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Morphometric Studies on Three Ostracod Species of the Genus *Digmocythere* Mandelstam from the Middle Eocene of Egypt

Ashraf M.T. Elewa

ABSTRACT

Canonical variate, eigenshape, relative warps, and thin plate spline analyses were applied to the ostracods *Cyamocytheridea*? sp., *Digmocythere omarai* Cronin, and Khalifa and *D*. *ismaili* Bassiouni. These analyses suggest that *Cyamocytheridea*? sp. is more similar to *D*. *ismaili* than *D*. *omarai* and, according to its taxonomy, should be described in a new species: *Digmocythere cronini*. The morphometric analyses support the suggestion of Boukhary et al. (1982) in placing *D*. *omarai* Cronin and Khalifa as the ancestor of *D*. *ismaili* (Bassiouni).

Ashraf M.T. Elewa. Geology Department, Faculty of Science, Minia University, Egypt. aelewa@link.net

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INTRODUCTION

Since multivariate techniques for studying the morphological changes of animals and plants using multivariate statistical analyses were introduced, their development has rapidly increased. Subsequently, a new era of multivariate morphometry, namely geometric morphometry, emerged (Reyment 1995a). Bookstein (1989, 1991) was the first to enhance the theory and practice of analyzing variation in shape by geometric methods.

Geometric morphometry in biology was pioneered by Thompson (1917) who expressed changes in shape in organisms by transforming the data into coordinates observed at diagnostic sites on the organism. These sites of reference are known as landmarks, a term borrowed from craniometry and previously from topographic surveying. Data in the form of coordinates are more comprehensive than those expressed as lengths, heights and breadths and "distances between" because they encompass not only all information on the relative positions of the points observed but also the distances between these points (see Reyment 1995a for details on general categories of landmarks and how to choose sites for landmarks).

It can be difficult to distinguish between ornamented and unornamented fossil ostracods. In taxonomic studies of this group, ornamented forms can be identified by standard methods of character recognition with a greater degree of confidence than can be accomplished with unornamented forms. In the absence of information about the internal characters of the carapace, the use of multivariate morphometric techniques can help resolve

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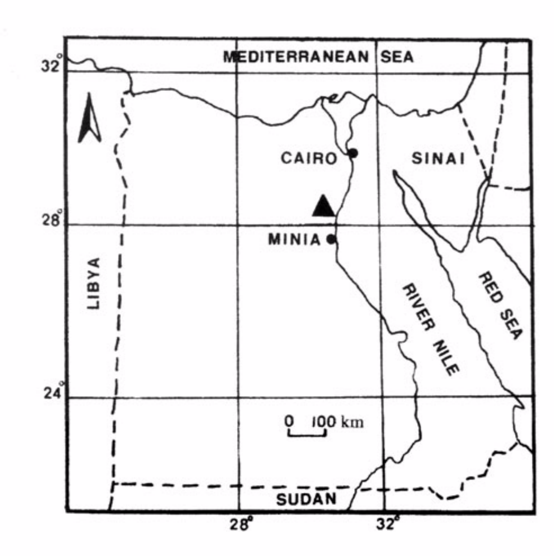

Figure 1. Location map. Black triangle represents location of the section from which specimens of the new species were collected.

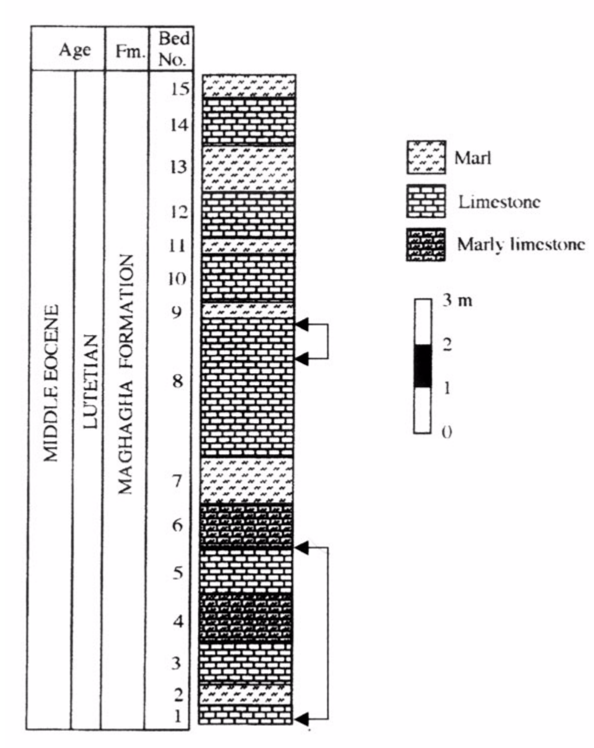

Figure 2. Columnar stratigraphic section of the middle Eocene Maghagha Formation from which specimens of the new species were collected.

this dilemma, by providing additional information about the shape parameters of unornamented forms, so that they can be more easily differentiated.

Through study of the middle Eocene ostracods of a section on the western bank of the Nile Valley (Upper Egypt), the author has recognized that specimens of *Cyamocytheridea*? sp. Elewa (1994) have many characters different from that genus (see the taxonomic section below), but which may be attributed to the genus *Digmocythere* based on the shape of the carapace (note that all the specimens are closed carapaces and analysis of the internal characters is not available). Three species of the Family Brachycytheridae have been selected for the present study: *Cyamocytheridea*? sp. (defined as *Digmocythere cronini* n. sp. in the conclusion of this study), *Digmocythere ismaili* (Bassiouni), and *Digmocythere omarai* Cronin and Khalifa. These species were collected from the middle Eocene Maghagha Formation, from a section that lies opposite of Beni Mazar city on the western bank of the Nile Valley, about 50 km north of Minia city (Figure 1). The Maghagha Formation was first proposed by Bishay (1966) to designate the chalk-marl complex exposed in the Maghagha district on the Nile Valley in substitution for the informal “B formation” of Barker (1945). Taxa analyzed in this study were collected from a section of the Maghagha Formation illustrated in Figure 2. This section consists of yellowish white, moderately hard limestone alternating with yellow to yellowish brown, soft to moderately hard marl and marly limestone comprising a thickness of about 14 m and all within the Maghagha Formation of Bishay (1966). Twenty-one samples from 15 beds were collected by the author from the studied section; only bed numbers 1-5 and the top of bed number 8 contain specimens of the new species. For more detailed information about the age and lithology of the section from which the specimens were collected, see Elewa (1997). For descriptions and illustrations of holotypes of *D. ismaili* and *D. omarai*, see Bassiouni (1971, p. 170, pl. 7, figs. 5-6) and Cronin and Khalifa (1979, p. 403, pl. 1, figs. 9-10), respectively.

The purpose of this study is to differentiate between the shapes of the three related ostracod forms by means of multivariate statistics and geometric morphometrics, to establish whether there is adequate shape variation between the forms separating them into different species, and to describe any resulting new species.

METHODS

Four common morphometric methodologies were used: 1) canonical variate analysis; 2) eigenshape analysis; 3) relative warps analysis; and 4) the thin plate spline method. In the following section, a brief description of these techniques is introduced.

Canonical Variate Analysis

Canonical variate analysis is one of the more interesting morphometric applications of multivariate statistics. The technique is used to examine the interrelationships between a number of populations simultaneously with a goal of objectively representing the interrelationships graphically in few dimensions (ideally only two or three). The axes of variation are chosen to maximize the separation between the populations relative to the variation within each of the populations.

In algebraic terms, the first canonical variate is the linear combination of variables that maximizes the ratio of between-groups sums of squares to the within-groups sums of squares for a one-way multivariate analysis of variance of the canonical variate scores.

For ***k*** groups (characters) and ***p*** variables (populations), the canonical variate scores are obtained from the following equation:

$$Y_{ij} = \mathbf{c}^{\mathrm{T}} x_{ij},$$

where c^{T} is the transpose of the canonical vectors and $\boldsymbol{x_{ij}}$ denotes the *i*-th of ***N*** observations for the *j*-th group. The first canonical vector **c** is derived so as to maximize the ratio:

$$F = \mathbf{c}^{\mathrm{T}}\mathbf{B}\mathbf{c} / \mathbf{c}^{\mathrm{T}}\mathbf{W}\mathbf{c}$$

where **B** is the between-groups matrix of sums of squares and cross products and **W** is the within-groups matrix of sums of squares and cross products.

The canonical vectors **c** and the canonical roots ***f*** satisfy the following equations:

$$(\mathbf{B} - f\mathbf{W})\mathbf{c} = \mathbf{0}$$

and

$$|\mathbf{B} - f\mathbf{W}| = \mathbf{0}$$

The canonical vectors are usually scaled so that

$$\mathbf{c}^{\mathrm{T}}\mathbf{W}\mathbf{c} = N_w$$

where $\boldsymbol{N_w}$ is the within-groups degrees of freedom.

For more information see Blackith and Reyment (1971), Reyment et al. (1984), and Reyment and Savazzi (1999).

Eigenshape Analysis

In 1983, Lohmann developed a Q-mode principal component technique for analyzing changes in the shape of an organism that he called eigenshape analysis. The observations consist of coordinate pairs determined at definite points around the circumference of the shell. In the present study, 11 landmarks were selected around the outline of each studied ostracod specimen to express these points.

The technique is a simple ordinating procedure that has as its starting point the ***x***, ***y*** coordinates of a set of ***p*** points along outlines of ***N*** objects of interest (here outline of the ostracod carapace). A transformation procedure is followed in the same manner as principal component analysis.

Thin Plate Spline and Relative Warps Analyses

Rohlf (1996) stated that there are two methods of comparison of shapes in geometric morphometrics. One of them is based on the least square method and is most efficient if overall similarity depends largely on few landmarks. The other method is thin plate spline analysis, which works best if the similarity depends on many landmarks.

The thin plate spline method is based on analogy of a two-dimensional morphological object to a thin homogeneous deformable metallic plate (Bookstein 1989, 1991); thus one specimen is fitted to another by stretching, and the numerical estimate of degree of such a smooth deformation is the *bending energy* coefficient.

The shape variation encompasses two components, an affine (uniform) part and non-affine (non-uniform) part (Bookstein 1991). In the affine change, the orthogonality of principal axes is preserved, and parallel lines remain parallel, like the deformation of a square into a parallelogram or a circle into an ellipse. The non-affine change is represented by the residual of size-free change that remains after the difference due to any affine change has been subtracted from the total change in shape. An example is when an initially flat object is twisted or warped. For some examples of the method, see Reyment (1993, 1995a, b and 1997), Reyment and Bookstein (1993), and Reyment and Elewa (2002).

THE MEASUREMENTS

Twenty-seven well-preserved, adult specimens from the three studied ostracod forms (14 males and 13 females; 12 specimens of *D. ismaili*, 6 specimens of *D. omarai* and 9 specimens of *C.*? sp.) were selected for multivariate morphometrics. The measurements for the canonical variate analysis are: the length of the carapace (L), the height of the carapace (H), the distance from the eye tubercle to the maximum end of the posterior margin (P), the distance from the eye tubercle to the maxi-

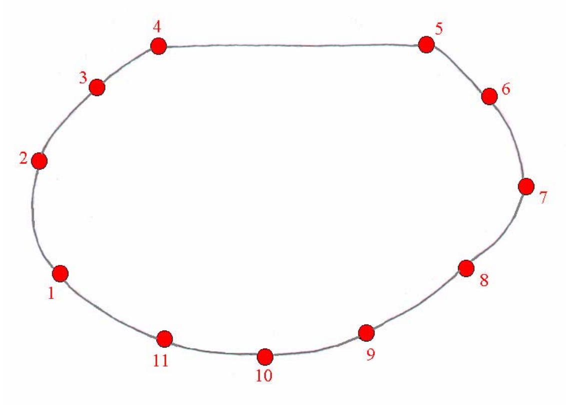

Figure 3. Sketch showing the locations of the 11 landmarks used in the present study. Figure based on *Digmocythere ismaili* (Bassiouni).

mum end of the ventral margin (V), and the length of the hinge (G). These measurements were taken based on SEM photographs of the specimens.

Eleven landmarks were selected for the eigenshape analysis and the thin plate spline and relative warps analyses (Figure 3): the mid-point along the antero-ventral margin (1), the maximum end of the anterior margin (2), the mid-point along the antero-dorsal margin (3), the location of the eye tubercle (4), the end of the hinge from the posterior side (5), the mid-point along the postero-dorsal margin (6), the maximum end of the posterior margin (7), the mid-point along the postero-ventral margin (8), and three landmarks at points of inflection of the ventral margin (9, 10, 11) and are therefore not as well established as the fixed-points (fixed-point here is used in spirit with the topographical surveying terminology embodied in the concept of landmarks).

These landmarks were digitized on the basis of SEM photographs using a computer program by Rohlf (1998a). Note that the observations of the studied left views of carapaces were rotated by 180 degrees to achieve compatibility with the studied right views of carapaces. Eigenshape analysis is usually based on a more thorough sampling of the outline of a specimen, but these 11 landmarks capture most of the aspects of the shape so they were used to allow more direct comparison with the relative warps results.

MULTIVARIATE ANALYSIS OF DISTANCE MEASUREMENTS

First, in order to examine the multivariate normality for each sample of the studied species, the Q-Q probability plot for each sample is made (Figures 4-6). This expression stands for Q(uantile)-Q(uantile) probability plot. It is nothing more than advisory in nature because it provides a graphical means of assessing one aspect of multivariate normality in a sample. The plot is made using the generalized statistical distances computed for each specimen in the sample. If there are strongly divergent specimens in the data, these will show up as isolated points at the top of the graph. Figures 4, 5, and 6 indicate that there are no markedly divergent specimens within each species and hence no indication of deviation from multivariate normality in the three samples.

Next, the five measured distances were subjected to canonical variate analysis using a program by Reyment and Savazzi (1999) to test the hypothesis that there are three different species.

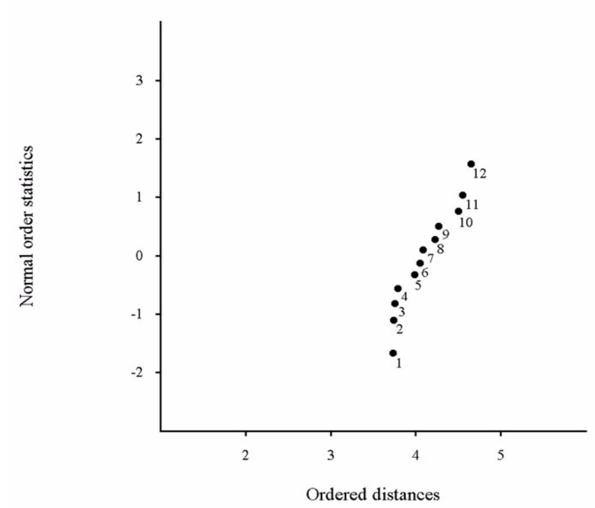

Figure 4. Q-Q plot of specimens of *Digmocythere ismaili* (Bassiouni).

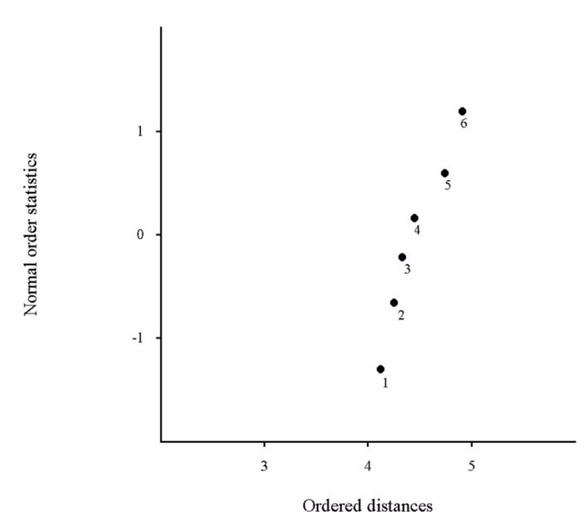

Figure 5. Q-Q plot of specimens of *Digmocythere omarai* Cronin and Khalifa.

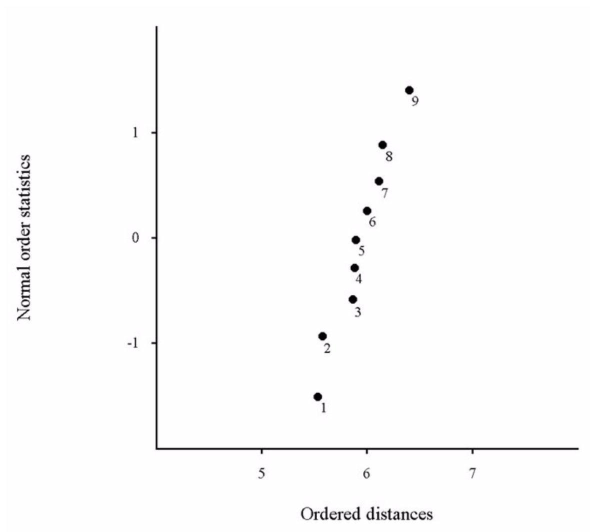

Figure 6. Q-Q plot of specimens of *Digmocythere cronini* n. sp.

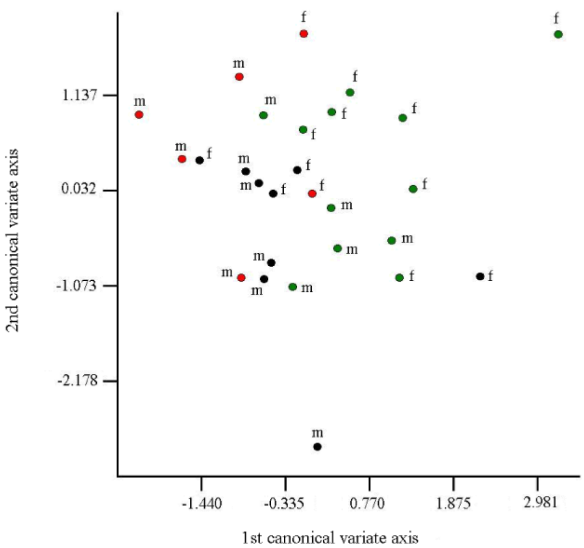

Figure 7. Plot of the 1st vs. 2nd canonical variate scores of the three studied species. Green solid circles: *Digmocythere ismaili*; red solid circles: *Digmocythere omarai*; black solid circles: *Digmocythere cronini*. f: females; m: males.

The results for the analysis yielded the ordination displayed in Figure 7. Table 1 reveals that the 1st and 2nd canonical roots represent all the variance (100%). This table shows that the 1st normalized canonical vector may represent the relationship between the length (1 in Table 1), the height (2) and the distance of the hinge (5). The 2nd normalized canonical vector shows the relationship between the height (2) and the length of the hinge (5). From Figure 7, it can be concluded that the analysis could successfully distinguish males from females for each species; however, it failed to differentiate between the shapes of the three species.

EIGENSHAPE ANALYSIS

The program used for the eigenshape analysis is contained within a package named "PAST" (version 1.04 for the year 2003). The results of the analysis (Table 2) indicate that the 1st and 2nd eigenshape components account for more than 74% of the variance. As a result, the plot of the 1st versus 2nd components shown in Figure 8 gives the same results as the canonical variate analysis in separating males (in the upper section of the graph) and females (in the lower section of the graph). Based on this preliminary data, the use of both canonical variate and eigenshape analyses seems to be of little use for interpreting shape complexities in these taxa.

GEOMETRIC MORPHOMETRY

Relative Warps

The program for relative warps analysis was written by Rohlf (1998b, version 1.2).

Non-affine Shape Differentiation in the Three Forms. The ordination for the 1st and 2nd warps (Figure 9) represents the non-affine (= non-uniform) shape variation. The first singular value for these data constitutes 20.85% of the variance, the second one comprises 17.59% of the variance, the third one is 15.33% and the fourth one is 13.03%. Thus, more than 66% of the variance is included within the first four relative warps, which is sufficient for interpreting the shape variation within the studied data. Figure 9 shows a plot of the 1st vs. 2nd relative warps and indicates that the 1st relative warp has a tendency to separate most specimens with acute posterior ends (at the left; like 20, 12, 8, 10, 13) from those with broad posterior ends (at the right; like 17, 2, 9, 15, 16). The 2nd relative warp shows no distinct relation between the specimens studied. Figure 10 compares the 1st vs. 3rd relative warps and shows that the 3rd axis separates most male specimens (in the upper section; like 14, 9, 20, 16) from females (in the lower section; like 15, 3, 21, 12). Figure 11, plotting the 1st vs. 4th axes, shows a tendency for the 4th axis to separate suboval shapes (in the upper section; like 19, 23, 15, 24, 9, 12, 21) from subtriangular ones (in the lower section; like 1, 3, 4, 20, 13).

Affine Shape Differentiation in the Three Forms. Although this study does not deal with growth, the uniform relative warps analysis is

Table 1. Summary of canonical variate analysis.

No.	Canonical root	Percent	Cum. percent
1	.5281	71.320	71.320
2	.2124	28.680	100.000
Distance measures	1st normalized canonical vector	2nd normalized canonical vector	
1	-0.4464	-0.2191	
2	0.4517	0.5092	
3	-0.3105	-0.0738	
4	0.2817	0.3521	
5	0.6488	-0.7548	

Table 2. Summary of eigenshape analysis.

Components	Eigenvalues	% variance
1	0.101	57.28
2	0.029	16.76
3	0.017	9.88
4	0.010	5.917

expected to give additional information about the growth of these ostracods because most growth in crustacean shells is of uniform (= affine) origin owing to the molting process. Figure 12, which plots the 1st vs. 2nd uniform axes, shows the tendency to separate most of the specimens of *D. ismaili* (Bassiouni) in the upper section of the graph, and most specimens of *C.*? sp. in the lower section of the graph. Specimens of *Digmocythere omarai* Cronin and Khalifa are distributed between these two species. It is clear that the affine differentiation could successfully differentiate between most females (at the upper section; like 7, 8, 3, 10) from most males (at the lower section; like 25, 20, 19, 27). Unexpectedly, the affine projection does not appear to provide additional information about the relationship between the three studied forms. Like the results of the distance measurements, there is a strong overlap between the three forms studied.

The Thin Plate Spline

The program used for the thin plate spline analysis is that of Rohlf (1997, version 2.13). This technique is a graphical representation of mapping from one shape to another. Left views of three females of the three studied forms (one specimen for each) were considered as typical (reference) specimens for the analysis. Figure 13 portrays the mapping of the non-affine case of *Digmocythere ismaili* into *C.*? sp. and suggests strong deformation, coupled with a bending energy of 0.11407. The posterior zone is more affected than the anterior zone. A weak dilatation towards the anterior

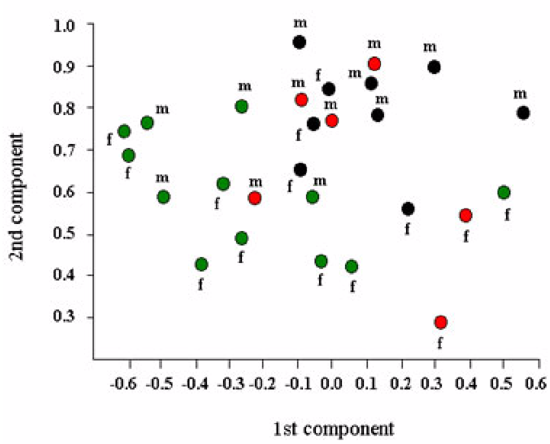

Figure 8. Plot of the 1st vs. 2nd eigenshape components of the three studied species. Coloured circles are same as Figure 7.

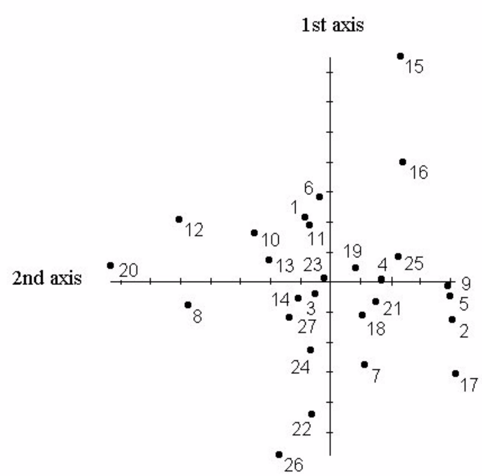

Figure 9. Ordination by the non-affine shape 1st and 2nd components for the three studied species. 1-12: *Digmocythere ismaili*, 13-18: *Digmocythere omarai*, 19-27: *Digmocythere cronini*.

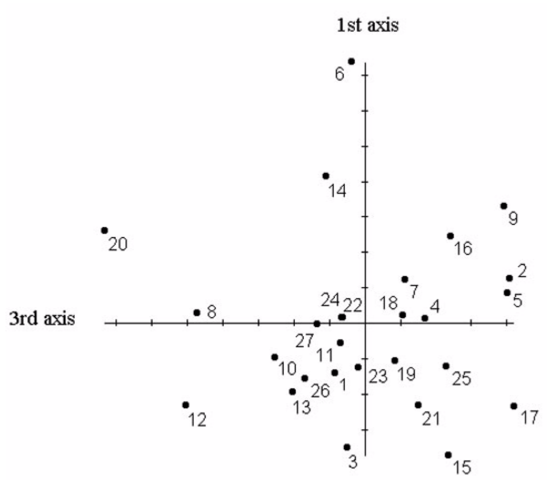

Figure 10. Ordination by the non-affine shape 1st and 3rd components for the three studied species. Numbers are the same as in Figure 9.

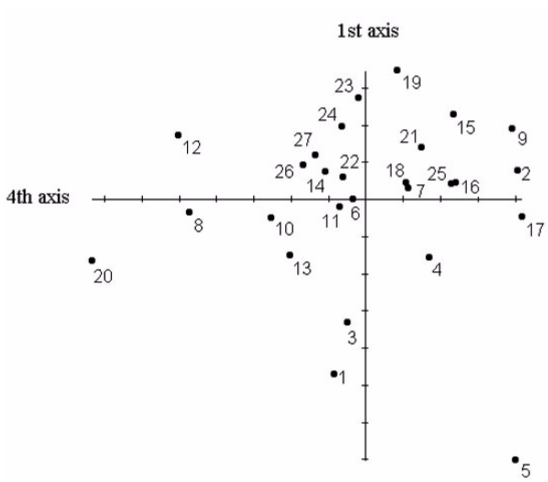

Figure 11. Ordination by the non-affine shape 1st and 4th components for the three studied species. Numbers are the same as in Figure 9.

detected. Figure 14 displays the warp of *Digmocythere ismaili* into *D. omarai*. The bending energy is 0.06381, and the effect is not so strong. The figure shows that the postero-dorsal margin is more affected than other sides. There is strong dorsal compression and posterior-anterior dilatation that increases in the anterior direction. Figure 15, showing the warp of *Digmocythere omarai* into *C.*? sp., suggests that the deformation is greater than the previous two cases, with bending energy equal 0.24868. The posterior zone is more affected than the anterior one, and there is a weak dilatation toward the posterior margin and a strong dorsal compression.

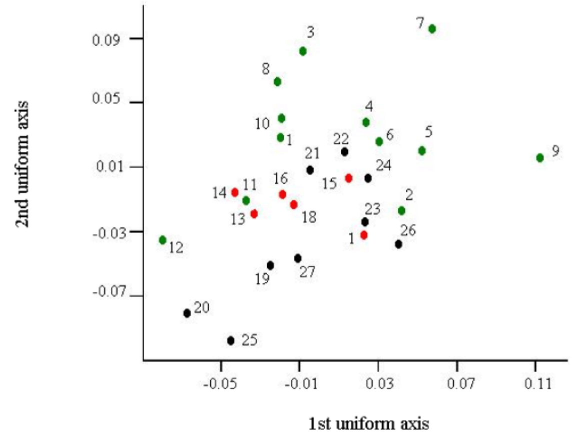

Figure 12. Ordination by the affine shape component for the three studied species. Numbers are the same as in Figure 9.

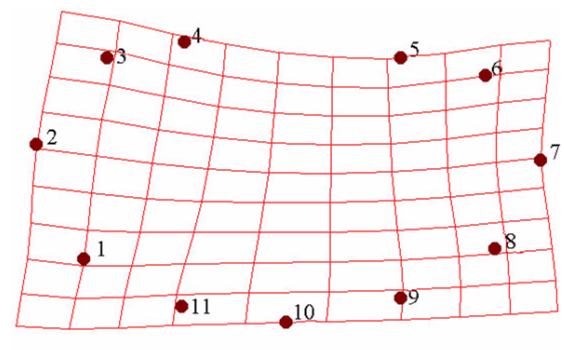

Figure 13. The non-affine deformation for the comparison between *Digmocythere ismaili* and *D. cronini*.

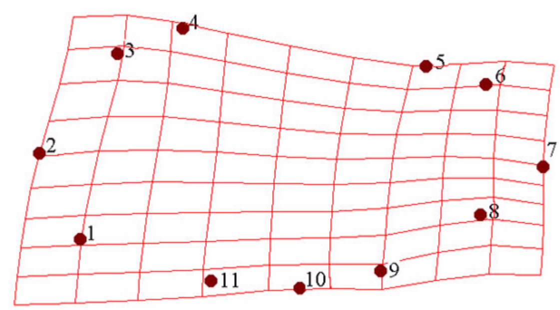

Figure 14. The non-affine deformation for the comparison between *Digmocythere ismaili* and *D. omarai*.

The three comparisons indicate that the postero-dorsal zone is the most affected area in the three cases. *Digmocythere omarai* and *C.*? sp. show the most divergent shape categories, while *Digmocythere ismaili* and *D. omarai* exhibit convergent shape categories.

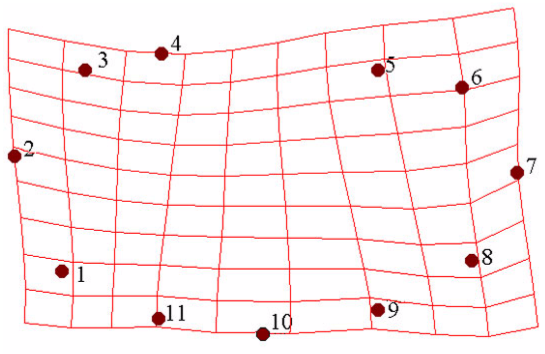

Figure 15. The non-affine deformation for the comparison between *Digmocythere omarai* and *D. cronini*.

DISCUSSION AND CONCLUSIONS

The successful application of multivariate statistical techniques as well as geometric morphometry to the study of taxonomic problems encourages the use of these methods for solving problems arising from lack of internal morphometric characters in ostracods.

The results indicate that the geometric measurements were marginally more helpful in differentiating the three studied species, whereas the distance measures were not. However, the distance measurements can help differentiate males from females.

The thin-plate spline results suggest that *C.*? sp. is a distinct species, which is more similar to *D. ismaili* than it is to *D. omarai*. Additionally, the deformation between *D. omarai* and *D. ismaili* is not as strong as one might have expected. This may be due to one of the following: 1) the older species (*Digmocythere omarai*) is the ancestor of the younger (*D. ismaili*) as suggested by Boukhary et al. (1982); and 2) these two species could be two morphs of one species.

Because the dorsal zone is more deformed in the warping of *D. ismaili* into *D. omarai* than the other zones, I therefore, support the first suggestion that the second species is the ancestor of the first. The dorsal margin contains the hinge which in general tends to evolve towards shorter length relative to the length of the carapace (Kaesler In: Boardman et al. 1987). This is the present case, where *Digmocythere ismaili* has shorter hinge distance (G; in the measurements of the present study) relative to the carapace length than *Digmocythere omarai.*

Finally, this study points out that benefits can be expected by applying geometrical morphometrics and, as an auxiliary tool, multivariate statistical analyses for solving problems in the field of systematics.

SYSTEMATIC PALEONTOLOGY

Subclass OSTRACODA Latreille, 1806
Order PODOCOPIDA Müller, 1894
Suborder PODOCOPINA Sars, 1866
Family BRACHCYTHERIDAE Puri, 1954
Digmocythere cronini n. sp.
Figure 16 (1-5)

1994 *Cyamocytheridea*? sp. Elewa, p. 145, pl. 2, figs. 11-12.

Etymology - The species is named after Thomas Cronin, US Geological Survey, USA, who with Hamed Khalifa, Geology Department, Faculty of Science, Assiut University, Egypt, were the first authors to recognize this form.

Diagnosis - A species with elliptical shape, smooth carapace with a prominent projection just behind mid-length and rounded anterior and posterior margins.

Material - Fifty-four specimens are referred to the new species. The holotype (A 10132) and the paratypes (A 10133 to A 10185) are deposited at the Geological Museum of the Geology Department, Faculty of Science, Minia University in Elewa's personal collection.

Type locality and stratum - A section west of Beni Mazar city, bed no. 1, yellowish white limestone, the Maghagha Formation, middle Eocene.

Dimensions	Length (mm)	Height (mm)	Width (mm)
A 10132 (Holotype) (Female)	0.690	0.375	0.260
A 10133 (Paratype) (Male)	0.700	0.370	0.240

Description - Carapace elliptical in lateral view, with a slight ventral convexity; dorsal margin straight to slightly convex; ventral margin convex, with a prominent projection just behind mid-length; antero-ventral margin slightly concave; postero-ventral margin straight to slightly convex; anterior margin rounded; posterior margin rounded. The right valve slightly overlaps the left valve, especially ventrally. Maximum height at mid-length. Surface smooth. In dorsal view, carapace elliptical, narrow; maximum width at mid-length. Internal characters were not observed.

Sexual dimorphism - Presumed female carapaces are wider and shorter than presumed male ones.

Remarks - The new species resembles a species described as belonging to an uncertain family and genus by Khalifa and Cronin (1979, p. 181, pl. 1, figs. 5-6) from Gebel El Sheikh Fadl east of Beni

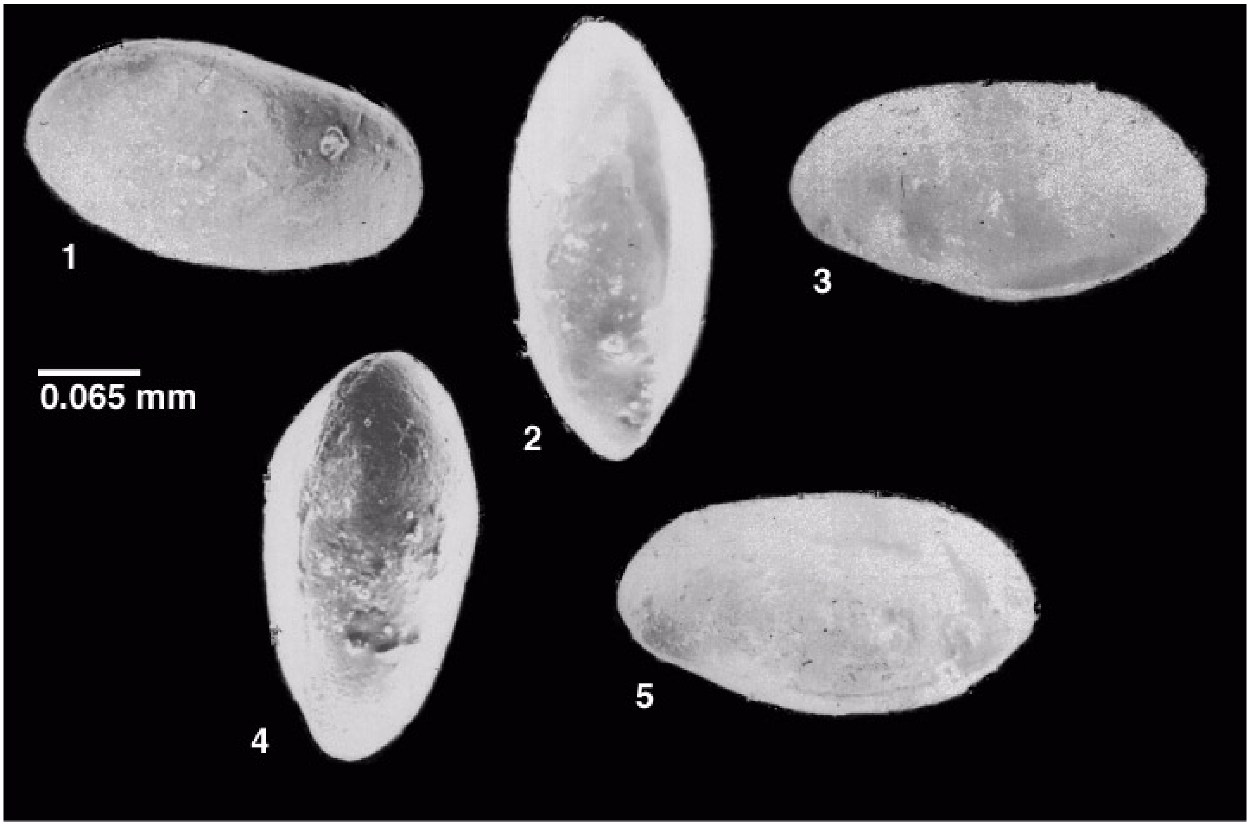

Figure 16. *Digmocythere cronini* n. sp. from the middle Eocene Maghagha Formation of Upper Egypt. All the illustrated specimens have x 150 magnification, and were collected from sample 1 of bed 1; the middle Eocene (Lutetian) of a section west of Beni Mazar city on the Nile Valley, Egypt. 1. Holotype (A 10132), Left side view of female carapace; 3, 5. Right side view of female carapaces; 2, 4. Ventral view of female carapaces.

Mazar city. Unfortunately, all the previous and presently studied specimens are complete carapaces; as a result, the internal features could not be observed. However, the new species externally differs from *Cyamocytheridea* Oertli, 1956, in having a distinct projection just behind mid-length and acuminate anterior and posterior margins. The maximum width is at mid-length in the new species, while it is posteriorly in *Cyamocytheridea*. Therefore, this form should not be assigned to *Cyamocytheridea*. On the other hand, because the new species has almost the same external characters of the genus *Digmocythere*, it is placed under that genus until the internal characters become available from a new material. Unfortunately, the characters essential for assignment of species to *Digmocythere* are the internal features (particularly the hinge). Further, the validity of that genus is questionable because of several factors: 1) the genus was named by a worker who used only published descriptions, but without actual observation of any specimens of the species; 2) the essential character for assignment to *Digmocythere*, a crenulate anterior hinge element, occurs in closely related species that are assigned to other genera; and 3) the American species and the northern African species, all of which were apparently shallow-water taxa, were separated by the Atlantic Ocean during the Eocene, so it is not clear how they are genetically related. Only observation of the muscle scars and the hinge will give clues regarding the phylogenetic distance of these species.

Occurrence - The Maghagha Formation; the middle Eocene of a section west of Beni Mazar city, bed nos. 1-5 and top of bed no. 8.

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APPENDIX

Raw data used for the canonical variate analysis

Measurements were made twice from scanned SEM photographs, one after discarding the magnification factor and the other with considering it. The results of the analysis were approximately the same in both cases indicating that the magnification factor was not affecting the analysis as a result of the constant ratio of the dimensions measured for each specimen. The following measurements are based on discarding the magnification.

The length of the carapace (L), the height of the carapace (H), the distance from the eye tubercle to the maximum end of the posterior margin (P), the distance from the eye tubercle to the maximum end of the ventral margin (V) and the length of the hinge (G)

Digmocythere cronini

L	*H*	*P*	*V*	*G*
3.3	1.6	2.8	1.9	2.1
3.5	1.7	3.0	2.0	2.2
4.8	2.8	4.0	3.0	2.5
4.9	2.9	4.4	3.0	2.6
4.7	2.6	3.7	2.6	2.2
6.1	3.7	5.0	4.0	3.5
4.7	2.2	3.7	2.5	3.0
3.5	1.9	3.0	2.1	2.0
3.4	1.8	2.8	2.0	1.9

Digmocythere omarai

L	H	P	V	G
3.6	2.0	2.8	2.1	2.1
5.2	3.0	4.8	3.2	2.5
2.2	1.4	1.8	1.5	1.3
3.9	2.2	2.8	2.3	1.8
4.1	2.2	3.2	2.2	1.8
4.3	2.3	4.0	2.5	2.5

Digmocythere ismaili

L	H	P	V	G
3.6	2.2	2.9	2.3	2.0
4.0	2.3	3.6	2.6	2.4
3.5	2.2	3.0	2.4	2.0
4.1	2.3	3.1	2.5	2.5
4.0	2.3	3.1	2.4	2.0
4.2	2.5	3.4	2.6	2.2
5.1	3.2	4.2	3.5	2.7
5.6	3.5	4.5	4.8	3.0
5.4	2.9	4.8	3.5	3.0
4.1	2.5	3.4	2.7	2.5
4.2	2.2	3.4	2.7	2.5
5.3	3.0	4.0	3.2	3.0