Chapter 3

A BIOMETRICAL STUDY OF THE NERINEACEA FROM THE WHITE LIMESTONE (BATHONIAN)

'By a small sample we may judge of the whole piece.'

Cervantes (Don Quixote: 1605-1615)

Introduction

The application of biometrics and biostatistics to palaeontological problems is just one facet of the changing nature of palaeontology in recent years. Initially largely qualitative procedures were used for systematic descriptions and classifications which then formed the bases for most biostratigraphic and evolutionary studies. However, advances in biology, especially in the fields of ecology and population genetics, are now influencing current palaeontological thinking. Aided by a greater understanding of mathematical and statistical methods together with the availability of high-speed computers for complex, time-consuming calculations, the science has entered a more mature, quantitative phase.

Brief resumés of the development of biostatistics and their application to geological problems in general can be found in Sokal and Rohlf (1973); Miller and Kahn (1962) and Davis (1973).

As far as the present author is aware the present study is the first to apply biometrical techniques to Nerineid gastropods. Two aspects of Nerineid shell morphology seemed to be particularly interesting and amenable to quantitative analysis.

A) the ontogenetic development of the turreted Nerineid shell
B) the "intra-specific" morphological variability.

The growth of the Palaeocene Turritella moretoni Conrad has been recently documented, using biometric analysis, by Andrews (1974). Comparisons between the ontogenetic growth of the ubiquitous post-Mesozoic Turritellidae and the dominant Mesozoic turreted gastropod superfamily, the Nerineacea, show differences which can probably be related to differences in their modes of life. The study of morphological variability in Nerineids is essential in order to obtain shell parameters which were both easily applicable and reliable in the discrimination of several externally similar Nerineid genera and species. The application of these parameters to members of the Aphanoptyxidae produced some interesting results which are summarised below.

The choice of parameters

The general descriptive terminology for gastropod shells was mainly formulated by nineteenth century malacologists, such as Sowerby (1842) and Woodward (1851). The terms were later standardised by Cox (1955 and 1960). Although largely qualitative in their application, many of these terms can be expressed numerically and have been used with varying degrees of sophistication in studies by Sadlick and Nielsen (1963); Batten (1966); Eldridge (1968); Gould (1969); Andrews (1974) and Ambroise et Geyssant (1974). Three dimensional descriptive parameters based upon mathematical formulae expressing the helicospiral coiling of gastropod shells were developed by Moseley (1838 and 1842) and Thompson (1942). These were later modified and adapted for computer simulation of gastropod morphologies by Raup (1961, 1962, 1963 and 1966). Subsequent work extended the applicability of Raup's parameters to other classes of the Mollusca, especially the cephalopoda and also encompassed most of the morphologies exhibited by the brachiopoda (Raup 1966, 1967; Raup and Chamberlin 1967; Chamberlin 1969). Vermeij (1971) used three of the parameters developed by Raup in order to examine differences in morphological diversity amongst several major taxonomic groups of Recent gastropods. The self-evident conclusion was reached that gastropods with their axes of coiling highly inclined to the substrate are a) the more primitive forms i.e. the Archaeogastropoda and 'lower' Caenogastropoda, b) always associated with simple generating curves, and c) morphologically less diverse than more advanced forms with their axes of coiling at a lower angle of elevation to the substrate. Unless this type of analysis is combined with extensive ecological and palaeontological data, it is unlikely to significantly advance our knowledge concerning the evolution of gastropod morphology. However, in general, the four parameters developed by Raup (op. cit.):- the shape of the generating curve; the whorl expansion rate; the position of the generating curve with respect to the axis of coiling and the rate of whorl translation down the axis, have not been extensively applied in detailed morphological studies. Raup's parameters have not been used in this study of Nerineid gastropods for the following reasons;

1) The shape of the generating curve in Nerineid gastropods is not a simple curve and is therefore difficult to express quantitatively. As noted by Raup (1966, p. 1179) the generating curve "can only rarely be defined mathematically.... More generally, however, a line drawing is used to describe the shape".

2) Consequently one is unable to define the centre of the generating curve and cannot therefore measure r_c (the distance of the centre of the initial generating curve from the axis of coiling) which is necessary to

solve the equation for helicone coiling given by Raup (1966, p. 1179, eqn. 3)

$$y\theta = yo.W^{\theta/2\pi} + r_c.t\,(W^{\theta/2\pi} - 1)$$

Unless the parameter r_c can be measured, the translation rate, t, in the form used by Raup (op. cit.) cannot be calculated for Nerineid gastropods.

In order to utilise the concept of the whorl translation rate, a modification of Raup's equation (1966, p. 1179) which omits r_c is necessary. This can be achieved by utilising the junction of successive whorls (point X in Fig. 3:1) as the points which are being translated.

Footnote

An earlier paper; Raup (1962), appears to contain typological and arithmetical errors. In Fig. 2 (Raup, 1962, p. 151), the translation rates should obviously be transposed to read:- Fig. 2a, t = 5.0; 2b, t = 1.8; 2c, t = 0.8; 2d, t = 0.6 and 2e, t = 0.2. Not only should the translation rate values be transposed, but the actual value for Figs. 1 and 2b appear to be incorrect. Transposing the equation for helicone coiling (Raup, 1966, p. 1179, eqn. 3 - see above)

$$t = \frac{y\theta - yo.W^{\theta/2\pi}}{r_c\,(W^{\theta/2\pi} - 1)}$$

Using the above formula, the present author calculated the translation rates for successive whorls on an enlargement of Raup's Fig. 1 (Raup, 1962, p. 151) and obtained t values of 2.495, 2.335 and 2.402 (mean t = 2.30) for successive whorls from apex to aperture: not 0.6 as given by Raup (op. cit.) or 1.8 if the t values are transposed.

If the value yo in Raup's Fig. 1 (1966, p. 1180) is reduced to zero and the distance from point X to the coiling axis is taken as r_x then a 'relative' translation rate tr can be used and is expressed by,

$$tr = \frac{y\theta}{r_x \left(W^{\theta/2\pi} - 1\right)}$$

This formula was also used on an enlargement of Fig. 1 in Raup (1962, p. 151) and when compared with the translation rates obtained by Raup's method, the two were found to be empirically related as follows,

$$tr = t^c$$

where c 2.43 for Fig. 1. (Raup, 1962, p. 151). The use of the two formulae is shown in Fig. 3:1. Whorl expansion and relative translation rates (w and tr) were calculated by the present author for the following Nerineid species.

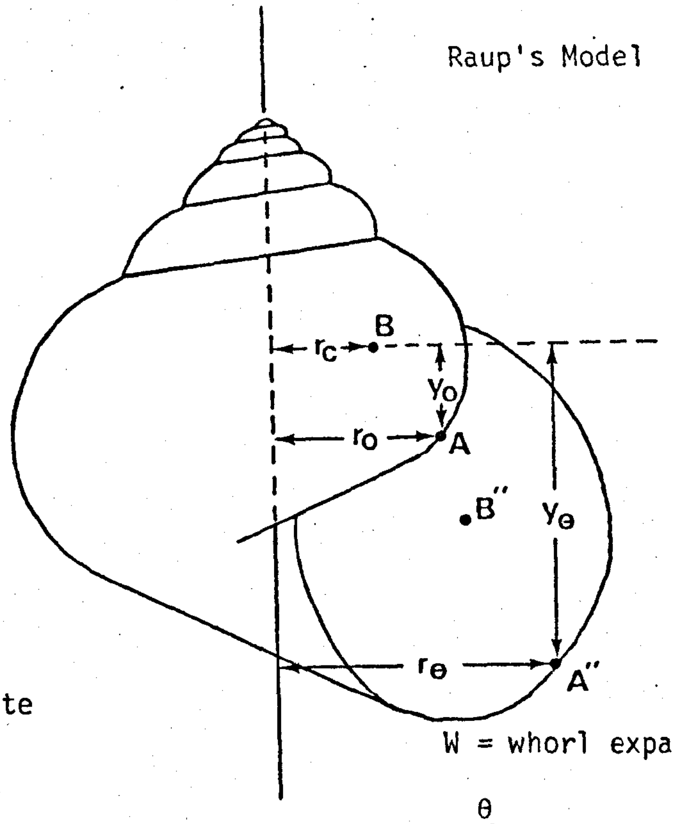
a) *Bactroptyxis implicata* Dagham Downs Quarry
M.J.B. coll. ref. no. D.D.23

b) *Nerinea requieniana* - reproduced from Knight *et*. *al*., 1960, p. 108, Fig. 65.

c) *Aphanoptyxis bladonensis* - reproduced from Arkell, 1947, p. 43, Fig. 5. Also Oxford University Museum specimen: J843.

d) *Aphanoptyxis ardleyensis* - reproduced from Arkell, 1947, p. 43, Fig. 5. Also Oxford University Museum specimens: J830 (paratype) and J828 (paratype).

Raup's Model



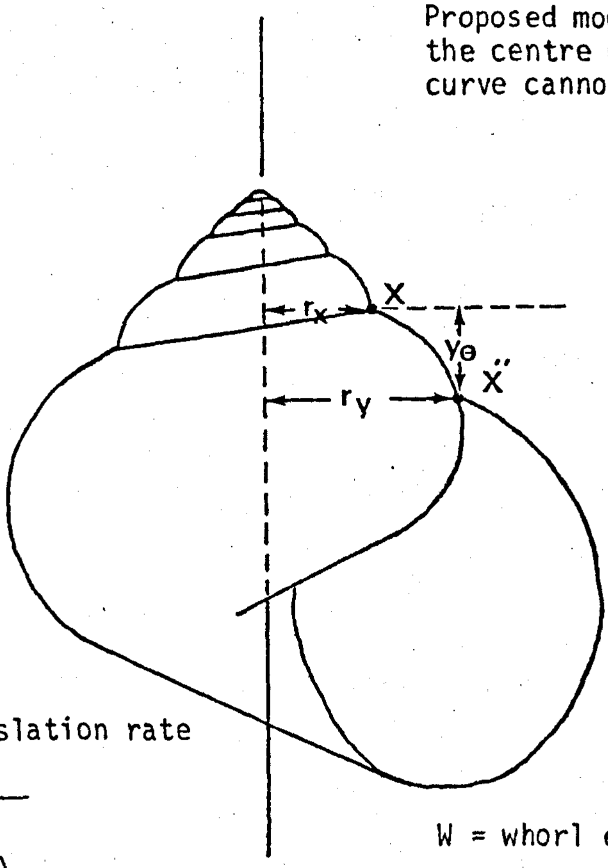
t = translation rate

$$t = \frac{y\theta - yo.W^{\frac{\theta}{2\pi}}}{r_c\ (W^{\frac{\theta}{2\pi}} - 1)}$$

W = whorl expansion rate

$$W^{\frac{\theta}{2\pi}} = \frac{r\theta}{ro}$$

Proposed modification where the centre of the generating curve cannot be defined.



tr = relative translation rate

$$tr = \frac{y\theta}{rx\ (W^{\frac{\theta}{2\pi}} - 1)}$$

W = whorl expansion rate

$$W^{\frac{\theta}{2\pi}} = \frac{ry}{rx}$$

Fig. 3.1. Raup's model for helical coiling and a proposed modification.

Both the whorl expansion rates and the relative translation rates were found to vary considerably within a single specimen. In the case of A. bladonensis the following results were obtained

a) Fig. 5, Arkell, 1947,

Mean tr = 5.11, range 4.55 - 5.53, n = 7.

Mean w = 1.08, range 1.24 - 1.33, n = 7.

b) O.U.M. J843

Mean tr = 5.39, range 5.09 - 5.79, n = 5.

Mean w = 1.29, range 1.24 - 1.39, n = 5.

Further examples are graphically shown in Fig. 3:2. Because of the variability of the results and the time consuming nature of this method, it was decided that these parameters would not be used in this study. As noted by Gould (1969, p. 42), "Raup abstracts the general form of coiled shells with as few parameters as possible" and the present author concludes that these parameters are inappropriate for detailed morphological analyses.

The choice of variables to measure was constrained by three major factors.

1) Most Nerineid specimens could not satisfactorily be removed from their matrix without some loss of the shell and therefore axial cross-sections of the gastropods proved to be the most practical method of study. For all detailed measurements, enlarged photographs were prepared from acetate peels of the axial sections.

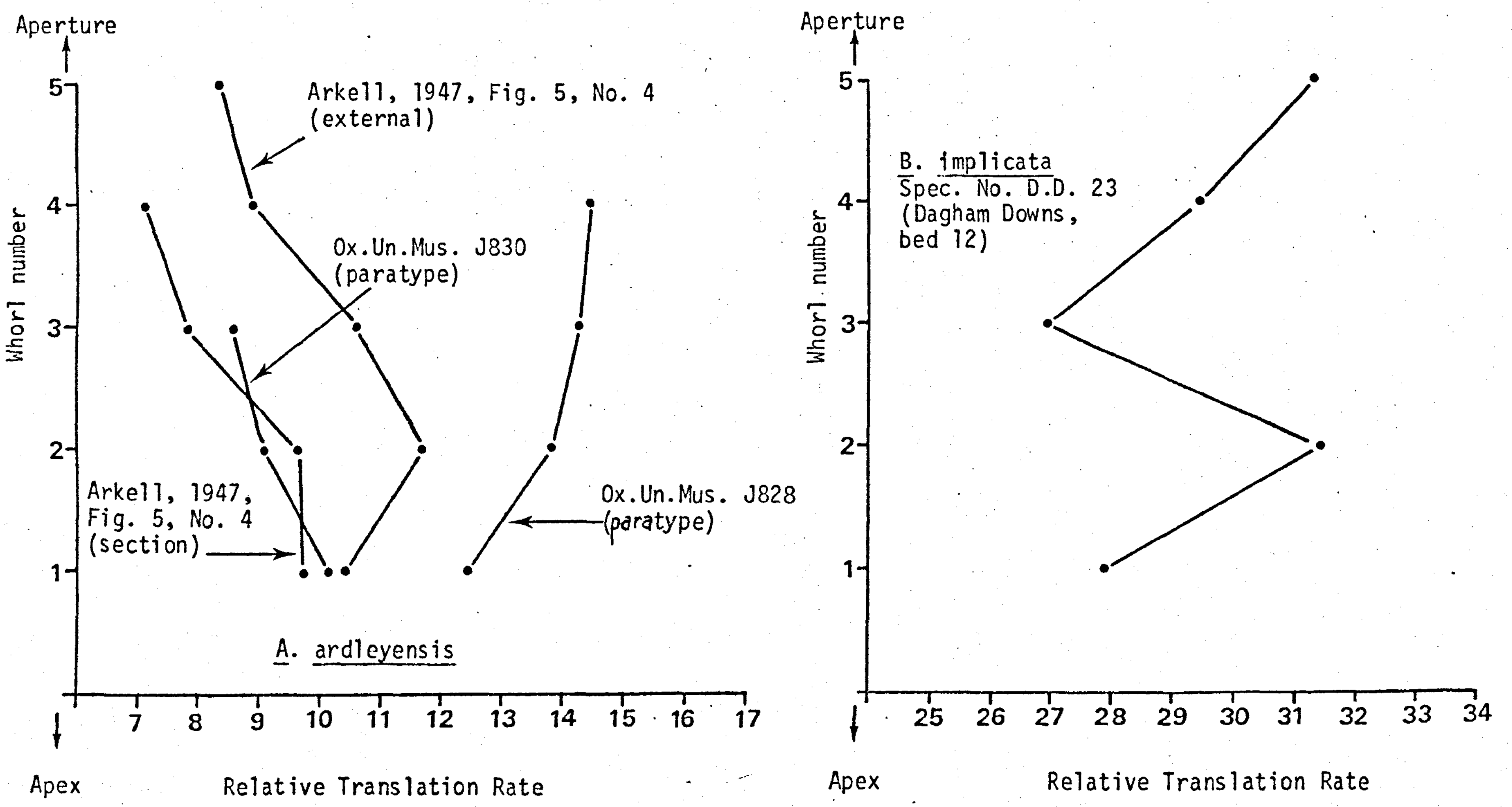


Fig. 3.2. Variation in the Relative Translation Rates in A. ardleyensis and B. implicata

2) Since Nerineids continue to grow throughout their life, the aperture lacks terminal growth features defining an adult stage. Furthermore, no Nerineid protoconch has been observed by the present author. These two features make it impossible to obtain whorl measurements which can be related to a physiologically meaningful point in the shell development such as a definable adult stage or a post-protoconch growth stage.

In a study of ontogenetic variation amongst Middle Carboniferous Pleurotomarian gastropods in which the apical region was rarely preserved, Sadlick and Nielsen (1963) used a "zero-point" where the whorl height equalled some arbitary value in order to give some reference point to which successive whorl measurements could be related. However, this method relies upon good three-dimensional shell preservation and was obviously inapplicable to those Nerineids which necessitated sectioning.

3) As noted by Sylvester-Bradley (1958, p. 216) "A formidable argument against the adoption of quantitative techniques is that they are so time-consuming". For each of the 335 specimens used in this study, the retrieval of data for analysis involved,

a) the cutting and polishing of an axial cross-section,

b) the preparation of an acetate peel,

c) the production of an enlarged photograph,

d) the recording of various qualitative data, such as epifauna, state of preservation, etc., by examination under a binocular microscope, and

e) the measurement of the various biometric parameters discussed below.

This procedure took a minimum time of about three hours per specimen. For every specimen processed in this way, several others were discarded at various intermediate stages.

Consequently the biometric parameters chosen must provide information which adequately describes Nerineid growth as well as intra-specific morphological variation and which subsequently help in species discrimination. They must also be easily measurable, even on poorly preserved specimens.

The variables chosen were:-

a) the apical (or spiral) angle:

This is an obvious and easily measured feature in these high-spired gastropods. In terms of Raup's parameters, this variable is a product of the interaction of the whorl translation rate with the whorl expansion rate.

b) the sutural angle:

The size of the sutural angle is directly related to the rate of increase in the whorl height i.e. this parameter is primarily influenced by the whorl translation rate.

c) the successive whorl width/height ratios:

The accretionary growth of the gastropod shell preserves a complete record of the ontogeny of the individual. The measurement of the width/height ratios of successive whorls records that ontogeny and enables growth curves to be constructed from several individual ontogenies. On the other hand, if only one set of measurements is made per specimen, the ontogeny must be inferred from a mass curve composed of measurements derived from juvenile and adult specimens. There is no a priori reason why such curves should reflect individual ontogeny in any way (see Gould, 1966a and Ghose, 1970).

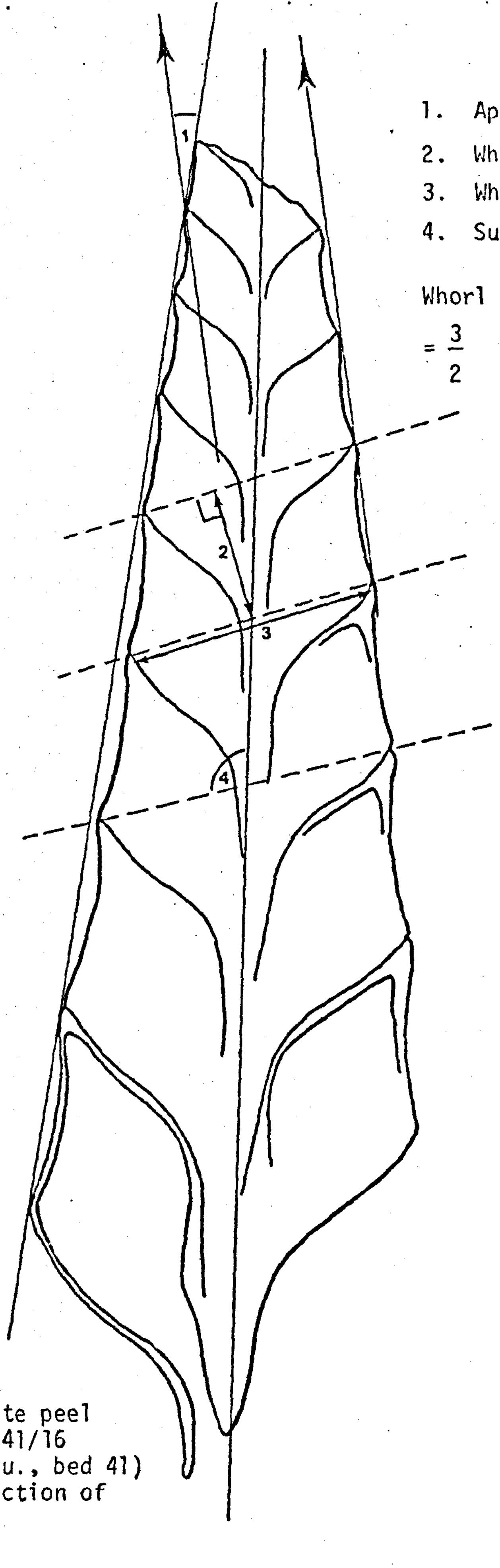
The parameters measured are shown in Fig. 3:3.

Growth in Bathonian Nerineid gastropods

Since the ontogeny of a Nerineid shell can be expressed by successive whorl width/height measurements, a simple bivariate plot of these parameters should yield a quantifiable relative growth-line. Because of the inherent variability of biological material, associated with secondary errors induced by preservation, sampling and measurement, the data do not exactly plot on a single growth-line. The growth-line is therefore mathematically computed by regression analysis which takes into account the variability of the data. In early studies, least squares regression was the method used. However, in most bivariate plots derived from biological material neither variable can be regarded as independent and a method which considers the variation in both is preferable. The 'Reduced Major Axis' or 'line of organic correlation' (Teissier, 1948; Kermack and Haldane, 1950) has therefore been used by many authors (Imbrie, 1956; Hallam, 1960; Gould, 1969). When the correlation between the variates is high, least squares regressions and Reduced Major Axes give almost identical results.

The striking thing about these and other organic growth-lines is that they are closely approximated by the equation of simple allometry;

$$y = bx^k \qquad \text{(Huxley 1924, 1932).}$$



1. Apical angle
2. Whorl height
3. Whorl width
4. Sutural angle

Whorl width/height ratio

$= \frac{3}{2}$

A. ardleyensis

Drawn from acetate peel
of spec. no. AF 41/16
(Ardley Fields Qu., bed 41)
- personal collection of
author.

Fig. 3.3. The shell parameters measured.

The logarithmic transformation of this power function,

$$\log g = k(\log x) + \log b$$

gives a rectilinear plot on logarithmic co-ordinates. k is the slope of the growth line and is the ratio of the specific growth rates of y and x. b is the y value at X = 0, although this is frequently biologically meaningless (Gould, 1966; White and Gould, 1965). When k is greater than unity, the allometry is positive and when k is less than unity, the allometry is negative. The allometric equation therefore implies change of shape with increase in size. In the special case, k = 1, there is no change in shape during growth (isometry) and the data can be plotted on arithmetic co-ordinates in the form,

$$y = ax + b$$

where a is the slope of the growth line and represents the constant ratio between y and x. The application of these equations to the generalised morphology of high-spired gastropod shells is shown in Fig. 3:4.

The use of the Reduced Major Axis in regression analysis and the allometric growth equation for the description of growth are now well established palaeontological technqiues. Fuller explanations of the theory and practise relating to these methods may be found in Imbrie (1956); Simpson _et_. _al_. (1960); Gould (1966); Miller and Kahn (1962) and Ghose (1970).

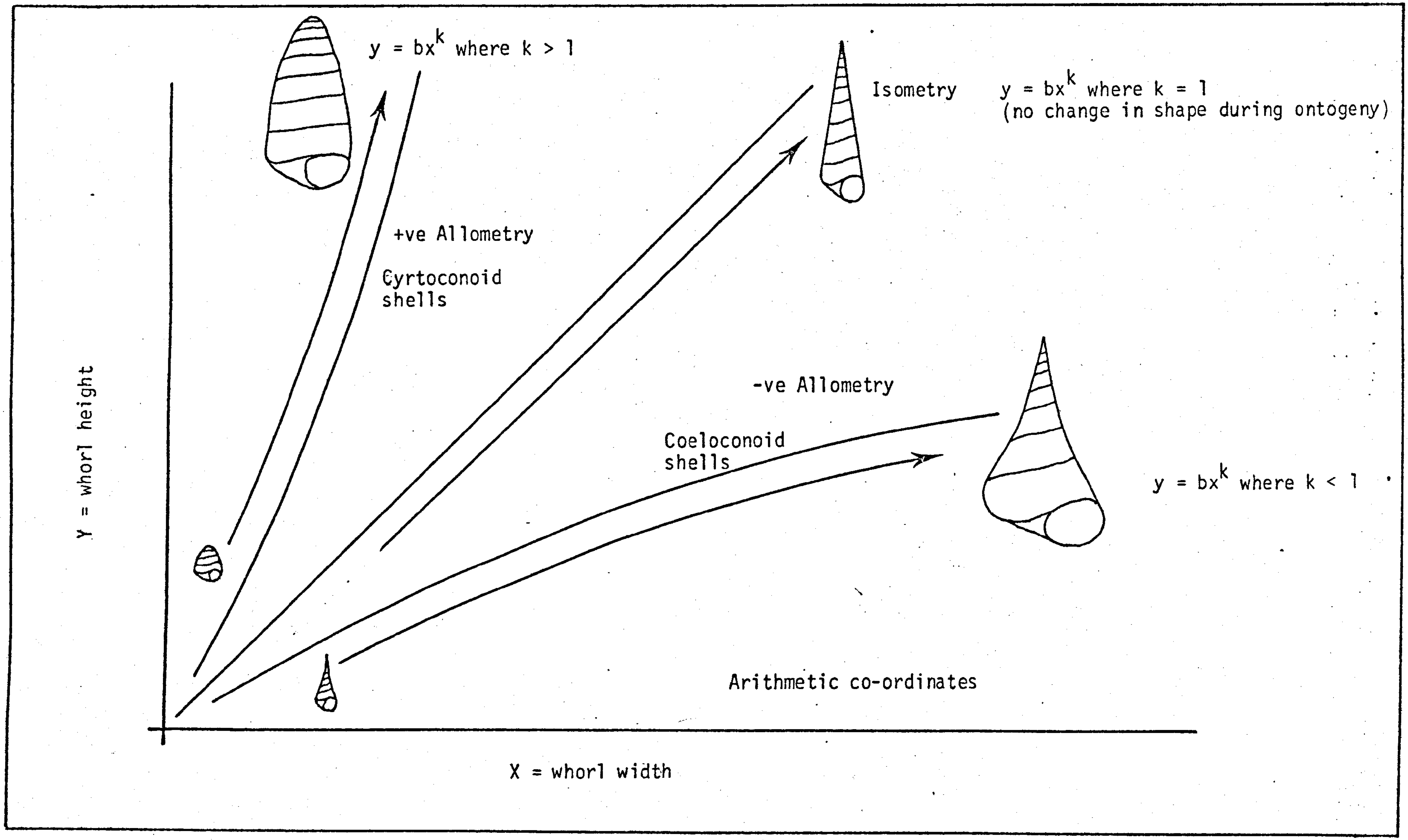


Fig. 3.4. The application of the allometric growth equation, $y = bx^k$, to high-spired gastropods.

The whorl width/height measurements from the various Nerineid species in the White Limestone were processed with a PDP8 computer to fit a) the isometric equation $y = ax + b$ and b) the allometric equation $y = bx^k$.

The output from the isometry program was of the form:

cx: = standard deviation of sample variate X, i.e. the whorl width.
cy: = standard deviation of sample variate Y, i.e. the whorl height.
cc: = correlation coefficient.
sx: = standard deviation of X.
sy: = standard deviation of Y.
a: = slope of the Reduced Major Axis + standard error.
b: = the intercept on the Y axis when X = 0.
B: = the regression coefficient.

The output from the allometry program was of the form:

cx:)
)
cy:)
)
cc:) as above.
)
sx:)
)
sy:)
k: = the ratio of the specific growth rates of X and Y.
b: = slope of the reduced major axis + standard error.

Growth-lines which can be defined by the allometric equation $y = bx^k$ will not be accurately described by the isometric growth equation, $y = ax + b$, and therefore the correlation coefficient (i.e. the closeness of the points to the growth-line) will be lower in data anomalously fitted to the isometric growth equation. However, those data correctly described by the isometric growth-line $y = ax + b$ can also be fitted to the allometric growth equation, $y = bx^k$, but only where $k = 1$ and the correlation coefficients in these cases will have the same value. In all Bathonian Nerineid species studied by the present author, the fitting of the data to allometric and isometric growth equations yielded the same correlation coefficients and in the allometric equations, k closely approximated to unity (see Table 3A). One infers, therefore, that within the range of the data plotted, the growth of Bathonian Nerineid gastropods was isometric. It is noticeable that in all the species studied, except for A. excavata sp. nov. from Sturt Farm (see Fig. 3:5), where the correlation coefficient was 0.879, the correlation coefficients were extremely high; greater than 0.9 and frequently in excess of 0.95 (see Figs. 3:5 and 3:6).

When the Reduced Major Axes are extrapolated they pass through or close to the origin of the axes which suggests that most, if not all, of the post-larval growth in these Nerineids was also isometric. However, extrapolation of the Reduced Major Axis of Fibuloptyxis witchelli indicates that the initial whorl of this species possessed a finite width at a whorl height of 0; which is obviously impossible.

Table 3A

Species: *Aphanoptyxis ardleyensis* Arkell 1931

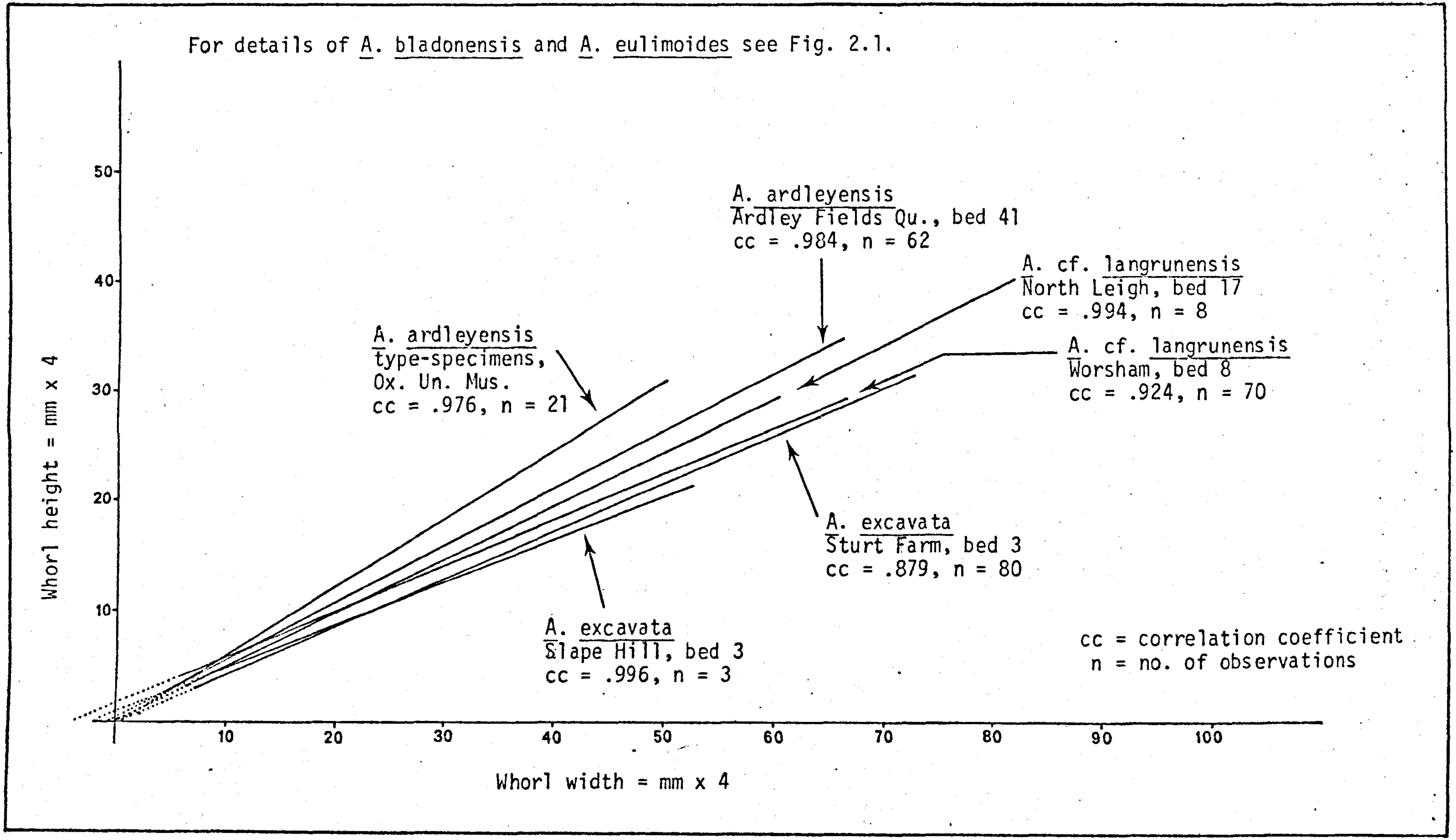
Origin: Oxford University Museum

J 829	Lectotype
J 828	Paratype
J 885	Paratype

Locality: White Limestone in Ardley-Fritwell railway cutting (see Arkell, 1931; Arkell, Richardson and Pringle, 1933).

Reduced Major Axes:

	Allometric equation $y = bx^k$	Isometric equation $y = ax + b$
cx	5.914	5.914
cy	3.612	3.612
cc	0.977	0.977
sx	1.272	1.272
sy	0.777	0.777
	$k = 1.006$	$a = 0.611$
	$b = 0.597$	$b = -0.056$
		$B = 0.092$



For details of A. bladonensis and A. eulimoides see Fig. 2.1.

Fig. 3.5. Relative growth lines (Reduced Major Axes) for some Bathonian *Aphanoptyxis* spp.

Eunerinea arduennensis samples

1. Ardley Fields Quarry, bed 34

   cc = .938, n = 17

2. Slape Hill, bed 5

   cc = .967, n = 324

3. Croughton, bed 7

   cc = .99, n = 51

4. North Leigh, bed 17

   cc = .987, n = 79

5. Slape Hill, bed 3

   cc = .977, n = 39

6. Foss Cross, bed 4

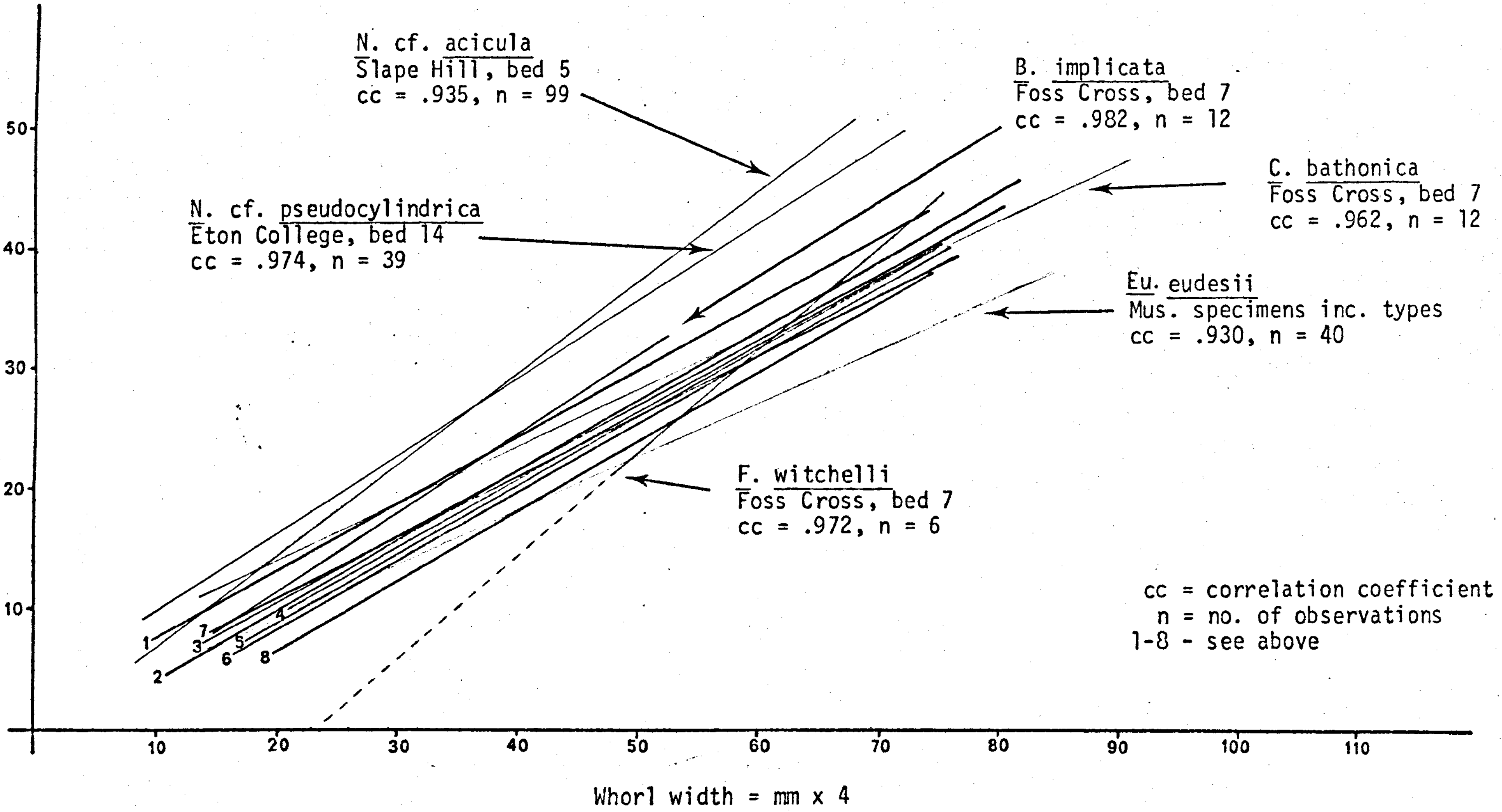
   cc = .988, n = 19

7. Foss Cross, bed 7

   cc = .925, n = 45

8. Slape Hill, bed 7

   cc = .977, n = 79


N. cf. acicula
Slape Hill, bed 5
cc = .935, n = 99
B. implicata
Foss Cross, bed 7
cc = .982, n = 12
C. bathonica
Foss Cross, bed 7
cc = .962, n = 12
N. cf. pseudocylindrica
Eton College, bed 14
cc = .974, n = 39
Eu. eudesii
Mus. specimens inc. types
cc = .930, n = 40
F. witchelli
Foss Cross, bed 7
cc = .972, n = 6
cc = correlation coefficient
n = no. of observations
1-8 - see above
1
2
3
4
5
6
7
8
Whorl height = mm x 4
Whorl width = mm x 4
10
20
30
40
50
10
20
30
40
50
60
70
80
90
100
110

The correlation coefficient of the measured data is high (0.972) and in this range the growth of F. witchelli is clearly best defined by an isometric equation. Probably the early growth of F. witchelli was allometric, becoming isometric at a later stage (see Fig. 3:6).

Examination of the successive whorl width/height ratios in individual specimens should also reveal allometric growth if present. Positive allometric growth was recorded in Nerinella? varioplicata by Wieczorek (1974) who noted a decrease in the whorl height/width ratios from 1.0 in the apical whorls to 0.80-0.85 m in later whorls. No such definite trends could be identified in Bathonian Nerineids (Fig. 3:7) which again suggests that their growth was isometric.

Statistical discrimination between the several Reduced Major Axes involves the formulation of the null hypothesis that the two samples were drawn from populations having identical growth patterns. To test the hypothesis that the slopes of the Reduced Major Axes characterising the populations from which the two samples were drawn are the same, the statistic z is calculated where,

$$z = \frac{a_1 - a_2}{\sqrt{\sigma_{a_1}^2 + \sigma_{a_2}^2}}$$

$a = \frac{sy}{sx}$ = slope of the Reduced Major Axis

$\sigma_a = \frac{sy}{sx}\sqrt{\frac{1 - cc^2}{n}}$ = standard error of the slope.

The test statistic, z, has a frequency distribution which is a standardised normal distribution.

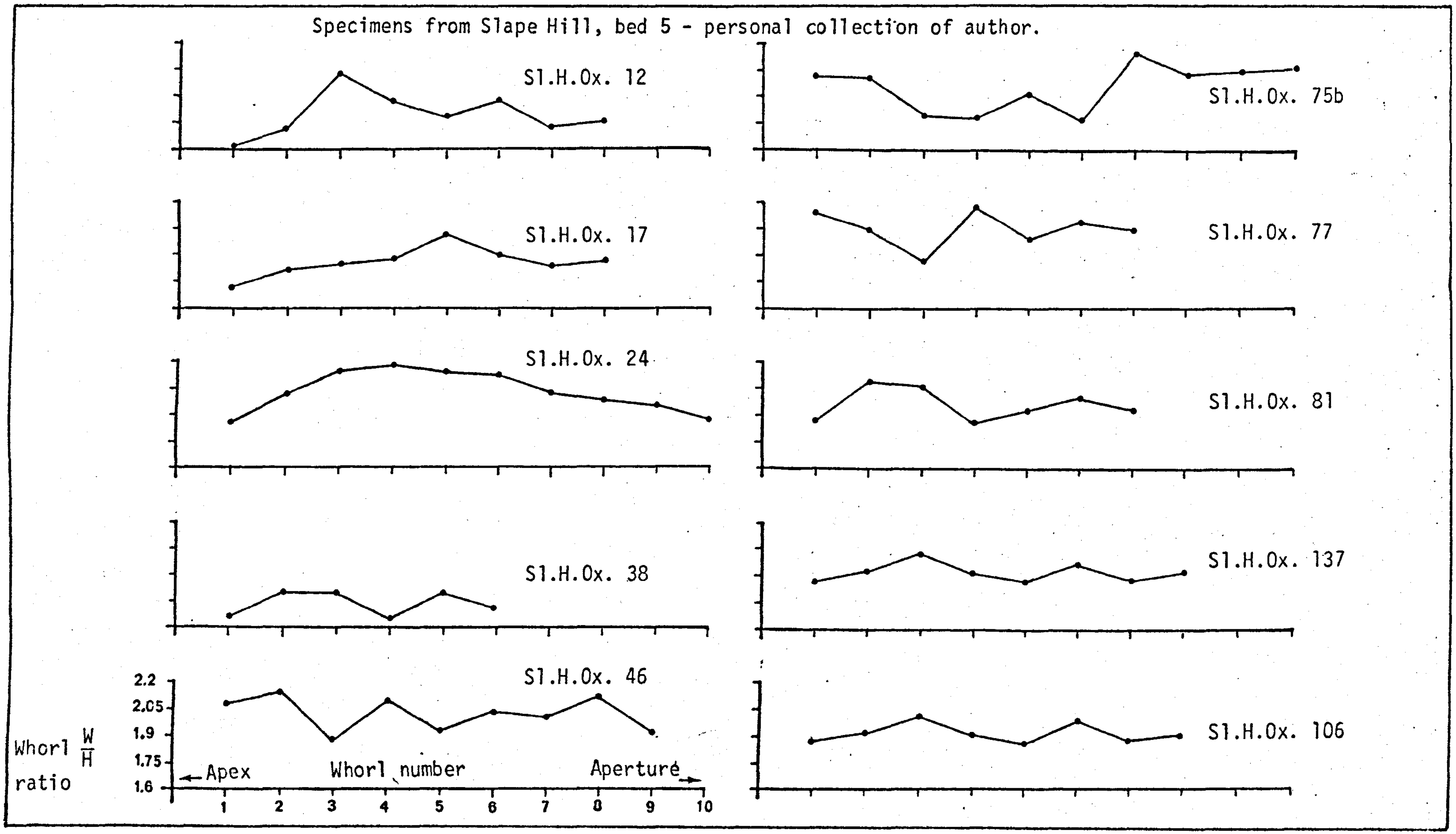


Fig. 3.7. Variation in whorl width/height ratios in specimens of Eu. arduennensis.

If the observed value of z is greater than 1.96, the probability (P) that the observed difference between the slopes ($a_1 - a_2$) arose by chance is greater than 0.05 and the hypothesis of equal slopes is rejected, the observed difference being considered statistically significant at the 5% level.

A matrix of the values of z for the various Bathonian Aphanoptyxis spp. is shown in Table 3B. The slopes of the Reduced Major Axes of the various Cossmannea, Eunerinea and Nerinella spp., together with B. implicata (all from the White Limestone) were similarly statistically compared by a matrix of z values (Table 3C).

Fig. 3:5 and Table3B reveal a systematic, statistically significant change in the slope of the Reduced Major Axes in certain members of the genus Aphanoptyxis. There is a gradual progressive increase in the slope of the Reduced Major Axes from those specimens of Aphanoptyxis found near the base of the White Limestone through to A. ardleyensis near the top of theWhite Limestone. The morphological expression of this change is a progressive increase in the relative whorl height of the Aphanoptyxis spp. as one passes up the White Limestone. Examination of Fig. 3:6 suggests that the two samples of Nerinella sp. taken from the White Limestone (Slape Hill, bed 5 and Eton College, bed 12a; see Figs. 1:5 and 1.11) have different growth patterns. This is supported statistically ($P < 0.001$; see Table 3C and the two samples probably represent two distinct species.

	A. ardleyensis		A. cf. langrunensis		A. excavata sp. nov.		
	Oxford Univ. Mus.	Ardley bed 41	N. Leigh bed 17	Worsham bed 8a	Sturt Fm. bed 5	Slape Hill bed 3	A. bladonensis
Ardley bed 4	86 3.11 **						
North Leigh bed 17	32 3.21 **	68 0.68 NS					
Worsham bed 8a	94 4.83 ***	130 3.23 ***	76 2.22 *				
Sturt Farm bed 5	119 4.48 ***	165 2.74 **	201 1.89 *	163 0.18 NS			
Slape Hill bed 3	27 5.61 ***	63 4.33 ***	9 3.27 **	71 1.12 NS	96 1.23 NS		
A. bladonensis	167 4.29 ***	203 2.39 **	149 1.01 NS	211 1.73 *	236 1.36 NS	144 2.96 **	
A. eulimoides	67 6.23 ***	103 5.73 ***	49 3.82 ***	111 1.09 NS	36 1.21 NS	44 0.26 NS	184 3.78 ***

value of 'z'
degrees of freedom - 86 | 3.11 / **
significance

NS = not significant
* = < 0.05 = significant
** = < 0.01 = v. significant
*** = < 0.001 = v.v. significant

Table 3B

Comparison of slopes of Reduced Major Axes of Bathonian Aphanoptyxis spp. using 'z' statistic

	1	2	3	4	5	6	7	8	9	10	11	12
	N. cf. acicula	N. cf. pseudocyl.	B. implicata	C. bathonica	Eu. eudesii	Eunerinea arduennensis						
	Slape Hill	Eton Coll.				Ardley bed 34	Croughton bed 7	Slape Hill bed 7	Slape Hill bed 5	Slape Hill bed 3	North Leigh bed 17	Foss Cross bed 7
2	135 3.66 ***											
3	108 2.64 **	49 0.31 NS										
4	108 6.75 ***	49 4.14 ***	22 3.70 ***									
5	136 8.56 ***	77 5.71 ***	50 4.71 ***	50 0.49 NS								
6	103 2.01 *	44 0.54 NS	17 1.43 NS	17 1.38 NS	45 1.68 *							
7	147 7.45 ***	88 3.66 ***	61 2.75 **	61 2.29 *	89 3.81 ***	22 0.34 NS						
8	122 5.04 ***	63 1.64 NS	36 1.55 NS	36 2.77 **	64 3.96 ***	31 0.08 NS	75 1.33 NS					
9	420 6.35 ***	361 2.31 *	334 1.87 *	334 3.18 ***	362 4.98 ***	329 0.11 NS	373 2.35 **	348 0.08 NS				
10	135 5.57 ***	76 1.96 *	49 1.75 *	49 2.83 **	77 4.18 ***	44 0.13 NS	88 1.38 NS	63 0.14 NS	361 0.10 NS			
11	170 7.10 ***	109 3.23 ***	84 2.47 **	84 2.57 **	112 4.18 ***	79 0.37 NS	123 0.75 NS	98 0.93 NS	396 1.60 NS	111 0.90 NS		
12	141 7.02 ***	82 4.07 ***	55 3.50 ***	55 0.62 NS	83 1.31 NS	50 1.11 NS	94 1.91 NS	69 2.47 **	367 3.01 **	82 2.55 **	117 2.26 *	
Foss Cross bed 4	115 5.74 ***	56 2.15 *	29 1.89 *	29 2.69 **	57 4.00 ***	24 0.20 NS	68 1.12 NS	43 0.32 NS	341 0.02 NS	56 0.20 NS	91 0.65 NS	62 2.38 *

degrees of freedom - 135 3.66 *** — value of 'z', significance

NS = not significant
* = < 0.05 = significant
** = < 0.01 = v. significant
*** = < 0.001 = v.v. significant

Table 3C

Comparison of the slopes of Reduced Major Axes of Bathonian Nerineids excl. Aphanoptyxisidae using 'z' statistic

With one exception, all the White Limestone Eunerinea horizons sampled by the present author show no significant differences ($P > 0.05$) between the slopes of their Reduced Major Axes suggesting that they all had the same growth pattern and they represent several populations of a single species. The partial exception is the sample of Eunerinea sp. from the Fibuloptyxis bed at Foss Cross Quarry (see Fig. 1:7). The slope of the Reduced Major Axis of this sample is not statistically significantly different ($P > 0.05$) from that of Eu. eudesii, nor is it statistically significantly different ($P > 0.05$) from the Reduced Major Axes of the Eunerinea sp. found at Ardley Fields Quarry (bed 34, see Fig. 1:18) and Croughton (bed 7, see Fig. 1:19). However, it is statistically significantly different ($P < 0.05$) from the remaining Eunerinea sp. horizons within the White Limestone (see Table 3C).

The abundant White Limestone Eunerinea sp. was identified by Arkell (1931) as N. eudesii; later revised by Cox and Arkell (1948-50) to C. eudesii. However, the Reduced Major Axis of Eu. eudesii (= Cossmannea eudesii of Cox and Arkell op. cit.) obtained by measurement of the type material (Lectotype - Geol. Surv. Museum No. GSM 8288, Para/Topotypes GSM 49428 and 49429) together with specimens from Oxford University Museum. (J 13076-7, J 833-5), is statistically very significantly different ($P < .001$) from all other Eunerinea sp. samples taken from the White Limestone (with the exception of the Eunerinea sp. from the Fibuloptyxis bed at Foss Cross - noted above). The identification of the White Limestone Eunerinea sp. as Eu. eudesii must therefore be suspect. The isometric growth of Bathonian Nerineids is similar to that of Turritella spp. A biometrical analysis of T. mortoni by Andrews (1974) revealed that the only allometric growth component in the ontogeny of this species is an increase in the basal convexity of the whorls. This can be functionally best interpreted as an ontogenetic increase in the cross-sectional area of the inhalent portion of the aperture, thereby increasing the ciliary feeding capacity of this largely sessile gastropod as the volume of the animal increases. Only Fibuloptyxis witchelli amongst the Bathonian gastropods studied by the present author is believed to exhibit significant allometric growth during its ontogeny.

Morphological variation in Bathonian Nerineid gastropods

The simple shell form and isometric growth of Bathonian Nerineids produces little morphological variation within the various samples, although depending upon the stratigraphical position, the variation between the samples can be quite large.

The variation in the apical angle and whorl width/height ratios amongst the samples of Aphanoptyxis spp. are shown in Tables 3D and 3F. The variation between samples is statistically compared using Students' 't' test and the results are shown in Tables 3E and 3G. The use of the Students' 't' test in the comparison of the means of samples is well known and fully dealt with elsewhere (Simpson, Roe and Lewontin, 1960; Sokal and Rohlf, 1973). The formula used is

Table 3D

Apical angle variation in Bathonian species of Aphanoptyxis

(The samples are arranged in stratigraphical order workings downwards)

A. bladonensis

Oxford University Museum, Nos. J 840 - Holotype
J 837-43 - Paratypes
J 13021-45 - Topotypes
J 13069 - Topotype
J 13054-5

N = 65
X̄ = 23.9°
Observed Range = 18.0°-32.0°
Standard Deviation = 2.9°

A. ardleyensis

Ardley Fields Quarry, bed 34

N = 14
X̄ = 16.3°
Observed Range = 14.0°-18.5°
Standard Deviation = 1.5°

Oxford University Museum,
Nos. J 828-9 - Para. & lectotype resp.
J 885 - Paratype

N = 3
X̄ = 12.8°
Observed Range = 11.0°-15.5°
Standard Deviation = 2.4°

A. cf. langrunensis

Worsham, bed 8a

N = 16
X̄ = 18.5°
Observed Range = 15.0°-21.5°
Standard Deviation = 1.8°

Eton College, bed 12a

N = 8
X̄ = 19.4°
Observed Range = 15.0°-23.0°
Standard Deviation = 2.3°

North Leigh, bed 17

N = 1
X̄ = 17.0°
Observed Range = -
Standard Deviation = -

A. excavata sp. nov.

Sturt Farm, bed 5

N = 27
X̄ = 24.8°
Observed Range = 19.0°-31.0°
Standard Deviation = 3.3°

Slape Hill, bed 3

N = 1
X̄ = 27.0°
Observed Range = -
Standard Deviation = -

A. eulimoides

Oxford University Museum, Nos. J 845 - Holotype
J 844 - Paratype
J 23536
J 23538-44

N = 10
X̄ = 21.5°
Observed Range = 17.5°-25.0°
Standard Deviation = 2.2°

Mean standard deviation of all Aphanoptyxis spp. expressed as % = 12.2%

			A. ardleyensis		A. cf. langrunensis			A. excavata sp. nov.	
		A. bladonensis	Ardley Fields Quarry	Oxford Univ. Mus.	Worsham bed 8a	Eton Coll. bed 12a	North Leigh bed 17	Sturt Farm bed 5	Slape Hill bed 3
A. ardleyensis	Ardley Fields Quarry	77 9.50 ***							
	Oxford Univ. Mus.	66 6.20 ***	15 3.34 **						
A. cf. langrunensis	Worsham bed 8a	79 7.05 ***	28 3.61 ***	17 4.82 ***					
	Eton College bed 12a	71 4.22 ***	20 3.84 ***	9 4.20 **	22 1.05 NS				
	North Leigh bed 17	64 2.36 ** Δ	13 0.45 NS Δ	2 1.52 NS Δ	15 0.81 NS Δ	7 0.98 NS Δ			
A. excavata sp. nov.	Sturt Farm bed 5	90 1.30 NS	39 9.12 ***	28 6.08 ***	41 7.021 ***	33 4.31 ***	26 2.32 * Δ		
	Slape Hill bed 3	64 1.06 NS Δ	13 6.89 *** Δ	2 5.12 * Δ	15 4.58 *** Δ	7 3.12 ** Δ	Δ	26 0.65 NS Δ	
	A. eulimoides	73 2.50 **	22 6.90 ***	11 5.91 ***	24 3.34 ***	16 1.97 *	9 1.95 * Δ	35 7.88 ***	9 2.38 * Δ

degrees of freedom - 77 | 9.50 — value of 't'
*** — significance

NS = not significant
* = < 0.05 = significant
** = < 0.01 = v. significant
*** = < 0.001 = v.v. significant

Table 3E

Δ - modified formula used (see Simpson, Roe & Lewontin, 1960, p. 183).

Comparison of means of apical angles in British Bathonian *Aphanoptyxis* spp. using Students 't' test

Table 3F

Whorl width/height ratio variation in Bathonian species of Aphanoptyxis

(The samples are arranged in stratigraphical order working downwards).

A. bladonensis

Oxford University Museum, Nos. J 840 - Holotype
J 837-43 - Paratypes
J 13021-45 - Topotypes
J 13069 - Topotype
J 13054-5

N = 143
$\bar{X}$ = 2.06
Observed Range = 1.33 -2.80
Standard Deviation = 0.27

A. ardleyensis

Ardley Fields Quarry, bed 34	Oxford University Museum, Nos. J 828-9 - Para.& Lectotype resp. J 885 - Paratype
N = 62	N = 21
$\bar{X}$ = 1.91	$\bar{X}$ = 1.65
Observed Range = 1.69 -2.15	Observed Range = 1.38 -2.09
Standard Deviation = 0.11	Standard Deviation = 0.18

A. cf. langrunensis

Worsham, bed 8a	Eton College, bed 12a	North Leigh, bed 17
N = 70	N = 10	N = 8
$\bar{X}$ = 2.07	$\bar{X}$ = 1.99	$\bar{X}$ = 1.95
Observed Range = 1.78 -2.55	Observed Range = 1.71 -2.26	Observed Range = 1.86 -2.13
Standard Deviation = 0.24	Standard Deviation = 0.16	Standard Deviation = 0.10

A. excavata sp. nov.

Sturt Farm, bed 5	Slape Hill, bed 3
N = 80	N = 3
$\bar{X}$ = 2.29	$\bar{X}$ = 2.29
Observed Range = 1.68 -2.81	Observed Range = 2.23 -2.35
Standard Deviation = 0.22	Standard Deviation = 0.06

A. eulimoides

Oxford University Museum, Nos. J 845 - Holotype
J 844 - Paratype
J 23526
J 23538-44

N = 43
$\bar{X}$ = 2.09
Observed Range = 1.79 -2.63
Standard Deviation = 0.20

Mean standard deviation of all Aphanoptyxis spp. expressed as % = 8.49%

			A. ardleyensis		A. cf. langrunensis			A. excavata sp. nov.	
		A. bladonensis	Ardley Fields Quarry	Oxford Univ. Mus.	Worsham bed 8a	Eton Coll. bed 12a	North Leigh bed 17	Sturt Farm bed 5	Slape Hill bed 3
A. ardleyensis	Ardley Fields Quarry	203 4.22 ***							
	Oxford Univ. Mus.	162 6.73 ***	81 7.87 ***						
A. cf. langrunensis	Worsham bed 8a	211 0.26 NS	130 4.82 ***	89 7.41 ***					
	Eton College bed 12a	151 0.81 NS	70 1.20 *	29 5.09 ***	78 1.02 NS				
	North Leigh bed 17	149 1.14 NS	68 0.98 NS	27 4.43 ***	76 1.39 NS	16 0.62 NS			
A. excavata sp. nov.	Sturt Farm bed 5	221 6.50 ***	140 12.44 ***	99 12.28 ***	148 5.86 ***	88 4.17 ***	86 4.31 ***		
	Slape Hill bed 3	144 1.47 NS	63 5.91 ***	22 6.01 ***	71 1.58 NS	11 3.10 **	9 5.42 ***	81 0.00 NS	
	A. eulimoides	184 0.73 NS	103 5.92 ***	62 8.53 ***	121 0.46 NS	51 1.47 NS	49 1.92 *	121 4.96 ***	44 1.71 *

degrees of freedom - 203 | 4.22 value of 't'
*** significance

NS = not significant
* = < 0.05 = significant
** = < 0.01 = v. significant
*** = < 0.001 = v.v. significant

Table 3G

Comparison of means of whorl width/height ratios in British Bathonian Aphanoptyxis spp. using Students 't' test

$$t = \frac{\bar{x}_1 - \bar{x}_2 \sqrt{\dfrac{N_1 . N_2}{N_1 + N_2}}}{\sqrt{\dfrac{(N_1 - 1)\ S.D._1^{\ 2} + (N_2 - 1)\ S.D._2^{\ 2}}{N_1 + N_2 - 2}}}$$

Where one of the samples is a single specimen only, and therefore has no standard deviation, comparison with other samples is possible using a modified formula;

$$t = \frac{\bar{x}_1 - x_2 \dfrac{\sqrt{N_1}}{N_1 - 1}}{S.D._1}$$

Discussion

In the following section, the various samples of Aphanotpyxis sp. have been specifically identified as described in Chapter 2. This in no way implies that the species categories pre-empted the statistical analyses and their inclusion below is purely to clarify the discussion.

The general conclusions to be drawn from these samples of the several Aphanoptyxis species present in the White Limestone are;

1) A. eulimoides appears to be a distinct species.
2) A. bladonensis appears to be a distinct species, (the inability to statistically discriminate ($P < 0.05$) A. bladonensis from A. excavata at Slape Hill is probably due to the small size of the Slape Hill sample).

3) The differences between the samples of A. excavata at Sturt Farm and Slape Hill were not statistically significant at the 5% level (i.e. $P < 0.05$).

4) The Sturt Farm and Slape Hill samples of Aphanoptyxis excavata were statistically very significantly different (i.e. $P < 0.001$) from those samples of Aphanoptyxis cf. langrunensis taken from adjacent, stratigraphically higher, horizons (i.e. North Leigh, Worsham and Eton College).

5) The sample of A. ardleyensis from Ardley Fields Quarry is statistically significantly different ($P > 0.05$) from the samples of Aphanoptyxis cf. langrunensis from Worsham and Eton College but not significantly different ($P < 0.05$) from the North Leigh sample. Possibly this is a reflection of the small sample size from North Leigh.

6) The type-specimens of A. ardleyensis Arkell 1931 are statistically significantly different ($P > 0.05$) from all other Aphanoptyxis spp. samples, including a sample of Aphanoptyxis ardleyensis from Ardley Fields Quarry:- adjacent to the type locality in the Ardley-Fritwell railway-cutting. Two explanations are possible:-
   a) Bias in favour of the more acicular end members when the type-specimens were collected and designated.
   b) The type-specimens may have been collected from the Upper Ardleyensis Bed whereas the specimens from Ardley Fields Quarry were collected from the Lower Ardleyensis Bed. Only one Ardleyensis Bed was recorded by Arkell (1931) (See Chapter 1; Barker and Torrens, in press).

Table 3H

Apical angle variation in Bathonian species of *Eunerinea* and *Nerinella*

Nerinella cf. *pseudocylindrica*

Eton College, bed 12a

N = 12

$\overline{X}$ = 6.0°
Observed Range = 4.0°-8.5°
Standard Deviation = 1.28°

Nerinella cf. *acicula*

Slape Hill, bed 5

N = 20

$\overline{X}$ = 9.0°
Observed Range = 7.0°-11.5°
Standard Deviation = 1.09°

Eunerinea eudesii Geological Survey Museum GSM 8288 - Lectotype
GSM 49428-9 - Para /Topotypes
Oxford University Museum J 13076-7
J 833-5

N = 3 (only J 13077, GSM 8288 and 49429 measureable)
$\overline{X}$ = 20.5°
Observed Range = nil
Standard Deviation = nil

Eunerinea arduennensis

Foss Cross, *Fibuloptyxis* bed - bed 7

N = 12

$\overline{X}$ = 14.45°
Observed Range = 11.0°-17.5°
Standard Deviation = 1.45°

Foss Cross, bed 4

N = 11

$\overline{X}$ = 11.8°
Observed Range = 10.5°-13.5°
Standard Deviation = 1.08°

Slape Hill, bed 3

N = 10

$\overline{X}$ = 13.35°
Observed Range
= 10.0°-17.5°
Standard Deviation
= 2.09°

Slape Hill, bed 5

N = 61

$\overline{X}$ = 13.4°
Observed Range
= 10.0°-18.0°
Standard Deviation
= 1.61°

Slape Hill, bed 7

N = 5

$\overline{X}$ = 14.2°
Observed Range
= 11.0°-17.0°
Standard Deviation
= 2.36°

North Leigh, bed 17

N = 16

$\overline{X}$ = 13.06°
Observed Range
= 11.0°-14.5°
Standard Deviation
= 1.1°

Ardley Fields, bed 34

N = 8

$\overline{X}$ = 11.43°
Observed Range
= 10.5°-14.0°
Standard Deviation
= 1.23°

Croughton, bed 7

N = 12

$\overline{X}$ = 13.08°
Observed Range
= 12.0°-14.5°
Standard Deviation
= 1.01°

Mean standard deviation of all *Eunerinea* and *Nerinella* spp. expressed as % = 12.383%

	N. cf. pseudocylindrica	N. cf. acicula	Eu. eudesii	Eunerinea arduennensis						
	Eton Coll.	Slape Hill		Foss Cross bed 7	Foss Cross bed 4	Slape Hill bed 3	Slape Hill bed 5	Slape Hill bed 7	North Leigh bed 17	Ardley Fields bed 34
N. cf. acicula Slape Hill	30 7.06 ***									
Eu. eudesii	11 10.88 *** Δ	19 10.30 *** Δ								
Foss Cross bed 7	22 15.13 ***	30 12.09 ***	11 4.01 ** Δ							
Foss Cross bed 4	21 11.69 ***	29 6.86 ***	10 7.71 *** Δ	21 4.93 ***						
Slape Hill bed 3	20 10.14 ***	28 7.55 ***	9 3.26 ** Δ	20 1.45 NS	19 2.17 *					
Slape Hill bed 5	71 14.99 ***	79 11.37 ***	60 4.37 *** Δ	71 2.10 *	70 3.16 **	69 0.09 NS				
Slape Hill bed 7	15 9.40 ***	23 7.45 ***	4 2.44 * Δ	15 0.27 NS	14 2.86 **	13 0.71 NS	64 1.03 NS			
North Leigh bed 17	26 15.67 ***	34 11.06 ***	15 6.56 *** Δ	26 2.89 **	25 2.95 **	24 0.77 NS	75 0.80 NS	19 1.49 NS		
Ardley Fields bed 34	18 9.44 ***	26 5.14 ***	7 6.95 *** Δ	18 4.83 ***	17 0.70 NS	16 2.29 *	67 3.33 ***	11 2.81 **	22 3.29 **	
Croughton bed 7	22 15.04 ***	30 10.53 ***	11 7.06 *** Δ	22 2.94 **	21 2.94 **	20 0.40 NS	71 0.66 NS	15 1.41 NS	26 0.05 NS	18 3.28 **

degrees of freedom 30 | 7.06 (value of 't') | *** (significance)

NS = not significant
* = < 0.05 = significant
** = < 0.01 = v. significant
*** = < 0.001 = v.v. significant

Table 3I

Δ - modified formula used (see Simpson, Roe & Lewontin, 1960, p. 183).

Comparison of means of apical angles in British Bathonian *Nerinella* and *Cossmannea* spp. using Students 't' test

Table 3J

Whorl width/height ratio variation in Bathonian species of *Eunerinea* and *Nerinella*

Nerinella cf. *pseudocylindrica*

Eton College, bed 12a

N = 39

X̄ = 1.49
Observed Range = 1.20-1.62
Standard Deviation = 0.09

Nerinella cf. *acicula*

Slape Hill, bed 5

N = 99

X̄ = 1.39
Observed Range = 1.19-1.86
Standard Deviation = 0.10

Eunerinea eudesii

Geological Survey Museum GSM 8288 - Lectotype
GSM 49428-9 - Para/Topotypes
Oxford University Museum J 13076-7
J 833-5

N = 40

X̄ = 2.24
Observed Range = 1.80-2.61
Standard Deviation = 0.19

Eunerinea arduennensis

Foss Cross, *Fibuloptyxis* bed, bed 7

N = 45

X̄ = 2.03
Observed Range = 1.58-2.30
Standard Deviation = 0.14

Foss Cross, bed 4

N = 19

X̄ = 1.90
Observed Range = 1.66-2.10
Standard Deviation = 0.11

Slape Hill, bed 3

N = 39

X̄ = 1.90
Observed Range = 1.71-2.16
Standard Deviation = 0.13

Slape Hill, bed 5

N = 324

X̄ = 1.87
Observed Range = 1.40-2.28
Standard Deviation = 0.17

Slape Hill, bed 7

N = 27

X̄ = 2.13
Observed Range = 1.72-2.43
Standard Deviation = 0.16

North Leigh, bed 17

N = 79

X̄ = 1.91
Observed Range = 1.61-2.29
Standard Deviation = 0.15

Ardley Fields, bed 34

N = 7

X̄ = 1.73
Observed Range = 1.68-1.84
Standard Deviation = 0.07

Croughton, bed 7

N = 51

X̄ = 1.85
Observed Range = 1.63-2.17
Standard Deviation = 0.10

Mean standard deviation of all *Eunerinea* and *Nerinella* spp. expressed as % = 6.83%

	N. cf. pseudocylindrica	*N. cf. acicula*	*Eu. eudesii*	*Eunerinea arduennensis*						
	Eton Coll.	Slape Hill		Foss Cross bed 7	Foss Cross bed 4	Slape Hill bed 3	Slape Hill bed 5	Slape Hill bed 7	North Leigh bed 17	Ardley Fields bed 34
N. cf. acicula Slape Hill	136 5.44 ***									
Eu. eudesii	77 22.32 ***	137 34.37 ***								
Foss Cross bed 7	82 20.66 ***	142 31.25 ***	83 5.84 ***							
Foss Cross bed 4	56 15.12 ***	116 20.04 ***	57 7.24 ***	62 3.60 ***						
Slape Hill bed 3	76 16.19 ***	134 24.70 ***	77 9.26 ***	82 4.39 ***	58 0.00 NS					
Slape Hill bed 5	361 13.72 ***	421 26.71 ***	362 12.81 ***	367 6.03 ***	341 0.76 NS	361 1.07 NS				
Slape Hill bed 7	64 20.73 ***	124 29.59 ***	65 2.47 **	70 2.78 ***	44 5.42 ***	64 6.45 ***	349 7.67 ***			
North Leigh bed 17	116 16.09 ***	176 27.64 ***	117 10.34 ***	122 4.39 ***	96 0.27 NS	116 0.36 NS	401 1.91 *	104 6.47 ***		
Ardley Fields bed 34	411 6.68 ***	104 8.82 ***	45 6.97 ***	50 5.53 ***	24 3.79 ***	44 3.35 ***	329 1.55 NS	32 6.40 ***	84 3.13 **	
Croughton bed 7	88 17.67 ***	148 26.69 ***	89 12.61 ***	94 7.31 ***	68 1.81 *	88 2.06 *	373 0.82 NS	76 9.50 ***	128 2.52 **	56 3.06 **

value of 't'
degrees of freedom - 136 5.44 ***
significance

NS = not significant
* = < 0.05 = significant
** = < 0.01 = v. significant
*** = < 0.001 = v.v. significant

Table 3K

Comparison of means of whorl width/height ratios in British Bathonian *Nerinella* and *Cossmannea* spp. using Students 't' test

7) The mean variability of the apical angle standard deviations amongst the samples of *Aphanoptyxis* spp. was ± 8.5%.
8) The mean variability of the whorl width/height ratio standard deviations amongst the samples of *Aphanoptyxis* spp. was ± 12.2%.

The morphological variability between the samples of *Eunerinea* spp. and *Nerinella* spp. from the White Limestone was also statistically compared using the Students' 't' test. The apical angle variation and whorl width/height variation are shown in Tables 3H and 3J respectively. The results of the Students' 't' tests are shown in Tables 3J and 3K.

The general conclusions to be drawn from the statistical comparisons between the various samples of *Eunerinea* spp. and *Nerinella* spp. are as follows.

1) The two samples of *Nerinella* sp. (Eton College and Slape Hill) are statistically very significantly different ($P < 0.001$) and probably represent two species. This reinforces the earlier conclusions obtained by comparing the slopes of the Reduced Major Axes of the *Nerinella* sp. samples.
2) The sample of *Eunerinea eudesii* (including the type specimens) is statistically very significantly different ($P < 0.001$) from other *Eunerinea* sp. samples in the White Limestone. Once again this suggests that the abundant *Eunerinea* sp. in the White Limestone is *not* *Eu. eudesii* as previously recorded (Arkell, 1931).
3) Both the mean apical angle and the mean whorl width/height ratio in the sample of *Eunerinea* sp. from the *Fibuloptyxis* Bed at Foss Cross Quarry are statistically significantly different ($P < 0.005$) from most other White Limestone *Eunerinea* samples. Only the mean

apical angle of two Slape Hill samples (bed 5 and bed 7) are not statistically different ($P > 0.05$).

4) Comparisons between the remaining samples of Eunerinea sp. do show some differences which are statistically significant ($P < 0.05$). However, these differences appear to be inconsistent in their distribution, e.g. the mean apical angle of the Foss Cross bed 4 sample is not statistically significantly different from that of the Ardley sample but the mean whorl width/height ratios are significantly different. Whereas when the Eunerinea sample from Slape Hill, bed 5, is compared with that from Ardley, the situation is reversed.

Certainly the numerical values of the Students' 't' tests between the Eunerinea sp. samples are much lower than those produced when the Nerinella spp. and Eunerinea eudesii samples are compared with each other and with the Eunerinea sp. samples. This suggests that whilst the differences between the Eunerinea sp. samples are statistically significantly different (at $P < 0.05$), they may not be biologically significantly different.

5) The mean variability of the apical angle standard deviations amongst the samples of Eunerinea spp. and Nerinella spp. was ± 12.4%.
6) The mean variability of the whorl width/height ratio standard deviations amongst the samples of Eunerinea spp. and Nerinella spp. was ± 6.8%.

The discrimination of Nerineid gastropod species

In many instances, the gastropod material available for study consists of type-specimens (which cannot be sectioned) or specimens in which the body-chamber has not been filled with sediment and therefore the fold pattern is not preserved. Furthermore, the limited variation of the internal folding of Nerinella and Eunerinea species (3 folds) and the absence of folding amongst the various species of Aphanoptyxis, predetermines a reliance upon the external morphologies for discrimination between the species. If the external shell parameters measured previously can be used as species discriminants then such material can be profitably studied. It is also clearly desirable to know which of the variables measured are the most useful in separating the various Nerineid species.

In order to assess the discriminatory value of the parameters (variables) previously measured (i.e. the apical angle, sutural angle, whorl width, whorl height and whorl width/height ratio) a stepwise multivariate disciminant anlysis was used. The program used (B.M.D. 07 M) is one of the B.M.D. Biomedical Computer programs produced by the University of California, Los Angeles Medical Centre. Full details of these programs may be found in Dixon (1968). The programs have been adapted for use with the ICL 4130 computer at Portsmouth Polytechnic and the revised reference manuals for these programs (B.M.D., a statistical package for the ICL 4130, vols. I-V) are available from the Department of Mathematics at Portsmouth Polytechnic. The geological use of the B.M.D. computer programs is also noted by Davis (1973, pp. 539-40).

Basically the program, B.M.D. 07 M, is designed to classify a set of discriminating variables by using these variables to achieve the best multidimensional separation between a number of groups (up to a maximum of 5) which the operator selects.

In this study the groups were gastropod samples from selected Nerineid horizons in the White Limestone. The samples chosen were:-

1) *Nerinella* cf. *acicula*; Slape Hill bed 5; (N = 97)
2) *Eunerinea* *arduennensis*; Slape Hill bed 5; (N = 324)
3) *Aphanoptyxis* *ardleyensis*; Ardley Fields Quarry; (N = 58)
4) *Aphanoptyxis* cf. *langrunensis*; Worsham bed 8a; (N = 64)
5) *Aphanoptyxis* *excavata*; Sturt Farm bed 5; (N = 111)
6) *Aphanoptyxis* cf. *langrunensis*; Eton College bed 12a; (N = 10)

The first five samples were carefully selected not only to provide groups with large numbers, but also groups which were undoubtedly different at the generic level (i.e. *Nerinella*, *Eunerinea* and *Aphanoptyxis*) as well as groups which were specifically different (i.e. *A*. *ardleyensis*, *A*. cf. *langrunensis* and *A*. *excavata*. Furthermore, considering the results of the 'z' tests on the Reduced Major Axes and the results of the Students' 't' tests on the means of the apical angles and means of the whorl width/height ratios, the possibility of further separating the various samples of *Aphanoptyxis* spp. (which at this stage had *not* been further subdivided) into valid species could not be ignored.

As a check upon the stratigraphical validity of any separation the program might produce, the last sample (*Aphanoptyxis* cf. *langrunensis*; Eton College bed 12a) was excluded from the discrimination procedure but was still classified and plotted in the later stages and also in the canonical analysis which formed the final part of the program.

The variables entered for each of the 664 cases distributed amongst the six samples were:

1) the apical angle
2) the sutural angle
3) the whorl width
4) the whorl height
5) the whorl width/height ratio.

Results and Conclusions

The initial part of the output gave the mean and standard deviation for each variable for each of the groups. The variables were then compared by a 'within groups covariance matrix', shown below.

	Apical angle	Sutural angle	Whorl width	Whorl height	Whorl W/H ratio
Apical angle	3.69482				
Sutural angle	-0.49082	5.19089			
Whorl width	-3.45034	3.91064	168.99918		
Whorl height	-2.82693	2.20990	91.36374	53.26590	
Whorl W/H ratio	0.09225	0.00720	-0,30151	-0.36986	0.02436

The variance of a variable, X, is its variation about the mean value of X. The covariance shows how two variables, X and Y, are distributed about a common mean. The greater the numerical value of the covariance, the greater the variability within a group. The above covariance matrix shows that the whorl width and the whorl height are very variable whereas the apical angle, sutural angle and whorl width/height ratios show little variation within a group.

The mutual interaction of the variables is the next feature assessed by the computer program using a 'within groups correlation matrix', the results of which are shown below.

	Apical angle	Sutural angle	Whorl width	Whorl height	Whorl W/H ratio
Apical angle	1.00000				
Sutural angle	-0.11207	1.00000			
Whorl width	-0.13808	0.13203	1.00000		
Whorl height	-0.20151	0.13290	0.96296	1.00000	
Whorl W/H ratio	0.30748	0.02025	-0.14859	-0.32467	1.00000

The high correlation coefficient (0.96296) between the whorl width and the whorl height indicates a high degree of mutual dependence in these variables whereas the other variables are almost completely independent (i.e. changes in the apical angle, for instance, produce very little corresponding predictable change in the other variables).

The next part of the program is the stepwise discriminant analysis. At each step a variable is entered into the set of discriminating variables. The variables are only included if they make a sufficiently large decrease in the ratio of within groups generalised variance to total generalised variance amongst the samples. This ratio is known as the F-ratio. At each step the variate entered is the one with the highest F-ratio, i.e. the variable with the greatest discriminating ability between the groups. The initial F-ratios were as follows;

Apical angle - 999.0212
Sutural angle - 497.8042
Whorl W/H ratio - 448.7962
Whorl width - 10.5275
Whorl height - 10.4569

These variables were then successively entered into the discriminant function in the above order. During the course of analysis, the whorl height variable no longer accounted for a significant proportion of within group to total generalised variance and was therefore not included after step 4 in the procedure. The order in which the variables were entered into the discriminant function showed that if only one variable was to be used to achieve the best separation of the samples, the apical angle was by far the best variable to use. The sutural angle and whorl width/height ratio were approximately equal in their discriminatory ability but the whorl width (and hence the whorl height because of the high correlation between these two variables) was of little use in descriminating between the groups.

After the final step, all cases in each of the groups are classified and for each case the square of the Mahanalobis' generalised distance, D^2, from each of the group means and the posterior probability of belonging to each group, are calculated. Each case is then classified as belonging to the group with the highest posterior probability (i.e. as belonging to the group where the distance from the group mean to the case in point - the Mahanalobis generalised distance, D^2, - is at a minimum). Two examples from the 664 cases used in this study are shown below.

computer re-classification

A. ardleyensis group	*A. ardleyensis*	*A. cf. langrunensis*	*A. excavata*	*Nerinella*	*Eunerinea*
	Ardley Fields	Worsham	Sturt Farm	Slape Hill	Slape Hill
Case No. 5 Square of Mahanalobis' generalised distance D^2	0.322	4.891	28.410	31.262	1.012
Posterior probability	0.552	0.056	0.000	0.000	0.391

therefore Case 5 correctly belongs to the *A. ardleyensis* group.

Case No. 33 Square of Mahanalobis' generalised distance D^2	3.959	13.362	45.959	16.667	3.945
Posterior probability	0.496	0.004	0.000	0.001	0.499

therefore Case 33 of the *A. ardleyensis* group should be placed in the *Eunerinea* group.

The net result is that the initial groups used in the stepwise discriminant analysis are re-classified on the basis of the results of that analysis. At this stage the group which was excluded from the discriminant analysis (*Aphanoptyxis* cf. *langrunensis*, Eton College bed 12a) is now classified and plotted. The full classification matrix is shown overleaf.

The interpretation of this matrix is interesting and has important stratigraphic implications. The sample of *Nerinella* cf. *acicula* is distinct and easily separable from all other samples. The external morphologies of the *Eunerinea arduennensis* sample show some overlap (13% of the sample) with the range of morphologies shown by the sample of *Aphanoptyxis ardleyensis*. Similarly, 15% of the *A. ardleyensis* sample show morphological overlap with the *Eunerinea arduennensis* sample. Since these two genera can usually be separated by the presence or absence of internal folds, there is little danger of taxonomic confusion. However, the computer analysis does provide an 85%, or better, separation based upon external morphologies and if this degree of separation can be obtained with other samples which do not have criteria such as the presence or absence of folding to separate them, this suggests that such differences between these samples may at least be of specific rank.

The samples of *Aphanoptyxis* were chosen from three of the four *Aphanoptyxis* horizons in the White Limestone. *A. bladonensis* at the top is very distinctive and because the number of groups used in the program was limited to five, it was not included in this study. *A. ardleyensis*

	re-classification of cases into groups, based upon computer output				
original groups ↓	*A. ardleyensis*	*A. cf. langrunensis* Worsham	*A. excavata* Sturt Farm	*Nerinella*	*Eunerinea*
A. ardleyensis	40	9	0	0	9
A. cf. *langrunensis* Worsham	13	51	0	0	0
A. excavata Sturt Farm	0	19	92	0	0
Nerinella Slape Hill	0	0	0	97	0
Eunerinea Slape Hill	43	2	0	0	279
A. cf. *langrunensis* Eton College	1	8	0	0	1

occurs at the top of the Ardley Beds and another *Aphanoptyxis* horizon (*A*. cf. *langrunensis* from which the Worsham sample used in this study was taken) occurs at the base of the Ardley Beds. The sample of *Aphanoptyxis* from Sturt Farm (*A*. *excavata* sp. nov.) occurs at the top of a new basal member of the White Limestone Formation, the Excavata Beds (see Chapter 1) and these occur below the Ardley Beds.

Of the 58 cases in the *A*. *ardleyensis* sample, 9 (15%) show morphological overlap with the stratigraphically lower *A*. cf. *langrunensis* sample from Worsham. Similarly 20% of the Worsham sample show morphologies more typical of *A*. *ardleyensis*. Neither of these two groups show any overlap with the stratigraphically lowest *Aphanoptyxis* *excavata* sample from Sturt Farm, although 17% of the Sturt Farm sample are morphologically indistinguishable from the Worsham sample.

The matrix now classifies the sample of *Aphanoptyxis* cf. *langrunensis* from Eton College and on the basis of the foregoing discriminant analysis, 80% of the Eton College sample are indistinguishable from the *Aphanoptyxis* cf. *langrunensis* sample from Worsham; with a small overlap into the *A*. *ardleyensis* range and the *Eunerinea* *arduennensis* range. The present author had previously concluded (Chapter 1) on other grounds that the *Aphanoptyxis* horizons at Worsham (Bed 8a) and Eton College (Bed 12a) are laterally equivalent and the computer analysis shows quite independently that the gastropod samples are almost identical.

One therefore concludes that the morphological parameters of the various *Aphanoptyxis* populations are changing in a regular, predictable manner through the White Limestone and that biometrical analysis of these *Aphanoptyxis* populations can provide valuable stratigraphic information.

The final part of the program gives the results of a canonical analysis of the included variables. The four included variables may be taken to represent vectors in a four-dimensional space with the samples variously distributed in that space. This is extremely difficult to adequately represent in two-dimensions but canonical analysis is a means of mathematically 'rotating' this four-dimensional space (by calculating the eigen vectors) until the maximum separation of the samples in two dimensions is obtained. This two-dimensional surface is defined by the first and second canonical variables. All the groups can then be plotted by the computer on a two-dimensional graph of the first canonical variable against the second canonical variable, the results of which are shown in Fig. 3:8.

The results graphically express the relationships between the groups shown in the classification matrix above. The clear separation of the Sturt Farm *Aphanoptyxis excavata* sample (the lowest *Aphanoptyxis* horizon in the White Limestone) from the stratigraphically higher *A. ardleyensis* sample, with the *Aphanoptyxis* cf. *langrunensis* samples from intermediate horizons overlapping both fields is particularly evident.

The application of results to other Nerineid samples

The results of the stepwise multivariate discriminate analysis clearly indicate that, of the variables measured, the apical angles together with the sutural angles and whorl width/height ratios are the best discriminators amongst samples of Nerineid gastropods. The most practicable application of these results to other Bathonian Nerineid samples not included in the above study is a bivariate plot of the

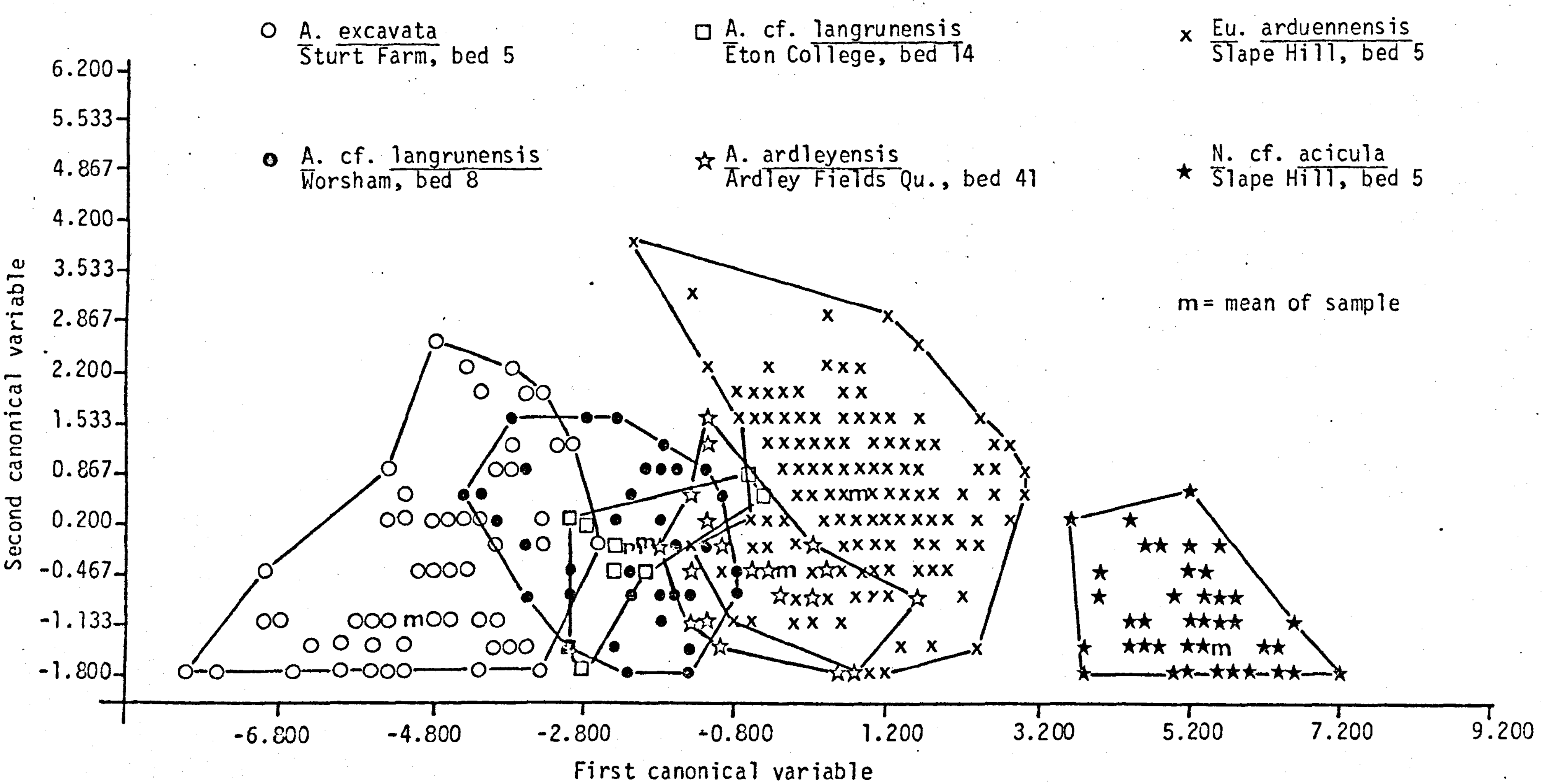


Fig. 3.8. Graphical output from canonical analysis of selected Nerineid populations from the White Limestone.

apical angle means together with some measure of their variation against the mean and variation of either the sutural angle or the whorl width/height ratio. Since there is little difference in discriminatory value between the sutural angles and the whorl width/height ratios, the decision to use the whorl width/height ratios was based upon convenience. The successive whorl widths and heights of the specimens had to be measured in order to provide data for regression analyses and growth studies and consequently it was easier to calculate the whorl width/height ratios than measure the sutural angles.

The bivariate plots of the apical angles and the whorl width/height ratios of the various Eunerinea and Nerinella samples taken from the White Limestone (including the samples used in the computer analysis) are shown in Fig. 3:9 and similarly the Aphanoptyxis samples are shown in Fig. 3:10.

The measure of variation used was ± one standard deviation about the mean, which encompasses 68.27% of the population, assuming that the population was normally distributed as most biological material is (Simpson, Roe and Lewontin, 1960, pp. 53-4). The results are discussed below.

General conclusions

The various Nerineid samples from the White Limestone have been subjected to biometrical analysis. Growth in Nerineids has been studied by regression analysis using the Reduced Major Axis and the slopes of the relative growth lines statistically compared using the 'z' test.

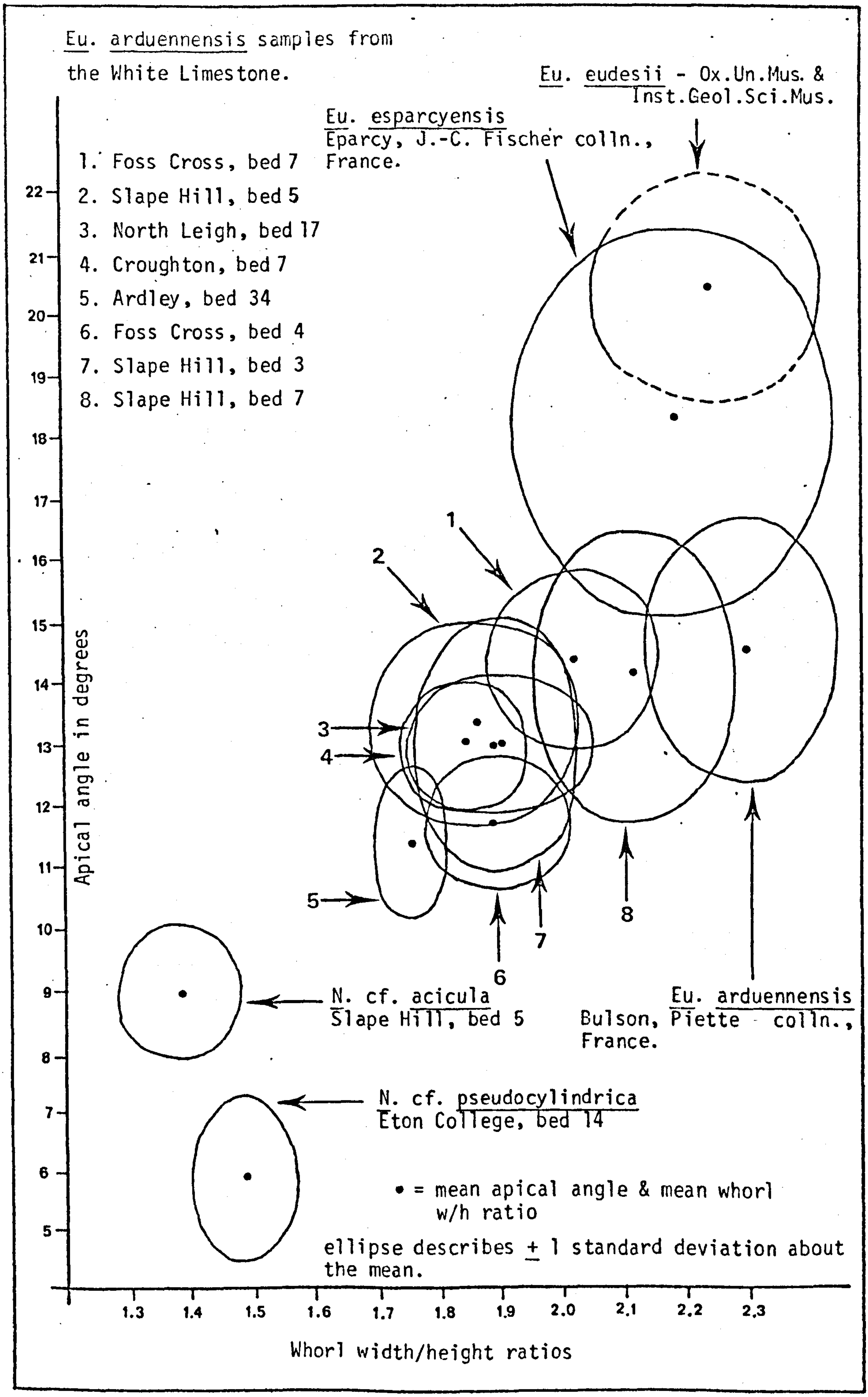


Fig. 3.9. Variation in apical angles and whorl w/h ratios in Nerinella and Eunerinea spp.

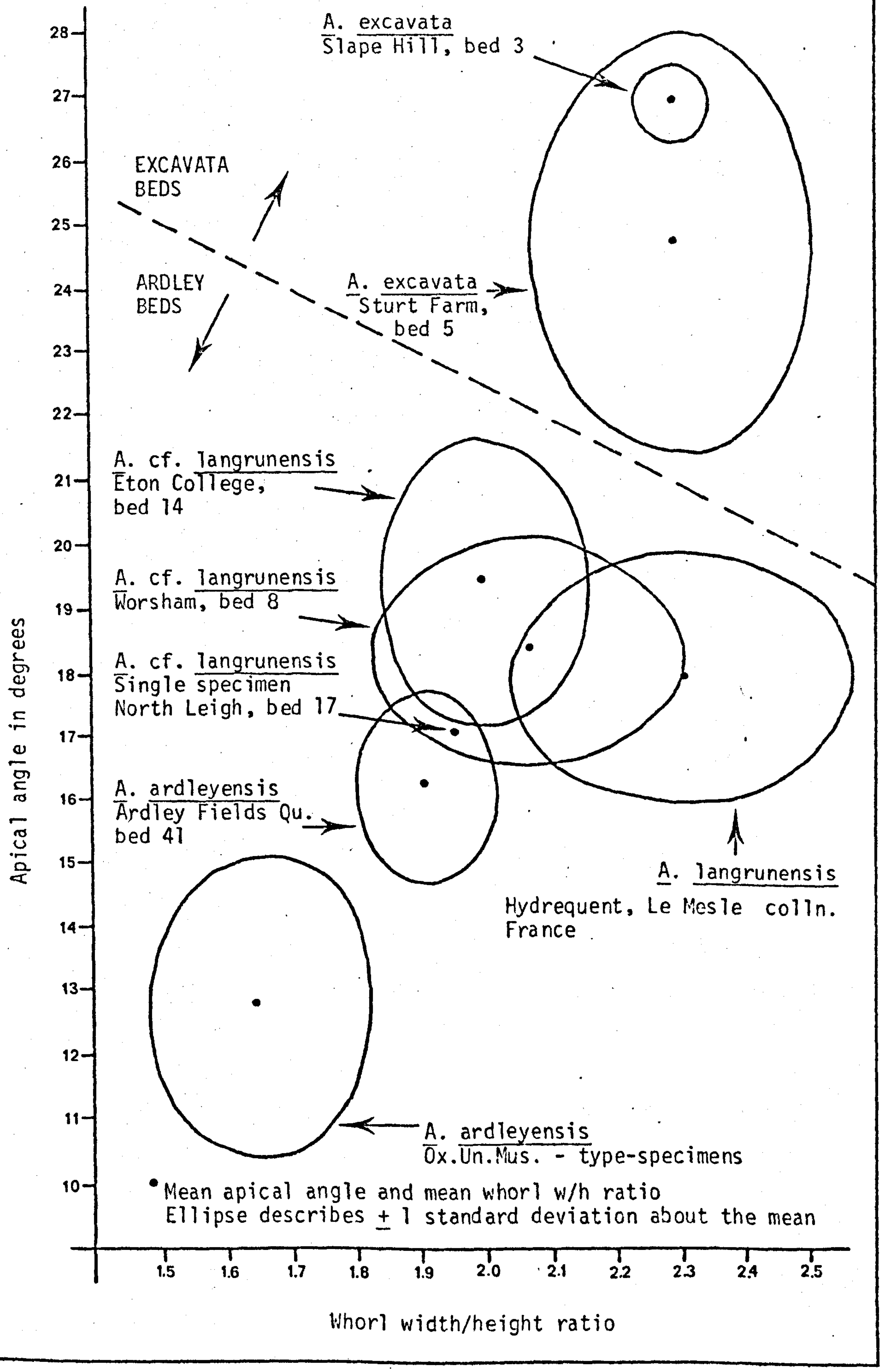


Fig. 3.10. Variation in apical angles and whorl w/h ratios in *Aphanoptyxis* spp.

The mean apical angles and mean whorl width/height ratios of the samples have been calculated and the results statistically evaluated using Students' 't' test.

The discriminatory ability of the variables measured on the Nerineid shells has been assessed by the use of a computer program, BMD 07 M - a stepwise multivariate discriminant analysis, and using the results of this program, the various Nerinella, Eunerinea and Aphanoptyxis samples have been plotted using the two best discriminant variables (Fig. 3:9 and Fig. 3:10).

The general conclusions are as follows;

1) The two Nerinella samples represent two species (N. cf. acicula and N. cf. pseudocylindrica - see Chapter 2).
2) The various samples recorded as Eunerinea sp. represent samples from several populations of the same species. No stratigraphic or geographic trend is discernable in the pattern of morphological overlap of the samples (see Fig. 3:9).
3) This Eunerinea sp. is not Eu. eudesii as previously recorded (Arkell, 1931).
4) The samples of Aphanoptyxis from the Ardley and Excavata Beds show morphological trends which can be correlated with their stratigraphic position.

The examples of Aphanoptyxis from the Excavata Beds have larger apical angles and relatively wider whorls than stratigraphically higher examples of the same genus. There is no morphological overlap with other higher Aphanoptyxis samples in the Ardley Beds. Possibly the period of time represented by the hard-ground which usually separates the Excavata Beds from the Ardley Beds also represents a period of evolution in the Aphanoptyxis lineage for which there are now no known representatives. It is therefore considered that the samples from Sturt Farm (bed 5) and Slape Hill (bed 3) represent a new species of Aphanoptyxis - to be called A. excavata (see Chapter 2 for diagnosis).

Four Aphanoptyxis samples from the Ardley Beds have been analysed. Three of these (Worsham, Eton College and North Leigh) are from the lowest Aphanoptyxis horizon in the Ardley Beds. The fourth sample is from the lower Aphanoptyxis ardleyensis bed, near the top of the Ardley Beds at Ardley Fields Quarry. The statistical tests suggests that the Worsham and Eton College samples are from the same population or almost identical populations. Furthermore, these two samples are statistically significantly different ($P < 0.05$) from the stratigraphically higher sample from the Lower A. ardleyensis bed. The sample from North Leigh is unfortunately a single specimen and the statistical extrapolation of the morphological parameters of this specimen is unlikely to be representative of the population to which it once belonged. It is therefore somewhat unfortunate that this specimen falls in the fields of morphological overlap of the Worsham and Ardley Fields samples. However, based upon the data at present available, there nevertheless seems to be a distinct trend, probably evolutionary, in the morphology of Aphanoptyxis in the Excavata and Ardley Beds. The apical angle becomes smaller and the whorls become relatively higher as one samples successively higher horizons in these beds. The present author is of the opinion that the Aphanoptyxis sp. present at the base of the Ardley Beds at Worsham, Eton

College and North Leigh is a distinct intermediate species between A. ardleyensis and A. excavata sp. nov. This species is provisionally diagnosed as Aphanoptyxis cf. langrunensis (d'Orb.). A small sample (4 specimens) of A. langrunensis (a common French species) from the Bathonian of Hydrequent - Pas de Calais: le Mesle collection in the Muséum National d'Histoire Naturelle, Paris) has been studied by the present author. The only apparent difference between the British and French species is in the degree of convexity of the basal whorl. The taxonomic implications of this feature are discussed in Chapter 2.

5) The somewhat extreme position of the type-specimens of A. ardleyensis (see Fig. 3:10) is probably due to some combination of three factors

a) the small sample size (3 specimens)

b) bias in the selection of type-specimens

c) the possibility of collection from a higher stratigraphic horizon - the upper A. ardleyensis bed, thus continuing the evolutionary trend of the earlier examples.

Chapter 4

THE INTERNAL MORPHOLOGY OF THE NERINEACEA

'In the carriages of the past you can't go anywhere'

Maxim Gorky, The Lower Depths, 1903.

Introduction

In the previous chapter the author has endeavoured to utilise the basic external morphology of the high-spired Nerineid gastropods to achieve a quantitative discrimination between Nerineids at generic and specific levels.

The various aspects of the internal morphology of the Nerineacea which are less amenable to quantitative study will be discussed in the present chapter.

Shell micro-structure

The almost invariable association of Nerineids with carbonate environments means that they are subject to the complex diagenetic changes which carbonate sediments and their enclosed fauna undergo during lithification. With the sole exception of *Nerinella* cf. *multistriata* (Cossmann *ex* Piette) from the Upper Bajocian at Inver Tote, Isle of Skye (G.R. NG 506606, see later), all British Nerineids examined by the present author have undergone shell replacement via a cavity stage. The original aragonite shell and shell structures have been replaced by a mosaic of calcite crystals (see chapter 6). Even the Isle of Skye specimens, which show the incremental growth stages of the fold development, do not retain the original shell structure.

Stimulated by the work of Bøggild (1930) and the widespread availability of the scanning electron microscope, the evolutionary and taxonomic implications of molluscan shell structures have been the subject of a considerable number of recent studies (Erben, Flajs & Siehl, 1968; Hudson, 1968; McClintock, 1967; Taylor, Kennedy and Hall, 1969 and 1973; Taylor, 1973; Wise, 1970). Considering the uncertain taxonomic affinities of the Nerineacea, the possibility of utilising the shell microstructure in systematic studies could not be ignored.

The only recorded occurrence of the original shell micro-structure in a Nerineid gastropod seems to be that of Delpy (1937). In this case, the Corallian *Eunerinea salinensis* (d'Orb.) was colonised by the ectoproct *Millepodium* cf. *fasciculatum* Yabe and Sugiyama. The ectoproct evidently grew over the base of the shell and as the growth of the gastropod shell continued over the colony, the last whorl became disjunct. The ectoproct colony eventually completely enveloped the terminal whorl of the gastropod thus protecting the shell structures from alteration during diagenesis. Lacking similar protection, the rest of the shell did not retain its internal structure. As noted by Delpy (*op. cit.*, pp. 355-6) it was impossible at that time to ascertain by comparison with other specimens whether the presence of the ectoproct between the whorls or the change in growth vector had produced abnormal shell structures in the Nerineid.

Delpy's description of the shell structure was as follows (*op. cit.*, p. 356) - "D'épaisser assez considérable, il comporte une couche externe semblant formée de prismes perpendiculaires à la surface, une couche moyenne de lamelles entrecroisées et une couche interne dont le lamelles sont plus régulierment paralléles. L'épaisseur de la couche externe prismatique est à peu près $1/_{13}$ de l'épaisseur totale". Her conclusion was (op. cit., p. 356), "L'allure génerale du test vu en section rappelle plutôt le Fissurellida, les Lamellibranches anisomyaires, et Dentalium."

The photographs of Delpy (op. cit., pl. XXII and XXIII) are reproduced on plates 4:A and 4:B.

Only a complex crossed lamellar middle layer can be identified with certainty. The supposedly prismatic outer layer can only be seen in the enlarged photograph (plate 4:B), although no prismatic structure is visible at this magnification (50x). A possible inner layer is visible in plate 4:A, although structural details have not been resolved in the photograph. The disposition of finely spaced lamellae within this layer suggests that it is either a nacreous layer or a laminated honogeneous layer (see Taylor, Kennedy and Hall, op. cit., pp. 50-52). Unfortunately, the area of shell which Delpy (op. cit.) chose for an enlarged (50x) photograph in order to show the details of the shell structure, is that region where the gastropod itself generates secondary shell growth in order to seal the juxtasutural slit, i.e. the enlarged photograph of Delpy (op. cit.) is taken across the selenizone. It is not possible in the region of the selenizone to identify the 3 shell layers of Delpy with certainty. The laths of the complex crossed-lamellar layer gradually become larger, more regularly orientated until they are almost parallel to the inner surface.

Dr. N. J. Morris (British Museum, Natural History) kindly brought to the present author's attention the fact that the Trigoniacea preserved in the Gosau Beds (Cenomanian - Turonian, south-east of Saltzburg, Austria) regularly exhibit the original nacreous shell structure whilst the associated Nerineid gastropods apparently do not. This suggests that the inner nacreous/homogeneous layer of Delpy was either erroneous or not universally present in these gastropods. Subsequently an acetate peel was prepared from a Gosau specimen of Laevinerinea cf. nobilis (Münster) - specimen number 96987 (British Museum, Natural History) and is shown in plate 4:C. In spite of considerable brittle fracture, probably due to compaction, and a later phase of extension producing tension gashes, the shell microstructure and incremental growth are beautifully preserved in this specimen.

At least four shell layers are present each exhibiting well-developed crossed-lamellar structure, with the first order lamells approximately at right angles to the growth surface. No other type of shell microstructure was observed, although the external surface of the specimen was not preserved. Plate 4:D shows enlargements of an adapertural columellar fold and a part of the intraumbilical adapertural carina, both of which exhibit the growth increments and the shell structure.

Two explanations are possible to satisfactorily explain the apparent discrepancy in shell structure between Eu. salinensis and Laevinerinea cf. nobilis. Either Nerineid gastropods exhibited several types of shell structure or, more plausibly in the opinion of the present author, the enveloping ectoproct in Eu. salinensis produced abnormal shell growth and shell structures in this gastropod. No information has yet been found to support or refute the suggestion that abnormal growth in molluscs, whether induced by epifaunal colonisation or injury, etc., may produce atypical shell microstructures.

Support for this latter hypothesis has very recently been found. A silicified specimen of *Aptyxiella portlandica* from a chert nodule found in the Portland Freestone (U. Jurassic, Isle of Portland) exhibited a small area of the original crossed-lamellar structure in an otherwise completely recrystallised shell. Thus two Nerineacean genera (*Eunerinea* and *Aptyxiella*) are now known to possess a crossed-lamellar structure.

Unfortunately, the taxonomic implications of these shell microstructures are equally uncertain. The shell structure in *Eu. salinensis* is apparently a 'primitive' type in that it compares most closely with Prosobranch gastropods and, when the presence of the selenizone is considered, particularly the Archaeogastropoda such as the Fissurellidae and the Pleurotomariidae, as noted by Delpy (*op. cit.*, p. 357).

However, the crossed lamellar structure found in *Laevinerinea* cf. *nobilis* is the most common type of shell microstructure to be found amongst the gastropods, occurring frequently in representatives of the Mesogastropoda, Neogastropoda, Opisthobranchia and Pulmonata and is apparently without taxonomic significance.

The taxonomic position of the Nerineid gastropods is discussed more fully in Chapter 7.

Fold Terminology

Amongst Nerineid gastropods the cross-sectional shape of the whorls is usually quadrate thus allowing a more or less precise subdivision into the columellar, upper, outer (labral) and basal walls which may bear columellar, parietal, labral and basal folds respectively (see Cox, 1954, p. 12; 1955, pp. 198-99; Delpy, 1939, p. 149). Over a number of years a numerical abbreviation has developed in order to simplify the description of Nerineid genera (Levasseur, 1934; Delpy, 1939, pp. 151-2 and Cox, 1954). The number and arrangement of the internal folds of the shell are indicated by a brief formula (the fold diagnosis) which enumerates the folds borne respectively by the columella, parietal region, outer lip and base. This is illustrated, together with the fold terminology in Fig. 4.1.

Although helpful in general surveys, the use of fold diagnoses in more detailed studies is extremely limited. They cannot serve to distinguish two species of the same genus. Furthermore when comparing two genera, fold diagnoses do not indicate which of the several folds is the more strongly developed or precisely where a particular fold lies on the columellar wall or labrum, etc. Difficulty in formulating a fold diagnosis may also be encountered in those Nerineids in which the whorl cross-section is not quadrate. It may then become impossible to distinguish between the columellar wall and parietal region or the labral wall and the base; as in such genera as Phaneroptyxis and Itieria.

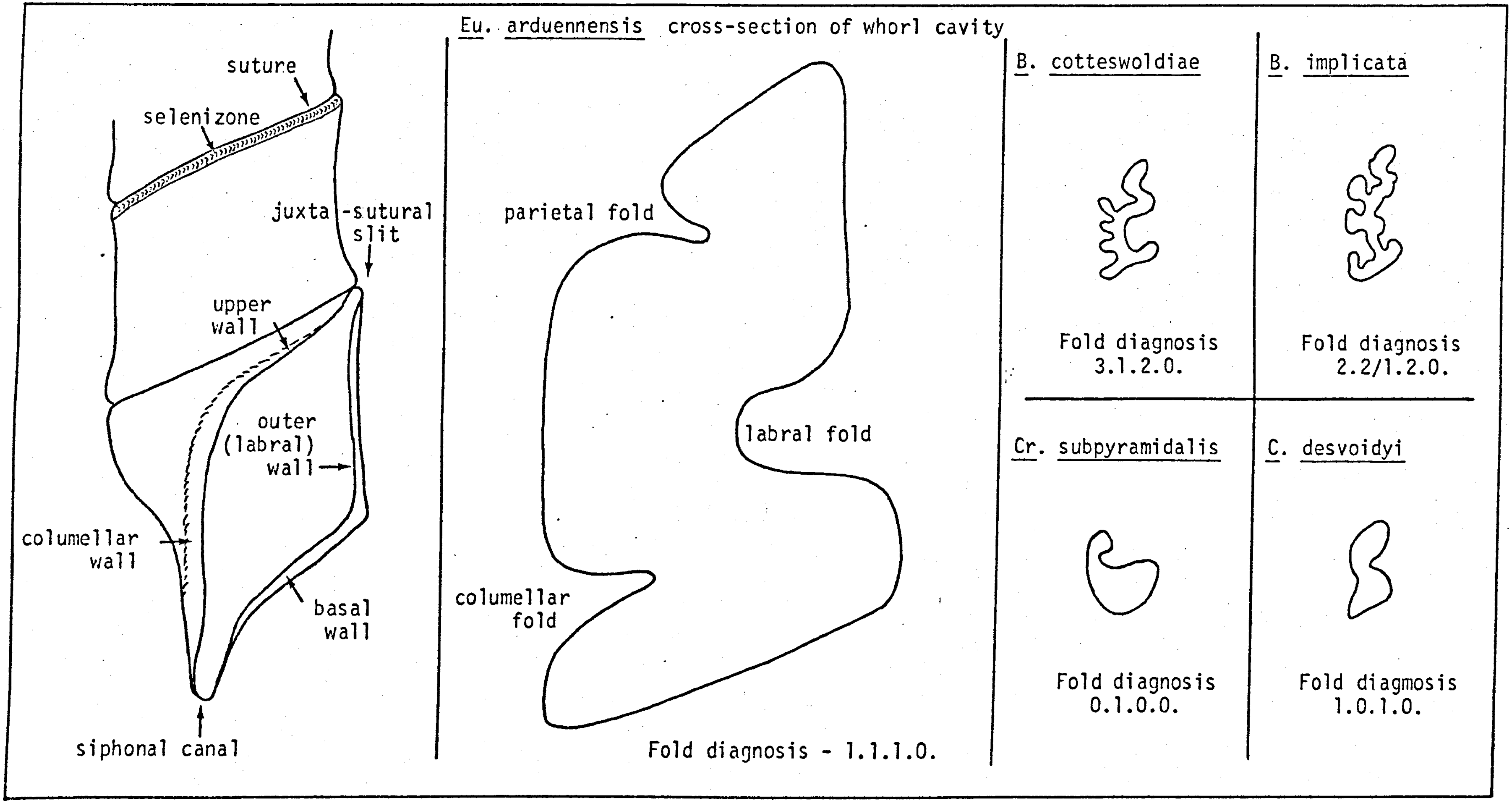


Fig. 4.1. The terminology of the aperture and folds in Nerineacean gastropods and the use of fold diagnoses.

Variation in Fold development

In a given Nerineid gastropod species there are two types of variation which can modify the fold pattern; the minor intraspecific variability in the mature fold configuration and the more pronounced ontogenetic changes in fold development which all fold-bearing Nerineid gastropods exhibit.

In the normal ontogenetic development, the apical whorls of a Nerineid gastropod are fold-less. Gradually the folds are secondarily emplaced as the animal grows but the aperture and last whorl remain fold-free throughout growth.

The examination of the early whorls of Nerineids is difficult. Often they are not preserved due to damage associated with transport or compaction but the most serious problem encountered is that the carbonate sediment cannot easily enter the very small apical whorls. Subsequently diagenetic deposition of calcite in the empty whorl cavity combined with the aragonite-calcite shell transformation results in a mosaic of interlocking calcite crystals in the apical whorls, the body chamber and shell then become indistinquishable. This problem is particularly acute in Nerineids with complex fold patterns such as Bactroptyxis spp. and Ptygmatis spp.

The absence of folds at the apertures of Nerineid gastropods is a feature that has been noticed by virtually every author from Voltz (1836) to Wieczorek (1975). However, no attempt seems to have been made to explain this phenomenon in relation to the physiology of the gastropod. The absence of the folds would have been a physiological necessity in order not to impair the function of the vital organs such as the stomach, ctenidia and particularly the mantle-cavity. It is noticeable in all Nerineids examined by the present author that the labral fold is the last to be developed whilst the columellar and parietal folds are quickly emplaced within approximately half a whorl of the apertural lip (see plates 4:E, F). This is almost certainly related to the position of the mantle-cavity. The presence of a labral fold in the final whorl would reduce the volume of the mantle-cavity which would in turn reduce respiratory and excretory efficiency. Further aspects of the biology of the Nerineacea are discussed in Chapter 5.

Only two authors have described the complete ontogenetic fold development of a Nerineid gastropod. Delpy (1939, p. 150) described _Nerinea schiosensis_ Pirona and Wieczorek (1974 and 1975) described _Nerinella? varioplicata_ Wieczorek and _Nerinea_ sp. (= _Fibuloptygmatis_ Pchelintsev, 1965) respectively. These are shown in Figure 4:2. The ontogenetic developments of _B. implicata_, _Eunerinea arduennensis_ and _Nerinella_ cf. _acicula_ are shown in plates 4:E, 4:F and 4:G. The main morphological stages in their development are outlined below.

B. implicata (see Fig. 4:3)

a) Apical whorls

1) No folds present.

2) A broad, open labral fold is inserted.

3) Much smaller parietal and columellar folds are developed almost simultaneously.

4) The upper columellar fold appears soon after (3).

5) The labral fold becomes narrower and extends deeper into the whorl cavity. It starts to subdivide. The parietal and columellar folds deepen.

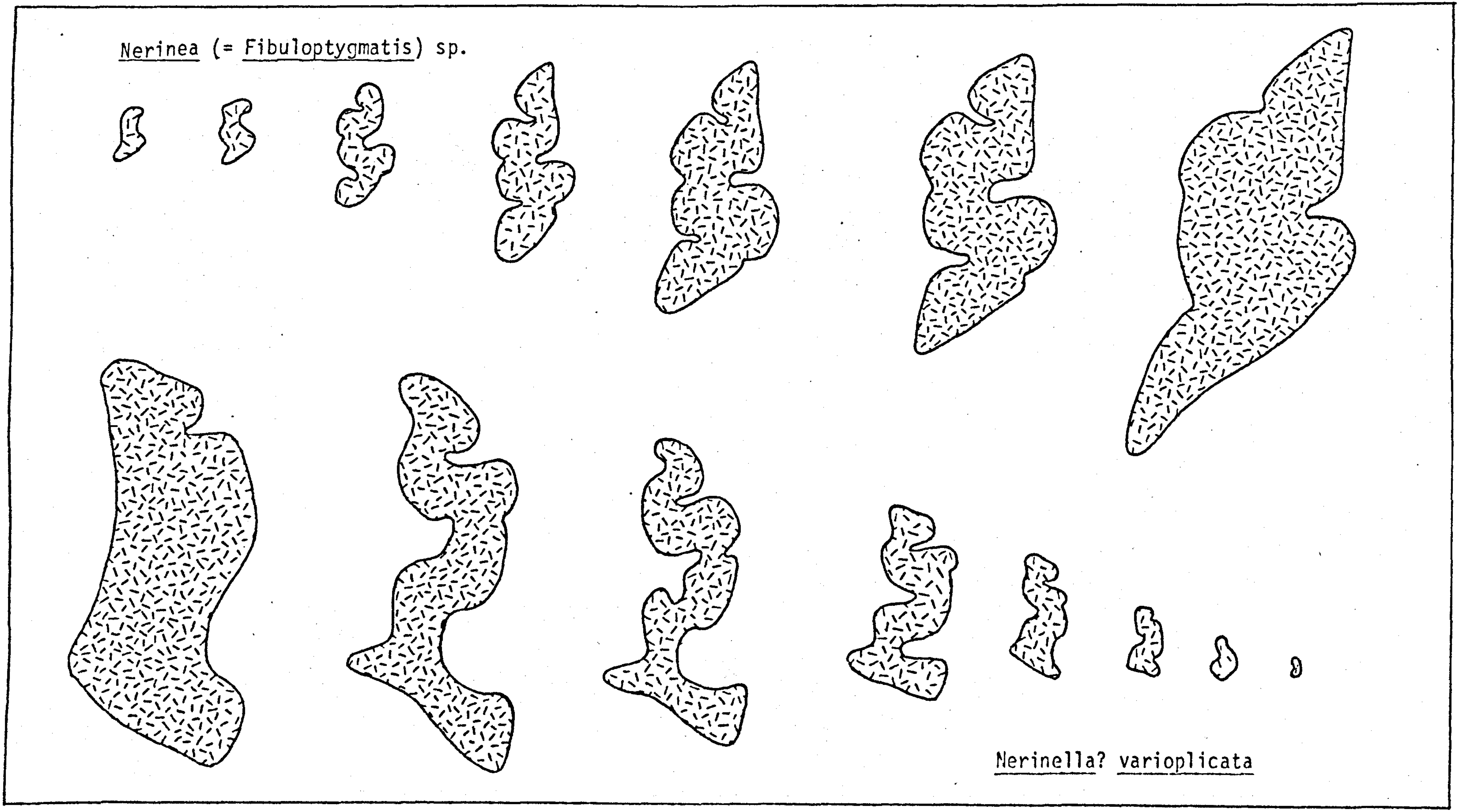


Fig. 4.2. Ontogenetic development of folds in Nerinea (= Fibuloptygmatis) sp. and N? varioplicata - after Wieczorek (1974, 1975)

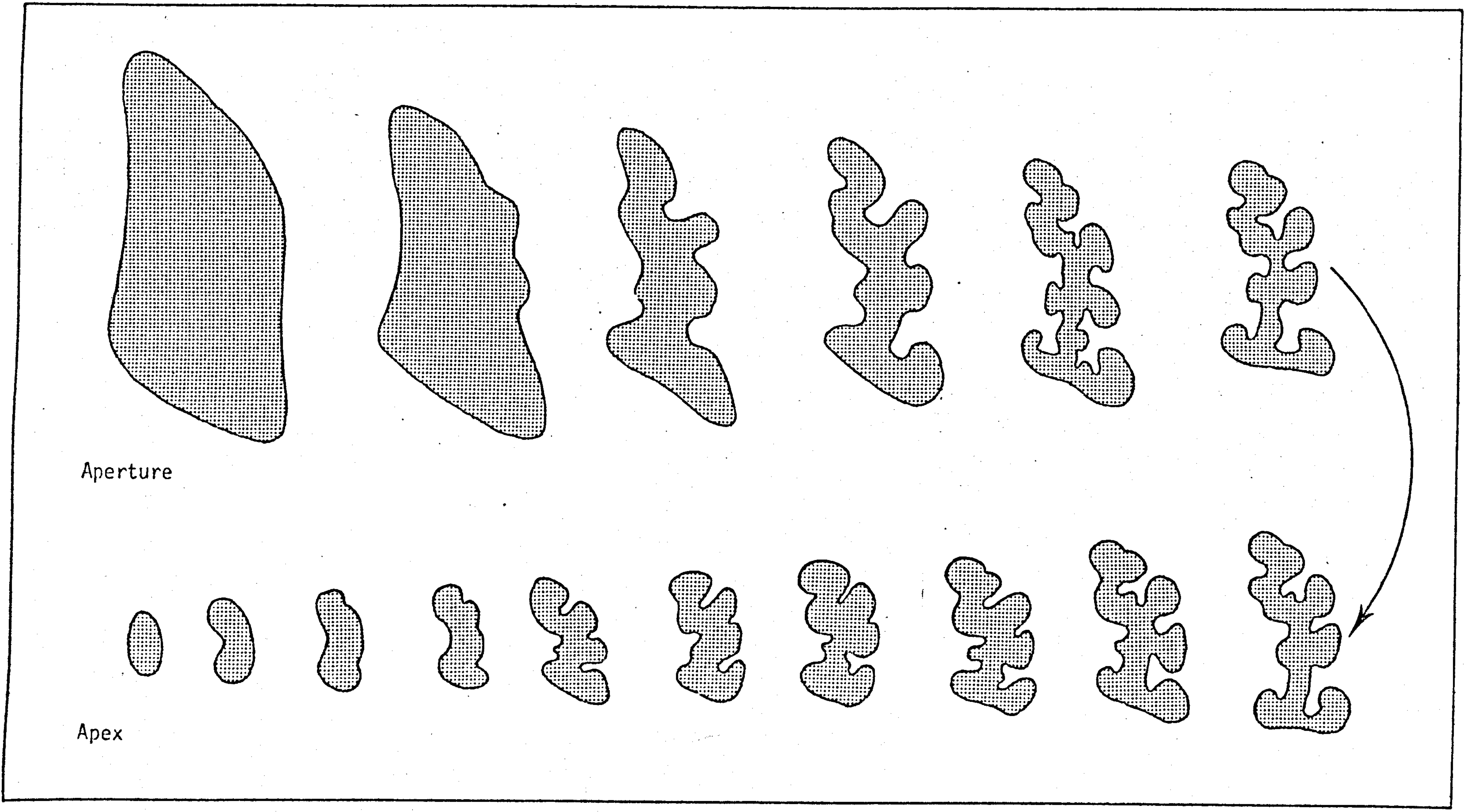


Fig. 4.3. Ontogenetic development of folds in Bactroptyxis implicata.

6) The upper labral fold appears.
7) The lower columellar fold subdivides.
8) The second parietal fold appears.
9) The first parietal fold subdivides.
10) A small labral fold is inserted between the previous two labral folds.
11) Continued subdivision of the first parietal, first columellar and first labral fold.
12) Subdivision of the secondary lobes of the first labral fold.

b) Terminal whorls

The reduction of folds as the aperture is approached is almost the reverse of the above sequence but the labral fold disappears very quickly (in reality, in fact, it is the last fold to be emplaced). Most of the intense folding is developed in approximately half-a-whorl. The total development of the mature fold configuration from a foldless aperture is usually accomplished in one or one and a half whorls.

Eunerinea _arduennensis_ (see Fig. 4:4)

a) Apical whorls

1) No folds present.
2) A broad, open labral fold is inserted.
3) A small, acute parietal fold appears.
4) The labral fold becomes narrower and deeper.
5) The columellar fold is inserted.
6) All folds become narrower and extend further into the whorl cavity.

b) Terminal whorls

A simultaneous and rapid reduction of the parietal and labral folds. The columellar fold is also reduced but persists for longer.

Nerinella cf. acicula (see Fig. 4:5)

a) Apical whorls

1) Parietal, columellar and labral folds develop simultaneously. Initially the parietal fold is a small median fold parallel to the shell axis.

2) Deepening of all folds and the parietal fold moves near the parietal-columellar angle and is no longer parallel to the shell axis.

b) Terminal whorls

All folds start to disappear simultaneously becoming broader and shallower. The emplacement of the labral fold occurs at a slightly earlier stage in this species (i.e. the labral fold does not disappear as quickly on approaching the aperture from the apex).

The variation in fold morphology within a single Nerineid species and its taxonomic implications are more fully dealt with in Chaper 2.

The secondary nature and incremental growth of Nerineid folds can be clearly demonstrated in specimens of Nerinella cf. multistriata where the growth lamellae are preserved because the shell transformation from aragonite to calcite took place by aggrading neomorphism rather than via a cavity stage. The clarity of preservation is also partially due to the presence of bituminous compounds in the sediment which have stained the growth lamellae (or more probably stained the original organic matrix between the growth lamellae). The excellent preservation of Laevinerinea cf. nobilis from the Gosau Beds also retains the original growth increments.

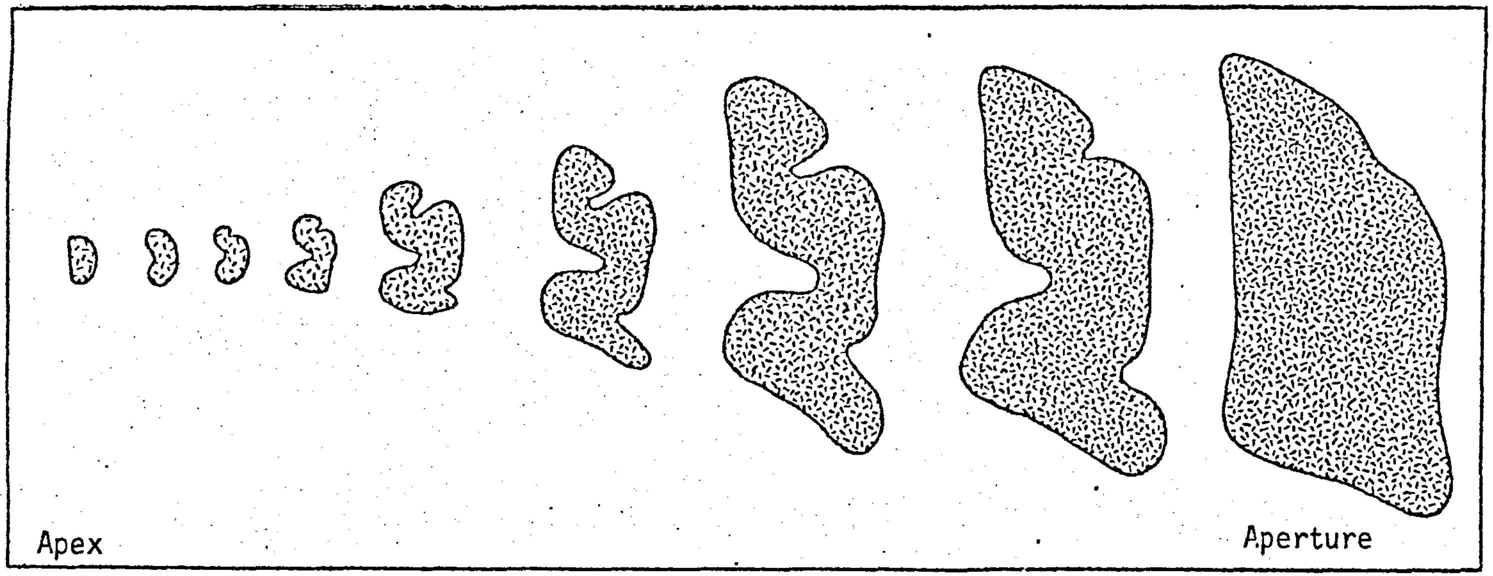


Fig. 4.4. Ontogenetic development of folds in *Eunerinea arduennensis*.

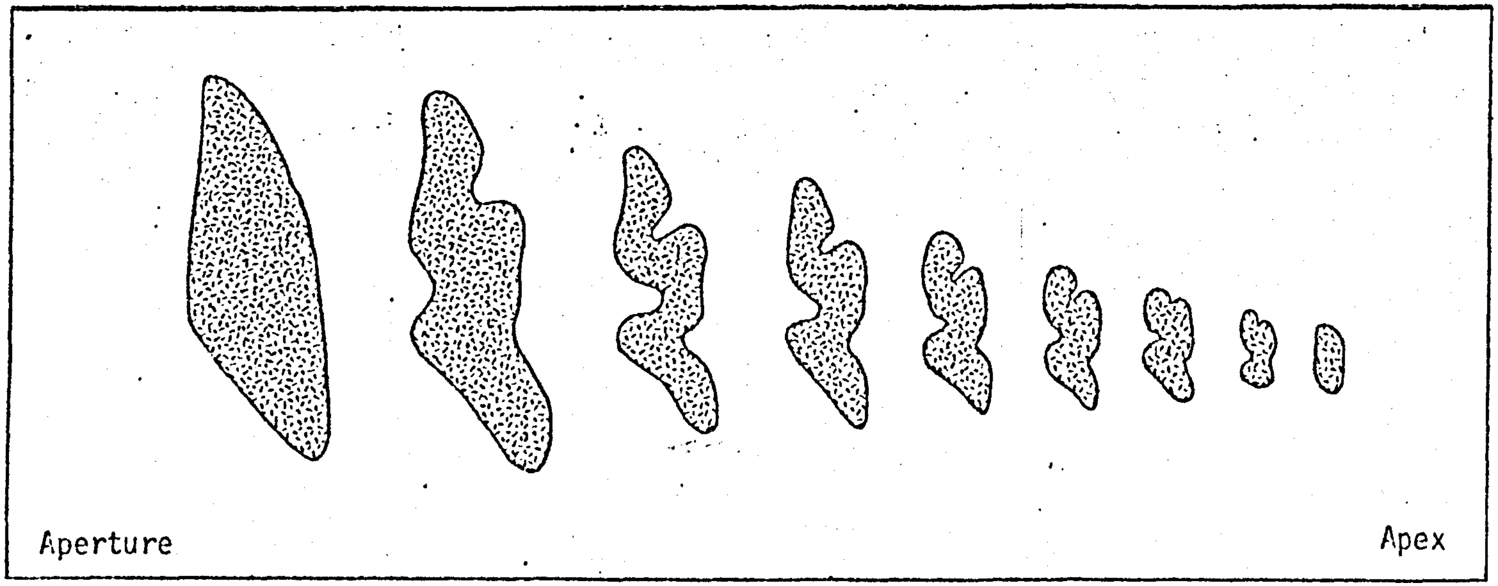


Fig. 4.5. Ontogenetic development of folds in *Nerinella* cf. *acicula*.

Although discontinuities exist between groups of growth lamellae it is not at this stage possible to relate these discontinuities to either regular environmental periodity or more irregular physiological phenomena such as cessation of growth due to predation or intermittent inadequate feeding, etc.

The shell microstructure of *Eu. salinensis* (d'Orb.) from Delpy, 1937, pls. XXII and XXIII.

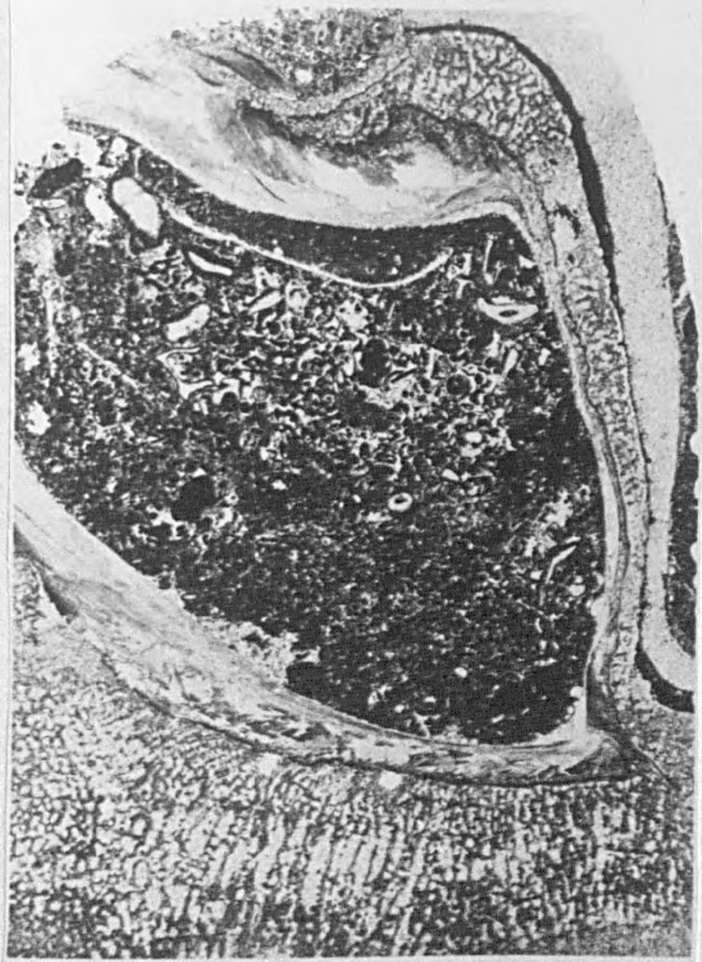
Plate 4.A.

Plate 4.B.

Note de Geneviève Delpey

Bull. Soc. Géol. de France

S. 5 ; t. VII ; pl. XXII



Cl. H. Ragot

Phototypie Mémin, Arcueil (Seine)


2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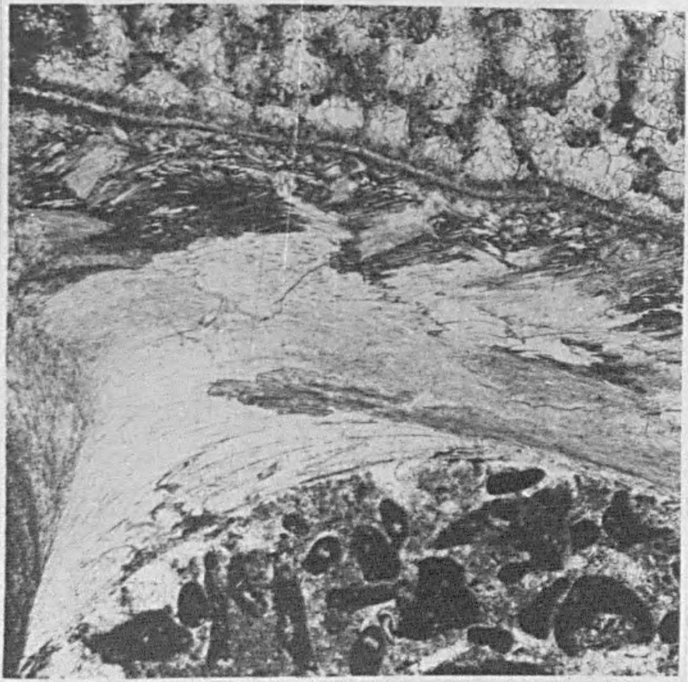

Cl. H. Ragot

1

The shell microstructure of *Laevinerinea* cf. *nobilis* (Münster)

Specimen 96987 (B.M.N.H.),

Acetate peel, x5.

Plate 4.C.

Crossed-lamellar structure in Laevinerinea cf. nobilis (Münster)

Details of Plate 4.C.

Upper photograph - Adapertural columellar fold

Lower photograph - Intraumbilical adapertural carina

Acetate peels, x20.

Plate 4.D.

The ontogenetic fold development in *B. implicata*

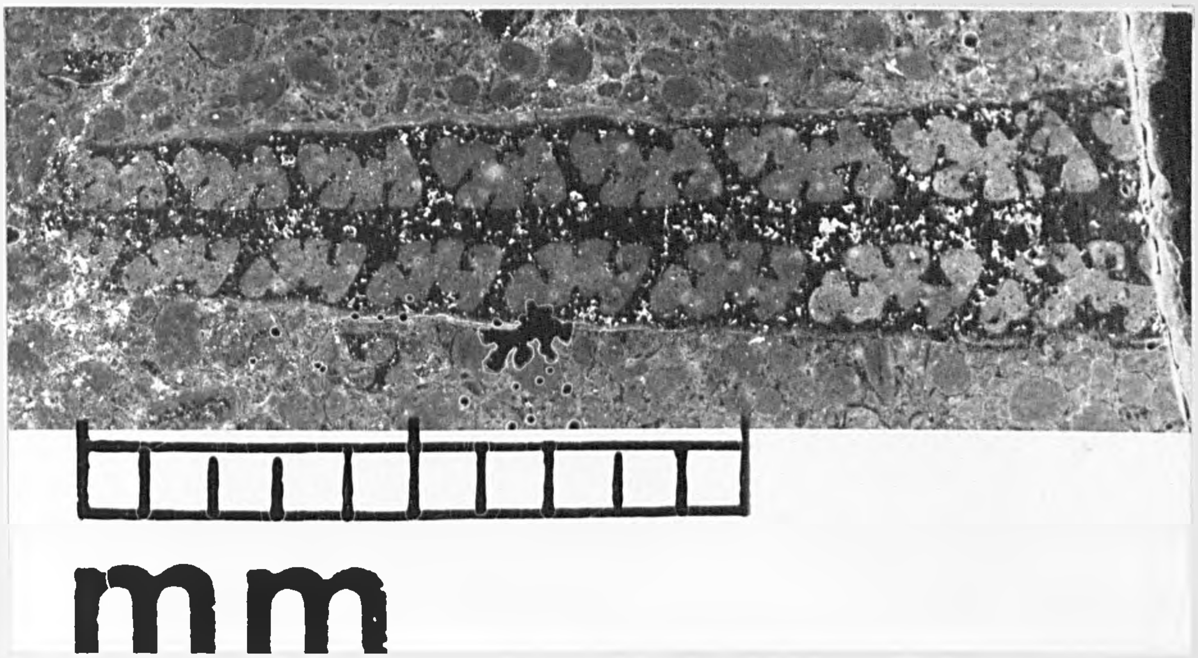
Apertural development

Specimen D.D.1 - Dagham Downs, Bed 12,
Acetate peel. M.J.B. colln.

Apical development

Specimen D.D. 8a - Dagham Downs, Bed 12,
Acetate peel. M.J.B. colln.

Plate 4.E.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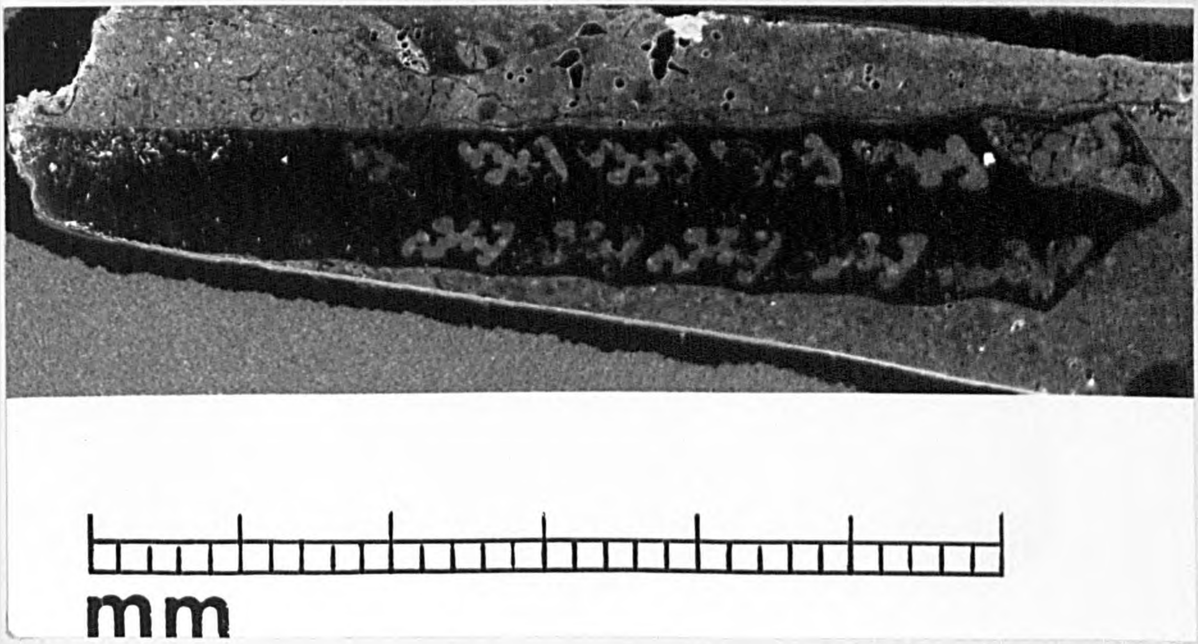
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The ontogenetic fold development in *Eu. arduennensis*

Apical development

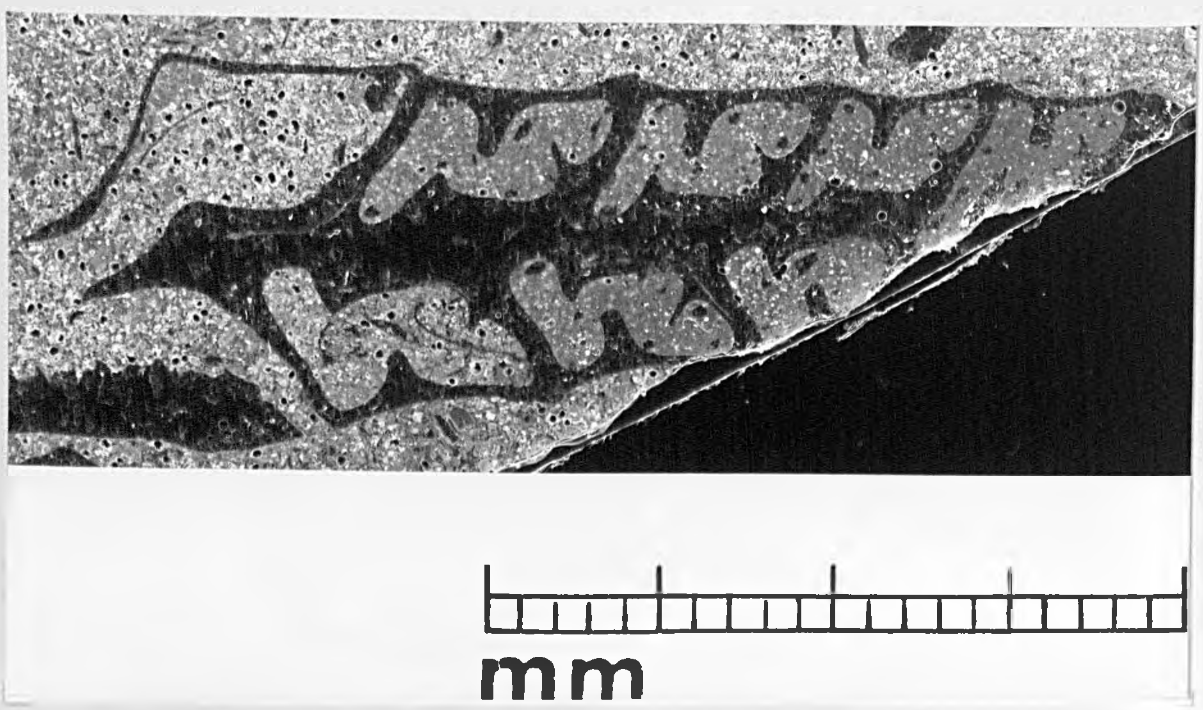
Specimen FXS 34a - Foss Cross, Bed 10,
Thin section, plane polarised light
note oncolite envelopment

Apertural development

Specimen Sl.H.Ox. 136 - Slape Hill, Bed 5
Acetate peel

Both specimens M.J.B. colln.

Plate 4.F.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The ontogenetic fold development in N. cf. acicula

Apical development

Specimen Sl.H.Ox. 111 - Slape Hill, Bed 5,

Acetate peel

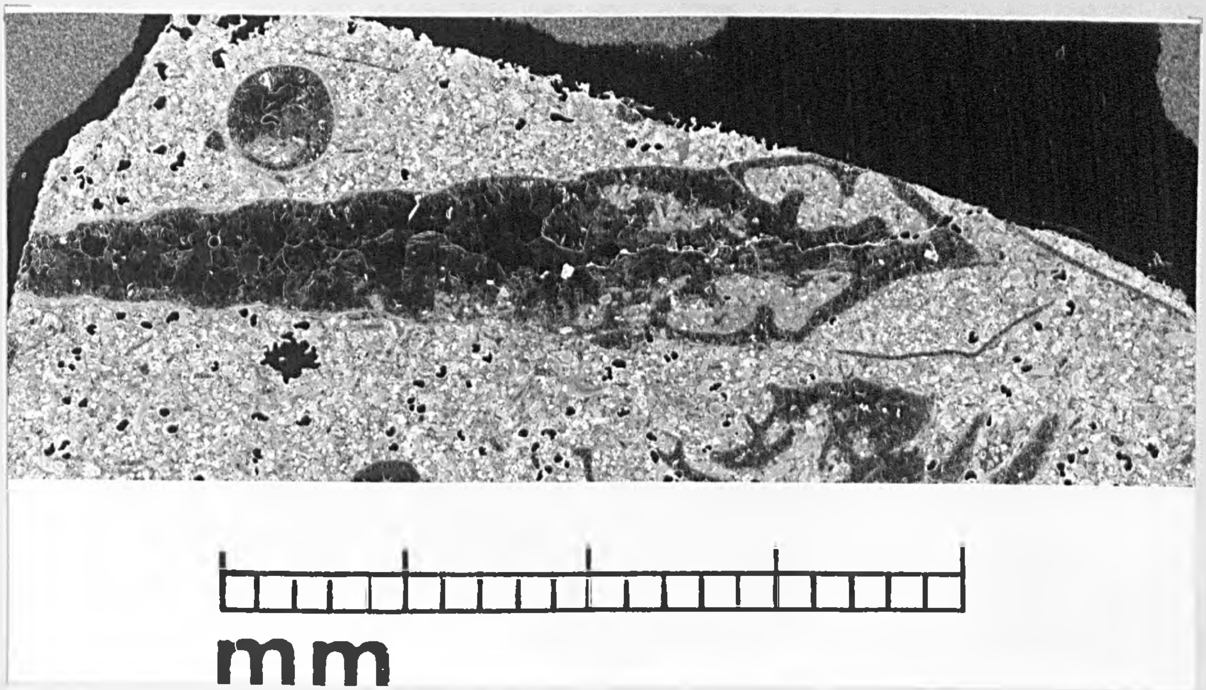
Apertural development

Specimen Sl.H.Ox. 59 - Slape Hill, Bed 5

Acetate peel

Both specimens M.J.B. colln.

Plate 4.G.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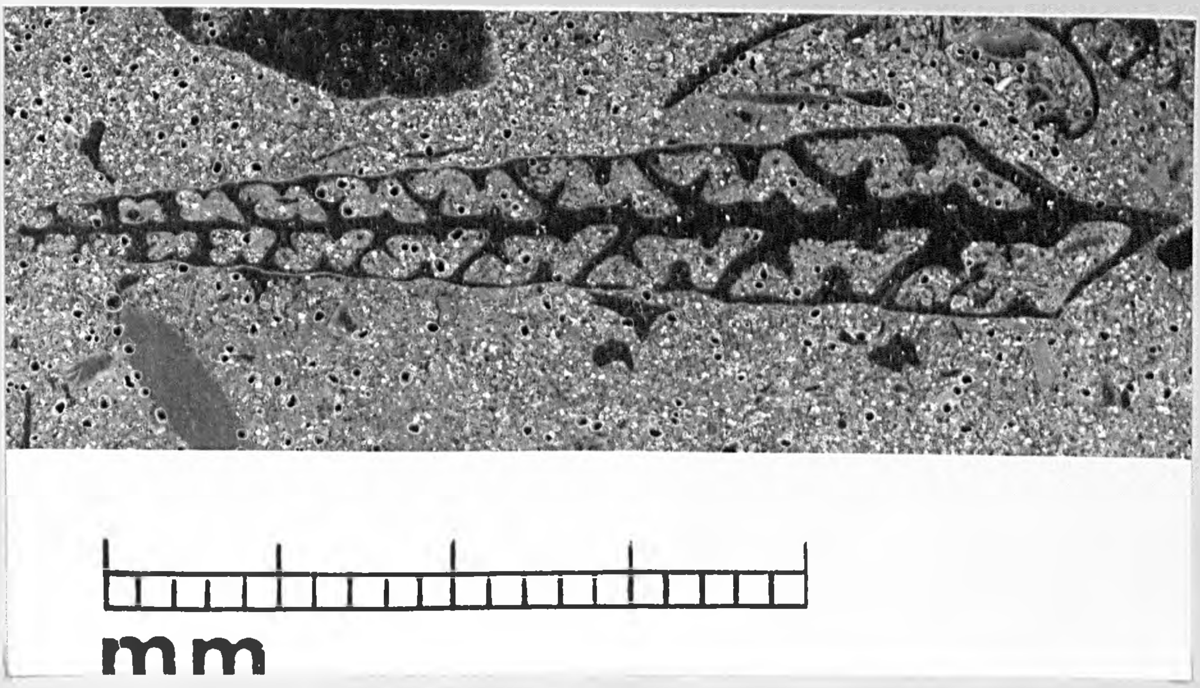
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Chapter 5

THE PALAEOBIOLOGY OF THE NERINEACEA

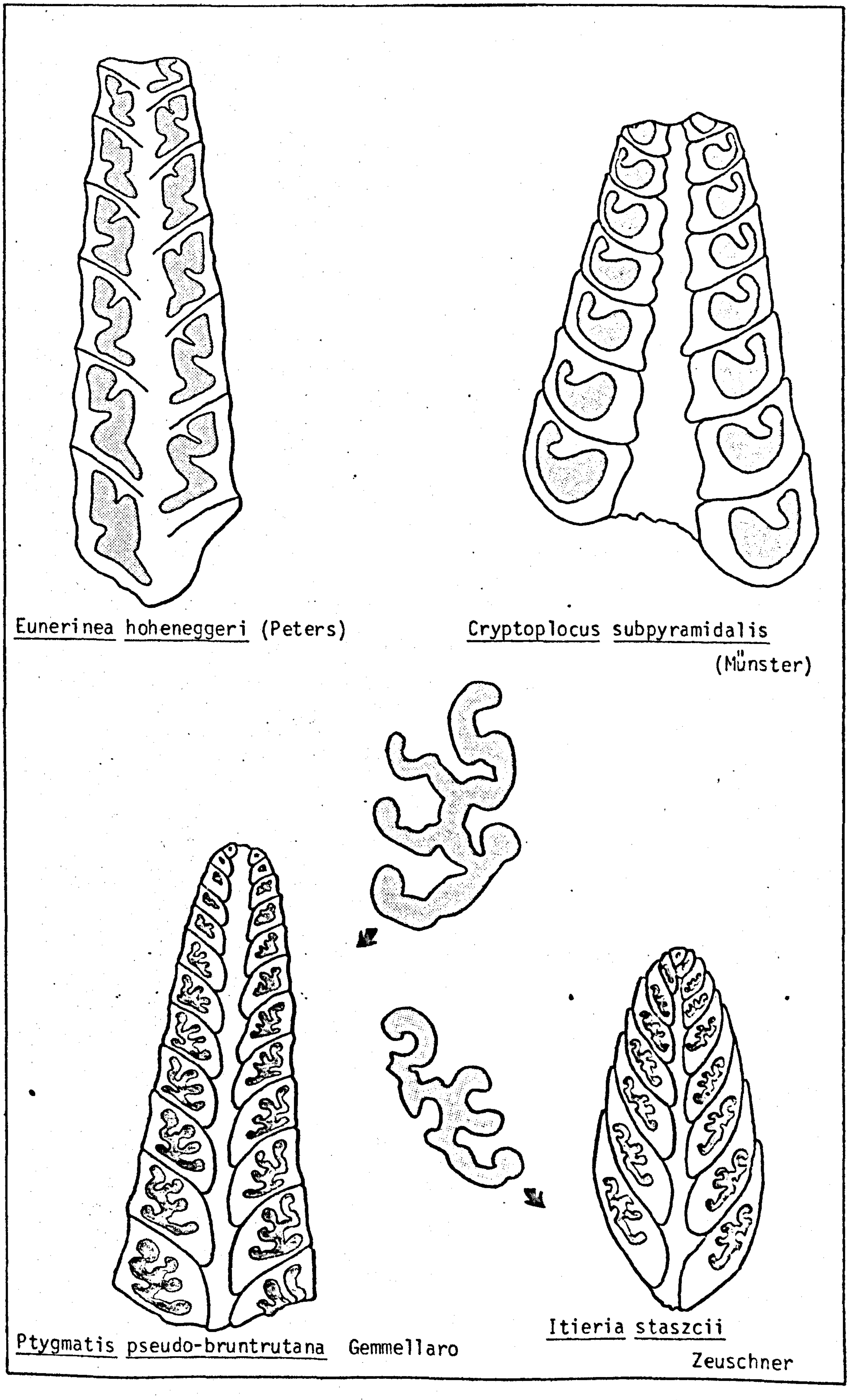
'Es bedarf sonach noch genauer Untersuchungen über die Nerineenfalten,
ihre Enstehung, Bedeutung, Funktion.'

Dietrich, 1925, p. 3

Generally, the normally simple shell morphology of the gastropods and the lack of Recent ecological data which can be applied to fossil forms has precluded detailed palaeobiological analyses of fossil gastropod faunas. In spite of major advances in fossil gastropod taxonomy during the nineteenth century, (Cossmann, 1885, 1898, 1895-1925; d'Orbigny, 1850-1852; Hudleston, 1887-96; Gemmellaro, 1865, 1869; Zekeli, 1852 and Zittel, 1873), and early part of the twentieth century, (Dietrich, 1925; Haber, 1932-1934; Pchelintsev, 1927, 1934, 1965 and Wenz, 1938-44), only occasional studies, such as those by Gould (1969) and Sohl (1969), have demonstrated the palaeobiological and palaeogeographical potential of gastropods.

The most striking and unique feature of the Nerineacea is the possession of internal spiral calcareous folds, sometimes of great complexity, within the body-chamber (Fig. 5:1). Obviously these folds must have been intimately related to the soft tissue within the high-spired gastropod and presumably were of some biological significance to the animal. Therefore, when considering the palaeobiology of the Nerineacea as a whole, one must first ascertain the nature and significance of these folds (Dietrich, 1925, p. 3).

Despite an extensive literature on all aspects of the Nerineacea, this fundamental relationship seems to have been ignored, or at best treated superficially, by previous authors. Most authors (including important contributions by Bronn, 1836; Cox, 1949, 1954; Delpy, 1939; Eudes-Deslongchamps, 1842; Fischer, 1969; Hudleston, 1884, 1887-96; Levasseur, 1935; d'Orbigny, 1850-1852; Rollier, 1909; Quenstedt, 1881-1884 and Zittel, 1873) offer no explanation for the presence of folds in the Nerineacea.



Eunerinea hoheneggeri (Peters)

Cryptoplocus subpyramidalis (Münster)

Ptygmatis pseudo-bruntrutana Gemmellaro

Itieria staszcii Zeuschner

Fig. 5.1. Internal folds in selected Nerineacean gastropod species.

The first attempt to interpret the folds of Nerineid gastropods was made by Peron (1901, p. 4-5) who considered, "Leur coquille si menue est entièrement renforcée dans sa lonqueur par de gros plis longitudinaux qui, tant du côté ombilical que du côté externe, out pour effet du lui donner une grande solidité. Ces plis de la coquille des Nérinées ne sont pas comme certaines nodosités ou crêtes qui renforcent seulement les bords de l'ouverture dans certains autres gastropods; ils s'étendent sur toute la longueur de la coquille et persistent pendant tout son développement.

Ce sont de véritables piliers et contreforts spiraux qui, d'une part, forment de l'axe central une véritable vis d'Archiméde et lui donne anisi une grande rigidité, et, d'autre part, soutiennent la paroi externe et luid donnent une grande résistance à l'écrasement."

Subsequently, Arkell (1931); Dietrich (1925); Geiger (1901); Pchelintsev (1965) and Wenz (1938-44) accepted the interpretation of Peron (op. cit.) that the folds were a means of strengthening the shell against physical damage.

The present author rejects this hypothesis. A turretted gastropod is most likely to suffer serious physical damage, other than by abrasion of the shell, in three regions; a) the apex, b) the aperture and c) the suture.

a) the Apex: the thin walled protoconch and apical whorls of the teleoconch are only rarely preserved in turretted gastropods. Presumably compaction is the main taphonomic agent which destroys this part of the shell in fossil gastropods although apparently this region may also be lost during the animal's life-time.

Andrews, (1974), has shown that T. mortoni is capable of both secondary shell thickening and the formation of 'septae' in the apical region. These are primarily a protection against damage and, in the event of shell breakage, to seal off the apex. The secondary nature of these deposits is evident when one compares the apices of thin-shelled juveniles with the thicker-shelled apices of adult forms. No difference in shell thickness, other than that produced by normal ontogenetic growth, has been observed between the adult and juvenile stages of Nerineid gastropods.

In a grab sample, (N = 148), of a living Turritella communis community (see Table 5A for further details) only 54 (36.5%) of the specimens were found with the protoconch in-tact.

b) the Aperture: Recent work on Turritella by the present author has confirmed the susceptibility of the apertural margin to damage. The modern Turritella communis Risso is a shallow infaunal, largely sedentary, ciliary suspension feeder living in argillaceous sediment (Yonge, 1946). Andrews (1974) has argued that the Palaeocene Turritella mortoni had a similar mode of life. Presumably damage to the apertural lip is either of physical origin or, more likely in the low-energy environments inhabited by Turritella, the result of predation. Whatever the cause, the mantle tissue at the edge of the aperture was evidently capable of repairing such damage and any repair is preserved in the ontogenetic development of the shell. Table 5A shows the incidence of major shell regeneration of the aperture in two Turritella populations.

Table 5A

Species: *Turritella communis* Risso

Age: Recent Locality: Isle of Cumbrae, Scotland

Origin: Grab sample

No. of specimens: 148

Average No. of whorls per specimen: 11.26 range 7-14

Standard Deviation: 1.35

No. of specimens showing damage
involving 3 or more growth lines: 142 (98.6%)

Average No. of damaged areas per specimen: 2.62 range 0-7

Standard Deviation: 1.39

Species: *Turritella imbricataria*

Age: Eocene-London Clay Locality: Swanwick, Hants. (G.R. SU 509101)

No. of specimens: 35

Average No. of whorls per specimen: 8.71 range 5-12

Standard Deviation: 2.19

No. of specimens showing damage
involving 3 or more growth lines: 20

Average No. of damaged areas per specimen: 1.09 range 0-4

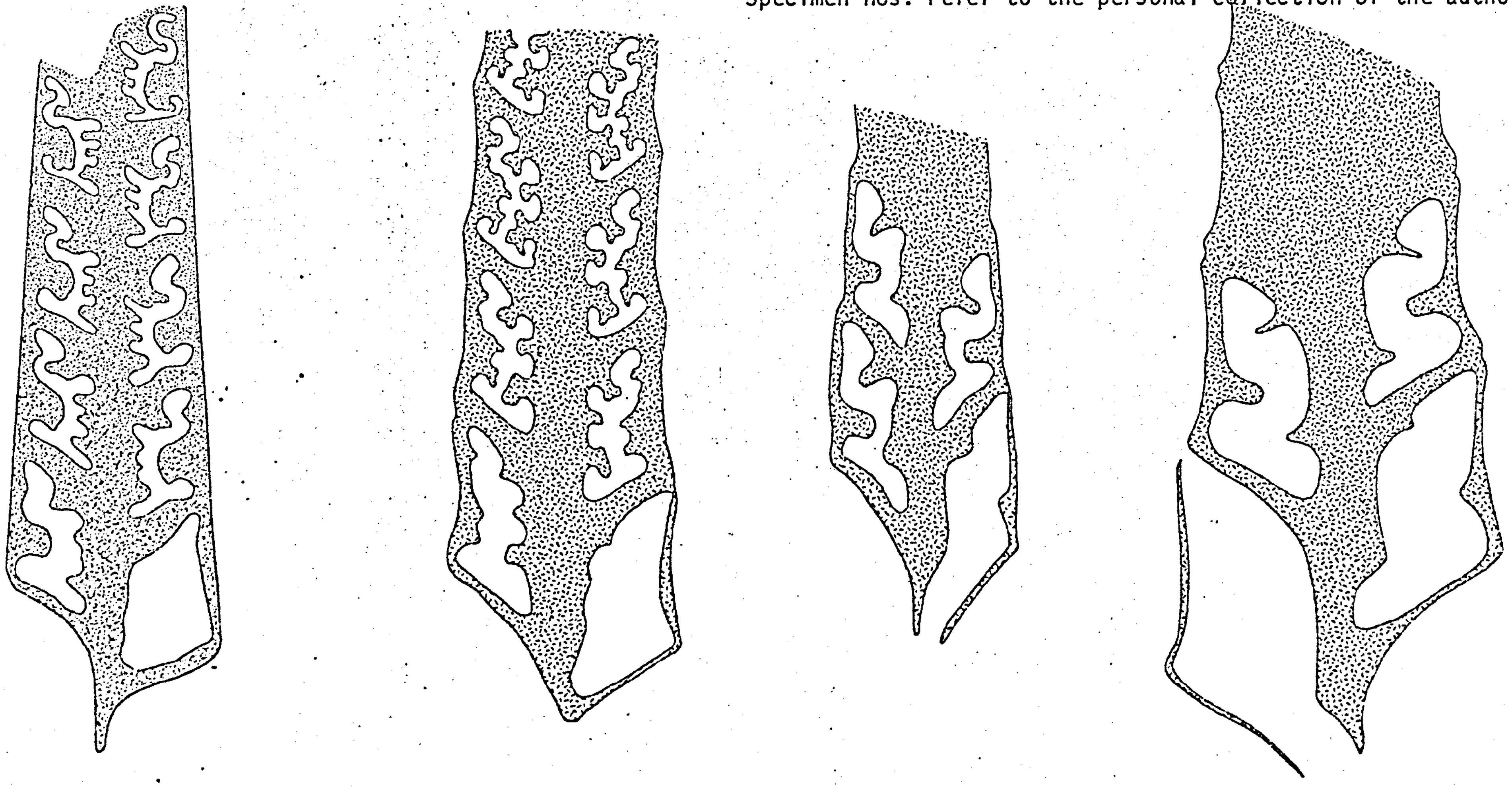
Standard Deviation: 1.17

The present author has not observed repair of growth lines in any Bathonian Nerineid. The significance of this will be discussed later.

c) the Suture: On breaking a specimen of Turritella or any other high-spired gastropod across the axis, the initial break is always along the suture, not across the whorl.

The folds in the Nerineacea do not protect any of these regions. Folding is only barely observable in the early whorls of Nerineid gastropods and is probably absent in the protoconch and first whorls of the teleoconch (Wieczorek, 1975). Folding is also absent at the apertural margin and normally starts to appear approximately one quarter of a whorl from the aperture. In most cases the folding is only fully developed after approximately one and a half whorls (see Fig. 5:2). In general previous authors have noted the absence of folds in the aperture of Nerineids but have failed to appreciate the biological significance, although Hudleston, (1887-96, p. 195), thought this feature was to "give the animal additional space". The absence of shell repair in Nerineid shells cannot therefore be attributed to the protective function of the folds, not do the folds protect the sutures between whorls. No hypothesis exists therefore to adequately explain the presence and significance of folding in the Nerineidae. Indeed Cossmann, (1896, p. 6), considered, "A cette particularité, (i.e. the folds) dont le but anatomique m'échappe absolement...." and that, (1898, p. 139), "... on se demande vraiment comment un mollusque pouvait vivre et se mouvoir dans un espace aussi linèaire, gèné par de pareils obstacles dont on ignore encore le but biologique". Subsequent authors such as

Specimen nos. refer to the personal collection of the author.



B. cotteswoldiae (Lycett)
(reconstruction based upon several specimens)

B. implicata (d'Orbigny)
(spec. no. D.D.1. - Dagham Downs, bed 12)

N. cf. *acicula* (d'Arch)
(spec. no. Sl.H.Ox. 124 - Slape Hill, bed 5)

Eu. arduennensis (Buv.)
(spec. no. Sl.H.Ox. 54 - Slape Hill, bed 5)

Fig. 5.2. The reduction of folds at the apertures of selected Nerineacean gastropod species.

Tiedt (1958), Vogel (1968), Awad (1952), Pchelintsev (1967) and Wieczorek (1975) have discussed the ecology of various Nerineacean genera without reference to the biological significance of the folds. Two of these interpretations are particularly interesting. Pchelintsev (1967) speculated upon the mode of life of the Tithonian-L. Cretaceous genus Diozoptyxis. He considered that members of this genus hung vertically from coral branches by means of a 'hook-shaped' siphonal canal! Another, more bizarre, interpretation of Nerineid ecology was offered by Awad (1952). All Nerineas, according to Awad, were sessile and (p. 34) "... if a gastropod like this lay always on one side, fixed to the sea bottom, the peristome which is always changing direction with the growth of the shell, will after 180° of growth, face downwards, or lie in the mud as one might say. This difficulty has to be met one way or the other". Therefore (p. 35) "... it appears that to get over the difficulty of having their face in the mud, the Nerineas build up the wall of the last whorl rapidly so that the peristome faces upwards again the the minimum of time and then remained in that position for a long time, and during this normal position utilised the orthogenetic lime secreting activity of the mantle in building up and thickening the wall of the spiral cavity by development of these folds and then elaboration. Thus the folds simply represent varices corresponding to resting stages in the growth of the shell while the animal, fixed to the sea bottom enjoyed a respite from having its face in the mud". Such an improbable mode of life would result in;

a) asymmetric growth of the Nerineid shell,

b) growth lines which reflect the varying growth rates as it "hurried through the mud" ,

c) a distinct discontinuity between the folds and the wall of the shell,

d) asymmetric colonisation by epifauna and asymmetric damage by abrasion or predation to one half of the shell.

The present author believes that these two interpretations do not seriously consider the functional requirements of a once living gastropod.

Some early authors (Defrance, 1825 and d'Orbigny, 1854), considered that the apertural columellar folds of certain extant Pyamidellidae were homologous with those of the Nerineacea. However, later authors, such as Cossmann (1896, p. 7) and Dietrich (1925, p. 1), have justifiably rejected this hypothesis. As well as some Pyramidellids many other modern gastropods, such as Clausilia, (a stylommatophoran pulmonate), various Volutidae, Strombidae, Cypraeidae etc., possess apertural folds. Although the folds of these gastropods exhibit a superficial similarity to those of the Nerineacea, they differ in that,

a) the folds are always visible at the aperture,

b) they do not usually continue throughout the length of the shell,

c) they rarely exhibit parietal, basal or palatal folds.

Dall, (1894), suggests that apertural folds reflect folding of the shell-secreting mantle edge and that this is a mechanical consequence of the withdrawal into the aperture of the head-foot complex. Whilst this may be partially true, it is equally likely that the function of apertural columella folds is to increase the surface area for the attachment of the pedal retractor muscles.

The relationship between the internal anatomy, the folds and the mode of life of the Nerineacea

a) The internal anatomy of the Nerineacea.

Within the Nerineacea, polished median axial sections regularly show certain unique structures inside the sediment-filled folded section of the body cavity (see Figs. 5:3 and 5:4). As far as the present author is aware, these structures have never previously been described although they have been figured by Hudleston (1887-96, see especially plate XIII, Figs. 4c and 10c). However, only the first three plates of the Nerineacea (plates XII-XIV) show these features; the remaining two plates (XV and XVI) were prepared by a different lithographer who seemingly omitted these details. Apparently, Hudleston (*op. cit.*) was also unaware of them as they are not mentioned in the text. In cross-section these structures appear as small calcite 'dots', coarsely crystalline in the centre, with a rim of microcrystalline calcite (see Fig. 5:5). In outline they are usually circular and within any one specimen, remarkably uniform in diameter. After examining approximately 100 specimens, of various genera and species, which contain these dots, it is apparent that their spatial

Section of *B. implicata* showing 'dots' (sections across the ducts of the digestive gland/gonad) within the sediment filled body-cavity.

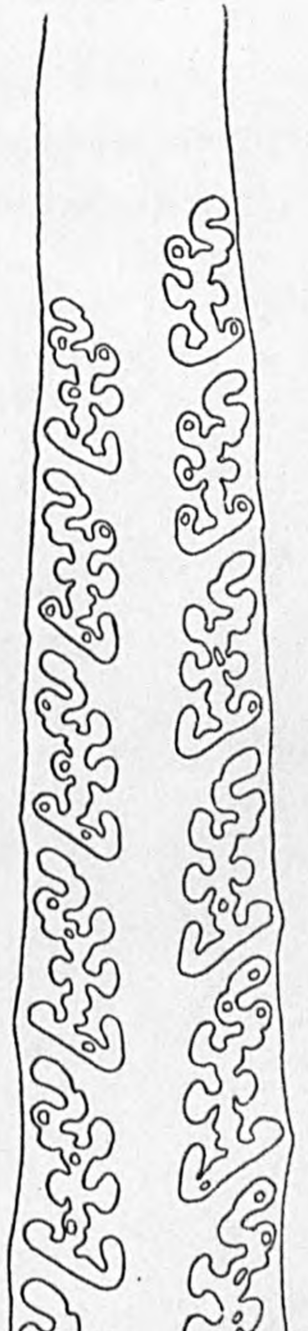
Specimen D.D. 20 - Dagham Downs, Bed 12.

Acetate peel. M.J.B. colln.

Bleached photograph with 'dots'

inked in for comparison.

Figure 5.3.

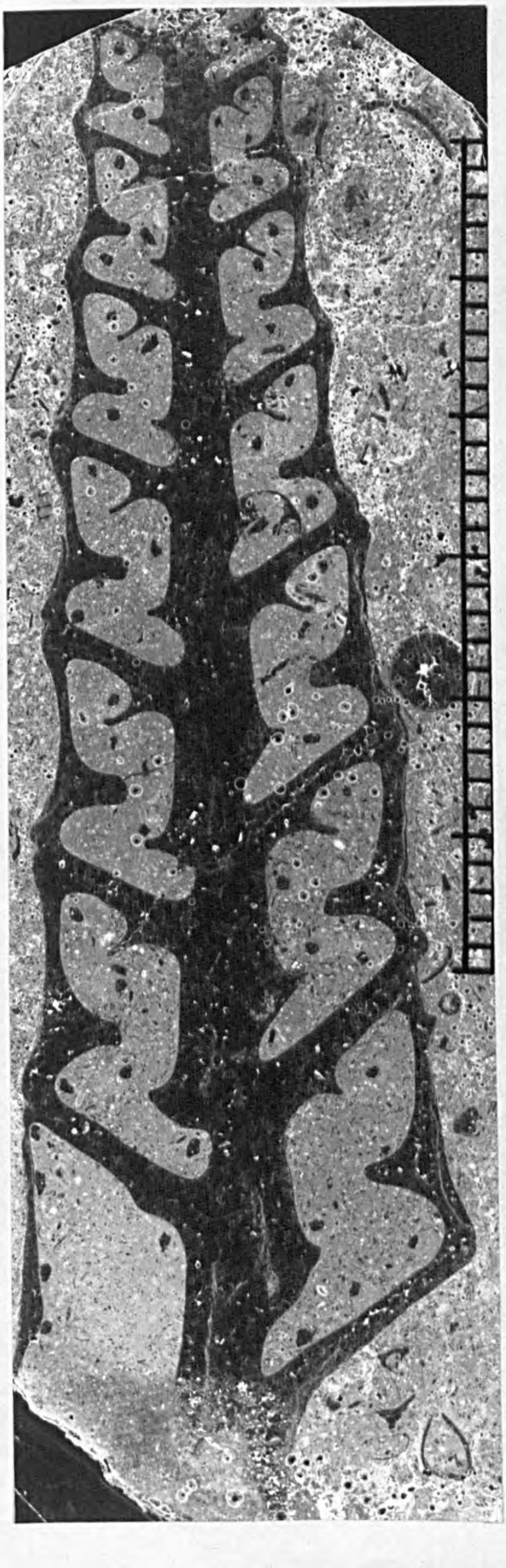


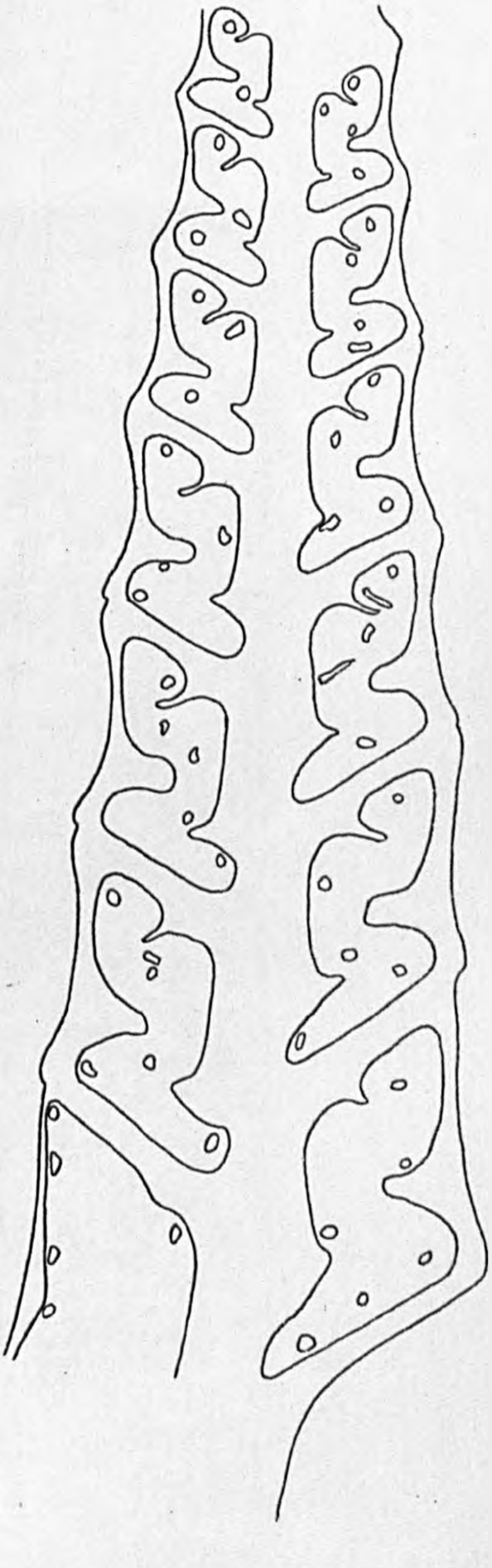
Section of Eu. arduennensis showing 'dots' (sections across the ducts of the digestive gland/gonad) within the sediment filled body-cavity.

Specimen CR 10/21 - Croughton, Bed 10.
Acetate peel. M.J.B. colln.

Bleached photograph with 'dots'
inked in for comparison

Figure 5.4.

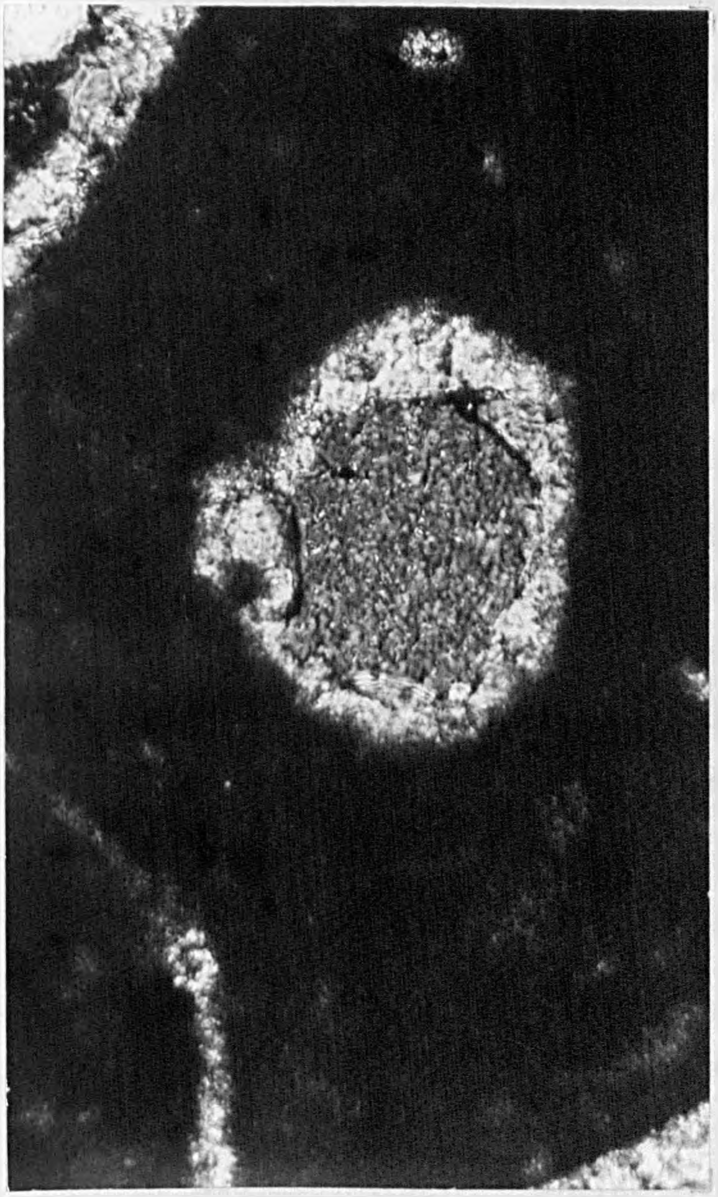




The petrography across a duct of the digestive gland/gonad within *B. implicata*

Specimen St. Fig. 13 - Stony Furlong, Bed 13c.
Thin section, x20,
crossed polars. M.J.B. colln.

Figure 5.5.



distribution within the internal body cavity is not random (see Figs. 5:6 and 5:7). They are preferentially located, especially in members of the Bactroptyxidae, in the centre of the major lobes of what was probably the digestive gland/gonad complex (see below).

Serial sectioning of specimens in which these 'dots' are exceptionally well preserved shows them to be sections across a system of helically coiled calcite rods supported within the internal body cavity and having no contact with the body wall. A broken specimen of Bactroptyxsis cotteswoldiae (Lycett) was ground down by hand along one of these helically coiled rods. Fig. 5:8 shows the rod continuity and its spatial disposition in this specimen. In other specimens, especially amongst species belonging to the genera Eunerinea and Nerinella, lack of continuity and contact with the body wall is presumably due to breakage and subsequent partial collapse of such delicate structures when sediment entered the internal cavity. Where the rods have been broken, re-orientation sometimes allows short segments to be longitudinally sectioned during preparation. These occasionally reveal smaller side branches as in Fig. 5:9.

The following genera and species (mainly from the Bathonian White Limestone) have yielded specimens with remnants of this rod system. For details of sections see Chapter 1.

Fibuloptyxis witchelli (Cox & Arkell): Foss Cross, Cirencester.

Bactroptyxis implicata (d'Orb.): Foss Cross, Stony Furlong, Worsham, Dagham Downs.

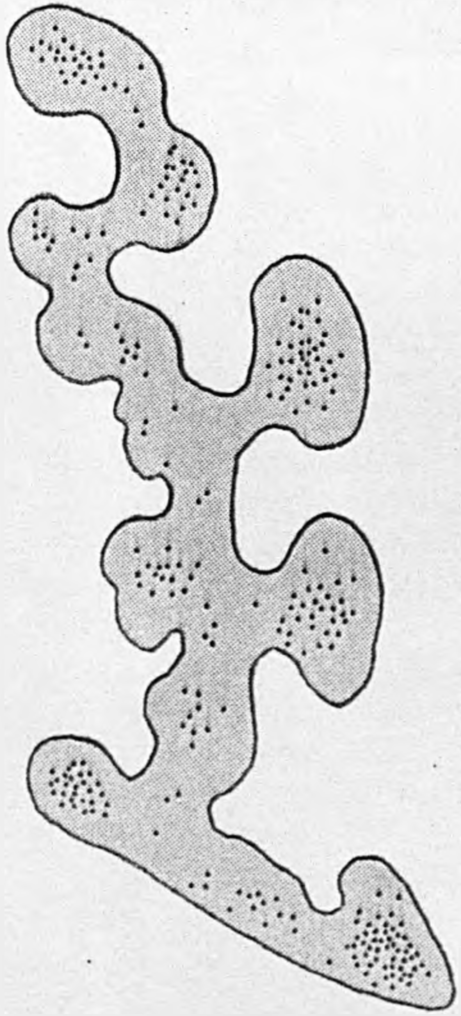


Fig. 5.6. *B. implicata* - 70 specimens

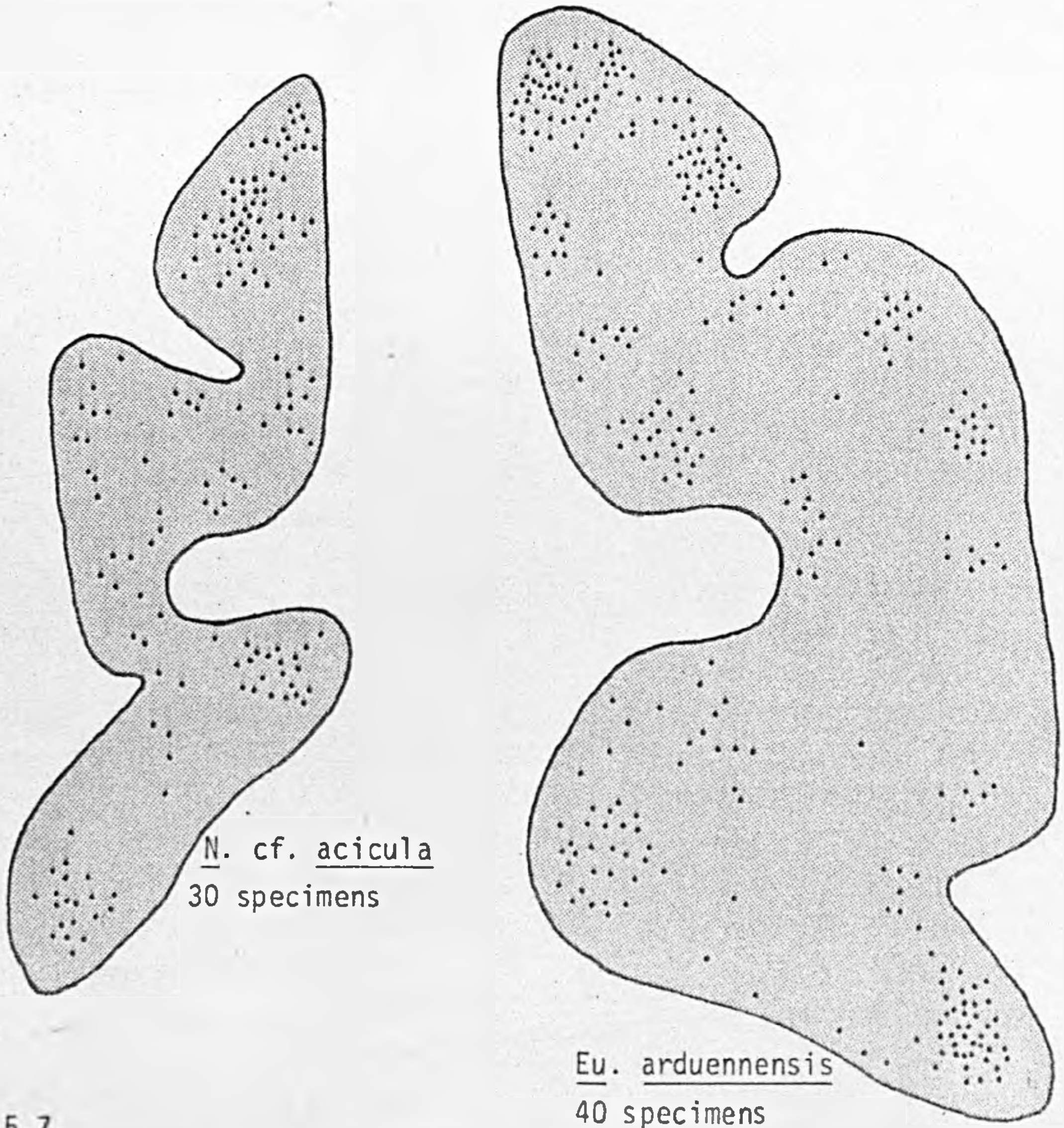


Fig. 5.7.

Figs. 5.6. and 5.7. The distribution of calcite 'dots' in three Bathonian species of Nerineacean gastropods.

The spatial disposition and 3D continuity of a duct in *B. cotteswoldiae*

Median axial section

Specimen G.P.5 - Grange Pit, Bed 1.

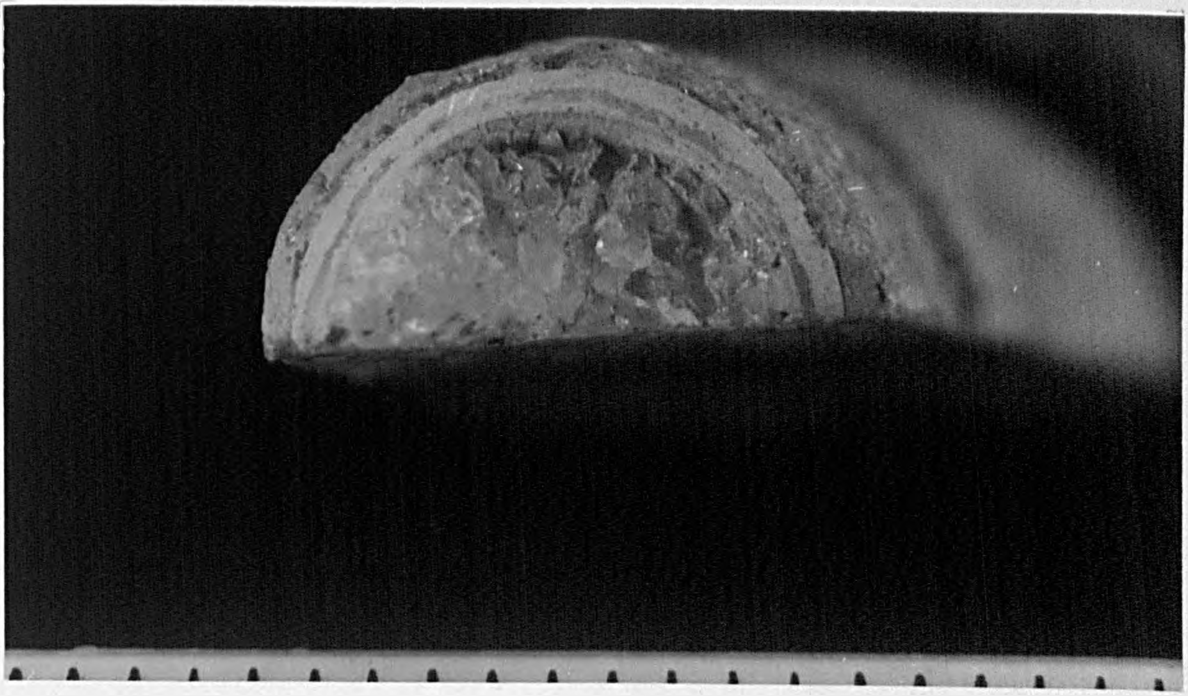
x4. M.J.B. colln.

top view of same specimen.

Helically sectioned showing
duct within sediment filled
body-cavity.

x7

Figure 5.8.



Broken, re-orientated, longitudinally-sectioned segments of the duct system of the digestive gland/gonad in *B. implicata*.

Specimen FXS 4 - Foss Cross, Bed 10

Thin section, x45, crossed polars

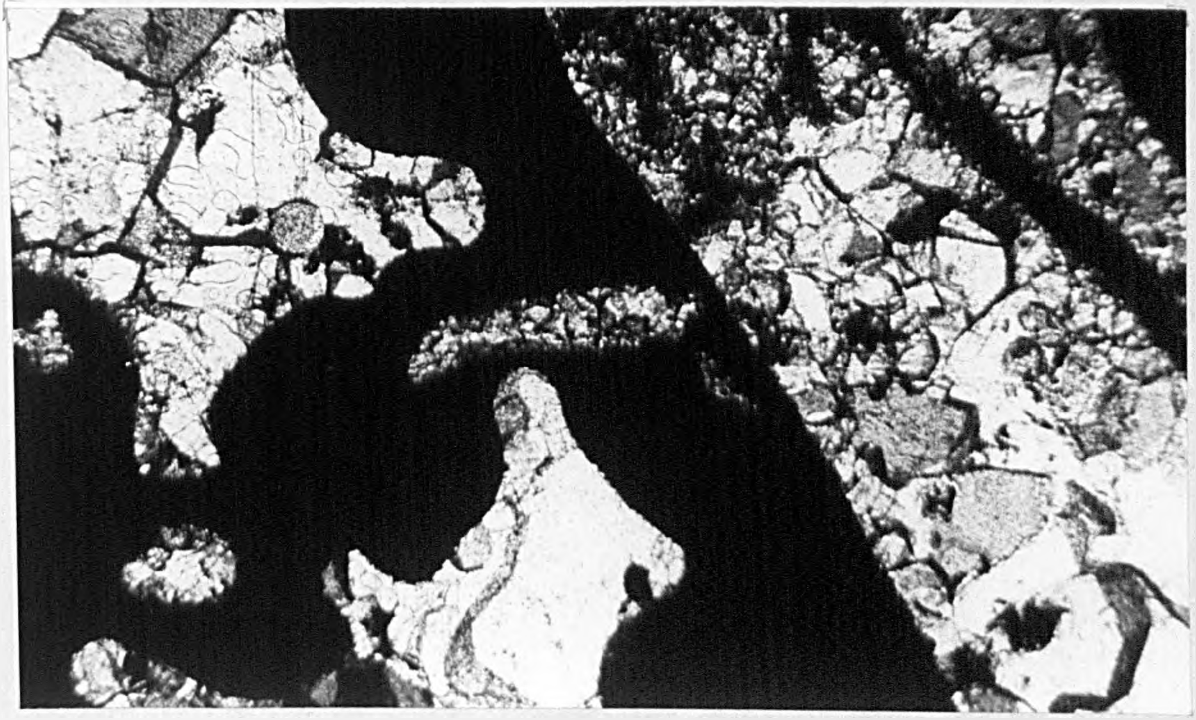
Note side branch

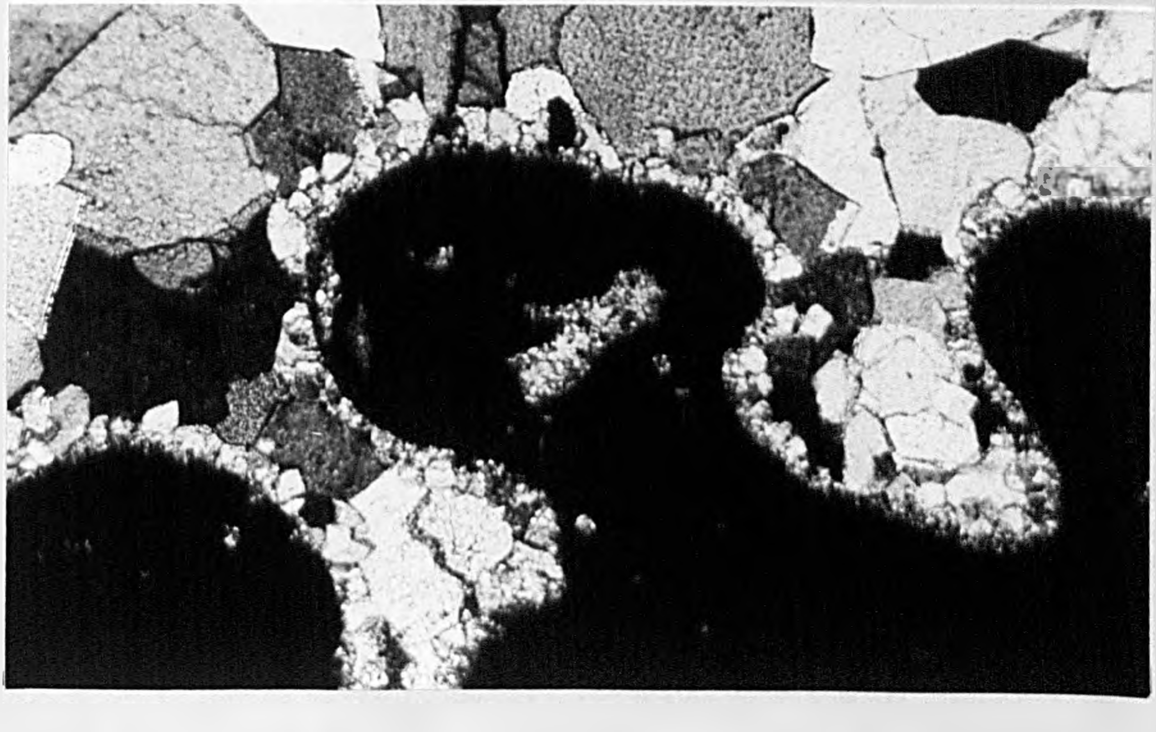
Specimen FXS 7 - Foss Cross, Bed 10

Thin section, x45, crossed polars

Both specimens M.J.B. colln.

Figure 5.9.





Nerinella cf. *acicula* (d'Archiac): Slape Hill.

Nerinella cf. *pseudocylindrica* (d'Orbigny): Eton College.

Eunerinea eudesii (Morris & Lycett): Geological Survey Museum and Oxford University Museum.

Eunerinea arduennensis (Buvignier): localities throughout the White Limestone.

Cossmannea bathonica (Rigaux et Sauvage): Foss Cross, Ardley Fields Quarry.

Zenoplocus microplicatus gen. et sp. nov. - see Chapter 2 for details.

Endiaplocus munieri (Rigaux et Sauvage): Ardley Fields Quarry.

Melanioptyxis altararis (Cossmann): Ardley Fields Quarry.

Bactroptyxis cotteswoldiae (Lycett)) Grange pit, Geddington.
)
)
Nerinella subcingenda (Hudleston)) Bajocian (Lower Lincolnshire
)
) Limestone). (See Barker & Torrens,
)
) 1971).

No traces have been positively identified in any species of *Aphanoptyxis*. This may mean the foldless genus *Aphanoptyxis* did not possess these structures or that the subsequent history precluded their preservation.

At any one Nerineid gastropod horizon, the presence or absence of these rod structures appears to be positively correlated with the type of carbonate sediment filling the spine. If the sediment contains large clasts and bioclastic debris, i.e. a relatively high-energy sediment, no traces of the rods are found. Where the sediment in the spire is a low-energy type, usually a fine grained intra/pel micrite, the rods are preserved. Table 6B shows the frequency of preservation of the rods from four gastropod horizons in the White limestone (Bathonian) containing Bactroptyxis implicata.

Table 5B

	Dagham Downs bed 12	Foss Cross bed 10	Stony Furlong bed 13c	Worsham bed 10
No. of specimens	19	38	29	14
No. with rods preserved	4	14	17	2
% with rods preserved	21.1	36.8	58.6	14.3

Interpretation

The fabric within the rods usually shows two generations of spar growth. Occasionally it is just a gradation from a fine grained spar at the edge to a coarser grained calcite in the centre, but more often a distinct microcrystalline calcite rim is found. The calcite of the rods falls within the term "cement" as defined by Bathurst (1971). Of the fabric criteria for cement given by Bathurst (op. cit., p. 417-8), the calcite in the rods of the Nerinacea fulfil the following: 2-8, 11-13, 15-17. The term cement is used "to include all passively precipitated, space filling carbonate crystals which grow attached to a free surface", (Bathurst op. cit., p.416). This fabric therefore suggests the rods were originally hollow tubes. For further discussion of carbonate fabrics see Chapter 6.

If the shell is removed from a modern gastropod such as Turritella, Buccinum or Helix, it will be seen that approximately 1½ whorls from the aperture, the spire contains a complex combination of the digestive gland and the gonad. The internal anatomy of Turritella communis Risso and Buccinum undatum Linné is shown in Fig. 5:10. This part of the spire in modern high-spired gastropods corresponds closely with that part of the spire in Nerineids in which the folds are fully developed, (see Fig. 5:2).

All gastropods have a digestive gland which is usually conspicuous. It has been variously called the digestive diverticulata, midgut gland, liver, hepato-pancreas or hepatic tissue. In this work the term digestive gland will be used. In some gastropods, the digestive gland and gonad are easily separable; in others, e.g. Thais lamellosa (Gmelin) and the abalones Haliotis cracherodii and H. rufescens Swainson, the digestive gland is physically inseparable from the gonad (Giese, 1959; Boolootian et. al., 1962; Stickle, 1973). The size of the digestive gland in modern molluscs exhibits a distinct seasonal, inverse relationship to the size of the gonad, both being governed by the reproductive cycle of the organism (Galtsoff, 1961; Lawrence et. al., 1965; Sastry, 1966; Ropes, 1968; Sastry & Blake, 1971). Fig. 5:11 is reproduced from Boolootian et. al. (1962) and shows the relationship between the annual cycles of the gonad and digestive gland in H. cracherodii. During maturation and gametogenesis, the gonad grows, largely, but not exclusively at the expense of the stored nutrients within the digestive

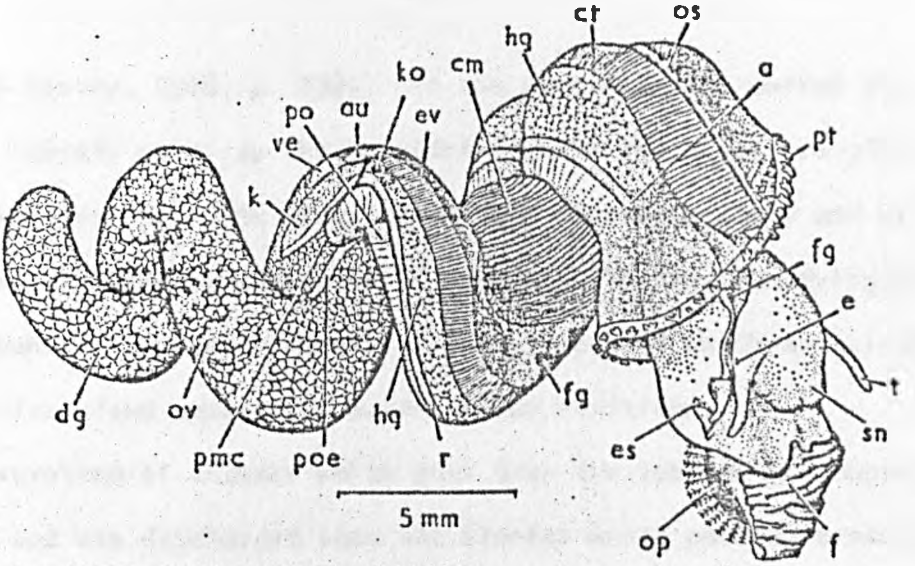


Fig. 57.—*Turritella communis*: animal removed from shell, seen from the right.
a, position of anus; au, auricle; cm, columellar muscle; ct, ctenidium, by transparency; dg, digestive gland; e, eye; es, exhalant siphon; ev, efferent branchial vessel; f, foot; fg, food groove; hg, hypobranchial gland; k, kidney; ko, kidney opening, by transparency; op, operculum; os, osphradium; ov, ovary; pmc, posterior limit of mantle cavity; po, pallial oviduct; poe, posterior oesophagus; pt, pallial tentacle; r, rectum; sn, snout; t, tentacle; ve, ventricle.

After Fretter and Graham, 1962.

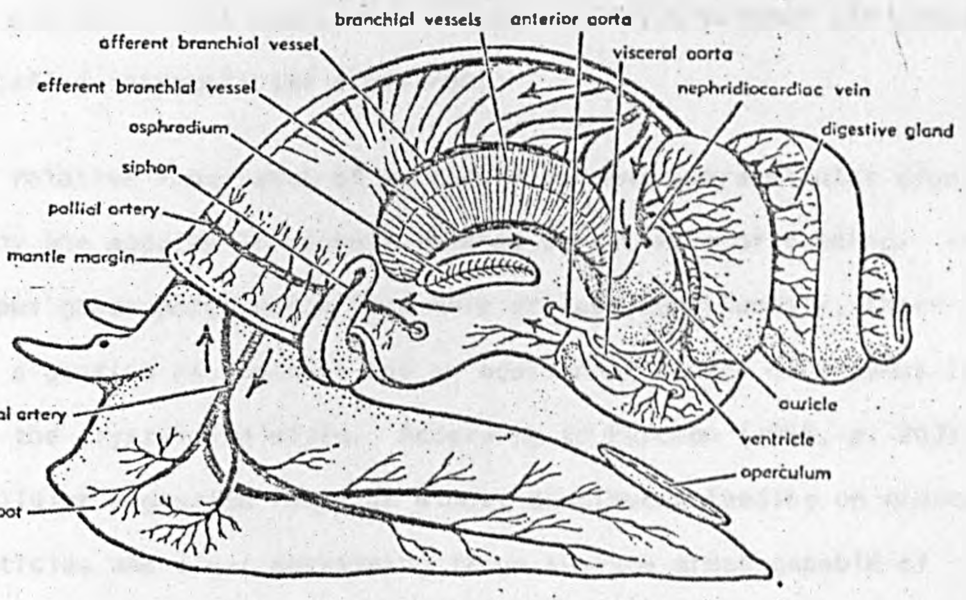


Fig. 58. *Buccinum undatum* Linné, diagrammatic representation of respiratory system, slightly enlarged (115n).

After Knight et. al., 1960.

Note that most of the spire is occupied by the digestive gland/gonad.

Fig. 5.10. The internal anatomy of T. communis (above) and B. undatum (below).

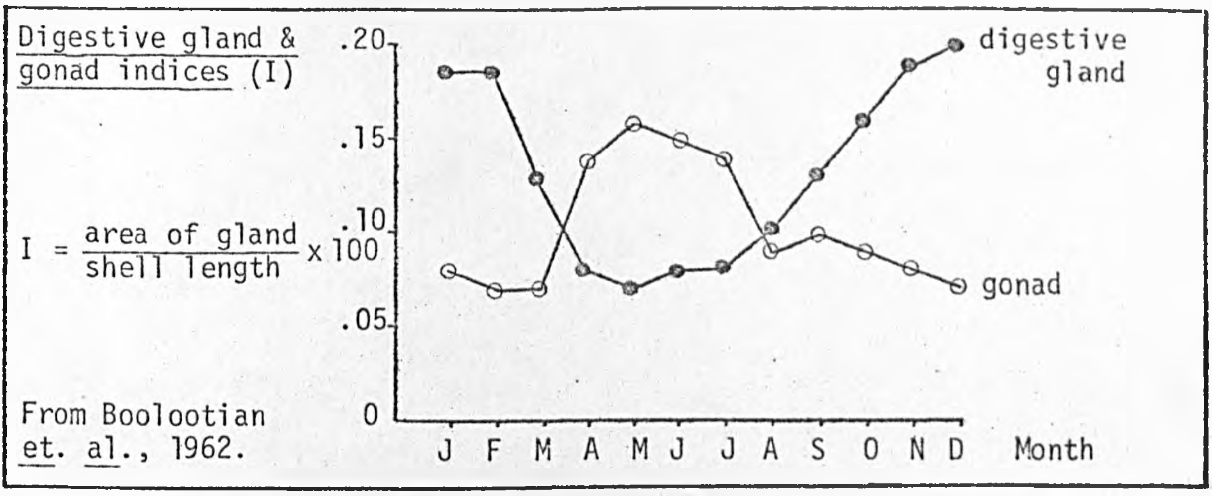
gland (see Sastry, 1966, p. 130). In the post spawning period the gastropod rapidly makes up the nutrient loss in the digestive gland by increased feeding. The structure of the digestive gland and of the gonad in modern gastropod species is acinous with many ramifying blind tubules opening into major canals or ducts, some of which are ciliated. The digestive gland apparently performs two functions,

a) The secretion of enzymes which pass down the tubules and ducts of the gland and are discharged into the stomach where partial breakdown of the food occurs. This is called extracellular digestion.

b) The epithelial cells lining the ducts and tubules phagocytose and absorb particulate material passed from the stomach into the digestive glands by peristaltic muscular action and/or cilia. Material ingested by the cells and not immediately required, is absorbed and stored as glycogen and fat in the connective tissue and cells between the tubules. This is called intracellular digestion.

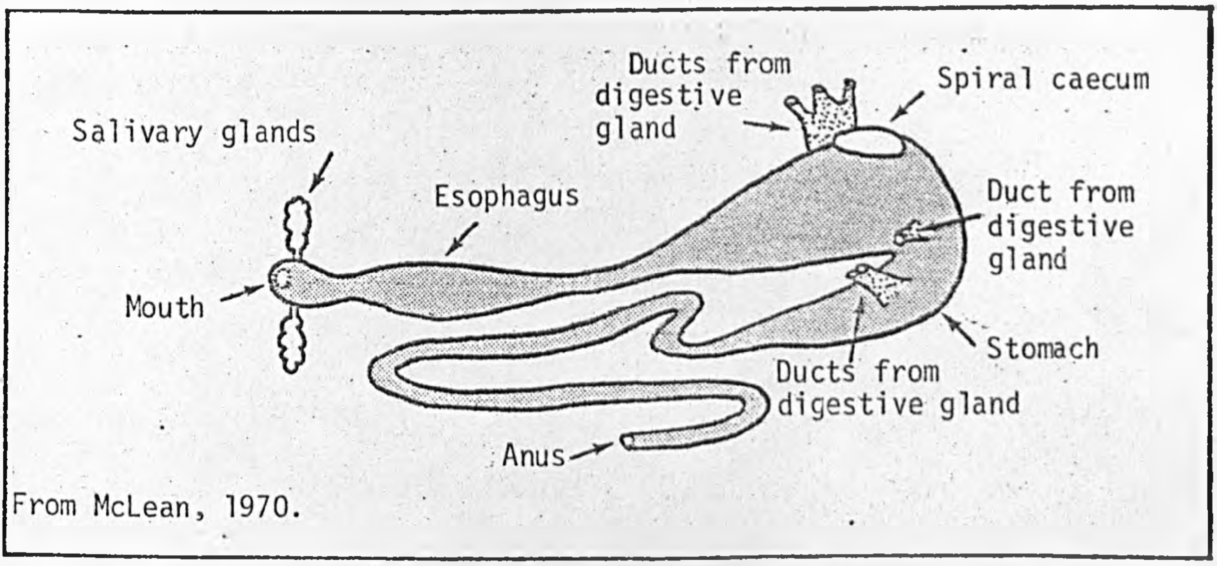
The relative importance of extracellular and intracellular digestion within any one species is closely related to the mode of feeding. In herbivorous gastropods, which feed more or less continuously, intracellular digestion is dominant and an additional source of enzymes is found in the crystalline style. According to Purchon (1968, p. 207), "intracellular digestion requires almost continuous feeding on minute food particles and a gut possessing large surface areas capable of phagocytosing suitably small particles and efficient ciliary sorting mechanisms; this is thought to have been the primitive method of digestion in the Mollusca." In those herbivores which feed discontinuously and especially in carnivorous or in scavenging genera, extracellular digestion appears to dominate, the main source of enzymes being the digestive gland. Most gastropods utilise both intra and extracellular digestion. When compared with the internal structure of modern gastropods, it appears probable that the rods in the Nerinacea represent the remnants of the duct system in the digestive gland/gonad complex. The side branching occasionally seen in longitudinally sectioned segments supports this hypothesis. Fig. 5:12 is reproduced from McLean (1970) and shows a schematic diagram of the digestive tract of the modern archaeogastropod Haliotis rufescens Swainson which has six major ducts leading from the digestive gland into the stomach. In the modern pulmonate Helix pomatia (Fig. 5:13), the digestive gland is divided into separate left and right lobes. The left lobe is further sub divided into three accessory lobes each with a main duct and the right lobe which occupies the apical part of the spire has one main duct. Thus H. pomatia has four distinct lobes and four major ducts within its digestive gland (Marshall and Hurst, 1946).

A reconstruction of the duct systems in Bactroptyxis implicata and a typical Eunerinea/Nerinella is shown in Figs. 5:14 and 5:15. The density distributions shown in Figs. 5:6 and 5:7 are less conclusive in locating the ducts for Eunerinea and Nerinella. This is probably a reflection of the greater ease of collapse of the rods in the open three fold arrangement of Eunerinea and Nerinella than in the more complicated lobate structure of B. implicata, from which it would be more difficult for the rods to fall. It therefore seems likely that the Nerinacean folds could be in some way intimately associated with the digestive gland/gonad complex. The attenuation of the folds in Nerineids as the aperture is approached would have been necessary in order not to adversely affect the vital organs, mantle cavity and the head-foot complex of the organism.



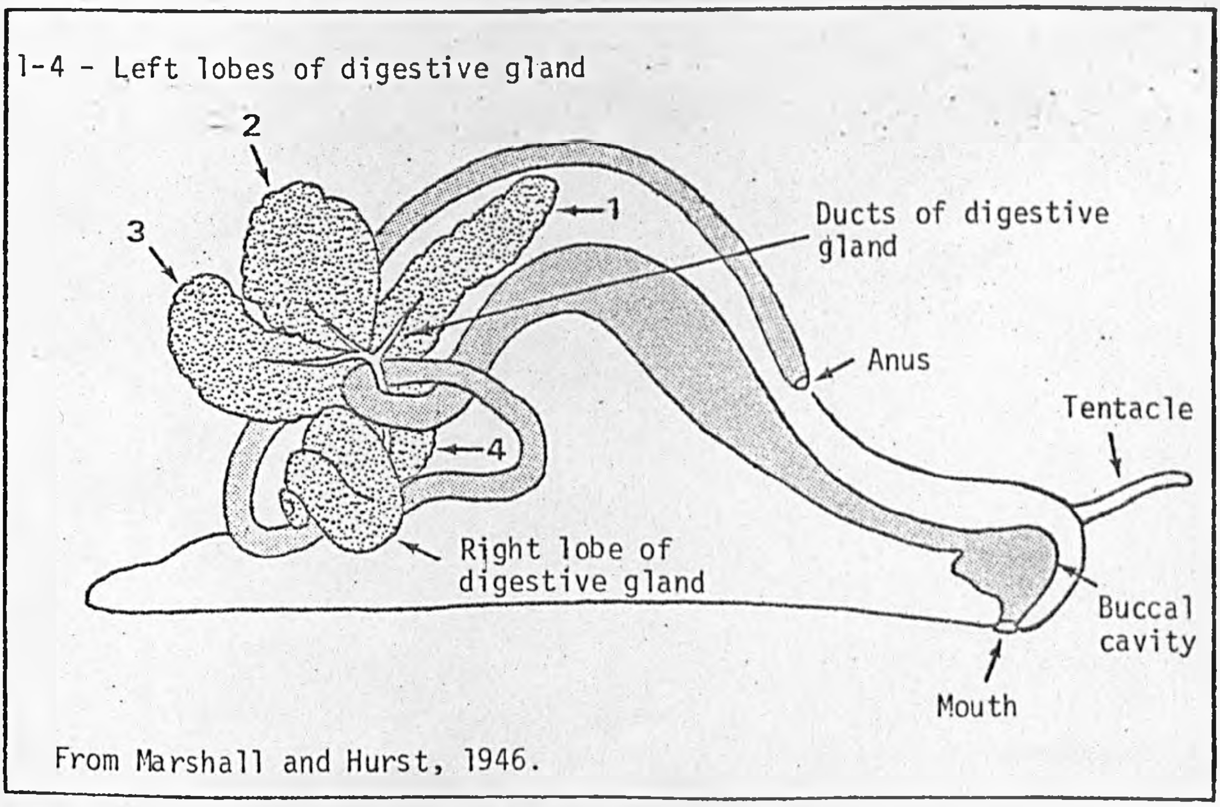
From Boolootian et. al., 1962.

Fig. 5.11. Annual cycles in the gonad and digestive gland of *H. cracherodii*



From McLean, 1970.

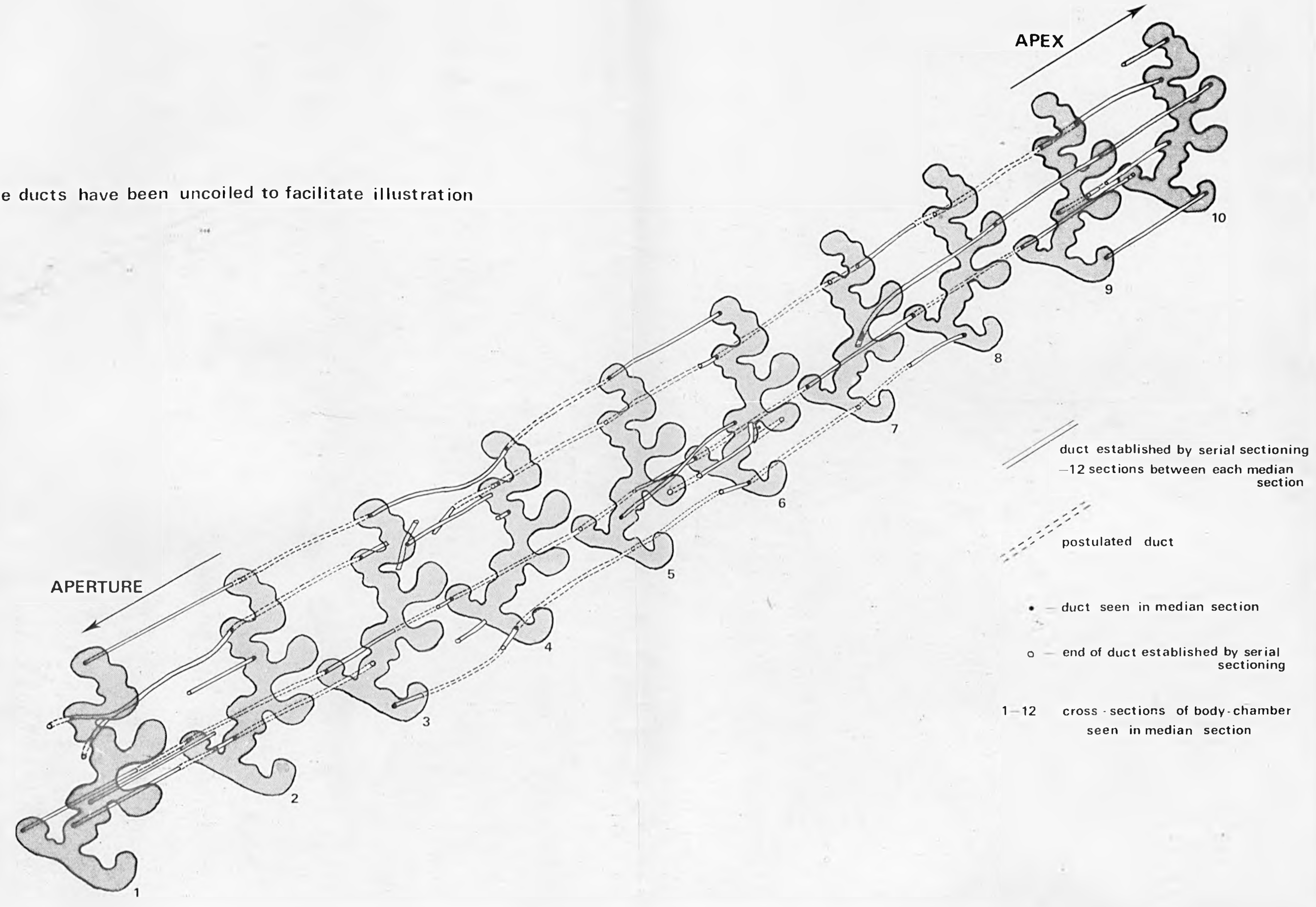
Fig. 5.12. Digestive tract of the Recent *H. rufescens*



From Marshall and Hurst, 1946.

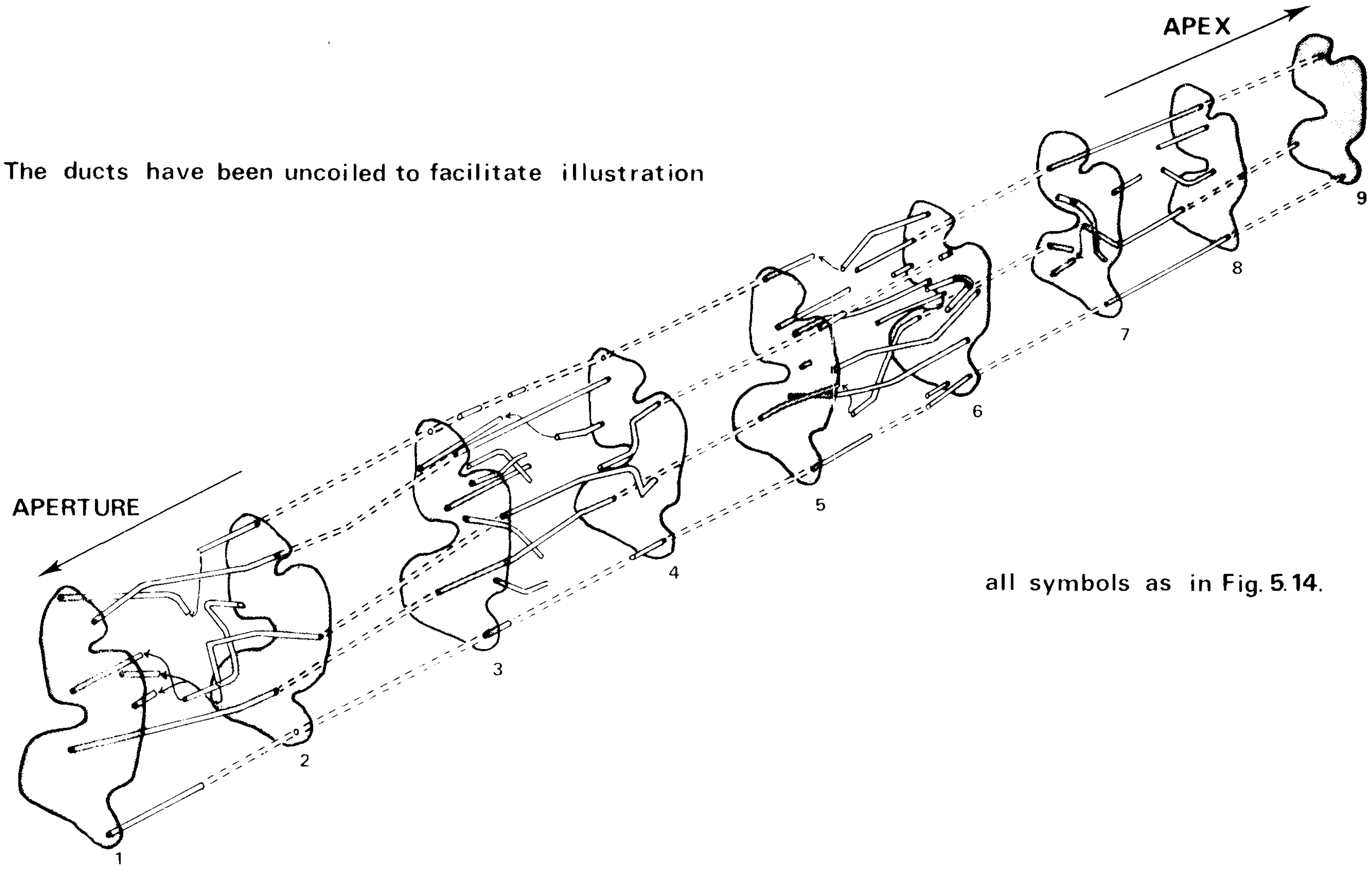
Fig. 5.13. Digestive tract of the Recent *Helix pomatia*

The ducts have been uncoiled to facilitate illustration



Specimen No. DD 20 (Dagham Downs, bed12) — personal collection of author

Fig. 5.14 The duct system in the digestive gland/gonad of B. implicata



The ducts have been uncoiled to facilitate illustration

all symbols as in Fig. 5.14.

Specimen No. G.P. 15 (Grange Pit, bed 1 see Barker and Torrens, 1971) personal collection of author

Fig. 5.15. The duct system in the digestive gland/gonad of Nerinella cf. subcingenda

The preservational mechanism poses some problems. The outer surface of the digestive gland/gonad complex would have been covered, as in all modern gastropods, by a thin mantle integument. The epithelial cells of this integument would have secreted the folds. Whatever the original source of the $CaCO_3$, aqueous or particulate, its metabolic pathway could only be through the digestive gland. 'Calciferous' cells have been identified in histological studies of digestive glands in all three orders of modern gastropods. These cells contain granules or spherules that react positively to histochemical tests for calcium. The calcium apparently exists as calcium phosphate and is bound to a protein base (Hyman, 1967). These calcium rich cells are most abundant in the epithelia of the ducts in the digestive gland and may buffer the acid contents of the ducts and stomach (Purchon, 1968).

The oxidative and bacterial processes associated with the decay of organic tissue are highly efficient, usually enzyme based mechanisms. A major function of the digestive gland is to secrete enzymes in order to breakdown ingested organic tissue. The epithelia cells of the duct need therefore to be resistant themselves to certain groups of enzymes and are probably more resistant to decay than the surrounding cells of the connective tissue. In most organisms the epithelial cells of ducts and tubes also tend, in general, to be thicker walled and stronger than the remaining soft tissue (see Schäfer, 1971, p. 37). Very early partial mineralisation of these ducts combined with slow sediment infill during, or immediately after, decay could preserved this duct system more or less intact and with its original 3D. configuration. The modification of the local geochemical environment caused by the process of decay within the gastropod spire could effect very early precipitation of $CaCO_3$ by utilising elements released through decomposition of the soft tissue. As any free oxygen was used up, the Eh would be reduced and there would be an initial lowering of the pH. However the main agents responsible for the breakdown of organic tissue are sulphate reducing and denitrifying bacteria, both capable of initiating the precipitation of $CaCO_3$ in spite of the initial reduction in pH. Russian workers ascribe a biochemical origin via these two types of bacteria to the fine grained $CaCO_3$ found in the muds accumulating in the anerobic bottom environment of the Black Sea (Caspers, 1957, pp. 820-1, 830). These Black Sea muds contain 7-10 gms./cc. of $CaCO_3$ in the sediment. Zangerl (1971) discusses the importance of bacterially induced precipitation of $CaCO_3$ in the early diagenetic history of concretions in Mississippian and Pennsylvanian black shales. The role of bacteria in the precipitation of calcium carbonate in modern carbonate environments is reviewed by Bathurst (1971) and in a series of articles, Berner (1966, 68, 69) examined the biogeochemistry and thermodynamics of bacterial decay in fishes and bivalves. In the presence of $CaCO_3$, decomposition of soft tissue first produces a fall in pH to between 5.6 and 6.2. Later production of ammonia due to the action of denitrifying bacteria increases the pH to between 7.8 and 8.8 but this does not itself bring about the precipitation of $CaCO_3$. Dissolved Ca^{2+} derived from the soft tissue is precipitated, (presumably as $CaCO_3$), only when there is extensive bacterial sulphate reduction. If the 'calciferous' cells in the epithelia of the ducts in Nerineacean digestive glands acted as substrates for bacterially precipitated $CaCO_3$, this could preserve the ducts in their original position until they were supported by the fine grained sediment infill. The goethite particles which sporadically occur around the edges of the ducts in some Nerineid specimens were probably FeS_2 particles initially, since most of the gastropod bearing limestones of the White limestone (Bathonian) and the Lower Lincolnshire limestone (Bajocian) are blue hearted and the insoluble residues after acid digestion contain appreciable amounts of particulate FeS_2. This suggests that at the time of deposition, reducing conditions existed below the sediment water interface. Similar conditions have been reported from many modern fine grained sediments e.g. the carbonate sediments of the Bahamas bank (Newell et. al., 1959, p. 191).

The more vigorous the inflow of sediment into the spire, or the longer the time between decay and the sediment infill, the less likely, and the less precisely, the duct system will be preserved. In the former case, the ducts would be physically broken and in the latter case they would have completely decayed. All states exist between excellent preservation (as in Fig. 5:4) and complete destruction.

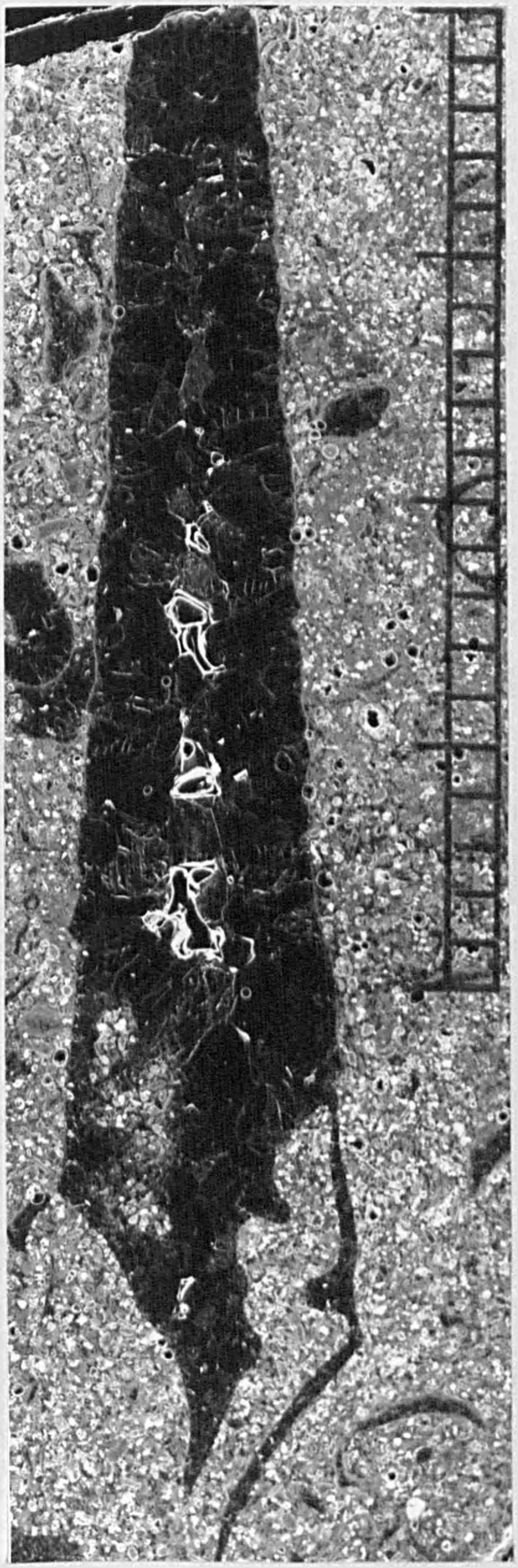
Sediment can enter the spire in two ways; via the aperture, or via holes, as a result of damage to the apex or whorl sides. In most modern gastropods, death is accompanied by contraction of the columella muscles and the viscera are drawn up into the shell. Frequently Nerineids are preserved with the first 1 or 1½ whorls filled with sediment (Fig. 5:16) and the spire contains no sediment, only cavity precipitated cement. This probably represents a "plugged aperture" with the viscera tightly drawn up into the shell (see also Chapter 6). If no further openings in the shell are available, delayed decomposition or the production of gases

Plugged aperture in *N.* cf. *acicula*

Specimen Sl.H.Ox. 134 - Slape Hill, Bed 5.

Acetate peel. M.J.B. colln.

Figure 5.16.



through putrifaction will prevent sediment entering the spire. For sediment to have entered the whole spire in the acicular Bactroptyxidae with their much reduced internal body cavity, some form of damage to the spire would be necessary in order a) to have provided another means of sediment access other than the aperture and b) to have allowed the products of decomposition (both gaseous and liquid) to escape, thereby relieving the pressure build-up which prevented sediment entering.

b) Mode of life.

Part I. The ecological relationships of modern gastropod faunas.

After the establishment of that class of molluscs we call the Gastropoda, their highly successful evolutionary diversification was based largely upon modification, developments and transformations of the original feeding mechanisms. They established representatives in a wide variety of habitats with the capacity to efficiently exploit a surprising diversity of food sources. "With the exception of aerial locomotion, the Gastropoda have successfully undertaken every possible mode of life", (Purchon, 1968). Most gastropods can be conveniently grouped into one or more of the following modes of life: predator, scavenger, parasite, grazer, algal browser, suspension feeder or deposit feeder. Within each group, some members are highly specialised (e.g. host-specific parasitic Pyramidellids), others are more generalised, especially the scavengers and browsers. These various modes of life are associated with differences in internal anatomy. Food sorting mechanisms in the gut and the relative importance of intracellular and extracellular digestion are dietically controlled (see previously).

Deposit feeders and suspension feeders are not commonly found amongst modern gastropod faunas. These are, of course, the main modes of life within the Bivalvia. Despite the obvious adaptability of the buccal mass and radula to a wide variety of food gathering mechanisms, deposit feeding and suspension feeding have not been extensively used by gastropods, largely, in the opinion of the present author, because gastropods have less efficient particle sorting mechanisms than the Bivalvia. In the Bivalvia, the ciliated ctenidia (also the labial palps in detritus feeders such as the Nuculoida and Solemyidae) are the main food gathering organs. Amongst the Gastropoda the ctenidia are much less concerned with food sorting than with respiration. The food in the majority of gastropods is passed straight into the mouth and any necessary sorting is done by ciliary action in the stomach, not prior to ingestion as in the Bivalvia.R.Newell (1965) reported that deposit feeders do not digest particulate organic matter in the sediment, but they mainly assimulate the bacterial coating and microorganisms associated with organic decomposition found on the sediment grains and organic particles. He suggests that much of the organic detritus is expelled unaltered in the faeces of the organisms and postulates a correspondence between the sediment grain size and the abundance of deposit feeders, viz (op. cit., p. 41). "In coarse deposits, breakdown of autotrophs is slow owing to the small, population of microorganisms and the population of deposit feeders is also small. In fine deposits, however, the organic debris is decomposed more rapidly owing to the presence of an abundant population of microorganisms providing a food source for a population of deposit feeders whose density is hence closely related to the grade of deposit".

The spatial distribution and relationships of the various molluscan feeding mechanisms in modern environments has not been extensively studied. However, this approach was utilised by Taylor (1968) who examined the ecological composition of molluscan communities around the Island of Mahé in the Seychelles. Of the habitats he recognised, only the *Thalassia* marine grass beds and the carbonate sands to the seaward of the grass beds, could possibly be taken as analogues of the environments in which the Nerinacea must have lived. Sediment composition and sedimentary environments around Mahé have been treated more fully by Lewis (1969) who states "These water and climatic conditions preclude the formation of carbonate deposits such as oolitic sediments, which are characteristic of regions of high water temperature and excessive evaporation rates, such as the Bahamas and the Persian Gulf. The carbonate grains in the sediment around Mahé are therefore, of wholly skeletal origin". The composition of the molluscan faunas in the *Thalassia* and carbonate sand habitats of Mahé are shown in Tables 5C and 5D.

Organism communities in relation to the Bahamas bank sediments have been studied by Newell *et*. *al*. (1959). West of Andros Island, the pellet sand lithology is occupied by the *Strombus costatus* community of Newell *et*. *al*. (*op*. *cit*.). Examination of their faunal lists reveals a similar pattern to that shown by the molluscan fauna in Mahé. The gastropods are mainly algal browsers, predators or scavengers. The algal browsers are epifaunal (*S*. *costatus*, *Cerithium* spp.) whereas the predators and scavengers may be epifaunal

Table 5C

Molluscan fauna from Thalassia beds Mahé.

(data from Taylor, 1968)

Fauna 55% Prosobranchia. 45% Bivalvia.

Prosobranchia

30% algal grazers e.g. Strombus, Cerithium, Cypraea and neritids

35% predators e.g. Conus, Natica and Drupa

15% faunal grazers

also large numbers of scavenging Nassarius arcularis and N. albescens.

The gastropods are dominantly epifaunal except for a few shallow/ partial burrowers especially Conus, Natica and Terebra.

Bivalvia

75% suspension feeders e.g. Pinna, venerids and lucinids

15% deposit feeders e.g. Scissulina, Leptomya and tellinids

Bivalves dominantly infaunal.

Table 5D

Molluscan fauna from Sands seaward of Thalassia beds at Mahé.

(data from Taylor, 1968)

Coarse, clean, rippled carbonate sand stabilised by extensive algal growths of Sargassum and Turbinaria. Encrusting calcareous and coralline algae abundant.

Fauna 75% Prosobranchia. 25% Bivalvia.

Prosobranchia

45% predators e.g. naticids, Conus and Pleuroploca

25% algal grazers especially Cerithium

rest are scavengers (Oliva and Nassarius spp.) or parasitic (Pyramidellacea)

Bivalvia

55% depost feeders. Mainly tellinids, e.g. Tellinella and Quadrans - species diversity high but numbers of individuals low.

45% suspension feeders e.g. lucinids and venerids

The epifaunal gastropods frequently have an epibiota of calcareous algae e.g. Cerithium echinatum encrusted with Monotrema rubra

(Nassarius and Bulla) or infaunal (Natica). The bivalves are either deposit feeders (mainly tellinids such as Tellina and Macoma) or suspension feeders (Lucina and Laevicardium). However the ecological analysis of the Bahamian fauna is less rigorous than that of Taylor (op. cit.) and Newell et. al. (op. cit., p. 183) further state that, "The Bahamian fauna and flora are not well known and long sustained effort by many collectors and taxonomic specialists is required before the specific composition of the bottom biota can become really well known".

Part 2. The proposed relationship between the internal folds and the mode of life of the Nerineacea, especially the Bactroptyxidae.

The digestive gland/gonad complex performs three important functions in modern gastropods (Fretter & Graham, 1962).. It is the site for

a) the absorption of foodstuffs and the excretion of waste matter in the digestive gland;

b) the production of gametes in the gonad;

c) the storage of the products of digestion as glycogen and fat in the connective tissue.

Occupying most of the spire, the digestive gland/gonad complex represents the only region in a gastropod where large amounts of $CaCO_3$ could be internally deposited without serious detrimental consequences to the animal. The decrease in volume of the soft tissue due to fold development inside the spire is very marked, especially within the genus Bactroptyxis. The calculated percentage volume reduction caused by the folds in several genera and species is shown in Fig. 5:17. Of the three vital functions listed above, only the

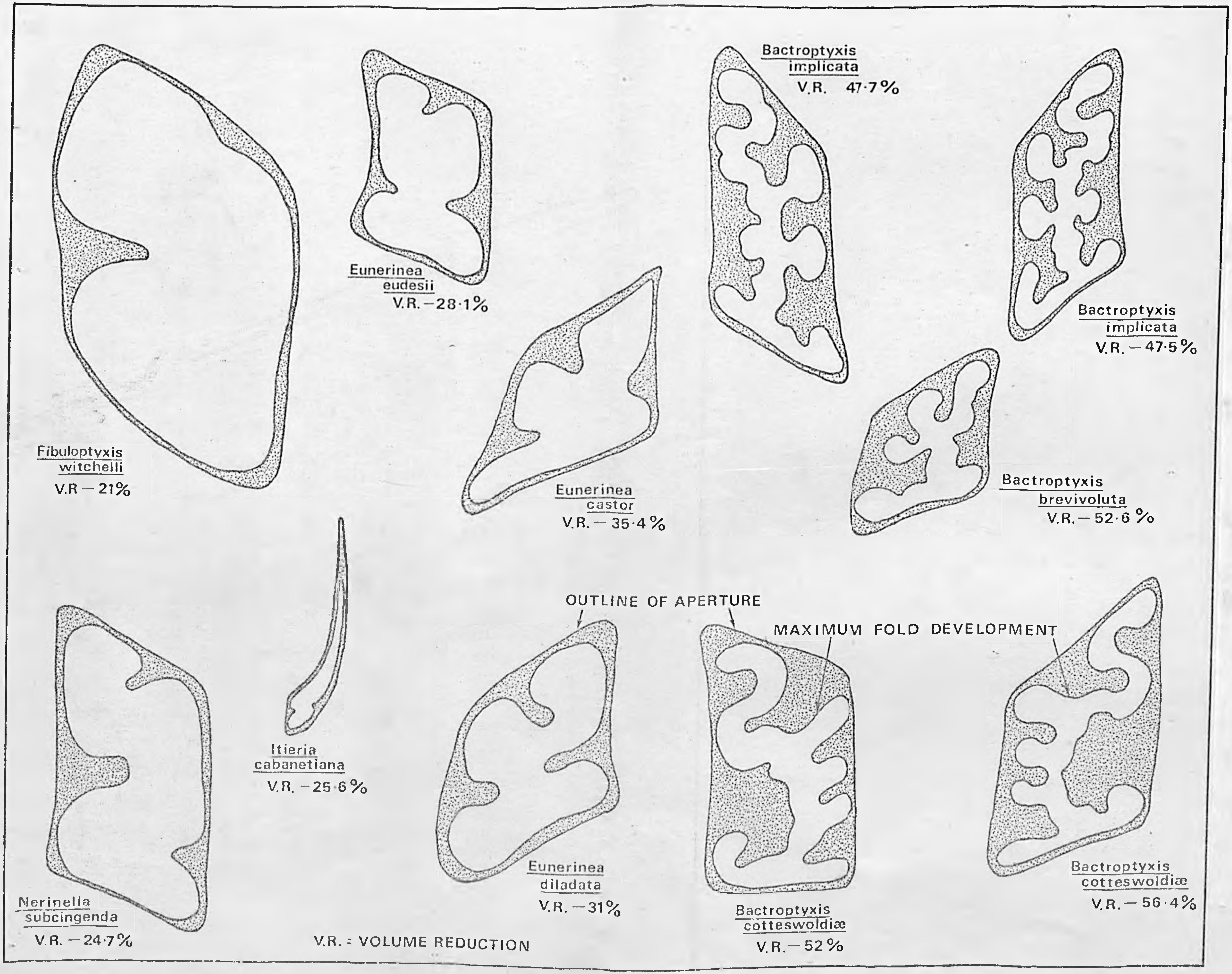


Fig. 5.17. Volume reduction in body cavity due to the development of internal spiral folds.

storage capacity is dispensable and then only if the metabolism of the organism can be adequately and constantly maintained. Continuous feeding on abundantly available food is the only means of providing a constant energy input. As the Nerineacea had well developed duct systems and were extremely abundant, there is no reason to suppose functions a) and b) were in any way impaired by the development of folds. It is suggested that the folds of the Nerineacea were developed at the expense of the nutrient storage capacity, and were emplaced between the major lobes of the digestive gland/gonad complex. The primary function of any storage cells that remained was probably to supply the gonads during the reproductive cycle.

Of the diverse feeding mechanisms exhibited by gastropods, only those involving a herbivorous diet could ensure the continuous supply of food necessary to a) sustain the metabolism of an organism with such a reduced capacity for energy storage and b) provide enough food for the vast numbers of individuals usually found in the Nerineid bearing horizons. Predation and scavenging do not supply regular meals.

If the hypothesis that the Nerineid metabolism was sustained by regular, almost continuous feeding is correct, considerable amounts of waste material would be ingested and would need to be evacuated from the alimentary tract as faecal pellets.

Fig. 5:18 is reproduced from Barker and Torrens (1971) and shows the modal analyses of the basal 1.80 m of the Lower Lincolnshire limestone (Bajocian discites subzone) from Grange Pit, Geddington,

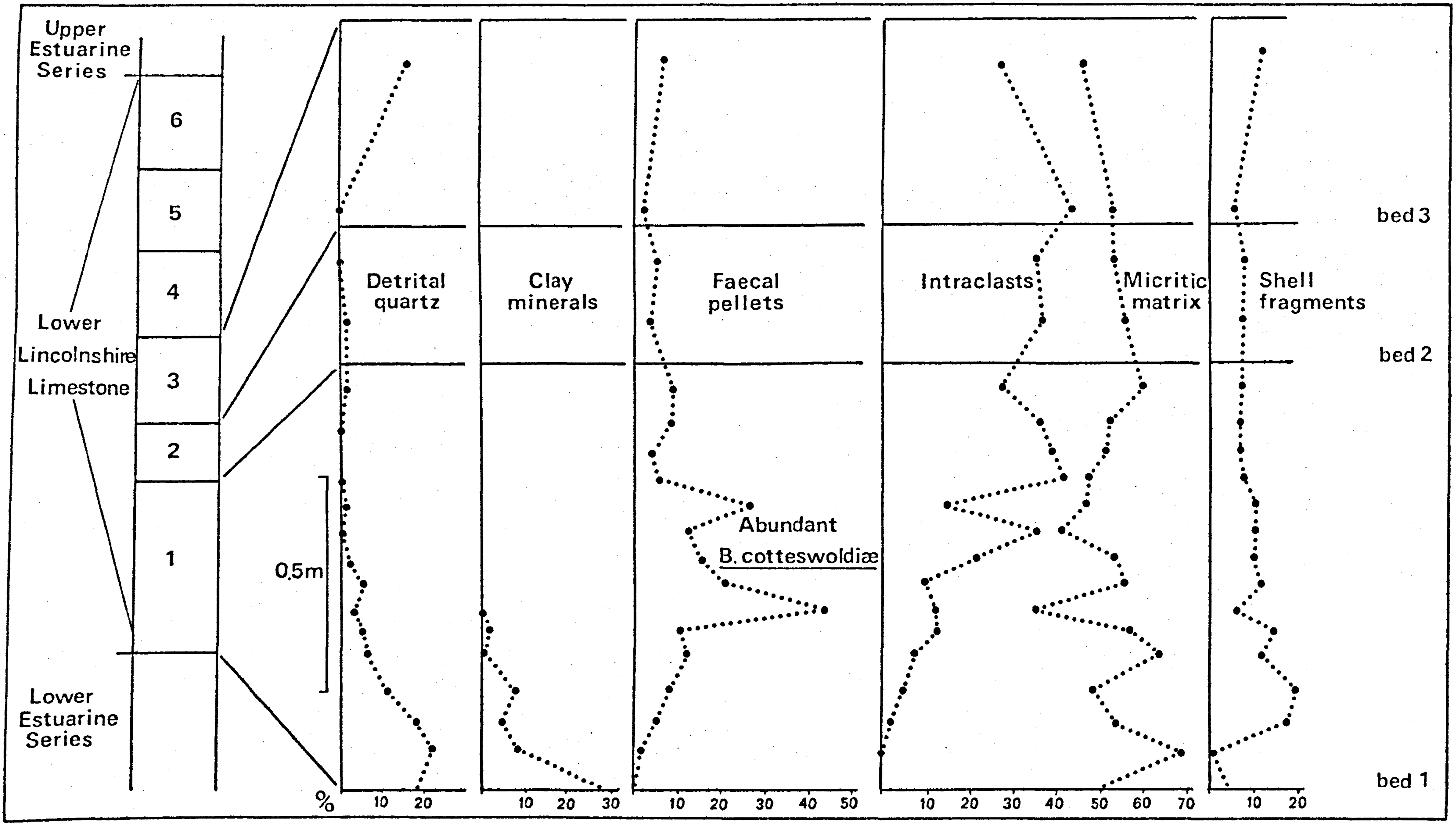


Fig. 5.18 Modal analysis of basal Lower Lincolnshire Limestone (Sowerbyi Zone, Discites Subzone) at Grange Pit, Geddington (SP867824) (after Barker and Torrens, 1971)

north of Kettering. Faecal pellets are abundant at two horizons; 0.42 m and 0.66 m from the base. The Nerineid Bactroptyxis cotteswoldiae (Lycett) is considerably more abundant at these levels than at other horizons and in view of the scarcity of other fauna (see Barker & Torrens, op. cit., p. 52) it is reasonable to ask whether the faecal pellets originated from this gastropod. However, one cannot exclude the possibility that the pellets were derived from some other soft bodied group of organisms, such as polychaete worms, which would not be preserved. The association of herbivorous gastropods and faecal pellets is well known in modern molluscan faunas e.g. Cerithidea off Andros Island, Bahamas and Cerithium and Mitrella at Abu Dhabi (Bathurst, op. cit. and Gatrell, pers. comm., 1970). These three genera are all epifaunal browsers/detritus feeders and are closely associated with faecal pellet/aragonitic mud lithologies.

Two groups of modern gastropods ingest large amounts of detritus, the epifaunal algal browsers and the infaunal deposit feeders. The algal browsers utilise the algal film on surface sediment particles. They remove the surface film and usually some of the top layers of sediment, some taking very little detritus, others taking in considerable volumes. The ingested material is passed straight into the mouth and sorting takes place in the alimentary tract. Some authors (Carriker, 1946; Owen, 1966) suggest the intake of inert particulate matter is essential in providing a physical breakdown (trituration) of the organic matter inside the stomach. Except for some predators, modern infaunal gastropods are either suspension filter feeders or deposit feeders. They are unique amongst the gastropods in that they use the ciliary sorting capabilities of the ctenidium in the mantle cavity, in the same way as most bivalves. This means that some particle size sorting takes place before the sediment is passed into the mouth and alimentary tract.

Two modern infaunal deposit feeding gastropods with contrasting feeding mechanisms are Aporrhais and Struthiolaria, both of which lie buried in the surface layers of marine deposits of firm muddy gravel or firm muddy sand. In Struthiolaria the main source of food is particulate matter stirred up from the surface of the muddy sand (Morton, 1951). Aporrhais, on the other hand, exhibits the more archaic method of foraging for organic debris, pieces of algae and diatoms by protruding its proboscis and grasping prospective food material by its radular teeth.

Fox (1957) gives an account of feeding in the marine prosobranch Littorina planaxis from La Jolla, California. This gastropod is an algal browser living on compacted siltstone. The sediment has an average organic matter content of 2.6% and the average amount of siliceous material passed through the gut of the gastropods is 2336 mgm/year/individual. In these environments the sediments contain little or no carbonate material apart from comminuted shell debris, which is unlikely to form a significant component within the grain size range utilised by algal browsers and deposit feeders. Most of the non-organic particulate detritus is terrestrial in origin, essentially inert, usually comprising degraded clay mineral lattices and silt size quartz grains.

Carbonate environments exhibit a similar range of physical properties and a similar variability in the amount of organic matter available in the sediment (cf. the Thalassia beds and open sands around Mahé; Taylor, op. cit.) but differ in that the non-nutriative carbonate fraction would not be as chemically inert in the molluscan gut as material of terrestrial origin. The enzymes of the digestive system (both in the stomach and in the digestive gland) of modern gastropods show optimal activities with a pH range of 5-6. This probably means that $CaCO_3$ is unavoidably assimilated in the metabolic cycle of those gastropods ingesting large volumes of particulate carbonate detritus. Rapid passage through the gut would reduce this absorption but the problem would be acute in organisms ingesting fine grained carbonate sediment. In modern gastropods unwanted products of metabolism both inorganic and organic, which have no excretory pathway via the gut, are often incorporated in the shells of the organism concerned. This is the source of most colour banding in molluscs, (Cox, 1960, p. 123-4). In epifaunal gastropods inhabiting carbonate sediments, excess $CaCO_3$ due to adsorption of ingested particulate carbonate matter can be deposited by the mantle as extra shell layers, spines and other shell ornament, as in Strombus, Lambis, Astraea and Columbella, all of which are thick shelled, heavily ornamented epifaunal genera occurring in the S. costatus community in the Bahamas. The development of spines and other extraneous shell ornament in a motile, infaunal gastropod would considerably reduce the mobility of the gastropod through the sediment and seriously impair its feeding efficiency.

It is thought that Bactroptyxis, at least, was an infaunal Nerineacean for the following reasons:

a) the extremely long, slender spire would require protection. Some broken specimens of B.implicata have been found with an apertural diameter of 12 mm. The average apical angle of B. implicata is 4° which gives a total projected length, including the siphonal canal, of approximately 190 mm. All extremely high-spired modern gastropods, such as Terebra, are at least partially infaunal (Taylor, J.D., pers. comm., 1971).

b) the presence of an apertural canal suggests the necessity for an extensile siphon for respiration/feeding in a position from which it would not be possible without it.

c) the present author has never seen evidence of shell regeneration caused by injury or predation in any specimen of Bactroptyxis. Recent epifaunal gastropods such as Buccinum, Nassarius and Littorina, together with very shallow infaunal forms such as Turritella, frequently show shell regeneration. Amongst the fossil forms associated with the Nerineacea, Purpuroidea, Proconulus and Leptomaria have been found with repaired growth lines.

d) Bactroptyxis and other elongate high-spired genera lack an epifauna which colonised the shell during life. For discussion on post-mortem epifaunal colonisation see Chapter 6.

e) The sediments in which Bactroptyxis and other Nerineids are found are extensively bioturbated.

In order to live in the fine grained, subtidal, carbonate sediments, *Bactroptyxis* had to adapt and accommodate extra $CaCO_3$ in its metabolism. This could not be deposited externally as this would reduce its feeding efficiency, so the $CaCO_3$ was deposited internally between the lobes of the digestive gland. The nutrient storage capacity was thereby reduced but as the animal had a regular supply of energy obtained by continuous gross feeding, its metabolic efficiency was probably not impaired. Amongst other Bathonian Nerineids, both *Fibuloptyxis* and *Melanoptyxis* were evidently epifaunal. Specimens can be found in which the growing gastropod shell has enveloped the attached epibionts (see Chapter 6). These colonising organisms include algal borings, oysters, ectoprocts and serpulid worms. The Bathonian representatives of *Fibuloptyxis* and *Melanoptyxis* seem to be associated with relatively high-energy carbonate substrates, being particularly abundant in the Minchinhampton facies where the streamlined shell shapes of these two genera were probably advantageous.

Another Bathonian Nerineid, *Eparciella*, was also apparently confined to the Minchinhampton facies. This small gastropod is heavily ornamented, a very unusual feature in Nerineids, and was probably also epifaunal. The heavy ornamentation implies a capability for both internal and external secretion of $CaCO_3$ in this genus.

The ecological interpretation of the remaining White Limestone Nerineid genera is more difficult. *Eunerinea* spp. and *Nerinella* spp. frequently occur together and often in large numbers (e.g. Slape Hill, bed 5, see Fig. 1:5). *Nerinella* spp. and *Aphanoptyxis* spp. are similarly distributed (e.g. Eton College, bed 12a, see Fig. 1:11). However, Eunerinea spp. and Aphanoptyxis spp. show a distinct inverse relationship and never occur together in large numbers in the White Limestone, (see Chapter 1). One concludes that either the Eunerinea spp. and the Aphanoptyxis spp. were ecologically competitive or that they had dissimilar ecological nichés with only marginal overlap whereas the Nerinella spp. had a broad ecological niché and could associate with either. No unequivocal evidence has been found to suggest an epifaunal or infaunal mode of life for any of these three genera, i.e. no regenerated growth lines or shell enveloped epifauna have been observed.

All species of Aphanoptyxis are foldless and presumably, therefore, their food source did not contain more $CaCO_3$ than could be accommodated in the normal metabolic processes of shell formation. This implies an epifaunal mode of life, perhaps as an algal browser, on the surface of the fine-grained intrapelmicrites in which they are normally preserved. In this environment one might expect abundant oncolite encrustation together with other epifaunal colonisation. However, undoubted epifaunal species associated with the various Aphanoptyxis spp., such as Amberleya bathonica, Neritoma (Neridomus) cooksonii and Chartroniella infrastriata, do not show any such epifauna. Perhaps the environments in which the Aphanoptyxis spp. lived were unsuitable for oncolite formation and epifaunal colonisation or possibly the Aphanoptyxis spp. proved unsuitable substrates.

The slender, high-spired form of *Nerinella* cf. *acicula* and *Nerinella* cf. *pseudocylindrica* suggest they were an infaunal species. Tiedt (1958) has reported shell regeneration in the Senonian Nerineids *Aptyxiella (Acroptyxis) gracilis* (Zekeli) and *A*. (*A*.) *granuiligera* Tiedt. The subgenus *A*. (*Acroptyxis*) is morphologically intermediate between *Aptyxiella* and *Nerinella*. Like *Nerinella*, *A*. (*Acroptyxis*) has three folds but the columellar and parietal folds are much weaker. Ecological diversification from a shallow, infaunal Nerinellid ancestor into an epifaunal existence may explain the presence of shell regeneration and the incomplete fold development in *A*. (*Acroptyxis*).

The inverse relationship between the *Aphanoptyxis* spp. and the *Eunerinea* spp. and its possible ecological basis has been noted earlier. The large size, concave whorls and robust nature of the *Eunerinea* shell is consistent with an epifaunal mode of life. The sediments associated with the *Eunerinea* spp. seem to reflect a higher-energy depositional régime than in the sediments in which the *Aphanoptyxis* spp. are found which probably accounts for the relationship between these two genera.

The remaining Bathonian Nerineid genus, the umbilicate, trochiform *Endioplocus* would almost certainly have been epifaunal, perhaps feeding in much the same manner as the Recent *Trochus niloticus* and other trochiform gastropod species.

With the exception of occasional monospecific horizons, it is noticeable throughout the White Limestone that beds containing several Nerineid gastropod species are numerically dominated by only two of those species, one an infaunal species (either a *Bactroptyxis* sp. or a *Nerinella* sp.) and the other an epifaunal species (either a *Fibuloptyxis* sp., *Melanoptyxis* sp., *Eunerinea* sp. or *Aphanoptyxis* sp.).

The above ecological considerations clearly suggest a close relationship between the Nerineid fauna and the carbonate sediment they occupy. The Bathonian White Limestone Formation of England is divisible into the Bladon Beds at the top, the Ardley Beds and the Excavata Beds at the base (see Chapter 1 and Barker and Torrens in prep). Generally the individual gastropod horizons in the White Limestone show little or no vertical change in the sediment or fauna. However, north-east of Sturt Farm Quarry (G.R. SP286102), the basal member of the Ardley Beds exhibits a marked lithological transition from dark clays immediately above the *A. excavata* bed, passing through sandy, decalcified limestone into a biointrasparite at the top of the bed. The lower part of the carbonate lithology is particularly fossiliferous at two localities, Ardley Fields Quarry (G.R. SP541265) and Slape Hill Quarry (G.R. SP425196). The sections at Slape Hill and Ardley Fields are approximately 14 km. (8.5 miles) apart and are shown in Figs. 1:5 and 1:18. A detailed study of the vertical changes in the fauna and sediment was undertaken in order to examine the relationship between the fauna and the sediment as well as assess the potential correlative value and lateral continuity of benthonic faunas.

The decalcification at the base of the carbonate sediment evidently progressed much further around Ardley than elsewhere. The fossils in the basal fossiliferous layer are found as moulds and casts in a well developed Roach-stone (see Chapter 1). Blocks of the Roach-stone can be found scattered around Ardley Fields Quarry and the nearby Ardley Station Quarry (G.R. SP539269). With a little excavation the Roach-stone can be examined *in situ* in Ardley Fields Quarry and in the adjacent railway cutting. At the Slape Hill the equivalent bed is not decalcified and is well exposed in the working quarry. Beautifully weathered-out specimens can be obtained from joint faces. The taxonomic and ecological composition of these fossil faunas is shown in the following tables and figures.

Fig. 5:19	Bivalvia: Gastropoda ratios
Table 5E	Taxonomic composition of the Bivalvia
Table 5F	Taxonomic composition of the Gastropoda
Fig. 5:20	Distribution of Bivalvia taxa
Fig. 5:21	Distribution of Gastropoda taxa
Table 5G	Modes of life - Bivalvia
Fig. 5:22	Distribution of modes of life - Bivalvia
Table 5H	Modes of life - Gastropoda
Fig. 5:23	Epifaunal-infaunal relationships of Slape Hill fauna
Fig. 5:24	Epifaunal-infaunal relationships of Ardley fauna
Fig. 5:25	Feeding habits of Slape Hill fauna
Fig. 5:26	Feeding habits of Ardley fauna

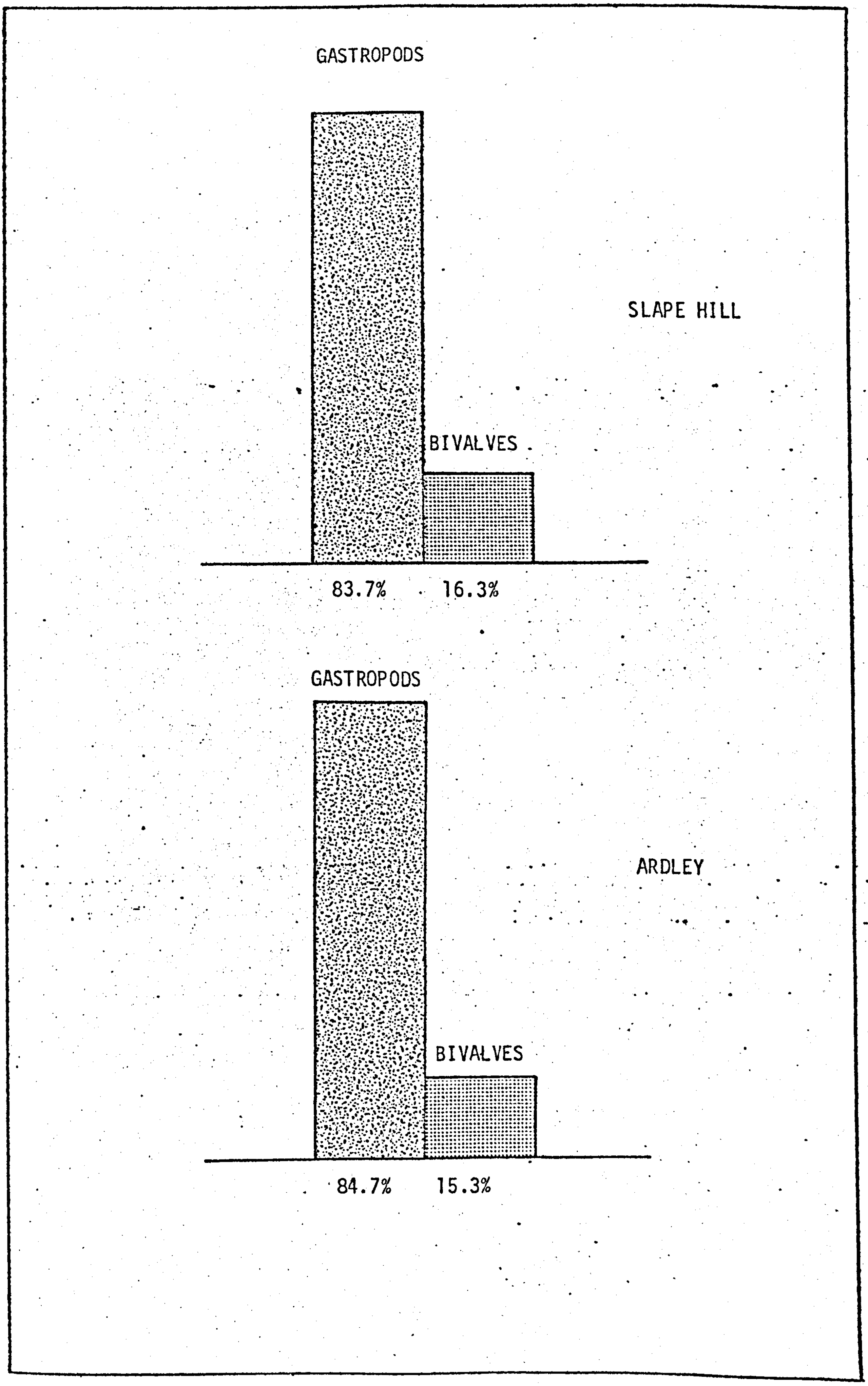


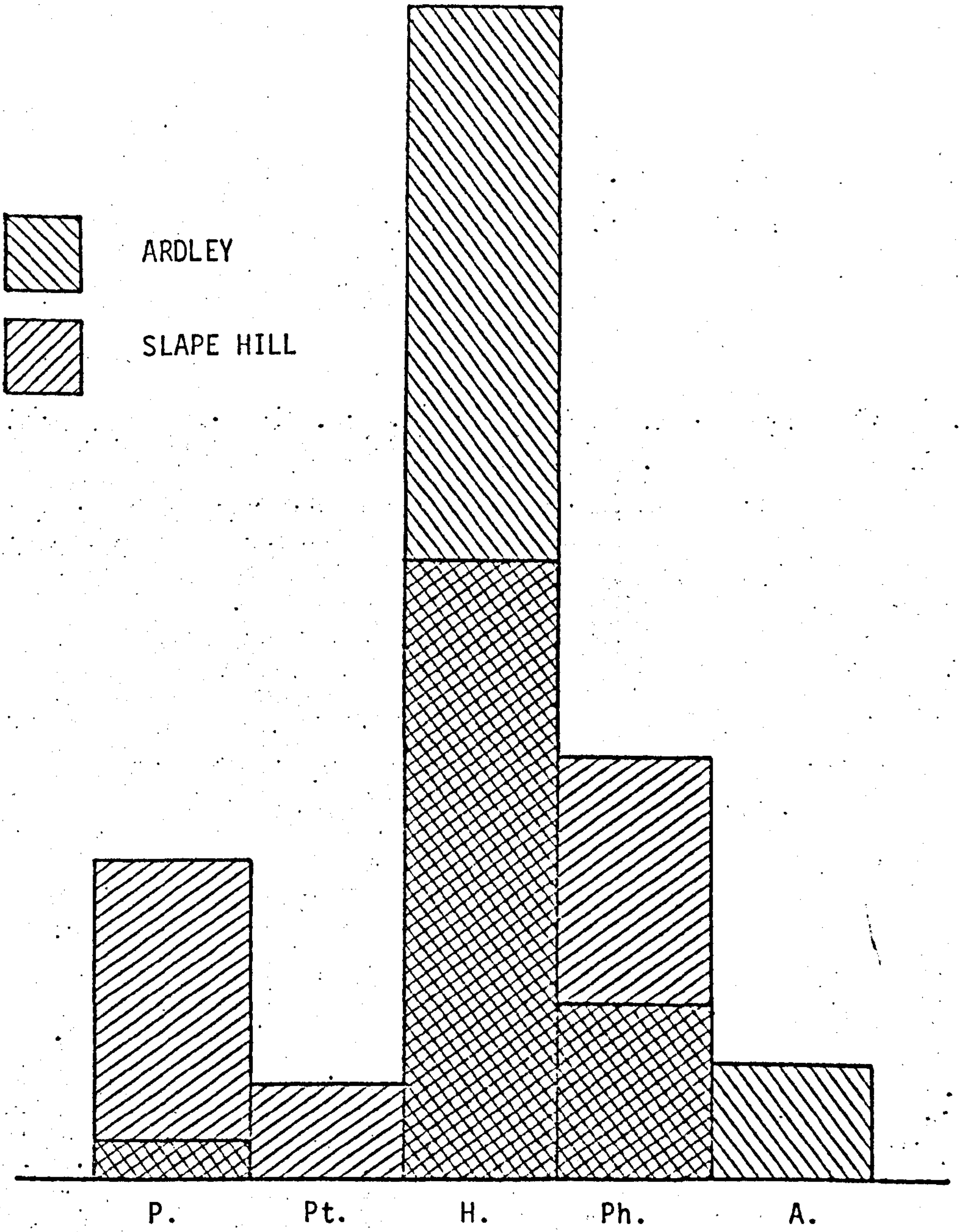
Fig. 5.19. The ratio of Gastropods to Bivalves in the Lower Ardley Bed.

Table 5E - Bivalvia

Subclass Pteriomorphia	Slape Hill		Ardley	
	No.	%	No.	%
Entolium sp.			1	1.3
Gervillella sp.			1	1.3
Praeexogyra hebridica (Forbes)	2	13.8		
Praeexogyra sp.	11			
Cucullaea	1	1.0		
Pteroperna cf. *costulata* (E. Deslongchamps)	6	6.4		
Palaeotaxodonta				
Nucula (Palaeonucula) waltoni (Morris & Lycett)	6	6.4		
Heterodonta				
Protocardia stricklandi (Morris & Lycett)	4	33.7	8	61
Protocardia cf. *buckmanni* (M. & L.)	28			
Protocardia sp.			39	
Cavilucina (Mesomiltha) bellona (d'Orb.)	10	10.6	1	1.3
Astarte sp.			3	3.9
Anisocardia sp.			8	10.4
Corbis sp.			1	1.3
Palaeoheterodonta				
Trigonia (Vaugonia) cf. *moretoni* (Morris & Lycett)	16	27.7	4	11.7
Trigonia pullus J. de C. Sow	10		15	
Anomalodesmata				
Pleuromya cf. *uniformis* (J. Sow)			6	7.8

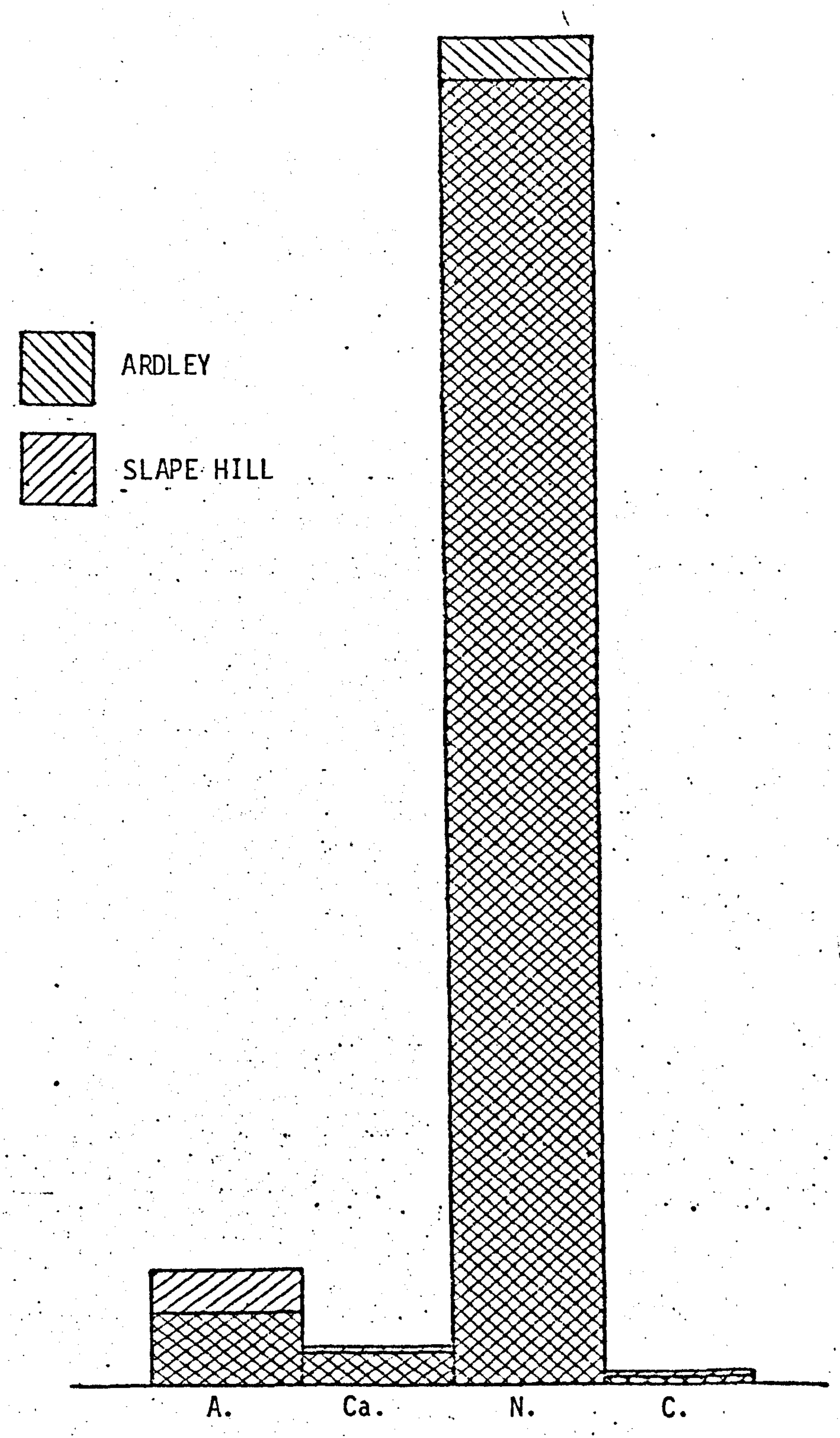
Table 5F - Gastropoda

	Slape Hill		Ardley	
Order Archaeogastropoda	No.	%	No.	%
Amberleya bathonica Cox & Arkell	1	0.2	1	0.3
Neritoma (*N.*) cf. *cooksonii* (E.Desl.)	11	2.0	12	3.0
Chartroniella infrastriata (C. & A.)	24	4.4	3	0.8
Nummocalcar polygonium (d'Archiac)	3	0.5	2	0.5
Metriomphalus sp.	4	0.7	3	0.8
Discohelix cf. *turbiniformis* (Lycett)	1	0.2		
Caenogastropoda				
Globularia sp.	1	0.2	2	0.5
Dicroloma cf. *pupaeformae* (d'Archiac)	2	0.4	6	1.5
Dicroloma laevigatum (M. & L.)	4	0.7	1	0.3
Procerithium (*Rhabdocolpus*) *pulchrum* (Lycett)	4	0.7		
Procerithium (*Cosmocerithium*) *betulae* (d'Orb.)	1	0.2	1	0.3
Naricopsina subcaniculata (M. & L.)	1	0.2		
Pseudomelania sp.	2	0.4		
"Nerineidae" (see Chapter 2)				
Aphanoptyxis cf. *langrunensis* (d'Orb)			28	7.1
Eunerinea arduennensis (Buvignier)	236	43.1	36	9.1
Nerinella cf. *acicula* (d'Archiac)	249	45.4	297	75.4
Ceritella sp.	1	0.2		
Cephalaspidea				
Cylindrites caniculatus (Lycett)	1	0.2		
Cylindrites cf. *altus* (C. & A.)			2	0.5
Goniocylindrites brevis (M. & L.)	2	0.4		



	Slape Hill	Ardley
P. - Pteriomorphia	21.2%	2.6%
Pt.- Palaeotaxodonta	6.4%	0.0%
H. - Heterodonta	44.3%	77.9%
Ph.- Palaeoheterodonta	27.7%	11.7%
A. - Anomalodesmata	0.0%	7.8%

Fig. 5.20. The distribution of Bivalve sub-classes in the L. Ardley Bed.



	Slape Hill	Ardley
A. - Archaeogastropoda	8.0%	5.4%
Ca.- Caenogastropoda	2.8%	2.6%
N. - Nerineacea	88.7%	91.6%
C. - Cephalaspidea	0.6%	0.5%

Fig. 5.21. The distribution of Gastropod orders in the Lower Ardley Bed.

Table 5G - Mode of Life - Bivalves

		Superfamily	Genus	Slape Hill	Ardley
Infauna	Active burrowers	Cardiacea	*Protocardia*	68.0	88.3
		Trigonacea	*Trigonia*		
		Nuculacea	*Nucula*		
		Lucinacea	*Corbis*		
		Crassatellacea	*Astarte*		
		Articacea	*Anisocardia*		
	Inactive burrowers	Pleuromyacea	*Pleuromya*	10.6	9.1
		Lucinacea	*Cavilucina*		
Epifauna	Sessile	Ostreacea	*Praeexogyra*	21.3	1.3
		Arcacea	*Cucullaea*		
		Pteriacea	*Pteroperna*		
			Gervillia		
	Free swimming	Pectinacea	*Entolium*		1.3

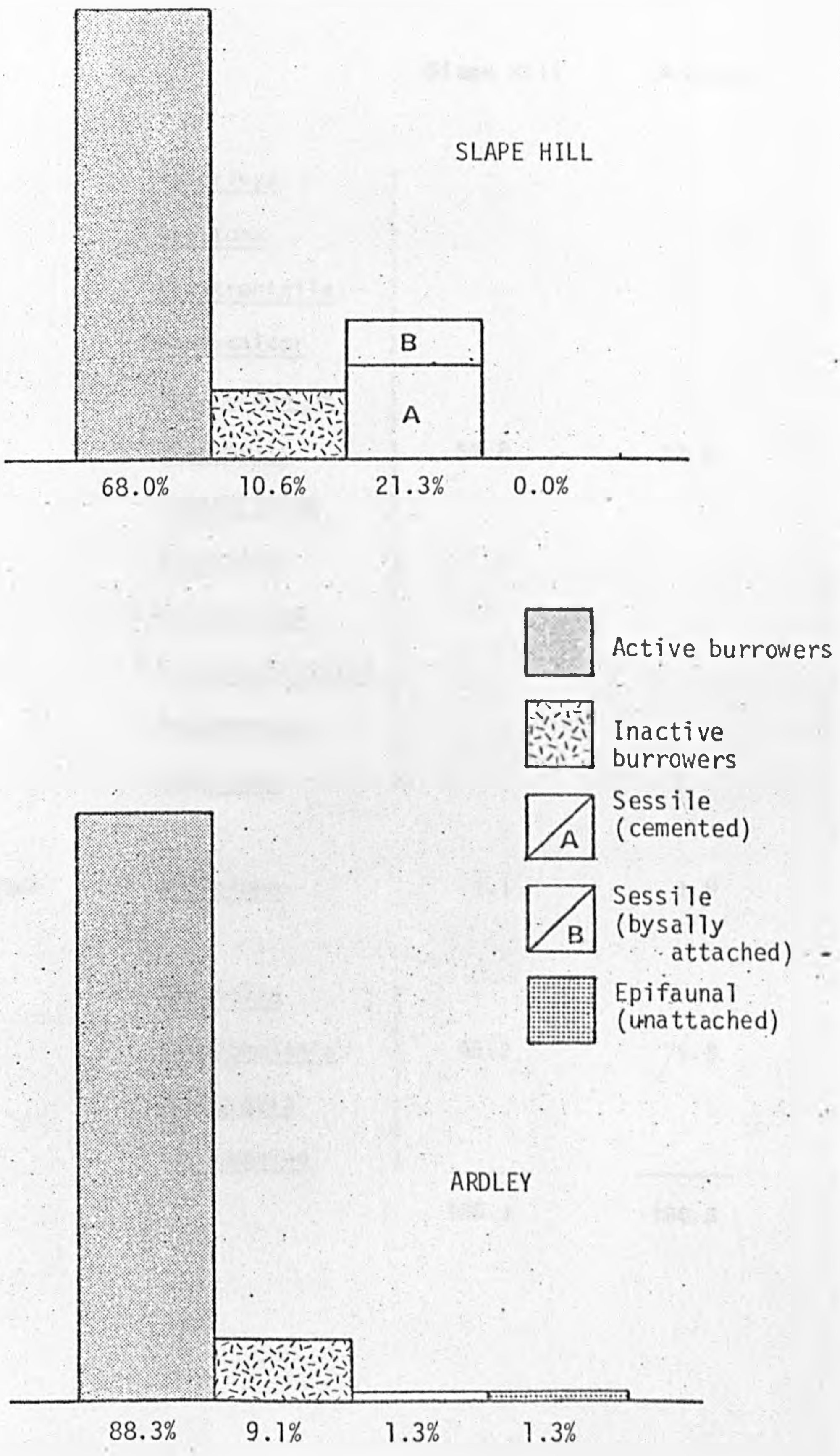


Fig. 5.22. Modes of life in the Bivalve fauna in the Lower Ardley Bed.

Table 5H - Mode of life - Gastropods

		Slape Hill	Ardley
Epifaunal	*Amberleya*	52.8	22.4
	Neritoma		
	Chartroniella		
	Nummocalcar		
	Metriomphalus		
	Discohelix		
	Procerithium		
	Ceritella		
	? *Cylindrites*		
	? *Goniocylindrites*		
	Aphanoptyxis		
	Eunerinea		
Shallow Infaunal	*Dicroloma*	1.1	1.8
Infaunal	*Nerinella*	46.2	75.8
	Pseudomelania		
	Globularia		
	Naricopsina		
		100.1	100.0

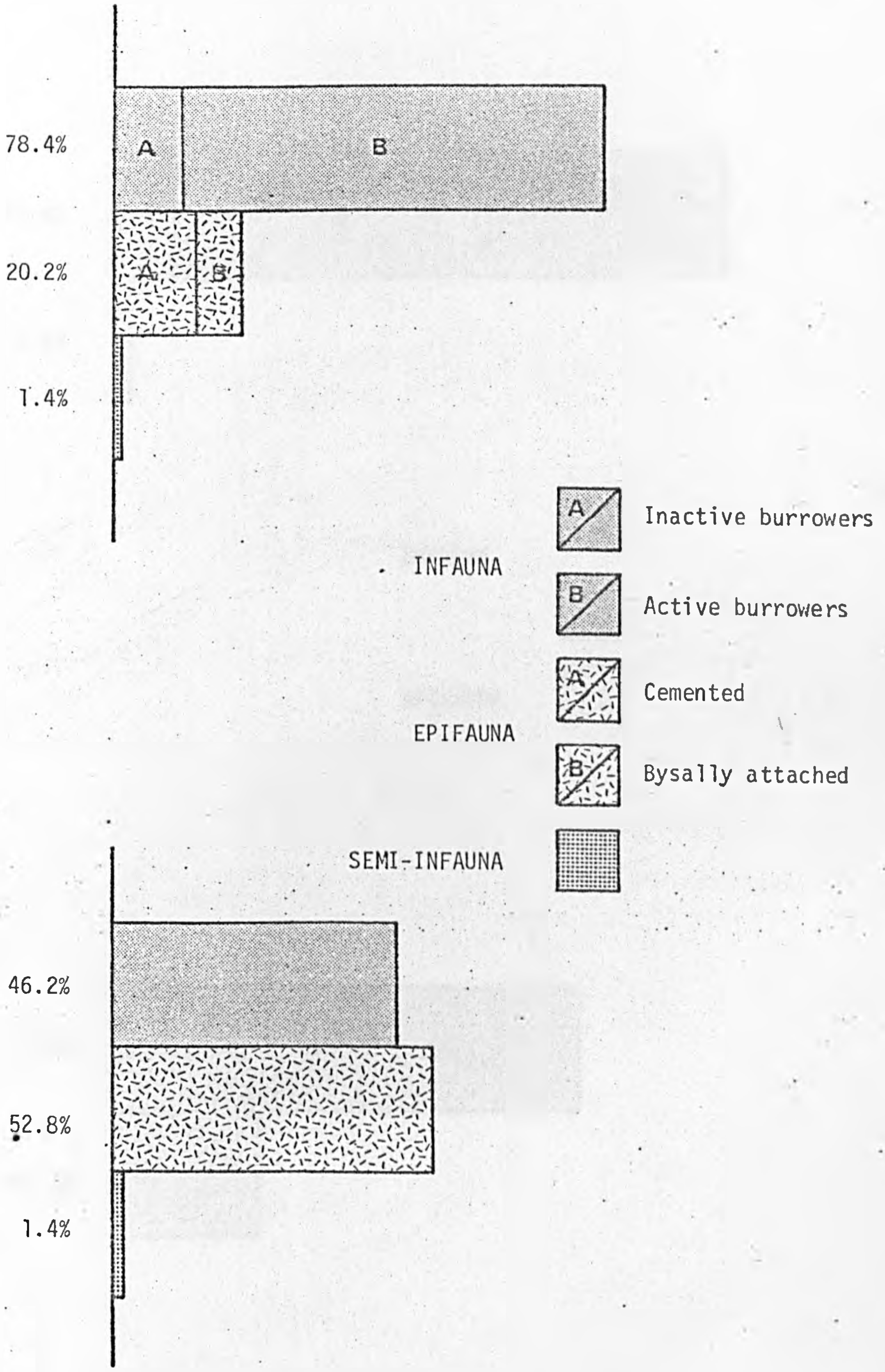


Fig. 5.23. Epifaunal-Infaunal relationships in the Slape Hill fauna.

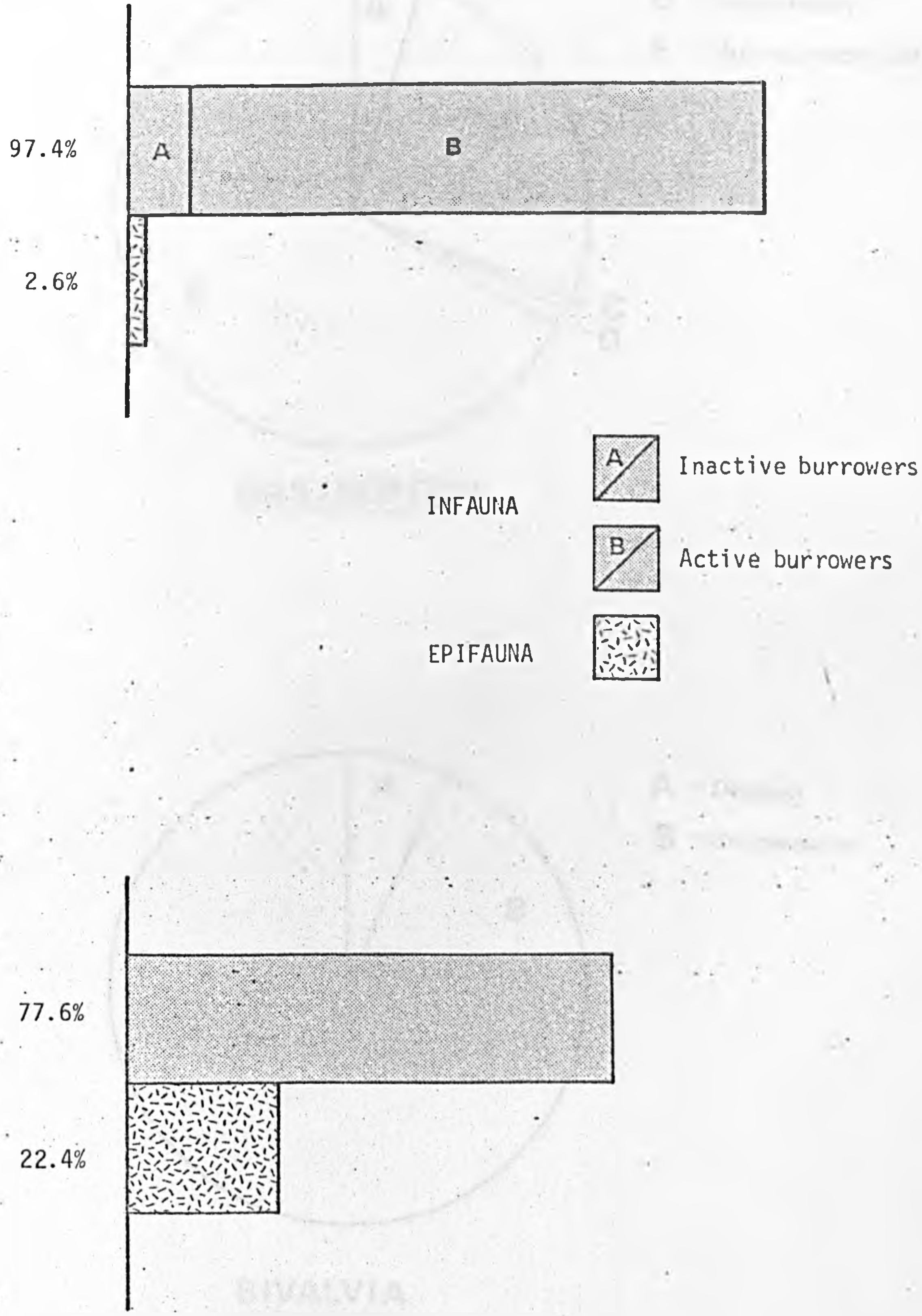
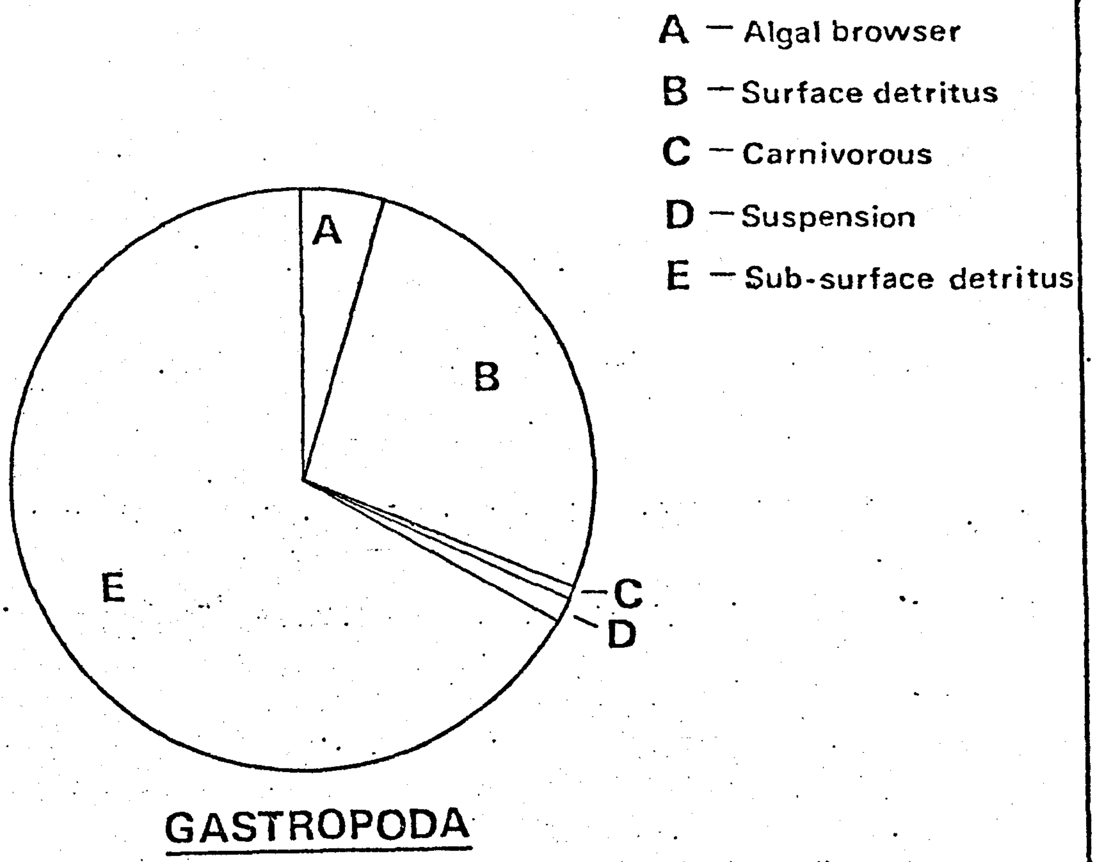


Fig. 5.24. Epifaunal-Infaunal relationships in the Ardley fauna.



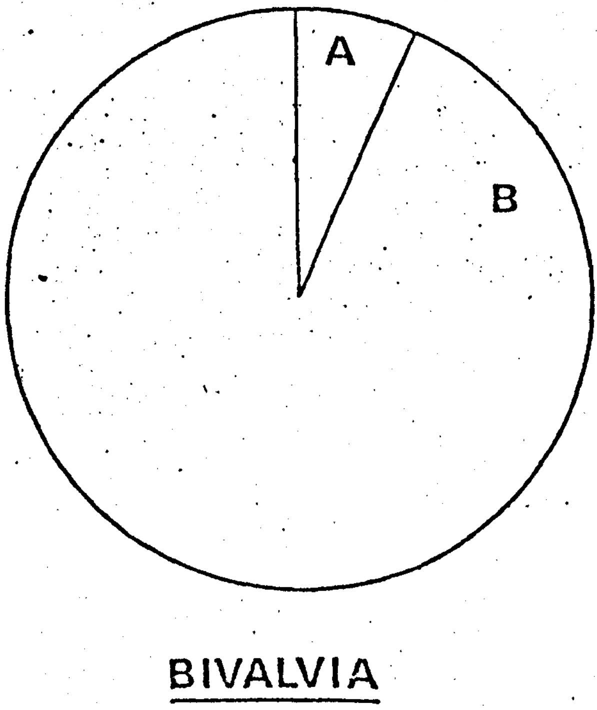
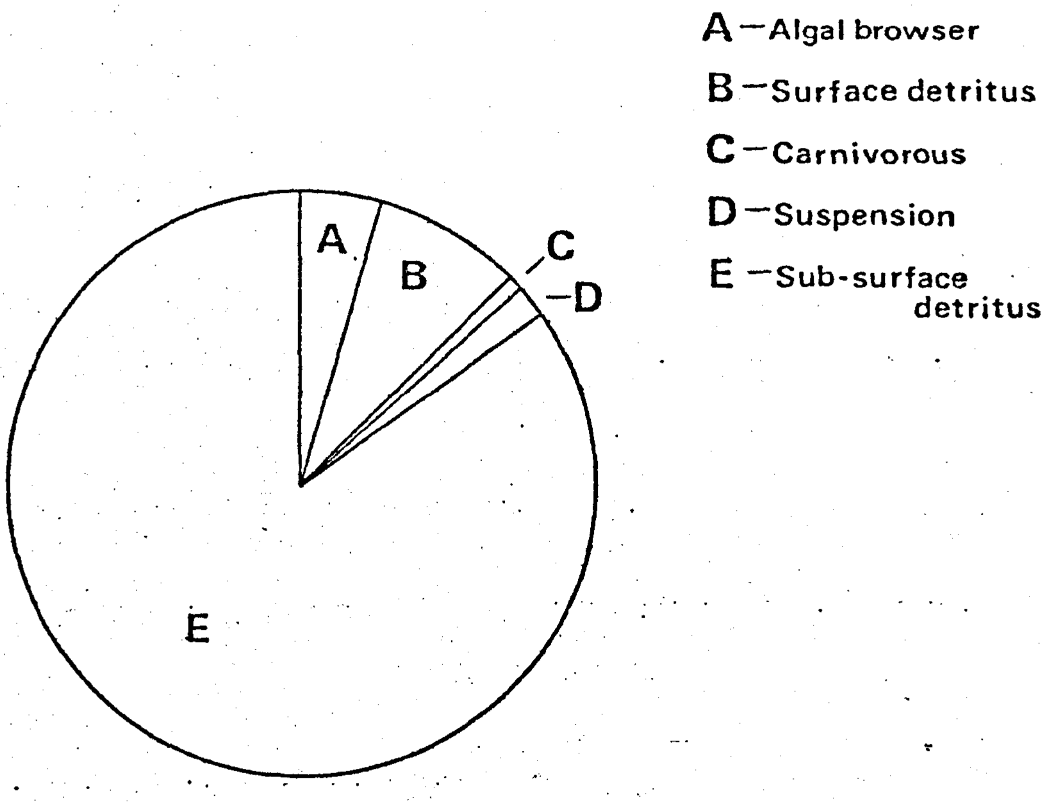
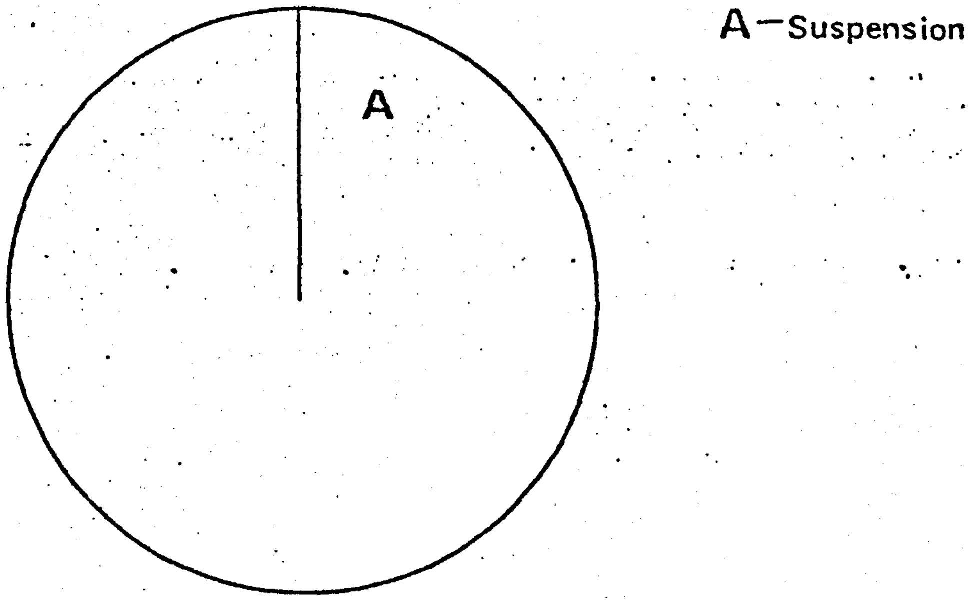


Fig. 5.25. Feeding habits of the Slape Hill fauna from the L. Ardley Bed.



GASTROPODA



BIVALVIA

Fig. 5.26. Feeding habits of the Ardley fauna from the Lower Ardley Bed.

The fossil faunas in both cases probably represent an assemblage very similar to that of life. Bioturbation is extensive throughout the beds but large scale transportation has probably not occurred. The evidence for minimal transportation can be summarised as follows:

1) Most Bivalves, especially Protocardia spp. are articulated. Disarticulated valves where present are generally complete and unworn.

2) Flume based orientation studies of high spired gastropods (e.g. Turritella) have shown that under unidirectional flow regimes of quite small velocities, a preferred orientation is easily obtained (Brenchley & Newall 1970). However the high spired Nerineids occurring at Slape Hill and Ardley show no evidence of such current orientation.

3) The organisms present show considerable size variation.

4) The Nerineid gastropods show few signs of damage and transport. They frequently occur with a sparry calcite infill probably due to preservation with the viscera still intact, (see previously). Transport at the sediment/water interface would mean a) the viscera would decay or be scavenged, and b) the spire would then be filled with sediment, broken and/or abraded.

5) The fauna is predominantly an infauna. Transportation by erosive agencies powerful enough to exhume an infaunal assemblage would be reflected in the lithology. The lithology shows a uniform and gradual change with no evidence of erosion.

6) The fossil assemblages are ecologically viable.

The more important similarities between Slape Hill and Ardley are as follows:

1) The proportion of bivalves to gastropods is almost identical in the two beds.

~~2) The proportion of infaunal to epifaunal bivalves is almost the same~~.

2) The bivalves are dominated by active burrowing forms belonging to the subclass Heterodonta.

3) Both the epifaunal and infaunal gastropods are dominated by the Nerineidae.

Eunerinea arduennensis and *Nerinella* cf. *acicula* are extremely abundant at both localities. If the faunal assemblages are ecologically viable, interspecific competition between these two gastropod species must have been minimal, possibly one (*Nerinella*) feeding on sub-surface detritus, the other (*Eunerinea*) feeding on surface detritus (see previously). Gastropods representing the order Archaeogastropoda are all epifaunal and of the six genera present, five are common to Slape Hill and Ardley. Of the five Caenogastropod genera found, one is epifaunal, one is shallow infaunal and the rest are probably deeper infaunal. The epifaunal form *Procerithium* (*Rhabdocoplus*) *pulcrum* and the two infaunal forms *Pseudomelania* sp. and *Naricopsina subcaniculata* are only found at Slape Hill. The remaining forms, two species of *Dicroloma* (shallow infaunal) and *Globularia* sp. (infaunal) are present in both beds. The Cephalapsidea are poorly represented by *Cylindrites caniculatus* in both beds and *Goniocylindrites brevis* only at Slape Hill.

In the distribution of the bivalves, as with the gastropods, Slape Hill contains a greater proportion of epifaunal forms than Ardley. These are mostly represented by *Praeexogyra* sp. and *Pteroperna costulata*. *Gervillella* and *Entolium* are the only epifaunal bivalves occurring at Ardley. The epifaunal bivalves consist of byssally attached forms (*Pteroperna*, *Gervillella* and *Cucullaea*), cemented forms (*Praeexogyra*) and a free-swimming Pectenid (*Entolium*). Their presence above the substrate suggests the hydrodynamic conditions were not excessively turbulent. *Protocardia* and *Trigonia* dominate the infaunal bivalves of both beds.

Feeding Relationships

In adapting Turpaeva's work (1957) for use with western terminology Walker (1972) suggests that marine bethonic fauna can be divided into four trophic groups:

1) High-level suspension feeders.
2) Low-level suspension feeders.
3) Sediment surface feeders.
4) Animals feeding with the sediment.

Most of the fauna found at Slape Hill and Ardley can be divided into these trophic groups.

High-level suspension: Possibly byssally attached epifauna e.g. *Pteroperna*.

Low-level suspension: Oysters, most shallow burrowing suspension feeding bivalves.

Sediment surface feeders: Epifaunal gastropods, some detritus feeding bivalves, Eunerinea and Aphanoptyxis.

Animals feeding within the sediment: Infaunal gastropods, some bivalves.

It is interesting to note that the four major ecological groups of fossils at Slape Hill and Ardley, i.e. epifaunal bivalves and gastropods and infaunal bivalves and gastropods, fall into these four trophic groups. This reflects the maximum utilisation of all ecological niches to minimise interspecific competition.

According to Turpaeva (1957) the trophic relationships amongst benthonic organisms show the following characteristic features:

1) A community is usually dominated by one trophic group.

2) If the most dominant species (in terms of biomass) in the community belongs to one particular trophic group, the next most dominant species belongs to a different group. Often the third most dominant species belongs to a third group.

3) Among the various species of the community which belong to a given trophic group, a single species commonly dominates the group in terms of biomass.

4) Thus the most dominant species in the benthic community use the available food resources more fully than if they feed at a single level and feeding competition is minimised.

Turpaeva's work was based upon relative abundances in terms of biomass which is not directly applicable to fossil faunas. However some indication may be gained by looking at the relative abundances of the fossil species. A major problem is the unavailability of soft-bodied organisms in the fossil fauna because of their non-preservability. Walker (*op. cit.*) suggested the use of burrows in such analysis but the lack of well defined trace fossils (only a ubiquitous bioturbation) negated the inclusion of soft bodied benthos in this study. The most abundant species and their possible trophic groupings are listed below:

Slape Hill

	Fauna	(Nos. of individuals)	Trophic group
1.	*Nerinella* cf. *acicula*	(249)	Detritus within sediment
2.	*Eunerinea arduennensis*	(236)	Sediment surface feeder - ? detritus
3.	*Protocardia* cf. *buckmani*	(28)	Low-level suspension feeder
4.	*Chartroniella infrastriata*	(24)	Sediment surface feeder - ? algal browser/scavenger

Ardley

	Fauna	(Nos. of individuals)	Trophic group
1.	*Nerinella* cf. *acicula*	(297)	Detritus within sediment
2.	(*Eunerinea arduennensis*	(36)	Sediment surface feeder -
	(*Aphanoptyxis* sp.	(28)	? detritus
3.	*Protocardia* sp.	(39)	Low-level suspension feeder
4.	*Neritoma* (*N.*) *cooksonii*	(12)	Sediment surface feeder - ? algal browser/scavenger

The sediment surface would provide a wide variety of food types and ecological niches. Quite possibly these were exploited by small numbers of the various vagile epifaunal genera (such as Eunerinea, Aphanoptyxis, Chartroniella and Neritoma) without producing excessive interspecific competition.

Very few identifiable faecal pellets have been found in the beds but this may be due to several factors, viz: 1) the faecal pellets being largely composed of organic matter. 2) The pellets were probably a nutrient supply for other organisms especially the interstital fauna. 3) Diagenetic processes may have obliterated any definite pelloidal shape. 4) Most of the intraclasts are micritic with no internal structure and are therefore difficult to distinguish from pellets.

Lithology

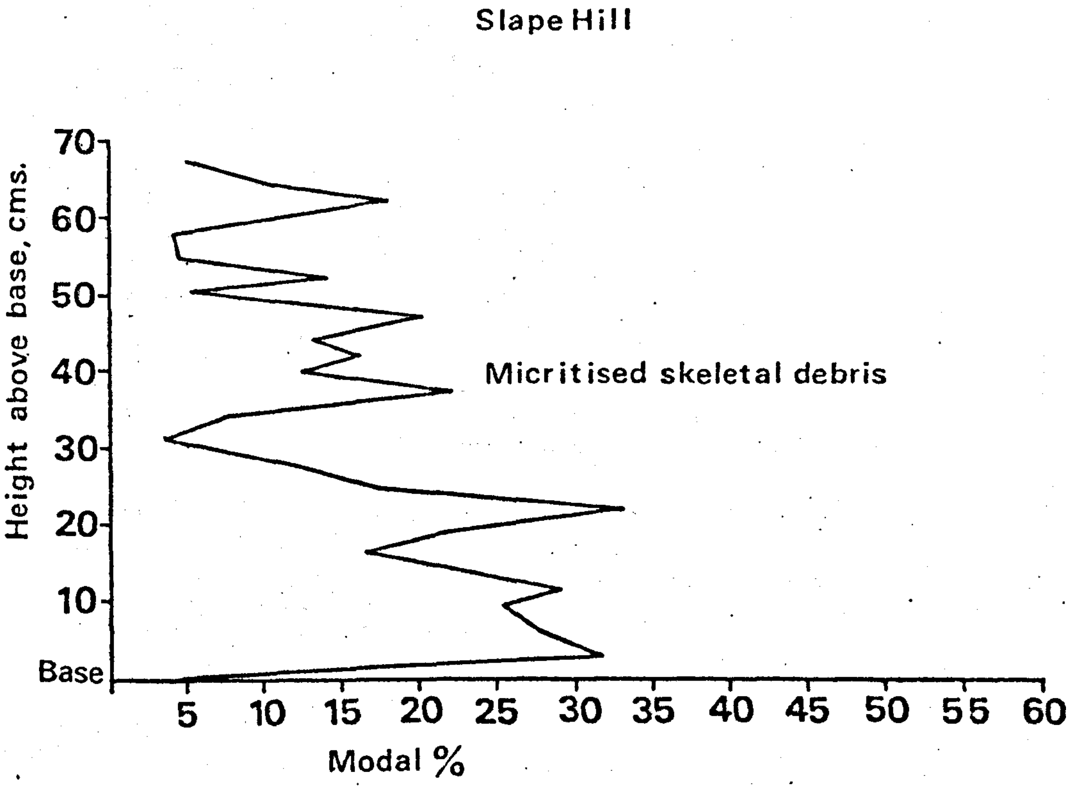
Large specimens of both beds were taken from the respective quarries. Vertical cores were taken at right angles to the bedding, a one inch core from the Slape Hill specimen and, because of the friable nature of the Roach, a three inch core from the Ardley specimen. The core from Ardley was impregnated with Epoxy resin several times to facilitate sectioning. Twenty-five thin sections, between 1 and 3 cm. apart were taken from the Slape Hill core and twenty-two sections from the Ardley core. In order to determine the vertical variation in sedimentary composition in the two beds, modal analyses (based on 800 points per section) were made from all thin sections. Although the use of 500 points per section has been considered sufficient in other modal analyses of carbonate sediments, both modern and fossil (Purdy, 1963a; Wilson, 1965, 1968), it was felt that 800 points per slide would yield more accurate results, especially in the coarser fractions (see also Chayes, 1956). Particle nomenclature was based on Bathurst (1971) and Wilson (1967).

Grain size analyses were made on selected thin sections from both beds. The thin sections were projected onto a screen at a known magnification and the long axes of grains were measured. Approximately 250 measurements were taken of both the detrital quartz grains (not those as nuclei of intraclasts) and intraclasts for each thin section. It is obvious that these measurements represent only the two dimensional sizes of the various clasts. Friedman (1958) has suggested how thin section data can be converted to equivalent sieve sizes, however, as the grain sizes were used on a comparative basis within the bed, no conversion was attempted.

Intraclasts, the most abundant allochem at both localities, are mainly composed of microcrystalline calcium carbonate and devoid of any internal structure. Consequently, a meaningful distinction bewteen pellets and regularly shaped intraclasts proved impossible in these modal analyses (Wilson, 1965 + see above). Oöids are rare in these sediments; no true Oöids are found and superficial oöids are uncommon.

Vertical variation in composition

The variation in composition with height for the two beds is shown in Figs. 5:27 - 5:31. The change in lithologies at the two localities



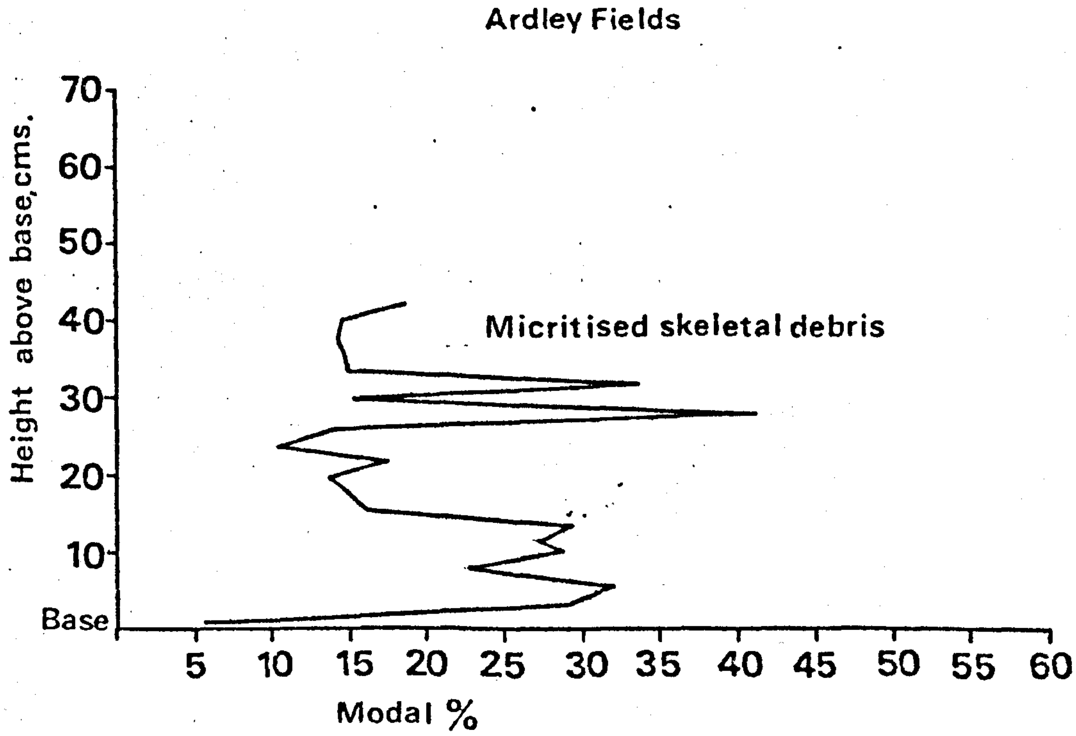


Fig. 5.27. Vertical variation in clast composition:
Basal Ardley Bed; Slape Hill and Ardley Fields.

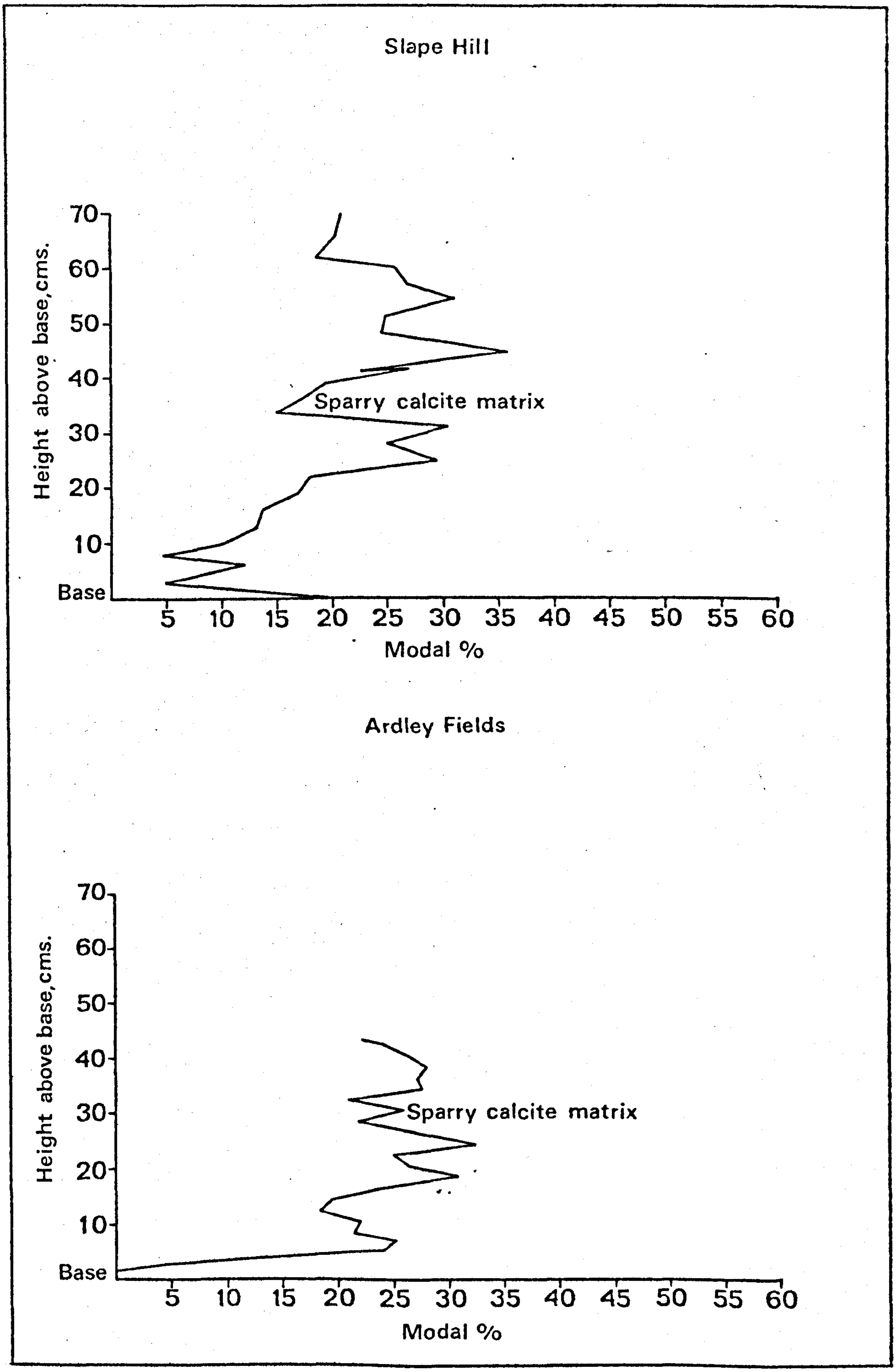
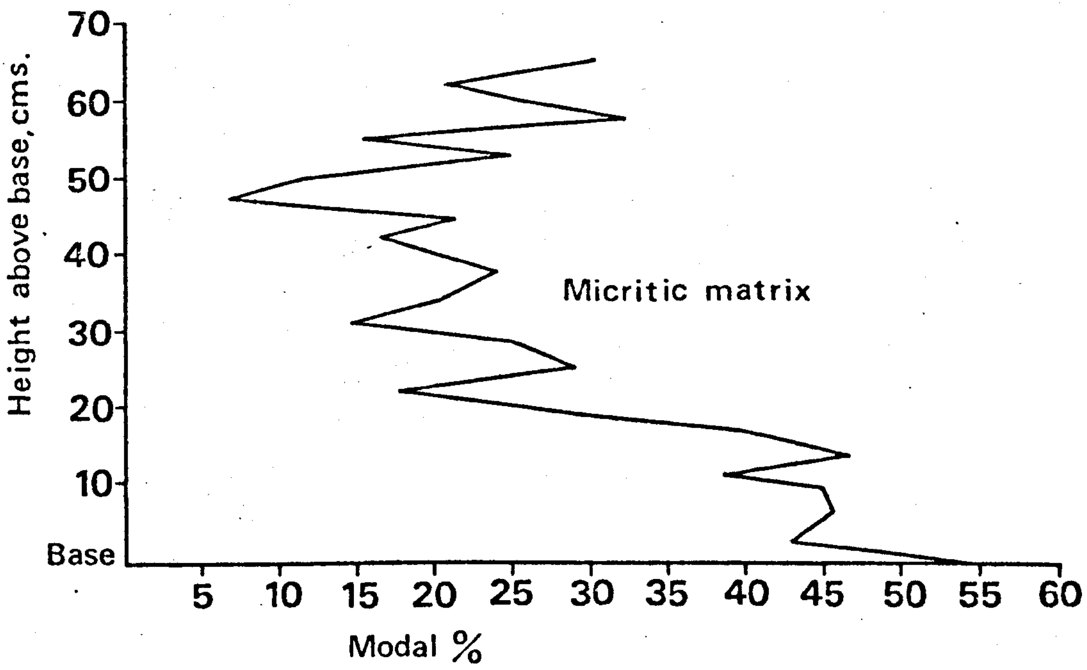


Fig. 5.28. Vertical variation in clast composition: Basal Ardley Bed; Slape Hill and Ardley Fields.

Slape Hill



Ardley Fields

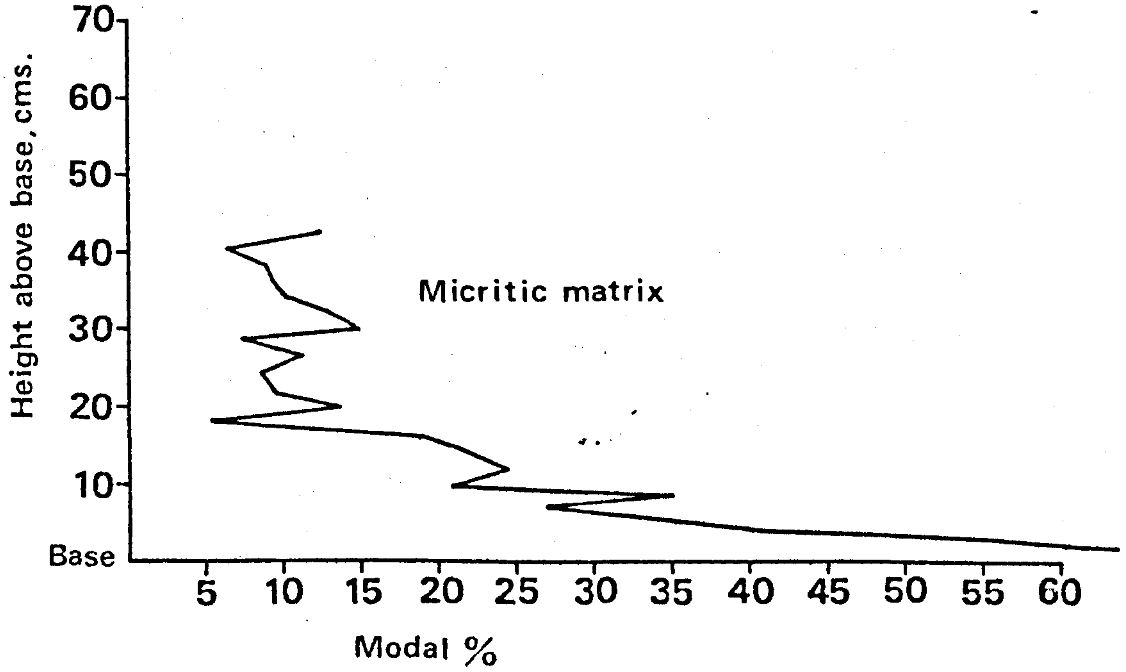
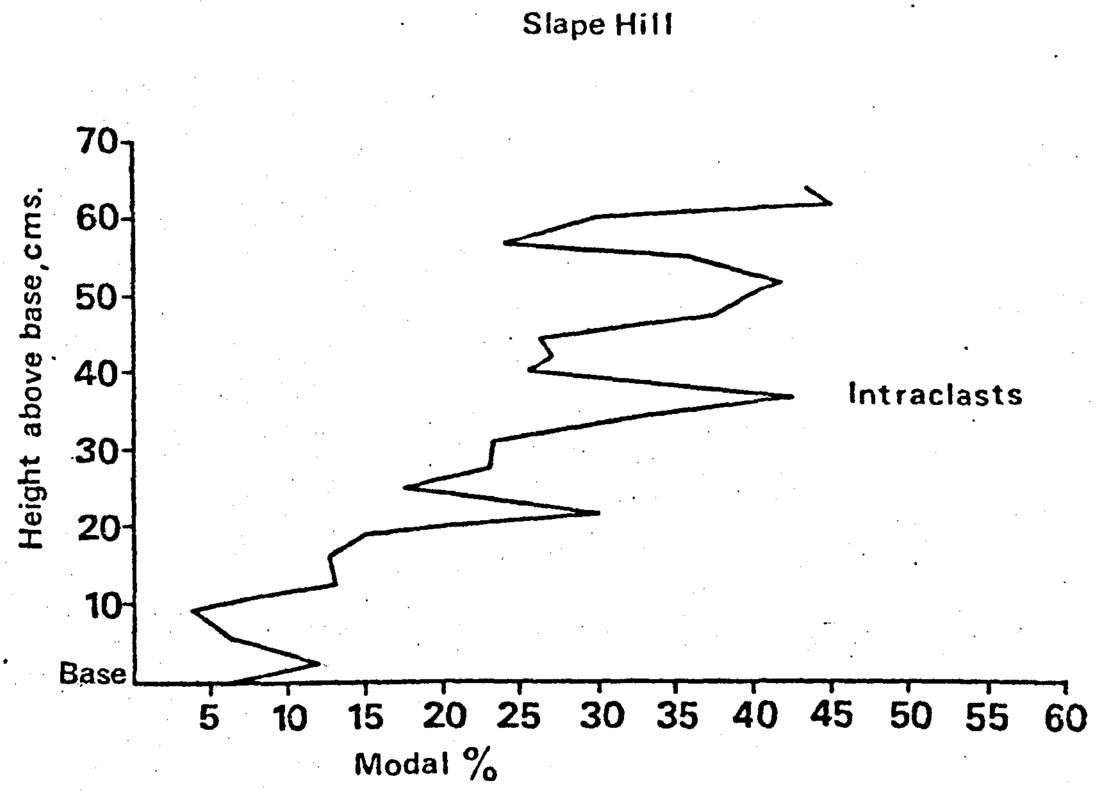


Fig. 5.29. Vertical variation in clast composition: Basal Ardley Bed; Slape Hill and Ardley Fields.



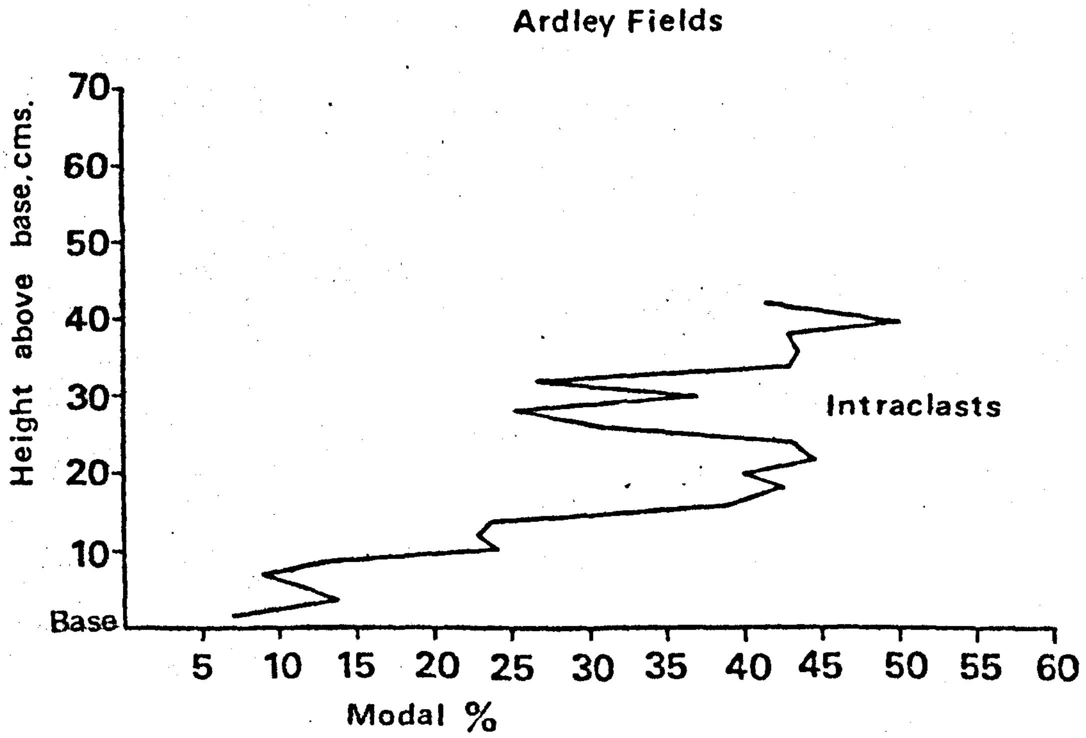


Fig. 5.30. Vertical variation in clast composition: Basal Ardley Bed; Slape Hill and Ardley Fields.

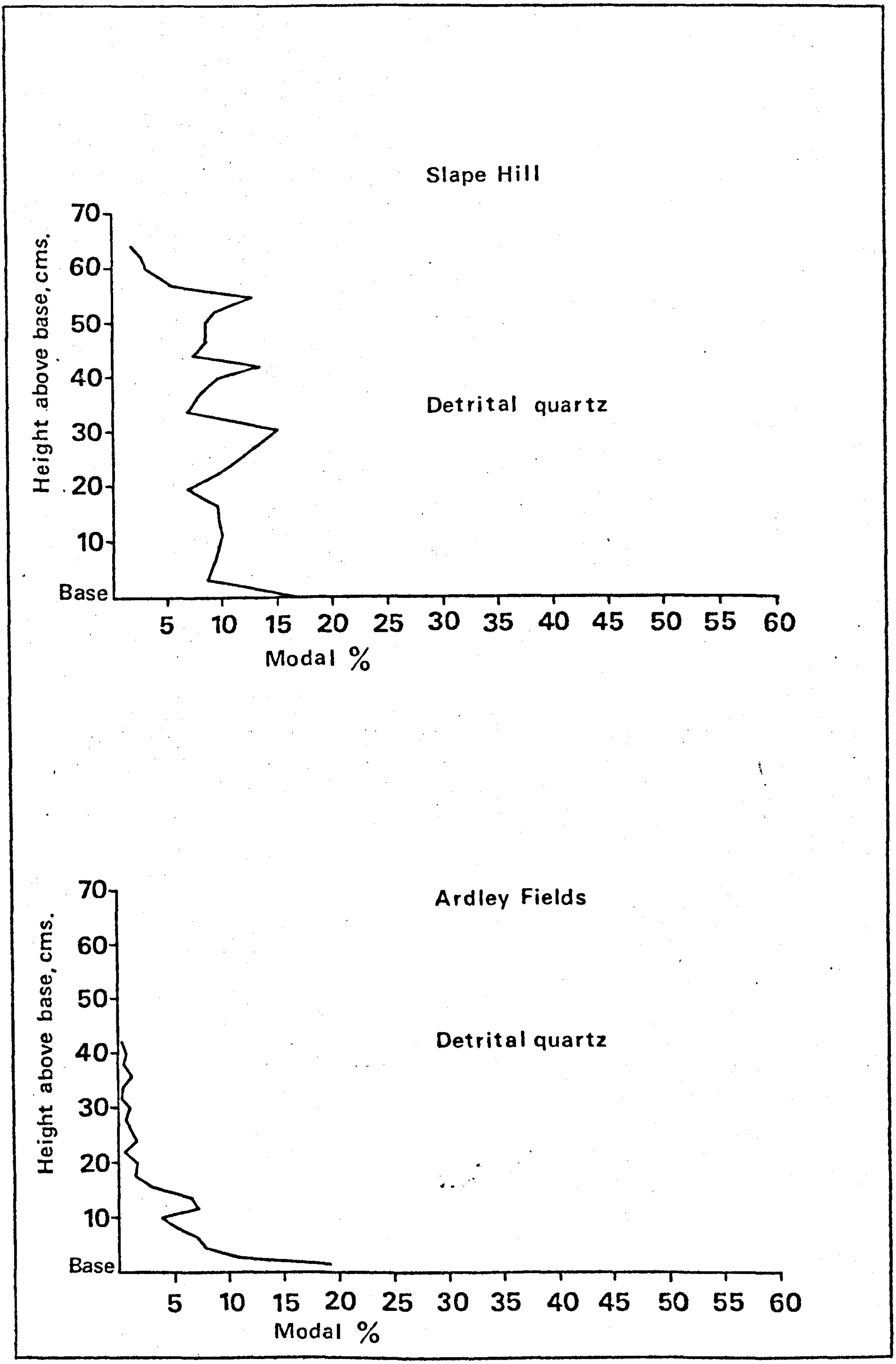


Fig. 5.31. Vertical variation in clast composition: Basal Ardley Bed; Slape Hill and Ardley Fields.

is remarkably similar. The major similarities passing upwards through the beds may be summarised as follows:

a) Decrease in percentage of quartz.

b) Decrease in percentage of micritic matrix.

c) Increase in percentage of intraclasts.

d) Increase in percentage of sparry calcite matrix.

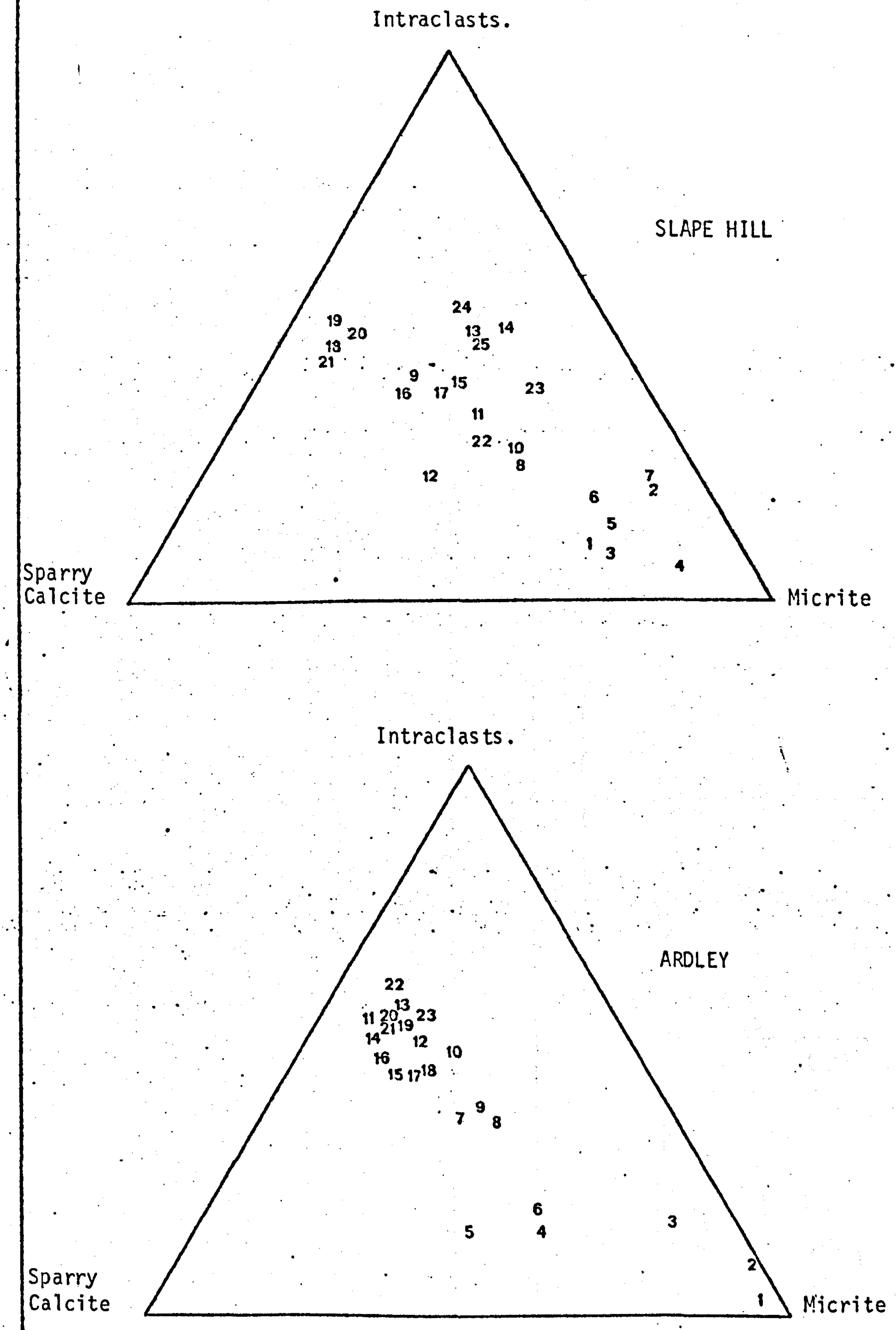
The graph showing the variation of micritised skeletal debris at Ardley shows a pronounced second peak between 0.25-0.35 m. above the base. This is a second fossiliferous horizon above the Roach Bed (the first peak in the graph) which is not readily apparent in the field, the fossils not being decalcified.

The silty clay base proved difficult to section but the decrease in clay mineral content as one passes up into the carbonate rich horizons is comparable with the decrease in quartz content.

The triangular component diagrams of Fig. 5:32 show very similar trends in the vertical variation of lithology between Slape Hill and Ardley.

Vertical variation in grain size

The grain size analyses (Figs. 5:33 and 5:34) show a gradual increase in grain size with height at both localities. This is most promounced at Slape Hill but nevertheless can still be recognised at Ardley. The size frequency distribution of quartz show a change in skewdness from a positive skew at the base to a more symmetrical distribution (or negative skew at Ardley) at the top of the beds. The



Numbers correspond with those in Fig. 5.27.

Fig. 5.32. Triangular component diagrams for the Lower Ardley Bed.

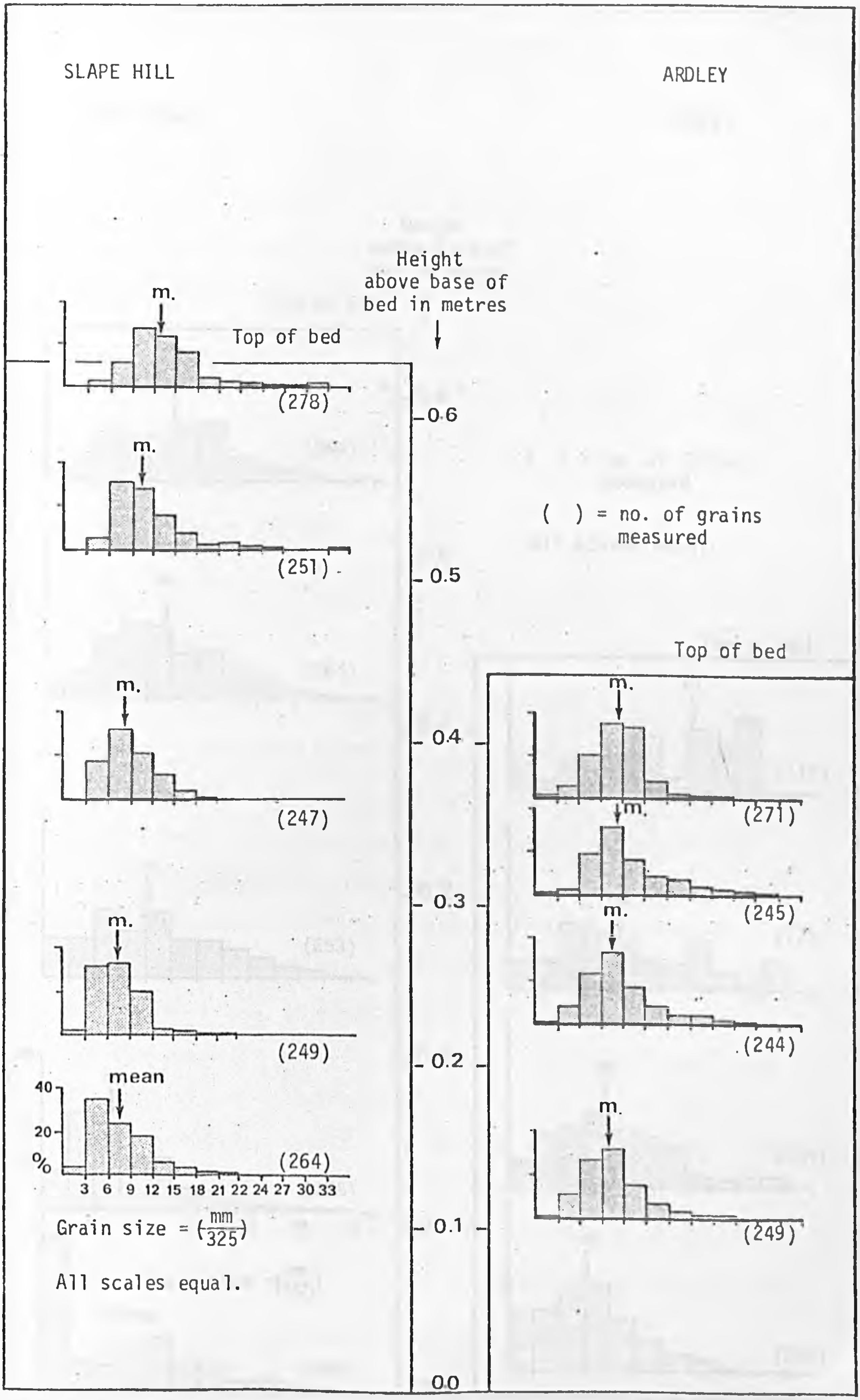


Fig. 5.33. Size-Frequency analysis of intraclasts in the L. (= Basal) Ardley bed

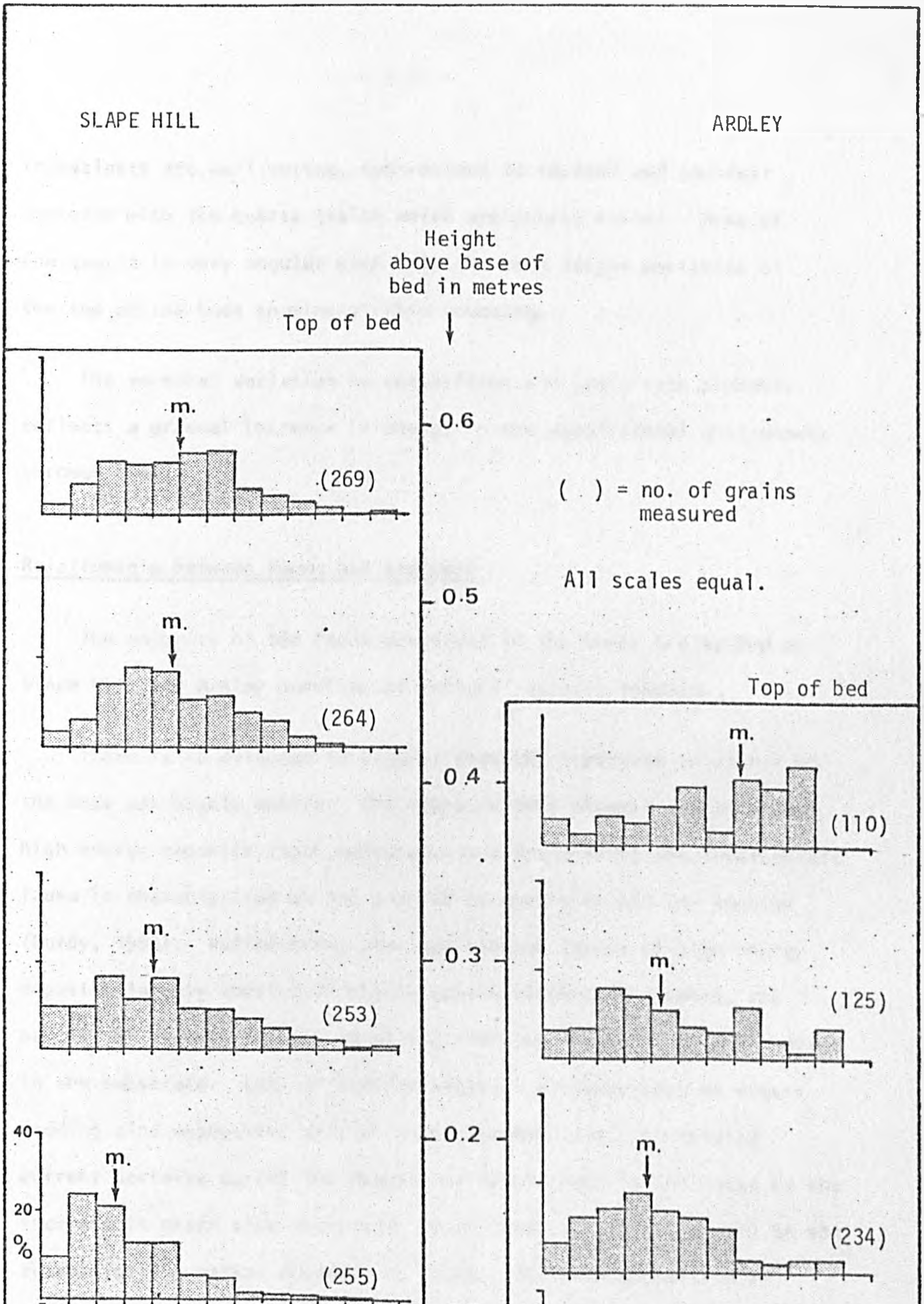


Fig. 5.34. Size-Frequency analysis of quartz in the L. (=Basal) Ardley bed.

intraclasts are well sorted, sub-rounded to rounded and contrast markedly with the quartz grains which are poorly sorted. Most of the quartz is very angular with only the rare larger particles at the top of the beds showing visible rounding.

The vertical variation in composition and grain size probably reflects a gradual increase in energy in the depositional environment through time.

Relationship between fauna and sediment

The majority of the fauna preserved in the Lower Ardley Bed at Slape Hill and Ardley consists of infaunal deposit feeders.

There is no evidence to suggest that the substrate in either of the beds was highly mobile. The fauna is very diverse and in modern high energy deposits (both calcareous and arenaceous) the invertebrate fauna is characterised by low population densities and few species (Purdy, 1963). Furthermore, the invertebrate faunas of high energy deposits largely consist of highly mobile suspension feeders, the paucity of deposit feeders resulting from the dearth of organic matter in the substrate. Lack of sedimentological evidence such as cross-bedding also emphasises minimal substrate mobility. Increasing current activity during the deposition of the beds is indicated by the increase in grain size vertically up the beds and this may well be the reason for the marked decrease in fauna. The high proportion of micrite at the base of the beds would have had a binding effect on the substrate as well as providing the organic matter for the deposit feeders (i.e. the infaunal gastropods and some deposit feeding bivalves such as Nucula). Presumably, the suspension feeding bivalves found enough organic matter in the water above the sediment. The decrease in micritic matrix and increase in both grain size and proportion of intraclasts indicate increasing current activity with the substrate becoming a) more mobile and b) providing less organic matter, both within the sediment and in the waters above. Hence the absence of fauna, probably due to migration to more favourable substrates.

The detailed comparison between these beds leaves little doubt that they are laterally equivalent, being formed under a single sedimentary episode under almost identical conditions and with closely similar faunas. These conclusions are important in that lithological and related faunal changes in the benthos can be demonstrated to be both widespread and useful in correlation.

An almost identical relationship between fauna and sediment has been outlined by Barker and Torrens (1971) where the gradual transition from the Lower Estuarine Series into the Lower Lincolnshire Limestone is documented and is closely comparable with the White Limestone example outlined above. However, in this Bajocian example it was possible to distinguish between faecal pellets and intraclasts. The fauna is similarly dominated by infaunal deposit feeding gastropods, (Bactroptyxis cotteswoldiae (Lycett), and subordinate Nerinella cf. subcingenda (Hudleston)), with Pholadomya fidicula J. Sowerby representing the infaunal suspension feeding bivalves. Gervillella sp. and

Trigonia sp. are again present. This Bajocian fauna occurs in the same lithological setting as the Slape Hill and Ardley faunas. The two peaks in the faecal pellet modal analysis correspond with the maximum abundance of B. cotteswoldiae. The absence of fauna in the higher parts of the bed is again probably due to higher energy conditions. Because of the transitional nature of the junction of the two formations, Barker and Torrens (op. cit., p. 54) concluded that "the best basis for the recognition of the base of the Lincolnshire Limestone here is the incoming of Nerineid gastropods".

The occurrence of these two faunas, of differing ages but within the same lithological setting is, in the opinion of the present author, not only controlled by the substrate conditions but also by a change in salinity from reduced salinities in the clays below to fully marine conditions in the limestones above in both cases. The presence of Melanioptyxis altararis in the Hampen Marly Beds at Danes Hill (see Chapter 1) may also be partially controlled by salinity. In those instances (such as those given above) where clays containing a fauna suggestive of reduced salinities (e.g. Praeexogyra, Eomiodon, Corbula and Protocardia) pass transitionally into limestones containing a marine fauna (corals, Trigonia etc.) the change in lithologies may be a reflection of the increase in salinity. Furthermore the first abundant invertebrate group found in the limestone is the Nerineacea which suggest that they were rapid colonisers of new carbonate substrates as soon as the salinities became tolerable for them, which was possibly before other invertebrate groups.

The ecological diversification of the Nerineacea.

The Bathonian stage was an important developmental period in the geological history of the Nerineid gastropods. The expansion and diversification of Nerineid gastropods during the Bathonian is reflected in both the numerical abundance and in the multigeneric composition of Nerineid bearing horizons found in the White Limestone.

During the Lias the establishment of the Nerineid superfamily resulted in two fossil genera, *Nerinella* (3 folds) and *Pseudonerinea* (0 folds), both being high-spired and acicular. Most of our subsequent knowledge of the early expansion of the Nerineids is presently based upon the Bajocian and Bathonian of England and France. British representatives of Bajocian genera descended from the two Liassic genera include; *Bactroptyxis* (5 folds, e.g. *B. cotteswoldiae* and *B. implicata*), *Nailsworthia* (1 fold, e.g. *N. gracilis*), *Aptyxiella* (0 folds, e.g. *A. subconica*) together with the original genus *Nerinella* (e.g. *N. cingenda*). Again these genera are all high-spired and acicular.

The diversification of Bathonian representatives was not merely a continuation of the previous theme of fold elaboration (the basic types had already been established in the Lias/Bajocian). We now find 5 Bathonian genera (*Nerinella*, *Cossmannea*, *Fibuloptyxis*, *Melanoptyxis* and *Eparcyella*) which possess 3 folds but their external morphologies are very different. Heavy ornamentation is found for the first time in the genus *Eparcyella*. More robust shells with broader bases are found in *Fibuloptyxis*, *Melanoptyxis* and *Aphanoptyxis* and two genera (*Endiaplocus* and *Pseudotrochalia* - a genus with 2 folds from the Bathonian of France) are conspicuously umbilicate.

This early generic and morphological evolution represents an ecological diversification of the Nerineids into the expanding carbonate depositional environments of the Middle Jurassic in N.W. Europe. The low-energy, subtidal carbonate sediments found in the White Limestone of England and France provided advantageous substrates for the rapidly evolving Nerineid gastropods. The ability to feed on, and in, fine-grained carbonate muds conferred a unique selective advantage upon them and it is hardly surprising that the gastropod faunas of low energy Mesozoic carbonate sediments are dominated by Nerineids. However, they also expanded into higher-energy carbonate environments to give one of the most distinctive Mesozoic faunal associations, the Tethyan Nerineid - Rudist - Coral association.

This faunal association has been recorded many times (e.g. Peron, 1901; Dietrich, 1925; Levasseur, 1935; Montagne, 1938; Tiedt, 1958; Ronchetti and Mirelli, 1965; Vogel, 1968 and Wieczorek, 1975) and these authors have reasoned that the fauna lived in a high-energy reef, or peri-reefal, environment. Some of these authors, (e.g. Peron, op. cit. and Dietrich, op. cit.), have therefore erroneously inferred that the occurrence in these environments of high-spired acicular Nerineids would not have been possible without the protective, strengthening function of complex internal folds (see previously).

Examination of the Nerineid faunas from Nerineid - Rudist - Coral occurrences reveals that the gastropod assemblages are multigeneric and that the Nerineids exhibit a variety of morphologies with each genus occupying a different ecological niche amongst the many available in such environments. Furthermore, most of the genera are thick-shelled, often umbilicate, robust forms such as *Plesioptygmatis*, *Laevinerinea*, *Acrostylus*, *Adiozoptyxis*, *Trochalia*, *Iteria*, *Itruvia* and *Phaneroptyxis*, all probably capable of an epifaunal mode of life in such high-energy environments. One would therefore expect to find shell damage and epifaunal colonisation (particularly oncolitic coatings and algal-sponge borings) indicating transport and exposure at the sediment-water interface. Such features have been reported several times (Tiedt, *op*. *cit*., Vogel, *op*. *cit*., Janicke, *op*. *cit*., and Wieczorek, *op*. *cit*.).

Acicular species of *Nerinella*, *Bactroptyxis* and *Aptyxiella* also constitute a small proportion of the Nerineid gastropod genera found in the Nerineid - Rudist - Coral association, (Tiedt, *op*. *cit*. and Janicke, *op*. *cit*.), although how the slender *Aptyxiella* (with no internal folding) could survive has somehow escaped comment! If the reported occurrences are correct, their presence must be due to either transportation from quieter environments or an extension of the original infaunal, protected, mode of life seen in the White Limestone species of *Nerinella* and *Bactroptyxis*, into higher-energy carbonate regimes. More research on the detailed palaeoecology of Nerineid - Rudist - Coral associations is clearly needed.

The above palaeobiological interpretations seek to understand Nerineid gastropods as functioning organisms which are associated with and interact with other biota.

Chapter 6

TAPHONOMIC PROCESSES

'Penetrating so many secrets, we cease to believe in the unknowable. But there it sits nevertheless, calmly licking its chops.'

H. L. Mencken, Minority Report (1956).

Post-mortal movement of high-spired gastropods

Apart from sedimentological criteria, orientation studies on fossil collections of high-spired gastropods [redacted] are a means of ascertaining whether significant *post-mortem* transport has occurred.

Flume experiments with dead *Turritella* show that, under experimental conditions, very low current velocities produce a remarkable preferred orientation with the apices of the gastropods upstream. In the experiments of Brenchley and Newall (1970, pp. 185-220), the initial movement of *Turritella* took place at 13 cms./sec. water velocity on a bed of medium sand (mean grain size, 0.4 mm.). The results obtained by Brenchley and Newall (*op. cit.*) are shown in Fig. 6:1. As noted by these authors (*op. cit.*, p. 213) additional buoyancy due to air trapped in the apertural end of the spiral shell of *Turritella* would reduce resistance to current orientation as the apex of the shell would act as a frictional anchor on the substrate.

The direct application of such experimental results to the exhumation and orientation of infaunal high-spired gastropods must be treated with some caution. It is doubtful whether buried gastropods (alive or dead) would contain entrapped air within their spires, thus modifying the weight and buoyancy distribution. The shells would contain either the soft tissue of the animal, sediment or, if the shell were empty, water and presumably would not behave in the same manner as the empty *Turritella* shells used in the flume experiments even under identical water flow and substrate conditions. When alive, the Recent *Turritella communis* is a predominantly sessile, infaunal species.

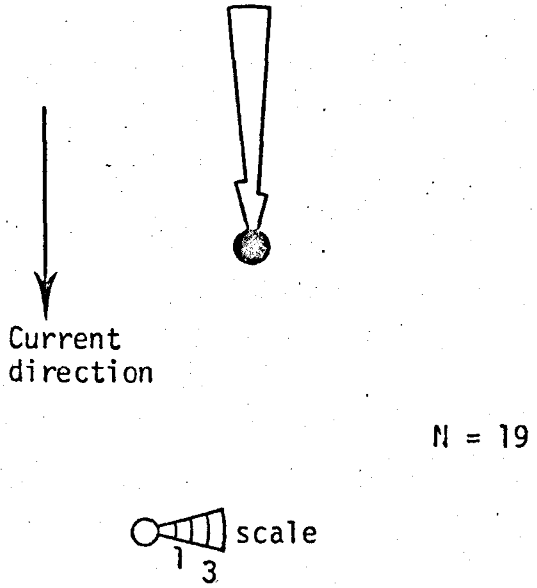
The ciliary suspension feeding mechanism and general ecology have been elucidated by Graham (1938) and Yonge (1946) respectively.

The accurate measurement of elongate objects in solid rock can also present problems and almost invariably one relies upon natural sections of bedding planes. Such sections were available at Eton College Quarry (bed 14, Fig. 1.11) and the results are shown in Fig. 6.1. The Lower *Nerinea* Bed at Snowshill Hill (G.R. SP 131322, bed 4a of Barker and Torrens, in Torrens, 1969, pp. 16-18) is a friable, sandy oolite and the prolific *Aphanoptyxis eulimoides* contained in the bed can thus easily be excavated and their orientation measured, the results being shown in Fig. 6.1. In the case of particularly well-lithified limestones, a useful technique is to cut blocks of the limestone into slices approximately 2.0 cms. thick, parallel to the bedding, and photograph by X-ray radiography. The orientation diagram of *B*. *cotteswoldiae* and *Nerinella* cf. *subcingenda* from the Lower Lincolnshire Limestone (Bajocian, Discites Subzone) at Geddington (G.R. SP 867824; bed 1 of Barker and Torrens, 1971, p. 51) was produced by this method (see Fig. 6.1).

Clearly no preferred orientation of the high-spired Nerineid gastropods exists in either the Eton College or Geddington samples. Together with the associated fine-grained matrix, wide size-range of the shells and lack of major shell damage, these orientation diagrams suggest that post-mortem transport was minimal or nil in these environments and that current velocities and lateral sediment transport were slight. Furthermore, the gastropods were probably

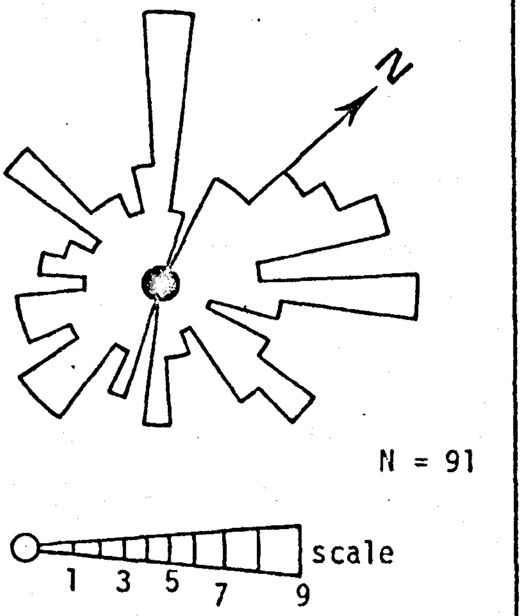
T. communis

Flume experiments of Brenchley & Newall, 1970.



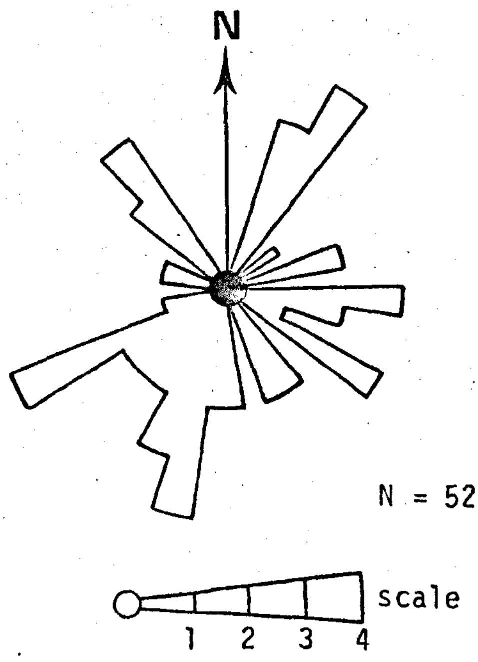
A. cf. *langrunensis* &
N. cf. *pseudocylindrica*

Lower Ardley Beds
Eton College Quarry, Bed 14 (Fig.1.11)



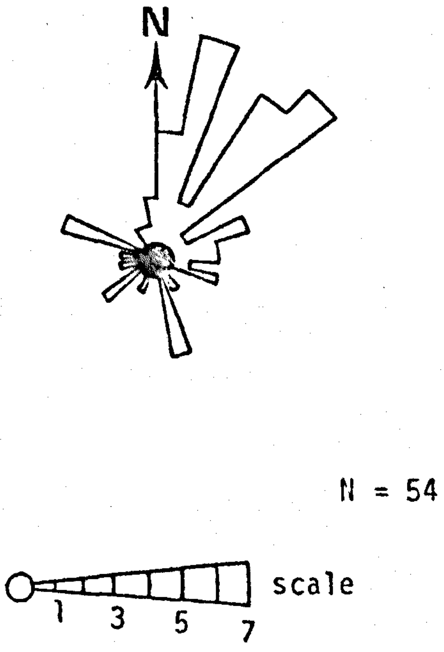
B. cotteswoldiae &
N. cf. *subcingenda*

Lower Lincolnshire Limtestone
Grange Pit, Geddington, Bed 1
(Barker & Torrens, 1971)



A. eulimoides

Sharps Hill Beds
Snowshill Hill, Glos., Bed 4a
(Barker & Torrens, in Torrens, 1969)



10^o Class intervals N = number of specimens Apices plotted buried deep enough in the sediment to avoid any local current scour that did occur. The present author considers that most of the White Limestone Nerineid horizons are low energy deposits and show little evidence of post-mortem transport.

However, in certain horizons evidence of higher energy conditions and more mobile substrates is very obvious. The Nerineids can be at least partially current-orientated as in the cases of A. eulimoides at Snowshill Hill (see Fig. 6.1), Eu. arduennensis in the White Limestone at Slape Hill (bed 3, Fig. 1.5) and B. implicata at Worsham (bed 10, Fig. 1.12). The orientations are never as perfect as in the flume experiments of Brenchley and Newall (op. cit. and see Fig. 6.1), presumably because either the greater weight and less buoyancy of exhumed specimens requires greater current velocities to orientate them perfectly or the current velocities, even in the higher-energy White Limestone depositional environments, were not as great as those used in the flume experiments. Other clear indications of transport include breakage of specimens and breaching of whorl walls, loss of ornamentation, general shell comminution and larger clast size of the matrix.

Mixed horizons, where some of the gastropods have been exhumed (either by current scour or by the bioturbation of other organisms) whilst others have remained buried in the sediment, can also be recognised (for example the Solenopora Bed, Foss Cross Quarry, bed 10, Fig. 1.7). The specimens which remained buried were gastropods which died within the sediment, usually with the viscera contracted into the shell. The subsequent history of these specimens must have depended upon the interaction of several post-depositional processes, the principal ones being;

a) the rate of decay of the soft tissue in the spire,
b) the rate of lithification of the sediment,
c) the grain-size of the sediment,
d) the presence and movement of interstitial waters,
e) the Eh of the interstitial waters,
f) the activity of sub-surface micro-organisms.

Frequently, sediment entered the aperture of the gastropod, was quickly lithified and prevented any further ingress of sediment into the spire, even after the subsequent decay of the soft tissue. The resultant fossil has a 'plugged aperture' with sediment occupying the first half-whorl or so but the spire is composed of cavity-fill calcite (see Fig. 5.16). Since the fossils have never at this stage been exhumed, they

a) show no signs of damage,
b) never have sediment in the spire, and
c) the surface of the shells are not colonised by an epifauna.

In those specimens which were post-mortally exhumed and exposed at the sediment-water interface, the soft tissue quickly decayed and the movement and rolling of the shell together with shell damage soon filled the spire with sediment (noticeably in these cases without the preservation of the duct system). These specimens were also quickly colonised by epifaunal organisms, particularly calcareous algae, as discussed below (see Plate 6.A). Intermediate stages existed where specimens were exhumed and only a small amount of sediment entered the spire before re-burial. Also where lithification was delayed, very soft water-saturated sediment was, in some cases, pushed up the spire of buried gastropods (probably due to compaction) as the soft tissue decayed and the duct system of the digestive gland/gonad was occasionally preserved (see Chapter 5). In the latter case, the sediment in the spire is always a very fine micrite, with very small or no clasts whereas the sediment in the spire of exhumed specimens shows a distinct clast structure comparable with that of the surrounding matrix. These various states of preservation and variations in sedimentary infill are diagrammatically summarised in Fig. 6.2.

If the postulated infaunal mode of life for Bactroptyxis and Nerinella is correct (see Chapter 5) then the inclination of the shell axes in a plane at right angles to the bedding in non-drifted assemblages would perhaps confirm the life-orientation of these infaunal gastropods. Blocks of limestone containing Eu. arduennensis from Foss Cross Quarry (bed 4, Fig. 1.7) were cut into slabs approximately 1 cm. in thickness at right angles to the bedding plane. The sections of the gastropods were traced onto large glass plates which could be positioned and orientated so as to show the inclination of the shell axes. The results are shown in Fig. 6.3.

Not unexpectedly, a substantial majority of the shells are approximately horizontal, a position assumed by most mobile, infaunal gastropod species. Those specimens at other angles were probably post-mortally disturbed and re-orientated by other burrowing infauna.

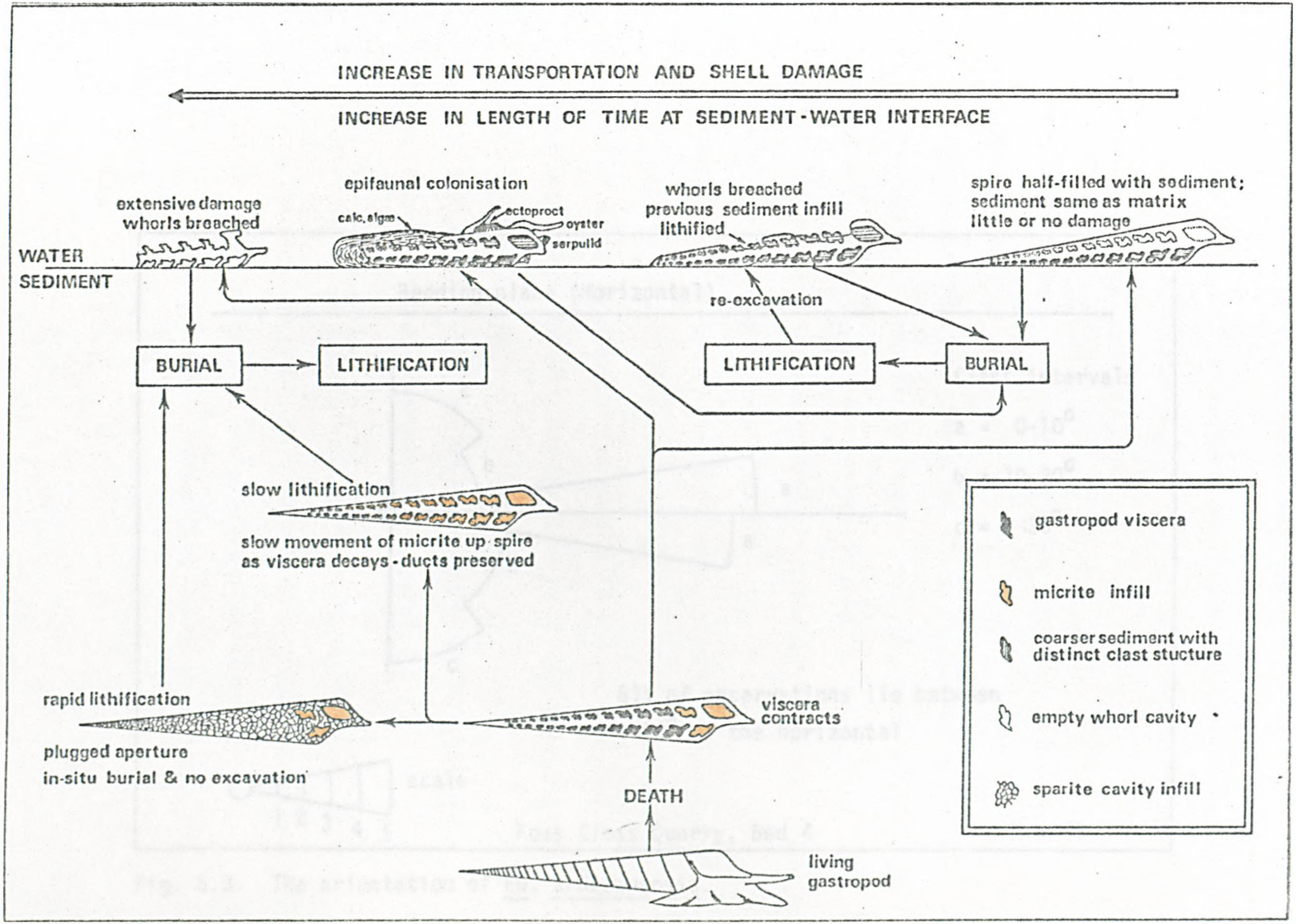


Fig. 6.2. The post-mortem preservation, colonisation and destruction of Nerineid gastropod shells.

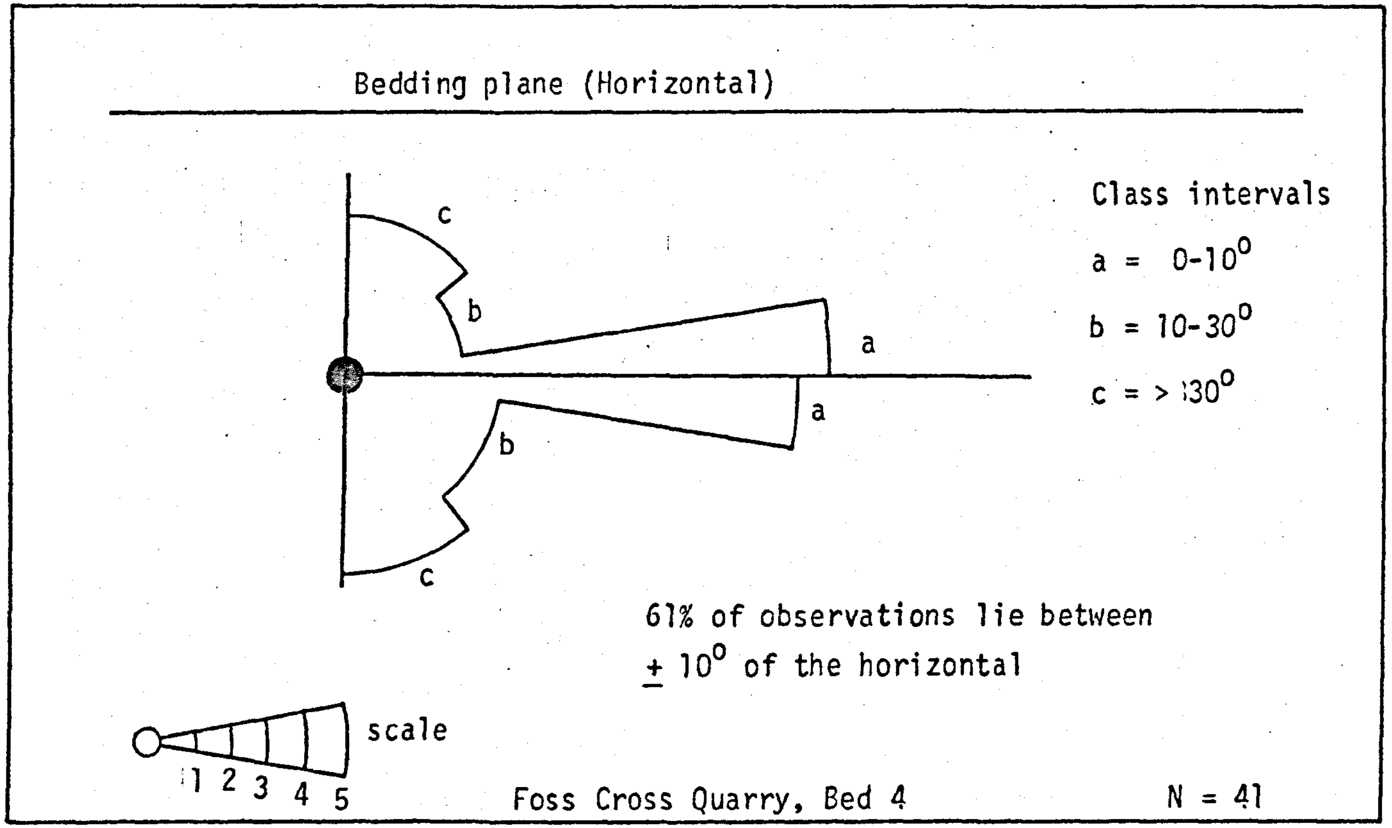


Fig. 6.3. The orientation of Eu. arduennensis.

Damage to Nerineid shells during transportation

The destruction of the Nerineid shell with progressive transportation and abrasion is accomplished in several recognisable stages from minor damage to complete destruction.

1) Damage to the apex: the protoconch and juvenile whorls of the teleoconch are lost.
2) Damage to the aperture: the outer lip is broken and the juxtasutural selenizone is reduced in length. However, folds are not yet visible at the aperture and the ornamentation is still visible.
3) The ornamentation is progressively lost through abrasion, although the sutures between whorls remain visible.
4) Absence of all ornament: the sutures become indistinguishable and the shell is reduced in thickness.
5) Further damage to the aperture results in the folds on the columella and outer lip being exposed. The whorl walls are now breached in various places on the spire.
6) Continued progressive breakage of the whorl walls eventually reducing the shell to an abraded columella only.

Unfortunately the problems of specimen extraction from well indurated limestones prevent the illustration of this progressive destruction of Nerineids with examples from the Bathonian White Limestone, although the latter stages (4-6 in the above scale) can readily be identified in sectioned gastropods (plate 6.B).

However, in the more friable Upper Lincolnshire Limestone (Bajocian) specimens are relatively easily extracted and Plate 6.C shows the varying stages of shell destruction in several Nerineid gastropods taken from a single block of limestone at Kingscliffe (G.R. TL013967) - see also Sylvester-Bradley and Ford (1968, p. 226).

Most specimens which exhibit extensive shell destruction show only one phase of sedimentary infill, the sediment which fills the breached whorls being the same as the surrounding matrix. Occassionally specimens are found in which the shell destruction post-dates a previous phase of sedimentary infill which was lithified before exhumation and abrasion. In these cases, when the whorls are breached the earlier sedimentary infill retains the configuration of the whorl cavity and contrasts markedly with the surrounding matrix (plate 6.D).

It is difficult to assess to what extent the destruction of the shells was accompanied by structural weakening due to the action of micro-boring organisms such as fungi, algae and sponges, etc. Apart from thin micritic envelopes, there is usually little direct evidence of their activity (noteable exceptions being in specimens of N. cf. multistriata from Inver Tote, Isle of Skye) because any larger, unsupported, borings would have collapsed during the mineralogical transformation of the shell from aragonite to calcite via a cavity stage. The presence and effect of micritic envelopes during diagenesis is discussed below.

Epibiontic colonisation of Nerineid shells

In certain circumstances the shells of those Nerineid gastropods exposed at the sediment-water interface, whether they are dead or alive, provided hard substrates upon which epibionts lived. Two groups of epibionts are found on Nerineid shells; the endolithic shell destructive type, represented by boring algae and the enveloping epibionts, represented by oncolitic calcareous algae, ectoprocts, serpulid worms and oysters.

Boring algae

Amongst Middle Jurassic Nerineid gastropods from Britain, only *Nerinella* cf. *multistriata* (Upper Bajocian - ? Garantiana zone, Inver Tote, Isle of Skye) consistently reveals the presence of shell boring algae. The almost total absence of boring algae in other Nerineid gastropods can probably be ascribed to the diagenetic transformation of the shell from aragonite to calcite via a cavity stage, rather than a lack of algal colonisation.

As noted by Bromley (1970, p. 54), it is often extremely difficult to differentiate between fossil algae and fossil fungi (see also Golubic, 1969). However, whilst the borings in the shells of *N.* cf. *multistriata* are abundant, much of the finer detail has been lost due to their preservation in pyrite.

Most, if not all, of the borings appear to be algal in origin and at least two types are present. There is a dense envelope of shallowly penetrating tubes, probably of mixed algal types with at least one of these algae being composed of tubes very similar to those described as *Ortonella* by Brown (1963, pp. 566-7). The tubes are circular, approximately 30µ in diameter and show repeated dichotomous, 60° branching (see plate 6:E). The other recognisable algal boring consists of very fine parallel tubes which penetrate much more deeply into the shell (plate 6:E). Branching has not been observed in this type and it seems identical to the tubes described from the Great Estuarine Series of the Hebrides by Hudson (1970, p. 24) as like the modern *Schizothrix* and described from the White Limestone by Elliot (1975, p. 355) as Myxophyte threads. However, it is important to note that neither *Ortonella* nor *Schizothrix* are endolithic algae having been reported only from stromatolitic occurrences and are not known to bore into carbonate substrates. As noted by Bromley (1970, p. 55), some algae show a chemotactic affinity for iron and the preservation of Nerineid algal tubes in pyrite might suggest that they were iron-fixing members of the Cyanophyceae. However, the InverTote gastropod shells are found in an angular, medium-grained slightly calcareous sandstone which is black in colour due to bitumen staining (Bed 3 of Hudson in Torrens, 1969, p. 30). Post-depositionally precipitated pyrite is present in the matrix and this suggests that the origin of the pyrite in the algal tubes is also secondary in nature..

It seems likely that the boring algae found in *Nerinella* cf. *multistriata* belong to either the Myxophyceae or the Chlorophyceae (see Bathurst, 1971, p. 381). Boring representatives of the Chlorophyceae (green algae) are widespread in modern calcareous environments and according to Elliot (1975, p. 35), living representatives of the Myxophyceae (blue-green algae) are frequently abundant in the littoral zone. Clearly although the algal associations and occurrences are not identical to those found by Hudson (*op. cit.*), the colonisation of the Nerineid shells by boring algae almost certainly took place in clear shallow waters with good light penetration. The association of *Cayeuxia* and *Schizothrix*-like tubes in 'algal nodules' from the Great Estuarine Series of the Hebrides has been compared with intergrowths of *Scytonema* and *Schizothrix* from modern supratidal Bahaman deposits by Hudson (1970, pp. 24-26).

The question of whether the algal colonisation of *Nerinella* cf. *multistriata* was an *in-vivo* or *post-mortem* process is an important one; as only the former can provide data relevant to the mode of life of the gastropod. Unequivocal evidence of the activities of boring algae during the life of the gastropod is provided by enveloped algal borings where the growing gastropod shell has enclosed algal tubes penetrating the base of the previous whorl (see plate 6:F). This demonstrates that *N*. cf. *multistriata* was epifaunal for at least part of its life and lived in the photic zone.

Clionid sponge borings have been observed in Nerineid shells from the Gosau Beds of Austria (Tiedt, 1958) and the Lower Kimmeridgian of Poland (Wieczorek, 1975).

As noted by Hudson (in Torrens, 1969, p. 31) it is unusual to find a Nerineid gastropod in an arenaceous facies. It is likely that much of the fauna in this bed was subjected to *post-mortem* transport because the shells are usually broken and markedly abraded. The present author has seen Cossmannea desvoidyi (d'Orb.) from the Oxfordian of Saudi Arabia preserved in a similar arenaceous facies.

Oncolitic algal overgrowths

The occurrence of oncolites in the White Limestone at Dagham Downs has been briefly described by Elliot (1975, p. 355). Oncolitic coatings upon Nerineid shells have been observed by the present author at Foss Cross (beds 7 and 10) Stony Furlong (bed 13c) and Worsham (bed 10) as well as at Dagham Downs (bed 7). As noted by Elliot (op. cit.) oncolites require movement during growth to produce the typical rounded, concentrically laminated form and most of the Nerineid shells with oncolitic encrustations show evidence of exhumation and transportation. In extreme examples, the oncolite has protected the shell whilst the regions without the algal coating are extensively abraded (see plate 6:G). Details of Recent intertidal and subtidal analogues together with the environments in which they are found have been given by Ginsburg (1960).

Oysters, serpulids and ectoprocts

The hard substrates provided by Nerineid shells on the sediment surface could be colonised by oysters, serpulids or ectoprocts. Evidently some minimum shell size was necessary before the spat of these organisms could settle and grow, as it is usual to find only the larger shells with these epibionts present. Generally, colonisation was a post-mortem process, although this is difficult to prove in those cases in which only the sides of the shell are colonised. Plate 6:H shows examples of the three epifaunal organisms which have been found on Nerineid shells. Occasionally the epifaunal organism grows over or in the aperture of the gastropod or upon an abraded shell, thus clearly demonstrating that colonisation took place after the death of the host animal (plate 6:I). However, occasional specimens of M. altararis (Ardley Fields Quarry, bed 34) are found in which oysters and serpulids have colonised the last whorl of a living representative and have been subsequently enveloped by the growing gastropod (plate 6:J). This clearly demonstrates that M. altararis (like Nerinella cf. multistriata) was at least partially an epifaunal species. It is interesting to note that both these epifaunal Nerineids are a) robust, large-shelled species and b) have only three internal folds.

The distinctive geographical distribution of the colonising epifauna is probably a reflection of the varying environmental conditions that existed at any one time during the White Limestone depositional régime. Oncolites have only been found in abundance in the south-west of the White Limestone outcrop whereas the oysters and serpulids are much more characteristic of the north-eastern part. The ectoprocts are apparently more evenly distributed in the White Limestone. The ecology of oysters and their distribution in the Middle Jurassic of Britain have been discussed by Arkell (1934) and Hudson and Palmer (1976, pp. 79-93). The occurrence of the oysters as epifaunal overgrowths in this part of the White Limestone is consistent with the proximity of the London-Ardennes landmass to the east where run-off from the land would provide both terrigenous clastic detritus and fresh-water contamination, providing a more favourable habitat for oyster growth (cf. Hampen Marly Beds and Upper Estuarine Series). Nevertheless the overall environment in this part of the White Limestone remained that of a low-energy subtidal/intertidal carbonate mud flat and at this time the influence of the London-Ardennes landmass upon the depositional environment was slight.

To the south-west the carbonate deposits of the White Limestone are in general those of higher-energy hydrodynamic régimes; the resulting sediments being coarser and in places cross-bedding is well-developed. Not unexpectedly, it is in this region where the oncolites are found, associated with water movement and sediment transport. Furthermore, evidence of exhumation, abrasion and shell damage are more readily apparent in the gastropod faunas in the south-western part of the White Limestone than in the north-east. The White Limestone passes south-west into the Minchinhampton 'shoal' region which consists of high-energy shelly facies, probably condensed and probably deposited at the edge of the 'Cotswold shelf' (see Chapter 1).

The diagenetic history of Nerineid shells

The various types of sedimentary infill that may occur in Nerineid whorl cavities and their origins have been briefly discussed previously and are summarised in Fig. 6.2. The remaining post-depositional processes affecting Nerineid gastropods are mainly concerned with the lithification of the sediment and the diagenetic transformation of the aragonitic shell to calcite; the latter process always post-dating the sedimentary infill phase.

With the sole exception of Nerinella cf. multistriata from Inver Tote, Isle of Skye, all British Bathonian (and Bajocian) Nerineid gastropods examined by the present author have undergone the transformation from an aragonitic to a calcite shell via a cavity stage. The general sequential stages of this mineralogical transformation in molluscan shells have been documented in detail by Bathurst (1958, 1964b, 1966 and 1971) and the following stages can be recognised in Nerineid gastropods from the White Limestone.

In those cases where the soft tissue of the gastropod decayed and the spire was empty for some (indeterminate) period of time, a distinct micrite envelope developed inside the spire on the sides of the whorl cavity (see plate 6:K). Subsequently the spire became either filled with carbonate sediment or remained empty. If after burial the spire and whorl cavity remained empty, later solution of the aragonitic shell resulted in two cavities (i.e. the space previously occupied by the shell together with the empty whorl cavity) which were separated only by a thin, three-dimensionally coiled, micritic envelope. At a later stage these cavities were simultaneously infilled by two generations of cavity precipitated calcite cement (plate 6:K).

Where the spire was wholly or partially filled with sediment, the infill took place before the solution of the shell. Upon solution of the aragonitic shell, the sediment infilled whorl cavity was suspended in the void gastropod shell which was later infilled by two generations of cavity calcite cement (plate 6:L).

During the cavity stage, movement of the sediment, perhaps due to compaction, occasionally ruptured the delicate empty micritic envelope which, without the support of the shell, then collapsed (see plate 6:H). In some cases, similar movement also fragmented the sediment infilled whorl cavity which then telescoped and collapsed into the empty gastropod mould (see plate 6:H). It is noticeable that both the collapse of the micritic envelope and the sediment infilled whorl cavity were evidently due to brittle fracture and the original shapes of the micritic envelope and whorl cavity are not distorted, merely broken and disorientated.

The diagenetic implications of this brittle nature of the micritic envelope have been discussed by Bathurst (1971, pp. 333-4). Clearly if the micritic envelope consisted only of the elastic organic substrate (the walls of the algal tubes) then distortion and stretching would have occurred during the collapse and breakage.

Both aragonite and high-magnesian calcite have been reported from Recent micritic envelopes (Bathurst, op. cit., pp. 333-4). Presumably if the algal bores in the micritic envelope in Nerineid gastropods were originally filled with aragonitic micrite, this would also have dissolved at the same time as the aragonitic shell, unless the aragonite in the envelope was either rendered metastable, perhaps by association with the organic matrix, or transformed to calcite. Alternatively, if the algal tubes were filled with high-magnesian calcite, this would not have dissolved and the micritic envelope would have remained mineralised, and hence brittle, during the cavity stage.

The broken but not disturbed fragments of the sedimentary infilled whorl cavity indicate that the sediment was at least partially lithified and also capable of brittle fracture before the solution of the aragonitic shell occurred. In all cases observed by the present author, the breakage of the micritic envelopes and the sediment infilled whorl cavities preceded the two observable phases of cavity cement. The early first generation of cement consists of small scalenohedral calcite crystals which form a cavity druse lining all free surfaces, including the broken edges of the micritic envelopes and the fractured surfaces of collapsed sediment infilled whorl cavities (see plate 6:M). The second generation of cement consists of much larger rhombohedral calcite crystals which completely fill the remaining spaces. No phase of cementation earlier than the two observed in the cavity cement has been found within the interstices of the grains comprising the sediment in the whorl cavities and hence the nature of the pre-cavity stage lithification of this sediment remains unknown.

It is unusual to find a Nerineid gastropod from the White Limestone in which the outer micritic envelope of the shell has been ruptured during diagenesis. This suggests that compaction of the sediment was minimal during the lithification of these molluscan biointrasparites. Movement was just sufficient to occasionally break delicate micritic envelopes and sediment infilled whorl cavities both precariously suspended in the void gastropod shell but not great enough to induce wholesale collapse of empty gastropod and bivalve moulds which were bounded on all sides by grain supported carbonate sediment.

The various stages in the diagenetic history are outlined in Fig. 6.4.

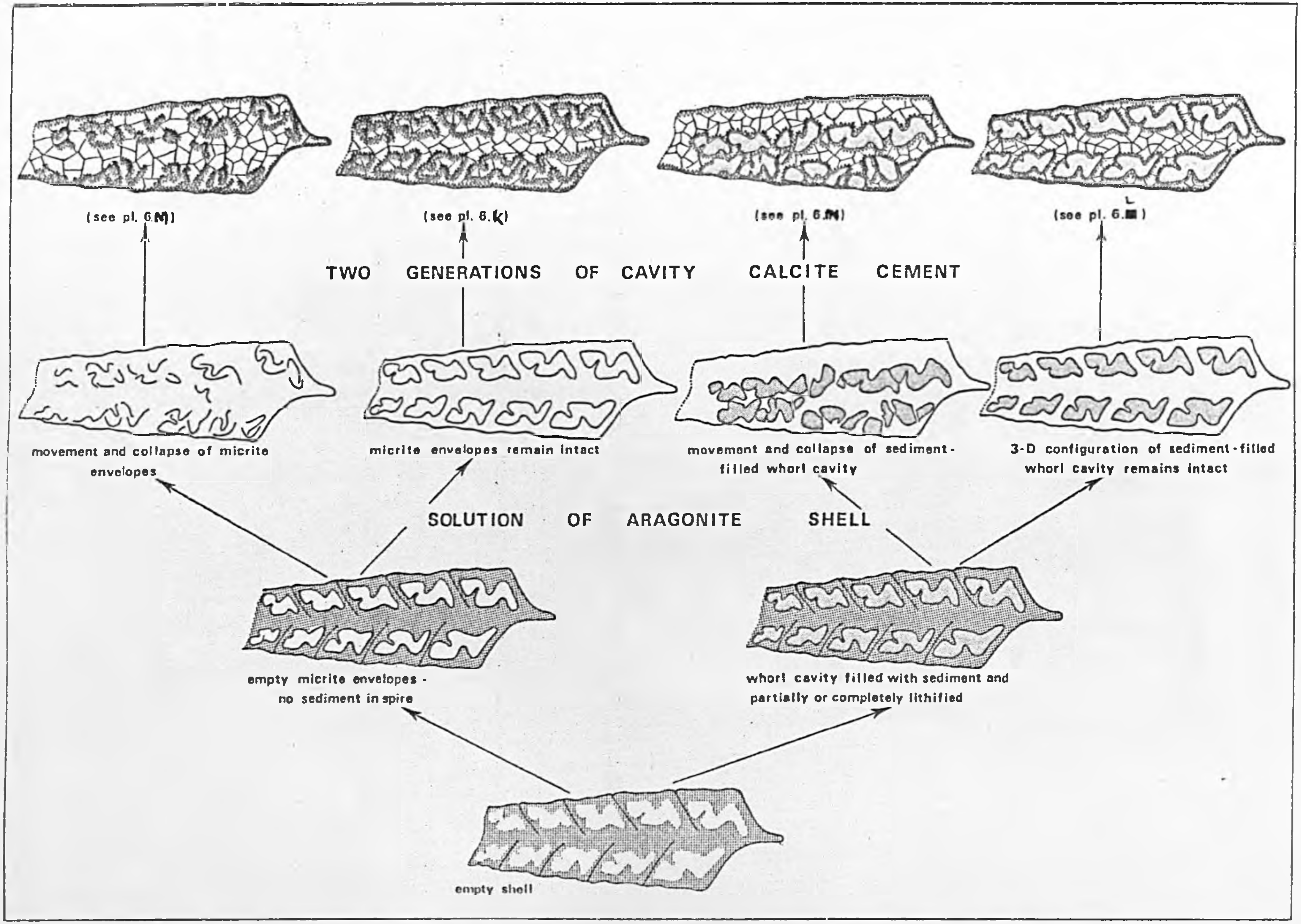


Fig. 6.4. The main stages of shell transformation and diagenesis in Nerineid gastropod shells.

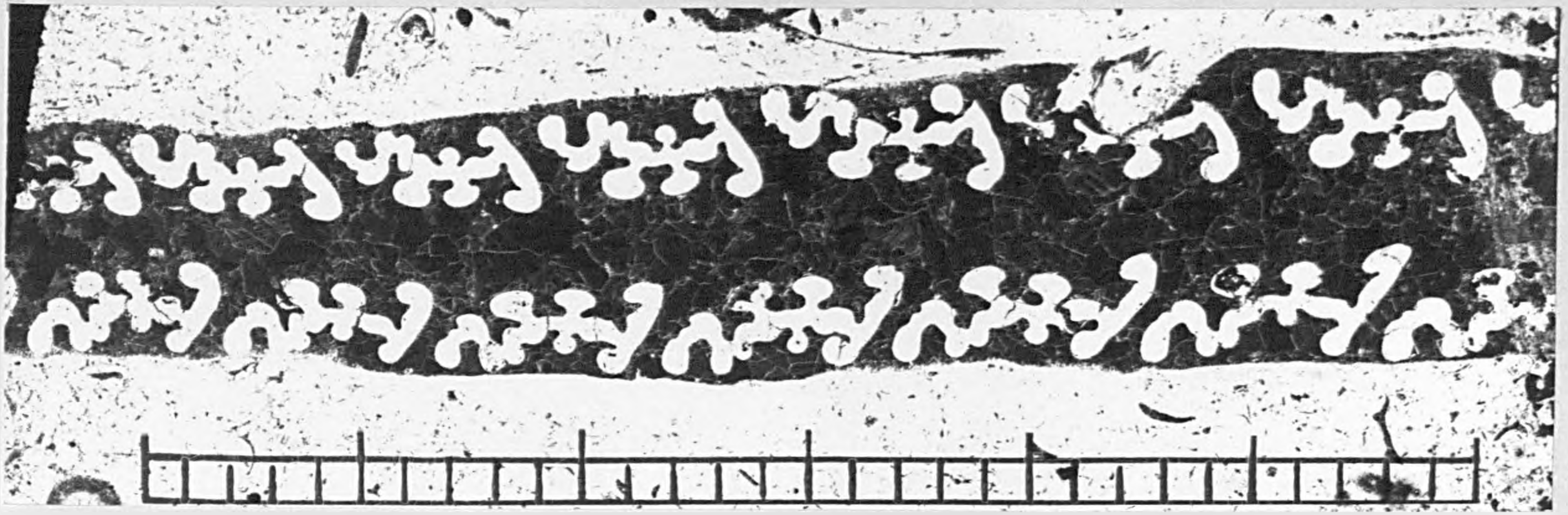
Exhumed and abraded specimen of B. *implicata*

Specimen St. Fig. 2 - Stony Furlong, Bed 13c.

Thin section, plane polarised light. M.J.B. colln.

Note shell damage and absence of duct system in the whorl cavity

Plate 6.A.



Progressive destruction of _B_. _implicata_

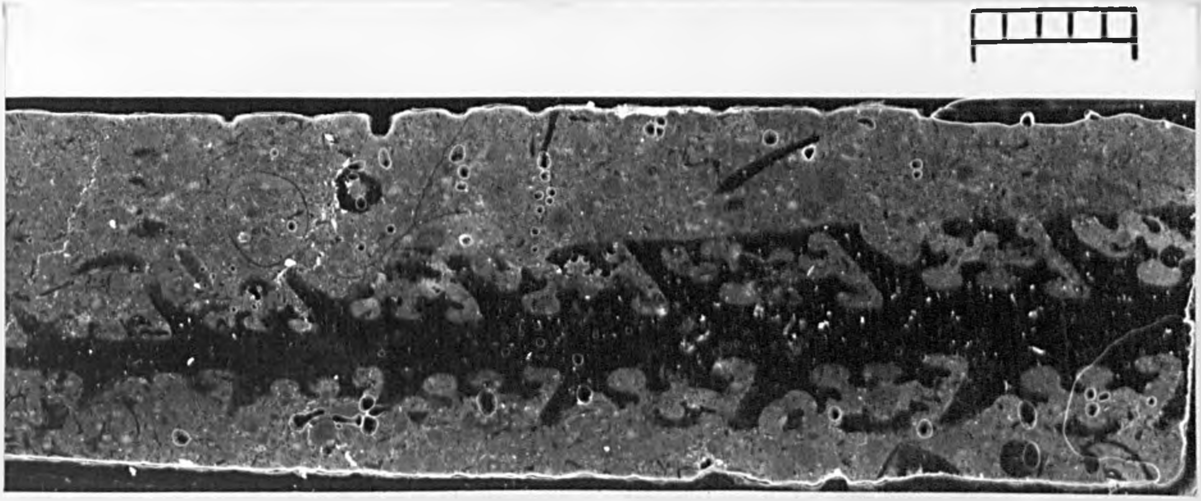
Specimen D.D.8.	Specimen D.D.13.	Specimen D.D.7.
Stage 4	Stage 5	Stage 6

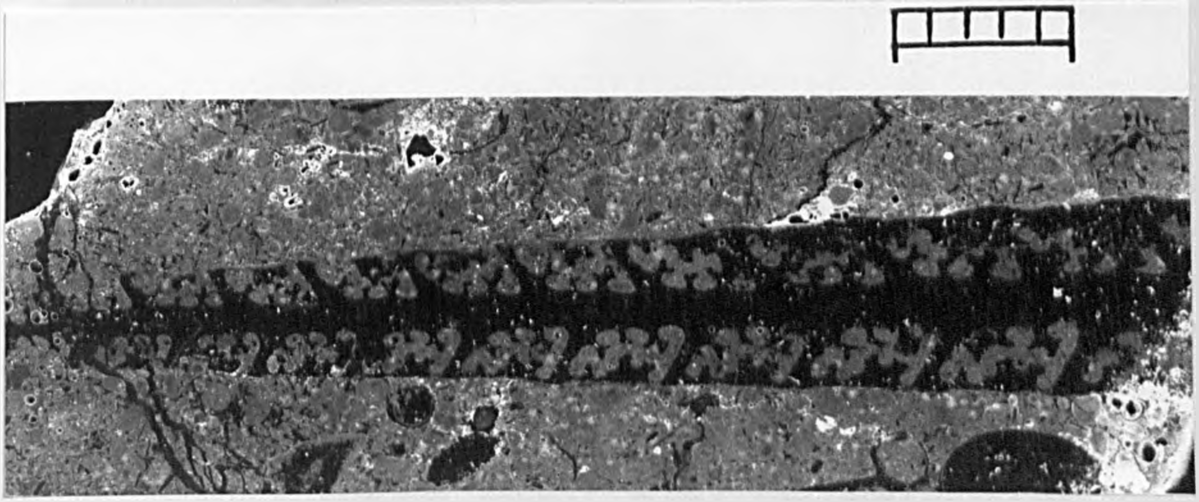
(stages of destruction as given on p. 6.6)

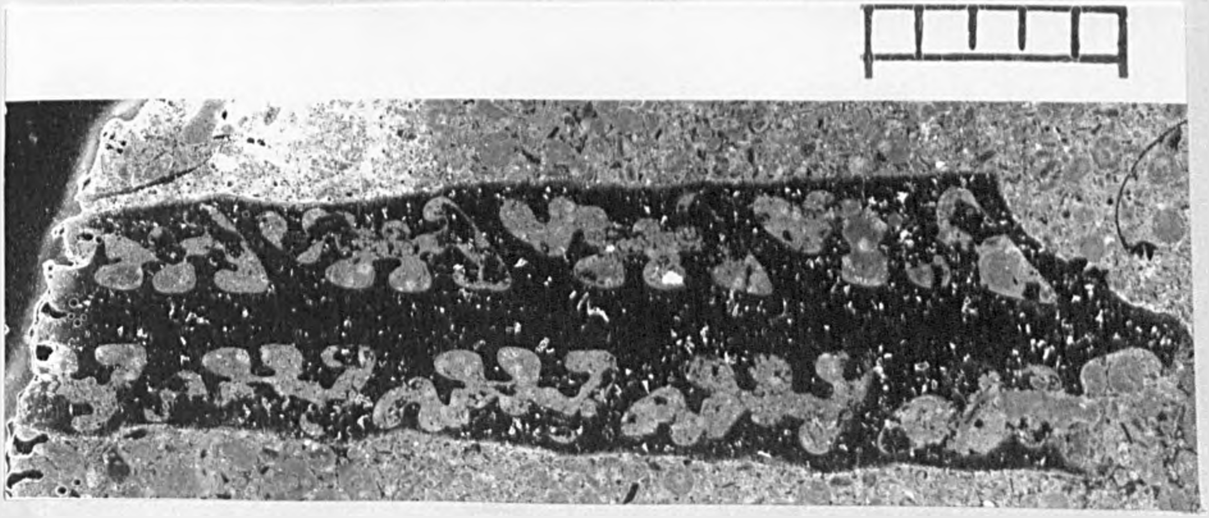
All from Dagham Downs, Bed 12.

All acetate peels. All specimens M.J.B. colln.

Plate 6.B.







Progressive destruction of Bajocian Nerineids from Kingscliffe (Upper Lincolnshire Limestone)

Numbers below specimens refer to stages of destruction
given on p. 6.6

Specimens from M.J.B. colln.

Plate 6.C.

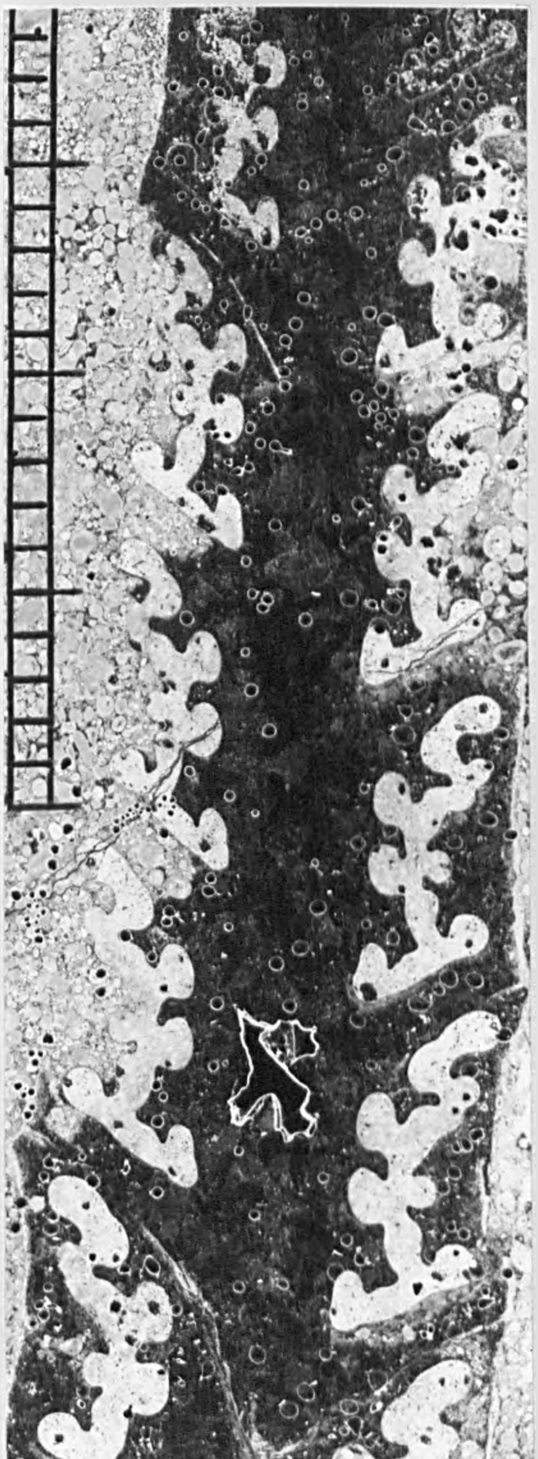

2
3
3
4
5
6
6

Shell destruction of _B_. _implicata_ post-dating an earlier phase of sediment infill in the body cavity (with preservation of the duct system).

Specimen W 10/1 - Worsham, Bed 10

Acetate peel. M.J.B. colln.

Plate 6.D.



Shell boring algae in *Nerinella* cf. *multistriata*

Specimen I.T./B

cf. *Ortonella*

Thin section

plane polarised light

x200

(Margins of shells on the right-hand side: note also the incremental growth of labral folds)

cf. *Schizothrix*

Specimen I.T./F

Thin section

crossed polars

x25

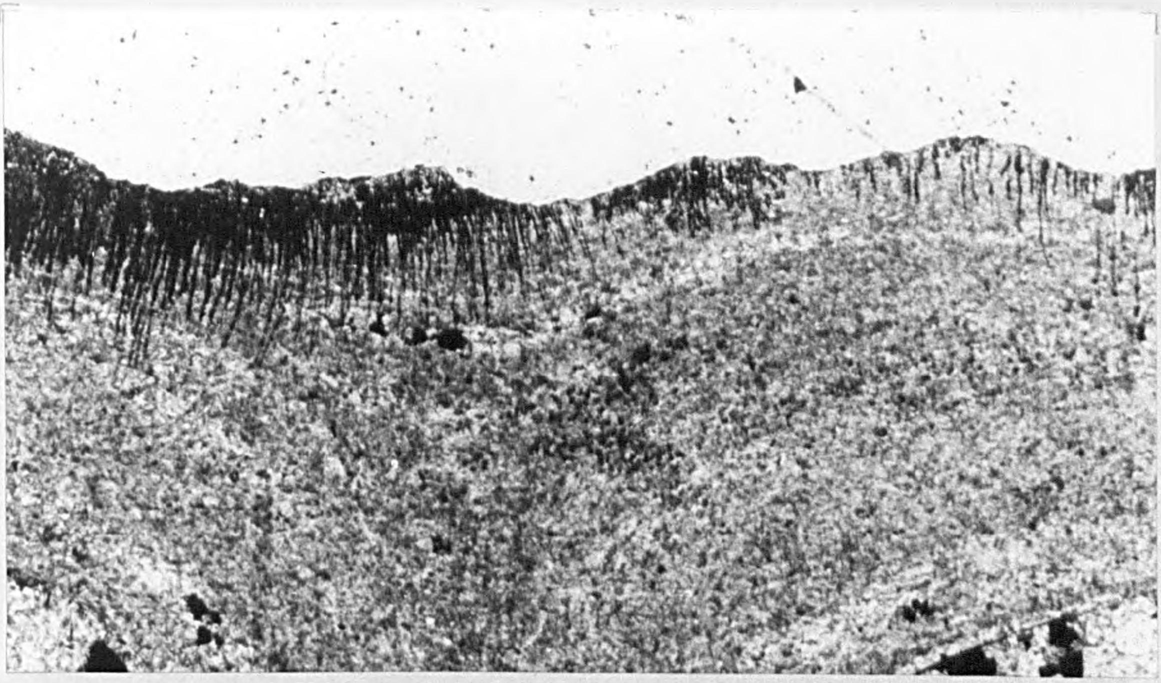
Specimen I.T./H

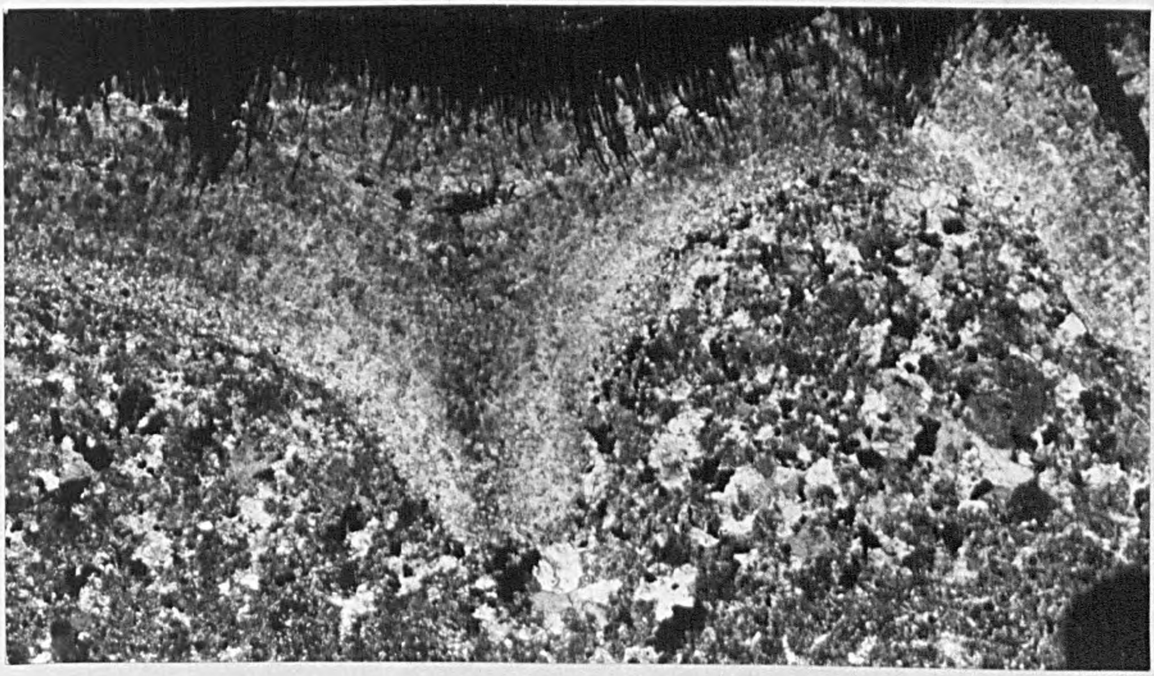
Thin section

plane polarised light

x25

Plate 6.E.





Enveloped algal borings in *Nerinella* cf. *multistriata*

Upper Photograph

Specimen I.T./R

Thin section,

x45.

Plane polarised light.

Lower Photograph

Specimen I.T./J

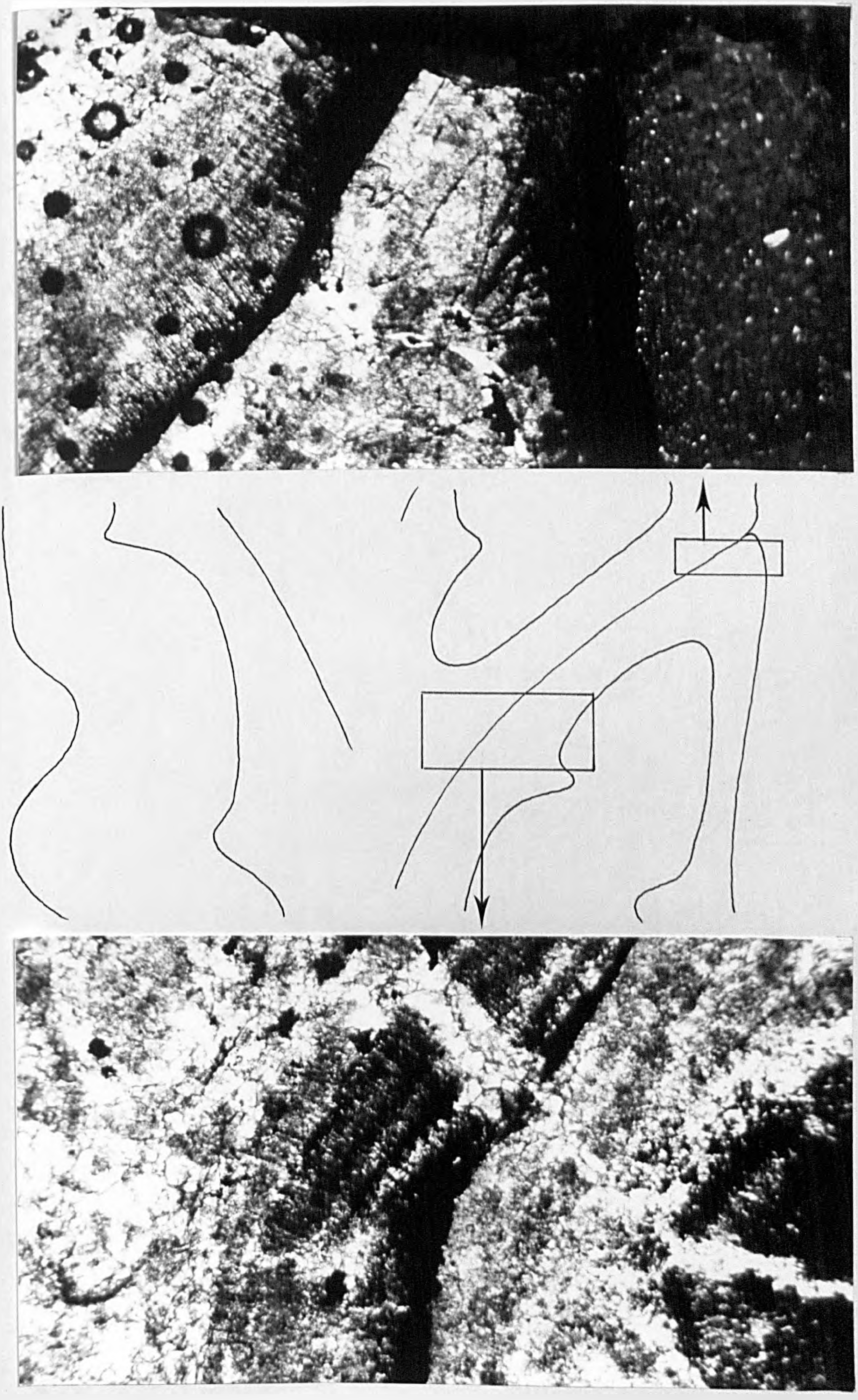
Thin section,

x45.

Plane polarised light.

Both specimens M.J.B. colln.

Plate 6.F.



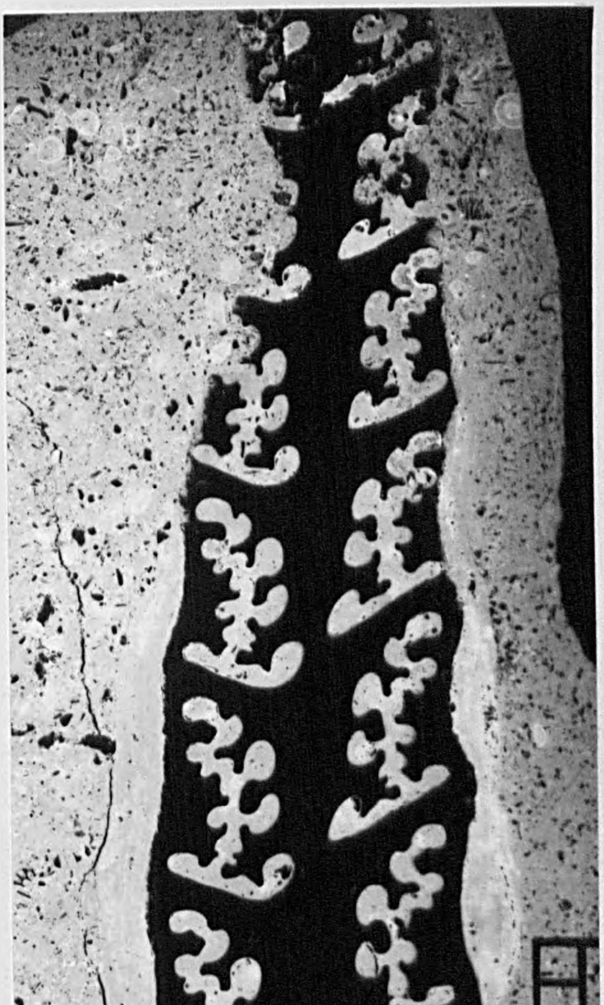
Specimen of B. implicata with adapertural region of shell protected from destruction by oncolite envelopment.

Specimen FXS. 1 - Foss Cross, Bed 10.

Thin section, plane polarised light.

M.J.B. colln.

Plate 6.G.



Epifaunal colonisation of Nerineid shells.

Left hand photograph - Melanioptyxis altararis with an epifauna of oysters.

Specimen AR. 34/11 - Ardley Fields Quarry, Bed 34.

Acetate peel.

Upper right hand photograph - Eu. arduennensis with an epifauna of serpulid worms.

Specimen Sl.H.Ox. 54 - Slape Hill, Bed 5.

Acetate peel.

Lower right hand photograph - M. altararis with an epifauna of ectoproct colonies and serpulids.

Specimen AR. 34/5 - Ardley Fields Quarry, Bed 34.

Acetate peel.

All specimens M.J.B. colln.

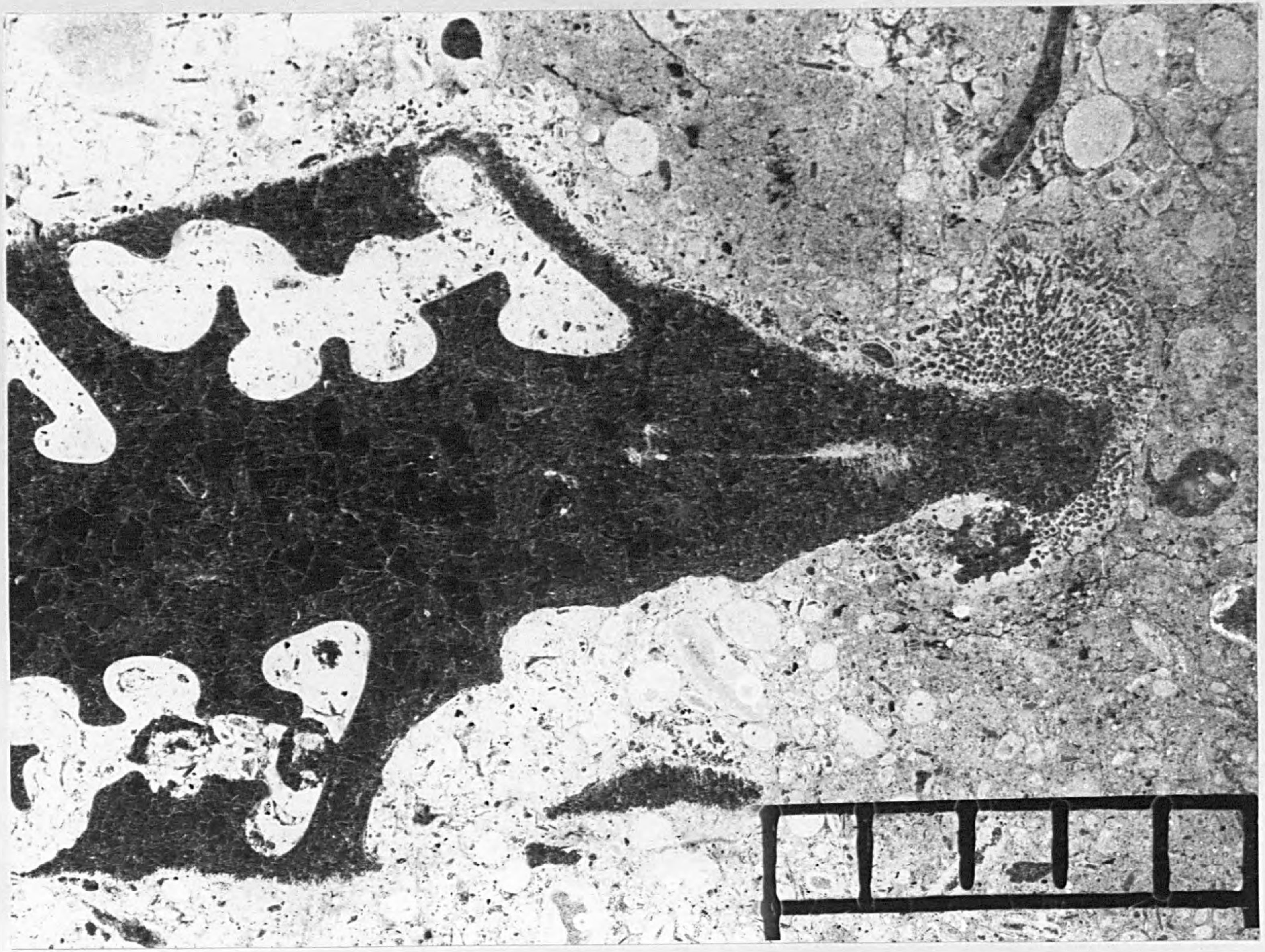
Plate 6.H.

Post-mortem colonisation of an abraded
specimen of *B. implicata* by ectoproct colonies

Specimen W 10/18. Worsham, Bed 10
Thin section, plane polarised light.

M.J.B. colln.

Plate 6.1.



Epifauna enveloped by growing gastropod

Serpulid enveloped by *M. altararis*

Specimen AR. 34/32 - Ardley Fields Quarry, Bed 34

Acetate peel

Oyster enveloped by *M. altararis*

Specimen AR. 34/38 - Ardley Fields Quarry, Bed 34

Acetate peel

Both specimens M.J.B. colln.

Plate 6.J.

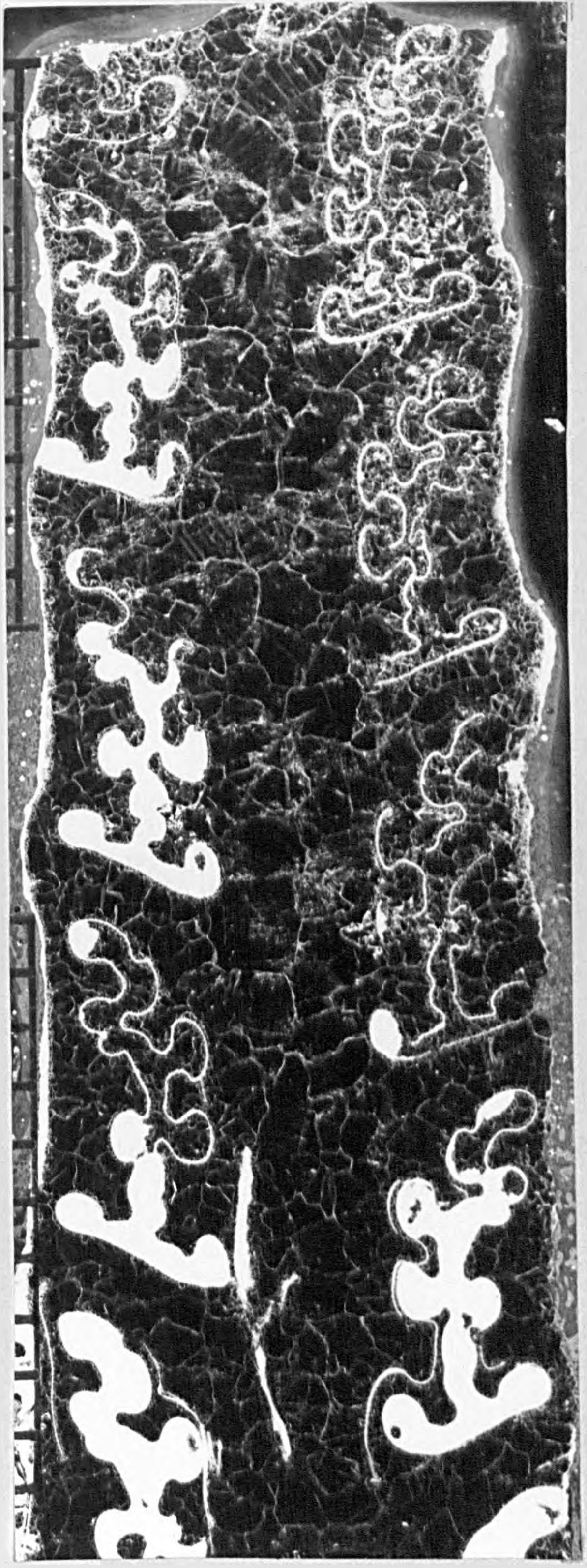
Micritic envelopes developed upon the inside of the empty whorl cavity in a specimen of B. implicata: Shell replaced by and whorl cavity filled by two generations of cavity pptd. calcite cement.

Specimen FXS 210 - Foss Cross, Bed 10.

Thin section, plane polarised light.

M.J.B. colln.

Plate 6.K.



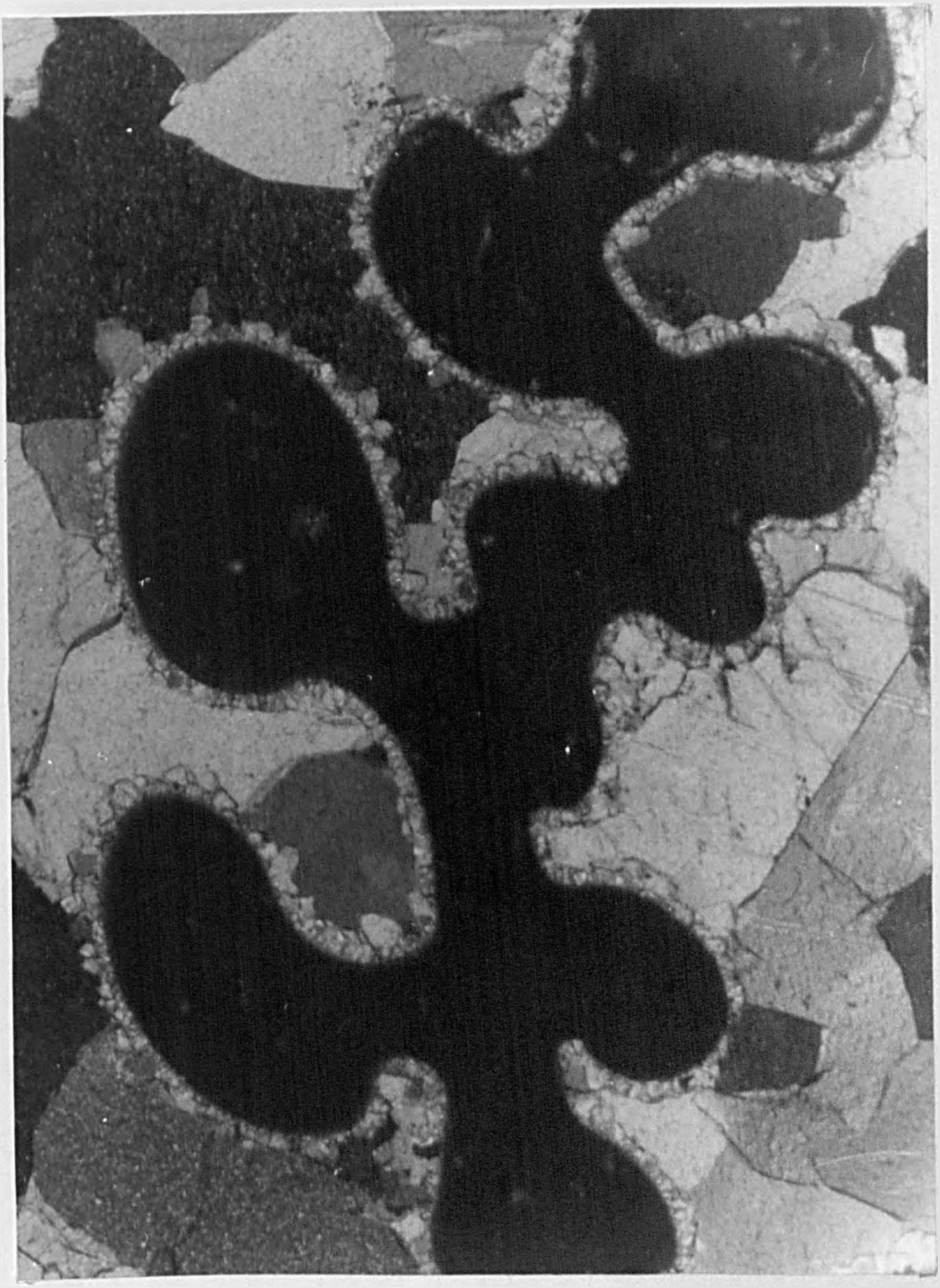
Whorl cavity in B. implicata infilled with sediment: Shell replaced by two generations of cavity pptd. calcite cement.

Specimen FXS/1W - Foss Cross, Bed 10.

Thin section, crossed polars, x50.

M.J.B. colln.

Plate 6.L.



Micrite envelopes and sediment filled whorl cavities showing breakage and collapse

Eu. arduennensis

Specimen AR 34/51 - Ardley Fields Qu., Bed 34
Acetate peel

Eu. arduennensis

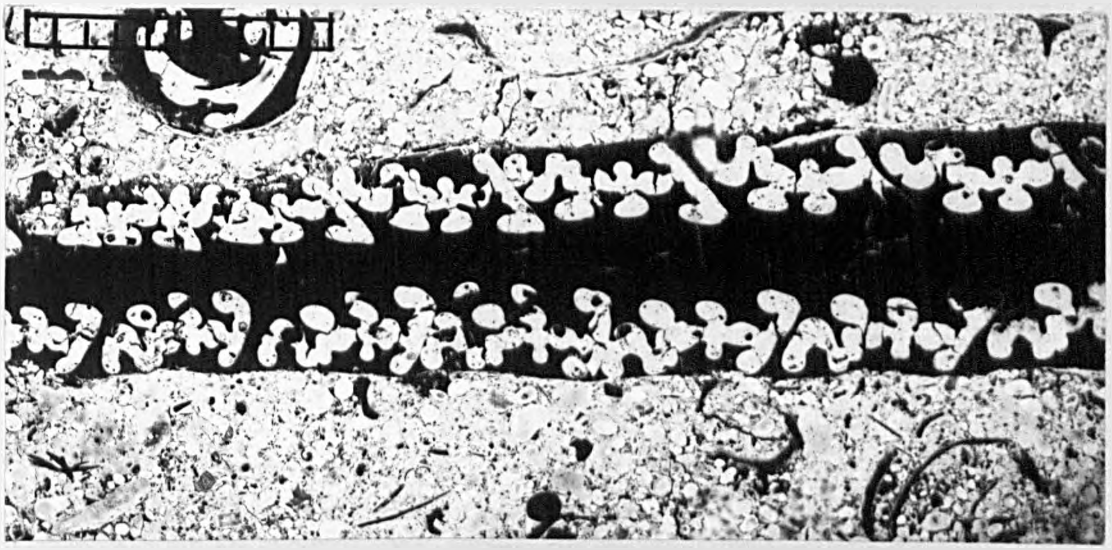
Specimen SH/L.G.H./34-
Slape Hill, Bed 3.
Acetate peel

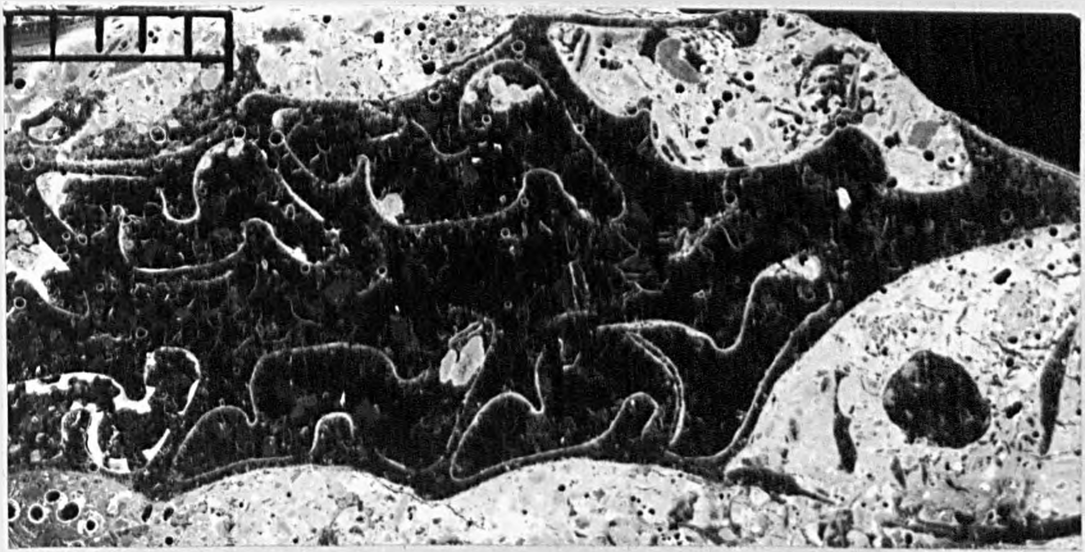
B. implicata

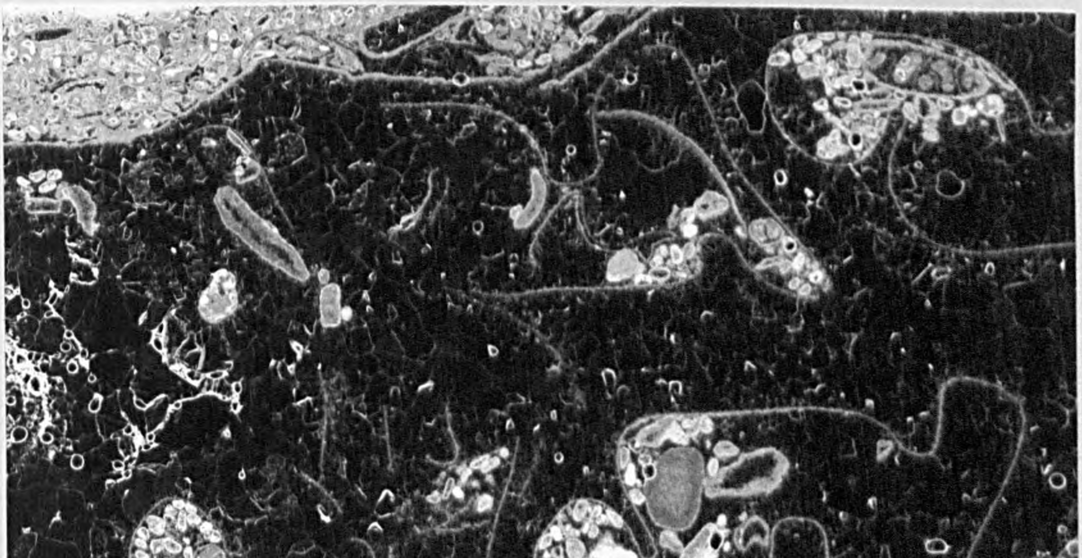
Specimen St. Flg. 13 - Stony Furlong, Bed 13c
Thin section, plane polarised light

All specimens M.J.B. colln.

Plate 6.M.







Chapter 7

A BRIEF GEOLOGICAL HISTORY OF THE NERINEACEA

'The historical sense involves a perception, not only of the pastness of the past, but of its presence.'

T. S. Elliot, Tradition and the Individual Talent, 1919.

Introduction

As far as the present author is aware, 90 Nerineacean generic names have so far been published and 146 species categories (not all valid) have been named from the Bathonian strata of Western Europe alone! Clearly, considering that Nerineids are generally abundant in Jurassic and Cretaceous strata throughout the world the total number of species might eventually reach several thousand. During the course of the present study, the author has attempted to apply a more biologically orientated species-concept to some of these gastropods. This has resulted in considerable taxonomic changes amongst Bathonian forms (mainly English) and the extension of these methods to other described Nerineid 'species' might result in similar changes. Thus the extent to which one can rely upon published Nerineacean 'species' categories (which constitute the primary taxobases of any classification) is unknown, although this problem is by no means unique to Nerineid gastropods.

However, there are also no generally accepted criteria for generic discrimination or for an adequate suprageneric classification and indeed there is even no agreement as to whether this group of gastropods constitutes a family, superfamily or order. Perhaps the most difficult and controversial aspect of Nerineid gastropods concerns their affinities with other gastropod groups and they have been variously assigned amongst the Archaeogastropoda, Mesogastropoda, Neogastropoda and the Opisthobranchia.

Clearly many difficult problems exist particularly:

1) Are the described species reliable in the context of the modern palaeontological species concept?

2) How can one adequately distinguish between Nerineid genera which are frequently not clearly delineated from each other e.g. Eunerinea and Nerinella?

3) Do Nerineid gastropods constitute a monophyletic and homogenous group which are therefore all genetically related? If so, can a practical phylogenetic classification be constructed and on what basis?

4) What 'kind' of gastropod are the Nerineids?

One answer to most of these problems would be to try and evaluate all described Nerineid species on the basis of the experience gained from Bathonian forms. It might then be possible to construct both a consistent generic taxobasis and a phylogenetic classification but although a start has been made, this will clearly involve considerable further research before such a situation can be realised. Indeed L. R. Cox, a noted Nerineid specialist, did not attempt a phylogenetic classification of the Nerineacea when he produced a manuscript for the projected Treatise volume dealing with the Gastropoda ex Archaeogastropoda. He merely listed the major, well-defined genera on the basis of the number of folds they possessed and the presence or otherwise of an umbilicus. In recent years, only Pchelintsev (1965) has attempted a phylogenetic classification of the Nerineid gastropods, although, in the opinion of the present author, the validity of many of the relationships proposed by Pchelintsev (op. cit.) is very questionable and will be discussed later. At this stage, the origin, affinities and basic classification of the Nerineacea together with a broad outline of their geological history can be profitably discussed. The construction of a detailed phylogeny must await further research.

The origin and affinities of the Nerineacea

The morphological variability of the Nerineacean shell is such that many gastropod families and genera have been variously proposed as their possible ancestors and descendants. Objectivity on this matter is difficult, if not impossible and inevitably if author A believes that the Nerineacea are Opisthiobranchia, he searches for an ancestor, amongst pre-Mesozoic opisthobranchs (and usually suggests the Pyramidellidae or the Actaeonidae) whereas author B, believing that the Nerineids are Archaeogastropods, not surprisingly considers that the Murchisoniidae are the ancestors of the Nerineids.

The unity and homogeneity of the Nerineacea was effectively established by Cossmann (1896 - see later) and if one accepts this, the following features should be examined and critically evaluated when considering the affinities of the group.

1) The presence of a juxtasutural selenizone in all members of the group.

2) The presence of a rudimentary siphonal canal or notch in all members of the group.

3) The development of internal, spiral folds, usually on the columella and the outer lip but also variously on the basal lip and parietal region, together with their total absence in other representatives. We must also note the absence of folds at the aperture of all fold-bearing Nerineid gastropods.

4) The reported occurrence of heterostrophic protoconchs in certain Nerineids.

5) The considerable morphological diversity of the group.

1) The juxtasutural selenizone

All Nerineid gastropods possess a narrow, deep adapical slit on the whorl sides, adjacent to the suture, which is secondarily (abaperturally) infilled by the animal to produce a selenizone with characteristic 'chevron' ornamentation and associated opisthocline growth lines on the whorl sides.

Amongst fossil and recent gastropods only the Pleurotomariacea and the Murchisoniacea exhibit a comparable (even identical) development of the slit and selenizone. However, in these two superfamilies, the slit is not juxtasutural but in a more or less median position on the whorl sides. In this respect, an important point was made by Delpy (1939) who noted that the growth lines on the whorls of the disjunct <u>Nerinella libanotica</u> were symmetrical and opisthocline about the selenizone. Therefore, the detailed morphology of the Nerineacean selenizone is exactly the same as that in the Pleurotomariacea and Murchisoniacea, only displaced towards the suture.

Since Mikardotrochus is extant, the slit and selenizone of Pleurotomariacean gastropods can be demonstrated to contain the median exhalent current from the mantle cavity and presumably the same function can be ascribed to all the fossil representatives of the Pleurotomariacea and also, presumably, the Murchisoniacea. The presence of this slit is also associated with the retention of at least some of the original primitive molluscan bilateral symmetry, seen particularly in the presence of paired bipectinate ctenidia in Mikardotrochus. If the juxtasutural slit and selenizone of the Nerineacea were homologous with those found in the Pleurotomariacea and Murchisoniacea, the change in position might conceivably represent a greater degree of assymetry (probably involving a loss of at least the right ctenidium) in the Nerineid soft anatomy.

The importance of the slit and selenizone was stressed by Zittel (1873) and Geiger (1901) who both inferred a close relationship between the Nerineacea and the Pleurotomariacea.

Several other groups of gastropods have shallow median or marginal sinuses and the occasional presence of 'folds' in these groups has led to various attempts to homologise the Nerineid slit and selenizone with these shallow sinuses. Thus the Conidae (Prosobranchia:Neogastropoda) possess a shallow juxtasutural sinus as noted by Cox (1960, p. 257) and Brookes-Knight (in Cox, Treatise M.S.). A similar marginal sinus is present in the Actaeonidae (Opisthobranchia) and their decendants, the Actaeonellidae, possess well-developed internal folds on the columella, so bearing a remarkable resemblance in shell morphology and internal structure to one group of the Nerineacea - the Itieriidae. Kollman (1967) considered that the Nerineacea along with the Actaeonellidae were descended from the Actaeonidae and objections to this theory will be discussed later. Certain members of the Cerithiacea, Loxonematacea and Pyramidellacea possess shallow median sinuses at the aperture. Martin (1889) reported the presence of a median, labral sinus together with columellar and basal internal folds in the Recent cerithiid genus *Vicarya* (*V*. *verneuilli* from India and *V*. *callosa* from Java) and the Pliocene genus *Telescopicum*. Internal columellar and basal folds are found in the Cenomanian-Recent cerithiid genus *Campanile* and both Martin (*op*. *cit*.) and Delpy (1939) suggest that a close relationship existed between the Nerineacea and Cerithiacea, as did certain earlier authors (e.g. Deslongchamps, 1842; and Blainville, 1825-27). However, Delpy (*op*. *cit*., pp. 207-208) considered that the relationship was one of descent, the Campanilidae being descended from the Nerineacea and that the ancestors of the Nerineacea were elongate Pleurotomariidae, close to the Loxonematidae.

The Pyramidellacea, members of which also possess a shallow median sinus, have long enjoyed popularity as the ancestors of the Nerineacea, mainly because of the presence of folding in the Pyramidellids and their elongate shell shape, rather than the median sinus.

The present author feels that it is important to note that the Cerithiacea, Loxonematacea and Pyramidellacea, together with the Conacea and Actaeonacea, do *not* possess slits and selenizones comparable with those of the Nerineacea; they possess only shallow sinuses. The anatomical function of these sinuses is not as yet fully understood although both Cossmann (1896, p. 10) and Cox (1960, p. 254) considered that their presence in these groups did not indicate the same anatomical organisation as that found in the Pleurotomariiacea. The juxtasutural sinus in the Actaeonacea is probably associated with the pallial caecum (Fretter and Graham, 1954, p. 567).

2. The siphonal canal

The siphonal canal present in all Nerineid gastropods is very short and frequently lost through damage and poor preservation. However, the inference is that the Nerineacea possessed an inhalent siphon, a feature which in living gastropods is confined to certain representatives of the Caenogastropoda (= Mesogastropoda + Neogastropoda; see Cox, 1960 and Brookes-Knight et. al., 1960, p. 142). This is consistent with the adoption by the Nerineids of a more advanced, less symmetrical anatomy which effectively separated the inhalent and exhalent mantle currents.

3. The internal folds

As noted previously and in Chapter 5 several extant and fossil gastropod families exhibit internal folds. The presence of internal folding has been used to postulate a relationship between the Nerineacea and the Pyramidellacea (d'Orbigny, 1842-43; Cossmann, 1896; Taylor and Sohl, 1962; Stoliczka, 1867-1868 and Wenz, 1938-44). However, several other groups also possess internal folds e.g. the

Auriculidae and Clausiliidae (Pulmonata), the Actaeonellidae (Opisthobranchia), the Strombidae and Cassididae (Prosobranchia; Mesogastropoda) and Terebridae (Prosobranchia; Neogastropoda).

In all the above cases, the folds are present and have their maximum development at the apertural margin of the gastropod whereas in the Nerineacea, the folds are not present at the aperture (see Chapters 4 and 5). It is not therefore possible to homologise the folds of the Nerineacea with the folds of other gastropods (with two notable exceptions - see later). The presence of folding at the aperture of a gastropod can be explained in two ways; the columellar folds (which are more numerous and better developed than other folds) give an increased area of attachment for the pedal retractor muscles whereas the occasional labral, parietal and basal fold are probably a consequence of mantle folding as the animal is withdrawn and compressed into the shell (Dall, 1894). The functional significance of Nerineid folds and their postulated relationship to the Nerineacean biology have been fully discussed in Chapter 5.

Apparently only two gastropod genera have a fold development comparable with that found in the Nerineacea; the Permian Labridens Yochelson (Subulitacea) and the Jurassic Rigauxia Cossmann (Zygopleuridae:Loxonematacea). In both cases, folding is absent at the aperture and a labral fold is well developed. However, neither Labridens nor Rigauxia possess the slit and associated selenizone found in true Nerineid gastropods. The morphology together with the distribution of Rigauxia varicosa (Rigaux et Sauvage) in the Excavata Beds (lower member of the White Limestone: see Chapter 1), as well as its association with known Nerineid gastropods, suggests that *Rigauxia* was an isochronous homeomorph of the Nerineids. Since *Rigauxia*, a member of the Loxonematacea, was apparently homeomorphic with the Nerineids, we may suppose that the origins of the Nerineacea are not to be found within this superfamily.

The shell morphology of the Permian gastropod genus *Labridens* (from W. Texas, U.S.A.) bears a superficial resemblance to the genus *Brouzetia*, Cossmann (Nerineacea; Itieriidae: Cretaceous of France). However, the fold morphologies of the two genera are different and *Labridens* does not possess the Nerineid slit and selenizone. Yochelson (1956) suggested that a relationship existed between the Subulitacea and the Nerineacea but the typical subulitid morphology (as represented by *Labridens*) does not in any way resemble the morphologies shown by the early Nerineacean genera and the present author is of the opinion that the superficial similarity of *Labridens* and *Brouzetia* may be one of heterochronous convergence. This should not therefore be taken to represent an evolutionary relationship. Furthermore, the taxonomic position of the Subulitacea is at present uncertain, for whilst Knight (1944) and Yochelson (1956) consider that members of this superfamily are the earliest representatives of the Neogastropoda, Taylor and Sohl (1962) place the Subulitacea in the Mesogastropoda and Wenz (1938-44) places them in the Archaeogastropoda.

4. Heterostrophic protoconchs in Nerineid gastropods

The reported presence of heterostrophic protoconchs in two Nerineacean genera *Ceritella* and *Pseudonerinea* has been widely used to support the idea that Nerineid gastropods are Opisthobranchs

(Cossmann, 1895; Wenz, 1938-44; Taylor and Sohl, 1962). This was further reinforced when following Fretter and Graham (1949), the Pyramidellidae were transferred to the Opisthobranchia.

Cossmann (1895, p. 91) described the genus *Ceritella* Morris and Lycett as having a heterostrophic protoconch and in the subsequent descriptions of the known species, Cossmann (*op. cit.*) notes that two species (*C. plicata*, p. 102 and *C. blanda*, p. 110) have heterostrophic protoconchs but neither have been figured or described in detail. Indeed the only figure of a Nerineid with a supposedly heterostrophic protoconch is that subsequently given by Bigot (1896, p. 29) of *Pseudonerinea clio* and this diagram does not show the junction of the teleoconch with the protoconch. From the evidence presently available, it is not possible to ascertain whether the protoconchs of the Nerineacean gastropods were generally heterostrophic or whether this feature was confined to the Ceritellidae (which according to Cossmann, 1895, includes *Ceritella* and *Pseudonerinea*) or whether the reported occurrences are even erroneous. Certainly Cox (1960, p. 257) was uncertain as to whether heterostrophic protoconchs were a general feature of the Nerineids and even if all the Ceritellidae possessed heterostrophic protoconchs, at least one author (Dietrich, 1925) does not include the Ceritellidae in the Nerineid gastropods.

However it is a known fact that all shell bearing Opisthobranch gastropods have heterostrophic protoconchs and these protoconchs are also hyperstrophic (i.e. the protoconch is *sinistrally* coiled but contains a dextrally organised animal and the teleoconch is also dextrally coiled). If the presence of hyperstrophic heterostrophic protoconchs could be established in Nerineid gastropods, this would present overwhelming evidence in favour of Opisthobranch affinities; as it is, the only figured Nerineid protoconch (Bigot, op. cit.) does not appear to be coiled at all! The occurrence of heterostrophic protoconchs is not however confined to the Ophisthobranchs (although apparently the occurrence of hyperstrophy in the protoconch is) and certain prosobranchs, particularly the Architectonicidae (Mesogastropoda) also show this feature.

5. The Morphological Diversity of the Nerineacea

Considering the very diverse shell forms of the Nerineacea, it is not unexpected that other gastropod groups, both fossil and extant, should have utilised at least part of the range of shell morphologies found in the Nerineid gastropods. In such relatively simple animals as gastropods, the shell is usually a poor reflection of the internal anatomy; its major function being protective. When several unrelated taxonomic groups occupy the same broad ecological niché they will develop the same structural answers, in terms of shell morphology, in response to the same environmental pressures. This morphological parallelism when occupying similar life habitats has been established in many groups e.g. Mactracean and non-Mactracean bivalves, the Ammonitina and on a larger scale by the marsupial and placental mammals. Consequently the resemblance of certain Nerineid genera to other gastropods e.g. Ceritella spp. and Brouzetia to the Subulitids; Itieria to the Actaeonellids; Nailsworthia and Pseudonerinea to Pseudomelania; Pseudotrochalia to Trochus and certain trochiform

Pleurotomariidae; Eparciella to Procerithium and Phaneroptyxis to Terebra is best explained by the diverse ecological adaptations of the Nerineacea rather than by speculative phylogenetic affinities to other gastropods.

Because of the resemblance of Itieria to Actaeonella, Kollmann (1967, p. 249) suggests that the Nerineacea and the Actaeonellidae were both derived from the primitive opisthobranch family the Actaeoninidae. He further suggests (p. 251) that the Pyramidellids were descended from the Nerineacea. The Opisthobranch affinities of the Nerineacea are unequivocally accepted by Kollmann (op. cit.) without reservation or discussion and in the present author's opinion a derivation of Nerineid gastropods from the Actaeoninidae does not fit the observable facts. The early Nerineacean genera include Ceritella, Nerinella, Bactroptyxis, Aptyxiella, Pseudonerinea (all established during the Lias-Bajocian) and none of these bear the slightest resemblance to the Actaeoninidae. Indeed, Itieria, the only Nerineid genus which does resemble the opisthobranch Actaeoninidae or the Actaeonellidae, has not been recorded from strata earlier than the Upper Oxfordian according to Cox (Treatise manuscript) or Kimmeridgian according to Pchelintsev (1965). Consequently a derivation of the Nerineacea from the Actaeoninidae seems unlikely.

The postulated descent of the Pyramidellidae from the Nerineacea by Kollmann (op. cit.) is even more surprising considering that known Pyramidellids (e.g. Donaldina, Platyconcha and Streptacis) have been recorded from the Lower Carboniferous through to the Middle Permian (Knight et. al., 1960). The Nerineacean genus which resembles the

Pyramidellid morphology most closely is Itruvia which is only known from Cenomanian to Turonian strata but is preceded by approximately 100 million years of intense Nerineid evolutionary activity.

The robust shells of the Nerineacea contrast markedly with the Opisthobranchia in which the shells are characteristically reduced or even absent. Only the Pyramidellidae and Actaeonellidae amongst the Opisthobranchs possess fully developed shells and in most of these, the shells are noticably delicate (e.g. Actaeonina).

When considering the above discussions and previous authors' works, it is difficult to decide which of the several conchological aspects of the Nerineacea, if any, are phylogenetically most significant. In the opinion of the present author, the constant presence in Nerineid gastropods of the juxtasutural slit and selenizone together with the rudimentary siphonal canal clearly suggest Prosobranch affinities. The position of the selenizone at the suture probably reflects greater assymmetry in the soft anatomy, associated with the loss of the right ctenidium in the mantle cavity and the rudimentary siphonal canal suggests the presence of inhalent and exhalent currents - both features of the Caenogastropoda (= Mesogastropoda + Neogastropoda). Therefore, whilst the morphology of the slit and selenizone is that of an Archaeogastropod (cf. the Pleurotomariiacea and the Murchisoniacea), the spatial disposition of this feature suggests a Caenogastropod anatomy. Consequently the present author considers that the Nerineacea consitute a primitive superfamily of the Caenogastropoda whilst retaining some Archaeogastropod features.

Any Opisthobranch affinities of the Nerineacea cannot be justified in the light of evidence at present available.

The classification of the Nerineacea

Leaving aside the question of the higher affinities of Nerineid gastropods, the taxonomic status of the group as a whole has, in common with most organisms, undergone progressive elevation due to continued research spanning nearly 150 years.

Prior to the classic works of Cossmann (1896 and 1898), previous authors, particularly Woodward (1851-1856), Zittel (1873) and Fischer (1880-1887), had largely accepted and modified Sharpe's (1850) classification of the genus *Nerinea* into four subgenera; *Nerinea* (*Nerinea*), *N.* (*Nerinella*), *N.* (*Trochalia*) and *N.* (*Ptygmatis*). Various new subgenera were added e.g. *N.* (*Cryptoplocus*) by Pictet et Campiche (1861-1864); *N.* (*Aptyxis*) by Zittel (*op. cit.*), later amended to *N.* (*Aptyxiella*) by Fischer (*op. cit.*) and the subgenus *Itieria* (Mathéron, 1842) was by now included in the genus *Nerinea*. Subsequently a radical reappraisal of Nerineid systematics was undertaken by Cossmann (1896 and 1898). Nine new subgenera were created (*Campichia*, *Acrostylus*, *Melanioptyxis*, *Diozoptyxis*, *Aphanoptyxis*, *Bactroptyxis*, *Endiaplocus* in 1896, together with *Endiatrachelus* and *Aphanotaenia* in 1898) and a new genus *Phaneroptyxis* Cossmann, 1896, was also established. Following his monograph on the French Jurassic "Opisthobranchs" (Cossmann, 1895), Cossmann (1896) later re-organised the then known Nerineid taxa into three new faimilies, the Tubiferidae, the Nerineidae and the Itieriidae and combined all three in a new suborder the Entomotaeniata. Furthermore, Cossmann (1896) seems to have been the first author to cite type-species for many of the taxa and his classification is given below (type-species are given in parentheses).

Suborder Entomotaeniata

Family Tubiferidae

genus *Ceritella* subgenus *Ceritella* (*C. acuta* Morris & Lycett)
subgenus *Fibula* 'section' *Fibula*
(*F. undulosa* Piette)
'section' *Sequania*
(*Cerithium cotteaui* de Loriol)

genus *Pseudonerinea* (*P. blauenensis* de Loriol)

Family Itieriidae

genus *Itieria* subgenus *Itieria* (*Actaeon cabanetianus* d'Orb.)
subgenus *Campichia*
(*Itieria truncata* Pictet et Campiche)

genus *Itruvia* (*Pyramidella canaliculata* d'Orb.)

genus *Phaneroptyxis* (*Nerinea moreana* d'Orb.)

Family Nerineidae

genus *Nerinea* subgenus *Nerinea* 'section' *Nerinea*
(*N. tuberculosa* Defrance but see Chapter 2 for discussion)

'section' Acrostylus

(N. trinodosa Voltz)

'section' Melanioptyxis

(N. altararis Cossmann)

subgenus Diozoptyxis (N. monilifera d'Orb.)

subgenus Ptygmatis (N. bruntrutana Thurmann)

subgenus Aphanoptyxis (Cerithium defancii
Deslongchamps)

genus Nerinella subgenus Nerinella (N. dupiniana d'Orb.)

subgenus Bactroptyxis (N. implicata d'Orb.)

subgenus Aptyxiella (N. sexcostata d'Orb.)

genus Trochalia subgenus Trochalia (N. annulata Sharpe)

subgenus Cryptoplocus (N. depressa Voltz)

subgenus Endiaplocus (Turritella roissyi d'Archiac)

Cossmann's unification of the Tubiferidae, Nerineidae and Itieriidae was partially on the basis of the common possession of a juxtasutural selenizone and slit together with the siphonal notch/canal. The presumed common occurrence by Cossmann (op. cit.)of heterostrophic protoconchs in all members was unwarranted (see previously). Nevertheless most subsequent workers accepted, with modifications, this three-fold division of the Nerineid gastropods, although only Taylor and Sohl (1962) considered that the ordinal taxon Entomotaeniata was justified and only Pchelintsev (1965) retained the familial taxon Tubiferidae.

Wenz (1938-44) considered that Nerineid gastropods should be united as a superfamily, the Nerineacea (= Entomotaeniata), with families Ceritellidae (= Tubiferidae), Nerineidae and Itieriidae and later workers such as Cox (1949, 1960, Treatise manuscript) and Fischer (1969) have usually accepted these amendments to Cossmann's (op. cit.) classification. The present author agrees with this classification which ranks the Nerineacea with the Pleurotomariiacea, Murchisoniacea, Patellacea, Cerithiacea etc. An ordinal rank for the Nerineid gastropods would seem to be unjustified although Taylor and Sohl (op. cit.) on the basis of a supposedly close relationship between the Pyramidellids and the Nerineids resurrect Cossmann's (op. cit.) sub-order, the Entomotaeniata, and raise it to an ordinal category of the Opisthobranchia, a position with which the present author cannot agree.

Amongst the western European workers, only Dietrich (1925) considered that Cossmann's (op. cit.) tripartite division of the Nerineid gastropods was inappropriate. According to Dietrich (op. cit. p. 1), "Die Tubiferidae (= Ceritellidae of Wenz) haben mit den Nerineidae das nähtständige Band gemeinsam,es fehlen ihnen dagegen mit wenig Ausnahmendie Falten und der eigentliche Nerineenschlitz an der Mündung." Dietrich (op. cit.) concludes that (p. 1) " ... die Bezeichnung Entomotaeniata zu verwerfen ist, weil es auch ausser den genannten Familien noch Gastropoden mit Schlitzband gibt

(z. B. Pleurotomaria) erscheint die Vereinigung der Tubiferidae, Itieriidae und Nerineidae deswegen wilkürlich." The older classification of Zittel (op. cit.) and others is revised by Dietrich (op. cit.) so that the family Nerineidae (sensu Dietrich) comprises the Nerineidaeand Itieriidae of Cossmann. The belief of Dietrich (op. cit.) that the absence of folds, the reported presence of heterostrophic protoconchs and the supposed absence of the 'true Nerinea slit at the aperture' (see above) in the Ceritellidae necessitates their removal from the Nerineid gastropods may have some validity. However, the presence of a juxtasutural selenizone and siphonal notch/canal is surely an equally valid argument for their retention.

Cox (1949, p. 249) suggested that the subgenera of Cossmann (op. cit.) were well-defined and that their inclusion as subgenera of only a few genera was both unjustified and anomalous. He therefore suggested that they should be elevated to generic status and later, in preparation for the projected Treatise volume, Cox (1954) named several new genera of the superfamily Nerineacea.

In Eastern Europe, V.F. Pchelintsev (U.S.S.R.) was apparently the only worker considering the systematic position and classification of Nerineid gastropods. In a series of publications (particularly 1927, 1954, 1960 - in Orlov, 1963 and 1965) one can observe an 'evolution' in the taxonomy of Nerineid gastropods from a modified Cossmann (1896) classification (Pchelintsev, 1927) into one in which the Nerineids are subdivided into four superfamilies (Tubiferacea, Nerineacea, Nerinellacea and Itieriacea) each containing several new families and new genera (Pchelintsev, 1965). This taxonomic elevation has proceeded so far that it will be difficult to reconcile Pchelintsev's (1965) classification with the current Western European terminology outlined previously. For example, the family Ptygmatisidae contains (according to Pchelintsev, 1965) the following genera, *Ptygmatis*, Sharpe 1850; *Aphanoptyxis*, Cossmann 1896; *Fibuloptygmatis*, Pchelintsev 1965 (= *Nerinea sensu stricto* - see Chapter 2); *Trochoptygmatis*, Pchelintsev 1965; *Scalaeptygmatis*, Pchelintsev 1965 and *Megaptyxis*, Pchelintsev 1965. Working in the Crimea, Caucasus, Armenia and Azerbaydzhan, Pchelintsev has created a large number of new species and many of the genera are based soley on those species - e.g. *Megaptyxis* with three known species according to Pchelintsev (1965) - *M. caucasica* Pchelintsev, *M. taurica* Pchelintsev and *M. suatensis* (Pchelintsev). Clearly any attempt to evaluate the work of Pchelintsev will prove very difficult with the attendant problems of language and the availability of type-specimens. The task would be made easier if some systematic conceptual basis/bases for Pchelintsev's (1965) classification were apparent but, as will be discussed later, it is difficult to ascertain a clear 'theme' upon which this classification was based.

The earliest classification given by Pchelintsev (1927) concerns only those Nerineid gastropods which constitute the family Nerineidae (*sensu* Cossmann, 1896) which according to Pchelintsev (1927) comprises:

Genus *Nerinea* subgenus *Nerinea*
    subgenus *Cossmannea* subgen. nov.
        (type-species *N. desvoidyi* d'Orb.)
    subgenus *Melanioptyxis*
    subgenus *Endiatrachelus*

Genus *Nerinella* subgenus *Nerinella*
    subgenus *Bactroptyxis*
    subgenus *Polyptyxis* subgen. nov.
        (type-species *Ptyg. nodosa* Voltz)
    subgenus *Triptyxis* subgen. nov.
        (type-species *N. acutecochleata* Broili)
    subgenus *Aptyxis* subgen. nov.
        (type-species *Aptyxiella infravalanginensis* Chottat)

Genus *Ptygmatis* subgenus *Ptygmatis*
    subgenus *Aphanoptyxis*

Genus *Diozoptyxis*

Genus *Cryptoplocus* subgenus *Cryptoplocus*
    subgenus *Endiaplocus*

Genus *Diptyxis*

The family Nerineidae is placed by Pchelintsev (1927) in the Prosobranchia.

In his final work (Pchelintsev, 1965) all Nerineid gastropods (= Entomotaeniata of Cossmann, 1896; superfamily Nerineacea of Wenz, 1938-44 and Cox, 1954) are included in a new order the Murchisoniata (Prosobranchia) which includes the following,

Superfamily Murchisoniacea	
Superfamily Tubiferacea	Family Ceritellidae
	Family Pseudonerineidae
Superfamily Nerineacea	Family Fibuloptyxisidae
	Family Nerineidae
	Family Ptygmatisidae
	Family Cryptoplocusidae
	Family Diozoptyxisidae
	Family Diptyxisidae
Superfamily Nerinellacea	Family Nerinellidae
	Family Elatiorellidae
	Family Bactroptyxisidae
	Family Elegantellidae
	Family Auroraellidae
	Family Upellidae
	Family Polyptyxisidae
	Family Triptyxisidae
Superfamily Itieriacea	Family Itieriidae
	Family Phaneroptyxisidae
Superfamily Procerithiacea	
Superfamily Cerithiacea	
Superfamily Turritellacea	
Superfamily Scalacea	

Pchelintsev's definition of the new order Murchisoniata (of equal rank to the Archaeogastropoda, Mesogastropoda and Neogastropoda) is as follows (1965, p. 4)

"Comprising neritic marine organisms that are often associated with coral colonies, the order ranges from the Cambrian through the Recent. Shells are small to large and conical - or oval-turreted with the mantle notch in the middle of the lateral surface of the whorls or at the top, directly at the suture line; rarely the mantle notch is in the lower half. The whorls are contiguous, slightly overlapping or completely enveloping each other. Suture line is often found on the sutural ridge formed by elevation of margins of successive whorls. Shells smooth or with longitudinal and transverse ribs or rows of tubercles. Umbilicus of varying width or absent. The aperture is oval, oval-tetragonal, or rhombic. As many as seven interior spiral folds may protrude into the apertural cavity. In its anterior part the aperture either has a siphonal notch or, more commonly, is extended to form a short siphonal canal."

It has already been suggested previously that the Nerineid slit and selenizone cannot be considered homologous with the median sinuses of the Turritellacea and other groups, and furthermore, median sinuses together with siphonal notches or canals are not universal features of the Procerithiacea, Cerithiacea or Turritellacea. On the basis of the above definition, it is difficult to understand why other groups of gastropods such as the Loxonematacea and the Pyramidellacea have been excluded from the order Murchisoniata. The present author believes that the creation of a new order is, at present, unjustified and the various superfamilies above can be adequately distributed amongst the three conventional orders of the Prosobranchia (or two orders if one accepts Cox, 1960, where the Mesogastropoda and Neogastropoda are combined into the Caenogastropoda).

Within the Nerineid gastropods, Pchelintsev (1965) has retained two of Cossmann's (1896) families - the Tubiferidae (now elevated to a superfamily, the Tubiferacea) and the Itieriidae (also elevated to a superfamily, the Itieriacea). The family Nerineidae (sensu Cossmann, 1896; Wenz, 1938-44 and Cox, Treatise manuscript) has been divided into two superfamilies, the Nerineacea and the Nerinellacea. This much, at least, can be equated between the Western European workers and Pchelintsev's work. Indeed the principle of a fourfold division of Nerineid gastropods (first proposed by Pchelintsev, 1960) was later accepted by Taylor and Sohl (1962, p. 11) and incorporated in their gastropod classification.

The only points of general agreement amongst Nerineid workers are that the Ceritellidae (= Tubiferidae) and Itieriidae are two distinct groups of Nerineid gastropods. Pchelintsev (1960 and 1965) divides the remainder into two groups, the Nerineacea and Nerinellacea which may initially seem justified but the bases upon which this subdivision was made seem to be both arbitary and illogical (see later). The present author therefore continues to place the remaining Nerineid genera in the family Nerineidae.

It has already been suggested that the status of Nerineid gastropods is comparable with that of the Pleurotomariacea, Murchisoniacea, Conacea, etc. and therefore the Western European usage of the superfamily Nerineacea is followed as defined below.

Subclass Prosobranchia Milne Edwards

Order Caenogastropoda Cox

Superfamily Nerineacea Wenz

Shell very diverse in form, usually highly acute and multispiral but ovate or even obconical and involute in certain genera. Protoconch reportedly heterostrophic in Ceritella and Pseudonerinea but otherwise unknown. Aperture usually with a distinct siphonal outlet, either a notch or a short canal. Outer lip of aperture strongly opisthocline, ending apically in a deep slit which generates a narrow juxtasutural selenizone. Walls of whorls frequently bearing, internally, a series of folds which restrict the whorl cavity but are absent at the aperture.

Family Nerineidae Zittel

Aciculate to broadly conical, with or without umbilicus, shell wall thick. Protoconch unknown. Whorls numerous with little overlap, whorl section rectangular or rhomboidal; proportionate height of last whorl small. Sutures never much impressed and often located on a bulging band. Ornament absent or consisting of spiral threads or of rows of tubercles which are only occasionally joined by axial ridges. Peristome interrupted by a siphonal notch or short canal but rarely almost entire. Outer lip opithocline with a well developed slit and selenizone just below the suture. Whorl cavity of spire usually constructed by folds, either simple or complicated, variously present on the columella, upper outer or lower walls.

Family Itieriidae Cossmann

Ovate, ovate-conical or cylindrical, with or without umbilicus. Aperture narrow and occupying at least one-third, and sometimes the whole, of the total shell height. Shell wall thick and protoconch unknown. Whorls flat or feebly convex, smooth or tuberculate, each widely overlapping the preceding one. Whorl section narrow, curved and axially elongate. Siphonal outlet a notch. Outer lip, as in the Nerineidae, with a deep slit and juxtasutural selenizone. Whorl cavity reduced by a series of internal folds.

Family Ceritellidae Wenz
(= Tubiferidae Cossmann)

Moderately acute to squat, with a conical spire of numerous whorls and a rather globose or subcylindrical last whorl occupying up to one-half, but often a much smaller proportion, of the shell height. Umbilicus narrow or absent. Protoconch reportedly heterostrophic in _Ceritella_ and _Pseudonerinea_. Siphonal outlet an ill-defined notch. No internal folds.

Further subdivision of the Nerineacean families

The problems of further subdivision of the Nerineacean families (or Soviet equivalents, see previously) have not yet been satisfactorily solved. As noted by Cox (1949, p. 249) "There has been much difference of opinion as to which characters (e.g. general shell-form, presence of umbilicus, number of apertural folds, nature of external ornament) are of most importance, the classifications proposed differ considerably in the status accorded to each."

The proposed relationship between the mode of life and the number of folds in Nerineid gastropods has been outlined in Chapter 5. If the number and development of folds is ecologically controlled, then presumably the classificatory value of the fold morphology in the various Nerineid genera is of little phylogenetic significance. In this context it is interesting to note that most authors have been intuitively wary about the use of Nerineid fold configurations in any proposed classification e.g. Cossmann (1896, p. 9) who regarded "les différences résultant du nombre ou de l'absence des plis ne paraissent avoir qu'une valeur accessoire au point de vue de la séparation des familles, et justifient tout au plus la séparation des genres et des sous-genres dans chaque famille." In spite of this statement, the genera, subgenera and 'sections' of Cossmann's (1896) classification (see previously) were not in general based upon the fold patterns but upon external shell morphology (see Cossmann, 1896, pp. 29-31).

However, surely exactly the same problems which exist with Nerineid fold morphology, exist with all features of Nerineid shell morphology. The presence or absence of an umbilicus in modern gastropods is consistent within a species although some species vary in the degree of conspicuousness of the umbilicus (e.g. Gibbula umbilicalis, G. cineraria and Monodonta lineata - pers. comm. Prof. A. Graham, 1971). Likewise within a single family of modern gastropods, some genera are umbilicate and some are not (e.g. in the Turbinidae, Turbo is non-umbilicate and Angaria is umbilicate). Therefore can the presence or absence of an umbilicus in Nerineid gastropods be considered as significant other than at the specific or generic level?

When considering the extensive morphological diversity of the Nerineacea (see previously), it is surely not unlikely that much of this variation is ecologically based, the major constraints upon Nerineid shell design being mobility through the substrate in infaunal forms and stability together with hydrodynamic streamlining in epifaunal forms (cf. Bactroptyxis and Melanioptyxis). Therefore are variations in Nerineid shell morphology any more reliable for classification than the number of folds?

The problem of the evaluation of Nerineid shell characters is perhaps one that is not capable of a final solution although two possibilities exist which will at least make Nerineid systematics less unwieldy. One can either abandon the concept of a phylogenetic classification and erect an essentially monothetic grouping which would at least provide an identification key for the various Nerineid genera or one can attempt a polythetic arrangement which places together organisms on the basis of the greatest number of shared features with the possibility that this may reflect Nerineid phylogeny.

The first solution was attempted by Delpy (1939) and Cox (Treatise manuscript) whilst Pchelintsev (1965) attempted a phylogenetic classification. Delpy (1939) accepted the earlier tripartite division of the family Nerineidae (sensu Cossmann, 1896) based upon external shell morphology, into Nerinella, Nerinea and Trochalia.

These genera were each then divided into several subgenera distributed amongst seven 'grades' of fold development i.e. grade 1 = no folds; grade 3 = 2 folds, 1 columellar and 1 parietal; grade 7 = 4 folds, 2 equal columellar, 1 parieto-columellar and 1 labral etc. However, Delpy (op. cit.) was forced to conclude that representatives of some of the grades were unknown and the classification proved of little practical value.

In a similar manner, Cox (Treatise manuscript) divided the Nerineidae into groups of genera characterised by a) genera with four or more folds, b) genera with 1-3 folds, umbilicus absent or narrow, c) genera with 1-3 folds and broad umbilicus, d) genera without internal folds.

The inconsistencies produced by these classifications places Aptyxiella, Nerinella and Bactroptyxis (i.e. all acicular Nerineidae) together as subgenera of Nerinella, according to Delpy (op. cit.) whilst the classification of Cox (op. cit.) - with the number of folds being the primary taxobase - places these three genera into three separate groups (Bactroptyxis in group a, Nerinella in group b and Aptyxiella in group c).

The classification of Pchelintsev (1965) similarly provides many anomalies. The division of the Nerineidae of Western European workers into two superfamilies, the Nerineacea and the Nerinellacea, might seem reasonably justified on the basis that previous workers, particularly Cossmann (1896) and Delpy (1939), had distinguished the genus Nerinella (together with subgenera Aptyxiella, Bactroptyxis, *Nerinella* etc.).because of the common possession of an acicular, turreted shape.

Presumably this is the basis of Pchelintsev's classification for he states (1965, p. 19) "Members of this superfamily (i.e. the Nerineacea) have fairly stocky, conical outlines, reaching considerable size and are thereby sharply differentiated from both earlier and coeval forms of the Nerinellacea" and (p. 87) "Compared with the superfamily Nerineacea described above, members of the new superfamily (i.e. the Nerinellidae) are distinguished by their much greater diversity. The predominant shell outline is narrow, elongate and turreted with a very small spiral angle."

However, the genera *Turbinea* Pchelintsev 1965 and *Funiptyxis* Pchelintsev 1965 are both placed by Pchelintsev (*op. cit.*) in the Nerineacea: family Nerineidae. *Turbinea* (type-species *Nerinea contorta* Buvignier) is extremely acicular and no explanation is offered for the occurrence of a typical Nerinellid morphology in the Nerineacea. Concerning the relationships of *Turbinea*, Pchelintsev (1965, p. 26) states "Phylogenetically the new genus (i.e. *Turbinea*) appearing first in Bathonian times, is associated with such typical members of Nerinea, as *N. bathonica* Rigaux and Sauvage, and this fact determines its systematic position. Curiously we find a similar group of species with the same kind of external adaption to life among stones in a littoral zone also in the family Nerinellidae". The present author is at a loss to explain how the presence of *Turbinea* with *N. bathonica* defines the systematic position of the former.

The speculative phylogenetic proposals of Pchelintsev (op. cit.) also seem to lack supporting evidence. Thus the relationships of the genera comprising the Diozoptyxisdae are as follows (Pchelintsev, op. cit., p. 85) "Examination of the systematic position of Neoptyxis Pchelintsev, described below, has shown Diozoptyxis Cossmann to be the original genus of this family. From it, in turn, descends the genus Plesioptygmatis Böse which is a short phylogenetic branch. Also from Diozoptyxis Cossmann derives the genus Neoptyxis Pchelintsev, from which Plesioplocus Pchelintsev and Laevinerinea Dietrich branched off in the Upper Cretaceous. Neoptyxis Pchelintsev is a local form, found only in the eastern Crimean-Caucasian province, whereas Plesioplocus Pchelintsev and Plesioptygmatis Böse developed mainly in the upper Cretaceous of Transcaucasia and Soviet Central Asia. At the same time Diozoptyxis Cossmann developed mainly in Western Europe and the Crimea, where it is represented by an almost identical species composition." No evidence is provided for the relationships proposed which also fail to adequately account for the fact that Diozoptyxis, Plesioptygmatis and Laevinerinea all originated in the Tithonian (U. Jurassic).

Similarly in the family Ptygmatisidae, Pchelintsev (op. cit.) considers that (p. 51) "We thus have a straight phylogenetic series from Aphanoptyxis Cossmann, which starts in the Bathonian deposits, to Ptygmatis Sharpe from which independant phylogenetic branches of the genera Fibuloptygmatis Pchelintsev (= Nerinea sensu stricto - see Chapter 2). Megaptyxis Pchelintsev, Trochoptygmatis Pchelintsev and *Scalaeptygmatis* Pchelintsev split off in the middle of the Lusitanian." He further states (p. 51) that "The direct ancestors of the genus *Aphanoptyxis* were Middle Jurassic Nerineaceans of the type *Nerinea batonica* Piette." The suggestion that *N. batonica* Piette (3 folds and no umbilicus) evolved into *Aphanoptyxis* (no folds and no umbilicus) which later evolved into *Ptygmatis* (5 folds and umbilicus) is both unsupported and unlikely.

The ambiguities of Pchelintsev's (1965) classification, which admittedly fails to satisfactorily accommodate such a well-defined genus as *Trochalia* Sharpe (see Pchelintsev, *op. cit.*, p. 70), clearly does not solve the problem of the classification of Nerineid gastropods.

In the opinion of the present author, a satisfactory classification of the Nerineacea may never be realised although any attempt to reconstruct Nerineid phylogeny must be based not only upon the various shell characters outlined above but also upon much more detailed stratigraphic and palaeogeographic data than have hitherto been used.

The stratigraphical distribution of the Nerineacea

The oldest recorded Nerineid gastropods are two supposedly Hettangian species of '*Nerinella*'; '*N.*' *grossouvrei* Cossmann from Simon-la-Vineuse, Vendée, France and '*N.*' *norigliensis* (von Tausch) from Sega di Noriglio in N. Italy. Other early species include '*Nerinella*' *ficalhoi* Choffat from the Sinemurian of Vacarica, Portugal and '*Eunerinea*' *timorensis* (Wanner) from the Middle Lias of Timor.

Stratigraphically, the earliest undoubted Nerineid species found in Britain is *Bactroptyxis xenos* (Hudleston) which according to

Hudleston (1887-96, p. 193) occurs "in the shell-bed below the Lower Limestone at Crickley Hill (Aalenian, at the junction of the Opalinum zone, Scissum subzone and the Murchisonae zone, Haugi subzone). Other Aalenian occurrences of Nerineid gastropods in the Cotswolds include "fragments of two species in the Lower Limestone, several feet below the Pea Grit at Selsley" (Witchell, 1886, footnote to p. 29) but no further details are given. However, Witchell (*op. cit.*) also records *B. implicata* (d'Orb.), *Nerinella altivoluta* (Witchell), *Nerinella attenuata* (Witchell) and *Nerinella cingenda* (Phillips) from the stratigraphically higher Pea Grit (Aalenian; Murchisonae zone, Murchisonae subzone).

There was a considerable increase in both specific and generic diversity during the Bathonian stage with 13 Nerineacean genera being recorded from British Bathonian strata compared with 6 from the preceding Bajocian stage of which 5 are common to both.

The expansion and development of Nerineacean gastropods during the Middle Jurassic seems to have been a widespread feature. The generic diversities of Nerineid gastropods during the Jurassic and Cretaceous are shown in Figs. 7:1 and 7:3. The genera comprising the superfamily Nerineacea (*sensu* Wenz, 1938-44; Cox, Treatise manuscript and the Entomotaeniata of Cossmann, 1896) are shown in Fig. 7:1 and the stratigraphic distributions of the three Nerineacean families are shown in Fig. 7:2. The genera comprising the Mesozoic representatives of Pchelintsev's (1965) Murchisoniata are shown in Fig. 7:3. In spite of the generic proliferation of Pchelintsev (*op. cit.*), the overall stratigraphic distributions of the Nerineid gastropods are strikingly

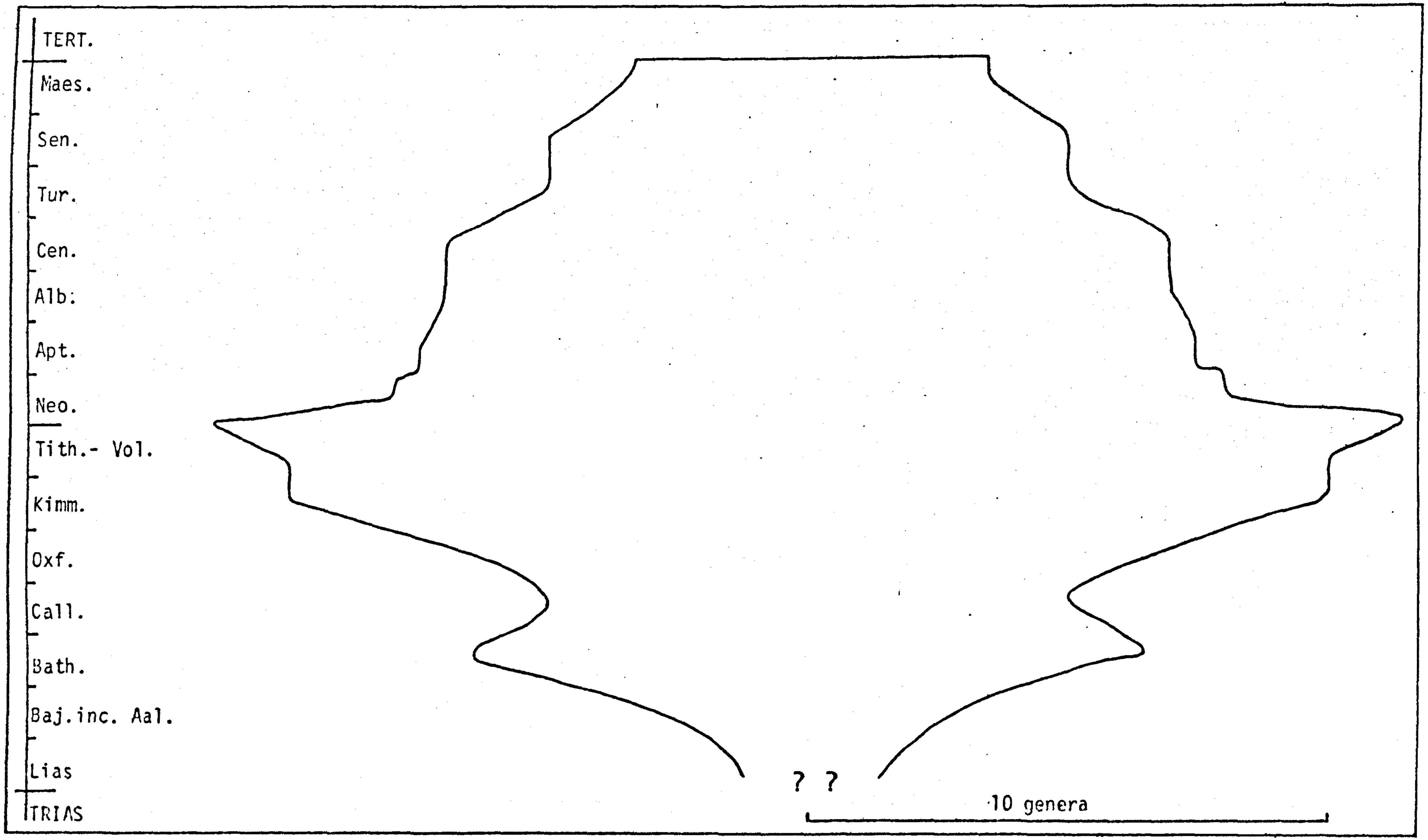


Fig. 7.1. The generic diversity of the superfamily Nerineacea (after Western European workers).

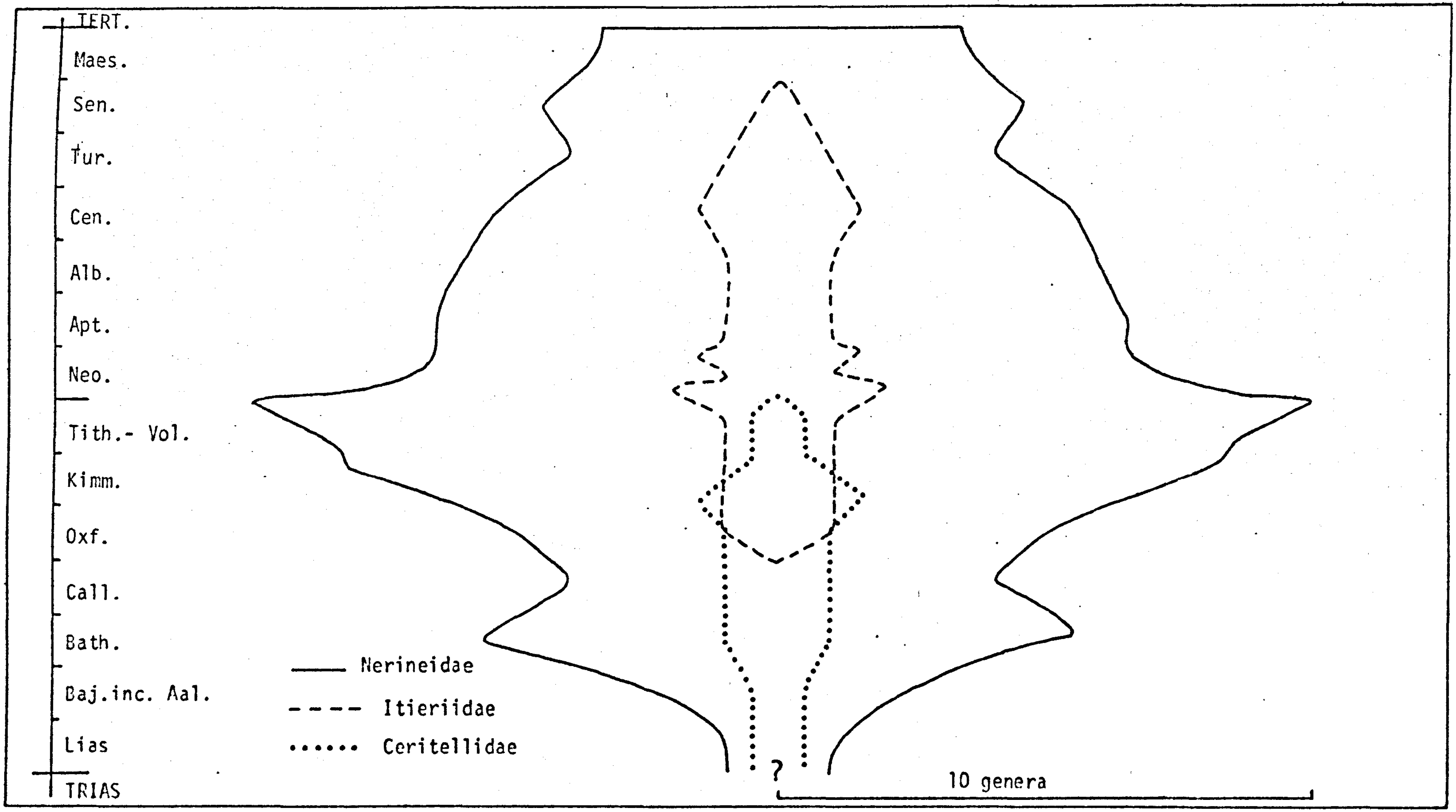


Fig. 7.2. The generic diversity of the Nerineidae, Itieriidae and Ceritellidae (after Western European workers)

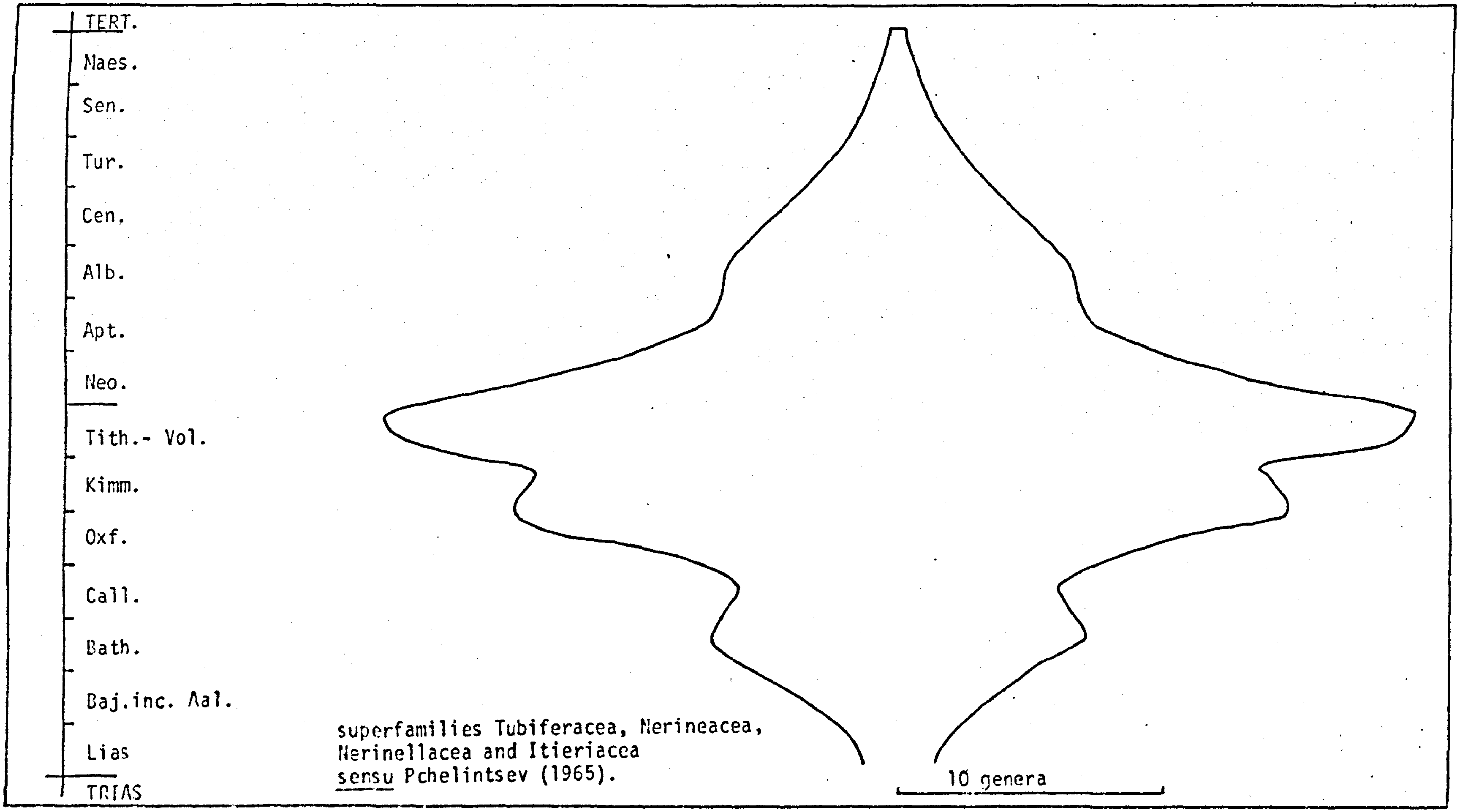


Fig. 7.3. The generic diversity of the Mesozoic representatives of Pchlintsev's (1965) Murchisoniata.

similar. Although some of the peaks in the distributions may be thought of as 'monographic bursts' (e.g. the Middle Jurassic Peak - largely based upon the works of d'Archiac, 1843; Cossmann, 1885, 1896, 1907; Hudleston, 1887-96; Cox and Arkell, 1948-50 etc.), the distribution of the genera also follows the distribution of available carbonate facies suitable for Nerineid gastropods e.g. the reduction in genera during the Callovian reflects the widespread development of clayey facies in Europe at this stage. Hence it seems likely that these diagrams are reasonably accurate reflections of the evolutionary development of Nerineid gastropods in Europe. It is noticable that the acme of Nerineid generic diversity was in the Upper Jurassic, although only one species, <u>Aptyxiella</u> <u>portlandica</u> (J. de C. Sowerby) is recorded from the Upper Tithonian-Volgian (= Portlandian)of Britain. This was followed by a slow decline in generic diversity throughout the Cretaceous until their demise, presumably as part of the world-wide faunal changes at the end of this period.

To what extent this European evolutionary picture will be modified by data from other parts of the world is, as yet, unknown. Nerineid gastropods, like the Rudist Bivalves, reef corals, larger Foraminifera and some Brachiopods (see Adams and Ager, 1967; Hughes, 1973, and Hallam, 1975) are a charactersitic and integral part of the Tethyan fauna and as such have been recorded from Texas (Craigin, 1905) through to Japan (Dietrich, 1925). Many of the Nerineid occurrences outside Europe are still poorly documented. According to Sohl (1965, p. 23) "Nerineid gastropods are among the most common snails found in the

Jurassic rocks of the Western Interior" but they have yet to be described in detail. Later, in a survey of gastropod faunas from North and Central America, Sohl (1969, pp. 1610-1614) noted the Tethyan affinities and restriction of Cretaceous Nerineids to the Caribbean,Central America and Southern U.S.A. region, commenting particularly on the lack of information from the Caribbean.

In this general region, Nerineid faunas of Cretaceous age have been reported from Cuba (Knipscheer, 1938; Woodring, 1952), Jamaica (Dietrich, 1939), St. Domingo and Haiti (Dietrich, 1925) as well as the 'Urgonian' facies of Venuzuala (Von der Osten, 1957) and the Neocomian of Mexico (Böse, 1906 and Cserna, 1956). Further east, preliminary reports of Nerineid gastropods have come from the Aptian of Yasin, West Pakistan (Douvillé, 1926; Ronchetti and Mirelli, 1965) and the Tithonian of Liangdaohe, Northern Tibet (Yin, 1962). Dietrich (1925, p. 4) reports undescribed Nerineid faunas from the Upper Jurassic of Daodkhel in the Western Saltrange, West Pakistan; the Neocomian of the Torinosu formation of Japan and the Neocomian of Somalia. It would appear therefore that, as in Europe, the major phase of Nerineid evolutionary expansion in the Tethyan realm took place in the Upper Jurassic-Lower Cretaceous, although further work is required before a clearer picture of the overall evolution and distribution of Nerineid gastropods emerges.

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