STUDIES ON THE PALAEONTOLOGY

OF THE LOWER OXFORD CLAY

OF SOUTHERN ENGLAND

A thesis submitted for the degree of Doctor of Philosophy

in the Faculty of Science

of the University of Leicester.

by

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ABSTRACT

The Lower Oxford Clay (Middle Callovian, Upper Jurassic) of southern England has been studied in detail, in order to elucidate the stratigraphy, bivalve taxonomy and palaeoecology of the formation.

Examination of four quarries in the Midlands, between Peterborough and Calvert (Bucks.), has allowed a detailed stratigraphy to be established, based upon that of Callomon (1968), and to which it has been possible to relate the range and occurrence of all the invertebrate species collected. The position of the Obductum – Grossouvrei Subzonal boundary at Stewartby (Bedford), which was not located by Callomon, has been established, on the basis of recurrent bivalve populations.

The taxonomy of the bivalve fauna has been treated monographically, 48 species, 7 of which are new, having been described. One new genus, Byssentolium gen. nov. is introduced, with B. hudsoni sp. nov. as its type species. The subgenus Trautscholdia Cox & Arkell is elevated to full generic rank, and the generic assignations of several of the most well-known Upper Jurassic bivalve species are amended. The remainder of the Lower Oxford Clay invertebrate fauna has been considered in general terms, and its palaeoautecology inferred; the palaeo- autecology of the bivalve fauna has been dealt with in detail.

By using the mass of detailed information collected at the four major quarries, a palaeoecological reconstruction of the environmental conditions established during the deposition

of the Lower Oxford Clay has been made. Ten biofacies types
have been defined and recognised at all the major quarries,
and are characterised by 5 ecologically defined parameters.

The benthonic fauna of several other Jurassic and
Cretaceous Clay Formations has been compared with that of the
Lower Oxford Clay, showing that only the Upper Lias of England
is closely comparable.

Consideration of the composition of deposit-feeder
dominated communities since the Lower Palaeozoic has shown the
major difference to be the replacement of the suspension-feeding
brachiopods by suspension-feeding bivalves, a consequence of
mantle fusion and siphon formation.

iii.

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v.

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CHAPTER 1

GENERAL INTRODUCTION

The Lower Oxford Clay (M. Callovian, U. Jurassic) is a series of up to 18 m of dark grey-green bituminous shales, bounded below by the sandy Kellaways Rock (L. Callovian) and above by the lighter grey, more plastic, non-bituminous clays of the Middle and Upper Oxford Clay (U. Callovian - L. Oxfordian). The British Callovian deposits represent a major marine transgressive phase after the regressive, dominantly lagoonal and estuarine, deposits of the Bathonian, and show what is believed to be a deepening water sequence of sediments, from near-shore sands and limestones, through bituminous shales, into massive unlaminated clays. The shales of the Lower Oxford Clay were chosen for study because of the interest in bituminous shale ecology, together with the diversity and abundance of fossils which they contain. Originally, it was hoped to produce an overall ecological synthesis of conditions of deposition within the whole of the English Oxford Clay, but it very quickly became apparent that this was an impossible task in the time available. The main cause of this realisation was the discovery that the Oxford Clay bivalve fauna, although diverse and abundant, was very poorly-known, and so needed a taxonomic basis before ecological work could properly be conducted. Accordingly the aims became modified, so that the major part of the project became a taxonomic study of the bivalves of the Lower part of the Oxford Clay, together with an ecological study of the same

part. This is how the project has developed, and the bias is obvious from the relative size of the Chapters.

Lithologically, the Lower Oxford Clay consists dominantly of well-laminated bituminous shales, with occasional shell-beds, more calcareous clays, and some silts at the base. The detailed lithologies are discussed in Chapter 2. There is a very diverse and often abundant fauna to be found in the Lower Oxford Clay, dominated by molluscs, with cephalopods and bivalves being overwhelmingly the most common elements, although gastropods are frequent, and scaphopods locally abundant. There is, however, a varied accessory fauna consisting of inarticulate brachiopods (Lingula), which are locally common in the bituminous shales, rhynchonellid brachiopods, small decapod crustacea, annelid worm tubes, occasional ophiuroids and some trace fossils. A well-known characteristic of the Lower Oxford Clay is the presence of well-preserved and relatively common vertebrate remains, especially reptiles (Ichthyosaurs, Plesiosaurs, Pliosaurs) and fish, the skeletons of the reptiles are often articulated, although isolated skeletal fragments such as teeth, ribs and centra are fairly common in the shell beds.

The thesis considers several aspects of the palaeontology of the Lower Oxford Clay of southern England. There are two Chapters, Chapter 2 being a monographic study of the Lower Oxford Clay bivalve fauna, and also comprising the major part of the thesis, and Chapter 3 being a study of the palaeoecology of the Lower Oxford Clay of central England. Finally, there is a short chapter summarising the conclusions reached from the

work. Both Chapters 2 and 3 have been written in a style
suitable for publication, and have been submitted to the
Palaeontographical Society and to the journal 'Palaeontology'
respectively. Thus each of these chapters is completely self-
contained, with introduction, methods and results, conclusions
and bibliography; for this reason, a general bibliography is
not given separately at the end of the thesis.

The work is the result of three years study of the Lower
Oxford Clay as seen at four quarries owned by the London Brick
Company between Peterborough (Hunts.) and Calvert (Bucks.).
These exposures have been compared with those seen on the Dorset
coast in the area around Weymouth. The sections seen at the
four L.B.C. pits have been described by Callomon (1968), and
these measured sections formed the basis of the detailed
collections made in this study. Some minor discrepancies between
this work and that of Callomon (op. cit.) were found, and the
sections measured by the author are shown in Fig. 2.3 and
Appendix 1. As the revised sections were measured, extensive
collections of the contained fauna were made, and it is these
collections which form the basis of the work in both Chapters
2 and 3. However, in order to make the monographic work as
comprehensive as possible, collections housed in all the major
British museums were also examined.

The remainder of this introductory chapter will present
a general summary of the contents of the two major chapters in
this thesis.

Chapter 2 occupies the bulk of the thesis, and comprises a monographic study of the bivalve fauna of the Lower Oxford Clay of southern England. A general introduction is followed by a consideration of previous work, which discusses earlier work on the stratigraphy, taxonomic palaeontology and palaeoecology of the Lower Oxford Clay. The most obvious point which becomes apparent from this section of the work, is the need for taxonomic revision of virtually all of the invertebrate groups present in the Lower Oxford Clay, especially the molluscs (excluding the ammonites).

The next section (2.3) considers the stratigraphy of the Midlands Lower Oxford Clay at some length. Notes on the geographic extent and thickness of the deposit are followed by detailed facies analysis and description of the four quarries examined. Five lithofacies types are recognised in the Midlands, which may be divided, on the basis of their combined fauna, into ten biofacies. Each biofacies may be recognised at all of the quarries (with the exception of the blocky claystone, which is peculiar to Calvert), and is usually found in the same stratigraphical position relative to the other biofacies. Section 2.3.4 describes the biostratigraphy of each of the quarries, and compares them in very general terms. More detailed comparison, together with consideration of the overall environmental conditions, is given in Chapter 3. These descriptions, in section 2.3, are the basic stratigraphic framework for further study of the Lower Oxford Clay fauna, and complement Callomon's (op. cit.) consideration of the subzonal stratigraphy of the Middle Callovian.

Section 2.4 deals with the palaeoautecology of the
bivalves, with the species being first placed in feeding
groups, and then being considered individually. The autecology
of each species has been determined by a combination of functional
morphology and consideration of the life habits of Recent
related species. Detailed assemblage studies have not been
considered here, but are left until Chapter 3. The main aim of
the palaeoautecology section is to consider the life habits of
the individual bivalve species. This section is brought to a
close by a description of the rest of the invertebrate fauna of
the Lower Oxford Clay, where the faunal elements other than
bivalves are discussed. However, the species here are not
treated taxonomically; the aim of the section is to show the
diverse invertebrate fauna present in the Lower Oxford Clay.
Most groups are in need of thorough taxonomic revision.

Chapter 2 is concluded by a section on conventions and
techniques (2.5), in which terminology, type material, variation
within species, preparation methods and taxonomic considerations
are discussed, and by a section (2.6) on preservation in the
Lower Oxford Clay. Four main preservation types are seen in the
Lower Oxford Clay; preservation as primary shell material
(calcite or aragonite), primary shell with pyrite overgrowths
(usually only on shells with nacreous aragonite), primary shell
with calcite overgrowths, and complete replacement of the shell
material by pyrite. These preservation types are considered in
section 2.6, and it is proposed to study Lower Oxford Clay shell
preservation in more detail. The effects of crushing of shells

are also considered, showing that articulated shells, containing
a void between the valves, are more likely to suffer crushing
than are single disarticulated valves.

The "introductory" part of Chapter 2 ends with
acknowledgements and a comprehensive bibliography, before going
on to the taxonomic part of the work, in which 48 species of
bivalve, 7 new and 3 undescribed but as yet indeterminate, are
described. One new genus, Byssentolium gen. nov. is described,
with Byssentolium hudsoni as its type species; this genus is
separated from Entolium s.s. on the basis of the presence of a
byssal notch throughout life. In all the specimens of the type
species of Entolium, E. demissum, which have been examined,
there is no evidence of a byssal notch in any development stages,
including the earliest. One subgenus, Trautscholdia Cox &
Arkell is elevated to full generic rank, and the generic
placement of several well-known Upper Jurassic bivalve species
has been changed.

There has been some overlap of species in this study with
those considered by Arkell (1929-1937) in his monograph of
Corallian lamellibranchs, and those considered by Morris &
Lycett (1851-1855) and Lycett (1863) in their monographs on the
Mollusca of the Great Oolite. In the case of the Great Oolite
monographs, the species were in need of redescription, which
has been done here, whilst the work of Arkell has proved to be
still valid in most cases. Thus, in the case of the species
described by Arkell, unless new information has come to light,
the descriptions and remarks given herein supplement, rather than
supercede, those of Arkell.

Chapter 3 is a consideration of the palaeoecology of the Lower Oxford Clay of central England, and in particular, is concerned with the status of the Lower Oxford Clay as a bituminous shale. As it is written in the style required by the journal 'Palaeontology', the lay-out is completely different to that of Chapter 2. The introduction and section on the stratigraphy in many ways repeat what has been said in Chapter 2, to which frequent reference is made; the same is broadly true of the section on the nature of the fauna and preservation. After these introductory sections, there is a general consideration of the methods of ecological analysis used here, in which the uses of five parameters are discussed, together with a general section on palaeoecological assumptions. The ten biofacies characterised in Chapter 2 are then considered at some length, by the use of the five parameters noted above, triangular plots, rarefaction curves, trophic nuclei, trophic group composition and diversity index.

Having described the biofacies divisions, and their relationship to each other at all the major exposures, a synthesis of the environment of deposition of the Lower Oxford Clay in central England is presented, showing the presence of two cycles of deposition over the whole of the area studied. Central England, between Peterborough and Buckinghamshire is shown to be an area of gradual subsidence throughout Middle Callovian times, with similar environmental conditions being present over most of the area, although the thinning of the M. Callovian sequence northwards, and the presence of marginal

deposits of this age in Yorkshire (Wright, 1968), indicate that the shoreline lay to the north.

Comparison of the Lower Oxford Clay bituminous shales with other Jurassic and Cretaceous dark or bituminous shale facies reveals that the Lower Oxford Clays is, in many ways, unique, in that there is frequently a fauna dominated by infaunal deposit-feeding protobranchs and epifaunal suspension-feeding bivalves such as Bositra, Oxytoma and Meleagrinella. The palaeoautecology of these three genera has been considered in Chapter 2, showing them to almost certainly have been attached to floating organic material at some distance above the seafloor (the "pendent" mode of life). Such an association of species is not recorded from any of the other British Jurassic or Cretaceous Clay Formations, with the exception of the Upper Lias (Melville, 1956), and so environmental conditions during this time must have been rather unusual. The work of Hallam (1967a) on the depth significance of bituminous shales is of relevance here, and his hypothesis that bituminous shales are deposited early in the history of a major marine transgression, seems valid in this case. Other Clay Formations are compared, and shown, in most cases, to be characteristic of rather better-aerated water than was present during the deposition of the Lower Oxford Clay.

As a final consideration, the relative importance of evolutionary changes in the development of deposit-feeder dominated bivalve communities has been discussed, and it becomes apparent that the role of the slowly-evolving deposit-feeding

Nuculacea has remained constant since the Lower Palaeozoic. The main change appears to be the replacement of epifaunal suspension-feeding brachiopods by bivalves, the development of mantle fusion in the bivalves rendering them much more competitive, leading to the replacement by them of brachiopods as the main epifaunal elements of Mesozoic assemblages.

The final chapter summarises the major conclusions of the work.

REFERENCES

ARKELL, W.J. 1929-1937   See p. 68

CALLOMON, J.H. 1968   See p. 72

HALLAM, A. 1967a   See p. 451

LYCETT, J. 1863   See p. 83

MELVILLE, R.V. 1956   See p. 451

MORRIS, J. & J. LYCETT 1851-1855   See p. 85

WRIGHT, J.K. 1968   See p. 95

A MONOGRAPH OF THE LOWER OXFORD CLAY

BIVALVIA OF SOUTHERN ENGLAND

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CHAPTER 2

THE BIVALVE FAUNA OF THE LOWER OXFORD CLAY OF SOUTHERN ENGLAND

2.1   Introduction and general remarks

This work constitutes Part I of a three-part study of the
bivalve fauna of the British Oxford Clay (Jurassic, Middle
Callovian - Middle Oxfordian), and is concerned only with the
bivalves found in the Lower Oxford Clay (Middle Callovian) of
southern England.   Part II will deal with the Middle and Upper
Oxford Clay (Upper Callovian - Lower Oxfordian) of England, and
Part III with the Oxford Clay (Lower Callovian - Middle
Oxfordian) of Scotland.   The bivalve faunas of much of the
British Middle and Upper Jurassic are well-known, due to the
monographs of Morris & Lycett (1853-1855), Lycett (1863) and
Lycett (1872-1879) on Great Oolite bivalves, Blake (1905-1907)
on the Cornbrash, and Arkell (1929-1937) on the Corallian.
However, certain parts of the Jurassic, including the Oxford
Clay, have very poorly documented bivalve faunas, in spite of
the abundance of molluscan remains, and in the course of studies
on the palaeoecology of the Lower Oxford Clay of southern
England, the need for such a monograph became apparent.
Accordingly, large collections have been made from the British
Oxford Clay, and it is the specimens in these, together with the
collections housed in the major museums, which make up the
material described here.

The outcrop of the Lower Oxford Clay (Fig. 2.1) runs from
the Dorset coast at Weymouth, across England to the Yorkshire

coast at Scarborough, and is considered in more detail in section 2.3.1. Fossils are abundant throughout, molluscs dominating the fauna, which is discussed in general terms in section 2.2 on "previous work" and at the end of the "palaeoecology" section (Section 2.4.4). Preservation is variable, but usually very good, the original shell material often being preserved unchanged; the abundance of well-preserved specimens allow variation studies to be made.

There is some overlap in species with both the Great Oolite beneath, and the Corallian above, and as monographs exist for both these formations, the coverage of the species in question is amended accordingly. In the few cases where Bathonian species persist into the Oxford Clay, it has been necessary to redescribe and discuss the species in question, as there has been no adequate modern study of British Bathonian bivalves, with the exception of Cox & Arkell's synoptic supplement of 1948-1950. This causes overlap with the work of Morris & Lycett (1853-1855), Lycett (1863) and Lycett (1872-1879), but in view of the many advances in the last century, the author is of the opinion that this is fully justified. However, the work of Arkell (1929-1937) on the Corallian bivalve fauna is much more thorough in its treatment of morphology and synonymy, and the problems of overlap are much greater. In order to bring the species in question (about 10) in line with the others considered here, and in view of Arkell's sometimes scant descriptions, the diagnoses and description are given in detail, while the discussions are structured such that they are

complementary to those of Arkell, except on points of contention, which are considered more fully. As regards the synonymies of species described by Arkell, only the first record and selected important British records are given here, together with records made since Arkell's work was published. For a comprehensive synonymy list, the lists herein should be used in conjunction with those of Arkell.

The synonymies of species not discussed by Arkell are given in full, the British figured and cited specimens having been examined where available. In the case of foreign species and records, the type specimens or photographs of them, have been examined where possible, although several appear to have been lost. The system advocated by Richter (1948) and discussed by Matthews (1973), of attaching signs to the synonymy list to indicate the degree of confidence with which a record is referred to any species, is used in this work. Matthews (op. cit.) defines the signs used as follows:

 1881   Year in italics: this work has a mention of the species, but no description or illustration.

 1881   Year in roman: the work has a description and/or illustration, and contributes to our knowledge of the species.

    /cop. Anton 1856/: the illustration merely copies that of Anton, 1856.

*1881   * in front of year: with the publication of this work, the species can be regarded as valid under the terms of Article 11 of the ICZN.

.1881   . in front of year: we accept responsibility for attaching this reference to the species in question.

1881   no sign in front of year: we have no right expressly to accept responsibility for attaching this reference to the species under discussion; but at the same time, we have no cause to doubt such an allocation.

?1881   ? in front of year: the allocation of this reference must be subject to some doubt because of the way in which it was presented.

v1881   v in front of year: we have checked the deposited specimen that relates to the work cited, and on this evidence have chosen the additional sign used. Thus:

     v*1881   we have seen the type of the species.

     v.1881   because of the evidence of the deposited specimens we are able to take responsibility for this assignment.

     v 1881   we do not accept responsibility.

     v?1881   the condition of the original specimens is such that no clear decision is possible.

2.2   Previous work

Early workers on the Jurassic tended to be concerned with general fauna and stratigraphy, rather than on any specific

formation such as the Oxford Clay, although many fossils from
the Oxford Clay were figured by Phillips (1829), J. Sowerby
(1812-1823) and J. de C. Sowerby (1823-1829). Later workers
studied specific faunal elements found in the Oxford Clay, such
as the ammonites (Pratt, 1841; Leckenby, 1859; Buckman, 1909-
1930; Brinkmann, 1929a; Arkell, 1939a; Callomon, 1955;
Tintant, 1963), belemnites (Owen, 1844; Pearce, 1847; Mantell,
1848, 1850; Phillips, 1865-1870), crustacea (McCoy, 1849;
Carter, 1886; Woods, 1924-1931) or mollusca (Morris, 1850;
Leckenby, 1859; Hudleston, 1884-1885; Arkell, 1939a; Walker,
1972). In spite of this, no comprehensive study has been made
of any part of the invertebrate fauna of the Oxford Clay, with
the exception of Tintant's (1963) work on the Kosmoceratidae
(Mollusca: Ammonoidea) from the Lower and Middle Callovian of
Western Europe.

The status of the Oxford Clay within the Jurassic, and its
local stratigraphy, were discussed at length by Woodward (1895),
Brinkmann (1929), Arkell (1933a) and Callomon (1955, 1968);
these last works, together with those of Buckman (1913), Morley
Davies (1916) and Neaverson (1925), attempting to fit the Oxford
Clay into the standard system of Jurassic zones. The zonal
sequence for the Callovian used here (Table 2.1), is that
ratified by the International Geological Congress at their
Luxembourg colloquium of 1962 (Callomon, 1964, p. 288), a
modification of that originally introduced by Callomon (1955,
p. 256). This sequence has been exhaustively discussed by
Callomon (1955, 1964, 1968), and does not need further

consideration here. Earlier zonal systems, often based on local occurrences of various ammonites, were suggested by Buckman (1913), Morley Davies (1916) and Neaverson (1925), and are compared with modern usage in Table 2.2.

2.3   Stratigraphy

The Lower Oxford Clay occupies the whole of the Middle Callovian, and parts of the Upper and Lower Callovian stages, and is delimited at its base by the junction with the sandy Kellaways Rock. This junction usually occurs in southern England at the base of the Enodatum Subzone, although the change from silt to clay is gradual, and sometimes is not completed until the top of the Medea Subzone. The top of the Lower Oxford Clay is not so clearly marked palaeontologically or lithologically, and is placed about one-third of the way up the Athleta Zone. The junction with the Middle Oxford Clay divides the bituminous shales with abundant crushed aragonitic fossils of the Lower Oxford Clay, from the blue or grey-green, plastic, apparently unstratified, clays with fewer crushed fossils, of the Middle Oxford Clay; this change also heralds the appearance of pyritic ammonites.

This subdivision of the Oxford Clay only applies to the areas of England south of the Humber, as north of the Market Weighton region, most of the Middle Callovian is cut out by an unconformity at the base of the Grossouvrei Subzone (Wright, 1968, p. 366), and what remains of the Middle Callovian is developed in a much more marginal facies of sandstones and

limestones (Fig. 2.2). In Yorkshire, the Grossouvrei Subzone is up to 20m thick (Wright, op. cit., p. 368), and is represented by massive or flaggy fine and medium-grained sandstones, the Langdale Beds, in which bivalves are not frequent. The overlying Hackness Rock (up to 2.40m thick) belongs to the Athleta and Lamberti Zones, and consists of poorly sorted sandy limestones and calcareous sandstones, becoming a chamosite oolite towards the top. Wright (op. cit., p. 385) showed that there was another period of erosion at the base of the Hackness Rock, the oldest parts of the Hackness Rock appearing to be of Upper Callovian age, with rocks of Lower Athleta Zone age being absent. Thus the only rocks of Middle Callovian age proved in Yorkshire are the Langdale Beds.

Early workers (Damon, 1860, 1884; Judd, 1875; Roberts, 1889, 1892) on the Oxford Clay divided the formation into beds on the basis of preservation and fossil types, but it was not until the classic work of Brinkmann (1929), on the Lower and Middle Oxford Clay of Peterborough, that detailed bed by bed sections were recorded. Woodward (1895) and Arkell (1933a) summarized the early records of Oxford Clay exposures, but these are now of little more than historical interest. Detailed descriptions of parts of the Middle and Upper Oxford Clay of Buckinghamshire and Wiltshire were given by Arkell (1939a, 1941), and of the Lower Oxford Clay of the Midlands by Callomon (1955, 1968).

2.3.1 Geographical extent and thickness of the Oxford Clay

The Oxford Clay crops out in a wide belt extending from the Dorset coast at Weymouth across southern and eastern England to the Humber (Fig. 2.1). There it disappears in the area of Market Weighton, to reappear from beneath the Chalk cover further north, before swinging around the Vale of Pickering to meet the Yorkshire coast in the region of Scarborough. The clay facies is only to be found in its full development south of Market Weighton, as in the northern part of the Yorkshire outcrop, the clay facies does not begin until the Mariae Zone, and much of the Middle Callovian is absent.

Maximum thickness (up to 200m) appears to be in the Wiltshire region (Callomon, 1968, p. 264), with the sequence thinning northwards and southwards, 130-170m of Oxford Clay being seen at Weymouth (Arkell, 1947, p. 25), 150m in Berkshire (Falcon & Kent, 1960, p. 14) and 85m in Huntingdonshire (Callomon, op. cit., p. 264). The northward thinning is due in part to decrease in the amount of sediment deposited, and in part to subsequent erosion, there being particularly well-marked erosion surfaces at the base of the Ampthill Clay (Upper Oxfordian) and of the Lower Greensand (Aptian).

The Lower Oxford Clay has a fairly constant thickness of between 16-25m in the Midlands (Callomon, 1968, p. 265), and 20m in Dorset (Smith in Torrens, 1969, p. A42), but data for the regions north of Huntingdonshire is not available, although it seems likely that there is overall thinning of all divisions of the Oxford Clay towards Market Weighton.

2.3.2 Exposures in the Lower Oxford Clay

At the present time, exposures are very limited, the only natural section being in the cliffs of the East Fleet near Charlestown, Weymouth (Nat. Grid SY6478-6479), where bituminous shales of the Jason, Coronatum and Athleta Zones are intermittently exposed in the low degraded cliffs and on the foreshore. The nature of the exposures is such that detailed stratigraphic data are unobtainable, although it is possible to find the zonal ammonites. Better sections are available in the disused brickpit owned by the Dorset Brick & Tile Co. at Crook Hill, Chickerell (SY 644797), where Smith (in Torrens, 1969, p. A41) has described a detailed succession of beds belonging to the Jason - U. Athleta Zones. Lower zones (Koenigi - Medea Subzones) used to be visible in the adjacent Putton Lane brickyard (SY 649798), but the pit is now flooded and used for the culture of water plants. The section at Putton Lane was described by Arkell (1947, p. 27), and many specimens from this locality are preserved in the major museums.

The only other permanent exposures in the Lower Oxford Clay of England are in the series of brickpits, mostly owned by the London Brick Company, between Calvert (Bucks.) and Peterborough (Hunts.). These pits, which are concentrated in four areas (Calvert, Fletchley, Bedford and Peterborough), have been described in detail by Callomon (1968), and it is his sections which have provided the basis for detailed collecting at the pits, although some slight modifications to his stratigraphy have been made. The revised sections are shown in Fig. 2.3.

The detailed descriptions may be found in Appendix 1.

2.3.3 Facies analysis of the Lower Oxford Clay

Study has revealed the presence of several different lithologies within the apparently homogeneous mass of shale, each having several biofacies developed within it. Each biofacies will now be briefly discussed, with reference to its lithological and faunal characteristics.

2.3.3.1 Silts and silty clays

These represent the transition beds between the silts and sandstones of the underlying Kellaways Rock and the overlying Oxford Clay, and are greenish silts, and clays with a variable silt content, both showing strong bioturbation. Fossils often occur concentrated into plasters, usually consisting dominantly of ammonites or oysters, although many other bivalves, especially Pinna, Trautscholdia, Protocardia, Meleagrinella and Corbula occur throughout, and belemnites are often abundant.

2.3.3.2 Shell Beds

Four different types of shell bed, each characterised by a different faunal association, have been recognised, a shell bed here being defined as an accumulation of shells, regardless of the lithology in which it occurs. Occasionally the shells within a shell bed have been replaced by pyrite, or have pyrite overgrowths.

a) Nuculacean shell beds

These have a restricted-diversity bivalve fauna,
dominated by the Nuculaceans Palaeonucula and Mesosaccella,
accompanied by ammonites, belemnites, and reptile bones. Other
bivalves and gastropods occur, but are not usually of numerical
importance.

b) Gryphaea shell beds

This type of shell bed is intimately associated with the
Kellaways Beds - Oxford Clay transition beds, occurring most
frequently in the Enodatum and Medea Subzones, and consists of
an accumulation of solid shell debris, mainly gryphaeate oysters,
belemnites, ammonites and bone fragments. It appears to
represent a high energy environment, in which all but very robust
skeletal material was destroyed.

c) Grammatodon shell beds

These have a diverse fauna of epifaunal and infaunal
suspension-feeding bivalves, the dominant genera being
Grammatodon , Oxytoma, Isocyprina, Discomiltha, Protocardia,
Trautscholdia, Neocrassina, Myophorella, Ostrea and arcids.
Although these shell beds are commonest in the upper parts of the
Coronatum Zone, the 'basal' shell bed at Calvert, and beds 11 and
13 at Norman Cross also belong here.

d) Meleagrinella shell beds

Most commonly, these occur as packed masses of Meleagrinella
(up to 0.20m thick), with diagenetic overgrowths of secondary
calcite on their shells. The secondarily thickened shells
occur in a gritty clay matrix, the gritty feel being imparted by

calcite growth within the clay, and there is a sparse subsidiary fauna of deposit-feeding bivalves (Palaeonucula and Mesosaccella) and gastropods (Procerithium).

Within the deposit-feeder bituminous shale biofacies there are occasional plasters, less than 1 cm thick, consisting solely of abundant Meleagrinella shells (often articulated), which are thought to represent phases of mass mortality.

2.3.3.3 Bituminous shales

This is the dominant lithology within the Lower Oxford Clay, attaining its maximum development at Bletchley and Calvert, where the whole of the Jason and Obductum Subzones, and much of the Grossouvrei Subzone, are developed in this lithology. The rocks are olive-green in colour when fresh, blocky, usually fissile and well-laminated, and contain a variable fauna of infaunal and epifaunal bivalves. Three biofacies may be recognised within this facies:

a) Deposit-feeder bituminous shales

In this biofacies there is a rich fauna of benthonic deposit-feeders (Palaeonucula, Mesosaccella and Procerithium), usually associated with a prolific fauna of epifaunal suspension-feeders (Oxytoma, Meleagrinella, Bositra), which are thought to have lived attached to floating weed or wood ("pendent" - see 'Palaeoecology', section 2.4.2, for explanation of this term); a few shallow infaunal suspension-feeders (Pinna, Corbula, Solemya) occur sporadically. A notable feature of this biofacies is the preservation of fragile faunal elements such as

articulated ophiuroids, crustacea (Mecocheirus) and brachiopods (Lingula), together with bivalve spat, fish teeth and fish scales. This suggests that conditions on the seafloor were extremely quiet, and that predation must have been negligible at times.

b) Grammatodon-rich bituminous shales

In this biofacies, the lithology and faunal content is similar to that of the deposit-feeder bituminous shales, but infaunal suspension-feeding bivalves (Grammatodon, Isocyprina, Thracia) have appeared, and are an important component of the fauna (15-20%). Deposit-feeders are still common, but are not the only abundant benthonic bivalves. Pendent epifaunal suspension-feeders are also much less abundant than in the deposit-feeder bituminous shales.

c) Foram-rich bituminous shales

The shaly clays of this biofacies are often greener and better laminated than the other types of bituminous shales, and contain abundant foraminifera (Brotzenia). The benthonic macrofauna is sparse, not abundant, and limited to forms such as Mesosaccella and Corbula, together with some pendent epifaunal suspension feeders (Bositra, Inoceramus). Ammonites and scaphopods (Prodentalium) are locally abundant, and usually well-preserved.

2.3.3.4 Blocky claystone

This unusual lithology is restricted to bed 3B (Jason Subzone) at Calvert, where it is about 1.00m thick, and may be

easily distinguished from the bituminous shales by virtue of
its much lighter colour (pale grey), lack of clearly-developed
lamination, and different faunal content. Black streaks of
organic material are abundant throughout, and there is also much
disseminated fine organic matter. The fauna is dominated by
'pendent' epifaunal suspension-feeders (Bositra and Meleagrinella
comprise 55% of the total fauna), with deposit-feeders such as
Palaeonucula, Mesosaccella and Procerithium making up only 17%
of the fauna. The most characteristic faunal element is
Lingula, which comprises 11% of the fauna, and is locally the
only benthonic organism present. A unique feature of this
facies is the occurrence of uncrushed body chambers of a
macroconch kosmoceratid, named Kosmoceras (Gulielmites) effulgens
by Buckman (1925, pl. 597, fig. A, B), but which is probably
referable to K. (Zugokosmoceras) jason (Reinecke). The
occurrence of these body chambers may be due either to
exceptional preservation being possible in the claystone facies,
perhaps caused by greater resistance to flattening, or it may be
that the deposits represented at Calvert by bed 3B have been cut
out at the other pits by a non-sequence. A third possibility
is that the blocky claystone was only a local deposit, limited
to the area near Calvert.

2.3.3.5 Calcareous clays

At the four pits examined, the upper part of the Grossouvrei
Subzone consists of an alternation of Meleagrinella shell beds
and Calcareous clays, in beds about 0.20m thick. The Calcareous

clays are light grey or grey-green, rather plastic, apparently
unlaminated, and have a soluble fraction as high as 40%, the
equivalent figure for the bituminous shales being 10-20%
(Fig. 2.4, and Appendix 2). Faunally, deposit-feeding
Nuculacea (Mesosaccella, Palaeonucula) persist, but are joined
by a new fauna of infaunal and benthonic epifaunal suspension-
feeders such as Discomiltha, Isocyprina, Myophorella, Byssentolium
and Ostrea, together with the annelid worm Genicularia.
Particularly characteristic of this biofacies is the abundance
of small specimens of Byssentolium hudsoni, this species
comprising 10-35% of the fauna.

2.3.3.6 Concretionary limestones

Two major types of limestone are developed within the
Lower Oxford Clay, a band of septarian concretions, and a band
of lenticular earthy limestone, both having formed after
deposition of the clay/shale sequence.

a) Septarian concretions

These take the form of isolated wheel-shaped concretions
up to 2.00m in diameter and 0.20m thick, which
occur at a different level in each pit. In the southernmost
pit (Calvert), the septaria occur just below the top of the
Obductum Subzone, but as the concretions are traced northwards,
they become gradually lower, appearing low in the Obductum
Subzone at Bletchley and Stewartby, and at the base of the Jason
Subzone at Norman Cross. At all localities the nodules are
clearly septarian, consisting of a fine microsparite veined with

calcite, with some local variation in accessory minerals; at Calvert, vugs containing calcite, baryte and celestite, often associated with collapse structures with an earthy infill, occur within the septaria, whilst at Bletchley, some of the septaria have the calcite veins lined with a thin film of pyrite, and a pyritic outer skin to the concretion.

There is no obvious correlation between the position of the septaria and the lithology in which they occur, although at all the pits other than Bletchley the concretions are sandwiched between, or in close proximity to, distinct shell beds. At Norman Cross and Calvert the septaria occur within a thin band of Foram-rich bituminous shale, whilst at Stewartby they are found within a particularly thick Meleagrinella shell bed, and at Bletchley within a thick development of deposit-feeder bituminous shales.

Fossils within the nodules are usually uncrushed, and often show the effects of expansion, being rather strained and cracked, which together with the carbon and oxygen isotope values (Hudson, Ms.), suggest early formation of the concretion itself, but late formation of the calcite veins.

b) Earthy limestones

The main earthy limestone, known as the Acutistriatum Band (after the ammonite Kosmoceras (Spinikosmoceras) acutistriatum Buckman), occurs at the base of the Athleta Zone at Stewartby, Bletchley and Calvert, but is absent at Norman Cross, although the non-limestone facies of the Acutistriatum band is present. The limestone occurs as lenticular masses which pass laterally

into bituminous shales   , weathered surfaces of the
limestone clearly showing the presence of the same primary
sedimentary structures as can be seen in the interdigitated
shales, indicating the replacement origin of the limestone. The
limestone itself is of microsparite grade   , but is
more earthy and contains more relict clay material than the
septaria. Locally, there is some late-stage calcite veining
within the Acutistriatum Limestone, especially at Calvert, where
subregular concentric veins, joined by cross-veins, are present
in most of the lenticles   . The limestone has
developed within several lithologies, and often transgresses
into the beds above and below the bituminous shales of the
Acutistriatum Band proper, with the result that at all the three
pits where the limestone is developed, the shell beds beneath
the Acutistriatum Band are also sometimes developed in the
limestone facies. Within the limestone, preservation is similar
to that within the surrounding shales, with crushing of the
ammonites, and some solution of aragonitic bivalve shells.
Carbon and oxygen isotopes (Hudson Ms.) support the view that
this limestone formed during diagenesis, and after some burial.

Lenticles of a similar earthy limestone, but without the
calcite veining, occur within the pyritic shell bed (bed 14) at
the top of the Obductum Subzone at Bletchley. These lenticles
are much smaller than those of the Acutistriatum Band, rarely
exceeding a diameter of 0.50m and a thickness of 0.15m, and
show similar preservation to that found in the Acutistriatum
Band limestone.

2.3.4 Descriptions of the four major pits examined

The detailed successions at these pits are shown in Fig. 2.3 and recorded in Appendix 1, so only general points will be considered here. In all the pits except Calvert, the lowest beds seen are the transition beds from the Kellaways Beds to the Oxford Clay, these being followed by a clear section up into the Athleta Zone. At Calvert, however, the pit is worked down to a tough pyritic shell bed within the Jason Subzone, and the transition beds below are not seen.

The Acutistriatum Band forms a well-defined marker horizon, instantly recognisable on palaeontological and lithological grounds, and as this represents the highest marker band seen at all four pits, detailed ecological and stratigraphical studies have been restricted to the beds below and including the Acutistriatum Band. Collections made from the deposit feeder bituminous shales of the Lower Athleta Zone reveal that faunally these shales belong with the Lower Oxford Clay, as noted by Callomon (1968, p. 274), but they have not been studied in detail.

In the placement of the subzonal and zonal boundaries, the work of Callomon (1968) has been largely used, especially within the thick shale sequences at Stewartby, Bletchley and Calvert. Examination of Fig. 2.3 shows the variation in thickness of the various subzones between Calvert and Norman Cross, and reveals that there is a general thickening of the subzones southwards from Peterborough. This is most marked in the Enodatum and Medea Subzones, which are very condensed at Norman Cross and

thicken rapidly southwards, reaching their greatest thicknesses
in the Bletchley area. The Obductum and Grossouvrei Subzones
have a much more constant thickness over the whole of the East
Midlands region (with the exception of the Obductum Subzone at
Stewartby), indicating that conditions had become stable over a
more widespread area by that time. This view is supported by
the succession seen in the Grossouvrei Subzone at all four pits,
where Grammatodon-rich bituminous shales are followed by
Foram-rich bituminous shales and then an alternation of
Calcareous Clays and Meleagrinella Shell Beds, the subzone
being capped by a shell-bed. No such close correlation of the
sequences is possible within the Calloviense or Jason Zones,
partly because of the variation in thickness, and partly because
the Jason Zone is usually represented by a thick horizon of
bituminous shale.

2.3.4.1 Norman Cross, Peterborough (TL 172916)

The sequence here is more condensed than at any of the
other pits, but the presence of a large drainage sump in the
floor of the pit allows examination of the transition beds and
the uppermost part of the Kellaways Rock, in addition to the
Lower Oxford Clay.

The lowest 1.00m exposed belongs to the Calloviense
Subzone, and consists of massive yellow-green microcross-
laminated silts and siltstones, becoming more clayey towards
the top, with occasional partings of green shaly clay; this is
all placed within the Kellaways Rock. The fauna is dominated by

belemnites (Cylindroteuthis) and oysters (Catinula - Gryphaea
grade), with local lenses rich in Trantscholdia, Meleagrinella
and Grammatodon concinna.

The Enodatum and Medea Subzones are very thin (0.63m
combined thickness), and consist of an alternation of Gryphaea
shell beds and shaly clays, dominated by gryphaeate oysters and
belemnites. The shaly clays are green and fissile, although not
as well-laminated as the bituminous shales to be found higher
in the sequence, and have a fauna dominated by Bositra,
Meleagrinella and G. concinna. These transition beds are taken
as belonging to the Oxford Clay, the junction with the Kellaways
Rock being placed at the top of the Calloviense Subzone, with
the disappearance of the cross-laminated silts.

At the base of the Jason Subzone are two shell beds,
separated by a thin band of papery bituminous shale containing
occasional septarian concretions; the concretions often contain
uncrushed ammonites preserved in aragonite infilled by sparry
calcite. The shell bed above the paper shale has a rich
fauna of G. concinna, Trantscholdia and Protocardia, with an
ammonite plaster at its base. The rest of the Jason Subzone,
and the whole of the Obductum Subzone, with the exception of a
thin Nuculacean shell bed at their junction, consists of a
thick sequence of deposit-feeder bituminous shales, with
occasional Meleagrinella plasters, especially towards the top.

The base of the Grossouvrei Subzone coincides with the
appearance of Grammatodon minima, a situation which prevails
throughout the East Midlands, and which also appears to be true

of the succession in Dorset, as collecting at Crook Hill, Chickerell, has shown. The 'normal' Grossouvrei Subzone succession, as detailed above in section 2.3.4, and in Fig. 2.3, is developed at Normal Cross, except that the place of the Calcareous Clay facies is sometimes replaced by deposit-feeder bituminous shale. The topmost bed of the Grossouvrei Subzone here, as at all the pits in the East Midlands (except Stewartby), is the Comptoni Bed, named from the ammonite 'Binatisphinctes' comptoni (Pratt), which consists of a Nuculacean shell bed containing abundant specimens of ammonites transitional between perisphinctidae and Peltoceras. This is overlain by the deposit-feeder bituminous shales of the Acutistriatum Band, heralding the base of the Athleta Zone; there is no concretionary limestone development at this level at Normal Cross.

2.3.4.2 Stewartby (Bedford) (SP017412)

In the Bedford region, the silts of the Kellaways Rock continue to the top of the Enodatum Subzone, where they are overlain by the pyritic 'basal shell bed' (bed 5). Close examination reveals that the 'basal shell bed' consists of two shell beds separated by 2 cm of green clay containing Bositra and many comminuted shell fragments, the shell beds belonging to different biofacies. The upper shell bed consists of an ammonite plaster at the top, resting on a Grammatodon shell bed with a diverse bivalve fauna also containing occasional reptile bones and fish teeth, whilst the lower shell bed is a Gryphaea shell bed with Gryphaea, belemnites and ammonites.

The Medea, Jason and lower half of the Obductum Subzones
are developed in the deposit-feeder bituminous shale facies, the
fauna being dominated by Palaeonucula, Mesosaccella, Procerithium
and 'pendent' epifaunal suspension-feeders. The upper half of
the Obductum Subzone differs from its development elsewhere in
that the bituminous shale facies is replaced by a thick
Meleagrinella shell bed, and 0.75m of Foram-rich bituminous
shale, with a pyritic shell bed immediately beneath the
Meleagrinella shell bed. Isolated septarian nodules occur
towards the top of the Meleagrinella shell bed, but are notably
less clearly septarian than at other pits, and contain fewer
uncrushed fossils.

The Obductum - Grossouvrei Subzonal boundary at this pit
was not defined by Callomon (1968, p. 281), and the authors
collections have also proved inconclusive as to where
K. (Zugokosmoceras) grossouvrei replaces K. (Z.) obductum,
although other species may also be of use in defining the
boundary. The appearance of K. (Spinikosmoceras) pollux and
species of Hecticoceras are features usually associated with
the start of the Grossouvrei Subzone, but as shown at the other
three pits, the appearance of G. minima is possibly as useful.
At Stewartby, the appearance of G. minima, K. (Sp.) pollux and
Hecticoceras is almost synchronous, G. minima appearing in
bed 9, while both K. (Sp.) pollux and Hecticoceras appear in
bed 10D, only 0.10m higher, and so for this reason, the base of
the Grossouvrei Subzone is placed at the base of bed 9, a well-
developed pyritic shell bed. The Grossouvrei Subzone shows the

same development as at the other East Midlands pits, except at the top, where the Comptoni Band (bed 19) lies above the Acutistriatum Band limestone (bed 17), the two being separated by 0.35m of deposit-feeder bituminous shales. The concretionary limestone is developed within the same lithology as the overlying bed, but there is a total lack of the diagnostic index, K. (Sp.) acutistriatum Buckman, which is only found above the Comptoni Band, indicating that the term Acutistriatum Band should not be applied to the concretionary limestone at Stewartby; the Athleta Zone does not start until some 0.40m above the concretionary limestone.

2.3.4.3 Bletchley (SP 862325)

As between Norman Cross and Stewartby, the transition beds between the Kellaways Beds and the Oxford Clay continue to become progressively younger southwards, and reach up almost to the top of the Medea Subzone. Again, these beds consist of an alternation of silts and silty clays, shell beds and bituminous shales, all in rapid alternation; the shell beds are all Gryphaea shell beds with a gryphaeate oyster-belemnite-ammonite association, whilst the bituminous shales are of deposit-feeder type.

The Jason Subzone has a thin pyritic shell bed (Gryphaea shell bed) at its base, overlain by a very thin Meleagrinella shell bed, passing up into a thick sequence of deposit-feeder bituminous shales which persist for the remainder of the Jason Subzone and virtually the whole of the Obductum Subzone, except for a Nuculacean shell bed at its top. The septarian concretions

occur near the middle of the Obductum Subzone, but seem to be spread randomly within a metre band of deposit-feeder bituminous shale, rather than occurring at one well-defined horizon. Some of the concretions have a pyritic coating, and fine pyrite linings to the calcite veins. Occasional earthy limestone concretions occur within the shell bed at the top of the Obductum Subzone, a feature unique to this pit.

The normal Grossouvrei Subzone succession is developed here, although it is slightly thinner than at Norman Cross and Stewartby. There is also a slight discrepancy in that the alternation of Meleagrinella shell beds and calcareous clays gives way to an alternation of deposit-feeder bituminous shales and calcareous clays immediately beneath the Comptoni Band. The Acutistriatum Band has earthy limestone concretions developed within it, the concretions being notable for the well-preserved ammonites to be found in them.

2.3.4.4 Calvert (SP 695232)

The lowest beds seen here belong to the Jason Subzone, although Callomon (1968, p. 287) records 0.28m of Medea Subzone beneath this. From the data given by him, it appears that the transition beds must lie within the Enodatum Subzone, as the Medea Subzone is said to consist of an alternation of bituminous shales and shell beds, with no silty horizons.

The base of the Jason Subzone consists of a well-developed pyritic shell bed (Grammatodon shell bed) with a rich and diverse fauna of bivalves and ammonites, all of which are

pyritised and very well-preserved. This is overlain by a thin band of deposit-feeder bituminous shale, and then 1.05m of blocky claystone, the only place from which this lithology is known. The claystone forms a clear marker horizon near the base of the pit, its light grey colour being very distinctive. Faunally it is also rather distinctive, the dominant fauna being Meleagrinella and Bositra, with accessory Lingula, Solemya and Palaeonucula, and a good deal of wood. Above the blocky claystone there is a reversion to deposit-feeder bituminous shale, although in the lowest metre there is a fauna dominated by Lingula, the aporrhaid gastropod Dicroloma, 'pendent' epifaunal suspension-feeders (Bositra, Oxytoma) and protobranchs, suggesting a continuation of the fauna of the blocky claystone beneath. Above this rather unusual biofacies, the normal deposit-feeder bituminous shale returns, and persists for the remainder of the Jason Subzone and virtually all of the Obductum Subzone, very much as at Stewartby. The topmost part of the Obductum Subzone consists of two thin pyritic Nuculacean shell beds, separated by a thin band of Foram-rich bituminous shales containing many scaphopods (Prodentalium calvertensis Palmer Ms.), and the septarian concretions, these concretions are unique in the Lower Oxford Clay in that they contain vugs filled with calcite, celestite and baryte.

The basal bed of the Grossouvrei Subzone shows the development of lenses of fibrous calcite up to 4mm thick, within the deposit feeder bituminous shale biofacies, a feature not usually seen outside the Meleagrinella shell beds, where

the fibrous calcite never attains such a thickness. This is
followed by the normal Grossouvrei Subzone succession, of
about the same thickness as that seen at Bletchley, with the
Comptoni Band shell bed being overlain by the lenticular lime-
stone of the Acutistriatum Band. Here, the Acutistriatum
limestone facies often extends down into the Comptoni Band
beneath, so that many lenticles of limestone contain both the
Comptoni and Acutistriatum faunas. A characteristic feature of
the Acutistriatum Band is the frequent occurrence of large
(30 mm diameter) ammonites transitional between perisphinctids
and Peltoceras, a situation also seen at Bletchley.

2.4   Palaeoecology

A palaeoecological reconstruction of the environments of
deposition within the Lower Oxford Clay will be published
elsewhere (Duff, in prep.; see also Chapter 3), but
nevertheless, it is useful to consider the modes of life of the
bivalves at this point, as it adds substantially to our
understanding of the bivalves themselves. There are of course
many difficulties involved in attempting to deduce the modes
of life of fossil species, especially in groups which have
left no living relatives, and even where there is documentation
of the habits of Recent species, there are often problems of
interpretation. However, by utilising the observation made by
Stanley (1968, p. 217), namely that all living representatives
of any given superfamily fall within one, or rarely two,
feeding groups, coupled with an analysis of the functional

morphology of each genus, it is possible to decide with a high level of confidence what feeding habits and ecological niche any genus occupied. Stanley (1970) has further considered the field of bivalve functional morphology in great detail, and it is his observations which have been used as a basis for many of the interpretations of life habits suggested here. Previous workers, such as Yonge (1939, 1946, 1949, 1953) and Allen (1958) had concentrated on the functional adaptations of particular taxonomic groupings, but Stanley went much further, and produced a general study of the relationships between the form of the bivalve shell and the mode of life of the animal which lived within it. One of the most important observations made by Stanley was that some structural adaptations occur in more than one taxonomic group, although the animals which possess them occupy similar niches, indicating that there has been parallel evolution of morphological features. Observations of this type are the basis from which interpretations of functional morphology are made.

There have been many suggestions as to ways in which bivalves may be united into "meaningful" ecological groups, the most popular groupings being based on mode of life, substrate type or feeding groups. Hudson & Palframan (1969) used mode of life and feeding groups in their study on the palaeoecology of the Middle-Upper Oxford Clay of Woodham (Bucks.), while Rhoads et al. (1972) have emphasized the importance of feeding groups in palaeoecological analysis, and suggested that it is sedimentary and hydrographic conditions which most closely control the

distribution of both deposit and suspension feeding bivalves.
The latter authors have recognised several trophic groupings in
an Upper Cretaceous bivalve assemblage from South Dakota on
this basis. The distribution of suspension-and deposit-feeding
bivalves is controlled in part by the sediment grain size and
texture, by the degree of bottom turbidity and by the
availability of food resources, suggesting that feeding groups
are the most valid means of splitting bivalves into ecological
groups, as data gleaned from substrate type is also used.
Mode of life observations may be used to further subdivide the
feeding groups.

On this basis, three major feeding groups may be
recognised in most Recent and fossil assemblages, including the
Lower Oxford Clay. The suspension-feeders are divided by mode
of life into epifaunal and infaunal types, while all deposit-
feeding bivalves are infaunal although epifaunal deposit-feeding
gastropods are known. In the sections below, each major feeding
group is considered in general terms, and individual genera
are then discussed. Table 2.3 gives a summary of the life
habits, siphon lengths and feeding groups of the bivalve genera
occurring in the L. Oxford Clay, and relates these to the
various superfamilies present.

2.4.1 Epifaunal suspension-feeders

Bivalves of this type lived on or above the sediment
surface, and most were attached by a byssus at some stage in
their life history, although there is some doubt as to whether

all genera were attached to objects on the sea floor. The
animals fed by filtering suspended food particles out of the
water which was drawn over the ctenidia by ciliary currents.
The recognition of epifaunal suspension-feeders in the Oxford
Clay is relatively easy, as most species possess a byssal notch,
and most belong to the Pectinacea.

Modiolus   A nestling mytilid (Stanley, 1972, p. 171), byssally
            attached to the substrate, the byssus emerging through
            the anterior ventral region, although there appears
            to be no byssal gape in the Oxford Clay forms.

Parainoceramus   An equivalve pteriacean lacking an obvious
            byssal apparatus, and possessing hinge teeth in
            addition to the multiple ligament pits. Kauffman
            (1967, p. 104) believed that _Inoceramus (Mytiloides)_
            labiatus (Schlotheim), an Upper Cretaceous species
            comparable to P. subtilis, lay weakly attached or
            free on the substrate, and was most abundant in
            middle shelf clays. A similar mode of life seems
            probable for P. subtilis, although there is a
            tendency for the species to occur in clusters, and
            Sykes (1973, pers. comm.) has noted inoceramid
            plasters associated with wood bands in the Oxford
            Clay of Scotland. Stanley (1972, p. 189) on the other
            hand, compared I. (Mytiloides) labiatus with mytilids,
            and suggested that it was semi-infaunal and byssally
            attached. In view of the clustering of the specimens

found in the Lower Oxford Clay, this interpretation seems unlikely.

Pteroperna   A subequivalve pteriacean with a long pointed posterior auricle, but no apparent byssal notch. Recent species of Pteria, a genus rather similar in form to Pteroperna, often live byssally attached to alcyonarian sea whips (Stanley, 1972, p. 189), the posterior auricle serving as a means of keeping the inhalent and exhalent currents separate. A similar mode of life is here assumed for Pteroperna, although preservation does not allow the recognition of a byssal notch; it is also unlikely that the attachment substrate was an alcyonarian.

Pinna   Yonge (1953) has shown that Recent pinnids live vertically embedded in the sediment, pointed anterior end downwards, with much of the shell protruding above the sediment surface. A similar life style is invoked for the Jurassic species, some specimens of P. mitis from the Oxford Clay of Woodham being found upright in presumed life position (Hudson & Palframan, 1969).

Bositra   The palaeoecology of B. buchii is considered in depth by Jefferies & Minton (1965), and in the taxonomic part of this work (p. 193), so the arguments concerning its mode of life will not be repeated here. B. buchii is thought to have been nektoplanktonic, but may possibly have been attached to floating weed,

or other organic material, although it is possible that the organic material was rooted to the sea floor. The term pendent is here used for this mode of life.

Oxytoma   An inequivalve pectinacean with a deep byssal notch, but no ctenolium, although some specimens have weak nodes on the external surface of the right anterior auricle. There is a marked tendency for specimens of O. inaequivalvis to occur in clusters. In view of the very soft nature of the Oxford Clay substrate, it is unlikely that a pectinacean could have survived lying directly on the sea floor, so an attached mode of life is postulated. As with Bositra, it is believed that Oxytoma was byssally attached to floating or rooted organic material, although there is no direct evidence for the existence of either.

Meleagrinella Another subequivalve pectinacean with a deep byssal notch but no ctenolium, often found in clusters. The same arguments apply as for Oxytoma, and it is believed to have lived byssally attached to organic material, not directly on the sea floor.

Entolium   A thin-shelled subequivalve pectinid, sometimes byssally attached in its juvenile stages, but rapidly losing the byssus and byssal notch. The large umbonal angle (about 100°) and the thinness of the shell, together with the lack of a byssus in the adult state, suggests a free-living form, capable of swimming.

Byssentolium   A small pectinacean with a byssal notch but no
ctenolium, only becoming abundant in the calcareous
clays at the top of the Grossouvrei Subzone. The
small size, and persistence of the byssal notch
indicate a functional byssus. The most likely mode
of life for this genus is byssally attached to near-
bottom or floating organic material, the soft nature
of the sediment surface precluding attachment directly
to the sea floor.

Camptonectes   Strongly byssate in all life stages, with a well-
developed ctenolium; attached closely to the
substrate through life. For further details see
Speden (1967, p. 17).

Chlamys   Both *Chlamys* s.s. and *C.* (*Radulopecten*) are
inequivalve pectinids with clearly developed byssal
notches, the M. Callovian forms (with the exception
of *C.* (*R.*) *scarburgensis*) being of small size. The
latter species may have been free-swimming in the
adult state, but it is probable that all the other
species were byssally attached throughout life, to
objects on the sea floor.

Plicatula   A cemented inequivalve pectinacean, attached to
the substrate by the right valve throughout life
(Yonge, 1973).

Gryphaea   Free-living oyster, cemented to the substrate
in its juvenile stages, but lying free at the sediment
surface for most of its life, convex left valve

downwards, lid-like right valve horizontal. Sessile
after spat settlement.

Nanogyra   A cemented oyster, fixed to the substrate by
the left valve throughout life, although in a few
cases, the attachment may be lost, the shell then
lying free in the sediment.

2.4.2 Infaunal suspension-feeders

Stanley (1968, p. 217) recognised the existence of three
groups of infaunal suspension-feeding bivalves, all of which
may be found in the Oxford Clay. Infaunal non-siphonate
suspension-feeders are mostly active burrowers (Trigonacea,
Astartacea, some Carditacea and Arcacea), which move about at or
near the sediment/water interface, and draw in water currents
through the sediment. Infaunal siphonate suspension-feeders
have shown the greatest evolutionary radiation, this life habit
being known in 15 superfamilies; they burrow to varying depths,
draw in water currents through their inhalent siphons, and may
be active or more or less sedentary. Stanley (op. cit., p. 220)
pointed out that the great adaptive radiation of infaunal
siphon feeders in the Mesozoic was due to the development of
mantle fusion, allowing the formation of separate inhalent and
exhalent siphons. The third group — infaunal mucus-tube feeders —
are represented solely by the Lucinacea (and possibly Thracia as
well), and draw water into the mantle cavity through a long
anterior mucus-lined tube constructed by the foot (Allen, 1958).

2.4.2.1 <u>Infaunal non-siphonate suspension feeders</u>

<u>Grammatodon</u>   Although Stanley (1970) lists several criteria
for distinguishing infaunal from epifaunal arcids,
and states that free-burrowing forms do not appear
until the Cretaceous (op. cit., p. 22), the functional
morphology of the M. Callovian species does not
support this view. All three Lower Oxford Clay
species lack byssal sinuses, possess entire margins,
and have the maximum region of inflation placed near
the dorsal margin, which together with the broadly
truncate flattened posterior region, are features
indicative of burrowers. In contrast, the L/H ratio
of all three species is greater than 1.35, which
according to Stanley suggests that they were epifaunal.
The weight of evidence seems to point more strongly
towards a shallow burrowing infaunal mode of life,
the posterior region placed at or near the sediment
surface, although there is a slight possibility that
the M. Callovian species were semi-infaunal nestlers,
with a very weak byssal apparatus.

<u>Myophorella</u>   The only living representative of the Trigonacea,
<u>Neotrigonia margaritacea</u> Lamarck, is a very active
shallow burrower, with a large byssal apparatus
functional only in juveniles (Gould, 1969, p. 1129).
<u>Myophorella</u> possesses many features, such as a thick
shell, strong ornamentation and divaricate ribbing
(at least in the irregularly-ribbed forms), which

suggest a similar shallowly-buried rapid-burrowing mode of life. Stanley (1970, p. 75) notes that many short, robust shallow burrowers (such as cardiids) have a flattened posterior margin which lies at or just beneath the sediment surface, and it seems probable that the posterior area of trigoniids fulfils a similar function.

Neocrassina   A small suborbicular astartid of low inflation, the shell form suggesting that it was a rapid burrower which used a large angle of rotation in burrowing. Most Recent astartids live just beneath the sediment surface, posterior end uppermost, and move slowly through the sediment; this mode of life is assumed for N. ungulata and N. calvertensis.

Trautscholdia   Another small astartid, of high inflation, with a suborbicular outline and strong concentric ribs. The high inflation, strong ribbing pattern and thick shell are all features which slow down the burrowing rate, and the denticulate ventral margin suggests that it is a shallow burrower. A similar mode of life to Neocrassina is postulated here, the animal moving slowly through the sediment, just beneath the surface.

2.4.2.2 Infaunal siphonate suspension-feeders

Solemya   Stanley (1970, p. 120) shows that Recent Solemya maintain a deep open U-tube burrow, resting at its deepest point, and drawing in a water current

anteriorly; the suspended food material is then sorted on the gills. Stanley also notes the existence of a deep vertical extension to the burrow, and suggests that it may supply nutrients such as bacteria. As in Recent species, S. woodwardiana has a very thin shell, which gives a low whole-animal density, a feature which allows Recent species to make rapid swimming movements; in view of the similarity between Recent and fossil species of Solemya, it is probable that S. woodwardiana was also capable of swimming movements when necessary, although for most of the time, it presumably functioned as a deep-burrowing siphonate suspension-feeder.

Protocardia   A small cardiacean with a radially ribbed flattened posterior area, and high inflation. Stanley (1968, p. 216) classes all members of the Cardiacea as infaunal siphon feeders, although pallial sinuses are rarely seen in marine forms. It is most likely that Protocardia lived just beneath the surface, its posterior region lying more or less at the sediment/water interface, the radial ribbing perhaps helping to camouflage the shell when covered with a thin veneer of sediment.

Rollierella   A suborbicular, globose arcticacean, with very fine cancellate ornament, and tightly enrolled umbones. The globose nature of the shell, together

with the cancellate ornament, are indicative of a slow
burrower, as also is the ventral marginal
denticulations. As with Recent Arcticacea, it is
believed that Rollierella lived just below the
sediment surface, its very short siphons only just
protruding from the shell, there being no pallial
sinus present.

Anisocardia   Closely related to Rollierella, but differs by
being less inflated and more rostrate. The mode of
life must have been similar to that of Rollierella,
but the lesser inflation suggests a more rapid
burrower, and the more clearly-developed rostrum
suggests a slightly deeper burrower, although, as in
Rollierella, there is no pallial sinus.

Isocyprina   A medium sized, suborbicular, compressed
arcticacean with a smooth, polished external shell
surface. The compressed nature of the shell, coupled
with the smooth surface, suggests that it was a rapid
burrower, and the heterodont dentition is suggestive
of a shallow burrower. Some specimens have a slight
pallial sinus, but it is unlikely that Isocyprina
lived very far beneath the sediment surface.

Corbulomima   Yonge (1946) has shown that some Recent corbulids
are shallow-burrowing siphonate suspension-feeders,
some of which plant byssal threads and become
sedentary; the siphons lie or move less flush with

the sediment surface. C. macneillii and C. obscura
have rather truncate posterior margins, suggesting
that they lived more shallowly than the more rostrate
C. mosae, in which siphon development was presumably
greater.

Pleuromya   Although very similar in form to Recent species
of Mya, P. alduini and P. uniformis lack commissure
gapes anteriorly and posteriorly, suggesting that the
valves were either permanently open, or else the
siphons could be completely retracted into the shell;
the large size of the pallial sinus makes it possible
that the siphons could not be fully retracted. All
other features, such as the desmodont dentition,
thin largely unornamented shell and large pallial
sinus, are features typical of a deep-burrowing
siphon feeder. If, as seems likely, the siphons were
too large to be fully retracted, Pleuromya must have
been virtually sessile after the attainment of the
adult state. The more elongate and cylindrical
form of P. uniformis suggests that it may have been
a deeper and more effective burrower than
P. alduini.

2.4.2.3 Infaunal mucus-tube feeders

Discomiltha   A typical lucinoid with an elongate anterior
adductor muscle scar and a strong posterior sulcus.
The lucinoid mode of life has been described by
Allen (1958) and seems to have continued more or
less unchanged since the Palaeozoic, the animal
living deep below the sediment surface with an
anterior inhalent and a posterior exhalent mucus-
lined tube reaching to the surface; strong water
currents are produced by the cilia of the elongate
anterior adductor muscle scar and the gills. Once
settled, lucinoids seem to be more or less
sedentary.

Thracia   A deep burrowing suspension-feeder showing
all the typical features seen in Pleuromya, although
the more triangular shape of Thracia suggests that
it was less deeply buried. Yonge (1937, p. 338)
showed that Thracia is notable for the production
of mucus-lined tubes through which the inhalent
and exhalent currents flow; this apparently
enables the siphons to be free of the danger of
predation, and allows the animal to burrow slightly
deeper, as the siphons need not be permanently
extended so far.

2.4.3 Deposit-feeders

Bivalves which belong to this feeding group collect and digest organic material that has settled to the sea floor, and is either incorporated into the sediment, or forms a thin veneer on the sediment surface. This deposited material is collected in two ways: the Nuculoida are infaunal, and feed on material within the sediment, collecting it by means of labial palps, while the Tellinacea (which are also infaunal) feed on the thin veneer of organic matter at the sediment surface, using slender siphons which suck the organic material into the mantle cavity. In the Oxford Clay, only the Nuculoida are represented.

Palaeonucula   A short triangular shelled form, very similar in outline to Recent species of Nucula, the modes of life of which have been described by Yonge (1939). All nuculids live just beneath the sediment surface, moving sluggishly about in search of food, which is collected by the ventrally-emergent palp proboscides. No siphons are present, and the weak inhalent current is drawn directly through the sediment.

Mesosaccella   An elongate cylindrical malletiid with a clearly developed pallial sinus and a wholly external ligament. Mesosaccella closely resembles Recent species of Yoldia, a nuculanid whose life habits were noted by Yonge (1939); it is likely that it occupied a similar niche, buried anterior downwards with the siphons reaching to the surface, collecting organic material from within the sediment by means of the palp proboscides.

2.4.4 Other fauna

In addition to the rich bivalve fauna of the Lower Oxford
Clay, there is also an abundant invertebrate and vertebrate
fauna, most of which was described in the last century. The
authors of the major works on the invertebrate fauna are listed
in the section on 'previous work' (Section 2.2).

The most common associates of the bivalves are ammonites,
mainly belonging to the Kosmoceratidae (see Buckman, 1909-1930;
Brinkmann, 1929a; Callomon, 1955 and Tintant, 1963), although
Hecticoceratidae (Pratt, 1841; Zeiss, 1956), Pachyceratidae
(Morris, 1850) and some Perisphinctidae transitional to Peltoceras
(Pratt, 1841; Mangold, 1970) become locally abundant in the
Coronatum Zone. Callomon (1968) gives a useful summary of the
ammonite faunas of the Lower Oxford Clay. Together with the
ammonites, there is also an abundant fauna of belemnites,
Cylindroteuthis puzosiana (d'Orbigny) being common throughout,
Belemnopsis sulcata (Miller) restricted to the transition beds
at the base, and Belemnoteuthis antiquus Pearce being common
in the bituminous shales of the Jason Zone.

Gastropods occur throughout, but are not a diverse element
of the fauna, only five species having been recognised. The
most frequently occurring species are Dicroloma bispinosa
(Phillips), D. trifida (Phillips) and "Procerithium" damonis
(Lycett), although Spinigera spinosa d'Orbigny and an unidentified
Pleurotomariid have also been found. By analogy with the Recent
species Aporrhais serresiana (see Yonge, 1937), it seems
probable that the Jurassic species of Dicroloma were infaunal,

had mucus-lined tubes for the inhalent and exhalent currents,
and collected deposited vegetal material with their mobile
proboscis. Both D. bispinosa and D. trifida are found most
commonly in the deposit-feeder bituminous shales, conditions
which agree well with those described for A. serresiana by Yonge
(op. cit.). Procerithium is thought to feed on a probable
detrital algal film at the sediment surface (M. Barker, 1973,
pers. comm.), and so may be described as an epifaunal deposit-
feeder. Procerithium occurs most frequently in the deposit-
feeder and Grammatodon-rich bituminous shales, but is found in
all other lithologies too, and does not seem as closely
controlled by the substrate as Dicroloma. The gastropod fauna
of the British Callovian is very poorly known, and in urgent
need of revision, the last work of any consequence being that of
Hudleston (1884-1885). Scaphopods (Prodentalium calvertensis
Palmer Ms.) are abundant in bed 6 at Calvert, and occur
sporadically elsewhere.

In the deposit-feeder bituminous shales of the Jason
Zone, and more rarely in the Coronatum Zone, a malacostracan
crustacean, Mecocheirus pearcei McCoy, is locally very abundant,
and although crushed flat, is extremely well-preserved. The
ecology and relationships of this species have been considered
by Förster (1971). The calcified shells of polychaet worms,
identified as Genicularia vertebralis (J. de C. Sowerby), are
common constituents of the Coronatum Zone fauna, being particularly
characteristic of the Calcareous Clays. In the Jason Zone, and
parts of the Coronatum Zone, there are occasional specimens of

poorly-calcified serpulid worms, as yet unidentified.

Inarticulate brachiopods — Lingula craneae Davidson — are a
fairly common member of the Jason Zone fauna at all the pits,
and are especially abundant in the deposit-feeder bituminous
shales and the blocky claystone. Crushed Rhynchonellids have
been found in the silts and silty clays at Norman Cross and
Bletchley. The final constituent of the invertebrate fauna is
an ophiuroid, still to be described, which occurs rarely in the
deposit-feeder bituminous shales. It is possible that it is
identifiable as 'Ophioderma' weymouthensis Lycett (in Damon),
from the Oxford Clay of Weymouth.

The Oxford Clay is famous for the profusion of well-
preserved vertebrate remains to be found in it, especially in
its lower parts. The abundant reptile fauna includes
ichthyosaurs, described by Andrews (1910) and Appleby (1956,
1958, 1961, 1967), plesiosaurs (Andrews, 1910; Persson, 1963),
pliosaurs (Andrews, 1913; Tarlo, 1960) and crocodiles (Andrews,
1913; Leeds, 1908; Lydekker, 1899; A.S. Woodward, 1885).
More recent general reviews of the Oxford Clay reptile fauna
have been published by Leeds (1956) and Delair (1958-1960, 1966).
In the well-laminated bituminous shales of the Lower Oxford Clay,
it is not unusual to find complete articulated skeletons of
representatives of all the reptile groups listed above, although
disarticulated bones are more common in the shell beds. The
most commonly found disarticulated bones are centra, ribs,
teeth and paddle bones. In addition to the varied reptile fauna,
there is also a diverse fauna of fish, represented by

disarticulated bones (mainly scales, teeth and centra) and
occasional complete skeletons. There are many papers concerned
with the Oxford Clay fish fauna, the most important being those
by Egerton (1844), A.S. Woodward (1888, 1889-1901, 1890,
1892, 1896, 1897) and Jain & Robinson (1963).

2.5   Conventions and Techniques

2.5.1   Terminology

The morphological terms used in this work are broadly
those listed and defined by Cox (1969, p. N102-N109) and
Stenzel (1971, p. N1028-N1034) in the Treatise on Invertebrate
Paleontology, although some terms, such as escutcheon and
corcelet, have been amended in the taxonomic discussions.
However, there is some ambiguity over the parameters used for
measurements, so these are discussed below, and shown in Fig.
2.5. Measurements were made using a pair of stainless steel
vernier calipers, giving measurements correct to 0.1 mm, although
in crushed specimens, and in some specimens which proved
impossible to isolate from the matrix, the accuracy is to the
nearest mm. Angular measurements were made with a simple
contact goniometer constructed from a clear plastic protractor.

Length (L) was measured parallel to the long axis of the
ligament in most heterodonts (Fig. 2.5a) and the Trigonacea
(Fig. 2.5c). This axis is nearly parallel to the line joining
the centres of the adductor muscle scars, thus enabling
measurements to be made on specimens with a poorly defined
ligament. In superfamilies possessing a long straight hinge

line (Fig. 2.5b), length was measured parallel to the hinge line, at the widest point of the shell.

Height (H) in all superfamilies was measured as the maximum dimension perpendicular to the length, passing through the umbones and the ventral margin.

Likewise, in all superfamilies, inflation (I) was measured perpendicular to length and height, and is the distance between the plane of the commissure and the point on the shell exterior furthest away from this plane perpendicularly. All the measurements given in the tables are for the combined inflation of both valves, except in the Pteriacea and Pectinacea, where the inequivalve nature of the shells means that the inflation of opposing valves of the same specimen is different. The inflation of each valve is listed separately in these superfamilies.

Anterior length (AL) is defined as the distance from the points of the umbones to the anterior margin of the shell, measured parallel to length (Fig. 2.5a-5c).

In the Arcacea, Pteriacea, Pectinacea and Mytilacea (Fig. 2.5b) it is possible to measure the length of the straight hinge line (Lh), which can be further subdivided into the portions anterior (ALh) and posterior (PLh) to the umbones. In the Nuculoida, hinge line lengths are measured directly along their long axes, regardless of the axis of shell length.

In the four superfamilies mentioned above (Fig. 2.5b), it is also possible to measure the degree of obliquity of the shell in two ways: the oblique length (OL) is measured from the umbones to the posteroventral angle, while the angle θ is the

angle between the hinge line and the oblique length. In some Arcacea, the posterodorsal angle is also measured.

In the Trigonacea (Fig. 2.5c), the presence of the posterior area introduces more terms which may be used to define shell form. The escutcheon length (LE) is measured from the umbones to the point where the escutcheon carina meets the margin, while the length of the area (LA) is measured from the umbones to the posteroventral angle. Both these measurements are taken as straight lines, and do not follow the contours of the shell. The escutcheon width (EW) is measured across both valves, perpendicular to the plane of the commisure. The number of tubercle rows is represented by the letters TR.

In the Pinnacea (Fig. 2.5d), length is measured from the umbones, which are placed anteriorly, to the point where the median carina meets the posterior margin; height is measured perpendicular to this, near the posterior extremity. The length of the dorsal margin (LDM) is measured in a straight line from the umbones to the posterodorsal angle. In many specimens, the posterior is incomplete, making precise measurement impossible.

Where the terms length and height are applied to features such as muscle scars, the features are measured parallel to the major shell dimensions. In the tables length is recorded in mm, and the other measurements are recorded as percentages of it, in order to facilitate comparisons between species, and give a clear idea of the variation of each measured character. Measurements of the figured specimens are given in the taxonomic

descriptions, and details of all other measured specimens are
given in Appendix 3. In the descriptions, the terms small,
medium and large are defined by the following size ranges:
small, up to 10 mm long; medium, 11-30 mm; large, over 31 mm.
This classification is designed for the bivalves of the Lower
Oxford Clay, which are generally smaller than other bivalve
assemblages. The criterion of adulthood in all species is the
crowding of growth-lines towards the ventral margin.

2.5.2 Type Material

In the taxonomic work, the following abbreviations are
used to denote the repositories containing collections of type
and other relevant material, the more important collections
being shown in brackets.

BM	British Museum (Natural History), London.
	(Sowerby colln.)
SM	Sedgwick Museum, Cambridge. (Leckenby colln.)
GSM	Institute of Geological Sciences, London.
	(Morris & Lycett; Lycett; Arkell)
OUM	University Museum, Oxford. (Phillips; Arkell)
YM	The Yorkshire Museum, York. (Phillips; Reed)
CMB	City Museum, Bristol. (Pratt; Chaning Pearce)
CML	City Museum, Leicester.
BU	University of Bristol.
LU	University of Leicester. (Authors colln.)
RMH	Roemer Museum, Hildesheim, Germany. (Roemer colln.)
MHNP	Laboratoire Paléontologique du Musée National
	d'Histoire Naturèlle, Paris. (d'Orbigny colln.)

2.5.3 Variation

Study of the large collections made by the author has revealed a high degree of variability in Middle Callovian bivalves, in both form and ornamentation. Variation is usually continuous, however, and there are no reasons for separating distinct variants at any horizon, meaning that some way of presenting this variation data must be found. Simple statistics are used here, and are presented in Appendix 3, although basic parameters, such as N, $\overline{x}$, Max, Min and OR are tabulated in the species descriptions. The terms used here were discussed at length by Imbrie (1956), so only a brief summary of their value will be given here. For more involved statistics, and a critical discussion of their importance, the work of Temple (1968) and Cooper (1973) should be consulted.

The terms used in this work are tabulated below:

N   =   number of observations made.

$\overline{x}$ =   arithmetic mean of the observations.

Max   =   maximum observed value of each group of observations.

Min   =   minimum observed value of each group of observations.

OR   =   observed range of the observations.

s   =   standard deviation: this gives a measure of absolute variation of the sample. It is expressed in the same units as the original data, and may be compared directly with the mean.

$$s = \sqrt{\frac{\sum (d^2)}{N-1}} \qquad \text{where } d = x - \bar{x}$$

s^2 = variance: the mean of the squares of deviations from the arithmetic mean.

V = coefficient of variation $\dfrac{100s}{\bar{x}}$; it is

used to compare the variability of animals of different sizes.

$\sigma_{\bar{x}}$ = standard error of the mean $\dfrac{s}{\sqrt{N}}$;

the population mean cannot be directly measured, as it is impossible to observe the entire local fossil population; thus standard error is used to judge the reliability of the arithmetic mean as an estimate of the population mean.

In addition to the numerical data listed above, scatter diagrams and regression lines have been plotted for certain species where it is required that a contrast between different populations should become apparent. The slopes and positions of the regression lines were obtained by using a Hewlett-Packard Model 10 programmable calculator, and plotted on arithmetic scales; the results are discussed at the relevant points in the text. However, in certain species, such as _Palaeonucula triangularis_ and _Trautscholdia phillis_, variation is so great that it is not possible to give a complete picture of the variation pattern in this way, and the pictograph technique

has been used, supplemented by a larger number of plate figures.

2.5.4 Localities

The grid references for the localities of the authors collections from England are given below. Fig. 2.6 shows the geographical locations of the localities.

Chickerell brickyard, near Weymouth, Dorset	SY644798
Fleet Shore, near Weymouth, Dorset	SY638791
Calvert brickpit, Bucks.	SP695232
Newton Longville brickpit, Bletchley, Bucks.	SP862325
Marston Moretaine brickpit, Bedfordshire	SP001402
Stewartby brickpit, Bedfordshire	SP017412
Norman Cross brickpit, Peterborough, Hunts.	TL172916
Cayton Bay, near Scarborough, Yorks.	TA075841

It is not possible to give details of the provenance of most museum specimens, as the details provided in the museum registers are frequently inadequate, and often the locality itself is in doubt.

2.5.5 Preparation

In view of the softness of the matrix containing most of the specimens, preparatory techniques were usually restricted to picking with a mounted needle. However, in some of the limestone bands and pyritised shell beds it was necessary to use a 'Burgess' vibro-engraver, or even a Desoutter VP2 compressed air-pen, to remove harder matrix. The friability of the shell of many species meant that it was essential to harden the shell material to prevent breakage, and for this purpose, a solution

of Vinamul 6525 dissolved in toluene proved the most useful,
although it sometimes gave a slight gloss to the surface, making
photography slightly more difficult.

Serial sections were made of one species of bivalve
(Rollierella minima), in order to show details of the dentition.
To produce these sections, the specimen was mounted in
'Cristablik' and the resulting block stuck onto a metal plate
with Lakeside 70 adhesive. Serial sections were then taken at
regular intervals by grinding down the block on a Speedlap
rotary grinder, and making an acetate peel of the resulting
surface.

Rubber casts were made of many specimens preserved as
external moulds, using a mixture of ICI Silkoset 105 and carbon
black. This meant that the resulting casts were the ideal
colour for coating with ammonium chloride for photographic
purposes. The fine-grained nature of the shales and clays is
very conducive to the making of good casts.

The photographs were taken by the author with a Leica
camera and bellows, the specimens first being coated with a
film of ammonium chloride to give evenness of tone and emphasize
the surface ornament. Many specimens were first darkened with
a thin solution of Barlows opaque before chloriding, to bring
out the shell detail.

2.5.6 Taxonomic considerations

The classification of the bivalves used here is that
utilised by Newell (1969, N205) in the Treatise on Invertebrate

Paleontology (part N, Mollusca 6, Bivalvia), a slight emendation
of the system first introduced by Newell in 1965. In only one
case has it been necessary to alter the placement of a genus,
Mesosaccella Chavan having been transferred from the Nuculanidae
to the Malletiidae on the basis of the absence of an internal
ligament. All other genera are placed as in the Treatise.
Likewise, most of the generic descriptions and synonymies are
based on data given in the Treatise, although it has proved
expeditions to amend them on occasion. Where this has occurred,
the fact is noted in the relevant generic discussion. Generic
ranges are not given; for this data, the relevant entry in the
Treatise should be consulted.

2.6 Preservation

Several different modes of preservation are present in
the Lower Oxford Clay, and will be discussed in detail elsewhere
(Duff, in preparation). However, preservation plays
an important role in determining how much detail may be seen in
any particular shell, and so is given some consideration here.

Most of the bivalves found are preserved with their
original shell mineralogy, which is dominantly aragonite, except
for the mainly calcitic Pectinacea and Ostreacea. The original
shell material may be preserved in a crushed or uncrushed
state, often dependent upon the degree of inflation of the
species, and whether it is an isolated valve or an articulated
shell. In general, articulated shells are much more frequently
crushed than are isolated valves, probably due to the fact that

they were buried without having the space between the valves
completely filled with clay. It is difficult to extract
aragonitic valves from the rock in an unbroken state, and it
is usually only possible to examine one surface of any
aragonitic bivalve specimen. However, examination of many
specimens allows a complete picture of the morphology to be
built up, especially when the species sometimes occurs as
pyritised casts, as in the Nuculoida. The aragonite usually
shows no signs of having been even partially dissolved, although
it is never as strong as the aragonite of Recent shells,
suggesting that there must have been some slight chemical change;
it is so well-preserved that it is possible to recognise the
shell micro-structure.

Calcite shells appear to be more resilient than aragonitic
ones, and are usually preserved uncrushed, either as isolated
valves or articulated shells. It is often possible to extract
calcitic shells from the rock, so both inner and outer
surfaces of the same specimen may be examined. Again,
preservation is so good that shell micro-structure is easily seen.

Many shells, both aragonitic and calcitic, have variably
developed overgrowths of pyrite, particularly in the more
bituminous horizons. The pyrite is usually rather patchily
developed on shells found in the massive shaly clays, and in
these beds, seems to be concentrated on aragonitic shells such
as Thracia, Pinna and Palaeonucula, where it occurs as small
patches on the surfaces of the shell. Hudson & Palframan
(1969, p. 404) describe a somewhat similar situation in the

Middle and Upper Oxford Clay of Woodham, Bucks., where pyrite
is patchily developed on the surfaces of bivalves preserved as
clay moulds, with no aragonite preserved. They attribute the
pyrite formation to local sulphate reduction by bacteria acting
on the organic matrix of the dissolving shell. It is possible
that the patchy pyrite developed on aragonitic shells in the
Lower Oxford Clay formed in a similar manner, although the
aragonite has not disappeared. In the shell beds belonging to
the transition beds between the Kellaways Rock and the Oxford
Clay, Gryphaea dilobotes is frequently found thickly encrusted
with pyrite, the pyrite having grown from the shell surfaces.
This pyrite is much too abundant to have formed by local
bacterial reduction of sulphates, and as in the other shell beds,
it is believed that the pyrite formed by combination of Fe^{++}
from one source, and S^{--} from another source, the shell bed
acting as a sort of aquifer (Berner 1969, 1971).

The shell beds developed in the Jason and Coronatum Zones
often contain shells and valves which have been completely
replaced by pyrite, rather than merely having pyrite over-
growths. The same mode of preservation is sometimes seen in the
transition beds as well, and affects Palaeonucula, Mesosaccella,
Myophorella, Discomiltha, Cucullaea, Grammatodon, Trautscholdia,
Neocrassina and Isocyprina. Most of the pyrite is a stable
form which does not rapidly disintegrate, and it is from these
pyrite-replaced valves that details of the dentition and shell
interior may frequently be obtained. Because of its origin as
a replacive material, no shell microstructure is visible in

these pyritised moulds. The pyrite presumably originates in the same way as that which encrusts oysters in the transition beds.

At Norman Cross, Peterborough, crushed articulated shells of Palaeonucula are often preserved in pinkish calcite, indicating late replacement of the originally aragonitic shell by calcite. This is a very unusual preservation type, only found in beds 17-18 at Norman Cross, and must indicate a particularly chemically active phase of diagenesis.

A final preservation type is that where the original shell material, calcite or aragonite, has been wholly or partially covered with a layer of secondary calcite, which has the effect of obscuring surface detail. The calcite is not easily removed, and often will not part from the original shell material, rendering the making of detailed observations impossible. This type of preservation is dominant in the Meleagrinella shell beds at the top of the Grossouvrei Subzone, but also occurs throughout the Lower Oxford Clay. It is seen most frequently on Pteriacea and Pectinacea, although Palaeonucula and Mesosaccella are also particularly susceptible.

It must be emphasized that unlike the situation described from Woodham by Hudson & Palframan (op. cit.), these preservation types are not controlled by shell mineralogy, as several different preservation types are known in most species. This suggests that in the more bituminous Lower Oxford Clay, it was physico-chemical factors, rather than the original shell composition, which governed the type of preservation to occur. Because of the range of preservation types found in many species,

it is sometimes possible to get more detailed information than
it would be if there was only a single mode of preservation.
For example, it is easy to see details of the cardinal regions
on pyritised shells, but in order to examine the shell micro-
structure, specimens preserved as the original shell material
must be used. It is also possible to see colour banding in
some aragonitic specimens of _Palaeonucula_, although it is
uncertain whether or not this represents original shell
markings.

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SYSTEMATIC DESCRIPTIONS

Class BIVALVIA Linnaeus, 1758

Subclass PALAEOTAXODONTA Korobkov, 1954

Order NUCULOIDA Dall, 1889

Superfamily NUCULACEA Gray, 1824

Family NUCULIDAE Gray, 1824

Genus NUCULOMA Cossmann, 1907 (p.124)

Type species. By monotypy, Nuculoma castor Cossmann ex
d'Orbigny, 1907, p.124, pl.2, figs. 14, 15, from the Callovian
Oxford Clay of the Haute-Marne, France.

Diagnosis.   Medium sized genus (up to 26.0 mm L), subtrigonal
to subtrapezoidal in outline, well-inflated; umbones very
strongly opisthogyrate, usually markedly enrolled, often near
terminal; posterodorsal area usually deeply impressed, cordate
in outline; anterodorsal margin evenly arched and convex,
ventral margin evenly convex, often straightening posteriorly
and becoming sinuate; anterior margin bluntly rounded; anterior
row of teeth evenly arched, much larger than the posterior row,
which has only about 4-6 teeth, placed more or less vertically
above each other; ornament of fine interdigitate concentric
striae, or fine regular concentric striae without interdigitation.

Remarks   _Nuculoma_ is an easily recognised Jurassic genus
characterised by its strongly opisthogyrate, enrolled umbones,
and its distinctive ornament pattern, and as noted below (in
discussion of _Palaeonucula_ /p.106_7) is clearly distinguished
from _Palaeonucula_. Although the umbones are terminal, or nearly
so, in the type species, in species such as _N. pollux_ (Raspail
ex d'Orbigny), the umbones are more centrally placed (AL $\overline{x}$ 66.5%).
However, it is very difficult to compare measurements of nuculids
given by different authors, as the orientation of the measurements
is not constant. Most authors have measured length in nuculids
parallel to the direction of the anterodorsal margin, thus
virtually ensuring that the posterodorsal margin is vertical, and
the umbones almost terminal. The present author sees no reason
to measure nuculids any differently from other dimyarian
bivalves, and so length is measured parallel to a line drawn
through the adductor muscle scars. Examination of steinkerns
shows the adductor scars to be placed at the distal ends of
the hinge line, and so the measurement of length is made between
the posteroventral angle and the anterodorsal angle. This has
the effect of reducing the AL % of many species, notably those
placed in _Nuculoma_, and increasing the H %. The author
believes that standardisation of measurements allows easier
comparisons at the generic level, and should be adopted where
possible.

The development of interdigitate ornamentation within
Nuculoma is, as yet, of uncertain distribution, apparently
absent from the type species (Cossmann, 1907; Cottreau, 1925)

and some Indian Upper Jurassic species described by Cox (1940,

p.23, p.24), but present in N. pollux Raspail ex d'Orbigny and

N. chassyana Cottreau ex d'Orbigny. There is no reason to doubt

that the type species lacks interdigitate ornament, as the

phenomenon is recognised in N. pollux and N. chassyana by

Cottreau (pl. 39, fig. 27; pl. 40, fig. 5), although it is

usually on a microscopic scale, and is easily overlooked. It

is possible that forms with interdigitate ornament may prove

distinct from forms with regular concentric ornament, but as

yet there is no reason to separate them, and there are too many

other close similarities.

1.   Nuculoma pollux (Raspail ex d'Orbigny, 1901) Pl. 1,

        figs. 1a-1d.

. 1850   Nucula Pollux sp. nov.; d'Orbigny, p.339, no. 179.

* 1901   N. Pollux d'Orbigny; Raspail, p.194, pl.12, fig.13.

. 1925   N. Pollux d'Orbigny; Cottreau, p.22, pl.39, figs.25,26,27.

Type specimen   The specimen figured by Raspail (op. cit.) has

not been traced, but agrees perfectly with the type specimen of

d'Orbigny's earlier nomina nuda, figured in 1925 (pl.39, fig.

25-27) by Cottreau. D'Orbigny's holotype is preserved in the

d'Orbigny collection (no. 3347A) in the Laboratoire Paleontologique

du Musee National d'Histoire Naturelle in Paris.

Diagnosis   Medium-sized species (up to 18.9 mm L), trigonal

in outline, height about 80% of length (H 70.9-83.7%, $\bar{x}$ 79.1%)

posterodorsal margin evenly concave, anterodorsal margin of

approximately equal length, very gently convex; ventral margin
short, evenly convex, not sinuate, inflation always slightly
less than anterior length (I 55.6-64.1%, x̄ 58.7%; AL 63.6-
70.2%, x̄ 66.5%); umbones slightly posterior to median, rounded
markedly opisthogyrate, slightly enrolled; corcelet large,
cordate, excavate, escutcheon well-developed, cordate, with a
marked escutcheon pout protruding above about half of the
posterodorsal margin; lunule elongate, lanceolate, clearly
differentiated; ornament interdigitate.

Measurements

See Appendix 3.

	L	H	I	AL
N	7	7	6	3
x̄	15.1 mm	79.1 %	58.7 %	66.5 %
Max	18.9	83.7	64.1	70.2
Min	9.9	70.9	55.6	63.6
OR	9.0	12.8	8.5	6.6

Description

Small to medium-sized species, equivalve, inequilateral,
umbones posterior to median (x̄ 66.5%), opisthogyrate, rounded,
slightly enrolled, salient about 2 mm above the hingeline.
Outline trigonal, anterodorsal, posterodorsal and ventral
margins of subequal length, variably curved; anterodorsal
margin straight to gently convex, posterodorsal margin markedly
concave, ventral margin evenly convex, with no posterior

sinuosities; posteroventral angle sharp, prominent, but not produced, about a right angle; anteroventral angle more rounded, and less prominent than the posteroventral angle. Outline of the posterodorsal margin broken by the prominent, evenly convex escutcheon pout (Fig. 2.7), which protrudes above about half the length of the posterodorsal margin. Ornament consisting of interdigitate concentric striae over the body of the shell, with no apparent growth halts; dorsal areas ornamented with faint growth striae, not interdigitate.

Corcelet large, excavate, cordate, occupying the whole of the posterodorsal region, bounded by sharp umbonal carinae running to the posteroventral angles; escutcheon smaller, prominent, cordate, two arcuate elevated ridges running from the umbones to the posterior end of the hingeline, protruding above the posterodorsal margin as the escutcheon pout; inner part of the escutcheon excavate; corcelet and escutcheon ornamented by fine growth striae. Lunule elongate, lanceolate, extending from the umbones to the anteroventral angle, bounded by rounded carinae; lunule biconcave in outline, a slight rise occurring along the commissure and dividing the lunule into two separated excavate areas; ornamented by faint growth striae. Ligament internal.

Dentition, details of ligament and musculature unknown.

Remarks   This easily recognised species may be distinguished from the similarly-shaped Palaeonucula triangularis sp. nov. by its much more concave posterodorsal margin, its more enrolled

umbones, its lower inflation and its interdigitate ornament.
These two species have many close similarities of form, but
because of differences in ornament pattern and twisting of the
umbones, are placed in different genera. N. pollux is less
inflated, and has much more median umbones than the genotype,
N. castor, and may clearly be separated from other European
Upper Jurassic species of Nuculoma, such as N. chassyana
(Cottreau ex d'Orbigny). The clear development of a differentiated
lunule is an unusual feature in nuculids, but is well seen in
N. pollux, although it is not as prominent as the corcelet.
N. pollux has been recorded only from France (d'Orbigny, 1850;
Raspail, 1901; Cottreau, 1925), and seems to be rare, as such
a distinctive species is hardly likely to have been continually
overlooked elsewhere. Two specimens from the Oxford Clay of
Wiltshire (YM KD1974/1), whose exact horizon and locality are
unknown, belong to this species and are described above.

Range and occurrence   Oxford Clay of Wiltshire; Middle
to Upper Oxford Clay (Athleta - Mariae Zones) of Villers-sur-Mer
(France).

2.   Nuculoma kathryni sp. nov. Pl. 1, figs. 2-6.

Type specimen   Holotype, GSM 114030, from the Oxford Clay
(horizon unknown) of Lydlinch (Wiltshire). Nine paratypes from
the same locality and horizon (GSM 114031 - 114039).

Diagnosis   Small species (up to 10.8 mm L), subtrigonal
in outline, usually rather elongate in form (H 76.5-84.7%,

$\overline{x}$ 81.0%); posterodorsal margin evenly concave, much shorter than anterodorsal margin, usually interrupted by a large escutcheon pout; anterodorsal margin gently concave to gently convex, ventral margin evenly convex, sometimes straightening posteriorly; well-inflated (I 61.9-74.4%, $\overline{x}$ 70.9%), but inflation always less than anterior length (AL 76.5-85.7%, $\overline{x}$ 81.1%); umbones prominent, rounded, strongly opisthogyrate, enrolled, placed near the posterior extremity of the shell; corcelet broad, cordate, lightly impressed, the bounding carinae rounded in outline; escutcheon well-developed, with a prominent escutcheon pout; lunule not differentiated; ornament interdigitate; posterior part of hinge with up to 8 teeth.

Measurements

See Appendix 3.

	L	H	I	AL
N	6	6	5	6
$\overline{x}$	9.8 mm	81.0 %	70.9 %	81.1 %
Max	10.8	84.7	74.4	85.7
Min	8.5	76.5	61.9	76.5
OR	2.3	7.8	12.5	9.2

Description   Small, equivalve, inequilateral, elongate-subtrigonal in outline, with the anterodorsal and ventral margin of subequal length, about twice the length of the posterodorsal margin; anterodorsal margin usually gently convex, but occasionally straight or slightly concave, the anteroventral angle prominent, rounded, produced; posterodorsal

margin evenly concave, the outline usually broken by the well-developed escutcheon pout, which occupies about half the length of the posterodorsal margin; posteroventral angle sharply rounded, produced, about a right angle; ventral margin gently and evenly convex, sometimes straightening posteriorly and becoming subparallel to the anterodorsal margin. Inflation high, (I $\bar{x}$ 70.9%) giving the shell a globular appearance. Umbones prominent, inflated, rounded, strongly opisthogyrate, enrolled, placed close to the posterior extremity of the shell (AL $\bar{x}$ 81.1%), salient about 1 mm above the hingeline. Ornament consisting of interdigitate concentric striae, except on the dorsal areas, where there are only faint growth lines.

Corcelet broad, cordate, not deeply excavated, occupying the whole of the posterodorsal region to the posteroventral angle, the bounding umbonal carina being rounded and not prominent. Escutcheon small, cordate, prominent, reaching about halfway to the posteroventral angle, the two arcuate ridges broad and clearly elevated as the escutcheon pout. Lunule not differentiated, lacking bounding carinae and distinctive ornament pattern. Ligament internal.

Hinge line 72.9% of length of dorsal margins (only measurable on one specimen), the anterior part twice as long as the dorsal part (48.6% to 24.3%), the two parts set at an angle of about 110°; the anterior tooth row is gently convex and contains 15 small, chevron-shaped taxodont teeth, the angles of the chevrons pointing towards the umbones, the teeth increasing in size distally; the posterior row is straight and

has 8 small, similarly-shaped teeth, more closely spaced than the anterior row; chondrophore tooth not visible, but preservation in the umbonal region is poor. Resilifer placed on a short, narrow, anteroventrally directed chondrophore, which only protrudes very slightly into the shell cavity.

Musculature largely obscured, the adductor muscle scars suborbicular, subequal, normally placed, the anterior scar slightly larger than the posterior; no other muscle scars visible. Pallial line entire.

Remarks   N. kathryni is superficially similar to N. castor, but there are several important differences, notably the more enrolled, nearly terminal, umbones of the latter species. These cause reduction of the posterior tooth row, so that, as shown by Couffon (1919, pl. 5, fig. 14g) and Schenck (1934, pl. 4, fig. 5c), there are only about four small peglike teeth, arranged subvertically, in N. castor. In contrast, N. kathryni has the posterior part of the hinge plate longer with 8 teeth. The escutcheon and escutcheon pout are much better developed in N. kathryni, the specimens of N. castor figured by Schenck and Couffon (op. cit.) appearing to lack a clearly-differentiated escutcheon, presumably due to reduction of the posterior tooth row.

Range and occurrence   The species is known solely by 10 specimens from the Oxford Clay (horizon unknown) of Lydlinch (Wiltshire), preserved in the Geological Survey Museum, London (GSM 114030-114039).

Genus PALAEONUCULA Quenstedt, 1930 (p. 110)

Type species   Originally designated by Quenstedt, 1930, p. 110, pl. 2, fig. 9, Nucula hammeri Defrance, 1825, p. 217, from the U. Lias of France.

Diagnosis   Medium sized genus (up to ≈ 35 mm L), elongate, subtrapezoidal to subtrigonal in outline, well inflated; umbones slightly opisthogyrate, sometimes gently enrolled, posteriorly placed, occasionally terminal; postero-dorsal area often deeply impressed, cordate in outline; anterodorsal margin usually slightly arched, ventral margin gently convex, often sinuate posteriorly; anterior margin bluntly rounded; anterior row of teeth often gently arched, posterior row shorter than anterior, its length dependent upon how near the posterior the umbones are placed; ornament consisting of irregularly spaced concentric growth lines of variable strength, no radial sculpture; valve margins not denticulate.

Remarks   Quenstedt's original diagnosis (1930, p. 112) has been emended by Schenck (1934, p. 36) and Cox (1940, p. 11), as it was not strictly applicable to the genotype. Schenck (op. cit.) recognised a 'chondrophore tooth', adjoining the posterior margin of the chondrophore in several specimens of N. hammeri, the type-species; Quenstedt (op. cit.) believed a chondrophore tooth to be absent, but this conclusion was based on examination of an incomplete specimen.

The relationships between the Jurassic nuculid genera
Palaeonucula and Nuculoma, and the Cretaceous-Recent genus
Nucula s.l., have been a source of great confusion in the past,
mostly due to imprecise understanding of the type species.
Quenstedt (1930) believed all three genera to be distinct, as
did Schenck (1934), although the latter author thought
Palaeonucula to be a subgenus of the Palaeozoic genus Nuculopsis
Girty. As noted by Cox (1940, pl. 12), Nuculopsis has a rather
more primitive type of chondrophore than Palaeonucula, the
chondrophore being wider and shorter, and not projecting into
the shell cavity; accordingly, Cox placed Palaeonucula as a
subgenus of Nucula, and accepted Nuculoma as a valid genus.
Later (1965, pl 25), Cox placed Palaeonucula as a subgenus of
Nuculoma, an opinion based on the shell structure studies of
Van de Poel (1955). At the present time, the name Nucula s.l. is
restricted to forms with radial ribbing on the shell exterior
(Keen, 1969, pl. N231), and thus Nucula s.l. must be considered
distinct from Palaeonucula and Nuculoma, not appearing until
the Cretaceous. Study of the genotypes of the two Jurassic
genera reveals several important differences, enabling a clear
distinction to be made between them. The diagnostic features of
Nuculoma are discussed above, the main differences between it
and Palaeonucula being its more opisthogyrate, strongly enrolled
umbones which overhang the posterior margin, and the fine
concentric ribbing, occasionally interdigitate, all over the
shell.

1.   Palaeonucula triangularis sp. nov. Pl. 1, figs. 7-11,
                                        Pl. 2, figs. 1-12.

Type specimen   Holotype, BM LL27713 from L. Oxford Clay,
Bed 7 (Callomon, 1968), Coronatum Zone, Obductum Subzone of
Stewartby, Bedfordshire. Paratypes (BM LL27714-27721) from the
same locality and horizon.

Diagnosis   Medium-sized species (up to 18.4 mm L),
subtrigonal (H 73.0-88.1%, $\bar{x}$ 79.6%) in outline, with posterior
margin straight to gently concave, the posteroventral angle
about 90°, often produced; corcelet broad, cordate, its
margins clearly defined by the ridge running from the umbones to
the posteroventral angle; ventral margin short, evenly convex,
sometimes straightening and becoming slightly sinuate posteriorly;
escutcheon cordate, elevated, usually protruding above the
posterior margin as a slight pout; anterior margin straight to
gently convex, anteroventral angle rounded; well inflated
(I 56.1-82.0%, $\bar{x}$ 66.9%); umbones posterior of median (AL 55.8-
80.0%, $\bar{x}$ 70.1%), opisthogyrate, not enrolled; sculpture of
irregularly spaced concentric growth lines, locally coarsened
as growth halts.

Measurements

See Appendix 3.

	L	H	I	AL
N	158	158	158	158
$\bar{x}$	14.7 mm	79.6%	66.9%	70.1%
Max	18.4	88.1	82.0	80.0
Min	10.7	73.0	56.1	55.8
OR	7.7	14.9	25.9	24.2

Description   Small to medium-sized species, trigonal to
subtrigonal in outline, with anterior and ventral margins of
approximately equal length; anterior margin straight to gently
convex, the outline of the body of the shell obscuring the
hingeline (as seen laterally) for most of its length; the
anterior extremity of the hinge line not elevated above the
anterior margin; posterior margin straight to gently concave,
the body of the shell obscuring the hingeline for all of its
length, except where the escutcheon pout protrudes above the
margin for a short way; posteroventral angle about a right
angle, ofter produced, thus emphasizing the concavity of the
posterior margin, and the sinuosity of the posteroventral margin;
ventral margin evenly convex, often straightening posteriorly,
and often becoming very slightly sinuate in forms with a produced
posteroventral angle; anteroventral angle acute, rounded,
passing evenly between the ventral and anterior margins.
Umbones prominent, opisthogyrate, placed posterior of median
(AL $\overline{x}$ 70.1%), salient up to 2 mm above the hinge line, not
enrolled. Well inflated (I $\overline{x}$ 66.9%), inflation tending to
increase throughout ontogeny. Ornament consisting solely of
irregularly spaced concentric growth lines over the whole shell
surface, including the dorsal regions; no interdigitate
ornament, but on some very well preserved specimens, there are
very faint traces of radial striae in places.

   Posterodorsal region of the shell generally rather
flattened, corcelet and escutcheon well-developed lunuliform;
corcelet large, broad, cordate, occupying the whole of the

posterodorsal region of the shell, bounded by the ridges running from the umbones to the posteroventral angle; corcelet flattened to excavate in outline, ornamented by concentric growth lines which continue onto the body of the shell. Escutcheon shorter and narrower, cordate, placed within the corcelet, extending about two-thirds of the way to the posteroventral angle; its outer margin taking the form of a rounded ridge extending in an arc from the umbones to the commissure, usually protruding above the outline of the posterodorsal margin as an escutcheon pout; inside the marginal ridge, the escutcheon slopes gently to the commissural margin. Lunule absent.

Hinge line about two-thirds of the length of the dorsal margin (Lh 61.8-72.6%, $\overline{x}$ 67.8% $\underline{/\text{Lh}}$ as % of Ldn$\underline{/}$), anterior part straight to very gently convex, posterior part gently convex, with known maxima of 16 anterior teeth and 10 posterior teeth. Dentition taxodont, teeth chevron-shaped, the points of the chevrons directed towards the umbo, projecting about 1 mm above the commissure; teeth becoming more widely spaced distally, the largest tooth occurring about 3 teeth from the distal end of each tooth row; the proximal teeth of the anterior row continue above the chrondrophore as very small peglike teeth which prove impossible to count. A strong chondrophore tooth occurs at the anterior end of the posterior tooth row of the left valve, forming the posterior margin of the chondrophore, the next three or four teeth of the posterior row being narrow and blade-like; the chondrophore tooth is matched by a socket in the right valve. Resilifer located on a short, excavate chondrophore directed

anteroventrally from the umbo and projecting a little way into the shell cavity.

Muscle insertion areas weakly impressed, best seen on steinkerns. Adductor scars subequal, ovate, placed close to the dorsal margin, immediately beneath the distal ends of the hinge line marked by prominent growth lines. Posterior adductor scar slightly more ovate than the anterior, with a slight buttress dorsally and anterodorsally; anterior adductor scar buttressed dorsally and posterodorsally. Pedal muscles unequal, sited near the commissure; anterior scar L-shaped, slightly longer than posterior scar, the long arm of the L running parallel to the commissure from the posterior end of the anterior adductor scar, about one-third of the way to the umbones, the short arm perpendicular to it, about one-third of the length of the long arm, parallel to the posterior margin of the anterior adductor scar; posterior scar about two-thirds of the length of the anterior scar, straight, subparallel to the commissure, running anterodorsally from the dorsal margin of the posterior adductor scar, about halfway to the umbones; both pedal scars ornamented with fine growth lines. Visceral muscle impressions occupy a marked channel on the steinkerns, running anteroventrally from the anterior side of the umbones, fading at the level of the dorsal margins of the adductor scars; two or three suborbicular discrete muscle scars may sometimes be seen at the ventral end of the groove (Fig. 2.8). Pallial line simple. Valve margins not crenulate.

Remarks   The large collections of pyritized whole shells to be found in many of the pyritic shell beds of the Lower Oxford Clay allow detailed studies of variation to be made in P. triangularis, revealing its polymorphic nature (Fig. 2.9). The variation is continuous, however, and no valid reasons for further subdivision have been found. The 'norm' of the population is a shell of trigonal outline, relatively short (H ≃ 82%) and well-inflated (I ≃ 72%), with a short, smoothly-curved ventral margin. Elongation varies quite considerably (H 73.0-88.1 %, $\bar{x}$ 79.6 %), the ventral margin becoming more gently curved as length increases; elongation is often coupled with increasing concavity of the posterior margin, and slight sinuosities which appear at the posterior end of the ventral margin. Inflation does not vary systematically with any shell parameter except perhaps overall size (measured as L), small shells tending to have a lower I percentage, but this relationship does not always hold. The development of the escutcheon pout is a very inconsistent feature, which cannot be directly correlated with any other major shell parameter, but which seems to be related to the degree of convexity of the posterior row of teeth; the more arched the teeth, the more pronounced is the pout. The degree of excavation of the corcelet is apparently unrelated to the strength of the escutcheon pout.

The terms escutcheon and corcelet are used as defined by Carter (1967, p. 261), and although they have not traditionally been used in the description of nuculids, the author feels that they may usefully be employed in the description of the

posterodorsal area in this family. The escutcheon is defined as representing the track on the outer surface of the valve of the posterodorsal edge of the hinge during shell growth, and even a cursory glance at specimens of P. triangularis shows that the escutcheon corresponds with the posterior end of the tooth row. The corcelet is rather more loosely defined, but represents a further differentiated area posterior to the umbones, outside the escutcheon; its structural significance is unknown.

The musculature is best seen on limestone steinkerns which may occasionally be extracted from the septarian concretions that occur in the Lower Oxford Clay of the Midlands, especially at Stewartby. Careful removal of the inner nacreous layer reveals well preserved adductor and pedal muscle scars, and a faint channel representing the visceral muscle attachment area (Fig. 2,8). The pedal musculature of Jurassic nuculids is not well-documented, and these specimens are valuable in that the pedal musculature of Palaeonucula is described for the first time. Terminology for the musculature is taken from Speden (1970, p. 30), who described the muscle scars of two Cretaceous species of Nucula s.s.; these differ from Palaeonucula in the shape of the pedal scars, and the shape and position of the visceral muscle scars, thus showing that the musculature is of some taxonomic importance in this family.

There are many available specific names for Callovian and Oxfordian nuculids, but none of them are applicable to the species described here. In general outline, P. triangularis is close to Nuculoma pollux (Raspail ex d'Orbigny), but N. pollux is less

inflated (I $\overline{x}$ 58.7%), and has the interdigitate concentric ribbing which places it in Nuculoma. The specimen figured by Makowski (1952, p. 5, pl. 5,figs. 2,2a) as Nucula calliope d'Orbigny is probably also referable to N. pollux, although it is a little more inflated than the type. In general outline, Makowski's specimen is similar to P.triangularis but again, it has interdigitate ornament. Nucula calliope Couffon (1919, p. 79, pl. 5, fig. 13, 13a-13i) appears to belong to Palaeonucula, lacking regular concentric ornament, but the posterior margin is not concave enough, and the escutcheon pout not pronounced enough for P. triangularis.

Range and occurrence   Abundant in the L. Oxford Clay, Jason – L. Athleta Zones of the English Midlands (Calvert, Bletchley, Stewartby, Norman Cross) and Dorset (Crook Hill).   ? Jason Zone, M4 Road Cutting, Dodford Farm, Christian Malford, Wilts. (OUM J28238).   Also Calloviense Zone, Enodatum Subzone of Stewartby and Bletchley and Peterborough;   four specimens (GSM Bx7515) from the Geological Survey borehole at Upwood (Hunts.), and one specimen from the Oxford Clay of Christian Malford (Wilts.) (GSM Lowe Collection, 14).

2.   Palaeonucula cottaldi (de Loriol, 1875). Pl. 2, figs. 13-19.

v?   1829 Nucula (cast); Phillips, pl. 5, fig. 4.

      1850 Nucula Calliope sp. nov.; d'Orbigny, p. 339, no. 177.

      1856 N. pectinata Zieten; Quenstedt, p. 505, pl. 67, fig. 24.

      1860 N. ornata Quenstedt; Damon, pl. 2, figs. 6-8 (non
            Quenstedt).

1875 <u>N. Cottaldi</u> sp. nov.; de Loriol in de Loriol and Pellat,
p. 295, pl. 17, figs. 11-15.

non 1883 <u>N. Calliope</u> d'Orbigny; Lahusen, p. 86, pl. 2, figs.
21a-b, 22a-b.

1897 <u>N. Cottaldi</u> de Loriol; de Loriol p. 113, pl. 14, figs.
15, 15a-b, 16, 17, 17a-b, 18.

1901 <u>N. Calliope</u> d'Orbigny; Raspail, p. 194, pl. 11, fig. 16.

non 1904 <u>N. Calliope</u> d'Orbigny; Borissiak, p. 36, pl. 2, fig. 2.

non 1907 <u>N. Cottaldi</u> de Loriol; Cossmann, p. 9, pl. 3, figs. 10,11.

non 1915 <u>N. Calliope</u> d'Orbigny; Krenkel, p. 306, pl. 26, figs.
19-22 /figs. 19-21 = <u>N. chassyana</u> d'Orbigny, fig. 22 =
<u>N. inconstans</u> Roeder/.

non 1919 <u>N. Calliope</u> d'Orbigny; Couffon, p. 79, pl. 5, figs.
13, 13a-13i.

1925 <u>N. Calliope</u> d'Orbigny; Cottreau, p. 21, pl. 39, figs. 21,22.

1952 <u>N. ornati</u> Quenstedt; Makowski, p. 5, pl. 5, figs. 1-1a
(non Quenstedt).

non 1952 <u>N. calliope</u> d'Orbigny; Makowski, p. 5, pl. 5, figs. 2-2a.

<u>Type specimen</u>   Lectotype here designated, the specimen
figured by de Loriol in de Loriol & Pellat, 1875, p. 295, pl. 17,
figs. 11-15, as <u>Nucula Cottaldi</u>, from the Oxfordian
of Boulogne-sur-Mer, France. Preserved in the Polytechnicum à
Zurich.

<u>Diagnosis</u>   Medium-sized species (up to 19.0 mm L),
subrectangular (H 67.4-81.8%, $\overline{x}$ 75.0%) in outline, the
posterodorsal margin short, straight to gently concave, the

posteroventral angle rounded, greater than 90°, not produced;
anterodorsal margin markedly concave in outline, a faint carina
running from the umbo to the anteroventral angle, the anterior
part of the hinge line protruding above the level of the overall
shell outline to give the anterior end of the shell a sub-
rectangular outline; the whole shell outline giving the
impression of being elongated posteriorly; well inflated (I 61.8-
74.8%, $\overline{x}$ 67.3%); umbones markedly opisthogyrate, placed close
to the posterior margin (AL 73.3-84.4%, $\overline{x}$ 79.1%), not enrolled;
corcelet shorter and narrower than in P. triangularis, its
margins not so clearly defined, and of a generally concave
outline; escutcheon small, not well-developed, pout not visible
above the posterior margin; sculpture of irregularly spaced
concentric growth lines.

Measurements

See Appendix 3.

	L	H	I	AL
N	9	9	7	8
$\overline{x}$	16.4 mm	75.0 %	67.3 %	79.1 %
Max	19.0	81.8	74.8	84.4
Min	14.4	67.4	61.8	73.3
OR	4.6	14.4	13.0	11.1

Description   Small to medium sized, equivalve,
inequilateral, subrectangular to subelliptical in outline, the
whole shell appearing to be elongated posterodorsally. Posterior
margin short, gently concave or straight, depending on the

inflation of the umbones; posteroventral angle sharply rounded, greater than a right angle (approximately 120°), not produced posteriorly; outline of anterodorsal margin concave, the anterior end of the hinge line appearing above the outline of the body of the shell in its anterior half; the hinge line itself is straight; the outline of the anterior part of the umbonal region is continued to the anteroventral angle as a rounded carina, marking off a broad, lanceolate, obliquely sloping anterodorsal area; anterior margin short, oblique, truncate, straight to very gently concave or convex, forming an angle of about 145° with the hinge line; anteroventral angle slightly produced, evenly rounded, about a right angle; ventral margin evenly convex, not straightening anteriorly, and without sinuousities. Umbones prominent, rounded, opisthogyrate, not enrolled, placed close to the posterior margin (AL $\overline{x}$ 79.1%). Well inflated (I $\overline{x}$ 79.1%), at maximum near the centre of the shell. Ornament consisting of irregularly spaced concentric growth lines, often coarsened into prominent growth halts near the ventral margin; the growth lines continue uninterrupted over the dorsal areas; no radial elements or interdigitate pattern.

Posterodorsal region of the shell slightly excavate, corcelet and escutcheon poorly developed, cordate; corcelet small, suboval, not deeply impressed, gently concave in outline; its margins marked by a rounded carina running from the umbones to the posteroventral angle, but not as clearly marked as in P. triangularis. Escutcheon small, cordate, very weakly developed, only a very faint arcuate ridge developed; escutcheon pout very small, not protruding above the outline of the posterior margin.

Anterodorsal area of the shell differentiated into two areas, both of lanceolate shape; the inner area extends from the umbones to the anterodorsal angle, its margins being marked by faint carinae sometimes ornamented by darkened patches of shell slightly elongated along growth lines; its floor is flat. The outer area extends from the umbones to the posteroventral angle, lies outside the inner area, and is limited by the umbonal carina running to the posteroventral angle; it slopes obliquely downwards from the umbonal carina to the bounding carina of the inner area. Both areas are ornamented by concentric growth lines continuous onto the body of the shell. Ligament internal.

Hinge line occupying nearly the whole of the dorsal margin, reaching as far as the anterodorsal angle and nearly to the posterodorsal angle; anterior tooth row straight to very gently convex, maximum number of teeth seen being 20; posterior row gently convex, the hingeline broken in the only available specimen, so the number of teeth is unknown, but at least 6. Dentition taxodont, teeth chevron-shaped, details as in P. triangularis. Chondrophore and resilifer not seen because of breakage of the only available shell, but probably as in P. triangularis.

Muscle insertions deeply impressed, best seen on steinkerns. Adductor scars subequal, the anterior scar slightly larger, both scars subovate, placed immediately beneath the distal ends of the hingeline, ornamented by prominent growth lines. Posterior scar slightly more ovate than the anterior, which tends to be slightly subtrigonal, a weak buttress developed dorsally; the

anterior scar more strongly buttressed dorsally and posteriorly. Pedal muscles of unequal size and different shape anteriorly and posteriorly, both placed close to the commissure; anterior scar triangular, about 1 mm long, the long axis of the triangle directed towards the umbones, subparallel and very close to the commissure, located immediately anterior of the anterior adductor scar; posterior scar elongate, as in P. triangularis about 1.5 mm long, located about midway between the posterior adductor and the umbo, its long axis subparallel to the commissure and directed umbonally; both scars ornamented with fine growth lines. Visceral muscle scars faint, two elongate muscle scars placed in line, running directly ventrally from the anterior side of the umbo, fading at about the level of the dorsal margin of the adductor scars; just anterior to these scars, a faint groove on the steinkern runs towards the anteroventral angle, fading at about the same level as the visceral scars. Pallial line simple. Valve margins not crenulate.

Remarks   The description is based on well-preserved material from Lukow, Poland, kindly donated by Dr. A. Radwanski, together with reference to the descriptions and figures of de Loriol (1897) and Cottreau (1925). Variation is not as great as in P. triangularis, degree of elongation being the most variable feature, inflation and anterior length tending to be more constant. D'Orbigny's original (1850, p. 339) diagnosis was very brief - "Espece voisine du N. Caecilia, mais plus renflee, plus courte dans son ensemble, tronquee sur la region anale" - and from the diagnosis alone, recognition is difficult,

several authors (see synonomy) having misidentified the species
before Cottreau figured the type. The first valid description
of the species is that of de Loriol (1875 in de Loriol & Pellat),
who ignored d'Orbigny's name, and introduced the name
Nucula cottaldi; his figures show it to be indistinguishable
from d'Orbigny's species, and so his name takes priority.
Nucula ornati Quenstedt (1856, p. 505, pl. 67, figs. 22, 23) has
been confused with N. calliope by authors such as Damon (1860)
and Makowski (1952), but Quenstedt's figure is clearly of a
different species, being more elongate, and with the umbones
more centrally placed; it is probably conspecific with
N. caecilia d'Orbigny. The composite mould figured by Phillips
(1829, pl. 5, fig. 4) as Nucula (cast), from the Mariae
Zone Oxford Clay of Scarborough, is preserved in the Yorkshire
Museum (YM Tsp 880), together with several topotypes, and it
is likely that this represents the earliest figure of the species
as the specimens agree well with the continental specimens.
Phillips figure is reversed.

The musculature is more deeply impressed than in
P. triangularis, a feature probably related to the greater
thickness of the shell in P. cottaldi. Placement of the
muscles is similar to that seen in P. triangularis, but there are
marked differences in the pedal muscle scars, the anterior scar
being triangular rather than L-shaped, and smaller than the
posterior scar. The visceral muscle scars are more disjunct in
P. cottaldi, most likely due to increased shell thickness.

<u>Range and occurrence</u>   Mariae Zone, Scarborough (YM Tsp

and Warboys, Hunts. (GSM Dr 2829);   Cordatum Zone, Warboys,

Hunts. (GSM Dr 2508, Dr 2526, Dr 2538);   Oxford Clay, Osmington,

Dorset (GSM Y2049).

Callovian of France (d'Orbigny, 1850;   Cottreau, 1925),

Lukow, Poland (Lamberti - Athleta Zones, Makowski, 1952), and

Germany (Quenstedt, 1856).   Oxfordian of Switzerland (de Loriol,

1897).   Type specimens from the   Oxfordian

of Boulonge-sur-Mer,   France,   (de Loriol in de Loriol &

Pellat, 1875).

Superfamily NUCULANACEA   H. Adams & A. Adams, 1858

Family MALLETIIDAE   H. Adams & A. Adams, 1858

Genus MESOSACCELLA Chavan, 1946 (p.   197)

<u>Type Species</u>   Originally designated by Chavan, 1946, p. 197,

<u>Nucula fӧrsteri</u> Mu̎ller, 1847, p. 17, pl. 2, fig. 1, from the

U. Cretaceous of Germany.

<u>Diagnosis</u>   Elongate oval in outline, inflated, the

antero- and posterodorsal margins straight, set at an obtuse

angle to each other, the posterodorsal margin about $1\frac{1}{2}$ to 2 times

the length of the anterodorsal margin;   posterodorsal angle

sharply rounded, about a right angle, the posterior margin

truncate to gently convex, posteroventral angle more evenly

rounded;   no resilifer, ligament external, amphidetic, nymphs

elongate and very small;   slight depression beneath the umbo

between the anterior and posterior rows of teeth; anterior and posterior rows of teeth straight, not gently concave, as in the similarly-shaped Saturnia; ornament of irregular concentric growth lines; pallial sinus small.

Remarks   Puri (1969, p. N235) placed Mesosaccella in the Nuculanidae, although as Chavan (1946, p. 197) originally observed "Le ligament reste donc externe, en marge du bord immediatement derriere le crochet, ce qui exclut l'attribution aux vraies Nuculana et notamment au sous-genre Saccella". The lack of a resilifer, the ligament being wholly external, indicates that Mesosaccella should properly be classified in the Malletiidae, and it is here   placed in that family. The range is here extended down to the Callovian, the genus only being known previously from the Campanian and Maestrichtian (U. Cretaceous).

Cox (1937, p. 192) referred M. morrisi to the genus Palaeoneilo Hall, a genus originally described from the Devonian of the United States, on the basis of similarities in outline and dentition. However, Palaeoneilo, although believed by some authors to extend into the Mesozoic, is primarily a Palaeozoic genus, characterised by a faint radial posterior sulcus, and with the end teeth of the posterior series tending to pass above the anterior series in the area beneath the umbo. This means that there can be no development of a slight depression beneath the umbo, a necessary feature of Mesosaccella. Examination of well-preserved specimens of M. morrisi reveals the presence of

this slight fossette, thus invalidating their placement in

Palaeoneilo; M. morrisi also lacks the posterior radial groove,

and is much more elongate and subequilateral than Palaeoneilo.

Cox also maintained (1937, p. 193; 1940, p. 6) that in

Palaeoneilo (including P. morrisi), the pallial line was entire,

with no sinus, and in his 1940 paper, this caused him to place

Palaeoneilo in the Ctenodontidae, a family characterised by the

lack of a pallial sinus. Specimens of M. morrisi from the

English Midlands show the presence of a clearly developed pallial

sinus, and so Cox's conclusions about the Jurassic species he

assigned to Palaeoneilo must be amended. The status of Palaeoneilo

has been considered, and a series of probable topotypes of the

type species figured, by McAlester (1968, p. 41, pl. 15, figs. 1-15).

Mesosaccella morrisi (Deshayes, 1853). Pl. 3, figs. 1-19.

? 1828 Nucula nuda sp. nov.; Young & Bird (Bean, Ms.), p.230.

v? 1829 N. nuda Young & Bird; Phillips, pl. 5, fig. 5.

1850 Nucula (Leda) Phillipsii sp. nov.; Morris, p.318, pl. 30,

figs. 1, 1a. (non N. phillipsii McCoy, Carboniferous species).

1850 Leda alpina sp. nov.; d'Orbigny, p. 336, no. 136.

1853 Leda morrisii nom. nov.; Deshayes, p. 282. (nom. nov.

pro N. phillipsii Morris non McCoy).

? 1904 Palaeoneilo choroschowensis sp. nov.; Borissiak, p. 32,

pl. 2, figs. 11a; 11b.

? 1925 Leda alpina d'Orbigny; Cottreau, p. 11, pl. 38, fig. 3.

v. 1937 Palaeoneilo phillipsii (Morris); Cox, p.192, pl.15, figs.1-3.

1940 P. morrisii (Deshayes); Cox, p.6.

<u>Type specimen</u>   The holotype of Morris'1850 (pl. 30, figs. 1,

1a) figure of <u>Nucula (Leda) Phillipsii</u> is not preserved with the

rest of Morris' types in the BM (NH), and must be considered lost.

The specimen figured by Cox (1937, pl. 15, fig. 1) from the Oxford

Clay of Christian Malford, Wiltshire (the type locality) is here

designated neotype (BM L67154). The two other specimens figured

by Cox (op. cit., figs. 2, 3) from the same locality are

neoparatypes (BM L67155, BM L67148 respectively).

<u>Diagnosis</u>   Medium-sized species (up to 17.6 mm L),

equivalve, subequilateral, subovate in outline (H 48.8-73.8%,

$\overline{x}$ 60.4%); inflation relatively high (I 41.1-56.8%, $\overline{x}$ 51.1%),

always greater than anterior length in any particular shell

(AL 34.5-52.3%, $\overline{x}$ 41.5%). Umbones small, broadly rounded,

orthogyrate, only very slightly salient to the hinge line (max.

salience 1 mm), no umbonal sulcus or carina present. Dorsal

margin an acute angle ($\sphericalangle$ 131-160°, $\overline{x}$ 141.2°), posterodorsal

part straight to very slightly concave, anterodorsal part straight

to very slightly convex. Ornament consisting of fine growth

lines, occasionally coarsened into growth rugae.

May be distinguished from the closely-related <u>M. galatea</u>

(Dumortier ex d'Orbigny) /See Cox 1936, p. 465; 1937, p. 191/

by its much greater inflation, greater anterior length (AL 32.3-

38.7%, $\overline{x}$ 34.5% in <u>M. galatea</u>), smaller umbonal angle (< 146-

157°, $\overline{x}$ 150.8° in M. galatea) and difference in ornament;

<u>M. galatea</u> is ornamented by very fine, regularly spaced, incised

concentric striae, slightly oblique to the growth lines.

Measurements

See Appendix 3.

	L	H	I	AL	<
N	125	124	35	122	111
$\overline{x}$	11.4 mm	60.4%	51.1%	41.5%	141.2°
Max	17.6	73.8	56.8	52.3	160
Min	4.8	48.8	41.4	34.5	131
OR	12.8	25.0	15.4	17.8	29

M. galatea (Measurements from Cox, 1937)

	L	H	I	AL	<
N	4	4	-	4	4
$\overline{x}$	8.6 mm	57.9%		34.5%	150.8°
Max	11.1	61.8		38.7	157
Min	7.1	55.1		32.3	146
OR	4.0	6.7		6.4	11°

Description   Small to medium-sized species (L up to 17.6 mm), equivalve, inequilateral to subequilateral, subovate in outline, posterior elongate to a varying extent. There is a relationship between overall size (measured as length), and the outline of the shell, smaller specimens (up to about 10 mm L) tending to be subequilateral, with submedian umbones and relatively high H, while large specimens tend to be much more elongate, with the posterior becoming lengthened, the umbones moving anteriorly, and the height decreasing relative to L. Umbones small, pointed, placed between submedian and about 34.5% of the length behind the anterior margin (AL $\overline{x}$ 41.5%), orthogyrate, rounded, moderately prominent, but only slightly salient ($\simeq$ 1 mm)

to the hinge margin. Dorsal margin an obtuse angle about the
slightly salient umbones ($< \bar{x}$ 141.2^o), the anterodorsal margin
short (AL $\bar{x}$ 41.5%), very slightly concave in juveniles,
straight to slightly convex in larger specimens; anterodorsal
angle evenly rounded, not produced; posterodorsal margin
elongate, straight to slightly concave in all specimens;
posterodorsal angle sharply rounded, even in juvenile forms,
passing via a slightly obtuse angle into the rounded truncate
posterior margin; posterior part of the shell not rostrate, but
evenly produced; ventral margin evenly convex to elongate,
convexity often dependent upon length, the median part of the
ventral margin often tending to become straight in large forms,
although not invariably; anteroventral angle not demarcated, the
anterior margin passing evenly into the ventral margin, and being
sharply rounded; posteroventral angle variably developed,
usually an evenly rounded angle of about 90°, but often not
clearly developed, the ventral and posterior margins being
continuously curved. Ornament consisting of faint concentric
growth lines, sometimes locally coarsened to form growth rugae;
no radial or regular concentric ribbing developed. Shell margin
entire, with no gapes.

Dorsal areas clearly differentiated; a small ovate
depression (up to about 1.5 mm long) immediately in front of the
umbones, and a lanceolate, slightly impressed area (up to about
2.0 mm long), located immediately posterior to the umbones,
which represents the attachment site for the external amphidetic
ligament. A longer (up to about 6.5 mm long) shallower,

lanceolate depression, delimited laterally by a sharp break of slope, lies immediately posterior to the umbones, and reaches almost to the posteroventral angle; this probably represents a primitive escutcheon.

Hinge teeth arranged in two straight rows, set at an obtuse angle of about 141° to each other, not meeting, each terminating just either side of the umbo, leaving a gap occupied by a very faint depression immediately beneath the umbo; this depression probably foreshadows a resilifer, but is not well enough developed to be a functional attachment site for an internal ligament. Teeth normally developed, taxodont, chevron-shaped, the points directed towards the umbo, interlocking well with the teeth of the opposite valve, increasing in size distally, the posterior row about 30% longer than the anterior row, a specimen 10.3 mm long possessing 21 posterior teeth and 16 anterior teeth. Anterior adductor muscle scar small, subovate (about 1 mm long in a specimen 14.7 mm long), placed immediately ventral of the anterior end of the hinge plate; posterior adductor muscle scar small (1.5 mm long in the specimen mentioned above), subrectangular, less deeply impressed than the anterior scar, placed immediately ventral of the posterior end of the hinge plate, about 4 teeth from the posterior extremity. Posterior pedal retractor muscle scars very narrow and elongate, deeply impressed, placed parallel to the posterodorsal margin, immediately ventral of the hinge plate, reaching from above the posterior adductor scar almost to the umbones (Fig. 2.10). Anterior pedal retractor scars narrow and short, placed parallel

to the anterodorsal margin, immediately ventral of the hinge
plate, located about one-third of the distance between the
anterior adductor scar and the umbo. A narrow elongate scar
often runs anteroventrally from the anterior point of the umbo
towards the pallial line, dying out just above and anterior to
the anterior adductor scar (Fig. 2.10); this scar could perhaps
be analogous with the visceral mass integument scar found in
species of Solemya, or could represent the intestinal scar
(Stoll, 1939, p. 351).

Remarks   The specimen figured by Phillips (1829, pl. 5,
fig. 5) as Nucula nuda Young & Bird, from the Oxford Clay of
Scarborough, Yorkshire, is preserved in the Yorkshire Museum
(YM Tsp 188), and is a poorly-preserved steinkern showing no
diagnostic features. No dentition or muscle scars are visible,
and the only similarities with M. morrisi are ones of general
shape. It is possible that N. nuda Phillips is conspecific with
M. morrisi, but in view of the poor preservation of the type
material of the former species, and the lack of better preserved
topotypes, it is not possible to unite the two species; a
further point of note is that no certain specimens of M. morrisi
have yet been found above the Athleta Zone. The name Nucula nuda
was introduced by Young & Bird (1828, p. 230) from a Bean Ms
name, for "a smaller nucula, a little more oblong, ... from
the second shale at Scarborough", and was a nomen nudum until
figured by Phillips the following year.

The species was first described properly by Morris in 1850,
based on specimens collected from the Oxford Clay of Christian

Malford, Wiltshire, but he unfortunately gave it a name already
preoccupied by a Carboniferous species, Nucula phillipsii McCoy.
Three years later, Deshayes (1853, p. 282) renamed the species
Leda morrisii, and this specific name has remained valid since
that date.

Leda alpina d'Orbigny (1850, p. 336, no. 136) from the
Callovian of Castellane (France), figured by Cottreau (1925, pl.
38, fig. 3), is clearly close to M. morrisi, but the posterodorsal
margin seems much too concave for this species, and the posterior
margin too elongate and pointed. Further study of a population
of topotype material would greatly aid in the proper interpretation
of this French species.

Borissiak (1904, p. 31) described five species of
Palaeoneilo from the ? Volgian of the Moscow region, one of
which, P. choroschowensis, agrees very well with the English
specimens of M. morrisi. However, in view of the age of
Borissiak's specimens, it is possible that they belong to
M. dammariensis (Buvignier), a Portlandian species with a clearly-
developed umbonal carina and a markedly truncate posterior margin.
The specimen figured by Borissiak (op. cit., pl. 2, figs. 11a,
11b) appears to lack the carina, and the posterior margin is of
M. morrisi type, so on purely morphological grounds, reference
to M. morrisi is possible. On the same plate, Borissiak figured
four other species of Palaeoneilo from the same horizon, all of
which could lie within the range of variation of a single species.
Taken from this point of view, the overall population is rather
more equilateral and less elongate than the British Callovian
species.

Nucula symmetrica Borissiak (Makowski, 1952, p. 6, pl. 5,
figs. 3, 3a) from the Callovian of Lukow, Poland (specimen
courtesy of Dr. A. Radwanski), lacks a pallial sinus, and
clearly cannot be assigned to *Mesosaccella*. In general outline,
it closely resembles Recent species of *Malletia*, with a faint
posterior carina giving a truncate posterior margin, but
differs from *Malletia* in the lack of a pallial sinus (Fig. 2.10).

The large collections of this species which may be made
at many localities in central England indicate that this is a
very variable species, the greatest variation being in degree
of elongation and inflation, anterior length and height
normally being dependent on overall length. There does seem to
be an increase in elongation up the stratigraphical sequence,
Grossouvrei Subzone specimens tending to be more elongate, with
more rounded ventral and posterior margins, than specimens from
the Medea Subzone, which are often more subequilateral.
However, there is no reason to split the species into
chronological subspecies, as there is an overlapping range of
variation at all levels, and no clear-cut distinctions may be
made between 'varieties'.

Pyritized specimens from Stewartby, Beds., (bed 7), and
some other well-preserved specimens from bed 8B at the same
locality and at Kempston, Beds. (GSM 75695-75703), show the
dorsal regions very clearly, allowing the recognition of small
external ligament sutures on either side of the umbones. Thus
Chavans (1946, p. 197) statement that the ligament in
Mesosaccella is posterior needs slight emendation. Speden (1970,

p. 42) described similar ligament sutures in the U. Cretaceous _Malletia evansi_. The interpretation placed on the anterior and posterior pedal retractor scars is based on the descriptions of _M. evansi_ given by Speden (op. cit., p. 43), the main difference being in the position of the anterior pedal retractors.

Range and occurrence   Lower Oxford Clay of England, very abundant in the Jason – Athleta Zones at all exposures. Possibly present in the Mariae Zone Upper Oxford Clay of Scarborough, Yorkshire. Possible records also from the Callovian of France (d'Orbigny, 1850).

Subclass CRYPTODONTA Neumayr, 1884

Order SOLEMYOIDA Dall, 1889

Superfamily SOLEMYACEA H. Adams & A. Adams, 1857

Family SOLEMYIDAE H. Adams & A. Adams, 1857

Genus SOLEMYA Lamarck, 1818 (p. 488)

Synonyms: _Solenimya_   Bowdich, 1822

Solenomya   Children, 1823

Stephanopus   Scacchi, 1833

Solenymia   Swainson, 1840

Solenymya   Schaufuss, 1869

Type species   Subsequently designated by Children, 1823, p.   27 , _Solemya mediterranea_ Lamarck, 1818, p.488 (= _Tellina togata_ Poli, 1795, p.42), Recent, Mediterranean, C. Atlantic, N. Pacific.

Mediterranean - W. Atlantic.

Diagnosis   Elongate-oval in form, compressed, umbones placed near the posterior margin, and level with hinge margin; valves with narrow anterior and posterior gapes; ligament opisthodetic to slightly amphidetic, located between dorsal shell margin and large internal chondrophore; anterior adductor scar large, with a continuation ascending obliquely posteriorly from the posteroventral corner of the adductor, towards the dorsal margin, where it broadens out, marking the visceral mass attachment area; pallial line obscure, but entire; ornament consisting of irregularly arranged radial ribs.

Discussion   Solemya has been divided into several subgenera on the basis of internal shell features, such as the relative positions of the ligament and chondrophore, thus making determination of fossil forms very difficult. 'S'. woodwardiana has an internal ridge running from below the umbones (Fig. 2.11) obliquely towards the posteroventral margin, which suggests that it is not a Solemya s.s., but in the absence of better-preserved material, it is not possible to make a subgeneric assignation. The discovery of better preserved specimens should allow subgeneric placement.

Roemer (1839, p. 43) states that in S. voltzii (U. Lias, Germany) "Jede Schale hat einen breiten, zusammengedrückten, sehr schrägen, das halb äusserliche, halb innerliche Band aufrehmenden Zahn." This suggests the presence of a chondrophore, as Solemya is edentulous, which necessitates placement within

Solemya s.l., rather than Acharax or Adulomya.

Solemya woodwardiana Leckenby, 1859, Pl. 3, figs. 20-31.

v* 1859 S. woodwardiana sp. nov.; Leckenby, p. 14, pl. 3, fig. 7.

Type specimen   The holotype of Leckenbys pl. 3, fig. 7 and
three paratypes, all from the "Kelloway Rock" of Scarborough,
Yorkshire, are preserved in the Sedgwick Museum, Cambridge
(SM J6008, J12568-12570).

Diagnosis   Compressed Solemya with riblets radiating
from the umbonal area, more marked towards the anterior and
posterior extremities.

Measurements

See Appendix 3.

	L	H	AL
N	19	19	19
$\bar{x}$	19.5 mm	45.6 %	78.5 %
Max	38.0	50.0	84.6
Min	11.0	39.1	72.7
OR	27.0	10.9	11.9

Description   Medium to large in size (up to 38 mm long),
equivalve, inequilateral, elongate-elliptical in shape (H 39-
50%, $\bar{x}$ 46%) with umbones situated close to the posterior
margin (AL 73-84%, $\bar{x}$ 78%); dorsal and ventral margins
subparallel, anterior and posterior margins almost semicircular
in smaller forms, becoming more pointed in larger forms;

inflation low, but not accurately measurable; umbones not prominent, but apparently opisthogyrate; hinge edentulous, ligament not visible; lunule and escutcheon apparently absent; shell thin and fragile, ornamented by riblets radiating from the umbonal area, more marked at the anterior and posterior extremities, especially in large forms, and by faint concentric growth lines, with relict colour banding of brown and buff in some examples; adductor scars unequal (Fig. 2.11), anterior scar larger, with a visceral mass integument scar running from its posteroventral corner obliquely towards the dorsal margin; posterior scar small and obscure, its anterior margin marked by a radial ridge on the shell interior, running obliquely posteroventrally from the umbonal area; ventral margin cracked radially in some examples, a feature associated with cracking of the periostracum in Recent species of 'Solemya'.

Remarks   S. woodwardiana occurs as 2 distinct geographical morphotypes in Great Britain, with the type series (SM J6006, J12568-70) holding an intermediate position. In the Lower Oxford Clay of the Midlands, the species occurs as a small, finely striated form up to 17 mm long, whilst in the Athleta Zone shales of Brora, Sutherlandshire, a larger, more coarsely ribbed form, up to 38 mm long, is found. The holotype, and three paratypes, from the "Kelloway Rock" of Scarborough are intermediate in both size and ornament, with a maximum observed length of 25 mm, and the beginnings of coarse radial riblets over the posterior parts of the valves. The early growth lines of the Scottish specimens reproduce the shell form of the

smaller morphotypes from Yorkshire and the Midlands, and in
addition, the early stages are smooth or finely striated,
exactly as in the English forms. The bulk of the evidence, then,
is in favour of uniting these three series of geographically
separated populations into a single variable species, the
variability most probably being environmentally controlled.
Length/height and length/anterior length regression lines (Fig.
2.12) show the close correlation between the three populations.

The radial ridge which delimits the anterior margin of
the posterior adductor scar (Fig. 2.11), originates beneath the
chondrophore in Recent species of 'Solemya', and is usually
confined to forms with a chondrophore, suggesting that in S.
woodwardiana, a chondrophore is present, although it has not
been definitely seen. A specimen from the Lower Oxford Clay of
Wiltshire, presented to the author by Mr. S.R.A. Kelly, shows a
depression on the inner surface of the dorsal margin which may
mark the position of the chondrophore (Fig. 2.13).

The cracking seen at the ventral extremities of the shell
in specimens of S. woodwardiana from Brora may represent a
parallel to the condition seen in Recent Solemya (Solemyarina),
where the ventral margins of the shell are frequently seen to
break along wide radial fissures (Cox, 1969a, p. 242, fig. 2a).
This is associated with radial lines of weakness in the
periostracum, which extends beyond the shell margins in the
Solemyidae.

S. voltzii Roemer (1839, p. 43, pl. 19, fig. 20) from the
L. Toarcian Posidonienschiefer of Germany is closely related, as

noted by Leckenby (1859, p. 14), but appears to be slightly more elongate (AL $\overline{x}$ 71.7%; H $\overline{x}$ 37.7%) than the British forms, and is probably distinct. Roemer mentioned (op. cit.) that the umbones were closer to the anterior (sic) margin than shown in his plate, and so the AL valve should be greater than that measured from his plate. However, the lack of comparative material from the type area, and the uncertainty about the location of the type material, make specific comparison difficult.

Range and occurrence   Common in the L. Oxford Clay of the English Midlands (Jason and Grossouvrei Subzones at Calvert; Grossouvrei Subzone at Bletchley; Obductum and Grossouvrei Subzones at Stewartby, Jason and Grossouvrei Subzones at Norman Cross), where the small, finely-ribbed form is found; the same form also occurs in the Grossouvrei Subzone of Crook Hill brickpit, near Weymouth. The intermediate form is found in the Hackness Rock (Athleta - Lamberti Zones) of Scarborough, Yorkshire, and the large, coarsely-ribbed form in the Athleta Zone Oxford Clay (Brora Brickclay Member of Sykes, 1973, pers. comm.) of Brora, Sutherlandshire. The overall range of the species thus appears to be M - U Callovian (Jason - Athleta Zones).

Subclass PTERIOMORPHIA Beurlen, 1944

Order ARCOIDA Stoliczka, 1871

Superfamily ARCACEA Lamarck, 1809

Family PARALLELODONTIDAE Dall, 1898

Subfamily GRAMMATODONTINAE Branson, 1942

Genus GRAMMATODON Meek & Hayden, 1861 (p. 419)

Synonyms: Pseudomacrodon Stoll, 1934

Type species   Originally designated by Meek & Hayden, 1861,
p. 419, Arca (Cucullaea) inornata Meek & Hayden, 1859, p. 51,
from the L. Jurassic of the Black Hills, Dakota, U.S.A.

Diagnosis   Subrectangular to ovate in form, height
greater than 50% length, umbones placed about 30-35 % behind
the anterior margin; valve flanks smooth or costellate; valve
margins closed; inner margin of hinge plate straight or
slightly curved, with several nearly parallel and horizontal
posterior pseudolaterals, and a series of small, oblique,
cardinals, mainly anterior, converging to a point below the
umbones;

Subgenus GRAMMATODON s.s.

Diagnosis   Umbonal carina well-developed, marking off
a distinctly-ornamented posterior area with closely spaced
radial striae; coarsening of the radial riblets on the
anterior extremity is often present.

Discussion   The generic status of Grammatodon was
discussed by Arkell (1930b), who considered it (together with
Beushausenia) to be a subgenus of Parallelodon, a view which

cannot (as pointed out by Branson 1942, p. 248) be considered valid, as Grammatodon has priority as a name. Thus Branson (op. cit.) unites Grammatodon, Parallelodon and Cosmetodon (nom. nov. pro Beushausenia Cossmann), but considers them as subgenera of Grammatodon. Cox (1940) was followed by Dickins (1963) and Newell (1969) in separating Parallelodon and Grammatodon, a decision based mainly on external dissimilarities, Parallelodon being more elongate, often posteriorly alate and having a well-marked byssal sinus; Parallelodon also has fewer posterior pseudolaterals and anterior cardinals.

1.   Grammatodon (Grammatodon) minima (Leckenby, 1859), Pl. 4, figs. 1-11.

v*   1859   Cucullaea minima sp. nov.; Leckenby, p. 13, pl. 3, fig. 5.

      1881   Macrodon pictum sp. nov.; Milaschewitsch, p. 145 (nom. nov. pro Cucullaea cancellata Rouillier, 1846).

?   1883   M. pictum Milaschewitsch; Lahusen, p. 80, pl. 2, figs. 13a, 13b.

      1905   M. pictum Milaschewitsch; Borissiak, p. 15, pl. 2, figs. 16a-c, 17a-c.

      1905   M. pictum Milaschewitsch; var. a nov.; Borissiak, p. 18, pl. 2, figs. 18a-d.

      1905   M. pictum Milaschewitsch var. b nov.; ibid, p. 18, pl. 2, figs. 19a-c.

      1905   M. pictum Milaschewitsch var. c nov.; ibid, p. 19, pl. 3, figs. 2a, 2b.

      1905   M. pictum Milaschewitsch var. d nov.; ibid, p. 19, pl. 3, figs. 1a-c.

? 1905 <u>M. cf. pictum</u> Milaschewitsch; ibid, p. 17, pl. 3,
        figs. 6a, 6b.

? 1911 <u>Cucullaea sp.</u>; Boden, p. 65, pl. 7, figs. 7, 7a.

   1915 <u>M. pictum</u> Milaschewitsch; Krenkel, p. 309, pl. 26,
        figs. 9, 10.

   1919 <u>Arca (Nemodon) Goldfussi</u> (Roemer); Couffon, p. 68,
        pl. 5, figs. 1-1c.

   1923 <u>Cucullaea couffoni</u> nom. nov.; Cossmann p. 12, pl. 6, figs.
        5-7 (nom. nov. pro <u>A. (Nemodon) Goldfussi</u> Couffon non
        Roemer)

   1930a <u>Parallelodon (Grammatodon) Schourovskii</u> (Rouillier);
        Arkell, p. 340, pl. 15, figs. 7-7b. (non Rouillier).

   1930a <u>P. (G.) pictum</u> (Milaschewitsch); Arkell, p. 341, pl. 15,
        figs. 8-8b.

? 1934 <u>Pseudomacrodon pictum</u> (Milaschewitsch); Stoll, p. 9,
        pl. 1, fig. 12.

<u>Type specimen</u>   Holotype of Leckenby (1859, p. 13, pl. 3,
fig. 5) preserved in the Sedgwick Museum, Cambridge (SM J6007),
together with 1 paratype (SM J12359), both from the 'Kelloway
Rock' of Scarborough, Yorkshire.

<u>Diagnosis</u>   Medium-sized (up to 15 mm L), subrectangular
to subquadrate species (H 62-84%, $\bar{x}$ 73%), with variable but
often high inflation (I 36-76%, $\bar{x}$ 55%); outline extremely
variable, subquadrate to elongate - oval in form; hinge line
length correlates closely with shell height (Lh 66-82%, $\bar{x}$ 73%);
posterodorsal angle varies from 99-120° ($\bar{x}$ 111°); sculpture

dominated by regular concentric riblets, with faint radial
threads over the whole of the valve surface, producing a finely
cancellate pattern; no coarsening of radial threads at the
anterior extremity of the valves, a major point of difference
from most other species of Grammatodon; margin entire; 3-5
horizontal posterior pseudolaterals, 5-7 oblique anterior
cardinals, converging to a point below the umbones.

Measurements

See Appendix 3.

	L	H	I	AL	Lh	<
N	47	47	27	47	46	46
$\bar{x}$	10.3 mm	72.6%	55.1%	41.4%	73.4%	110.9°
Max	14.5	84.3	76.1	50.5	82.1	118
Min	6.0	62.4	36.5	31.0	66.4	99
OR	8.5	21.9	39.6	19.5	15.7	19

Description   Small to medium sized, subrectangular to
subquadrate, inequilateral, equivalve species, with an extremely
variable form; umbones situated between 30-50% of the shell length
behind the anterior margin (AL $\bar{x}$ 41.0%), prominent, inflated and
slightly prosogyrate, salient up to 3 mm above the hinge-margin,
not contiguous; ligament area of variable form, but usually
occurring as an elongate diamond, up to 3 mm wide in very
inflated specimens; area stretches almost the entire length of
the hinge-margin, and is ornamented by chevron-shaped grooves
radiating from beneath the umbones; dorsal margin straight to
slightly concave, often having the anterodorsal angle protruding

above the general level of the dorsal margin; anterior margin
very strongly convex, its anteriormost point lying anterior to
the anterodorsal angle, curving evenly into the gently convex
to straight ventral margin; form of the ventral margin depends
on shell length, being evenly curved with the anterior margin in
short forms, and becoming straight, but not parallel to the hinge-
margin, in more elongate forms; in elongate forms, the ventral
margin is oblique to the hinge margin, and if extended, would
meet the hinge-margin at a distance of about $1\frac{1}{2}$ x shell length
behind the posterodorsal angle; posterior margin obliquely
truncate and very slightly convex, meeting the ventral margin at
the prominent, but rounded, posteroventral angle; posterodorsal
angle variable from $99-120^{\circ}$ ($\overline{x}$ 111°), tending to be greater
in the more elongate forms; umbonal carina present, of variable
sharpness depending on valve inflation, more inflated forms
having more rounded carinae, and forms with low inflation having
more angular carinae; sculpture distinctive, with concentric
riblets dominant over rather faint radial striae, which become
slightly stronger anteriorly and posteriorly, giving a very
finely cancellate pattern over the whole of the shell; there is
no marked coarsening of the radial striae on the anterior or
posterior extremities; margin entire, and not crenulated;
adductor scars suborbicular, subequal, not raised on buttresses,
and placed close to the hinge plate; pallial line entire;
dentition of typical Grammatodon type, with 3-5 horizontal
posterior pseudolaterals, and 5-7 oblique anterior cardinals
converging on a point beneath the umbones (Fig. 2.14); dorsal

and ventral margins of all teeth are very finely crenulate.

Remarks   G. minima is a very distinctive species, whose main diagnostic features are the subquadrate form, and the finely cancellate ornament pattern. Leckenby's holotype (SM J6007) is a well-preserved left valve which shows the ornament particularly well; on the same slab is a paratype (un-numbered) showing more closely-packed concentric riblets, and allowing examination of the ligament area. Both specimens agree closely with the abundant material from the Lower Oxford Clay, and there can be no doubt that they are conspecific.

G. minima is identical to the species from the Oxfordian of Russia whose variation has been discussed at length by Borissiak (1905, p. 49), and which was placed by him in M. pictum Milaschewitsch. Borissiak recognised five varieties of M. pictum, based on slight differences in outline, inflation and position of the umbones, occurring in beds dated as Oxfordian - Sequanian at several localities. Exactly the same range of variation may be seen in the British material, collected mainly at Calvert and Stewartby, where the great abundance of the species allows detailed study of the variation to be made. Whereas Borissiak found that two of his varieties (var. c. and var. d.) were apparently restricted to deposits of 'Sequanian' age, specimens fitting with all his varieties may be found together in the same bed in Britain, suggesting that variation is continuous, and not stratigraphically controlled. In the Lower Oxford Clay of the English Midlands, G. minima appears quite · suddenly at the base of the Grossouvrei Subzone (Coronatum Zone),

invariably in great numbers, and study reveals that continuous variation does occur, giving a species of very diverse form, and which it is not advisable to split into stratigraphical subgroups. Study of pl. 4 and the statistical data (Appendix 3) reveal the range of variation of the species, the most variable characters (inflation and anterior length) having high values of V and s^2.

The most marked difference between individuals is in degree of inflation, very tumid and very flat specimens being found side by side, and if large samples were not available, it is likely that Borissiak's classification would be accepted. The degree of inflation has a profound effect on the width and shape of the ligament area, wider, rather triangular areas occurring in very tumid specimens, whilst specimens of low inflation usually have areas of lanceolate form. It is also noticeable that it is only the very inflated forms (I > 60%) which show the development of an obliquely elongate ventral margin, more subquadrate forms usually being considerably less inflated. Examination of the very inflated forms reveals that it is only in the late stages of growth that high inflation and obliquity develop, the latest-formed parts of the shell being very steep-sided, together with the relatively rapid expansion of the anterior parts of the shell. The most obvious difference between the specimens described by Borissiak and the British forms, is one of maximum size; the largest British specimen known is 14.5 mm long, whilst the maximum size of Borissiak's specimens is 23 mm. However, all other parameters have the same

range of proportions as the British specimens, and the most likely explanation is that the Russian forms are larger due to genetic or ecological effects.

A good deal of variation in the strength of the fine radial striae occurs in G. minima, there being a gradation from forms where the flanks of the shell are almost devoid of radial elements to forms in which radial striae are much more obvious, and a clear cancellate pattern is developed. There is no apparent correlation between strength of radial striae and any other shell parameter, cancellate development occurring in each morphotype to varying degrees. All specimens share, however, the lack of conspicuous radial riblets on the anterior extremities, although there is slight coarsening of the striae anteriorly and posteriorly. This is in direct contrast to most other Jurassic species of Grammatodon, including G. concinna and G. montaneyensis, which usually have up to 6 prominent anterior radial riblets. The same is true of the posterior area, which in other species of Grammatodon is usually ornamented with 12-15 coarsened radial striae, whilst in G. minima, although there is slight coarsening of the radial striae on the posterior area, they are still very fine, and need to be examined under the microscope.

Borissiak's description and figures suggest that Russian forms of the species have more prominent radial sculpture over the whole shell, although a good deal of variation may be seen from his figures. In view of the variation in strength of ornament to be found in British forms, it seems most unlikely that this feature is of use in specific separation of collections

from the two areas, and when all the other similarities are taken into account, there can be little doubt that the Russian and British forms belong to the same species.

The specimen figured by Lahusen (1883, p. 80, pl. 2, figs. 13a, 13b) as M. pictum appears also to be decorated with rather prominent radial striae, which are coarsened over the anterior and posterior areas, and there is some doubt as to whether or not his identification is correct.

Stoll (1934, p. 9) erected the new genus Pseudomacrodon, with Macrodon pictum Milaschewitsch as type, on the premise that the dentition is not that of Macrodon (now known as Parallelodon) or Cucullaea, although it is closer to the former. Pseudomacrodon is synonymous with Grammatodon.

Range and occurrence Abundant in the Lower Oxford Clay (Grossouvrei Subzone) of Central and Southern England (found at Weymouth, Calvert, Bletchley, Stewartby and Norman Cross at this level), sometimes also occurring as rare individual specimens in the Jason and Obductum Subzones at these localities: Hackness Rock (Athleta - Lamberti Zones) of Scarborough, Yorkshire, the type locality.

On the continent, it has been recorded from the Callovian of Maine-et-Loire and Deux-Sevres (France) by Couffon (1919) and Cossmann (1922); the M. Callovian of Pommerania (Stoll, 1934); the "M.-U. Kelloway, Jason - Ornaten horizont" (Jason - Coronatum Zones) and "Lamberti - Schichten" (Lamberti Zone) of Popilani, Russia (Krenkel, 1915); the Cordatum Zone of Russia (Lahusen, 1883; Boden, 1911), and the "Oxfordien und Sequanien"

of Central Russia (Borissiak, 1905).

Thus the overall range in Britain and N.W. Europe appears to be Jason - Lamberti Zones, whilst in Russia it continues to the top of the Oxfordian.

2,   Grammatodon (Grammatodon) concinna (Phillips, 1829)

        Pl. 4, figs. 12-21.

v*   1829 Cucullaea concinna sp. nov.; Phillips, pl. 5, figs.
             9, 31 (?).

.   1850 Arca gnoma sp. nov.; d'Orbigny, p. 339, no. 186.

v.non 1853 Cucullaea concinna Phillips; Morris & Lycett, p. 50,
             pl. 5, fig. 7. /= Grammatodon bathonicus Cox & Arkell7

.?   1856 Cucullaea concinna Phillips; Quenstedt, p. 504, pl. 67,
             figs. 15, 16.

non   1882 C. cf. concinna Phillips; Roeder, p. 64, pl. 1, figs.
             5a-5e.

        1883 C. concinna Phillips; Lahusen, p. 86, pl. 2, fig. 17.

        1897 Arca (Macrodon) concinna (Phillips); de Loriol, p. 109,
             pl. 14, figs. 5-11.

?   1899 A. (Macrodon) concinna (Phillips); de Loriol, p.
             pl. 10, figs. 6-6a, 7-7a.

        1901 A. gnoma d'Orbigny; Raspail, p. 194, pl. 11, fig. 10.

?   1919 A. (Nemodon) gnoma d'Orbigny; Couffon, p. 68, pl. 5,
             figs. 2-2c, 3-3b.

non   1919 A. (Beuschausenia) concinna (Phillips); Couffon, p. 71,
             pl. 5, figs. 6-6c.

        1923 Parallelodon gnoma (d'Orbigny); Cossmann, p. 14, pl. 6,
             figs. 8-12.

1925 <u>A. gnoma</u> d'Orbigny; Cottreau, p. 23, pl. 40, figs. 8, 9

    (non figs. 10, 11).

. 1930a <u>Parallelodon (Grammatodon) concinnum</u> (Phillips); Arkell,

    p. 341, pl. 15, figs. 2-4.

v.? 1972 <u>G. concinnus</u> (Phillips); Walker, p. 118.

<u>Type specimen</u>   Holotype of Phillips (1829, pl. 5, fig. 9) is preserved in the Phillips collection at the Yorkshire Museum, York (Tsp 135), from the Oxford Clay (Mariae Zone), near Scarborough, Yorkshire. A clay steinkern.

<u>Diagnosis</u>   Moderately elongate <u>Grammatodon</u> (H $\bar{x}$ 62.1%) with a prominent umbonal carina; posterior area ornamented by 12-15 fine radial striae, anterior area with 3-5 coarse radial riblets; the striae are often developed over the flanks of the shell, being more elevated towards the posterior; ventral margin smoothly convex, curving evenly into the anterior margin, posterior margin oblique, with a clear posterodorsal angle ($\bar{x}$ 106°).

<u>Description</u>   Equivalve, inequilateral, umbones placed anterior of median (AL 32.6-45.7%, $\bar{x}$ 39%); large sized shells (up to 24 mm L), obliquely subrectangular in outline (H 52.2-73.5%, $\bar{x}$ 62.1%), with a long straight hingeline occupying nearly the whole length of the shell (Lh 69.4-96.8%, $\bar{x}$ 83.2%); umbones small, prosogyrate, distinctly salient to the hingeline (up to 3 mm) and not contiguous (up to 3 mm separation observed); straight dorsal margin truncated anteriorly by the sharp anterodorsal angle, approximating a right angle; anterior and

ventral margins evenly and convexly curved, meeting the oblique posterior margin at the ventral end of the umbonal carina and forming the acute posteroventral angle; posterodorsal angle obtuse (92-126°, $\overline{x}$ 106°). Sharply defined umbonal carina runs from the posterior side of the umbones more or less directly to the posteroventral angle, marking off the radially striated posterior area (12-15 striae); flanks of the shell often ornamented by fine radial striae, giving a finely cancellate pattern where they cross the growth lines; 3-5 coarse, widely-spaced radial riblets diverge from the anterior side of the umbones, and are separated by intercalatory fine radial striae. Inflation moderate (40.0-64.8%, $\overline{x}$ 56.0% for both valves). Ligament duplivincular, cardinal area broad, widening with age, well-defined and ornamented with chevron-shaped grooves radiating from beneath the umbones.

Dentition taxodont, teeth radiating upwards from a point immediately beneath the umbones, the anterior series being short and oblique, while the posterior series flex over and run subparallel to the hinge margin. Margins entire, not crenulated. Musculature not seen.

Measurements

See Appendix 3.

	L	H	AL	(2 valves) I	Lh	Posterodorsal <
N	37	37	37	12	35	36°
$\overline{x}$	17.3 mm	62.1%	39.0%	56.0%	83.2%	106°
Max	24.0	73.5	45.7	64.8	96.8	126°
Min	14.0	52.2	32.6	40.0	69.4	92°
OR	10.0	21.3	13.1	24.8	27.4	34°

Remarks   Etheridge (1875, p. 326), in the 3rd edition

of Phillips 'Geology of Yorkshire', claimed that the holotype of

G. concinna was in the Bean collection, although the specimen

in the Yorkshire Museum labelled as the holotype bears a label

referring it to the Reed collection. There is thus some doubt

as to the authenticity of the supposed holotype, although the

specimen bears a label in Phillips handwriting, and agrees with

the original figure. The balance of evidence seems to suggest

that Etheridge's record was in error. Phillips paratype from

the 'Kelloway Rock' (1829, pl. 5, fig. 31), an indeterminate

steinkern, is not in the Phillips collection at York, and must

be considered lost.

          G. concinna is a very variable species (see Appendix 3),

as may easily be seen from study of populations from Yorkshire

and the English Midlands. The holotype, and all other topotypes

seen, are steinkerns with no preserved shell material, so

relationships with shelled specimens are rather difficult to

establish with certainty, but the external form measurements, and

ornament of the Yorkshire specimens agree well with those from

the Lower Oxford Clay of central and southern England, with

which they are united here. The most notable difference between

the two populations is in the value of the posterodorsal angle,

the Yorkshire specimens having a slightly greater angle (110-120°)

than the central England ones (92-126°). Other measurements are

more or less equally variable (Appendix 3), with overlap between

the two regions. Within the Midlands population, strength of

cancellate ornamentation on the flanks of the shell is the most

variable feature, some specimens having virtually no radial striae whilst others have a strongly cancellate pattern. In all specimens, however, the anterior and posterior radial riblets and striae remain clearly defined. The presence of the anterior and posterior riblets and striae on the Yorkshire steinkerns suggest that they are in fact composite internal and external moulds, but no evidence of radial striae on the flanks is apparent.

Cottreau's (1925) figures of d'Orbigny's types, preserved in the Institut Paleontologique du Musee Nationale d'Histoire Naturelle in Paris, leave no doubt that Arca gnoma d'Orbigny is synonymous with G. concinna. Cottreau also suggested (op. cit., p. 23) that A. gnoma is merely a juvenile form of A. galathea d'Orbigny (1850, p. 339, no. 183), as both species occur together, with similar preservation, at Villers-sur-Mer, A. gnoma being consistently smaller and having finer (but similar) ornament. Study of the specimens in question (d'Orbigny colln. numbers 3358 and 3359 respectively) reveals that A. galathea has a considerably different shape to A. gnoma, and is probably a Cucullaea. A. gnoma Couffon (1919) lacks anterior radial riblets, and cannot be considered synonymous.

The specimens figured by Morris & Lycett (1853) as Cucullaea concinna, from the Great Oolite (Bathonian) of Gloucestershire, differ from the Oxford Clay species in being more subrectangular in outline, and having distinct regular concentric ornament. This species was renamed G. bathonicus by Cox & Arkell (1948), and both the holotype (GSM 49029) and three

topotypes (GSM 9465, 83402, 83403) are preserved in the
Geological Survey Museum, London. Walkers (1972) figure of
G. concinnus from the Kellaways Rock of South Cave (Yorkshire)
show a specimen with subparallel anterior and posterior tooth
rows, suggesting closer affinities with Cucullaea. Study of
Walkers specimens, preserved in the Hull University Geology
Department supports this view.

Range and occurrence   Kellaways Rock to Lower Oxford Clay
(Calloviense to Jason Zones) of central and southern England;
Kellaways Rock of Yorkshire (Walker); Oxford Clay (Mariae Zone)
of Yorkshire (the type area); Callovian - Oxfordian of France,
Germany, Switzerland and Poland.

3.   Grammatodon (Grammatodon) montaneyensis (de Loriol, 1901)
       Pl. 4, figs. 22-24.

.   1850 Arca hersilia sp. nov.; d'Orbigny, p. 368, no. 343
          (nom. nud.)

.? 1888 A. Quenstedtii nom. nov.; Lycett in Damon, pl. 2, fig. 9.
          (nom. nov. pro A. aemula Quenstedt, non Phillips)

*   1901 A. (Macrodon) montaneyensis sp. nov.; de Loriol, p. 83,
          pl. 5, figs. 12-14.

.   1919 Arca (Beushausenia) concinna (Phillips); Couffon, p. 71,
          pl. 5, figs. 6-6c. (non Phillips)

.   1927 A. hersilia d'Orbigny; Cottreau, p. 59, pl. 47, figs. 12,13.

.   1930a Parallelodon (Grammatodon) montaneyensis (de Loriol);
          Arkell, p. 341, pl. 15, fig. 6.

<u>Type specimen</u>   Lectotype designated herein, the specimen
figured by de Loriol (1901, pl. 5, fig. 12) as <u>Arca (Macrodon)</u>
<u>montaneyensis</u> sp. nov., from the Oxfordian of Montaney.
Specimen preserved in the Polytechnicum à Zurich.

<u>Diagnosis</u>   Large subrectangular <u>Grammatodon</u> (up to 28
mm L) with a prominent umbonal carina; posterior area
ornamented by 6-8 radial riblets, with faint intercalated
secondaries, anterior area ornamented by 4-6 coarse radial
riblets; flanks of the shell covered by regular radial striae,
occasionally becoming obsolete; ventral margin subparallel to
dorsal margin, anterior and posterior margins also subparallel,
giving some specimens a rather rhomboidal outline.

<u>Measurements</u>

See Appendix 3.

	L	H	I	AL	Lh	posterodorsal ∢
			(2 valves)			
N	5	5	4	5	5	5
$\overline{x}$	23.8 mm	63.0%	58.0%	38.5%	85.8%	108.8°
Max	28.0	66.7	62.8	42.9	91.1	116
Min	20.0	58.8	55.0	35.3	80.0	99
OR	8.0	7.9	7.8	8.6	11.1	17

<u>Description</u>   Equivalve, inequilateral, with umbones
situated anterior of median (AL 35.3-42.9%, $\overline{x}$ 38.5%); outline
subrectangular (H 58.8-66.7%, $\overline{x}$ 63.0%), with most of the length
being occupied by the long straight hingeline (Lh 80.0-91.1%,
$\overline{x}$ 85.8%); hingeline meeting the oblique posterior margin at the

obtuse posterodorsal angle (99-116°, $\overline{x}$ 108°); posteroventral angle well-marked, about a right angle, located at the point where the umbonal carina reaches the ventral margin; anterodorsal angle about a right angle, anterior margin curving evenly into the straight to slightly convex ventral margin, itself sub-parallel to the dorsal margin. Umbones inflated, prosogyrate, anterior of median, salient up to about 3 mm above the hingeline, not contiguous. Umbonal carina delimits the posterior area, which is ornamented with 6-8 radial riblets and faint inter-calatories; the anterior parts of the valves are covered by 4-6 coarse radial riblets, diverging from beneath the umbones; flanks of the shell covered by regular radial striae which continue onto the anterior and posterior areas as the intercalatories; concentric growth lines of variable strength, occasionally showing marked growth halts. Overall inflation of both valves about equal to that of G. concinna (I 55.0-62.8%, $\overline{x}$ 58.0%), giving a rather tumid shell, with maximum inflation slightly ventral of the hinge line. Ligament duplivincular, cardinal area broad (widening with growth), ornamented by chevron-shaped grooves radiating from beneath the umbones.

Dentition taxodont, with short oblique anterior cardinal teeth and long posterior pseudolaterals subparallel to the hinge margin; point of origin of the teeth is below the umbones, and the teeth radiate upwards. Margins entire, not denticulate. Musculature not seen.

Remarks   The first record of this species is attributable to d'Orbigny (1850) in the Prodrome, but his

description was not diagnostic, and not being accompanied by a figure, must be considered as a nomen nudum. The species was validated by Cottreau in 1927, but by then, the species had already been described under another name by de Loriol (1901), accompanied by a recognisable description and figures, and so de Loriol's name must stand. There are similarities in general form between this species and G. concinna, as is apparent from comparison of the measurement tables and the regression lines (Fig. 2.15) although G. montaneyensis is slightly more rectangular. The main differences concern the position of the posteroventral angle, which in G. montaneyensis is not the most ventral part of the shell, the greater tendency for the ventral margin of G. montaneyensis to be parallel to the hinge line, and the much more regular radial striae on the flanks of the latter species. The differences between these two species are not great, as is seen above, but none of the British specimens of G. concinna approach the subrectangular outline of G. montaneyensis, nor do they show such regular ribbing. However, a specimen assigned to G. concinna, from the Kellaways Rock of Sutton Benger, Wilts. (GSM Zr 1699), occurs in association with two specimens of G. montaneyensis at the same locality (GSM Zr 1698, 1700), and it is possible that G. montaneyensis is merely an extreme variant of G. concinna. The differences in riblet and striae density on the anterior and posterior areas remain, however, and until further specimens become available, the two species will be considered to be separate.

Arca subtetragona Morris (1850, p. 318, pl. 30, figs. 5-5b),

from the Kellaways Rock of Wiltshire, resembles G. montaneyensis

in its strongly rectangular outline, but is not as elongate, and

lacks the radial striae on the flanks of the shell. The

specimen figured by Morris is lost, and no comparable specimens

are preserved in any of the major museums, so the status of

this species must remain uncertain. Arca Quenstedtii Lycett in

Damon (1888), from the Oxford Clay of Weymouth raises similar

problems, as it closely resembles A. subtetragona, differing

only in the possession of regular radial striae on the flanks

of the shell. In this respect, the similarities between

A. Quenstedtii and G. montaneyensis are very close, but again,

Lycett's figured specimen is lost, and the exact status of the

former species must remain in doubt.

Range and occurrence   Kellaways Rock (Calloviense Zone) of

Wiltshire, and possibly the Lower Oxford Clay (Jason Zone) of

central England (Stewartby). Oxfordian of France and Switzerland.

4.   Grammatodon (Grammatodon) clathrata (Leckenby, 1859).
        Pl. 4, figs. 25-26, Pl. 5, figs. 1-4.

v* 1859 Cucullaea clathrata sp. nov.; Leckenby, p. 13, pl. 3,
          fig. 4.

v. 1863 C. clathrata Leckenby; Lycett, p. 44, pl. 39, figs. 4, 4a.

.   1867 C. clathrata Leckenby; Laube, p. 34, pl. 2, fig. 11.

.   1905 C. cf. clathrata Leckenby; Borissiak, p. 56, pl. 3,
          figs. 15, 15a.

.   1948 C. clathrata Leckenby; Cox & Arkell, p. 2. (pars).

Type specimen   Holotype of Leckenby, 1859, pl. 3, fig. 4,
a left valve from the Hackness Rock (Athleta - Lamberti Zones)
of Castle Hill, Scarborough, Yorkshire, preserved in the
Leckenby collection at the Sedgwick Museum, Cambridge (SM J6005).

Diagnosis   Large elongate Grammatodon (H $\bar{x}$ 60.9%),
rather variable in form, up to 50.7 mm long;   inflation moderate
($\bar{x}$ 48.6%), umbones anterior of median (AL $\bar{x}$ 35.4%);   hingeline
shorter than in other species (Lh $\bar{x}$ 72.0%), posterodorsal angle
larger ($\bar{x}$ 135°);   ornament finely cancellate, with wider,
flatter radial riblets over the posterior parts of the shell.
Differs from 'Cucullaea' contracta Phillips by virtue of being
more elongate, less inflated, and lacking the coarsened radial
ornament on the anterior flank, having instead coarse flattened
radial posterior ribs.

Description   Equivalve, inequilateral species, of large
size (up to 50.7 mm L) and subtrapezoidal outline (H 53.9-66.7%,
$\bar{x}$ 60.9%), with the umbones placed 27.5-40.2% of shell length
($\bar{x}$ 35.4%) behind the anterior margin;   umbones inflated,
prominent, prosogyrate, salient up to about 4 mm above the hinge-
line, not contiguous. Hingeline straight, relatively short
(Lh 68.4-76.6%, $\bar{x}$ 72.0%), meeting the obliquely truncate
posterior margin at an angle of about 135° (posterodorsal angle
126-140°, $\bar{x}$ 135°);   anterior margin evenly curved, meeting the
dorsal margin at an obtuse angle of between 100-120°, passing
smoothly into the ventral margin, which is itself subparallel
to the hingeline;   posteroventral angle acute, marking the point

at which the rounded umbonal carina reaches the ventral margin.
Ornament consists of fine radial riblets over the anterior and
median parts of the valves, becoming wider and flatter over the
posterior regions; fine concentric growth lines produce a
cancellate pattern where they cross the costellae. Ligament
duplivincular, cardinal area diamond-shaped and clearly-defined,
ornamented with chevron-shaped grooves diverging from beneath
the umbones. Inflation moderate (I 40.0-56.8%, $\overline{x}$ 48.6%).

Dentition taxodont, with the pseudolaterals being
subparallel to the hingeline at both ends of the hingeline, and
having fine crenulations running vertically up their dorsal and
ventral faces. Margin entire, with no denticulations. Adductor
muscle scars subequal in size, the posterior scar slightly the
larger, but not being raised on a myophoric buttress; scars
ovate, placed beneath the anterior and posterior ends of the
hingeline; pallial line entire.

Measurements

See Appendix 3.

	L	H	I	Al	Lh	posterodorsal ∢
N	9	9	9	8	7	8
$\overline{x}$	33.3 mm	60.9%	48.6%	35.4%	72.0%	135.5°
Max	50.7	66.7	56.8	40.2	76.6	140
Min	23.5	53.9	40.0	27.5	68.4	126
OR	27.2	12.8	16.8	12.7	8.2	14

Remarks   The variability of G. clathrata may be seen
from the table of measurements and the plates, and agrees in

this respect with Arkell's (1929, p. 42) description of
'Cucullaea' contracta Phillips from the Corallian, a species
which it resembles in form. The dentition and musculature of
'C'. contracta are not known, so its exact generic position is
uncertain. These two are, however, distinct species, differing
in form and ornamentation, as noted in the diagnosis above.
'C'. contracta has an average height of 72.7%, and an inflation
of 65.2%, both considerably higher than in G. clathrata. The
specimens from the Lower Oxford Clay of Stewartby and Chippenham
(GSM 113414) are less inflated than the Yorkshire Cornbrash and
Hackness Rock specimens, and very similar in all other respects,
so it is likely that these differences are merely ecologically
or geographically controlled.

The pyritised valves from Stewartby allow close examination
of the dentition and ligament areas, and show them to be of
rather abnormal grammatodontinid type. Both the anterior and
posterior pseudolaterals are horizontal, with very little
evidence of either central vertical teeth, or oblique anterior
pseudolaterals. In this respect they are very similar to the
condition seen in the Cucullaeidae, although the pseudolaterals
are somewhat shorter and more massive in that family. However,
in the other typically cucullaeid features, such as a prominent
series of central subvertical teeth, a prominent posterior
myophoric buttress, and a subquadrate outline, G. clathrata is
notably lacking, and the balance of evidence favours placement
within the Grammatodontinae. It should be noted that this is
the first occasion on which the species has been placed in this

family, previous authors having referred it to Cucullaea on the

basis of its external form and ornament. The ornament pattern

differs from that of a 'typical' grammatodontinid in that it

lacks the strengthened anterior and posterior radial striae

seen so often in the subfamily, and in this respect, agrees well

with G. minima. The good state of preservation also allows

recognition of the finely crenulated sides of the pseudolaterals,

a feature which gives tighter interlocking of the two valves.

Many British and Continental species of 'Cucullaea'

closely resembling G. clathrata have been described in the

literature, although it is doubtful whether they are in fact

true cucculaeids. Arca harpax d'Orbigny (1850) was shown by

Cottreau (1928, p. 57, pl. 47, figs. 4-6) to be superficially

close to G. clathrata, and have similar Cucullaea-like dentition.

However, Arkell (1935, p. vii) united A. harpax and A. halie

d'Orbigny (1850) in C. contracta Phillips, as he could recognise

overlap in the variation ranges of the three species, and all

were of Oxfordian age. The French Oxfordian specimens agree

with the English specimens of 'C'. contracta in being more elongate

and less inflated than G. clathrata. C. cancellata Phillips

(1829, pl. 9, fig. 24) from the Scarborough Limestone (Bathonian)

of Yorkshire is also closely related, but study of topotypes in

the Yorkshire Museum reveals that the radial ornament is

virtually obsolete, and the posterior margin is more truncate

than oblique. Also, elongation is considerably less.

Cox & Arkell (1948, p. 2) unite Lycett's (1963) figures

of C. corallina Damon (p. 43, pl. 39, fig. 3) and G.clathrata

Leckenby (p. 44, pl. 39, fig. 4) in C. clathrata, together with
C. corallina Lycett in Damon of Laube (1867). The originals of
Leckenby's figures are preserved in the Sedgwick Museum
Cambridge (SM J5670, J5669 respectively), and appear to
represent two distinct species, vindicating Lycett's
identifications. In addition to SM J5670, from the Cornbrash of
Yorkshire, there are four specimens of C. corallina from the
Yorkshire 'Kelloway Rock' in the Sedgwick Museum (SM J12360-
J12363), all of which are clearly distinct from G. clathrata.
They agree well with Arkell's (1929, p. 42) conception of
C. contracta Phillips (of which C. corallina Lycett in Damon is
a junior synonym) in form and ornamentation. In the absence of
specimens transitional between G. clathrata and 'C'. contracta,
it seems best to extend the range of 'C'. contracta down to the
Cornbrash, so as to include the Yorkshire Cornbrash and 'Kelloway
Rock' forms. C. corallina Laube (1867, p. 34, pl. 2, fig. 11)
fits into the extended range of the species.

Range and occurrence Cornbrash, Scarborough (the paratypes);
Lower Oxford Clay (Medea Subzone, Jason Zone), Stewartby;
Hackness Rock (Athleta - Lamberti Zones), Scarborough (the type
locality); Oxford Clay, Chippenham, Wilts. (horizon unknown).

Order MYTILOIDA Ferussac, 1822
Superfamily MYTILACEA Rafinesque, 1815
Family MYTILIDAE Rafinesque, 1815
Subfamily MODIOLINAE Keen, 1958

Genus MODIOLUS Lamarck, 1799 (p. 87) nom. subst. pro Volsella

Scopoli, 1777 (ICZN Opin. 325, 1955).

Synonymy: Modiola Lamarck, 1801

Perna Adams & Adams, 1858

Eumodiolus Ihering, 1900

Nudiola Monterosata, 1917

Type species   Subsequently designated by Gray, 1847, p. 198,
Mytilus modiolus Linnaeus, 1758, p. 706, Recent, European seas.

Diagnosis   Shell more or less trapeziform in outline,
usually transversely elongate, with angle of obliquity usually
less than 45°; inflation variable; anterior margin usually
convex, protruding in front of the umbones, which are never
terminal; anteroventral region expanded, usually marked off
from the body of the shell by a rounded ridge running from the
umbones to the posteroventral margin; hingeline smooth, lacking
teeth; ligament external, long; shell smooth, or with
concentric ornament.

Subgenus MODIOLUS s.s.

Diagnosis   Shell transversely elongate, well-inflated,
umbonal region frequently prominent and inflated; diagonal
bounding ridge of the anteroventral area well-defined; shell
smooth, sometimes with weak concentric plications; periostracum
hirsute in Recent specimens.

Remarks   After introducing Modiolus in 1799, Lamarck

decided two years later (1801, p. 113) to amend the name to

Modiola, the latter name then becoming generally accepted by

himself and later workers. However, priority must take

precedence over usage, and the ICZN ruling of 1955 (Opinion 325)

declared Modiola to be invalid, thus reintroducing Modiolus into

general acceptance.

Modiolus is a very long-ranging genus (Devonian - Recent),

in which several subgenera have been distinguished, all (except

Gibbomodiola Sacco /Oligocene - Recent7) of Recent age. The

fossil species of Modiolus do not readily lend themselves to

subgeneric classification, and most are left in Modiolus s.s.

(Cox, 1940, p. 63). The status of Modiolus, and its relationship

with Mytilus and other Mytilidae, is discussed by Cox (1937,

p. 339).

Modiolus (Modiolus) bipartitus J. Sowerby. Pl. 5, figs. 5-12.

v* 1818 Modiola bipartita sp. nov.; J. Sowerby, 3, p. 17,
          pl. 210, fig. 4 (non fig. 3).

.   1829 M. bipartita J. Sowerby; Phillips, pl. 4, fig. 30.

.   1860 M. bipartita J. Sowerby; Damon, pl. 2, fig. 12.

.   1860 M. cuneata J. Sowerby; Damon, pl. 2, fig. 13 (non J.
          Sowerby).

.   1871 M. bipartita J. Sowerby; Phillips, pl. 13, fig. 25.

?   1901 M. Villersensis (Oppel); Raspail, p. 193, pl. 12, fig. 10.

.   1911 M. aequiplicata Strombeck; Boden, p. 68, pl. 7, figs.
          13, 13a only.

.   1915   M. tulipaea Lamarck; Cossmann, p. 10, pl. 5, fig. 10.

v. 1928   M. bipartita J. Sowerby; Douglas & Arkell, p. 174,

           pl. 12, figs. 8, 9.

v. 1929   M. bipartita J. Sowerby; Arkell, p. 55, pl. 2, figs. 1-4.

?   1934   M. aequiplicata Strombeck; Stoll, p. 23, pl. 2, fig. 29.

v. 1940   M. cf. bipartitus J. Sowerby; Cox, p. 67, pl. 5, figs.

           11, 12.

.   1948   Modiolus bipartitus J. Sowerby; Cox & Arkell, p. 4.

    1952   Modiola aequiplicata Strombeck; Makowski, p. 18, pl. 1,

           fig. 15.

<u>Type specimen</u>   Lectotype, designated by Arkell, 1929, p. 56,
the specimen figured by J. Sowerby, 1818, p. 17, pl. 210, fig. 4,
from the Oxford Clay, Osmington, Dorset, as <u>Modiola bipartita</u>,
preserved in the Sowerby Colln. at the BM (NH), specimen no.
BM 43231.

<u>Diagnosis</u>   Large species (up to 70 mm L), elongately
oblique (θ about 30°), height very variable (H 66.0-100.2%, $\overline{x}$
77.6%); hingeline about half the length of the shell (Lh 35.7-
58.0%, $\overline{x}$ 45.4%), straight to very gently convex, passing via a
rounded posterodorsal angle into the long, gently convex
posterior margin; anterior margin short, truncate, slightly
convex, the anteroventral angle variable rounded, about a right
angle, passing into the sinuate ventral margin, which is often
subparallel to the posterior margin; umbones subterminal, small,
prosogyrate, their tips enrolled; umbonal ridge runs from the
umbones in a straight line towards the posteroventral angle,

marking off the bulging anteroventral area; inflation equal to about half the length of the shell (I 39-54.5%, $\overline{x}$ 45.8%), at a maximum in the central part of the body of the shell, not along the umbonal ridge; ornament of concentric growth lines, locally raised into growth rugae, not imbricate.

Measurements

See Appendix 3.

	L	H	I	Lh
N	29	29	25	26
$\overline{x}$	50.1 mm	77.6 %	45.8 %	45.4 %
Max	70.0	100.2	54.5	58.0
Min	36.5	66.0	39.0	35.7
OR	33.5	34.2	15.5	22.3

Description   Medium to large sized, equivalve, markedly inequilateral and oblique, umbones subterminal; elongate elliptical to subtrapezoidal in outline, very variable in relative proportions of length and height (H 66.0-100.2%, $\overline{x}$ 77.6%). Hinge line long, about half the length of the shell (Lh $\overline{x}$ 45.4%), straight or gently convex, reaching anteriorly to the umbones; anterior margin short, obliquely truncate, convex, the anteroventral angle varying from a sharply-rounded right angle to a continuous smooth curve, passing into the gently convex anteroventral margin; the ventral margin becomes gently concave in the region where the umbonal sulcus reaches the margin, then straightens out posteriorly and becomes convex again, passing evenly into the sharply convex, semicircular,

posteroventral angle; posterior margin meeting the hinge line at a variably rounded angle of about 150°, the margin itself being obliquely elongate and gently convex, often subparallel to the posteroventral margin, passing smoothly into the posteroventral angle. Umbones small, pointed, subterminal, prosogyrate, their tips tightly enrolled, salient up to about 5 mm above the hinge margin. A rounded ridge runs from the apex of the umbones in a more or less straight line to the anterior side of the postero-ventral angle, dividing the inflated body of the shell from the small, trigonal, anteroventral region of the shell; a prominent rounded depression runs along the anteroventral side of the umbonal ridge; the anteroventral region bulges prominently anteriorly, and attains its maximum inflation near the anterior margin; maximum inflation of the body of the shell ($I \; \overline{x} \; 45.8\%$) occurs in the median region of the shell, not along the umbonal ridge. Ornament consisting of irregularly spaced concentric growth lines, locally coarsened and elevated as growth rugae; no imbricate ornament.

Ligament elongate, external, opisthodetic, parivincular, nymphs long, parallel to the hinge line. Hinge teeth absent. Musculature and pallial line not visible.

Remarks   The synonomy of this very common Upper Jurassic species has been discussed by Arkell (1929, p. 56) and Cox (1940, p. 68), and little need be added to their conclusions. Arkell showed that the holotype of Modiola tulipaea Lamarck (refigured by de Loriol, 1897, pl. 15, fig. 1-3) agrees perfectly with that of M. bipartita J. Sowerby, thus simplifying the

continental usage considerably. The holotype of <u>Mytilus halesus</u>
d'Orbigny, from the Callovian of Pas-de-Jeux, figured by
Cottreau (1925, pl. 40, fig. 21-22) is a poorly preserved
specimen which seems close to <u>M. bipartitus</u>, but more topotype
materials needs to be examined before definite conclusions can
be drawn. The specimen figured by Corroy (1932, op. cit.) as
<u>Modiola holesa</u> (d'Orbigny), from the L. Callovian of the Paris
Basin, agrees perfectly with topotypes of <u>M. bipartitus</u>, as does
the specimen figured by Makowski (1952, op. cit.) from the M.
Callovian of Lukow as <u>Modiola aequiplicata</u> Strombeck. Several
topotypes of Makowski's species have been generously presented
to the author by Dr. A. Radwanski of Warsaw University, and
show, without any doubt, that the species is identical to
<u>M. bipartita.</u>

 <u>M. aequiplicata</u> Strombeck, a species usually recorded
from the Oxfordian and Kimmeridgian of Europe, was considered by
Cox on several occasions (1935, p. 162; 1940, p. 66; 1965, p. 36)
to be synonymous with <u>Modiola imbricata</u> J. Sowerby (1818, p. 21,
pl. 212, figs. 1, 3), a Bajocian to Callovian species. Cox
believed that no valid distinctions could be drawn between these
two species, and that they should be united in <u>M. imbricatus</u>,
which had its range extended to include forms found in deposits
of Bajocian to Kimmeridgian age. <u>M. imbricatus</u> seems to be
restricted to the Bajocian - Callovian in Britain, and differs
from <u>M. bipartitus</u> in its style of ornament (it has fine
concentric threads, with pronounced growth lamellae, imbricated
at irregular intervals) and in its overall form. <u>M. imbricatus</u>

is usually less elongately oblique than M. bipartitus, with a
less well-developed anteroventral bulge, the umbonal ridge
being arcuate, usually fading before it reaches the ventral
margin; the point of maximum shell inflation is also located
on the umbonal ridge.

The holotype of Mytilus Consobrinus d'Orbigny, figured by
Cottreau (1928, op. cit.) also agrees well with topotypes of
M. bipartitus from Weymouth. Arkell (1929, p. 56) cleared up the
confusion over the provenance and identity of the type specimen
of M. bipartitus, designating Sowerby's plate 210, fig. 4 (BM
43231) as lectotype. Most continental authors seem to have
been led into error by Sowerby's admittedly sparse notes on this
species.

A species of Modiolus occurs rarely in the Lower Oxford
Clay of the Midlands, but is invariably crushed flat and
considerably distorted, and as yet, no specimens identifiable at
the specific level have been found. It is likely that these
specimens belong to M. bipartita, as identifiable examples of
the species occur in the Calloviense Zone at Stewartby and the
Athleta Zone at Woodham, and the crushed Lower Oxford Clay
specimens seem to show no distinguishing features.

Range and occurrence   Cornbrash - Corallian of Great Britain,
especially common in the Cornbrash, Upper Oxford Clay and
Corallian, but also being found in the Kellaways Rock, Lower
and Middle Oxford Clay. Specimens recorded from the Enodatum
and Grossouvrei Subzones at Stewartby, Medea Subzone at Bletchley,
Obductum and Grossouvrei Subzones at Calvert, and Athleta Zone of

Woodham.

Many records from the Callovian - Oxfordian of Europe and India (Arkell, 1929; Cox, 1940).

Superfamily PINNACEA Leach, 1819

Family PINNIDAE Leach, 1819

Genus PINNA Linnaeus, 1758 (p.707)

Synonyms: Chimaeroderma Poli, 1795

Pinnarius Dumeril in Froriep, 1806

Pinnigenus Renier, 1807

Pinnula Rafinesque, 1815

Pinnites von Schlotheim, 1820

Pennaria Mörch, 1853 (non Oken, 1815)

Pinua Seguenza, 1877

Pina Koch, 1922

Type species   Subsequently designated by Children, 1823, p. 34, Pinna rudis Linnaeus, 1758 , as figured in Lamarck, 1819, p. 60, pl. 2, fig. 80. Recent, West Indies.

Diagnosis   Equivalve, wedge-shaped, umbones terminal; valves with median carina, at least in juvenile stages; ribbing predominantly radial, but sometimes with growth undulations on the ventral region.

Subgenus PINNA s.s.

Synonyms: Chimaera Poli, 1795 (non

Linnaeus, 1758)

Sulcatopinna Hyatt, 1892

Sulcatipinna Girty, 1915

Quantulopinna Iredale, 1939

Subitopinna Iredale, 1939

Diagnosis   Wedge-shaped; ventral margin straight to concave in outline; median carina well-defined; sculpture of radial ribs or rows of scales.

1.   Pinna (Pinna) mitis Phillips, 1829. Pl. 6, figs. 2-10.

v* 1829 Pinna mitis sp. nov.; Phillips, pl. 5, fig. 7.

?   1850 P. rugoso-radiata sp. nov.; d'Orbigny, p. 340, no. 190.

    1883 P. mitis Phillips; Lahusen, p. 86, pl. 2, fig. 12.

    1907 P. rugoso-radiata d'Orbigny; Cossmann & Thierry, p. 51,
          pl. 3, fig. 1.

?   1925 P. rugoso-radiata d'Orbigny; Cottreau, p. 24, pl. 40,
          figs. 14-16.

v   1933 P. mitis Phillips; Arkell, p. 222, pl. 26, fig. 7.

?   1934 P. mitis Phillips; Stoll, p. 19, pl. 2, fig. 9.

?   1940 P. cf. mitis Phillips; Cox, p. 132, pl. 10, fig. 11.

v. 1952 P. mitis Phillips; Makowski, p. 16, pl. 1, fig. 14.

Type specimen   Holotype, the original of Phillips (1829, pl. 5, fig. 7) figure of Pinna mitis from the Oxford Clay

(Mariae Zone) of Scarborough, Yorkshire, preserved in the
Yorkshire Museum (YM Tsp 219).

Diagnosis   Large wedge-shaped Pinna with the dorsal
margin straight to slightly convex, and the ventral margin
strongly convex, ornamented with 13-22 fine, closely-packed
radial ribs on the dorsal part of the valves, and 6-14 on the
ventral part. Ventral part also covered with coarse, sub-
concentric growth rugae. P. mitis may easily be distinguished
from P. lanceolata by its much smaller size, concave ventral
margin, lack of puckerings on the posterior parts of the shell,
and much finer ornament (fig. 2.16); P. lanceolata has about
8-10 radial ribs on the dorsal part of each valve, and 3-5 on
the ventral part.

Measurements

See Appendix 3.

	L	H	No. Dorsal ribs	No. Ventral ribs
N	21	12	18	18
$\bar{x}$	48.2 mm	44.2 %	14.7 ribs	9.2 ribs
Max	82.4	50.9	22	14
Min	25.0	35.1	14	6
OR	57.4	15.8	8	8

Description   Medium to large sized Pinna, up to 83 mm
long, with low inflation and rapidly diverging dorsal and
ventral margins; maximum height varies from 35-50% of length,
with mean at 44.2%. Umbones terminal, pointed, but often rather
eroded. Dorsal margin straight to very slightly convex, ventral

margin markedly concave for up to 40 mm from umbones, then becoming straight or slightly convex, curving evenly into the rounded truncate posterior margin; posterodorsal angle about 110°, clear and well-marked. Median carina weak and not clearly visible, apparently because of the low inflation; region dorsal to the carina ornamented by 13-22 fine, densely packed radial riblets, with more intercalatories coming in posteriorly, the riblets being crossed by faint concentric growth lines, giving a fine reticulate pattern under the microscope; ventral region with 6-14 fine radial riblets, increasing in number posteriorly occupying only the half of the region nearer the carina, crossed by concentric growth welts strongest at the ventral margin and rarely reaching the median carina. No internal features are visible on any of the specimens examined, as the shell is so thin and fragile.

Remarks   There has been a good deal of confusion in faunal lists about the name to be given to the Oxford Clay Pinna. Arkell (1933, p. 222) clarified the position by figuring the type of P. mitis and comparing it with P. lanceolata Sowerby, from the Corallian. Study of the diagnosis above and the plates show that the two are clearly distinct, P. lanceolata tending to expand gently away from the umbones, while P. mitis widens rapidly to give a fan-shaped shell. (See Fig. 2.16). At first sight, it appears to be a clear cut distinction between the large, slowly-widening P. lanceolata of the Corallian, and the smaller, wider P. mitis of the Oxford Clay. However, specimens from the Oxford Clay of Wiltshire (Christian Malford,

Chippenham and Wootton Bassett) preserved in the major museums all appear to belong to the form with widely-spaced ribs of lanceolata-type. They are mostly fragmentary, and so overall shape is hard to judge. The level is dateable by ammonites to top Coronatum - low Athleta zones, where one would expect to find P. mitis, as it occurs above and below this in other parts of England. Their general shape appears to fit better the mitis-form, as the dorsal margin is straight, not concave, and there is no suggestion of the curved form so typical of lanceolata. It is possible that these specimens belong to a coarsely-ribbed variant of P. mitis, or even that they are just conceivably a new species. Unfortunately, not enough specimens are preserved to allow a clear decision to be made, and it is better at this stage to keep them in P. mitis. It should be noted, however, that they closely resemble some of the small forms of P. lanceolata from the Malton Oolite (Corallian), figured by Arkell (1933, pl. 29, figs. 1, 2). They share the same style of ribbing, with few, rather strong, wire-like ribs, and no intercalatories.

P. mitis and P. lanceolata may easily be distinguished, as noted in the diagnosis, by their different overall shape (Fig. 2.16). Young forms are rather more difficult to separate, as the similarities are greater in the juvenile stages. However, the ribbing in P. lanceolata is stronger and more wire-like, and also lacks the fan-shape of the rapidly expanding P. mitis.

P. rugosa-radiata d'Orbigny, from the Callovian of Pizieux, and also recorded by Cossmann from the Haute-Marne and Deux-

Sevres is synonymous with P. mitis, as study of the holotype
reveals.

P. cf. mitis Cox, from the Callovian - Divesian of Kachh
is probably identical, but appears to have rather weak concentric
growth welts on the ventral parts of the valves, unlike the
British specimens. Intercalation of ribs as growth proceeds is
well seen in this specimen.

Range and occurrence   Abundant in the Jason - Coronatum Zones
of the Lower Oxford Clay of the English Midlands, occurring at
all the pits; Athleta - Mariae Zones (M.-U. Oxford Clay) of
Woodham, Bucks.; Mariae Zone Oxford Clay of Scarborough,
Yorkshire; Cordatum Zone of Warboys, Hunts.; Coronatum -
Athleta Zones of Wiltshire; Kellaways Rock of Wiltshire.

Also found in the Callovian of France, Germany, Poland,
European Russia, and probably India.

2.   Pinna (Pinna) lanceolata J. Sowerby, 1821 Pl. 6, figs.11-14.

v* 1821 Pinna lanceolata sp. nov.; J. Sowerby,   p. 145, pl. 281.

    1822 P. capricornus sp. nov.; Young & Bird, p. 240, pl. 9,
          fig. 5.

    1829 P. lanceolata J. Sowerby; Phillips, pl. 4, fig. 33.

v. 1933 P. lanceolata J. Sowerby; Arkell, p. 219, pl. 28, fig. 5;
          pl. 29, figs. 1-3; pl. 55, fig. 3.

Type specimen   Neotype designated by Arkell, 1933, p. 222,
pl. 28, fig. 5, from the Lower Calcareous Grit, Olivers Mount,
Scarborough, Yorks; probable topotype. Preserved in the

Sedgwick Museum, Cambridge, SM J511.

<u>Diagnosis</u>   Very large, long (over 220 mm occasionally),
narrow <u>Pinna</u> with dorsal and ventral margins diverging regularly,
not unevenly as in <u>P. mitis</u>. Dorsal margin gently concave,
ventral margin gently convex. Valves with median carina well-
marked, and inflation much greater than in <u>P. mitis</u>. Dorsal
part of valve ornamented with 8-10 sharp wire-like radial ribs,
fading posteriorly, ventral part with 3-5 radial ribs, on part
of valve nearest median carina; subconcentric growth welts on
ventral margin. Posterior part of valves marked by coarse
concentric growth puckers, along growth lines.

<u>Measurements</u>

See Appendix 3.

	L	H	I	No. dorsal ribs	No. ventral ribs
N	7	7	6	7	5
x̄	90.1 mm	34.6 %	17.1 %	7.3 ribs	4.2 ribs
Max	170.0	38.9	26.5	8	5
Min	37.6	24.3	11.0	6	3
OR	132.4	14.6	15.5	2	2

<u>Remarks</u>   This well-known Corallian species has been
well-described by Arkell (1933, p. 219) and needs no further
description; the differences between it and <u>P. mitis</u> are
considered above, and shown in Fig. 2.16. The range of
<u>P. lanceolata</u> is extended downwards to include two specimens
from the Mariae Zone Oxford Clay of Scarborough, collected by

Leckenby, and preserved in the Sedgwick Museum, Cambridge
(SM J26725, J26726). These two examples of the species are
indistinguishable from specimens found in the Corallian
(especially the Lower Calcareous Grit), and although they raise
questions about the genetic relationships with the smaller
P. mitis, morphological criteria demand their separation. It is
tempting to suggest that P. lanceolata represents the adult
stage, and P. mitis the juvenile, of a single species, but this
is unlikely on two grounds. Firstly, there is always a difference
in lateral outline of the two species (Fig. 2.16), P. mitis
being more wedge-shaped, and as there is no shell resorption in
bivalves, it is necessary to assume that these shape differences
are original. Secondly, the rib density and strength differs
markedly, P. mitis always having more, finer, ribs than even the
very early stages of P. lanceolata. Added to this the fact that
the two forms are only rarely found together (the Mariae Zone
Oxford Clay of Yorkshire is the only known occurrence), it
becomes unlikely that the two species represent different growth
stages of a single species.

Range and occurrence   Oxford Clay (Mariae Zone) of Scarborough,
Yorkshire, where it is rare; abundant in the Corallian (Arkell,
1933) in many parts of Britain. There is one specimen in the
Sedgwick Museum, Cambridge (SM J28813) from the Kellaways Rock
of South Cave, Yorkshire, which may belong to P. lanceolata.

Order PTERIOIDA Newell, 1965

Suborder PTERIINA Newell, 1965

Superfamily PTERIACEA Gray, 1847

Family PTERIIDAE Gray, 1847

Genus PTEROPERNA Morris & Lycett, 1853 (p. 16)

(ex Lycett, 1850 (p. 413, 420), nom. nud.

Synonymy: Pterinoperna Whitfield, 1891

Type species   Originally designated by Morris & Lycett,
1853, p. 17, Gervillia costatula Eudes-Deslongchamps, 1824,
p. 131, pl. 5, figs. 3-5, from the Bathonian of Europe.

Diagnosis   Subequivalve (left valve more convex than
right valve), inequilateral, oblique, bialate, with a long
pointed posterior auricle and a short, rounded or pointed,
anterior auricle; hinge line long, straight, thickened and
transversely crenulated anteriorly, with one (LV) or two (RV)
elongate posterior lateral teeth, subparallel to the hinge
margin; resilifer wide, flattened, triangular, running postero-
ventrally from beneath the points of the umbones; externally,
the posterior auricle bears up to four elongate grooves,
subparallel to the hinge margin, the lowest of which corresponds
to the lateral teeth; ornament dominantly concentric, but
radial ribs present on the early growth stages in some species.

Remarks   The name Pteroperna was first introduced by
Lycett (1850, op. cit.) for a species (P. gibbosa Lycett, nom.

nud.) from the Inferior Oolite of Gloucestershire, but no figures
of the genus or species were published, and it was not until
three years later that the name was validated (with a different
type-species) by Morris & Lycett (op. cit.).

Cox (1940, p. 88) pointed out that the ligamental area of
Pteroperna is external and obtusely triangular, not "internal
and nearly parallel with the external margin", as stated by
Morris & Lycett (1853, p. 17). The external grooves subparallel
to the hinge margin are of use in distinguishing Pteroperna
from Pteria and most bakevelliids, although similar grooves may
sometimes be seen in some species of Bakevellia s.s. These
grooves are of considerable use in specimens where it is not
possible to see the interior of the hinge, and where only
external features may be used in generic placement. Morris &
Lycett (1853, op. cit.) also claim that a small anterior adductor
scar is present, but the existence of this scar is doubtful
(Cox, op. cit.).

Pteroperna? pygmaea (Dunker) Pl. 5, figs. 13-17, Pl. 6, fig. 1.

*   1837 Avicula pygmaea sp. nov.; Dunker, in Koch & Dunker,
              p. 37, pl. 3, figs. 6a-6d.

v.non 1853 Pteroperna pygmea (Dunker); Morris & Lycett, p. 19,
              pl. 2, figs. 11, 11a /= P. costatula (Eudes-
              Deslongchamps)_7.

      1874 Gervillia pygmaea (Dunker); Brauns, p. 309.

?   1882 Avicula pygmaea Dunker; Roeder, p. 59, pl. 3, figs. 1a,1b.

1915 <u>Pteroperna pygmaea</u> (Dunker); Krenkel, p. 290, pl. 25,
fig. 43.

non 1915 <u>P. pygmaea</u> (Dunker); Krenkel, p. 290, pl. 26, figs. 1,2.

non 1934 <u>P. pygmaea</u> (Dunker) var. <u>baltica</u> nov.; Stoll, p. 16,
pl. 2, figs. 3, 4.

v.non 1972 <u>Gervillia pygmaea</u> (Dunker); Walker, p. 121, pl. 8,
fig. 18.

<u>Type specimen</u>   Lectotype, here designated, the specimen
figured in Dunker, 1837, pl. 3, figs. 6a, 6b, as <u>Avicula pygmaea</u>
sp. nov., from the Corallian of Hannover. Present location of
the type specimen unknown.

<u>Diagnosis</u>   Small to medium-sized species (up to 15.3 mm
L), markedly inequilateral, oblique; hinge line long, straight,
almost as long as the body of the shell (Lh 80.7-93.8%, $\bar{x}$ 86.8%),
the anterior auricle about half as long as the posterior auricle
(ALh 20.8-32.3%, $\bar{x}$ 27.4%; PLh 50.5-68.8%, $\bar{x}$ 59.5%); anterior
auricle relatively large and deep, posterior auricle pointed,
with two strong ridges subparallel to the hinge margin, neither
auricle clearly marked off from the body of the shell; height
57.3-73.0%, $\bar{x}$ 63.0%; oblique length 78.6-100.0%, $\bar{x}$ 88.7%;
angle of obliquity 30-38°, $\bar{x}$ 32.9^{o}; ornament consisting of
fine, regularly spaced concentric lines, about 0.5 mm apart,
becoming more densely packed on the auricles.

<u>Measurements</u>

See Appendix 3, and fig. 2.17 for the measurements used.

	L	Lh	ALh	PLh	OL	H	θ
N	11	11	9	9	11	11	9
$\bar{x}$	11.5 mm	86.8%	27.4%	59.5%	88.7%	63.0%	32.9°
Max	15.3	93.8	32.3	68.8	100.0	73.0	38
Min	5.1	80.7	20.8	50.5	78.6	57.3	30
OR	10.2	13.1	11.5	18.3	21.4	15.7	8

Description   Small to medium sized species, subequivalve, left valve slightly more inflated than the right valve, inequilateral, oblique, pteriiform.   Hinge margin long (Lh $\bar{x}$ 86.8%), straight, the anterior part about half the length of the posterior part (ALh $\bar{x}$ 27.4%; PLh $\bar{x}$ 59.5%); antero-dorsal angle sharp, acute, passing into the sinuate anterior margin; anterior margin of auricle convex, becoming concave in the area where the faint bounding sulcus reaches the margin, then convex again, passing smoothly into the evenly convex ventral margin; posterior margin emarginate and deeply concave dorsally, becoming gently convex ventrally, and passing into the ventral margin via a sharply rounded, acute, posteroventral angle; shell markedly oblique, the angle between the hinge line and the oblique length about 33°, the oblique length usually slightly greater than the length of the hinge margin. Umbones small, rounded, slightly prosogyrate, placed about a quarter of the shell length behind the anterior margin (AL $\bar{x}$ 27.4%), those of the left valve salient about 0.5 mm to the hinge line, those of the right valve hardly salient. Posterior auricle longer and narrower than anterior auricle, with a sharp-topped ridge running from the umbones to the posterior emargination,

presumably marking the position of the posterolateral tooth; another ridge, slightly less elevated, runs along the posterior part of the hinge margin of the posterior auricle; posterior auricle marked off from the body of the shell by a wide sulcus running to the dorsal side of the posteroventral angle. Anterior auricle shorter, deeper, with a faint ridge along the hinge margin, marked off from the body of the shell by a very faint depression running subperpendicularly from the hinge margin. Ornament consisting of faint concentric lines, regularly spaced on the body of the shell, about 0.5 mm apart, becoming more closely packed on the posterior auricle; at the dorsal extremities of the anterior auricle the lines bifurcate and become more elevated; on the body of the shell the concentric lines are seen to be fine grooves.

Ligament area external, oblique, flattened, the small resilifer placed immediately below the umbo, and running posteroventrally from it. The hinge margin anterior to the umbones is obliquely flattened, and has a series of about 12 very fine, rather faint, vertical teeth. Just anterior to the umbo, on the ventral edge of the hinge margin of the left valve, is a rounded peglike apophysis, with a central depression on the upper surface; immediately anterodorsal of the apophysis is a slightly smaller triangular-shaped socket (Fig. 2.18). Posteriorly, a long, narrow posterior lateral tooth runs from the umbo about two-thirds of the way to the posterior end of the hinge line, immediately ventral of the ligamental area. Musculature and pallial line unknown. Inner ostracum of nacreous aragonite, outer ostracum of prismatic calcite.

Remarks   Five well-preserved specimens of

P? pygmaea from the Oxford Clay of Christian Malford (Wiltshire),

housed in the Bristol City Museum (BCM Cb4777-4781), are the

basis of the above description, and between them they demonstrate

clearly the nature of the species. In size, shape and ornament,

they agree closely with the specimens described and figured by

Dunker from the Corallian of the Hannover area, and there can be

little doubt of their identity. In one of the Bristol Museum

specimens (Cb4777), it has been possible to remove the shell

from the clay steinkern and examine the hinge (Fig. 2.18), thus

proving that the specimens concerned are pteriids rather than

bakevelliids, as they lack multiple ligament pits. In most

respects, the hinge of P.? pygmaea agrees with that of the type

species (P. costatula), but differs in possessing a peglike

divided tooth just anterior to the umbo of the left valve, and

in the much weaker development of the series of short anterior

teeth. In some ways, P.? pygmaea is closer to Pteria than

Pteroperna, especially in the presence of the toothlike

processes below the umbo and the single posterior lamina, making

exact generic placement within the Pteriidae uncertain. It

appears to represent a transitional stage between Pteria and

Pteroperna, having certain features (i.e. the 'dentition')

typical of Pteria, and others (i.e. the external grooves on the

posterior auricle) typical of Pteroperna. Further material

would greatly help in clarification of the generic relationships,

but unfortunately, the shell is so fragile that examination of

the hinge almost invariably results in the destruction of the

specimen. Thus in our present state of knowledge, it is not possible to place this species with certainty, but as a concession to historical usage, it is left, for the moment, in Pteroperna.

There has been a good deal of confusion over the identity of P. pygmaea in the literature, few authors having correctly interpreted the species. Morris & Lycett (1853, op. cit.) figured two specimens from the Bathonian of Minchinhampton under the name P. pygmaea, but this is a misidentification of P. costatula (Deslongchamps), characterised by the sharply-differentiated, finger-like anterior wing, and frequent radial ribbing on the early growth stages. P. emarginata Morris & Lycett (1853, p. 19, pl. 2, fig. 10), from the same horizon and locality, has a minute anterior wing, and is clearly different. Avicula pygmaea Roeder (op. cit.) is undoubtedly closely related to Dunker's species, but is much too large (H 45 mm) and has rather a short hinge (Lh 71.9%); identity with P. pygmaea is doubtful. Krenkel (1915) appears to have caused much of the subsequent confusion by figuring a Gervillella, which clearly shows the serial ligament pits (pl. 26, figs. 1, 2), under the name P. pygmaea. On the previous plate (pl. 25, fig. 43) he figured a correctly identified P. pygmaea, but this figure has been largely overlooked by later authors (Cox, 1940, p. 90; Walker, 1972, p. 121). Stoll (1934, pl. 2, figs. 3, 4) figured two specimens of P. pygmaea var. baltica nov. which are specifically distinct from P. pygmaea, being much larger (L 35 mm), with very narrow, elongate posterior auricles, and

a virtually obsolete anterior auricle. Her figures also seem to have suffered by being mercilessly trimmed around the edges, and it is quite possible that some of the outline has been lost. Gervillia pygmaea Walker (1972, pl. 8, fig. 18) is far too oblique (θ 21°), has too short a hinge line (LH 67.0%) and not great enough height (H 35.2%) for P. pygmaea. Walker accepts Krenkels figure (pl. 26, figs. 1, 2) showing the serial ligament pits as belonging to P. pygmaea, and on this basis places his species in Gervillia.

Other similar species are P? blakei Cox (1940, p. 89, pl. 6, fig. 8) from the Athleta Zone of Cutch (India), in which the anterior auricle is far too elongate, narrow and pointed; Avicula obliqua Buvignier (1852, p. 27, pl. 16, figs. 38-40) from the Kimmeridgian of France, similar in form to P? blakei; and Avicula polyodon Buvignier (in Sauvage & Buvignier, 1842, p. 533, pl. 4, figs. 1, 2) from the Corallian, which is much closer to P. costatula than P. pygmaea.

Range and occurrence   Occurs rarely in the Lower Oxford Clay (Enodatum Subzone - Athleta Zone) of the Midlands, and in the Coronatum - Athleta Zone Oxford Clay of Christian Malford, Wilts.

The type series comes from the Corallian of the Hannover area, Germany, and specimens are also recorded from the M. Callovian of Lithuania (Krenkel, 1915).

Family INOCERAMIDAE Giebel, 1852

Genus PARAINOCERAMUS Voronetz, 1936 (p. 23)

Type species   Subsequently designated by Cox, 1954, p. 47,
Parainoceramus bulkurensis Voronetz, 1936, p. 34, pl. 1, figs.
2, 8, 10, from the U. Triassic (Carnian) of Russia.

Diagnosis   Medium to large-sized genus (up to at least
80 mm H), equivalve, moderately inflated, rectangular to
trapeziform in outline, with hingeline of variable length;
posteriorly subalate, wing not clearly differentiated from the
body of the shell; umbones protruding only slightly above the
hinge margin, subterminal, prosogyrate; anterior face of shell
flattened, more or less impressed; ligament area flat, with
variable number of pits; short anterior and elongate posterior
teeth present in some species, at least in early growth stages;
surface smooth or with weak concentric plication; shell
structure of normal inoceramid type.

Remarks   Parainoceramus was introduced by Voronetz
(1936) to contain the Triassic to Jurassic equivalve inoceramids
with an impressed, flattened anterior region and small, only very
slightly salient umbones; it is also the only inoceramid genus
to have hinge teeth, although they are not always present.
P. subtilis (Lahusen) shows all the features typical of the
genus, and is one of the toothed species, having two small
mytiliform teeth beneath the umbo of the right valve. The
fragility of the shell renders the hinge of P. subtilis difficult

to develop, but from the few specimens seen which show the hinge, it is apparent that there are fewer ligament pits than in other species of Parainoceramus, only five being seen in any specimen. As in other genera of inoceramids, there is a great deal of variation in ribbing strength and density within any species of Parainoceramus, including P. subtilis, and all intermediate stages between an almost smooth form and a form with regular concentric ribs may be seen.

Parainoceramus subtilis (Lahusen). Pl. 7, figs. 1-9.

* 1883 Perna subtilis sp. nov.; Lahusen, p. 86, pl. 2, figs. 10, 11.

.? 1904 Mytilus nikitiniensis sp. nov.; Ilovaisky, p. 253, pl. 8, fig. 9.

Type specimen   Lectotype, here designated, the specimen figured by Lahusen (1883) as pl. 2, fig. 10, from the Coronatum Zone Oxford Clay of Tschulkowo, Russia. Present location of the specimen unknown, probably lost.

Diagnosis   Large species (up to 72.5 mm L), equivalve, subrectangular in outline, with umbones small, subterminal, slightly prosogyrate, not prominent; height exceeding length (H 110.3-143.0 %, $\bar{x}$ 124.3 %), hinge line length about half overall shell length (Lh 40.9-67.2 %, $\bar{x}$ 53.0 %); anterior margin straight to evenly convex, forming an obtuse angle with the hinge line; posterior margin straight to evenly convex, continuous with the ventral margin; inflation low; ligament

narrow, only five pits seen, the interspaces wider than the ligament pits; two small mytiliform teeth lie beneath the umbo of the right valve; ornament very variable, from almost smooth to forms with regular concentric ridges.

Measurements

See Appendix 3, and Fig. 2.19 for the measurements used.

	L	H	Lh
N	25	25	25
$\bar{x}$	20.9 mm	124.3 %	53.0 %
Max	72.5	143.0	67.2
Min	3.3	110.3	40.9
OR	69.2	32.7	26.3

Description   Large species, equivalve, inequilateral, subrectangular to subovate in outline, of low inflation. Hinge margin straight, posterodorsal angle rounded, obtuse, sometimes clearly marked, in other specimens not well angulated; posterior margin straight to evenly and fully convex, passing into the evenly curved ventral margin without angulation; anterior margin evenly convex, occasionally almost straight in the half nearest the umbones, forming an obtuse angle with the hinge margin, passing smoothly into the ventral margin. Umbones small, rounded, only very slightly salient to the hinge margin, gently prosogyrate, not enrolled, often subterminal. Anterior area flattened more or less at right angles to the commissure; no anterior auricle. Posterior part of the shell subalate, slightly compressed, but not clearly separated from the body of the shell.

No differentiated dorsal areas. Ornament of faint concentric growth lines, with variable development of irregular or regular concentric ridges, sometimes restricted to the umbonal regions and fading distally, but usually persisting to the ventral margin; the spacing and elevation of the ridges varies within individual specimens. Outer ostracum of prismatic calcite, inner ostracum of nacreous aragonite; inner layer well-developed. Commissure planar, lacking gapes.

Ligament area narrow, elongate, flattened, with five widely spaced, convex-sided ligament pits, the interspaces between the pits being at least as wide as the pits themselves, except in the region immediately beneath the umbo, where the pits become crowded together; ventral margins of the pits are convex, but protrude only very slightly into the shell cavity. Immediately beneath the umbo of the right valve, two small Λ-shaped teeth mark the anterior extremity of the hinge line, the anterior tooth being narrow, bladelike and elevated, the posterior tooth wider, lower and more peglike; between them is a small socket divided horizontally into two, the lower part being about twice the size of the upper part (Fig. 2.20).

Musculature and pallial line not visible.

Remarks   Lahusen's two specimens from the Coronatum Zone of Russia are indistinguishable from specimens to be found in the Lower Oxford Clay of England, and although he gives no indication of the nature of the hinge, there can be little doubt that Lahusen's figures represent an inoceramid. The hinge is occasionally seen in well-preserved specimens, showing that the

ligament pits are fewer and more widely spaced than in other species of *Parainoceramus*, such as *P. substriata* (Münster in Goldfuss) from the L. Lias. The short anterior teeth sometimes found in *Parainoceramus* are well seen in *P. subtilis* (Fig. 2.20), but the elongate posterior teeth have not been seen, due to incompleteness of the shells examined. *P. substriata* (Münster) closely resembles *P. subtilis* in shape, but is more inflated and has more densely packed ligament pits.

Perna lamellosa Lahusen (1883, p. 91, pl. 2, fig. 9) is closely related to *P. subtilis*, but is much narrower and higher, with rather prominent umbones forming an acute angle between the antero- and posterodorsal margins. No specimens of *P. subtilis* comparable with *P. lamellosa* have been seen.

Mytilus nikitiniensis Ilovaisky, from the Cordatum Zone of the Moscow region closely resembles *P. subtilis*, and undoubtedly is an inoceramid rather than a mytilid. Ilovaisky's figure shows a specimen with a slightly more acute umbonal angle than is seen in *P. subtilis*, but agrees well in all other respects, and could be synonymous.

Inoceramus inoceramoides (Hudleston) from the British Corallian, well-described and figured by Arkell (1933, p. 217, pl. 28, figs. 1, 1a), is clearly different, being markedly suborbicular with prominent umbones, the antero- and posterodorsal margins being concave in outline. *I. nitiscens* Arkell (1933, p. 218, pl. 28, figs. 2, 3), also from the Corallian, differs in having regularly spaced, distant, concentric lines over the whole shell, and in its much more equilateral outline, with

prominent submedian umbones, and a concave anterior margin.

Range and occurrence   Common in the Lower Oxford Clay (Enodatum Subzone - Athleta Zone) of the English Midlands, occurring at all the major pits, and at Chickerell, Weymouth, and Chippenham, Wilts.

Also known from the Coronatum Zone (type horizon) and possibly from the Cordatum Zone (Ilovaisky, 1904) of Russia.

Superfamily PECTINACEA Rafinesque, 1815

Family POSIDONIIDAE Frech, 1909

Genus BOSITRA de Gregorio, 1886 (p. 11)

Type species   Subsequently designated by Cox, 1964, p. 47, Posidonia ornati Quenstedt, 1856, p. 501, pl. 67, fig. 27, from Brown Jura 3 of Gammelshaufen, Germany.

Diagnosis   Ovate to subquadrate shells with regular concentric undulations; auricles absent or poorly developed in adults; ligament alivincular.

Remarks   The name Bositra is here applied to the posidoniids occurring in abundance in the Toarcian - Oxfordian of Europe, and which have been described under various specific names (see synonomy below). The main point in which Bositra differs from Posidonia is in the possession of an alivincular ligament of a pteriid, rather than an arcid type, i.e. it lacks the external ligament chevrons on the dorsal part of the cardinal area.

Bositra buchii (Roemer, 1836). Pl. 7, figs. 10-18.

.* 1836   Posidonia buchii sp. nov.; Roemer, p. 81, pl. 4, fig. 8.

. 1851   Posidonia ornati sp. nov.; Quenstedt, p. 517, pl. 42,
          fig. 16.

. 1852   Posidonomya alpina sp. nov.; Gras, p. 11, 48, pl. 1,
          fig. 1.

. 1856   Posidonia ornati Quenstedt; Quenstedt, p. 501, pl. 67,
          fig. 27.

. 1856   Posidonia Parkinsoni sp. nov.; Quenstedt, p. 501,
          pl. 67, fig. 28.

. 1856   Posidonia ornati Quenstedt; Quenstedt, p. 551, pl. 72,
          fig. 29.

   1883   Posidonomya ornati (Quenstedt); Lahusen, p. 86, pl. 2,
          fig. 8.

. 1928   Posidonomya alpina Gras; Guillaume, p. 22, pl. 10,
          figs. 4-13.

. 1934   Posidonomya alpina Gras; Stoll, p. 19, pl. 2, fig. 14.

. 1940   Posidonia ornati Quenstedt; Cox, p. 103, pl. 7, figs. 10-11.

   1964   ? Bositra buchii (Roemer); Cox, p. 39.

v. 1965   Bositra buchi (Roemer); Jefferies & Minton, p. 156,
          pl. 19, figs. 1-4, 6-9.

   1965   Bositra buchii (Roemer); Cox, p. 50, pl. 6, fig. 1.

Type specimen   Holotype of Roemer's p. 81, pl. 4, fig. 8,
from the Walker - Erde (Fullers Earth, Bathonian) of Geerzen,
Germany, not present in the Roemer collection at the Roemer Museum
in Hildesheim, W. Germany, and must be considered lost.

<u>Diagnosis</u>   Small to medium in size, up to 15 mm high,
with strong concentric folds. Shell extremely thin and fragile;
rather variable in shape, although generally suborbicular.
Differs from 'Posidonia' <u>bronni</u> Goldfuss in being rather smaller
and more oblique.

<u>Measurements</u>

See Appendix 3.

	L	H	Lh	AL
N	50	50	50	50
$\bar{x}$	7.7 mm	83.9 %	48.8 %	35.1 %
Max	15.0	97.7	62.1	45.0
Min	2.4	67.7	40.0	22.4
OR	12.6	30.0	22.1	22.6

<u>Description</u>   Equivalve, inequilateral, suborbicular,
with height 67.7-97.7 % of length, $\bar{x}$ 83.9 %. Umbones prosogyrate,
anterior to median (AL 22.4-45.0 %, $\bar{x}$ 35.1 %), only slightly
salient to the hingeline; maximum shell height located posterior
to the umbones, giving a slightly oblique appearance. Dorsal
margin straight, the rest of the shell margin a continuous
sweeping curve. Ornament consists of strong concentric folds
affecting the whole thickness of the shell; crests of the folds
rounded, being separated by angular furrows; spacing of folds
varies within a population, but is usually fairly constant
within any given specimen. Wide anterior and posterior gapes.
Shell very thin, with prismatic calcite outer layer and nacreous
inner layer. Cardinal area thicker shelled than the rest of the

shell, consisting of a central triangular resilifer (approx. 45% length of hingeline) bordered anteriorly and posteriorly by the external ligament attachment areas, each approx. 27% length of hingeline.

Remarks   It was Cox (1964, p. 39) who first tentatively referred Posidonia buchii to the genus Bositra, although he noted that more detailed work on the hinge structure was necessary before such a placement could be verified. Consequently, the work of Jefferies & Minton (1965), who figured an internal view of a M. Callovian specimen (reproduced here as Fig. 2.21), showed that Cox's tentative assignment was in fact correct.

The taxonomy and mode of life of this long-ranging species have been considered in detail by Jefferies & Minton (1965), who concluded that Posidonia buchii, P. ornati and Posidonomya alpina were synonymous. Comparison of the original figures of P. ornati and P. alpina leaves no doubt that those two species were in fact one, but the relationship between them and P. buchii is a little more difficult to ascertain. Roemer's figure of P. buchii shows a rather smooth-shelled elongate form, with the umbones situated close to the anterior margin, and a rather produced posterior. Elongate forms of the other species do occur, however, and the most likely conclusion is that Roemer's figure is of a poorly preserved form, rather more elongate than usual. The fact that Roemer (p. 81) says that P. buchii is thin-shelled, and has a straight hingeline, and is shown in his plate in the characteristic valves-open position, leaves little doubt that it represents the same species as were described by Quenstedt and Gras.

The thinness of the shell makes study of the hinge area
very difficult, as the shell is so fragile. No specimens
showing details of the cardinal area have been found by the
author, so Fig. 2.21, showing the cardinal area, has been
reproduced from Jefferies & Minton (their fig. 1, p. 157).
Evidence for anterior and posterior gapes has been taken from
the same source (Fig. 2.22).

Ecology   Because the ecology of this species is of
great importance in the understanding of the environmental
conditions existing during the deposition of the Lower Oxford
Clay, and because it is well-documented, it is considered here.

B. buchii is a very widespread species with pelagic
facies relationships, occurring abundantly where there is no
benthos, as well as in facies with a rich benthonic fauna; it
also appears to be independent of lithofacies. Two main modes
of life have been postulated for B. buchii because of its
unusual facies relations. Ichikawa (1958) suggested that
posidoniids were pseudoplanktonic, being attached to floating
seaweed, whilst many other authors, such as Molengraaf (1917),
Krumbeck (1921) and Guillaume (1928) favoured a free-swimming
pelagic habit, Krumbeck comparing them with pteropods. Jefferies
& Minton (1965), using the evidence of facies, geographical
distribution and functional morphology, attempted to show that
B. buchii was nektoplanktonic, having a free-swimming pelagic
habit similar to that originally postulated by Molengraaf (op. cit.).
Their studies showed that wide anterior and posterior gapes were
present, that the valves had a wide angle of opening in life, and

that the shell was very thin. They concluded that the mantle was fringed by prominent tentacles, and that the animal was nektoplanktonic.

There are, however, some problems concerning this interpretation, such as the apparent lack of large attachment scars for the adductors; a free-swimming valve-clapping ~~pteriid~~ *Pectinacean* would surely have needed well-developed adductor muscles to enable valve-clapping. On the other hand, adults are totally non-auriculate, and equivalve, and so the existence of a functional byssus seems rather unlikely. The commonest mode of occurrence of B. buchii, especially in the L. Oxford Clay, is as articulated shells, with the valves spread wide open, and Jefferies & Minton (op. cit.) point out that this would be most likely to occur if the living shell was able to gape very widely; wide-gaping potential would be expected to be greatest in a valve-clapping swimmer.

A benthonic mode of life is precluded because of the very wide geographical spread of the species, and its frequent occurrence in sediments with little or no benthos. The likelihood of such a small suspension feeder being able to live on a seafloor of very soft unstable mud is small, and there are no structural features which suggests byssal attachment. On balance, however, it seems necessary to invoke a byssally attached mode of life, probably via only a very few byssal threads, to floating or rooted organic material. The reason for this is primarily the fact that no nektoplanktonic bivalves are known at the present time, and it seems an unlikely mode of life for a bivalve,

especially one without well-developed muscle scars. Attachment
to organic material would also explain the clustering of
individuals which so commonly occurs in the L. Oxford Clay. The
absence of a byssal notch may be explained by the animal having
only a few byssal threads, and not needing a functional ctenolium.

Range and occurrence The species ranges from the Toarcian -
Oxfordian, and is of almost cosmopolitan extent, having been
recorded from Europe, Russia, E. Africa, Madagascar, S. America
and India. In Britain, it is found in the Fullers Earth
(Bathonian) and Oxford Clay, apparently commonest in lithologies
with a sparse benthonic fauna. The youngest British specimen so
far recorded is from the Mariae Zone, and it is abundant in the
Jason and Coronatum Zones, less common above this.

Family OXYTOMIDAE Ichikawa, 1958

Genus OXYTOMA Meek, 1864, (p. 39)

Type species   Originally designated by Meek, 1864, p. 39,
Avicula münsteri Bronn, 1830, p. 164 (the species first being
figured by Goldfuss, 1836, p. 131, pl. 118, figs. 2a-2h), from
the Braunjura delta of Thurnau (Oberfranken), Germany.

Diagnosis   Suborbicular and acline to ovate, or broadly
lunate and prosocline, inequivalve, left valve larger than the
right valve; left valve convex in section, variably inflated,
right valve flat or feebly convex; bialate, posterior auricles
of both valves produced and sharply pointed, with a variably

developed sinus below them; left anterior auricle small, blunt, right anterior auricle short and prominent; byssal notch deep, acute, usually with ctenolium, angular projection of shell margin extending on inner side of notch; ligamental area subparallel to commissure in left valve, subperpendicular to commissure in right valve; edentulous.

Subgenus OXYTOMA s.s.

Diagnosis   Medium sized shell; left valve ornamented with ribs and riblets developed to three orders of strength, although only primaries and secondaries are present in some specimens; primaries well separated, interspaces much wider than the ribs; right valve smooth, or with weak radial threads; adductor scar placed posteriorly.

Remarks   Bronn first introduced the name Avicula münsteri in 1829 (p. 76), and mentioned it again in 1830 (p. 164), but both these records are nomina nuda; the species was not figured until 1836, by Goldfuss (p. 131, pl. 118, figs. 2a-2h), and since then, it has often been accepted that this species is synonymous with the earlier described A. inequivalvis J. Sowerby (1819). However, Ichikawa (1958, pl. 24, figs. 1, 2) has refigured the types of A. münsteri Bronn in Goldfuss, together with several other examples of the species (op. cit., pl. 24, figs. 3-7), and shown them to be equivalve, thus precluding them from being conspecific with the markedly inequivalve A. inequivalvis. This invalidates the conclusions

of Cox (1940, p. 92), who believed the two species to be
synonymous.

Meleagrinella is closely related to Oxytoma, but may
readily be distinguished by the greater inflation of its left
valve, the finer ornament pattern, the smaller posterior auricle
(and the lack of a left anterior auricle), and the presence of
a tooth-like protuberance on the ventral margin of the cardinal
plate.

Oxytoma (Oxytoma) inequivalvis (J. Sowerby). Pl. 7, figs. 19-23,
                                            Pl. 8, figs. 1-13.

v* 1819 Avicula inequivalvis sp. nov.; J. Sowerby,   p. 78,
          pl. 244, figs. 2, 3.

.   1851 Monotis inequivalvis (J. Sowerby); Quenstedt, p. 518,
          pl. 42, figs. 18, 19.

v. 1855 Avicula münsteri Bronn; Morris & Lycett, p. 129, pl. 14,
          fig. 6 (non Bronn).

v.? 1863 A. subcostata Roemer; Lycett, p. 36, pl. 40, fig. 24
          (non Roemer).

    1882 A. (Oxytoma) Münsteri Bronn; Roeder, p. 58, pl. 1,
          figs. 10a, 10b (non Bronn).

    1883 A. inaequivalvis J. Sowerby; Lahusen, p. 91, pl. 2, fig. 5.

    1904 A. cf. Münsteri Bronn; Ilovaisky, p. 252, pl. 8, figs.
          18, 19 (non Bronn).

    1907 A. (Oxytoma) inaequivalvis J. Sowerby; Cossmann &
          Thierry, p. 49, pl. 3, figs. 5-7.

    1909 Oxytoma inaequivalvis (J. Sowerby) var. borealis nov.;
          Borissiak, p. 19, pl. 1, figs. 3-8.

1909 <u>O. inaequivalvis</u> (J. Sowerby); Borissiak, p. 19, pl. 1, fig. 10.

? 1909 <u>O. cf. interlaevigata</u> (Quenstedt); Borissiak, p. 21, pl. 1, fig. 9.

1915 <u>O. inaequivalvis</u> (J. Sowerby) var. <u>borealis</u> Borissiak; Krenkel, p. 289, pl. 25, figs. 25-31.

1915 <u>Pteria phillipsi</u> nom. nov.; Rollier, p.   (nom. nov. pro <u>A. inequivalvis</u> J. Sowerby, 1819, pl. 244, fig. 2).

1919 <u>A. (Oxytoma) inaequivalvis</u> J. Sowerby; Couffon, p. 62, pl. 4, figs. 7-7c.

1924 <u>Oxytoma inaequivalvis</u> (J. Sowerby); Gillet, p. 450.

v* 1933 <u>O. inaequivalvis</u> (J. Sowerby); Arkell, p. 194, pl.24, fig.9.

1935 <u>O. inequivalve</u> (J. Sowerby); Cox, p. 165, pl.15, figs.11,12.

1939a <u>O. interlaevigata</u> (Quenstedt); Arkell, p. 137.

1940 <u>O. inequivalve</u> (J. Sowerby); Cox, p. 98, pl. 6, figs. 9-12.

1948 <u>O. inequivalve</u> (J. Sowerby); Cox & Arkell, p. 7.

1958 <u>O. (Oxytoma) sp.</u>; Ichikawa, p. 161, pl. 24, fig. 8.

1965 <u>O. inequivalvis</u> (J. Sowerby); Cox, p. 47, pl. 5, fig. 7.

<u>Type specimen</u>   Lectotype (designated by Arkell, 1933, p. 194) of <u>Avicula inequivalvis</u> J. Sowerby, 1819, p. 78, pl. 244, fig. 2 (the left hand figure), from the M. Lias of Dursley, Gloucester-shire, preserved in the BM (NH), number 43259.

<u>Diagnosis</u>   Medium to large sized species (up to 39.8 mm L), very inequivalve, right valve about half the size of the left valve; bialate, posterior auricles long and pointed, right anterior auricle short and pointed, left anterior auricle small,

blunt; inflation relatively high (I LV $\bar{x}$ 25.0 %); hingeline
long, invariably broken, seen to be up to 91.2 % of shell
length; ornament very variable, left valve usually with primary
and secondary ribs, sometimes with tertiaries also, occasionally
with primaries alone, or with primaries and tertiaries only;
right valve smoother, ornamented with faint radial riblets of
only one strength.

Measurements

 See Appendix 3.

LV		L	H	I	AL	OL	Lh	θ
	N	30	30	13	23	19	14	5
	$\bar{x}$	23.1 mm	89.0%	25.0%	27.1%	101.0%	71.6%	31.2°
	Max	39.8	108.9	33.8	33.7	126.6	91.2	40
	Min	11.4	72.6	18.8	20.0	86.7	50.4	27
	OR	28.4	36.3	15.0	13.7	39.9	40.8	13
RV								
	N	19	19	17	16	6	12	
	$\bar{x}$	14.0 mm	90.3%	15.2%	32.6%	94.7%	79.2%	
	Max	19.6	99.4	17.4	38.2	111.6	100.0	
	Min	7.4	63.5	10.7	25.7	67.6	46.8	
	OR	12.2	35.9	6.7	12.5	44.0	53.2	

Description Medium to large sized, suborbicular to
obliquely subovate in outline, prosocline; inequilateral,
umbones slightly prosogyrate, rounded, salient about 2 mm above
the hinge margin, placed within the anterior third of the shell
(LV AL $\bar{x}$ 27.1%; RV AL $\bar{x}$ 32.6%); strongly bialate, inequivalve,

left valve about twice the size of the right valve.

Left valve obliquely subovate to suborbicular in outline
(H 72.6-108.9 %, $\overline{x}$ 89.0 %), inflated (I 18.8-33.8 %, $\overline{x}$ 25.0 %),
with umbones placed near the anterior margin (AL 20.0-33.7 %,
$\overline{x}$ 27.1 %); oblique length variable, about equal to overall
shell length (OL 86.7-126.6 %, $\overline{x}$ 101.0 %). Hingeline long
(Lh 50.4-91.2 %, $\overline{x}$ 71.6 %), straight, most of its length placed
posterior to the umbones, forming the dorsal margin of the
strongly developed posterior auricle; posterior auricle elongate,
flattened, pointed, with a deep subauricular sinus; the
posterior auricle is well differentiated from the body of the
shell by a deep auricular sulcus; posterior margin of the body
of the shell gently concave to straight, passing via the smoothly
rounded posteroventral angle into the evenly and gently convex
ventral and anterior margins, which form a long, sweeping curve;
at its dorsal extremity, the anterior margin straightens, and
sometimes reflects back a little to meet the small, vestigial
anterior auricle; anterior auricle small, not clearly
differentiated from the body of the shell, bluntly terminated at
the anterior end. Ornament very variable, consisting of
arrangements of primary, secondary and tertiary radial riblets,
the primaries usually strong and wirelike, extending all the way
to the umbo, the secondaries becoming intercalated between the
primaries about 15-20 mm from the umbo, and the tertiaries
appearing between these; in some forms, such as those from the
Kellaways Clay of Chickerell, Dorset, only primaries and very
faint tertiaries occur, whilst forms from the Lower Oxford Clay

usually show primaries and secondaries, sometimes with tertiaries also. The primaries carry onto the anterior auricle, but not onto the posterior auricle, although faint radial threads are sometimes visible on the posterior auricle. On the body of the shell, the riblets are crossed by scalloped concentric growth lines, better seen on some specimens than others, but the interaction of growth lines and riblets never produces a reticulate pattern.

Right valve smaller, suborbicular to subovate (H 63.5-99.4 %, $\overline{x}$ 90.3 %), of very low thickness (I 10.7-17.4 %, $\overline{x}$ 15.2 %), more or less flat, with umbones placed about a third of the shell length behind the anterior margin (AL 25.7-38.2 %, $\overline{x}$ 32.6 %); umbones small, slightly prosogyrate, pointed, not salient to the hinge margin. Hingeline long (LH 46.8-100.0 %, $\overline{x}$ 79.2 %), but fragile, and easily broken; well-preserved specimens from the Lower Oxford Clay have maximum shell length along the hingeline, so it is probable that the measurements of hingeline length on other shells are rather too low. Posterior auricle large, flattened, very elongate, sharply pointed, with a less well-developed subauricular sinus than occurs in the left valve; anterior auricle small, pointed, with a deep byssal notch beneath it, the whole auricle well-differentiated from the body of the shell by a strong auricular sulcus; no auricular sulcus separates the posterior auricle from the shell body. Posterior margin of shell straight to evenly convex, passing smoothly into the semicircular sweeping curve of the ventral and anterior margins. Ornament consisting of faint radial striae,

becoming slightly stronger ventrally, but without secondaries
and tertiaries; these striae do not continue onto the auricles;
concentric growth lines hardly visible, but there are occasional
well-marked growth halts.

Ligamental area of the left valve (Fig. 2.23) subparallel
to the commissure, the resilifer present as a narrow triangular
area running posteroventrally from immediately beneath the umbo,
reaching almost to the auricular sulcus. There is a slight
elongate depression parallel to the hinge margin, and immediately
beneath it at its anterior end, for receipt of the anterior part
of the hinge area of the right valve. Interior of the posterior
auricle flattened, dropping sharply into the shell cavity along
the line of the auricular sulcus. Posterior adductor muscle
scar large, elliptical, with the concave side placed dorsally,
its posterior margin reaching to the auricular sulcus, and its
anterior margin reaching halfway to the midaxis; the scar is
slightly closer to the cardinal plate than to the ventral margin.
Curving anterodorsally from the anteroventral margin of the
posterior adductor scar is a disjunct pallial line (Fig. 2.23)
consisting of about 25 tiny pallial muscle scars, running beneath
the cardinal plate at the point where the anterior articulation
for the right valve is situated; anterior adductor scar not seen.

Ligamental area of right valve (Fig. 2.24) flattened
subperpendicular to the commissure, the resilifer a narrow
triangular depression running posteroventrally from immediately
beneath the umbo, reaching to the area of the posterior auricle.
A deeply incised byssal notch is present beneath the anterior

auricle, running obliquely into the shell interior; a ctenolium appears to be absent. Posterior adductor muscle scar suborbicular, placed slightly nearer to the ventral margin than to the cardinal plate, its posterior margin meeting the edge of the posterior auricle, and its anterior margin reaching to approximately below the midpoint of the resilifer. Running anterodorsally from the ventral margin of the adductor scar is a disjunct pallial line (Fig. 2.24) consisting of about 18-20 tiny pallial muscle scars; the anterior adductor muscle scar is very small, suborbicular, and placed on the lower margin of the cardinal plate, about 1.5 mm posterior of the inner end of the byssal notch.

Remarks   In his original description of O. inequivalvis, J. Sowerby (1819, p. 78, pl. 244, figs. 2, 3) figured two forms, identified as var. α and var. β , from the M. Lias and Kellaways Rock respectively, the two being distinguished by their different styles of ribbing. Var. α (said by Sowerby to have come from the Kellaways Rock of Dursley, Gloucestershire, but actually from the M. Lias /Arkell 1933, p. 194/) was described as having slender striae between the divergent primary ribs, while var. β had strong striae between the primaries, but Sowerby did not believe these differences to be of specific importance. In the years since Sowerby, some authors, notably Arkell (1933, p. 194), have claimed that the M. Lias and Kellaways Rock forms should be considered as distinct species, on the basis of differences in ornament pattern and overall size. Arkell (op. cit.) believed that the M. Lias species, which he referred

to as O. inaequivalvis, had 14-15 primary ribs, no secondaries, and numerous tertiaries, whilst the Kellaways Rock species, referred to O. expansa (Phillips), had 16-20 primaries, with a secondary between each pair, and numerous tertiaries. However, re-examination of the lectotype block (BM 43259) and several other specimens from the Sowerby collection (BM 66351) reveals that there is much variation in ribbing style in M. Lias specimens, examples possessing secondary ribs being by no means uncommon. Likewise, populations from the Lower Oxford Clay, which Arkell (op. cit., p. 195) would probably have referred to O. expansa, contain many specimens lacking secondary ribs and which are indistinguishable from M. Lias forms.

Cox (1940, p. 99) considered the O. inequivalvis problem, and having examined specimens from many horizons within the British, European and Asian Jurassic, followed Waagen (1901) and Gillet (1924) in concluding that there was but one species, showing no gradual evolutionary change in any particular direction between the Rhaetic and the L. Cretaceous, and that the name O. inequivalvis had priority. Cox's work showed that although there may be local races at any given horizon, most of these morphological types were imitated at a different horizon in a different region, and that no pattern could be made out for this variation; the only workable conclusion was to consider them all as part of a single, very variable species.

Having examined many specimens from the British Lias, Cornbrash, Kellaways Rock, Oxford Clay and Corallian, the author believes that O. inequivalvis is a very variable species

(Fig. 2.25), ranging at least from the Lias to the Oxford Clay, but that it is indeed distinct from O. expansa Phillips, a species appearing in abundance in the European Corallian. However, the basis for the separation of these two species is not the ornament pattern, but rather the relative sizes of the two valves. As the name suggests, O. inequivalvis is markedly inequivalve, the left valve being about twice as long and high as the right valve, whilst in O. expansa, the two valves are of approximately equal size. Waagen (1901) believed that the apparent smaller size of the right valve of O. inequivalvis was caused by the right valve being formed of more delicate tissue (sic) than the left, and was more easily abraded, but bivalved specimens from the Kellaways Rock of Kellaways, and elsewhere, reveal that the size difference between the two valves was original. Owing to the greater size attained by the right valves of O. expansa, the ribbing is much coarser than in O. inequivalvis, and the division into primaries, secondaries and tertiaries is rather irregular. There is also a difference of inflation, O. expansa having an extremely flat left valve, even in large specimens, the average inflation being 18%, compared with 25% in O. inequivalvis.

The ornament pattern and the prominence of the auricles are of no value in the specific discrimination of the two species, as O. inequivalvis is so variable, and often parallels the form of the left valve of O. expansa. Indeed, it is very difficult to separate these two species in the absence of associated left and right valves, the character of inflation being on its own an

unreliable index, and where only single valves are found in the Corallian, it is probably best to identify them as Oxytoma sp. For this reason, the lower end of the range of O. expansa is not known with certainty, as no associated left and right valves have been found lower than the Corallian, although Arkell (1933, p. 195), and Cox & Arkell (1948, p. 7) record O. expansa from the Cornbrash, Kellaways Beds. and Hackness Rock. These records cannot be verified until articulated or associated valves are found at these horizons.

An unusual feature of O. inequivalvis is its apparent lack of a ctenolium, there being no sign of one on the well-preserved right valves from the Lamberti Zone Oxford Clay of Woodham, Bucks. It is uncertain whether this is merely an unusual feature of specimens from this horizon, or whether it is true of the species as a whole, specimens from other horizons not being well enough preserved to show the feature. In a species with such a well-developed byssal notch as O. inequivalvis, it seems strange that a ctenolium should be absent, unless there were so few byssal threads that the ctenolium became unnecessary.

The specimens from the Kellaways Clay of Putton Lane brickyard, Chickerell, Weymouth, Dorset, mentioned in Arkell (1933, p. 194) are preserved in the Sedgwick Museum (SM J47646) and Oxford University Museum (OUM J8612, J13127). The specimens (about 35 in all) are mostly left valves, preserved in 3 small concretions, showing very strong, wire-like primary ribs, separated by wide interspaces bearing only very faint tertiaries in some specimens. By virtue of the ribbing style, the wire-like nature of the ribs, and the slightly greater inflation,

Arkell separated these specimens from O. inequivalvis and
O. expansa. However, these specimens agree well in ribbing style
with many specimens from the Lower Oxford Clay, which themselves
grade into forms indistinguishable from O. inequivalvis,
although there are four specimens with very strongly divergent
primary ribs of a style not seen elsewhere. Regarded as a
population, these specimens belong to O.inequivalvis, being merely
one of the more extreme local races which sporadically occurred.

The synonomy of this species is relatively straight
forward as regards the British specimens, but notoriously
complex with regard to foreign ones, in view of the many races
occurring at different horizons in different areas. For this
reason, only the British references, and the most important
continental ones are recorded here. The few British specimens
which have been referred to O. münsteri (Morris & Lycett, 1855,
p. 129, pl. 14, fig. 6) are inequivalved examples, and cannot be
considered to belong to Bronn's species. Examination of Morris
& Lycett's figured specimen (SM J4109), from the Inferior Oolite
of Yorkshire, reveals that it clearly belongs within
O. inequivalvis. The same is true of the specimens figured by
Roeder (1882, p. 58, pl. 1, figs. 10a, 10b) from the Zweischalerbank
(Corallian) of Oberlarg, Germany, which are clearly inequivalve,
and extend the range of O. inequivalvis up into the Oxfordian.

Rollier (1914 , p. 400) believed the specimens figured
by Sowerby as his figs. 2 and 3 of pl. 244 to belong to different
species, accepted Sowerby's pl. 244, fig. 3 as A. inequivalvis
sensu stricto, and introduced the name Pteria phillipsi nom. nov.

for Sowerby's pl. 244, fig. 2. As this specimen was later designated lectotype of A. inequivalvis by Arkell (op. cit.), Rollier's name is a synonym of A. inequivalvis.

Arkell (1939, p. 137) thought that the species of Oxytoma which occurs in the Lamberti Limestone (Lamberti Zone) and basal Mariae Zone of Woodham, Bucks., was distinct from both O. inequivalvis and O. expansa, and referred it to O. interlaevigata (Quenstedt) on the basis of the figure of that species given by Borissiak (1909, p. 21, pl. 1, fig. 9). Examination of a population of 'O. interlaevigata' from Woodham reveals that this species properly belongs with O. inequivalvis.

Range and occurrence   Lias - Kimmeridgian of Europe, widespread. In Britain, it occurs in the Lias, Inferior Oolite, Great Oolite, Fullers Earth, Kellaways Rock, Oxford Clay and extends into the Kimmeridge Clay (Cox & Arkell, 1948, p. 7). It is abundant in the Kellaways Rock (Calloviense Zone) of southern England, and throughout the L. Oxford Clay, occurring most commonly in the bituminous shale facies. It is more restricted in the M. Oxford Clay, but is abundant in the upper part of the Lamberti Zone at Woodham (the Lamberti Limestone), and is rare in the U. Oxford Clay. It occurs throughout the Kellaways Rock and Hackness Rock of Yorkshire.

Genus MELEAGRINELLA Whitfield, 1885 (p. 71)

Synonyms: Clathrolima Cossmann, 1908

Echinotis   Marwick, 1935

Echinotus   Cox, 1969

Type species   Subsequently designated by Cox, 1941, p. 134,
Avicula curta Hall, 1852, p. 412, pl. 2, fig. 1, from the Upper
Jurassic of the U.S.A.

Diagnosis   Small to medium sized shells, suborbicular
in outline;   left valve strongly convex, right valve flat or
very feebly convex, the left valve much larger than the right;
both valves usually with small pointed posterior auricles,
right valve with small anterior auricle, and a deep, narrow,
subauricular notch;   left valve lacking anterior auricle;
ligament area almost in plane of valve margins in left valve,
perpendicular to it in right valve;   resilifer broadly trigonal,
with toothlike protuberance anterior to it in the left valve;
left valve ornamented with narrow squamose radial riblets, right
valve smooth or with weak radial riblets.

Remarks   As Cox (1941, p. 133) has shown, Meleagrinella
is the earliest valid name for the group of small pectinacea
which includes Avicula echinata Smith. This name was overlooked
by Cossmann (1908, p. 296) and Marwick (1935, p. 301), who
introduced the names Clathrolima and Echinotis for the same group.
Several specimens of Avicula curta Hall, the type species, are
preserved on a slab of rock from the Oxfordian Sundance Formation
of South Dakota, U.S.A., now in the BM (NH) (no. L 58878)
and show many close similarities to the British Callovian
species M. braamburiensis (Phillips).

<u>Meleagrinella braamburiensis</u> (Phillips ex J. de C. Sowerby Ms)

Pl. 8, figs. 14-21, Pl. 9, figs. 1-10, 12.

.   1829 <u>Avicula braamburiensis</u> sp. nov.; J. de C. Sowerby in
          Murchison, p. 323 (nom. nud.)

v*   1829 <u>A. braamburiensis</u> sp. nov.; Phillips, pl. 6, fig. 6.

v.non 1855 <u>A. braamburiensis</u>   Phillips ; Morris & Lycett,
          p. 129, pl. 15, figs. 6, 7   <u>M. lycetti</u> (Rollier).

.?   1860 <u>Pecten sp.</u>; Damon, pl. 3, fig. 2.

.   1883 <u>Pseudomonotis subechinata</u> sp. nov.; Lahusen, p. 85,
          pl. 2, figs. 6, 7.

.non 1894 <u>A. braamburiensis</u>   Phillips ; Woodward, p. 44,
          fig. 13. = <u>M. lycetti</u> (Rollier)

.   1909 <u>P. subechinata</u> Lahusen; Borissiak, p. 24, pl. 2, figs.
          14-21.

.   1915 <u>P. subechinata</u> Lahusen; Krenkel, p. 290, pl. 26,
          figs. 13-15.

v*   1932 <u>P. braamburiensis</u> (Phillips); Douglas & Arkell, p. 163,
          pl. 12, figs. 5, 6.

.   1934 <u>P. ornati</u> (Quenstedt); Stoll, p. 17, pl. 2, fig. 5
          (non Quenstedt).

.   1934 <u>P. substriata</u> (Munster); Stoll, p. 18, pl. 2, fig. 6.

v.   1972 <u>Meleagrinella braamburiensis</u> (Phillips); Walker,
          p. 122, pl. 7, fig. 5.

<u>Type specimen</u>   Neotype designated by Douglas & Arkell,
1932, p. 168, pl. 12, fig. 6, from the Hackness Rock of
Scarborough, Yorkshire, preserved in the Yorkshire Museum

(no. YM 872). The specimen figured by Phillips (1829, pl. 6, fig. 6) is lost (Arkell, op. cit.).

Diagnosis   Medium to large sized species (up to 33.7 mm L), suborbicular, left valve about twice the size of the right valve; left valve suborbicular to subquadrangular, convex, usually slightly higher than long (H 91.7-122.2 %, $\overline{x}$ 103.2 %), of low inflation (I 20.8-44.6 %, $\overline{x}$ 33.0 %), with umbones slightly anterior of median (AL 42.2-46.5 %, $\overline{x}$ 46.5 %); right valve suborbicular, flattened to gently convex (I 18.4-29.7 %, $\overline{x}$ 23.3 %), height less than length (H 83.4-100.7 %, $\overline{x}$ 93.5 %), with submedian umbones (AL 44.3-51.9 %, $\overline{x}$ 49.5 %); left valve ornamented with 35-55 fine primary radial riblets, usually squamose, with intercalated secondaries on the middle regions of the shell; right valve smooth (in juveniles), or ornamented with 35-50 fine radial riblets, more delicately squamose, sometimes with faint secondaries.

Measurements

See Appendix 3.

LV		L	H	I	AL	Lh
	N	59	58	14	8	4
	$\overline{x}$	19.6 mm	103.4 %	33.0 %	46.5 %	46.9 %
	Max	33.7	122.2	44.6	46.5	51.8
	Min	8.0	91.7	20.8	42.2	38.2
	OR	25.7	30.5	23.8	4.3	13.6

RV	L	H	I	AL	Ih
N	21	21	5	5	1
$\overline{x}$	15.2 mm	93.5 %	23.2 %	49.8 %	48.6 %
Max	26.5	100.7	29.7	51.9	48.6
Min	7.0	83.4	18.4	44.3	48.6
OR	19.5	17.3	11.3	7.6	0

<u>One specimen</u>   (Stewartby, bed 6E).

LV   33.7 mm L

RV   17.5 mm L (51.9 %).

<u>Description</u>   Medium to large sized species, suborbicular
to subquadrangular in outline, inequilateral, inequivalve,
left valve about twice the size of the right valve; left
valve subquadrangular in outline, up to 33.7 mm long, usually
slightly higher than long (H $\overline{x}$ 103.4 %); left valve with a
short, prominent, pointed posterior auricle, its dorsal margin
straight, its posterior margin oblique, giving rise to a slight
concavity in the posterior shell margin; no left anterior
auricle; anterior part of the dorsal margin short, straight,
passing into the evenly convex anterior margin via a rounded
angle; anterior margin curved continuously with the ventral
margin; posterior margin oblique, nearly straight to gently
convex, never as rounded as the anterior margin; posteroventral
angle rounded, not prominent; umbones slightly anterior (AL $\overline{x}$
46.5 %), inflated, rounded, orthogyrate, salient about 2 mm
above the hinge margin; inflation variable, but usually low
(I $\overline{x}$ 30.0 %). Left valve ornamented with 35-55 fine primary

radial riblets, separated by interspaces about three times the width of the ribs, and extending onto the posterior auricle, often with secondary riblets becoming intercalated ventrally; usually the riblets are squamose, to a variable extent, although in many examples there is no evidence of squamosity; the squamae occur at the junctions of the radial riblets and the concentric growth lines. Hingeline straight, about half the length of the shell (Lh 38.2-51.8 %, $\overline{x}$ 46.9 %), two-thirds of its length being anterior to the umbones; resilifer subrectangular in outline, deep, located below and posterior to the umbones, placed more or less in the plane of the commissure, extending almost halfway to the posterior end of the hinge margin. Immediately anterior of the resilifer is a prominent, rounded, tooth-like protuberance which projects ventrally into the shell cavity (Fig. 2.26a). On the anterodorsal extremities of the shell, directly adjacent to the anterior end of the hingeline, are several obliquely directed corrugations, which may represent byssal grooves. Posterior adductor muscle scar placed halfway between the cardinal plate and the ventral margin, elliptical in shape, with its concave side ventrally, its anterior extremity just posterior of the midaxis of the shell, and its posterior extremity almost reaching to the posterior margin; anterior adductor not visible. Pallial line not seen.

Right valve about half the size of the left valve, suborbicular (H $\overline{x}$ 93.5 %) in outline, inequilateral, bialate; posterior auricle broad, flattened, pointed, not clearly differentiated from the body of the shell; anterior auricle

very small, pointed, marked off from the body of the shell by
a deep auricular sulcus, with a well-developed byssal notch
beneath it. Hingeline straight, about half the length of the
shell (Lh $\bar{x}$ 48.6 %), almost all of its length being posterior
to the umbones; anterior, ventral and posterior margins
continuously curved to give a suborbicular outline, the dorsal
part of the posterior margin sometimes gently reflexed, sweeping
into the obliquely truncate posterior margin of the posterior
auricle. Umbones submedian (AL $\bar{x}$ 49.5 %), small, pointed,
orthogyrate, hardly salient to the hinge margin. Inflation low,
but valves always convex in section (I $\bar{x}$ 23.3 %). Ornamented
by 35-50 fainter primary radial riblets, with some intercalated
secondaries, becoming more prominent as the shell increases in
size; in larger examples (L > 20 mm), weak squamae may
sometimes be seen, but more often, only a faint reticulate
pattern of ornamentation is visible, and in most smaller
specimens, concentric growth-lines dominate over radial elements;
when present, the radial ribs continue onto the posterior auricle.
Resilifer small, triangular, located immediately posterior of
the umbo, and placed almost perpendicular to the plane of the
commissure on a flat cardinal platform (Fig. 2.26b). Byssal
notch deep and narrow, placed directly beneath the anterior
auricle, ctenolium apparently absent. Posterior adductor muscle
scar large, orbicular, its centre about two-thirds of the shell
height below the hinge margin, its anterior edge just posterior
to the mid-axis of the shell, the scar reaching almost to the
posterior margin of the valve; anterior scar not visible,

pallial line simple.

Remarks   The name *Avicula braamburiensis* was published
independently by both J. de C. Sowerby and Phillips in 1829,
for specimens from Brora and Scarborough respectively, but as
Sowerby's record was a nomen nudum, whilst Phillips was
accompanied by a figure, Phillips specimen must be taken as the
type. It is now known that both Sowerby's and Phillips' records
refer to specimens from approximately the same horizon
(Athleta - Lamberti Zones) and comparison of specimens from the
two areas shows that they do in fact belong to the same species.
It also seems probable that Phillips followed Sowerby in using
the name *A. braamburiensis*, as the name comes from the locality
where Murchison collected the specimens later identified by
Sowerby, Braambury Hill, Brora, Sutherlandshire, and it is
difficult to see from where else Phillips could have derived his
name. It would thus be more correct to record the species as
A. braamburiensis Phillips (J. de C. Sowerby Ms). The type is
lost, and a neotype has been designated by Douglas & Arkell
(York. Mus. YM 872).

In 1932, Arkell (in Douglas & Arkell, p. 163) redescribed
and figured topotypes of this species from the Hackness Rock of
Scarborough, placing them in the genus *Pseudomonotis*, but the
material he used in his study consisted solely of steinkerns,
and details of the ornament pattern could not be made out.
Arkell (op. cit. p. 164) states that *P. braamburiensis* has
"the left valve ornamented with 25-30 fine, thread-like ribs,
which are faintly knotted at long intervals where crossed by some

of the more prominent of the indistinct growth-lines".
However, not all the ribs on the shell of this species are
strongly enough impressed to show up on a steinkern, and so
Arkell's diagnosis of the number of ribs is too low.

Variation within a population of M. braamburiensis is
very great, and is reflected mainly in the degree of inflation,
and the style of ornamentation (Fig. 2.27). Variation between
populations found at different levels in the Lower Oxford Clay
is even greater, but on the basis of general features of the
populations, the range of variation within each, and the lack of
any systematic variation, there is no justification for splitting
the species into geographical or stratigraphical subspecies.
At most horizons within the Callovian where M. braamburiensis
is common, the dominant form is one of small to medium size, with
low inflation and an ornament pattern of strong radial riblets,
with traces of squamosity. At a few horizons, such as bed 12F
(Grossouvrei Subzone) of Stewartby, the dominant form is of
medium size, low inflation, and strongly squamose, agreeing
perfectly with the specimens figured by Borissiak (1909, p. 24,
pl. 2, figs. 14-21) as Pseudomonotis subechinata Lahusen. In
association with this strongly squamose form are more 'normal'
forms with much fainter squamae, suggesting that variation is
continuous. In both these forms there is a strong tendency for
the young specimens to be very much more inflated than the older
ones (assuming a simple relationship between age and size), and
so at any one horizon it is possible to find three apparently
different morphotypes, which prove to grade into one another if

a large enough population is studied. For this reason it seems unwise to introduce further confusion by splitting the species, although perhaps the coarsely squamose form could be referred to var. subechinata Lahusen.

Most of the Lower Oxford Clay specimens are too fragile to allow close examination of the hinge area, but four specimens from the Oxford Clay (horizon unknown) of Cock Hill, Trowbridge, Wilts. (GSM Y2087-Y2090, Hudleston Colln.) are thicker-shelled than the specimens from the Midlands, and show the cardinal area clearly. The most obvious feature is the tooth-like protuberance anterior to the umbo of the left valve, which apparently fits into a corresponding socket in the right valve, acting as a safeguard against excessive lateral movement of the valves. There is usually a slight depression anterior to the protuberance, which accommodates the small right anterior auricle. The arrangement of the ligament is such that the resilifers of the left and right valves are set at right angles to one another, their ventral margins more or less touching.

There are marked differences between M. braamburiensis and its close stratigraphical relatives M. echinata (Smith) from the Cornbrash, and M. ovalis (Phillips) from the Corallian. M. echinata may be distinguished by its smaller size (L up to 20 mm); its greater inflation; its fewer number (up to 40) of wire-like, more widely spaced ribs on the left valve, the ribs being densely squamose, especially on the anterior and posterior extremities; the more elongate and pointed posterior auricle of both valves; and the ornament of the right valve, which is only

very slightly smaller than the left valve, and has an ornament
pattern of up to 16 low, faint, very divergent radial riblets
with no squamae. Cox (1940, p. 95) believed, on the basis of
specimens of Pseudomonotis echinata from the Bathonian of Cutch
(India), that the form present in the English Lower Cornbrash,
and identified as P. echinata, was merely a fairly well-defined
race of a long-ranging species, which showed much greater
variability in other parts of the world. However, the British
Bathonian and Callovian species of Meleagrinella are clearly
separable, and the author believes that it is more useful to
retain them as two separate species, rather than unite them, as
Cox would have liked.

M. ovalis is more difficult to separate from M. braamburiensis,
but nevertheless, several features serve to distinguish them: in
M. ovalis, the posterior auricle is much smaller and less well-
developed; the hingeline of the left valve is rather longer
(Lh $\bar{x}$ 61.9 %); the ribbing style consists of densely-packed
fine radial riblets on both valves, the difference between this
style and the ribbing on the right valve of M. braamburiensis
being particularly well-marked; neither are the squamae clearly
developed in M. ovalis, although the concentric elements of
ornamentation are much stronger than in M. braamburiensis.

The specimens collected from boreholes in the Kellaways
Rock and L. Oxford Clay of the Kent coalfield, mentioned by
Lamplugh & Kitchin (1911) and Lamplugh, Kitchin & Pringle
(1923) as Pseudomonotis sp. nov. are preserved in the Geological
Survey Museum and have been examined by the author. Lamplugh &

Kitchin (1911) stated that this species was characterised by its "relatively greater height than length, its strongly inflated left valve and its low obliquity" and had "fine radial ribs, showing no asperities, with irregularly intercalated secondary ribs". Study of the specimens reveals that they are all referable to M. braamburiensis, showing a range of variation compatible with that seen elsewhere, and that in fact, inflation is not any greater than in topotypes of M. braamburiensis; there is also a greater range of obliquity than Lamplugh & Kitchin admitted, and most of the specimens are steinkerns with remnants of imperfectly preserved shell material.

Monotis substriata Münster seems closely comparable with M. braamburiensis, although it appears to lack the squamae so often seen in the British species. The specimen figured by Damon (1860, pl. 3, fig. 2) as Pecten sp. is now unfortunately lost, but appears to be the right valve of a Meleagrinella. Pseudomonotis echinata Lahusen (1883) agrees well with the strongly squamose variety of M. braamburiensis, and is almost certainly synonymous.

Range and occurrence   Common in the Kellaways Beds (L. Callovian) of the Kent coalfield, and Wiltshire. Abundant throughout the L. Oxford Clay of England (Calloviense – Athleta Zones), and in the Hackness Rock of Yorkshire (Athleta – Lamberti Zones). Also recorded from the Kellaways Rock of Yorkshire, the Shales of the Cornbrash, Yorkshire (Wright, 1968), and the Clynelish Quarry Sandstone of Brora, Sutherlandshire.

In Europe, it is found in the Callovian of Germany and Russia.

Family ENTOLIIDAE Korobkov, 1960

Genus ENTOLIUM Meek, 1865 (p. 478)

Type species   Originally designated by Meek, 1865, p. 478, Pecten demissus Phillips, "as illustrated by Quenstedt, 1858, p. 353, pl. 48, figs. 6, 7" (non Phillips; = Pecten disciforme Schuebler in Zieten, 1833, p. 69, pl. 53, figs. 2), from the Aalenian of Germany.

Diagnosis   Byssal notch absent in all stages of development; margins closed laterally; incised ligamental area usually present and extending parallel to the hingeline on either side of the resilifer; cardinal crura variably developed, auricular crura present; inner layer of foliated calcite, outer layer radially fibrous.

Subgenus Entolium s.s.

Synonymy: Protamusium Verrill, 1897

Protamussium Paris & Richardson, 1915

Protomusium Stewart, 1930

Entholium Tzankov & Boncev, 1932

Etolium McLearn, 1948

Diagnosis   Shell exterior smooth;   auricles of left
valve projecting above the hinge line, usually as angular wings.

Discussion   Hertlein (1969, p. N346) believed that
Quenstedt's figure (1858, pl. 48, figs. 6, 7) of E. demissum
(Phillips) from the Aalenian represents a species distinct from
that of Phillips (1829, pl. 6, fig. 5), and is referable to
E. disciforme (Schuebler in Zieten, 1833, p. 69, pl. 53, fig. 2).
Other authors, including Cox (1952, p. 34) have united these
two species into a long-ranging one, to which Phillips name
was applied.   In either case, Meek (1865, p. 478) designated
Quenstedt's figures as the genotype.

There is some doubt as to which valve is which in
Entolium, as the adductor muscle scars have not been seen, and
traditionally the valve with the elevated dorsal wings has been
thought of as the right valve.   Newell (1969a, p. N347) suspects,
by analogy with Pernopecten Winchell from the Upper Palaeozoic,
that it is in fact the left valve which possesses elevated
dorsal auricles, and his views are followed here.

Speden (1967, p. 15) has discussed the generic status
of Entolium, and in particular, its relationships with
Syncyclonema Meek, a genus often placed in the synonymy of
Entolium, even though it predates Entolium.   Much of the
confusion concerning the two genera was caused by the fact
that the original diagnosis and figures of Syncyclonema (Meek,
1864, p. 31; figured in Hall & Meek, 1856, p. 31, pl. 1, figs.
4a-4c as Pecten rigida sp. nov. /non J. Sowerby, 1818/) were
brief and inadequate.   However, Speden has redescribed the type

species (P. rigida Hall & Meek /non J. Sowerby7 = P. halli Gabb),
designated and figured a lectotype, and shown Syncyclonema to be
a valid genus, distinct from Entolium on the basis of external
and internal shell morphology. Syncyclonema has a chlamyiid
shape, with a deep byssal notch, strong cardinal crura, and no
auricular crura.

Entolium (Entolium) corneolum (Young & Bird). Pl.9,figs.11,13-16,21.

*   1828   Pecten corneolus sp. nov.; Young & Bird, p. 234,
              pl. 9, fig. 5.

?   1829   Pecten sp.; Phillips, pl. 5, fig. 11.

v   1829   P. demissus sp. nov.; Phillips, pl. 6, fig. 5.

.?   1833   P. phillipsii nom. nov.; Voltz in Thurmann, p. 32
              (nom. nov. pro Pecten sp. Phillips, 1829).

       1836   P. demissus Phillips; Goldfuss, p. 74, pl. 99, fig. 2.

non   1836   P. cingulatus nom. nov.; Goldfuss, p. 74, pl. 99,
              figs. 3a, 3b. (nom. nov. pro Pecten sp. Phillips,
              1829. non Phillips).

v.   1855   P. demissus Phillips; Morris & Lycett, p. 127,
              pl. 14, fig. 7.

non   1858   P. demissus Phillips; Quenstedt, p. 353, pl. 48,
              figs. 6, 7 (= E. disciforme Schübler).

.   1858   P. demissus Phillips; Quenstedt, p. 553, pl. 72, fig. 27.

v.   1859   P. demissus Phillips; Leckenby, p. 8.

       1860   P. demissus Phillips; Damon, pl. 9, fig. 3.

v.   1930   Entolium demissum (Phillips); Arkell, p. 91, pl. 7,
              fig. 4; pl. 9, fig. 8.

. 1932   E. demissum (Phillips); Spath, p. 112, pl. 26, fig. 2.

v. 1932   E. Rhypheum (Schlippe ex d'Orbigny); Douglas & Arkell,
           p. 157.

. 1934   Pecten (Entolium) demissus Phillips: Stoll, p. 22,
           pl. 2, fig. 21.

v. 1935   E. demissum (Phillips); Arkell, p. x, pl. 53, fig. 3.

. 1935   P. corneolus Young & Bird; Arkell, p. xi.

. 1948   E. corneolum (Young & Bird); Cox & Arkell, p. 15.

. 1965   E. corneolum (Young & Bird); Cox, p. 51.

v. 1967   E. demissum (Phillips); Speden, p. 15, pl. 3, fig. 3.

Type specimen   Holotype of Young & Bird's p. 234, pl. 9,
fig. 5, from the Corallian of Malton, Yorkshire, is lost, the
whereabouts of none of Young & Bird's specimens being known.
The specimen figured by Arkell (1930, pl. 7, fig. 4) from the
Osmington Oolite Series (Corallian) of Malton, Yorkshire,
preserved in the Oxford University Museum (OUM J8151), is herein
designated neotype.

Diagnosis   Very variable species, suborbicular to
subovate in form, large to small in size (H 11.1-72.0 mm), length
80.2-95.2 %, $\bar{x}$ 88.5 %; auricles subequal, those of the left
valve projecting above the hingeline; lacking the pair of narrow
sharp-edged internal laminae diverging from the umbo and making
a very acute angle with the auricular margin, distinguishing it
from the group containing E. proteus (d'Orbigny), E. renevieri
(Oppel), E. cingulatum (Goldfuss) and E. partitum (J. de C.

Sowerby); ornament consisting solely of very fine concentric growth lines, not paired, thus differentiating it from E. briconense (Cossmann); occasionally with faint radial growth striae or crumples; E. disciforme (Schübler in Zieten), from the Bajocian, is lower and more orbicular, usually having the length greater than the height.

Measurements

See Appendix 3.

	H	L	umbonal angle
N	15	15	7
$\overline{x}$	29.7 mm	88.5 %	100.7 $^{\circ}$
Max	72.0	95.3	110
Min	11.1	80.2	95
OR	60.9	15.1	15

Description   Valves, excluding auricles, equilateral, equivalve, suborbicular to subovate, up to 72 mm high; auricles small, subequal, those of the left valve projecting above the level of the hingeline, most marked at the distal extremities, meeting the anterodorsal and posterodorsal margins close to the umbo, at an obtuse angle (95-110 $^{\circ}$, $\overline{x}$ 100.7 $^{\circ}$). Length variable (80.2-95.3 % of H, $\overline{x}$ 88.5 %), but always less than height, giving a subovate outline, although the outline becomes almost suborbicular in some forms with a relatively large length/ height ratio; shell outline appears to be independent of size, both subovate and suborbicular forms being found in the juvenile and adult stages. Umbones small, median, pointed, orthogyrate,

not salient to the dorsal margin. Anterodorsal margin straight to very gently concave, byssal notch absent; posterodorsal margin gently concave, diverging at an umbonal angle of about $100°$ ($\angle$ $110°$ – $95°$, $\bar{x}$ $100.7°$); anterior, posterior and ventral margins forming a continuous sweeping curve, of near semicircular outline; anterodorsal and posterodorsal angles rounded, placed about one-third of the shell height below the umbones. Auricular sulcus well-developed, the auricles being clearly marked off from the body of the shell. Ornament of both valves similar, consisting of regular closely-packed, concentric growth lines, occasionally slightly elevated into very faint concentric riblets, and sometimes showing marked growth halts; in well-preserved material, very faint radial striae may be seen to cover the entire body of the shell, giving rise to a fine cancellate pattern of ornament on a submacroscopic level; some small specimens from the Inverbrora Shale Member (Medea Subzone) of Brora show faint radial growth crumples in the shell exterior, superimposed on the fine concentric growth lines. Shell thin, often shiny and 'smooth', with a foliated calcitic inner layer, and a radially fibrous calcitic outer layer. Margin entire, closed.

Ligament placed in a small triangular resilifer, but rarely seen, due to fragility of the shell; incised ligamental area parallel to the dorsal margin not visible for the same reason. Cardinal crura faint, narrow, one on either side of the ligament on each valve, placed very close to the dorsal margin, becoming more clearly defined distally. Auricular crura clearly developed,

reflecting in part the well-defined exterior auricular sulcus, becoming more elevated above the auricles as they are traced distally, and usually swelling out into a small tubercle at the distal extremity (Fig. 2.28). Byssal notch absent in all stages of development, ctenolium absent. Adductor muscle scar and pallial line not visible.

Remarks   This species was covered by Arkell (1930, p. 91) in his monograph of British Corallian Lamellibranchs, and a full synonymy was given there. The synonomy given above refers to the most important British references to the species, and also lists many occurrences not recorded by Arkell; it should be referred to in conjunction with that of Arkell.

The variability of this species may be well seen in populations collected from horizons such as the Hackness Rock and the Corallian, where narrow subovate specimens occur together with much wider suborbicular forms. Arkell (1930, p. 93; 1935, p. xi) originally claimed to be able to distinguish Middle from Upper Jurassic specimens of Entolium, and referred the Bathonian forms to E. Rhyrheum (Schlippe ex d'Orbigny), on the basis of their more orbicular outline and larger umbonal angle. However, he later (Cox & Arkell 1948, p. 15) amended this view, and agreed that the Bathonian forms were indistinguishable from the Upper Jurassic forms, on the basis of the great range of variation at all horizons. Study by the author of collections of British Middle and Upper Jurassic Entolium in all the major British museums, has led him to agree with the view that E. corneolum is a very variable, long-ranging species, specimens

from the Bathonian being indistinguishable from many occurring
in the Upper Jurassic.

The specimen of Pecten sp. figured by Phillips (1829, pl. 5,
fig. 11) from the Oxford Clay may be referable to E. corneolum,
but the holotype is lost, and no topotypes have been seen in the
major British collections. The subequal nature of the auricles,
the apparent lack of a byssal notch, and its general outline
suggest that it is an Entolium, although the dorsal margins
seem a little too concave; this could be due to poor preservation
or bad drawing, but in the lack of comparable specimens, no
definite conclusions can be drawn. Voltz, in Thurmann (1833,
p. 32), proposed the name Pecten phillipsii nom. nov. for
Phillips figure, and so this name should also be noted. Goldfuss
(1836, p. 74, pl. 99, figs. 3a, 3b) compounded the confusion by
introducing the name Pecten cingulatus nom. nov. for the specimen
figured by Phillips, (ignoring the prior name of Voltz),
figuring a specimen clearly different from that of Phillips, in
that it possessed a pair of sharp-topped radial laminae on the
inner shell surface, passing almost to the ventral margin.
E. cingulatum (Goldfuss) has recently been well-figured by Cox
(1965, p. 52, pl. 6, fig. 5). The identity of Pecten vitreus
Roemer and P. solidus Roemer with E. corneolum were noted by
Arkell (1930, p. 93).

The small specimens of E. corneolum from the Inverbrora
Shale Member of Brora (Sutherlandshire) are particularly note-
worthy for the fact that they show the inner surface of the
valves, enabling examination of the cardinal plate and auricular

areas to be made for the first time. Most British specimens of
E. corneolum are seen only in external view, and details of the
hinge area were not previously known, although Speden (1967,
p. 15) noted the hinge structure of some other species of
Entolium (Fig. 2.28).

E. corneolum belongs to the group of species which lacks
internal laminae, but the generic significance of these internal
laminae is still uncertain, as noted by Speden (op. cit.), and
more work on Jurassic Entolium in general is needed to clarify
this matter.

Range and occurrence   This species has been recorded at most
levels from the Inferior Oolite to the Kimmeridge Clay (Cox &
Arkell, 1948, p. 15). In the English Lower Oxford Clay, it is
found in the Jason Subzone of Calvert, the Enodatum, Medea and
Jason Subzones of Norman Cross, the Calloviense Subzone at
Stewartby, and the Medea and Jason Subzones of Bletchley. It is
also common in the Hackness Rock (Athleta - Lamberti Zones) of
Scarborough, the Calloviense and Jason Zones of Brora, the
Oxford Clay of the Kent coalfield, the Athleta - Lamberti Zones
(M. Oxford Clay) of Woodham, Bucks., and the Kellaways Rock of
Wiltshire.

It has been recorded at equivalent levels in the Callovian -
Oxfordian of France, Germany, Switzerland, Poland, Russia,
Greenland and India.

? Family ENTOLIIDAE Korobkov, 1960

Genus BYSSENTOLIUM gen. nov.

Type species.   Byssentolium hudsoni sp. nov., from the
Grossouvrei Subzone, Coronatum Zone, Lower Oxford Clay of the
East Midlands.

Diagnosis   Shell externally resembling Entolium, but
differing from it in the possession of a byssal notch beneath
the right anterior auricle throughout life, giving a slightly
chlamyiid shape (Fig. 2.29); no ctenolium; auricles small,
subequal, the anterior slightly larger than the posterior, those
of the right valve tending to project a little way above the
dorsal margin; auricular crura well-developed; cardinal crura
weakly-developed, that of the anterior auricle of the right
valve most clearly-developed; hinge edentulous.

Remarks   Some species of Entolium (Cteniopleurium)
are thought to have a byssal notch in their juvenile stages
(Hertlein, 1969, p. N347), but this is a rare feature, and most
Entolium lack a byssal notch at all stages of growth; an
exception is E. frontalis (Dumortier), which appears to possess
a notch throughout life (N.J. Morris, 1973, pers. comm). Meeks
original diagnosis (1865, p. 478) of Entolium stated that a
byssal notch is absent, and study of many examples of the type
species - E. demissum (Phillips) - supports this observation, as
even in their very young stages (heights of 5 mm or less) there
is no trace of a byssal notch. The abundant material of

Byssentolium hudsoni to be found in the Grossouvrei Subzone
Oxford Clay of the English Midlands reveals that even in the
largest specimen known (H 12.3 mm), a byssal notch is still
clearly developed, although there is never any trace of a
ctenolium. For this reason, B. hudsoni must be considered
separate from the E. demissum group.

The relationship of B. hudsoni to other species of
Entoliidae is not clear, placement in that family being based
on the many gross similarities to Entolium. The projection of
the auricles of the right valve above the hingeline, the well-
developed auricular crura, the posterior crus swelling out into
a prominent peglike feature at its distal extremity, and the
overall similarity of ornament all serve to emphasize the close
relationships between Byssentolium and Entolium s.s. It can be
demonstrated that in B. hudsoni it is the right valve which has
the auricles projecting above the hingeline, as the same valve
has the byssal notch. This appears to support the 'traditional'
view that it is the right valve of Entolium which has elevated
auricles, not the left, as was suggested by Newell (1969a, p.
N347) on the premise of analogy with Pernopecten, an Upper
Palaeozoic Entoliid. However, until the discovery of muscle
scars in Entolium s.s., it is not possible to make clear cut
decisions.

The overall chlamyiid shape of Byssentolium could equally
well suggest that the genus should be placed in the Pectinidae,
but it is difficult to decide where it should belong if that was
the case; in view of the several similarities to Entolium, it

is best placed in the Entoliidae in our present state of
knowledge.

Byssentolium hudsoni sp. nov.   Pl.9,figs.17-20, Pl.10,figs.1-2,4.

Type specimen   Holotype from bed 30, Grossouvrei Subzone,
Coronatum Zone of Norman Cross brickpit, Peterborough,
BM LL27723 . Paratypes (BM LL27724,   27746   ) from the
same locality and horizon, BM LL27748   from bed 14G, Calvert,
LU 69939   -   69940   from bed 14E, Calvert, LU 69936
from bed 25, Norman Cross, LU 69934   -   69935   from bed 15,
Stewartby and BM LL27750   -   27751   from bed 33, Norman
Cross, all from the Grossouvrei Subzone.

Diagnosis   Small to medium-sized species (up to 12.3 mm
high), suborbicular to subovate in outline, length always less
than height (L 80.2-93.8 %, $\bar{x}$ 87.3 %); umbones small, median,
orthogyrate, not salient to the dorsal margin; byssal notch
beneath right anterior auricle in all stages of growth;
ctenolium absent. Cardinal crura weakly-developed, except for
the right anterior crus, which is usually stronger. Auricular
crura strongly-developed. Auricles of right valve projecting
above the hingeline.

Measurements

See Appendix 3.

	H	L	umbonal angle
N	15	15	11
$\overline{x}$	7.3 mm	87.3 %	100.9 °
Max	12.3	93.8	105
Min	4.3	80.2	93
OR	8.0	13.6	12

Description   Small to medium-sized species, equivalve,
inequilateral, of chlamyiid shape, with a marked byssal notch
beneath the right anterior auricle; height always greater than
length ($\overline{x}$ 87.3 %), giving a subovate outline in forms with a low
L value and a suborbicular outline in forms with a high L value.
Umbonal angle 93 - 105°, $\overline{x}$ 100.9°. Left valve not seen.
Dorsal margin straight to gently concave, often with the
auricles elevated slightly above the level of the hingeline;
auricles subequal, the anterior auricles larger than the
posterior, longer and higher, meeting the anterior margin
further away from the dorsal margin than does the posterior
auricle; a well-developed byssal notch is present beneath the
right anterior auricle, giving the anterior margin a concavo-
convex outline as it is followed ventrally (Fig. 2.29);
ctenolium absent; posterior margin slightly concave to evenly
convex, the posterior margin curved continuously with the ventral
margin in forms where the posterior margin is convex; anterior
angle variably rounded, never angular, passing smoothly into the
semicircular ventral margin. Ornament not visible, the shells
being coated with overgrowths of secondary calcite, but as the
ornament is reproduced in other species preserved in this way,

it is likely that they are virtually smooth; the translucent shell, viewed from the inside, shows faint regular concentric markings, which may be faintly represented on the external surface; no radial elements visible. Auricles appear to be smooth.

Auricular crura well-developed, that of the anterior auricle stronger and wider than that of the posterior, the posterior crus swelling out distally into an elevated tubercle. Cardinal crura faint, narrow, placed very close to the hinge margin, formed of the inner shell layer only; the anterior crus much more prominent than the posterior, both becoming better-developed as traced away from the resilifer (Fig. 2.29); Resilifer not seen, all the shells being broken in the centre of the cardinal plate, but judging from the height of the cardinal plate, the resilifer must be very small; no ligament band seen. Adductor muscle scar not visible. Margin entire.

Remarks   The uncertain taxonomic position of B. hudsoni has been discussed above, and need not be considered further here. It appears to be a very restricted species, only having been found in the Grossouvrei Subzone of central England (Calvert to Peterborough), and also at Crook Hill, near Weymouth. However, whenever it occurs, the species is found in great abundance, being commonest in the calcareous clay facies, although it also occurs in the Grammatodon shell bed facies and the Meleagrinella shell bed facies, always in the Grossouvrei Subzone. There also seems to be a close relationship between the appearance of B. hudsoni and the onset of rapidly alternating

facies which occurs in the upper part of the Grossouvrei Subzone, and it seems probable that if similar lithologies were found elsewhere, they would contain B. hudsoni. Further study will hopefully reveal the geographical extent of such facies alternations. No comparable species has been recorded or figured in the literature, although in view of the small size, and frequently poor preservation of the species, this is not totally unexpected.

Range and occurrence   Abundant in the upper part of the Grossouvrei Subzone (Coronatum Zone) of central and southern England. One specimen recorded from the Medea Subzone (Jason Zone) of Norman Cross, Peterborough.

Family PECTINIDAE Rafinesque, 1815

CAMPTONECTES Group Hertlein, 1969

Genus CAMPTONECTES Agassiz in Meek, 1865 (p. 28, 39)

Type species   Subsequently designated by Stoliczka, 1871, p. 425, Pecten lens J. Sowerby, 1818, p. 3, pl. 205, figs. 2, 3 (= Chamites auritus Schlotheim, 1813, p. 103), from the Corallian of the Oxford district.

Diagnosis   Inequivalve, left valve more inflated than right; large byssal notch developed beneath the right anterior auricle; ornament consisting of fine curved divaricate striae, a punctate pattern being produced by their intersection with the fine concentric growth lines.

Subgenus CAMPTONECTES s.s.

Synonymy: Campstonectes von Teppner, 1922

Campitonectes Salisbury, 1939

Camponectes Vyalov & Korobkov, 1939

Diagnosis   As Camptonectes s.l., but with very fine
concentric growth lines, never elevated into ribs; radial
elements consisting of fine divaricate striae, never strengthened
into radial ribs.

Remarks   Camptonectes is one of the best known genera
of British Jurassic Pectinacea, and nothing need be said about
its identity. There has, however, been some controversy over
the authorship of the genus, the name first being used by Meek
(1865, p. 39). In his diagnosis of Camptonectes, Meek (op. cit.)
clearly indicates that the concept of the genus was due to
Agassiz (Ms), and thus under the ICZN rules, the name should be
credited to Agassiz. Meek neglected to designate a type species,
and it was not until 1871 that Stoliczka (1871, p. 425) designated
Pecten lens Sowerby as the type species. The status of
Camptonectes has recently been discussed by Speden (1967, p. 17).

Camptonectes (Camptonectes) auritus (Schlotheim). Pl.10,figs.3,5-6.

    1676 Pectinites Plot; p. 104, pl. 4, fig. 11.
    1813 Chamites auritus sp. nov.; Schlotheim, p. 103
          (reference to Lister, 1678, pl. 9, fig. 51).

1818   <u>Pecten lens</u> sp. nov.; J. Sowerby, p. 3, pl. 205,

       figs. 2, 3.

1818   <u>P. arcuatus</u> sp. nov.; J. Sowerby, p. 3, pl. 205,

       figs. 5, 7.

1822   <u>P. maltonensis</u> sp. nov.; Young & Bird, p. 235, pl. 9,

       fig. 1.

1828   <u>P. maltonensis</u> Young & Bird; Young & Bird, p. 233,

       pl. 9, fig. 1.

?   1828   <u>P. lens</u> J. Sowerby; Young & Bird, p. 234, pl. 9, fig. 18.

1845   <u>P. lens</u> J. Sowerby; d'Orbigny, p. 476, pl. 42, figs. 1,2.

non 1846   <u>P. lens</u> J. Sowerby; Rouillier, pl. C, fig. 13.

non 1853   <u>P. lens</u> J. Sowerby; Morris & Lycett, p. 11, pl. 2,

       fig. 1. (= <u>P. laminatus</u> J. Sowerby, Bathonian).

non 1853   <u>P. arcuatus</u> J. Sowerby; Morris & Lycett, p. 11, pl. 1,

       fig. 18 (= <u>P. rigida</u> J. Sowerby, Bathonian).

1871   <u>P. lens</u> J. Sowerby; Phillips, pl. 13, fig. 24.

1901   <u>P. lens</u> J. Sowerby; Raspail, p. 193, pl. 12, fig. 14.

1930   <u>Camptonectes lens</u> (J. Sowerby); Arkell, p. 94, pl. 7,

       fig. 1; pl. 9, figs. 4-7.

1935   <u>C. lens</u> (J. Sowerby); Arkell, p. xii.

1936   <u>C. lens</u> (J. Sowerby); Dechaseaux, p. 30, pl. 4,

       figs. 9, 9a, 11, 14.

1948   <u>C. auritus</u> (Schlotheim); Cox & Arkell, p. 14.

1952   <u>C. auritus</u> (Schlotheim); Cox, p. 23, pl. 2, fig. 6.

1967   <u>C. auritus</u> (Schlotheim); Speden, p. 17, pl. 4, figs.

       1, 3, 6.

1972   <u>C. auritus</u> (Schlotheim); Walker, p. 123, pl. 7, fig. 10.

Type specimen   The holotype of Chamites auritus Schlotheim,
1813, p. 103 was stated by Schlotheim to be the figure of
Lister (1678, pl. 9, fig. 51), which is itself a copy of the
figure of Pectinites given by Plot (1676, p. 104, pl. 4, fig. 11),
Plot's specimen coming from the Corallian of Headington,
Oxfordshire. The specimen figured by Plot is lost, and so a
neotype is here designated. The two syntypes of Pecten lens J.
Sowerby also come from the Corallian ("Shell-cum-Pebble bed") of
Headington, and are preserved in the Sowerby collection at the
BM (NH), numbers L80525, L80526, and as these are the earliest
figured topotypes still extant, one (BM L80525, J. Sowerby,
1818, pl. 205, fig. 2) is designated neotype. It has been
refigured by Arkell (1930, pl. 9, fig. 4).

Diagnosis   Medium to large sized species (H up to 58 mm),
suborbicular in outline, with length only slightly less than
height (L 86.8-98.5 %, $\overline{x}$ 94.6 %), and umbonal angle 105 $^{\circ}$ -
110 $^{\circ}$; ornament similar on both valves at all growth stages,
consisting of closely packed, fine divaricate radial striae,
densely punctate, rendered finely reticulate by a series of
lightly impressed concentric growth lines. Auricles small, those
of the left valve, especially the anterior auricle, covered by
densely packed, fine vertical growth lines; posterior auricle
of the right valve with punctate radial striae only.

    C. auritus may easily be distinguished from the closely
related, but slightly older (Bajocian - Bathonian) C. laminatus
(J. Sowerby, 1818), as the latter species is narrower and more
subovate (L $\overline{x}$ 85 %, umbonal angle $\overline{x}$ 90 $^{\circ}$), has a tendency for

the ornament of the left valve to coarsen in larger specimens,
the divaricate striae becoming almost riblets, and has different
ornament patterns on the auricles; the anterior auricle of the
left valve has about 10 conspicuous, raised vertical lamellae,
and the posterior auricle of the right valve has a similar
pattern of ornament.

Measurements

See Appendix 3.

	H	L	umbonal angle
N	8	8	7
$\bar{x}$	39.5 mm	94.6 %	107.0 °
Max	58.0	98.5	110
Min	28.0	86.8	104
OR	30.0	11.7	6

Description

Medium to large sized shell (up to 58 mm
high), inequivalve, planoconvex, the right valve almost flat,
the left valve convex; inequilateral, auricles small, unequal,
the anterior auricles larger than the posterior, the anterior
auricle of the right valve larger than that of the left valve,
with a large byssal sinus beneath it. Outline suborbicular to
subovate, height always slightly greater than length (L 86.8–
98.5 %, $\bar{x}$ 94.6 %), umbonal angle 105–110 °, widest in the
suborbicular forms.

Anterior auricle of right valve elongate, dorsal margin
straight to very gently concave, anterior margin truncate,
becoming more convexly rounded ventrally, passing into the

concavely rounded byssal fasciole, and meeting the anterodorsal margin of the body of the shell at about a right angle; auricular sulci deeply impressed on all four auricles; the right anterior auricle also with a well-developed ridge running from the umbo to the posteroventral tip of the main part of the auricle, forming the dorsal edge of the byssal fasciole; right posterior auricle with straight dorsal margin, shorter than that of the anterior auricle, its posterior margin obliquely truncate, becoming gently concave ventrally, and meeting the posterodorsal margin of the body of the shell at an obtuse angle; anterior auricle of the left valve not as elongate as that of the right valve, its dorsal margin straight, the anterior margin obliquely truncate to gently convex, meeting the body of the shell at a very obtuse angle; left posterior auricle short, its dorsal margin gently convex, the posterior margin obliquely truncate, meeting the body of the shell at a very obtuse angle. Auricles of the left valve ornamented with tightly packed fine vertical growth lines, particularly well seen on the anterior auricle; right posterior auricle with punctate diagonal radial striae, anterior auricle with fine concentric growth lines.

Main body of shell suborbicular; umbones small, submesial, orthogyrate, not elevated above the dorsal margin, rounded. Valves of similar outline, but unequally inflated, the right valve almost planar, the left valve markedly convex. Anterodorsal margin evenly concave, the anterior auricle meeting it at about its midpoint; anterior angle sharply rounded, passing evenly into the semicircular ventral margin; postero-

dorsal margin gently convex, the posterior angle more rounded
than the anterior, passing smoothly into the ventral margin.
Ornament of both valves similar, consisting of closely packed,
fine, divaricate striae, densely punctate, markedly divergent at
the anterior and posterior extremities; fine concentric growth
lines interact with the divaricate striae to produce a finely
reticulate pattern upon which the punctae are superimposed.

Inner surface of hinge margin with fine vertical ridges
and grooves, particularly well-developed anterior of the
resilifer, for articular restraint. Resilifer not seen, but it
must be small, because of the low height of the hinge plate in
the umbonal region. One cardinal crus on each valve, anterior
and posterior to the resilifer, placed very close to the hinge
margin and parallel to it, the crura becoming more strongly
developed distally. Auricular crura absent (Fig. 2.30). A
strong ridge runs from the area of the resilifer to the postero-
ventral extremity of the main part of the right anterior auricle,
marking the dorsal edge of the byssal fasciole; a second ridge
runs from the resilifer to the part of the right anterior
auricle above the byssal notch, which may represent a vestigial
auricular crus, although crura are absent on the posterior
auricle of the right valve and on both auricles of the left
valve. Ctenolium well-developed, placed along the anterodorsal
margin of the right valve, immediately anterior to the location
of the byssal notch. Pallial line and musculature unknown.

Remarks   The provenance of J. Sowerby's two syntypes
of P. lens, said to be "the forest marble near Oxford", has
been shown by Arkell (1930, p. 95) to actually be the Corallian
(Berkshire Oolite Series) of Headington, Oxford. Arkell has also
shown that several species of Camptonectes may be distinguished
in the Middle and Upper Jurassic of Europe, and that there is
no justification for uniting all Middle and Upper Jurassic
specimens in C. lens, as was done by Staesche (1926). Arkell
also noted that much of the confusion over the species of
Camptonectes was caused by French and German workers using
Sowerby's several names without checking the types. The common
Callovian - Kimmeridgian species C. auritus may be distinguished
from the Bajocian - Bathonian C. laminatus (J. Sowerby), in
details of outline and ornament, as noted in the diagnosis above.

Several entries omitted by Arkell have been placed in
the synonomy here. Pecten maltonensis Young & Bird is clearly
conspecific, their figure showing a well-preserved right valve,
and it is probable that their 1828 (pl. 9, fig. 18) figure of
P. lens represents a poorly-preserved left valve, although there
seems to be a lack of divaricate ornament. Couffons (1919)
figure of P. lens shows a poorly preserved steinkern of similar
shape to Camptonectes, but lacking all external ornament.

Range and occurrence Upper Cornbrash, Kellaways Rock, Hackness
Rock, Corallian and Kimmeridge Clay of Britain. Also in the
Inverbrora Shale (Callovian) of Brora (Sykes collection). In
the Lower Oxford Clay of the Midlands, it has been found in
the transition beds (Enodatum Subzone) at Stewartby, and in a

similar lithology (Medea Subzone) at Bletchley. Arkell (1930,
p. 96) records a possible occurrence from the Forest Marble of
Chippenham (GSM 49043).

Widespread in the Callovian - Kimmeridgian of Europe;
see Arkell, 1930, p. 94.

Genus CHLAMYS Röding, 1798 (p. 161) /ex Bolten Ms/

Type species   Subsequently designated by Herrmannsen,
1847, p. 231, Pecten islandicus Müller, 1776, p. 248. Recent,
circumboreal.

Diagnosis   Suborbicular, often slightly higher than
long, commonly somewhat oblique; both valves convex, left
valve usually more so than the right valve, but in some species,
valves of almost equal convexity; auricles clearly delimited,
usually large, with large byssal notch beneath the right
anterior auricle; ctenolium usually present; sculpture of
radial (usually stronger) and concentric elements, with
scalelike spines often developed at their junctions, especially
on the left valve; in the adult stages, intercalatory ribs
are often present in the interspaces; margin scalloped;
cardinal crura variable in number and size.

Subgenus CHLAMYS s.s.

Synonymy: Clamys Leach, 1815

Chalmys Dollfus & Dautzenberg,
1886

Actinochlamys Roberto, 1898

Myochlamys von Ihering, 1907

Chlamydina Cossmann, 1907

Zygochlamys von Ihering, 1907

Belchlamys Iredale, 1929

Mimachlamys Iredale, 1929

Scaeochlamys Iredale, 1929

Talochlamys Iredale, 1929

Veprichlamys Iredale, 1929

Diagnosis   Usually higher than long, anterior auricles longer than posterior auricles; sculpture of numerous, generally grooved or striated and spinose, radial ribs; inner margin commonly with rounded, grooved, weak riblets; cardinal crura weak or nearly obsolete.

Remarks   Chlamys s.s. is readily distinguished from other Jurassic subgenera such as Radulopecten by virtue of its much greater rib density, which often gives a strong, finely reticulate ornament pattern on both valves. The ornament is similar to that seen in Camptonectes (Camptochlamys), a member of the Camptonectes group, where strong concentric lamellae interact with radial riblets to give a similar, but slightly coarser, reticulate pattern. Camptochlamys may also be distinguished by the presence of faint Camptonectes-type ornament on the auricles and adjacent areas, and by its larger byssal notch and fasciole.

In Chlamys s.s., the strength of the concentric lamellae
is rather variable, most Recent species, including the type
species C. islandicus, having only very faint concentric
ornament, usually developed as spinose protuberances on the
radial riblets. In contrast, most Jurassic species, such as
C. bedfordi sp. nov., C. splendens (Dollfus), C. nattheimensis
de Loriol and C. qualicosta (Etallon) have stronger concentric
lamellae, often forming conspicuous features which give rise
to a marked reticulate ornament pattern.

Chlamys (Chlamys) bedfordi sp. nov. Pl. 10, figs. 7-11.

Type specimen   Holotype, BM LL27724   , from bed 10A,
Grossouvrei Subzone, Coronatum Zone, M. Callovian of Calvert,
Bucks. Four syntypes (BM LL27725 -   27728   ) from bed 10D,
Stewartby (Obductum Subzone); bed 10D, Calvert (Grossouvrei
Subzone); bed 16, Norman Cross (Grossouvrei Subzone), and bed 6,
Calvert (Obductum Subzone).

Diagnosis   Small species (up to 9.7 mm L), suborbicular,
with length and height about equal (H 100-103.0 %, $\overline{x}$ 101.5 %;
right valve with a narrow byssal notch below the anterior
auricle, byssal fasciole small; right valve slightly more
convex than the left valve; both valves ornamented by very
fine, densely packed radial riblets, about 70 in the right
valve, and 40 in the left valve, crossed by regular fine
concentric lamellae, to give a microscopically reticulate
pattern.

Measurements

See Appendix 3.

		L	H	Lh	AL	umbonal angle
Overall	N	5	5	2	4	5
	$\overline{x}$	8.6 mm	101.5 %	66.0 %	48.9 %	109.6 °
	Max	9.7	103.0	71.4	53.2	113
	Min	6.6	100.0	60.6	42.4	107
	OR	3.1	3.0	10.8	10.8	6
RV	N	3	3	1	2	3
	$\overline{x}$	6.8 mm	100.7 %	60.6 %	53.2 %	111.0 °
	Max	9.7	101.1	60.6	53.2	113
	Min	9.4	100.0	60.6	53.2	109
	OR	0.3	1.1	0	0	4
LV	N	2	2	1	2	2
	$\overline{x}$	7.3 mm	102.8 %	71.4 %	44.6 %	107.5 °
	Max	7.7	103.0	71.4	46.8	108
	Min	6.6	102.6	71.4	42.4	107
	OR	1.1	0.4	0	4.4	1

Description   Small species (up to 9.7 mm L), suborbicular
in outline (H $\overline{x}$ 101.5 %), subequilateral, bialate, subequivalve,
the right valve slightly more inflated than the left valve.
Hingeline straight, about two-thirds of the overall length of
the shell (Lh 60.6-71.4 %, $\overline{x}$ 66.0 %), the auricles of the left
valve subequal, those of the right valve unequal, the right

anterior auricle higher and longer than the posterior. In the
right valve, the anterodorsal margin of the shell is gently
concave, and marks the position of the deeply excavate
auricular sulcus; the posterodorsal margin is very gently
concave in the region where it abuts against the excavate
auricular sulcus, then becomes gently convex; there is no
perceptible angle between the posterodorsal margin and the
ventral margin, which is evenly rounded in a semicircular
outline; the anterodorsal angle is more clearly defined, and
takes the form of a rounded obtuse angle. The right anterior
auricle is marked off from the body of a shell by a deeply
excavate auricular sulcus, but as there is no well-marked byssal
fasciole, the auricle is closely applied to the body of the
shell; the outer surface of the auricle is gently arched, the
anterior end curving gently down to the anterodorsal margin. The
posterior auricle of the right valve is shorter and more trigonal
than the anterior, but is clearly marked off from the body of
the shell by a deep auricular sulcus; its posterior margin forms
an obtuse angle of about 115 $^{\circ}$ with the hingeline, and is gently
concave in outline, meeting the posterodorsal margin not far
below the hingeline.

In the left valve, both the antero- and posterodorsal
margins are very gently concave, the subequal, trigonal auricles
being marked off from the body of the shell by deep auricular
sulci; at the anterior and posterior extremities of the valve,
the margins become more convex, and pass evenly into the semi-
circular shaped ventral margin, with no clearly differentiated

antero- or posterodorsal angles. In both valves, the umbones are placed in a submedian position (AL 42.4-53.2 %, $\overline{x}$ 48.9 %).

Both valves are ornamented by densely-packed fine radial riblets, the right valve bearing about 70, and the left valve about 40 at the ventral margins; faint intercalatory riblets appear in some of the interspaces towards the ventral margin in both valves; these are crossed by regularly-spaced fine concentric lamellae, which are present over the whole of the body of the shell, and give rise to a microscopically reticulate pattern. Both the concentric lamellae and the radial riblets persist onto the auricles, where the lamellae are strengthened relative to those on the body of the shell; the lamellae are very narrow and wirelike, and usually rather finer than the radial riblets.

A pair of small, weak cardinal crura is present on the cardinal plate of each valve, each crus being short, low and placed subparallel to the hinge margin, and fading distally (Fig. 31). Resilifer not seen. Auricular crura absent, but there is a slight ridge along the line of the auricular sulcus of the right anterior auricle; this being cut in the region of the byssal sinus by the narrow, deeply excavate, transverse byssal notch, which runs subparallel to the hinge margin. Ctenolium not visible. Ventral margin of the shell finely scalloped where the radial riblets reach the margin. Inner shell layer of nacreous aragonite, outer layer of crossed-lamellar calcite.

<u>Remarks</u>   This small, distinctive species, which occurs
sporadically throughout the Lower Oxford Clay of southern
England, does not appear to have been described before; its
small size, high rib density and suborbicular outline make it
an unmistakable member of the fauna. There are similarities in
overall size, general outline and preservation, to specimens of
<u>Byssentolium</u>, but <u>C. bedfordi</u> may easily be distinguished by its
ribbing style and larger auricles.

   <u>Pecten mantochensis</u> Etallon, a small, densely ribbed
species from the Portlandian of France, is rather similar to
<u>C. bedfordi</u>, but differs in being higher and more trigonal than
the British Callovian species. <u>Chlamys subtextoria</u> (Münster),
from the Upper Jurassic of Europe has similar ornamentation to
C. bedfordi, and shares its small size, but the density of
ribbing is much less, only 33 ribs being present; it is also
rather higher and more trigonal than <u>C. bedfordi</u>.

<u>Range and occurrence</u>   A rare constituent of the Lower Oxford
Clay fauna of central England, occurring in the Coronatum Zone
of Calvert, Stewartby and Norman Cross.

Subgenus RADULOPECTEN Rollier, 1911 (p. 158)

<u>Type species</u>   Originally designated by Rollier, 1911,
p. 158, <u>Pecten hemicostatus</u> Morris & Lycett, 1853, p. 10, pl. 1,
fig. 16, from the Great Oolite (Bathonian) of Minchinhampton,
Gloucestershire.

<u>Diagnosis</u>   Right valve usually more inflated than the
left valve, but not always so. Ornamentation variable, typically
with 5-6 pairs of twinned ribs on the right valve, but in many
species this twinning is faint or obsolete, in which case there
are 11-12 prominent radial ribs; left valve ornament closely
allied to that of the right valve, with 5-6 radial ribs in forms
with twinned ribs on the right valve, and 10-11 radials in
forms without paired ribs; right valve also ornamented with
faint regular concentric growth lines, the left valve with
prominent, regular, wire-like concentric lamellae.

<u>Remarks</u>   Cox's (1952) emended interpretation of the
nature of ribbing in <u>Radulopecten</u> has been accepted here, so
that the subgenus includes all of the Jurassic species placed by
Staesche (1926) in the "Group of <u>Aequipecten fibrosus</u> Sowerby".
Thus forms with poorly developed paired ribs on the right valve,
such as <u>C. (R.) fibrosus</u> and some specimens of <u>C. (R.) scarburgensis</u>
and <u>C. (R.) drewtonensis</u> may be included, together with the more
'typical' members of the subgenus, such as <u>C. (R.) hemicostatus</u>.
In essence, <u>Radulopecten</u> now includes most of the Jurassic species
referred to <u>Chlamys</u>.

1.   <u>Chlamys (Radulopecten) scarburgensis</u> (Young & Bird).
        Pl.10, figs. 12-15, Pl. 11, figs. 1-6, 8.

    1822   <u>Pecten Scarburgensis</u> sp. nov.; Young & Bird, p. 234,
            pl. 9, fig. 10.

    1828   <u>P. Scarburgensis</u> Young & Bird; Young & Bird, p. 235,
            pl. 9, fig. 13.

1829   P. fibrosus J. Sowerby; Phillips, pl. 6, fig. 3.
        (non J. Sowerby).

1845   P. discrepans nom. nov.; Brown, p. 157, pl. 65, fig. 17.
        (nom. nov. pro P. fibrosus Phillips non J. Sowerby).

? 1860 P. fibrosus J. Sowerby; Damon, pl. 3, figs. 1, 1a.
        (non J. Sowerby).

1883   P. fibrosus J. Sowerby; Lahusen, p. 23, pl. 2, fig. 3.
        (non J. Sowerby).

1901   P. fibrosus J. Sowerby; Raspail, p. 193, pl. 12, fig. 9.
        (non J. Sowerby).

1924   P. fibrosus J. Sowerby; Cossmann, p. 28, pl. 4, figs.
        19-21. (non J. Sowerby).

1932   Chlamys fibrosa (J. Sowerby); Corroy, p. 188, pl. 27,
        figs. 15, 16. (non J. Sowerby).

1934   Pecten (Aequipecten) fibrosus J. Sowerby var.
        duplicostatus nov.; Stoll, p. 21, pl. 2, fig. 16 only
        (non figs. 17, 18; = C. (R.) fibrosa).

1935   Chlamys scarburgensis (Young & Bird); Arkell, p. xiii.

1936   Aequipecten fibrosus (J. Sowerby); Dechaseaux, p. 47,
        pl. 6, figs. 15, 18, 18a, 19; pl. 7, fig. 1 (non J.
        Sowerby).

1948   Chlamys (Radulopecten) scarburgensis (Young & Bird);
        Cox & Arkell, p. 13.

Type specimen   Neotype, here designated, Sedgwick Museum
Cambridge, SM J12398, Leckenby collection, from the Hackness
Rock (Athleta - Lamberti Zones), Scarborough, Yorkshire (topotype).
Neoparatypes, SM J12399-J12401, same locality and horizon, also

Leckenby collection.

<u>Diagnosis</u>   Medium to large-sized species, up to 76 mm
long, with 9-11 narrow, flat- or round-topped radial ribs on
each valve; these ribs are equal in width or narrower than the
intervening sulci; right valve slightly more convex than the
left valve; radial striae absent from the sulci; ribs on the
left and right valves are of equal prominence; height usually
greater than length (H $\bar{x}$ 108 %), inflation low ($\bar{x}$ 30.5 %);
umbonal angle 83-108 °, $\bar{x}$ 97 °.

        Differs from <u>C. (R.) fibrosa</u> (J. Sowerby) in having fewer,
more divergent ribs, of equal prominence on each valve, the ribs
being narrower than in <u>C. fibrosa</u>; it also lacks the radial
striae which occur in the sulci of <u>C. (R.) fibrosa</u>. <u>C. (R.)</u>
<u>drewtonensis</u> Neale differs in that the left valve is slightly
more inflated than the right, and in the possession of a very
prominent anterior auricle on the right valve. The anterior
auricle is ornamented by 9 fine radial striae in its proximal
6.5 mm.

<u>Measurements</u>

        See Appendix 3.

	L	H	I	Umbonal angle	Ribs
N	12	12	5	10	12
$\bar{x}$	27.1 mm	108.0 %	30.5 %	97.2 °	9.7 ribs
Max	41.5	116.3	34.3	108	11
Min	10.4	99.4	28.3	83	9
OR	31.1	16.9	6.0	25	2

<u>Description</u>　　　　　Medium to large-sized species, up to 76 mm
long, inequivalve, the right valve slightly more inflated than
the left, inequilateral; umbonal angle very variable (83-108 $^{\circ}$,
$\overline{x}$ 97.2 $^{\circ}$), height slightly greater than length (H 99.4-116.3 %,
$\overline{x}$ 108.0 %); suborbicular in outline, with prominent, subequal
auricles; in the right valve, the anterior auricle is slightly
larger than the posterior auricle, has a distinct byssal notch
beneath it, and is ornamented by fine sinuous concentric growth
lines, with no radial elements; the posterior auricle of the
right valve is ornamented by fine vertical striae, the hinge
margin having about 8 coarse tuberculations acting as hinge
teeth; left valve auricles subequal, but not known in detail;
auricular sulci well-developed; ornament of right valve
consisting of 9-11 coarse radial ribs, usually round-topped, but
occasionally flattened and showing pairing of the ribs, the
ribs being equal in width or narrower than the intervening sulci;
the ribs are markedly divergent, the sulci widening towards the
ventral margin, rather than having the ribs widening, as is the
case in <u>C. (R.) fibrosa</u>; the radial ribs are crossed by fine
concentric striae, crossing both ribs and sulci, numbering about
55 to the centimetre; in some specimens, the anterior- and
posteriormost ribs have weakened radial elements, and are
marked more clearly by a line of squamae which represent coarsened
concentric striae; ornament on the left valve similar to that
of the right valve, the ribs being round-topped, of approximately
equal strength, numbering 9-11, and again being markedly
divergent; the sulci are wider than the ribs, often as much as

twice as wide; the ribs and sulci of the left valve are crossed by coarse, wire-like concentric costellae, numbering about 17 to the centimetre, the spacing remaining constant throughout growth. Ventral margin scalloped.

Remarks   C. (R.) scarburgensis, having been described in Young & Bird's (1822) somewhat obscure work on the geology of the Yorkshire coast, was overlooked for over a century before Arkell (1935, p. xiii) recognised its existence as a valid species. At least part of the confusion was caused by the similarity between this species and C. (R.) fibrosa (J. Sowerby), which ranges from the Kellaways Rock to the Upper Oxfordian, and must be considered a very close relative. There are, however, marked differences between the two species, as noted in the diagnosis above, and it is possible to separate even young forms on the basis of rib density and divergence. The neotype (SM J12398), from the Hackness Rock of Scarborough is the largest specimen known (L 41.5 mm), but Young & Bird (1822, p. 234) in their original diagnosis state that "some specimens are three inches long", and it is from this measurement that the maximum size (L 76 mm) is inferred.

Phillips (1829, pl. 6, fig. 3) figured a topotype of C. (R.) scarburgensis, which he identified as P. fibrosus J. Sowerby, but there can be little doubt from Phillips plate that his specimen, now lost, does not belong to Sowerby's species. Brown (1845, p. 157) realised that Phillips had misidentified his specimen, and renamed it Pecten discrepans nom. nov., overlooking Young & Bird's prior name. Several continental

authors (see synonymy) followed Phillips in misidentifying
Sowerby's species, and referred specimens of C. (R.) scarburgensis
to C. (R.) fibrosa. Stoll (1934, p. 21, pl. 2, figs. 16-20)
described Pecten (Aequipecten) fibrosus J. Sowerby, together
with two new varieties of the species, from erratic boulders of
Upper Jurassic age in N.W. Germany. Study of large collections
of C. (R.) fibrosa and C. (R.) scarburgensis shows the
variability in form of the two species, and from this it is
clear that all of Stoll's figures, except her plate 2, figure 16,
belong to C. (R.) fibrosa s.s. The specimen mentioned above
agrees well in size and ribbing style with topotypes of
C. (R.) scarburgensis, and is here assigned to that species.
Dechaseaux (1936, p. 47) also confused the two species, placing
all her specimens in Aequipecten fibrosus, but it is clear from
her plates (pl. 6, figs. 15-20; pl. 7, figs. 1-3) that more
than one species is represented. In fact, Dechaseaux figured
specimens referable to more than two species, her pl. 6, figs. 17,
17a, and 20 being clearly different from both C. (R.) fibrosa
and C. (R.) scarburgensis, as are her pl. 7, figs. 2, 3. Much
work on her actual specimens is needed before they may be
correctly interpreted, but from her two plates, it seems likely
that the specimens she figured on pl. 6, figs. 15, 18, 18a, 19,
and pl. 7, fig. 1 may be placed in C. (R.) scarburgensis.

Range and occurrence   In Britain, this species is known from
the Upper Cornbrash of Scarborough, the Kellaways Rock of
Kellaways, Wiltshire, the Hackness Rock of Scarborough, and the
Oxford Clay of Brill, Wiltshire (GSM 42985). One fragmentary

specimen is known from bed 5 (Enodatum Subzone) of Stewartby, but the species is more abundant in the Middle - Upper Oxford Clay of Oxfordshire and at Woodham (many specimens in the Oxford University Museum).

On the continent, the species appears to have been widespread, being known from the Callovian of Germany (Stoll, 1934), France (Raspail, 1901; Cossmann, 1924) and Russia (Lahusen, 1883), and the Oxfordian of France (Dechaseaux, 1936). The range agrees well with that known in Britain, and this appears to be an essentially Callovian species.

2. Chlamys (Radulopecten) fibrosa (J. Sowerby). Pl. 11,
    figs. 7, 9-12, 16.

    1816 Pecten fibrosus sp. nov.; J. Sowerby, p. 84, pl. 136,
          figs. 1, 2.

    1822 P. fibrosus J. Sowerby; Young & Bird, p. 233, pl. 9,
          fig. 12.

    1822 P. sulcatus sp. nov.; Young & Bird, p. 233, pl. 9,
          fig. 3. (non P. sulcatus Bosc).

non 1829 P. fibrosus J. Sowerby; Phillips, pl. 6, fig. 3.

    1860 P. vagans J. de C. Sowerby; Damon, pl. 9, fig. 4.
          (non P. vagans J. de C. Sowerby, 1826, Bathonian species).

non 1860 P. fibrosus J. Sowerby; Damon, pl. 3, figs. 1, 1a.
          (= C. (R.) scarburgensis).

non 1882 P. fibrosus J. Sowerby; Roeder, p. 50, pl. 1, figs.
          11a, 11b.

non 1901 P. fibrosus J. Sowerby; Raspail, p. 193, pl. 12,
fig. 9. (= C. (R.) scarburgensis)

non 1919 Chlamys fibrosus (J. Sowerby); Couffon, p. 119, pl. 3,
figs. 17, 17a, 18.

non 1924 P. fibrosus J. Sowerby; Cossmann, p. 28, pl. 4,
figs. 19-21. (= C. (R.) scarburgensis)

1926 Aequipecten fibrosus (J. Sowerby); Arkell, p. 546,
pl. 34, figs. 2-5.

1927 Chlamys (Aequipecten) fibrosus (J. Sowerby); Arkell,
p. 165, pl. 2, figs. 6a, 6b.

1931 C. (A.) fibrosa (J. Sowerby); Arkell, p. 112, pl. 11,
figs. 6-12.

1934 Pecten (Aequipecten) fibrosus (J. Sowerby); Stoll,
p. 21, pl. 2, fig. 19.

1934 P. (A.) fibrosus (J. Sowerby) var. duplicostatus nov.;
Stoll, p. 21, pl. 2, figs. 17, 18.

1934 P. (A.) tenuicostatus nom. nov.; Stoll, p. 22, pl. 2,
fig. 20. (nom. nov. pro P. fibrosus Goldfuss, non
J. Sowerby).

1936 Aequipecten fibrosus (J. Sowerby); Dechaseaux, p. 47,
pl. 6, figs. 16, 16a.

non 1936 A. fibrosus (J. Sowerby); Dechaseaux, p. 47, pl. 6,
figs. 15, 17, 17a, 18, 18a, 19, 20; pl. 7, figs.
1, 2, 3. (non J. Sowerby)

1952 Chlamys (Radulopecten) fibrosa (J. Sowerby) var.;
Chavan, p. 36, pl. 2, fig. 14.

Type specimens   The two syntypes figured by J. Sowerby (1816, p. 84, pl. 136, figs. 1, 2) are preserved in the Sowerby Collection at the BM (NH), both numbered 43305. The former (the left hand figure of Sowerby) is labelled "? Cornbrash, Chatley, near Frome", and the latter (the right hand figure of Sowerby) comes from the Corallian of Oxfordshire. Arkell (1931, p. 114) designated the latter specimen as lectotype, and suggested that it is probable that the other specimen came not from the Cornbrash, but from the Kellaways Rock (Arkell, in Douglas & Arkell, 1928, p. 165).

Diagnosis   Medium to large-sized species, up to 35 mm long, with 11-14 tightly packed radial ribs, flat-topped in the right valve, and rounded in the left valve; the ribs of the right valve are markedly flat-topped, often show evidence of pairing, and are wider than the sulci; in contrast to C. (R.) scarburgensis, it is the ribs, rather than the sulci, which broaden ventrally; the ribbing of the left valve is much more prominent than on the right valve, and the ribs are narrower, often not being as wide as the sulci; radial striae occur in the sulci of both the left and the right valves; height exceeds length, varying from 104-114 %, $\overline{x}$ 110 %, umbonal angle 89-104 $^{\circ}$, $\overline{x}$ 97 $^{\circ}$.

The differences between this species and C. (R.) scarburgensis have been discussed in the diagnosis of the latter species. C. (R.) drewtonensis Neale, from the Calloviense Zone of the Kellaways Rock of South Cave, Yorkshire, is undoubtedly closely related, but differs in the nature of ornament on the

anterior auricle, C. (R.) drewtonensis having radial striae on the proximal part of the right anterior auricle, and in the wider, flatter, more prominent ribs on the angle valve of Neale's species.

Measurements

        See Appendix 3.

	L	H	umbonal angle	ribs
N	11	11	11	9
$\overline{x}$	25.8 mm	110.2 %	97.2 °	12.3 ribs
Max	34.2	113.9	104	16
Min	12.3	104.5	89	11
OR	21.9	9.4	15	5

Description   Medium to large, up to 35 mm long, inequilateral, subequivalve, left and right valves with very marked differences in ornamentation; umbonal angle very variable (89-104 °, $\overline{x}$ 97.2 °) appearing to increase with growth, height slightly greater than length; auricles subequal, the right anterior auricle with a byssal sinus beneath it; ornament of right anterior auricle consists of sinuous raised commarginal striae, the striae being commarginal and vertical in the posterior auricle; in the left valve the auricles are subequal, and both anterior and posterior are ornamented by slightly coarse, vertical, raised commarginal striae; there are no radial elements present on any of the auricles; right valve ornamented by 11-14 wide, flat-topped radial ribs, always considerably wider than the intervening sulci, and widening

ventrally; in large specimens there is a tendency for the wide
primary ribs to become paired at their ventral margins; faint
radial striae are present in the sulci; both ribs and sulci
are crossed by regular fine concentric striae, numbering about
70 to the cm, which pass onto the auricles as the commarginal
striae; ornament of left valve more prominent, with narrower,
higher, round-topped radial ribs, which are narrower than the
sulci; as in the right valves of large specimens, there is a
tendency for intercalation of secondary ribs in the sulci towards
the ventral margin; both ribs and sulci alike are crossed by
coarse, wire-like concentric striae, numbering about 15 to the
cm, and passing onto the auricles as the commarginal striae;
faint radial striae are present within the sulci of both the
left and right valves; ventral margin scalloped.

Remarks   The synonomy and range of variation of this
species has been fully discussed by Arkell (1931, p. 112), and
little need be added here. As with many of Sowerby's types, the
horizon of the syntype (BM 43305) is uncertain, being labelled
Cornbrash, but Douglas & Arkell (1928, p. 165) believe that it
did in fact come from the Kellaways Rock. Certainly, specimens
referable to C. (R.) fibrosa occur in the Hackness Rock of
Yorkshire, and the Lower Oxford Clay of Bedfordshire and
Northamptonshire, and so the extension of this mainly Corallian
species down to the L. Callovian is quite acceptable.

The few Oxford Clay specimens known, from Stewartby,
Norman Cross and "Chippenham", are medium-sized specimens which
show clearly the wide flat-topped ribs on the right valve, 11-16

in number, and the commarginal striae passing over the auricles. GSM 113408, from the "Oxford Clay of Chippenham" is unusual in that there appear to be about 16 radial ribs on the right valve, but as it is only possible to gain an internal view of the valve, style of ornament and rib pattern cannot be examined, and this specimen is assigned to C. (R.) fibrosa only spectulatively. However, the ctenolium, and the vertical ridge and groove system along the hinge margin, to aid articulation, are very well seen, and it may be inferred from this that there was a functional byssus in the adult. A pair of cardinal crura, radiating from the apex of the resilifer and running subparallel to the hinge margin is also well seen (Fig. 2.32). Another unusual feature of this specimen is the size and extension of the anterior auricle, which seems rather too large for C. (R.) fibrosa. However, in the lack of other specimens, it is better to mention the specimen here than to assign it elsewhere.

Stoll's (1934, p. 21) division of C. (R.) fibrosa into three is, as noted by Arkell (1934, p. xiii), unacceptable, as all her figured specimens fit the variation seen within Sowerby's species. Chavan's (1952, op. cit.) C. (R.) fibrosa var. also belongs to the range of variation of this species. Only one of Dechaseaux's (1936, p. 47, pl. 6, figs. 16, 16a) specimens may be referred to C. (R.) fibrosa, the other specimens belonging to C. (R.) scarburgensis, as well as at least two other species.

Range and occurrence   This species is abundant at many levels
between the Kellaways Rock and Corallian (Arkell, 1931, op. cit.),
and occurs sparingly within the Oxford Clay of England, having
been found in the Medea and Grossouvrei Subzones of Stewartby,
and in the Medea and Jason Zones at Norman Cross; the specimen
from the "? Oxford Clay of Chippenham" (GSM 113408) probably
belongs here, as does a specimen from the Kellaways Rock of the
Snowsdown borehole, Kent (GSM K1342). It also occurs in the
Middle - Upper Oxford Clay of Oxfordshire (OUM), and in the
Hackness Rock of Scarborough (SM J12610).

On the continent, it has been recorded from many localities
in the Callovian and Oxfordian of France, Germany, Switzerland
and Russia (see Arkell, 1931, and the synonymy above).

3.   Chlamys (Radulopecten) drewtonensis Neale. Pl. 11,
        figs. 14-15.

v* 1956 Chlamys (Radulopecten) drewtonensis, sp. nov.; Neale,
          p. 371, pl. 28, figs. 1-5.
.   1972 C. (R.) drewtonensis Neale; Walker, p. 122.

Type specimens   Holotype of Chlamys (Radulopecten)
drewtonensis, figured by Neale, 1956, pl. 28, figs. 2, 3,
preserved in the BM (NH), number L88737, together with one
paratype, no. L88738 (Neale, pl. 28, fig. 1); both specimens
from the Kellaways Rock (Calloviense Zone), South Cave,
Yorkshire. Two additional paratypes from the same horizon and

locality are preserved in the Geological Collections of Hull University (figured in Neale, pl. 28, figs. 4, 5).

Diagnosis   Large species (up to 37.5 mm L), with the left valve slightly more inflated than the right valve; umbonal angle about 100 $^{\circ}$, height about 108 % length; right anterior auricle very produced, ornamented by sinuous commarginal striae, together with 9 radial striae on the proximal 6.5 mm; ribs of the right valve wide and flat-topped, 11 in number, the posterior three or four becoming paired by the development of a median sulcus along each primary rib; right valve ornamented by fine concentric growth lines, about 40 to the centimetre, these growth lines tending to become accentuated on the anterior and posterior extremities; left valve ornamented by 11 narrower, round-topped ribs which are not as wide as the sulci, there being also a tendency towards the development of secondary radial ribs in the posterior three sulci, corresponding with the pairing of the ribs in the right valve; concentric growth lines stronger than on the right valve, but not as wire-like as in C. (R.) fibrosa and C. (R.) scarburgensis; auricles ornamented with fine commarginal striae.

Measurements

See Appendix 3.

	L	H	umbonal angle	ribs
N	2	2	2	2
$\overline{x}$	36.5 mm	109.7 %	100 $^{\circ}$	11 ribs
Max	37.5	111.3	100	11
Min	35.5	108.0	100	11
OR	2.0	3.3	0	0

Description   Neale's (1956, p. 371) description remains
valid, and is not repeated here. Walker (1972, p. 123) noted
that the posterior auricle of the left valve, which was not
seen by Neale, is ornamented by vertical lamellae, the spaces
between them widening away from the umbo.

Remarks   C. (R.) drewtonensis is apparently restricted
to the Calloviense Zone of the Kellaways Rock in East Yorkshire,
only having been found at two quarries in the area of South
Cave. It appears to have certain affinities with both C. (R.)
fibrosa and C. (R.) scarburgensis, although it is not possible
to unite it with either because of a shortage of material. The
ribbing style of the right valve recalls that of C. fibrosa
insofar as the ribs are wide and flat-topped, but no examples of
the latter species with such marked pairing of the ribs have
been seen. The density of concentric striae on the right valve
is also less than in C. fibrosa. The most obvious differences,
however, are the presence of radial striae on the anterior
auricle of C. drewtonensis, a feature not seen in the other
species, and the weaker concentric ornament on the left valve of
C. drewtonensis. It is possible that the discovery of more
material will show that this species may be united with either
C. fibrosa or C. scarburgensis, but until that time, it is best
left as a separate species.

Range and occurrence   Kellaways Rock (Calloviense Zone,
Enodatum Subzone) of Kettlethorpe Main Quarry, South Cave,
Yorkshire (Neale, 1956, p. 372; Walker, 1972, p. 123), and South

Cave Station Quarry (Walker, op. cit., p. 123).

Family PLICATULIDAE Watson, 1930

Genus PLICATULA Lamarck, 1801 (p. 132)

Synonymy: Plicatuligenus Renier, 1807

Micatula Carpenter, 1859

Plycatula Monterosato, 1877

Type species   Subsequently designated by Schmidt,
1818 , Spondylus plicatus Linnaeus, 1764, p. 511, Recent, Java.

Diagnosis   Small to medium-sized genus, subequivalve,
the right valve usually more convex than the left valve;
attachment area small to moderately large;   cardinal area small,
resilifer acutely triangular;   crura straight, narrow, prominent,
narrowly-divergent, crenulated, those in the right valve adjacent
to the resilifer;   adductor scar situated in a relatively
posterior position.

Subgenus PLICATULA s.s.

Synonymy: Harpax Parkinson, 1811

Plicatulopecten Neumann, 1907

Diagnosis   Auricles absent or very poorly defined; most
species having radial ornament, which may range from fine
costellae to broad costae, and with imbricating growth lamellae;

short spines present in many forms.

Remarks   Yonge (1973), having studied the anatomy and
shell structure of Recent species of Plicatula and Spondylus,
has shown that the teeth and ligament structure of Plicatula
are radically different from those of Spondylus and other
Pectinacea. Yonge suggested that evolution of the four
Pectinacean families began in the Palaeozoic, with modifications
of the organs of the mantle cavity, all four families having
the same original set of structures. In the Propeamussiidae
and Pectinidae, it was the organs of the mantle cavity which
evolved, whilst in the Plicatulidae and Spondylidae, the ligament
became adapted, the organs of the mantle cavity remaining
virtually unchanged. However, the great differences between the
ligament and hinge of Plicatulidae and Spondylidae led Yonge
(op. cit., p. 205) to suggest that perhaps the Plicatulidae
should be elevated to the status of a new superfamily.

Plicatula cf. fistulosa Morris & Lycett.   Pl. 11, figs. 13, 17,
                                            Pl. 12, figs. 2-4.

1853 Plicatula fistulosa sp. nov.; Morris & Lycett, p. 15,
      pl. 2, fig. 5.

1907 P. fistulosa Morris & Lycett; Cossmann, p. 273, pl. 1,
      figs. 1, 2.

1923 P. fistulosa Morris & Lycett; Lissajous, p. 150, pl. 29,
      figs. 10-18.

1948 P. fistulosa Morris & Lycett; Cox & Arkell, p. 15.

Type specimen   Holotype of *Plicatula fistulosa* Morris &
Lycett, 1853, p. 15, pl. 2, fig. 5, preserved in the GSM,
London (no. 9166), from the Great Oolite (Bathonian) of
Minchinhampton, Gloucestershire.

Diagnosis   Large-sized species (up to 31.8 mm L), of
very irregular and variable outline, covered with tubiform
spines arising from ill-defined radial ribs; left valve
slightly less spinose than the right valve.

Measurements   See Appendix 3.

L $\overline{x}$	H $\overline{x}$	I (both valves) $\overline{x}$	AL $\overline{x}$
29.9 mm	112.8 %	31.3 %	56.0 %

Description   Large -sized species (up to 31.8 mm L), subovate
in outline, inequivalve, the left valve flatter than the right;
inequilateral, the posterior region slightly produced, no
differentiated auricles. Umbonal region rounded, passing
smoothly into the evenly and continuously-rounded anterior and
ventral margins; posterior margin rounded, slightly produced,
the posterodorsal margin slightly convex, umbones situated
just posterior of median (AL 56.0 %). Inflation low (I both
valves 31.3 %). Margins closed.

Right valve slightly convex, with a suboval attachment
area   11.5 mm high by 8.2 mm long, in the umbonal region; the
remainder of the external surface of the valve is covered by
irregular rows of sharply tubiform spines, with a central
hollow core; the spines are roughly arranged in radial rows,

about 15 in number, and there are about six spines per row. Left valve very slightly convex, bearing a xenomorphic attachment area in the umbonal region; as in the right valve, much of the rest of the valve is covered with hollow tubiform spines, of slightly larger size than those of the opposing valve, which are best developed along the ventral margin; the radial arrangement of the spines is less well-marked than on the right valve, and spines are fewer in number.

As the specimen is preserved as a pyritised articulated shell, it is not possible to see any of the internal structures of the shell

Remarks   Damon (1860, pl. 9, fig. 7) described P. wey-mouthiana from the Trigonia clavellata Beds of the Corallian, and since then, many other specimens have been found in the Corallian (Arkell, 1928, p. 91). This is the first record of a Callovian Plicatula in Britain, and in view of the lack of other material, and the known variability of Plicatulids, it is not possible to unite these specimens with this species, although there are similarities of shape and ornamentation with Damon's species. The spines of the Oxford Clay species appear to be rather more delicate than those of P. weymouthiana however, and are not so well-aligned on radial elevations.

It seems probable that the Oxford Clay species is more closely related to P. fistulosa Morris & Lycett (1855, p. 15, pl. 2, fig. 5) from the Great Oolite of Minchinhampton, a much more finely-ribbed species of similar shape; however, in view of the rarity of the Callovian specimen, it is impossible

to assign it to P. fistulosa at the present time.

Range and occurrence   Lower Oxford Clay, bed 10 (Medea Subzone),
Jason Zone) of Peterborough and bed 14 (Obductum Subzone, Coronatum
Zone) of Bletchley, Bucks. The known range of P. fistulosa Morris
& Lycett is Inferior Oolite to Great Oolite (Bajocian - Bathonian).

Suborder OSTREINA Ferussac, 1822

Superfamily OSTREACEA Rafinesque, 1815

Family GRYPHAEIDAE Vyalov, 1936

Subfamily GRYPHAEINAE Vyalov, 1936

Genus GRYPHAEA Lamarck, 1801, p. 398

Synonyms: Gryphoea Bosc, 1802

Gryphaeigenus Renier, 1807

Gryphites Schlotheim, 1813

Griphaea de Blainville, 1821

Griphoea de Blainville, 1821

Griphea Brongniart, 1822 in Cuvier &
                            Brongniart

Gryphea Brongniart, 1823

Liogryphaea Fischer, 1886

non   Gryphaea Fischer, 1886 (= Crassostrea
                            Sacco, 1897)

Gryphaae White, 1887

Liogryphaea Douville, 1904

Ghyphaea Scalia, 1912

<p style="text-align:center">Lyogryphaea Couffon, 1917</p>

<p style="text-align:center">Jurogryphaea Arkell, 1934</p>

<p style="text-align:center">Incurva Arkell, 1934</p>

<p style="text-align:center">Gryphaca Jaworski, 1935</p>

<p style="text-align:center">Rygepha Vyalov, 1946</p>

<p style="text-align:center">Liogriphaea Vyalov, 1948</p>

<p style="text-align:center">Liographaea Charles, 1949</p>

<p style="text-align:center">Liogryphanaea Krach, 1951</p>

<p style="text-align:center">Gruphea Ciric, 1951</p>

<p style="text-align:center">Griphea Ciric, 1951</p>

<p style="text-align:center">Cryphaea Zaprudskaya, 1953</p>

Type species   Subsequently designated by ICZN opinion number 338, p. 127 , 1955, Gryphaea arcuata Lamarck, 1801, p. 398, from the L. Lias of France.

Diagnosis   Shell medium to large in size (up to 160 mm L), very inequivalve, with left valve strongly convex and enrolled, and right valve slightly concave, flat or slightly convex; shape very variable, ranging from high narrow forms, where H greatly exceeds L, through suborbicular forms (L > H) to triangulate forms, with or without the development of bilobation; left valve with posterior radial sulcus, weak or strong, forming the anterior margin of the posterior flange, which is of varying size and prominence; the deeper the sulcus, the more prominent is the flange; umbones slightly opisthogyrate to orthogyrate; left valve ornamented by concentric growth squamae or undulations, occasionally smooth, with or without radial elements; umbo of

left valve often strongly coiled, although it is frequently
terminated by an attachment area; right valve ornamented with
concentric growth squamae or undulations, with or without radial
striae; adductor scar slightly posterior to the midline, and
placed nearer the hinge than the ventral margin; dorsal margin
always convex, ventral margin usually slightly elevated;
quenstedt muscle insertions close to the hinge-plate and
posterior to the midline; umbonal cavity below the hinge-plate
is small, and almost entirely filled by shell material; resilifer
excavate, varying from one to five times the length of each
bourrelet; resilifer of right valve terminates the dorsal
margin of the valve at a right angle to the body of the shell,
and projects ventrally into the shell cavity, where it is
supported by a buttress; commissural shelf well developed, but
lacking chomata.

<center>Subgenus BILOBISSA Stenzel, 1971 (p. N1099)</center>

<center>Synonymy: Bilobata Arkell, 1934</center>

Type species   Originally designated by Stenzel, 1971,
p. N1099, Gryphaea bilobata J. de C. Sowerby, 1840, p. 4, from
the Inferior Oolite (Bajocian) of England. (= G. dilatata var. β
J. Sowerby, 1816, p. 113, pl. 149, fig. 2).

Diagnosis   Small to medium in size (up to about 90 mm
L), left valve with strongly developed posterior radial sulcus,
and very well-marked and pronounced posterior flange; radial

elements present only as faint striae on the right valve; attachment area often large.

Remarks   The generic synonymy reveals much about the controversy concerning the taxonomic position of Gryphaea, and it was not until the ICZN ruling of 1955 (Opinion no. 338), that the identity and type species of the genus were clarified. Gryphaea is now restricted to fossil species, of Triassic to Jurassic age, with a variably developed posterior sulcus. A full taxonomic revision of the Gryphaeidae has recently been produced by Stenzel (1971, p. N1097).

Stenzel took the unusual step of erecting the subgenus Bilobissa in the Treatise on Invertebrate Paleontology, for the reception of the strongly bilobate Gryphaea with a well-developed posterior flange from the Middle - Upper Jurassic. The provenance and horizon of the type species — G. (Bilobissa) bilobata — has been a source of much confusion since J. de C. Sowerby (1835, p. 244) introduced the name for the specimen figured by J. Sowerby (1816, p. 113, pl. 149, fig. 2) as G. dilatata var β , from the "Kellaways Rock". Study of the type specimen of G. bilobata, preserved in the Sowerby Collection at the BM (NH) (no. 43349   ) led Richardson (1923 Ms) to the conclusion that it came from the Inferior Oolite. C. P. Palmer (1973, pers. comm.) has examined the matrices of the type, and specimens from the Inferior Oolite and Kellaways Rock, and shown that the type of G. bilobata has a whitish-oolitic matrix adhering to the right valve, exactly as in other specimens from the Inferior Oolite. Until the work of Stenzel (op. cit.), the

horizon of G. bilobata had always been taken as Kellaways Rock,
and the name applied to Lower and Middle Callovian Gryphaea in
general. Thus a new name is required for the Lower – Middle
Callovian forms and the name G. dilobotes Sylvester-Bradley Ms
is introduced here.

1.   Gryphaea (Bilobissa) dilobotes nom. nov. (Sylvester-
          Bradley Ms). Pl. 12, figs. 5-15, Pl. 13, figs. 1-6, Pl. 14,
              figs. 1-5, Pl. 15, figs. 1-7, Pl.16,figs.1-5,8.

? 1829 Gryphaea dilatata var. ß . J. Sowerby; Phillips, pl. 6,
          fig. 1.

   1892 G. bilobata J. de C. Sowerby; Fox-Strangways, p. 279,
          pl. 14, fig. f.

   1892 G. dilatata J. Sowerby; Fox-Strangways, p. 293, pl. 15,
          fig. a.

   1895 G. bilobata J. de C. Sowerby; Woodward, p. 11, fig. 8.

   1898 G. bilobata J. de C. Sowerby; Strahan, p. 17, fig. 31.

   1904 G. bilobata J. de C. Sowerby; Fox-Strangways, p. 29,
          fig. 3f.

   1915 G. dilatata J. Sowerby; Krenkel, p. 300, pl. 25, figs.
          36-39.

? 1919 G. (Lyogryphaea) bullata J. Sowerby; Couffon, p. 52,
          pl. 3, figs. 14-14b.

   1932 G. bilobata J. de C. Sowerby; Arkell, p. 172.

   1934a G. bilobata J. de C. Sowerby; Arkell, p. 58, 60.

   1934a Ostrea (Bilobata) gryphaea nom. nov.; Arkell, p. 64.

   1947 G. bilobata J. de C. Sowerby; Arkell, p. 27.

   1947a Ostrea (Gryphaea) bilobata (J. de C. Sowerby); Arkell, p.68.

1952 G. bilobata J. de C. Sowerby; Cox, p. 81, pl. 8, figs. 1,2,4.

1955 G. bilobata J. de C. Sowerby; Callomon, p. 221.

1958 G. dilobotes Ms nom. nov.; Sylvester-Bradley, p. 2,3.

1968 G. bilobata auctt; Callomon, p. 270.

1970 G. bilobata J. de C. Sowerby; Cope & Cox, p. 122.

1971 G. aff. bilobata J. de C. Sowerby; Callomon, p. 168.

1972 G. bilobata J. de C. Sowerby; Walker, p. 124.

Type specimen   Holotype, from the Enodatum Subzone, Calloviense
Zone, of Stewartby, Beds., preserved in the BM (NH), number
LL 27729.

Diagnosis   Large species, up to 80 mm L, very variable
in form, but usually subtrigonal to suborbicular in outline, with
the antero- and posterodorsal margins forming an acute or obtuse
angle with each other (θ 66-128 $^{\circ}$, $\overline{x}$ 97.7 $^{\circ}$); height usually
greater than length (H 89.3-144.8 %, $\overline{x}$ 114.7 %), other
characters very variable (see measurements); umbones prominent,
rounded, opisthogyrate; posterior flange generally well-developed,
although of variable width ($\triangleleft$ 11-42 $^{\circ}$, $\overline{x}$ 31 $^{\circ}$), placed high
on the posterior margin, the deeply excavate bounding posterior
radial sulcus not usually reaching more than two-thirds of the
way to the ventral margin; attachment area often large, and
frequently xenomorphic; right valve often with radial striae.

The distinctions between G. dilobotes, G. lituola and
G. dilatata are considered in the discussion below, but the most
important difference in respect of G. dilobotes is its variable
height, and the position of the posterior flange, placed high on the
posterior margin.

Measurements   See Appendix 3 and Fig. 2.33 for measurements used.

Left valve

	L	H	I	AL	Llig	Hlig	Lab	Lpb	His	Hi	Θ	α
N	66	66	66	63	27	40	25	25	34	63	65	56
x̄	44.2mm	114.7%	57.6%	46.0%	12.9%	12.2%	6.1%	5.9%	64.5%	101.8%	97.7°	27.7°
Max	80.0	144.8	87.9	57.4	17.8	22.1	9.1	10.3	102.1	133.3	128	42
Min	13.1	89.3	28.7	28.6	8.3	6.3	2.1	3.4	45.2	76.8	66	11
OR	66.9	55.5	59.2	28.8	9.5	15.8	7.0	6.9	56.9	61.5	62	31

Right valve

	L	H	I	AL	Llig	Hlig	Lab	Lpb	His	Hi	Θ	α
N	20	20	16	18	6	15	6	5	17	19	19	8
x̄	38.6mm	107.9%	27.1%	49.6%	11.9%	13.6%	6.4%	5.4%	68.4%	107.8%	92.7°	28.1°
Max	73.4	130.2	35.7	59.2	15.9	20.0	7.7	6.9	100.0	130.2	110	34
Min	14.5	84.0	15.0	33.1	10.0	6.2	5.7	4.5	54.6	84.0	70	24
OR	58.9	46.2	20.7	26.1	5.9	13.8	2.0	2.4	45.4	46.2	40	10

<u>Description</u>   Large species, up to about 80 mm in length, of very variable form, outline subtrigonal to subovate, often with a well-developed posterior flange. Very inequivalve, left valve strongly inflated (I 28.7-87.9 %, $\overline{x}$ 57.6 %) and highly convex, right valve flat or slightly concave. Umbones prominent, rounded, slightly opisthogyrate and not tightly coiled, the extremity often truncated by a large attachment area, xenomorphic on the right valve. Anterior margin slightly concave to slightly convex, curving smoothly into the evenly-rounded ventral margin; posterior margin usually produced into a well-developed posterior flange, delimited anteriorly by a deeply excavate posterior radial sulcus, angle α varying between 11-42 ° ($\overline{x}$ 27.7 °) in the left valve, and 24-34 ° ($\overline{x}$ 28.1 °) in the right valve; the posterior radial sulcus tends to be subparallel to the posterior margin, but never reaches to the ventral margin, usually terminating about two-thirds of the way to the ventral margin; this places the posterior flange high on the shoulders of the valve, quite distinct from the body of the shell, usually as a clearly triangular feature; posterior margin deeply concave where the posterior radial sulcus reaches the margin; posterior flange often not well-developed in young forms (up to 35 mm L), these tending to be high and subtrigonal in outline. Surface of left valve covered by coarse concentric growth squamae, with faint radial elements sometimes visible in the juvenile stages; right valve ornamented similarly, but the radial elements tend to be stronger and more apparent.

Adductor muscle scar placed slightly closer to the dorsal than the ventral margin, or subequidistant (HMS 45-102 %, $\overline{x}$ 64.5 % in the left valve; 54.6-100.0 %, $\overline{x}$ 68.4 % in the right valve), and just posterior to the mid-axis; shape variable, but usually more or less orbicular to subquadrate in the left valve, suborbicular to subovate in the right valve. Quenstedt muscle small, situated close to the hinge-axis, posterior to the mid-axis, usually more or less below the posterior bourrelet in both valves. Resilifer up to 5 times the length of each bourrelet, covered by fine parallel growth lines which cross onto the bourrelets; bourrelets not well differentiated from the resilifer (Fig. 2.33). In the right valve, the resilifer projects ventrally into the shell cavity, forming a small ligamentary buttress, the whole ligament area being perpendicular to the plane of the valve. Commissural shelf present on the dorsal half of the left valve, but not strongly developed. Proximal gill wheal faint, stretching from the vicinity of the quenstedt muscle to the branchitellum. Umbonal cavity shallow. Hinge edentulous.

Flat ecomorphs from the basal shell beds and the clay facies. In the population of G. dilobotes from the basal shell bed (Medea Subzone) at Stewartby, there is a large number of individuals with very large attachment areas, which greatly affects the overall shape of the shells. In their juvenile stages, the left valves took the form of a negative mould of the substrate to which they were attached, with the right valve assuming a xenomorphic positive mould of the substrate. Stenzel

(1971, p. N1021) gives a good discussion of the nature and mechanics of xenomorphism in oysters. As the oysters grew, and became too large and heavy to remain in their original post-larval settlement position, they toppled over onto their left valves and then developed in the manner usual for Gryphaea, i.e. resting free, half-buried in the sediment, with the right valve uppermost in a more or less horizontal position (Stenzel, 1971, p. N1072). By the time that the shells were large and heavy enough to overbalance, they were also strong enough to withstand the attacks of most predators, and so the attached encrusting life habit was no longer necessary.

This gives a population of two distinct morphotypes — the juveniles, of flattened shape with the whole or most of the left valve directly attached to the substrate, and the gryph-shaped 'adults', with large residual attachment areas. The size at which the onset of the gryph-shape occurred is variable, apparently depending on the size of the shell fragment being used as a substrate, but most individuals appear to have assumed independence of the post-larval settlement site by the time they were 10 mm high.

The spat appear not to have been specific in their choice of settlement site, as they are found attached to ammonites, belemnites, bivalves, indeterminate shell material, fragments of wood, and occasionally to other oysters. The commonest attachment site is an ammonite shell or fragment, but this is probably due to ammonites being more numerically abundant and easily recognised as fragments. Attachment to the ammonites Kosmoceras

(Gulielmiceras) spp., Kosmoceras spp. s.l., the belemnite
Cylindroteuthis and the bivalves Meleagrinella, Oxytoma and
Gryphaea (Bilobissa) has been observed.

The adoption of this fixed juvenile mode of life has led
to peculiarities in the hinge area in many young individuals,
the commonest being the blurring of the distinction between the
resilifer and bourrelets, and an overall lengthening of the
ligamental area. As growth proceeds, and the gryph-shape is
acquired, the ligament area develops normally.

The probable explanation for this dimorphic population is
that the individuals were reacting to the environment, the high
number of examples with large attachment areas being due to the
greater number of potential post-larval settlement sites. The
fact that the substrate, being much richer in shells and shell
fragments, was likely to have been harder and more coherent than
the silty sands of the Kellaways Beds or the mud of the Oxford
Clay, may also have meant that it was necessary to remain
attached to a stable area for a longer part of post-larval
development, not only for stability, but also for protection from
predators capable of breaking smaller shells. Bottom turbulence
may also have been greater, necessitating the growth of a thicker
shell before the free-living stage could be assumed.

Similarly-shaped ecomorphs may be collected from the clay
facies throughout the Lower Oxford Clay, and may be interpreted
as being ecologically equivalent to the forms in the transition
beds at the base of the Oxford Clay. In the clay facies,
however, the dominant form is rather small and flat, and often

encrusts other shells or fragments of wood. Characteristically, the left valves (which are much less commonly found than right valves) have a large xenomorphic attachment area, occupying up to 50% of the external surface of the valve, the remainder of the valve being gently cup-shaped; the large size of the attachment area prevents the acquisition of the true gryph-shape with enrolled umbones. In form, many of these left valves agree closely with similar valves found in the shell beds. As in the transition beds forms, the right valves are generally flat or gently concave in outline, sometimes with faint radial striae, and often bear a large positive xenomorphic mould of the substrate. In a few rare cases, a truly gryph-shaped individual develops, showing the strong posterior sulcus and relatively loose coiling of G. dilobotes, but these are very much the exception to the rule. The dominant form of oyster in the bulk of the Lower Oxford Clay is a flattened, non-gryphaeate form of G. dilobotes, truly gryphaeate oysters not reappearing in the English Oxford Clay until the Middle Athleta Zone (Upper Callovian), with the appearance of G. lituola.

Remarks   The questions of the name of the Kellaways Beds and Lower Oxford Clay Gryphaea, and of the provenance of the holotype of G. bilobata have been considered above (in the subgeneric discussion) and need not be repeated here. Examination by the author of the holotype of G. bilobata J. de C. Sowerby (BM (NH) 43349   ) convinces him that it did come from the Inferior Oolite, having a yellow-whitish oolitic matrix. Rollier (1915, p. 582) overlooked J. de C. Sowerby's name G. bilobata

and introduced the name <u>Ostrea (Gryphaea) calloviensis</u> for the specimen figured by J. Sowerby (1816, p. 113, pl. 149, fig. 2) as <u>G. dilatata var ß</u> , believing it to be of Callovian age. However well he may have meant, his name must be considered a junior synonym of <u>G. bilobata,</u> and cannot be used for the Lower Callovian species.

Sylvester-Bradley (1958, p. 2, fig. 4) introduced three manuscript names for species of <u>Gryphaea</u> in the Calloviense Zone of Britain, <u>G. renata</u>, <u>G. connexiva</u> and <u>G. dilobotes</u>, the three species being successive forms in a continuously evolving lineage. No diagnoses, descriptions or figures were given for the species, and so the names must rank as nomina nuda. Sylvester-Bradley (1973, pers. comm.) believes <u>G. dilobotes</u> to be the youngest of these three species, characterised by a well-developed posterior lobe, its type horizon being the Enodatum Subzone (Kellaways Rock) of South Cave, Yorkshire. This appears to be the earliest applicable name for the strongly bilobate Lower Callovian <u>Gryphaea,</u> and its use is here validated. The question of the status of Sylvester-Bradley's two other Ms species, <u>G. renata</u> and <u>G. connexiva</u> is uncertain, and will be considered at a later date, but at the present time, the author favours using <u>G. dilobotes</u> to include all the Calloviense Zone <u>Gryphaea.</u>

Phillips (1829, pl. 6, fig. 1) applied J. Sowerby's name to a form found in the 'Kellaway Rock' (= Hackness Rock?) of Hackness. The specimen, claimed to be in the Yorkshire Museum, seems to be lost, and so it is not possible to tell whether this is a <u>G. dilobotes</u> or a <u>G. lituola.</u> The horizon (Athleta Zone of

Hackness Rock is correct) suggests the latter, and if so, then the likelihood is that the figure represents a bilobate form of that species close to G. dilobotes. Arkell (1932, p. 160) placed Phillips specimen in G. dilatata, but the horizon is too low, and the form far too bilobate.

Lissajous (1912), Couffon (1919) and Cossmann (1924) separated the Callovian species of Gryphaea from G. dilatata, but overlooked the name bilobata, and referred it instead to G. bullata J. Sowerby, a species from the Kimmeridge Clay, which is not lobate. Krenkel (1915, pl. 25, figs. 36, 38) figured two right valves with good xenomorphic attachment areas.

The characters measured in G. dilobotes and the other species of Gryphaea are shown in Fig. 2.33, and are largely self-explanatory, although they differ from the parameters used by Hallam (1968). As in all other bivalves, length is measured parallel to the hinge axis, and most other orientations are related to this basic parameter. Hi is measured from the tip of the umbo (the apex of the resilifer) to the ventral margin, and gives a measure of how much of the umbo is dorsal to the hinge line. HMS, measured from the hingeline to the ventral margin of the adductor scar, gives the location of the adductor scar, and is easily measured, as the ventral margin of the scar is raised above the general shell surface. Angle θ, measured from the tip of the resilifer to the most anterior and posterior points of the shell gives a measure of elongation, and angle α , measured from the resilifer tip to the posterior margin and the posterior radial sulcus, gives a measure of the development of

the posterior flange. Lengths of the bourrelets and resilifer
are taken parallel to the hinge margins, and height of the
resilifer perpendicular to it. Study of the measurements table
above shows the great variability of all the main characters, a
feature better appreciated diagrammatically (Fig. 2.34). The
most obviously variable characters are height, inflation and
development of the posterior flange, but other than there being
a tendency for young forms to be higher and have weaker flanges,
systematic variation is not obvious.

Three species of Gryphaea (Bilobissa) may be recognised
in the British Oxford Clay, G. dilobotes in the Kellaways Beds
and lowermost Oxford Clay, G. lituola in the Middle Oxford Clay,
and G. dilatata in the Upper Oxford Clay. Traditionally, their
status has been confused, and it was not until 1932 that Arkell
clarified the differences between G. lituola and G. dilatata,
with a passing reference to G. bilobata. All three species are
extremely variable in all their characters, but it is nevertheless
possible to distinguish specimens of each, although distinction
is more suitably carried out on large populations. The differences
may be considered under several headings:

a) Size. G. dilatata attains a very large size (up to
198 mm H), gerontic specimens becoming very high, and with great
extension of the ligament. Both G. lituola and G. dilobotes
attain an approximately equal length (≃ 80 mm), but G. lituola
tends to be slightly higher (H up to 150 %).

b) Shape. All three species have a posterior flange
developed, which affects the gross shell outline to varying

degrees, being most marked in G. dilobotes and least in
G. dilatata. Disregarding gerontic specimens, G. dilatata may
be distinguished by its low height (90-106 %) from G. dilobotes
(89-145 %, $\overline{x}$ 115 %) and G. lituola (102-128 %, mean 116 %),
and also by its low inflation — 20-50 %, compared with 28-88 %
($\overline{x}$ 58 %) in G. dilobotes and 54-77 % ($\overline{x}$ 66 %) in G. lituola.
As is obvious, G. dilobotes and G. lituola cannot easily be
separated using these criteria. In overall shape, G. dilatata
tends to be wide and flat, with the posterior flange usually
only weakly developed, and the umbones are not strongly incurved,
often forming an approximate right angle to the plane of the
commissure. The low degree of inflation and low prominence of
the umbones may be seen from the fact that Hi is only slightly
less than H. G. dilobotes and G. lituola are similar in shape,
being subtrigonal in outline and well-inflated, but the umbones
of G. lituola tend to be more incurved than those of G. dilobotes,
even when terminated by a large attachment area. The shell of
G. lituola is also thicker than in G. dilobotes, and the
commissural platform better-developed and more extensive, with
consequent elongation of the ligament area perpendicular to the
hinge axis.

c) Posterior flange. The position and degree of
development of this feature is the most useful in separating the
three species. As the sequence dilobotes - lituola - dilatata
is traced stratigraphically upwards, the posterior flange moves
posteroventrally and widens, so that in typical forms of
G. dilobotes, the flange is placed high on the posterior margin

and forms a well-differentiated, relatively small, triangular feature; the posterior radial sulcus rarely reaches more than $\frac{2}{3}$ of the way to the ventral margin. G. lituola is characteristically not as markedly bilobate, although strongly bilobed individuals do occur, the posterior radial sulcus reaching almost to the ventral margin, and marking off a poorly-differentiated posterior flange which is not well-separated from the body of the shell, but is still roughly triangular in form. Finally, in G. dilatata, the posterior radial sulcus usually extends all the way to the ventral margin, the posterior flange is not well-differentiated from the body of the shell, and tends to be subrectangular or subovate in outline.

d) Ligament. In the loosely coiled G. dilobotes, the ligament area on the left valve tends to be low and poorly-developed, even in very large (L 80 mm) specimens. The tighter coiling seen in G. lituola necessitates continuous growth of the ligament area in a direction perpendicular to the hinge axis, giving a very high ligament, even in small specimens. The same is true of G. dilatata, although the reason seems to be slightly different; after the attainment of the 'adult' stage (at a height of about 115 mm) growth proceeds mainly by accretion of shell at the ventral margin, and so in order to maintain equilibrium in the substrate, and allow the valves to open, the ligament attachments must also move ventrally, and so a very high, often parallel-sided ligament area is formed. Elongation of the ligament is more marked in G. dilatata than in G. lituola, and is accompanied by the development of a very wide

commissural platform. (New term introduced here for the areas postero- and anterodorsally where the growth squamae of the valve margins form a flattened area outside the mantle-covered area).

The problem of homoeomorphy in oysters is relevant here, as although it is simple to separate the three species above when large populations are examined, the occurrence of some specimens of G. lituola which are markedly bilobate could lead to difficulties in the interpretation of very small samples. The recognition of these three distinct species with certainty, requires the possession of populations of at least 10 specimens, to make allowances for intra-specific variation, which in Gryphaea is great.

Range and occurrence   Abundant in the Kellaways Beds (Calloviense Zone) and basal Oxford Clay (Medea Subzone, Jason Zone) of England, and at equivalent levels, sometimes ranging a little higher when the lithology is favourable, in France, Germany and Poland.

2.   Gryphaea (Bilobissa) lituola Lamarck. Pl. 16, figs. 6-7, 9,
                                        Pl. 17, figs. 1-4,9.

1819 Gryphaea lituola sp. nov.; Lamarck, p. 199.

1822 G. dilatata J. Sowerby; Young & Bird, p. 239, pl. 10, fig. 4.

1860 G. dilatata J. Sowerby; Damon, pl. 3, fig. 7.

1910 G. lituola Lamarck; Cossmann, no. 201.

1932 G. lituola Lamarck; Arkell, p. 170, pl. 19, figs. 2, 3.

<u>Type specimen</u>   Holotype of <u>Gryphaea lituola</u> Lamarck, 1819,
p. 199, figured by Cossmann, 1910, as no. 201 in the
Palaeontologia Universalis, from the Middle Oxford Clay of
France (Calvados?) preserved in the Lamarck collection at the
Institute Paléontologique du Musée National d'Histoire Naturèlle
in Paris.

<u>Diagnosis</u>   Large species (up to 115 mm H), rather
variable in form, but usually subtrigonal to subelliptical in
outline, although a few specimens are bilobate; posterior radial
sulcus not usually prominent, reaching about 80-90 % of the way
to the central margin, posterior flange generally small and not
well-differentiated from the body of the shell (α 20-46 $^{\circ}$,
$\bar{x}$ 27.7 $^{\circ}$), and not wing-like as in <u>G. dilobotes</u>; posterior
radial sulcus and flange better developed in wider specimens,
which tend also to be less incurved than narrower ones. Umbones
strongly incurved, much more so than in <u>G. dilobotes</u> or
<u>G. dilatata</u>, causing great increase in the height of the
ligament area (H.lig. 14.7-26.5 %, $\bar{x}$ 21.7 %). Height variable,
but always greater than length (H 102.9-128.4 %, $\bar{x}$ 116.3 %),
inflation high, always greater than half the length (I 54.4-77.3 %,
$\bar{x}$ 66.3 %), variability of other characters shown in the table
of measurements.

The differences between <u>G. lituola</u> and the other two species
of Oxford Clay <u>Gryphaea</u> have been discussed above, so it only needs
to be noted that <u>G. lituola</u> is narrower and more inflated than
<u>G. dilatata</u>, with the posterior radial sulcus reaching only 80-90%
of the way to the ventral margin, and less markedly bilobate than

Measurements   See Appendix 3.

LV	L	H	I	AL	L.lig	H.lig	Lab	Lpb	HdS	Hi	θ	α
N	13	13	13	10	2	4	2	2	4	13	13	13
$\bar{x}$	69.9 mm	116.3%	66.3%	49.4%	12.8%	21.7%	7.1%	7.6%	53.2%	93.3%	102.7°	27.7°
Max	75.7	128.4	77.3	56.4	15.2	26.5	7.7	8.6	58.1	100.2	118	46
Min	43.5	102.9	54.4	42.6	10.4	14.7	6.5	6.5	45.3	87.1	88	20
OR	32.2	25.5	22.9	13.8	4.8	11.8	1.2	2.1	12.8	13.1	30	26

L.lig (all)	N4	$\bar{x}$ 28.5	Max 31.2	Min 26.7	OR 4.5
L.add.scar	N4	$\bar{x}$ 17.9	Max 21.5	Min 14.7	OR 6.8
H.add.scar	N4	$\bar{x}$ 19.8	Max 24.2	Min 16.1	OR 3.1

RV	L	H	I	AL	L.lig	H.lig	Lab	Lpb	HdS	Hi	θ	α
N	2	2	–	2	1	2	1	1	2	2	2	–
$\bar{x}$	51.1 mm	101.5%	–	46.9%	16.3%	18.3%	8.4%	8.2%	57.1%	101.5%	95.5°	–
Max	52.2	107.3	–	47.5	16.3	21.5	8.4	8.2	63.0	107.3	98	–
Min	49.9	95.6	–	46.3	16.3	15.0	8.4	8.2	51.1	95.6	93	–
OR	2.3	11.7	–	1.2	0	6.5	0	0	11.9	11.7	5	–

L.lig (all)	N2	$\bar{x}$ 30.6	Max 32.5	Min 28.7	OR 3.8
L.add.scar	N2	$\bar{x}$ 17.2	Max 17.6	Min 16.8	OR 0.8
H.add.scar	N2	$\bar{x}$ 15.8	Max 17.6	Min 14.0	OR 3.6

G. dilobotes, with the posterior flange less clearly
differentiated from the body of the shell, and placed lower on
the posterior margin.

Description   Large species (up to 115 mm high), of rather
variable form, subtrigonal to subovate in outline (H 102.9-
128.4 %, $\overline{x}$ 116.3 %), occasionally markedly rostrate (var.
obliqua Arkell), with a variably developed posterior radial
sulcus and flange. Height always greater than length, often
very much so, giving high, subtrigonal shells which are slightly
wider than in G. dilobotes (θ 88-118 $^{\circ}$, $\overline{x}$ 102.7 $^{\circ}$). Very
inequivalve, left valve strongly convex (I 54.3-77.3 %, $\overline{x}$ 66.3 %),
and often markedly incurved in the umbonal region, right valve
flat or slightly concave, suborbicular to subovate in outline,
seldom very bilobate. Umbones prominent, rounded, inflated (Hi $\overline{x}$
23% less than overall height), slightly opisthogyrate, often
strongly incurved and generally terminated by an attachment area
of variable size, reflected xenomorphically on the right valve.
Anterior margin slightly concave to slightly convex, depending
on the prominence of the umbones, curving smoothly into the evenly-
rounded ventral margin with no angulation; posterior margin
variably produced into a posterior flange, usually weakly
developed, not clearly separated from the body of the shell by
the generally faint posterior radial sulcus (α 20-46 $^{\circ}$, $\overline{x}$
27.7 $^{\circ}$); posterior flange does not stand out from the body of
the shell in a wing-like fashion, and usually extends further
down towards the ventral margin than in G. dilobotes; occasional
forms (var. obliqua Arkell) with the posterior flange drawn out

into a long rostrate feature are found, but these are rare. Surface of left valve ornamented by irregular concentric growth squamae, not as coarse as in G. dilatata, radial elements rare; right valve ornament similar, but the radial striae are better-developed, especially in the umbonal region.

Adductor muscle scar posterior to mid-axis, placed subcentrally between dorsal and ventral margins, or slightly closer to the ventral margin (HMS 45.3-58.1 %, $\overline{x}$ 53.2 % in LV. 51.1-63.0 %, $\overline{x}$ 57.1 % in RV), suborbicular to subovate in outline (L adductor scar 14.7-21.5 %, $\overline{x}$ 17.9 % in the left valve, 16.8-17.6 %, $\overline{x}$ 17.2 % in the right valve; H adductor scar 16.1-24.2 %, $\overline{x}$ 19.8 % in left valve, 14.0-17.6 %, $\overline{x}$ 15.8 % in the right valve), its ventral margin often slightly elevated above the general inner surface of the shell, ornamented by subconcentric growth lines. Quenstedt muscle scar rarely seen, very small, located immediately beneath the posterior bourrelet in the only left valve in which it is visible; located beneath the posterior bourrelet in the right valve, but not obscured by it. Commissural shelf narrow, developed only in the dorsal regions, and more strongly developed on the posterior side; commissural platform well-developed, becoming flattened in very large specimens, but usually sloping towards the shell interior. Ligament area of the left valve tending to become elongated perpendicular to the hinge-axis, with the distinction between the resilifer and bourrelets becoming faint (overall L.lig. 26.7-31.2 %, $\overline{x}$ 28.5 %; H.lig. 14.7-26.5 %, $\overline{x}$ 21.7 %), often assuming a slight twist towards the posterior; ornamented by

concentric growth-lines. Ligament area of right valve flattened, clearly triangular in outline, with little differentiation of resilifer and bourrelets (overall L.lig. 28.7-32.5 %, $\overline{x}$ 30.6 %; H.lig. 15.0-21.5 %, $\overline{x}$ 18.3 %); ventral margin produced into the shell interior as a ligamentary buttress; sometimes with a slight posterior twist.

Remarks   This Middle Oxford Clay species has been referred to G. dilatata on several occasions in the nineteenth century, Lamarck's name being overlooked, but there can be no doubt that it is specifically distinct from both G. dilobotes and G. dilatata. Arkell (1932, p. 170) clarified the nomenclatorial position, and resurrected the name lituola for these Middle Oxford Clay forms. He also made the unusual error of placing Damon's 1860 figure (pl. 3, fig. 7) of 'G. dilatata' in the synonomy of both G. dilatata (p. 160) and G. lituola (p. 170). Damon's figure shows a relatively high, narrow form, viewed from the right, which could represent a narrow form of G. dilatata or a 'normal' form of G. lituola. In the absence of the specimen (it has not been traced in the BM (NH)), no definite conclusion on its identify may be made.

G. dilatata Young & Bird (1822, p. 239, pl. 10, fig. 4) is recorded from the "hard sandstone at the foot of Scarborough castle", presumably a reference to the Kellaways or Hackness Rock, and so is likely to be a specimen of either G. dilobotes or G. lituola. Their figure is of a faintly sulcate form resembling G. lituola, but in the absence of the specimen, its identity is uncertain.

As with G. dilobotes, there is a good deal of variation
in G. lituola, some forms closely resembling 'typical' forms of
G. dilobotes, but when the population as a whole is considered,
this U. Callovian species may be seen to be distinct from
G. dilobotes on account of its less strongly flanged nature,
greater degree of incurvature and narrower outline. A
characteristic of G. lituola, and often G. dilatata too, is the
frequent occurrence of an encrusting epifauna of serpulids,
foraminifera, bryozoa and oysters, attached to the exterior of
the left and right valves, and occasionally on the inner
surfaces of the valves. It is probable that at least some of
these epizoic elements, notably the foraminifera, bryozoa and
oysters lived at the same time as the oysters, but this will be
discussed elsewhere. In view of the lack of these epizoic
elements in the more organic-rich shales and clays of the L.
Oxford Clay and Kellaways Beds, it is likely that their
distribution is related to environmental conditions rather than
to host specificity.

Range and occurrence   Middle Oxford Clay, Athleta to Lamberti
Zones of England, known from Woodham, Stewartby, Wolvercote
(Oxford), and the Argile de Dives, Calvados (France) of similar
age. Probably Hackness Rock also, and maybe Corallian (Arkell,
1932, p. 171). More work needs to be done on the stratigraphical
and geographical distribution of this species.

Subfamily EXOGYRINAE Vyalov, 1936

Genus NANOGYRA Beurlen, 1958 (p. 206)

Synonymy: Palaeogyra Mirkamalov, 1963

Type species   Originally designated by Beurlen, 1958,
p. 206, Gryphaea nana J. Sowerby, 1822, p. 114, pl. 383, from
the Kimmeridge Clay of Oxfordshire.

Diagnosis   Small, inequivalve, very variable in shape
and form; left valve globular to moderately convex, suborbicular
or subtrigonal in outline, or elliptical to ovate; all specimens
spirally twisted, but degree of spiralling variable. Left valve
bilobate in some specimens, spiral groove dividing it into two
unequal lobes; spiral groove reaches valve margin dorsal of
branchitellum. Right valve flat, gently concave or gently
convex, suborbicular to subovate in outline, comma-shaped,
auriform or lingulate at branchitellum; left valve covered with
fine radial ribs or rough concentric growth squamae, often with
growth halts; right valve with few marginal growth squamae,
except along anterior margin, which has many crowded upturned
growth squamae. Spiral umbones of left valve coil tightly over
the ligament area, largely obscuring it; ligamental area
variably spiralled, anterior and posterior bourrelets of
approximately equal length, the posterior one not narrower than
the anterior.

Remarks   Beurlen (1958) separated the Jurassic and

Cretaceous Exogyrinae into two distinct genera, Nanogyra and

Exogyra, believing the former to be the most primitive member

of the Exogyrinae, transitional between Liostrea and Exogyra.

The spiral groove on the left valve of some specimens of

Nanogyra was thought to be homologous to that of Gryphaea,

suggesting that the Exogyrinae had their origins in the

Gryphaeinae. Nanogyra may be distinguished from Exogyra by

virtue of its small size, low degree of spirality of the left

valve, lack of commissural shelf covered with vermiculate

chomata, and equality of size of the bourrelets. The overall

taxonomic position of Nanogyra and other members of the Exogyrinae

are discussed by Stenzel (1971, p. N1115) and Pugaczewska (1971,

p. 220), the latter being more comprehensive, although the

overall conclusions are similar.

Nanogyra nana (J. Sowerby). Pl. 17, figs. 5-8.

v* 1822 Gryphaea nana sp. nov.; J. Sowerby, p. 114, pl. 383.

.   1829 G. mima sp. nov.; Phillips, pl. 4, fig. 6.

v. 1853 Exogyra auriformis (Goldfuss); Morris & Lycett, p. 5,
          pl. 1, fig. 7. (non Goldfuss).

v. 1932 E. nana (J. Sowerby); Arkell, p. 175, pl. 17, figs. 2-21;
          pl. 18, figs. 3-11; pl. 19, figs. 4, 4a.

.   1948 E. nana (J. Sowerby); Cox & Arkell, p. 20.

.   1952 E. nana (J. Sowerby); Cox, p. 92, pl. 10, figs. 2-4.

.   1965 E. nana (J. Sowerby); Cox, p. 73, pl. 11, figs. 5, 6a, 6b.

. 1971 Nanogyra nana (J. Sowerby); Pugaczewska, p. 281, pl. 1,
     figs. 3-5, 7; pl. 2, figs. 1-4; pl. 24, figs. 1-6;
     pl. 25, figs. 1-7; pl. 26, figs. 1-6; pl. 27, figs. 1-6.

Type specimen   Lectotype (designated by Arkell 1932, p. 180),
the left hand figure of J. Sowerby's plate 383 (1822), from the
Kimmeridge Clay of Shotover Hill, near Oxford. Preserved in the
Sowerby collection at the BM (NH), no. 43340.

Measurements

     Specimen from Calvert, bed 9Ac. A right valve.

     L   11.2 mm   HMS   11.9 mm (106.3%)

     H   18.7   (167.9%)   L.lig. 1.3   (1.0)

     I   2.5   (22.3)   H.lig. 0.9   (0.8)

     AL   11.2   (100.0)

Description   The single specimen known from the Lower
Oxford Clay is a small right valve 11.2 mm long. Outline
elliptical, tapering ventrally, with height considerably greater
than length (H 167.9%); dorsal margin evenly and convexly
curved into an approximately semicircular shape, passing smoothly
into the straight to very gently convex anterior margin; ventral
margin sharply rounded, narrower than the dorsal margin, but
without postero- or anteroventral angles; anterior margin
straight to gently sinuate; umbones small, very strongly
spirally coiled in an opisthogyrate direction, terminal on the
posterior margin (AL 100.0%). Shell flattened, very thin
(I 2.5 mm, 22.3 %), the anterior margin thickened, with a series
of steeply-stepped growth squamae sweeping round from the umbo

to the midpart of the anterior margin; posterior margin thin, tapered. External ornament consisting of faint subconcentric growth squamae, with no marked growth halts. No xenomorphic imprint of the attachment area is seen.

Ligament area very short (L.lig. 1.0 %), height slightly less than length (H.lig. 0.8 %), anterior and posterior bourrelets very short, approximately equal in length, but not measurable; ligament area ornamented by concentric growth lines; umbonal tip overhangs the apex of the ligament area. Adductor muscle scar slightly crescentic, concave towards the dorsal margin, placed considerably nearer to the hinge than to the ventral margin (HMS 106.3 %), its ventral margin slightly elevated above the body of the shell interior; muscle scar located about halfway between the anterior and posterior margins. Slight commissural shelf along the anterior margin. Quenstedt muscle scar not visible.

Remarks   The single specimen found in the Lower Oxford Clay (Grossouvrei Subzone of Calvert) agrees exactly with many specimens from the Corallian and Kimmeridge Clay of Britain, and must be united with them. Its occurrence in a Grammatodon shell bed suggests that during a pause in sedimentation, spat spawned elsewhere was able to settle in an area outside its usual habitat, although development of a new population did not occur. The range of variation, geographical and stratigraphical distribution in Britain, and the taxonomic relationships of N. nana were fully discussed by Arkell (1932, p. 175), and nothing need be added here. More recently, Pugaczewska (1971,

p. 281) in an important work on the Jurassic Ostreidae of
Poland, has described a collection of over 500 individuals of
this species, with emphasis on their variation, and for further
information on this point, her paper should be consulted. Cox's
(1952, 1965) records of N. nana from India and East Africa
show how geographically widespread this species must have been,
as it is also known from all over Europe and parts of Russia
(Pugaczewska 1971, p. 285).

Range and occurrence   Bathonian - Portlandian of Great Britain,
most of western Europe and parts of Russia, India, Asia and
Africa. The specimen recorded here is from the Grossouvrei
Subzone (Middle Callovian) of the English Midlands.

Subclass PALAEOHETERODONTA Newell, 1965

Order TRIGONIOIDA Dall, 1889

Superfamily TRIGONIACEA Lamarck, 1819

Family TRIGONIIDAE Lamarck, 1819

Genus MYOPHORELLA Bayle, 1878 (expl. pl. 120)

Type species   Subsequently designated by Crickmay, 1932,
p. 458, Myophorella nodulosa Bayle, 1878, pl. 120, figs. 1, 2, 6
(= Trigonia nodulosa Lamarck, 1801, p. 117), from the Oxfordian
of France.

Diagnosis   Trigonally ovate to oblong in outline,
strongly inequilateral, anterior margin fully and evenly curved,

posterior margin rostrate to a varying extent; posterior area
clearly separated from the body of the shell, with a completely
different ornament pattern; marginal carina obtuse, not
separated from the ornamented part of the valve by a smooth
band; escutcheon shallow; area divided by a variably developed
median carina; ornamented usually by concentric striae; flanks
of shell bearing rows of tubercles or tuberculate costae,
usually oblique, but occasionally subconcentric.

Subgenus MYOPHORELLA s.s.

Synonymy: Haidaia Crickmay, 1930

Scaphotrigonia Crickmay, 1930

Scaphitrigon Crickmay, 1930

Clavotrigonia Lebküchner, 1932

Clavitrigonia Leanza, 1942

Promyophorella Kobayashi & Tamura,1955

Diagnosis   Area transversely ridged or smooth, never
with radial ornament; escutcheon smooth; costae on flanks may
be uninterrupted throughout growth in some species, or
discontinuous and broken up anteriorly in later growth stages
in others.

Remarks   Crickmay (1932) designated Bayle's figure
of Myophorella nodulosa as the type species of Myophorella,
believing that the species figured by Bayle was not the same as
Trigonia nodulosa Lamarck, but Favre (1876), in refiguring

Lamarck's holotype, showed it to belong to the same species as
that figured by Bayle in his plate 120, figs. 1, 2, 6. There
has been a good deal of confusion concerning the type species of
several genera of trigoniids, and for some time, T. nodulosa was
accepted as type of Trigonia s.s., until an ICZN ruling (Opin. 327)
confirmed Venus sulcata Hermann as the type of that genus. Cox
(1952) gives a clear summary of the problem of trigoniid
nomenclature.

1.   Myophorella (Myophorella) irregularis (Seebach) Pl. 18,
        figs. 8-13, Pl. 19, figs. 1-4.

      1860 Trigonia clavellata J. Sowerby; Damon, pl. 2, fig. 3.
              (non J. Sowerby).

      1864 T. irregularis nom. nov.; Seebach, p. 117 (nom. nov.
              pro T. clavellata Damon non J. Sowerby).

      1872 T. irregularis Seebach; Lycett, p. 39, pl. 5, figs. 1a,
              1b, 2; pl. 7, fig. 6.

non 1877 T. irregularis Seebach; Lycett, p. 39, pl. 39, fig. 3.

      1879 T. irregularis Seebach; Mansell-Pleydell, p. 117,
              pl. 2, fig. 3.

      1911 T. irregularis Seebach; March, p. 8, text-figs. 7a, 7b.

non 1925 T. irregularis Seebach; Cox in Cunnington, p. 197.
              (= M. scarburgensis).

non 1932 T. irregularis Seebach; Arkell, p. 45. (=
              M. scarburgensis).

Type specimen   The holotype, figured by Damon (1860, pl. 2, fig. 3) is not preserved in the Damon collection at the BM (NH), and must be considered lost. Accordingly, the topotype figured by Lycett (1872, pl. 5, figs. 1a, 1b) is here designated neotype. It is preserved in the GSM (no. 11423), and comes from the Oxford Clay (horizon unknown) of Weymouth, Dorset.

Diagnosis   Large species (up to 88 mm L), elongate, markedly rostrate, the posterodorsal margin very concave and the posterior part of the ventral margin often reflexed; 10-16 tubercle rows, varying in regularity, the tubercles rising straight from the flanks of the shell, not elevated on subconcentric ribs; tubercles sometimes crowded anteriorly, but never coalescing, not crowded posteriorly; carinae strongly tuberculate, tubercles often persisting to the posteroventral angle; narrow, but prominent, smooth band runs posteroventrally between the marginal carina and the posterior end of the tubercle rows. H 64.7-78.9 %, $\overline{x}$ 71.1 %; I 33.8-52.5 %, $\overline{x}$ 41.5 %; AL 17.4-33.9 %, $\overline{x}$ 23.6 %; LE 46.4-61.5 %, $\overline{x}$ 55.1 %; LA 81.4-95.8 %, $\overline{x}$ 85.9 %; EW 15.0-25.4 %, $\overline{x}$ 20.1 %; TR 9-16, $\overline{x}$ 12.9.

Measurements   See Appendix 3, and fig. 2.35 for measurements used.

	L	H	I	AL	LE	LA	EW	Number of tubercle rows
N	30	30	30	29	28	29	30	29
$\overline{x}$	61.1mm	71.1%	41.5%	23.6%	55.1%	85.9%	20.1%	12.9
Max	88.0	78.9	52.5	33.9	61.5	95.8	25.4	16
Min	26.5	64.7	33.8	17.4	46.4	81.4	15.0	9
OR	61.5	14.2	18.7	16.5	15.1	14.4	10.4	7

Description   Large sized, elongate-oval to subtrapezoidal
in outline (H $\overline{x}$ 71.2 %), rostrate, well inflated (I $\overline{x}$ 41.8 %),
equivalve, inequilateral, the umbones situated within the
anterior third of the shell (AL $\overline{x}$ 23.6 %); umbones prominent,
small, pointed, opisthogyrate, contiguous, only slightly salient
to the hinge margin. Anterior margin gently convex, anteroventral
angle varying from a sharply rounded right angle to an even
curve into the ventral margin; ventral margin evenly and gently
convex, often sinuate posteriorly; posteroventral angle sharp,
about a right angle, the posterior margin biconvex, the median
carina forming an obtuse angle of about 135 ^{o} where it meets the
posterior margin; posterodorsal angle sharp, obtuse, about 125 ^{o},
marking the posterior limit of the gently to markedly concave
posterodorsal margin; the central part of the escutcheon, along
the dorsal margin, usually protrudes slightly above the outline
of the posterodorsal margin to form a slight convexity in the
outline. On the extreme anterior part of the valves, perpendicular
to the plane of the commissure, is a narrow smooth band, up to
about 5 mm wide, separating the anterior ends of the tubercle
rows from the commissure; a more prominent smooth band, up to
10 mm wide, extends from the umbones to the posteroventral angle,
anterior to the marginal carina, separating the posterior ends
of the tubercle rows from the marginal carina. The flanks of
the shell are ornamented by 9-16 rows of clavellate tubercles,
varying in regularity, with young forms (up to about 55 mm L)
often showing no irregularity in tubercle arrangement, and having
only subconcentric tubercle rows, meeting the marginal carina at

about 90 $^{\circ}$; larger specimens often show great irregularity of tubercle arrangement, the tubercle rows being sinuous or indistinct, with intercalatory half-rows in the anterior region; some large specimens, however, show a more regular arrangement of the tubercle rows, similar to that seen in younger specimens. The tubercles themselves increase in size with age, and usually number about 8-9 per row; they also tend to rise straight from the flanks of the shell, and are not usually placed on distinct, elevated tubercle rows. Marginal carina strong, concave in outline, taking the form of a ridge, topped at regular intervals by varices elongated along growth lines; median carina and escutcheon carina similarly ornamented, the varices being strongest on the escutcheon carina; there is very little tendency for the varices to get weaker posteroventrally; median sulcus shallow; area usually flat, oblique, ornamented by strong concentric ribs in the 10 mm nearest the umbones, these ribs then fading rapidly, leaving the remainder of the area covered in irregularly-spaced concentric growth lines, giving a slightly imbricate appearance; these growth lines continue onto the flanks of the shell, and affect even the tubercles. Escutcheon elongate, lanceolate, wide (EW $\overline{x}$ 20.1 %), deeply biconcave to almost flat, but always with the median part, along the commissure, elevated; proximally there is a prominent, lanceolate external ligament, with strong nymphs.

Dentition normal for Trigoniacea, dental formula

$$\frac{5a \quad\quad 3a \quad\quad 3b}{4a \quad\quad 2 \quad\quad 4b}$$

with 2 large, bifid, 4b and 5a short, lamellar, and 3a, 3b, and 4a

long and ridgelike, all the cardinal teeth bearing clearly-marked vertical crenulations. Adductor muscle scars subequal, the posterior scar subovate and slightly larger than the subelliptical anterior scar, the posterior scar more deeply impressed, especially along its anterior margin; posterior scar placed posteroventrally of the end of the hinge plate, separated from it by the small, suborbicular posterior pedal retractor scar; anterior adductor scars placed immediately anterodorsal to the anterior end of 3a, and below the end of 4a (Fig. 2.35).

Three short ridges on the inner surface of the rostrum mark the positions of the escutcheon, median and marginal carinae on the exterior, and serve to divide the rostrum into two areas, probably corresponding to the siphon positions. Pallial line entire.

Remarks   The exact horizon of the type specimen, and the numerous specimens labelled 'Oxford Clay, Weymouth' is unknown, as no examples have been collected in the area for nearly a century due to obliteration of the exposures, notably that at Radipole Backwater. In view of the fact that all the Zones of the Oxford Clay above the Lamberti Zone are still well-exposed in the cliffs of Weymouth Bay and the Fleet Backwater, and do not yield any specimens of M. irregularis, it seems probable that the specimens came from the Callovian Oxford Clay, coupled with the evidence from the 1" Geological Map (Sheet 342), which shows that most of Radipole Backwater is situated on the lower part of the Oxford Clay. The Athleta, Coronatum and part of the Jason Zones are exposed in the brickyard at Crook Hill, Chickerell, and again have not yielded any specimens of M. irregularis. In fact, the

only record of M. irregularis from this area in recent times is
that of Arkell (1947, p. 27) from the Koenigi Zone of Putton Lane
Brickyard, Chickerell, and this is a juvenile (SM J47645). Hence
it is still not possible to locate the horizon from which the
numerous topotypes of M. irregularis came, although the weight
of evidence suggests to the author that they are likely to have
come from the lower parts of the Oxford Clay, or perhaps even
from the Kellaways Beds.

The records of M. irregularis given by Cox (in Cunnington,
1925, p. 197) and Arkell (1932a, p. 45) refer to specimens found
in the beach of the West Fleet shore, about 1 mile west of
Langton Herring, Dorset, supposedly with other fossils of
Callovian age. However, Arkell later (1940, p. 44) showed that
the fauna was in fact of Fuller's Earth (Bathonian) age, and that
the trigoniids belonged to M. scarburgensis (Lycett).

March (1911) studied the ornament of some clavellate Upper
Jurassic trigoniids from the viewpoint of development of the
ornament pattern, and concluded (p. 9) that the ornament of
M. irregularis was ecologically controlled, and that the species
should be considered as a variety of M. clavellata. In view of
the many obvious morphological distinctions between these two
species, and their clearly separated stratigraphic levels, this
opinion is open to question.

The specimen figured by Lycett (1879) from the Kimmeridge
Clay of Wootton Bassett bears some superficial resemblance to
M. irregularis, but the tubercle rows are too regular and there
are too many tubercles per row for it to belong here. No
specimens of M. irregularis have been seen from the Kimmeridge Clay.

M. irregularis, like other trigoniids, is notable for the variation in form which may be found within a population of topotypes or other specimens; this is most obviously seen in the ornament pattern, but may also be noted in the shape of the shells. Most adult shells (over about 55 mm L) show the distinctive rostrum at the posterior end, with the variably reflexed posteroventral margin, but in younger specimens, this feature is not nearly as well seen, although some specimens are clearly rostrate. Tracings of the growth lines of large specimens (Fig. 2.36) reveal that the rostrum becomes better developed as growth proceeds. The lack of a prominent rostrum makes it difficult to identify juvenile specimens of M. irregularis in the absence of a large population, the only distinction being that the ribbing on juveniles of this species tends to be a little more regular than in species such as M. scarburgensis.

The major change in ornamentation style seems to take place at about the same time as rostrum development (L ≃ 55 mm), when there is a change from regular subconcentric rows of tubercles, to irregular rows with sinuous outlines and intercalatory half-rows. Occasional specimens of large size are found with simple tubercle rows, but these are not frequent, although many specimens show only a slight sinuosity near the anterior margin. At the other extreme are forms such as that figured by Damon (1860, pl. 2, fig. 3) where the tubercles have attained a very large size, and the subconcentric basic pattern has been almost totally obliterated.

In the description above, the teeth have been numbered according to the Bernard convention, on the assumption that all

the teeth are cardinals. However, Ohdner (1918) suggested that the teeth of Trigoniacea may in fact represent the cardinals and laterals, and introduced a modified system of notation, whereby the dental formula would be

$$\frac{3a \quad 1 \quad 3b + P_I}{2a \quad 2b \quad P_{II}}$$

As yet, there is no conclusive evidence either way, and Cox (1969b, p. N471) refrained from using dental formulae for Trigoniacea in the 'Treatise on Invertebrate Paleontology' for this reason. Both formulae have been given above to avoid confusion, although the former is the one which has been used more frequently in the past. D. W. Boyd (1973, pers. comm.) suggests that in order to avoid all this confusion caused by homologies of teeth, it would be better to use a modified Steinmann notation, and advocates using capital letters to indicate major dental elements, and small letters to indicate minor but persistent elements. A small n would represent the ligament nymph. Thus Boyd's hinge formula would be

	Posterior					Anterior
RV	n o 1 0 1 0
LV	n i 0 0 1

This very distinctive species may easily be distinguished from its close stratigraphic neighbours M. scarburgensis (Lycett) and M. rupellensis (Lycett) /non d'Orbigny/ on the basis of its rostrate form, and the way in which the tubercles rise straight from the flanks of the shell. There are apparently no certain records of it from the continent although Trigonia aff. irregularis has been recorded from the Callovian (Wohlegemuth, 1883) and

Oxfordian (Klüpfel, 1919) of France, without having been figured.

Range and occurrence   The type material came from the 'Oxford
Clay of Weymouth', horizon unknown, but probably Callovian;
Also from the Kellaways Beds (Koenigi Zone) of Putton Lane brick-
pit, Chickerell, Weymouth (SM J47645), Oxford Clay (horizon
unknown) of Loudon, Wilts. (Hudleston collection, GSM Y2078-2080),
Oxford Clay (horizon unknown) of Trowbridge, Wilts. (GSM Y2014),
Oxford Clay (horizon unknown) of Chippenham, Wilts. (GSM Y2027),
L. Oxford Clay, Jason Zone Medea Subzone (Bed 5), Stewartby,
Beds.; Coronatum Zone, Obductum subzone (Bed 7), Marston Moretaine,
Beds.; Coronatum Zone, Grossouvrei Subzone (Bed 9AA), Calvert,
Bucks.; Coronatum Zone, Obductum subzone (Bed 10C), Marston
Moretaine, Beds.

2.   Myophorella (Myophorella) caytonensis nom. nov. Pl. 19,
        figs. 5a-b, Pl. 20, figs. 1-3.

v*   1872 Trigonia Rupellensis d'Orbigny; Lycett, p. 28, pl. 8,
            fig. 4. (non d'Orbigny).

v.   1877 T. Rupellensis d'Orbigny; Lycett, p. 199, pl. 36,
            figs. 1, 2, 3, 4. (non d'Orbigny).

.non 1915 T. rupellensis d'Orbigny; Krenkel, p. 312, pl. 27,
            fig. 16. (non d'Orbigny).

.non 1929 T. Rupellensis d'Orbigny; Cottreau, p. 85, pl. 54, fig.1.

.?   1934 T. clavellata J. Sowerby; Stoll, p. 10, pl. 1, fig. 18.
            (non J. Sowerby).

v.   1972 Myophorella rupellensis (d'Orbigny); Walker, p. 124,
            pl. 8, fig. 20. (non d'Orbigny).

<u>Type specimen</u>   Holotype of <u>T. rupellensis</u> Lycett (non

d'Orbigny), from the Kellaways Rock of Cayton Bay, Scarborough,

(Lycett, 1872, p. 28, fig. 4) is preserved in the SM, no. J11377,

and is here made the holotype of <u>M. caytonensis</u> nom. nov.

<u>Diagnosis</u>   Large (up to 88 mm L), clavellate,

trigoniform, not rostrate, ovately trigonal to elongate-oval in

outline (H 70.0-86.4 %, $\bar{x}$ 79.6 %), inflation extremely variable

(I 36.5-66.7 %, $\bar{x}$ 46.4 %); umbones usually placed about a third

of the shell-length behind the anterior margin (AL 19.2-45.2 %,

$\bar{x}$ 31.2 %); ornament of flanks irregular, the first 6 tubercle

rows subconcentric, subsequent tubercle rows usually sinuate,

often forming a V pointing towards the posteroventral angle;

there are often intercalatory half-rows anteriorly; the tubercles

never become coalesced into a rib anteriorly, and at their

posterior extremities, the tubercle rows bend abruptly upwards

to the marginal carina, meeting it at a very obtuse angle. LE

51.0-75.5 %, $\bar{x}$ 59.2 %; LA 79.2-96.7 %, $\bar{x}$ 87.2 %; EW 9.1-23.3 %,

$\bar{x}$ 18.4; TR 10-17, $\bar{x}$ 13.9.

<u>Measurements</u>

See Appendix 3.

	L	H	I	AL	LE	LA	EW	TR
N	18	18	17	18	16	17	14	17
$\bar{x}$	64.5mm	79.6%	46.4%	31.2%	59.2%	87.2%	18.4%	13.9 ribs
Max	88.0	86.4	66.7	45.2	75.5	96.7	23.3	17
Min	29.5	70.0	36.5	19.2	51.0	79.2	9.1	10
OR	58.5	10.4	30.2	26.0	24.5	17.5	14.2	7

Description   Large species, equivalve, inequilateral, with umbones usually placed within the anterior third of the shell (AL $\overline{x}$ 31.2 %); subtrigonal to elongate oval in outline, but not rostrate. Umbones prominent, small, pointed, contiguous, of opisthogyrate, salient about 2 mm to the hinge margin. Posterodorsal margin straight to gently concave, markedly concave anteriorly, where the umbones protrude above it, and sometimes with a small convexity where the central part of the escutcheon stands out along the commissure; posterodorsal angle obtusely rounded, about 150 $^{\circ}$, passing into the gently convex and oblique posterior margin; posteroventral angle rounded, obtuse, about 120 $^{\circ}$. passing into the evenly convex ventral margin; there is no posterior sinuosity in the ventral margin; anterior margin very gently convex, meeting the ventral margin in either an evenly rounded curve, or a rounded angle of about 90 $^{\circ}$. Marginal carina long, concave in outline, taking the form of an elongate ridge with occasional well-marked subconcentric varices on some specimens; median carina faint, with very poorly developed varices, median sulcus obscure; escutcheon carina strong, ridgelike, with well-developed tuberculate varices. Area long (LA $\overline{x}$ 87.2 %), flat to gently convex in outline, sometimes becoming slightly concave in the proximal regions, oblique to the flanks of the shell at an angle of about 135 $^{\circ}$. Escutcheon elongate (LE $\overline{x}$ 59.2 %), narrow (EW $\overline{x}$ 18.4 %), lanceolate, biconcave in section, rising to a high point along the commissure, the greatest elevation being just posterior to the end of the ligament nymphs; ligament up to 15 mm long, narrow, lanceolate, opisthodetic, nymphs strong; both the area and the escutcheon

are ornamented with concentric growth striae, often coarsened
on the area to give an imbricate appearance; the proximal 10 mm
of the area is ornamented with strong concentric ribs, which fade
distally.

Flanks of the shell ornamented by 10-17 ($\overline{x}$ 13.9) rows of
rounded tubercles, each row with about 12 tubercles, the rows
tending to be raised on elevated ribs, rather than rising
straight from the flanks of the shell; approximately the first
6 tubercle rows are simple and subconcentric in form, but there-
after the tubercle rows become sinuate and very irregular, often
assuming a falcate form, the anterior part of each row being
relatively straight, the row then swinging posteroventrally before
it curves back towards the marginal carina; the posterior part
of each tubercle row is abruptly reflected towards the marginal
carina, meeting it at an angle of about 130 $^{\circ}$; in the anterior
regions, intercalatory half-rows of tubercles between the major
rows are often present; the anterior parts of the tubercle rows
do not coalesce into ribs. Where the ribs meet the anterior
margin, they are not paired, but interdigitate.

Internal features not seen, but probably normal for
Trigonacea.

Remarks   The figuring by Cottreau (1929, pl. 54, fig. 1)
of the holotype of T. rupellensis d'Orbigny revealed that Lycett's
conception of the species differed from that of d'Orbigny. Thus
Lycett's species is in need of renaming, M. caytonensis being
introduced herein. D'Orbigny's species came from the 'Corallien'
(actually the Cymodoce Zone of the L. Kimmeridge Clay) of La
Rochelle, Calvados, France, and is a densely ribbed form with a

wide, smooth band between the marginal carina and the posterior end of the tubercle rows, more correctly placed in the genus Laevitrigonia Lebkūchner. Lycett's figures show the great variation in form and ornamentation present in this species, as do the measurements (see above), which reveal that many characters (I, AL, LE) have a range of over 20 %. In form, there is gradation from subtrigonal forms, such as the holotype, through more elongate forms, to a markedly elongate form such as that figured by Lycett in his pl. 36, fig. 4 (GSM 11439); this form variation is independent of overall size. In ornament, there is a gradation from relatively regularly-tuberculate forms, with subparallel tubercle rows (i.e. the holotype) to forms with very irregular ribbing, such as Lycett's pl. 36, fig. 2 (GSM 11437) and fig. 3 (GSM 11438), where the subparallel nature of the tubercle rows is lost, and where there are several intercalatory half-rows of tubercles.

The specimen figured by Krenkel (1915, pl. 27, fig. 16) as T. rupellensis is certainly a Myophorella, not a Laevitrigonia, but is probably to be placed in M. scarburgensis rather than M. caytonensis, as the tubercles are coalescent over much of the anterior part of the shell, and the tubercle rows do not reflect upwards to the marginal carina. Krenkel's figure agrees closely with Lycett's figure (1863, p. 48, pl. 37, fig. 1) of the holotype of T. scarburgensis (GSM 10610). Krenkel (op. cit. p. 313) believed that T. scarburgensis and T. rupellensis Lycett (non d' Orbigny) were one and the same, but study of populations of topotypes of each species reveals that this is not so, T. scarburgensis having the anterior tubercles in each row joined

together into a rib, lacking the posterior reflection of the ribs towards the marginal carina, and tending to have different ornament patterns on each valve. There is also a stratigraphic discrepancy, M. scarburgensis ranging from the Cornbrash (the type locality) down to the Fuller's Earth, while M. caytonensis appears to be restricted to the Yorkshire Kellaways Rock.

T. clavellata Stoll (non J. Sowerby), from the M. Callovian of Pomerania (Stoll, 1934, pl. 1, fig. 18) is poorly figured and not described, but bears several resemblances to M. caytonensis, in which it is tentatively placed. The specimens figured by Walker (1972, pl. 8, fig. 20) as M. rupellensis, from the Kellaways Rock of South Cave, Yorkshire, agree closely with the Cayton Bay specimens of M. caytonensis, and are placed in that species. Walker's statement (op. cit., p. 125) that typical specimens from the South Cave area are indistinguishable from Krenkel's figure of T. rupellensis is misleading, as almost certainly Krenkel figured a specimen of M. scarburgensis, and Walker's specimens certainly do not belong to that species.

M. caytonensis seems to be restricted to the Kellaways Beds (Calloviense Zone) of Yorkshire, abundant material being available at Cayton Bay, and less well-preserved material in the South Cave area. Presumably this may represent an ecological effect, M. caytonensis only being found in more arenaceous lithologies, its place in the more argillaceous Kellaways Beds to the south possibly being taken by M. irregularis.

Range and occurrence   Calloviense Zone (L. Callovian), Kellaways Rock, Cayton Bay, Scarborough (the type locality); also the Calloviense Zone Kellaways Rock of South Cave Station Quarry and

South Newbald Quarry, South Cave, Yorkshire.

Perhaps also the M. Callovian of N. Germany (Stoll, 1934).

Subclass HETERODONTA Neumayr, 1884

Order VENEROIDA H.Adams & A.Adams, 1858

Superfamily LUCINACEA Fleming, 1828

Family LUCINIDAE Fleming, 1828

Subfamily MYRTEINAE Chavan, 1969

Genus DISCOMILTHA Chavan, 1952 (p. 95)

Type species   Originally designated by Chavan, 1952, p.95,
Discomitha oehlerti Bigot Ms in Chavan, 1952, p. 95, pl. 4,
figs. 38-40, from the Sables Astartiens (U. Oxfordian) of
Cordebugle, Calvados, France.

Diagnosis   Moderately large, suborbicular, flattened,
of low inflation; sculpture of well-spaced feeble, concentric
ribs and finer striae; posterior area well-marked; lunule very
asymmetrical, narrow, long, larger in the left valve than the
right; ligament projecting, inframarginal; hinge teeth
comprising only two weak cardinals, partly obscured by lunular
expansion; shell interior punctate and grooved; anterior
adductor muscle scars elongate, narrow, distant from the pallial
line; shell margin smooth internally.

Remarks   Chavan, in the Treatise on Invertebrate
Paleontology (1969, p. N492) divided the Lucinidae into three
subfamilies, the Lucininae, Myrteinae and Milthinae, on the basis
of shell thickness and outline, and length of the anterior

adductor muscle scars. The Myrteinae are characterised by thin, more or less quadrangular or transverse shells, of moderate inflation, and with medium-sized anterior adductor scars, usually divergent from, and within, the pallial line.

The good preservation of several specimens of Lucina lirata Phillips from the Grossouvrei Subzone (Coronatum Zone) of Calvert, Bucks., allows study of the internal features of the valves, and it is immediately apparent that this species belongs in Discomiltha, by virtue of its external form and ornament, the length of the narrow anterior adductor scar, and the pustulose nature of the shell interior. Particularly characteristic is the obliquely truncate posterior margin of Discomiltha, with a variably developed indentation in the posteroventral margin marking the position of the posterior radial sulcus.

Superficially, Discomiltha resembles Saxolucina Stewart, a member of the Milthinae, but although there are close similarities in ornament, outline, and details of the musculature, Saxolucina has more clearly developed teeth (2 and 3b often being bifid), together with traces of anterior laterals; the asymmetry of the lunule is reversed in Saxolucina, the right valve bearing the larger part. Several other genera of Lucinidae, such as Monitilora Iredale, Plastomiltha Stewart and Gardnerella Chavan are also internally pustulose, but may be distinguished from Discomiltha by their shorter anterior adductor scars and differences in the dentition. The presence of internal pustules on the shell is of uncertain significance, but is of great taxonomic value at generic level, as very few genera possess these features, and those which do are confined to the Myrteinae and

Milthinae; no Lucininae with pustules are known.

Discomiltha lirata (Phillips). Pl. 17, figs. 10-11, Pl. 18,
figs. 1-7.

*   1829 *Lucina lirata* sp. nov.; Phillips, p. 140, pl. 6, fig.11.

.non 1830 *L. lirata* Phillips; Zieten, p. 84, pl. 63, fig. 1.

                (non Phillips; = *L. zieteni* nom. nov. d'Orbigny).

.non 1843 *L. lyrata* Phillips var. *transversa* nov.; d'Archiac,

                pl. 26, figs. 3a, 3b. (non *L. lirata* Phillips; non *L.*

                transversa Bronn, 1831; = *L. bellona* nom. nov.

                d'Orbigny).

v.   1934 *L. lirata* Phillips; Arkell, p. 278, pl. 41, figs. 1-3,7.

Type specimen   Neotype, designated herein, the specimen
figured by Arkell (1934, p. 278, pl. 41, fig. 7) from the Hackness
Rock of Scarborough, Yorkshire, preserved in the BM (NH), number
BM LL10077.

Diagnosis   Large species, up to about 50 mm long,
suborbicular to subrectangular in outline (H 80.1-98.4 %, $\overline{x}$
90.9 %), compressed (I 35.1-45.4 %, $\overline{x}$ 39.8 %); posterior region
of shell slightly flattened, marked off from the body of the
shell by a variably developed, but usually faint, radial sulcus
extending to the posteroventral angle; posterior margin straight,
obliquely truncate; anterior part of shell not markedly
produced, umbones submedian (AL 46.3-58.1 %, $\overline{x}$ 51.3 %);
ornamented by irregularly spaced concentric lamellae, often about
1.5 mm apart, with fine concentric growth lines in the
interspaces; shell interior pustulose; anterior adductor scar
long, narrow.

Measurements

See Appendix 3.

	L	H	I	AL
N	18	18	7	9
$\overline{x}$	34.2 mm	90.9 %	39.8 %	51.3 %
Max	47.0	98.4	45.4	58.1
Min	21.6	80.1	35.1	46.3
OR	25.4	18.3	10.3	11.8

Description   Large species, equivalve, inequilateral, suborbicular to subrectangular in outline, with umbones submedian (AL $\overline{x}$ 51.3 %), small, fairly prominent, pointed, prosogyrate, salient about 2 mm above the dorsal margin. Anterodorsal margin gently concave, variably produced, passing either evenly, or via a rounded anterodorsal angle, into the evenly convex anterior margin; occasionally, the anterior margin is rather less convex, and more nearly straight, in which case the anterodorsal angle is more marked; the fully rounded anterior margin passes smoothly into the more gently convex ventral margin, with no perceptible anteroventral angle; at its posterior end, the ventral margin becomes slightly more convex, and meets the rounded, but prominent, posteroventral angle, the latter often being marked by a clear indentation caused by the posterior radial sulcus meeting the posterior margin; in some specimens, the sulcus is very weak, and the posteroventral angle very ill-defined, the ventral and posterior margins then curving more smoothly into one another; posterior margin straight to gently convex, occasionally very slightly concave, obliquely truncate, meeting the posterodorsal margin in a rounded obtuse angle;

posterodorsal margin straight to gently convex. A posterior area, bounded by the variably developed posterior radial sulcus, is usually clearly developed, and takes the form of an obliquely flattened region between the umbo and the posteroventral angle; often the ornament becomes slightly coarsened on the posterior area, the concentric lamellae being strengthened and slightly elevated. The remainder of the shell exterior is ornamented with irregularly developed narrow concentric lamellae, spaced about 1.5 mm apart, separated by wider interspaces containing concentric growth striae; in the Lower Oxford Clay specimens, the lamellae are not well-developed, and are only slightly coarser than the growth lines, giving a more even pattern of ornamentation; no radial elements are present on the shell exterior.

Dorsal areas well-differentiated, prominent. Lunule small, elongate, narrow, sharply bounded by two carinae, asymmetric, the part of the lunule on the left valve being wider than that on the right. Escutcheon absent, being obscured by the external ligament, which occupied the whole of the posterodorsal margin between the umbo and the posterodorsal angle, and is deeply inset into the dorsal margin.

Dentition unknown. Anterior adductor muscle scar elongate, narrow, arcuate, parallel-sided, reaching about two-thirds of the way to the ventral margin, and placed within the pallial line, from which it diverges markedly; posterior adductor muscle scar subovate, elongated dorsoventrally, located mostly within the posterior area, sometimes crossing the posterior sulcus, and reaching into the body of the shell; pallial line entire, lacking a pallial sinus, although there is often a slight

reflection where the pallial line crosses the posterior radial
sulcus. The shell interior within the pallial line is strongly
pustulose, and a faint radiating pattern may be made out within
this pustulose area. Inner shell margin smooth, lacking
marginal denticulations.

Remarks   The holotype of *Lucina lirata* Phillips is
said by Etheridge (in Phillips, 1875, p. 326) to be in the
author's collection, but search of the Phillips collections at
the Yorkshire Museum and the Oxford University Museum has not
revealed this specimen; neither is it present in the British
Museum (Natural History), Sedgwick Museum, Cambridge or the
Geological Survey Museum, London, and must be considered lost.
The topotype figured by Arkell (1934, pl. 41, fig. 7; BM LL10077)
is here designated neotype.

        Phillips figure (1829, pl. 6, fig. 11) is rather stylized,
and shows a specimen with a much more oblique posterodorsal
margin than is normal, but there are many topotypes available
from the Hackness Rock which show the true nature of the species,
and which reveal that Phillips exaggerated the truncation of the
posterior margin. The most variable feature of this species is
the elongation, and degree of prominence of the anterior part of
the shell, which are often, but not always related. Frequently,
the most elongate specimens have rather inflated and produced
anterior regions, the more suborbicular specimens being not nearly
so anteriorly produced, although a few elongate, but not
anteriorly-inflated examples occur. Inflation is not as variable
as height, and appears to be unrelated to degree of elongation;
it is also the most difficult parameter to measure, as most of

the specimens occur as disarticulated valves, and accurate measurement of the inflation is not possible. Maximum inflation always occurs in the middle regions of the shell, never on the produced anterior regions.

The modes of preservation found in D. lirata make study of the dentition and dorsal regions very difficult, and as yet, no specimens showing the teeth have been seen, although it is hoped that further collecting from the Lower Oxford Clay shell-beds will yield suitable examples. Lacking the dentition, it is very difficult to place this species with certainty, but the presence of the pustules, and the elongation of the anterior adductor scar make it almost certain that it belongs in Discomiltha. Comparison with Chavan's original figures (1952, pl. 4, figs. 38-40) of the type species shows that D. oehlerti is very close to Lucina lirata, and that until evidence to the contrary is found, the latter species is best placed in Discomiltha. The topotypes of L. lirata are all steinkerns, occasionally with a few remnants of shell remaining, and none of them are well enough preserved in the umbonal regions to allow study of the dentition. However, the examples which occur in the shell beds of the Lower Oxford Clay are single valves, of great fragility, but showing internal structures, and it can only be a matter of time before a specimen showing the teeth comes to light.

Arkell (1934, p. 278) has shown that the Bathonian species Lucina bellona d'Orbigny (= L. lyrata d'Archiac non Phillips) is closely related to D. lirata, but differs in being more elongate, less protuberant at the anterior part of the ventral margin, and

having shorter and wider anterior adductor scars.

The Callovian - Oxfordian species L. rotundata (Roemer), common in the arenaceous facies of the Callovian at Brora, and throughout the Corallian of Britain and north-west Europe, differs from D. lirata in its greater inflation (I 50-63 %), its rounded posterior margin without a posterior sulcus, and its ornament style, lacking the concentric lamellae; in general outline, it is much more rounded and globose than D. lirata.

Range and occurrence   D. lirata occurs throughout the L. Oxford Clay of central and southern England, although it is never abundant, except locally in some of the condensed shell beds; Calloviense - Athleta Zones. Also from the Hackness Rock of Scarborough, Yorkshire (the type locality), and abundant throughout the British Corallian (see Arkell, 1934, p. 278).

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Superfamily CRASSATELLACEA Ferussac, 1822

Family ASTARTIDAE d'Orbigny, 1844

Subfamily ASTARTINAE d'Orbigny, 1844

Genus NEOCRASSINA Fischer, 1886 (p. 1016)

(nom. subst. pro Crassinella Bayle, 1878 (non Guppy, 1874)

Synonymy: Puschia Rouillier & Vossynski, 1847

Oreadia Rouillier & Vossynski, 1847

Pruvostiella Agrawal, 1955

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Type species   Subsequently designated by Dall, 1903,
p. 1487, <u>Astarte obliqua</u> Deshayes, 1830, p. 80 (= <u>Cypricardia</u>
<u>obliqua</u> Lamarck, 1819, p. 29), from the Bajocian of western
France.

Diagnosis   Ovate to subtrapezoidal in outline,
inequilateral, often with umbones pointed and slightly produced;
concentric ribs developed in umbonal regions, fading in adults,
leaving merely strong growth lines. Hinge formula:

$$\frac{A_I \quad 3a \quad 3b \quad PI}{A_{II} \quad 2 \quad 4b \quad PII}$$

with trigonal cardinals and strong posterior laterals; ligament
nymph broad and flattened. Marginal denticulation present or
absent.

Subgenus NEOCRASSINA s.s.

Diagnosis   Shape and ornament as in <u>Neocrassina</u> s.l.;
P_{II} placed well behind the ligament nymph, elongate, laminar;
lunule only slightly depressed; escutcheon narrow, external.

Remarks   <u>Neocrassina</u> was introduced by Fischer (1886)
to accommodate the Jurassic to L. Cretaceous astartids with two
trigonal cardinals and a strong posterior lateral tooth in each
valve, and was a substitute name for <u>Crassinella</u> Bayle (1878),
Guppy having introduced <u>Crassinnella</u> four years earlier as a
genus of Recent Crassatellidae. The shell of <u>Neocrassina</u> is
often thick and heavy with a wide hingeplate, as in <u>N. (N.)</u>
<u>ungulata</u>, but in other species, such as <u>N. (N.) calvertensis</u>, it

is thinner-shelled with a narrow hingeplate.

Neocrassina s.s. is distinguished from N. (Coelastarte) by having a more posteriorly placed posterior lateral tooth (P_{II}), together with a less well-excavated lunule and less penetrating escutcheon. The hinges of several Russian Upper Jurassic species of Neocrassina s.s. have been well-figured by Zakharov (1970, pl. 12, figs. 4, 5), and show the wide cardinal plate with elongate cardinal teeth.

1.   Neocrassina (Neocrassina) ungulata (Lycett). Pl. 20,
       figs. 4-12.

1829   Astarte lurida sp. nov.; Phillips, pl. 5, fig. 2. (non J.
       Sowerby, U. Lias species).

1863   A. ungulata nom. nov.; Lycett, p. 72, pl. 35, fig. 20.
       (nom. nov. pro A. lurida Phillips non J. Sowerby).

1934   A. ungulata Lycett; Arkell, p. 244.

1948   A. ungulata Lycett; Cox & Arkell, p. 26.

Type specimen   The holotype of Astarte ungulata Lycett (1863, p. 72, pl. 35, fig. 20), from the Cornbrash of Yorkshire, is preserved in the Leckenby collection at the Sedgwick Museum, Cambridge (SM B10715). The specimen figured by Phillips (1829, pl. 5, fig. 2) as Astarte lurida sp. nov. (non J. Sowerby), from the Oxford Clay of Scarborough, is preserved in the Yorkshire Museum (YM 873), together with two syntypes (YM 874, 875).

Diagnosis   Medium sized species (up to 21.2 mm L) of low inflation (I 32.9-44.4 %, $\overline{x}$ 40.3 %), very variable in outline from suborbicular to subquadrate (H 85.6-110.1 %, $\overline{x}$ 95.3 %);

umbones sharp, prosogyrate, of varying prominence, rather produced in subquadrate forms, hardly salient above the hinge margin in suborbicular forms; ornament consisting of strong concentric ribs in the umbonal regions, fading to mere concentric growth lines at about 8 mm from the umbo. Hinge plate wide, with 3b, 2, 4b elongate; dental formula normal for genus. Margin denticulate.

Measurements

See Appendix 3.

	L	H	I	AL
N	10	10	3	8
$\overline{x}$	16.7 mm	95.3 %	40.3 %	37.9 %
Max	21.2	110.1	44.4	42.3
Min	13.8	85.6	32.9	32.0
OR	7.4	25.5	11.9	10.3

Description   Medium-sized species (up to 21.2 mm L), inequilateral, umbones small, prosogyrate, pointed, variably produced, placed 32.0-42.3 % ($\overline{x}$ 37.9 %) behind the anterior margin; outline suborbicular, with length approximately equal to height, and umbones not prominent, to subquadrate, with length about 10-15 % greater than height, and umbones rather produced; anterior margin almost straight to slightly concave, curving smoothly into the continuously rounded anterior and ventral margins; posterodorsal margin gently convex, posterodorsal angle obtusely rounded; posterior margin subtruncate and gently convex in subquadrate individuals, passing into the ventral margin via a prominent rounded posteroventral angle, or evenly rounded, and

passing into the ventral margin without a posteroventral angle
in suborbicular forms. Inflation variable (32.9-44.4 %, $\overline{x}$
40.3 %) but low, most of it usually being due to the thickness
of the valves rather than enlargement of the shell cavity.
Ornament consists of a variable number, up to 13, of strong
concentric ribs, separated by sulci approximately equal in width
to the ribs; the ribs fade out at a distance of about 7 mm from
the umbones, and only faint, irregularly spaced concentric growth
lines remain; very occasionally coarser growth lines develop in
the ventral regions to form one or two ribs. Lunule elongate,
extending almost to the anterodorsal angle, narrow, lanceolate
in outline, obliquely flattened and only slightly depressed.
Escutcheon elongate, lanceolate, reaching almost to the postero-
dorsal angle, obliquely flattened and external.

Cardinal plate heavy and wide, the cardinal teeth being
elongate and subparallel to one another (Fig. 2.38). Dental
formula:

$$\frac{A_I \quad 3a \quad 3b \quad P_I}{A_{II} \quad 2 \quad 4b \quad P_{II}}$$

with A_{II} and P_I forming the dorsal margin; 3b, 2, 4b elongate,
trigonal, narrow, 2 and 4b subparallel; 3a shorter and more
oblique; laterals laminar, P_I and P_{II} placed well behind the
nymph. Nymph broad and flattened, ligament suture placed along
the dorsal margin.

Adductor muscle scars placed immediately beneath the ends
of the cardinal plate, subequal, the posterior being slightly
larger and subrectangular, the anterior subelliptical; anterior
pedal retractor muscle scar very small, subovate, placed on the

ventral slope of the cardinal plate, just posterior of the anterior adductor;   posterior pedal retractor scar subovate, placed on the ventral slope of the cardinal plate immediately beneath cardinal tooth 2. Pallial line entire. Margin denticulate.

Remarks   The relationships of the Upper Jurassic species of Neocrassina are rather complex, in view of the great amount of variation which may be present in each species, and it is advisable to work with populations rather than with individuals. N. (N.) ungulata shows the normal wide range of variation in outline, but all specimens are characterised by the wide cardinal plate, with elongate cardinal teeth (Fig. 2.38), which serves to distinguish them from N. (N.) calvertensis. It is perhaps possible that variation in development of the cardinal plate is merely an intraspecific feature, but the two hinge types are never found together, and so in the lack of an overlap of the two types of cardinal plate, it is necessary to separate them at the specific level. The discovery of further material may clarify this point.

The holotype of N. ungulata is from the Cornbrash of Yorkshire (SM B10715) and is suborbicular in outline, but topotypes reveal that this is merely one morphotype, and that more subquadrate forms, similar to those figured by Phillips (1829, pl. 5, fig. 2) from the Mariae Zone Oxford Clay of Scarborough, also occur (i.e. GSM 113012). Syntypes of A. lurida Phillips (non J. Sowerby) preserved in the Yorkshire Museum (nos. YM 873-875) show that a similar range of variation occurs in the Yorkshire Oxford Clay. The specimens which occur in the

Yorkshire Oxford Clay are preserved as composite clay steinkerns, with details of the exterior and interior superimposed; specimens such as these show the nature of the dentition quite clearly, revealing the presence of a wide cardinal plate and elongate cardinals (SM J26767-68 show this particularly well). The dentition is best seen in a specimen (BCM 3324) from the Oxford Clay of Trowbridge, Wiltshire, which agrees particularly well in outline with Lycett's holotype. Some small specimens of the closely-related N. striato-costata (Münster in Goldfuss) from the Callovian of Lukow, Poland, presented to the author by Dr. A. Radwanski of Warsaw University, are extremely well-preserved, and show the nature of the musculature particularly well (Fig. 2.39). It is from these specimens that the details of the pedal musculature have been determined. N. striato-costata, with which should be grouped N. trembiazensis (de Loriol, 1901) is very near N. ungulata, as Makowski's (1952, p. 10) figures show. This continental species may, however, be distinguished from N. ungulata by virtue of its consistently smaller size (up to 13.5 mm L), and more pointed and prominent umbones, which give a marked concavity to the posterior part of the lunular area. The length-height relationships are also different, the height of N. striato-costata slightly exceeding the length.

A. philea d'Orbigny and A. pelops d'Orbigny (figured in Cottreau, 1927, pl. 46, figs. 1, 2, and 3, 4 respectively) closely resemble N. ungulata in their suborbicular outline and low inflation, but are placed by Arkell (1934, p. 241) in the synonymy of Astarte nummus Sauvage. All three names apply to Corallian species, which may be distinguished from N. ungulata

by their tendency to have ribbing over the whole shell surface.

Range and occurrence   Cornbrash of Yorkshire (the type horizon);
"Kelloway Rock" (= Hackness Rock) of Scarborough, and widespread
in parts of the Oxford Clay, specimens being known from the
Oxford Clay of Trowbridge and Chippenham (BCM 3324/1-5),
Fairford, Gloucestershire (BU 14708), and the Mariae Zone of
Scarborough, Yorkshire (numerous specimens). Also found in the
?Lamberti Zone of Lukow, Poland.

2.   Neocrassina (Neocrassina) calvertensis sp. nov. Pl. 21,
      figs. 1-7.

Type specimen   Holotype, from the L. Oxford Clay (Bed 2C),
Jason Subzone, Jason Zone of Calvert, Bucks., preserved in the
BM (NH), number LL 27730.

Diagnosis   Small to medium sized species (up to 20.7 mm
L) of low inflation (I 19.3-37.3 %, $\bar{x}$ 28.0 %), suborbicular to
subovate in outline (H 88.3-96.9 %, $\bar{x}$ 90.7 %), usually slightly
elongate; umbones small, pointed, not very prominent,
prosogyrate; ornament consisting of concentric ribs in the
umbonal region, fading into growth lines at a distance of about
5 mm from the umbo; dentition normal for genus, but cardinal
plate narrow and slight, with cardinal teeth short and peglike;
margin denticulate.

Measurements

See Appendix 3.

	L	H	I	AL
N	7	7	4	6
$\overline{x}$	16.7 mm	90.7 %	28.0 %	36.0 %
Max	20.7	96.9	37.3	43.5
Min	13.8	88.3	19.3	26.8
OR	6.9	8.6	18.0	16.7

Description   Small to medium-sized species (L up to 20.7
mm) of variable outline, but usually suborbicular, with small,
prosogyrate, pointed, slightly salient umbones, or subovate with
slightly more prominent umbones (H 88.3-96.9 %, $\overline{x}$ 90.7 %); the
most common forms tend to be subovate, slightly drawn out antero-
posteriorly, with a more concave anterodorsal margin;
anterodorsal margin straight to gently concave, the concavity
being greatest in more elongate forms; anterodorsal angle
rounded, obtuse, passing evenly into the continuously rounded
anterior and ventral margins; ventral margin almost straight to
evenly convex in outline, dependent upon elongation; posterodorsal
margin gently convex, passing into the truncate or gently convex
posterior margin via an obtuse posterodorsal angle which is very
clearly developed in elongate forms; posteroventral angle
obsolete. Umbones small, pointed, hardly protruding above the
general level of the shell outline, situated about one-third of
the length behind the anterior margin (AL 26.8-43.5 %, $\overline{x}$ 36.0 %).
Inflation low (I 19.3-37.3 %, $\overline{x}$ 28.0 %), most of this usually
being due to the thickness of the valves rather than inflation
of the shell cavity. Ornament consisting of 8-10 concentric ribs

in the umbonal region, fading into mere concentric growth lines
at a distance of about 5 mm from the umbones; the rest of the
shell is ornamented only with these growth lines. Lunule and
escutcheon elongate, lanceolate, shallow, only slightly
depressed, reaching to the anterodorsal and posterodorsal angles
respectively.

Cardinal plate narrow and slight, the cardinal teeth
short and peglike; dental formula:

$$\frac{A_I \quad\quad 3a \quad\quad 3b \quad\quad P_I}{A_{II} \quad\quad\quad 2 \quad\quad 4b \quad\quad P_{II}}$$

with 3a+3b, and 2+4b short and divergent; A_I, P_I, A_{II}, P_{II}
laminar. A_{II} and P_{II} placed along the dorsal margin, allowing
overlap of the opposite valve margin, P_I and P_{II} placed well
behind the nymph (Fig. 2.40). Nymph relatively wide (but not
as wide as in N. ungulata) and flattened, ligament suture located
along the dorsal margin. Musculature as in N. ungulata, pallial
line entire. Margin denticulate.

Remarks   Many individuals of this species occur in
bed 5 (Enodatum Subzone) at Stewartby and bed 2C (Medea Subzone)
at Calvert, all possessing a narrow hinge plate with short,
peglike cardinal teeth (Fig. 2.40). Comparison with N. ungulata
reveals that the latter species also differs in having a higher
number of concentric ribs in the umbonal region, the fading into
growth lines not occurring until 8 mm from the umbo, as
compared with 5 mm in N. calvertensis. As noted in the
discussion of   N. ungulata, there is no overlap of characters
of these two species, and it is necessary at the present time to
separate them. The species appears to be restricted to the

Kellaways Rock - Lower Oxford Clay boundary, not having been found elsewhere.

Two comparable species of Neocrassina have been described from the Callovian - Oxfordian of the continent, N. striato-costata (Münster in Goldfuss) and N. trembiazensis (de Loriol), but both of these species (which are probably synonymous) differ in possessing a wide cardinal plate, and are more closely related to N. ungulata. No comparable forms of Neocrassina with a narrow hinge plate are known.

Range and occurrence   Enodatum Subzone, Stewartby (bed 5), Medea Subzone of Colvert (bed 2C) and Bletchley (bed 6). Not common.

Genus TRAUTSCHOLDIA Cox & Arkell, 1948 (p. 27)
emend Duff herein

Type species   Originally designated by Cox & Arkell, 1948, p. 27, Astarte cordata Trautschold, 1860, p. 347 (nom. nov. pro Astarte cordiformis Rouillier, 1846, pl. D, figs. 15a-g, non Deshayes), from the Upper Jurassic of Galiowa, Russia.

Diagnosis   Small, subtrigonal to suborbicular in outline, very inflated, globose, umbones high, inflated, often produced to give a cordate appearance; ornament of regular concentric ribs, often with concentric growth lines superimposed on them and the intervening sulci; inner margin usually crenulate; lunule cordiform, escutcheon lanceolate, both broad and well-defined; hinge formula:

A_I	A_{III}	3a	3b	5b	P_{III}	
	A_{II}		2	4b	P_{II}	P_{IV}

with laminar laterals and short stout cardinals.

Remarks   Cox & Arkell (1948, p. 27) introduced the subgenus _Trautscholdia_, to be placed in _Astarte_ s.s., giving an adequate diagnosis except for the nature of the dentition, which was stated to be "of normal astartid type". However, the type species of _Astarte_, _A. sulcata_ da Costa (a Recent species) lacks the cardinal tooth 3a, and as 3a is well-developed in _Trautscholdia_, the dentition does not conform to the normal astartid type. Chavan (1969, p. N567), having been misled by Cox & Arkell's description of the dentition, places _Trautscholdia_ as a subgenus of _Nicaniella_ Chavan (1945, p. 43), a genus which also lacks 3a. The ultimate cause of the confusion appears to be Rouillier's 1846 figure (pl. D, fig. 15a) of the dentition of the type species _A. cordata_, which is unfortunately a figure of a left valve. The socket in the left valve to receive 3a is never very clear, and is easily overlooked; there is, however, a suggestion of a socket in the appropriate place in Rouillier's figure. Trautschold (1860, p. 347) in his description of _A. cordata_ does not mention the dentition. Study of topotypes of _A. cordata_ (BM (NH) L66752-66760) reveals that 3a is present, and so _Trautscholdia_ does not belong with _Nicaniella_. Accordingly, the diagnosis has been emended, and _Trautscholdia_ elevated to full generic rank.

1. <u>Trautscholdia carinata</u> (Phillips). Pl. 21, figs. 8-14,17.

v* 1829 <u>Astarte carinata</u> sp. nov., Phillips, pl. 5, fig. 3.

non 1850 <u>A. carinata</u> Phillips; Morris, p. 317, pl. 30, figs.
    2-2e. (= <u>T. phillis</u> Cottreau ex d'Orbigny).

non 1860 <u>A. carinata</u> Phillips; Damon, pl. 2, fig. 4. (=
    <u>T. phillis</u>).

<u>Type specimen</u> Holotype of Phillips figure of 1829 (pl. 5, fig. 3), from the Mariae Zone Upper Oxford Clay of Scarborough, is preserved in the Yorkshire Museum (YM 876), together with one syntype (YM 877). Phillips original figure is reversed.

<u>Diagnosis</u> Small, inflated species of <u>Trautscholdia</u> (up to 9.1 mm L), with 8-12 regularly spaced concentric ribs; suborbicular to subtrigonal in outline, height only slightly less than length (H 88.1-96.3 %, $\overline{x}$ 93.2 %), inflation about 85 %; umbones of variable prominence, but occasionally rather produced to give a strongly trigonal outline; posterior flank of the shell often marked by a variably-developed carina running from the umbones to the ventral margin.

  <u>T. phillis</u> may be readily distinguished from <u>T. carinata</u> by its greater number of more tightly packed ribs (12-21), and its more elongate outline (H 69.9-96.2 %, $\overline{x}$ 81.7 %).

<u>Measurements</u> See Appendix 3.

	L	H	I	AL	Ribs
N	5	5	1	3	9
$\overline{x}$	5.0 mm	93.2 %	87.8 %	41.6 %	9.4
Max	9.1	96.3	87.8	43.9	12
Min	6.6	88.1	87.8	38.1	8
OR	2.5	8.2	0	5.8	4

<u>Description</u>   Inequilateral, suborbicular to subtrigonal
in outline (H 88.1-96.3 %, $\overline{x}$ 93.2 %), with umbones moderately
prominent (occasionally very prominent), slightly prosogyrate,
salient above the hingeline to a variable extent, submesial
(AL 38.1-43.9 %, $\overline{x}$ 41.6 %), inflated. Anterodorsal and
posterodorsal margins straight to slightly concave,
anteroventral and posteroventral angles clearly defined;
ventral margin evenly rounded, often semicircular in outline,
crenulate over its entire length. Dorsal areas not well-seen,
but both the lunule and the escutcheon seem to be well-developed;
ligament not seen. Ornament consists of 8-12 regularly spaced
sharp concentric ribs, most commonly 8-10 in number, with fine
concentric striae between the ribs. A variably developed
umbonal carina runs from the umbones to the ventral margin,
meeting the margin just anterior of the posteroventral angle.

        Dentition and musculature not known.

<u>Remarks</u>   The available material of <u>T. carinata</u> is
poorly preserved, consisting only of clay steinkerns from the
Upper Oxford Clay of Scarborough and Oxford, so it is not
possible to make out any details of the dentition, ligament or
musculature. Consequently, the generic assignment of this
species is based solely on external shape, and its close
resemblance to <u>T. phillis</u>.

        The variation in form is large, although not as much
material is available as for <u>T. phillis</u>, but it is nevertheless
possible to distinguish the latter species by the greater number
of ribs and more elongate form of the population as a whole. In
<u>T. carinata</u> the umbones are often slightly produced, as in the

holotype, although never as much as in T. cordata and T. mosae
(d'Orbigny). The relationships of the Upper Jurassic species
of Trautscholdia with produced umbones are uncertain, and more
material, from a wide geographical and stratigraphical range,
is needed before definite conclusions may be drawn. It seems
likely, however, that T. mosae (d'Orbigny) is synonymous with
T. cordata (Trautschold), although they come from slightly
different horizons, the former from the U. Callovian of France,
and the latter from the L. Oxfordian (Cordatum Zone) of Russia.

The exact status of this species is, as yet, still
uncertain, as although the Scarborough population may be readily
distinguished from T. phillis, elsewhere the distinction does not
seem to be so great, and T. carinata has not been recognised with
certainty at any locality other than Scarborough. This raises
the possibility that the Scarborough population is perhaps a
local race of T. phillis which has become very well-differentiated
from the rest of the populations. In such a case, it would
perhaps be more correct to consider T. carinata as a variety of
T. phillis, but at the present time, this is pure supposition.

Range and occurrence   Common in the U. Oxford Clay (Mariae
Zone) of Scarborough, also occurring in the M. - U. Oxford Clay
(Lamberti - Mariae Zones) of St. Edmund Hall, Oxford. Also the
Oxford Clay (horizon unknown) of Radipole Backwater, Weymouth
(BM L20715).

2.   Trautscholdia phillis (Cottreau ex d'Orbigny). Pl. 21,
        figs. 15-16, 18-32, Pl. 22, figs. 1-3.

1850　Astarte carinata Phillips; Morris, p. 317, pl. 30,

　　　figs. 2-2e. (non Phillips).

1850　Astarte phillis sp. nov.; d'Orbigny, p. 363, no. 253.

1860　A. carinata Phillips; Damon, pl. 2, fig. 4. (non

　　　Phillips).

?　1875　A. sauvagei sp. nov.; de Loriol & Pellat, p. 96, pl. 15,

　　　figs. 33, 34.

?　1911　A. Sauvagei de Loriol; Boden, p. 64, pl. 6, figs. 18-18b,

　　　19.

1915　Gouldia cordata (Trautschold); Krenkel, p. 320, pl. 26,

　　　figs. 16-18. (non Trautschold).

1919　G. cordata (Trautschold); Couffon, p. 90, pl. 6, figs.8-8e.

　　　8-8e. (non Trautschold).

v*　1927　A. phillis d'Orbigny; Cottreau, p. 49, pl. 46, figs. 6,7.

1952　A. cordata Trautschold; Makowski, p. 10, pl. 5, fig. 6.

1972　A. multiformis Roeder; Walker, p. 127, pl. 8, figs. 11-17.

Type specimen　　　The holotype of Astarte phillis d'Orbigny
(1850, p. 363, no. 253), refigured by Cottreau (1927, pl. 46, figs.
6, 7), from the calcaire-blanc (Coral Rag, Corallian) of
Neuvizy, France, preserved in the d'Orbigny collection (no. 3669)
at the Museum Nationale d'Histoire Naturelle in Paris.

Diagnosis　　　Medium-sized species (up to 12.4 mm long),
inflated (I 56.6-100.0 %, $\overline{x}$ 77.2 %) Trautscholdia with umbones
slightly anterior of median (AL 26.9-43.2 %, $\overline{x}$ 34.1 %);
ornament consisting of 12-21 regularly spaced concentric ribs,
with the mode at about 15; outline subtrigonal to suborbicular,
with height significantly less than length (H 69.9-96.2 %, $\overline{x}$

85.4 %), giving an elongate rather than a suborbicular
outline, although occasional suborbicular varieties occur.

The distinctions between this species and T. carinata
have been discussed above.

Measurements

See Appendix 3.

	L	H	I	AL	Ribs
N	84	84	73	15	68
$\overline{x}$	8.7 mm	85.4 %	77.2 %	34.1 %	14.8
Max	12.4	96.2	100.0	43.2	21
Min	4.8	69.9	56.6	26.9	10
OR	6.3	26.3	43.4	16.3	11

Description   Medium-sized species, inflated, equivalve,
inequilateral, umbones placed slightly anterior of median
(AL $\overline{x}$ 34.1 %); outline dominantly subtrigonal, with length
considerably greater than height, but suborbicular forms, with
length only just exceeding height, are also found; umbones
prominent, inflated, prosogyrate, salient up to 2 mm above
the hingeline, rounded in lateral profile. Anterodorsal
margin slightly concave, posterodorsal margin slightly concave
to slightly convex; anterodorsal angle sharply rounded,
passing into the evenly convex ventral margin; posterodorsal
angle variably developed, a rounded obtuse angle passing
evenly into the ventral margin in suborbicular forms, or a
more sharply angular posterodorsal angle, passing into a short
truncate posterior margin, which passes into the ventral

margin via a rounded posteroventral angle in elongate forms;
in the elongate forms there is a tendency for a weak umbonal
ridge to develop between the umbones and the posteroventral
angle. Ligament nymph short but well-defined, located
immediately above cardinal tooth 5b in the right valve, and
above and behind 4b in the left valve. Lunule strongly-
developed, cordiform, deeply concave, its anterior extremity
reaching virtually to the anterodorsal angle; escutcheon
lanceolate, bounded by a sharp escutcheon carina, extending
to the posterodorsal angle; both lunule and escutcheon
ornamented by fine concentric growth striae. Ornament of
flanks of valve consists of 12-21 regularly spaced concentric
ribs, with faint concentric intercostal striae; the ribs are
somewhat more tightly-packed than in T. carinata, but the exact
number of ribs varies between populations; the spaces between
the ribs are usually about 3 times as wide as the ribs
themselves. Margin denticulate in its entirety, denticulations
extending to the ends of the lateral teeth.

Dental formula:

$$\frac{A_I \quad A_{III} \quad 3a \quad 3b \quad 5b \quad P_{III}}{A_{II} \qquad\quad 2 \quad 4b \quad P_{II} \quad P_{IV}}$$

with paired laminar laterals posteriorly in the left valve and
anteriorly on the right valve; 2 and 4b prominent, rounded,
peglike; 3a and 3b strongly developed, with 3b almost median
and a strong 3a reaching anteriorly from its dorsal margin, and
5b poorly developed, parallel to, and often fused with, the
shell margin (Fig. 2.41). Transposed dentition occurs

occasionally, with transposition of either the anterior
laterals or the cardinals (Fig. 2.42). Adductor muscle scars
subequal, the posterior scar slightly larger, subquadrate, the
anterior scar elongate-elliptical and slightly smaller;
pallial line entire.

Remarks   The variation within this species (Fig. 2.43)
is very great, as may be deduced from the study of large
populations such as that collected from bed 2C at Calvert.
Although the dominant form in that population is markedly
elongate, suborbicular forms are fairly common, together with
all intermediate stages, showing variation to be continuous;
the variation in number of ribs is also well shown in this
population, the overall range being 13-19. Other populations
of comparable age, but from different localities, show a
similar range of variation, although they occupy different
positions within the range. For example, the small population
from the Oxford Clay of Chippenham (GSM Y2066-Y2070, GSM 113419-
113427) are of a similar shape to the Calvert population, but
have fewer ribs, ranging from 12-15, with one specimen having
17 ribs. Variation may best be appreciated from a study of
the plates, and Fig. 2.43. In all populations of this species,
the dominant shape is subtrigonal, with length considerably
greater than height, and it is this feature, together with the
consistently high rib density, that separates it from
T. carinata. Regression lines for different populations of
T. phillis (Fig. 2.44) show the similarity between all
populations when their L/H and L/I ratios are considered.

T. phillis is a common Kellaways Rock - L. Oxford Clay species in England, although its upper range is as yet uncertain, and it seems to occur at higher levels in the Callovian and Oxfordian on the continent. It was first described from the L. Callovian by Morris (1850), who erroneously assigned it to Astarte carinata, being followed by Damon (1860). Also in 1850, d'Orbigny introduced the name A. phillis for an Oxfordian species found in the Corallian of Neuvizy (France), the type being figured by Cottreau in 1927, showing that the French species was indistinguishable from the British Lower Callovian one, in spite of the age difference. The fact that the holotype of T. phillis comes from the Corallian creates uncertainty about the placement of the Callovian forms, but the figure given by Cottreau is of a shell indistinguishable from the typical Callovian form, although there is a possibility that the French specimen is not a typical member of the population from which it came. In the absence of a population of topotypes, there is no reason to doubt the identity of the English and French species. Arkell (1934, p. 247) united A. phillis with A. Contejeani de Loriol (1875, p. 92), and figured two specimens of the latter species from the Corallian of Weymouth; however, the specimens figured by Arkell do not match the figures given by Cottreau.

Astarte robusta Lycett is probably also referable to Trautscholdia, and is superficially very similar to A. phillis, having 16-18 ribs, but differs in its more suborbicular outline, with length and height being approximately equal. The

holotype came from the Cornbrash of Scarborough, and is

preserved in the Sedgwick Museum, Cambridge (SM J5682)

Astarte cordata Trautschold has been misidentified

several times (Krenkel, 1915; Couffon, 1919; Makowski, 1952),

the figures showing specimens identifiable as T. phillis.

T. cordata is clearly distinct (Rouillier, 1846, pl. D, figs.

15a-15g), having very pronounced umbones.

Roeder (1882) discussed variation in T. multiformis

(Roeder), and showed it to be an extremely polymorphic species

in both form and ornamentation. It closely parallels the

situation seen in T. phillis, to which it must be closely

related, but consistently differs from that species by being

much more orbicular, with length about equal to height. Arkell

(1934, p. 239) suggested that this species might be synonymous

with A. extensa Phillips.

Hinge transposition is fairly common in the Astartidae

(Cox, 1969, p. 57), Popenoe & Findlay (1933) noting that one

specimen in 130 showed this phenomenon. There appears to be

variation in the part of the hinge affected by transposition,

Popenoe & Findlay (op. cit.) and Newell (1939) reporting that

the cardinals and anterior laterals were transposed separately

from the posterior laterals, supporting Bernard's observation

that the anterior laterals and the cardinals develop from one

lamella, and the posterior laterals from another, while Eggleton

& Davies (1962) showed that in a population of the Recent

freshwater genus Sphaerium, 18.5 % of the population showed

transposition of the complete hinge. The specimens of T. phillis

showing transposition of the dentition lend support to the observations of Newell and Popenoe & Findlay, a right valve from the Oxford Clay of Chippenham (GSM 113425) showing transposition of the cardinals and anterior laterals (Fig. 2.42a), while a right valve from bed 2C at Calvert merely shows transposition of the posterior laterals (Fig. 2.42b), with the result that the former has no laminar laterals on the right valve, whilst the latter has paired laminar laterals anteriorly and posteriorly.

<u>Range and occurrence</u> Widespread in the Kellaways Rock of Southern England, and in the transition beds between the Kellaways Rock and the Oxford Clay, occurring in the Jason Subzone at Calvert, the Medea Subzone at Bletchley and Stewartby, and in the Medea and Jason Subzones at Norman Cross. It also occurs rarely in the clay facies (Obductum Subzone of Calvert, Stewartby and Norman Cross).

T. phillis is known from various horizons in the Callovian and Oxfordian of France, Germany, Poland and Russia.

<div align="center">

Superfamily CARDIACEA Lamarck, 1809

Family CARDIIDAE Lamarck, 1809

Subfamily CARDIINAE Keen, 1951

Genus PROTOCARDIA von Beyrich, 1845 (p. 17)

Synonym: Hassbergia Krumbeck, 1939

</div>

<u>Type species</u>   Subsequently designated by Herrmannsen,
1847, p. 336, <u>Cardium hillanum</u> J. Sowerby, 1813, p. 41
pl. 14, upper fig. , from the Upper Cretaceous of
England.

<u>Diagnosis</u>   Subquadrate to subovate, umbones
subcentral; posterior slope with radial ribs, not usually
spinose, remainder of shell ornamented by concentric ribs;
hinge long and slightly arched, left valve with A_I, 2, 4b, P_I,
right valve with A_{II}, A_{IV}, 3a, 3b, P_{II}, with 2 and 3b peglike;
pallial line mostly entire, sometimes a small sinus near the
posterior adductor scar.

Subgenus PROTOCARDIA s.s.

<u>Diagnosis</u>   Posterior slope clearly marked off from
the rest of the shell by its well-developed radial riblets;
remainder of shell with concentric growth lines only.

1.   <u>Protocardia (Protocardia) striatulum</u> (J. de C. Sowerby).
      Pl. 22, figs. 6-11.

*   1829 <u>Cardium striatulum</u> sp. nov.; J. de C. Sowerby, p. 101,
          pl. 553, fig. 1.
v. 1859 <u>Cardium Crawfordii</u> sp. nov.; Leckenby, p. 14, pl. 3,
          figs. 9a, 9b.
v. 1859 <u>C. cognatum</u> Phillips; Leckenby, p. 14, pl. 3, figs. 8a,
          8b. (non Phillips).

v. 1860   C. striatulum Sowerby; Damon, pl. 3, fig. 3.

1934   C. crawfordii Leckenby; Arkell, p. 305.

v. 1955 Protocardia citrinoidea (Phillips); Calloman, p. 221.
(non Phillips).

v. 1972 P. crawfordii Leckenby; Walker, p. 128, pl. 7, fig. 7.

Type specimen   Holotype of J. de C. Sowerby's plate 553,
fig. 1, from the Roofbed of the Brora Coal (Kellaways Beds,
Calloviense Zone) of Brora, Sutherlandshire, is preserved in
the Sowerby collection at the BM (NH), number 43154.

Diagnosis   Medium sized Protocardia (up to 24.1 mm L),
subquadrate to suborbicular in outline (H $\bar{x}$ 91.9 %), with
umbones just anterior of median (AL $\bar{x}$ 44.7 %); inflation high
(I $\bar{x}$ 70.4 %), but more marked in smaller specimens than in
large ones; anterior margin slightly shorter than posterior
margin; ornament of fine concentric striae on the shell flanks,
with no concentric ribs; posterior area with radial striae
clearly differentiated.

Measurements

See Appendix 3.

	L	H	I	AL
N	15	15	13	14
$\bar{x}$	13.1 mm	91.9 %	70.4 %	44.7 %
Max	24.1	101.4	85.5	54.8
Min	7.3	81.4	59.0	32.8
OR	16.8	20.0	26.5	22.0

<u>Description</u>   Equivalve, inequilateral, umbones placed just anterior of median (AL 32.8-54.8 %, $\overline{x}$ 44.7 %); medium-sized species (up to 24.1 mm L), subrectangular to subquadrate in outline (H 81.4-101.4 %, $\overline{x}$ 91.9 %), the regularity of outline broken by the prominent umbones. Hinge margin slightly reflexed, almost straight, the anterior and posterior parts meeting in a very obtuse angle immediately beneath the umbones; posterior margin obliquely truncate to gently convex, meeting the posterodorsal margin at a rounded obtuse angulation; anterodorsal margin curving smoothly into the slightly produced, rather rounded anterior margin; anterodorsal angle weakly angular, but sometimes prominent; ventral margin smoothly and convexly curved, passing evenly into the anterior and posterior margins, without angulation. There is no clearly-developed umbonal carina, the posterior area being delimited solely by the ornament pattern, not by a change in slope of the shell flanks. Umbones large, prominent, just anterior of median (AL $\overline{x}$ 44.7 %), slightly prosogyrate, their anterior and posterior borders gently rounded, salient up to 4 mm above the hingeline, almost contiguous at their extremities. Ligament external, parivincular, very short, rather deeply impressed; no lunule or escutcheon. Ornament consists of up to 20 fine radial riblets on the posterior part of the shell, occupying the area between the posterior margin and the posterior part of the umbo; the posterior area is not delimited from the flanks of the shell by an umbonal carina; the radial riblets are coarsest in the central part of the area,

becoming finer anteriorly and posteriorly; the remainder of
the shell is ornamented solely by fine concentric growth
lines. Inflation high (I 59.0-85.5 %, $\overline{x}$ 70.4 %), more
marked in small specimens.

Dentition heterodont, with a pair of triangular
cardinal teeth in each valve, arranged in a Λ-shaped pattern
immediately beneath the umbones; left valve with an elongate
anterior and posterior lateral tooth, right valve with two
elongate anterior laterals and one posterior lateral (Fig. 2.45).
Margin entire, crenulate along the margin of the area, where
the radial riblets reach the shell margin. Musculature not
seen.

Remarks   As may be seen from the synonymy, the
nomenclature of British Upper Jurassic Protocardia is confused,
and in need of clarification. In common with several other
species which were described from the Brora Roof Bed
(= Kellaways Beds) of Sutherlandshire by J. de C. Sowerby in
1829, Cardium striatulum was largely overlooked by subsequent
workers, who had presumably been misled by its being referred
to in the Index to the Mineral Conchology (1829) as occurring
in the "Inferior Oolite?" The only worker to recognise
Sowerby's species was Damon (1860), who correctly identified
this species from the Oxford Clay of Weymouth. Study of a
large collection of P. striatulum from the type locality
(comprised of specimens in the authors collection, specimens
in the Oxford University Museum and specimens in the BM (NH))

shows a marked size variation in this species, from small
subquadrate specimens to medium-sized suborbicular ones.
Were it not for the existence of specimens gradational in form
and size between the large and small specimen, it is likely
that they would be thought of as distinct species, as the two
forms are not obviously identical. The small specimens agree
perfectly with the ones described from the 'Kelloways Rock' of
Scarborough by Leckenby (1859) as Cardium Crawfordii sp. nov.,
and also occurring in the Kellaways Rock of Wiltshire (Arkell,
1934) and Yorkshire (Walker, 1972). These tend to be much
smaller, more subquadrate, with subparallel anterior and
posterior margins, and more inflated (making them much more
globose) than the larger, flatter, more suborbicular forms
from the Brora Roof Bed (referred to P. striatulum), in which
the anterior and posterior margins are evenly curved. The
holotype of C. crawfordii, from the 'Kelloway Rock' of
Scarborough, is preserved in the Sedgwick Museum Cambridge
(SM J6010).

Cardium cognatum Phillips (holotype in the Yorkshire
Museum, Tsp. 117) from the Grey Limestone (Bathonian) to
'Kelloways Rock' of Yorkshire has been referred to the genus Pro-
tocardia by several authors (Cox & Arkell, 1948; Walker,
1972), but examination of the holotype reveals the absence of
any radial ornamentation on the posterior area, thus precluding
it from placement in Protocardia. In a note found with the
holotype in the Yorkshire Museum (in Arkell's handwriting),
it is suggested that there are faint traces of radial striae on

the extreme posterior of the shell, but they are not obvious on the specimen, and must be discounted. The specimen figured by Leckenby (1859) as C. cognatum, is a large Protocardia agreeing perfectly with specimens of P. striatulum from the Brora Roof Bed, and clearly does not belong with Phillips conception of his species. Likewise, the specimen mentioned by Callomon (1955, p. 221) as belonging to Protocardia citrinoidea (Phillips), from the Lower Oxford Clay of Kidlington (OUM J9719), cannot be reconciled with Phillips original figure (1829, pl. 7, fig. 7) of that species, which shows a specimen with regular concentric ribs, and no evidence of radial striae. The holotype of C. citrinoidea is missing from the Yorkshire Museum, but several topotypes from the Upper Cornbrash of Scarborough agree well with Phillips figure, and clearly do not belong to Protocardia. Callomon's specimen agrees perfectly with the many small specimens of P. striatulum.

Arkell (1934, p. 304) described P. dyonisea (Buvignier) from the Corallian of England, and compared it with P. crawfordii, with which it agrees well in size. As Arkell noted, P. crawfordii is less elongate, and the anterior and posterior margins are more truncate and less rounded; the umbones are also more acute, and the anterior part of the shell more inflated. P. intexta (Münster), also from the British Corallian (Arkell, 1935, p. 372), more closely resembles the large form of P. striatulum, but is more perfectly orbicular, much less inflated, and has the umbones much less prominent than in P. striatulum.

Range and occurrence   Locally abundant in the Kellaways Rock
(Calloviense Zone) of Dorset, Wiltshire, the Midlands,
Yorkshire and Scotland;   this species also occurs sporadically
in the Lower Oxford Clay (Jason Zone) of the Midlands, the
Hackness Rock (Athleta - Lamberti Zones) of Yorkshire, and the
Upper Oxford Clay of Huntingdonshire.

2.   Protocardia (Protocardia) sp. Pl. 22, figs. 4-5.

Description   Large (up to 32.5 mm L) Protocardia of low
inflation and suborbicular to subtrigonal outline, ornamented
by a series of fine radial ribs on the posterior area, and
regular fine concentric ribs on the remainder of the shell.
In the only measurements available, height is measured at
92.6 % and anterior length at 33.7 %. The umbones appear to
be rather more rounded, and considerably less prominent than in
P. striatulum;   it is likely that they are more nearly median
in position than the AL indicates, as there seems to be some
distortion caused by crushing. The radial ribs on the posterior
area are strongest in the middle part of the area, and diminish
in strength anteriorly and posteriorly;   concentric ribs are
strongest near the anterior margin and in the umbonal region,
but never very highly elevated. Ligament, dentition and
musculature not seen.

Measurements

L	H	AL
32.5 mm	30.1 mm (92.6 %)	
30.6		10.3 mm (33.7 %)

Remarks   This species is represented by six
disarticulated, pyritised valves from the Obductum Subzone
(bed 7) of Marston Moretaine and Stewartby. Unfortunately,
because of their relatively large size and fragility, burial
and compaction in a shell bed has led to considerable distortion
and breakage of the valves, and a full description is impossible.
There can, however, be no doubt that they are Protocardia, as
they clearly show the differentiated radially ribbed posterior
area, and the concentrically ribbed flanks. The strength of the
ribbing over the flanks of the shell serves to separate this
species from P. striatulum, which has only very faint growth
lines. The ornament style resembles that seen in P. stricklandi
(Morris & Lycett), from the Great Oolite (Bathonian), and it
is possible that the Lower Oxford Clay species may belong with
it. However, in view of the poor preservation of the Callovian
specimens, specific identification is impossible until better-
preserved material becomes available. Until then, all that
can be done is to record the species, and record similar
species from other horizons.

Range and occurrence   Lower Oxford Clay (Obductum Subzone,
Bed 7), Marston Moretaine, and Stewartby, Bedfordshire.

Superfamily ARCTICACEA Newton, 1891

Family ARCTICIDAE Newton, 1891

Genus ROLLIERELLA Cossmann, 1924 (p. 48)

Synonyms: <u>Rollieria</u> Cossmann 1923 (non <u>Rollieria</u>

<u>Rollieria</u> Cossmann 1924   Cossmann 1920

/Nuculanacea/)

<u>Type species</u>   Originally designated by Cossmann, 1924,

p. 48, <u>Isocardia laubei</u> Rollier, 1913, p. 209 , nom. nov. pro

<u>Isocardia cordata</u> Laube, 1867, p. 41 , pl. 4, fig. 1 (non J.

Buckman, 1845); from the Brown Jura of Balin, Germany.

<u>Diagnosis</u>   Subtrigonal to orbicular, gibbose, inflated;

umbones prominent, produced, strongly prosogyrate and enrolled;

lunule well-marked, escutcheon absent; surface smooth or with

radial threads; hinge formula:

$$\frac{A_I \quad 3a \quad 1 \quad 3b \quad P_I}{A_{II} \quad 2a \quad 2b \quad 4b \quad P_{II}}$$

with 1 arcuate and projecting, 3a-3b a continuous angulate

structure, 3b bifid; 2a short and curved, 2b massive and

peglike, 4a elongate and arcuate; pallial line entire.

<u>Remarks</u>   The genus was discussed, and the dentition

described (Fig. 2.46), by Cox (1947), who mentioned that

several specimens from the Bathonian of Noyen and Langrune

(France), referred by Douville (1921, p. 121, figs. 13, 14) to

'Eotrapezium' (mistake for <u>Pseudotrapezium</u>) <u>tenerum</u> (J. Sowerby),

are present in the BM (NH). These are not true <u>Anisocardia</u>

<u>tenera</u>, however, and the species, now needing a new name, is

not known to occur in Britain. The present record is thus the

first authenticated British record of the genus.

Externally, there are strong resemblances to
Anisocardia, to which A. minima has been traditionally
referred, in that the umbones are rather pronounced and
twisted, and generic separation is based on dental characters.
Rollierella may be distinguished from Anisocardia by virtue of
its strong, continuous, angulated 3a-3b, the same teeth barely
meeting at an acute angle in Anisocardia; 2b is also very
distinctive, being large and peglike in Rollierella, and
markedly bifid in Anisocardia.

Rollierella minima (J. Sowerby). Pl. 22, figs. 12-22, 25-26.

   1821   Isocardia minima sp. nov. J. Sowerby, p. 171, pl.
          295, fig. 1.

   1829   I. tumida sp. nov.; Phillips, pl. 4, fig. 25. (non
          Pygocardia tumida Nyst).

? 1829   I. minima J. Sowerby; Phillips, pl. 7, fig. 6.

   1850   I. campaniensis sp. nov.; d'Orbigny, p. 338, no. 168.

? 1850   I. villersensis sp. nov.; d'Orbigny, p. 338, no. 169.

   1853   I. tenera J. Sowerby; Morris & Lycett, p. 66, pl. 7,
          figs. 1, 1a. (non J. Sowerby).

non 1860 I. minima J. Sowerby; Damon, pl. 4, fig. 7.
          (= Anisocardia anisocardiodes Blake & Hudleston).

   1863   I. tenera J. Sowerby; Lycett, p. 57, pl. 38, figs.
          5-5b. (non J. Sowerby).

non 1863 I. minima J. Sowerby; Lycett, p. 56, pl. 36, figs. 1,
          1a. (= Anisocardia globosa (Roemer)).

1913 Anisocardia oolithica sp. nov.; Rollier, pl 198 (nom.

nov. pro I. tenera Morris & Lycett non J. Sowerby).

1913 A. lycetti sp. nov.; Rollier, p. 210 (nom. nov. pro

I. tenera Lycett non J. Sowerby).

1915 I. campaniensis d'Orbigny var. dassei nov.; Cossmann,

p. 6, pl. 1, figs. 3, 4; pl. 3, fig. 17.

1925 I. campaniensis d'Orbigny; Cottreau, p. 18, pl. 39,

figs. 13, 14.

? 1925 I. villersensis d'Orbigny; Cottreau, p. 19, pl. 39,

figs. 15, 16.

1934 A. minima (J. Sowerby); Arkell, p. 275, pl. 36,figs.8-11.

1947 A. minima (J. Sowerby); Cox, p. 170, text-figs. 43a,43b.

1948 A. minima (J. Sowerby); Cox & Arkell, p. 31.

1952 A. tenera (J. Sowerby); Makowski, p. 12, pl. 5, fig. 7.

(non J. Sowerby).

1965 A. minima (J. Sowerby); Cox, p. 112, pl. 18, fig. 8.

Type specimen   Holotype of J. Sowerby's pl. 295, fig. 1,

Isocardia minima, from the ?Cornbrash of Wiltshire, preserved

in the Sowerby collection at the BM (NH), number 43164.

Holotype refigured by Arkell (1934, pl. 36, fig. 8).

Diagnosis   Medium-sized species (up to 24 mm L) with

very prominent, enrolled, not contiguous, strongly prosogyrate

umbones; ornament consists of regular fine radial riblets all

over the shell, except on the lunule, which has only concentric

growth lines; anterodorsal angle very well-marked, prominent

and acute, posterior margin evenly rounded; inflation high

($\overline{x}$ 88.1 %); pseudolunule wide and bowl-shaped.

Differs from the closely-related Anisocardia tenera in being more inflated (I 76-98 % in R. minima, 52-70 % in A. tenera), in the possession of a much sharper and more prominent anterodorsal angle, in having more inflated and enrolled umbones, and in lacking the slightly rostrate posterior margin of A. tenera. R. minima may easily be distinguished from the two other species figured by Arkell (1934) from the Corallian, A. anisocardioides (Blake & Hudleston) and A. globosa (Roemer) in external shape and inflation. A. anisocardioides has a much more rounded anterodorsal angle, and the umbones are not as strongly produced or enrolled. A. globosa is more inflated, again has a more rounded anterodorsal angle, and a well-marked posterior carina delimiting the anterior margin of a distinct posterior flange.

Measurements

See Appendix 3.

	L	H	I	AL	PW
N	33	33	31	32	4
$\overline{x}$	17.5 mm	93.1 %	88.0 %	31.0 %	55.3 %
Max	24.0	99.4	98.7	42.3	59.9
Min	7.0	84.3	76.4	24.2	46.0
OR	17.0	15.1	22.3	17.1	13.9

Description   Medium-sized shells (up to 24 mm L), subtrigonal in outline, inequilateral, equivalve, with margins entire; umbones prominent, inflated, salient up to 4 mm above

the hingeline, not contiguous, up to 5 mm apart at umbonal extremities, strongly prosogyrate and enrolled; dorsal margin arched at an obtuse angle of about 120 $^\circ$, the anterior part slightly concave, the posterior part slightly convex; anterodorsal angle very prominent and produced, rounded at its extremity, posterodorsal angle much more evenly curved; ventral margin smoothly curved between the antero- and posterodorsal angles; height 84.3-99.4 %, $\bar{x}$ 93.1 %, inflation high, 76.4-98.7 %, $\bar{x}$ 88.0 %; umbones placed in about the anterior third of the shell, AL 24.2-34.3 %, $\bar{x}$ 31.0 %. Valves sculptured with closely-spaced fine radial riblets, crossed by densely packed fine radial riblets to give a fine cancellate pattern over the whole shell surface, except for the pseudolunule, where radial riblets are absent; pseudolunule large, wide, PW 46.0-59.9 %, $\bar{x}$ 55.3 %, its edge marked by an impressed line parallel to the radial riblets and extending from the umbones almost to the anteroventral angle, enclosing an area ornamented solely by growth lines (Fig. 2.48). Lunule small, arcuate, flattened, marked off from the pseudolunule by a deeply impressed line, forming an obtuse angle with the pseudolunule; escutcheon absent. Ligament external, opisthodetic, nymph situated immediately behind and beneath the umbonal terminations; ventral margin finely crenulate.

Hinge heterodont, dental formula:

A_I	3a	1	3b	P_I
A_{II}	2a	2b	4b	P_{II}

with the cardinal teeth of the left valve anterior to those of
the right valve; in the right valve, A_I is short and peglike,
and situated immediately beneath the anterior end of 1, which
itself is arcuate, concave ventrally and strongly developed;
3a small, continuous with 3b, closely applied to the upper
surface of 1; 3b elongate and bifid, forming a continuous
angulated tooth with 3a; P_I long and well-developed. In the
left valve, A_{II} is short, and situated immediately below the
anterior end of 2a; 2a short and curved, attached posteriorly
to the massive, peglike 2b; 4b elongate and gently concave
ventrally; P_{II} elongate and well-developed (Fig. 2.47).
Pallial line entire; anterior adductor scar elongate and
arcuate, located immediately dorsal of the anteroventral angle
and reaching almost to the cardinal plate; posterior adductor
scar subquadrate, located just ventral to the posterior end of
the posterolateral teeth.

Remarks   In four exceptionally well-preserved
specimens of R. minima from the Upper Callovian of Lukow,
Poland, donated to the author by Dr. A. Radwanski of the
University of Warsaw, it has been possible to develop the
hinge for the first time, thus enabling correct generic
placement of the species. The use of normal development techniques,
supplemented by serial sectioning, has shown the dentition to be
of Rollierella type, with 3a + 3b a continuous, angulate, well-
developed tooth, rather than two separate elements, as occurs
in Anisocardia. Fig. 2.49 shows a comparison of the dentition
of these genera. 1 is strongly developed and arcuate in form.

Thus the suspicions of Cox (1947), that the globose <u>Anisocardia</u>-like forms may belong to <u>Rollierella</u>, are seen to be correct. It is possible that the same is true of <u>Anisocardia tenera</u>, but the dentition has never been seen in this species, and with the lack of evidence to the contrary, it is better to leave it in <u>Anisocardia</u>.

Of all the proportions, inflation is seen to be the most variable, whilst the ranges of height and anterior length are smaller and approximately equal. There does not seem to be any positive correlation between size and proportions, and the most likely explanation is that variation in shell proportions is normally distributed.

The term pseudolunule (Fig. 2.48) is used for the large area anterior to the umbones, and marked off from the body of the shell by a fine impressed radial line which extends from the umbo to the dorsal margin, reaching almost to the anterodorsal angle. The pseudolunular area includes the lunule, which is itself marked off from the body of the pseudolunule by a more deeply impressed line radiating from the umbones. There is a marked angular discordance between the surface of the lunule and the pseudolunule, the two areas also being distinguished by an important difference in ornamentation, the latter area lacking radial sculpture.

The synonymy and general remarks about this species are considered at length by Arkell (1934, p. 275).

Range and occurrence   This long-ranging species is known from
the Bathonian – Oxfordian of Britain (Cox & Arkell, 1948, p. 31),
and is particularly abundant in the Cornbrash and Kellaways
Rock; although it occurs in the top Kellaways Rock of the
Midlands, and in the transition beds to the Oxford Clay, it has
not been found in the clay facies. Arkell (1934, p. 276)
listed the foreign Callovian records of specimens referable to
R. minima, the species being known from France, Germany, Poland
and East Africa.

Genus ANISOCARDIA Munier-Chalmas, 1863 (p. 288)

Synonymy: Apocardia Dollfus, 1863
            Cardiodonta Laube, 1867

Type species   By monotypy, Anisocardia elegans Munier-
Chalmas, 1863, p. 288, pl. 11 , figs. 5 – 8 , from
the Kimmeridgian of Le Havre, France.

Diagnosis   Ovate to subtrigonal or trapeziform,
sometimes slightly truncate posteriorly; lunule superficial,
escutcheon absent; surface smooth or with radial threads;
hinge formula:

$$\frac{A_I \quad 1 \quad 3a \quad 3b \quad P_I}{A_{II} \quad 2a \quad 2b \quad P_{II}}$$

with 1 projecting, 3a laminar and elongate, 3b bifid, 2b chevron-
shaped, 2a laminar, not well differentiated from A_{II}, P_I strong,
elongate, P_{II} confluent with margin of hinge plate; pallial

line markedly truncate posteriorly, but not sinuate.

Subgenus ANISOCARDIA s.s.

Diagnosis   Subtrigonal, posterior margin usually
truncate or rostrate; umbones very prominent, strongly
prosogyrate, often very markedly salient above the dorsal
margin; ornamented by radial threads and concentric growth
lines; hingeline strongly arched, anterior laterals very
reduced; ventral margin finely crenulated.

Remarks   The status of Anisocardia has been discussed
at some length by Casey (1952) and Cox (1947), with emphasis on
the dentition. There is some doubt concerning the generic
placement of species such as Anisocardia minima, A. tenera and
A. gibbosa (Münster), which have been referred to Anisocardia
since the work of Zittel (1881). The external features of the
shell, if studied in isolation, would suggest that these gibbose
species belong to Rollierella, which differs from Anisocardia
only in details of the hinge, as discussed above. Development
of the hinge of 'A'. minima has shown that it does in fact
belong in Rollierella, and this increases the possibility that
'A'. tenera and 'A'. gibbosa also belong to this genus, but it
has not been possible to examine the hinges of these species, so
it seems better to leave them in Anisocardia until they can be
proved to belong elsewhere.

Anisocardia is unusual in that in the right valve, 1 is
usually placed anterior of 3a, thus posing problems of tooth

numeration. The lamina 3a-3b is, however, seen to be of normal Arcticacean type, and it is possible that 1 merely represents a rather unusual development of A_I, and that 1 itself is obsolete. It is in cases such as this that the Bernard system of numbering teeth runs into difficulties. In the lack of ontogenetic series, the problem cannot yet be resolved. The same is true to some extent in Rollierella, although 3a is often placed dorsal, rather than posterior to, 1.

Anisocardia (Anisocardia) tenera (J. Sowerby). Pl. 22, figs. 23-24, 27-29.

    1821 Isocardia tener sp. nov.; J. Sowerby, p. 171, pl. 295,
          fig. 2.

    1829 I. tenera nom. nov.; J. de C. Sowerby, p. 48

non 1853 I. tenera J. Sowerby; Morris & Lycett, p. 66, pl. 7,
          figs. 1, 1a. (= R. minima).

non 1863 I. tenera J. Sowerby; Lycett, p. 57, pl. 38, figs. 5-5b.
          (= R. minima).

?   1904 Anisocardia tenera (J. Sowerby); Ilovaisky, p. 258,
          pl. 9, fig. 10.

?   1915 A. tenera (J. Sowerby); Krenkel, p. 325, pl. 26, fig. 37.

non 1919 A. tenera (J. Sowerby); Couffon, p. 92, pl. 4,
          figs. 14-14b.

    1934 A. tenera (J. Sowerby); Stoll, p. 13, pl. 1, fig. 39.

non 1952 A. tenera (J. Sowerby); Makowski, p. 12, pl. 5,
          figs. 7-7a. (= R. minima).

?   1972 A. tenera (J. Sowerby); Walker, p. 130, pl. 8, figs. 8, 9.

Type specimen   Holotype of J. Sowerby's plate 295, fig. 2,
Isocardia tener, from the Kellaways Rock of Wiltshire, is
preserved in the BM (NH), number 43165.

Diagnosis   Large species (up to 25 mm L), with
prominent prosogyrate umbones, which are not enrolled; ornament
as in R. minima, with very fine radial riblets all over the
shell, except on the lunule; anterodorsal angle prominent, but
more rounded than in R. minima; posterior margin slightly
truncate and rostrate, more angular than in R. minima; inflation
considerably lower than in R. minima (52-71 %, $\bar{x}$ 60.3 %).

The differences between this species and R. minima have
been discussed in the diagnosis of the latter species. Other
British Middle - Upper Jurassic Anisocardia have been well
diagnosed and described by Cox (1947), and it is not necessary
to consider them here.

Measurements

See Appendix 3.

	L	H	I	AL
N	14	14	14	14
$\bar{x}$	20.5 mm	89.9 %	60.3 %	33.6 %
Max	25.2	98.3	70.5	39.0
Min	12.7	83.0	52.6	27.3
OR	12.5	15.3	17.9	11.7

Description   Large shells (up to 25.2 mm L),
subrectangular to subtrigonal in outline (H 83.0-98.3 %,

$\bar{x}$ 89.9 %), inequilateral, equivalve; umbones prominent, prosogyrate, but not strongly enrolled, placed within the anterior third of the shell (AL 27.3-39.0 %, $\bar{x}$ 33.6 %), only slightly salient (up to 2 mm) above the hingeline; dorsal margin arched at 100-110 °, the anterior part gently concave, becoming convex anteriorly, the posterior part gently convex, becoming more strongly convex into the posteroventral margin; anterodorsal angle prominent and rounded, posterodorsal angle rounded, passing into the obliquely truncate posterior margin, which is slightly rostrate; anterior margin rounded, passing evenly into the gently convex ventral margin; posteroventral angle rounded; an umbonal carina runs from the umbones to the posteroventral angle, delimiting a small, flattened posterior area. Inflation not great, 52.6-70.5 %, $\bar{x}$ 60.3 %. Sculpture consisting of densely packed fine radial riblets, crossed by closely spaced concentric growth lines, to give a finely cancellate pattern to all of the shell surface except the pseudolunule, which lacks radial ornament; pseudolunule width 22.7 %, marked off from the body of the shell by a slightly impressed radial line; lunule not visible, escutcheon absent; ligament external, opisthodetic, placed as in R. minima.

Dentition not seen. Pallial line entire, anterior adductor scar elongate and arcuate, placed near the anterodorsal angle; posterior adductor scar not seen. Ventral margin finely crenulate.

Remarks   As noted above, the dentition of this species has not been seen in British specimens, but, however, figures of the dentition of closely related species do exist. Boden (1911) figured some specimens identified as Anisocardia Choffati de Loriol, although study of de Loriol's original descriptions (1904, p. 162, pl. 20, figs. 6-8) reveals that Boden's assignation is incorrect. Comparison with British material leads to the conclusion that at least part of Boden's series of specimens (his pl. 6, figs. 6-8, and possibly fig. 9) may belong to A. tenera. Unfortunately, it is his fig. 9 which shows the dentition, and as it is not certain that this figure belongs to A. tenera, the nature of the dentition of this species remains uncertain. However, Boden's figure is reproduced here (Fig. 2.50), and the dental formula of the right valve is given thus:

$$A_I \quad 1 \quad 3a \quad 3b \quad (5b) \quad P_I$$

As mentioned in the subgeneric remarks, Anisocardia is unusual in having 1 placed anterior to 3a, as a clear continuation of the laminar A_I; 3a is small, elongate and closely pressed against the hinge margin, while 3b is stout and oblique. Boden's figure suggests also the presence of a fairly well-developed 5b. Cox's figure (1947) of the hinge of the type species of Anisocardia is reproduced above in Fig. 2.49.

Statistically, the differences between A. tenera and R. minima are most obvious in the L/I regression lines (Fig. 2.51a), the L/H and L/AL regressions for the two species being rather similar (Figs. 2.51b, 2.51c); in view of the measurements

of the two species (Appendix 3), this is not unexpected. It should be remembered that the regressions shown here are simple arithmetic plots, which assume constant growth rates; this assumption has not been proved conclusively to be either true or false.

There is a long history of confusion in the literature over the identity of A. tenera and R. minima, caused in the most part by the scantiness of Sowerby's descriptions, and the apparent similarity of his two figures. Examination of the holotypes, or even collections of topotypes, reveals that the differences between the two are clear cut. However, study of the synonymies shows that the two species have often been confused, notably by Morris & Lycett (1853) and Lycett (1863) in the British literature, and by several continental authors such as Goldfuss (1837), Couffon (1919) and Makowski (1952). Anisocardia clarissima (Leckenby, 1859), from the Hackness Rock of Scarborough, is closely related to A. tenera, but specific identity is unlikely. The holotype (SM J6006) and several paratypes (SM J12456-12460) are more elongate than A. tenera (H $\bar{x}$ 83.0 %, compared with 89.9 % in A. tenera), and also more inflated (I $\bar{x}$ 68.0 %, compared with 60.3 %). Both these values for A. clarissima lie further from the mean of A. tenera than one standard deviation, and are thus considered to be significantly different. A. clarissima is also much more markedly rostrate than A. tenera.

Range and occurrence   In Britain, this species is apparently
restricted to the Kellaways Rock, being found in Wiltshire
and Yorkshire, as well as being cited from the Kellaways Rock
in several Geological Survey memoirs.   Four specimens from
the Hudleston collection (GSM Y2071-2074), labelled "Oxford
Clay, Loudon" also seem to belong to this species, but the
preservation is poor, and the horizon unknown.

On a wider geographical scale, Stoll (1934) records
this species from the U. Bathonian (Oppelia aspidoides Zone)
and M. Callovian of Pommerania (N. Germany), whilst Boden
(1911) records it from the "Unteren Oxford" (probably Cordatum
Zone) of Popilany, Lithuania.   Ilovaisky (1904) figured a
specimen identified as A. tenera, from the Cordatum Zone of the
Moscow region, but this is probably more closely related to
A. anisocardioides (Blake & Hudleston) from the Corallian.
A. tenera Krenkel (1915), from the Athleta and Lamberti Zones
("Oberes Kelloway") of Popilany, is probably correctly
identified.   However, as these foreign specimens have not been
examined, and their ranges are rather different to that of
British specimens, it cannot be certain that they are conspecific,
and so they are merely recorded here.

Genus ISOCYPRINA Roeder, 1882 (p. 90)

Type species   Subsequently designated by Cossmann, 1921,
p. 23, Cardium cyreniformis Buvignier, 1852, p. 15, pl. 13,
figs. 23-27, from the Upper Oxford Clay (Oxfordian) of the
Ardennes.

Diagnosis   Suborbicular to ovate, evenly inflated or
with a weak umbonal carina; lunule faint, mostly bounded by
an impressed line, escutcheon absent; ornamented by faint
concentric lines, or smooth; hinge formula:

A_I (A_{III}) (1) $(3a)$ P_I / A_{II} $(2a)$ $2b$ $4b$ (P_{II});
lamina A_{II} (+ 2a) joined to 2b by vinculum, P_{II} merged into
margin; P_I strong, elongate.

<center>Subgenus ISOCYPRINA s.s.</center>

Diagnosis   Hinge with 2a differentiated from A_{II};
laterals smooth; other characters as in the generic diagnosis.

Remarks   Arkell (1934, p. 263) suggested that there
is a possibility that the distinction between forms with and
without cardinal tooth 3a may be of generic or subgeneric
significance. However, Casey (1952, p. 136) has concluded,
after studying many species of Jurassic and Cretaceous
Isocyprina including the type species I. cyreniformis, that no
taxonomic significance should be ascribed to these variations in
dentition. He believed that in I. cyreniformis, 3a is present,
although extremely reduced, and is represented by a minute
sliver of shell pressed against the valve margins (Fig. 2.52).
Chavan (1945, p. 80) followed Arkell in noting that the species
described by Roeder (1882) as I. cyreniformis was not identical
with that originally described by Buvignier (1852), on the basis
of the dentition, there being no 3a in Buvignier's species,

although he recognised that other Jurassic and Cretaceous
species possessed 3a. This led Chavan to conclude that all
the Mesozoic species of Isocyprina bearing 3a should be
placed in the subgenus Eotrapezium Douville, and that
Isocyprina (Eotrapezium) roederi should be chosen as the
'typical form'. However, Keen & Casey (1969, N648) restricted
Eotrapezium to Upper Trias - Lower Jurassic forms with 1
scarcely differentiated from A_I, no 2a, and lamina A_{III} - 3a
usually suppressed, with the effect that the Jurassic and
Cretaceous forms must be replaced in Isocyprina s.s.

Isocyprina (Isocyprina) roederi Arkell. Pl. 23, figs. 1-8.

1882 Cyprina (Isocyprina) cyreniformis Buvignier; Roeder,
      p. 91, pl. 2, figs. 5a, 5b; pl. 4, figs. 11a, 11b.
      (non I. cyreniformis Buvignier).

1934 Isocyprina roederi nom. nov.; Arkell, p. 263, pl. 35,
      fig. 21.

1945 I. (Eotrapezium) roederi Arkell; Chavan, p. 81.

Type specimen   Holotype, the specimen figured by Roeder
(1882, pl. 2, fig. 5b) as Cyprina (Isocyprina) cyreniformis,
from the Oxfordian of Pfirt, Germany. Present location of the
type series is unknown.

Diagnosis   Medium sized Isocyprina (up to 20 mm L),
orbicular, with very small, but slightly salient umbones;
very compressed, with low inflation (I $\overline{x}$ 35.3 %); umbonal

carina extremely faint, lunule very small; pallial sinus
small. Differs from the closely related species I. simplex
Arkell in possessing a clearly developed 3a on the right valve.
It may be distinguished from other Jurassic Isocyprina by
virtue of its very orbicular outline and low inflation.

Measurements

    See Appendix 3.

	L	H	I
N	14	14	3
$\overline{x}$	15.5 mm	90.1 %	35.3 %
Max	20.0	96.3	42.2
Min	6.5	83.3	30.9
OR	13.5	13.3	11.3

Description   Equivalve, subequilateral (umbones more or
less median), medium-sized species (up to 20 mm L), suborbicular
to subovate in outline (H 83.3-96.3 %, $\overline{x}$ 90.1 %); anterodorsal
and posterodorsal margins gently convex, except for a slight
concavity just anterior of the umbones which indicates the
position of the very small lunule; anterior, ventral and
posterior margins continuously and evenly curved to give a semi-
circular outline to the remainder of the shell margin.
Inflation low (I 30.9-42.2 %, $\overline{x}$ 35.3 %). Umbones small,
submedian, prosogyrate, not prominent, only very slightly
salient to the hinge margin, not contiguous. Shell exterior
smooth, with irregularly-spaced faint concentric growth lines;
no radial elements.

Hinge formula as for subgenus:

$$\frac{A_I \quad 1 \quad 3a \quad 3b \quad P_I}{A_{II} \quad (2a) \quad 2b \quad 4b}$$

except that 2a is not clearly differentiated from A_{II}; laterals strong, laminar, smooth, A_I usually colaminar with, and not differentiated from, cardinal 1; 3a thin, closely pressed against the valve margin, 3b strongly triangular, more or less bifid; 2b stoutly triangular, its anterior limb aligned with A_{II} and joined to it by a vinculum; 4b long, slender. Margin entire, without denticulations. Adductor muscle scars unequal, the posterior scar being higher and more elongate than the anterior scar, both scars elongated dorsoventrally; very small pallial sinus in many specimens (Fig. 2.53).

Remarks   As noted above, in the subgeneric discussion, the species figured by Roeder (1882) as I. cyreniformis Buvignier differs from Buvignier's species in the possession of tooth 3a, and the first available name is I. roederi Arkell. This rather distinctive species is, unfortunately, rarely well enough preserved to allow examination of the hinge, although one pyritised right valve from Marston Moretaine shows almost all of the cardinal plate (Fig. 2.54). 3a is clearly recognisable, and so the species may be separated from I. simplex Arkell. These two species are undoubtedly very closely related, as a study of external form reveals, and were it not for the dentition, they could be united. However, as Arkell (1934, p. 269) noted, no right valves of I. simplex

showing the dentition properly have been seen, and it is
uncertain how strongly 3a is developed. Arkell (op. cit.)
notes that the hinge is "as I. cyreniformis", and so it is
necessary to assume, in the absence of evidence to the contrary,
that 3a is very weak or absent. The discovery of better-
preserved material of I. simplex would clarify the position,
but in the light of available evidence, it seems best to
separate the two species at the moment.

Arkell (op. cit., p. 261) recognised five species of
Isocyprina (excluding I. roederi) in the British Corallian, and
was responsible for the clarification of the position of several
of d'Orbigny's (1850) nomina nuda species. As in several of his
species, d'Orbigny seems to have united individuals belonging
to more than one species, notably in the case of his Cyprina
dimorpha, which was figured by Cottreau in 1927 (pl. 46, figs.
15-17). Arkell (p. 265) accepted Cottreau's fig. 17 as being
synonymous with I. cyreniformis, but questioned the placement of
figs. 15 and 16, suggesting that they may belong with I. simplex.
This seems probable, as the age is equivalent, and there are
great similarities of form; the absence of a view of the
cardinal plate precludes placement in I. roederi.

I. depressiuscula Morris & Lycett (1853) from the
Bathonian (holotype GSM 9703), is another smooth species of
low inflation, but is clearly distinct from I. roederi in that
it possesses a much more produced anterior angle, breaking the
regular suborbicular outline and exaggerating the prominence
of the umbones. I. politula Bean (1839) from the Cornbrash of

the Yorkshire coast also has two prominent umbones, which are slightly hooked, and is immediately distinguishable.

Range and occurrence   Oxford Clay (Coronatum - Athleta Zones) of central and southern England; Inverbrora Shale (Calloviense to Jason Zones) of Brora, Sutherlandshire; Oxford Clay (Cordatum Zone) of Eigg, Inverness-shire; Oxfordian of Germany (type material).

Order MYOIDA Stoliczka, 1870

Suborder MYINA Stoliczka, 1870

Superfamily MYACEA Lamarck, 1809

Family CORBULIDAE Lamarck, 1818

Subfamily CORBULINAE Gray, 1823

Genus CORBULOMIMA Vokes, 1945 (p. 10)

Type species   Originally designated by Vokes, 1945, p. 10, Corbulomima nuciformis sp. nov., p. 10, pl. 2, figs. 5-8, from the Aptian (L. Cretaceous) of Lebanon.

Diagnosis   Moderately inflated, smooth, very slightly rostrate, lacking special structures for the reception of the resilifer in both valves; single large triangular cardinal tooth in the right valve, received in a socket in the left valve.

Remarks   Chavan (1952, p. 121, 122) has described two corbulids referable to Corbulomima from the Sable Astartiens (U. Oxfordian) of Calvados, France, C. glosensis (Zittel &

Goubert) and C. suprajurensis (d'Orbigny). Figures of the
hinge (Chavan, pl. 4, figs. 73, 74, 77, 79) show the typical
cardinal arrangement as defined by Vokes (1945), and there can
be no doubt as to the correct placement of these two species.

1.   Corbulomima macneillii (Morris). Pl. 23, figs. 9-18,
                                        Pl. 24, figs. 1-8.

1850   Corbula ?macneillii sp. nov.; Morris, p. 318, pl. 30,
        fig. 4.

1899   Corbula Greppini sp. nov.; de Loriol, p. 146 , pl. 10,
        fig. 1.

Type specimen   Neotype, designated herein, GSM 113999,
from the Kellaways Rock of Trowbridge, Wiltshire. The Morris
collection is believed to have been sold (Cox & Arkell, 1948,
p. xxii), although a few Bathonian types are still preserved
in the BM (NH), London; however, the holotype of C. macneillii
is not among these, and in order to clarify the differences
between this species and C. obscura (J. de C. Sowerby), it has
been necessary to designate a neotype.

Diagnosis   Small (up to 6.8 mm L), smooth, suborbicular,
inflated Corbulomima, with a prominent rounded posterior margin
and a quadrate posterior margin, a small posterior area being
delimited by an umbonal carina. The species differs from
C. obscura (J. de C. Sowerby) in being more inflated (I $\bar{x}$ 72.0 %
compared with 61.1 %), less elongate (H $\bar{x}$ 83.3 % compared with
70.5 %) and having a markedly less rostrate posterior margin.

Measurements

See Appendix 3.

	L	H	I	AL
N	132	132	119	132
$\bar{x}$	5.0 mm	83.3 %	72.0 %	37.0 %
Max	6.8	100.0	90.0	48.5
Min	3.4	67.2	56.5	29.5
OR	3.4	32.8	33.5	19.0

Description   Inequivalve, right valve slightly larger
than the left valve, and overhanging it along the ventral
margin; inequilateral, umbones placed clearly anterior of
median (AL 29.5-48.5 %, $\bar{x}$ 37.0 %); small species (up to 6.8
mm L), suborbicular to subtrigonal in outline (H 67.2-100.0 %,
$\bar{x}$ 83.3 %), globose (I 56.5-90.0 %, $\bar{x}$ 72.0 %), with maximum
inflation in the region of the hingeline. Dorsal margin
reflexed, forming an obtuse angle diverging from below the
umbones, posterior part straight to gently convex, dependent
upon the development of the posterior area, anterior part
concave; no lunule; anterior margin rounded, rather produced
into a semicircular shape, passing smoothly into the gently
convex ventral margin; posterior margin obliquely truncate,
meeting the posterodorsal margin at an angle of about 125 $^{\circ}$;
posteroventral angle acute, well-developed, located at the point
at which the umbonal carina reaches the ventral margin;
carina rounded, gently convex towards the posterior, the
posterior area sloping very steeply down from it towards the
posterior margin. Umbones small, submedian, inflated,

prosogyrate, rather salient, not contiguous. Escutcheon absent. Ligament internal, external nymph not present. Shell very thin, with an internal nacreous layer, ornamented solely by very faint concentric growth lines. Dentition appearing to consist of a single large triangular tooth on the right valve, with no chondrophore; dentition of left valve unknown. Margins entire, ventral margin of the right valve overlapping that of the left. Musculature not seen.

Remarks   The basis of this description is a large collection of recrystallised calcite steinkerns from the Lower Oxford Clay cementstones of Wiltshire, preserved in the Oxford University Museum (OUM J28229-28231 collective), which show the various features much more clearly than the clay steinkerns of the Midlands Lower Oxford Clay. In one of the specimens from Wiltshire (OUM J28231), it was possible to prepare the hinge of the right valve, revealing the presence of a single large triangular cardinal tooth (Fig. 2.55), which confirmed the placement of this species within Corbulomima. No special structures (such as a chondrophore) for the attachment of the internal ligament were seen, Vokes (1945, p. 10) believing that the ligament was attached to the posterior part of the socket in the left valve in this genus, the socket being too elongate to accept only the cardinal tooth. No interior views of any left valves of C. macneillii have been seen, but the internal view of a left valve of the closely related Corbula oxfordiensis d'Orbigny given by Cottreau (1926, pl. 45, fig. 16) suggests that the dentition is normal for a Corbulomima.

Corbulomima obscura (J. de C. Sowerby), from the Roof
Bed (= Kellaways Rock) of Brora, Sutherlandshire, is very close
to C. macneillii in both age and form, but differs in being
less inflated, more elongate, and having a more reflexed
posterior margin, giving a slightly rostrate appearance. The
range of variation in form of these two species is shown in
Fig. 2.56. Plotted on a simple length/height scatter diagram
(Fig. 2.57), C. obscura and C. macneillii can be seen to follow
the same general trend of growth, although at any given length,
the height measurement is slightly less in C. obscura. This
trend is made even more apparent when the data is replotted to
give regression lines (Fig. 2.58), the line for C. obscura having
a markedly steeper slope than those of four populations of
C. macneillii from different parts of England. In view of the
consistent differences in both form and growth rates of these
two geographically separated species, the balance of evidence
favours their taxonomic separation, and it seems possible that
in Corbulomima, speciation may be allopatric.

Morris (1850, p. 318) stated that Corbula cucullaeaeformis
Koch & Dunker (1837, p. 31, pl. 2, figs. 6a-6c) is "extremely
close" to C. macneillii. However, study of Koch & Dunker's
original plate shows that their species is a much more rostrate
species, with orthogyrate umbones, and cannot be considered
synonymous. Corbula Greppini de Loriol (1899), from the Lower
Oxfordian of the Bernese Jura agrees well with the English Lower
Oxford Clay specimens, and is probably synonymous with
C. macneillii. Corbula oxfordiensis d'Orbigny (see Cottreau,

1926, p. 47, pl. 45, figs. 16-18) from the Upper Oxford Clay of Normandy differs from both C. macneillii and C. obscura in having regular concentric ornament, a feature shared by Corbula mosae d'Orbigny (1850).

Range and occurrence   Kellaways Rock (Calloviense Zone) of Wiltshire, the type area; Lower Oxford Clay (Jason - Athleta Zones) of central and southern England; Hackness Rock (Athleta - Lamberti Zones) of Yorkshire; Upper Oxford Clay (Praecordatum Zone) of southern England. Upper Oxford Clay of the Bernese Jura.

2.   Corbulomima obscura (J. de C. Sowerby). Pl. 24, figs. 9-13.

1827 Corbula sp. nov.; J. de C. Sowerby in Murchison, p. 320.
1827 Corbula obscura sp. nov.; J. de C. Sowerby, p. 140, pl. 572, fig. 5.

Type specimen   Holotype of J. de C. Sowerby's plate 572, fig. 5, from the "?Inferior Oolite" (= Kellaways Rock) of Brora, Sutherlandshire, is preserved in the Sowerby collection at the BM (NH), number 43044.

Diagnosis   Small (up to 5.2 mm L), smooth, subrectangular Corbulomima with umbones rather less salient than in C. macneillii, and a more pronounced, slightly reflexed rostrum; both height ($\bar{x}$ 70.5 %) and inflation ($\bar{x}$ 61.1 %) are considerably less than in C. macneillii; umbonal carina tending to be concave in outline towards the posterior, unlike C. macneillii in which it is convex.

Measurements

See Appendix 3.

	L	H	I
N	7	7	2
$\overline{x}$	4.3 mm	70.5 %	61.1 %
Max	5.2	73.8	62.2
Min	4.0	67.5	60.0
OR	1.2	6.3	2.2

Description   Inequivalve, right valve slightly overlapping
the left along the ventral margin, inequilateral, umbones just
anterior of median; small species (up to 5.2 mm L),
subrectangular to subtrigonal in outline (H 67.5-73.8 %, $\overline{x}$
70.5 %), gently inflated (I 60.0-62.2 %, $\overline{x}$ 61.1 %). Dorsal
margin reflexed, the angle more obtuse than in C. macneillii,
with gently concave to straight anterodorsal and posterodorsal
outlines; anterior margin rounded, slightly produced, passing
smoothly into the gently concave ventral margin; posterior
margin gently convex to oblique, meeting the posterodorsal
margin at an angle of 120-125 °; posteroventral angle acute,
marking the point where the umbonal carina reaches the ventral
margin; umbonal carina rounded, less sharp than in C. macneillii,
the posterior area being slightly wider and flatter than in
C. macneillii, as the carina is concave towards the posterior;
a slight reflection of the posterior part of the ventral margin
is characteristic, giving a slightly rostrate appearance.
Umbones small, submedian, just anterior to the mid-axis,
prosogyrate, only slightly salient to the hingeline, not markedly

inflated. No lunule or escutcheon, ligament internal. Shell
surface smooth, with very faint concentric growth lines, no
radial elements. Dentition and musculature unknown.

Remarks   Corbulomima obscura is another of Sowerby's
species which has largely been overlooked in the literature,
at least as regards Upper Jurassic records. This is due to
the fact that in the index to volume 6 of the 'Mineral
Conchology', the species was said to have come from the
"Inferior Oolite?", although in the description of the species
(op. cit., p. 140), its horizon is recorded as the Brora Roof
Bed. However, at the time of writing (1827), the Scottish
Middle - Upper Jurassic succession was very poorly understood,
and it is probable that Sowerby believed the Roof Bed to be of
Inferior Oolite age. Whatever the cause, the effect was that
subsequent authors have regarded it as a Middle Jurassic form,
and ignored it when considering Upper Jurassic corbulids.

As mentioned in the discussion of the preceding species,
the differences between C. macneillii and C. obscura are fairly
small, but nevertheless constant, and are deserving of specific
separation. These are the only two European Callovian - L.
Oxfordian corbulids known which are smooth and lack prominent
concentric ribbing, and thus form a closely related species
pair. All other contemporaneous European corbulids are also
markedly more rostrate, and have a greater valve overlap along
the ventral margin. It is possible that these strongly ribbed
species should be referred to a genus other than Corbulomima.
C. cucullaeaeformis Koch & Dunker, mentioned above belongs to

this latter group, and need not be further considered here.

The only exception to this observation is <u>Corbulomima</u> <u>suprajurensis</u> (d'Orbigny), figured by Chavan (1952, p. 122, pl. 4, figs. 72-75) from the Upper Oxfordian of Normandy. This species seems to have characters common to both the groups of Upper Jurassic corbulids, as the small, subrectangular form with only faint concentric ornament is typical of the <u>macneillii</u> - <u>obscura</u> group, while the strong posterior reflection of the ventral margin is more characteristic of the <u>carinata</u> group. The evidence of the hinge mechanism, well seen in figures 73 and 74 of Chavan's plate 4, places this species undoubtedly in <u>Corbulomima</u>, but it cannot be considered synonymous with either of the two British species.

<u>Range and occurrence</u>   Roof Bed (Calloviense Zone), Brora, Sutherlandshire, the type locality and horizon. At this locality, the Roof Bed is divided into two lithologically distinct units, which Sykes (1973, pers. comm.) believes represent the Koenigi (lower part) and Calloviense (upper part) Subzones; <u>C. obscura</u> is found only in the Calloviense Subzone.

<div align="center">

Subclass ANOMALODESMATA Dall, 1889

Order PHOLADOMYOIDA Newell, 1965

Superfamily PHOLADOMYACEA Gray, 1823

Family PLEUROMYIDAE Dall, 1900

Genus PLEUROMYA Agassiz, 1842 (p. 439)

</div>

Synonymy: Myacites Schlotheim, auctt.

Amphidesma Phillips, 1829 (non Lamarck)

Myopsis Agassiz, 1840 (pars)

Anaplomya Kraus, 1843

Hapalomya Roeder, 1882

Hapalomia Roeder, 1882

? Fogiella Krumbeck, 1913

Type species   Subsequently designated by Herrmannsen, 1847, p. 297, Mya gibbosa J. de C. Sowerby, 1823, p. 19, pl. 419, from the Upper Oxford Clay near Weymouth, Dorset. (= Donacites Alduini Brongniart, 1821, p. 571, pl. 7, figs. 6a, 6b).

Diagnosis   Subequivalve, right valve slightly larger than the left, oval, oblong or trapeziform, moderately to strongly inflated; umbones placed within the anterior half, and generally close to the anterior margin, inflated, not prominent; lunule and escutcheon absent; no true hinge teeth. Main part of ligament external, opisthodetic, with short nymphs; below and anterior to the umbones of each valve is a short rounded protuberance; deep pallial sinus, well-developed posterior gape; surface with or without concentric ribbing.

1.   Pleuromya alduini (Brongniart). Pl. 24, figs. 14-24,
                                        Pl. 25, figs. 1, 7.

1821   Donacites Alduini sp. nov.; Brongniart, p. 571, pl. 7, figs. 6a, 6b.

1823 Mya gibbosa sp. nov.; J. de C. Sowerby, p. 19, pl. 419.

(non Mactra (Lutraria) gibbosa J. Sowerby, 1812,

Inferior Oolite species).

1829 Panopaea oblata nom. nov.; J. de C. Sowerby, p.4

(nom. nov. pro M. gibbosa J. de C. Sowerby). /1840/.

1829 Amphidesma recurvum sp. nov.; Phillips, pl. 5, fig. 25.

1851 Potamomya ? sowerbyii sp. nov.; Forbes, p. 112, pl. 5,

figs. 2a, 2b.

1860 Homomya oblata (J. de C. Sowerby); Damon, pl. 3, fig. 4.

1863 Myacites recurvum (Phillips); Lycett, p. 81, pl. 36,

figs. 4, 4a.

1871 M. recurvus (Phillips); Phillips, pl. 13, fig. 28.

1910 Donacites (Pleuromya) alduini Brongniart; Cossmann, no. 230.

1915 Pleuromya agassizi Chapuis; Krenkel, p. 331, pl. 27, fig. 6.

1934 P. alduini (Brongniart); Arkell, p. 321, pl. 44, figs. 1-9.

1934 P. recurva (Phillips); Stoll, p. 14, pl. 1, fig. 44.

1948 P. alduini (Brongniart); Cox & Arkell, p. 40.

Type specimen   Holotype of Brongniart's (1821) pl. 7, figs.
6a, 6b, from "Writhenterton, England" (probably Winterton,
Lincolnshire, from Boulder Clay - Arkell, 1934, p. 323),
refigured by Cossmann (1910) as number 230 in the Palaeontologia
Universalis. Holotype preserved in the Institute Paléontologique du
Musée National d'Histoire Naturelle, Paris.

Diagnosis   Large sized (up to 66 mm L), subquadrate to
subtrigonal species, ornamented with conspicuous well-developed
concentric ribs; height 53.8-87.4 % ($\overline{x}$ 69.2 %), inflation
37.1-67.4 % ($\overline{x}$ 49.8 %), anterior length 20.7-35.7 % ($\overline{x}$ 27.9 %),

the first two characters being very variable; anterior margin
short, gently concave to gently convex, truncate, with rounded
anteroventral angle of about 90 $^{\circ}$; posterior margin produced
into a rounded angle; ventral margin strongly convex;
posterodorsal margin subparallel to ventral margin.

Differs from P. uniformis (J. Sowerby) in possessing
strong regular concentric ribs, and in being relatively higher
(H $\overline{x}$ 58 % in P. uniformis) and more inflated (I $\overline{x}$ 40.2 % in
P. uniformis). The latter species is smooth except for some
low irregular growth rugae. Both these species are notable for
their great range of variation. P. calceiformis (Phillips) is
much more elongate (H $\overline{x}$ 43 %) than P. alduini, and is also
smooth-shelled.

Measurements

See Appendix 3.

	L	H	I	AL
N	70	70	48	67
$\overline{x}$	39.4 mm	69.2 %	49.8 %	27.9 %
Max	65.9	87.4	67.4	35.7
Min	18.5	53.8	37.1	20.7
OR	47.4	33.2	30.3	15.0

Description   Large species (up to 66 mm L), inequilateral,
subequivalve, the right valve overlapping the left valve along
the dorsal margin; subrectangular to elongate - subtrigonal in
form, with the posterior margin often produced into a rounded
angle; height $\overline{x}$ 69.2 %, inflation 49.8 %, anterior length

27.9 %, limits of variation given above; umbones situated close to the anterior margin, prosogyrate, often contiguous, not very prominent, elevated up to 6 mm above the dorsal margin; anterodorsal margin merged into anterior margin, gently concave to gently convex, truncate, forming about a right angle with the posterodorsal margin at the umbo; posterodorsal margin straight to gently concave, often subparallel to the ventral margin; posteroventral angle produced and acutely rounded, passing evenly into the strongly convex ventral margin; antero-ventral angle rounded, forming an angle of about 90 $^{\circ}$ with the ventral margin; the anterior part of the ventral margin and the anterior part of the posterodorsal margin are often parallel, then swing round posterodorsally towards the posterior angle; lunule and escutcheon absent, but the area on the dorsal margin immediately anterior to the umbones is often deeply excavated; ligament external, opisthodetic, inserted upon short prominent nymphs; ornament consists of prominent, regularly spaced concentric ribs, becoming wider away from the umbones; superimposed upon the pattern of concentric ribs are very fine concentric growth striae, well seen in specimens from the Lower Calcareous Grit which retain the shell; radial elements absent; in a few specimens, a faint shallow sulcus runs from the umbones to the ventral margin, reaching the margin just behind the anteroventral angle and causing a slight sinuosity in the anterior part of the ventral margin.

No true hinge teeth present, there being only a small rounded protuberance of the dorsal margin below and slightly

anterior of the umbo of each valve, the protuberance being hollowed out above, with a small niche behind; protuberance of right valve fits above that of left valve (Fig. 2.59), a small internal ligament possibly occupying the space between them (Cox, 1969, p. N842). Anterior adductor muscle scar subrectangular, elongated dorsoventrally, about 6 mm high, posterior scar suborbicular, 6 mm long by 5 mm high; pallial sinus well-developed, lower limb not confluent with the pallial line (Fig. 2.60). Prominent posterior gape in most specimens, slight anterior gape in a few.

Remarks   The synonomy of P. alduini is fully listed and discussed by Arkell (1934, p. 321), and little need be added about this long-ranging species of wide geographical extent.

Study of large populations reveals the extreme nature of variation in this species, both height and inflation having a range of over 30%. There is, however, no consistent pattern of variation at different stratigraphical levels, and the evidence indicates the presence of a single species, ranging from the Bathonian to the Kimmeridgian. As noted by Arkell (1934, p. 323), P. alduini appears to have had a preference for clay environments, being particularly common at some levels in the Oxford and Kimmeridge Clays. The small specimens found so commonly at the top of the Grossouvrei Subzone at Peterborough are typical of the species in all respects, although crushing has affected the inflation, which it is not possible to measure. Uncrushed specimens from septarian concretions in the Lower Oxford Clay of Wiltshire (OUM J28241-42) show the form present

in the Lower Oxford Clay to be exactly comparable with those
from the Red Nodule Beds of Weymouth, and elsewhere in the
Oxford Clay.

Range and occurrence   Fullers Earth Rock (Bathonian) of
Dorset and Somerset (Arkell, 1939, p. 170); Belemnite Sands
(Bathonian) of Staffin Bay, Skye; Cornbrash, Kellaways Beds,
Oxford Clay, Corallian and Lower Kimmeridge Clay, widespread.

On the continent P. alduini has been recorded from beds
of Callovian to Kimmeridgian age, in France, Germany and Russia.

2.   Pleuromya uniformis (J. Sowerby). Pl. 24, figs. 25-27,
                    Pl. 25, figs. 2-4, Pl. 26, figs. 11-16.

1813   Unio uniformis sp. nov.; J. Sowerby, p. 83, pl. 33, fig. 4.

1821   Lutraria ? Jurassi sp. nov.; Brongniart, p. 555, 570, pl.
        7, figs. 4-4b.

1829   Amphidesma decurtatum sp. nov.; Phillips, pl. 7, fig. 11.

1836   Lutraria tenuistriata sp. nov.; Münster in Goldfuss,
        p. 257, pl. 153, figs. 2a-2c.

1836   L. elongata sp. nov.; Münster in Goldfuss, p. 258, pl. 153,
        figs. 4a, 4b.

1840   Amphidesma ? ovale sp. nov.; J. de C. Sowerby, pl. 21,
        fig. 11.

1840   A. ? hians sp. nov.; J. de C. Sowerby, pl. 21, fig. 12.

1851   Potamomya ? Sedgwickii sp. nov.; Forbes, p. 113, pl. 5,
        figs. 3a, 3b.

1855   Myacites Terquemea (Buvignier); Morris & Lycett, p. 115,
        pl. 12, figs. 6, 6a. (non Buvignier).

1855 M. securiformis (Phillips); Morris & Lycett, p. 136, pl.

13, fig. 15. (non Phillips).

1855 M. decurtatus (Phillips); Morris & Lycett, p. 137, pl. 15,

figs. 10a, 10b.

1860 M. decurtatus (Phillips); Damon, pl. 4, fig. 6.

1888 M. jurassi (Brongniart) var. portlandica nov.; Damon, pl.

19, fig. 9.

1910 Lutraria (Pleuromya) Jurassi Brongniart; Cossmann, no. 231.

1915 Pleuromya tellina Agassiz; Krenkel, p. 329, pl. 27, fig. 7.

1915 P. polonica sp. nov.; Krenkel, p. 330, pl. 27, fig. 5.

1932 P. decurtata (Phillips); Spath, p. 117, pl. 6, fig. 5;

pl. 7, fig. 6.

1934 P. jurassi (Brongniart); Stoll, p. 14, pl. 1, fig. 47.

1935 P. uniformis (J. Sowerby); Cox, p. 15, pl. 2, figs. 9, 10.

1935 P. uniformis (J. Sowerby); Arkell, p. 325, pl. 45, figs.1-13.

1936 P. tellina Agassiz; Spath, p. 128, pl. 45, figs. 4a, 4b;

pl. 50, figs. 1a, 1b.

1948 P. uniformis (J. Sowerby); Cox & Arkell, p. 40.

1955 P. uniformis (J. Sowerby); Callomon, p. 221.

1965 P. uniformis (J. Sowerby); Cox, p. 131, pl. 20, fig. 6.

1972 P. uniformis (J. Sowerby); Walker, p. 134.

Type specimen   Holotype of J. Sowerby's plate 33, fig. 4,
from the Cornbrash of Felmersham, Bedfordshire, refigured by
Arkell (1935, pl. 45, figs. 4, 4a), preserved in the Sowerby
collection at the BM (NH), number 43224.

<u>Diagnosis</u>   Large sized species (up to 71.2 mm L),
elongate elliptical in form, with height 49.8-74.1 %, $\overline{x}$ 58.4 %,
inflation 33.1-45.5 %, $\overline{x}$ 40.2 %, and anterior length 29.3-
41.9 %, $\overline{x}$ 34.3 %. Ornament consists of irregularly-spaced
concentric growth rugae of uneven development. Posterior part
of the shell tapers into a rounded angle; a sulcus running
from the umbones to the anterior part of the ventral margin
causes a slight sinuosity in the ventral margin; sulcus of
variable strength, but almost always present; umbones low, not
markedly prominent.

          Differs from <u>P. alduini</u> in lacking the coarse regular
concentric ribs, and in being more elongate and less inflated;
the umbones are also much less prominent. <u>P. calceiformis</u>
shares the lack of regular concentric ribs, but is much more
elongate (H $\overline{x}$ 43.0 %) and has the posterior drawn out into a
long round-ended 'rostrum'.

<u>Measurements</u>

          See Appendix 3.

	L	H	I	AL
N	29	29	18	29
$\overline{x}$	39.3 mm	58.4 %	40.2 %	34.3 %
Max	71.2	74.1	45.5	41.9
Min	27.1	49.8	33.1	29.3
OR	44.1	24.3	12.4	12.6

<u>Description</u>   Large sized species, elongate-elliptical
to subrectangular in outline, inequilateral, subequivalve, with

the right valve slightly overlapping the left valve along the dorsal margin; height $\overline{x}$ 58.4 %, inflation 40.2 %; umbones placed about one-third of the shell length behind the anterior margin (AL 29.3-41.9 %, $\overline{x}$ 34.3 %), prosogyrate, contiguous, not prominent or inflated, elevated up to about 4 mm above the dorsal margin; anterodorsal margin short, gently concave, with no lunule, passing smoothly into the evenly rounded anterior margin; anteroventral angle variable, usually rounded and not angular, but becoming almost a right angle in forms with a very strong anterior sulcus; ventral margin long and very gently convex, with a variably-developed sinuosity near the anterior extremity marking the position of the anterior sulcus; the convexity of the ventral margin becomes stronger posteriorly, where it passes smoothly into the posterior margin; clearly defined posteroventral and posterodorsal angles lacking, the posterior margin passing evenly into the dorsal and ventral margins; escutcheon absent; ligament external, opisthodetic, nymph short but clearly defined.

Ornament consists of fine concentric growth lines, with irregularly spaced growth rugae being developed to variable extents in most specimens; occasionally almost smooth. Very well-preserved specimens show the whole of the shell surface to be covered with minute radial striae. Posterior adductor muscle scar suborbicular, placed very close to the dorsal margin at the point where the posterior margin begins to diverge from the dorsal margin; anterior adductor scar unknown; pallial line with large pallial sinus, reaching halfway to the anterior margin,

the lower limb of the pallial sinus not confluent with the pallial line; dentition unknown, but probably of normal pleuromyid type; margins closed, with no anterior or posterior gapes.

Remarks   The synonymy of P. uniformis has been discussed fully by Arkell (1935, p. 327), and Cox & Arkell (1948, p. 40), and nothing need be added to their conclusions. The species has been given many names by continental authors, the most common being P. jurassi (Brongniart), P. tellina Agassiz, P. Voltzii Agassiz and P. elea (d'Orbigny). Arkell (op. cit.) has shown that all these names refer to the same species, the earliest available name being P. uniformis (J. Sowerby), a name overlooked until 1935 when Cox (1935, p. 15) used it for specimens from the 'Argovian' of India. Sowerby's name appears to have been overlooked because it was assigned to Unio, a freshwater genus.

The range of variation in this species, as in P. alduini, is very great, but attempts to separate stratigraphically distinct populations into discrete species or varieties have not been successful, an overlapping range of variation occurring at all levels from the Inferior Oolite to the Portland Beds (Arkell, 1935, p. 327; Lewinski, 1923, p. 80). Specimens studied in the course of this work lend support to this conclusion. P. uniformis seems to occur most commonly in sandy and calcareous deposits, being rather rare in shales and clays, and thus there appears to be ecological separation between it and P. alduini.

Range and occurrence   Inferior Oolite to Portland Beds

of Great Britain, being especially common in the Fullers Earth

Rock, Cornbrash, Kellaways Rock, Corallian, Kimmeridge Clay and

Portland Beds. It occurs sporadically at all intermediate

levels, but rarely in great abundance. Although it is known

from the Upper Oxford Clay of Dorset, it has not been found in

the Lower Oxford Clay.

On the continent, P. uniformis has been recorded from

the Bathonian - Portlandian of France, Germany, Switzerland,

Russia and Poland. It is also known from the Upper Jurassic of

Greenland and India.

Superfamily PANDORACEA Rafinesque, 1815

Family THRACIIDAE Stoliczka, 1870

Genus THRACIA J. de C. Sowerby, 1844 (p. 41)

Synonymy: Osteodesma de Blainville, 1825

Odoncineta Costa, 1829

Odontocineta Agassiz, 1843

Cinetodonta Agassiz, 1843

Corymya Agassiz, 1843

Throna Carpenter, 1859

Corimya Fischer, 1887

Coromya Fischer, 1887

Homoeodesmata Fischer, 1867

Eximiothracia Iredale, 1924

Cetothrax Iredale, 1949

Type species   Subsequently designated by Anton, 1839,
p. 2, Thracia pubescens Lamarck, 1819, p. 83 (= Mya pubescens
Pulteney, 1799, p. 27, pl. 4, fig. 6), Recent, Atlantic Ocean.

Diagnosis   Subequilateral, inequivalve, right valve
larger than the left valve, which it overlaps; umbones
opisthogyrate, prominent; adductor scars small, pallial line
with sinus; posterior margin truncate, with a gape; faint
umbonal ridge runs to the posteroventral margin.

Subgenus THRACIA s.s.

Diagnosis   Shell with concentric ornament, surface
granulate; umbones contiguous and perforate; ligament
external; cardinal plate with fissure occupied by lithodesma;
chondrophore moderately long.

Remarks   Some authors (Agassiz, 1843; Stoliczka,
1871) have used the genus Corimya Agassiz for the Jurassic
species referred to Thracia, but as Terquem (1855, p. 93) and
Arkell (1936, p. 354) pointed out, there is no satisfactory
evidence for separating Mesozoic from Tertiary and Recent species,
and so Thracia is retained. Jurassic forms occur only as
steinkerns, often crushed, with some thin remnant shell, thus
details of the dentition are not seen, although the position of
the external ligament nymphs is clear.

Thracia (Thracia) depressa (J. de C. Sowerby). Pl. 25,
figs. 5-6, 8-10, 14-15.

1823 _Mya depressa_ sp. nov.; J. de C. Sowerby, p. 19, pl. 418.

1836 _Mya_ or _Panopaea depressa_ J. de C. Sowerby; J. de C.
      Sowerby in Fitton, p. 347, pl. 23, fig. 9.

1836 _Tellina incerta_ sp. nov.; Thurmann in Roemer, p. 121, pl.
      8, figs. 7a, 7b.

1888 _Thracia depressa_ (J. de C. Sowerby); Damon, pl. 19, fig. 14.

1892 _T. depressa_ (J. de C. Sowerby); Fox-Strangways, p. 378,
      pl. 21, fig. f.

1911 _T. incerta_ (Thurmann); Boden, p. 55, pl. 5, figs. 21, 22.

1929 _T. depressa_ (J. de C. Sowerby); Cox, p. 172, pl. 5, fig. 3.

1934 _T. undulata_ (Schlippe); Stoll, p. 16, pl. 2, fig. 2.

1936 _T. depressa_ (J. de C. Sowerby); Arkell, p. 354, pl. 50,
      figs. 7-10.

1948 _T. depressa_ (J. de C. Sowerby); Cox & Arkell, p. 46.

Type specimen   The specimens figured by J. de C. Sowerby
(1823) are not preserved with the Sowerby collection at the BM
(NH), and must be considered lost. Accordingly, the specimen
figured by Damon (1888, pl. 19, fig. 14) from the Oxford Clay of
Weymouth (a topotype) is here designated neotype. It is
preserved in the BM (NH), number L 6797.

Diagnosis   Large sized shells (up to 65.1 mm L), very
variable in form, with height considerably less than length
(H 63.7-92.3 %, $\overline{x}$ 74.1 %), low to medium inflation (I 29.9-
60.8 %, $\overline{x}$ 41.7 %), and umbones placed just posterior of median

(AL 51.2-69.4 %, $\overline{x}$ 60.5 %).

Differs from the superficially similar T. incerta Cox
(non Thurmann) from the Portlandian, which is markedly more
elongate (H 66.3 % in Cox's figure) and has the umbones situated
more anteriorly (AL 45.3 %).

Measurements

See Appendix 3.

	L	H	I	AL
N	36	36	14	36
$\overline{x}$	46.4 mm	74.1 %	41.7 %	60.5 %
Max	65.1	92.3	60.8	69.4
Min	19.9	63.7	29.9	51.2
OR	45.2	28.6	30.9	18.2

Description   Large shells (up to 65.1 mm L), inequilateral,
inequivalve, with right valve larger than the left valve;
subtrigonal, subrectangular to elongate elliptical in form,
very variable; umbones prominent, opisthogyrate, contiguous,
placed posterior to median (AL $\overline{x}$ 60.5 %), bounded posteriorly
by strongly-developed ligament nymphs. Anterodorsal margin
gently convex, steepness of slope to the anterior margin dependent
upon the height of the shell; posterodorsal margin strongly to
gently concave, the area immediately posterior to the umbones
being occupied by the short, but prominent, ligament nymphs.
Anterior margin evenly rounded, passing smoothly into the gently
convex ventral margin; posterior margin slightly rostrate, with
a variably developed umbonal carina marking off the posterior

area, truncate or rounded in outline, with a strong posterior
gape. Inflation very variable (I 29.9-60.8 %, $\overline{x}$ 41.7 %),
point of maximum inflation located about 30 % of the height
below the dorsal extremity of the umbones; lunule absent, but
the area anterior to the umbones is marked by a deep channel;
ligament opisthodetic, nymphs producing a bisulcate feature on
the dorsal margin immediately posterior to the umbones;
escutcheon absent. Sculpture consists of irregularly spaced
growth lines, occasionally coarsened into growth rugae, crossed
by very fine radial striae which are not always visible.

Dentition unknown. Pallial line with large pallial
sinus, the lower limb of the sinus nearly confluent with the
pallial line.

Remarks   The great variability of this species may be
seen in large collections of uncrushed specimens, where all
intermediates between relatively short, high, subtrigonal
forms and more elongate, lower elongate-elliptical forms may
usually be found; the variation which occurs in the Upper
Oxford Clay, Corallian, Kimmeridge Clay and Portlandian examples
of the species has been discussed by Arkell (1936, p. 355). The
same range of variation is to be found in the Lower and Middle
Oxford Clay specimens which are, unfortunately, always crushed.
There is a tendency for the Lower Oxford Clay forms to be
slightly more elongate than forms from high in the Oxfordian,
as may be seen from the measurements in Table 2.4, but such is
the variation range, that forms agreeing exactly in shape with

Upper Oxfordian examples are often found, and there is no justification for considering them to be a different species. Regression lines for the two stratigraphically separated groups are shown in Fig. 2.61, and although having slightly different intercepts on the y axis, have similar slopes, and are not significantly different. It is likely that shell proportions have been slightly distorted by crushing in the Lower Oxford Clay, but it is improbable that the differences in form are due to this effect.

The synonymy of this species has been well covered by Arkell, but one point needs to be added here. Thracia incerta (Thurmann in Roemer) has been accepted as a distinct species occurring in the Kimmeridgian and Portlandian by many authors (Goldfuss, 1836; Agassiz, 1843; Leymerie, 1846; Thurmann & Etallon, 1861-1864; de Loriol, 1868, 1872, 1875; Lewinski, 1923 and Cox, 1929), supposedly differing from T. depressa by way of its being more elongate, and having anteriorly-placed umbones. Thurmann's figure in Roemer (1836, p. 121, pl. 8, figs. 7a, 7b) shows a form indistinguishable from typical British Oxfordian forms, and the author sees no reason to retain it as a distinct species, as the range overlaps with that of T. depressa. There are, however, very elongate forms with anterior umbones in the English Portland Beds, which Cox (1929, p. 173, pl. 5, fig. 6) has referred to T. incerta, and which may indeed represent a separate species; study of large collections should reveal whether or not the two 'species' grade into one another.

Range and occurrence   In Britain, T. depressa occurs

in the Fullers Earth (Bathonian) of Somerset and Dorset

(Arkell, 1939a, p. 171), throughout the Oxford Clay, and at

various horizons in the Corallian, Kimmeridge Clay and Portland

Beds.

It has also been recorded from the Upper Jurassic

(Callovian - Portlandian) of France, Germany, Switzerland and

Russia.

INCERTAE SEDIS

The two species described below are too small and poorly-

preserved to allow generic or even familial placement, although

it seems probable that they belong to the subclass Anomalodesmata.

Anomalodesmatan sp. A.   Pl. 25, figs. 11-13, Pl. 26, figs. 1,6,9.

Description   Small species, up to 14.0 mm long,

equivalve, inequilateral, subrectangular to subovate in outline

(H 60.2-80.2 %, $\overline{x}$ 69.3 %). Umbones small, rounded, contiguous,

prosogyrate, placed about one-third of the shell length behind

the anterior margin (AL 30.0-38.7 %, $\overline{x}$ 35.2 %), only very

slightly salient to the hinge margin. Posterodorsal margin

passing smoothly into the evenly-rounded posterior margin,

without a clearly marked posterodorsal angle, the posteroventral

angle often more apparent, forming a rounded right angle, or

occasionally, a more even curve; ventral margin straight to

gently convex, subparallel to the posterodorsal margin;

anterodorsal margin gently concave, passing into the short, sharply-curved anterior margin; anteroventral angle sharply rounded; in some specimens, the anterior part of the ventral margin is straight, and oblique to the posterodorsal margin, giving the anterior part of the shell a slightly rostrate appearance. Inflation low.

Ornament consists of low concentric growth striae and rugae, placed rather irregularly, and of variable strength; no radial elements. Shell of friable aragonite.

Measurements

See Appendix 3.

	L	H	AL
N	26	26	19
$\overline{x}$	9.4 mm	69.3 %	35.2 %
Max	14.0	80.2	38.7
Min	5.5	60.2	30.0
OR	8.5	20.0	8.7

Remarks   This small species is widespread in all lithologies of the Lower Oxford Clay of southern England, but is always poorly preserved, and its taxonomic position uncertain. It is usually preserved as clay steinkerns, often of articulated, wide-open shells, with a very thin layer of aragonitic shell material on the outer surface; because of this, nothing is known of the ligament, cardinal area or musculature, there being no sign of muscle scars on either the steinkerns or the shell material. For the same reason, the orientation of the shells

is unknown, the umbones being described as prosogyrate merely to facilitate description; there is no means of telling whether they are in fact prosogyrate or opisthogyrate.

In external form, this species is unlike any other known from the Lower Oxford Clay, although the ornament is sometimes reminiscent of Pleuromya, and it is just possible that these specimens may be juvenile Pleuromya. However, the early growth stages of both Pleuromya alduini and P. uniformis, as seen from larger specimens, do not fit the outline of anomalodesmatan sp. A., and this possibility seems unlikely. The larger specimens are markedly inequilateral, the posterior region being much more expanded than the rather narrow anterior region, and again, the outline does not agree with small specimens of P. alduini or P. uniformis; there is also no indication of any shell gapes. The only other Lower Oxford Clay species which is in any way comparable is Thracia depressa, which occasionally shows forms similar in shape to this species, and which generally occurs in the same beds, although more rarely. However, in general, the shape of the early growth lines of T. depressa does not fit with the species described here. Some Recent species of Thracia, such as the type species T. pubescens (Pulteney), resemble this species in that they have one end (the anterior) very fully expanded, whilst the other is more rostrate, but it is not clear whether or not anomalodesmatan sp. A. is equivalve; if it is, it cannot be a thraciid. There seems more chance of this species being a juvenile Thracia than a juvenile Pleuromya, but the author

believes both possibilities to be unlikely.

Range and occurrence   Lower Oxford Clay (Calloviense –
Athleta Zones) of central and southern England; very common.

Anomalodesmatan sp. B.   Pl. 26, figs. 2-5, 7-8, 10.

Description   Small species, up to 9.6 mm long,
equivalve, subequilateral, subovate in outline (H 61.7-70.5 %,
$\overline{x}$ 66.7 %), with umbones slightly anterior of median (AL 37.9–
50.0 %, $\overline{x}$ 44.2 %); umbones small, rounded, hardly salient above
the hingeline, prosogyrate. Anterodorsal margin gently concave
to gently convex, forming a continuous even curve with the
anterior margin; ventral margin gently convex, not as curved
as the anterior and posterior margins, and passing smoothly
into them without angulations; posterior margin evenly convex,
curved smoothly with the posterodorsal margin. The most usual
form found is rather elongate, with an almost straight ventral
margin, but smaller forms tend to be shorter and more perfectly
ovate, with a higher L/H ratio. Inflation low.

Ornament very faint, consisting of very fine, irregularly
spaced concentric growth lines, occasionally with faint growth
rugae; no radial elements. The ornament pattern is much
finer than that of the preceding species, and the two species
are further distinguished by virtue of their differences in
outline. Shell material consisting of very thin, friable
aragonite.

Measurements

See Appendix 3.

	L	H	AL
N	12	12	7
$\overline{x}$	7.8 mm	66.7 %	44.2 %
Max	9.6	70.5	50.0
Min	5.6	61.7	37.9
OR	4.0	8.8	12.1

Remarks   Preservation is similar to that of the
preceding species, and again, nothing may be seen of the
ligament, cardinal plate or musculature, making taxonomic
placement impossible. The shell seems to be thinner than in
sp. A., and is rarely preserved, except in patches along the
dorsal margin; removal of the shell in that area does not help
in the elucidation of the structure of the cardinal plate, as
the shell has not been deeply enough impressed into the rock,
and the resulting steinkern shows no detail of the dental region
or musculature.

In external outline, sp. B. has no really distinctive
features, and parallels the shape of many bivalve genera, making
generic placement impossible. This species is much rarer than
sp. A., although it occurs sporadically throughout the Lower
Oxford Clay of southern England, and does not seem to be
associated with any other species of which it could possibly
be a juvenile stage.

Range and occurrence   Lower Oxford Clay (Jason - Athleta Zones)
of central and southern England, widespread, but nowhere abundant.

CHAPTER 3

PALAEOECOLOGY OF A BITUMINOUS SHALE: THE LOWER OXFORD CLAY OF

CENTRAL ENGLAND

Palaeoecological studies on Mesozoic clay sequences are
of great importance in building up an understanding of
environmental conditions, and until the last 10 years, had been
largely ignored. Most thick clay sequences appear at first
glance to be homogeneous masses of rock, but close inspection
reveals many lithological and faunal variations, which when
interpreted, show many interesting features. This is especially
true of bituminous shale sequences, which until the work of
Hallam (1960), were usually thought of as being homogeneous
deposits. Hallam (op. cit.) showed that in the Blue Lias,
several lithologies, each with a characteristic fauna, could be
recognised, only some of them showing the lack of benthonic
fossils thought so typical of bituminous shales. Since then,
many other studies have been made on this type of rock sequence,
to which the Lower Oxford Clay belongs, and it is the purpose
of this paper to show the high variability, in both lithology
and faunal content, that exists within the Lower Oxford Clay.

STRATIGRAPHY

The Callovian deposits of England represent a transgressive
marine phase after the lagoonal and estuarine conditions of the
Bathonian, the base of the transgression being marked by the

Upper Cornbrash, which passes upwards into the Kellaways Clay
and Kellaways Rock. After the deposition of the Kellaways Rock,
conditions appear to have stabilised, with deposition of a thick
argillaceous sequence of bituminous shales, shaly clays and
more calcareous clays. The Yorkshire succession (Text - Fig. 1)
differs in that it is developed in a more marginal facies, and
has been well described by Wright (1968). In this paper, only
the clay facies will be considered in detail. The Lower
Oxford Clay has been defined by Callomon (1968), and occupies
the whole of the Middle Callovian, together with the topmost
subzone of the Lower Callovian and the lowermost part of the
Upper Callovian (Text - Fig. 2). It consists of about 16-25 m
of grey bituminous shaly clays with other minor lithologies
developed within them (Text - Fig. 3). The stratigraphy is
discussed elsewhere (Duff, in prep., and Chapter 2).
Economically, the Lower Oxford Clay is of great importance for
brickmaking, and is extensively quarried between Peterborough
and Aylesbury. Higher parts of the Oxford Clay are more plastic,
less bituminous, and not so easily used for brickmaking;
consequently, exposures are rarer.

The zonal divisions (Text - Fig. 2) have been considered
at length by Callomon on several occasions (1955, 1964, 1968),
and are now widely accepted by most Jurassic stratigraphers.
Previous workers on the Oxford Clay have concerned themselves
mainly with the general stratigraphy of the formation, and paid
scant attention to the Lower Oxford Clay itself (Woodward, 1895;
Morley Davies, 1916; Neaverson, 1925; Arkell, 1933), although

Brinkmann (1929, 1929a) and Callomon (1955, 1968) have dealt
with that part of the formation in considerable detail.
Palaeoecological studies have been few, and are limited to those
of Rutten (1956) and Hudson & Palframan (1969).

NATURE OF THE FAUNA

The composition of the Lower Oxford Clay fauna is considered
in detail elsewhere (Duff, in prep., and Chapter 2), molluscs
being overwhelmingly dominant, and mostly represented by
cephalopods and bivalves. Other characteristic members of the
macrofauna include gastropods, scaphopods, brachiopods,
crustacea, annelids and occasional echinoderms; a diverse and
well preserved vertebrate fauna has been described by several
authors (Duff, op. cit.). A full faunal list of the macro-
invertebrates, showing their distribution, is given in Table 1.
The microfauna is considerably more restricted than that of the
Middle and Upper Oxford Clays, the foraminifera having been
studied by Cordey (1962, 1963, 1963a) and Barnard (1952, 1953),
the ostracodes by Whatley (1966, 1970), and the coccoliths by
Rood, Hay & Barnard (1971) and Rood & Barnard (1972).
Apparently, the darker, more organic rich shaly clays of the
Middle Callovian were less conducive to the development of a
diverse benthonic microfauna than were the more calcareous
clays of the Upper Callovian - Lower Oxfordian.

This paper is based on detailed quantitative studies
made on the Lower Oxford Clay in 1970 - 1971 at 4 brickpits in

central England (Text - Fig. 4), collecting being carried out
on beds of Calloviense - Coronatum Zone age. The beds are
well exposed in continuously accessible profiles, and are
clearly marked off at the base by the sandy Kellaways Rock, and
at the top by a concretionary limestone bed, the Acutistriatum
Band (Text - Fig. 3); this marker horizon was shown by Callomon
(1968) to be the basal bed of the Athleta Zone. The ecological
analysis is based on quantitative data, the palaeoautecology of
the benthos having been described elsewhere (Duff, in prep.,
and Chapter 2), and summarized in Tables 2 and 3. The methods
of analysis used here are a combination of those introduced by
workers on both Recent and fossil faunas, and have not previously
been applied to Mesozoic clay deposits. This creates the draw-
back of there being a lack of comparative data, and in order to
compare the Lower Oxford Clay with other Mesozoic sediments,
especially clays, it has been necessary to use rather more
qualitative data.

Preservation   The Lower Oxford Clay is notable for the
preservation of original shell aragonite in the shales,
especially in the bituminous shales. This is a feature known
from many argillaceous sequences, and seems to be caused by the
impervious nature of the sediment. Aragonite preservation in
the Oxford Clay has been discussed by Hudson & Palframan (1969)
and Duff (in prep., and Chapter 2). However, the fine grain-
size of the sediment has also meant that there was little
resistance to post-depositional compaction, and many of the

fossils are crushed, especially those in which voids unfilled by sediment remained; because of this, most of the ammonites, gastropods, crustacea and articulated bivalve shells have been crushed, often more or less flat.

In some of the more porous lithologies, notably the shell beds, there has been replacement of the original aragonite by secondary calcite, precipitated from calcareous fluids moving through the rock, or by recrystallization of shell material in situ. A more notable post-depositional preservational change has been the growth of pyrite in many of the shell beds, and in local pockets within the shales. It appears that the porous shell beds have acted as "aquifers" along which sulphide-rich fluids moved, and that when the pyrite was precipitated, it became concentrated in the central parts of the shell beds. This is particularly noticeable in many of the Nuculacean shell beds, where the central part of the shell bed is strongly pyritised, with pyritisation decreasing towards the margins. Study of pyritised shells reveals that many of them have had the shell material replaced by pyrite, rather than having had pyrite grow outward from the shell surface.

Within the bituminous shales, many shells have developed pyrite overgrowths to a varying extent. The pyrite is usually rather patchily developed on shells found in the bulk of the bituminous shales, and often seems to be concentrated on aragonitic shells such as Thracia, Pinna and Palaeonucula, where it occurs as small patches on the surfaces of the shells. Hudson & Palframan (1969, p. 404) describe a somewhat similar

situation in the Middle and Upper Oxford Clay of Woodham, Bucks., where pyrite is patchily developed on the surfaces of bivalves preserved as clay moulds. They attribute the pyrite formation to local sulphate reduction by bacteria acting on the organic matrix of the dissolving shell. It is possible that the patchy pyrite developed on aragonitic shells in the Lower Oxford Clay formed in a similar manner, although the aragonite has not totally disappeared.

Another characteristic feature of the Lower Oxford Clay is the presence of concretionary limestones at certain levels (Text - Fig. 3). Hudson (1974, pers. comm.) has demonstrated the existence of two phases of concretion development, one pre- and the other post-compaction, each with distinctive carbon and oxygen isotopic compositions. The early pre-compaction concretions are septarian, and are the ones found within the various Lower Oxford Clay bituminous shales and shell beds (Text - Fig. 3); they contain uncrushed fossils preserved in partially dissolved aragonite or secondary calcite. The later, post-compaction concretions occur as lenticular limestones within the Acutistriatum Band (Text - Fig. 3), and contain crushed fossils, usually preserved in secondary calcite. Both limestones are clearly of diagenetic origin, and contain the same fauna as the enveloping shales.

Methods of analysis   At the four pits studied (Text - Fig. 4), the Lower Oxford Clay is up to 18 m thick, and worked in large opencast pits by means of "walking draglines", giving

sloping faces which may be collected from with ease, and on
which a continuous profile may be measured. As the sections
were measured, detailed counts were made of all the fossils
found in each bed, collection continuing until no new species
appeared in the sample. In the case of beds over 50 cm thick,
each bed was arbitrarily divided into 50 cm units, each of which
was then considered as a separate sample; this gave a method
for evaluating the faunal similarity of different parts of the
thicker units. In addition to these field counts (usually
conducted on up to 2000 specimens), blocks from each sampled
bed were taken back to the laboratory and broken up under more
controlled conditions to check the accuracy of the field counts.
While this sometimes revealed the presence of one or two
additional species (in small quantities), in most cases it
merely confirmed the picture supplied by the field counts, so
the analysis presented here is based on the data collected in
the field.

Measures of the physical properties of the beds were
gained from analyses of the organic carbon and insoluble residue
percentages, which are shown in Table 4 and Text – Fig. 5
respectively. The organic carbon content gives a measure of
the amount of the detrital organic matter available for
collection by feeding organisms, while the insoluble residue
determinations give a measure of the amount of lime present in
the sediment, either as cement or as original particles of shell
or other carbonate. Organic carbon contents of over 3% in
Recent mud deposits have been shown by Bader (1954) to cause a

diminution in bivalve diversity, with infaunal deposit-feeding protobranchs becoming dominant. The organic carbon contents of many of the Lower Oxford Clay samples (Table 4) show that they belong to this type of lithology, with an impoverished benthonic fauna. The degree of correlation between the organic carbon contents of Recent muds and fossil shales is uncertain, and it is not possible to tell whether or not the values obtained from compacted rocks are true reflections of the primary organic carbon content. Comparison of Bader's (op. cit.) values with those from the Lower Oxford Clay suggests that in some cases, they are.

In order to extract the maximum information on bottom conditions from the collected data, most analysis was carried out on the benthonic fauna only, with the nektonic elements (such as the cephalopods) removed from consideration. However, before the nektonic elements were removed, the relative percentages of nektonic predators and scavengers were calculated, showing that in the bituminous shales they constitute 10-15 % of the fauna. Having removed the nektonic elements, the data for the remaining benthos were recalculated to give percentages of epifaunal suspension, infaunal suspension and deposit-feeders only. The bivalves were also treated in this way, these last two groups forming the basis of this work. The reasons for using feeding groups were discussed by Rhoads et al. (1972), who suggested that it is sedimentary and hydrographic conditions which most closely control the distribution of bivalves, with sediment grain-size and texture, bottom turbidity and food

availability all being of importance in determining the spatial
distribution of suspension and deposit-feeding bivalves. The
status and mode of life of bivalve feeding groups in general
have been exhaustively studied by Stanley (1970). The
ecological positions of the various bivalve genera are shown in
Table 2.

The data for the bivalves was then further subdivided,
because of the high proportion of epifaunal suspension-feeders
such as Bositra, Oxytoma, Meleagrinella, Parainoceramus, and
Pteroperna in some beds. As discussed by Duff (in prep., and
Chapter 2), it seems very likely that these genera were not
strictly benthonic, but lived byssally attached to organic
matter at some distance above the seafloor, as there appears to
be a lack of suitable benthonic attachment areas, and the genera
show a marked tendency to occur in clusters. There is also the
possibility that Bositra was pseudoplanktonic (Jefferies &
Minton, 1965). This group of genera is grouped together as
"pendent" epifaunal suspension-feeders, and as they tend to be
rather abundant in the bituminous shales, thereby obscuring the
relative importance of the more strictly benthonic elements, the
bivalve percentages were recalculated to omit them. Consideration
of the whole bivalve assemblage then shows the overall faunal
composition of a bed, the relative abundance of the strictly
benthonic species being seen after the removal of the pendent
species.

Biofacies analysis   In an earlier work, Duff (in prep.,
and Chapter 2) recognised ten biofacies within the Lower
Oxford Clay of the Midlands, the major lithofacies groupings
being subdivided by faunal content; the data are summarized in
Table 5, while Text - Fig. 6 shows the distribution of each of
these facies at the major pits. The data were then analysed in
five ways to give a synthesis of the palaeoecology, the plots
used being

  a)   triangular plots

  b)   rarefaction curves

  c)   trophic nuclei

  d)   trophic group composition

  e)   diversity index

The triangular diagrams are based on bivalve feeding
groups, the corners of the triangles representing 100% epifaunal
suspension-feeders (ES), 100% infaunal suspension-feeders (IS)
and 100% infaunal deposit-feeders (ID). Each sample has both
the total bivalve fauna and the overall benthonic fauna
(excluding pendent genera) divided into these three groups, and
may then be represented on the diagram by a single point. It
can be seen from Text - Figs. 7 and 8 that each biofacies
yields a group of points, all falling within a certain field
of the triangle, with varying degrees of overlap.

The rarefaction curve method was conceived by Sanders
(1968) as a means of comparing the diversities of different
samples of benthonic organisms. He showed that most diversity
measurements were affected by sample size, as individuals are

added to a population at an arithmetic rate, while species are added at a decreasing logarithmic rate. The rarefaction method depends on the shape of the species abundance curve rather than the absolute number of specimens in a sample, and has the advantage that each sample generates a curve. The method of calculating and plotting rarefaction curves is discussed fully by Sanders (op. cit., p. 245), and will not be repeated here. Each aquatic environment was shown by Sanders to have its own characteristic rate of species increment, with its rarefaction curves lying in a particular field (Text – Fig. 9). It is interesting to note that the curves generated by the various Lower Oxford Clay biofacies (Text – Fig. 10) agree closely with those generated by Recent boreal shallow water samples, as Hallam (1969) placed the British area in his Boreal Province during Callovian times. It should, however, be remembered that the Boreal Province of the Jurassic is not necessarily equivalent to the Recent boreal area.

The trophic nucleus of an assemblage or community is defined as the numerically dominant species which make up 80% of the fauna (Neyman, 1967). Analysis of the composition of the trophic nucleus greatly assists in the understanding of the relationships between the various members of the assemblage, notably in the relative abundance of the species, and the importance of deposit-feeders. The trophic nucleus of most communities consists of up to five species, although in some tropical marine environments, high specific diversity greatly increases its size. Two tables showing the composition of the

trophic nuclei are shown here, one (Table 6) showing the overall nucleus of the whole benthonic fauna, whilst the other (Table 7) shows the nucleus after pendent bivalves have been removed. Columns 7-9 of each table show the percentage of the various kinds of deposit-feeders within each biofacies.

As well as determining the size of the trophic nucleus, it is useful to examine the trophic group composition of each biofacies, a technique introduced by Turpaeva (1948), and later refined by the same author in 1949 and 1957. This method of determining the trophic relationships of all the benthonic invertebrates in an assemblage was considered in depth by Walker (1972), who showed it to be a useful method of ecological analysis. Turpaeva's work on the Recent faunas of the Barents Sea revealed several generalisations which apply to most Recent communities, while Walker (op. cit.) showed that they could also be applied to many Lower Palaeozoic communities; the evidence from the Lower Oxford Clay suggests that they are also applicable to Mesozoic assemblages. Turpaeva (op. cit.) showed that

a) each community is dominated by a single trophic group.

b) each of the dominant species in the trophic nucleus belongs to a different trophic group.

c) one species dominates each trophic group in the community.

These generalisations led her to the conclusion that feeding competition is thus minimised. In most cases these

generalisations appear to be valid, although Rhoads et al.
(1972) showed the existence of heterogeneous trophic nuclei,
in which habitat partitioning allows maximum use to be made of
available food resources. In Text - Figs. 11-21, the trophic
groups introduced by Turpaeva are used, as they represent the
simplest and most clearly understood means of presenting the
data. "Swallowers" are infaunal deposit-feeders (Palaeonucula,
Mesosaccella, Dicroloma), which feed by ingesting large
quantities of sediment as they move through it; "collectors"
utilise organic detritus from the sediment surface, the category
including epifaunal deposit-feeders (Procerithium), scavengers
(Mecocheirus, ophiuroids, cephalopods) and browsing herbivores
(Pleurotomaria). "Low-filterers" are low level suspension-
feeders, filtering food from the water immediately above the
seafloor, and comprise Lingula, rhynchonellids, all infaunal
suspension feeding bivalves and some epifaunal bivalves
(Plicatula, Gryphaea, Modiolus), together with Genicularia and
serpulid worms. "High-filterers" are high level suspension-
feeders, collecting food from some distance above the seafloor,
and are represented by the pendent bivalves, together with
Pinna and Chlamys.

Diversity index is a parameter introduced by Ziegler et
al. (1968), and is defined as

$$\frac{\text{number of species}}{\text{log. number of individuals}}$$

giving a relationship between the number of species present in
an assemblage and the number of individuals counted; the

parameter is strongly sample-size controlled, but gives a value which can be directly compared with values for Silurian communities given by Ziegler et al. (op. cit.). Diversity index values are incorporated in Tables 6 and 7.

Palaeoecological assumptions   In common with most other palaeoecological analyses, this one is concerned solely with the skeletonised invertebrates, no account being taken of the soft-bodied fauna, which has left evidence of its existence only in the form of trace fossils. This is a factor well-recognised by palaeoecologists, Johnson (1964, p. 119) showing that about 70% of the animals in a Recent community are soft-bodied. Occasionally, exceptional preservation allows recognition of some of the soft-bodied animals usually lost (Whittington, 1971). Walker (1972) suggested that by study of the abundance and nature of the trace fossils, it should be possible to obtain an estimate of the abundance of the soft-bodied fauna, but this is not a viable proposition in the Lower Oxford Clay, where trace fossils are very rare.

The status of the terms community, assemblage and association has been much discussed in palaeoecological literature, especially by Johnson (1964, 1971), and need not be considered here. The author is of the opinion that it is not justified to use the term community in palaeoecology, and that recurrent quantitative groupings of fossils should be referred to as assemblages. Local assemblages not recurrent over wider areas will be referred to as associations.

Recent quantitative ecological studies are based on the concept of biomass, which is defined as "the weight of organisms per unit area sampled", usually expressed as g/m^2 (Rhoads et al., 1972). As this measurement is based on the overall wieght of both soft parts and skeletal material, it is not applicable to palaeoecological work, and Walker (1972) suggested the use of biovolume as a substitute. This method, however, also has difficulties, especially where there has been crushing of the fossils, and it is not readily applicable to the Oxford Clay assemblages. Simple numerical abundance has been used here, and as long as large enough samples are used, proves convenient. It must be remembered, however, that this method takes no account of biovolume or biomass, and so the bioenergetic relationships between the various species are not accurately represented. The problem is partially overcome by presenting the data as relative size histograms (Text - Figs. 11-21). As is discussed below, palaeoecological analysis is carried out at the generic level.

It has been assumed, at least for the shale facies (and most notably the bituminous shales), that the benthos is more or less indigenous, and that there has been virtually no transport of shells in from elsewhere. The assumption is justified because articulated shells are common, although rarely in life position; there are roughly equivalent numbers of left and right valves in most samples; most bivalve species have rather fragile shells, but few show signs of physically induced breakage; complete articulated skeletons of ophiuroids,

crustacea and vertebrates are not uncommon (Schäfer, 1972, p.
99) shows that the arms of ophiuroids begin to disintegrate
within 15 hours of death, while crustacea are also rapidly
disarticulated). The final point is that there is very little
evidence of current activity preserved in the sediment itself,
as intercalations of coarser particles are extremely rare, and
occur only as very thin films of sediment, whose thickness may
be measured in fractions of a millimetre. There is also no
conspicuous orientation of skeletal remains, and no sign of shell
concentrates (except the shell beds). However, in contrast, the
shells of many infaunal species, especially Thracia depressa,
Pinna mitis and Discomiltha lirata, rest flat on bedding planes,
and so there must have been at least slight winnowing to exhume
these shells from their life positions. Schäfer (op. cit., p.
474) points out that such occurrences indicate the presence of
discontinuities, showing there to have been numerous short
sedimentary pauses within the Lower Oxford Clay, a feature not
immediately apparent on examination of the rocks. Rhoads &
Young (1970) showed that in many Recent shallow shelf mud areas,
the nature of the mud-water interface is substantially controlled
by the activity of deposit feeders, giving an uncompacted fluid
surface consisting mainly of faecal pellets ("seston"), which
is very unstable in the presence of weak bottom currents.
However, as Rhoads (1973) later pointed out, it is only the
uppermost 2-3 cm which becomes resuspended, and it seems unlikely
that this zone of disturbance would be great enough to exhume
such deep burrowers as Thracia and Discomiltha; clearly a

mechanism more powerful than this is required to lay bare the
shells of such deep burrowers.

LOWER OXFORD CLAY ENVIRONMENTS

The Lower Oxford Clay is dominantly a series of dark
bituminous shales, the fauna being characterised by an abundance
of infaunal deposit-feeders (Palaeonucula and Mesosaccella) and
pendent epifaunal suspension-feeders (Bositra, Meleagrinella,
Oxytoma, Parainoceramus and Pteroperna). Although other
epifaunal and infaunal suspension-feeders occur throughout, they
are rarely of numerical importance. In common with other
bituminous shales, such as parts of the Lias, the Lower Oxford
Clay fauna is very well-preserved, with non-solution of
original aragonitic shells, and it seems probable that most of
the skeletonised invertebrate fauna has been preserved. There
are, however, differences between the bituminous shales of the
Lias and the Oxford Clay, benthonic fossils being fairly common
in the Oxford Clay, in direct contrast to the Lias, where the
only common fossils in such lithologies are cephalopods and
fish fragments (Hallam, 1960). This indicates that the bottom
conditions during Lower Oxford Clay times were not anaerobic,
and so the depositional environment must have been rather
different to that prevailing during the deposition of the Lias
bituminous shales described by Hallam. The main characteristic
of the laminated bituminous shales described by Hallam is the
presence of uniform alternations, on a microscopic scale, of

carbonaceous and calcitic-clay laminae, which have remained
undisturbed by burrowing organisms. Thin sections of the
Lower Oxford Clay do not show these laminations, and many
benthonic burrowers are present in the sediment, so it is clear
that bottom conditions in the Middle Callovian were less
anaerobic than those prevailing in the bituminous shales of
the L. Lias. Insofar as it has a fauna dominated by deposit-
feeders and pendent bivalves, the Oxford Clay holds an almost
unique position among British shale facies, as the Lower and
Middle Lias fauna (Hallam, 1960, 1967; Palmer, 1971) has a
much higher proportion of suspension-feeders, and relatively
few deposit-feeders, as do the Kimmeridge Clay and the Gault
(Price, 1879). The only comparable Formation is part of the
Upper Lias (Melville, 1956). In many ways, the bituminous shales
are most closely related to parts of the "dark-gray shale
lithofacies" recognised by Scott (1971) in the Lower Cretaceous
of the United States, in particular his Nuculana-association.
These similarities will be discussed later.

The monotony of the shale sequence within the Lower
Oxford Clay is broken most obviously by the various shell beds
which occur at certain levels, most commonly at the base of a
subzone. Four types of shell bed have been recognised, the fine
distinctions between them being considered below. The most
notable feature of all the types of shell bed is the fact that
they contain the same species as the shales in which the shell
bed occurs, only in much greater abundance; thus Nuculacean
shell beds occur within the deposit-feeder bituminous shales,

while Grammatodon shell beds occur in the Grammatodon-rich
bituminous shales. In the case of all the shell beds occurring
within the clay facies, it seems most likely that they formed
by concentration of shells in situ, due to slow deposition of
sediment rather than by accumulation of shells transported in
from elsewhere. The most telling pieces of evidence supporting
this interpretation are the facts that there is no reason to
suspect marked shallowing of the sea (no oyster concentrations),
the relative proportions of the species are similar to those of
the shales, and the studies of Brinkmann (1929) on the ammonite
fauna. He showed that whilst there was continuous evolution of
shell features during shale deposition, there was a marked
discontinuity produced by the shell beds (Text - Fig. 22),
indicating that a long period of time was represented by the
thin shell beds. This interpretation is supported by the fact
that most of the more important shell beds occur at subzonal
boundaries (Text - Fig. 3). Schäfer (1972) has shown that in
the North Sea, shells are winnowed out of their life position
by weak currents, which may or may not also move them laterally,
and that if current activity at the depositional site is too
small to move the shells, but too great to allow the settlement
of suspended sediment, a bed consisting almost entirely of
shells and shell fragments, with very little interstitial matrix
is formed. This appears to have been the case in the Lower
Oxford Clay.

Despite the general homogeneity of the Lower Oxford Clay,
several different facies may be recognised, characterised by

differences in lithological and faunal associations, as
evidenced by the various ecological parameters; these are
grouped as biofacies associations. In this consideration of
the palaeoecology, analysis was carried out at the generic level,
as most of the Lower Oxford Clay genera are represented by only
one species, and even where there is more than one species per
genus, ecological differences are very small; where two species
belonging to the same genus occur together, niche partitioning
between them is discussed at the relevant point. A full list
of the species present in the Lower Oxford Clay is given in
Table 1. The various biofacies will now be considered.

Silts and silty clays   This alternation of silts and
silty clays occurs within the transition beds from the Kellaways
Rock to the Oxford Clay, and is characterised by a high content
of infaunal and epifaunal suspension-feeders (82% by number of
the overall benthonic fauna), infaunal and epifaunal species
being of about equal importance (Text - Figs. 7a, 7b). Deposit
feeders are of minor importance, epifaunal and infaunal species
being present in about equal quantities (Table 6). The high
diversity of the trophic nucleus (Table 6) is also reflected in
the position of the rarefaction curve for this facies (Text -
Fig. 10), and in conjunction with the data of the trophic group
composition (Text - Fig. 11), shows the domination of this
facies by niche-separated filter-feeders. Removal of the
pendent bivalves from consideration does little to change the
appearance of the faunal characteristics of the facies, as they

are of minor importance. The high aeration of the water, and
presumably rich food supply, allowed the establishment of a
diverse fauna, dominated by infaunal and epifaunal suspension-
feeders, unlike any other seen in the Lower Oxford Clay. The
low organic carbon content (1%) and abundant fauna of trace
fossils (Rhizocorallium and indeterminate burrows, plus a
high level of bioturbation) is further evidence of the high
aeration and stronger current activity, and together with the
small scale cross-bedding, suggests deposition in shallow water,
relatively near shore, a situation postulated by Farrow (1966)
for Rhizocorallium-rich beds in the Bajocian of Yorkshire.

Bituminous shales   This facies is represented by
well-laminated shaly clays with a high organic carbon content
(3.0-4.7 %) and a high insoluble residue content (90 %), and
comprises the bulk of the Lower Oxford Clay of central England.
Three biofacies may be recognised, deposit-feeder bituminous
shales, Grammatodon-rich bituminous shales and foram-rich
bituminous shales, the first two being mutually exclusive, while
the latter is a foram-rich variant of either of the first two.
The trophic nuclei of the three biofacies may be compared from
Tables 6 and 7, the trophic group composition from Text - Figs.
13-16 and the various diversity measurements from Tables 6 and
7. Rarefaction curves (Text - Fig. 10) show how similar the
diversity of each biofacies is, whilst the triangular plots
(Text - Figs. 7c-8a) present the most convincing diagrammatic
arguments for separating the biofacies.

The deposit-feeder bituminous shales occupy the largest part of the Lower Oxford Clay, and can be seen from Text - Fig. 13 to be dominated by pendent bivalves (Bositra and Meleagrinella), the truly benthonic fauna being dominated by deposit-feeders such as Procerithium, Mesosaccella, Dicroloma and Nuculoma, and a few of the more tolerant infaunal suspension-feeders (Corbulomima and Lingula). There is also a wide diversity in numbers of species of infaunal and epifaunal suspension-feeders (23 species, each comprising less than 1% of the fauna), although they are not abundant. Essentially, this biofacies seems to have been the least well-aerated of the bituminous shales, with an impoverished benthonic fauna of tolerant deposit-feeders. The quiet nature of sedimentation, largely undisturbed by the activity of scavengers, is further evidenced by the presence of articulated crustacea and ophiuroids. Niche partitioning is not clearly developed in this biofacies (Text - Fig. 13), with two high level suspension-feeders in positions 1 and 2, and three swallowers in positions 4, 5 and 7. This may be explained by postulating a superabundance of food, which will be dealt with below.

One of the most interesting features of the deposit-feeder bituminous shales is the trophic group composition (Text - Fig. 13), which shows the facies to be dominated by two species of pendent bivalves, Bositra buchii and Meleagrinella braamburiensis. Four of the next five positions in the assemblage are occupied by deposit-feeding bivalves and gastropods, and it is necessary to explain how such a fauna,

utilising essentially the same food source, could survive. The abundance of pendent bivalves occupying the first two trophic positions may be explained by there being a superabundance of suspended food material, which allows two species, of the same trophic group, to coexist without deleterious effects on either. As Rhoads (1973) has demonstrated, suspension-feeders are frequently excluded from assemblages in and on a mud bottom, as the substrate is too unstable, and creates problems of mantle-clogging. If, however, suspension-feeders are placed in racks above the seafloor, but within the zone of greatest turbidity (up to 3 m above the bottom), Rhoads (op. cit.) showed that they would thrive. It is probable that a similar situation prevailed during the deposition of the deposit-feeder bituminous shales, the pendent bivalves being attached to organic material within the zone of maximum turbidity (not necessarily 3 m thick in M. Callovian times), allowing use to be made of the superabundant food source. As regards the truly benthonic fauna of this biofacies, it appears to closely resemble the phenomenon of trophic group amensalism described by Rhoads & Young (1970), in which one trophic group is excluded from a deposit either by nature of the substrate or activity of other members of the fauna. Clearly, the seafloor during deposit-feeder bituminous shale phases of deposition was not suitable for colonisation by byssally attached suspension-feeders, and was dominated instead by deposit-feeders, showing fairly well-developed niche partitioning. Procerithium is thought to have browsed more or less at the surface, on a

probable algal film, while Mesosaccella, Dicroloma and Palaeonucula burrowed through the sediment, ingesting it as they went. The coexistence of these three species again suggests a super-abundance of deposited food material, perhaps combined with a vertical separation of the three species within the sediment. Although Rhoads (1973) showed that in Recent sediments of Buzzards Bay, only 0.5-2.0% of the annual sediment supply of organic detritus on a soft mud bottom was actually deposited permanently, the high organic carbon contents of the deposit-feeder bituminous shales suggests that it is quite possible that transient amounts of organic material were much greater in Middle Callovian times.

Examination of the relevant triangular plots (Text - Figs. 7c-7f) shows that the Grammatodon-rich bituminous shales lie in a different field to the deposit-feeder bituminous shales, and have a considerably lower content of pendent bivalves. The dominant species of this biofacies are deposit-feeders (Procerithium and Mesosaccella, which constitute 57.2% of the fauna), with pendent bivalves being relatively unimportant (Bositra and Meleagrinella only 15.8%). The most characteristic elements of the fauna are infaunal suspension feeding bivalves (Grammatodon, Corbulomima, Thracia, Isocyprina and ?anomalodesmatan sp. A.), which together make up 16.6% of the fauna. Unlike the situation in the deposit-feeder bituminous shale, there is strong evidence for niche partitioning amongst the dominant species (Text - Fig. 15), but as in the deposit-feeder shales, there is a fairly diverse fauna of rare

suspension feeders, 13 species each constituting less than 1% of the fauna.

The foram-rich bituminous shales are a rather unusual biofacies typified by the abundance of foraminifers (Brotzenia) in a normal bituminous shale type sediment. As is apparent from the trophic group composition (Text - Fig. 16), they are usually more closely related to the deposit-feeder bituminous shales, being dominated by pendent bivalves, with deposit-feeders in the next dominance positions. However, they do sometimes fall within the Grammatodon-rich bituminous shales, and form a wide spread on the triangular plot (Text - Fig. 8a). The only way in which they can be distinguished is by the presence of large numbers of foraminifers, which presumably had a rather localised distribution, as they are not confined to any particular stratigraphical level. Hence the foram-rich bituminous shales do not really represent more than a local variation on the main twofold division of the bituminous shales, although they have a slight effect on the macrofauna in that wherever forams occur, scaphopods become very much more common, and it has been shown that many scaphopods feed selectively upon foraminifers (Dinamani, 1963).

Shell beds   Four types of shell bed have been recognised in the Lower Oxford Clay, distinguished by their faunas. The relative diversities of species may be seen from the rarefaction curves (Text - Fig. 10), which shows the low diversity of the Nuculacean shell beds as compared to the relatively higher diversities in the Gryphaea and Grammatodon shell beds. Comparison of the trophic nuclei (Tables 6 and 7), trophic group

composition data (Text - Figs. 12, 17-19) and the triangular
plots (Text - Figs. 8b-8d), graphically shows the differences
in composition of the various shell beds. _Meleagrinella_ shell
beds are not shown on the triangular plots because of the
difficulty of collecting accurate quantitative data, the beds
containing _Meleagrinella_ in such great abundance.

The Nuculacean shell beds show the lowest dominance
diversity (Sanders, 1968) of the shell bed biofacies, having
75% of the fauna consisting of infaunal deposit-feeding
Nuculaceans. The next most abundant genera are _Meleagrinella_
and _Procerithium_ (18.2 %), leaving the remaining 7% of the fauna
distributed between 15 species of infaunal and epifaunal
suspension-feeders. The faunal composition (Text - Fig. 17) is
grossly similar to that of the deposit-feeder bituminous shales,
and there seems little doubt that these shell beds represent
pauses in deposition of normal deposit-feeder bituminous shale.
It is this type of shell bed which is often found at subzonal
boundaries, and frequently contains quantities of wood and bone
fragments, suggesting that it represents a significant pause in
deposition.

Grammatodon shell beds occur within the _Grammatodon_-rich
bituminous shales, and have a very similar trophic group
composition to them (Text - Fig. 18), with deposit-feeders
dominating, pendent species being very subordinate, and infaunal
suspension-feeders such as _Grammatodon_, _Corbulomima_,
Trautscholdia and _Thracia_ being particularly characteristic.
The triangular plots (Text - Figs. 8c, 8d) show the relationship
between this and the preceding biofacies, indicating that there

is some degree of overlap. However, the two biofacies are easily distinguished by both their faunal content, and the lithology in which they occur. Again, this biofacies is thought to be a product of a reduced rate of sedimentation, caused by a slight increase in current activity.

Gryphaea shell beds, like the two preceding types, are restricted to a particular lithology, the transition beds between the Kellaways Rock and the Oxford Clay. They too have a low dominance diversity, with Gryphaea constituting 62.2 % of the fauna (Text - Fig. 12), the remaining 37.8 % being fairly evenly distributed between 12 species of suspension-feeder (28.7 %) and 3 species of deposit-feeder (8.5 %). Amongst the dominant species, there is clear evidence of niche separation, although in general, the biofacies is characterised by suspension-feeders. The high oyster content places the field of this biofacies close to the epifaunal suspension-feeder corner of the triangle (Text - Figs. 8c, 8d). Again, the fauna is similar to that of the beds in which the shell beds occur, and the sediment seems to be another shell concentrate formed more or less in situ. There is, however, some evidence to suggest that the fossils found in this biofacies may have been transported to some extent, as bivalves occur as disarticulated shells rather than articulated shells, many of the valves are fragmented, and there are disproportionate amounts of left and right valves. Added to this the fact that broken cephalopod fragments, reptile bones and fish teeth are fairly common, it seems likely that the Gryphaea shell beds represent a transported

fossil assemblage (Fagerstrom, 1964). Facies associations
(their occurrence in the silts and silty clays), and
consideration of the mode of life of the various faunal elements,
particularly the oysters (Stenzel, 1971), suggest that these
were deposited in shallower water than the bulk of the Lower
Oxford Clay, subject to wave-scouring at times.

Meleagrinella shell beds are largely confined to the
upper part of the Grossouvrei Subzone, where they are inter-
bedded with calcareous clays, and consist overwhelmingly of a
concentration of broken and unbroken specimens of Meleagrinella
braamburiensis. Accurate quantitative counts are very difficult
to make, and consequently the data used in Text - Fig. 19 is
rather less accurate than that of other biofacies. Over 70 %
of the fauna is Meleagrinella, the remainder of the fauna
consisting of well niche-partitioned species occupying several
habitats. An important feature associated with these shell
beds is the fact that most of them are bounded above or below
by burrowed surfaces, where fragments of the overlying bed are
piped down into the bed beneath. Burrowed horizons are very
rare elsewhere in the Lower Oxford Clay (except in the silts),
and it seems probable that they represent phases of very slow
or non-deposition, with increased current activity. The over-
whelming abundance of Meleagrinella almost certainly represents
an original feature, as the shells are too fragile to have
withstood much postmortem transport, and if it did represent a
current-concentrated shell bed, one would expect a much larger
content of larger, heavier shells. To explain the high

Meleagrinella content of these beds and bearing in mind the inferred pendent mode of life of the genus, it seems necessary to invoke the presence of a large amount of floating organic matter to which Meleagrinella may have been attached; the resulting environmental reconstruction presumably bears some resemblance to the Recent Sargassum-dominated environments (Friedrich, 1965). However, this deduction is tentative, as most of the epifauna of Sargassum is soft-bodied, and would leave no traces, and there is no direct evidence for large amounts of floating organic material in the Lower Oxford Clay. The existence of such material, as noted above, is deduced from the presence of abundant thin-shelled byssally-attached Pteriacea and Pectinacea in sediments such as bituminous shales, where the substrate would have been too soft to allow such animals to live on the seafloor.

Blocky claystone.   This unique lithology, known only from the Jason Subzone (Bed 3B) of Calvert, and discussed in detail elsewhere (Duff, in prep., and Chapter 2) has a number of interesting faunal and sedimentological properties. As with the deposit-feeder bituminous shales (within which it occurs), the first two dominance positions are occupied by pendent bivalves (58.4 %), whilst the remainder of the fauna is dominated by an alternation of infaunal-deposit and suspension-feeders, Lingula and Solemya being the characteristic members of the latter group (Text - Fig. 20). The total number of species found is small (only 11), but there is a relatively high dominance

diversity, with only two of the species being represented by less than 1% of the fauna. Lithologically, this is a very distinctive rock type consisting of very light grey, rather plastic non-fissile clay, with a good deal of black organic fragments spread throughout it. Many of the Lingula are preserved upright in life position, a condition not known elsewhere in the Oxford Clay, and suggesting that there was no deep scouring of the seafloor. The overall trophic nucleus (Table 6) is similar in composition to the normal bituminous shales, due mainly to the large content of pendent species, and it is not until these are removed (Table 7) that the unusual nature of the fauna becomes apparent.

Calcareous clays   This facies is restricted to the upper part of the Grossouvrei Subzone, where it forms a regular alternation with the Meleagrinella shell beds, the junctions between the two invariably being burrowed. The main characteristic of the calcareous clays is their high dominance diversity, with 5 species each comprising more than 10 % of the fauna (Text - Fig. 21), and a relatively large trophic nucleus (Table 6). The most abundant species is an infaunal deposit-feeder (Mesosaccella), the next two species being pendent bivalves (Byssentolium and Meleagrinella), which together make up 60.8 % of the fauna. Byssentolium is the most characteristic faunal element of this facies, being known only rarely from other facies; the polychaet worm Genicularia is also typical. Further analysis of the fauna reveals that there is an

approximately equal distribution of deposit and suspension-feeders (Table 6), with most of the suspension-feeders being pendent; infaunal suspension-feeders are not numerically abundant (Text - Fig. 21), and it seems probable that the degree of aeration within the sediment was not great, a situation also apparently characteristic of the more calcareous Middle and Upper Oxford Clays. The low content of infaunal suspension-feeders is also very apparent from the triangular plots (Text - Figs. 8e-8f). The calcareous clays are rather rich in carbonate, and consequently have a low insoluble residue content (74 %), together with a low organic carbon content (1.1 %).

Relations between the biofacies   The overall succession in the Lower Oxford Clay at the major pits examined in the Midlands (Text - Fig. 6) is generally very similar, although there are local variations, especially at Stewartby and Calvert. Superimposed on these local variations in the details of the succession is a marked southward increase in thickness, the Enodatum - Grossouvrei Subzone succession being 12 m thick at Peterborough, and gradually increasing through 14 m at Stewartby, 17 m at Bletchley, to 18 m at Calvert. These thickness changes are likely to be associated with greater distance from the shoreline or a submarine swell, with consequent decrease in the number and thickness of shell beds. This is particularly noticeable in the case of the shell bed which occurs at or just above the base of the Obductum Subzone at Peterborough and Stewartby, the shell bed having disappeared from the Bletchley

section. Study of Text - Fig. 6 also reveals that most of the thickness variation occurs within the Jason and Calloviense Zones, which thicken from 0.5 m at Peterborough to over 3 m at Calvert, suggesting that during the deposition of the initial subzones of the Oxford Clay, conditions were rather more variable, and very much controlled by local configurations of the seafloor. By the time of the Coronatum Zone, conditions appear to have stabilised over the whole of the Midland area, giving a much more uniform thickness of Lower Oxford Clay.

The transition beds between the Kellaways Rock and the Oxford Clay are best developed, and best seen, at Peterborough and Bletchley, where they consist of an alternation of silts and silty clays, Gryphaea shell beds and deposit-feeder bituminous shales. At Peterborough, the transition beds occupy the whole of the Enodatum and Medea Subzones (0.5 m), but at Bletchley are restricted to the Medea Subzone (2.0 m), Kellaways Rock deposition having continued until the top of the Enodatum Subzone. At Stewartby, the transition beds appear to be absent, a bipartite shell bed, the upper part a Grammatodon shell bed and the lower part a Gryphaea shell bed, resting directly on the silts of the Kellaways Rock, which are dated as Enodatum Subzone; deposit-feeder bituminous shales of the Medea Subzone follow directly on from these shell beds. It thus appears that Kellaways Rock deposition ended earlier in the northern parts of the Midlands, Oxford Clay not reaching the south Midlands until the end of Enodatum Subzone times, suggesting that the shoreline lay to the south during this time.

At that time, there then appears to have been rather variable
current activity, phases of shallowing and increased current
activity giving Gryphaea shell beds, whilst in the intermittent
quiet phases, silts or bituminous shales were laid down. The
presence of the bituminous shales indicates that the influence
of the offshore clay facies was becoming more strongly felt at
that time, and that distance from shore, together probably with
water depth, was gradually increasing. The transition beds are
not exposed at Calvert, the pit ending in the Jason Subzone,
although Callomon (1968, p. 287) records 10 feet of combined
Medea and Enodatum Subzones in a borehole there.

Gradual recession of the shoreline throughout the period
of deposition of the transition beds eventually allowed the
establishment of quiet water conditions in which bituminous
shales were laid down. At Peterborough, Bletchley and Calvert,
this phase seems to have begun more or less at the start of
Jason Subzone times, while at Stewartby, similar conditions
became established slightly earlier. At all the pits, the
lowermost few cm of the shales are markedly fossiliferous, and
contain the same species as the underlying shell beds, indicating
the gradual dying out of the fauna of the preceding bed. There
then followed a thick sequence of dominantly deposit-feeder
bituminous shales, which occupy the whole of Jason and Obductum
Subzone time at Peterborough, Bletchley and Calvert, with the
exception of the 1m band of blocky claystone near the base at
Calvert. During this time, bottom conditions were very quiet,
and water circulation was rather poor, producing an impoverished

benthonic fauna dominated by deposit-feeding bivalves and gastropods, with benthonic suspension-feeders being rare. Living above the bottom, attached to postulated organic material, were large numbers of pendent epifaunal suspension-feeding bivalves, dominated by _Bositra_, _Meleagrinella_ and _Oxytoma_. The suspension-feeder dominated nature of the fauna is unusual, and almost certainly caused by a superabundance of the suspended food source, as discussed above.

The general sequence seen in the Lower Oxford Clay of the Midlands, Kellaways Rock through transition beds to bituminous shales and then to more fossiliferous shales, adds substance to the suggestion of Hallam (1967a) that bituminous shales are often laid down in relatively shallow water. Hallam suggested that near the base of transgressive sequences, widespread bituminous shale deposition was characteristic, and that it was followed by more fossiliferous, deeper-water clays and shales, laid down as water circulation improved, and sediment oxygenation increased. The Kellaways Beds – Upper Oxford Clay sequence agrees well with this model, the bulk of the Lower Oxford Clay representing the bituminous shale part of the cycle.

The presence of the 1m band of blocky claystone near the base of the Jason Subzone at Calvert indicates that environmental conditions were slightly different in that area during much of the Jason Subzone times, as the _Lingula_-rich nature of the blocky claystone fauna continues for much of the remainder of the subzone. Both _Lingula_ and _Solemya_ have been considered by previous authors to be genera tolerant of poorly-aerated water

conditions, and this, together with the low organic carbon content, the increased thickness, and reduced benthonic fauna, suggests that in the south Midlands area, this part of the sequence was laid down more rapidly than the deposit-feeder bituminous shales, possibly in slightly deeper water.

At Stewartby, the Obductum Subzone sequence is completely different to that seen at any of the other pits, a thin development of deposit-feeder bituminous shale, containing two very well-developed Nuculacean shell beds, being followed by a very thick Meleagrinella shell bed and a development of foram-rich bituminous shale. The combination of the two Nuculacean shell beds, being followed by a very thick Meleagrinella shell bed, suggests that current activity in this area must have been greatly increased at this time, probably on a local swell. The foram-rich bituminous shale above the Meleagrinella shell bed shows a return to quieter, deeper-water conditions, with well-developed niche partitioning within the benthonic fauna.

Throughout the Midlands, the end of the Obductum Subzone is marked by a widespread phase of slow deposition, marked by Nuculacean or Grammatodon shell beds. Brinkmann (1929) showed that at Peterborough, the shell bed at the top of the Obductum Subzone represents a significant pause in sedimentation (Text - Fig. 22), and it seems likely that a similar situation prevailed over much of the Midlands. This phase of condensed deposition is followed at all the pits by a similar succession in the Grossouvrei Subzone, and so it will be considered in rather general terms. The well-aerated conditions existing during the

deposition of the Nuculacean and Grammatodon shell beds persisted
into the next phase of bituminous shale deposition, giving a
sequence of Grammatodon-rich bituminous shales, rich in infaunal
suspension-feeders such as Grammatodon, Isocyprina and Thracia.
There appears to have been some stratigraphical control
operating at this time, as the start of the Grossouvrei Subzone
sees the first appearance in the Oxford Clay of Grammatodon
minima, and also marks the arrival of abundant Isocyprina. This
event can be recognised at the same level in Dorset, and is
extremely useful for defining the base of the Grossouvrei
Subzone. Phases of increased current activity during this time
are marked by Grammatodon shell beds. As subsidence continued,
and oxygenation of the water gradually decreased, the Grammatodon-
rich bituminous shales were replaced by foram-rich bituminous
shales, in which deposit-feeders became more abundant at the
expense of infaunal suspension-feeders, although conditions
such as those prevailing in the deposit-feeder bituminous
shales never became re-established.

Later in Grossouvrei Subzone times, there was a renewed
phase of shallowing, producing the very characteristic
alternation of calcareous clays and Meleagrinella shell beds,
which bring the Middle Callovian to a close in southern England.
As suggested above, this sequence must have been characterised
by periodic explosions in colonisation by organic matter,
allowing dense Meleagrinella shell beds to accumulate, and
producing many small non-sequences. Aeration in the calcareous
clays must have been relatively good, as they supported a

diverse fauna of suspension-feeders, and there is a sudden
increase in the abundance of tube building annelid worms.
Grossouvrei Subzone deposition was concluded over the whole
area by a thick Nuculacean shell bed - the Comptoni Bed - which
again represents a phase of greatly increased current activity,
and a long pause in sedimentation (Text - Fig. 22). This part
of the sequence is usually capped by a concretionary diagenetic
limestone, the Acutistriatum Band, which is developed within a
band of very bituminous foram-rich shaly clay, and which
represents the basal bed of the Athleta Zone.

Thus within a relatively thin sequence of Lower Oxford
Clay (12-18 m), occupying just over two ammonite zones, there are
two cycles of environmental conditions. Firstly there is the
deepening sequence from the Kellaways Rock through the transition
beds into the deposit-feeder bituminous shales of the Jason –
Obductum Subzones, with indications of shallowing towards the
top, and then the more balanced cycle of the Grossouvrei Subzone,
which shows distinct deepening and shallowing phases, ending
with a pronounced non-sequence.

COMPARISONS WITH OTHER FACIES

In view of the lack of comparable quantitative data from
other similar environments, comparisons must be limited to
rather more qualitative observations, largely gleaned from the
literature. In particular, the work of Melville (1956), Hallam
(1960, 1967), Palmer (1966, 1966a, 1973) and Sellwood (1972) on

the Lias, Hudson & Palframan (1969) on the Middle and Upper
Oxford Clay, Price (1879) on the Gault, and Scott (1970) on
the Lower Cretaceous of the United States, has been used for
comparison of clay faunas, and shows the Lower Oxford Clay to
be unusual because of its very high content of pendent epifaunal
suspension-feeders and infaunal deposit-feeders. With the
exception of the work of Scott (op. cit.), no quantitative data
was given, fossils merely being recorded, or being said to be
rare, common or occur, and thus comparison is sometimes difficult.

There is also the problem of the relative importance of
evolutionary and environmental considerations when the
palaeoecology of rocks of different ages is being compared.
However, in the rocks under consideration here, which are mostly
of Jurassic age, the importance of evolutionary changes appears
to be minor, as there is very little change in the overall
composition of the fauna, although there is much variation in
the relative importance of different species within it. It is
well-known that protobranch bivalves are a notably slowly-
evolving group, so evolutionary effects in this protobranch-
dominated assemblage are likely to have been negligible. In
general terms, it appears to be environmental conditions which
have exercised the greater control over benthonic assemblages
during Jurassic and Lower Cretaceous times. The importance of
evolutionary changes will be considered in the next section.

The shales of the Oxford Clay have most frequently been
compared with those of the Lias, but study of the published
data on Lias faunas tends to emphasise differences between the

two deposits. Hallam (1960) described the bituminous shales
of the Blue Lias of Dorset and Glamorgan, and showed them to
have a very high organic carbon content (3.9-8.0 %), and a
fauna consisting almost entirely of ammonites, fish scales
and bivalve spat, indicating that bottom conditions must have
been anaerobic, allowing no benthonic fauna to become
established. Most of the fossils are preserved in the marls
and limestone bands, which Hallam (op. cit.) showed to be
essentially of primary origin, although he later (1964) amended
his views, but similarities with the Lower Oxford Clay are
negligible, as in the Lias limestones there is a rich and varied
fauna of normal infaunal and epifaunal suspension-feeders, while
deposit-feeders and pendent bivalves are rare. It thus seems
very likely that the limestone part of the Blue Lias rhythm
was considerably better-aerated than the Lower Oxford Clay, as
it contains a much more varied fauna, including gastropods,
brachiopods and echinoderms.

The work of Sellwood (1972) on the Sinemurian-Pliensbachian
Lias of England gives similar results to those of Hallam (1960)
insofar as the fauna is dominated by infaunal and epifaunal
suspension-feeders, with few deposit-feeders. Rocks of this
age over most of Britain are clearly less bituminous and more
well-aerated than the bituminous shales of the Blue Lias, and
contain many genera which are also characteristic of the Lower
Oxford Clay, but again there is a lack of abundant pendent
bivalves and deposit-feeders. The same is true of the Middle
and Lower Lias described by Melville (1956) from the Stowell

Park borehole in Gloucestershire, pendent bivalves and deposit-feeders again not being abundant, the fauna being dominated by infaunal and epifaunal suspension-feeders. Palmer's (1973) work on the upper parts of the Lower Lias in Gloucestershire shows a faunal list rather similar to that of the Lower Oxford Clay, but yet again, pendent bivalves and deposit-feeders are neither abundant nor widespread. Work on parts of the Middle Lias (Palmer, 1966, 1966a; Hallam, 1967) shows similar conditions to have prevailed during deposition of the more sandy shales being laid down at that time.

The Upper Lias (Melville, 1956; Hallam, 1967) of Britain is probably the most similar deposit to the Lower Oxford Clay, consisting of dark shales and shaly clays with a sparse benthonic bivalve fauna, dominated by deposit-feeding Nuculaceans such as Nuculana and "Nucula", often with a pendent bivalve fauna of Bositra radiata and Inoceramus dubius. These shales, which are also particularly rich in cephalopods and Procerithium, often contain local concentrations of comminuted fish debris, insect remains and crustacea, emphasising the similarity with the bituminous shales of the Lower Oxford Clay. Quantitative work on the fauna of the Upper Lias shales would be of great interest for the making of detailed comparisons with the Oxford Clay.

Hudson & Palframan (1969) have described the palaeoecology of part of the Middle-Upper Oxford Clay of the Midlands, and shown that there are clear differences between the fauna of this part of the Oxford Clay, and the Lower Oxford Clay. The dark grey, well-laminated bituminous shales have been

replaced by light grey, rather calcareous clays, often rich in fossils preserved as pyritic internal moulds, with no preserved aragonite. The Spinosum Clays (Athleta - Lamberti Zones) have a sparse benthonic fauna, dominated by shallow infaunal species (mostly deposit-feeders), with the epifauna characteristically rich in Chlamys and Gryphaea; other Pectinacea are locally common. Near the top, Gryphaea beds appear, alternating with the normal clay facies, and having, in addition to the abundant Gryphaea lituola, suspension-feeders dominating over deposit-feeders. However, these Gryphaea beds are not equivalent to those of the Lower Oxford Clay, as they merely consist of a concentration of oysters (estimated at 4 per square foot) in slightly harder and more calcareous clay, and do not represent phases of non-deposition, although there must have been some slowing of sedimentation. The rest of the Spinosum Clays make up a sequence of quiet water muds, similar to, but not equivalent to the bituminous shales of the Lower Oxford Clay. The faunal density is also by no means as great as in the Lower Oxford Clay, and there are none of the abundant Bositra, Meleagrinella or Oxytoma so typical of the Middle Callovian. The abundance of Astarte s.l. in the Spinosum Clays suggests that the bottom sediments must have been fairly well-aerated.

The Mariae Clays (Mariae Zone) are darker and more organic-rich than the Spinosum Clays, and have a different faunal composition. The benthonic fauna is much reduced in variety, and is almost entirely infaunal, with Dicroloma, Procerithium and Nuculacea being abundant, and Pinna being the

only common suspension-feeder. This part of the Upper Oxford Clay is much more similar to the Lower Oxford Clay in faunal content, although the presence of pyritic ammonites is a notable difference, and the shales are not well-laminated. It seems likely, however, that during at least part of the Mariae Zone, conditions were somewhat similar to those of the Lower Oxford Clay.

The fauna of the Gault Clay (Cretaceous, Albian) has been summarised by Casey (1966), but a more comprehensive faunal list was given by Price (1879), who charted the distribution of the bivalve fauna. Price recognised 86 bivalve species in the English Gault, 14 of which are deposit-feeders, almost all being species of "Nucula". In spite of this apparently high diversity of deposit-feeding protobranchs, they are not as abundant as they are in the Lower Oxford Clay, nor are there so many siphonate forms. There are, however, large swarms of Inoceramus throughout the Gault, and so in this respect, there are close similarities with the L. Oxford Clay. The main difference is in the much greater diversity of infaunal and epifaunal suspension-feeders, especially deep burrowers. The Gault has long been divided into two lithological parts, the Upper Gault consisting of light coloured rather calcareous clay, while the Lower Gault is much darker, less calcareous, and is generally more similar to the Lower Oxford Clay, although it is not bituminous. Casey (1966) records Inoceramus and Nuculacea (Nucula spp., Acila and Mesosaccella) as the most abundant bivalves of the L. Gault, with infaunal suspension-feeders

becoming more abundant in the Upper Gault. Most of the molluscs preserved in the Lower Gault retain the original unaltered aragonite of their shells, although the cephalopods in particular, as well as some of the bivalves and gastropods, are usually pyritised. As in the Lower Oxford Clay, preservation of aragonite is related to the very impervious nature of the sediment.

Scott (1970) has described the palaeontology and palaeo-ecology of the Kiowa Formation (L. Cretaceous, Aptian – Cenomanian) of Kansas, and recognised six lithofacies groupings, of which one, the dark-gray shale lithofacies, is comparable with the Lower Oxford Clay. It is a dark grey, fissile, well-laminated shale, with a general lack of small-scale sedimentary structures, and Scott believes the fossil assemblages to represent "disturbed neighbourhood" and mixed fossil assemblages. This lithofacies is characterised by the Nuculana association, dominated by Nuculana, Yoldia, Nucula, (nuculaceans), Breviarca (Arcacea), Pholadomya, Turritella, Drepanocheilus and Lingula, which constitute 18-84 % of the fauna; most of the remainder of the fauna is composed of a corbulid.

The other comparable lithofacies recognised by Scott is his shell conglomerate facies, which corresponds closely to the Gryphaea shell beds of the Lower Oxford Clay. Points of similarity are many, and include the high content of Gryphaea (51-100 %), the common occurrence of calcitic shells, and the laterally discontinuous nature of the shell beds. There are, however, some sedimentary structures present which suggest that

the Kiowa shell conglomerates were deposited in very shallow water, possibly by storm-generated currents, and there is no direct evidence that this is the case for the Lower Oxford Clay Gryphaea shell beds.

Evolutionary changes - comparison with Palaeozoic and Recent assemblages   Deposit-feeder dominated assemblages are known from many argillaceous deposits, from the Ordovician to the present day. In general trophic composition, the assemblages are clearly similar, but marked evolutionary changes have altered the structure of the younger ones, showing the importance of evolutionary changes over a long period of time. The main changes are in the composition of the suspension-feeding part of the fauna since the Lower Palaeozoic, bivalves having taken the place of the articulate brachiopods, as a result of the development of mantle fusion and siphon formation (Stanley, 1968). The suspension-feeder groups present in the Lower Palaeozoic have also been replaced by more highly-evolved superfamilies, leaving only the slowly-evolving deposit-feeding Nuculoida as a conservative stock. Most Recent deposit-feeder dominated mud assemblages are characterised by a high content of soft-bodied polychaets, but as noted above, the importance of such animals in fossil assemblages is virtually impossible to assess.

The most similar assemblages to those of the Lower Oxford Clay are the various Lingula "communities" described from the British and American Palaeozoic (Bretsky, 1970; Ziegler et al.,

1968; Craig, 1955). The data for these communities have been
replotted by Walker (1972) to show the trophic structure of
the assemblages, and it is clearly apparent that both the
Ordovician and the Lower Carboniferous Lingula assemblages
(described by Bretsky and Craig respectively), are dominated by
deposit-feeders, and show well-developed niche partitioning.
As in parts of the deposit-feeder bituminous shale biofacies,
Lingula is an important constituent of the fauna, and occupies
second place in the assemblage; the dominant species in both
these Lower Palaeozoic assemblages is an infaunal nuculoid. In
the Ordovician Lingula community described by Bretsky (op. cit.),
3rd and 5th places are occupied by archaeogastropods, which
functioned as epifaunal browsing herbivores. These elements
are absent from the equivalent Mesozoic assemblages. Similar
archaeogastropod-rich assemblages are known from the Devonian
of New York (the Bellerophon community of Bowen et al., 1974),
with bellerophontid gastropods occupying niche 1, and two
infaunal deposit-feeding nuculoids in positions 2 and 3. Other
minor elements of the fauna are shallow infaunal and epifaunal
suspension-feeding bivalves, and articulate brachiopods.

Ziegler et al. (1968) have described several "communities"
from the Silurian of the Welsh borderlands, the Lingula community
being particularly relevant here. The commonest species is an
epifaunal suspension-feeding brachiopod (Camarotoechia), with
Lingula and Palaeoneilo (a nuculanid) occupying the next two
positions; the epifaunal pterioid Pteronitella is also
characteristic. This assemblage has a low diversity (Diversity

Index 6.2), but shows a wide range of feeding types, although
it differs from the other Palaeozoic Lingula associations in
having a high content of filter-feeders; Walker (1972) has
suggested that perhaps this is not a true example of the Lingula
assemblage, which he recognises as existing, more or less
unchanged, from the Ordovician to the Permian. This particular
Lingula community is usually developed in a more marginal
facies, consisting mainly of sandstones, and so epifaunal
suspension-feeders, such as Camarotoechia, are most abundant.
The main point here is that Lingula communities may be of
varying type, and developed in several lithologies; only shale
occurrences are of relevance here. The Diversity Index value
for Ziegler's Lingula community (6.2) agrees well with the
values from the Lower Oxford Clay (5.9-6.7 in the bituminous
shales), although the other brachiopod-dominated Silurian
communities have much higher diversities (DI 7.8-11.8), due to
their low dominance diversity.

In general terms, there are close similarities between
Palaeozoic and Mesozoic deposit-feeder dominated assemblages,
most notably in the abundance of infaunal deposit-feeding
bivalves and infaunal suspension-feeding Lingula. Insofar as
the Nuculoida have not evolved markedly since the Lower Palaeozoic,
there are close parallels at the superfamily or even family
level between Palaeozoic and Mesozoic assemblages, the greatest
differences being in the composition of the suspension-feeding
part of the fauna. In the Mesozoic, many of the niches
originally occupied by the brachopods have been largely taken

over by the bivalves, many of the new superfamilies still being extant. One of the major differences between the Lower Oxford Clay and the Palaeozoic assemblages just discussed, is the lack of a rich fauna of pendent epifaunal suspension-feeding bivalves, although they occur sporadically in some of the assemblages (i.e. the _Posidonia_ band of Craig, 1955).

Recent offshore soft mud communities have been described by many authors, and are broadly comparable with the Lower Oxford Clay assemblages, although there are several conspicuous differences. The silt-clay facies occupying the central axis of Buzzards Bay (Massachusetts) has been studied by Sanders (1960), Rhoads & Young (1970) and Rhoads (1973), and shown to be dominated by deposit-feeders, both infaunal and epifaunal. Sanders (op. cit.) identified the fauna as belonging to the _Nucula proxima_ - _Nephthys incisa_ community, with these two species (the latter a polychaet) making up 76 % by number of the specimens collected. Five other species are represented by over 1% of the fauna (2 polychaets, a crustacean, an opisthobranch gastropod and a suspension-feeding bivalve) and 95 % of the fauna is accounted for by only 11 species; there is a very varied accessory fauna, with 68 species making up the last 5% of the fauna. The trophic nucleus consists of 3 deposit-feeders, _Nucula proxima_ being the most abundant, and suspension-feeders are of very minor importance; no pendent epifaunal suspension-feeding bivalves are known. The same is true of other offshore mud communities (Jones, 1950, 1951), which are usually dominated by deposit-feeding protobranchs and

polychaets, usually with a conspicuous associated fauna of infaunal suspension-feeding bivalves. In this respect, the similarities with the various Lower Oxford Clay biofacies are many when the strictly benthonic fauna alone is considered, but again, there is a noticeable lack of pendent suspension-feeders. The only known Recent assemblage with a high content of pendent epifaunal species is that found on _Sargassum_ weed (Friedrich, 1965), but molluscs are not of great importance, only 5 species having been described from this habitat. Stanley (1970) has recorded the fact that many Recent species of _Pteria_ attach preferentially to alcyonarian sea-whips, a method of obtaining stable fixation in a very agitated environment. Recent parallels for the mode of life postulated for the Oxford Clay pendent bivalves are not known, and this may be accounted for by evolutionary effects. Alcyonarians did not appear until the Jurassic, and gorgonaceans until the Cretaceous (Stanley, 1972), so it is possible that the lack of abundant rooted organic material during the Jurassic led to the colonisation of floating or rooted organic material (including algae) by species that needed to live above, rather than on, a soft mud substrate. In this context it is easy to see that the Lower Oxford Clay bituminous shale assemblages were both differently structured, and occupied slightly different environments, to Palaeozoic and Recent offshore mud assemblages, a consequence of evolutionary, rather than environmental changes.

CONCLUSIONS

Hallam (1967a) suggested that bituminous shales were relatively shallow-water deposits laid down in quiet, but not invariably stagnant water, below wave base, in contrast to the deep-water "barred basin" model postulated by many earlier authors. The evidence supplied by the Oxford Clay appears to support this hypothesis, as it clearly represents a deepening sequence, from the sands and silts of the Kellaways Rock, through the laminated bituminous shales of the Lower Oxford Clay into the more massive calcareous clays of the Middle - Upper Oxford Clay; the many small scale alternations of lithology within the Lower Oxford Clay are indicative of relatively shallow-water deposition, where a slight change in water depth could have a marked effect on hydrographic conditions.

Faunally, bituminous shale sequences show variability through time, with Palaeozoic black shales being either completely lacking in benthonic elements (the graptoloitic shales), or with a benthonic fauna dominated by deposit-feeding nuculoids and suspension-feeding linguloids. At various times, pendent or benthonic byssally-attached bivalves were fairly common, but were never as important as in the Mesozoic. In the European Jurassic, bituminous shales are particularly important in the L. Hettangian, L. Toarcian and the M. Callovian, and all tend to show a fauna consisting mainly of nuculoids and pendent bivalves. Recent organic-rich mud communities appear to have rather more infaunal suspension-feeders, and no pendent bivalves, but again,

nuculoids are numerically dominant. The role of the infaunal deposit-feeding protobranchs seems to have persisted more or less unchanged since the Lower Palaeozoic, their mode of life (inhabiting quiet water muds in areas of environmental stability) meaning that there has been little need of adaptive change. The replacement of brachiopods by bivalves as the dominant members of the epifauna after the Palaeozoic is a function of mantle fusion and siphon formation in the Bivalvia, and marks the main change in the composition of the faunas of organic-rich shales since the Palaeozoic.

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CHAPTER 4

SUMMARY OF CONCLUSIONS

From the detailed work on the bivalve taxonomy and palaeoecology of the Lower Oxford Clay of southern England, the following conclusions may be drawn.

1) The detailed stratigraphy of the Lower Oxford Clay, as described by Callomon (1968) has been confirmed, as broadly speaking, the divisions recognised by Callomon have been identified and described by the author (Fig. 2.3 and Appendix 1). The lithological details given by Callomon (op. cit.) are mostly confined to elucidation of the subzonal stratigraphy, and recording the ranges of most of the ammonite species. Exhaustive collecting by the author at the four L.B.C. quarries has added to this basic store of information by giving the range and occurrence of all the bivalve species, together with all the other invertebrate species collected. In only one case, that of the Obductum – Grossouvrei subzonal boundary at Stewartby, has it been necessary to amend Callomon's zonal scheme, with the placing of the boundary at the level of Callomon's bed 9. This conclusion is based on the first appearance of abundant Grammatodon minima, a character proved at the other pits to be diagnostic of the base of the Grossouvrei Subzone; Callomon was unable to split the Coronatum Zone by using ammonites.

2) Ten different biofacies types, broadly based on a combination of bivalves and lithology have been recognised at the four major quarries, and their faunal content, lithological

characters and distribution considered in sections 2.3.3,
2.3.4 and Chapter 3.

3)   The palaeoautecology of each of the 33 bivalve
genera described from the Lower Oxford Clay has been considered
in detail, together with general remarks on the feeding group
classification so widely used in modern palaeoecological work.
The nature and inferred palaeoautecology of the non-bivalve
part of the fauna has been described in section 2.4.4, the first
exhaustive treatment of the ecology of the whole of the Lower
Oxford Clay fauna. The nature of the fauna has also been
considered in Chapter 3.

4)   Two new morphological terms, to be applied to various
bivalve groups, have been introduced: pseudolunule (in
Rollierella minima) and commissural platform (in Gryphaea
dilobotes). These terms are defined in the description and
remarks sections of the systematic descriptions. Several
measurement parameters, such as length of the straight hinge
line (Lh), degree of obliquity (angle θ), oblique length (OL),
escutcheon length (LE), length of the area (LA), escutcheon
width (EW) and number of tubercle rows (TR) are defined in
section 2.5, and widely used in the description of the various
bivalve species. An arbitrary decision as to the meaning of
the terms small, medium and large-sized, as applicable to Lower
Oxford Clay bivalves, has been made as follows: small, up to
10 mm long; medium, 11-30 mm; large, over 31 mm.

Several simple statistical terms are used in Appendix 3
to characterise the degree of variation within each species;

these are shown and defined in section 2.5.3.

5)   Four main preservation types have been recognised in the Lower Oxford Clay (section 2.6), the preservation type often determining how much detail may be seen on any particular shell. The major types are: a) preservation as primary shell material, either calcite or aragonite; b) preservation as primary shell with pyrite overgrowths, usually only on shells with nacreous aragonite; c) primary shell with calcite over-growths, on shells which were either calcite or aragonite; and d) complete replacement of the shell material by pyrite. There are occasional examples of originally aragonitic shell material (the shell of the ammonite *Erymnoceras*) which has been completely replaced by sparry calcite; this type is, however, rare. As mentioned in section 2.6, the degree of crushing is dependent on whether the specimen in question is preserved as an articulated shell, or as a disarticulated valve.

6)   In the systematic descriptions of the bivalve fauna (Chapter 2), 48 species, 7 of which are new, are described monographically, and one new genus, *Byssentolium*, with its type species *B. hudsoni* sp. nov., is erected; it is distinguished from *Entolium* s.s. by the presence of a persistent byssal notch throughout its life. One subgenus, *Trautscholdia* Cox & Arkell, has been elevated to full generic rank, on the basis of dental characters. Two well-known Upper Jurassic bivalve species are placed in different genera, a decision based on study of their internal characters; *Lucina lirata* Phillips is placed in *Discomiltha*, and *Anisocardia minima* (J. Sowerby) in *Rollierella*.

The well-known oyster species _Gryphaea bilobata_ J. de C. Sowerby, selected by Stenzel (1971) as the type species of his new subgenus _Bilobissa_, has had the nomenclatorial problems surrounding it elucidated, and it is proven that the holotype of _G. bilobata_ come from the Inferior Oolite, not the Kellaways Rock, and is a different species to the Callovian one; hence it has proved necessary to introduce a new name for the Callovian _Gryphaea_, _Gryphaea (Bilobissa) dilobotes_ nom. nov.

7) Five parameters aiding the understanding of the palaeosynecology of the Lower Oxford Clay are defined in Chapter 3: triangular plots, rarefaction curves, trophic nuclei, trophic group composition and diversity index. After definition, the advantages and disadvantages of each method are discussed, and the ten biofacies previously defined in Chapter 2 are then considered using these five parameters. It may be seen from the relevant figures (Table 5; Figs. 7a-8f; Fig. 10; Tables 5, 6; Figs. 11-21) that each biofacies has characteristics of its own which enable it to be easily recognised using these parameters, which are thereby proved to be valid indicators of palaeosynecology in this case.

8) Using these parameters, together with lithological and faunal characteristics, the environmental history of the Middle Callovian stage in central England has been elucidated. The whole sequence seems to agree with Hallam's (1967a) hypothesis of bituminous shales being typical of deepening water in the early stages of a major marine transgression, as the Lower Oxford Clay bituminous shales follow shallow-water silts

and sandstones, and are followed by more massive, plastic clays, with very poor lamination. Throughout central England, the Jason Zone and Obductum Subzone sequences show a general thickening when traced southwards, showing that deposition was more continuous in the south, with fewer phases of reduced sedimentation; this evidence is strengthened by the presence of marginal deposits of M. Callovian age in Yorkshire (Wright, 1968), indicating that the shoreline during this time lay to the north. The sequence up as far as the top of the Obductum Subzone shows what appears to be a deepening-water phase, from the silts and sands of the Kellaways Rock beneath, through into laminated bituminous shales; there seems also to have been a slight shallowing phase towards the end of the Obductum Subzone, as the subzone is capped by a well-developed Nuculacean or Grammatodon-rich shell bed at all the quarries, formed during a period of increased current activity and winnowing, almost certainly in fairly shallow water. Within the four quarries studied there are minor variations in both lithology and biofacies, showing there to have been local variation in environmental conditions, although the overall conditions seem to have been relatively stable.

The onset of the Grossouvrei Subzone heralded a greater uniformity of environmental conditions over the whole of central England, as the same sequence of biofacies may be recognised at all the quarries. Suspension-feeder bituminous shales start the sequence, and are followed by laminated foram-rich bituminous shales, and an alternation of calcareous clays and Meleagrinella

shell beds, the subzone being concluded by another well-developed
Nuculacean shell bed. This sequence is interpreted as showing
an initial deepening phase, from Grammatodon-rich shell beds,
through suspension-feeder bituminous shales, into foram-rich
bituminous shales, being followed by a shallowing phase, with
the alternation of calcareous clays and Meleagrinella shell beds,
and the capping Nuculacean shell bed.

Thus within the 18 m of Lower Oxford Clay present in the
Midlands, two cycles of environmental conditions may be recognised,
each one showing deepening and then shallowing of the water.

9)   Comparison with other British Jurassic Clay
Formations reveals that the Lower Oxford Clay is an unusual
deposit, with a fauna dominated by epifaunal 'pendent' suspension-
feeders and infaunal deposit-feeding Nuculaceans. The only truly
comparable sequence is the Upper Lias described by Melville
(1956) from the Stowell Park borehole in Gloucestershire, where
dark bituminous shales have a fauna dominated by Nuculacea and
the 'pendent' suspension feeders Bositra radiata and Inoceramus
dubius, together with Procerithium; this particular fauna seems
to be characteristic of much of the Upper Lias of Britain, and
also of Europe, as the Toarcian stage marked another major
marine transgression (Hallam, 1967a). Other parts of the Lias,
the Middle and Upper Oxford Clay, the Gault, and parts of the
Lower Cretaceous of the U.S.A., in which there are thick clay or
shale sequences, do not show faunas of this kind, and so cannot
be considered as ecologically equivalent to the Lower Oxford Clay.

10)   The composition of assemblages dominated by mud-dwelling deposit-feeders from the Lower Palaeozoic to the Recent has been considered, and it is clearly apparent that although the same ecological niches may be recognised, they are occupied by different groups of animals. Study of Recent offshore soft mud communities has shown that these communities are usually dominated by infaunal and epifaunal deposit-feeders, with polychaet worms being of great importance (often constituting 75% of the fauna); as noted in the early part of Chapter 3, the abundance of soft-bodied invertebrates in fossil sediments is virtually impossible to assess.

In the Palaeozoic, the suspension-feeder part of the assemblage was dominated by brachiopods, but with the development of mantle fusion and siphon formation in the bivalves at the end of the Palaeozoic, the brachiopods were rapidly replaced by suspension-feeding bivalves, which have occupied these niches right up to the Recent. Only the slowly-evolving deposit-feeding Nuculoida have remained in the same niche since the Lower Palaeozoic, showing how they have become well-adapted to their particular niche.

REFERENCES

CALLOMON, J.H. 1968	See p. 72
HALLAM, A. 1967a	See p. 451
MELVILLE, R.V. 1956	See p. 451
STENZEL, H.B. 1971	See p. 91
WRIGHT, J.K. 1968	See p. 95

ABSTRACT

The Lower Oxford Clay (Middle Callovian, Upper Jurassic)
of southern England has been studied in detail, in order to
elucidate the stratigraphy, bivalve taxonomy and palaeoecology
of the formation.

Examination of four quarries in the Midlands, between
Peterborough and Calvert (Bucks.), has allowed a detailed
stratigraphy to be established, based upon that of Callomon
(1968), and to which it has been possible to relate the range
and occurrence of all the invertebrate species collected. The
position of the Obductum - Grossouvrei Subzonal boundary at
Stewartby (Bedford), which was not located by Callomon, has been
established, on the basis of recurrent bivalve populations.

The taxonomy of the bivalve fauna has been treated
monographically, 48 species, 7 of which are new, having been
described. One new genus, Byssentolium gen. nov. is introduced,
with B. hudsoni sp. nov, as its type species. The subgenus
Trautscholdia Cox & Arkell is elevated to full generic rank, and
the generic assignations of several of the most well-known Upper
Jurassic bivalve species are amended. The remainder of the
Lower Oxford Clay invertebrate fauna has been considered in
general terms, and its palaeoautecology inferred; the palaeo-
autecology of the bivalve fauna has been dealt with in detail.

By using the mass of detailed information collected at
the four major quarries, a palaeoecological reconstruction of
the environmental conditions established during the deposition

of the Lower Oxford Clay has been made. Ten biofacies types have been defined and recognised at all the major quarries, and are characterised by 5 ecologically defined parameters.

The benthonic fauna of several other Jurassic and Cretaceous Clay Formations has been compared with that of the Lower Oxford Clay, showing that only the Upper Lias of England is closely comparable.

Consideration of the composition of deposit-feeder dominated communities since the Lower Palaeozoic has shown the major difference to be the replacement of the suspension-feeding brachiopods by suspension-feeding bivalves, a consequence of mantle fusion and siphon formation.

STUDIES ON THE PALAEONTOLOGY

OF THE LOWER OXFORD CLAY

OF SOUTHERN ENGLAND

A thesis submitted for the degree of Doctor of Philosophy

in the Faculty of Science

of the University of Leicester.

by

Keith Leslie Duff B.Sc. (University College, Cardiff)

Volume II, Figures, Plates and Appendices

November 1974

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Byssentolium hudsoni gen. et sp. nov.

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_C._ (_Radulopecten_) _scarburgensis_ (Young & Bird)

2.11   _C._ (_R._) _scarburgensis_ (Young & Bird)

_C._ (_R._) _fibrosa_ (J. Sowerby)

Plicatula cf. _fistulosa_ Morris & Lycett

_C._ (_R._) _drewtonensis_ Neale

P. fistulosa Morris & Lycett

2.12   _P. weymouthiana_ Damon

_P._ cf. _fistulosa_ Morris & Lycett

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2.16   _G. dilobotes_ nom. nov.

G. lituola Lamarck

2.17   _G. lituola_ Lamarck

Nanogyra nana (J. Sowerby)

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2.18   _D. lirata_ (Phillips)

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2.20   _M. caytonensis_ nom. nov.

Neocrassina ungulata (Lycett)

Appendices

1. Detailed descriptions of the stratigraphical sections seen at the four major pits examined.

2. Soluble fractions of each bed at the four major pits examined.

3. Measurements and measurement statistics for the specimens examined during the course of the monographic work.

In pocket at end of Volume II.

4a-d. Number of specimens of each species found in each bed at each pit.

CHAPTER 2

A monograph of the Lower Oxford Clay

bivalvia of southern England

Figs.   2.1 - 2.61

Tables   2.1 - 2.4

Plates   2.1 - 2.26
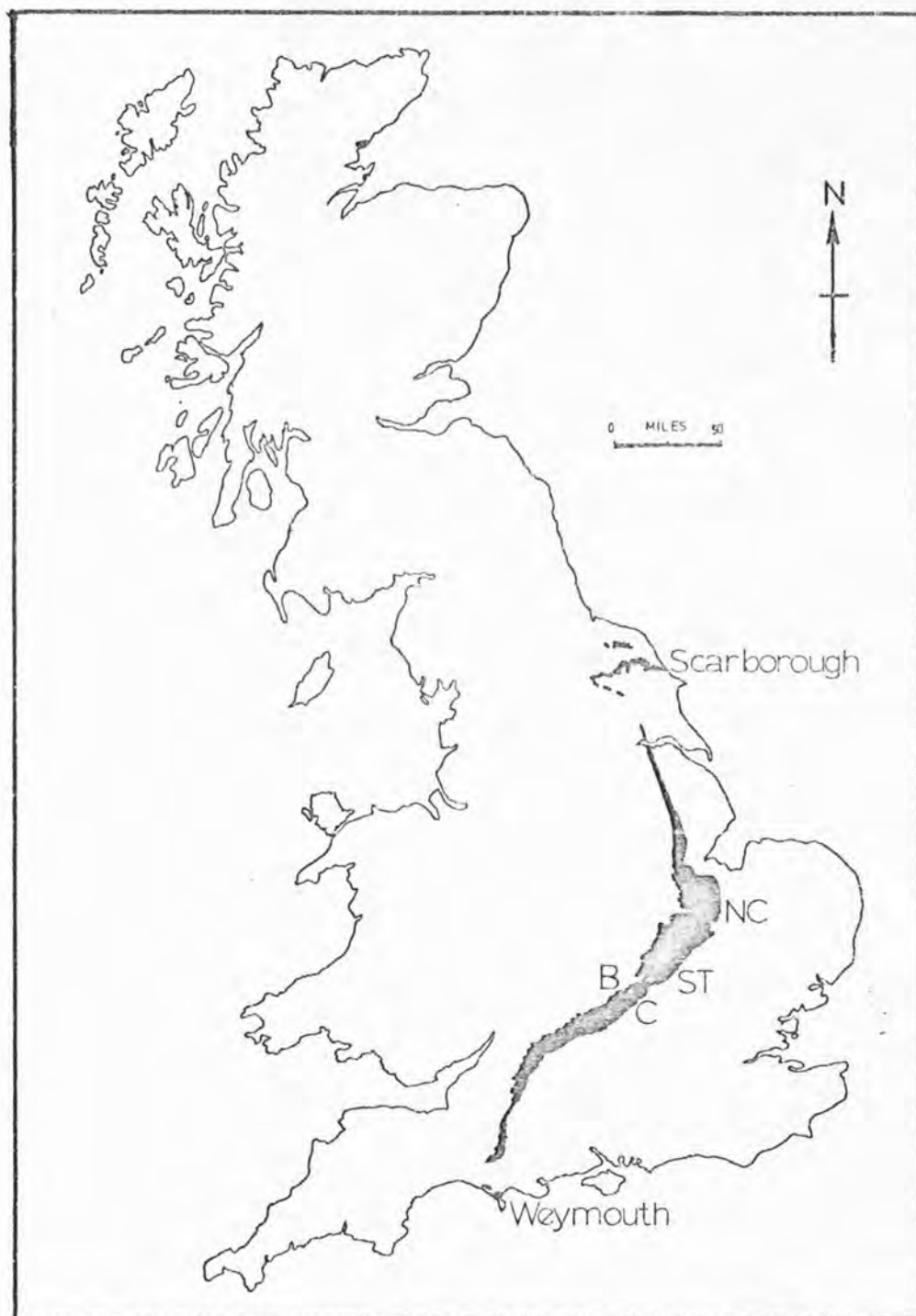
Fig. 2.1. The outcrop of the Oxford Clay in England, and the
location of the main sections studied. B = Bletchley,
C =€alvert, NC = Norman Cross, ST = Stewartby.

North-east Yorks.		ZONE	Central & Southern England		STAGE
Yorkshire Oxford Clay		Mariae		U. Oxford Clay	L. Oxfordian
Hackness Rock		Lamberti		M. Oxford Clay	U. Callovian
		Athleta			
hiatus					
Langdale Beds		Coronatum		L. Oxford Clay	M. Callovian
hiatus		Jason			
Kellaways Rock		Calloviense		Kellaways Rock	L. Callovian
Shales of the Cornbrash		Macro-cephalus		Kellaways Clay	
U. Cornbrash				U. Cornbrash	
U. Deltaic Series		Discus		L. Cornbrash	U. Bathonian

Fig. 2.2. A comparison of the basal part of the Upper Jurassic of northeast Yorkshire with that of central and southern England.

FIG. 2.3

Lithological sections measured at the four pits
examined in central England.

KEY

Limestone
Laminated bituminous shales
Shell bed
Calcareous clays
Meleagrinella shell bed

Bituminous shales
Blocky claystone
Siltstone and silty clay

CALVERT SP 695232
BLETCHLEY SP 862325
STEWARTBY SP 017412
NORMAN CROSS TL 172916

ATHLETA ZONE

GROSSOUVREI SUBZONE

OBDUCTUM SUBZONE

JASON SUBZONE

MEDEA SUBZONE

ENODATUM SUBZONE
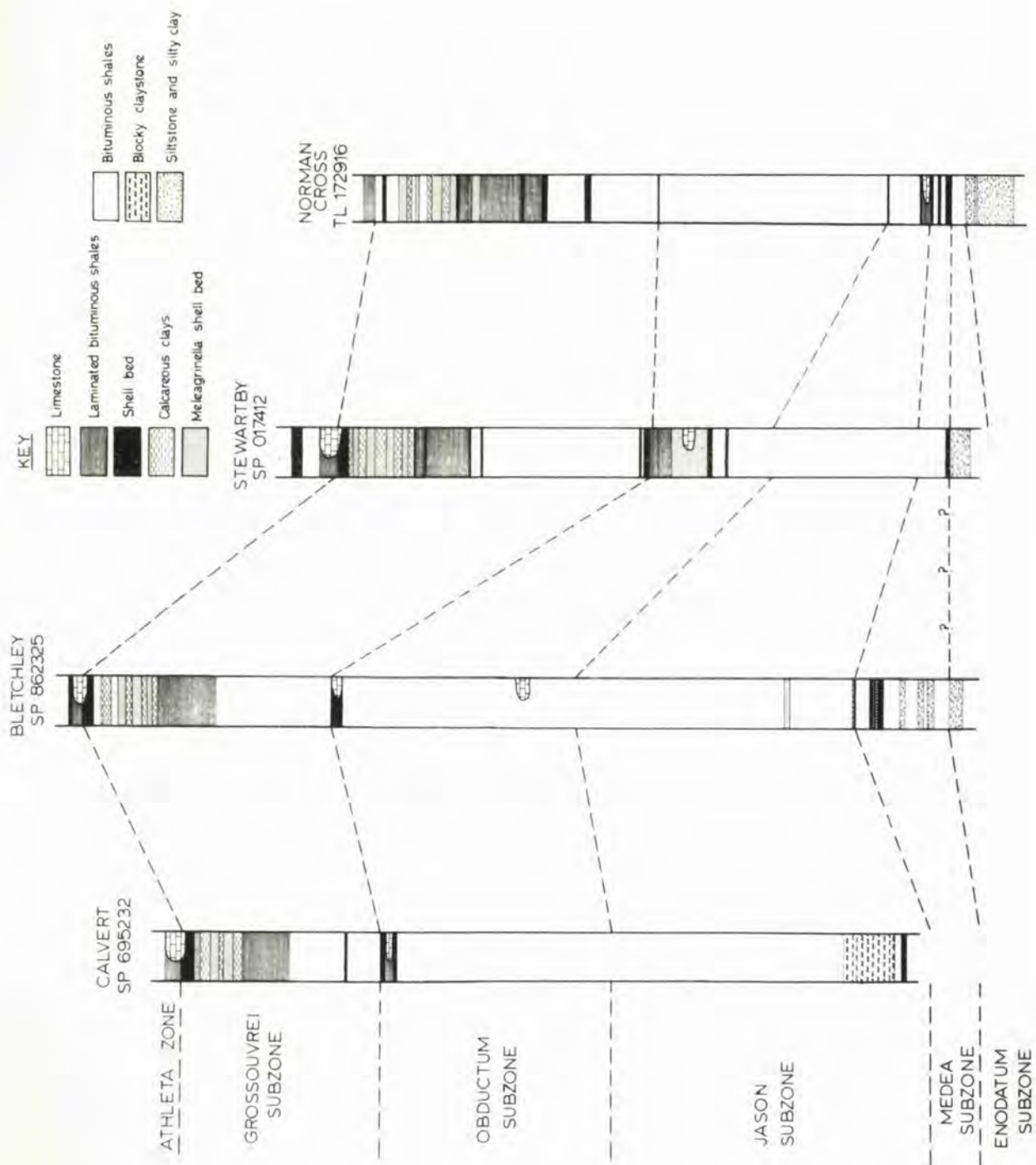
FIG. 2.4

Soluble fractions determined for the various beds
at each of the four pits examined.

NORMAN CROSS

STEWARTBY

BLETCHLEY

CALVERT

Vertical scale – 1 cm represents 0·5 m
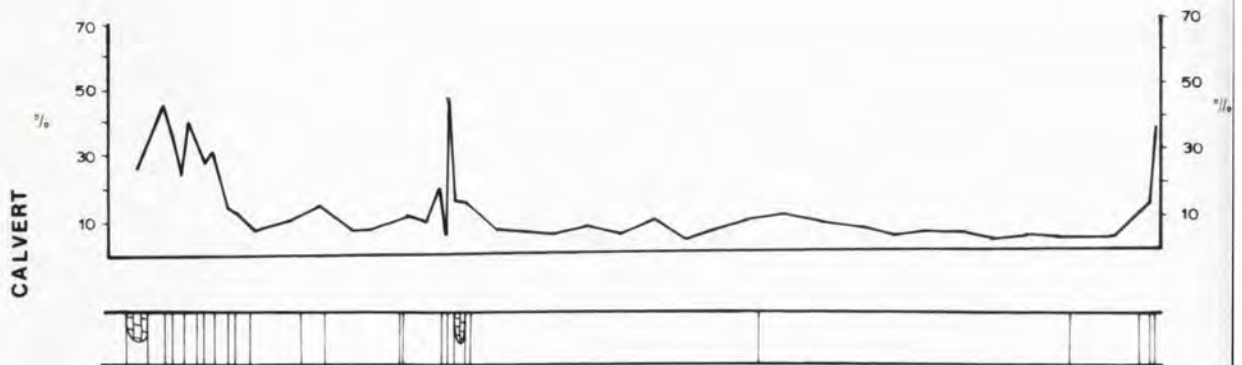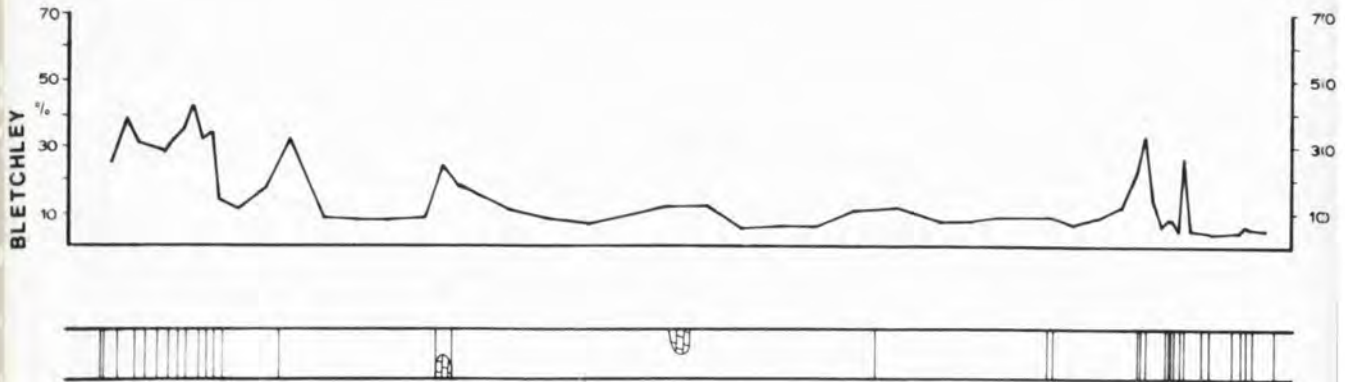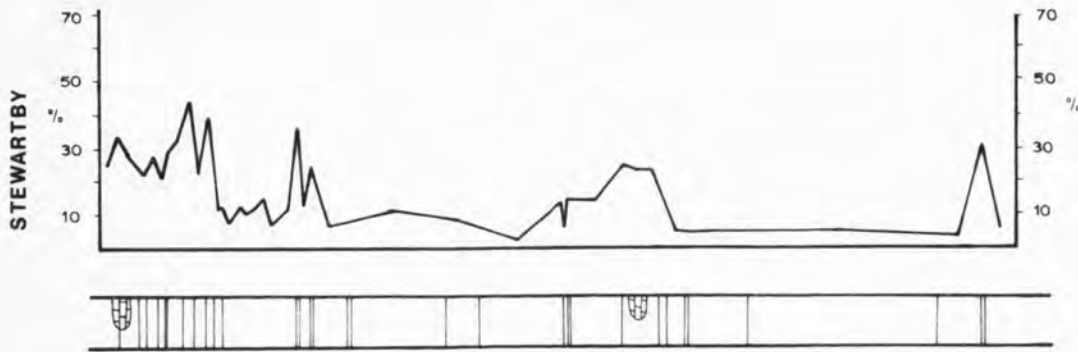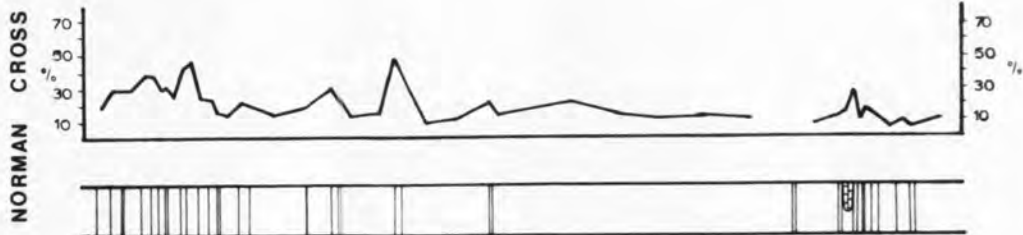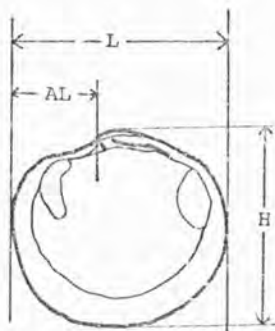
a) Astartacea, Cardiacea, Myacea,
Arcticacea, Solemyacea, Pholadomyacea,
Lucinacea, Pandoracea, Nuculacea,
Nuculanacea.
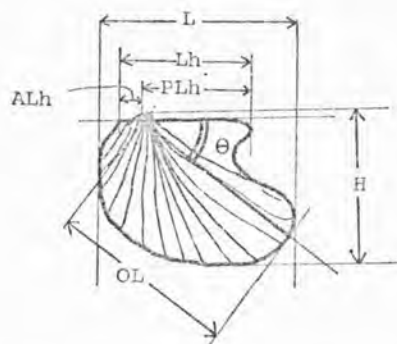
b) Arcacea, Pteriacea, Pectinacea,
Mytilacea.
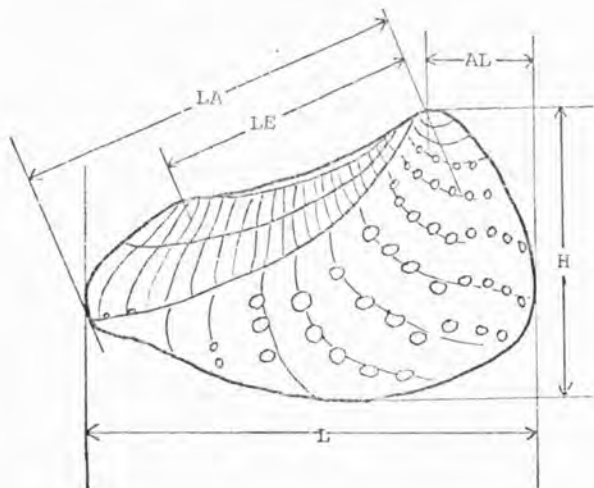
c) Trigonacea.
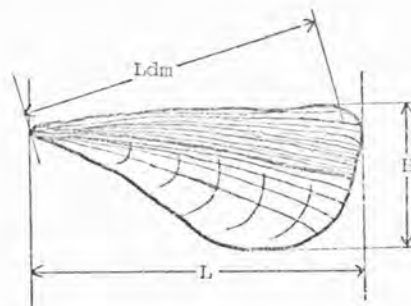
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Fig. 2.5. Schematic view of representatives of each of the four major bivalve
outlines present in the Lower Oxford Clay, showing the measurement parameters
used in the descriptions of the species.
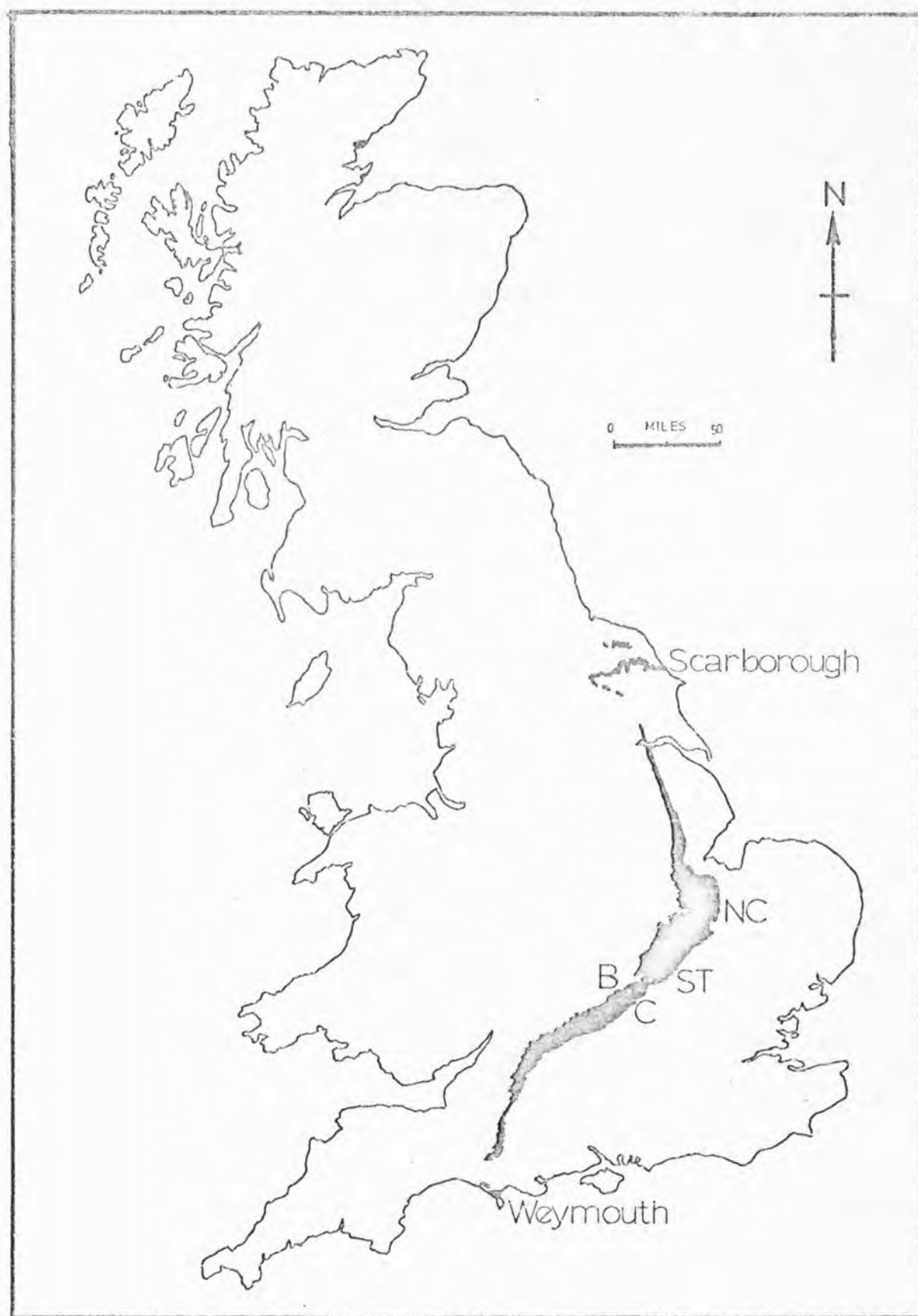
Fig. 2.6. Location of the major outcrops examined.
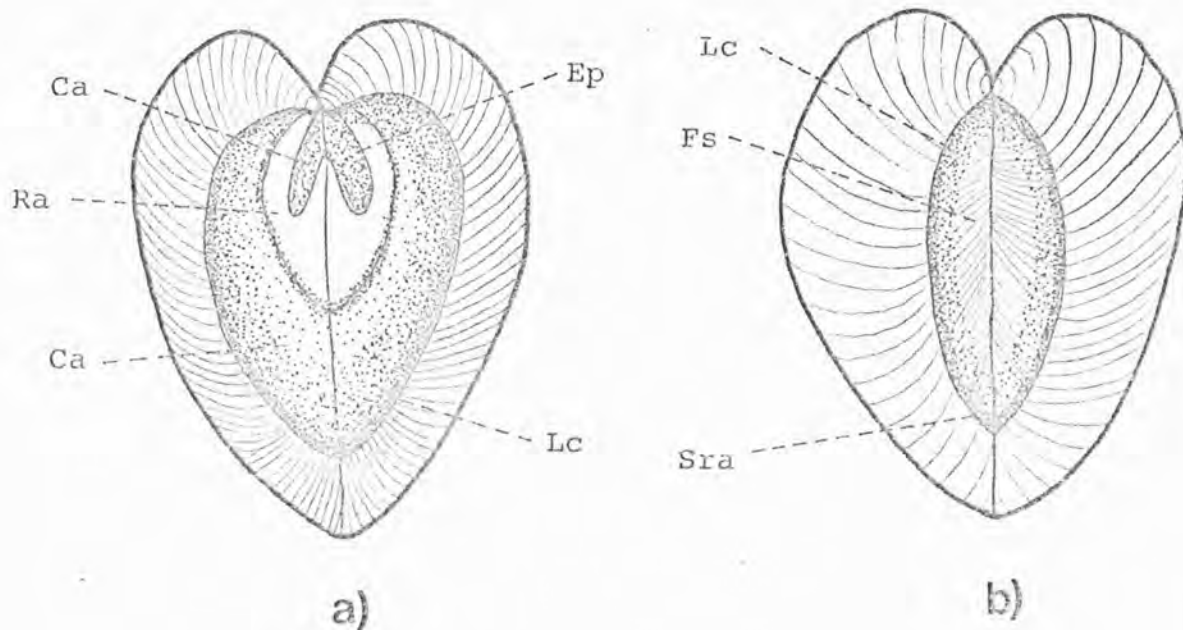
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the Oxford Clay of Wiltshire (YM KD 1974/1). x 6. The form
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in fig. a.
Ca = Concave area; Ep = Escutcheon pout; Fs = Fine striae;
Lc = Lateral carina; Ra = Raised area; Sra = Slightly raised
area.
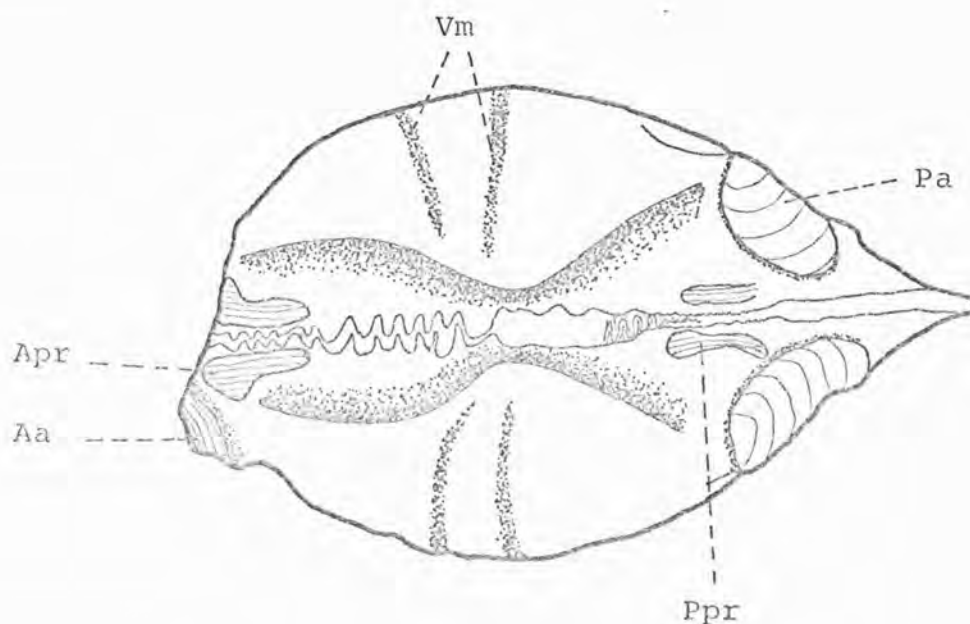
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(LU 68611), showing the disposition of the various muscle
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Aa = Anterior adductor scar; Apr = Anterior pedal retractor
scar; Pa = Posterior adductor scar; Ppr = Posterior pedal
retractor scar; Vm = Visceral muscle scars.

FIG. 2.9

Sketch-pictograph showing the main lines of variation

in Palaeonucula triangularis sp. nov.
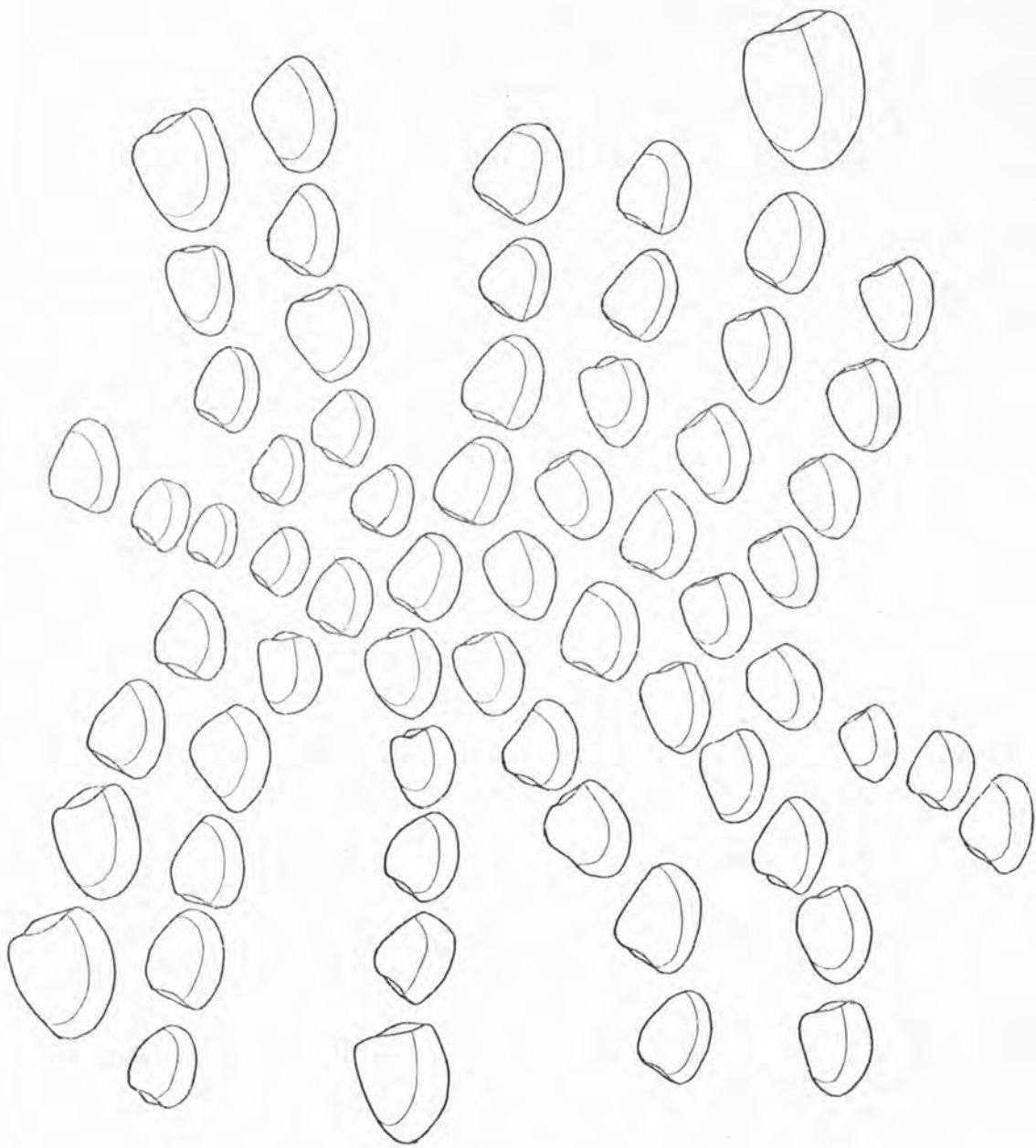
Fig. 2.9.
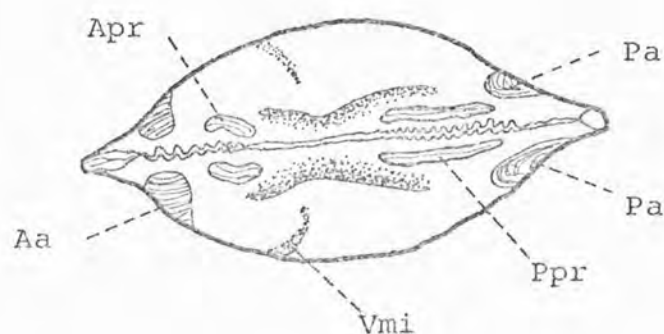
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mould of Mesosaccella morrisi (Deshayes), from the
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disposition of the various muscle scars.   x 6.
Aa = Anterior adductor scar; Apr = Anterior pedal
retractor scar; Pa = Posterior adductor scar;
Ppr = Posterior pedal retractor scar; Vmi = Visceral
mass integument scar.
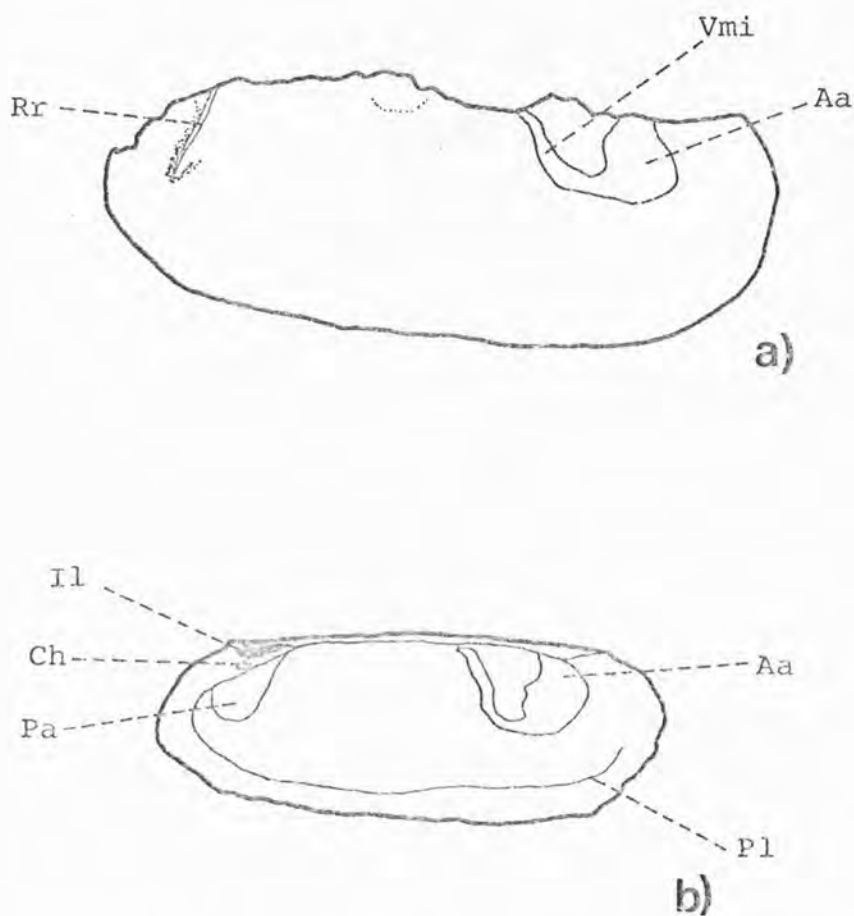
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x2. Figure after Cox (1969, Fig B1,3.). Aa = Anterior
adductor scar; Pa = Posterior adductor scar; Vmi = Visceral
mass integument scar; Pl = Pallial line; Rr = Radial rib;
Ch = Chondrophore; Il = Internal ligament.
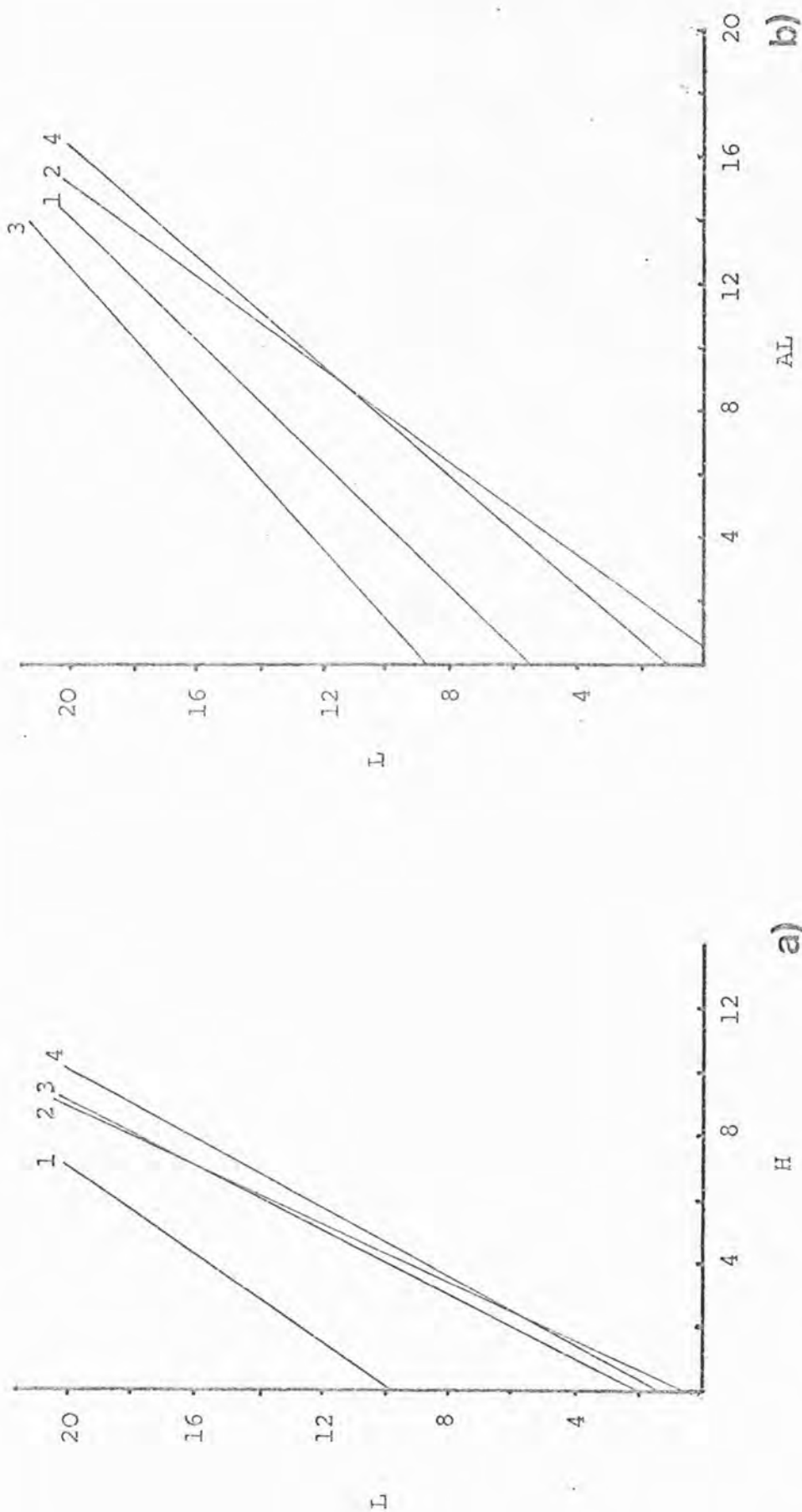
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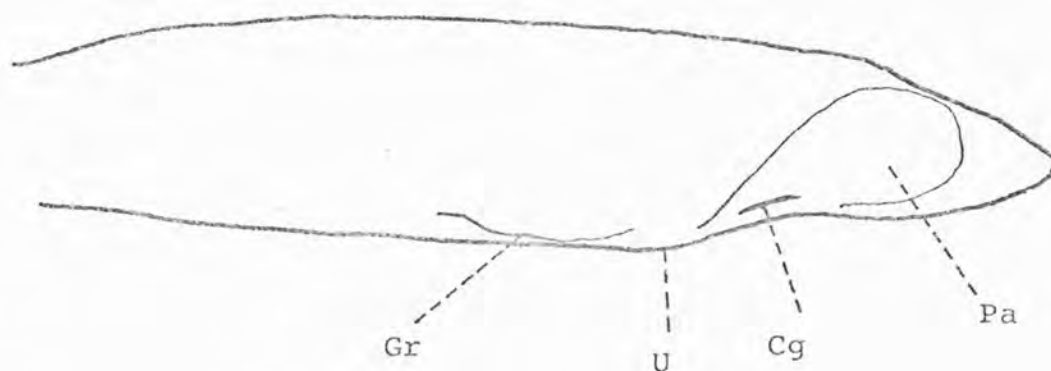
Fig. 2.13. Schematic view of the dorsal region of an internal mould of a right valve of _Solemya woodwardiana_ Leckenby, showing the position of the posterior adductor scar, and a short deep groove just posterior of the umbo which may represent the chondrophore groove. Specimen from the Lower Oxford Clay of Wiltshire (LU 69932), x 6.

Cg = Chondrophore groove; Gr = Groove; Pa = Posterior adductor scar; U = umbo.
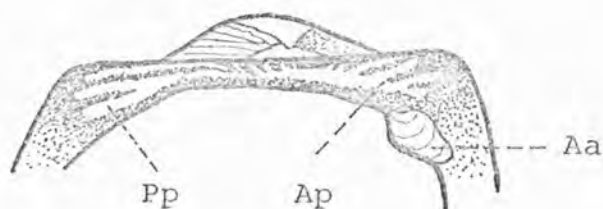
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Subzone; Coronatum Zone) of Stewartby, Beds. (LU 68627),
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pseudolateral teeth to the subhorizontal posterior
pseudolaterals. x 6.
Aa = Anterior adductor scar; Ap = Anterior pseudolaterals;
Pp = Posterior pseudolaterals.
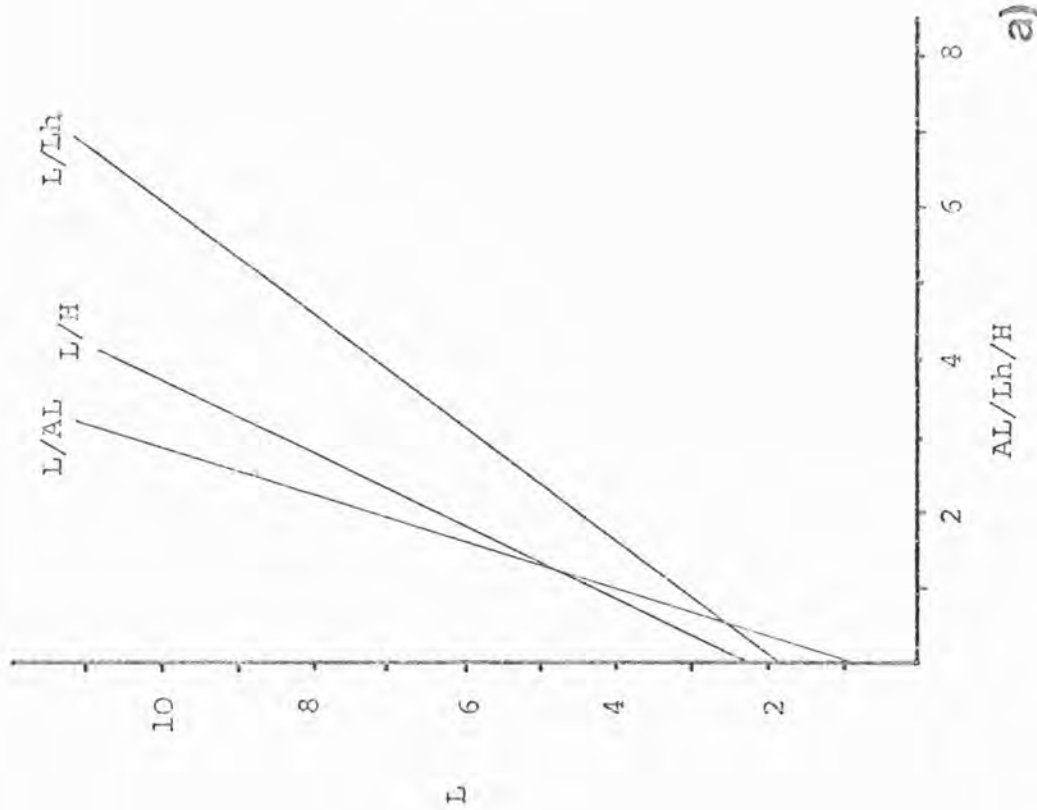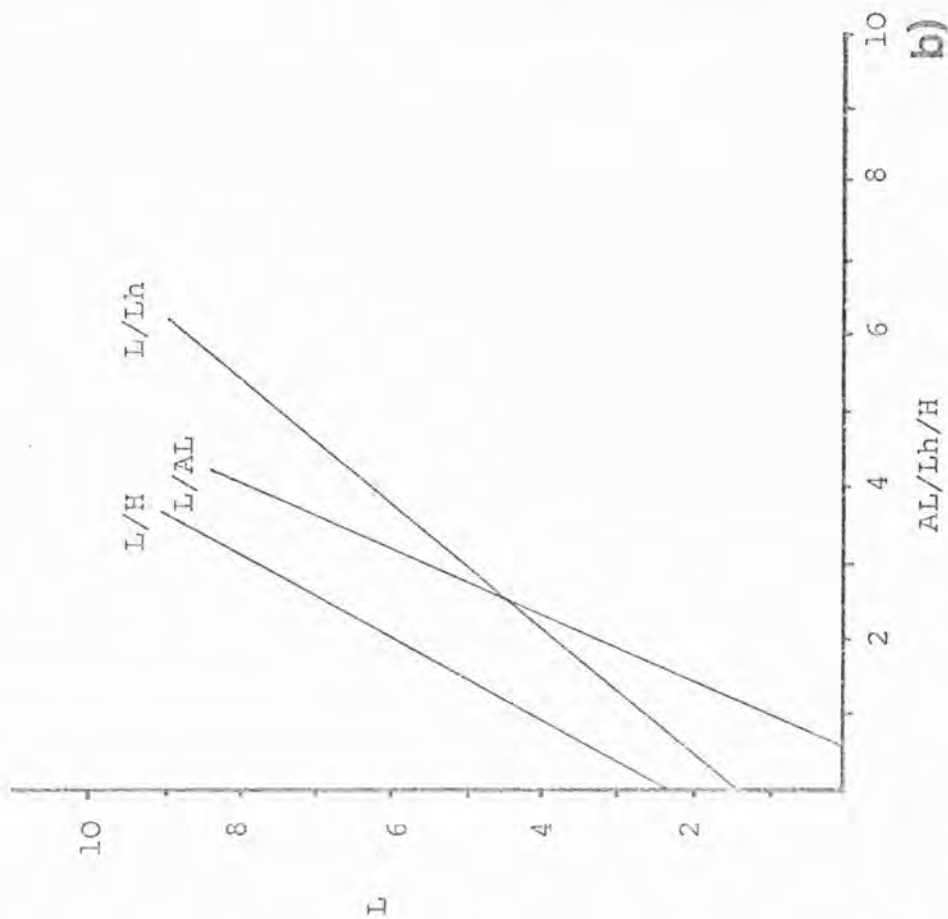
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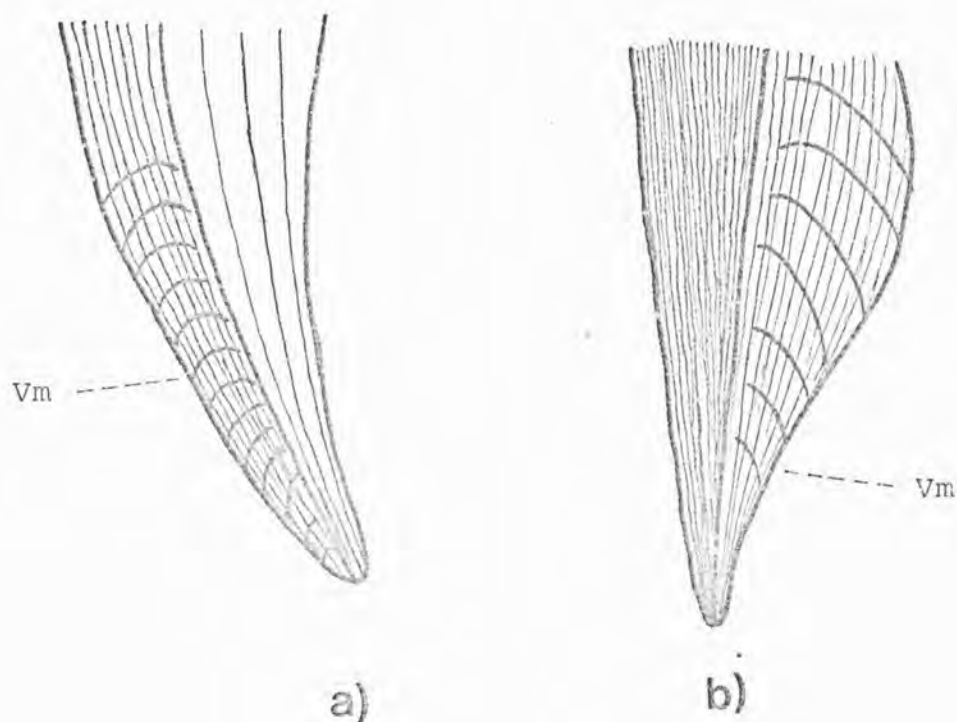
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showing the concavo-convex ventral margin, and much higher rib
density. Both x 1.5.
Vm = Ventral margin.
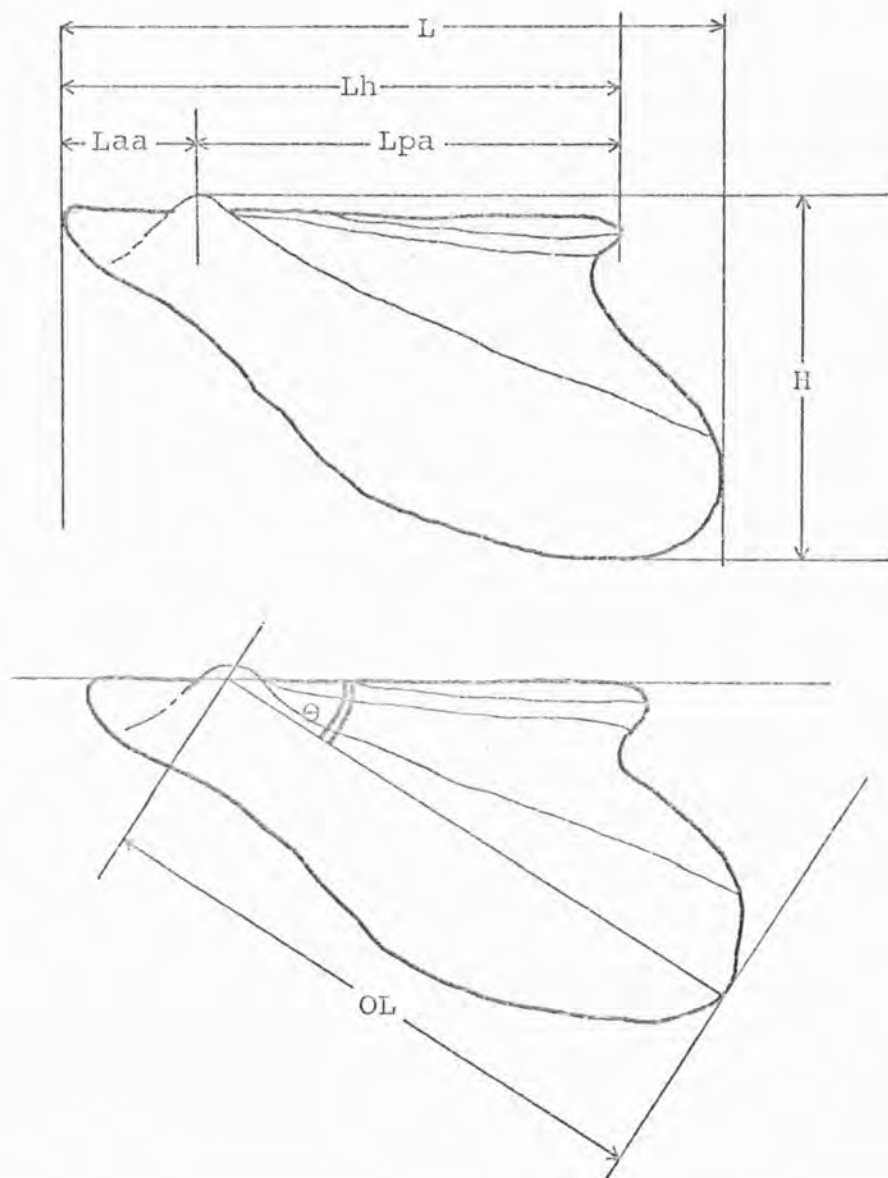
Fig. 2.17. Schematic view of the exterior of a left
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measurements used in the description of this species.
L = Length; Lh = Length of the hingeline; Laa = Length
of the anterior auricle; Lpa = Length of the posterior
auricle; H = Height; OL = Oblique length; θ = angle
of obliquity.
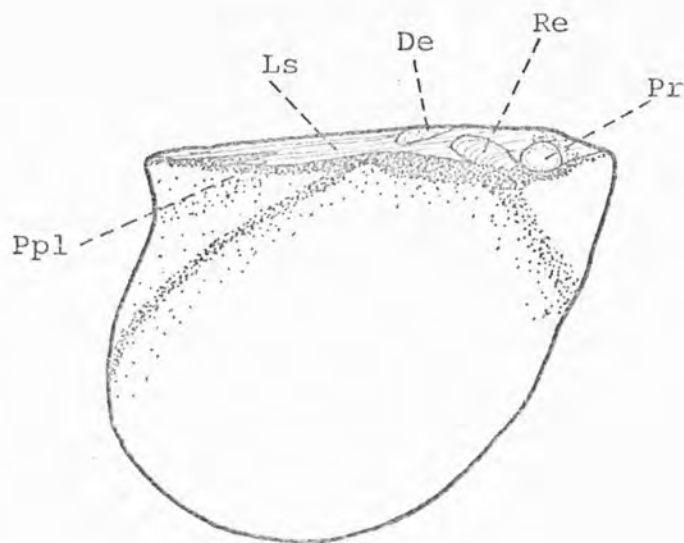
Fig. 2.18. Schematic view of the interior
of the left valve of a specimen of Pteroperna
pygmaea (Dunker) from the Lower Oxford Clay
of Wiltshire (BCM Cb 4777), showing details
of the cardinal area. x6.
De = slight depression; Ls = find longitudinal
striae; Ppl = Posterior pseudolateral tooth;
Pr = rounded protuberance; Re = Resilifer pit.
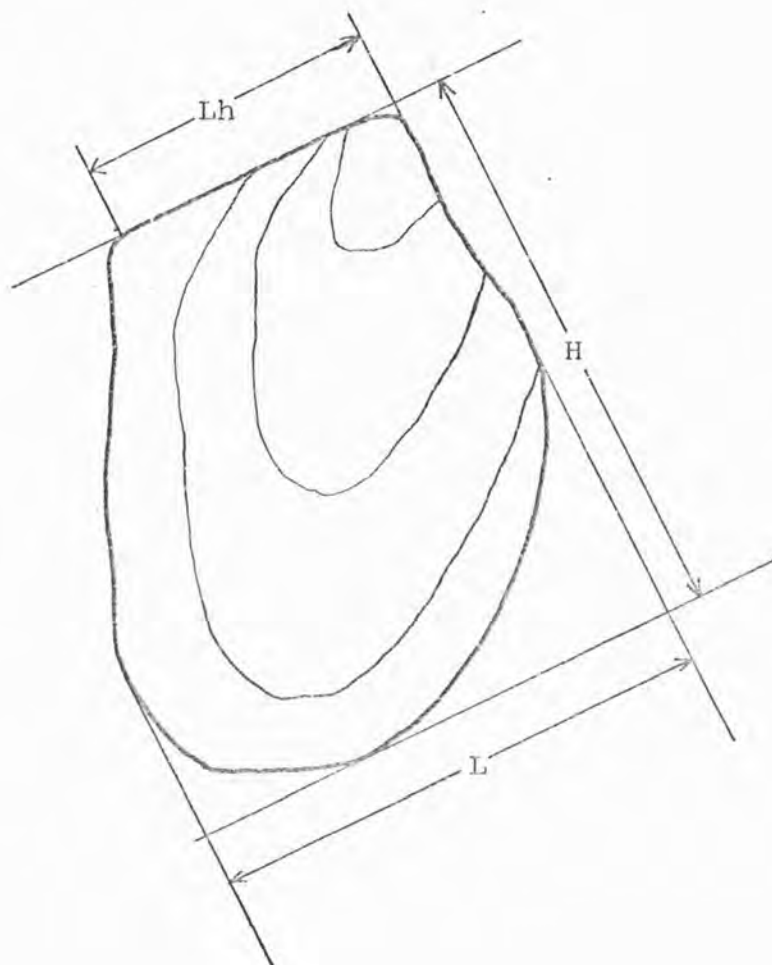
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the measurements used in the description. Lh = Length of
the straight part of the hinge line; H = Height, measured
perpendicular to Lh; L = Length, measured parallel to Lh.
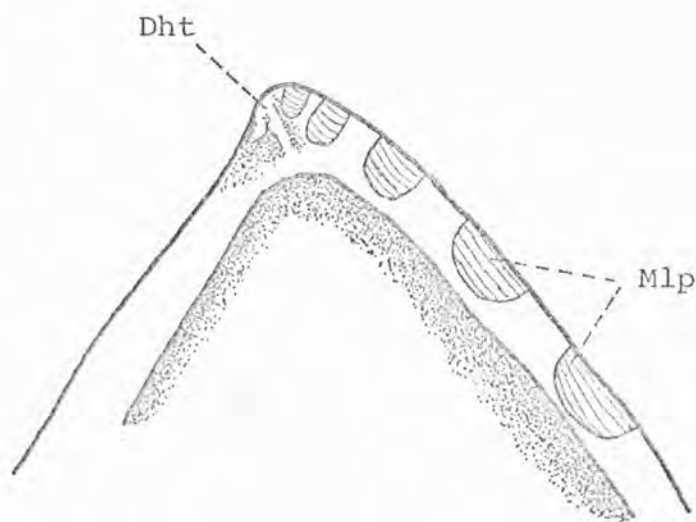
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placed immediately beneath the umbones, and the multiple
ligament pits along the posterodorsal margin. x 6.
Dht = Divergent hingeteeth; Mlp = Multiple ligament pits.
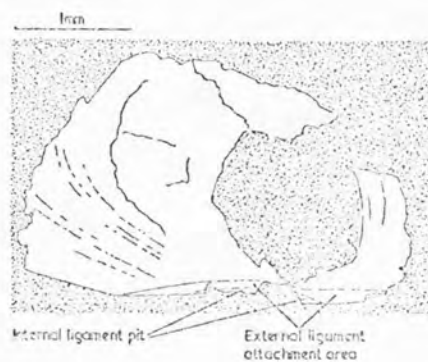
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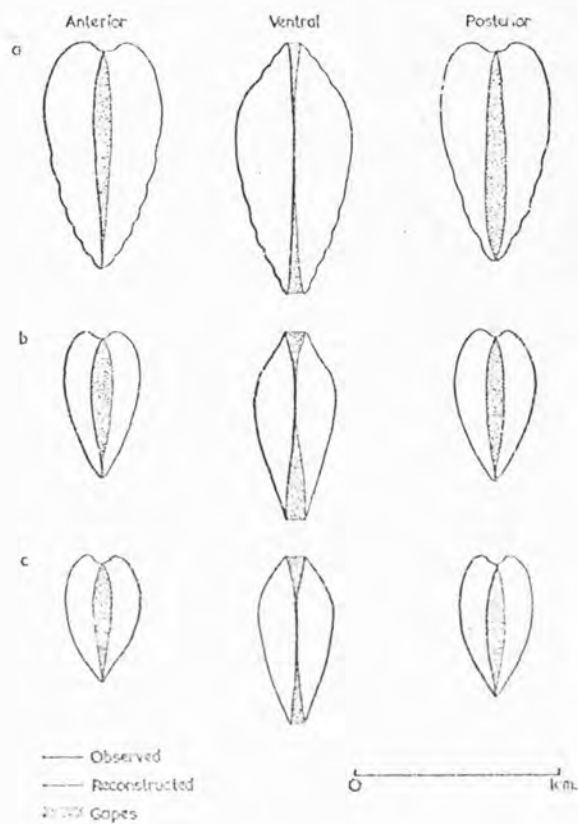
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(1965), Text-Fig. 3. x 2.75.
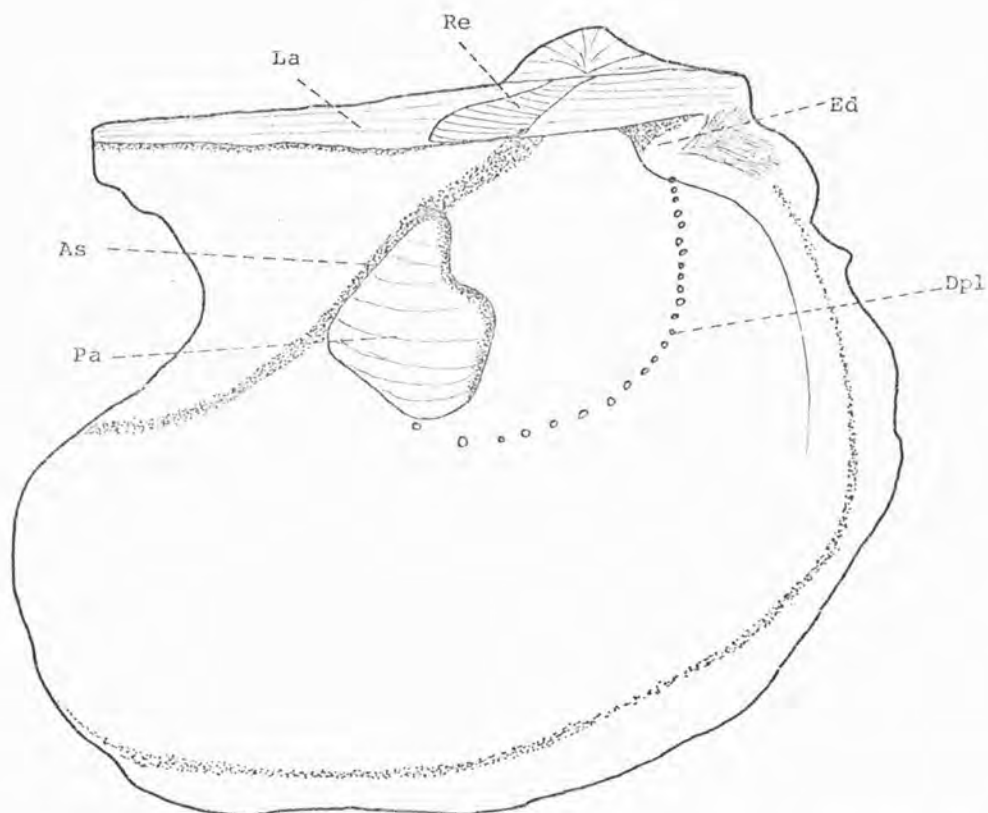
Fig. 2.23. Schematic internal view of a left valve of <u>Oxytoma inequivalvis</u> (J. Sowerby), from the Middle Oxford Clay of Woodham, Bucks. (LU 52673), showing details of the musculature and the cardinal area. Note the elongate depression anteroventral of the umbo for articulation with the pointed anterior auricle of the right valve. x 6.

As = Auricular sulcus; Dpl = Disjunct pallial line; Ed = Elongate depression; La = Ligament area; Pa = Posterior adductor scar; Re = Resilifer.
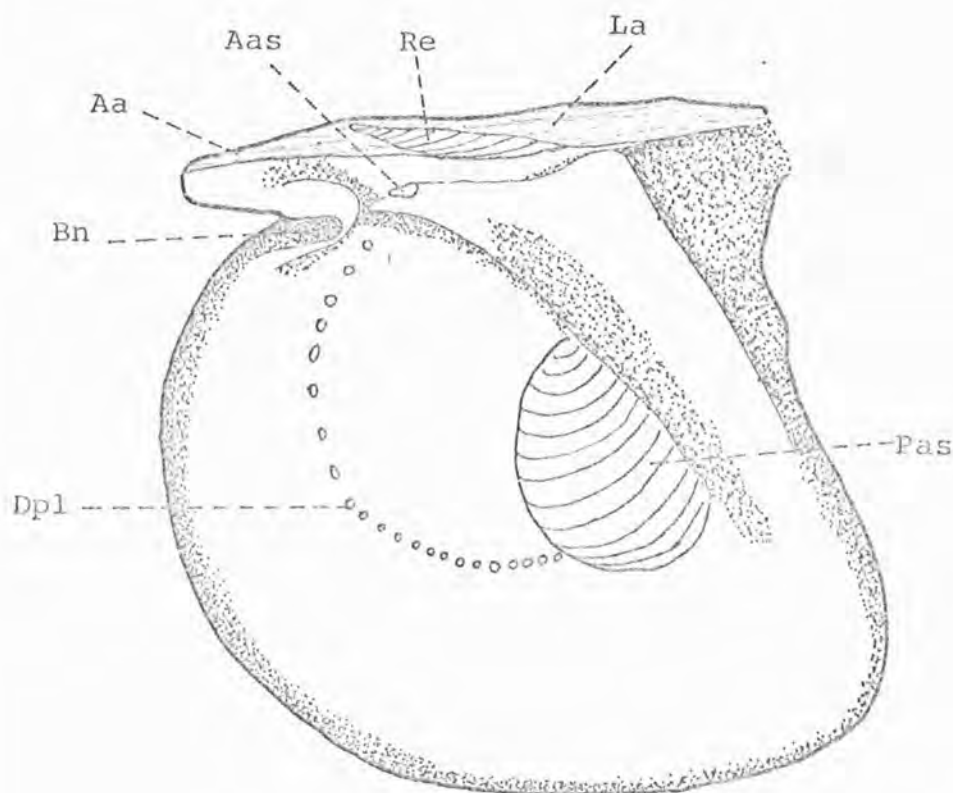
Fig. 2.24. Schematic internal view of a right valve of Oxytoma
inequivalvis (J. Sowerby), from the Middle Oxford Clay of
Woodham, Bucks. (LU 52675), showing details of the musculature
and the cardinal plate. Note the small anterior adductor scar
beneath the resilifer. x 6.

Aa = Anterior auricle; Aas = Anterior adductor scar; Bn = Byssal
notch; Dpl = Disjunct pallial line; La = Ligamental area;
Pas = Posterior adductor scar; Re = Resilifer.
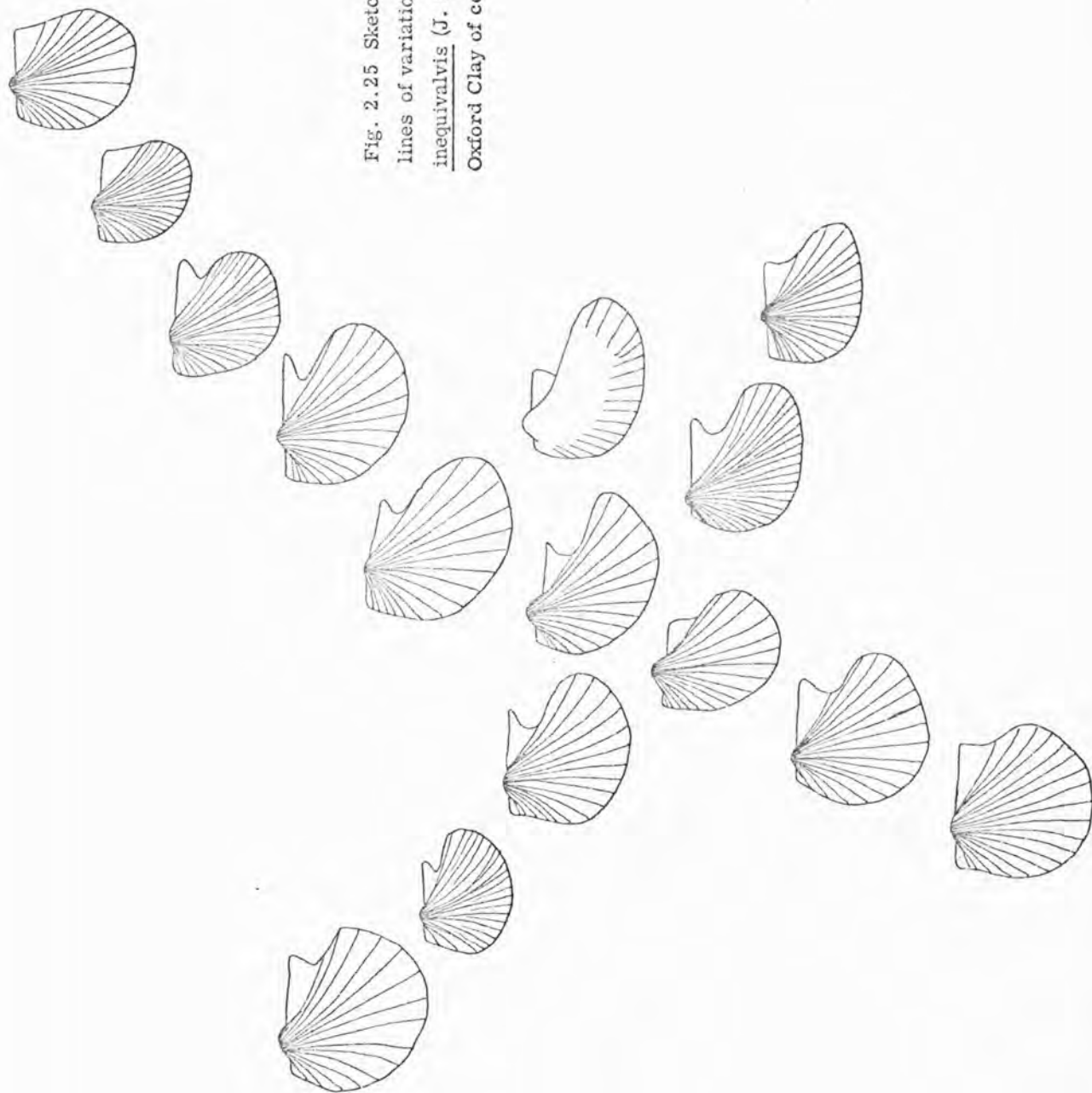
Fig. 2.25 Sketch-pictograph showing the main lines of variation present in Oxytoma inequivalvis (J. Sowerby). Specimens from the Oxford Clay of central England, x1.
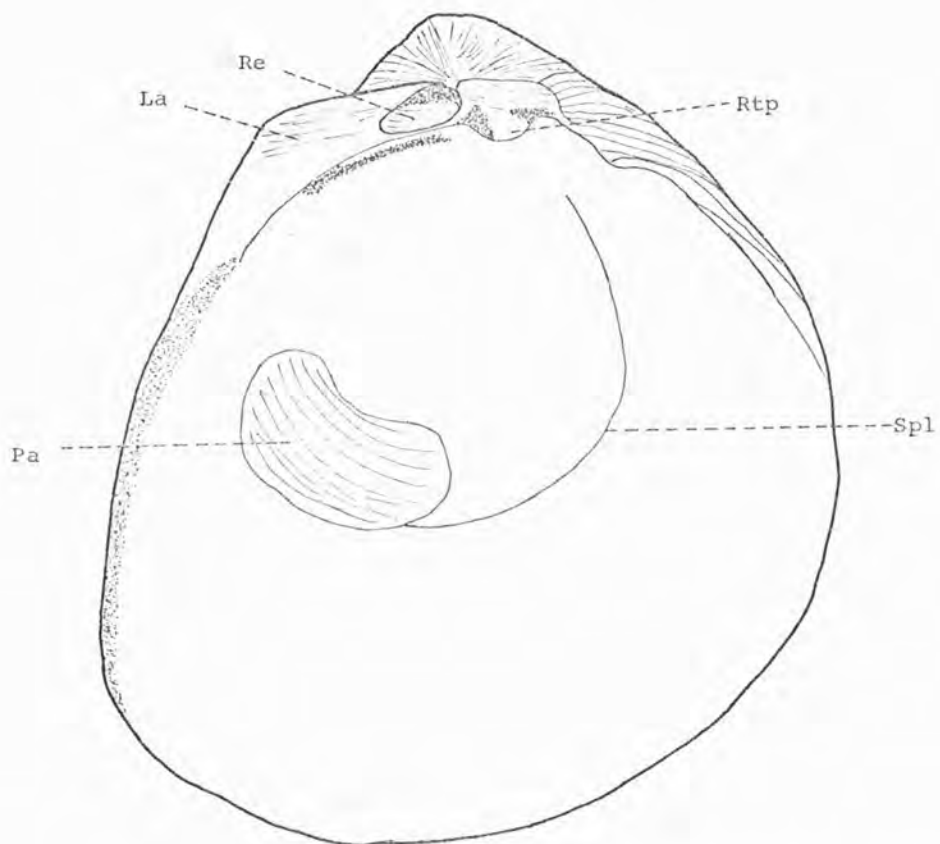
Fig. 2.26a. Schematic internal view of a left valve of _Meleagrinella braamburiensis_ (Phillips) from the Oxford Clay of Wiltshire (GSM Y2088), showing details of the cardinal area and musculature. Note the prominent rounded toothlike protuberance anterior of the resilifer. x 6.

La = Ligament area; Pa = Posterior adductor scar; Re = Resilifer; Rtp = Rounded toothlike protuberance; Spl = Simple pallial line.
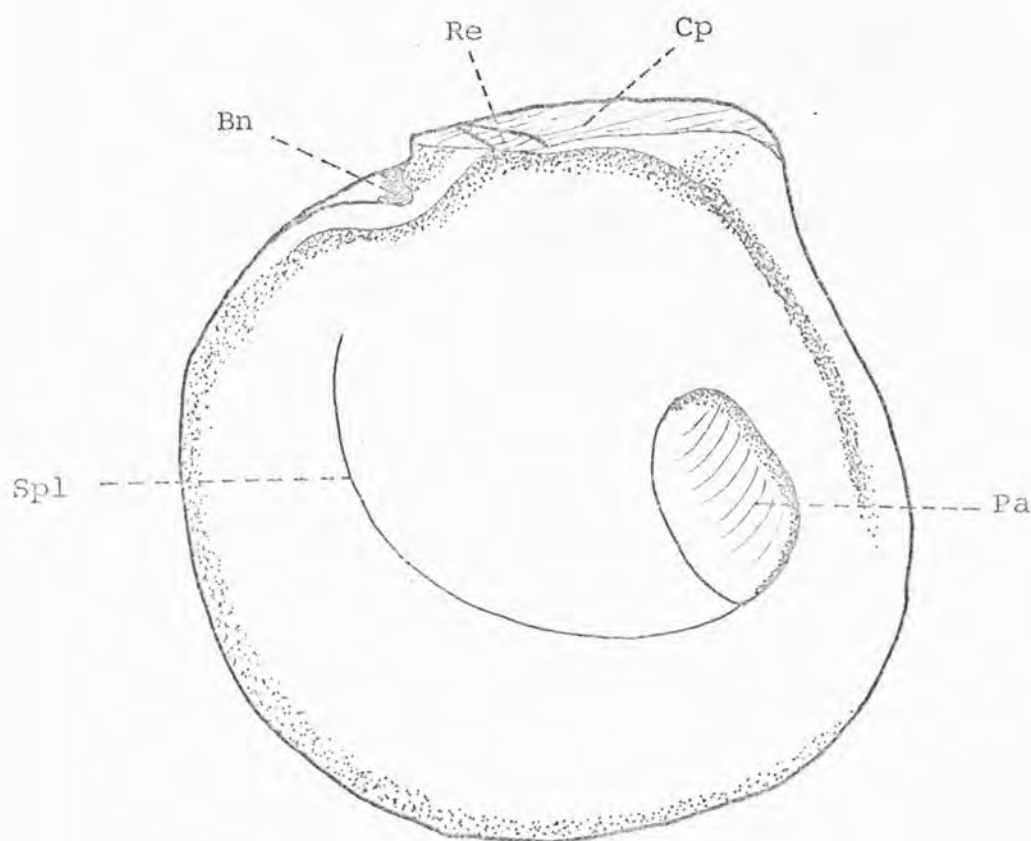
Fig. 2.26b. Schematic internal view of a right valve of
Meleagrinella braamburiensis (Phillips), from the Oxford Clay
of Wiltshire (GSM Y2090), showing details of the musculature
and the cardinal plate. Note the narrow resilifer placed
on the broad cardinal platform with a deep byssal notch beneath
the broken right anterior auricle. x 6.
Bn = Byssal notch; Cp = Cardinal platform; Pa = Posterior
adductor scar; Re = Resilifer; Spl = Simple pallial line.
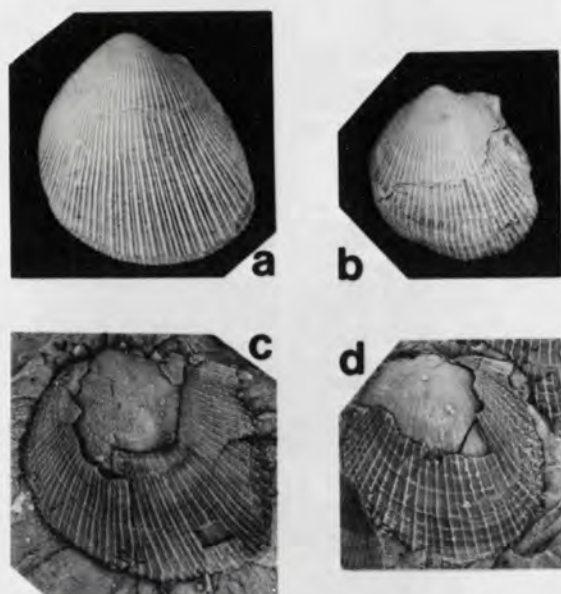
Fig. 2.27. Variation in ornament style in
Meleagrinella braamburiensis.

   a) Simple radial primaries with intercalated
secondaries.

   b) Simple radial primaries with intercalated
secondaries and some faint concentric elements,
especially well-developed at the anterior and
posterior.

   c) Radial primaries and secondaries, with
concentric growth lines strengthened, and
becoming spinose on the posterior flanks.

   d) Radial primaries and secondaries,
together with strong concentric growth lines,
strongly spinose on the posterior flanks.
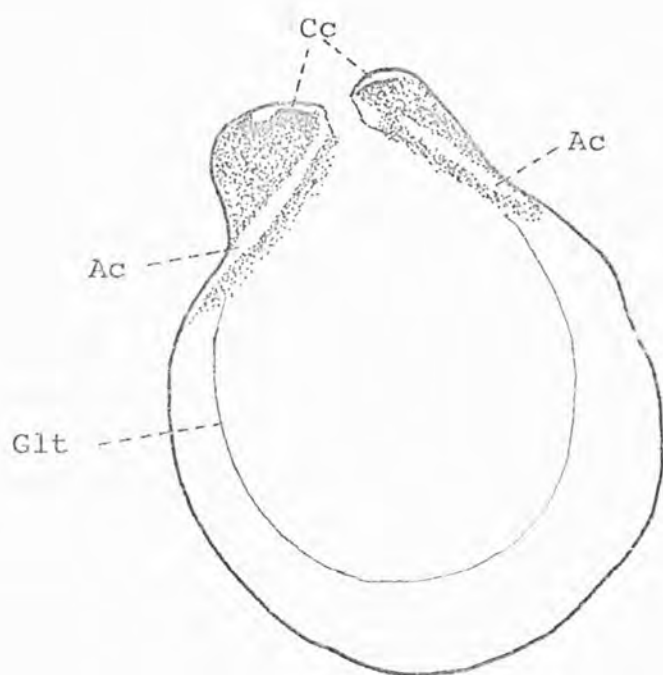
Fig. 2.28. Schematic internal view of a left valve of _Entolium_
corneolum (Young & Bird), from the Oxford Clay of Brora, Suther-
landshire, in the authors collection, showing the crura on the
cardinal plate. x 6.

Ac = Auricular crus; Cc = Cardinal crura; Glt = Growth-line trace.
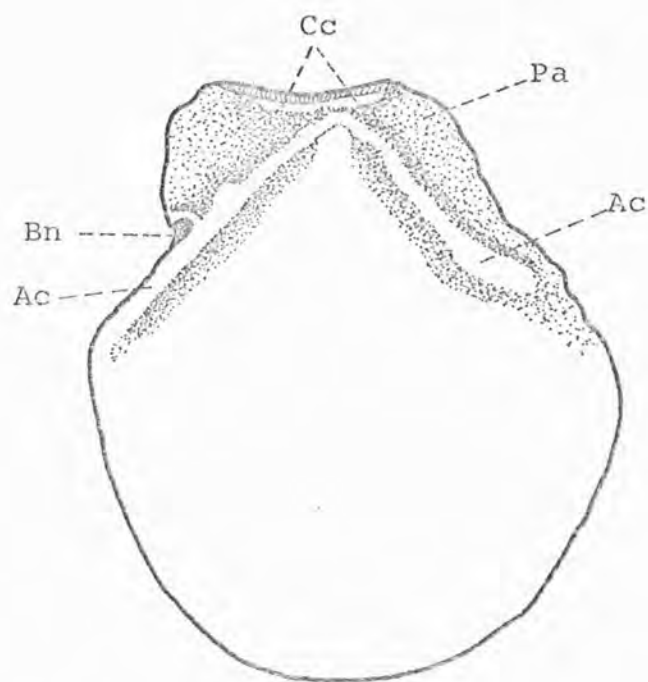
Fig. 2.29. Internal view of a right valve of Byssentolium
hudsoni sp.nov., showing details of the cardinal plate.
x 12. Note the small, but prominent byssal notch, and the
clearly-developed cardinal and curicular crura.
Aa = Anterior auricle; Ac = Auricular crus; Bn = Byssal
notch; Cc = Cardinal crura; Pa = Posterior auricle.
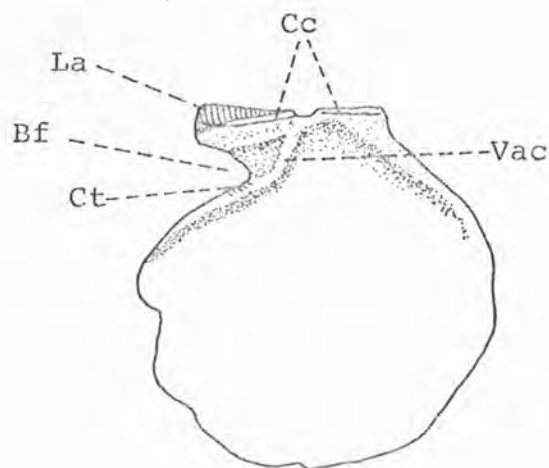
Fig. 2.30. Internal view of a right
valve of Camptonectes auritus (Schlotheim),
from the Corallian of England (BM LL2445),
showing details of the cardinal plate.
The specimen was originally figured by
Speden (1967) pl.4, figs. 1, 3, 6. x 1.
Bf = Byssal fasciole; Cc = Cardinal
crura; Ct = Ctenolium; La = Ligamental
area; Vac = Vestigial auricular crus.
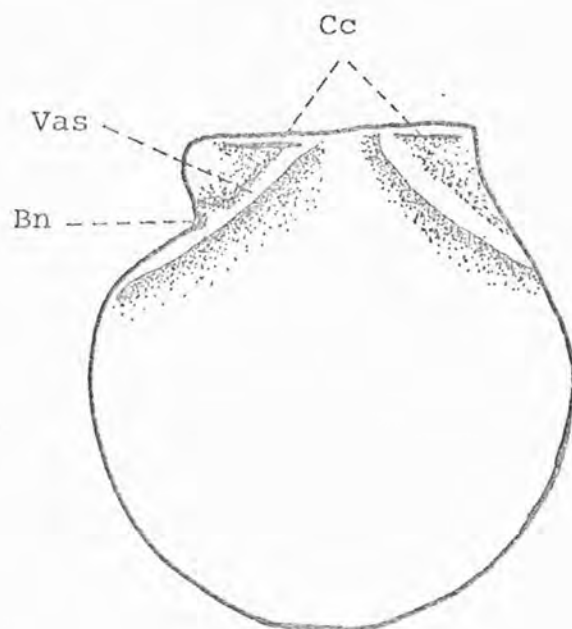
Fig. 2.31. Schematic internal view of a right
valve of Chlamys (Chlamys) bedfordi sp. nov.,
from the Lower Oxford Clay (Grossouvrei
Subzone, Coronatum Zone) of Peterborough
(BM LL27727), showing detail of the cardinal
plate. Note the well-developed cardinal
crura, and the vestigial auricular crus; central
part of the hinge plate broken. x 6.
Bn = Byssal notch; Cc = Cardinal crura;
Vas = Vestigial auricular crus.
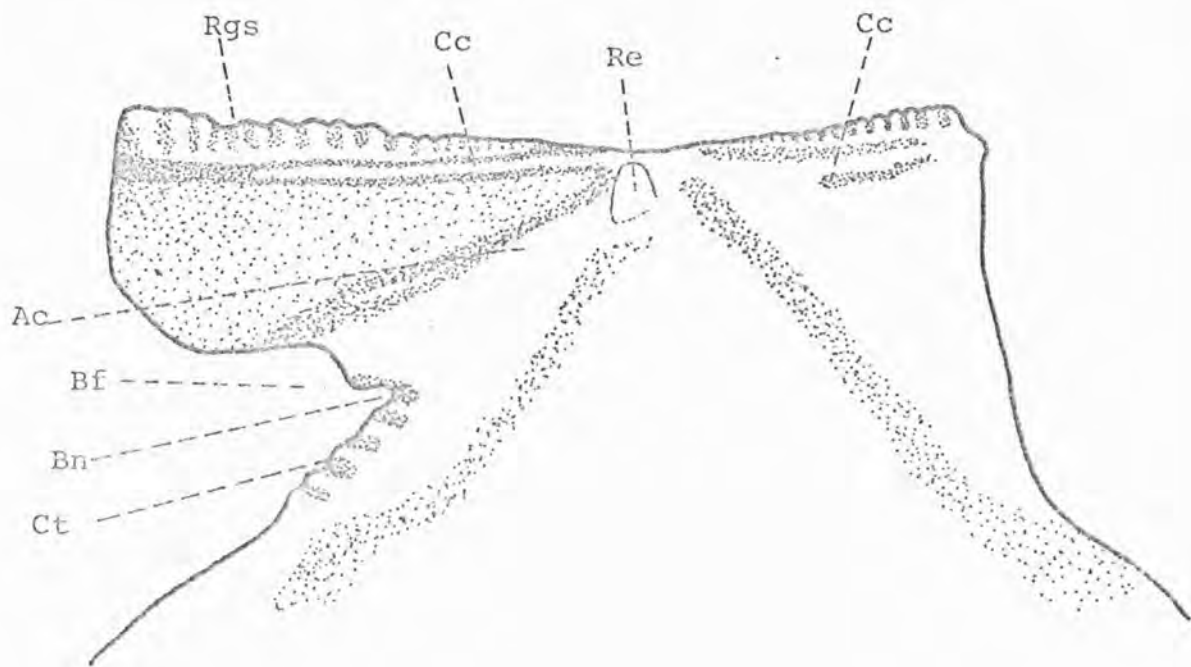
Fig. 2.32. Internal view of a right valve of Chlamys
(Radulopecten) fibrosa (J. Sowerby) from the Oxford Clay
of Chippenham, Wiltshire (GSM 113408), showing details
of the cardinal plate. x 6.

Ac = Auricular crus; Bf = Byssal fasciole; Bn = Byssal
notch; Cc = Cardinal crus; Re = Resilifer; Rgs = Ridge
and groove system to aid articulation, and to prevent
lateral shearing of the hinge plates.
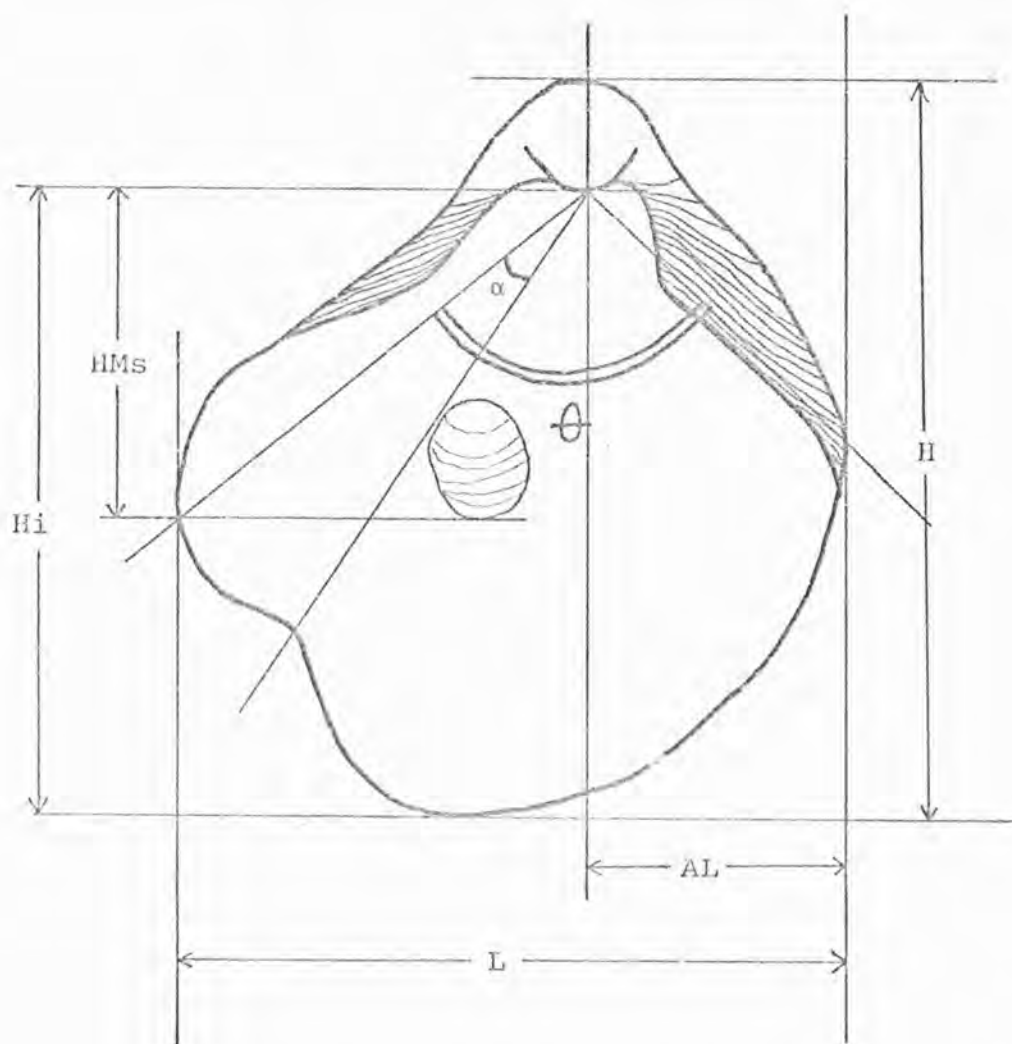
Fig. 2.33. Schematic internal view of a left valve of
Gryphaea dilobotes nom. nov. from the Lower Oxford Clay,
showing the measurements used in the description of
gryphaeate oysters. Many details of shell ornament
omitted for clarity. x 1.

AL = Anterior length; H = Height; Hi = Internal height,
measured from the top of the umbo to the ventral margin;
HMs = Height of the base of the muscle scar beneath the
hinge axis; Angle α measures the angle between the lines
radiating from the tip of the resilifer to the posterior
margin and the branchitellum; Angle θ measures the angle
between the lines radiating from the tip of the resilifer
to the anterior and posterior margins.
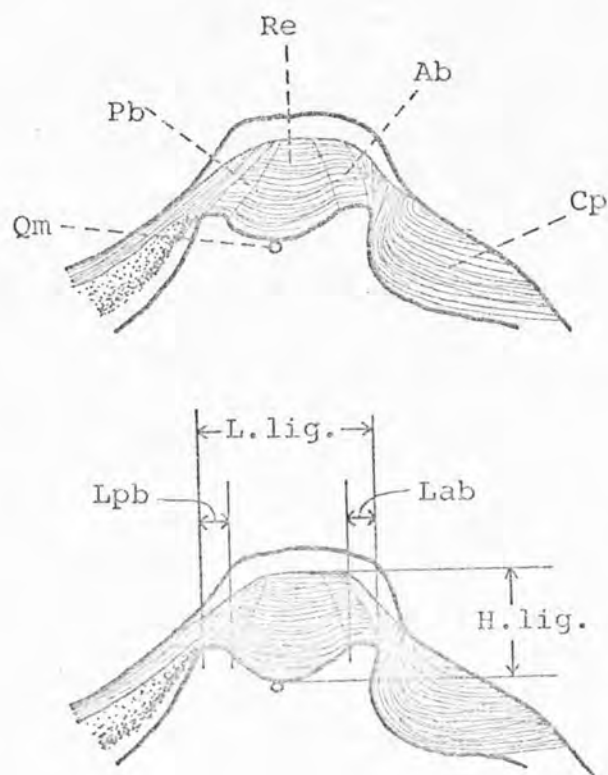
Fig. 2.33a. Schematic views of the ligamental
area of a left valve of *Gryphaea (Bilobissa)*
dilobotes nom. nov., showing the main features
present and the characters measured. x 1.5.
Ab = Anterior bourrelet; Cp = Commissural
platform; H.lig. = Overall height of the
ligament ; Lab = Length of the anterior bourrelet;
Lpb = Length of the posterior bourrelet; L.lig. =
Overall length of the ligament (resilifer +
bourrelets); Pb = Posterior bourrelet; Qm =
Quenstedt muscle scar; Re = Resilifer.

FIG. 2.34

Sketch pictograph showing the main lines of variation
present in collections of Gryphaea (Bilobissa)
dilobotes nom. nov. from the Kellaways Rock and Lower
Oxford Clay of England. All specimens x 0.3.
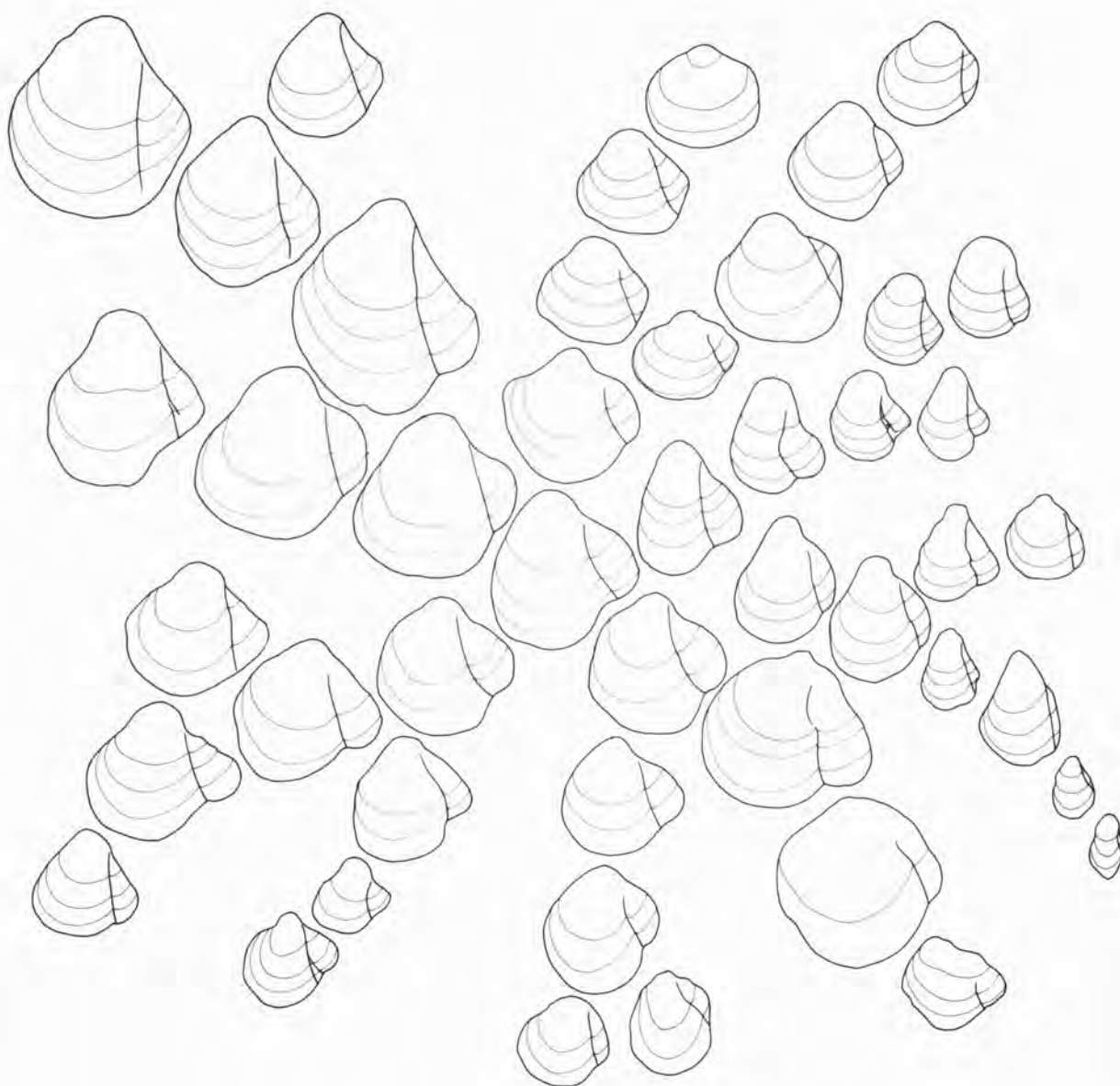
Fig. 2.34
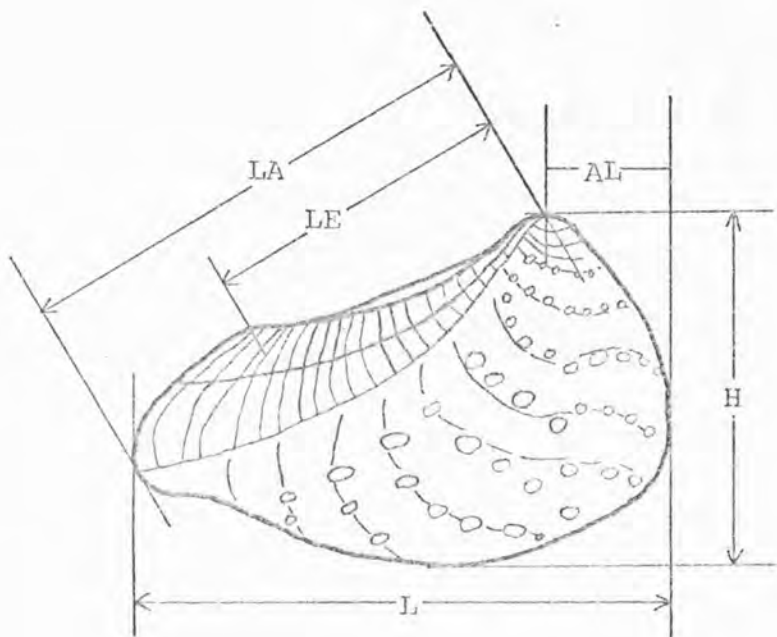
Fig. 2.35. Schematic external view of a right valve
of <u>Myophorella irregularis</u> (Seebach), from the Oxford
Clay of Weymouth, Dorset (YM KD 1974/40), showing
the measurements used in the description of trigoniids.
Tubercle rows shown diagrammatically.
AL = Anterior length; H = Height; L = Length;
LA = Length of the area; LE = Length of the escutcheon.
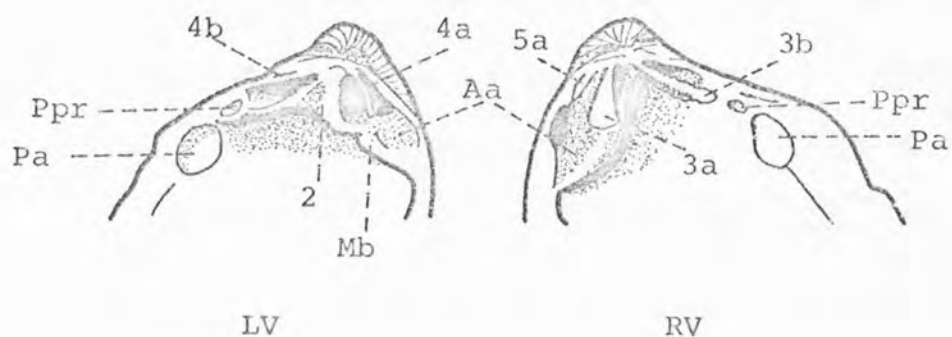
Fig. 2.36. Internal views of the left and right
valves of Myophorella, showing details of the
musculature and the cardinal plate. After Cox
(1952, p.47). x 1.
Aa = Anterior adductor scar; Mb = Myophoric
buttress (fused with 3a in the right valve);
Pa = Posterior adductor scar; Ppr = Posterior
pedal retractor scar.
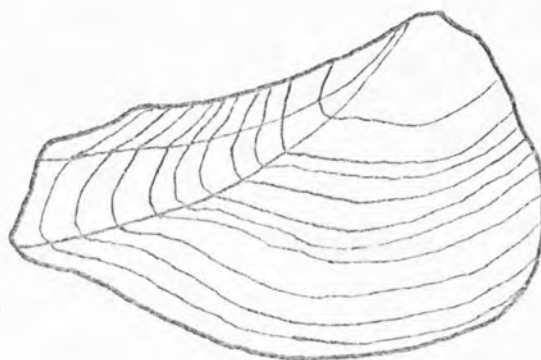
Fig. 2.37. Growth line traces of a large specimen of <u>Myophorella irregularis</u> (Seebach), from the Oxford Clay of Weymouth, Dorset (YM KD 1974/40), showing the development of a rostrate form through growth. x 1.
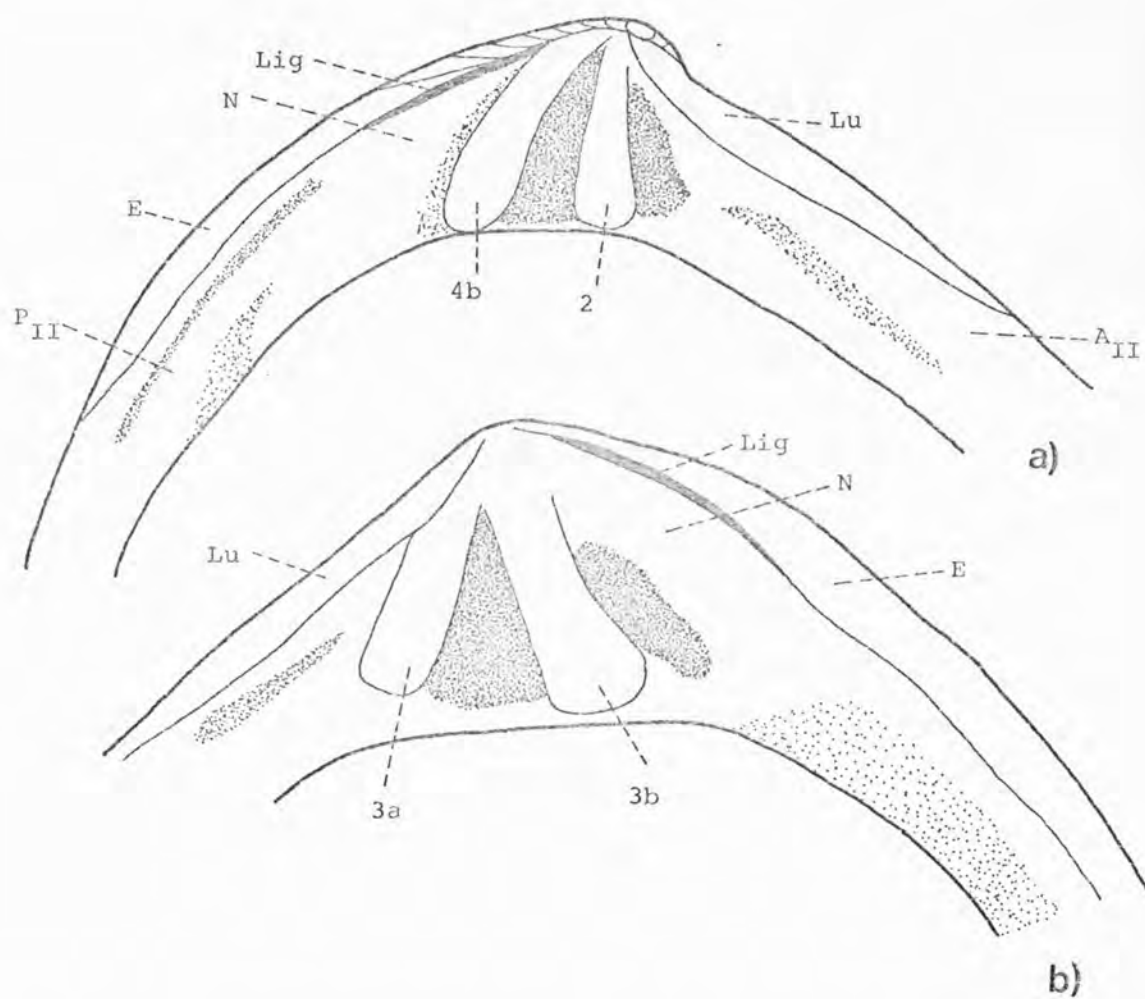
Fig. 2.38. Schematic views of the hinge areas of left (a) and right (b) valves of *Neocrassina ungulata* (Lycett), from the Kellaways Rock of Trowbridge, Wiltshire (BCM 3324), showing the broad hinge plate with elongate cardinal teeth. x 12.

E = Escutcheon; Lig = Ligament; Lu = Lunule; N = Nymph.

Fig. 2.39. Internal view of a right valve of _Neocrassina_
striato-costata (Münster), from the Oxford Clay of Lukow,
Poland, to show the musculature and internal features of a
typical species of _Neocrassina_. Specimen courtesy of
Dr. A. Radwanski.   x 12.

Aa = Anterior adductor scar; Apr = Anterior pedal retractor
scar; E = Escutcheon; Lig = Ligament; Lu = Lunule; Md =
Marginal denticulations; N = Nymph; Pa = Posterior adductor
scar; Pl = Pallial line; Ppr = Posterior pedal retractor
scar.

Fig. 2.40. Schematic internal views of the right (a) and left (b) valves of Neocrassina calvertensis sp. nov., from the Jason Subzone (Jason Zone) of Calvert (Bucks.), showing details of the cardinal plate. Note the narrower, thinner hinge plate, with shorter, more peglike cardinal teeth than in N. ungulata (Lycett). x 12.
E = Escutcheon; Lig = Ligament; Lu = Lunule; N = Nymph.
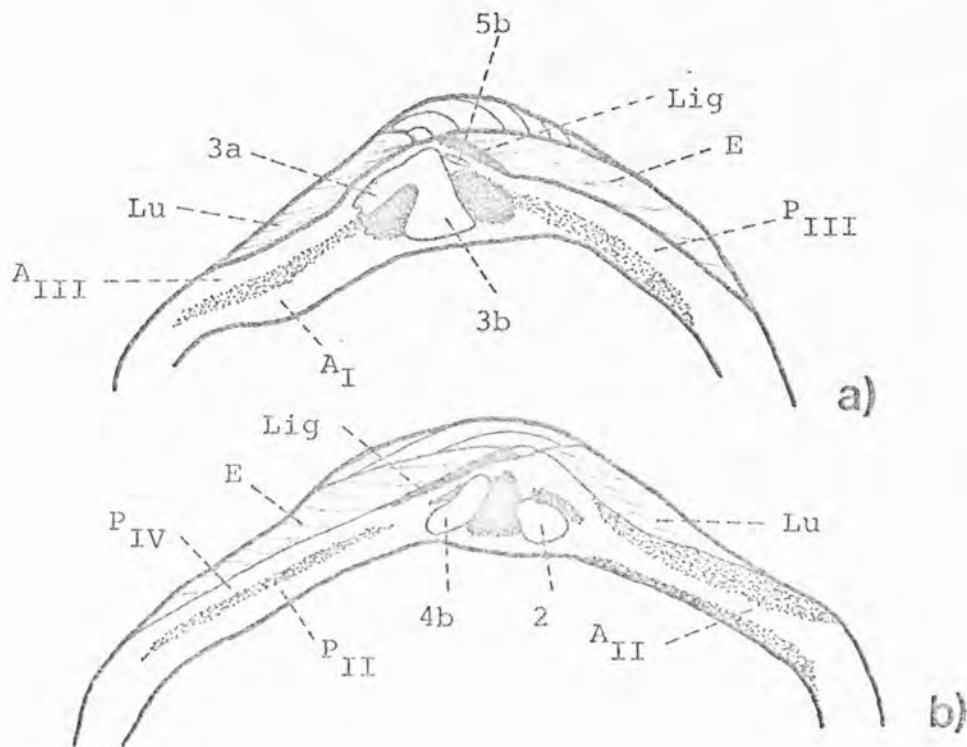
Fig. 2.41. Schematic internal views of the right (a) and
left (b) valves of _Trautscholdia phillis_ (Cottreau), from
the Lower Oxford Clay of Wiltshire (GSM Zn 2544) and the
Kellaways Rock of Wiltshire (GSM 113422) respectively,
showing the normal dentition for the species, with 3
cardinals in the right valve and 2 in the left valve. x 12.
E = Escutcheon; Lig = Ligament; Lu = Lunule.
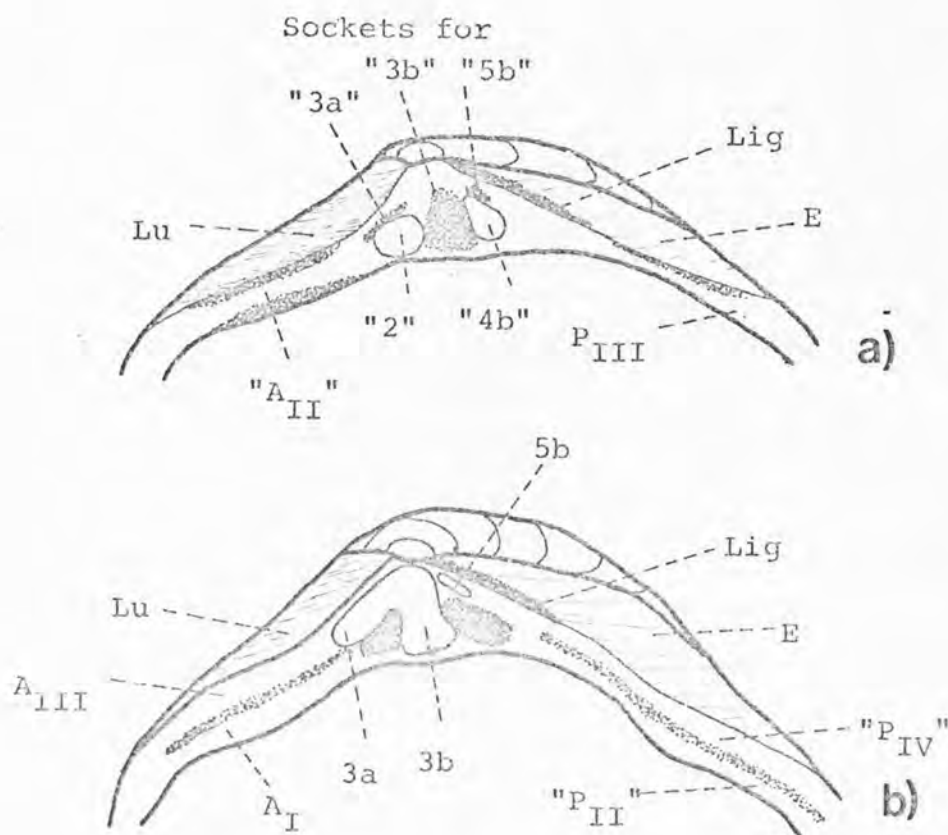
Fig. 2.42. a, b. Schematic internal views of two right valves of _Trautscholdia phillis_ (Cottreau) from the Kellaways Rock of Wiltshire (GSM 113425) and the Lower Oxford Clay (Jason Subzone, Jason Zone) or Calvert, Bucks. (LU 69943) respectively, showing two types of hinge transposition. a) Transposition of the cardinal and anterior lateral teeth, with "2" and "4b" replacing the normal 3a and 3b, and "A_{II}" replacing the normal A_I and A_{III}. b) Transposition of the posterior lateral teeth, with "P_{II}" and "P_{IV}" replacing the normal P_{III}. x 12.

E = Escutcheon; Lig = Ligament; Lu = Lunule.
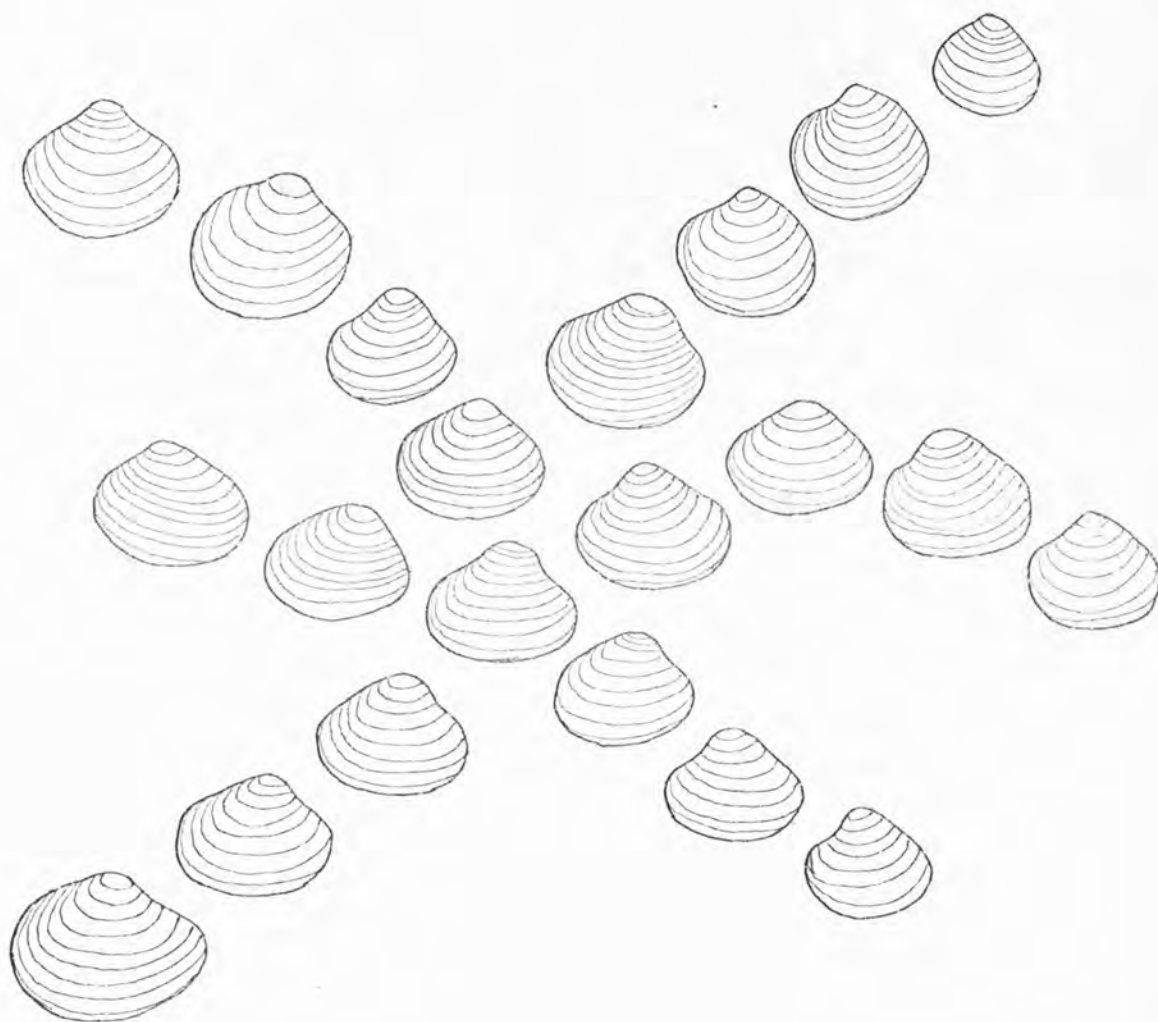
Fig. 2.43. Sketch-pictograph showing the main lines of variation
in shape and ornament in _Trautscholdia phillis_ (Cottreau) from
the Lower Oxford Clay (Calloviense - Jason Zones) of southern
England. x 2.
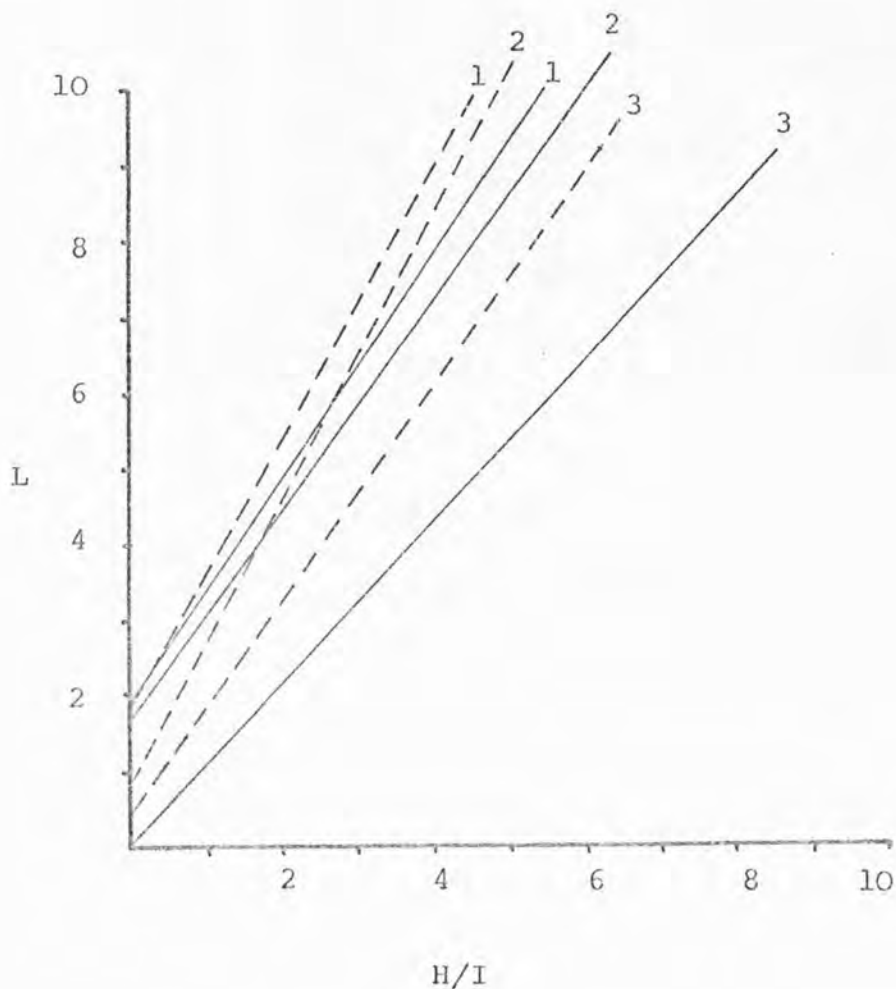
Fig. 2.44. Comparison of the regression lines for various pairs of parameters in three populations of _Trautscholdia phillis_ (Cottreau). Dashed lines represent L/I regression lines, and unbroken ones L/H regressions. Population 1 comes from the Lower Oxford Clay of Calvert (Bucks.), population 2 from the Kellaways Rock of Wiltshire (specimens in the GSM and SM), and population 3 also from the Kellaways Rock of Wiltshire (specimens in the BCM). Note the close correspondence of the lines for each of these populations, and also the close grouping of L/I and L/H lines, showing the similar growth rates for these two characters. Scale in mm.
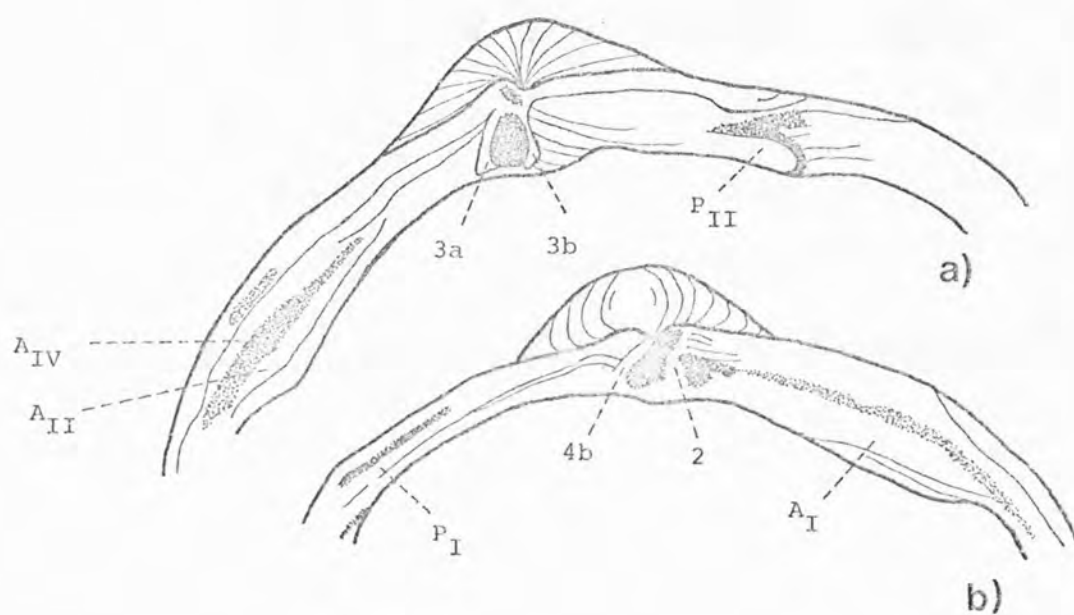
Fig. 2.45. Internal views of the right (fig. a) and the left (fig. b) valves of the type species of Protocardia, P. hillanum (J. Sowerby), from the Upper Cretaceous of England, showing details of the cardinal plate. Figure after Woods (1908). x 3.
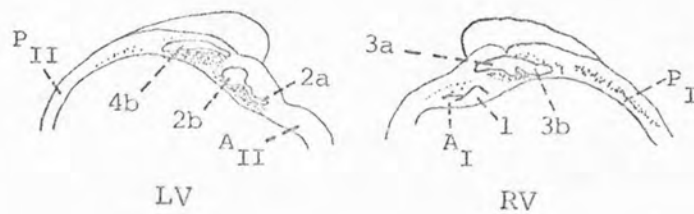
Fig. 2.46. Internal view of both valves
of Rollierella sp. from the Bathonian of
Noyen, Sarthe (after Douvillé), showing
the characteristic dentition of the genus.
Figure reproduced from Cox (1947, p. 145,
figs. 3a, 3b).
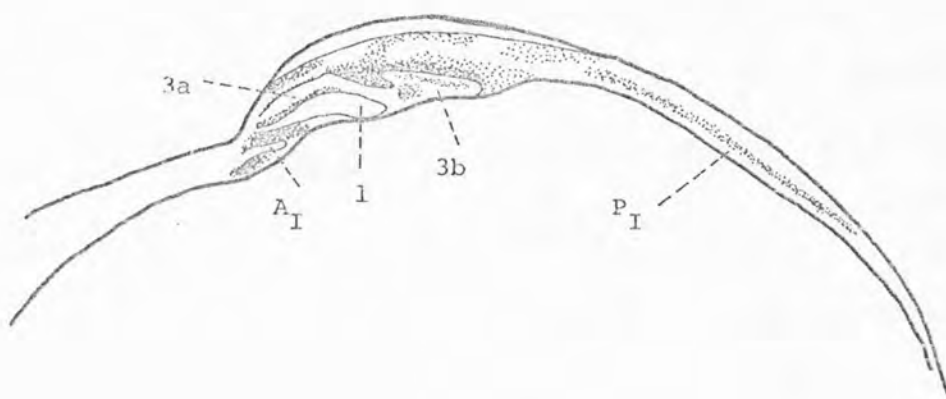
Fig. 2.47. Schematic internal view of a right valve of Rollierella
minima (J. Sowerby), from the Oxford Clay of Lukow, Poland,
showing details of the hinge plate. Drawing from a positive
latex mould made from a limestone internal mould. The teeth
3a and 3b are formed into a continuous lamina, with 3b bifid,
and 3a closely applied to the dorsal surface of the arcuate 1.
A_I is short and peglike, and placed just ventral of the anterior
end of 1. Specimen in the authors collection. x 6.
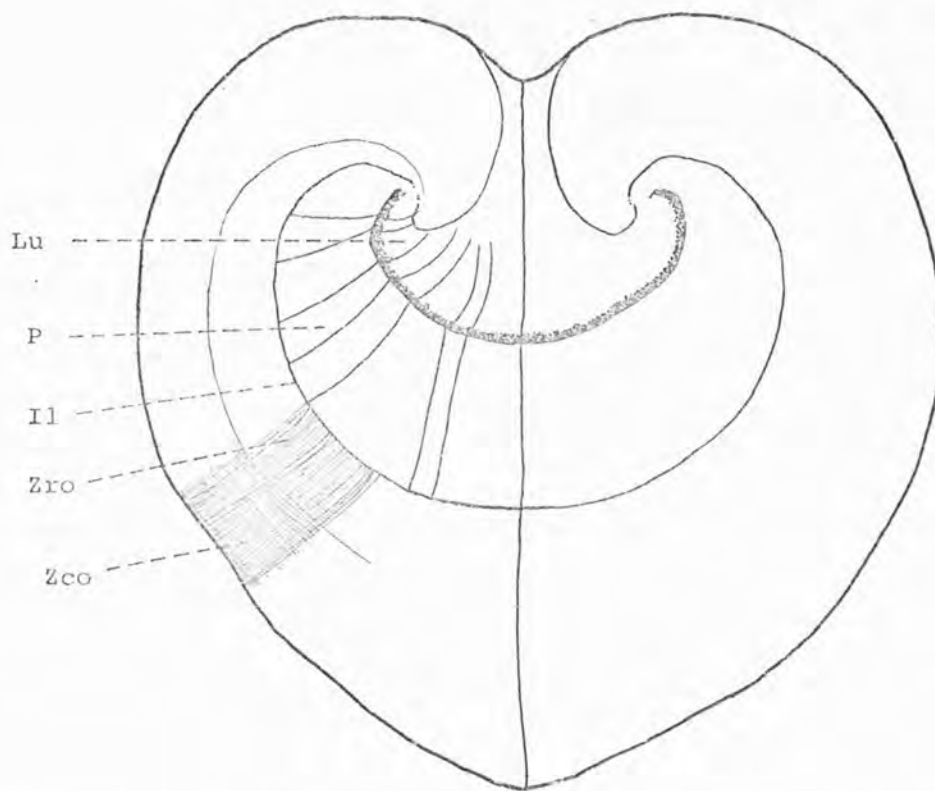
Fig. 2.48. Schematic view of the anterior of a specimen of _Rollierella minima_ (J. Sowerby) from the Oxford Clay of Lukow, Poland, showing the differentiation of the lunule and the pseudolunule. The lunule is flattened, and separated from the obliquely-sloped pseudolunule by an impressed line, making an obtuse angle between the two areas. The two zones of ornamentation on the body of the shell are shown diagrammatically, a narrow zone of radial ornament adjacent to the pseudo-lunule being replaced on the flanks of the shell by finely cancellate ornamentation. x 6. Il = Impressed line; Lu = lunule; P = Pseudolunule; Zco = Zone of cancellate ornament; Zro = Zone of radial ornament.
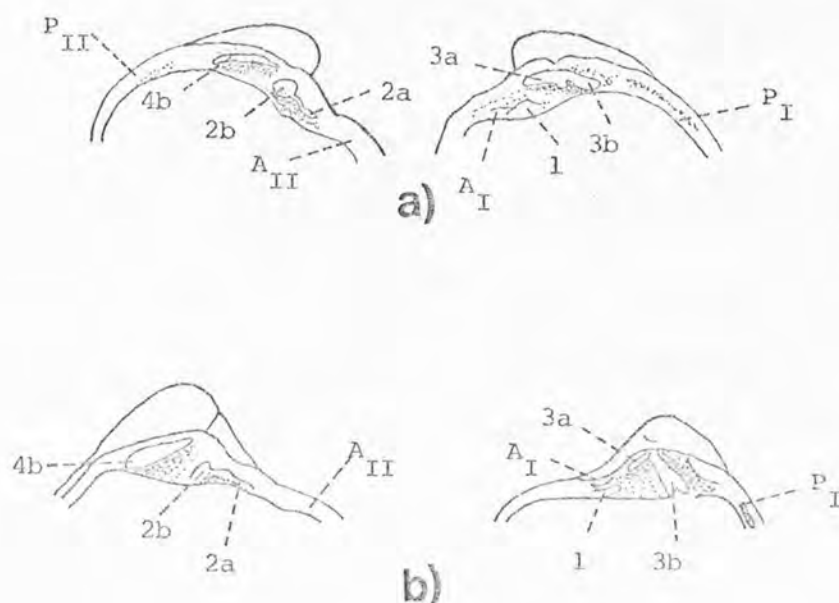
Fig. 2.49. Schematic views of the dentition of Anisocardia and Rollierella. a) The dentition of Rollierella sp. from the Bathonian of Noyen, Sarthe (after Douvillé), from Cox, 1947, p. 145. b) The dentition of Anisocardia elegans Munier-Chalmas, from the Kimmeridgian of France (after Cox, 1947, p. 145). Both x 1. The major difference is in the dentition of the right valves, 3a and 3b being united into a broad, continuous lamina in Rollierella, with 3a lying more or less directly above 1. In the left valve, 2b in Rollierella is much stouter, and more peglike, than its counterpart in Anisocardia.
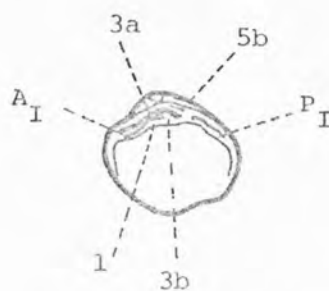
Fig. 2.50. Schematic internal view of a right valve
of <u>Anisocardia choffati</u> Boden (non de Loriol), from
the Upper Jurassic of Germany (after Boden, 1904,
p.61, pl.6, fig.9), showing the dentition typical
of <u>Anisocardia</u>, with a large 3b, laminar 3a, vestigial
5b, and 1 + P_I as a continuous lamina; 1 again is
anterior to 3a, and 3a is not applied to the dorsal
surface of 1. x 1.
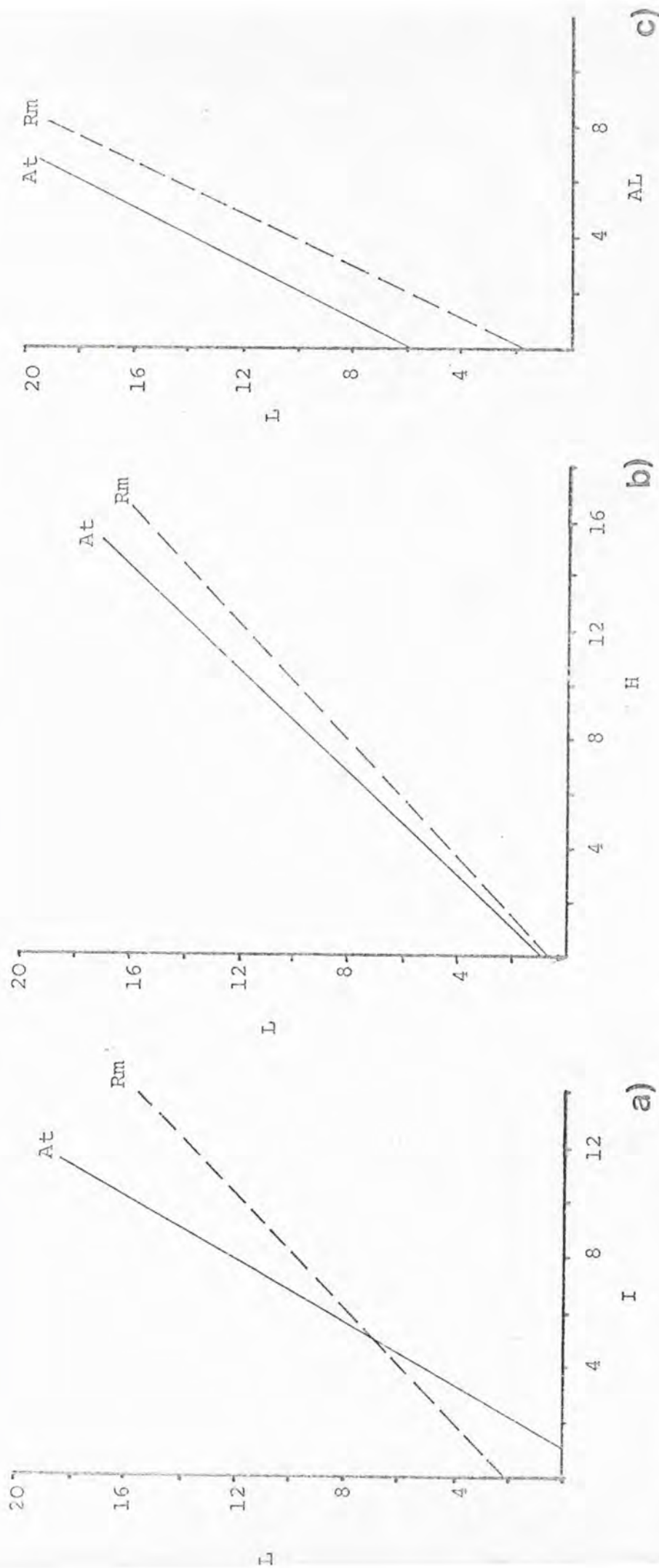
Fig. 2.51. Comparison of the L/I, L/H and L/AL regression lines for *Anisocardia tenera* (J. de C. Sowerby) and *Rollierella minima* (J. Sowerby). Fig. a) shows the average L/I regressions for several populations of the two species; note the obvious difference in growth rates, with *R. minima* being much more inflated. Fig. b) shows the L/H regressions, and Fig. c) the L/AL regressions; in both these pairs of parameters, the growth rates for the two species are similar. Scale in mm.

At = *Anisocardia tenera*; Rm = *Rollierella minima*.
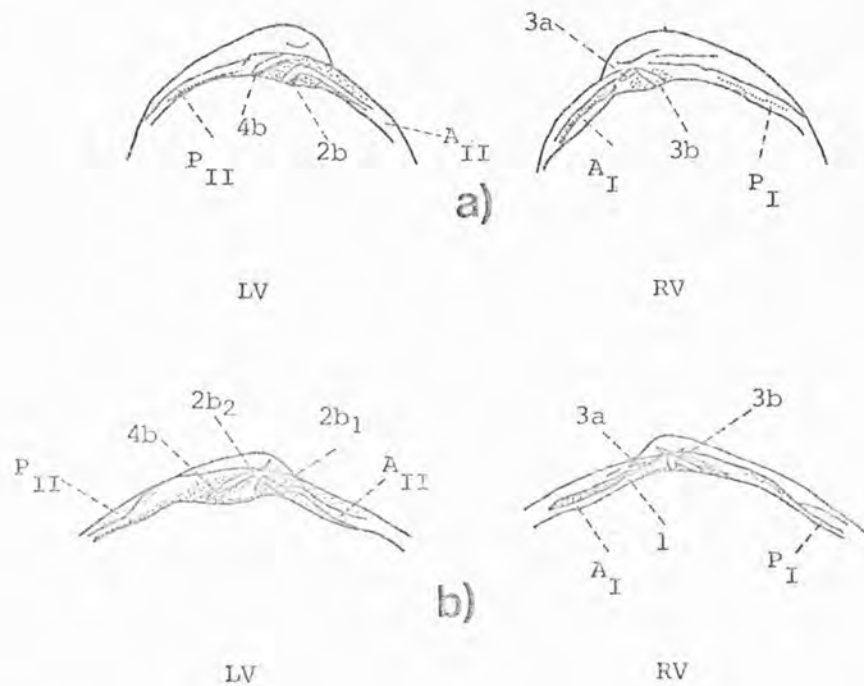
Fig. 2.52. Schematic views of the hinges of Isocyprina;
a) Internal views of the left and right valves of Isocyprina
cyreniformis (Puvignier), from the Oxfordian of France.
Note the vestigial 3a in the right valve. After Cox (1947,
p. 145), x 1. b) Internal views of the hinge of I. sharpi
Cox, from the Bathonian of Oxfordshire; again, 3a is
vestigial. After Casey (1952, p. 135), x 1.
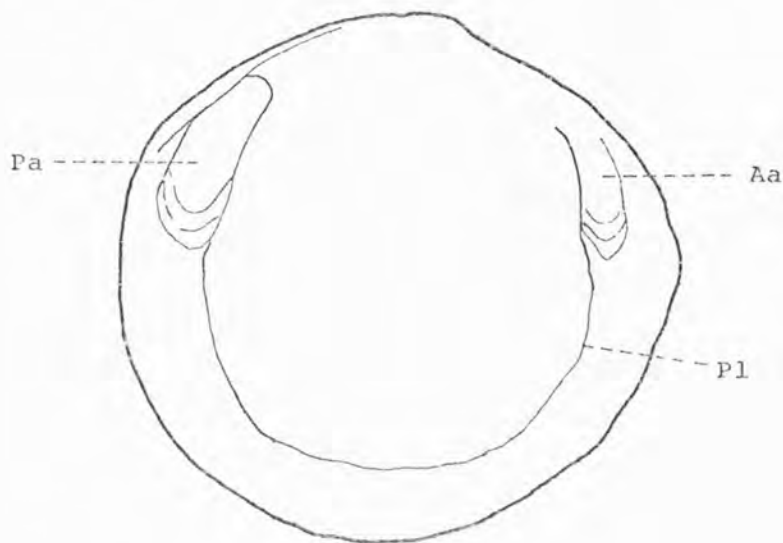
Fig. 2.53. Schematic internal view of a left valve of _Isocyprina_
roederi Arkell, from the Lower Oxford Clay (Grossouvrei Subzone,
Coronatum Zone) of Stewartby, Beds. (LU 69832), showing the musculature.
Note that the posterior adductor scar is considerably larger than
the anterior, both lying mainly outside the pallial line; note also
the lack of a pallial sinus in this specimen. x 6.
Aa = Anterior adductor scar; Pa = Posterior adductor scar;
Pl = Pallial line.
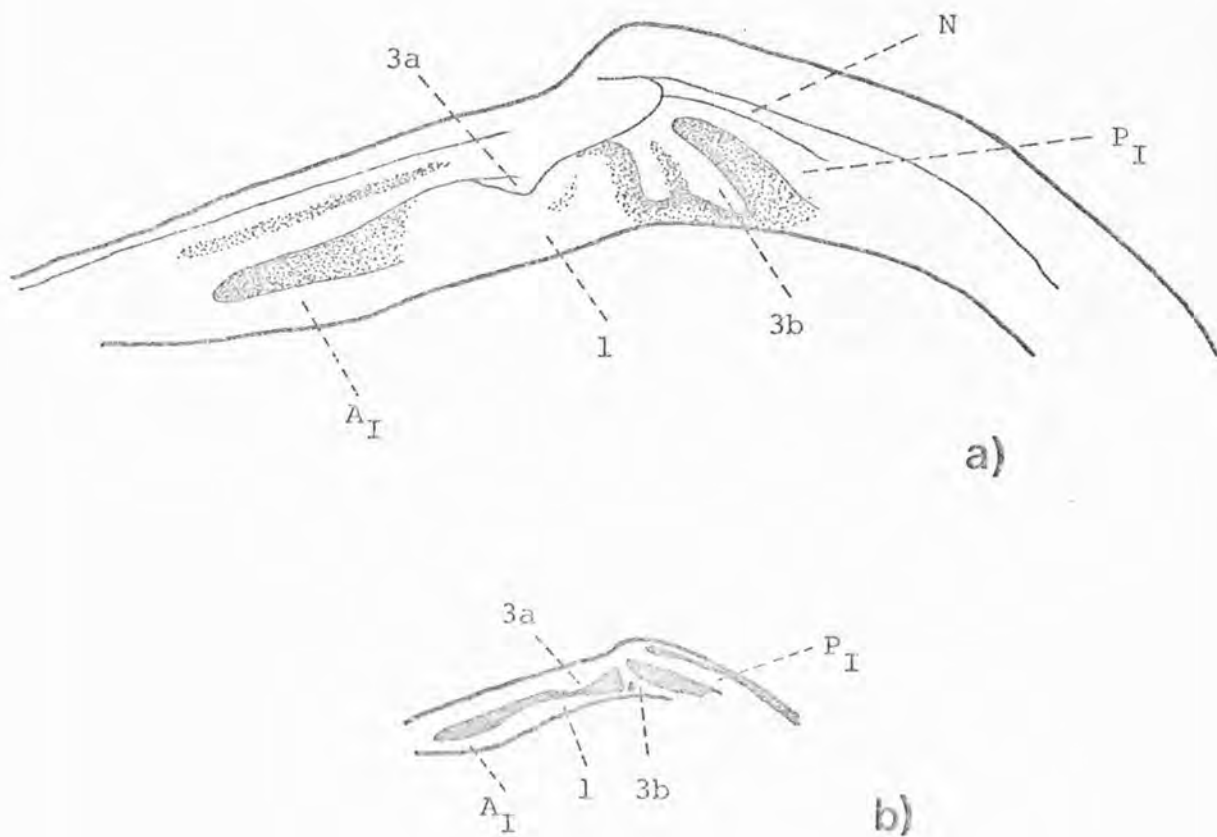
Fig. 2.54. a) Schematic internal view of a pyritised right
valve of _Isocyprina roederi_ Arkell, from the Grossouvrei
Subzone (Coronatum Zone) of Marston Moretaine, Beds. (LU 69941),
showing details of the hinge. The anteroventral part of the
cardinal plate is broken, so it is not possible to determine
whether or not A_I and 1 are united. x 12.

        b)   Low power sketch of the hinge of the same
specimen, showing a probable reconstruction of the complete
hinge; A_I and 1 are thought to be united. x 4.
N = Nymph.
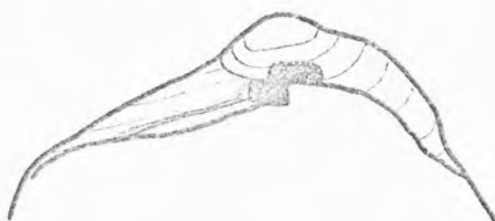
Fig. 2.55. Schematic internal view
of a right valve of *Corbulomima
macneillii* (Morris), from the Lower
Oxford Clay of Wiltshire (OUM J28230
collective), showing the presence of
a single large cardinal tooth immediately
beneath the umbo. x 12.

Fig. 2.56. Outline sketch pictograph showing the main lines of variation in the population of _Corbulomima macneillii_ (Morris), from the Lower Oxford Clay of Wiltshire. (OUM 28230 - 28231 collective)
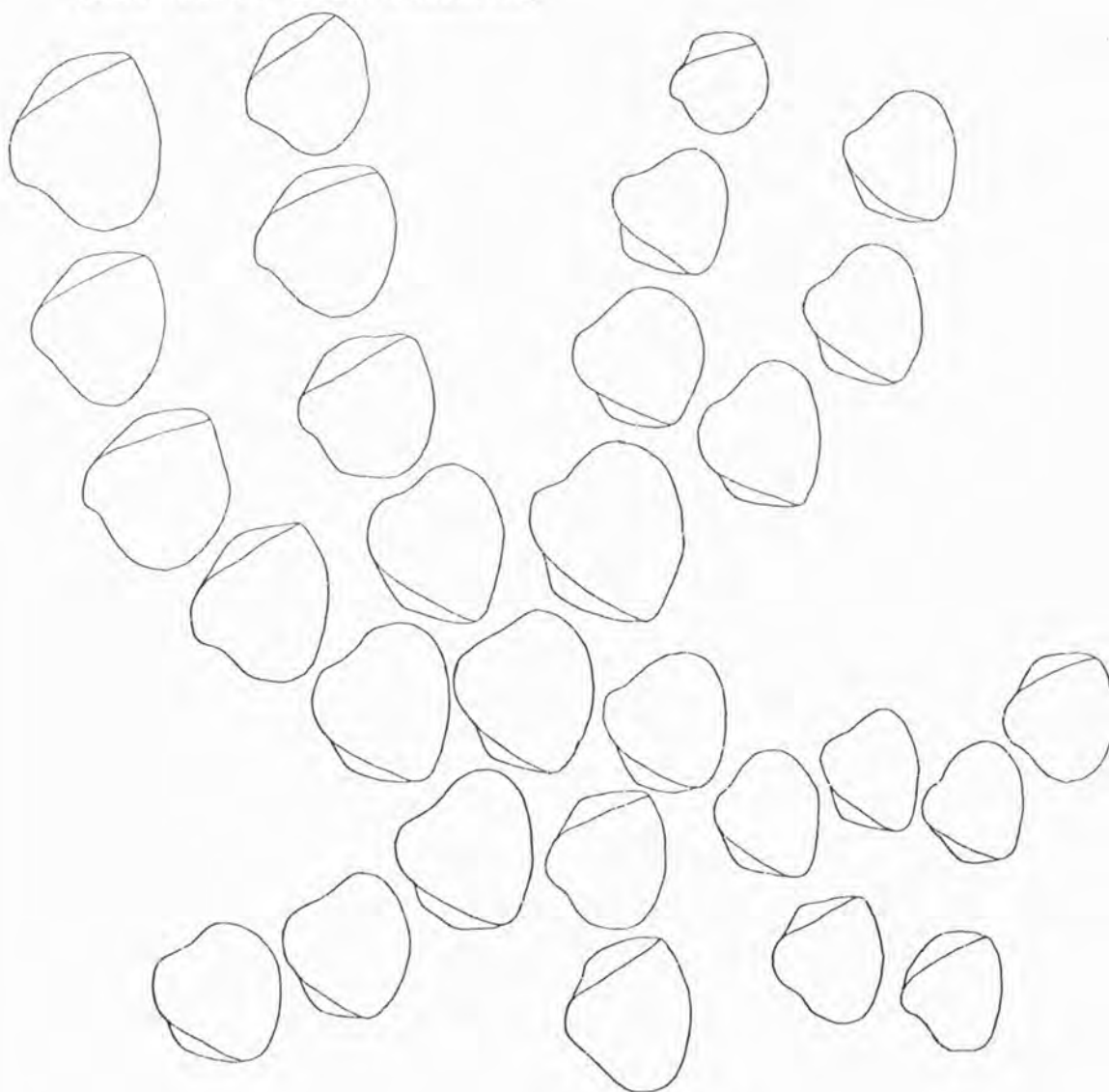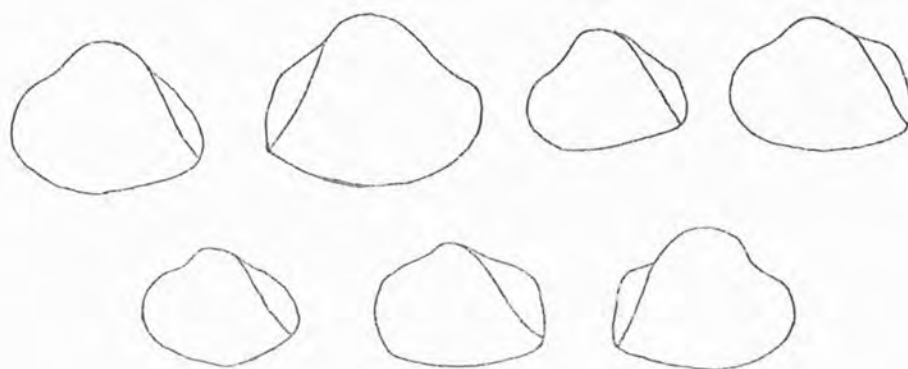
Fig. 2.56a. Schematic views of the outlines of seven specimens
of Corbulomima obscura (J. de C. Sowerby), to show the variation
in form present within the species. All specimens from the
Brora Roof Bed, Brora. Comparison with the outlines of
C. macneillii (Fig. 2.56) shows C. obscura to be more elongate
and to possess a slightly reflexed postero-ventral angle.
All x 6.
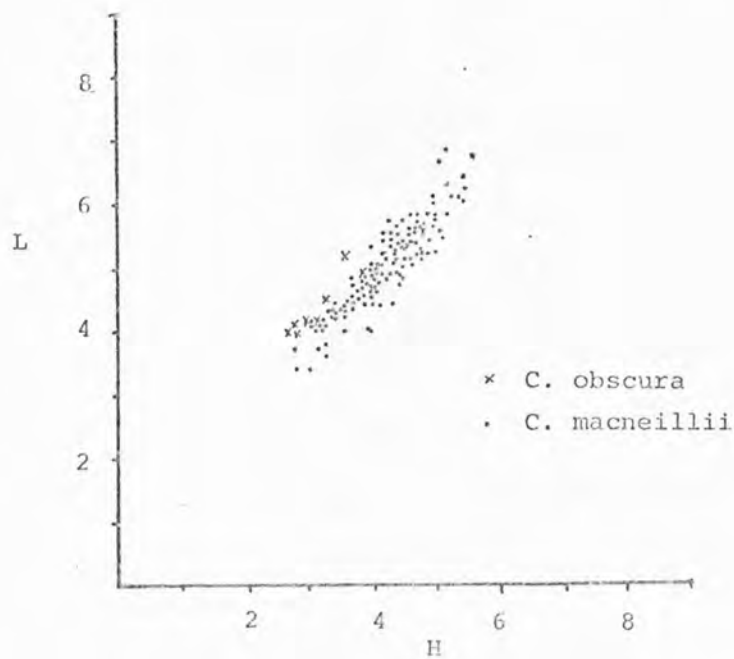
Fig. 2.57. Scatter diagram showing the length-height ratio of Corbulomima obscura (J. de C. Sowerby) and C. macneillii (Morris). Note that the points for C. obscura indicate a lower value for H than do those of C. macneillii. Scale in mm.
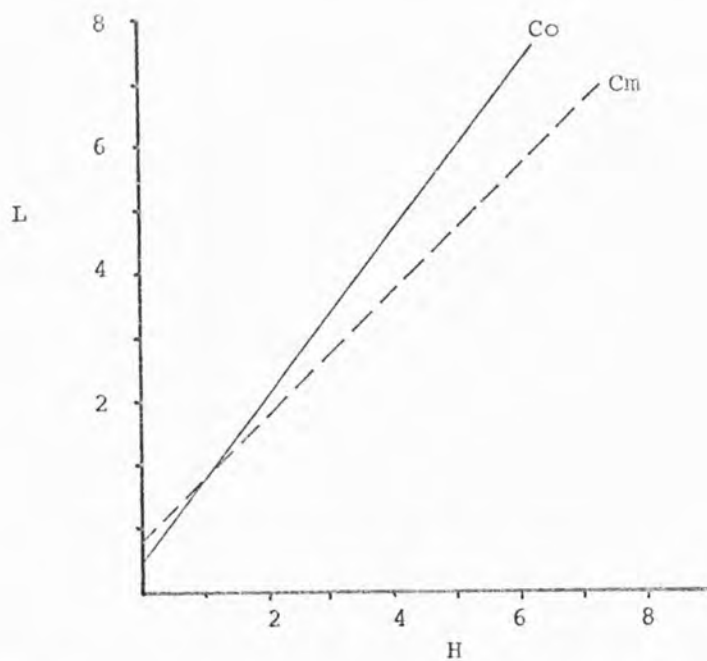
Fig. 2.58. Length-height regression lines for the scatter diagram above. The relationship between the L/H ratio of the two species now becomes more apparent. Scale in mm.
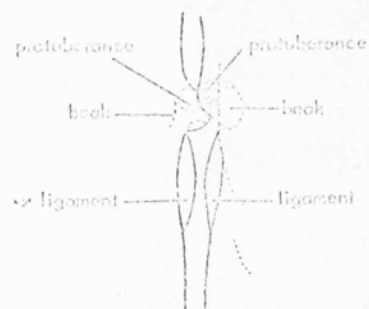
Fig. 2.59. Schematic diagram of the hinge area of
Pleuromya marginata Agassiz, from the Bathonian of
France, showing the relationship between the
protuberances on the hinge margin of each valve;
left valve to the left, view from dorsal. (After
Douvillé, 1907). Enlarged.
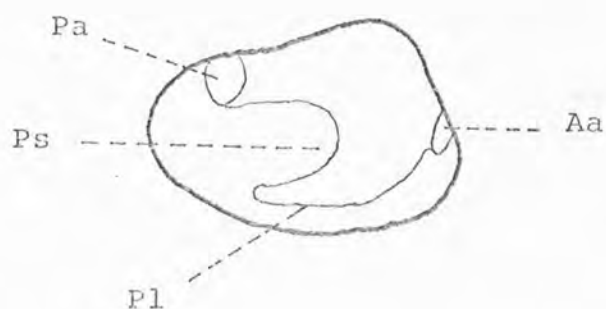
Fig. 2.60. Schematic view of an internal cast of a
specimen of Pleuromya alduini (Brongniart), from the
Kellaways Rock of Kington Langley, Wilts. (GSM Ka609),
showing the musculature and the very large pallial
sinus. Note that the posterior adductor scar is about
twice the size of the anterior, and that the lower limb
of the pallial sinus is not confluent with the pallial
line. Seen from the right; ribs not shown. x 1.
Aa = Anterior adductor scar; Pa = Posterior adductor
scar; Pl = Pallial line; Ps = Pallial sinus.
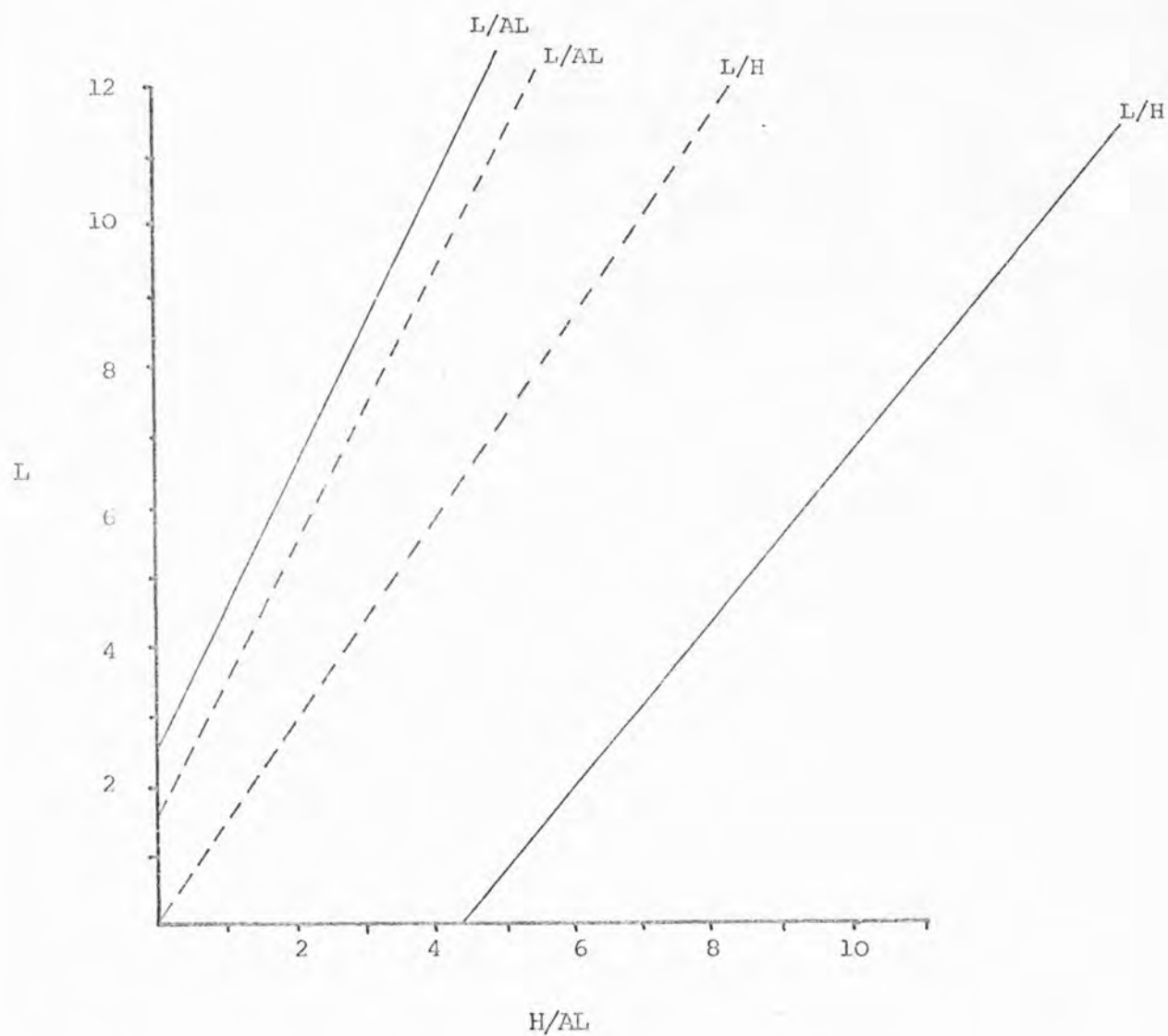
Fig. 2.61. Comparison of the L/H and L/AL regression lines for populations of Thracia depressa (J.de C. Sowerby) from the Lower (dashed lines) and Upper (unbroken lines) Oxford Clay of England. The L/AL regressions for the two horizons compare closely, but those of L/H vary considerably, with the Upper Oxford Clay forms being higher and less elongate. Scale in mm.

Stages		Zones	Subzones	Divisions
OXFORDIAN	LOWER	Cardioceras cordatum	C. cordatum	UPPER OXFORD CLAY
			C. costicardia	
			C. bukowskii	
		Quenstedtoceras mariae	C. praecordatum	
			C. scarburgense	
CALLOVIAN	UPPER	Quenstedtoceras lamberti		MIDDLE OXFORD CLAY
		Peltoceras athleta	Upper Middle Lower	
	MIDDLE	Erymnoceras coronatum	K.(Zugokosmoceras) grossouvrei	LOWER OXFORD CLAY
			K.(Zugokosmoceras) obductum	
		Kosmoceras jason	K.(Gulielmites) jason	
			K.(Gulielmites) medea	
	LOWER	Sigaloceras calloviense	S.(Catasigaloceras) enodatum	
			Sigaloceras calloviense	KELLAWAYS ROCK
			Proplanulites koenigi	
		Macrocephalites macrocephalus	M.(Kamptokephalites) kamptus	KELLAWAYS CLAY
			M.(Macrocephalites) macrocephalus	UPPER CORNBRASH

Table 2.1. The Zones of the Callovian and Lower Oxfordian.

WOODWARD 1895	BUCKMAN 1913	MORLEY-DAVIES 1916	NEAVERSON 1925	BRINKMANN 1929	ARKELL 1933	CALLOMON 1968	DIVISIONS
	Lamberti	Renggeri	Lamberti	Lamberti	Lamberti	Lamberti	Middle Oxford Clay
Ornatus	Athleta Ornatum	Athleta U. Ornatum	Athleta/ Duncani	Spinosum	Athleta	Athleta	
	Coronatum	Coronatum	Castor Coronatum Elizabethae Conlaxatum	Castor/Pollux	Reginaldi	Coronatum	Lower Oxford Clay
	Anceps	L. Ornatum		Jason	Jason	Jason	
Calloviensis	Calloviense			Macrocephalus	Calloviense	Calloviense	Kellaways Rock
	Koenigi				Koenigi	Macrocephalus	Kellaways Clay

TABLE 2.2. Zonal schemes applied to the Lower Oxford Clay between 1895 and 1968.

GENERA AND FEEDING GROUPS	MAXIMUM SHELL LENGTH (mm)	EPIFAUNAL				INFAUNAL						TAXONOMIC POSITION
		SWIMMING	FREE-LIVING OR CEMENTED	BYSSALLY ATTACHED	"PENDENT"	NON-SIPHONATE	SHORT SIPHONS	LONG SIPHONS	MUCUS-TUBE FEEDERS	BYSSALLY ATTACHED	MOBILE	
DEPOSIT-FEEDERS												SUPERFAMILY
PALAEONUCULA	18.4										X	NUCULACEA
MESOSACCELLA	17.6										X	NUCULANACEA
SUSPENSION-FEEDERS												
SOLEMYA	38.0							X				SOLEMYACEA
GRAMMATODON	28.0					X					X	ARCACEA
MODIOLUS	70.0			X								MYTILACEA
PINNA	82.4			X								PINNACEA
PTEROPERNA	15.3				X							PTERIACEA
PARAINOCERAMUS	72.5				X							PTERIACEA
BOSITRA	15.0				X							PECTINACEA
OXYTOMA	39.8				X							PECTINACEA
MELEAGRINELLA	33.7				X							PECTINACEA
ENTOLIUM	31.0	X										PECTINACEA
BYSSENTOLIUM	12.3			X								PECTINACEA
CAMPTONECTES	58.0			X								PECTINACEA
CHLAMYS	9.7			X								PECTINACEA
RADULOPECTEN	76.0			X								PECTINACEA
PLICATULA	26.8		X									PECTINACEA
GRYPHAEA	80.0		X									OSTREACEA
NANOGYRA	11.2		X									OSTREACEA
MYOPHORELLA	88.0					X					X	TRIGONACEA
DISCOMILTHA	47.0						X	X				LUCINACEA
NEOCRASSINA	21.2					X					X	ASTARTACEA
TRAUTSCHOLDIA	12.5					X					X	ASTARTACEA
PROTOCARDIA	30.3						X				X	CARDIACEA
ANISOCARDIA	25.0						X				X	ARCTICACEA
ISOCYPRINA	20.0						X				X	ARCTICACEA
ROLLIERELLA	24.0						X				X	ARCTICACEA
CORBULOMIMA	6.8						X			X		MYACEA
PLEUROMYA	71.0							X				PHOLADOMYACEA
THRACIA	65.0							X	X			PANDORACEA

Table 2. 3. Life habits of the bivalve genera represented in the Lower Oxford Clay.

TABLE 2.4. Comparison of the measurements and variation statistics for populations of _Thracia_ _depressa_ (J. de C. Sowerby) from the Lower and Upper Oxford Clay of England.

	LOWER OXFORD CLAY		UPPER OXFORD CLAY		
	H	AL	H	I	AL
N	20	20	16	14	16
$\bar{x}$	70.5%	61.3%	78.6%	41.7%	59.4%
Max	77.1	66.9	92.3	60.8	69.4
Min	63.7	54.3	71.5	29.9	51.2
OR	13.4	12.6	20.8	30.9	18.2
s	3.84	3.21	5.84	7.89	6.34
s^2	14.77	10.30	34.10	62.30	40.19
V	5.45	5.23	7.43	12.67	10.67
	0.86	0.72	1.46	2.11	1.59

views. Lower Oxford Clay, Coronatum
Zone, Stewartby, Bedfordshire, x 1.6.
BM LL27713.

8a-8b.   Paratype. External view of left valve and
dorsal view. Same horizon and locality
as above, x 1.6. BM LL27714.

9.   Paratype. Internal view of right valve.
Same horizon and locality as above,
x 1.6. BM LL27715.

10a-10d.   Paratype. External view of left valve,
right valve, posterodorsal and dorsal
views. Same horizon and locality as
above, x 1.6. BM LL27716.

11.   Paratype. Internal view of left valve.
Same horizon and locality as above,
x 1.6. BM LL27717.

PLATE 1.

Nuculoma pollux (Raspail)

Fig.

1a-1d.   External view of left valve, right valve,
dorsal view and detail of the ornament.
Oxford Clay, Wiltshire, x 2.2 (Figs.
1a-1c), x 3.3 (Fig. 1d). YM KD1974/1.

Nuculoma kathryni sp. nov.

2a-2c.   Holotype. External view of left valve,
anterodorsal view and posterior view.
Oxford Clay, Wilts., x 1.9. GSM 114030.

3a-3b.   Paratype. Internal and external views of
right valve. Same horizon and locality
as above, x 1.9. GSM 114035.

4.   Paratype. External view of right valve.
Same horizon and locality as above, x
1.9. GSM 114032.

5.   Paratype. External view of right valve.
Same horizon and locality as above,
x 1.9. GSM 114033.

6.   Paratype. External view of left valve.
Same horizon and locality as above, x
1.9. GSM 114031.

Palaeonucula triangularis sp. nov.

7a-7d.   Holotype. External views of left valve,
right valve, posterodorsal and dorsal

PLATE 1
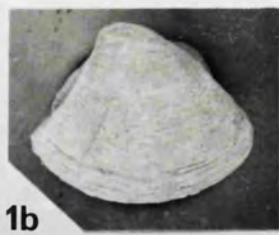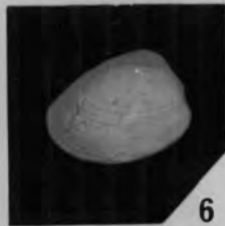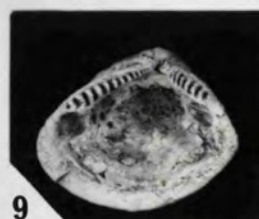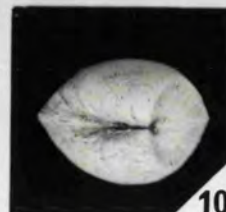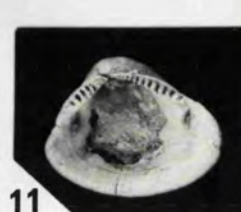
17.   External view of right valve, internal
        mould. Upper Oxford Clay, Cordatum
        Zone, Warboys, Hunts., x 1.2. GSM Dr2526.

18.   External view of left valve, internal
        mould. Same horizon and locality as
        above, x 1.2.   GSM Dr2508.

19.   Dorsal view of internal mould. Oxford Clay,
        Lukow, Poland, x 1.5. KD Lukow 9.

8.   Paratype. External view of right valve.
Lower Oxford Clay, Jason Zone, same
locality as above, x 1.9. LU 68607.

9.   Paratype. External view of left valve,
Coronatum Zone, same locality as
above, x 1.9. LU 68608.

10.   Paratype. External view of right valve,
same horizon and locality as above,
x 1.9. LU 68609.

11.   Paratype. External view of left valve,
internal mould. Coronatum Zone,
Stewartby, Beds., x 1.5. LU 68610.

12.   Paratype. Dorsal view of internal mould.
Same locality and horizon as above,
x 1.7. LU 68611.

Palaeonucula cottaldi (de Loriol)

13.   Internal view of right valve. Oxford Clay,
Wiltshire, x 0.8. GSM Y2082.

14a-b.   Dorsal view and external view of left valve.
Same horizon and locality as above,
x 1.1. GSM Y2083.

15.   External view of left valve. Oxford Clay,
"Near Osmington", Dorset, x 1.1. GSM Y2049.

16.   External view of left valve. Upper Oxford
Clay, Mariae Zone, Scarborough,
Yorkshire, x 1.3. YM KD1974/59.

PLATE 2.

Palaeonucula triangularis sp. nov.

Fig.

1a-1c.   Paratype. External view of left valve,
right valve and dorsal view. Lower
Oxford Clay, Coronatum Zone, Stewartby,
Bedfordshire, x 1.6. BM LL27718.

2a-2b.   Paratype. External view of right valve
and dorsal view. Same horizon and
locality as above, x 1.7. BM LL27719.

3.   Paratype. External view of left valve.
Same horizon and locality as above,
x 1.6. BM LL27720.

4.   Paratype. Internal view of left valve.
Same horizon and locality as above,
x 1.6. BM LL27721.

5.   Paratype. External view of left valve.
Lower Oxford Clay, Coronatum Zone,
Calvert, Buckinghamshire, x 2.0.
LU 68604.

6.   Paratype. External view of right valve.
Lower Oxford Clay, Jason Zone,
Stewartby, Beds., x 1.9. LU 68605.

7.   Paratype. External view of left valve.
Lower Oxford Clay, Coronatum Zone,
Norman Cross, Huntingdonshire, x 1.9.
LU 68606.

PLATE 2
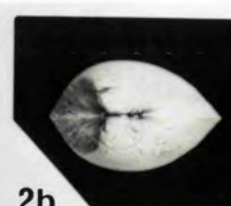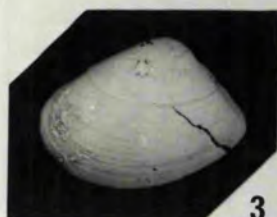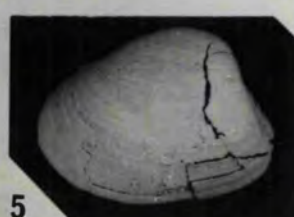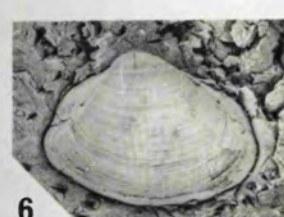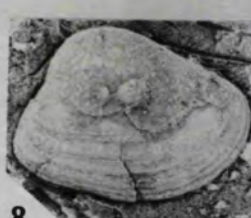
25.   External view of left valve. Same horizon
        and locality as above, x 1.1. LU 69755.

26.   External view of both valves. Same horizon
        and locality as above, x 1.8. LU 69754.

27.   External view of right valve. Lower Oxford
        Clay, Grossouvrei Subzone, Norman
        Cross, Huntingdonshire, x 1.1.
        LU 69750.

28.   External view of right valve. Lower Oxford
        Clay, Grossouvrei Subzone, Calvert,
        Bucks., x 1.1. LU 69758.

29a-b. Internal view of left valve, magnified and
        natural size. Same horizon and
        locality as above, x 1.2 (12a), x 2.9
        (12b). LU 69756.

30.   External view of left valve. Lower Oxford
        Clay, Jason Subzone, Calvert, Bucks.,
        x 1.5. LU 69749.

31.   External view of left valve. "Kelloway Rock",
        Castle Rock, Scarborough, Yorkshire,
        x 1.3. Leckenby Collection, SM J12569.

17.   External view of left valve, internal mould. Same horizon and locality as above, x 1.9. LU 68622.

18a,18b.   External view of left valve and dorsal view, internal mould. Same horizon and locality as above, x 1.9. LU 68623.

19.   Dorsal view. Oxford Clay, Kempston, Beds., x 1.9. GSM 75702.

Solemya woodwardiana Leckenby

20.   Holotype. External view of left valve. "Kelloway Rock", Castle Rock, Scarborough, Yorkshire, x 1.3. Leckenby Collection. SM J6008. Figured by Leckenby, 1859, pl. 3, fig. 7.

21.   Paratype. External view of left valve. Same horizon and locality as above, x 1.3. Leckenby Collection, SM J12570.

22.   External view of right valve. Lower Oxford Clay, Brora, Sutherlandshire, x 1.0. LU 69744.

23.   External view of left valve. Same horizon and locality as above, x 0.9. LU 69743.

24.   External view of right valve. Lower Oxford Clay, Grossouvrei Subzone, Calvert, Buckinghamshire, x 1.5. LU 69752.

8.   External view of right valve. Same horizon
          and locality as above, x 1.9.
          GSM 75698.

9.   External view of left valve. Lower Oxford
          Clay, Obductum Subzone, Stewartby,
          Bedfordshire, x 2.0. LU 68613.

10.   External view of left valve. Same horizon
          and locality as above, x 2.0.
          LU 68614.

11.   External view of right valve. Same horizon
          and locality as above, x 2.0.
          LU 68615.

12a,12b. External view of left valve and dorsal
          view. Same horizon and locality as
          above, x 2.0. LU 68616.

13.   External view of right valve. Grossouvrei
          Subzone, Stewartby, Beds., x 2.0.
          LU 68617.

14.   External view of right valve. Same horizon
          and locality as above, x 1.9.
          LU 68618.

15.   Internal view of left valve. Grossouvrei
          Subzone, Marston Moretaine, Beds.,
          x 1.9. LU 68619.

16.   Dorsal view. Obductum Subzone, Stewartby,
          Beds., x 1.9. LU 68621.

PLATE 3.

Mesosaccella morrisi (Deshayes)

Fig.

1. Neotype. Internal view of right valve.
   Lower Oxford Clay, Christian Malford,
   Wiltshire, x 1½. BM L67154.

2. Neoparatype. External view of right
   valve. Same horizon and locality as
   above, x 1.7. BM L67155.

3. External view of left valve, internal mould.
   Upper Oxford Clay, Scarborough,
   Yorkshire, x 1.3. YM Tsp.188.
   Holotype of Nucula nuda Phillips, 1829,
   pl. 5, fig. 5.

4. External view of right valve, internal mould.
   Same horizon and locality as above,
   x 1.3. YM 881.

5. Internal view of left valve. Lower Oxford
   Clay, Obductum Subzone, Stewartby,
   Bedfordshire, x 1.7. Authors collection,
   KD 500.

6. External view of right valve. Same horizon
   and locality as above, x 2.0. LU 68612.

7. External view of right valve. Oxford Clay,
   Kempston, Bedfordshire, x 1.9.
   GSM 75700.

PLATE 3
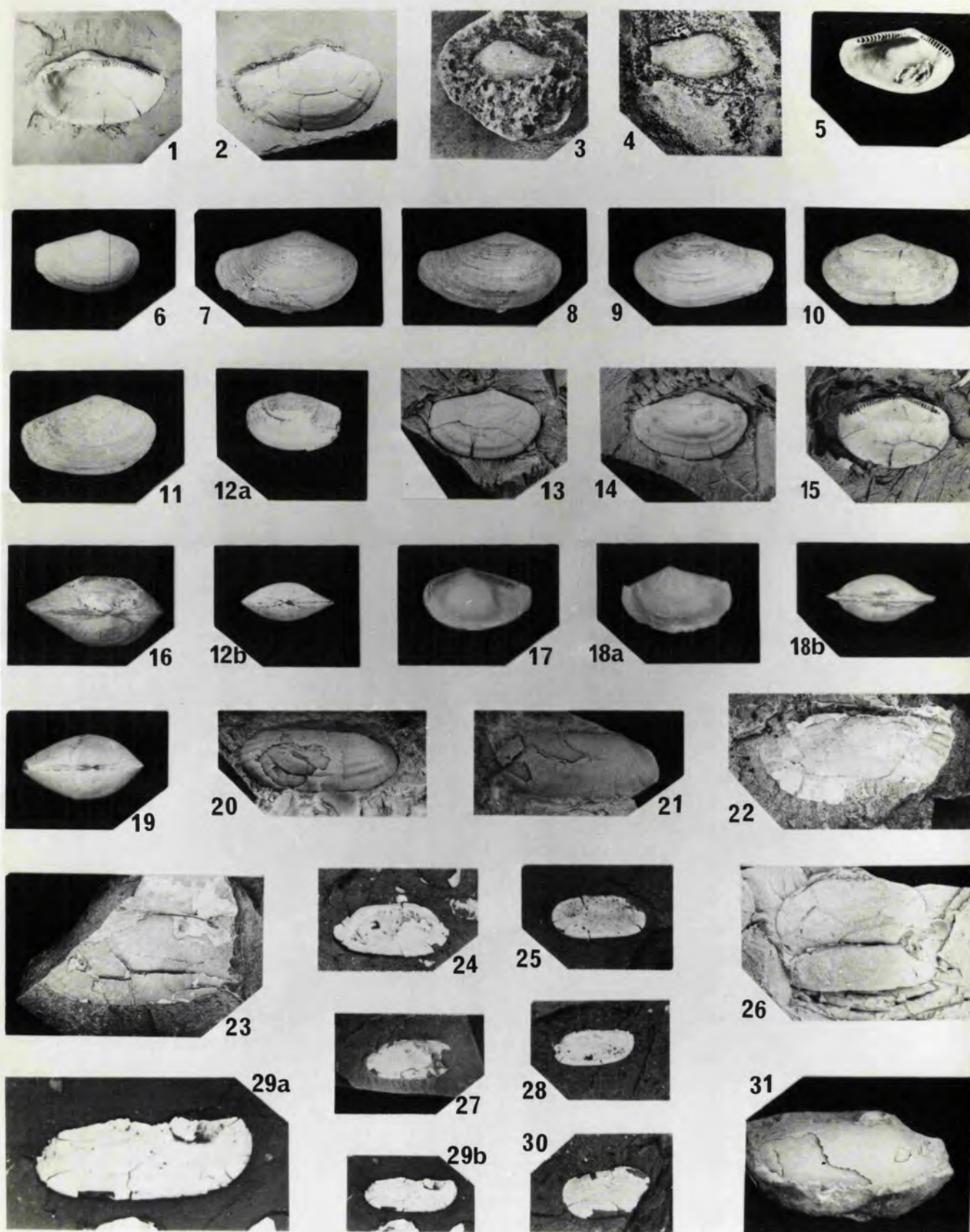
24a-b.   External view of left valve and dorsal view.

               Oxford Clay, Chippenham, Wilts.,

               x 1.4. GSM 52300.

Grammatodon (*Grammatodon*) *clathrata* (Leckenby)

25.   External view or right valve. Cornbrash,

               Scarborough, Yorkshire, x 0.8.

               YM KD1974/9.

26.   Holotype. External view of left valve.

               Hackness Rock, Scarborough, Yorkshire,

               x 1.1. Leckenby Collection, SM J6005.

16.   External view of left valve. Same horizon

           and locality as above, x 1.2.

           LU 68646.

17a-c.   External view of right valve, left valve

           and dorsal view. Medea Subzone,

           Stewartby, Beds., x 1.3. LU 68647.

18.   External view of left valve. Lower Oxford

           Clay, Jason Subzone, Calvert, Bucks.,

           x 1.1. LU 68648.

19.   External view of right valve. Same horizon

           and locality as above, x 1.1.

           LU 68649.

20.   External view of right valve, 'Silcoset'

           cast. Lower Oxford Clay, Jason

           Subzone, Norman Cross, Hunts., x 1.1.

           LU 68650.

21a-c.   External view, internal view and dorsal

           view of right valve. Kellaways Rock,

           Sutton Benger, Wiltshire, x 1.1.

           GSM Zr1699.

Grammatodon (_Grammatodon_) _montaneyensis_ (de Loriol)

22.   External view of right valve, internal mould.

           Lower Oxford Clay of Snowsdown, Kent

           (borehole), x 2.0. GSM K113.

23.   External view of left valve. Kellaways Rock,

           Sutton Benger, Wilts., x 1.2.

           GSM Zr1700.

8.   External view of left valve, 'Silcoset'
                cast. Same horizon and locality as
                above, x 2.4. LU 69761.

9.   External view of left valve, 'Silcoset'
                cast. Same horizon and locality as
                above, x 3.3. LU 69762.

10.   External view of left valve. Lower Oxford
                Clay, Grossouvrei Subzone, Stewartby,
                Beds., x 1.8. LU 69765.

11.   Internal view of right valve. Same horizon
                and locality as above, x 1.6. LU 68627.

Grammatodon (*Grammatodon*) *concinna* (Phillips)

12.   Holotype. External view of left valve,
                internal mould. Upper Oxford Clay,
                Mariae Zone, Scarborough, Yorkshire,
                x 1.7. Phillips Collection, YM Tsp 135.
                Figured by Phillips, 1829, pl. 5, fig. 9.

13.   External view of left valve. Lower Oxford
                Clay, Jason Subzone, Norman Cross,
                Hunts., x 1.4. LU 68624.

14.   External view of right valve. Lower Oxford
                Clay, Jason Subzone, Calvert, Bucks.,
                x 1.2. LU 68644.

15.   External view of left valve. Same horizon
                and locality as above, x 1.2.
                LU 68645.

PLATE 4.

Grammatodon (*Grammatodon*) *minima* (Leckenby)

Fig.

1.   Holotype. External view of left valve.
          Hackness Rock, Scarborough, Yorkshire,
          x 2.1. Leckenby Collection, SM J6007a.

2.   Paratype. External view of right valve.
          Same horizon and locality as above,
          x 1.5. Leckenby Collection, SM J6007b.

3.   External view of left valve, 'Silcoset' cast.
          Lower Oxford Clay, Grossouvrei Subzone,
          Chickerell, Dorset, x 1.4. LU 69759.

4.   External view of right valve, 'Silcoset'
          cast. Same horizon and locality as
          above, x 2.6. LU 69764.

5.   External view of left valve, 'Silcoset'
          cast. Lower Oxford Clay, Grossouvrei
          Subzone, Stewartby, Beds., x 1.7.
          LU 69790.

6.   External view of left valve. Same horizon
          and locality as above, x 1.7.
          LU 68626.

7.   External view of left valve, 'Silcoset' cast.
          Lower Oxford Clay, Grossouvrei
          Subzone, Calvert, Bucks., x 2.7.
          LU 69763.

PLATE 4
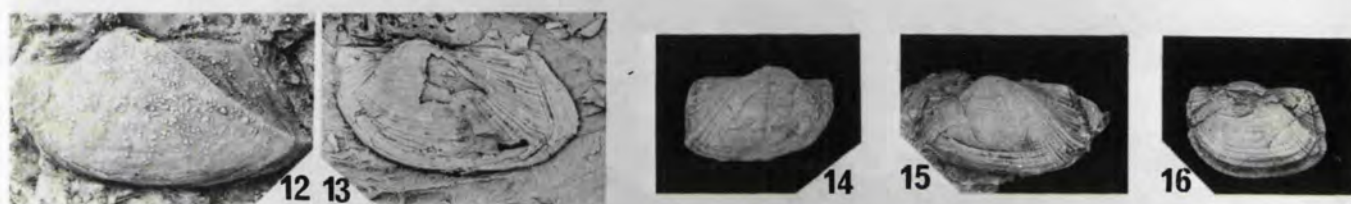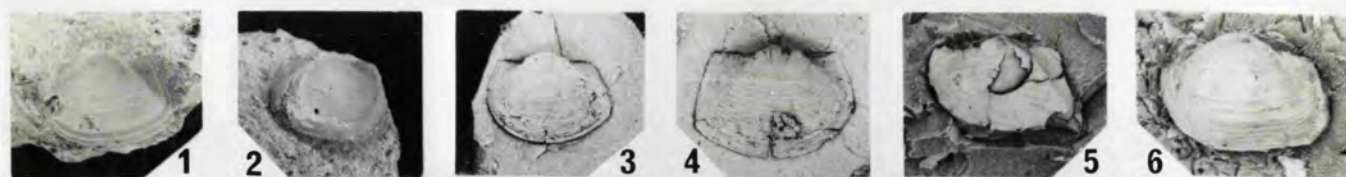
8.   Holotype. External view of right valve.
Upper Oxford Clay, Cordatum Zone
("Red Nudule Beds"), Weymouth, Dorset,
x 1. Sowerby Collection, BM 43251.

9.   External view of left valve, Same horizon
and locality as above, x 1.
YM KD1974/13.

10a-10b. External view of left valve and posterodorsal
view. Same horizon and locality as
above, x 1. YM KD1974/11.

11.   External view of left valve. Lower Oxford
Clay, Coronatum Zone, Calvert,
Buckinghamshire, x 1. LU 70015.

12.   External view of left valve. Oxford Clay,
Lukow, Poland, x 1. KD Lukow 4.

Pteroperna ? *pygmaea* (Dunker)

13.   External view of left valve. Lower Oxford
Clay, Wiltshire, x 2. BCM Cb4778.

14.   External view of left valve. Same horizon
and locality as above, x 2. BCM Cb4780.

15.   External view of left valve. Same horizon
and locality as above, x 2. BCM Cb4781.

16.   External view of left valve. Same horizon
and locality as above, x 2. BCM Cb4779.

17.   Internal view of left valve, 'Silcoset' cast.
Same horizon and locality as above,
x 2. BCM Cb4777.

PLATE 5.

Grammatodon (*Grammatodon*) *clathrata* (Leckenby)

Fig.

1a-1b.   External view of right valve and dorsal

                view. Cornbrash, Scarborough,

                Yorkshire, x 1.   YM KD1974/10.

2.   External view of left valve. Oxford Clay,

                Chippenham, Wiltshire, x 1.   GSM 113414.

3.   External view of left valve. Lower Oxford

                Clay, Jason Zone, Stewartby,

                Bedfordshire, x 1.   LU 68656.

4a-4c.   External, internal and dorsal views of left

                valve. Same locality and horizon as

                above, x 1. LU 68658.

            Modiolus bipartitus J. Sowerby

5.   External view of left valve. Middle Oxford

                Clay, Lamberti Zone, Woodham,

                Buckinghamshire, x 1. LU 69943.

6.   Posterodorsal view. Lower Oxford Clay,

                Calloviense Zone, Stewartby, Beds.,

                x 1.   LU 69944.

7a-7c.   External view of right valve, posterodorsal

                and anterodorsal views. Lower

                Calcareous Grit (Oxfordian),

                Scarborough, Yorks., x 1. YM KD1974/14.

PLATE 5
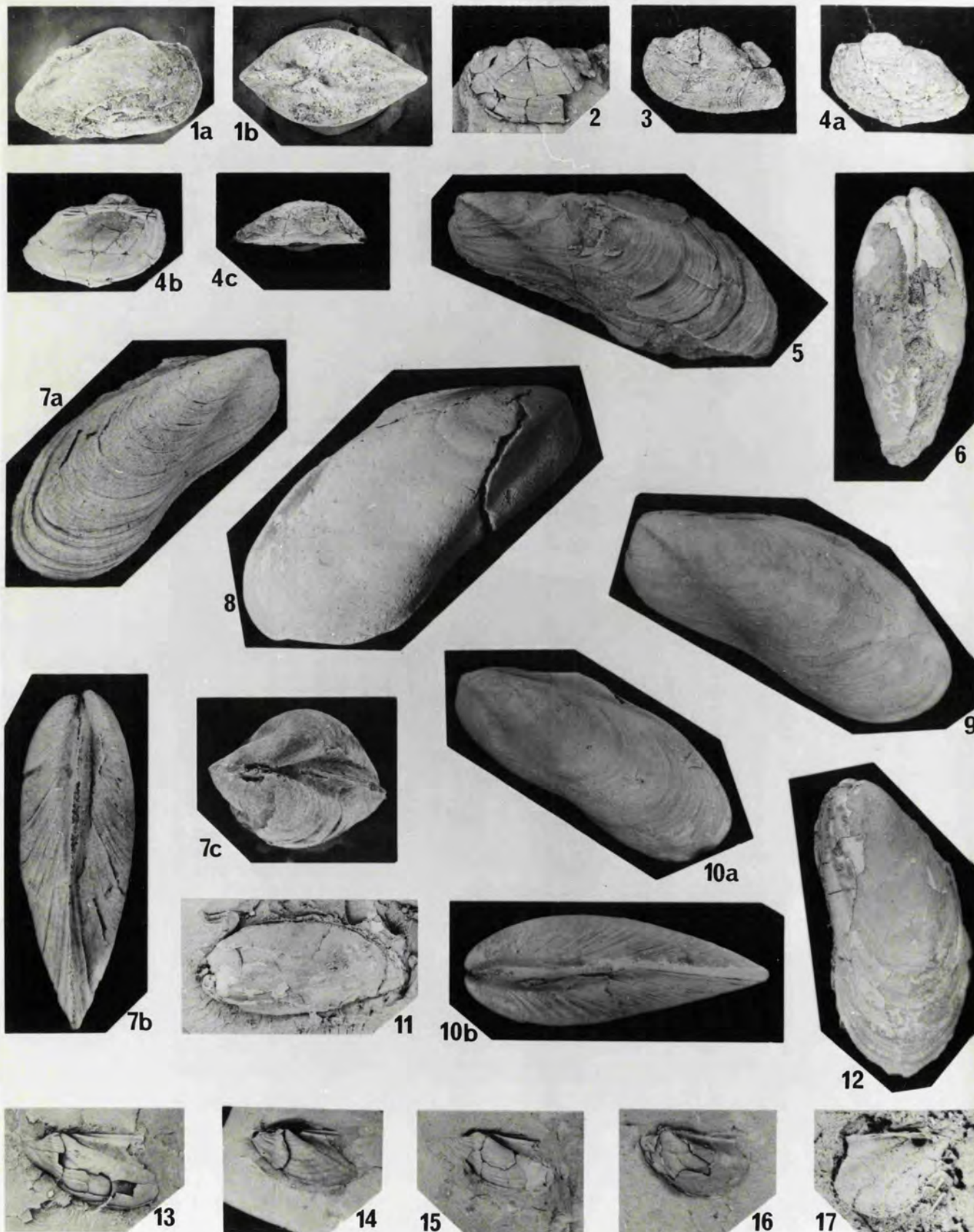
8.   External view of right valve. Lower Oxford
                 Clay, Wiltshire, x 1.1. BM L9728.

9.   External view of left valve. Same horizon
                 and locality as above, x 1.1.
                 BM 34469.

10.   External view of right valve. Upper Oxford
                 Clay, Mariae Zone, Scarborough,
                 Yorkshire, x 1.3. YM KD1974/18.

<div align="center">

Pinna lanceolata J. Sowerby

</div>

11.   External view of left valve. Coralline
                 Oolite (Oxfordian), Malton, Yorkshire,
                 x 1. YM KD1974/22.

12.   External view of left valve. Lower
                 Calcareous Grit (Oxfordian),
                 Scarborough, Yorkshire, x 0.7.
                 YM KD1974/26.

13.   External view of left valve. Coralline
                 Oolite (Oxfordian), Malton, Yorkshire,
                 x 1. BM 66884.

14.   External view of left valve. Lower
                 Calcareous Grit (Oxfordian),
                 Scarborough, Yorkshire, x 1.
                 YM KD1974/20.

PLATE 6.

Pteroperna ? pygmaea (Dunker)

Fig.

1.   Internal view of left valve, 'Silcoset' cast.
        Lower Oxford Clay, Wiltshire, x 5.4.
        BCM Cb4777.

Pinna mitis Phillips

2.   External view of left valve. Kellaways
        Rock, Chippenham, Wiltshire, x 1.
        SM J12887.

3.   External view of left valve, 'Silcoset' cast.
        Lower Oxford Clay, Jason Zone,
        Bletchley, Buckinghamshire, x 1.
        LU 69945.

4.   External view of left valve, 'Silcoset' cast.
        Lower Oxford Clay, Jason Zone,
        Stewartby, Bedfordshire, x 1. LU 68660.

5.   Holotype. External view of right valve.
        Upper Oxford Clay, Mariae Zone,
        Scarborough, Yorkshire, x 1.0.
        Phillips Collection, YM Tsp219.

6.   External view of left valve. Same horizon
        and locality as above, x 1. Leckenby
        Collection, SM J26740.

7.   Dorsal view. Upper Oxford Clay, Mariae
        Zone, Woodham, Bucks., x 0.9.
        OUM J30186.

PLATE 6
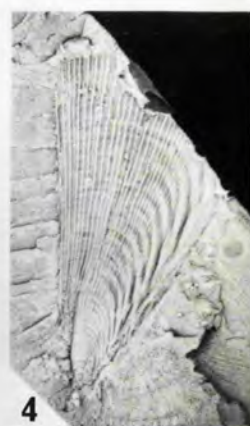
17.   External view of right valve. Jason Zone,
            Stewartby, Beds., x 1.8. LU 68705.

18.   External view of left valve. Same horizon
            and locality as above, x 1.8.
            LU 68706.

Oxytoma inequivalvis (J. Sowerby)

19.   External view of right valve. Lower Oxford
            Clay, Jason Zone, Stewartby, Beds.,
            x 2.0. LU 68752.

20.   External view of left valve, 'Silcoset'
            cast. Lower Oxford Clay, Coronatum
            Zone, Calvert, Buckinghamshire, x 1.6.
            LU 69949.

21.   External view of left valve. Kellaways
            Clay, Putton Lane, Chickerell, Dorset,
            x 1.4. Arkell Collection, SM J47646a.

22.   External view of left valve. Same horizon
            and locality as above, x 1.3. Arkell
            Collection, SM J47646b.

23.   External view of left valve. Same horizon
            and locality as above, x 1.2. Arkell
            Collection, OUM J8612.

9.   External view of right valve. Lower Oxford
          Clay, Jason Zone, Stewartby, Beds.,
          x 3.3. LU 68676.

                    Bositra buchii (Roemer)

10a-b.   External view of both valves. Lower Oxford
          Clay, Coronatum Zone, Stewartby,
          Beds., x 2.4 (10a), x 1.8 (10b).
          LU 68701.

11.   External view of right valve. Lower Oxford
          Clay, Jason Zone, Stewartby, Beds.,
          x 1. LU 68696.

12.   External view of right valve. Lower Oxford
          Clay, Coronatum Zone, Stewartby,
          Beds., x 1.8. LU 68702.

13.   External view of left valve. Lower Oxford
          Clay, Jason Zone, Stewartby, Beds.,
          x 1.9. LU 68703.

14.   External view of right valve, 'Silcoset'
          cast. Same horizon and locality as
          above, x 1.5. LU 68698.

15.   External view of left valve, 'Silcoset'
          cast. Same horizon and locality as
          above, x 1.4. LU 68697.

16.   External view of many specimens. Jason Zone,
          Crook Hill, Chickerell, Dorset, x 1.6.
          LU 68704.

PLATE 7.

Parainoceramus subtilis (Lahusen)

Fig.

1.   External view of right valve. Lower Oxford
            Clay, Wiltshire, x 1. BCM Cb4774.

2.   External view of left valve. Lower Oxford
            Clay, Coronatum Zone, Marston
            Moretaine, Bedfordshire, x 1.2.
            LU 68675.

3.   External view of left valve. Lower Oxford
            Clay, Coronatum Zone, Stewartby,
            Beds., x 3.4. LU 68685.

4.   Internal view of right valve. Lower Oxford
            Clay, Coronatum Zone, Marston
            Moretaine, Beds., x 2.0. LU 69946.

5.   External view of left valve. Lower Oxford
            Clay, Coronatum Zone, Stewartby, Beds.,
            x 1.8. LU 68687.

6.   External view of left valve. Same horizon
            and locality as above, x 1.5.
            LU 69947.

7.   External view of left valve. Same horizon
            and locality as above, x 1.7.
            LU 68695.

8.   Internal view of right valve. Same horizon
            and locality as above, x 3.3.
            LU 69948.

PLATE 7
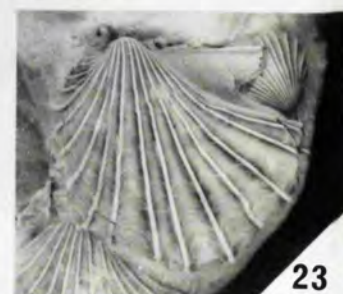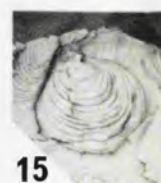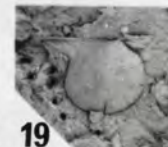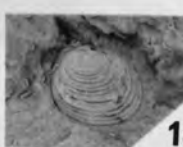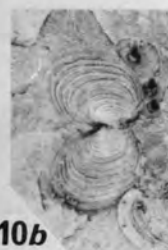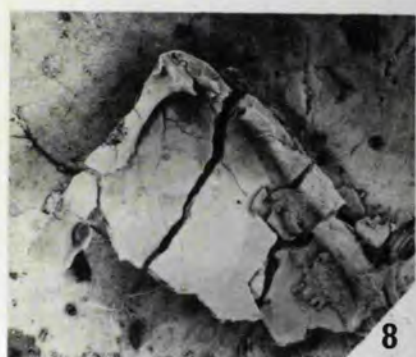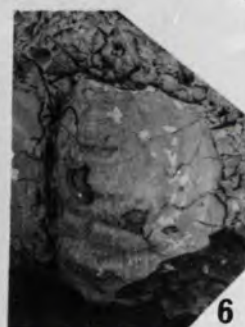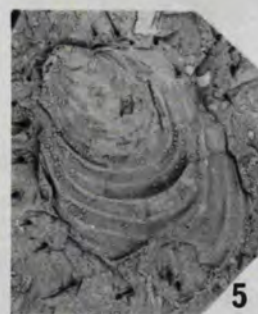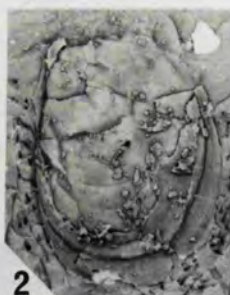
16.   Neotype. External view of left valve, internal mould. Hackness Rock, Scarborough, Yorkshire, x 1.2. YM 872.

17.   Neotype. External view of left valve, internal mould. Same horizon and locality as above, x 1. YM 872, KD1974/32.

18a-c.   External, internal and magnified internal views of left valve. Oxford Clay, Trowbridge, Wiltshire, x 1 (18a-b), x 3.3 (18c). GSM Y2088.

19.   External view of right valve. Lower Oxford Clay, Coronatum Zone, Norman Cross, Huntingdonshire, x 1. LU 69953.

20.   External view of left valve. Lower Oxford Clay, Jason Zone, Calvert, Bucks., x 3.7. LU 69954.

21.   Internal view of left valve. Oxford Clay, Trowbridge, Wilts., x 3.3. GSM Y2087.

8a-8b.   Internal and external views of right valve.
           Same horizon and locality, 8a x 2.3,
           8b x 1.7. LU 52676.

9.   Lectotype. External view of left valve.
           Middle Lias, Dursley, Gloucestershire,
           x 1. Sowerby Collection. BM L43259a.

10.   Syntype. External view of left valve. Same
           horizon and locality as above, x 1.
           BM L43259b.

11.   External view of left valve. Kellaways
           Rock, Tytherton Lucas, Wiltshire,
           x 1. BU 11435.

12.   External view of right valve. Lower Oxford
           Clay, Jason Zone, Calvert, Bucks.,
           x 3.5. LU 69951.

13.   External view of left valve. Lower Oxford
           Clay, Calloviense Zone, Stewartby,
           Beds., x 2.9. LU 69952.

           Meleagrinella _braamburiensis_ (Phillips)

14.   External view of left valve. Oxford Clay,
           Chippenham, Wiltshire, x 1.6.
           BCM 3324a.

15.   External view of left valve. Same horizon
           and locality as above, x 1.1.
           GSM 113410.

PLATE 8.

Oxytoma inequivalvis (J. Sowerby)

Fig.

1. External view of left valve, 'Silcoset' cast. Lower Oxford Clay, Jason Zone, Stewartby, Bedfordshire, x 3.3. LU 68749.

2. External view of left valve, 'Silcoset' cast. Same horizon and locality, x 1.8. LU 68748.

3. External view of left valve. Kellaways Rock, Putton Lane, Chickerell, Dorset, x 1.4. OUM J28250.

4. External view of left valve. Lower Oxford Clay, Coronatum Zone, Stewartby, Beds., x 1.8. LU 69950.

5. External view of left valve. Hackness Rock, Scarborough, Yorkshire, x 1. YM KD1974/31.

6. External view of left valve, 'Silcoset' cast. Lower Oxford Clay, Jason Zone, Stewartby, Beds., x 2.3. LU 68747.

7a-7c. Internal view, external view and dorsal view of left valve. Middle Oxford Clay, Lamberti Zone, Woodham, Buckinghamshire, 7a, 7c x 1.4, 7b x 1.0 LU 52673.

PLATE 8
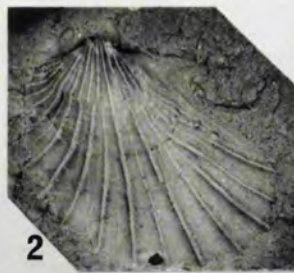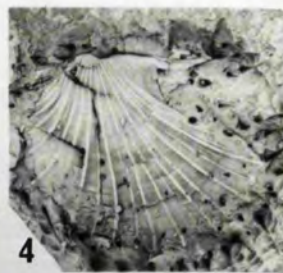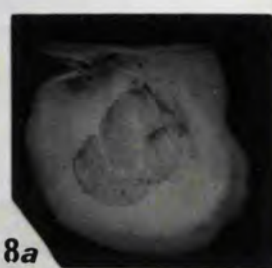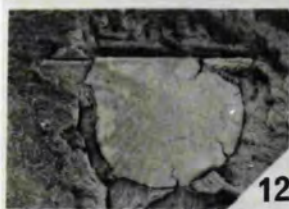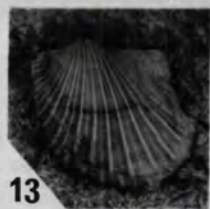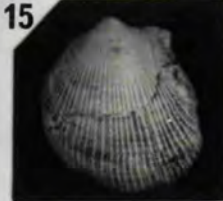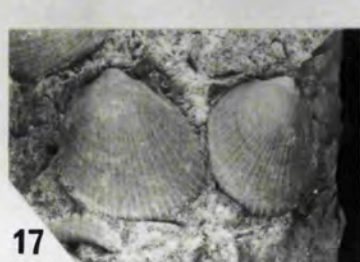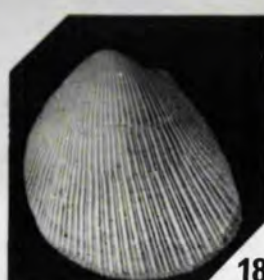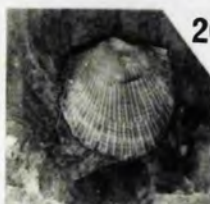
Byssentolium hudsoni gen. et sp. nov.

17.   Paratype. Internal view of right valve.

Lower Oxford Clay, Coronatum Zone,

Norman Cross, Hunts., x 4.6.

BM LL27722.

18.   Holotype. Internal view of right valve.

Same horizon and locality as above,

x 4.6. BM LL27723.

19.   Paratype. Internal view of right valve.

Same horizon and locality as above,

x 4.2. BM LL27750.

20.   Paratype. Internal view of right valve.

Same horizon and locality as above,

x 5.6. BM LL27751.

9. External view of left valve, 'Silcoset'
    cast. Same horizon and locality as
    above, x 2.5. LU 68761.

10. External view of right valve, 'Silcoset'
    cast. Same horizon and locality as
    above, x 2.5. LU 69957.

12. External view of right valve. Oxford Clay,
    Trowbridge, Wilts., x 1. GSM Y2090.

        Entolium corneolum (Young & Bird)

11. External view of left valve. Hackness
    Rock, Scarborough, Yorkshire, x 1.
    YM Tsp 119. Holotype of *Pecten*
    demissus Phillips, 1829, pl. 6, fig. 5.

13. External view of left valve. Kellaways Rock,
    Scarborough, Yorkshire, x 1.
    Leckenby Collection, SM J12397.

14. External view of left valve. Same horizon
    and locality as above, x 1. Leckenby
    Collection, SM J12396.

15. External view of left valve. Same horizon
    and locality as above, x 1. BM 47443.

16. Internal view of right valve. Lower Oxford
    Clay, Brora, Sutherlandshire, x 1.8.
    LU 69958.

21. External view of right valve. Same horizon
    and locality as above, x 1.9.
    LU 69959.

PLATE 9.

Meleagrinella braamburiensis (Phillips)

Fig.

1a-1c.   External, posterior and internal views of
          left valve. Oxford Clay, Trowbridge,
          Wiltshire, x 1.4. GSM Y2087.

2.   External view of left valve. Lower Oxford
          Clay, Coronatum Zone, Calvert,
          Buckinghamshire, x 1.8. LU 68756.

3.   External view of left valve, 'Silcoset'
          cast. Lower Oxford Clay, Coronatum
          Zone, Stewartby, Bedfordshire, x 1.8.
          LU 69955.

4.   Internal view of right valve. Oxford Clay,
          Trowbridge, Wilts., x 3.0. GSM Y2090.

5.   External view of right valve. Lower Oxford
          Clay, Coronatum Zone, Stewartby,
          Beds., x 2.9. LU 68771.

6.   External view of left valve. Lower Oxford
          Clay, Coronatum Zone, Norman Cross,
          Huntingdonshire, x 1.9. LU 69956.

7.   View from right side of both valves. Lower
          Oxford Clay, Coronatum Zone,
          Stewartby, Beds., x 1.2. LU 68758.

8.   External view of left valve. Lower Oxford
          Clay, Coronatum Zone, Calvert,
          Bucks., x 1.8. LU 68753.
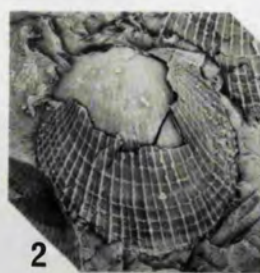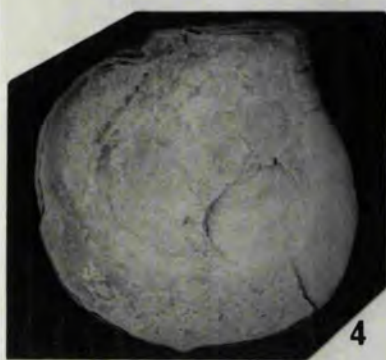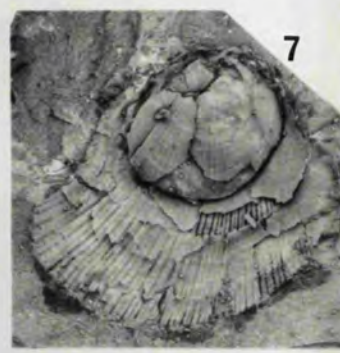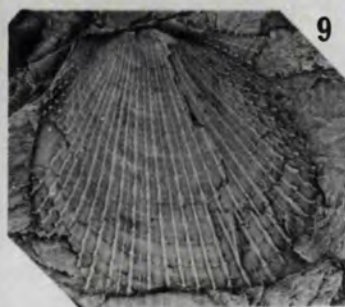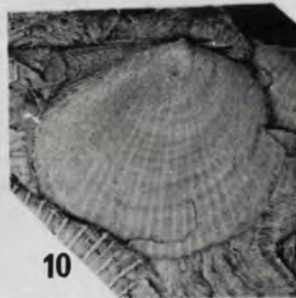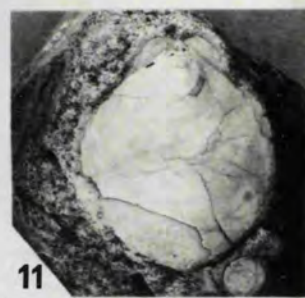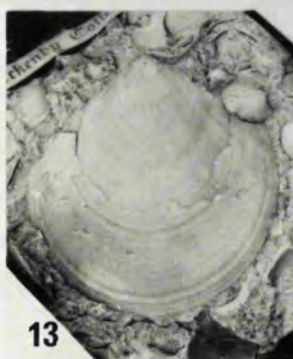
PLATE 9
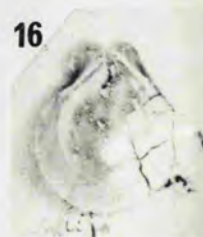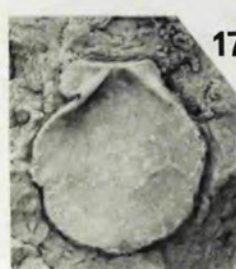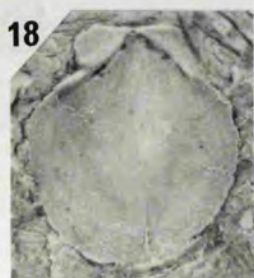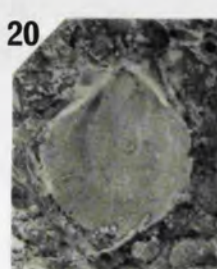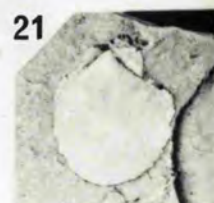
14.   External view of right valve. Same horizon

        and locality as above, x 1.

        BM L8958a.

15.   Neotype. External view of left valve.

        Hackness Rock, Scarborough, Yorkshire,

        x 1. Leckenby Collection, SM J12398.

Chlamys (Chlamys) bedfordi sp. nov.

7.   Paratype. Internal view of left valve.
        Lower Oxford Clay, Coronatum Zone,
        Calvert, Bucks., x 3.1. BM LL27728.

8.   Paratype. External view of right valve.
        Lower Oxford Clay, Coronatum Zone,
        Stewartby, Beds., x 3.0. BM LL27725.

9.   Paratype. Internal view of right valve.
        Lower Oxford Clay, Coronatum Zone,
        Norman Cross, Huntingdonshire, x 3.1.
        BM LL27727.

10.   Paratype. External view of left valve,
        'Silcoset' cast. Lower Oxford Clay,
        Coronatum Zone, Calvert, Bucks., x 2.8.
        BM LL27726.

11a-b. Holotype. External view of right valve, and
        details of ornament. Same horizon and
        locality as above, x 3.3 (11a), x 6.6
        (11b). BM LL27724.

Chlamys (Radulopecten) scarburgensis (Young & Bird)

12.   Internal view of left valve. Upper Oxford
        Clay, Mariae Zone, Warboys, Hunts.,
        x 1. Peterborough Museum 299/G.

13.   External view of left valve. Upper Oxford
        Clay, Oxfordshire, x 1.3. BM L8958c.

PLATE 10.

Byssentolium *hudsoni* gen. et sp. nov.

Fig.

1.   Paratype. Internal view of right valve.

            Lower Oxford Clay, Coronatum Zone,

            Calvert, Buckinghamshire, x 4.3.

            BM LL27748.

2.   Paratype. External view of right valve.

            Same horizon and locality as above,

            x 4.2. LU 69960.

4.   Paratype. External view of right valve.

            Lower Oxford Clay, Coronatum Zone,

            Stewartby, Bedfordshire, x 4.6.

            LU 69937.

Camptonectes *auritus* (Schlotheim)

3.   Internal view of right valve. Kellaways

            Rock, Stewartby, Beds., x 3.3.

            LU 70016.

5a-5b.   External and internal views of right valve.

            Coralline Oolite (Oxfordian),

            Malton, Yorkshire, x 1. BM LL2445.

6.   External view of left valve. Berkshire

            Oolite Series (Oxfordian), Headington,

            Oxfordshire, x 1. BM L80525.

            Syntype of *Pecten* *lens* J. Sowerby,

            1818, pl. 205, fig. 2.

PLATE 10
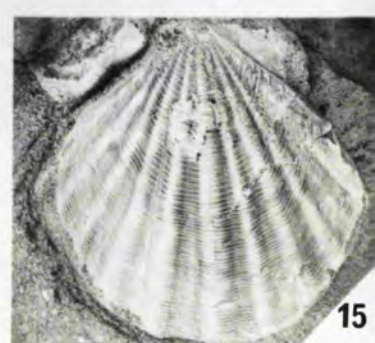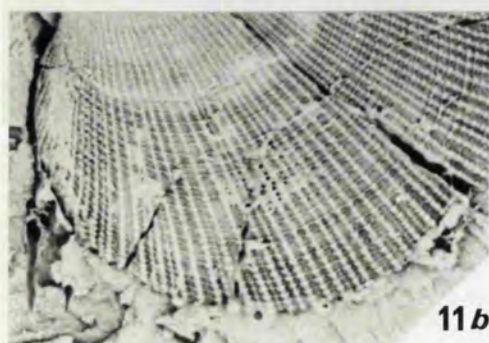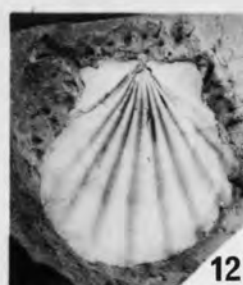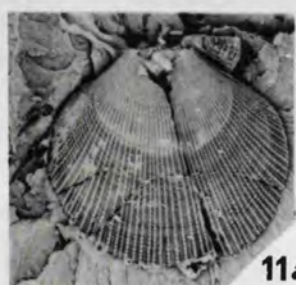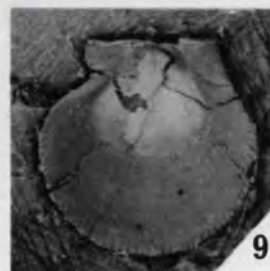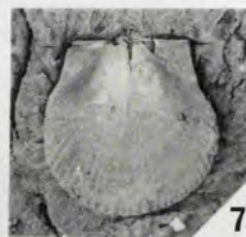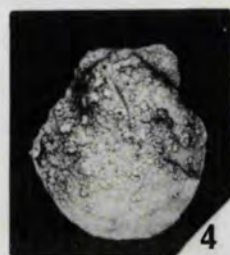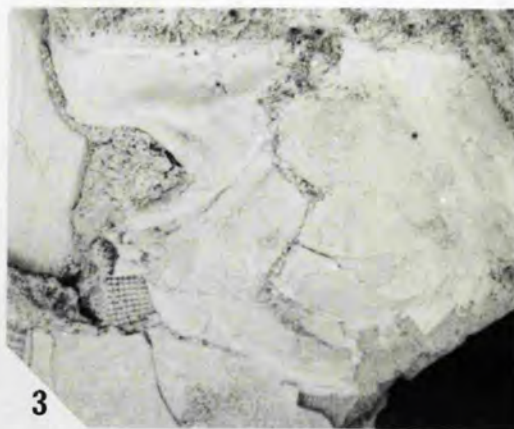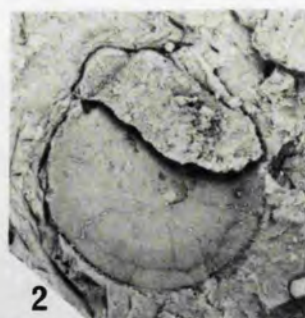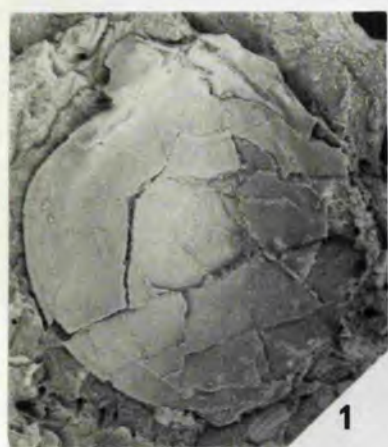
17.   Holotype of <u>Plicatula</u> <u>fistulosa</u> Morris &

          Lycett. External view of left valve.

          Great Oolite (Bathonian), Minchinhampton,

          Gloucestershire, x 1. Morris & Lycett

          Collection, GSM 9166. Figured by

          Morris & Lycett, 1853, pl. 2, fig. 5.

          <u>Chlamys</u> (<u>Radulopecten</u>) <u>drewtonensis</u> Neale

14.   Paratype. External view of left valve.

          Kellaways Rock, South Cave, Yorkshire,

          x 1.2. BM L88738. Figured by Neale,

          1956, pl. 28, fig. 1.

15.   Holotype. External view of right valve,

          plaster cast. Same horizon and

          locality as above, x 1. BM L88737.

          Figured by Neale, 1956, pl. 28, fig. 3.

Chlamys (_Radulopecten_) _fibrosa_ (J. Sowerby)

7. Lectotype. External view of right valve.
Cornbrash (?), Chatley, Wiltshire,
x 1. Sowerby Collection, BM 43305.
Figured by J. Sowerby, 1816, pl. 136,
left hand figure, as one of the two
syntypes of _Pecten fibrosus_.

9a-b. Internal view of right valve, magnified and
natural size. Oxford Clay,
Chippenham, Wiltshire, x 1.8 (9a),
x 1 (9b). GSM 113408.

10. External view of both valves, 'Silcoset'
cast. Lower Oxford Clay, Jason Zone,
Norman Cross, Huntingdonshire, x 1.5.
LU 69962.

11. External view of left valve. Kellaways Rock,
Scarborough, Yorks., x 1.9. SM J12610.

12. External view of right valve. Lower
Calcareous Grit (Oxfordian), Scarborough,
Yorkshire, x 1.9. YM KD1974/59.

16. External view of left valve. Lower Oxford
Clay, Coronatum Zone, Stewartby, Beds.,
x 2.2. LU 69963.

Plicatula (_Plicatula_) cf. _fistulosa_ Morris & Lycett

13. External view of left valve. Oakley Beds
(Oxfordian), Ampthill, Beds., x 1.
BM L91702.

PLATE 11.

Chlamys (*Radulopecten*) *scarburgensis* (Young & Bird)

Fig.

1.   Neoparatype. External view of left valve.
        Hackness Rock, Scarborough, Yorkshire,
        x 1. Leckenby Collection, SM J12400.

2.   Neoparatype. External view of right valve.
        Same horizon and locality as above,
        x 1. Leckenby Collection, SM J12401.

3.   Neoparatype. External view of right valve.
        Same horizon and locality as above,
        x 1. Leckenby Collection, SM J12399.

4.   External view of right valve. Same horizon
        and locality as above, x 1. GSM 54616.

5a-b.   External view of right valve and left valve.
        Upper Oxford Clay, Oxfordshire, x 1.
        BM L8958b.

6.   External view of left valve, detail of
        ornament. Lower Oxford Clay, Jason
        Zone, Stewartby, Bedfordshire, x 1.7.
        LU 69961.

8.   Dorsal view. Upper Oxford Clay, Oxford
        Oxfordshire, x 1. OUM J14548.

PLATE II
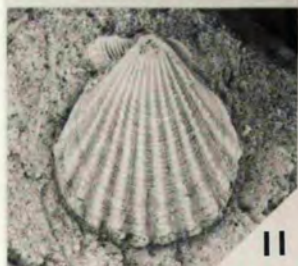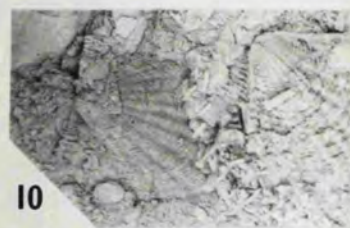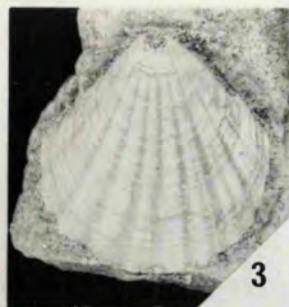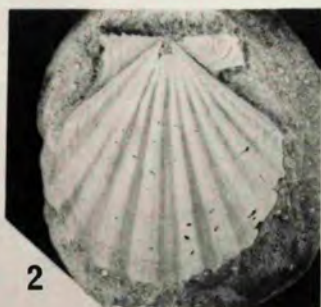
7. External view of left valve. Lower Oxford
    Clay, Calloviense Zone, Stewartby,
    Beds., x 1. BM LL27752.

8a-b. Internal and external views of left valve.
    Same horizon and locality as above,
    x 1. BM LL27753.

9a-c. External, internal and posterior views of
    left valve. Lower Oxford Clay, Jason
    Zone, Stewartby, Beds., x 1. BM LL27754.

10. External view of left valve. Lower Oxford
    Clay, Calloviense Zone, Norman Cross,
    Hunts., x 1. LU 69965.

11. External view of left valve. Lower Oxford
    Clay, Coronatum Zone, Norman Cross,
    Hunts., x 1. BM LL27755.

12. External view of left valve. Lower Oxford
    Clay, Coronatum Zone, Stewartby, Beds.,
    x 1. LU 69966.

13a-b. Internal and external views of left valve.
    Lower Oxford Clay, Jason Zone, Calvert,
    Buckinghamshire, x 1. BM LL27756.

14. External view of left valve. Lower Oxford
    Clay, Calloviense Zone, Stewartby,
    Beds., x 1. LU 69967.

15. Internal view of right valve. Lower Oxford
    Clay, Jason Zone, Calvert, Bucks., x 1.
    LU 69968.

PLATE 12.

Plicatula (Plicatula) weymouthiana Damon

Fig.

1a-b.   Holotype. External views of right and left

                  valves. Corallian, Weymouth, Dorset,

                  x 1. Damon Collection, BM L6786.

                  Figured by Damon, 1860, pl. 9, fig. 7.

Plicatula (Plicatula) cf. fistulosa Morris & Lycett

2.   External view of right valve. Lower Oxford

                  Clay, Jason Zone, Peterborough,

                  Huntingdonshire, x 1. BM L87302.

3a-b.   External views of left and right valves.

                  Lower Oxford Clay, Coronatum Zone,

                  Bletchley, Buckinghamshire, x 1.

                  LU 68775.

4.   External view of right valve. Lower Oxford

                  Clay, Jason Zone, Norman Cross,

                  Hunts., x 1. LU 68778.

Gryphaea (Bilobissa) dilobotes nom. nov.

5a-5d.   External and internal views of left and

                  right valves. Lower Oxford Clay,

                  Calloviense Zone, Stewartby, Beds.,

                  x 1. LU 69964.

6.   External view of left valve. Lower Oxford

                  Clay, Jason Zone, Stewartby, Beds.,

                  x 1. BM LL27751.
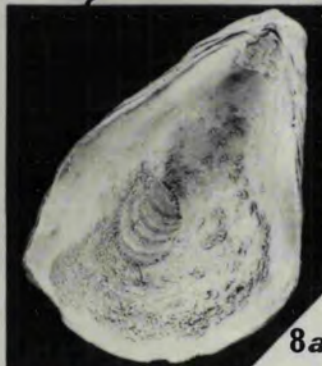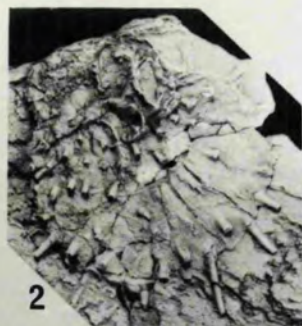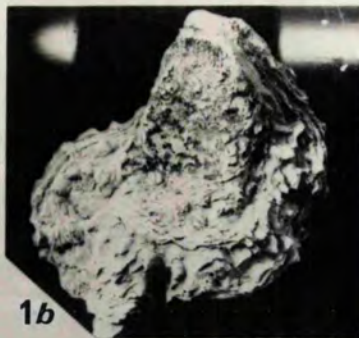
PLATE 12

PLATE 13.

Gryphaea (*Bilobissa*) *dilobotes* nom. nov.

Fig.

1.   Holotype. External view of left valve.
          Lower Oxford Clay, Calloviense Zone,
          Stewartby, Bedfordshire, x 1.
          BM LL27729.

2a-b.   External views of left and right valves.
          Lower Oxford Clay, Calloviense Zone,
          Norman Cross, Huntingdonshire, x 1.
          LU 69969.

3.   External view of left valve. Lower Oxford
          Clay, Calloviense Zone, Stewartby,
          Beds., x 1. LU 69970.

4.   External view of left valve. Same horizon
          and locality as above, x 1. LU 69971.

5.   External view of left valve. Lower Oxford
          Clay, Jason Zone, Stewartby, Beds.,
          x 1. LU 69972.

6a-b.   External views of left and right valves.
          Lower Oxford Clay, Calloviense Zone,
          Stewartby, Beds., x 1. LU 69973.

PLATE 13
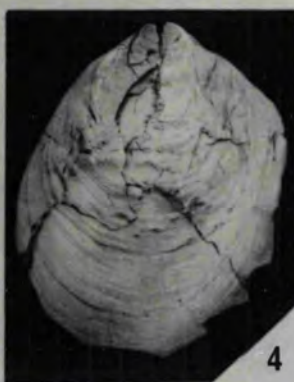
PLATE 14.

Gryphaea (Bilobissa) dilobotes nom. nov.

Fig.

1a-c.   External and internal views of left valve
         and external view of right valve.
         Lower Oxford Clay, Calloviense Zone,
         Stewartby, Bedfordshire, x 1.
         LU 69974.

2.   External view of left valve. Same horizon
         and locality as above, x 1. LU 69975.

3a-b.   External views of left and right valves.
         Lower Oxford Clay, Jason Zone,
         Stewartby, Beds., x 1. LU 69976.

4.   External view of left valve. Same horizon
         and locality as above, x 1. LU 69977.

5.   External view of left valve. Lower Oxford
         Clay, Calloviense Zone, Stewartby,
         Beds., x 1. LU 69978.

PLATE 14

1a

1b

1c

2

3a 3b

4

5
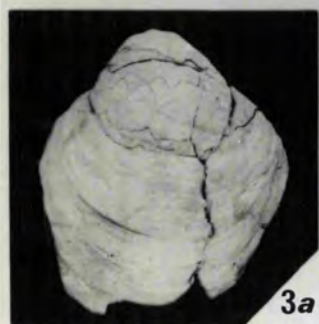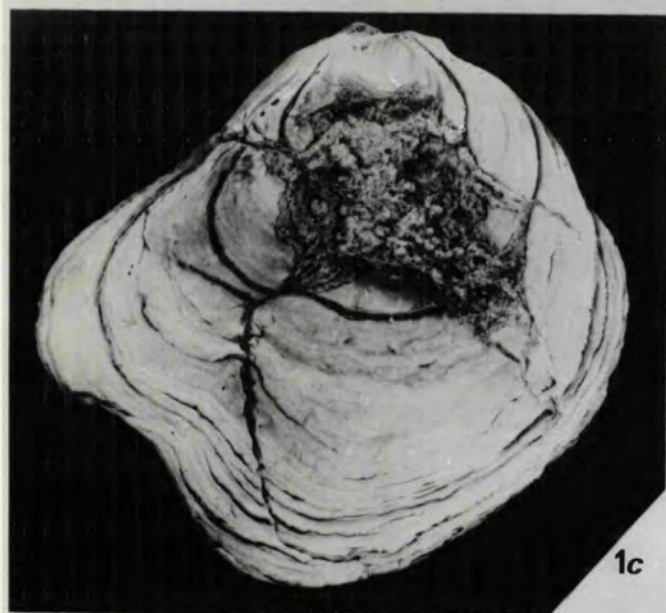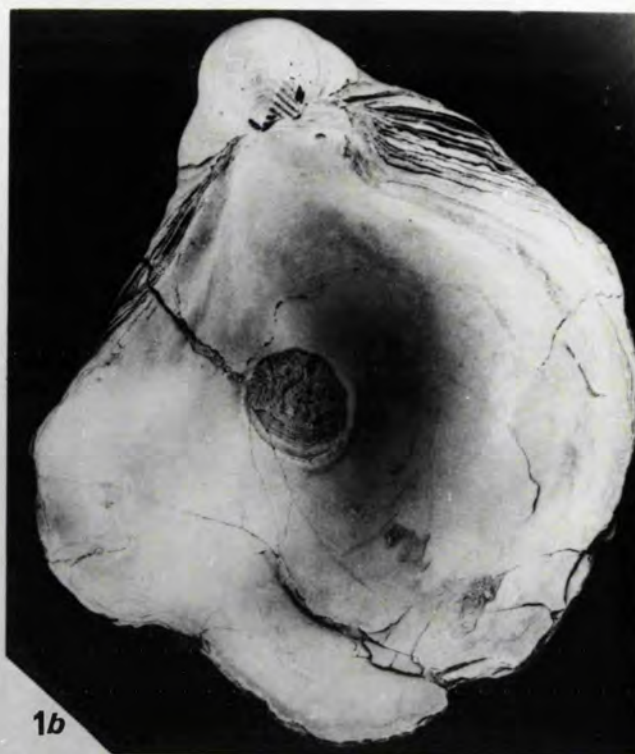
PLATE 15.

Gryphaea (*Bilobissa*) *dilobotes* nom. nov.

Fig.

1.   External view of left valve. Lower Oxford
            Clay, Jason Zone, Stewartby, Beds.,
            x 1. LU 69979.

2a-b.   External and internal views of left valve.
            Lower Oxford Clay, Calloviense Zone,
            Stewartby, Beds., x 1. LU 69980.

3a-b.   External and posterior views of left valve.
            Same horizon, Norman Cross,
            Huntingdonshire, x 1. LCM 523 1961 29a.

4a-b.   External views of left and right valves.
            Kellaways Rock, Drewton, North Cave,
            Yorkshire, x 1. YM KD1974/60.

5.   External view of left valve. Lower Oxford
            Clay, Calloviense Zone, Stewartby,
            Beds., x 1. LU 69981.

6a-b.   External views of left and right valves.
            Lower Oxford Clay, Jason Zone,
            Stewartby, Beds., x 1. LU 69982.

7.   External view of left valve. Lower Oxford
            Clay, Calloviense Zone, Norman Cross,
            Hunts., x 1. LU 69983.

PLATE 15
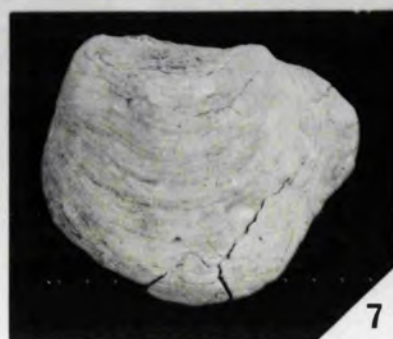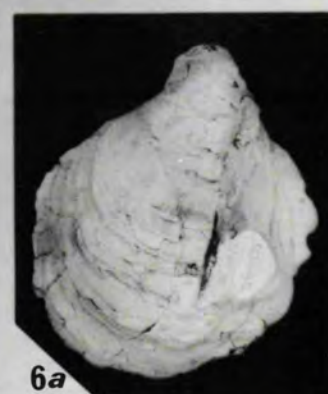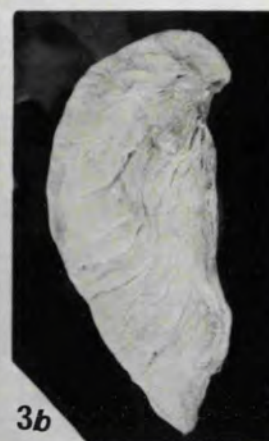
9a-c.   External and posterior views of left valve

and external view of right valve.

Same horizon and locality as above,

x 1.   LU 68775.

PLATE 16.

Gryphaea (*Bilobissa*) *dilobotes* nom. nov.

Fig.

1.   External view of left valve. Lower Oxford
                Clay, Calloviense Zone, Norman Cross,
                Huntingdonshire, x 1. LU 69984.

2a-b.   External views of right and left valves.
                Lower Oxford Clay, Jason Zone, Stewartby,
                Bedfordshire, x 1. LU 69985.

3.   External view of left valve. Same horizon
                and locality as above, x 1. LU 69986.

4.   External view of left valve. Lower Oxford
                Clay, Calloviense Zone, Norman Cross,
                Hunts., x 1. LU 69987.

5.   External view of left valve. Lower Oxford
                Clay, Calloviense Zone, Stewartby,
                Beds., x 1. LU 69988.

8.   External view of right valve. Same horizon
                and locality as above, x 1. LU 69991.

Gryphaea (*Bilobissa*) *lituola* Lamarck

6.   External view of left valve. Middle Oxford
                Clay, Athleta Zone, Stewartby, Beds.,
                x 1. LU 68777.

7a-b.   External and internal views of right valve.
                Same horizon and locality as above,
                x 1. LU 68783.

PLATE 16
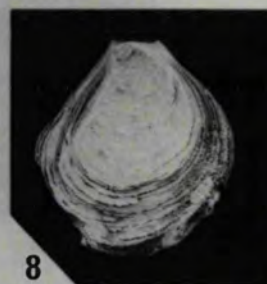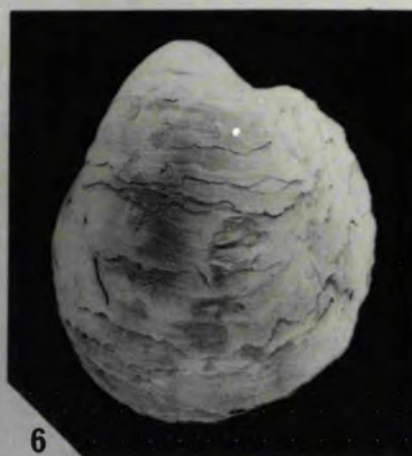
7.   Syntype. External view of left valve.

        Kimmeridge Clay, Shotover Hill,

        Oxfordshire, x 1. BM 43340a.

8a-b.   Syntype. External view of right valve and

        anterior view. Same horizon and

        locality as above, x 1. BM 43340b.

        Discomiltha lirata (Phillips)

10.   Neotype. External view of left valve.

        Hackness Rock, Scarborough, Yorkshire,

        x 1. BM LL10077. Figured by Arkell,

        1934, pl. 41, fig. 7 as Lucina lirata

        Phillips.

11.   External view of right valve. Same horizon

        and locality as above, x 1.

        YM KD1974/47.

PLATE 17.

Gryphaea (Bilobissa) lituola Lamarck

Fig.

1a-b.   External views of left and right valves.

          Middle Oxford Clay, Athleta Zone,

          Stewartby, Bedfordshire, x 1. LU 68782.

2.   External view of left valve. Same horizon

          and locality as above, x 1. LU 68778.

3.   External view of left valve. Same horizon

          and locality as above, x 1. LU 69989.

4.   External view of left valve. Same horizon

          and locality as above, x 1. LU 68776.

9.   External view of left valve. Same horizon

          and locality as above, x 1. LU 68773.

          Nanogyra nana (J. Sowerby)

5a-b.   Lectotype. External and internal views of

          left valve. Kimmeridge Clay,

          Shotover Hill, Oxfordshire, 5a x 1,

          5b x 1.2. Sowerby Collection,

          BM 43340c. Figured by J. Sowerby

          1822, pl. 383, left hand figure, as

          Gryphaea nana.

6a-b.   Internal and external views of right valve.

          Lower Oxford Clay, Coronatum Zone,

          Calvert, Buckinghamshire, x 1. LU 68784.

PLATE 17
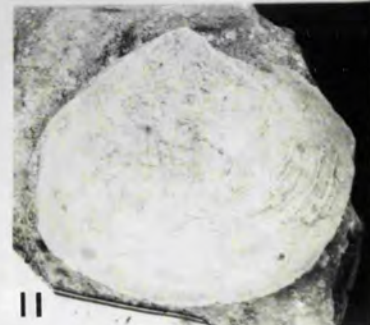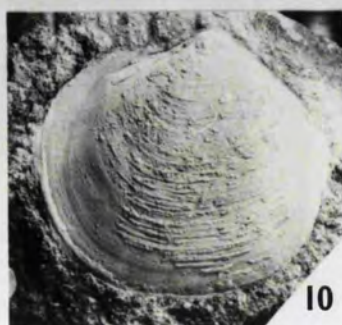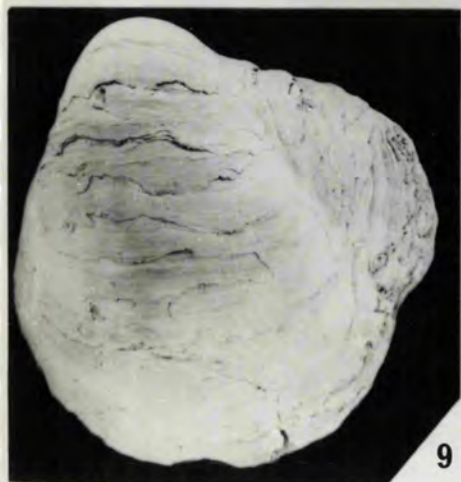
Myophorella (Myophorella) irregularis (Seebach)

8.   External view of right valve. Oxford Clay,
          Weymouth, Dorset, x 1. YM KD1974/40.

9.   External view of left valve. Same horizon
          and locality as above, x 1. Reed
          Collection, YM KD1974/37.

10a-b.   External view of right valve and dorsal view.
          Same horizon and locality as above,
          x 1. GSM 43053.

11a-b.   Internal and external views of right valve.
          Lower Oxford Clay, Jason Zone,
          Stewartby, Beds., x 1. LU 54481.

12.   External view of left valve. Same horizon
          and locality as above, x 1.1.
          LU 68785.

13.   External view of right valve. Kellaways
          Rock, Putton Lane, Chickerell,
          Dorset, x 1. Arkell Collection,
          SM J47645.

PLATE 18.

Discomiltha lirata (Phillips)

Fig.

1.   External view of left valve. Lower Oxford
        Clay, Coronatum Zone, Marston
        Moretaine, Bedfordshire, x 1.1.
        LU 68789.

2.   External view of right valve. Same horizon
        and locality as above, x 1.5.
        LU 68787.

3.   Internal view of right valve. Same horizon
        and locality as above, x 1.1.
        LU 69990.

4a-b.   External view of right valve and dorsal
        view. Coralline Oolite (Oxfordian),
        Hildenley, Yorkshire, x 1. YM Tsp 170.

5.   External view of right valve. Lower Oxford
        Clay, Coronatum Zone, Marston
        Moretaine, Beds., x 1. LU 68786.

6.   External view of right valve, internal mould.
        Hackness Rock, Scarborough, Yorkshire,
        x 1. YM KD1974/44.

7.   External view of left valve. Lower Oxford
        Clay, Jason Subzone, Calvert,
        Buckinghamshire, x 1.4. LU 69992.

PLATE 18
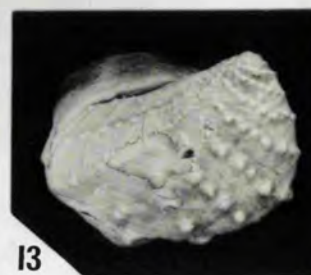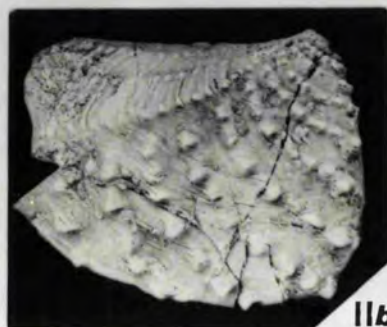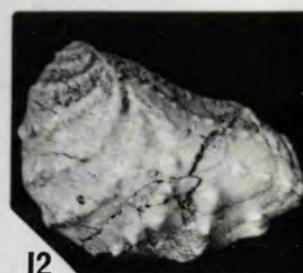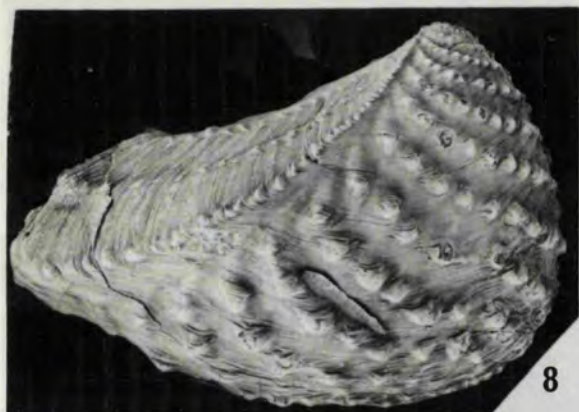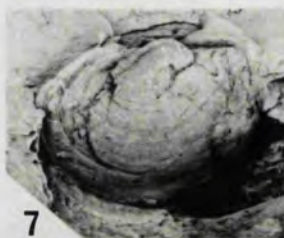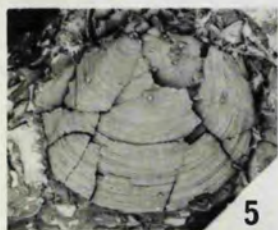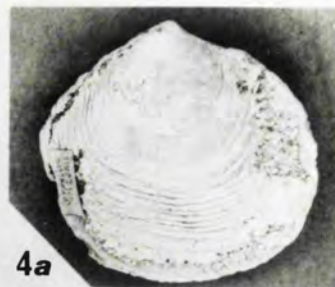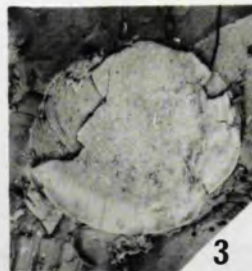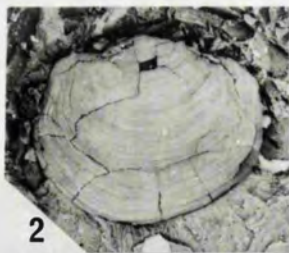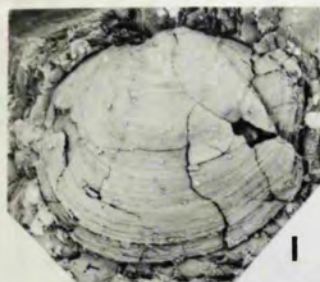
PLATE 19.

Myophorella (Myophorella) irregularis (Seebach)

Fig.

1a-c.   External, internal and oblique internal
            views of left valve. Oxford Clay,
            Weymouth, Dorset, x 1. YM KD1974/39.

2.   External view of left valve. Oxford Clay,
            Trowbridge, Wiltshire, x 1.5.
            GSM Y2080.

3a-b.   External views of right and left valves.
            Oxford Clay, Weymouth, Dorset, x 1.
            YM KD1974/61.

4a-c.   External view of right valve, dorsal view
            and external view of left valve.
            Same horizon and locality as above,
            x 1. YM KD1974/41.

Myophorella (Myophorella) caytonensis nom. nov.

5a-b.   External views of left and right valves.
            Cornbrash, Scarborough, Yorkshire,
            x 1. Lycett Collection, GSM 112893.

PLATE 19
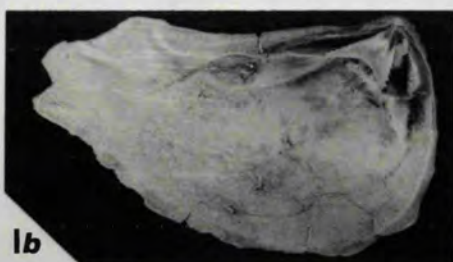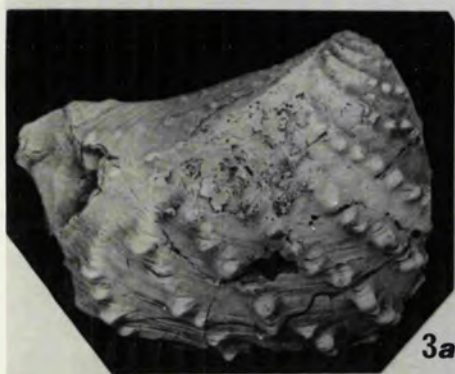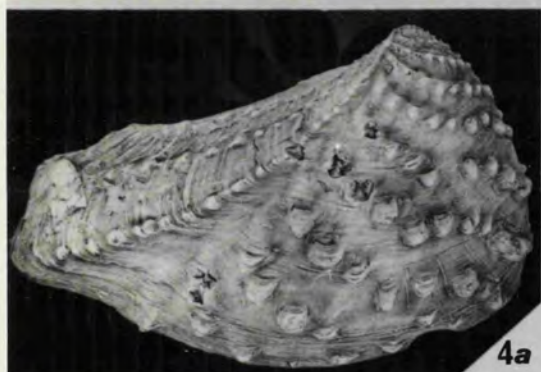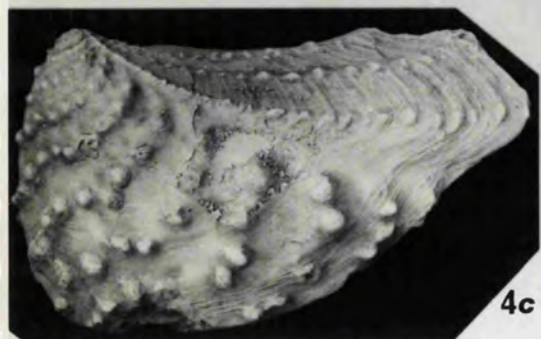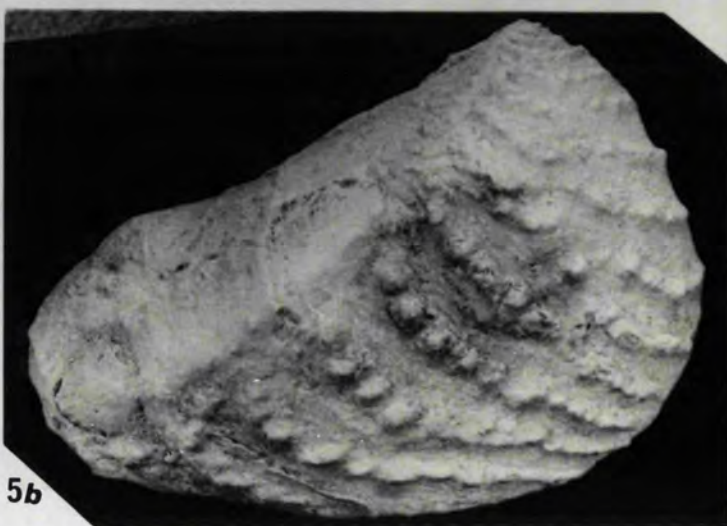
1a   1b   2   1c   3a   3b   4a   4b   4c   5a   5b

7.   External view of right valve, composite
        internal mould. Upper Oxford Clay,
        Mariae Zone, Scarborough, Yorkshire,
        x 1.5. SM J26767.

8.   External view of right valve, composite
        internal mould. Same horizon and
        locality as above, x 1.5. YM 873,
        holotype of *Astarte* *lurida* Phillips,
        1829, pl. 5, fig. 2 (non *A. lurida* J.
        Sowerby).

9.   External view of both valves, composite
        internal mould. Same horizon and
        locality as above, x 1.5. SM J26766.

10.   External view of right valve, composite
        internal mould. Same horizon and
        locality as above, x 1.5 . YM KD1974/48.

11a-b. External view of left valve and posterodorsal
        view. Oxford Clay, Fairford, Wiltshire,
        x 1.4. BU 14708.

12a-b. Dorsal view and external view of left valve.
        Oxford Clay, Trowbridge, Wilts., x
        2.0. BCM 3324a.

PLATE 20.

Myophorella (*Myophorella*) *caytonensis* nom. nov.

Fig.

1a-d.   Holotype. External views of right and left

          valves, dorsal and anterior views.

          Kellaways Rock, Scarborough, Yorkshire,

          x 1. SM J11377.

2.   External view of left valve. Same horizon

          and locality as above, x 1. GSM 11436.

          Figured by Lycett, 1877, pl. 36, fig.

          1 as *Trigonia Rupellensis* d'Orbigny.

3.   External view of left valve. Same horizon

          and locality as above, x 1. GSM 11438.

          Figured by Lycett, 1877, pl. 36, fig.

          3 as *Trigonia Rupellensis* d'Orbigny.

Neocrassina (*Neocrassina*) *ungulata* (Lycett)

4.   Internal view of right valve. Oxford Clay,

          Trowbridge, Wiltshire, x 1.9.

          BCM 3324d.

5a-b.   External views of left and right valves.

          Same horizon and locality as above,

          x 1.9. BCM 3324c.

6a-b.   Oblique internal and internal views of left

          valve. Same horizon and locality as

          above, x 1.9. BCM 3324b.

PLATE 20
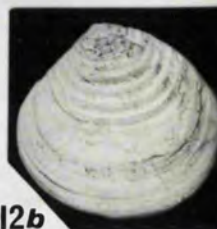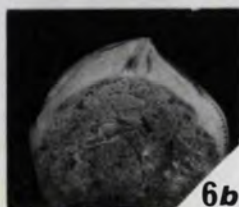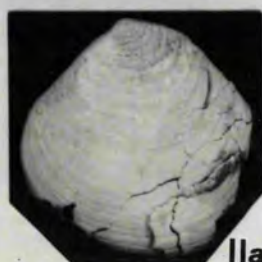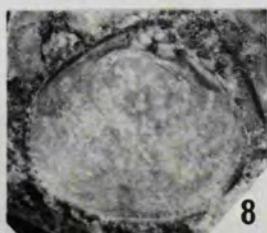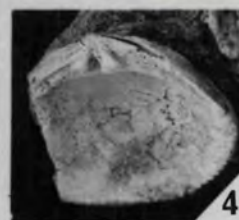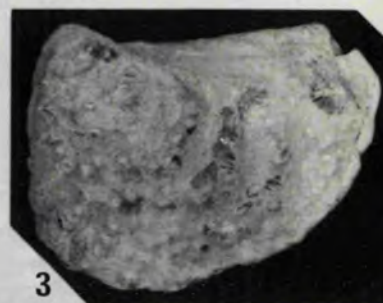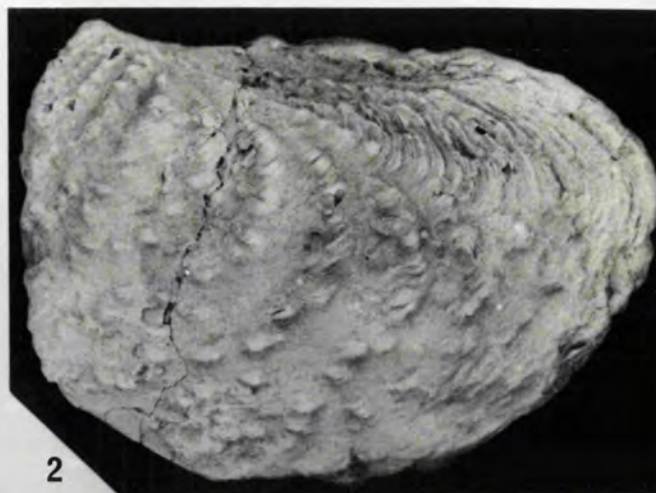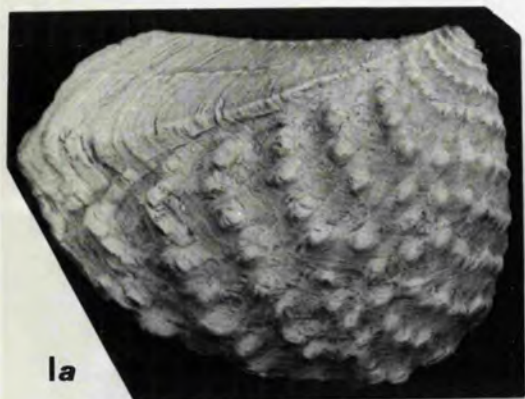
23.   Internal view of right valve, showing

transposed dentition. Same horizon

and locality as above, x 2.7.

LU 69943.

24.   External view of right valve. Lower Oxford

Clay, Jason Zone, Stewartby, Beds.,

x 2.7. LU 69998.

25.   External view of left valve. Lower Oxford

Clay, Jason Zone, Calvert, Bucks.,

x 2.7. LU 69812.

26.   External view of left valve. Same horizon

and locality as above, x 2.7. LU 68795.

27.   Dorsal view. Same horizon and locality as

above, x 2.7. LU 68793.

28.   Dorsal view. Lower Oxford Clay, Jason Zone,

Stewartby, Beds., x 2.7. LU 69998.

29.   External view of right valve. Same horizon

and locality as above, x 2.7. LU 69999.

30.   External view of right valve. Lower Oxford

Clay, Jason Zone, Calvert, Bucks.,

x 2.7. LU 68792.

31.   Internal view of left valve. Same horizon

and locality as above, x 2.7. LU 68798.

32.   External view of right valve. Same horizon

and locality as above, x 2.7. LU 68799.

17.   External view of left valve. Same horizon
               and locality as above, x 1.5.
               YM KD1974/50.

               Trautscholdia phillis (Cottreau)

15.   External view of right valve. Lower Oxford
               Clay, Jason Zone, Calvert, Bucks.,
               x 2.7. LU 69805.

16.   External view of left valve. Same horizon
               and locality as above, x 2.7.
               LU 69802.

18.   External view of right valve. Same horizon
               and locality as above, x 2.7.
               LU 69996.

19a-b.   External and internal views of left valve.
               Same horizon and locality as above,
               x 2.7. LU 69800.

20a-b.   Internal and external views of right valve.
               Lower Oxford Clay, Coronatum Zone,
               Marston Moretaine, Beds., x 2.7.
               LU 69814.

21.   Internal view of right valve. Lower Oxford
               Clay, Jason Zone, Calvert, Bucks.,
               x 2.7. LU 69997.

22a-b.   External view of left valve and dorsal view.
               Same horizon and locality as above,
               x 2.7. LU 69801.

7.   Paratype. Internal view of right valve.
         Lower Oxford Clay, Jason Zone,
         Calvert, Bucks., x 1.6. LU 69995.

         Trautscholdia carinata (Phillips)

8.   Holotype. External view of right valve.
         Upper Oxford Clay, Mariae Zone,
         Scarborough, Yorkshire, x 1.5.
         Phillips Collection, YM 876.

9.   External view of right valve. Same horizon
         and locality as above, x 1.6.
         SM J26747.

10.   External view of right valve. Same horizon
         and locality as above, x 1.6.
         YM KD1974/62.

11.   External view of right valve. Same horizon
         and locality as above, x 1.5.
         SM J26745.

12.   External view of left valve. Same horizon
         and locality as above, x 1.1.
         YM KD1974/49.

13.   External view of left valve. Same horizon
         and locality as above, x 1.6.
         YM KD1974/51.

14.   External view of right valve. Same horizon
         and locality as above, x 1.6.
         SM J26746.

PLATE 21.

Neocrassina (_Neocrassina_) _calvertensis_ sp. nov.

Fig.

1a-b.   Holotype. External and internal views of
         right valve. Lower Oxford Clay, Jason
         Zone, Calvert, Buckinghamshire, x 2.5.
         BM LL27730.

2.   Paratype. External view of left valve.
         Lower Oxford Clay, Jason Zone,
         Stewartby, Bedfordshire, x 1.5.
         LU 68790.

3a-b.   Paratype. Internal and external views of
         left valve. Lower Oxford Clay, Jason
         Zone, Calvert, Bucks., x 1.6. LU 69993.

4a-c.   Paratype. External views of right and left
         valves and dorsal view. Same horizon
         and locality as above, x 1.5.
         BM LL27732.

5.   Paratype. External view of right valve.
         Same horizon and locality as above,
         x 1.6. BM LL27733.

6a-b.   Paratype. Internal and external views of
         left valve. Lower Oxford Clay, Jason
         Zone, Stewartby, Beds., x 1.5.
         LU 69994.

PLATE 21
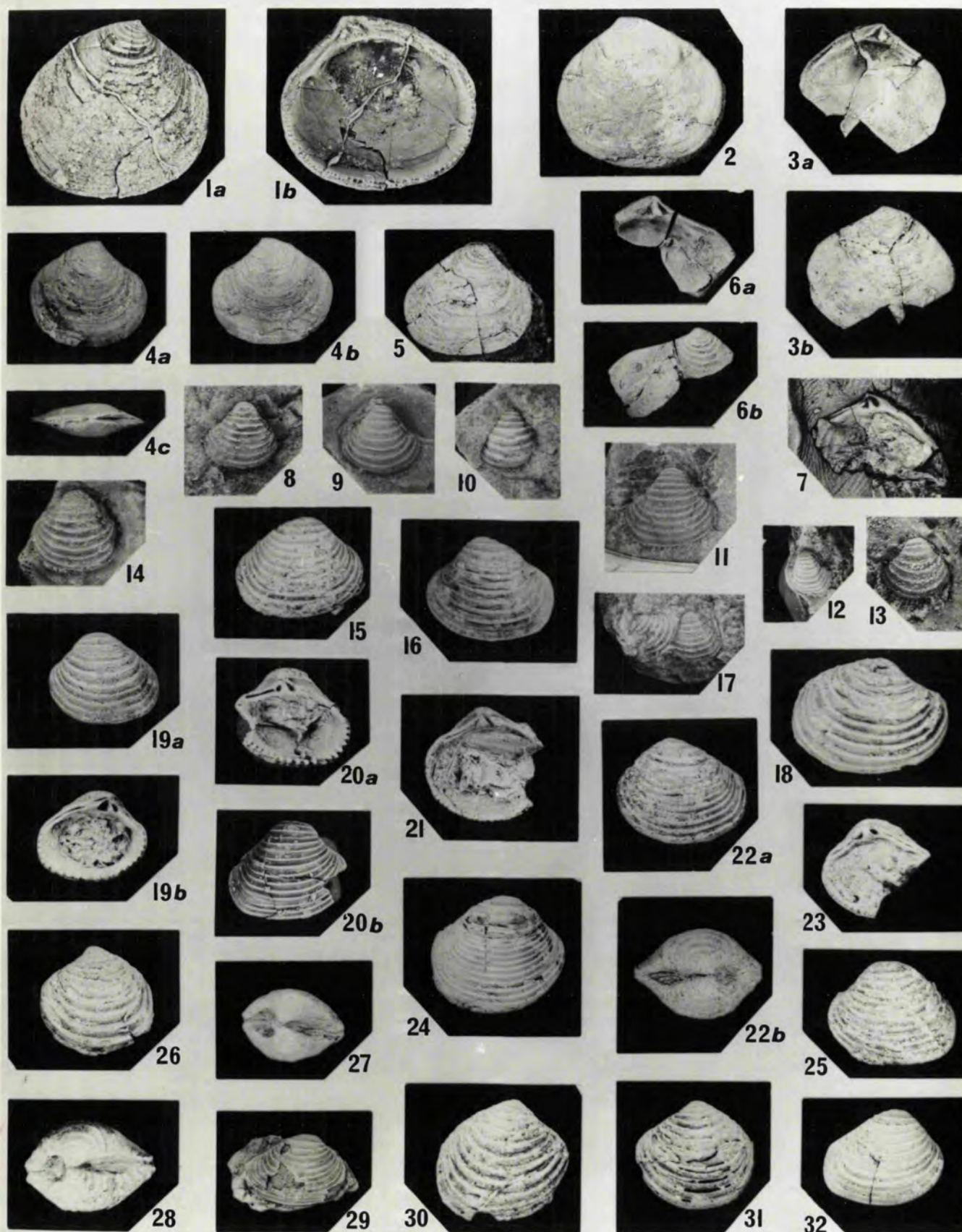
25.   Holotype. External view of left valve.

           Cornbrash, Wiltshire, x 1.1. Sowerby

           Collection, BM 43164. Figured by J.

           Sowerby, 1821, pl. 295, fig. 1. as

           Isocardia minima.

26.   External view of left valve. Kellaways

           Rock, Chippenham, Wilts., x 1.

           GSM 42919.

           Anisocardia (Anisocardia) tenera (J. de C. Sowerby)

23a-b.   Holotype. External view of right valve and

           anterior view. Kellaways Rock,

           Wiltshire, x 1.3. Sowerby Collection,

           BM 43165. Figured by J. Sowerby, 1821,

           pl. 295, fig. 2. as Isocardia tener.

24.   External view of right valve. Kellaways

           Rock, Chippenham, Wilts., x 1.

           GSM 114041.

27.   External view of left valve. Same horizon

           and locality as above, x 1.

           GSM 114043.

28a-b.   External view of left valve and anterior view.

           Kellaways Rock, Loudon, Wilts., x 1.

           Hudleston Collection, GSM Y2072.

29a-b.   Anterior view and external view of right

           valve. Kellaways Rock, Chippenham,

           Wilts., x 1. GSM 114040.

14. Internal view of right valve, 'Silcoset' cast. Same horizon and locality as above, x 2. KD Lukow 8.

15. External view of left valve. Kellaways Rock, Kellaways, Wiltshire, x 1.4. Chaning Pearce Collection, BCM Cb 4770.

16a-b. Anterior view and external view of left valve. Kellaways Rock, Chippenham, Wilts., x 1. GSM 42916.

17. Anterior view. Same horizon and locality as above, x 1. GSM 42917.

18. External view of right valve. Kellaways Rock, Kellaways, Wiltshire, x 1.4. Chaning Pearce Collection, BCM Cb 4771.

19. External view of right valve. Kellaways Rock, Calloviense Zone, Stewartby, Beds., x 1. LU 70001.

20a-b. External view of right valve and posterior view. Lower Calcareous Grit (Oxfordian), Scarborough, Yorkshire, x 1. YM KD1974/54.

21. External view of right valve. Kellaways Rock, Calloviense Zone, Stewartby, Beds., x 1. LU 70002.

22. External view of right valve. Kellaways Rock, Chippenham, Wiltshire, x 1. GSM 42917.

8.   External view of right valve. Lower Oxford

              Clay, Jason Zone, Kidlington,

              Oxfordshire, x 1. OUM J9719.

9a-b.   Holotype. Dorsal view and external view of

              right valve. Kellaways Rock, Brora

              Roof Bed, Brora, Sutherlandshire, x

              1.1. Sowerby Collection, BM 43154.

              Figured by J. de C. Sowerby, 1829,

              pl. 553, fig. 1, as Cardium striatulum.

10.   External view of left valve. Lower Oxford

              Clay, Wiltshire,

              x 1. OUM J28240.

11a-c.   External views of left valve and right valve

              and dorsal view. Kellaways Rock,

              Scarborough, Yorkshire, x 1.

              Leckenby Collection, SM J6010,

              holotype of Cardium crawfordii

              Leckenby, 1859, pl. 3, figs. 9a, 9b.

              Rollierella minima (J. Sowerby)

12.   Internal view of right valve, 'Silcoset'

              cast. Oxford Clay, Lukow, Poland,

              x 2. KD Lukow 6.

13.   Internal view of right valve, 'Silcoset'

              cast. Same horizon and locality as

              above, x 2. KD Lukow 5.

PLATE 22.

Trautscholdia phillis (Cottreau)

Fig.

1.   External view of right valve. Lower Oxford
            Clay, Jason Zone, Calvert,
            Buckinghamshire, x 2.7. LU 69824.

2.   External view of right valve. Lower Oxford
            Clay, Jason Zone, Stewartby,
            Bedfordshire, x 2.7. LU 70000.

3.   External view of right valve. Lower Oxford
            Clay, Jason Zone, Calvert, Bucks.,
            x 2.7. LU 69824.

Protocardia sp.

4.   External view of right valve. Lower Oxford
            Clay, Coronatum Zone, Marston
            Moretaine, Beds., x 1. LU 70005.

5.   External view of left valve. Same horizon
            and locality as above, x 1. LU 70006.

Protocardia (_Protocardia_) _striatulum_ (J. de C. Sowerby)

6.   External view of left valve. Kellaways Rock,
            Brora Roof Bed, Brora, Sutherlandshire,
            x 1.5. LU 69832.

7.   External view of right valve, internal mould.
            Same horizon and locality as above,
            x 1. LU 69833.
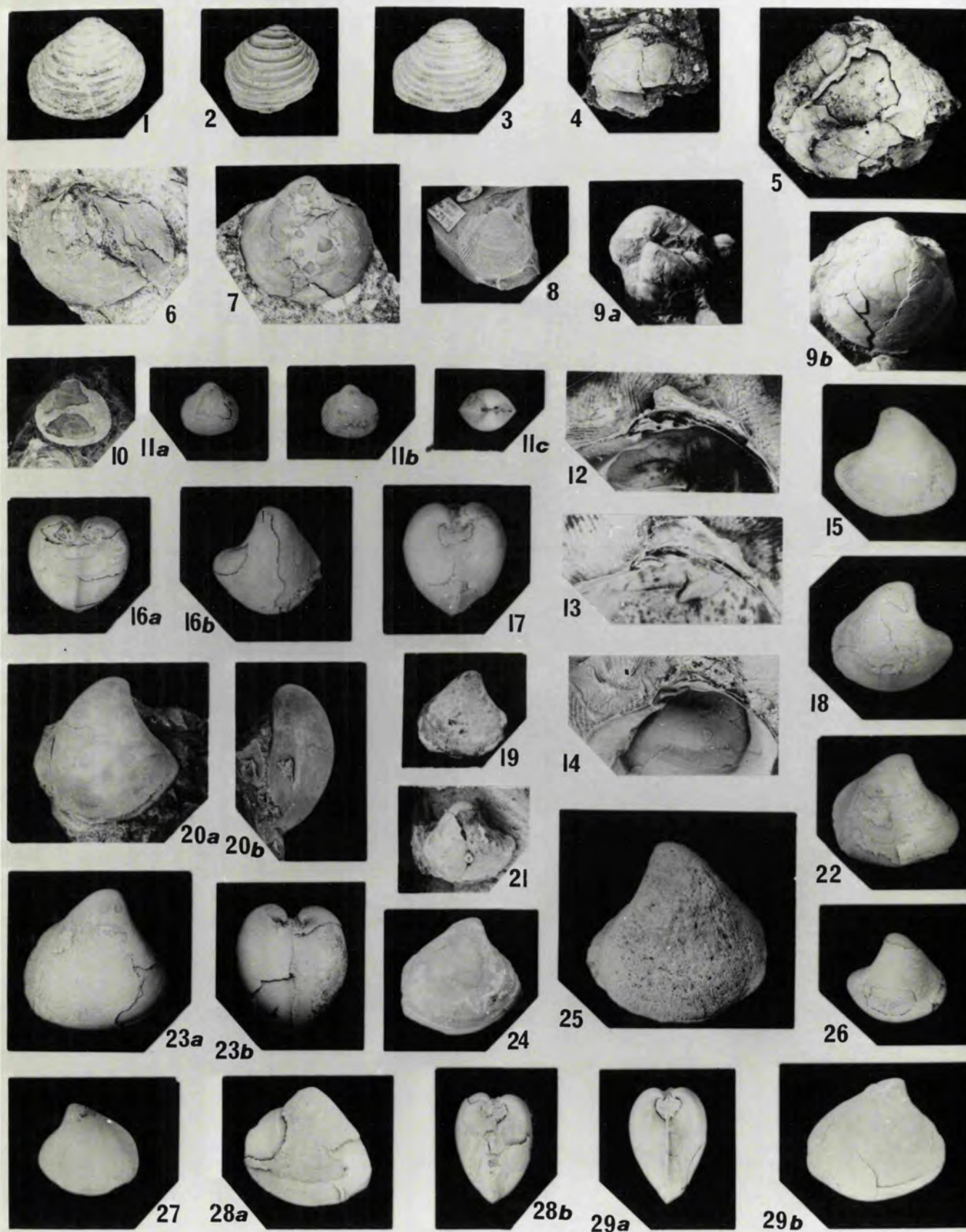
PLATE 22

16a-b.   External view of right valve, normal size
          and magnified. Lower Oxford Clay,
          Jason Zone, Stewartby, Beds., x 1
          (16a), x 5.4 (16b). LU 69852.

17a-b.   External views of left and right valve.
          Lower Oxford Clay, Jason Zone,
          Wiltshire, x 5.4. OUM J28230.

18a-b.   External view of right valve and dorsal
          view. Lower Oxford Clay, Dauntsey,
          Wiltshire, x 5.4. LU 70018.

8.   Internal view of right valve. Lower Oxford
          Clay, Coronatum Zone, Marston
          Moretaine, Beds., x 1.4. LU 69846.

          Corbulomima macneillii (Morris)

9a-c.   External views of right and left valve and
          dorsal view. Kellaways Rock,
          Trowbridge, Wiltshire, x 5.8.
          GSM 113985.

10a-c.   Neotype. External views of right and left
          valves and dorsal view. Same horizon
          and locality as above, x 5.1.
          GSM 113999.

11.   External view of left valve. Kellaways
          Rock, Chippenham, Wilts., x 4.3.
          BCM 3324b.

12a-c.   External views of right and left valves and
          dorsal view. Same horizon and locality
          as above, x 5.6. BCM 3324c.

13.   External view of left valve. Kellaways
          Rock, Trowbridge, Wilts., x 5.9.
          GSM 114017.

14a-c.   External views of right and left valves and
          dorsal view. Lower Oxford Clay,
          Dauntsey, Wilts., x 5.9. LU 70017.

15.   External view of right valve. Kellaways
          Rock, Chippenham, Wiltshire, x 4.3.
          BCM 3324a.

PLATE 23.

Isocyprina (*Isocyprina*) *roederi* Arkell

Fig.

1.   External view of right valve, internal
        mould. Lower Oxford Clay, Coronatum
        Zone, Stewartby, Bedfordshire, x 1.
        LU 69833.

2.   External view of right valve. Same horizon
        and locality as above, x 1.4.
        LU 69839.

3.   External view of left valve, internal mould.
        Lower Oxford Clay, Coronatum Zone,
        Crook Hill, Chickerell, Dorset, x 1.4.
        LU 70007.

4.   External view of right valve. Lower Oxford
        Clay, Coronatum Zone, Stewartby,
        Beds., x 1.4. LU 69837.

5.   Internal view of left valve. Same horizon
        and locality as above, x 1.5. LU 70003.

6.   External view of left valve. Same horizon
        and locality as above, x 1.5.
        LU 69845.

7.   Internal view of left valve. Same horizon
        and locality as above, x 1.4.
        LU 70008.

PLATE 23
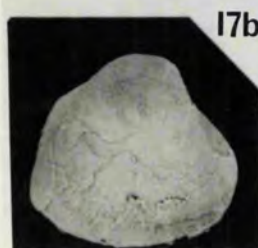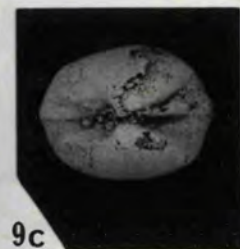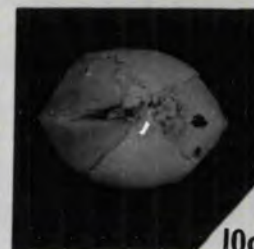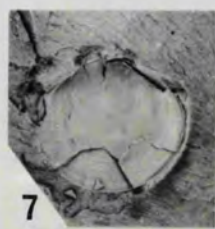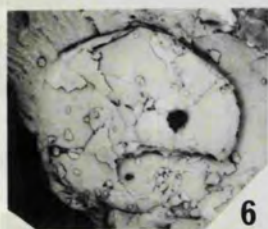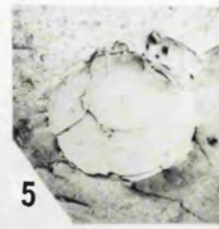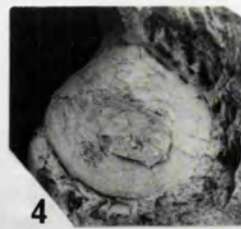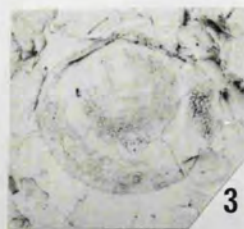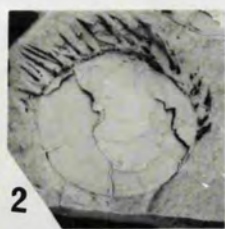
26a,b.   Dorsal view and external view of left

         valve. Kellaways Rock, Stewartby,

         Beds., x 1. LU 70010.

27.   External view of right valve. Belemnite

         Sands (L. Callovian), Staffin Bay,

         Isle of Skye, x 1. LU 70011.

16.   External view of right valve. Lower Oxford
                Clay, Jason Zone, Calvert,
                Buckinghamshire, x 1. LU 69881.

17.   External view of right valve. Lower Oxford
                Clay, Jason Zone, Wilts., x 1.
                OUM J28242.

18.   External view of left valve. Same horizon
                and locality as above, x 1.
                OUM J28241.

19.   External view of left valve. Lower Oxford
                Clay, Coronatum Zone, Norman Cross,
                Hunts., x 1. LU 69879.

20.   External view of right valve. Same horizon
                and locality as above, x 1. LU 70100.

21.   External view of left valve. Same horizon
                and locality as above, x 1. LU 69880.

22.   External view of right valve. Same horizon
                and locality as above, x 1. LU 69883.

23.   External view of left valve. Same horizon
                and locality as above, x 1. LU 69884.

24.   External view of right valve. Same horizon
                and locality as above, x 1. LU 69882.

Pleuromya uniformis (J. Sowerby)

25.   External view of right valve. Belemnite
                sands (L. Callovian), Staffin Bay,
                Isle of Skye, x 1. LU 70009.

Corbulomima obscura (J. de C. Sowerby)

9.   Holotype. External view of right valve.
Kellaways Rock, Brora Roof Bed,
Brora, Sutherlandshire, x 4.7.
Sowerby Collection, BM 43044.
Figured by J. de C. Sowerby, 1827,
pl. 572, fig. 5 as Corbula obscura.

10a-c.   External views of right valve and left
valve and dorsal view. Same horizon
and locality as above, x 4.7.
LU 69870.

11.   External view of left valve. Same horizon
and locality as above, x 4.7.
LU 69868.

12.   External view of left valve. Same horizon
and locality as above, x 4.7.
LU 69871.

13.   External view of left valve. Same horizon
and locality as above, x 4.7.
LU 69872.

Pleuromya alduini (Brongniart)

14.   External view of left valve. Lower Oxford
Clay, Coronatum Zone, Norman Cross,
Hunts., x 1. LU 69875.

15.   External view of left valve. Same horizon
and locality as above, x 1. LU 69877.

PLATE 24.

Corbulomima macneillii (Morris)

Fig.

1a-b.   External view of right valve and dorsal
         view. Lower Oxford Clay, Jason Zone,
         Wiltshire, x 5.4. OUM J28230.

2.   External view of left valve. Lower Oxford
         Clay, Jason Zone, Dauntsey, Wilts.,
         x 5.4. LU 70019.

3.   External view of left valve. Kellaways
         Rock, Chippenham, Wilts., x 5.4.
         BCM 3324d.

4a-b.   External view of right valve, normal size
         and magnified. Lower Oxford Clay,
         Jason Zone, Stewartby, Beds., x 1
         (4a), x 4.7 (4b). LU 69859.

5.   External view of right valve. Kellaways
         Rock, Chippenham, Wilts., x 5.4.
         BCM 3324e.

6.   External view of right valve. Lower Oxford
         Clay, Jason Zone, Stewartby, Beds.,
         x 4.5. LU 69861.

7.   External view of left valve. Same horizon
         and locality as above, x 4.2.
         LU 69853.

8.   External view of right valve. Same horizon
         and locality as above, x 4.6. LU 69855.

PLATE 24
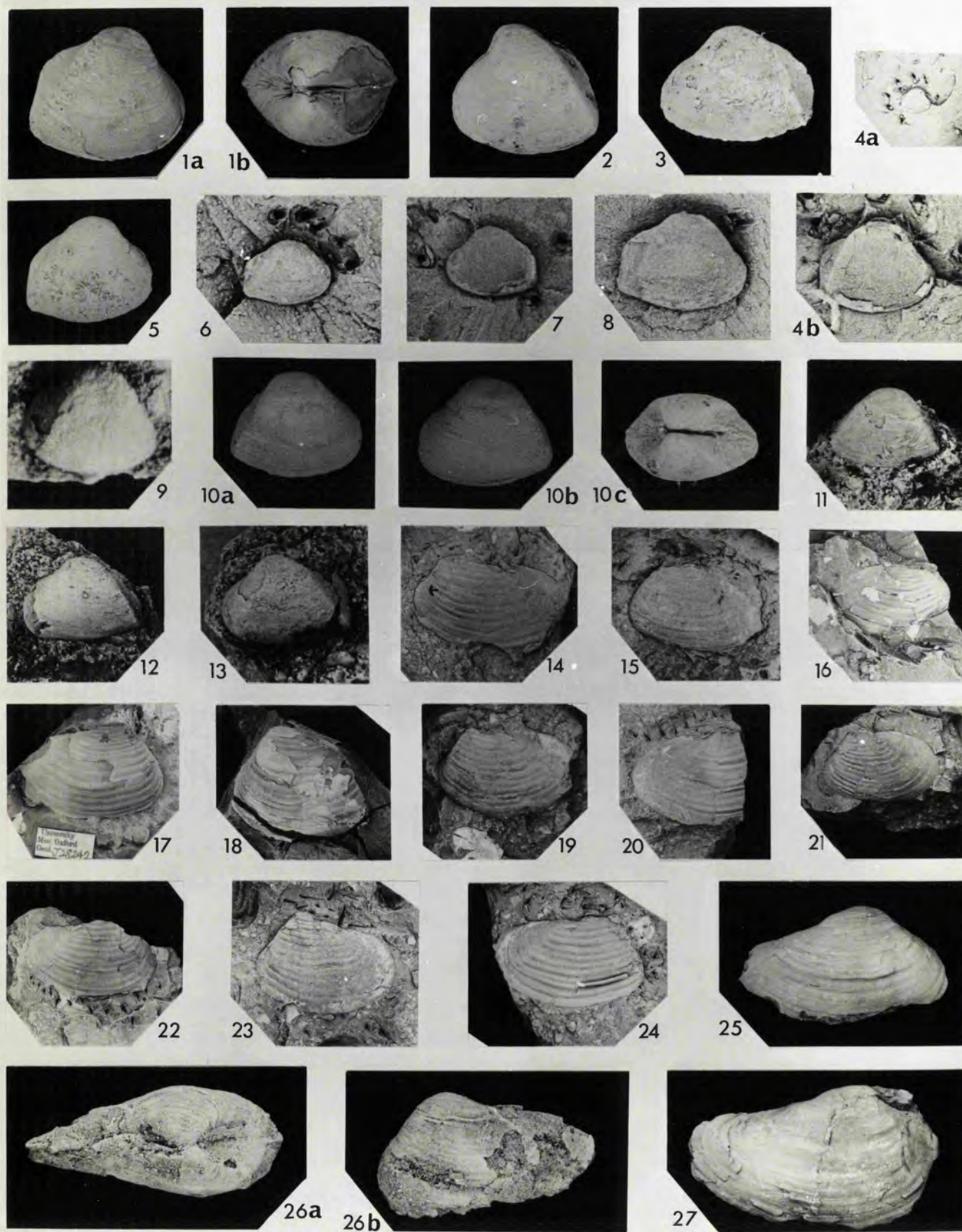
12.   External view of ? left valve. Lower

       Oxford Clay, Coronatum Zone, Stewartby,

       Beds., x 1.7.   BM LL27736.

13.   External view of both valves. Same horizon

       and locality as above, x 2.2.

       LU 70040.

6.   External view of left valve. Lower Oxford
               Clay, Coronatum Zone, Calvert,
               Buckinghamshire, x 1. LU 69888.

8.   Neotype. External view of left valve.
               Upper Oxford Clay, Cordatum Zone (Red
               Nodule Beds), Weymouth, Dorset, x 1.
               Damon Collection, BM L6979. Figured
               by Damon, 1888, pl. 19, fig. 14 as
               Thracia _depressa._

9.   External view of left valve. Lower Oxford
               Clay, Corcnatum Zone, Stewartby,
               Beds., x 1. LU 69901.

10.   External view of left valve. Upper Oxford
               Clay, Mariae Zone, Scarborough,
               Yorkshire, x 1. YM KD1974/58.

14a-b.   External view of left valve and anterior
               view. Upper Oxford Clay, Cordatum
               Zone (Red Nodule Beds), Weymouth,
               Dorset, x 1. GSM GSa 3649.

15.   External view of left valve. Same horizon
               and locality as above, x 1.
               GSM GSa 3648.

Anomalodesmatan sp. A.

11.   External view of ? left valve. Lower
               Oxford Clay, Coronatum Zone, Crook
               Hill, Chickerell, Dorset, x 1.6.
               BM LL27735.

PLATE 25.

Pleuromya alduini (Brongniart)

Fig.

1.   External view of right valve. Kellaways

        Rock, Kington Langley, Wiltshire,

        x 1. GSM Ka 608.

7.   External view of left valve. Lower Oxford

        Clay, Calloviense Zone, Stewartby,

        Bedfordshire, x 1. LU 70014.

        Pleuromya uniformis (J. Sowerby)

2.   External view of left valve. Belemnite

        Sands (L. Callovian), Staffin Bay,

        Isle of Skye, x 1. LU 70012.

3.   Holotype. External view of left valve.

        Cornbrash, Felmersham, Beds., x 1.

        Sowerby Collection, BM 43224. Figured

        by J. Sowerby, 1813, pl. 33, fig. 4

        as *Unio uniformis*.

4.   External view of right valve. Belemnite

        Sands (L. Callovian), Staffin Bay,

        Isle of Skye, x 1. LU 70013.

        Thracia (*Thracia*) *depressa* (J. de C. Sowerby)

5.   External view of left valve. Lower Oxford

        Clay, Calloviense Zone, Stewartby,

        Beds., x 1. LU 69889.

PLATE 25
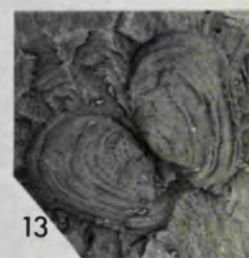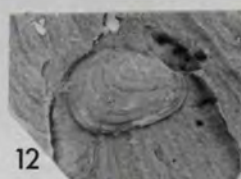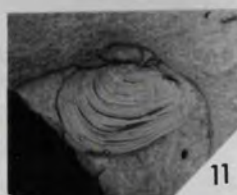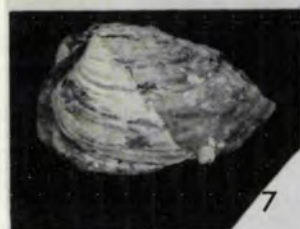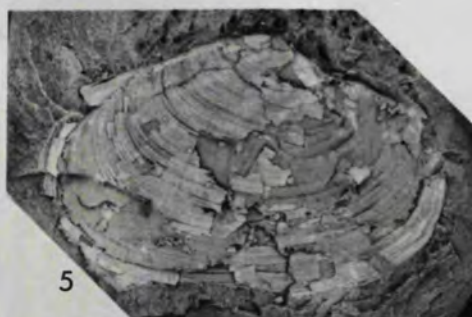
7.   External view of both valves. Lower Oxford
      Clay, Coronatum Zone, Calvert,
      Buckinghamshire, x 2.2. LU 70031.

8.   External view of ? right valve. Same
      horizon and locality as above, x
      2.2. LU 70032.

10.   External view of ? left valve. Lower Oxford
      Clay, Coronatum Zone, Stewartby,
      Beds., x 1.6. LU 70033.

Pleuromya uniformis (J. Sowerby)

11a-b. External view of right valve and dorsal
        view. Belemnite Sands (L. Callovian),
        Staffin Bay, Isle of Skye, x 1.
        LU 70034.

12.   External view of right valve. Same horizon
      and locality as above, x 1. LU 70035.

13.   External view of left valve. Same horizon
      and locality as above, x 1. LU 70036.

14a,b. External view of left valve and dorsal
        view. Same horizon and locality as
        above, x 1. LU 70037.

15a,b. External views of right and left valves.
        Same horizon and locality as above,
        x 1. LU 70038.

16a,b. External view of left valve and dorsal
        view. Same horizon and locality as
        above, x 1. LU 70039.

PLATE 26.

Anomalodesmatan sp. A.

Fig.

1.   External view of both valves. Lower Oxford
            Clay, Coronatum Zone, Stewartby,
            Bedfordshire, x 2.2. LU 70024.

6.   External view of ? left valve. Lower
            Oxford Clay, Jason Zone, Stewartby,
            Beds., x 1.6. LU 70025.

9.   External view of ? left valve. Lower
            Oxford Clay, Coronatum Zone,
            Stewartby, Beds., x 1.6. LU 70026.

Anomalodesmatan sp. B.

2.   External view of both valves. Same horizon
            and locality as above, x 2.2.
            LU 70027.

3a-b.   External view of both valves, magnified and
            normal size. Lower Oxford Clay,
            Jason Zone, Stewartby, Beds., x 2.2
            (3a), x 1 (3b). LU 70028.

4a-b.   External view of both valves, magnified and
            normal size. Same horizon and
            locality as above, x 2.2 (4a), x 1
            (4b). LU 70029.

5.   External view of both valves. Same horizon
            and locality as above, x 2.2. LU 70030.
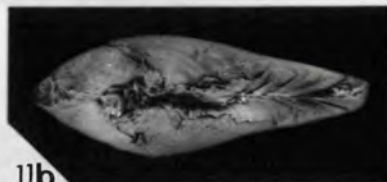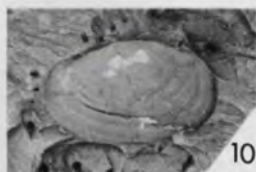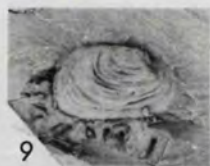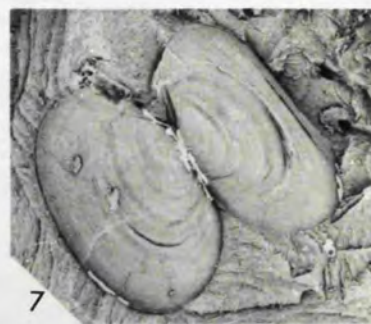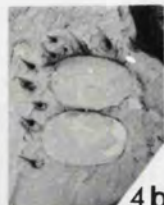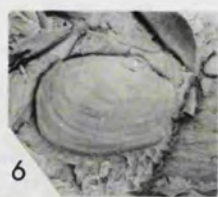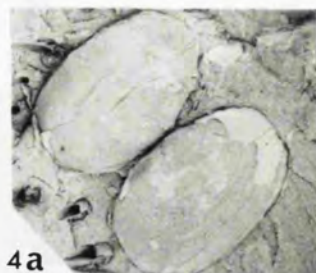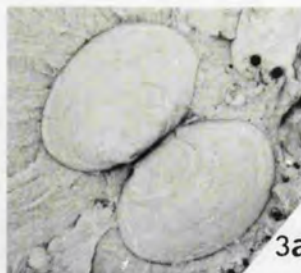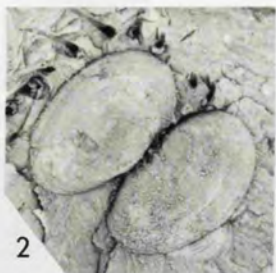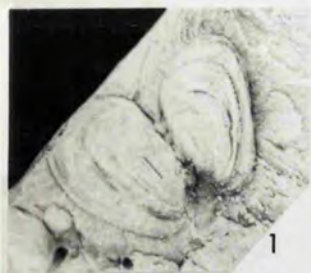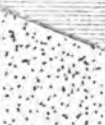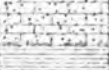
PLATE 26

CHAPTER 3

Palaeoecology of a bituminous shale:

the Lower Oxford Clay of central England

Text-Figs. 1 - 22

Tables   1 - 7

North-east Yorks.		ZONE	Central & Southern England		STAGE
Yorkshire Oxford Clay		Mariae		U. Oxford Clay	L. Oxfordian
Hackness Rock		Lamberti		M. Oxford Clay	U. Callovian
		Athleta			
hiatus					
Langdale Beds		Coronatum		L. Oxford Clay	M. Callovian
hiatus		Jason			
Kellaways Rock		Calloviense		Kellaways Rock	L. Callovian
Shales of the Cornbrash		Macro-cephalus		Kellaways Clay	
U. Cornbrash				U. Cornbrash	
U. Deltaic Series		Discus		L. Cornbrash	U. Bathonian

Text-Fig. 1. Comparison of the lower part of the Upper Jurassic of Yorkshire and southern England, showing the development of a marginal facies in Yorkshire during Callovian times. After Wright (1968). All Zones drawn to equal thickness, therefore the lithological sections are not to scale.

Stages		Zones	Subzones	Divisions
OXFORDIAN	LOWER	Cardioceras cordatum	C. cordatum	UPPER OXFORD CLAY
			C. costicardia	
			C. bukowskii	
		Quenstedtoceras mariae	C. praecordatum	
			C. scarburgense	
CALLOVIAN	UPPER	Quenstedtoceras lamberti		MIDDLE OXFORD CLAY
		Peltoceras athleta	Upper Middle Lower	
	MIDDLE	Erymnoceras coronatum	K. (Zugokosmoceras) grossouvrei	LOWER OXFORD CLAY
			K. (Zugokosmoceras) obductum	
		Kosmoceras jason	K. (Gulielmites) jason	
			K. (Gulielmites) medea	
	LOWER	Sigaloceras calloviense	S. (Catasigaloceras) enodatum	
			Sigaloceras calloviense	KELLAWAYS ROCK
			Proplanulites koenigi	
		Macrocephalites macrocephalus	M. (Kamptokephalites) kamptus	KELLAWAYS CLAY
			M. (Macrocephalites) macrocephalus	UPPER CORNBRASH

Text-Fig. 2. The Zones of the Callovian and Lower Oxfordian. After Callomon (1968).

Lithological sections measured at the four quarries
examined in central England.
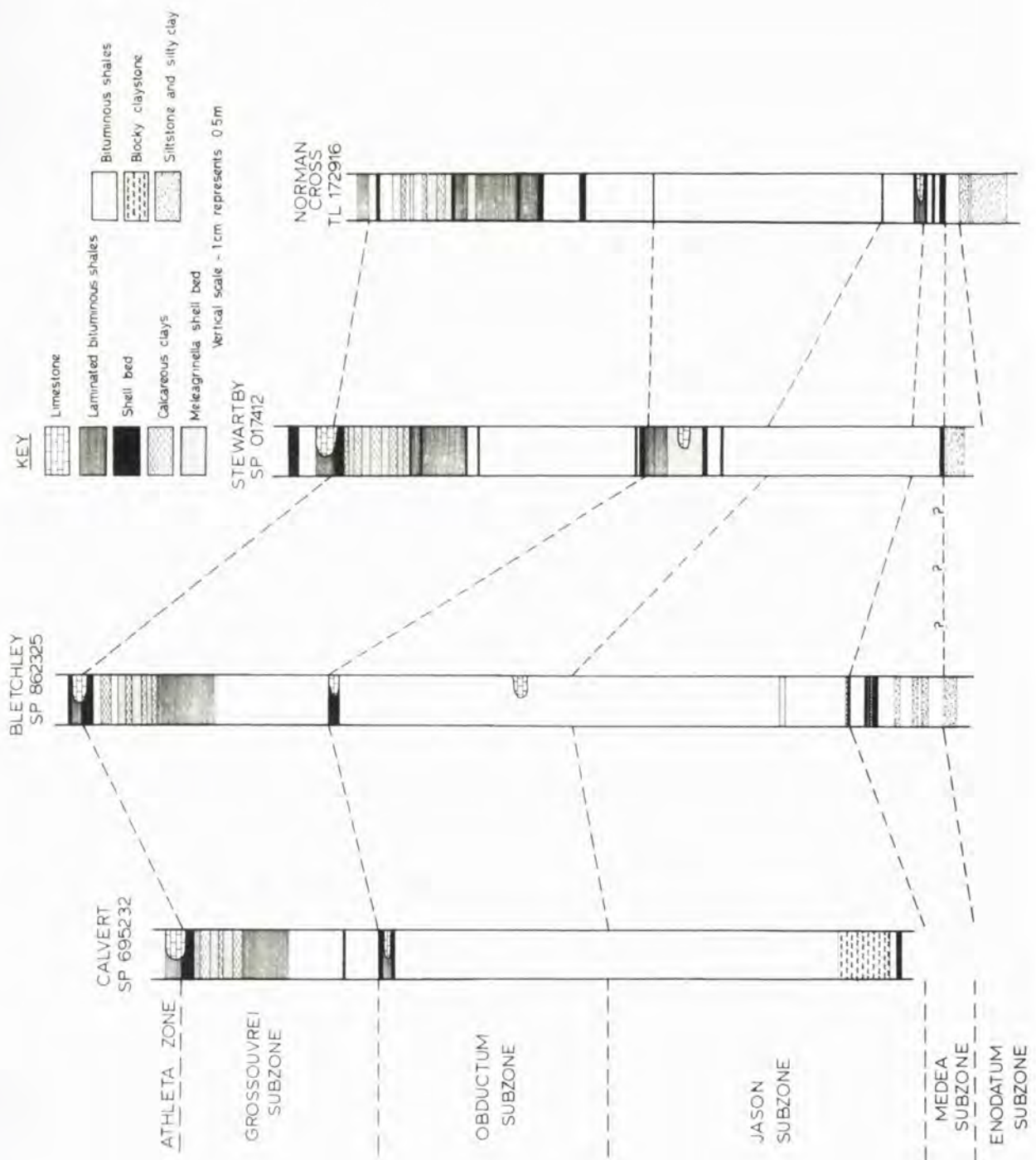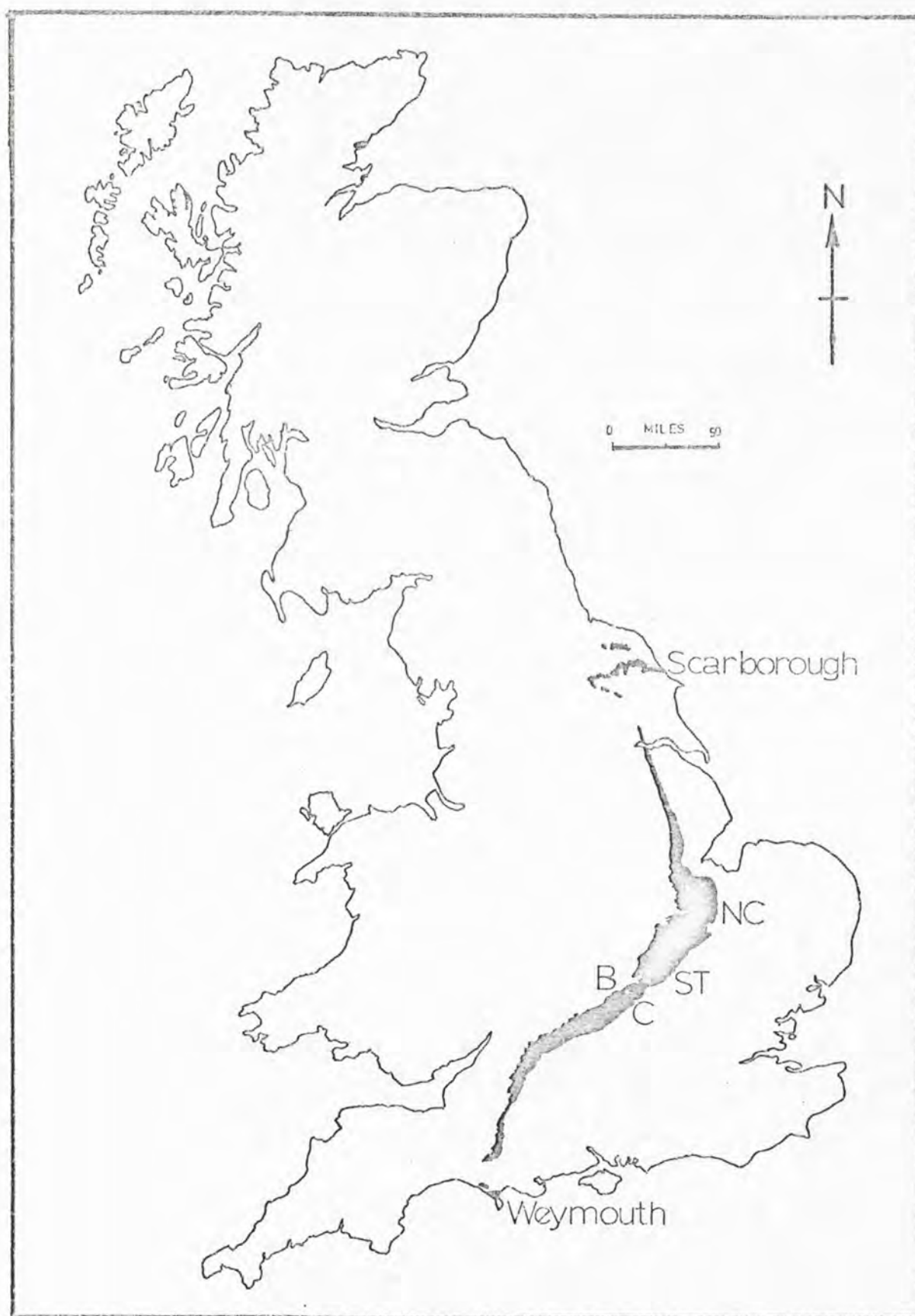
Text-Fig. 4. The outcrop of the Oxford Clay in England, showing the location of the major sections examined.

TEXT-FIG. 5.

The soluble fraction of the Lower Oxford Clay of the
Midlands, related to lithology and biofacies.
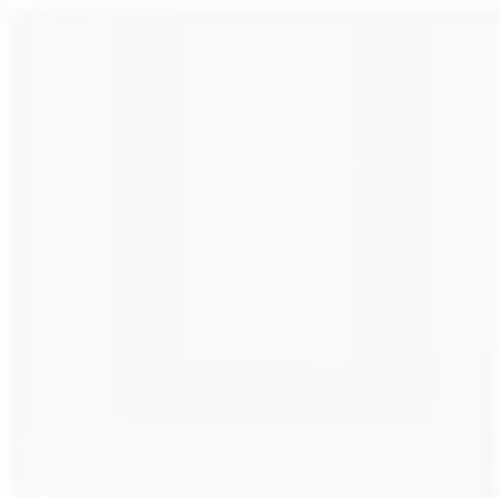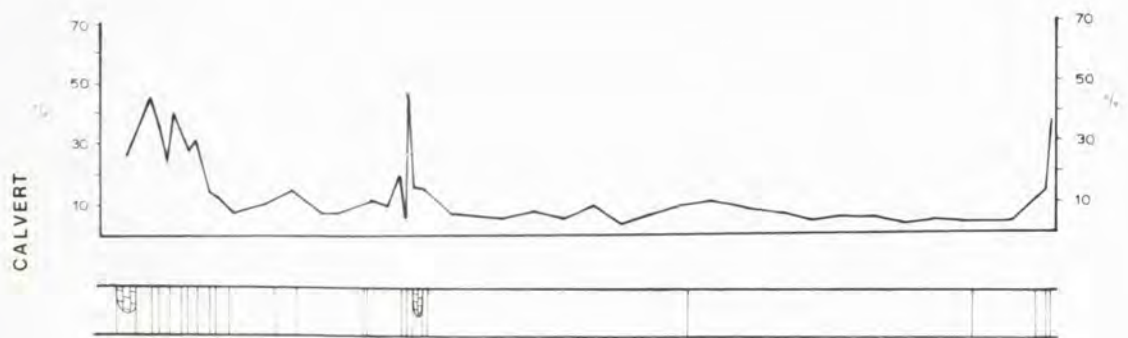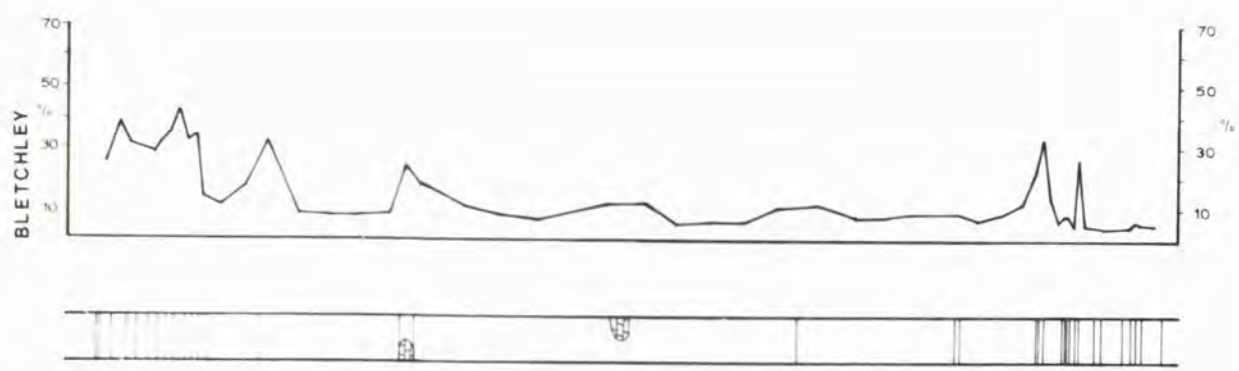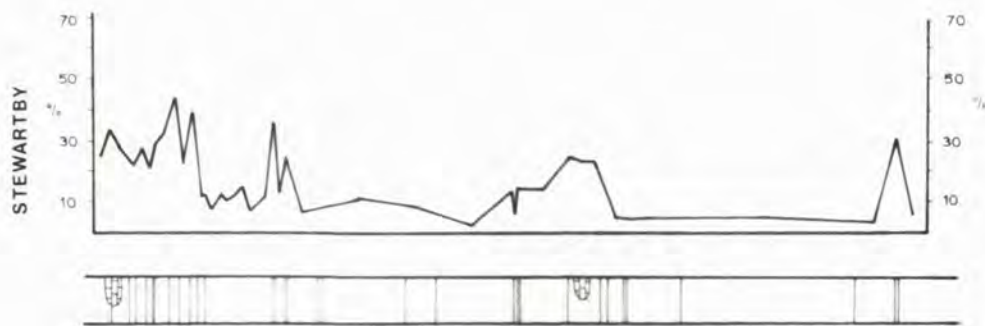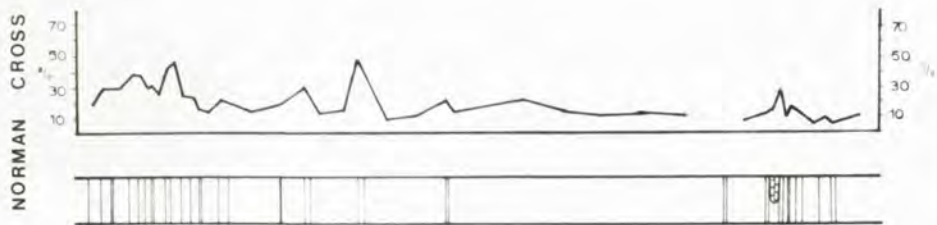
TEXT-FIG. 6.

Distribution of the ten biofacies at each of the four Midlands quarries.

KEY

Silts and silty clays
Blocky claystone
Calcareous clays
Meleagrinella shell beds
Gryphaea shell beds

Nuculacean shell beds
Grammatodon shell beds
Deposit-feeder bituminous shale
Grammatodon-rich bituminous shale
Foram-rich bituminous shale

Vertical scale - 1 cm represents 0.5 m

CALVERT
SP 695232

BLETCHLEY
SP 862325

STEWARTBY
SP 017412

NORMAN
CROSS
TL 172916

ATHLETA ZONE

GROSSOUVREI
SUBZONE

OBDUCTUM
SUBZONE

JASON
SUBZONE

MEDEA
SUBZONE

ENODATUM
SUBZONE

TEXT-FIG. 7.

Triangular plots of bivalve feeding groups for three
of the Lower Oxford Clay biofacies. a. Silts and
silty clays, all bivalves; b. Silts and silty clays,
pendent bivalves removed; c. Deposit-feeder
bituminous shales, pendent bivalves, removed; e.
Grammatodon-rich bituminous shales, all bivalves;
f. Grammatodon-rich bituminous shales, pendent bivalves
removed.
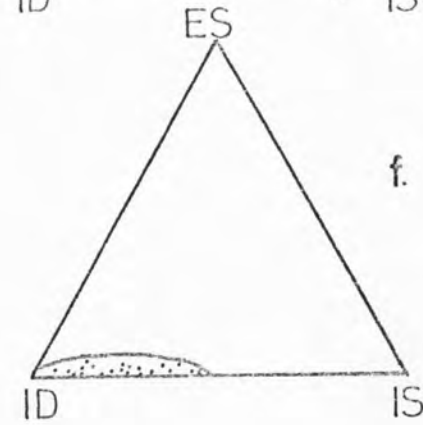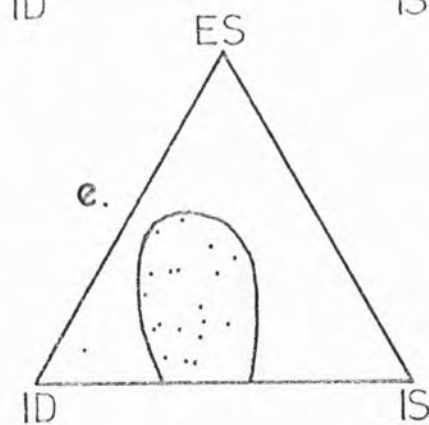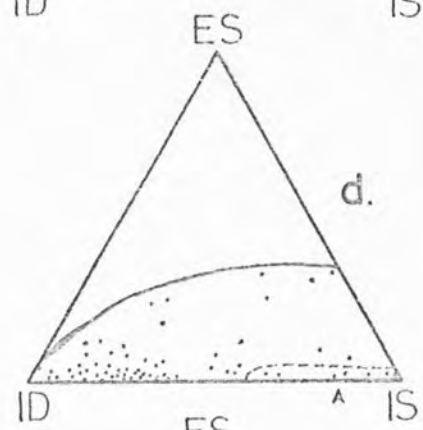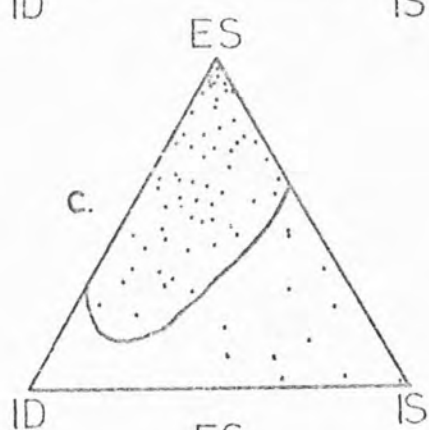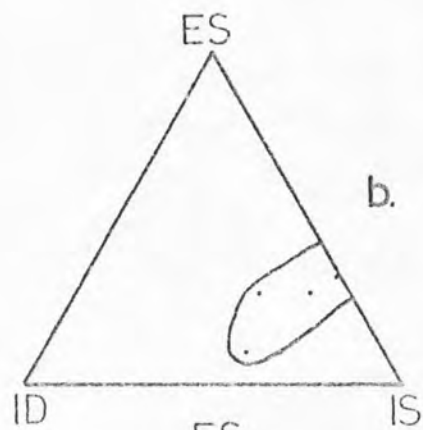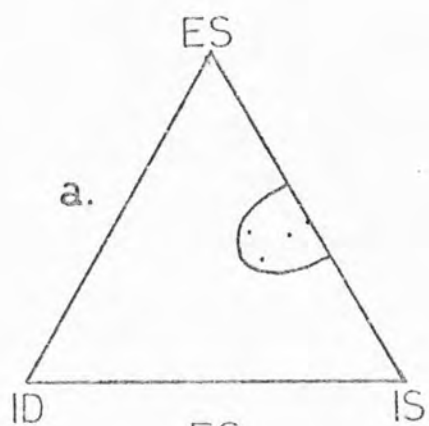
Triangular plots of bivalve feeding groups for the remaining biofacies. a. Foram-rich bituminous shales, all bivalves; b. _Meleagrinella_ shell bed, all bivalves (A); Blocky claystone, all bivalves (B); c. Shell beds, all bivalves; _Gryphaea_ shell beds (A), Nuculacean shell beds (B), _Grammatodon_ shell beds (C); d. Shell beds, pendent bivalves removed; _Gryphaea_ shell beds (A), Nuculacean shell beds (B), _Grammatodon_ shell beds (C); e. Calcareous clays, all bivalves; f. Calcareous clays, pendent bivalves removed.
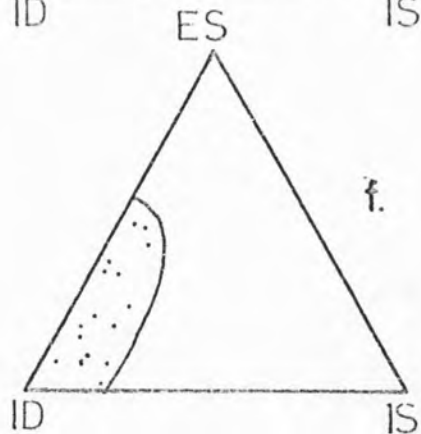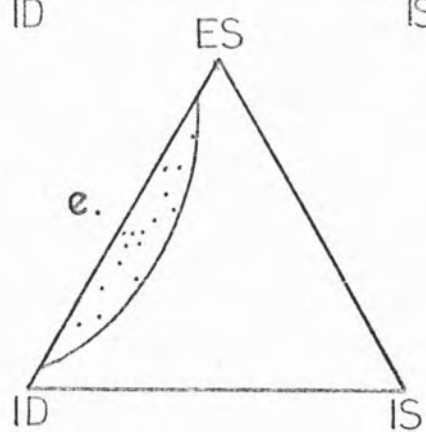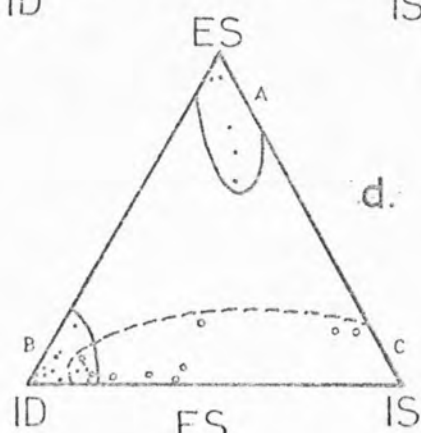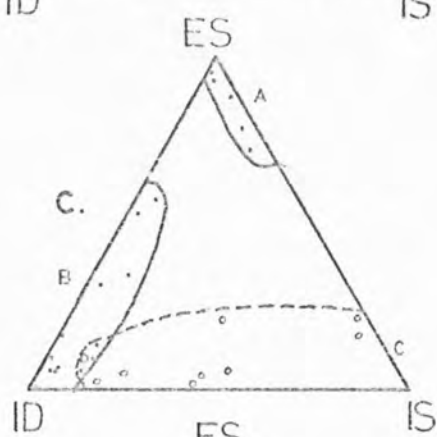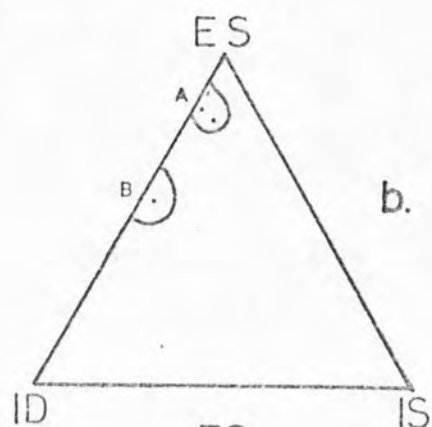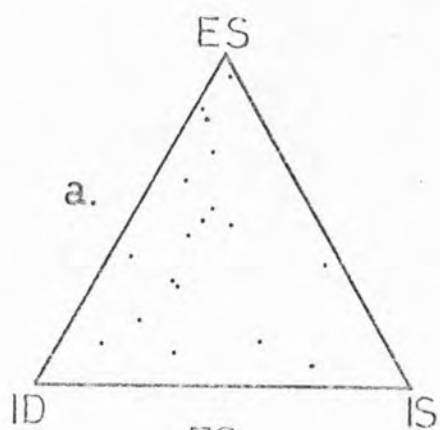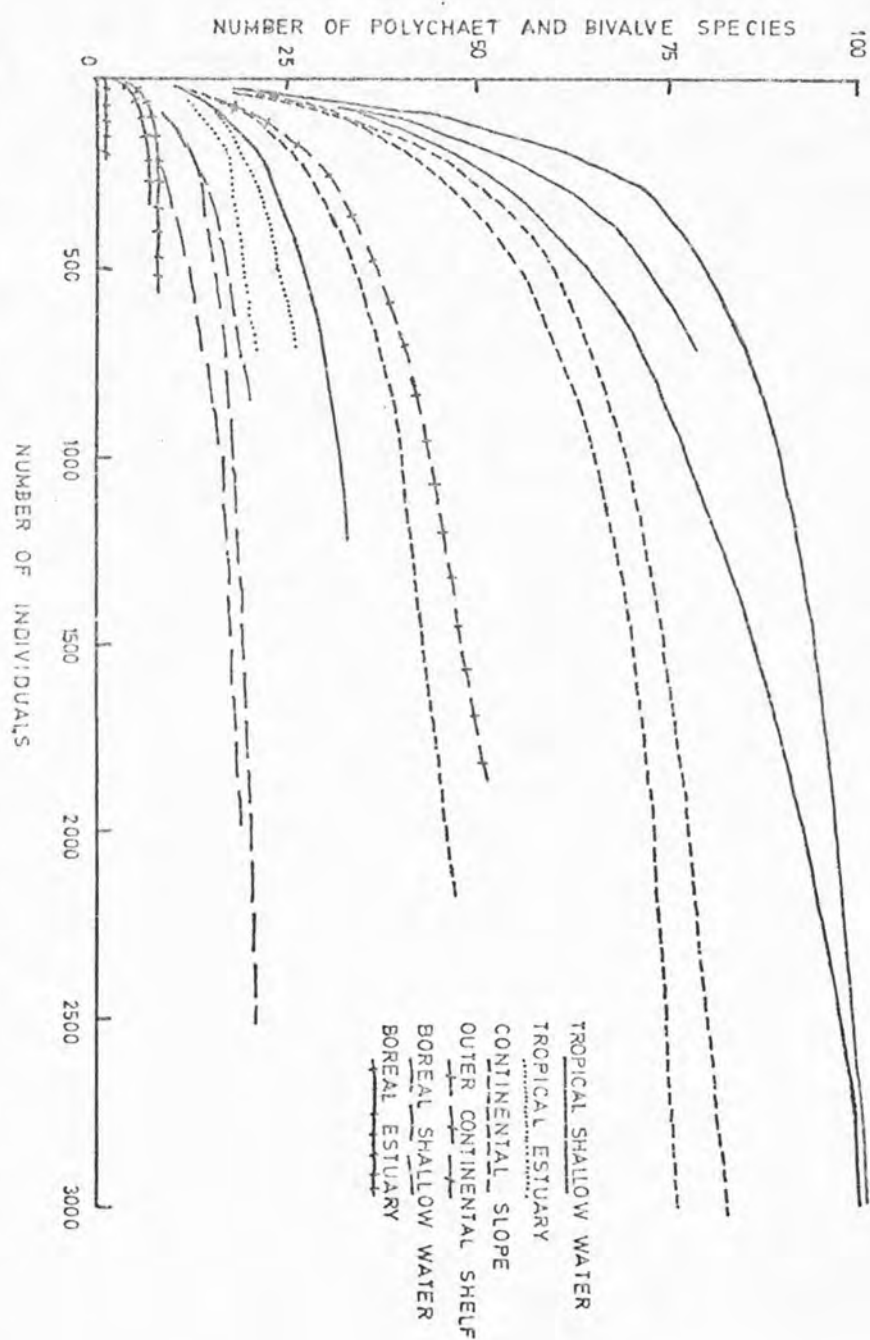
Text-Fig. 9. Rarefaction curves for a range of aquatic environments. From Sanders (1968).

TEXT-FIG. 10.

Rarefaction curves for the Lower Oxford Clay biofacies.
a. Silts and silty clays; b. Deposit-feeder
bituminous shales; c. Grammatodon-rich bituminous
shales; d. Foram-rich bituminous shales;
e. Nuculacean shell beds; f. Grammatodon shell beds;
g. Gryphaea shell beds; h. Blocky claystone;
j. Calcareous clays.

Number of individuals

Number of species
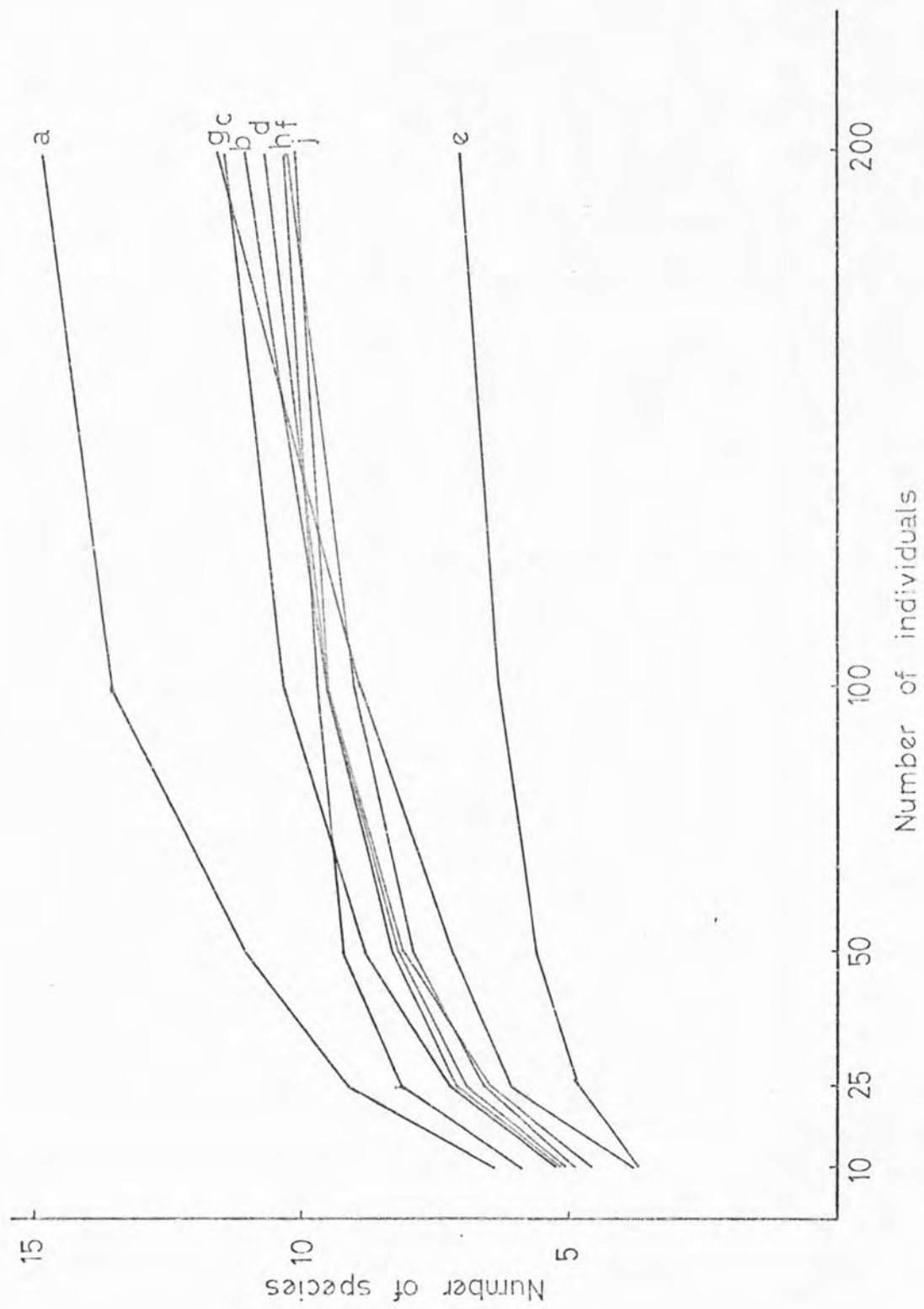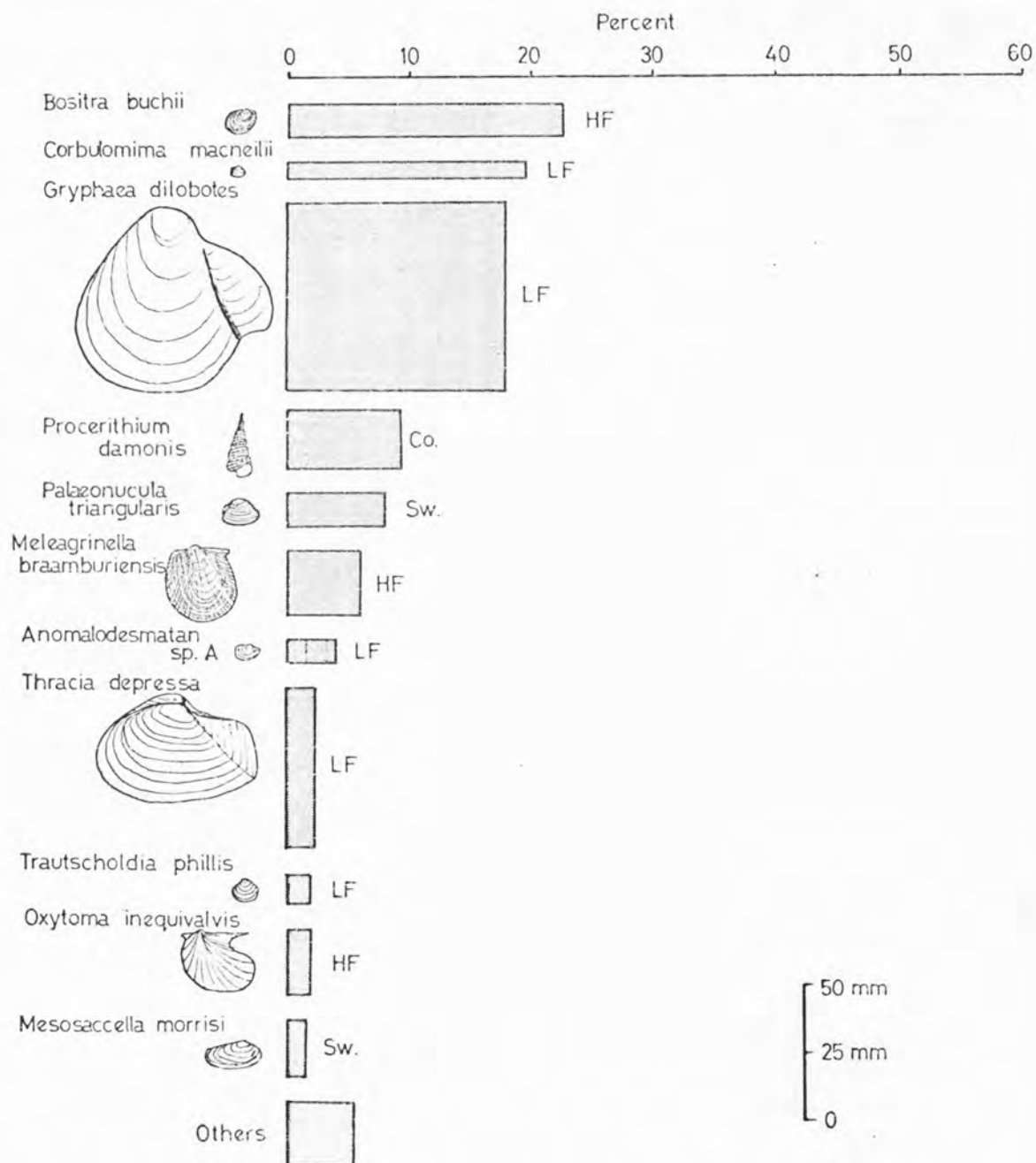
Text-Fig. 11. Trophic group composition of the silts and silty clays biofacies. All benthos included.
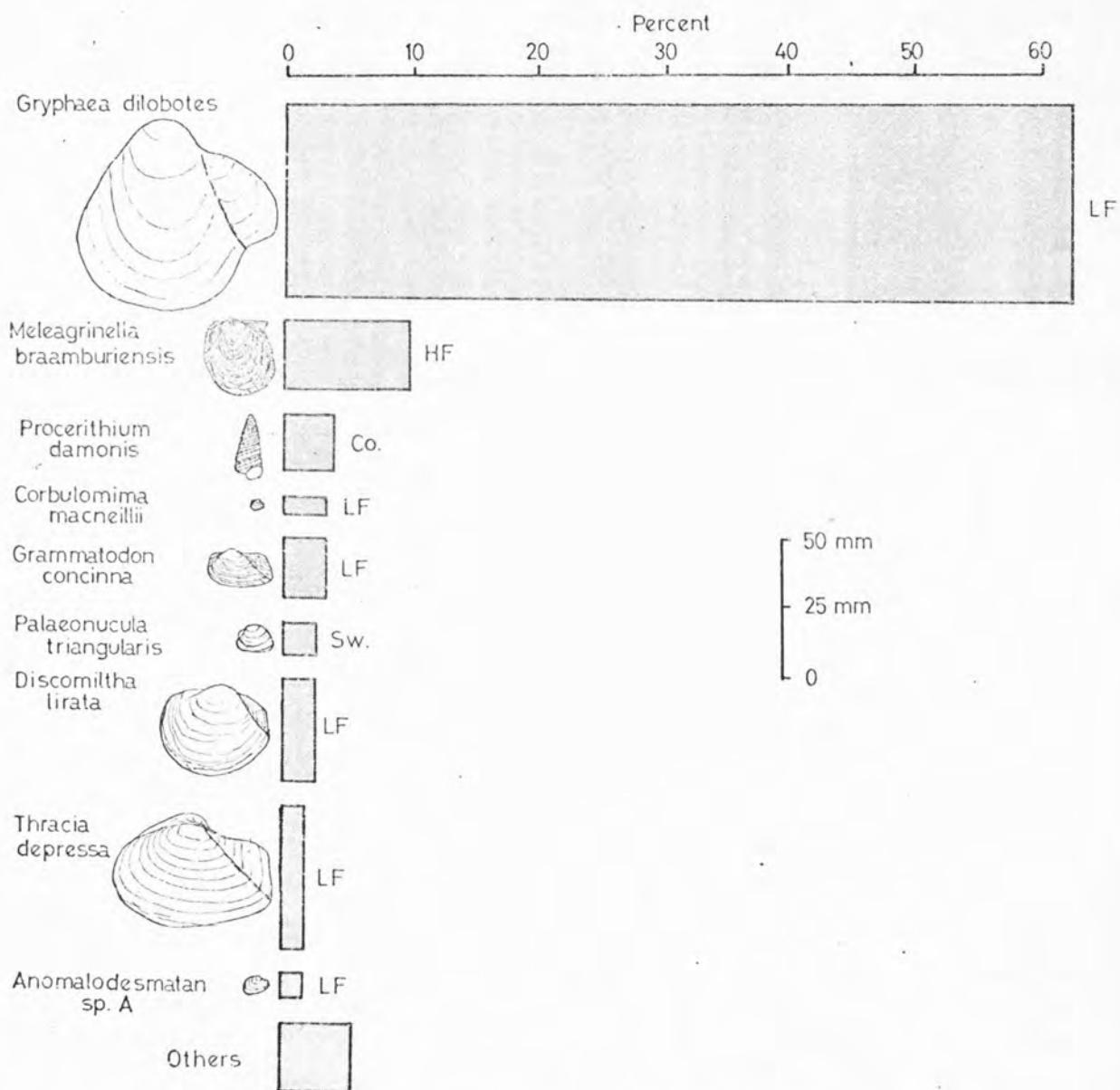
Text-Fig. 12. Trophic group composition of the Gryphaea shell bed
biofacies. All benthos included.
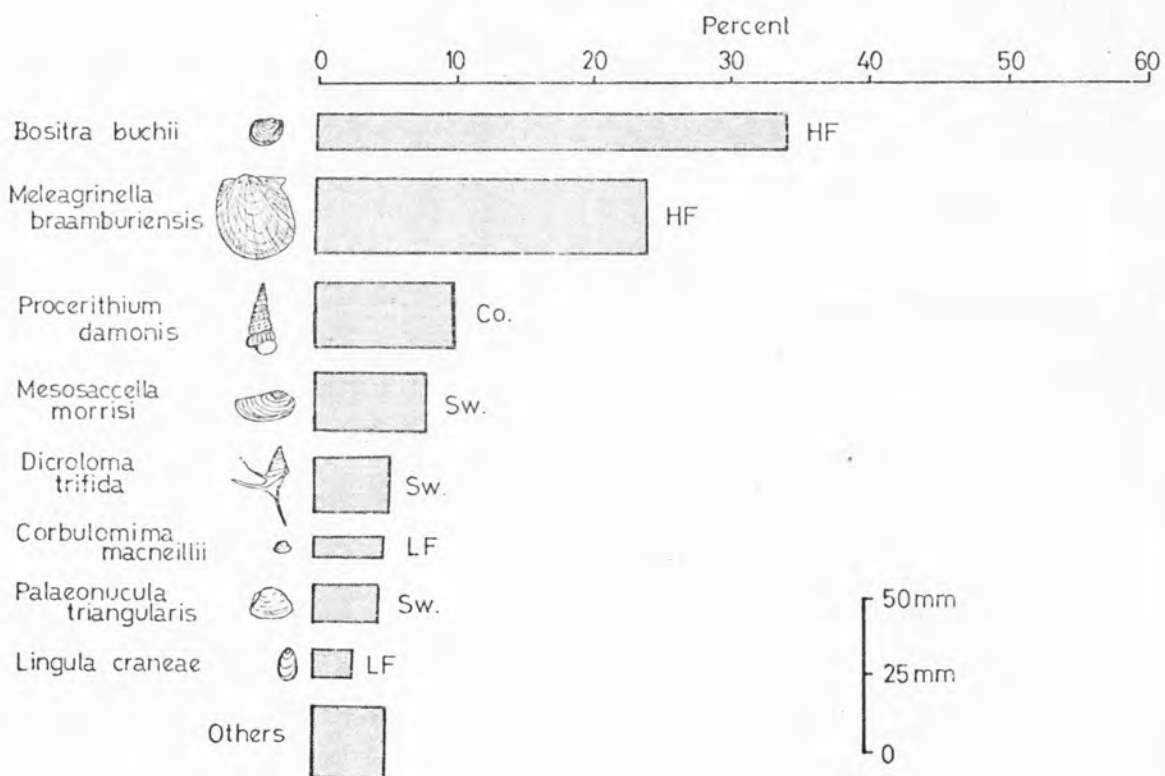
Text-Fig. 13. Trophic group composition of the Deposit-feeder
bituminous shale biofacies. All benthos included.
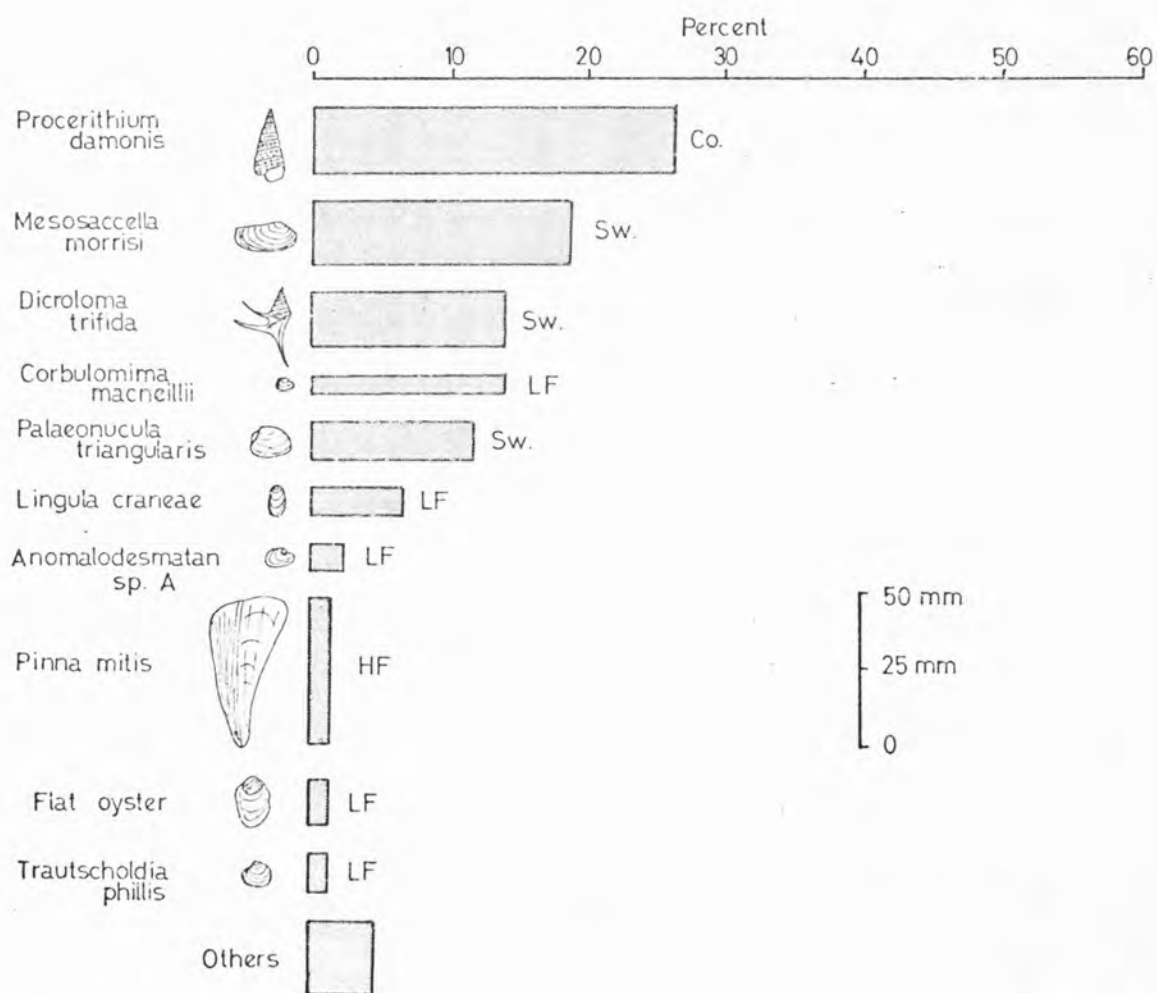
Text-Fig. 14. Trophic group composition of the Deposit-feeder bituminous shale biofacies. Pendent bivalves removed.
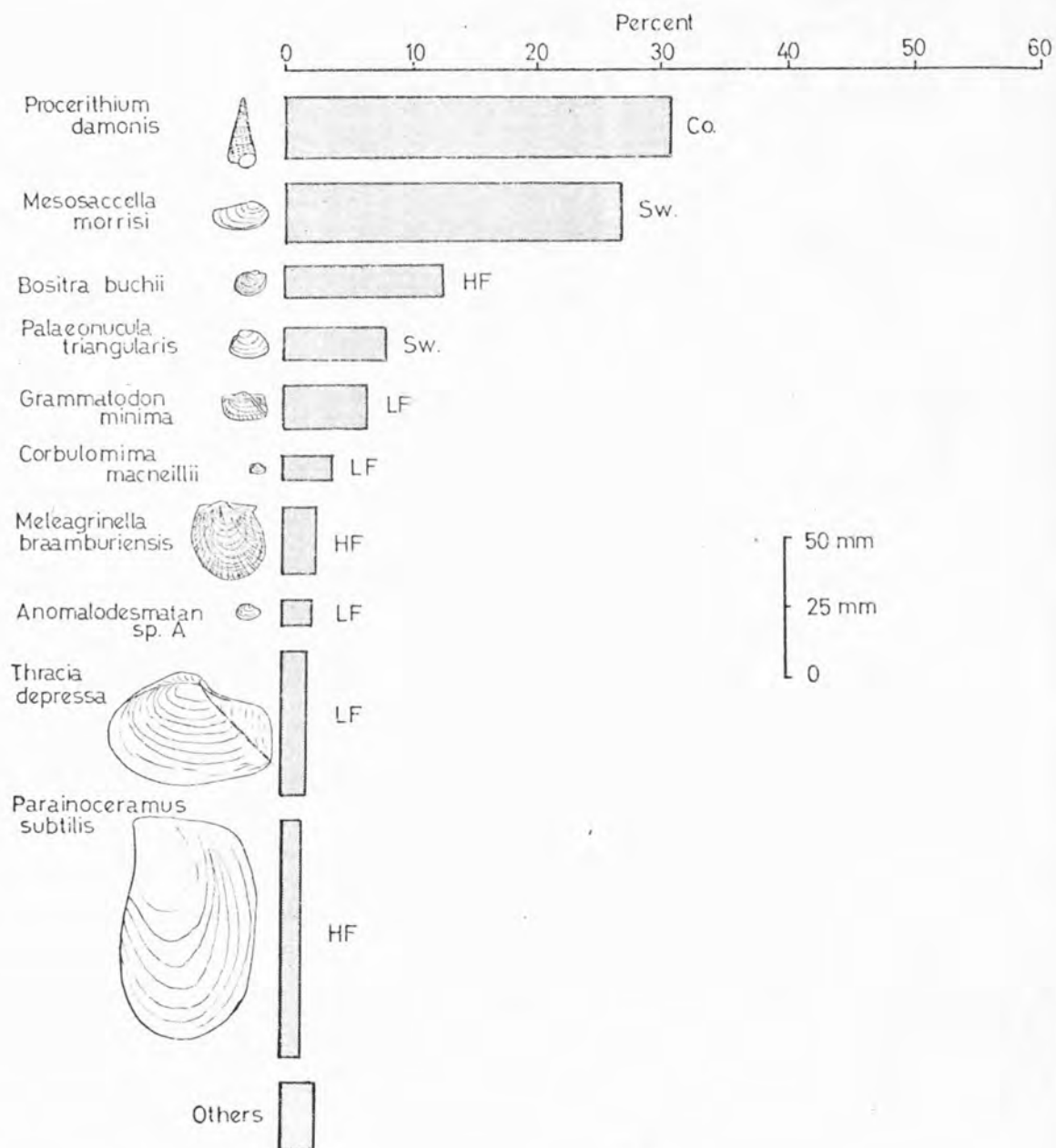
Text-Fig. 15. Trophic group composition of the Grammatodon-rich
bituminous shales. All benthos included.
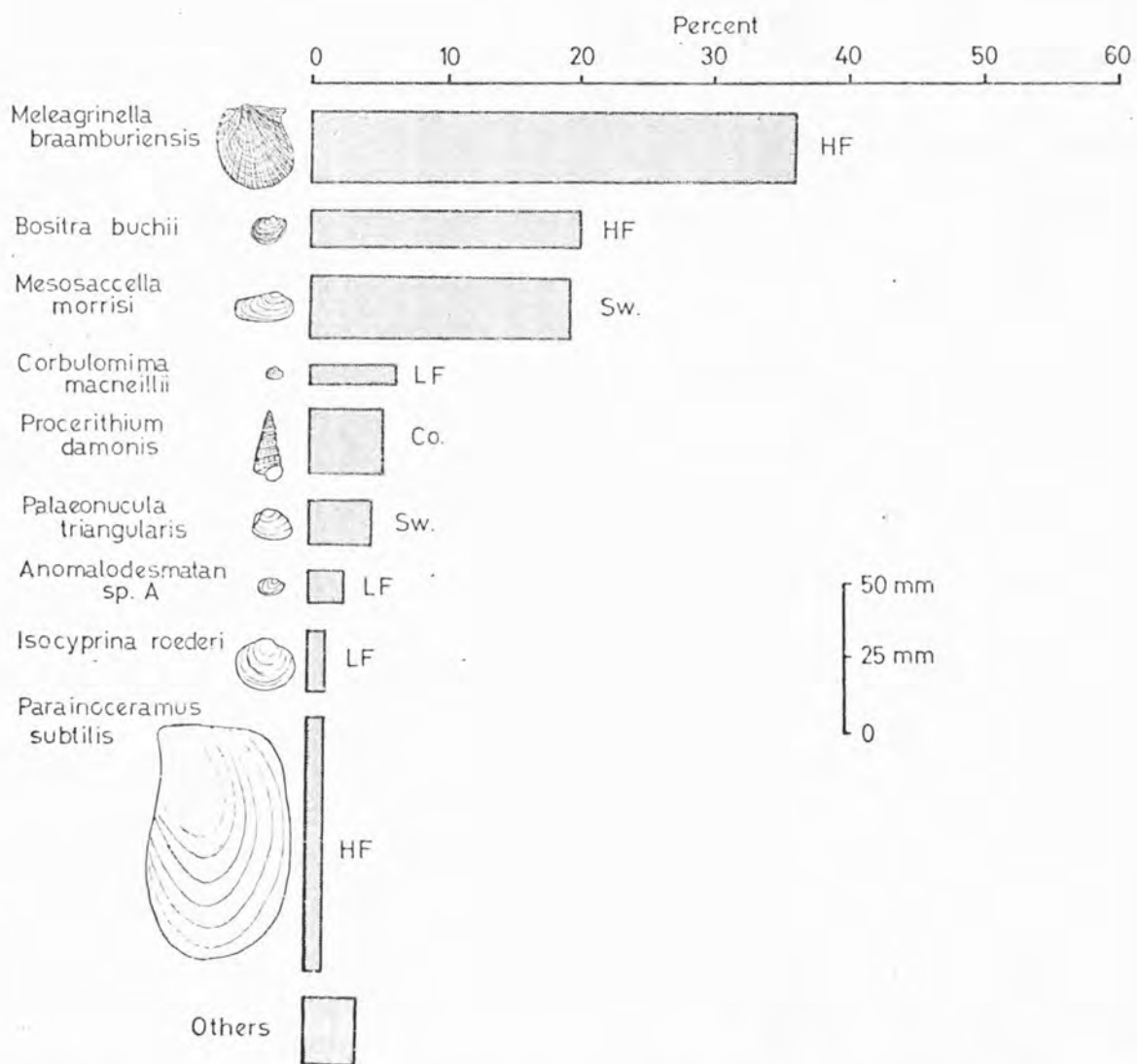
Text-Fig. 16. Trophic group composition of the Foram-rich
bituminous shale biofacies. All benthos included.
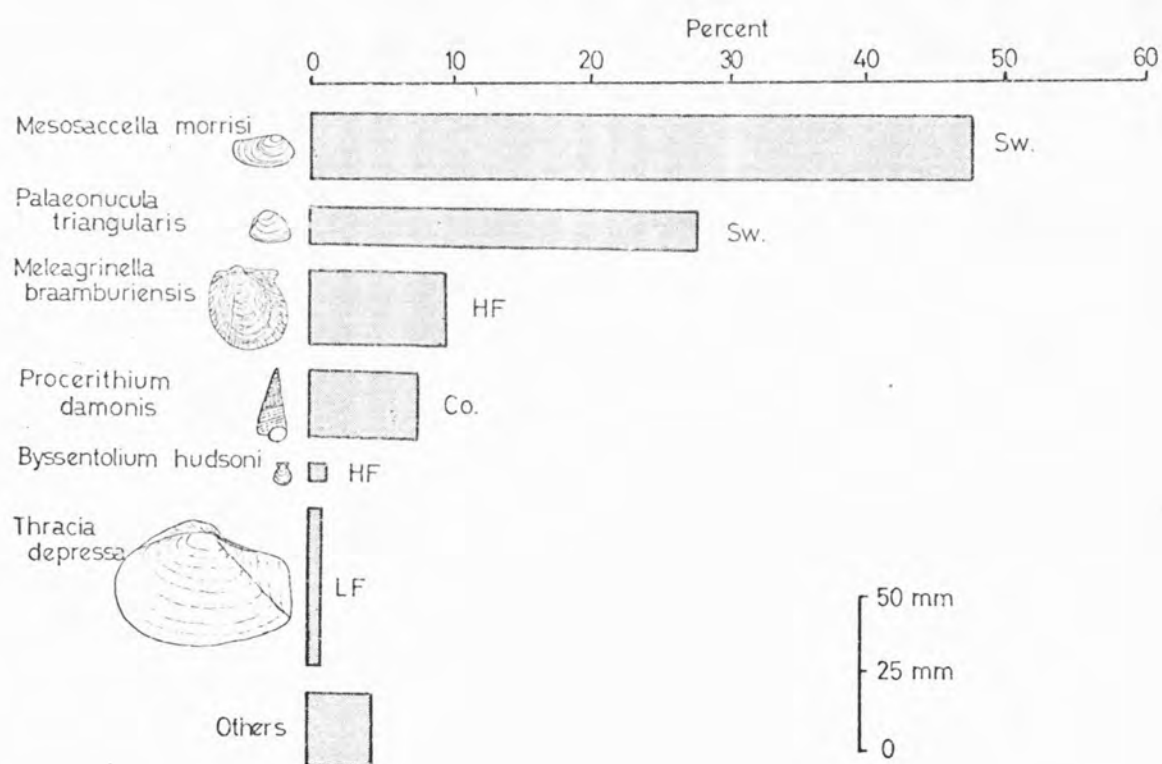
Text-Fig. 17. Trophic group composition of the Nuculacean
shell bed biofacies. All benthos included.
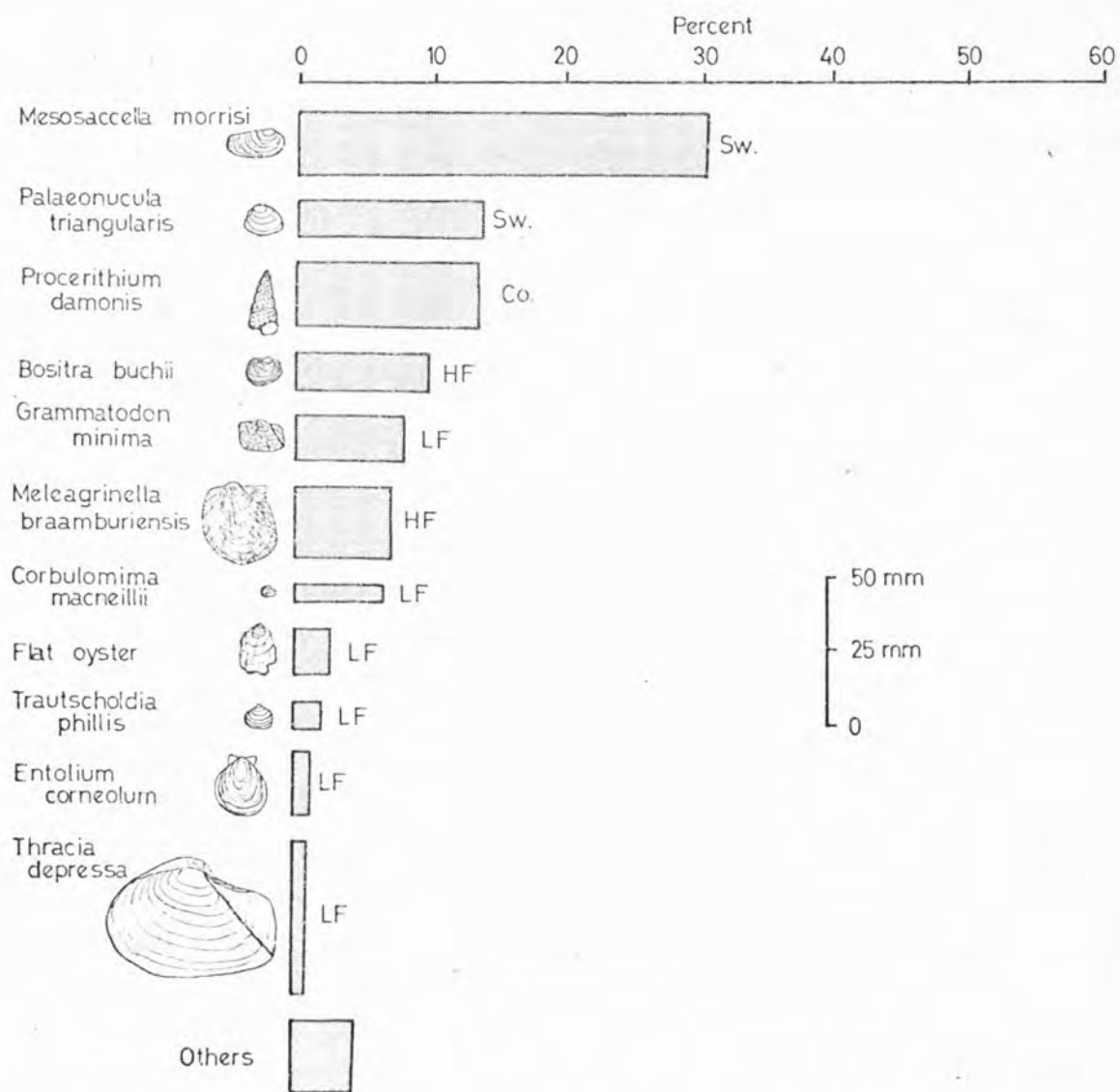
Text-Fig. 18. Trophic group composition of the Grammatodon shell bed biofacies. All benthos included.
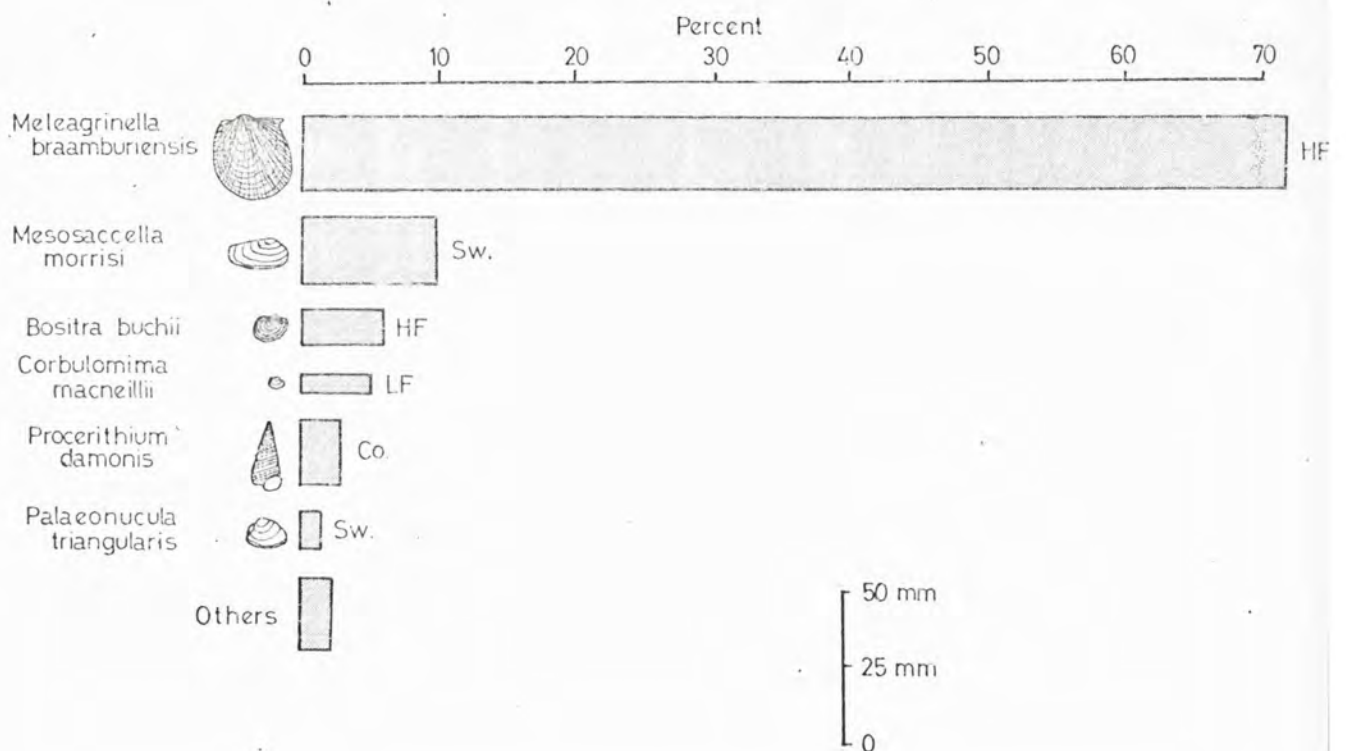
Text-Fig. 19. Trophic group composition of the _Meleagrinella_ shell bed biofacies. All benthos included.
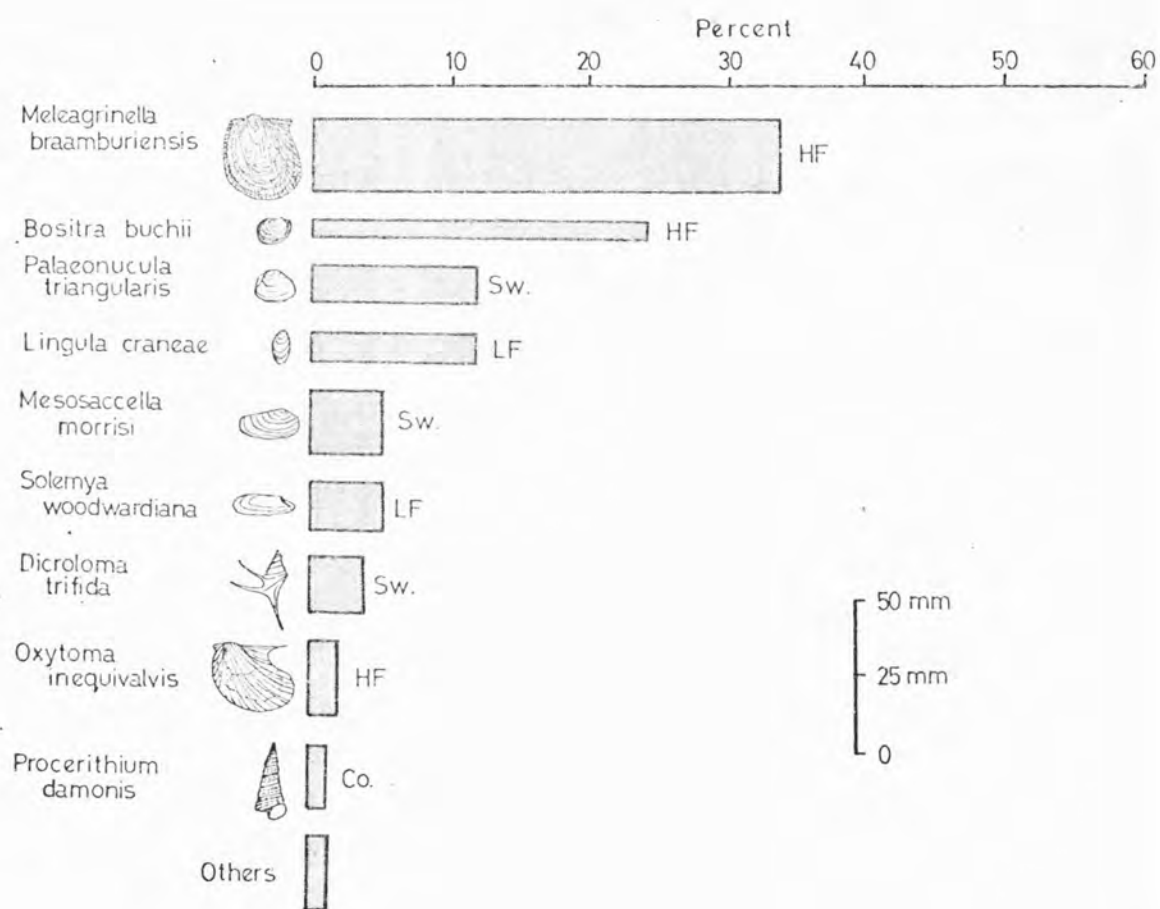
Text-Fig. 20. Trophic group composition of the Blocky Claystone
biofacies. All benthos included.
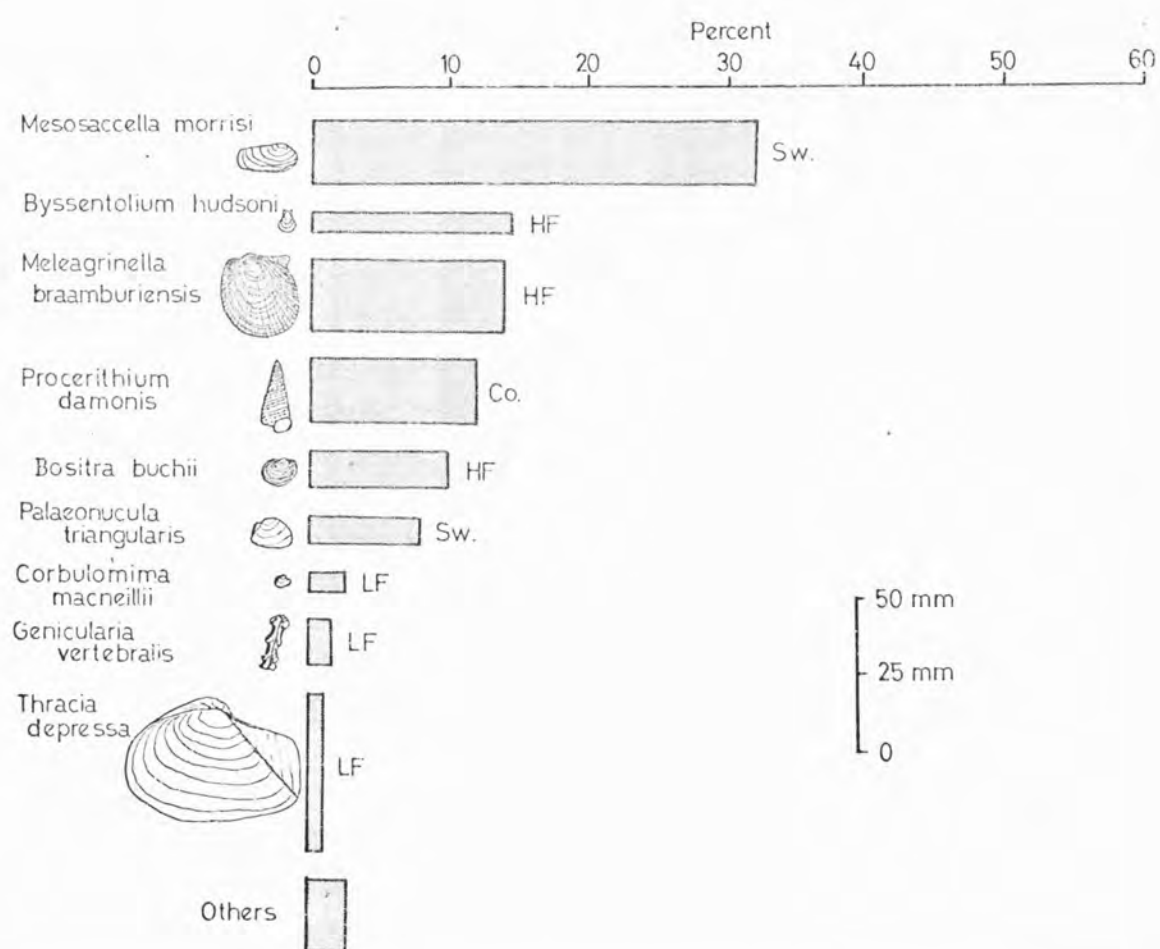
Text-Fig. 21. Trophic group composition of the Calcareous Clays
biofacies. All benthos included.
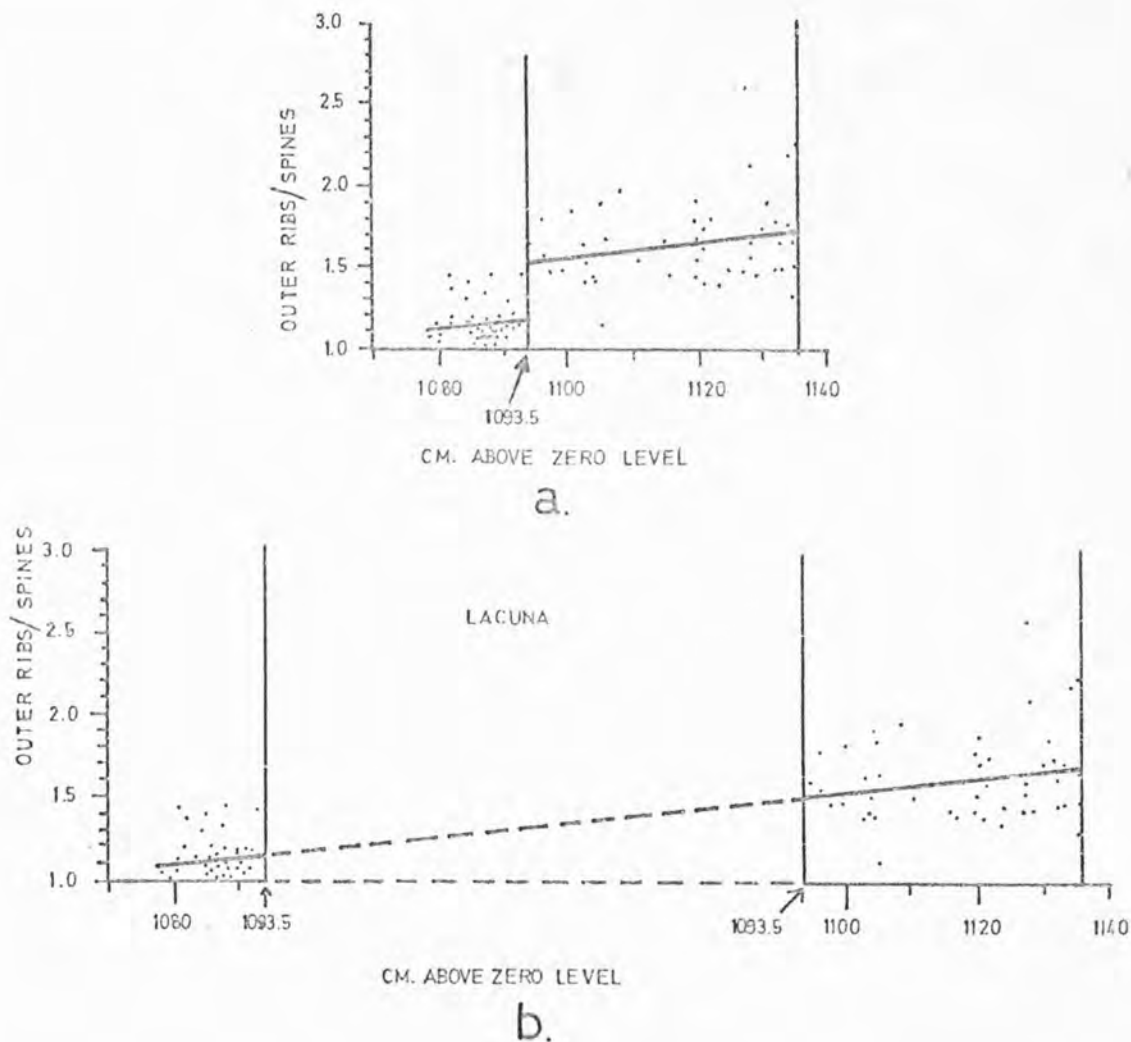
Text-Fig. 22. Regression lines plotted for the rib bundling ratio of
Spinikosmoceras in the shales above and below the
Coronatum - Athleta Zone boundary at Peterborough.
The marked break in the regression line at 1093.5cm
above the zero level in Fig. a. is represented in Fig.
b. by a long sedimentary pause. This assumes a
constant rate of sedimentation and evolution. After
Brinkmann (1929).

TABLE 1.   Faunal list of the macroinvertebrates found in the
           Lower Oxford Clay.

POLYCHAETA

Genicularia vertebralis (J. de C. Sowerby)

Serpula sp.

CEPHALOPODA

'Binatisphinctes' comptoni (Pratt)

'B.' fluctuosus (Pratt)

'B.' spp.

Choffatia spp.

Erymnoceras spp.

Hecticoceras spp.

Kosmoceras (Gulielmiceras) gulielmi (J. Sowerby)

K. (K.) baylei Tintant

K. (K.) grossouvrei Douville

K. (K.) nodosum Callomon

K. (Spinikosmoceras) aculeatum (Eichwald)

K. (Sp.) acutistriatum Buckman

K. (Sp.) castor (Reinecke)

K. (Sp.) pollux (Reinecke)

K. (Zugokosmoceras) enodatum (Nikitin)

K. (Z.) jason (Reinecke)

K. (Z.) medea Callomon

K. (Z.) obductum (Buckman)

K. (Z.) zugium (Buckman)

Pseudocadoceras spp.

Reineckeia spp.

Sigaloceras calloviense (J. Sowerby)

Belemnopsis sulcata (Miller)

Belemnoteuthis antiquus Pearce

Cylindroteuthis puzosianus (d'Orbigny)

BIVALVIA

Anisocardia (Anisocardia) tenera (J. de C. Sowerby)

Bositra buchii (Roemer)

Byssentolium hudsoni Duff

Camptonectes (Camptonectes) auritus (Schlotheim)

Chlamys (Chlamys) bedfordi Duff

C. (Radulopecten) fibrosa (J. Sowerby)

C. (R.) scarburgensis (Young & Bird)

Corbulomima macneillei (Morris)

Discomiltha lirata (Phillips)

Entolium (Entolium) corneolum (Young & Bird)

Grammatodon (Grammatodon) clathrata (Leckenby)

G. (G.) concinna (Phillips)

G. (G.) minima (Leckenby)

G. (G.) montaneyensis (de Loriol)

Gryphaea (Bilobissa) dilobotes Duff

Isocyprina (Isocyprina) roederi Arkell

Meleagrinella braamburiensis (Phillips)

Mesosaccella morrisi (Deshayes)

Modiolus (Modiolus) bipartitus J. Sowerby

Myophorella (Myophorella) irregularis (Seebach)

Nanogyra nana (J. Sowerby)

Neocrassina (Neocrassina) calvertensis Duff

N. (N.) ungulata (Lycett)

Nuculoma kathryni Duff

N. pollux (Raspail ex d'Orbigny)

Oxytoma (Oxytoma) inequivalvis (J. Sowerby)

Palaeonucula cottaldi (de Loriol)

P. triangularis Duff

Parainoceramus subtilis (Lahusen)

Pinna (Pinna) mitis Phillips

Plicatula (Plicatula) cf. fistulosa Morris & Lycett

Pleuromya alduini (Brongniart)

P. uniformis (J. Sowerby)

Protocardia (Protocardia) striatulum (J. de C. Sowerby)

Protocardia sp.

Pteroperna ? pygmaea (Dunker)

Rollierella minima (J. Sowerby)

Solemya woodwardiana Leckenby

Thracia (Thracia) depressa (J. de C. Sowerby)

Trautscholdia phillis (Cottreau ex d'Orbigny)

GASTROPODA

Dicroloma bispinosa (Phillips)

D. trifida (Phillips)

Pleurotomaria reticulata (J. Sowerby)

'Procerithium' damonis (Lycett)

Spinigera spinosa d'Orbigny

SCAPHOPODA

Prodentalium calvertensis Palmer

BRACHIOPODA

Lingula craneae Davidson

'_Orbiculoidea_' sp.

'_Rhynchonella_' sp.

CRUSTACEA

Mecocheirus pearcei McCoy

ECHINODERMATA

Unidentified ophiuroids

GENERA AND FEEDING GROUPS	MAXIMUM SHELL LENGTH (mm)	EPIFAUNAL				INFAUNAL						TAXONOMIC POSITION
		SWIMMING	FREE-LIVING OR CEMENTED	BYSSALLY ATTACHED	"PENDENT"	NON-SIPHONATE	SHORT SIPHONS	LONG SIPHONS	MUCUS-TUBE FEEDERS	BYSSALLY ATTACHED	MOBILE	
DEPOSIT-FEEDERS												SUPERFAMILY
PALAEONUCULA	18.4										X	NUCULACEA
MESOSACCELLA	17.6										X	NUCULANACEA
SUSPENSION-FEEDERS												
SOLEMYA	38.0							X				SOLEMYACEA
GRAMMATODON	28.0					X					X	ARCACEA
MODIOLUS	70.0			X								MYTILACEA
PINNA	82.4			X								PINNACEA
PTEROPERNA	15.3				X							PTERIACEA
PARAINOCERAMUS	72.5				X							PTERIACEA
BOSITRA	15.0				X							PECTINACEA
OXYTOMA	39.8				X							PECTINACEA
MELEAGRINELLA	33.7				X							PECTINACEA
ENTOLIUM	31.0	X										PECTINACEA
BYSSENTOLIUM	12.3			X								PECTINACEA
CAMPTONECTES	58.0			X								PECTINACEA
CHLAMYS	9.7			X								PECTINACEA
RADULOPECTEN	76.0			X								PECTINACEA
PLICATULA	26.8		X									PECTINACEA
GRYPHAEA	80.0		X									OSTREACEA
NANOGYRA	11.2		X									OSTREACEA
MYOPHORELLA	88.0					X					X	TRIGONACEA
DISCOMILTHA	47.0							X	X			LUCINACEA
NEOCRASSINA	21.2					X					X	ASTARTACEA
TRAUTSCHOLDIA	12.5					X					X	ASTARTACEA
PROTOCARDIA	30.3						X				X	CARDIACEA
ANISOCARDIA	25.0						X				X	ARCTICACEA
ISOCYPRINA	20.0						X				X	ARCTICACEA
ROLLIERELLA	24.0						X				X	ARCTICACEA
CORBULOMIMA	6.8						X			X		MYACEA
PLEUROMYA	71.0							X				PHOLADOMYACEA
THRACIA	65.0							X	X			PANDORACEA

Table 2. Life habits of the bivalve genera recognised from the Lower
Oxford Clay of England.

TABLE 3.   Life habits of the benthonic invertebrates other
           than bivalves which occur in the Lower Oxford Clay.

Suspension-feeders

    Genicularia vertebralis   Epifaunal

    Serpula sp.   "

    'Orbiculoidea' sp.   "

    'Rhynchonella' sp.   "

    Lingula craneae   Infaunal

Deposit-feeders

    Procerithium damonis   Epifaunal

    Dicroloma bispinosa   Infaunal

    Dicroloma trifida   "

    Spinigera spinosa   "

    Prodentalium calvertensis   "

Scavengers

    Mecocheirus pearcei

    ophiuroids

Browsing herbivores

    Pleurotomaria reticulata

TABLE 4.   Organic carbon contents measured in the various Lower

Oxford Clay biofacies. N = number of samples,

Max = maximum observed value, Min = minimum observed

value.

Biofacies	N	Max	Min	Mean
Silts & silty clays	1	1.0	1.0	1.0
Deposit-feeder bituminous shales	10	3.5	2.1	2.9
Grammatodon-rich bituminous shales	2	6.1	3.4	4.8
Foram-rich bituminous shales	3	4.9	3.5	4.1
Nuculacean shell beds	1	1.8	1.8	1.8
Gryphaea shell beds	1	1.7	1.7	1.7
Meleagrinella shell beds	4	3.8	2.3	2.9
Calcareous clays	1	1.1	1.1	1.1

TABLE 5. Table showing the main faunal and lithological characteristics of the ten Lower Oxford Clay biofacies.

Biofacies	Lithology	Dominant faunal elements	Organic carbon	Insoluble residue
Silts and silty clays	Silts and silty clays	Cephalopods, Pinna, Protocardia, Trautscholdia, Corbulomima, Meleagrinella.	1%	95%
Deposit-feeder bituminous shales	Dark olive-green shaly clays	Pendent epifaunal suspension-feeders (Bositra, Meleagrinella and Oxytoma), together with Palaeonucula and Mesosaccella.	2.9%	90%
Grammatodon-rich bituminous shales	Dark olive-green shaly clays	Bositra, Oxytoma, Meleagrinella, Palaeonucula, Mesosaccella, together with infaunal suspension-feeders such as Grammatodon, Thracia and Isocyprina.	4.8%	90%
Foram-rich bituminous shales	Light green, rather fissile, shaly clays.	Bositra, Parainoceramus, Mesosaccella, Corbulomima, Prodentalium, foraminifers (Protozoa).	4.1%	87%
Nuculacean shell beds	Shell concentrate	Palaeonucula, Mesosaccella.	1.8%	79%
Grammatodon-rich shell beds	Shell concentrate in clay matrix	Grammatodon, Isocyprina, oysters, Oxytoma, Discomiltha, Protocardia, Trautscholdia, Neocrassina, Myophorella.	—	80%
Gryphaea shell beds	Shell concentrate	Gryphaeate oysters, bone fragments, cephalopods.	1.7%	82%
Meleagrinella shell beds	Shell concentrate	Meleagrinella.	2.9%	69%
Blocky claystone	Light grey plastic clay with dark streaks.	Bositra, Meleagrinella, Palaeonucula, Mesosaccella, Procerithium, Lingula, Solemya.	—	96%
Calcareous clays	Light grey or grey-green, rather plastic, clay.	Palaeonucula, Mesosaccella, Discomiltha, Isocyprina, Myophorella, Byssentolium, Genicularia, oysters.	1.2%	74%

TABLE 6

Trophic nuclei of the Lower Oxford Clay biofacies, all

benthos included.

TROPHIC NUCLEUS DOMINANCE POSITIONS

BIOFACIES	1.	2.	3.	4.	5.	Ed	Id	SD	Div. TN	DI	No. spp.
SILTS & SILTY CLAYS	BOSITRA 23.3	CORBULOMIMA 19.4	GRYPHAEA 17.6	PROCERITHIUM 9.2	PALAEONUCULA 7.4	9.2	8.8	18.0	6	7.1	21
DEPOSIT-FEEDER BITUMINOUS SHALES	BOSITRA 34.9	MELEAGRINELLA 24.0	PROCERITHIUM 10.1	MESOSACCELLA 7.4	DICROLOMA 5.2 CORBULOMIMA 5.2	10.1	17.1	27.2	6	6.7	31
GRAMMATODON-RICH BITUMINOUS SHALES	PROCERITHIUM 30.5	MESOSACCELLA 26.7	BOSITRA 12.9	PALAEONUCULA 8.0	GRAMMATODON MINIMA 6.9	30.5	34.8	65.3	5	5.9	24
NORAW-RICH BITUMINOUS SHALES	MELEAGRINELLA 35.7	BOSITRA 19.6	MESOSACCELLA 19.1	CORBULOMIMA 6.0		5.2	23.9	29.1	4	6.1	24
NUCULACEAN SHELL BEDS	MESOSACCELLA 47.0	PALAEONUCULA 28.2	MELEAGRINELLA 10.4			7.8	75.4	83.2	3	5.2	19
GRAMMATODON-RICH SHELL BEDS	MESOSACCELLA 30.1	PALAEONUCULA 13.6	PROCERITHIUM 13.5	BOSITRA 9.9	GRAMMATODON MINIMA 8.1 MELEAGRINELLA 7.4	13.5	44.0	57.5	6	6.1	24
GRYPHAEA SHELL BEDS	GRYPHAEA 62.2	MELEAGRINELLA 9.8	PROCERITHIUM 4.1	CORBULOMIMA 3.4	GRAMMATODON CONCINJA 3.2	4.1	4.4	8.5	5	5.6	16
MELEAGRINELLA SHELL BEDS	MELEAGRINELLA 71.4	MESOSACCELLA 10.2				3.0	11.6	14.5	2	4.5	16
BLOCKY CLAYSTONE	MELEAGRINELLA 34.2	BOSITRA 24.2	LINGULA 11.1	PALAEONUCULA 11.1		1.7	20.6	22.3	4	4.3	11
CALCAREOUS CLAYS	MESOSACCELLA 32.4	BYSSENTOLIUM 24.4	MELEAGRINELLA 24.0	PROCERITHIUM 12.4	BOSITRA 10.4	12.4	41.3	53.7	5	5.8	22

TABLE 7

Trophic nuclei of the Lower Oxford Clay biofacies,
pendent bivalves removed.

TROPHIC NUCLEUS DOMINANCE POSITIONS

BIOFACIES	1.	2.	3.	4.	5.	Ed	Id	%D	Div. TN	DI	No. spp.
SILTS & SILTY CLAYS	CORBULOMINA 28.5	GRYPHAEA 26.0	PROCERITHIUM 13.5	PALAEONUCULA 11.0		13.5	13.0	26.5	4	6.1	17
DEPOSIT-FEEDER BITUMINOUS SHALES	PROCERITHIUM 25.2	MESOSACCELLA 19.1	DICROLOMA 13.5	CORBULOMINA 13.4	PALAEONUCULA 11.6	25.2	44.2	69.6	5	6.1	25
GRAMMATODON-RICH BITUMINOUS SHALES	PROCERITHIUM 36.9	MESOSACCELLA 32.4	PALAEONUCULA 9.6	GRAMMATODON MINIMA 8.4		36.9	42.1	79.0	4	5.0	20
FORAM-RICH BITUMINOUS SHALES	MESOSACCELLA 44.5	CORBULOMINA 13.8	PROCERITHIUM 12.1	PALAEONUCULA 10.5		12.1	55.7	67.8	4	5.4	14
NUCULACEAN SHELL BEDS	MESOSACCELLA 53.5	PALAEONUCULA 32.1				8.8	85.8	94.6	2	3.9	14
GRAMMATODON-RICH SHELL BEDS	MESOSACCELLA 37.4	PALAEONUCULA 16.9	PROCERITHIUM 16.6	GRAMMATODON MINIMA 10.0		16.8	54.7	71.5	4	5.0	19
GRYPHAEA SHELL BEDS	GRYPHAEA 71.4	PROCERITHIUM 4.7	CORBULOMINA 3.8			4.7	5.0	9.7	3	4.7	13
MELEAGRINELLA SHELL BEDS	MESOSACCELLA 45.3	CORBULOMINA 25.6	PROCERITHIUM 13.5			13.5	51.7	65.2	3	4.5	13
BLOCKY CLAYSTONE	PALAEONUCULA 28.2	LINGULA 28.2	SOLEMYA 13.4	MESOSACCELLA 13.4		4.2	52.2	56.4	4	3.7	8
CALCAREOUS CLAYS	MESOSACCELLA 43.2	BYSSENTOLIUM 19.2	PROCERITHIUM 16.5	PALAEONUCULA 11.7		16.5	55.0	71.5	4	4.5	17

APPENDICES

APPENDIX 1

Detailed descriptions of the stratigraphical sections
seen at the four major pits examined. Bed numbers are those used
by the author, and broadly speaking, do not correlate with those
used by Callomon (1968). The Zonal and Subzonal boundaries are,
however, broadly those placed by Callomon (op. cit.).

These descriptions should be consulted in conjunction with
Fig. 2.3, Text - Fig. 6 in Chapter 3, and Appendix 4, which give
more detailed or more graphic descriptions of the various aspects
of the beds.

CALVERT (SP 695232)

ATHLETA ZONE

Bed 12   32 cm.   Green-brown very fissile shaly clay with a
background of very small indeterminate shell
fragments. Macrofauna not very diverse or
abundant, being dominated by crushed lappeted
ammonites, Corbulomima, Bositra, Parainoceramus
and Mesosaccella, together with a few specimens
of several other bivalve genera. Locally, there
occur massive lenticles of concretionary
limestone, with radial and concentric calcite
veins, which often force the bedding apart above
and below. "The Acutistriatum Band".

CORONATUM ZONE, GROSSOUVREI SUBZONE

11   25 cm.   Nuculacean shell bed, partially pyritic, with a
strongly pyritised part in the top 5 cm, in
which kosmoceratids and pseudoperisphinctids are
abundant. In addition to the abundant ammonites
and Nuculacea, Procerithium, Meleagrinella and a
diverse, but sparse, fauna of bivalves occur.
"The Comptoni Band".

10K   12 cm.   Meleagrinella shell bed, with abundant
Meleagrinella valves and fragments covered in
secondary calcite. Other characteristic genera
are Mesosaccella, Parainoceramus, Bositra,

Corbulomima, Isocyprina and Palaeonucula. Base
burrowed.

10J   19 cm.   Green-grey massive, rather calcareous clay, with
a rich fauna dominated by Mesosaccella,
Hecticoceras, Discomiltha, Byssentolium and
Genicularia. Some local growth of pyrite on
Palaeonucula valves. Accessory fauna both diverse
and abundant, with Isocyprina, Dicroloma,
Procerithium, Thracia, Protocardia and
Corbulomima being particularly important. Base
burrowed.

10H   15 cm.   Meleagrinella shell bed of the normal type, with
kosmoceratids and Mesosaccella as the dominant
accessory elements of the fauna. Other character-
istic genera are Bositra, Parainoceramus,
Palaeonucula and Corbulomima. Base burrowed.

10G   10 cm.   Green sticky calcareous clay, very fossiliferous.
Most of the fossils preserved in primary
aragonite, with some local pyritisation on Thracia
and Palaeonucula. Fauna dominated by kosmoceratids,
Nuculacea, Discomiltha, Byssentolium, Procerithium,
Genicularia and Meleagrinella. Base burrowed.

10F   18 cm.   Meleagrinella shell bed of normal type, with very
little other than Meleagrinella covered with
secondary calcite. Kosmoceratids and Mesosaccella

dominate the accessory fauna. Base burrowed.

10E   20 cm.   Greenish sticky calcareous clay, again very fossiliferous, with a high diversity. Ammonites, Mesosaccella, Meleagrinella, Bositra, Procerithium, Isocyprina and Corbulomima dominate.

10D   1.43 m.   Green-brown very fissile bituminous shale with an extremely dense fauna of foraminifera. Preservation mainly as primary aragonite, with variable developments of secondary calcite, and variable amounts of foram and broken shell background. Fauna both diverse and abundant, with abundant Meleagrinella, Mesosaccella, Bositra, kosmoceratids, Isocyprina, Procerithium, and Palaeonucula, with accessory Parainoceramus, flat oysters, Corbulomima, Grammatodon minima, Discomiltha, Solemya, Lingula, Pinna and Dicroloma.

10C   1.09 m.   Olive-green fissile shaly clay with a fairly abundant fauna spread throughout the clay, with local shell concentrations. Preservation as primary aragonite, with some local pyritisation affecting Procerithium, Thracia, Palaeonucula and kosmoceratids. Fauna dominated by Mesosaccella, Procerithium, Parainoceramus, Palaeonucula, Isocyprina, Grammatodon minima, Corbulomima and

Thracia, with Meleagrinella and flat oysters
becoming more abundant towards the top. There
is also a diverse, but relatively sparse,
accessory fauna of bivalves and gastropods.

10B 6 cm. Grammatodon shell bed, with abundant G. minima,
Isocyprina, Mesosaccella, Thracia, Corbulomima
and kosmoceratids. Accessory Palaeonucula,
oysters, Oxytoma and Pleuromya alduini.

10A 50 cm. Olive-green fissile shaly clay, with a fairly
sparse fauna spread irregularly throughout the
clay. Fauna dominated by kosmoceratids,
Mesosaccella, Palaeonucula, G. minima, Procerithium,
Bositra, Corbulomima and Parainoceramus. Several
other bivalves are characteristics, but rare,
such as Solemya, Oxytoma, Thracia and Isocyprina.

9 8 cm. Olive-green shaly clay with two well-developed
Grammatodon shell beds, very rich in G. minima,
Mesosaccella, Isocyprina, Discomiltha, Procerithium,
Palaeonucula, flat oysters, Oxytoma and
kosmoceratids.

8 11 cm. Greenish bituminous shale, extremely rich in
lenses of "beefy" brown secondary calcite up to
4 cm. thick, but not showing cone in cone structure.
Fauna fairly sparse, and not very heavily covered
with secondary calcite, dominated by Mesosaccella,

Corbulomima, Bositra and kosmoceratids. Accessory fauna of sparse bivalves and Lingula.

CORONATUM ZONE, OBDUCTUM SUBZONE

7   9 cm.

Pyritic shell bed, rich in Mesosaccella and Palaeonucula preserved in unstable pyrite. Other characteristic faunal elements are kosmoceratids, Erymnoceras, Cylindroteuthis and sharks teeth. Top and base transitional, with lenses of bed 7 incorporated into the top of bed 6 and the base of bed 8.

6   14 cm.

Green-brown very fissile bituminous shale, with a good background of broken shell fragments and foraminifera. Well-preserved kosmoceratids are characteristic, as are scaphopods (Prodentalium calvertensis Palmer Ms). Other fauna consists of abundant Mesosaccella, Palaeonucula, Meleagrinella, Corbulomima and Lingula, with accessory Parainoceramus, Procerithium, Dicroloma, Bositra, Thracia and Mecocheirus. Ellipsoidal septarian concretions occur within this bed, the septarian cracks filled with calcite, although there are also some vugs filled with celestite or barytocelestite.

5   8 cm.

Pyritic shell bed, of the Nuculacean type, with abundant Mesosaccella and Palaeonucula preserved in very unstable pyrite. Other more abundant

elements are kosmoceratids, lignite, reptile bones
and Meleagrinella, with accessory belemnites,
oysters and bivalves.

4 4.28 m. Olive-green shaly clay with a diverse benthonic
fauna, with Meleagrinella becoming commoner
towards the top. There are many local variations
in faunal density and composition, but in general
the fauna is dominated by Nuculacea, Meleagrinella,
Bositra, Procerithium, Dicroloma and kosmoceratids,
with a diverse and often abundant accessory fauna
of Thracia, Corbulomima, Lingula, Anomalodesmatan
sp. A., serpulids, Modiolus, Protocardia and
Oxytoma.

Light background throughout, usually composed
mainly of indeterminate shell fragments, but
locally including forams. Preservation mainly as
primary aragonite, with a little solution of the
shell, and without the development of secondary
calcite.

JASON ZONE, JASON SUBZONE

3C 4.60 m. Olive-green shaly clay with a diverse benthonic
fauna, preserved mainly as primary aragonite.
There is a general increase in both diversity and
abundance upwards, the basal part being fairly
sparse in fossils, although Lingula is common,
especially in the bottom metre, where it is

sometimes the single most abundant form. Locally, there is a rich background of forams, but in general, they are not very abundant. The same is true of the development of secondary calcite, which affects Bositra and Meleagrinella most frequently. Diverse fauna dominated by kosmoceratids, Lingula, Dicroloma, Bositra, Solemya, Procerithium, Meleagrinella, with accessory Mesosaccella, Palaeonucula, Corbulomima, Discomiltha, Oxytoma, Anomalodesmatan sp. A. and sp. B., Parainoceramus, "Rhynchonella", Protocardia, Isocyprina and Thracia.

3B 1.05 m. Light grey, massive clay, rather plastic, and not at all fissile, with many small dark carbonaceous particles throughout. It dries to a very light grey colour, and becomes extremely tough, and is a unique lithology, not seen at any of the other pits. (The blocky claystone facies). Fossils are sparse, the ones that do occur often being clustered together, especially Bositra, Meleagrinella and Solemya.

Preservation as primary aragonite, no secondary calcite, and a characteristic feature is the occurrence of uncrushed body chambers of a macroconch kosmoceratid known as Kosmoceras effulgens Buckman, but actually belonging in K. jason (Reinecke).

Fauna is relatively diverse, but rather sparse, the most common genera being Palaeonucula, Lingula, Meleagrinella, Solemya and Bositra, with accessory kosmoceratids, Mesosaccella, Cylindroteuthis, Procerithium, Dicroloma, Discomiltha and Oxytoma.

3A 15 cm. Olive-green shaly clay with a rich background of shell fragments and forams. This appears to be a transition between the shell bed beneath and the blocky claystone above. Preservation mainly as primary aragonite, with slight development of secondary calcite on Oxytoma, Bositra and worm tubes. Fairly high diversity fauna, dominated by kosmoceratids, Bositra, Protocardia, flat oysters, Dicroloma and Mesosaccella, with a diverse accessory fauna including Oxytoma, Parainoceramus, Procerithium, Trautscholdia, Meleagrinella and Palaeonucula.

2C 8 cm. Pyritic shell bed packed with well-preserved shells and valves of Trautscholdia, Neocrassina, Grammatodon concinna, Discomiltha, Palaeonucula and ammonites. The pyrite is stable, and does not rot. There are also concentrations of belemnites and oysters together with reptile bone fragments.

Locally, large ellipsoidal cementstone concretions are developed within this bed, and contain the same fauna as the pyritic shell bed.

BLETCHLEY (SP862326)

ATHLETA ZONE

Bed 18   20 cm.   Greenish brown, very well-laminated bituminous shales with a sparse macro-fauna, dominated by well-preserved crushed kosmoceratids. Corbulomima and Mesosaccella are the commonest bivalves. "The Acutistriatum Band". Lenticles of earthy concretionary limestone occur at this level.

CORONATUM ZONE, GROSSOUVREI SUBZONE

17K   24 cm.   Nuculacean shell bed with abundant Palaeonucula, Mesosaccella, Procerithium and Corbulomima; pseudoperisphinctids are also characteristic, and there is a diverse accessory bivalve fauna. Some low-grade pyritisation, and a little development of secondary calcite. "The Comptoni Band".

17J   15 cm.   Greenish laminated bituminous shale, with a rich background of small indeterminate shell fragments. Fauna of low diversity, dominated by kosmoceratids, Mesosaccella, Corbulomima, Meleagrinella and Bositra.

17H   18 cm.   Greenish-grey calcareous clay with abundant Nuculacea and Procerithium in a matrix of clay with abundant shell fragments. Meleagrinella, Corbulomima, Procerithium and Byssentolium also characteristic. Some local low-grade pyritisation.

17G   14 cm.   Fissile green shaly clay, similar to that of 17J,
with a good background of shell and Bositra
fragments. Macrofauna dominated by kosmoceratids,
often lappeted, together with Nuculacea, Bositra,
Meleagrinella, Corbulomima and Parainoceramus.
Accessory fauna includes Mecocheirus, Pteroperna
and Pleuromya alduini. Top burrowed.

17F   14 cm.   Meleagrinella shell bed, with abundant valves and
shell fragments of Meleagrinella covered in
secondary calcite. Accessory fauna dominated by
Mesosaccella, Corbulomima and Palaeonucula.

17E   14 cm.   Greyish rather calcareous clay with a diverse
fauna of bivalves, dominated by Mesosaccella,
Byssentolium, Procerithium, Corbulomima and
Palaeonucula. No secondary calcite, but some low-
grade pyritisation.

17D   18 cm.   Meleagrinella shell bed of normal type, although
secondary calcite seems to be largely restricted
to the pectinacea. Dominant accessory fauna of
Mesosaccella, Palaeonucula, Procerithium and
kosmoceratids.

17C   12 cm.   Grey-green rather calcareous clay with a very rich
fauna, including one gryphaeate oyster. Rich
fauna includes abundant Nuculacea, Procerithium and
Meleagrinella, with Byssentolium, Thracia,

Discomiltha and arcids as characteristic accessory
genera. Base burrowed.

17B   11 cm.   _Meleagrinella_ shell bed of normal type, with very
little macrofauna other than _Meleagrinella_, even
ammonites being rare. _Bositra_, _Procerithium_,
Mesosaccella and _Parainoceramus_ were the only
genera seen, and only comprise about 3% of the
overall fauna. A thin band of pyritisation occurs
4 cm above the base of the bed. Burrowed base.

17A   12 cm.   Greenish slightly shaly clay very rich in shell
fragments. Very diverse benthonic fauna, dominated
by _Mesosaccella_, _Meleagrinella_ and _Procerithium_,
with a rich accessory fauna of _Thracia_, _Byssentolium_,
Corbulomima, _Palaeonucula_ and kosmoceratids.

16   88 cm.   Very fissile green shaly clay with a rich fauna
of foraminifera and a variable amount of thin
secondary calcite, which affects most species.
Meleagrinella, _Mesosaccella_, _Procerithium_,
Isocyprina, _Thracia_, _Corbulomima_, _Palaeonucula_,
Bositra and _Grammatodon_ _minima_ are the most common
of the accessory elements of the fauna.

15   2.30 m.   Olive-green bituminous shale with a fairly sparse,
but well-preserved fauna, preserved mainly as
primary aragonite, although secondary calcite
becomes common in the top 20 cm. The typical
Grossouvrei Subzone fauna of _G. minima_, _Isocyprina_

and Mesosaccella in abundance appears at this level, together with abundant Palaeonucula, Procerithium, Corbulomima, Thracia and Anomalodesmatan sp. A., with a diverse, but sparse accessory fauna of bivalves and kosmoceratids.

CORONATUM ZONE, OBDUCTUM SUBZONE

14 20 cm.   Nuculacean shell bed, with a pyritic fauna of Nuculacea, kosmoceratids and Erymnoceras, and a good deal of lignite and belemnites. Occasional cementstone concretions, with a rich fauna, occur within the shell bed. Accessory fauna partly obscured by the abundance of Nuculacea, but includes Plicatula, Discomiltha, Procerithium, flat oysters, Thracia, Pleuromya alduini and Meleagrinella.

13 6.30 m.   Greenish shaly bituminous clay with a diverse fauna, largely dominated by deposit-feeders, or species able to tolerate less well-oxygenated conditions. Fauna dominated by kosmoceratids, Nuculacea, Bositra, Procerithium, Corbulomima, Lingula and Dicroloma, with an accessory fauna of Thracia, Meleagrinella, Oxytoma, Mecocheirus, Parainoceramus and Pinna; Meleagrinella becomes more abundant towards the top of the bed. Secondary calcite variably developed, being abundant at certain levels, and absent at others. At about 2.80 m above the base, there is a band of

ellipsoidal cementstone septarian concretions,
spread throughout about 1.00 m of shaly clay.
Septarian cracks are well-developed in these
concretions, and are often lined by pyrite;
fossils are sparse in them.

JASON ZONE, JASON SUBZONE

12   3.90 m.   Light green shaly clay, more massive towards the
base, with a fairly sparse, but relatively diverse,
fauna. Much of the fauna either consists of
"pendent" suspension-feeders or very tolerant
deposit-feeders, especially in the bottom 2.00 m;
above this, the fauna becomes more diverse and
more abundant. Dominant fauna of kosmoceratids,
Bositra, Meleagrinella, Mesosaccella, Dicroloma,
Corbulomima, Lingula and Palaeonucula, with
accessory Oxytoma, Mecocheirus, Thracia,
Anomalodesmatan sp. A., and sp. B., Pinna,
Discomiltha and Parainoceramus. Preservation mostly
as crushed valves which have suffered a high degree
of aragonite solution, making the shells very
fragile. Locally there is some secondary calcite,
but it is not widespread. A 10 cm Meleagrinella
shell bed occurs 1.25 m above the base, and there
are occasional Meleagrinella plasters towards the
top of the bed.

11   3 cm.   <u>Meleagrinella</u> shell bed of normal type, with few
                 other species except kosmoceratids, <u>Mesosaccella</u>
                 and <u>Corbulomima</u>.

10   3 cm.   Pyritic shell bed containing mainly kosmoceratids
                 and <u>Cylindroteuthis</u>, together with bone fragments
                 and fish teeth. The whole bed is very rich in
                 comminuted indeterminate shells. Oysters
                 transitional between the ostreate and the
                 gryphaeate form are fairly abundant, together with
                 occasional specimens of <u>Belemnopsis</u> <u>sulcata</u>.

JASON ZONE, MEDEA SUBZONE

9   30 cm.   Olive-green well-laminated shaly clay with a fauna
                 dominated by kosmoceratids, <u>Corbulomima</u>,
                 <u>Procerithium</u> and <u>Bositra</u>; there is also a diverse
                 fauna of rare accessory genera, such as <u>Thracia</u>,
                 <u>Meleagrinella</u>, <u>Entolium</u>, <u>Pinna</u>, <u>Parainoceramus</u>,
                 <u>Mesosaccella</u>, <u>Palaeonucula</u> and terebratulids. Near
                 the top is an 8 cm band of darker shale rich in
                 <u>Bositra</u> and <u>Pinna</u>, often preserved in secondary
                 calcite, and with ammonite plasters.

8   2 cm.   <u>Gryphaea</u> shell bed, with abundant <u>Gryphaea</u> and
                 <u>Cylindroteuthis</u>, as well as a fairly diverse
                 accessory fauna of <u>Discomiltha</u>, <u>Palaeonucula</u>,
                 <u>Procerithium</u>, <u>Thracia</u>, <u>Bositra</u> and <u>Corbulomima</u>.

7   3 cm.   Green shaly clay with a diverse fauna, and
              indeterminate worm burrows. Preservation as both
              primary aragonite, and with secondary calcite.
              Fauna dominated by ammonites, oysters and
              Meleagrinella, with accessory Procerithium,
              Bositra, Corbulomima and rhynchonellids.

6   2 cm.   Pyritic shell bed, with abundant Gryphaea and
              Cylindrotheuthis, together with kosmoceratids,
              Meleagrinella and a diverse, but sparse, accessory
              fauna of bivalves and cephalopods.

5B 10 cm.   Shaly, rather silty clay, grading downwards into a
              shell bed (5A), with a rich fauna of small bivalves
              such as Protocardia and Corbulomima. Kosmoceratids,
              oysters, Bositra, Procerithium, Meleagrinella,
              Entolium, Oxytoma, G. clathrata, Thracia, Lingula
              and rhynchonellids are also characteristic.
              Trace fossils (indeterminate) are fairly abundant.

5A 3 cm.   Gryphaea shell bed, rich in oysters, belemnites and
              ammonites, together with a diverse benthonic fauna
              of sparse bivalves and gastropods such as
              Discomiltha, Oxytoma and Thracia.

4E 70 cm.   Green shaly clay, with a 10 cm silt band with a
              basal shell plaster in the centre. The shaly clay
              has a diverse fauna, dominated by kosmoceratids,
              Palaeonucula, Procerithium, Corbulomima and Bositra,

together with many other species of bivalve,
gastropod, brachiopod and cephalopod. The silt
band is rather strongly bioturbated and contains a
diverse molluscan fauna similar to that of the
shales; the basal shell plaster is rich in
kosmoceratids, oysters, belemnites, Thracia and
Meleagrinella.

4D 12 cm.   Intensely bioturbated silt and clayey silt, with
very little else other than trace fossils. Fauna
dominated by kosmoceratids and Cylindroteuthis,
but there is also a diverse and sparse bivalve
fauna, including Modiolus, Thracia and Protocardia.

4C 8 cm.   Greenish shaly clay, rather well-laminated, with a
very rich molluscan fauna, dominated by
kosmoceratids, Palaeonucula, Meleagrinella,
Trautscholdia, Grammatodon concinna, Protocardia,
Corbulomima and Bositra. There is also a rich
accessory bivalve fauna.

4B 10 cm.   Bioturbated silty clay rich in trace fossils, with
a not very diverse fauna, dominated by
kosmoceratids, Trautscholdia, Meleagrinella
and oysters.

4A 32 cm.   Olive-green fissile shaly clay, locally with a
background of foraminifera, and with lenses of
shells throughout, together with some plasters of

either ammonites or oysters plus <u>Pinna</u>. These
three, together with <u>Trautscholdia</u>, <u>Bositra</u> and
<u>Corbulomima</u>, are the dominant genera, but there is
also a diverse accessory fauna.

<u>CALLOVIENSE ZONE, ENODATUM SUBZONE</u>

3B 25 cm seen. Very sticky silty clay, with a fauna consisting
almost entirely of kosmoceratids and gryphaeate
oysters.

STEWARTBY (BEDFORD) SP017412

    SUBZONES MODIFIED BY DUFF.

ATHLETA ZONE

Bed 19   20 cm.   Very shelly grey-green clay, packed with

                  Nuculacea, Procerithium and Perisphinctids.   "The

                  Comptoni Band" shell bed.   Basal layer of the bed

                  contains pyritic ammonites.

18   35 cm.   Greenish bituminous shale, rather shelly in the

                  basal 7 cm.   Fauna dominated by Nuculacea,

                  Meleagrinella and Bositra.

17   37 cm.   Dark grey-black,well-laminated bituminous shales,

                  rich in crushed ammonites, many with lappets,

                  Nuculacea, Inoceramus and Meleagrinella.   Lenses

                  of concretionary limestone occur within this band,

                  and make a clear marker band about halfway up the

                  face.   "The Acutistriatum Band".

CORONATUM ZONE, GROSSOUVREI SUBZONE

15   20 cm.   Nuculacean shell bed.   Very shelly clay with

                  abundant Nucula and Mesosaccella.   Procerithium

                  and Meleagrinella also very common.

14I 12 cm.   Light grey-green, rather calcareous clay, with

                  quite a lot of broken shell debris.   Normal fauna

                  of Nuculaceans, Meleagrinella, kosmoceratids and

                  Hecticoceratids.   Inoceramus.

14H   11 cm.   Meleagrinella shell bed, consisting mainly of valves of Meleagrinella covered with honey-brown coloured secondary calcite in a clayey matrix.

14G   17 cm.   Light grey-green, calcareous clay, with a good background of shell hash. Nuculacea abundant, Meleagrinella, Inoceramus, Kosmoceras common.

14F   20 cm.   Meleagrinella shell bed with shells covered by 2° calcite. Nuculacea of subsidiary importance.

14E   23 cm.   Light grey-green clay with many black Meleagrinella shell fragments. Dominant fauna is again Nuculacea, with subsidiary Procerithium, Thracia, Genicularia and Kosmoceratids.

14D   17 cm.   Meleagrinella shell bed as normal. Junction with 14C below burrowed, as are most of the junctions within bed 14. Nuculacea are dominant subsidiary fauna.

14C   16 cm.   Grey-green clay, not very well-laminated. Nuculacea and Procerithium dominate, Bositra quite common too.

14B   12 cm.   Meleagrinella shell bed, with burrowed base and top. Usual high content of Meleagrinella with 2° calcite.

14A 13 cm.   Grey-green calcareous clay, very shelly at the
base, and rich in bivalves throughout. <u>Thracia</u>,
<u>Inoceramus</u>, oysters and <u>Procerithium</u> common,
together with abundant Nuculacea.

13   3 cm.   Pyritic shell plaster, the pyrite being rather
unstable, and occurring often as irregular black
nodules within a finely pyritic clay, often iron-
stained. Fauna difficult to see because of
pyrite-rot, but contains ammonites and Nuculacea.

12   1.05 cm. Olive-green rather fissile, well-laminated shaly
clay, with a rich and obvious fauna of
Foraminifera. Rich fauna dominated by <u>Bositra</u>,
<u>Meleagrinella</u>, <u>Procerithium</u> and Nuculacea, but
also with a diverse fauna of accessory bivalves.
A rich shelly band occurs between 85 - 90 cm
above the base, in which the same species occur as
in the clays, but much more abundantly.

11   3 cm.   Pyritic shell bed, mainly pyritic <u>Meleagrinella</u> in
a Foram-rich clay. Oysters, ammonites and
Nuculacea also characteristic.

10D 15 cm.   Olive-green, rather fissile shaly clay, with a
very abundant fauna of Foraminifera, and also
with very common <u>Meleagrinella</u>. <u>Bositra</u> and
<u>Mesosaccella</u> characteristic.

10C   3.23 m.   Blocky greenish shaly clay, not as fissile as 10D,
and lacking the rich fauna of foraminifera. Very
rich and diverse bivalve fauna, dominated by
Nuculacea, but characterised by a varied fauna of
infaunal suspension-feeders, in which Grammatodon,
Isocyprina and Thracia are dominant. Many other
bivalves too.

10B   2 cm.   Thin Grammatodon shell bed, dominated by Nuculacea,
Grammatodon, Procerithium and Kosmoceratids.
Other bivalves diverse, but not numerically
abundant.

10A   6 cm.   Very shelly greenish clay, as in 10C.

9   6 cm.   Pyritic shell bed, passing upwards into a non-
pyritised shell bed. Very rich in bivalves and
ammonites, especially Nuculacea, oysters,
Grammatodon, Lucina and Procerithium. This is
the first appearance of Grammatodon minima, and is
taken as the base of the Grossouvrei Subzone.
"20 foot shell bed" of Callomon

CORONATUM ZONE, OBDUCTUM SUBZONE

8B   45 cm.   Green shaly clay with a rich fauna of Foraminifera.
Nuculacea, Bositra, Corbula and ammonites are the
characteristic members of the macrofauna.

8A   70 cm.   Mainly a thick Meleagrinella shell bed, with large numbers of Meleagrinella shells with 2° calcite. Parts of the bed do, however, consist of lenses of more shaly clay similar to that of 8B above. Fauna dominated by Meleagrinella, with Mesosaccella, Corbula and Procerithium as characteristically abundant members of the fauna. Within this bed, there occur lensoid septarian concretions up to 25 cm thick, of a wheel-like shape. These are post-depositional, and form a useful marker band.

7   10 cm.   Strongly pyritic shell bed, the most obvious and stable shell bed in the whole section. A rich mass of Nuculacea and ammonites, with Kosmoceras dominating, but the most characteristic are the large specimens of Erymnoceras which occur. Many other bivalves and snails. "16' shell bed".

6E   28 cm.   Grey-green shaly clay, with a background of some shell hash, and a fauna consisting mainly of Nuculacea, Meleagrinella, Procerithium, Dicroloma and Corbula.

6D   10 cm.   Shell bed, consisting of a Meleagrinella shell bed with 2° calcite in the lowermost 7 cm, with occasional seams of fibrous calcite ("beef") up to 1 cm thick. Upper 3 cm is a pyritic shell bed, of unstable pyrite. Nuculacea and Meleagrinella

common in upper part.

6C   90 cm.   Olive-green blocky shaly clay, with a clear
background of shell hash. Fauna dominated by
Bositra, Meleagrinella, Dicroloma, Procerithium,
Corbula and Nuculacea. Base taken at a very thin
seam of pyrite-shot clay, apparently filling
burrows. Base of Coronatum Zone.

JASON ZONE, JASON SUBZONE

6B   2.95 m.   Olive-green blocky shaly clay, as in 6C above.
Very abundant fauna of Bositra, with Corbula,
Nuculacea, Procerithium, Dicroloma and Kosmoceras
common. Lingula and crustacea locally fairly
abundant also. Meleagrinella of subsidiary
importance.

JASON ZONE, MEDEA SUBZONE

6A   69 cm.   Olive-green rather well-laminated shaly clay,
rather similar to that of 6B and 6C. Fauna again
dominated by Bositra, with Meleagrinella much more
common than in 6B above. Procerithium and
Kosmoceras also characteristic, together with
Dicroloma and Pinna.

5B   1 cm.   Crushed pyritic ammonites, together with a shell
bed (pyritic) containing abundant Nuculacea,
Grammatodon concinna, Trigonia, Astarte, together
with reptile bones and wood fragments.

5A   5 cm.   Oyster bed consisting of numerous specimens of
Gryphaea dilobotes in a matrix of silt and silty
clay. Other bivalves which preferred a soft
substrate for burrowing are also more common —
Pleuromya, Anisocardia, Astarte. 5A separated
from 5B by a thin band of silt, as in 5A, but
without the abundant oysters.

CALLOVIENSIS ZONE, ENODATUM SUBZONE

4   20 cm. +   Green silt, with lenses of silty clay, and
locally grey silt. Markedly bioturbated in
places, and with abundant trace fossils.
Several thin shell beds containing Gryphaea and
belemnites occur within bed 4.

NORMAN CROSS (PETERBOROUGH) (TL172916)

ATHLETA ZONE

Bed 38   20 cm.   Brown, well-laminated bituminous shale rich in
crushed ammonites, mainly kosmoceratids, with
Corbulomima, Mesosaccella and Pleuromya alduini
also being characteristic. "The Acutistriatum
Band".

CORONATUM ZONE, GROSSOUVREI SUBZONE

37   17 cm.   Greenish shaly clay, pseudoperisphinctids
continuing on from the underlying bed, with
kosmoceratids and hecticoceratids also being
characteristic. Corbulomima, Procerithium and
Mesosaccella are the most abundant benthonic
molluscs. Trace fossil burrows common in the
uppermost 2 cm.

36   5 cm.   Nuculacean shell bed in a greenish shaly clay
matrix; pseudoperisphinctids abundant. Many of
the shells are broken, and there seems to have been
winnowing. Same dominant fauna as in bed 37.
"The Comptoni Band".

35   25 cm.   Greenish shaly clay with a rich background of small
Bositra fragments. Benthonic fauna not very
diverse, but fairly abundant, with Mesosaccella,
Palaeonucula, Corbulomima and Meleagrinella being
the most characteristic.

34 16 cm.   Meleagrinella shell bed. Abundant valves of
             Meleagrinella, with Nuculacea, Corbulomima and
             Byssentolium, all often covered with secondary
             calcite. Top and base burrowed.

33 10 cm.   Light grey-green, rather plastic, calcareous clay,
             with a good background of broken black
             Meleagrinella shell fragments. Virtual absence
             of secondary calcite. Base burrowed. Nuculacea
             abundant, together with Byssentolium and
             Corbulomima.

32 12 cm.   Greenish shaly clay, with a light background of
             broken Bositra fragments. A little secondary
             calcite. Benthonic fauna dominated by Nuculacea,
             Pleuromya alduini, Corbulomima, Meleagrinella and
             Parainoceramus. Top burrowed.

31 6 cm.   Meleagrinella shell bed. Abundant valves and
             broken fragments of Meleagrinella and Bositra
             covered in secondary calcite. Mesosaccella and
             Corbulomima dominate the remainder of the fauna.
             Base burrowed.

30 18 cm.   Greenish shaly clay, with a background of Bositra
             fragments becoming commoner towards the top.
             Benthonic fauna dominated by Nuculacea,
             Procerithium, Byssentolium, Meleagrinella and
             Corbulomima.

29   9 cm.   Grey-green, rather plastic calcareous clay, with a
good background of black Meleagrinella fragments.
No secondary calcite. Benthonic fauna dominated
by Mesosaccella and Byssentolium, with Meleagrinella
and Palaeonucula also being characteristic.

28   18 cm.   Meleagrinella shell bed. Abundant valves and
shell fragments of Meleagrinella and Bositra,
covered in secondary calcite; few valves are
unbroken. Mesosaccella, Procerithium and
Corbulomima also characteristic. Burrowed base.

27   17 cm.   Grey-green, rather plastic clay, transitional into
28 above. Shells spread uniformly throughout the
bed, with local lenses of shell fragments. Some
secondary calcite on Bositra, Mesosaccella and
kosmoceratids. Ammonite plaster at the base.
Fauna dominated by Bositra and Meleagrinella, with
a rich accessory fauna of Corbulomima, Procerithium
and Byssentolium.

26   15 cm.   Meleagrinella shell bed, of normal type. Secondary
calcite virtually restricted to Meleagrinella.
Accessory fauna dominated by Nuculacea and
Procerithium. Burrowed top and base.

25   3 cm.   Thin shell bed, rich in Bositra and Meleagrinella,
with Nuculacea, Procerithium and Byssentolium
also being characteristic.

24 27 cm. Well-laminated green shaly clay, with secondary calcification affecting most members of the fauna. Rich fauna of foraminifera. Abundant and rather varied benthonic fauna, characterised by Meleagrinella, Bositra, Nuculacea, Procerithium, Anomalodesmatan sp. A. and Thracia.

23 15 cm. Meleagrinella shell bed. Abundant Bositra and Meleagrinella fragments covered by secondary calcite. Top and base strongly burrowed. Large, well-preserved macroconch kosmoceratids occur frequently. Accessory fauna diverse, but not very abundant — Mesosaccella, Parainoceramus, Procerithium, Anomalodesmatan sp. A.

22 85 cm. Greenish well-laminated shaly clay, with a rich background of forams. A little secondary calcite on some shells; also, there are occasional crushed articulated shells of Palaeonucula preserved in secondary pink calcite. Macrofauna dominated by Bositra and Meleagrinella, with Nuculacea, Procerithium, Anomalodesmatan sp. A. and kosmoceratids; several other bivalve genera are also characteristic.

21 1 cm. Ammonite plaster, rich in macroconch kosmoceratids, together with Nuculacea and Procerithium.

20 38 cm.   Greenish well-laminated shaly clay, rich in forams.
Secondary calcite developed on most species, and
some pink calcitic Palaeonucula shells occur.
Fauna dominated by Bositra and Meleagrinella, with
Nuculacea, Anomalodesmatan sp. A., and kosmoceratids
as the most abundant species, but also with
Thracia, Dicroloma, "Ostrea", Procerithium and
Corbulomima.

19 10 cm.   Shell bed, dominated by Bositra and Meleagrinella,
the latter often attaining a large size (H > 30 mm),
and having a thick coating of secondary calcite.
Remainder of the fauna dominated by Mesosaccella
and Procerithium.

18 75 cm.   Olive-green shaly clay, rich in forams, and with
many horizontal worm burrows, filled with fine
shell fragments. Pink calcitic Palaeonucula shells
common. Secondary calcite affects every species,
but not all the specimens. Fauna dominated by
Nuculacea and Procerithium, with accessory Thracia,
Grammatodon minima, Bositra, Parainoceramus, and
several other species more rarely.

17 10 cm.   Partially pyritic shell bed, pyritisation fading
towards the edges. Fauna dominated by Nuculacea
and G. minima, with kosmoceratids and flat oysters.

16 1.35 m.   Greenish, very fissile shaly clay, with a light
                background of broken shell fragments. Fauna
                fairly diverse, but not particularly abundant,
                dominated by Bositra, Nuculacea, G. minima,
                Procerithium, Oxytoma, Parainoceramus, Thracia,
                Corbulomina and Anomalodesmatan sp. A. Some
                secondary calcite, mainly on Mesosaccella, but
                never abundant.

CORONATUM ZONE, OBDUCTUM SUBZONE

15 5 cm.   Pyritic shell bed, dominated by Mesosaccella and
                Palaeonucula, and also rich in lignite and
                disarticulated reptile bones. Also, there's
                quite a lot of secondary calcite. Accessory fauna
                of kosmoceratids, lignite, flat oysters,
                Cylindroteuthis and Erymnoceras. A good example
                of a winnowed shell bed.

14 4.55 m.   Olive-green blocky shaly clay, with an abundant
                pendent bivalve fauna of Bositra and Meleagrinella,
                and a rather impoverished benthonic fauna dominated
                by Nuculacea. There is also a rather diverse
                fauna of other species, which are not usually
                very common, including Dicroloma, Mecocheirus,
                Lingula, Belemnoteuthis, and several other species
                which occur rarely. Occasional Meleagrinella
                plasters occur, especially towards the top.
                Secondary calcite is developed on most species,
                but varies in its importance throughout the bed.

JASON ZONE, JASON SUBZONE

13   5 cm.   Shell bed consisting dominantly of shell fragments
                    in a dark sticky clay matrix; some weak
                    pyritisation of shells towards the top, and
                    secondary calcite is characteristic throughout.
                    Kosmoceratids abundant, together with Meleagrinella,
                    Palaeonucula, G. concinna and flat oysters. A
                    diverse, but not abundant accessory fauna of
                    bivalves and gastropods is also present.

12   62 cm.   Olive-green blocky shaly clay, with a patchy
                    distribution of fossils, some horizons being
                    apparently unfossiliferous. An unusual feature of
                    this bed is that Protocardia appears to have
                    replaced Palaeonucula. Dicroloma dominates over
                    Procerithium. A little development of secondary
                    calcite on some species. Bositra abundant, with
                    a rich accessory fauna dominated by Protocardia,
                    Grammatodon concinna, Oxytoma, and kosmoceratids.
                    Other rather rarer elements include Mesosaccella,
                    Meleagrinella, Parainoceramus, Lingula,
                    Procerithium and flat oysters.

11   5 cm.   Grammatodon-rich shell bed, with an ammonite
                    plaster at the base, although ammonites are not
                    particularly abundant within the rest of the bed.
                    Fauna dominated by G. concinna, Trautscholdia,
                    Protocardia, Dicroloma and flat oysters. Bositra
                    and Meleagrinella rare.

10   15 cm.   Dark, very well-laminated bituminous shales, with
a rich fauna of crushed macroconch kosmoceratids,
and many horizontal trace-fossil burrows, often
up to 2 cm wide. Diverse benthonic fauna,
dominated by G. concinna, Parainoceramus and
Dicrolona, with accessory Pinna, Oxytoma,
Trautscholdia, Meleagrinella, Chlamys and Bositra.
Fish fragments — scales, teeth and centra are also
characteristic. Contained within these shales is
a band of wheel-shaped septarian concretions, up
to 19 cm thick, with macroconch and microconch
kosmoceratids preserved in sparry calcite in the
septarian cracks.

JASON ZONE, MEDEA SUBZONE

9   7 cm.   Dark olive-green clay with many shells, slightly
pyritic at the base, and not particularly fissile.
Fauna dominated by G. concinna, Gryphaea,
Trautscholdia, Bositra and Belemnopsis sulcata.

8   8 cm.   Fairly massive, slightly silty clay, very
fossiliferous towards the top, with a fauna
similar to that of bed 9. Towards the base,
oysters become larger and more abundant. Fauna
dominated by kosmoceratids, Gryphaea, G. concinna
and Meleagrinella.

7   3 cm.   Non-pyritic shell bed, rich in Gryphaea and
Cylindroteuthis. Remainder of the fauna rather
impoverished, and containing the same species as in
bed 8.

6 9 cm.   Slightly shaly clay with a rather sparse fauna,
            not rich in ammonites. Palaeonucula absent,
            Mesosaccella rare. Dominant benthos is G. concinna,
            Gryphaea, Bositra, Oxytoma and Procerithium.

5 10 cm.   Very shelly clay, containing abundant Gryphaea
            and Cylindroteuthis, together with crushed
            kosmoceratids, in a matrix of broken shells and
            blackish-green clay. Sparse accessory fauna as in
            bed 6.

CALLOVIENSE ZONE, ENODATUM SUBZONE

4 26 cm.   Shaly clay, becoming silty towards the base, with an
            ammonite plaster containing K. (Zugokosmoceras)
            enodatum 12 cm below the top. Fauna diverse, but
            very sparse, with G. concinna, Oxytoma, Meleagrinella
            and Bositra being dominant.

CALLOVIENSE ZONE, CALLOVIENSE SUBZONE

3 20 cm.   Massive micro-crosslaminated silts, with no
            parallel, horizontal bedding obvious; some
            bioturbation. Fauna very sparse, and not diverse,
            with Meleagrinella, Trautscholdia, Thracia,
            Protocardia and Gryphaea.

2 6 cm.   Olive-green shaly clay with a characteristic fauna
            of small bivalves. Fauna not very diverse, but
            slightly more abundant than in bed 3. Dominated
            by Trautscholdia, Protocardia, Meleagrinella and
            Bositra.

1   70 cm. seen. Massive yellow-green sandy silts, micro-cross
     laminated. Fauna dominantly <u>Gryphaea</u> and
     <u>Cylindroteuthis</u>, with some kosmoceratids. Large
     concretionary doggers of calcareous sandstone
     occur within this bed. Trace fossils such as
     <u>Rhizocorallium</u> are locally abundant.

APPENDIX 2

Soluble fractions of each bed at the four major quarries examined.

Measurements made by treating samples with 10% HCl, and calculating the weight loss as a percentage of the original weight. The measurements given are averaged from analysis of three samples per bed.

The bulk of the soluble fraction is thought to be $CaCO_3$, but also includes unknown percentages of other carbonates, sulphates and other acid-soluble salts.

CALVERT

Bed	Soluble fraction	Bed	Soluble fraction
12B	69.20 %	4JC	5.18 %
12A	26.60	4JB	8.92
11	44.52	4JA	6.76
10R	35.41	4H	6.03
10Q	24.36	4G	5.36
10P	40.80	4F	7.98
10N	35.88	4E	5.49
10MA	35.71	4D	9.04
10M	27.69	4C	3.70
10L	31.18	4BB	13.15
10K	14.04	4BA	6.19
10J	12.33	4A	9.31
10HB	10.73	3L	10.96
10HA	7.62	3K	8.39
10G	10.98	3JB	7.70
10F	14.34	3JA	6.18
10E	7.84	3H	4.30
10D	8.74	3G	5.68
10B	11.60	3F	5.50
10A	9.52	3E	3.03
9AC	20.27	3D	4.63
9AB	13.75	3C	3.70
9AA	7.08	3B	4.13
8	46.91	3A	12.77
7	15.06	2C	30.59
6	15.21		

BLETCHLEY

Bed	Soluble fraction	Bed	Soluble fraction
18 (limestone)	75.01 %	13E	11.74 %
18 (clay)	25.96	13D	4.87
17K	37.28	13C	5.42
17J	30.11	13B	5.20
17G	28.63	13A	10.07
17F	31.45	12J	11.23
17E	35.43	12I	7.24
17D	42.43	12H	6.03
17C	31.93	12G	8.22
17B	34.00	12F	8.66
17A	13.94	12D	8.28
16C	10.34	12C	6.77
16B	11.14	12B	8.20
16A	17.87	12A	12.07
15E	32.67	11	22.38
15D	8.04	10	33.30
15C	7.70	9B	13.16
15B	7.81	9A	5.62
15A	8.52	8	8.40
14	24.15	7	7.96
13M	18.17	5B	4.51
13J	10.77	5A	26.04
13I	7.75	4EA	4.23
13H	6.01	4D	4.07
13G	8.58	4C	5.54
13FA	29.99	4B	5.30
13F	11.26	4A	4.69

STEWARTBY

Bed	Soluble fraction	Bed	Soluble fraction
18 (top)	26.57 %	11	35.73 %
18 (base)	24.63	10J	12.40
17 (clay)	33.13	10I	23.99
17 (limestone)	75.96	10H	6.77
15	27.51	10F	10.14
14I	21.85	10E	7.65
14H	27.00	10D	2.47
14G	20.55	10C	13.59
14F	28.61	10B	5.20
14E	31.98	10A	14.00
14D	43.03	8D	33.85
14C	22.85	8C	24.16
14B	39.63	8B (clay)	23.00
14A	11.02	8B (limestone)	84.72
13	12.03	8A	22.74
12H	7.08	7	61.18
12G	12.04	6E	4.61
12F	10.08	6D	4.12
12E	11.98	6C	4.22
12D	14.77	6B	4.72
12C	6.26	6A	3.58
12B	8.24	5	30.42
12A	11.19	4	5.96

NORMAN CROSS

Bed	Soluble fraction	Bed	Soluble fraction
38	19.61 %	17	47.36 %
37	29.10	16A	6.93
36	29.04	16	8.57
35	29.42	15	18.37
34	38.13	14G	11.14
33	37.43	14F	14.97
32	29.31	14E	19.96
31	30.09	14D	12.33
30	24.77	14C	9.93
29	40.90	14B	11.08
28	44.61	14A	8.54
27	23.24	12	7.20
26	22.81	11	12.92
25	14.94	10	14.21
24	13.27	9	27.18
23	19.33	8	8.99
22	12.47	7	17.72
21	17.43	5	11.94
20	20.74	4	5.46
19	28.75	3	9.77
18A	11.24	2	5.90
18	13.01	1	10.51

APPENDIX 3

Measurements and variation statistics of the specimens

examined in the course of the monographic work.

The measurements and statistical parameters are defined

in sections 2.5.1. and 2.5.3. respectively.

Basic measurements are in mm, with the percentage of

each measurement parameter compared with L shown in

brackets. Angular measurements are given in degrees.

<u>Nuculoma pollux</u> (Raspail)

spec. no.	L	H	I	AL
d'Orbigny 3374A (HT)	18.9	14.3 (75.7)	10.9 (57.7)	12.4 (65.6)
Raspail pl.12 fig.13	9.9	8.1 (81.8)		6.3 (63.6)
YM KD1974/1	12.9	10.8 (83.7)	7.5 (58.1)	9.0 (70.2)
KD1974/2	12.4	10.3 (83.0)	6.9 (55.6)	
GSM 25/46-1	16.9	13.2 (78.1)	10.3 (60.9)	
25/46-2	17.9	12.7 (70.9)	10.0 (55.9)	
25/46-3	16.9	13.4 (80.2)	10.7 (64.1)	

N	7	7	6	3
$\bar{x}$	15.1 mm	79.1 %	58.7 %	66.5 %
Max	18.9	83.7	64.1	70.2
Min	9.9	70.9	55.6	63.6
OR	9.0	12.8	8.5	6.6
s	3.35	4.56	3.25	3.38
s^2	11.21	20.78	10.56	11.45
V	22.19	5.77	5.53	5.09
$\sigma_{\bar{x}}$	1.27	1.72	1.33	1.95

Nuculoma kathryni sp. nov.

spec. no.	L	H	I	AL
GSM 114030	10.8	8.3 (76.9)	7.9 (73.1)	8.9 (82.4)
114031	9.8	7.5 (76.5)	7.1 (72.4)	7.5 (76.5)
114032	9.0	7.0 (77.8)	6.7 (74.4)	7.3 (81.1)
114033	10.1	8.7 (86.1)		8.4 (83.2)
114034	10.5	8.8 (83.8)	6.5 (61.9)	9.0 (85.7)
114035	8.5	7.2 (84.7)	6.2 (72.9)	6.6 (77.6)

N	6	6	5	6
$\bar{x}$	9.8 mm	81.0 %	70.9 %	81.1 %
Max	10.8	84.7	74.4	85.7
Min	8.5	76.5	61.9	76.5
OR	2.3	7.8	12.5	9.2
s	0.88	4.36	5.11	3.48
s^2	0.78	18.97	26.08	12.13
V	9.04	5.38	7.20	4.30
$\sigma \frac{}{x}$	0.36	1.78	2.28	1.42

Palaeonucula triangularis sp. nov.

spec. no.	L	H	I	AL
(HT) BM LL27713	16.1	12.6 (78.3)	10.8 (67.1)	10.4 (64.6)
27714	13.2	10.6 (80.3)	8.6 (65.2)	9.5 (72.0)
27715	16.6	14.0 (84.3)	12.3 (74.1)	10.5 (63.3)
27716	14.8	12.4 (83.8)	10.7 (72.3)	10.2 (68.9)
27717	14.3	11.8 (82.5)	9.4 (65.7)	9.0 (62.9)
27718	13.8	10.6 (76.8)	8.2 (59.4)	8.5 (61.6)
27719	14.5	12.0 (82.8)	10.3 (71.0)	9.3 (64.1)
27720	17.4	13.0 (74.7)	11.0 (63.2)	11.7 (67.2)
27721	14.5	11.3 (77.9)	9.2 (63.4)	10.5 (72.4)
LU 69500	15.7	12.0 (76.4)	9.9 (63.1)	9.9 (63.1)
69501	13.4	10.4 (77.6)	8.8 (65.7)	8.7 (64.9)
69502	17.8	15.4 (86.5)	11.7 (65.7)	10.7 (60.1)
69503	16.3	13.2 (81.0)	10.4 (63.8)	10.5 (64.4)
69504	15.7	12.0 (76.4)	11.1 (70.7)	10.3 (65.6)
69505	15.5	11.7 (75.5)	9.8 (63.2)	10.0 (64.5)
69506	16.4	13.1 (79.9)	11.0 (67.1)	10.6 (64.6)
69507	15.8	12.5 (79.1)	11.0 (69.6)	10.5 (66.5)
69508	12.6	10.0 (79.4)	7.9 (62.7)	8.6 (68.3)
69509	13.2	10.2 (77.3)	8.5 (64.4)	8.2 (62.1)
69510	16.6	14.2 (85.5)	12.0 (72.3)	13.0 (78.3)
69511	16.3	13.9 (85.3)	12.5 (76.7)	12.7 (77.9)
69512	13.1	10.7 (81.7)	9.0 (68.7)	9.1 (69.5)
69513	12.7	9.9 (78.0)	8.7 (68.5)	9.3 (73.2)
69514	13.2	11.3 (85.6)	9.3 (70.5)	9.2 (69.7)
69515	14.6	11.6 (79.5)	9.4 (64.4)	10.1 (69.2)
69516	14.5	10.9 (75.2)	9.2 (63.4)	9.4 (64.8)
69517	14.2	12.0 (84.5)	11.2 (78.9)	9.7 (68.3)
69518	15.5	12.7 (81.9)	9.9 (63.9)	9.3 (60.0)
69519	15.2	12.4 (81.6)	11.5 (75.7)	10.8 (71.1)
69520	14.9	12.3 (82.6)	10.7 (71.8)	11.0 (73.8)
69521	14.9	11.8 (79.2)	9.3 (62.4)	10.7 (71.8)
69522	15.1	11.7 (77.5)	9.5 (62.9)	10.2 (67.5)
69523	14.0	11.0 (78.6)	10.0 (71.4)	11.2 (80.0)

Palaeonucula triangularis (cont.)

spec. no.	L	H	I	AL
LU 69524	14.6	12.0 (82.2)	8.5 (58.2)	10.6 (72.6)
69525	13.2	10.8 (81.8)	9.7 (73.5)	9.1 (68.9)
69526	13.5	10.5 (77.8)	8.5 (63.0)	9.8 (72.6)
69527	14.2	10.8 (76.1)	10.4 (73.2)	10.0 (70.4)
69528	11.4	9.6 (84.2)	8.1 (71.1)	8.4 (73.7)
69529	12.6	10.0 (79.4)	8.0 (63.5)	8.9 (70.6)
69530	11.5	9.8 (85.2)	7.3 (63.5)	8.5 (73.9)
69531	16.3	13.1 (80.4)	9.9 (60.7)	11.6 (71.2)
69532	13.0	10.0 (76.9)	8.1 (62.3)	8.8 (67.7)
69533	11.9	9.5 (79.8)	7.9 (66.4)	8.2 (68.9)
69534	14.1	10.9 (77.3)	8.0 (56.7)	10.5 (74.5)
69535	14.7	12.0 (81.6)	10.4 (70.7)	10.5 (71.4)
69536	16.5	13.0 (78.8)	11.5 (69.7)	11.3 (68.5)
69537	17.2	12.6 (73.3)	10.3 (59.9)	10.5 (61.0)
69538	15.0	12.3 (82.0)	10.6 (70.7)	10.9 (72.7)
69539	16.8	12.9 (76.8)	10.7 (63.7)	11.9 (70.8)
69540	14.1	11.9 (84.4)	10.0 (70.9)	10.6 (75.2)
69541	14.7	11.9 (81.0)	10.9 (74.1)	10.5 (71.4)
69542	15.2	12.3 (80.9)	11.4 (75.0)	10.7 (70.4)
69543	15.4	11.8 (76.6)	9.6 (62.3)	11.6 (75.3)
69544	12.5	10.2 (81.6)	7.9 (63.2)	9.2 (73.6)
69545	15.8	12.2 (77.2)	10.7 (67.7)	10.9 (69.0)
69546	15.9	12.0 (75.5)	9.6 (60.4)	11.2 (70.4)
69547	16.8	13.1 (78.0)	11.3 (67.3)	11.6 (69.0)
69548	15.5	12.7 (81.9)	11.0 (71.0)	11.5 (74.2)
69549	14.8	12.7 (85.8)	9.5 (64.2)	10.7 (72.3)
69550	15.4	12.6 (81.8)	12.0 (77.9)	12.0 (77.9)
69551	14.6	10.9 (74.7)	9.2 (63.0)	10.1 (69.2)
69552	13.5	10.5 (77.8)	8.6 (63.7)	9.3 (68.9)
69553	14.7	11.6 (78.9)	10.0 (68.0)	11.0 (74.8)
69554	14.2	11.2 (78.9)	9.2 (64.8)	9.9 (69.7)
69555	14.1	11.4 (80.9)	9.6 (68.1)	9.1 (64.5)

Palaeonucula triangularis (cont.)

spec. no.	L	H	I	AL
LU 69556	18.4	14.0 (76.1)	14.0 (76.1)	13.8 (75.0)
69557	13.8	10.5 (76.1)	9.2 (66.7)	10.1 (73.2)
69558	12.3	9.5 (77.2)	7.2 (58.5)	8.7 (70.7)
69559	15.8	12.6 (79.7)	11.0 (69.6)	11.1 (70.3)
69560	14.7	11.9 (81.0)	9.3 (63.3)	10.9 (74.1)
69561	16.9	14.2 (84.0)	12.0 (71.0)	10.7 (63.3)
69562	12.3	10.2 (82.9)	8.4 (68.3)	8.3 (67.5)
69563	15.5	12.9 (83.2)	10.0 (64.5)	10.6 (68.4)
69564	16.4	13.1 (79.9)	10.2 (62.2)	12.4 (75.6)
69565	13.4	10.9 (81.3)	8.0 (59.7)	9.6 (71.6)
69566	15.1	12.1 (80.1)	9.9 (65.6)	11.7 (77.5)
69567	16.9	13.4 (79.3)	12.2 (72.2)	11.7 (69.2)
69568	13.1	10.0 (76.3)	8.3 (63.4)	8.6 (65.6)
69569	15.9	12.4 (78.0)	10.0 (62.9)	10.5 (66.0)
69570	15.9	11.6 (73.0)	10.9 (68.6)	11.0 (69.2)
69571	13.1	10.3 (78.6)	8.5 (64.9)	9.2 (70.2)
69572	16.4	12.3 (75.0)	11.1 (67.7)	11.3 (68.9)
69573	13.0	9.8 (75.4)	8.0 (61.5)	9.3 (70.8)
69574	16.9	13.0 (76.9)	12.3 (72.8)	11.1 (65.7)
69575	13.0	10.9 (83.8)	8.9 (68.5)	8.4 (64.6)
69576	14.0	11.3 (80.7)	9.6 (68.6)	10.2 (72.9)
69577	15.5	12.0 (77.4)	10.3 (66.5)	11.2 (72.3)
69578	16.0	12.8 (80.0)	11.2 (70.0)	11.4 (71.3)
69579	16.2	12.9 (79.6)	11.3 (69.8)	11.0 (67.9)
69580	16.1	12.2 (75.8)	10.4 (64.6)	11.1 (68.9)
69581	18.4	14.4 (78.3)	12.4 (67.4)	14.2 (77.2)
69582	14.1	11.6 (82.3)	9.9 (70.2)	10.2 (72.3)
69583	13.4	10.8 (80.6)	9.0 (67.2)	9.0 (67.2)
69584	12.1	10.3 (85.1)	8.1 (66.9)	8.2 (67.8)
69585	14.9	12.4 (83.2)	10.8 (72.5)	10.3 (69.1)
69586	16.0	12.8 (80.0)	10.4 (65.0)	11.4 (71.3)
69587	12.9	10.2 (79.1)	8.5 (65.9)	9.0 (69.8)

Palaeonucula triangularis (cont.)

spec. no.	L	H	I	AL
LU 69588	15.3	11.7 (76.5)	10.0 (65.4)	10.6 (69.3)
69589	12.1	8.9 (73.6)	7.4 (61.2)	8.6 (71.1)
69590	15.6	11.9 (76.3)	11.3 (72.4)	12.1 (77.6)
69591	16.5	14.3 (86.7)	10.1 (61.2)	11.7 (70.9)
69592	15.7	12.7 (80.9)	10.5 (66.9)	11.1 (70.7)
69593	17.0	12.8 (75.3)	10.3 (60.6)	12.0 (70.6)
69594	15.9	12.2 (76.7)	11.3 (71.1)	11.2 (70.4)
69595	15.8	12.6 (79.7)	10.7 (67.7)	11.4 (72.2)
69596	14.5	11.8 (81.4)	10.8 (74.5)	11.2 (77.2)
69597	15.6	12.1 (77.6)	10.8 (69.2)	11.0 (70.5)
69598	15.3	12.0 (78.4)	10.4 (68.0)	10.7 (69.9)
69599	16.4	12.1 (73.8)	11.1 (67.7)	10.9 (66.5)
69600	16.3	12.8 (78.5)	10.9 (66.9)	11.2 (68.7)
69601	16.2	13.5 (83.3)	11.2 (69.1)	10.2 (63.0)
69602	15.0	12.1 (80.7)	9.9 (66.0)	10.3 (68.7)
69603	13.9	10.9 (78.4)	9.9 (71.2)	10.1 (72.7)
69604	13.2	10.6 (80.3)	8.3 (62.9)	9.4 (71.2)
69605	17.5	15.0 (85.7)	11.2 (64.0)	12.0 (68.6)
69606	13.5	11.1 (82.2)	9.6 (71.1)	10.0 (74.1)
69607	13.7	10.6 (77.4)	8.6 (62.8)	9.5 (69.3)
69608	11.0	8.7 (79.1)	7.0 (63.6)	7.6 (69.1)
69609	15.4	11.8 (76.6)	9.7 (63.0)	10.4 (67.5)
69610	14.3	11.7 (81.8)	10.3 (72.0)	10.1 (70.6)
69611	12.4	9.6 (77.4)	8.1 (65.3)	8.6 (69.4)
69612	14.3	11.6 (81.1)	9.8 (68.5)	10.3 (72.0)
69613	12.3	9.6 (78.0)	6.9 (56.1)	7.5 (61.0)
69614	16.3	13.6 (83.4)	11.4 (69.9)	9.1 (55.8)
69615	17.0	12.6 (74.1)	9.9 (58.2)	10.4 (61.2)
69616	15.0	12.2 (81.3)	10.1 (67.3)	10.3 (68.7)
69617	14.1	11.9 (84.4)	8.7 (61.7)	11.1 (78.7)
69618	16.0	12.6 (78.8)	11.2 (70.0)	12.0 (75.0)
69619	14.3	11.7 (81.8)	10.2 (71.3)	9.7 (67.8)

Palaeonucula triangularis (cont.)

spec. no.	L	H	I	AL
LU 69620	14.7	11.8 (80.3)	9.8 (66.7)	10.5 (71.4)
69621	15.2	12.9 (84.9)	10.6 (69.7)	11.2 (73.7)
69622	11.9	9.3 (78.2)	7.2 (60.5)	8.0 (67.2)
69623	13.4	11.1 (82.8)	8.6 (64.2)	9.4 (70.1)
69624	17.9	13.8 (77.1)	13.6 (76.0)	12.4 (69.3)
69625	14.3	11.4 (79.7)	9.6 (67.1)	10.9 (76.2)
69626	13.3	11.1 (83.5)	10.9 (82.0)	9.9 (74.4)
69627	13.4	10.3 (76.9)	9.4 (70.1)	10.0 (74.6)
69628	13.6	11.0 (80.9)	9.7 (71.3)	10.3 (75.7)
69629	13.5	10.4 (77.0)	8.0 (59.3)	9.5 (70.4)
69630	15.0	12.2 (81.3)	10.2 (68.0)	9.9 (66.0)
69631	15.6	11.9 (76.3)	10.6 (67.9)	10.9 (69.9)
69632	15.6	12.8 (82.1)	10.7 (68.6)	11.2 (71.8)
69633	12.7	10.1 (79.5)	8.6 (67.7)	9.3 (73.2)
69634	14.6	11.9 (81.5)	10.2 (69.9)	10.9 (74.7)
69635	10.7	8.3 (77.6)	6.2 (57.9)	8.2 (76.6)
69636	12.8	9.8 (76.6)	8.3 (64.8)	9.3 (72.7)
69637	14.4	11.2 (77.8)	9.4 (65.3)	9.1 (63.2)
69638	13.0	10.2 (78.5)	8.4 (64.6)	9.2 (70.8)
69639	15.1	13.3 (88.1)	12.2 (80.8)	10.8 (71.5)
69640	12.1	9.2 (76.0)	6.9 (57.0)	9.1 (75.2)
69641	11.3	8.8 (77.9)	8.0 (70.8)	7.8 (69.0)
69642	13.0	10.9 (83.8)	8.6 (66.2)	9.0 (69.2)
69643	16.3	12.4 (76.1)	10.5 (64.4)	10.5 (64.4)
69644	13.8	11.6 (84.1)	10.0 (72.5)	10.0 (72.5)
69645	14.3	11.3 (79.0)	10.3 (72.0)	10.7 (74.8)
69646	13.3	10.3 (77.4)	8.7 (65.4)	9.8 (73.7)
69647	12.5	9.2 (73.6)	7.4 (59.2)	9.5 (76.0)
69648	13.4	10.2 (76.1)	7.9 (59.0)	9.4 (70.1)
69649	17.0	12.3 (72.4)		11.4 (67.1)
69650	15.1	11.9 (78.8)		11.1 (73.5)
69651	13.5	10.8 (80.0)	8.5 (63.0)	8.8 (65.2)

Palaeonucula triangularis (cont.)

spec. no.	L	H	I	AL
LU 69652	17.5	12.4 (70.9)		11.8 (67.4)
69653	12.6	10.0 (79.4)	8.0 (63.5)	7.8 (61.9)

N	163	163	160	163
$\overline{x}$	14.7 mm	79.5 %	66.9 %	70.0 %
Max	18.4	88.1	82.0	80.0
Min	10.7	73.0	56.1	55.8
OR	7.7	14.9	25.9	24.2
s	1.60	3.27	4.88	4.25
s^2	2.57	10.68	23.8	18.07
V	10.95	4.11	7.30	6.07
$\sigma_{\overline{x}}$	0.13	0.26	0.39	0.33

<u>Palaeonucula cottaldi</u> (de Loriol)

spec. no.	L	H	I	AL
(HT)de Loriol pl.17 fig.11	16.5	12.2 (73.9)	10.3 (62.4)	13.4 (81.2)
(ST)de Loriol pl.17 fig.14	15.3	11.3 (73.9)	9.6 (62.7)	12.4 (81.0)
KD Lukow 1	14.4	10.4 (72.2)	8.9 (61.8)	11.3 (78.5)
KD Lukow 2	16.7	13.4 (80.2)	12.3 (73.7)	13.9 (83.2)
KD Lukow 3	14.7	11.5 (78.2)	11.0 (74.8)	12.4 (84.4)
GSM Y2049	20.1	13.9 (69.2)	12.6 (62.7)	16.2 (80.6)
GSM Dr 2508	17.8	12.4 (69.7)	14.8 (83.1)	
GSM Dr 2526	15.4	12.4 (80.5)	12.4 (80.5)	
GSM Dr 2538	18.4	13.7 (74.5)	11.7 (63.6)	13.6 (73.9)

N	9	9	9	7
$\overline{x}$	16.6 mm	74.7 %	69.5 %	80.4 %
Max	20.1	80.5	83.1	84.4
Min	14.4	69.2	61.8	73.9
OR	5.7	11.3	21.3	10.5
s	1.89	4.17	8.58	3.43
s^2	3.57	17.39	73.62	11.76
V	11.39	5.58	12.35	4.27
$\sigma\,\overline{x}$	0.63	1.39	2.86	1.30

Mesosaccella morrisi (Deshayes)

spec. no.	L	H	I	AL	∠
(LT) BM 48830	12.6	7.5 (59.5)		4.9 (38.9)	146°
BM L67155	14.2	8.8 (62.0)		5.6 (39.4)	149
BM L67148	13.5	8.3 (61.5)		5.2 (38.5)	131
GSM 44/16-1	13.1	7.3 (55.7)			
GSM 44/16-2	11.6	6.5 (56.0)			
GSM 44/16-3	11.2		5.5 (49.1)		
GSM 43041	15.1	9.1 (60.3)	8.8 (58.3)	5.5 (36.4)	
GSM Lowe-1	15.5	9.0 (58.1)		5.9 (38.1)	
GSM Lowe-2	14.4	8.6 (59.7)		5.8 (40.3)	
GSM 75695	11.9	7.0 (58.8)		4.8 (40.3)	141
75697	17.0	10.0 (58.8)		7.2 (42.4)	147
75698	13.8	8.1 (58.7)	6.9 (50.0)	5.1 (37.0)	142
75700	13.6	8.0 (58.8)	7.3 (53.7)	5.5 (40.4)	139
75701	14.5	7.9 (54.5)	8.0 (55.2)	5.7 (39.3)	144
75702	12.3	7.5 (61.0)	6.6 (53.7)	5.4 (43.9)	145
75703	8.4	5.4 (64.3)	4.0 (47.6)	3.3 (39.3)	144
KD 500	12.9	7.5 (58.1)	7.0 (54.3)	4.4 (33.3)	
LU 68612	10.4	6.3 (60.6)		4.0 (38.5)	
68613	13.2	7.3 (55.3)	7.2 (54.5)	5.4 (40.9)	139
68614	13.1	6.5 (49.6)	7.0 (53.4)	5.3 (40.4)	138
68615	13.0	7.8 (60.0)	6.2 (47.7)	5.1 (39.2)	139
68616	8.9	5.8 (65.2)	3.8 (42.7)	3.4 (38.2)	145
68617	10.3	6.8 (66.0)		4.3 (41.7)	148
68618	11.0	6.5 (59.1)		4.5 (40.9)	147
68619	11.0	7.2 (65.5)		5.1 (46.4)	
68621	13.7	8.1 (59.1)	7.2 (52.6)	5.5 (40.1)	139
68622	10.7	6.7 (62.6)	4.8 (44.9)	4.4 (41.1)	138
68623	10.3	6.3 (61.2)	4.8 (46.6)	4.0 (38.8)	143
69654	14.8	7.4 (50.0)	6.8 (45.9)	6.3 (42.6)	142
69655	12.9	7.3 (56.6)	6.9 (53.5)	5.3 (41.1)	144
69656	13.7	7.7 (56.2)	7.3 (53.3)	5.3 (38.7)	140
69657	14.6	8.6 (58.9)	7.1 (48.6)	6.1 (41.8)	139

Mesosaccella morrisi (cont.)

spec. no.	L	H	I	AL	∠
LU 69658	12.2	7.2 (59.0)	6.6 (54.1)	5.3 (43.4)	148°
69659	13.0	7.7 (59.2)	6.8 (52.3)	5.4 (41.5)	139
69660	13.9	8.2 (59.0)	7.8 (56.1)	5.5 (39.6)	142
69661	13.7	8.0 (58.4)	6.4 (46.7)	5.4 (39.4)	139
69662	15.0	8.3 (55.3)		5.7 (38.0)	140
69663	13.3	8.3 (62.4)		5.5 (41.4)	142
69664	12.5	7.5 (60.0)	6.2 (49.6)	5.1 (40.8)	144
69665	11.1	6.6 (59.5)	4.6 (41.4)	4.7 (42.3)	141
69666	12.0	6.8 (56.7)	5.9 (49.2)	4.9 (40.8)	140
69667	12.2	7.8 (63.9)	5.5 (45.1)	5.6 (45.9)	138
69668	12.5	7.4 (59.2)	7.0 (56.0)	5.0 (40.0)	139
69669	11.3	6.9 (61.1)	5.9 (52.2)	4.8 (42.5)	146
69670	8.3	5.9 (71.1)		3.6 (43.4)	160
69671	6.2	3.9 (62.9)		2.9 (46.8)	160
69672	4.8	3.3 (68.8)		2.3 (47.9)	139
69673	9.2	6.0 (65.2)		3.9 (42.4)	142
69674	9.6	5.6 (58.3)		4.0 (41.7)	138
69675	8.3	5.3 (63.9)		3.3 (39.8)	145
69676	8.4	5.6 (66.7)		4.0 (47.6)	146
69677	8.1	5.3 (65.4)		3.6 (44.4)	145
69678	9.7	5.8 (59.8)		3.9 (40.2)	137
69679	9.5	6.4 (67.4)		4.2 (44.2)	140
69680	11.5	6.8 (59.1)		4.9 (42.6)	142
69681	14.3	8.3 (58.0)		5.4 (37.8)	141
69682	13.3	7.6 (57.1)		5.2 (39.1)	139
69683	14.1	7.9 (56.0)		5.7 (40.4)	141
69684	10.3	6.4 (62.1)		4.9 (47.6)	143
69685	11.2	6.4 (57.1)		4.4 (39.3)	148
69686	9.4	4.9 (52.1)		4.2 (44.7)	142
69687	12.2	6.5 (53.3)		4.9 (40.2)	139
69688	11.4	6.2 (54.4)		4.6 (40.4)	139
69689	8.7	5.8 (66.7)		3.5 (40.2)	150

Mesosaccella morrisi (cont.)

spec. no.	L	H	I	AL	∠
LU 69690	13.8	8.4 (60.9)		6.0 (43.5)	140°
69691	10.2	6.4 (62.7)		4.7 (46.1)	142
69692	11.2	6.2 (55.4)		5.2 (46.4)	142
69693	8.1	5.0 (61.7)		3.8 (46.9)	147
69694	9.1	5.8 (63.7)		3.7 (40.7)	138
69695	12.7	6.6 (52.0)		4.8 (37.8)	139
69696	10.7	5.8 (54.2)		4.6 (43.0)	143
69697	9.6	6.3 (65.6)		4.1 (42.7)	137
69698	7.2	4.8 (66.7)		2.9 (40.3)	148
69699	9.1	5.7 (62.6)		3.6 (39.6)	138
69700	11.2	6.4 (57.1)		4.6 (41.1)	141
69701	11.3	6.2 (54.9)		4.4 (38.9)	133
69702	13.3	8.1 (60.9)		5.0 (37.6)	139
69703	11.3	6.3 (55.8)		4.7 (41.6)	136
69704	9.9	5.7 (57.6)		4.3 (43.4)	144
69705	15.0	7.6 (50.7)		5.9 (39.3)	140
69706	10.2	5.6 (54.9)		4.0 (39.2)	146
69707	9.6	6.1 (63.5)		4.5 (46.9)	137
69708	9.5	5.3 (55.8)		4.0 (42.1)	141
69709	16.8	8.2 (48.8)		6.3 (37.5)	136
69710	6.4	4.5 (70.3)		2.9 (45.3)	133
69711	7.8	5.0 (64.1)		3.7 (47.4)	135
69712	12.3	6.6 (53.7)		4.7 (38.2)	132
69713	8.6	5.4 (62.8)		3.8 (44.2)	138
69714	10.7	6.5 (60.7)		4.6 (43.0)	140
69715	10.8	6.4 (59.3)		4.7 (43.5)	
69716	9.3	5.4 (58.1)		3.9 (41.9)	
69717	9.6	5.5 (57.3)		5.0 (52.1)	
69718	5.9	3.9 (66.1)		2.5 (42.4)	
69719	9.4	6.3 (67.0)		4.4 (46.8)	137
69720	8.8	6.1 (69.3)		4.6 (52.3)	143
69721	8.0	5.0 (62.5)		3.1 (38.8)	135

Mesosaccella morrisi (cont.)

spec. no.	L	H	I	AL	∠
LU 69722	8.9	5.6 (62.9)		3.6 (40.4)	144°
69723	9.0	5.9 (65.6)		3.2 (35.6)	153
69724	7.0	4.6 (65.7)		3.0 (42.9)	142
69725	14.0	7.8 (55.7)		5.5 (39.3)	143
69726	9.7	6.3 (64.9)		4.6 (47.4)	138
69727	10.7	6.0 (56.1)		4.4 (41.1)	137
69728	17.6	9.6 (54.5)		7.2 (40.9)	145
69729	14.7	7.9 (53.7)		6.2 (42.2)	142
69730	12.7	7.7 (60.6)		5.3 (41.7)	144
69731	11.8	7.0 (59.3)		4.9 (41.5)	143
69732	12.8	7.4 (57.8)		4.9 (38.3)	141
69733	6.8	4.6 (67.6)		2.8 (41.2)	144
69734	7.7	5.2 (67.5)		3.6 (46.8)	140
69735	8.0	5.9 (73.8)		3.2 (40.0)	148
69736	15.7	9.1 (58.0)		5.7 (36.3)	133
69737	17.1	10.3 (60.2)		5.9 (34.5)	133
69738	13.9	9.2 (66.2)		5.5 (39.6)	138
69739	8.3	5.7 (68.7)		3.6 (43.4)	
69740	14.2	8.3 (58.5)		5.4 (38.0)	138
69741	13.5	7.8 (57.8)		5.2 (38.5)	134
69742	17.3	9.2 (53.2)		6.3 (36.4)	145
LU 40608	11.8	8.0 (67.8)	6.7 (56.8)	4.7 (39.8)	139
40599	13.3	7.6 (57.1)	7.3 (54.9)	5.8 (43.6)	139
40606	12.2	6.9 (56.6)	6.6 (54.1)	5.2 (42.6)	144
40593	10.9	7.2 (66.1)	5.3 (48.6)	4.7 (43.1)	148
40591	12.1	7.2 (59.5)	6.4 (52.9)	4.9 (40.5)	143
40598	12.5	8.3 (66.4)	6.6 (52.8)	5.3 (42.4)	136
40596	12.3	7.3 (59.3)		5.0 (40.7)	139
40594	10.9	7.5 (68.8)		4.5 (41.3)	139
40604	10.3	7.0 (68.0)	5.7 (55.3)	4.4 (42.7)	140

Mesosaccella morrisi (cont.)

N	125	124	35	122	111
$\overline{x}$	11.4 mm	60.4 %	51.1 %	41.5 %	141.2°
Max	17.6	73.8	56.8	52.3	160
Min	4.8	48.8	41.4	34.5	131
OR	12.8	25.0	15.4	17.8	29
s	2.61	4.95	4.22	4.89	4.52
s^2	6.79	24.47	17.80	23.95	20.43
V	22.77	8.19	8.25	11.89	3.20
$\sigma\,\overline{x}$	0.23	0.44	0.71	0.44	0.43

Solemya woodwardiana Leckenby

spec. no.	L	H	AL
(HT) SM J6008	23.3	9.1 (39.1)	18.4 (79.0)
(PT) SM J12568	24.5	9.7 (39.6)	18.6 (75.9)
(PT) SM J12569	24.3	9.6 (39.5)	18.4 (75.7)
(PT) SM J12570	24.1	9.8 (40.7)	18.8 (78.0)
LU 69743	38.0	18.0 (47.4)	28.0 (73.7)
69744	38.0	18.0 (47.4)	30.0 (78.9)
69745	34.0	16.0 (47.1)	26.0 (76.5)
69746	12.0	5.5 (45.8)	10.0 (83.3)
69747	13.0	6.5 (50.0)	11.0 (84.6)
69748	11.0	5.0 (45.5)	9.0 (81.8)
69749	11.0	5.0 (45.5)	8.0 (72.7)
69750	17.0	8.0 (47.1)	13.0 (76.5)
69751	11.0	5.0 (45.5)	8.5 (77.3)
69752	14.5	7.0 (48.3)	11.0 (75.9)
69753	15.0	7.0 (46.7)	11.5 (76.7)
69754	16.0	7.5 (46.9)	13.5 (84.4)
69755	16.5	8.0 (48.5)	13.5 (81.8)
69756	14.0	7.0 (50.0)	11.0 (78.6)
69757	13.0	6.0 (46.2)	10.5 (80.8)

N	19	19	19
$\bar{x}$	19.5 mm	45.6 %	78.5 %
Max	38.0	50.0	84.6
Min	11.0	39.1	72.7
OR	27.0	10.9	11.9
s	8.94	3.40	3.44
s^2	79.92	11.56	11.83
V	45.85	7.46	4.38
$\sigma \bar{x}$	2.05	0.78	0.79

Grammatodon minima (Leckenby)

spec. no.	L	H	I	AL	Lh	∢
SM J6007a	9.0	7.0 (77.8)	5.9 (65.6)	3.8 (42.2)	7.1 (78.9)	106°
SM J6007b	11.0	7.8 (70.9)	6.2 (57.4)	4.8 (43.6)	8.2 (74.5)	111
SM J12359	14.0	11.8 (84.3)	10.0 (71.4)	5.0 (35.7)		
LU 69759	11.6	8.3 (71.6)	5.8 (50.0)	4.6 (39.7)	8.5 (73.3)	115
69760	10.4	8.0 (76.9)	3.8 (36.5)	4.0 (38.5)	7.0 (67.3)	115
69761	12.1	9.0 (74.4)	5.9 (48.8)	4.3 (35.5)	8.5 (70.2)	113
69762	9.9	7.6 (76.8)		4.0 (40.4)	7.6 (76.8)	102
69763	10.8	7.7 (71.3)	4.1 (38.0)	4.0 (37.0)	7.7 (71.3)	110
69764	8.1	5.7 (70.4)	3.9 (48.1)	3.1 (38.3)	5.8 (71.6)	104
69765	13.3	8.3 (62.4)	6.7 (50.4)	4.9 (36.8)	10.3 (77.4)	117
69766	10.3	7.5 (72.8)	4.8 (46.6)	4.1 (39.8)	7.1 (68.9)	108
69767	12.5	9.6 (76.8)	7.3 (58.4)	4.4 (35.2)	8.3 (66.4)	105
69768	7.8	5.8 (74.4)	3.3 (42.3)	3.7 (47.4)	5.9 (75.6)	99
69769	11.5	8.7 (75.7)	6.8 (59.1)	4.4 (38.3)	7.8 (67.8)	114
69770	10.9	7.8 (71.6)	6.0 (55.0)	4.8 (44.0)	7.9 (72.5)	114
69771	6.8	4.8 (70.6)	3.2 (47.1)	2.6 (38.2)	4.6 (67.6)	107
69772	11.4	8.4 (73.7)	8.0 (70.2)	4.2 (36.8)	8.4 (73.7)	106
69773	11.2	8.4 (75.0)	7.6 (67.9)	4.6 (41.1)	8.2 (73.2)	112
69774	7.0	4.9 (70.0)	3.8 (54.3)	2.3 (32.9)	4.9 (70.0)	113
69775	14.0	9.6 (68.6)	10.4 (74.3)	5.9 (42.1)	10.8 (77.1)	118
69776	7.5	5.6 (74.7)		3.2 (42.7)	5.7 (76.0)	111
69777	9.3	6.5 (69.9)	4.3 (46.2)	4.3 (46.2)	6.6 (71.0)	110
69778	7.2	5.0 (69.4)	4.8 (66.7)	2.9 (40.3)	5.7 (79.2)	104
69779	10.0	7.3 (73.0)		4.8 (48.0)	7.5 (75.0)	107
69780	12.1	9.2 (76.0)		5.0 (41.3)	9.3 (76.9)	108
69781	11.5	8.6 (74.8)		4.8 (41.7)	8.2 (71.3)	116
69782	14.5	10.4 (71.7)	9.3 (64.1)	4.5 (31.0)	11.9 (82.1)	106
69783	11.2	8.7 (77.7)		4.6 (41.1)	7.8 (69.6)	114
69784	11.5	8.0 (69.6)	6.8 (59.1)	4.9 (42.6)	8.4 (73.0)	112
69785	10.6	8.3 (78.3)		4.5 (42.5)	8.0 (75.5)	115
69786	10.5	7.6 (72.4)		4.6 (43.8)	7.2 (68.6)	115
69787	10.2	6.8 (66.7)		4.5 (44.1)	7.2 (70.6)	118

Grammatodon minima (cont.)

spec. no.	L	H	I	AL	Lh	∠
LU 69788	11.6	8.4 (72.4)	4.4 (37.9)	3.9 (33.6)	8.5 (73.3)	118°
69789	8.8	6.1 (69.3)		4.0 (45.5)	6.8 (77.3)	114
69790	11.4	7.3 (64.0)	4.7 (41.2)	4.8 (42.1)	8.7 (76.3)	112
69791	9.5	6.8 (71.6)		4.3 (45.3)	6.8 (71.6)	110
69792	11.0	8.3 (75.5)		4.7 (42.7)	7.8 (70.9)	108
69793	13.0	9.2 (70.8)		5.9 (45.4)	9.7 (74.6)	106
69794	10.4	7.7 (74.0)		4.3 (41.3)	7.7 (74.0)	111
69795	9.6	6.8 (70.8)		4.3 (44.8)	7.1 (74.0)	116
69796	9.8	7.5 (76.5)		4.8 (49.0)	7.4 (75.5)	110
69797	6.2	4.2 (67.7)		2.3 (37.1)	4.3 (69.4)	112
69798	6.0	4.1 (68.3)		2.7 (45.0)	4.1 (68.3)	109
69799	10.0	7.8 (78.0)		4.9 (49.0)	7.4 (74.0)	110
68625	9.1	6.5 (71.4)		4.6 (50.5)	7.2 (79.1)	113
68626	13.8	9.6 (69.6)	10.5 (76.1)	5.7 (41.3)	10.7 (77.5)	115
68627	12.5	9.0 (72.0)	6.9 (55.2)	5.6 (44.8)	9.6 (76.8)	112

N	47	47	27	47	46	46
$\bar{x}$	10.5 mm	72.6 %	55.1 %	41.4 %	73.4 %	110.9°
Max	14.5	84.3	76.1	50.5	82.1	118
Min	6.0	62.4	36.5	31.0	66.4	99
OR	8.5	21.9	39.6	19.5	15.7	19
s	2.06	3.97	11.58	4.40	3.69	4.45
s^2	4.24	15.76	134.1	19.35	13.63	19.83
V	19.62	5.47	21.01	10.62	5.03	4.02
$\sigma_{\bar{x}}$	0.30	0.58	2.23	0.64	0.54	0.66

Grammatodon concinna (Phillips)

spec. no.	L	H	I	AL	Lh	∢
(HT)YMTsp135	24.0	14.0 (61.5)		8.0 (33.3)	20.4 (85.0)	110°
YM KD1974/3	20.0	11.5 (57.5)		7.6 (38.1)	14.5 (72.4)	117
1974/4	18.0	11.2 (62.4)	11.6 (64.4)	8.2 (45.5)	12.5 (69.4)	120
1974/5	18.5	11.7 (63.2)		6.8 (36.8)	16.4 (88.6)	110
1974/6	22.0	14.7 (66.9)		9.3 (42.3)	18.8 (85.5)	115
1974/7	22.0	12.5 (56.6)		8.7 (39.3)	17.9 (81.4)	110
LU 68624	23.0	12.0 (52.2)		7.5 (32.6)	18.5 (80.4)	126
68644	17.0	11.0 (64.7)	11.0 (64.7)	7.0 (41.2)	15.0 (88.2)	102
68645	19.0	11.5 (60.5)	11.0 (57.8)	8.0 (42.1)	15.0 (78.9)	102
68646	16.0	11.0 (68.8)		6.0 (37.5)	14.0 (87.5)	98
68647	17.0	12.5 (73.5)	10.0 (58.8)	7.0 (41.2)	13.0 (76.5)	104
68648	15.0	9.0 (52.6)		5.5 (36.7)	13.5 (90.0)	103
68649	17.0	11.0 (60.0)		6.5 (38.2)	13.0 (76.5)	105
68650	16.5	11.0 (52.2)		6.0 (36.4)	15.0 (90.9)	102
68628	14.0	9.0 (64.3)		5.5 (39.3)	12.0 (85.7)	102
68629	9.5	6.0 (63.2)		4.0 (42.1)	8.5 (89.5)	92
68630	17.0	10.5 (61.8)	9.0 (53.0)	6.0 (35.3)	15.0 (88.2)	95
68631	16.0	10.5 (65.6)	8.0 (50.0)	6.0 (37.5)		107
68632	15.5	10.0 (64.5)	10.0 (64.6)	5.5 (35.5)	14.5 (93.5)	100
68633	17.5	11.0 (62.9)	7.0 (40.0)	8.0 (45.7)	14.0 (80.0)	102
68634	18.0	11.0 (61.1)		7.0 (38.9)	15.0 (83.3)	105
68635	17.0	10.0 (58.8)		7.5 (44.1)	13.5 (79.4)	108
68636	14.0	9.5 (67.9)		5.5 (39.3)	11.5 (82.1)	103
68637	17.0	10.5 (61.8)		6.5 (38.2)	15.0 (88.2)	104
68638	20.0	12.5 (62.5)		8.5 (42.5)	16.5 (82.5)	104
68639	17.5	11.0 (62.9)		7.0 (40.0)		
68640	17.0	10.5 (61.8)	10.0 (58.8)	7.0 (41.1)	13.5 (79.4)	102
68641	20.0	12.5 (62.5)		7.0 (35.0)	15.0 (75.0)	103
68642	15.5	10.0 (64.5)		6.0 (38.7)	15.0 (96.8)	108
68643	16.0	10.0 (62.5)		6.5 (40.6)	12.5 (7 .1)	118
68651	19.0	10.0 (52.6)		8.0 (42.1)	15.0 (78.9)	104
68652	14.0	9.0 (64.3)		5.0 (35.7)	11.5 (82.1)	109

Grammatodon concinna (cont.)

spec. no.	L	H	I	AL	Lh	∢
LU 68653	20.0	13.0 (65.0)		7.0 (35.0)	16.5 (82.5)	110°
68654	19.0	11.0 (57.9)		7.0 (36.8)	17.0 (89.5)	102
68655	20.0	13.0 (65.0)	11.0 (55.0)	7.0 (35.0)	17.0 (85.0)	99
GSM Zr 1699	20.0	12.5 (62.5)	12.0 (60.0)	8.0 (40.0)	17.0 (85.0)	101
d'Orbigny 3359	20.0	11.5 (57.5)	9.0 (45.0)	7.5 (37.5)	15.5 (77.5)	115

N	37	37	12	37	35	36
$\bar{x}$	17.3 mm	62.1 %	56.0 %	39.0 %	83.2 %	106°
Max	24.0	73.5	64.8	45.7	96.8	126
Min	14.0	52.2	40.0	32.6	69.4	92
OR	10.0	21.3	24.8	13.1	27.4	34
s	2.82	4.40	3.93	3.09	6.02	7.08
s^2	7.95	19.33	15.45	9.55	36.21	50.09
V	16.30	7.09	14.04	7.92	7.23	6.68
$\sigma_{\bar{x}}$	0.46	0.72	1.13	0.51	1.02	1.18

Grammatodon concinna (cont.)

Grammatodon montaneyensis (de Loriol)

spec. no.	L	H	I	AL	Lh	∠
HT de Loriol pl.5 fig.12	25.5	15.0 (58.8)	16.0 (62.8)	9.0 (35.3)	21.0 (82.4)	116°
ST de Loriol pl.5 fig.14	27.5	16.5 (60.0)		10.0 (36.4)	22.0 (80.0)	116
d'Orbigny 3711	28.0	18.0 (64.3)	16.0 (57.2)	12.0 (42.9)	25.5 (91.1)	105
GSM Zr 1700	21.0	14.0 (66.7)	12.0 (57.0)	9.0 (42.9)	19.0 (90.5)	108
GSM 52300	20.6	12.9 (62.6)	12.4 (60.2)	7.4 (35.9)		115

N	5	5	4	5	5	5
$\bar{x}$	24.5 mm	63.0 %	58.0 %	38.5 %	85.8 %	108.8°
Max	28.0	66.7	62.8	42.9	91.1	116
Min	21.0	58.8	55.0	35.3	80.0	99
OR	7.0	7.9	7.8	8.6	11.1	17
s	3.52	3.39	3.34	4.05	4.90	7.33
s^2	12.39	11.51	11.16	16.41	24.01	53.70
V	14.37	5.38	5.78	10.52	5.71	6.74
$\sigma \bar{x}$	1.58	1.52	0.84	1.81	2.19	3.28

Grammatodon clathrata (Leckenby)

spec. no.	L	H	I	AL	Lh	∠
HT SMJ6005	39.6	23.7 (59.8)	19.4 (49.0)	14.5 (36.6)	28.1 (71.0)	140°
SM J12358	50.7	29.1 (57.4)	27.4 (54.0)	20.4 (40.2)		134
YM KD1974/8	30.0	20.0 (66.7)	14.0 (46.6)	10.0 (33.3)	22.0 (73.3)	140
1974/9	38.0	20.5 (53.9)	19.0 (50.0)	14.0 (36.8)	26.0 (68.4)	136
1974/10	37.0	22.0 (59.5)	21.0 (56.8)	14.0 (37.8)	28.0 (75.7)	
GSM 113414	23.5	15.0 (63.8)	10.0 (42.6)	8.5 (36.2)	18.0 (76.6)	126
LU 68656	25.5	15.0 (58.8)	11.0 (43.2)		18.0 (70.6)	134
68657	30.0	18.5 (61.7)	12.0 (40.0)	10.5 (35.0)		136
68658	25.5	17.0 (66.7)	14.0 (55.0)	7.0 (27.5)	17.5 (68.6)	138

N	9	9	9	8	7	8
$\bar{x}$	33.3 mm	60.9 %	48.6 %	35.4 %	72.0 %	135.5°
Max	50.7	66.7	56.8	40.2	76.6	140
Min	23.5	53.9	40.0	27.5	68.4	126
OR	27.2	12.8	16.8	12.7	8.2	14
s	8.79	4.26	5.94	3.78	3.27	4.50
s^2	77.21	18.14	35.32	14.26	10.67	20.29
V	26.38	6.99	12.23	10.66	4.53	3.32
$\sigma_{\bar{x}}$	2.93	1.42	1.98	1.33	1.23	1.59

Modiolus bipartitus J. Sowerby

spec. no.	L	H	I	Lh
(HT)BM 43231	70.6	52.1 (73.8)	30.5 (43.2)	34.8 (49.3)
Arkell				
pl.2 fig.1	54.0	36.7 (68.0)	27.0 (50.0)	24.1 (44.6)
pl.2 fig.2	51.9	39.3 (75.7)		23.1 (44.5)
pl.2 fig.3	41.9	32.2 (76.8)		20.8 (49.6)
pl.2 fig.4	35.4	31.2 (88.1)	18.0 (50.8)	16.9 (47.7)
GSM 42865	52.0	47.1 (90.6)	22.4 (43.1)	23.0 (44.2)
GSM 42866	47.0	31.4 (66.8)	20.4 (43.4)	24.9 (53.0)
GSM 42864	41.5	35.9 (86.5)	22.6 (54.5)	19.2 (46.3)
GSM Zr 1702	38.6	33.4 (86.5)		22.4 (58.0)
GSM Y2148	51.8	34.6 (66.8)	25.6 (49.4)	22.2 (42.9)
GSM Fr 26	38.5	27.3 (70.9)		20.5 (53.2)
GSM 52282	43.7	35.8 (81.9)	19.9 (45.5)	17.9 (41.0)
GSM KA 537	48.6	34.2 (70.4)	23.5 (48.4)	21.7 (44.7)
GSM 43027	46.6	32.5 (69.7)	20.7 (44.4)	26.4 (56.7)
GSM 25-23	53.3	47.6 (89.3)	28.9 (54.2)	
GSM GSa 3634	52.9	34.9 (66.0)	23.4 (44.2)	
3636	48.0	34.2 (71.3)	20.6 (42.9)	
GSM KD1974-1	36.5	26.1 (71.5)	16.3 (44.7)	16.9 (46.3)
GSM 3100	56.6	38.0 (67.1)	25.8 (45.6)	29.9 (52.8)
GSM 3099	50.3	45.2 (89.9)	21.8 (43.3)	18.5 (36.8)
GSM 57520	53.8	42.2 (78.4)	28.3 (52.6)	23.8 (44.2)
GSM 57521	37.9	31.0 (81.8)	16.0 (42.2)	17.8 (47.0)
GSM GSa 3635	45.2	36.7 (81.2)	21.3 (47.1)	19.7 (43.6)
SM J12394	56.9	44.4 (78.0)	23.8 (41.8)	26.6 (46.7)
KD Lukow 4	46.2	38.8 (84.0)	19.5 (42.2)	18.1 (39.2)
YM KD 1974/11	55.9	38.5 (68.9)	24.1 (43.1)	24.2 (43.3)
1974/12	53.9	40.0 (74.2)	22.3 (41.4)	23.3 (43.2)
1974/13	67.2	45.2 (67.3)	26.9 (40.0)	25.6 (38.1)
1974/14	57.4	47.3 (82.4)	22.4 (39.0)	21.7 (37.8)

Modiolus bipartitus (cont.)

	L	H	I	Lh
N	29	29	25	26
$\bar{x}$	50.1 mm	77.6 %	45.8 %	45.4 %
Max	70.0	100.2	54.5	58.0
Min	36.5	66.0	39.0	35.7
OR	33.5	34.2	15.5	22.3
s	9.49	9.17	4.39	5.83
s^2	90.13	84.09	19.27	33.96
V	18.94	11.82	9.59	12.83
$\sigma \bar{x}$	1.76	1.70	0.88	1.14

Pinna mitis Phillips

spec. no.	L	H	Dr	Vr
YM Tsp 219 (HT)	43.8			8+
YM KD1974/15	42.2		15	6
1974/16	52.5	26.7 (50.9)	15	10+
1974/17	74.5			
1974/18	50.9	23.8 (46.8)	14	8
1974/19	41.4	15.3 (37.0)		
OUM J30186	68.0		22	9+
SM J26739	36.6	17.3 (47.3)	17	13
26740	49.4	22.0 (44.5)	15+	8+
LCM G1955/257a	82.4	29.5 (35.8)	18	13
LCM G1955/257b	58.0		14	9
LU 68659	78.9	32.9 (41.7)	17	12
68660	49.3	24.1 (48.9)	18	12
68661	54.9	23.6 (43.0)	14	14
68662	32.4		14+	
68663	39.8	16.0 (40.2)	13	10
68664	38.3		14	7
68665			16	
68666	27.9	14.0 (50.2)	8+	4+
68667			13	8
68668	25.0			6
68669	40.1	16.2 (40.4)		
68670	36.2		14	
68671	50.0	25.0 (50.0)	17	11
68672	25.9	9.1 (35.1)	9	6

Pinna mitis (cont.)

	L	H	Dr	Vr
N	23	14	20	19
$\bar{x}$	47.8 mm	44.2 %	14.7	9.2
Max	82.4	50.9	22	14
Min	25.0	35.1	8	6
OR	57.4	15.8	14	8
s	16.06	5.84	3.07	2.79
s^2	257.9	34.13	9.42	7.78
V	33.60	13.22	20.88	30.33
$\sigma\,\bar{x}$	3.35	1.69	0.69	0.64

Pinna lanceolata J. Sowerby

spec. no.	L	H	I	Dr	Vr
BM 47399	49.7	18.4 (37.0)	13.1 (26.4)		
BM 66884	43.2	16.8 (38.9)			
SM J26725	147.5	66.8 (45.3)	43.0 (29.2)	9	6
26726	116.9	51.0 (43.6)	31.1 (26.6)	9	
YM KD1974/20	170.0	66.2 (38.9)	34.6 (20.4)	7	5
1974/21	52.7	16.2 (31.5)	5.8 (11.0)	8	5
1974/22	50.2	17.0 (33.9)	7.2 (14.3)	7	4
1974/23	37.6	13.2 (35.1)	4.4 (11.7)	7	
1974/24	84.0	28.8 (34.3)		6	3
1974/25	67.9	20.1 (29.6)	18.0 (26.5)	8	
1974/26	168.0	65.0 (38.7)	31.4 (18.7)	8	4

N	11	11	9	9	6
$\bar{x}$	89.8 mm	36.9 %	20.5 %	7.67	4.50
Max	170.0	45.3	29.2	9	6
Min	37.6	29.6	11.0	6	3
OR	132.4	15.7	18.2	3	3
s	51.54	4.78	7.01	1.00	1.05
s^2	26.56	22.85	49.14	1.00	1.10
V	57.39	12.95	34.20	13.04	23.3
$\sigma_{\bar{x}}$	15.54	1.44	2.34	0.33	0.43

Pteroperna ? pygmaea (Dunker)

spec. no.	L	Lh	ALh	PLh	OL	H	Θ
Dunker pl.3 fig.6a(LT)	11.4	9.2 (80.7)	3.2 (28.1)	6.0 (52.6)	10.4 (91.2)	7.6 (66.7)	38
pl.3 fig.6c	9.6	9.0 (93.8)	2.4 (25.0)	6.6 (68.8)	9.0 (93.8)	5.5 (57.3)	30
Krenkel pl.25 fig.43	24.0	20.1 (83.8)	5.0 (20.8)	15.1 (63.0)	23.0 (95.8)	14.4 (60.0)	33
SM J12446	15.3	13.2 (86.3)			15.3 (100.0)	10.2 (66.7)	
BCM Cb 4778	12.8	11.5 (89.8)	3.4 (26.6)	8.1 (63.2)	11.5 (89.8)	8.3 (64.8)	33
4779	10.5	9.4 (89.5)	3.2 (30.5)	6.2 (59.0)	8.7 (82.9)	6.1 (58.1)	31
4777	11.1	9.9 (89.2)	3.0 (27.0)	6.9 (62.2)	10.5 (94.6)	8.1 (73.0)	36
4780	10.3	8.3 (80.6)	3.1 (30.1)	5.2 (50.5)	8.1 (78.6)	6.2 (60.2)	32
4781	10.4	9.1 (87.5)	2.7 (26.0)	6.4 (61.5)	8.9 (85.6)	6.5 (62.5)	31
LU 68673	6.2	5.4 (87.1)	2.0 (32.3)	3.4 (54.8)	5.0 (80.6)	4.0 (64.5)	32
68674	5.1	4.4 (86.3)			4.2 (82.4)	3.0 (58.8)	
N	11	11	9	9	11	11	9
$\bar{x}$	11.5 mm	86.8 %	27.4 %	59.5 %	88.7 %	63.0 %	32.9°
Max	15.3	93.8	32.3	68.8	100.0	73.0	38
Min	5.1	80.7	20.8	50.5	78.6	57.3	30
OR	10.2	13.1	11.5	18.3	21.4	15.7	8
s	4.99	3.96	3.42	5.86	7.05	4.73	2.57
s^2	24.89	15.68	11.68	34.33	49.69	22.41	6.61
V	43.31	4.56	12.49	9.85	7.95	7.52	7.82
$\sigma\overline{x}$	1.50	1.19	1.14	1.95	2.13	1.43	0.36

Parainoceramus subtilis (Lahusen)

spec. no.	L	H	Lh
GSM 42987	31.9	.37.5 (117.6)	18.8 (58.9)
GSM 25-15	72.5	80.0 (110.3)	31.7 (43.7)
BCM Cb 4774	46.8	62.0 (132.5)	23.8 (50.9)
4775	39.8	46.0 (115.6)	16.9 (42.5)
LU 68675	20.9	28.0 (134.0)	11.9 (56.9)
68676	4.5	6.1 (135.6)	2.6 (57.8)
68677	9.0	11.7 (130.0)	4.8 (53.3)
68678	3.3	4.3 (130.3)	2.1 (63.6)
68679	5.8	6.7 (115.5)	3.9 (67.2)
68680	24.2	31.3 (129.3)	9.9 (40.9)
68681	7.8	8.6 (110.3)	4.2 (53.8)
68682	8.6	12.3 (143.0)	4.9 (57.0)
68683	6.3	8.0 (127.0)	3.6 (57.1)
68684	7.6	9.2 (121.1)	3.6 (47.4)
68685	7.3	8.5 (116.4)	4.6 (63.0)
68686	9.5	12.9 (135.8)	5.1 (53.7)
68687	15.6	17.9 (114.7)	8.1 (51.9)
68688	61.3	71.0 (115.8)	27.7 (45.2)
68689	29.3	32.4 (110.6)	14.6 (49.8)
68690	14.4	17.7 (122.9)	7.8 (54.2)
68691	8.6	11.8 (137.2)	4.7 (54.7)
68692	24.0	30.2 (125.8)	12.8 (53.3)
68693	18.1	22.1 (122.1)	8.9 (49.2)
68694	28.5	31.8 (111.6)	12.6 (44.2)
68695	16.2	23.1 (142.6)	8.7 (53.7)

Parainoceramus subtilis (cont.)

	L	H	Lh
N	25	25	25
$\overline{x}$	20.9 mm	124.3 %	53.0 %
Max	72.5	143.0	67.2
Min	3.3	110.3	40.9
OR	69.2	32.7	26.3
s	18.05	10.32	6.67
s^2	325.85	106.59	44.54
V	86.49	8.31	12.60
$\sigma \overline{x}$	3.61	2.06	1.33

Parainoceramus subtilis (cont.)

Bositra buchii (Roemer)

spec. no.	L	H	Lh	AL	Ribs
LU 68696	15.0	12.6 (84.0)	6.5 (43.3)	5.3 (35.3)	23
68697	10.0	8.6 (86.0)	5.0 (50.0)	4.5 (45.0)	20
68698	10.8	9.1 (84.3)	5.3 (49.1)	4.6 (42.6)	24
68699	10.7	7.7 (72.0)	5.2 (48.6)	3.3 (30.8)	29
68700	4.3	3.7 (86.0)	2.1 (48.8)	1.3 (30.2)	18
68701	7.8	6.3 (80.8)	4.4 (56.4)	2.7 (34.6)	20
68702	12.6	11.6 (92.1)	6.0 (47.6)	4.8 (38.1)	23
68703	11.4	8.9 (78.1)	5.0 (43.9)	4.5 (39.5)	31
68704	8.0	6.6 (82.5)	3.6 (45.0)	2.3 (28.8)	19
68705	4.9	3.6 (73.5)	2.4 (49.0)	1.5 (30.6)	21
68706	4.9	3.9 (79.6)	2.7 (55.1)	1.7 (34.7)	18
68707	8.4	6.7 (79.8)	4.0 (47.6)	3.3 (39.3)	27
68708	6.8	6.0 (88.2)	3.2 (47.1)	2.4 (35.3)	23
68709	7.5	6.2 (82.7)	3.2 (42.7)	2.7 (36.0)	28
68710	7.0	5.8 (82.9)	2.8 (40.0)	2.3 (28.8)	37
68711	6.7	5.7 (85.1)	3.8 (56.7)	1.5 (22.4)	28
68712	5.7	4.9 (86.0)	3.1 (54.4)	2.0 (35.1)	17
68713	5.0	4.1 (82.0)	2.9 (58.0)	2.1 (42.0)	24
68714	5.3	4.6 (86.8)	2.4 (45.3)	1.8 (34.0)	19
68715	12.3	10.7 (87.0)	6.4 (52.0)	5.1 (41.5)	
68716	8.2	7.1 (86.6)	3.8 (46.3)	3.1 (37.8)	17
68717	4.4	4.3 (97.7)	2.1 (47.7)	1.6 (36.4)	26
68718	3.2	3.0 (93.8)	1.5 (46.9)	1.2 (37.5)	19
68719	10.2	9.0 (88.2)	4.5 (44.1)	3.7 (36.3)	17
68720	7.9	6.5 (82.3)	3.9 (49.4)	3.3 (41.8)	26
68721	9.3	6.3 (67.7)	4.2 (45.2)	3.2 (34.4)	28
68722	8.4	7.3 (86.9)	4.9 (58.3)	2.8 (33.3)	22
68723	8.1	6.5 (80.2)	4.0 (49.4)	3.2 (39.5)	24
68724	9.5	7.7 (81.1)	4.4 (46.3)	3.3 (34.7)	30
68725	7.2	6.1 (84.7)	3.0 (41.7)	2.3 (31.9)	33
68726	6.3	5.1 (81.0)	2.9 (46.0)	2.3 (36.5)	33
68727	8.4	7.7 (91.7)	3.9 (46.4)	2.9 (34.5)	21

Bositra buchii (cont.)

spec. no.	L	H	Lh	AL	Ribs
LU 68728	12.5	10.6 (84.8)	5.5 (44.0)	4.6 (36.8)	26
68729	5.6	5.1 (91.1)	2.6 (46.4)	2.2 (39.3)	18
68730	6.2	5.5 (88.7)	3.4 (54.8)	2.7 (43.5)	52
68731	6.8	5.9 (86.8)	3.3 (48.5)	1.7 (25.0)	46
68732	6.8	5.3 (77.9)	3.6 (52.9)	2.3 (33.8)	36
68733	7.0	6.0 (85.7)	3.5 (50.0)	2.6 (37.1)	38
68734	8.2	7.1 (86.6)	3.4 (41.5)	2.4 (29.3)	35
68735	7.3	7.0 (95.9)	3.8 (52.1)	2.4 (32.9)	43
68736	6.9	5.3 (76.8)	3.1 (44.9)	2.8 (40.6)	34
68737	6.5	5.5 (84.6)	3.1 (47.7)	1.9 (29.2)	29
68738	7.1	5.8 (81.7)	3.6 (50.7)	2.1 (29.6)	32
68739	5.1	4.5 (88.2)	2.6 (51.0)	1.9 (37.3)	26
68740	5.8	5.1 (87.9)	3.6 (62.1)	2.5 (43.1)	21
68741	7.9	6.4 (81.0)	3.5 (44.3)	2.7 (34.2)	36
68742	6.3	4.8 (76.2)	3.2 (50.8)	1.9 (30.2)	39
68743	6.6	5.5 (83.3)	3.4 (51.5)	1.6 (24.2)	35
68744	5.5	4.3 (78.2)	2.7 (49.1)	1.9 (34.5)	29
68745	5.7	4.5 (78.9)	2.8 (49.1)	2.0 (35.1)	32

N	50	50	50	50	49
$\bar{x}$	7.6 mm	83.9 %	48.8 %	35.1 %	27.6 Ribs
Max	15.0	97.7	62.1	45.0	52
Min	3.2	67.7	40.0	22.4	17
OR	11.8	30.0	22.1	22.6	35
s	2.42	5.68	4.81	4.94	8.08
s^2	5.86	32.24	23.13	24.37	65.29
V	31.84	6.77	9.86	14.07	29.3
$\sigma\,\overline{x}$	0.34	0.80	0.68	0.70	1.15

Oxytoma inequivalvis (J. Sowerby)

Left valves

spec. no.	L	H	I	AL	OL	Lh	θ	Primary Ribs
BM 43259 (LT)	26.8	25.3 (94.4)						
OUM J8612	27.3	25.1 (91.9)		7.8 (28.6)	24.6 (90.1)	21.0 (76.9)		15
OUM J13127	22.4	21.1 (94.2)		6.4 (28.6)	21.4 (95.5)			16
SM J12431	28.0	23.8 (85.0)				17.5 (62.5)		
GSM 3113	17.9	15.3 (85.5)				12.0 (67.0)		
GSM 25/11a	20.4	16.5 (80.9)		5.5 (27.0)				
GSM 25/11b	18.2	16.2 (89.0)		4.3 (23.6)				
GSM 25/10	29.6	25.3 (85.5)	6.4 (21.6)					
GSM Y2053	20.1	19.4 (96.5)	5.5 (27.4)	5.7 (28.4)		13.3 (66.2)		
Y2054	14.9	15.6 (104.7)	2.8 (18.8)					
SM J47646a	25.1	20.2 (80.5)		6.4 (25.5)	24.4 (97.2)	17.8 (70.9)	30	18
J47646b	22.6	21.9 (96.9)		6.2 (27.4)		15.1 (66.8)		17
BU 11435/1	25.1	20.7 (82.5)		6.9 (27.5)	24.2 (96.4)	18.9 (75.3)		18
11435/2	20.0	20.2 (101.0)	5.4 (27.0)	6.4 (32.0)	20.1 (100.5)	12.6 (63.0)		17
YM KD1974/27	39.8	29.2 (73.4)		9.1 (22.9)	40.1 (100.8)		29	17
1974/28	35.1	27.7 (78.9)	9.0 (25.6)	8.1 (23.1)	35.7 (101.7)		30	21
1974/29	26.5	19.7 (74.3)	5.3 (20.0)	5.3 (20.0)	28.1 (106.0)		27	18
1974/30	23.7	25.8 (108.9)	8.0 (33.8)	6.9 (29.1)	30.0 (126.6)		40	12
1974/31	36.3	27.4 (75.5)		7.6 (20.9)	35.5 (97.8)			19
LU 52681	23.2	20.9 (90.1)	5.2 (22.4)	6.8 (29.3)	24.0 (103.4)	15.7 (67.7)		18
52672	23.7	23.4 (98.7)	6.9 (29.1)	5.9 (24.9)	26.0 (109.7)	18.3 (77.2)		19

Oxytoma inequivalvis (cont.)

spec. no.	L	H	I	AL	OL	Lh	θ	Primary Ribs
LU 52673	24.6	20.8 (84.6)	6.2 (25.2)	7.8 (31.7)	24.1 (98.0)			17
52679	24.6	20.5 (83.3)	4.8 (19.5)	5.8 (23.6)	25.0 (101.6)			
52671	15.8	14.7 (93.0)	4.3 (27.2)					
52680	15.4	16.3 (105.8)	4.3 (27.9)					
68746	16.8	14.2 (84.5)		5.0 (29.8)	16.5 (98.2)	14.7 (87.5)		
68747	11.4	9.3 (81.6)		3.7 (32.5)	11.4 (100.0)	10.4 (91.2)		
68748	19.0	18.2 (95.8)		6.4 (33.7)	20.1 (105.8)			
68749	14.0	13.8 (98.6)		4.2 (30.0)	14.4 (102.9)	11.1 (79.3)		
68750	22.6	16.4 (72.6)		5.1 (22.6)	19.6 (86.7)	11.4 (50.4)		

	L	H	I	AL	OL	Lh	θ
N	30	30	13	23	19	14	5
$\bar{x}$	23.1 mm	89.0 %	25.0 %	27.1 %	101.0 %	71.6 %	31.2°
Max	39.8	108.9	33.8	**33.7**	126.6	91.2	40
Min	11.4	72.6	18.8	20.0	86.7	50.4	27
OR	28.4	36.3	15.0	13.7	39.9	40.8	13
s	6.62	9.96	4.37	3.83	8.19	10.61	5.07
s^2	43.83	99.13	19.14	14.70	67.05	112.67	25.70
V	28.67	11.19	17.47	14.16	8.11	14.83	16.25
$\sigma \bar{x}$	1.21	1.82	1.21	0.80	1.88	2.84	2.27

Oxytoma inequivalvis (cont.)

Right valves

spec. no.	L	H	I	AL	OL	Lh
GSM 3113	9.4	9.0 (95.7)				4.4 (46.8)
GSM Y2055	15.9	15.8 (99.4)	2.2 (13.8)	5.7 (35.8)		12.5 (78.6)
Y2056	15.5	14.2 (91.6)	2.1 (13.5)	5.4 (34.8)		
Y2057	14.9	14.3 (96.0)	1.8 (12.1)	4.9 (32.9)		13.4 (89.9)
Y2058	17.0	15.4 (90.6)	2.6 (15.3)	5.6 (32.9)		10.3 (60.6)
Y2059	15.5	14.5 (93.5)	2.0 (12.9)	5.1 (32.9)		
Y2060	14.7	13.3 (90.5)	2.1 (14.3)	4.3 (29.3)		
Y2061	15.4	12.9 (83.8)	2.1 (13.6)	4.7 (30.5)		10.6 (68.8)
Y2062	13.9	12.4 (89.2)	2.3 (16.5)	4.4 (31.7)		
Y2063	14.4	13.0 (90.3)	1.6 (11.1)	5.5 (38.2)		
Y2064	13.1	12.3 (93.9)	2.1 (16.0)	4.6 (35.1)		11.2 (85.5)
Y2065	9.7	9.1 (93.8)	1.6 (16.5)	3.6 (37.1)		8.1 (83.5)
LU 52678	19.6	17.6 (89.8)	2.1 (10.7)	6.0 (30.6)	19.8 (101.0)	13.7 (69.9)
52677	14.9	14.8 (99.3)	2.5 (16.8)		16.0 (107.4)	
52674	15.8	15.1 (95.6)	2.5 (15.8)			
52675	13.8	13.9 (94.2)	2.4 (17.4)	4.3 (31.2)	15.4 (111.6)	11.7 (84.8)
52676	14.0	12.9 (73.4)	2.4 (17.2)	5.0 (35.7)	14.0 (100.0)	11.5 (82.1)
68751	11.9	8.7 (73.1)		3.3 (27.7)	9.6 (80.7)	11.9 (100.0)
68752	7.4	4.7 (63.5)		1.9 (25.7)	5.0 (67.6)	7.4 (100.0)

Oxytoma inequivalvis (cont.)

N	19	19	17	16	6	12
$\bar{x}$	14.0 mm	90.3 %	15.2 %	32.6 %	94.7 %	79.2 %
Max	19.6	99.4	17.4	38.2	111.6	100.0
Min	7.4	63.5	10.7	25.7	67.6	46.8
OR	12.2	35.9	6.7	12.5	44.0	53.2
s	2.83	20.48	2.16	3.43	38.06	14.82
s^2	8.02	419.56	4.67	11.77	1448.82	219.69
V	20.17	23.80	14.81	10.51	4.85	19.17
$\sigma\bar{x}$	0.65	4.70	0.54	0.86	15.54	4.47

Meleagrinella braamburiensis (Phillips)

Left valves

spec. no.	L	H	I	AL	Lh
YM 872 (NT)	18.7	20.3 (108.6)			
YM KD1974/32	17.0	17.6 (103.5)			
1974/33	18.8	19.5 (103.7)			
GSM K1329	21.3	22.0 (103.3)	5.5 (25.8)		
K1340	15.5	15.7 (101.3)			
K228	13.6	13.9 (102.2)	4.2 (30.9)		
K1426	26.9	28.2 (104.8)	7.7 (28.6)		
K1332	20.9	23.6 (112.9)	5.4 (25.8)		
K1333	17.5	20.0 (114.3)			
K1433a	27.6	27.0 (97.8)			
K1433b	25.0	25.0 (100.0)			
K1433c	20.9	21.6 (103.3)			
K1433d	28.8	28.5 (99.0)			
K209	14.8	15.1 (102.0)			
K1331	23.8	24.2 (101.7)			
K1336	20.3	20.6 (101.5)			
K1420	29.3	29.1 (99.3)			
K1323	12.0	13.2 (110.0)			
K1322	19.0	19.0 (100.0)			
K1328	18.4	19.1)(103.8)			
K1325	18.4	18.9 (102.7)	5.9 (32.1)		
K1344	23.5	22.6 (96.2)			
K198	17.7	19.3 (109.0)			
K1324	19.3	19.3 (100.0)			
K1339	20.4	20.1 (98.5)			
K1429	29.1	29.4 (101.0)			
K1418	19.2	19.2 (100.0)			
K212	16.5	16.6 (100.6)			
K196	20.0	19.8 (99.0)			
K239	18.0	19.3 (107.2)			
K1425	29.2	29.3 (100.3)	8.9 (30.5)		

Meleagrinella braamburiensis (cont.)

spec. no.	L	H	I	AL	Lh
GSM K1334	25.7	25.5 (99.2)			
K197	16.7	15.8 (94.6)			
SM J12407	28.9	31.6 (109.3)	9.6 (33.2)		
J12444	16.8	18.3 (108.9)			
J12445	13.5	16.5 (122.2)			
GSM 42971	14.5	15.5 (106.9)		6.7 (46.2)	
42972	16.6	13.1 (78.9)		7.0 (42.2)	
42961	13.8	13.8 (100.0)	4.8 (34.8)	5.9 (42.8)	
42962	15.4	15.4 (100.0)	4.3 (27.9)	6.5 (42.2)	
LU 68753	19.1	18.5 (96.9)			
68754	26.0	27.2 (104.6)			
68755	12.3	12.8 (104.1)			
68756	15.4	16.1 (104.5)			
68757	8.0	8.6 (107.5)			
68758	33.7	30.9 (91.7)			
68759	24.3	23.5 (96.7)			
68760	24.2	25.0 (103.3)			
68761	15.3	16.8 (109.8)			
68762	16.7	17.6 (105.4)			
68763	16.0	16.7 (104.4)			
68764	28.1	29.0 (103.2)			
GSM Y2087	21.8	22.5 (103.2)	8.1 (37.2)	10.0 (45.9)	11.3 (51.8)
Y2088	20.4	22.6 (110.8)	9.1 (44.6)	9.4 (46.1)	7.8 (38.2)
Y2089	15.7	15.9 (101.3)	5.8 (36.9)	7.3 (46.5)	7.5 (47.8)
113409	13.3	14.0 (105.3)			
113410	16.3	17.2 (105.5)	6.0 (36.8)	7.4 (45.4)	8.1 (49.7)
BCM 3324a	12.2	12.9 (105.7)	4.4 (36.1)		
3324b	13.4	14.2 (106.0)			

Meleagrinella braamburiensis (cont.)

N	59	58	14	8	4
$\overline{x}$	19.6 mm	103.4 %	32.9 %	44.7 %	46.9 %
Max	33.7	122.2	44.6	46.5	51.8
Min	8.0	91.7	20.8	42.2	38.2
OR	25.7	30.5	23.8	4.3	13.6
s	5.46	5.12	5.23	1.91	6.01
s^2	29.84	26.19	27.32	3.64	36.12
V	27.87	4.95	15.87	4.27	12.82
$\sigma\,\overline{x}$	0.71	0.67	1.40	0.67	3.00

Right valves

spec. no.	L	H	I	AL	Lh
GSM K1341	8.6	8.4 (97.7)			
K195	14.7	14.7 (100.0)			
K1326	14.3	13.4 (93.7)			
K1427	21.1	17.6 (83.4)			
K197	13.8	12.9 (93.5)			
GSM 42966	17.4	17.1 (98.3)	3.2 (18.4)	8.7 (50.0)	
42968	12.9	12.4 (96.1)	2.6 (20.2)	6.7 (51.9)	
42969	10.1	9.8 (97.0)	3.0 (29.7)	5.1 (50.5)	
42970	7.0	6.9 (98.6)	1.9 (27.1)	3.1 (44.3)	
GSM Y2090	14.4	14.5 (100.7)	3.0 (20.8)	7.3 (50.7)	7.0 (48.6)
LU 68765	20.8	18.8 (90.4)			
68766	18.3	16.2 (88.5)			
68767	26.5	24.4 (92.1)			
68768	16.8	14.5 (86.3)			
68769	7.2	6.8 (94.4)			
68770	22.5	20.8 (92.4)			
68771	9.8	9.1 (92.9)			
68772	9.8	9.0 (91.8)			

Meleagrinella braamburiensis (cont.)

spec. no.	L	H		I	AL	Lh
LU 68773	20.9	19.6 (93.8)				
68774	14.6	13.3 (91.1)				
68759	17.5	15.8 (90.3)				

	N	21	21	5	5	1
$\bar{x}$		15.2 mm	93.5 %	23.2 %	49.8 %	48.6 %
Max		26.5	100.7	29.7	51.9	48.6
Min		7.0	83.4	18.4	44.3	48.6
OR		19.5	17.3	11.3	7.6	0
s		5.46	5.12	5.23	1.91	6.01
s^2		29.84	26.19	27.32	3.64	36.12
V		27.87	4.95	15.87	4.27	12.82
$\sigma \, \bar{x}$		0.71	0.67	1.40	0.67	3.00

Entolium corneolum (Young & Bird)

spec. no.	H	L	∠
YM Tsp. 119	30.7	25.7 (83.7)	100°
YM KD1974/34	11.1	9.9 (89.2)	
1974/35	29.6	28.2 (95.3)	
1974/36	15.3	13.4 (87.6)	
SM J12396	30.4	27.9 (91.8)	108
J12397	33.7	31.0 (92.0)	109
J60363	18.7	15.0 (80.2)	95
J60364	13.2	12.2 (92.4)	96
J60365	14.1	11.5 (81.6)	99
J60366	13.1	11.8 (90.1)	98
BM L66462	15.3	12.2 (79.7)	
47433	35.9	32.3 (80.0)	
Arkell 1930			
p.91 a	72.0	66.0 (92.0)	
b	43.0	37.5 (87.0)	
c	47.0	41.0 (87.0)	
d	47.0	42.0 (89.0)	
e	27.0	24.0 (89.0)	

N	17	17	7
$\overline{x}$	29.2 mm	87.5 %	100.7°
Max	72.0	95.3	109
Min	11.1	79.7	95
OR	60.9	15.6	14
s	16.39	4.86	5.59
s^2	268.6	23.62	31.25
V	56.1	5.55	5.55
$\sigma\,\overline{x}$	3.97	1.18	2.11

Byssentolium hudsoni sp. nov.

spec. no.	H	L	∢
BM LL27722	5.9	5.2 (88.1)	101°
LL27723(HT)	7.3	6.3 (86.3)	102
27746	5.9	5.3 (89.8)	93
27747	7.3	6.2 (84.9)	104
27748	12.3	10.9 (88.6)	100
27749	8.0	7.3 (91.3)	102
27750	6.0	5.4 (90.0)	103
27751	4.3	3.5 (81.4)	98
LU 69934	8.1	6.5 (80.2)	
69935	8.2	6.9 (84.1)	98
69936	5.5	5.0 (90.9)	105
69937	6.1	5.3 (86.9)	
69938	4.8	4.5 (93.8)	
69939	12.2	11.1 (91.0)	104
69940	7.9	6.5 (82.3)	

N	15	15	11
$\bar{x}$	7.3 mm	87.3 %	100.9°
Max	12.3	93.8	105
Min	4.3	80.2	93
OR	8.0	13.6	12
s	2.34	4.04	3.51
s^2	5.49	16.30	12.32
V	32.01	4.62	3.48
$\sigma \frac{}{x}$	0.60	1.04	1.06

Camptonectes auritus (Schlotheim)

spec. no.		H	L	⊿
BM L80525		34.3	34.3 (100.0)	
L80526		46.1	47.4 (102.8)	
SM J12402		33.9	31.5 (92.9)	106°
J12403		28.0	26.2 (93.6)	108
J12404		29.6	25.7 (86.8)	104
J12405		38.0	36.8 (96.8)	103
J12406		30.6	28.0 (91.5)	
Arkell 1930 p.94	a)	58.0	57.0 (98.5)	106
	b)	54.0	53.0 (98.5)	108
	c)	46.0	45.0 (98.0)	110

	N	10	10	7
	$\overline{x}$	39.9 mm	95.9 %	107.0°
	Max	58.0	102.8	110
	Min	28.0	86.8	103
	OR	30.0	16.0	7
	s	10.58	4.71	2.44
	s^2	111.9	22.18	5.95
	V	26.52	4.91	2.28
	$\sigma_{\overline{x}}$	3.35	1.49	0.92

Chlamys (Chlamys) bedfordi sp. nov.

spec. no.	L	H	Lh	AL	$\angle$	valve
BM LL27724	9.7	9.8 (101.0)			111°	RV
27725	9.4	9.4 (100.0)		5.0 (53.2)	113	RV
27726	6.6	6.8 (103.0)		2.8 (42.4)	107	LV
27727	9.4	9.5 (101.0)	5.7 (60.6)	5.0 (53.2)	109	RV
27728	7.7	7.9 (102.6)	5.5 (71.4)	3.6 (46.8)	108	LV

Left valve

N	2	2	1	2	2
$\bar{x}$	7.2 mm	102.8 %	71.4 %	44.6 %	107.5°
Max	7.7	103.0	71.4	46.8	108
Min	6.6	102.6	71.4	42.4	107
OR	1.1	0.4	0	4.4	1
s	0.78	0.28		3.11	0.70
s^2	0.61	0.08		9.68	0.49
V	10.88	0.28		6.98	0.65
$\sigma\,\bar{x}$	0.55	0.20		2.20	0.50

Right valve

N	3	3	1	2	3
$\bar{x}$	9.5 mm	100.7 %	60.6 %	53.2 %	111.0°
Max	9.7	101.0	60.6	53.2	113
Min	9.4	100.0	60.6	53.2	109
OR	0.3	1.0	0	0	4
s	0.17	0.58			2.52
s^2	0.03	0.33			6.35
V	1.82	0.57			2.27
$\sigma\,\bar{x}$	0.10	0.33			1.45

Chlamys (Radulopecten) scarburgensis (Young & Bird)

spec. no.	L	H	∠	no. ribs
SM J12398 (NT)	41.5	42.9 (103.4)	108°	10
J12399	29.9	32.1 (107.4)		10
J12400	41.2	41.6 (101.0)		10
J12401	30.0	32.5 (108.3)		10
J47648	20.8	22.5 (108.2)		10
GSM 42847	32.6	35.4 (108.6)	101	10
42985	26.8	28.4 (106.0)	105	10
BM L8958a	34.4	37.7 (109.6)		
L8958b	37.8	36.0 (95.2)		
L8958c	22.6	24.3 (107.5)		

N	10	10	3	7
$\bar{x}$	31.8 mm	105.5 %	104.7°	10 ribs
Max	41.5	109.6	108	10
Min	20.8	95.2	101	10
OR	20.7	14.4	7	0
s	7.18	4.47	3.51	
s^2	51.55	19.98	12.32	
V	22.58	4.24	3.35	
$\sigma \frac{}{x}$	2.27	1.41	2.03	

Chlamys (Radulopecten) fibrosa (J. Sowerby)

spec. no.	L	H
BM 43305 (ST)	34.8	39.5 (113.5)
43305 (ST)	22.2	24.3 (109.5)

N	2	2
$\overline{x}$	28.5 mm	111.5
Max	34.8	113.5
Min	22.2	109.5
OR	12.6	4.0
s	8.9]	2.83
s^2	79.39	8.00
V	31.26	2.54
$\sigma \overline{x}$	6.30	2.00

Chlamys (Radulopecten) drewtonensis Neale

spec. no.		H	L	∡
BM L88737 (HT)		40.3	38.5 (104.7)	100°
L88738		41.3	38.1 (108.4)	100
	N	2	2	2
	$\bar{x}$	40.8 mm	106.6 %	100°
	Max	41.3	108.4	100
	Min	40.3	104.7	100
	OR	1.0	3.7	0

Plicatula cf. fistulosa Morris & Lycett

spec. no.	L	H	I	AL
LU 68775	26.8	26.8 (100.0)	8.4 (31.3)	15.0 (56.0)
68776	31.1			
68777		24.6		
68778		26.3		
BM L87302	31.8	39.9 (125.5)		

N	3	2	1	1
$\bar{x}$	29.9 mm	112.8 %	31.3 %	56.0 %
Max	31.8	125.5	31.3	56.0
Min	26.8	100.0	31.3	56.0
OR	5.0	25.5	0	0
s	2.71	18.03		
s^2	7.34	325.0		
V	9.06	15.98		
$\sigma_{\bar{x}}$	1.56	12.75		

Gryphaea dilobotes nom. nov.

	BM LL 27729 (HT) LV	LU 69972 LV	LU 69973 LV
L	59.3 mm	66.9	75.9
H	62.0 (104.6 %)	72.4 (108.2)	84.8 (111.7)
I	25.7 (43.3)	32.2 (48.1)	40.7 (53.6)
L. lig.	6.3 (10.6)		11.2 (14.8)
H. lig.	4.5 (7.6)	7.8 (11.7)	
L.a.b.	2.0 (3.4)		3.8 (5.0)
L.p.b.	2.8 (4.7)		4.4 (5.8)
HMS	33.3 (56.2)		44.0 (58.0)
Hi	58.6 (98.8)	67.9 (101.5)	71.9 (94.7)
AL	24.6 (41.5)	35.3 (52.8)	33.1 (43.6)
θ	95°	92	98
∝	28°	26	26

	LU 70041 RV	LU 70042 LV	LU 70043 LV
L	68.3	57.9	50.8
H	70.1 (102.6)	69.4 (119.9)	64.7 (127.4)
I	24.4 (35.7)	37.2 (64.2)	33.1 (65.2)
L. lig.		8.5 (14.7)	
H. lig.		7.3 (12.6)	
L.a.b.		3.7 (6.4)	
L.p.b.		2.3 (4.0)	
HMS	41.3 (60.5)	33.0 (57.0)	
Hi	70.4 (103.1)		
AL	30.5 (44.7)	24.6 (42.5)	22.3 (43.9)
θ	106	106	92
∝		31	24

Gryphaea dilobotes (cont.)

	LU 69969 LV	LU 70044 LV	LU 69974 LV	LU 69974 RV
L	53.7	42.6	80.0	73.4
H	64.9 (120.9)	55.1 (129.3)	90.7 (113.4)	67.4 (108.9)
I	33.4 (62.2)	35.8 (84.0)	39.8 (49.8)	
L.lig.			10.5 (13.1)	7.5 (10.2)
H.lig.			10.4 (13.0)	12.2 (16.6)
L.a.b.			3.2 (4.0)	4.5 (6.1)
L.p.b.			4.6 (5.8)	3.9 (5.3)
HMS			44.0 (55.0)	
Hi	50.8 (100.0)	36.8 (86.4)	76.8 (96.0)	
AL	27.9 (52.0)	17.7 (41.5)	36.8 (46.0)	28.0 (38.1)
θ	97	126	103	102
∝	39	38	29	29

	LU 69979 LV	LU 69970 LV	LU 70045 LV	LU 69988 LV
L	68.0	70.0	68.4	58.8
H	75.0 (110.3)	66.9 (95.6)	67.5 (98.7)	63.2 (107.5)
I	40.6 (59.7)	31.7 (45.3)	28.8 (42.1)	30.8 (52.4)
L.lig.		6.0 (8.6)		7.6 (12.9)
H.lig.				7.0 (11.9)
L.a.b.		3.2 (4.6)		3.0 (5.1)
L.p.b.		2.5 (3.6)		5.0 (8.5)
HMS		31.8 (45.4)	36.7 (53.7)	
Hi	62.4 (91.8)	57.0 (81.4)	61.5 (89.9)	49.8 (84.7)
AL	32.2 (47.4)	29.7 (42.4)	26.6 (38.9)	25.4 (43.2)
θ	113	117	113	115
∝	32	42	29	28

Gryphaea dilobotes (cont.)

	LU 70046 LV	LU 70047 LV	LU 70048 LV	LU 69980 LV
L	46.8	61.6	61.1	42.7
H	48.0 (102.6)	61.3 (99.5)	68.8 (112.6)	44.3 (103.7)
I	24.7 (52.8)	23.2 (37.7)	34.3 (56.1)	23.4 (54.8)
L.lig.	3.9 (8.3)			5.5 (12.9)
H.lig.	5.0 (10.7)			7.5 (17.6)
L.a.b.	3.1 (6.6)			3.3 (7.7)
L.p.b.	2.5 (5.3)			4.4 (10.3)
HMS	25.9 (55.3)			23.9 (56.0)
Hi	43.1 (92.1)	57.7 (93.7)	58.9 (96.4)	39.2 (91.8)
AL	19.0 (40.6)	26.0 (42.2)	30.1 (49.3)	24.5 (57.4)
θ	101	100	117	90
∝	38	26	34	31

	LU 70049 LV	LU 69981 LV	LU 70050 LV	LU 70051 LV
L	55.5	54.0	34.5	66.6
H	65.5 (118.0)	60.8 (112.6)	36.7 (106.4)	68.1 (102.3)
I	34.7 (62.5)	28.0 (51.9)	19.8 (57.4)	25.5 (38.3)
L.lig.		5.5 (10.2)	4.1 (11.9)	7.6 (11.4)
H.lig.		3.4 (6.3)	3.7 (10.7)	7.6 (11.4)
L.a.b.				4.4 (6.6)
L.p.b.				4.7 (7.1)
HMS		35.4 (65.6)	21.2 (61.4)	
Hi	54.9 (98.9)	54.6 (101.1)	33.9 (98.3)	67.3 (101.1)
AL	24.1 (43.4)	20.9 (38.7)	16.4 (47.5)	22.4 (33.6)
θ	110	101	94	113
∝	20	31	30	29

Gryphaea dilobotes (cont.)

	LU 70052 LV	LU 70053 RV	LU 70054 LV	LU 70055 LV
L	29.9	42.6	67.3	50.7
H	32.9 (110.0)	49.8 (116.9)	79.2 (117.7)	51.0 (100.6)
I	14.7 (49.2)	12.6 (29.6)	38.0 (56.5)	26.5 (52.3)
L.lig.			12.0 (17.8)	
H.lig.			8.8 (13.1)	6.7 (13.2)
L.a.b.			1.4 (2.1)	
L.p.b.			3.2 (4.8)	
HMS		34.3 (80.5)	38.2 (56.8)	
Hi	30.9 (103.3)	49.8 (116.9)	68.9 (102.4)	49.1 (96.8)
AL	13.7 (45.8)			22.4 (44.2)
θ		97	106	107
∝		24	35	35

	BM LL27753 LV	LU 69976 LV	LU 70056 LV	LU 70057 LV
L	33.9	34.0	24.0	21.0
H	49.1 (144.8)	39.6 (116.5)	29.4 (122.5)	25.8 (122.9)
I	25.6 (75.5)	19.9 (58.5)	13.2 (55.0)	17.4 (82.9)
L.lig.	5.7 (16.8)	3.5 (10.3)		
H.lig.	7.3 (21.5)	3.2 (9.4)		2.8 (13.3)
L.a.b.	2.3 (6.8)	2.0 (5.9)		
L.p.b.	2.5 (7.4)	1.5 (4.4)		
HMS	34.6 (102.1)	17.9 (52.6)		
Hi	46.9 (138.3)	35.5 (104.4)	29.4 (122.5)	23.7 (122.9)
AL	17.0 (50.1)	17.4 (51.2)		8.4 (40.0)
θ	66	107	87	81
∝	11	24		20

Gryphaea dilobotes (cont.)

	LU 70058	LU 70059	LU 70060	LU 70061
	LV	LV	LV	RV
L	32.4	32.1	18.1	18.0
H	38.6 (119.1)	35.0 (109.0)	21.4 (118.2)	21.7 (120.6)
I	20.9 (64.5)	17.6 (54.8)	11.4 (63.0)	6.1 (33.9)
L.lig.	5.6 (17.3)			
H.lig.	5.2 (16.0)			3.6 (20.0)
L.a.b.	2.6 (8.0)			
L.p.b.	1.9 (5.9)			
HMS	22.6 (69.8)			18.0 (100.0)
Hi	35.9 (110.8)	30.6 (95.3)	21.4 (118.2)	21.7 (120.6)
AL	17.5 (54.0)	15.0 (46.7)		
θ	98	107	78	75
α	22	26		

	LU 70062	LU 70063	LU 70064	LU 70065
	RV	RV	LV	LV
L	14.5	39.9	21.3	23.4
H	15.0 (103.4)	42.1 (105.5)	24.7 (116.0)	23.3 (99.6)
I	3.4 (23.4)		15.2 (71.4)	13.4 (57.3)
L.lig.		4.0 (10.0)	3.1 (14.6)	
H.lig.	2.0 (13.8)	3.9 (9.8)	2.9 (13.6)	
L.a.b.		2.4 (6.0)	1.5 (7.0)	
L.p.b.		2.2 (5.5)	1.2 (5.6)	
HMS	9.4 (64.8)	23.0 (57.6)		
Hi	15.0 (103.4)	42.1 (105.5)	24.6 (115.5)	23.3 (99.6)
AL	4.8	20.0 (50.1)	10.3 (48.4)	9.8 (41.9)
θ	80	105	82	98
α		26		

Gryphaea dilobotes (cont.)

	LU 70066 LV	LU 70067 LV	LU 70068 LV	LU 70069 RV
L	16.0	35.9	64.4	58.4
H	19.2 (120.0)	44.2 (123.1)	66.9 (103.9)	58.5 (100.2)
I	12.0 (75.0)	28.9 (80.5)	28.4 (44.1)	
L.lig.			7.3 (11.3)	
H.lig.			4.8 (7.5)	
L.a.b.			5.1 (7.9)	
L.p.b.			3.9 (6.1)	
HMS	12.1 (75.6)			36.0 (61.6)
Hi	16.6 (103.8)		65.2 (101.2)	58.5 (100.2)
AL	7.2 (45.0)	19.9 (55.4)	31.1 (48.3)	28.1 (48.1)
θ	81	88	105	96
$\propto$		23	33	27

	LU 70070 LV	LU 70071 LV	LU 70072 RV	LU 70073 RV
L	46.4	56.0	45.4	26.8
H	49.5 (106.2)	67.4 (120.4)	42.2 (93.0)	28.1 (104.9)
I	27.9 (59.9)	28.9 (51.6)	14.1 (31.1)	5.3 (19.8)
L.lig.				3.3 (12.3)
H.lig.	5.2 (11.2)		3.4 (7.5)	5.0 (18.7)
L.a.b.				1.8 (6.7)
L.p.b.				1.2 (4.5)
HMS	28.8 (61.8)	37.3 (66.6)	24.8 (54.6)	17.3 (64.6)
Hi	45.0 (96.6)	61.9 (110.5)	42.2 (93.0)	28.1 (104.9)
AL	18.7 (40.1)	28.7 (51.3)	19.8 (43.6)	13.6 (50.7)
θ	98	92	101	96
$\propto$	23	20	33	

Gryphaea dilobotes (cont.)

	LU 70074	LU 70075	LU 70076	LU 70077
	RV	RV	LV	LV
L	24.6	18.0	53.5	65.3
H	24.4 (99.2)	21.4 (118.9)	63.3 (118.3)	65.0 (99.5)
I	4.3 (17.5)	2.7 (15.0)	30.7 (57.4)	31.0 (47.5)
L.lig.	3.9 (15.9)			9.0 (13.8)
H.lig.	4.2 (17.1)		5.6 (10.5)	7.8 (11.9)
L.a.b.	1.9 (7.7)			2.4 (3.7)
L.p.b.	1.7 (6.9)			2.2 (3.4)
HMS	16.6 (67.5)			35.1 (53.8)
Hi	24.4 (99.2)	21.4 (118.9)	53.5 (100.0)	56.0 (85.8)
AL	12.8 (52.0)	9.1 (50.6)	26.8 (50.1)	31.9 (48.9)
θ	103	79	91	116
∝			23	36

	LU 70078	BM LL27754	LU 70079	LU 70080
	LV	LV	LV	LV
L	62.6	34.6	49.8	37.4
H	76.0 (121.4)	39.5 (114.2)	48.0 (96.4)	41.3 (110.4)
I	41.2 (65.8)	24.5 (70.8)	23.2 (46.6)	22.9 (61.2)
L.lig.	7.9 (12.6)	5.3 (15.3)	7.4 (14.9)	
H.Lig.	9.7 (15.5)	5.4 (15.6)	4.9 (9.8)	3.9 (10.4)
L.a.b.	5.7 (9.1)	2.3 (6.6)	2.9 (5.8)	
L.p.b.	4.8 (7.7)	1.8 (5.2)	2.2 (4.4)	
HMS	36.9 (58.9)	24.6 (71.1)	26.8 (53.8)	24.8 (66.3)
Hi	60.3 (96.3)	36.2 (104.6)	43.6 (87.6)	35.5 (94.9)
AL	31.6 (50.5)	16.2 (46.8)	24.8 (49.8)	19.6 (52.4)
θ	98	86	128	108
∝	28	25	40	23

Gryphaea dilobotes (cont.)

	LU 70081 LV	BM LL27752 LV	LU 70082 RV	LU 70083 RV
L	26.8	30.8	27.4	28.3
H	32.0 (119.4)	40.5 (131.5)	35.6 (129.9)	30.2 (106.7)
I	18.6 (69.4)	18.0 (58.4)	7.8 (28.5)	6.8 (24.0)
L.lig.	3.5 (13.1)			
H.lig.	2.4 (9.0)	3.5 (11.4)	2.3 (8.4)	4.2 (14.8)
L.a.b.	1.6 (6.0)			
L.p.b.				
HMS		18.0 (58.4)	21.1 (77.0)	18.8 (66.4)
Hi	29.0 (108.2)	34.0 (110.4)	35.6 (129.9)	30.2 (106.7)
AL	12.3 (45.9)	15.1 (49.0)	15.0	13.4 (47.3)
θ	81	84	70	94
$\propto$	20	25		29

	LU 70084 RV	LU 70085 RV	LU 70086 RV	LU 70087 LV
L	21.8	16.2	52.4	44.8
H	26.0 (119.3)	21.1 (130.2)	53.6 (102.3)	40.0 (89.3)
I	5.2 (23.9)	4.8 (29.6)	16.1 (30.7)	15.1 (33.7)
L.lig.				
H.lig.	2.7 (12.4)	3.0 (18.5)	6.3 (12.0)	3.0 (6.7)
L.a.b.				
L.p.b.				
HMS	17.0 (78.0)	14.3 (88.3)	32.7 (62.4)	
Hi	26.0 (119.3)	21.1 (130.2)	53.6 (102.3)	34.4 (76.8)
AL	11.2 (51.4)	9.4 (58.0)	26.5 (50.6)	22.9 (51.1)
θ	83	76	110	128
$\propto$				30

Gryphaea dilobotes (cont.)

	LU 70088 RV	LU 70089 LV	LU 70090 LV	LU 70091 LV
L	49.3	29.3	62.0	58.9
H	46.8 (94.9)	29.8 (101.7)	74.6 (120.3)	61.0 (103.6)
I	13.2 (26.8)	14.3 (48.8)	27.3 (44.0)	19.6 (33.3)
L.lig.				
H.lig.		2.5 (8.5)		
L.a.b.				
L.p.b.				
HMS				36.6 (62.1)
Hi	46.8 (94.9)	29.4 (100.3)	69.1 (111.5)	59.0 (100.2)
AL	26.7 (54.2)	11.5 (39.2)	28.9 (46.6)	33.3 (56.5)
θ	108	113	99	106
∝		28	25	37

	LU 70092 LV	LU 70093 LV	LU 70093 RV	LU 70094 RV
L	51.1	76.0	69.8	40.2
H	62.8 (122.9)	70.0 (92.1)	58.6 (84.0)	44.6 (110.9)
I	30.0 (58.7)	21.8 (28.7)		12.3 (30.6)
L.lig.	5.5 (10.8)	6.3 (8.3)	7.2 (10.3)	5.2 (12.9)
H.lig.	6.7 (13.1)	4.9 (6.4)	4.3 (6.2)	5.0 (12.4)
L.a.b.	3.7 (7.2)	4.4 (5.8)	4.2 (6.0)	2.3 (5.7)
L.p.b.	3.3 (6.5)	4.9 (6.4)		2.0 (5.0)
HMS	41.1 (80.4)		39.9 (57.2)	22.5 (56.0)
Hi	55.6 (108.8)	67.5 (88.8)	58.6 (84.0)	44.6 (110.9)
AL	27.3 (53.4)	38.4 (50.5)	41.3 (59.2)	19.4 (48.3)
θ	87	94	102	80
∝	29	31	34	

Gryphaea dilobotes (cont.)

	LU 69978 LV	LU 70095 LV	LU 70096 LV	LU 70097 LV
L	26.5	20.5	13.1	14.5
H	37.8 (142.6)	26.9 (131.2)	16.1 (122.9)	16.5 (113.8)
I	20.7 (78.1)	11.5 (56.1)	6.8 (51.9)	8.9 (61.4)
L.lig.	4.5 (17.0)			
H.lig.	4.1 (15.5)		1.4 (10.7)	2.1 (14.5)
L.a.b.	2.3 (8.7)			
L.p.b.	1.9 (7.2)			
HMS	21.2 (80.0)		10.8 (82.4)	9.0 (62.1)
Hi	31.3 (118.1)	24.8 (121.0)	14.7 (112.2)	16.5 (113.8)
AL	13.9 (52.5)	7.4 (36.1)	4.9 (37.4)	6.5 (44.8)
θ	75	74	84	89
∝	23			

	LU 70098 LV	LU 70099 LV	LU 70100 LV	LU 70101 LV
L	68.7	74.9	42.1	35.3
H	80.4 (117.0)	72.6 (96.9)	45.4 (107.8)	44.8 (126.9)
I	38.6 (56.2)	41.6 (55.5)	19.3 (45.8)	22.5 (63.7)
L.lig.			6.8 (16.2)	
H.lig.			5.9 (14.0)	
L.a.b.			3.0 (7.1)	
L.p.b.			2.3 (5.5)	
HMS				
Hi	73.1 (106.4)	65.6 (87.6)	42.0 (99.8)	39.5 (111.9)
AL	31.4 (45.7)	32.5 (43.4)	22.2 (52.7)	16.1 (45.6)
θ	90	108	101	84
∝	26	33	22	18

Gryphaea dilobotes (cont.)

	LU 70102 LV	BM LL27751 LV	LU 70103 LV	LU 70104 RV
L	42.3	35.7	34.3	36.0
H	55.7 (131.7)	43.0 (120.4)	48.2 (140.5)	37.7 (104.7)
I	21.0 (49.6)	22.8 (63.9)	23.7 (69.1)	11.8 (32.8)
L.lig.		3.6 (10.1)		
H.lig.	4.9 (11.6)	4.9 (13.7)	5.9 (17.2)	5.7 (15.8)
L.a.b.		1.8 (5.0)		
L.p.b.		1.9 (5.3)		
HMS	28.9 (68.3)	25.3 (70.9)	26.5 (77.3)	23.5 (65.3)
Hi	53.9 (127.4)	38.6 (108.1)	42.2 (123.0)	37.7 (104.7)
AL	12.1 (28.6)	13.0 (36.4)	14.3 (41.7)	21.0 (58.3)
θ	95	79	86	96
$\propto$	18	24	19	

	LU 70105 LV	LU 70106 LV	LU 70107 LV
L	24.7	20.4	55.5
H	35.1 (142.1)	29.5 (144.6)	60.9 (109.7)
I	21.7 (87.9)	17.8 (87.3)	34.1 (61.4)
L.lig.			
H.lig.	2.1 (8.5)	4.5 (22.1)	
L.a.b.			
L.p.b.			
HMS	17.0 (68.8)	17.2 (84.3)	
Hi	21.7 (87.9)	23.1 (113.2)	52.2 (94.1)
AL	13.7 (55.5)	9.9 (48.5)	24.4 (44.0)
θ	83	75	106
$\propto$	15		29

Gryphaea dilobotes (cont.)

Left valves

	N	x̄	Max	Min	OR	s	s²	V	σ x̄
L	66	44.2 mm	80.0	13.1	66.9	18.73	350.65	42.37	2.31
H	66	114.7 %	114.8	89.3	55.5	17.53	307.14	15.47	2.16
I	66	57.6 %	87.9	28.7	59.2	14.00	195.79	24.94	1.71
L.lig.	27	12.9 %	17.8	8.3	9.5	2.81	7.88	21.68	0.54
H.lig.	40	12.2 %	22.1	6.3	15.8	3.63	13.15	29.67	0.57
L.a.b.	25	6.1 %	9.1	2.1	7.0	1.69	2.87	27.84	0.34
L.p.b.	24	5.9 %	10.3	3.4	6.9	1.60	2.57	27.32	0.33
HMS	34	64.5 %	102.1	45.2	56.9	12.13	147.15	18.81	2.08
Hi	63	101.8 %	138.3	76.8	61.5	12.02	144.55	11.82	1.51
AL	63	46.0 %	57.4	28.6	28.8	5.82	33.84	12.64	0.73
θ	65	97.7 °	128	66	62	12.25	203.19	14.59	1.77
∝	56	27.7 °	42	11	31	6.68	44.66	24.16	0.89

Gryphaea dilobotes (cont.)

Right valves

	N	$\bar{x}$		Max	Min	OR	s	s^2	V	$\sigma\bar{x}$
L	20	38.6	mm	73.4	14.5	58.9	18.66	348.27	48.39	4.17
H	20	107.9	%	130.2	84.0	46.2	11.89	141.46	11.03	2.66
I	16	27.1	%	35.7	15.0	20.7	3.97	35.59	22.05	1.49
L.lig.	6	11.9	%	15.9	10.0	5.9	2.29	5.24	19.19	0.93
H.lig.	15	13.6	%	20.0	6.2	13.8	4.85	23.53	39.12	1.25
L.a.b.	6	6.4	%	7.7	5.7	2.0	0.73	0.53	11.48	0.30
L.p.b.	5	5.4	%	6.9	4.5	2.4	0.90	0.81	16.52	0.40
HMS	17	68.4	%	100.0	54.6	45.4	12.45	154.99	18.21	3.02
Hi	19	107.8	%	130.2	84.0	46.2	12.21	148.98	11.32	2.80
AL	18	49.6	%	59.2	33.1	26.1	6.74	45.40	13.58	1.59
Φ	19	92.7	°	110	70	40	12.51	156.47	13.46	2.80
∤	8	28.1	°	34	24	10	3.63	13.14	12.56	1.37

Gryphaea lituola Lamarck

	HOLOTYPE LV	LU 52695 LV	LU 52694 LV	LU 52690 LV
L	67.4	75.7	57.8	58.3
H	96.5 (143.2)	92.7 (122.5)	70.1 (121.3)	60.0 (102.9)
I	50.0 (74.2)	51.0 (67.4)	35.5 (61.4)	36.3 (62.3)
L.lig.				
H.lig.				
L.a.b.				
L.p.b.				
HMS				
Hi	72.6 (107.7)	70.0 (92.5)	57.9 (100.2)	51.8 (88.9)
AL	37.1 (55.0)	42.7 (56.4)	26.0 (45.0)	
θ	95	107	107	102
∝	22	22	23	

	LU 52692 LV	LU 68775 LV	LU 68776 LV	LU 68777 LV
L	43.6	47.0	58.8	43.5
H	56.0 (128.4)	56.2 (119.6)	60.5 (102.9)	51.2 (117.7)
I	33.7 (77.3)	31.8 (67.7)	32.0 (54.4)	28.6 (65.7)
L.lig.				
H.lig.				
L.a.b.				
L.p.b.				
HMS				
Hi	43.3 (99.3)	43.6 (92.8)	52.6 (89.5)	42.9 (98.6)
AL			30.3 (51.5)	23.1 (53.1)
θ	99	103	95	88
∝	38	21	21	25

Gryphaea lituola (cont.)

	LU 68778	LU 68779	LU 68780	LU 68781
	LV	LV	LV	LV
L	58.9	62.5	56.7	55.1
H	69.4 (117.8)	73.4 (117.4)	69.1 (121.9)	65.0 (118.0)
I	39.8 (67.6)	40.9 (65.4)	41.9 (73.9)	41.7 (75.7)
L.lig.				
H.lig.			15.0 (26.5)	14.1 (25.6)
L.a.b.				
L.p.b.				
HMS			30.9 (54.5)	32.0 (58.1)
Hi	57.2 (97.1)	59.5 (95.2)	51.0 (89.9)	48.0 (87.1)
AL	28.0 (47.5)	32.2 (51.5)	28.6 (50.4)	23.5 (42.6)
θ	104	118	107	99
∝	29	46	38	20

	LU 68782	LU 68782	LU 68783	LU 68783
	LV	RV	LV	RV
L	64.3	52.2	57.0	49.9
H	71.5 (111.2)	56.0 (107.3)	63.2 (110.9)	47.7 (95.6)
I	39.8 (61.9)		35.1 (61.6)	
L.lig.	9.8 (15.2)	8.5 (16.3)	5.9 (10.4)	
H.lig.	12.7 (19.8)	11.2 (21.5)	8.4 (14.7)	7.5 (15.0)
L.a.b.	4.2 (6.5)	4.4 (8.4)	4.4 (7.7)	
L.p.b.	4.2 (6.5)	4.3 (8.2)	4.9 (8.6)	
HMS	35.2 (54.7)	32.9 (63.0)	25.8 (45.3)	25.5 (51.1)
Hi	59.4 (92.4)	56.0 (107.3)	50.6 (88.8)	47.7 (95.6)
AL	30.1 (46.8)	24.8 (47.5)	27.8 (48.8)	23.1 (46.3)
θ	96	93	110	98
∝	21		28	

Gryphaea lituola (cont.)

Left valves

	N	$\bar{x}$	Max	Min	OR	s	s^2	V	$s_{\bar{x}}$
L	14	57.6 mm	75.7	43.5	32.2	8.82	77.79	15.31	2.36
H	14	116.3 %	128.4	102.9	25.5	10.17	103.4	8.75	2.72
I	14	66.3 %	77.3	54.4	22.9	6.53	42.64	9.85	1.74
L.lig.	2	12.8 %	15.2	10.4	4.8	3.39	11.49	26.49	2.40
H.lig.	4	21.7 %	26.5	14.7	11.8	5.50	30.25	25.35	2.75
L.a.b.	2	7.1 %	7.7	6.5	1.2	0.85	0.72	11.97	0.60
L.p.b.	2	7.6 %	8.6	6.5	2.1	1.48	2.19	19.47	1.05
HMS	4	53.2 %	58.1	45.3	12.8	5.49	30.14	10.32	2.74
Hi	14	93.3 %	100.2	87.1	13.1	5.74	32.95	6.15	1.54
AL	11	49.4 %	56.4	42.6	13.8	4.22	17.81	8.54	1.27
Θ	14	102.7 °	118	88	30	7.58	57.46	7.38	2.03
$\curlyvee$	14	27.7 °	46	20	26	8.34	69.56	30.10	2.31

Gryphaea lituola (cont.)

Right valves

	N	$\bar{x}$	Max	Min	OR	s	s^2	V	$\sigma_{\bar{x}}$
L	2	51.1 mm	52.2	49.9	2.3	1.63	2.66	3.19	1.15
H	2	101.5 %	107.3	95.6	11.7	8.27	68.39	8.15	5.85
L.lig.	1	16.3 %	16.3	16.3	0				
H.lig.	2	18.3 %	21.5	15.0	6.5	4.60	21.16	25.14	3.25
L.a.b.	1	8.4 %	8.4	8.4	0				
L.p.b.	1	8.2 %	8.2	8.2	0				
HmS	2	57.1 %	63.0	51.1	11.9	8.41	70.79	14.73	5.95
Hi	2	101.5 %	107.3	95.6	11.7	8.27	68.39	8.15	5.85
AL	2	46.9 %	47.5	46.3	1.2	0.85	0.72	1.81	0.60
Θ	2	95.5 °	98	93	5	3.54	12.53	3.71	2.50

Nanogyra nana (J. Sowerby)

spec. no.	L	H	I	AL	HMS	H.lig.	L.lig.
BM43340a(ST)	23.0	16.5 (71.7)	15.3 (66.5)				
43340b(ST)	13.1	23.3 (177.9)	9.4 (71.8)				
43340c	15.0	21.0 (140.0)	10.4 (69.3)				
43340d	17.6	22.2 (126.1)	10.6 (60.2)				
LU 68784 (RV)	11.2	18.7 (167.9)	2.5 (22.3)	11.2 (100.0)	11.9 (106.3)	1.3 (1.0)	0.9 (0.8)
N	5	5	5	1	1	1	1
$\bar{x}$	16.0 mm	136.7 %	58.0 %	100.0 %	106.3 %	1.0 %	0.8 %
Max	23.0	177.9	71.8	100.0	106.3	1.0	0.8
Min	11.2	71.7	22.3	100.0	106.3	1.0	0.8
OR	11.8	106.2	49.5	0	0	0	0
s	4.58	41.89	20.43				
s^2	20.98	17.55	417.4				
V	28.63	30.64	35.22				
$\sigma \bar{x}$	2.05	18.73	9.14				

Myophorella irregularis (Seebach)

spec. no.	L	H	I	AL	LE	LA	EW	TR
GSM GSa 3640	75.5	53.5 (70.9)	35.5 (47.0)	15.0 (19.9)	43.0 (57.0)	69.0 (91.4)	16.0 (21.2)	16
3628	74.0	54.0 (73.0)	29.0 (39.2)	16.0 (21.6)	40.0 (54.1)	68.0 (91.9)	13.0 (17.6)	15
3629	64.0	46.0 (71.9)	28.0 (43.8)	17.0 (26.6)	34.0 (53.1)	54.0 (84.4)	13.0 (20.3)	12
3630	73.0	53.0 (72.6)	34.0 (46.6)	17.0 (23.3)	42.0 (57.5)	62.0 (84.9)	15.0 (20.5)	15
GSM T33-1	69.0	46.0 (66.7)	27.0 (39.1)	12.0 (17.4)	35.0 (50.7)	58.0 (84.1)	14.0 (20.3)	13
T33-2	67.5	48.5 (71.9)	27.5 (40.7)	13.5 (20.0)	40.0 (59.3)	59.5 (88.1)	14.0 (20.7)	13
T33-3	51.0	33.0 (64.7)	21.0 (41.2)	12.5 (24.5)	24.5 (48.0)	42.0 (82.4)	9.0 (17.6)	10
T33-4	52.5	39.0 (74.3)	22.0 (41.9)	12.0 (22.9)	29.5 (56.2)	43.0 (81.9)	13.0 (24.8)	11
GSM 25/36-1	71.0	47.0 (66.2)	30.0 (42.3)	16.0 (22.5)	38.5 (54.2)	59.0 (83.1)	15.0 (21.1)	13
25/36-2	75.0	48.5 (64.7)	29.5 (39.3)	17.0 (22.7)	41.0 (54.7)	65.0 (86.7)	13.0 (17.3)	15
25/36-3	73.5	52.5 (71.4)	28.5 (38.8)	18.0 (24.5)	39.0 (53.1)	63.0 (85.7)	13.0 (17.7)	14
25/36-4	73.5	50.0 (68.0)	29.5 (40.1)	18.0 (24.5)	39.0 (53.1)	61.5 (83.7)	15.0 (20.4)	13
GSM 43051	77.0	52.0 (67.5)	33.0 (42.9)	18.0 (23.4)	41.0 (53.2)	67.0 (87.0)	15.0 (19.5)	13
43053	68.0	46.0 (67.6)	31.0 (45.6)	17.0 (25.0)	39.0 (57.4)	58.0 (85.3)	15.5 (22.8)	14
51647	65.0	46.0 (70.8)	30.0 (46.2)	17.0 (26.2)	34.0 (52.3)	53.0 (81.5)	14.5 (22.3)	13
GSM 25/37	88.0	60.0 (68.2)	34.0 (38.6)	24.0 (27.3)	49.0 (55.7)	74.5 (84.7)	16.5 (18.8)	14
GSM Y2014	61.0	44.0 (72.1)	21.0 (34.4)				14.0 (23.0)	12
Y2079	28.0	20.0 (71.4)	11.5 (41.1)	8.0 (28.6)	13.0 (46.4)	23.0 (82.1)	6.0 (21.4)	9
Y2078	35.0	25.5 (72.9)	12.5 (35.7)	10.0 (28.6)	17.0 (48.6)	29.5 (84.3)	8.0 (22.9)	10
Y2027	29.5	23.0 (78.0)	15.5 (52.5)	10.0 (33.9)		24.0 (81.4)	7.5 (25.4)	
Y2080	26.5	20.2 (76.2)	12.0 (45.3)	6.8 (25.7)	15.1 (57.0)	22.1 (83.4)	4.7 (17.7)	9

Myophorella irregularis (cont.)

spec. no.	L	H	I	AL	LE	LA	EW	TR
SM J47645	35.3	27.8 (78.8)	17.2 (48.7)	7.4 (21.0)	21.7 (61.5)	32.1 (90.9)	6.3 (17.8)	11
LU 18075	73.0	53.0 (72.6)	30.0 (41.1)	17.0 (23.3)	42.5 (58.2)	61.0 (83.6)	13.0 (17.8)	13
YM KD1974/37	77.0	51.0 (66.2)	26.0 (33.8)	15.0 (19.5)	45.0 (58.4)	69.5 (90.3)	13.0 (16.9)	14
1974/38	66.0	47.0 (71.2)	24.0 (36.4)	15.0 (22.7)	37.0 (56.1)	57.0 (86.4)	11.0 (16.7)	14
1974/39	54.0	36.0 (66.7)	21.0 (38.9)	9.5 (17.6)	31.0 (57.4)	48.0 (88.9)	11.0 (20.4)	14
1974/40	74.0	54.0 (73.0)	31.0 (41.9)	18.0 (24.3)	41.0 (55.4)	65.5 (88.5)	13.0 (17.6)	16
1974/41	70.0	48.0 (68.6)	26.0 (37.1)	14.0 (20.0)	37.0 (52.9)	61.0 (87.1)	10.5 (15.0)	13
LU 68785	35.5	28.0 (78.9)	18.0 (50.7)	7.0 (19.7)	21.0 (59.2)	34.0 (95.8)	9.0 (25.4)	11
LU 54481	51.0	39.0 (76.5)	23.0 (45.1)	14.5 (28.4)	31.0 (60.8)	42.0 (82.4)	12.0 (23.5)	13
N	30	30	30	29	28	29	30	29
$\bar{x}$	61.1 mm	71.7 %	41.5 %	23.6 %	55.1 %	85.9 %	20.1 %	12.9 ribs
Max	88.0	78.9	52.5	33.9	61.5	95.8	25.4	16
Min	26.5	64.7	33.8	17.4	46.4	81.4	15.0	9
OR	61.5	14.2	18.7	16.5	15.1	14.4	10.4	7
s	17.17	4.02	5.36	3.68	3.71	3.60	2.76	1.88
s^2	294.87	16.17	28.77	13.51	13.80	12.94	7.63	3.55
V	28.10	5.65	12.91	15.55	6.75	4.19	13.71	14.65
$\sigma \bar{x}$	3.13	0.73	0.98	0.68	0.70	0.67	0.50	0.35

Myophorella caytonensis nom. nov.

spec. no.	L	H	I	AL	LE	LA	EW	TR
GSM 11436	86.0	72.0 (83.7)	33.0 (38.4)	16.5 (19.2)	55.0 (64.0)	80.0 (93.0)	16.0 (18.6)	17
11437	88.0	64.0 (72.7)	33.0 (37.5)	31.0 (35.2)	47.0 (53.4)	72.0 (81.8)	8.0 (9.1)	16
11438	51.0	39.0 (76.5)	22.0 (43.1)	17.0 (33.3)	26.0 (51.0)	41.0 (80.4)	8.5 (16.7)	13
11439	65.0	45.5 (70.0)	30.0 (46.2)	18.0 (27.7)	35.5 (54.6)	55.5 (85.4)	11.0 (16.9)	15
GSM T57	59.0	51.0 (86.4)	23.0 (45.2)	23.0 (45.2)	34.0 (57.6)	51.0 (86.4)	12.0 (20.3)	12
GSM 24/39	63.0	52.0 (82.5)	23.0 (36.5)	24.0 (38.1)	33.0 (52.4)	53.0 (84.1)	9.0 (14.3)	13
GSM 54622	72.0	57.0 (79.2)	32.0 (44.4)	22.0 (30.6)	37.0 (51.4)	57.0 (79.2)		17
42869	67.0	54.0 (80.6)	35.0 (52.2)	19.0 (28.4)		57.0 (85.1)		14
GSM Y2165	71.0	56.0 (78.9)	34.5 (48.6)	19.0 (26.8)	43.0 (60.6)	64.0 (90.1)	15.0 (21.1)	16
Y2166	52.0	43.0 (82.7)	27.0 (51.9)	14.0 (26.9)				12
GSM T55-1	79.0	61.5 (77.8)	33.0 (41.8)	32.0 (40.5)	48.0 (60.8)	65.0 (82.3)	15.0 (19.0)	14
T55-2	33.5	27.0 (80.6)	19.0 (56.7)	10.0 (29.9)	19.5 (58.2)	30.5 (91.0)	7.0 (20.9)	11
T55-3	29.5	24.5 (83.1)	13.0 (44.1)	13.0 (44.1)	18.5 (75.5)	27.5 (93.2)		10
T55-4	79.0	61.5 (77.8)	34.0 (43.0)	25.0 (31.6)	44.0 (55.7)	71.0 (89.9)	18.0 (22.8)	
T55-5	30.0	25.0 (83.3)	20.0 (66.7)	10.0 (33.3)	18.5 (74.0)	29.0 (96.7)	7.0 (23.3)	10
SM J11377	67.1	57.3 (85.4)	31.6 (47.1)	18.9 (28.2)	41.5 (61.8)	61.3 (91.4)	11.9 (17.7)	13
J12391	83.1	60.7 (73.0)	37.4 (45.0)	16.2 (19.5)	50.0 (60.2)	71.2 (85.7)	15.7 (18.9)	16
J12392	85.1	67.1 (78.8)		20.1 (23.6)	47.1 (55.3)	73.2 (86.0)	15.0 (17.6)	17

Myophorella caytonensis nom. nov. (cont.)

N	18	18	17	18	16	17	14	17
$\bar{x}$	64.5 mm	79.6 %	46.4 %	31.2 %	59.2 %	87.2 %	18.4 %	13.9
Max	88.0	86.4	66.7	45.2	75.5	96.7	23.3	17
Min	29.5	70.0	36.5	19.2	51.0	79.2	9.1	10
OR	58.5	16.4	30.2	26.0	24.5	17.5	14.2	7
s	18.89	4.49	7.44	7.39	7.21	4.95	3.62	2.39
s^2	356.72	20.20	55.31	54.65	52.01	24.54	13.13	5.74
V	29.30	5.65	16.04	23.67	12.19	5.68	19.73	17.25
$\sigma_{\bar{x}}$	4.45	1.06	1.80	1.74	1.80	1.20	0.97	0.58

Discomiltha lirata (Phillips)

spec. no.	L	H	I	AL
BM LL10077 (NT)	38.6	35.9 (93.0)		
SM J12469	27.0	24.5 (90.7)		15.7 (58.1)
J12470	38.9	38.2 (98.2)		20.6 (53.0)
J12471	42.6	40.6 (95.3)	15.0 (35.2)	19.8 (46.5)
J12472	38.7	37.3 (96.4)	17.4 (45.0)	21.5 (55.6)
J12486	47.0	41.1 (87.4)		25.4 (54.0)
YM Tsp. 169	32.5	31.1 (95.7)	13.7 (42.2)	
170	37.4	34.3 (91.7)	14.5 (38.8)	
YM KD1974/42	37.2	36.6 (98.4)	16.9 (45.4)	
1974/43	40.0	35.3 (88.3)	14.8 (37.0)	
1974/44	26.3	25.7 (97.7)		
1974/45	23.9	21.0 (87.9)		
1974/46	33.3	31.4 (94.3)	11.7 (35.1)	
1974/47	43.1	37.8 (87.7)		
LU 68786	29.5	25.7 (87.1)		13.8 (46.8)
68787	21.6	17.3 (80.1)		10.0 (46.3)
68788	30.1	26.9 (89.4)		15.9 (52.8)
68789	33.9	27.3 (80.5)		16.6 (49.0)

N	18	18	7	9
$\bar{x}$	34.2 mm	90.9 %	39.8 %	51.3 %
Max	47.0	98.4	45.4	58.1
Min	21.6	80.1	35.1	46.3
OR	25.4	18.3	10.3	11.8
s	7.00	5.54	4.40	4.34
s^2	49.03	30.64	19.37	18.84
V	20.48	6.09	11.06	8.45
$\sigma \bar{x}$	1.65	1.30	1.66	1.45

Neocrassina ungulata (Lycett)

spec. no.	L	H	I	AL
YM 873	19.7	17.9 (90.9)		
YM KD1974/48	21.2	20.3 (95.8)		
SM J26767	17.4	14.9 (85.6)		6.1 (35.1)
J26768	17.8	17.8 (100.0)		5.7 (32.0)
J26766	19.0	17.3 (91.1)		6.9 (36.3)
BCM 3324a	14.4	13.5 (93.8)	6.4 (44.4)	5.4 (40.0)
3324b	14.0	13.2 (94.3)	4.6 (32.9)	5.7 (40.7)
3324c	14.0	13.1 (93.6)		4.9 (35.0)
GSM 113011	15.6	15.3 (98.1)		6.6 (42.3)
113012	13.8	15.2 (110.1)	6.0 (43.5)	5.8 (42.0)

N	10	10	3	8
$\overline{x}$	16.7 mm	95.3 %	40.3 %	37.9 %
Max	21.2	110.1	44.4	42.3
Min	13.8	85.6	32.9	32.0
OR	7.4	25.5	11.5	10.3
s	2.70	6.55	6.40	3.82
s^2	7.30	42.94	40.90	14.58
V	16.19	6.87	15.88	10.07
$\sigma_{\overline{x}}$	0.85	2.07	3.69	1.35

Neocrassina calvertensis sp. nov.

spec. no.	L	H	I	AL
BM LL27730	14.2	12.8 (90.1)	5.3 (37.3)	3.8 (26.8)
27731	18.4	16.5 (89.7)	4.8 (26.1)	7.4 (40.2)
27732	14.7	13.2 (89.8)	4.3 (29.3)	6.4 (43.5)
27733	15.4	13.6 (88.3)		4.3 (27.9)
27734	13.8	12.4 (89.9)		5.8 (42.0)
LU 68790	20.7	18.7 (90.3)	4.0 (19.3)	7.3 (35.3)
68791	19.5	18.9 (90.9)		

N	7	7	4	6
$\overline{x}$	16.7 mm	90.7 %	28.0 %	36.0 %
Max	20.7	96.9	37.3	43.5
Min	13.8	88.3	19.3	26.8
OR	6.9	8.6	18.0	16.7
s	2.80	2.80	7.47	7.22
s^2	7.85	7.86	55.83	52.12
V	16.80	3.09	26.68	20.08
$\sigma \overline{x}$	1.06	1.06	3.73	2.95

Trautscholdia carinata (Phillips)

spec. no.	L	H	I	AL	Ribs
YM 876 (HT)	9.1	8.7 (95.6)		3.9 (42.9)	12
YM KD1974/49	8.2	7.9 (96.3)	7.2 (87.8)		12
1974/50	6.6	6.1 (92.4)		2.9 (43.9)	8
1974/51	8.4	7.4 (88.1)		3.2 (38.1)	10
OUM J29089	7.7	7.2 (93.5)			11

N	5	5	1	3	5
$\bar{x}$	8.0 mm	93.2 %	87.8 %	41.6 %	10.6 ribs
Max	9.1	96.3	87.8	43.9	12
Min	6.6	88.1	87.8	38.1	8
OR	2.5	8.2	0	5.8	4
s	0.93	3.24		3.10	1.67
s^2	0.86	10.50		9.61	2.79
V	11.63	3.48		7.45	15.75
$\sigma \bar{x}$	0.42	1.45		1.79	0.75

Trautscholdia phillis (Cottreau)

spec. no.	L	H	I	AL	Ribs
LU 68792	9.2	8.5 (92.4)	6.6 (71.7)		18
68793	6.2	6.0 (96.8)	5.2 (83.9)		15
68794	8.4	8.1 (96.4)	6.7 (79.8)		17
68795	8.3	7.7 (92.8)	6.8 (81.9)		16
68796	8.0	7.7 (96.3)	6.3 (78.8)		17
68797	7.3	6.2 (84.9)	5.2 (71.2)		14
68798	8.5	7.6 (89.4)	7.2 (84.7)		17
68799	8.0	7.0 (87.5)	6.0 (75.0)		15
68800	8.6	7.3 (84.9)	7.2 (83.7)		14
68801	7.6	6.3 (82.9)	4.9 (64.5)		16
68802	7.8	6.5 (83.3)	6.2 (79.5)		13
68803	8.1	7.1 (87.7)	6.3 (77.8)		15
69800	7.8	6.6 (84.6)	6.4 (82.1)		16
69801	9.1	7.4 (81.3)	6.4 (70.3)		16
69802	9.0	7.4 (82.2)	7.2 (80.0)		13
69803	9.2	7.0 (76.1)	6.4 (69.6)		15
69804	8.5	6.9 (81.2)			14
69805	8.9	7.4 (83.1)	7.0 (78.7)		14
69806	9.0	7.2 (80.0)	6.8 (75.6)		17
69807	8.7	7.1 (81.6)	6.1 (70.1)		16
69808	9.0	7.2 (80.0)			13
69809	9.9	7.1 (71.7)	7.4 (74.7)		14
69810	8.2	7.9 (96.3)	6.8 (82.9)		15
69811	8.5	6.9 (81.2)	6.5 (76.5)		13
69812	9.1	7.3 (80.2)	5.8 (63.7)		15
69813	8.1	7.1 (87.7)	7.0 (86.4)		16
69814	10.8	8.8 (81.5)	8.4 (77.8)		21
69815	9.9	8.3 (83.8)	8.4 (84.8)		16
69816	8.4	8.0 (95.2)	7.4 (88.1)		17
69817	9.9	8.3 (83.8)	7.0 (70.7)		15
69818	10.2	8.1 (79.4)			16
69819	9.2	8.3 (90.2)	6.5 (70.7)		
69820	10.6	8.6 (81.1)			

Trautscholdia phillis (cont.)

spec. no.	L	H	I	AL	Ribs
LU 69821	11.2	9.2 (82.1)			17
69822	10.2	9.1 (89.2)			18
69823	9.7	8.1 (83.5)	6.3 (64.9)		14
69824	8.9	7.9 (88.8)	7.3 (82.0)		
69825	7.6	6.2 (81.6)	6.2 (81.6)		
69826	9.3	6.5 (69.9)	6.4 (68.8)		
69827	7.2	6.0 (83.3)	6.0 (83.3)		
69828	10.0	7.8 (78.0)	6.3 (63.0)		
69829	8.4	6.8 (81.0)	4.1 (48.8)		
GSM 31506	6.3	5.7 (90.5)	5.2 (82.5)		10
31507	7.6	6.5 (85.5)	6.0 (78.9)		11
GSMZn2544	7.1	6.3 (88.7)	6.4 (90.1)		14
Y2070	6.8	5.8 (85.3)	5.0 (73.5)		11
Y2069	7.2	5.9 (81.9)	5.8 (80.6)		
Y2068	8.8	7.2 (81.8)	6.4 (72.7)		14
Y2066	8.3	7.0 (84.3)	7.8 (93.9)		12
Y2067	8.7	7.1 (81.6)	7.0 (80.4)		12
31513	10.4	8.8 (84.6)	8.4 (80.8)		18
31511a	9.2	8.0 (87.0)			15
31511b	8.6	7.9 (91.9)			
31515a	4.8	4.2 (87.5)	3.6 (75.0)		17
31515b	5.2	5.0 (96.2)			19
31514	4.8	5.1 (106.3)	3.2 (66.7)		17
113419	6.7	5.7 (85.1)	5.2 (77.6)		11
113420	6.9	6.1 (88.4)	5.8 (84.0)		11
113421	10.6	9.4 (88.7)	8.8 (83.0)		17
113422	8.3	6.6 (79.5)	6.2 (74.7)		13
113423	8.0	6.8 (85.0)	5.6 (70.0)		12
113424	7.4	6.0 (81.1)	5.6 (75.7)		12
113425	7.4	6.1 (82.4)	6.4 (86.5)		12
113426	7.7	6.3 (81.8)	6.2 (80.5)		12
113427	9.0	7.3 (81.1)	6.6 (73.3)		13
Y2051	8.8	8.0 (90.9)	7.0 (79.5)	3.8 (43.2)	11

Trautscholdia phillis (cont.)

spec. no.	L	H	I	AL	Ribs
43054	11.1	9.8 (88.3)		4.2 (37.8)	13
43056	6.1	5.4 (88.5)			8
31516	11.7	9.6 (82.1)	8.5 (72.6)	4.8 (41.0)	
31517	12.4	10.3 (83.1)	9.6 (77.4)	4.8 (38.7)	
31518	10.9	9.3 (85.3)	7.3 (67.0)		
31519	10.5	8.7 (82.9)	8.2 (78.1)	3.8 (36.2)	
31520	10.6	7.2 (67.9)	6.0 (56.6)	3.9 (36.8)	
31521	6.3	5.4 (85.7)	4.8 (76.2)	2.2 (34.9)	
SM J28877	7.1	6.4 (90.1)	4.2 (59.2)		11
BCM 3324a	10.4	8.9 (85.6)	7.9 (76.0)	3.0 (28.8)	16
3324b	10.1	9.0 (89.1)	7.8 (77.2)	2.9 (28.7)	17
3324c	9.2	8.4 (91.3)	7.9 (85.9)	2.9 (31.5)	16
3324d	10.4	9.6 (92.3)	9.3 (89.4)	2.8 (26.9)	21
3324e	9.4	8.4 (89.4)	7.7 (81.9)	2.8 (29.8)	16
3324f	10.0	7.2 (72.0)	8.4 (84.0)	3.1 (31.0)	18
3324g	8.8	7.7 (87.5)	7.8 (88.6)	3.0 (34.1)	13
3324h	9.6	8.6 (89.6)	9.6 (100.0)	3.0 (31.7)	15
Morris pl. 30 fig.2	11.8	10.6 (89.8)	9.3 (78.8)		17

		L	H	I	AL	Ribs
	N	84	84	73	15	68
	$\bar{x}$	8.7 mm	85.4 %	77.2 %	34.1 %	14.8 ribs
	Max	12.4	96.2	100.0	43.2	21
	Min	4.8	69.9	56.6	26.9	10
	s	1.54	6.18	8.52	4.84	2.56
	s^2	2.38	38.21	72.54	23.38	6.55
	V	17.72	7.24	11.03	14.19	17.35
	$\sigma \bar{x}$	0.17	0.67	1.00	1.25	0.31

Protocardia striatulum (J. de C. Sowerby)

spec. no.	L	H	I	AL
BM 43154 (HT)	22.3	21.1 (94.6)	13.9 (62.3)	
SM J12509	10.5	9.4 (89.5)	7.4 (70.5)	4.0 (38.1)
J12510	7.6	7.0 (92.1)	5.5 (72.4)	3.4 (44.7)
J6010	10.6	9.8 (92.5)	8.0 (75.5)	4.6 (43.4)
YM KD1974/52	14.0	13.3 (95.0)	10.1 (72.1)	6.5 (46.4)
1974/53	14.4	12.0 (83.3)	9.8 (68.1)	
OUM J9719	14.5	14.1 (97.2)	9.6 (66.2)	6.4 (44.1)
OUM J28233	7.3	7.4 (101.4)	4.5 (61.6)	4.0 (54.8)
J28234	8.8	8.1 (92.0)	6.2 (70.5)	4.0 (45.5)
J28235	8.6	7.9 (91.9)	6.1 (70.9)	4.5 (52.3)
J28240	15.6	12.7 (81.4)	9.2 (59.0)	6.7 (42.9)
LU 69830	13.1	12.1 (92.4)	11.2 (85.5)	6.0 (45.8)
LU 69831	14.9	13.3 (89.3)	11.8 (79.2)	6.0 (40.3)
LU 69832	20.0	18.3 (91.5)		8.6 (43.0)
LU 69833	24.1	22.6 (93.7)		12.4 (51.5)

N	15	15	13	14
$\bar{x}$	13.1 mm	91.9 %	70.4 %	44.7 %
Max	24.1	101.4	85.5	54.8
Min	7.3	81.4	59.0	32.8
OR	16.8	20.0	26.5	22.0
s	5.19	4.90	7.24	4.77
s^2	26.94	24.01	52.42	22.75
V	39.62	5.33	10.28	10.67
$\sigma \bar{x}$	1.34	1.26	2.01	1.32

Rollierella minima (J. Sowerby)

spec. no.	L	H	I	AL	LW
BM 43164(HT)	31.1	31.0 (99.7)	27.6 (88.8)		
GSM 42906	22.8	21.3 (93.4)	20.3 (89.0)	5.8 (25.4)	
42907	21.0	18.2 (86.7)	19.0 (90.5)	5.6 (26.7)	
42908	23.0	20.5 (89.1)	20.5 (89.1)	6.6 (28.7)	
42909	19.5	16.7 (85.6)	17.5 (89.7)	5.9 (30.3)	
42910	21.7	18.3 (84.3)	17.4 (80.2)	6.1 (28.1)	
42911	18.6	16.9 (90.9)	15.9 (85.5)	5.6 (30.1)	
42912	16.4	15.7 (95.7)	14.1 (86.0)	4.7 (28.7)	
42913	14.8	13.6 (91.9)	12.4 (83.8)	4.9 (33.1)	
42914	12.6	11.0 (87.3)	10.7 (84.9)	4.3 (34.1)	
42915	10.4	9.6 (92.3)	8.6 (82.7)	4.4 (42.3)	
42916	20.6	19.8 (96.1)	19.2 (93.2)	8.2 (39.8)	
42918	16.0	15.8 (98.8)	14.2 (88.8)	5.6 (35.5)	
42919	18.5	16.7 (90.3)	15.2 (82.2)	5.7 (30.8)	
42921	15.9	14.7 (92.5)	14.0 (88.1)	5.5 (34.6)	
42922	13.8	11.7 (84.8)	12.2 (88.4)	5.8 (42.0)	
42923	10.6	9.7 (91.5)	8.1 (76.4)	2.7 (25.5)	
42924	10.8	9.6 (88.9)	9.3 (86.1)		
42925	7.0	6.4 (91.4)	5.6 (80.0)	2.3 (32.9)	
KD Lukow 5	21.7	21.3 (98.2)	19.9 (91.7)	5.6 (25.8)	12.4 (57.1)
Lukow 6	20.7	20.2 (97.6)	19.2 (92.8)	5.0 (24.2)	12.4 (59.9)
Lukow 7	15.0	14.6 (97.3)	12.8 (85.3)	3.8 (25.3)	6.9 (46.0)
Lukow 8	24.0	23.2 (96.7)	22.7 (94.6)	5.9 (24.6)	14.0 (58.3)
SM J12461	21.2	20.7 (97.6)	20.5 (96.7)	6.6 (31.1)	
YM KD1974/54	27.5	27.3 (99.3)	13.3 (96.8)	10.8 (39.3)	
1974/55	27.0	26.7 (98.9)	11.8 (97.4)	9.8 (36.3)	
LU 70001	15.5	15.4 (99.4)	15.3 (98.7)	4.5 (29.0)	
LU 70002	15.8	14.7 (93.0)		5.2 (32.9)	
BCM Cb 4767	16.2	15.6 (96.3)	14.9 (92.0)	5.6 (34.6)	
4768	16.0	14.7 (91.9)	13.9 (86.9)	4.5 (28.1)	
4769	16.8	15.3 (91.1)	15.0 (89.3)	4.8 (28.6)	
4770	16.2	14.7 (90.7)	13.6 (84.0)	4.4 (27.2)	

Rollierella minima (cont.)

spec. no.	L	H	I	AL	LW
BCM Cb 4771	16.2	15.1 (93.2)	14.2 (87.7)	4.5 (27.8)	
4772	14.1	13.9 (95.7)	12.5 (88.7)	4.4 (31.2)	

N	34	34	33	32	4
$\bar{x}$	17.9 mm	93.2 %	88.4 %	31.1 %	55.3 %
Max	31.1	99.7	98.7	42.3	59.9
Min	7.0	84.3	76.4	24.2	46.0
OR	24.1	15.4	22.3	18.1	13.9
s	5.20	4.47	5.23	5.02	6.32
s^2	27.04	19.98	27.35	25.20	39.94
V	29.05	4.80	5.92	16.14	11.43
$\sigma\,\bar{x}$	0.89	0.77	0.91	0.89	3.16

Anisocardia tenera (J. Sowerby)

spec. no.	L	H	I	AL	PLW
BM 43165(HT)	23.2	20.6 (88.8)	17.0 (73.3)	6.8 (28.0)	
GSM 24/53-1	19.9	16.7 (83.9)	13.0 (65.3)	6.9 (34.7)	
24/53-2	21.7	20.5 (94.5)	14.2 (65.4)	6.6 (30.4)	7.2 (22.7)
24/53-3	18.3	16.7 (91.3)	11.3 (61.7)	5.0 (27.3)	
24/53-4	17.6	17.3 (98.3)	12.4 (70.5)	5.8 (33.0)	
24/53-5	12.7	11.7 (92.1)	8.7 (68.5)	4.6 (36.2)	
25/45-1	25.2	22.4 (88.9)	14.9 (59.1)	7.6 (30.2)	
25/45-2	21.6	18.2 (84.3)	12.5 (57.9)	7.3 (33.8)	
25/45-3	21.9	20.2 (92.2)	12.7 (58.0)	7.8 (35.6)	
25/45-4	16.6	15.5 (93.4)	10.5 (63.3)	6.2 (37.3)	
25/45-5	18.2	15.1 (83.0)	10.2 (56.0)	7.1 (39.0)	
Y2071	22.8	21.6 (94.7)	12.0 (52.6)	6.6 (28.9)	
Y2072	23.1	21.3 (92.2)	12.5 (54.1)	9.0 (39.0)	
Y2073	22.5	19.0 (84.4)	12.2 (54.2)	8.2 (36.4)	

N	14	14	14	14	1
$\bar{x}$	20.5 mm	89.9 %	60.3 %	33.6 %	22.7 %
Max	25.2	98.3	73.3	39.0	22.7
Min	12.7	83.0	52.6	27.3	22.7
OR	12.5	15.3	20.7	11.7	0
s	3.34	4.88	5.59	3.99	
s^2	11.16	23.78	31.27	15.93	
V	16.29	5.42	9.27	11.90	
$\sigma \frac{}{x}$	0.89	1.30	1.49	1.07	

Isocyprina roederi Arkell

spec. no.	L	H	I
LU 70003	13.5	13.0 (96.2)	
70004	18.0	16.5 (91.6)	7.6 (42.2)
69834	18.0	16.0 (88.8)	
69835	14.0	12.0 (85.7)	
69836	16.5	15.2 (92.1)	
69837	16.0	14.6 (91.2)	
69838	6.5	6.0 (92.3)	
69839	15.2	14.3 (94.1)	5.0 (32.9)
69840	17.5	15.0 (85.7)	5.2 (30.9)
69841	19.2	18.5 (96.3)	
69842	15.5	13.2 (85.1)	
69843	14.4	13.0 (89.6)	
69844	12.0	10.0 (83.3)	
69845	20.0	18.0 (90.0)	
69846		20.5	9.0

N	14	14	3
$\bar{x}$	15.5 mm	90.1 %	35.3 %
Max	20.0	96.3	42.2
Min	6.5	83.3	30.9
OR	13.5	13.3	11.3
s	3.42	4.07	6.03
s^2	11.70	16.60	36.37
V	22.06	4.53	17.08
$\sigma \bar{x}$	0.92	1.09	3.48

Isocyprina roederi Arkell

Corbulomima macneillii (Morris)

spec. no.	L	H	I	AL
LU 69847	5.4	4.9 (90.7)	4.3 (79.6)	2.1 (38.9)
69848	5.0	4.6 (92.0)	3.8 (76.0)	2.0 (40.0)
69849	5.3	4.3 (81.1)	4.1 (77.4)	2.4 (45.3)
69850	5.3	4.9 (92.5)	4.0 (75.5)	2.0 (37.7)
69851	5.6	4.8 (85.7)	4.0 (71.4)	2.7 (48.2)
OUM J28230-1	5.6	5.0 (89.3)	4.5 (80.4)	2.2 (39.3)
J28230-2	5.8	5.0 (86.2)	4.3 (74.1)	2.1 (36.2)
J28230-3	5.3	4.5 (84.9)	3.9 (73.6)	2.2 (41.5)
J28230-4	4.5	4.0 (88.9)	3.2 (71.1)	1.8 (40.0)
J28230-5	5.6	4.8 (85.7)	4.4 (78.6)	1.8 (32.1)
J28230-6	5.8	5.4 (93.1)	4.8 (82.8)	2.1 (36.2)
J28230-7	6.5	5.5 (84.6)	4.2 (64.6)	2.1 (32.3)
J28230-8	5.5	4.8 (87.3)	4.0 (72.7)	2.0 (36.4)
J28230-9	5.2	4.4 (84.6)	3.8 (73.1)	1.7 (32.7)
J28230-10	5.4	5.0 (92.6)	4.0 (74.1)	1.8 (33.3)
J28230-11	5.8	4.9 (84.5)	4.1 (70.7)	2.0 (34.5)
J28230-12	5.2	4.6 (88.5)	4.2 (80.8)	2.0 (38.5)
J28230-13	4.5	3.9 (86.7)	3.0 (66.7)	1.8 (40.0)
J28230-14	4.3	3.7 (86.0)	3.2 (74.4)	1.6 (37.2)
J28230-15	3.7	3.6 (97.3)	2.8 (75.7)	1.5 (40.5)
J28230-16	6.3	5.6 (88.9)	5.0 (79.4)	2.2 (34.9)
OUM J28231-1	5.0	4.4 (88.0)	3.4 (78.0)	1.8 (36.0)
J28231-2	5.0	4.3 (86.0)	3.6 (72.0)	1.8 (36.0)
J28231-3	5.4	4.7 (87.0)	3.7 (68.5)	2.1 (38.9)
J28231-4	4.6	4.0 (87.0)	3.0 (65.0)	1.9 (41.3)
J28231-5	5.5	4.5 (81.8)	3.5 (63.6)	2.0 (36.4)
J28231-6	5.4	4.2 (77.8)	3.2 (59.3)	2.0 (37.0)
J28231-7	5.4	4.8 (88.9)	3.8 (70.4)	2.3 (42.6)
J28231-8	4.8	4.5 (93.8)	3.6 (75.0)	1.9 (39.6)
J28231-9	4.4	3.7 (84.1)	3.2 (72.7)	1.4 (31.8)
J28231-10	5.0	4.1 (82.0)	3.2 (64.0)	1.8 (36.0)
J28231-11	4.7	4.0 (85.1)	3.2 (68.1)	1.9 (40.4)
J28231-12	5.4	4.9 (90.7)	3.9 (72.2)	2.0 (37.0)

Corbulomima macneillii

spec. no.	L	H	I	AL
OUM J28231-13	4.6	3.5 (76.1)	2.9 (63.0)	1.4 (30.4)
J28231-14	4.2	3.3 (78.6)	2.8 (66.7)	1.4 (33.3)
J28231-15	4.4	4.3 (97.7)	3.1 (70.5)	1.3 (29.5)
J28231-16	4.9	4.5 (91.8)	3.2 (65.3)	1.6 (32.7)
J28231-17	4.5	4.2 (93.3)	3.0 (66.7)	1.5 (33.3)
J28231-18	4.5	3.7 (82.2)	2.8 (62.2)	1.5 (33.3)
J28231-19	4.3	3.3 (76.7)	2.8 (65.1)	1.5 (34.9)
J28231-20	4.8	4.1 (85.4)	3.0 (62.5)	1.8 (37.5)
J28231-21	4.8	4.2 (87.5)	3.1 (64.6)	1.7 (35.4)
J28231-22	4.3	3.8 (88.4)	2.8 (65.1)	1.6 (37.2)
J28231-23	3.8	3.1 (81.6)	2.6 (68.4)	1.7 (44.7)
GSM 113966	5.4	4.6 (85.2)	3.7 (68.5)	2.1 (38.9)
113967	4.3	3.4 (79.1)	3.0 (69.8)	1.8 (41.9)
113968	4.3	3.7 (86.0)	3.1 (72.1)	1.5 (34.9)
113969	4.2	3.3 (78.6)	3.0 (71.4)	1.5 (35.7)
113970	5.1	4.4 (86.3)	3.8 (74.5)	1.9 (37.3)
113971	4.0	3.3 (82.5)	2.9 (72.5)	1.4 (35.0)
113972	5.5	4.6 (83.6)	4.3 (78.2)	2.3 (41.8)
113973	5.5	4.7 (85.5)	3.6 (65.5)	1.9 (34.5)
113974	4.6	3.3 (71.7)	2.6 (56.5)	1.6 (34.8)
113975	5.8	4.7 (81.0)	4.1 (70.7)	1.9 (32.8)
113976	5.2	4.3 (82.7)	3.8 (73.1)	1.8 (41.9)
113977	4.6	4.0 (87.0)	3.4 (73.9)	1.4 (30.4)
113978	6.7	5.6 (83.6)	5.2 (77.6)	2.3 (34.3)
113979	4.2	3.4 (81.0)	2.9 (69.0)	1.5 (35.7)
113980	5.4	4.3 (79.6)	3.7 (68.5)	2.2 (40.7)
113981	5.3	4.5 (84.9)	4.0 (75.5)	2.1 (39.6)
113982	4.5	3.7 (82.2)	3.6 (80.0)	1.7 (37.8)
113983	5.5	4.6 (83.6)	3.6 (65.5)	1.9 (34.5)
113984	4.4	3.7 (84.1)	3.3 (75.0)	1.6 (36.4)
113985	4.2	3.1 (73.8)	2.8 (66.7)	1.6 (38.1)
113986	4.4	3.9 (88.6)	3.3 (75.0)	1.7 (38.6)
113988	4.1	3.2 (78.0)	3.0 (73.2)	1.5 (36.6)

Corbulomima macneillii

spec. no.	L	H	I	AL
GSM 113989	4.9	4.0 (81.6)	3.8 (77.6)	2.0 (40.8)
113991	4.6	3.8 (82.6)	3.4 (73.9)	1.7 (37.0)
113992	4.8	3.7 (77.1)	3.6 (75.0)	1.7 (35.4)
113993	5.2	4.9 (94.2)	4.2 (80.8)	1.8 (34.6)
113995	5.3	4.4 (83.0)	3.7 (69.8)	1.9 (35.8)
113996	5.6	4.7 (83.9)	4.1 (73.2)	2.0 (35.7)
113997	4.0	4.0 (100.0)	3.5 (87.5)	1.4 (35.0)
113998	5.5	4.8 (87.3)	4.2 (76.4)	2.0 (36.4)
113999 (NT)	5.0	4.3 (86.0)	4.2 (84.0)	2.0 (40.0)
114000	4.0	4.0 (100.0)	3.6 (90.0)	1.6 (40.0)
114001	4.8	4.0 (83.3)	3.4 (70.8)	1.8 (37.5)
114002	4.1	3.3 (80.5)	3.0 (73.2)	1.5 (36.6)
114004	4.3	3.4 (79.1)	3.1 (72.1)	1.4 (32.6)
114005	4.9	4.0 (81.6)	3.8 (77.6)	1.8 (36.7)
114006	4.8	4.0 (83.3)	3.6 (75.0)	1.9 (39.6)
114007	4.6	4.0 (87.0)	3.0 (65.2)	1.7 (37.0)
114008	4.0	3.2 (80.0)	3.0 (75.0)	1.5 (37.5)
114009	3.8	3.3 (86.8)	2.6 (68.4)	1.3 (34.2)
114010	4.1	3.3 (80.5)	3.3 (80.5)	1.6 (39.0)
114011	5.8	5.0 (86.2)	4.7 (81.0)	1.9 (32.8)
114012	4.0	3.6 (90.0)	3.2 (80.0)	1.6 (40.0)
114013	3.4	3.0 (88.2)	2.3 (67.6)	1.1 (32.4)
114014	5.7	4.3 (75.4)	4.0 (70.2)	2.4 (42.1)
114015	5.2	4.4 (84.6)	3.6 (69.2)	2.0 (38.5)
114016	5.8	4.6 (79.3)	3.7 (63.8)	2.0 (34.5)
114017	4.8	3.9 (81.3)	3.6 (75.0)	1.6 (33.3)
114018	4.9	4.0 (81.6)	4.0 (81.6)	1.9 (38.8)
114019	6.1	5.3 (86.9)	4.4 (72.1)	2.3 (37.7)
114021	5.5	4.2 (76.4)	3.9 (70.9)	2.1 (38.2)
114022	5.5	4.3 (78.2)	3.9 (70.9)	2.0 (36.4)
114023	5.4	4.5 (83.3)	3.8 (70.4)	1.8 (33.3)
114024	6.1	5.0 (82.0)	4.9 (80.3)	2.6 (42.6)
114025	5.5	5.1 (92.7)	3.4 (61.8)	2.0 (36.4)

Corbulomima macneillii

spec. no.	L	H	I	AL
GSM 114026	4.5	3.8 (84.4)	3.3 (73.3)	1.6 (35.6)
113994	6.6	5.1 (77.3)	4.0 (60.6)	3.2 (48.5)
BCM 3324-1	6.3	5.2 (82.5)	4.9 (77.8)	2.3 (42.9)
3324-2	5.6	4.4 (78.6)	4.2 (75.0)	2.0 (35.7)
3324-3	5.0	4.1 (82.0)	4.0 (80.0)	1.8 (36.0)
3324-4	6.8	5.2 (76.5)	4.3 (63.2)	2.6 (38.2)
3324-5	5.3	4.5 (84.9)	4.0 (75.5)	2.0 (37.7)
3324-6	4.0	2.9 (72.5)	2.6 (65.0)	1.5 (37.5)
3324-7	5.5	4.4 (80.0)	3.7 (67.3)	2.1 (38.2)
3324-8	5.7	4.5 (78.9)	3.7 (64.9)	2.1 (36.8)
3324-9	5.7	5.0 (87.7)	4.3 (75.4)	1.9 (33.3)
3324-10	5.0	4.0 (80.0)	3.7 (74.0)	1.7 (34.0)
3324-11	5.1	4.3 (84.3)	3.6 (70.6)	2.2 (43.1)
3324-12	5.2	4.7 (90.4)	3.8 (73.1)	2.1 (40.4)
3324-13	5.8	4.9 (84.5)	3.8 (65.5)	2.0 (34.5)
3324-14	5.3	4.5 (84.9)	4.1 (77.4)	2.0 (37.7)
3324-15	4.8	3.9 (81.3)	3.5 (72.9)	1.6 (33.3)
LU 69852	5.4	4.7 (87.0)	3.6 (66.7)	1.9 (35.2)
69853	4.1	3.1 (75.6)		1.3 (31.7)
69854	3.9	3.0 (76.9)		1.4 (35.9)
69855	5.2	4.1 (78.8)		2.0 (38.5)
69856	6.1	5.4 (88.5)	3.8 (62.3)	2.1 (34.4)
69857	6.1	4.1 (67.2)		2.0 (32.8)
69858	5.0	3.8 (76.0)		2.0 (40.0)
69859	4.6	4.1 (89.1)		1.8 (39.1)
69860	3.4	2.6 (76.5)		1.3 (38.2)
69861	3.7	2.8 (75.7)		1.4 (37.8)
69862	5.6	4.6 (82.1)	4.2 (75.0)	1.8 (32.1)
69863	4.6	3.4 (73.9)		1.5 (32.6)
69864	5.4	4.2 (77.8)		1.8 (33.3)
69865	5.9	4.9 (83.1)		2.3 (39.0)
69866	4.5	3.3 (73.3)		1.6 (35.6)
69867	4.8	4.5 (93.8)		1.9 (39.6)

Corbulomima macneillii (cont.)

N	132	132	119	132
$\overline{x}$	5.0 mm	83.3 %	72.0 %	37.0 %
Max	6.8	100.0	90.0	48.5
Min	3.4	67.2	56.5	29.5
OR	3.4	32.8	33.5	19.0
s	0.71	5.84	6.09	3.42
s^2	0.50	34.09	37.05	11.66
V	14.2	7.01	8.45	9.23
$\sigma_{\overline{x}}$	0.06	0.51	0.56	0.30

Corbulomima obscura (J. Sowerby)

spec. no.	L	H	I
LU 69868	4.5	3.3 (73.3)	2.8 (62.2)
69869	4.0	2.8 (70.0)	
69870	5.2	3.6 (69.2)	
69871	4.2	3.0 (71.4)	
69872	4.2	3.1 (73.8)	
69873	4.1	2.8 (68.3)	
69874	4.0	2.7 (67.5)	2.4 (60.0)

N	7	7	2
$\overline{x}$	4.3 mm	70.5 %	61.1 %
Max	5.2	73.8	62.2
Min	4.0	67.5	60.0
OR	1.2	6.3	2.2
s	0.43	2.43	1.56
s^2	0.18	5.89	2.42
V	10.00	3.44	2.55
$\sigma_{\overline{x}}$	0.16	0.92	1.71

Pleuromya alduini (Brongniart)

spec. no.	L	H	I	AL
GSM 24/58-1	45.1	29.2 (64.7)	21.0 (46.6)	12.1 (26.8)
24/58-2	38.0	26.9 (70.8)	21.3 (56.1)	9.6 (25.3)
GSM KA 590	35.8	23.9 (66.8)		10.4 (29.1)
KA 542	37.4	25.8 (69.0)	17.6 (47.1)	10.1 (27.0)
KA 603	41.1	26.7 (65.0)	21.8 (53.0)	10.6 (25.8)
KA 609	39.3	27.4 (69.7)	18.3 (46.6)	11.9 (30.3)
GSM 42946	38.1	28.1 (73.8)	21.6 (56.7)	8.4 (22.0)
42945	46.7	28.4 (60.8)	20.8 (44.5)	12.6 (27.0)
42936	39.0	27.5 (70.5)	18.8 (48.2)	10.5 (26.9)
42937	42.8	27.3 (63.8)	19.3 (45.1)	12.2 (28.5)
42938	36.7	26.9 (73.3)	17.6 (48.0)	11.1 (30.2)
42939	29.2	17.8 (61.0)	13.1 (44.9)	8.2 (28.1)
Y2020	30.2	20.8 (68.9)	13.0 (43.0)	10.6 (35.1)
42947	47.8	32.7 (68.4)	26.5 (55.4)	12.7 (26.6)
42940	47.3	32.7 (69.1)	26.4 (55.8)	14.3 (30.2)
GSM GSa 3759	35.9	23.9 (66.6)	15.7 (43.7)	9.0 (25.1)
3760	34.3	23.7 (69.1)	17.3 (50.4)	10.7 (31.2)
3761	33.7	23.6 (70.0)	15.7 (46.6)	9.7 (28.8)
GSM 42941	35.5	23.7 (66.8)	16.2 (45.6)	11.8 (33.2)
42942	38.4	25.6 (66.7)	18.0 (46.9)	11.4 (29.7)
42943	32.4	21.1 (65.1)	12.8 (39.5)	11.1 (34.3)
42944	29.2	18.1 (62.0)	12.8 (43.8)	10.3 (35.3)
GSM Zr 1704	38.8	26.7 (68.8)	16.6 (42.8)	11.4 (29.4)
GSM GSa 3762	38.3	22.5 (58.7)	14.2 (37.1)	11.9 (31.1)
3763	49.4	26.6 (53.8)	22.1 (44.7)	13.4 (27.1)
3764	46.7	27.9 (59.7)	23.6 (50.5)	13.3 (28.5)
3644	43.0	33.3 (77.4)	25.4 (59.1)	9.4 (21.9)
3645	42.7	34.5 (80.8)	24.4 (57.1)	10.2 (23.9)
3646	42.7	30.9 (70.7)	23.8 (54.5)	11.2 (25.6)
3647	46.5	35.8 (77.0)	25.8 (55.5)	11.1 (23.9)
GSM 25/47-1	65.9	49.5 (75.1)	39.2 (59.5)	15.6 (23.7)
43060	41.3	28.8 (69.7)	18.9 (45.8)	11.9 (28.8)
43061	30.5	22.1 (72.5)	14.3 (46.9)	9.2 (30.2)

Pleuromya alduini (cont.)

spec. no.	L	H	I	AL
GSM 43059	53.7	35.8 (66.7)	23.8 (44.3)	13.4 (25.0)
Y2075	34.0	22.0 (64.7)	14.3 (42.1)	10.0 (29.4)
52295	39.8	31.5 (79.1)	26.0 (65.3)	8.8 (22.1)
52296	37.1	30.7 (82.7)	21.0 (56.6)	10.5 (28.3)
52298	30.5	24.1 (79.0)	16.1 (52.8)	8.7 (28.5)
SM J12531	54.9	38.5 (70.1)	25.5 (46.4)	17.1 (31.1)
J12532	44.8	33.8 (75.4)	24.5 (54.7)	12.8 (28.6)
J12533	44.8	34.9 (77.9)		11.2 (25.0)
J12534	38.0	33.2 (87.4)	25.6 (67.4)	10.2 (26.8)
J12535	45.0	33.1 (73.6)	26.7 (59.3)	11.1 (24.7)
J12536	35.5	23.7 (66.8)	17.2 (48.5)	8.3 (23.4)
J26843	43.1	31.5 (73.1)	22.6 (52.4)	15.4 (35.7)
J26844	44.3	29.6 (66.8)	21.1 (47.6)	12.9 (29.1)
J26845	38.5	26.3 (68.3)	19.8 (51.4)	12.1 (31.4)
J26846	34.3	24.6 (71.7)	16.5 (48.1)	11.2 (32.7)
LU 69875	27.1	18.2 (67.2)		6.8 (25.1)
69876	26.1	16.7 (64.0)		6.3 (24.1)
69877	24.1	16.2 (67.2)		6.6 (27.4)
69878	18.5	11.4 (61.6)		
69879	24.9	16.1 (64.7)		5.8 (23.3)
69880	21.3	13.6 (63.8)		7.6 (35.7)
69881	20.7	12.2 (58.9)		6.6 (31.9)
69882	27.4	17.0 (62.0)		
69883	24.1	15.7 (65.1)		
69884	25.4	18.9 (74.4)		8.7 (34.3)
OUM J28242	28.5	17.4 (61.1)		7.4 (26.0)
YM KD1974/56	33.8	21.8 (64.5)		9.0 (26.6)
1974/57	49.1	36.2 (73.7)	23.8 (48.5)	11.9 (24.2)
Arkell pl.44 fig. 1	39.8	29.4 (73.9)	18.1 (45.5)	11.1 (27.9)
fig. 2	45.0	31.2 (69.3)		9.3 (20.7)
fig. 3	46.6	35.2 (75.5)		10.7 (23.0)
fig. 4	48.0	34.5 (71.9)		13.3 (27.7)

Pleuromya alduini (cont.)

spec. no.	L	H	I	AL
Arkell pl.44				
fig. 5	46.0	34.4 (74.8)		11.4 (24.8)
fig. 6	50.3	37.3 (74.2)		13.7 (27.2)
fig. 7	61.2	39.7 (64.9)		19.5 (31.9)
fig. 8	50.2	35.3 (70.3)		13.1 (26.1)
fig. 9	51.3	35.6 (69.4)		15.7 (30.6)
N	70	70	48	67
$\bar{x}$	39.4 mm	69.2 %	49.8 %	27.9 %
Max	65.9	87.4	67.4	35.7
Min	18.5	53.8	37.1	20.7
OR	47.4	33.2	30.3	15.0
s	8.26	6.12	6.43	3.62
s^2	68.30	37.42	41.36	13.10
V	20.96	8.84	12.91	12.96
$\sigma \bar{x}$	0.99	0.73	0.93	0.44

Pleuromya uniformis (J. Sowerby)

spec. no.	L	H	I	AL
SM J12526	31.4	17.7 (56.4)	11.7 (37.3)	11.1 (35.4)
J12527	38.9	22.2 (57.1)	15.4 (39.6)	12.8 (32.9)
J12528	32.9	19.3 (58.7)	11.8 (35.9)	11.4 (34.7)
J12529	40.1	20.2 (50.4)	16.7 (41.6)	11.8 (29.4)
J12530	43.2	24.3 (56.3)	19.5 (45.1)	12.9 (29.9)
J12537	29.2	15.4 (52.7)		11.9 (40.8)
J12538	36.5	18.7 (51.2)		12.7 (34.8)
J12539	36.7	18.8 (51.2)		14.9 (40.6)
GSM 24/57-1	54.9	31.3 (57.0)	20.3 (37.0)	18.4 (33.5)
24/57-2	34.7	18.0 (51.9)	12.1 (34.9)	11.0 (31.7)
24/57-3	29.3	17.7 (60.4)	11.9 (40.6)	10.1 (34.5)
24/57-4	28.0	16.2 (57.9)	12.2 (43.6)	8.9 (31.8)
SM J49979	47.6	27.0 (56.7)	19.6 (41.2)	14.8 (31.1)
J49980	71.2	39.0 (54.8)	23.6 (33.1)	29.8 (41.9)
J49981	27.1	16.1 (59.4)	10.5 (38.7)	9.2 (33.9)
J49982	32.2	19.7 (61.2)	13.4 (41.6)	9.8 (30.4)
Arkell pl. 45				
fig. 1	40.0	26.8 (67.0)	17.1 (42.8)	13.7 (34.3)
fig. 2	40.5	23.4 (57.8)	18.3 (45.2)	15.7 (38.8)
fig. 3	47.8	28.8 (60.3)	19.7 (41.2)	17.0 (35.6)
fig. 4	35.0	22.0 (62.9)	14.2 (40.6)	10.7 (30.6)
fig. 5	44.4	25.8 (58.1)	19.0 (42.8)	15.9 (35.8)
fig. 6	39.8	21.7 (54.5)		12.3 (30.9)
fig. 7	46.1	26.5 (57.5)		17.0 (36.9)
fig. 8	39.7	29.4 (74 1)		14.6 (36.8)
fig. 9	37.5	25.0 (66.7)		14.3 (38.1)
fig. 10	37.2	26.2 (70.4)		13.1 (35.2)
fig. 11	33.4	20.2 (60.5)		10.8 (32.3)
fig. 12	30.7	19.0 (61.9)		10.4 (33.9)
fig. 13	53.6	26.7 (49.8)		15.7 (29.3)

Pleuromya uniformis (cont.)

	L	H	I	AL
N	29	29	18	29
$\overline{x}$	39.3 mm	58.4 %	40.2 %	34.3 %
Max	71.2	74.1	45.5	41.9
Min	27.1	49.8	33.1	29.3
OR	44.1	24.3	12.4	12.6
s	9.45	5.82	3.42	3.45
s^2	89.29	33.85	11.68	11.89
V	24.05	9.96	8.51	10.04
$\sigma_{\overline{x}}$	1.75	1.08	0.81	0.64

Thracia depressa (J. de C. Sowerby)

spec. no.	L	H	I	AL
BM L6979 (NT)	53.9	40.8 (75.7)	20.7 (38.4)	34.6 (58.1)
GSM 25/52	52.5	38.9 (74.1)	24.0 (45.7)	29.6 (56.4)
25/50	59.4	47.2 (79.5)	24.5 (41.2)	31.4 (52.9)
43067	56.8	52.4 (92.3)	25.6 (45.1)	30.7 (54.0)
43068	52.3	45.9 (87.8)	31.8 (60.8)	26.8 (51.2)
43058	29.4	23.4 (79.6)	13.4 (45.6)	18.4 (62.6)
43064	53.9	40.8 (75.7)		37.4 (69.4)
57522	47.9	36.4 (76.0)	21.4 (44.7)	31.6 (66.0)
SM 26894	57.2	46.5 (81.3)	27.6 (48.3)	30.6 (53.5)
26895	46.6	34.4 (73.8)	17.4 (37.3)	27.4 (58.8)
26896	61.2	44.6 (72.9)	24.0 (39.2)	32.0 (52.3)
26897	44.6	31.9 (71.5)		23.6 (52.9)
26898	46.2	34.5 (74.7)	13.8 (29.9)	30.2 (65.4)
GSM GSa 3648	55.8	42.0 (75.3)	20.0 (35.8)	35.1 (62.9)
3649	58.5	49.1 (83.9)	25.3 (43.2)	39.9 (68.2)
LU 69885	58.6	48.9 (83.4)	18.9 (32.3)	38.8 (66.2)

	L	H	I	AL
N	16	16	14	16
$\overline{x}$	51.8 mm	78.6 %	41.7 %	59.4 %
Max	59.4	92.3	60.8	69.4
Min	29.4	71.5	29.9	51.2
OR	30.0	20.8	30.9	18.2
s	7.98	5.84	7.89	6.34
s^2	63.61	34.10	62.30	40.19
V	15.40	7.43	12.67	10.67
$\sigma_{\overline{x}}$	1.99	1.46	2.11	1.59

Thracia depressa (cont.)

Lower Oxford Clay specimens

spec. no.	L	H	AL
YM KD1974/58	39.0	27.3 (70.0)	23.7 (60.8)
LU 69886	49.5	33.4 (67.5)	33.1 (66.9)
69887	52.1	35.3 (67.8)	31.6 (60.7)
69888	59.1	41.5 (70.2)	36.2 (61.3)
69889	52.9	35.6 (67.3)	32.3 (61.1)
69890	63.9	42.8 (67.0)	38.8 (60.7)
69891	29.7	20.6 (69.4)	19.5 (65.7)
69892	28.9	18.4 (63.7)	17.5 (60.6)
69893	65.1	48.9 (75.1)	36.7 (56.4)
69894	37.8	28.7 (75.9)	24.3 (64.3)
69895	26.8	18.1 (67.5)	17.2 (64.2)
69896	22.2	17.0 (76.6)	13.7 (61.7)
69897	37.5	28.9 (77.1)	22.1 (58.9)
69898	38.4	28.2 (73.4)	22.8 (59.4)
69899	45.1	33.3 (73.8)	27.6 (61.2)
69900	57.6	42.4 (73.6)	31.3 (54.3)
69901	42.4	29.7 (70.0)	25.4 (59.9)
69902	27.7	18.8 (67.9)	16.1 (58.1)
69903	19.9	13.9 (69.8)	12.7 (63.8)
69904	44.2	29.3 (66.3)	29.3 (66.3)

N	20	20	20
$\bar{x}$	42.0 mm	70.5 %	61.3 %
Max	65.1	77.1	66.9
Min	19.9	63.7	54.3
OR	45.2	13.4	12.6

Thracia depressa (cont.)

	L	H	AL
s	13.65	3.84	3.21
s²	186.28	14.77	10.30
V	32.50	5.45	5.23
σ x̄	3.05	0.86	0.72

Overall

	L	H	I	AL
N	36	36	14	36
x̄	46.4 mm	74.1 %	41.7 %	60.5 %
Max	65.1	92.3	60.8	69.4
Min	19.9	63.7	29.9	51.2
OR	45.2	28.6	30.9	18.2
s	12.36	6.26	7.89	4.87
s²	152.86	39.17	62.30	23.72
V	26.67	8.45	12.67	8.05
σ x̄	2.06	1.04	2.11	0.81

Anomalodesmatan sp. A.

spec. no.	L	H	AL
BM LL27735	11.1	8.1 (73.0)	4.3 (38.7)
27736	9.3	7.0 (75.3)	2.9 (31.2)
27737	13.6	10.5 (77.2)	4.9 (36.0)
27738	7.8	4.9 (62.8)	2.8 (35.9)
27739	12.5	8.3 (66.4)	
27740	9.0	6.4 (71.1)	3.4 (37.8)
LU 69905	9.8	6.3 (64.3)	3.4 (34.7)
69906	7.3	5.0 (68.5)	2.7 (37.0)
69907	13.7	9.6 (70.1)	5.3 (38.7)
69908	10.8	7.4 (68.5)	3.8 (35.2)
69909	6.7	5.0 (74.6)	
69910	8.6	6.9 (80.2)	2.6 (30.2)
69911	14.0	10.8 (77.1)	4.8 (34.3)
69912	6.8	4.2 (61.8)	
69913	8.3	5.7 (68.7)	
69914	8.7	6.1 (70.1)	3.2 (36.8)
69915	8.5	6.0 (70.6)	3.2 (37.6)
69916	8.8	5.3 (60.2)	2.7 (30.7)
69917	10.6	6.9 (65.1)	3.9 (36.8)
69918	9.3	6.5 (69.9)	3.2 (34.2)
69919	5.5	3.5 (63.6)	
69920	12.0	8.3 (69.2)	3.6 (30.0)
69921	6.0	4.2 (70.0)	
69922	7.6	5.0 (65.8)	
69923	10.0	7.1 (71.0)	3.8 (38.0)
69924	7.6	5.1 (67.1)	2.7 (35.5)

Anomalodesmatan sp. A. (cont.)

	L	H	AL
N	26	26	19
$\bar{x}$	9.4 mm	69.3 %	35.2 %
Max	14.0	80.2	38.7
Min	5.5	60.2	30.0
OR	8.5	20.0	8.7
s	2.35	4.95	2.83
s^2	5.54	24.54	8.02
V	25.08	7.15	8.04
$\sigma_{\bar{x}}$	0.46	0.97	0.65

Anomalodesmatan sp. B.

spec. no.	L	H	AL
BM LL27741	8.9	5.7 (64.0)	4.1 (46.1)
27742	9.2	6.1 (66.3)	4.6 (50.0)
27743	9.0	6.0 (66.7)	4.4 (48.9)
27744	9.6	6.4 (66.7)	4.2 (43.8)
27755	7.1	4.6 (64.8)	2.7 (38.0)
LU 69925	7.9	5.5 (69.6)	
69926	6.6	4.5 (68.2)	2.5 (37.9)
69927	8.1	5.0 (61.7)	
69928	5.6	3.8 (67.9)	
69929	6.1	4.3 (70.5)	
69930	7.3	4.7 (64.4)	
69931	8.1	5.6 (69.1)	3.6 (44.4)
N	12	12	7
$\bar{x}$	7.8 mm	66.7 %	44.2 %
Max	9.6	70.5	50.0
Min	5.6	61.7	37.9
OR	4.0	8.8	12.1
s	1.28	2.59	4.79
s^2	1.63	6.69	22.94
V	16.39	3.88	10.85
$\sigma\,\overline{x}$	0.37	0.75	1.81

APPENDIX 4

(In pocket inside back cover)

Percentage faunal composition of each bed at each pit.

4A		Calvert
4B		Bletchley
4C		Stewartby
4D		Norman Cross

AZ	=	Athleta Zone
CZ	=	Calloviense Zone
CSZ	=	Calloviense Subzone
ESZ	=	Enodatum Subzone

A	=	Abundant
✓	=	Present