A QUANTITATIVE STUDY OF VARIATION WITHIN THE MESOZOIC ECHINOID NUCLEOLITES.

David Gordon Attilio Scurry, B.Sc.
Department of Geology
Bedford College, London.

Submitted for the degree of Doctor of Philosophy.

1979
A quantitative study of variation within the Mesozoic echinoid *Nucleolites*. D.G.A. Scurry.

**ABSTRACT**

Bivariate (reduced major axes) and multivariate (discriminant functions, canonical variates, principal components, cluster analysis) computer techniques are used to analyse quantitative measurements on fifteen test dimensions of the Mesozoic cassiduloid echinoid *Nucleolites* and its probable living descendant *Apatopygus recens*. A modification to standard techniques is described for analysis of reduced major axes and the cluster analysis.

Twenty samples are analysed. They include nine species of *Nucleolites* from the Jurassic (*N. amplus*, *N. burgundiae*, *N. elongatus*, *N. latiporus*, *N. micraulus*, *N. scutatus*, *N. woodwardii*) of England and France and Cretaceous (*N. rotundus*, *N. subquadratus*) of France and North Africa.

The genotype, *Nucleolites scutatus*, is represented by seven samples. Significant intraspecific variation occurs primarily in size, shape and position of the periproct and in the length of the anal sulcus. A large periproct correlates with large sediment grain size.

No such differences are proved between three samples of *N. latiporus* (= *N. clinicularis* auct.). Statistical differences between *N. latiporus* and *N. scutatus* are of the same order as between intraspecific samples of *N. scutatus*.

Samples of the seven remaining fossil species are compared to the genotype. Quantitatively, differences can be expressed in terms of two test variables, always including either the length of the periproct and/or its distance from the apical disc. The size of the periproct is facies dependent. Within the Jurassic species, the length of the anal sulcus is consistently shorter in the stratigraphically younger species. This trend is not continued in the Cretaceous species. Overall, the distance of the apical disc from the anterior of the test becomes consistently shorter in the stratigraphically younger of the nine species studied.

*N. scutatus* shows a similar range of variation to intraspecific samples of *Apatopygus recens* from New Zealand. *A. recens* burrows completely in a coarse substrate and injects large substrate particles. *N. scutatus* probably did likewise. These habits are therefore of ancient origin in the Cassiduloida.
CONTENTS

Abstract p. 2

1. Introduction p. 4

2. Stratigraphy p. 11

3. Systematics p. 22

4. Methods of Study p. 90

5. Intraspecific variation within Nucleolites scutatus p. 126

6. Biometrics of Nucleolites latinorus p. 158

7. Biometrics of some other Jurassic nucleolitids p. 189


10. Discussion p. 304

11. Summary p. 321

12. References p. 326

List of Plates

Nucleolites scutatus pl. 1
Nucleolites amplus pl. 2
Nucleolites woodwardii pl. 2
Nucleolites elongatus pl. 3
Nucleolites latinorus pl. 3
Nucleolites micralus pl. 4
Nucleolites subquadatus pl. 4
Nucleolites rotundus pl. 5
Apatopygus recens pl. 5
1 A) The genus NUCLEOLITES

Nucleolites is an important Mesozoic irregular echinoid genus because of its common occurrence; its numerous species; its long stratigraphic range; the fact that it is one of the earliest known and arguably one of the most primitive of the cassiduloid echinoids; and because of its presumed ancestry of or close affinity with all other members of the order Cassiduloida.

The first undoubted occurrence of Nucleolites is in the parkinsoni zone of the middle Jurassic upper Bathonian stage. The genus becomes diverse in number of species and locally abundant in number of individuals for the first time in the succeeding Bathonian stage. It seems to reach its acme, judged by common occurrence of individuals and extensive geographic range, in the Oxfordian, N. scutatus Lamarck especially being common in the Corallian (middle and upper Oxfordian) of England and France. Subsequently the genus is represented by less common individuals but comprises species showing a greater range in morphology. In the Cretaceous it gives rise to many new genera but also disappears from England by this time. It is then of frequent occurrence only in eastern France, Germany and Switzerland. By the upper Cretaceous it is found mainly in Morocco, Algeria and Tunisia, the last undoubted Nucleolites species, N. rotundus (Peron & Gauthier), occurring in the Cenomanian of Algeria (Kier, 1962).

The genus is diverse with over eighty named species (sensu Lambert & Thiéry, 1909). They occur most commonly in limestones and in the north west European area. The greatest
number of species as opposed to individuals occurs in the Neocomian (fig.1,1).

The total range of the genus from upper Bajocian to Cenomanian represents a time span of some sixty nine million years (Harland et al., 1964). This is significantly longer than most other cassiduloid genera (sensu Kier, 1962).

In that it occurs in the Bajocian, barely two stages later than the earliest known cassiduloid (Galeropygus Cotteau, 1856) in the Toarcian (Kier, 1977), Nucleolites is an early cassiduloid. Kier (1962, 1966) considers it to be not only the type but the ancestral genus of the family Nucleolitidae. The family Nucleolitidae Agassiz & Desor, 1847, is itself one of the largest and oldest families of the Cassiduloida. All other families of the Cassiduloida, with the exception of the contemporary Clypeidae Lambert, 1898, and the ancestral Galeropygidae Lambert 1911, are probably derived from the Nucleolitidae (sensu Kier, 1962).

Nucleolites is therefore an early and long ranging genus which probably formed the root stock of its family and most of the order Cassiduloida (Kier, 1962). The cassiduloids themselves constitute one of the five principal orders of irregular echinoids.

1 B) Taxonomy

Because it is common, Nucleolites has been studied for 300 years. Because it is diverse, and its species widespread throughout west Europe, there has been considerable duplication of nomenclature at both generic and species level.

A number of genera are synonymous. Pomel (1883), for example, erected eight new genera on slight differences in shape and position of the periproct and length of the sulcus. All are now
Figure 1.1. Occurrence of species of *Nucleolites*. (Based on Lambert & Thiéry (1909) and Parisian collections.)
considered synonymous with *Nucleolites* by most authors. There has been considerable controversy related to the use of the names *Nucleolites* and *Echinobrissicus* and this is discussed fully below (p. 22). Wright, Mortenson and Kier, among others, have pointed out the difficulty in distinguishing between species attributed to *Nucleolites*. Cotteau figured many specimens in his works on French echinoids in the latter half of the nineteenth century. Unfortunately his artist made many inaccurate drawings and in the case of *Nucleolites* consistently drew specimens with single pores rather than double pores in each half ambulacrum beyond the petals. This feature has subsequently been found to be of great evolutionary importance within cassiduloid echinoids; single extra-petaloid pores found in only post-Albian cassiduloids (Kier, 1962).

There is need, therefore, to clarify the taxonomy of the genus and its constituent species. *Nucleolites scutatus* Lamarck, 1816, is here confirmed as the genotype.

1 C) Quantitative methods

In order to discriminate effectively between species, some assessment of variation is required at both infra and inter specific level.

Biometrical methods are adopted here because of the particular suitability of echinoids to statistical analysis. The test of echinoderms is internal and so preserves more features suitable for study than most other invertebrates. The approach has been applied to the fossil spatangoid *Micraster* (e.g. Rowe, 1899; Kermack, 1954) and to living spatangoids (e.g. Nichols, 1959, 1962) but not significantly hitherto to cassiduloids. Roman's (1956, 1957) attempts to differentiate species of *Echinolampas* on the basis of
museum collections are the only comparable studies with respect to this order.

1. D) Computer techniques

It is shown that at least 56 different measurements may be taken in order to characterise the form of the Nucleolites test. However, 15 measurements are usually adequate to define the morphology of a local species population.

This study describes samples ranging in size from three to one hundred and thirty three specimens, comprising in total twenty two samples allocated to ten species. Computer techniques are employed to handle this volume of data and perform multidimensional analyses. The techniques themselves (principal components, discriminant functions, canonical variates and cluster analysis) are standard computer procedures, but have not been fully applied to many palaeontological studies in this way.

All specimens data, listings of computer programs RMA, TEST and HIGROUP, and all computer output used in this study have been deposited in the British Museum (Natural History), B.M. (N.H.) specimen numbers are included with the data. Copies of computer programs are available from the author.

1. E) The genus APATOPYGUS

Apatopygus is an extant cassiduloid found mainly in the waters around New Zealand and is probably the closest living descendant of Nucleolites. Indeed it was first described as Nucleolites recens Milne Edwards, 1836, because of its remarkable morphological similarity to the fossil form. Hawkins (1920) removed it from Nucleolites because of the monobasal apical disc in the adult, shorter petals, ambulacral plates beyond the petals having single pores and the possession of 'pyrinid' plating. Kier (1962) has further
removed the genus to a separate family, the Apatopygidae. However, Ooloxygus d'Orbigny has single pores beyond the petals and yet is retained as a nucleolitid by Kier. It has also been shown recently (Kier, 1974) that the apical system is only superficially monobasal in the adult of Apatopygus, and the remaining characters do not appear to justify its exclusion to a separate monogeneric family.

A biometrical comparison between Nucleolites and Apatopygus is made to assess their affinities and clarify evolutionary trends linking the two genera. The palaeoecology of Nucleolites and possible functional significance of intraspecific variation is inferred through the known ecology of its extant relative.

1 F) Acknowledgements

Sincere thanks are extended to Dr. E. P. F. Rose, Bedford College, London for research supervision, guidance with the completion of this thesis and encouragement throughout the course of this study.

I would like to thank those who have given me assistance with field work, both in this country and abroad. They include Dr. H. S. Torrens, University of Keele; Dr. J. M. Hancock, King's College, London; Dr. Simon Kelly, Goldsmiths College, London; Dr. Andrew Scott, Trinity College, Dublin; Dr. Tim Palmer, Oxford and Prof. Tintant, Universite de Dijon. Amongst the museums that have allowed me access to their collections I would like to acknowledge the help I received from Dr. R. F. S. Jefferies, Dr. Hugh Owen and Mr. David Lewis of the B.M.(N.H.); Mr. N. P. Powell, University Museum, Oxford; Dr. Jean Roman, Musee National d'Histoire Naturelle, Paris; Dr. D. Pajaud, Universite de Paris-6 and Prof. Roger and Mme. D. Gaspard, Universite d'Orsay. I would also like to thank Rene Panchaud, Naturhistorisches Museum, Basel for research information. Special thanks are due to M. Rioult, Universite de Caen for the loan of much of the Trouville material and for help and advice with field locations in Normandy.
I am grateful for all the help I received as a research student at Bedford College. I would especially like to thank Mr. Jack Keith and the technical staff of the Geology Department; Miss Jane Olver and Mrs. Orapin Dawson for many hours of useful discussions; Mr. J. D. Valentine, Psychology Department, for help with the statistical work and Dr. P. Pal and the computer terminal staff for their invaluable assistance with the many computing problems that arose during the course of the research work.

I would also like to thank those at Oxford Polytechnic that have helped me with the completion of the thesis. Mr. Colin Bridger for the use of departmental facilities; Mr. David Rees, Department of Mathematics, Statistics and Computing, Mr. Nick Butler, Computer Manager and to Dr. Peter Morris, Department of Biology for their valuable help and also to my colleagues within the Geology Unit for their encouragement and patience during the completion of this work. I am also very grateful to Mr. Phil Cameron and Mr. Martin Eagle for much help and assistance with the photography and to Mrs. Angela Morris for typing the thesis.

I would finally like to thank my wife Geraldine for continued help and encouragement and for assistance with field work.

This research was carried out whilst in receipt of a University of London Postgraduate Scholarship. Fieldwork was financed by grants from the Central Research Fund of the University of London.
CHAPTER 2 - STRATIGRAPHY

The genus Nucleolites ranges in age from the uppermost Bajocian to Cenomanian in age. Examples of the oldest species, *N. latiporus* and *N. woodwardii*, and youngest, *N. rotundus* (Kier, 1962) have been sampled in the present study. Figure 2.1 shows the stratigraphic distribution of the nine species studied with details of the ages of the samples used.

*Nucleolites* has been collected from a number of horizons from the middle Jurassic to the lower Cretaceous in England and France. Figure 2.2 shows the location of all the major sites from which samples have been collected. The present study includes a museum collection of *N. rotundus* from the Cenomanian of North Africa, also shown in the insert. The exact location of the English samples is given by grid reference in Chapters 5 to 7 and in figure 2.5. The locations of the French samples are shown in figure 2.3 a - c.

At some localities *Nucleolites* is found only at certain horizons. Figure 2.4 gives detailed stratigraphic sections of these localities showing the horizons and associated sediments in which *Nucleolites* has been found. Figure 2.5 lists references which give further stratigraphic descriptions of these localities.

Figure 2.5 also details each sample used in the biometric analyses. The samples are arranged by species. The sample name used in the text, the computer codes, sedimentary facies, numbers of specimens collected and used and the ages are given for each sample. The initial letter of the computer name is used as a code to identify specimens of particular samples on computer print-out. Where there is a risk of confusion between samples of similar name, an alternative
Figure 2.1. Stratigraphic distribution of *Nucleolites* species described in the text. Stages and zones follow British Mesozoic Fossils (B.M.(Y.H.), 1972) subzones modified after Wright, (1972).

0 = sample used in quantitative study herein, and other specimens collected by the author.

X = other known occurrences (from literature and museum collections)
Figure 2.2. Map showing localities sampled.

J = Jurassic strata
C = Cretaceous strata
Figure 2,3a. Location of the French samples of Devecey, Doubs; Signy l'Abbaye, Thin-le-Moutier and Villers-le-Tourneur, Ardennes. + = location of sample. Scale: 1cm to 2km.
Figure 2,3b. Location of the French samples of Selongey and Talant, Cote d'Or. + = location of sample. Scale: 1cm to 2km.
Figure 2,3c. Location of the French samples of Luc-sur-Mer, Ranville, Vaches Noires and Trouville, Calvados. + = location of sample.
Scale: 1cm to 2km.
name is also listed. Further details of the sedimentary facies and palaeoecology associated with each sample and the number of specimens collected at each locality are given under the appropriate species description in Chapter 3. The column listing numbers of specimens refers to the total number of Nucleolites collected at each locality for a particular species. Also included are the number of 'perfect' specimens found upon which fifteen variables could be measured. Details of the variables are given in Chapter 4. For many analyses a larger number of specimens could be utilised as all fifteen variables are not always taken into account in the multivariate computer programs. The number of 'perfect' specimens therefore represents the minimum number used in the analysis. For bivariate computer programs all specimens collected are used in analyses.
Figure 2,4. Stratigraphical sections of some of the localities sampled.
Fig. 2, 4. cont.
<table>
<thead>
<tr>
<th>Species</th>
<th>Locality</th>
<th>Sample Name</th>
<th>Computer name and code</th>
<th>Facies</th>
<th>No.spec. collected perfect</th>
<th>Age</th>
<th>Recent Stratigraphic Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>N. scutatus</td>
<td>Bran Point, Dorset (SY 743814)</td>
<td>Bran Point</td>
<td>DORSET D</td>
<td>Fine grained blue-grey marl</td>
<td>28 16</td>
<td>antecedens</td>
<td>Cope &amp; Torrens 1969</td>
</tr>
<tr>
<td></td>
<td>Dry Sandford Quarry Oxon., (SU 466996)</td>
<td>Cothill</td>
<td>HILL H</td>
<td>Fine calc. sandstone</td>
<td>38 17</td>
<td>antecedens</td>
<td>Callomon 1960</td>
</tr>
<tr>
<td></td>
<td>Hennequeville, Calvados</td>
<td>TROUVLE T</td>
<td>TROUVLE T</td>
<td>Dark oomericite</td>
<td>62 47</td>
<td>antecedens</td>
<td>Arkell 1930</td>
</tr>
<tr>
<td></td>
<td>Hennequeville, Calvados</td>
<td>TROUVLE T</td>
<td>TROUVLE T</td>
<td>Grey oosparite</td>
<td>140 60</td>
<td>antecedens</td>
<td>Arkell 1930</td>
</tr>
<tr>
<td></td>
<td>Calne, Wilts., (ST 99765)</td>
<td>Calne</td>
<td>CALNE C</td>
<td>Bionlike</td>
<td>8 5</td>
<td>plicatilias</td>
<td>White 1925</td>
</tr>
<tr>
<td></td>
<td>M4 Wootton Bassett Wilts., (SU 073843)</td>
<td>M4 W.B.</td>
<td>W.B. M</td>
<td>Coarse oosparite</td>
<td>52 17</td>
<td>plicatilias</td>
<td>White 1925</td>
</tr>
<tr>
<td></td>
<td>Upware, Cambs., (TL 542723)</td>
<td>Upware</td>
<td>UPWARE U</td>
<td>Coarse intramicrite</td>
<td>133 76</td>
<td>parandieri</td>
<td>Callomon 1960</td>
</tr>
<tr>
<td>N. latinicus</td>
<td>Stratton Audley Oxon., (SP 602253)</td>
<td>Stratton</td>
<td>6STRAT 6</td>
<td>Bionlike</td>
<td>14 9</td>
<td>discus</td>
<td>Douglas &amp; Arkell 1932</td>
</tr>
<tr>
<td></td>
<td>Hydrequent</td>
<td>HYD M</td>
<td>MHYD M</td>
<td>? Museum collection</td>
<td>8 7</td>
<td>Low or mid</td>
<td>Ager &amp; Wallace 1966</td>
</tr>
<tr>
<td></td>
<td>Pas de Calais</td>
<td>HYD H</td>
<td>TALAL 1</td>
<td>Rubby oolite</td>
<td>10 5</td>
<td>macroceph.</td>
<td>pers. comm.</td>
</tr>
<tr>
<td></td>
<td>Talant, Cote d'Or</td>
<td>Talant</td>
<td>CALNE C</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Figure 2,5. Summary of stratigraphic data for localities sampled and computer descriptions used in figs. 5, 1 to fig. 9, 11.
<table>
<thead>
<tr>
<th>Species</th>
<th>Location</th>
<th>Code</th>
<th>Site</th>
<th>E</th>
<th>Biomicrite</th>
<th>Zone</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>N. elongatus</td>
<td>Stratton Audley, Oxon. (SF 602253)</td>
<td>EL</td>
<td>E</td>
<td>7</td>
<td>2</td>
<td>discus zone</td>
<td>Douglas &amp; Arkell 1932</td>
</tr>
<tr>
<td>N. amplus</td>
<td>Signy l'Abbeye, Ardennes</td>
<td>ABBAYE</td>
<td>A</td>
<td>39</td>
<td>10d</td>
<td>discus zone</td>
<td>Fischer 1969</td>
</tr>
<tr>
<td>N. woodwardii</td>
<td>Marquise, Pas de Calais</td>
<td>MARQU</td>
<td>H</td>
<td>7</td>
<td>4d</td>
<td>Bathonian</td>
<td>Museum coll.</td>
</tr>
<tr>
<td>N. burgundiae</td>
<td>Selongey, Cote d'Or</td>
<td>BURG</td>
<td>B</td>
<td>4</td>
<td>0</td>
<td>Bathonian</td>
<td>Museum coll.</td>
</tr>
<tr>
<td>N. micraulus</td>
<td>Villers-le-Tourne, Ardennes</td>
<td>VILLER</td>
<td>V</td>
<td>45</td>
<td>25</td>
<td>Lower Oxfordian</td>
<td>None</td>
</tr>
<tr>
<td>N. subquadratus</td>
<td>Devecsey, Doubs.</td>
<td>QUAD</td>
<td>Q</td>
<td>25</td>
<td>13</td>
<td>Neocomian</td>
<td>None</td>
</tr>
<tr>
<td>N. rotundus</td>
<td>Bou Saada, Algeria</td>
<td>RGT</td>
<td>R</td>
<td>3</td>
<td>3</td>
<td>Cenomanian</td>
<td>Cotteau et al 1878</td>
</tr>
<tr>
<td>A. recens c</td>
<td>Nelson, New Zealand</td>
<td>NELSON</td>
<td>N</td>
<td>18</td>
<td>4e</td>
<td>Recent</td>
<td>None</td>
</tr>
<tr>
<td></td>
<td>Wellington Harbour, NZ</td>
<td>WELL</td>
<td>W</td>
<td>23</td>
<td>0e</td>
<td>Recent</td>
<td>None</td>
</tr>
</tbody>
</table>

(a) S is used as computer code for combinations of various samples of N. scutatus.
(b) L is used as computer code for combinations of various samples of N. latiporus.
(c) N is used as computer code for combinations of various samples of A. recens.
(d) For the Signy and Marquise samples, totals of 28 and 7 specimens respectively are used for many analyses by excluding variable E.
(e) Many A. recens specimens have spines intact and many analyses excluded variables H and N4.

Figure 2.5 (cont.)
CHAPTER 3 - SYSTEMATICS

3 A) Introduction

1. General problems in the systematics of NUCLEOLITES.

It has long been recognised, perhaps since Pomel's unsuccessful attempt to classify species of Nucleolites into ten different genera (Pomel, 1883), that the taxonomy of this genus is in a much confused state. The confusion originates from two major factors; the variability and widespread occurrence of Nucleolites and the long history of research into the genus.

Since Nucleolites is a variable genus, both widespread and common in many countries in N.W. Europe, authors of many different nationalities have independently designated in total a large number of species, many of them possibly synonymous. There has therefore been a long history of discussion in the literature on this genus (e.g. d'Orbigny 1855, Cotteau 1871, Mortensen 1948, Kier 1962), its nomenclature, number of species, synonymous species and stratigraphic range. The various 'species' of Nucleolites were often described and figured by pre-Linnaean authors and such designations were frequently accepted as valid during the nineteenth and twentieth centuries contrary to the modern rules of zoological nomenclature. Species, including the 'types', were often inadequately defined and described being originally set up to encompass groups of fossils now considered to belong to different families. A confused state of nineteenth century taxonomy resulted from frequent redefinitions of the genus Nucleolites (e.g. Agassiz & Desor 1847, d'Orbigny 1855, Desor 1857, and Pomel 1883) and innumerable duplication of species.
An attempt is therefore made here to solve some of the more important taxonomic problems associated with the nucleolitid echinoids, initially to establish whether Nucleolites or Echinobrissus, or even both names, should be retained as the generic name; to remove from Nucleolites species belonging to other genera; and to redefine, and where necessary synonymise selected species.

The names Nucleolites and Echinobrissus are the two main contenders for the generic title, all other names being generally accepted as invalid or unnecessary (e.g. Mortensen 1948, Kier 1962). The continued use of both names appears to result from convenience and an unwillingness to alter long established names. The retention of long established names is not in itself a bad practice but cannot be accepted when it results in ambiguous and highly subjective taxonomic categories.

This author agrees with Cooke's short analysis according to the rules of the International Code of Zoological Nomenclature (I.C.Z.N.), of the Nucleolites - Echinobrissus problem (Cooke, 1946). It is necessary however to re-examine the pre-Linnaean literature in an effort to understand the nineteenth century concept of Nucleolites as reference is always made to this early literature.

It is also necessary, in such an analysis, to be able to distinguish more critically the two important and very similar species *N. scutatus* and *N. clunicularis*, both used as types for the different generic names Nucleolites and Echinobrissus respectively.

In the following account reference is made to 'scutatus' and 'clunicularis' nucleolitids. The names are used only in a descriptive sense and apply to the generally accepted forms of *N. scutatus* from the Corallian and *N. clunicularis* from the Inferior Oolite, Great Oolite and Cornbrash. The names, at this
stage, do not imply any strict taxonomic categories.

2. Pre-Linnaean concepts of the genus NUCLEOLITES

The earliest reference to a nucleolitid echinoid is that of Plot (1676 p.92) in his Natural History of Oxfordshire. Plot does not name the fossil and figures it with no anal sulcus, but comments on the similarity between Clypeus, Nucleolites and Micraster the three "being flat and depressed on their bases having also some resemblance of a star of five points." He continues to describe Nucleolites by comparing it to Clypeus.

"Found in the fields about Ifley, whose rays like those of Polar Stone (Clypeus) are made of double ranks of transverse lines, whereof the outermost are much longer and extend likewise to the rim of the stone; its substance also like that seems to be a yellow rubble, but not cased that I can perceive with any such laminated substance, or adorned with annulets (tubercles), yet the umbilicus (apical disc) of some of them, it being sometimes divided and foliated like a rose." (probably reference to the larger madreporite of Clypeus which obscures the genital plates of the apical system).

Ifley is to the south-east of Oxford on Corallian strata so it is probable that this record describes 'scutatus' specimens.

This work is followed two years later by Lister's latin account of 'Historie Animalium Angliae' (1678), in which he attempts a systematic classification of known fossils. He groups echinoids with gastropods and belemnites under 'circular stones', but further separates regular and irregular echinoids, grouping together specimens which would now be ascribed to 'Nucleolites', 'Clypeus', 'Micraster' and 'Echinocorys'. A specimen which is clearly Nucleolites is described
under Titular 26 as "Echinites e lapide selenite, quinis radius e duplici serie transversarum lineolarum conflatis." He refers, with a question mark, to Plot's figure as Plot shows no anal sulcus, and states that it is found in large whitish calcareous stones at quarries near Newton Grange fields. Lister's excellent drawing of the specimen shows open petals, a deep groove at the posterior border, and a sulcus reaching the apical system. This probably represents a large elongate variety of 'clunicularis', a form not found in 'scutatus' populations.

Llhwyd (1698) makes a more detailed description of British fossils and names many for the first time. In paragraph 988 (p. 48) he quotes Lister's original Latin description of "Nucleolites" and refers to the specimens of both Lister and Plot, to which he gives the name Echinites clunicularis. He also lists a variety of localities in the Great Oolite, Cornbrash and Corallian of Oxford and Northamptonshire, indicating that he made no distinction between 'scutatus' and 'clunicularis' forms and that the original name E.clunicularis applied to both groups.

In the early eighteenth century two Swiss authors, Scheuchzer and Lang introduced much confusion into the nomenclature by conflating the forms described by the earlier English authors with those now referred to "Micraster", confusion which continued into post-Linnaean literature.

Thus Scheuchzer (1702) figures a fossil spantagoid which he calls Echinites Spatagoides, and yet makes reference not only to the "micrasters" of Lister and Llhwyd but also to Lister's description of "Nucleolites" and "Clypeus". This lack of discrimination between Micraster and Nucleolites is continued in Lang (1708). His genus, Echinites cordatus spatagoidaeus appears to be a spantagoid
from the figures, but he uses Lister's description of "Nucleolites" to describe each of three species assigned to it. Of the three species, distinguished by size only, the larger form is referred to Llwyd's "Micraster" and Scheuchzer's E. spatagoides, while the medium sized species is referred to Llwyd's E. clunicularis as well as the specimens of Lister and Plot. He makes no reference to any previous literature when describing the figures attributable to Nucleolites which he names Echinites cordatus subluteus.

Morton (1712) in the Natural History of Northamptonshire describes three types of echinoid under Llwyd's Echinites clypeatus (i.e., Clypeus). He figures all three specimens; Plate ten, figure 9 is described as "a third sort of a more raised shape" and is taken to be the Echinata clunicularis of Llwyd, found near Peterborough. This probably represents a 'clunicularis' form as Peterborough is adjacent to Bathonian strata, Morton's figure also being elongate with the sulcus reaching the apical system.

Breynius (1732) in an important work solely concerned with echinoids defines the genus and uses the name Echinobrissus for the first time, making reference to Llwyd's Echinites clunicularis by quoting the name 'Luidio clunicularis' in his description. He describes two species, Echinobrissus planior and E. elatior which later authors (e.g., Wright, Cotteau) consider to represent 'clunicularis' and 'scutatus' forms respectively. Breynius is therefore the first author to use a separate generic name for Nucleolites and to distinguish between 'clunicularis' and 'scutatus' forms although he rightly considered both to represent Llwyd's original E. clunicularis.

Other eighteenth century works containing relevant echinoid material include Bourguet (1742) who reproduces many of Lang's
figures giving short redescriptions of each type, and Davila (1767) who describes Echino-spatagites, a Miceraster from the chalk.

3. Post-Linnaean concepts of the genus NUCLEOLITES

The first post-Linnaean author to describe specimens of a nucleolitid echinoid was Leske (1778). He figures a large quadrat specimen under the specific name depressus but placed in the genus Spatangus of Klein. However, his description of the species included a lot of references to species which would now be ascribed to both "Nucleolites" and "Miceraster." He rightly identified his Spatangus depressus with both Echinobrissus species of Breynius and to the Echinolites cordatus subluteus of Lang, and also includes E.spatagoides of Scheuchzer and Echino-spatagites of Davila. Leske was possibly confused by the anterior groove of Miceraster and Lang's damaged specimen of Nucleolites which had only four visible ambulacra.

Leske also describes another species S.subgloboe, an obvious spatangoid to which he refers not only the Echinospatangus cordiformis of Breynius, and a spatangoid of Morton, but also the nucleolitid specimens of Lister, Llhwyd, Morton and Lang already included by Breynius in Echinobrissus. Thus although Leske is the first post-Linnaean author to describe species of Nucleolites (i.e. S.depressus), his generic concept is confused. He separates the Echinobrissus of Breynius from the E.clunicularis of Llhwyd, although these were previously grouped by Breynius, and also included within his species apparently heart-shaped forms of quite different genera. Indeed only Bruguiere (1791), Schlotheim (1820) and Blainville (1830, 1834), have used the name Nucleolites depressa. The name therefore can safely be suppressed, becoming a nomen
oblitum (I.C.Z.N. Article 23 b).

At the beginning of the nineteenth century Lamarck uses the generic name Nucleolites for the first time in his Système des Animaux sans Vertèbres (1801). His description reads:

"Corps ovale ou cordiforme garni des plusieus rangées des prés qui forment des ambulacres complete, rayonnant du sommet à la base. Bouche subcentrale, anus au-dessus du bord."

He makes no reference to earlier works and is apparently unaware of Echinobrissus of Breynius.

Lamarck (1816) further expands his work by redescribing his genus and notes (my translation) "the nucleolites, from the position of the anus closely resemble the cassidulids, they however have incomplete ambulacra which distinguish them whereas in the nucleolites the ambulacra radiate from the summit to the base."

He therefore observes that the more petaloid ambulacra of the cassiduloids distinguish them from the nucleolitids with their long open petals. Lamarck describes four species, the first of which, Nucleolites scutata is described as 'elliptical, subquadrate, convexo-depressed, broad posterior, five complete ambulacra, anus dorsal.' To this species, the type species of Nucleolites, he refers to Echinobrissus planior, Spatangus depressus and Echinites cordatus subluteus as synonyms, again grouping probable 'scutatus' and 'clunicularis' forms under a single specific name. He also lists a second variety to which he refers Echinobrissus elatior of Breynius.

Lamarck is therefore the author of Nucleolites since he is the first post-Linnaean author to use a separate generic name for this group, of which the first described species is Nucleolites scutatus. The only other post-Linnaean author to which Lamarck...
refers to Leske, whose figure (Leske, 1778: plate 61) represents the type form, a large quadrate form found among individuals of 'scutatus' (see also Wright 1859, Cotteau 1871).

The first post-Linnaean author to use the name Echinobrissus is Gray (1825). His description is a direct translation of Lamarck's original definition of *Nucleolites* of 1801. Gray's description reads: "Body ovate or cordiform, rather convex grooved in front, ambulacra ten in pairs radiating without interruption from vertex to mouth. Mouth subcentral anus dorsal." His first described species, and therefore genotype is *Nucleolites scutatus* Lamarck to which he refers *Echinobrissus planior* of Breynius.

*Echinobrissus* Gray is clearly therefore a junior objective synonym of *Nucleolites* Lamarck, both having the same genotype *Nucleolites scutatus* Lamarck. The name *Nucleolites* Lamarck became well established during the first half of the nineteenth century; important redescriptions are given by Eudes Deslongchamps 1824, Defrance et al. 1825, Goldfuss 1826, Blainville 1830 and Agassiz 1839. D'Orbigny (1854) however, restored the generic name *Echinobrissus* Breynius on the grounds that when Lamarck defined *Nucleolites* he was unaware of the earlier description by Breynius, who is therefore the senior author. This interpretation was accepted by Desor (1857), Wright (1859) and Cotteau (1856), all of whom reversed the nomenclature of their previous publications.

Desor (1857) used d'Orbigny's restoration of *Echinobrissus* but also kept the name *Nucleolites* because of its popular usage and attempted to redefine the genus in order to distinguish it from *Echinobrissus*, following Agassiz and Desor (1847). The important points of Desor's redescription are that *Nucleolites* is small, long; petals lanceolate, straight poriferous zones, conjugate
pores; summit always eccentric anteriorly; sulcus never reaches the summit. Peristome eccentric anteriorly, pentagonal, transverse or oblique, floscelle rudimentary without bourrelets; range Cretaceous to Tertiary. The definition, age range and species included within the genus indicate that Desor was referring largely to Nucleopygus, although he had used the name Nucleopygus earlier in his work. This use of Nucleolites is contrary to I.C.2.N., in that Nucleolites is an occupied name, unavailable for redefinition. Desor's distinction between Nucleolites and Echinobrissus on the presence or absence of conjugate pores cannot be maintained, as this character is seen to be variable in single specimens as pointed out by A. Agassiz (1872) and Duncan (1887).

However, despite this arbitrary use of generic names the misconception of the existence of two separate genera has persisted to relatively recent times, with the continued misuse of the name Nucleolites in the sense of Desor (e.g., Cotteau and Triger 1867, A. Agassiz 1872) or a further redefinition (e.g., Pomel 1883, Lambert and Thiéry 1921, Zittel 1879). Many authors (e.g., A. Agassiz 1872, Cotteau 1871, Duncan 1887, Mortensen 1948) have admitted the inadequacies of any distinction between Echinobrissus and Nucleolites and yet "... because of the great number of species it is practical to keep these genera, even though it may in several cases be questionable to which of them some species should be referred" (Mortensen 1948, p.173). Such interpretations are neither helpful to taxonomy nor valid under the rules of the International Code of Zoological Nomenclature, and therefore one generic name only must be used.

4. Summary

It is apparent that only one generic name is applicable to this group of nucleolitid echinoids, a view supported by
Wright 1859, Beurlen 1933, Cooke 1946, Durham & Melville 1957 and Kier 1962, although Wright and Beurlen suppressed *Nucleolites* in favour of *Echinobrissus*. However, it has been shown that *Nucleolites* Lamarck 1801 is without doubt the senior name and that *Echinobrissus* Gray 1825, the first post-Linnaean use of this name, is a junior objective synonym. The generally accepted authorship of *Echinobrissus* Breynius is invalid under Article 50 as the name is pre-Linnaean and not available under Article II(a).

It can also be shown that the generally accepted type species of *Echinobrissus*, *E. clunicularis*, is a junior subjective synonym of *Nucleolites scutatus*, the genotype of *Nucleolites* (see p. 62).

**3 B) The genus NUCLEOLITES**

Order *Cassiduloida* Claus, 1880

Family *Nucleolitidae* Agassiz & Desor, 1847

Remarks

The family name 'Nucleolides' was first proposed by Agassiz and Desor (1847) and, although not a latinized name, the present author disagrees with Mortensen (1948:119) that it therefore has no legal priority against d'Orbigny's (1855) correctly latinized form *Echinobrissidae*. Article IIc (ii) and (iii) of I.C.Z.N. states that a family group published before 1900, but not latinized, is still available in properly amended form. The name *Nucleolitidae* is therefore adopted here, following Kier (1962, 1966).

*Nucleolitidae* and *Echinobrissidae* appear to be the only two names that have been used for the family.
Genus *Nucleolites* Lamarck, 1801 (non Desor, 1857)

**Synonymy**

1825 *Echinobrissus* Gray, p. 429.
1883 *Clitopygus* Pomel, p. 59.
1883 *Holcaepygus* Pomel, p. 59.
1883 *Notopygus* Pomel, p. 59.
1883 *Lophopygus* Pomel, p. 59.
1883 *Cliniculus* Pomel, p. 59.
1883 *Acromazus* Pomel, p. 59.
1883 *Thigopygus* Pomel, p. 59.
1883 *Taphropygus* Pomel, p. 59.

The generic names of Pomel (1883), with the exception of *Clitopygus*, have never been generally accepted. However, because of the long history of the genus and the frequent misuse of the name *Echinobrissus* in the literature both *Nucleolites* and *Echinobrissus* are listed here in detailed synonymy.

1732 *Echinobrissus*; Breynius, p. 62.
1801 *Nucleolites*; Lamarck, p. 347.
1816 " ; Lamarck, v. 3, p. 36.
1824 " ; Eudes Deslongchamps, p. 570.
1825 " ; DeFrance, p. 213.
1825 *Echinobrissus*; Gray, p. 429.
1826 *Nucleolites*; Goldfuss, p. 137.
1830 " ; Blainville, p. 188.
1834 " ; Blainville, p. 206.
1836 " ; Agassiz, p. 19.
1837 " ; Bronn, v. 1, p. 281.
1837 " ; Desmoulins, p. 356.
1839 " ; Agassiz, p. 39.
1840 Nucleolites; Agassiz, p.4.
1840 " ; Dujardin, v.3, p.341.
1847 " (non Type B); Agassiz & Desor, p.95.
1854 Echinobrissus; d'Orbigny, p.24.
1855 " ; d'Orbigny, v.6, p.388.
1855 Nucleolites; Aradas, p.12.
1857 Echinobrissus; Desor, p.257.
1859 " ; Wright, p.331.
1862 " ; Dujardin & Hupé, p. 578.
1867 " ; Cotteau & Triger, p.418.
1871 " ; Cotteau, v.9, p.233.
1871 " ; Desor & Loriol, p.305.
1872 Echinobrissus; Agassiz, p.108.
1873 " ; Loriol, p.254.
1874 " ; Quenstedt, p.433.
1879 " ; Zittel, p.529.
1879 Echinobrissus; Zittel, p.528.
1881 " ; Cotteau, Peron & Gauthier, p.161.
1883 " ; Cotteau, p.108.
1883 " ; Pomel, p.58.
1883 Nucleolites; Pomel, p.57.
1887 Echinobrissus; Duncan, p.429.
1889 " ; Gauthier, p.47.
1891 " ; Duncan, p.157.
1898 Nucleolites; Lambert, p.25.
1903 " ; Delage & Herouard, p.264.
1904 " ; Meissner, p.1385.
1913 " ; Jackson, p.289.
1921 " ; Lambert & Thiery, p.244.
1921 Echinobrissus; Lambert & Thiéry, p.343.
1932 " ; Mercier, p.227.
1933 " ; Beurlen, p.31.
1935 Nucleolites; Smiser, p.50.
1936 " ; Maury, p.276.
1946 " ; Clark, p.354.
1946 " ; Cooke, p. 222.
1948 " ; Mortensen, p.175.
1948 Echinobrissus; Mortensen, p.171.
1957 Nucleolites; Durham & Melville, p.269.
1962 " ; Kier, p.56.

Type species

N.scutatus Lamarck 1816, by subsequent designation,
Lambert, 1898, p.168.

N.scutatus is the first species described by Lamarck
under his genus Nucleolites. Two other species listed in the
earlier (Lamarck 1801) work are not described but are still
available under I.C.Z.N. Article 16 a (v). However, the names have
not been used since 1801 and each becomes a nomen oblitum under
Article 236.

Description

Small to medium size cassiduloid echinoid; test oval,
round or subquadrate; greatest width posterior to centre;
moderately inflated; ambulacra petaloid, petals long, open and flush
with test; the outer pore elongate, the inner pore small and round;
ambulacral plates double pored beyond petals; phyllodes little
developed, narrow with two series of pores in each half ambulacrum.

Apical system central or anterior, tetrabasal with or
without complementary or catenal plates; very variable in form.

Periproct supramarginal in a deep sulcus extending from the periproct to the posterior border; periproct may be in contact with the apical system or some distance from it and may not be visible from the aboral surface; area between the apical system and periproct may be a depression or groove, a continuation of the anal sulcus, or flat if the periproct is widely separated from the apical system.

Peristome pentagonal, anterior depressed, with no buccal pores or bourrelets.

Tubercles perforate, crenulate, larger adorally than aborally.

Distinguishing Features

In general morphology Nucleolites is most similar to Phyllobriessus but is distinguished by its more oval, wider test, more anterior periproct, lack of bourrelets, and a generally less well developed floscelle.

The floscelle also distinguishes Nucleolites from Clypeopygus in which the phyllodes are broad and bourrelets well developed. The test of Clypeopygus is depressed as opposed to the inflated test of Nucleolites.

Range

Middle Jurassic (Bajocian) to Upper Cretaceous (Cenomanian) of Europe, North Africa and Malagasy.

Discussion

Nucleolites has been shown (e.g., Kier 1962) to be closely related to Clypeus but is distinguished from it as Clypeus has a central apical system, wide petals and broader poriferous zones, and a test usually wider than long. Clypeus also has a well developed floscelle, with longer phyllodes containing three series
of pores in each half ambulacrum and more distinct bourrelets.

Mortensen (1948) rightly points out that larger forms of Clypeus are easily distinguishable from Nucleolites as no nucleolitids grow to a size comparable with the majority of Clypeus species. However, some small species are less easily placed into either genus because of the intermediate nature of some character distinguishing the large clypeoids from Nucleolites. Indeed many genera of the Clypeidae and Nucleolitidae have characters intermediate between the two families (Kier 1962), e.g., Astrolampas, Bothryopneustes and Clypeopygus. Kier (1962) acknowledges this close relationship at the family and generic levels between the two groups, and the intermediate character of many of the species. However, he then includes some species in Nucleolites that clearly resemble Clypeus.

An example is N. amplius Agassiz, a species with wide poriferous zones, elongate slit-like outer pores, central apical disc, long phyllodes often with three series of pores in each half-ambulacra and bourrelets. The peristome is also star-shaped as in Clypeus, the floscelle being well developed. Kier has included this and other ambiguous species in Nucleolites by expanding the normal generic description to include forms with moderately developed bourrelets. However, all early authors have used the lack of bourrelets in Nucleolites to distinguish it from other genera. Indeed Blainville (1830), perhaps the first author to describe Clypeus (Echinoclypeus of Blainville) and Nucleolites in the same work distinguishes five deep grooves around the mouth in Clypeus but does not recognise such features in Nucleolites. Agassiz (1839) also uses the presence and absence of bourrelets to distinguish between the two genera. Agassiz and Desor (1847),
d'Orbigny (1855) and Desor (1857) use the absence of bourrelets in *Nucleolites* to distinguish it from *Catopygus*, *Clypeopygus*, and *Clypeus* and *Clypeopygus* respectively. Cotteau (1871) further states that *Echinobrissus* has no floscelle, is less petaloid and has a more anterior apical disc, characters which he uses to differentiate this genus from *Clypeus*.

However even the absence or presence of bourrelets is open to interpretation by individual authors; faintly, poorly or moderately developed being various intermediate conditions.

Clearly, therefore, single morphological features should not be used as definitive characteristics to distinguish between such closely related groups.

See below for a numerical analysis of the differences and affinities between *N.amplus*, *N.woodwardii* and other *Nucleolites* species.

3 C) Species descriptions

*Nucleolites scutatus* Lamarck, 1816

(Plate 1, fig.1a-d)

Description of the type species

Synonymy

*Listed in synonymy for the genus and species described here are all references which contribute significant data on the morphology, nomenclature, stratigraphic range and geographical distribution of the taxa concerned. Other minor references have been omitted for brevity, or where species identifications could not be verified from published descriptions or museum collections.*

1676 Plot, p.92, table ii, fig.12

1708 *Echinites cordatus subluteus* Lang, p.320, pl.35, figs 1-2.

1732 *Echinbrissus elatior* Breynius, p.63, pl.6, fig.3.

1778 *Spatangus depressus* (in pars) Leske, p.238, pl.51, figs 1-2.
1791 " " (in pars) Leske; Bruguiere, pl.154, figs 5-6.

1816 *Nucleolites scutata* Lamarck, v.3, p.36.

1817a *Clypeus* Smith, pl.6.

1817b *Clypeus clunicularis* (Llwyd); Smith, p.54.

1820 *Echinites depressus* (Leske); Schlotheim, p.313.

1822 *Clypeus clunicularis* Smith; Conybere & Phillips, p.188.

1822 *Nucleolites scutatus* Lamarck; Parkinson, p.126.

1824 " " Lamarck; Eudes Deslongchamps, v.2, p.570
1825 " " Lamarck; Defrance, v.25, p.213.

1826 " " Lamarck; Goldfuss, v.1, p.160, pl.43 fig.6.

1828 *Clypeus clunicularis* Smith; Fleming, p.479.

1829 *Clypeus dimidiatus* Phillips, p.127, pl.3, fig.16.

1830 *Nucleolites depressus* (Leske); Blainville, v.60, p.188.

1834 " " (Leske); Blainville, p.206, pl.16, fig.1.

1836 *Nucleolites scutatus* Lamarck; Agassiz, p.186.

1836 *Nucleolites dimidiatus* (Phillips); Agassiz, p.186.

1837 " " (Phillips); Des Moulins, p.367, No.25.

1837 " " (Phillips); Agassiz, p.279.

1837 *Nucleolites scutatus* Lamarck; Agassiz, p.279.

1837 " " Lamarck; Bronn, p.281, pl.17a, fig.13.

1837 *Nucleolites clunicularis* (in pars); Bronn, p.281.

1837 *Nucleolites goldfussi* Des Moulins, p.367, No.49.

1839 *Nucleolites scutatus* Lamarck; Agassiz, p.45, pl.12, figs 19-20.

1840 " " Lamarck; Agassiz, p.4.

1840 *Nucleolites goldfussi* Des Moulins; Agassiz, p.4.
1840 *Nucleolites paraplesius* Agassiz, p.4.
1840 *Nucleolites scutatus* Lamarck; Dujardin, v.3, p.343.
1840 *Nucleolites dimidiatus* (Phillips); Dujardin, v.3, p.343.
1840 *Nucleolites goldfussi* Des Moulins; Dujardin, v.3, p.343.
1843 *Nucleolites dimidiatus* (Phillips); Morris, p.55.
1843 *Nucleolites scutatus* Lamarck; Morris, p.55.
1847 "
1847 *Nucleolites diamidiatus* (Phillips); Agassiz & Desor, p.95.
1848 "
1848 *Nucleolites goldfussi* Des Moulins; Bronn, p.818.
1848 *Nucleolites paraplesius* Agassiz; Bronn, p.818.
1848 *Nucleolites scutatus* Lamarck; Bronn, p.818.
1849 *Nucleolites clinicularis* (in pars); Forbes, pl.9.
1849 *Nucleolites dimidiatus* (Phillips); Forbes, p.7.
1850 "
1850 *Nucleolites scutatus* Lamarck; d'Orbigny, v.1, p.379, No.507.
1851 "
1851 *Nucleolites dimidiatus* (Phillips); Wright, p.38.
1852 *Nucleolites scutatus* Lamarck; Wright, p.25.
1852 "
1852 *Nucleolites scutatus* Lamarck; Giebel, p.322.
1854 *Echinobrissus scutatus* (Lamarck); d'Orbigny, p.24.
1854 *Nucleolites scutatus* Lamarck; Forbes, p.84.
1857 *Echinobrissus scutatus* (Lamarck); Desor, p.267.
1857 *Nucleolites scutatus* Lamarck; Pictet, v.4, p.217.
1857 *Nucleolites dimidiatus* (Phillips); Pictet, v.4, p.217.
1857 *Echinobrissus elatior* Breynius; d'Orbigny, v.6, p.392.
1857 *Echinobrissus scutatus* (Lamarck); d'Orbigny, v.6, p.392.
1858 "
1858 " (Lamarck); Oppel, p.609
1858 *Echinobrissus dimidiatus* (Phillips); Oppel, p.609.

1859 *Echinobrissus scutatus* (Lamarck); Cotteau & Triger, p.129, pl.22, figs.3-7.

1859 *""* (Lamarck); Wright, p.346, pl.26, fig.2,4.

1859 *Echinobrissus dimidiatus* (Phillips); Wright, p.350, pl.26, fig.3.

1860a *Echinobrissus scutatus* (Lamarck); Etallon, p.18.

1862 *Echinobrissus goldfussii* (Des Moulins); Thurmann & Etallon, p.300, pl.24, fig.4.

1863 *""* (Des Moulins); Credner, p.6, 12, 33.

1864 *Nucleolites scutatus* Lamarck; Bonjour, p.28.

1864 *Echinobrissus goldfussii* (Des Moulins); Etallon, p.331.

1864 *Echinobrissus scutatus* (Lamarck); Seebach, p.52, 74.

1865 *""* (Lamarck); Schauroth, p.142.

1865 *""* (Lamarck); Huxley & Etheridge, p.243.

1867 *Echinobrissus goldfussii* (Des Moulins); Greppin, p.71.

1867 *Nucleolites scutatus* Lamarck; Eichwald, p.252.

1868 *Echinobrissus scutatus* (Lamarck); Guillier, p.29.

1869 *""* (Lamarck); Cotteau & Triger, p.420.

1870 *""* (Lamarck); Greppin, p.83.

1871 *""* (Lamarck); Desor & Loriol, p.315, pl.49, figs.8-10.

1871 *""* (Lamarck); Cotteau, v.9, p.280, pl.76, pl.77, figs.1-5.

1913 *Nucleolites scutatus* Lamarck; Jackson, Fig.408c,d.

1921 *Nucleolites scutatus* Lamarck; Lambert & Thiéry, p.344.

1925 *""* Lamarck; Deecke, p.447, p.456.

1933 *""* Lamarck; Beurlen, p.56, figs.8-9.

1948 *""* Lamarck; Mortensen, p.176, figs.154e,155.

1962 *""* Lamarck; Kier, p.59, figs.1-3, text-figs,30-32,41.

1966 *""* Lamarck; Kier, p.503, figs.389,1a-c, fig.390,1.

1973 *""* Lamarck; Brookfield, p.265.
Type specimen
Location unknown, (Kier, 1962).

Description
Test small to medium sized, sub-quadrate, anterior margin rounded, posterior bilobed and indented by anal sulcus, aborally inflated but rarely conical, margins tumid, adorally concave and undulated with ambulacra depressed and interambulacral areas prominent, peristome depressed; ambulacra petaloid, the petals being long, open, flush with test; interporiferous zone wider than poriferous zone, outer pore elongate, inner pore small and round; posterior interambulacral area is wider than postero-lateral pair which are in turn wider than the anterior pair,

Apical system anterior, tetrabasal, variable in form with catenal and complementary plates rarely present.

Periproct supramarginal, large, rarely in contact with the apical system usually lying between one-third and one-half the distance from the disc to the posterior border, in deep, wide anal sulcus which reaches to the posterior border, usually slight groove between periproct and apical system.

Peristome anterior, depressed, pentagonal, moderately large; floscelle hardly conspicuous, phyllodes narrow, bourselets only slightly developed.

Tubercles perforate, crenulate.

Distinguishing features
N. scutatus Lamarck is most similar to N. latiporus Agassiz (syn. = N. clunicularis), in fact no single diagnostic character
separates the two forms, as noticed by Smith (1817b). However the gross morphology of samples of the two species show that generally the periproct is larger and further from the apical system in *N. scutatus*, the test narrower relative to the length and often more conical in *N. latiporus*. Moreover *N. scutatus* is restricted in range to the Corallian whilst *N. latiporus* ranges from the Upper Inferior Oolite to the Cornbrash (e.g. Arkell, 1933). Biometrical analyses (see Chapter 6) shows that when a sample of *N. scutatus* is compared with a sample of *N. latiporus* homeomorphy does occur in some specimens but the group means are a significant distance apart, indicating that the samples, as a whole, are distinct from one another.

It is distinct from species of similar age, e.g. *N. micraulus*, *N. pulvinatus* and *N. brodiei* as in these species the periproct is nearer the posterior border. This character, the distance between the periproct and the apical system, is considered to be of evolutionary significance in *Nucleolites* (Jesionek-Szymanska, 1968) but the distance is not diagnostic of any particular species or group, contrary to Pomel's system of classification (1883).

**Range**

Middle Oxfordian (cordatum zone) to Lower Kimmeridgian (cymodoce zone) of England, France and Switzerland.

**Discussion**

It has been shown that *N. scutatus* Lamarck 1816 is the type species of *Nucleolites* Lamarck 1801 (see p. 28), although there has been much discussion on the nomenclature of the genus due to its long pre-Linnaean history. All early descriptions, to which many authors refer, did not in fact discriminate between the two species *N. scutatus* and *N. latiporus*, a mistake followed by William Smith (1817b).
resulting in the commonly used name for the Middle Jurassic species, N. clinicularis, becoming invalid.

Material

Measured specimens used in the biometrical analyses:

Collection of the Université de Caen from the type locality, Trouville, Calvados; antecedens sub-zone, 175 specimens.

Personal collections from:
Trouville, Calvados; antecedens sub-zone, 27 specimens.
Bran Point, Dorset; antecedens sub-zone, 28 specimens.
Calne, Wiltshire; plicatilis zone, 8 specimens.
Wootton Bassett, Wilts.; Corallian, 52 specimens.
Cothill, Oxfordshire; antecedens sub-zone, 48 specimens.
Upware, Cambridgeshire; parandieri sub-zone, 133 specimens.

Specimens collected but not used in the biometrical analyses:
Beckley, Oxfordshire; parandieri sub-zone, 18 specimens.
Shellingford Cross-roads, Oxon.; antecedens sub-zone 43 specimens.
Wath, North Yorkshire; antecedens sub-zone 13 specimens.
Appleton-le-street, North Yorks.; vertebralis sub-zone, 34 specimens.
Swinton Grange, North Yorks.; vertebralis sub-zone, 42 specimens.
Lyons Plantaion, North Yorks.; vertebralis sub-zone, 17 specimens.
Vache Noire, Calvados; antecedens sub-zone, 24 specimens.
Bran Point, Dorset; antecedens and parandieri sub-zones, 25 specimens.
Sandhills, Oxfordshire; plicatilis zone, 10 specimens.
North Grimston, North Yorks.; vertebralis sub-zone, 8 specimens.

Additional material:

Cotteau collection, Université de Paris sud, Orsay, 3 figured specimens in Cotteau (1871).
Lambert collection, Université de Paris - 6.
The location of Lamarck's type specimens is unknown. It is proposed to establish the author's personal collection from Trouville, Calvados, the type locality, as neotypes. All measurements taken on these specimens are deposited at B.M.(N.H.).

Palaeoecology

Nucleolites scutatus is found in a variety of calcareous sediments including marls at Bran Point, calcareous sandstone at Cothill, bioclastic limestone at Beckley and oolitic limestones in Yorkshire. The species is perhaps most commonly found in oolitic sediments with a high percentage of bioclastic fragments.

It occurs in 3 of the 17 macroinvertebrate associations of Fursich (1976a & b) usually in association with oysters, infaunal bivalves, pectinids and high spired gastropods. These are, according to Fursich, invariably found in his offshore shelf or lagoonal sequences. However N. scutatus is rarely found with a varied fauna, often only occurring with burrowing bivalves and gastropods. At Upware it is found in great numbers with the irregular echinoids Holecypus depressus, Collyrites bicordata and Pygaster and Hyboclypus although other fossils are rare. At Wootton Bassett it is found with a fauna of small burrowing bivalves, pectinids, gastropods, regular echinoids and small solitary corals.

N. scutatus is most commonly found within sediments in which the dominant allochems are oolites. These are usually high energy sparites e.g. Swinton Grange, Wootton Bassett, Shellingford Cross-roads, Trouville (cliff-section), although some of the oolitic sediments have a micritic matrix e.g. Lyons Plantation, Trouville (shore-section).
Bioclastic fragments are also an important constituent, becoming the dominant allochem at Beckley (biosparite) and Calne (biomicrite). Echinoid, brachiopod, gastropod and bivalve debris is recognisable in most of the sediments under thin section. Quartz is also common within the sediments occurring as either the main grains e.g. calcareous sandstone, Cothill, as the nuclei to the ooliths, e.g. Wootton Bassett, Shellingford Cross-roads, or as silt sized particles scattered throughout the sediment e.g. Swinton Grange, Lyons Plantation.

*N. scutatus* therefore seems to have been well adapted to a variety of environments as it occurs in large numbers in these sediments. The environments represented range from very low energy marls to very high energy oolite shoals, from very shallow water sandstones to perhaps deeper water offshore bioclastic lime muds. Despite its thin test and association with high energy environments *N. scutatus* is unusually well preserved, even in bioclastic and oolitic sediments in which most of the other fauna has been broken down to sand sized particles.

The author has never found *N. scutatus* in association with other nucleolitid echinoids.

Brookfield (1973) includes *N. scutatus* in a list of fauna from the Abbotsbury Ironstone (lower Kimmeridgian, *cymodoce* zone) of England. It occurs in limonitic, fine quartz sandstone beds with a diverse fauna dominated by infaunal and epifaunal bivalves and gastropods. Brookfield interprets this facies as representing a quiet, offshore shelf environment.
**Nucleolites amplus** Agassiz, 1847

(Plate 2, fig. 1a-d)

1847 *Nucleolites amplus* Agassiz, p. 96.

1854 *Echinobrissus amplus* (Agassiz); d'Orbigny, p. 24.

1855 " " (Agassiz); d'Orbigny, v. 6, p. 393.

1857 *Nucleolites amplus* Agassiz; Pictet, 2nd ed., v. 4, p. 217.

1857 *Echinobrissus amplus* (Agassiz); Desor, p. 266.

1859 " " (Agassiz); Wright, p. 357.

1867a " " (Agassiz); Moesch, p. 36.

1867b " " (Agassiz); Moesch, p. 97.

1867 " " (Agassiz); Greppin, p. 55.

1870 " " (Agassiz); Greppin, p. 51.

1871 " " (Agassiz); Desor & Lorio1, p. 310, pl. 49, figs. 3-5.

1871 " " (Agassiz); Cotteau, v. 9, p. 255, pl. 68, figs. 6-11, pl. 69, figs. 1-8.

1921 " " (Agassiz); Lambert & Thiery, p. 344.

1932 " " (Agassiz); Mercier, p. 231, pl. 10, fig. 6.

1962 *Nucleolites amplus* Agassiz; Kier, p. 57, fig. 8, text-fig. 42.

1969 " " Agassiz; Fischer, p. 202, pl. 19, fig. 11.

**Type specimen**

*Nucleolites amplus* Agassiz, 1847, in the Musée d'Histoire Naturelle, Basle, Switzerland.

**Description**

Medium size test, sub-circular to sub-quadrate, posterior margin not bilobed; aborally inflated, flattened apically, rarely sub-conical; margins tumid, adorally flat or slightly concave with ambulacra in depressions and interambulacral areas often prominent; peristome slightly depressed; ambulacra strongly petaloid; outer pore very elongate, slit-like, inner pore small, circular; poriferous
zones as wide or wider than interporiferous zones; petals long, narrowing distally in slight groove on aboral surface; all ambulacra of equal length.

Apical system central, tetrabasal.

Periproct supramarginal, small, often not visible from the aboral view, reaching to apical system in deep narrow sulcus that extends from the periproct to posterior border.

Peristome anterior, pentagonal, star shaped, small; phyllodes long, narrow, pores crowded, up to three rows in each half ambulacrum; moderately developed bourrelets; distinct floscelle.

Distinguishing features

This species is most similar to *N. woodwardii* and may be conspecific with it. Desor & Loriol (1871) discriminated between the species through the flatter test of *N. woodwardii*. Height is a very variable character in irregular echinoids and this may not, therefore, be a safe diagnosis.

It is distinct from other larger orbiculoid echinoids. In *N. burgundiae* the sulcus is some distance from the apical disc and the general morphology is less tumid. *N. orbicularis* is more convex, the sides taper and are less tumid, the base concave, ambitus more circular and the petals longer than in *N. amplus*.

Range

Bathonian of northern France and Switzerland.

Discussion

*N. amplus* is a species which possesses characteristics of both the Clypeidae and Nucleolitidae. Features of the floscelle and petals appear to link it very closely to the Clypeidae, but its general form and growth patterns show affinities to the Nucleolitidae.
This could indicate either that the intermediate character of *N. amplus* shows the division of early cassiduloids between clypeids and nucleolitids is not justified, or that *N. amplus* is a *Clypeus* with growth characteristics similar to *Nucleolites*.

**Material**

Measured specimens used in the biometrical analysis:

Personal collection from:-

Signy l'Abbaye, Ardennes; discus zone, 41 specimens.

Additional material:


**Palaeoecology**

*Nucleolites amplus* occurs at Signy l'Abbaye in association with *N. elongatus* within a sequence of bioclastic peloid limestones, mostly representing moderate energy conditions. The succession is summarised in fig. 2, 4. Six beds are identified on small differences in lithological and faunal composition. Only bed 5 (see fig. 2, 4) yields complete nucleolitids but all beds contain echinoderm fragments as seen under thin section.

The section is composed of two fining upward sequences of peloidal limestones with micrite becoming more common in the finer units. The lower beds of the two sequences (i.e. beds 1 and 4) are also less fossiliferous and more poorly sorted than the higher units. High-spired gastropods (*Nerinella*, *Pleurotomaria*, *Pseudomelania*, *Bactroplyxis*) and rhyynchonellid brachiopods (*Kallihrynchia deliciosa*, *Burmirhynchia turgida*, *Isjuminella thierachensis*) are common throughout, most of the brachiopods tending to be large and spherical. Solitary corals (*Montlivaltia tenuiradiata*, *Chromatoseris orbilites*) and colonial corals (*Bathycoenia hemisphaerica*, *Thamnasteria rumignyensis*, *T. dissimilis*, *Thecosmilia sp.*) occur throughout the
sequence. Bivalves seem to be restricted to the upper units of
the two sequences (beds 2,3,5 and 6) but deep burrowers e.g.

Pleuromya and Homomya are found only in bed 5 in association with
Nucleolites.

Bed 5 is very fossiliferous and is dominated by cassiduloid
echinoids and infaunal bivalves. Nucleolites amplus is the most
common irregular echinoid but single specimens of N.elongatus,

Hyboclypus gibberulus, Holecotypus depressus and fragments of large
clypeulds were also found. Pseudomelania sp., Kallirhynchia delicosa,

Burmirhynchia turgida and echinoid spines are common whilst a rare
fragment of an ammonite, small corals and some terebratulids
(e.g. Eudesia cardium and Ceresithyris intermedia) were also
found. The infaunal bivalves include the deep burrowers Pleuromya
calceiformis, P.uniformis, Homomya gibbosa and the shallower
Sphaeriola madridi, Opis (Trigonopsis) sp., Anisocardia islipensis.

In thin section bed 5 is a poorly washed peloidal parite of
closely packed, mostly rounded peloids. Most peloids contain an
internal pattern of tubules and may be of crustacean origin
(Horowitz & Potter, 1971). Some small ooliths and much bioclastic
debris is also present along with large patches of micrite. The
micrite may have been brought in by burrowers. Bivalves, gastropods,
brachiopods, echinoids, crinoids and bryozoa are all recognisable
in thin section. Some echinoid fragments have been bored and infilled
with micrite. Although grains are in contact there are large
cavities filled with coarsely crystalline calcite. The rock gives
the appearance of being well sorted, although this may not be a
meaningful observation in a peloidal sediment.

The sediment is bioturbated and was probably deposited
in an environment of moderate energy. There seems to be no direct
evidence, from an examination of the sediment, as to the reason for
the occurrence of Nucleolites in bed 5 and not in the other units
of similar lithology.

Most of the above identifications follow Fischer (1969).

Nucleolites burgundiae (Cotteau), 1871.

1871 Echinobrissus burgundiae Cotteau, v. 9, p. 259, pl. 69, figs. 9-11,
pl. 7.
1908 " " Cotteau; Cotteau, p. 158, pl. 2, figs. 6 & 6a.
1921 Clitopygus burgundiae (Cotteau); Lambert & Thiery, p. 346.
1922 " " (Cotteau); Lambert, p. 35.
1933 Echinobrissus burgundiae Cotteau; Kier, p. 57, text-fig. 36,44.
1962 Nucleolites burgundiae (Cotteau); Kier, p. 57, text-fig. 36,44.

Type specimen

Echinobrissus burgundiae Cotteau, 1871, in the Cotteau
Collection, Université de Paris-sud, Orsay. (Examined and used in
biometrical analysis). Specimens b903, b904 and b905 (a & b).

Description

Test medium sized, sub-circular, slightly longer than wide;
aboral surface uniformly inflated, sometimes conical; base concave
towards the mouth; petaloid, petals of unequal length, posterior
pair longer and flexuous.

Apical disc sub-central, tetrabasal, madreporite large.

Periproct oval, lying one third of the distance from the
apical disc to the ambitus, at the top of a deep sulcus.

Peristome pentagonal, anterior, no distinct floscelle.

Tubercles small, more numerous towards the mouth.
Distinguishing features

*N. burgundiae* is distinguished from *N. orbicularis* by the periproct being separated from the apical disc in *N. burgundiae*. The diagnostic features that distinguish it from *N. amplus* have been discussed above (see p.47).

Range

Bathonian of central France.

Discussion

This species was first described by Cotteau (1871) and placed in the genus *Echinobrissus* after d'Orbigny (1854). It was transferred to Pome's genus *Clitopygus* by Lambert & Thiery because the anal sulcus is separated from the apical system, a character thought to be of no specific value by later authors. It is placed in *Nucleolites* by Kier (1962). The specimen from the Bathonian of Malagasy figured by Cotteau (1908) is a small damaged specimen and may be *N. woodwardii*.

Material

Measured specimens used in the biometrical analyses:

Cotteau's type specimens, Selongey, Cote d'Or; Bathonian (personal communication from Prof. Tintant, Université de Dijon), 4 specimens.

Seyney l'Abbaye, Ardennes; discus zone, 1 specimen.

Specimens collected but not used in the biometrical analyses:

Selongey, Cote d'Or; Bathonian (possibly discus zone), 6 specimens.

Additional material:

Cotteau collection, Université de Paris-sud, Orsay.

Lambert collection, Université de Paris - 6.

Palaeoecology

Little is known of the palaeoecology of *N. burgundiae*. 
Only type specimens, from the Cotteau collection, Orsay, were used in the biometrical analyses and no detailed stratigraphic or palaeoecology data were supplied with them.

Specimens collected from the type locality, Selongey, were from fields and were too badly damaged to be used in the study. The specimens, however, were found in association with large Pholadomya fidicula up to 11 cms. long and smaller, ornate P. deltoidea. Small brachiopods were also found including Epityris, Wattonityris and Sphenorhynchus. Other echinoids included N. latiporus and Holoecyptus sp.

The sediment attached to the fauna is a rubbly bioclastic limestone similar to the English Cornbrash. The strata may indeed be Cornbrash in age as Cipy (1964:17) in a short description of the Bathonian of the Dijon area describes a limestone facies in the Upper Bathonian rich in organic debris. Present are bryozoans, echinoderms, oysters, brachiopods and rare ammonites, one of the ammonites being Clydoniceras discus, giving a lower Cornbrash age to the sediments.

In thin section the rock is a brachiopod-bivalve rich biomicrite, with alignment of the tabular fossil allochems. This may indicate current activity but not enough activity to wash the microcrystalline ooze from the sediment.

The massive nature of the infaunal bivalves and the attached epifauna of brachiopods also seem to suggest an environment of moderate energy.

* Nucleolites elongatus Agassiz 1840
  (plate 3, fig. la-d)

1840 Nucleolites elongatus Agassiz, p. 4.

1847 " " Agassiz; Agassiz & Desor, p. 95.
1848 **Nucleolites elongatus** Agassiz; Bronn, p.818.
1850 **"** **"** Agassiz; d'Orbigny, v.1,p.345,no.260.
1854 **Echinobrissus elongatus** (Agassiz); d'Orbigny, p.24.
1857 **"** **"** (Agassiz); d'Orbigny, p.391.
1857 **"** **"** (Agassiz); Desor, p.365.
1857 **"** **"** (Agassiz); Pictet, p.217.
1857 **"** **"** (Agassiz); Cotteau & Triger, p.55, pl.10, figs. 8-11.
1859 **"** **"** (Agassiz); Wright, p.356.
1859 **Echinobrissus quadratus** Wright; p.344, pl.26, fig.1.
1863 **Nucleolites elongatus** Agassiz; Bonjour, p.19.
1864 **"** **"** Agassiz; Bonjour, p.28.
1865 **"** **"** Agassiz; Ogerien, v.3, p.675.
1867 **Echinobrissus elongatus** (Agassiz); Greppin, p.55.
1869 **"** **"** (Agassiz); Cotteau & Triger, p.419.
1871 **"** **"** (Agassiz); Cotteau, p.264, pl.72.
1921 **"** **"** (Agassiz); Lambert & Thiery, p.343.
1932 **Echinobrissus clunicularis** var. **elongatus** (Agassiz); Mercier, p.229, pl.10, fig.3.
1962 **Nucleolites elongatus** Agassiz; Kier, p.57, text-fig.46.
1968 **"** **"** Agassiz; Jesionek-Szymanska, figs. 7e & f.
1969 **Nucleolites clunicularis** var. **elongatus** Agassiz; Fischer, p.202, pl.19, fig.15.
1974 **Nucleolites elongatus** Agassiz; Kier, fig.276.

**Type specimen**

Location unknown; not in Musée d'Histoire Naturelle, Basle (R. Panchaud, personal communication, 1977).
Description

Test small to medium sized, longer than wide, quadrate, rounded anteriorly, truncated posteriorly with a deep indentation formed by the anal sulcus at the posterior border; convex dorsal surface, concave to flat base; petaloid, narrow poriferous zones, anterior ambulacrum straight, posterior pair longer and flexuous.

Apical system anterior, tetrabasal, elongate.

Periproct small, not visible from the dorsal surface in adult specimens, at the top of an anal sulcus that reaches to the apical disc.

Peristome small, rounded to sub-pentagonal, anterior, distinct phyllodes, faint floccellae.

Tubercles small.

Distinguishing features

*N. elongatus* is superficially similar to *N. latiporus* and, being often found in the same horizon, mixed samples are difficult to separate into the two species. However, a detailed examination of the periproct, breadth relative to length, and peristome will reveal species with different growth patterns but similar juvenile morphologies. Individual specimens of adult *N. elongatus* are distinguished in possessing a smaller peristome and periproct, the periproct not being visible from the dorsal surface in adults, more elongate and quadrate form, and a deeper indentation made by the anal sulcus at the posterior border. The species is probably conspecific with the other large bilobed forms such as *N. triangularis* and *N. cordatus*. *N. elongatus* is quite different from the large elongate form of *N. latiporus*, termed *N. oblongus* by d'Orbigny, as in this variety the periproct is large and remote from the apical disc.
Range

Bathonian (possibly Cornbrash only) of England and France.

Discussion

This species, first listed by Agassiz (1840), is probably conspecific with Wright's *N. quadratus* 1859 also from the Cornbrash. Mercier (1932) considered *N. elongatus* a variety of *N. latiporus* (Mercier's *N. clunicularis*), probably because of the similarity of juvenile specimens of the two species. Mercier's interpretation is shared by Fisher (1969). This species is endocyclic, as described by Jesionek-Szymanska (1968).

Material

Measured specimens used in the biometrical analyses:
Lambert Collection, Université de Paris-6, 1 specimen labelled *N. elongatus*, Bathonian.

Personal collections from:
Stratton Audley, Oxfordshire; discus zone, 7 specimens.
Signy L'Abbaye, Ardennes; discus zone, 1 specimen.

Palaeoecology

*N. elongatus* is found at Stratton Audley in a typical Cornbrash lithology; a very fossiliferous, coarse bioclastic limestone.

The fauna is dominated by brachiopods and bivalves. The brachiopods are represented mainly by terebratulids e.g. the globose *Obovothyris magnobovata*, large *Cererithyris* and the globose rhynchonellid *Kallirhynchia*. The bivalves occur mainly as burrowers and small epifauna e.g. many *Pleuromya* and *Meleagrinella echinata*. There are also many oysters, pectinids and large and small *Pholadomya*. Other fauna includes casts of large gastropods, small solitary corals and belemnites.
N. elongatus is also found in association with other echinoids e.g. the smaller N. latiporus, the small hemicidaroid Hypodiadema and fragments of large clypeids.

The sediment is a poorly washed bivalve-brachiopod biosparite. The bioclastic allochems are dominated by small tabular fragments of bivalves and brachiopods often bound by trapped micrite. Although large patches of micrite are present in the sediment, there is a sparry calcite cement and drusy calcite infillings within recrystallised molluscan fragments.

The skeletal fragments are coated with micrite. These include large and small fragments of punctate and inpunctate brachiopods and thick shelled bivalves, some gastropods, tabular echinoid plates, foraminifera and some ostracods infilled with micrite. A few algal oncoliths and coralline algae are also present. No ooliths can be seen in thin section but there are some large round to elongate amorphous peloids composed of light micritic allochems. The rock as a whole is poorly sorted.

Although much micrite has been left unwashed from the sediment large amounts of highly abraded small tabular bioclastic fragments have been brought into the area by currents. This may, therefore, indicate an original sedimentary environment of moderate energy conditions.

One specimen of N. elongatus was also found at Signy l'Abbaye, Ardennes, in association with N. amplus, and fragments of clypeids within a sequence of bioclastic peloidal limestones. Although the specimen is broken it shows no signs of wear or encrustation due to transportation. The succession at Signy again seems to represent an environment of moderate energy and organic rich sediments (see p. 48 ).
Nucleolites latiporus Agassiz, 1839

(Plate 3, fig. 1a-d)

1678 Lister, p.233, pl.7, fig.26.
1699 Echinites clunicularis (in pars), Llhyd, p.48.
1712 " " Llhyd; Morton, p.233, pl.10, fig.9.
1732 Echinobrissus planior Breynius, p.63, pl.6, figs.1-2.
1817b Clypeus clunicularis (Llhyd)(in pars); Smith, p.69,110.
1828 Clypeus lobatus Fleming, p.479.
1829 Clypeus clunicularis (pars); Phillips, p.115, pl.7, fig.2.
1830 Nucleolites clunicularis (Smith); Blainville, v.60, p.188.
1834 " " (Smith); Blainville, p.206, pl.16, fig.1.
1836 " " (Smith); Agassiz, p.186.
1837 " " (Llhyd); Bronn, p.282, (form A), pl.17a, fig.13.
1837 " " (Smith); Des Moulins, p.358, no.15.
1837 " " (Smith); Agassiz, p.278.
1840 " " Agassiz; Agassiz, p.4.
1840 Nucleolites clunicularis (Phillips); Dujardin, v.3, p.345, no.7.
1843 " " (Phillips); Morris, p.55.
1845 Clypeus clunicularis (Phillips); Buckman & Strickland, p.73.
1847 Nucleolites clunicularis (Smith); Agassiz & Desor, p.95.
1847 Nucleolites latiporus Agassiz; Agassiz & Desor, p.95.
1847 Nucleolites thurmanni Agassiz & Desor, p.95.
1848 Nucleolites clunicularis (Llhyd); Bronn, p.818.
1848 Nucleolites latiporus Agassiz; Bronn, p.818.
1848 " " Agassiz; Marcou, p.79.
1848 Nucleolites thurmanni Agassiz & Desor; Marcou, p.79.
1849 Nucleolites clunicularis (Llhyd); Forbes, pl.9.
1850 " " (Llhyd); Cotteau, v.1, p.65, pl.4, figs.7-12.
1850 Nucleolites conicus Cotteau; v.1, p.64, pl.4, figs.4-6.
1850 Nucleolites edmundi Cotteau; v.1, p.67, pl.5, figs.1-3.
1850 Nucleolites clunicularis (Llhyd); d'Orbigny, v.1, p.319, no.402.
1850 Nucleolites latiporus Agassiz; d'Orbigny, v.1, p.290, no.499.
1850 Nucleolites conicus Cotteau; d'Orbigny, v.1, p.319, no.405.
1850 Nucleolites thurmanni Agassiz & Desor; d'Orbigny, v.1, p.319, no.404.
1851 Nucleolites clunicularis (Llhyd); Wright, p.297.
1851 " " (Llhyd); Bronn, p.152.
1852 Nucleolites latiporus Agassiz; Giebel, p.322.
1853 Nucleolites clunicularis (Llhyd); Gueranger, p.25.
1854 " " (Llhyd); Forbes, p.84.
1854 Echinobrissus clunicularis (Llhyd); d'Orbigny, p.24.
1854 Echinobrissus latiporus (Agassiz); d'Orbigny, p.24.
1854 Echinobrissus thurmanni (Agassiz & Desor); d'Orbigny, p.25.
1854 Nucleolites pyramidalis M'Coy, p.63.
1856 Echinobrissus clunicularis (Llhyd); Wright, p.310.
1857 " " (Llhyd); d'Orbigny, v.6, p.391.
1857 Echinobrissus latiporus (Agassiz); d'Orbigny, v.6, p.391.
1857 Echinobrissus sarthacensis (d'Orbigny); d'Orbigny, v.6, p.391.
1857 Echinobrissus conicus (Cotteau); d'Orbigny, v.6, p.391.
1857 Echinobrissus edmundi (Cotteau); d'Orbigny, v.6, p.391.
1857 Echinobrissus thurmanni (Agassiz & Desor); d'Orbigny, v.6, p.391.
1857 Nucleolites clunicularis (Llhyd); Pictet, v.4, p.217, atlas, pl.94, fig.10.
1857 **Nucleolites clunicularis** (Llhwyd); Etallon, p.22.
1857 **Echinobrissus clunicularis** (Llhwyd); Desor, p.263, pl.30, figs.18-20.
1857 **""** (Llhwyd); Cotteau, p.52, pl.10, fig.7.
1858 **Nucleolites clunicularis** (Llhwyd); Oppel, p.457.
1858 **""** (Llhwyd); Leymerie & Raulin, p.622.
1858 **Nucleolites conicus** Cotteau; Leymerie & Raulin, p.623.
1858 **Nucleolites edmundi** Cotteau; Leymerie & Raulin, p.623.
1859 **Echinobrissus clunicularis** (Llhwyd); Wright, p.332.
1859 **""** (Llhwyd); Chapuis, p.106, pl.20, fig.2
1859 **""** (Llhwyd); Wright, p.25.
1863 **Nucleolites clunicularis** (Llhwyd); Bonjour, p.17.
1864 **Nucleolites conicus** Cotteau; Bonjour, p.20.
1864 **Nucleolites latiporus** Agassiz; Bonjour, p.20.
1864 **Nucleolites thurmanni** Agassiz & Desor; Bonjour, p.20.
1864 **Nucleolites clunicularis** (Llhwyd); Bonjour, p.24.
1864 **Echinobrissus clunicularis** (Llhwyd); Zejszner, table.
1864 **""** (Llhwyd); Seebach, p.43, p.74.
1864 **Nucleolites latiporus** Agassiz; Winkler, p.200.
1865 **Echinobrissus clunicularis** (Llhwyd); Huxley & Etheridge, p.222.
1865 **""** (Llhwyd); Eudes Deslongchamps, p.155.
1865 **Nucleolites conicus** Cotteau; Ogerien, p.736.
1865 **Nucleolites latiporus** Agassiz; Ogerien, p.736.
1865 **Nucleolites thurmanni** Agassiz & Desor; Ogerien, p.736.
1865 **Nucleolites clunicularis** (Llhwyd); Ogerien, p.736.
1867 **Echinobrissus clunicularis** (Llhwyd); Moesch, p.36.
1867 **""** (Llhwyd); Moesch, p.97.
1867 **""** (Llhwyd); Laube, p.2, pl.1, fig.1.
1867 **""** (Llhwyd); Greppin, p.55.
1868 **""** (Llhwyd); Dewalque, p.354.
1868 *Echinobrissus clunicularis* (Llwyd); Guillier, p.25.
1869 “ “ (Llwyd); Cotteau & Triger, p.419.
1869 “ “ (Llwyd); Brauns, p.64.
1869 “ “ (Llwyd); Wright, p.49.
1870 “ “ (Llwyd); Greppin, p.51,p.56.
1871 “ “ (Llwyd); Desor & Loriot, p.305, pl.48,figs.3-8.
1871 “ “ (Llwyd); Cotteau
1913 *Nucleolites clunicularis* (Llwyd); Jackson, fig.408,a,b.
1921 *Echinobrissus clunicularis* (Llwyd); Cotteau,Lambert & Thiery,p.343
1925 “ “ (Llwyd); Deecke, p.440.
1932 “ “ (Llwyd); Mercier, p.227,pl.10,fig.1.
1932 *Echinobrissus latiporus* (Agassiz); Mercier, p.232,pl.10,fig.5.
1933 *Echinibrissus clunicularis* (Llwyd); Beurlen, p.53,fig.8.
1948 “ “ (Llwyd); Mortensen, p.172,figs.149, 151,154(e).
1962 *Nucleolites clunicularis* (Phillips); Kier, p.63.
1967 “ “ (Smith); B.M.N.H., pl.44,fig.2 (pars).
1968 “ “ (Llwyd); Jesionek-Szymanska, fig.8a.
1974 “ “ (Phillips); Kier,fig.27c.

**Type specimen**

Location unknown; the specimen belongs to the Gressly collection (N.Panchaud,personal communication) but is not at Basle or mentioned in the Solothurn Museum type catalogue (Ledermann,1967).

**Description**

Test subquadrate to elongate, anterior margin rounded, posterior bilobed; aborally inflated, often conical, adorally flat, concave towards the peristome, slight depression formed by anterior
ambulacrum only on adoral surface; ambulacra petaloid, open, long.

Apical system sub-central, tetrabasal.

Periproct large, supramarginal, in deep, wide sulcus that usually reaches to the apical disc, although the periproct may not be in contact with the disc; sulcus widens towards the posterior margin.

Peristome circular, becoming pentagonal in the adult, anterior; no bourrelets, poor development of the floscelle.

Distinguishing features.

*N. latiporus* is most similar to *N. scutatus*. The affinities and differences of these two species are discussed under the systematic palaeontology of *N. scutatus*. *N. latiporus* occurs throughout strata of Upper Bajocian and Bathonian age, but is rarely as numerically abundant at any one horizon as *N. scutatus* is in the Upper Oxfordian. For this reason, perhaps, complete ranges in form typical of a large living population are not seen in the fossil state. Many names have therefore been established for the different morphological variants, most now considered to be synonymous with *N. latiporus* (e.g. Cotteau 1871).

*N. latiporus* is similar to *N. elongatus*, in fact juvenile specimens of both species are very difficult to distinguish from each other. Mercier (1932) considered *N. elongatus* as only a variety of his *Echinobrissus clunicularis*. Young forms of *N. elongatus* are distinguished by their more elongate shape and smaller periproct, while adult forms are distinguished by their smaller peristome, deeper indentation of the posterior border and eccentrically posterior apical disc. *N. latiporus* differs from the larger, orbicular nucleolitids, such as *N. amplus*, *N. burgundiae* and *N. orbicularis* in its more elongate, conical, subquadrate shape and bilobed form.
As yet no significant differences have been found to distinguish between the Inferior Oolite, Great Oolite and Cornbrash specimens, which therefore must, for the present, be regarded as conspecific.

Range

parkinsoni zone to mariae zone (upper Bajocian to lower Oxfordian) of England, France and the Swiss and German Jura, according to current usage; parkinsoni zone to top of Callovian as defined herein (p. 313).

Discussion

Although Llwyd (1698) is considered by most later workers to be the author of _N. clunicularis_ (e.g. d'Orbigny 1857, Cotteau 1871, Lambert & Thiery 1921, Mortensen 1948) there is obviously no validity in this designation under Article 11a. of the rules of the I.C.Z.N. The first post-Linnaean use of this specific name among nucleolitid echinoids is by William Smith when describing Corallian, Cornbrash, Great and Inferior Oolite specimens of a small irregular echinoid for which he gave a full systematic description to the Coral Rag form (Smith 1817a, p. 59). The holotype of Smith's material, a Corallian specimen from Maggot's Hill (illustrated in Smith 1817b), is identified only as Clypeus, but in his 'Observations on Echini' (Smith 1817a) he refers again to this species as Clypeus species no. 2 (clunicularis Llwyd). He notices that it occurs repeatedly in these strata although '... a considerable difference in appearance may be traced between the specimens from the Pisolite and others from the Cornbrash and Oolites. These last are thinner at the edge, with a more undulated base and flatter sides, particularly that side containing the groove.' Smith further shows that although a change in morphology is apparent he was unable to isolate
diagnostic characters distinguishing the two forms which we must therefore conclude to have been considered conspecific.

Conybere & Phillips (1822, p.188) and Phillips (1829) refer to 'Clypeus clunicularis (Smith, fig.6)' from the Coral Rag. Phillips also following Smith's range for the species by listing its occurrence in the Middle Jurassic. Smith is therefore clearly considered the author of *N. clunicularis* having described, named and figured this species in 1817, his 'figure 6' being designated the holotype by Conybere & Phillips (1822), Fleming (1828) and Phillips (1829).

However, when the author examined Smith's holotype (B.M. no. E.495), from the Corallian of Maggot's Hill, Coleshill, it was apparent that it is a specimen of *N. scutatus* Lamarck, 1816. The specimen has the morphological characteristics of *N. scutatus* in being rounded, depressed, having tumid sides, a periprostlying some distance from the apical system, a deep indentation on the posterior margin made by the sulcus and an undulated base. See also p. 181 for a computer classification of this specimen. Smith's paratypes, from the Cornbrash and Inferior Oolite, are all considered good specimens of *N. clunicularis*.

*Nucleolites clunicularis* (Smith) auct. is therefore a junior subjective synonym of *Nucleolites scutatus* Lamarck and the next available name has been sought under Article 23e (iii) of the I.C.Z.N.

*N. sowerbyi* Defrance, 1825, has been considered synonymous with *N. clunicularis* by some authors (e.g. Cotteau 1871) although when first described by Defrance and Blainville (1825) the genus contained many species since removed to other genera. In a later volume of the same work Blainville (1830) establishes the new genus *Echinoclypeus* (syn. *Clypeus* Leske), distinguished on the
presence of a floscelle, into which he placed *N. sowerbyi* and *N. patella* (syn. *Clypeus plotii* Leske). Blainville also includes *N. clunicularis* amongst the nucleolitids for the first time making reference to Fleming (1828) and Smith's figure 6. It therefore seems unlikely that *N. sowerbyi* and *N. clunicularis* are synonymous, a view apparently shared by Agassiz (1836, 1839) who also places the two species in *Clypeus* and *Nucleolites* respectively.

*C. lobatus* Fleming, 1828, is probably synonymous with *N. clunicularis*. He refers Lister's Bathonian specimen (Lister 1678) to his new species, describing it with 'the groove deep and dividing the margin into two lobes.' (Fleming 1828). He rightly considers *C. lobatus* distinct from *C. clunicularis* of Smith, describing it simply as 'oval', this species having been established as synonymous with *N. scutatus* (see above). Indeed *N. scutatus* is characterised as being more oval and less lobate than *N. clunicularis*. However the specific name *N. lobatus* Fleming never appears to have been used in the literature since 1828 and therefore becomes a _nomen oblitum_ under Article 23b of the I.C.Z.N.

The next available name is *N. latiporus* Agassiz, 1839, considered synonymous with *N. clunicularis* by many authors (e.g. Wright 1859, Cotteau 1871), but rightly considered a different species to *N. clunicularis* of Smith and Fleming by Agassiz himself (Agassiz and Desor 1847). The specific name of *N. latiporus* has often been used for varieties of *N. clunicularis* (e.g. Mercier 1932) that are considered somewhat flatter than usual, but an inspection of the excellent figures of Agassiz (1839) and of his casts (see Biometrical analysis below) shows the two names to be synonymous. Under the rules of the I.C.Z.N. *Nucleolites latiporus* Agassiz is therefore the valid name for *N. clunicularis* (Smith) auct.
Material

Measured specimens used in the biometrical analysis:
Lambert Collection, Hydrequent, Pas-de-Calais; Bathonian, 9 specimens.
William Smith's type collection, British Museum (Natural History),
4 specimens.
d'Orbigny's 'type' specimens, Cotteau Collection, Université de Paris-sud,
Orsay, 5 specimens.

Personal collections from:
Stratton Audley, Oxfordshire; discus zone, 15 specimens.
Talant, Côte d'Or; macrocephalus zone, 10 specimens.

Specimens collected but not used in the biometrical analyses:
Burton Bradstock, Dorset; discus zone, 2 specimens.
Kirtlington, Oxfordshire; discus zone, 4 specimens.
Lower Stanton-le-Quentin, Wilts; discus zone, 1 specimen.
Ranville, Calvados; discus zone, 5 specimens.
Luc-sur-Mer, Calvados; discus zone, 3 specimens.
Thin-le-Moutier, Ardennes; zigzag zone, 6 specimens.
Cranford St. John, Northants; subcontractus zone, 6 specimens.
Aston Blank, Gloucestershire; parkinsoni zone, 4 specimens.
Chatel Censoir, Yonne; Bathonian, 2 specimens.
Ferques, Pas de Calais; Lower Bathonian, 2 specimens.
Selongey, Côte d'Or; Bathonian, 1 specimen.
Villers-le-Tourneur, Ardennes; Lower Oxfordian, 1 specimen.

Additional material examined:
Lambert collection, Université de Paris 6.
Collection of Université de Dijon.

Palaeoecology

*N. latiporus*, unlike *N. scutatus*, is found associated with a varied fauna in coarse bioclastic limestones, especially within
the Cornbrash where it appears to be most abundant. Indeed it is rare to find it alone, it nearly always occurs with other echinoids often other species of Nucleolites. It is commonly found with rhyynchonellid and terebratulid brachiopods, shallow infaunal and epifaunal bivalves, wide-angle spired gastropods, solitary corals, clypeiids and regular echinoids.

In the Cornbrash of Stratton Audley N. latiporus is found in association with N. elongatus, Hypodiadema and fragments of large clypeiids in a poorly washed bivalve-brachiopod biostratite representing moderate energy conditions (see also p. 55 for a detailed description of the palaeoecology of Stratton Audley). It also occurs in a very similar facies of the Cornbrash at Kirtlington with fragments of clypeiids. Douglas & Arkell (1932) record it occurring with epifaunal pectinids, Lima, deep burrowing bivalves such as Pleuromya and Homomya, shallow burrowing bivalves such as Trigonia and Astarte and the brachiopods Cererithyris intermedia and Obovothyris magnobovata in a rubbly and marly limestone.

At Selongey it occurs with N. burgundiae and Holocotypus in a bivalve-brachiopod biomicrite representing moderate energy conditions (see also p. 51). In the Clypeus Grit of Aston Blank it is found with N. woodwardii and Clypeus plotii in a very poorly washed oosparite, again probably representing moderate energy environments (see also p. 82). At Thin-le-Moutier it occurs in a well washed, well sorted pelsparite with only small patches of micrite present. There are two distinct sizes of peloids - more numerous small peloids and scattered larger peloids about thirty times as large which are elongate to rounded. The fauna includes gastropods and tabular bivalve fragments. In the Blisworth Limestone of Cranford St. John it occurs in a fine grained muddy bioclastic
limestone with *Holoctypus depressus* and *Acrosalenia*, all the echinoids being very small in size. The fauna is dominated by brachiopods.

At Villers-le-Tourneur it is found associated with *N. micraulus*, *Collyrites bicordata*, *Hyboclypus sandelinus* and *Holoctypus depressus*. However it seems to be associated with the derived epifauna and may not be an inhabitant of this high energy environment (see also p.70).

The palaeoenvironments seem to be of fairly shallow water muddy shell gravels with burrowing and epifaunal elements. However it is difficult to speculate on the palaeoecology of *N. latiporus*, as defined herein, as the species is found in a variety of sedimentary facies over a wide time range, from the Upper Bajocian to the Lower Oxfordian.

**Nucleolites micraulus** Agassiz, 1839

(Plate 4, fig.1-4)

<table>
<thead>
<tr>
<th>Year</th>
<th>Author</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>1839</td>
<td>Nucleolites micraulus Agassiz</td>
<td>p.43, pl.7, figs. 16-18.</td>
</tr>
<tr>
<td>1840</td>
<td>&quot;</td>
<td>Agassiz; Agassis, p.4.</td>
</tr>
<tr>
<td>1847</td>
<td>&quot;</td>
<td>Agassiz; Agassiz &amp; Desor, p.96.</td>
</tr>
<tr>
<td>1848</td>
<td>&quot;</td>
<td>Agassiz; Bronn, p.818.</td>
</tr>
<tr>
<td>1848</td>
<td>&quot;</td>
<td>Agassiz; Marcou, p.94.</td>
</tr>
<tr>
<td>1850</td>
<td>&quot;</td>
<td>Agassiz; d'Orbigny, v.1, p.345, No.459.</td>
</tr>
<tr>
<td>1852</td>
<td>&quot;</td>
<td>Agassiz; Buvignier, p.238.</td>
</tr>
<tr>
<td>1852</td>
<td>Nucleolites dimidiatus (non Phillips); Quenstedt</td>
<td>p.585, pl.50, fig.5.</td>
</tr>
<tr>
<td>1854</td>
<td>Echinobrissus micraulus (Agassiz); d'Orbigny</td>
<td>p.25.</td>
</tr>
<tr>
<td>1857</td>
<td>&quot;</td>
<td>(Agassiz); d'Orbigny, p.392.</td>
</tr>
<tr>
<td>1857</td>
<td>Echinobrissus goldfussi (non Desmoulins); Desor</td>
<td>p.267.</td>
</tr>
<tr>
<td>1857</td>
<td>&quot;</td>
<td>(non Desmoulins); Cotteau &amp; Triger, p.86, pl.19, figs.1-2.</td>
</tr>
</tbody>
</table>
1857 *Echinobrissus goldfussi* (non Desmoulins); Wright, p.358.
1857 *Nucleolites micraulus* (Agassiz); Etallon, p.252.
1860b *Echinobrissus goldfussi* (non Desmoulins); Etallon, p.300, pl.44, fig.4.
1864 " " (non Desmoulins); Etallon, p.18.
1868 " " (non Desmoulins); Guillier, p.26.
1869 " " (non Desmoulins); Cotteau & Triger, p.491.
1871 *Echinobrissus micraulus* (Agassiz); Desor & Loriol, p.313, pl.50, figs.1-2.
1874 " " (Agassiz); Cotteau, v.9, p.276, pl.75.
1921 *Clitopygus micraulus* (Agassiz); Lambert & Thiery, p.346.
1925 *Echinobrissus micraulus* (Agassiz); Deecke, p.451.
1933 " " (Agassiz); Beurlen, p.65, fig.11.

**Type specimen**

Location unknown. The type belongs to the Gressly collection, but, as with *N. latiporus* is neither at Basle (R. Panchaud, personal communication) nor listed in the Solothurn Museum type catalogue (Ledermann, 1967).

**Description**

Test small to medium sized, longer than wide, rounded anteriorly, only slightly indented by anal sulcus at posterior border; inflated aboral surface, tumid sides, concave base, depressed towards the mouth; ambulacra petaloid, long, open, outer pore elongate, poriferous zone narrow; phyllodes depressed, interambulacral areas prominent on adoral surface.

Apical system central, small, tetrabasal.

Periproct small, hardly visible from aboral view, two-thirds of the distance between apical disc and posterior border, in deep short sulcus; test between periproct and apical disc undepressed.

Peristome pentagonal, eccentric anteriorly, very faintly developed floscelle.
Distinguishing features

*N. micraulus* is most similar to *N. scutatus* but occurs earlier in the Oxfordian and is distinguished by the much shorter sulcus and its greater separation from the apical disc.

It is very similar to other Upper Jurassic nucleolitids such as *N. brodiei* and *N. pulvinatus*, forms that are also elongate with a short sulcus. It is distinguished from *N. brodiei* (a Portlandian) species by its more inflated test, tumid sides and narrower sulcus and from *N. pulvinatus* by its more marginal sulcus.

In some characters, such as the separation of the periproct from the apical disc and the central position of the apical system, *N. micraulus* has some resemblance to the Bathonian *N. burgundiae*, but is otherwise easily distinguished from it.

Range

(?! Callovian); Oxfordian of France and Switzerland.

Discussion

This species, first described in detail and well figured by Agassiz (1839), was subsequently confused with a variety of *N. scutatus* designated *N. goldfussii* by Desmoulins (1837) who considered that Goldfuss' figure of *N. scutatus* (Goldfuss 1826) did not represent the true Lamarckian species. This confusion is exemplified by Wright (1857:347) who states that he has found many species of *N. scutatus* which agree with the figure of Goldfuss, but then (Wright, 1857:358) describes *N. goldfussii* Desmoulins as a separate species in the same work. The name *N. goldfussii* Desmoulins is therefore considered a junior subjective synonym of *N. scutatus* Lamarck. Moreover, the reinterpretation of the name by Desor (1857) is invalid, *N. micraulus* Agassiz being the senior synonym.
Etallon (1857) lists this species from the Callovian of the Haut-Jura.

Material

Measured specimens used in the biometrical analyses:

Cast of type specimen of *N. micraulus*, B.M.(N.H.), an Agassiz mould.

Personal collection from:-

Villers-le-Tourneur, Ardennes; Lower Oxfordian, 50 specimens.

Additional material:

Cotteau collection, Université de Paris-sud, Orsay.

Lambert collection, Université de Paris - 6.

Palaeoecology

*N. micraulus* is found at Villers-le-Tourneur in association with a fauna rich in *individuals* as well as species within a soft, brown limonitic oolitic limestone.

The fauna is diverse, belonging to most major marine habitats (see fig. 3.1). Nektic elements are dominated by ammonites, the epifauna by byssate and cemented bivalves, shallow infauna by irregular echinoids and deep burrowers by siphonate suspension feeding bivalves.

The fauna seems to be well preserved, although the epifauna, as would be expected in an oolitic environment, is often broken and fragmented. Some groups, however, show unusual preservation. For example, the stems of the crinoids are often well preserved, of many joined ossicles and recognisably cirrate, but in some cases the ossicles, although joined in a long stem, are worn smooth so that only traces of the cirri are evident. It is noted that the crinoids have been silicified. Similarly, the shallow infaunal trigoniids *Myophorella* and *Vaugonia* are fragmented but fine detail
<table>
<thead>
<tr>
<th>Habitat</th>
<th>Fauna</th>
<th>Mode of life*</th>
<th>Originally aragonitic(*) or partly aragonite (+)</th>
<th>Silicified (*)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nekton</td>
<td>Microsophinctes sp.</td>
<td>)</td>
<td></td>
<td>*</td>
</tr>
<tr>
<td></td>
<td>Cardioceras alphacordatum</td>
<td>)</td>
<td></td>
<td>*</td>
</tr>
<tr>
<td></td>
<td>Cardioceras sp.</td>
<td>)</td>
<td>nektic cephalopods</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Dichotomosphinctes sp.</td>
<td>)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Epifauna</td>
<td>C.(Aequipecten) sp.</td>
<td>capable of swimming</td>
<td>byssate fissure dweller</td>
<td>*</td>
</tr>
<tr>
<td></td>
<td>C.(Raduloplecten) sp.</td>
<td>)</td>
<td>byssate fissure dweller</td>
<td>*</td>
</tr>
<tr>
<td></td>
<td>Ctenostreon sp.</td>
<td>)</td>
<td>cemented</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Spondylus sp.</td>
<td>)</td>
<td>cemented</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Lopho gregarea</td>
<td>)</td>
<td>attached by pedicle</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Postepithysis sp.</td>
<td>)</td>
<td>cemented</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Crinoids</td>
<td>)</td>
<td>vagrant</td>
<td>*</td>
</tr>
<tr>
<td></td>
<td>Nerinida</td>
<td>)</td>
<td>vagrant</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Holecypus depressus</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>?epifaunal</td>
<td>Gervillia aviculoides</td>
<td>?byssate</td>
<td></td>
<td>*</td>
</tr>
<tr>
<td>Semi-infaunal</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Shallow infaunal</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Myophorella sp.</td>
<td>)</td>
<td>very shallow burrowers</td>
<td>*</td>
</tr>
<tr>
<td></td>
<td>Vaugonia sp.</td>
<td>)</td>
<td></td>
<td>*</td>
</tr>
<tr>
<td></td>
<td>Nucleolites latiporus</td>
<td>)</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Nucleolites micratus</td>
<td>)</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Collarytes bicordata</td>
<td>)</td>
<td>deposit feeders</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Hybeciphus sandelinus</td>
<td>)</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Pseudomelania sp.</td>
<td>)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Deep infaunal</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Pleuromya sp.</td>
<td>)</td>
<td>siphonate burrowers</td>
<td>*</td>
</tr>
<tr>
<td></td>
<td>Sowerbya sp.</td>
<td>)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Unknown</td>
<td>Bathrotomaria sp.</td>
<td></td>
<td>(archaeogastropod)</td>
<td>*</td>
</tr>
</tbody>
</table>


Fig.3.1 Fauna from Villers-le-Tourneur.
of the shell is preserved, as with the epifaunally cemented pectinid *Spondylus*. These three genera are also silicified.

Amongst the shallow infaunal irregular echinoids many are broken or damaged, but, unlike the silicified forms, are poorly preserved. The undamaged specimens, however, do show fine detail and enough well preserved *N. micraulus* have been collected to justify their inclusion in multivariate statistical analyses. No specimen of *N. micraulus*, *Colyrites bicordata* or *Hybocyclus sandelinus* is silicified. In contrast to these echinoids the epifaunal, or possibly very shallow infaunal, echinoid *Holectypus depressus* is broken and damaged but still retains fine detail of the test. This is also the case with *Nucleolites latiporus*, both specimens again being silicified.

Silicified specimens are, therefore, usually fragmentary, showing signs of transportation, but retaining fine preservation of ornament. Specimens preserved as calcareous internal moulds or casts, however, are either undamaged with fine preservation or damaged and poorly preserved.

Silification does not appear to correlate with recrystallisation of originally aragonitic forms and the non-recrystallisation of calcitic genera. For example, the aragonitic ammonites are preserved as calcareous moulds whilst the nerinid gastropods are silicified. In contrast, the calcitic brachiopod *Postepithyris* and some echinoids, e.g. *Holectypus*, have been silicified whilst other echinoids such as *Nucleolites micraulus* and *Colyrites bicordata* are still calcareous.

Silification, instead, seems to be confined largely to the epifaunal elements irrespective of original shell mineralogy. In fact all the recognisable epifauna is silicified along with the
very shallow infaunal trigoniids and the possibly infaunal
*Nucleolites latiporus*. No other infaunal genera are silicified,
nor are the nektic ammonites.

Now, as noted above, the silicified specimens also show
signs of wear, probably due to transportation. The retention of
fine ornament, however, suggest that silification of the shells
took place prior to transportation and redeposition. Amongst the
calcitic infauna the poor preservation of damaged specimens
may mean that fragmentation took place soon after death. However,
it is unlikely that these specimens have been transported very
far, as, for example amongst the echinoids, there is also good
preservation within an otherwise thin shelled fauna e.g. *N.micraulus*
and *C.bicordata*. The reworking and transportation of an epifauna
originally buried within a rapidly silicifying environment would
account for the presence of so many attached forms. Attached
brachiopods (*Postepithyris*), byssate fissure dwellers (*Radulpecten,*
*Ctenostreon*), cemented bivalves (*Spondylus, Lopha*), and cemented
stalked crinoids would seem to be more at home within a reef
environment than an unstable oolitic environment.

It would therefore appear that only the non-silicified
fauna of irregular echinoids and deep burrowing bivalves is in
situ, a more plausible assemblage for an oolitic environment.
The ammonites, being nektic, would have drifted into the area,
are not derived as the other epifauna and are therefore not
silicified.

In thin section the sediment is in fact seen to be a
skeletal oncotic sparite. The oncolites are algal nodules
that have incorporated fragments of shell and sediment, including
siderite, in the nucleus. The skeletal allochems are mainly echinoid
spines, recrystallised bivalve fragments and occasional foraminifera and seems to be representative only of the original infauna.

The rock is cemented by sparite which also fills the voids left by the aragonitic bivalves. There are also patches of geopetal micrite, seen especially around the larger bivalve fragments. These larger fragments may also be coated by micrite.

The oncolites are well rounded, very well sorted and coated by limonite. This staining predates cementation as the sparite is clear and unstained and may therefore have occurred prior to transportation. The nature of the oncolites and the lack of micrite, except for geopetal infillings, would seem to indicate a high energy, unstable environment with most of the material being derived.

This sediment may therefore represent a reef talus type of environment with the algal nodules and epifauna being derived from the nearby reef.

Nucleolites rotundus (Peron & Gauthier)

(Plate 5, fig. 1a-d)

1879 Echinobrissus rotundus Peron & Gauthier; Cotteau, Peron & Gauthier, v.1, part 4, p.147, pl.19, figs. 9-13.

1921 Clitopygus rotundus (Peron & Gauthier); Lambert & thiey, p.347.

1962 Nucleolites rotundus (Peron & Gauthier); Kier, p.59, pl.7, fig.7, text-fig. 41.

Type specimen

Location unknown; specimens in the Lambert collection are not labelled type specimens, and no types were found in the Cotteau collection.
Description

Test small to medium sized, oval to subquadrate, rounded anteriorly, truncated posteriorly; inflated aboral surface, sides tumid, indentation of posterior margin by anal sulcus, base slightly concave; petaloid, petals expanded, narrowing distally but remaining open, poriferous zones almost as wide as interporiferous zones.

Apical system very eccentric anteriorly, tetrabasal.

Periproct large, elongate, about half the distance between the apical disc and the posterior border, at the head of a relatively shallow groove; area between apical disc and periproct undepressed.

Peristome large, pentagonal; all ambulacral plates of the phyllodes double pored, floscelle indistinct; tubercles small.

Distinguishing features

*N. rotundus* is one of the few Cretaceous nucleolitids to retain the tumid, subquadrate morphology of the more common Jurassic forms such as *N. scutatus*. However it can be distinguished from such forms by the greater separation of the apical disc and periproct, shorter petals and more anterior apical disc.

Range

Cenomanian of North Africa.

Discussion

This species is considered by Kier (1962) to be the latest occurring *Nucleolites*, as most other post-Cenomanian species have single-pored phyllodes and can be referred to other genera.

Material

Measured specimens used in the biometrical analyses:
Lambert collection, Université de Paris - 6; Cenomanian, 3 specimens. Specimen CE 01 is figured by Kier (1962), pl. 7, fig. 7.
Palaeoecology

According to Cotteau et al (1878) N. rotundus occurs at Bou Saada in a massive, yellow, fossiliferous calcareous marl in association with a wide variety of regular and irregular echinoids, ammonites, bivalves and gastropods. These authors define a zone of the Cenomanian around Bou Saada characterised by the presence of N. rotundus (Cotteau et al., 1878:62).

Cotteau et al describe the following echinoids from this zone: the cassiduloids *Nucleolites*, *Nucleopygus*, *Archiacia* and *Phyllobrissus*; the spatangoid *Hemiaspaster*; the holecryptoid *Holectypus*; the hemicidaroids *Pseudodiadema* and *Heterodiadema*; the arbacioid *Goniopygus*; and the orthopsid *Orthopsis*; (*Pseudodiadema*, however, does not occur in strata younger than the Aptian according to Fell & Pawson, (1966)). *Nucleolites rotundus* also occurs with a variety of molluscs including the ammonites *Turritites* and *Hamites* and the epifaunal bivalves *Lima*, *Pecten* and *Ostrea*. Cotteau et al. also note the presence of many poorly preserved bivalves and gastropods. These are presumably aragonitic forms preserved as internal moulds.

*Nucleolites subquadratus* Agassiz, 1839.

(Plate 4, fig. 2a-d)

1839 *Nucleolites subquadratus* Agassiz, p.41, pl.7, figs.1-3.
1840 " " Agassiz; Agassiz, p.4.
1847 " " Agassiz; Agassiz & Desor, p.96.
1848 " " Agassiz; Marcou, p.147.
1850 " " Agassiz; d'Orbigny, v.2, p.88.
1854 *Echinobrissus subquadratus* (Agassiz); d'Orbigny, p.24.
1857 *Clypeopygus subquadratus* (Agassiz); d'Orbigny, p.423, pl.965, figs.7-9.
1857 *Echinobrissus subquadratus* (Agassiz); Desor, p.268.

1862 *Clypeopygus subquadratus* (Agassiz); Dujardin & Hupe, p.579.

1863 *Echinobrissus subquadratus* (Agassiz); Loriol, p.164,pl.19,fig.11.

1865 *"" (Agassiz); Duncan, p.355-356.

1869 *"" (Agassiz); Loriol, p.43,pl.6,fig.1.

1921 *Clypeopygus subquadratus* (Agassiz); Lambert & Thiery, p.348.

1962 *Nucleolites subquadratus* Agassiz; Kier, p.57,pl.6,fig.9, text-fig.48.

**Type specimen**

Belongs to the Renaud-Comte collection, which is housed at Besançon (Lambert & Jeannet, 1928).

**Description**

Test small, oblong, narrow anteriorly, produced posteriorly, conical towards the apical disc but test slopes gently to posterior border, sides tapered, base concave; petals expanded slightly and narrowing distally; poriferous zones narrow, ambulacra straight.

Apical system close to anterior border, tetrabasal.

Periproct oval, two-thirds of the distance between the apical disc and posterior border, at head of deep sulcus that hardly indentates the margin.

Peristome pentagonal, large with faint bourrelets and floscelle, anterior, interambulacral areas prominent. Some specimens have a distinctly oblique peristome whilst in others it appears normal.

**Distinguishing features**

*N. subquadratus* is distinguished from the Jurassic nucleolitids by its produced posterior border and the anterior eccentricity of the apical system. It is similar to *N.rotundus* but this species has tumid sides and a more bilobed posterior margin.
Range

Neocomian of the French and Swiss Jura, Albian of Arabia.

Discussion

Another species well described and figured by Agassiz (1839) but transferred from Nucleolites to Echinobrissus by d’Orbigny (1854). D’Orbigny (1857) further removed the species to his new genus Clypeopygus. Loriol (1863) however considered d’Orbigny’s specimen to be a flattened form. Kier (1962) agrees that the test is too inflated and the petals too narrow for Clypeopygus and restores it to its original genus, Nucleolites.

Material

Measured specimens used in the biometrical analyses:
Cast of the type specimen of N. subquadratus, B.M. (N.H.), an Agassiz mould.

Personal collection from:
Devecey, Doubs; Neocomian, 20 specimens.

Additional material:
Cotteau collection, Université de Paris-sud, Orsay.
Lambert collection, Université de Paris -6.

Palaeoecology

N. subquadratus occurs at Devecey in association with another cassiduloid, Phyllobriussus, Holaster and the small hemicidaroid Trochotiara in a coarse bioclastic limestone. The rest of the macrofauna is limited to brachiopods, bivalves and serpulid worm tubes.

The small terebratulid Musculina is the most common representative of the epifauna. Also present is the ribbed terebratulid Gemmarcula, a strongly ribbed Inoceramus and small fragmented pectinids. The many worm tubes are found either coiled or in
aggregates of parallel tubes. These may be referable to *Glomerula gordialis* and *Sarcinella plexus* respectively. Internal moulds of the large, elongate deep burrowing bivalves *Phalodomya* and *Pleuromya* are also present in association with smaller more ovate moulds of shallow burrowers.

In thin section the sediment can be classed as an algal-echinoid biomicrite.

Many very well preserved algal oncolites are present enclosing patches of sediment or are sometimes themselves bound into elongate peloidal spheres. Patches of partly recrystallised coralline algae are also present. The echinoid debris is either preserved as tabular fragments, which may be bored and infilled with micrite, or as spines. The very rich fauna includes gastropods, bivalves, bryozoa, rhynchonellid and terebratulid brachiopods and small conical foraminifera. The bryozoa are often found in close association with (encrusting?) other skeletal fragments. The molluscan fragments are coated in micrite and have undergone coarse recrystallisation of the shelly material.

There are also large grains composed of small sediment particles bound by a thick layer of light coloured micrite. These may represent algal-bound sediment, large faecal pellets or true intraclasts.

There seems to be no preferred orientation to the long tabular bivalve, brachiopod and echinoid fragments, the sediment as a whole being poorly sorted.

The sediment therefore seems to represent an environment of moderate energy, an environment in which micrite is retained in the sediment but in which much of the fauna is broken down into small fragments.
Nucleolites woodwardii Wright, 1854.
(Plate 2, fig. 2a-d)

1854 Nucleolites woodwardii Wright, p. 321, pl. 12, fig. 5a-e.
1854 " " Wright; Forbes, p. 8, ad, sp.
1857 Echinobrissus woodwardii (Wright); Desor, p. 268.
1859 " " (Wright); Wright, p. 337, pl. 24, fig. 2.
1921 " " (Wright); Lambert & Thiery, p. 344.
1933 " " (Wright); Beurlen, p. 37.

Type specimen
Wright has not stated a type in his original description,
but refers to one specimen (B.M.(N.H.) El590) from Salperton
Tunnel (D. Lewis, personal communication, 1977).

Description
Test small to medium sized, thin, circular to sub-quadrat;
aboral surface flatly convex, sides tumid, posterior margin hardly
indented by anal sulcus, adoral surface flat; ambulacra depressed
and interambulacral areas prominent.

Apical system small, central, individual plates not distinct;
ambulacra petaloid, poriferous zone narrow, outer pore elongate.

Periproct supramarginal, small, in narrow sulcus which extends
from apical system to posterior border.

Peristome eccentric anteriorly, in slight depression,
pentagonal, star-shaped, small; bourrelets distinct, phyllodes narrow.

Distinguishing features
This species is most like N. amplus but is distinguished
by the narrow petals, narrower poriferous zones and less crowded
phyllodes. It may be conspecific with N. amplus as there is little
overall morphological difference between them.

It is distinguished from *N. orbicularis* on the same grounds that *N. amplus* is distinguished from that genus. It is distinguished from *N. scutatus* and other upper Jurassic forms by the narrower anal sulcus which always extends to the apical system, and from *N. latiporus* by its flatter, non-bilobed appearance.

**Range.**

Upper Bajocian (*parkinsoni* zone) to upper Bathonian (*aspidoides* zone) of England and northern France.

**Discussion**

This species, first described by Wright (1852), was placed in the genus *Nucleolites* because of its small size and apparent lack of a well defined floscelle. The species was transferred to *Echinobrissus* by Desor (1857) following d'Orbigny (1854). The specimen of *N. burgundiae*, figured by Cottreau (1908) from the Bathonian of Malagasy, has the general form of *N. woodwardii* although it is a small and damaged specimen. Specimen L6, from the middle Bathonian of Fosse Cross Quarry, has genital 5 intact and the periproct surrounded by oculars V and I in a similar manner to the *N. elongatus* described by Jesionek-Szymanska (1968:55) (J. Olver, pers. comm.).

**Material**

Measured specimens used in the biometrical analyses:

Lambert collection, Université de Paris - 6; 7 specimens identified as *N. woodwardii* from Marquise, Pas de Calais, Bathonian.

Additional material:

Fosse Cross, Gloucestershire; *morrisi* zone, 21 specimens.

Wiggold Cutting, Glos: probably *morrisi* zone, 1 specimen.

81
Palaeoecology

*N. woodwardii* has been found in a series of fine grained sediments, frequently occurring with clypeiids and molluscs.

At Aston Blank a single specimen was found within the well known *Clypeus* Grit. This yellow marly coarse oolitic limestone contains much bioclastic debris and is named from the many large *Clypeus plotii* which dominate the fauna. Other echinoids present include *N. latiporus* and *Holecypthus depressus*. In thin section the rock is a very poorly sorted oosparite with a very fine sparry cement. Ostracods and gastropods are recognisable as are the tabular bivalve fragment which often form the centres of the ooliths. There are also patches of coralline algae, brachiopods and some echinoid spines although there is a noticable rarity of larger echinoderm fragments. The sediment is on the whole poorly sorted. The persistence of unwashed micrite in the sediment seems to indicate an environment of moderate energy conditions.

*N. woodwardii* has also been found in Middle Bathonian strata at three localities. At Fosse Cross quarry it is found in association with a very small disc-like *Clypeus* and the small solitary coral *Discocyathus* in a yellow rubbly limestone. Terebratulids are concentrated in lenses throughout the rock, which also contains rhychnonellids, gastropods and some burrowing bivalves (e.g., *Lucina*). Most of the fossils are well preserved and only rarely worn. The sediment, however, appears almost conglomeratic in nature being composed of a yellow peloidal limestone containing large fragments of whitish porcelaneous limestone.
In thin section the rock is very poorly sorted, poorly washed pelsparite. Large patches of micrite and some intraclastic fragments are present. The fauna includes echinoid, crinoid bivalve, foraminiferal and coral debris. The larger fragments of porcelaneous limestone are of very fine pelsparites whereas the yellow peloidal limestone is composed of coarser peloids within a limonite stained matrix. The two limestones appear to grade into each other in thin section with no sharp divisions.

At Slape Hill *N.woodwardii* is found in association with small fragmented specimens of *Clypeus* and the high spired gastropod *Nerinea eudesii* in a medium grained bioclastic limestone. In thin section the rock is a poorly washed pelsparite with large tabular fragments of echinoids and punctate brachiopods, crinoids, ostracods, patches of algae and small echinoid spines. There is no specific orientation to the larger tabular fragments.

At Ardley it is again found in association with fragments of *Clypeus* in a fine, white bioclastic limestone. *N.woodwardii* occurs in a bed capped by a hardground that Palmer (1973) suggests was formed subaqueously. It occurs with a diverse fauna of shallow burrowing bivalves (e.g. *Lucina*), pectinids, gastropods, terebratulids (e.g. *Epithyris*), rhynchonellids and regular echinoid spines. In section the sediment is very fine pelmicrite with distinct patches of coralline algae.

These Middle Bathonian peloidal limestones all seem to represent environments of moderate energy conditions in which the muddy fraction is rarely washed completely from the sediment. The close association of *N.woodwardii* with *Clypeus* is also noted.
3 D) The genus APATOPYGUS

Family Apatopygidae Kier, 1962

Remarks

Kier (1962) removed the genus Apatopygus Hawkins, 1920 from the Nucleolitidae to a separate monogenic family, the Apatopygidae, on the grounds that the presence of single pored plates and pyrinid plating in the ambulacra beyond the petals and a monobasal apical system in the adults are differences of too great a significance to include Nucleolites and Apatopygus in the same family. However, Mortensen (1948) attaches no special importance to the pyrinid structure, dismissing it as "simply an arrangement of triads after the echinoid structure", and it has since been shown (Kier, 1974) that the apical system is only superficially monobasal in the adult.

The principal character of importance in distinguishing the two type genera is, therefore, the presence of single pored phyllodes in Apatopygus. However, Kier (1962) includes within the family Nucleolitidae the Senonian Oolopygus, a genus also possessing single pored phyllodes.

This taxonomic problem will perhaps only be resolved when phylogenetic relationships have been established amongst rare Tertiary forms that will ultimately link Apatopygus to its closest Cretaceous ancestor.


Synonymy

1920 Apatopygus Hawkins, p.396.
1922 " ; Lambert, p.31.
1924 *Apatopygus*; Lambert & Thiery, p.396.
1925 "; Lambert & Thiery, p.585.
1925 "; Clark, p.179.
1929 "; Brighton, p.313.
1946 "; Clark, p.355.
1948 "; Mortensen, p.179.
1962 "; Kier, p.223.

**Type species**


**Description**

Small to medium sized test, depressed, ovoid, elongate, greatest width posterior to centre; oral surface concave, sunken towards the peristome; ambulacra petaloid, petals narrow, open, extending about half the distance from the apical system to the ambitus; inner pore rounded, small, outer pore only slightly elongate; ambulacral plates single pored beyond the petals.

Apical system eccentric anteriorly, superficially monobasal in the adults, tetrabasal in the juveniles.

Periproct supramarginal, longitudinal, situated midway between apical disc and posterior margin, large, in a deep sulcus extending to the posterior border.

Peristome anterior, often slightly transversely oblique; bourelets moderately developed, phyllodes narrow with two rows of pores in each half ambulacrum; no distinctly larger buccal pores; pyrinid plating in ambulacra beyond petals.

Tubercles perforate, crenulate, spines short.
**Distinguishing features**

Apatopygus is most similar in appearance to Nucleopygus but is generally larger, more oval and has more conspicuous petals. It is distinguished in detail by the lack of buccal pores, tetrabasal apical system in the young and pyrinid plating in the ambulacra beyond the petals. None of these differences, however, are good diagnostic characters.

Apatopygus differs from Nucleolites in having single pored ambulacral plates beyond the petals and a monobasal apical system in the adult.

**Range**

Eocene to Recent of the Mediterranean and New Zealand.

**Discussion**

The recent A. recens of New Zealand is represented by a fossil form of supposed Pliocene age from the Chatham Islands (Brighton, 1929; Kier 1962, 1966) now dated as Eocene (Rose, pers. comm. 1977). A new species has recently been found (Rose, 1975) from the Miocene of the Mediterranean.

**Description of the type species**

Apatopygus recens (Milne Edwards)  
(Plate 5, fig. 2a-d)

1836 Nucleolites recens Milne Edwards, pl. 14, fig. 3.  
1847 " " Milne Edwards; Agassiz & Desor, p. 153.  
1854 Echinobrissus recens (Milne Edwards); d'Orbigny, p. 24.  
1857 Nucleolites recens (Milne Edwards); Desor, p. 257.  
1859 " " Milne Edwards; Wright, p. 330, pl. 41, fig. 1.
1862 Echinobrissus recens (Milne Edwards); Dujardin & Hupe, p.578, pl.10, figs.9-10.

1872 " " (Milne Edwards); Agassiz, p.108, pl.14a, figs.2-4, pl.21b, figs.1-2, pl.38, figs.30-31.

1872 " " (Milne Edwards); Hutton, p.13.

1898 " " (Milne Edwards); Farquhar, p.321.

1904 " " (Milne Edwards); Hutton, p.228.

1907 " " (Milne Edwards); Farquhar, p.128.

1917 Oligopodia recens (Milne Edwards); Clark, p.108, pl.144, figs.8-11.

1920 Apatopygus recens (Milne Edwards); Hawkins, p.394.

1921 Nucleopygus recens (Milne Edwards); Lambert & Thiery, p.347.

1921a Echinobrissus (Oligopodia) recens (Milne Edwards); Mortensen, p.184, pl.8, figs.1-4.

1921b " " " (Milne Edwards); Mortensen, p.117, pl.11, figs.4-5.

1922 Apatopygus recens (Milne Edwards); Lambert, p.30.

1924 " " (Milne Edwards); Lambert & Thiery, p.396.

1925 " " (Milne Edwards); Lambert & Thiery, p.587.

1925 " " (Milne Edwards); Clark, p.179.

1925 Echinobrissus recens (Milne Edwards); Mortensen, p.391.

1929 " " (Milne Edwards); Young, p.161.

1929 Apatopygus recens (Milne Edwards); Brighton, p.308.

1948 " " (Milne Edwards); Mortensen, p.181, pl.1, figs.22-25, 31, 32, 34, 35.

1962 " " (Milne Edwards); Kier, p.223, pl.34, figs.4-7, text-fig.182.

1966 " " (Milne Edwards); Kier, p.522, fig.413, la-c.

1974 " " (Milne Edwards); Kier, Fig.28c.
Type specimen

Location unknown.

Description

Characters of the genus.

Range

?Eocene to Recent of New Zealand.

Discussion

This species, first placed within Nucleolites by Milne Edwards (1836) on the grounds of close morphological similarity, is the only known extant form of the 'nucleolitid'-type cassiduloids. It is, therefore, of great interest ecologically. Due to the absence of well established Tertiary intermediates the affinities of this species have been the subject of much discussion. Apart from Nucleolites the species has also been placed within Echinobrissus, Nucleopygus and Oligopodia. Hawkins (1920) established the genus Apatopygus soley for this extant species because of the presence of pyrinid plating in the phyllodes.

Material

Measured specimens used in the biometrical analyses:

Collection of the Department of Zoology, B.M.(N.H.), from Nelson, New Zealand; Recent, 18 specimens.

Sample donated by Dr. D. Pawson from Wellington Harbour, New Zealand; Recent, 23 specimens.

Ecology

A. recens is found around the New Zealand coasts, generally in coarse shell gravels, at depths of between 3 and 150 metres (Higgins, 1974), although Mortensen (1948:183) gives depths of between
This species is now known to be a shallow burrower (Higgins, 1974; Kier, personal communication) and Kier's (1962) earlier hypothesis may now be invalid for most extant cassiduloids and possibly for fossil species as well. Kier (1962) suggested, partly from the lack of relevant ecological data, but mainly from observations on general morphology, length of petals and the lack of any specialised burrowing organs, that cassiduloids may only partly burrow up to the edge of the petals. He showed in diagrammatic form (Kier, 1962; chart 4) that an evolutionary sequence within the cassiduloids could be established in which the length of the petals shorten with time. This was taken to indicate that these cassiduloids were gradually able to bury more deeply throughout the Mesozoic and Cenozoic.

Higgins (1974), however, has observed _A. recens_ burrowing into its native substrate in an aquarium. It is able to burrow completely beneath the surface of the substrate with no apparent connexion with the overlying water column. It appears that the association of _A. recens_ with a relatively porous, coarse substrate obviates the requirement to maintain a direct connexion to the overlying sea-water, e.g. through the construction of a respiratory burrow.

_A. recens_ is a deposit feeder and an almost continuous discharge of sediment particles from the anus was observed by Higgins during normal feeding behaviour. This feeding behaviour is selective in that larger particles will not be ingested.
CHAPTER 4 - METHODS OF STUDY

4 A) Aims

The aim of the biometrical work in this and subsequent chapters is twofold. First, to characterise samples of selected Nucleolites species by multidimensional measurements of the test. Second, to compare samples to assess both inter and infraspecific variation. This permits distinction of those variables which can be shown to be objectively significant from those which are insignificant in quantitative terms. For the data to be valid care has been taken in sampling, measurement and the application of appropriate techniques.

4 B) Sampling

Each sample used in this study is a collection of nucleolitids from a specific horizon at a single locality of limited geographical extent. During sampling all echinoids within a particular horizon were collected as were examples of the sediment and representative members of the accompanying fauna. I was careful to ensure that collection of Nucleolites was unbiased and, therefore, the size of the sample was limited only by the abundance of specimens within each horizon. There are, of course, large differences in the numerical abundance of Nucleolites at particular localities and sample sizes vary correspondingly. Amongst museum collections, samples are again limited by the amount of material available for study.

It was, therefore, impossible in practice to collect large samples at every locality or to collect samples all of a similar size. This is a common problem in biological research, as noted
by Simpson et al (1960:150). "In zoology the sample size is usually fixed by what can be obtained. Instances in which a sample can be made of any desired size are rare, and it is a good general principle to use all available information." They conclude that even single specimens or very small samples contribute some information of the original population range and should not be ignored. Gilbert (1973), however, suggests that, as the values of Student's 't' do not change much once there are 12 or more degrees of freedom, this should be a minimum number for biometrical samples.

Gilbert (1973), however, suggests that, as the values of Student's 't' do not change much once there are 12 or more degrees of freedom, this should be a minimum number for biometrical samples.

Amongst modern statistical studies there has been great variation in the sizes of samples used. For example, in echinoid biometrics Nichols (1959) uses samples ranging in size from 15 to 30 specimens, whilst Kermack (1954), working on a museum collection, is able to study samples of between 27 and 271 specimens. Some recent multivariate studies also show wide range of sample sizes. Mares (1976) uses discriminant functions and cluster analysis in a study of rodent species in which species are characterised by samples ranging from 1 to 20 individuals. Pingitore (1976) uses Biomed program BMD 07M in an analysis of coral diagenesis. He quantifies 12 variables on two samples of 13 and 27 specimens in order to classify unknown material.

There does not appear to be a consensus of opinion on minimum or maximum sample size, the number of specimens usually being related to the problem at hand. The smallest sample used in the present study is of three type specimens of *N. rotundus* from the Cotteau collection at Orsay. The smallest collection made by the author was seven specimens of *N. elongatus* amongst the
21 nucleolitids found at Stratton Audley. Most collected samples used in the biometrical analyses below contain over ten specimens. The largest sample is of 133 specimens of *N. scutatus* from Upware.

It was found that little additional information is gained by the use of very large samples. For example, the sample of *N. scutatus* from Trouville, Calvados, has been characterised in two ways. First, by the use of the full number of 107 perfect specimens from both the cliff and shore localities. Second, by the inclusion of only 19 specimens from the shore collected by myself. Both methods produce similar results in multivariate analyses (see p. 150) indicating that the data are consistent for both large and small samples. Samples of the order of 20 individuals would therefore seem adequate to characterise their local population (see also p. 296).

Specimens were cleaned by a variety of modern techniques. Most were prepared with air abrasive apparatus, using fine or soft powders, and a Dentsply Cavitron, an ultrasonic vibrating probe. Specimens covered in a soft matrix were first cleaned in an ultrasonic bath, whilst a dental drill with carborundum hand pieces was used on some very hard limestones.

All specimens were measured using a Swift travelling microscope. Definition of test dimensions is given below (p. 83).

Measurements of the test morphology were tested for their reproducibility following the methods of Kermack (1954).

4 C) Measurement

1. Introduction

Past workers in numerical taxonomy have been limited in the number of variables they have been able to use to define fossil
samples by the calculation and handling of the large amounts of data involved. Relatively recently, Sylvester-Bradley (1958) stated that quantitative methods were only able to examine one or two characters in a series of specimens while the human eye is able to compare many characters instantaneously in single specimens. He concluded that typological comparison was therefore a more useful tool as a basis for taxonomy. However the parallel growth of computer analyses and multidimensional techniques have made the first part of this statement outmoded as palaeontologists are now able, to a great extent, to combine the analysis of variation in n dimensions with analysis of a great number of specimens. Computers can be programmed to calculate complex formulae such as the reduced major axis, an important regression line of best fit that has had only limited application in the past because of the time involved in deriving the coefficients for each pair of variates.

If an objective study of the taxonomy of fossil samples is attempted, as many variables as possible should be used so that subjective assessment is kept to a minimum. Paradoxically, however, the selection of variables to be measured is perhaps the most subjective element in the compilation of data for biometrical analysis, as those characters which are chosen are deemed more important by the taxonomist, and are in effect weighted in favour of those characters not chosen. If, for example, only the length, breadth and height of specimens are used to distinguish between samples then these variables alone have necessarily been pre-selected as the only characters important in the taxonomy of the groups concerned.

A full range of measurements is therefore imperative
in order to obtain maximum information on the morphology of specimens and to limit the degree of subjectivity that weighted characters introduce.

2. The selection of characters on NUCLEOLITES

It has been possible in the present work to incorporate many variables that have been used in recent years in statistical studies of echinoids as well as characters that were used in the original classifications of nucleolitids.

Recent British statistical work on Mesozoic echinoids has been concentrated on the Cretaceous spatangoid Micraster. Elementary studies have been applied to the Cretaceous holasteroid Echinocorys (Willcox, 1953). Although the measurements of some characters of the test used in these studies cannot be applied to cassiduloids, most of the variables concerned with morphology are used in the present work. The author's variables A to E, G and H are basically the same as those used by Kermack (1954) for Micraster, although the exact position of measurement may differ due to the differences in overall shape between Micraster and Nucleolites. Nichols (1959), in a palaeoecological study of Micraster, concentrates mainly on petal characteristics and pore counts plotted against size number. These are represented by variables P to V and variable W respectively herein. Stokes (1972) suggests that the height of the periproct is more useful in distinguishing between samples of Micraster than the presence or absence of a sub-anal fasciole, the height of the periproct being incorporated as variable N₄ in the present work.

In France, Roman (1956, 1957) uses characters of the petals and eccentricity of the apex and peristome in statistical studies of
the variation in some Eocene species of the cassiduloid *Echinolampas*.

In petals 1 and 2 he measures the length (variables Q1 and Q2 of the present work) the maximum width of the petals (V1, V2) width of the interporiferous zone (U1, U2) and calculates the width of the two poriferous zones (T1 and T2) by subtracting the width of the interporiferous zone from the maximum width of the petal. Roman (1956) also uses the projection of the ambulacra above the surface of the test, but this could not be measured in the essentially planar surface of the test of *Nucleolites*. Roman (1957) measures the length of the two poriferous zones independently as well as the differences in width of interambulacral areas II and III to show asymmetry within specimens of *Echinolampas*. Asymmetry of petal characters appears to be an advanced adaptive character (Kier, 1962 p.11) amongst cassiduloid echinoids and is not apparent in *Nucleolites*. However the variables were measured on all petals so that differences between the left and right ambulacra could be seen. Detailed structures such as the length of the anterior and posterior poriferous zones of individual petals appear to be constant in *Nucleolites*.

In non-statistical work various authors have suggested that certain characters are useful in distinguishing within and between groups of nucleolitids.

Kier (1962, p.57) states that the genus *Nucleolites* can be distinguished from *Clypeopygus* by its more inflated test (variable C) and from *Phyllobrissus* by its wider test and more anterior periproct (variables B and J). Kier (p.62) also claims that within the genus *N. scutatus* can be distinguished from *N. clunicularis* (*N. latiporus*) only by slight differences in shape (variables A to D, G and H) and length of the anal groove.
(variable J). He also observes (p.10 and Chart 4) that there is an evolutionary trend within the cassiduloids from Jurassic forms in which the petals are long and extend almost to the margin to forms with higher tests and shorter petals in the Cretaceous and Tertiary. Measurements of the length of the petal are represented by variables Q1-5 for each ambulacrum and variable X, the average petal length. Other evolutionary trends recognised by Kier (1962) concern the width of the petal and elongation of the outer pore. Measurements on the poriferous zones are taken on each ambulacrum across the widest part of the petal, these being variables R to V in the present work.

Jesionek-Szymanska (1967) recognises a gradual posterior movement of the periproct through time in the nucleolitids, resulting in a greater separation between the apical system and periproct, and therefore a shortening of the anal sulcus. These measurements are represented by variables N1 and J.

Many of Wright's (1859) observations on Nucleolites have been incorporated in this study. He frequently uses the length of the sulcus (variable J), ambitus increasing in diameter towards the posterior (variable H), the width of the sulcus (variable K), position of the disc (variable M), size of the peristome (variable F) and elongation of the test (variables A and B) to distinguish between the various British species.

Many of the early workers in France and Switzerland use characters of the peristome and floscele to distinguish between Nucleolites and other cassiduloids. Agassiz (1839) uses the absence of bourrelets in Nucleolites to distinguish it from Clypeus. Agassiz and Desor (1847) use bourrelets to separate Nucleolites from Catopygus while d'Orbigny (1857) establishes two new genera from...
the *Nucleolites* of Agassiz on characters of the peristome; *Clypeopygus* on the presence of bourrelets and well developed phyllodes, and *Trematopygus* (= *Plagiochasma*) on the presence of an oblique peristome. Kier (1962) however in making observations on evolutionary trends in the phyllodes of the cassiduloids picks out a 'nucleolitid' trend in which the phyllodes of genera of the Nucleolitidae and species of *Nucleolites* show a consistency in length and arrangement throughout the Jurassic and Lower Cretaceous.

It was also found that for the purpose of a biometrical study characters of the floscelle were very difficult to define objectively. The pores of the phyllodes often alternate either side of a straight line from the peristome for some distance towards the ambitus. It is therefore difficult to determine the beginning of the phyllodes or the number of pores in each inner row. For this reason and because of the observations made by Kier it was not considered expedient to attempt to take measurements or counts on the phyllodes. The bourrelets were also difficult to measure, observations usually being limited to subjective assessments of presence/absence or degree of development. The measurements taken on the peristome were therefore limited to the size of the mouth (variable F) and its position (variable E).

The presence of a shallow groove or depression between the periproct and the apical disc, apparently an extension of the sulcus above the periproct found in early species of *Nucleolites*, has been used in the taxonomy of nucleolitids (Wright 1859, Pomel 1883). This again was a character that was virtually impossible to measure objectively, as was the size, degree or pattern of tuberculation.

Some of the evolutionary trends recognised by Kier (1962, p.4-15) could, however, be represented by a binary system of notation based
on the presence or absence of characters. For example, the presence or absence of buccal pores, bourrelets, the possession of double or single pores beyond the petals or between tetrabasal and monobasal apical systems. However such measurements of attributes cannot be compared with direct measurements of size as both are completely different methods of characterising data. Attributes are basically qualitative descriptions whilst measurements based on an interval scale are truly quantitative. The biometrical analyses in this thesis are therefore based on measurements or counts which have objective definition, but are limited to data on the interval scale.

Of the variables chosen for measurement, A to N4 and W were measured on all specimens, whilst P to V and X were taken on two selected groups only.

3. Definition of measurements

<table>
<thead>
<tr>
<th>Variable</th>
<th>Definition</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>Greatest length of test.</td>
</tr>
<tr>
<td>&quot;</td>
<td>Greatest breadth of test taken at right angles to A.</td>
</tr>
<tr>
<td>&quot;</td>
<td>Greatest height of test.</td>
</tr>
<tr>
<td>&quot;</td>
<td>Height of the apical system; from base of test to madreporite.</td>
</tr>
<tr>
<td>&quot;</td>
<td>Distance from anterior of test to centre of peristome, measured in an antero-posterior direction.</td>
</tr>
<tr>
<td>&quot;</td>
<td>Antero-posterior diameter of the peristome.</td>
</tr>
<tr>
<td>&quot;</td>
<td>Distance from the anterior of test to most anterior point of the sulcus at the posterior margin.</td>
</tr>
<tr>
<td>&quot;</td>
<td>Distance from anterior of test to the widest part of the test.</td>
</tr>
<tr>
<td>&quot;</td>
<td>Vertical height of the periproct.</td>
</tr>
<tr>
<td>&quot;</td>
<td>Length of the anal sulcus measured from the anterior of the periproct to the posterior margin of the test.</td>
</tr>
</tbody>
</table>
"K" : Width of the sulcus measured at the point of greatest width of the periproct.

"L" : Horizontal length of the periproct.

"M" : Distance from the anterior margin of test to the apical disc, measured to the anterior of the madreporite.

"N1" : Distance from the apical system, measured from the anterior edge of the madreporite, to the anterior edge of the periproct.

"N2" : Depth of the anal sulcus at the posterior margin of the test, measured in the antero-posterior direction.

"N3" : Difference between the apical height and greatest height.

"N4" : Vertical distance from the base of test to the base of the periproct.

"P1-" : Number of pores in the petaloid portion of each half-ambulacrum.

"Q1-V" : Length of each petal.

"R1-V" : Width of outer pore measured at the point of greatest width of the petal (average from zones a and b).

"S1-V" : Width of inner pore measured at the point of greatest width of the petal (average from zones a and b).

"T1-V" : Greatest width of poriferous zone at the point of greatest width of the petal (average from zones a and b).

"U1-V" : Greatest width of interporiferous zone at the point of greatest width of the petal.

"V1-V" : Greatest width of petal.

"W" : Size number, calculated by A x B x C.

"X" : Average length of the five petals calculated from variable Q.

Variables A to N4 are the 15 major test dimensions used in the majority of analyses detailed below.
Measurements P to V were taken for each ambulacrum and recorded separately, the ambulacra being numbered in the conventional method (Melville & Durham, 1966:221). Variables R to V were recorded at the point of greatest width of the petal.

The length of the petal, variable Q, is defined as the distance from the distal edge of the oculax plate to the most distal pores which are not orientated obliquely to each other, like the pores at the ambitus (see fig. 4,1). The extent of the petal is relatively easy to recognise in practice. In the genus Apatopygus the petal includes only double pored ambulacral plates.

All measurements except variable P, a pore count, were taken with a Swift Travelling microscope to 0.01 mm. Variable P, being a count is, by definition, a discrete measurement based on an interval scale whilst all other variables are continuous measurements. Although the two units of measurement are not strictly comparable, they can be used in the same data matrix if the discrete units have large values. This is the case with variable P as usually P \( \geq 25 \). Fig. 4,2 gives diagrammatic illustration of variables A to N4.

The measurements of variables A, B, G, H, J, K, L, M, N1 and N2 were taken in the horizontal plane from the aboral surface, variable E and F from the adoral surface.

Variables C, D, I, N3 and N4 were taken from the posterior in the vertical plane.

4. Reproduceability of measurements

The methods used by Kermack (1954, p. 386) in the assessment of the errors of measurement have been employed in the present work.

A random sample of fifty specimens of *N. scutatus* from the marly oolite of Trouville was measured twice to test the
Figure 4.1. Length of petal, variables P and Q, as defined in the text. Drawing of apical disc and anterior ambulacrum of \textit{Nuculeolites elongatus} (O 15) from the Cornbrash (Upper Bathonian, discus zone) of Stratton Audley, Oxfordshire.
Figure 4.2. Definition of variables A – N4. See text for exact definition of measurements.
reproduceability of measurements, the effect of secular errors and the total contribution of errors to the population variance. Kermack (1954) gives an account of the theoretical bases for these procedures, which he used on two congeneric species from the same chalk horizons. However, because the present work encompasses fossil groups from differing sedimentary facies, these procedures were also followed for the Cothill sample of *N. scutatus* from a sandy horizon.

It was found that despite difference in size, geography and sedimentary environments variables *F* and *K* consistently failed tests of reproduceability amongst the two fossil samples (see data). Variable *F*, the size of the peristome, was found to be of a small but uniform size amongst the samples studied. The variance is therefore correspondingly small and any errors of measurement contribute a larger percentage to the population variance than with a more variable character. Variable *K*, width of the sulcus, was difficult to define as the walls of the anal sulcus are rounded, no easily fixed point being present from which measurement can be made. These variables were therefore not measured in other fossil samples.

Most specimens within the two recent samples of *A. recens* have the spines and periproctal membrane intact. Measurements of the test, especially those of the periproct, were difficult to make; variable *I* could not be measured accurately on any Wellington Harbour specimens. The total errors of measurement of *I* and *K* were found to be unacceptably large (differed significantly from zero at the 1% level) and were, therefore, omitted in later analyses.
4D) STATISTICS

1. Bivariate analysis

Kermack (1954:391) has been followed in the use of bivariate analysis of the fossil samples. Due to the effects of mortality rates, chance of burial, fossilization and preservation, the fossil samples are unlikely to be representative in size of individuals of the original population. Through the use of bivariate statistics, however, the 'shape' parameters so produced more accurately reflect the growth of the population than univariate statistics such as means and standard deviations. Reduced major axis regression lines fitted to growth curves, using the equation of allometric growth \( y = \beta x^\alpha \), can be compared to test the significance of the differences between such lines, after the methods of Kermack (1954) and Imbrie (1956).

2. Multivariate analysis

Multivariate methods of analysis are an extension of bivariate methods into \( n \)-dimensional space. Many techniques have been developed during the last forty years for multivariate analysis. Examples include the transformation of variables into a smaller number of vectors that express the same variability as the original matrices, or the use of multiple regression lines. These methods are obviously very useful as all the information gathered on samples can be used in one analysis instead of a series of bivariate analyses.

Multiple regression, a logical progression from successive bivariate analyses, was not found to be useful in the present work.

The basic problem of using multiple regression techniques is the necessity of using a dependent variable. Dependent variables
are those variables about which all other characters vary, such as time or distance in a mathematical problem. In biologically variable samples, however, no dependent variables exist as in no instance does an increase in one variable necessarily mean that another variable will increase correspondingly. This is the case even between components with a high degree of correlation.

Neither the use of dummy variables nor arbitrary numbering of geographic locations as dependent variables produced usable results.

However other multivariate programmes available on the University of London Computer Centre computers were found to be useful in the analysis of fossil samples. These included Principal Component Analysis, Cluster Analysis, Discriminant Functions and Canonical Variates.

**Principal Component Analysis**

When there are no _a priori_ patterns of interrelationships readily observable within the structure of a set of multivariate observations, then principal component analysis (PCA) may be able to pick out dependence structures occurring within these observations. The multivariate set may be a single sample, and therefore the presence of subgroups may be sought, or the set may consist of two or more samples in which case PCA can be used to test whether the individual cases fall into their natural groupings. Furthermore, the nature of the differences between these groupings is important. PCA is able to isolate the dependence structure of sets of cases between the groups or sets of variables within the groups.

Principal component analysis is a widely used technique in the analysis of multivariate data. As Temple (1975) has pointed out, the method can be used both as a statistical technique and
for the graphical representation of multivariate samples.

PCA identifies sets of original variates \( x_1, x_2, \ldots, x_n \) that vary together but are instead represented by new independent variables \( y_1, y_2, \ldots, y_n \). These new variables are completely independent of each other as they are orthogonal, unlike the original variates which are often highly correlated one to the other. These new variates are known as principal components or eigenvectors, the variances of which are represented by eigenvalues.

The total variance of the original data matrix is preserved by this orthogonal transformation to principal components. However, since the eigenvalue of the first vector is never less than, and may be much greater than, the second eigenvalue,

such that \( \lambda_1 \geq \lambda_2 \geq \lambda_3 \geq \cdots \geq \lambda_n \)

(\( \lambda_1 \) is the first eigenvalue)

then the total variance may be expressed in a small number of eigenvalues.

The eigenvectors therefore describe the relationships between cases with economy and a large proportion of the sample dispersions may be accounted for by \( K \leq n \) dimensions. Also since \( \lambda_1 \) is the largest of the roots it absorbs a large, potentially very large, percentage of the total variance. It is therefore possible that only a few vectors are needed to summarise most of the variability of the original variates. The object of the analysis is a "parsimonious summarization of a mass of observations", (Seal, 1964). Principal components analysis is a method for reducing \( p \) correlated measurement variables to a smaller set of statistically independent linear combinations having certain unique properties with regard to characterising individual differences (Overall & Klett, 1972).
Sneath & Sokal (1973) state that the vectors give the directions of a set of K orthogonal axes in p dimensional space. The coordinates of these axes are linear combinations of the original variates and summarise the major dimensions of variation. Thus the first axis is inclined along the direction of maximum variability among the p dimensional observations. The second is then inclined at right angle to the first and in the direction of next greatest variability and so on. If for simplicity we are dealing with three dimensions only then a plot of each case may produce a cluster of points in the shape of a rugby ball. The principle axis will be aligned along the long axis of the ball and will account for the largest percentage of the total variance. The other two axes will be at right angles to the first axis, be shorter and therefore account for smaller percentages of the dispersion. PCA is able to extend this concept into n dimensions where the cases form a hyperdimensional cloud. The first principal component is the normalised linear combination (i.e. the sums of squares of coefficients being unity) with maximum variance, and so on.

The account of Biomed program BMO 0IM Principal Component Analysis (see section 4E,5) is summarised from Dixon (1973). It is noted (Till & Colley, 1973; Temple, 1975) that this principal component analysis is performed on the correlation matrix, so as to remove the effects of different absolute sizes of the original variates and is equivalent to using standardised data. This in order that small variates may contribute equally with large variates to the total variances attributable to each eigenvalue. It can therefore be appreciated that this method is far superior to bivariate plots as two vectors may depict the simultaneous variation in several characters. Furthermore, the mutual orthogonality
of the eigenvectors allows conclusions to be drawn about the independence of variation represented by these eigenvectors' (Temple, 1975).

It is noted that in this work, as shown in the major texts (e.g. Seal, 1964; Blackith & Reyment, 1971) the first eigenvector will generally only have positive components and be an indicator of general size. It is therefore often the second and third vectors which reveal variations within the sample which are independent of size. That is, overall differences between groups not related to growth differences or differences in size between the groups.

A general rule of thumb for the analysis of PCA is to only consider those eigenvectors with roots larger than 1 as contributing significantly to total variation. Sneath & Sokal (1973) recommend that it is customary to extract only enough eigenvectors to remove the majority, say 75 per cent, of the total variance of the data matrix. Within each vector it may be necessary to only consider those original variates which have a high absolute value, say 0.7 of the highest weighted variate, as contributing significantly to that vector.

This author has used the method recommended by Seal (1964) and based the PCA on variates measured on the same scale. For this reason counts of the number of pore pairs in each half ambulacrum of each petal, variate P, should not be used in conjunction with the other, continuous, measurements.

Seal (1964) gives a detailed mathematical treatment of PCA, Blackith & Reyment (1971) give examples of the biological and palaeontological applications of the technique, and Sneath & Sokal (1973) show its uses within numerical taxonomy.
Discriminant Function Analysis

Discriminant function analysis, as described by Blackith & Reyment (1971), can be considered in terms of hyperdimensional clusters of cases representing known groups. In the present work the cases are represented by fossil specimens upon which K measurements have been made. The groups, therefore, are represented by the specimens collected at known stratigraphic horizons, at particular geographic localities, referred to by the locality name. Thus the Cothill group is simply a hyperdimensional cloud of points constructed through measurement of all fifteen dimensions on each specimen of *N. scutatus* collected at that locality. Therefore with discriminant function analysis, in contrast to PCA, a structure is imposed on the data matrices as groups are defined through reference to their geographic location.

In the case of two clusters which are reasonably well defined from the samples drawn from them, a linear discriminant function is constructed on the basis of the K variables and the two samples of sizes $N_1$ and $N_2$. On the grounds of measurements on the same K variables on a newly found individual, this new specimen can be assigned to one of the clusters with the least chance of making a mistake. As pointed out by Blackith & Reyment (1971:46) this new specimen, in a palaeontological context, may not belong to either cluster in reality but may be close morphometrically to either. This is an important point to consider in identifying relationships between individual specimens.

The linear discriminant function between two samples may be defined as

$$Y = (\bar{x}_1 - \bar{x}_2)^T S^{-1} x,$$

where $\bar{x}_1$ and $\bar{x}_2$ are the mean vectors for the respective samples.
A mean vector is the centre of the cluster of points in K dimensional Cartesian space, i.e. the estimated centre of the data universe. $S^{-1}$ is the reciprocal of the pooled sample dispersion matrix and $X$ is a vector of variables.

The coefficients of the discriminant functions are defined as

$$a = S^{-1} (\bar{x}_1 - \bar{x}_2)$$

where $a$ is the vector of coefficients.

The logical extension of the case of two groups is the concept of linear discriminant functions between many groups. Thus $g$ discriminant functions are constructed between each of $g$ groups (Blackith & Reyment, 1971:49).

A difficult problem to overcome, however, is the fact that all the usual methods of discriminant analysis assume that the dispersion matrices of the groups are homogeneous, i.e. the clusters are of much the same size, shape, and have multivariate normal distributions (Sneath & Sokal, 1973:404).

**Canonical Variates**

The relationship between the groups and the variates within the groups can be represented through canonical variates analysis. Canonical variates can be used to construct generalized distance charts (Blackith & Reyment, 1971:88) in which the underlying axes of variation are first constructed and then used to plot the positions of the various groups. Now as each of the $g$ groups will form a swarm of points in $k$-variante space the calculation for canonical variates is similar to that for principal components with transformed axes being produced. The first axis is inclined in the direction of greatest variability between the means of the $g$ groups. The second is perpendicular to the first and inclined...
in the direction of next greatest variability, and so on for subsequent axes. In PCA the vectors are orthogonal but with canonical variates this is generally not the case. However the canonical variates are also linear combinations of original variables in each of the sets that have maximum correlation, but each linear combination is uncorrelated with other linear combinations. Canonical variates are therefore able to analyse the correlation between the variables of one set with those of other sets, (Anderson, 1958).

Canonical variates are found from the vectors and eigenvalues (or roots) of the determinantal equation

\[
/B - zW/ = 0
\]

where \( z \) represents the eigenvalues, \( B \) is the 'among matrix of sums of squares and cross products' matrix and \( W \) the 'within sums of squares and cross product' matrix (Blackith & Reyment, 1971:89).

It is noted that if there are more variates than groups, i.e. if \( k > g - 1 \), then there will only be \( g - 1 \) non-zero roots. This can be shown in the following manner. If two groups are used then their two mean vectors can be joined by a single line. With three groups the mean vectors can be projected onto a plane, i.e. in two dimensions, and so on.

The vectors corresponding to the eigenvalues \( z \) are found from

\[
(B - zW)t = 0
\]

and are the \( K \) - component vectors, \( t \).

Program BMD 07M is a stepwise discriminant function analysis and is essentially a two part multivariate analysis programme (Mares, 1976). First, sample groups are assigned on the strength
of their geographic and/or stratigraphic horizon and variates which
maximise the between-group variances are added singly while within-
group variances are minimised. Therefore the variate which
discriminates most highly between the groups is used first to
construct a discriminant function and then the second best variate
is added, and so on. Variates which do not contribute significantly
to a discrimination of the groups are omitted from consideration.

Second, a canonical variate analysis is performed and group
means are plotted on canonical axes. The square of the Mahalanobis
distance ($D^2$) of each case from its group mean is also computed
and the probabilities of the inclusion of a case into a particular
group are listed. On this basis newly found individuals can be
assigned to the group they most resemble.

The account of Biomed program BMD 07M Stepwise Discriminant
Analysis (see section 4.5, 6) is taken from Dixon (1973).
Sneath & Sokal (1973) note that discriminant functions and $D^2$
are less sensitive to general size factors than taxonomic distance.
Therefore, despite the use of absolute measurements for the
discriminating procedure, the morphological shape of individuals
is more important for separating groups than overall size. Furthermore,
they point out that discriminant functions have most value for
very close clusters that partly overlap. This has certainly been
found to be the case in the present work.

**Cluster Analysis**

Cluster Analysis, as the name implies, is the grouping of
cases in multivariate space into disjoint sets. As Blackith
& Reyment (1971) explain, individuals or groups which are more
closely related morphologically are brought together into a cluster
which is then considered to be differentiated from other associations forming separate clusters. This technique can therefore be used to try to determine sub-groups, with specific characteristics, within an original sample, or to test the mutual exclusiveness of two or more samples. It can be used when no a priori groupings within a sample are readily observable or alternatively to test the separation of predetermined groupings. Thus Cluster Analysis can be used to complement either PCA or canonical variates.

Broadly speaking clustering techniques may involve the grouping of cases into larger sets from smaller grouping or it may involve the breakup of a complete sample into increasingly smaller sets. These two methods are known as agglomerative and divisive methods respectively.

There are in fact many clustering methods available using either agglomerative or divisive procedures, some of which are able to use different types of data. Many authors differ in their recommendations of the most suitable methods available, indeed the two main texts in this field, Blackith & Reyment (1971) and Sneath & Sokal (1973), advise the use of completely different types of clustering procedures. Blackith & Reyment recommend divisive techniques e.g. the method of Edwards & Cavalli-Sforza (1965). However, they admit that computing time may be prohibitive as these methods involve the examination of similarities between \(2^{n-1}-1\) possible splits between \(n\) cases simply for the initial clustering into 2 sets. They also point out (Blackith & Reyment, 1971:285) that clustering by means of ordination on charts whose axes are vectors (PCA and canonical variates) virtually meets all the requirements of a divisive technique. Sneath & Sokal in contrast recommend the use of agglomerative techniques based on matrices.
of similarity coefficients between cases or between sets of cases. Starting with a set of n separate entities agglomerative techniques group these into successively fewer than n sets arriving eventually at a single set containing all n cases.

Within these techniques, different types of data may be employed. In general presence/absence data and/or quantitative measurements of morphology can be used to characterise cases. These data can then be used in a weighted or unweighted state i.e. different variates can be weighted if they are considered more important than other variates in the clustering procedure. Unweighted methods are equally weighted procedures.

Program Higroup, employed in the present work, has been adapted by the Computer Terminal Staff at Bedford College, London from Davis (1973) and a dendrogram constructing subroutine added, (see section 4E4).

It is a SAHN technique as defined by Sneath & Sokal (1973:214), i.e. a sequential, agglomerative, hierarchic, non-overlapping clustering method using unweighted data. It is sequential as at each clustering stage the similarity between each pair of individuals or clusters is tested in a recursive sequence of operations. It is hierarchic as each smaller set can only be combined in full with another set as the clustering procedure advances. For example, no individual can be linked with another individual at one stage and then separated from it at a later stage. In this way a discrete hierarchy of clusters is built up. It is non-overlapping as any one individual or group of individuals may only belong to one set at a particular stage in the clustering procedure.

This simple type of hierarchical, non-overlapping procedure gives the familiar nested classification often represented by
dendrograms found in many multivariate morphometric studies (e.g., Mares, 1976:50). However, in the present study it is found that this type of cluster analysis rarely provided information on differences within or between groups not provided by PCA, discriminant functions or canonical variates. It is used mainly as a 'checking' routine.

4E) Computer programs

1. Introduction

In the following descriptions of computational procedures normal statistical/computer language has been used. Each sample from a particular locality, stratigraphic horizon or museum collection is referred to as a 'group'. Each group is composed of a series of individual fossil specimens referred to as 'cases' and a series of measurements, 'variables', taken on each case. Therefore in all programs the number of cases, number of variables and the actual measurement of each variable on each case is needed for the analysis.

In addition to this information, the number of groups used in the analysis and the number of cases in each group is needed to perform the Stepwise Discriminant Analysis. Program Test uses only the output from program RMA. The descriptions of Biomed computer program BMD 01M (a principal component analysis) and program 'BMD 07M (a discriminant functions and canonical variates analysis) are taken from Dixon (1973).

2. Program RMA

Program RMA was written by me to produce reduced major axes for every pair of variates within a data matrix characterising a single group (see data * for program listing).
Sets of sample statistics are first produced and then each reduced major axis is calculated through the conversion of data to logarithms. This allows the calculation of the allometric growth curve from the formula for a straight line (i.e., where \( y = bx^a \equiv \log b + a \log x \)). For a straight line of the form \( y = b + ax \)

\[
a = \frac{s_y}{s_x}
\]

\[
\sigma_a = a \sqrt{\frac{1 - r^2}{N}}
\]

\[
b = \bar{y} - \bar{x}a,
\]

where

- \( a \) = growth ratio (slope of the line)
- \( b \) = initial growth index
- \( \sigma_a \) = standard error of \( a \)
- \( \bar{x} \) = mean of \( x \)
- \( \bar{y} \) = mean of \( y \)
- \( s_x \) = standard deviation of \( x \)
- \( s_y \) = standard deviation of \( y \)
- \( r \) = correlation coefficient

(from Imbrie, 1956).

For each pair of variates the program checks for missing data from damaged specimens i.e., that for every case both variates have been measured and then the above statistics are derived. Statistics \( a, b \) and the error of \( a \) are calculated from the formula for a straight line and the results printed and also punched onto cards for use with Program Test. A correlation matrix is then constructed and eigenvectors and eigenvalues derived for comparison with those produced by Principal Components Analysis (BMD OLM).
3. Program Test

Program Test was written by me to compare pairs of reduced major axes calculated by Program RMA. It uses punch cards produced by that program (see data for program listing).

The program prints the locality data information of each pair of groups to be compared. Differences between the slopes of each pair of reduced major axis is calculated such that

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

See 4E section 2 for a description of notations.

For those slopes that are not significantly different the significance of the distance between the slopes is tested. At the first step a combined estimate of the true slope (\(\hat{a}\)) based on both samples is found such that

\[ \hat{a} = \frac{a_1 \sigma_{a_2}^2 + a_2 \sigma_{a_1}^2}{\sigma_{a_1}^2 + \sigma_{a_2}^2} \]

and the variance of \(\hat{a}\) is

\[ \text{var}(\hat{a}) = \frac{\sigma_{a_1}^2 \sigma_{a_2}^2}{\sigma_{a_1}^2 + \sigma_{a_2}^2} \]

New estimates of \(b_1\) and \(b_2\) for each sample can then be derived. The significance of the distance between the two lines can then be calculated (Kermack, 1954:409) such that

\[ z = \frac{\dot{B}_1 - \dot{B}_2}{\text{Var}(\dot{B}_1 - \dot{B}_2)} \]

where

\[ \text{var}(\dot{B}_1 - \dot{B}_2) = \frac{\sigma_y^2}{n_1} + \frac{\dot{a}^2 \sigma_{x_1}^2}{n_1} + \frac{2\dot{a} \sigma_x \sigma_y r_1}{n_1} + \frac{\sigma_y^2}{n_2} + \frac{\dot{a}^2 \sigma_{x_2}^2}{n_2} - \frac{2\dot{a} \sigma_x \sigma_y r_2}{n_2} + \]

\[ (\bar{x}_1 - \bar{x}_2) \cdot \text{var} \hat{a} \]
The program prints out lists of each pair of variates in which the slopes are:

- a) significantly different ($t < 1\%$)
- b) probably significantly different ($1\% < t < 5\%$)
- and c) not significantly different ($t > 5\%$)

Of the slopes that are not significantly different two lists are printed of slopes that are:

- a) a significant distance apart ($t < 1\%$)
- and b) not a significant distance apart ($t > 1\%$)

### 4. Program Higroup

Program Higroup was written by the Bedford College Computer Terminal staff to perform a cluster analysis on multivariate data (see data for program listing) and is a SAHN technique using an unweighted arithmetic pair-group method of clustering.

Data are first standardised in order to equalise the effects of differences in the units and magnitude of the measurements. Then similarity coefficients are constructed from the data matrices of each possible pair of cases, $\sum_{i=1}^{n-1} n_i$ coefficients being produced by this method. The pair with the highest coefficients are then grouped together and their data matrices pooled. This method is sequentially repeated grouping individuals into larger and larger sets until one final cluster is formed containing all cases. The program therefore uses a pair-group method of clustering as only one case or set at a time and the dendograms will show simple bifurcations.

The output includes a dendrogram of the clusters produced by this technique but it lies with the individual worker to decide at which point the program starts to group together disparate
sets. In general, a sudden increase in size of the 'error' produced at each stage of the procedure will indicate that unlike sets are being combined. In this case the immediately proceeding clusters form a grouping of cases into reasonably discrete sets (see example, page 270).

5. Principal Component Analysis (BMD O1M)

This is available as a library program (Dixon, 1973).

After the original data matrix is centered and normed the eigenvalues and corresponding eigenvectors of the correlation matrix C are found, solving the system

\[(C - \lambda I)B = 0\]

where \(\lambda_j\) is the \(j^{th}\) eigenvalue and \(B = (b_{kj})\) the matrix whose columns are the corresponding eigenvectors. \(k, j = 1, 2, \ldots, p\) number of original variables.

The matrix multiplication is then performed

\[z = \sqrt{n-1} \cdot WB\]

which transforms the W data into their orthogonal components. W is the centered and normal data matrix.

The value of each principal component is given for each case in a ranked order so that components can be plotted on bivariate graphs.

6. Stepwise Discriminant Functions (BMD O7M)

This is available as a library program (Dixon, 1973).

At the first step of the analysis the F value for each variable is calculated. For the \(j^{th}\) variable

\[F_j = \frac{(b_{jj} - a_{jj})/(g-1)}{a_{jj}/(n-r-g)}\]
where $b_{jj}$ represents diagonal elements of the total cross-product matrix and $a_{jj}$ the diagonal elements of the within group cross-products matrix, with $g-1$ and $n-r-g$ degrees of freedom.

$g = \text{number of groups used for analysis}$

$n = \text{total number of cases}$

$r = \text{the number of variables included so far in the analysis.}$

The variable selected for entry is the one with the greatest $F$ value.

Now at each further step of the programme the $F$ values are again computed for each variable and one variable is added or removed from the discriminating set according to one of the following rules:

a) If there are one or more variables which have been entered which have an $F$ value less than the originally specified "$F$ level for deletion", then the one with the smallest $F$ will be deleted. If variable $j$ has been entered

$$F_j = \frac{(a_{jj} - b_{jj})/(g-1)}{b_{jj}/(n-r-g+1)}$$

b) If no variable satisfies a) then from among those variables which have not been included, which pass the tolerance test, i.e. has an $F$ value greater than the originally specified "Tolerance level", one is selected with the greatest $F$ value, providing this value is greater than the originally specified "$F$ level for inclusion".

At each step of the procedure the variables are divided into 2 disjoint sets; those included in the discriminant functions and those not included.

For the first $r$ variables included the following statistics are computed:

120
a) The coefficients and constant terms of the classification functions

\[ c_{ki} = (n-g) \sum_{j=1}^{r} \bar{x}_{kj} a_{ij} \]

\[ c_{k0} = \frac{1}{2} \sum_{i=1}^{r} c_{ki} \bar{x}_{ki} \]

Where \( i = 1, 2, \ldots, r \) number of variables included.

\( k = 1, 2, \ldots, g \) number of groups used for the analysis.

\( \bar{x}_{kj} \) is the mean value of the \( j^{th} \) variable in group \( k \).

\( a_{ij} \) is the within group cross-product matrix.

b) The square of the Mahalanobis distance between each pair of groups. This allows each case to be classified into the group it most resembles given the number of variables used so far in the discriminating procedure.

The likelihood of a case being included in its correct group will increase as more variables are included.

c) The F values for testing differences between each pair of groups.

\[ F_{ml} = \frac{(n-g-r+1) n_m n_l}{r(n-g)(n_m + n_l)} \frac{D^2_{ml}}{D^2_{ml}} \]

Where \( m \) and \( l \) are pairs of groups taken in turn.

\( D^2_{ml} \) is the Mahalanobis distance between the pair of groups concerned.

\( n_m \) is the number of cases in group \( m \) and similarly for group \( l \).

\( n \) is the total number of cases.

\( r \) is the number of variables so far included.

This calculation is tested with \( r \) and \( n-g-r+1 \) degrees of freedom.
d) Wilks' $\Lambda$ to test the equality of group means

$$U = \frac{|W|}{|T|}$$

Where $|W|$ is the determinant of the within group cross-product matrix and $|T|$ is the determinant of the total cross-product matrix.

According to Dixon (1973) this statistic is tested with $r,g-1$ and $n-g$ degrees of freedom. Overall & Klett (1972) compute the statistic

$$X^2 = -m \log_e \Lambda$$

where $m = n-1-\frac{1}{2}(p+k)$

and $n = \text{total number of cases}$.

$k = \text{number of groups}$.

$p = \text{number of variables used}$.

$X^2$ can be tested with $(k-1)p$ degrees of freedom, i.e. with Dixon's $(g-1)r$ degrees of freedom. However the statistic $n-g$ of Dixon (1973) is always greater than $m$ of Overall & Klett (1972) and this can effect the $X^2$ statistic to some degree.

Rao (1965) advocates the use of a variance ratio to test the value of $\Lambda$. For small values of $k$ the exact variance ratio is given as:

(1) where $k = 2$; $V.R. = \frac{1-\Lambda}{\Lambda} \frac{n-1-p}{p}$ with $p, n-1-p$ d.f.

(2) where $k = 3$; $V.R. = \frac{1-\sqrt[3]{\Lambda}}{\sqrt[3]{\Lambda}} \frac{n-1-p-1}{p}$ with $2p, 2(n-1-p-1)$ d.f.

For higher values of $k$ a good approximation is to use

$$F = \frac{1-\Lambda^{1/s}}{\Lambda^{1/s}} \frac{ms - 2\lambda}{p(k-1)}$$

where $s = \sqrt[4]{\frac{p^2(k-1)^2}{p^2 + (k-1)^2} - 4}$

$$\lambda = \frac{p(k-1) - 2}{4}$$
with p(k-1) and (ms-2 \wedge ) degrees of freedom. According to Rao (1975) this provides a better approximation than \( \chi^2 \).

e) Approximate F statistic to test equality of group means

\[ F = \frac{1 - \frac{u_1}{s}}{\frac{u_1}{s}} \]

where

\[ s = \sqrt{\frac{r^2q^2 - 4}{r^2 + q^2 - 5}} \quad \text{if} \quad r^2 + q^2 \neq 5 \]

\[ s = 1 \quad \text{if} \quad r^2 + q^2 = 5 \]

with ms + 1 - rq/2 and rq degrees of freedom,

where \( r = r_q + 3 \) and \( q = g - 1 \).

The approximate F gives similar results to the test for Wilks' \( \Lambda \).

The F values for each variable are then calculated again for entry or deletion at the next step.

When all steps are completed, i.e., all variables are entered except those not passing the tolerance test, then the following are computed for classification purposes.

a) The value of the \( m^{th} \) classification function evaluated at case \( k \) of group \( 1 \)

\[ s_{1mk} = c_{m0} + \sum_{j=1}^{r} c_{mj} x_{1kj} \]

where \( 1 = 1, 2, \ldots, t \) total number of groups.

\( m = 1, 2, \ldots, g \)

\( k = 1, 2, \ldots, n_1 \) the total number of cases in the groups \( 1 \).

\( c_{m0} \) is the discriminant constant for group \( m \).

\( c_{mj} \) is the discriminant coefficient for variable \( j \) of group \( m \).

b) Posterior probability of case \( k \) in group \( 1 \) having come
from group m.

\[ P_{lmk} = \frac{p_m \exp(s_{lmk})}{\sum_{i=1}^{g} p_i \exp(s_{lik})} \]

where \( p_m \) is the prior probability of group m. The probability of case k belonging to group m is lower as \( P_{lmk} \) approaches zero.

c) The square of the Mahalanobis distance of case k in group m from group 1.

This value, \( D_{lnk}^2 \), can be used as a chi-square variable with \( r \) degrees of freedom for classification purposes.

Therefore, for a particular case the probability of it belonging to each of the groups used in the analysis can be tested.

A canonical variate analysis is then performed and the eigenvalue problem

\[ Bu_i = \lambda_i Wu_i \quad i = 1, 2, \ldots, p \]

is solved to find the coefficients \( u_i \) of the canonical variables and the amount of dispersion, \( \lambda_i \), explained by each canonical variable where \( B = T - W \). In this case \( W \) and \( T \) are the within and total sum of product matrices of the p variables included after the last step.

The vectors are normalised so that

\[ u_i^T W u_j = \delta_{ij} \]

The canonical correlations \( p_1, p_2, \ldots, p_p \) relative to the groups are then computed where

\[ p_i = (\lambda_i / (1 + \lambda_i))^{1/2} \]
For each case the canonical variables, \( z \), are computed

\[ z_{mki} = \sum_{j=1}^{r} u_{ji}(x_{mki} - \bar{x}_j) \]

where \( m = 1, \ldots, g \)

\( k = 1, \ldots, n \) total number of cases.

\( i = 1, \ldots, z \) canonical variables.

and the first two plotted on a scatter diagram.
CHAPTER 5 -INFRASPECIFIC VARIATION WITHIN NUCLEOLITES SCUTATUS

5A) Introduction

The aim of biometrical analysis here is to make comparisons and hence infer interrelationships between the collected samples from an objective appraisal of their degree of morphological similarity. Differences between samples of the same species, all of similar age, indicate facies dependent characters and the variation to be expected within a species. The analysis is then extended to similar species of different ages to determine whether the same facies dependent characters are important in distinguishing samples at other times. The analysis is then further extended to morphologically distinct species of different ages and of different facies to differentiate facies (environment) dependent from time dependent variables. From the broad evolutionary pattern demonstrated for the echinoids by Kier (1974) the time dependent variables are expected to show overall evolutionary trends within the genus which reflect adaptations to various facies changes through time. Adaptation to a new environment and improved adaptation to a particular mode of life are two trends which are inexorably interwoven, as the ability to adapt to differing habitats is necessarily limited by previous specialisations and morphological changes. Details of these trends are differentiated below (Chapter 10). Finally comparison is made between previously established supra-generic groupings to test their validity and the relationships of species between these groups.

Nomenclature of the species groups has been confused. The author has therefore been careful to confirm Lambert's (1898 p.168) designation of N. scutatus Lamarck 1816, as the genotype of
Nucleolites Lamarck, 1801, N. scutatus apart from its systematic importance, is also the most abundant and morphologically variable species studied. It is a species ideal for a biometrical analysis; a species doubly useful as a standard comparison with other species. Fig. 5.1 is a summary of analyses carried out in this Chapter.

5B) Stratigraphy

The two biometrically important features of N. scutatus are its local abundance and its variability. The numerical profusion in the upper Oxfordian has been well known to stratigraphers and palaeontologists for many years, giving rise to local stratigraphical names such as the Urchin Marls of Oxfordshire and the Urchin Dirt Beds of Yorkshire. No account of the variability within the species has been published, a fact that is surprising, as differences between some samples are marked and taken in isolation would normally, on many grounds, be considered of sufficient importance to split the species into more taxa.

Samples from seven localities have been used in the present study (see Fig. 2, 5). All but two samples are personal collections made by the author. Further collections of N. scutatus were made but were not used in the analysis because of an insufficient number of specimens or particularly poor preservation.

The largest sample of specimens of N. scutatus is from the type area (Wright 1852, 1859) of Trouville, Calvados, France. The specimens come from two horizons, the lower dark grey marly oolites of the shore of Hennequeville (referred to as Trouville shore) and secondly the overlying light grey oolitic limestone at the base of the cliff at the small promontory to the west (referred to as Trouville cliff). These localities are shown in figure 2, 3c. Samples of 42 specimens
<table>
<thead>
<tr>
<th>Sample</th>
<th>Comparison sample</th>
<th>Page</th>
<th>Var.</th>
<th>Spec.</th>
<th>Technique</th>
<th>Sig. of difference</th>
<th>Imp. variables</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Trouville shore</td>
<td>Trouville cliff</td>
<td>133</td>
<td>15</td>
<td>83</td>
<td>S.D.F.</td>
<td>P&gt;5%</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>134</td>
<td>12</td>
<td>166</td>
<td>S.D.F.</td>
<td>P&lt;5%</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>134</td>
<td>12</td>
<td>127</td>
<td>S.D.F.</td>
<td>P&lt;5%</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>134</td>
<td>15</td>
<td>83</td>
<td>H.C.</td>
<td>Clustering not into original groups</td>
<td></td>
</tr>
<tr>
<td>2. Trouville</td>
<td>Cothill</td>
<td>136</td>
<td>15</td>
<td>36</td>
<td>S.D.F.</td>
<td>P&lt;1%</td>
<td>N2,I,H,B,A,</td>
</tr>
<tr>
<td></td>
<td></td>
<td>139</td>
<td>15</td>
<td>250</td>
<td>R.M.A.</td>
<td>P&lt;1% between 7 pairs of slopes</td>
<td>L</td>
</tr>
<tr>
<td>3. Cothill</td>
<td>W.Bassett</td>
<td>140</td>
<td>15</td>
<td>34</td>
<td>S.D.F.</td>
<td>P&lt;1%</td>
<td>L,I,N4</td>
</tr>
<tr>
<td></td>
<td></td>
<td>142</td>
<td>15</td>
<td>34</td>
<td>P.C.A.</td>
<td>Separation along 2nd vector</td>
<td>L,N2,N4</td>
</tr>
<tr>
<td>4. Trouville</td>
<td>Cothill, W.Bassett</td>
<td>145</td>
<td>15</td>
<td>53</td>
<td>S.D.F.</td>
<td>P&lt;1%</td>
<td>L,N2,I</td>
</tr>
<tr>
<td></td>
<td></td>
<td>146</td>
<td>15</td>
<td>53</td>
<td>P.C.A.</td>
<td>Greatest separation along 2nd vector</td>
<td>L,J</td>
</tr>
<tr>
<td>5. Trouville</td>
<td>Cothill, Dorset,</td>
<td>146</td>
<td>15</td>
<td>99</td>
<td>S.D.F.</td>
<td>P&lt;1%</td>
<td>I,L,J,N3,N4,B,A,H</td>
</tr>
<tr>
<td></td>
<td>W.Bassett, Upware</td>
<td>152</td>
<td>15</td>
<td>463</td>
<td>R.M.A.</td>
<td>P&lt;1% between 3-7 pairs of slopes</td>
<td>L</td>
</tr>
<tr>
<td>6. Trouville</td>
<td>Cothill, Dorset,</td>
<td>152</td>
<td>15</td>
<td>468</td>
<td>S.D.F.</td>
<td>P&lt;1%</td>
<td>I,L,N4,J,H,B,A</td>
</tr>
<tr>
<td></td>
<td>Colne, W.Bassett, Upware</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Figure 5.1. Summary of important analyses run in Chapter 5 for N.scutatus samples. See fig. 4.2. for details of variables. S.D.F. = Stepwise discriminant functions; (BMD O7M: This program includes the construction of discriminant functions and a canonical variates analysis. See p.94); P.C.A. = Principal components analysis (BMD O1M); H.C. = Hierarchical clustering; R.M.A. = Reduced major axes; Class = Classification routine of stepwise discriminant functions.
from the shore horizon and 133 from the cliff arc from the collection
of the Université de Caen, kindly lent by Dr. M. Rioult. These samples
were supplemented by a further 20 specimens from the shore and 7
from the cliff collected by the author.

Within the samples from Trouville a much better preservation
was seen in the specimens collected from the shore horizon, where the
test is usually intact and the specimens are rarely crushed or
cracked, whereas in the cliff sample the test easily breaks away
from the internal mould in many specimens. This is reflected in the
number of specimens in which all 15 morphological variables could
be measured. Of the 42 specimens from the Caen collection of the shore
horizon all measurements could be taken on 28 specimens and only
one measurement, usually variable E, was missing from a further 8.
Of 133 specimens from the cliff horizon, it was only possible to take
all measurements on 55 fossils and all but one measurement on a
further 30.

The specimens are from beds of the Oolithe de Trouville
lying within the sub-zone of Perisphinctes antecedens (Arkell, 1930).
They would therefore appear to be of the same age as the beds of
Cothill, Bran Point and possibly Wootton Bassett although the oolites
of Upware are possibly of a younger age.

Of the other samples used in the analysis all were personally
collected by the author. The localities are:

a) Bed 4 (see fig. 2, 4) Bran Point, Dorset (G.R. SY743814).

This bed was chosen as it contained far more specimens of N. scutatus
than the other six beds yielding the species. In this sample, from a
soft blue-grey marl, many specimens were found to be very distorted,
crushed and broken, possibly due to compaction of the marl during
diagenesis. Some other specimens were perfectly preserved and amongst
the finest specimens of *N. scutatus* found. Within the sample of 28 specimens in which any sort of reasonable measurement could be made, all measurements are possible on 16. The beds are near the top of the Osmington Oolite Group (Arkell 1936) and therefore near to the boundary between the *transversariurn* and *plicatilis* zones (Wilson 1968). The beds are placed within the *parandieri* sub-zone by Fursich (1976, a), but within the *antecedens* sub-zone by Cope & Torrens (1969).

b) The old quarry in the town, Calne, Wiltshire (G.R. ST998765). This small sample from a soft chalky oolite contained well preserved specimens with the test intact. The bed is within the famous Coral Rag of Calne placed between the *transversariurn* and *plicatilis* zones (Wilson 1968). All measurements could be taken on five out of eight specimens collected.

c) The M4 motorway cutting at Wootton Bassett, Wiltshire (G.R. SU073343). These specimens, from oolitic limestone, are usually found as moulds, as the test tended to adhere to the rock when the fossils were extracted. Therefore, although the specimens are not often crushed, a full set of measurements could be taken on only 17 from a sample of 52 specimens. They are of presumed *plicatilis* age, from comparison with the closest comparable strata (White, 1925).

d) Quarry at Cothill, Oxfordshire (G.R. SU466996). These specimens from the sandy horizons (see fig. 2, 4) are frequently broken and have probably suffered much pre-burial abrasion. A full set of measurements is therefore possible on only 17 from a sample of 38 specimens. The sample is from the Urchin Marls of Oxfordshire, within the *antecedens* sub-zone (Callomon 1960).

e) Quarry at Upware, Cambridgeshire (G.R. TL542723). This large sample from the Upware reef inlier is from a coarse, but soft marly pisolite with abundant irregular echinoids. The specimens were generally well-preserved with the tests intact and
in good condition revealing much detail. All measurements could be taken on 76 specimens from a sample size of 133, and only one measurement, usually variable E, was missing on a further 15. The oolites are placed within the parandieri sub-zone with perhaps "traces of the antecedens sub-zone" (Callomon, 1960).

Thus a total of 461 specimens of *N. scutatus* was used in the biometrical analysis. As far as could be determined all the samples were collected from horizons within the plicatilis and transversarium zones which lie each side of the middle-upper Oxfordian boundary (Wright, 1972).

5C) **Preservation**

From a subjective appraisal all the samples appear to be very similar to each other; no distinguishing features separate any group from any other group. However, some generalisations can be made about the samples.

Firstly, that there is an overall size difference in the specimens between samples, although of course, considerable overlap does occur. The samples can be ordered according to the average size of specimens, i.e., the smallest being Bran Point, followed by Cothill, Trouville (the samples from both horizons being very similar), Calne, Wootton Bassett and the sample with the generally largest specimens being Upware.

Another feature that is noticeable is the difference in the states of preservation between the samples. In the only sample from a distinctly siliceous horizon, the Cothill sample, the specimens are often broken and abraded but the test is always intact, moulds being rare. In the remaining samples, all from dominantly calcareous horizons, two states of preservation are observed. There are those
samples with specimens that are well preserved, tests intact and showing fine detail, and secondly those samples with specimens that are mainly preserved as moulds with a light brown test often adhering to the matrix in which the fossil is found. Those in the former group, the Bran Point, Trouville shore, Calne and Upware samples are all found in sediments with a high proportion of micrite whilst those from the latter, Trouville cliff and Wootton Bassett are from sparry oolitic limestones. It seems that replacement of the test is associated with sparry cements precipitated from percolating pore fluids in the grain supported sparites and that less post-depositional alteration occurs in mud supported micrites as these sediments contain fewer primary pore spaces. The specimens from the pure marl horizon at Bran Point have suffered more post-depositional compression than those from the marly oolites. The presence of coarse ooliths appears to limit the amount of compaction of the sediments.

5D) **Comparison between the Trouville shore and the Trouville cliff samples.**

Comparisons is first made between the sample from the lower marly oolite of the Trouville shore and the sample from the upper oolite of the Trouville cliff (samples from the Caen collection with 42 and 133 specimens in each group respectively). Differences in the state of preservation between the two samples allow all 15 variables to be measured on a higher proportion of specimens from the lower horizon. Comparison was made between the samples because of the slight differences in sedimentary facies and stratigraphic horizon between the two.

The aim of the analysis was to detect whether a significant change had occurred during this slight change in facies and time.

Four tests were utilised. Three first of all using a small
number of near perfect specimens. These tests were then repeated using a larger number of specimens by adding less well preserved individuals, and a fourth test added.

1. Discriminant Functions

Using the stepwise discriminant function programme, BMD07M, on those specimens with 15 measured variables (28 specimens from the lower and 55 from the upper horizon) it was found that there are no significant differences between the two samples.

Step 14 (final)
Variable not included; NL
F value = 2.1 (Significance of the difference between group means; $P > 5\%$)
U-statistic = .701 (Significance of the inequality of group means; $P > 5\%$)
Specimens classified wrongly by posterior probability; 20%.

2. Chi-square

$\chi^2$ tests were carried out on the Mahalanobis distance between each specimen and all group means, produced by program BMD 07M, in order to assess the probability of a particular specimen belonging to a particular group. In this analysis only three specimens, two from Trouville cliff and one from Trouville shore, were a highly significantly distance ($P < 1\%$) from the opposing group. This indicates that the probability is high ($P > 5\%$) that most specimens might belong to either group and substantiates the F statistic that there is no significant difference between the groups. In the case of the two specimens noted above it was found that they also have a low probability ($P < 5\%$) of belonging to their correct group and therefore appear to be unusual specimens. See fig. 5,4 as an example of classification output.
3. Canonical variates

A plot of the first two canonical variables, (fig. 5, 2) representing 100% of the variability of the 14 variables used was produced by program BMD 07M and shows the degree of overlap between the two samples.

As many specimens in the original samples were only slightly abraded it was decided to increase the number of specimens in the analysis by reducing the number of variables used to define the samples. Two test runs were undertaken in which firstly variables I, M and N were excluded so that it was possible to use 106 specimens, and secondly, 127 specimens without variables E, I or L. It was found that there was a marginal increase in the significance of the difference between the group means (P = 5%), shown by the $U$ statistic, ($\eta^2 = .8$) but that the number of specimens classified into the wrong group at the end of the analysis rose to over 30%.

No certain significant difference is therefore evident between the samples from the shore and cliff horizons and they have therefore been treated as a single sample in many later analysis.

The computer has shown therefore that although the two samples are different, as any two samples must be to a certain extent, even a comparison in 14 dimensions cannot produce a significant separation, and it is inferred that only a minimal amount of change occurred in the two populations during the time between the deposition of the marly oolite and the oolitic limestones at Trouville.

4. Cluster analysis

On performing a hierarchical cluster analysis on the complete Trouville sample, two quite distinct groups are formed
Figure 5.2. Distribution of Trouville cliff (T) and Trouville shore (O) specimens on the first two canonical axes. Group centroids indicated by large lettering. Mean coordinates; Trouville cliff $0.447, 0.000$, Trouville shore $-0.878, 0.000$. 

$O =$ Trouville shore  
$T =$ Trouville cliff
by the programme, although the errors of grouping beyond the fourth step are large in comparison with earlier groupings. However, the two sub-groups so formed can be characterised as adjacent and remote factions amongst the sample. The smaller adjacent group being characterised in general by a larger, lower periproct, a shallower groove at the posterior border and the periproct being close to the apical disc, i.e. variables L, N4, N2 and N1 respectively. The specimens of the adjacent group tend to be the smaller in size of the two groups although the groups are not differentiated by size alone, and specimens from both the shore and cliff samples are evenly distributed throughout the two groups. The adjacent group is also the more homogeneous in character being formed by the cluster analysis at the stage of formation of five groups. Thus, although the computer distinguishes two groups within the total sample, these do not correspond to the two different horizons.

There is no significant difference between the sample of N. scutatus from the Trouville shore and that from Trouville cliff.

5B) Comparison between the Trouville and Cothill samples

Comparison was extended to a sample from a completely different sediment of the same subzonal age, the calcareous sandstone of Cothill.

All Cothill and Trouville specimens of the author's collection, in which all 15 variables are present were used for the comparison (comprising 17 and 19 specimens respectively) in a discriminant function analysis. The small Trouville sample was used to satisfy a recommendation of discriminant function analysis i.e. near equal sample sizes. (See Ch. 4D).
Step 1
Variable N2 entered.

Step 5
Variables I, M, B and A added.

U-statistic = 0.39 (Significance of the inequality of group means; 
\[ P = 1\% \])

Step 13 (final)
Variables not included; D and N4

F value = 3.6 (Significance of difference between group means; 
\[ P = 1\% \])

U-statistic = 0.320 (Significance of the inequality of group means; 
\[ P = 1\% \])

Specimens classified wrongly by posterior probability; 6%.

\[ \chi^2 \] tests of the probability of each specimen belonging to a particular group showed that roughly a fifth of the cases in each group have a low probability (\( P < 5\% \)) of belonging to the opposing group. This is a marked contrast to the previous analysis (p.133) which indicated that nearly all specimens from Trouville shore and Trouville cliff could belong to either sample.

Comparison of figure 5.3 with figure 5.2, shows there is a much greater distance between the two group means and less overlap in the Cothill - Trouville comparison. In the Trouville sample 17 specimens are classified correctly with only two wrongly, and in the Cothill sample all 17 are correct, giving an incorrect classification of 11% and 0% of the specimens respectively.

Simpson (1961) and Cooper (1973) have used a figure of 25% or less overlap between samples to define a sub-species. This evidence, therefore, taken in isolation would suggest that
Figure 5.3. Distribution of Trouville (T) and Cothill (H) specimens on the first two canonical axes. Group centroids indicated by large lettering. Mean coordinates; Trouville 1.341 .000
Cothill -1.499 .000
two sub-species are present in the foregoing analysis.

It can be argued, however, that the 17 perfect specimens are not representative of all 38 specimens of the Cothill sample. The multivariate analysis cannot accept missing data from incomplete specimens. However, a bivariate approach can be used to test the difference between all specimens in the two samples.

When reduced major axes are constructed for variable A and all other variables, comparisons of the two samples reveal significant differences between only two slopes. These are for A with C ($P < 1\%$) and D ($1\% < P < 5\%$). Although no significant differences can be proved between any other pair of slopes, in all but one case, A and N4, the slopes are a significant distance apart.

It is noted that N4 is entered at step 12 on DFA. The rate of increase of C during growth seems to be very different between the two samples. For example, when reduced major axes are constructed for C with all other variables then high significant differences ($P < 1\%$) are found with the slopes involving variables A, B, G, J, L and N2 and probable significant differences ($1\% < P < 5\%$) for C and H. This involves over half of the variables measured. An even greater degree of difference is found between the reduced major axes when all variables are used with a variable such as L. In this case seven slopes, L with C, D, I, M, N1, N2 and N3, are all found to be highly significantly different ($P < 1\%$) between the two samples.

It should be noted that the variables important in distinguishing between the two samples through bivariate analysis need not be the same as those found to be important in discriminant analysis. This is because the former is concerned with growth ratios of variables and the latter with absolute values. Nevertheless,
significant differences are observable between the Trouville and Cothill samples of *N. scutatus*.

5F) **Comparison between the Cothill and Wootton Bassett samples**

The significant difference between the Cothill and Trouville samples might have reflected the geographical isolation of these localities. The Cothill sample was therefore compared with the geographically closer Wootton Bassett sample to test for a closer morphological similarity. These samples are from horizons only 40 kms apart and are of the same presumed *plicatilis* zonal age (see p.130).

Using the discriminant analysis programme, BMD 07M, a dramatic difference between the samples was observed.

**Step 3**

Variables L, I and N4 entered.

F value = 26.4 (Significance of difference between group means; 

\[ P = 1\% \]

Specimens classified wrongly by posterior probability; 0%.

**Step 16 (final)**

F value = 9.2 (Significance of difference between group means; 

\[ P < .1\% \]

U-statistic = .128 (Significance of the inequality of group means; 

\[ P < .1\% \]

Specimens classified wrongly by posterior probability; 3%.

The majority of specimens were classified as 100% representative of their own group (fig. 5,4).

Although specimens of the Wootton Bassett sample are on average larger in size than those of the Cothill sample, measurements of the gross morphology of the test e.g. variables A, B, C, D, G and H,
<table>
<thead>
<tr>
<th>Group with Largest Prob.</th>
<th>Square of Distance from and Posterior Probability for Group</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Group</td>
</tr>
<tr>
<td>1</td>
<td>Hill</td>
</tr>
<tr>
<td>2</td>
<td>Hill</td>
</tr>
<tr>
<td>3</td>
<td>W.B.</td>
</tr>
<tr>
<td>4</td>
<td>Hill</td>
</tr>
<tr>
<td>5</td>
<td>Hill</td>
</tr>
<tr>
<td>6</td>
<td>Hill</td>
</tr>
<tr>
<td>7</td>
<td>Hill</td>
</tr>
<tr>
<td>8</td>
<td>Hill</td>
</tr>
<tr>
<td>9</td>
<td>Hill</td>
</tr>
<tr>
<td>10</td>
<td>Hill</td>
</tr>
<tr>
<td>11</td>
<td>Hill</td>
</tr>
<tr>
<td>12</td>
<td>Hill</td>
</tr>
<tr>
<td>13</td>
<td>Hill</td>
</tr>
<tr>
<td>14</td>
<td>Hill</td>
</tr>
<tr>
<td>15</td>
<td>Hill</td>
</tr>
<tr>
<td>16</td>
<td>Hill</td>
</tr>
<tr>
<td>17</td>
<td>Hill</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Group</th>
<th>W.B.</th>
<th>Case</th>
<th>W.B.</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>W.B.</td>
<td>20.799</td>
<td>.000</td>
<td>9.974</td>
</tr>
<tr>
<td>2</td>
<td>W.B.</td>
<td>33.428</td>
<td>.000</td>
<td>12.624</td>
</tr>
<tr>
<td>3</td>
<td>W.B.</td>
<td>59.953</td>
<td>.000</td>
<td>14.810</td>
</tr>
<tr>
<td>4</td>
<td>W.B.</td>
<td>51.569</td>
<td>.000</td>
<td>20.153</td>
</tr>
<tr>
<td>5</td>
<td>W.B.</td>
<td>40.594</td>
<td>.000</td>
<td>14.328</td>
</tr>
<tr>
<td>6</td>
<td>W.B.</td>
<td>22.398</td>
<td>.000</td>
<td>6.720</td>
</tr>
<tr>
<td>7</td>
<td>W.B.</td>
<td>55.399</td>
<td>.000</td>
<td>23.775</td>
</tr>
<tr>
<td>8</td>
<td>W.B.</td>
<td>39.474</td>
<td>.000</td>
<td>5.544</td>
</tr>
<tr>
<td>9</td>
<td>W.B.</td>
<td>25.532</td>
<td>.001</td>
<td>11.196</td>
</tr>
<tr>
<td>10</td>
<td>W.B.</td>
<td>21.963</td>
<td>.000</td>
<td>5.354</td>
</tr>
<tr>
<td>11</td>
<td>W.B.</td>
<td>37.071</td>
<td>.000</td>
<td>13.494</td>
</tr>
<tr>
<td>12</td>
<td>W.B.</td>
<td>36.923</td>
<td>.000</td>
<td>8.560</td>
</tr>
<tr>
<td>13</td>
<td>W.B.</td>
<td>42.449</td>
<td>.000</td>
<td>6.485</td>
</tr>
<tr>
<td>14</td>
<td>W.B.</td>
<td>22.982</td>
<td>.001</td>
<td>8.513</td>
</tr>
<tr>
<td>15</td>
<td>W.B.</td>
<td>51.208</td>
<td>.000</td>
<td>15.120</td>
</tr>
<tr>
<td>16</td>
<td>W.B.</td>
<td>38.419</td>
<td>.000</td>
<td>15.305</td>
</tr>
<tr>
<td>17</td>
<td>W.B.</td>
<td>42.997</td>
<td>.000</td>
<td>14.291</td>
</tr>
</tbody>
</table>

Figure 5.4 Classification output for the Cothill (Hill) and Wotton Bassett (W.B.) samples at the final step of the discriminant function analysis. Tabulation of the Mahalanobis distances and posterior probability for each specimen.
did not figure highly in discriminating between the two samples. Indeed the first size variable to be entered was variable B (Breadth) at step 4, indicating the more elongate character of the Cothill specimens. The first three variables of importance in the discriminating procedure were all concerned with the size and position of the periproct. Measurements on the position of the apical system, i.e. M and N1, figure only at steps 10 and 13.

A plot of the principal components (fig. 5,5) shows a similar but more scattered distribution of points for the same two samples. This perhaps is a more objective view of the differences between the samples in multidimensional space, as all 34 specimens are treated as one group, the scatter of points being a representation of their position relative to multivariate correlations for the group as a whole. Again a small degree of overlap is evident between the two groups, which have a wide and almost equal scatter.

Figure 5,6 tabulates eigenvalues and direction cosines for the first four principal components. The first component is composed of the main morphological or size/shape variables, i.e. A, B, C, D, E, G, H and M. The second component is made up of variables concerned with the periproct and sulcus, i.e. L and N4, the length and position of the periproct, and J and N2 the length of the sulcus and its depth at the posterior border. As can be seen from a plot of the first two components it is the distribution along component 2, that produces the separation between the groups. Moreover, as all vectors are orthogonal (see Ch. 4,02) the differences in the periproct and sulcus, between the two samples, are independent of size. For example, a specimen from Cothill would be very different in the length of the periproct and sulcus when compared to a specimen from Wootton Bassett of exactly the same size. Therefore variables of
Figure 5.5. Distribution of Cothill (H) and Wootton Bassett (W) specimens along Principal Components 1 and 2 based on a 15 variable analysis. Components 1 and 2 account for 71% of total variation.
PRINCIPAL COMPONENT ANALYSIS

Cothill and Wootton Bassett samples

15 variables, 34 cases.

Eigenvalues

<p>| | | | |</p>
<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>8.31</td>
<td>2.38</td>
<td>1.14</td>
<td>1.09</td>
</tr>
</tbody>
</table>

Cumulative proportions of total variance

<p>| | | | |</p>
<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>55%</td>
<td>71%</td>
<td>79%</td>
<td>86%</td>
</tr>
</tbody>
</table>

Eigenvectors

<table>
<thead>
<tr>
<th></th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>-.34</td>
<td>-.07</td>
<td>.02</td>
<td>.04</td>
</tr>
<tr>
<td>B</td>
<td>-.32</td>
<td>-.18</td>
<td>.04</td>
<td>.00</td>
</tr>
<tr>
<td>C</td>
<td>-.30</td>
<td>.26</td>
<td>-.19</td>
<td>-.09</td>
</tr>
<tr>
<td>D</td>
<td>-.30</td>
<td>.25</td>
<td>-.23</td>
<td>-.14</td>
</tr>
<tr>
<td>E</td>
<td>-.31</td>
<td>-.09</td>
<td>.17</td>
<td>.06</td>
</tr>
<tr>
<td>G</td>
<td>-.34</td>
<td>-.12</td>
<td>.04</td>
<td>.03</td>
</tr>
<tr>
<td>H</td>
<td>-.33</td>
<td>-.01</td>
<td>-.02</td>
<td>.09</td>
</tr>
<tr>
<td>I</td>
<td>-.21</td>
<td>-.09</td>
<td>.21</td>
<td>-.58</td>
</tr>
<tr>
<td>J</td>
<td>-.21</td>
<td>-.41</td>
<td>-.23</td>
<td>.04</td>
</tr>
<tr>
<td>L</td>
<td>-.09</td>
<td>-.47</td>
<td>-.36</td>
<td>.35</td>
</tr>
<tr>
<td>M</td>
<td>-.24</td>
<td>-.20</td>
<td>-.32</td>
<td>.03</td>
</tr>
<tr>
<td>N1</td>
<td>-.23</td>
<td>.18</td>
<td>.31</td>
<td>-.18</td>
</tr>
<tr>
<td>N2</td>
<td>-.14</td>
<td>.43</td>
<td>-.09</td>
<td>.23</td>
</tr>
<tr>
<td>N3</td>
<td>-.11</td>
<td>.20</td>
<td>.47</td>
<td>.63</td>
</tr>
<tr>
<td>N4</td>
<td>-.22</td>
<td>.33</td>
<td>-.47</td>
<td>.07</td>
</tr>
</tbody>
</table>

Figure 5, 6. Eigenvalues and direction cosines of the first four eigenvectors for the Cothill and Wootton Bassett samples. The first two eigenvectors are plotted in fig. 5, 5.
the periprot again figure prominently in the discrimination
between two samples of *N. scutatus* of approximately the same age
but from different horizons.

The degree of difference between the samples from Cothill
and Wootton Bassett is at a higher level than between the Cothill
and Trouville samples, since significant differences are achieved
by the use of fewer variables. Indeed the evidence for the two
English samples, coming from two close localities, might suggest that
they represent two separate species.

5G Comparison between Cothill, Wootton Bassett and Trouville samples

The analysis can be extended further to include all three
groups so far studied. For this purpose the discriminant analysis
programme was used in an attempt to observe further the differences
between the samples, especially the large differences found to
exist between the Cothill and Wootton Bassett samples.

Step 3
Variables L, N2 and I entered.

**U-statistic = .40** (Significance of the inequality of group means;

\[ P < 1\% \])

Step 8

F matrix indicated that all group means were highly significantly
different \( (P < 1\%) \) from all other groups.

Step 13

**U-statistic = .12** (Significance of the inequality of group means;

\[ P < .1\% \])

Specimens classified wrongly by posterior probability;

Cothill 6%, Trouville 16%, Wootton Bassett 12%.
An interesting point to note is that the Trouville sample occupied an intermediate position between the two English samples in having some specimens classified wrongly into either group, whilst no Cothill specimens was classified with the Wootton Bassett samples or Wootton Bassett specimens with the Cothill samples. In fact the only specimen to be classified wrongly in the previous analysis, specimen X79 from Cothill, was classified with the Trouville sample. The intermediate nature of the Trouville sample is borne out in the canonical plot, figure 5,7, which shows the two English samples lying in peripheral areas to the central French sample.

A plot of the first two principal components also showed a complete separation between the Cothill and Wootton Bassett sample, the Trouville sample again occupied a central position between them. These two components in general represent the same variables as those used in the Cothill - Wootton Bassett plot.

The Cothill and Wootton Bassett samples are end members of a series linked by the intermediate and overlapping Trouville sample. It is therefore inferred that the Cothill and Wootton Bassett samples do not belong to separate species. Since the morphological sequence Cothill - Trouville - Wootton Bassett is not the geographical sequence of samples, the differences between samples are not primarily a function of geographic isolation.

5H) Comparison between all large N.scutatus samples

The five major samples of N.scutatus from Bran Point, 16 specimens; Cothill, 17 specimens; Trouville, 19 specimens; Wootton Bassett, 17 specimens and a random sample of 30 specimens from Upware, were used together in an analysis to further test the significance of the differences between groups within this diverse species.
Figure 5,7. Distribution of Trouville (T), Cothill (H) and Wootton Bassett (W) specimens on the first two canonical axes. Group centroids indicated by large lettering.
Mean coordinates;
Trouville 0.261 -1.310
Cothill -2.307 0.595
Wootton Bassett 2.016 0.870

H = Cothill
T = Trouville
W = Wootton Bassett
Again it was found that the first variable to be entered by the stepwise discriminating procedure were those concerned with the periproct.

**Step 1**
Variable I entered.

$U$-statistic = .41 (Significance of the inequality of group means; $P < .1\%$)

**Step 2**
Variable L entered.

Upware sample became probably significantly different ($P < 5\%$) from all other groups except Wootton Bassett.

**Step 8**
Variables J, N3, N4, B, A and H added.

$F$ matrix indicated all groups were highly significantly different ($P < 1\%$) from every other group.

**Step 14 (final)**
Variable not included; C

$U$-statistic = .05 (Significance of the inequality of group means; $P < .1\%$)

Specimens classified wrongly by posterior probability; 13%

It was seen therefore that the size variables A to H were not important in distinguishing between individual specimens from different samples although there are overall size differences between the samples.

The plot of the first two canonical variates shows the distribution of the five groups relative to each other, although it should be noted that the plot represents only 85% of the total dispersion (figure 5, 8). It can readily be seen that there are no distinct groups formed, the samples overlap and the specimens
Figure 5.8. Distribution of Bran Point (D), Cothill (H), Trouville (T), Wootton Bassett (W) and Upware (U) specimens on the first two canonical axes. Group centroids indicated by large lettering.
Mean coordinates:
Bran Point  -2.372  1.312
Cothill     -2.301  -1.672
Trouville  -0.498  0.315
Wootton Bassett  0.526  0.469
Upware     2.586  -0.217

D = Bran Point
H = Cothill
T = Trouville
W = Wootton Bassett
U = Upware
therefore probably represent one diverse species. However certain patterns can be discerned from within the plot.

First, it is evident that each group mean is quite separate from all other group means. (The statistical significance of this difference is given in the F - matrix). The two most similar groups are Trouville and Wootton Bassett samples yet only 18% of the Wootton Bassett sample is classified as more typical of Trouville specimens and 5% of the Trouville sample classified with Wootton Bassett.

Second, the means of the four 'calcareous' samples, Bran Point, Trouville, Wootton Bassett and Upware, lie close together and occur in a simple linear progression. This is roughly coincident with increasing sediment grain size (fig. 5, 11). The Cothill sample, from a siliceous horizon, stands apart from, and has much less overlap with, these other groups.

It was found that between 75% and 100% of the specimens in each sample were assigned into their locality group. This applies when either all 107 Trouville specimens are used or only 19 specimens collected by the author.

Fig. 5, 9 tabulates the probability of specimens in each sample belonging to a particular group based on \( \chi^2 \) tests of Mahalanobis distances, \( D^2 \), of each case from all group means. The linearity of the samples from Bran Point, Cothill, Trouville, Wootton Bassett to Upware is emphasised by an examination of the percentage of specimens within each sample with a low probability (\( P < 5\% \)) of belonging to each group. The percentage increases in a linear manner away from the correct group. Therefore, there are many specimens from Upware with a low probability (\( P < 5\% \)) of belonging to Cothill but considerably fewer with a low probability.
<table>
<thead>
<tr>
<th>Original Sample</th>
<th>Group</th>
<th>Bran Point</th>
<th>Cothill</th>
<th>Trouville</th>
<th>W. Bassett</th>
<th>Upware</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bran Point</td>
<td>6.3%</td>
<td>31.3%</td>
<td>18.8%</td>
<td>31.3%</td>
<td>100%</td>
<td></td>
</tr>
<tr>
<td>Cothill</td>
<td>35.3%</td>
<td>11.8%</td>
<td>29.4%</td>
<td>47.1%</td>
<td>88.2%</td>
<td></td>
</tr>
<tr>
<td>Trouville</td>
<td>21.1%</td>
<td>26.3%</td>
<td>0.0%</td>
<td>10.5%</td>
<td>21.1%</td>
<td></td>
</tr>
<tr>
<td>W. Bassett</td>
<td>64.7%</td>
<td>70.6%</td>
<td>41.2%</td>
<td>17.6%</td>
<td>35.3%</td>
<td></td>
</tr>
<tr>
<td>Upware</td>
<td>96.7%</td>
<td>93.3%</td>
<td>36.7%</td>
<td>23.3%</td>
<td>0.0%</td>
<td></td>
</tr>
</tbody>
</table>

Figure 5, 9. Percentage of specimens within each sample with a low probability (P<5%) of belonging to each group, based on $\chi^2$ tests of $D^2$ for each case.
of belonging to its statistical neighbour Wootton Bassett.

Fig. 5, 10 shows the degree of difference between all five \textit{N. scutatus} samples when reduced major axes are constructed for variable A with all other variables. Again, in general terms, the sample from Upware is seen to be the most distinct group. However, if an important discriminating variable, such as L, is used as the main variable for comparison then a large number of slopes are found to be highly significantly different (P < 1%).

\textit{N. scutatus} is thus a highly variable species. Significant differences in sample means indicate generalised differences between local populations, but the high degree of overlap implies that only a single species is involved.

51) Extension of the analysis to include the small Calne sample

The discriminant analysis was extended to include the small Calne sample of 5 specimens and to split the Trouville group into its original shore and cliff collections.

It was found that the pattern of discrimination was the same as with the previous analyses. No significant differences were observed between the two Trouville samples so justifying their inclusion as a single group. The plot of all the samples showed the Calne group to lie between the Trouville and Wootton Bassett groups. It was not significantly different (P > 5%) from any other group, probably a result of its small sample size. The maximum grain size of the Calne sediment is also intermediate between that of Trouville and Wootton Bassett, supporting the inference that there is a relationship between echinoid morphology and the associated substrate.
A) Variable A with all other variables

<table>
<thead>
<tr>
<th>Bran Point</th>
<th>Cothill</th>
<th>Trouville</th>
<th>W.Bassett</th>
<th>Upware</th>
</tr>
</thead>
<tbody>
<tr>
<td>A. 0</td>
<td>B. 1</td>
<td>C. 13</td>
<td>D. 3</td>
<td></td>
</tr>
<tr>
<td>A. 1</td>
<td>B. 0</td>
<td>C. 13</td>
<td>D. 2</td>
<td></td>
</tr>
<tr>
<td>A. 0</td>
<td>B. 0</td>
<td>C. 14</td>
<td>D. 1</td>
<td></td>
</tr>
<tr>
<td>A. 1</td>
<td>B. 2</td>
<td>C. 3</td>
<td>D. 2</td>
<td></td>
</tr>
<tr>
<td>A. 11</td>
<td>B. 0</td>
<td>C. 11</td>
<td>D. 0</td>
<td></td>
</tr>
</tbody>
</table>

B) Variable L with all other variables.

<table>
<thead>
<tr>
<th>Bran Point</th>
<th>Cothill</th>
<th>Trouville</th>
<th>W.Bassett</th>
<th>Upware</th>
</tr>
</thead>
<tbody>
<tr>
<td>A. 4</td>
<td>B. 0</td>
<td>C. 10</td>
<td>D. 1</td>
<td></td>
</tr>
<tr>
<td>A. 3</td>
<td>B. 1</td>
<td>C. 10</td>
<td>D. 3</td>
<td></td>
</tr>
<tr>
<td>A. 5</td>
<td>B. 0</td>
<td>C. 9</td>
<td>D. 0</td>
<td></td>
</tr>
<tr>
<td>A. 3</td>
<td>B. 0</td>
<td>C. 11</td>
<td>D. 0</td>
<td></td>
</tr>
</tbody>
</table>

Figure 5.10. Comparison of reduced major axes between each of five *N. scutatus* samples. A= slopes that are highly significantly different (P<1%); B= slopes that are probably significantly different (1%<P<5%); C= slopes in which no significant difference can be proved (P>5%); D= slopes within C which are not a significant distance apart (P>1%).

153
5J) Conclusions

The computer analyses show that variables L, I and N4 are primarily used for discrimination between all sample groups and that A, B, H and J are less frequently but occasionally important. Thus, the size of the periproct and its position within the sulcus are significantly different between groups, the overall size and elongation of the test are characters of secondary significance, and all other morphological variables account for little significant variation within _N. scutatus_.

The samples are all from two adjacent subzones. However, no phylogenetic sequence of changes is discernable. The computer did not even divide the samples clearly into two age groups. Fig. 5, 5 shows a clear distinction between two of the samples. Taken in isolation, it might suggest that the groups be characterised taxonomically as separate species. However, fig. 5, 8 demonstrates the occurrence of intermediate groups, and it is concluded that only a single variable species is represented.

There is no direct correlation between the morphological and geographical separation of the groups. Fig. 5, 7 shows the French sample from Trouville to be placed morphologically between the two English samples of Cothill and Wootton Bassett. There is no graphical overlap between the latter samples although the localities are only 40 km apart. Morphological distinction between groups is therefore not simply a function of geographic distance. Geographic isolation rather than distance may, however, be of some importance. The distinct Cothill and Wootton Bassett samples were separated by a submarine swell (Wilson, 1968) which may have formed a physical barrier. The distinction of the Upware group (e.g. fig. 5, 8) may reflect separation of this area of carbonate deposition from the
main outcrop by the Ampthill Clay facies, a facies inhospitable to echinoids. However the Trouville samples, geographically a similar distance from the main English outcrop of carbonates as the Upware group, plot as intermediate between the Bran Point, Cothill and Wootton Bassett groups. The distinction of the Upware group may also reflect its slightly younger age.

The most obvious distinction (e.g. figs. 5, 5; 5, 7 and 5, 8) between samples corresponds with differences in the enclosing sediment and presumably original substrate. The general good state of preservation of this small thin-shelled echinoid seems to indicate little post-mortem transportation. The Cothill sample (from a sediment with siliceous grains) is clearly different from the other samples (from sediments with calcareous grains). Moreover, the four calcareous samples form a linear series: Bran Point, Trouville, Wootton Bassett to Upware. This corresponds with an increase in grain size of the sediment from a fine micrite, medium grained oomicrite, oosparite to coarse oncolitic intramicrite. Apart from the unusual algal oncolite facies of Upware this progression also represents an increase in the energy of the original depositional environment (Folk, 1962). Even the Cothill sample, from a fine-grained calcareous quartz sandstone, plots most closely with the samples from the finer grained carbonates.

Fig. 5, 11 plots the average length of the periproct, \( L \), and the maximum grain size against locality. It is seen that in all cases the periproct is larger than the largest ooliths or other large grains within the sediment. Furthermore, the average periproct length increases as the sediment becomes coarser. This is borne out in fig. 5, 12, a plot of the average periproct area \( \bar{I} \times \bar{L} \) against the size of the largest oolith within the sediment at each locality.
Figure 5,11. Plot of mean periproct length (P), largest grain size (X) and largest oolith (O) against locality. Bran Point (D), Cothill (H), Trouville shore (Ts), Trouville cliff (Tc), Wootton Bassett (W), Upware (U).

Figure 5,12. Plot of largest oolith grain size against mean periproct area (T x L) of samples in fig. 5,11. Within the nonoolitic sediments of Bran Point and Cothill the largest grain size has been plotted.
The correlation coefficient is 0.92 and differs significantly from zero at the 1% level.

It is therefore concluded that the differences in the size and position of the periproct between samples are primarily a function of the grain size and energy index of the sediment (Scurry, 1978).

5K) The selection of neotypes for *N. SCUTATUS*.

It is proposed to establish the author's collection from the shore at Trouville, Calvados, France, specimens X462 - X481, to be neotypes for *N. scutatus*. The reasons for the choice of these specimens are both historical and statistical.

Wright (1852, 1859) states that Trouville is the type area of Lamarck's *N. scutatus*. He was indeed sent specimens by M. Deslongchamps of Caen from the area on that understanding. This locality also contains the most prolific number of specimens of this species so far discovered by the author, therefore allowing a wide variety of individuals to be collected from this single locality.

From the multivariate analyses made of the various samples of *N. scutatus* it was found that the Trouville specimens occupy a central position amongst the groups so far studied. The Trouville specimens used by the author are also the only group to exhibit morphological overlap with samples from all other localities studied.

For these reasons it appears reasonable to propose that the author's Trouville specimens be accepted as typical representatives of the diverse species *N. scutatus* if any one sample need be selected for taxonomic purposes.
CHAPTER 6 - BIOMETRICS OF NUCLEOLITES LATIPORUS

6A) Introduction

Only three samples of this species are studied biometrically here. Specimens were found at a great number of localities in the middle Jurassic and it appears to be a widespread and common species, especially in the Cornbrash. However it is not so abundant in any one locality as "scutatus", many of the localities yielding fewer than 10 specimens, and the specimens were generally broken and abraded and therefore not suitable for a full biometrical analysis. Although Douglas & Arkell (1928, 1932) list many localities in the Cornbrash of England where "latiporus" (syn. "clunicularis") occurs many are now overgrown, disused or destroyed. Few samples can still be collected which contain abundant individuals. Fig. 6, 1, is a summary of analyses carried out in this Chapter.

6B) Stratigraphy

Three samples are analysed below:-

a) Collection from Stratton Audley, Oxfordshire (G.R. SP602253).

From the Cornbrash at the top of a large quarry working the underlying Bathonian White Limestone. The horizon yielding the specimens is typically Lower Cornbrash, a coarse bioclastic limestone, very fossiliferous, but with only moderately preserved echinoids. A total of 21 nucleolitid echinoids was collected. All 15 measurements as defined above (p. 99) could be made on 11 specimens whilst one variable was missing from a further 3. However 3 other large specimens all had the same 5 characters missing (i.e. variables C, D, M, N1, N3) as the dorsal surfaces were not preserved.

b) A sample from the large quarry at Talant, Dijon, Cote d'Or, France (see figure 2, 3b). The specimens were found in rubble which
<table>
<thead>
<tr>
<th>Sample</th>
<th>Comparison sample</th>
<th>Page</th>
<th>Var.</th>
<th>Spec.</th>
<th>Technique</th>
<th>Sig. of difference</th>
<th>Imp. variables</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Stratton Audley</td>
<td></td>
<td>163</td>
<td>9.</td>
<td>17</td>
<td>P.C.A.</td>
<td>Separation along 1st. (size) vector</td>
<td></td>
</tr>
<tr>
<td>2. Stratton Audley (N.latiporus)</td>
<td>Hydrequent (N.latiporus)</td>
<td>166</td>
<td>15</td>
<td>16</td>
<td>S.D.F.</td>
<td>P&gt;5%</td>
<td></td>
</tr>
<tr>
<td>3. Stratton Audley (N.latiporus)</td>
<td>Hydrequent, Talant (N.latiporus)</td>
<td>168</td>
<td>15</td>
<td>21</td>
<td>S.D.F.</td>
<td>P&gt;5%</td>
<td></td>
</tr>
<tr>
<td>4. Stratton Audley, Hydrequent (N.latiporus)</td>
<td>Trouville (N.scutatus)</td>
<td>172</td>
<td>15</td>
<td>35</td>
<td>S.D.F.</td>
<td>P&lt;1%</td>
<td>N4, J, L, M, C</td>
</tr>
<tr>
<td>7. S. Audley, Talant, Hydherent</td>
<td>Cothill, Dorset, W.B.</td>
<td>176</td>
<td>15</td>
<td>495</td>
<td>R.M.A.</td>
<td>P&lt;1% between 2-11 pairs of slopes</td>
<td>L</td>
</tr>
<tr>
<td>8. S. Audley, Talant, Hydherent</td>
<td>Trouville</td>
<td>176</td>
<td>15</td>
<td>123</td>
<td>H.C.</td>
<td>Clustering not into original groups</td>
<td></td>
</tr>
<tr>
<td>9. All N.latiporus samples</td>
<td>All N.scutatus samples</td>
<td>178</td>
<td>15</td>
<td>166</td>
<td>S.D.F.</td>
<td>P&lt;1%</td>
<td>B, N, C, J</td>
</tr>
</tbody>
</table>

Figure 6.1 Summary of important analyses run in Chapter 6 for *N. latiporus* and *N. scutatus* samples. See fig. 5.1. for key.
<table>
<thead>
<tr>
<th>Sample</th>
<th>Comparison sample</th>
<th>Page</th>
<th>Var.</th>
<th>Spec.</th>
<th>Technique</th>
<th>Sig. of difference</th>
<th>Imp. variables</th>
</tr>
</thead>
<tbody>
<tr>
<td>10. Smith's holotype (Coleshill)</td>
<td>Trouville (N. scutatus) S. Audley, Hydrequent, Talant (N. latiporus)</td>
<td>181</td>
<td>12</td>
<td>129</td>
<td>Class</td>
<td>Trouville 91% Hydrequent 5% S. Audley 4%</td>
<td></td>
</tr>
<tr>
<td>11. Smith's paratype (Trowle)</td>
<td>as above</td>
<td>182</td>
<td>15</td>
<td>129</td>
<td>Class</td>
<td>St. Audley 99% Hydrequent 1%</td>
<td></td>
</tr>
<tr>
<td>12. Smith's paratype (Wroxhall)</td>
<td>as above</td>
<td>184</td>
<td>14</td>
<td>129</td>
<td>Class</td>
<td>St. Audley 100%</td>
<td></td>
</tr>
<tr>
<td>13. Smith's paratype (Churchill)</td>
<td>as above</td>
<td>184</td>
<td>11</td>
<td>129</td>
<td>Class</td>
<td>Hydrequent 39% Trouville 38% St. Audley 23%</td>
<td></td>
</tr>
<tr>
<td>14. Agassiz type</td>
<td>as above</td>
<td>184</td>
<td>10</td>
<td>129</td>
<td>Class</td>
<td>St. Audley 87% Trouville 11% Hydrequent 2%</td>
<td></td>
</tr>
<tr>
<td>15. d'Orbigny's types</td>
<td>As above + N. elongatus group</td>
<td>185</td>
<td>15</td>
<td>129</td>
<td>Class</td>
<td>Always classified with a sample of N. latiporus</td>
<td></td>
</tr>
</tbody>
</table>

Figure 6.1 continued
appeared to originate from hard brown, gritty oolitic beds (Fig. 2, 4). The beds are above the base of the zone of M. macrocephalus (personal communication, Prof. Tintant, Université de Dijon), and are therefore Callovian in age, equivalent to the Upper Cornbrash of England, also known to contain N. latiporus (Douglas & Arkell, 1928, 1932). The specimens are poorly preserved, all fifteen measurements being possible on only 5 of the original 10 specimens found.

c) Sample from the Lambert Collection housed at the Université de Paris - 6. It contains 8 well preserved specimens of varying sizes, only 1 specimen being imperfect with variable E missing. The specimens have anoolitic limestone matrix. Locality data for the sample is the 'Vesuvian of Hydrequent'. Hydrequent is a small town in the Boulonnais, France, an area with many large quarries originally working the Upper Palaeozoic rocks and exposing the overlying middle and upper Jurassic strata as overburden. The author has collected some nucleolitid specimens from a similar nearby quarry at Ferques, Pas de Calais.

The Vesuvian of the Boulonnais has been correlated with the Upper Inferior Oolite of Great Britain particularly the parkinsoni zone of the Cotswolds (Gignoux, 1950). However Lambert's stratigraphy was probably based on the earlier interpretation of the Vesuvian stage which equated it with the lower and middle Bathonian (Arkell, 1933). Bigot (1930) also correlated the Vesuvian with the Lower Bathonian Caen Limestone which is of zigzag and progracilis zone age. Ager & Wallace (1966) support these early views by stating that there are no Bajocian strata exposed in the Boulonnais. The sample thus probably originates from middle Bathonian oolites.
6C) Type material

Two 'type' collections from the British Museum (Natural History) London and the Cotteau Collection, Université de Paris-sud, Orsay, were also analysed.

a) The British Museum specimens are William Smith's holotype and paratypes of *N. clunicularis* (Smith). Four specimens were measured from the collection:-

i) Holotype, E495, from the Coral Rag of Coleshill, (Wiltshire?) (Smith 1817 b, figure 6).

ii) Paratype, E572, from the Cornbrash of Trowle.

iii) Paratype, E511, from the Cornbrash of Wraxhall.

iv) Paratype, E564a, from the Inferior Oolite of Churchill; the more conical specimen of the two being measured.

b) The specimens from the Cotteau Collection are d'Orbigny's five types, varieties and accompanying specimens of *Echinobrissus clunicularis* (Llwyd) d'Orbigny 1853. All of d'Orbigny's specimens have been termed varieties of *E. clunicularis* by Cotteau (1871).

i) 'Type', No. b 236, from the Bathonian of the area around Alençon, Orne.

ii) 'Accompanies type', No. b 894, from Davage, Saone et Loire.

iii) 'Variété déprimée (*E. edmundi*), No. b 238, from the Bathonian of Asnieres, Yonne.

iv) 'Accompanies *E. edmundi* from the same locality, No. b 895.

v) 'Variété élongée (*E. oblongus*) from the same locality.

Measurements were also taken on a cast of the Agassiz type specimen of *N. latiporus* at the British Museum (Natural History), London.
6d) Analysis of the Stratton Audley sample

This sample of 21 specimens from the same locality and horizon (Cornbrash) appeared from a preliminary evaluation to be inhomogeneous, composed of two species; a small round, rather conical type, and a large elongate form, with no intermediates between the two. The two forms were subjectively placed in *N. latiporus* Agassiz and *N. elongatus* Agassiz. When this morphological separation had been made on the basis of test size and shape the two species were examined in greater detail. It was observed that the peristome was reduced in size, the periproctal opening was not visible from the dorsal surface and that the apical disc occupied a more central position in the larger elongate *N. elongatus*. One of the smaller specimens (specimen 03) was additionally seen to be more elongate, have a more central disc and have a smaller peristome and periproct than the generalised *N. latiporus* form.

To test whether this subjective two-fold division of the sample was objectively verifiable a hierarchical clustering and a component analysis were run on the total Stratton Audley samples. Such tests are ideal for such a problem since no prior information on groupings is required.

The plot (fig. 6,2) of the first and second principal components, accounting for 88% of total variability of the nine characters common to most specimens, shows a division purely on size, component 1. The small elongate specimen therefore lies within the area of the group previously defined as *N. latiporus*. Figure 6,3 tabulates the eigenvalues and direction cosines for the first four eigenvectors.

The same sample can be run on the Hiegroup programme in order to compare results with the groupings produced by the
Figure 6.2. Distribution of Stratton Audley specimens along Principal Components 1 and 2 based on a 9 variable analysis. Components 1 and 2 account for 88% of total variation.
PRINCIPAL COMPONENT ANALYSIS

Stratton Audley sample.
9 variables, 17 cases.

Eigenvalues

<p>| | | | |</p>
<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>7.23</td>
<td>.73</td>
<td>.61</td>
<td>.26</td>
</tr>
</tbody>
</table>

Cumulative proportions of total variance

<p>| | | | |</p>
<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>80%</td>
<td>88%</td>
<td>95%</td>
<td>98%</td>
</tr>
</tbody>
</table>

Eigenvectors

<table>
<thead>
<tr>
<th></th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>.37</td>
<td>.04</td>
<td>.08</td>
<td>.00</td>
</tr>
<tr>
<td>E</td>
<td>.37</td>
<td>-.01</td>
<td>.12</td>
<td>.06</td>
</tr>
<tr>
<td>G</td>
<td>.37</td>
<td>.05</td>
<td>.06</td>
<td>.03</td>
</tr>
<tr>
<td>H</td>
<td>.37</td>
<td>.09</td>
<td>.00</td>
<td>.05</td>
</tr>
<tr>
<td>I</td>
<td>.25</td>
<td>.66</td>
<td>-.57</td>
<td>-.28</td>
</tr>
<tr>
<td>J</td>
<td>.33</td>
<td>.16</td>
<td>.21</td>
<td>.77</td>
</tr>
<tr>
<td>L</td>
<td>.33</td>
<td>.38</td>
<td>-.26</td>
<td>.47</td>
</tr>
<tr>
<td>N2</td>
<td>.36</td>
<td>-.03</td>
<td>.16</td>
<td>-.24</td>
</tr>
<tr>
<td>N4</td>
<td>.23</td>
<td>-.62</td>
<td>-.71</td>
<td>.21</td>
</tr>
</tbody>
</table>

Figure 6,3. Eigenvalues and direction cosines of the first four eigenvectors for the Stratton Audley sample. The first two eigenvectors are plotted in fig.6,2.
component analysis. As can be seen from the dendrogram (fig.6,4) of the results, the sample splits clearly into the two subjectively defined groups, the small specimen (03) being grouped with the larger specimens of N.elongatus.

The two tests thus both substantiate the subjective distinction into the same two morphological groups, but differ in their placement of the small specimen 03. The difference can be explained by the fact that in the hiergroup clustering procedure the raw data is standardised so that the value of every variable ranges between 0 and 1. This minimises the effect of size, by allowing variables with only small ranges of absolute measurements to vary as much as measurements of large magnitude. This is not always possible with component analysis as the first vector is generally governed by size. Taking this evidence, together with that produced by the principal component analysis, the small specimen is here regarded as N.elongatus and only the specimens numbered 02,04-14,021-22 are included in further analysis as N.latiporus.

6E) Comparison between the three N.LATIPORUS samples

Discriminant function analysis between the two geographically closest groups, of Stratton Audley and Hydrequent, showed no significant differences between the groups.

Step 16 (final)

Variable not included; A,D and G.

U-statistic = .27 (Significance of the inequality of group means; P > 5%)

Specimens classified wrongly by posterior probability; 6%

In a re-run of the analysis, variables B and E were ignored
Figure 6.4. Dendrogram of the clustering routine for the Stratton Audley sample.
in order to be able to include more less perfect specimens
(B and E had only been entered late at the 12th and 14th step respectively of the previous analysis). The same pattern was produced.

**Step 10 (final)**

Variable not included; C, G, M, N1 and N2.

U-statistic = .31 (Significance of the inequality of group means; P > 5%)

These results are influenced by the small size of the samples but are noteworthy considering the age difference between the two groups. One sample came from middle and the other from uppermost Bathonian. Although there is a difference in age there is no proved significant difference in morphology between the samples.

All three groups were tested by the inclusion of the Callovian Talant sample using discriminant function analysis. Again no significant differences were found between the group means but the Talant sample lay at a greater distance from the other samples and overlapped to a much lesser degree.

**Step 12 (final)**

Variables not included; A, C and G.

U-statistic = .065 (Significance of the inequality of group means; P > 5%)

Specimens classified wrongly by posterior probability;

Hydrequent 14%, Stratton Audley 11%, Talant 0%.

Figure 6, 5 tabulates \( \chi^2 \) tests of \( D^2 \) for each specimen.

It is apparent that the three groups can be ordered according to an increasing high percentage of specimens with a low probability (P < 1%) of belonging to particular groups. This order corresponds to age differences between the samples. Again it is seen that the
<table>
<thead>
<tr>
<th>Group</th>
<th>Hydrequent</th>
<th>Strat. Aud.</th>
<th>Talant</th>
</tr>
</thead>
<tbody>
<tr>
<td>Original Sample</td>
<td>0%</td>
<td>14.3%</td>
<td>100%</td>
</tr>
<tr>
<td>Hydrequent</td>
<td>11.1%</td>
<td>0%</td>
<td>77.8%</td>
</tr>
<tr>
<td>Strat. Aud.</td>
<td>80.0%</td>
<td>60.0%</td>
<td>0%</td>
</tr>
</tbody>
</table>

Figure 6.5. Percentage of specimens within each sample with a low probability ($P<1\%$) of belonging to each group, based on $\chi^2$ tests of $D^2$ for each case.
Talent sample is the most distinctive of the three groups.

The discriminant function analysis, therefore, showed little proved significant difference between the three samples of *N. latiporus* although the samples are from rocks of different age, facies and geographic location (Stratton Audley and Talent are about 720 kms apart). The degree of difference between the groups is less than that shown between the various *N. scutatus* samples which are all from two adjacent sub-zones and closer geographic proximity. However this may reflect sample size, and be accounted for by the smaller size of the *N. latiporus* samples.

To try to overcome the problem of small sample size by the utilization of more data, programmes RMA and TEST were run in order to test the significance of the differences between the reduced major axes of the samples. The results also reflect the age differences between the samples to a greater extent than the discriminant analysis.

When the group of intermediate age, the upper Bathonian Stratton Audley sample, was compared to both the other groups then only three slopes in each of the two comparisons were shown to be at least probably significantly different (*1% < P < 5%*). In the comparison with the lower Callovian Talent sample these slopes were variable A with L, B and G, whilst in comparison with the middle Bathonian Hydrequent sample the slopes were A with E, B, and N3. However, when the two samples showing the greatest age range were compared, i.e. Talent and Hydrequent, then three slopes were shown to be highly significantly different (*P < 1%*), A with B, C, and N3 and one slope, A with G was shown to be probably significantly different. Moreover, in this comparison, parallel slopes were all proved to be a significant distance apart. This pattern was repeated
A) Variable A with all other variables

<table>
<thead>
<tr>
<th>Talant</th>
<th>Strat. Aud.</th>
</tr>
</thead>
<tbody>
<tr>
<td>A. 1</td>
<td>2</td>
</tr>
<tr>
<td>B. 2</td>
<td>1</td>
</tr>
<tr>
<td>C. 11</td>
<td>1</td>
</tr>
<tr>
<td>D. 11</td>
<td></td>
</tr>
</tbody>
</table>

B) Variable L with all other variables

<table>
<thead>
<tr>
<th>Talant</th>
<th>Strat. Aud.</th>
</tr>
</thead>
<tbody>
<tr>
<td>A. 4</td>
<td>8</td>
</tr>
<tr>
<td>B. 0</td>
<td>0</td>
</tr>
<tr>
<td>C. 10</td>
<td>6</td>
</tr>
<tr>
<td>D. 3</td>
<td></td>
</tr>
</tbody>
</table>

Figure 6.6. Comparison of reduced major axes between each of three *N. latiporus* samples. Key as for fig. 5.10.
when L is used with all other variables (fig. 6,6).

There appeared to be slightly greater degrees of difference between the three *N. latiporus* samples than between the five major groups within the *N. scutatus* species range (compare figs 5,10 with fig 6,6).

**6f) Comparison between *N. SCUTATUS* and *N. LATIPORUS***,

The variation to be expected within a single, diverse species has been assessed above for both *N. scutatus* and *N. latiporus*. The variation between these two species is now assessed to indicate more precisely the taxonomic level at which the various morphotypes of *N. scutatus* can be placed; and to determine whether subjective differences between the species *N. scutatus* and *N. latiporus* are greater than differences detected between populations of *N. scutatus*

*N. scutatus* and *N. latiporus* are obviously closely related, few pre-nineteenth century authors being able to distinguish between the two species. However since Linnaeus most authors have stated that these are indeed good species (e.g. Wright, 1859; Mortensen, 1948; and Kier, 1962) but with some notable exceptions (e.g. Smith, 1817a & b, and Forbes, 1849). It thus appears that there are subjective differences between the two species but exactly what the true differences are has not been established. It is generally assumed that *N. latiporus* is solely middle Jurassic in age and that *N. scutatus* is restricted to the upper Oxfordian and lowest Kimmeridgian. (*vide* Lambert & Thiery, 1921). However, some specimens of either species could easily be placed in the other taxon on purely morphological grounds.

A discriminant analysis between the *N. scutatus* sample from Trouville and the *N. latiporus* samples from Stratton Audley and Hydrequent showed significant differences (P < 1%) between the
group means of the samples of the two species but not between the
*N. latiporus* samples themselves. This is to be expected as no proved
differences were found between the middle Jurassic samples when
taken in isolation.

**Step 5**
Variable N4, J, L, M and C entered.
F matrix indicated that the Trouville group mean became highly
significantly different (*P* < 1%) from Bathonian groups.

**Step 12 (final)**
Variables not included; C, G and Nl.

U-statistic = .30 (Significance of the inequality of group means;

\[ P < .1\% \].

Trouville specimens classified with the Stratton Audley group
by posterior probability; 2%.

However this distinction does not seem to be as complete
as would be expected from species separated by almost two stages
of the Jurassic homeomorphy obviously occurring between the samples.
The characters that were found to be most useful in distinguishing
between the two species were the same as those used to distinguish
between the various samples of *N. scutatus* itself, the degree of
separation and the significance of the difference between the group
means also being at about the same level.

However \( \chi^2 \) tests of \( D^2 \) for each specimen revealed that
between 66% and 88% of cases within each species had a low probability
(*P* < 5%) of belonging to the other species. The \( \chi^2 \) tests showed,
therefore, a higher degree of difference between these two species
than between the various groups of *N. scutatus* alone. This pattern
was repeated when the Talant sample was included in the analysis.

A discriminant function analysis was therefore carried
out between the Stratton Audley sample and the two *N. scutatus* samples previously shown to exhibit a good separation - the Cothill and Wootton Bassett samples.

**Step 5**
Variables *L, N2, B, A* and *I* were entered. F matrix indicated that the Wootton Bassett sample became highly significantly different (*P < 1%*) from the other groups.

**Step 13 (final)**
Variables not included; *C* and *G*.

U-statistic = .07 (Significance of the inequality of group means; *P < .1%*)

F matrix indicated that all group means were highly significantly different (*P < 1%*) from each other.

One specimen from each of the *N. scutatus* samples classified with the Stratton Audley group by posterior probability. All Stratton Audley specimens were classified correctly.

Both *N. scutatus* groups contain homeomorphs of the older *N. latiporus* sample, but each group was equally different from each other.

To test this further, the Stratton Audley sample was included in a discriminant function analysis of all the major *N. scutatus* groups. Figure 6,7 shows the canonical variate plot of 75% of the total dispersion; compare with fig.5,8. From this plot it is seen that the differences between the Stratton Audley and the various *N. scutatus* samples are of the same order of magnitude as differences between samples within the *N. scutatus* groupings. From the group posterior probability table it was seen that again Stratton Audley is a group into which specimens from most other groups were classified, indicating that many *N. scutatus* samples contain specimens which are homeomorphic of the stratigraphically older *N. latiporus*. 

174
Figure 6, 7. Distribution of Stratton Audley (6) (N. latiporus) and Bran Point (D), Cothill (H), Trouville (T), Wootton Bassett (W) and Upware (U) (N. scutatus) specimens on the first two canonical axes. Group centroids are indicated by large lettering. Mean coordinates:

Stratton Audley  -0.930 0.281
Bran Point     -2.014 1.392
Cothill        -2.193 -1.626
Trouville      -0.327 0.420
Wootton Bassett 0.562 0.469
Upware         2.485 0.268
Variable not included; C.

F matrix indicated that all group means were highly significantly different ($P < 1\%$) from all other group means.

U-statistic = .04 (Significance of the inequality of group means; $P < .1\%$)

This pattern of discrimination is the same as for earlier comparisons which included only five *N. scutatus* groups (see Ch.5, H).

It can therefore be concluded from the last two analyses that *N. latiporus* samples are only as different from *N. scutatus* as infraspecific samples of *N. scutatus* are from each other.

In bivariate analysis of differences between reduced major axes of the various *N. scutatus* and *N. latiporus* samples, it is difficult to distinguish patterns or trends as only pairs of samples can be analysed at any one time. Fig. 6, 8 tabulates comparisons of reduced major axes for A and the important discriminating variable L with all other variables between the three *N. latiporus* and five *N. scutatus* groups. In general terms there are about the same degrees of difference between the groups representing the two species as differences within the two species (compare with fig. 5, 10 and fig. 6, 6).

A hierarchical analysis of all *N. latiporus* and the Trouville sample of *N. scutatus* showed a pattern of grouping similar to that shown by the Trouville sample by itself (see p.134), in that a clustering into 'remote' and 'adjacent' groups was achieved. The penultimate clustering into 2 groups was the last to show no great increase in the 'error' value over the previous clustering and it would normally be supposed that 2 natural groupings were present. The pattern of clustering was, however, seen to be similar to that
A) Variable A with all other variables

<table>
<thead>
<tr>
<th>Hydrequent</th>
<th>Strat.Aud.</th>
<th>Talant</th>
</tr>
</thead>
<tbody>
<tr>
<td>A. 0</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>B. 3</td>
<td>12</td>
<td>11</td>
</tr>
<tr>
<td>C. 11</td>
<td>2</td>
<td>1</td>
</tr>
<tr>
<td>D. 1</td>
<td>2</td>
<td>1</td>
</tr>
</tbody>
</table>

Bran Point

<table>
<thead>
<tr>
<th>Hydrequent</th>
<th>Strat.Aud.</th>
<th>Talant</th>
</tr>
</thead>
<tbody>
<tr>
<td>A. 1</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>B. 0</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>C. 12</td>
<td>12</td>
<td>11</td>
</tr>
<tr>
<td>D. 0</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>

Cothill

<table>
<thead>
<tr>
<th>Hydrequent</th>
<th>Strat.Aud.</th>
<th>Talant</th>
</tr>
</thead>
<tbody>
<tr>
<td>A. 1</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>B. 0</td>
<td>0</td>
<td>3</td>
</tr>
<tr>
<td>C. 13</td>
<td>12</td>
<td>9</td>
</tr>
<tr>
<td>D. 1</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>

Trouville

<table>
<thead>
<tr>
<th>Hydrequent</th>
<th>Strat.Aud.</th>
<th>Talant</th>
</tr>
</thead>
<tbody>
<tr>
<td>A. 1</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>B. 12</td>
<td>13</td>
<td>11</td>
</tr>
<tr>
<td>C. 11</td>
<td>13</td>
<td>11</td>
</tr>
<tr>
<td>D. 0</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>

W. Bassett

<table>
<thead>
<tr>
<th>Hydquent</th>
<th>Strat.Aud.</th>
<th>Talant</th>
</tr>
</thead>
<tbody>
<tr>
<td>A. 1</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>B. 3</td>
<td>0</td>
<td>3</td>
</tr>
<tr>
<td>C. 10</td>
<td>12</td>
<td>9</td>
</tr>
<tr>
<td>D. 0</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>

Upware

B) Variable L with all other variables

<table>
<thead>
<tr>
<th>Hydrequent</th>
<th>Strat.Aud.</th>
<th>Talant</th>
</tr>
</thead>
<tbody>
<tr>
<td>A. 3</td>
<td>7</td>
<td>11</td>
</tr>
<tr>
<td>B. 0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>C. 11</td>
<td>7</td>
<td>3</td>
</tr>
<tr>
<td>D. 1</td>
<td>2</td>
<td>0</td>
</tr>
</tbody>
</table>

Bran Point

<table>
<thead>
<tr>
<th>Hydquent</th>
<th>Strat.Aud.</th>
<th>Talant</th>
</tr>
</thead>
<tbody>
<tr>
<td>A. 5</td>
<td>5</td>
<td>7</td>
</tr>
<tr>
<td>B. 0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>C. 9</td>
<td>9</td>
<td>7</td>
</tr>
<tr>
<td>D. 0</td>
<td>0</td>
<td>1</td>
</tr>
</tbody>
</table>

Cothill

<table>
<thead>
<tr>
<th>Hydquent</th>
<th>Strat.Aud.</th>
<th>Talant</th>
</tr>
</thead>
<tbody>
<tr>
<td>A. 2</td>
<td>8</td>
<td>12</td>
</tr>
<tr>
<td>B. 0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>C. 12</td>
<td>6</td>
<td>2</td>
</tr>
<tr>
<td>D. 1</td>
<td>0</td>
<td>1</td>
</tr>
</tbody>
</table>

Trouville

<table>
<thead>
<tr>
<th>Hydquent</th>
<th>Strat.Aud.</th>
<th>Talant</th>
</tr>
</thead>
<tbody>
<tr>
<td>A. 4</td>
<td>8</td>
<td>8</td>
</tr>
<tr>
<td>B. 1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>C. 9</td>
<td>6</td>
<td>6</td>
</tr>
<tr>
<td>D. 0</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>

W. Bassett

<table>
<thead>
<tr>
<th>Hydquent</th>
<th>Strat.Aud.</th>
<th>Talant</th>
</tr>
</thead>
<tbody>
<tr>
<td>A. 3</td>
<td>7</td>
<td>11</td>
</tr>
<tr>
<td>B. 2</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>C. 9</td>
<td>7</td>
<td>3</td>
</tr>
<tr>
<td>D. 0</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>

Upware

Figure 6,8. Comparison of reduced major axes between five N. scutatus samples and three N. latiporus samples. Key as for fig. 5,10.
of the previous Trouville analysis, the Trouville specimens generally falling into the same groups. In this analysis it was seen that the *N. latiporus* specimens likewise fell into one of these two groups rather than into a separate group, and the majority fell into the 'adjacent' group as previously defined (p. 136). Only specimen 164 from Hydrequent, 014 from Stratton Audley and specimens P1 and P2 from Talent were grouped with the 'remote' forms.

It appears that groups are not established by associating specimens of similar geographic, stratigraphic or sedimentary origin.

In a final discriminant analysis two groups were formed of all specimens from within the two species. That is, all specimens from the five *N. scutatus* samples were characterised as 'scutatus' cases and the *N. latiporus* samples were similarly distinguished. In this analysis the pattern of discrimination was completely different from earlier runs as now generalised differences between the species were sought rather than specific differences between samples.

**Step 4**
Variables B, N4, C and I entered.

F matrix indicated a highly significant difference (P < 1%) between both group means.

**Step 16 (final)**
Variable not entered; C (removed at step 16)

U-statistic = .61 (Significance of inequality of group means; 

\[ P < .1\% \])

Specimens classified wrongly by posterior probability; 10%

For the first time measurements of the gross morphology of the test were used as important discriminating variables. *N. latiporus* tends to be more streamlined but more domed than typical...
tests of Mahalanobis distances between each specimen and the two group means revealed that few specimens had a low probability (P < 1%) of belonging to the wrong species whilst not being a significant distance (P > 5%) from the correct group mean. For example, within the N. scutatus group, from a total of 145 specimens analysed, only four specimens fulfilled the above criteria whilst a further two specimens had a low probability (P < 1%) of belonging to the N. scutatus group but were not being a significant distance (P > 1%) from the N. latiporus group mean.

Figure 6.9 is a plot of the first two canonical variates representing 100% of the total dispersion. No significant separation is achieved between the groups and overlap is at a similar scale to that shown to exist between samples from within the N. scutatus plexus.

Classification of N. LATIPORUS according to types.

Stepwise Discriminant Analysis is only able to discriminate between samples comprising two or more specimens. Single holotypes cannot therefore be treated as samples in the analysis unless the 'classification' procedure is adopted. By this method the holotypes, or any other group designated in the program, are omitted from the stepwise discriminating procedures so that groups are formed in the usual manner. During the final step, when the group probabilities are calculated, the holotypes are then placed by the program within the existing group to which they are most likely to be members. In this way the specimen is classified by reference to the mean of a group of specimens. In contrast, normal typological procedure compares all specimens individually to the holotype. Although the
Figure 6.9. Distribution of all *N. scutatus* (S) and *N. latiporus* (L) specimens on the first two canonical axes. Group centroids indicated by large lettering. Mean coordinates:

* N. scutatus  \(-0.301, 0.000\),
  N. latiporus  \(2.079, 0.000\).
computer comparison is not carried out in the normal typological manner, this method does allow a sample as a whole to be compared to a single type specimen.

To be reasonably sure that a holotype is more characteristic of one group than any other, it is necessary that the groups be originally distinctive, and this is not strictly the case between _N. scutatus_ and _N. latiporus_ (see previous analysis). Homeomorphy does occur in some specimens, but this is usually only about 10% of the samples and there is usually a highly significant difference ($P < 1\%$) between group means.

Bearing these limitations in mind, the type specimens of Smith, d'Orbigny and Agassiz were classified with reference to the collected samples of _N. scutatus_ and _N. latiporus_. In some cases specimens were classified individually in separate analyses so that all variables measured on each specimen could be fully utilized every time.

Smith must be considered to be the author of the name _N. clunicularis_ (see p. 62 Systematic Palaeontology). His holotype (BM, No. E 495) is from the Corallian of Coleshill on the Wiltshire-Oxfordshire border, which is possibly the locality of Coltswell mentioned by Llwyd (Llwyd 1698, No. 989) in his original description of _Echinites clunicularis_. However, the specimen has all the characters of _N. scutatus_ being flattened aborally, having a deep posterior groove, and periproct well removed from the apical disc. Smith's Cornbrash and Inferior Oolite paratypes appear to be good specimens of ' _N. clunicularis_ ' auctorum.

It is possible to measure only 12 variables on Smith's holotype, the periproct being infilled with matrix. Variables I, L and N4 are therefore omitted. These variables are important in distinguishing
between *N. scutatus* and *N. latiporus* and because these variables are omitted the Trouville sample was found to be only probably significantly different (1% < P < 5%) from the other 3 samples in the discriminant analysis. However, the U-statistic, at .43, indicates that the groups as a whole were significantly different at the .1% level. The holotype is shown to lie very closely to the group mean of the Trouville sample (Fig.6,10) and was classified into this group in the posterior probability table. Data for the likelihood of belonging to a particular group are Trouville 91%, Hydrequent 5% and Stratton Audley 4%. A $X^2$ test of the Mahalanobis distance of the specimen from each group mean showed a low probability (P < 5%) of Smith's holotype belonging to either the Stratton Audley or Hydrequent samples and a very low probability (P = .2%) of belonging to the Talant sample. No significance (P > 10%) can be attached to its distance from the Trouville sample. This therefore confirms the subjective, typological and stratigraphic evidence that Smith's holotype of *N. clunicularis* is a true *N. scutatus* Lamark.

The 'classification' procedure was continued with three paratypes from Smith's collection. The paratype from the Cornbrash of Trowle (B.M. No,E572) was classified using all 15 variables. This resulted in a highly significant difference (P < 1%) between the *N. scutatus* and *N. latiporus* groups as well as between the Talant and Hydrequent samples and a probable significant difference (1% < P < 5%) between the Stratton Audley and Talant samples. The Trowle specimen was classified with the Cornbrash Stratton Audley sample, the results being Stratton Audley 99%, Hydrequent 1%. A $X^2$ test of the Mahalanobis distance of the specimen from each group mean showed a very low probability (P < .1%) of the specimen belonging to either the Trouville or Talant samples, and a low
Figure 6.10. Distribution of Trouville (*N. scutatus*) and Hydrequent, Stratton Audley and Talant (*N. latiporus*) specimens on the first two canonical axes. Smith's holotype of *N. clunicularis* (S) is plotted according to its discriminant score along these two axes. Group centroids indicated by large lettering. Mean coordinates:

- Smith's holotype (S) 1.377 - .394
- Trouville (T) .844 -.767
- Hydrequent (H) .603 1.230
- Stratton Audley (6) -.375 1.007
- Talant (1) -3.377 -.621
probability \( (1% < P < 5\%) \) of belonging to the Hydrequent sample. No significance \( (P > 20\%) \) can be attached to its distance from the Stratton Audley sample.

The paratype from the Cornbrash of Wraxhall \( (B.M. \text{ No. E511}) \), using 14 variables as \( E \) is missing, was also classified with Stratton Audley sample, the results being Stratton Audley 100%. However the probability of this specimen belonging to any of the groups present was very low, being at the .1% level for Stratton Audley and lower than .1% for the remaining three groups.

Finally the Bajocian paratype from Churchill \( (B.M. \text{ No. E564}) \), using only 11 variables with \( E, I, L \) and \( N4 \) missing, was classified with the middle Bathonian Hydrequent sample, the figures being Hydrequent 39\%, Trouville 38\%, Stratton Audley 23\%. Similarly the probability of the specimen belonging to any of the groups present is high \( (P > 20\%) \), except for the Talant sample \( (P < .5\%) \). The latter figures of the group probability for the Churchill specimens are very closely balanced, as with only 11 variables no significant separation is achieved between the various groups.

From this method it is seen that each of Smith's specimens can be classified by posterior probability with a sample from a stratigraphic horizon of a similar age. Each specimen was assigned to its age group within the first two steps of the procedure. All of Smith's specimens used in the analysis except the holotype, were also shown to be specimens of \( N. \text{latiporus} \) as defined herein.

An Agassiz cast of the type specimen of \( N. \text{latiporus} \) Agassiz was measured in order to ascertain its similarity to the three collected samples of \( N. \text{latiporus} \), although all specimens appear to be conspecific with Agassiz' original description and figures \( (\text{Agassiz}, 1839) \). No detailed measurements of the periproct or apical
disc are possible from the cast and therefore variables D, I, L, N3 and N4 were omitted. The same groups as those employed with Smith's holotypes are used in this analysis, but as only 10 variables were used the groups were, at the most, only probably significantly different (1% < P < 5%). The type specimen was classified as Stratton Audley 87%, Trouville 11% and Hydrequent 2%.

In the classification of d'Orbigny's types all 15 variables were utilized, the _N. elongatus_ specimens (see later analysis) also being included as d'Orbigny's _N. oblongus_ specimen bears a superficial resemblance to this species.

All the pairs of group means are at least probably significantly (P < 5%) different at the end of the analysis with the exception of the Stratton Audley and Hydrequent samples (P > 5%). Figure 6.11 tabulates firstly, the degree of probability of each specimen belonging to a particular group by posterior probability and secondly, a $\chi^2$ test of the specimens' distance to each group mean.

Most of d'Orbigny's type collection, therefore falls within the bounds of _N. latiporus_ as defined herein, rather than with the closely related _N. scutatus_ or _N. elongatus_. However specimens of _N. oblongus_ and the "accompanying specimen" of _N. clunicularis_ from Saône et Loire appear to be very unlike any of the groups sampled in the present work.

It has been shown that Smith's holotype of _N. clunicularis_ is stratigraphically, morphologically and statistically a specimen of _N. scutatus_ Lamarck, and therefore the name _N. clunicularis_ is a junior subjective synonym of _N. scutatus_ (see p. 63). Smith's paratypes, Agassiz's _N. latiporus_ and d'Orbigny's type specimens are all shown to be statistically similar to samples collected from middle Jurassic strata and that they are probably all conspecific.
<table>
<thead>
<tr>
<th>Species</th>
<th>Post.Prob</th>
<th>Hydrequent</th>
<th>Strat. Aud.</th>
<th>Talant</th>
<th>Trouville</th>
<th>N. elongatus group</th>
</tr>
</thead>
<tbody>
<tr>
<td>E. clunicularis Sp. b236</td>
<td>X²</td>
<td>&gt;20%</td>
<td>&gt;20%</td>
<td>&lt;.1%</td>
<td>1%</td>
<td>&lt;.1%</td>
</tr>
<tr>
<td>E. clunicularis Sp. b894</td>
<td>X²</td>
<td>74%</td>
<td>26%</td>
<td>&lt;.1%</td>
<td>&lt;.1%</td>
<td>&lt;.1%</td>
</tr>
<tr>
<td>E. edmundi Sp. b238</td>
<td>X²</td>
<td>&lt;.1%</td>
<td>95%</td>
<td>1.5%</td>
<td>&lt;.1%</td>
<td>5%</td>
</tr>
<tr>
<td>E. edmundi Sp. b895</td>
<td>X²</td>
<td>&lt;.1%</td>
<td>58%</td>
<td>41%</td>
<td>1%</td>
<td>1%</td>
</tr>
</tbody>
</table>

Figure 6.11 Probability values (P) of group assignment for D'Orbigny specimens based on DFA classification procedures.
N. latiporus Agassiz is the first valid name under the rules of the I.C.Z.N., 15th Session, for the species (see p. 64).

6.4) Conclusions

Multivariate comparisons between the three samples of N. latiporus show no significant differences between the samples despite large separation in stratigraphic age and geographic position. The apparent similarity between the groups may, however, be a function of small sample size. Indeed, a bivariate comparison of reduced major axes showed that differences between samples are at least as great as the differences proved between the five N. scutatus samples. These differences may be correlated with the stratigraphic age of the sample. The reduced major axis length with breadth varies consistently between all three samples, indicating differences in streamlining of the test with time.

Although significant differences exist between N. scutatus and N. latiporus samples these differences are of the same type and order as those shown to occur within N. scutatus itself. There is overlap within and between species whilst the size and position of the periproct are again the main discriminating characters. Differences between species are of the same order and magnitude as differences between samples within species. Samples of N. latiporus are, accordingly, placed in a correct position relative to grain size within the framework previously constructed for N. scutatus (periproct and grain size dimensions are very similar between Trouville and Stratton Audley samples).

Direct comparison between the two species reveals no significant separation, with homeomorphy being evident even in 15 dimensions. There is no single character or group of variables
that can be used to distinguish *N. scutatus* from *N. latiporus* although the average specimens from each species are clearly distinct. Again variable B, breadth, is the most important discriminating variable indicating that *N. latiporus* is generally characterised by a more streamlined test than the ovate *N. scutatus*.

In general terms, there is conflicting evidence concerning the scale of difference between samples from within the two species. Discriminant function analysis indicates that no significant difference exists between samples of *N. latiporus* but that samples of *N. scutatus* are highly significantly different (i.e. *N. scutatus* has higher infraspecific variability). Comparisons of reduced major axes, however, show higher degrees of difference between samples of *N. latiporus* than between samples of *N. scutatus* (i.e. the converse, that *N. latiporus* has higher infraspecific variability). A greater equality in numbers of specimens is, however, needed to determine whether this apparent discrepancy is the result of different statistical methodology or differences in sample size.

Overall differences between the two species do not seem to be great. See Chapter 10 for a discussion of these differences in comparison with other species.

From comparison of various type material with samples collected by the author, *N. latiporus* Agassiz, 1839, appears to be the correct name for this group of nucleolitid echinoids.
CHAPTER 7 - BIOMETRICS OF SOME OTHER JURASSIC NUCLEOLITIDS

7 A) Introduction

*N. scutatus* is the genotype and most common upper Jurassic species of *Nucleolites*. *N.latiporus* is the most common and widespread middle Jurassic *Nucleolites*. Lambert & Thiery (1921) list in addition 67 other species which would be ascribed to *Nucleolites* (sensu Kier, 1962). Most of these are rare; were obtained from rocks no longer exposed; were obtained from localities too vaguely defined to be located and visited for further collection; or do not occur in N.W. Europe.

Samples of Jurassic species in addition to *N. scutatus* and *N. latiporus* were, however, collected by the author and these are analysed below. They include the endocyclic (and therefore primitive) *N. elongatus*, the orbicular (clypeiform) *N. amplus*, *N. woodwardii* and *N. burgundiae*, together with *N. micraulus* which has the periproct well separated from the apical disc (possibly an advanced evolutionary character). A range of potentially significant morphologies is therefore included.

Four of the species (*N. elongatus*, *N. amplus*, *N. woodwardii*, *N. burgundiae*) are of middle Jurassic age, one (*N. micraulus*) of upper Jurassic age. *N. elongatus* is considered first since it is both a primitive form and found in association with *N. latiporus*, just described. A sample of *N. amplus* is then analysed since this is the largest sample representative of a similarly middle Jurassic, but orbicular species, *N. woodwardii* and *N. burgundiae* are analysed subsequently in decreasing order of sample size. Finally, analysis is made of the upper Jurassic *N. micraulus* sample.

Fig. 7.1 is a summary of analyses carried out in this chapter.
<table>
<thead>
<tr>
<th>Sample</th>
<th>Comparison sample</th>
<th>Page</th>
<th>Var.</th>
<th>Spec.</th>
<th>Technique</th>
<th>Sig. of difference</th>
<th>Imp variables</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. S.Audley (N. elongatus)</td>
<td>S.Audley (N.latiporus)</td>
<td>194</td>
<td>15</td>
<td>21</td>
<td>R.M.A.</td>
<td>$p&lt;1%$ between all 14 pairs of slopes</td>
<td>L</td>
</tr>
<tr>
<td>2. S.Audley (N. elongatus)</td>
<td>Trouville (N.scutatus)</td>
<td>195</td>
<td>10</td>
<td>33</td>
<td>S.D.F.</td>
<td>$p&lt;1%$</td>
<td>L,N4,C</td>
</tr>
<tr>
<td></td>
<td></td>
<td>196</td>
<td>15</td>
<td>223</td>
<td>R.M.A.</td>
<td>$p&lt;1%$ between all 14 pairs of slopes</td>
<td>L</td>
</tr>
<tr>
<td></td>
<td></td>
<td>199</td>
<td>15</td>
<td>32</td>
<td>S.D.F.</td>
<td>$p&lt;1%$</td>
<td>L,N4,M</td>
</tr>
<tr>
<td>3. Signy (N.amplus)</td>
<td></td>
<td>202</td>
<td>14</td>
<td>30</td>
<td>P.C.A.</td>
<td>0.67 separated along 2nd vector</td>
<td>N4,N2</td>
</tr>
<tr>
<td>4. Signy (N.amplus)</td>
<td>Trouville (N.scutatus)</td>
<td>203</td>
<td>14</td>
<td>47</td>
<td>S.D.F.</td>
<td>$p&lt;1%$</td>
<td>M,N1</td>
</tr>
<tr>
<td></td>
<td></td>
<td>206</td>
<td>14</td>
<td>47</td>
<td>H.C.</td>
<td>Final 2 groups = original groups</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>206</td>
<td>15</td>
<td>241</td>
<td>R.M.A.</td>
<td>$p&lt;1%$ between all 14 pairs of slopes</td>
<td>L</td>
</tr>
<tr>
<td></td>
<td></td>
<td>206</td>
<td>13</td>
<td>47</td>
<td>P.C.A.</td>
<td>Separation on plot of 1,2 vectors</td>
<td>1st - size</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>2nd - N1,N2</td>
</tr>
<tr>
<td>5. Signy (N.amplus)</td>
<td>S. Audley (N.latiporus)</td>
<td>207</td>
<td>14</td>
<td>55</td>
<td>S.D.F.</td>
<td>$p&lt;1%$</td>
<td>M,N1,B</td>
</tr>
<tr>
<td></td>
<td>Trouville (N.scutatus)</td>
<td>207</td>
<td>14</td>
<td>56</td>
<td>P.C.A.</td>
<td>Separation on plot of 1,2 vectors</td>
<td>1st - size</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>2nd - N1</td>
</tr>
<tr>
<td>6. Signy (N.amplus)</td>
<td>S.Audley (N.latiporus)</td>
<td>210</td>
<td>10</td>
<td>43</td>
<td>S.D.F.</td>
<td>$p&lt;1%$</td>
<td>L,N2,B,A,N4</td>
</tr>
</tbody>
</table>

Figure 7.1 Summary of important analyses run in Chapter 7. See fig. 5.1 for key.
<table>
<thead>
<tr>
<th>Sample</th>
<th>Page</th>
<th>Var.</th>
<th>Spec. Technique</th>
<th>Sign of difference</th>
<th>Imp. variables</th>
<th>L, X, NI</th>
<th>L, X, Y, NI</th>
</tr>
</thead>
<tbody>
<tr>
<td>7. Sigry (N. amplus)</td>
<td>210</td>
<td>210</td>
<td>S. audley (N. latipes)</td>
<td>211</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>8. Sigry (N. amplus)</td>
<td></td>
<td>213</td>
<td>S. audley (N. elongatus)</td>
<td>215</td>
<td>R.M.A.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>9. Marquise (N. woodwardii)</td>
<td>214</td>
<td>214</td>
<td>Sigry (N. amplus)</td>
<td>215</td>
<td>S.D.F.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>10. Marquise (N. woodwardii)</td>
<td></td>
<td>217</td>
<td>Trouville (N. scutatus)</td>
<td>217</td>
<td>R.M.A.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>11. Marquise (N. woodwardii)</td>
<td></td>
<td>217</td>
<td>S. audley (N. latipes); S. elongatus</td>
<td>217</td>
<td>S.D.F.</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Figure 7.1 continued
<table>
<thead>
<tr>
<th>Sample</th>
<th>Comparison sample</th>
<th>Page</th>
<th>Var.</th>
<th>Spec.</th>
<th>Technique</th>
<th>Sig. of difference</th>
<th>Imp. variables</th>
</tr>
</thead>
<tbody>
<tr>
<td>12. Marquise(N.woodwardii)</td>
<td>As above + Trouville</td>
<td>221</td>
<td>14</td>
<td>80</td>
<td>S.D.F.</td>
<td>P&lt;1%</td>
<td>M,Ni,B,N2</td>
</tr>
<tr>
<td>13. Marquise(N.woodwardii)</td>
<td>S.Audley (N.latiporus)</td>
<td>223</td>
<td>15</td>
<td>21</td>
<td>R.M.A.</td>
<td>P&lt;1% between 6 pairs of slopes</td>
<td>L</td>
</tr>
<tr>
<td>14. Marquise(N.woodwardii)</td>
<td>S.Audley (N.elongatus)</td>
<td>223</td>
<td>15</td>
<td>14</td>
<td>R.M.A.</td>
<td>P&lt;1% between 8 pairs of slopes</td>
<td>L</td>
</tr>
<tr>
<td>15. Selongey(N.burgundiae)</td>
<td>Trouville (N.scutatus)</td>
<td>225</td>
<td>11</td>
<td>22</td>
<td>S.D.F.</td>
<td>P&lt;1%</td>
<td>N1</td>
</tr>
<tr>
<td>16. Selongey(N.burgundiae)</td>
<td>Trouville (N.scutatus)</td>
<td>225</td>
<td>11</td>
<td>50</td>
<td>S.D.F.</td>
<td>P&lt;1%</td>
<td>M,Ni,N2</td>
</tr>
<tr>
<td></td>
<td>Signy (N.amplus)</td>
<td>227</td>
<td>11</td>
<td>50</td>
<td>P.C.A.</td>
<td>Separation along 3rd vector</td>
<td>N2</td>
</tr>
<tr>
<td></td>
<td></td>
<td>228</td>
<td>11</td>
<td>50</td>
<td>H.C.</td>
<td>Clustering not into original groups</td>
<td></td>
</tr>
<tr>
<td>17. Selongey(N.burgundiae)</td>
<td>All previously examined species</td>
<td>228</td>
<td>11</td>
<td>83</td>
<td>S.D.F.</td>
<td>P&lt;1%</td>
<td>M,Ni,B,N2</td>
</tr>
<tr>
<td>18. Villers(N.micraulus)</td>
<td></td>
<td>231</td>
<td>15</td>
<td>25</td>
<td>P.C.A.</td>
<td>V45 separated along 3rd vector</td>
<td>L,N2</td>
</tr>
<tr>
<td>19. Villers(N.micraulus)</td>
<td>Trouville(N.scutatus)</td>
<td>232</td>
<td>15</td>
<td>43</td>
<td>S.D.F.</td>
<td>P&lt;1%</td>
<td>L,N1</td>
</tr>
<tr>
<td></td>
<td></td>
<td>235</td>
<td>15</td>
<td>43</td>
<td>P.C.A.</td>
<td>Separation along 2nd vector</td>
<td>L,N1,J</td>
</tr>
<tr>
<td></td>
<td></td>
<td>235</td>
<td>15</td>
<td>131</td>
<td>H.C.</td>
<td>Final 2 groups = original groups</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>238</td>
<td>15</td>
<td>246</td>
<td>R.M.A.</td>
<td>P&lt;1% between 13 pairs of slopes</td>
<td>N1</td>
</tr>
</tbody>
</table>

Figure 7.1 continued
<table>
<thead>
<tr>
<th>Sample</th>
<th>Comparison samples</th>
<th>Page</th>
<th>Var.</th>
<th>Spec.</th>
<th>Technique</th>
<th>Sig. of difference</th>
<th>Imp. variables</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>239</td>
<td>15</td>
<td>507</td>
<td>R.M.A.</td>
<td>P&lt;1% between 8-13 pairs of slopes</td>
<td>N1</td>
</tr>
<tr>
<td>21. Villers (N. micraulus)</td>
<td>Trouville (N. scutatus), Signy (N. amplus)</td>
<td>241</td>
<td>14</td>
<td>71</td>
<td>S.D.F.</td>
<td>P&lt;1%</td>
<td>j, L, N1</td>
</tr>
<tr>
<td></td>
<td></td>
<td>241</td>
<td>13</td>
<td>71</td>
<td>P.C.A.</td>
<td>Separation on plot of 1,2 vectors</td>
<td>1st - size 2nd - N1, L</td>
</tr>
<tr>
<td></td>
<td></td>
<td>242</td>
<td>14</td>
<td>71</td>
<td>H.C.</td>
<td>Final 3 groups = original groups</td>
<td></td>
</tr>
<tr>
<td>22. Villers (N. micraulus)</td>
<td>As above + Marquise (N. woodwardii), Hydrenquint, Talant, S. Aud. (N. latiporos)</td>
<td>245</td>
<td>14</td>
<td>188</td>
<td>S.D.F.</td>
<td>P&lt;1%</td>
<td>L, J, N1, B</td>
</tr>
<tr>
<td>23. Villers (N. micraulus)</td>
<td>Trouville (N. scutatus), Signy (N. amplus), N. elongatus group</td>
<td>245</td>
<td>14</td>
<td>75</td>
<td>S.D.F.</td>
<td>P&lt;1%</td>
<td>N1, B, N2, L, A</td>
</tr>
<tr>
<td>24. Specimen V45 (Villers)</td>
<td>Trouville (N. scutatus), Villers (N. micraulus), S. Audley, Hydrenquint, Talant (N. latiporos), Devecey (N. subquadratus), N. elongatus group</td>
<td>248</td>
<td>15</td>
<td>82</td>
<td>Class</td>
<td>100% Stratton Audley</td>
<td></td>
</tr>
<tr>
<td>25. Agassiz type</td>
<td>As above</td>
<td>249</td>
<td>13</td>
<td>82</td>
<td>Class</td>
<td>100% Villers</td>
<td></td>
</tr>
</tbody>
</table>

Figure 7,1 continued.
1. Introduction

This middle Jurassic species is represented in the present study by seven specimens found with the *N. latiporus* sample of Stratton Audley and originally considered to be adult specimens of this latter species. Mercier (1932) and Fisher (1969) considered *N. elongatus* to be only a variety of *N. latiporus*, but it is shown here that the morphological and growth characteristics indicate that both are probably true species. Indeed, Jesionek-Szymanska (1968) has shown the two species to be at quite different levels of evolutionary advancement in the transition from the endocyclic to exocyclic condition in irregular echinoids. Biometrical analysis supports Jesionek-Szymanska (1968) in that *N. elongatus* is considered to be quite distinct from other species studied in the present work.

Two other specimens were subsequently found to be similar to the *N. elongatus* specimens of Stratton Audley. The first specimen, number 067, was found with the Signy l'Abbaye sample of *N. amplus* (see p. 202 for locality data). The second numbered 068 in the present study, is a specimen labelled *N. elongatus* from Ranville, Calvados from the Lambert Collection, Paris, the age also probably being upper Bathonian.

2. Comparison with *N. LATIPORUS* of Stratton Audley

For an evaluation of the Stratton Audley sample using component and cluster analysis see p. 163.

Using the groupings formed by the above analysis, reduced major axis coefficients for the two species were compared to show the number of slopes that can be proved to be significantly different. This estimation of the differences between the groups
was not expected to show reliably the total number of axes that are different as only a small number of specimens is involved and the confidence intervals of the coefficients are correspondingly large. This necessitates a greater distinction between the groups for a given probability level than if a larger number of specimens is used. It should also be noted that as the two species within the Stratton Audley sample are distinguished mainly by size, a discriminant analysis would not be totally satisfactory as this method uses absolute values and not growth trends to discriminate between groups.

From the bivariate analyses of reduced major axes comparisons it was seen that for A with all other variables six slopes (A with B, C, D, L, N1 and N3) were at least probably significantly different (1% < P < 5%) between the two samples. Only one pair of axes, A with M, could not be shown to be different in any way. However, for L with all other variables every pair of axes was shown to be highly significantly different (P < 1%) indicating a very high degree of difference in the increase in length of the periproct during growth between the two samples. An examination of the coefficients of correlation for L within the N. elongatus group showed it to be highly negatively correlated with all other variables. Therefore, L decreases during growth within N. elongatus whilst there is rarely a significant correlation between L and other variables within the N. latiporus group.

The degree of difference between these two species, from the same horizon at the same locality is much greater than between any two samples of N. latiporus and N. scutatus so far studied.

3. Comparison with N. LATIPORUS and N. SCUTATUS

N. latiporus is certainly very different from the contemporary
**N. elongatus**, as so far defined; much more so than it is from the younger **N. scutatus**. This can be confirmed by a discriminant analysis of the three species. This is justifiable as specimens of **N. scutatus** range up in size to those of **N. elongatus** and therefore discrimination will not be made on size differences alone.

The analysis, using 10 variables, the two Stratton Audley groups and the Trouville sample, shows **N. elongatus** to be well removed from the **N. latiporus - N. scutatus** grouping with **N. latiporus** occupying a somewhat central position. In a canonical variate plot the smaller **N. elongatus** specimens lie closer to the **N. latiporus** group than do the larger specimens, confirming a closer similarity of form between young members of the two species (fig.7,2).

**Step 3**

Variables L, N4 and G entered

F matrix indicated that the **N. elongatus** group became highly significantly different (P < 1%) from the other two groups.

**Step 6**

Variables B, I and H added

F matrix indicated that all groups were highly significantly different (P < 1%) from each other.

The central position of **N. latiporus** between **N. scutatus** and **N. elongatus** is borne out by bivariate analysis of the reduced major axes of the latter two species.

In this comparison seven slopes were found to be highly significantly different (P < 1%) when axes were constructed for A with all other variables (i.e. A with B, C, D, E, L, N1 and N3) whilst A with G was probably significantly different (1% < P < 5%). All slopes were highly significantly different for L with all other variables.
Figure 7.2. Distribution of Trouville and Stratton Audley specimens on the first two canonical axes. Group centroids indicated by large lettering. Mean coordinates:

- Trouville: $-2.538 \quad .612$
- S. Audley (N.latiporus): $0.138 \quad -1.664$
- S. Audley (N.elongatus): $9.395 \quad .672$
This is the lowest degree of similarity so far encountered between two groups. This can be contrasted with the results of the Stratton Audley (N.latiporus) and Stratton Audley (N.elongatus) comparisons, p. 195, and the Stratton Audley (N.latiporus) and Trouville comparisons, fig. 6,8. Again the N.latiporus sample is seen to occupy a central position as it is more similar to the N.elongatus and N.scutatus samples than the latter two samples are to each other.

However, it should be noted that the results of these comparisons may not reflect original differences between the populations as, due to the poor preservation of the N.elongatus sample, many reduced major axes are calculated on data from only two 'perfect' specimens. If this is the case then a straight line is easily fitted between the two points on a bivariate graph resulting in a correlation coefficient of unity and no statistical error in \( \alpha \), the slope of the line. This produces a mathematically highly accurate but completely unnatural picture of growth lines, which makes comparison with other axes somewhat dubious.

4. Classification of specimens 067 and 068

The classification of specimens 067 and 068, inferred to be N.elongatus, was carried out within the framework of samples yet to be discussed i.e. the Signy L'Abbaye and Marquise samples. In this way all middle Jurassic nucleolitid groups sampled in the present study were used. This increased the likelihood that the specimens were classified into the species to which they were most likely to belong. The computer program must classify into an existing group and is unable to conclude that the specimens do not belong to any groups present. For this reason as wide a variety of species as possible was included in such analyses.
The *N. elongatus* group of Stratton Audley contains only two specimens on which the standard 15 measurements can be used.

Discriminant function analysis placed specimens 067 and 068 within the *N. elongatus* group (fig. 7,3). The posterior probability for membership of the *N. elongatus* group was 100% in both cases. $\chi^2$ tests of the Mahalanobis distances however showed a low probability ($P < 1\%$) of either specimen belonging to any group.

Using fewer variables so that more specimens from Stratton Audley could be used in the classification procedure, a re-run of the analysis show the smaller Lambert specimen (No. 068) to lie closer to the Marquise sample of *N. woodwardii* than to *N. elongatus*. However the smaller *N. elongatus* specimen from Stratton Audley also lay in this direction, which exposes the problems encountered when using only a few pre-selected variables to define samples rather than all possible information. A $\chi^2$ test of Mahalanobis distances of the specimens from each group mean shows specimen 067 to have a very low probability ($P < 1\%$) of belonging to any group except the Stratton Audley group of *N. elongatus* ($P = 2.5\%$). Specimen 068 has a very low probability ($P < 1\%$) of belonging to any of the groups sampled.

Specimens 067 and 068 are therefore included with the *N. elongatus* specimens from Stratton Audley in analyses below. For the purposes of clarity, when reference is made to the *N. elongatus* sample from Stratton Audley this will refer to the seven specimens found at Stratton Audley only. The term - the 'N. elongatus group' - will refer to these seven specimens plus the two additional specimens from Signy l'Abbaye and the Lambert collection.

A re-run of the discriminant analysis between the Trouville and both Stratton Audley samples was performed using all 15 variables.
Figure 7.3. Distribution of Signy, Marquise, Talant, Stratton Audley and Hydrequent specimens on the first two canonical axes. Specimens 067 and 068 are plotted according to their discriminant scores along these two axes. Group centroids indicated by large lettering. Mean coordinates;
Signy 5.887 1.375
Marquise 3.370 2.728
Talant -4.169 .167
Stratton Audley (N.latiporus) -2.919 .173
Hydrequent 3.762 1.238
Stratton Audley (N.elongatus) .101 -6.947
Specimen 067 .464 -3.080
Specimen 068 -2.224 -4875
and including specimens 067 and 068.

**Step 3**

Variables L, N4 and M entered

The F matrix indicated that the *N. elongatus* sample became highly significantly different ($P < 1\%$) from the other two samples.

**Step 12 (final)**

Variables not entered; A, C and J.

$U$-statistic = .018 (Significance of inequality of group means; $P < .1\%$)

Specimens classified wrongly by posterior probability: 0%.

The third variable to be entered, M, was one of five variables (C, D, M, N1 and N3) not included in the earlier analysis (see p. 196). The plot of the first two canonical variates was very similar to that of fig. 7.1.

The two specimens 067 and 068 were also included in a re-calculation of reduced major axes and derivation of new coefficients for the Stratton Audley sample of *N. elongatus*. On comparison with the Stratton Audley sample of *N. latiporus* when reduced major axes were constructed for A with all other variables, only one slope was significantly different ($P < 1\%$) and two were shown not to be a significant distance apart ($P > 5\%$). On comparison with the Trouville sample of *N. scutatus* three slopes were highly significantly different ($P < 1\%$) and one probably significantly different ($1\% < P < 5\%$). All slopes were highly significantly different ($P < 1\%$) in both comparisons when L was used with all other variables.

However it must be pointed out that as the two additional specimens are not from the same sample the error of $\alpha$, the slope of the line, is likely to be very much larger than the error within
a natural sample. This requires a more rigorous proof of non-parallelism between the slopes resulting in a greater number of lines not proved to be significantly different. It must be remembered that the statistical proof of non-parallelism between two axes is a function of sample size as well as absolute differences. It therefore appears to be unwise to mix specimens from different localities and, therefore, probably different local populations in the construction of reduced major axes.

The analyses show the Trouville sample to be more distinct from the *N. elongatus* group than from the *N. latiporus* sample.

7C) NUCLEOLITES AMPLUS

1. Introduction

A single, but large and fairly well preserved, sample of this problematical species is used in the present study. The sample is from the middle Jurassic of Signy L'Abbaye, Ardennes, France. The locality is described by Fischer (1969). It is located herein on fig. 2, 3a. See p. 46 for discussion of the systematic palaeontology of *N. amplus* and description of the palaeoecology and sedimentology of the Signy sample.

The specimens are unusual in that, although generally well preserved, in a great majority the peristome is missing and therefore variable E could not be measured. This variable is therefore excluded from many analysis so that a reasonably large number of specimens can be utilized.

2. Analysis of the Signy sample

This sample of 41 specimens from the same horizon and locality contains one specimen, No. 067 which is very distinct from the normal morphology of *N. amplus*. This specimen is elongate
sub-quadrate and possesses a deep groove at the posterior margin.

To test the homogeneity of the sample a component analysis was run, a plot of the principal components being given in fig. 7, 4. Fig. 7, 5 tabulates eigenvalues and direction cosines for the first four principal components. Component 1 comprises the usual size/shape parameters, component 2 is composed mainly of variables N2 and N4, which are measures of the posterior sulcus, and component 3 is basically variable I, the vertical height of the periproct. It is seen from the plot of components 2 and 3 that specimen 067 is distinguished from the N.amplus group along the axis of component 2. It possesses a much deeper groove at the posterior margin, variable N2, and a lower than average periproct, variable N4.

In a discriminant function 'classification' procedure, see p. 198, specimen 067 is placed within the group of N.elongatus, a species to which it can easily be assigned subjectively. It is therefore omitted from the Signy sample of N.amplus during further analyses.

3. Comparison between the Signy and Trouville samples

A discriminant analysis between the Signy and Trouville samples indicates the major differences in form between N.amplus and N.scutatus. In this analysis 14 variables only were used, variable E being omitted.

Step 2
Variables M and N1 entered

F matrix indicated that the group means were highly significantly different (P < 1%)

Specimens classified wrongly by posterior probability; 0%

Step 11 (final)

Variables not entered; C, G and J.
Figure 7.4. Distribution of Signy specimens along Principal Components 2 and 3 based on a 14 variable analysis. Components 2 and 3 account for 21% of total variation.
Coordinates for specimen 067: 1.45 -3.97
The ordinate is Component 2, the abscissa is Component 3.
PRINCIPAL COMPONENT ANALYSIS

Signy sample.  
14 variables, 30 cases.

Eigenvalues

<p>| | | | |</p>
<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>7.35</td>
<td>1.63</td>
<td>1.26</td>
<td>1.09</td>
</tr>
</tbody>
</table>

Cumulative proportions of total variance

<p>| | | | |</p>
<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>52%</td>
<td>64%</td>
<td>73%</td>
<td>81%</td>
</tr>
</tbody>
</table>

Eigenvectors

<p>| | | | |</p>
<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>2</td>
<td>3</td>
<td>4</td>
</tr>
<tr>
<td>A</td>
<td>.36</td>
<td>-.15</td>
<td>.00</td>
</tr>
<tr>
<td>B</td>
<td>.35</td>
<td>-.06</td>
<td>-.00</td>
</tr>
<tr>
<td>C</td>
<td>.32</td>
<td>.30</td>
<td>.01</td>
</tr>
<tr>
<td>D</td>
<td>.31</td>
<td>.34</td>
<td>.01</td>
</tr>
<tr>
<td>G</td>
<td>.36</td>
<td>-.10</td>
<td>-.02</td>
</tr>
<tr>
<td>H</td>
<td>.39</td>
<td>-.26</td>
<td>-.01</td>
</tr>
<tr>
<td>I</td>
<td>.12</td>
<td>.15</td>
<td>-.72</td>
</tr>
<tr>
<td>J</td>
<td>.29</td>
<td>-.06</td>
<td>-.29</td>
</tr>
<tr>
<td>L</td>
<td>-.07</td>
<td>.32</td>
<td>.28</td>
</tr>
<tr>
<td>M</td>
<td>.33</td>
<td>-.17</td>
<td>.04</td>
</tr>
<tr>
<td>N1</td>
<td>.26</td>
<td>.04</td>
<td>.34</td>
</tr>
<tr>
<td>N2</td>
<td>.09</td>
<td>-.50</td>
<td>.21</td>
</tr>
<tr>
<td>N3</td>
<td>.01</td>
<td>-.22</td>
<td>.26</td>
</tr>
<tr>
<td>N4</td>
<td>.21</td>
<td>.49</td>
<td>.30</td>
</tr>
</tbody>
</table>

Figure 7.5. Eigenvalues and direction cosines of the first four eigenvectors for the Signy sample. The second and third eigenvectors are plotted in fig. 7.4.
U-statistic = .04 (Significance of the inequality of group means; 
\[ P < .1\% \]
Specimens 100% characteristic of the sample to which they belonged 
(using posterior probability); 100%
Specimens with a low probability (\( P < .1\% \)) of belonging to the 
opposing group (using \( \chi^2 \) tests of \( D^2 \)); 100%
Variables M and N1 were not previously encountered as 
important discriminating characters.
This separation was borne out by a cluster analysis of the 
Trouville and Signy samples which showed a simple clustering 
of specimens into their respective groups. These two multivariate 
methods illustrate the sharp distinction in morphology between the 
two species which along with the possession of bourrelets, wide 
poriferous zone, and long crowded phyllodes of \( N.amplus \) seems to 
indicate that no close relationship exists between it and \( N.scutatus \).

Bivariate analyses between the two samples showed that 
three axes were highly significantly different (\( P < 1\% \)) and four 
probably significantly different (1% < \( P < 5\% \)) for A with all 
other variables. The axes were A with I, L and N3 and A with 
E, G, J and N2 respectively. Again all slopes were significantly different 
for L and all other variables. The degree of difference between the 
two groups was higher than that between \( N.latiporus \) and \( N.scutatus \) 
samples but not as high as in the \( N.scutatus - N.elongatus \) comparison. 

Using variable M (the important discriminating variable isolated 
through discriminant functions) with all other variables four 
slopes were found to be highly significantly different (\( P < 1\% \)).

In a principal component analysis of the two samples the first 
component, which represented 67% of the total variability, was a 
combination of all the major size variables, whilst the second
component, representing a further 15%, was composed mainly of variables N1 and N2. Fig. 7,7 tabulates eigenvalues and direction cosines for the first four principal components. A plot of the first two components (fig. 7,6) reveals a sharp distinction between the two forms. For a given size a Trouville specimen has a deeper groove at the posterior margin (N2) and the periproct is more removed from the apical system (N1) than in the Signy specimen.

4. Comparison between the Signy sample and other nucleolitid species.

In a discriminant analysis between the Signy, Trouville and Stratton Audley samples, representing N.amplus, N.scutatus and N.latiporus respectively, N.amplus was seen to be remote from the other two species which overlap and lie relatively close to each other.

Step 2
Variables M and N1 entered.
Signy specimens classified wrongly by posterior probability; 0%

Step 3
Variable B added
F matrix indicated a highly significant difference (P < 1%) — between Signy and the other two group means.

Step 14 (final)

U-statistic = .01 (Significance of inequality of group means; P < .1%)
Specimens classified wrongly by posterior probability; 0%
F matrix and the canonical variate plot showed the Signy sample to be well removed from the other two related groups.

In a component analysis of the representative samples of N.scutatus, N.latiporus and N.amplus, the plot of the principal
Figure 76. Distribution of Trouville and Signy specimens along Principal Components 1 and 2 based on 13 variable analysis. Components 1 and 2 account for 83% of total variation.
### Principal Component Analysis

Signy and Trouville samples

13 variables, 47 cases.

#### Eigenvalues

<p>| | | | |</p>
<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>8.68</td>
<td>2.15</td>
<td>.75</td>
<td>.54</td>
</tr>
</tbody>
</table>

#### Cumulative proportions of total variance

<p>| | | | |</p>
<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>67%</td>
<td>83%</td>
<td>89%</td>
<td>93%</td>
</tr>
</tbody>
</table>

#### Eigenvectors

<p>| | | | |</p>
<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>2</td>
<td>3</td>
<td>4</td>
</tr>
<tr>
<td>A</td>
<td>.33</td>
<td>-.01</td>
<td>.03</td>
</tr>
<tr>
<td>B</td>
<td>.33</td>
<td>-.06</td>
<td>.00</td>
</tr>
<tr>
<td>C</td>
<td>.32</td>
<td>.15</td>
<td>.06</td>
</tr>
<tr>
<td>D</td>
<td>.32</td>
<td>.16</td>
<td>.08</td>
</tr>
<tr>
<td>G</td>
<td>.33</td>
<td>-.03</td>
<td>.07</td>
</tr>
<tr>
<td>H</td>
<td>.30</td>
<td>.11</td>
<td>.03</td>
</tr>
<tr>
<td>I</td>
<td>.28</td>
<td>-.11</td>
<td>-.32</td>
</tr>
<tr>
<td>J</td>
<td>.30</td>
<td>-.28</td>
<td>.10</td>
</tr>
<tr>
<td>L</td>
<td>-.21</td>
<td>.34</td>
<td>.29</td>
</tr>
<tr>
<td>M</td>
<td>.32</td>
<td>-.11</td>
<td>-.02</td>
</tr>
<tr>
<td>N1</td>
<td>.02</td>
<td>.62</td>
<td>.17</td>
</tr>
<tr>
<td>N2</td>
<td>.06</td>
<td>.45</td>
<td>-.80</td>
</tr>
<tr>
<td>N4</td>
<td>.22</td>
<td>.36</td>
<td>.35</td>
</tr>
</tbody>
</table>

Figure 7.7. Eigenvalues and direction cosines of the first four eigenvectors for the Signy and Trouville samples. The first two eigenvectors are plotted in fig.7,6.
components showed a pattern similar to that of the Trouville - Signy plot (see fig. 7,5), the components basically representing the same variables as in that analysis. All the specimens of the Stratton Audley sample lay completely within and along the N. scutatus growth axis, and were quite distinct from the Signy sample.

A discriminant analysis performed on the four species so far studied produced similar results to the discriminant analysis between the Signy, Stratton Audley and Trouville samples. The inclusion of the N. elongatus sample from Stratton Audley, using only 10 variables, showed this sample to be more closely associated with the 'scutatus - latiporus' group than to the N. amplus group, but like the Signy sample to be highly significantly different (P < 1%) from all other samples.

In a comparison of reduced major axes a slightly higher degree of similarity was seen to exist between Signy and the contemporaneous Stratton Audley sample of N. latiporus than between the Trouville and Signy samples.

For A and all other variables only one slope, A with L, was highly significantly different (P < 1%) between the two former samples. In many cases reduced major axes for the main discriminating variables (e.g. J, L, M and N4) showed a greater degree of similarity between the Signy and Stratton Audley samples than between the Signy and Trouville samples.

Reduced major axis comparisons between the Signy and Stratton Audley sample of N. elongatus showed the two groups to be very different. For A with all other variables a total of eight axes were at least probably significantly different (1% < P < 5%). Furthermore, for each of the major discriminating variables L, M and N1 nine axes were highly significantly different (P < 1%).
1. Introduction

This middle Jurassic species is represented by a collection of specimens from the vicinity of Cirencester, Gloucestershire. Also by 7 well preserved specimens of the Lambert Collection, Paris, from Marquise. Marquise is a small quarrying town in the Boulonnais and the specimens are labelled Bathonian in age.

The specimens from Gloucestershire are too broken and poorly preserved for the purposes of a biometrical study and the analysis is therefore concentrated on the French specimens. Wright (1852) in his original description of the species comments on the thin test of *N. woodwardii* and the rarity of well preserved specimens.

The 7 specimens from Marquise are all perfectly preserved except that in 3 specimens the peristome is missing and variable E cannot be measured. This, and the similarity in form between *N. woodwardii* and *N. amplus*, indicates a close phylogenetic relationship between the two species, possibly even that the specimens from the two samples are con-specific.

The width of the poriferous zone in the Hydrequent sample is broader than Wright's (1852, 1859) drawings which show a narrow zone. This could not be confirmed as the author was unable to locate any of Wright's type material. The French sample may not be truly representative of *N. woodwardii*.

2. Comparison with the Signy sample

To test the hypothesis that the Signy and Marquise samples are con-specific a discriminant function analysis was carried out using the 14 common variables (omitting variable E) and 28 and 7 specimens respectively, fig.7, 8.
Figure 7.8 Distribution of Signy and Mirquise specimens on the first two canonical axes. Group centroids indicated by large lettering.

Mean coordinates;
Signy 0.561 0.000
Mirquise -2.242 0.000
Step 10 (final)

Variables not entered; D, G, N1 and N2

\( U \)-statistic = 0.43 (Significance of inequality of group means; \( P = 4\% \))

Specimens classified wrongly by posterior probability; 3%.

From an analysis of \( X^2 \) tests of Mahalanobis distances it appeared that 50% of the specimens from each group had a low probability (\( P < 5\% \)) of belonging to the opposing sample. This is about the same degree of difference as between samples of \( N.\text{scutatus} \) and \( N.\text{latiporus} \).

Bivariate analyses showed a surprisingly high number of reduced major axes to be different between the two samples. For A with all other variables four slopes were found to be highly significantly different (\( P < 1\% \)), whilst variables L and I, both dimensions of the periproct, were found to be very different between all the samples. For variable L with all other variables all slopes were highly significantly different (\( P < 1\% \)), and for I all slopes were similarly different. These results appear to be in conflict with the previous analysis as they indicate a much greater degree of difference, comparable with that between the Trouville and Signy samples.

The discriminant analysis program was re-run with all 15 variables used but the number of specimens reduced. Only 10 and 4 specimens represented the Signy and Marquise samples respectively. However, the three specimens omitted from the Marquise sample were the largest.

Step 2

Variables N4 and E entered (E was therefore important in discriminating between the two groups).
Specimens classified wrongly by posterior probability; 0%

**Step 12 (final)**

Variables not entered; C, G and M

\[ U\text{-statistic} = .019 \] (Significance of the inequality of group means; \[ P = 7\% \])

Specimens classified wrongly by posterior probability; 0%

This analysis has shown that although good separation is achieved between these two samples, no significance can be attached to these differences.

Similar results were achieved with a hierarchical grouping. Using only 14 variables no distinction was made between the two groups, both being mixed throughout the clustering procedure. Using all 15 variables but reducing the number of specimens, the samples separated to a better degree, only specimen 053 from Signy being grouped wrongly.

These results are open to two opposing interpretations. First, that the position of the peristome, variable E, is a character of taxonomic importance and that without its inclusion in analyses the samples do not reflect true differences between the original populations. Second, that the preservation of the peristome in some specimens may be due to unidentified test characteristics and therefore not random, resulting in an extreme bias when examining these small numbers of specimens.

Due to the results provided by the U-statistic, see above, and in order to minimise bias, variable E will, in many cases, be omitted from further comparisons so that as many specimens as possible can be used in subsequent analyses.

**3. Comparison between the Marquise, Signy and Trouville samples.**

A discriminant analysis between these three samples using
14 variables, is in effect a combination of two previous analyses between the Marquise and Signy and the Signy and Trouville samples. It produces a multivariate picture of the relationships between these groups.

**Step 2**
Variables M and Nl entered
F matrix indicated a significant difference ($P < 1\%$) between the group means of the Trouville and Signy samples. Trouville specimens classified wrongly by posterior probability; 0%

**Step 9**
F matrix indicated that all group means are highly significantly different ($P < 1\%$) from each other
Signy and Marquise specimens classified wrongly by posterior probability; 9%.

**Step 13 (final)**
Variable not entered; G
Trouville specimens classified as 100% representative of their own group (using posterior probability); 100%
Signy specimens classified wrongly by posterior probability; 7%

Fig. 7, 9 shows the distribution of specimens along the first two canonical variates representing 100% of total dispersion.

A clear distinction was therefore made between the Trouville and the two Bathonian forms. The Signy and Marquise samples lie relatively close together with overlap between the groups. This supports the subjective view that *N.amplus* and *N.woodwardii* are more closely related to each other than they are to *N.scutatus*.

A hierarchical grouping of these three samples, using 15 variables, showed a similar pattern of grouping between the Marquise and Signy samples as described in the previous section (see p. 214).
Figure 7,9. Distribution of Signy, Marquise and Trouville specimens on the first two canonical axes. Group centroids indicated by large lettering. Mean coordinates:
Signy 3.219 -.646
Marquise 2.717 2.738
Trouville -5.746 -.057
At the formation of four groups an 'adjacent' and 'remote' Trouville, a Signy, and a mainly Marquise group were formed. The two Trouville groups were then combined at the next stage of clustering, while the Signy and Marquise groups were joined at the stage of formation of two groups. This analysis again underlined the close association between the two 'orbiculoid' species.

In a principal component analysis of the three groups a similar situation emerged to the analysis of the Signy and Trouville samples (see p.206). The value and composition of each of the first four principal components was virtually identical to that of the preceding components analysis. The pattern of the various plots was also the same. For example, the first and second components showed parallel growth lines between the Trouville and Signy samples with an increase in size associated with an increased value of \( N_l \). The Marquise sample lay with and was indistinguishable from, the Signy group showing that the size/\( N_l \) growth ratio was similar between these two groups but quite distinct from that of the Trouville sample.

In a comparison of reduced major axes for the three samples it was seen that there is about the same degree of difference between any of the different pairs of groups involved (Fig.7,10).

4. Comparison between the Marquise sample and other nucleolitid species

In a discriminant analysis between all Bathonian forms so far studied i.e. the samples of Signy, Marquise, Hydrequent, Talant and the two samples from Stratton Audley (together representing the species \( N.amplus, N.woodwardii, N.latiporus \) and \( N.elongatus \)) it was seen that three major groupings emerge (Fig.7,11). The three \( N.latiporus \) samples are grouped together,
A) Variable A with all other variables.

<table>
<thead>
<tr>
<th></th>
<th>A</th>
<th>B</th>
<th>C</th>
<th>D</th>
<th>Signy</th>
<th>Trouville</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>4</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>B</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>C</td>
<td>9</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>D</td>
<td>0</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

B) Variable J with all other variables.

<table>
<thead>
<tr>
<th></th>
<th>A</th>
<th>B</th>
<th>C</th>
<th>D</th>
<th>Signy</th>
<th>Trouville</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>2</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>B</td>
<td>2</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>C</td>
<td>10</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>D</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

C) Variable M with all other variables.

<table>
<thead>
<tr>
<th></th>
<th>A</th>
<th>B</th>
<th>C</th>
<th>D</th>
<th>Signy</th>
<th>Trouville</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>2</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>B</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>C</td>
<td>11</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>D</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

D) Variable N1 with all other variables.

<table>
<thead>
<tr>
<th></th>
<th>A</th>
<th>B</th>
<th>C</th>
<th>D</th>
<th>Signy</th>
<th>Trouville</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>3</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>B</td>
<td>5</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>C</td>
<td>6</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>D</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Figure 7,10. Comparison of reduced major axes between the Trouville, Signy and Marquise samples. Key as for fig.5,10.
Figure 7.11. Distribution of Signy, Marquise, Hydrequent, Stratton Audley and Talant specimens on the first two canonical axes. Group centroids indicated by large lettering. Mean coordinates:

- Signy: 3.378, 0.492
- Marquise: 2.493, -1.415
- Hydrequent: -4.553, 1.261
- S. Audley (N. latiporus): -4.556, 0.218
- Talant: -6.568, -0.667
- S. Audley (N. elongatus): -0.883, -6.291
as are the Signy and Marquise samples whilst the *N.elongatus* sample lies some distance from, but in a central position between, the other groups. The *N.elongatus* sample, although consisting of only two specimens in which 14 variables could be measured, is still highly significantly different from all other groups.

**Step 4**
Variables M, N2, B and N1 entered
F matrix indicated that the group means of the 'orbiculoid' samples became highly significantly different (P < 1%) from the 'latiporus' samples.

**Step 5**
Variable H entered
F matrix indicated that the *N.elongatus* group became highly significantly different (P < 1%) to all other groups except the Marquise sample.

**Step 7**
Variables D and L added.
U-statistic = .005 (Significance of inequality of group means; P < .1%)

Samples from within the larger groupings were at most only-probably significantly different (1% < P < 5%) from each other but each sample was highly significantly different (P < 1%) from samples from any other grouping.

Variables M, N1 and B have all been important in previous analyses between the orbiculoid and other nucleolitid groups. Variable B is probably of importance because of the wide difference in roundness of morphology between these groups.

As in the previous analyses between Marquise, Signy and Trouville, measurements of the length of specimens were not found to be good discriminating variables. The discrimination procedure
was therefore not conducted on the absolute size of specimens as considerable overlap in size range occurred between samples. In the final group probability table it was only specimens from the oldest samples within each grouping that were all classified correctly, whilst the younger samples contained specimens classified wrongly into the older sample. For example, within the *N. latiporus* grouping only specimens from the middle Bathonian Hydrequent sample were all classified as most likely to belong to Hydrequent, whilst the Stratton Audley sample contained two specimens classed with the Hydrequent sample. One specimen from Talant was also classed with the Hydrequent sample. The same pattern was found in the 'orbiculoid' group where three Signy specimens were classified with the Marquise sample.

The analysis was also extended to include the *N. scutatus* sample from Trouville, which, from previous analysis would be expected to occupy a position close to the *N. latiporus* group. For this analysis only the author's 19 specimens of the Trouville shore sample were used in order to satisfy the 'similar sample size' requirement of discriminant analysis. (It had been found previously that no important statistical changes occurred from the use of the full sample of 107 specimens.) In addition, the two single specimens of *N. elongatus* were used to supplement the two perfect specimens from Stratton Audley.

The pattern of discrimination between the samples and groupings was the same as in the previous analysis. The Trouville sample was indeed found to lie in a peripheral position within the *N. latiporus* grouping in an area opposed to that of the *N. elongatus* group. However some minor changes were observed.
**Step 4**
Variables M, N1, B and N2 entered.

F matrix indicated that the group means of samples within the
major groupings became highly significantly different ($P < 1\%$)
from samples from within other groupings.

**Step 5**
Variable J added

F matrix indicated that the *N. elongatus* became highly significantly
different from all other groups.

**Step 11 (final)**
Variables not entered; A, D and G.

$U$-statistic = .003 (Significance of inequality of group means;
$P < .1\%$)

F matrix indicated that the majority of samples were at most only
probably significantly different ($1\% < P < 5\%$) from other samples
from within their own group.

The group probability table showed that the *N. elongatus* group
was quite discrete, lying in a position equidistant from the
Stratton Audley sample of *N. latiporus* and the Marquise sample of
*N. woodwardii*.

Variable N1 became the second most important discriminating
variable indicating an increase in importance of the separation
of the periproct and apical system with the inclusion of the
stratigraphically younger Trouville sample.

On the plot of the first two canonical variates the samples
occupied the same positions (the co-ordinates of the group means
were also very similar) as during the previous analysis.

Discriminant and component analysis, using only the principal
members of the major groupings so far discussed, produced the
same results as when a full analysis was executed using all samples. Therefore for the sake of simplicity and clarity some future analyses will be recorded using only those principal members, i.e. Signy sample omitting Marquise, and the Trouville sample, omitting the Hydrequent, Stratton Audley and Talant samples of N.latiporus. On all occasions when this method was used the pattern of discrimination and the composition of components remained unchanged. This procedure was used in previous analyses when the Trouville sample represented all the combined N.scutatus groups.

Figure 7,12 tabulates results of comparisons of reduced major axes for the important discriminating variables with all other variables between Marquise and the two Stratton Audley samples of N.latiporus and N.elongatus. In almost every case the Marquise sample shows a higher degree of similarity to the N.latiporus sample. However the degree of similarity, in both comparisons, may be overestimated due to the small sample sizes used.

7: E) NUCLEOLITES BURGUNDIAE

1. Introduction

The final middle Jurassic species examined is Cotteau’s N.burgundiae from the Bathonian of Selongey, Cote d’Or, France. The four type specimens of this species from the Cotteau Collection at Orsay were measured and although poorly preserved were used in some preliminary analyses. These specimens were supplemented by specimens collected by the author from the type locality. However as these are even more poorly preserved than the type material they are omitted from the analysis.

N.burgundiae is characterised by its large circular form.
<table>
<thead>
<tr>
<th>Variable</th>
<th>Strat. Audley N.latiporus</th>
<th>Strat. Audley N.elongatus</th>
<th>Marquise</th>
</tr>
</thead>
<tbody>
<tr>
<td>Variable A</td>
<td>2</td>
<td>3</td>
<td>2</td>
</tr>
<tr>
<td>Variable B</td>
<td>2</td>
<td>3</td>
<td>2</td>
</tr>
<tr>
<td>Variable L</td>
<td>6</td>
<td>8</td>
<td>6</td>
</tr>
<tr>
<td>Variable M</td>
<td>1</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td>Variable N1</td>
<td>1</td>
<td>6</td>
<td>6</td>
</tr>
<tr>
<td>Variable N2</td>
<td>2</td>
<td>1</td>
<td>1</td>
</tr>
</tbody>
</table>

Figure 7,12. Comparison of reduced major axes between Marquise and the two Stratton Audley samples of N.latiporus and N.elongatus for the variables shown and all other variables. Key as for fig.5,10.
conical shape and periproct well removed from the apical system. The type specimens all have the periproct obscured by matrix, and therefore variables I, L and N4 could not be measured on them. The peristome is also missing from the most well preserved specimens and variable E consequently omitted from analysis. However, even allowing for these missing variables only 3 out of 4 type specimens could be utilised in analysis employing 11 remaining variables.

2. Comparison between the Selongey and other nucleolitid samples.

Results of a discriminant function analysis between the Trouville and Selongey samples:

Step 1
Variable N1 entered
Specimens classified wrongly by posterior probability; 0%

Step 4
Variables N2, N3 and H added
F matrix indicated a significant difference (P < 1%) between group means.

Step 9
Variables not entered; A, D, H and M.
U-statistic = .13 (Significance of the inequality of group means; P < .1%)
Specimens with a low probability (P < .1%) of belonging to the opposing group (using $\chi^2$ tests of $\psi^2$); 100%.

The large periproct to apical system distance (N1) is important in the characterisation of the Selongey sample.

The analysis was repeated with the inclusion of another 'orbiculoid' species sample to determine whether there was a
statistical similarity between species of apparently similar gross morphology, comparable to that found between the Signy and Marquise samples. The analysis was repeated using the Selongey, Trouville and Signy samples, with the same 11 variables.

**Step 2**
Variables M and N entered.
Specimens classified wrongly by posterior probability; 0%
F matrix indicated that the Signy sample became highly significantly different (P < 1%) from the other two groups.

**Step 3**
Variable N2 added
All group means became highly significantly different (P < 1%) from each other.

**Step 8 (final)**
Variable not entered; A, C and G
U-statistic = .01 (Significance of the inequality of group means; P < .1%)
Specimens classified as 100% representative of their own group (using posterior probability); 100%

A combination of a central apical disc and a more extremely posterior periproct, represented by the first two entered variables, distinguishes the Selongey specimens from both the Signy and Trouville samples, as the latter groups do not possess both characters together.
The first four discriminating variables are the same as those used in the analysis of four middle Jurassic species (see p. 217) and appear to be important for discriminating between nucleolitid echinoids of this epoch.

From the canonical variate plot it was seen that, quite unexpectedly, the 'orbicular' middle Jurassic Selongey sample lay
closer to the non-orbicular, upper Jurassic Trouville sample than to the similarly orbicular and middle Jurassic Signy sample. Moreover, the Trouville sample occupied a somewhat central position between the groups. There was therefore no statistical similarity between the two orbiculoid species.

In a component analysis between the same three samples the composition and plots of the vectors were similar, but not exactly the same as in the analysis between the Trouville and Signy samples, although the growth axes did follow the same trends (see p206). In the present analysis the second eigenvector, which together with the first vector contributed 86% of the total variance, was made up of variables N1 and J in inverse proportions. This appears to be a logical measure of variability within these samples as, assuming a stable position for the apical disc for a given size of specimen, an increase in the distance between the apical disc and the periproct must result in a corresponding decrease in the length of the periproctal sulcus. The plot of the first two components placed the Selongey specimens within the growth axis of the Trouville sample, as a combination of a well separated apical disc and periproct with a short sulcus easily distinguish the Selongey group from the _N_amplus sample of Signy. The Selongey specimens were seen to lie at the extremity of the Trouville growth axes due to their large size.

They were further distinguished from both the Trouville and Signy samples along the axis of the third component, composed of only variable N2; the Selongey specimens possessing only a shallow indentation of the posterior border relative to their large size.
A hierarchical grouping of the same specimens also placed the Selongey sample within the Trouville cluster, rather than with the Signy specimens. The 3 Selongey specimens were brought together at the stage of formation of 5 groups and clustered with 4 Trouville specimens. These 4 specimens, numbers X463, 465, 473 and 480 are all characterised by relatively large variables M, N1 and C, variables which are similarly large in N. burgundyae. At the stage of formation of 3 groups the clusters were organised into Trouville and Signy groups plus a group including both Selongey and the four Trouville specimens. At the stage of formation of two groups the latter group was combined, with a large increase in error, with the Trouville cluster. One Signy specimen, 056, was placed within the Trouville cluster. Although an earlier analysis (p. 206) using 14 variables showed a clear distinction between the Signy (N. amplus) and Trouville (N. scutatus) samples, a clear distinction was not made in this analysis, which used only 11 variables. The lack of distinction is therefore inferred to reflect the relative paucity of data.

The discriminant function analysis was extended further to include all previously studied species, and the pattern of discrimination found to be the same as in earlier analyses.

**Step 2**
Variables M and N1 entered.
Selongey specimens classified wrongly by posterior probability: 0%.

**Step 3**
Variable B entered.
F matrix indicated that the Selongey sample became highly significantly different ($P < 1\%$) from all other group means.

**Step 4**
Variable N2 entered.
F matrix indicated that the group means of samples within the major groupings were highly significantly different ($P < 1\%$) from samples within other groupings.

At the end of the analysis the Selongey sample lay on the opposite side of the canonical variate plot to the *N. elongatus* group and closest to the Trouville sample (fig. 7, 13). Its polarity on the graph to the *N. elongatus* is apparently due to four features: (1) the periproct being remote from, as opposed to being in contact with, the apical system (variable N1); (2) its rounded as opposed to elongate form (variable B); (3) shallow, as opposed to deep indentation of the posterior border (variable N2); (4) short as opposed to long anal sulcus (variable J).

Thus the genotype and five middle Jurassic species are clustered into four species groups, distinguished on the graph by two orthogonal vectors. One vector trends from bottom left to top right of the graph, and distinguishes round (bottom left) from elongate (top right) forms. The second vector distinguishes forms with the periproct close to the apical disc (top left) from those where the periproct is at some distance from the apical disc (bottom right). Neither vector is directly correlated with the stratigraphic ages of the samples.

7 F) NUCLEOLITES MICRAULUS

1. Introduction

This upper Jurassic species is characterised by an elongate form, a small periproct and short sulcal groove. It is represented in analyses by a large sample collected by the author from Villers-le-Tourneur, Ardennes, France. The sample is from an iron-stained, poorly consolidated, soft, but very fossiliferous
Figure 7.13. Distribution of Signy, Marquise, Talant, Stratton Audley, Hydrequent, Trouville, Selongey and N. elongatus group specimens on the first two canonical axes. Group centroids indicated by large lettering. Mean coordinates:
Signy  -3.968  -.622
Marquise  -3.154  .161
Talant  3.387  2.821
Stratton Audley  2.367  .747
Hydrequent  2.273  .582
Trouville  3.238  -.385
Selongey  5.813  -6.139
N. elongatus group  -.548  4.131
oosparite in which 45 specimens were considered sufficiently well preserved for measurement. Many specimens are broken and fragmentary and not suitable for analysis. All 15 measurements could be made on only 25 of the 45 specimens. Two other specimens had only one character missing, variable B, whilst variables I, J, L could not be measured on the majority of the remainder of the sample.

A cast in the British Museum (Natural History) of the Agassiz type specimen was also used in the analysis. Specimens of _N. micraulus_ from Villers-le-Tourneur in the Cotteau Collection are labelled as lower Oxfordian.

2. Analysis of the Villers-le-Tourneur sample

One specimen of this sample, V45, is less elongate, more bilobed and has the periproct closer to the apical disc than in the type _N. micraulus_. It more closely resembles the _N. scutatus—N. latiporus_ form and so a principal component analysis was carried out on the Villers sample to ascertain whether this specimen stood apart from the rest of the group.

The first component was as usual the size/shape component; the specimen was seen to lie at one end of this axis because of its small size. The second component was composed of variables J, L and N4, all related to the size and position of the periproct. The specimens plotted amongst those with the largest periproct. The third component, which sets the specimen well apart from the rest of the sample, is composed of L and N2. The depth of the groove at the posterior border, (N2), which was noted subjectively as giving the specimen a bilobed appearance is thus an important discriminating character. Although other Villers specimens possess a deeper groove this is usually associated with a very small periproct. It is a multivariate character, the combination of a large periproct and
groove, which distinguishes this specimen from the rest. The proportion of the total variance of the three principal components is 59%, 10% and 10% respectively. Fig.7,14 shows the second component against the third, so eliminating any size dependent characters of the specimens. Fig.7,15 tabulates eigenvalues and direction cosines of the first four principal components.

Specimen V45 is seen to be well separated from the other *N. micraulus* specimens and is therefore omitted from further analyses.

3. Comparison between the Villers and Trouville samples

The results of a discriminant function analysis between the two samples are:

**Step 2**

Variables L and N1 entered

*F* matrix indicated a highly significant difference (*P* < 1%) between group means.

Specimens classified wrongly by posterior probability; 2%

**Step 3**

Variable B added

Specimens classified wrongly by posterior probability; 0%

**Step 12 (final)**

Variables not entered; A, D and J

*U*-statistic = .13 (Significance of inequality of group means; *P* < .1%)

Specimens classified as 100% representative of their group (using posterior probability); 99%

Specimens with a low probability (*P* < .1%) of belonging to the opposing group (using *X* squared tests of *D* squared); 98%. Specimen X489 (Trouville) had a 1% probability of belonging to the Villers group.
Figure 7.14. Distribution of Villers specimens along Principal Components 2 and 3 based on a 15 variable analysis. Components 2 and 3 account for 20% of total variation.

Coordinates of specimen V45:
3.22    -1.27.

The ordinate is Component 2, the abscissa is Component 3.
PRINCIPAL COMPONENT ANALYSIS

Villers sample.

15 variables, 25 cases.

Eigenvalues

<p>| | | | |</p>
<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>8.84</td>
<td>1.58</td>
<td>1.46</td>
<td>1.07</td>
</tr>
</tbody>
</table>

Cumulative proportions of total variance

<p>| | | | |</p>
<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>59%</td>
<td>69%</td>
<td>79%</td>
<td>86%</td>
</tr>
</tbody>
</table>

Eigenvectors

<p>| | | | |</p>
<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>2</td>
<td>3</td>
<td>4</td>
</tr>
<tr>
<td>A</td>
<td>-.33</td>
<td>-.05</td>
<td>.06</td>
</tr>
<tr>
<td>B</td>
<td>-.32</td>
<td>-.02</td>
<td>.07</td>
</tr>
<tr>
<td>C</td>
<td>-.30</td>
<td>-.16</td>
<td>-.22</td>
</tr>
<tr>
<td>D</td>
<td>-.30</td>
<td>-.19</td>
<td>-.24</td>
</tr>
<tr>
<td>E</td>
<td>-.30</td>
<td>.01</td>
<td>.18</td>
</tr>
<tr>
<td>G</td>
<td>-.33</td>
<td>-.06</td>
<td>.03</td>
</tr>
<tr>
<td>H</td>
<td>-.27</td>
<td>.20</td>
<td>-.03</td>
</tr>
<tr>
<td>I</td>
<td>-.26</td>
<td>.31</td>
<td>.25</td>
</tr>
<tr>
<td>J</td>
<td>-.11</td>
<td>-.49</td>
<td>.24</td>
</tr>
<tr>
<td>L</td>
<td>-.10</td>
<td>-.47</td>
<td>.45</td>
</tr>
<tr>
<td>M</td>
<td>-.29</td>
<td>-.10</td>
<td>.21</td>
</tr>
<tr>
<td>N1</td>
<td>-.27</td>
<td>.23</td>
<td>-.35</td>
</tr>
<tr>
<td>N2</td>
<td>-.13</td>
<td>.28</td>
<td>.51</td>
</tr>
<tr>
<td>N3</td>
<td>-.13</td>
<td>.26</td>
<td>.17</td>
</tr>
<tr>
<td>N4</td>
<td>-.23</td>
<td>-.36</td>
<td>-.26</td>
</tr>
</tbody>
</table>

Figure 7,15. Eigenvalues and direction cosines of the first four eigenvectors for the Villers sample. The second and third eigenvectors are plotted in fig.7,14.
This degree of discrimination is similar to that between the Trouville and Signy samples.

This distinction between the Villers and Trouville samples was confirmed by principal component and cluster analysis. Both separate the two samples perfectly into their correct groupings. In the principal component analysis the second component separated the two samples. The first component is the size component, (Fig.7,17) accounting for 62% of the variability, but unusually excluding J.

The second component, accounting for a large proportion of the variance at 22%, is composed of variables J, L and an inverse proportion of variable NL. This is to be expected since if the apical disc is in a constant position, a shortening of the anal sulcus would result in the periproct becoming increasingly distal to the apical system, and vice versa. The length of the periproct (L) increases as the length of the anal sulcus (J) increases. The third component, comprising only 6% of the variability, is composed of variable I and N4 in inverse proportions showing that a general increase in size of the vertical height of the periproct results in a lowering of its position so that it lies closer to the adoral surface.

Fig.7,16 is a plot of the second and third components, which, therefore eliminates differences due to variation in test size between the samples. It consequently accounts for only 28% of the variability but the plot is able to distinguish perfectly between the two samples. Fig.7,17 tabulates eigenvalues and direction cosines for the first four principal components.

A hierarchical grouping of the two samples showed the Villers sample to be more homogeneous in morphology than the Trouville sample. This could be simply a reflection of the larger sample size of the Trouville group, producing greater diversity of form.
Figure 7.16. Distribution of Villers (N. micraulus) and Trouville (N. scutatus) specimens along Principal Components 2 and 3 based on a 14 variable analysis. Components 2 and 3 account for 23% of total variation. The ordinate is Component 2, the abscissa is Component 3.

T = Trouville
V = Villers
**Principal Component Analysis**

Trouville and Villers samples.

14 variables, 43 cases.

**Eigenvalues**

<p>| | | | | |</p>
<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>8.72</td>
<td>3.11</td>
<td>.77</td>
<td>.58</td>
</tr>
</tbody>
</table>

**Cumulative proportions of total variance**

<p>| | | | | |</p>
<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>62%</td>
<td>84%</td>
<td>90%</td>
<td>94%</td>
</tr>
</tbody>
</table>

**Eigenvectors**

<table>
<thead>
<tr>
<th></th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>-.33</td>
<td>-.12</td>
<td>.05</td>
<td>-.18</td>
</tr>
<tr>
<td>B</td>
<td>-.33</td>
<td>.03</td>
<td>.05</td>
<td>-.15</td>
</tr>
<tr>
<td>C</td>
<td>-.32</td>
<td>.01</td>
<td>-.31</td>
<td>.13</td>
</tr>
<tr>
<td>D</td>
<td>-.32</td>
<td>-.01</td>
<td>-.34</td>
<td>.13</td>
</tr>
<tr>
<td>E</td>
<td>-.32</td>
<td>-.03</td>
<td>.18</td>
<td>-.08</td>
</tr>
<tr>
<td>G</td>
<td>-.32</td>
<td>-.15</td>
<td>.03</td>
<td>-.24</td>
</tr>
<tr>
<td>H</td>
<td>-.29</td>
<td>-.07</td>
<td>.34</td>
<td>.04</td>
</tr>
<tr>
<td>I</td>
<td>-.27</td>
<td>.11</td>
<td>.44</td>
<td>.22</td>
</tr>
<tr>
<td>J</td>
<td>-.09</td>
<td>.50</td>
<td>.03</td>
<td>-.44</td>
</tr>
<tr>
<td>L</td>
<td>-.02</td>
<td>.55</td>
<td>.04</td>
<td>-.16</td>
</tr>
<tr>
<td>M</td>
<td>-.32</td>
<td>-.04</td>
<td>.04</td>
<td>-.24</td>
</tr>
<tr>
<td>N1</td>
<td>-.15</td>
<td>-.50</td>
<td>-.03</td>
<td>.08</td>
</tr>
<tr>
<td>N2</td>
<td>-.18</td>
<td>.32</td>
<td>.19</td>
<td>.70</td>
</tr>
<tr>
<td>N4</td>
<td>-.25</td>
<td>.19</td>
<td>-.63</td>
<td>.15</td>
</tr>
</tbody>
</table>

Figure 7,17. Eigenvalues and direction cosines of the first four eigenvectors for the Trouville and Villers samples. The second and third eigenvectors are plotted in fig. 7,16.
At the stage of formation of four groups the Villers sample had been fully and correctly clustered whilst the Trouville sample was divided between the remaining three groups. These three Trouville groups were gradually combined with increasingly larger errors with the 'adjacent' and 'remote' grouping of earlier analyses being formed (see p.134). At the stage of formation of two groups all specimens were clustered into their original samples.

Bivariate analyses of reduced major axes between the two samples showed a degree of difference as great as that between _N.scutatus_ and _N.elongatus_. When axes were constructed for _A_ with all other variables, five slopes (_A_ with _E,L,N1,N2_ and _N3_) were highly significantly different (_P_ < 1%) between the two samples and a further two slopes (_A_ with _B_ and _N4_) were probably significantly different (1% < _P_ < 5%). Reduced major axes for the two important discriminating variables _L_ and _N1_ with all other variables were very different between the two samples. For example, for _L_ a total of eleven slopes were highly significantly different (_P_ < 1%) and the other three were probably significantly different (1% < _P_ < 5%).

In the case of _N1_ thirteen slopes were highly significantly different (_P_ < 1%).

Thus although the samples from Villers and Trouville come from the same stage of the upper Jurassic, they are clearly distinct, and represent two different species, _N.micraulus_ and _N.scutatus_ respectively.

4. Comparison between the Villers and all N.SCUTATUS samples

The discriminant analysis of the previous comparison was extended to include the five major samples of _N.scutatus_, i.e. Cothill, Bran Point, Trouville, Wootton Bassett and Upware, to determine whether
the Villers sample bore a close resemblance to any particular
N. scutatus group.

At the end of the analysis the two species were well
separated from each other, and to a much greater extent than between
N. scutatus and N. latiporus. The U-statistic, at .03, showed a high
significant difference between group means at the .1% level. All,
except one Villers specimen, were 100% representative of their own
group, no overlap occurring between the two groups. Moreover the
group mean of the Villers sample was highly significantly different
from all other samples, although it was possibly closer, as revealed
by a lower F statistic, to the Cothill and Bran Point groups. These
are N. scutatus groups with small periprocts.

Bivariate analyses also showed a higher degree of similarity
between Villers and Cothill than between Villers and Trouville,
although this may have been due to differences in sample size.
For variables found to be important in distinguishing between
N. scutatus and N. micraulus in the previous analysis, i.e. L and Nl,
fewer axes were different between samples when Villers was compared
with Cothill than when it was compared to Trouville. For A with
all other variables five slopes are highly significantly different
( P < 1%) and one probably significantly different (1% < P < 5%).
For L the results are seven and one slopes and for Nl eight and
three slopes respectively.

The two upper Jurassic species, N. micraulus (Villers) and
N. scutatus (from five localities) are clearly distinct both
subjectively and statistically. The N. scutatus sample which most
closely resembles N. micraulus is that from Cothill, from a similarly
fine-grained matrix ( ? = substrate).
5. Comparison between the Villers, Trouville and Signy samples

The large Villers (N. micraulus) and Signy (N. amplus) samples have been shown above to be important groups in biometrical analysis, in that they are easily distinguishable from N. scutatus both subjectively and statistically. Indeed they form standard points of reference that stand apart from the genotype and its antecedent species N. latiporus (e.g., Fig. 7, 13). One other species, N. woodwardii is close to N. amplus, in the same way that N. scutatus is close to N. latiporus. The fourth major grouping to emerge is the Stratton Audley sample of N. elongatus, a very small and poorly preserved sample that can only be used effectively with conspecific specimens from other collections. The distinctness of this group and the equally small and poorly preserved sample from Selongey representing N. burgundiae is therefore questionable. This section therefore makes comparison between the three largest groups.

It is seen that at this higher taxonomic level, certain samples can represent the spread of morphological variation within the larger groups in the same way that the Trouville sample has been used as the single representative of N. scutatus. This is achieved without detriment to the statistical certainty of results. It also allows a clearer picture of relationships to emerge by reducing the number of specimens plotted per graph. The four samples which will be used to characterise these major groups are:

a) Trouville, representing the N. scutatus - N. latiporus plexus.

b) N. elongatus group represented by the Stratton Audley sample and the two single specimens from Signy and the Lambert collection.

c) Signy, representing the N. amplus - N. woodwardii plexus.

d) Villers, representing N. micraulus.
In order to explore the differences between the three large groups, a discriminant function analysis was therefore carried out limited to the Trouville, Signy and Villers samples. Only the 14 variables usually employed for the Signy sample were used.

**Step 2**
Variables J and L entered.

F matrix indicated that the Signy sample became highly significantly different \((P < 1\%)\) from all other group means.

**Step 3**
Variable Nl entered.
All groups became highly significantly different \((P < 1\%)\) from each other.

**Step 4**
Variable B added
Specimens classified wrongly by posterior probability; 0%

**Step 11 (final)**
Variables not entered; C, G and M

U-statistic = .004 (Significance of the inequality of group means; \(P < .1\%\))

Specimens classified as 100% representative of their own group (using posterior probability); 100%

Variable M is not used in the discriminating procedure whereas previously (see p. 203) it was the first variable to be used in distinguishing between the Trouville and Signy samples.

The canonical variate plot showed three distinct homogeneous groups, all well separated, with the Trouville sample occupying a central position.

In a principal component analysis a closer relationship was seen between two of the samples. The second principal component
formed was the usual size/shape component, producing a growth element in the graphs. The plot of these two components, comprising 78% of the total variance, produced only two distinct growth lines; one formed by the Villers specimens, the other by the Signy and Trouville specimens intermixed. This second component was similar to the second component of the Villers - Trouville plot except that it excluded variable J to a greater degree. Variable N1 was also the co-contributor, along with N2, to the second component of the Signy - Trouville analysis.

The principal component analysis apparently equated the Signy and Trouville samples because of the smaller value of N1 in these groups as opposed to the 'remote' condition of the Villers sample. Therefore, despite the similarities in age and overall morphology between Villers and Trouville, the latter sample is placed with the older Signy sample on the evidence of the larger periproct and its proximity to the apical system. (Fig.7,18).

A similar pattern was produced in a plot of the first and third components, the third component adding 9% to the variability and being composed of variables L, N1, N2 and N4 in almost equal proportions. In this plot a clear distinction was again found between the Villers and Trouville samples, the Signy specimens however spanning both growth lines. This is the result of the Signy specimens having some morphological affinities to the Villers sample in possessing a small periproct and a smaller indentation of the posterior border (L and N2) whilst the periproct and apical system lie in close proximity (N1) as in the Trouville sample. Fig.7,19 tabulates eigenvalues and direction cosines for the first four principal components.

A hierarchical clustering of the same specimens showed
Figure 7,18. Distribution of Villers (N.micraulus), Trouville (N.scutatus), and Signy (N.amplus) specimens along Principal Components 1 and 2 based on a 13 variable analysis. Components 1 and 2 account for 78% of total variation.
PRINCIPAL COMPONENT ANALYSIS

Signy, Trouville and Villers samples.

13 variables, 71 cases.

Eigenvalues

<p>| | | | |</p>
<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>8.55</td>
<td>1.57</td>
<td>1.22</td>
<td>.65</td>
</tr>
</tbody>
</table>

Cumulative proportions of total variance

<p>| | | | |</p>
<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>66%</td>
<td>78%</td>
<td>87%</td>
<td>92%</td>
</tr>
</tbody>
</table>

Eigenvectors

<p>| | | | |</p>
<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>2</td>
<td>3</td>
<td>4</td>
</tr>
<tr>
<td>A</td>
<td>-.33</td>
<td>-.15</td>
<td>.02</td>
</tr>
<tr>
<td>B</td>
<td>-.33</td>
<td>.01</td>
<td>.10</td>
</tr>
<tr>
<td>C</td>
<td>-.32</td>
<td>-.07</td>
<td>-.20</td>
</tr>
<tr>
<td>D</td>
<td>-.32</td>
<td>-.09</td>
<td>-.22</td>
</tr>
<tr>
<td>G</td>
<td>-.33</td>
<td>-.17</td>
<td>.05</td>
</tr>
<tr>
<td>H</td>
<td>-.28</td>
<td>-.18</td>
<td>-.13</td>
</tr>
<tr>
<td>I</td>
<td>-.29</td>
<td>.09</td>
<td>.17</td>
</tr>
<tr>
<td>J</td>
<td>-.28</td>
<td>.32</td>
<td>.30</td>
</tr>
<tr>
<td>L</td>
<td>.12</td>
<td>.50</td>
<td>-.45</td>
</tr>
<tr>
<td>M</td>
<td>-.33</td>
<td>-.01</td>
<td>.15</td>
</tr>
<tr>
<td>N1</td>
<td>.12</td>
<td>-.63</td>
<td>-.41</td>
</tr>
<tr>
<td>N2</td>
<td>-.15</td>
<td>.37</td>
<td>-.42</td>
</tr>
<tr>
<td>N4</td>
<td>-.25</td>
<td>.08</td>
<td>-.44</td>
</tr>
</tbody>
</table>

Figure 7,19. Eigenvalues and direction cosines of the first four eigenvectors for the Signy, Trouville and Villers samples. The first two eigenvectors are plotted in fig.7,18.
that the same homogeneity exists within each of the three samples. At the stage of formation of six groups each sample was split between two clusters, after which each pair of clusters was combined until the three original samples were formed. At the stage of formation of two groups the Signy and Trouville samples were combined although not without a large increase in error, again exemplifying the distinctive morphology of the Villers specimens.

To confirm the validity of using single samples of major species groups, a discriminant function analysis was performed on both the orbicular samples (Signy, Marquise) and four *N. latiporus - N. scutatus* groups (Stratton Audley, Hydrequent, Talant, Trouville) as well as the Villers sample. Groupings of samples and species emerged as in previous analyses (e.g. Fig. 7, 11).

The Villers sample (*N. micraulus*) is thus clearly distinct from *N. amplus* (Signy) as well as *N. scutatus* (Trouville).

6. Comparison of the Villers sample with previously examined species

The analysis was further extended to include the *N. elongatus* group, a group found to be distinct in earlier analyses, through the use of discriminant function analysis.

**Step 1**
Variable NL entered (NL became important when the range of samples was extended in time or morphological variety, achieved by the addition of this elongate middle Jurassic species sample).

**Step 2**
Variable B entered.

F matrix indicated that the Villers sample became highly significantly different (*P < 1%*) from all other group means. The Trouville and Signy samples also became highly significantly different.

Villers specimens classified wrongly by posterior probability; 0%
Step 5
Variables N2, L and A entered
F matrix indicated that all major groupings became highly significantly
different (P < 1%) from each other.

Step 6
Variable J added
Absence of overlap in classification of specimens between major
groupings.

Again variable M is not used in this analysis. Possibly the
increased importance of N1, itself closely governed in size by the
length of M, negates the discriminating power of M (distance of the
apical disc from the anterior of the test).

Fig. 7, 20 is a plot of a canonical variate analysis carried
out on only the representative members of each major grouping, the
pattern of discrimination being almost identical to that of all
samples. The first two canonical variables represent over 92% of
the total dispersion, a higher percentage than if all samples are
used, and therefore producing a more representative distribution of
specimens. It is seen that the elongate Oxfordian Villers sample
lies in a comparable position to its contemporaneous rounded
Trouville sample as the elongate Bathonian N. elongatus group does to its
contemporaneous rounded Signy sample. Separation is achieved by
two orthogonal vectors. The first (a shape vector) trends from top
left to bottom right, and separates elongate (top left) from rounded
forms (bottom right). The second (an age vector) separates middle
Jurassic species (top right) from upper Jurassic species (bottom
left). This second (age) vector correlates with the size of J
(length of the anal sulcus), a shorter sulcus being characteristic
of stratigraphically younger species.
Figure 7, 20. Distribution of Signy, N. elongatus group, Trouville and Villers specimens on the first two canonical axes. Group centroids indicated by large lettering.

Mean coordinates:
- Signy: 6.802, -3.369
- Trouville: 7.510, 1.103
- Villers: 1.254, 4.867
The major discriminating variables were in general the same throughout all analyses involving the Villers sample, but they assume a different degree of importance with the addition of the stratigraphically older, elongate _N. elongatus_ group. _N. micraulus_ is as distinct both subjectively and statistically from _N. elongatus_ as it is from _N. amplus_ and _N. scutatus_.

7. Classification of Villers specimen V45

Specimen V45 possesses the morphology of the _N. scutatus_ - _N. latiporus_ group of samples, and was eliminated from analysis with the Villers sample (p. 231). It was classified by discriminant function analysis within the framework of the species studied here by referring it to the group with which it bore most resemblance. The samples used in this procedure were those apparently most similar: the three _N. latiporus_ samples, the Trouville sample of _N. scutatus_, the _N. elongatus_ group, the Villers sample of _N. micraulus_ and the sample (not yet discussed) from Devecey representing _N. subquadratus_. At the end of the 'classification' procedure specimen V45 was classified 100% representative of the Stratton Audley sample of _N. latiporus_ and at no time in the procedure was it classified with samples representing other species. However, a $\chi^2$ test of the Mahalanobis distance indicated a low probability ($P < .5\%$) of the species belonging to the Stratton Audley sample of _N. latiporus_ but an even more remote probability ($P < .1\%$) of belonging to any other group. The group mean of the Stratton Audley sample was highly significantly different from all other samples representing different species, including Trouville. However as has been observed before, homeomorphy can occur between _N. latiporus_ and _N. scutatus_ but not with samples from other major groupings. Specimen V45 is therefore
very likely to be a specimen of *N. latiporus* or possibly *N. scutatus*
but certainly not *N. elongatus, N. micraulus, N. subquadratus* or any
other species so far studied outside the *N. scutatus - N. latiporus*
plexus.

8. Classification of Agassiz type specimen of *N. MICRAULUS*

The same samples and procedures were adopted for the
classification of a cast from the British Museum (Natural History)
of the Agassiz type specimen. Variables D and N3 could not be
accurately measured on the cast and were therefore omitted from the
classification. At the completion of the analysis the specimen
labelled MIC was classified as 100% representative of the Villers
sample, which was itself highly significantly different (P < 1%)
from any other sample with no overlap occurring between itself and
any other group. Furthermore a $\chi^2$ test of the Mahalanobis distance
indicated an extremely low probability (P < .01%) of the Agassiz
specimen belonging to any other group except the Villers sample
(P = .3%). This evidence suggests that the Villers sample is correctly
named *N. micraulus*.

7 G) Conclusions

Computer comparisons of these five Jurassic species indicate
that two distinct levels of groupings are present. At the first
level it is shown above that *N. woodwardii* is not easily separated
from *N. amplus*. In all multivariate comparisons *N. woodwardii* is seen
to lie very close to, and overlap with, *N. amplus* in a similar manner
to the *N. scutatus - N. latiporus* groupings. At the second level,
the four species, *N. elongatus, N. amplus, N. burgundiae* and *N. micraulus*
are distinct from each other and can be distinguished from the type
species through the use of only two measured variables. At least one of the two characters is either N1 or L. It is noted that no significance can be attached to the differences between *N.woodwardii* and *N.amplus*. More specimens are needed, and the type specimen of *N.woodwardii* should be located, before further judgements can be made on its taxonomic position.

It is evident from a comparison of results that selected samples can be used to characterise larger groupings of samples in many biometrical analyses. Accordingly, the author's Trouville shore sample can be used to define the position of all seven samples of *N.scutatus* and also the three samples of *N.latiporus* in multivariate comparisons. Similarly, the Signy sample can be used to represent both Signy and Marquise in many analyses.

*N.scutatus* is distinguished from *N.elongatus* subjectively by differences in the outline of the test, the former species being ovate and the latter elongate. In biometrical analyses however, the length of the periproct, L, its height within the sulcus, N4, and the position of the apical disc, M, are of primary discriminating importance. In *N.elongatus* variable L is highly negatively correlated with other measurements of the gross morphology of the test, whilst in *N.scutatus* there is no significant correlation between these variables. Furthermore, the periproct is consistently lower in position within the anal sulcus and the apical disc occupies a more central position within specimens of *N.elongatus* than in specimens of *N.scutatus*. Growth patterns within the two species are also very different. Reduced major axes for length with breadth, height, position of the peristome and the distance between the apical disc and the periproct are significantly different. These data support the subjective appraisal of *N.elongatus* as a narrower and flatter species.
than *N. scutatus* with the periproct in closer contact with the apical disc.

*N. elongatus* occurs with *N. latiporus* in Cornbrash strata, and comparisons of reduced major axes reveal similar differences to those found to exist between *N. elongatus* and *N. scutatus*. Although a generally larger species, the area of the periproct of *N. elongatus* is consistently smaller than in *N. latiporus*, as is the size of the peristome. This is an interesting factor in the light of evidence advanced for a grain inesting habit for *N. scutatus* and probably, therefore, for *N. latiporus* as well. It may therefore be possible to infer that within the biomicritic sediments of the Cornbrash *N. latiporus* inhabited a niche in which it inested primarily larger bioclastic fragments whilst *N. elongatus* was restricted, because of the small size of its alimentary canal, to a diet of organic rich carbonate mud.

The two species may have inhabited different but adjacent microenvironments, and only transported tests be found together. However, sympatric species of echinoids are known from both recent (Chesher, 1968) and fossil (Nichols, 1959) occurrences.

*N. amplus* is distinguished from *N. scutatus* through variables *M* and *Nl*, the positions of the periproct and apical disc on the aboral surface of the test. In *N. amplus* the apical disc occupies a central position and is also in close contact with the periproct. In *N. scutatus* the apical disc is in a slightly anterior position and well separated from the periproct. *N. amplus* is generally broader than long whilst the reverse is usually the case in *N. scutatus*. Finally, the indentation of the posterior border is deeper in *N. scutatus*, whilst reduced major axes involving measurements of the periproct, variables *L* and *I*, are also consistently different between the two species. The morphology of the periproct is, therefore, very different.
although the area of the periproctal opening is similar. Within *N. amplus* the vertical dimension of the periproctal opening is large, whilst its horizontal length along the aboral surface is small. Within *N. scutatus* the opening is generally as high as it is long. Similarity in the area of the periproctal opening between the two species is matched by a similarity in grain size of the enclosing sediment.

Due to the poor preservation of the type material of *N. burgundiae*, only a few preliminary conclusions can be made on differences with the type species. *N. burgundiae* can be distinguished from *N. scutatus* solely on the distance between the apical disc and the periproct, this distance being about 30% of the total length in the former species and about 20% in the latter. The apical disc is in a similar position on both species, being slightly anterior to centre. Therefore, the combination of this feature and the distance between the apical disc and the periproct results in the anal sulcus being shorter in *N. burgundiae* than in *N. scutatus*. The indentation at the posterior border is also much smaller in *N. burgundiae*.

Figure 7.13 shows an arrangement of samples representing all these six species (*N. scutatus*, *N. latiporus*, *N. amplus*, *N. woodwardii*, *N. elongatus*, *N. burgundiae*). One vector, composed of *N1* and a small component of *M* in inverse proportions, trends from the top left of the graph to the bottom right. A second vector, along the Y axis, can also be identified. This is composed of *N2* and a small component of *B* in an inverse relationship.

*N. micraulus* can be distinguished from *N. scutatus* through variables *L*, *N1* and *B*. *N. micraulus* is more elongate in outline and the periproct is smaller and lies in a more posterior position than in *N. scutatus*. In the former species the overall area of the periproct is small, its length on the aboral surface being particularly short.
Again, there may be a correlation between grain size and periproct size as the sediment at Villers is slightly finer grained than at Trouville.

Principal component analysis reveals that complete separation between the two species is achieved along a vector composed mainly of L, J, and an inverse proportion of Nl. Again, the size and position of the periproct is of primary discriminating importance. Reduced major axes involving variables L and Nl are also very different between the two species.

Canonical plots of *N. scutatus*, *N. amplus* and *N. elongatus* place the three species along two orthogonal vectors that can be interpreted as representing age and elongation of samples respectively. The age vector, represented mainly by Nl and M, is displaced along the X axis, and the elongation vector, represented mainly by B and N4, is displaced along the Y axis. Supporting evidence for the composition of such vectors is provided by *N. micraulus*. It can be predicted that as *N. micraulus* is an elongate species of a similar age to *N. scutatus*, specimens should plot in a position between *N. scutatus* and *N. elongatus* at the extremities of the two vectors. Fig. 7 shows that this is the case. The two vectors are almost orthogonal, indicating that elongation of species occurs independent of age. Furthermore, the age component is now more closely correlated with J and M, and this vector bisects two other, almost orthogonal, vectors. The first is composed of I, C, and an inverse proportion of Nl orientated along the X axis. The second is composed of L along the Y axis.

This illustrates that Nl (the distance between periproct and apical disc) does not increase consistently with decreasing stratigraphic age, although there is an overall tendency for it to increase and L (the length of the periproct) to decrease up the
stratigraphic column. The only feature which consistently decreases up the stratigraphic column is J, the length of the anal sulcus.
CHAPTER 8 - BIOMETRICS OF SOME CRETACEOUS NUCLEOLITIDS

8 A) Introduction

Lambert & Thiéry (1921) list 31 species of Nucleolites from the Cretaceous. The genus became extinct during this period, although its descendants flourished in the Cainozoic.

Of the Cretaceous species, most occur outside N.W. Europe. Perhaps only 12 are European. Most were defined during the 19th century, and were obtained from localities not precisely recorded or from localities where good rock exposures no longer exist. None have been recorded from Britain. Numerous localities in France and Switzerland were examined by the author but only one yielded Nucleolites, of the single species N. subquadratus.

According to Kier (1962, 1966) the last known species of Nucleolites is N. rotundus from the Cenomanian of North Africa. An analysis is included here of a museum collection of this species because of its phylogenetic significance.

Fig. 8.1 is a summary of analyses carried out in this chapter.

8 B) NUCLEOLITES SUBQUADRATUS

1. Introduction

This lower Cretaceous species is characterised by specimens with a large, low periprost; large, sometimes oblique peristome; and anterior apical system. It is represented by a sample of 25 specimens from the Neocomian of Devecey, Doubs, France. The specimens are from a hard, white bioclastic limestone from which it is difficult to extract specimens without causing damage to them. For this reason all measurements could be taken on only 14 specimens.
<table>
<thead>
<tr>
<th>Sample</th>
<th>Comparison sample</th>
<th>Page</th>
<th>Var.</th>
<th>Spec</th>
<th>Technique</th>
<th>Sig. of diff.</th>
<th>Imp. variables</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Devecey</td>
<td>(N. subquadratus)</td>
<td>258</td>
<td>15</td>
<td>14</td>
<td>P.C.A.</td>
<td>BA 25 separated along 3rd vector</td>
<td>I, J, L, N4</td>
</tr>
<tr>
<td>2. Devecey</td>
<td>Trouville (N. scutatus)</td>
<td>258</td>
<td>15</td>
<td>32</td>
<td>S.D.F.</td>
<td>P&lt;1%</td>
<td>N4, N1, J</td>
</tr>
<tr>
<td></td>
<td></td>
<td>259</td>
<td>14</td>
<td>32</td>
<td>P.C.A.</td>
<td>Separation along 2nd vector</td>
<td>N1, I, N4</td>
</tr>
<tr>
<td></td>
<td></td>
<td>259</td>
<td>15</td>
<td>32</td>
<td>H.C.</td>
<td>Final 2 groups = original groups</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>262</td>
<td>15</td>
<td>227</td>
<td>R.M.A.</td>
<td>P&lt;1% between 9 pairs of slopes</td>
<td>I</td>
</tr>
<tr>
<td>3. Devecey</td>
<td>Villers (N. micraulus)</td>
<td>262</td>
<td>15</td>
<td>37</td>
<td>S.D.F.</td>
<td>P&lt;1%</td>
<td>L, D, J</td>
</tr>
<tr>
<td></td>
<td></td>
<td>264</td>
<td>15</td>
<td>37</td>
<td>H.C.</td>
<td>Final 2 groups = original groups</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>264</td>
<td>15</td>
<td>69</td>
<td>R.M.A.</td>
<td>P&lt;1% between 10 pairs of slopes</td>
<td>N4</td>
</tr>
<tr>
<td>4. Devecey</td>
<td>Trouville (N. scutatus), Villers (N. micraulus)</td>
<td>264</td>
<td>15</td>
<td>50</td>
<td>S.D.F.</td>
<td>P&lt;1%</td>
<td>L, N4, N1</td>
</tr>
<tr>
<td></td>
<td>Villers (N. micraulus)</td>
<td>265</td>
<td>14</td>
<td>50</td>
<td>P.C.A.</td>
<td>Separation along 2nd vector</td>
<td>L, J, N1</td>
</tr>
<tr>
<td>5. Devecey</td>
<td>Trouville (N. scutatus, Villers (N. micraulus), Signy (N. amplius)</td>
<td>267</td>
<td>14</td>
<td>84</td>
<td>H.C.</td>
<td>Final 4 groups = original groups</td>
<td>1st size 2nd N1</td>
</tr>
<tr>
<td></td>
<td></td>
<td>267</td>
<td>13</td>
<td>84</td>
<td>P.C.A.</td>
<td>Separation on plot of 1, 2 vectors</td>
<td></td>
</tr>
<tr>
<td>6. Devecey</td>
<td>As above + N. elongatus group</td>
<td>271</td>
<td>14</td>
<td>88</td>
<td>S.D.F.</td>
<td>P&lt;1%</td>
<td>J, L, N4, N1, B, A</td>
</tr>
</tbody>
</table>

Figure 8.1 Summary of important analyses run in Chapter 8. See fig. 5.1 for key.
<table>
<thead>
<tr>
<th>Sample</th>
<th>Comparison sample</th>
<th>Page</th>
<th>Var.</th>
<th>Spec.</th>
<th>Technique</th>
<th>Sig. of diff.</th>
<th>Imp. variables</th>
</tr>
</thead>
<tbody>
<tr>
<td>7. Agassiz type</td>
<td>( N_{\text{elliptus}} ) group, Trouville ( N_{\text{scutatus}} ), Villers, ( N_{\text{micranthus}} ), Devececy, ( N_{\text{subquadratus}} ), Bou Saada ( N_{\text{rotundus}} ).</td>
<td>272</td>
<td>10</td>
<td>64</td>
<td>Class</td>
<td>99% Devececy 1% Bou Saada</td>
<td></td>
</tr>
<tr>
<td>8. Bou Saada ( N_{\text{rotundus}} )</td>
<td>Trouville ( N_{\text{scutatus}} )</td>
<td>274</td>
<td>15</td>
<td>22</td>
<td>S.D.F.</td>
<td>P&lt;1%</td>
<td>N1,D,H,B</td>
</tr>
<tr>
<td>9. Bou Saada ( N_{\text{rotundus}} )</td>
<td>Trouville ( N_{\text{scutatus}} ), Villers ( N_{\text{micranthus}} ), Devececy ( N_{\text{subquadratus}} )</td>
<td>275</td>
<td>15</td>
<td>59</td>
<td>S.D.F.</td>
<td>P&lt;1%</td>
<td>L,N1,D,T,J,B,G,E</td>
</tr>
<tr>
<td></td>
<td></td>
<td>276</td>
<td>15</td>
<td>59</td>
<td>H.C.</td>
<td>Clustering not into original groups</td>
<td></td>
</tr>
<tr>
<td>10. Bou Saada ( N_{\text{rotundus}} )</td>
<td>Signy ( N_{\text{amplus}} ), ( N_{\text{elliptus}} ) group, Trouville ( N_{\text{scutatus}} ), Villers ( N_{\text{micranthus}} ), Devececy ( N_{\text{subquadratus}} )</td>
<td>278</td>
<td>15</td>
<td>73</td>
<td>S.D.F.</td>
<td>P&lt;1%</td>
<td>J,L,N4,N1,E,N2,B,M</td>
</tr>
</tbody>
</table>

Figure 8.1 continued.
A cast, in the British Museum (Natural History) of the Agassiz type specimen was also used in the analysis.

2. Analysis of the Devecey sample

The sample contains one specimen, BA 25, which is well rounded and has a shorter sulcus and smaller periproct than typical N. subquadratus specimens. Moreover, the smoothly inflated adoral surface is in sharp contrast to the Agassiz original description, in which he specifically comments on the sharply angled posterior surface.

A principal component analysis of the sample revealed that specimen BA 25 was well separated from the other Devecey specimens along the axis of the third component, this vector being composed of I, J, L and an inverse proportion of N4, all variables concerned with the size and position of the periproct. The specimen has a small periproct (I, L) and short sulcus (J) but the periproct lies some distance from the adoral surface (N4), explaining the inverse value of N4 in this vector. The specimen was therefore eliminated from further analyses involving this sample. On general morphology, specimen BA 25 can be ascribed to the genus Phyllobrissus.

3. Comparison between the Devecey and Trouville samples

The results of a discriminant function analysis between the Devecey and Trouville samples showed a sharp distinction at about the same degree of difference as between the Trouville and Villers samples (p. 232).

Step 3

Variables N4, N1 and J entered

F matrix indicated that both group means became highly significantly different (P < 1%) from each other

Specimens classified wrongly by posterior probability: 0%
Step 13 (final)

Variables not entered; C and G

U-statistic = .15 (Significance of inequality of group means; P < .1%)

Specimens classified as 100% representative of their own group
(using posterior probability); 100%

Specimens with a low probability (P < .1%) of belonging to the
wrong group (using $\chi^2$ tests of D^2); 100%

Variable N4 had not previously been encountered as a primary
discriminating variable.

A clear distinction between the two samples was also made
by reference to the first two vectors of a principal component
analysis. The first component was the usual size/shape vector
contributing 66% of variability but excluding I and J, variables that
usually contribute to this element. The samples, however, were distinguished
along the second vector, contributing a further 15% and being composed of
I, N1 and an inverse proportion of N4. The two vectors thus plot growth
positions of specimens from increases in I and N1 and decreases in N4
against specimen size. The second vector tabulates greater scores for the
Deveccey sample than for the Trouville sample for a given specimen size,
(fig. 8, 2). During growth within the Deveccey sample the periproct
increases in size but in so doing becomes further removed from the
apical system and lower in position. The Trouville specimens in
contrast show only limited changes in the relative magnitude of these
three variables with increased size. Most Trouville specimens
therefore lie in a line parallel to the axis of the first component.
The analysis does show, however, an increasing similarity of form
between the smaller specimens of the two samples. Fig. 8, 3 tabulates
eigenvalues and direction cosines for the first four principal components.

A hierarchical grouping was able to cluster specimens into
Figure 8.2. Distribution of Trouville (*N. scutatus*) and Dececy (*N. subquadaratus*) specimens along Principal Components 1 and 2 based on a 14 variable analysis. Components 1 and 2 account for 81% of total variation.
**PRINCIPAL COMPONENT ANALYSIS**

Trouville and Devecey samples

14 variables, 32 cases.

**Eigenvalues**

<table>
<thead>
<tr>
<th></th>
<th>9.19</th>
<th>2.19</th>
<th>1.01</th>
<th>.86</th>
</tr>
</thead>
</table>

**Cumulative proportions of total variance**

<table>
<thead>
<tr>
<th></th>
<th>66%</th>
<th>81%</th>
<th>88%</th>
<th>95%</th>
</tr>
</thead>
</table>

**Eigenvectors**

<table>
<thead>
<tr>
<th></th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>.31</td>
<td>-.17</td>
<td>.17</td>
<td>.10</td>
</tr>
<tr>
<td>B</td>
<td>.32</td>
<td>.09</td>
<td>.02</td>
<td>-.00</td>
</tr>
<tr>
<td>C</td>
<td>.31</td>
<td>.08</td>
<td>-.17</td>
<td>-.20</td>
</tr>
<tr>
<td>D</td>
<td>.31</td>
<td>.08</td>
<td>-.19</td>
<td>-.22</td>
</tr>
<tr>
<td>E</td>
<td>.32</td>
<td>-.03</td>
<td>-.02</td>
<td>-.05</td>
</tr>
<tr>
<td>G</td>
<td>.30</td>
<td>-.20</td>
<td>.15</td>
<td>.15</td>
</tr>
<tr>
<td>H</td>
<td>.28</td>
<td>-.14</td>
<td>.30</td>
<td>.11</td>
</tr>
<tr>
<td>I</td>
<td>.19</td>
<td>-.45</td>
<td>-.34</td>
<td>-.07</td>
</tr>
<tr>
<td>J</td>
<td>.20</td>
<td>.17</td>
<td>.25</td>
<td>.71</td>
</tr>
<tr>
<td>L</td>
<td>.17</td>
<td>.15</td>
<td>-.73</td>
<td>.32</td>
</tr>
<tr>
<td>M</td>
<td>.31</td>
<td>.10</td>
<td>.06</td>
<td>.05</td>
</tr>
<tr>
<td>N1</td>
<td>.14</td>
<td>-.58</td>
<td>.06</td>
<td>-.18</td>
</tr>
<tr>
<td>N2</td>
<td>.22</td>
<td>.32</td>
<td>.26</td>
<td>-.44</td>
</tr>
<tr>
<td>N4</td>
<td>.24</td>
<td>.42</td>
<td>-.03</td>
<td>-.18</td>
</tr>
</tbody>
</table>

Figure 8.3. Eigenvalues and direction cosines of the first four eigenvectors for the Trouville and Devecey samples. The first two eigenvectors are plotted in fig. 8.2.
the two samples with no overlap or wrongly grouped specimens.

Bivariate analyses of the two samples revealed a degree of
difference at about the same level as between those of Trouville
(Oxfordian) and Signy(Bathonian) but less than between Trouville
and Villers (Oxfordian). A comparison of reduced major axes for A
with all other variables showed three slopes, A with I, L and N2,
to be highly significantly different (P < 1%) and a further three,
A with B, E and N3, to be probably significantly different (1% < P < 5%).

Both discriminant functions and principal components analysis
picked out N4 as an important discriminating variable. This was
borne out in bivariate analyses (Fig. 8,4). Variable L was not isolated
as an important discriminating variable and consequently fewer slopes
were shown to be different in comparison with some earlier analyses,
e.g. Trouville and Signy (p.206) and Trouville and Villers (p.238).
However, the other measure of the size of the periproct, I, was isolated
as an important discriminating character by principal component
analysis. Bivariate analyses supported this finding (Fig. 8,4).

4. Comparison between the Devecey and Villers samples.

Previous analyses showed that the degree of difference between
the Devecey and Trouville, and Villers and Trouville samples was at
about the same level. The Devecey sample was therefore compared
to that of Villers to see if it was similarly different or alternatively
another quite distinct group.

The results of a discriminant function analysis are:-

Step 3
Variables L, D and J entered

U-statistic = .17 (Significance of the inequality of group means;
P < 1%)
A) Variable A with all other variables.

<table>
<thead>
<tr>
<th></th>
<th>A.</th>
<th>B.</th>
<th>C.</th>
<th>D.</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>3</td>
<td>3</td>
<td>8</td>
<td>0</td>
</tr>
</tbody>
</table>

B) Variable L with all other variables.

<table>
<thead>
<tr>
<th></th>
<th>A.</th>
<th>B.</th>
<th>C.</th>
<th>D.</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>5</td>
<td>5</td>
<td>4</td>
<td>0</td>
</tr>
</tbody>
</table>

C) Variable I with all other variables.

<table>
<thead>
<tr>
<th></th>
<th>A.</th>
<th>B.</th>
<th>C.</th>
<th>D.</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>9</td>
<td>2</td>
<td>3</td>
<td>1</td>
</tr>
</tbody>
</table>

D) Variable N4 with all other variables.

<table>
<thead>
<tr>
<th></th>
<th>A.</th>
<th>B.</th>
<th>C.</th>
<th>D.</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>7</td>
<td>2</td>
<td>5</td>
<td>0</td>
</tr>
</tbody>
</table>

Figure 8.4. Comparison of reduced major axes between the Trouville and Devecey samples. Key as for fig. 5.10.
Specimens classified wrongly by posterior probability; 0%

Measurements of the height, either C or D, had not previously found to be of value in discriminating between groups. The relationship between these two samples is therefore unlike their relationship to the Trouville sample.

A hierarchical analysis also showed the samples to be quite distinct, every specimen clustered into its original sample at the stage of formation of two groups.

A comparison of reduced major axes between the Villers and Deveccey samples revealed a degree of difference similar to that found between Trouville and Deveccey. For A and all other variables only two slopes were at most probably significantly different in angle, \(1\% < P < 5\%)\) and two slopes not even significantly different in angle or separation \(P > 5\%). Although this indicated a close similarity between the two groups, reduced major axes for the main discriminating variables (e.g. I, J, L, N1 and N4) showed a degree of difference similar to the results produced in the Deveccey - Trouville comparison.

5. Comparison between Deveccey, Trouville and Villers samples

The Deveccey, Villers and Trouville samples were next grouped in a single discriminant function analysis. Using the full 15 variables and the Trouville sample of 19 specimens the analysis produced results that were similar to, and a combination of, the two previous analyses.

Step 1
Variable L entered
No overlap in classification between Trouville and Villers samples

Step 3
Variables N4 and N1 entered
F matrix indicated that all group means became highly significantly
different ($P < 1\%$) from each other.

Trouville specimens classified wrongly by posterior probability; 0%

**Step 6**

Variable C, J, and B added (C is equivalent to D in the previous analysis)

Specimens classified wrongly by posterior probability; 0%

**Step 14 (final)**

Variables not entered; A, D, and M

Specimens classified as 100% representative of their own group (using posterior probability); 100%

The F matrix and group probability table indicated, during the stepwise procedure, that the Villers and Devecey samples lay closer together than to the Trouville sample. This is highlighted in a plot of the first two canonical variates (fig.8,5).

A principal component analysis of the three groups selected variables concerned with the horizontal size and position of the periproct (L, J, and inversely N1) as the second vector and variables of the vertical size and position of the periproct (I and inversely N4) as the third vector. These two components contributed 18% and 10% of total variability respectively whilst the important size/shape component accounted for a further 60%.

The three samples were separated from each other along the vector of the second component, Trouville specimens having on average large values of J and L to small values of N1, whereas Villers specimens were distinguished by short J and L to large N1. As noted previously, J, and N1 must vary in inverse proportions given a stable value for variable M, the position of the apical disc. The Devecey specimens lay in an intermediate position between the two extreme cases along this vector. Component three, on the other hand, tended to isolate the Devecey sample from an admixture of Villers and Trouville specimens.
Figure 8.5. Distribution of Villers, Trouville and Devecey specimens on the first two canonical axes. Group centroids indicated by large lettering. Mean coordinates:
Trouville  -6.172  .031
Villers     3.133  -2.181
Devecey    3.238   3.983
specimens. This component characterises typical Devecy specimens, which have a large but low periproct. A plot of the second and third components, which eliminates any overall size variation between the samples shows how clearly the groups are distinguished (Fig. 8, 6). Fig. 8, 7 tabulates eigenvalues and direction cosines for the first four principal components.

6. Comparison between Devecy, Villers, Trouville and Signy

The four samples from Signy, Trouville, Villers and Devecy were tested one to the other for interspecific variation by hierarchical grouping. Previously it was seen that the Signy and Trouville specimens could be grouped before addition of the Villers specimens (p. 245) indicating a closer link between the former pair of samples.

During clustering the Devecy sample showed the same degree of homogeneity exhibited by the three other samples. At the stage of formation of eight groups the specimens in each sample were split between two groups. Pairs of groups were then combined until, at the stage of formation of four groups, all specimens were clustered into their original samples. From this stage obviously only samples themselves can be combined, earliest combinations indicating closer similarity. It is seen that Villers and Devecy are joined at the stage of formation of three groups whilst Signy and Trouville are not joined until the penultimate stage, indicating a closer resemblance in morphology between the former pair of samples (fig. 8, 8).

With the introduction of Signy the vectors of a principal component analysis took on a different composition to the earlier analysis. The principal component, now 65% of the variability, included variable J again, whilst the second component was composed almost entirely of Nl and contributed a further 12%. A plot of these
Figure 8,6. Distribution of Trouville (N. scutatus), Villers (N. micraulus) and Devecey (N. subquadraatus) specimens along Principal Components 2 and 3 based on a 14 variable analysis. Components 2 and 3 account for 28% of total variation. The ordinate is Component 2, the abscissa is Component 3.
PRINCIPAL COMPONENT ANALYSIS

Trouville, Villers and Devecey samples.
14 variables, 56 cases.

Eigenvalues

<p>| | | | |</p>
<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>8.36</td>
<td>2.61</td>
<td>1.33</td>
<td>.61</td>
</tr>
</tbody>
</table>

Cumulative proportions of total variance

<p>| | | | |</p>
<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>60%</td>
<td>78%</td>
<td>88%</td>
<td>92%</td>
</tr>
</tbody>
</table>

Eigenvectors

<table>
<thead>
<tr>
<th></th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>-.33</td>
<td>-.08</td>
<td>-.14</td>
<td>-.21</td>
</tr>
<tr>
<td>B</td>
<td>-.34</td>
<td>.04</td>
<td>.05</td>
<td>-.06</td>
</tr>
<tr>
<td>C</td>
<td>-.32</td>
<td>.01</td>
<td>.16</td>
<td>.34</td>
</tr>
<tr>
<td>D</td>
<td>-.32</td>
<td>-.00</td>
<td>.17</td>
<td>.36</td>
</tr>
<tr>
<td>E</td>
<td>-.33</td>
<td>.00</td>
<td>-.04</td>
<td>-.00</td>
</tr>
<tr>
<td>G</td>
<td>-.33</td>
<td>-.11</td>
<td>-.17</td>
<td>-.20</td>
</tr>
<tr>
<td>H</td>
<td>-.29</td>
<td>-.03</td>
<td>-.18</td>
<td>-.39</td>
</tr>
<tr>
<td>I</td>
<td>-.19</td>
<td>.09</td>
<td>-.63</td>
<td>.43</td>
</tr>
<tr>
<td>J</td>
<td>-.05</td>
<td>.53</td>
<td>-.21</td>
<td>-.38</td>
</tr>
<tr>
<td>L</td>
<td>-.01</td>
<td>.56</td>
<td>-.22</td>
<td>.32</td>
</tr>
<tr>
<td>M</td>
<td>-.32</td>
<td>-.01</td>
<td>.10</td>
<td>-.19</td>
</tr>
<tr>
<td>N1</td>
<td>-.18</td>
<td>-.49</td>
<td>-.18</td>
<td>.10</td>
</tr>
<tr>
<td>N2</td>
<td>-.17</td>
<td>.34</td>
<td>.26</td>
<td>-.12</td>
</tr>
<tr>
<td>N4</td>
<td>-.25</td>
<td>.14</td>
<td>.52</td>
<td>.17</td>
</tr>
</tbody>
</table>

Figure 8,7. Eigenvalues and direction cosines of the first four eigenvectors for the Trouville, Villers and Devecey samples. The second and third eigenvectors are plotted in fig.8,6.
Figure 8.8. Dendrogram of the clustering routine of the Signy (O), Trouville (X), Villers (V), and Devecey (BA) specimens.
two components showed two growth lines, formed respectively by the Signy - Trouville and Villers - Devecey specimens and highlighted the relationships revealed in the hierarchical clustering. The graph showed a similarity in growth within the two groupings, the value of N1 increasing much more rapidly with size in the Villers - Devecey samples.

Thus, both hierarchical clustering and principal components analysis indicate that the two Oxfordian species (Trouville and Villers) are very different from each other, and have separate morphological affinities with Bathonian and Neocomian species respectively. Again the smaller specimens from within each grouping were most similar to the other group.

7. Comparison of Devecey and other nucleolitid samples

The final multivariate analysis is the discriminant function analysis of senior members of the major groupings of earlier analysis, i.e., Signy, the N. elongatus group, Trouville, Villers, and Devecey.

Step 3
Variables J, L and N4 entered
F matrix indicated that the Signy and Villers samples became highly significantly different (P < 1%) from all other group means except the N. elongatus group.
Devecey specimens classified wrongly by posterior probability; 0%

Step 6
Variables N1, B and A added
All group means highly significantly different (P < 1%)
Specimens classified wrongly by posterior probability; 0%

Step 11 (final)
Variables not entered; C, G and M
U-statistic = .0005 (Significance of inequality of group means; P < .1%).
Specimens with a low probability (P < 5%) of belonging to a wrong group (using $X^2$ tests of $\chi^2$); 97%. Three Villers specimens were not a significant distance (P > 5%) from the Devecey group mean. Specimens classified as 100% representative of their own group (using posterior probability); Signy, 100%; N. elongatus group, 100%; Trouville, 100%; Villers 88%; Devecey, 77%.

The F matrix and the group probability table indicated that the Villers and the Devecey samples lay relatively close to each other. This close proximity is also seen in a plot of the first two canonical variates (fig. 8, 9).

8. Classification of Agassiz type specimen of N. SUBQUADRATUS

The following samples were used to classify the cast of Agassiz type specimen; N. elongatus group, the Trouville sample of N. scutatus, the Villers sample of N. micraulus, the Devecey sample of N. subquadratus and the Bou Saada sample (dealt with in the following section) of N. rotundus. Variables of the height of the apical disc and of the periproct (D, I, L, N3 and N4) could not be measured on the cast and were therefore omitted from the classificatory procedure. The type specimen was classified with the Devecey sample throughout every step of the program and at the completion of the analysis had a posterior probability of Devecey 99%, Bou Saada 1%. Every group was highly significantly different (P < 1%) from every other group with very little overlap between groups. A $X^2$ test of the Mahalanobis distance of the cast from each group mean showed a low probability (P < 5%) of it belonging to any group except the Devecey sample (P > 20%). This evidence suggests that the Devecey sample is correctly named N. subquadratus.
Figure 8,9. Distribution of Signy, *N. elongatus* group, Trouville, Villers and Debecay specimens on the first two canonical axes. Group centroids indicated by large lettering. Mean coordinates;
Signy    7.717  .767
*N. elongatus* group    1.642  2.951
Trouville   .232  -3.334
Villers   -5.927  1.818
Debecay  -6.519  -1.042
RC) NUCLEOLITES ROTUNDUS

1. Introduction

This sample, from the Cenomanian of North Africa, represents a species considered by Kier (1962) to be the last Nucleolites. The sample is however, small. The three specimens used are from the Lambert Collection, Paris. Specimen CE1 is that figured by Kier (1962, text fig. 41, pl. 7, fig. 7). This, and specimens CE2 are from the same box in the Collection, labelled Bou Saada, Algeria. Specimen CE3 is from a separate box but similarly labelled.

The sample is in good condition. The full fifteen measurements could be taken on all specimens and therefore some preliminary analyses are carried out on the group. The sample was compared first with the genotype, and subsequently other Nucleolites species.

2. Comparison between Trouville and Bou Saada

A discriminant function analysis was used to demonstrate a clear cut distinction between the Trouville and Bou Saada samples.

Step 2
Variables N1 and D entered
Specimens classified wrongly by posterior probability; 0%

Step 4
Variables H and B added
F matrix indicated a highly significant difference (P < 1%) between group means.

Step 11 (final)
Final variable to be entered; L
Variables not entered; A, C, J and N3
U-statistic = .08 (Significance of inequality of group means; P < .1%)
Specimens with a low probability \( P < .01\% \) of belonging to the opposing group (using \( X^2 \) tests of \( D^2 \)); 100%

Variables such as \( L \) and \( J \), previously found to be important, were of little or no value in distinguishing between groups in this analysis.

3. Comparison between Cretaceous and Upper Jurassic nucleolitid samples

The analysis was extended to include the other Upper Jurassic and Lower Cretaceous samples.

Discriminant function analysis was carried out between the Trouville, Villers, Devecey and Bou Saada samples produced similar primary discriminating variables to earlier analyses. Due to the similarity of form between the latter three samples, eight variables were needed in order to discriminate fully between the four groups.

Step 3

Variables \( L, N_1 \) and \( D \) entered.

F matrix indicated that the Trouville samples became at least probably significantly different \( (1\% < P < 5\%) \) from all other group means.

Trouville and Villers specimens classified wrongly by posterior probability; 0%.

Step 4

Variable \( I \) entered.

Villers and Devecey group means become highly significantly different \( (P < 1\%) \).

Devecey specimens classified wrongly; 0%.

Step 5

Variable \( J \) entered.

F matrix indicated that all group means (except between Devecey and
Bou Saada) were highly significantly different (P < 1%)

**Step 7**
Variables B and G entered
All group means became highly significantly different (P < 1%)

**Step 8**
Variable E added
Specimens classified wrongly by posterior probability; 0%

**Step 12 (final)**
Variable not entered; A, C and M

U-statistic = .003 (Significance of inequality of group means; P < .1%)

Specimens classified as 100% representative of their own group
(using posterior probability); 98%. Specimen CE 2 from Bou Saada
has probability figures of Bou Saada 81%, Villers 19%.
Specimens with a low probability (P < 5%) of belonging to a wrong
group (using \( \chi^2 \) tests of \( D^2 \)); 98%. Specimen CE 2 did not lie a
significant distance (P > 5%) from either the Bou Saada or Villers
groups.

The probability table and \( D^2 \) indicated that the Bou Saada
sample lay morphologically closer to Villers than the Deveceey
sample (see above). This is also indicated in the matrix and
portrayed in the canonical plot (fig. 8, 10).

A hierarchical grouping of the same samples revealed that
specimen CE 2 was again more easily clustered with the Villers sample,
and was combined with the Villers specimen V 9 at an early stage.
Specimens CE 1 and CE 3 on the other hand were grouped with Deveceey
specimens. The Bou Saada sample does not show, therefore, the homogeneity
of other samples, a feature which may be the result of using museum
specimens.
Figure 8,10. Distribution of Trouville, Villers, Devecey and Bou Saada specimens on the first two canonical axes. Group centroids indicated by large lettering. Mean coordinates; Trouville 6.282 .064 Villers -3.101 -2.178 Devecey -3.368 3.386 Bou Saada -.383 .251
Reduced major axes were not constructed for the Bou Saada sample as the three specimens are unlikely to have been drawn from the same population. Such groups have previously been found (p.201) to produce data unreliable for comparison with other samples.

4. Comparison between all Cretaceous and Jurassic nucleolitid samples

The Bou Saada sample, when incorporated into a discriminant function analysis of all senior members of the major groupings and using the full 15 measurements, was seen to occupy a position close to the other Cretaceous sample, from Devecey.

Step 5
Variables J, L, N4, N1 and E entered
F matrix indicated that all group means were at least probably significantly different (1% < P < 5%) from each other.
Signy, N. elongatus group, Trouville and Villers specimens classified wrongly by posterior probability; 0%

Step 8
Variables N2, B and M added
All group means became highly significantly different (P < 1%)
Specimens classified wrongly by posterior probability; 0%

Step 12
Variables not entered; A, D and G
U-statistic = .0002 (Significance of inequality of group means; P < .1%)
All specimens are 100% representative of their own group (using posterior probability) except Devecey specimen BA 15 (Devecey 98%, Bou Saada 2%) and Bou Saada specimen CE 2 (Bou Saada 65%, Villers 35%).

Clearly, therefore, there is not the hard and fast distinction in morphology between the Bou Saada, Devecey and Villers samples.
as there is between the Trouville, Signy and the *N. elongatus* group.

3 D) Conclusions

Both *N. subquadratus* and *N. rotundus* are statistically quite different from the genotype, *N. scutatus*, at about the same level of difference from it as *N. amplus* and *N. micraulus*. Only a small number of variables are needed to define these differences and all specimens are characteristic of their own group. There is no overlap with the type in any discriminant function analyses. *N. subquadratus* is therefore a distinct species at the 'second level' of grouping as outlined on p.249. *N. rotundus* often appears distinct but may overlap to a small extent with either *N. subquadratus* or *N. micraulus*. This, again, may be a function of small sample size and the use of museum specimens.

*N. subquadratus* can be subjectively distinguished from *N. scutatus* as being more elongate, having a sharper domed aboral surface and a generally more streamlined appearance. In detail, however, multivariate analyses pick out *N4, N1* and *J* to be of primary discriminating importance. The distance between the apical disc and the periproct (*N1*) is large in *N. subquadratus* and the length of the anal sulcus (*J*) is correspondingly small. The position of the periproct within the anal sulcus (*N4*) is also much lower in *N. subquadratus*. The greatest width of the specimen, *B*, and the height of the periproct, *I*, are also important discriminating variables. Reduced major axes involving *N4* and *I* are consistently different between the two species.

*N. subquadratus* was equally different in comparisons with *N. micraulus*, but is distinguished on separate criteria. Here the morphology of the periproct, *L* and *I*, the length of the anal sulcus, *J*,
and the apical height, $D$, are of primary discriminating importance. $N_l$ and $N_4$ are not important in this analysis and, as expected, a combination of most of the above variables is used to distinguish between $N_{subquadratus}$, $N_{scutatus}$, and $N_{micraulus}$ in both discriminant functions and principal components analyses.

The earlier interpretation of canonical plots (p. 253) is further confirmed by the positioning of the $N_{subquadratus}$ sample. It can be predicted that this stratigraphically young, elongate species will be expected to plot at the extremities of two vectors characterising these traits. Figure 8, 9 shows this to be the case: a vector representing decreasing stratigraphic age plotting from top right to bottom left of the figure and a vector representing increasing test elongation from bottom right to top left. The $N_{subquadratus}$ group plots beyond the Villers and Trouville samples along the 'age' vector to the bottom left of the graph, (corresponding with its young age) and with the Villers and $N_{elongatus}$ samples along the orthogonal 'elongation' vector. The 'age' vector corresponds more closely with $M$ than $N_l$. Two other, orthogonal, vectors composed of $N_l$ and $L$, orientated parallel with the $X$ and $Y$ axes respectively, can still be recognised.

$N_{rotundus}$ is represented by three museum specimens only and, therefore, only a few preliminary conclusions can be made. It is easily distinguished from $N_{scutatus}$ through variables $N_l, D, H$ and $B$, being a large nucleolitid with the periproct situated in a posterior position.

Comparisons with all other species studied show $N_{rotundus}$ to be closely associated with $N_{micraulus}$ and $N_{subquadratus}$ and to be well separated from $N_{scutatus}$, e.g., fig. 8, 10. In some analyses overlap occurs with $N_{micraulus}$, but this may be due to the use of
a museum collection rather than a naturally occurring sample.

Nevertheless, in analyses involving all the important species studied, the samples can still be considered to be distributed with respect to stratigraphic age and test elongation in canonical plots. Therefore, the Upper Cretaceous, elongate *N. rotundus* lies very close to the Lower Cretaceous, elongate *N. subquadratus*, although the distribution of groups is not as clear as in the previous plots. Stratigraphic age is now more closely correlated with increases in M and a small weighting of NL, whilst the two vectors lying parallel to the X and Y axes can be interpreted as being composed of J and L respectively.
CHAPTER 9 - BIOMETRICS OF APATOPYGUS RECENS

9 A) Introduction

This species, the only supposed living descendant of *Nucleolites* (Kier, 1962), is represented by two samples from the seas around New Zealand. One sample, from the collection of the Department of Zoology, British Museum (Natural History), is of 18 specimens all, except four, having the spines intact and the peristome and periproct covered by a membrane of small plates. The label gives as locality Golden Bay, Nelson, South Island. The other sample, given to the author by Dr. D. Pawson, is of 23 much larger specimens from Wellington Harbour, North Island. All specimens are covered in spines and have the peristomal and periproctal membranes intact. The two samples are from localities 120 km apart.

The species is typically elongate with a large peristome and periproct and anterior apical system. Variable I was found to have unacceptable errors of measurement and was omitted from all analyses involving the New Zealand specimens. Variable N4 could not be measured on any specimen with the periproctal membrane intact.

Fig. 9.1 is a summary of analyses carried out in this chapter.

9 B) Analysis of the two A.RECENS samples

The two samples of *A. recens* can be compared in a similar manner to earlier analyses involving fossil species.

A stepwise discriminant function analysis, omitting variables H, I, and N4, in order to retain as large a sample as possible, produced very similar results to comparisons between samples of *N. scutatus* (Chapter 5)

**Step 5**

Variables J, N3, N1, C and N2 entered
<table>
<thead>
<tr>
<th>Sample</th>
<th>Comparison sample</th>
<th>Page</th>
<th>Var</th>
<th>Spec</th>
<th>Technique</th>
<th>Sig. of diff.</th>
<th>Imp. Variables</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>284</td>
<td>12</td>
<td>31</td>
<td>P.C.A.</td>
<td>Separation mainly along 1st vector</td>
<td>Size variables</td>
</tr>
<tr>
<td></td>
<td></td>
<td>284</td>
<td>12</td>
<td>31</td>
<td>H.C.</td>
<td>Clustering not into original groups</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>284</td>
<td>13</td>
<td>41</td>
<td>R.M.A.</td>
<td>P&lt;1% between 11 pairs of slopes</td>
<td>N 2</td>
</tr>
<tr>
<td>2. New Zealand (A.recent)</td>
<td>Trouville (N.scutatus)</td>
<td>288</td>
<td>13</td>
<td>45</td>
<td>S.D.F.</td>
<td>P&lt;1%</td>
<td>N1,C</td>
</tr>
<tr>
<td></td>
<td></td>
<td>289</td>
<td>13</td>
<td>45</td>
<td>P.C.A.</td>
<td>Separation on plot of 1,2 vectors</td>
<td>1st – size</td>
</tr>
<tr>
<td></td>
<td></td>
<td>289</td>
<td>12</td>
<td>50</td>
<td>H.C.</td>
<td>Final 2 groups = original groups</td>
<td>2nd – N2</td>
</tr>
<tr>
<td></td>
<td></td>
<td>289</td>
<td>14</td>
<td>243</td>
<td>R.M.A.</td>
<td>P&lt;1% between 11 pairs of slopes</td>
<td>N 2</td>
</tr>
<tr>
<td>3. Nelson, Wellington, (A.recent)</td>
<td>Trouville, Cothill, Dorset, W. Basset, Upware (N.scutatus)</td>
<td>293</td>
<td>12</td>
<td>176</td>
<td>S.D.F.</td>
<td>P&lt;1%</td>
<td>N1,N1,L</td>
</tr>
<tr>
<td>4. All A.recent (treated as one group)</td>
<td>All N.scutatus samples (treated as one group)</td>
<td>295</td>
<td>12</td>
<td>176</td>
<td>S.D.F.</td>
<td>P&lt;1%</td>
<td>N1,C</td>
</tr>
<tr>
<td>5. New Zealand (A.recent)</td>
<td>Trouville (N.scutatus), Villers (N.microclus), Devecy (N.subquadruatus), Bou Saada (N.rotundus)</td>
<td>296</td>
<td>13</td>
<td>85</td>
<td>S.D.F.</td>
<td>P 1%</td>
<td>L,N1,C,E,N2</td>
</tr>
<tr>
<td></td>
<td></td>
<td>297</td>
<td>12</td>
<td>90</td>
<td>H.C.</td>
<td>Clustering not into original groups</td>
<td></td>
</tr>
<tr>
<td>6. New Zealand (A.recent)</td>
<td>As above + N.elongatus group, Signy (N.amplus)</td>
<td>297</td>
<td>13</td>
<td>98</td>
<td>S.D.F.</td>
<td>P&lt;1%</td>
<td>L,J,N1,C,E,N2</td>
</tr>
<tr>
<td></td>
<td></td>
<td>300</td>
<td>14</td>
<td>361</td>
<td>R.M.A.</td>
<td>P&lt;1% between 10–11 pairs of slopes</td>
<td>N2</td>
</tr>
</tbody>
</table>

Figure 9.1. Summary of important analyses run in Chapter 9. See fig. 5.1 for key.
Specimens classified wrongly by posterior probability; 97%

Step 9 (final)

Variables not entered; G, L and M

U-statistic = .25 (Significance of inequality of group means; \( P < .5\% \))

Specimens classified as 100% representative of their own group (using posterior probability); 97%

Specimens not a significant distance \( (P > 5\%) \) from either group (using \( \chi^2 \) tests of \( D^2 \)); 35%. Compare with fig. 5, 9.

Figure 9, 2 is a canonical variate plot of the multivariate distribution of specimens (compare with fig. 5, 3).

Fig. 9, 3 is a plot of the first two eigenvectors of a principal component analysis using the same specimens and variables as in the previous analysis. Fig. 9, 4 tabulates the eigenvalues and direction cosines for the first four eigenvectors. The first component is a size vector composed of variables A to N1 and including variable L. The second vector is weighted heavily for N2. The plot of these two components, accounting for 86% of total variance, reveals overlap between the groups with maximum differentiation occurring along the size vector.

The hierarchical grouping program was not able to distinguish adequately between the groups. All clusters formed in the final stages of the analysis were composed of specimens from both groups.

A comparison of reduced major axes for the Wellington and Nelson samples revealed a degree of similarity close to that found to occur between various \( N. scutatus \) samples (compare with fig. 5, 10). Thirteen variables were used for comparison, omitting I and N4, and, therefore, only twelve slopes can be constructed for each variable. For A with all other variables only two slopes were highly significantly different \( (P < 1\%) \) and a further slope was probably significantly
Figure 9.2. Distribution of Nelson and Wellington specimens on the first two canonical axes. Group centroids indicated by large lettering. Mean coordinates:
Nelson  -2.593  .000
Wellington  1.061  .000
Figure 9.3. Distribution of Nelson and Wellington specimens along Principal Components 1 and 2 based on a 12 variable analysis. Components 1 and 2 account for 86% of total variation.
PRINCIPAL COMPONENT ANALYSIS

Nelson and Wellington samples.
12 variables, 31 cases.

Eigenvalues

<p>| | | | |</p>
<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>9.39</td>
<td>98</td>
<td>88</td>
<td>40</td>
</tr>
</tbody>
</table>

Cumulative proportions of total variance

<p>| | | | |</p>
<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>78%</td>
<td>86%</td>
<td>94%</td>
<td>97%</td>
</tr>
</tbody>
</table>

Eigenvectors

<table>
<thead>
<tr>
<th></th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>-.33</td>
<td>-.03</td>
<td>-.02</td>
<td>-.05</td>
</tr>
<tr>
<td>B</td>
<td>-.32</td>
<td>.04</td>
<td>-.05</td>
<td>-.07</td>
</tr>
<tr>
<td>C</td>
<td>-.31</td>
<td>.01</td>
<td>.01</td>
<td>-.08</td>
</tr>
<tr>
<td>D</td>
<td>-.31</td>
<td>-.02</td>
<td>-.10</td>
<td>-.10</td>
</tr>
<tr>
<td>E</td>
<td>-.32</td>
<td>-.00</td>
<td>-.04</td>
<td>-.04</td>
</tr>
<tr>
<td>G</td>
<td>-.33</td>
<td>.02</td>
<td>-.03</td>
<td>-.07</td>
</tr>
<tr>
<td>J</td>
<td>-.30</td>
<td>.20</td>
<td>-.09</td>
<td>.35</td>
</tr>
<tr>
<td>L</td>
<td>-.28</td>
<td>.25</td>
<td>-.19</td>
<td>.60</td>
</tr>
<tr>
<td>M</td>
<td>-.32</td>
<td>-.07</td>
<td>.15</td>
<td>-.17</td>
</tr>
<tr>
<td>N1</td>
<td>-.30</td>
<td>-.15</td>
<td>.18</td>
<td>-.54</td>
</tr>
<tr>
<td>N2</td>
<td>-.12</td>
<td>-.89</td>
<td>.18</td>
<td>.34</td>
</tr>
<tr>
<td>N3</td>
<td>-.12</td>
<td>.26</td>
<td>.92</td>
<td>.14</td>
</tr>
</tbody>
</table>

Figure 9.4. Eigenvalues and direction cosines of the first four eigenvectors for the Nelson and Wellington samples. The first two eigenvectors are plotted on fig.9.3.
different ($1\% < P < 5\%$). N2 contributed most variability in the second vector of the principal components analysis described above. In comparisons of reduced major axes it is found that this variable produced most dissimilar slopes. Only the slopes formed from N2 with H were not significantly different ($P > 5\%$) between the two samples but even these slopes were a significant distance apart ($P < 1\%$).

The analyses indicate that the range of variation between these conspecific samples is of a similar nature to that found between the samples of N. scutatus. The actual variables that distinguish between the groups are, however, different. Differentiation between the two samples of A. recens is primarily a function of test size, and may merely reflect age separated groups. The two samples can, therefore, be combined to take account of a fuller age range in comparison with other samples. The two combined samples will be referred to as the New Zealand sample in subsequent analyses.

9 C) Comparison with N. SCUTATUS samples

A step wise discriminant function analysis reveals a sharp distinction between the two samples of A. recens and the Trouville sample of N. scutatus.

Step 2
Variables N1 and C entered
F matrix indicated a highly significant difference ($P < 1\%$) between group means.
Specimens classified wrongly by posterior probability; 0%

Step 12 (final)
Variable not entered; D
U-statistic = .06 (Significance of inequality of group means; $P < .1\%$)
Specimens classified as 100% representative of their own group (using posterior probability); 100%
Specimens with a low probability ($P < .1\%$) of belonging to the opposing group (using $\chi^2$ tests of $D^2$); 100%

Fig. 9.5 is a plot of the first two vectors of a principal component analysis using the same specimens and variables as the previous analysis. From a tabulation of the eigenvalues and direction cosines of the first four eigenvectors, fig. 9.6, it can be seen that the composition of these first two vectors is very similar to the analysis of the two New Zealand samples (compare with fig. 9.4). Again the first vector is a size component composed of variables A to N1 and the second vector is weighted heavily for N2. The plot of these two vectors, accounting for 86% of the total variability, produces two growth axes with increasing size correlated with increasing indentation of the posterior border. Smaller members of the two groups plot in a similar position, but increases in N2 proceed much slower with increase in size within the New Zealand sample of A. recens than within the N. scutatus group. Differentiation between the groups is, therefore, possible with most members of the two groups.

A hierarchical grouping program differentiated perfectly between the two groups.

A comparison of reduced major axes, between the Trouville and New Zealand samples, omitting variable I, revealed large differences between the groups (see part of fig. 9.7). Only four axes were not significantly different ($P > 5\%$) for both A and L with all other variables. In the case of the important discriminating variables, N1 and N2, the figures were one and two slopes respectively. This degree of difference is higher than in comparisons between any other pair of samples used in the present study, e.g. compare with the Trouville - Villers comparison, Chapter 7F, 3.

Using the 12 variables common to most New Zealand specimens, comparisons were extended to include stepwise discriminant function
Figure 9.5. Distribution of New Zealand and Trouville specimens along Principal Components 1 and 2 based on a 13 variable analysis. Components 1 and 2 account for 86% of total Variation.
PRINCIPAL COMPONENT ANALYSIS

New Zealand and Trouville samples.

13 variables, 44 cases.

Eigenvalues

<p>| | | | | |</p>
<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>9.45</td>
<td>1.77</td>
<td>.82</td>
<td>.38</td>
<td></td>
</tr>
</tbody>
</table>

Cumulative proportions of total variance

<p>| | | | |</p>
<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>73%</td>
<td>86%</td>
<td>93%</td>
<td>96%</td>
</tr>
</tbody>
</table>

Eigenvectors

<table>
<thead>
<tr>
<th></th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>-.32</td>
<td>-.06</td>
<td>.05</td>
<td>.15</td>
</tr>
<tr>
<td>B</td>
<td>-.32</td>
<td>.05</td>
<td>.04</td>
<td>.02</td>
</tr>
<tr>
<td>C</td>
<td>-.27</td>
<td>.36</td>
<td>-.07</td>
<td>-.35</td>
</tr>
<tr>
<td>D</td>
<td>-.26</td>
<td>.40</td>
<td>.05</td>
<td>-.37</td>
</tr>
<tr>
<td>E</td>
<td>-.32</td>
<td>-.08</td>
<td>.06</td>
<td>.22</td>
</tr>
<tr>
<td>G</td>
<td>-.32</td>
<td>-.09</td>
<td>.05</td>
<td>.13</td>
</tr>
<tr>
<td>H</td>
<td>-.30</td>
<td>.02</td>
<td>.08</td>
<td>.19</td>
</tr>
<tr>
<td>J</td>
<td>-.30</td>
<td>-.22</td>
<td>-.04</td>
<td>-.30</td>
</tr>
<tr>
<td>L</td>
<td>-.27</td>
<td>-.31</td>
<td>.08</td>
<td>-.39</td>
</tr>
<tr>
<td>M</td>
<td>-.30</td>
<td>.19</td>
<td>.15</td>
<td>.00</td>
</tr>
<tr>
<td>N1</td>
<td>-.29</td>
<td>-.14</td>
<td>.05</td>
<td>.54</td>
</tr>
<tr>
<td>N2</td>
<td>-.00</td>
<td>.69</td>
<td>-.11</td>
<td>.29</td>
</tr>
<tr>
<td>N3</td>
<td>-.15</td>
<td>-.09</td>
<td>-.97</td>
<td>.03</td>
</tr>
</tbody>
</table>

Figure 9.6. Eigenvalues and direction cosines of the first four eigenvectors for the New Zealand and Trouville samples. The first two eigenvectors are plotted in fig. 9.5.
### Variables

<table>
<thead>
<tr>
<th></th>
<th>A</th>
<th>L</th>
<th>N1</th>
<th>N2</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Signy</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>A.</td>
<td>4</td>
<td>12</td>
<td>7</td>
<td>11</td>
</tr>
<tr>
<td>B.</td>
<td>1</td>
<td>1</td>
<td>3</td>
<td>0</td>
</tr>
<tr>
<td>C.</td>
<td>8</td>
<td>0</td>
<td>3</td>
<td>2</td>
</tr>
<tr>
<td>D.</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><strong>Trouville</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>A.</td>
<td>7</td>
<td>4</td>
<td>10</td>
<td>11</td>
</tr>
<tr>
<td>B.</td>
<td>2</td>
<td>5</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>C.</td>
<td>4</td>
<td>4</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>D.</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><strong>Villers</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>A.</td>
<td>4</td>
<td>3</td>
<td>5</td>
<td>10</td>
</tr>
<tr>
<td>B.</td>
<td>2</td>
<td>3</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>C.</td>
<td>7</td>
<td>7</td>
<td>8</td>
<td>2</td>
</tr>
<tr>
<td>D.</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td><strong>Devecey</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>A.</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>11</td>
</tr>
<tr>
<td>B.</td>
<td>1</td>
<td>2</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>C.</td>
<td>11</td>
<td>10</td>
<td>11</td>
<td>1</td>
</tr>
<tr>
<td>D.</td>
<td>0</td>
<td>1</td>
<td>2</td>
<td>0</td>
</tr>
</tbody>
</table>

**Figure 9,7.** Comparison of reduced major axes between the combined New Zealand samples and the four important samples of Signy, Trouville, Villers and Devecey for the variables shown with all other variables. Key as for fig. 5, 10.
analysis of all important *N. scutatus* samples. Firstly, seven groups were constructed from the two *A. recens* and five *N. scutatus* samples used in Chapter 5H. Secondly, the same specimens were arranged into two groups, representing the two species, in a similar manner to comparisons between *N. scutatus* and *N. latiporus* (Chapter 6F).

In the first of these analyses the results were:

**Step 3**
Variables NL, M and L entered

F matrix indicated that the group means of all samples became highly significantly different (*P* < 1%) from the group means of any sample from the opposing species.

**Step 4**
Variable C added

Specimens classified with the wrong species by posterior probability; 0%

**Step 12 (final)**
U-statistic = .02 (Significance of inequality of group means; *P* < .1%)

All group means, except Wootton Bassett and Trouville (1% < *P* < 5%), were highly significantly different (*P* < 1%).

Specimens with a low probability (*P* < 5%) of belonging to a group from the wrong species (using *X*² tests of *D*²); 0%

Fig. 9, 8 is a canonical plot of the multivariate distribution of specimens used in the discriminant analysis and represents 90% of total dispersion. Between species differences are maximised along the axis of the first canonical variate, the coefficients of which are highly weighted for original variables G and NL. NL, the distance between the apical disc and the periproct, is the primary discriminating variable in the stepwise discriminant function procedure. G (the distance from the anterior of the test to the most anterior point of the sulcus at the posterior border) is used as a measure of length.
Figure 9.8. Distribution of Nelson and Wellington (A. recens) and Bran Point, Cothill, Trouville, Wootton Bassett and Upware (N. scutatus) specimens on the first two canonical axes. Group centroids indicated by large lettering. Mean coordinates:

Nelson -5.660 -1.173
Wellington -5.489 .688
Bran Point .900 -2.341
Cothill .833 -1.999
Trouville 1.092 -1.073
W. Bassett 1.635 -.144
Upware 1.245 1.180
rather than A (the greatest length of the test) as the depth of the sulcus is usually larger within *N. scutatus* than *A. recens*. G is equivalent to A - N2. Overall differences between samples of the two species can be summarised in terms of length, depth of the posterior notch and the distance between the apical disc and periproct.

Within species differences are maximised along the axis of the second canonical variate, the coefficients of which are highly weighted for C, D and L. L (the length of the periproct) is the third discriminating variable to be entered in the stepwise discriminating procedure. It is also a primary discriminating variable in analyses of various *N. scutatus* samples. C (the greatest height of the test), which is highly correlated with D (the apical height) is the fourth discriminating variable in the above analysis of the two *A. recens* samples.

The first canonical variate is discriminating between species, whilst the second is discriminating within species. This second vector is correlated in part with a facies dependent character.

In the second analysis all specimens were grouped into their correct species. The results were:

**Step 2**
Variables N1 and C entered
F matrix indicated a highly significant difference (P < 1%) between group means

**Step 5**
Variables J, B and E added
Specimens classified wrongly by posterior probability; 0%

**Step 12 (final)**
Variables not entered; C and N2 (C was removed at the last step of the analysis)
U-statistic = .13 (Significance of inequality of group means; P < .1%)
Specimens with a low probability (P < 5%) of belonging to the wrong group (using $\chi^2$ tests of $D^2$); 100%

The first five variables to be entered were used in exactly the same order and achieved the same results as in the Trouville - New Zealand analysis (see above) and justify the use of a single group, such as Trouville, to represent a complete species or even chronospecies in multivariate comparisons.

The above analyses show a much greater degree of difference between the groups than between samples of $N$.scutatus and $N$.latiporus.

9 D) Comparison with other nucleolitid samples

The degree of difference between $N$.scutatus and $A$.recens was further assessed by adding other post-middle Jurassic samples to the analysis. Using 13 variables, by omitting I and N4, a stepwise discriminant function analysis was carried out on the Trouville, Villers, Devecey, Bou Saada and New Zealand samples.

**Step 5**
Variables L, N1, C, E and N2 entered
Jurassic specimens classified wrongly by posterior probability; 0%
Most group means were highly significantly different (P < 1%) from each other. The bou Saada sample was not significantly different (P > 4%) from either the Devecey or New Zealand groups.

**Step 12 (final)**
Variable not entered; D

U-statistic = .004 (Significance of inequality of group means; P < .1%)
F matrix indicated that the Bou Saada sample was only probably significantly different (1% < P < 5%) from the Devecey and New Zealand samples.
Specimens classified wrongly by posterior probability; Trouville 0%, Villers 0%, Devecey 8%, Bou Saada 0%, New Zealand 4%.

Fig. 9 is a canonical variate plot of the groups representing 90% of total dispersion. The slight overlap in post-Jurassic groups is graphically illustrated.

A cluster analysis of the Villers, Devecey, Bou Saada and New Zealand samples produced similar results. The Bou Saada specimen CE 2 was again grouped with the Villers group at an early stage, whilst there was considerable overlap of grouping between the Devecey, Bou Saada and New Zealand specimens.

The final analysis involved all seven major groups sampled. It added the two middle Jurassic samples of Signy and _N. elongatus_ to those used in the previous discriminant function analysis. The same 13 variables were used.

**Step 6**
Variables L, J, N1, C, E and N2 entered

F matrix indicated that most group means were highly significantly different (P < 1%) from each other. Bou Saada was only probably significantly different (1% < P < 5%) from the Devecey and New Zealand samples. Signy, _N. elongatus_, Trouville and Villers specimens classified wrongly by posterior probability; 0%

**Step 12 (final)**
Variables not entered; D

U-statistic = .0002 (Significance of inequality of group means; P < .1%)

Group probability table showed:

- Devecey specimens classified with Bou Saada; 8%
- New Zealand specimens classified with Devecey; 4%

Fig. 9, 10 tabulates the probability of specimens belonging to
Figure 9.9. Distribution of New Zealand (A. recens), Bou Saada (N. rotundus), Devecey (N. subquadriatus), Villers (N. micraulus) and Trouville (N. scutatus) specimens on the first two canonical axes. Group centroids indicated by large lettering. Mean coordinates: New Zealand -2.822 2.590 Bou Saada .500 .566 Devecey -1.536 -.737 Villers -.568 3.422 Trouville 5.709 1.194
<table>
<thead>
<tr>
<th>Original Sample</th>
<th>Group</th>
<th>Signy</th>
<th>N.elongatus</th>
<th>Trouville</th>
<th>Villers</th>
<th>Devecey</th>
<th>Bou Saada</th>
<th>N.Zealand</th>
</tr>
</thead>
<tbody>
<tr>
<td>Signy</td>
<td>0%</td>
<td>100%</td>
<td>100%</td>
<td>100%</td>
<td>100%</td>
<td>100%</td>
<td>100%</td>
<td>100%</td>
</tr>
<tr>
<td>N.elongatus</td>
<td>100%</td>
<td>50%</td>
<td>100%</td>
<td>100%</td>
<td>100%</td>
<td>100%</td>
<td>100%</td>
<td>100%</td>
</tr>
<tr>
<td>Trouville</td>
<td>100%</td>
<td>100%</td>
<td>0%</td>
<td>100%</td>
<td>100%</td>
<td>100%</td>
<td>100%</td>
<td>100%</td>
</tr>
<tr>
<td>Villers</td>
<td>100%</td>
<td>100%</td>
<td>100%</td>
<td>4%</td>
<td>62%</td>
<td>83%</td>
<td>100%</td>
<td></td>
</tr>
<tr>
<td>Devecey</td>
<td>100%</td>
<td>100%</td>
<td>100%</td>
<td>77%</td>
<td>8%</td>
<td>69%</td>
<td>100%</td>
<td></td>
</tr>
<tr>
<td>Bou Saada</td>
<td>100%</td>
<td>100%</td>
<td>100%</td>
<td>66%</td>
<td>66%</td>
<td>0%</td>
<td>66%</td>
<td></td>
</tr>
<tr>
<td>New Zealand</td>
<td>100%</td>
<td>100%</td>
<td>100%</td>
<td>96%</td>
<td>92%</td>
<td>68%</td>
<td>12%</td>
<td></td>
</tr>
</tbody>
</table>

Figure 9,10. Percentage of specimens within each sample with a low probability (P<5%) of belonging to each group, based on \( \chi^2 \) tests of \( D^2 \) for each case.
a particular group (using \( \chi^2 \) tests of \( D^2 \)). The linearity of the samples with time is well illustrated.

Fig. 9, 11 is a canonical variate plot of the specimens used in the discriminant function analysis but, because of the large number of groups used, represents only 76% of the total dispersion. The discreteness of the four Jurassic samples compared with the three post-Jurassic groups is, however, well illustrated. Apart from the apparent anomalous position of the _N. elongatus_ sample, there is a general trend indicating decreasing age towards the upper right hand corner of the graph. This vector corresponds closely to an anterior movement of the apical disc, variable M.

Fig. 9, 7 summarises comparisons of reduced major axes between _A. recens_ and fossil samples of _Nucleolites_. The comparisons are arranged in terms of increasing similarity (fewer significant differences) to the New Zealand sample. This order corresponds closely to a decrease in the stratigraphic age of the sample. The youngest sample of _Nucleolites_ is most similar to the Recent _A. recens_.

**9. E) Conclusions**

Comparison between the two _A. recens_ samples revealed a degree of difference at a very similar level to that found to exist between the various samples of _N. scutatus_, and adds weight to the argument that the _N. scutatus_ samples are conspecific. The nature of the difference between the conspecific samples is, however, different. For example, within _A. recens_ the two samples can be distinguished on size and a size variable, C, is entered at step four in discriminant analysis. Variables _N1_, _N2_ and _M3_ are important in distinguishing between the two Recent samples whereas they are rarely important in analyses involving _N. scutatus_ samples. Variable J is an important discriminating
Figure 9, 11. Distribution of New Zealand, Bou Saada, Devecey, Villers, Trouville, Signy and \textit{N. elongatus} group specimens on the first two canonical axes. Group centroids indicated by large lettering. Mean coordinates:

- New Zealand: 3.415 2.891
- Bou Saada: 2.654 -.129
- Devecey: 3.189 -.889
- Villers: 1.467 3.200
- Trouville: -3.089 -.018
- Signy: -9.335 .460

\textit{N. elongatus} group: -4.488 3.037
variable in both analyses.

Fig.9,3 is a plot of _A.recens_ specimens along the first two vectors of a principal component analysis. It reveals that the major differentiation between the groups is along the size component, unlike analyses involving _N.scutatus_ groups which show between sample differences that are independent of size (e.g. fig.5,5). This indicates that the two _A.recens_ samples may represent size differentiated, migratory age groups of a similar nature to those observed in living spatangoids (Buchanan,1966).

_A.recens_ can be distinguished from _N.scutatus_ through the use of variables N1 and C only, _A.recens_ being a flatter species with the apical disc lying some distance from the periproct, i.e. about 29% of the total length as compared to around 21% in _N.scutatus_. Mahalanobis distances and posterior probability indicate a differentiation between the two types at the 'second level' of grouping as outlined on p.249. Principal component analysis and comparisons of reduced major axes reveal that the depth of the posterior groove, variable N2, increases much more slowly during growth in _A.recens_ than in _N.scutatus_. Variables J,B and E are also important in stepwise discriminant function analysis between the two species. Variable M becomes important in analyses that discriminate between all samples of _A.recens_ and _N.scutatus_.

In comparisons with other nucleolitid samples it is found that _A.recens_ is more similar in morphology to the younger Cretaceous samples than to the older Jurassic groups. Neither discriminant functions nor cluster analyses are able to distinguish fully between the post-Jurassic samples. Canonical variate plots of the various groups do, however, show a consistent trend with earlier analyses (e.g. figs.7,10 and 8,9). For example fig.9,9 shows that the New
Zealand sample lies at the extreme end of an age vector running towards the top left of the graph. An orthogonal vector indicates a distinctiveness between Trouville and the more elongate samples of Villers, Devecey, Bou Saada and New Zealand.

In a canonical variate plot of all major samples (fig. 9, 11) there is again a trend towards decreasing age (towards the top right of the graph), which corresponds closely with decreases in variable M. Within the middle Jurassic Signy and *N. elongatus* groups the apical disc is in a central position on the aboral surface. M is 47% of total length, A, in *N. amplus* and 50% of total length in *N. elongatus*. Within the upper Jurassic samples its position is 41% in *N. scutatus* and 39% in *N. micraulus*. Within the three post-Jurassic samples the apical disc lies consistently 34% of the distance along the aboral surface from the anterior of the test. The vector parallel with the X axis of the graph is composed of N1 and N2 in inverse proportions. This indicates only a general trend towards an increase in the distance between the periproct and apical disc with time. There is, however, a degree of variation in this distance between species at any given stratigraphic stage.
10 A) The ecological significance of variation within N. SCUTATUS

The samples of N. scutatus used in this study represent a single, widespread species showing a distinctive morphological diversity which can be correlated with substrate type. Each sample can, therefore, be considered to represent a local population adapted to a particular sedimentary environment. Each individual population is not isolated from other local populations since variation within the species is shown to be continuous. This continuous variation is demonstrated by the considerable overlap in morphology between the samples with no combination of variables characterising all specimens of one group sufficiently distinctly to differentiate them all from specimens of another group.

Genetic differences between these fossil groups cannot be determined. However, the samples are unlikely to represent ecotypes (a group of organisms from within a larger biotype showing a genotypic response to a particular habitat, Turreson, 1922) as considerable overlap in form is a characteristic of the samples. Even if the groups do represent populations which were genetically isolated by ecology or as allopatric populations, then isolation had not occurred for long enough to allow identifiable morphological characteristics to become unique to particular samples. Ecotypes and even ecospecies (ecotypic populations, between which gene flow is impeded to some extent, Heslop-Harrison, 1969) are difficult to recognise in the fossil record, but such groups may exist close to each other given sufficiently strong environmental gradients. (Heslop-Harrison, 1969).

Modern species of echinoids are known to occur in age differentiated groups with juveniles living further from the shore.
than adults (Moore, 1936; Nichols, 1962; and Ernst & Seibertz, 1978). Differences in mean size between the samples studied have been recognised, but it is unlikely that the samples represent migratory age groups within a single, large population for two reasons. Firstly, because there is no direct correlation between size and nearness to shore as here interpreted. (The Upware sample contains the largest individuals, and although belonging to an isolated reef complex, is found within a low energy micritic algal limestone rather than a high energy near-shore facies. On the other hand, the high energy near shore calcareous sandstone of Cothill contains small individuals.) Secondly, because the groups show a large size range and can only be differentiated on mean sizes. (Each sample contains a normally distributed group of individuals with very small and very large specimens.) Multivariate comparisons between the groups also show that differences occur independent of size (e.g. fig. 5, 5). Specimens of the same size within the different groups show real differences in the size and position of the periproct and in the length of the anal sulcus, which are highly correlated with differences in the enclosing sediment (fig. 5, 12). The differences between groups are not, therefore, a function of allometric growth between age grouped samples.

It is possible that *N. scutatus* shows phenotypic variation in response to local environmental factors and that the samples represent ecads (forms showing adaptation to a particular habitat in which the adaptive characters are not genetically determined but are imposed by environmental agencies, Turreson, 1922). Each sample shows adaptations to a particular habitat in that the periproct and sulcus vary in direct relationship with sediment size. These adaptive features are interpreted here as phenotypic responses to the environment because of the very strong correlation between
periproct morphology and sediment grain size. It is envisaged that each local population underwent somatic adaptation to a particular environment resulting in distinct but continuous phenotypes within the species. *N. scutatus* shows plasticity of form in relation to substrate conditions. As so much overlap in form occurs, then it is probable that the samples belong to a single biotype (a collection of individuals which are genotypically all essentially the same) and that one taxonomic species covers the total range of variation.

The highly significant correlation between periproct size and sediment particle size suggest a grain ingesting habit for *N. scutatus*. In general morphology and, therefore, probably habit and habitat, *N. scutatus* closely resembles the Recent *Apatopygus recens*. Both are abundantly associated with a coarse substrate. *A. recens* burrows completely, though shallowly, in a coarse sediment and injests substrate grains for food (Higgins, 1974). From its similar form and facies association it is probable that *N. scutatus* did likewise.

A large periproct would be required to defecate large substrate grains; a small periproct would serve to defecate small grains.

The burrowing and feeding behaviour of *A. recens* have been described by Higgins (1974) who notes that there is no connection between the urchin and the overlying sea water column by way of a respiratory burrow and that it becomes completely embedded in the substrate to a depth of about 3cm. He suggests that respiration is maintained through the interstitial water of the relatively porous, coarse grained substrate. Higgins (1974) also notes that the feeding activity of *A. recens* is selective in that large particles will not be ingested. Higgins’ recorded observations on the maximum size of ingested particles correspond closely to the average periproct size for specimens of *A. recens* used in the present study.
Another limiting factor on maximum grain size injection may be the stickiness of the mucous of the tube-feet related to the weight of the particles as suggested by Nichols (1959) for modern spatangoids. *N. scutatus*, like its morphologically similar living descendant *A. recens*, probably derived food from organic materials adhering to individual sediment particles. The high organic content of the mud coated oolitic grains (Bathurst, 1975:80) found in association with *N. scutatus* may have been able to fulfil this nutritional requirement. Furthermore, the usually excellent preservation of this thin shelled echinoid in mobile oolitic environments suggest that it was able to burrow completely within the substrate away from the area of maximum sediment activity at the surface. The absence of specialist burrowing organs does not negate this hypothesis (c.f. Rose, 1978).

Many other recent cassiduloids also inhabit coarse substrates and maintain a grain injecting habit (Mortensen, 1948). Agassiz (1873:555) states that *Rhyncholampas pacificus* burrows only to the aboral extremities of its petals. Higgins (1974) suggests that in cases where cassiduloids occupy habitats insufficiently coarse to maintain an adequate water flow a partial burrowing habit may be adopted. This may indeed have been the case for populations of *N. scutatus* occupying muddy environments such as that at Bran Point.

Furthermore, oxygen depletion within this particular fine grained sediment may also account for the smaller specimen sizes.

Supporting evidence for this interpretation may be derived from the work of Buchanan (1966), who has shown also that populations of the recent spatangoid *Echinocardium cordatum* are smaller, grow at a slower rate and burrow to a shallower depth in silty as opposed to clean sandy substrates. The size differentiation between the two populations studied by Buchanan (1966) living within different substrates is comparable to size differences observed between the
samples of *N. scutatus*. A close association between populations of echinoids and particular substrate particle size has been observed by Lawrence & Ferber (1971) in the recent spatangoid *Lovenia elongata*.

Nichols (1959, 1962) has noted that the periproctal organs of all British burrowing echinoids are greatly affected by the type of substrate. Nichols (1962) studied conspecific populations of *E. cordatum* in which differences occur in the shape of the sub-anal fascicle. Nichols interpreted this phenomenon as an adaptation by each local population to the building of a sanitary drain of an optimum shape according to the physical properties of the particular sediment type. Nichols concluded that either genetic or environmental factors could produce such differences. Stokes (1976) also used the periproct to distinguish between sympatric species of *Micraster*. In this case the height of the periproct above the adoral surface was used.

Similar investigation of morphological variability within species of brachiopods have been made (e.g. Dubois, 1916; Mc Kerrow, 1954; and Alexander, 1975). Dubois (1916) demonstrated the plasticity of living terebratulids. Normally tear-shaped specimens developed a gibbous geometry when transplanted into a more agitated environment. Mc Kerrow (1953) showed distinctive morphological variability within the Jurassic terebratellids *Ornithella* and *Rugitela* along the length of outcrop of the English Fullers Earth Rock. Lateral changes in variation of the brachiopods were interpreted to reflect regional changes in environment. Alexander (1975), in a study of the Ordovician strophomenid *Rafinesquina alternata*, demonstrated distinctive phenotypic plasticity related to sedimentological regimes. Relationship of benthic organisms to their substrate is therefore well established. The nature of the substrate played
an important role in the ecology and evolution of the marine benthos.

*N. scutatus* responded to different substrates in a similar manner to modern burrowing echinoids, such as spatangoids and the closely related cassiduloid *A. recens*. Possible explanations of the infraspecific variation studied within *N. scutatus* are that it could be either genetically or environmentally controlled. Nichols (1962) states that in the case of the former factor it is assumed that the range of variation in progeny of any population extends to the limits displayed by any population. Observed differences in adult populations are then a result of different selection forces at work as the echinoids grow. However, there does not seem to be a similarly great range of variation within juveniles of *N. scutatus* as observed by Nichols in samples of *E. cordatum*.

The alternative environmental explanation offered by Nichols (1962) for *E. cordatum* seems to be particularly appropriate to the observed differences within *N. scutatus*. "If the differences are environmental, on the other hand, it suggest that the urchins, relatively non-variable in genetic make-up, become differently influenced in each locality at an early age in response to some feature in the substratum, possibly pertaining to its particle size" (Nichols, 1962:118).

10 B) Taxonomic implication of variation between species of NUCLEOLITES

Within the analysis of these nucleolitid echinoids, two different levels of taxonomic differentiation can be distinguished through the use of multivariate techniques. Some generalised statements can be made about these grades of discrimination.

The first level represents grade of evolution within a lineage. It can be characterised by the comparisons of the various samples within *N. scutatus* and *A. recens*, or between *N. scutatus* and *N. latiporus*, and *N. Woodwardii* and *N. amplus*. Usually about five to
nine variables are needed to distinguish between the groups through the use of discriminant functions. Discrimination between samples involves no more than the establishment of significant differences between group means. There is always overlap between groups, although usually occurring at about the level of 10% of specimens being classified wrongly by posterior probability. Usually only up to 50% of specimens have low probabilities ($P < 1\%$) of belonging to opposing groups. Comparisons of reduced major axes involving measurements of the gross morphology of the test, e.g., variable A (length of test), reveal many slopes to be not significantly different ($P > 5\%$). Normally 10 to 13 from a maximum total of 14 slopes are not significantly different between pairs of groups (e.g., fig. 5, 10). When important discriminating variables are used, such as variable L, the number of slopes shown not to be significantly different drops to between 6 and 9 slopes. Principal components and cluster analysis are unable to facilitate satisfactory discrimination between such groups.

Measurements of the periproct are invariably important discriminating characters in many analyses. For example, variables I (the vertical height of the periproct) and L (horizontal length of the periproct) are the two most important variables in distinguishing between samples of *N. scutatus*. Furthermore, variable I is an important discriminating variable in the *N. scutatus - N. latiporus* comparisons as it is in the *N. woodwardii - N. amplus* analyses. Comparisons of reduced major axes involving variable L also produce the greatest degree of dissimilarity between groups.

The second level of taxonomic differentiation represents distinction of separate lineages. It is evident from comparisons between *N. scutatus*, *N. amplus*, *N. micraurus*, *N. subquadratus* and *A. recens*. A comparison of *N. scutatus* with *N. burgundiae*, *N. elongatus* and *N. rotundus*
produces similar results but the analyses involve only a small number of specimens. Discrimination of samples is totally complete in the majority of the analyses. Group means are highly significantly different after the entry of only two or four variables. All specimens are classified as 100% characteristic of their own group by posterior probability and each specimen has a very low probability ($P < 1\%$) of belonging to any opposing group. Comparisons of reduced major axes involving variable A usually show that between 6 and 9 slopes are not proved to be significantly different ($P > 5\%$), whilst in comparisons between important discriminating variables all slopes are often shown to be highly significantly different ($P < 1\%$).

Principal components and cluster analysis facilitated distinction between all such species.

Biometrical analyses thus reveal inconsistencies in the levels of differentiation used to distinguish between species of Nucleolites. If $N. scutatus$ and $N. latiporus$ are defined as separate species then $N. amplus$, $N. micraulus$ and $N. subquadratus$ could, with justification, be considered to represent genera or subgenera of Nucleolites. Conversely, if $N. amplus$ is considered to be distinguished from $N. scutatus$ at the specific level, then $N. latiporus$ should be treated as a subspecies of $N. scutatus$, since it is quantitatively less distinct. To raise each of the clearly defined species of Nucleolites, such as $N. amplus$, to the rank of subgenus or genus would be cumbersome and without historical precedent.

From a historical viewpoint, it has been shown (Chapter 3A) that up to and including William Smith (Smith, 1817a, b) there was considerable confusion concerning the differences between $N. scutatus$ and $N. latiporus$ (syn. $N. clunicularis$), few pre-Linnaean authors distinguishing between the two forms. This uncertainty continued
into the twentieth century (e.g. Mortensen, 1948; Kier, 1962), and is clearly a function of the close similarity between the two forms. On purely biometrical grounds *N. latiporus* cannot be considered to be more than a subspecies of *N. scutatus*, and it can be argued that differences may not even be of this order. Similarly, *N. woodwardii* could be lowered to the rank of subspecies of *N. amplus*.

This procedure may appear clumsy, particularly since the close morphological similarity between *N. latiporus* and *N. scutatus* probably represents an ancestor - descendant relationship. The groups can, therefore, be considered as chronospecies (Valentine, 1973:41) rather than as subspecies. A chronospecies "has whatever (stratigraphic) range conventional agreement is prepared to give it" (George, 1956:129), and the form of any individual is no guide to its place in the lineage. *N. latiporus* can, therefore, be defined as specimens that are morphologically similar to *N. scutatus* occurring in the middle Jurassic (Aalenian to Callovian as defined by Hallam, 1975:14) whilst *N. scutatus* is restricted to the upper Jurassic. This procedure seems justified as significant differences between sample means can usually be demonstrated, and yet no significant differences can be proved between the samples of *N. latiporus* that occur in Callovian, upper and middle Bathonian strata. With time there is a general trend for specimens from within the lineage to become wider, flatter and with a taller periproct lying higher in the sulcus. The historically valid species names *N. latiporus* and *N. scutatus* are both maintained here, but to characterise chronospecies rather than biospecies following conventional usage (e.g. Arkell, 1933).

A similar definition can be applied to the middle Jurassic *N. woodwardii - N. amplus* plexus, the taxon *N. amplus* being restricted to Cornbrash specimens, *N. woodwardii* to upper Bajocian to middle Bathonian specimens. However, as the lineage only appears to extend
the length of a stage, from the topmost zone of the Bajocian to the topmost zone of the Bathonian, a more detailed study may reveal that there is no need to differentiate between these forms at the species level. In general terms *N.woodwardii* possess a taller periproct lying in a lower position within a shorter sulcus and the apical system is in a more central position.

Following the historical (post-Linnean) tradition of dividing the *N.latiporus - N.scutatus* plexus into two species, an arbitrary division can be made at the Callovian - Oxfordian boundary. The overall differences between the chronospecies are not the same as the differences within the *N.scutatus* samples based on sediment dependent characters. Neither are they the same as the overall time dependent characters recognised throughout the genus. Yet within the *N.amplus - N.woodwardii* plexus the two groups are found within similar peloidal sediments and a close similarity in the area of the periproct is evident. The movement of the apical system towards the anterior is an evolutionary trend as defined in 10 C.

It is therefore concluded that the species *N.scutatus*, *N.amplus*, *N.elongatus*, *N.burgundiae*, *N.micraulus*, *N.subquadratus* and *N.rotundus* are all morphologically distinct whilst *N.latiporus* and *N.woodwardii* are chronospecies of the first two species respectively. The adoption of such a solution is a reversal of normal palaeontological aims in that stratigraphy has been used to define species rather than species strata. It is also the case that if a hypothetical sample with the exact characteristics of, say, the Stratton Audley sample of *N.latiporus* was found in the Corallian then justifiably the name *N.scutatus* would be applied. Figure 6,7 demonstrates that samples of *N.latiporus* fall within the morphological range of *N.scutatus* and a division between the two can only be made on
stratigraphical grounds. This seems, however, to be a more rational solution in view of the alternative use of subspecies and the abolition of a well used, albeit subjective, division of species.

The arbitrary stratigraphic division does lead to certain apparent anomalies. For example, the lower Oxfordian specimen V45 from Villers-le-Tourneur (see Chapter 7E:7) must by definition be assigned to *N. scutatus* although by posterior probability it most resembled the *N. latiporus* sample of Stratton Audley. Moreover, the Mahalanobis distance reveals that it had a low probability of belonging to any of the groups sampled. This characteristic has been encountered in previous analyses and seems to be within the range of variation of specimens known to belong to *N. scutatus* and *N. latiporus*. Therefore, in this case, as with some specimens from within all *N. scutatus* samples, the biometrical conclusion that specimens belong to the species *N. latiporus* must be overruled in the light of geological evidence and placed within *N. scutatus*.

Using purely quantitative data *A. recens* would be placed, as indeed it was first described, within the genus *Nucleolites*. It is only as different from the type species as the other species studied in the present work despite the larger time gap involved. It is distinguished on the basis of two characters in all analyses. However, a single character, the presence of single pores in ambulacral plates beyond the petals, distinguishes it from all other species within the genus. On this single, time dependent character of great evolutionary significance (Kier, 1962), a non-overlapping, objective, non-arbitrary division can be made between *N. scutatus* and *A. recens* which is considered to be of greater importance than the simple morphological distinctiveness of other species of *Nucleolites*. There seems, therefore, ample justification for the maintenance of the two genera on this
single character although future work may reveal transitory groups between the two genera possessing single and double pores in the phyllodes.

The retention of a separate, monogeneric family for *Apatopygus* (sensu Kier, 1962) however seems unjustified. A close morphological similarity between *Apatopygus* and *Nucleolites* has been demonstrated as has a probable similar habit and habitat for the two type species. Certain other criteria for dividing the families have since been shown to be unwarranted, e.g. the superficially monobasal apical system of *Apatopygus* (Kier, 1974). Furthermore, Kier (1962, 1966) includes one genus, *Oolopygus*, within the *Nucleolitidae* which also possesses single pored phyllodes. Therefore, there seems no great need or justification for excluding *Apatopygus*.

It is proposed that the family *Apatopygidae* Kier, 1962, in the absence of any firm data to the contrary, be abolished and *Apatopygus* be restored as the only extant member of the *Nucleolitidae* Agassiz and Desor, 1847.

10 C) The evolutionary significance of variation within the genus *Nucleolites*

It has been demonstrated (e.g. Chapters 7G, 8D and 9E) that certain metric changes in the test dimensions of species of *Nucleolites* are highly correlated with time. It has also been demonstrated that changes in these characters are usually uncorrelated with other test dimensions or recognisable palaeoenvironmental changes and that some changes in test characteristics are completely independent of time.

For example fig. 7, 20 is a canonical variate plot of the important Jurassic species studied. It represents over 92% of total
dispersion. The age of the sample decreases from the Bathonian at
the top right to the Oxfordian at bottom left. The length of the anal
sulcus, \( J \), is correlated with this vector so that decrease in age
corresponds to decrease in \( J \). However, the width of the test, \( B \),
changes along a vector at right angles to the age vector. Within the
Cornbrash there are elongate (\( N. \text{elongatus} \)) and rounded (\( N. \text{amplus} \))
species, and again in the Oxfordian there are elongate (\( N. \text{micraulus} \))
and rounded (\( N. \text{scutatus} \)) forms. Elongation, therefore, occurs independently
of age. Two other vectors, orthogonal to each other, can also be
determined. One is composed mainly of \( L \), the length of the periproct,
and the other of \( C \) (height of test), \( I \) (height of periproct) and an
inverse \( N_1 \) (distance between apical disc and periproct). This indicates
that \( C \) and \( I \) decrease as \( N_1 \) increases and that these changes are
independent of changes in the length of the periproct. This is an
interesting observation as it has been demonstrated that the area
of the periproct, calculated from \( L \times I \), is correlated with substrate
grain size in some species, e.g. within \( N. \text{scutatus} \) (Scurry, 1978) and
probably within \( N. \text{amplus}, N. \text{elongatus} \) and \( N. \text{micraulus} \).
The canonical plot suggests that although area correlates closely
with grain size, the shape of the periproct can be highly variable
between species. For example, the height of the periproct, \( I \), can be
smaller than \( L \) (\( N. \text{scutatus} \)) or much larger (\( N. \text{amplus} \)). However,
the orthogonality of the two vectors indicates that as \( N_1 \) increases
there is a tendency for the periproct to become shallower in height,
as in the above example, but that the length of the periproct, \( L \),
varies independently of \( N_1 \).

It must be noted that all vectors may not be independent
of each other as each canonical variate is not necessarily orthogonal
to every other variate (see p. 110). Therefore, there is only a
very general trend for \( N_l \) and \( L \) to increase and for \( C \) and \( I \) to
decrease with time, and that this trend is not constant in manner.
For example, in the Bathonian \( N.m.amplus \) \( N_l \) and \( L \) are short, \( C \) and \( I \)
large, whilst in the Oxfordian \( N.m.micraulus \) \( L \) and \( I \) are short and \( N_l \)
and \( C \) are large. These changes are not regular or consistent
with time.

Different patterns of discrimination are found within a
particular Jurassic stage where the distribution of samples with
time is limited. For example, fig. 7, 11 is a canonical plot of some
Bathonian samples and represents 93% of total dispersion. In this
analysis \( M \), the position of the apical disc, is the major discriminating
variable followed by \( N_2 \) (indentation of posterior border), \( B \) (width
of test) and \( N_l \). The plot indicates an elongation vector from
bottom left to top right and an orthogonal vector composed mainly of
\( M \). Neither vector is, however, correlated with time. Two vectors
parallel to the axes of the graph are composed of \( N_2 \) (parallel with
the \( Y \) axis) and \( J \) and inverse \( L \) (parallel with the \( X \) axis). A stage
is therefore too short a period in which to recognise evolutionary
change.

Variable \( N_l \) becomes important only when the time element is
extended as in the analysis described on p. 221. Hence with the
addition of the Oxfordian sample of \( N.scutatus \) from Trouville to
the above analysis, \( N_l \) becomes the second most important discriminating
variable after \( M \).

When the time element is extended by including Cretaceous
samples also (e.g. fig. 8, 9 and 8, 10), the nature of the age vector
changes slightly and is now closely correlated with \( M \) and a small
weighting of \( N_l \). Again the orthogonal vector is composed mainly of
\( B \), whilst the other two vectors mentioned above correspond closely
to changes in \( J \) and \( L \). The distance of the apical disc from the
anterior of the test decreases constantly with time. The length of the anal sulcus tends to decrease with time but the length of the periproct does not.

The predictability of such plots is confirmation that the vectors can be interpreted in terms of age and elongation of species. For example, as explained in 7G and 8D, the position of the young, elongate *N. subquadratus* and the younger rounded *N. rotundus* are indeed placed in expected areas (e.g. fig. 8, 9) with respect to these two vectors.

With a further extension of time to include the extant *A. recens* another change is noted in canonical variate analysis. Although *A. recens* plots in a correct position along the age vector, there is now no direct correlation with *N*. Within this extant species the distance between the apical disc and periproct is a smaller proportion of absolute size than in *N. micraulus, N. subquadratus* or *N. rotundus*. The age vector now more closely corresponds to decreasing values of *M*, as explained in Chapter 9E.

From the final analysis involving all major groups (see p. 297) it is evident that the position of the apical disc and periproct are of primary discriminating importance. Variables J, NL and M are entered at steps 2, 3 and 8 respectively in discriminant function analysis. J and NL themselves virtually defining M for a given length of specimen.

The most important variable in distinguishing between species is, however, *L*, a variable that has also been found to be of primary importance in distinguishing groups within species, for example *N. scutatus* (Chapter 5H). As discussed in that section, *L* is probably a facies dependent variable that changes within local populations according to the grain size of the sediment, a particular periproct.
length becoming narrowly adapted to a particular substrate. The length of the periproct is, therefore, a very 'plastic' character. As all seven species used in the final analysis are found within different sedimentary facies it is expected that the periproct length would be very different between groups. It is also unlikely that the length of the periproct would change regularly with time as species have adapted to a variety of facies.

This situation does seem to be the case within the species studied. For example, within the older forms there are species with long (*N. scutatus*) and short (*N. amplus*) periprocts, whilst the same is true of younger species (large in *A. recens* and small in *N. subquadratus*). The palaeoecology of each species, as discussed in Chapter 3, indicates that the periproct size is closely correlated with sediment grain size and L can be considered to represent a facies dependent variable.

The major consistent evolutionary trend within the seven species studied is the location of the apical system on the aboral surface of the test, variable M. The disc gradually moves to a more anterior position with time from a central position within Bathonian species to a position only one-third of the test length from the anterior within the Recent *A. recens*.

Jesionek-Szymanska (1968) has detailed the migration of the periproct from within the apical system and the attainment of exocyclism within *Nucleolites*, suggesting that this is an important evolutionary trend within early members of the genus. Certainly the periproct lies in close proximity to the apical system in the Bajocian - Bathonian chronospecies *N. woodwardii* and *N. amplus* and the Bathonian endocyclic *N. elongatus* (Jesionek-Szymanska, 1968: fig. 8, f). However by the Oxfordian there are species with the periproct
lying one-fifth of the test length from the apical disc (21% in *N. scutatus*) and other species in which it lies one-third of this distance (35% in *N. micraulus*). This figure continues to vary with time being 34% in the Cenomanian *N. rotundus* but only 29% in the Recent *A. recens*. The movement of the periproct towards the posterior does not seem to be a consistent trend between the species studied and is not even a major factor within the two lineages of chronospecies. See p.211 for differences between *N. woodwardii* and *N. amplus* and p.178 between *N. latiporus* and *N. scutatus*.

A shortening of the anal sulcus, *J*, is also a generalised trend that is not consistent with time. The distance of the peristome from the anterior, *E*, remains fairly constant within the species studied being about 40% of test length. This is also the case with the 'streamlining' of the test, the point of greatest width of the test, *H*, being close to 60% of the test length for all species except in the very rounded *N. amplus* in which the figure is only 55%.

The elongation of the test, breadth *B* / length *A*, varies independently of time so that rounded and elongate forms may be found at any time during the evolution of the genus. For example, *N. elongatus* (Bathonian) is as narrow (breadth is 88% of length) as the Recent *A. recens* (breadth 89% of length).

The span of time involved in the study of the evolution of the genus is, therefore, vitally important to any conclusions made. It has been shown that different overall trends become apparent when three different time units are considered; the middle to upper Jurassic; the middle Jurassic to upper Cretaceous; and middle Jurassic to Recent.
CHAPTER 11 - SUMMARY

1. The taxonomy of each of the ten species studied is discussed.
   Echinobri\textsuperscript{is}sus Gray 1825 is a junior objective synonym of Nucleolites
   Lamarck 1801. N.scutatus Lamarck 1816 is confirmed as the type species
   of Nucleolites Lamarck 1801. N.clunicularis (Smith) 1817 is a
   junior subjective synonym of N.scutatus Lamarck 1816 and N.latiporus
   Agassiz 1839 is the next available name for this group of middle
   Jurassic cassiduloids. It is proposed that Apatopygus Hawkins 1920
   be retained within the Nucleolitidae, contrary to Kier (1962, 1966, 1974).

2. Of the four computer analyses used in this study, stepwise
   discriminant function analysis was found to be the most useful
   technique in determining infra and interspecific variation between
   samples. Principal component analysis also proved useful in determining
   differences between small numbers of samples and in isolating
   heterogeneity within samples. Reduced major axes and cluster analysis
   were used to confirm results produced by the other techniques.

3. Infraspecific variation within the genotype, Nucleolites scutatus,
   from the Oxfordian of England and Normandy is correlated with grain
   size of the enclosing sediment. Significant differences occur
   between samples, primarily in the size, shape and position of the
   periproct and in the length of the periproctal sulcus. A large
   periproct correlates with large sediment grain size rather than
   with differences in the stratigraphic age or geographic location
   of the samples.

4. It is inferred that infraspecific variation within N.scutatus
   reflects phenotypic variation between populations in response to
   local environmental factors such as substrate grain size. The samples
   may, therefore, represent ecads. The degree of morphological overlap
between samples indicate that all individuals belong to a single biotype and that one taxonomic species covers the total range of variation.

5. No such differences are proved between three samples of *N. latiporus* from the middle Jurassic (Bathonian to Callovian) of England and France, despite wide geographic and stratigraphic separation. Statistical differences between *N. latiporus* and *N. scutatus* are of the same order as between infraspecific samples of *N. scutatus*.

6. Samples of five Jurassic species (*N. elongatus*, *N. amplus*, *N. woodwardii*, *N. burgundiae*, *N. micraulus*) are compared to the genotype. Quantitatively, differences can be expressed in terms of only two test variables, always including either the horizontal length of the periproct and/or its distance from the apical disc. The size of the periproct is again facies dependent. The length of the anal sulcus, however, is consistently shorter in stratigraphically younger species.

7. A sample of each of two Cretaceous species (*N. subquadratus*, *N. rotundus*) is compared with the Jurassic species. These two samples are as distinct from the genotype as are the Jurassic species, excluding *N. latiporus*. Differences between all nine species relate partly to the size of the periproct (a facies dependent variable) and partly to the distance of the apical disc from the anterior of the test (a dimension which becomes consistently shorter in the stratigraphically younger species). The length of the anal sulcus, significantly different between middle and upper Jurassic species, does not become significantly shorter in the Cretaceous species studied.

8. Comparison of the two samples of the Recent *Apatopygus recens*, from different localities off the New Zealand coast, shows infraspecific
variation similar to that observed for *N. scutatus*. *A. recens* is known to burrow completely within a coarse substrate and ingest large substrate particles for food. It is inferred from its close morphological similarity and similar sedimentary associations that *N. scutatus* also burrowed completely within coarse, mainly oolitic sediments. The relationship between size of periproct and sediment grains established for *N. scutatus* indicates that it similarly ingested large substrate grains. These habits are therefore of ancient origin in the order Cassiduloida.

9. Biometrical analyses reveal inconsistencies in the levels of taxonomic differentiation between species of *Nucleolites*. First, a low level of discrimination is evident between *N. scutatus* and *N. latiporus* and also between *N. amplus* and *N. woodwardii*. Second, a higher level of differentiation distinguishes the remaining species from each other and from the genotype, *N. scutatus*.

At the first, low level of discrimination species can only be effectively distinguished by stratigraphy and may therefore represent chronospecies within evolutionary lineages. The second level may represent distinction of separate lineages.

10. In the absence of significant morphological distinction between *N. latiporus* and *N. scutatus* it is proposed that the nomenclature of the lineage should be defined on stratigraphic criteria following conventional usage. Distinction within this lineage is, therefore, made at the middle-upper Jurassic boundary. The taxon *N. latiporus* Agassiz 1839 is restricted to samples of Bajocian to Callovian age. *N. scutatus* Lamarck 1816 is restricted to samples of Oxfordian to Kimmeridgian age.

It may only be possible to distinguish between *N. amplus* Agassiz and *N. woodwardii* in a similar manner.
11. Examination of canonical variate plots indicates that vectors characterising different test dimensions can be identified. One vector, usually characterising the position of the apical disc on the aboral surface or the length of the anal sulcus, is highly correlated with the stratigraphic age of the samples. Another, orthogonal, vector is closely correlated with test elongation, and is a time independent character. The predictability of such vectors is confirmation that the vectors can be interpreted in terms of age and elongation of species. The interpretation of such vectors is important in identifying evolutionary (time dependent) trends within fossil groups. Detailed objective methods of analysis may only be possible through the use of such multivariate techniques.

12. Figure 11.1 is a summary of phylogenetic relationships between the 10 species studied. The phylogenetic diagram is based on biometrical analyses alone.
<table>
<thead>
<tr>
<th></th>
<th>Rounded</th>
<th>Elongate</th>
</tr>
</thead>
<tbody>
<tr>
<td>Quaternary</td>
<td></td>
<td>recens</td>
</tr>
<tr>
<td>Pliocene</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Miocene</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Oligocene</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Eocene</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Palaeocene</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Maastrichtian</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Senonian</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Turonian</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cenomanian</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Albian</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Aptian</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Neocomian</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Portlandian</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Kimmeridgian</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Oxfordian</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Callovian</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bathonian</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bajocian</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Aalenian</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lias</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Trias</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Figure 11.1. Summary of phylogenetic relationships between the species studied as inferred from biometrical analyses only. Double-lined stratigraphical ranges indicate endocyclic species; ringed lineages indicate chronospecies as defined herein.


327


Cotteau, G.H. 1883. Échinides du sud-ouest de la France.


Cotteau, G.H. & Triger, J. 1869. Échinides du département de la Sarthe, descriptions des familles et des genres.


Guillier, A. 1868. Notice géologique et agriculture à l'appui des profiles géologiques des routes importantes de la Sarthe.


Fig. 1  *Nucleolites scutatus* Lamarck.
Specimen X544 from Upware Quarry, Cambridgeshire, Parandieri Subzone (Oxfordian).
Specimen size; Length (A) = 25.6 mm, Breadth (B) = 24.3 mm, Height (C) = 13.9 mm.

On all plates specimens are lettered as follows:–

a - aboral view
b - adoral view
c - posterior view
d - ambitus viewed from left (ambs IV and V visible)
Fig. 1  *Nucleolites amplus* Agassiz.
Specimen 027 from Signy l'Abbaye, Ardennes, Discus Zone (Bathonian). Specimen size;
Length (A) = 30.9 mm, Breadth (B) = 31.3 mm,
Height (C) = 16.3 mm.

Fig. 2  *Nucleolites woodwardii* Wright.
Specimen L137 from Marquise, Pas-de-Calais, Bathonian. (From the Lambert Collection, Paris, specimen 989). Specimen size; Length (A) = 29.4 mm, Breadth (B) = 28.6 mm, Height (C) = 13.8 mm.
Fig. 1  *Nucleolites latiporus* Agassiz.
Specimen 010 from Stratton Audley, Oxfordshire, Discus Zone (Bathonian). Specimen size;
Length (A) = 22.4 mm, Breadth (B) = 20.9 mm,
Height (C) = 11.8 mm.

Fig. 2  *Nucleolites elongatus* Agassiz.
Specimen 068 from Ranville, Calvados, Bathonian.
(From the Lambert Collection, Paris).
Specimen size; Length (A) = 26.2 mm, Breadth (B)
= 20.4 mm, Height (C) = 11.5 mm.
Fig. 1  *Nucleolites micraulus* Agassiz.
Specimen V8 from Villers-le-Tourneur, Ardennes, Lower Oxfordian. Specimen size;
Length (A) = 21.1 mm, Breadth (B) = 19.4 mm,
Height (C) = 11.2 mm.

Fig. 2  *Nucleolites subquadratus* Agassiz.
Specimen BA2 from Devecey, Doubs, Neocomian.
Specimen size; Length (A) = 23.1 mm, Breadth (B)
= 20.6 mm, Height (C) = 11.4 mm.
PLATE 5

Fig. 1 **Nucleolites rotundus** (Peron & Gauthier).
Specimen CE1 from Bou Saada, Algeria, Cenomanian.
(From the Lambert Collection, Paris).
Specimen size; Length (A) = 31.7 mm, Breadth (B) = 29.4 mm, Height (C) = 16.2 mm.

Fig. 2 **Apatopygus recens** (Milne Edwards).
Specimen ZZ39 from Wellington Harbour, New Zealand, Recent. Specimen size; Length (A) = 27.7 mm, Breadth (B) = 25.3 mm, Height (C) = 12.2 mm.