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Relative Warp and Correlation Analysis based on Distances of the Morphological shell shape patterns among freshwater gastropods (Thiaridae: Cerithimorpha)

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Abstract. Shell morphology has various details in their architecture that contributes effectively to gastropod identification and classification. A conventional approach has been made to study shell morphology using descriptions of biological shapes. However, descriptions can be strengthened by applying additional quantitative tools. Relative Warp Analysis and Correlation Analysis based on Distances (CORIANDIS) were used to determine shell shape divergence and ascertain factors associated with the shell shape variation in three species of the genus Melanoides of the family Thiaridae namely, *Melanoides granifera, Melanoides maculata,* and unknown *Melanoides* species belonging to the family Thiaridae. Relative warp summarizes the vectors of shape variation within samples. CORIANDIS on the other hand, examines similarities among samples and interpreted in terms of congruence among traits. Results of the relative warp analysis showed significant shell shape variation among the Thiaridae species in the height of the spire, aperture, and apical shapes. Distance matrices were also constructed for the three data sets of shell characters: ventral/aperture, dorsal, and top/whorl shell. Results of the comparison via correlation analyses of distances among the species showed that an unknown *Melanoides* species is closely related to *M. maculata* than *M. granifera*. The results of the present study clearly show the importance of geometric morphometric analysis determination of systematic relationship in Thiarid snails.
Key Words: Relative Warp Analysis, CORIANDIS, shell shape, Thiaridae, shell characters.

Introduction. The freshwater gastropods of the family Thiaridae is a worldwide family primarily circum-tropical in distribution and with many extremely widespread species (Glaubrecht 1999). It is one of the richest in freshwater faunas but are least known. There are numerous descriptions of the species but the taxonomic status of which remain unresolved (Kohler & Glaubrecht 2003). The identification of species boundaries remains difficult especially in the search for useful characters or attributes of the organisms. In the description of gastropods, the shell is traditionally used in classifications and taxon descriptions. Shell morphometry and sculpture are regarded as essential for species discrimination (Kohler 2003). The external form of the shell was the principal character used in gastropod species-level taxonomy. Evaluation of characters is sometimes based on qualitative descriptions of the biological structure. However, many problems are raised on this approach as how will one do the scoring in defined and continuous change of shape in metric terms that measure the difference between regions (Gutierrez et al 2011). For these past years, the study of biological form progressed from qualitative to quantitative. This has been accomplished by several new methodological and analytical tools that have been developed to facilitate the acquisition, interpretation and presentation of shape data collectively referred to as geometric morphometric (GM) techniques. This method was developed to analyze shape differences within, between and among groups of organisms based on anatomical landmarks defined by x and y Cartesian coordinates. Geometric morphometric (GM) methods accomplish this by comparing the coordinates collected from different specimens after removing the effects of size, position, and orientation, allowing the evaluation of shape differences only (Adams et al 2004). Image analysis coupled with GM has proven important in the quantitative shape analysis of many biological structures. While most GM studies are concerned only with the analysis of only one character and since various characters of a species may and usually do vary independently, new methodology were developed which calculates intergroup similarity averaged over multiple data sets, and can be used in the assessment of the overall similarity among the species. This method is correlation analysis based on distances (CORIANDIS) (Marquez & Knowles 2007). CORIANDIS provides set of graphical and analytical tools to study associations among multivariate datasets, using distances among measured individuals. These methods of analysis are done by taking one set of character at a time as a basis to look into variability and relationship between the populations especially in discriminating confused species as the case of the freshwater gastropod, Thiaridae.

Material and Method. The freshwater gastropods of Family Thiaridae were collected from Guillian stream Balangao, Diplahan, Zamboanga Sibugay and Mimbalot Falls, Buru-un, Iligan City (Fig. 1). A total of 192 specimens were obtained comprising of three Thiarid species namely *Melanoides maculata* (71 samples), *Melanoides granifera* (75 samples), and including one unknown species of the genus *Melanoides* (46 samples).

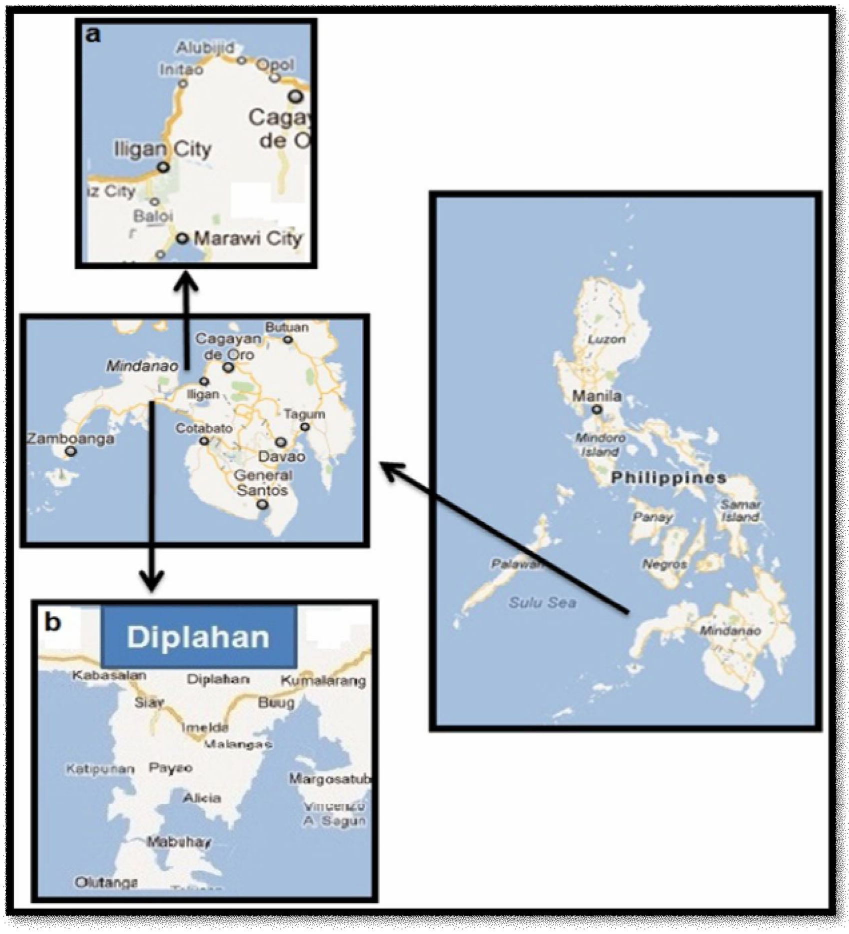

Fig. 1. Map showing the study area, (a) Mimbalot Falls, Buru-un, Iligan City and (b) Guillian stream Balangao, Diplahan, Zamboanga Sibugay.

Shells were photographed by a digital camera Images of the shell will always be in the same position with the columella at 90° of the x-axis in an aperture view or in the orientation in which the apex is visible. Obtained images were then subject to geometric morphometric. Digital images (ventral, dorsal and top view) were taken for each sample using a standardized procedure (Fig. 2).

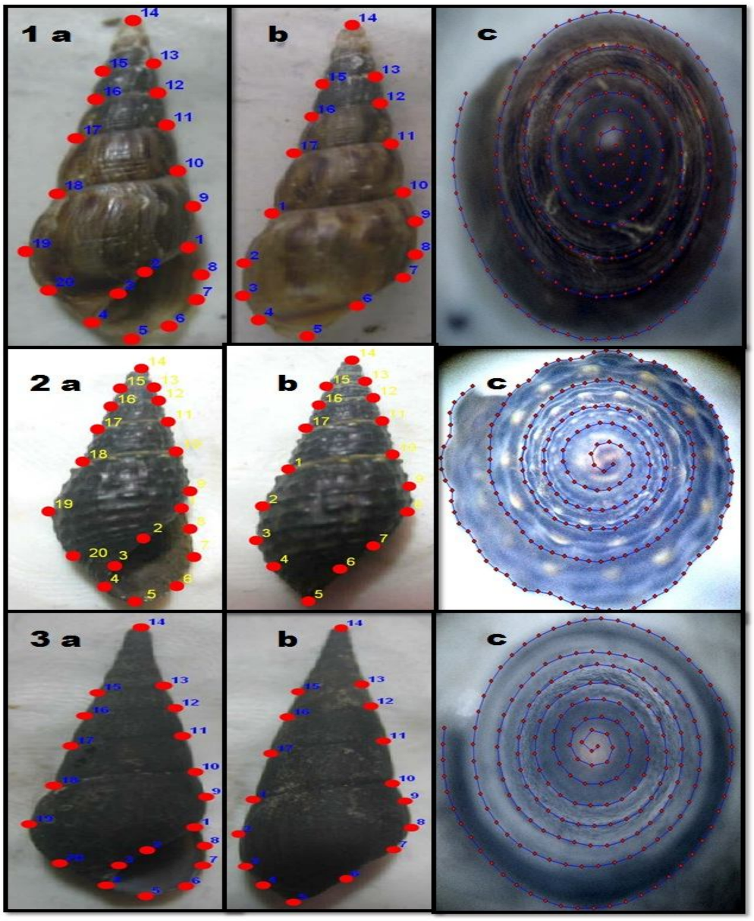

Figure 2. Landmarks used to describe the shape of the (a) ventral/aperture (b) dorsal and (c) top/whorl view of the shell of (1) *Melanoides maculata,* (2) *Melanoides granifera,* and (3) *Melanoides* sp.

Shell shape was studied using a landmark-based methodology that eliminates the effect of variation in the location, orientation, and scale of the specimens. Twenty anatomical landmarks located along the outline of the ventral or apertural portion (Fig. 2a) of the shell and seventeen anatomical landmarks along the dorsal portion (Fig. 2b) of shell were defined and used. This was made possible using an image analysis and processing software Tps Dig freeware 2.12. Tps Dig facilitates the statistical analysis of landmark data in morphometrics by making it easier to collect and maintain landmark data from digitized images (Rholf 2008a).

These coordinates were then transferred to Microsoft Excel application for organization of the data into groups (based on species). The two-dimensional coordinates of these landmarks were determined for each shell specimen. Then the generalized orthogonal least squares Procrustes average configuration of landmarks was computed using the generalized Procustes Analysis (GPA) superimposition method. GPA was performed using the software tpsRelw, ver. 1.46 (Rholf 2008b).

After GPA, the relative warps (RWs, which are the principal components of the covariance matrix of the partial warp scores) were computed using the unit centroid size as the alignment-scaling method. Histogram and box plots were generated using PAST software (Hammer et al 2009) from the relative warps of the shell shapes. Histogram and box plots are a powerful display for comparing distributions. They provide a compact view of where the data are centered and how they are distributed over the range of the variable. Kruskal-Wallis test was used to analyze whether or not the species differ significantly with regards to its shell shape (Demayo et al 2011). Canonical Variance Analysis (CVA) was also used in order to compare patterns of population variation.

The top or whorl (Fig. 2c) portion of the shell were outlined with 199 outline points using tpsDig program and the tps curve outline was converted to landmarks (corresponding x and y) using tpsUtil ver. 1.44 (Rholf 2009). The collective coordinates of all individuals were then subjected to Principal Component Analysis (PCA) using geometric morphometric computer application Paleontological Statistics (PAST) software developed by Hammer et al (2009). PCA was used to summarize the information of the variations and mean shapes contained in the coefficients of landmark descriptors.

Landmark data obtained for the three shell characters were analyzed using CORIANDIS: Correlation analysis based on distances version 1.1 beta (Marquez & Knowles 2007). This was used to determine associations among multivariate datasets, projections on compromise space, trait variance or disparity, congruence and multivariate covariance measure on how similar the interspecific locations of characters of three different species of snails belonging to family Thiaridae. The software was used to determine associations between species of freshwater snails as defined by different multivariate data. The option “Projections on compromise space” was selected, this was done such that all specimens/groups and traits/sets are plotted in the same space, obtained by projecting each dataset plus their weighter average (‘compromise’) onto the compromise space. Then, the squared distances of each group to the origin are computed for each of the shape data sets, and plotted in a stacked bar graph to give an overall impression of the differences between the three species of freshwater snails (Tabugo et al 2010 and Gutierrez et al 2011). After that, the scores obtained in the analysis are used in Cluster analysis.

Results and Discussion. Using the landmarks in the ventral, dorsal and top/whorl portion of the shell, CVA scatter plots of the three species of *Melanoides* showed differences between them (Fig. 3). Significant differences in shell shapes of the 3 species were observed indicating that with the number of landmarks used, species differentiation can be observed based on the distribution of the samples along the first canonical variate axes (Table 1).

Figure 4 illustrates a summary of the descriptions of the shapes of the shell showing the consensus morphology and variation in ventral/apertural (Fig. 4A) and dorsal (Fig. 4B) shell shape pattern of the 3 *Melanoides* species. Projections on the left side of the histogram are considered to be variations in shell shape foreseen as negative deviations of the mean in the axis of the relative warps. Then, on the right side are variations in shell shape foreseen as positive deviations of the mean in the axis of the relative warps. The topmost figure is the mean shape of the samples obtained.

Table 2 shows the results of the Kruskal-Wallis test for significant differences in mean shapes of the ventral/aperture and dorsal portion of the Thiarid shell respectively. Descriptions of the overall shape variation in the ventral/apertural and dorsal shell of the 3 *Melanoides* species were shown in Table 3.

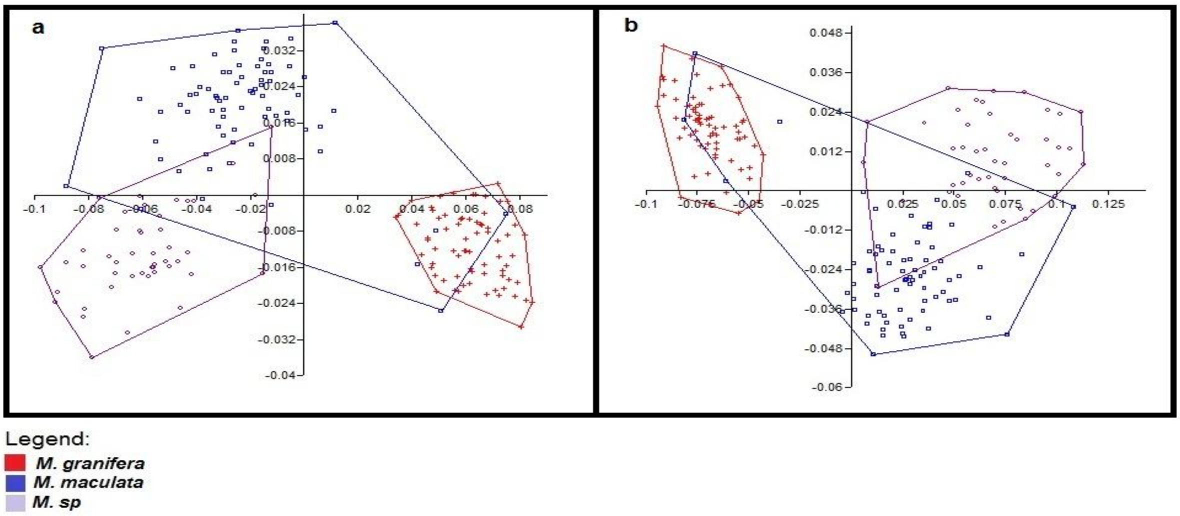

Figure 3. CVA scatter plot of the (a) ventral/apertural and (b) dorsal shell of the freshwater snails of the genus Melanoides belonging to Family Thiaridae.

Table 1

Results of the Multivariate Analysis of Variance (MANOVA) p-values between Thiaridae

Orientation	(p-value)	Remarks
Ventral/aperture	$3.288E^{-88}$	Significant
Dorsal	$3.054E^{-86}$	Significant

Table 2

Results of the Kruskal-Wallis test for significant differences in mean shapes of the ventral/apertural and dorsal view of the shells among the freshwater Thiarid snails

		VENTRAL / APERTURAL		
Relative Warp	**Species**	**a**	**b**	**c**
1	(a) *M. granifera*		**1.69E-23***	**8.28E-20***
	(b) *M. maculata*	**5.06E-23***		**2.92E-12***
	(c) *M.* sp.	**2.48E-19***	**8.77E-12***	
2	(a) *M. granifera*		**8.36E-12***	**2.08E-20***
	(b) *M. maculata*	**2.52E-11***		**2.92E-12***
	(c) *M.* sp.	**6.23E-6***	**1.16E-14***	
3	(a) *M. granifera*		**2.39E-8***	0.7504
	(b) *M. maculata*	**7.16E-08***		**5.88E-15***
	(c) *M.* sp.	1	**1.76E-6***	
		DORSAL		
Relative Warp	**Species**	**a**	**b**	**c**
1	(a) *M. granifera*		**3.42E-23***	**8.28E-20***
	(b) *M. maculata*	**1.03E-22***		**7.09E-12**
	(c) *M.* sp.	**2.48E-19***	**2.13E-11***	
2	(a) *M. granifera*		**7.17E-16***	**4.21E-06***
	(b) *M. maculata*	**2.15E-15***		**8.07E-16***
	(c) *M.* sp.	**1.26E-05***	**2.61E-15***	

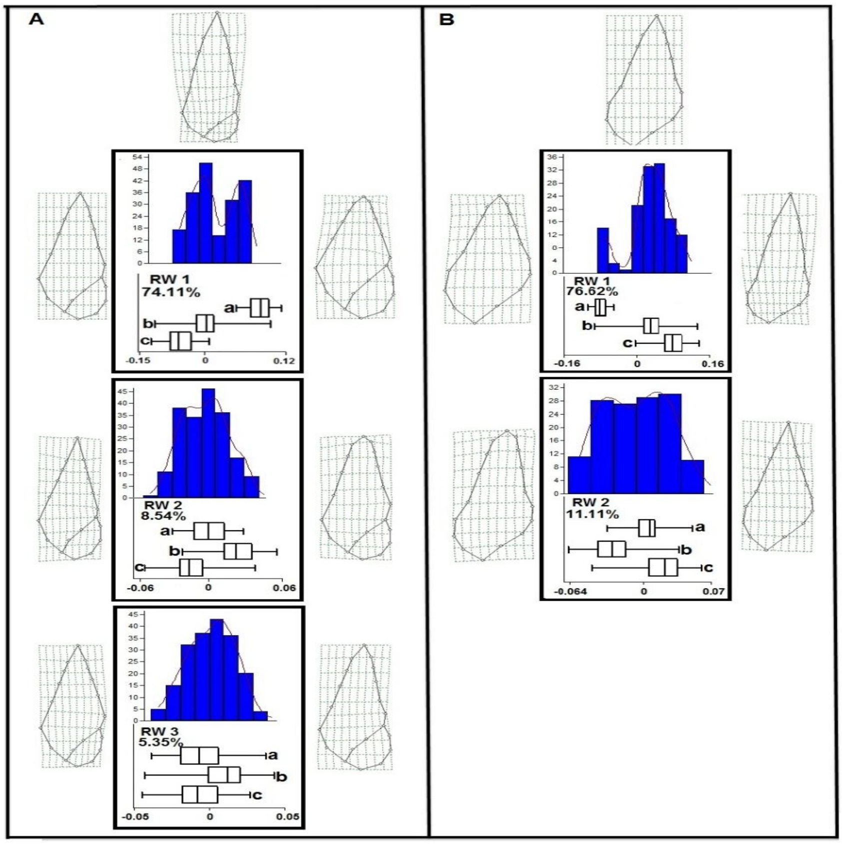

Figure 4. Relative warp box plot and histogram showing variations in shape of the (A) ventral/aperture and (B) dorsal shell of the Thiarid freshwater snails. Legend: (a) *Melanoides granifera*, (b) *Melanoides maculata*, and (c) *Melanoides* sp.

Table 3

Percentage variance and overall shape variation in the ventral/apertural and dorsal shell of the freshwater snails of family Thiaridae as explained by significant relative warps

RW	% variation	Ventral/apertural shell	% variation	Dorsal shell
1	74.11%	There is a bimodal distribution of the population in the first relative warp which strongly suggests two separate normally distributed populations or groups as depicted in the histogram in Figure 4A. RW1 explains differences in the apertural shell shapes and spires. Samples with low negative scores along the first relative warp axis have have conical shape leading to higher spire compared to those with high positive RW 1 scores which is elongate to elongate-ovate in shape with much shorter spires. *Melanoides granifera* draws towards the positive first relative warp axis, indicating *M. granifera* has short spire and elongate to elongate ovate in shape while *Melanoides maculata* and *Melanoides* sp. have higher spire and is conical in shape which lies along the negative first	76.62%	RW1 explains differences in the posterior margin of the outer dorsal lip and differences in the dorsal shell shape which accounts for 76.62%% of the total shape variation. Samples with high positive RW1 score have the posterior margin of the outer dorsal lip slightly depressed towards the center of the shell opening. *M. maculata* and *M.* sp. display this characteristic which lies on the positive RW1 axis. In terms of the dorsal shell shape, samples with high positive RW1 scores have elongate to elongate-ovate dorsal shell shape. On the other hand, samples with a low negative RW1 scores have conical dorsal shell shape.

Table 3 Continuation

Percentage variance and overall shape variation in the ventral/apertural and dorsal shell of the freshwater snails of family Thiaridae as explained by significant relative warps

RW	% variation	Ventral/apertural shell	% variation	Dorsal shell
1	74.11%	relative warp axis. Also these samples, *M. maculata* and *M.* sp., are seen to have shorter and narrower apertural opening. Variation in the ventral/apertural shell shape in the first relative warp is considered to be significant as indicated in the result of the Kruskal-Wallis test for significant differences in mean shapes of the apertural view of the shell (Table 2).	76.62%	*M. granifera* have negative RW1 score indicating elongate to elongate-ovate shape leading to much shorter spire for this species in the dorsal view. *M. maculata* and *M.* sp. containing higher spire have conical shape which lies in the positive RW1 axis.
2	8.54%	RW2 which is attributed to differences in the whorls, explains 8.54% of the total variance in shape. A low negative RW2 score means that a shell has more pronounced body whorl and elevated apex. While, samples with a high positive RW2 score has shell with less pronounced body whorl relative to its shorter apical shape. In terms of the shape of the body whorls, samples with low negative RW2 scores have narrower body whorl compared to those with high positive RW2 scores which have shells with broader body whorl. Samples which have broader and less pronounced body whorl are freshwater species belonging to *M. maculata*. *M.* sp., on the other hand, lies on the negative RW2 axis showing narrower and more pronounced body whorl and highly elevated spires. Results of the Kruskal-Wallis in Table 2 confirm significant sources of variation in the second relative warp axis.	11.11%	The RW2 explains 11.11% of the total variance and describes differences in the body whorl. Samples with low negative RW2 score have shell with less pronounced body whorls, while high positive RW2 score has more pronounced body whorl and highly elevated apex. *M.* sp. has positive RW2 scores suggesting narrower and pronounced body whorl and elevated apex. On the other hand, *M. maculata* has broader body whorl less pronounced spire on the apical portion of the dorsal shell. Moreover, *M. granifera* lies on either positive or negative RW2 axis suggesting that *M.* granifera has shell with either broader or narrower body whorl. Kruskal-Wallis test (Table 2) for significant differences in the mean shapes of the dorsal shell showed highly significant variation.
3	5.35%	RW3 describes differences in the opening of the aperture where the operculum is located. RW3 explains more than 5% of the total variation. Samples with high positive RW3 scores are species belonging to *M. maculata,* which have wider and longer opening of the aperture. *M. granifera* and *M.* sp, on the other hand, lies on the negative RW3 axis indicating less pronounced and narrower apertural opening. Kruskal-Wallis test showed significant variation between *M. granifera* and *M.* sp to *M. maculata*.		

For the top/whorl portion of the shell, the outline coefficients (199 outlines) were interpreted using the multivariate Principal Component Analysis (PCA) to identify sources of variation from the whorl shell shape pattern. Figure 5 illustrates the mean shell shape (top/whorl portion) of freshwater gastropod of the Family Thiaridae: (a) *Melanoides granifera*, (b) *Melanoides maculata,* and (c) *Melanoides* sp.

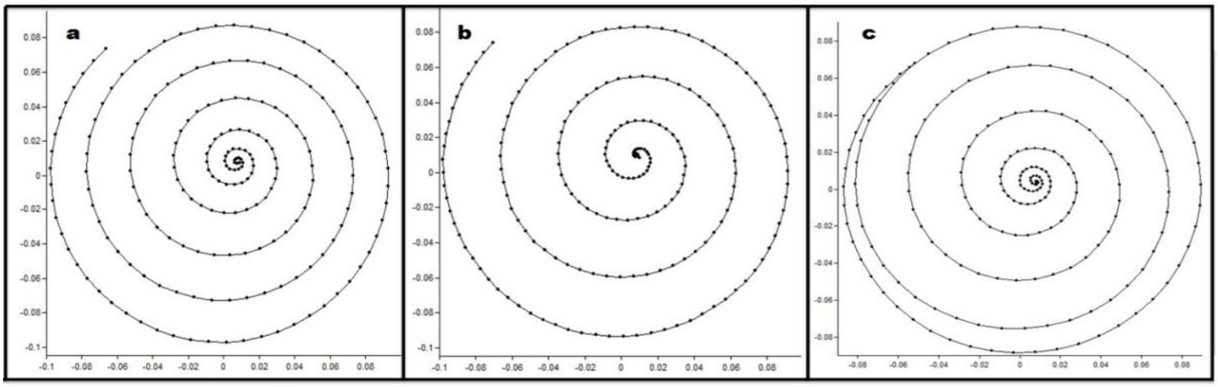

Figure 5. Principal deformations from the mean shape of the top/whorl shell portion of the Thiarid snails, (a) *Melanoides granifera,* (b) *Melanoides maculata,* and (c) *Melanoides* sp.

The top/whorl portion of the shell obtained nine principal components (PC1-PC9) for both *M. granifera* and *M. maculata* and eight principal components (PC1-PC8) for *M.* sp. These components were considered to be significant since their Eigenvalues are above the Jollifee cut-off score. However, the first and second principal components (PC1 and PC2) were only considered since the first two components provide a good summary of the variation for the top/whorl portion of the shell. Results in Table 4 showed the percentage variance value of the significant components in the top/whorl portion of the thiarid shell. *M. granifera* accounted for 88.237% of the total variance and more than 85% and 90% of the total variance for *M. maculata* and *M.* sp. respectively. Results indicate high variation in the top/whorl portion of the shell.

Table 4

Percentage variance values of the significant components in the top/whorl portion of the shell of freshwater snails belonging to Family Thiaridae

	Melanoides granifera		*Melanoides maculata*		*Melanoides* sp.	
PC	EV	V (%)	EV	V (%)	E	V (%)
PC1	0.07386	64.481	0.0748119	58.995	0.162923	62.118
PC 2	0.0272117	23.756	0.0336104	26.504	0.0745078	28.408
TOTAL		88.237		85.499		90.526

Legend: PC- Principal Component, EV- Eigenvalue, V- Variance

Correlation analysis based on distances (CORIANDIS) was also applied to integrate all the three characters to observe underlying relationships and sources of variability among groups in terms of congruence among characters (Abdi et al 2005, 2007 and Tabugo et al 2010). Using this analysis, the ventral/apertural, dorsal, and top/whorl portion of the shell were analyzed. Figure 6 is a plot of the principal components of “compromise” space axis accounting for 70.41% and 25.59% of the total compromise variance. The quality of the compromise is 99.69%.

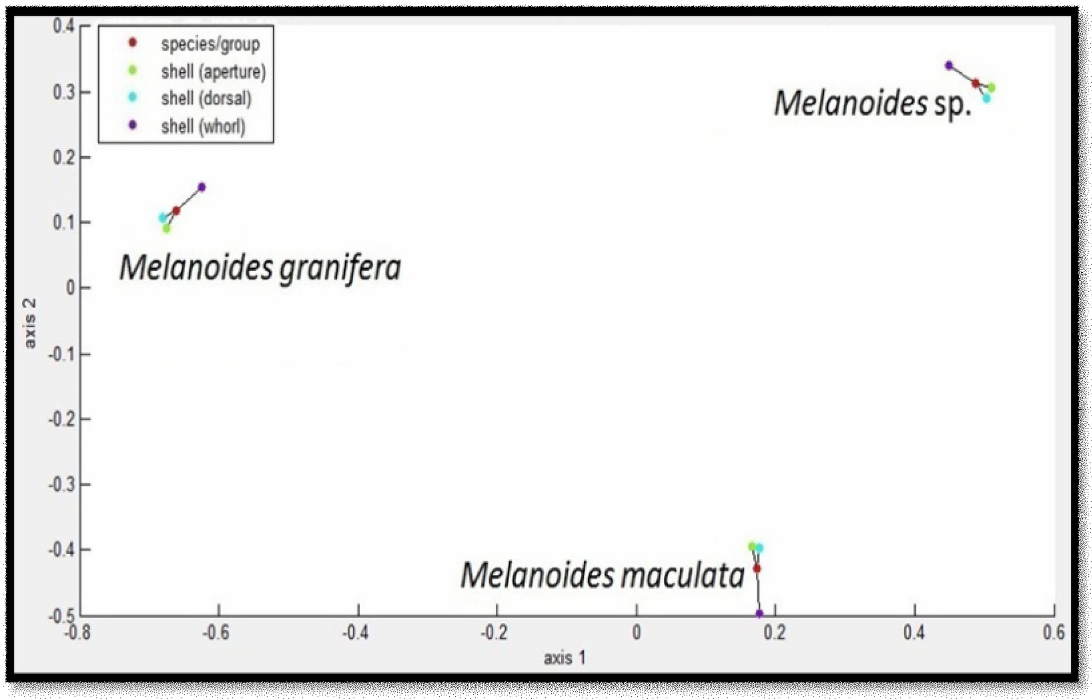

Figure 6. Plot of the principal components of “compromise” space axis of the freshwater gastropod belonging to Family Thiaridae.

The figure above indicates the congruence and multivariate measure on how related the interspecific locations of traits/characteristics (represented as colored points) are in this space. If two traits tend to be consistently different or similar between pairs of species, they are said to be (positively) congruent, and will show in this plot as a general tendency to cluster together within species (Gutierrez et al 2011). The result shows a general tendency for each species to cluster out together implying great differences between the three species with regards to the three shell shape datasets.

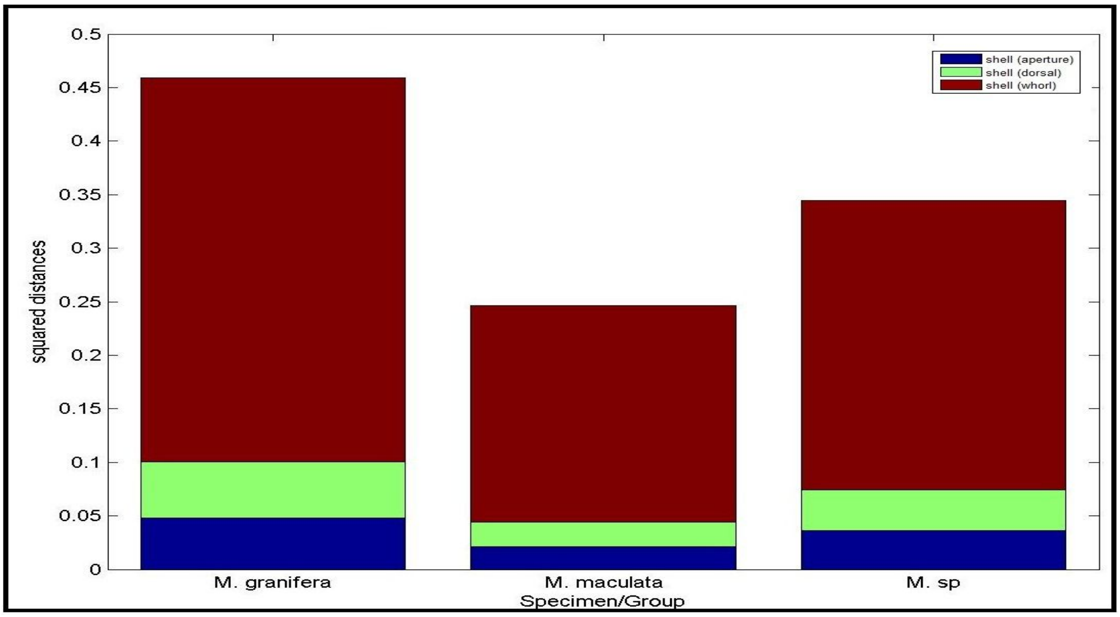

Figure 7. Stacked bar graphs showing disparity among the three (3) species of freshwater snails belonging to Family Thiaridae with regards to the shape of the ventral/aperture, dorsal, and top/whorl shell portion.

Figure 7 is a disparity plot showing the relative contribution of different characters to species' divergence. The total height of the stacked bar chart results from the addition of the squared distances of each trait separately (a measure of trait disparity), this shows how much each population differs from the rest by interpreting such differences in terms of individual character (Gutierrez et al 2011). This chart can therefore be interpreted as a decomposition of species distinctness from other species in terms of specific traits. The heights of the stacked bar graphs were different between species in *M. granifera*, *M. maculata,* and *M.* sp. implying morphological differences in the shapes of the shell between the species.

The overall relationship among the Thiarid snails on compromise space is shown as a dendrogram in Figure 8. The snails are divided into two groups based on the shell characters analyzed. The members of the first cluster comprised of *M. maculata* and *M.* sp. *M. maculata* indicate 82% resemblance to *M.* sp. This indicates that unknown species *M.* sp. is closely related to *M. maculata.* Although these species are similar, the two species vary significantly in color which can also be considered a taxonomic trait and variability in their color might be attributed to their habitat. On the other hand, the other cluster is composed of *M. granifera*. It is well separated in the group, because it has smaller shell shape pattern compared with the other thiarid snails.

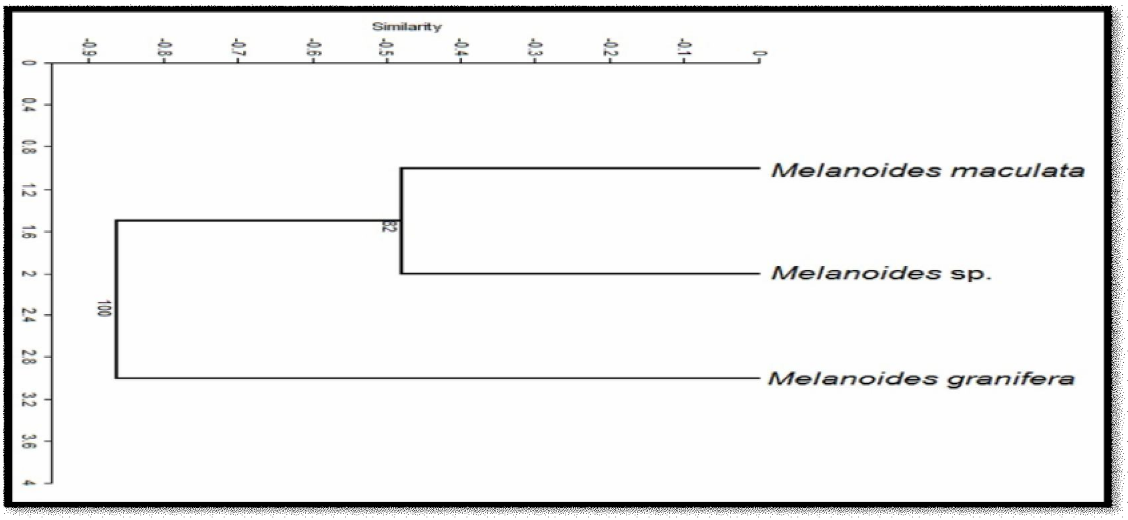

Figure 8. Plot showing the degree of similarity of characters between three (3) different species of Thiarid snails.

Results of this study have shown that the three shell characters could be used to discriminate between species. As to the ecological adaptations of the variations in shapes, it is argued that species with high spire are able to burrow at soft substrate and could survive periods of droughts for months because they are hidden in the bottom of the mud (Cain 2007 and cited by Borra 2006). *M. maculata* and *M.* sp. were observed to have much higher spires which may indicate long periods of survival. However, though *M. granifera* has shorter spire compared to other species, its spire is also used for the same purpose. Differences in the apex of the shell was also observed, among the three species *M. maculata* displayed a blunt and short apex. Dissolved and short apical portions of shells in *M. maculata* could be a physiological response that may be explained as a constraint of growth due to a low-calcium present in freshwater environment (Chiu et al 2002). Other extrinsic factors due to environmental conditions might also induce variation in the shell shape of the snails. The shape of the apertural opening where the operculum is located also contributes to variation among thiarid snails. Differences in shape of the aperture with respect to the body whorl could be linked to predatory defense of the snail. It has been reported by DeWitt (2000) that shape of the aperture is the best way to deter shell entry as frequently performed by the predators such as decapods. Narrow apertures are a potentially important defense in freshwater. Conversely, wider aperture indicates vulnerability to predation (Williams 2005). It could be inferred that predators may affect apertural shape of the freshwater snails.

Patterns of variation among the three gastropod species may also be symptomatic of processes occurring on several levels. Different proportions of individuals in the populations within the species imply genetic diversity, which in turn has implications for phenotypic diversity. It may also be due to varying strength of predation inducing different ecological and morphological strategies for survival. Autoregulatory developmental processes may also vary from species to species in their ability to buffer against environmental or genetic perturbations (Callier 2006). Thus, genetic, ecological and developmental sources of phenotypic variation may have contributed to morphological differences within and between the three species of freshwater gastropods of the genus Melanoides.

Conclusions. The results of this study suggest that Relative Warp Analysis (RWA), Principal Component Analysis (PCA) and Correlation analysis based on distances (CORIANDIS) can be used as tools for the study of morphological differences in gastropod shell pattern using various characters like ventral/aperture, dorsal, and top/whorl portion of the shell. It clearly indicates that various geometric morphometric methods are useful in detecting subtle differences between groups and to understand the patterns of shell shape variation. Thus, it represents advances for taxonomic and microevolutionary studies of gastropods.

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