Australian Journal of Basic and Applied Sciences, 4(9): 4323-4335, 2010
ISSN 1991-8178

# Sexual Dimorphism and Morphological Disparity in the Shapes and Sizes of the Cranium, Scapula, Mandible and Pelvis of Selected Murid Rodents

[1]Mark Anthony J. Torres, [2]Roxan Eupeña and [1]Cesar G. Demayo

[1]Department of Biological Sciences College of Science and Mathematics MSU-Iligan Institute of Technology Iligan City

**Abstract:** The sex of a captured rodent is usually determined based on external features only such as the presence of testes and teats in mature males and females, respectively, posing impediments in the identification of the sex of specimens based on some skeletal elements. Recent advances in geometric morphometrics (GM) and multivariate analyses can help remedy the discrepancy. Thus, this study was conducted to observe, describe and compare the differences in the shapes and sizes of the cranium, scapula, pelvis, mandible and between sexes among the four species of murid rodents, namely: *Mus musculus* Linnaeus, *Rattus argentiventer* Robinson and Kloss, *R. norvigicus* Berkenhaut, and *R. rattus mindanensis* Mearns. Results show that the magnitude of sexual dimorphism with regards to the shape of the skeletal elements differs among species - the largest between the sexes of *R. r. mindanensis*. However, subtle differences in sizes can be seen among the species. Shape disparity between the females of *R. r. mindanensis* and *R. argentiventer* is large and is observed to be a function of differences in the shape of the cranium as seen from the lateral and dorsal orientations, pelvis, and scapula. However, differences can also be observed between the males of these species with regards to the shapes of the scapula with only subtle disparity in the shapes of the mandible. The females of these species differ in the size of the cranium when measured in both dorsal and ventral orientations. The results of the study underscore the need to incorporate GM methods in rodent taxonomy and in the identification of specific features rendering sexual dimorphism in murid rodents.

**Key words:** Murid, rodents, morphological shapes and sizes, geometric morphometrics, compromise space

## INTRODUCTION

The Philippines is home to at least 48 species of murid rodents (Heaney *et al.,* 1998; Stuart *et al*., 2007). Several of these species are of agricultural significance as they may be found living in and around ricefield ecosystems either as pest or beneficial vermivores that feed on invertebrate pests (Alfonso *et al.,* 1985; Vergara, 2001; Stuart *et al.,* 2007). Despite the growing number of papers describing species of murid rodents, their population ecology remains to be poorly understood (Heaney *et al*., 1998). Also, morphological resemblances between and among some species have caused confusion over the taxonomy and correct identification of pest species (Barbehenn *et al.,* 1973). For example, the close resemblance between *Rattus rattus mindanensis* Mearns and *R. argentiventer* Robinson and Kloss has caused much confusion among field workers in the Philippines so that, together with *R. r. umbriventer* Kellog, their names were used synonymously in the literature (Sanchez, 1977).

Knowledge of the true nature of rodent species may have a direct bearing on rodent control and should contribute to the formulation of better and more efficient control measures against pest species and at the same time enhance the diversity of beneficial vermivores. For example, different control strategies might be called for the control of two different destructive species as susceptibility to poisons as well as acceptance of baits are reported to vary among rodent pests (Sanchez, 1977). These subtle behavioral or physiological differences among target organisms may mean the success or failure in a control operation.

Thus, ecological and toxicological research for control methodology must be geared towards the lowest taxon for meaningful results. Despite the overwhelming need to know the true nature of the species important in agricultural systems, classical morphology-based rodent taxonomy still suffers from several important

---

**Corresponding Author:** Mark Anthony J. Torres, Department of Biological Sciences College of Science and Mathematics MSU-Iligan Institute of Technology Iligan City

problems. These include, among others, the difficulties in defining species boundaries because of the existence of overlaps in intra- and interspecific character variations. Comparisons of the characters of specimens providing the basis of their nomenclature and description are sometimes based on qualitative descriptions of the shapes of biological forms scoring the need for a natural approach in defining continuous change of shape in metrical terms that measures the difference between two regions.

The advent of geometric morphometrics (GM) was seminal in the improvement of shape quantification and found many applications in biodiversity studies (Loy *et al*., 1993; Adams and Rohlf, 2000; Douglas *et al.*, 2001). An important aspect of geometric morphometrics is the analysis of data in the form of 2-dimensional or 3-dimensional morphological landmarks digitized from images of biological specimens (Douglas, 1993; Douglas *et al*., 2001). However, most of the GM studies are concerned only with the analysis of a single character. However, the various characters of a species may and usually do vary independently such that operational taxonomic units (OTUs) agree, in some characters and differ in others. Recently, an approach was developed which could determine associations between and among OTUs by calculating intergroup similarity averaged over multiple data sets, and can be used in the assessment of the overall similarity among the species (Márquez and Knowles, 2008).

This study was conducted to gain further insight into the differences within, between and among the four species of rodents using the method of geometric morphometrics and study associations among them based on an assessment of multiple multivariate shape and size data sets. Taxonomic problems often stem-out from observations regarding the nature of character variation in organisms whereby infra-specific variability may often be greater than interspecific disparity resulting from large discrepancies in the characters between sexes. Thus, this study was also conducted to determine sexual dimorphism with regards to the shapes and sizes of the cranium, scapula, mandible and pelvis of the four rodent species.

The study was conducted from June 2007 to February 2008 at the genetics and Evolutionary Biology Laboratory, Department of Biological Sciences, College of Science and Mathematics, MSU-Iligan Institute of Technology, Iligan City.

## MATERIALS AND METHODS

A total of 53 samples of the rodents were used in this study. The rats were collected using a mousetrap and Sherman live traps. These traps were placed near ground holes, fallen logs, bamboo clumps, openings of the root systems of huge trees and stumps, overlying branches of trees and palms above the ground and along runways. The mice samples were purchased from a pet shop. After euthanasia, the rodents were skinned and the crania were removed and cleaned.

The samples were identified up to species level using the online key on the "Non-flying Mammals of Mindanao Island, Philippines" by Heaney *et al* (1998). Rat morphometrics, external features and information on sex and reproductive status were also taken. All of these are important aids for the identification of each rat species. While in the field, specimens were preserved using 10% buffered formalin. In the lab, samples were skinned and the flesh removed using a scalpel and dissecting needle. The specimens were then soaked overnight in a detergent and bleached by soaking them in an approximately 3% to 6% solution of hydrogen peroxide for about 45 minutes and then allowed to dry completely.

### *Geometric Morphometric (Gm) Analysis:*

*Image acquisition, landmark assignment and coordinate data.* The cranium, mandible, scapula and pelvic girdle of the rodent samples were scanned and digitized at different orientations using a Hewlett Packard flatbed scanner model 2400 at a resolution of 1200 vertical and horizontal dpi. Several landmarks were assigned to the prominent features of the specimens (Figs.1to7). The ScionImage software (http://www.scioncorp.com) was used to generate the x and y coordinates of the landmark points.

Size data. Sizes of the skeletal elements were approximated via Euclidean Distance matrix Analysis (EDMA) of the landmark data which measured all possible chords between landmarks just as if these linear distances have been painstakingly recorded using calipers (Fig. 8). The analysis is simple and not radically different from traditional morphometric approaches. The CORIANDIS ver. 1.1. Beta (Marquez & Knowles, 2007) was used to determine associations between sexes among the species of rodents as defined by the different multivariate data (consisting of 11 landmark and 11 inter-landmark data sets). First, non-metric multidimensional scaling (MDS) was performed on the matrix of Euclidean distances obtained for each of the data sets where intergroup distances in the matrix were used to obtain configuration of points, corresponding to the different sexes per species, in two dimensions, so that the Euclidean distances among these points approximate the distances in the original matrix. Then, a "compromise" is built reflecting the structure of the intergroup similarity averaged over the different data sets, plotted in two dimensions and used in the assessment of the overall similarity among the species of rodents. Weights were applied to each trait prior to computing the compromise. Weights were chosen so that the traits that are most congruent with other traits have a large influence on the computation of the compromise than traits that are too different from the rest. Then, the squared distances of each group to the origin are computed for each of the 11 shape and 11 size data sets, and plotted in a stacked bar graph to give an overall impression of the differences between sexes among the four species of rodents. Visualization of shape differences. The extent and nature of sexual dimorphism of the shapes of the skeletal elements were examined in detail via Procrustes superimposition, a technique done to remove non-shape features of biological form related to scaling (variation in size), translation (variation in the position of the specimens on the scanner bed), and rotation (variation in the orientation of the specimen). In this approach, the landmark coordinates for all the specimens were superimposed, such that the fit between all the specimens is as close as possible. Reference configurations per skeletal element were computed for each of the sexes per species and established as the mean of the fitted landmark coordinates. Procrustes superimposition was performed using the PAST program by Hammer *et al.* (2002).

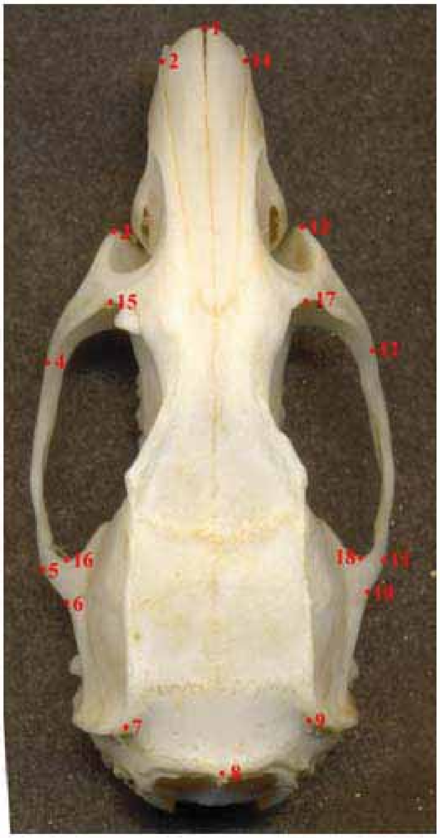

**Fig.1:** Landmarks used to describe the cranial shape (dorsal view) of rodents in geometric morphometric analyses. 1 = tip of the nasal at their anterior suture, 2 = most anterior point at left nasal-premaxillary suture, 3 = left anterior projection of zygoma, 4 = anterior left zygomatic arch, 5 = posterior left zygomatic arch, 6 = posterior inferior tip of squamosal root of left zygomatic bar, 7 = intersection of left parietal, interparietal and supraoccipital sutures, 8 = rearmost point of supraoccipital, 9 = intersection of right parietal, interparietal and supraoccipital sutures, 10 = posterior inferior tip of squamosal root of right zygomatic bar, 11 = posterior right zygomatic arch, 12 = anterior right zygomatic arch, 13 = Right anterior projection of zygoma, 14 = Most anterior point at right nasal-premaxillary suture, 15 = most anterior internal point of left zygomatic arch, 16 = most posterior internal point of left zygomatic arch, 17 = most anterior internal point of right zygomatic arch, 18 = most posterior internal point of right zygomatic arch.

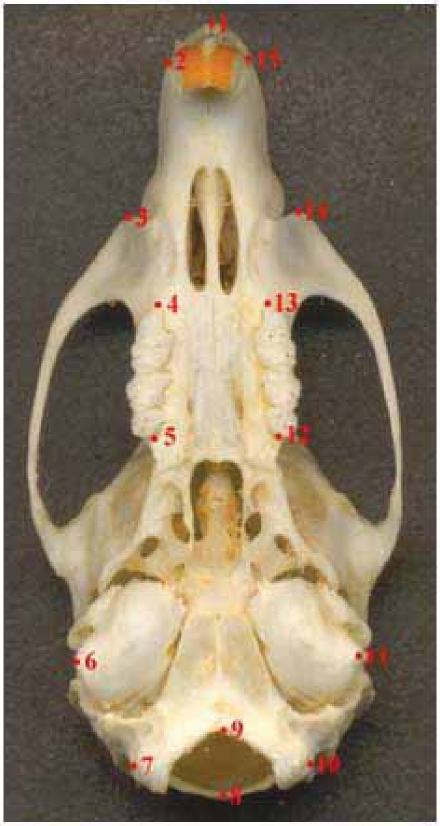

**Fig.2:** Landmarks used to describe the cranial shape (ventral view) of rodents in geometric morphometric analyses. 1= tip of the nasal at their anterior suture, 2 = anterior side most region of the incisor teeth, 3 = tip of the zygomatic plate, 4 = anterior margin of the 1st molar alveolus, 5 = posterior margin of the 3rd molar alveolus, 6 = anterior limit of external auditory meatus, 7 = lateral limit of the foramen magnum, 8 = posterior of the foramen magnum, 9 = anterior of the foramen magnum, 10= lateral limit of the foramen magnum, 11 = anterior limit of external auditory meatus, 12 = posterior margin of the 3rd molar alveolus, 13 = anterior margin of the 1st molar alveolus, 14 = tip of the zygomatic plate, 15 = anterior side most region of the incisor teeth.

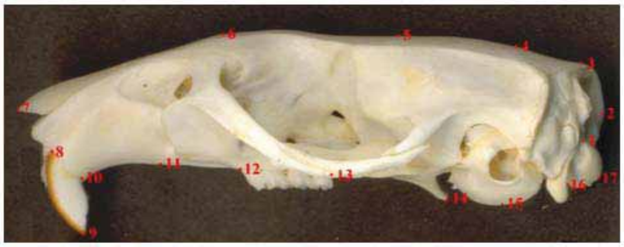

**Fig.3:** Landmarks used to describe the cranial shape (lateral view) of rodents in geometric morphometric analyses. 1 = upper part of the occipital condyle, 2 = point at the back of the skull over occipital, 3 = back of interparietal, 4= front of interparietal, 5 = front of parietal, 6 = frontal suture, 7 = anterior tip of the nasal, 8 = upper point of incisor, 9 = tip of the incisor, 10 = margin of the alveolus at the back of incisors, 11 = most curvature region between landmarks 10 and 12, 12 = front of the first molar, 13 = back of tooth row (over alveolus of last molar), 14 = tip of the pterygoid process, 15 = middle curvature region of the eustachian tube, 16 = lower part of the occipital condyle, 17 = middle most curvature point of the occipital condyle.

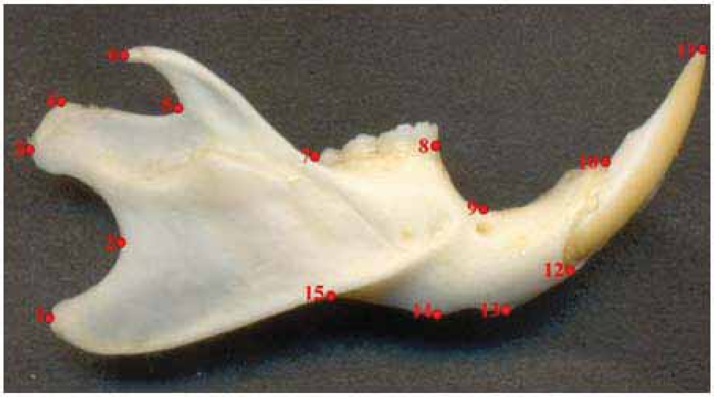

**Fig.4:** Landmarks used to describe the mandibular shape (lateral view) of rodents in geometric morphometric analyses. 1 = posterior extremity of the angular process, 2 = greatest curvature point between angular process and posterior tip of the condyle, 3 = posterior tip of the condyle, 4 = anterior tip of the condyle, 5 = incisura mandibulae , 6 = tip of the coronoid process, 7 = intersection of the dental ridge with the dorsal portion of the masseteric ridge (base of the coronoid process), 8 = anterior extremity of the maxillary toothrow (premolar alveolus), 9 = diastema, 10 = upper extreme anterior part of the incisor alveolus, 11 = tip of the incisor, 12 = lower extreme posterior part of the incisor alveolus, 13 = 1st protrusion of the horizontal ramus, 14 = 2nd protrusion of the horizontal ramus, 15 = intersection between the ascending ramus and alveolar process.

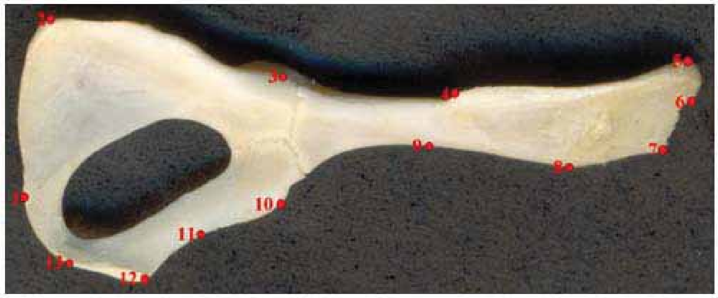

**Fig.5:** Landmarks used to describe the shape of the pelvis (medial orientation) of rodents in geometric morphometric analyses. 1 = ventral margin of the tuberosity of the ischium, 2 = dorsal margin of the tuberosity of the ischium, 3 = greatest curvature point near acetabulum area, 4 = posterior inferior spine of the ilium, 5 = dorsal margin of the crest of the ilium, 6 = anterior margin of the crest of the ilium, 7 = ventral margin of the crest of the ilium, 8 = curvature point near auricular surface, 9 = greatest depression on the body of the ilium, 10 = iliopectineal eminence, 11 = greatest depression between landmarks 11 and 12, 12 = pubic tubercle, 13 = greatest curvature on the ramus of the pubis.

## RESULTS AND DISCUSSION

Figure 9 is a plot of 8 clusters (stars), each corresponding to the two sexes per species. The locations of the species in the “compromise” space as indicated by the red dots reflect the overall similarity between them as implied by the 11 shape data sets. Likewise, the intra- and interspecific locations of the 11 data sets are indicated by the other colored points radiating from the “species” points in red.

The result shows a general tendency for the male and female members of *R. argitiventer*, *R. norvigicus* and *M. musculus* to cluster together implying minimal sexual dimorphism with regards to the 11 shape data sets. However, differences can be observed between the two sexes of *R. rattus mindanensis*.

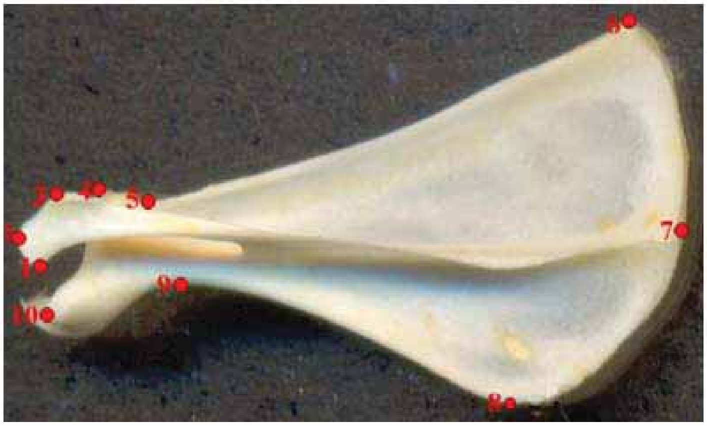

**Fig.6:** Landmarks used to describe the shape of the scapula (dorsal) of rodents in geometric morphometric analyses. 1 = dorsal end of acromio-clavicular articulation, 2 = ventral end of acromio-clavicular articulation, 3 = flexure marking the boundary between acromion and metacromion, 4 = dorsal end of glenoid fossa, 5 = depression between glenoid cavity and infraspinous fossa, 6 = tip of the axillary border, 7 = intersection of spine and vertebral border between infraspinous fossa, 8 = maximum curvature along anterior border, 9 = maximum curvature of the scapular notch, 10 = ventral end of glenoid fossa.

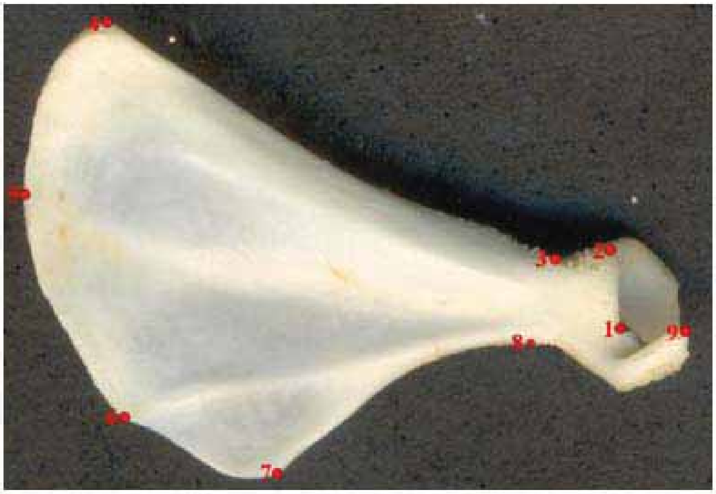

**Fig.7:** Landmarks used to describe the shape of the scapula (ventral) of rodents in geometric morphometric analyses. 1 = anterior extremity of glenoid cavity, 2 = posterior extremity of glenoid cavity, 3 = depression between glenoid cavity and infraspinous fossa, 4 = tip of the axillary border, 5 = intersection between scapular crest and posterior scapular border, 6 = intersection between scapular spine and scapular border between supraspinous and infraspinous fossa, 7 = maximum curvature along anterior border, 8 = maximum curvature of the scapular notch, 9 = coracoid process extremity.

The magnitude of sexual dimorphism with regards to the shape of the skeletal elements differs among the four species as shown in Figure 10. The total height of each bar results from the addition of the squared distances of each trait separately making it a measure of trait disparity. This chart can be interpreted as a decomposition of a species/sex distinctiveness from the other species/sex in terms of specific traits. Thus, the observed difference between sexes in *M. musculus* is largely a function of the shape of the dorsal left scapula and the pelvis. Specifically, males and females of this species differ in the shape of the posterior scapula border, and region between the pubic tubercle and ramus of the pubis (Figure 11).

For *R. argitiventer*, differences can be observed in the shape of the scapula (ventral view) and pelvis between males and females (Figure 10). Detailed comparison of the mean shapes of the skeletal elements in Figure 12 reveals that the differences can be observed with respect to the shape of the posterior scapular border and the region between the dorsal margin of the tuberosity of the ischium and the greatest curvature near the acetabulum area.

Minimal sex differences can be observed in *R. norvigicus* and seen as differences in the shapes of the scapula (ventral) and the pelvis based on the stacked bar graphs in Figure 10. However, the mean shapes of the cranium (lateral view) of the males and female samples examined showed differences with respect to the shape of the posterior part involving the tip of the incisor, tooth row, tip of the pterygoid process, and the occipital condyle (Figure 13). Minor differences can also be seen in the shapes of the posterior border of the scapula. *R. rattus mindanensis* exhibited the largest amount of sexual dimorphism. Males and females of this species show differences in the shape of the cranium, pelvis, and scapula. Of these, the two sexes differ largely on the shape of the cranium on the regions defined by landmarks 7 and 9 (point of intersection of the parietal, interparietal and supraoccipital sutures; dorsal view) and the upper point of incisor and lower part up to the middle most point of curvature of the occipital condyle (lateral view). Differences can also be observed with respect to the shape of the scapular border, and the region in the pelvis between the dorsal margin of the tuberosity of the ischium and the greatest point of curvature near acetabulum area and the ilium.

Shape disparity between the females of *R. r. mindanensis* and *R. argentiventer* is large and is observed to be a function of differences in the shape of the cranium as seen from the lateral and dorsal orientations, pelvis, and scapula. The former having a cranium similar in shape to that of the male and female specimens of *R. norvigicus.* However, differences can also be observed between the males of these species with regards to the shapes of the scapula with only subtle disparity in the shapes of the mandible. Not much difference can be observed in the cranium of the three species of *Rattus* when viewed laterally.

Minor size differences can be observed between sexes among the four species of rodents as evidenced in the scatter plot in Figure 15 showing the positions of the species in the "compromise" space. However, differences in the heights of the bar graphs in Figure 15 can be observed for *R. norvigicus* and *R. rattus mindanensis* which translates into saying that sexual size dimorphism can be observed in these species and can be seen as a function of differences in the size of the cranium.

The apparent disparity in the extent and magnitude of sexual dimorphism in the shapes and sizes of the skeletal elements of the rodent samples examined may be true for all species of Murids. In fact, among the four species of *Rhynchomys* in the Philippines, only *Rhynchomys isarogensis* shows moderate sexual size dimorphism with regards to the size of the adult body, external proportions, cranial, and dental measurements (Balete *et al.,* 2007).

Minimal size differences can be observed between the males of *R. r. mindanensis* and *R. argentiventer* (Figure 16). However, the females of these species differ in the size of the cranium when measured in both dorsal and ventral orientations. Subtle differences in the size of the pelvis can also be seen between them. Also, the two species do not differ in the sizes of their scapula. These two species can easily be distinguished from *R. norvigicus* based on the sizes of all skeletal elements considered.

The results of the study suggest that the sex of species of rodents may be determined from specific characteristics of selected skeletal elements. Traditionally, the sex of a captured rodent is usually determined based on external features, such as the presence of testes in mature males and teats associated with the subcutaneous mammary glands in adult females. Also, in juveniles, the distance between the anus and genital papilla can be used as an alternative to determine the sex of an individual where the distance is usually much greater in a juvenile male than in a juvenile female.

There are several taxonomic implications resulting from observations regarding the nature of character variation in the species examined whereby infra-specific variability may often be greater than interspecific disparity. From the results, *R. r. mindanensis* have high infra-specific metric characters because of their large degree of sexual dimorphism. In contrast, the other two *Rattus* species have low infra-specific variability. While morphometric scaling eliminates size differences, it does not eliminate shape differences related to the sex of the rodent specimen.

Wide disparities in the extent of sexual dimorphism also have implications in the use of a metric to measure population differentiation or determine subspecies of rodents in terms of the shapes and sizes of the skeletal elements. For example, the use of the Mahalanobis metric scales differences in terms of within-species variances and covariances, but does not consider higher moments of the distribution (Ahern *et al*., 2005). *R.*

*r. mindanensis* is highly bimodal in shape and size, while that of *R. argentiventer* and *R. norvigicus* are unimodal. Thus, comparing two *R. r. mindanensis* populations results in a larger mean distance, and comparing two *R. argentiventer* populations results in a smaller mean distance merely because the two species differ in infra-specific character variation.

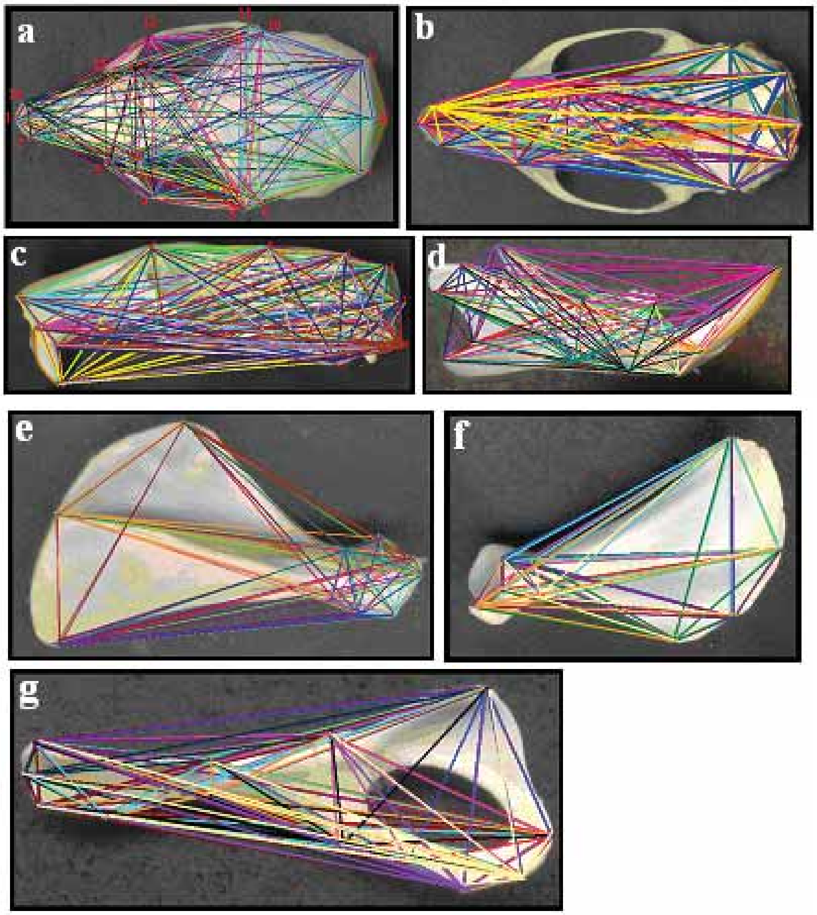

**Fig.8:** Euclidean Distance matrix Analysis (EDMA) interlandmark distances of the (a-c) cranium (dorsal, ventral, and lateral orientations, respectively), (d) mandible, (e) & (f) scapula (dorsal and ventral views, respectively), (g) pelvic girdle.

### *Conclusions and Recommendations:*

The results of this study shows that GM methods coupled with novel approaches in analysis of multiple multivariate data sets can be used as a supplement to the traditionally collected data that are used in rodent taxonomy and in determining specific features that differentiate the dimorphic sexes. This is particularly important especially in few species of rodents which possess uniquely diagnostic features, making it difficult to recognize closely related species. More typically, rodent taxonomists classify the species based on a unique combination of features. Even then, rodents are often quite difficult to identify to species level, especially among members of the family Muridae, the group that includes nearly two-thirds of living rodents, and almost all of the major pest species. This might be attributed to the fact that murid rodents have the remarkable ability to undergo major shifts in ecological adaptation with only minor changes in morphology. In this respect, the methods of GM are appropriate in identifying the gaps, discontinuities, discrepancies and overlaps in character shape and size variations. Thus, GM supplements traditional morphology-based rodent taxonomy. There might be other considerations in the use of GM to study the nature of infra- and interspecific character variations in murid rodents. First, almost all murid rodents undergo dramatic changes through life in body proportions, which means that juveniles, subadults, and adults of one species often differ more from each other when compared to the same growth stages of another species. Thus, future research directions should include a comparison of growth trajectories among species by comparing how the shapes of characters vary across different life stages. Finally, the methods of GM can be used to determine species boundaries as some rodents appear to be highly polymorphic and show a lot of morphological variations even within and between populations of a single species. Thus, population differentiation studies should be done extensively using all possible characters and if possible utilizing available methodologies. Such attempts lead to more natural classification and identification of species.

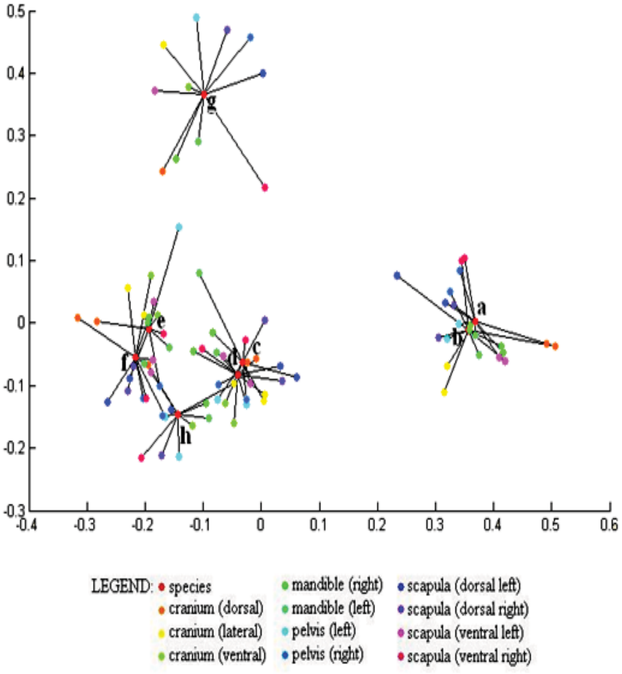

**Fig.9:** Plot of the first two principal components of the "compromise" SSCP shape matrix accounting for 54.92% of the total variance. Quality of the compromise is 91.04%. (a-b) M. musculus male and female, respectively (c-d) Rattus argentiventer Robinson and Kloss male and female (e-f) Rattus norvigicus Berkenhaut male and female (g-h) Rattus rattus mindanensis Mearns male and female.

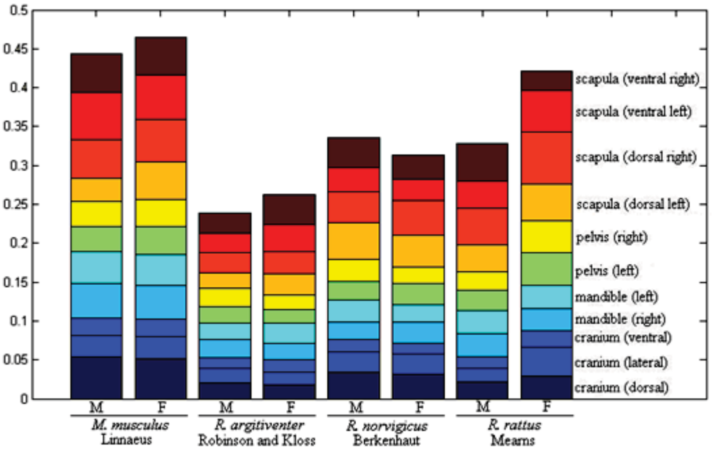

**Fig.10:** Stacked bar graphs showing disparity between sexes among the four species of rodents with regards to the shape of the cranium, mandible, pelvis, and scapula.

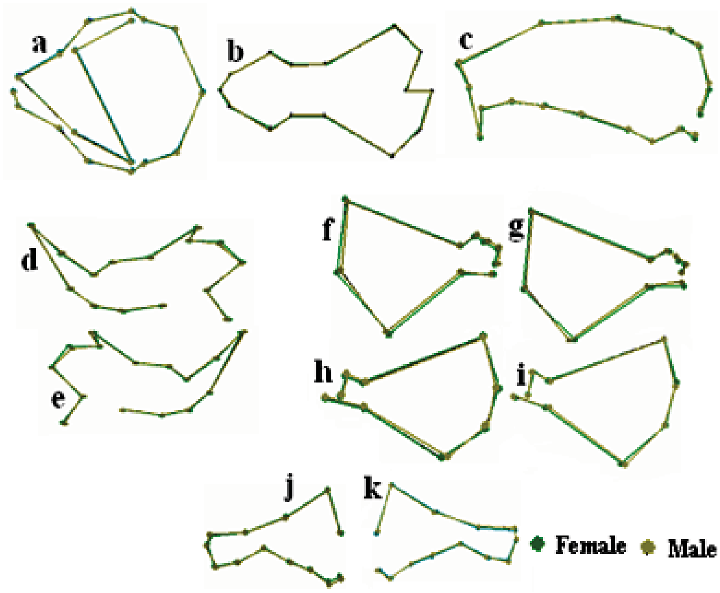

**Fig.11:** Superimposed mean shapes of the (a-c) cranium (dorsal, ventral and lateral orientation, respectively), (d-e) left and right mandible, (f-g) left and right scapula (dorsal view), (h-i) left and right scapula (ventral view), and (j-k) left and right pelvic girdle of the male and female individuals of Mus musculus Linnaeus.

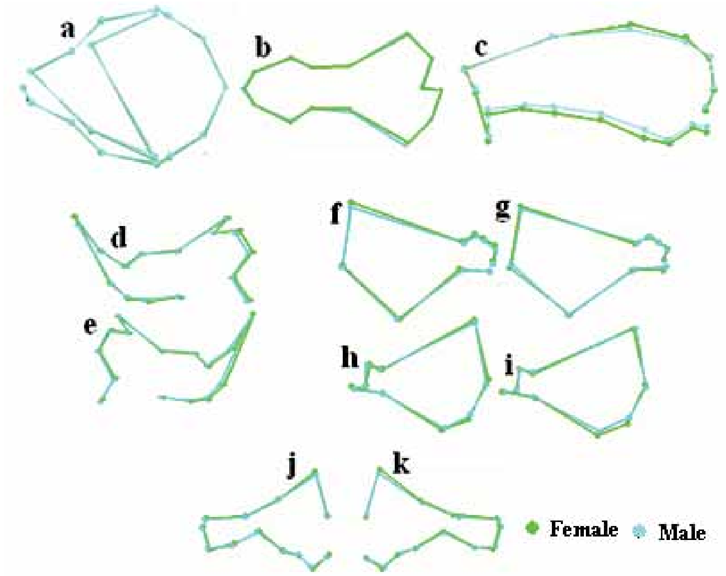

**Fig.12:** Superimposed mean shapes of the (a-c) cranium (dorsal, ventral and lateral orientation, respectively), (d-e) left and right mandible, (f-g) left and right scapula (dorsal view), (h-i) left and right scapula (ventral view), and (j-k) left and right pelvic girdle of the male and female individuals of Rattus argentiventer Robinson and Kloss.

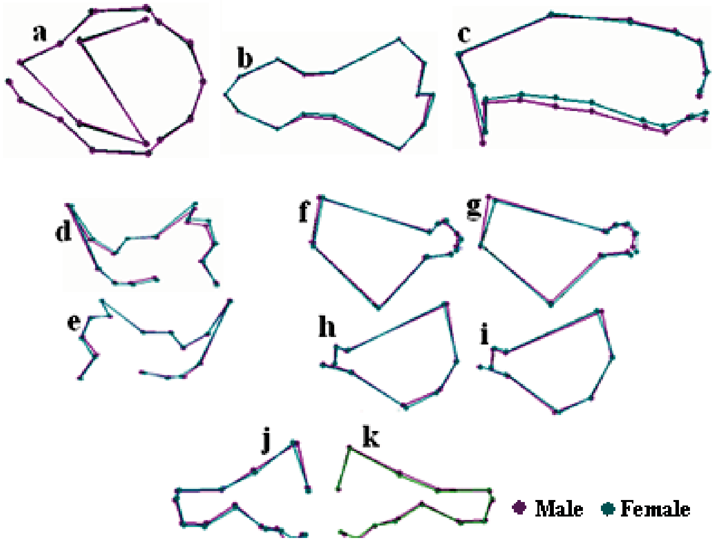

**Fig.13:** Superimposed mean shapes of the (a-c) cranium (dorsal, ventral and lateral orientation, respectively), (d-e) left and right mandible, (f-g) left and right scapula (dorsal view), (h-i) left and right scapula (ventral view), and (j-k) left and right pelvic girdle of the male and female individuals of Rattus norvigicus Berkenhaut.

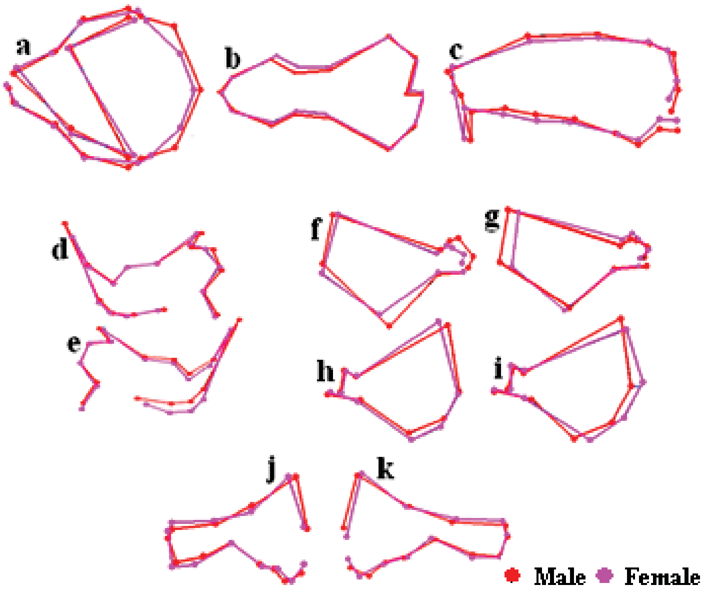

**Fig.14:** Superimposed mean shapes of the (a-c) cranium (dorsal, ventral and lateral orientation, respectively), (d-e) left and right mandible, (f-g) left and right scapula (dorsal view), (h-i) left and right scapula (ventral view), and (j-k) left and right pelvic girdle of the male and female individuals of Rattus rattus mindanensis Mearns.

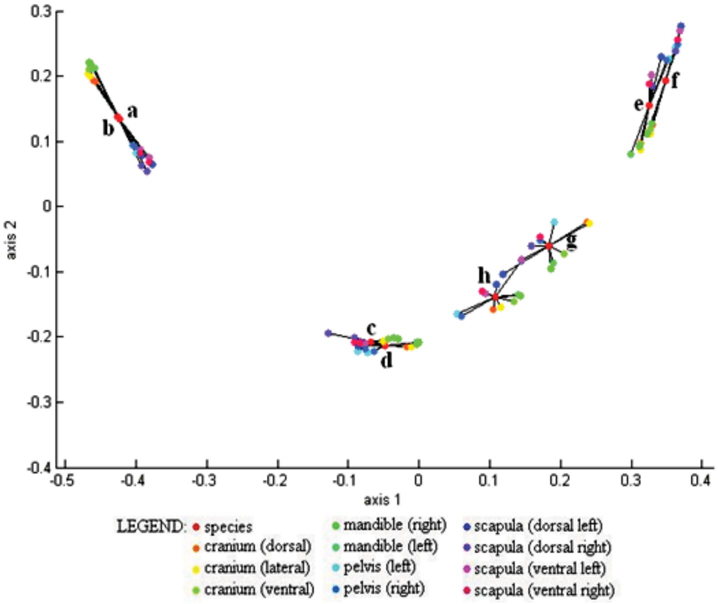

**Fig.15:** Plot of the first two principal components of the "compromise" SSCP size matrix accounting for 84.91% of the total variance. Quality of the compromise is 97.82%. (a-b) Mus musculus Linnaeus male and female, respectively (c-d) Rattus argentiventer Robinson and Kloss male and female (e-f) Rattus norvigicus Berkenhaut male and female (g-h) Rattus rattus mindorensis Mearns male and female.

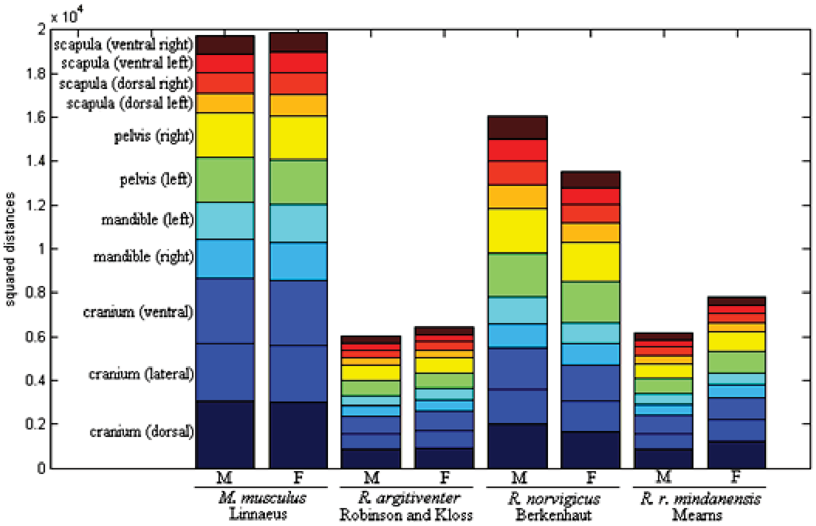

**Fig.16:** Stacked bar graphs showing disparity between sexes among the four species of rodents with regards to the size of the cranium, mandibles, pelvis, and scapula.

## REFERENCES

Adams, D.C., and F.J. Rohlf., 2000. Ecological character displacement in *Plethodon*: biomechanical differences found from a geometric morphometric study. Proceedings of the National Academy of Sciences, 97: 4106-4111.

Ahern, J.C.M., J.D. Hawks and S.H. Lee, 2005. Neandertal taxonomy reconsidered… again: a response to Harvati *et al*. (2004). Journal of Human Evolution, 48: 647-652.

Alfonso, P.J., L.A. Fiedler and J.P. Sumangil, 1985. Rodents. In: F.F. Sanchez, E.A. Benigno, editors. Rodent Biology and Control (with special reference to the Philippines). Laguna, Philippines: University of the Philippines at Los Baños College. pp: 9-24.

Aplin, K.P., P.R. Brown, J. Jacob, C.J. Krebs and G.R. Singleton, 2003. Field methods for rodent studies in Asia and the Indo-Pacific. ACIAR Monograph No. 100, pp: 223.

Balete, D.S., E.A. Rickart, R.G.B. Rosell-Ambal, S. Jansa and L.R.Heaney, 2007. Descriptions of two new species of Rhynchomys Thomas (Rodentia: Muridae: Murinae) from Luzon Island, Philippines. Journal of Mammalogy 88(2): 287-301.

Barbehenn, K.R., J.P. Sumangil and J.L. Libay., 1973. Rodents of the Philippine Croplands. Philippine Agriculturist, 56: 217-242.

Douglas, M.E., 1993. An analysis of sexual dimorphism in an endangered cyprinid fish (*Gila cypha* Miller) using video image technology. Copeia, (2): 334-343.

Douglas, M.E., M.R. Douglas, J.M. Lynch and D.M. McElroy, 2001. Use of geometric morphometrics to differentiate *Gila* (Cyprinidae) within the Upper Colorado River basin. Copeia, 2: 389-400.

Hammer, Ø, D.A.T Harper and P.D. Ryan., 2001. PAST: Palaeontological Statistics Software package for education and data analysis. Paleontologia Electronica, 4(1): 9.

Heaney, L.R., D.S. Balete, M.L. Dolar, A.C. Alcala, A.T.L. Dans, P.C. Gonzales, N.R. Ingle, M.V. Lepiten, W.L.R. Oliver, P.S. Ong, E.A. Rickart, B.R. Jr. Tabaranza, R.C.B. Utzurrum. 1998. A synopsis of the mammalian fauna of the Philippine Islands. Fieldiana Zoology new series, 88: 1-61.

Loy, A., M. Corti and L.F. Marcus., 1993. Landmark data: size and shape analysis in systematics: a case study on old world Talpidae (Mammalia: Insectivora), pp: 215-240. In: Contributions to Morphometrics. L.F. Marcus, E. Bello, and A. García-Valdecasas (eds.). Monograph of the National Museum of Natural Sciences, Madrid, Spain.

Márquez, E.J. and L.L. Knowles 2007. Correlated evolution of multivariate traits: detecting co-divergence across multiple dimensions. Journal of Evolutionary Biology, 20: 2334-2348.

Sanchez, D.C., 1977. Population patterns of sympatric rodents: *Rattus r. mindanensis* Mearns and *R. argentiventer* Robinson and Kloss associated with the rice crop in Oriental Mindoro. [MS Thesis]. College, Laguna, Philippines: University of the Philippines Los Baños. pp:78. http://www.scioncorp.com/pages/scion_image_windows.htm.

Stuart, A.M., C.V. Prescott, G.R. Singleton, R.C. Joshi and L.S. Sebastian., 2007. The rodent species of the Ifugao Rice Terraces, Philippines – Target or non-target species for management? International Journal of Pest Management, 53(2): 139-146.

Vergara, B.S., 2001. Ricefields, biodiversity and landscapes. Manila, Philippines: Island Publishing House, Inc. pp: 22.