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MORPHOMETRIC RELATIONSHIPS AMONG UPPER CRETACEOUS SAMPLES OF *Oertliella tarfayensis* REYMENT (CRUSTACEA, OSTRACODA)

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ABSTRACT

The single species analysed in this paper is from the Tarfaya Basin, southwestern Morocco; the material studied range in age from Turonian to Santonian. At least two morphotypes differentiated by their reticulum size may be distinguished. This ornamental variation seems discontinuous in nature. Continuous polymorphism occur also within all morphotypes, as far as can be judged from the variable expression of the reticulum muri. The Santonian part of the sequence is dominated by a punctate morphotype which is ornamentally distinctly different from other forms in the sequence studied, although it cannot be distinguished with respect to size and shape according to pertinent multivariate statistics.

Keywords: Ostracoda, Cretaceous, Polymorphism, Multivariate analysis, Morphometry.

RESUMEN

La única especie de ostracodos estudiada aquí proviene de la cuenca sedimentaria de Tarfaya en el suroeste de Marruecos. La edad de los cortes estudiados es Turoniense a Santoniense. Dos o tres morfotipos pueden diferenciarse en cuanto al tamaño de los hoyos de la reticulación. Se trata probablemente de una expresión de polimorfismo discontinuo, aunque hay también polimorfismo continuo en la reticulación de cada morfotipo. Sin embargo, el Santoniense está dominado por un morfotipo bien definido por sus hoyos pequeños. El mismo morfotipo no se diferencia de los otros en lo que concierne al tamaño y forma del caparazón, según los resultados de un detallado análisis estadístico.

Palabras clave: Ostracodos, Cretácico, Polimorfismo, Análisis estadístico multivariante, Morfometría.

INTRODUCTION

According to Reyment (1985, 1988a, 1988b), there are different types of polymorphism known to affect the carapace morphology of ostracods. The most common is the continuous "ecophenotypic polymorphism" which is mainly produced by ambiental variation in salinity, temperature and depth. A continuous variation may, however, also be produced by genetical variation, although genetical variation is more easily identified when the expression is discontinuous (i.e. producing discrete morphotypes without the presence of intermediates). Clark (1976) introduced the term "environmentally cued polymorphism" for a kind of variation where an interaction between the genome and environmental stimuli in time favor the expression of a particular, discrete morphotype.

Polymorphism occurs in the material investigated here. The collection derives from a composite section in Tarfaya, southwestern Morocco, and comprises a single species ranging from Upper Turonian to Santonian. Oertli (1966) gave a brief account of this composite section and a detailed description of the species. He differentiated three discrete morphotypes, and claimed that at least two of these occur together and alternate at different frequencies throughout the entire section. The presence of what may be environmentally cued polymorphism is a common phenomenon among Tarfayan ostracods, as has been shown by Reyment (1978, 1982a). This phenomenon may have evolutionary significance and may play a major role in speciation transition (Reyment 1982a, 1988a).

The ecological history of the Tarfayan basin during the Mid- and Upper Cretaceous is difficult to interpretate, but have been evaluated by Wiedmann *et al.* (1978) who claimed that the sediments are typically of deep-sea origin. However, according to Reyment (1982a), this interpretation is far from unchallengeable, because the fossil evidence is hardly in favor of such an interpretation. An abundance of stranded ammonite shells of various morphologies is indicative of near-shore environments. Nevertheless, the conditions were such as to allow of the presence of a monotypic fauna of *Oertliella tarfayensis.*

Twelve to fifteen samples containing a single ostracod species and without information on chemical and physical properties of the sediment (cf. Reyment 1988b, pp. 258-261), cannot provide enough information for an evolutionary analysis. The object of the present report is simply to express, quantitatively, the morphological variation exhibited by the species throughout the sequence, by using various multivariate statistical methods. This is attempted mainly by determining the relationship between size, shape of carapace outline and type of ornament from sample to sample, and by investigating whether the variation among these parameters is integrated in any manner.

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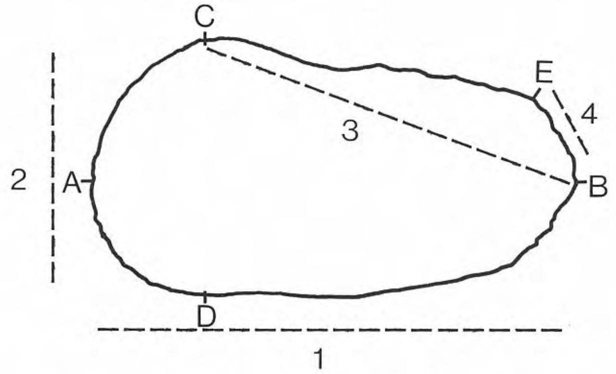

Figure 1. The distance measures of the carapace, defined as distances between landmarks A, B, C, D and E.

MATERIAL AND METHODS

The location and stratigraphical position of the Tarfayan, ostracods dealt with here, are reviewed by Oertli (1966, figs. 2, 3). The present study was restricted to less than half of the 36 samples reviewed by Oertli (1966). The yielded only *Veenia* n. sp. Oertli, 1966.

Apart from basic univariate statistics, the methods of eigenshape analysis, principal coordinates, discriminant analysis, principal components and canonical variates were used for analysing size and shape variation within the species. Males and females were treated separately by the three former methods, all 15 sample-levels for females, but only 12 for males, due to an insufficient number of specimens of this sex in three samples. For the same reason, the female samples had to be reduced to 12 in number, and the male samples to 11, before they simultaneously were subjected to a canonical variate analysis. Between 6 and 12 specimens were analysed in most samples. In addition to this, six of the male samples and six of the female samples, respectively, were analysed with respect to their shape coordinates by a method known as tensor biometrics, in order to analyse shape variation.

The characters chosen for study (cf. Fig. 1) are four distance measures of the left valve: (1) the length of the carapace, (2) the maximum height of the carapace measured at the anterior cardinal angle, (3) the distance between the eye-tubercle and the posterior extremity, and (4) the length of the posterodorsal margin. These were the characters analysed by all statistical methods mentioned above, except for the eigenshape analysis.

SYSTEMATICS

Oertliella tarfayensis Reyment, 1978

Plate I, figs. A-L; Plate II, figs. A-U.

? 1959	Ostracode B3, Glintzboeckel & Magné, 58, pl. 3, fig. 25.
? 1965	*Anticythereis?* sp. 1, Masoli, 123, pl. 1, figs. 5a.
1966	*Veenia?* n. sp. Oertli, 268-271, pl. 2.
1978	*Oertliella? tarfayensis* Reyment, 26, pl. 1, figs. 1-14, pl. 2, figs. 1-3.
1979	*Oertliella tarfayensis* Reyment; Reyment, 40, pl. 1, figs. 1-6.
1982a	*Oertliella tarfayensis* Reyment; Reyment, 411, figs. 2e-f,h.
1982b	*Oertliella tarfayensis* Reyment; Reyment, 295, pl. 1, figs. 1-16.

The speciments treated here were originally studied by Oertli (1966). They are particularly difficult to assess taxonomically due to their extreme ornamental variability. They are here assigned to *Oertliella tarfayensis,* a species which, according to Reyment's (1978) description, displays an even greater variability. In that description, the stratigraphical range of the species is given as Late Cenomanian to Early Turonian, whereas the present specimens are known from Turonian to Santonian. Apart from the ornamental variability, the specimens display a prominent sexual dimorphism with males being longer and more rectangular than females.

I have not followed Vivière (1985) who referred *Oertliella tarfayensis,* among other West African forms, to *Reticulocosta* gr. *vitiliginosa* Apostolescu, although a further examination of his conclusion may prove to be valid. This is needed, but beyond the scope of this investigation. See Vivière (1985) for further details concerning the synonymy of *Reticulocosta* gr. *vitiliginosa.*

According to Oertli (1966), the specimens may be differentiated into three ornamental types. The first two types show notable plications of the valve surface. The first type, which dominates the Turonian, displays a pattern of reticulation with comparatively wide fossae, and differs from the second type in lacking secondary subdivision of the primary fossae. The second type alternates with the first during the Turonian and Coniacian. However, the present investigation has not been succesful in differentiating between these two types (see below). The third type (Plate I, figs. K, L; Plate II, figs. R, S, T, U), which emerges in the transition zone Coniacian-Santonian and dominates the Santonian, is quite

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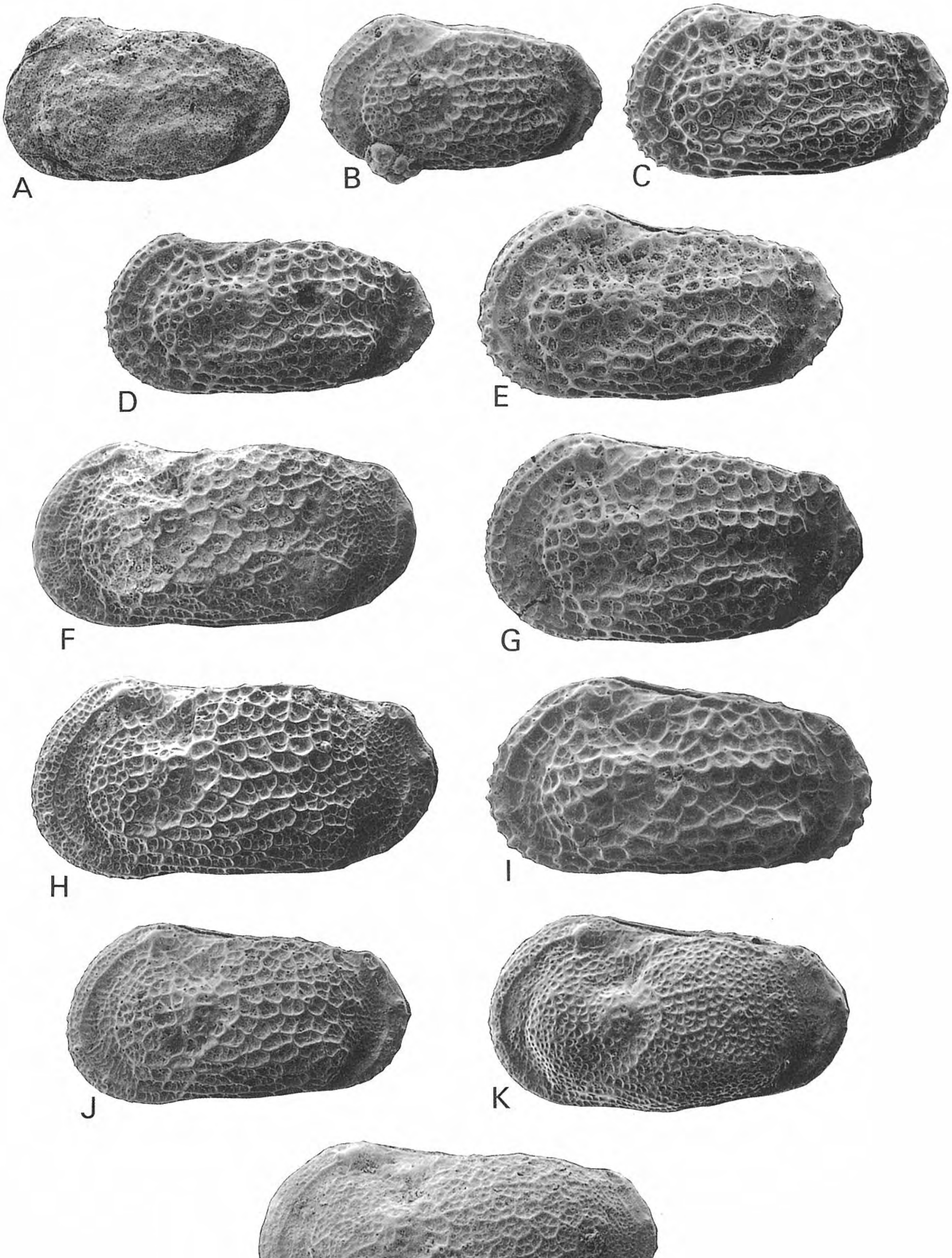
Plate I

Carapaces in left lateral view. All photographs approximately x 60. **A.** female from sample T416, **B.** female from sample T226, **C.** female from sample T105, **D.** male from sample T86, **E.** female from sample T106, **F.** male from sample T232, **G.** female from sample T405, **H.** male from sample T30, **I.** female from sample T406, **J.** female from sample T32, **K.** female from sample T34, **L.** male from sample T36.

Plate I



distinctive in lacking plications on the regularly inflated valve surface. The surface displays 5-10 secondary fossae within each of the primary ones creating an almost punctate pattern. The term "transition zone" was preliminary introduced by Oertli (1966), and refers to a range including the Coniacian-Santonian boundary; the latter cannot be determined due to lack of faunal documentation.

Contrary to the earlier forms, minute denticles are almost completely reduced in the third morphotype. According to Oertli (1966), there is a significant increase in average-size across the Turonian-Coniacian boundary, whereas there is no significant size fluctuation among later representatives. Oertli (1966), however, did not give any statistical evidence for this.

In connection with the present research, specimens from the entire sequence were studied using the SEM. These SEM-photos demonstrate that there is no rigid distinction between the first and second morhotypes of Oertli (1966). There are very few individuals, if any, that entirely lack secondary subdivision of the primary fossae, particularly on the dorso- and ventromedian regions of the valve surface. Oertli (1966, p. 271) also mentioned these difficulties even between ornamental type 2 and 3. Another feature common to all morphotypes, is a variable expression of the primary muri, although part of the underlying causes of this variation might be diagenetic. The ornamental features of specimens from each stratigraphical level are here investigated in ascending order (cf. Oertli 1966, p. 270). The results are summarized below:

T 416 - Turonian. Only females available. Valve surface poorly preserved, irregular and appearing granular in its present state (Plate I, fig. A; Plate II, fig. A).

T 478 - Coniacian. Primary reticulation with comparatively large fossae, rough and irregular muri. Secondary muri interconnecting the primary occur (Plate II, fig. B).

T 226 - Coniacian. Primary reticulation with irregular, granular muri. Irregular secondary muri interconnecting the primary also occur. Antero- and posteromarginal region with indistinct reticula (Plate I, fig. B; Plate II, figs. C, E).

T 105 - Coniacian. Variable expression of the reticulum. Some individuals with smooth, prominent primary muri, others with thinner, less regular muri. Secondary muri hardly discernible centrally, but more abundant ventromedianly. Individuals with prominent median muri also display rectangular fossae antero- and posteromarginally (Plate I, fig. C; Plate II, figs. D, F).

T 86 - Coniacian. Reticulum with smooth, prominent primary muri. Secondary muri only dorso- and ventromedianly. Anteromarginal area with rectangular fossae (Plate I, fig. D; Plate II, fig. G).

T 207 - Coniacian. Reticulum with irregular, moderately developed primary muri. Secondary muri only vaguely discernible centrally (Plate II, fig. H).

T 106 - Transition zone Coniacian-Santonian. Reticulum with smooth, stout primary muri centrally. Secondary muri sparse in this region. Anteromarginal area with rectangular fossae (Plate I, fig. E; Plate II, fig. I).

T 232 - Transition zone Coniacian-Santonian. Primary muri variably expressed. Feebly developed on some individuals where they almost merge with the underlying surface; more protruding and irregular on other individuals. The latter forms also show tiny secondary muri centrally, and display a dense network of antero- and posteromarginal foveolae (Plate I, fig. F; Plate II, figs. J, K).

T 405 - Transition zone Coniacian-Santonian. Primary reticulation with stout muri; minute secondary muri present centrally; more abundant and prominent ventrally. Antero- and posteromarginal reticulum comparatively indistinct (Plate I, fig. G; Plate II, fig. L).

T 242 - Transition zone Coniacian-Santonian. Primary reticulum with comparatively wide fossae centrally, and prominent, irregular muri. Minute secondary muri also present centrally (Plate II, fig. M).

T 30 - Transition zone Coniacian-Santonian. Reticulation variable. On some individuals, comparatively large fossae occur centrally with thick, somewhat irregular, primary muri but no secondary muri. The same region on other individuals displays smooth slender primary muri which are interconnected by secondary muri. The latter forms bear a dense network of antero- and posteromarginal foveolae (Plate I, fig. H; Plate II, figs. N, O).

T 406 - Transition zone Coniacian-Santonian. Primary reticulum with comparatively large fossae, and somewhat irregular primary muri. Secondary muri only feebly developed centrally. Antero- and posteromarginal region with large rectangular fossae (Plate I, fig. I; Plate II, fig. P).

T 32 - Santonian. Primary muri somewhat irregular and interconnected by secondary muri centrally. Size of primary fossae variable, very large to moderate. Antero- and posteromarginal areas foveolate (Plate I, fig. J; Plate II, fig. Q).

T 34 - Santonian. The ornament corresponds to Oertli's (1966) morphotype 3, although the reticulation is variably expressed. Some individuals are almost smooth, showing only ghost-like traces of reticula. The surface of other, more abundant individuals, appear punctate since it is barely possible to distinghish between primary and secondary muri. The fossae are small and rounded, and diminish in size towards the antero- and posteromarginal region (Plate I, fig. K; Plate II, figs. R, S).

T 36 - Santonian. This ornament also corresponds to Oertli's (1966) morphotype 3. The expression of the reticulum is also variable. Some individuals show feebly developed muri almost completely merging with the valve surface. However, contrary to the individuals of level T 34, there is a distinct difference in the strength of the expression of the primary and secondary reticula on the more prominent reticulated morphotypes. There are 5-10 secondary fossae within each primary fossa. Antero- and posteromarginal area foveolate (Plate I, fig. L; Plate II, figs. T, U).

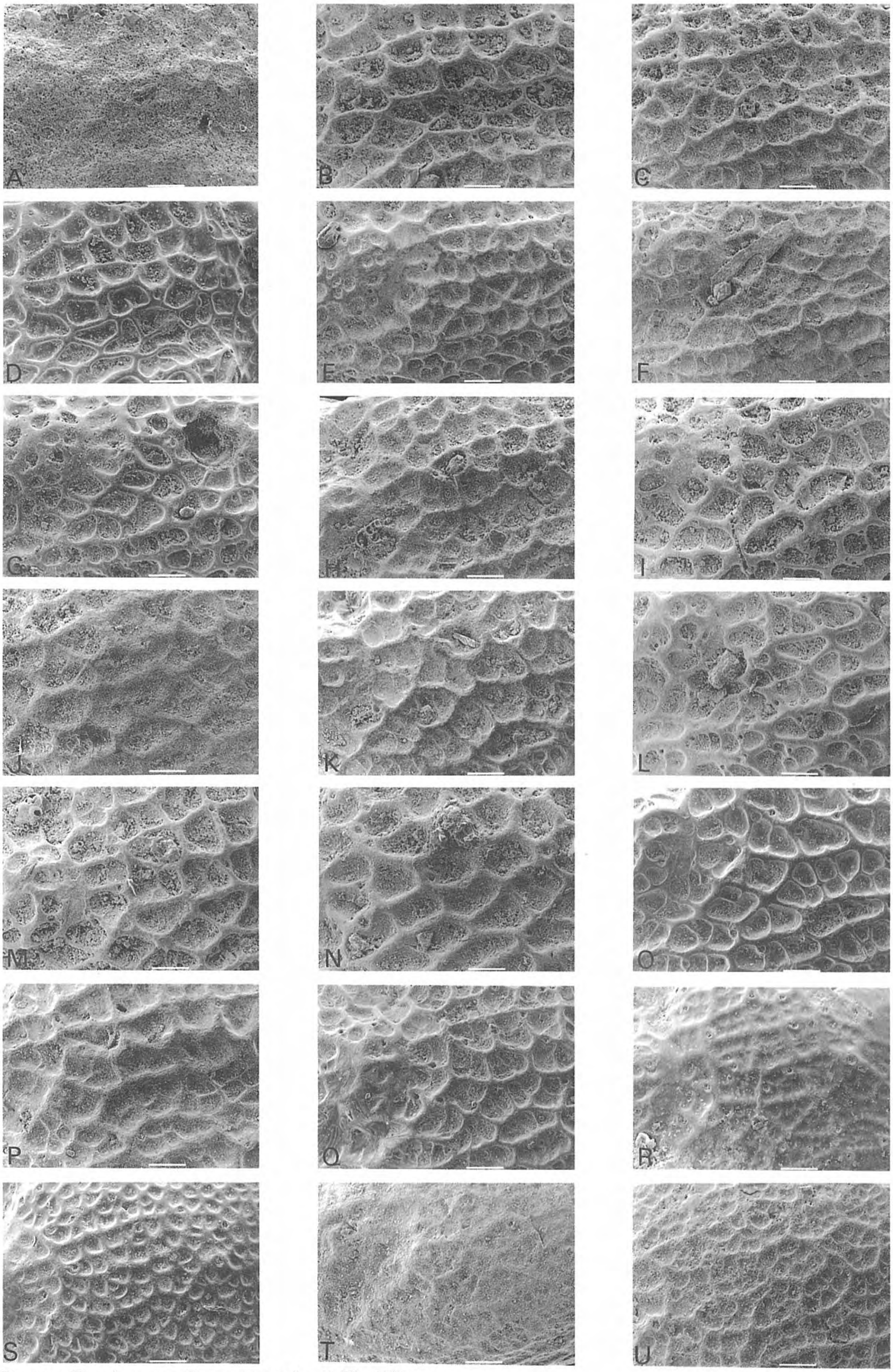
STATISTICAL ANALYSIS

The basic statistics concerning all samples of

Plate II

Details of carapace ornament of females in lateral view. All photographs approximately x 125. **A.** T416, **B.** T478, **C.** T226, **D.** T105, **E.** T226, **F.** T105, **G.** T86, **H.** T207, **I.** T106, **J.** T232, **K.** T232, **L.** T405, **M.** T242, **N.** T30, **O.** T30, **P.** T406, **Q.** T32, **R.** T34, **S.** T34, **T.** T36, **U.** T36.

Plate II



	Means and standard deviations var1	var2	var3	var4
Females	0.951	0.510	0.760	0.183
(N=134)	(0.046)	(0.023)	(0.038)	(0.012)
Males	1.133	0.545	0.913	0.202
(N=91)	(0.060)	(0.028)	(0.046)	(0.016)
Females & Males	1.024	0.524	0.822	0.191
(N=225)	(0.104)	(0.031)	(0.086)	(0.017)

Table 1. Basic statistics for all samples of *Oertliella tarfayensis;* values within brackets are standard deviations.

	var1	var2	var3	var4
var1	1.000	0.786**	0.929**	0.363**
var2		1.000	0.741**	0.370**
var3			1.000	0.343**
var4				1.000

Table 2. Pooled correlation matrix based on 23 samples of males and females (N = 217) (the characters ** indicate a statistically significant value at $p < 0.01$).

Oertliella tarfayensis are given in Table 1. The correlations among the variables are given in Table 2. According to an univariate analysis of variance (ANOVA), all differences among all sample means for all variables are highly significant ($p < 0.01$). This test concerns the raw data as well as the logarithmically transformed data. The results of the logarithmic data are given in Table 3.

Although Oertli (1966) distinguished three ornamental morphotypes, he called attention on the fact that it is not always easy to assign a particular specimen to a particular morphotype, since there are intermediates between the first and the second as well as between the second and the third morphotypes. The present investigation, although based on a considerably smaller number of specimens, confirms and emphasizes the difficulties in differentiating between members of the first and the second morphotype, whereas the third, punctate morphotype, which dominates the Santonian, appears perfectly distinct. According to Oertli (1966, fig. 2), at least two of the morphotypes, sometimes all three, are found together, although in differing proportions. In the present study, however, it has not been possible (in samples T416-T30) to distinguish between the first and second

Table 3a-h. One- and two-way analysis of variance (ANOVA) for all logarithmically transformed variables of the two sexes, respectively.

a) 1st variable for females.

Source	df	ss	ms	f
A	14	0.1957	0.0140	18.0270
S/A	119	0.0923	0.0008	
Total	133	0.2880		

b) 2nd variable for females.

Source	df	ss	ms	f
A	14	0.1289	0.0092	10.6368
S/A	119	0.1030	0.0009	
Total	133	0.2320		

c) 3rd variable for females.

Source	df	ss	ms	f
A	14	0.1914	0.0137	13.4874
S/A	119	0.1206	0.0010	
Total	133	0.3120		

d) 4th variable for females.

Source	df	ss	ms	f
A	14	0.1583	0.0113	2.7228
S/A	119	0.4941	0.0042	
Total	133	0.6524		

e) 1st variable for males.

Source	df	ss	ms	f
A	11	0.2062	0.0187	26.6016
S/A	79	0.0557	0.0007	
Total	90	0.2618		

f) 2nd variable for males.

Source	df	ss	ms	f
A	11	0.1938	0.0176	24.0523
S/A	79	0.0579	0.0007	
Total	90	0.2516		

g) 3rd variable for males.

Source	df	ss	ms	f
A	11	0.1847	0.0168	21.3922
S/A	79	0.0620	0.0008	
Total	90	0.2467		

h) 4th variable for males.

Source	df	ss	ms	f
A	11	0.3146	0.0286	9.0920
S/A	79	0.2485	0.0031	
Total	90	0.5632		

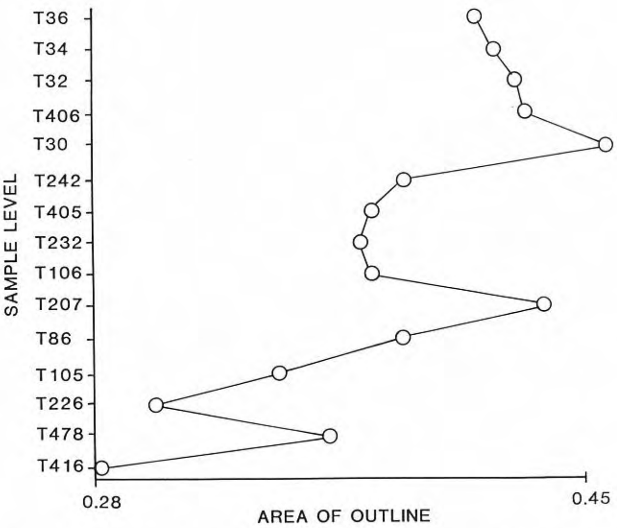


Figure 2. Plot of the average lateral areas against stratigraphical level for females, 15 samples.

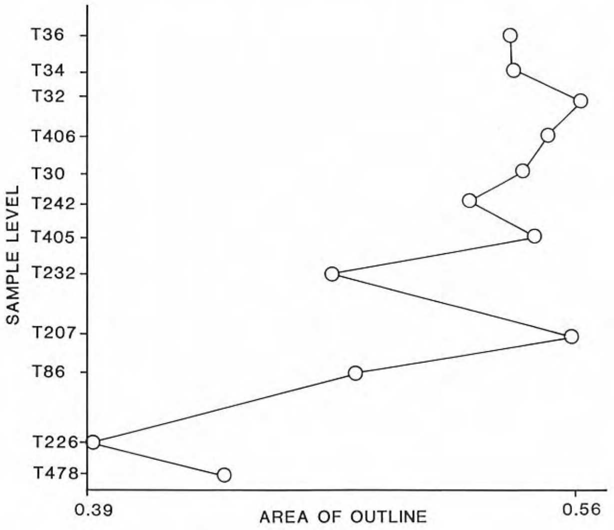


Figure 3. Plot of the average lateral areas against stratigraphical level for males, 12 samples.

morphotypes when subjected to the statistical analysis.

All individuals (males and females) were initially subjected to a principal component analysis and plotted in the plane of the first two principal components which together represent about 95 % of the total variation. The first component, with an eigenvalue of 3.39, is given by the following equation: $Y_1 = 0.53X_1 + 0.50X_2 + 0.52X_3 + 0.44X_4$; and the second component, with the considerably smaller eigenvalue of 0.41, by $Y_2 = 0.25X_1 + 0.25X_2 + 0.27X_3 - 0.90X_4$. The computations were made on the correlation matrix of the raw data. No clear groupings exist emong the samples except for the usual subdivision into males and females, which is expressed along the first principal component axis. This means that sexual dimorphism is mainly related to size differences.

In order to gain further information on the homogeneity of the samples, principal coordinate analysis, a technique which provides information on the geometrical distances between individuals was employed. Reyment *et al.* (1984) provide a detailed description of this method and discuss its biological significance. In the present connection, males and females were subjected independently to this method. After extracting the two first roots from the raw data, the percentage residual for this sum is 48.65 % for females and 41.79 % for males. Stabilizing the size variation by taking logarithms of the raw data did nothing to change the pattern displayed by a plot of the individuals in the plane of the first and second coordinate axes. The plots (Figs. 4, 5) disclose the familiar parabolic pattern, a phenomenon discussed by Seber (1984). They both (Figs. 4, 5) reveal that one end of the parabola is occupied by sample T207 and the other end by sample T226, whereas the median region is mixed by the other samples. The distribution of the specimens in the vectorial space (Figs. 4, 5) reveals that no morphometric trend exists.

These results were compared with the average-size of the carapace outline of each sample (Figs. 2, 3). The area of the outline was estimated by trapezoidal integration of cartesiane coordinates computed from points digitized along the carapace outline

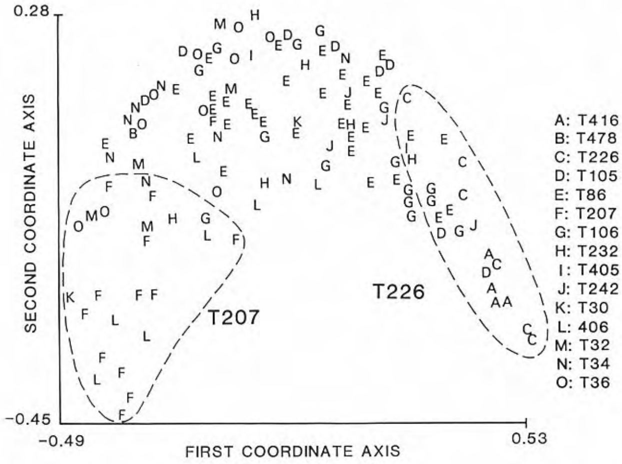


Figure 4. Principal coordinate analysis of females, 15 samples.

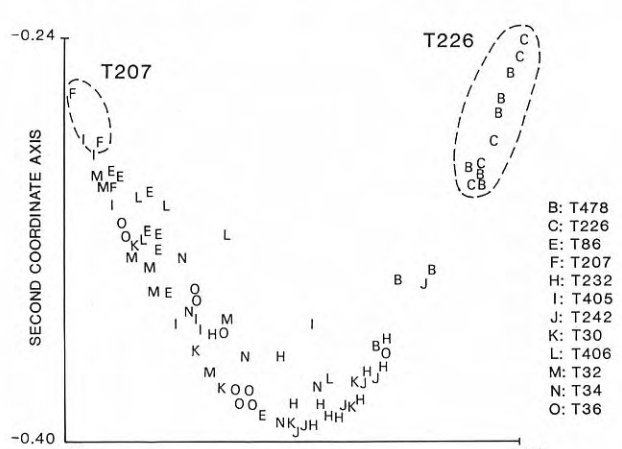


Figure 5. Principal coordinate analysis of males, 12 samples.

by a microprocessor-controlled video image digitizer. Figs. 2 and 3 reveal the fluctuations in average-size through time for males and females, respectively, and show mainly a semi-continuous trend towards increasing size. These trends were tested by Runs Test (cf. Davis 1986, p. 170), and a method which tests the significance of all increments together (cf. Raup & Crick 1981, p. 211). The results say that no statistically significant trend exists.

A technique known as eigenshape analysis was used here in order to unravel differences in outline among the samples. The method (Lohmann 1983), has the advantage of describing outline independently of size and orientation. Males and females were subjected independently to this analysis. The steps taken by Lohmann (1983) were followed in extracting the first eigenshape of each sample and submiting these to an additional eigenshape analysis in order to minimize within sample sources of shape variation. Schweitzer *et al.* (1986) and Maness & Kaesler (1987) have succesively applied this technique to the study of ontogenetic shape changes among ostracods. The result of the present analysis shows that no trend at all could be found along the second eigenshape, i.e. the shape vector responsible for the major contrast in shape, according to Lohmann (1983).

Another way of studying shape variation is by shape coordinates (cf. Bookstein *et al.* 1985; Bookstein 1986). Such methods are based on analysing landmarks that are homologous from form to form. In my case, the points A, B, C, D and E in Fig. 1 were selected, i.e. the endpoints of the distant measures used in the previous analysis above. For shape variation that is not too great, as expected in my case, the analysis and interpretation of changes in landmark locations proceed effectively when the landmarks are considered three at a time in a set of triangles distributed over the forms to be studied. A complete coverage of N landmarks requires N-2 triangles (cf. Bookstein 1986). The morphometric analysis of the shape of a triangle XYZ is equivalent to an ordinary normal model multivariate analysis of the pair of coordinates assigned to landmark Z in a cartesiane system for which X is always located at (0, 0) and Y at (1, 0). XY is referred to as the "baseline". This construction results in the shape coordinates of the triangle (cf. Bookstein *et al.* 1985, pp. 230-232).

In the present case the five landmarks A, B, C, D, and E were subjected to a shape coordinate analysis. Males and females were considered independently. Only six samples of males and females, respectively, were analysed, because the plots would be very crowded if all observations were to be included. Triangles ABC, ABD and ABE were analysed. In all cases, there were practically no discrimination when the results were plotted. The conclusion is therefore that the samples are very homogenous, and the shape variation slight indeed, according to this analysis; differences are therefore due to size.

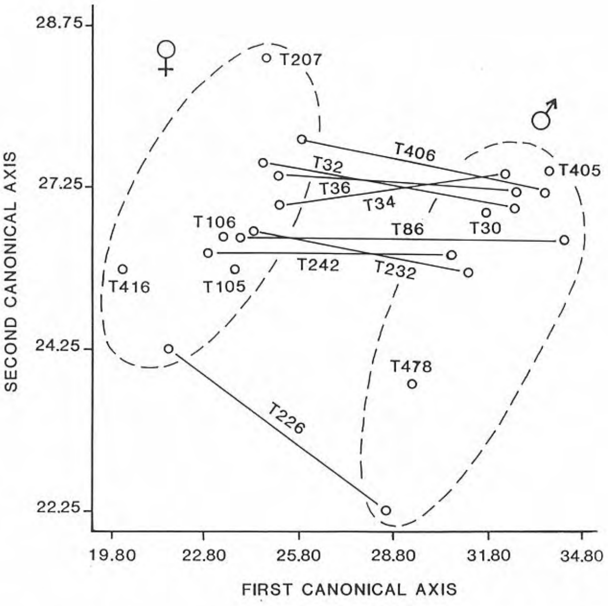


Figure 6. Canonical variate means for 23 samples (12 female samples and 11 male samples) plotted in the plane of the first and second standardized canonical variate axis.

Each sample was subjected to a Gaussian Q-Q probability plot, in order to detect atypical values at the multivariate level. A few atypical values were found in a few of the male and female samples, a circumstance which induced me to use the robust method of canonical variate analysis which reduces the effects of atypical values (Campbell & Reyment 1980). Compared with principal components and principal coordinates, canonical variate analysis has obviously a stronger discriminatory power, because contrary to the former methods, canonical variates is an allocation technique developed for discriminating among previously distinguished groups. The significance of this method and its applicability has been discussed at length by Reyment *et al.* (1984).

In the present case, the means of each group were plotted in the plane of the first and second standardized canonical variate axes (Fig. 6) which are specified by the equations: $Z_1 = 1.47X_1 + 0.38X_2 - 1.62X_3$ and $Z_2 = -0.77X_1 + 1.32X_2 - 0.42X_3$. The first canonical variate axes mainly reflects sexual dimorphism, whereas the second axes emphasizes mainly the segregation between samples T207 and T226. The results of the analysis are consistent with the general picture of homogeneity yielded by the previous multivariate methods. The analysis reveals that sex differences in the used parameters are more important than intersample differences.

The generalized Mahalanobis distances between consecutive samples were calculated using stepwise discriminant analysis, according to the program BMDP7M (Dixon & Brown 1979). When all four variables were included in the calculations, the following distances were significant for females ($P < 0.01$): T416-T478, T478-T226, T226-T105, T86-207, T207-T106 and T242-T30, but not T105-T86. For the males, the following distances were significant: T226-T86, T207-T232, T232-T405, T405-T242, T30-T406 and T406-T32, but not T86-T207.

SYNOPSIS

The most interesting event in the sequence studied, is the sudden dominance of the punctate morphotype (level T34-T36), which is morphologically easily distinguished from other morphotypes with respect to ornament, but not with respect to size and shape, according to the multivariate analysis. Despite the multivariate analysis, which mainly analysed size and shape variation, the ornamental differences between this morphotype and other forms are here regarded as discontinuous (i.e. of kind rather than degree), as far as can be judged from visual inspection.

The dominance of the punctate morphotype may possibly be an expression of environmentally cued polymorphism (Clark 1976), where the ecological conditions favor the expression of this morphotype at the expence of other forms. It seems, however, futile to discuss environmentally cued polymorphism, in this case, since there is no information available on whats going on in the environment.

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