org.uk/MorphoJ_page.htm (accessed 11 September 2015)
- Lestrel, P.E. (2000). *Morphometrics for the life sciences*. River Edge, NJ: World Scientific Publishing Co. Pte. Ltd.
- Matina, C, Kalcounis, R, Radmila P, Jessica, R.B., Catherine, C., Matthew, M.M., John, T.W., Olav, R., David, O.R., Jannet, P.C. (2010). Differences in Ultrasonic Vocalizations between Wild and Laboratory California Mice (*Peromyscus californicus*). *PlosOne*, 10.1371/journal.pone.0009705
- Michaux, J., Chevret, P., Renaud, S. (2007). Morphological diversity of Old World rats and mice (Rodentia, Muridae) mandible in relation with phylogeny and adaptation. *J. Zoo. Syst. Evol. Res.*, 45, 263-279.
- Olopade, J. O. (2006). *Morphometric analysis of the skull of three breeds of goats in Nigeria* Ph.D Thesis. Department of Veterinary Anatomy, faculty of Veterinary medicine, Univ. of Ibadan Nigeria.
- Olude, M.A., Olopade, J.O., Fatola, I.O., Onwuka, S.K. (2011). Some aspects of the neurocraniometry of the African giant rat (*C. gambianus* Waterhouse) *Folia Morphol.*, 68 (4), 224-227.
- Onar, V., Ozcan, S., Pazvant, G. (2001). Skull typology of the adult male Kangal dog. *Anat. Histol. Embryol.*, 30, 41-48.
- Onyeanus, B.I., Adeniyi, A.A., Ayo, J.O., Ibe, C.S. and Onyeanus C.G. (2009). A comparative study of the urinary system of the African giant rat (*C. gambianus*, Waterhouse) and the Wistar rat. *Pakist. J. Nutr.*, 8(7), 1043-1047.
- Pergams, O.R.W., Lawler, J.J. (2009). Recent and Widespread Rapid Morphological Change in Rodents *PloS One*, 4(7), e6452. doi:10.1371/journal.pone.0006452
- Renaud, S., Chevret, P., Michaux, J. (2007). Morphological vs. molecular evolution: ecology and phylogeny both shape the mandible of rodents. *Zool. Scr.* 36: 525-535
- Rohlf, F.J. 2000. Statistical power comparisons among alternative morphometric methods. *Am. J. Phys. Anthropol.*, 111, 463-478.
- Rohlf, F.J. (2006). *tpsRelw*, ver. 1.44. Department of Ecology and Evolution. State University of New York at Stony Brook.
- Rohlf, F.J. (2010). *Ecology and Evolution*. SUNY at Stony Brook.
- Rohlf, F.J. (2014). *TpsSmall* ver. 1.29. Department of Ecology and Evolution. State University of New York at Stony Brook.
- Samuels, J.X. (2009). Cranial morphology and dietary habits of rodents. *Zool. J. Linn. Soc.*, 156, 864-888.
- Serrat, M.A., King, D., Lovejoy, C.O. (2008). Temperature regulates limb length in homeotherms by directly modulating cartilage growth. *Proc. Nat. Acad. Sci. USA*, 105, 19348-19353.
- Tong, H. (1989). Origine et evolution des Gerbillidae (mammalia, Rodentia) en Afrique du nord. *Mem. Soc. geol. France*, 155, 1-120.
- Vinogradov, B.S., Argiropulo, A.I. (1941). Fauna of the U.S.S.R, mammals. *Zool. Inst. Acad. Sci. U.S.S.R New series*, 29, 243.
- Wright, S., Keeling, J., Gilman, L. (2006). The road from Santa Rosalia: A faster tempo of evolution in tropical climates. *Proc. Nat. Acad. Sci. USA*, 103, 7718-7722.
- Yigit, N.Q. (1999). A study of the Taxonomy and karyology of *Meriones persicus* (Blanford, 1875) (Mammaliae, Rodentia) in Turkey. *Turk. J. Zool.*, 23, 269-274.