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DIFFERENTIATION BETWEEN THE TRACES OF PREDATION OF MURICIDS AND NATICIDS IN SPANISH PLIOCENE *CHLAMYS*

S. Guerrero Alba* and R. A. Reyment**

RESUMEN

El análisis estadístico de los orificios perforados en las especies del género *Chlamys* del Plioceno Inferior del Sur de España aclara algunos aspectos muy interesantes sobre la predacción de los murícidos y natícidos. El análisis de la función discriminante se ha determinado como un método muy útil para identificar la naturaleza de los orificios, son muy pocos los errores de identificación para los especímenes analizados. En concreto, se ha podido establecer diferencias significativas en las relaciones entre los predadores y las presas. Se ha podido responder afirmativamente a la cuestión de cómo eligen los sitios preferentes para la localización de las perforaciones en el caso de los murídicos. También, para los murícidos la mayoría de las perforaciones observadas (74,1%) se ha concentrado en la región del músculo abductor; en cambio, para los natícidos no se ha observado este techo (sólo un 36,9%, de perforaciones en la región del músculo abductor). Para los natícidos se ha podido demostrar una asociación entre el lugar de la presa donde se producen las perforaciones y predador, únicamente cuando se toman en cuenta presas de muchas especies y géneros distintos. También existe una estrecha asociación entre el tamaño de la presa y el lugar donde perforan ambos grupos de predadores. No hay una evidencia decisiva que permita correlacionar la localización de las perforaciones para los natícidos, pero probablemente si la haya para los murícidos.

La estrategia de selección del lugar de la perforación para los murícidos se ha determinado en función del músculo abductor en los monomiarios *Chlamys* para facilitar el acceso a las vísceras.

En general, los métodos de análisis multivariado y en especial el método de correlaciones canónicas, se han encontrado como de gran ayuda en la interpretación de observaciones cuantitativas.

Palabras clave: *Predación de Gasterópodos, bivalbos, natícidos, murícidos, Plioceno, España.*

ABSTRACT

The statistical analysis of holes drilled in species of the bivalve genus *Chlamys* from localities in the Lower Pliocene of Southern Spain throws light on aspects of muricid and naticid predation. Discriminant function analysis was found to be a useful means of identifying the nature of boreholes, with but slight errors of identification for known specimens. In particular, significant differences in relationships between predators and prey could be established. The question as to whether preferred locations of boreholes occur could be answered affirmatively for muricids. Also for muricids, the majority of the observed boreholes (74.1%) are concentrated to the region fo the adductor muscle: such a relationship could not be definitely proven for naticids (36.9% within the adductor muscle field). An association between the site of the prey and predator could only be demonstrated for naticids in connexion with prey of several species and genera. There is a strong association between the size of the prey and the site chosen for drilling for both groups of predators. There is indecisive evidence for a correlation between the location and size a drillhole for naticids, but probably not for muricids.

The strategy of selection of a drilling site by muricids seems to be to weaken the function of the adductor muscle in the monomyarian *Chlamys*, hence facilitating access to the viscera.

In general, multivariate analytical procedures, and especially the method of canonical correlations, were found to aid greatly the interpretation of the quantitative observations.

Key words: *Gastropod predation, bivalves, naticids, muricids, Pliocene, Spain.*

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Introduction

Muricidds and naticids have been important predators of bivalves, gastropods, cirripedes, ostracods and foraminifers (Livan, 1937; Reyment, 1966) since the early Cretaceous, notwithstanding that their predational history extends much further back in time (Maddocks, 1988). Inasmuch as they leave unequivocal evidence of their predational activity, they are valuable ecological indicators. The traces left by these predators in molluscan shells, in particular, are usually identifiable. Thus, the holes drilled by muricids are characterized by having their external and internal openings of about the same size, with the external diameter only slightly greater which, because of the straight walls of thehole, confer a conical shape to the orifice. The holes drilled by naticids are usually countersunk in shape, with the external opening being considerably wider than the internal opening; the walls tend to follow a parabolic course. A detailed appraisal of the morphology of gastropod boreholes is to be found in Carriker and Yochelson (1968).

The aims of the present investigaiton are directed towards elucidating the following points: 1. The eventual usefulness of multivariate statistical analysis for distinguishing between holes drilled by naticids and muricids. 2. The association between the size of the prey and the dimensions of the borehole: 3. The eventual association between the holes made by the drills in *Chlamys* and the size of the prey. 4. Does the size of the borehole in *Chlamys* show a relationship with its position? 5. Is their a difference in the strategy employed by muricids in their predation on species of *Chlamys*?

Material and methods

The material studied here was obtained from exposures in the Lower Pliocene of the Río Padrón in the Province de Málaga (Spain) (fig. 1). These samples yielded several species of bivalves belonging to a number of genera which display abundant evidence of gastropod predation. In addition, species of the bivalve genus *Chlamys* (are indicated in figs. 3, 4, 5, 6, 7, 8) from various localities in the Lower Pliocene around the city of Málaga were available. These localities are indicated in fig. 1. They are all dated as belonging to the zone of *Globorotalia margaritae*.

The coordinates of the exposures sampled are: Arroyo Hornacinos, 36° 34' 4.5" latitudee N-5° 36' longitude E. Rio Padrón, 36° 33' 21.4" latitude Ní5° 39' 54" longitude E. Rio Velerin, 36° 33' 14.2" latitude N-5° 43' 12" longitude E. Rio Guadalmansa, 36°

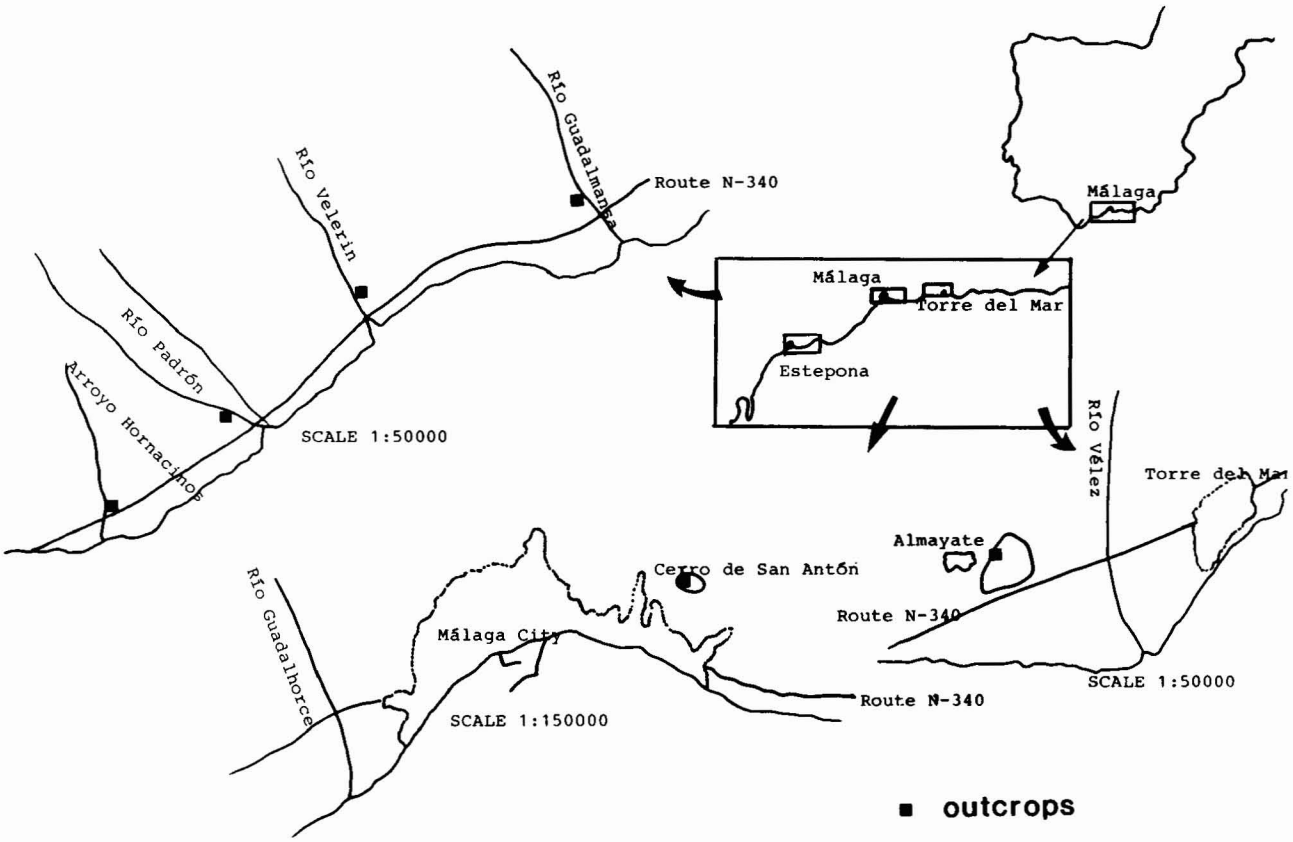

Fig. 1.—Sketch map showing the localities samples for the present study. These all lie in the Province of Málaga and are Pliocene in age.

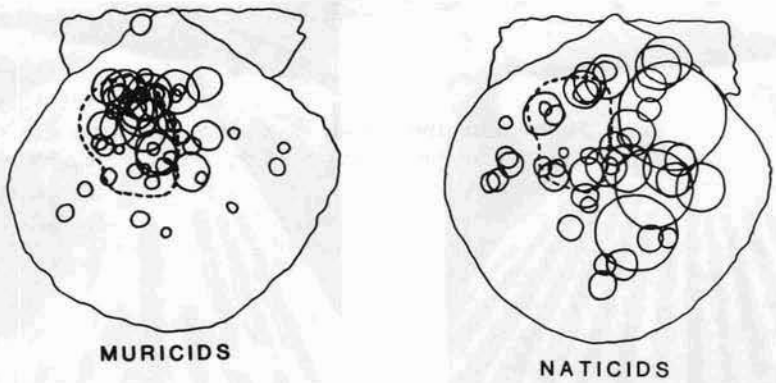

Fig. 2.—Pope diagrams displaying the locations of 54 drillholes made by muricids and 46 by naticids in *Chlamys*. The dashed lines denote the probably location of the adductor muscle. There are 40 muricid holes situated within the adductorial field (74.1%) and 17 naticid holes (36.9%) in this field.

32' 31.1" latitude N-5° 48' 27" longitude E. Cerro San Antón, 36° 45' 14.2" latitude N-4° 54' 35" longitude E. Almayate, 36° 45' 12" latitude N-4° 36' 9" longitude E.

Measurements were made on the following characteristics of the holes and prey: DE=external diameter of the drillhole; DI=internal diameter of the drillhole; DOU=distance of the centre of the role from the tip of the umbone; DOB=distance of the centre of a hole from the anterior margin; L=length of the shell; A=width of the shell; G=thickness of the shell substance; C=curvature of the shell.

The data thus obtained were analyzed by standard methods of univariate statistics and by the multivariate statistical methods of linear and quadratic discriminant functions, canonical correlation analysis, and principal components.

Descriptions of these methods in biological contexts are provided by Reyment *et al.* (1984). The special application of canonical correlational analysis to gastropod predation is reviewed in Reyment *et al.* (1987).

Univariate or multivariate analysis?

We shall begin by addressing ourselves to the question of the utility of multivariate analysis in the present connexion. This can be done conveniently by considering the differences between the means for the external, respectively, internal openings of muricid

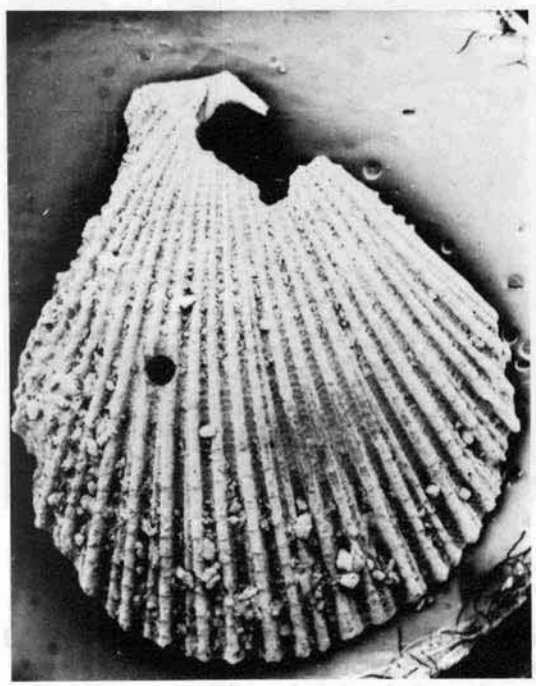

Fig. 3.—*Chlamys varia* displaying a muricid borehole. x10.

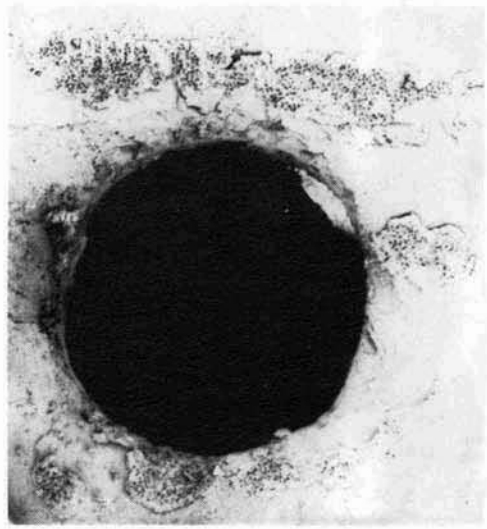

Fig. 4.—Enlargement of the borehole in fig. 3. x90.

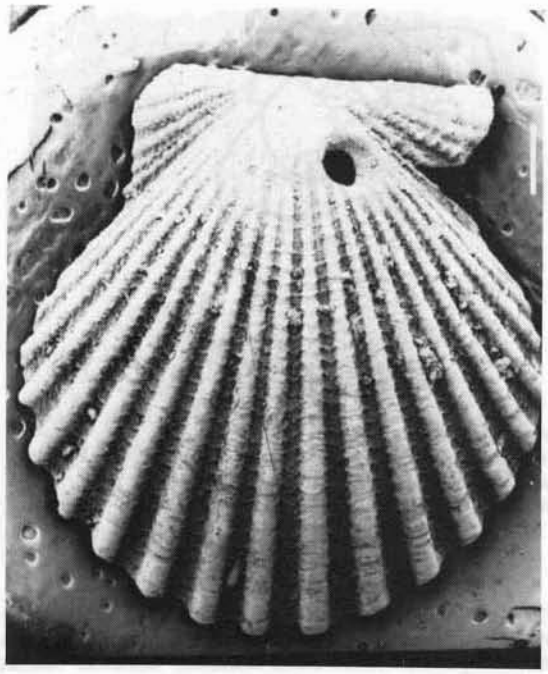

Fig. 5.—*Chlamys radians* displaying a naticid borehole. x10.

and naticid boreholes in species of *Chlamys*. A simple univariate test of the difference in external diameters, amounting to 0.507 mm., indicates a high level of significance, whereas the same test for the difference in internal diameters, to wit, 0.076 mm., is not statistically significant. A similar result was obtained for the mixed material from the Rio Padrón.

If, on the other hand, we examine the same set of

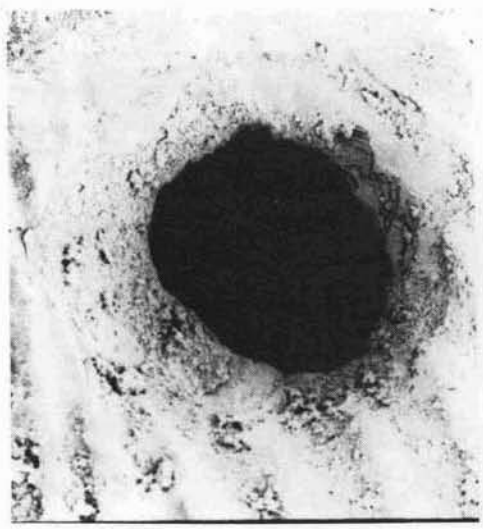

Fig. 6.—Enlargement of the hole shown in fig. 5. x70.

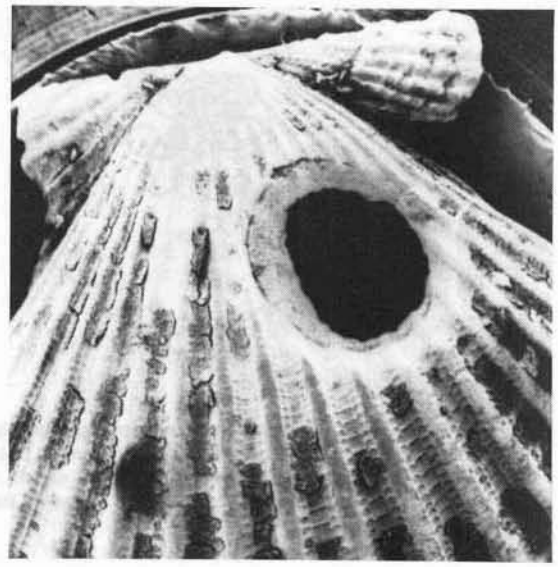

Fig. 7.—*Chlamys radians* showing a naticid borehole with marks made by the radula of the gastropod (upper right). x10.

Fgi. 8.—Enlargement of the radula traces of fig. 7. x300.

observations by means of the multivariate method of linear discriminant functions, using all variables on prey and predational holes, different conclusions are suggested. Table 1 summarizes the results for 54

Table 1.—**Linear discriminant function analysis for holes drilled by muricids and naticids in *Chlamys* spp. and the bivalves from the Rio Padrón.**

Chlamys	L	A	C	G	DE	DI	DOU	DOB
Vector of mean differences	—1.475	—1.646	—0.311	—0.064	0.507	0.076	0.075	—0.905
Linear discriminant coefficients	0.230	—0.142	—0.519	0.776	18.659	—19.041	—0.111	—0.004
Unbiassed generalized distance squared between groups=2.639								
Probability of misidentification=0.0935								
($N_{mur.}$=54; $N_{nat.}$=46)								
Rio Padrón	L	A	DE	DI				
Vector of mean differences	—2.554	—2.084	0.223	0.028				
Linear discriminant coefficients	—0.539	0.044	33.286	—37.095				
Unbiassed squared generalized distance=2.767								
Probability of misidentification=0.074								
($N_{mur.}$=33; $N_{nat.}$=49)								

muricid holes and 46 naticid holes drilled in *Chlamys* spp., and 39 muricid holes and 33 naticid perforations in the specimens from the Rio Padrón (using only variables L, A, DE and DI). In the first case, only 6.5% of the naticid holes were incorrectly located with those known to derive from muricids and, on the other hand, even less muricid holes were incorrectly allocated, namely, 3.7%.

In general, the linear discriminant function in table 1 for *Chlamys* provides an efficient means of distinguishing between naticid and muricid predation, as indicated by the highly significant value of the variance ratio $F_{8,77}$=23.13. The use of the corresponding quadratic discriminant function enabled a reduction in the levels of incorrect allocation to 1.85% for muricids and 6.5% for naticids, which is the same value as before.

In the case of the mixed sample of bivalves from the Rio Padrón, the discriminant function given in table 1 correctly identified allo but 8.2% of the naticid holes, and 3.0% of those made by muricids. The efficiency of this linear discriminant function is indicated by the highly significant value of $F_{4,77}$=39.78. The corresponding quadratic discriminant function produced exactly the same results as the linear function. As is apparent from table 1, almost all of the discriminatory effect is due to the properties of the boreholes, with little or no input from the dimensions of the prey.

To answer the question posed at the beginning of this section, the multivariate analyses were clearly able to provide a more nuanced and complete analysis of the data, in addition to giving us a means of allocating new material to one or other of the groups of predators on the basis of measurements on the borehole.

Sizes of predator and prey

The next question we ask is whether it is possible to establish a relationship between the size of the prey and that of the predator. Data on the prey are, naturally, easily enough come by. But how are we to estimated the size of the predator? This can be done, albeit in approximate terms, by making use of the fact that the dimensions of the accessory boring organ (ABO) are closely reflected in the size of the borehole. This observation derives from the careful work over more than 30 years of Carriker (1955, 1969, 1981); also Carriker *et al.* (1974). Valuable observations on this topic have been published by Wiltse (1980) and the growth-relationship between the ABO and the rest of the drill has been used by Reyment *et al.* (1987) for computing approximate sizes of drills. For our analyses, we made use of the rather complicated multivariate technique of canonical correlation analysis, in the expanded from, involving redundancy analysis (Coole and Lohnes, 1971), expounded in biological connexions by Pimentel (1979). The analyses based on the two measures on the boreholes and the length, width and thickeness of the shell of the prey indicated that for both groups of drills, the associations with the prey are far from achieving significance. In neither case does the degree of overlap between either groups (redundancy of one group given information on the other, i.e., the overlap between sets) reach a sufficiently high level for investing the canonical correlation in the entire sample. (N.B. canonical correlations are not representative of ranked fractions of total variation as is the case in principal component analysis.)

If we now proceed to the results obtained for the analysis of the material from the Rio Padrón, we find that, once again, there is no significant relationship between the size of the predator and the size of the drill for muricids and, in fact, the two sets are no

Table 2.—**Correlation matrices, standard deviations and means for species of *Chlamys* drilled by muricids and naticids.**

	Muricids (N=54)							Naticids (N=46)					
	DE	DI	L	A	C	G		DE	DI	L	A	C	G
DE	1.00	0.90	0.30	0.29	0.22	0.15	DE	1.00	0.95	0.15	0.15	0.12	0.16
DI		1.00	0.34	0.34	0.24	0.21	DI		1.00	0.05	0.04	0.01	0.05
L			1.00	1.00	0.92	0.84	L			1.00	0.99	0.92	0.79
A				1.00	0.92	0.85	A				1.00	0.94	0.82
C					1.00	0.90	C					1.00	0.83
SD	0.318	0.321	9.912	10.687	2.152	0.437	SD	0.515	0.425	8.258	8.700	1.689	0.371
Means	0.945	0.834	18.550	18.442	3.984	0.789	Means	1.452	0.910	17.075	16.796	3.673	0.734
	Ratio DI/DE=0.883							Ratio DI/DE=0.627					

Table 3.—**Correlation matrices, standard deviations and means for the bivalves from the Rio Padrón drilled by muricids and naticids.**

	Muricids (N=33)					Naticids (N=49)			
	L	A	DE	DI		L	A	DE	DI
L	1	0.85	—0.02	—0.01	L	1	0.78	0.59	0.62
A		1	1	0.02	A		1	0.54	0.57
DE			1	0.99	DE			1	0.97
SD	3.052	2.892	0.283	0.227	SD	2.262	3.087	0.394	0.310
Means	6.333	6.587	0.587	0.529	Means	3.779	4.503	0.810	0.538
	Ratio DI/DE=0.901					Ratio DE/DI=0.664			

more than in contact with each other. However, in the case of the naticid predation, a completely different situation emerges. The first set overlaps the second to the extent of 35.3% while the second overlaps the first by 38.5%; these values are quite high, and sufficiently so as to indicate that the corresponding canonical correlation is indeed representative of a true association in the varibles. The relevant details of the analysis for the muricids and naticids are listed in table 3 in which it will be seen that there is a alignment in the elements of the first principal component and the elements for the vector of morphological structure for three of four variables.

Principal component analysis: Principal component analyses were computed to supplement the foregoing results. In the case of the data for muricid holes in *Chlamys*, summarized in table 5, we observe that the first principal component, amounting to 66.42% of tr R, indicates covariation in all six variables, but with reduced participation by the dimensions of the boreholes. The second component, 27.45% of tr R and hence also important, is totally dominated by the two borehole dimensions. This results reflects amply the lack of correlation between the size of the predator and the size of the shells of *Chlamys*. The smallest (approximately invariant) principal component is almost exclusively indicative of a bipolar relationship in the length and width of the shell. The principal component

Table 4.—**Standardized canonical variate elements, morphological structure and first principal component for muricid and naticid drillholes in the bivalves from the Rio Padrón.**

	Muricids		
	Canonical vector elements	Morphological structure	Corresponding principal component
L	—5.905	0.525	0.004
A	6.415	0.895	0.026
DE	—4.079	0.448	0.707
DI	3.216	0.568	0.707
	First eigenvalue=49.8% of tr R		
	Overlap of second group by first=0.26%		
	Overlap of frist group by second=0.13%		

	Naticids		
	Canonical vector elements	Morphological structure	Corresponding principal component
L	—0.249	0.075	0.488
A	1.241	0.898	0.469
DE	0.700	0.959	0.507
DI	3.216	0.568	0.707
	First eigenvalue=76.03% of tr R		
	Overlap of second group by first=35.30%		
	Overlap of frist group by second=38.51%		

Table 5.—**Principal component analysis of the correlation matrix for muricids on *Chlamys* spp.**

	1	2	3	4	5	6
Eigenvectors:						
DE	0.227	— 0.672	—0.042	—0.640	0.293	—0.005
DI	0.247	— 0.653	—0.095	0.635	—0.316	—0.003
L	0.484	0.119	0.450	0.097	0.187	0.710
A	0.483	0.128	0.438	0.117	0.224	—0.703
C	0.471	0.196	—0.123	—0.380	—0.762	—0.023
G	0.445	0.230	—0.761	0.142	0.386	0.002
Eigenvalues:						
	3.985	1.647	0.193	0.114	0.059	0.002
% of tr R						
	66.417	27.450	3.217	1.900	0.983	0.033

Table 6.—**Principal component analysis of the correlation matrix for naticids on *Chlamys* spp.**

	1	2	3	4	5	6
Eigenvectors:						
DE	0.132	0.691	—0.0004	—0.097	0.703	—0.044
DI	0.074	0.708	0.024	0.063	—0.698	0.043
L	0.502	— 0.071	0.392	0.409	—0.009	—0.649
A	0.510	— 0.072	0.288	0.283	0.062	0.754
C	0.499	— 0.096	0.114	—0.843	—0.120	—0.064
G	0.464	— 0.050	—0.866	0.170	—0.050	
Eigenvalues:						
% of tr R	3.693	1.198	0.263	0.082	0.039	0.005
	61.550	19.967	4.383	1.367	0.650	0.008

analysis of the dimensions of the naticid holes in *Chlamys,* and the size of the prey, is summarized in table 6. These results agree closely with those obtained for the muricid holes. The angle between the smallest eigenvectors for both sets of data is only 9° 20', thus confirming the similarity in their structures.

A possible explanation of the principal component analyses might lie with the fact that the data considered derive from closely related morphologies of the genus *Chlamys,* noted for the great homogeneity it displays in the dimensions of the shell in its species.

The principal component analyses for the data from the Rio Padrón are summarized in tables 7 and 8. The results echo sharply those found for the *Chlamys* data in the case of the muricid holes. However, some aspects are more sharply outlined. We note that the first vector for muricids is dominated by the hole-dimensions, whereas this vector for naticids is marked by equal participation of all variables. The second vector for muricids is dominated by equal participation of the shell-dimensions at the expense of the hole-dimensions, whereas in the naticid material, the two shell-dimensions are in a negative relationship with the roughly equally represented hole-measures. Further inspection of the results in table 7 for the muricid boreholes discloses the interesting detail that each of the four vectors reflects a complete lack of correlation between the two sets (this is pointed to by the occurrence throughout of the pairwise loadings of [0.707], [0.707].

Finally, we observe that the angle between the two smallest eigenvectors in no more than 2° 42, thus indicating almost complete agreement in their structures.

Association between the size of the prey and the location of the drillholes

The same statistical methodology as used in the foregoing section was applied to the present problem. The four variables DE, DI DOU and DOB were weighed against the set of measures on the shell of the *Chlamys,* to wit, L, A, G, and the curvature, here denoted C. The canonical correlation between these sets for muricids is highly significant, with X^2 for the significance of the first latent value of the canonical analysis reaching 321 for five degrees of freedom. The significance for the naticids for the same latent

Table 7.—**Principal component analysis of the correlation matrix for size of prey and drillhole size for muricids on bivalves from the Rio Padrón.**

	1	2	3	4
Eigenvectors:				
L	0.004	— 0.707	0.707	0.002
A	0.026	— 0.707	—0.707	—0.008
DE	0.707	0.018	0.015	—0.707
DI	0.707	0.019	0.006	0.707
Eigenvalues:				
	1.991	1.849	0.150	0.010
% of tr R				
	49.8	46.2	3.7	0.2

Table 8.—**Principal component analysis of the correlation matrix for size of prey and drillhole size for naticids on bivalves from the Rio Padrón.**

	1	2	3	4
Eigenvectors:				
L	0.488	0.469	—0.736	—0.013
A	0.469	0.570	0.675	—0.020
DE	0.517	— 0.495	0.039	—0.697
DI	0.525	— 0.458	0.043	0.716
Eigenvalues:				
	3.041	0.713	0.219	0.026
% of tr R				
	76.025	17.825	5.475	0.650

values is also highly significant, being $X^2=239$ for five degrees of freedom.

The validity of the relationships are strongly supported by the exceptionally high overlaps between sets; thus, for the muricids, the first set overlaps the second to the extent of 79.92% and the second overlaps the first by 78.38%. Likewise, we find for the maticids, that the overlap of the second set by first is 66.22% and that by the second set of the first is 70.01%. The respective canonical correlation coefficients are 0.929, for muricid holes, and 0.919 for naticids.

The correlation matrix listed in table 9 shows that there is high correlation between variable of the two sets and, also, within sets. The naticids (table 9) also display quite high analogous correlations, but these are less marked than for the muricids. If we now examine the analytical results summarized in table 10, we observe that the vector for morphological structure for both sets of boreholes presents the same picture of equal participation of all variables. We also observe that the elements of the first principal component for both categories are close indeed. The angle between these vectors is 3° 38, thus documenting the agreement in structure.

The results of the principal component analyses for both categories are presented in tables 11 and 12. The good association between the size of the prey and the location of the borehole is clearly manifested in both cases. This result would seem to be interpretable in the same manner as before, namely, with respect to the homogeneity in length and width of the shell of the species of *Chlamys* encountered in

Table 9.—**Correlation matrix, standarrd deviations and means for the *Chlamys* drilled by muricids and naticids.**

	Muricids					
	DOU	DOB	L	A	C	G
DOU	1	0.76	0.84	0.85	0.83	0.78
DOB		1	0.89	0.88	0.83	0.73
L			1	1.00	0,92	0.84
A				1	0.92	0.85
C					1	0.90
SD	4.810	6.108	9.912	10.687	2.152	0.437
Means	7.349	10.050	18.550	18.442	3.984	0.798

	Muricids					
	DOU	DOB	L	A	C	G
DOU	1	0.59	0.76	0.76	0.69	0.59
DOB		1	0.85	0.85	0.79	0.61
L			1	0.99	0,92	0.79
A				1	0.94	0.82
C					1	0.83
SD	4.982	6.269	8.258	8.700	1.689	0.371
Means	7.425	9.145	17.075	16.796	3.673	0.734

Table 10—**Standardized canonical variate elements, morphological structure and first principal component for muricid and naticid drillholes in *Chlamys*.**

	Muricids		
	Canonical vector elements	Morphological structure	Corresponding principal component
DOU	0.481	0.860	0.391
DOB	0.584	0.883	0.394
L	—0.195	0.923	0.425
A	0.976	0.925	0.426
C	0.284	0.886	0.419
G	—0.056	0.802	0.394
	First eigenvalue=88% of tr R		
	Overlap of second group by first=79.92%		
	Overlap of frist group by second=78.38%		
	Naticids		
	Canonical vector elements	Morphological structure	Corresponding principal component
DOU	0.411	0.757	0.358
DOB	0.701	0.867	0.389
L	—0.044	0.909	0.440
A	1.289	0.909	0.441
C	—0.061	0.837	0.429
G	—0.243	0.669	0.382
	First eigenvalue=82.550% of tr R		
	Overlap of second group by first=66.22%		
	Overlap of frist group by second=70.01%		

the present study. If we once again direct attention to the smallest principal component, we note the close agreement in its elements for the both sets of observations. The angle between these vectors is 9°.

Association between the size of the drillhole and its location

Even this particular topic can be best treated in the same statistical manner as in the previous sections. The analysis accounted for here was made on the two dimensions of the borehole balanced against the twoi measures of its location on the shell.

The canonical correlation for the muricids is not significant, whereas that obtained for naticids was determined to be so, with $X^2=22$ for three degrees of freedom. The non-significant canonical correlation for muricids is reflected in the slight degree of overlap between sets for the muricid holes; in the case of the naticids, we have a strongly asymmetric relationship with set one overlapping set two by 20.87% whereas the value for set 2 overlapping set 1 is only 1.58%. The correlation matrix for muricids (table 13) indicated the between-group correlations to be low; likewise for the naticids (table 13). The canonical vector, morphological structural vector and first principal component listed in table 14 point to certain indicationns that were not shown up by the redundancy analysis in that the first principal component represents equal covariation in all four variables, a condition that is largely reproduced in the morphological structural relationship.

A similar result was found for the naticid holes (table 15), with respect to the agreement in morphological structure and principal components. However, in their case, the role of hole-size is very greatly reduced. Thus, the evidence seems to point to there being an association between the size of the drillhole and its location in naticids, but that this is not so for muricids.

The principal component analyses for both kinds of drillholes are summarized in tables 16 and 17. In addition to what has already been mentioned, we point to certain marked differences in the structure of

Table 11.—**Principal component analysis of the correlation matrix for the site of predation in *Chlamys* spp. by muricids.**

	1	2	3	4	5	6
Eigenvectors:						
DOU	0.391	— 0.152	—0.893	—0.161	0.013	0.029
DOB	0.394	0.668	0.168	—0.606	0.060	—0.015
L	0.425	0.134	0.089	0.503	0.164	0.706
A	0.426	0.157	0.050	0.500	0.203	—0.707
C	0.419	— 0.218	0.206	0.004	—0.857	—0.025
G	0.394	— 0.652	0.349	—0.323	0.440	0.016
Eigenvalues:						
	5.285	0.292	0.230	0.122	0.069	0.002
% of tr R						
	83.083	4.867	3.833	2.033	1.115	0.033

Table 12.—**Principal component analysis of the correlation matrix for the site of drillhole in *Chlamys* spp. by naticids.**

	1	2	3	4	5	6
Eigenvectors:						
DOU	0.358	— 0.900	0.076	0.187	0.147	0.011
DOB	0.389	0.241	—0.682	0.531	0.206	0.024
L	0.440	0.021	—0.116	—0.294	—0.556	0.631
A	0.441	0.051	—0.053	—0.231	—0.387	—0.771
C	0.429	0.180	0.097	—0.542	0.690	0.068
G	0.382	0.311	0.709	0.500	—0.032	0.058
Eigenvalues:						
	4.953	0.440	0.401	0.128	0.073	0.005
% of tr R						
	82.550	7.333	6.683	2.133	1.217	0.083

Table 13.—**Correlation matrices, standard deviations and means for the location and size of boreholes in *Chlamys*.**

	Muricids					Naticids			
	DE	DI	DOU	DOB		DE	DI	DOU	DOB
DE	1	0.90	0.09	0.25	DE	1	0.59	0.17	0.00
DI		1	0,15	0.29	DI		1	0.04	—0.05
DOU			1	0.76	DOU			1	0.95
Standard deviation	0.318	0.321	4.810	6.108	Standard deviation	4.928	6.269	0.515	0.425
Means	0.945	0.834	7.349	10.050	Means	7.425	9.145	1.452	0.910

Table 14.—**Standardized canonical variate elements, morphological structure and first principal component for muricid and naticid drillholes *Chlamys*.**

	Canonical vector elements	Morphological structure	Corresponding principal component
DE	0.252	0.940	0.532
DI	0.768	0.994	0.553
DOU	—0.613	0.439	0.410
DOB	1.383	0.917	0.493
		First eigenvalue=55.850% of tr R	

Table 15.—**Standardized canonical variate elements, morphological structure, and first principal component for naticids drillholes *Chlamys*.**

	Canonical vector elements	Morphological structure	Corresponding principal component
DE	3.341	0.307	0.193
DI	—3.179	0.008	0.117
DOU	1.064	0.966	0.700
DOB	—0.117	0.509	0.678
		First eigenvalue=49.450% of tr R	
	Overlap of second group by first=1.58%		
	Overlap of first group by second=20.87%		

the eigenvectors. The first two eigenvectors for the muricids do not differ very greatly with respect to the sizes of their eigenvalues, notably, 56% and 36%, respectively. This indicates that these two principal components represent real relationships in the two sets; thus the first vector seems to say that most variability in the data lies with bigger holes being located at certain sites. The second vector tells us that an essential part of the sample comprises holes that bear some inverse relationship to the site drilled, presumably indicating that a sizeable proportion of the holes drilled are not directly relatable to the location occupied by the hole in the shell. This conclusion is in harmony with the findings of the redundancy analysis.

In the case of the naticids (table 17), we see that location of the borehole and the size of the borehole are entirely unconnected and that each set has its own principal component, the first dominated by the geometrical location of the borehole, attached to about 49% of the variation, and the second entirely dominated by the dimensions fo the borehole, and connected

Table 16.—**Principal component analysis of the correlation matrix for sites and sizes of holes drilled by *muricids* in *Chlamys* spp.**

	1	2	3	4
Eigenvectors:				
DE	0.532	— 0.470	—0.011	—0.705
DI	0.553	— 0.427	—0.127	0.704
DOU	0.410	0.601	—0.682	—0.081
DOB	0.493	0.486	0.721	0.037
Eigenvalues:				
	2.234	1.439	0.225	0.102
% of tr R				
	55.850	35.975	5.625	2.550

Table 17.—**Principal component analysis of the correlation matrix for site and size of holes drilled by naticids in *Chlamys* spp.**

	1	2	3	4
Eigenvectors:				
DE	0.193	0.678	—0.696	0.136
DI	0.117	0.697	0.708	—0.017
DOU	0.700	— 0.096	—0.038	—0.707
DOB	0.678	— 0.213	0.115	0.694
Eigenvalues:				
	1.978	1.580	0.412	0.030
% of tr R				
	49.450	39.500	10.300	0.750

to almost 40% of the variation. Finally, we point to the structure of the smallest principal components: in the case of the muricids, this component is concerned entirely with the dimensions of the borehole, whereas the corresponding component for the naticids is almost entirely a representation of the localization of the borehole.

It is interesting to note that these two vectors are almost orthogonal, thus indicating their completely opposite nature. We may draw a further conclusion, to wit, that the factor of fundamental significance in the predational register of the naticids is the size of the borehole, as the process of feeding takes place through the hole drilled. On the other hand, the behaviour of some species of muricids, for example those of *Murex,* with respect to feeding is different in that the act of drilling is the means of obtaining access to the interior of the shell (see, for example, Barnes, 1985, p. 379). The size of the hole drilled is therefore not decisive for gaining access to the prey.

Predational strategies of muricids and naticids

As is shown by the Pope diagrams in figure 2, the holes drilled by muricids in *Chlamys* display a pronounced tendency to concentrate in a restricted part of the shell (74.1%), namely, in the zone of insertion of the adductor muscle; this pattern of distribution of boreholes (only 36.9%) is not seen to the same extent in the prey drilled by naticids. On the basis of the present investigation of predation on *Chlamys* spp., at least, it would seem that muricids manifest a capacity to select a certain site for initiating drilling.

Some species of muricids first drill their prey after wwhich they feed on the soft parts directly through the gaping valves. This second behavioural procedure is commonly adopted for feeding on carrion. Suitable prey is provided by monomyarian bivalves, sich a *Chlamys,* in which only one muscle requires to be neutralized. The concentration of holes to the location of the adductor muscle shown in figure 2 is clearly expressed.

Thus, it seems logical to conclude that the drilling behaviour of some muricids, in relation to monomyrian bivalves, has some kind of non-random component in the sense that it is aimed at weakening the function of the adductor muscle. Naticids are not invested with the same strategy of attack since they feed solely by means of the hole drilled. The efficiency of the muricid attack procedure seems to be relatively high in relaiton to naticids, with respect to the return of energy in relation to the effort expended.

Concluding remarks

The present study has as its aim the elucidation of certain aspects of gastropod predation, exemplified by the collections at our disposal. It is not meant to be a complete treatise on the general predatory behaviour of the two groups of interest. We have found that some groups of muricids may manifest a preferred interest for drilling a certain site in monomyrian bivalves, but that this behaviour is not obviously echoed in naticids. Inasmuch as many of the differences between the two kinds of boreholes are slight, and undetermined at the univariate level, multivariate statistical procedures have been resorted to; these have been found to yield excellent results and to sharpen greatly the interpretations.

It was thus established that notwithstanding the fact that the respective sizes of predator and prey are not usually highly correlated (cf. Reyment, 1966; Reyment *et al.,* 1978; Ansell, 1960; Thomas, 1976; Kitchell *et al.,* 1981), one sample did indeed display a high level of such association, notably, naticid holes in material from the Río Padrón.

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