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Non-functional sexually dimorphic mandibular differences in the African rodent *Thryonomys swinderianus(*Temminck, 1827)

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ABSTRACT

This study aimed to compare mandibular parameters in adult males and females of Greater cane rat or African cane rat (Thryonomys swinderianus). For this purpose,9lateral mandibular landmarks were analysed by means of geometric morphometrics. Based on data, and exclusion of the size related component of shape variation, males and females can be clearly discriminated according to mandible shape.In males the ventral point of first incisor alveolus tends to be more cranial, whereas the mental foramen presented a more caudal displacement in females, which moreover demonstrated a more slender mandible. Main biomechanical points (mandibular ramus flexure) showed no differences between genders. It may be concluded that morphological differences the in the mandible of both sexes of T. swinderianus are not due to a functional reasons, as masticatory behaviour would be. This is the first time to the best of our knowledge that geometric morphometric comparison of mandibles in this African rodent is reported, which has enabled the inference of identical biomechanical forces in males and females.

Key words: craniofacial, comparative morphometry, osteometry, sex assessment, *Thryonomydae*

INTRODUCTION

Greater cane rat or African cane rat (*Thryonomys swinderianus* Temminck, 1827) belongs to the family *Thryonomydae*. The specieshas been widely recorded over much of Subsaharan Africa, living in Liberian coast in the west to east African countries such as Kenya, Tanzania, and Gabon, and been reported in the South African enclave [1, 2]. Body weight is between 5-8 kg[3].

Rapidly extending geographic distribution of *T. swinderianus* has been observed in areas otherwise not reported especially islands and landlocked enclaves[4, 5, 6]. Their colonies comprise a male and about five females [3] making seasonal availability or scarcity of food, high temperature deviations, flooding and moonlight the limiting or promoting factors of interactions [7].

Literary information on head morphology of the *T. swinderianus* is rare despite an abundance of similar works in other small mammals, such as mole rat [8], mink[9], 1989), rabbit [10, 11] and African giant pouched rat[12], among many others.In the skeleton, male and female characteristics run through a continuum of morphologic configurations and metric values. A good understanding of the nature and factors of expression of sexual dimorphism is fundamental for the study of growth, development, and evolution. The isolation, interpretation, and quantification of manifestations of sex bias are essential parts of all skeletal analyses.The paucity of literary information in *T. swinderianus* justifies a necessity for this investigation.

The objective of this investigation was to compare sexually dimorphic variations in the macro anatomy of mandible morphology of this species. Osteometric approaches, such as discriminant function analysis, have shown that size alone is not the best indicator of sex, this study is performed using geometric morphometrics (GM) technique. GM employs the Cartesian coordinates of a set of topographically corresponding landmarks to compare the form of organisms and their organs. In two-dimensional analyses, the landmarks areusually digitized on images of organisms under study. To remove differences due to specimen orientation and position during data collection, and to separate the size and shape components, landmark configurations are first scaled to the same size, centered at their origin and rotated to minimize the distances among the corresponding landmarks (Generalized Procrustes Analysis or GPA). After the GPA, each landmark configuration corresponds to a point in a curved shape space and needs to be projected in a tangent Euclidean space to perform standard multivariate statistical analyses: this process is analogous to a flat map approximation of a small region of the earth's surface. The coordinates of the tangent space provide a set of shape variables that describe only those morphological features that do not change with scale, position and orientation

Some studies have pointed out the existence of a close relationship between feeding habits and skulls or mandibles morphology using classical and GM tools for quantification of shapes[13, 14, 15, 16]. We predicted that if mandibular shape, as revealed in the principal components analysis, would separates exes in *T. swinderianus*, it would be explained by different masticatory behaviour only if those differences were related to bony aspects linked to biomechanical mandibular properties, e.g., ramus flexure.

MATERIALS AND METHODS

A skull sampling of *T. swinderianus* (n=21, 11 males and 10 females) was used. It 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 [1, 12]. Initial heads maceration was done immediately after acquisition using procedures described by Onar and Parvant [17]. Mandibles were posteriorly disarticulated and two hemi-mandibles separated. No edentulous mandible appeared in the sampling.

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 in this study were primarily chosen (type 1 landmarks) 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 Tps Dig, v. 2.16 software [18]and processed with MorphoJ, v. 1.06c[19].

For the smallest shape variation around the point of tangency, the best point of tangency is the sample mean form. Tps Small, v. 1.20 software[20]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=0.997; slope, b=0.906), 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 skull is not a flat object, authors considered that the 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[21]. 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), 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 analysed 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[22].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

There were significant gender shape differences(p<.001).The proportion of correctly classified sex from discriminant function reached 100%. First two Principal Components in PCA explained a 80.44% of the total observed variance (PC1+PC2=53.96+26.48%) (Fig. 2and Table 2).It must be acknowledged that male specimens were more widely distributed on the first plane of the PCA than the females.Main differences were observed on ventral point of first incisor alveolus (2), on ventral point of mental foramen on mandible body (3), on the condylar ramus (6) and on mental foramen (8) (Figure 3). Average shape for each gender appears in Table 3.

DISCUSSION

Mandibular shape detected shape differences in males and females of greater cane rat or African cane rat (*Thryonomys swinderianus*). The results indicate that ventral point of first incisor alveolus, ventral point of mental foramen on mandible body, mental for a men and the condylar ramus assess the sex differentiation. No landmark on the mandibular ramus flexure contributed to the sex mandibular differentiation. In males the ventral point of first incisor alveolus tends to be more cranialand direct ventral point of mental foramen on mandible body more ventral, thus marking a more impressive “face”. In females the mental foramen tends to be more caudally displaced. But this foramen is just is the way by which mandibular division of the trigeminal nerve (V3) and mental vessels enters, so nonfunctional difference can be deduced from this more dorsal position. Moreover, minor locations variations may be phylogenetic related, at least in humans[23], and evidently it does not implies functional differences between human groups.

Bringing the incisors together or using them to chisel away at a surface requires muscles that forcefully brings the lower jaw forward. In rodents, this is done primarily by the masseter muscle. By moving the point of origin of parts of the masseteric musculature anteriorly, rodents gain both mechanical advantage and additional range of movement of the lower jaw. The masseter is on the lower jaw inserted along the lower part of the mandible at the rear, but condylar and angular processes of the ramus appeared to be similar in shape for both genders. This posterior part of the mandible would present differences if different biomechanical forces were present.

T. swinderianus utilizes high roughage and fibre content plant diet such as *Austrophia species* (spear grass), *Pennisetumpurpureum* (elephant grass) and *Saccharum species* (sugar cane)[1]. This fact is postulated to contribute to the characteristics of some mandible anatomic parameters and becomes important in formulation of captive animal diet. Such plant species becomes scarce between the months of September-April being the drier periods of the year [7, 24] serving as a substrate in overlap of 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 mammalian mandible arises from embryonicneural crest cells that migrate to the first mandibular arch, where they provide thee embryonicmesenchyma for mandibular skeletal, dental, and connective tissues[25]. After migration, mesenchymal cells aggregate, producing condensations that differentiate further and give rise to the variousmorphogenetic units of the mandible, which in adult individuals are recognized as semi-independent morphogenetic regions: the horizontal ramus; the molar and incisivealveolar regions, which support tooth roots; and the ascending ramus, which includes three muscular processes, the condyloid, coronoid, and angular processes [25]. This growth is directed and molded by numerous influences [26]. The effective number of cells in the condensations, the relative timing of the initiation of the condensation, and rates of cell migration, cell birth, and cell death are the developmental parameters known to be important in the production of mandibular shape[27, 25]. These developmental parameters of cell population dynamics are responsible for the assembling of a complex morphological structure such as the mandible, and alterations in each of these parameters may lead to developmental changes and morphological evolution [27].Genetically mediated changes affecting developmental parameters at the mesenchymal condensation stage will affect the entire mandibular structure, whereas changes in developmental parameters occurring at the stage where mesenchymal condensations already have differentiated will affect individual units of the mandible, for example, the angular, condylar, or alveolar regions[27], and therefore will have a localized effect on mandibular shape.

As is any bone, the mandible is subject to remodeling based on mechanical stress, changes in functional patterns. But, being male and female differences located on non-mechanical mandibular point, sexual divergence in morphological form of the mandible in *T. swinderianus* can be explained only by changes in some of those specific mandibular morphogenetic units rather than the development of musculature.

On the basis of our findings, we can conclude that differences in both sexes *T. swinderianus* are not due to a functional cause, as masticatory behaviour would be.

Table 1. Nine landmarks studied on lateral view of each mandible for *Thryonomys swinderianus*

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

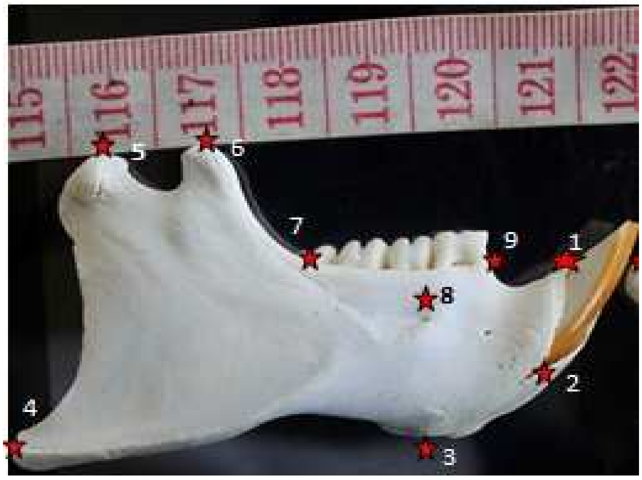

Figure 1.Right lateral mandible view of *Thryonomys swinderianus* with 9 landmark points. Numbers correspond to definitions in Table 1

Table 2. Principal Component Coefficients for Principal Component 1 (PC1) and 2 (PC2)for mandibles of *Thryonomys swinderianus*(n=21, 11 males and 10 females).PC1+PC2=53.96+26.48%. Procrustes which explained most of the differences (>[0.2]) appear in bold

	PC1	PC2
x1	-0.16242	-0.06677
y1	-0.05365	0.11176
x2	**-0.30982**	**0.28324**
y2	**-0.20138**	**0.37258**
x3	0.11697	**-0.48605**
y3	0.18244	-0.15865
x4	0.01878	-0.11949
y4	0.03000	0.10287
x5	0.00637	-0.13877
y5	-0.00704	-0.06604
x6	**-0.28348**	**0.42318**
y6	0.07881	-0.17794
x7	-0.08623	-0.18891
y7	0.01214	-0.00238
x8	**0.81374**	**0.40464**
y8	-0.10930	-0.17768
x9	-0.11395	-0.11109
y9	0.06795	-0.00454

Table 3. Average shape for *T. swinderianus* (n=21, 11 males and 10 females). Procrustes which explained most of the differences in PCA appear in bold

	Males		Females	
Lmk.	Axis 1 (x)	Axis 2 (y)	Axis 1 (x)	Axis 2 (y)
1	0.3314	0.0810	0.3446	0.0803
2	**0.3492**	**-0.0684**	**0.3590**	**-0.0697**
3	**0.1799**	-0.1896	**0.1796**	-0.1919
4	-0.4902	-0.2719	-0.4860	-0.2715
5	-0.4123	0.1609	-0.4134	0.1587
6	**-0.2397**	0.1817	**-0.2397**	0.1829
7	-0.0941	0.0499	-0.0818	0.0508
8	**0.1668**	**-0.0147**	**0.1207**	**-0.0039**
9	0.2090	0.0713	0.2171	0.0642

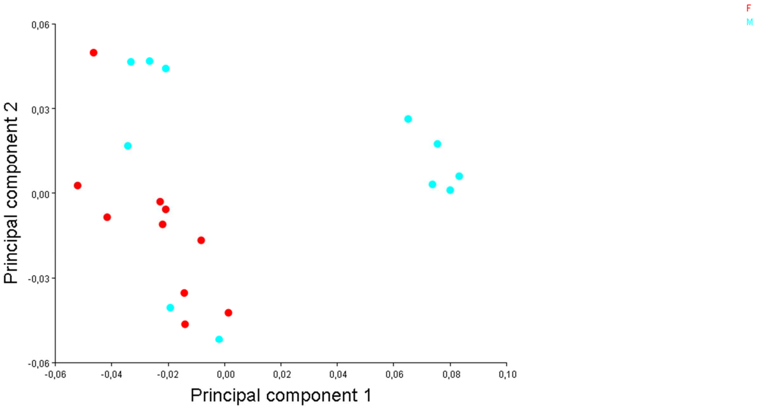

Figure 2. Principal Component Analysis for males and females of*Thryonomys swinderianus*(n=21, 11 males and 10 females). First two Principal Components in PCA explained a 80.44% of the total observed variance (PC1+PC2=53.96+26.48%). In the morphometric space described, both species were significantly distinguished from each other (p<0.001). It must be acknowledged that malespecimens are more widely distributed on the first plane of the PCA than the females

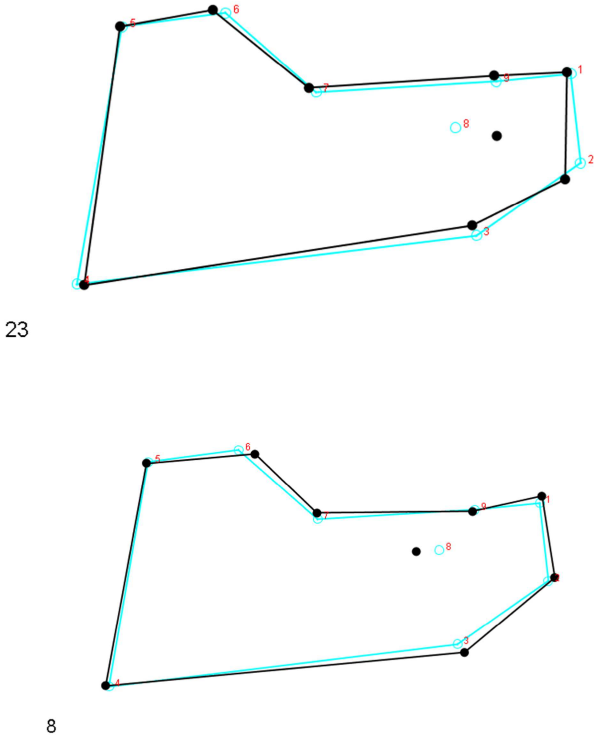

Figure 3. Plotting for each gender (extreme specimens 23 and 8) of *Thryonomys swinderianus*(male above; female below).Set of lines connecting the empty points on a shape represent the average data (males and females). Main differences between genderswere observed on ventral point of first incisor alveolus (2),ventral point of mental foramen on mandible body (3), mental foramen (8) and the condylar ramus (6).In males the ventral point of first incisor alveolustended to be more cranial and ventral point of mental foramen on mandible body more ventral, whereas mental foramen presented the presented a caudal displacement in females

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