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ISSN : 2348-1935

RESEARCH ARTICLE

Annals of Experimental Biology
2015, 3 (2):21-30

Geometric morphometrics of the skull of two African rodents, *Thryonomys swinderianus* and *Cricetomys gambianus*

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(Received: 09/07/15) *(Accepted: 05/08/15)*

ABSTRACT

Greater cane (Thryonomys swinderianus) and African giant pouched rats (Cricetomys gambianus) have sympatric ecological relations and identical body conformation characteristic, and inhabit similar ecological biome and sometimes synergize seasonal activities across species. The introduction of new variants due to genetic biodiversities and migrations as well as age related skull ambiguities has necessitated a survey of craniometrical data. For a geometric morphometric comparison, ten dorsal, ten lateral and fifteen ventral skull landmarks points landmarks were used. The study concluded that species with low leverage, long skulls and low mandible moment points utilize animal resources in diet and postulates utility of assessed parameters are important for home range exploration and diet partitioning, new colonization process, communication, tracking, trafficking, defense and sexuality signals; it also suggests the observed plasticity may be due to newer variants or an index of fauna quality, such data will be useful in solving phylogenetic difficulties, wildlife surveillance in age-population control, ration formulation in captive species, and eco-migration.

Key words: *Nesomydae*, *Thryonomydae*, morphometry, craniofacial, comparative craniometry

INTRODUCTION

African giant pouched rat (*Cricetomys gambianus*) and the greater cane rat or African cane rat (*Thryonomys swinderianus*) are two separated along family lines *Nesomydae* and *Thryonomydae* respectively. Ecological separation and home range overlaps exist as they share and interact in conflict or competitively but not necessarily exploitatively within territory limits [1, 2]. Rapidly extending geographic distribution of the species has been observed in areas otherwise not reported; especially islands and landlocked enclaves [3, 4, 5]. Liberian coast in the west to east African countries such as Kenya, Tanzania, and Gabon and has been reported in the South African enclave [1, 6]. The rodents share certain body conformation similarities (adults of *C. gambianus* and *T. swinderianus* weigh between 5-8kg and 3-5.8kg respectively irrespective of gender bias), ecological biome, habitat, diet, certain aspects of prehension and mastication [7]. Sub-Saharan African rodent types form an important link in maintaining the ecosystem; as natural resource, while contributing to a genetic biodiversity with utility in genetic surveillance of extant types. Further attestation to their relevance includes an economic value which derives from use as explosives sentinels, emerging alternative meat protein source, disease epidemiology in transmission of ebola virus and such invasive threats they pose to root crops [7, 8] in farms and barns.

Previous studies on the cranial morphology of rodents and similar species include those on mole rat [9], mink [10], rabbit [11], beaver [12], and [13] evaluated *C. gambianus.* The paucity of literary information on the comparative cranio-macro morphology and spatial interactive determinant indices between these two closely related rodents

justifies a necessity for this investigation. Relevant data obtained will be useful in bridging knowledge gap in anthropologic surveys, invasive species control, preservation, conservation through systematic population balance maintenance. The objective of the study was to compare certain inter-species dimorphic variations in the macro anatomy of skull morphology of both species which may be useful in solving taxonomic challenges.

MATERIALS AND METHODS

Two separate samples of *T. swinderianus* (n=25) and *C. gambianus* (n=25) were used. Each was comprised of 12 males and 13 females collected from a village locality in southwestern Nigeria between January to March and between July to October of year. The heads were macerated using procedures described by [14].

Pictures of skull parts were taken with a digital camera, Canon EOS1200D (Canon Inc. Tokyo Japan) equipped with EFS 18-58mm telephoto and Hama tripod with stabilizer on dorsal, ventral, right and left lateral views with two ruler points included non- biological landmark as the last two marks to scale for size. 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 for the dorsal, right lateral, ventral views of cranium were 10, 14, 13 and 9 in number respectively (Table 1). These landmarks were considered to define overall cranium shape. Specimens were aligned using Procrustes superimposition with the software TPSRelw v. 1.41 [15] which provided the consensus configuration of mean shapes. Thin Plate Spline functions were interpolated for deriving the uniform and non-uniform components of shape change, Partial Warp scores were calculated for describing the differences between each specimen (α=0). The relative warps (RW's) summarize the original variance of both samples and describes major trends in shape change [16, 17]. Principal component analysis methodology was used in assessing and interpretation of cranial morpho-space in the two species and in making inferences on phylogenetic, ecological and dietary dispositions within and between populations. Principal strain maps were computed (Thin-Plate spline) with area of highest strain (red color), medium and lowest strains in yellow and blue colors respectively

Ethic statement

The investigation did not involve endangered or protected species. No animal was sacrificed with intent for the purpose of investigation. 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

The relative warp analysis for the 10 landmarks describing the dorsal skull shape yielded 18 RW scores in both species of the present study. The first three principal components jointly contributed about 86% of the total variance in *T. swinderianus* but only the first two made up 97% in *C. gambianus* while the rest represented minor taxa related morphological differences.

Figure 1c illustrates the TPS of both dorsal skull typologies showing the inter-species expansion factors and the principal strains of skull shape change (in red) being mostly in the dorso-caudal direction in the neuro-cranium in *T. swinderianus* while the direction of shape change is in a ventro-caudal direction of the neuro-cranium in *C. gambianus* and produces more strain of shape changes. Deep vaulted cranial, bowed zygoma and shortened facial bones is observed in *T. swinderianus* but an elongated crania and facial bones, long zygoma with less pronounced infra-orbital foramen as shown by the TPS diagram in Figs 1c and 2c. The x-axis comparison in Figs. 1d and 2d displays little simmilarity in a reverse in scores situation in both species. The second RW (Figs. 1d and 2d) upper y-axis sharply discriminate morphological differences between the studied species with a lowest negative projections scores in *T. swinderianus*. Lower y-axis representing the second PC (Figs. 1d and 2d) further separates between the rodent species despite phylogenic proximity, the TPS diagram confirmed that *T. swinderianus* possess a deeper rostrum, a more anterio-ventrally oriented orbit whereas *C. gambianus* has a more caudally displaced orbital rim (Figs. 3d and 4d), most expansion factors and prncipal strains of skull morphology shape change occurs in the dorsal frontal bones in *T. swinderianus* but at the palatine and maxillary level ventrally (in red) in *C. gambianus* (Fig. 2c).

Ventral skull morphology- The landmarks assessed for ventral skull shape in *T. swinderianus* yielded 19 relative warps; the first five had significant eigenvalues contributing about 98% of the total variance while homologous landmarks in *C. gambianus* yielded 12 relative warps; the first five contributed approximately 100% of the total variance (see supporting information). Figure 3b visualized the vectors of skull shape deformation for the morpho-space defined by the first principal component (PC1). Significant scores correlation on the warps and centroid size between both species indicates allometric changes may not be exclusively responsible for the pattern of shape differences observed in the ventral surface of both skull types. The first principal component score and the scatter

plot discriminated both species on feeding basis before phylogenic proximities, both scored negatively on the first relative warps but to a greater extent in cane rats, Fig.3c also included a TPS showing a pattern of landmark displacement depicting a more concave and stout ventral surface in the more negative RW scores compared to *C. gambianus* ventral skull surface TPS. Finally, there exists a medially vaulted calvaria short rostrum and a bowed zygomatic arch in *T. swinderianus* relative to *C. gambianus* while a multivariate allometry assessment revealed a significant percentage component variation of 97.40% and 2.40% (*T. swinderianus* and *C. gambianus* respectively) in PC1.

DISCUSSION

Morpho-craniometric variation studies of African Giant Rat and the greater Cane Rat skull bones made it possible to determine species-specific skull and mandible characteristics. Seasonal activities of the species may be monitored to demonstrate sex-species-specific population type encountered within moon cycles in any particular eco environment.

Literary information on comparative investigations on skull morphology of the *T. swinderianus* and *C. gambianus* is rare despite an abundance of similar works in other rodent species: rodents [9, 10, 13], minks [18] and largomorphs [19].

Comparatively compact cheek teeth and surface for *M. pterygoideus lateralis* muscle in *T. swinderianus* is a discriminant factor of adaptation which favors fibrous diet type during the drier seasons compared to a reverse in *C. gambianus* mandibles Fig. 4e where PC1 alone made up 99% of its total variance where feeding habit was a subsidiary consideration to strong phylogenic *Cricetidae* family character evidenced by a more profound genealogic constraint in the species [20, 5]. A more highly placed and posteriorly oriented coronoid process relative to the articular condyle in *C. gambianus* is similar to ruminant's mandible [21] 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 [20] in some members of *Heteromydae* family [5].

Comparative skull data analyses derived from the present study revealed the nasal, frontal, premaxilla, and maxilla, and zygomatic bones exhibited remarkable morphologic variations between and within species. These results suggest that cranio-dental morphology may be used to infer extinct rodent diets [5, 12].

In comparing diet in these rodents, [1, 22] reported that 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 diet such as *Austrophia spp.* (spear grass), *Pennisetum purpureum* (elephant grass) and *Saccharum spp.* (sugar cane). This fact is postulated to contribute to the characteristics of some skull 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 [2, 23] 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 dental space length in *T. swinderianus* was found shortened compared to the *C. gambianus* and may be an adaptation for their diverse method of prehension, mastication and deglutition [6, 23]. Similar maxillo-dental construction obtains in both rodents, but larger sized in *T. swinderianus*; as partial adaptation for vigorous horizontal snapping movements of the head; thus resulting in differing specific alterations in morphological proportions of the skull and jaw. Fatalities resulting from brief occasional interactions between both species favor cane rats more often by means of such differences. Numerical increase in the presence of such adults is precursor of formation of new colonies and relocation of *C. gambianus spp.* [19, 22].

Though genetically related, both rodent species of the same superfamily do not crossbreed [1]. adaptive divergence revealed by the analyses of cranial variations in *T. swinderianus* and *C. gambianus waterhouse* demonstrated that highest coefficient of variations in *T. swinderianus* males occurred in neuro-cranial, orbital and nasal bone varied most in females. Investigations on cranial parameters in *C. gambianus* males revealed highest coefficient of variations in zygomatic and orbital regions observed higher and longer with a high relative warp coefficient in *C. gambianus* (male and females), a character associated with nocturnal ecology [13] despite its skull length compared to values obtained in *T. swinderianus* [18, 24, 25]. This phenotypic plasticity observed to be in agreement with [5] has been noted a substrate in evolutionary change in rodents.

Inference from the presented data observed a shortening of nasal bone length in *T. swinderianus* contributing to the exceptionally large infra orbital foramen observed in all specimens studied in that species. The skull in *C.*

gambianus has a high coefficient of variation and is suggested to contribute to the observed occipital area morphologic variations encountered [12, 18, 14, 21] and may give insight to age estimation in this rodent.

The skull height and length of the *T. swinderianus* was found longer compared to *C. gambianus,* a lower profile and gradient of the *C. gambianus* skull is suggested to be an eco-adaptation which is proposed to permits survival from predators in burrows for quick getaways from within narrow tunnels, a character not seen in *T. swinderianus* a more diurnal species. There is a shortening of the neuro-cranium with a concomitant negative correlation of extension of the viscero-cranium in *T. swinderianus*. A reverse of this observation existed in *C. gambianus*; this is speculated to be a characterizing index in regional population surveys for adequate taxonomy [5].

A comparison of the mean values of each variable assessed in both females and males in individual separate species identified significant differences and variations in neuro-cranial and skull sizes as between the species.

The greater cane rat has a generally globular skull morphology demonstrated by a larger index (skull height/width x 100) of 46.97% with a remarkably shorter (and arched maxilla) incisor to premolar distance compared to the more elongated skulls of the giant rat with a shorter value of 28.41%. This representation unlike in another rodent type and the rabbit [11] is the contribution of the curvature gradient of the nasal bone in the *C. gambianus* being less so than the *T. swinderianus* where it is shorter. The proximity to the olfactory neuro-epithelium is enhanced with the more forward displacement of the cribriform plates by the ethmoid bone in the latter specie (not included in the present study), thereby permitting a larger surface access of air to the neuro-epithelia filaments of the olfactory nerves cells- an attribute found utilizable in land mine detection [27], an essence in breeding as well as an adaptation for movement in light- subdued environments while residing in deep tunnels below surface [7, 13].

The *os incisivum* in the adult *T. swinderianus* is short and stout terminating in the alveolar sockets of the incisors on both sides; suggesting a stronger prehension and bite force of the cranium [28] corroborated by the zygomatic process (Fig. 3b) which is more bowed in this specie as it utilizes more fibrous plant diet than the giant rat and gives more surface for the attachment of the *m. temporalis* muscle [29, 30]. This bone, (incisive) is highly indented and grooved in *T. swinderianus* for lodgment of infraorbital nerve and vessels [27]. The study of skull typology of this species is relevant in craniometric paleontology, phylo-geography and tracking of eco-migrant species in wildlife conservation techniques [13, 19, 26].

In conclusion, comparative studies on skull typology of both rodents are relevant in phylogenetic investigations, domestication and diet research. In prolonged drought young *C. gambianus* species becomes exposed to risks of predators and as well contribute to economic losses in homes and farms, whereas the *T. swinderianus* lays in thickets most nights and relies on adipose reserves, it selectively ventures out during this period with comparatively less dietary challenges [1, 5, 6] body weight therefore remains relatively constant. Knowledge of craniometric and mandibular relationship of these species represented in the present investigation may be valuable in rodent taxonomic ambiguity [21, 23, 26] and localization. Sustained temperature deviations in weather events are also postulated to trigger deadly and population threatening interactions during roaming [25].

Species population density often determined by abundance and otherwise of favorable ecological conditions making inter-specific contacts more likely in moonlight of scarce food periods [2, 5, 12]. Tolerance among colonies is speculated to exceed territorial space among older males; more in the *C. gambianus* who dictates or charts new paths in the *fadamas* (dry straw irrigated grasslands in the dry seasons) for others [2, 8, 31]. The results of this study of both species taken from the location (fig. 5) exposed variations in some craniometric indices between *T. swinderianus* and *C. gambianus* species. These variations may be used for inter-specific contacts, diet, vocalization recognition studies [19, 21], ecoadaptation as well in weather phenomenon-driven species character change monitoring [5], and they may also find utility in head restraint designs for medication in wildlife management [7, 12].

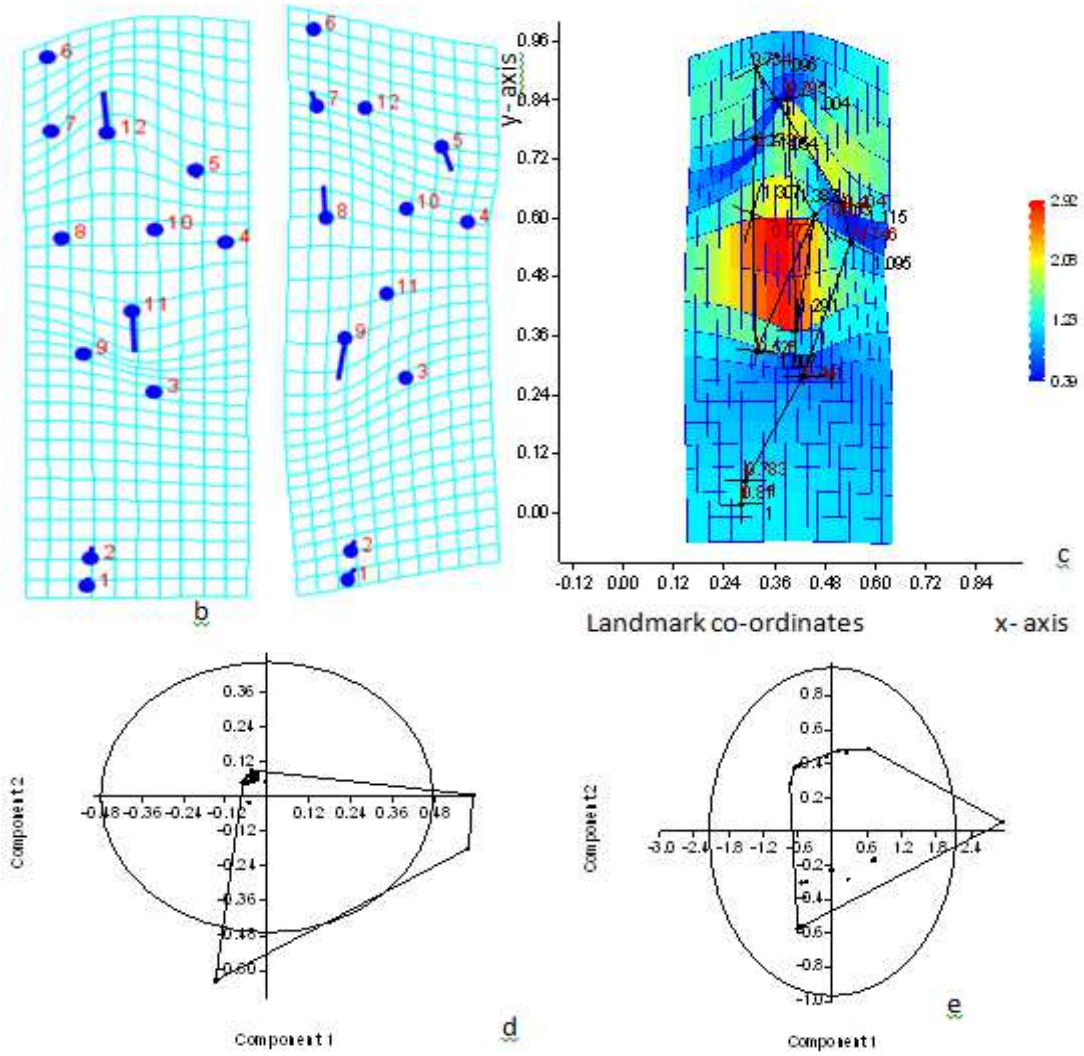


Figure 1b, c, d and e. (b) shows the shape changes associated with PC1 and PC2 using the Procrustes coordinates of landmarks on the skull of *T. swinderianus* and *C. gambianus* shape transformation grid showing principal components of shape change (PC1 and 2), (c) Mean Thin-plate Splines and Warps of dorsal view of *T. swinderianus* and *C. gambianus* with landmark links, principal strains (x, y) values and expansion factors color code (red=highest strain value of shape change and blue =lowest strain of shape change or contraction) (d and e) PCA scatter diagrams with convex hulls and 95% ellipses (PC1 and PC2 = x, y axis respectively) percentage variation in PC1 and PC2 is 37.57%, 36.24% and 74.03% and 15.15% for *T. swinderianus* and *C. gambianus* respectively.

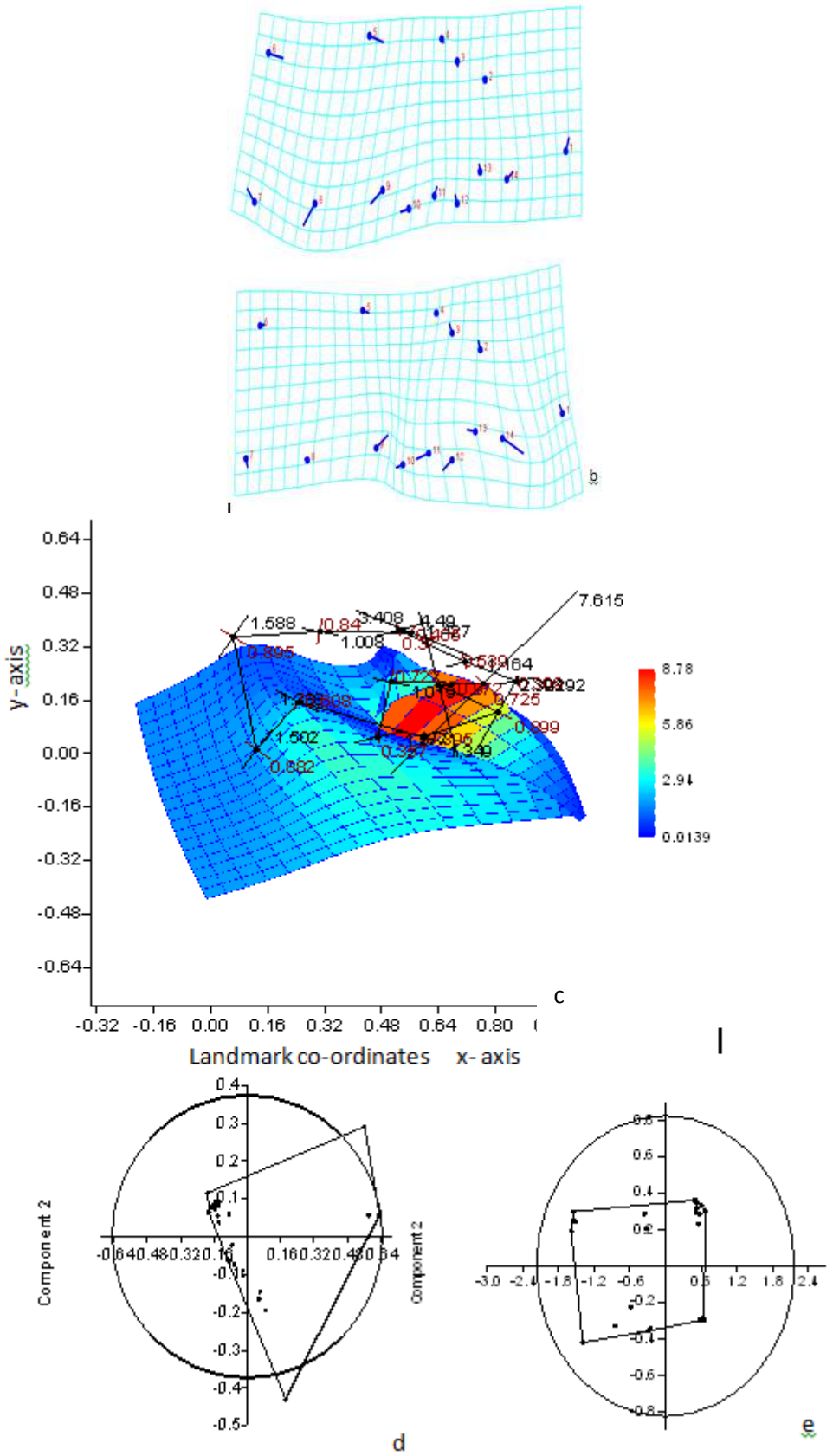


Figure 2b, c, d and e. (b) shows the shape changes associated with PC1 and PC2 using the Procrustes coordinates of landmarks on the skull of *T. swinderianus* and *C. gambianus* shape transformation grid showing principal components of shape change (PC1 and 2), (c)Mean Lateral Thin-plate Splines shape and Warps of lateral view of *T. swinderianus* and *C. gambianus* with landmark links, principal strains (x, y) values and expansion factors color code (red=highest strain value of shape change and blue =lowest strain of shape change) (d and e) PCA scatter diagrams with convex hull and 95% ellipses (PC1 and PC2= x, y axis respectively) percentage variation in PC1 and PC2 is 43.29%, 14.38% and 77.39% and 11.14% for *T. swinderianus* and *C. gambianus* respectively.

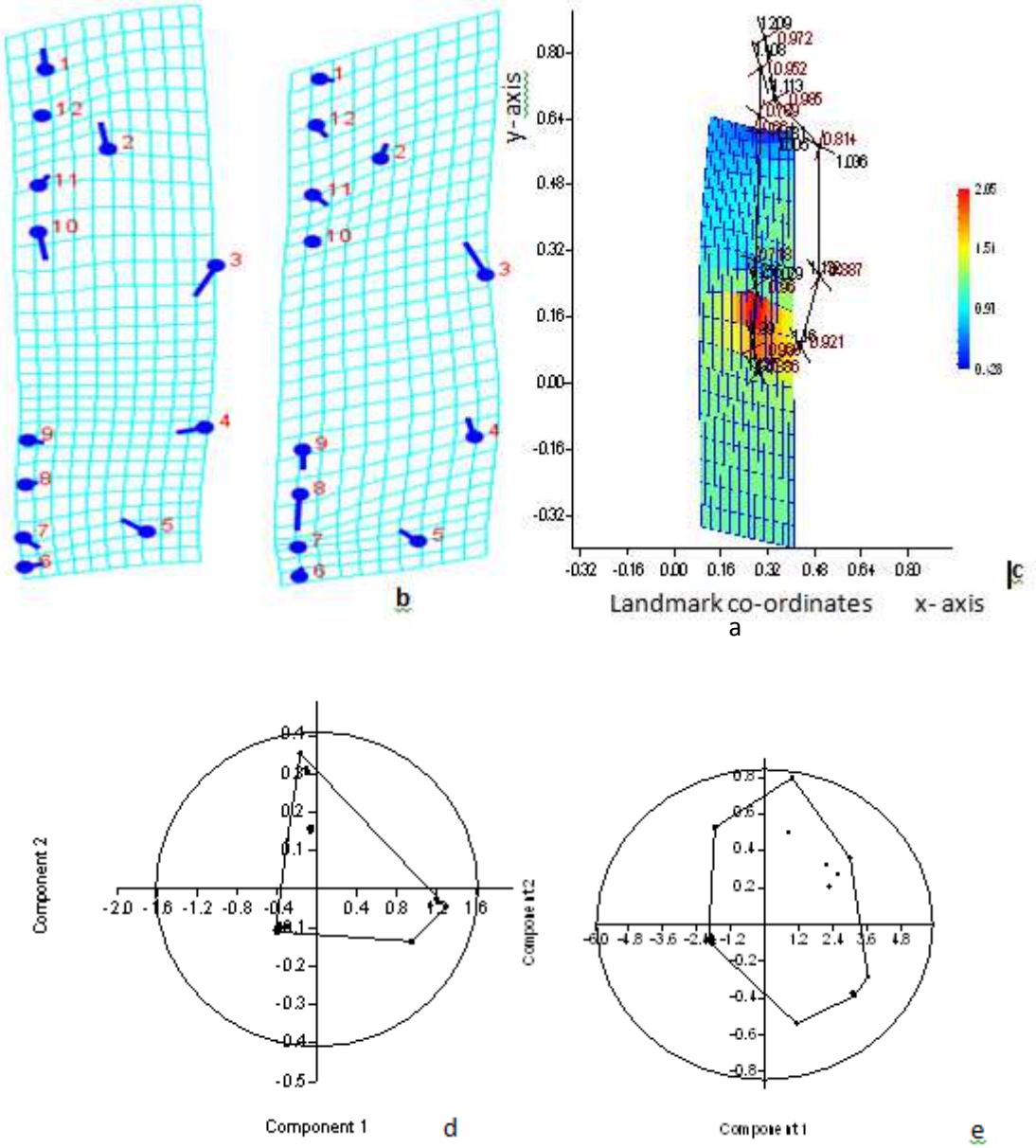
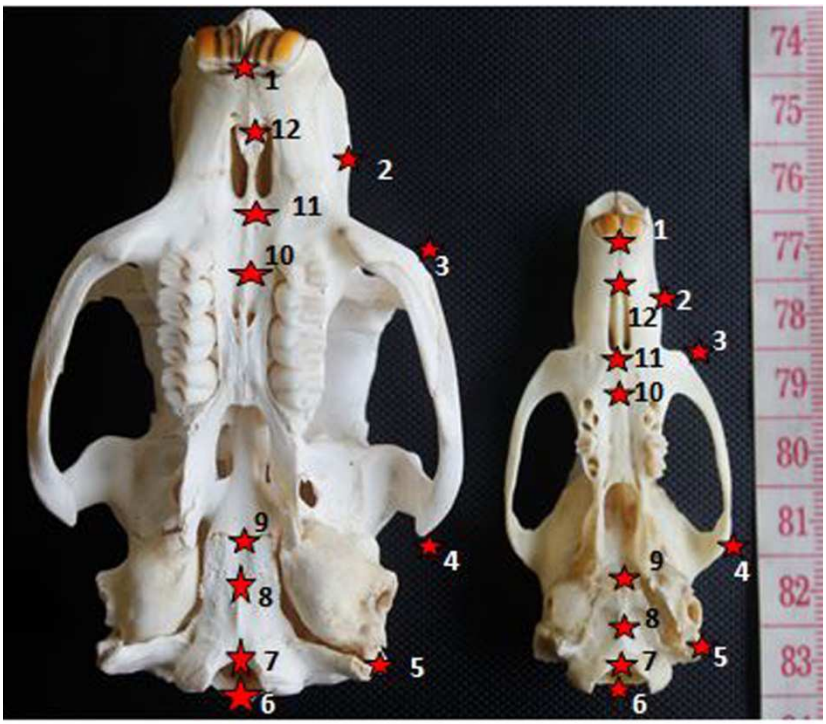
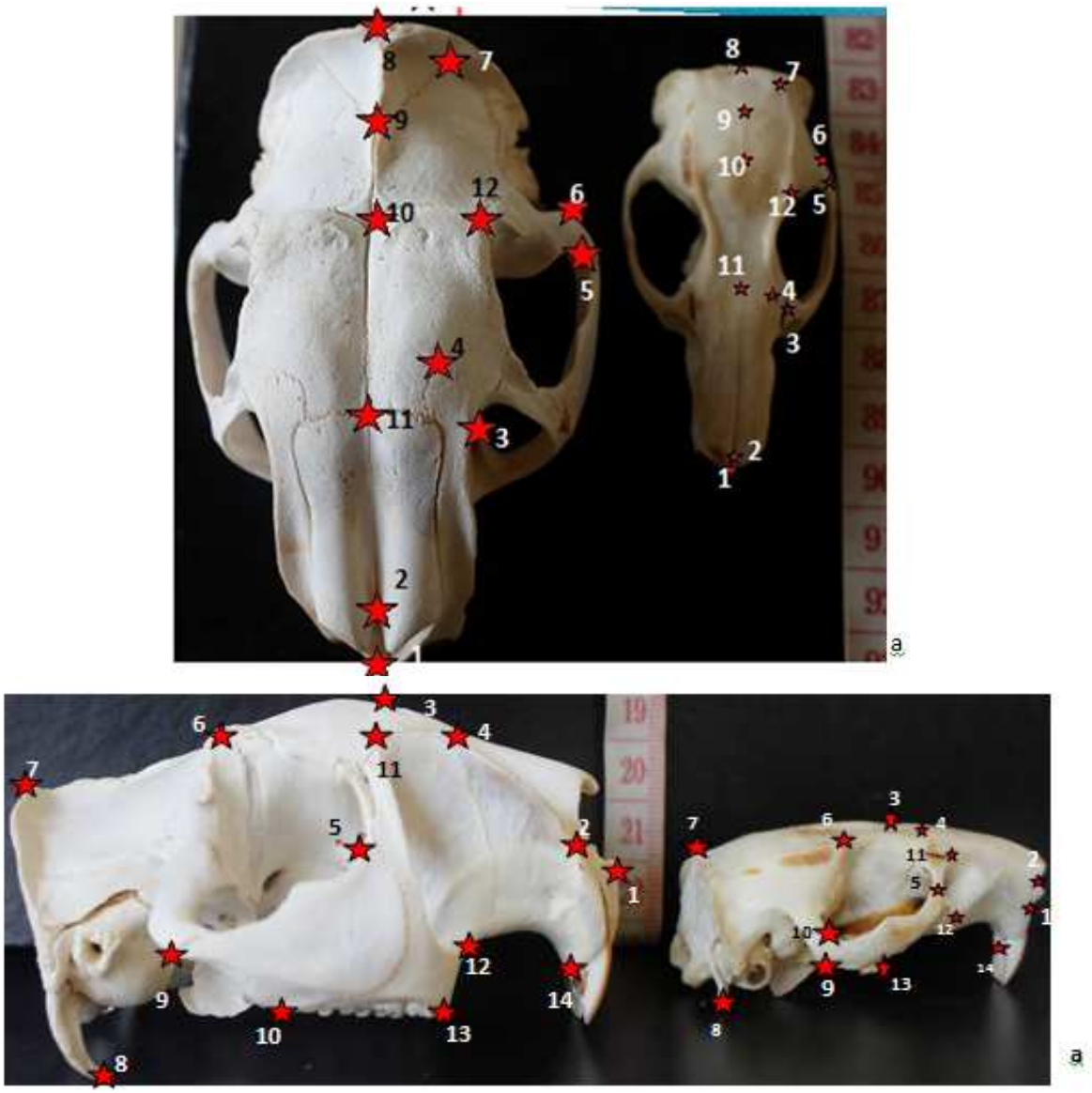


Figure 3b, c, d and e. (b) shows the shape changes associated with PC1 and PC2 using the Procrustes coordinates of landmarks on the skull of *T. swinderianus* and *C. gambianus* shape transformation grid showing principal components of shape change (PC1 and 2), (c) Mean ventral skull Thin-plate Splines shape and Warps of ventral view of *T. swinderianus* and *C. gambianus* with landmark links, principal strains (x, y) values and expansion factors color code (red=highest strain value of shape change and blue =lowest strain of shape change or contraction) (d and e) PCA scatter diagrams with convex hull and 95% ellipses (PC1 and PC2= x, y axis respectively) percentage variation in PC1 and PC2 is 93.30%, 5.96% and 97.92% and 1.95% for *T. swinderianus* and *C. gambianus* respectively.

Table 1. Landmarks on dorsal, lateral and ventral views of skulls. See images above.

Landmark no.	Dorsal view	Lateral view	Ventral view
1	rostral extremity of nasal bone	the most anterior point of premaxilla	caudal limit of the incisive alveolus
2	anterior-most of suture between the nasals and premaxillary	antero-lateral point of nasal bone with premaxilla	suture between the premaxillary and maxillary in the ventral photographic plane
3	suture between the premaxillary, maxillary and frontal	suture between nasal and frontal	intersection between the premolar and maxillary bone in the ventral view
4	dorsal point on the fronto-maxillary suture	suture between incisive and maxilla	suture between the maxillary and zygoma
5	on the suture between the zygomatic and temporal bone	the extent of frontal process of zygoma	tip of jugal process
6	caudal limit of the zygoma	lateral limit of fronto-parietal suture	tip of jugular process
7	occipito-parietal suture in the dorsal plane	occipital protuberance	most posterior point of foramen magnum
8	the external occipital protuberance	the jugular process point ventrally	most anterior point of foramen magnum
9	frontal bone suture on junction of the bilateral parieto-frontal suture	the zygomatic process intersection with the zygomatic process of the temporal bone	suture of basi-sphenoid, basi-occipital and tympanic bulla
10	sutural junction of nasal bone with the frontal bone	frontal process of the zygoma ventrally	suture of the pre-sphenoid and basi-sphenoid in the median plane
11		the most dorsal point of the infra-orbital foramen	most caudal limit of the incisive foramen
12		the base of the infra orbital foramen	most caudal limit of incisive foramen
13		caudal limit of dental space before the first premolar	most anterior point of the incisive foramen
14		anterior limit of dental space on the first incisor teeth	





Acknowledgements
This investigation was collaboratory in nature, carried out by departments of Veterinary Anatomy of three institutions mentioned above. We therefore acknowledge the effort of Professor S.K. Onwuka, head of Anatomy University of Ibadan who authorized the use of facilities employed for this work M.O Akpan assisted in the acquisition of African Cane rat skulls.

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