A QUANTITATIVE STUDY OF VARIATION WITHIN THE MESOZOIC ECHINOID NUCLEOLITES.
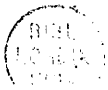
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A quantitative study of variation within the Mesozoic
echinoid <u>Nucleolites</u>.   D.G.A.Scurry.

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
<u>Nucleolites</u> and its probable living descendant <u>Apatopygus recens</u>.
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
<u>Nucleolites</u> from the Jurassic (<u>N.amplus</u>,<u>N.burgundiae</u>,<u>N.elongatus</u>,
<u>N.latiporus</u>,<u>N.micraulus</u>,<u>N.scutatus</u>,<u>N.woodwardii</u>) of England and
France and Cretaceous (<u>N.rotundus</u>,<u>N.subquadratus</u>) of France and
North Africa.

The genotype,<u>Nucleolites scutatus</u>,is represented by seven
samples. Significant infraspecific 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
<u>N.latiporus</u> (= <u>N.clunicularis</u> auct.). Statistical differences
between <u>N.latiporus</u> and <u>N.scutatus</u> are of the same order as between
infraspecific samples of <u>N.scutatus</u>.

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.

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

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CONTENTS

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 earliesc 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 Bajocian 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 & Thiery, 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
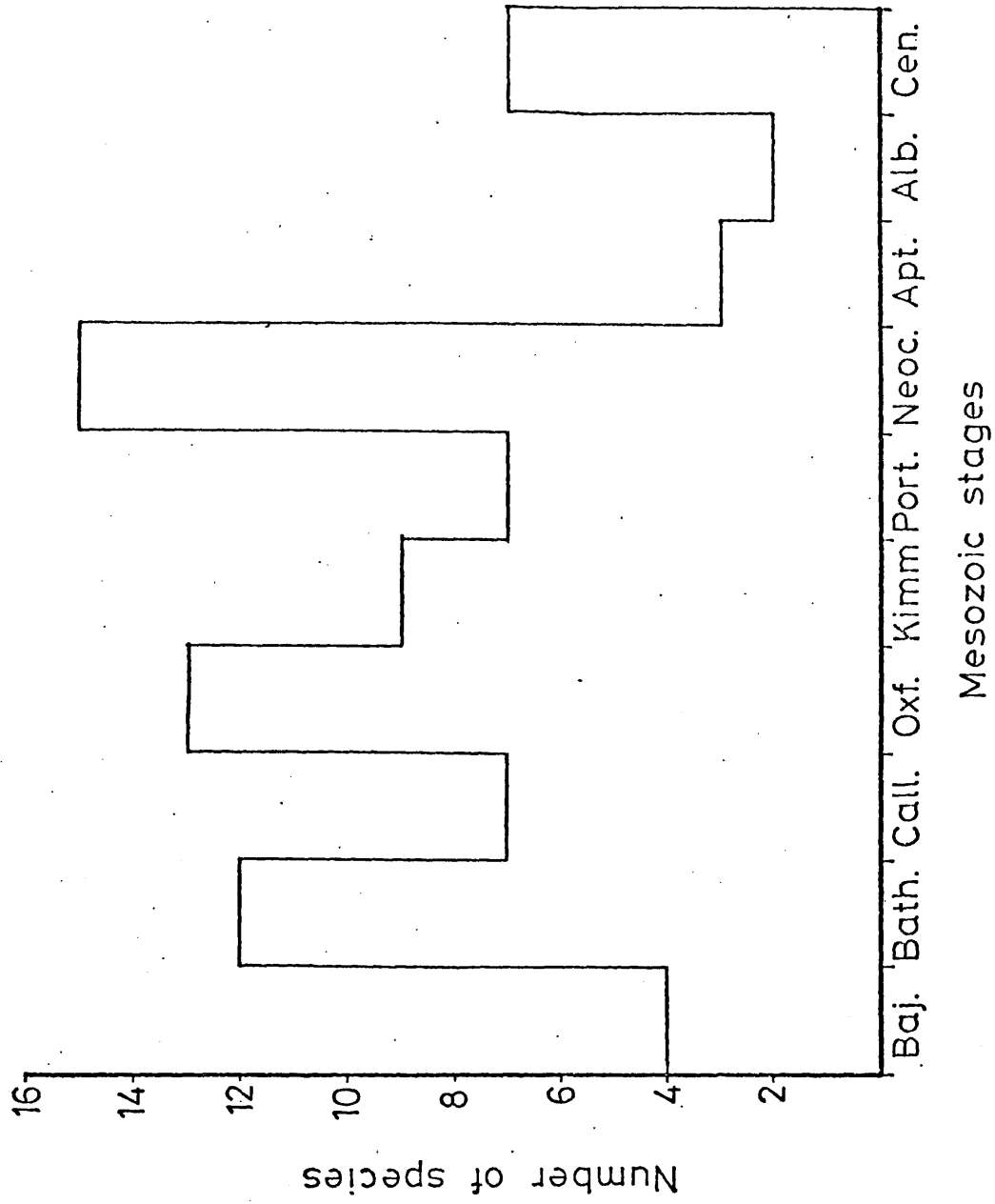
Figure 1.1. Occurrence of species of Nucleolites. (Based on. Lambert & Thiéry (1909) and Parisian collections.)

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considered synonymous with Nucleolites by most authors. There has

been considerable controversy related to the use of the names

Nucleolites and Echinobrissus 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, Oolopygus 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.

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.(N.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)

SYSTEM	STAGE	ZONE	SUB-ZONE	N.scutatus	N.amplus	N.burgundiae	N.elongatus	N.latiporus	N.micraulus	N.rotundus	N.subquadratus	N.woodwardii
CRETACEOUS	MAASTRICHT.											
	SENONIAN											
	TURONIAN											
	CENOMANIAN											
	ALBIAN										X	X
	APTIAN											O X
	BARREMIAN											
	HAUTERIVIAN											
	VALANGINIAN								O	O?	O	
	BERRIASIAN											
	PORTLANDIAN											
	U.KIMMERIDGE.											
	L.KIMMERIDGE.	pseudocordata										
		decipens		X								
		transversarium	cautisnigrae									
			nunningtonense									
			parandieri	O								
	OXFORDIAN	plicatilis	antecedens	O								
			vertebrale	O								
		cordatum	cordatum	O								
			costicardia									
			bukowski									
		mariae										
		lamberti										
		athleta								O		
	CALLOVIAN	coronatum										
		jason										
		calloviense										
		macrocephalus										
JURASSIC		discus	discus		O		O X	O O X X X X X O X O O			
			hollandi				X					
	BATHONIAN	aspidoides			X?	O?						
		retrocostatum										
		morrisi										
		subcontractus										
		progracilis										
		zigzag										
		parkinsoni										
		garantiana										
	BAJOCIAN	subfurcatum										
		humphriesianum										
		sowerbyi										
		concavum										
		murchisonae										
		scissum										
		opalinum										
	TOARCIAN											
	UP.LIENSBACH											
	L.LIENSBACH											
	SINEMURIAN											
	HETTANGIAN											

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.

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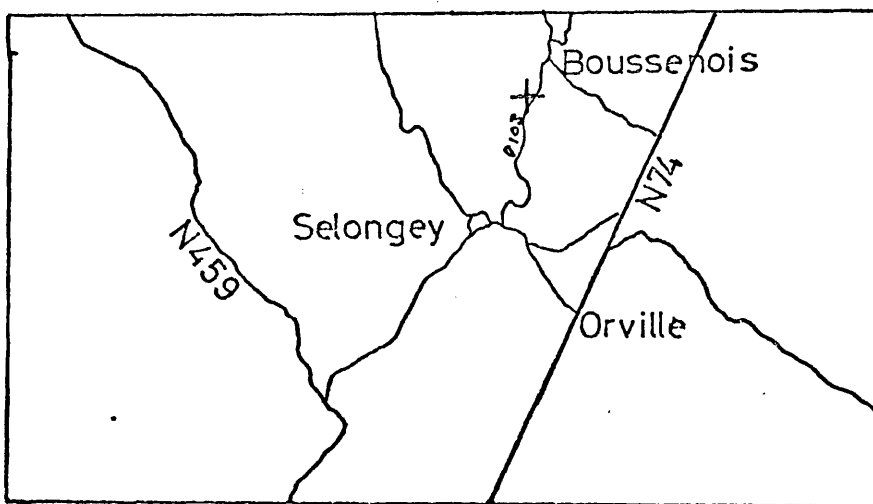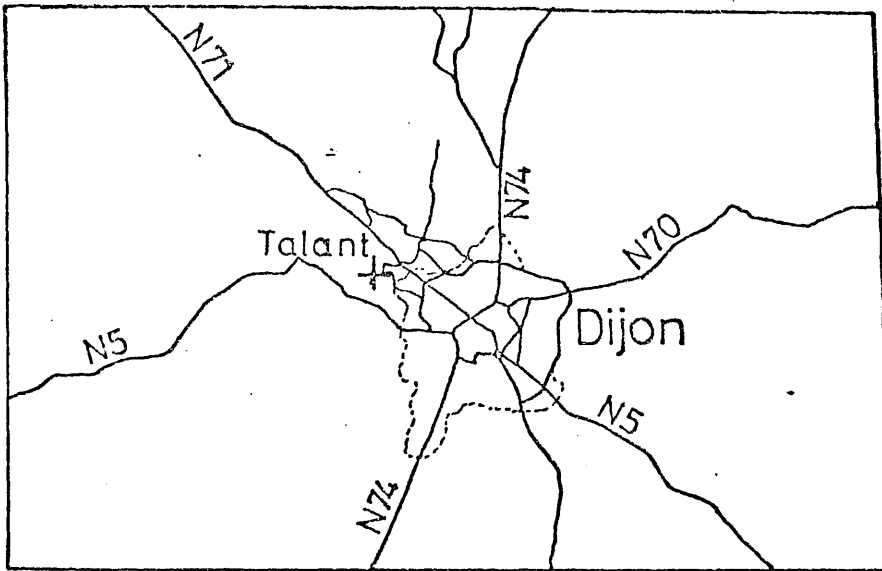
Figure 2,3b. Location of the French samples of Selongey
and Talant, Cote d'Or. + = location of
sample. Scale: 1cm to 2km.
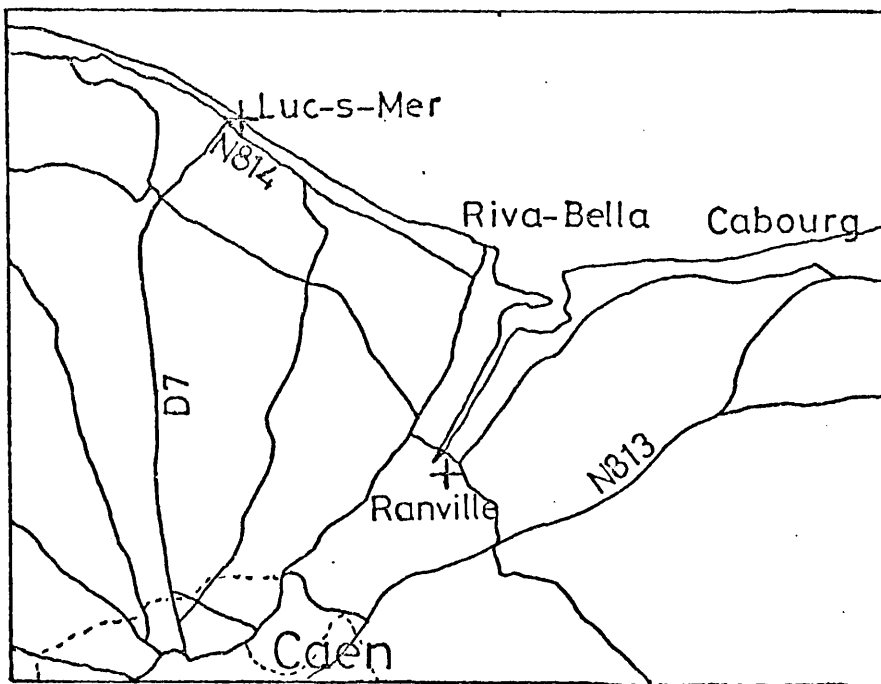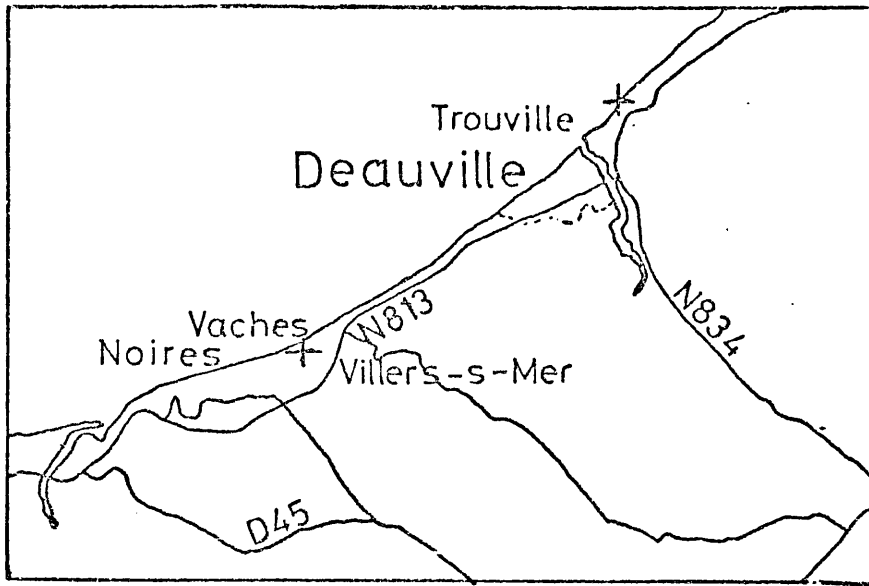
Figure 2,3c. Location of the French samples of Luc-sur-
Mer, Ranville, Vaches Noires and Trouville,
Calvados. + = location of sample.
Scale: 1cm to 2km.

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.
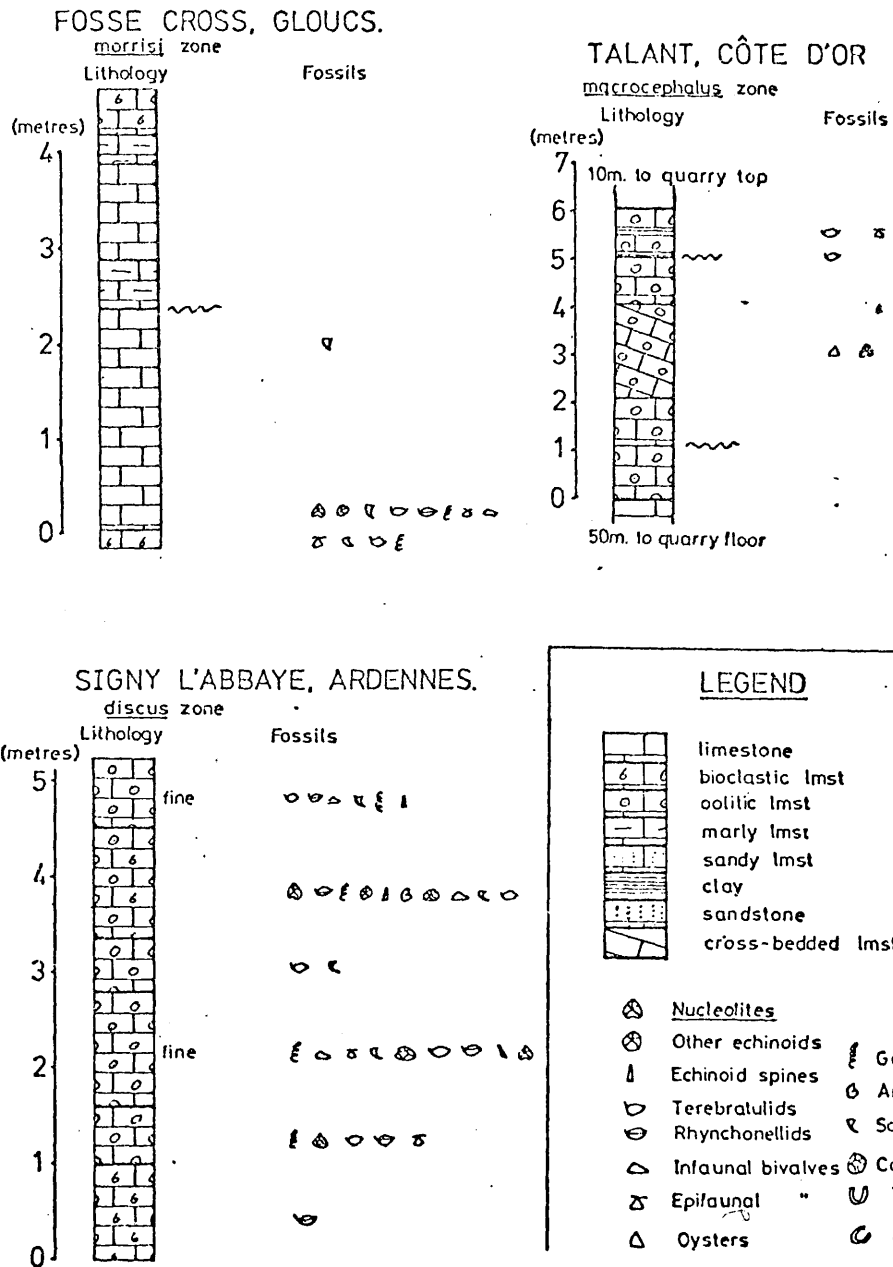
BECKLEY, OXON
parandieri subzone
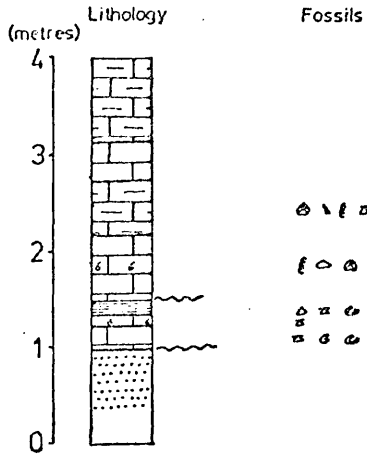
COTHILL, OXON.
antecedens subzone
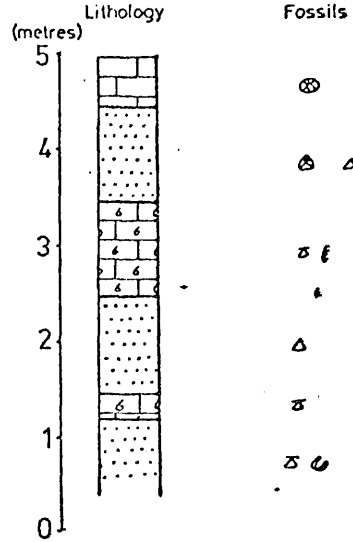
APPLETON LE STREET, N. YORKS.
vertebrale subzone
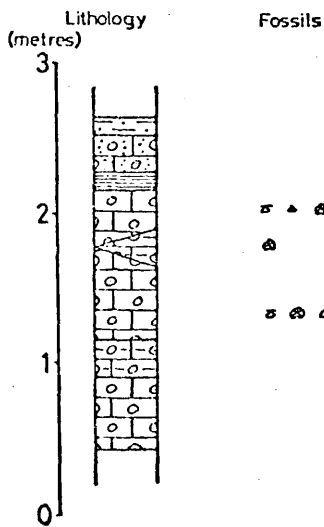
Fig. 2,4. cont.

BRAN POINT, DORSET
antecedens and parandieri sub-zones
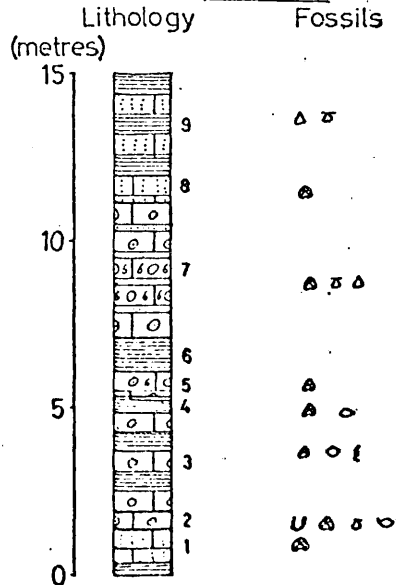
Species	Locality	Sample Name	Computer name and code	Facies	No.spec. collected /perfect		Age	Recent Stratigraphic Reference
N.scutatus[a]	Bran Point,Dorset (SY 743814)	Bran Point	DORSET D	Fine grained blue-grey marl	28	16	antecedens subzone	Cope & Torrens 1969
	Dry Sandford Quarry Oxon.,(SU 466996)	Cothill	HILL H	Fine calc. sandstone	38	17	antecedens subzone	Callomon 1960
	Hennequeville, Calvados	Trouville shore	TROUVL O'VLLE T O	Dark oomicrite	62	47	antecedens subzone	Arkell 1930
	Hennequeville, Calvados	Trouville cliff	TROUVL T	Grey oosparite	140	60	antecedens subzone	Arkell 1930
	Calne,Wilts. (ST 998765)	Calne	CALNE C	Biomicrite	8	5	plicatilis zone	White 1925
	M4 Wootton Bassett Wilts., (SU 073843)	Wootton Bassett	M4 W.B. M W	Coarse oosparite	52	17	plicatilis zone	White 1925
	Upware,Cambs., (TL 542723)	Upware	UPWARE U	Coarse intramicrite	133	76	parandieri subzone	Callomon 1960
N.latiporus[b]	Stratton Audley Oxon., (SP 602253)	Stratton Audley (N. latiporus)	6STRAT 6	Biomicrite	14	9	discus zone	Douglas & Arkell 1932
	Hydrequent Pas de Calais	Hydrequent	MHYD HYD M H	? Museum collection	8	7	Low or mid Bathonian	Ager & Wallace 1966
	Talant,Cote d'Or	Talant	1TAL 1	Rubbly oolite	10	5	macroceph. zone	pers. comm.

Figure 2,5.   Summary of stratigraphic data for localities sampled and computer descriptions used in figs.5,1 to fig.9,11.

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	Stratton Audley Oxon. (SP 602253)	Stratton Audley (N. elongatus)	EL	E				discus zone	Douglas & Arkell 1932
N.elongatus					Biomicrite	7	2	discus zone	
N.amplus	Signy l'Abbaye, Ardennes	Signy	ABBAYE	A	Pelsparite	39	10[d]	discus zone	Fischer 1969
N.woodwardii	Marquise, Pas de Calais	Marquise	HMARQU MARQU	H M	? Museum collection	7	4[d]	Bathonian	Museum coll.
N. burgundiae	Selongey, Cote d'Or	Selongey	BURG?	B	Biomicrite	4	0	Bathonian	Museum coll.
N.micraulus	Villers-le-Tourneur, Ardennes	Villers	VILLER	V	Limonitic oolite	45	25	Lower Oxfordian	None
N.subquadratus	Devecey, Doubs.	Devecey	QUAD	Q	Biomicrite	25	13	Neocomian	None
N.rotundus	Bou Saada, Algeria	Bou Saada	ROT	R	? Museum collection	3	3	Cenomanian	Cotteau et al 1878
A.recens [c]	Nelson, New Zealand	Nelson	NELSON	N	? Museum coll.	18	4[e]	Recent	None
	Wellington Harbour, New Zealand	Wellington	WELL	W	? Donation	23	0[c]	Recent	None

(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.)

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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 resemblence 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 spatangoid

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
Llhwyd's "Micraster"and Scheuchzer's E.spatagoidoeus,while the
medium sized species is referred to Llhwyd'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 Llhwyd'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 Llhwyd,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 Llhwyd'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 Llhwyd'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 Micraster 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 quadrate 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"Micraster". He rightly identified his Spatangus depressus with both Echinobrissus species of Breynius and to the Echinites 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 Micraster and Lang's damaged specimen of Nucleolites which had only four visible ambulacra.

Leske also describes another species S.subglobosus,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

<u>oblitum</u> (I.C.Z.N. Article 23 b).

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

"Corps ovale ou cordiforme garni des plusieus rangées des pres qui forment des ambulacres completes,rayonnant du somment à la base. Bouche subcentrale,anus au-dessus du bord." He makes no reference to earlier works and is apparently unaware of <u>Echinobrissus</u> 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,<u>Nucleolites scutata</u> is described as 'elliptical,subquadrate, convexo-depressed,broad posterior,five complete ambulacra,anus dorsal.' To this species,the type species of <u>Nucleolites</u>,he refers to <u>Echinobrissus planior</u>,<u>Spatangus depressus</u> and <u>Echinites cordatus subluteus</u> as synonyms,again grouping probable 'scutatus' and 'clunicularis' forms under a single specific name. He also lists a second variety to which he refers <u>Echinobrissus elatior</u> of Breynius.

Lamarck is therefore the author of <u>Nucleolites</u> since he is the first post-Linnaean author to use a separate generic name for this group,of which the first described species is <u>Nucleolites scutatus</u>. The only other post-Linnaean author to which Lamarck

refers is 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.Z.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 existance 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 Cluniculus 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, pp347.

    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 <u>Nucleolites</u>; Agassiz, p.4.

1840 " ; Dujardin, v.3, p.341.

1847 " (non Type B); Agassiz & Desor, p.95.

1854 <u>Echinobrissus</u>; d'Orbigny, p.24.

1855 " ; d'Orbigny, v.6, p.388.

1855 <u>Nucleolites</u>; Aradas, p.12.

1857 <u>Echinobrissus</u>; 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 <u>Echinobrissus</u>; Agassiz, p.108.

1873 " ; Loriol, p.254.

1874 " ; Quenstedt, p.433.

1879 " ; Zittel, p.529.

1879 <u>Echinobrissus</u>; Zittel, p.528.

1881 " ; Cotteau,Peron & Gauthier, p.161.

1883 " ; Cotteau, p.108.

1883 " ; Pomel, p.58.

1883 <u>Nucleolites</u>; Pomel, p.57.

1887 <u>Echinobrissus</u>; Duncan, p.429.

1889 " ; Gauthier, p.47.

1891 " ; Duncan, p.157.

1898 <u>Nucleolites</u>; Lambert, p.25.

1903 " ; Delage & Herouard, p.264.

1904 " ; Meissner, p.1385.

1913 " ; Jackson, p.289.

1921 " ; Lambert & Thiery, p.344.

1921 Echinobrissus;Lambert & Thièry, 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.

1966   "   ; Kier, p.501.

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 Phyllobrissus 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 clypeiids 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.amplus 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

describeClypeus (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

herein 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

1693 Echinites clunicularis (in pars) Llhwyd,p.48.

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 (Llhwyd); 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   "   "   Lamark; 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 scutaus Lamarck; Morris, p.55.

1847   "   "   Lamark; Agassiz & Desor, p.95.

1847   Nucleolites diamidiatus (Phillips); Agassiz & Desor,p.95.

1848   "   "   (Phillips); Bronn, p.818.

1848   Nucleolites goldfussi Des Moulins; Bronn, ·p.818.

1848   Nucleolites paraplesius Agassiz; Bronn, p.818.

1848   Nucleolites scutatus Lamarck; Bronn, p.818.

1848   Nucleolites planulatus M'Coy, v.2, p.116.

1849   Nucleolites clunicularis (in pars); Forbes, pl.9.

1849   Nucleolites dimidiatus (Phillips); Forbes, p.7.

1850   "   "   (Phillips); d'Orbigny, v.1,p.379,

                                         No.507.

1850   Nucleolites scutatus Lamark; d'Orbigny, v.1, p.379,No.505.

1851   "   "   Lamarck; Bronn, v.2,p.171,figs.a,b,c,·

1851   Nucleolites dimidiatus (Phillips); Wright, p.38.

1852   Nucleolites scutatus Lamarck; Wright, p.25.

1852   "   "   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   "   · "   (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 goldfussi (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 goldfussi (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 goldfussi (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,30-32,4

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,bourrelets 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.clunicularis, 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; antecendens sub-zone,27 specimens.

Bran Point,Dorset; antecendens sub-zone,28 specimens.

Calne,Wiltshire; plicatilis zone,8 specimens.

Wootton Bassett,Wilts.; Corallian,52 specimens.

Cothill,Oxfordshie; 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.;vertebrale sub-zone,34 specimens.

Swinton Grange,North Yorks.; vertebrale sub-zone,42 specimens.

Lyons Plantaion,North Yorks.; vertebrale 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.; vertebrale 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.

Collection of Musée d'Histoire Naturelle, Paris.

Collection of Université de Dijon.

Collection of the Musée d'Histoire Naturelle ,Neuchatel,Switzerland.

The location of Lamarck's type specimens is unkown. 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
Holectypus 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

particlesscattered 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 & Loriol, 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   Nulceolites 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
clypeiids 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:

Collection of Musée d'Histoire Naturelle, Paris..

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 rhynchonellid brachiopods (Kallirhynchia deliciosa,
Burmirhynchia turgida,Isjuminella thierachensis) are common
throughout,most of the brachiopods tending to be large and spherical.
Solitary corals (Montlivaltia tenuiradiata,Chromatoseris orbulites)
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,Holectypus depressus and fragments of large clypeiids were also found. Pseudomelania sp.,Kallirhynchia deliciosa, Burmirhynchia turgida and echinoid spines are common whilst a rare fragment of an ammonite,small corals and some terebratulids (e.g. Eudesia cardium and Cererithyris 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 pelsparite 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 appearence 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; Cottreau,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 b 903,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 firstdescribed by Cotteau (1871) and placed in the genus Echinobrissus after d'Orbigny (1854). It was transferred to Pomel'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 Cottreau (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. Signey l'Abbaye,Ardennes; discus zone,1 specimen.

Specimens collected but not used in the biometrical anayses: 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 11cms. long and smaller,ornate P.deltoidea. Small
brachiopods were also found including Epithyris,Wattonithyris and
Sphenorhynchia. Other echinoids included N.latiporus and
Holectypus 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 microcrystaline 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 floscelle.

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 brachiopodsare 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 clypeiids.

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 clypeiids 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

Nucleolites latiporus Agassiz, 1839

(Plate 3, fig. 1a-d)

1678		Lister, p.233, pl.7, fig.26.
1699	Echinites clunicularis	(in pars), Llhwyd, p.48.
1712	" "	Llhwyd; Morton, p.233, pl.10, fig.9.
1732	Echinobrissus planior	Breynius, p.63, pl.6, figs.1-2.
1817b	Clypeus clunicularis	(Llhwyd)(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	" "	(Llhwyd); Bronn, p.282, (form A), pl.17a, fig.13.
1837	" "	(Smith); Des Moulins, p.358, no.15.
1837	" "	(Smith); Agassiz, p.278.
1839	Nucleolites latiporus	Agassiz, p.63, pl.7, figs.13-15.
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 pyramidalis	M'Coy, v.2, p.116.
1848	Nucleolites eaqualis	M'Coy, v.2, p.116.
1848	Nucleolites clunicularis	(Llhwyd); 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   (Llhwyd); Forbes,pl.9.

1850   "   "   (Llhwyd); 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   (Llhwyd); d'Obigny, 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.

1850   Nucleolites edmundi   Cotteau; d'Orbigny, v.1,p.319,no.406.

1850   Nucleolites oblongus   d'Orbigny, v.1,p.319,no.407.

1850   Nucleolites sarthacensis   d'Orbigny, v.1,p.290,no.501.

1851   Nucleolites clunicularis   (Llhwyd); Wright,p.297.

1851   "   "   (Llhwyd); Bronn, p.152.

1852   Nucleolites latiporus   Agassiz; Giebel, p.322.

1853   Nucleolites clunicularis   (Llhwyd); Gueranger, p.25.

1854   "   "   (Llhwyd); Forbes, p.84.

1854   Echinobrissus clunicularis   (Llhwyd); 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   (Llhwyd); Wright, p.310.

1857   "   "   (Llhwyd); 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   (Llhwyd); 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 (Llhwyd); Guillier, p.25.

1869   "   "   (Llhwyd); Cotteau & Triger, p.419.

1869   "   "   (Llhwyd); Brauns, p.64.

1869   "   "   (Llhwyd); Wright, p.49.

1870   "   "   (Llhwyd); Greppin, p.51,p.56.

1871   "   "   (Llhwyd); Desor & Loriol, p.305,

                                      pl.48,figs.3-8.

1871   "   "   (Llhwyd); Cotteau

1913 Nucleolites clunicularis (Llhwyd); Jackson, fig.408,a,b.

1921 Echinobrissus clunicularis (Llhwyd); Cotteau,Lambert & Thiery,p.343

1925   "   "   (Llhwyd); Deecke, p.440.

1932   "   "   (Llhwyd); Mercier, p.227,pl.10,fig.1.   -

1932 Echinobrissus latiporus (Agassiz); Mercier, p.232,pl.10,fig.5.

1933 Echinibrissus clunicularis (Llhwyd); Beurlen. p.53,fig.8.

1948   "   "   (Llhwyd); 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   "   "   (Llhwyd); 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 Llhwyd (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 Artible 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 Llhwyd). 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 periproct lying 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.

<u>Material</u>

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; <u>discus</u> zone, 15 specimens.

Talant,Cote d'Or; <u>macrocephalus</u> zone, 10 specimens.

Specimens collected but not used in the biometrical analyses:

Burton Bradstock,Dorset; <u>discus</u> zone, 2 specimens.

Kirtlington,Oxfordshire; <u>discus</u> zone, 4 specimens.

Lower Stanton-le-Quentin, Wilts; <u>discus</u> zone, 1 specimen.

Ranville,Calvados; <u>discus</u> zone, 5 specimens.

Luc-sur-Mer,Calvados; <u>discus</u> zone, 3 specimens.

Thin-le-Moutier,Ardennes; <u>zigzag</u> zone, 6 specimens.

Cranford St.John, Northants; <u>subcontractus</u> zone, 6 specimens.

Aston Blank, Gloucestershire; <u>parkinsoni</u> zone, 4 specimens.

Chatel Censoir, Yonne; Bathonian, 2 specimens.

Ferques,Pas de Calais; Lower Bathonian, 2 specimens.

Selongey, Cote d'Or; Bathonian, 1 specimen.

Villers-le-Tourneur, Ardennes; Lower Oxfordian, 1 specimen.

Additional material examined:

Lambert collection,Université de Paris 6.

Collection of Musée d'Histoire. Naturelle ,Paris.

Collection of Université de Dijon.

<u>Palaeoecology</u>

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
rhynchonellid 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 biospatite
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 Holectypus
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 Holectypus 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 Holectypus 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 ,fig1a-d)

1839	Nucleolites micraulus	Agassiz, p.43,pl.7,figs. 16-18.
1840	" "	Agassiz; Agassis, p.4.
1847	" "	Agassiz; Agassiz & Desor, p.96.
1848	" "	Agassiz; Bronn, p.818.
1848	" "	Agassiz; Marcou, p.94.
1850	" "	Agassiz; d'Orbigny, v.1,p.345,No.459.
1852	" "	Agassiz; Buvignier, p.238.
1852	Nucleolites dimidiatus	(non Phillips); Quenstedt, p.585,pl.50,fig.5.
1854	Echinobrissus micraulus	(Agassiz); d'Orbigny, p.25.
1857	" "	(Agassiz); d'Orbigny, p.392. ·
1857	Echinobrissus goldfussi	(non Desmoulins); Desor, p.267.
1857	" "	(non Desmoulins); Cotteau & Triger,p.86,

pl.19,figs.1-2.

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.goldfussi 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.goldfussi Desmoulins as a separate species in the same work. The name N.goldfussi 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

Habitat	Fauna	Mode of life*	Originally aragonitic(*) or partly aragonite (+)	Silicified (*)
Nekton	Microsphinctes sp.	⎫	*	
	Cardioceras alphacordatum	⎬ nektic cephalopods	*	
	Cardioceras sp.	⎪	*	
	Dichotomosphinctes sp.	⎭	*	
Epifauna	C.(Aequipecten) sp.	capable of swimming	+	*
	C.(Radulopecten) sp.	byssate fissure dweller	+	*
	Ctenostreon sp.	byssate fissure dweller	+	*
	Spondylus sp.	cemented	+	*
	Lopha gregarea	cemented		*
	Postepithyris sp.	attached by pedicle		*
	Crinoids	cemented		*
	Nerinids	vagrant	*	*
	Holectypus depressus	vagrant		*
?epifaunal				
Semi-infaunal	Gervillia aviculoides	?byssate	+	
Shallow infaunal	Myophorella sp.	⎫	*	*
	Vaugonia sp.	⎬ very shallow burrowers	*	*
	Nucleolites latiporus	⎭		
	Nucleolites micraulus	⎫		
	Collyrites bicordata	⎬ deposit feeders		
	Hyboclypus sandelinus	⎪		
	Pseudomelania sp.	⎭	*	
Deep infaunal	Pleuromya sp.	⎫ siphonate burrowers	*	*
	Sowerbya sp.	⎭	+	
Unknown	Bathrotomaria sp.	(archaeogastropod)	*	

*Modes of life from Moore (1969), Fursich (1976).

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,Collyrites bicordata or Hyboclypus 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.

Silicification 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 silicifted. In contrast,the calcitic brachiopod
Postepithyris and some echinoids,e.g. Holectypus,have been silicified
whilst other echinoids such as Nucleolites micraulus and
Collyrites 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 silicifing environment would

account for the presence of so many attached forms. Attached

brachiopods (Postepithyris),byssate fissure dwellers (Radulopecten,

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 oncolitic 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 & thiery,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.

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 Hemiaster; the holectypoid 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 Turrilites 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 distincly 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 eccentricityy

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,Phyllobrissus,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,fog.2.

1921   "   "   (Wright); Lambert & Thiẻry, 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.) E1590) from Salperton

Tunnel (D.Lewis,personal communication,1977).

Description

Test small to medium sized,thin,circular to sub-quadrate;

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 distinguihed

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, Gloucs: probably morrisi zone, 1 specimen.

Slape Hill,Oxfordshire; subcontractus zone, 13 specimens.

Ardley,Oxfordshire; subcontractus zone, 18 specimens.

Aston Blank,Gloucs; parkinsoni zone, 1 specimen.

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 bioclasticdebris and is named from the many large

Clypeus plotii which dominate the fauna. Other echinoids present

include N.latiporus and Holectypus 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

rhynchonellids,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 monogeneric 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.

Genus Apatopygus   Hawkins,1920.

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.

1966 " ; Kier, p.522.

Type species

Apatopygus recens (Milne Edwards),1836 by monotypy and original designation of the author (Hawkins, 1920:395).

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; bourrelets 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.

pl.10,figs.9-10.

1872   "   "   (Milne Edwards); A.Agassiz, p.108,556,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.413,1a-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

10 and 40 m. only.

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. Bailey (1959) defines n < 30 as a small sample whilst also noting that much information can still be extracted from a small sample.

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 reproduceability 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 fasicole,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 echinoidsand 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 floscelle 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

Variable A : Greatest length of test.

" B : Greatest breadth of test taken at right angles to A.

" C : Greatest height of test.

" D : Height of the apical system; from base of test to madreporite.

" E : Distance from anterior of test to centre of peristome, measured in an antero-posterior direction.

" F : Antero-posterior diameter of the peristome.

" G : Distance from the anterior of test to most anterior point of the sulcus at the posterior margin.

" H : Distance from anterior of test to the widest part of the test.

" I : Vertical height of the periproct.

" J : Length of the anal sulcus measured from the anterior of the periproct to the posterior margin of the test.

"   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 ocular 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 $P > 25$. 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
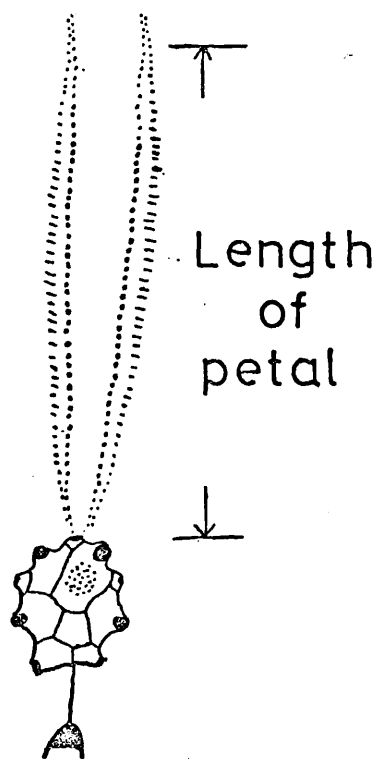
Figure 4,1. Length of petal, variables P and Q,
as defined in the text. Drawing of apical
disc and anterior ambulacrum of
Nucleolites elongatus (O 15) from the
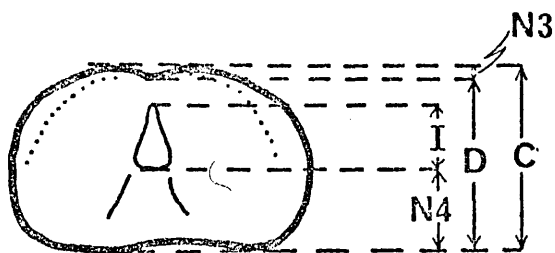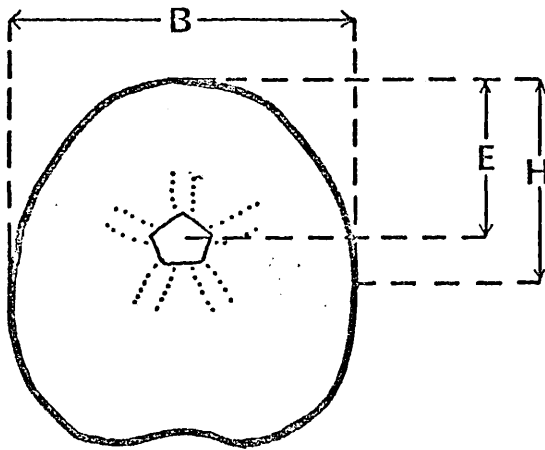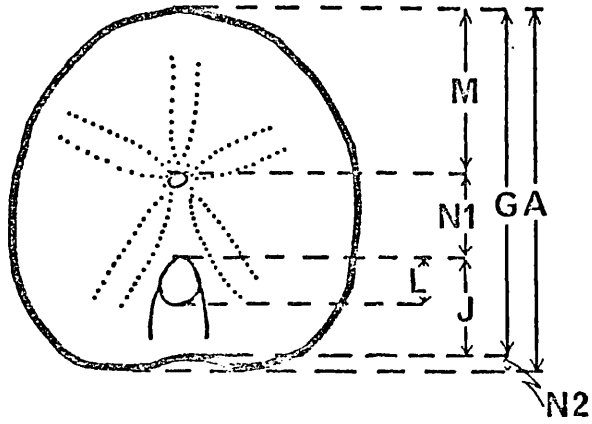Cornbrash (üpper Bathonian, discus zone)
of Stratton Audley, Oxfordshire.

Figure 4.2. Definition of variables A -- N4. See
text for exact definition of measurements.

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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 pricipal 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 $x_1, x_2 \ldots \ldots x_n$ that vary together but are instead represented by new independent variables $y_1, y_2 \ldots \ldots y_n$. 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 $\lambda_1 \geqslant \lambda_2 \geqslant \lambda_3 \ldots \ldots \lambda_n$

(λ_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 $K < n$ dimensions. Also since λ_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 O1M 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

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

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 - variate 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 conbinations 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_i are found

from

$$(B - zW)t = 0$$

and are the K - component vectors,t.

Progam BMD 07M is a stepwise dicriminant 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 BMO 07M Stepwise Discriminant

Analysis (see section 4.E,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

        σ_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 01M).

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

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

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 (á) based on both samples is found such that

$$á = \frac{a_1 \sigma_{a_2} + a_2 \sigma_{a_1}}{\sigma_{a_1} + \sigma_{a_2}}$$

and the variance of á is

$$\text{var } á = \frac{\sigma_{a_1} \sigma_{a_2}}{\sigma_{a_1} + \sigma_{a_2}}$$

New estimates of b ($\dot{B}_1$ and $\dot{B}_2$) 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 $\text{var}(\dot{B}_1 - \dot{B}_2) = \frac{\sigma_{y_1}^2 + á^2\sigma_{x_1}^2 - 2á\sigma_{x_1}\sigma_{y_1}r_1}{n_1} + \frac{\sigma_{y_2}^2 + á^2\sigma_{x_2}^2 - 2á\sigma_{x_2}\sigma_{y_2}r_2}{n_2} +$

$$(\bar{x}_1 - \bar{x}_2).\text{var } á$$

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 dendrograms 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 imediately proceeding clusters form a grouping of cases into reasonably discrete sets (see example, page 270).

5. Principal Component Analysis (BMD 01M)

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 λ_j is the jth 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

$$z = \sqrt{n-1} \; WB$$

which transforms the W data into their orthoganal 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 07M)

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 jth 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 elelments of the within group

cross-products matrix,with g-1 and n-r-g degrees of freedom.

g = number of groups used for analysis

n = total number of cases

r = 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:

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 jth 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.

$$F_{ml} = \frac{(n-g-r+1) \, n_m \, n_1}{r(n-g)(n_m + n_1)} \, D^2_{ml}$$

Where m and 1 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 1.

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' Λ to test the equality of group means

$$U = |W| / |T|$$

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

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

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

and n = total number of cases.

         k = number of groups.

         p = number of variables used.

χ^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 χ^2 statistic to some degree.

Rao (1965) advocates the use of a variance ratio to test

the value of Λ . For small values of k the exact variance ratio

is given as

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

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

For higher values of k a good approximation is to use

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

where s = $\sqrt{\dfrac{p^2(k-1)^2 - 4}{p^2 + (k-1)^2 - 5}}$

$$\lambda = \frac{p(k-1) - 2}{4}$$

with p(k-1) and (ms-2 λ) degrees of freedom. According to Rao (1975) this provides a better approximation than χ^2.

e) Approximate F statistic to test equality of group means

$$F = \frac{1 - U^{1/s}}{U^{1/s}}$$

where $s = \sqrt{\dfrac{r^2 q^2 - 4}{r^2 + q^2 - 5}}$ if $r^2 + q^2 \neq 5$

$s = 1$ if $r^2 + q^2 = 5$

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

where m n - $\dfrac{r + q + 3}{2}$ and q = g - 1.

The approximate F gives similar results to the test for Wilks' Λ.

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 mth 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,....t total number of groups.

    m = 1,2,....g

    k = 1,2,....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.

$$P_{1mk} = \frac{p_m \, \exp(s_{1mk})}{\displaystyle\sum_{i=1}^{g} p_i \, \exp(s_{1ik})}$$

where p_m is the prior probability of group m. The probability of case k belonging to group m is lower as P_{1mk} approaches zero.

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

This value, D^2_{1mk} , 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

$$Bu_i = \lambda_i \, Wu_i \qquad\qquad i = 1,2,\ldots\ldots\ldots p$$

is solved to find the coefficients, u_i, of the canonical variables and the amount of dispersion, λ_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

$$u_i' \, Wu_j = \delta_{ij}$$

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,......g

k = 1,......n total number of cases.

i = 1,......z canonical variables.

and the first two plotted on a scatter diagram.

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

Sample	Comparison sample	Page	Var.	Spec.	Technique	Sig. of difference	Imp. variables
1. Trouville shore	Trouville cliff	133	15	83	S.D.F.	P>5%	
		134	12	106	S.D.F.	P=5%	
		134	12	127	S.D.F.	P=5%	
		134	15	83	H.C.	Clustering not into original groups	
2. Trouville	Cothill	136	15	36	S.D.F.	P<1%	N2,I,M,B,A,
		139	15	250	R.M.A.	P<1% between 7 pairs of slopes	L
3. Cothill	W.Bassett	140	15	34	S.D.F.	P<1%	L,I,N4
		142	15	34	P.C.A.	Separation along 2nd vector	L,N2,J,N4
4. Trouville	Cothill, W.Bassett	145	15	53	S.D.F.	P<1%	L,N2,I
		146	15	53	P.C.A.	Greatest separation along 2nd vector	L,J
5. Trouville	Cothill, Dorset, W.Bassett, Upware	146	15	99	S.D.F.	P<1%	I,L,J,N3,N4,B,A,H
		152	15	463	R.M.A.	P<1% between 3-7 pairs of slopes	L
6. Trouville	Cothill, Dorset, Calne, W.Bassett, Upware	152	15	468	S.D.F.	P<1%	I,L,N4,J,H,B,A

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 07M: This program includes the construction of discriminant functions and a canonical variates
analysis. See p.94); P.C.A. = Principal components analysis (BMD 01M); 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 are 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 transversarium 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 transversarium 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. SU 073843). 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 Oxforshire,
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 antecendens 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 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 ocurred 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,BMDO7M,

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; N1

F value = 2.1 (Significance of the difference between group means;

$\qquad$ P $>$ 5%)

U-statistic = .701 (Significance of the inequality of group means; P $>$ 5%)

Specimens classified wrongly by posterior probability; 20%.

2. Chi-square

χ^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 N1 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,(Λ = .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 .447 .000,
Trouville shore -.878 .000.

O = Trouville shore
T = Trouville cliff
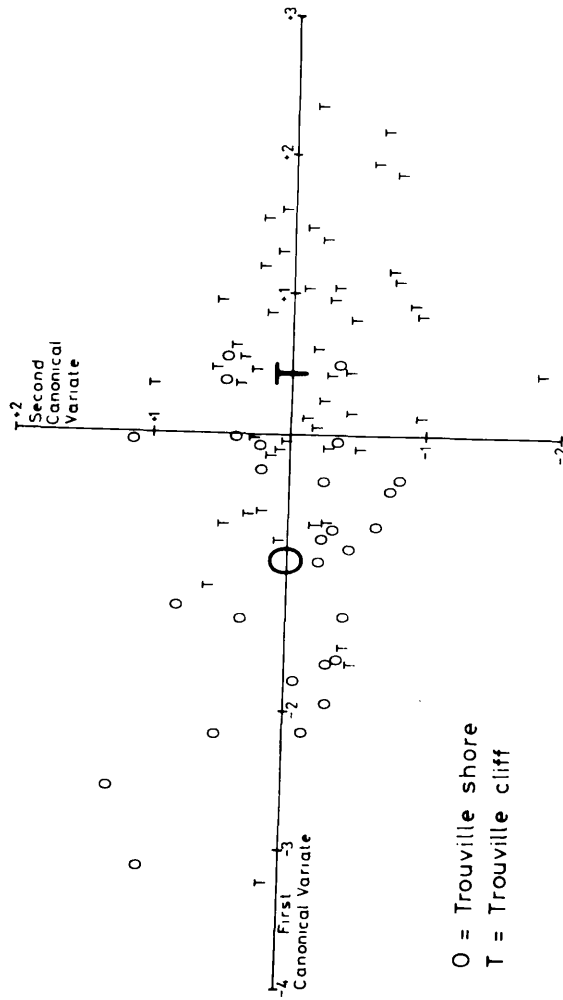
by the programme,although the errors of grouping beyond the fourth

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.

5E) 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).

<u>Step 1</u>

Variable N2 entered.

<u>Step 5</u>

Variables I,M,B and A added.

U-statistic = ·39 (Significance of the inequality of group means;

$$P = 1\%)$$

<u>Step 13 (final)</u>

Variables not included; D and N4

F value = 3.6 (Significance of difference between group means;

$$P = 1\%)$$

U-statistic = .320 (Significance of the inequality of group means:

$$P = 1\%)$$

Specimens classified wrongly by posterior probability; 6%.

χ^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
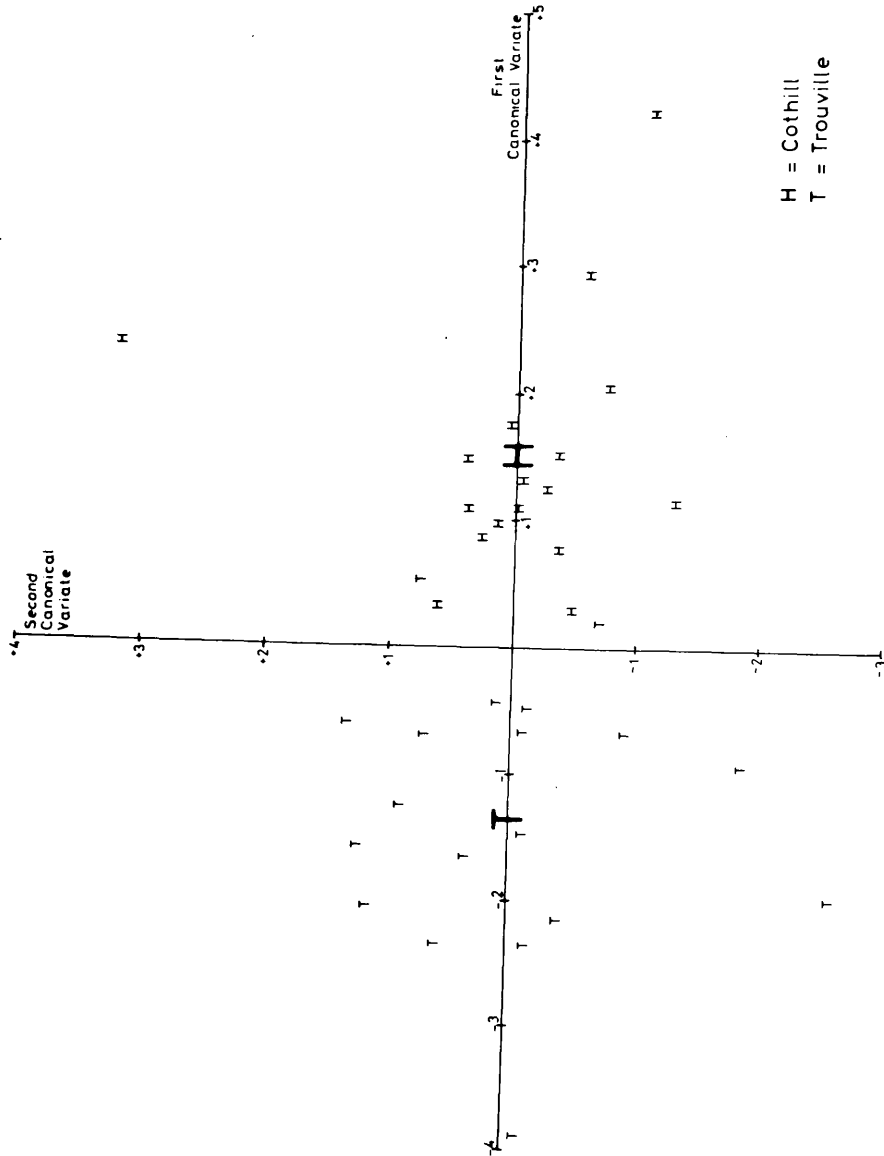
two sub-species are present in the foregoing analysis.

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,

		Square of Distance from and Posterior Probability for Group -			
Group Hill Case	Group with Largest Prob.	Hill		W.B.	
1	Hill	10.726	1.000,	50.542	.000
2	Hill	8.139	1.000,	27.629	.000
3	W.B.	10.467	.273,	8.511	.727
4	Hill	12.579	1.000,	35.153	.000
5	Hill	24.978	1.000,	51.952	.000
6	Hill	8.915	1.000,	43.104	.000
7	Hill	10.718	1.000,	41.007	.000
8	Hill	3.919	1.000,	24.245	.000
9	Hill	7.114	1.000,	23.297	.000
10	Hill	7.157	1.000,	26.550	.000
11	Hill	11.693	.998,	23.799	.002
12	Hill	11.902	1.000,	43.841	.000
13	Hill	29.416	1.000,	60.770	.000
14	Hill	16.233	1.000,	58.700	.000
15	Hill	7.894	1.000,	36.883	.000
16	Hill	13.359	1.000,	57.566	.000
17	Hill	11.358	1.000,	37.158	.000

Group W.B. Case		Hill		W.B.	
1	W.B.	30.799	.000,	9.974	1.000
2	W.B.	33.428	.000,	12.624	1.000
3	W.B.	59.953	.000,	14.810	1.000
4	W.B.	51.569	.000,	20.153	1.000
5	W.B.	40.894	.000,	14.328	1.000
6	W.B.	22.398	.000,	6.720	1.000
7	W.B.	55.399	.000,	23.778	1.000
8	W.B.	39.474	.001,	8.544	1.000
9	W.B.	25.952	.001,	11.196	.999
10	W.B.	21.963	.000,	5.564	1.000
11	W.B.	37.071	.000,	13.494	1.000
12	W.B.	36.623	.000,	8.566	1.000
13	W.B.	42.449	.000,	6.485	1.000
14	W.B.	22.982	.001,	8.513	.999
15	W.B.	51.208	.000,	15.120	1.000
16	W.B.	38.419	.000,	15.305	1.000
17	W.B.	42.997	.000,	14.261	1.000

Number of cases classified into group -

Group	Hill	W.B.
Hill	16	1
W.B.	0	17

Figure 5.4   Classification output for the Cothill (Hill) and Wootton 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,D2) 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.
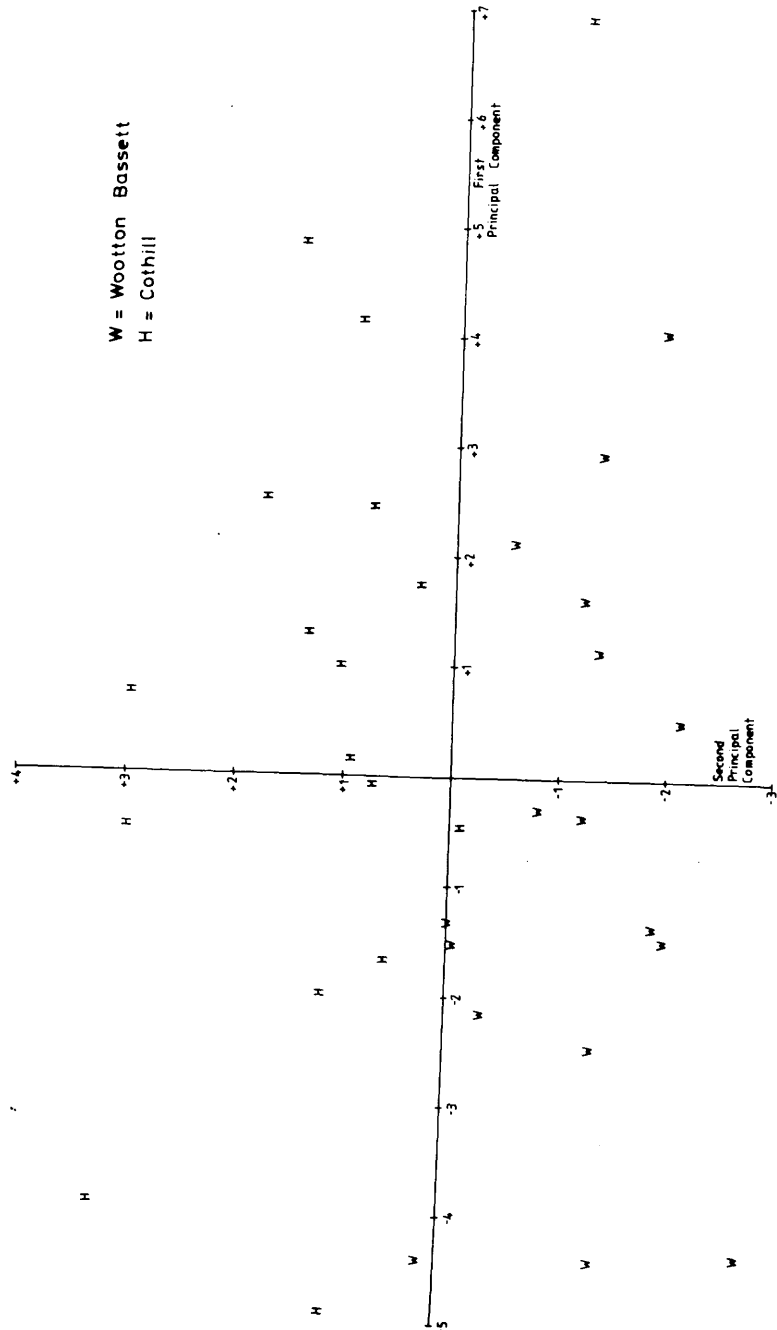
PRINCIPAL   COMPONENT   ANALYSIS

Cothill and Wootton Bassett samples

15 variables, 34 cases.

Eigenvalues

| 8.31 | 2.38 | 1.14 | 1.09 |

Cumulative proportions of total variance

| 55% | 71% | 79% | 86% |

Eigenvectors

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

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 periproct 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%.

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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 periƒeral 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.
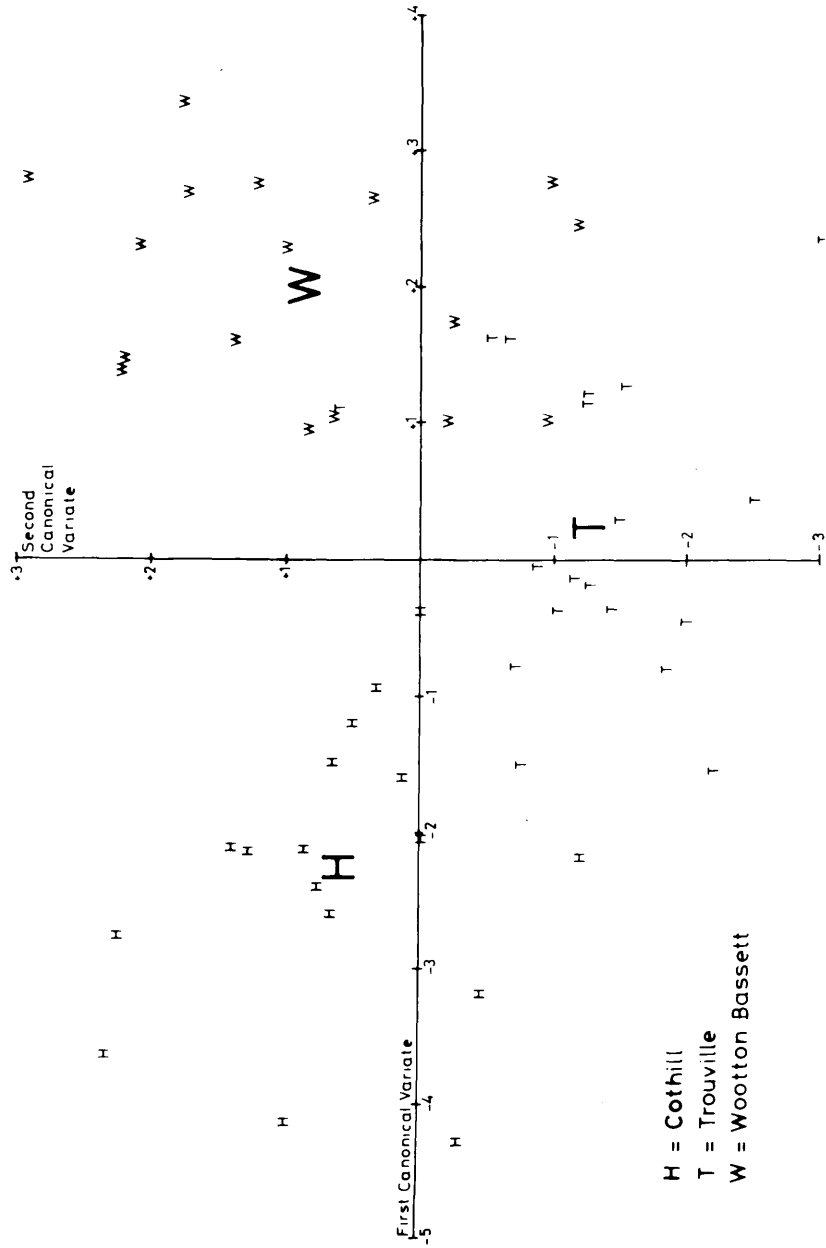
Figure 5.7. Distribution of Trouville
(T), Cothill (H) and Wootton Bassett
(W) specimens on the first two
canonical axes. Group centroids
indicated by large lettering.

Mean coordinates;

Trouville   .261   -1.310

Cothill   -2.307   .595

Wootton Bassett 2.016   .870

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

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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   -.498   .315
Wootton Bassett   .526   .469
Upware   2.586   -.217
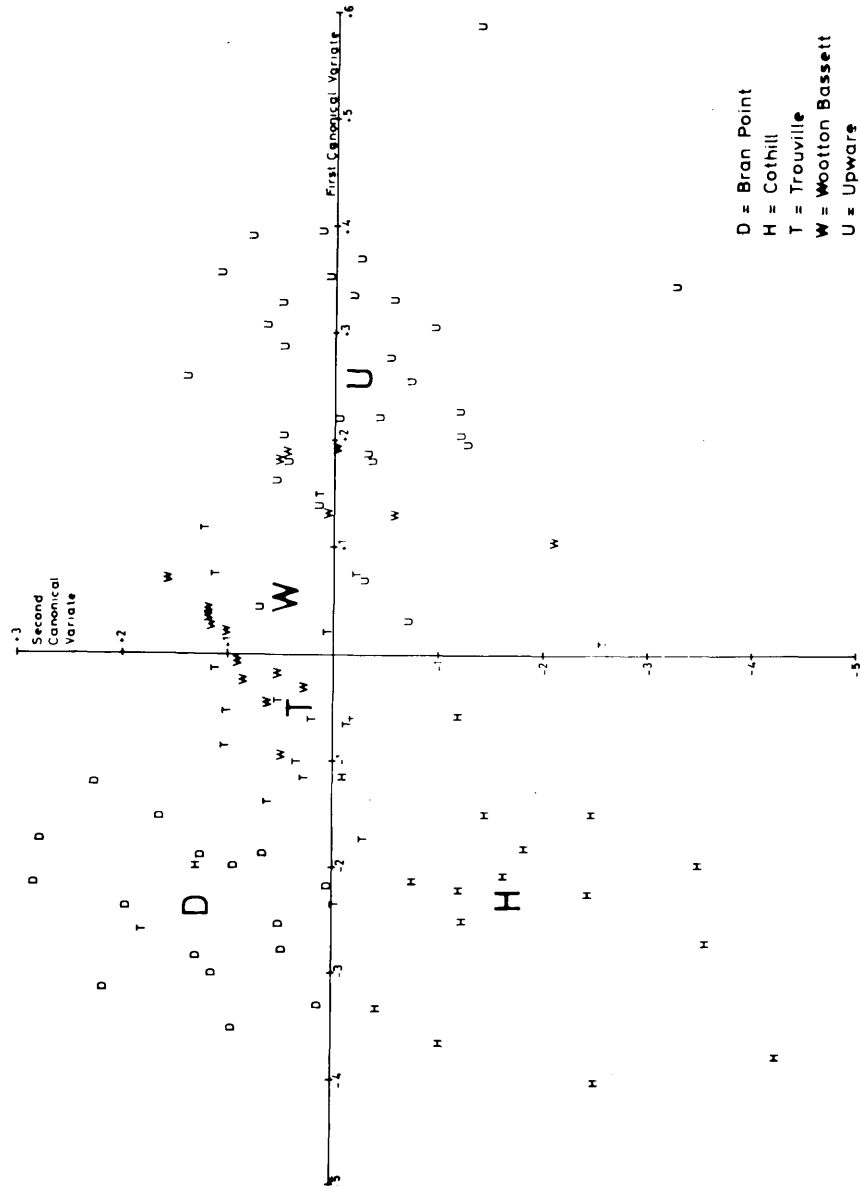
D = Bran Point
H = Cothill
T = Trouville
W = Wootton Bassett
U = Upware

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 χ^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

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Group \ Original Sample	Bran Point	Cothill	Trouville	W. Bassett	Upware
Bran Point	6.3%	31.3%	18.8%	31.3%	100%
Cothill	35.3%	11.8%	29.4%	47.1%	88.2%
Trouville	21.1%	26.3%	0.0%	10.5%	21.1%
W. Bassett	64.7%	70.6%	41.2%	17.6%	35.3%
Upware	96.7%	93.3%	36.7%	23.3%	0.0%

Figure 5,9. Percentage of specimens within each sample with a low probability (P<5%) of belonging to each group, based on χ^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
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%).

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.

5I) 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

Bran Point

	Bran Point	Cothill	Trouville	W.Bassett	Upware
A.	0				
B.	1				
C.	13		Cothill		
D.	3				
A.	1	1			
B.	0	1			
C.	13	12	Trouville		
D.	2	1			
A.	0	0	0		
B.	0	2	1		
C.	14	12	13	W.Bassett	
D.	1	0	0		
A.	1	3	2	1	
B.	2	0	3	0	
C.	11	11	9	13	Upware
D.	0	0	0	0	

B) Variable L with all other variables.

Bran Point

	Bran Point	Cothill	Trouville	W.Bassett	Upware
A.	4				
B.	0				
C.	10		Cothill		
D.	1				
A.	3	7			
B.	1	0			
C.	10	7	Trouville		
D.	3	0			
A.	5	4	6		
B.	0	0	0		
C.	9	10	8	W.Bassett	
D.	0	0	1		
A.	3	6	6	7	
B.	0	0	8	1	
C.	11	8	0	6	Upware
D.	0	0	0	1	

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%).

5J) <u>Conclusions</u>

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 significance variation within <u>N.scutatus</u>.

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 taxonimically 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 5,12. Plot of largest oolith grain size against mean periproct area ($\bar{1} \times \bar{L}$) of samples in fig. 5,11. Within the non-oolitic sediments of Bran Point and Cothill the largest grain size has been plotted.
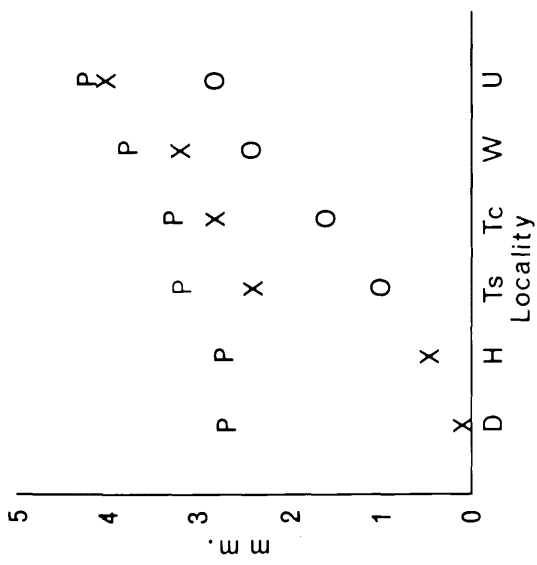

Figure 5,11. Plot of mean periproct length (P), largest grain size (X) and largest oolith (O) against locality. Bran Point (D), Cothill (H), Trouville shore (Ts), Trouville cliff (Tc), Wootton Bassett (W), Upware (U).
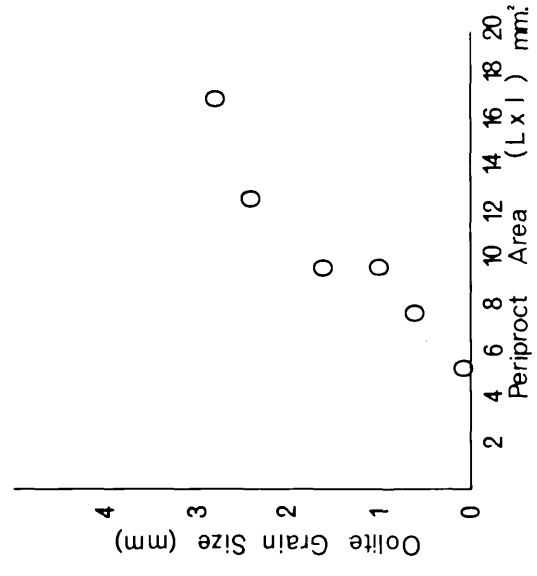
The correlation coefficient is 0.92 and differs significantly from zero at the 1% level.

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 esablish 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.

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 N.scutatus,many of the localities yielding fewer than 10 specimens,and the specimens were generally broken and abbraded and therefore not suitable for a full biometrical analysis. Although Douglas & Arkell (1928,1932) list many localities in the Cornbrash of England where N.latiporus (syn. N.clunicularis) occurs many are now overgrown,disused or destroyed. Few samples can still be collected which contain abundant individuals. Fig.6,1₀ 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

Sample	Comparison sample	Page	Var.	Spec.	Technique	Sig. of difference	Imp. variables
1. Stratton Audley		163	9	17	P.C.A.	Separation along 1st. (size) vector	
		163	9	17	H.C.	Separation into 2 recognised species	
2. Stratton Audley (N.latiporus)	Hydrequent (N.latiporus)	166	15	16	S.D.F.	P>5%	
		166	13	20	S.D.F.	P>5%	
3. Stratton Audley (N.latiporus)	Hydrequent, Talant (N.latiporus)	168	15	21	S.D.F.	P>5%	
		170	15	32	R.M.A.	P<1% between 4-12 pairs of slopes	L
4. Stratton Audley, Hydrequent (N.latiporus)	Trouville (N.scutatus)	172	15	35	S.D.F.	P<1%	N4,I,L,M,C
5. Stratton Audley (N.latiporus)	Cothill, W.Bassett (N.scutatus)	173	15	43	S.D.F.	P<1%	L,N2,B,A,I
6. Stratton Audley (N.latiporus)	Cothill, Dorset W.F. Upware, Trouville	174	15	108	S.D.F.	P<1%	I,L,N4,H,B,A,J,N3
7. S.Audley, Talant Hydrequent	Cothill, Dorset,W.B. Upware, Trouville	176	15	495	R.M.A.	P<1% between 2-11 pairs of slopes	L
8. S.Audley, Talant, Hydrequent	Trouville	176	15	123	H.C.	Clustering not into original groups	
9. All N.latiporus samples	All N.scutatus samples	178	15	166	S.D.F.	P<1%	B,N4,C,J

Figure 6,1   Summary of important analyses run in Chapter 6 for N. latiporus and N.scutatus samples. See fig. 5,1. for key.

Sample	Comparison sample	Page	Var.	Spec.	Technique	Sig. of difference	Imp. variables
10. Smith's holotype (Coleshill)	Trouville (N.scutatus) S.Audley,Hydrequent, Talant(N.latiporus)	181	12	129	Class	Trouville 91% Hydrequent 5% S. Audley 4%	
11. Smith's paratype (Trowle)	as above	182	15	129	Class	St. Audley 99% Hydrequent 1%	
12. Smith's paratype (Wraxhall)	as above	184	14	129	Class	St. Audley 100%	
13. Smith's paratype (Churchill)	as above	184	11	129	Class	Hydrequent 39% Trouville 38% St. Audley 23%	
14. Agassiz type	as above	184	10	129	Class	St. Audley 87% Trouville 11% Hydrequent 2%	
15. d'Orbigny's types	As above + N.elongatus group	185	15	129	Class	Always classified with a sample of N.latiporus	

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 'Vesulian 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 Vesulian 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 Vesulian stage which equated it with the lower and middle

Bathonian (Arkell,1933). Bigot (1930) also correlated the Vesulian

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) <u>Type material</u>

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 <u>N.clunicularis</u> (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 <u>Echinobrissus</u>

<u>clunicularis</u> (Llhwyd) d'Orbigny 1853. All of d'Orbigny's specimens

have been termed varieties of <u>E.clunicularis</u> by Cotteau (1871).

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

Alençon,Orne.

ii) 'Accompanies type', No.b894,from Davage,Saone et Loire.

iii) 'Varieté deprimée (<u>E.edmundi</u>), No. b 238,from the

Bathonian of Asnieres,Yonne.

iv) 'Accompanies <u>E.edmundi</u>' from the same locality, No.b 895.

v) 'Varieté elongée (<u>E.oblongus</u>) from the same locality.

Measurements were also taken on a cast. of the Agassiz

type specimen of <u>N.latiporus</u> at the British Museum (Natural History),

London.

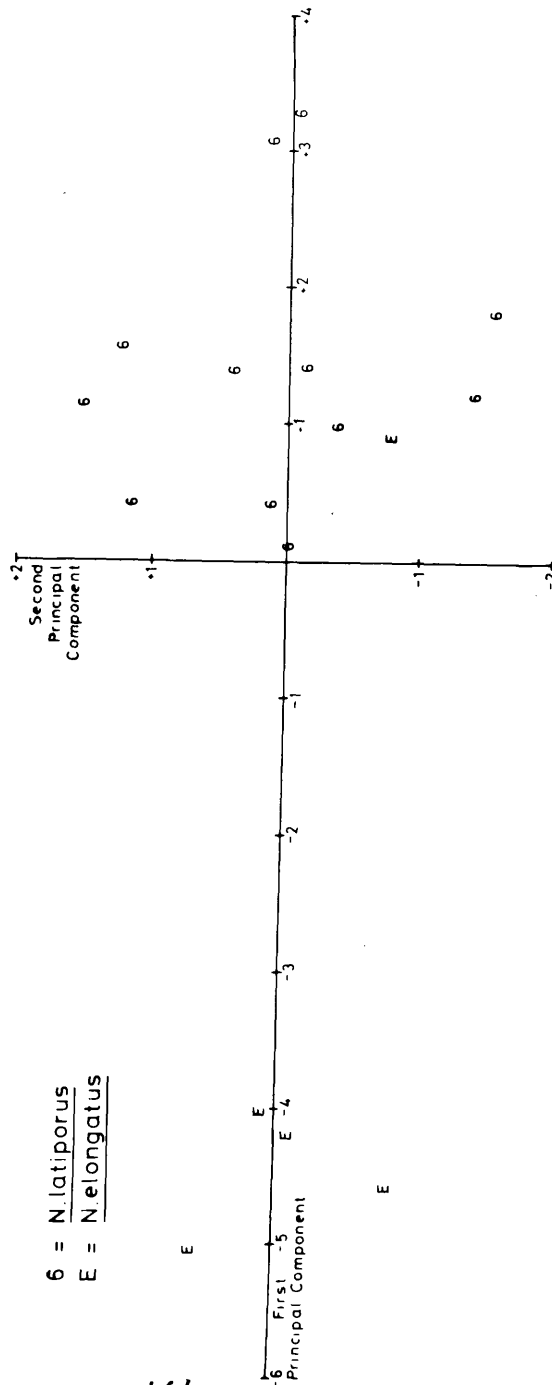6D) <u>Analysis of the Stratton Audley sample</u>

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 <u>N.latiporus</u> Agassiz and <u>N.elongatus</u> 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 <u>N.elongatus</u>. 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 <u>N.latiporus</u> 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 <u>N.latiporus</u>. 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.

6 = N.latiporus
E = N.elongatus

PRINCIPAL   COMPONENT ANALYSIS

Stratton Audley sample.

9 variables, 17 cases.

Eigenvalues

7.23	.73	.61	.26

Cumulative proportions of total variance

80%	88%	95%	98%

Eigenvectors

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

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 hiegroup 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.
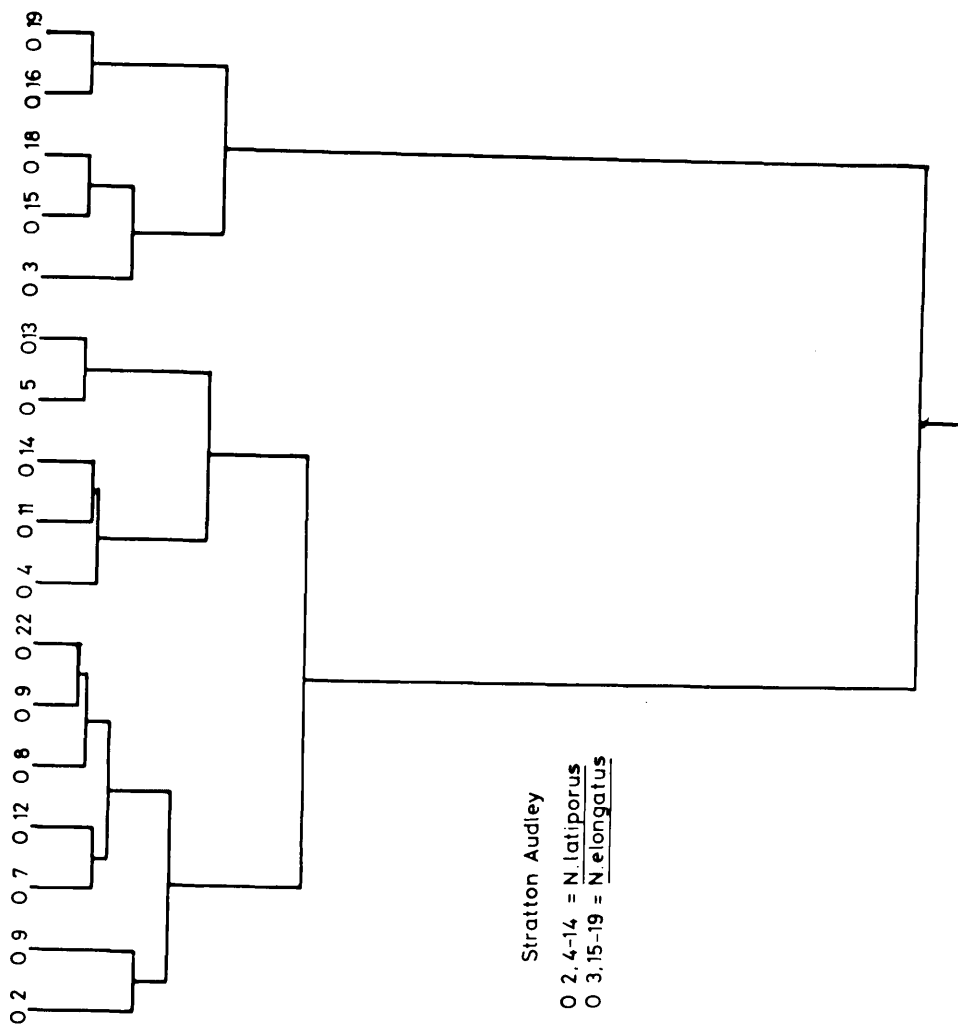
Step 16 (final)

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.

Stratton Audley

O 2. 4-14 = N. latiporus
O 3. 15-19 = N. elongatus

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 χ^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

Group	Hydrequent	Strat. Aud.	Talant
Original Sample			
Hydrequent	0%	14.3%	100%
Strat. Aud.	11.1%	0%	77.8%
Talant	80.0%	60.0%	0%

Figure 6,5, Percentage of specimens within each sample with a low probability (P<1%) of belonging to each group, based on χ^2 tests of D^2 for each case.

Talant 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 Talant 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 Talant 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. Talant 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

Talant

```
        ┌──────────────┐
A.      │  1           │
B.      │  2           │ Strat. Aud.
C.      │ 11           │
D.      │      1       │
        ├──────────────┼──────────────┐
A.      │  3           │    2         │
B.      │  1           │    1         │ Hydrequent
C.      │ 10           │   11         │
D.      │       0      │        1     │
        └──────────────┴──────────────┘
```

B) Variable L with all other variables

Talant

```
        ┌──────────────┐
A.      │  4           │
B.      │  0           │ Strat. Aud.
C.      │ 10           │
D.      │      3       │
        ├──────────────┼──────────────┐
A.      │ 12           │    8         │
B.      │  0           │    0         │ Hydrequent
C.      │  2           │    6         │
D.      │       0      │        0     │
        └──────────────┴──────────────┘
```

Figure 6,6 . Comparison of reduced major axes between each of
three <u>N.latiporus</u> 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,1817 a & 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

172

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 N1.

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 occuring 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 χ^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 χ^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 Woolton 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.

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: ·

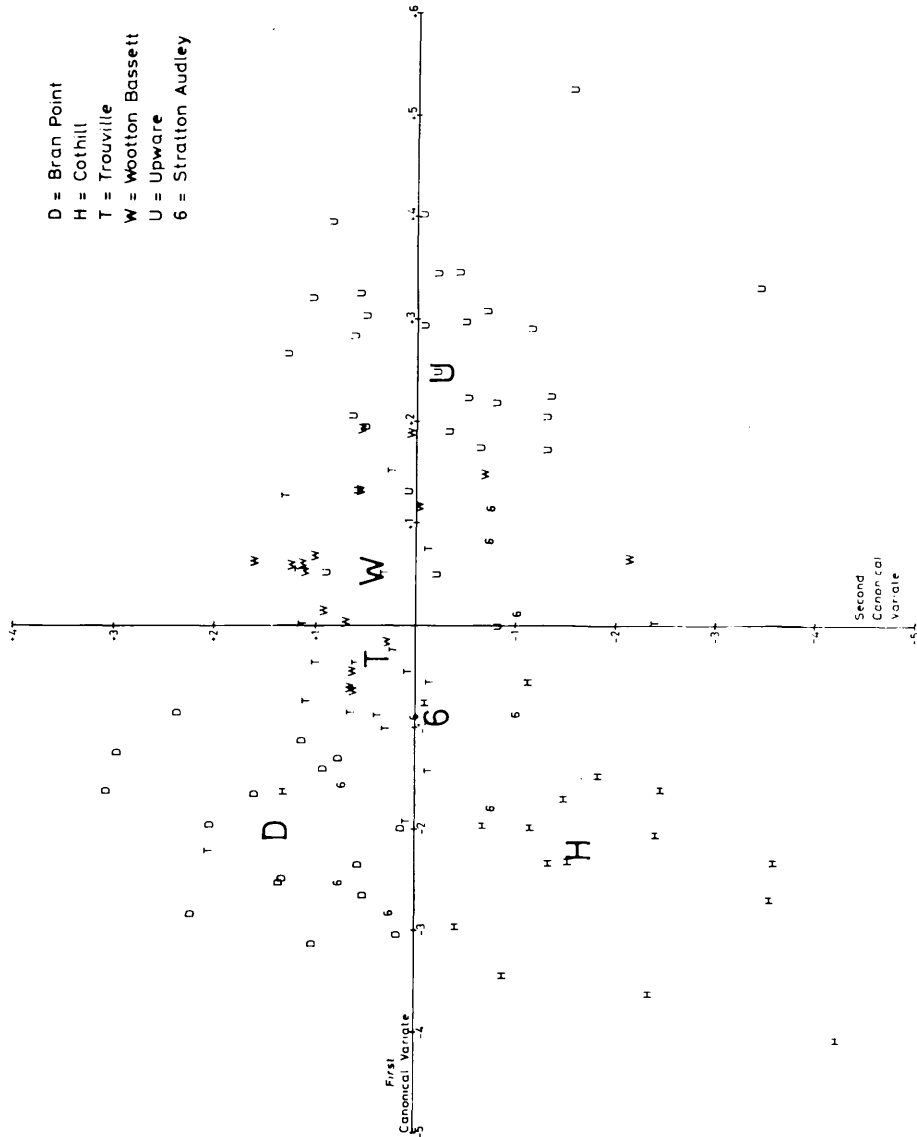|		
Stratton Audley	-.930	-.281
Bran Point	-2.014	1.392
Cothill	-2.193	-1.626
Trouville	-.327	.420
Wootton Bassett	.562	.469
Upware	2.485	-.268

D = Bran Point
H = Cothill
T = Trouville
W = Wootton Bassett
U = Upware
6 = Stratton Audley

Step 14 (final)

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

	Hydrequent	Strat.Aud.	Talant	
A.	0	1	2	
B.	3	1	1	Bran Point
C.	11	12	11	
D.	1	2	1	
A.	1	2	2	
B.	1	0	1	Cothill
C.	12	12	11	
D.	0	0	0	
A.	1	2	2	
B.	0	0	3	Trouville
C.	13	12	9	
D.	1	0	0	
A.	1	1	2	
B.	2	0	1	W. Bassett
C.	11	13	11	
D.	0	0	0	
A.	1	2	2	
B.	3	0	3	Upware
C.	10	12	9	
D.	0	0	0	

B) Variable L with all other variables

	Hydrequent	Strat.Aud.	Talant	
A.	3	7	11	
B.	0	0	0	Bran Point
C.	11	7	3	
D.	1	2	0	
A.	5	5	7	
B.	0	0	0	Cothill
C.	9	9	7	
D.	0	0	1	
A.	2	8	12	
B.	0	0	0	Trouville
C.	12	6	2	
D.	1	0	1	
A.	4	8	8	
B.	1	0	0	W. Bassett
C.	9	6	6	
D.	0	0	0	
A.	3	7	11	
B.	2	0	0	Upware
C.	9	7	3	
D.	0	0	0	

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
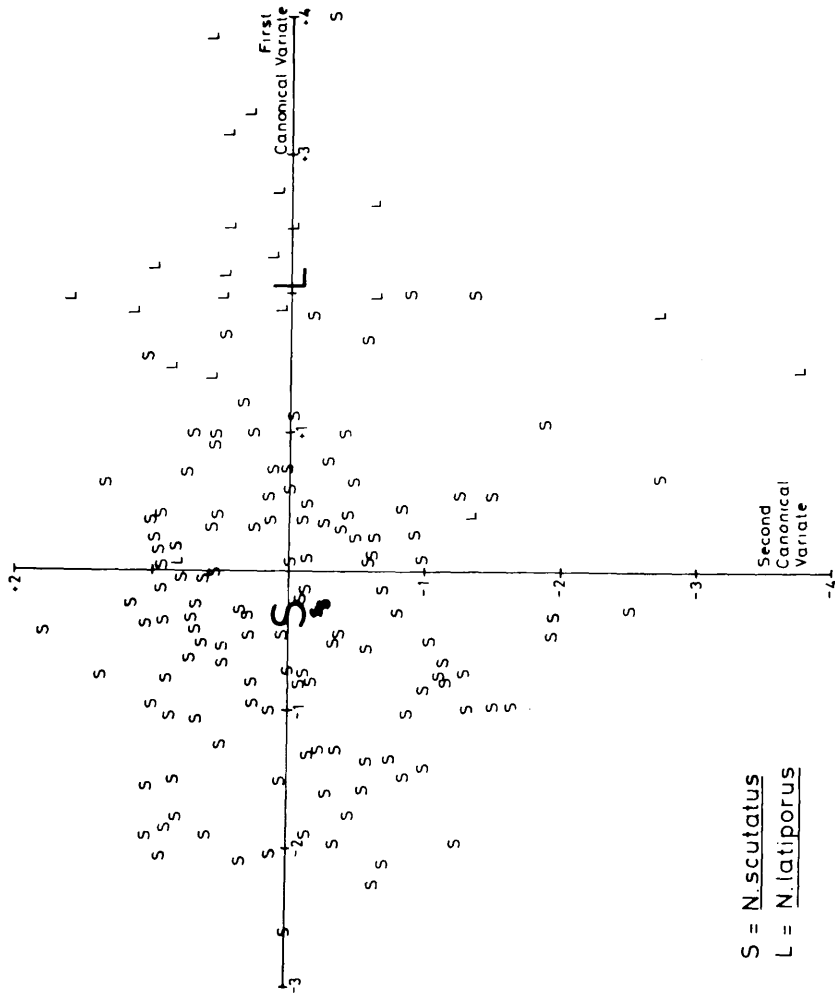
N.scutatus specimens.

X^2 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.

6G)   Classification of N.LATIPORUS according to types.

Stepwise Discriminant Ananlysis 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 programm,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. Distibution 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   -.301   .000,
N.latiporus   2.079   .000.

First
Canonical Variate

Second
Canonical
Variate

S = N.scutatus
L = N.latiporus

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 (B M. No.E 495) is from the Corallian of Coleshill on the Wiltshire-Oxfordshire border,which is possibly the locality of Coltswell mentioned by Llhwyd (Llhwyd 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%.
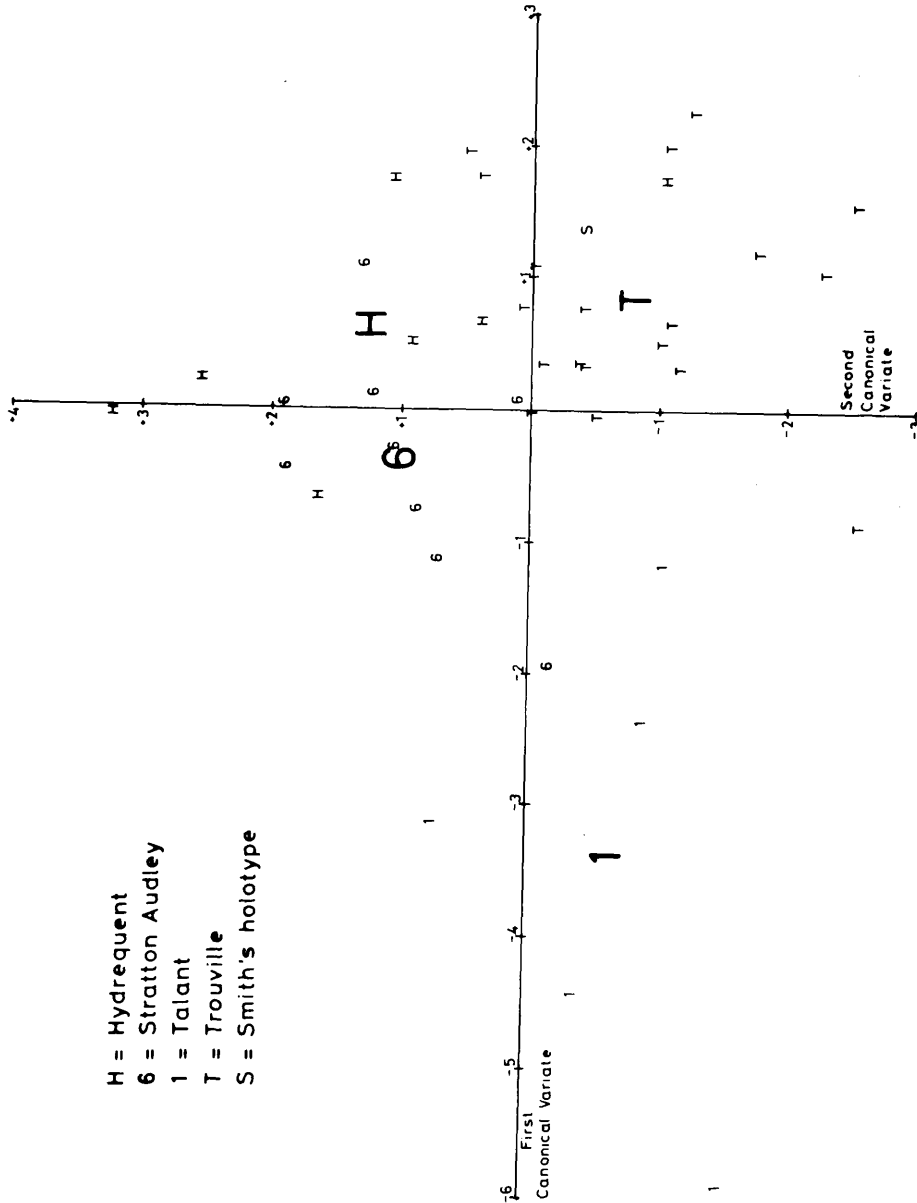
The 'classification' procedure was continued with three paratypes from Smith's collection. The paratype from the Cornbrash of Trowle (B.M. No.E572) was classified using all 15 variables. This resulted in a highly significant difference (P < 1%) between the N.scutatus and N.latiporus groups as well as 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

H = Hydrequent
6 = Stratton Audley
1 = Talant
T = Trouville
S = Smith's holotype

First Canonical Variate
Second Canonical Variate

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. 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. 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 tb be specimens of N.latiporus as defined herin.

An Agassiz cast of the type specimen of N.latiporus Agassiz was measured in order to ascertain its similarity to the three collected samples of N.latiporus,although all specimens appear to be conspecific with Agassiz' original description and figures (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 exeption
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 χ^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.

		Hydrequent	Strat. Aud.	Talant	Trouville	N.elongatus group
E.clunicularis Sp. b236	Post.Prob	55%	44%		1%	
	X^2	>20%	>20%	<.1%	3%	<.1%
E.clunicularis Sp. b894	Post.Prob	74%	26%			
	X^2	.1%	<.1%	<.1%	<.1%	<.1%
E.edmundi Sp. b238	Post.Prob		95%		5%	
	X^2	<.1%	1.5%	<.1%	.2%	<.1%
E.edmundi Sp. b895	Post.Prob		58%	41%	1%	
	X^2	<.1%	1.5%	1.5%	.1%	<.1%
E.oblongus	Post.Prob		99%		1%	
	X^2	<.1%	<.1%	<.1%	<.1%	<.1%

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   ).

6H)   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 c

collected by the author,N.latiporus Agassiz,1839,appears to be the

correct name for this group of nucleolitid echinoids.

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 & Thiéry (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.

Sample	Comparison sample	Page	Var.	Spec.	Technique	Sig. of difference	Imp variables
1. S.Audley (N. elongatus)	S.Audley (N.latiporus)	194	15	21	R.M.A.	P<1% between all 14 pairs of slopes	L
2. S.Audley (N.elongatus)	S.Audley (N.latiporus)	195	10	33	S.D.F.	P<1%	L,N4,G
	Trouville (N.scutatus)	196	15	223	R.M.A.	P<1% between all 14 pairs of slopes	L
		199	15	32	S.D.F.	P<1%	L,N4,M
3. Signy (N.amplus)		202	14	30	P.C.A.	0 67 separated along 2nd vector	N4,N2
4. Signy (N.amplus)	Trouville (N.scutatus)	203	14	47	S.D.F.	P<1%	M,N1
		206	14	47	H.C.	Final 2 groups = original groups	
		206	15	241	R.M.A.	P<1% between all 14 pairs of slopes	L
		206	13	47	P.C.A.	Separation on plot of 1,2 vectors	1st – size 2nd – N1,N2
5. Signy (N.amplus)	S. Audley (N.latiporus)	207	14	55	S.D.F.	P<1%	M,N1,B
	Trouville (N.scutatus)	207	14	56	P.C.A.	Separation on plot of 1,2 vectors	1st – size 2nd – N1
6. Signy (N.amplus)	S.Audley (N.latiporus) Trouville(N.scutatus) S.Audley (N.elongatus)	210	10	43	S.D.F.	P<1%	L,N2,B,A,N4

Figure 7,1 Summary of important analyses run in Chapter 7. See fig. 5,1 for key.

Sample	Comparison sample	Page	Var.	Spec.	Technique	Sig. of difference	Imp. variables
7. Signy (N.amplus)	S.Audley(N.latiporus)	210	15	53	R.M.A.	P<1% between all 14 pairs of slopes	L
8. Signy (N.amplus)	S.Audley(N.elongatus)	210	15	46	R.M.A.	P<1% between 9 pairs of slopes	L,M,N1
9. Marquise (N.woodwardii)	Signy (N.amplus)	211	14	35	S.D.F.	P=4%	L
		213	15	46	R.M.A.	P<1% between all 14 pairs of slopes	
		213	15	14	S.D.F.	P>5%	
		214	14	35	H.C.	Clustering not into original groups	
		214	15	14	H.C.	Clustering not into original groups	
10. Marquise(N.woodwardii)	Signy (N.amplus), Trouville (N.scutatus)	214	14	54	S.D.F.	P<1%	M,N1
		215	15	33	H.C.	Clustering not into original groups	
		217	13	54	P.C.A.	Separation on plot of 1,2 vectors	) 1st size) 2nd size N1
		217	15	247	R.M.A.	P<1% between all 14 pairs of slopes	
11. Marquise(N.woodwardii)	Signy (N.amplus); Hydrequent, Talant, S.Audley(N.latiporus); S.Audley(N.elorgatus)	217	14	59	S.D.F.	P<1%	M,N2,B,N1

Figure 7,1 continued

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

Figure 7,1 continued

Sample	Comparison samples	Page	Var.	Spec.	Technique	Sig. of difference	Imp. variables
20. Villers (N.micraulus)	W.Bassett,Dorset, Trouville,	238	15	257	S.D.F.	P<1%	L,I,N1,C,B,G,N3
	Cothill,Upware (N.scutatus)	239	15	507	R.M.A.	P<1% between 8-13 pairs of slopes	N1
21. Villers (N.micraulus)	Trouville(N.scutatus)	241	14	71	S.D.F.	P<1%	J,L,Ni
	Signy (N.amplus)	241	13	71	P.C.A.	Separation on plot of 1,2 vectors	1st – size 2nd – N1,L
		242	14	71	H.C.	Final 3 groups = original groups	
22. Villers (N.micraulus)	As above + Marquise (N.woodwardii), Hydrequent, Talant,S.Aud. (N.latiporus)	245	14	188	S.D.F.	P<1%	L,J,N1,B
23. Villers (N.micraulus)	Trouville(N.scutatus), Signy (N.amplus), N.elongatus group	245	14	75	S.D.F.	P<1%	N1,B,N2,L,A
24. Specimen V45 (Villers)	Trouville(N.scutatus), Villers(N.micraulus), S.Audley,Hydrequent, Talant(N.latiporus), Devecey(N.subquadratus, N.elongatus group.	248	15	82	Class	100% Stratton Audley	
25. Agassiz type	As above	249	13	82	Class	100% Villers	

Figure 7,1 continued.

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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 inv olved 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 s

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 proably 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   .612

S.Audley (N.latiporus)

.138 -1.664

S.Audley (N.elongatus)

9.395   .672
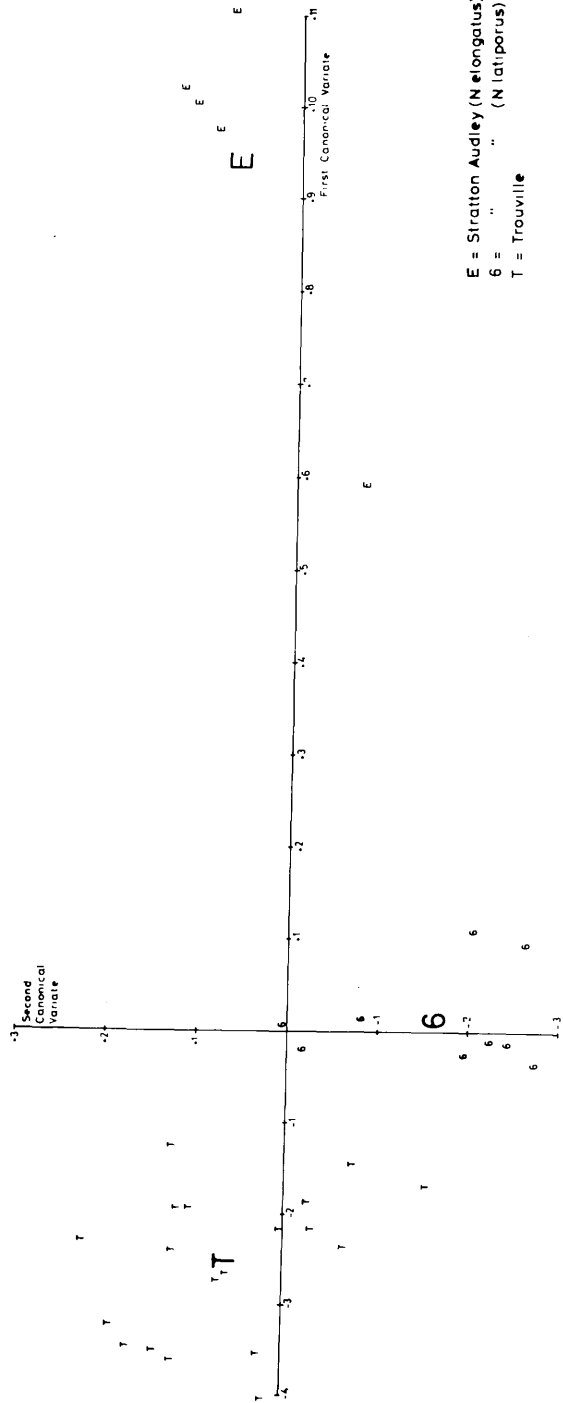
E = Stratton Audley (N.elongatus)
6 =   "   "   (N.latiporus)
T = Trouville

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 α ,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.

χ^2 tests of the Mahalanobis distances however showed a low

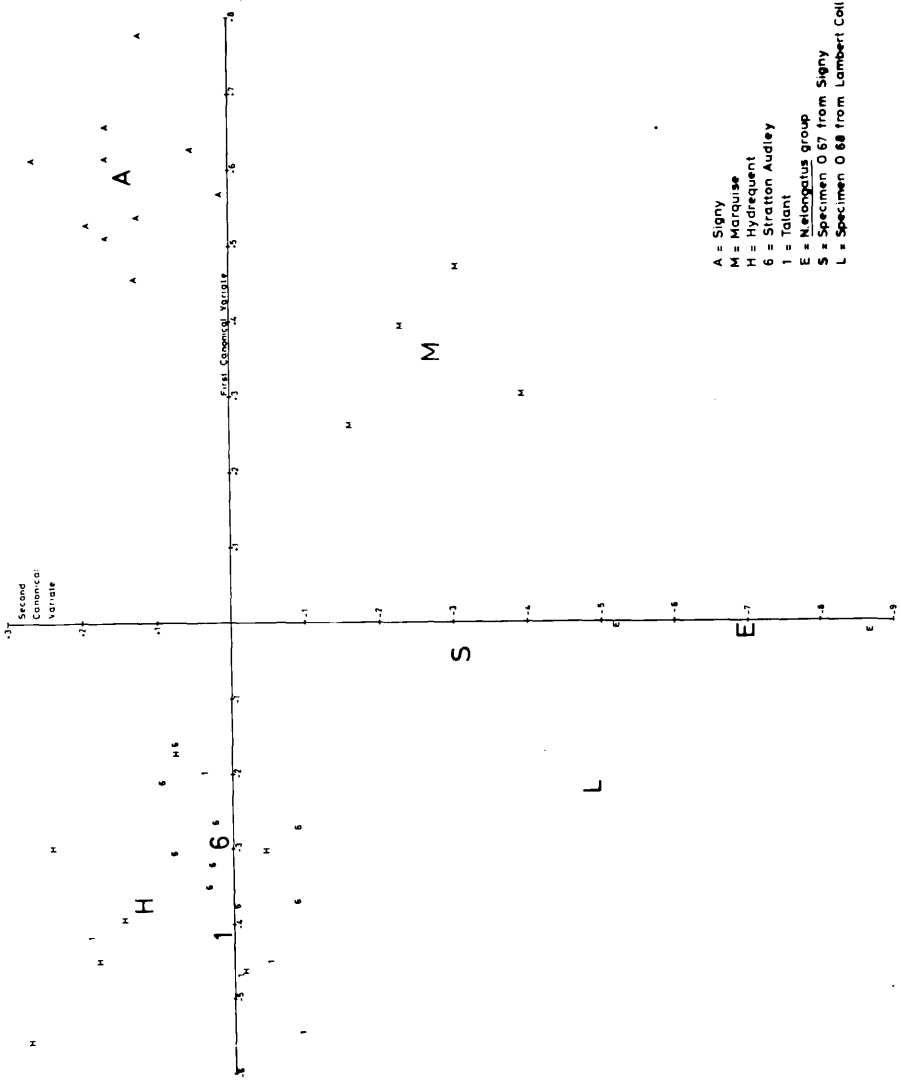probability (P < 1%) of either specimen belonging to any group.

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 χ^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

exept 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

A = Signy
M = Marquise
H = Hydrequent
6 = Stratton Audley
1 = Talant
E = N.elongatus group
S = Specimen O 67 from Signy
L = Specimen O 68 from Lambert Coll.

and including specimens 067 and 068.

Step 3

Variables L,N4 and M entered

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 α ,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.

7 C) 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%)

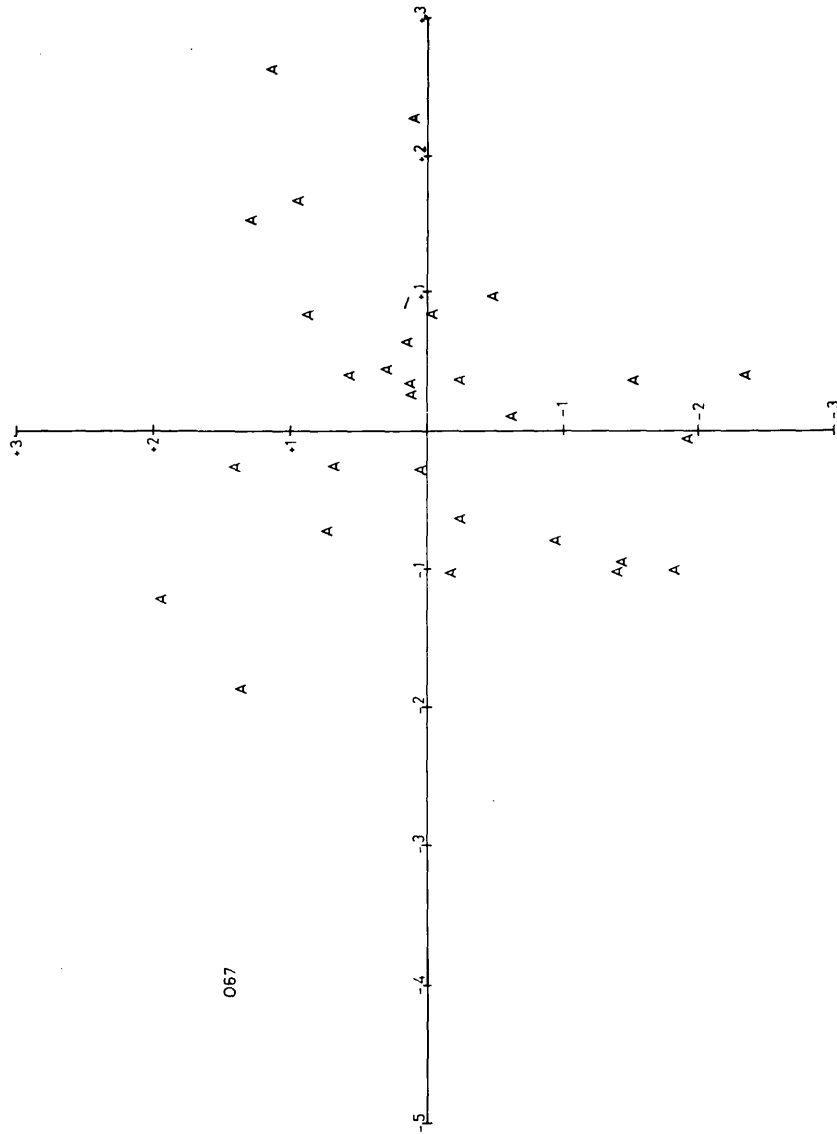Specimens classified wrongly by posterior probability; 0%

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

| 7.35 | 1.63 | 1.26 | 1.09 |

Cumulative proportions of total variance

| 52% | 64% | 73% | 81% |

Eigenvectors

	1	2	3	4
A	.36	-.15	.00	.08
B	.35	-.06	-.00	.03
C	.32	.30	.01	-.18
D	.31	.34	.01	-.08
G	.36	-.10	-.02	.07
H	.30	-.26	-.01	.14
I	.12	.15	-.72	.06
J	.29	-.06	-.29	-.21
L	-.07	.32	.28	.54
M	.33	-.17	.04	.25
N1	.26	.04	.34	.13
N2	.09	-.50	.21	.11
N3	.01	-.22	.26	-.67
N4	.21	.49	.30	-.22

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 χ^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 7.6. Distribution
of Trouville and Signy
specimens along Principal
Components 1 and 2 based
on a 13 variable analysis.
Components 1 and 2
account for 83% of total
variation.
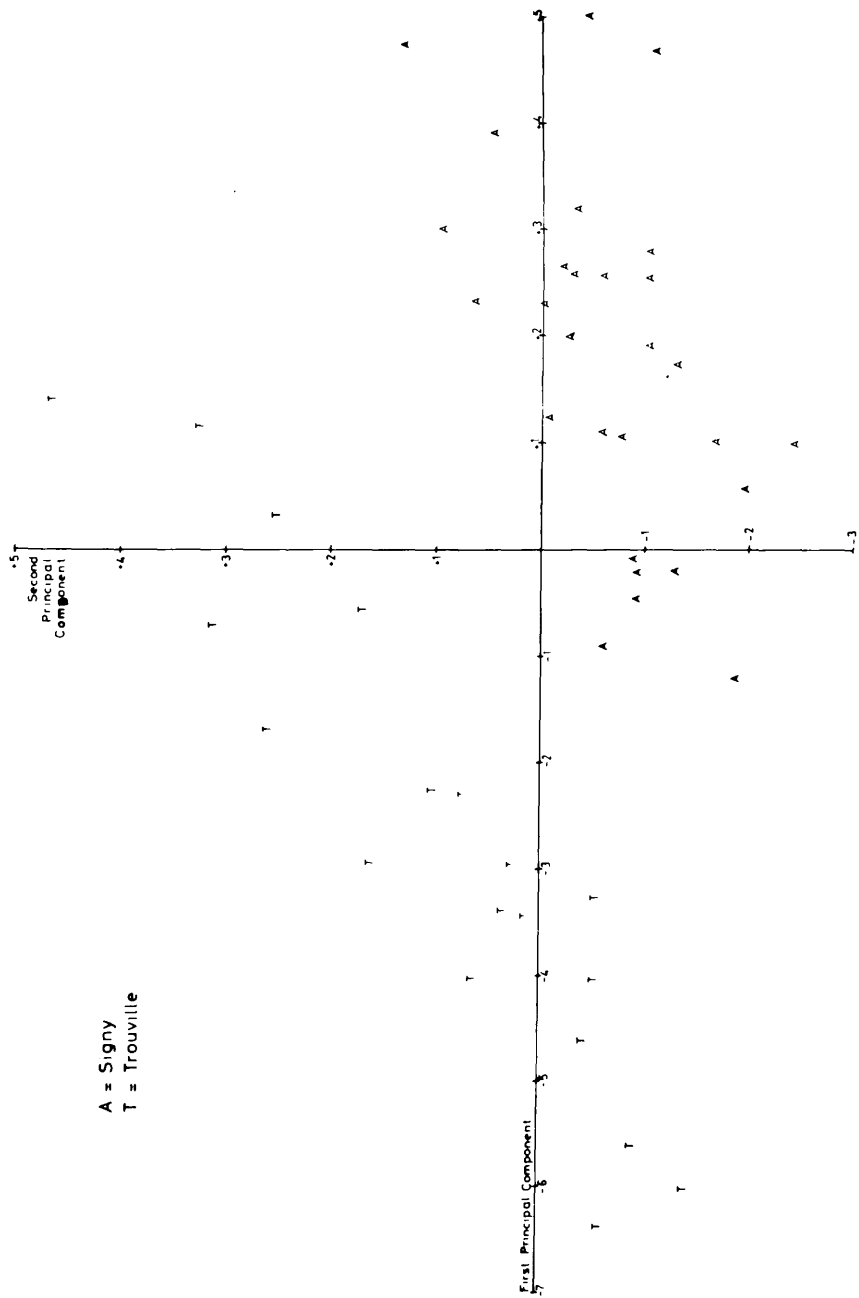
A = Signy
T = Trouville

PRINCIPAL COMPONENT ANALYSIS

Signy and Trouville samples

13 variables, 47 cases.

Eigenvalues

| 8.68 | 2.15 | .75 | .54 |

Cumulative proportions of total variance

| 67% | 83% | 89% | 93% |

Eigenvectors

	1	2	3	4
A	.33	-.01	.03	.12
B	.33	-.06	.00	.06
C	.32	.15	.06	-.17
D	.32	.16	.08	-.18
G	.33	-.03	.07	.13
H	.30	.11	.03	.37
I	.28	-.11	-.32	.33
J	.30	-.28	.10	.04
L	-.21	.34	.29	.50
M	.32	-.11	-.02	.08
N1	.02	.62	.17	.27
N2	.06	.45	-.80	-.13
N4	.22	.36	.35	-.55

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   A discriminant analysis performed on the four species so far studied produced similar results to the dicriminant 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 wit 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 then 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 exept 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 Marquise specimens on the first
two canonical axes. Group centroids
indicated by large lettering.
Mean coordinates;
Signy   .561   .000
Marquise -2.242   .000

M = Marquise
A = Signy

Second Canonical Variate

First Canonical Variate
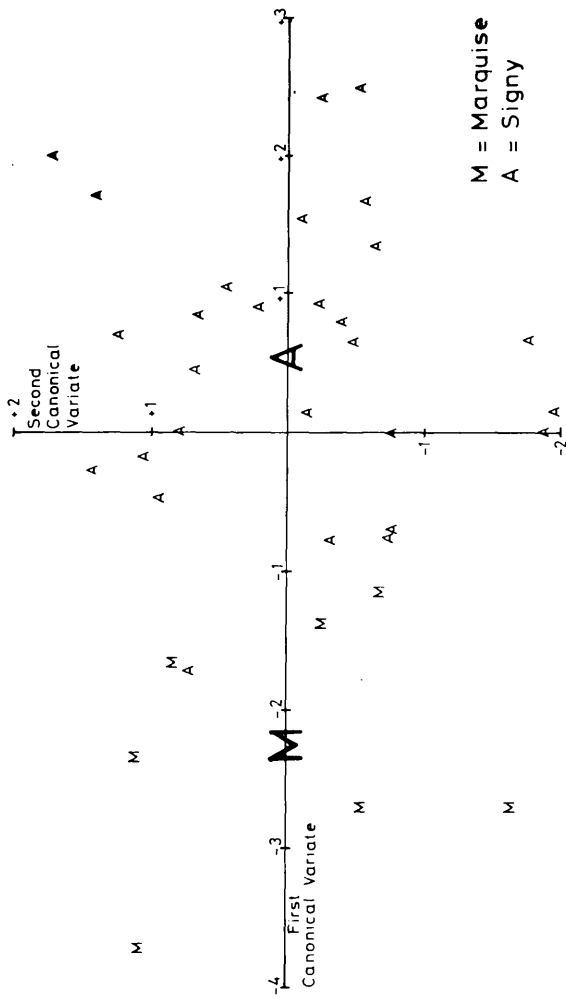
Variables not entered; D,G,N1 and N2

U-statistic = .43 (Significance of inequality of group means;

P = 4%)

Specimens classified wrongly by posterior probability; 3%.

From an analysis of χ^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.scutatus

and N.latiporus.

Bivariate analyses showed a suprisingly 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 eight

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-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 e 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 N1 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
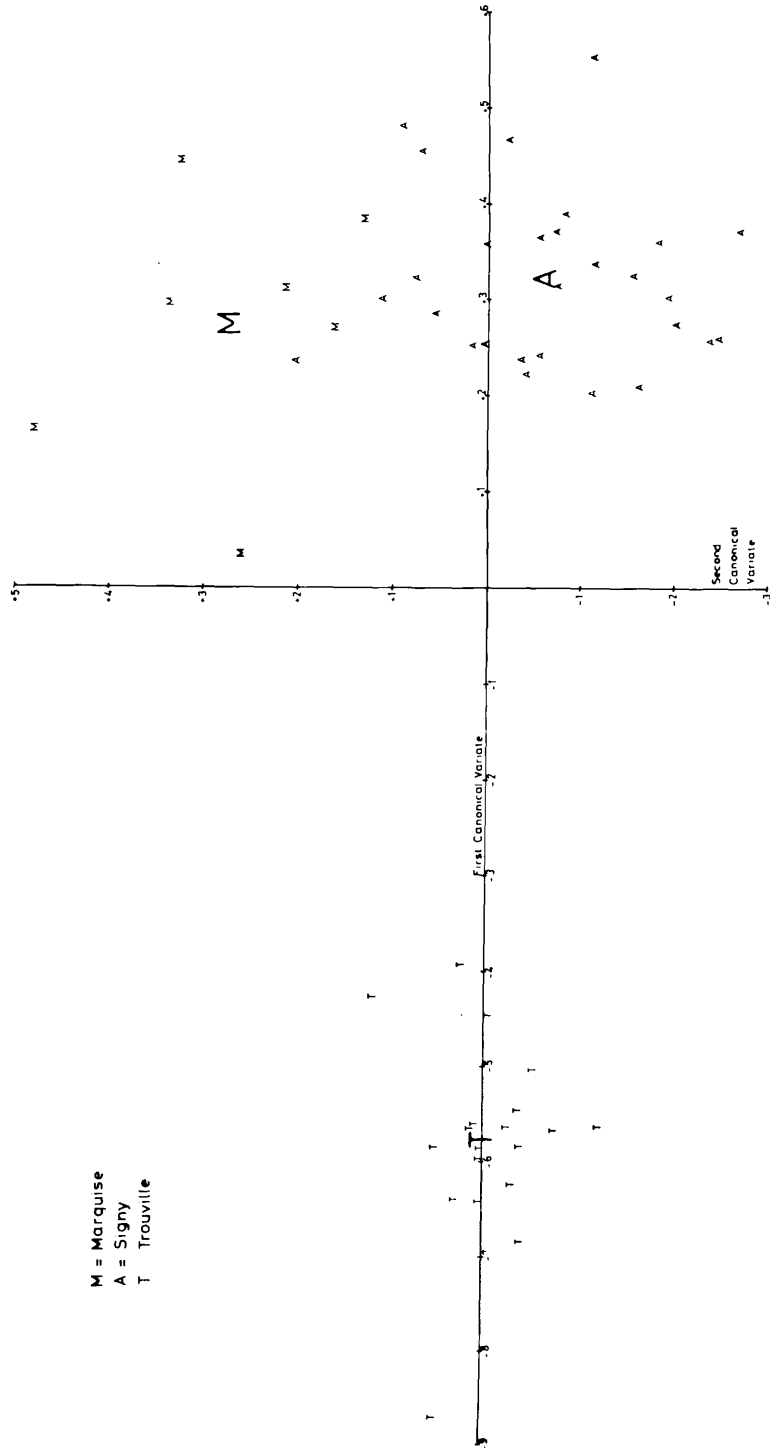
M = Marquise
A = Signy
T = Trouville

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 preceeding 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 Nl. The Marquise sample lay with,and was indistinguishable from,the Signy group showing that the size/Nl 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 diference 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.

Marquise

		Signy
A.	4	
B.	1	
C.	9	
D.		0

				Trouville
A.	2		3	
B.	2		4	
C.	10		7	
D.		0		0

B) Variable J with all other variables.

Marquise

		Signy
A.	2	
B.	2	
C.	10	
D.		1

				Trouville
A.	2		1	
B.	1		2	
C.	11		11	
D.		0		0

C) Variable M with all other variables.

Marquise

		Signy
A.	2	
B.	1	
C.	11	
D.		1

				Trouville
A.	2		4	
B.	0		1	
C.	12		9	
D.		0		0

D) Variable N1 with all other variables.

Marquise

		Signy
A.	3	
B.	5	
C.	6	
D.		1

				Trouville
A.	2		3	
B.	4		0	
C.	8		11	
D.		0		0

Figure 7,10. Comparison of reduced major axes between the Trouville, Signy and Marquise samples. Key as for fig.5,10.

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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   .492

Marquise   2.493   -1.415

Hydrequent -4.553   1.261

S.Audley (N.latiporus) -4.556
.218

Talant   -6.568   -.667

S.Audley (N.elongatus)   -.883
-6.291
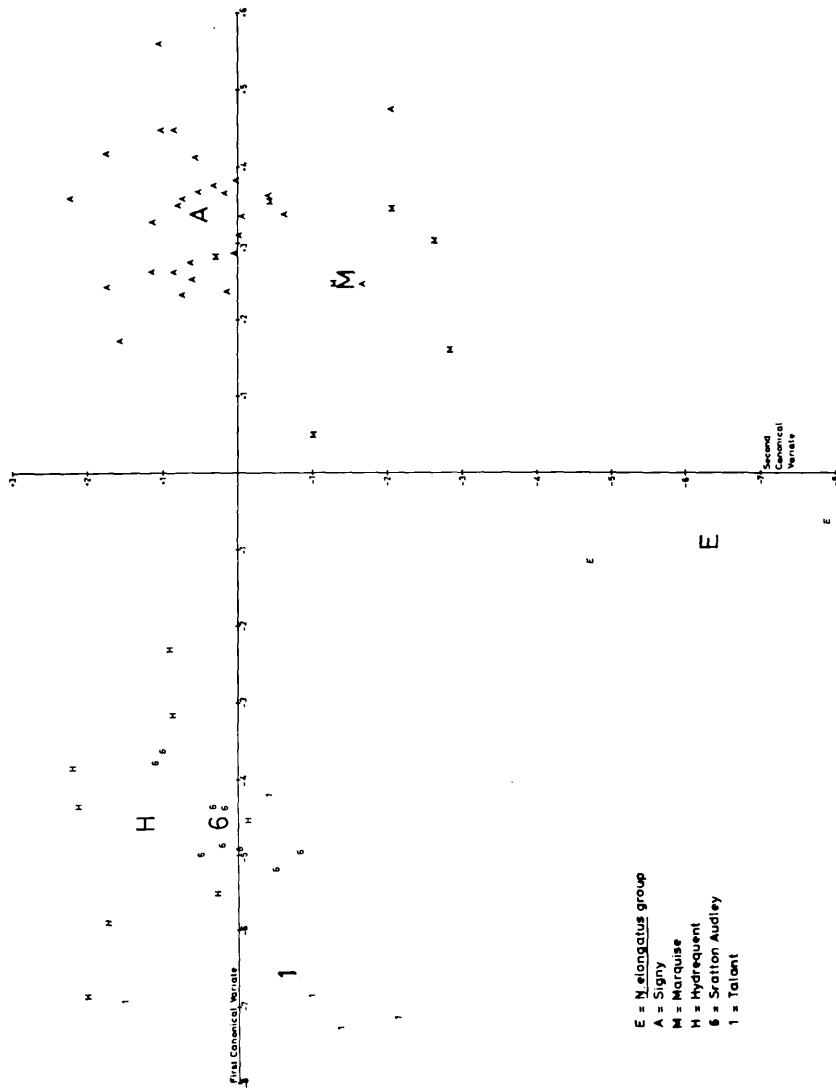
E = N.elongatus group
A = Signy
M = Marquise
H = Hydrequent
6 = Sratton Audley
1 = Talant

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 its 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,

	Strat. Audley N.latiporus	Strat. Audley N.elongatus	
Variable A	A. 2 B. 2 C. 10 D. 1	3 2 9 0	Marquise
Variable B	A. 2 B. 0 C. 12 D. 0	3 2 9 0	Marquise
Variable L	A. 6 B. 0 C. 8 D. 1	8 6 0 0	Marquise
Variable M	A. 1 B. 0 C. 13 D. 0	3 3 8 1	Marquise
Variable N1	A. 1 B. 4 C. 9 D. 0	6 2 6 0	Marquise
Variable N2	A. 2 B. 0 C. 12 D. 3	1 1 12 0	Marquise

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 χ^2 tests of D^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 N1 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 p.206).
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.burgundiae. 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 wi
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;
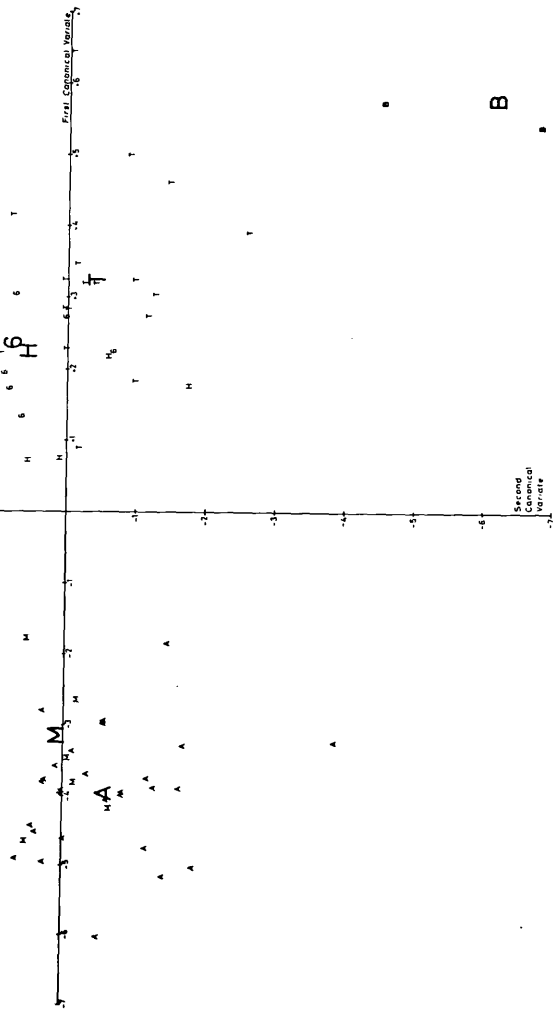
Signy	-3.968	-.622
Marquise	-3.154	.161
Talant	3.387	2.821
Stratton Audley	2.367	.747
Hydrequent	2.273	.582
Trouville	3.238	-.385
Selongey	5.813	-6.139
N.elongatus group	-.548	4.131

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% representaive of their group (using

posterior probability); 99%

Specimens with a low probability (P < .1%) of belonging to the

opposing group (using χ^2 tests of D^2); 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.
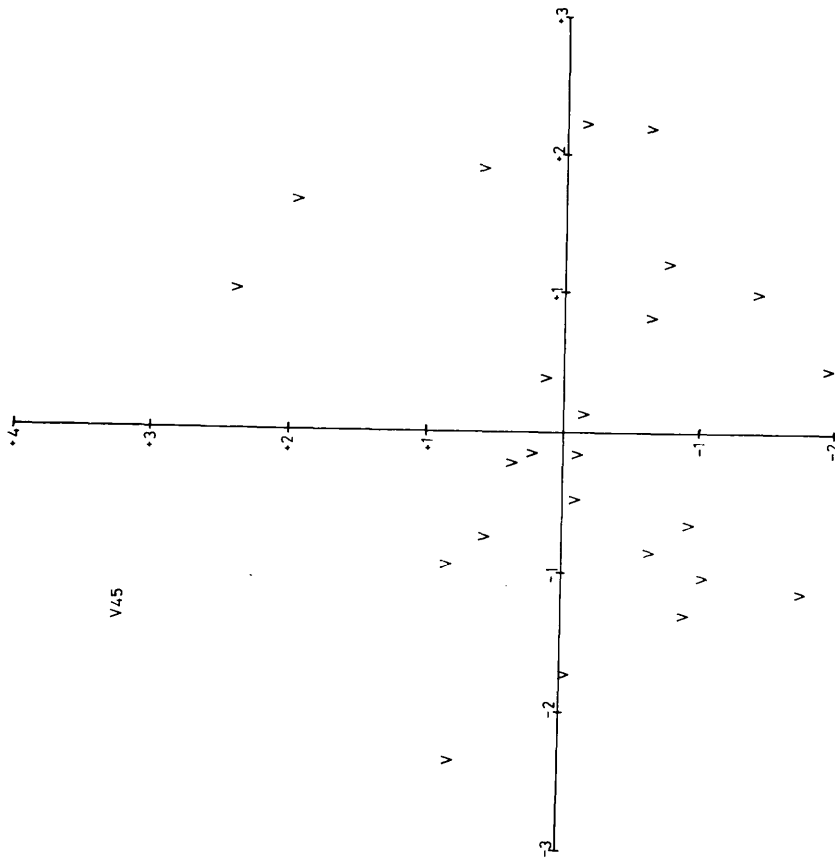
PRINCIPAL COMPONENT ANALYSIS

Villers sample.

15 variables, 25 cases.

Eigenvalues

8.84	1.58	1.46	1.07

Cumulative proportions of total variance

59%	69%	79%	86%

Eigenvectors

	1	2	3	4
A	-.33	-.05	.06	.07
B	-.32	-.02	.07	.07
C	-.30	-.16	-.22	-.17
D	-.30	-.19	-.24	-.22
E	-.30	.01	.18	.11
G	-.33	-.06	.03	.09
H	-.27	.20	-.03	.02
I	-.26	.31	.25	-.12
J	-.11	-.49	.24	.53
L	-.10	-.47	.45	-.27
M	-.29	-.10	.21	-.07
N1	-.27	.23	-.35	.02
N2	-.13	.28	.51	-.44
N3	-.13	.26	.17	.52
N4	-.23	-.36	-.26	-.23

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 N1. 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 28%
of total variation.

The ordinate is Component 2, the
abscissa is Component 3.

T = Trouville
V = Villers
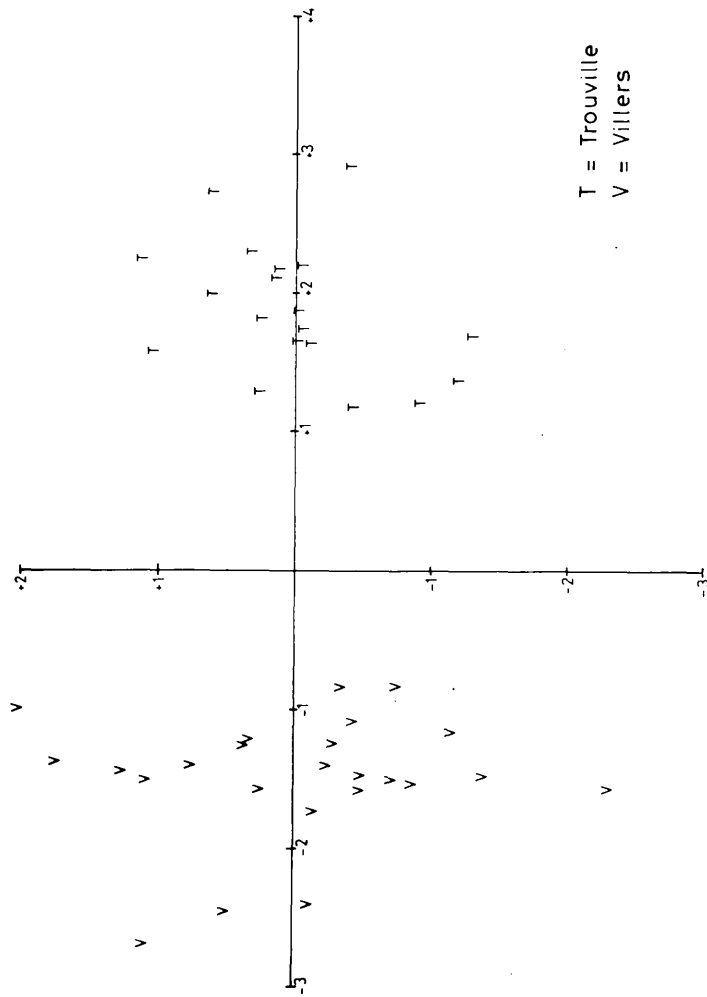
PRINCIPAL COMPONENT ANALYSIS

Trouville and Villers samples.

14 variables, 43 cases.

Eigenvalues

8.72	3.11	.77	.58

Cumulative proportions of total variance

62%	84%	90%	94%

Eigenvectors

	1	2	3	4
A	-.33	-.12	.05	-.18
B	-.33	.03	.05	-.15
C	-.32	.01	-.31	.13
D	-.32	-.01	-.34	.13
E	-.32	-.03	.18	-.08
G	-.32	-.15	.03	-.24
H	-.29	-.07	.34	.04
I	-.27	.11	.44	.22
J	-.09	.50	.03	-.44
L	-.02	.55	.04	-.16
M	-.32	-.04	.04	-.24
N1	-.15	-.50	-.03	.08
N2	-.18	.32	.19	.70
N4	-.25	.19	-.63	.15

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 significatnly

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 significatnly 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 con-specific 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 picure 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 N1 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 exept 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.
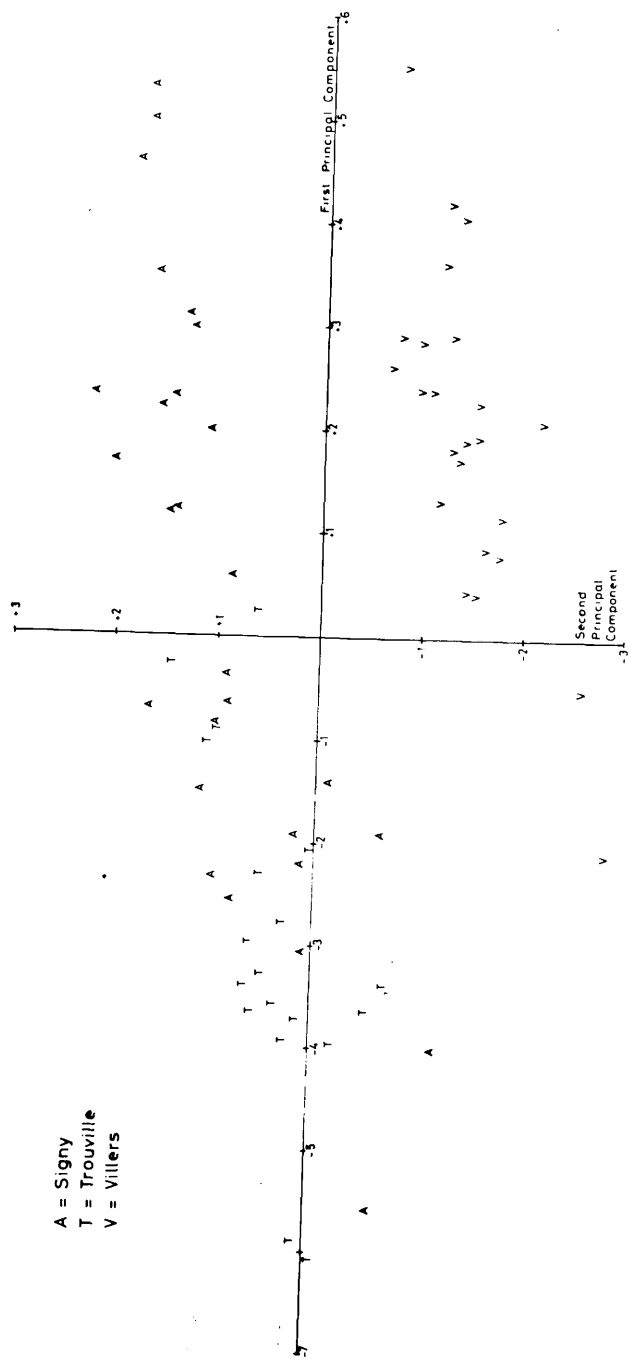
A = Signy
T = Trouville
V = Villers

Signy, Trouville and Villers samples.

13 variables,   71 cases.

Eigenvalues

| 8.55 | 1.57 | 1.22 | .65 |

Cumulative proportions of total variance

| 66% | 78% | 87% | 92% |

Eigenvectors

	1	2	3	4
A	-.33	-.15	.02	.03
B	-.33	.01	.10	.00
C	-.32	-.07	-.20	-.15
D	-.32	-.09	-.22	-.16
G	-.33	-.17	.05	-.02
H	-.28	-.18	-.13	.21
I	-.29	.09	.17	.30
J	-.28	.32	.30	-.16
L	.12	.50	-.45	-.20
M	-.33	-.01	.15	.00
N1	.12	-.63	-.41	.13
N2	-.15	.37	-.42	.70
N4	-.25	.08	-.44	-.49

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 anaysis 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 N1 entered (N1 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
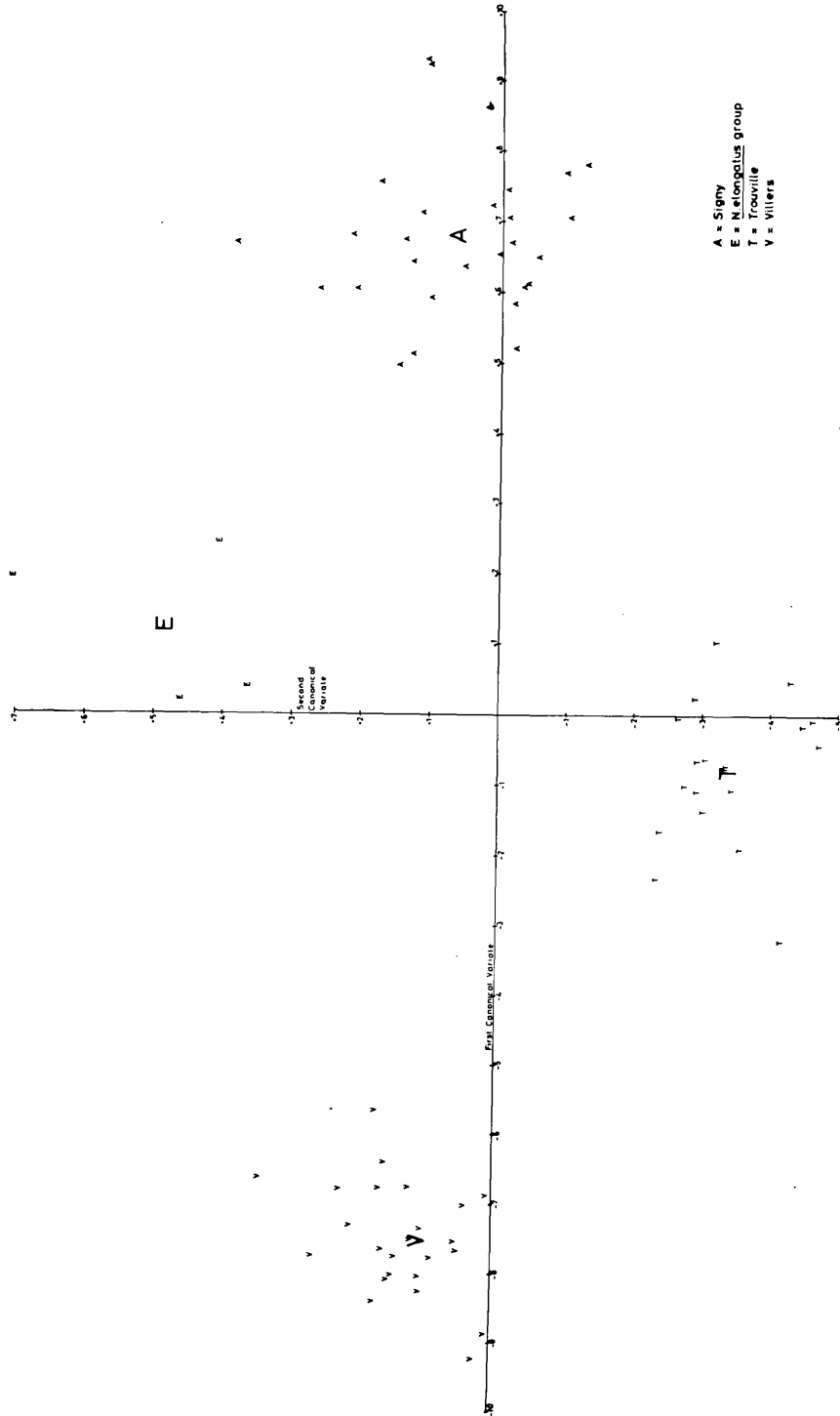by large lettering.

Mean coordinates;

Signy   6.802   .646

Trouville -.802 -3.369

Villers -7.510 1.103

N.elongatus group

1.254 4.867

A = Signy
E = N.elongatus group
T = Trouville
V = Villers

First Canonical Variate

Second
Canonical
Variate

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 χ^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 ommitted 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 χ^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 v

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 injesting 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 injested 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 N1,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.7,20 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

statigraphic 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.

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 periproct; 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.

Sample	Comparison sample	Page	Var.	Spec.	Technique	Sig. of diff.	Imp. variables
1.Devecey (N.subquadratus)		258	15	14	P.C.A.	BA 25 separated along 3rd vector	I,J,L,N4
2.Devecey (N.subquadratus)	Trouville (N.scutatus)	258	15	32	S.D.F.	P<1%	N4,N1,J
		259	14	32	P.C.A.	Separation along 2nd vector	N1,I,N4
		259	15	32	H.C.	Final 2 groups = original groups	
		262	15	227	R.M.A.	P<1% between 9 pairs of slopes	I
3. Devecey (N.subquadratus)	Villers (N.micraulus)	262	15	37	S.D.F.	P<1%	L,D,J
		264	15	37	H.C.	Final 2 groups = original groups	
		264	15	69	R.M.A.	P<1% between 10 pairs of slopes	N4
4. Devecey (N.subquadratus)	Trouville (N.scutatus), Villers (N.micraulus)	264	15	56	S.D.F.	P<1%	L,N4,N1
		265	14	56	P.C.A.	Separation along 2nd vector	L,J,N1
5. Devecey (N.subquadratus)	Trouville (N.scutatus), Villers (N.micraulus), Signy (N.amplus)	267	14	84	H.C.	Final 4 groups = original groups	
		267	13	84	P.C.A.	Separation on plot of 1,2 vectors	1st size 2nd N1
6. Devecey (N.subquadrutus)	As above + N.elongatus group	271	14	88	S.D.F.	P<1%	J,L,N4,N1,B,A

Figure 8,1 Summary of important analyses run in Chapter 8. See fig. 5,1 for key.

Sample	Comparison sample	Page	Var.	Spec.	Technique	Sig. of diff.	Imp. variables
7. Agassiz type	(N.elongatus group, Trouville (N.scutatus),Villers, (N.micraulus),Devecey, (N.subquadratus),Bou Saada (N.rotundus).	272	10	64	Class	99% Devecey 1% Bou Saada	
8. Bou Saada (N.rotundus)	Trouville (N.scutatus)	274	15	22	S.D.F.	P<1%	N1,D,H,B
9. Bou Saada (N.rotundus)	Trouville (N.scutatus), Villers (N.micraulus), Devecey (N.subquadratus)	275 276	15 15	59 59	S.D.F. H.C.	P<1% Clustering not into original groups	L,N1,D,I,J,B,G,E
10. Bou Saada (N.rotundus)	Signy(N.amplus),N.elongatus group, Trouville N.scutatus), Villers (N.micraulus), Devecey (N.subquadratus)	278	15	73	S.D.F.	P<1%	J,L,N4,N1,E,N2,B,M

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 sharpy 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%

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 χ^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

contibuting 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

Devecey sample than for the Trouville sample for a given specimen size,

(fig.8,2). During growth within the Devecey 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 hierarchial grouping was able to cluster specimens into

Figure 8.2. Distribution of Trouville (N.scutatus) and Devecey (N.subquadratus) specimens along Principal Components 1 and 2 based on a 14 variable analysis. Components 1 and 2 account for 81% of total variation.

T = Trouville
Q = Devecey

First Principal Component
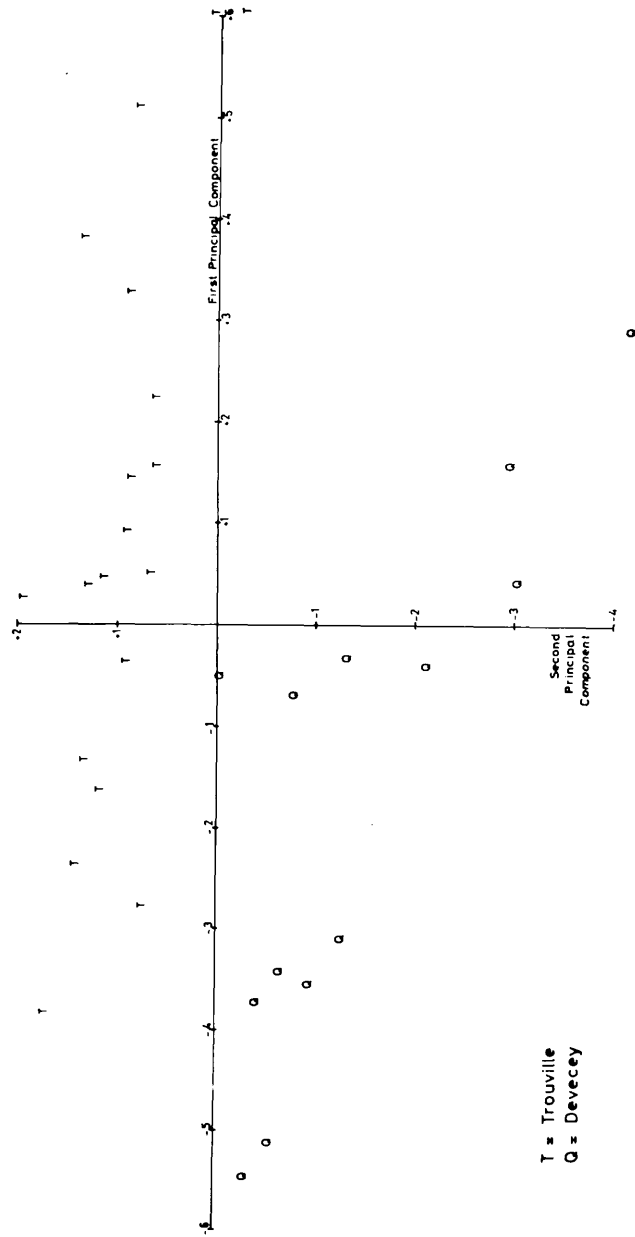
Second Principal Component

Trouville and Devecey samples

14 variables, 32 cases.

Eigenvalues

| 9.19 | 2.19 | 1.01 | .86 |

Cumulative proportions of total variance

| 66% | 81% | 88% | 95% |

Eigenvectors

	1	2	3	4
A	.31	-.17	.17	.10
B	.32	.09	.02	-.00
C.	.31	.08	-.17	-.20
D	.31	.08	-.19	-.22
E	.32	-.03	-.02	-.05
G	.30	-.20	.15	.15
H	.28	-.14	.30	.11
I	.19	-.45	-.34	-.07
J	.20	.17	.25	.71
L	.17	.15	-.73	.32
M	.31	.10	.06	.05
N1	.14	-.58	.06	-.18
N2	.22	.32	.26	-.44
N4	.24	.42	-.03	-.18

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 anlyses 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 significatnly 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 anayses 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.

A.	3
B.	3
C.	8
D.	0

B) Variable L with all other variables.

A.	5
B.	5
C.	4
D.	0

C) Variable I with all other variables.

A.	9
B.	2
C.	3
D.	1

D) Variable N4 with all other variables.

A.	7
B.	2
C.	5
D.	0

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

Devecey samples revealed a degree of difference similar to that

found between Trouville and Devecey. 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 Devecey - Trouville

comparison.

5. Comparison between Devecey,Trouville and Villers samples

The Devecey,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

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

Second Canonical Variate

First Canonical Variate

T = Trouville
V = Villers
Q = Devecey
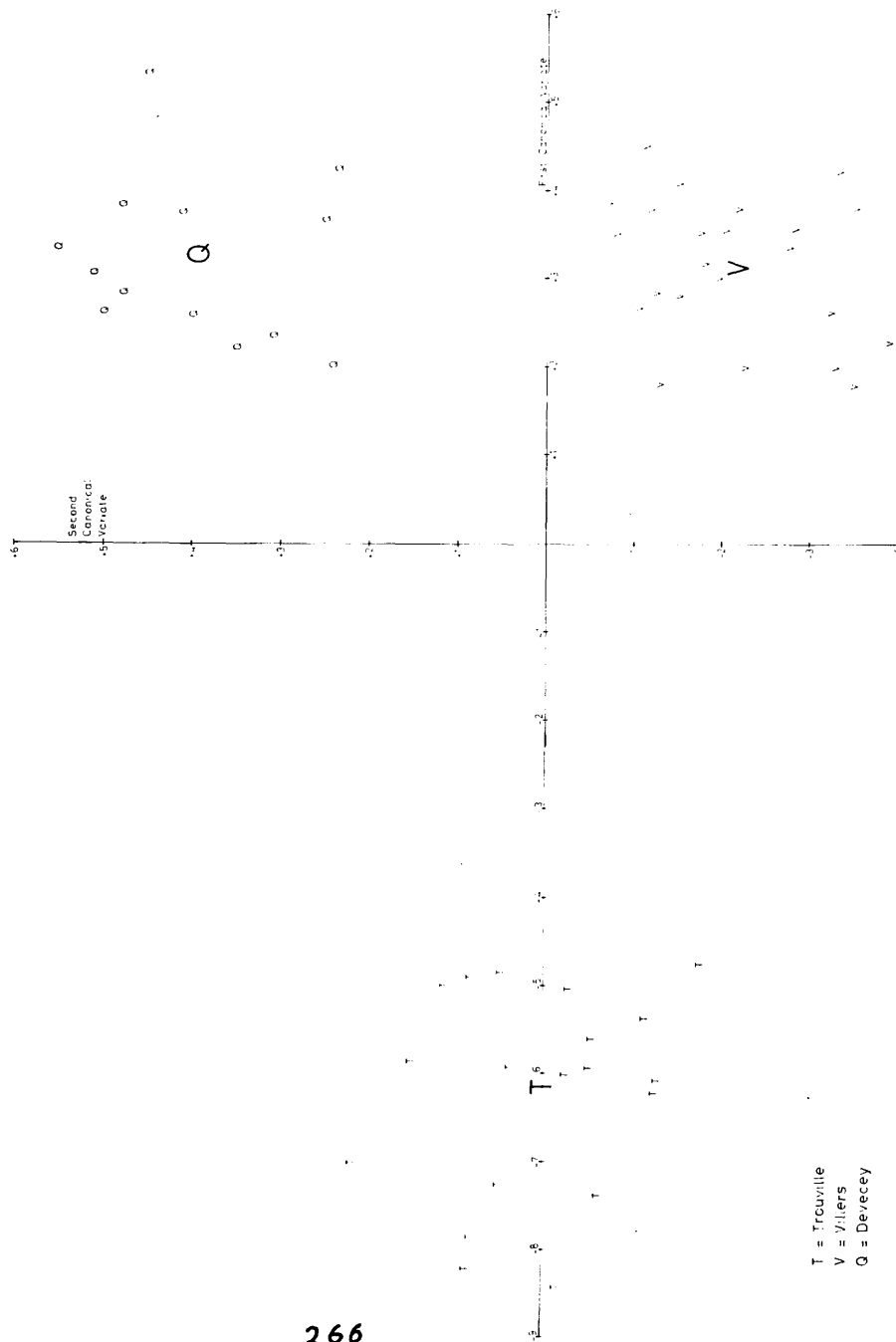
specimens. This component characterises typical Devecey specimens, which have a large but low periproct. A plot of the second and third components,which eliminates any overall size variation between the samples shows how clearly the groups are distinguished (Fig.8,6). Fig.8,7 tabulates eigenvalues and direction cosines for the first four principal components.

6. Comparison between Devecey,Villers,Trouville and Signy

The four samples from Signy,Trouville,Villers and Devecey 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 Devecey 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 Devecey 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 N1 and contributed a further 12%. A plot of these

Figure 8,6. Distribution of Trouville (N.scutatus), Villers (N.micraulus) and Devecey (N.subquadratus) 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.
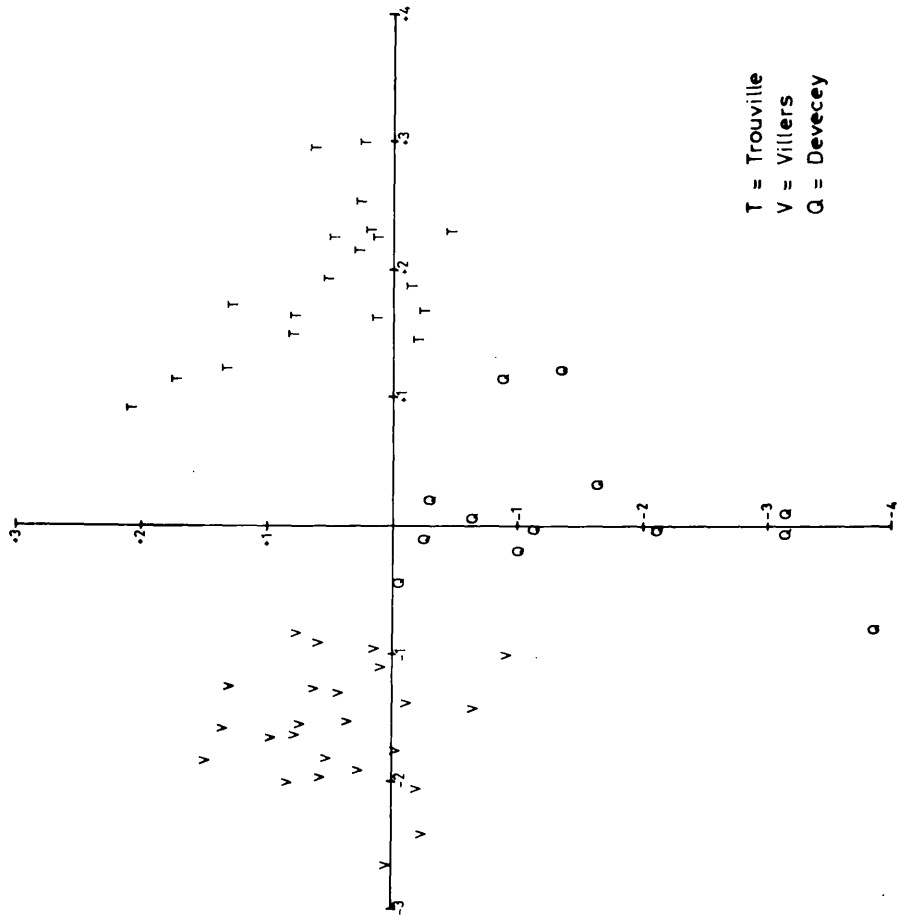
T = Trouville
V = Villers
Q = Devecey

PRINCIPAL COMPONENT ANALYSIS

Trouville, Villers and Devecey samples.

14 variables, 56 cases.

Eigenvalues

| | 8.36 | 2.61 | 1.33 | .61 |

Cumulative proportions of total variance

| | 60% | 78% | 88% | 92% |

Eigenvectors

	1	2	3	4
A	-.33	-.08	-.14	-.21
B	-.34	.04	.05	-.06
C	-.32	.01	.16	.34
D	-.32	-.00	.17	.36
E	-.33	.00	-.04	-.00
G	-.33	-.11	-.17	-.20
H	-.29	-.03	-.18	-.39
I	-.19	.09	-.63	.43
J	-.05	.53	-.21	-.38
L	-.01	.56	-.22	.32
M	-.32	-.01	.10	-.19
N1	-.18	-.49	-.18	.10
N2	-.17	.34	.26	-.12
N4	-.25	.14	.52	.17

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.

Prefix O = specimens from Signy
"   X =   "   "   Trouville
"   V =   "   "   Villers
"   BA =   "   "   Devecey
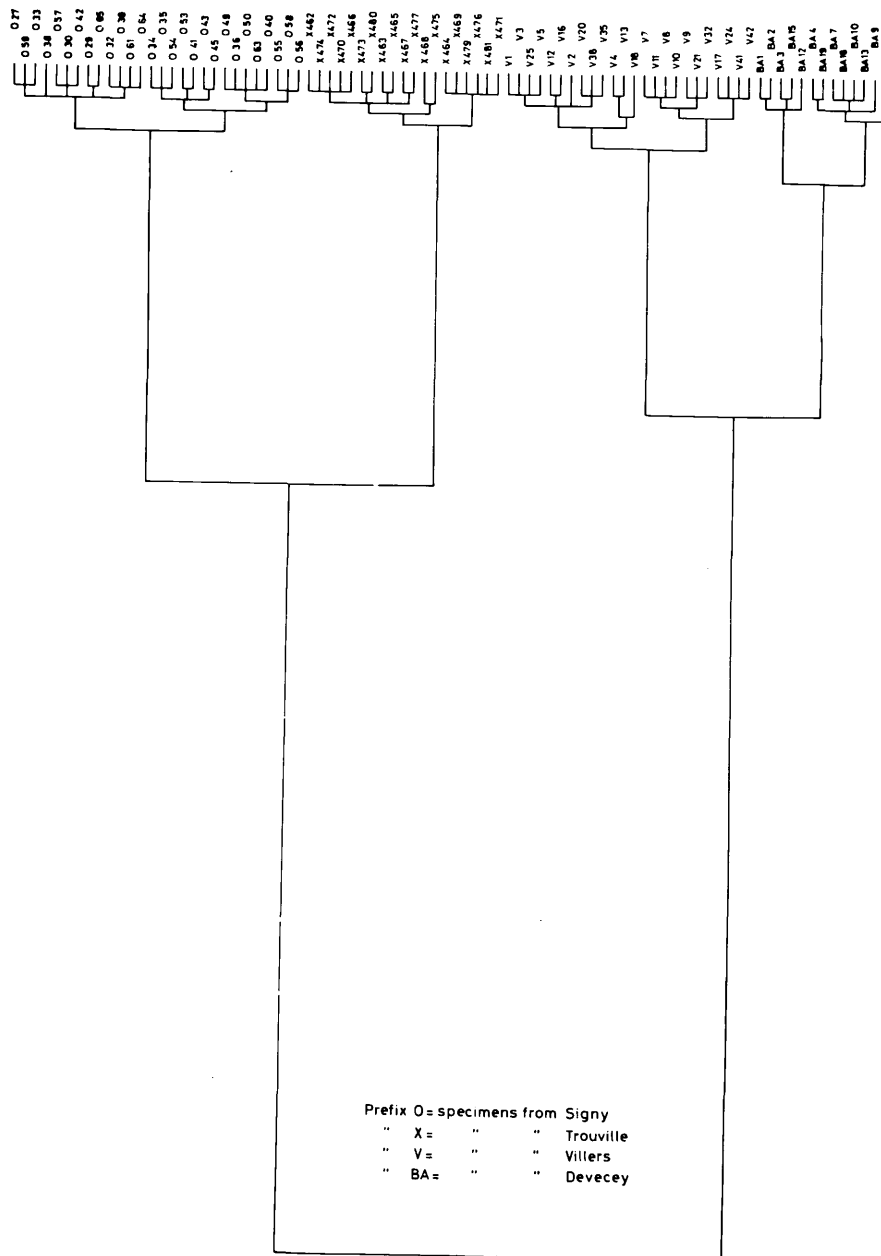
two components showed two growth lines,formed respectively by the Signy - Trouville and Villers - Devecey specimens and highlighted the relationships revealed in the hierarchical clustering. The graph showed a similarity in growth within the two groupings,the value of N1 increasing much more rapidly 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 indiacted 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 χ^2 tests of D^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 χ^2 test of the Mahalanobis distance of the cast from each group mean showed a low proabability (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 Devecey specimens on the first two canonical axes. Group centroids indicated by large lettering. Mean coordinates;

Signy   7.717   .767
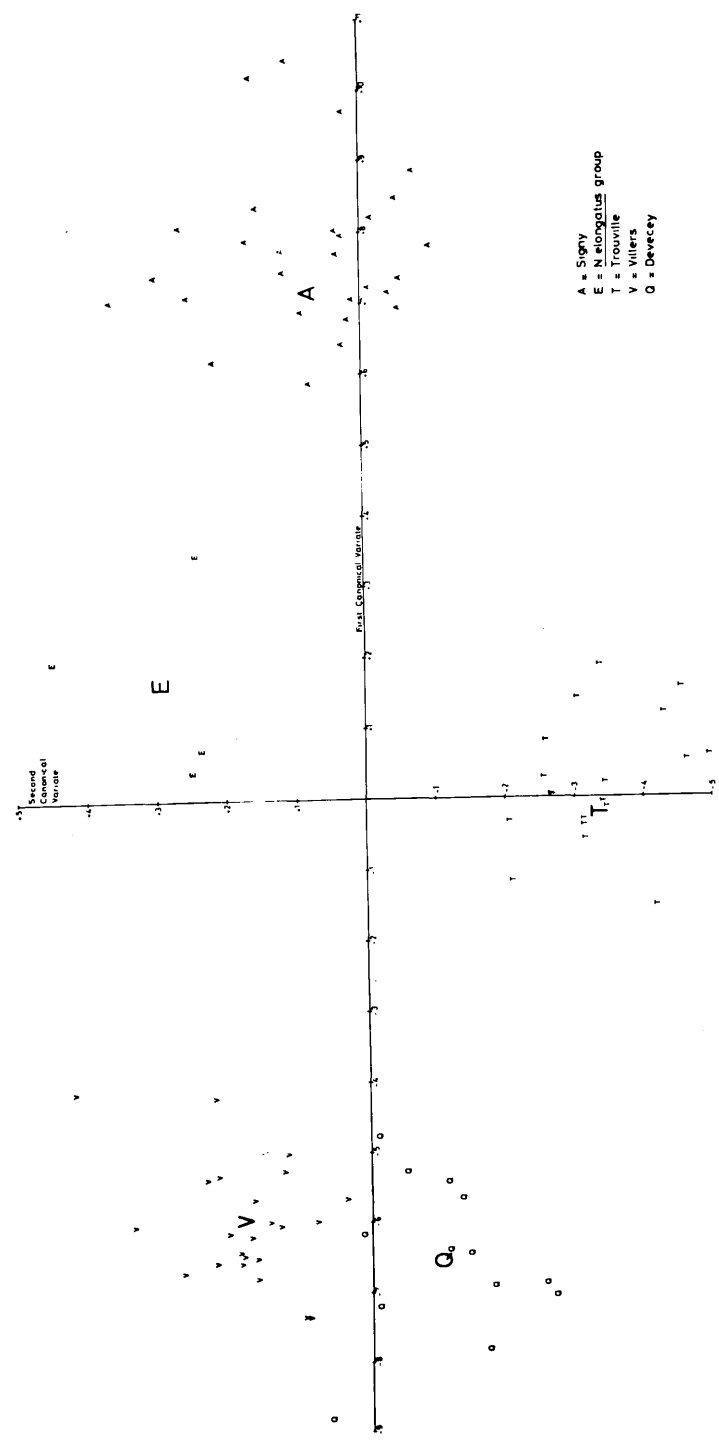
N.elongatus group
             1.642   2.951

Trouville   .232 -3.334

Villers   -5.927   1.818

Devecey   -6.519 -1.042

A = Signy
E = N.elongatus group
T = Trouville
V = Villers
Q = Devecey

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. Specimens 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 distintion 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 χ^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, Nl 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 χ^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 Devecey

sample (see above). This is also indicated in the F 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 Devecey

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.

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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;
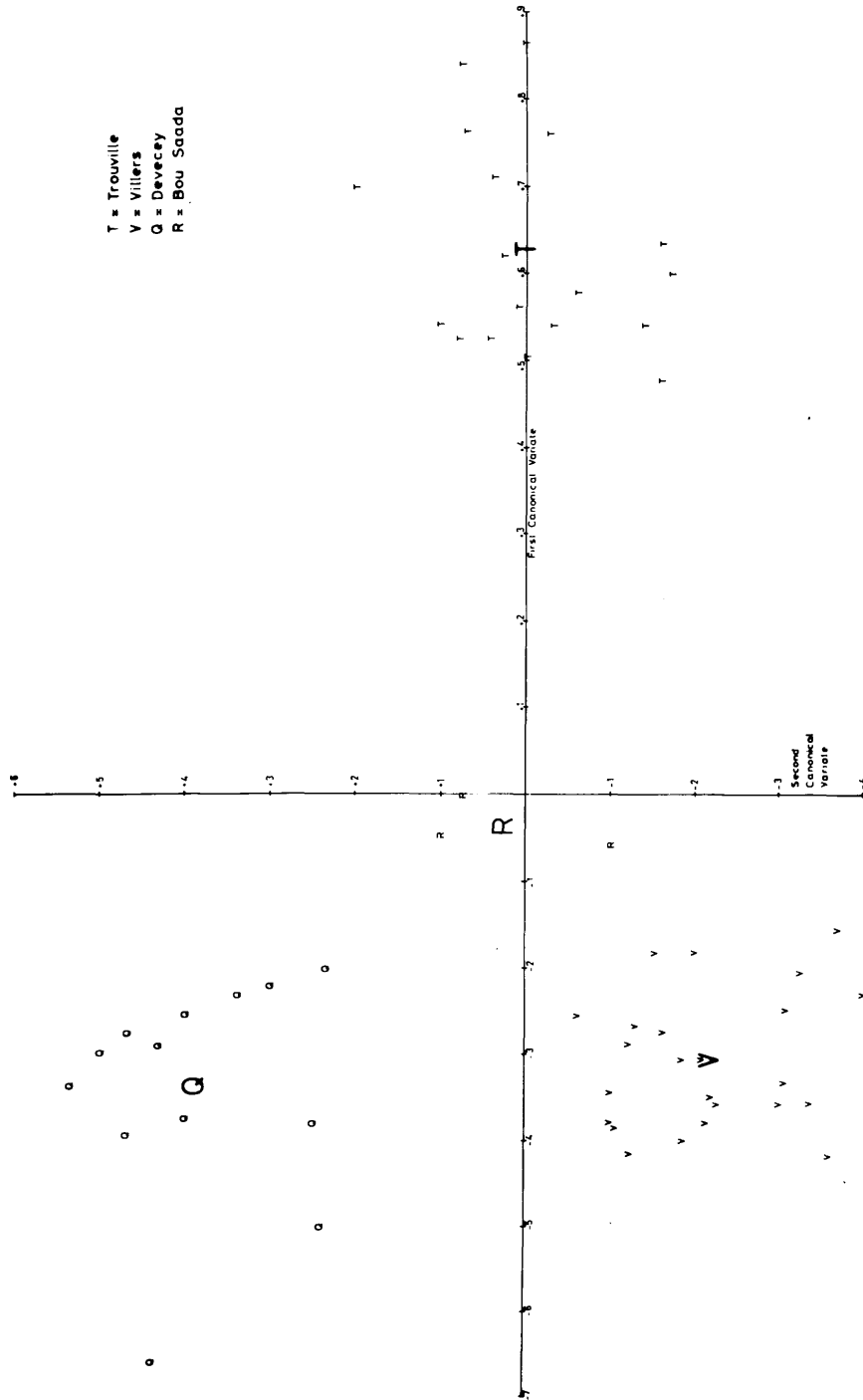
Trouville 6.282   .064
Villers   -3.101 -2.178
Devecey   -3.368   3.386
Bou Saada -.383   .251

T = Trouville
V = Villers
Q = Devecey
R = Bou Saada

First Canonical Variate

Second
Canonical
Variate

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 <u>N.elongatus</u> group.

8 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 corre spondingly 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.

N1 and N4 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 N1. Two other,orthogonal,vectors composed

of N1 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 N1,D,H and B,

being a large nucleolitid with the periproct situated in a posterior

position.

Comparisions 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

Sample	Comparison sample	Page	Var	Spec	Technique	Sig. of diff.	Imp. Variables
1. Nelson (A.recens)	Wellington (A.recens)	282	12	31	S.D.F.	P<1%	J,N3,N1,C,N2
		284	12	31	P.C.A.	Separation mainly along 1st vector	Size variables
		284	12	31	H.C.	Clustering not into original groups	
		284	13	41	R.M.A.	P<1% between 11 pairs of slopes	N 2
2. New Zealand (A.recens)	Trouville (N.scutatus)	288	13	45	S.D.F.	P<1%	N1,C
		289	13	45	P.C.A.	Separation on plot of 1,2 vectors	1st – size 2nd – N2
		289	12	50	H.C.	Final 2 groups = original groups	
		289	14	243	R.M.A.	P<1% between 11 pairs of slopes	N 2
3. Nelson, Wellington, (A.recens)	Trouville,Cothill,Dorset, W.Bassett, Upware (N.scutatus)	293	12	176	S.D.F.	P<1%	N1,M,L
4. All A.recens (treated as one group)	All N.scutatus samples (treated as one group)	295	12	176	S.D.F.	P<1%	N1,C
5. New Zealand (A.recens)	Trouville (N.scutatus) Villers(N.micraulus), Devecey(N.subquadratus) Bou Saada(N.rotundus)	296	13	85	S.D.F.	P 1%	L,N1,C,E,N2
		297	12	90	H.C.	Clustering not into original groups	
6. New Zealand (A.recens)	As above + N.elongatus group, Signy (N.amplus)	297	13	98	S.D.F.	P<1%	L,J,N1,C,E,N2
		300	14	361	R.M.A.	P<1% between 10-11 pairs of slopes	N2

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 χ^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;

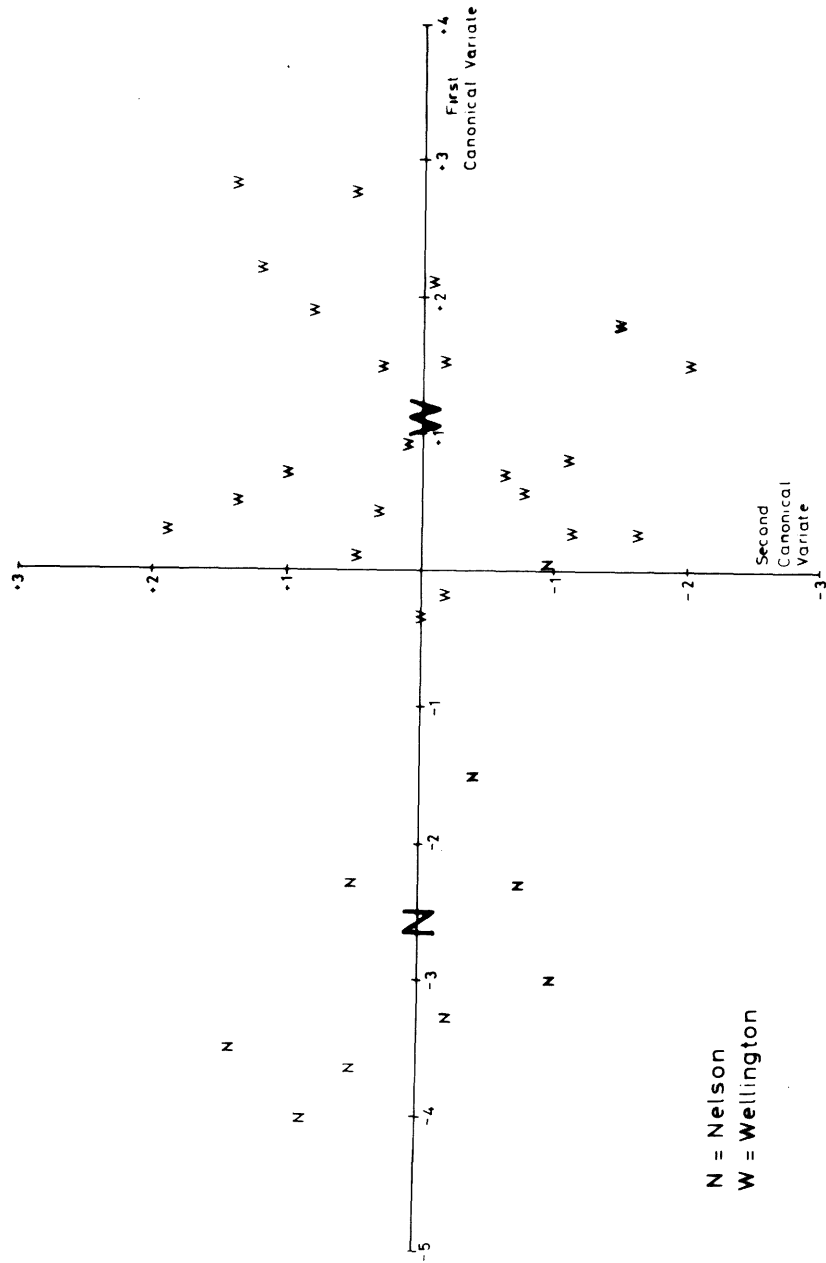Nelson   -2.593   .000
Wellington 1.061   .000

First Canonical Variate

Second Canonical Variate

N = Nelson
W = Wellington

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.

N = Nelson
W = Wellington

First Principal Component

Second Principal Component
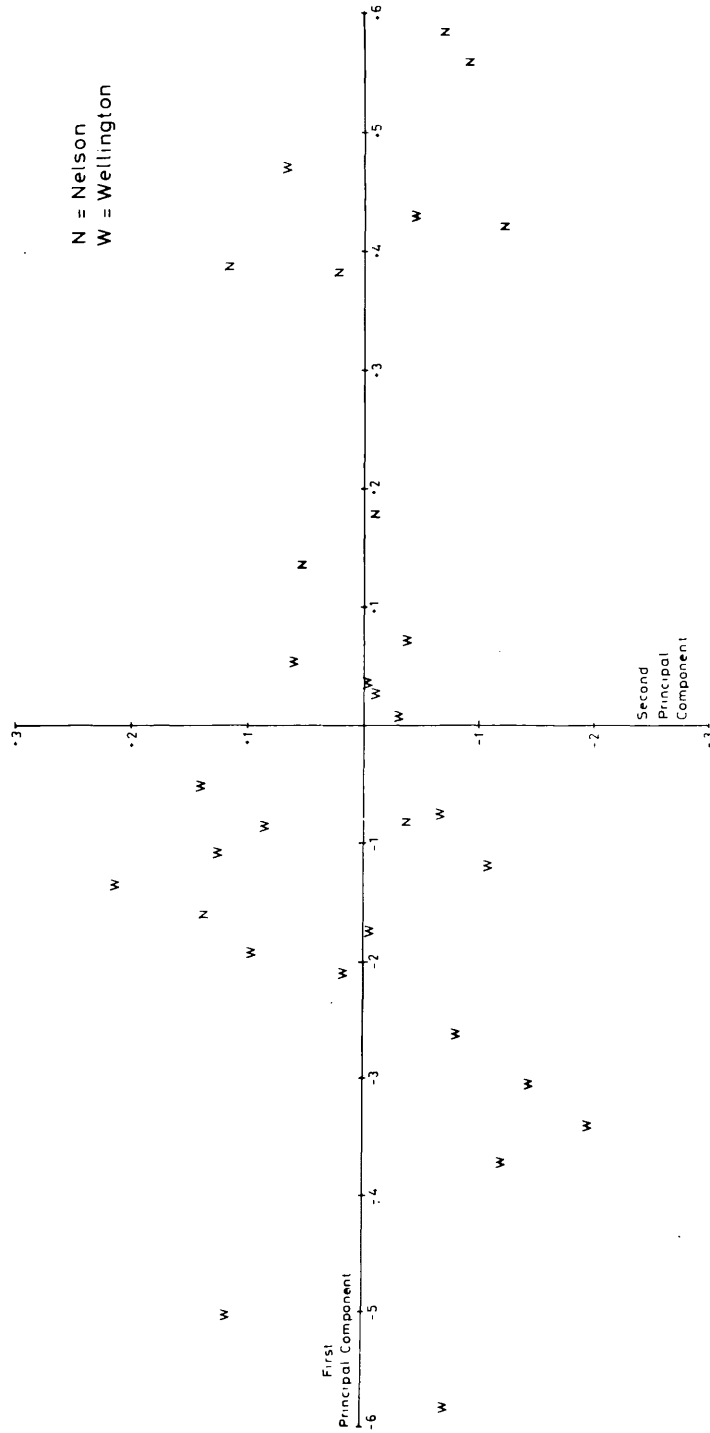
PRINCIPAL COMPONENT ANALYSIS

Nelson and Wellington samples.

12 variables, 31 cases.

Eigenvalues

| 9.39 | .98 | .88 | .40 |

Cumulative proportions of total variance

| 78% | 86% | 94% | 97% |

Eigenvectors

	1	2	3	4
A	-.33	-.03	-.02	-.05
B	-.32	.04	-.05	-.07
C	-.31	.01	.01	-.08
D	-.31	-.02	-.10	-.10
E	-.32	-.00	-.04	-.04
G	-.33	.02	-.03	-.07
J	-.30	.20	-.09	.35
L	-.28	.25	-.19	.60
M	-.32	-.07	.15	-.17
N1	-.30	-.15	.18	-.54
N2	-.12	-.89	.18	.34
N3	-.12	.26	.92	.14

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 χ^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 increse 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.

T = Trouville
N = New Zealand
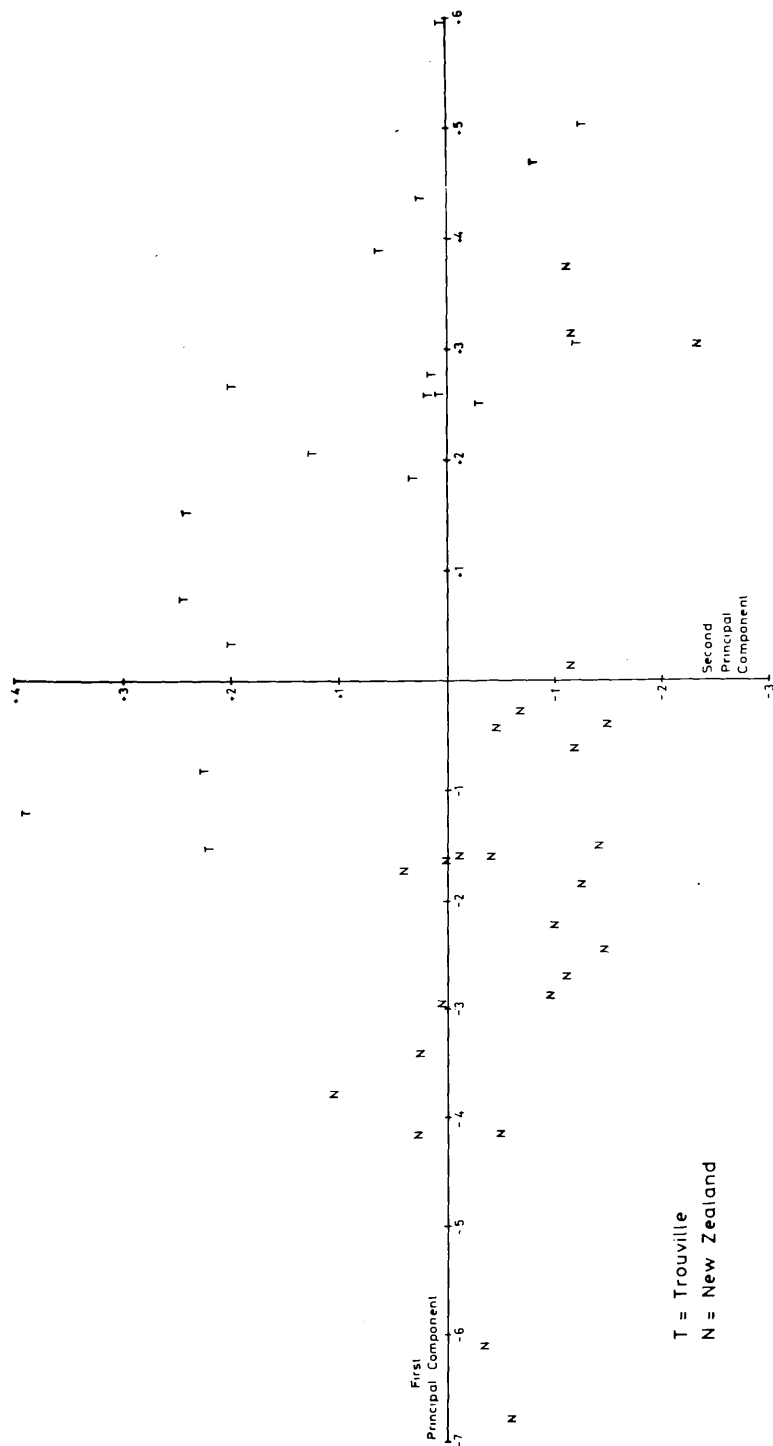
PRINCIPAL   COMPONENT   ANALYSIS

New Zealand and Trouville samples.

13 variables, 44 cases.

Eigenvalues

9.45	1.77	.82	.38

Cumulative proportions of total variance

73%	86%	93%	96%

Eigenvectors

	1	2	3	4
A	-.32	-.06	.05	.15
B	-.32	.05	.04	.02
C	-.27	.36	-.07	-.35
D	-.26	.40	.05	-.37
E	-.32	-.08	.06	.22
G	-.32	-.09	.05	.13
H	-.30	.02	.08	.19
J	-.30	-.22	-.04	-.30
L	-.27	-.31	.08	-.39
M	-.30	.19	.15	.00
N1	-.29	-.14	.05	.54
N2	-.00	.69	-.11	.29
N3	-.15	-.09	-.97	.03

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

		A	L	N1	N2
Signy	A.	4	12	7	11
	B.	1	1	3	0
	C.	8	0	3	2
	D.	0	0	0	0
Trouville	A.	7	4	10	11
	B.	2	5	2	0
	C.	4	4	1	2
	D.	0	0	0	0
Villers	A.	4	3	5	10
	B.	2	3	0	1
	C.	7	7	8	2
	D.	0	0	1	0
Devecey	A.	1	1	1	11
	B.	1	2	1	1
	C.	11	10	11	1
	D.	0	1	2	0

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. Firtsly,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 6 F).

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
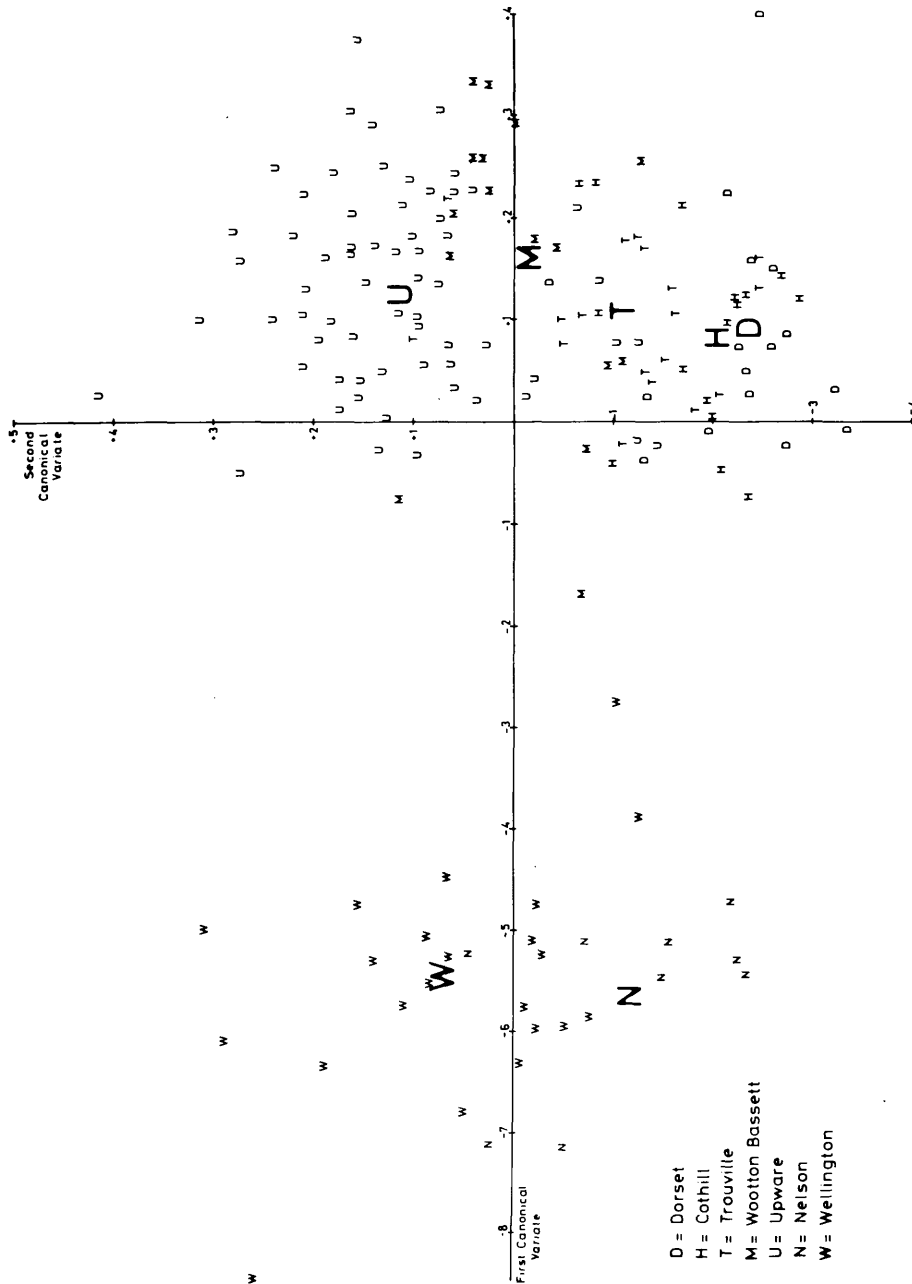
D = Dorset
H = Cothill
T = Trouville
M = Wootton Bassett
U = Upware
N = Nelson
W = Wellington

Second Canonical Variate

First Canonical Variate

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 χ^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.9,9 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.subquadratus), 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

T = Trouville
V = Villers
Q = Devecey
R = Bou Saada
N = New Zealand
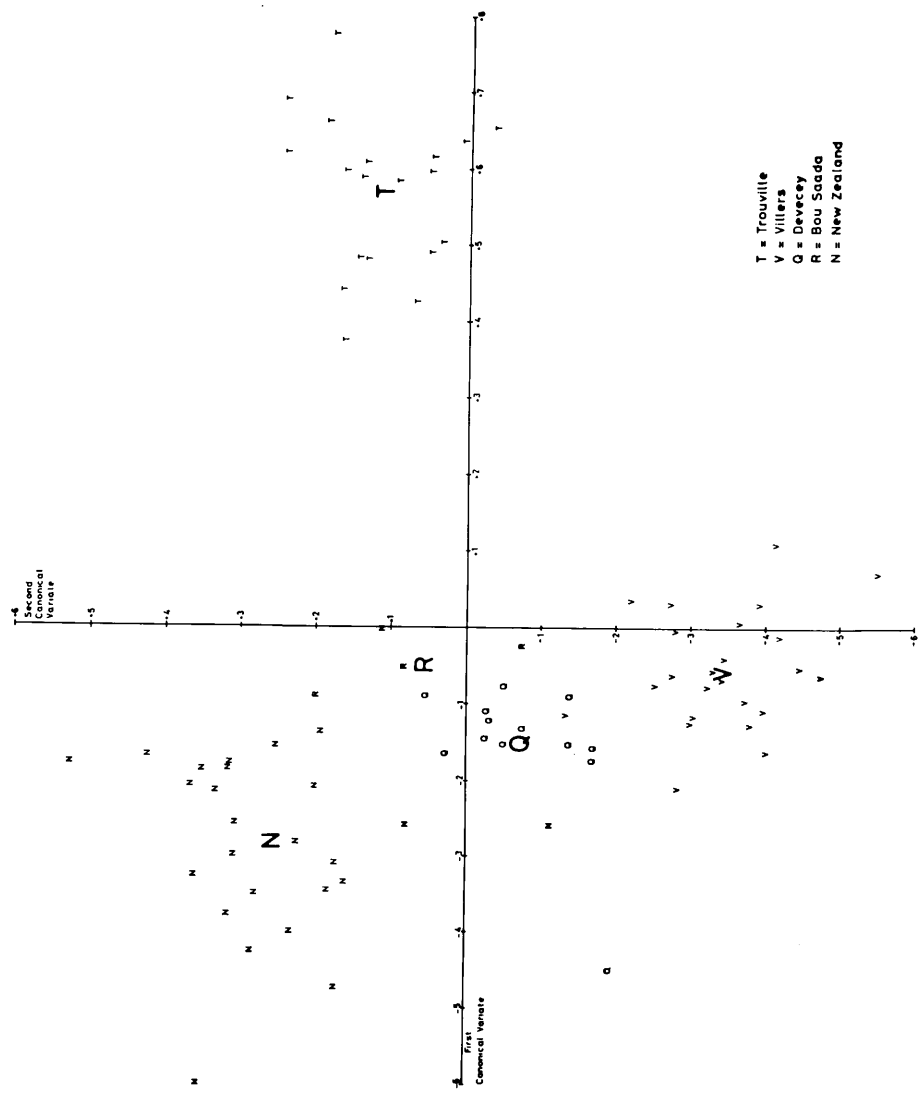
Original Sample \ Group	Signy	N.elongatus	Trouville	Villers	Devecey	Bou Saada	N.Zealand
Signy	0%	100%	100%	100%	100%	100%	100%
N.elongatus	100%	50%	100%	100%	100%	100%	100%
Trouville	100%	100%	0%	100%	100%	100%	100%
Villers	100%	100%	100%	4%	62%	83%	100%
Devecey	100%	100%	100%	77%	8%	69%	100%
Bou Saada	100%	100%	100%	66%	66%	0%	66%
New Zealand	100%	100%	100%	96%	92%	68%	12%

Figure 9,10. Percentage of specimens within each sample with a low probability (P<5%) of belonging to each group, based on χ^2 tests of D^2 for each case.

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a particular group (using χ^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 anomolous 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 dfferences) 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
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
N.elongatus group	-4.488	3.037
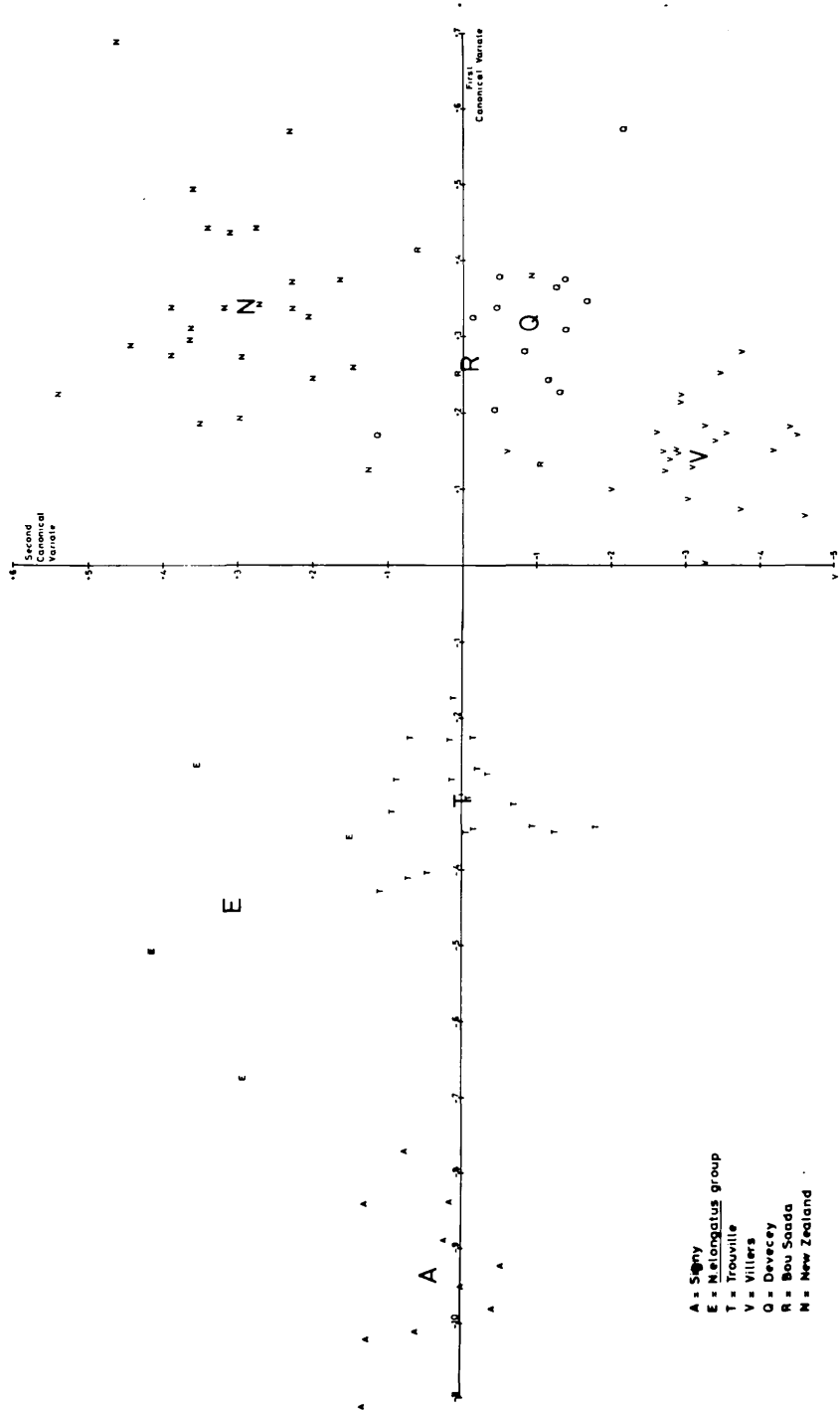
A : Signy
E : N.elongatus group
T : Trouville
V : Villers
Q : Devecey
R : Bou Saada
N : New Zealand

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 differentiatied,
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.

CHAPTER 10 - DISCUSSION

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 injested. 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 injestion 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 injesting 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 fasciole. 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; McKerrow,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.

McKerrow (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 interpretated

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 bethonic 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 spatagoids 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.micraulus,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 speciemens

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 Willian Smith (Smith,1817a,b) there was

considerable confusion concerning the differences between N.scutatus

and N.latiporus (syn.N.clunicularis), few pre-Linnean 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-arbitary

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 mophological 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

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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.elongatus) and rounded(N.amplus) species,and again in the Oxfordian there are elongate (N.micraulus) and rounded (N.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 Nl (distance between apical disc and periproct). This indicates that C and I decrease as Nl 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 $\bar{L}$ x $\bar{I}$, is correlated with substrate grain size in some species,e.g. within N.scutatus (Scurry,1978) and probably within N.amplus,N.elongatus and N.micraulus (see Chapter 7G). 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.scutatus) or much larger (N.amplus). However, the orthogonality of the two vectors indicates that as Nl 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 Nl.

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 N1 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.amplus N1 and L are short,C and I large,whilst in the Oxfordian N.micraulus L and I are short and N1 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 N2 (indentation of posterior border),B (width of test) and N1. 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 N2 (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 N1 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,N1 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 N1. 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

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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 N1. 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,N1 and M

are entered at steps 2,3 and 8 respectively in discriminant function

analysis,J and N1 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 overal 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.

1. The taxonomy of each of the ten species studied is discussed.
Echinobrissus 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
heterogenity 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

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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.

	Rounded	Elongate
Quaternary		recens
Pliocene Miocene		
Oligocene Eocene Palaeocene		
Maastrichtian Senonian Turonian Cenomanian	rotundus	
Albian Aptian Neocomian		subquadratus
Portlandian Kimmeridgian Oxfordian	scutatus	micraulus
Callovian Bathonian Bajocian Aalenian	amplus burgundiae woodwardii ?	elongatus latiporus
Lias		
Trias		

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.

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PLATE   1

Fig.1   <u>Nucleolites</u>   <u>scutatus</u>   Lamarck.

Specimen X544 from Upware Quarry,

Cambridgeshire, Parandieri Subzone (Oxfordian).

Specimen size; Length (A) = 25.6mm, 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)

PLATE 1
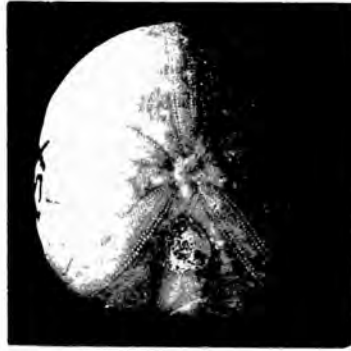
1a
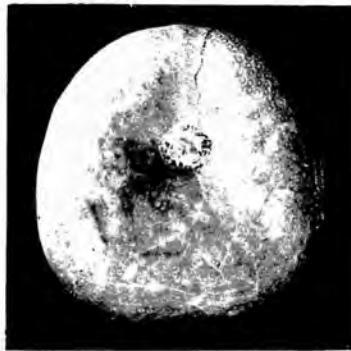
1b

1c

1d

339A

PLATE   2

Fig. 1   <u>Nucleolites</u> <u>amplus</u> 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   <u>Nucleolites</u> <u>woodwardii</u> 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.

PLATE 2

1a

1b

1c

1d

2a

2b

2c

2d

340A
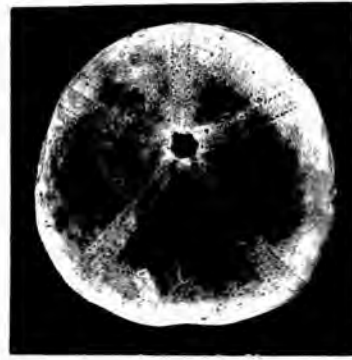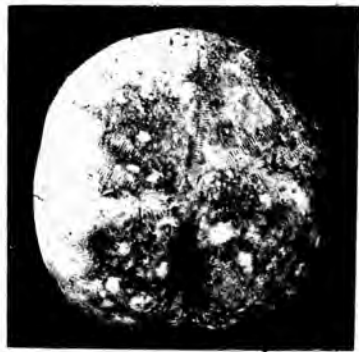
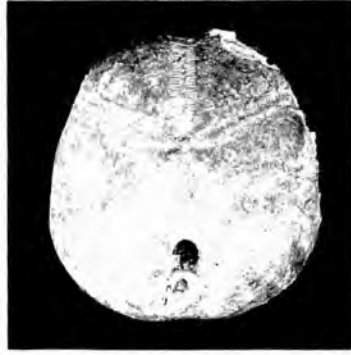PLATE   3

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.

341
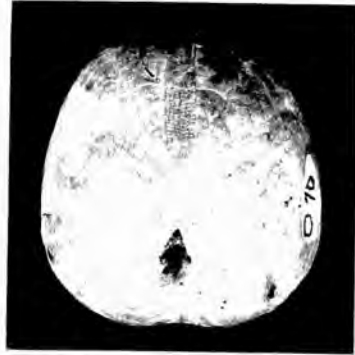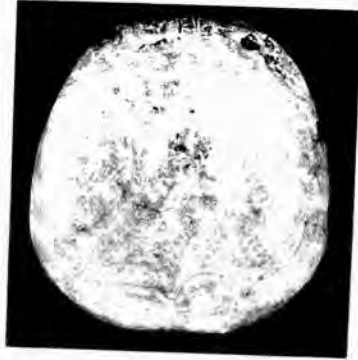
PLATE 3

1a 1b

1c 1d
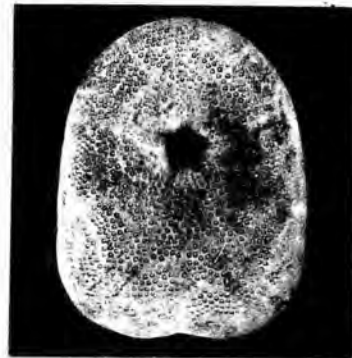
2a 2b

2c 2d

341A

PLATE   4

Fig. 1   <u>Nucleolites</u> <u>micraulus</u> 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   <u>Nucleolites</u> <u>subquadratus</u> Agassiz.

Specimen BA2 from Devecey, Doubs, Neocomian.

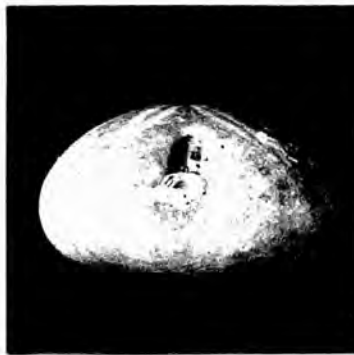Specimen size; Length (A) = 23.1 mm, Breadth (B)
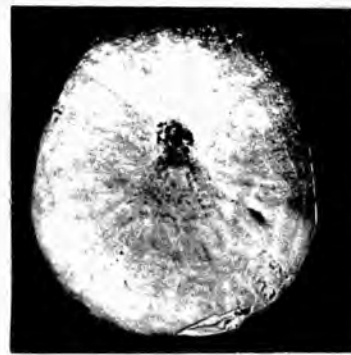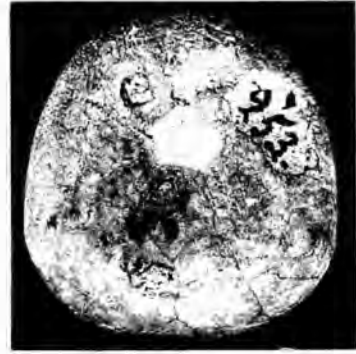
= 20.6 mm, Height (C) = 11.4 mm.

PLATE 4

1a

1b

1c

1d

2a

2b

2c

2d

BA.2

342A

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)
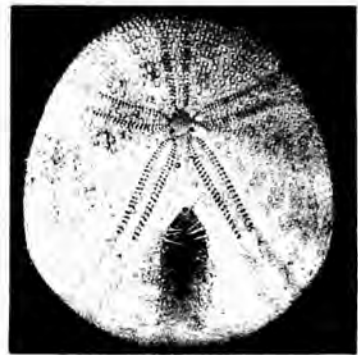
= 27.7 mm, Breadth (B) = 25.3 mm,

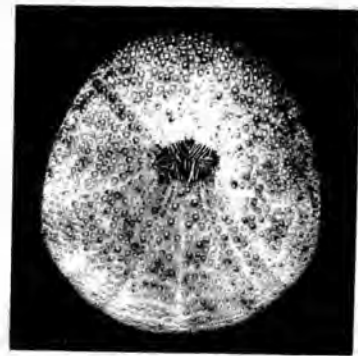Height (C) = 12.2 mm.

PLATE 5

1a 1b

1c 1d

2a 2b

2c 2d

343A