FOSSILS OF THE OXFORD CLAY

Edited by

David M. Martill
and
John D. Hudson

The Palaeontological Association

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DEDICATION

This book is dedicated to the memory of John Horrell, formerly Chief Geologist of the London Brick Company, who devoted his working life to the Oxford Clay, and most generously helped those who studied its fossils. Without his help many exciting fossil finds would not have been made.

ACKNOWLEDGEMENTS

A work of this nature depends very heavily on one's fellow workers. We take this opportunity to thank those many people who have assisted us with advice, facilities, the loan of specimens, and helpful discussions over many years. We apologize to anyone who may have inadvertently been missed here. We especially would like to mention staff of the Natural History Museum, Dr C. Patterson, Dr A. Milner, Dr M. K. Howarth, Dr P. D. Taylor, Dr A. Smith, Dr N. J. Morris and Mr R. J. Cleevely for allowing us to examine specimens in their care. Also, many thanks go to Dr B. M. Cox (British Geological Survey) and Dr J. K. Wright (Royal Holloway and Bedford College) for allowing us to use photographs. Professor J. H. Callomon (University College, London), Dr G. Chancellor (Peterborough City Museum), Mr Alan Dawn (Stamford), Dr D. T. Donovan (University College, London), Dr Tim Palmer (University of Wales at Aberystwyth), Dr Mike Barker (Portsmouth Polytechnic), Ms Liz Harper (Open University), Dr F. T. Fürsich (University of Würtzburg), and Dr R. G. Clements, Dr J. W. Faithfull and Mr R. Branson (Leicester University) all offered helpful advice. At Leicester Museum Dr M. A. Taylor and Dr A. Cruickshank offered helpful discussions on aspects of marine reptile palaeobiology. We have also drawn heavily on data from Dr A. Williams and Dr I. St. J. Fisher, both of whom have made important contributions to our knowledge of the geochemistry of the Oxford Clay. Ms S. Button, Mr J. Taylor and Mr A. Lloyd assisted with diagrams. Mrs D. Tye and Mrs W. D. Hebden helped type manuscripts. Dr Alistair Crame (British Antarctic Survey) and Dr Ed. Jarzembowski acted on behalf of the Palaeontological Association.

With the decision to produce this guide book we very rapidly found that specimens of many of the fossils were not represented in our collections. To remedy this we undertook several field visits to enrich the collections at Leicester University and the Open University. We therefore thank the London Brick Company for permission to visit their brick pits, and in particular thank Mr P. Furr (LBC Bletchley), Mr Keith Morton (LBC Stewartby) and Mr A. Robinson (LBC Calvert) for their help.

1. INTRODUCTION

by J. D. HUDSON *and* DAVID M. MARTILL *with a contribution by* KEVIN N. PAGE

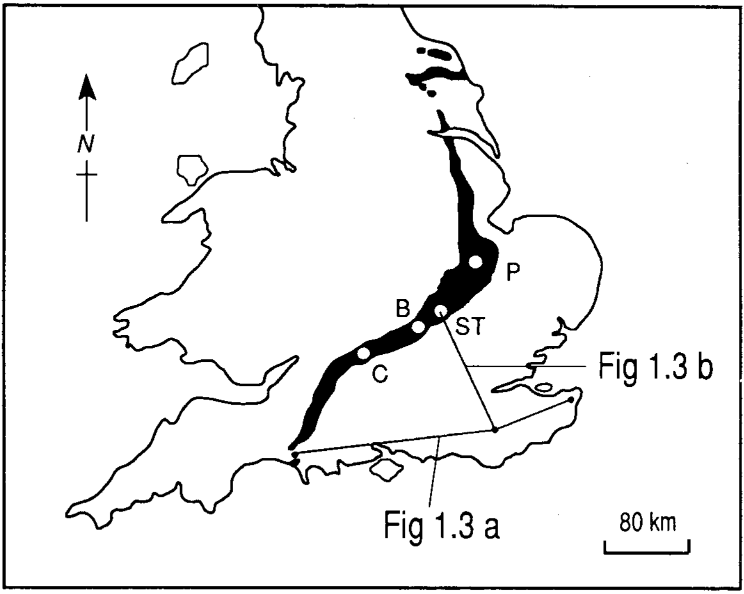
THE Oxford Clay is a famous source of beautifully-preserved fossils, yet it deserves more fame than it currently has, and it undoubtedly holds surprises still. We hope that this guide book will summarize what we know, facilitate accurate identification of Oxford Clay fossils, and perhaps most important of all, serve as a stimulus for further research.

The Oxford Clay is an argillaceous formation of Callovian to lower Oxfordian age occurring in the marine Jurassic succession of Southern and Midland England (text-fig. 1.1). Northwards, in Yorkshire, the clay facies declines in importance as sandy deposits dominate the succession. Clay facies occur at the same stratigraphical horizon in north-east and north-west Scotland, and contain many of the same fossils. The deposits occur in different basins, however, and are given different stratigraphic names: they are not comprehensively covered here. Nor do we describe all the fossils occurring in the non-argillaceous equivalents to the Oxford Clay in England although we do, for convenience, figure some specimens from them which also occur in the clays. More precise delimitation of the Oxford Clay is given below.

We have aimed to describe all known macrofossils and some of the more common microfossils of the Oxford Clay, and to mention doubtful species; rare but conspicuous forms are included. We also include less comprehensive treatments of microfossils and trace fossils. In the case of the vertebrates, emphasis is on the parts of disarticulated skeletons most likely to be found, such as teeth, ribs and vertebrae. Whereas this is primarily a handbook for identification, we have tried in our introduction to put the Oxford Clay fauna and flora in its stratigraphical, ecological and preservational context, for only then do the individual species come alive in our imaginations. We are the heirs of a great tradition, so we briefly describe the contributions of our predecessors, some of whose work has had significance in the fields of comparative anatomy and evolutionary palaeontology, going well beyond purely local concerns.

During the course of preparation of this book Dr Neville Hollingworth has discovered many new exposures, some of a temporary nature, of the seldom seen Middle and Upper Oxford Clay. Most of these are associated with gravel workings in the Thames Valley between Oxfordshire and Wiltshire and are highly fossiliferous.

In the Midlands several complete skeletons of marine reptiles were also discovered while the book was in preparation, demonstrating that it



TEXT-FIG. 1.1. Map of England showing the onshore outcrop of the Oxford Clay. Note the outcrop is almost continuous except for a small area north of Weymouth and in Yorkshire where the Oxford Clay is overstepped by Cretaceous strata. Extensive outcrops also occur on the sea bed in the English Channel and in the sea cliffs of Normandy, France. Lines indicate location of ribbon diagrams illustrated in text-fig. 1.3a–c. Based partly on Duff (1975).

is still possible to collect high quality specimens, even with today's highly mechanized extractive methods.

STRATIGRAPHY

The Oxford Clay is a succession of mudrocks with intermittent concretionary carbonate horizons that lies above the mainly sandy Kellaways Formation, and is overlain by a variety of facies formerly referred to the 'Corallian Beds'; in many localities its upper limit is a disconformity. Its age ranges from uppermost Lower Callovian to approximately the top of the Lower Oxfordian (Cope *et al.*, 1980a). Traditionally, the Oxford Clay has been divided into Lower, Middle and Upper divisions. Only the lowest, Lower Callovian, part of the sequence has been subject to recent formal stratigraphic revision (Page, 1989).

STAGE		ZONE	SUBZONE	STRATA
OXFORDIAN	LOWER	Cardioceras cordatum	C. cordatum	UPPER OXFORD CLAY
			C. costicardia	
			C. bukowskii	
		Cardioceras mariae	C. praecordatum	
			C. scarburgense	
CALLOVIAN	UPPER	Q. lamberti	Q. lamberti	MIDDLE OXFORD CLAY
			Q. henrici	
		Peltoceras athleta	K. spinosum	
			K. proniae	
			K. phaeinum	LOWER OXFORD CLAY
	MIDDLE	Erymnoceras coronatum	K. grossouvrei	
			K. obductum	
		Kosmoceras jason	K. jason	
			K. medea	
	LOWER	Sigaloceras calloviense	S. enodatum	
			S. calloviense	KELLAWAYS FORMATION
		Proplanulites koenigi	K. galilaei	
			K. curtilobus	
			K. gowerianus	
		Macrocephalites herveyi	M. kamptus	CAYTON CLAY FM
			M. terebratus	ABBOTSBURY CORNBRASH FM. (PART)
			K. keppleri	

TEXT-FIG. 1.2. Traditional lithostratigraphic subdivisions of the Oxford Clay with ammonite zone and subzone nomenclature. Based largely on Callomon 1968, Callomon *et al.* (1989), Cope *et al.* (1980a) and Page (1989). Relationships between lithostratigraphic divisions and zones are simplified, especially for the lower part of the succession.

On the other hand, the sequence of ammonite faunas, which is the basis of the bio- and chrono-stratigraphy, is now very well known for most parts of the succession.

As regards lithostratigraphy, we here follow recent practice as follows, paying most attention to the succession in the East Midlands. The base of the Oxford Clay is taken above the last siltstone bed of the Kellaways Formation; at Peterborough this corresponds to the base of the sequence measured by Brinkmann (1929a) and to the base of the Enodatum Subzone (see below). The top of the Lower Oxford Clay is a fairly sharp lithological change from organic-rich, fissile shale to grey mudstone, within the Athleta Zone. The Middle and Upper Oxford Clays are similar lithologically, but are separated in the South Midlands by an argillaceous limestone, the Lamberti Limestone, best known from the former brickpit at Woodham, Buckinghamshire (Arkell, 1939; Hudson & Palframan, 1969). This also marks the top of the Lamberti Zone and of the Callovian, and there has been a tendency to regard the Middle-Upper Oxford Clay (litho-stratigraphic) boundary as necessarily coinciding with the stage boundary (e.g. Cope *et al.*, 1980a). The top of the Oxford Clay is defined by the base of the overlying formation and is diachronous (Cope *et al.*, 1980a).

As already mentioned, the ammonites form the basis of the standard zonation of the Callovian and Oxfordian, which has been successively refined by, among others, Callomon & Donovan (1974), Cope *et al.* (1980a), Callomon, Dietl & Page (1989) and Page (1989). The outline stratigraphical classification that we use is shown in text-fig. 1.2. In the following section, Kevin Page summarizes the currently recognized chronozones and subzones of the relevant parts of the Callovian and Oxfordian. He also supplies lists of the ammonite faunas characterizing each zone, as developed in the Oxford Clay of England, with notes on rarities whose distribution needs further confirmation. We would welcome additional records, particularly of these rare forms, whose distribution may be highly significant for Jurassic palaeobiogeography. This list should be used in conjunction with the taxonomic treatment of the ammonites in Chapter 4.

AMMONITE ZONES AND SUBZONES

contributed by KEVIN N. PAGE

CALLOVIAN STAGE

LOWER CALLOVIAN SUBSTAGE

Calloviense Zone
Index: *Sigaloceras* (*S*.) *calloviense* (J. Sowerby).
Characteristic fauna: Corresponds to the range of *Sigaloceras* spp.
Comments: The base of the Oxford Clay, over much of Britain south of Humberside, lies within the upper part of the Calloviense Zone.

Calloviense Subzone
Index: As for Calloviense Zone.
Characteristic fauna: Species of *Sigaloceras* (*S*.), with compressed finely ribbed whorls and a tabulate venter throughout ontogeny.
The perisphinctid *Proplanulites* is often common: for fuller details see Callomon, Dietl & Page (1989) and Page (1989).

Enodatum Subzone
Index: *Sigaloceras* (*Catasigaloceras*) *enodatum* (Nikitin).
Characteristic fauna: Correlated by three successive species of *Sigaloceras* (*Catasigaloceras*), namely *S*. (*C*.) nov. (Page, MS), *S*. (*C*.) *enodatum* and *S*. (C.) *anterior* (Brinkmann).
Perisphinctids are only locally abundant and include *Homeoplanulites cardoti* (Petitclerc) and *H*. *difficilis* Buckman.
Cadoceras (*C*.) *durum* occurs occasionally, as well as extremely rare specimens of *Macrocephalites tumidus* (Reinecke).

MIDDLE CALLOVIAN SUBSTAGE

Jason Zone
Index: *Kosmoceras* (*Gulielmiceras*) *jason* (Reinecke).
Characteristic fauna: Corresponds to the range of *Kosmoceras* (*Gulielmiceras*) as here defined.

Medea Subzone
Index: *Kosmoceras* (*Gulielmiceras*) *medea* Callomon.
Characteristic fauna: *Kosmoceras medea* is typically abundant, and

accompanied by occasional perisphinctids (*Homeoplanulites* or *Indosphinctes*), *Cadoceras* (*C.*) sp. and rare *Reineckeia* aff. *anceps* (Reinecke). A hecticoceratid has also been recorded (Callomon, 1968, p. 282).

Jason Subzone
Index: *Kosmoceras* (*Gulielmiceras*) *jason* (Reinecke).
Characteristic fauna: Dominated by *K. jason*, a larger species than *K. medea*. Other taxa are rare, and include *Indosphinctes patina* (Neumayr), *Cadoceras* (*C.*) *compressum* (Nikitin) and *Reineckeia* (*R.*) *anceps* (Reinecke).

Coronatum Zone
Index: *Erymnoceras coronatum* (Bruguière).
Characteristic fauna: Correlated using species of *Kosmoceras* (*Zugokosmokeras*). *Erymnoceras* is locally common, mainly in the lower part of the Zone.

Obductum Subzone
Index: *Kosmoceras* (*Zugokosmokeras*) *obductum* (Buckman).
Characteristic fauna: The index is common, and accompanied by frequent *Erymnoceras coronatum*. Other taxa are rather rare, and include *Grossouvria* (*G.*) sp. and *Hecticoceras* (?*Lunuloceras*) cf. *lugeoni* (de Tsytovitch).

Grossouvrei Subzone
Index: *Kosmoceras* (*Zugokosmokeras*) *grossouvrei* (Douvillé).
Characteristic fauna: Large species of *K.* (*Zugokosmokeras*) are typical; the lower part of the Subzone contains *K.* (*Z.*) *posterior* (Brinkmann), the upper part *K.* (*Z.*) *grossouvrei*. *Erymnoceras coronatum* is locally common in the lower part of the Subzone, but is replaced by rarer *E. argoviense* (Jeannet) at higher levels. Associated faunas are now richer than at lower levels, especially near the top of the Subzone, where *Binatisphinctes comptoni* (Pratt) is abundant and *Hecticoceras* (*Sublunuloceras*) *lonsdali* (Pratt) common. Occasional *Grossouvria* (*G.*) and rare *Cadoceras* (*C.*) *milaschevici* (Nikitin) have been recorded from the lower part of the Subzone. Reineckeids are known very rarely and probably include *Reineckeia* (*Collotia*) *spathi* (Bourquin).

UPPER CALLOVIAN SUBSTAGE

Athleta Zone
Index: *Peltoceras* (*P.*) *athleta* (Phillips).
Characteristic fauna: Detailed subdivision is made on the basis of species

of *Kosmoceras* (*Lobokosmokeras*) and early *K.* (*Kosmoceras*), all with looped ribbing (see Chapter 4). Peltoceratids are abundant at certain levels, mainly in the middle and upper parts of the zone.

Phaeinum Subzone
Index: *Kosmoceras* (*Lobokosmokeras*) *phaeinum* (Buckman).
Characteristic fauna: Dominated by *K.* (*L.*) *phaeinum*, with occasional *Binatisphinctes comptoni*, *Hecticoceras* (*Sublunuloceras*) *lonsdali* and rather rarer *Longaeviceras laminatum* (Buckman) and *Reineckeia* (*Collotia*) *spathi*.

Proniae Subzone
Index: *Kosmoceras* (*Lobokosmokeras*) *proniae* Teisseyre.
Characteristic fauna: *K.* (*L.*) *proniae* is abundant, and accompanied by large *Peltoceras* ex grp. *athleta* (Phillips). Rarer faunal elements include *Pseudopeltoceras chauvinianum* (d'Orbigny), *Grossouvria* (*G.*) *sulcifera* (Oppel), *Alligaticeras* (*A.*) *rotifer* (Brown), *Hecticoceras* (?*Orbignyceras*) and *Longaeviceras placenta* (Leckenby) also, possibly, *Reineckeia* (*Collotia*) cf. *collotiformis* (Jeannet).

Spinosum Subzone
Index: *Kosmoceras* (*K.*) *spinosum* (J. de C. Sowerby).
Characteristic fauna: *Kosmoceras* (*K.*) *kuklikum* (Buckman) is abundant and accompanied by a more diverse fauna than that of the Proniae Subzone (Callomon & Sykes *in* Cope *et al.*, 1980, pp. 44–7), including *Peltoceras* (*P.*), *Grossouvria* (*G.*) *sulcifera*, *Alligaticeras* (*A.*) *rotifer*, *Distichoceras bicostatum* (Stahl), *Hecticoceras* (*Orbignyceras*) *pseudopunctatum* (Lahusen), plus very rare *Pachyceras* cf. *crassum* Douvillé and probably also *Longaeviceras placenta*.

Lamberti Zone
Index: *Quenstedtoceras lamberti* (J. Sowerby).
Characteristic fauna: Species of *Quenstedtoceras* are abundant; *Kosmoceras* (*K.*) occurs although mainly in the lower part of the Zone.

Henrici Subzone
Index: *Quenstedtoceras henrici* (Douvillé).
Characteristic fauna: *Q. henrici* is common and occurs in approximately equal numbers with *Kosmoceras* (*K.*) *spinosum* sensu stricto. A large peltoceratid occurs (Sykes, 1975, p. 57), possibly a species of *Peltoceras* (*Peltomorphites*), and may be accompanied by perisphinctids such as *Grossouvria* and *Alligaticeras* (*A.*), and hecticoceratids.

Lamberti Subzone

Characteristic fauna: *Q. lamberti* is abundant and accompanied by a diverse fauna, including *Peltoceras* (*Peltomorphites*) *subtense* (Bean), *Grossouvria* (*Poculisphinctes*) *poculum* (Leckenby), *Euaspidoceras clynelishense* (Arkell), *Hecticoceras* (*Putealiceras*) *puteale* (Leckenby) with rarer *Distichoceras bicostatum*, *Kosmoceras* (*K.*) cf. *spinosum* and *Alligaticeras* (*A.*) *alligatum* (Leckenby). Great rarities include *Pachyceras* (*P.*) *lalandeanum* (d'Orbigny) and *Reineckeia* (*Collotia*) *oxyptichoides* (Spath).

OXFORDIAN STAGE

LOWER OXFORDIAN SUBSTAGE

Mariae Zone

Index: *Cardioceras* (*Pavloviceras*) *mariae* Douvillé.
Characteristic fauna: Early *Cardioceras* of the subgenus *Pavloviceras* are abundant and characteristic.

Scarburgense Subzone

Index: *Cardioceras* (*Pavloviceras*) *scarburgense* (Young & Bird).
Characteristic fauna: *C.* (*P.*) *scarburgense* is abundant. Other faunal elements include *Peltoceras* (*Peltomorphites*) ex grp. *hoplophorus* (Buckman), *Hecticoceras* (*Putealiceras*) *bonarellii* de Loriol, *Creniceras renggeri* (Oppel), *Alligaticeras* (*Properisphinctes*) *bernensis* (*de Loriol*), *Euaspidoceras* cf. *babeanum* (d'Orbigny), *Scaphitodites navicula* (Buckman) and *Grossouvria* (*Klematosphinctes*) cf. *vernoni* (Young & Bird).

Praecordatum Subzone

Index: *C.* (*P.*) *praecordatum* Douvillé.
Characteristic fauna: *C.* (*P.*) *praecordatum* is abundant, and frequently accompanied by *Peltoceras* (*Peltomorphites*) *hoplophorus* (Buckman). The associated fauna is similar to that of the Scarburgense Subzone and includes *Creniceras renggeri*, *Euaspidoceras babaenum*, *Alligaticeras* (*Properisphinctes*) *bernensis*, *Grossouvria* (*Klematosphinctes*) *vernoni*, *Hecticoceras* (*Putealiceras*) *bonarellii* and *Ochetoceras* (*Campylites*) cf. *delmontanum* (Oppel).

Cordatum Zone

Index: *Cardioceras* (*C.*) *cordatum* (J. Sowerby).
Characteristic fauna: Species of *Cardioceras* (*C.*) are often common,

and accompanied by occasional perisphinctids, peltoceratids and *Euaspidoceras*.

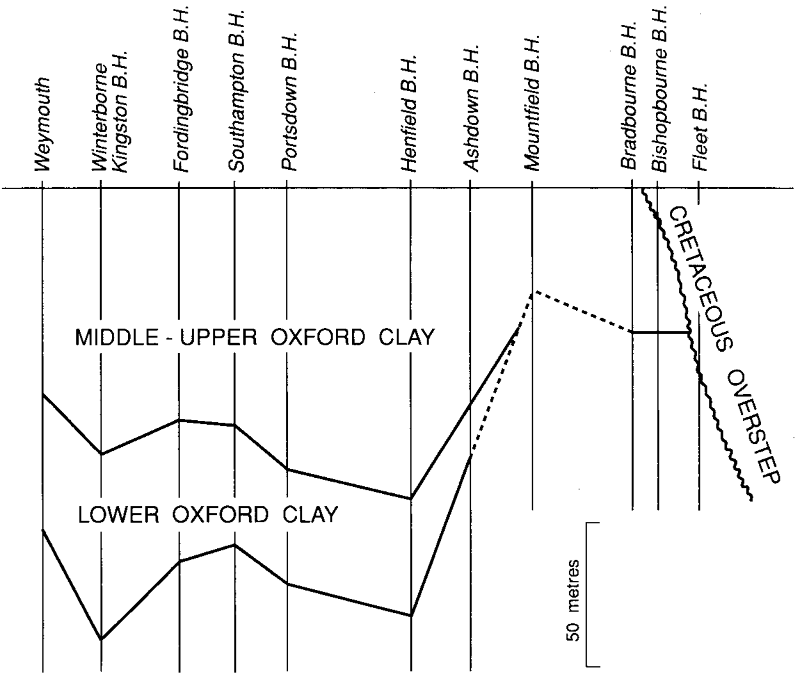
Bukowskii Subzone
Index: *Cardioceras* (*C.*) *bukowskii* Maire.
Characteristic fauna: *C.* (*C.*) *bukowskii* is abundant and characteristic; *Peltoceras* (*Peltomorphites*) *hoplophorus* Buckman is locally common. Other faunal elements are less common and include *Euaspidoceras douvillei* (Collot), *Alligaticeras* (*Properisphinctes*) *matheyi* (de Loriol), *Grossouvria* (*Klematosphinctes*) sp., *Ochetoceras* (*Campylites*) *delmontanum* (Oppel) and very rare *Pachyceras* (*Tornquistes*) *leckenbyi* Arkell. *Creniceras renggeri* occurs in the lowest part of the Subzone, and is replaced at higher levels by rare *C. crenatum* (Bruguiere).

Costicardia Subzone
Index: *Cardioceras* (*C.*) *costicardia* Buckman.
Characteristic fauna: The index is locally common, and accompanied by rarer *Peltoceras* (*Peltoceratoides*) *williamsoni* (Phillips), *Euaspidoceras acuticostatum* (Young and Bird) *Grossouvria* (*K.*) sp. and *Perisphinctes* (*P.*) sp.

Cordatum Subzone
Characteristic fauna: *C.* (*C.*) *cordatum* is locally common and *Euaspidoceras* sp. is frequent. Only one other taxon appears to have been recorded in England, *Ochetoceras* (*Campylites*) sp.; nevertheless, *Perisphinctes* (*P.*) may be expected.
Comment: Very locally, near Oxford, the Oxford Clay ranges up into the Cordatum Subzone (Wright, *In*: Cope *et al.*, 1980b, p. 69). No younger deposits in Oxford Clay facies are known along the English outcrop.

STRUCTURE AND PALAEOGEOGRAPHY

With the exception of South Dorset, the Oxford Clay outcrop is not affected by any strong tectonic movements and has never been deeply buried; in parts of the East Midland platform maximum cover probably never exceeded 300 or 400 m (Hudson, 1978; Emery *et al.*, 1988). Thickness variations are summarized in text-fig. 1.3. The Oxford Clay is absent under London and southern East Anglia, the 'London Landmass' of traditional palaeogeographies, but this is certainly due in part to pre-Cretaceous erosion and overstep. It cannot be proved that the 'landmass' was emergent during deposition of the Oxford Clay, although the occurrence of abundant 'driftwood', and especially of

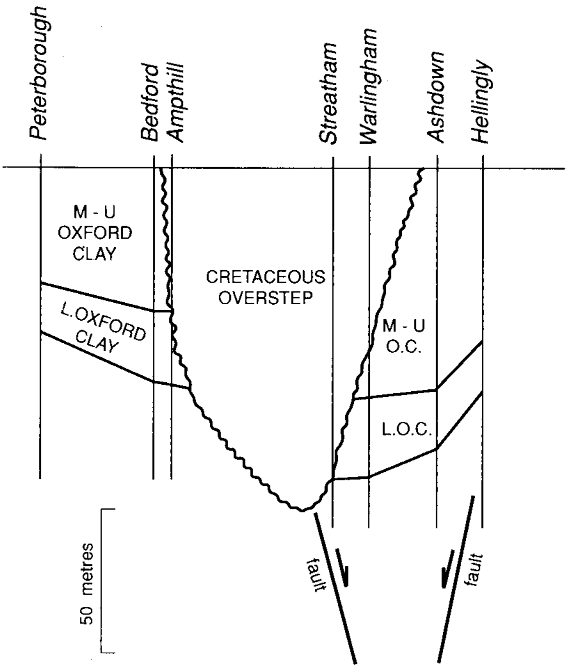


TEXT-FIG. 1.3a

terrestrial vertebrate remains in the Peterborough area, shows that land was not far away. The main influx of sediment was probably from the north or north-east, as shown by sandy facies in Yorkshire and offshore in the North Sea.

FACIES

The Oxford Clay exhibits two main facies with several sub-facies (Hudson & Palframan, 1969; Duff, 1975). The Lower Oxford Clay is composed predominantly of organic-rich mudstones that on exposure rapidly develop a shaly fissility. In this state the rock splits readily along the bedding, and almost every bedding plane reveals ammonites (mainly *Kosmoceras*), bivalves and gastropods, generally crushed but preserved in glistening aragonite. Particularly in the most organic-rich horizons

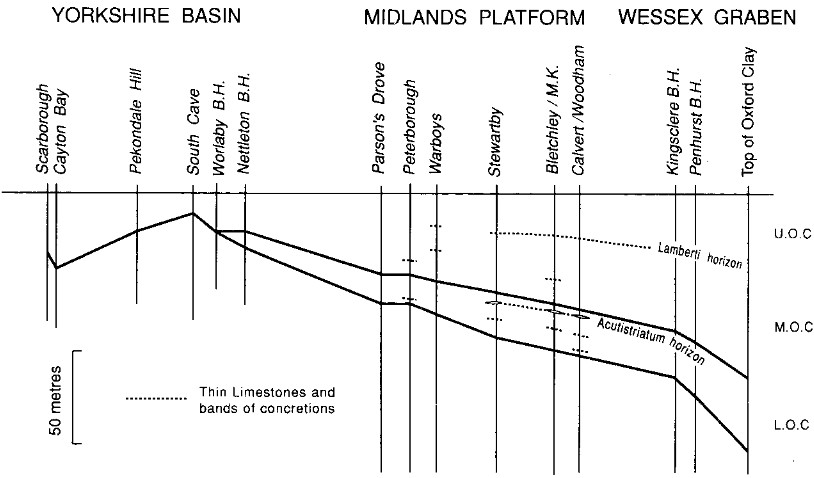


TEXT-FIG. 1.3b

whole articulated skeletons of fish and marine reptiles are not uncommon (Martill, 1985c). The main lithological variation is provided by shell-beds of several different kinds (Duff, 1975) and concretionary limestones (Hudson, 1978); see text-fig. 1.4. The Middle and Upper Oxford Clays are mainly blocky, non-fissile, rather calcareous mudstones, silty in places, which are less organic rich and contain far fewer macrofossils. Aragonite is not usually preserved, and the best-known fossils are pyritic internal moulds of ammonites. Shell beds are less well differentiated, but layers of *Gryphaea* occur. The Lamberti Limestone is notable for yielding large relatively uncrushed ammonites.

PALAEOECOLOGY

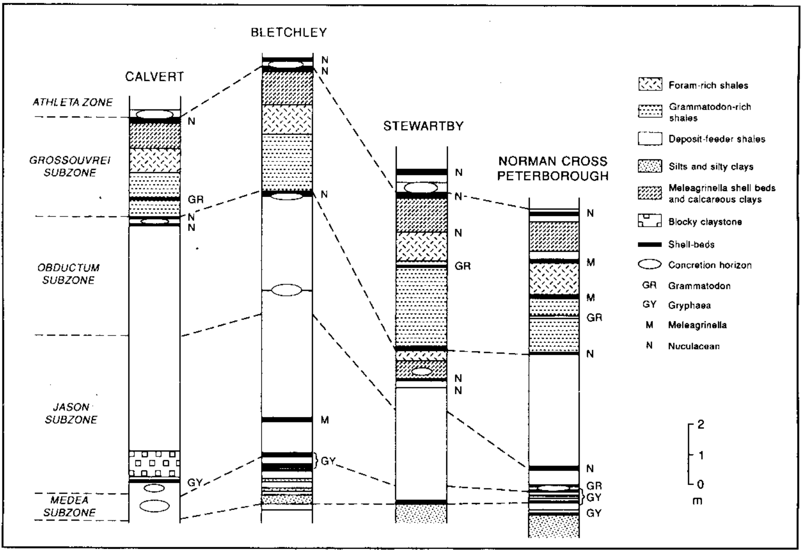
The palaeoecology of the Lower Oxford Clay benthos has been studied in detail by Duff (1975); that of the nekton is discussed by Martill (1988b) and Hudson & Martill (submitted). These papers should be consulted for detailed argumentation. Some general conclusions, by no means all



TEXT-FIG. 1.3c

TEXT-FIG. 1.3. Variations in thickness of the Oxford Clay in England. **a**, Dorset to Kent. **b**, Cambridgeshire to Sussex. **c**, Section approximately paralleling the line of outcrop from Yorkshire basin to the Wessex Graben. Notice the Cretaceous overstep in the Berkshire area appears to post date an erosional episode, rather than represent an area of non deposition. This suggests that the Oxford Clay transgressed the London Brabant 'landmass', at least in eastern England. Data derived from Arkell (1933), Bradshaw & Penney (1982), Brasier & Brasier (1978), Callomon (1955), Callomon & Cope (1971), Gallois & Worssam (1983), Gaunt *et al.* (1980), Osborne-White (1925), Strahan (1898), Wright (1968, 1985a,b), and numerous other sources.

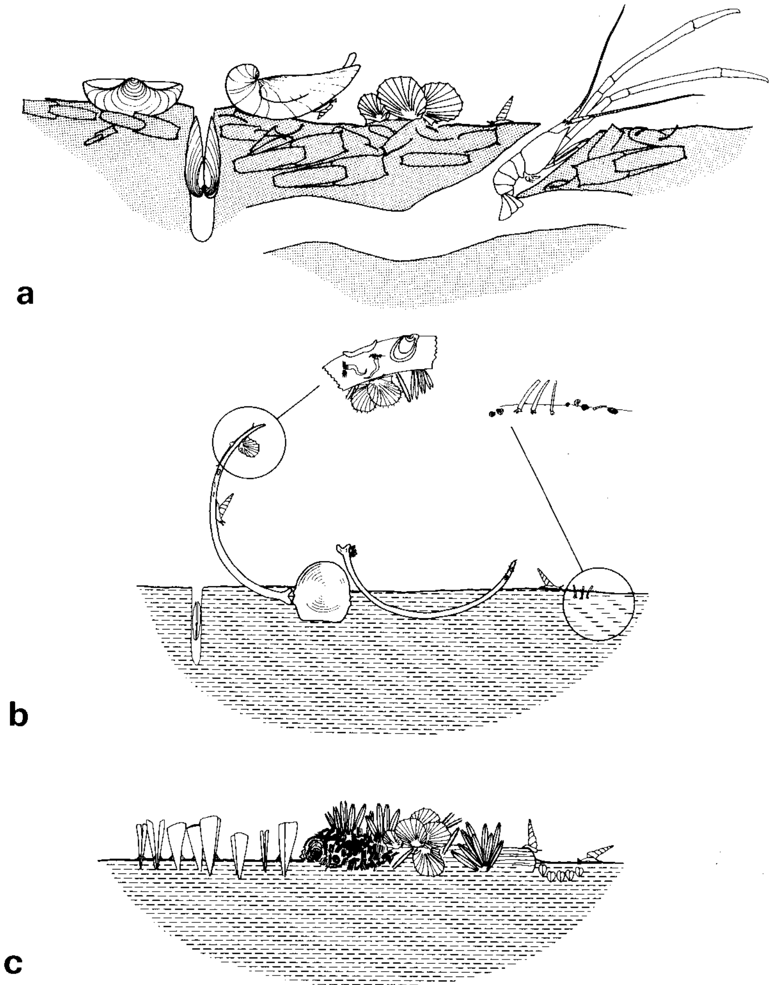
fully substantiated, follow. The Lower Oxford Clay accumulated in a wide, shallow (tens of metres?) epeiric sea at an early stage of a major transgression, far from any oceanic upwelling zone. Nevertheless, organic production was very high, as indicated by the trophic elaboration of the plankton and nekton (see below); the source of nutrients may have been nearby, well vegetated land. The sea floor accumulated fine-grained, organic-rich 'soupy' sediment; bottom water may have been hypoxic (or dysaerobic) but was rarely, if ever, anoxic. The soupy substrate encouraged, and was maintained by, a high abundance of shallow-burrowing, deposit-feeding organisms, especially nuculacean bivalves. Only a few deeper burrowers penetrated the 'stiffer' mud beneath. Sediment accumulation was discontinuous. Episodically-high sedimentation rates allowed the preservation of vertebrate skeletons, whilst some of the longer diastems are represented by shell-beds (Brinkmann, 1929). Minor variations in bottom oxygenation, sediment



TEXT-FIG. 1.4. Lithological variation and biofacies in the Lower Oxford Clay of the Midlands Platform. Simplified from Duff (1978). Notice that shell beds are more numerous towards the base and top of the sequence.

consistency etc. controlled the development of the different biofacies types recognized by Duff (1975). Reconstructions of aspects of the Oxford Clay seafloor are given in text-fig. 1.5. Whereas the benthic faunas are of fairly low diversity and are dominated by forms of low trophic levels, the nekton is extremely diverse (text-fig. 1.6) and some elements of the food chain can be reconstructed by a combination of functional morphology and study of bite-marks, stomach contents, etc. (Martill, 1988b). Oxygen isotope ratios of well-preserved ammonites suggest temperatures of around 20°C for the water column (Williams, 1988).

There has been less detailed work on the palaeoecology of the Middle and Upper Oxford Clays. One of the few published studies is that by Hudson & Palframan (1969). In general, the substrate was firmer than in the Lower Oxford Clay, with an increased importance of shallow-burrowing and suspension-feeding bivalves and fewer infaunal deposit-feeders. Discrete shell-beds are less prominent than in the Lower Oxford Clay, but layers of large *Gryphaea* are characteristic. The condensed horizon of the Lamberti Limestone is full of large ammonites and also has a distinct benthic fauna related to the availability of a shelly substrate, including a diverse assemblage of epizoans.



TEXT-FIG. 1.5. Variations in benthic palaeocommunities of the Lower Oxford Clay sea floor. **a**, the ammonite plaster/*Gryphaea* shell bed community, e.g. bed 11 at Peterborough. **b**, the benthic island community, this community is frequently encountered associated with marine reptile skeletons and large ammonites. **c**, organic-rich shale community, e.g. Bed 10 at Peterborough. Bed numbers from Callomon (1968).

PRESERVATION

Many of the fossils of the Oxford Clay are usually well-preserved, and some of them exceptionally so. A great many factors influence preservation or destruction of the parts of a potential fossil, and we cannot give a comprehensive discussion here. We give a brief account of some of the chief factors that affect the main fossil groups, and thus influence their identification and interpretation. One favourable circumstance for the Oxford Clay as a whole is lack of deep burial. Another is richness in fine-grained organic material, particularly in the Lower Oxford Clay. This renders the clay essentially impermeable to water, and also affects its fissility, which so greatly facilitates the examination of Lower Oxford Clay sections.

Preservation of original composition

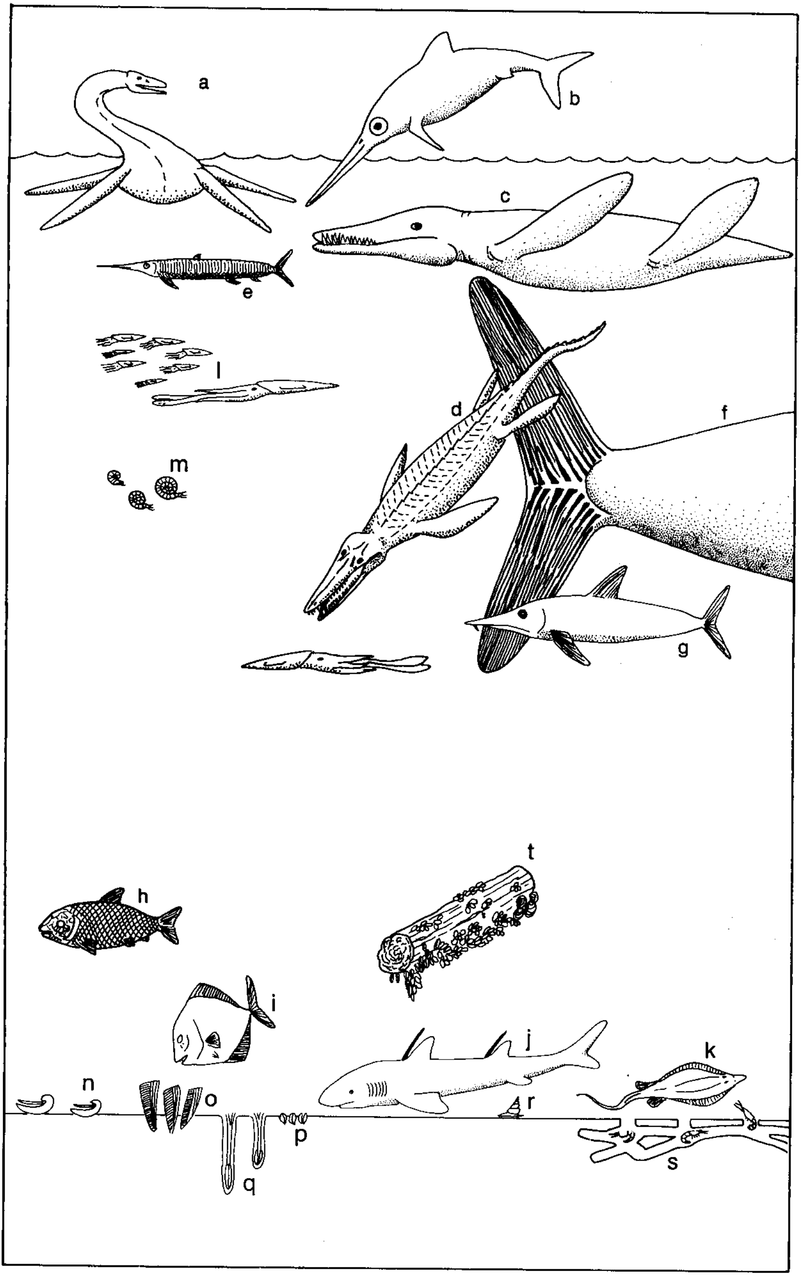
Organic matter. This is never preserved intact, but so-called biomarker molecules, which may be distinctive derivatives of particular biochemicals (e.g. chlorophyll) or of types of organisms (bacteria) are usually abundant. Their future study will greatly enhance our understanding of the origin and diagenesis of the organic matter. The resistant cysts of dinoflagellates and other microplankton may also be well preserved (Woollam, 1980; Woollam & Riding, 1983). The exceptional preservation of some aspects of soft-part morphology of certain cephalopods is discussed by Allison (1988) and in Chapter 5.

Most invertebrate hard parts were composed of aragonite, calcite, or calcium phosphate.

Aragonite is the more soluble form of calcium carbonate; ammonites (apart from their aptychi), belemnite phragmacones and most bivalves are composed of it. Its preservation correlates well with organic content, and most of the Lower Oxford Clay contains perfectly-preserved aragonite with microstructural detail and original chemical composition intact. In most of the Middle and Upper Oxford Clay, however, aragonite evidently dissolved in early diagenesis and fossils originally composed of it are preserved only as clay or mineral moulds, although at Ashton Keynes, Wiltshire, aragonite has survived and is associated with internal moulds of pyrite like those described below.

Calcite is more uniformly preserved and fossils composed of it are generally more robust than aragonite ones (e.g. *Gryphaea*, belemnite rostra, articulate brachiopods).

Calcium phosphate The inarticulate brachiopod *Lingula* is well-preserved as a rarity in the Lower Oxford Clay. The most important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phosphatic fossils are the vertebrates, whose preservation is discussed in Chapter 7.

Compaction

Three main factors determine whether a fossil retains its original, three dimensional shape or is crushed flat: the strength of the fossil itself, the compressibility of the sediment and the occurrence of mineralization within or around the fossil. The organic-rich Lower Oxford Clay has suffered more compaction, in general, than the Middle and Upper units. Within it, all large and/or relatively fragile fossils, notably ammonites, are squashed flat; small thick shelled bivalves, such as *Nucula*, may retain their shape.

Mineralization

The principal secondary minerals formed in and around Oxford Clay fossils are pyrite and calcite. Phosphate may be associated with arthropods and coprolites. Pyrite derives its sulphur from the sulphate contained in seawater; when organic matter is buried in reducing muds on the sea floor the sulphate is reduced to sulphide by the action of micro-organisms, and sulphide combines with iron to form pyrite, FeS_2. The chemical mechanisms are complex. A common result is that pyrite preferentially crystallizes in small enclosed voids, such as the inner phragmacone of an ammonite shell, forming a faithful internal mould. If the original shell was aragonite, it may subsequently dissolve, revealing the bright brassy pyrite to the collector. Many ammonites from the Middle and Upper Oxford Clay are preserved in this way, and they are very attractive fossils. In other cases pyrite less conspicuously fills the voids enclosed by shells of nuculid bivalves, as in Lower Oxford Clay shell-beds, or punctae in the shells of brachiopods. Less commonly, and only in the Lower Oxford Clay, pyrite *replaces* aragonitic shell material

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TEXT-FIG. 1.6. The vertebrate community of the Lower Oxford Clay. The great variety of vertebrates living in the Oxford Clay Sea occupied a wide range of trophic and living space niches. Many of the niches inhabited today by marine mammals were occupied by marine reptiles or large fish. Surface restricted, **a**, long necked plesiosaurs, **b**, ichthyosaurs, **c**, pliosaurs, **d**, marine crocodiles. Surface living fish, **e**, *Aspidorhynchus* sp. accompanied by shoals of '*Leptolepis*' (not illustrated). Mid water swimmers probably include the giant pachycormid, **f**, *Leedsichthys problematicus* and the smaller pachycormids, **g**, *Hypsocormus* spp., *Asthenocormus* sp., and *Sauropsis* sp. Benthic fishes included, **h**, *Lepidotes* spp., **i**, pycnodonts, **j**, *Asteracanthus ornatissimus*, and **k**, various small elasmobranchs. Invertebrates include **l**, **m**, surface and open water cephalopods. Benthic molluscs, **n**, *Gryphaea* sp., **o**, *Pinna* sp., **p**, deposit feeding bivalves, **q**, burrowing bivalves and **r**, grazing gastropods. Burrowing arthropods, **s**, may be common at some levels.

rather than merely filling cavities, and in some instances pyrite coats the exterior of shells. It may even replace bone. On weathering, pyrite readily oxidizes to brown iron oxides, mainly limonite, but morphological preservation may still be good. Discussion of pyrite types is given by Hudson & Palframan (1969), Hudson (1982) and Fisher (1986).

Calcite forms prominent layers of concretions at several horizons in the Lower Oxford Clay. Some of these formed early in burial, prior to compaction of the sediment. These may contain three-dimensional ammonites of species that occur crushed in shales outside the concretions, as in the Jason Zone at Peterborough. Other concretionary layers formed later and surround (but strengthen) already-crushed ammonites, as with the Acutistriatum Bed of the Bletchley-Calvert area. An unusual form of concretionary hardening is seen in the Jason Zone, Lower Oxford Clay at Calvert, Bucks. Sediment evidently infiltrated the body-chamber, but not the phragmacone, of large Kosmoceratid ammonites, and this became cemented. The phragmacone subsequently compacted, and only the body-chamber survives in good preservation. Fossils with voids that survived burial without crushing are usually filled with coarse, white or colourless calcite crystals. Similar calcite fills 'septarian' cracks in early diagenetic concretions, which may disrupt shells.

Examples of the effect of combinations of these preservational modes on the appearance of ammonites may be seen in the Plates of Chapter 4, e.g. Plate 12, Fig. 5 (crushed aragonitic shell), Fig. 15 (pyritic nucleus); Plate 14, Figs 2, 3 (uncrushed shell from a concretion).

FOSSIL GROUPS IN THE OXFORD CLAY

In summarizing the contribution of the various fossil groups to the fauna of the Oxford Clay it is useful to deal separately with the bottom-living fauna (the benthos), the swimming invertebrates (nekton), and the swimming vertebrates, fish and reptiles.

The benthic faunas provide our main evidence for conditions on the sea-floor, as summarized in the section on palaeoecology; the main contributions being by Hudson and Palframan (1969) and especially Duff (1975). There is a clear difference between the faunas of soft mud bottoms (most of the Lower Oxford Clay), stiff mud bottoms (most of the Middle and Upper Oxford Clay) and of shell beds.

Benthos. By far the dominant group is the **Bivalvia** (53 species; monograph by Duff, 1978). Notable features include the abundance of Nuculoida especially in the Lower Oxford Clay, and the relative diversity of surface-living Pterioida, which attached to a substrate by a byssus or by cementation; adult *Gryphaea* were free-lying recliners. This group also includes several species regarded by Duff (1975, 1978) as 'pendent'; that is attached to objects above the sea-floor, either floating or benthic algae. Controversy on their life habits continues, but their abundance does seem to vary independently of the 'normal' benthos. Many Oxford Clay bivalves occur in shell-beds, some of which are mere winnowed concentrations, but others formed distinct habitats, notably the *Gryphaea* shell-beds of the lower part of the Lower Oxford Clay. Bivalves requiring a firm sea-floor, including *Gryphaea* and most infaunal filter-feeders, are poorly represented in the main part of the Lower Oxford Clay, but re-appear in the Middle and Upper divisions, where diversity increases but abundance decreases.

Gastropods (5 species) and **Scaphopods** (1 species) are numerically minor members of the fauna but small *Dicroloma* and *Procerithium* species are abundant in the Lower Oxford Clay and appear in some of the trophic nuclei of Duff (1975).

Non-molluscan calcareous benthic macrofossils are very subordinate (**Brachiopods**, 6 spp.; **Coelenterates**, 2 spp.; **Bryozoans**, 4–5 species groups; **Annelids**, 3 spp.; **Cirripedes**, 2 spp.; **Echinoderms**, 6 spp.). The **Crustacea** excluding ostracods (12 species) were undoubtedly important and diverse members of the original fauna, and were responsible for constructing most of the recognizable trace fossils of the Oxford Clay, but their preservation is very patchy and they badly need modern study.

A distinctive part of the Oxford Clay biota is present as encrustations on large shells, particularly *Gryphaea* from the Middle and Upper Oxford Clay, or as 'bio-immured' faunas preserved on attachment scars (Taylor, 1990a,b). This fauna includes foraminifera, serpulids, bryozoa, and the small bivalve *Atreta*.

Nekton. The **ammonites** of the Oxford Clay are world famous, and their study has had a major influence on palaeontology and biostratigraphy. Specimens of *Kosmoceras* from Christian Malford are in virtually every major museum and many teaching collections. *Kosmoceras* from Peterborough were the subject of Brinkmann's classic research on statistical evolutionary palaeontology of 1929, which was given wider currency by Arkell (1933). Oxford Clay material figured prominently in Callomon's (1963) conclusive demonstration of sexual dimorphism in ammonites, whence a dimorphic pair grace the cover of Raup and Stanley's well known text-book (2nd edition, 1979); contemporaneous material from Poland inspired Makowski's (1962) independent and simultaneous proof of dimorphism. Palframan (1966, 1967) used beautifully-preserved pyritic nuclei from the Middle and Upper Oxford Clay in further, more detailed, studies on this topic. Because Britain occupies a critical position in Jurassic palaeogeography, between the Boreal and Tethyan realms, Oxford Clay ammonites are important in discussions of faunal provinciality, such as Callomon's (1985) wide-ranging survey of the evolution of the Cardioceratidae.

78 species of ammonite are recognized in this work. As discussed in Chapter 4, this number is much reduced because we have tried to include many named morphological variants, including sexual dimorphs, under one biospecies name. The sequence of faunas is detailed in the stratigraphical section, as the ammonites form the basis of the bio- and chrono-stratigraphy. The preservation of ammonites greatly affects their appearance and hence their appeal to the collector; this is also discussed above. In very general terms, the Lower Oxford Clay is dominated by Kosmoceratidae, the Middle Oxford Clay by Kosmoceratidae, Cardioceratidae, Perisphinctacea and Oppeliidae; the Upper Oxford Clay lacks Kosmoceratidae and has mainly a Cardioceratid-dominated fauna, with Perisphinctacea and Oppeliidae generally subordinate. Horizons of special preservation, such as the Lamberti Limestone, account for a disproportionate number of ammonite records.

Belemnites are very conspicuous in the Oxford Clay and because their rostra are so resistant they are among the fossils most commonly noticed by casual collectors. Six species are described here. Like ammonites, belemnites show faunal provincialism. More complete preservation of coleoid cephalopods also occurs in the Oxford Clay. Belemnites with phragmacone are quite common; rarely the pro-ostracum occurs also. The lightly calcified *Belemnotheutis* is not uncommon; other squid-like teuthids are virtually confined to the Christian Malford district, but their hooklets are common at most localities. **Nautilids** are surprisingly rare in the Oxford Clay, only one species being known.

Vertebrates. The **fish** fauna of the Oxford Clay is diverse both taxonomically and in mode of life (text-fig. 1.6); 32 species are described here. 17 are elasmobranchs—sharks, rays etc. which had cartilaginous skeletons but highly resistant teeth and fin-spines, which are quite common fossils. There are 16 species of actinopterygians, some of which bore well-calcified scales. The giant *Leedsichthys*, perhaps the largest fish of all time, was a filter-feeding analogue of the basking sharks and baleen whales of the present day.

Marine reptiles are by far the most spectacular fossils of the Oxford Clay. Isolated teeth, vertebrae, ribs and limb-bones are fairly common fossils, but the fame of the Oxford Clay rests on finds of articulated skeletons which are still being made (see Chapter 9) and which allow these beautiful animals to be reconstructed (text-figs 10.4, 10.7, 10.10, 10.11). There are 2 species of **ichthyosaur** both of the genus *Ophthalmosaurus* which, unlike Lias ichthyosaurs, generally lacked teeth, 5 species of long-necked plesiosaurs, 5 of short-necked pliosaurs and 4 of marine crocodiles. Thus the diversity of the Oxford Clay reptile fauna recalls that of the marine mammals of the present day, and a combination of functional morphology and the analysis of stomach contents allows the economy of the sea to be reconstructed with some confidence (Martill, 1988b).

Although it is fully marine, the Oxford Clay has yielded bones of 8 species of terrestrial dinosaurs, and 2 species of pterosaurs. These are invaluable in affording clues to life and environment on the contemporary land.

HISTORY OF RESEARCH

The Oxford Clay lacks the excellent coastal outcrops possessed by those other classic British Jurassic argillaceous formations, the Lias and the Kimmeridge Clay, and perhaps because of this its fossils did not attract the earliest investigators as those of the Lias, particularly, did. Instead, the best known collections of Oxford Clay fossils have come from inland exposures. In 1840–41 the Great Western Railway was constructed, and to enable it to cross the low-lying country of the Oxford Clay outcrop it was raised on an embankment. This was constructed from nearby borrow-pits which proved prolific sources of fossils. The most famous locality was near Christian Malford, but other cuttings made at the time near Trowbridge and later last century were also highly fossiliferous (Arkell, 1933; p. 345). These exposures yielded not only abundant crushed, but complete, ammonites but also soft-part preservations of coleoid cephalopods (Owen, 1844; Mantell, 1848, 1850).

The other major source of fossils, also from the Lower Oxford Clay, has been the numerous large brick-pits along the outcrop, and particularly around Peterborough. The large-scale brick industry dates from about 1880 (see below). The most notable collections were of vertebrates, assembled by the Leeds brothers late last century; see Chapter 8. Since mechanization of the brick-works collecting of vertebrates has become more difficult, but still continues. The continuous exposures afforded by the Peterborough pits were exploited in the classic work of Brinkmann (1929a,b) on ammonite evolution. Major advances in knowledge of the East Midlands brick-pits were summarized by Callomon (1968).

The higher parts of the Oxford Clay have never been as extensively exposed as the Lower division (although their coastal outcrop near Weymouth is far better). Two small brick-pits have been important this century. That at Woodham, Bucks., was described by Arkell in 1939; it was a prolific source of pyritic ammonite nuclei (Palframan, 1966, 1967; Hudson & Palframan, 1969) and also exposed the Lamberti Limestone with its giant ammonites. The pit at Warboys, Cambs., is in broadly similar facies but lies within the Upper Oxford Clay, overlain discomformably by Ampthill Clay. It was described by Spath (1939). Both these localities are also summarized by Callomon (1968).

In recent years Callomon (1968, 1984) has continued his researches on the ammonites and biostratigraphy of the Oxford Clay; Page (1989) has revised the stratigraphy of the Kellaways Formation and contiguous deposits. Duff (1975, 1978) has described the benthic faunas and monographed the bivalves of the Lower Oxford Clay. Martill (1983, 1984, 1985a,b,c, 1986a,b, 1987, 1988a,b, 1989a,b, 1990) has published a series of papers on the vertebrate fauna and its taphonomy.

FOSSIL–LAGERSTÄTTEN OF THE OXFORD CLAY

Seilacher *et al.* (1971) introduced the concept of fossil-lagerstätten (fossil ore-layers) as bodies of sediment that yield an unusual amount of palaeontological information (see Seilacher *et al.*, 1985). They are of two types, concentration- and preservation-lagerstätten, characterized respectively by quantity or quality of fossils preserved. Granted that no fossil is perfectly preserved, different types of preservation favour different types of study. Several parts of the Oxford Clay qualify as lagerstätten.

1. The Lower Oxford Clay in a general sense for the abundance and excellent preservation of its ammonites, which although crushed are frequently complete with body-chamber and aperture, and composed of their original nacreous aragonite with its elemental chemistry and isotopic composition intact. These properties favour both morphological (Brinkmann, 1929a) and geochemical (Williams, 1988) studies.
2. The Lower Oxford Clay, particularly the Jason Zone, at Peterborough, for its vertebrate fauna (see above, and Chapters 8, 9, 10).
3. The Lower Oxford Clay, mainly Phaeinum Subzone of Athleta Zone, of Christian Malford, Wilts, for exceptionally well-preserved ammonites accompanied by 'squids' with 'soft-part' preservation. This occurrence would well repay re-excavation.
4. The Middle-Upper Oxford Clay in Bucks. and Oxon. for the exquisite preservation of ammonites in the form of internal moulds, of the inner phragmacone only in large ammonites but including body chamber in small ones. This form of preservation allows detailed investigations of the early ontogeny, including development of the suture-line, but apertures are rarely preserved and no aragonite remains; thus the preservational bias is almost the opposite of that typical of the Lower Oxford Clay.

The Oxford Clay lagerstätten all involve phenomena such as richness in organic carbon, pyritization, and preservation of articulated vertebrate skeletons, that have sometimes been attributed to stagnant sea-floor conditions. Yet, with the possible exception of small thicknesses of sediment in the lowest Oxford Clay at Peterborough (and possibly of parts of the Christian Malford deposits?) the Oxford Clay always carries a benthic fauna. The preservation of the vertebrates probably depended more on the soft, almost soupy, nature of the sea-floor than on the state of oxygenation of the overlying water (Martill, 1987 and *in prep.*).

ECONOMIC GEOLOGY OF THE OXFORD CLAY

The Lower Oxford Clay supports the largest brick-making industry in the world. This account of it is based on Callomon (1968) and material supplied by the London Brick Company in 1980. The industry was relatively late to develop, for until the Fletton process of brick manufacture was developed at the end of the 19th century it had no particular advantages over other clays, and its hardness when fresh was a disadvantage. The key to the present industry's dominance lies in the uniformity (on a large scale) of the Lower Oxford Clay and its high content (averaging 5%) of organic matter of high calorific value and low combustion temperature. The uniformity enables highly mechanized extraction methods, and the organic content means that the bricks are virtually self-firing; low-grade coal is needed only to maintain and control, not to reach, the firing temperature of 1000°C. Other favourable circumstances include a low water content (around 20%), which means that the raw, unfired bricks are strong, and reduces heating costs, and an appropriate content of calcium carbonate (5–15%), enough to confer strength in firing but not enough to add to firing costs or cause 'blistering' during decomposition. In this connection fossils have economic significance. Large calcareous shells, particularly *Gryphaea* and belemnites, are unfavourable because even when crushed they can leave fragments large enough to burst a brick. Fortunately, they are abundant only in the lowest beds of the Oxford Clay, which are left in the floor of the pits, and in the Middle Oxford Clay above the worked levels. Larger fossils in the excavated clay are still removed by hand, but the old practice of rewarding the workers for each bucket full of fossils has sadly died.

From the point of view of the fossil collector the best period was undoubtedly that during which the Leeds brothers made their vertebrate collections (*circa* 1867–1917), after the Industrial Revolution created a vast demand for bricks, but before mechanization rendered the hand-working of the clay uneconomic. Along with mechanization has come an increasing concentration of the industry. The many original companies are now all part of the London Brick Company, itself since 1984 part of the Hanson Group.

The Middle and Upper Oxford Clays have never rivalled the Lower as sources of industrial materials; indeed the Middle Oxford Clay forms part of the overburden in some of the brick pits. However bricks were made from these units at Woodham from the 1930s to the 1960s, and the Upper Oxford Clay at Warboys was worked for extruded clay pipes for land-drains, etc. until the early 1980s. Its plasticity made it suitable for the extrusion process; large *Gryphaea* were removed by hand.

2. BIVALVES

by KEITH DUFF

THE bivalves of the Oxford Clay, although frequently abundant and diverse, especially in the Lower Oxford Clay, had not been described comprehensively prior to the early 1970s, when Duff undertook detailed palaeoecological and taxonomic studies (Duff, 1975, 1978). Previously, only selected members of the fauna had been figured by other authors, such as Arkell (1929–1937, 1930, 1947a, 1947b), Cottreau (1925–1932), Cox (1937), Cox & Arkell (1948–1950), Damon (1860, 1888), Jefferies & Minton (1965), Leckenby (1859), Lycett (1872–1883), Morris (1850), Morris & Lycett (1851–1855), Phillips (1829, 1871), Sowerby & Sowerby (1812–1846), Walker (1972), Woodward (1895) and Young & Bird (1822).

The rich bivalve fauna of the Oxford Clay is frequently very well preserved, often uncrushed, and sometimes pyritized. In the Lower Oxford Clay the original shell mineralogy and structure are often preserved, both as aragonite and calcite, and the original shell microstructure may sometimes be seen. Bivalves occur throughout the Oxford Clay, although they are usually most frequent in the concentrated shell beds which are so well developed in the Lower Oxford Clay. Some *Gryphaea*-rich horizons occur in the Middle and Upper Oxford Clay, but these are not as rich sources of fossils as the shell beds of the Lower Oxford Clay. Both isolated valves and articulated shells occur in the shell beds, and at certain horizons they are completely pyritized, giving very fine preservation of details of the shell morphology. Pyritized internal moulds are common in the Middle and Upper Oxford Clay. Few bivalves occur in life position, most being found lying parallel to the bedding surfaces, but generally they cannot have travelled far since even fragile shells are often preserved more or less complete. Their attitude might, in part, be due to rotation during compaction.

The morphological characters used to describe the species in these sections are those used by Cox (1969) and Stenzel (1971), but more detailed explanations of certain characters are given in Duff (1978). The latter publication also contains interpretations of the life habits of the Oxford Clay bivalve fauna, and gives detailed information on the individual species. The taxonomic framework is principally that defined by Newell (1969), but with modifications by Duff (1978), Waller (1978), Johnson (1984), Fürsich & Palmer (1982) and Fürsich & Werner (in press). In the descriptions, the terms small, medium, large and very large are defined by the following size ranges: small, up to 10 mm long; medium, 11–30 mm; large, 31–150 mm; very large, 151 mm and over. The criterion of adulthood in all species is the crowding of growth-lines towards the ventral margin.

SPECIES DESCRIPTIONS

Class BIVALVIA
Subclass PALAEOTAXODONTA
Order NUCULOIDA
Superfamily NUCULACEA
Family NUCULIDAE
Genus *NUCULOMA*

Nuculoma pollux (d'Orbigny)

Plate 1, fig. 1

Description. Medium sized (10–19 mm long) strongly triangular relatively compressed shell, with markedly opisthogyrate slightly enrolled umbones, set slightly posterior of median; posteroventral angle sharp and slightly produced; posterodorsal margin concave, broken by a prominent, evenly convex escutcheon pout. Ornament of interdigitate concentric striae on body of the shell; dorsal areas with faint growth striae, not interdigitate. Corselet large, excavate, cordate, occupying whole of posterodorsal region, bounded by sharp umbonal carinae running to the posteroventral angles. Escutcheon smaller, prominent, cordate, with two arcuate elevated ridges running from umbones to posterior end of hingeline. Lunule elongate, biconcave, lanceolate, bounded by rounded carinae. Taxodont hinge, ligament internal.

Remarks. Usually found as articulated closed shells. Distinguished from the similarly shaped *Palaeonucula triangularis* Duff by its much more concave posterodorsal margin, more enrolled umbones, lower inflation and interdigitate ornament. *Nuculoma castor* (d'Orbigny) is more inflated and has nearly terminal umbones. *N. kathrynae* Duff is more globular, has a more rounded posteroventral angle, and has more enrolled and nearly terminal umbones.

Age and distribution. Oxford Clay (undifferentiated) of Wiltshire, and Middle to Upper Oxford Clay (*athleta* to *mariae* Zones) of Oxfordshire.

Nuculoma kathrynae Duff

Plate 1, figs 5a,b

Description. Small to medium sized (8–11 mm long), obliquely triangular, globose shell, with strongly opisthogyrate enrolled umbones placed close to the posterior extremity of the shell; posteroventral angle rounded, not produced; posterodorsal margin straight to gently convex, with small escutcheon pout. Ornament of interdigitate concentric striae, except on dorsal areas where there are only faint growth lines. Corselet large, lightly impressed, with rounded umbonal margins. Escutcheon small, cordate, prominent, reaching about halfway to the posteroventral angle. Lunule not differentiated, no bounding carinae. Taxodont hinge, about 15 small chevron-shaped teeth anteriorly, and 8 posteriorly.

Remarks. Occurs as isolated valves and articulated shells. *N. castor* (d'Orbigny) has more enrolled and nearly terminal umbones, with only 4 posterior teeth, and lacks a clearly-differentiated escutcheon.

Age and distribution. Known only from the Oxford Clay (undifferentiated) of Wiltshire.

Genus *PALAEONUCULA*

Palaeonucula triangularis Duff
Plate 1, figs 4a,b

Description. Medium sized (10–19 mm long) strongly trigonal, well inflated shell, with prominent opisthogyrate umbones set slightly posteriorly, and not enrolled. Slight escutcheon pout. Posteroventral angle about a right angle and variably produced, giving a concave posterodorsal margin. Ornament of irregular concentric growth lines over the whole shell surface; not interdigitate; occasionally has very faint radial striae in very well preserved specimens. Corselet and escutcheon well-developed, lunuliform; escutcheon bounded by rounded margins. Lunule absent. Taxodont hinge, up to 16 teeth anteriorly and 10 posteriorly.

Remarks. Often well preserved, occurring as isolated valves, articulated shells, and internal moulds showing details of the musculature. The large quantities of shells found at horizons in the Lower Oxford Clay show this to be a very variable species in terms of shell dimensions and outline. Differs from *Nuculoma* in lacking interdigitate ornament.

Age and distribution. Abundant throughout England in the Lower and Middle Oxford Clay (*calloviense* to *athleta* Zones), often forming shell beds up to 10 cm thick in the Lower Oxford Clay.

Palaeonucula calliope (d'Orbigny)
Plate 1, figs 2 & 3

Description. Medium sized (14–19 mm long) subrectangular to subelliptical well-inflated shell, elongated posterodorsally, with prominent rounded opisthogyrate umbones placed close to the posterior margin.

Corselet and escutcheon poorly developed, with a very small escutcheon pout. Ornament of irregularly spaced concentric growth lines, often coarsened into prominent growth halts near the ventral margin; no radial elements. Taxodont hinge, up to 20 teeth anteriorly and at least 6 posteriorly.

Remarks. More subrectangular or subelliptical than *P. triangularis*, with a more elongated form, a much weaker corselet and escutcheon and more anterior teeth. *P. ornati* (Quenstedt) and *P. caecilia* (d'Orbigny) are more elongate and have more centrally placed umbones.

EXPLANATION OF PLATE 1

Fig. 1. *Nuculoma pollux* (d'Orbigny). Right valve; Oxford Clay, Wiltshire, × 1 (p. 36).

Figs 2, 3. *Palaeonucula calliope* (d'Orbigny). 2, right valve, Upper Oxford Clay (*mariae* Zone), Scarborough, Yorkshire, × 1. 3, left valve, Oxford Clay, Lukow, Poland, × 1 (p. 37).

Fig. 4a,b. *Palaeonucula triangularis* Duff. a, right valve, b, dorsal view, Lower Oxford Clay (*coronatum* Zone), Stewartby, Bedfordshire, × 1 (p. 37).

Fig. 5a,b. *Nuculoma kathrynae* Duff. a, right valve, b, anterior view, Oxford Clay, Wiltshire, × 1·5 (p. 36).

Figs 6, 7. *Mesosaccella morrisi* (Deshayes). 6, right valve, Lower Oxford Clay, Kempston, Bedfordshire, × 1·5. 7, left valve, internal view, Lower Oxford Clay (*coronatum* Zone), Stewartby, Bedfordshire, × 2 (p. 40).

Figs 8, 9. *Solemya woodwardiana* Leckenby. 8, left valve, Lower Oxford Clay (*coronatum* Zone), Calvert, Buckinghamshire, × 1. 9, left valve, Kellaways Rock, Scarborough, Yorkshire, × 0·75 (p. 41).

Figs 10, 11. *Dacryomya acuta* de Loriol. 10, left valve, Oxford Clay, Lydlinch, Wiltshire, × 1·5. 11, internal mould viewed from the right, Oxford Clay, St Ives, Cambridgeshire, × 1·5 (p. 40).

Fig. 12. *Grammatodon* (*Grammatodon*) *minimus* (Leckenby). Left valve, silicone rubber cast, Lower Oxford Clay (*coronatum* Zone), Calvert, Buckinghamshire, × 1·5 (p. 41).

Figs 13, 14. *Grammatodon* (*Grammatodon*) *clathratus* (Leckenby). 13, left valve, Hackness Rock, Scarborough, Yorkshire, × 1. 14, left valve, internal view, Lower Oxford Clay (*jason* Zone), Stewartby, Bedfordshire, × 0·75 (p. 42).

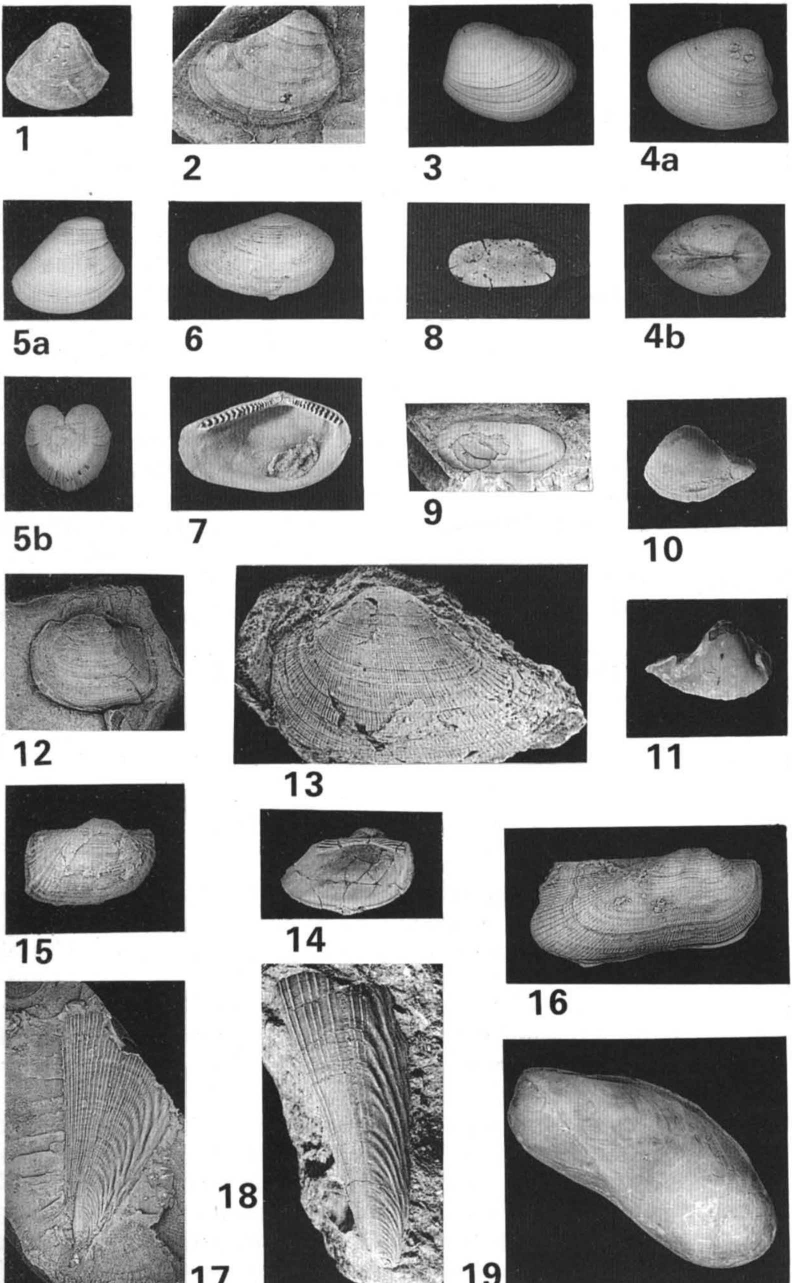
Fig. 15. *Grammatodon* (*Grammatodon*) *concinnus* (Phillips). Right valve, Lower Oxford Clay (*jason* Zone), Calvert, Buckinghamshire, × 1.(p. 42).

Fig. 16. *Grammatodon* (*Cosmetodon*) *keyserlingii* (d'Orbigny). Right valve, Oxford Clay, Lukow, Poland, × 1 (p. 43).

Fig. 17. *Pinna* (*Pinna*) *mitis* (Phillips). Left valve, silicone rubber cast, Lower Oxford Clay (*jason* Zone), Stewartby, Bedfordshire, × 0·75 (p. 44).

Fig. 18. *Pinna* (*Pinna*) *lanceolata* J. Sowerby. Left valve, Coralline Oolite (Oxfordian), Malton, Yorkshire, × 0·8 (p. 44).

Fig. 19. *Modiolus* (*Modiolus*) *bipartitus* J. Sowerby. Right valve, Upper Oxford Clay (*cordatum* Zone), Weymouth, Dorset, × 0·7 (p. 43).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Age and distribution. Widespread throughout England in the Middle and Upper Oxford Clay (*lamberti* to *cordatum* Zones).

Superfamily NUCULANACEA
Family MALLETIIDAE
Genus *MESOSACCELLA*
Mesosaccella morrisi (Deshayes)
Plate 1, figs 6 & 7

Description. Medium sized (5–18 mm long) shell, subovate in outline and posteriorly elongated, with small pointed orthogyrate umbones placed anterior of median; posterodorsal margin usually slightly concave, leading to a rounded and produced posterior margin. Taxodont hinge, with straight tooth rows set at an angle of about 140°; teeth chevron shaped, the posterior row about 30% longer than the anterior row, with up to 25 teeth posteriorly and 18 anteriorly. External amphidetic ligament. Ornament of faint concentric growth lines, locally coarsened into rugae. Shell margin entire, without gapes; pallial sinus present.
Remarks. An abundant and distinctive species which occurs as isolated valves, articulated shells and internal moulds. The Liassic species *M. galatea* (d'Orbigny) is shorter anteriorly, has a greater umbonal angle, and has incised concentric striae obliquely cutting across the growth lines.
Age and distribution. Lower to Upper Oxford Clay (*calloviense* to *cordatum* Zones), abundant throughout England.

Family NUCULANIDAE
Genus *DACRYOMYA*
Dacryomya acuta de Loriol
Plate 1, figs 10 & 11

Description. Medium sized species (up to 12 mm long), inflated, subtrigonal in outline, with a sharply-produced rostrate margin posteriorly. Umbones placed subcentrally, prominent, opisthogyrate. Posterodorsal margin concave in outline, ventral margin smoothly rounded. Prominent escutcheon, bounded by a well developed carina running from the umbones to the posterior angle, deeply impressed, with slight elevation along the hinge margin. Ornament of faint concentric growth lines over the whole shell surface. Taxodont hinge.
Remarks. Occurs as articulated shells and internal moulds, often pyritized in the Upper Oxford Clay. The latter are very distinctive, due to the barbed appearance of the posterior area, caused by pyritization of the deeply impressed posterior adductor muscle scars.
Age and distribution. Middle and Upper Oxford Clay (*lamberti* to *cordatum* Zones) throughout England.

Subclass CRYPTODONTA
Order SOLEMYOIDA
Superfamily SOLEMYACEA
Family SOLEMYIDAE
Genus *SOLEMYA*
Solemya woodwardiana Leckenby
Plate 1, figs 8 & 9

Description. Medium sized (11–17 mm long) elongate elliptical compressed shell, with umbones placed close to the posterior margin; umbones not prominent, opisthogyrate. Hinge edentulous. Shell thin and fragile, ornamented by riblets radiating from the umbonal area, most marked at anterior and posterior extremities, and by faint concentric growth lines. Anterior adductor muscle scar often pyritized, with a visceral mass integument scar running from its posteroventral corner obliquely towards the dorsal shell margin.
Remarks. Common at certain horizons within the Lower Oxford Clay, where it occurs as articulated wide open shells and as isolated valves. Larger, more coarsely ribbed forms up to 38 mm long are known from the *athleta* Zone shales of Brora in Sutherland.
Age and distribution. Common in the Lower Oxford Clay (*jason* and *grossouvrei* Subzones) of the Midlands and Dorset, and in the Brora Brickclay Member (*athleta* Zone) of Brora, Sutherland. Also known from the Hackness Rock (*athleta* to *lamberti* Zones) of Yorkshire.

Subclass PTERIOMORPHIA
Order ARCOIDA
Superfamily ARCACEA
Family PARALLELODONTIDAE
Subfamily GRAMMATODONTINAE
Genus *GRAMMATODON*
Subgenus *GRAMMATODON*
Grammatodon (*Grammatodon*) *minimus* (Leckenby)
Plate 1, fig. 12

Description. Medium sized (6–15 mm long) subrectangular to subquadrate well inflated shell, with prominent slightly prosogyrate umbones placed anteriorly. Ligament area of elongated diamond shape, up to 3 mm wide, and stretching almost the entire length of the hinge margin, with chevron shaped grooves radiating from beneath the umbones. Anterior margin smoothly curved with ventral margin. Sculpture distinctive, with concentric riblets and faint radial striae, becoming only slightly stronger anteriorly and posteriorly, giving a fine cancellate pattern. Hinge line straight, with 3–5 horizontal posterior pseudolaterals,

and 5–7 oblique anterior cardinal teeth converging to a point beneath the umbones.
Remarks. Characterized by its subquadrate form and the fine cancellate ornament pattern, without marked coarsening of the radial striae towards the anterior margin; this distinguishes the species from *G. concinnus* (Phillips). The ornament is considerably finer and much less regular than in *G. clathratus* (Leckenby).
Age and distribution. Abundant in the Lower Oxford Clay (*grossouvrei* Subzone) of England where its appearance in great numbers coincides with the base of the subzone; also occurs rarely in the *jason* and *obductum* Subzones and the *athleta* Zone. Hackness Rock of Yorkshire (*athleta* to *lamberti* Zones).

Grammatodon (*Grammatodon*) *concinnus* (Phillips)
Plate 1, fig. 15

Description. Medium sized (14–24 mm long) obliquely subrectangular shell, with long straight hingeline occupying nearly the whole length of the shell. Posterior margin oblique, with sharp umbonal carina running to the posteroventral angle, and marking off a radially striated posterior area with 12–15 prominent striae; flanks of shell often ornamented by fine radial striae; 3–5 coarse, widely-spaced radial riblets occur anteriorly, separated by fine intercalated radial striae. Broad cardinal area with duplivincular ligament. Dentition similar to *G. minimus*.
Remarks. Distinguished from *G. minimus* by the presence of coarse anterior and posterior riblets, and from *G. clathratus* by the less regular radial striae on the valve flanks and by the presence of a strong umbonal carina. In the Lower Oxford Clay the species occurs as isolated valves and articulated shells with the shell material preserved; occasionally the shell material is replaced by pyrite. In the Upper Oxford Clay shell material does not occur and preservation is as composite internal moulds, which display some of the external ornamentation.
Age and distribution. Kellaways Rock to Lower Oxford Clay (*calloviense* to *jason* Zones) of southern England, and Upper Oxford Clay (*mariae* Zone) of Yorkshire.

Grammatodon (*Grammatodon*) *clathratus* (Leckenby)
Plate 1, figs 13 & 14

Description. Large sized (23–50 mm long) subtrapezoidal shell with straight, relatively short, hinge line occupying less than three-quarters of the shell length. Umbones prominent, inflated, and with a broadly rounded umbonal carina. Posteroventral angle acute, giving the rear end of the shell a produced appearance. Ornament of fine radial riblets over the anterior and median parts of the valves, becoming wider and flatter posteriorly; no coarsening of riblets towards extremities. Dentition taxodont, with horizontal anterior and posterior pseudolaterals, and no vertical central teeth or oblique anterior pseudolaterals; faces of pseudolaterals finely crenulate.

Remarks. This species has traditionally been referred to "*Cucullaea*" on the basis of its external form and ornament, but it lacks the prominent series of subvertical central teeth and the prominent posterior myophoric buttress of that genus. The dentition and regular ornament pattern distinguish it from other Callovian species of *Grammatodon*.

Age and distribution. Lower Oxford Clay (*jason* Zone) of central and southern England and Hackness Rock (*athleta* to *lamberti* Zones) of Yorkshire.

Subgenus *COSMETODON*

Grammatodon (*Cosmetodon*) *keyserlingii* (d'Orbigny)

Plate 1, fig. 16

Description. Large sized (up to 50 mm long) elongate subcylindrical species, with a long straight hingeline occupying nearly the whole length of the shell. Posterior margin moderately produced and obliquely truncated. Ventral margin with a strongly developed sinus in its central part, running directly to the middle of the broad umbonal area. Flanks of the shell ornamented by regular fine radial riblets, crossed by irregularly spaced growth lines. Hinge plate wide, with 5–7 short narrow oblique anterior teeth, and 3 long narrow posterior teeth; anterior and posterior teeth converge towards a point well beneath the umbones.

Remarks. Externally, this species looks rather like a *Parallelodon*, especially in the presence of a strong umbonal sinus. However, the dentition is not that of a *Parallelodon*, and Branson (1942) designated this species as the type species of his new subgenus *Cosmetodon*.

Age and distribution. Middle and Upper Oxford Clay of England (*athleta* to *cordatum* Zones). Also known from the Kellaways Rock (*calloviense* Zone) of Yorkshire, and is common in the Corallian.

Order MYTILOIDA

Superfamily MYTILACEA

Family MYTILIDAE

Subfamily MODIOLINAE

Genus *MODIOLUS*

Subgenus *MODIOLUS*

Modiolus (*Modiolus*) *bipartitus* J. Sowerby

Plate 1, fig. 19

Description. Large sized (36–70 mm long) strongly oblique elongate-elliptical to subtrapezoidal shells, with a long straight to gently convex

hingeline and terminal umbones. Ventral margin markedly concave in outline, with a strong umbonal sulcus terminating in the central part of the concavity, and marking off a prominent anteroventral region which bulges anteriorly. Ornament of irregularly spaced concentric growth lines, locally coarsened and elevated as growth rugae; no radial or imbricate ornament. Ligament elongate, external, opisthodetic, parallel to the hingeline.
Remarks. A long ranging and well known species which occurs frequently at intervals through the Callovian and Oxfordian. It differs from *M. imbricatus* J. Sowerby (a Bajocian to Lower Callovian species) in lacking fine concentric threads, often strengthened into imbricate growth lamellae, on the shell flanks.
Age and distribution. Kellaways Clay (*calloviense* Zone) to Upper Oxford Clay (*cordatum* Zone) of England; especially common in the Lower and Middle Oxford Clay of central and southern England, and the Red Nodule Beds (Upper Oxford Clay) of Weymouth.

Superfamily PINNACEA
Family PINNIDAE
Genus *PINNA*
Subgenus *PINNA*
Pinna (*Pinna*) *mitis* Phillips
Plate 1, fig. 17

Description. Large sized (25–85 mm long) elongate fan-shaped shell, with terminal umbones. Outline of shell wedgelike, with straight dorsal margin and sinuous ventral margin which is initially concave and then becomes convex in outline. Weak median carina separates radially ribbed dorsal flank of shell from radially and concentrically ornamented ventral flank, in which growth lines are well marked; dorsal flank with 13–22 radial riblets and very fine reticulate ornament, ventral flank with 6–14 riblets.
Remarks. A very distinctive species, which differs from the larger *P. lanceolata* J. Sowerby in overall outline and density of ribbing. In *P. lanceolata* the ventral margin is convexly curved throughout its length rather than having the sinuous form of *P. mitis*, the dorsal part of the valve has only 8–10 sharp wire-like radial ribs, and the ventral area has only 3–5 radial ribs.
Age and distribution. Locally abundant in the Kellaways Clay (*calloviense* Zone) to Upper Oxford Clay (*cordatum* Zone) throughout England.

Pinna (*Pinna*) *lanceolata* J. Sowerby
Plate 1, fig. 18

Description. Very large elongate species, up to 220 mm long, in which the dorsal and ventral margins diverge regularly, the dorsal margin gently

concave and the ventral margin gently convex. Median carina well marked, with 8–10 radial ribs (fading posteriorly) on the dorsal flanks and 3–5 radial ribs ventrally; posterior part of valves marked by coarse concentric growth puckers.
Remarks. Common in the Corallian Beds (Oxfordian), but also occurs frequently in the Kellaways Rock of the South Cave area of Humberside, and occasionally in the Oxford Clay (*mariae* Zone) of Scarborough.
Age and distribution. Lower Callovian (*calloviense* Zone) of north Humberside and Lower Oxfordian (*mariae* Zone) of Scarborough.

Order PTERIOIDA
Suborder PTERIINA
Superfamily PTERIACEA
Family PTERIIDAE
Genus *PTEROPERNA*
Pteroperna pygmaea (Dunker)
Plate 2, fig. 8

Description. Medium sized (5–15 mm long) obliquely produced pteriiform shell with long straight hinge line and anterior and posterior auricles; posterior margin emarginate. Umbones small and placed in the front quarter of the hinge line. Posterior auricle longer and narrower than anterior auricle, with a sharp topped ridge running from the umbones to the posterior emargination; another ridge, slightly less elevated, runs along the posterior hinge margin. Umbonal carina runs to the posterior angle. Ornament of faint concentric growth lines becoming more closely packed on the posterior auricle; at the dorsal extremities of the anterior auricle the lines bifurcate and become more elevated. Hinge margin obliquely flattened, with about 12 very fine vertical teeth anteriorly; rounded peg-like apophysis on the left valve, just anterior of the umbones; long narrow posterior lateral teeth in each valve.
Age and distribution. This species occurs rarely in the Kellaways Rock and Lower Oxford Clay of Wiltshire and central England (*calloviense* to *athleta* Zones).

Family INOCERAMIDAE
Genus *PARAINOCERAMUS*
Parainoceramus subtilis (Lahusen)
Plate 2, fig. 11

Description. Large sized (up to 75 mm long) thin-shelled subrectangular to subovate species with straight hinge margin; hinge line about half the length of the shell. Umbones small, subterminal, gently prosogyrate. Ornament of faint concentric growth lines, with variably developed regular or irregular concentric ridges. Hinge plate with two small Λ-shaped mytiliform teeth immediately beneath the umbo of the right valve, and with five widely-spaced ligament pits, becoming more crowded towards the umbones.

Remarks. A variably shaped species in which the nacreous inner layer is usually well preserved, the outer calcitic layer being more fragile. It commonly occurs in clusters in the Lower Oxford Clay.

Age and distribution. Common in the Lower Oxford Clay (*calloviense* to *athleta* Zones) throughout central and southern England.

Family ISOGNOMONIDAE
Genus *ISOGNOMON*
Subgenus *ISOGNOMON*
Isognomon (*Isognomon*) *promytiloides* Arkell
Plate 2, fig. 10

Description. Large species (up to 70 mm long), rhomboidal to subquadrate in outline, slightly oblique, compressed. Very prominent, hooked, anteriorly-directed umbones, not protruding above the hingeline, and placed at the anterior extremity of the hingeline. Anterior margin concave in outline, especially beneath the umbones; posterior margin subparallel to anterior margin, meeting dorsal margin at an angle greater than 90°. Ornament of irregular concentric growth lines, locally prominent and sometimes slightly coarsened. Ligamental area broad, with numerous irregularly arranged ligamental grooves.

EXPLANATION OF PLATE 2

Figs 1, 2, 3. *Meleagrinella braamburiensis* (Phillips). 1, left valve, Oxford Clay, Trowbridge, Wiltshire, ×1. 2, left valve, silicone rubber cast, Lower Oxford Clay (*coronatum* Zone), Calvert, Buckinghamshire, ×1·75. 3, right valve, Lower Oxford Clay (*coronatum* Zone), Stewartby, Bedfordshire, ×2 (p. 49).

Figs 4, 5. *Oxytoma* (*Oxytoma*) *inequivalve* (J. Sowerby). 4, left valve, silicone rubber cast, ×1·5. 5, right valve, ×2·5. Lower Oxford Clay (*jason* Zone), Stewartby, Bedfordshire (p. 48).

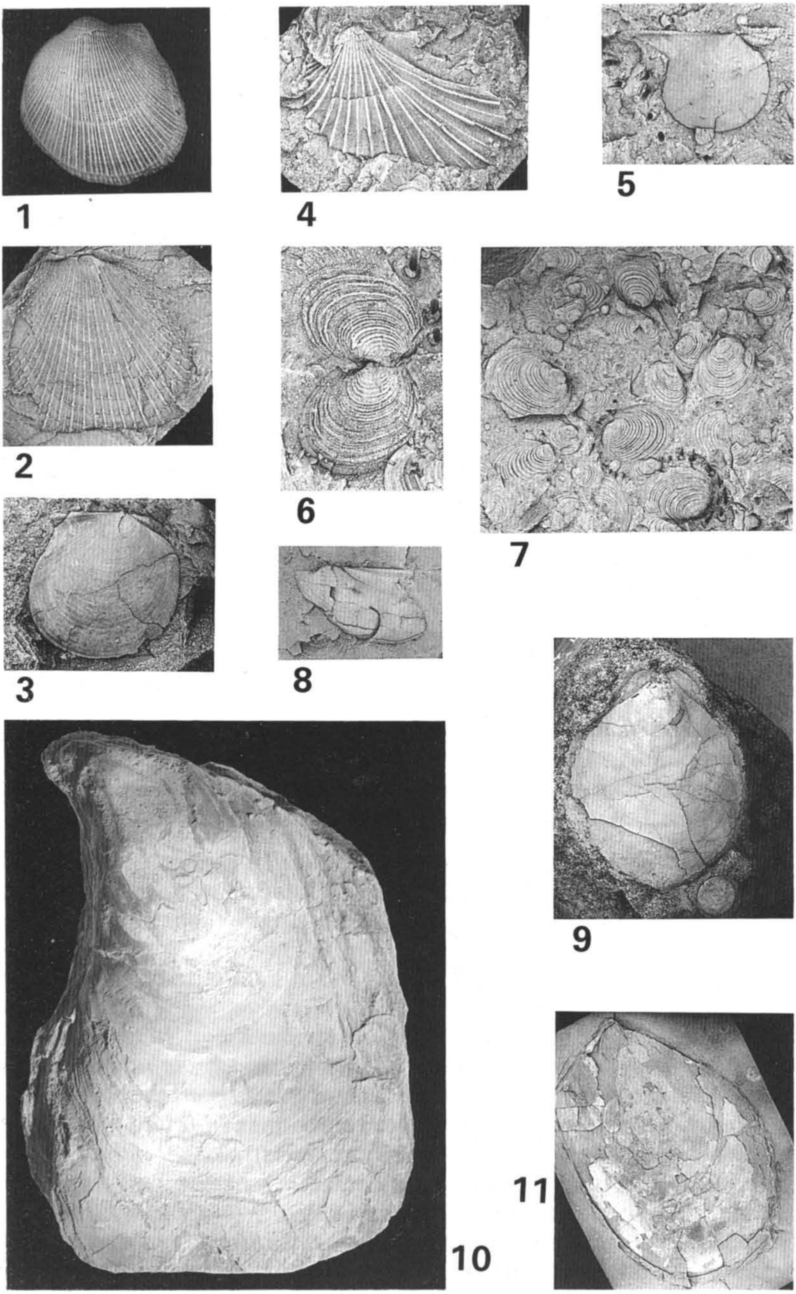
Figs 6, 7. *Bositra buchii* (Roemer). 6, articulated valves, Lower Oxford Clay (*coronatum* Zone), Stewartby, Bedfordshire, ×2·5. 7, typical 'plaster' of shells, Lower Oxford Clay (*jason* Zone), Chickerell, Dorset, ×1 (p. 48).

Fig. 8. *Pteroperna pygmaea* (Dunker). Left valve, Lower Oxford Clay, Wiltshire, ×1·5 (p. 45).

Fig. 9. *Entolium* (*Entolium*) *corneolum* (Young & Bird). Left valve, Hackness Rock, Scarborough, Yorkshire, ×1 (p. 50).

Fig. 10. *Isognomon* (*Isognomon*) *promytiloides* Arkell. Left valve, Oxford Clay, Radipole, Dorset, ×1 (p. 46).

Fig. 11. *Parainoceramus subtilis* (Lahusen). Right valve, Lower Oxford Clay, Wiltshire, ×0·75 (p. 45).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Remarks. A distinctive species characterized by its hooked umbonal shape and flattened form.
Age and distribution. Upper Oxford Clay (*cordatum* Zone) of Dorset.

Superfamily PECTINACEA
Family POSIDONIIDAE
Genus *BOSITRA*
Bositra buchii (Roemer)
Plate 2, figs 6 & 7

Description. Medium sized (3–15 mm long) very thin shelled, compressed, suborbicular species which usually occurs as articulated gaping shells. Dorsal margin straight, rest of margin a continuous sweeping curve. Ornament of strong concentric folds affecting the whole thickness of the shell; crests of folds rounded and separated by angular furrows. Wide anterior and posterior gapes. Very thin shell with prismatic calcite outer layer and nacreous inner layer; shell material frequently with a slight silvery-bluish tinge.
Remarks. An abundant species at many horizons within the Oxford Clay, frequently occurring in swarms, usually of wide open articulated shells. The mode of life of the species has been the subject of considerable debate, Jefferies & Minton (1965) suggesting it was nektoplanktonic, with a free-swimming pelagic habit, whilst Duff (1978) proposed that it was byssally attached to floating organic matter (driftwood and algal fronds), the so-called "pendent" life habit.
Age and distribution. The species is very long ranging, and is almost cosmopolitan in its distribution. It is known from rocks of Lower Jurassic (Toarcian) to Upper Jurassic (Oxfordian) age, and is abundant throughout the Oxford Clay (*calloviense* to *cordatum* Zones) of England.

Family OXYTOMIDAE
Genus *OXYTOMA*
Subgenus *OXYTOMA*
Oxytoma (*Oxytoma*) *inequivalve* (J. Sowerby)
Plate 2, figs 4 & 5

Description. Large sized species (up to 40 mm long), suborbicular to obliquely subovate in outline, with slightly prosogyrate umbones and valves of unequal size; left valve about twice as large as the right valve. Straight hinge line with well developed anterior and posterior auricles.

Left valve obliquely subovate to suborbicular, inflated, with umbones placed close to the anterior margin of the hingeline; very strongly developed posterior auricle, with deep subauricular sinus. Ornament very variable, consisting of arrangements of primary, secondary and tertiary radial riblets, crossed by scalloped concentric growth lines on the body of the shell; ribs absent from the auricles. Hinge plate with a long ligament area and a small triangular resilifer; an elongate depression lies immediately beneath, and parallel to, the anterior end of the hinge margin, to receive the anterior part of the hinge of the right valve. Disjunct pallial line consisting of up to 25 tiny pallial muscle scars.

Right valve much smaller and rounder in outline, more or less flat, and rather thicker than the left valve. Hinge line very long, but fragile and easily broken; posterior auricle very large, elongate, flattened, and sharply pointed, with subauricular sinus less well developed than in the left valve. Anterior auricle small, pointed, with a deep byssal notch beneath, and well differentiated from the body of the shell by a strong auricular sulcus; ctenolium absent. Ornament of faint radial striae, without secondaries or tertiaries; concentric growth lines hardly visible. Ligament area with triangular resilifer. Disjunct pallial line.

Remarks. This species shows considerable variation in ornament pattern, with a wide range of ribbing types. It is characterized by the left valve being about twice as large as the right valve in articulated specimens; the closely related *O. expansum* (Phillips) from the Corallian has valves of equal size, and also has consistently coarser ribbing.

Age and distribution. The species occurs from the Lower Jurassic (Hettangian) to the Upper Jurassic (Kimmeridgian), and occurs throughout the Kellaways Beds, Hackness Rock and Oxford Clay (*calloviense* to *cordatum* Zones), being particularly abundant in the *jason, coronatum* and *lamberti* Zones.

Genus *MELEAGRINELLA*

Meleagrinella braamburiensis (Phillips)

Plate 2, figs 1, 2 & 3

Description. Large sized species (up to 35 mm long), suborbicular to subquadrangular in outline, with left valve about twice the size of the right valve. Straight hinge line with posterior auricle only.

Left valve subquadrangular in outline, inflated, with a short prominent pointed posterior auricle; remainder of shell margin obliquely rounded. Umbones prominent, inflated. Ornament of 35–55 fine primary radial riblets, extending onto the posterior auricle, and often with intercalated secondaries; concentric growth lines often raised into squamae where they cross the primary riblets. Hingeline straight, about half the length of the shell, with broad ligament area and subrectangular resilifer posterior to the umbones; prominent rounded toothlike apophysis lies immediately anterior of the resilifer, projecting ventrally into the shell cavity. Pallial line simple.

Right valve suborbicular, of low inflation, and about half the size of the left valve. Posterior auricle broad, pointed, flattened, not clearly marked off from body of the shell; anterior auricle very small, pointed, separated from body of the shell by a deep auricular sulcus, with a well developed byssal notch beneath it; no ctenolium. Hinge line straight, rest of shell margin continuously curved. Ornamented by 35–50 faint primary radial riblets, with some intercalated secondaries; weak squamae sometimes seen in larger specimens, but usually only faint reticulation is seen. Small triangular resilifer lies behind umbo. Pallial line simple.

Remarks. Variation within populations of this species is considerable, and is even greater between populations from different horizons, being reflected mainly in style of ornamentation and degree of inflation. Specimens from the Lower Oxford Clay are generally of lower inflation and have a thinner and more fragile shell. *M. echinata* (Smith) from the Cornbrash is smaller, more inflated, has fewer ribs, and has the valves more equal in size. *M. ovalis* (Phillips) from the Corallian has a less well developed posterior auricle, and more densely packed radial riblets on both valves, without squamae.

Age and distribution. Kellaways Beds to Upper Oxford Clay (*calloviense* to *cordatum* Zones) throughout England.

Family PECTINIDAE
Genus *ENTOLIUM*
Subgenus *ENTOLIUM*
Entolium (*Entolium*) *corneolum* (Young & Bird)
Plate 2, fig. 9

Description. Large species (up to 72 mm high), of suborbicular to subovate outline, with small anterior and posterior auricles; on left valve, auricles project above the level of the hinge line; auricles marked off from shell body by auricular sulcus. Umbones small, median, pointed, not salient to dorsal margin. Ornament of regular, closely packed concentric growth lines, occasionally raised into very faint concentric riblets; in very well preserved specimens very faint radial striae can be seen over the entire shell, giving a very fine cancellate pattern. Shell thin. Ligament placed in small triangular resilifer, with faint cardinal crura running along the dorsal margin of the auricles, usually terminating distally in a small tuberosity. No byssal notch or ctenolium.

Remarks. A variable species of long stratigraphic range, occurring from the Inferior Oolite to the Kimmeridge Clay. Shell outline is the most widely ranging variable.

Age and distribution. Kellaways Rock (*calloviense* Zone) to Upper Oxford Clay (*cordatum* Zone) of central and southern England, and the Hackness Rock of Yorkshire.

Entolium (*Entolium*) ?*orbiculare* (J. Sowerby)
Plate 3, fig. 5

Description. Small to medium-sized species (4–13 mm high), of subovate to suborbicular outline, known only from right valves. Similar to *E. corneolum* but differs in possessing a well developed byssal notch beneath the anterior auricle of the right valve; ctenolium absent.
Remarks. This species occurs frequently in the *coronatum* Zone Lower Oxford Clay of central England, but is rare at all other horizons. Specimens are normally covered with a coating of secondary calcite on their external surface, preventing a view of the ornament, but it is likely that the species is smooth shelled. Byssate *Entolium* are rare, but Johnson (1984) suggests that the Oxford Clay species may belong to *E. orbiculare*. The species was described and figured in Duff (1978) as *Entolium* sp. A.
Age and distribution. Restricted to the Lower Oxford Clay of central England (*jason* to *coronatum* Zones), most commonly occurring in the calcareous clay biofacies of Duff (1975), although it also occurs sporadically in the *Grammatodon* and *Meleagrinella* shell bed biofacies.

Genus *CAMPTONECTES*
Subgenus *CAMPTONECTES*
Camptonectes (*Camptonectes*) *auritus* (Schlotheim)
Plate 3, fig. 1

Description. Large species (up to 58 mm high), suborbicular to subovate in outline, left valve inflated, right valve almost flat. Auricles small, unequal, anterior larger than posterior, and right valve with larger anterior auricle than left; byssal sinus beneath right anterior auricle, and with ctenolium. Right valve with elongate subrectangular anterior auricle, with well marked byssal fasciole below. Auricles of left valve 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. Umbones small, rounded, submedian. Both valves ornamented by closely packed fine divaricate striae, densely punctate, markedly divergent anteriorly and posteriorly; fine concentric growth lines interact with divaricate striae to produce a finely reticulate pattern upon which punctae are super-imposed. Inner surface of ligament area with fine vertical ridges and grooves, well developed anteriorly. One cardinal crus in each valve, close to and parallel with the hinge margin.
Remarks. Previously better known as *Camptonectes lens* (J. Sowerby), this well known Upper Jurassic species ranges from the Cornbrash to the

Kimmeridge Clay. The closely related *C. laminatus* (J. Sowerby) from the Bajocian to Bathonian is narrower, more subovate and has coarser ornamentation; the auricles also have conspicuous raised vertical lamellae.

Age and distribution. Kellaways Rock (*calloviense* Zone) to Middle Oxford Clay (*athleta* Zone) of central and southern England, and Hackness Rock of Yorkshire.

Genus *CHLAMYS*
Subgenus *CHLAMYS*
Chlamys (*Chlamys*) *bedfordensis* Duff
Plate 3, fig. 8

Description. Small species (up to 10 mm long), suborbicular in outline, bialate, right valve slightly more inflated than the left. Hinge line straight, umbones submedian. Right anterior auricle higher and longer than posterior, with deeply excavate auricular sulcus, and no significant byssal fasciole; narrow, deep byssal notch present; ctenolium absent. Other auricles marked off from body of shell by prominent auricular sulci. Each valve with a pair of small, weak cardinal crura, each crus

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EXPLANATION OF PLATE 3

Fig. 1. *Camptonectes* (*Camptonectes*) *auritus* (Schlotheim). Right valve, Coralline Oolite (Oxfordian), Malton, Yorkshire, ×0·75 (p. 51).

Figs 2, 3. *Radulopecten fibrosus* (J. Sowerby). 2, left valve, Kellaways Rock, Scarborough, Yorkshire, ×1. 3, right valve, internal view, Oxford Clay, Chippenham, Wiltshire, ×0·75 (p. 54).

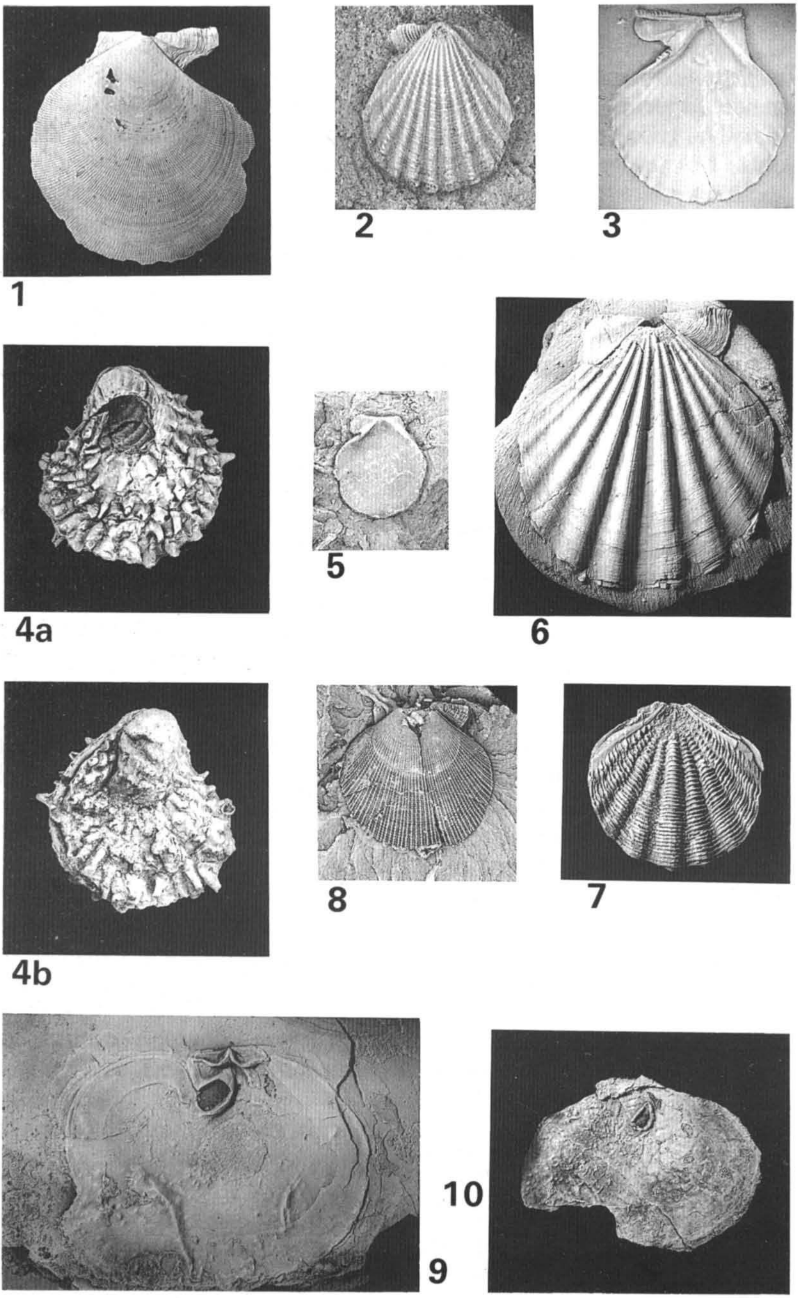
Fig. 4a,b. *Plicatula* (*Plicatula*) *fistulosa* (Morris & Lycett). a, left valve, b, right valve, Lower Oxford Clay (*coronatum* Zone), Bletchley, Buckinghamshire, ×1 (p. 55).

Fig. 5. *Entolium* (*Entolium*) ?*orbiculare* (J. Sowerby). Right valve, internal view, Lower Oxford Clay (*coronatum* Zone), Peterborough, Cambridgeshire, ×2 (p. 51).

Figs 6, 7. *Radulopecten scarburgensis* (Young & Bird). 6, right valve, 7, left valve, ×1, Upper Oxford Clay, Oxfordshire (p. 54).

Fig. 8. *Chlamys* (*Chlamys*) *bedfordensis* Duff. Right valve, Lower Oxford Clay (*coronatum* Zone), Calvert, Buckinghamshire, ×2 (p. 52).

Figs 9, 10. *Eonomia timida* Fürsich & Palmer. 9a, right valve, internal view showing prominent ligamental area and byssal foramen, Upper Oxfordian, Normandy, France, ×1. 10, right valve, internal view of typical 'English' preservation, showing byssal foramen, but weakly preserved ligamental area, Upper Oxford Clay (*mariae* Zone), Stanton Harcourt, Oxfordshire, ×1 (p. 56).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being short, low, subparallel to the hinge margin, and fading distally. Ornament of densely packed fine radial riblets, about 70 on the right valve, and 40 on the left valve; fine intercalatory riblets appear ventrally in some specimens. Riblets crossed by regularly spaced fine concentric lamellae, giving a microscopically reticulate pattern. Ornament extends onto auricles, where lamellae are stronger than on the body of the shell.

Remarks. A rare species, known only from the *coronatum* Zone Lower Oxford Clay of central England, characterized by its very fine ornamentation. Johnson (1984) suggests that this species may fall within *C.* (*C.*) *textoria* (Schlotheim), but more material from the Oxford Clay is needed before making a firm decision; *C. textoria* has significantly fewer riblets than *C. bedfordensis* at this growth stage.

Genus *RADULOPECTEN*

Radulopecten scarburgensis (Young & Bird)
Plate 3, figs 6 & 7

Description. Large species (up to 76 mm long), suborbicular in outline, with right valve slightly more inflated than the left, and with prominent subequal auricles. Right anterior auricle larger than right posterior, and with distinct byssal notch beneath it; auricular sulci well developed. Ornamentation of right valve consists of 9–11 coarse radial ribs, usually round topped but occasionally flattened and paired, with the ribs being equal in width or wider than intervening sulci; ribs markedly divergent, and both ribs and sulci crossed by fine concentric striae, numbering about 55 to the centimetre; left valve similarly ornamented, with 9–11 radial ribs, but with sulci wider than the ribs; ribs and sulci of left valve crossed by coarse wire-like concentric costellae, numbering about 17 to the centimetre. Ventral margin scalloped.

Remarks. A distinctive species, differing from *R. fibrosus* (J. Sowerby) by virtue of its fewer, more divergent ribs, which are of equal prominence in each valve (the ribs being narrower than in *R. fibrosus*), and the lack of radial striae in the intervening sulci.

Age and distribution. Occurs sporadically in the Upper Cornbrash to Upper Oxford Clay (*macrocephalus* to *cordatum* Zones) of central and southern England; also known from the Kellaways Rock of Wiltshire and the Hackness Rock of Yorkshire.

Radulopecten fibrosus (J. Sowerby)
Plate 3, figs 2 & 3

Description. Large species (up to 35 mm long), suborbicular in outline, with left and right valves showing marked differences in ornamentation.

Auricles subequal, right anterior auricle with byssal sinus and notch beneath it, with ctenolium; right anterior auricle with sinuous raised comarginal striae, posterior with vertical comarginal striae; left auricles both with slightly coarse, vertical, raised comarginal striae; no radial elements on the auricles. Ornament of right valve consists of 11–14 wide, flat-topped radial ribs, widening ventrally and always considerably wider than the intervening sulci; in large specimens the primary ribs tend to become paired at their ventral margins; ribs and sulci crossed by regular fine concentric striae, about 70 per centimetre; left valve ornamented by 11–14 more prominent, narrower, higher, round topped radial ribs, narrower than the sulci; intercalated secondaries appear ventrally; ribs and sulci crossed by coarse wire-like concentric striae, about 15 per centimetre. Faint radial striae in the sulci of both valves. Ventral margin scalloped.

Remarks. This species is abundant at many levels from the Kellaways Beds to the Corallian and has been considered in detail by Arkell (1929–1937). *R. drewtonensis* (Neale), from the Kellaways Rock of Humberside, is synonymous with this species (Johnson, 1984).

Age and distribution. Kellaways Clay (*calloviense* Zone) to Upper Oxford Clay (*cordatum* Zone) of England; also the Yorkshire Hackness Rock.

Family PLICATULIDAE
Genus *PLICATULA*
Subgenus *PLICATULA*
Plicatula (*Plicatula*) *fistulosa* Morris & Lycett
Plate 3, figs 4a,b

Description. Large species (up to 32 mm long), irregularly subovate in outline, left valve flatter than right, posterior region slightly produced, no differentiated auricles. Right valve slightly convex, with a suboval attachment area in the umbonal region; remainder of the shell ornamented by irregular rows of sharply tubiform spines with a central hollow core; spines roughly arranged in about 15 radial rows, with about 6 spines per row. Left valve flatter, often with a xenomorphic attachment area umbonally; spines slightly larger than those of right valve, and radial arrangement less well marked; number of spines fewer on left valve.

Remarks. A rare and distinctive species often found attached to driftwood, bone fragments and oyster shells in the Lower Oxford Clay. The spines are much more delicate than those of *P. weymouthiana* Damon from the Corallian Beds and not so well aligned along radial elevations.

Age and distribution. Lower to Middle Oxford Clay (*jason* to *lamberti*

Zones) of central England. Widely distributed in the Inferior Oolite and Great Oolite of southern England.

Superfamily DIMYACEA
Family DIMYIDAE
Genus *ATRETA*
Atreta blandina (d'Orbigny)
Plate 6, figs 8 & 10

Description. Medium sized species (up to 12 mm long), suborbicular in outline, with dorsal margin straight to gently convex. Right valve flattened to gently bowl-shaped in form, cemented to the substrate; with the edges of the shell elevated into a raised rim; external margins of rim marked by strong fine crenulations. Interior of right valve covered by fine but sharp bifurcating riblets, radiating outwards from the umbonal area. Left valve not seen.
Remarks. This distinctive and easily recognized species is one of the most frequent elements of the encrusting faunas found on oyster shells and bone fragments in the Upper Oxford Clay, although it has often been overlooked. The characteristic features are its subcircular outline, small size (normally no more than 10 mm long), bowl-shaped form, and radiating riblets ending in marginal crenulations; a hand lens is normally needed to see these features clearly.

The taxonomic status and position of *Atreta* has recently been reviewed by Fürsich & Werner (in press), who have demonstrated the unity of *Atreta* with the genus *Dimyodon*. They showed that the differences are due to diagenetic changes in the shell, with *Atreta* representing forms of *Dimyodon* where the internal aragonitic shell layers have been dissolved, thereby exposing the radiating riblets. The name *Atreta* takes precedence over the later erected name *Dimyodon*. Fürsich & Werner followed Waller (1978) in placing *Atreta* in the superfamily Dimyacea, rather than the Plicatulacea, because of important differences in the ligamental structure. This view is followed here.
Age and distribution. Locally common in the Upper Oxford Clay (*mariae* to *cordatum* Zones) of England, where it occurs as part of the encrusting fauna on oyster shells and bone fragments.

Superfamily ANOMIACEA
Family ANOMIIDAE
Genus *EONOMIA*
Eonomia timida Fürsich & Palmer
Plate 3, figs 9 & 10

Description. Large species (up to 80 mm high), circular or subcircular in outline (length exceeding height), and being flat or slightly bowl shaped according to the contours of the substrate to which it is cemented. Known only from right valves, seen in internal view. Well marked sub-circular byssal foramen present, lying just below the hingeline and just anterior of the dorsoventral axis; foramen up to 3.5 mm across. In very small specimens (less than 10 mm long) the byssal foramen takes the form of an open notch beneath the anterior auricle. Ligamental area with a dorsoventrally-flattened W-shape. Small tooth-like process runs posteroventrally from the posterior part of the ligamental area. Single subcircular adductor muscle scar subcentrally placed, lying below and behind the byssal foramen.

Remarks. A very distinctive species, found cemented to hard substrates such as oyster shells and bone fragments by pallial secretion, but overlooked until the work of Fürsich & Palmer (1982), who first described both the genus and the species. The species is known from Bathonian hardgrounds in Wiltshire and Normandy, and from the Upper Oxford Clay of Oxfordshire and Normandy. All known British specimens have incompletely preserved ligamental areas and lack the characteristic W-shape seen in French examples. However, the very well-marked byssal foramen is highly characteristic. This is the earliest anomiid known in the fossil record.

Age and distribution. Upper Oxford Clay (*mariae* to *cordatum* Zones) of central England. Also known from the Bradford Clay (Bathonian) of Wiltshire, and the Bathonian and Oxfordian of Normandy.

Superfamily LIMACEA
Family LIMIDAE
Genus *PLAGIOSTOMA*
Plagiostoma argillacea (Phillips)
Plate 6, fig. 9

Description. Large sized species (up to 35 mm long), obliquely ovate to subtrigonal in outline, length slightly exceeding height, of low inflation. Umbones placed within anterior third of the shell, towards the anterior end of the short straight hingeline. Shell covered by fine radial riblets, numbering about 30 to the centimetre, with the interspaces about twice as broad as the riblets. Very fine concentric comarginal growth striae cross the riblets, giving a fine cancellate ornament pattern. Occasional growth halts marked by strong growth lines.

Remarks. A rare species from the Middle and Upper Oxford Clay, easily recognized by its outline and ornament pattern.

Age and distribution. Middle and Upper Oxford Clay (*lamberti* to *cordatum* Zones) of England.

Suborder OSTREINA
Superfamily OSTREACEA
Family GRYPHAEIDAE
Subfamily GRYPHAEINAE
Genus *GRYPHAEA*
Subgenus *BILOBISSA*
Gryphaea (*Bilobissa*) *dilobotes* Duff
Plate 4, figs 1a,b, 2 & 3

Description. Large species (up to 85 mm long) of very variable form, subtrigonal to subovate in outline, with well developed posterior flange; left valve strongly inflated and highly convex, right valve flat or slightly concave. Umbones of left valve prominent, rounded, not tightly enrolled, often truncated by a large attachment area, xenomorphic on the right valve. Posterior margin of left valve usually drawn out into a well developed posterior flange, delimited anteriorly by a deeply excavate radial sulcus, the flange being placed relatively high on the shoulders of the valve and usually triangular in outline. Right valve of similar outline to left. Ornament of coarse concentric growth squamae, with faint radial elements sometimes present in juvenile stages; radial elements seen more clearly on right valves.

Remarks. This is the abundant *Gryphaea* of the Kellaways Beds and Lower Oxford Clay, frequently referred to as *G. bilobata* J. de C. Sowerby. However, as Duff (1978) showed, that species comes from the Inferior Oolite and is specifically distinct. Three species of *Gryphaea* occur in the Oxford Clay, *G.* (*B.*) *dilobotes* in the Lower Oxford Clay, *G.* (*B.*) *lituola* Lamarck in the Middle Oxford Clay, and *G.* (*B.*) *dilatata* J. Sowerby in the Upper Oxford Clay; Arkell (1929–1937) and Duff (1978) have defined their essential differences. All three species are extremely variable in their characters, but it is still possible to distinguish specimens of each, although distinction is more effectively achieved in large populations. The essential differences are:

1. *G.* (*B.*) *dilatata* attains a very large size (up to 200 mm high), and large specimens may have very extended ligaments. In general form this

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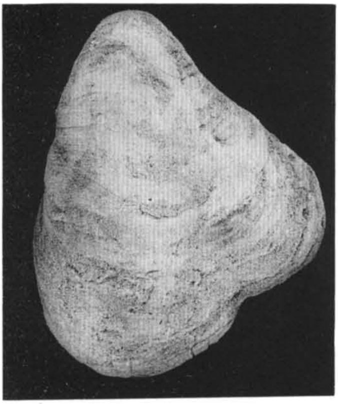
EXPLANATION OF PLATE 4

Figs 1a,b, 2, 3. *Gryphaea* (*Bilobissa*) *dilobotes* Duff. 1a,b, left and right valves, Lower Oxford Clay (*calloviense* Zone), Peterborough, Cambridgeshire, ×0·75. 2, left valve, Lower Oxford Clay (*jason* Zone), Stewartby, Bedfordshire, ×0·75. 3, left valve, Lower Oxford Clay (*calloviense* Zone), Stewartby, Bedfordshire, ×1 (p. 58).

Fig. 4a,b. *Gryphaea* (*Bilobissa*) *lituola* (Lamarck). a, left valve, b, right valve, Middle Oxford Clay (*lamberti* Zone), Stewartby, Bedfordshire, ×0·75 (p. 60).



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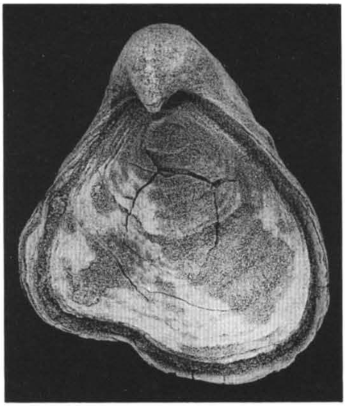

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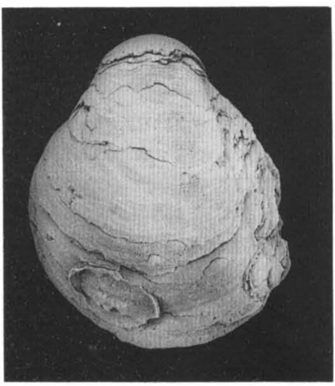
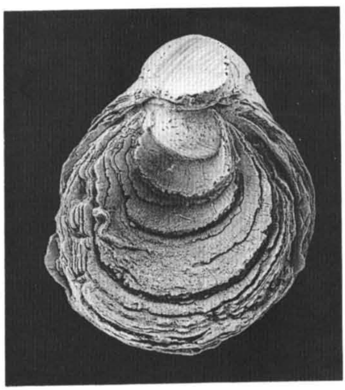


4a



4b

species is much wider and flatter than the other two, often being said to resemble a dinner plate. Height and length are about the same and inflation is only 20–50% of the shell length. The posterior flange is not well differentiated from the body of the shell, and tends to be subrectangular to subovate in outline; the flange extends all the way to the ventral margin.

2. *G.* (*B.*) *lituola* may be distinguished from *G.* (*B.*) *dilobotes* by virtue of its slightly greater inflation, more enrolled umbones, thicker shell, more extensive and better-developed commissural shelf, and by being less bilobate. In *G. lituola* the posterior radial sulcus reaches almost to the ventral margin and marks off a poorly-differentiated posterior flange which is not well-separated from the body of the shell, although it is still roughly triangular in shape. Also, in *G. lituola* the left valve ligament area is much higher due to tighter enrolling of the shell.

In the Lower Oxford Clay, *G.* (*B.*) *dilobotes* is abundant in the shell beds at the base, and frequently has very large attachment areas which greatly affect the shape of the shells. In their juvenile stages the left valves take 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. As the animals grew and became larger and heavier, they toppled over onto the left valves and developed the "normal" *Gryphaea* shape. In the shell beds, both morphotypes occur, but in the clays and shales of the Lower Oxford Clay the dominant form is small and flat, and is often found encrusting other shells or fragments of wood; gryph-shaped forms are rare, and do not reappear in abundance until the *athleta* Zone, where they have the form of *G.* (*B.*) *lituola*.

Age and distribution. Abundant in the Kellaways Beds and Lower Oxford Clay (*calloviense* to *coronatum* Zones) of central and southern England, including Humberside.

Gryphaea (*Bilobissa*) *lituola* Lamarck
Plate 4, figs 4a,b

Description. Large species (up to 115 mm high), subtrigonal to subovate in outline, rarely markedly rostrate, with posterior radial sulcus reaching nearly to the ventral margin. Height of shell always exceeds length. Umbones of left valve strongly enrolled, prominent, inflated, and generally terminated by an attachment area of variable size, reflected xenomorphically on the right valve. Ornamented by irregular concentric growth squamae, less coarse than in *G. dilobotes*, and with radial elements rare on left valve; ornament of right valve similar, but radial striae reasonably developed in the umbonal region. Ligament area of left valve elongated perpendicular to the hinge axis, with the distinction between resilifer and bourrelets becoming faint; area often with a slight twist posteriorly.

Remarks. In addition to the distinguishing features set out above, this species is also often characterized by the frequent occurrence of an epifauna of serpulid worms, foraminiferans, bryozoans and bivalves, attached to the exterior (and occasionally the inner) surfaces of the valves.

Age and distribution. Middle Oxford Clay (*athleta* to *lamberti* Zones) of England.

Gryphaea (*Bilobissa*) *dilatata* J. Sowerby
Plate 5, figs 1a,b

Description. Very large species (up to 200 mm high), suborbicular to subovate in outline, broad and of low inflation, with weak or absent posterior flange. Left valve often likened to a dinner plate. Umbones not tightly enrolled, but ligament area often very extended, perpendicular to the hinge margin; attachment area rarely seen. Ornamented by irregular concentric growth squamae, without radial elements on left valve; right valve sometimes shows radial striae in the umbonal area.

Remarks. This species has been well-described and illustrated by Arkell (1929–1937) and is the characteristic *Gryphaea* of the Upper Oxford Clay and Corallian Beds. Its very large size, low inflation and broad shell mark it out from the other Oxford Clay species. Very large specimens tend to show abnormalities and irregularities of form which distort the overall form of the shells in various ways; consequently this is a highly variable species. Both internal and external surfaces of the valves are frequently encrusted by epifaunal animals such as other bivalves, foraminiferans, bryozoans and worms.

Age and distribution. Abundant in the Upper Oxford Clay (*mariae* to *cordatum* Zones) of England and in the Corallian Beds.

Subfamily EXOGYRINAE
Genus *NANOGYRA*
Nanogyra nana (J. Sowerby)
Plate 6, figs 4 & 5

Description. Medium sized shell (up to 30 mm high), very variable in shape but generally ovate in outline, with left valve bowl-shaped and right valve flattened. Form of left valve varies according to the substrate to which the animal was attached. Umbones spirally coiled, particularly in the left valve, giving rise to obliquely extended ligament area which is obscured to varying degrees by the coiled umbones; not enrolled. Ornament of shell exterior normally consists of rough concentric growth squamae on both valves. Right valve flat, often comma-shaped, with spiral coiling well-seen in the umbonal area.

Remarks. This distinctive species of oyster is distinguished from adult and juvenile *Gryphaea* by virtue of its spiral growth form in the umbonal areas, with the spiralling being directed parallel to the plane of the commissure; in *Gryphaea*, the shells are enrolled (rather than spiralled) in a direction perpendicular to the plane of the commissure. The spiralling of the valves is best seen in the obliquely elongated shape of the ligament. *Nanogyra nana* is generally small, and usually occurs attached to *Gryphaea* shells or to bone fragments; it is rare to find it free-living in the Oxford Clay. The species has been well-described and figured by Arkell (1929–1937) and Pugaczewska (1971), and the overall taxonomic position of the genus was discussed by Stenzel (1971). *N. nana* is a long-ranging species of almost cosmopolitan extent, being found from the Bathonian to Portlandian of Europe, Russia, India, Asia and Africa.

Age and distribution. Occurs sporadically throughout the Oxford Clay of England, but is commonest as an encrusting species on other shells in the Middle and Upper Oxford Clay (*lamberti* to *cordatum* Zones).

Family OSTREIDAE
Subfamily LOPHINAE
Genus *LOPHA*
Subgenus *ACTINOSTREON*
Lopha (*Actinostreon*) *marshii* (J. Sowerby)
Plate 6, fig. 2

Description. Large species (up to 140 mm high), very variable in outline, but generally subrectangular to subtrigonal, and subequivalve. Powerful radial ornamentation on both valves, consisting of up to 15 angular plications, increasing in amplitude ventrally. Commissural margin of zig-zag form, being particularly strongly developed in the central part of the ventral margin. Growth halts well seen, giving rise to elevated shell thickenings and some development of tubercles at the intersections with the radial plicae. Ribs on the right valve tend to be less sharp.

Remarks. An easily recognized species of restricted distribution, which occurs sporadically in the Middle and Upper Oxford Clay. Other

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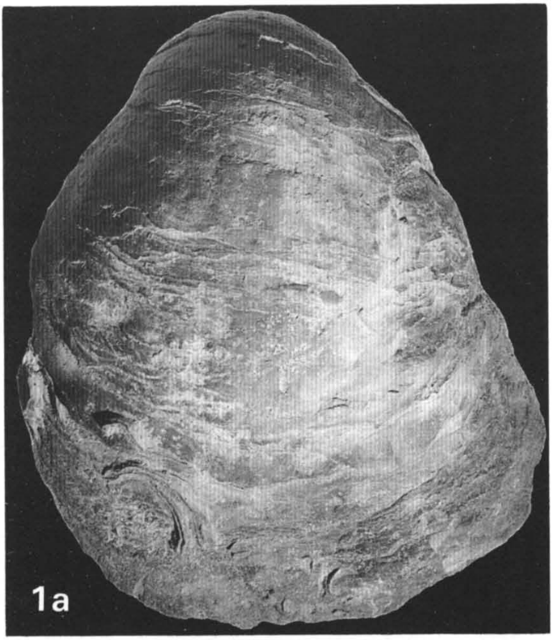
EXPLANATION OF PLATE 5

Fig. 1a,b. *Gryphaea* (*Bilobissa*) *dilatata* J. Sowerby. a, left valve, b, right valve, Upper Oxford Clay, Warboys, Cambridgeshire, ×0·5 (p. 61).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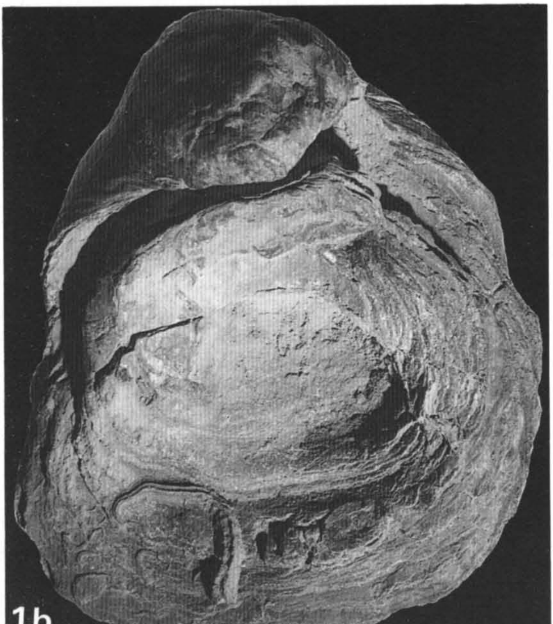
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well-known Upper Jurassic *Lopha*, such as *L.* (*A.*) *gregarea* (J. Sowerby) and *L.* (*A.*) *solitaria* (J. Sowerby), differ in having considerably more radial plicae, which are much smaller than those of *L.* (*A.*) *marshii*. The Corallian species *L.* (*A.*) *genuflecta* Arkell has similarities to *L.* (*A.*) *marshii*, but is much less equivalve, has a much thicker left valve, and the principal ribs rise into prominences resembling a bent knee.

Age and distribution. Sporadically distributed in the Middle and Upper Oxford Clay of England (*athleta* to *cordatum* Zones). Abundant in the Cornbrash of England, and also known from the Kellaways Clay and Kellaways Rock (*macrocephalus* to *calloviense* Zones).

Subclass PALAEOHETERODONTA
Order TRIGONIOIDA
Superfamily TRIGONIACEA
Family TRIGONIIDAE
Genus *TRIGONIA*
Subgenus *TRIGONIA*
Trigonia (*Trigonia*) *elongata* J. de C. Sowerby
Plate 6, fig. 6

Description. Large species (up to 45 mm long), subtrigonal in outline, well inflated, with prominent pointed subcentral opisthogyrate umbones. Very strong elevated marginal carina running to posteroventral angle, marking off a distinctive posterior area with cancellate ornament,

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EXPLANATION OF PLATE 6

Fig. 1. *Myophorella* (*Myophorella*) *caytonensis* Duff. Kellaways Rock, Scarborough, Yorkshire, ×0·75 (p. 66).

Fig. 2. *Lopha* (*Actinostreon*) *marshii* (J. Sowerby). Kellaways Clay, Fineshade, Northamptonshire, ×0·5 (p. 62).

Fig. 3. *Myophorella* (*Myophorella*) *irregularis* (Seebach). Oxford Clay, Weymouth, Dorset, ×0·6 (p. 66).

Figs 4, 5. *Nanogyra nana* (J. Sowerby). 4, right valve, Lower Oxford Clay (*coronatum* Zone), Calvert, Buckinghamshire. 5, left valve, internal view, Kimmeridge Clay, Oxfordshire. Both ×1 (p. 61).

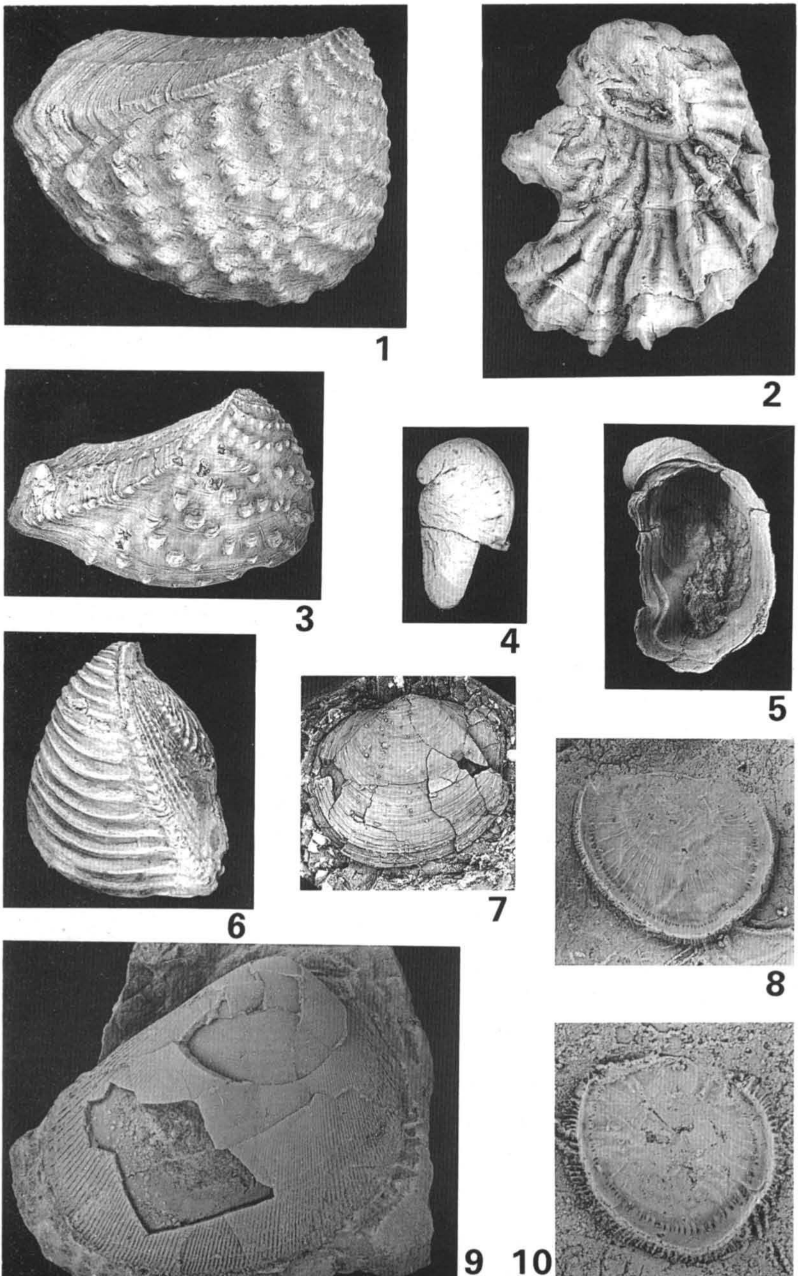
Fig. 6. *Trigonia* (*Trigonia*) *elongata* J. de C. Sowerby. Left valve, Oxford Clay, Radipole, Dorset, ×0·75 (p. 64).

Fig. 7. *Discomiltha lirata* (Phillips). Left valve, Lower Oxford Clay (*coronatum* Zone), Marston Moretaine, Bedfordshire, ×1 (p. 67).

Figs 8, 10. *Atreta blandina* (d'Orbigny). Right valve, internal views, Fig. 8 shows the radiating riblets well, and Fig. 9 shows the crenulated margins of the shell. Upper Oxford Clay (*mariae* Zone), Stanton Harcourt, Oxfordshire, ×2·5 (p. 56).

Fig. 9. *Plagiostoma argillacea* (Phillips). Right valve, Middle Oxford Clay (*lamberti* Zone), Woodham, Buckinghamshire, ×2·5 (p. 57).

PLATE 6



which occupies the posterior third of the shell. Escutcheon bounded by a carina with raised comarginal threads, and ornamented by raised concentric ridges, breaking into lines of closely spaced tubercles dorsally. Body of shell ornamented by 25–30 regularly spaced strong concentric ribs, separated by interspaces twice the width of the ribs; a narrow smooth radial band separates the posterior ends of the ribs from the marginal carina. Dentition of normal trigoniid type, with three large cardinal teeth in each valve, all bearing clearly marked vertical crenulations.

Remarks. This distinctive species was well-described by Lycett (1877), and is a well-known component of the Middle and Upper Oxford Clay fauna.

Age and distribution. Middle and Upper Oxford Clay (*athleta* to *cordatum* Zones) of England.

Genus *MYOPHORELLA*
Subgenus *MYOPHORELLA*
Myophorella (*Myophorella*) *irregularis* (Seebach)
Plate 6, fig. 3

Description. Large species (up to 90mm long), elongate-oval to subtrapezoidal in outline, rostrate, well inflated, with prominent pointed umbones located in the front third of the shell. Posterior margin drawn out, with slight reflection in ventral margin posteriorly, with posterior area marked off from the body of the shell by a strong marginal carina running from the umbo to the posteroventral angle; median and escutcheon carinae also present; carinae ornamented by strong varices elongated along growth lines; posterior area ornamented by irregularly spaced concentric growth lines, elevated into concentric ribs close to the umbo. Flanks of the shell ornamented by 9–16 curved rows of clavellate tubercles, varying in regularity and sinuosity but generally more irregular in larger shells; about 8–9 tubercles per row, not usually placed on distinct elevated rows. Dentition of normal trigoniid type.

Remarks. An easily recognized species, identified by its rostrate form and irregularly sinuous tubercle rows, with tubercles rising straight from the shell surface rather than being placed on ridges. There is considerable variation in sinuosity of the tubercle rows, some specimens having a completely regular form.

Age and distribution. Kellaways Clay (*macrocephalus* Zone) to Upper Oxford Clay (*cordatum* Zone) throughout England.

Myophorella (*Myophorella*) *caytonensis* Duff
Plate 6, fig. 1

Description. Large species (up to 90 mm long), subtrigonal to elongate oval in outline, not markedly rostrate. Posterior margin obliquely extended, but without posteroventral reflection. Marginal carina well marked, taking the form of an elongate ridge with occasional strong subconcentric varices on some specimens; median carina faint with poorly developed varices; escutcheon carina strong, ridge-like, with well developed tubercular varices. Flanks of the shell ornamented by 10–17 rows of rounded clavellate tubercles, placed on ribs, with about 12 tubercles per row; the first 5–6 rows of tubercles simple and subconcentric in form, the remainder sinuate and irregular, often falcate.

Remarks. Whilst this species has irregularities in tubercle rows it is clearly distinguished from *M. irregularis*. The species is characteristic of the Kellaways Rock of northern England, to which it is restricted.

Age and distribution. Kellaways Rock (*calloviense* Zone) of Humberside and Yorkshire.

Subclass HETERODONTA
Order VENEROIDA
Superfamily LUCINACEA
Family LUCINIDAE
Subfamily MYRTEINAE
Genus *DISCOMILTHA*
Discomiltha lirata (Phillips)
Plate 6, fig. 7

Description. Large species (up to 50 mm long), suborbicular to subrectangular in outline, with prominent pointed submedian umbones. Anterior margin somewhat inflated, rounded and slightly extended, posterior margin slightly rectangular, often with a weak radial sulcus running from the umbo to the posteroventral angle; posterior area delineated by radial sulcus, and often with slightly coarsened ornamentation, the concentric lamellae being strengthened and slightly elevated. Remainder of shell ornamented by irregularly developed narrow concentric lamellae, spaced about 1.5 mm apart, separated by wider interspaces containing concentric growth striae; the lamellae often not strongly developed in Lower Oxford Clay specimens; no radial ornament. Anterior adductor scar elongate and parallel-sided, diverging from the pallial line and reaching about two-thirds of the way to the ventral margin. Interior of shell surface within the pallial line strongly pustulose, with a faint radial pattern.

Remarks. Locally abundant in some of the shell beds within the Lower Oxford Clay, which yield well preserved shell material showing details of the musculature and pustulose inner texture of the shell. The Oxfordian species *D. rotundata* (Roemer) is considerably more inflated and globose, and lacks the posterior sulcus and subrectangular posterior margin of *D. lirata*.

Age and distribution. Occurs from the Kellaways Rock (*calloviense* Zone) to Middle Oxford Clay (*lamberti* Zone) of central and southern England, but is commonest in the condensed shell beds; also occurs in the Hackness Rock of Yorkshire, and throughout the Corallian Beds.

Superfamily CRASSATELLACEA
Family ASTARTIDAE
Subfamily ASTARTINAE
Genus *NEOCRASSINA*
Subgenus *PRESSASTARTE*
Neocrassina (*Pressastarte*) *ungulata* (Lycett)
Plate 7, figs 1 & 2

Description. Medium sized species (up to 22 mm long), suborbicular to subquadrate in outline, with small pointed prosogyrate umbones. Shell margins generally rounded. Inflation low, mostly due to thickness of the valves rather than enlargement of the shell cavity. Ornament of up to 13 strong concentric ribs, separated by sulci of approximately equal width; ribs fade out about 7 mm from the umbones and only faint growth lines remain; very occasionally growth lines near ventral margin are coarsened into riblets. Cardinal plate heavy and wide, cardinal teeth elongate and subparallel; each valve with two cardinals, plus one anterior and one posterior pseudolateral. Pallial line entire. Margin denticulate.
Remarks. Characterized by its wide and solid cardinal plate with elongate cardinal teeth, and thick shell.

EXPLANATION OF PLATE 7

Figs 1, 2. *Neocrassina* (*Pressastarte*) *ungulata* (Lycett). 1, left valve. 2, left valve, oblique internal view, Oxford Clay, Trowbridge, Wiltshire, × 2 (p. 68).
Fig. 3. *Isocyprina* (*Isocyprina*) *roederi* Arkell. Right valve, Lower Oxford Clay (*coronatum* Zone), Stewartby, Bedfordshire, × 1 (p. 73).
Figs 4a,b. *Neocrassina* (*Pressastarte*) *calvertensis* Duff. Right valve; a, external view, b, internal view, Lower Oxford Clay (*jason* Zone), Calvert, Buckinghamshire, × 1.5 (p. 70).
Figs 5, 8. *Anisocardia* (*Anisocardia*) *tenera* (J. Sowerby). Right valves, Kellaways Rock, Chippenham, Wiltshire, × 1 (p. 72).
Fig. 6. *Protocardia* (*Protocardia*) *striatula* (J. de C. Sowerby). Right valve, Kellaways Rock, Scarborough, Yorkshire, × 2 (p. 71).
Fig. 7. *Rollierella minima* (J. Sowerby). Right valve, Kellaways Rock, Kellaways, Wiltshire, × 1 (p. 72).
Fig. 9. *Nicaniella* (*Trautscholdia*) *carinata* (Phillips). Right valve, Upper Oxford Clay (*mariae* Zone), Scarborough, Yorkshire, × 1.5 (p. 70).
Fig. 10a,b. *Nicaniella* (*Trautscholdia*) *phillis* (d'Orbigny). Right valve; a, external view, b, internal view, Lower Oxford Clay (*coronatum* Zone), Marston Moretaine, Bedfordshire, × 1.5 (p. 70).

PLATE 7

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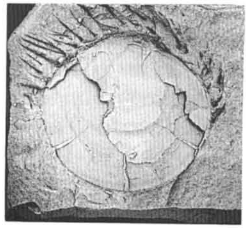

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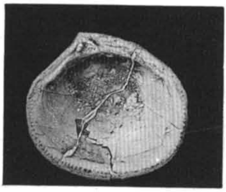

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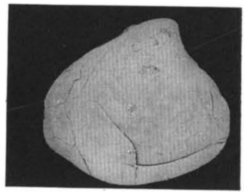

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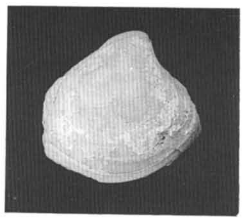

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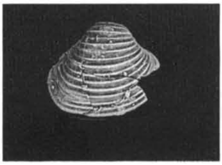

10b

Age and distribution. Cornbrash (*macrocephalus* Zone) of Yorkshire, Hackness Rock (*athleta* to *lamberti* Zones) of Yorkshire, Upper Oxford Clay (*mariae* Zone) of Yorkshire, and Oxford Clay (undifferentiated) of Wiltshire.

Neocrassina (*Pressastarte*) *calvertensis* Duff
Plate 7, figs 4a,b

Description. Medium sized species (up to 21 mm long), suborbicular to subovate in outline, of very low inflation, with small pointed prosogyrate umbones. Ornament of 8–10 concentric ribs in the umbonal region, fading into concentric growth lines about 5 mm from the umbones. Lunule and escutcheon elongate, lanceolate, shallow, reaching to the anterodorsal and posterodorsal angles. Cardinal plate narrow and slight, cardinal teeth short and peg-like; each valve with two cardinals, right valve with two anterior pseudolaterals; remainder of dentition as for *N.* (*P.*) *ungulata*. Pallial line entire. Margin denticulate.
Remarks. Characterized by its narrow cardinal plate with short peg-like cardinal teeth, and by the presence of two anterior pseudolaterals on the right valve. Also differs from *N.* (*P.*) *ungulata* by having fewer concentric ribs.
Age and distribution. Kellaways Rock to Lower Oxford Clay (*calloviense* to *jason* Zones) of central England.

Genus *NICANIELLA*
Subgenus *TRAUTSCHOLDIA*
Nicaniella (*Trautscholdia*) *carinata* (Phillips)
Plate 7, fig. 9

Description. Small species (up to 10 mm long), suborbicular to subtrigonal in outline, globular, with prominent produced submedian umbones. Dorsal margins slightly concave in outline, ventral margin evenly rounded, more or less semi-circular in outline, denticulate over its entire length. Ornament of 8–12 regularly spaced sharp concentric ribs (most commonly 8–10), with fine concentric threads between.
Remarks. Mainly found as clay internal moulds from the Middle and Upper Oxford Clay. Distinguished from *N.* (*T.*) *phillis* (d'Orbigny) by its fewer ribs and less elongate form.
Age and distribution. Common in the Middle to Upper Oxford Clay (*lamberti* to *mariae* Zones) of Oxfordshire and Yorkshire.

Nicaniella (*Trautscholdia*) *phillis* (d'Orbigny)
Plate 7, figs 10a,b

Description. Medium sized species (up to 13 mm long), generally subtrigonal in outline but occasionally suborbicular, with prominent, inflated umbones. Anterodorsal margin slightly concave, posterodorsal margin slightly concave to slightly convex; remainder of shell outline variably rounded, sometimes with angularities. Strongly developed deeply concave cordiform lunule; sharply defined lanceolate escutcheon. Ornament of 12–21 regularly spaced concentric ribs, with faint concentric intercostal threads; ribs more tightly packed than in *N.* (*T.*) *carinata*. Margin denticulate. Right valve with three cardinal teeth and left with two; paired laminar laterals anteriorly in right valve and posteriorly in the left; transposition of either the anterior laterals or cardinal teeth occurs occasionally. Pallial line entire.

Remarks. Large collections from the Lower Oxford Clay allow observation of the considerable range of variation which occurs in this species, but all populations show a consistently larger number of ribs, and greater elongation of the shell, than occurs in *N.* (*T.*) *carinata*.

Age and distribution. Widespread in the Kellaways Rock (*calloviense* Zone) of southern England, and in the Lower Oxford Clay (*calloviense* to *coronatum* Zones) of central and southern England.

Superfamily CARDIACEA
Family CARDIIDAE
Subfamily CARDIINAE
Genus *PROTOCARDIA*
Subgenus *PROTOCARDIA*
Protocardia (*Protocardia*) *striatula* (J. de C. Sowerby)
Plate 7, fig. 6

Description. Medium-sized species (up to 25 mm long), subrectangular to subquadrate in outline, inflated, with large prominent umbones. Hinge margin slightly reflexed, posterior margin obliquely truncate, ventral and anterior margins smoothly curved; no umbonal carinae. Ligament external and deeply impressed; lunule and escutcheon absent. Ornament of up to 20 very fine radial riblets on the posterior part of the shell, remainder of shell with fine concentric growth lines only; posterior shell margin crenulate where riblets reach margin.

Remarks. Easily recognized by its characteristic ornament pattern. Large *Protocardia* with regular fine concentric ribs on the body of the shell occur rarely in the *coronatum* Zone Lower Oxford Clay of the Midlands, and may represent a large form of this species. Their ornament pattern resembles that of *P. stricklandi* (Morris & Lycett) from the Great Oolite, but preservation is too poor to allow positive specific placement. The Corallian species *P. dyonisea* (Buvignier) and *P. intexta* (Münster), figured by Arkell (1929–1937), differ markedly in form.

Age and distribution. Locally abundant in the Kellaways Clay and Kellaways Rock (*calloviense* Zone) throughout England, and occurs sporadically throughout the Oxford Clay (*jason* to *cordatum* Zones) of England, and the Hackness Rock (*athleta* to *lamberti* Zones) of Yorkshire.

Superfamily ARCTICACEA
Family ARCTICIDAE
Genus *ROLLIERELLA*
Rollierella minima (J. Sowerby)
Plate 7, fig. 7

Description. Medium sized species (up to 25 mm long), strongly subtrigonal in outline, with extremely prominent produced umbones, strongly prosogyrate and enrolled. Anterodorsal angle very prominent and produced, with a rounded extremity. Very inflated shell. Ornament of closely spaced fine radial riblets, crossed by densely packed fine concentric threads to give a fine cancellate pattern over the whole shell. Pseudolunule large, wide, bowl-shaped, its edge marked by a sharply impressed line parallel to the radial riblets. Ventral margin finely denticulate. Each valve with three cardinal teeth and an anterior and posterior lateral.

Remarks. Differs from the superficially similar *Anisocardia tenera* (J. Sowerby) by being considerably more inflated, in having a much sharper and more prominent anteroventral angle, in having more inflated and more enrolled umbones, and in lacking a slightly rostrate posterior margin.

Age and distribution. Ranges from Bathonian to Oxfordian in Britain. Common in the Kellaways Rock (*calloviense* Zone) and basal Lower Oxford Clay (*calloviense* to *jason* Zones) of central and southern England.

Genus *ANISOCARDIA*
Subgenus *ANISOCARDIA*
Anisocardia (*Anisocardia*) *tenera* (J. Sowerby)
Plate 7, figs 5 & 8

Description. Medium sized species (up to 26 mm long), subrectangular to subtrigonal in outline, with prominent umbones (but not strongly enrolled or produced). Anterodorsal angle prominent and rounded, not produced, posterior margin obliquely truncate and slightly rostrate; umbonal carina reaches posteroventral angle and marks off a small flattened posterior area. Ornament of densely packed fine radial riblets, crossed by closely spaced concentric growth lines to give a finely cancellate pattern. Ventral margin finely denticulate.

Remarks. The dentition of this species has not been seen and it is possible that it belongs to *Rollierella*.

Age and distribution. Kellaways Clay and Kellaways Rock (*calloviense* Zone) throughout England.

Genus *ISOCYPRINA*
Subgenus *ISOCYPRINA*
Isocyprina (*Isocyprina*) *roederi* Arkell
Plate 7, fig. 3

Description. Medium sized species (up to 20 mm long), suborbicular to subovate in outline, with small inconspicuous submedian umbones. Shell margins evenly and continuously curved, except for a slight concavity just anterior of the umbones, indicating the position of the very small lunule; inflation low. Ornament consisting solely of very faint irregularly spaced growth lines; shell thin and fragile. Hinge with two cardinal teeth and an anterior and posterior lateral in each valve, the anterior laterals not clearly differentiated from the anterior cardinals. Margin entire, without denticulations; small pallial sinus. Both adductor muscle scars elongated dorso-ventrally, posterior higher and more elongate than anterior.
Remarks. An easily recognized, rather nondescript species, characterized by its orbicular form, inconspicuous umbones, and thin smooth fragile shell.
Age and distribution. Lower and Middle Oxford Clay (*coronatum* to *lamberti* Zones) of central and southern England.

Order MYOIDA
Suborder MYINA
Superfamily MYACEA
Family CORBULIDAE
Subfamily CORBULINAE
Genus *CORBULOMIMA*
Corbulomima macneillii (Morris)
Plate 8, figs 2, 3 & 6

Description. Small species (up to 7 mm long), suborbicular to subtrigonal in outline, globose, with right valve slightly larger than left and overhanging it along the ventral margin. Umbones small, inflated, placed anterior of median. Dorsal margin reflexed, lunule absent. Anterior margin well rounded, posterior margin obliquely truncate, with well marked postero-ventral angle and well developed umbonal carina. Ligament internal. Shell very thin, with internal nacreous layer; exterior ornamented solely by very faint concentric growth lines. Dentition of single large triangular tooth on right valve, without chondrophore.
Remarks. The smallest species of bivalve in the Oxford Clay, found abundantly in the Lower Oxford Clay. The size, shape and larger size of the right valve is characteristic. The comparable *C. obscura* (J. de C. Sowerby), from the Brora Roof Bed (*calloviense* Zone) of northern Scotland, is less inflated, more elongate and more rostrate. Most

other Upper Jurassic species have regular concentric ornament, which immediately distinguishes them from *C. macneillii.*
Age and distribution. Kellaways Clay (*calloviense* Zone) to Upper Oxford Clay (*cordatum* Zone) of England, and Hackness Rock (*athleta* to *lamberti* Zones) of Yorkshire.

Corbulomima mosae (d'Orbigny)
Plate 8, fig. 5

Description. Small species (up to 7 mm long), subrectangular in outline, and closely resembling *C. macneillii*, but with a fine concentric ornament pattern on the body of the shell, and having a more elongate shape; the umbonal carina is also more consistently developed. Dentition unknown.
Remarks. Very similar in form to *C. obscura* (J. de C. Sowerby), but differs in being concentrically ornamented.
Age and distribution. Upper Oxford Clay (*cordatum* Zone) of England.

Subclass ANOMALODESMATA
Order PHOLADOMYOIDA
Superfamily PHOLADOMYACEA
Family PHOLADOMYIDAE
Genus *PHOLADOMYA*
Subgenus *BUCARDIOMYA*
Pholadomya (*Bucardiomya*) *protei* (Brongniart)
Plate 8, fig. 1

Description. Large species (up to 60 mm long), subrectangular to

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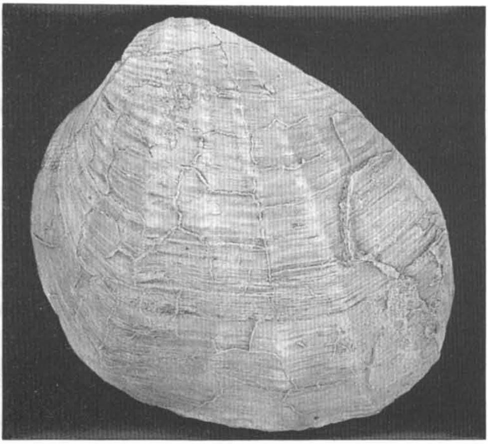
EXPLANATION OF PLATE 8

Fig. 1. *Pholadomya* (*Bucardiomya*) *protei* (Brongniart). Left valve, Oxford Clay, Radipole, Dorset, ×1 (p. 74).
Figs 2, 3, 6. *Corbulomima macneillii* (Morris). 2, 3, left valves, Lower Oxford Clay, Dauntsey, Wiltshire, ×2. 6, right valve, Lower Oxford Clay (*jason* Zone), Stewartby, Bedfordshire, ×2 (p. 73).
Fig. 4. *Pleuromya uniformis* (J. Sowerby). Right valve, Belemnite Sands (Lower Callovian), Staffin, Skye, ×0.75 (p. 76).
Fig. 5. *Corbulomima mosae* (d'Orbigny). Left valve, Upper Oxford Clay, Wiltshire, ×2 (p. 74).
Figs 7, 8. *Pleuromya alduini* (Brongniart). Right valves. 7, Kellaways Rock, Kington Langley, Wiltshire, ×0.75. 8, Lower Oxford Clay (*coronatum* Zone), Peterborough, Cambridgeshire, ×1 (p. 76).
Figs 9, 10. *Thracia* (*Thracia*) *depressa* (J. de C. Sowerby). Left valves, Upper Oxford Clay (*cordatum* Zone), Weymouth, Dorset, ×0.75 (p. 77).



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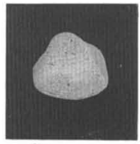

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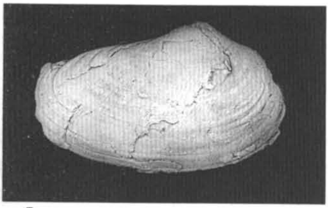

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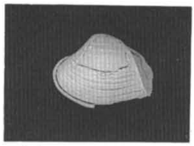

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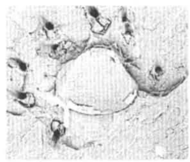

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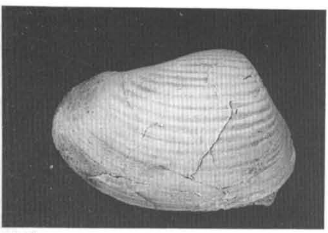

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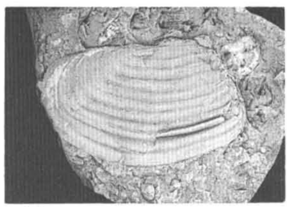

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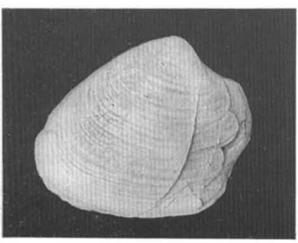

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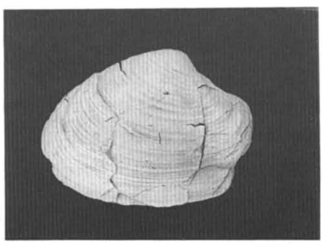

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obliquely subtrigonal in outline, strongly inflated; posterior margin slightly produced. Umbones prominent, placed anteriorly, and well inflated. Ornament of 4–6 strong radial ribs placed in the central part of the valve flanks, with smooth areas anteriorly and posteriorly; ribs variably elevated, marked by tubercular swellings where crossed by irregularly spaced concentric growth lines; ribs break up into fine rows of radial tubercles in the umbonal area. No escutcheon. Slight posterior gape.

Remarks. This common Corallian species also occurs sporadically in the Middle and Upper Oxford Clay, and is placed in the subgenus *Bucardiomya* because of its lack of elongation, and the absence of a differentiated escutcheon. It has markedly fewer ribs than the other Upper Jurassic species of *Pholadomya* described by Arkell (1929–1937) and is much less elongate in outline.

Age and distribution. Middle and Upper Oxford Clay (*athleta* to *cordatum* Zones) of England.

Family PLEUROMYIDAE

Genus *PLEUROMYA*

Pleuromya alduini (Brongniart)

Plate 8, figs 7 & 8

Description. Large species (up to 66 mm long), subrectangular to elongate trigonal in outline, with posterior margin often produced into a rounded angle; right valve overlaps left along dorsal margin. Umbones anteriorly placed, not prominent. Anterodorsal margin approximately straight, posteroventral angle produced and acutely rounded. Lunule and escutcheon absent; ligament external. Ornament of prominent, regularly spaced concentric ribs, becoming wider away from the umbones with fine concentric growth lines in addition. Pallial sinus well developed, lower limb not confluent with pallial line. Prominent posterior gape in most specimens, slight anterior gape in a few.

Remarks. A long ranging and variable species, known from the Fullers Earth Rock (Bathonian) to Kimmeridgian in Britain. The species is most abundant in clay rocks, and differs from *P. uniformis* (J. Sowerby) in possessing strong regular concentric ribs, being more inflated, and being more rectangular in outline.

Age and distribution. Kellaways Clay (*calloviense* Zone) to Upper Oxford Clay (*cordatum* Zone) of central and southern England.

Pleuromya uniformis (J. Sowerby)

Plate 8, fig. 4

Description. Large species (up to 72 mm long), elongate-elliptical to subrectangular in outline, with right valve overlapping left valve slightly along the dorsal margin. Umbones anteriorly placed, not prominent. Anterodorsal margin gently concave, anterior angle evenly rounded; posterior not produced, regularly rounded. Ornament of fine concentric growth lines, with irregularly spaced growth rugae variably developed; very well preserved specimens show the whole of the shell surface covered with minute radial threads. Pallial sinus large, not confluent with pallial line. Margins closed, without gapes.

Remarks. A very long ranging and variable species, recorded from the Inferior Oolite (Bajocian) to Portland Beds of Britain. The species is commonest in sandy and calcareous sediments, and rare in clays and shales.

Age and distribution. Kellaways Clay and Kellaways Rock (*calloviense* Zone) and Upper Oxford Clay (*cordatum* Zone) of central and southern England.

Superfamily PANDORACEA
Family THRACIIDAE
Genus *THRACIA*
Subgenus *THRACIA*
Thracia (*Thracia*) *depressa* (J. de C. Sowerby)
Plate 8, figs 9 & 10

Description. Large species (up to 66 mm long), subtrigonal, subrectangular or elongate-elliptical in outline, with prominent posteriorly-placed rear-facing umbones, bounded posteriorly by strongly developed ligament nymphs. Right valve larger than left. Anterodorsal margin long, gently convex, passing into evenly rounded anterior and ventral margins; posterior margin slightly rostrate, with variably developed umbonal carina marking off posterior area, which is often truncated; strong posterior gape. Inflation very variable. Ornament of irregularly spaced growth lines, occasionally coarsened into rugae, sometimes crossed by very fine radial threads. Large pallial sinus, lower limb almost confluent with pallial line.

Remarks. Long ranging and variable species, known from the Fullers Earth (Bathonian) to Portland Beds of Britain. The most well known forms of this species come from the Red Nodule Beds (*cordatum* Zone, Upper Oxford Clay) of Dorset, but the species is also common in the Lower and Middle Oxford Clay, where it is invariably crushed; specimens from these horizons tend to appear more elongate, but fall within the range of variation of the species. The Lower Oxford Clay forms have a thin and fragile shell, in which the silvery inner nacreous layer is often patchily pyritized.

Age and distribution. Kellaways Clay (*calloviense* Zone) to Upper Oxford Clay (*cordatum* Zone) of England.

3. GASTROPODS AND SCAPHOPODS

by N. T. J. HOLLINGWORTH

GASTROPODS and scaphopods are common throughout the Oxford Clay but have received little attention subsequent to the pioneering contributions of Hudleston (1884–1885) and Hudleston & Wilson (1892). There is considerable scope for a detailed systematic revision of the Oxford Clay gastropods and some of the names applied to the species selected here for description should be regarded as tentative. Despite high gastropod numerical abundance, especially in the Lower Oxford Clay, generic diversity is relatively low with only four families represented comprising the Pleurotomariidae, Procerithiidae, Amberleyidae and the Aporrhaidae. Only one species of scaphopod has been described from the Oxford Clay (Palmer 1975).

Most of the gastropods in the dominantly bituminous Lower Oxford Clay (Jason–Coronatum Zone) are preserved as crushed, friable aragonite. Well preserved specimens which are usually completely replaced by pyrite can be found weathering from the surfaces of large septarian concretions near the base of the Oxford Clay. Uncrushed specimens can also be found in large numbers from the numerous shell beds in the Lower Oxford Clay, where the gastropods have been completely replaced by early diagenetic pyrite (Hudson & Palframan, 1969) or as internal pyrite moulds with late diagenetic pyrite overgrowths (Hudson, 1982). Gastropods are less abundant in the Middle and Upper Oxford Clay (Athleta–Mariae Zones) and are generally preserved as pyrite internal moulds, and rarely as white, powdery aragonitic shells. Notable exceptions occur however, especially in the Lamberti limestone which was formerly exposed at Woodham Brickpit, Buckinghamshire, where specimens of *Ooliticia* and *Bathrotomaria* could be found in an excellent state of preservation as uncrushed or partly crushed calcite shells. A new locality with similar style preservation was recently discovered at Stanton Harcourt in Oxfordshire, but this is unfortunately only a temporary exposure.

Gastropod terminology follows recommendations by Moore (1960) and Arnold (1965). More detailed descriptions of families in which the Oxford Clay gastropods have been placed can also be found in Moore (1960), Wenz (1969) and Murray (1985). The palaeoecology of some of the Oxford Clay gastropods has been described by Duff (1975).

SPECIES DESCRIPTIONS

Order ARCHAEOGASTROPODA
Superfamily PLEUROTOMARIACEA
Family PLEUROTOMARIIDAE
Genus *BATHROTOMARIA*
Bathrotomaria reticulata (J. Sowerby)
Plate 9, figs 1 & 2

Description. Medium sized to large turbiniform shell, diameter almost equals height. Whorl profile broadly convex with selenizone forming periphery. Broad sutural ramp, sutures shallow. Base gently rounded, anomphalous. Selenizone is narrow, strongly convex forming a distinct cord situated at or just above mid-whorl. Ornament consists of spiral cords and collabral, opisthocyrt grooves which intersect to produce a reticulate pattern.
Remarks. The earliest whorls are not usually preserved on large individuals and there is considerable variation in shell morphology from distinctly trochiform to more depressed turbiniform types. Opportunistic herbivore, or algal grazer confined to semi-lithified or hard substrates.
Distribution. Rare or absent in the Lower and Middle Oxford Clay of central and southern England. Common in the Lamberti limestone in Buckinghamshire and Oxfordshire. Rare in the Upper Oxford Clay.

Superfamily AMBERLEYACEA
Family AMBERLEYIDAE
Genus *OOLITICIA*
Ooliticia oxfordiensis (d'Orbigny)
Plate 10, fig. 1

Description. Small to medium sized conical shell. Early whorls conical. Penultimate whorl broadly rounded. Sutures deep, well defined. Base is convex, anomphalous and ornamented with spiral cords only. Aperture subcircular. Columellar lip gently concave, thickened. Periphery evenly convex. Ornament of strong spiral cords with concave interspaces. Spiral cords intersect with opisthocyrt collabral threads to form pronounced nodose peripheral carinae.
Remarks. Commonly referred to in literature on the Oxford Clay as *Littorina*. Small individuals of *O. oxfordiensis* can be distinguished from *Procerithium* by their conical shells, larger size and distinct granulate spiral cords. ?Algal grazer.

Distribution. Rare or absent in the Lower and Middle Oxford Clay of central and southern England. Common in the Lamberti limestone of Buckinghamshire and Oxfordshire. Rare in the Upper Oxford Clay.

Order CAENOGASTROPODA
Superfamily CERITHIACEA
Family PROCERITHIIDAE
Genus *PROCERITHIUM*
Procerithium damonis (Lycett)
Plate 10, fig. 2

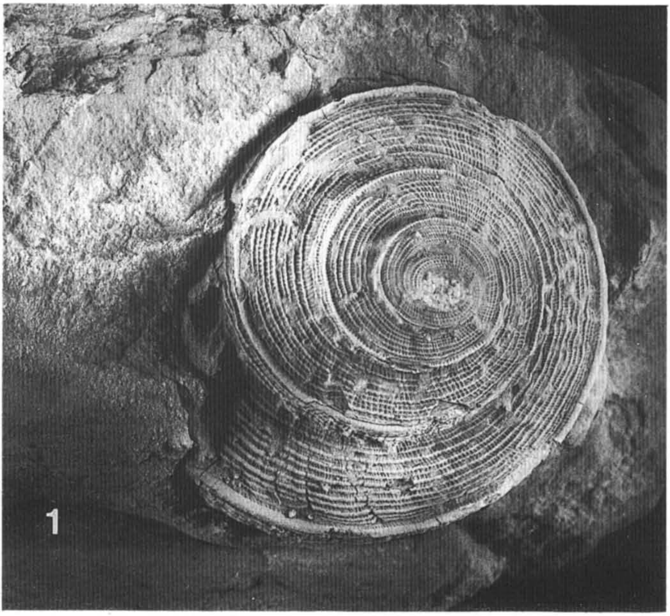
Description. Small, high spired turriculate shell with many whorls which are gently rounded and broadly convex. Sutures strongly impressed. Aperture with short siphonal canal, teardrop shaped. Base flattened, anomphalous. Early whorls strongly rounded, without ornament. Ornament on later whorls consists of strong intersecting collabral and spiral elements which produce pronounced varices that are most prominent on the last whorl. Epifaunal or semi-infaunal deposit feeder.
Distribution. Very abundant in the Lower Oxford Clay of central and southern England especially in the shell beds forming monospecific pyrite plaques. Less common in the Middle and Upper Oxford Clay, though widely distributed.

Superfamily STROMBACEA
Family APORRHAIDAE
Genus *DICROLOMA*
Dicroloma bispinosa (Phillips)
Plate 11, fig. 1

Description. High spired shell with few angular whorls, sutures shallow. Whorl profile strongly arched between sutures with well defined sutural ramp delineated at periphery by prominent spiral cords. Aperture elongate with pronounced siphonal notch. Outer lip expanded to produce wing with two recurved apertural spines. Whorls ornamented with fine spiral threads and major spiral cord which delineates the widest part of the whorl. Semi-infaunal deposit feeder or selective herbivore.

EXPLANATION OF PLATE 9

Fig. 1. *Bathrotomaria reticulata* (J. Sowerby). Apical view, Callovian, Lamberti Horizon, Lamberti Zone; Stanton Harcourt, Oxfordshire, × 1.5.
Fig. 2. *Bathrotomaria reticulata* (J. Sowerby). Adapertural view, Callovian, Lamberti Horizon, Lamberti Zone; Woodham, Buckinghamshire, × 1.5.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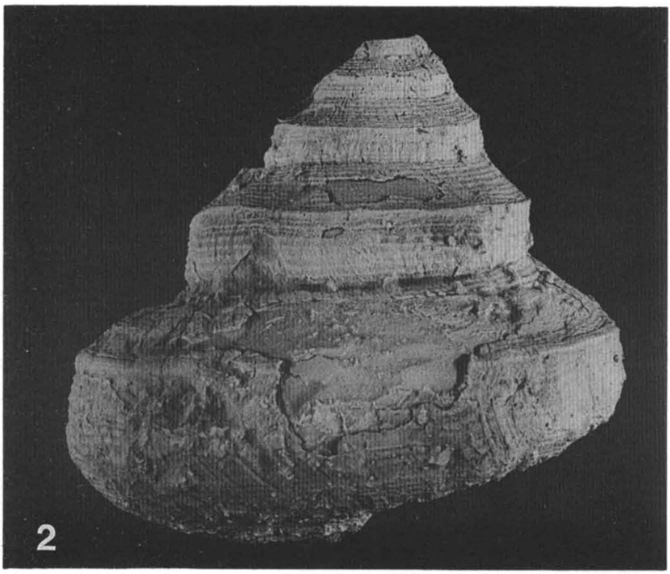
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Distribution. Common throughout the Oxford Clay although the best preserved and most easily recognizable specimens with intact spines are found in the more bituminous shales of the Lower Oxford Clay. Uncrushed specimens can be collected from septarian concretions, near the base of the Jason Zone in the Lower Oxford Clay exposed in the brickpits of central and southern England, although the spines usually break off upon extraction.

Dicroloma trifida (Phillips)
Plate 11, figs 2 & 3

Description. High-spired shell with four angular whorls, sutures shallow. Whorl profile angular with well defined sutural ramp delineated at the periphery by prominent spiral cord. Aperture elongate with siphonal notch. Outer lip expanded to produce wing with three recurved apertural spines. Ornament of spiral threads and major spiral cord which delineates the widest part of the whorl.
Remarks. *D. trifida* can easily be confused with *D. bispinosa* as their shell morphology is almost identical and the spines are not always completely preserved, or break upon extraction. Semi-infaunal deposit feeder or selective herbivore.
Distribution. Common throughout the Lower Oxford Clay. *D. trifida* may be represented in the Middle and Upper Oxford Clay but is usually too poorly preserved to enable identification to specific level.

Class SCAPHOPODA
Family DENTALIIDAE
Genus *PRODENTALIUM*
Prodentalium calvertensis Palmer
Plate 10, fig. 3

A single, but relatively abundant, small species of scaphopod has been reported from the Lower Oxford Clay of Central England (Palmer 1975). It is frequently associated with an abundance of the foraminiferan *Epistomina* sp. on which it is thought to have fed. Martill (1987) noticed

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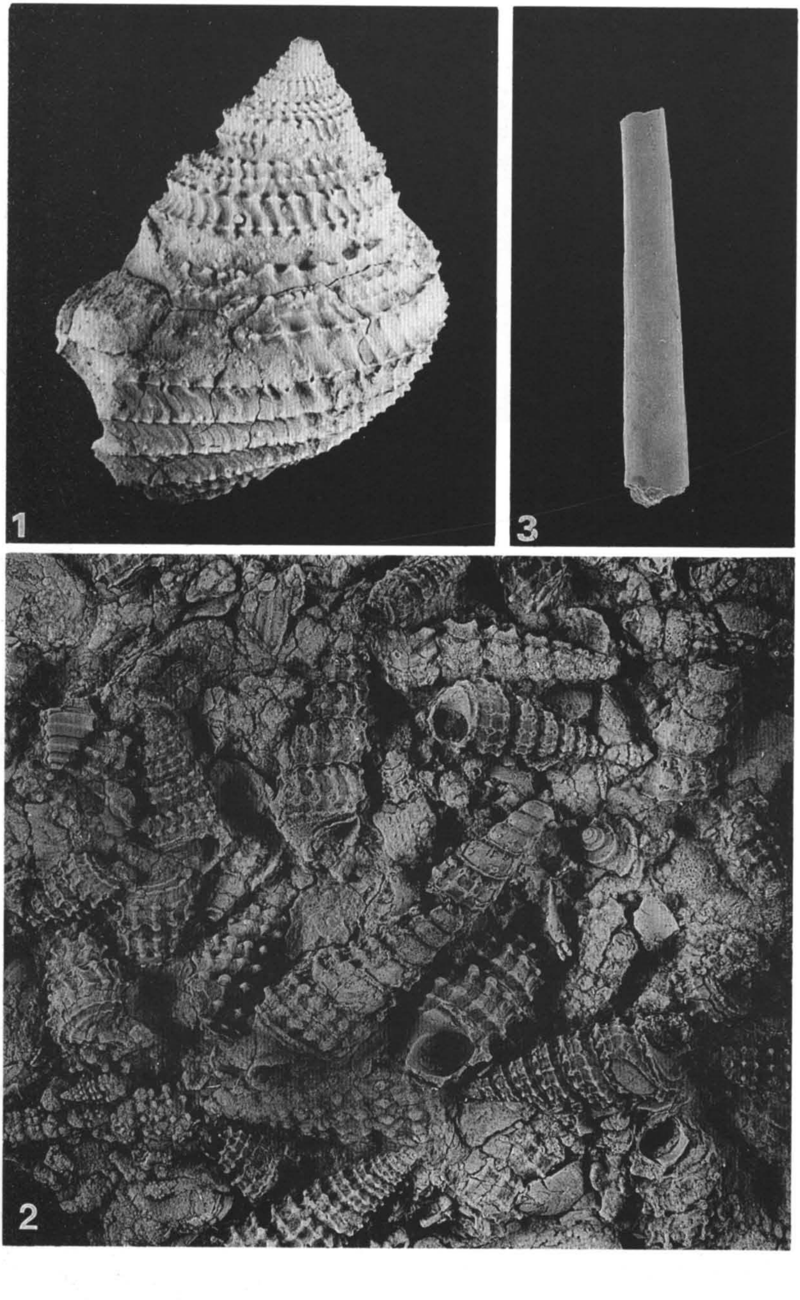
EXPLANATION OF PLATE 10

Fig. 1. *Ooliticia oxfordiensis* (d'Orbigny). Adapertural view, Callovian, Lamberti Horizon, Lamberti Zone; Stanton Harcourt, Oxfordshire, ×2.
Fig. 2. *Procerithium damonis* (Lycett). Preserved as pyrite casts. Callovian, Lower Oxford Clay. Newton Longville Brickworks, near Bletchley, Buckinghamshire, ×2.
Fig. 3. Scaphopod gen. et sp. indet. Middle Oxford Clay, Stanton Harcourt, Oxfordshire, ×10.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its occurrence associated with an ichthyosaur skeleton in Coronatum Zone of Buckinghamshire, and a small scaphopod is common in micro-palaeontological residues from the Lamberti horizon at Stanton Harcourt, Oxfordshire.

Diagnosis. Small, gently tapering, slightly curved tubular shell with numerous, fine, unequal, asymmetrical, longitudinal ribs. Up to forty ribs at the aperture.

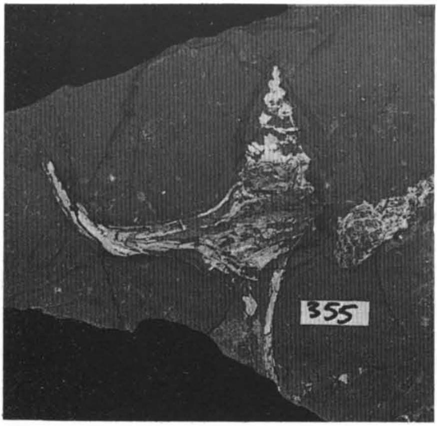
Remarks. The specimen illustrated in plate 10 Fig. 3, may represent a new species for the Oxford Clay as it lacks the fine ribbing characteristic of *Prodentalium calvertensis*.

Distribution. Common throughout the Lower, Middle and Upper Oxford Clay.

EXPLANATION OF PLATE 11

Figs 1, 2. *Dicroloma bispinosa* (Phillips). Crushed aragonitic original shell and uncrushed pyritic internal mould. Callovian, Lower Oxford Clay, Peterborough, Cambridgeshire, ×2.

Fig. 3. *Dicroloma trifida* (Phillips). Callovian, Lower Oxford Clay, Peterborough, Cambridgeshire. ×2.



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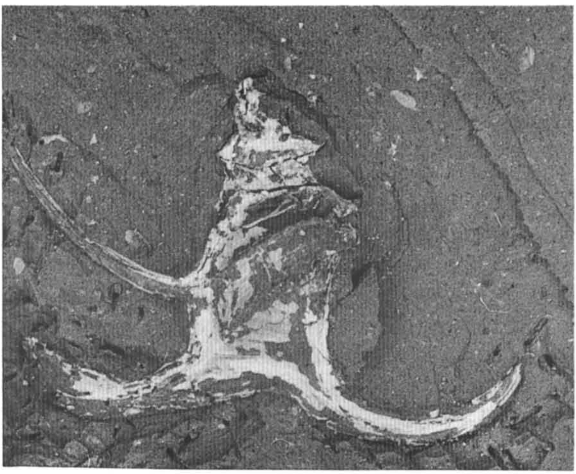

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4. AMMONITES

by KEVIN N. PAGE

ALTHOUGH the ammonites of the British Oxford Clay are world famous, surprisingly little detailed work has been published on them. Most studies are local in scope and only a few British groups have ever been monographed.

The earliest general work to cover British Callovian and Oxfordian species was that included in S. S. Buckman's 'Type Ammonites' (1909–1930). Buckman's aim was always towards achieving a more detailed chronology for the Jurassic, and, in the process, he founded large numbers of new genera and species. Unfortunately, many of the ages he assigned to his specimens were inferred, and some are now known to be incorrect. Nevertheless, he laid the foundations for subsequent detailed taxonomic and stratigraphical work.

R. Brinkmann studied the Oxford Clay around Peterborough and collected faunas of kosmoceratid ammonites, layer by layer. His published work is classic (1929a,b) and still represents one of the most detailed evolutionary and stratigraphical studies ever attempted; for a modern evaluation of Brinkmann's work see Raup & Crick (1982).

W. J. Arkell published several studies of Oxford Clay ammonite faunas (1933, 1941) including a detailed study of taxa recorded at Woodham, Buckinghamshire (1939) and a monograph of Cordatum Zone species (1935–1948). Most of the latter actually came from lateral equivalents of the Oxford Clay, in 'Lower Calcareous Grit' facies, as did some of the cardioceratids figured by Wright (1983) from the Lower Oxfordian in North Yorkshire. Callovian ammonites, mainly from sandstone facies in Yorkshire, are figured by Callomon & Wright (1989). Tintant (1963) monographed the Kosmoceratidae, and a monograph of Callovian perishpinctids has been commenced by B. M. Cox (1988).

NOMENCLATURE

As discussed at length by Callomon (1963, 1980) and Kennedy & Cobban (1975), ammonite shells are sexually dimorphic. The most obvious expression of this is in size, species being composed of a large and a small dimorph with a mature diameter ratio typically between 1:1·6 and 1:5. By analogy with modern cephalopods, the large forms are likely to have been female, and the small male, but as this has not yet been proved, the non-committal terms macro- and microconch are preferred (abbreviated to [M] and [m]). The contrasting size is accompanied usually by morphological differences associated with maturity. In many groups, the microconchs show only a limited change in ornament on the body chamber, but the final aperture often develops either paired lateral lappets or a ventral rostrum. In contrast, macroconchs tend to modify or lose ornamentation on the final whorl and usually have a relatively simple aperture.

Both dimorphs are morphologically variable, in some cases showing a spectrum of forms from inflated whorled, coarsely ornamented to compressed whorled, finely ribbed extremes. Historically, distinct morphological variants of each dimorph have tended to be assigned to different nominal species, and this is the reason for the vast number of names used to describe ammonite faunas. In the systematic section below *morphospecies* such as these have been grouped together to form *palaeo-biospecies*, that is, palaeontological approximations to neontological biospecies. Wherever possible, both dimorphs are discussed and typical variants described although only the most important morphospecies variants (or synonyms) are listed. This approach to ammonite taxonomy greatly simplifies the nomenclature as only one name is needed to describe a palaeo-biospecies, rather than the several, and more subjective, morphospecies names which are usually needed to describe a single assemblage. It also gives a more realistic picture of the actual faunal diversity which is often 'multiplied' five- or ten-fold in conventional lists.

Inevitably some species are better characterized than others, so the resolution of the paleo-biospecies described will differ from one lineage to another; i.e. the fact that one species has a greater stratigraphical range than another should not necessarily be taken to indicate slower morphological evolution.

The species are grouped into genera and, where appropriate, subgenera. Genera are used here primarily to distinguish separate evolutionary series or lineages, and subgenera to divide these lineages into convenient segments. The generic and subgeneric names used are the oldest appropriate to the group of dimorphic species being considered.

The suprageneric classification used here follows Callomon, Donovan & Howarth (1980).

PRESERVATION

Preservation styles vary considerably in the Oxford Clay (Chapter 1) and dramatically affect the appearance of specimens, sometimes making identification difficult or virtually impossible. Most specimens are crushed more or less flat in the clays and shales although occasionally 3-dimentional shells occur in calcareous or pyritic concretions. Only in the concretions can features such as ornament styles and whorl sections be appreciated fully. No two crushed specimens are identical as the angle of compression and shell-fracture patterns vary. Therefore, wherever possible, uncrushed specimens have been figured: some of these come from lateral equivalents of the Oxford Clay such as the Hackness Rock and 'Lower Calcareous Grit' of North Yorkshire.

APTYCHI

Ammonite jaw structures, or aptychi, occur sporadically in the Oxford Clay and usually only as isolated elements—shells with *in-situ* aptychi, preserved in their body chambers, are rare.

Most aptychi had an organic conchiolin composition (Kennedy & Cobban, 1975, p. 13) and consequently preservation is favoured in organic-rich sediments. Their patchy distribution, however, apparently reflects the distribution of those ammonite taxa with the most diagenetically resistant jaws.

Similarly, paired calcitic aptychi are rare—despite their great preservation potential—again largely due to the rarity of those species possessing such jaws.

BIO- AND CHRONOSTRATIGRAPHY

Ammonites are the most important biostratigraphic fossils for correlating marine Jurassic rocks. From an initial biozonation is derived a chronostratigraphical scheme or 'Standard Zonation' (Callomon & Donovan, 1974; Callomon, 1964, 1965; Cope *et al.*, 1980b). The sequence of ammonite faunas characterizing the zones currently recognized is given in Chapter 1.

Class CEPHALOPODA
Order AMMONOIDEA
Suborder PHYLLOCERATINA
Superfamily PHYLLOCERATACEAE
Family PHYLLOCERATIDAE
Subfamily CALLIPHYLLOCERATINAE
Genus *CALLIPHYLLOCERAS* Spath

Description. Involute, compressed with a rounded venter. Internal mould smooth with periodic sigmoidal constrictions, which occasionally have corresponding flares on the ventral shell surface. Ornament consists only of fine growth lines.

Suture typical for a phylloceratid; complex, with highly divided lobes ending in ovoid tips.

Dimorphism poorly known.

Calliphylloceras demidoffi (Rousseau)
Not illustrated

Description. Typical for genus. Includes giants; Arkell (1935–1948, p. 141) recorded a specimen with a septate diameter of 450 mm, suggesting a maximum size, with body chamber, of around 600 mm. Most other specimens are considerably smaller.
Range. Extremely rare in Britain apparently mainly in the Mariae Zone (Scarburgense Subzone).

Suborder LYTOCERATINA
Superfamily LYTOCERATACEAE
Family LYTOCERATIDAE
Subfamily LYTOCERATINAE
Genus *LYTOCERAS* Suess

Description. Evolute with round whorls. Shell surface with growth lines or riblets, sometimes crinkled. Some species with periodic flares, which often overlie constrictions on the internal mould. Suture typical for a lytoceratid, with highly divided lobes and saddles. Dimorphism poorly understood.

Lytoceras adeloides Kudern
Not illustrated

Description. Typical for genus.
Remarks. Poorly known in Britain; reaches at least 250 mm in diameter in Switzerland (Jeannet 1951, p. 30).
Range. Very rare, recorded from the Spinosum, Lamberti and Scarburgense Subzones (Arkell, 1935–1948).

Suborder AMMONITINA
Superfamily HAPLOCERATACEAE
Family OPPELIIDAE
Subfamily OPPELIINAE
Genus *PARALCIDIA* Spath

Description. *Macroconch*: Involute and compressed, with a sharp venter on inner whorls which becomes rounded on the body chamber. Virtually smooth, with weak traces of distant falcoid ribbing; aperture simple.
Microconch: Smooth, compressed, but less involute than macroconch and with a less triangular whorl section. Aperture lappeted.

Paralcidia glabella (Leckenby)
Plate 12, figs 1–3

Description. *Macroconch*: Typical for genus. Venter of inner whorls trimarginate. Mature at around 70 mm diameter (septate to 50 mm).
Microconch: Smooth. The maximum size seen is around 20 mm (septation ends at around 15 mm).
Range. Occurs rarely in the Athleta and Lamberti Zones.

Subfamily HECTICOCERATINAE
Genus *HECTICOCERAS* Bonarelli
Subgenus *LUNULOCERAS* Bonarelli

Description. *Macroconch*: Moderately evolute, compressed. Ribbing falcoid and may be strong, but commonly fades on the inner half of the whorl side. Aperture simple.
Microconch: More evolute than the macroconch; with lappets.

EXPLANATION OF PLATE 12

Figs 1–3. *Paralcidia glabella* (Leckenby). 1, 2, complete macroconch, $\times\frac{2}{3}$. 3, microconch, $\times 1$. (both preserved in chamositic oolite). Hackness Rock, Scarborough, North Yorkshire; Athleta or Lamberti Zone.

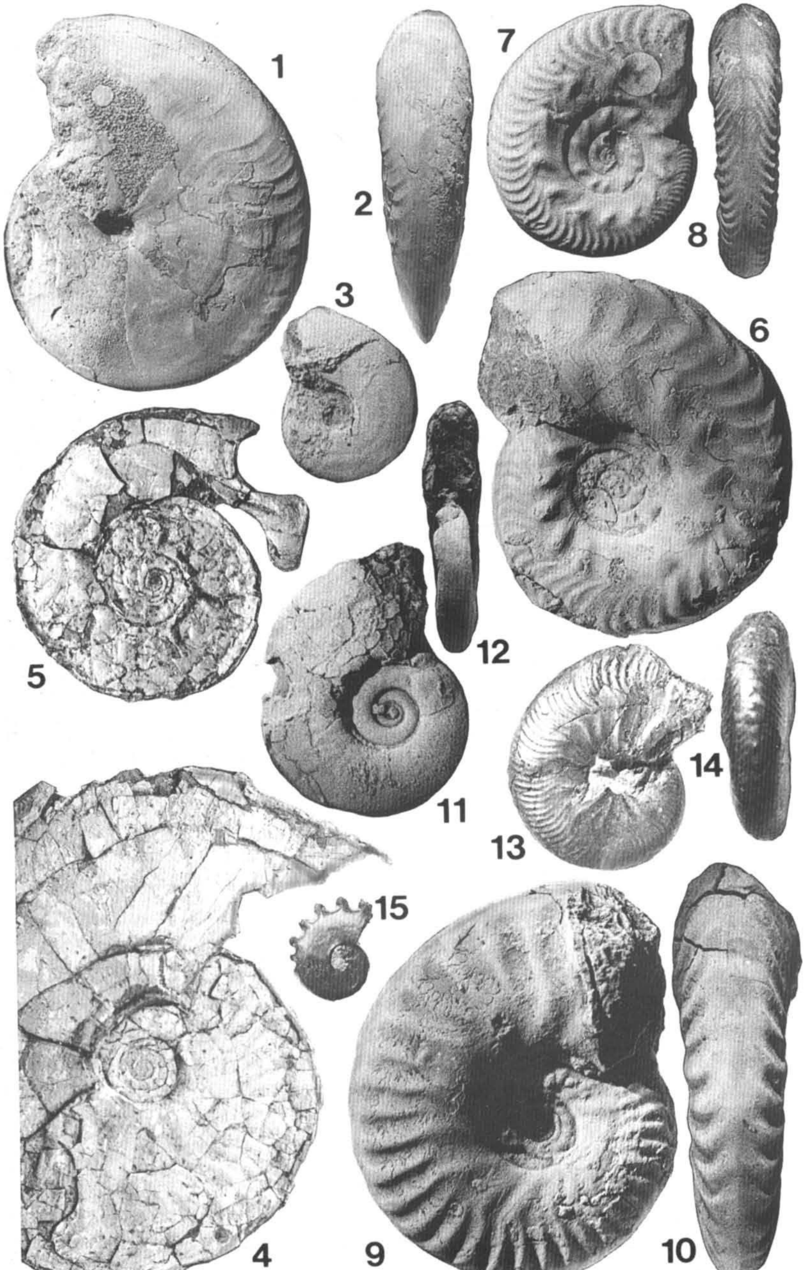
Figs 4, 5. *Hecticoceras* (*Sublunuloceras*) *lonsdali* (Pratt). 4, complete macroconch, $\times\frac{2}{3}$. 5, complete microconch, $\times 1$ (crushed shells in shale). Lower Oxford Clay, Christian Malford, Wiltshire; Athleta Zone, Phaeinum Subzone.

Figs 6–8. *Hecticoceras* (*Orbignyceras*) *pseudopunctatum* (Lahusen). 6, macroconch, Hackness Rock, Scarborough, North Yorkshire, $\times\frac{2}{3}$ (preserved in chamositic oolite). 7, 8, microconch, 'Middle' Oxford Clay, Oxford, $\times 1$ (pyritic internal mould). Athleta Zone.

Figs 9, 10. *Hecticoceras* (*Putealiceras*) *puteale* (Leckenby). Macroconch, $\times 1$ (pyritic internal mould). 'Upper' Oxford Clay, Weymouth, Dorset. Lamberti Zone.

Figs 11, 12. *Hecticoceras* (*Putealiceras*) *bonarellii* de Loriol. Inner whorls of ?macroconch, $\times 1$ (pyritic internal mould). 'Upper' Oxford Clay, Warboys, Cambridgeshire. Probably from the Mariae Zone, Praecordatum Subzone.

Figs 13–15. *Creniceras renggeri* (Oppel). 13, 14, macroconch, $\times 1$, 'Upper' Oxford Clay, Warboys, Cambridgeshire. Mariae Zone, Praecordatum Subzone or Cordatum Zone, Buckowskii Subzone. 15, complete microconch (lappets not preserved) $\times 1$, 'Upper' Oxford Clay, Woodham, Buckinghamshire. Mariae Zone, Scarburgense Subzone (pyritic internal moulds).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H. (?*Lunuloceras*) cf. *lugeoni* (de Tsytovitch)
Not illustrated

Comments. Hecticoceratids are rare in Britain below the Grossouvrei Subzone of the Coronatum Zone. Those that do occur are poorly characterized, however the morphology of typical specimens would fit the generalized subgeneric description given above.
Range. The earliest recorded Callovian hecticoceratid in Britain came from the Medea Subzone, but was not specifically determinable (Callomon, 1968, p. 282). Specimens recorded as *H. lugeoni* and *H. rossiense* occur rarely in the Obductum Subzone (Callomon, 1968, pp. 281–284).

Subgenus *SUBLUNULOCERAS* Spath

Description. *Macroconch*: Moderately involute and compressed, with a discoidal shape. Unicarinate, with weak falcoid ribbing. Simple aperture.
Microconch: similar to macroconch but virtually smooth and with large spatulate lappets.

H. (*Sublunuloceras*) *lonsdali* (Pratt)
Plate 12, figs 4, 5

Description. *Macroconch*: typical for genus. Ribbing fades on the body chamber leaving only swollen distant secondary ribs on the outer half of the whorl side. Mature at 70–110 mm diameter (septate to 45–70 mm).
Microconch: [= *H. brightii* (Pratt)] Inner whorls with very weak ribbing. Body chamber smooth, sometimes with a trace of secondary ribbing. Mature size 18–45 mm (septate to 10–22 mm).
Range. Upper Grossouvrei to Phaeinum Subzones.

Subgenus *ORBIGNYCERAS* Gerard and Contaut

Description. *Macroconch*: Moderately evolute. Whorl section compressed, with flattened whorl sides. Primary ribbing fades on the middle whorls leaving relatively sharp curved secondaries. The latter have a tendency to swell slightly on the outer part of the whorl side. Aperture simple.
Microconch: Relatively evolute and lappeted, with falcoid ribbing which either fades on the inner half of the whorl side or develops elongate bullae by swelling of the primaries.

H. (*Orbignyceras*) *pseudopunctatum* (Lahusen)
Plate 12, figs 6–8

Description. *Macroconch*: Typical for subgenus. Primary ribs typically faded by 30–40 mm. Septate to perhaps 60–70 mm, suggesting a mature size of at least 100 mm.

Microconch: Typical for subgenus.
Range. Proniae and Spinosum Subzones.

Subgenus *PUTEALICERAS* Buckman

Description. *Macroconch*: Moderately evolute with stouter whorls and stronger ribbing than *Orbignyceras*. Ribbing blunt and tends to develop a distinct club shape due to ventrolateral inflation. Venter unicarinate. Aperture simple.
Microconch: Relatively evolute, compressed. Typical specimens have the primary ribbing modified to form distant bullate tubercles on the inner part of the whorl side. External to the tubercules is fine secondary ribbing. Venter unicarinate. Aperture lappeted.

H. (*Putealiceras*) *puteale* (Leckenby)
Plate 12, figs 9, 10

Description. *Macroconch*: Typical for subgenus. Club-like secondary ribbing fades beside narrow keel. Septate to around 35–40 mm, probably mature at around 60 mm.
Microconch: Typical for genus. Probably mature at less than 30 mm diameter.
Range. Lamberti Zone, frequent in the Lamberti Subzone.

H. (*Putealiceras*) *bonarellii* de Loriol
Plate 12, figs 11, 12

Description. *Macroconch*: Moderately evolute, compressed with flat whorl sides. Generally smooth to at least 15 mm diameter, then gradually developing falcoid ribbing. The largest septate specimens seen have a diameter of around 28 mm, suggesting a body chamber to at least 40 mm.
Microconch: [=*H. matheyi* de Loriol] Evolute, compressed with flat whorl sides. Inner whorls smooth to *c.* 15–20 mm, thereafter developing modified falcoid ribbing. In some, the primary ribbing is reduced to distant nodes or is present only on the inner half of an otherwise smooth side. Secondary ribbing sometimes develops and may become relatively coarse on the body chamber. Septate to at least 18 mm, mature at around 26 mm.
Range. Common in the Scarburgense Subzone. Similar specimens also occur in the Praecordatum Subzone.

Subfamily DISTICHOCERATINAE
Genus *DISTICHOCERAS* Munier-Chalmas

Description. *Macroconch*: Involute with high, compressed whorls. Primary ribbing weak, secondaries ending on, or looped into, ventrolateral

nodes or clavi. Mid ventral keel weakly developed. Nucleus smooth but already with ventral ornament. Simple aperture.
Microconch: [=*Horioceras* Munier-Chalmas]. Moderately involute, compressed smooth whorled, but develops relatively large ventrolateral spines or clavi, which form a row on either side of the venter. Aperture lappeted.

Distichoceras bicostatum (Stahl)
Plate 13, figs 1–4

Description. *Macroconch*: Typical for genus, and losing ventro-lateral spines on the mature body chamber, which retains a tabulate venter. Septation ends at around 40 mm, mature at around 70 mm [includes *D. subornata* (Spath)].
Microconch: [=*Horioceras baugieri* (d'Orbigny)] Typical for genus. Mature at between 20–30 mm (septate to 15–20 mm?).
Remarks. The dimorphism and morphology of *D. bicostatum* are thoroughly discussed and illustrated by Palframan (1967).
Range. An occasional constituent of Athleta and Lamberti Zone faunas (Proniae or Spinosum to Lamberti Subzones).

Subfamily GLOCHICERATINAE
Genus *OCHETOCERAS* Haug
Subgenus *CAMPYLITES* Rollier

Description. *Macroconch*: Moderately involute, compressed. Ribbing blunt and falcoid, weakens and fades on outer whorls; the stronger secondary ribs have a distinct swollen appearance. Often develops a spiral band or groove on the middle of the whorl side. Venter tricarinate with median keel. Aperture simple.
Microconch: Inner whorls smooth, or weakly ornamented. Venter tending to become tricarinate. Aperture lappeted.

O. (*Campylites*) *delmontanum* (Oppel)
Plate 13, figs 5, 6

Description. *Macroconch*: Typical for subgenus. Maximum size seen is around 54 mm, although the mature size is certainly larger.
Microconch: Apparently typical for subgenus.
Range. Bukowskii Subzone, rare. A similar species has been recorded from the Praecordatum Subzone.

O. (*Campylites*) sp.
Not illustrated

Description. *Macroconch*: Inner whorls not seen. Large, mature at around 150 mm diameter (septate to 96 mm). Body chamber

compressed; venter sharp, trimarginate. Ribbing dies out soon after the end of septation.
Microconch: Not recorded.
Remarks. The single specimen described and figured by Arkell (1935–1948, p. 350; text-fig. 125), is stratigraphically distinct from other British species of *Ochetoceras*, but too incomplete for a more positive identification.
Range. Cordatum Subzone (very rare).

Subfamily TARAMELLICERATINAE
Genus *CRENICERAS* Munier-Chalmas

Description. *Macroconch*: [=*Lorioloceras* Spath; *Proscaphites* Rollier] Involute, with very small umbilicus. Generally moderately compressed. Finely or weakly ribbed and developing a beaded keel, usually flanked by ventro-lateral clavi. Aperture simple.
Microconch: Compressed, smooth, moderately involute. Venter develops characteristic 'Cocks-comb' serrations. Aperture lappeted.

Creniceras renggeri (Oppel)
Plate 13, figs 13–15

Description. *Macroconch*: [=*Taramelliceras richei* (de Loriol); *T. oculatum* (Phillips)] Typical for genus. A small species, septation ends at around 15–20 mm, body chamber to around 25–30 mm.
Microconch: Typical for genus with coarse serrations on the mature body chamber. Mature at around 10–16 mm (septate to 7–10 mm).
Remarks. Palframan (1966) describes in detail the dimorphism and variability of *C. renggeri*.
Range. Common at certain levels in the Scarburgense and Praecordatum Subzones, persisting into the lower part of the Bukowskii Subzone.

Creniceras crenatum (Bruguiere)
Not illustrated

Description. Apparently a larger species than *C. renggeri* with a macroconch possessing better developed ventral ornament and the microconch smaller serrations.
Remarks. Poorly known in Britain.
Range. Recorded by Spath (1939) from the upper part of the Bukowskii Subzone.

Genus *SCAPHITODITES* Buckman

Description. *Macroconch*: [=*Popanites*? Rollier] Involute, smooth with constricted and flared aperture.

Microconch: Small, smooth with rounded venter and markedly excentric body chamber. Aperture lappeted.

Scaphitodites navicula Buckman
Plate 13, figs 7, 8

Description. *Macroconch*: Not recorded.
Microconch: Typical for genus. Mature size around 10–13 mm (septate to *c*. 6–8 mm).
Range. Occasionally occurs in the Scarburgense Subzone.

Superfamily STEPHANOCERATACEAE
Family KOSMOCERATIDAE
Genus *SIGALOCERAS* Hyatt
Subgenus *CATASIGALOCERAS* Buckman

Description. *Macroconch*: Moderately involute, typically relatively compressed. Venter tabulate but becoming rounded on the mature body chamber. Ribbing fine, crossing venter on middle whorls but fading almost completely on the body chamber. Nuclei, however, show mid-ventral rib weakening and the development of small ventrolateral and

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EXPLANATION OF PLATE 13

Figs 1–4. *Distichoceras bicostatum* (Stahl). 1, 2, complete macroconch, $\times \frac{2}{3}$ (preserved in chamositic oolite), Hackness Rock, Scarborough, North Yorkshire, Athleta or Lamberti Zone. 3, 4, microconch, $\times 1$ (pyritic internal mould), 'Middle' Oxford Clay, Oxford, Athleta Zone.

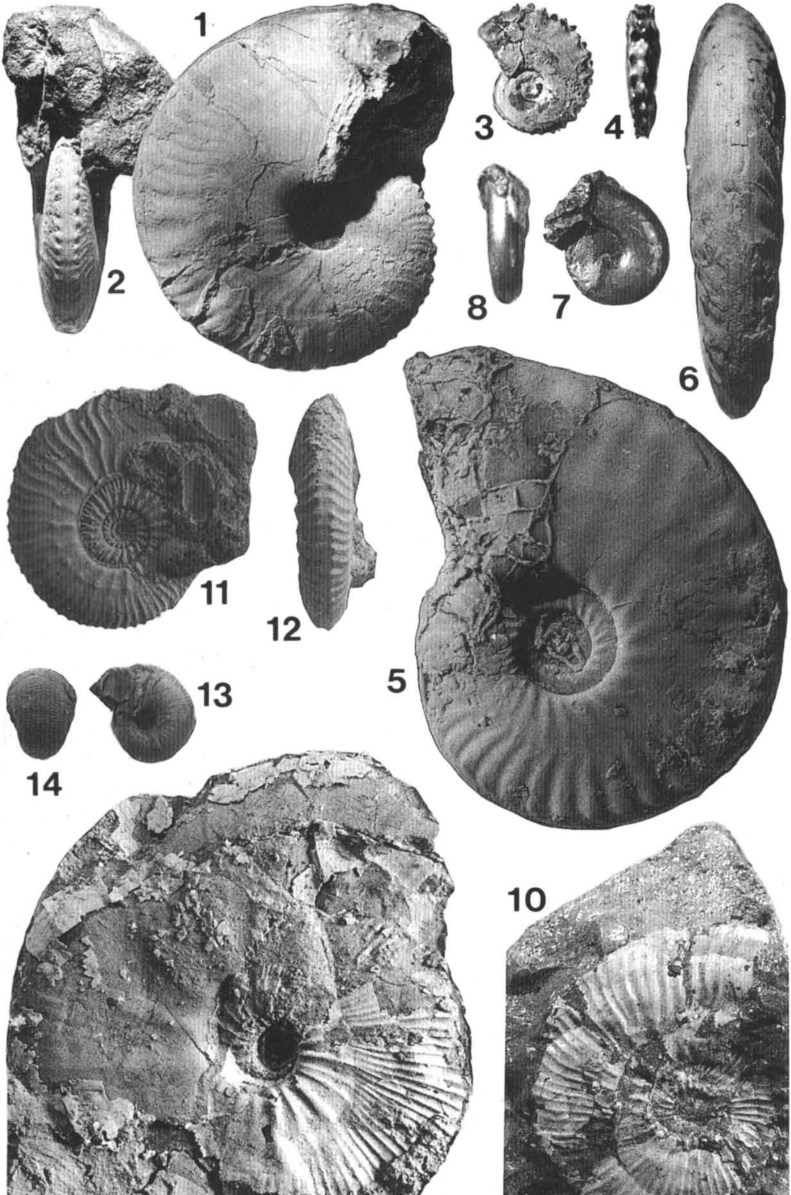
Figs 5, 6. *Ochetoceras* (*Campylites*) *delmontanum* (Oppel). Macroconch, $\times \frac{2}{3}$ (pyritic internal mould), Upper Oxford Clay, St. Ives, Cambridgeshire. Mariae Zone, Praecordatum Subzone.

Figs 7, 8. *Scaphitodites navicula* Buckman. Complete microconch with partial lappet, $\times 1$ (pyritic internal mould), Upper Oxford Clay, Woodham, Buckinghamshire. Mariae Zone, Scarburgense Subzone.

Figs 9, 10. *Sigaloceras* (*Catasigaloceras*) sp. nov. 9, complete macroconch, $\times 1$. 10, complete microconch, lappet not preserved, $\times 1$ (both crushed shells in sandy mudrock). Kellaways Formation to Oxford Clay transition facies, near Corscombe, Dorset. Calloviense Zone, lower part of Enodatum Subzone.

Figs 11, 12. *Sigaloceras* (*Catasigaloceras*) *enodatum* (Nikitin). Complete microconch with partial lappet, $\times 1$ (preserved in calcareous sandstone). Cave Rock (='Kellaways Rock' *s.l.*), South Cave, Humberside. Calloviense Zone, middle part of Enodatum Subzone.

Figs 13, 14. *Macrocephalites tumidus* (Reinecke). Nucleus, $\times 1$ (septarian nodule preservation), Weymouth, Dorset. Calloviense Zone, Enodatum Subzone.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lateral nodes. More coarsely ribbed, rounder whorled variants also occur. Aperture simple.
Microconch: Generally compressed, but more evolute than macroconchs. Nodes and tubercles better developed. Ventral smooth band present, virtually to the end of the mature body chamber. Ribbed to end; lappeted.

S. (*Catasigaloceras*) sp. nov.
Plate 13, figs 9, 10

Description. *Macroconch*: Assemblages are dominated by compressed variants with fine ribbing which fades entirely on the body-chamber. Rare stouter whorled variants retain some coarse ribbing at this stage. Typically mature at around 55–72 mm (septate to 50 mm).
Microconch: Inner whorls show a ventral smooth band flanked by small round tubercles. The ribbing tends to coarsen on the mature body chamber, but lateral nodes may weaken. Septate to around 20–23 mm, mature at up to 44 mm.
Range. Lower Enodatum Subzone, locally abundant.

S. (*Catasigaloceras*) *enodatum* (Nikitin)
Plate 13, figs 11, 12; Plate 15, fig. 1

Description. *Macroconch*: [= *S. planicerclus* (Buckman)] Compressed variants resemble a small *S*. sp. nov but tend to have a stouter whorl section and more evolute coiling. Relatively evolute and coarsely ornamented variants have ribbed body chambers. Mature size around 45–55 mm (septate to 35–38 mm).
Microconch: Smaller and more *Kosmoceras*-like than *S*. sp. nov. Typical variants have compressed whorls, fine ribbing and develop a double row of lateral nodes on the outer whorl. Ventrolateral nodes are relatively sharp on the body chamber. Mature size is less than 30 mm (septate to *c*. 20 mm).
Remarks. *S. enodatum* is the smallest kosmoceratid species known in Britain. Populations intermediate in size between *S. enodatum* and both the earlier *S*. sp. nov and the later *S. anterior* occur locally.
Range. Middle Enodatum Subzone; often abundant.

S. (*Catasigaloceras*) *anterior* (Brinkman)
Plate 14, fig. 1; Plate 15, fig. 2

Description. *Macroconch*: A larger species than *S. enodatum*, showing many features transitional to *Kosmoceras*. These include more evolute coiling, compressed high whorls with very fine ribbing, and incipient ventrolateral nodes. Mature at around 50–60 mm (septate to 40–45 mm).

Microconch: [=*Kosmoceras gulielmi anterior* Brinkman] Can superficially resemble microconchs of *S. enodatum*, but is larger; some variants are virtually indistinguishable from microconchs of *Kosmoceras medea* Callomon.
Remarks. A similarly sized species to *S.* sp. nov but distinguishable by its *Kosmoceras*-like characteristics.
Range. Upper Enodatum Subzone—locally abundant.

Genus *KOSMOCERAS* Waagen
Subgenus *GULIELMICERAS* Buckman

Description. *Macroconch*: [=*Gulielmites* Buckman] Moderately involute. Finely and sharply ribbed; inner and middle whorls with paired lateral tubercles. Venter tabulate, with sharp ventro-lateral tubercules separated by a smooth band. Coarsely ribbed variants occur but are relatively rare. Body chamber typically smooth with a rounded venter. Aperture simple.
Microconch: Ribbed throughout, often with some coarsening on the body chamber. Typically more evolute than macroconch with stronger tuberculation. Aperture lappeted.

K. (*Gulielmiceras*) *medea* Callomon
Plate 15, fig. 3

Description. *Macroconch*: Only outer row of lateral tubercules well developed; inner row incipient, formed due to the accentuation of the primary ribbing at the umbilical margin.

A small species typically mature at around 60–90 mm (septate to 35–65 mm).
Microconch: Typical for genus, but small (mature at 35–40 mm; septate to *c.* 25–30 mm).
Remarks. *K. medea* and the later *K. jason* (see below) are discussed at length by Callomon (1955).
Range. Medea Subzone—abundant and characteristic.

K. (*Gulielmiceras*) *jason* (Reinecke)
Plate 14, figs 2, 3; Plate 15, figs 4, 5

Description. *Macroconch*: [=*K. conlaxatum* Buckman] Typical for genus, with a well developed double row of lateral tubercules separated by a spiral smooth band. A large species, maturing at around 90–120 mm (septate to 60–70 mm?).
Microconch: [=*K. guliemi* (J. Sowerby)] Typical for genus, but larger than *K. medea*, mature at around 50–65 mm (septate to 35–45 mm?).
Range. Jason Subzone—abundant and characteristic.

Subgenus *ZUGOKOSMOKERAS* Buckman

Description. *Macroconch*: Broadly similar to *Gulielmiceras*, but with a tabulate venter and ribbing to the end of the body chamber. Finely fibbed variants have poorly developed tubercules on their middle and outer whorls although coarsely ornamented forms are also common. Aperture simple.
Microconch: Includes both relatively finely and also coarsely ribbed variants; the latter often with well developed ventrolateral spines. Aperture with long lappets.

K. (*Zugokosmokeras*) *obductum* (Buckman)
Plate 14, fig. 4; Plate 15, fig. 6

Description. *Macroconch*: A relatively small species, mature at around 90–100 mm (septate to 65–75 mm?). Ribbing comparatively coarse, ventral tubercules or ribs persisting onto the mature body chamber.
Microconch: Some like *K. jason*, but also including more coarsely ribbed and spinous forms [resembling *K. castor* (Reinecke)]. Mature size around 35–40 mm (septate to 25–30 mm?).
Range. Common in the Obductum Subzone.

EXPLANATION OF PLATE 14

Fig. 1. *Sigaloceras* (*Catasigaloceras*) *anterior* (Brinkman). Complete microconch, lappet not preserved, × 1 (crushed shell in shale). Lower Oxford Clay, Peterborough, Cambridgeshire. Calloviense Zone, upper part of Enodatum Subzone.

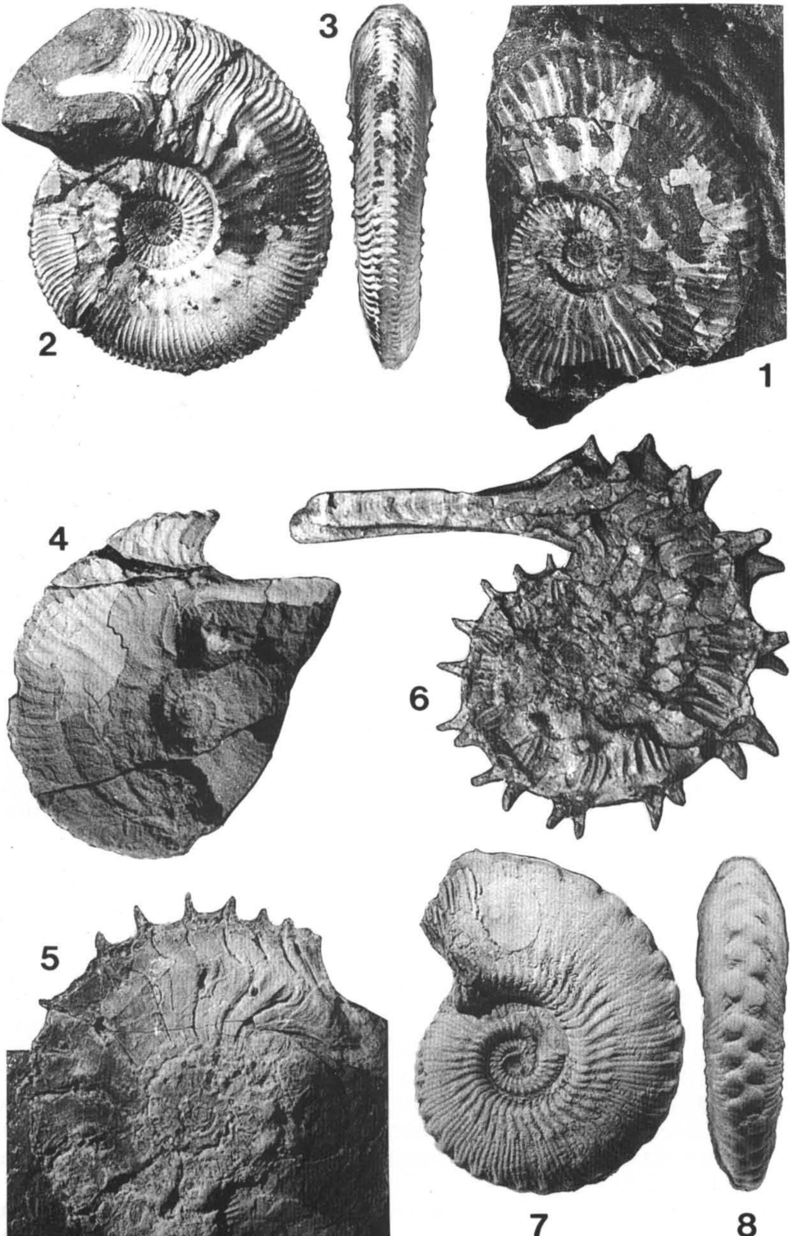
Figs 2, 3. *Kosmoceras* (*Gulielmiceras*) *jason* (Reinecke). Complete microconch × 1 (septarian concretion preservation). Lower Oxford Clay, Wiltshire. Jason Zone, Jason Subzone.

Fig. 4. *Kosmoceras* (*Zugokosmokeras*) *obductum* (Buckman). Complete microconch, × 1 (crushed shell in shale). Lower Oxford Clay, Swineshead, Bedfordshire. Coronatum Zone, Obductum Subzone.

Fig. 5. *Kosmoceras* (*Zugokosmokeras*) *grossouvrei* Douvillé. Complete microconch, × 1 (impression of crushed shell in shale). Lower Oxford Clay, Weymouth, Dorset. Coronatum Zone, Grossouvrei Subzone.

Fig. 6. *Kosmoceras* (*Lobokosmokeras*) *phaeinum* (Buckman). Complete microconch, coarsely ornamented variant, × 1 (crushed shell in shale). Lower Oxford Clay, Christian Malford, Wiltshire. Athleta Zone, Phaeinum Subzone.

Figs 7, 8. *Kosmoceras* (*Lobokosmokeras*) *proniae* Teisseyre. Microconch, × 1 (pyritic internal mould). 'Middle' Oxford Clay, Peterborough, Cambridgeshire. Athleta Zone, Proniae Subzone.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K. (Zugokosmokeras) posterior Brinkman
Not illustrated

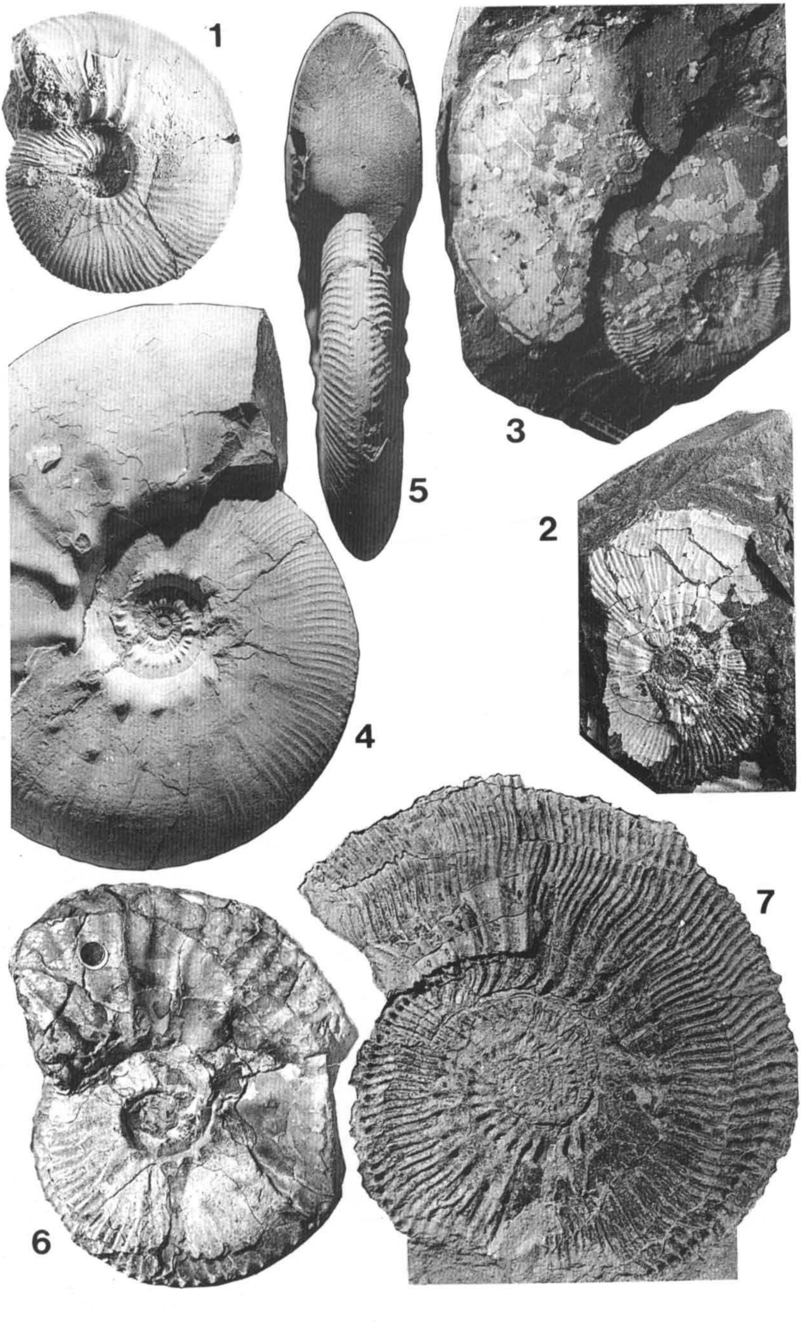
Description. *Macroconch*: [=*K. obductum posterior* Brinkman] Similar to *K. obductum* in coarseness of ribbing, but larger and more evolute and, therefore, transitional to *K. grossouvrei* Douvillé (see below). Mature at over 130 mm (septate to *c.* 100 mm?).
Microconch: Similar to *K. obductum* but including even coarser variants [resembling *K. pollux* Reinecke]. Mature probably around 60–70 mm.
Range. Common in the lower Grossouvrei Subzone.

K. (Zugokosmokeras) grossouvrei Douvillé
Plate 14, fig. 5; Plate 15, fig. 7

Description. *Macroconch*: Large relatively evolute, mature at around 160–180 mm (septate to 130–140 mm?). Finely ribbed variants are characteristic and very densely ribbed to the end of the mature chamber [=*K. zugium* (Buckman)]. Coarsely ribbed forms are common [=*K. pollucinum* (Teisseyre)]. On the outer whorls, ribs tend to cross the venter uninterrupted; only the middle and inner whorls retain a mid ventral smooth band and ventrolateral tubercules.
Microconch: Includes both finely ribbed variants and the more characteristic coarsely ornamented and spinous forms [=*K. castor* and *K. pollux*]. Mature at around 60–80 mm (septate to 45–60 mm?).
Range. Abundant above *K. posterior*, in the Grossouvrei Subzone.

EXPLANATION OF PLATE 15

Fig. 1. *Sigaloceras (Catasigaloceras) enodatum* (Nikitin). Complete macroconch, ×$\frac{2}{3}$ (crushed shell in muddy sand). Topmost Kellaways Sand, Peterborough, Cambridgeshire. Calloviense Zone, middle part of Enodatum Subzone.
Fig. 2. *Sigaloceras (Catasigaloceras) anterior* (Brinkman). Macroconch, ×$\frac{2}{3}$ (crushed shell in shale). Lower Oxford Clay, Peterborough, Cambridgeshire. Calloviense Zone, upper part of Enodatum Subzone.
Fig. 3. *Kosmoceras (Gulielmiceras) medea* Calloman. Macroconch, ×$\frac{2}{3}$ (crushed shell in shale). Lower Oxford Clay, Peterborough, Cambridgeshire. Jason Zone, Medea Subzone.
Figs 4, 5. *Kosmoceras (Gulielmiceras) jason* (Reinecke). Complete macroconch, ×$\frac{2}{3}$ (septarian concretion preservation). Lower Oxford Clay, ?Wiltshire. Jason Zone, Jason Subzone.
Fig. 6. *Kosmoceras (Zugokosmokeras) obductum* (Buckman). Complete macroconch, ×$\frac{2}{3}$ (septarian concretion preservation). Lower Oxford Clay, 'Huntingdonshire' (=part of north west Cambridgeshire?). Coronatum Zone, Obductum Subzone.
Fig. 7. *Kosmoceras (Zugokosmokeras) grossouvrei* (Douvillé). Macroconch, ×$\frac{2}{3}$ (impression of crushed shell in shale). Lower Oxford Clay, Weymouth, Dorset. Coronatum Zone, Grossouvrei Subzone.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Subgenus *LOBOKOSMOKERAS* Buckman

Description. *Macroconch*: Generally similar to *Zugokosmokeras*, but differing in ribbing style. In *Zugokosmokeras* the secondary ribs are joined only at the point of initial furcation on the whorl side. In *Lobokosmokeras*, however, the secondaries reunite in pairs or more at ventral tubercules. Tuberculation weakens on the outer whorl, and ribbing characteristically crosses the venter uninterrupted on the body chamber. Coarsely ribbed variants resemble *Kosmoceras* (*K*). [=*Hoplikosmokeras* Buckman]. Aperture simple.
Microconch: Variable, with finely ribbed and coarsely spinous variants [=*Spinikosmokeras* Buckman]. In all, however, looped secondary ribbing is typical. Aperture lappeted.

K. (*Lobokosmokeras*) *phaeinum* (Buckman)
Plate 14, fig. 6; Plate 16, fig. 1

Description. *Macroconch*: Similar to *K. grossouvrei* but with looped or bundled ribbing, which is best seen in the coarsely ribbed variants [=*K. hoplistes* (Buckman)]. Mature at around 120 mm (septate to *c*. 75 mm).
Microconch: [=*K. acutistriatum* (Buckman)] looped ribs prominent, and ventrolateral tubercles well developed and often spinous. Up to 56 mm diameter (septate to *c*. 35 mm).
Range. Common in and characteristic of the Phaeinum Subzone. Abundant in the Acutistriatum Band.

K. (*Lobokosmokeras*) *proniae* Teisseyre
Plate 14, figs 7, 8; Plate 16, figs 2, 3

Description. *Macroconch*: The typical variant is relatively compressed and finely ribbed. Umbilical tubercles are weak and separated from the stronger lateral tubercles by a spiral smooth band. Ventral tubercles also

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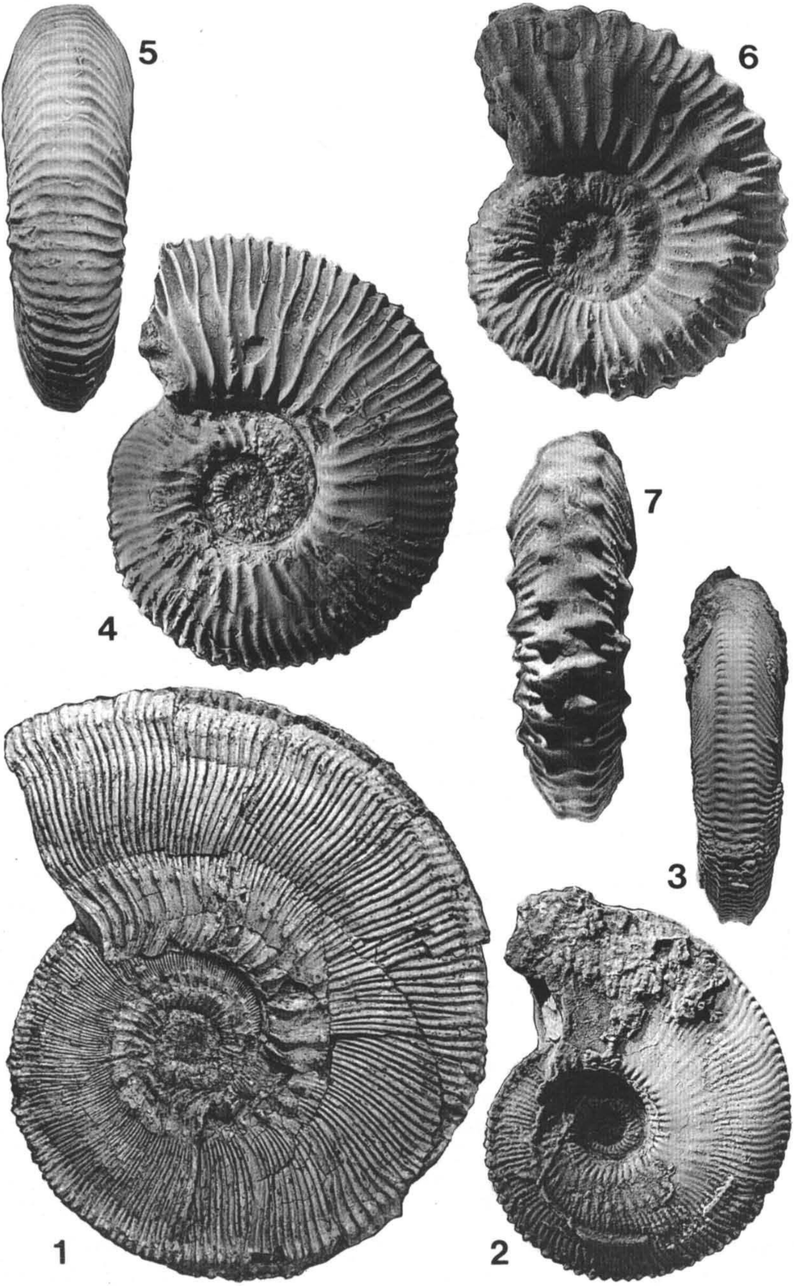
EXPLANATION OF PLATE 16

Fig. 1. *Kosmoceras* (*Lobokosmokeras*) *phaeinum* (Buckman). Complete macroconch, $\times\frac{2}{3}$ (crushed shell in shale). Lower Oxford Clay, Christian Malford, Wiltshire. Athleta Zone, Phaeinum Subzone.
Figs 2, 3. *Kosmoceras* (*Lobokosmokeras*) *proniae* Teisseyre. Macroconch, $\times\frac{2}{3}$ (pyritic internal mould). 'Middle' Oxford Clay, Peterborough, Cambridgeshire. Athleta Zone, Proniae Subzone.
Figs 4–7. *Kosmoceras* (*K.*) *spinosum* (J. de C. Sowerby). 4, 5, macroconch, $\times\frac{2}{3}$. 6, 7, inner whorls showing characteristic ornament, $\times 1$ (both are pyritic internal moulds). Oxford Clay, Weymouth, Dorset. Lamberti Zone.

PLATE 16



strong. Body chamber smooth on internal mould. More coarsely ribbed variants have rounder whorls and can resemble a typical *K. kuklikum* (see below), they are, however, infrequent. Mature at up to 115 mm (septate to around 70 mm).
Microconch: Typically compressed, with flexous looped ribbing. Ventral tubercles tending to become elongated and develop into clavi [=*K. duncani* (J. Sowerby)?]. Occasional coarsely ribbed and inflated whorled variants resemble *K. kuklikum*. Mature at around 55 mm (septate to 28–35 mm).
Range. Common in the Proniae Subzone.

Subgenus *KOSMOCERAS* Waagen

Description. *Macroconch*: Relatively evolute, typically with coarsely ornamented inner whorls. These have a rounded or even sub-hexagonal section with irregular ribbing and tuberculation. Umbilical tubercles are usually absent and primary ribs in turn link the lateral and large ventro-lateral tubercules. Body chamber often strongly ornamented with venter-crossing ribs. Aperture simple.
Microconch: Commonly compressed, with flexuous looped ribbing and ventro-lateral clavi. Aperture lappeted.

K. (*Kosmoceras*) *kuklikum* (Buckman)
Not illustrated

Description. *Macroconch*: Inner whorls typical of subgenus and resemble those of *K. spinosum* (see below). Outer whorls, however, commonly develop a compressed, finely ribbed morphology with venter-crossing secondaries. Although broadly resembling typical *K. proniae*, compressed variants of *K. kuklikum* tend to have a squarer whorl section and more evolute coiling. Entirely coarsely ribbed morphologies also occur. Maximum mature size is around 110–120 mm (septate to around 80 mm).
Microconch: Commonly compressed, typical for genus. Probably mature at around 35–45 mm (septate to 20–30 mm).
Remarks. *K. kuklikum* appears to be a correct name for the kosmoceratid species of the Spinosum Subzone. *K. spinosum* (J. de C. Sowerby) itself, as defined by its type, is a species of the Lamberti Zone. The inner whorls of *K. kuklikum* closely resemble those of *K. spinosum* sensu stricto, and it was for this reason that the latter was designated as the index of the Spinosum Subzone.
Range. Common in the Spinosum Subzone.

K. (*Kosmoceras spinosum*) (J. de C. Sowerby)
Plate 16, figs 4–7

Description. *Macroconch*: Inner whorls typical for genus, but developing a squarer, more compressed section on the middle and outer whorls.

This is combined with a change from the usual node and looped rib ornament to a simpler almost biplicate style. Maximum size poorly known, probably at least 100 mm.
Microconch: Poorly known, includes typical compressed variants.
Remarks. Includes *K. tidmoorense* Arkell which cannot be assigned to either a macro- or microconch adult.
Range. Lamberti Zone, including Lamberti Subzone.

Family SPHAEROCERATIDAE
Subfamily MACROCEPHALITINAE
Genus *MACROCEPHALITES* Zittel

Description. *Macroconch*: Large to giant. Typically involute, but varying between compressed whorled finely ribbed and inflated, or depressed whorled coarsely ribbed morphologies. Secondary ribs pass over the rounded venter uninterrupted. Body chamber smooth; aperture simple.
Microconch: More evolute than macroconch, with a similar range of variants, but with all tending to be more coarsely ribbed, the ornament persisting to the end of the body chamber. Aperture simple.

Macrocephalites tumidus (Reinecke)
Plate 13, figs 13, 14

Description. *Macroconch*: Typical for genus; depressed whorled, coarsely ribbed variants have a broad flattened venter and are characteristic [=*M. sphaericus* (Jeannet)]. Compressed variants are frequent [=*M. intermedius* (Jeannet)]. Giant, mature at 280–404 mm (septate to 170–240 mm).
Microconch: Mature at 95–125 mm (septate to 60–75 mm).
Range. Extremely rare in Britain; fragmentary specimens occur in the Enodatum Subzone.

Family CARDIOCERATIDAE
Subfamily ARCTOCEPHALITINAE
Genus *CHAMOUSSETIA* R. Douvillé

Description. *Macroconch*: Involute, with a very small umbilicus and an acute venter. Whorl section varies between compressed and stoutly triangular extremes, but the characteristic intermediates have a lanceolate section. Only innermost whorls ribbed, soon fading, but leaving a serrated keel. Aperture simple.
Microconch: Ribbed to end, simple aperture. Similar to innermost whorls of macroconch.

Chamoussetia funifera (Phillips)
Plate 18, figs 1, 2

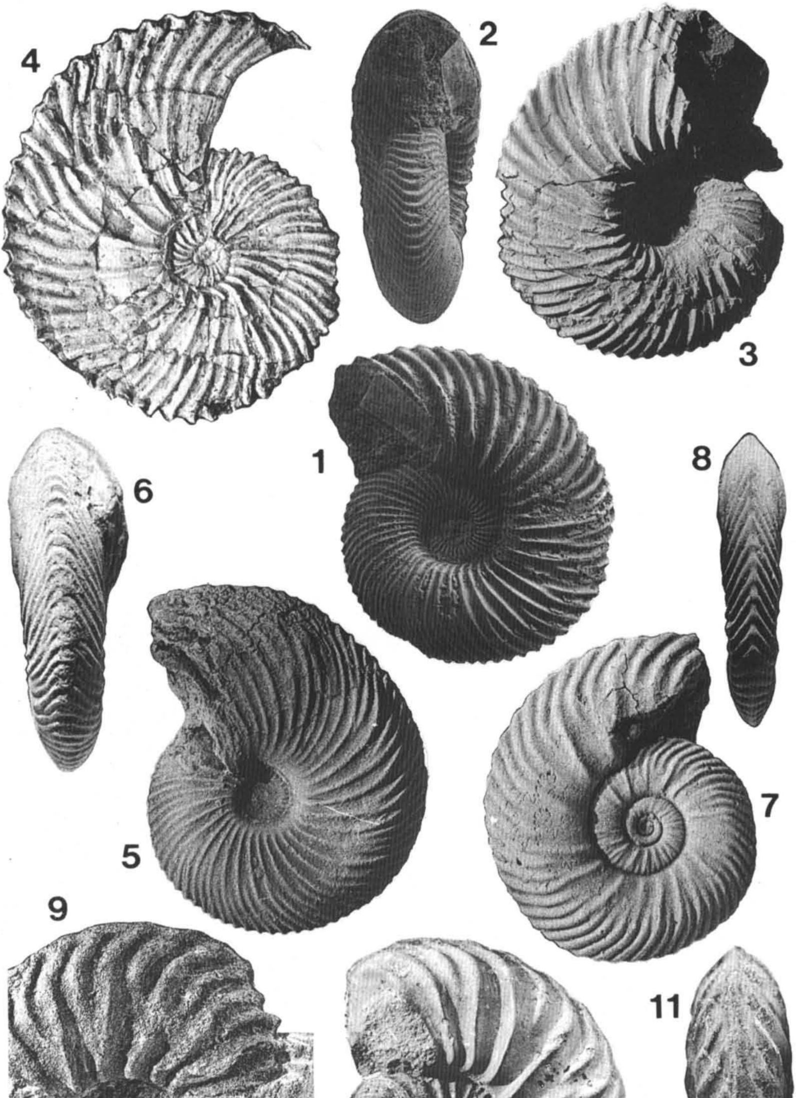
Description. *Macroconch*: Typical for genus; compressed variant characteristic. Mature size not known, probably septate to at least 60 mm.
Microconch: Very rare, typical for genus.
Range. Occurs rarely in the Athleta Zone.

Subfamily CADOCERATINAE
Genus *CADOCERAS* Fisher

Description. *Macroconch*: Inner whorls moderately involute, with fine ribbing which forms a forward-directed chevron on the acute venter. Middle whorls develop a depressed cadicone shape and ribbing fades leaving, in some, bullae on the angular umbilical edge. Body chamber smooth; aperture simple and constricted.
Microconch: Similar to inner whorls of macroconch, but relatively compressed and sharply ribbed to end of body chamber. Aperture simple, but developing short ventral rostrum.

EXPLANATION OF PLATE 17

Figs 1, 2 *Cadoceras durum* (Buckman). Complete microconch, × 1 (calcareous sandstone preservation). Cave Rock (= 'Kellaways Rock', *s.l.*), South Cave, Humberside. Calloviense Zone, Enodatum Subzone.
Fig. 3. *Cadoceras compressum* (Nikitin). Inner whorls of macroconch, × 1 (septarian concretion preservation). Lower Oxford Clay, Peterborough, Cambridgeshire. Jason Zone. Jason Subzone.
Fig. 4. *Longaeviceras laminatum* (Buckman). Complete microconch, × 1 (crushed shell in shale). Lower Oxford Clay, Christian Malford, Wiltshire. Athleta Zone, Phaeinum Subzone.
Figs 5, 6. *Longaeviceras placenta* (Leckenby). Microconch, × 1 (pyritic internal mould). 'Middle' Oxford Clay, Peterborough, Cambridgeshire. Athleta Zone, Proniae or Spinosum Subzone.
Figs 7, 8. *Quenstedtoceras lamberti* (J. Sowerby). Microconch, × 1 (pyritic internal mould). 'Upper' Oxford Clay, Weymouth, Dorset. Lamberti Zone, Lamberti Subzone.
Fig. 9. ?*Quenstedtoceras paucicostatum* (Lange). Microconch, × 1 (partially crushed internal mould in chamositic marl). Junction of Hackness Rock and 'Upper' Oxford Clay, near Scarborough, North Yorkshire. Lamberti Zone, topmost Lamberti Subzone.
Figs 10, 11. *Cardioceras* (*Pavloviceras*) *scarburgense* (Young & Bird). Complete microconch, × 1 (calcareous internal mould). Basal 'Upper' Oxford Clay, Scarborough, North Yorkshire. Mariae Zone, Scarburgense Subzone.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Cadoceras durum (Buckman)
Plate 17, figs 1, 2; Plate 18, figs 3, 4

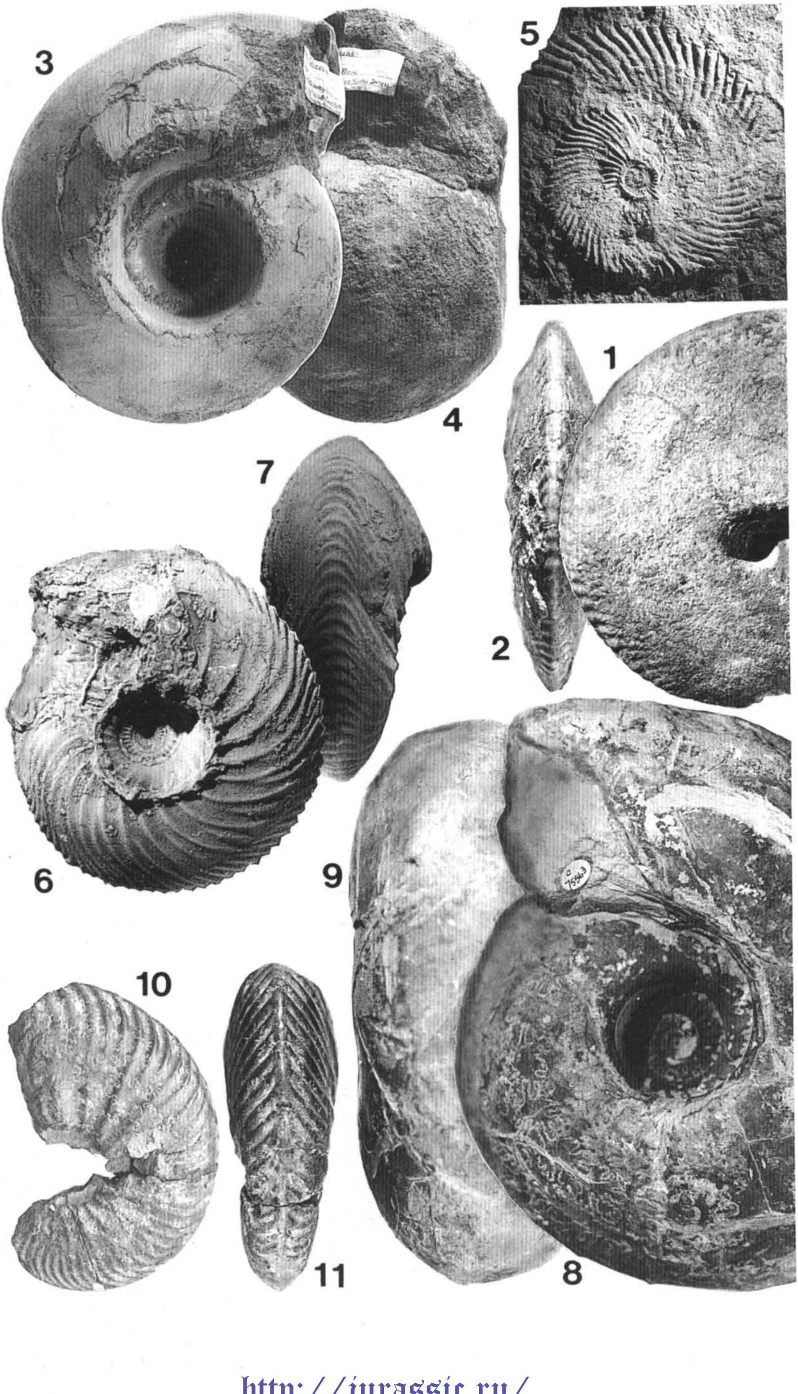
Description. *Macroconch*: Extreme morphologies for middle whorls are a compressed smooth form and a depressed sharply ribbed form. Mature adults are typical smooth cadicones. Large, up to 150 mm (septate to *c*. 105 mm).
Microconch: Typical for genus, but with more arcuate ribs than earlier species. Mature at around 45 mm (septate to 22–25 mm).
Range. Frequent in the middle Enodatum Subzone; a similar species occurs in the upper Enodatum Subzone.

Cadoceras compressum (Nikitin)
Plate 17, fig. 3

Description. *Macroconch*: Inner whorls relatively compressed with forward curved arcuate ribbing, resembling *Longaeviceras*. Relatively compressed and typical cadicone variants occur, both are smooth whorled from an early stage and without umbilical bullae. Mature size probably around 130–150 mm.
Microconch: Typical for genus and probably of a similar mature size to *C. durum*.
Range. A rare constituent of Jason Subzone faunas; a similar species occurs in the Medea Subzone.

EXPLANATION OF PLATE 18

Figs 1, 2. *Chamoussetia funifera* (Phillips). Macroconch, $\times\frac{2}{3}$ (preserved in chamositic oolite). Hackness Rock, Scarborough, North Yorkshire. Athleta Zone.
Figs 3, 4. *Cadoceras durum* (Buckman). Complete macroconch, $\times\frac{1}{3}$ (preserved in calcareous sandstone). Cave Rock (='Kellaways Rock' *s.l.*]. South Cave, Humberside. Calloviense Zone. Enodatum Subzone.
Fig. 5. *Longaeviceras laminatum* (Buckman). Macroconch, $\times\frac{1}{2}$ (crushed shell in argillaceous limestone). Acutistriatum Band, Lower Oxford Clay, Calvert, Buckinghamshire. Athleta Zone, Phaeinum Subzone.
Figs 6, 7. *Longaeviceras placenta* (Leckenby). Macroconch, $\times\frac{1}{2}$ (pyritic internal mould). 'Middle' Oxford Clay, Peterborough. Athleta Zone, Proniae or Spinosum Subzone.
Figs 8, 9. *Quenstedtoceras lamberti* (J. Sowerby). Complete macroconch, $\times\frac{1}{2}$ (internal mould in argillaceous limestone). Lamberti Limestone, Woodham, Buckinghamshire. Lamberti Zone, Lamberti Subzone.
Figs 10, 11. *Cardioceras* (*Pavloviceras*) *scarburgense* (Young & Bird). Macroconch, $\times\frac{1}{2}$ (calcareous internal mould). Basal 'Upper' Oxford Clay, near Scarborough, North Yorkshire. Mariae Zone, Scarburgense Subzone.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Cadoceras milaschevici Nikitin
Not illustrated

Description. Similar to *C. compressum*, with *Longaeviceras*-like inner whorls.
Remarks. Poorly known in Britain.
Range. Very rare, recorded from the lower part of the Grossouvrei Subzone (with *Kosmoceras* (*Z.*) *posterior* Callomon, 1968, p. 283).

Genus *LONGAEVICERAS* Buckman

Description. *Macroconch*: Involute; inner whorls compressed, with angular venter and open crater-like umbilicus, but still retaining an angular edge. Ribbing with distinct forward curve. Body chamber becomes smooth; shape varies between compressed and cadicone. Aperture simple.
Microconch: Similar ribbing style to macroconch but persisting to end of body chamber. Compressed with acute venter. Aperture simple, with short ventral rostrum.

Longaeviceras laminatum (Buckman)
Plate 17, fig. 4; Plate 18, fig. 5

Description. *Macroconch*: Apparently typical for genus, but poorly known. Mature size uncertain, but over 70 mm.
Microconch: Crushed specimens can resemble microconchs of *Cadoceras*, but have *Longaeviceras*-style ribbing. Mature around 45–55 mm (septate to 27–33 mm) [includes *L. concinnum* (Buckman)].
Range. Occurs rarely in the Phaeinum Subzone.

Longaeviceras placenta (Leckenby)
Plate 17, figs 5, 6; Plate 18, figs 6, 7

Description. *Macroconch*: Typical for genus, middle whorls have a distinct sub-triangular section. Septate to at least 80–90 mm, probably mature at around 140–150 mm.
Microconch: Typical for genus. Septate to *c*. 35 mm, mature at around 55 mm.
Range. Occurs rarely in the Proniae and Spinosum Subzones.

Longaeviceras staffinense Sykes
Not illustrated

Description. *Macroconch*: Relatively coarsely ribbed. Septate to at least 70 mm, with a mature size of around 130–140 mm.
Microconch: Relatively evolute for genus, with coarse forward-curved ribbing. Probably at least 60 mm in diameter when mature (septate to around 40 mm?).

Remarks. Poorly known in Britain; microconchs are recorded from Scotland (Sykes, 1975) and a probable macroconch figured by Wright (1983) from Yorkshire.
Range. Occurs very rarely in the Scarburgense Subzone.

Subfamily CARDIOCERATINAE
Genus *QUENSTEDTOCERAS* Hyatt

Description. *Macroconch*: High variable, including moderately involute forms with inflated whorls and blunt venters [= *Eboraciceras* Buckman], compressed forms with sharp venters [= *Lamberticeras* Buckman] and also relatively evolute compressed extremes [= *Prorsiceras* Buckman]. All are linked by intermediates, but the relative proportions of each extreme morphology varies at different stratigraphic levels. Umbilical edge rounded. Ribbing well differentiated, with relatively widely spaced and strong primaries and finer, closer secondaries. Ornament fades on the outer whorl but weak ventral ribs may persist to the beginning of the smooth body chamber. Aperture simple.
Microconch: Relatively evolute; compressed variants resemble '*Lamberticeras*' in ribbing style, but have a sharper almost carinate venters. Stout whorled very coarsely ribbed morphologies are frequent [= *Vertumniceras* Buckman].

Quenstedtoceras henrici (R. Douvillé)
Not illustrated

Description. *Macroconch*: Typical variants have inner whorls with a single secondary rib between each primary. Mature form typical for genus.
Microconch: Characteristic ribbing style similar to that of macroconch.
Remarks. In France and Germany faunas occur which are intermediate between *Q. henrici* and *Q. lamberti* and have referred to *Q. praelamberti* (R. Douvillé). These are also likely to occur in Britain but have not yet been separated and described. Characteristic *Q. praelamberti* have two secondary ribs between each primary whereas typical *Q. lamberti* (see below) have three to four (Makowski, 1960).
Range. Characteristic of the Henrici Subzone.

Quenstedtoceras lamberti (J. Sowerby)
Plate 17, figs 7, 8; Plate 18, figs 8, 9

Description. *Macroconch*: Typical for genus and highly variable, ranging from cadicones [= *Q. cadiforme* Buckman] to compressed forms [= *Q. lamberti* auctt.], and from involute morphologies [= *Q. sutherlandiae* (J. de C. Sowerby)] to relatively evolute forms [= *Q. gregarium* (Leckenby)]

(Callomon, 1985, text-fig. 5). Compressed, acute ventered, and intermediate forms with a stout whorl section and an arched venter [including *Q. dissimile* (Brown)] dominate most assemblages. Mature size varies between around 130 and 200 mm (septate to 130–140 mm).
Microconch: Typical for genus; compressed variants dominant [=*Q. flexicostatum* (Phillips)]. Coarse variants have blunt swollen ribbing [=*Q. leachi* J. Sowerby]. Mature size around 40–50 mm (septate to around 30 mm).
Range. Abundant in the Lamberti Subzone.

?*Quenstedtoceras paucicostatum* (Lange)
Plate 17, fig. 9

Description. *Macroconch*: Moderately involute with *Quenstedtoceras*-like ribbing; primaries well spaced and secondaries prominent on outer half of whorl side. Poorly known in Britain, but apparently septate to at least 90 mm (mature at over 130 mm).
Microconch: Characteristic forms are similar to coarse variants of the later *C. scarburgense* (see below). Typical specimens have a strong continuous keel and the ribbing does not form ventral chevrons. Mature size probably around 50 mm (septate to *c*. 33 mm).
Remarks. Wright (1983), following Marchand (1979), considered ?*Q. paucicostatum* to be a species of *Cardioceras* characterizing a basal horizon of the Oxfordian Stage. Callomon however (1990, in press), maintains that the species is a typical *Quenstedtoceras* and formally defines the base of the Oxfordian stage as lying above Marchand's *paucicostatum* horizon. ?*Q. paucicostatum* therefore becomes a species of the terminal Callovian.
Range. Uppermost part of the Lamberti Subzone.

Genus *CARDIOCERAS* Neumayr and Uhlig
Subgenus *PAVLOVICERAS* Buckman

Description. *Macroconch*: Very variable. Stout whorled morphologies have coarse wiry ribbing and well developed ventral rib chevrons. Depressed extremes, however, have straighter ribs. Compressed variants show the greatest rib differentiation, with relatively fine secondaries which become prominent on incipient ventrolateral whorl shoulders.
The mid ventral carina in early species develops into a keel in later forms. Body chamber smooth. Aperture simple.
Microconch: [=*Scarburgiceras* Buckman] Typically more compressed and evolute than macroconch, with greater ribbing differentiation and an acute carinate venter or keel. Ribbed to end. Aperture simple and developing short ventral rostrum.

C. (*Pavloviceras*) *scarburgense* (Young and Bird)
Plate 17, figs 10, 11; Plate 18, figs 10, 11

Description. *Macroconch*: Compressed variants characteristic, with relatively straight primary ribs which weaken on the sides of the middle whorls, and secondaries which curve on the outer part of the whorl side towards a carinate venter. Coarsely ribbed variants common and typical for subgenus. Septate to around 130–150 mm, probably mature at over 200 mm.
Microconch: Compressed forms have sharp carinate venters and relatively fine ribbing. Coarsely ribbed compressed forms also have carinate venters [= *C. woodhamense* Arkell] but stout whorled variants possess ventral rib chevrons [= *C. mariae* Douvillé].
Mature size around 50 mm (septate to 30–35 mm).
Range. Scarburgense Subzone. Coarsely ribbed and stout whorled variants are commonest in the lower part of the subzone, compressed variants dominate in the upper part (Callomon, 1968, p. 288; 1985, p. 72).

C. (*Pavloviceras*) *praecordatum* Douvillé
Plate 19, figs 1–4

Description. *Macroconch*: Compressed variants are characteristic and include forms with relatively widely spaced primary ribs and finer secondaries which curve back onto incipient whorl shoulders, but then twist outwards onto a keel [= *C. alphacordatum* Spath]. Coarser ribbed, stouter whorled morphologies are similar to variants of *C. scarburgense* and most have an arched venter [= *C. stibarum* Buckman?]. Septate to around 150–200 mm, mature at 200–280 mm.
Microconch: Typically compressed. Finely ribbed with straight primaries and secondaries which sweep strongly forwards on to gentle whorl shoulders, but twist outwards beside the narrow, serrated keel. Mature at around 60–80 mm (septate to *c*. 45–55 mm).
Range. Abundant in the Praecordatum Subzone.

Subgenus *CARDIOCERAS* Neumayr and Uhlig

Description. *Macroconch*: Moderately involute. Inner whorls of compressed variants have well differentiated ribbing; secondaries are projected on the whorl shoulders and sweep strongly backwards before twisting outwards onto a narrow serrated keel. Inflated variants have blunter stronger ribs and low keels with ventral rib chevrons [= *Goliathiceras* Buckman]; extremes have depressed whorls and broad weakly arched venters [= *Goliathites* Arkell]. Body chamber smooth.
Microconch: More evolute than macroconch, with greater differentiation and modification of ribbing. Compressed variants are similar to

the inner whorls of compressed macroconchs, but inflated extremes have very coarse ribbing and tend to become tuberculated, and also develop a broad tabulate venter and a strongly serrated keel [= *Vertebriceras* Buckman]. Ribbed to end; aperture simple, with ventral rostrum.

Cardioceras (*C.*) *bukowskii* Maire
Plate 19, figs 5–8

Description. *Macroconch*: Compressed variants have a triangular whorl section and a cordate keel which persists after the lateral ribbing has faded. Inner whorls have fine ribs which only weakly project on the whorl shoulders [= *C. excavatoides* Maire]. Inflated variants are frequent and typical for the genus [including *C. goliathus* (d'Orbigny). Giant, maturing at up to 320 mm; septate to over 200 mm.
Microconch: Compressed variants are very finely ribbed with a typical venter. Coarser variants have a stouter squarer whorl section and secondary ribs which are strongly projected on well developed whorl shoulders [includes *C. harmonicum* Arkell]. The extreme form has coarse biplicate ribbing, a broad venter and a coarsely serrated keel [= *C. bulbosum* Arkell].
In all variants of *C. bukowskii* tuberculation, if present, is weak. Mature size around 50–60 mm (septate to *c.* 35–40 mm).
Range. Common in the Bukowskii Subzone.

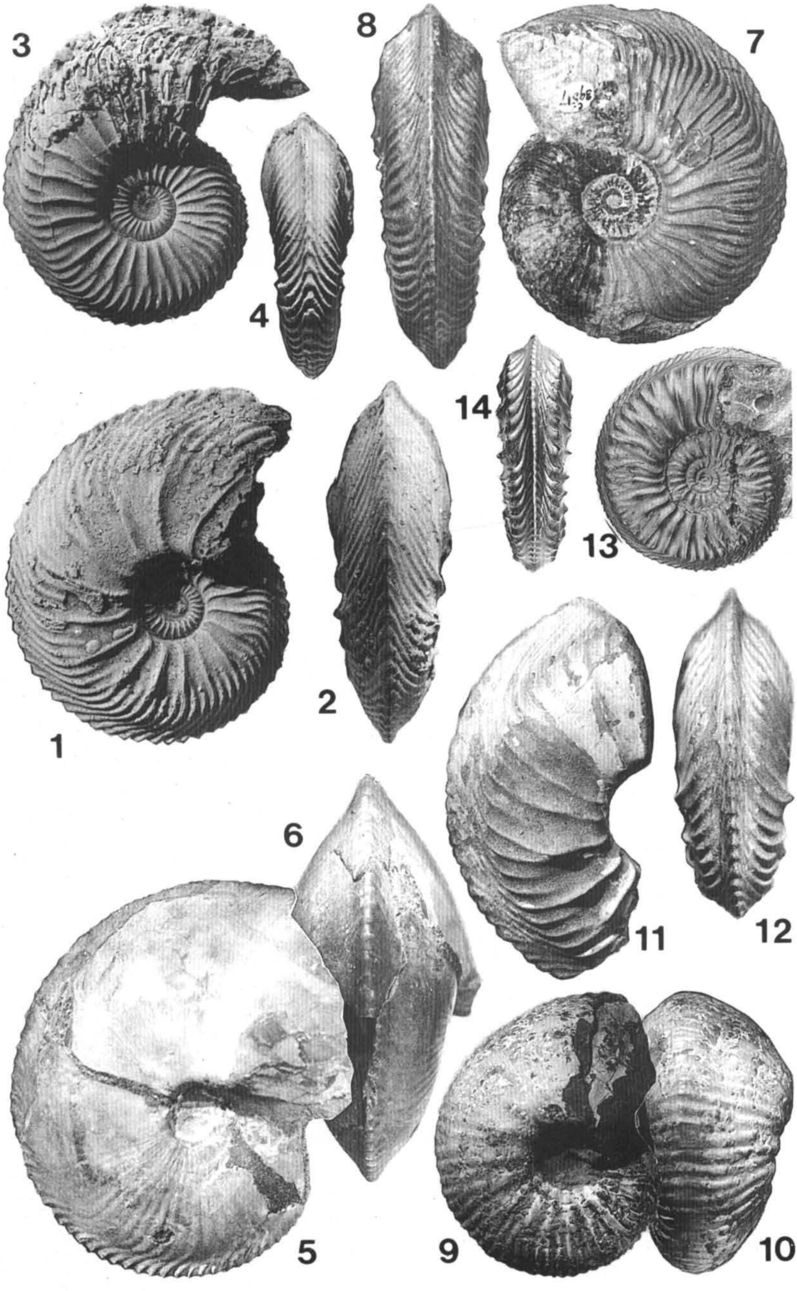
EXPLANATION OF PLATE 19

Figs 1–4. *Cardioceras* (*Pavloviceras*) *praecordatum* Douvillé. 1, 2, macroconch, $\times\frac{2}{3}$. 3, 4, complete microconch, $\times\frac{2}{3}$ (both pyritic internal moulds). 'Upper' Oxford Clay, St. Ives, Cambridgeshire. Mariae Zone, Praecordatum Subzone.

Figs 5–8. *Cardioceras* (*C.*) *buckowskii* Maire. 5, 6, macroconch, $\times\frac{1}{3}$ (typical of a moderately compressed variant of *Cardioceras* (*C.*)). 7, 8. Complete microconch, $\times\frac{2}{3}$ (both preserved in calcareous concretions). Tenants Cliff Member (='Ball Beds'), 'Lower Calcareous Grit', Scarborough, North Yorkshire. Cordatum Zone, Buckowskii Subzone.

Figs 9–12. *Cardioceras* (*C.*) *costicardia* Buckman. 9, 10, macroconch, $\times\frac{1}{3}$ (typical of an inflated variant of *Cardioceras* (*C.*)). 11, 12, microconch, $\times\frac{2}{3}$ (both preserved as sideritic limestone internal moulds). 'Red Nodule Beds', 'Upper' Oxford Clay,? Wootton Bassett, Wiltshire and Weymouth, Dorset, respectively. Cordatum Zone, Costicardia Subzone.

Figs 13, 14. *Cardioceras* (*C.*) *cordatum* (J. Sowerby). Complete microconch, $\times\frac{2}{3}$ (preserved in a calcareous concretion). Birdsall Calcareous Grit, Hambleton Hills, North Yorkshire. Cordatum Zone, Cordatum Subzone.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Cardioceras (*C.*) *costicardia* Buckman
Plate 19, figs 9–12

Description. *Macroconch*: Apparently typical for genus, with compressed and inflated whorled variants [the latter including *C. sidericum* (Arkell)]. The ribbing modification of inner whorls of compressed variants is similar to that of microconchs (see below). Complete specimens are rare; mature size probably similar to *C. bukowskii*.
Microconch: Compressed variants have secondary ribs projected on the whorl shoulders but then weakening ventrally beside a tall keel. Stouter

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EXPLANATION OF PLATE 20

Figs 1, 2. *Cardioceras* (*C.*) *cordatum* (J. Sowerby). Inner whorls of macroconch, $\times \frac{2}{3}$ (preserved in a calcareous concretion). Nothe Grit, near Weymouth, Dorset. Cordatum Zone, Cordatum Subzone.

Figs 3, 4. *Homeoplanulites cardoti* (Petitclerc). Complete microconch, $\times \frac{2}{3}$ (preserved in calcareous sandstone). Cave Rock (= 'Kellaways Rock' *s.l.*), South Newbold, Humberside. Calloviense Zone, Enodatum Subzone.

Figs 5, 6. *Grossouvria* (*G.*) *sulcifera* (Oppel). Microconch, × 1 (pyritic internal mould). 'Middle' Oxford Clay, Oxford, Athleta Zone, Proniae or Spinosum Subzones.

Fig. 7. *Grossouvria* (*Poculisphinctes*) *poculum* (Leckenby). Complete microconch, $\times \frac{2}{3}$ (internal mould in argillaceous limestone). Lamberti Limestone, 'Upper' Oxford Clay, Woodham, Buckinghamshire. Lamberti Zone, Lamberti Subzone.

Figs 8, 9. *Grossouvria* (*Klematosphinctes*) *vernoni* (Yound & Bird). Microconch, × 1 (pyritic internal mould). 'Upper' Oxford Clay, Warboys, Cambridgeshire. Mariae Zone, probably Praecordatum Subzone.

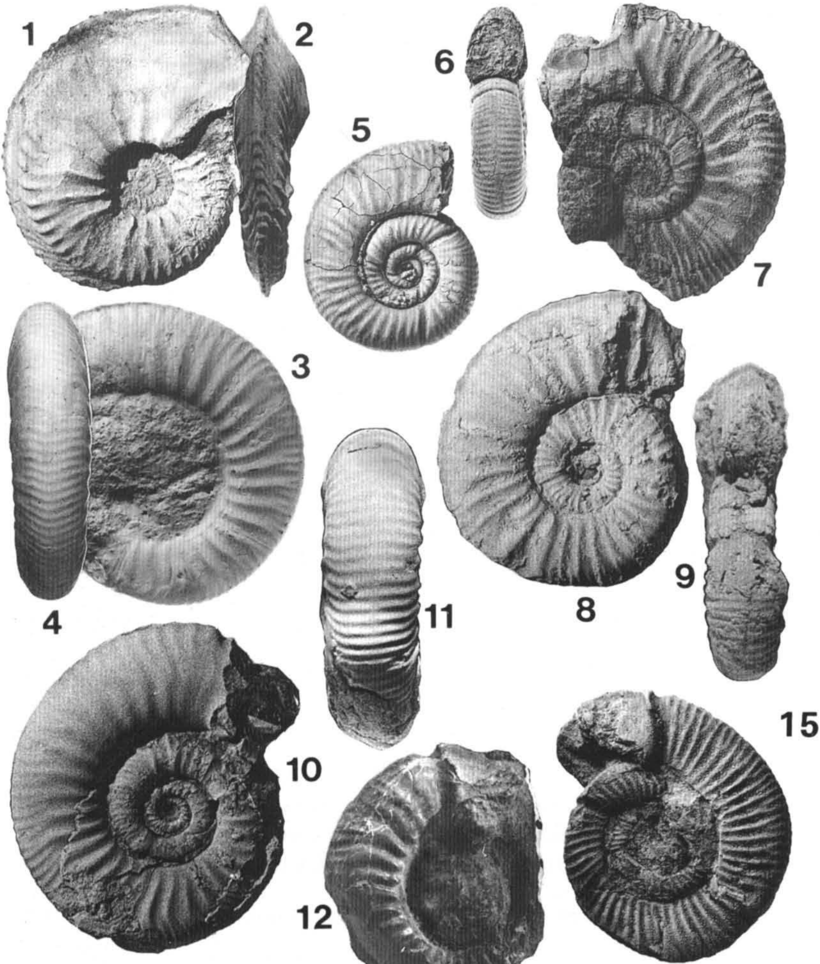
Figs 10, 11. *Grossouvria* (*Klematosphinctes*) sp.A. Microconch, × 1 (preserved in a calcareous concretion). Tenants Cliff Member (= 'Ball Beds'). 'Lower Calcareous Grit', Scarborough, North Yorkshire. Cordatum Zone, Buckowskii Subzone.

Fig. 12. *Grossouvria* (*Klematosphinctes*) sp.B. Complete microconch, × 1 (sideritic limestone internal mould). 'Red Nodule Beds', 'Upper' Oxford Clay, near Weymouth, Dorset. Cordatum Zone, Costicardia Subzone.

Figs 13, 14. *Alligaticeras* (*A.*) *rotifer* (Brown). Inner whorls of macroconch, × 1 (pyritic internal mould). 'Middle' Oxford Clay, Oxford. Athleta Zone, Proniae or Spinosum Subzone.

Fig. 15. *Alligaticeras* (*A.*) *alligatum* (Leckenby). Complete microconch, × 1 (internal mould in argillaceous limestone). Lamberti Limestone, 'Upper' Oxford Clay, Woodham, Buckinghamshire. Lamberti Zone, Lamberti Subzone.

Figs 16, 17. *Alligaticeras* (*Properisphinctes*) *matheyi* (de Loriol). ?Microconch, × 1 (preserved in a calcareous concretion). Tenants Cliff Member (= 'Ball Beds'), 'Lower Calcareous Grit', Scarborough, North Yorkshire. Cordatum Zone, Buckowskii Subzone.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whorled variants have stronger ribbing, often with tubercules at the end of the primaries. In extremely depressed variants the tubercules are large and the ornament extremely coarse [=*C. quadrarium* (Buckman)]. An unusual depressed morphology has a very weak keel and develops ventral rib chevrons [=*C. sagitta* (Buckman)].
Mature size around 80 mm (septate to 55–60 mm).
Range. Occurs in the Costicardia Subzone but is only common locally.

Cardioceras (*C.*) *cordatum* (J. Sowerby)
Plate 19, figs 13, 14; Plate 20, figs 1, 2

Description. *Macroconch*: Includes compressed variants with a triangular section which become virtually smooth by a diameter of 90–100 mm [=*C. galeiferum* (Buckman)?]. Inner whorls often have relatively widely spaced primaries ending in tubercles. Secondaries are strongly projected on the keeled venter but the link with the primaries weakens on middle whorls. Inflated variants probably resemble those of *C. costicardia*, etc. Mature size apparently over 210 mm (septate to at least 150 mm).
Microconch: A typical form is moderately evolute, with stout lateral tubercules, more or less angular shoulders and fine secondaries which sweep forwards at around 80° to the primaries [includes *C. persecans* Buckman]. Extremely finely ribbed forms are untuberculated [=*C. plasticum* Arkell]. Mature size at least 45–50 mm (septate to 30–35 mm?).
Range. Occurs in the Cordatum Subzone but is only locally common.

Superfamily PERISPHINCTACEAE
Family PERISPHINCTIDAE
Subfamily PEUDOPERISPHINCTINAE
Genus *HOMEOPLANULITES* Buckman

Description. *Macroconch*: [=*Loboplanulites* Buckman; *Parachoffatia* Mangold] Evolute. Compressed variants have flattened whorl sides and strong, long primary ribs. Secondaries branch on the outer third of the whorl side and weaken mid-ventrally. Round whorled variants have coarser blunter ribbing. Secondary ribbing tends to fade on the outer whorl, whereas blunt primary ribbing persists onto the body chamber. Occasional constrictions present particularly on inflated-whorled variants. Aperture simple.
Microconch: Compressed variant typical, ribbing style similar to compressed macroconchs, although finer, and secondaries persist to end of body chamber. Paired ventral parabolic nodes often present towards end of phragmocone or on beginning of body chamber. Aperture with short lappets.

Homeoplanulites cardoti (Petitclerc)
Plate 20, figs 3, 4; Plate 22, fig. 1

Description. *Macroconch*: Typical for genus. Mature at around 190–200 mm (septate to around 125 mm).
Microconch: Typical for genus, with secondary ribs tending to curve backwards slightly on ventral margin. Mature size 55–?70 mm (septate to 35–45 m).
Range. An occasional constituent of lower Enodatum Subzone faunas; a similar species may also occur higher in the Enodatum Subzone.

Homeoplanulites difficilis (Buckman)
Plate 22, figs 2, 3

Description. *Macroconch*: Inner whorls like a finely ribbed normal *Homeoplanulites*, but soon developing a typical compressed high-whorled shape and distinctive ribbing with short strong primaries and numerous fine secondaries. Stout whorled variants are also finely ribbed. Mature size around 170 mm (septate to *c.* 100–110 mm).
Microconch: Inner whorls as macroconch, but compressed high-whorled morphology develops only on the outer whorl. Body chamber characteristically virtually smooth, with only weak traces of ribbing. Mature size around 80–85 mm (septate to around 55 mm).
Range. Locally abundant in the middle Enodatum Subzone.

Genus *INDOSPHINCTES* Spath

Description. *Macroconch*: Typically compressed and moderately evolute, with flattened convergent whorl sides. Ribbing fine, characterized by low branching on the inner half of the whorl side and later branching on the outer part. Blunt primary ribs persist near the umbilical margin onto the otherwise smooth body chamber. Aperture simple.
Microconch: [=*Elatmites* Sheryrev] Ribbing style broadly similar to macroconch but persisting, in some, to end of body chamber. Aperture with relatively long lappets.

Indosphinctes patina (Neumayr)
Plate 22, figs 4–6

Description. *Macroconch*: Typical for genus. More evolute and often larger than *A. difficilis.* Mature size up to at least 270 mm (septate to around 145 mm).
Microconch: Ribbed to end of body chamber, secondaries tending to show a slight backward curve ventrally. Mature size around 90 mm (septate to *c.* 70 mm).

Range. Occurs occasionally in the Jason Subzone, a similar species may also occur in the Medea Subzone.

Genus *GROSSOUVRIA* Siemiradzki
Subgenus *GROSSOUVRIA* Siemiradzki

Description. *Macroconch*: Similar to *Homeoplanulites*, although smaller and with more irregularities of ornament such as constrictions and parabolic nodes. Aperture simple.
Microconch: Small; with numerous constrictions and parabolae. Ribbed to end, secondaries slightly backward-curved; aperture lappeted. Mid ventral rib-weakening characteristic of nuclei of both macro- and microconchs.

G. (*Grossouvria*) *cf. leptoides* (Till)
Not illustrated

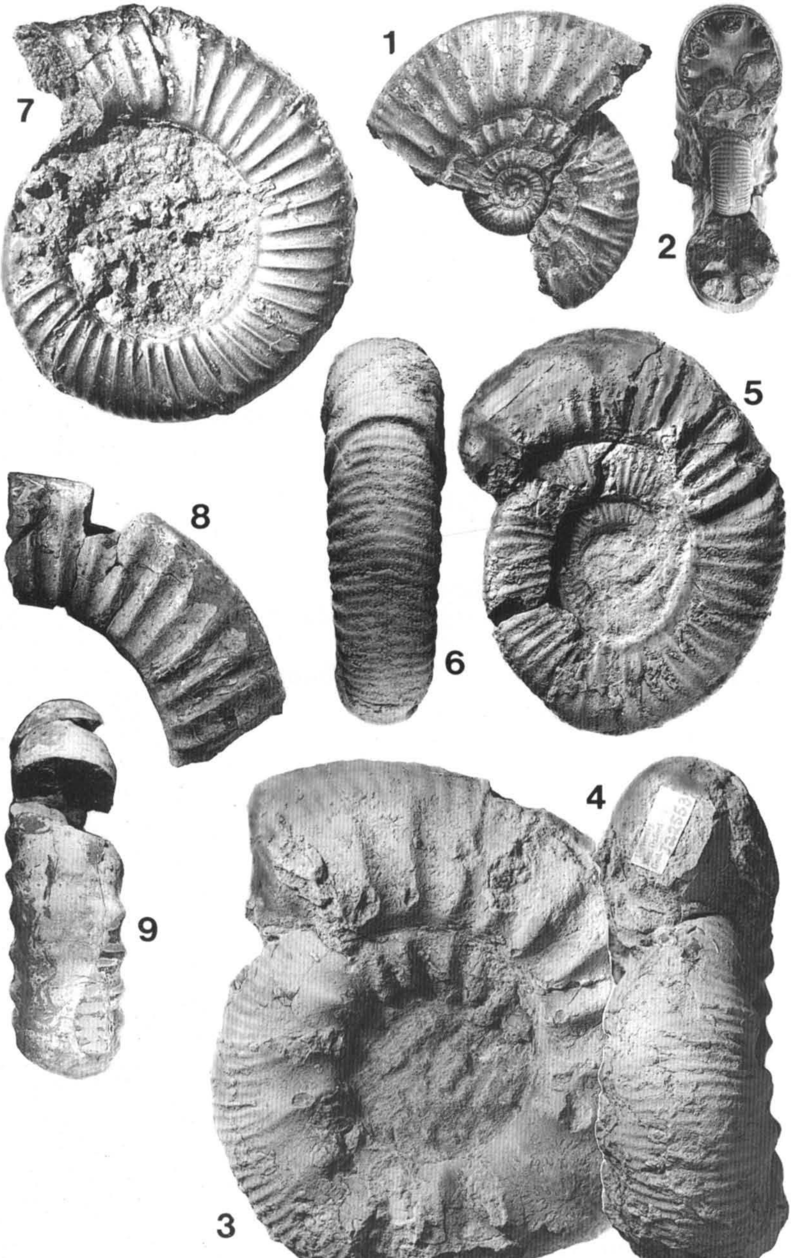
Remarks. Recorded by Callomon (1968, p. 283); poorly known in Britain.
Range. Lower Grossouvrei Subzone (with *K. posterior*).

G. (*Grossouvria*) *sulcifera* (Oppel)
Plate 20, figs 5, 6; Plate 21, figs 1, 2

Description. *Macroconch*: Nucleus relatively depressed; later whorl section more rounded. Apparently septate to around 70 mm (mature at over 110 mm?).

EXPLANATION OF PLATE 21

Figs 1, 2. *Grossouvria* (*G.*) *sulcifera* (Oppel). Inner whorls of macroconch, $\times\frac{2}{3}$ (pyritic internal mould). 'Middle' Oxford Clay, near Oxford. Athleta Zone, Proniae or Spinosum Subzone.
Figs 3, 4. *Grossouvria* (*Poculisphinctes*) *poculum* (Leckenby). Macroconch, $\times\frac{2}{3}$ (internal mould in argillaceous limestone). Lamberti Limestone, 'Upper' Oxford Clay, Woodham, Buckinghamshire. Lamberti Zone, Lamberti Subzone.
Figs 5, 6. *Alligaticeras* (*A.*) *alligatum* (Leckenby). Macroconch, $\times\frac{2}{3}$ (internal mould in argillaceous limestone). Lamberti Limestone, 'Upper' Oxford Clay, Woodham, Buckinghamshire. Lamberti Zone, Lamberti Subzone.
Fig. 7. *Alligaticeras* (*Properisphinctes*) *bernensis* (de Loriol). Macroconch, $\times\frac{2}{3}$ (pyritic internal mould). 'Upper' Oxford Clay, Warboys, Cambridgeshire. Probably from the Mariae Zone.
Figs 8, 9. *Perisphinctes* (*P.*) *sp.* ?nov. Macroconch, $\times\frac{1}{3}$ (sideritic limestone internal mould). 'Red Nodule Beds', 'Upper' Oxford Clay, Weymouth, Dorset. Cordatum Zone, Costicardia Subzone.



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Microconch: Typical for genus; mature at around 40 mm (septate to *c.* 25 mm).
Range. Occurs occasionally in the Proniae Subzone.

Subgenus *POCULISPHINCTES* Buckman

Description. *Macroconch*: Typical form is moderately evolute with stout rounded whorls and blunt, coarse and widely spaced primary ribbing; secondaries relatively fine. More compressed, finer ribbed variants also occur [= *Trinisphinctes* Buckman]. Blunt ribs persist onto mature body chamber. Aperture simple.
Microconch: Similar to *Grossouvria* s.s.. Ribbed to end, with short lappets.

G. (*Poculisphinctes*) *poculum* (Leckenby)
Plate 20, fig. 7; Plate 21, figs 3, 4

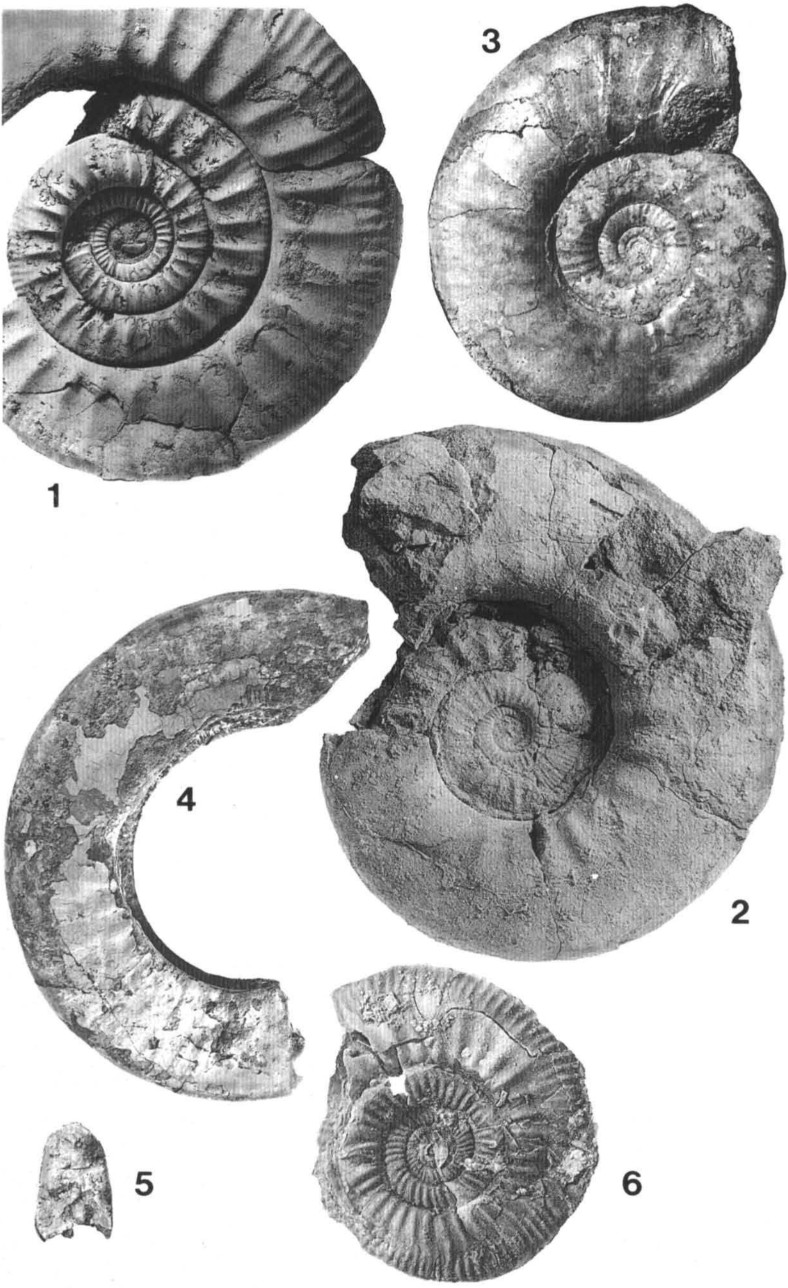
Description. *Macroconch*: Typical for subgenus. Mature size around 180 mm (septate to *c.* 110 mm). Finely ribbed variants may include *G. trina* (Buckman).
Microconch: Typical for subgenus. Finely ribbed variants with flattened sides to the body chamber are typical. Mature size around 40–55 mm (septate to 25–35 mm).
Range. A minor constituent of Lamberti Subzone faunas.

Subgenus *KLEMATOSPHINCTES* Buckman

Description. *Macroconch*: Small, with typical grossouvrid inner whorls, but more irregularly ribbed than *Grossouvria* (*G.*). Constricted, with numerous well-developed parabolic nodes. Body chamber apparently with slightly rursiradiate primary ribs, but secondaries tending to curve forward. Aperture simple.

EXPLANATION OF PLATE 22

Fig. 1. *Homeoplanulites cardoti* (Petitclerc). Complete macroconch, $\times\frac{1}{3}$ (preserved in calcareous sandstone). Topmost Kellaways Sand, South Cave, Humberside. Calloviense Zone, Enodatum Subzone.
Figs 2, 3. *Homeoplanulites difficilis* (Buckman). 2, complete macroconch, $\times\frac{1}{3}$; 3, complete microconch, $\times\frac{2}{3}$. Cave Rock, (= 'Kellaways Rock', *s.l.*), South Cave, Humberside. Calloviense Zone, Enodatum Subzone.
Figs 4–6. *Indosphinctes patina* (Neumayr). 4, 5, macroconch, $\times\frac{1}{4}$ (calcareous internal mould), Witney, Oxfordshire. 6, microconch, $\times\frac{1}{2}$ (crushed shell in shale), Calvert, Buckinghamshire. Jason Zone.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Microconch: (includes *Mirosphinctes* Schindewolf) Inner whorls similar to Macroconch, with many parablolic nodes. Ribbing style on body chamber also similar, but tends to be coarser. Lappets relatively long for genus

G. (*Klematosphinctes*) *vernoni* (Young and Bird)
Plate 20, figs 8, 9

Description. *Macroconch*: Poorly known, typical for subgenus. Mature size around 50–55 mm (septate to at least 33 mm).
Microconch: Typical for subgenus; but with a less coarsely ribbed body chamber than is typical of many later species. Mature size around 35–40 mm (septate to *c*. 25 mm).
Range. Occurs occasionally in the Scarburgense and Praecordatum Subzones.

G. (*Klematosphinctes*) sp. A
Plate 20, figs 10, 11

Description. *Macroconch*: Not recorded.
Microconch: Typical for genus, with very irregularly ornamented inner whorls. Matures at around 35–40 mm (septate to *c*. 25 mm).
Range. Bukowskii Subzone; rare.

G. (*Klematosphinctes*) sp. B
Plate 20, fig. 12

Description. *Macroconch*: Not recorded.
Microconch: Includes coarser ribbed variants than are typical of earlier species.
Mature size around 35 mm (septate to *c*. 22 mm).
Range. Costicardia Subzone; rare.

Subfamily PERISPHINCTINA
Genus *ALLIGATICERAS* Buckman
Subgenus *ALLIGATICERAS* Buckman

Description. *Macroconch*: Evolute with a round or slightly depressed whorl section. Constrictions conspicuous on inner and middle whorls. Relatively finely ribbed; primaries long, branching ventro-laterally; secondaries pass with virtually no interruption across venter; parabolae absent. Apparently ribbed to end of mature body chamber; aperture simple.
Microconch: Inner whorls as macroconch. Aperture lappeted.

Alligaticeras (*A.*) *rotifer* (Brown)
Plate 20, figs 13, 14

Description. *Macroconch*: Typical for subgenus; typified by specimens with a slightly depressed section. Some specimens show a slight

mid-ventral ribbing irregularity on inner whorls. Mature size probably around 100–110 mm (septate *c.* 65–70 mm).
Microconch: Inner whorls as macroconch, otherwise typical for subgenus. Mature size around 55 mm (septate to *c.* 35 mm).
Range. Occasionally found in the Proniae and Spinosum Subzones; the species may also occur in the Henrici Subzone (Cox, 1988, p. 52).

Alligaticeras (*A.*) *alligatum* (Leckenby)
Plate 20, fig. 15; Plate 21, figs 5, 6

Description. *Macroconch*: Typical for subgenus; with more quadrate and less depressed whorls than *A. rotifer*. Mature size probably at least 100 mm (septate to 65–70 mm).
Microconch: Typical for subgenus. Mature size around 38 mm (septate to *c.* 27 mm).
Range. Occasionally found in the Lamberti Subzone.

Subgenus *PROPERISPHINCTES* Spath

Description. *Macroconch*: Similar to *Alligaticeras* s.s., with a characteristic depressed nucleus. Middle whorls typically quadrate to compressed, with flattened sides and well-developed constrictions. Probably ribbed to end of mature body chamber; aperture simple.
Microconch: Inner whorls as macroconch; aperture lappeted.

A. (*Properisphinctes*) *bernensis* (de Loriol)
Plate 21, fig. 7

Description. *Macroconch*: Typical for subgenus. Mature size poorly known, septate to at least 50 mm.
Microconch: Typical for subgenus.
Range. Frequent in the Scarburgense and Praecordatum Subzones.

A. (*Properisphinctes*) *matheyi* (de Loriol)
Plate 20, figs 16, 17

Description. *Macroconch*: Poorly known, but apparently includes two distinct morphologies. The stouter whorled form has a sub quadrate section and can closely resemble *A. bernensis*. The compressed extreme, however, is more distinct with relatively flat whorl sides and finer ribbing. Mature size not known; maximum size seen around 60 mm.
Microconch: Includes variants with whorls similar to compressed macroconchs. Mature size around 38 mm (septate to *c.* 20 mm).
Range. Occurs rarely in the Bukowskii Subzone.

Genus *PERISPHINCTES* Waagen
Subgenus *PERISPHINCTES* Waagen

Description. *Macroconch*: Large to giant, with quadrate whorls. Inner and middle sharply ribbed, biplicate or triplicate; changing on outer whorls to strong, coarse, distant and swollen primaries, with smooth venter. Occasional deep constrictions present, particularly on depressed variants [= *Kranaosphinctes* Buckman]. Forms with flat whorl-sides are finer ribbed [= *Arisphinctes* Buckman]. Aperture simple.
Microconch: Typical forms similar to inner whorls of finer ribbed macroconch variants [= *Dichotomosphinctes* Buckman]. Occasional variants have more depressed whorls. Ribbed to end without modification. Aperture lappeted.

Perisphinctes (*P.*) sp. ?nov.
Plate 21, figs 8, 9

Description. *Macroconch*: Includes both depressed whorled and flat-sided forms. Apparently typical for genus, but known body chamber fragments do not appear to show varicostation. Giant, mature size not known but available fragments suggest a diameter of at least 300 mm.
Microconch: Poorly known; details not available, probably typical for genus.
Range. Occasionally found in the Costicardia Subzone.

Family REINECKEIIDAE
Genus *REINECKEIA* Bayle
Subgenus *REINECKEIA* Bayle

Description. *Macroconch*: Nucleus coronate, with depressed section and strong lateral nodes. Secondary ribs interrupted by mid-ventral smooth band throughout growth. Develops into a giant evolute shell. Coarse variants retain large lateral nodes; from these branch distinct forward sweeping secondary ribs. Compressed and relatively finely ornamented variants also occur. Body chamber often shows some weakening of ornament but never fades. Aperture simple.
Microconch: [= *Reineckeites* Buckman]. Nucleus coronate, but later shell usually develops a more compressed quadrate morphology (resembling finer ribbed macroconchs). Body chamber ribbed to end; aperture lappeted.

Reineckeia (*R.*) *anceps* (Reinecke)
Plate 23, figs 1–4

Description. *Macroconch*: Typical for subgenus. Giant, mature at around 380 mm (septate to *c.* 190 mm?).

Microconch: Typical for subgenus. Probably mature at around 85 mm (septate to 45–65 mm?).
Range. Occurs rarely in the Jason Subzone. A similar species occurs in the Medea Subzone.

Subgenus *COLLOTIA* de Grossouvre

Description. *Macroconch*: Nucleus coronate, like *Reineckeia* (*R.*) but developing a relatively compressed and finely ribbed morphology on the middle whorls. Outer whorl often with characteristic trituberculation. Aperture simple.
Microconch: Similar to inner whorls of macroconch, but does not develop tuberculation. Aperture lappeted.

R. (*Collotia*) *spathi* Bourquin
Plate 23, fig. 5

Description. *Macroconch*: Giant; poorly characterized.
Microconch: Typical for subgenus. Large; mature size around 120 mm (septate to *c*. 60 mm?).
Remarks. May include specimens recorded as *Reineckia* cf. *anceps* and *R. substeinmanni* by Callomon (1955, p. 254; 1968, p. 280 respectively).
Range. Upper Grossouvrei and lower Phaeinum Subzones. Very rare.

R. (*Collotia*) cf. *collotiformis* (Jeannet)
Not illustrated

Comments. Poorly known in Britain, probably includes specimens recorded as *R. stuebeli* (Steinmann) and *R. multicostata* Petitclerc by Arkell (1935–1948, p. 29).
Range. Proniae or upper Phaeinum Subzone. Very rare.

R. (*Collotia*) *oxyptychoides* Spath
Plate 23, figs 6, 7

Description. *Macroconch*: Typical for subgenus; with a trituberculate outer whorl. Large, reaching at least 250–300 mm.
Microconch: Not recorded.
Range. Lamberti Subzone; very rare.

Family PACHYCERATIDAE
Genus *ERYMNOCERAS* Hyatt

Description. *Macroconch*: Inner whorls typically coronate, with large lateral nodes and strong, blunt secondary ribbing which passes uninterrupted across the broadly rounded venter. Ventral ribs weaken on

later whorls and lateral nodes disappear on the mature body chamber. Finer ornamented forms have a more compressed section and strong primary ribbing which only forms incipient nodes [=*Erymnoceratites* Jeannet]. Aperture simple.
Microconch: [=*Rollierites* Jeannet] Relatively evolute, with a round whorl section and coarse untuberculated ribbing, which persists to the end of the body chamber. Aperture with lappets.

Erymnoceras coronatum (Bruguière)
Plate 23, fig. 8; Plate 24, figs 1, 2

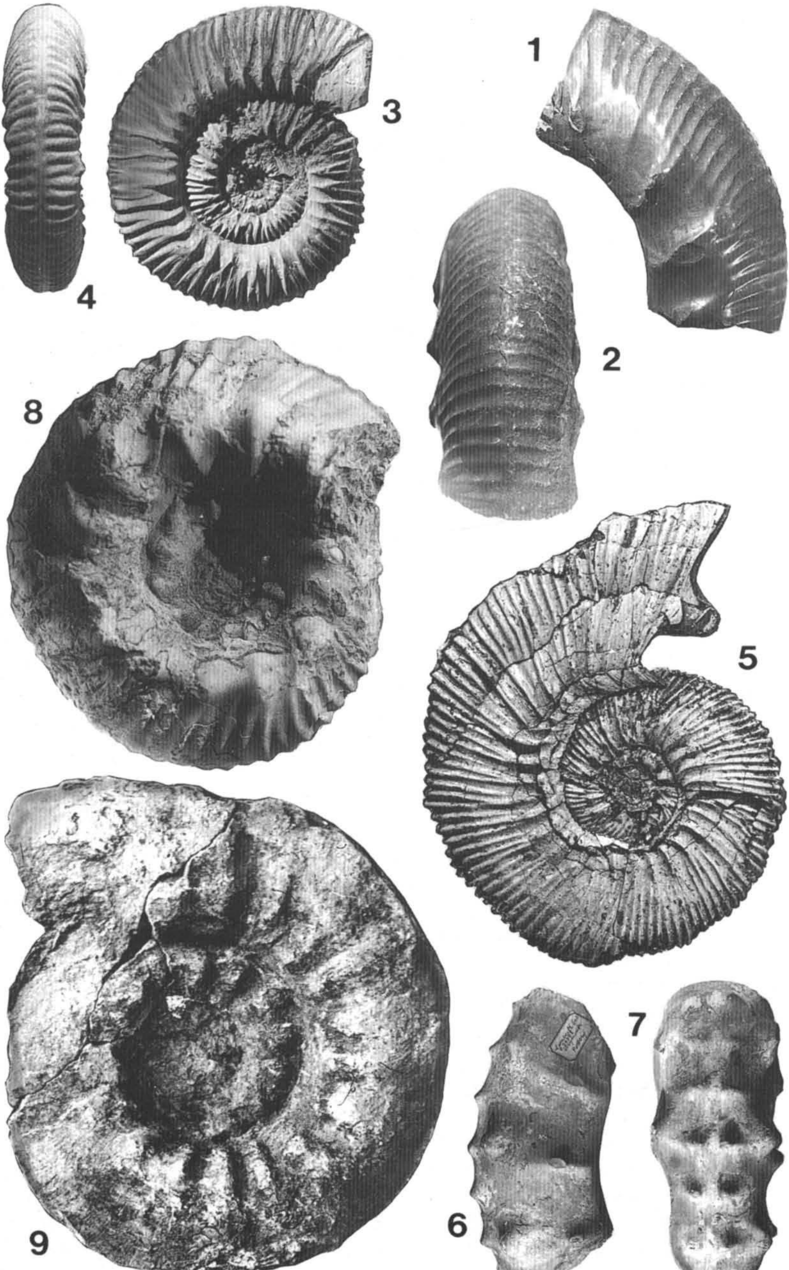
Description. *Macroconch*: [=*E. reginaldi* (Morris)] Typical for genus, with well-developed coronate inner whorls. Mature size at least 450 mm (septate to around 280–300 mm).
Microconch: Typical for genus. Mature size around 70–120 mm (septate to 50–90 mm?).
Range. Locally common in the Obductum and the lower part of the Grossouvrei Subzones.

Erymnoceras argoviense (Jeannet)
Plate 23, fig. 9

Description. *Macroconch*: Typically finer ornamented than *E. coronatum*, with lateral nodes tending to be replaced by strong primary ribbing. Mature size at least 200 mm (to septate to over 120 mm?).
Microconch: Typical for genus; not recorded in Britain?
Range. Locally common in the upper part of the Grossouvrei Subzone.

EXPLANATION OF PLATE 23

Figs 1–4. *Reineckeia* (*R.*) *anceps* (Reinecke). 1, 2, macroconch, ×$\frac{1}{4}$ (concretion preservation), Lower Oxford Clay, Higham Ferrers, Northamptonshire. 3, 4, microconch, ×$\frac{1}{2}$ (concretion preservation), Lower Oxford Clay, ?Weymouth, Dorset. Jason Zone.
Fig. 5. *Reineckeia* (*Collotia*) *spathi* Bourquin. Complete microconch, ×$\frac{1}{2}$ (crushed shell in shale). Lower Oxford Clay, Christian Malford, Wiltshire. Athleta Zone, Phaeinum Subzone.
Figs 6, 7. *Reineckeia* (*Collotia*) *oxyptychoides* Spath. Macroconch, ×$\frac{1}{4}$ (calcareous infil to body chamber). Oxford Clay, Weymouth, Dorset. Lamberti Zone.
Fig. 8. *Erymnoceras coronatum* (Bruguière). Macroconch, ×$\frac{1}{3}$ (septarian concretion preservation). Lower Oxford Clay, Weymouth, Dorset. Coronatum Zone, Obductum Subzone.
Fig. 9. *Erymnoceras argoviense* (Jeannet). Macroconch, ×$\frac{1}{3}$ (preserved in calcareous sandstone). Langdale Member, near Scarborough, North Yorkshire. Coronatum Zone, Grossouvrei Subzone.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Genus *PACHYCERAS* Bayle
Subgenus *PACHYCERAS* Bayle

Description. *Macroconch*: Involute, with compressed *Macrocephalites*-like shape. Ribbing strong and blunt, tending to fade on the inner half of the whorl sides. Initially rounded venter may become acute on the smooth body chamber. Aperture simple.
Microconch: [Probably includes *Pachyerymnoceras* Breisthoffer]. More evolute than macroconch with a rounder whorl section and coarse blunt ribbing to end of mature body chamber. Aperture lappeted.

Pachyceras (*P.*) cf. *crassum* Douvillé
Plate 24, fig. 3

Comments. Poorly known in Britain; apparently typical for subgenus.
Range. Probably Spinosum Subzone; very rare.

Pachyceras (*P.*) *lalandeanum* (d'Orbigny)
Plate 24, figs 4, 5

Description. *Macroconch*: Typical for subgenus. Mature size over 280 mm (septate to over 200 mm).
Microconch: Typical for subgenus. Moderately compressed variants show slight weakening of ribbing on outer whorl. Mature size around 90 mm (septate to *c*. 55 mm).
Range. Lamberti Subzone; rare.

Subgenus *TORNQUISTES* Lemoine

Description. *Macroconch*: Coarser ribbed and stouter whorled than typical *Pachyceras* (*P.*), with a rounder venter. Ornament fades on mature body chamber. Aperture simple.

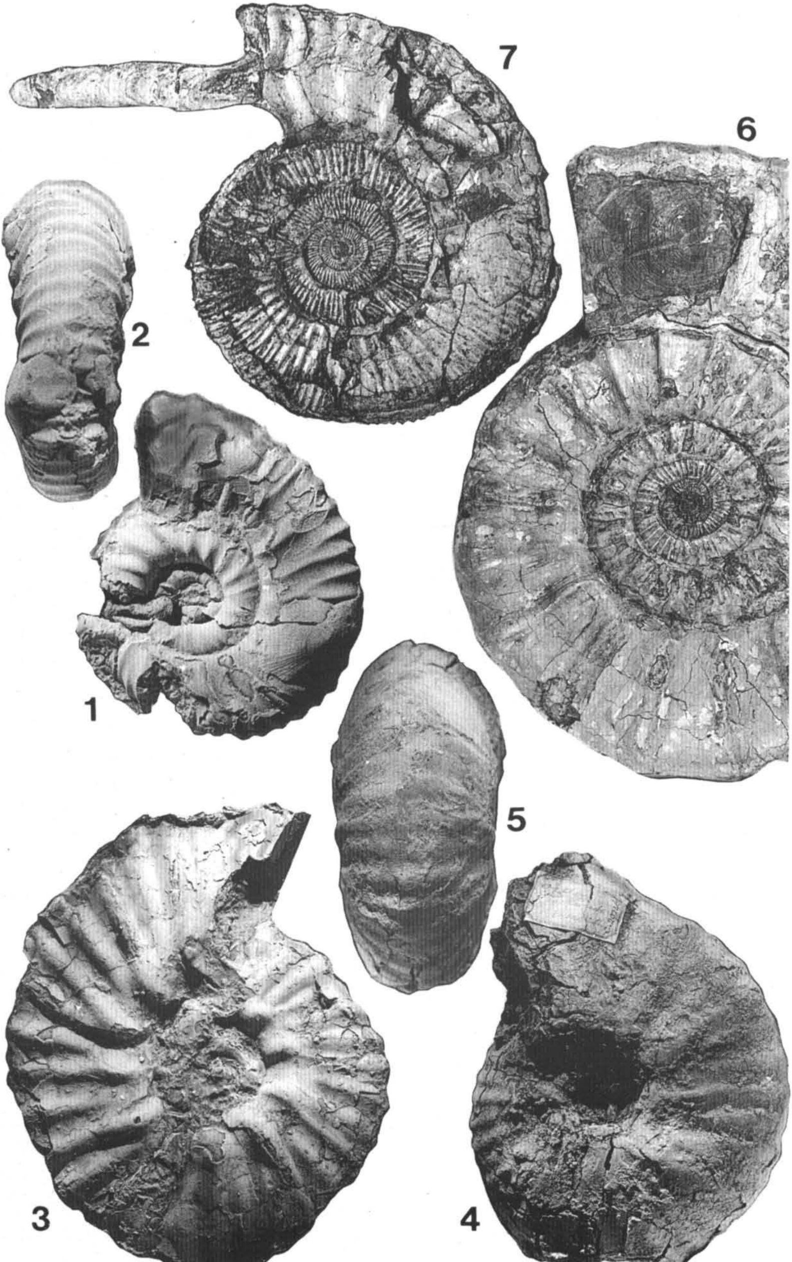
EXPLANATION OF PLATE 24

Figs 1, 2. *Erymnoceras coronatum* (Bruguière). Microconch, $\times\frac{2}{3}$ (septarian concretion preservation). Lower Oxford Clay, Weymouth, Dorset. Coronatum Zone, Obductum Subzone.

Fig. 3. *Pachyceras* (*P.*) cf. *crassum* Douvillé. ?Macroconch, $\times\frac{1}{2}$ (crushed shell in shale). 'Middle' Oxford Clay, Woodham, Buckinghamshire. Probably from the Athleta Zone, Spinosum Subzone.

Figs 4, 5. *Pachyceras* (*P.*) *lalandeanum* (d'Orbigny). Macroconch, $\times\frac{1}{2}$ (pyritic internal mould). 'Upper' Oxford Clay, near Weymouth, Dorset. Lamberti Zone, ?Lamberti Subzone.

Figs 6, 7. *Binatisphinctes comptoni* (Pratt). 6, ?Complete macroconch, $\times\frac{1}{3}$. 7, complete microconch, $\times\frac{2}{3}$ (crushed shells in shale). Lower Oxford Clay, Christian Malford, Wiltshire. Athleta Zone, Phaeinum Subzone.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Microconch: Similar to *Pachyceras* (*P*.). Strongly ribbed, but with coarsening on the mature body chamber. Aperture lappeted.

P. (*Tornquistes*) *leckenbyi* Arkell
Not illustrated

Description. *Macroconch*: Not recorded.
Microconch: Typical for subgenus. Mature size around 120–140 mm (septate to *c*. 100 mm).
Range. Bukowskii Subzone; very rare.

Family ASPIDOCERATIDAE
Subfamily PELTOCERATINAE
Genus *BINATISPHINCTES* Buckman

Description. *Macroconch*: Morphologically intermediate between large pseudoperisphinctids (*Grossouvria*, etc.) and peltoceratids. Moderately evolute with sharp perisphinctoid ribbing on inner whorls, which weakens or fades mid-ventrally. Outer whorls develop strong, distant primary ribbing. Aperture simple.
Microconch: Inner whorls as macroconch, sometimes coarsening on the mature body chamber. Ventral smooth band prominent at this state. Aperture with long lappets. Aptychus with concentric striations [= *Praestriaptychus* (text-fig. 4.1).

Binatisphinctes comptoni (Pratt)
Plate 24, figs 6, 7

Description. *Macroconch*: [= *B. fluctuosus* (Pratt)]. Typical for genus, with strong, distant but straight primary ribs on the outer whorls. Mature size around 200–250 mm (septate to *c*. 170 mm).
Microconch: Ribbing fine on inner whorls but weakening on mature body chamber. Mature size between 50 and 100 mm (septate to *c*. 30–60 mm).
Range. Upper Grossouvrei and lower Phaeinum Subzones.

Binatisphinctes hamulatus (Buckman)
Plate 25, figs 1–3

Description. *Macroconch*: Apparently typical for genus, with strong, straight primary ribs on the outer whorls. Mature size at least 280 mm (septate to *c*. 200 mm).
Microconch: Round whorled variants with relatively coarsely ribbed outer whorls are characteristic. More compressed variants resemble typical *B. binatus* (see below).

TEXT-FIG. 4.1. Ammonite aptychi, probably from the perisphinctid *Binatisphinctes* sp. Specimen from Acutistriatum horizon, Lower Oxford Clay, × 1.

Microconch: Mature size around 15–85 mm (septate to *c*. 55 mm).
Range. Athleta Zone, uncommon.

Binatisphinctes binatus (Leckenby)
Plate 25, fig. 4

Description. *Macroconch*: Characterized by variants with compressed, flat-sided whorls and a prominent mid-ventral smooth band. Mature size not known.
Microconch: Poorly known, apparently similar to inner whorls of macroconch.
Range. Lamberti Zone, probably including Lamberti Subzone; rare.

Genus *PSEUDOPELTOCERAS* Spath

Description. *Macroconch*: Morphology intermediate between *Binatisphinctes* and *Peltoceras*. Outer whorls typically massive and quadrate, but the strong primary ribs develop ventrolateral tubercles. Innermost whorls poorly known. Aperture simple.
Microconch: Not recorded.
Remarks. The dimorphism, variability and affinities of British species assigned to *Pseudopeltoceras* are poorly understood. The classification adopted here is, therefore, provisional.

Pseudopeltoceras chauvinianum (d'Orbigny)
Plate 25, fig. 5

Description. *Macroconch*: Typical for genus, with strong, curved and tuberculate primary ribs. Mature size at least 220 mm, possibly larger (septate to over 150 mm?). May include *P. leckenbyi* Spath.
Microconch: Not recorded in Britain.
Range. ?Proniae Subzone; rare.

Pseudopeltoceras famulum Spath
Plate 25, figs 6, 7

Description. ?*Macroconch*: Apparently a small species, with depressed, finely ribbed inner whorls. Rapidly develops strong distant primary ribs and incipient ventro-lateral nodes on the mature body chamber. Mature size around 100 mm (septate to *c*. 67 mm).
Microconch: Not recorded.
Range. Athleta and/or Lamberti Zones; very rare.

Genus *PELTOCERAS* Waagen
Subgenus *PELTOCERAS* Waagen

Description. *Macroconch*: Nucleus evolute, with sharp often biplicate ribbing, without ventral interruption. Rapidly develops two rows of massive lateral tubercles, the outer developing first and often remaining strongest. Venter flat, initially with sharp biplicate or triplicate secondary ribs linking the outer tubercles; becoming smooth on later whorls. Aperture simple.
Microconch: [=*Rursiceras* Buckman] Inner whorls as nucleus of macroconch, but does not develop tubercles. Becoming strongly rursiradiate on the outer whorl. Aperture lappeted.

EXPLANATION OF PLATE 25

Figs 1–3. *Binatisphinctes hamulatus* (Buckman). 1, 2, macroconch, $\times\frac{1}{3}$. 3, microconch, $\times\frac{1}{2}$ (preserved in chamositic oolite). Hackness Rock, Scarborough, North Yorkshire. Athleta Zone.

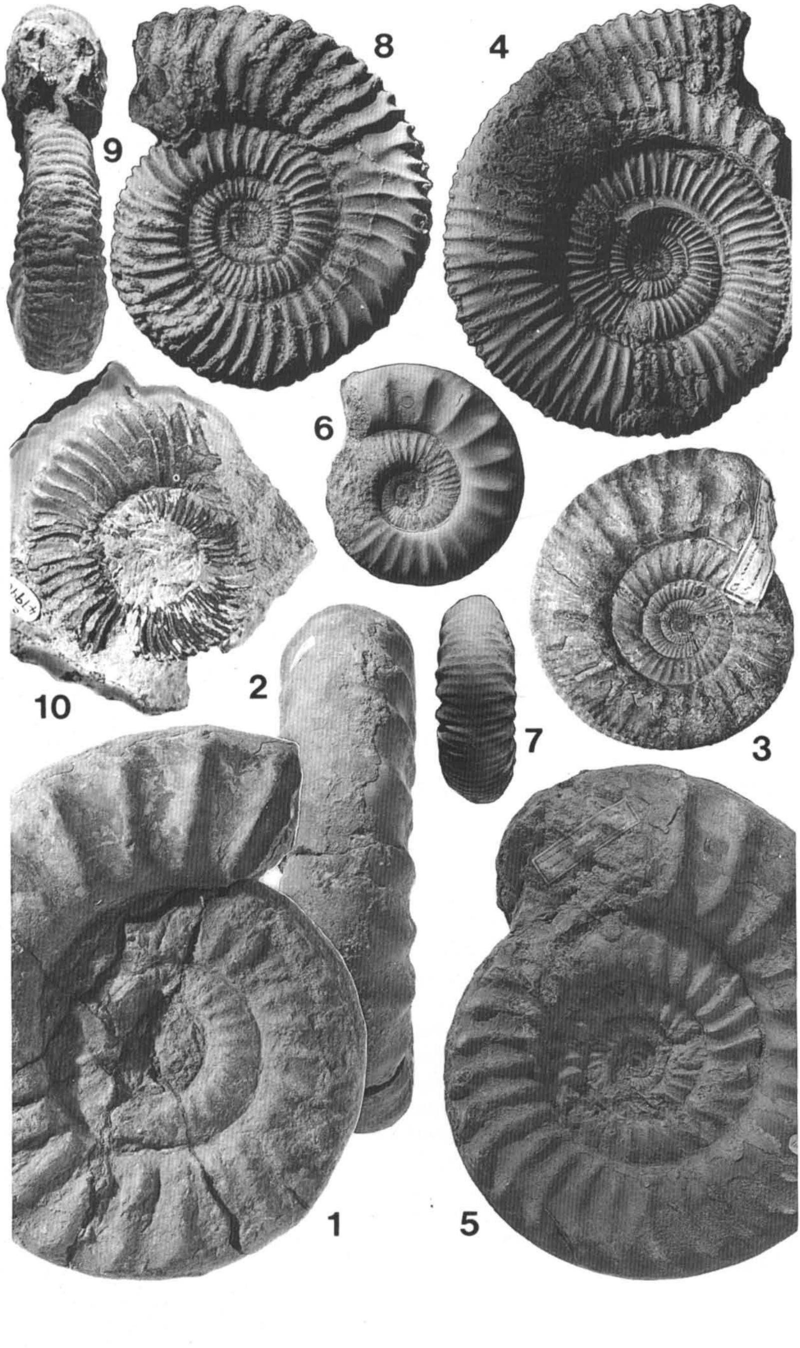
Fig. 4. *Binatisphinctes binatus* (Leckenby). ?Microconch, $\times\frac{2}{3}$ (pyritic internal mould). ?'Upper' Oxford Clay, Peterborough, Cambridgeshire. Probably Lamberti Zone.

Fig. 5. *Pseudopeltoceras chauvinianum* (d'Orbigny). Macroconch, $\times\frac{1}{3}$ (preserved in chamositic oolite). Hackness Rock, Scarborough, North Yorkshire. Athleta Zone.

Figs 6, 7. *Pseudopeltoceras famulum* Spath. Macroconch, $\times\frac{1}{3}$ (preserved in chamositic oolite). Hackness Rock, Scarborough, North Yorkshire. ?Lamberti Zone.

Figs 8, 9. *Peltoceras* (*P.*) ex grp. *athleta* (Phillips). Microconch, $\times\frac{2}{3}$ (pyritic internal mould). 'Middle' Oxford Clay, Peterborough, Cambridgeshire. Athleta Zone, ?Proniae Subzone.

Fig. 10. *Peltoceras* (*Peltomorphites*) *subtense* (Bean). Microconch, $\times\frac{2}{3}$ (crushed internal mould in argillaceous limestone). Lamberti Limestone, 'Upper' Oxford Clay, Woodham, Buckinghamshire. Lamberti Zone, Lamberti Subzone.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Peltoceras (*P.*) ex grp. *athleta* (Phillips)
Plate 25, figs 8, 9; Plate 26, figs 1, 2

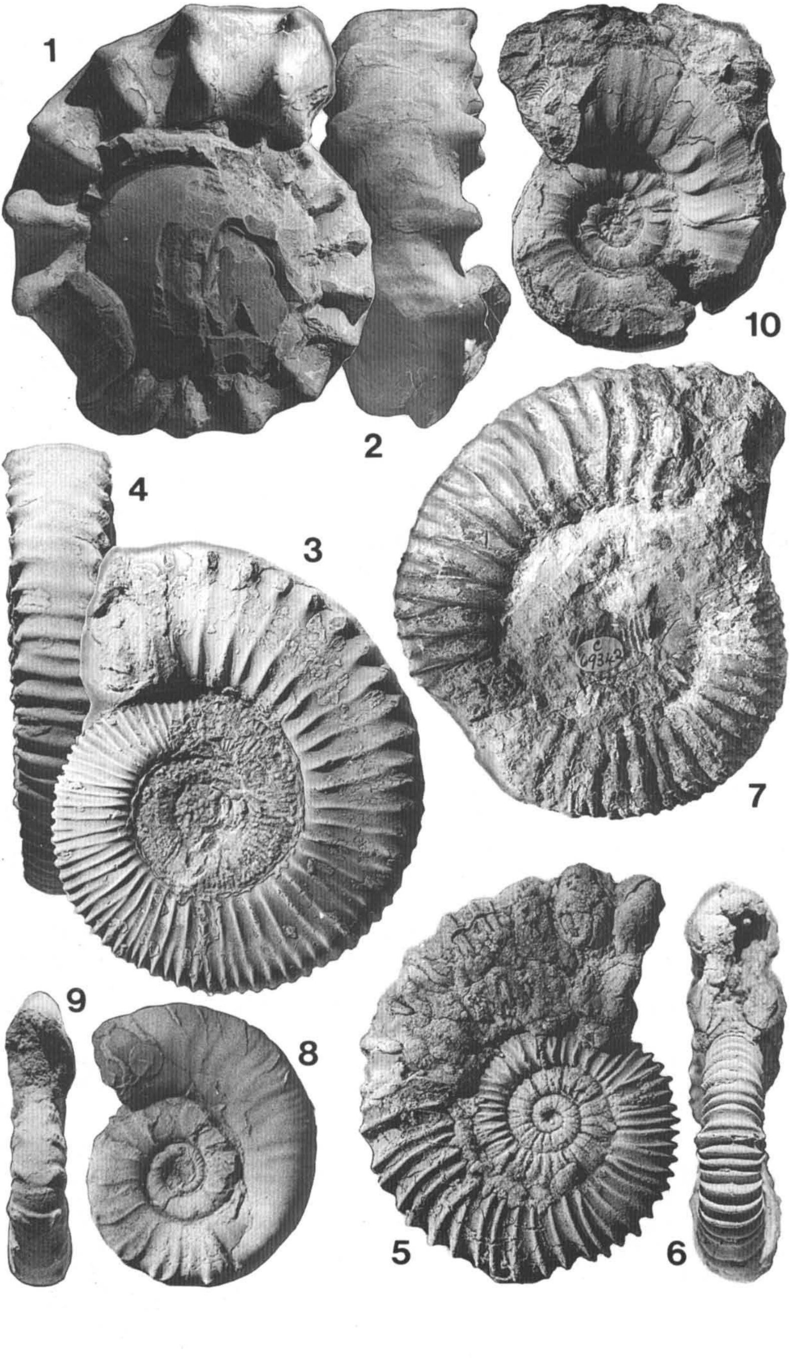
Description. *Macroconch*: Typical for subgenus, developing tubercles at only 25–35 mm diameter. Outer whorls with two rows of large tubercles. Mature size at least 250 mm.
Microconch: Typical for subgenus. Mature size around 55–65 mm (septate to *c.* 40 mm).
Remarks. *P. athleta* sensu stricto is a species of the uppermost Phaeinum Subzone (J. H. Callomon, pers. comm., 1989). Similar species of *Peltoceras* (*P.*), including *P.* (*P.*) *trifidum* (Quenstedt), occur in the later Proniae and Spinosum Subzones but are not readily distinguishable due to considerable intra-specific variation.
Range. Late Phaeinum to Spinosum Subzones; common in the Proniae Subzone.

Subgenus *PELTOMORPHITES* Buckman

Description. *Macroconch*: Inner whorls similar to *Peltoceras*, but ribbing tending to branch near the umbilical margin. Later whorls become bituberculate and spinous. The outer row of tubercles is always strongest and sharpest and, in some, splits to form a third row. Inner row of (lateral) tubercles tending to be elongated. Ornament weakens on mature body chamber. Aperture simple.

EXPLANATION OF PLATE 26

Figs 1, 2. *Peltoceras* (*P.*) ex grp. *athleta* (Phillips). Macroconch, $\times\frac{1}{2}$ (calcareous nodule preservation). 'Middle' Oxford Clay, Weymouth, Dorset. Athleta Zone, probably Proniae Subzone.
Figs 3, 4. *Peltoceras* (*Peltomorphites*) *subtense* (Bean). Macroconch, $\times\frac{2}{3}$ (pyritic internal mould). ?'Upper' Oxford Clay, east Midlands. Lamberti Zone.
Figs 5, 6. *Peltoceras* (*Peltomorphites*) *hoplophorus* (Buckman). Microconch, $\times\frac{2}{3}$ (pyritic internal mould). 'Upper' Oxford Clay, St. Ives, Cambridgeshire. Mariae Zone, probably Praecordatum Subzone.
Fig. 7. *Peltoceras* (*Peltoceratoides*) *williamsoni* (Phillips). Microconch, $\times\frac{2}{3}$ (sideritic limestone nodule preservation). 'Red Nodule Beds', 'Upper' Oxford Clay, Weymouth, Dorset. Cordatum Zone, Costicardia Subzone.
Figs 8, 9. *Euaspidoceras babeanum* (d'Orbigny). Microconch, × 1 (pyritic and calcareous internal mould). 'Upper' Oxford Clay, east Midlands. Mariae Zone.
Fig. 10. *Euaspidoceras douvillei* (Collot). Microconch, $\times\frac{2}{3}$ (preserved in a calcareous concretion). Tenants Cliff Member, 'Lower Calcareous Grit', Scarborough, North Yorkshire. Cordatum Zone, Buckowskii Subzone.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Microconch: [=*Parawedekindia* Schindewolf] Inner whorls similar to macroconch; with marked tendency for ribs to bifurcate near the umbilical margin. Untuberculated and sharply ribbed to end; with rursiradiate outer whorl. Aperture lappeted.

Peltoceras (*Peltomorphites*) *subtense* (Bean)
Plate 25, fig. 10; Plate 26, figs 3, 4; Plate 27, fig. 1

Description. *Macroconch*: Typical for subgenus, with relatively compressed and bituberculate middle and outer whorls. Mature size around 250–270 mm (septate to *c*. 210 mm).
Microconch: Typical for subgenus, with a relatively compressed and quadrate outer whorl. Mature size around 60 mm (septate to *c*. 42 mm).
Range. A minor constituent of Lamberti Subzone faunas.

Peltoceras (*Peltomorphites*) *hoplophorus* (Buckman)
Plate 26, figs 5, 6; Plate 27, figs 2, 3

Description. *Macroconch*: Innermost whorls typical for subgenus. Inner row of tubercules tend to remain weak on middle whorls, but outer row forms a distinctive doublet. On outer whorls, however, the latter develop into a single blunt spine. At this stage the inner tubercules may also become bluntly spinous, giving an *Euaspidoceras*-like body chamber. Mature size probably around 350 mm (septate to *c*. 240–300 mm).

EXPLANATION OF PLATE 27

Fig. 1. *Peltoceras* (*Peltomorphites*) *subtense* (Bean). Complete macroconch, $\times\frac{1}{4}$ (preserved in chamositic oolite). Hackness Rock, Scarborough, North Yorkshire. Lamberti Zone. ?Lamberti Subzone.

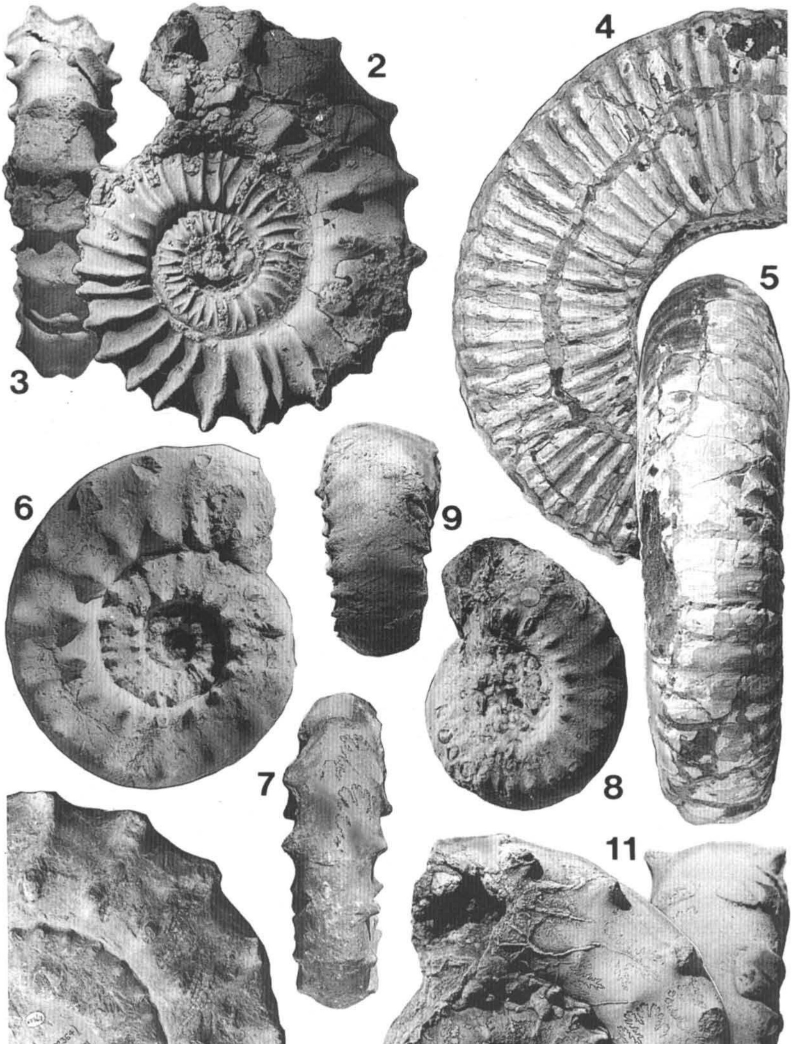
Figs 2, 3. *Peltoceras* (*Peltomorphites*) *hoplophorus* (Buckman). Macroconch, $\times\frac{1}{2}$ (pyritic internal mould). 'Upper' Oxford Clay, St. Ives, Cambridgeshire. Mariae Zone, ?Praecordatum Subzone.

Figs 4, 5. *Peltoceras* (*Peltoceratoides*) *williamsoni* (Phillips). Macroconch, $\times\frac{1}{2}$ (sideritic calcareous concretion preservation). 'Red Nodule Beds', 'Upper' Oxford Clay, Wootton Bassett, Wiltshire. Cordatum Zone, Costicardia Subzone.

Figs 6, 7. *Euaspidoceras hirsutum* (Bayle). Macroconch, $\times\frac{1}{3}$ (preserved in chamositic oolite). Hackness Rock, Scarborough, North Yorkshire. Lamberti Zone, probably Lamberti Subzone.

Figs 8, 9. *Euaspidoceras babeanum* (d'Orbigny). Macroconch, $\times\frac{1}{2}$ (pyritic internal mould). 'Upper' Oxford Clay, St. Ives, Cambridgeshire. Mariae Zone, probably Praecordatum Subzone.

Figs 10, 11. *Euaspidoceras douvillei* (Collot). Macroconch, $\times\frac{2}{3}$ (pyritic internal mould). Warboys, Cambridgeshire. Probably Cordatum Zone, Buckowskii Subzone.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Microconch: Typical for subgenus. Inner whorls have a rounded section which becomes squarer on the mature body chamber. Commonly resembles *P. arduennensis* (d'Orbigny). Mature size around 70–80 mm (septate to *c*. 55 mm).
Range. Common in the Praecordatum and Bukowskii subzones. A similar species occurs in the Scarburgense Subzone.

Subgenus *PELTOCERATOIDES* Spath

Description. *Macroconch*: Nucleus similar to *Peltomorphites*, but later whorls develop a flat-sided, compressed quadrate shape. Primary ribbing relatively fine, ending in small ventro-lateral tubercles. Middle whorls have a tendency to form looped ribs linking outer tubercles to an incipient inner row. Aperture simple.
Microconch: Similar to *Peltomorphites*, but with squarer whorls. Aperture lappeted.

Peltoceras (*Peltoceratoides*) *williamsoni* (Phillips)
Plate 26, fig. 7; Plate 27, figs 4, 5

Description. *Macroconch*: Typical for subgenus. Mature size at least 410 mm (septate to *c*. 310 mm).
Microconch: Typical for subgenus, mature at around 80 mm (septate to *c*. 50 mm).
Range. Costicardia Subzone; uncommon.

Subfamily ASPIDOCERATINAE
Genus *EUASPIDOCERAS* Spath

Description. *Macroconch*: Nucleus rapidly develops a quadrate, often depressed morphology, with tubercles developing from parabolic nodes. Outer row develops first, inner initially weak and linked to the former by irregular, even looped, ribs. Venter smooth from earliest stages. Later whorls bituberculate, with some weakening or modification towards the end of the mature body chamber. Aperture simple.
Microconch: Inner whorls have ventro-lateral nodes, frequently looped primary ribs and generally resemble the nuclei of macroconchs. They do, however, have a more planulate form. Body chamber relatively smooth, with very fine weak ribs. Aperture unknown, presumably lappeted.

Euaspidoceras hirsutum (Bayle)
Plate 27, figs 6, 7

Description. *Macroconch*: [Includes *E. ferrugineum* Jeannet and *E. clynelishense* Arkell] Typical for genus with medium sized tubercles and

a quadrate section. Mature size between 200 and 250 mm (septate to *c*. 130–150 mm).
Microconch: Poorly known, typical for genus.
Range. Locally common in the Lamberti Zone.

Euaspidoceras babeanum (d'Orbigny)
Plate 26, figs 8, 9; Plate 27, figs 8, 9

Description. *Macroconch*: [=includes *E. ivesense* Spath) Typified by variants with stout, depressed whorls, a broad venter and relatively small nodes. Maximum size poorly known but some may reach nearly 440 mm (septate to around 320 mm).
Microconch: Relatively small, apparently typical for genus. Maximum size known is around 40 mm (septate to *c*. 30 mm).
Range. Occasionally found in the Scarburgense and Praecordatum Subzones.

Euaspidoceras douvillei (Collot)
Plate 26, fig. 10; Plate 27, figs 10, 11

Description. *Macroconch*: Inner whorls typical for genus, outer whorl develops massive spines. Matures by at least 350 mm (septate to at least 270 mm).
Microconch: Typical for genus. Mature at around 60–70 mm (septate to *c*. 40 mm).
Range. Occasionally found in the Bukowskii Subzone.

Euaspidoceras acuticostatum (Young and Bird)
Not illustrated

Description. *Macroconch*: Outer tubercles relatively small for genus; inner row may be more prominent, but elongated to form weak rib. Outer whorl develops strong ribs, especially on the body chamber where they occasionally cross the venter. Mature size at least 390 mm (septate to *c*. 310–320 mm).
Microconch: Not recorded.
Range. Occasionally found in the Costicardia Subzone. A similar species may occur in the Cordatum Subzone.

5. OTHER CEPHALOPODS

by KEVIN N. PAGE AND PETER DOYLE

BELEMNITES (Peter Doyle and Kevin N. Page)

BELEMNITES are conspicuous in the Oxford Clay and at certain horizons they occur in such abundance that they pose considerable problems to the brick manufacturers. Despite such local abundance, detailed study has been limited. Historically, William Smith figured a belemnite from the Clunch [Oxford] Clay of Gloucestershire in his *Strata Identified by Organized Fossils* (1816–1819). This specimen, preserved in the British Museum (Natural History) (BMNH C. 640), is now known to be a *Cylindroteuthis*. Other nineteenth-century authors also recognized the importance of the Oxford Clay belemnites, including Owen (1844) and Mantell (1848, 1850), but the only monographic study remains that of Phillips (1869).

The Oxford Clay has yielded some spectacularly preserved specimens; complete tests exhibiting rostrum, phragmocone and pro-ostracum (text-fig. 5.1) which helped to shape the initial development of thought on belemnite morphology (e.g. Owen 1844; Mantell 1848). Such examples were first described by these authors from Trowbridge and Christian Malford in Wiltshire.

The Oxford Clay belemnites are divisible into two groups. The Cylindroteuthididae are Boreal, or northern derived, and are distinguished by their cylindrical to cylindriconical shape and a ventral apical groove which commences at the apex and dies out anteriorly. *Cylindroteuthis* is the most common of these belemnites in the Oxford Clay, although *Pachyteuthis* and the rarer, Arctic basin derived, *Lagonibelus* also occur. The Belemnopseidae are Tethyan, or southern derived, and are characterized by their hastate or double-tapering form, and a ventral alveolar groove which commences in the alveolar region and dies out posteriorly before reaching the apex. *Belemnopsis* and *Hibolithes* are its most familiar representatives in the Oxford Clay. Further details of the morphology and distribution of these belemnites may be found in Doyle and Kelly (1988).

The cylindroteuthid belemnites first appeared in Britain in the Lower Callovian, their appearance paralleling that of the Boreal kosmoceratid and cardioceratid ammonites (Doyle 1987). They dominate the British Oxford Clay belemnite fauna, although they are rarer in the Lower Oxfordian where the belemnopseid *Hibolithes* is locally common. Cylindroteuthid and belemnopseid belemnites occur side-by-side in approximately equal numbers only in the Lamberti Zone (Upper Callovian).

Subclass COLEOIDEA
Order BELEMNITIDA
Suborder BELEMITINA
Family CYLINDROTEUTHIDIDAE
Genus *CYLINDROTEUTHIS* Bayle
Cylindroteuthis puzosiana (d'Orbigny)
Plate 28, figs 1–4; Text-fig. 5.1

Description. Large rostrum, commonly attaining a length of 150–170 mm but reaching a maximum of approximately 240–250 mm. Rostrum cylindrical to cylindriconical, and symmetrical or almost symmetrical in outline (lateral aspect) and profile (ventral or dorsal aspect). The apex is acute, although in some examples it may be rounded. Transverse sections of the rostrum are slightly compressed and subcircular to subquadrate in form, often with a flattened venter. A sharply defined ventral groove is restricted to the apical quarter of the rostrum. Indistinct elongate depressions (lateral lines) are present on both flanks, and are especially well-defined in juvenile examples. The phragmocone is frequently absent from the alveolus, which penetrates up to one-quarter of the length of the rostrum.

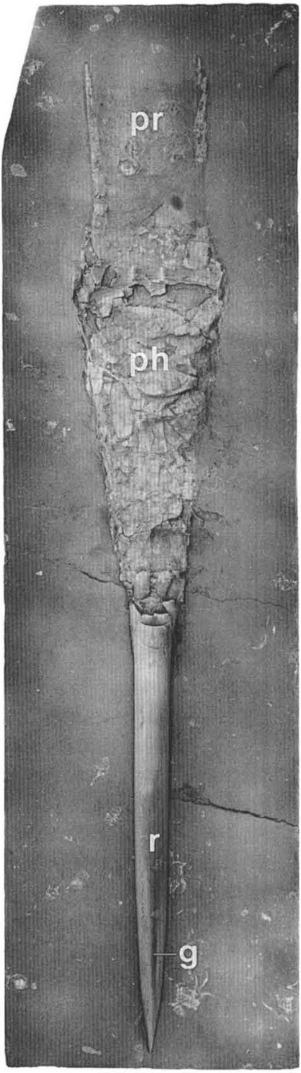
Remarks. Owen (1844), Morris (1854) and Phillips (1869) have all previously used the name *Belemnites owenii* Pratt for this species, a name first proposed by Pratt in Owen's (1844) paper. d'Orbigny's name was first used for this species in 1842 (d'Orbigny 1842), and thus has priority of usage.

Specimens preserved with rostrum, phragmocone and pro-ostracum are known from Christian Malford and Trowbridge in Wiltshire (e.g. Owen 1844; Mantell 1848) (text-fig. 5.1). One such specimen, preserved in the British Museum (Natural History) (BMNH C. 45079), has a rostrum 220 mm long, a phragmocone 170 mm long and a pro-ostracum of 130 mm; this represents a total shell length of around 520 mm yet possibly only one-third of the total body length.

Range. Very abundant. Lower Callovian (Calloviense Zone, Enodatum Subzone) to Lower Oxfordian (Mariae Zone, Praecordatum Subzone). Commonest in the Lower and Middle Callovian; very rare in the Lower Oxfordian.

Genus *LAGONIBELUS* Gustomesov
Lagonibelus beaumontiana (d'Orbigny)
Plate 29, figs 1 & 2

Description. Rostrum of medium size, attaining a maximum length of approximately 180 mm. Cylindriconical in form with a symmetrical outline and profile, and a moderately acute apex. Transverse sections of



TEXT-FIG. 5.1. *Cylindroteuthis puzosiana* (d'Orbigny), × 0·5. Exceptionally well-preserved specimen, probably from the Lower Oxford Clay (Athleta Zone, Phaeinum Subzone) of Wiltshire, in the Mantell collection (BMNH C59568). This specimen has the three elements of the belemnite shell preserved: rostrum (r), phragmocone (ph) and proostracum (pr). At the apex of the rostrum is a ventral groove (g) typical of the genus.

the rostrum are (dorso-ventrally) depressed and elliptical in the stem and apical regions, becoming more (laterally) compressed and subcircular in the alveolar region. A long ventrical groove commences at the apex as a narrow furrow, broadening substantially in the stem of the rostrum, where it is frequently secondarily deepened by weathering, and finally dies out as a broad flattened area in the alveolar region. Indistinct depressions (lateral lines) are present on each flank. The phragmocone penetrates up to one-third of the length of the rostrum.

Remarks. This species, which is commonest in the high Boreal regions, has frequently been confused with the Tethyan derived genus *Belemnopsis* because of the depth and length of its groove. However, an important distinction is that the groove in *Lagonibelus* is present at the apex and dies out anteriorly, the reverse situation to that occurring in *Belemnopsis*.

Range. Common in the Upper Callovian, mainly the Spinosum to Lamberti Subzones. Rare in the lower part of the Scarburgense Subzone.

Genus *PACHYTEUTHIS* Bayle
Pachyteuthis abbreviata (Miller)
Plate 30, figs 1 & 2

Description. Stout rostrum with a maximum length of approximately 150–170 mm. Cylindriconical in form with a symmetrical outline and profile. The apex is acute and often recurved towards the venter. Transverse sections of the rostrum are rounded and subquadrate to subtrapezoidal with both flanks flattened and excavated. The apical groove is only poorly defined or absent altogether, apart from a slight depression in the apical region. Both flanks bear strongly defined lateral depressions (lateral lines) causing the distinctive excavated form of the transverse sections. The phragmocone and alveolus penetrate one-half to two-thirds of the length of the rostrum.

Remarks. This species is the stoutest of the Oxford Clay cylindroteuthids, and is easily identified by its lateral depressions and resulting excavated transverse sections.

Range. Generally uncommon in the Cordatum Zone (Costicordatum or Cordatum Subzone) but ranging up to Middle or Upper Oxfordian. There is a single record of a Callovian *Pachyteuthis* sp. from the Phaeninum Subzone (Callomon 1968, p. 285).

Suborder BELEMNOPSEINA
Family BELEMNOPSEIDAE
Genus *BELEMNOPSIS* Bayle
Belemnopsis bessina (d'Orbigny)
Plate 29, figs 5 & 6

Description. Elongate, slender, needle-like rostrum of maximum length around 70 mm. Rostrum symmetrical, hastate or weakly hastate in

outline and cylindrical in profile. The profile may be slightly arcuate, and the apex is very acute. Transverse sections are notably depressed and reniform (kidney-shaped) because of the presence of a deep ventral groove. This groove commences in the alveolar region and broadens towards the apex, finally dying out in a flattened area approximately 5 mm from the apex. Lateral lines are present on each flank in the form of a pair of closely parallel double lines. The alveolus penetrates only the anterior-most portion of the rostrum.
Remarks. This species is easily distinguished from the other Oxford Clay belemnites by its slender, needle-like form and long, deep groove.
Range. Common in the Middle Callovian (Jason Zone).

Belemnopsis depressa (Quenstedt)
Plate 29, figs 3 & 4

Description. Elongate rostrum with a typical length of 100 mm. Rostrum symmetrical, hastate in outline and subhastate to cylindrical in profile. The apex is acute to rounded in outline. Transverse sections are depressed and generally elliptical, although made reniform due to the ventral groove in the stem; becoming subcircular in the alveolar region. The ventral groove is relatively narrow and deep, commencing in the alveolar region and dying out approximately 10–15 mm from the apex. Lateral lines are present on each flank as a pair of closely parallel double lines. The alveolus penetrates approximately one-sixth of the length of the rostrum.
Remarks. This species is common in mainland Europe, and is distinguished from *Belemnopsis bessina* by its more hastate and robust form.
Range. Rare. Probably occurs in the Jason or Coronatum zones of the Middle Callovian.

Genus *HIBOLITHES* Montfort
Hibolithes hastata Montfort
Plate 30, figs 3–6

Description. Rostrum attaining a maximum length of 170 mm, but generally small specimens of approximate length 50 mm are found.

EXPLANATION OF PLATE 28

Figs 1, 2. *Cylindroteuthis pusoziana* (d'Orbigny), Middle Callovian, Dogsthorpe, near Peterborough, Cambridgeshire, BMNH C. 46435: 1, ventral outline. 2, right profile (venter to right), × 1.
Figs 3, 4. *Cylindroteuthis pusoziana* (d'Orbigny), Middle Callovian, Fletton, near Peterborough, Cambridgeshire, BMNH C. 42265. 3, ventral outline. 4, right profile, × 1.

1 2 3 4

Rostrum is symmetrical and hastate in outline and profile, often with a bulbous stem and apex, and the maximum diameter is close to the apex. Transverse sections are depressed or weakly depressed and subcircular to elliptical in the stem and apex, becoming circular in the alveolar region. A sharply defined ventral groove commences in the alveolar region and is present for approximately one-half of the rostrum, dying out anteriorly. Closely parallel double lateral lines are present on each flank. The phragmocone penetrates only the anterior-most part of the rostrum. The alveolar region is frequently found in a semi-decomposed form.

Remarks. Few large specimens of this genus have been recorded from England, a fact first noted by Phillips (1869, p. 111), most being relatively small, often less than 50 mm in length. Despite this, the bulbous form and sharp, relatively short groove of many smaller English specimens are characteristic of *Hibolithes hastata*. There is, however, some indication of a stratigraphical change in morphology of belemnite rostra commonly identified as this species in the Oxford Clay. Specimens from the Lamberti Zone often have a relatively narrow rostrum while those from the Mariae Zone are often more bulbous. Available evidence suggests that those few large specimens collected (e.g. that illustrated by Phillips 1869, pl. XXVIII, fig. 67) come from a higher stratigraphic horizon, possibly within the Cordatum Zone. Future research and collecting may indicate the need for the separation of these groups into separate species, but this is not attempted here.

Range. Common in the Lamberti Zone (Lamberti Subzone). Also found in the Athleta Zone (Proniae and Spinosum subzones). Occasionally found in the Mariae Zone (mainly Praecordatum Subzone) and the lower Cordatum Zone.

NAUTILID AND 'TEUTHID' CEPHALOPODS (Kevin N. Page)

Ammonites and belemnites dominate all known Oxford Clay cephalopod faunas, but they are by no means the only representatives of the class in this formation. Rare finds indicate a much greater diversity of

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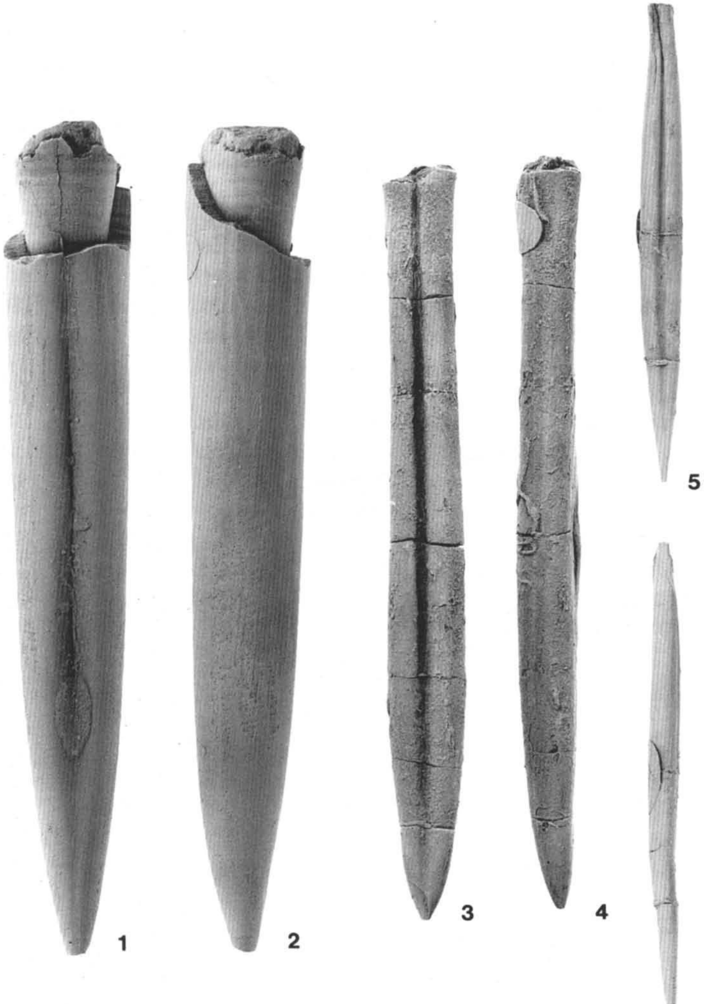
EXPLANATION OF PLATE 29

Figs 1, 2. *Lagonibelus beaumontiana* (d'Orbigny), Upper Callovian, Somerton, Oxfordshire, BMNH C. 11081: 1, ventral outline. 2, right profile (venter to right), × 1.

Figs 3, 4. *Belemnopsis depressa* (Quenstedt), Middle Callovian, Trowbridge, Wiltshire, BMNH C. 58921. 3, ventral outline. 4, right profile, × 1.

Figs 5, 6. *Belemnopsis bessina* (d'Orbigny), Middle Callovian, probably Jason Zone, Dogsthorpe, near Peterborough, Cambridgeshire, BMNH C. 46435. 5, ventral outline. 6, right profile, × 1.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cephalopods than would otherwise be suspected—these additional groups include nautilids, the belemnite-like *Belemnotheutis* and probable vampyromorph squids.

As nautilids have coiled aragonitic shells, broadly similar to those of ammonoids, they might be expected to occur wherever the latter are preserved—their rarity in the Oxford Clay is therefore a true reflection of original abundance. In the case of squid-like cephalopods (or 'teuthids') with their fragile shells, great rarity is in contrast much more likely to be a reflection of preservation potential.

As discussed below, most known specimens of these coleoids come from a single stratigraphic level in southern England. In this region, particularly in Wiltshire, unusual sea-bed conditions in the late Lower Oxford Clay facilitated the preservation of organic body-tissues which would normally have entirely decomposed. In consequence, a number of squid-like forms, with few mineralized structures, have been exceptionally well preserved.

The concentration of a rich cephalopod fauna at only one stratigraphic level does not, therefore, represent a chance immigration, but more likely a chance preservation of a 'normal' Oxford Clay biota. In other words, ammonites, belemnites and various other squid-like coleoids were likely to have been constant companions in Callovian and Oxfordian seas, and it is the selective preservation of calcareous shell material in other faunas that gives a biased faunal composition. Only the nautilids appear to have been truly rare.

NAUTILIDS

Only one genus of nautilid *Paracenoceras*, has been recorded from the Oxford Clay and specimens are rare.

The only publication to cover a British Callovian or Oxfordian nautilid species adequately is J. F. Blake's monograph of 1905. All his

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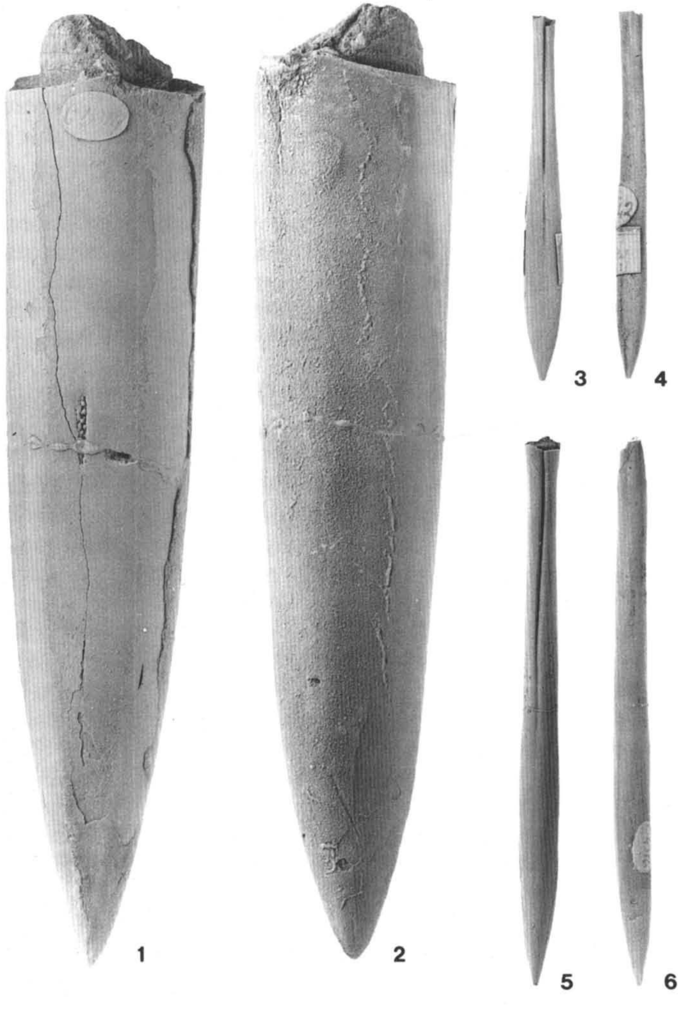
EXPLANATION OF PLATE 30

Figs 1, 2. *Pachyteuthis abbreviata* (Miller), Lower Oxfordian, St. Ives, Cambridgeshire, BMNH C. 4319. 1, ventral outline. 2, right profile (venter to the right), × 1.

Figs 3, 4. *Hibolithes hastata* Montfort, Lower Oxfordian, ?Mariae Zone, St. Ives, Cambridgeshire, BMNH C. 12042. 3, ventral outline. 4, right profile, × 1.

Figs 5, 6. *Hibolithes hastata* Montfort, Lower Oxfordian, ?Mariae Zone, St. Ives, Cambridgeshire, BMNH C. 4316. 5, ventral outline. 6, right profile, × 1.



1 2 3 4 5 6

specimens, however, came from the early Callovian 'Cornbrash', and appear to represent a different species from that known in the later Oxford Clay.

Unlike ammonoids, the sexual dimorphism observed in shells of living *Nautilus* takes the form of little more than variations in the inflation of adult body chambers. In the absence of well preserved and complete specimens, it remains to be convincingly demonstrated in *Paracenoceras*. The description below is therefore 'monomorphic'.

The suprageneric classification follows Kummel (1964).

PRESERVATION

Post Palaeozoic nautiloids, such as *Paracenoceras*, have coiled and chambered aragonitic shells, generally similar to those of ammonoids, but differing in microstructure and with simpler septal design.

All the preservational styles cited for Oxford Clay ammonites (see chapter 1) could therefore also apply to nautilids. In contrast to most ammonites, however, nautilid jaw structures, or rhyncolites, are calcitic. They clearly have a high preservational potential but no records appear to exist of their occurrence in the British Oxford Clay—a likely case of collection failure.

Order NAUTILIDA
Superfamily NAUTILACEAE
Family PARACENOCERATIDAE
Genus *PARACENOCERAS* Spath

Involute nautilid with a subtrapezoidal whorl section. Flattened whorl sides typically converge towards a flattened venter, which may be slightly concave on mature specimens.

The suture shows shallow ventral and lateral lobes. Surface ornament consists only of growth lines. Spiral lines on the innermost whorls produce a reticulate (netted) pattern.

Paracenoceras calloviense (Oppel)
Plate 31, fig. 1

Description. Typical for genus, showing a range of variation from relatively compressed forms resembling *P. truncatum* (Blake) to squarer whorled forms resembling *P. hexagonum* (J. de C. Sowerby). *P. truncatum* is characteristic of the older Abbotsbury Cornbrash Formation; *P. hexagonum* occurs in the overlying Corallian Group.

Mature size is not well known, most available specimens being inner whorls. One giant is around 380 mm in maximum diameter, another

specimen shows septal crowding, suggesting maturity, at only 90 mm (suggesting a maximum diameter of around 120 mm). This extreme size range may indicate that more than one species is present, although the paucity of available material makes their separation difficult or impossible. A single name is, therefore, used here.
Range. ?Koenigi to Lamberti Zones; commonest in the Lamberti Subzone.

BELEMNOTHEUTIS AND OTHER COLEOIDS

Commonly referred to collectively as 'teuthids', non-belemnite coleoids are rare constituents of certain Oxford Clay faunas.

Only the possible belemnoid *Belemnotheutis* had any significantly mineralized structures, all remaining groups being poorly mineralized. The characteristic remains of belemnotheutids are small, conical aragonitic phragmocones with an aragonitic rostrum in the form of a sheath. Most specimens are crushed, and as such can resemble the detached phragmocones of true belemnites, with which they are frequently confused.

In the 1840s, during the construction of the Great Western Railway near Christian Malford in Wiltshire, a number of exceptionally complete belemnotheutids were discovered (Pratt 1841; Owen 1844, 1856; Donovan 1977, 1983; Allison 1988). In addition to complete phragmocones with pro-ostraca, many specimens had mineralized soft-parts, including the mantle, head, arms and even ink sacs (Donovan 1977).

The same locality also yielded virtually the only known specimens of several other species of squid-like cephalopod—these include the probable vampyromorph *Mastigophora* (Donovan 1983) and the cuttle-fish like *Trachyteuthis*. A third species is known only from a single specimen and can be tentatively compared with the genus *Romaniteuthis*. All three species lack a true shell, its place being taken by a rigid organic or poorly mineralized internal support, analogous to the horny 'pen' of modern squids. This support is termed a gladius.

PRESERVATION

The delicate aragonitic phragmocones of belemnotheutids are typically preserved virtually unaltered in the Oxford Clay, although invariably in a crushed condition. The pro-ostracum was evidently poorly mineralized and is only known from localities where soft-part preservation occurs.

Despite their greater fragility, preservational styles similar to those of ammonite shells characterize belemnotheutid phragmocones at most levels in the Oxford Clay. In addition to phragmocones, belemnotheutid arm-hooks are occasionally recovered as isolated elements, both on sediment surfaces and in microfossil preparations—they appear to have a relatively resistant organic composition.

The soft-part preservation of the Christian Malford fauna is considerably different from the 'normal' fossilization processes which have affected virtually all other Oxford Clay cephalopods. It clearly represents a 'rare event, that requires exceptional physical and chemical conditions' (Allison 1988, p. 403).

As already discussed in Chapter 1, the mantle and arms of *Belemnotheutis* and the vampyromorph squids are frequently preserved as a film of calcium phosphate. All known specimens came from a single stratigraphic level in the upper part of the Lower Oxford Clay; dated by the abundant accompanying ammonites as Athleta Zone, Phaeinum Subzone. Laterally equivalent beds, in railway cuttings near Trowbridge, also in Wiltshire, have yielded elements of the same coleoid fauna, but without true soft part preservation (Mantell 1848). An isolated record of *Mastigophora*, from Weymouth (Carreck 1960), is also likely to have come from a similar level. The fauna therefore appears to be widespread, at least in southern England, although soft part preservation may only occur at the 'type' locality.

Belemnotheutis is known sporadically at other levels in the Oxford Clay, but always remains inconspicuous—its phragmocone resembles a broken belemnite and arm-hooks are often overlooked due to their small size. Similarly, the relatively tough organic or poorly mineralized internal supports of groups such as *Mastigophora* would tend to be discarded as indeterminate organic 'scraps' when poorly preserved and fragmentary.

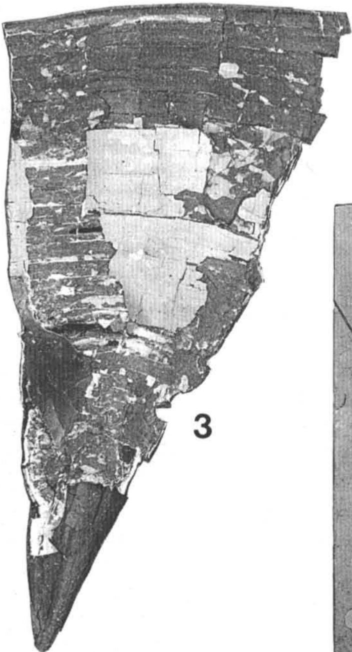
Subclass COLEOIDEA
Order BELEMNITIDA
Family BELEMNOTHEUTIDIDAE
Genus *BELEMNOTHEUTIS*
Belemnotheutis antiquus Pearce
Plate 31, figs 2 & 3

Description. Phragmocone conical, with slight dorsal curve. Apical portion covered by a thin rostrum-like layer up to 2 mm thick, which thins

EXPLANATION OF PLATE 31

Fig. 1. *Paracenoceras calloviense* (Oppel). Inner whorls or juvenile, ×1. Lower Oxford Clay, Peterborough, Cambridgeshire. Jason Zone, ?Jason Subzone.

Figs 2, 3. *Belemnotheutis antiquus* Pearce. 2, complete specimen with preserved mantle and showing arm hooklets, ×0·5; Lower Oxford Clay, Christian Malford, Wiltshire. Athleta Zone, Phaeinum Subzone. 3, phragmocone, crushed, ×1·5; Lower Oxford Clay, Stewartby, Bedfordshire, Middle Callovian.



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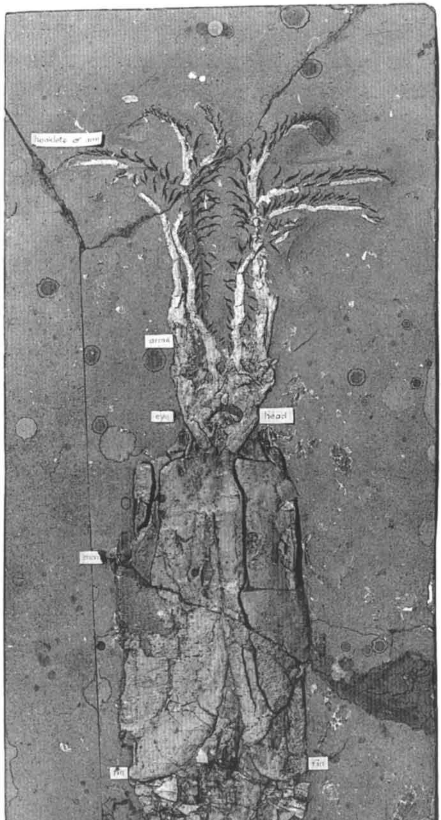

and disappears anteriorly. Two short ridges lie either side of the mid dorsal line, at the apex of the rostrum. Pro-ostracum bluntly pointed and slightly longer than the phragmocone.

Pro-ostraca are extremely rare, most specimens consisting only of a crushed phragmocone. The largest known are around 90 mm long, although most specimens tend to be less than 30 mm; apparently largely due to preservation of only the anteriorly thickened portion.

The exceptionally preserved specimens from Christian Malford indicate that the phragmocone was situated at the posterior of a squid-like animal. In these specimens, the front of the shell is covered by the mantle, the ink sack lying near the junction.

The animal's head probably possessed 10 arms, although fewer are visible in most specimens (Donovan 1977, p. 28). Each bore at least 25 pairs of hooks and rare specimens also show suckers (D. T. Donovan, *pers. comm.*, 1989). The maximum length known is around 300 mm.

Remarks. Donovan (1977, pp. 26–39) redescribes and discusses *B. antiquus*, its relatives and systematic position. The spelling '*Belemnotheutis*', rather than '*Belemnoteuthis*', follows Pearces' original (D. T. Donovan, *pers. comm.*, 1989).

Range. *B. antiquus* sensu stricto occurs in the Upper Callovian (Athleta Zone, Phaeinum Subzone). Belemnotheutid phragmocones are also known from the Lower Callovian (Koenigi Zone, Curtilobus Subzone; Calloviense Zone, Calloviense and Enodatum Subzones), Middle Callovian (Jason Zone; Coronatum Zone, Obductum and Grossouvrei Subzones) and the Lower Oxfordian (Mariae Zone or Cordatum Zone, Buckowskii Subzone).

Order VAMPYROMORPHA
Suborder MESOTEUTHINA
Family TRACHYTEUTHIDIDAE
Genus *TRACHYTEUTHIS*
Trachyteuthis sp. nov.
Plate 32, fig. 1

Description. Only incomplete specimens of the gladius are known, soft parts such as arms are not preserved.

EXPLANATION OF PLATE 32

Fig. 1. *Trachyteuthis* sp. *nov*. Gladius, damaged, ×0·32. Lower Oxford Clay, Christian Malford, Wiltshire. Athleta Zone, Phaeinum Subzone.

Fig. 2. *Mastigophora brevipinnus* (Owen). Complete specimen with preserved mantle and showing ink-sack, ×0·5. Lower Oxford Clay, Christian Malford, Wiltshire. Athleta Zone, Phaeinum Subzone.

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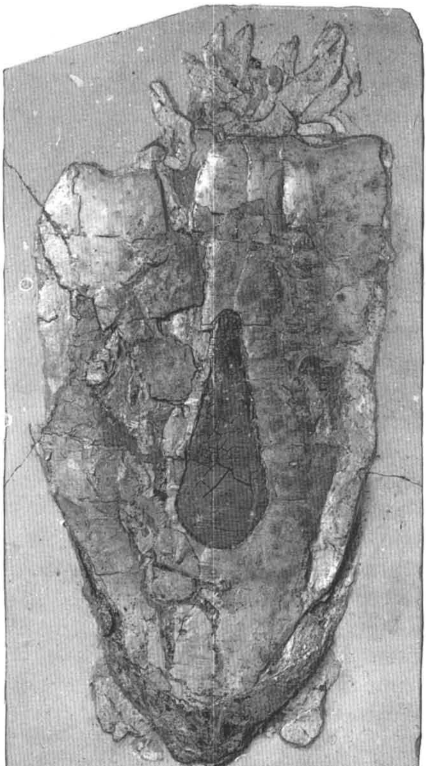


The outline is broad, with posterior lobes, and resembles that of modern cuttle-bones. A radial sculpture originates from the posterior apex and a concentric sculpture is present at the anterior and lateral margins. Traces of rugose dorsal ornamentation are present and are characteristic of the genus. No trace of phragmocone can be seen in the two specimens in the British Museum (Natural History; BM C46977 and C46969). The former is the most complete and measures around 420 mm in length.

Remarks. *Trachyteuthis* is discussed by Donovan (1977, pp. 31–33) who considers the genus to be a true cuttle-fish or sepiid (Order Sepioidea).

Hewitt and Wignall (1988) however, discuss Kimmeridgian trachyteuthids and believe that the phosphatic mineralogy and absence of a phragmocone refutes this classification. *Trachyteuthis* is therefore provisionally included with the Order Vampyromorpha.

Range. Known only from the Christian Malford fauna (Athleta Zone, Phaeinum Subzone).

Suborder LOLIGOSEPIINA
Family LOLIGOSEPIIDAE
Genus *MASTIGOPHORA*
Mastigophora brevipinnus Owen
Plate 32, fig. 2; text-fig. 5.2

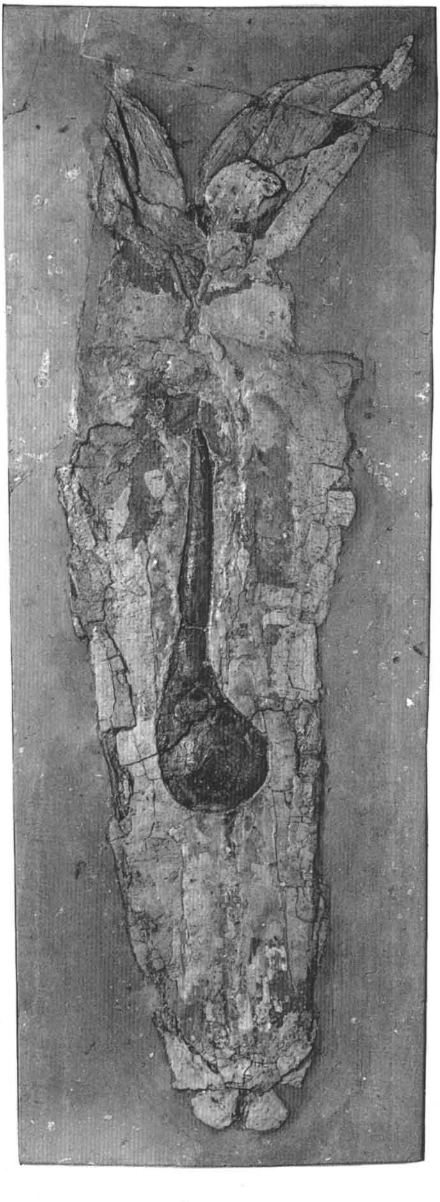
Description. Gladius with narrow triangular central field and blunt anterior. Lateral fields have a concentric striation. Specimens from Christian Malford typically have mineralized soft parts and have been described in detail and fully illustrated by Donovan (1983).

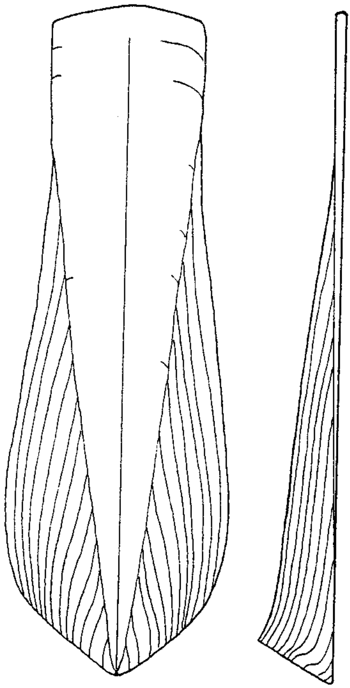
The gladius is enclosed in a stoutly triangular body which possessed a pair of postero-lateral fins. The ink sac is centrally placed and the mantle shows transverse striations. The head gives rise to eight short, unhooked arms. A small dark rhomboidal or V-shaped area in some specimens represents the jaws. A maximum size for complete specimens is around 180 to 190 mm.

Range. Known primarily from the Christian Malford fauna (Athleta Zone, Phaeinum Subzone). An additional specimen has been recorded from the Coronatum Zone (presumably Grossouvrei Subzone) near Weymouth, Dorset (Carreck 1960).

EXPLANATION OF PLATE 33

?*Romaniteuthis* sp. Complete specimen with preserved mantle and showing ink-sack, ×0·37. Lower Oxford Clay, Christian Malford, Wiltshire. Athleta Zone, Phaeinum Subzone.





TEXT-FIG. 5.2. Dorsal and lateral reconstructions of the gladius of *Mastigophora brevipinnus* Owen, × 0·75. After Donovan (1983).

Genus ?*ROMANITEUTHIS*
?*Romaniteuthis* sp.
Plate 33

Description. Similar to *Mastigophora*, but with a longer, more elongated body. In the figured specimen, the gladius cannot be seen and the number of arms is not discernible. An ink sac is, however, visible. The body measures 280 mm, but would be over 400 mm when including arms.
Comments. The identification is provisional and only one specimen has been seen (BM 34025).
Range. Christian Malford fauna (Athleta Zone, Phaeinum Subzone).

6. BRACHIOPODS

by COLIN D. PROSSER

BRACHIOPODS comprise only a relatively small part of the invertebrate fauna of the Oxford Clay. They have a patchy distribution and although rare in the Oxford Clay as a whole, they may be locally abundant. Brachiopod diversity was low in the muddy soft-bottomed conditions which prevailed in the Oxford Clay sea and it seems likely that they did not favour this environment. The inarticulate brachiopod *Lingula* is locally abundant in the Lower Oxford Clay whilst articulate brachiopods are more common in the Middle and Upper Oxford Clay. This sparse fauna has attracted little research in the past and is now in great need of taxonomic revision. The earliest records date back to Sowerby (1818) and Conybeare & Phillips (1822) whilst Davidson (1851–1882) is the most recent publication describing this fauna. Confusion exists over names used for most of the taxa and alternative names are given below. This guide does not give priority of nomenclature; this must await a full revision of the brachiopod fauna. For further details of morphological terms used see Moore (1965).

Class INARTICULATA
Order LINGULIDA
Superfamily LINGULACEA
Family LINGULIDAE
Genus *LINGULA*
Lingula craneae Davidson
Text-fig. 6.1, fig. 1

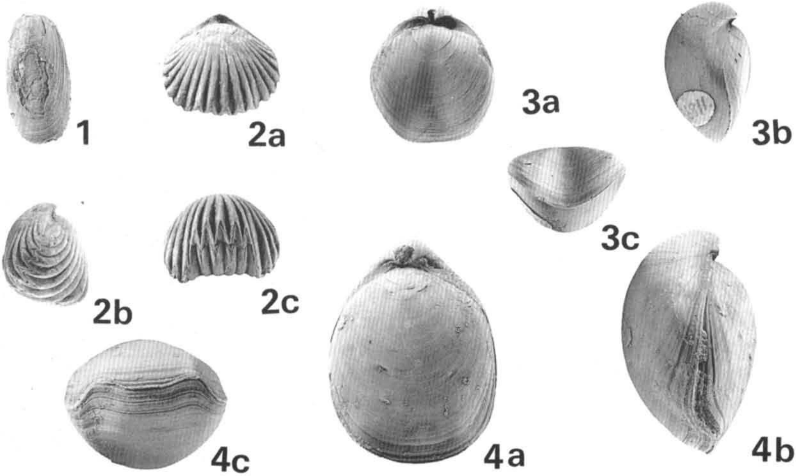
Description. Small, biconvex lingulid. Oval in outline with the anterior margin of the valves somewhat flattened. Valves about twice as long as wide. Well defined growth lines visible.
Range. This species has not been positively recorded outside the Lower Oxford Clay.
Remarks. A horizon rich in *L. craneae* occurs at the base of the *jason* Zone at Calvert brick pit. Early accounts sometimes refer this species to *L. ovalis*, recorded from the Kimmeridge Clay (Davidson 1851–1882).

Order ACROTRETIDA
Superfamily DISCINACEA
Family DISCINIDAE
Subfamily ORBICULOIDEINAE
Genus *ORBICULOIDEA*
Orbiculoidea latissima (Sowerby)
(not figured)

Remarks. Phillips (1829) listed amongst the fossils of the Oxford Clay of Yorkshire *Patella latissima.* He did not figure this species but referred the reader to Sowerby's 'Mineral Conchology of Great Britain'. Sowerby figured two specimens of *P. latissima* (1815–1818, tab. CXXXIX, figs 1 & 5) both of which are clearly discinid brachiopods not representative of the gastropod genus *Patella.* Sowerby gave little stratigraphic or locality data but Phillips (1829) recorded specimens from the Oxford Clay of Yorkshire and Conybeare & Phillips (1822) recorded the species from the Oxford Clay of Lincolnshire. Specimens have been recorded in boreholes from southern England but clearly these brachiopods are very rare and no specimens were located during the course of this present study.

Class ARTICULATA
Order RHYNCHONELLIDA
Superfamily RHYNCHONELLACEA
Family WELLERELLIDAE
Subfamily LACUNOSELLINAE
Genus *RHYNCHONELLOIDELLA*
Rhynchonelloidella socialis (Phillips)
Text-fig. 6.1, 2a–c

Description. Small, strongly uniplicate rhynchonellids with an oval outline. The fold in the brachial valve starts to appear about half way down the valve and corresponds with a well defined fairly wide sulcus in the pedicle valve. The valves are ornamented by about 18–22 subrounded to subangular costae that run the full length of the shell but which become less well defined posteriorly. About 6 costae are usually raised in the fold. The beak is suberect to erect with sharp beak ridges bordering a well defined interarea. The foramen is oval and surrounded by disjunct or just conjunct deltidial plates. Delicate closely packed growth lines are visible on the valves of many specimens.
Range. This species has been recorded from the Middle and Upper Oxford Clay along most of the outcrop but is rare in the Lower Oxford Clay. It has been accurately collected from the upper part of the *athleta* Zone (Callomon 1968).



TEXT-FIG. 6.1. Brachiopods of the Oxford Clay. 1, *Lingula craneae* Davidson, Oxford Clay; Weymouth, Dorset, ×1. 2a,b,c, *Rhynchonelloidella socialis* (Phillips). Oxford Clay; St Ives, Cambridgeshire, ×1. 3a,b,c, *Aulacothyris bernadina* (d'Orbigny). Oxford Clay; Bardney, Lincolnshire, ×1. 4a,b,c, *Cererithyris*? *oxoniensis* (Davidson). Oxford Clay; St Ives, Cambridgeshire.

Remarks. Davidson (1851–1884) listed a number of varieties of *Rhynchonella varians* which may be synonyms for *Rhynchonelloidella socialis*. Revision of all these varieties is required to confirm that *R. socialis* is the correct name for the species which occurs in the Oxford Clay. The following names have been used for Oxford Clay rhynchonellids at one time or another: *Rhynchonella spathica*, *Rhynchonella varians* and *Rhynchonella thurmanni*. Childs (1969) reviewed the genus *Thurmannella* and figured specimens which are very similar to *R. socialis*. This suggests that this species may be referrable to *Thurmannella*.

Family RHYNCHONELLIDAE
Subfamily ACANTHOTHYRIDINAE
Genus *ACANTHORHYNCHIA*
Acanthorhynchia lorioli (Rollier)
(not figured)

Remarks. A single specimen of this spinose rhynchonellid was recorded by Arkell (1939) from the Middle Oxford Clay of Woodham. This species was reviewed by Childs (1969) but was not recorded as being known from Britain. It is clearly extremely rare in the Oxford Clay.

Order TEREBRATULIDA
Superfamily ZEILLERACEA
Family ZEILLERIIDAE
Genus AULACOTHYRIS
Aulacothyris bernadina (d'Orbigny)
Text-fig. 6.1, figs 3a–c

Description. Shell small to medium sized with a subpentagonal outline. The anterior commissure is sulcate. The pedicle valve is convex with a fairly strong fold. The brachial valve displays a well defined sulcus running the full length of the valve. Both valves are smooth although growth lines may be quite prominent anteriorly. The beak is small and strongly incurved. The beak ridges enclose a small, narrow interarea.
Range. Recorded from the Middle and Upper Oxford Clay. It is fairly common in Cambridgeshire and Buckinghamshire and has been reported from other areas including Lincolnshire and Yorkshire.
Remarks. This distinctive brachiopod has sometimes been referred to by other authors as '*Terebratula impressa*' or '*Waldheimia impressa*'. A study of the internal characters of this Oxford Clay species is required to dispel any doubts as to its designation to *Aulacothyris*.

Superfamily TEREBRATULACEA
Family TEREBRATULIDAE
Subfamily TEREBRATULINAE
Genus *CERERITHYRIS*?
Cererithyris? *oxoniensis* (Davidson)
Text-fig. 6.1, figs 4a–c

Description. Shell medium sized with oval to subpentagonal outline. Biconvex with the pedicle valve being the more convex of the two valves. Anterior commissure moderately sulciplicate. Beak short and suberect to erect. Foramen large, permesothyridid. Valves smooth except for concentric growth lines.
Range. Davidson (1876–1878) recorded this species from the Oxford Clay of St Ives. Specimens examined at the BM(NH) confirmed this limited geographical and vague stratigraphical occurrence.
Remarks. This taxon appears to have been totally neglected since Davidson originally described it using Walker's unpublished manuscript name. A number of specimens exist in the collections of the BM(NH) labelled as *Terebratula oxoniensis* or *Cererithyris*? *oxoniensis*. Due to this species external similarity to species of *Cererithyris* which occur in the Cornbrash, *T. oxoniensis* is tentatively referred here to this genus pending a detailed study of the Oxford Clay brachiopods.

7. OTHER INVERTEBRATES

by DAVID M. MARTILL

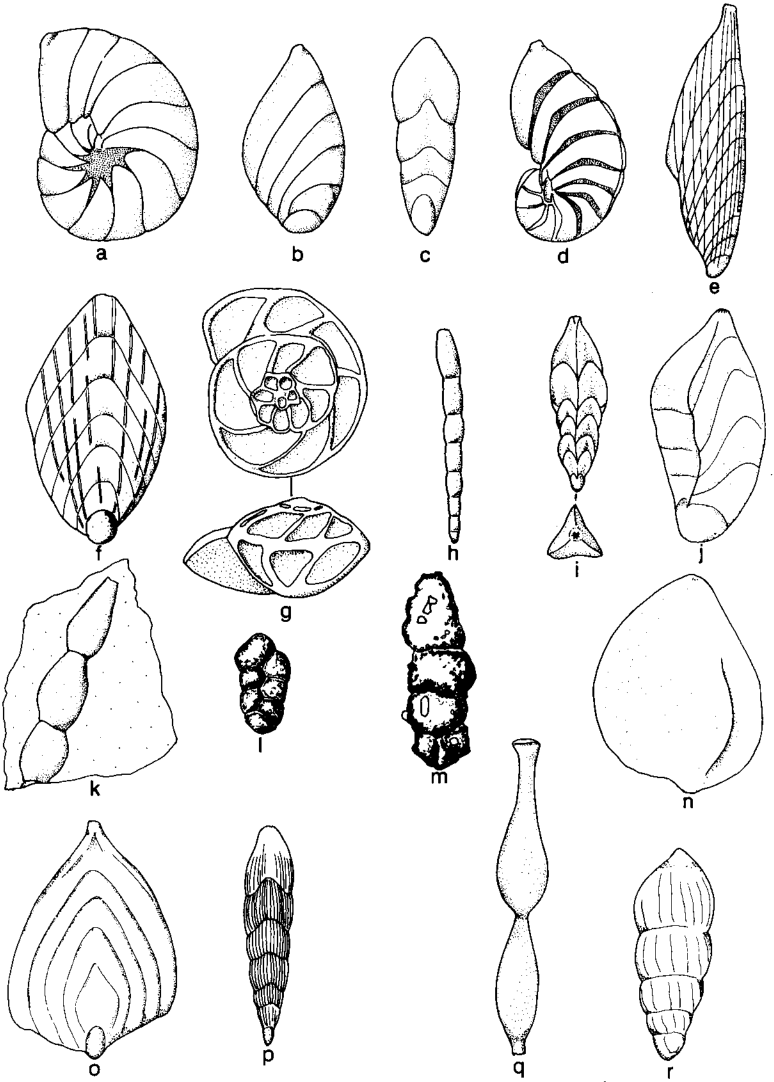
A NUMBER of invertebrate groups are represented in the Oxford Clay by one or two species only, insufficient in terms of diversity to justify devotion of a complete chapter, while others occur as microfossils which are not readily apparent in the field. These 'other' invertebrates have been assembled under a single chapter for the sake of convenience. Many are important members of the Oxford Clay marine community, and should not be considered as insignificant because of this treatment. Some macroinvertebrates may dominate shell beds, while the microfossils are important contributors to the rock record.

FORAMINIFERA

Foraminifera are extremely abundant in the Oxford Clay. Duff (1975) even used the term 'foram-rich bituminous shales' for a facies in the Lower Oxford Clay rich in *Epistomina* sp. Early accounts date back to the last century (Crick, 1887; Sherborn, 1888; Whittaker, 1886), but these records are of historic interest only. They have been extensively studied in recent years due to their importance in biostratigraphy (Barnard, 1952, 1953; Coleman, 1974, 1981; Richardson, 1979; Shipp & Murray, 1981). Clays and shales equivalent to the English Oxford Clay on the east coast of Scotland and on the Isle of Skye have yielded faunas similar to those in south-east England (Cordey, 1962; Gordon, 1967).

The fauna is easily collected by bulk sampling of the less bituminous clay horizons and washing through sieves down to a mesh size of 100 microns. Encrusting foraminifera can easily be sampled by carefully examining the surface of large grypheate oysters from the Upper Oxford Clay, especially at Warboys, Cambridgeshire and Stanton Harcourt, Oxfordshire. In an unpublished Ph.D. thesis, Shipp (1978) recorded thirty-five foraminifera species from the Lower Oxford Clay, fifty-seven from the Middle Oxford Clay, and fifty-four from the Upper Oxford Clay. The slightly reduced fauna from the Lower Oxford Clay may be a reflection of slightly lower oxygen levels caused by a higher organic carbon input.

It has only been possible to figure a few of the more common species (text-fig. 7.1). The foram enthusiast is referred to Shipp & Murray (1981) and to Coleman (1981) for more extensive figures and diagnoses. The foraminifera listed in Appendix 1 are derived from these authors.



TEXT-FIG. 7.1. Some common foraminifera from the Oxford Clay of south-east England. **a**, *Lenticulina muensteri*, ×25. **b**, *Planularia anceps*, ×40. **c**, *Frondicularia franconica*, ×50. **d**, *Marginulina ectypa*, ×75. **e**, *Citharina flabellata*, ×25. **f**, *Frondicularia moelleri*, ×25. **g**, *Epistomina stelligera*, ×50. **h**, *Dentalina filiformis*, ×50. **i**, *Tristix* sp. ×45. **j**, *Saracenaria oxfordiana*, ×40. **k**, *Nubeculinella bigoti*, ×50. **l**, *Textularia jurassica*, ×45. **m**, *Ammobaculites suprajurassica*, ×25. **n**, *Guttulina pera*, ×75. **o**, *Citharina* sp. ×25. **p**, *Lingulina longiscala*, ×40. **q**, *Dentalina* sp. ×50. **r**, *Pseudonodosaria radiata*, ×60.

COELENTERATES

Class ANTHOZOA

Anthozoa are represented in the Oxford Clay by a single species of the ahermatypic coral *Trochocyathus*. However, when it occurs, it is relatively abundant. The general absence of corals in the Oxford Clay sea may be a consequence of high sediment input, and possibly reduced light levels. *Trochocyathus* today is found in waters greater than 30 metres deep.

SPECIES DESCRIPTIONS

Order SCLERACTINIA
Suborder CARYOPHYLLINA
Superfamily CARYOPHILLIICAE
Family CARYOPHYLLIIDAE
Subfamily CARYOPHILLIINAE
Genus *TROCHOCYATHUS*
Trochocyathus magnevillianus Michelin
Plate 35, fig. 5

Description. Small, solitary cup coral, outline circular, depressed, slightly conical. Septa prominent on theca. Columella fasciculate.
Remarks. Common in the Middle Oxford Clay, where it rarely reaches more than one centimetre diameter.

Class HYDROZOA

Order HYDROIDA
Genus *PROTULOPHILA*
Protulophila gestroi Roverto
(not figured)

Diagnosis. A branching network of stolons and polyps preserved as bioimmurations in the tubes of calcareous serpulid worms. Stolon tubes usually between 0·04 and 0·05 mm diameter, forming diamond to hexagonal network on surface of serpulid tube. Polyp chambers conical, generally between 0·24 and 0·40 mm broad by 0·76 and 1·20 mm long.
Remarks. *Protulophila* stolons and polyp chambers were incorporated into the serpulid tube during growth of the serpulid. This indicates that the infestation of the serpulid was symbiotic. For a full discussion of the affinities and ecology of *Protulophila* see Scrutton (1975).
Range. Associated with *Serpula sulcata* from the Oxford Clay of St Ives, Cambridgeshire, Ludgershall, Wiltshire and Jordans Cliff, Weymouth. All presumably Upper Oxford Clay (Lower Oxfordian).

BRYOZOANS

Bryozoans are generally rare in the Oxford Clay, but may be locally abundant in condensed parts of the *lamberti* Zone in Oxfordshire. They are also common in the more shelly Oxford Clay equivalents of Normandy, France. In the earliest account Phillips (1871) records bryozoans from the Middle Oxford Clay of St Clement's, Oxfordshire. All early accounts of Oxford Clay bryozoans assign encrusting forms to the species *Berenicea diluviana* (e.g. Gregory, 1896). *B. diluviana* is a *nomen dubium*, and it is likely that Oxford Clay examples encompass at least four distinct species, some of which can be referred to the genera *Hyporosopora* and *Plagioecia*. No detailed account of Oxford Clay bryozoans is available, but Pitt & Thomas (1969) discuss the presence of at least three species.

Bryozoans are found in three states of preservation in the Oxford Clay: as encrusting colonies on the surfaces of oysters and belemnites; as borings in oysters and belemnites; and as bioimmured colonies where oysters have overgrown existing colonies attached to other substrates. In the latter case it may be possible to find organic walled forms that would not otherwise be preserved (Taylor, 1990a,b). Encrusting bryozoans should be looked for on the surfaces of large grypheate oysters occurring at minor non-sequences, especially those that are encrusted with large serpulid worms. Boring bryozoans can be found on the same oysters and belemnites colonized by encrusters. A common boring is attributable to the ctenostome *Ropalonaria*? *arachne* (Fischer) (see Pohowsky, 1978). Bioimmured bryozoans should be looked for as external moulds on the xenomorphic attachment areas of oysters. The species most likely to be encountered is the ctenostome *Arachnidium smithii* (Phillips) (see Taylor, 1990a and b) which occurs at Stanton Harcourt, Oxfordshire. A good description of bryozoan morphology is given by Taylor (1987). For an account of Jurassic bryozoan systematics see Walter (1970).

SPECIES DESCRIPTIONS

Order CYCLOSTOMATA
Suborder TUBULINOPORINA
Family PLAGIOECIIDAE
Genus *HYPOROSOPORA*
Hyporosopora spp.
Plate 34, figs 1, 2

Description. Flat encrusting sheet-like colonies. Often fan shaped when young, becoming circular.

Range. Middle and Upper Oxford Clays. Oxfordshire, Buckinghamshire, and Cambridgeshire.
Remarks. Flat, sheet-like, encrusting colonies of bryozoans from the Oxford Clay have usually been classified as *Berenicea*. In the Oxford Clay there are probably four distinct species, two of which may be referred to *Hyporosopora* on the basis of their reproductive polymorphs (gynozooids) (P. D. Taylor, *pers. comm.*). Appears to be very rare, but this may in part be due to lack of collecting effort. Can be common on oysters and belemnites in the *lamberti* Zone south of Oxford. Names under which these bryozoans may appear include *Berenicea diluviana* and *B. archiaci* (see Pitt & Thomas, 1969).

Genus *PLAGIOECIA*
Plagioecia sp.
Plate 34, figs 3, 5

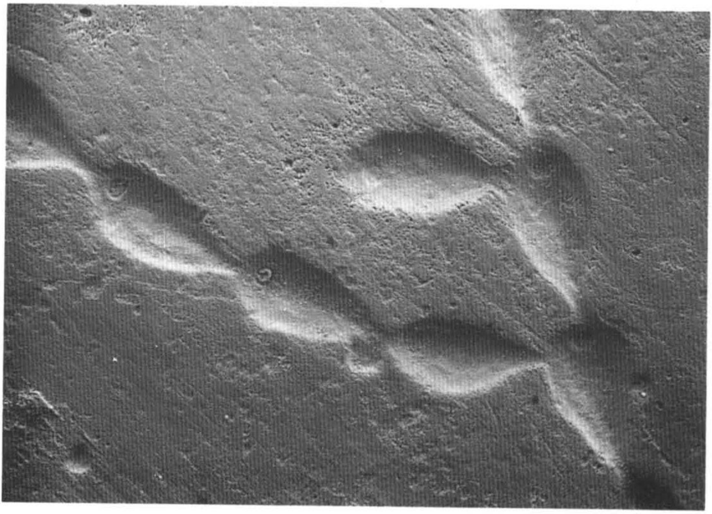
Description. Flattish, encrusting colonial bryozoan.
Range. Known only from the *lamberti* Zone at Stanton Harcourt, Oxfordshire.

Family STOMATOPORIDAE
Genus *STOMATOPORA*
Stomatopora spp.
(not figured)

Remarks. A small, encrusting, dichotomously branching bryozoan. Recorded from the Woodham brick pit, Buckinghamshire, by Pitt & Thomas (1969) as *S. dichotoma* (Lamouroux, 1821). A collecting effort in 1989 in coeval beds at Stanton Harcourt, Oxfordshire showed this bryozoan to be common on large *Gryphaea* spp. Several species may be represented (P. D. Taylor, *pers. com.*).

Order CTENOSTOMATA
Suborder CARNOSA
Family ARACHNIDIIDAE
Genus *ARACHNIDIUM*
Arachnidium smithii (Phillips)
Text-fig. 7.2

Description. Organic walled encrusting bryozoan with regular repeated budding of zooecia arranged in branched chains. Well preserved specimens may show terminal zooecipore on zooecia.
Range. *Arachnidium* is reported from the Oxford Clay equivalents of Villers-sur-mer, Normandy, France where the specimen in fig. 7.2



TEXT-FIG. 7.2. *Arachnidium smithii* (Phillips). A bioimmured specimen from the Oxfordian of Villers-sur-Mer, Normandy, France. This specimen should appear as a series of depressions, lit from the north-east. × 35.

is from. Recently however P. D. Taylor (*pers. comm.*) has discovered bioimmured specimens at Stanton Harcourt, Oxfordshire.

Remarks. This taxon is usually only preserved if it is overgrown by an oyster or serpulid. It can be found by examining oyster attachment areas, or by carefully removing serpulids from their substrates with a fine chisel. Specimens will appear as depressions on the attachment surface.

EXPLANATION OF PLATE 34

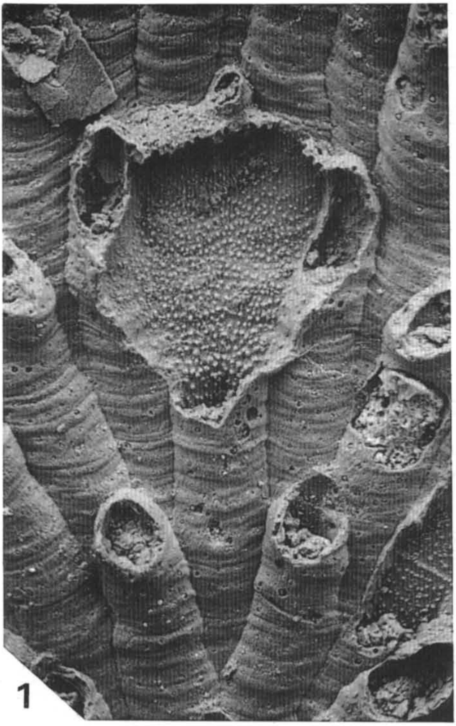
Fig. 1. *Hyporosopora* sp. with large gynozooid. Middle/Upper Oxford Clay boundary, Stanton Harcourt, Oxfordshire, × 50.

Fig. 2. *Hyporosopora* sp. entire colony, Middle/Upper Oxford Clay boundary, Stanton Harcourt, Oxfordshire, × 3.

Fig. 3. *Plagioecia* sp. entire colony encrusting oyster shell. Middle/Upper Oxford Clay boundary, Stanton Harcourt, Oxfordshire, × 1·5.

Fig. 4. Oyster shell showing variety of borings. Some of these may be attributable to boring bryozoans and cirripedes. Middle/Upper Oxford Clay boundary, Stanton Harcourt, Oxfordshire, × 2.

Fig. 5. *Plagioecia* sp. with large gynozooid. Middle/Upper Oxford Clay boundary, Stanton Harcourt, Oxfordshire, × 50.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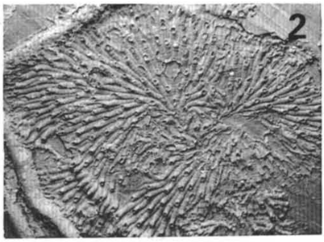
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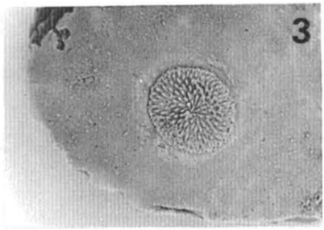
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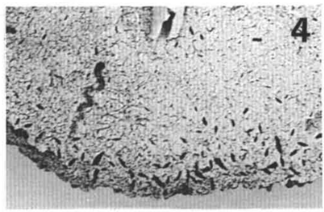
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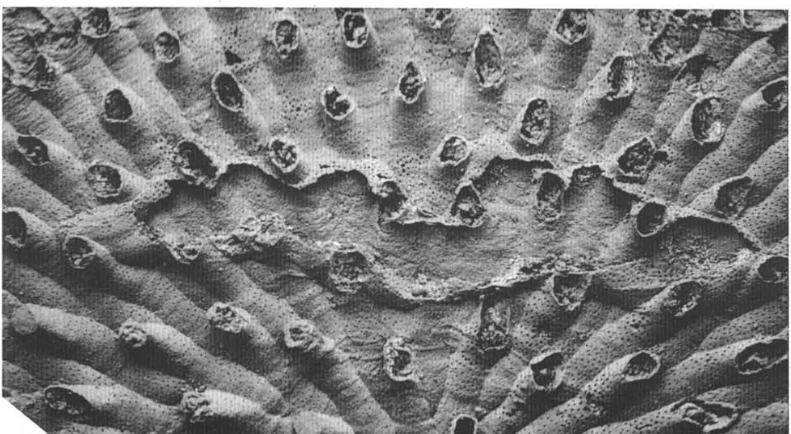
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ANNELIDS

Annelids were abundant in the Oxford Clay Sea. The preserved fauna is not diverse, consisting of only three or so forms with calcareous tubes, but early diagenetic pyrite frequently preserves burrows of possible annelids, suggesting a much more diverse soft-bodied fauna. Cemented forms such as *Serpula* are usually associated with breaks in sedimentation, where they are commonly cemented to shells of *Gryphaea* spp. *Genicularia* on the other hand, is frequently found in the shales, suggesting perhaps that it was infaunal, or possibly pendent. Some serpulids may have lived attached to free-swimming ammonites.

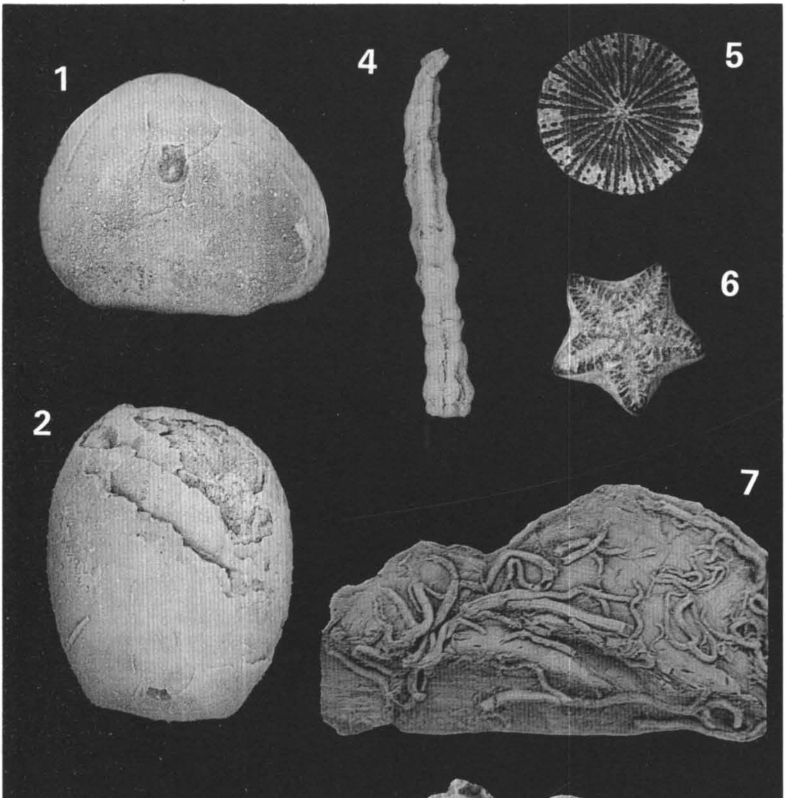
SPECIES DESCRIPTIONS

Class POLYCHAETIA
Order SEDENTARIDA
Family SERPULIDAE
Genus *SERPULA*
Serpula sulcata
Plate 35, fig. 8

Description. Large, cemented serpulid, irregularly sinuous, with longitudinal keel or sulcus. Larger specimens may be spinose apically. Some specimens display an apertural flange.
Remarks. *S. sulcata* is very abundant in the Middle and Upper Oxford Clay where it is found cemented to large grypheate oyster shells. It is often associated with cemented foraminifera. Specimens may show bioimmurations of the hydroid *Protulophila gestroi* Roverto.

EXPLANATION OF PLATE 35

Figs 1, 2, 3. *Disaster granulosus.* Middle Oxford Clay, Stanton Harcourt, Oxfordshire, ×2.
Fig. 4. *Genicularia vertebralis,* Lower Oxford Clay, Peterborough, Cambridgeshire, ×2.
Fig. 5. *Trochocyathus magnevillianus.* Middle Oxford Clay, Coronation Pit, Stewartby, Bedfordshire, ×3.
Fig. 6. *Isocrinus ?fisheri.* Ossicle. Middle Oxford Clay, Bletchley, Buckinghamshire, ×2.
Fig. 7. *'Serpula'* sp. Middle Oxford Clay, Stanton Harcourt, Oxfordshire, ×2.
Fig. 8. *Serpula sulcata.* Middle/Upper Oxford Clay boundary, Stanton Harcourt, Oxfordshire, ×2.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'*Serpula*' sp.
Plate 35, fig. 7

Description. Small, encrusting, meanderine serpulids. More slender than *S. sulcata*. Many show faint, longitudinal ridges.
Range. Most of the Oxford Clay.
Remarks. Occasionally found in the Lower Oxford Clay encrusting ammonite shells, wood, bones, and very rarely on belemnites. Common in the Middle Oxford Clay on belemnites and oysters.

Genus *GENICULARIA*
Genicularia vertebralis (J. de C. Sowerby)
Plate 35, fig. 4

Description. Straight or slightly curved tubular annelid. Shell elongate, sub-quadrate cross-section, regularly ornamented with smooth, globose bullae.
Range. Common in the *coronatum* and *athleta* Zones of the Lower Oxford Clay.
Remarks. Very common in the more calcareous parts of the Lower Oxford Clay, sometimes forming thin shell beds with the gastropod *Procerithium*.

ARTHROPODS
MALACOSTRACA

Malacostracan crustaceans were abundant in the Oxford Clay seas, and were fairly diverse. Unfortunately they are only well preserved at a few localities, and very little has been written on them in recent times; most of our knowledge coming from the work of Bate (1881), Woods (1891, 1922–29), Carter (1886), McCoy (1849), and Pearce (1841). The most recent account considers only the specialized decapod *Mecochirus* (Forster, 1971). There are two localities from which most of the best-known material has been collected; St Ives, Cambridgeshire, and Christian Malford, Wiltshire, but there is no longer any exposure at either site. Additional localities at which crustaceans have been reported include the Lower Oxford Clay of Peterborough and Calvert where they are common, and the Middle Oxford Clay of Scarborough and Weymouth.

The specimens from St Ives probably come from the top of the Upper Oxford Clay, but there is some doubt as to the precise stratigraphic position of the locality. They may be from the base of the Elsworth Rock. The specimens are preserved three-dimensionally in small phosphatic concretions. If these represent a remanie deposit, they may still be of Oxford Clay age, having been derived from the eroded top of the Oxford Clay proper. Only new exposures will resolve this problem. Most of the specimens represent shed portions of exoskeleton (exuviae). Christian Malford specimens are from the *athleta* Zone of the Lower Oxford Clay. They are highly crushed, but often are complete. A less well-known horizon yielding crustaceans was discovered by Callomon (1968) at the top of the *K. jason* Zone at Peterborough. Here it is possible to find complete specimens of the decapod *Mecochirus* still in its burrow system. This probably represents the only horizon currently available for the serious collecting of Oxford Clay malacostraca.

The following genera have been recognized by Carter (1886): *Eryon* 1 sp., *Eryma* 6 sp., *Glyphaea* 2 sp., *Magila* 3 sp., *Mecochirus* 2 sp., *Goniochirus* 1 sp., ?*Pseudastacus* 1 sp., and ?*Pagurus* 1 sp. For more complete diagnoses and taxonomy the reader is referred to the Treatise on Invertebrate Paleontology (Brooks *et al.*, 1969).

SPECIES DESCRIPTIONS

Class CRUSTACEA
Subclass MALACOSTRACA
Order DECAPODA
Suborder PLEOCYAMATA
Infraorder ANOMURA
Superfamily PAGUROIDEA
Family PAGURIDAE
Subfamily PAGURINAE
Genus *PAGURUS*
Pagurus sp.
Text-fig. 7.3h

Description. Robust chelae with few small tubercles posteriorly, many small circular pits anteriorly, pits in rows on dactylopodite.
Remarks. The validity of much of the Oxford Clay material assigned to this genus must remain suspect until a thorough review of the crustacean fauna is undertaken.

Subfamily uncertain
Genus *GONIOCHIRUS*
Goniochirus cristatus Carter
Text-fig. 7.3f

Description. Chela short with inflated external surface and flat internal surface. Ornamented with few small papillae.
Remarks. Poorly known decapod crustacean. Small fragments of claw and carapace common in phosphatic concretions from the Upper Oxford Clay.

Superfamily THALASSINOIDEA
Family AXIIDAE
Genus *MAGILA*
Magila dissimilis Carter
Text-fig. 7.3k

Description. Carapace weakly calcified with straight keels anteriorly. Highly serrated chelae, dactylopodite with two prominent serrations and faint ornamentation of small tubercles.

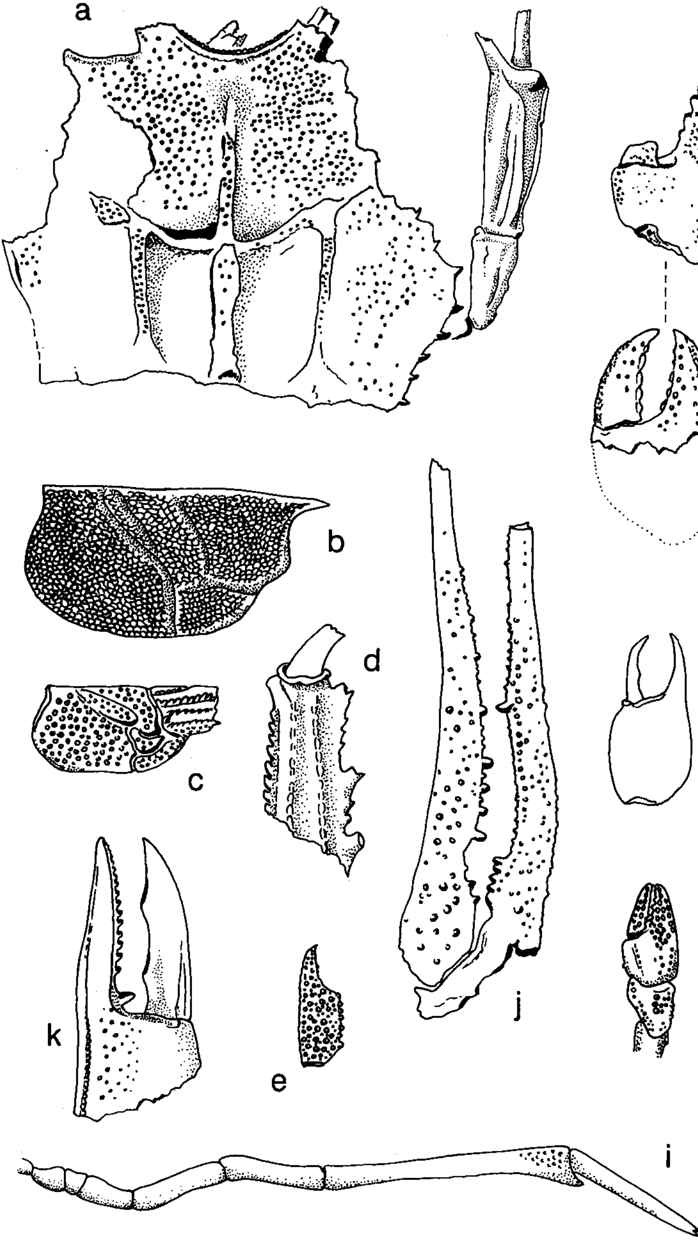
Magila levimana Carter
Text-fig. 7.3g

Description. Chelae smooth, not serrated, dactylopodite slender with single serration.

Infraorder PALINURA
Superfamily GLYPHEOIDEA
Family GLYPHEIDAE
Genus *GLYPHAEA*
Glyphaea rostrata Carter
Text-fig. 7.3c,d

Description. *Glyphaea* is characterized by a short carapace with short pointed rostrum, steeply inclined, and deep cervical groove.
Remarks. Two species are recorded from the Oxford Clay by Carter (*G. hispida* and *G. rostrata*), but Woods (1922–1929) considers them to be conspecific. Phillips (1871) figured a claw belonging to *Glyphaea* under the name *G. stricklandi* Bean.
Distribution. Upper Oxford Clay of Cambridgeshire, possibly Upper Oxford Clay of St Clement's, Oxfordshire.

TEXT-FIG. 7.3. Decapod crustacea from the Oxford Clay. **a**, *Eryon sublevis* Carter, carapace with right first propodite. ?Upper Oxford Clay, St Ives, Cambs., × 1. **b**, *Eryma mandelslohi* Meyer, carapace, ?Upper Oxford Clay, St Ives, Cambs., × 2. **c–d**, *Glyphaea* sp., carapace and distal portion of propodite, ?Upper Oxford Clay, St Ives, Cambs., **c** × 1, **d** × 2. **e**, ?*Pseudastacus serialis* Carter, propodite of first pair of limbs, possibly Lower Oxford Clay, Fletton, Cambs., × 1. **f**, *Goniochirus cristatus* Carter, ?Upper Oxford Clay, St Ives, Cambs., chelae of first pair of limbs, × 1. **g**, *Magila levimana* Carter, chelae of first pair of limbs, ?Upper Oxford Clay, St Ives, Cambs., × 2. **h**, *Pagurus* sp., portion of first limb, including chela, ?Upper Oxford Clay, St Ives, Cambs., × 1. **i**, *Mecochirus pearcei* M'Coy, first limb, Lower Oxford Clay, Christian Malford, Wiltshire, × 1. **j**, *Eryma* sp., dactylopodite and portion of fixed finger of first pair of limbs, ?Upper Oxford Clay, St Ives, Cambs., × 1. **k**, *Magila dissimilis* Carter, Chela of first pair of limbs, ?Upper Oxford Clay, St Ives, Cambs., × 3.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Family MECOCHIRIDAE
Genus *MECOCHIRUS*
Mecochirus pearcei Meloy
Text-fig. 7.3i, 7.4

Description. Decapod crustacean characterized by highly extended first periopods, and thin carapace with oblique cervical groove.
Remarks. Easily recognized by the very long periopods. Two species of *Mecochirus* are recorded from the Oxford Clay, *M. pearcei* (McCoy), and *M. socialis* (Meyer). Complete, but crushed specimens are relatively abundant at the top of the *jason* Zone at Peterborough. Also from Christian Malford, Calvert, and from a borehole in Kent (Lamplugh *et al.*, 1923).

Superfamily ERYONIDEA
Family ERYONIDAE
Genus *ERYON*
Eryon sublevis Carter
Text-fig. 7.3a

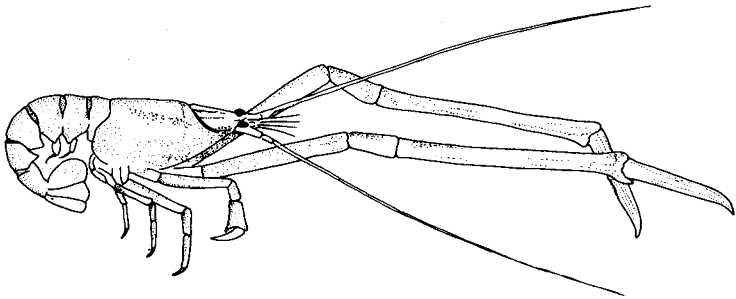
Description. Carapace broader than long, arched transversely. Frontal border emarginate with row of small tubercles. Postero-lateral margin inclined medially, with prominent spines.
Remarks. Very rare. So far only recorded from the ?Upper Oxford Clay of St Ives.

Infraorder ASTACIDEA
Family ERYMIDAE
Subfamily ERYMINAE
Genus *ERYMA*
Eryma mandelslohi von Meyer
Text-fig. 7.3b,j

Description. Cephalothorax longer than high, with prominent sulci. Ornamentation of closely packed pits with polygonal borders. Some fine tuberculations on cephalic and scapular portions.
Remarks. Carter lists some six species of *Eryma* from St Ives. He suggests that *E. mandelslohi* is the most abundant.

Family NEPHROPIDAE
Genus *PSEUDASTACUS*
Pseudastacus? *serialis* Carter
Text-fig. 7.3e

Description. Carapace granulate, with deep transverse groove and triangular rostrum. The first chelae are long and slender with elongate fingers.



TEXT-FIG. 7.4. Reconstruction of the decapod crustacean *Mecochirus* sp. Based on a figure in Brooks *et al.* (1969).

Remarks. Carter considered that two species from the Oxford Clay might be referable to *Pseudastacus*, but the affiliation remains uncertain.

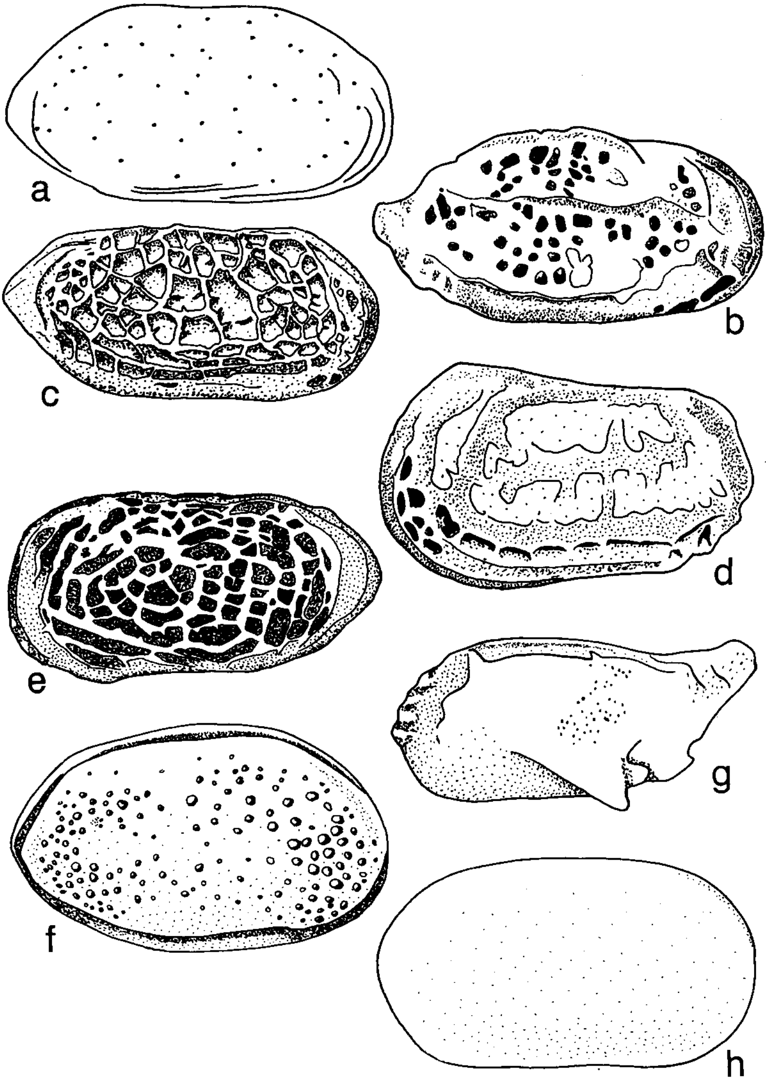
OSTRACODS

Ostracods are common in the Middle and Upper Oxford Clay, but are surprisingly infrequent in the Lower Oxford Clay. This might in part be due to reduced oxygen levels within the basin, or due to the soft nature of the substrate. Callovian and Oxfordian ostracod faunas have been examined by Whatley (1964, 1970), but most of the important work remains unpublished (Whatley, 1965).

A zonal scheme based on ostracod faunas has been erected for the British Upper Jurassic, but it is incomplete, and can only be applied in part to the Oxford Clay (Kilenyi, 1978). The top of the Lower Oxford Clay and the Middle Oxford Clay corresponds approximately to the *Lophocythere interrupta* biozone, while the Upper Oxford Clay appears to lie wholly within the *Nophocythere oxfordiana* biozone. An ostracod biozone has not been erected for the base of the Lower Oxford Clay. A small sample of forms recorded from the Oxford Clay of southern England is illustrated in text-fig. 7.5.

CIRRIPEDES

Cirripedes have been reported from the Oxford Clay of Christian Malford. Morris (1845) described and figured a remarkable specimen which he assigned to *Pollicipes concinnus*, in which several individuals are preserved with peduncles and articulated plates and are attached to



TEXT-FIG. 7.5. Ostracods of the Oxford Clay. Drawn from Kilenyi (1978). **a**, *Glabellacythere nuda* Wienholz, right valve, female, ×75. **b**, *Nophrecythere cruciata intermedia* (Lutze), right valve, male, ×95. **c**, *Lophocythere interrupta* Triebel, right valve, male, ×50. **d**, *Terquemula flexicosta lutzei* (Whatley), left valve, male, ×56. **e**, *Pseudoperissocytheridea parahieroglyphia* Whatley, left valve, ×115. **f**, *Praeschuleridea batei* Whatley, right valve, ×70. **g**, *Pedicythere anterodentina* Whatley, left valve, ×140. **h**, *Cytherella fullonica* (Jones & Sherborn), right valve, ×70.

an ammonite. He also describes a second species, *P. planulatus* based on isolated plates. Darwin (1851) included Morris' species in his now famous monograph on the fossil cirripedes of Great Britain. Darwin confirmed the cirripede nature of the specimens, and also commented on the exceptional preservation of the type specimen of *P. concinnus* Morris, although Darwin does say he was unable to see the original specimen, relying on a figure in Sowerby's mineral conchology (1815–1818, pl. 647). This species appears to be rare, there being no record of any new material since Morris' original description.

Class CIRRIPEDIA
Order THORACICA
Suborder LEPADOMORPHA
Family SCALPELLIDAE
Genus *POLLICIPES*
Pollicipes concinnus Morris
(not figured)

Description. Colonial, encrusting stalked cirripede. Peduncle may be more than twice length of capitulum. Capitulum composed of 18 or more plates. All umbones point apically. Lower latera arranged in whorls.
Range. Known only from the Oxford Clay of Christian Malford. The type and only specimen displays a group of several individuals of various sizes attached to an ammonite resembling *Peltoceras* sp., suggesting derivation from the upper part of the Lower Oxford Clay or the basal part of the Middle Oxford Clay.
Remarks. Known only from the type specimen. It might be worth looking for isolated capitular plates in micropalaeontological residues.

P. planulatus Morris
(not figured)

Remarks. This species is based on an isolated tergum figure by Morris (1845), also from the Oxford Clay of Christian Malford. Although Darwin (1851) also figured this species, he commented that the material described by Morris was of little value. The validity of this species is therefore in doubt.

ECHINODERMS

Echinoderms do not form an obviously important part of the Oxford Clay biota, but they may be locally abundant at some horizons.

Complete echinoids are frequently found in the Lamberti horizon in Oxfordshire, and complete ophiuroids were discovered by Duff (pers. comm.) in the Lower Oxford Clay of Stewartby, Bedfordshire. Holothurians are known from wheel-shaped spicules in the Upper Oxford Clay of Weymouth, Dorset, and were described by Hodson *et al.* (1956). Fragmentary portions of crinoid stems are common in the Middle and Upper Oxford Clay, but complete cups have only been reported rarely (Baily, 1860). The only recent systematic work of importance on Oxford Clay echinodermata is concerned with the ophiuroids (Hesse, 1964).

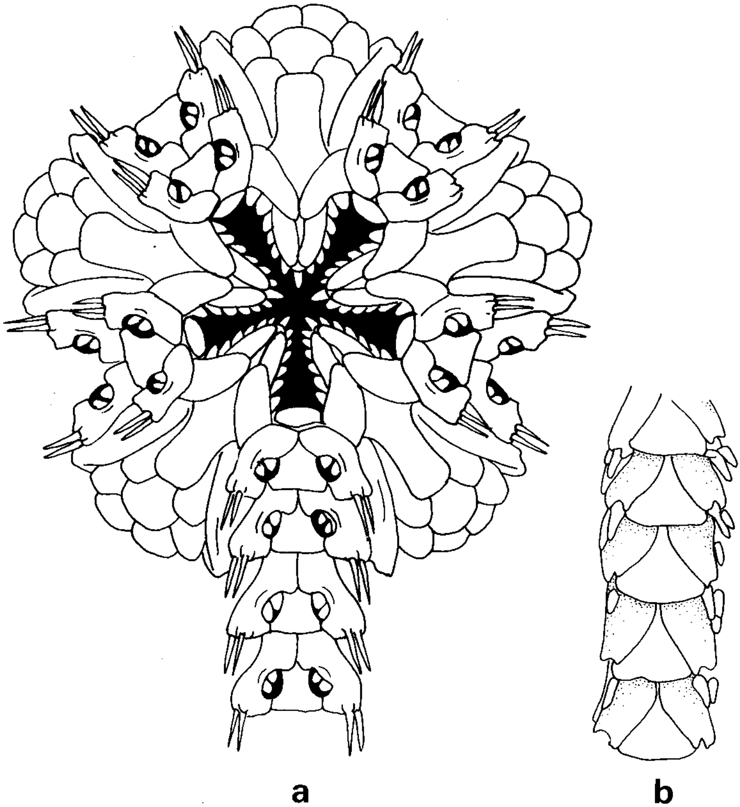
SPECIES DESCRIPTIONS

Class OPHIUROIDEA
Order OPHIUROIDA
Family OPHIURIDAE
Genus *OPHIOMUSIUM*
Ophiomusium weymouthiense (Damon)
Text-figs 7.6a, 7.7a

Description. Small ophiuroid with circular central disc. Five slender radial arms.
Remarks. Complete specimens are not common, but when found, often occur in abundance. Isolated ophiuroid vertebrae and plates can be common in micropalaeontological residues. Only certainly recorded from Weymouth (see Damon, 1844, 1880).

Family OPHIONEREIDIDAE
Genus *OPHIOCHITON*?
Ophiochiton? *pratti* (Forbes)
Text-fig. 7.6b

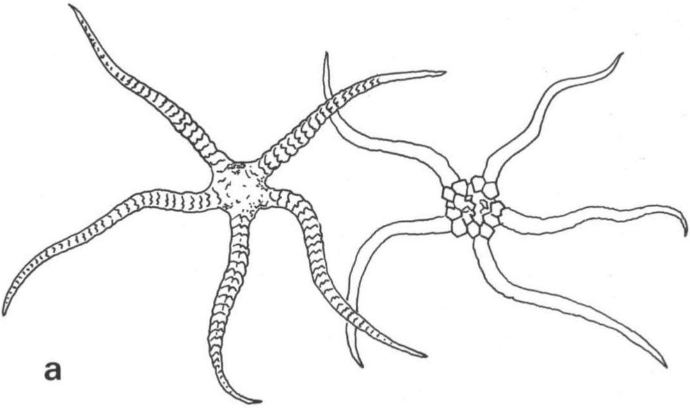
Remarks. A single specimen from the Lower Oxford Clay of Christian Malford, Wiltshire was described as *Amphiura pratti* by Forbes in 1844. Subsequently Hesse (1964) considered this specimen to probably be referable to *Ophiochiton*. *Ophiochiton* is a recent genus and assignment to this genus should be treated with caution.
Note. A small ophiuroid has been recorded from the Lower Oxford Clay of Bedfordshire, but this form appears to be distinct from both *Ophiomusium* and *Ophiochiton* (text-fig. 7.7b).



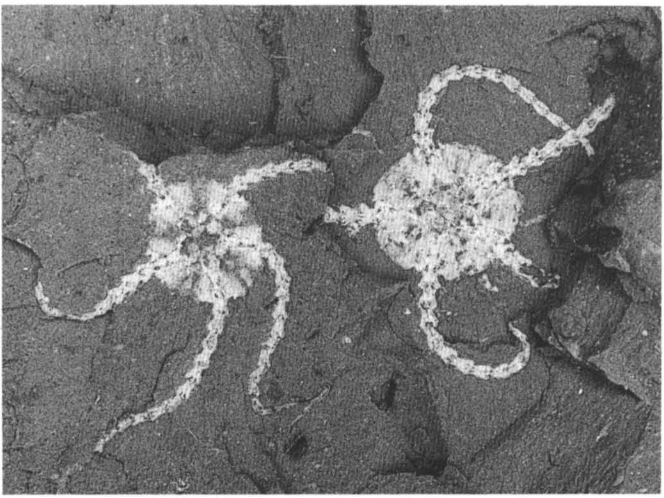
TEXT-FIG. 7.6. Ophiuroids from the Oxford Clay, based on figures in Hesse (1964). **a**, *Ophiomusium weymouthiense*, oral disc and vertebrae of arm, greatly magnified. **b**, *Ophiochiton*? *pratti*, vertebrae of arm.

Class CRINOIDEA
Subclass ARTICULATA
Order ISOCRINIDA
Family ISOCRINIDAE
Genus *ISOCRINUS*
Isocrinus fisheri (Forbes)
Plate 35, fig. 6

Description. Calyx small, five radial plates, five pentagonal brachial plates, each plate giving rise to two long rays. Rays repeatedly bifurcate. Stem slender, with pentagonal, petal-like columnar ossicles. A number of small cirri articulate with every eighth ossicle.



a



b

TEXT-FIG. 7.7. Ophiuroids from the Oxford Clay. **a**, *Ophiomusium weymouthiense*, entire test after Damon (1884). **b**, an undescribed species of ophiuroid from the Lower Oxford Clay of Bedfordshire. Approximately ×4.

Remarks. Originally described as coming from the Kimmeridge Clay, this was an error. Early accounts of this crinoid (Baily, 1860) suggest that it occurs in profusion on some bedding planes. Only recorded from Dorset, but isolated isocrinid cups and portions of stem from the Middle and Upper Oxford Clay may be referable to *I. fisheri*.

Class ECHINOIDEA

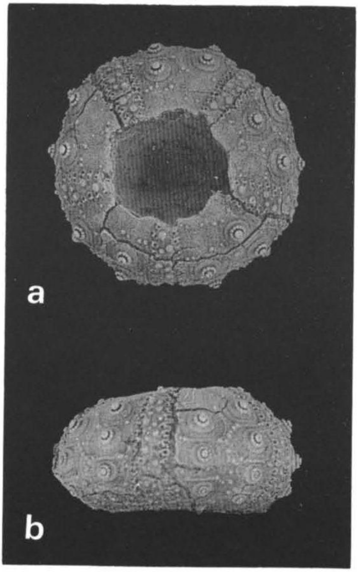
The echinoids of the Oxford Clay have received little attention, probably due to their rarity and generally poor state of preservation. Both regular and irregular echinoids have been reported, mostly from the Middle and Upper Oxford Clays. Isolated spines have been found in micropalaeontological residues from the Lower Oxford Clay. The preservation of echinoids is usually as flattened tests in shales or as pyrite internal moulds; neither style of preservation is helpful for accurate identification. Possibly for this reason, most Oxford Clay irregular echinoids have been referred to the relatively common Oxfordian genus *Collyrites*. New material from the *lamberti* Zone at Stanton Harcourt, which is three-dimensional, and has original shell preserved, indicate the presence of the genus *Disaster*.

Subclass EUECHINOIDEA
Order HOLASTEROIDA
Family DISASTERIDAE
Genus *DISASTER*
Disaster granulosus (Goldfuss)
Plate 35, figs 1, 3

Description. Small, irregular echinoid, usually less than three centimetres in length. Test squarely truncate posteriorly, ambulacral pores very small, but pores of ambulacrum III may be larger, genital 2 larger than other genital plates, posterior oculars separated from antero-apical system. Periproct oval, small, not in groove, and contiguous with oculars.
Range. From the *lamberti* Zone and possibly upper part of *athleta* Zone at Stanton Harcourt, Oxfordshire. Probably all the localities mentioned by Arkell (1947) as yielding *Collyrites*.
Remarks. For a review of the Disasteridae see Mintz (1968). Complete echinoids are rare in the Oxford Clay, but small tests of *Disaster* may be common at Stanton Harcourt, Oxfordshire.

Superorder DIADEMATACEA
Order DIADEMATOIDA
Family ASPIDODIADEMATIDAE
Genus *EOSALENIA*
Eosalenia sp. nov.
Text-fig. 7.8

Description. Small regular echinoid in which ambulacral plates are compounded triads, except adapically where they are arranged in diads.



TEXT-FIG. 7.8. *Eosalenia* sp. nov. An undescribed species rarely encountered in the Middle and Upper Oxford Clay. **a**, aboral view, **b**, lateral view. ×2.

Apical system large, but structure unknown. Primary tubercles crenulated.

Remarks. Well known from the Oxfordian of France, it is here reported for the first time in the UK. Several specimens from the Lamberti Horizon at Stanton Harcourt were obtained by N. Hollingworth and confirmed by A. Smith (pers. comm.). Small spines possibly belonging to this echinoid are frequent in micropalaeontological samples from most of the Oxford Clay.

Class HOLOTHURIDAE

Holothurian sclerites have been reported from the Upper Oxford Clay of Redcliff, near Weymouth, Dorset by Hodson *et al.* (1956), and are also known from the Upper Oxford Clay of Warboys, Cambridgeshire. Most have been assigned to form taxa, but some associated sclerites are known. It is suggested that most sclerites from the Oxford Clay are assigned to the genus *Theelia*. The sclerites are commonly wheel shaped with varying numbers of spokes, but anchor and rod shapes have also been described. A number of plate-like forms with perforations have also been doubtfully assigned to holothurians.

Family THEELIDAE
Genus *THEELIA*
Theelia wessexensis Hodson *et al.*

Description. Wheel-shaped sclerites with six or seven radially arranged spokes. Internal and external margins of wheel rim smooth. Usually circular outline but may appear slightly polygonal. Central hub boss-like on convex surface.

Remarks. The following form species of holothurians were also described and figured by Hodson *et al.*, 1956. Most probably belong to the same animal.

Family ACHISTRIDAE
Genus *ACHISTRUM*
A. issleri (Croneis)
A. gamma Hodson *et al.*
A. monochordata Hodson *et al.*
Text-fig. 7.9b

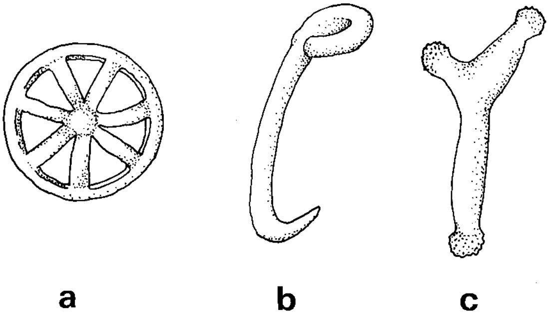
Family STICHOPTIDAE
Genus *RHABDOTITES*
R. divergens Hodson *et al.*
R. bifidus Hodson *et al.*
R. tridens Hodson *et al.*
Text-fig. 7.9c

TRACE FOSSILS

Trace fossils, including burrows, borings and coprolites are common at some levels within the Oxford Clay. Although trace fossils occur largely in the clay facies, and are less collectable than body fossils, some well-cemented sandstone lenses at the base of the Lower Oxford Clay in the Peterborough district have well-preserved trace fossil assemblages where the sandy sediment has filled burrows in the clays beneath.

Burrows of *Thalassinoides* are abundant in some parts of the Lower Oxford Clay, a particularly well-developed horizon occurring at the top of bed 10 (Callomon, 1968) at Peterborough. It is possible that most of these branching burrows were produced by *Mecochirus* sp. which may have remained hidden in its burrow, with its highly specialized, elongate peripods remaining poised for catching passing prey. Burrows attributable to *Ophiomorpha* can be found in the *jason* and *coronatum* Zones at Peterborough.

Petrological examination of the Lower Oxford Clay in early diagenetic concretions shows that much of the sediment was deposited as faecal



TEXT-FIG. 7.9. Isolated holothurian sclerites from the Upper Oxford Clay at Weymouth, Dorset. **a**, *Theelia* sp. **b**, *Achistrum* sp. **c**, *Rhabdotites* sp. Based on figures in Hodson *et al.* (1956). Approximately × 100.

pellets, sometimes called seston. It is not entirely clear whether the sediment was pelleted on the sea floor, or was pelleted in the water column by zooplankton. However, some pelletal material may be found within the camerae of ammonites, perhaps suggesting pellet formation took place at least in part on the sea floor. A lack of distinct lamination, even in the most organic and fissile parts of the Lower Oxford Clay indicates that considerable bioturbation took place. What is interesting is a general lack of easily recognizable trace fossils in the Lower Oxford Clay. This might be due to several factors, including complete bioturbation, lack of contrasting lithologies, and intense compaction. The more plastic Middle and Upper Oxford Clays are also highly bioturbated, but here burrows are often pyritized, especially around internal moulds of ammonites and large oysters. At least some of this bioturbation can be attributed to arthropods, but annelids, nematodes, bivalves and a host of other organisms must also be responsible.

An interesting aspect of the trace fossil assemblage in the Lower Oxford Clay is the general lack of unequivocal burrows of *Chondrites*. *Chondrites* burrows have been recorded from the Upper Oxford Clay at Warboys (Horton & Horrell, 1971), and Weymouth, Dorset.

Borings in hard substrates are common in the Lamberti Limestones at Stanton Harcourt, especially in the shells of large *Gryphaea* spp. Several distinct boring morphotypes occur, including elongate, sigmoidal borings parallel to the shell surface, small vertical borings and larger vertical borings (plate 34, fig. 4). Horton & Horrell (1971) recorded borings of *Lithophaga* in shells of large *Gryphaea* sp. from the Upper Oxford Clay at Warboys, Cambridgeshire. Micro-borings in shark teeth have been attributed to fungal activity by Martill (1989), and referred to the ichnotaxon *Mycelites enameloides*, after their apparent restriction to the enamel layer of the tooth.

Phosphatized coprolites are especially common in the Lower Oxford Clay in the Peterborough district. They are usually cylindrical, commonly with a diameter of between two and ten millimetres, and lengths of three to fifty millimetres. Larger, more irregular coprolites occur, and rarely contain small fish bones and cephalopod hooklets. Some specimens show evidence of activity by coprophagous organisms, perhaps echinoids. This usually takes the form of fine, almost straight scratch marks, but may also be in the form of a pelletized surface coprolite.

An unusual occurrence of circular lesions on the fin spines of the hybodont shark *Asteracanthus ornatissimus* was noted by Maisey (1978). These may represent areas of attachment by parasitic organisms of unknown affinities.

8. INTRODUCTION TO VERTEBRATE FOSSILS

by DAVID M. MARTILL

THE Oxford Clay is famous for the abundance and exceptional preservation of its vertebrate fauna. In the days when the Oxford Clay was dug manually for brick manufacture, many fine articulated skeletons of marine reptiles and fish were discovered (see Leeds, 1956). However, the earliest accounts go back to the construction of the Great Western railway near Christian Malford, Wiltshire (Egerton, 1843). These specimens were brought to the attention of a number of amateur collectors including Alfred Leeds and his brother Charles (Leeds, 1956). Between them they assembled one of the largest collections of fossil marine reptile skeletons ever brought together. Their collection is now dispersed around the world, but is still the most important assemblage of Middle Jurassic fish and marine reptiles known.

The following accounts are as comprehensive as can be within the scope of this guide, but emphasis is placed on the more easily recognized skeletal elements or those most commonly encountered: vertebrae and teeth.

Fine collections of vertebrates have recently been made from the Lower Oxford Clay; see Appendix 2. In particular, the London Brick Company's pits of the Peterborough district have been productive, especially at Dogsthorpe (TF 219019), Orton (TL 165937), and Yaxley (TL 178932) (Martill, 1985, 1988, 1989). In these pits clay is excavated by dragline which produces a considerable amount of spoil from which vertebrate remains weather out. Pits in the Whittlesey district employ shale planers which leave very clean faces and offer little opportunity for collecting. Occasionally however, drainage ditches in the bottoms of the pits are highly productive. Gravel pits in the Fens are often floored by Lower Oxford Clay and occasionally yield vertebrates, especially near Maxey (TF 135075). Other London Brick Company pits near Stewartby, Bedfordshire (TL 030420), Bletchley, Buckinghamshire (SP 855315) and Calvert, Buckinghamshire (SP 695234), also yield fragmentary vertebrates. Calvert Pit has recently (autumn 1989) yielded articulated skeletons of marine reptiles (Martill, 1990).

The famous locality of Christian Malford, Wiltshire (ST 956775), formerly yielded large numbers of articulated fish (Egerton, 1843) and a few reptiles, but there is no longer any exposure at this site. Coastal sections near Weymouth occasionally yield vertebrates but they are uncommon. The Oxford Clay of the Yorkshire coast has also yielded rare fish remains. Vertebrate remains have always been rare in the Middle and Upper Oxford Clay.

VERTEBRATE ABUNDANCE

Although vertebrate fossils are not ubiquitous in the Oxford Clay, their remains occur frequently in the Lower Oxford Clay around Peterborough, Bedford and Calvert. They also occur in the Lower Oxford Clay of Weymouth, and were widely reported from the Oxford Clay (presumably Lower Oxford Clay) of Christian Malford, Wiltshire. Martill (1985) demonstrated that in the Peterborough district articulated remains were concentrated in the lower parts of the succession, especially in the highly organic-rich parts of the *jason* Zone.

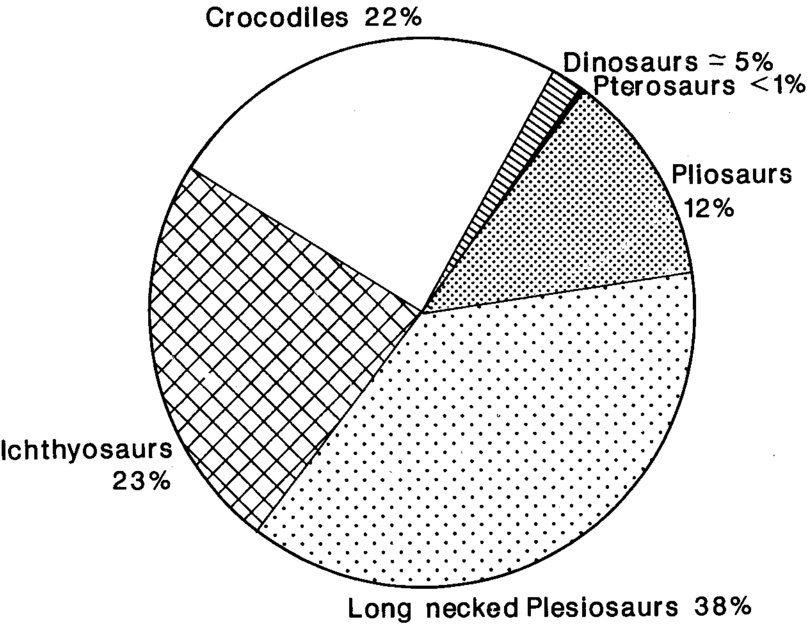
The remains of fish are probably the most common, especially as isolated elements in micropalaeontological residues. In some shell beds otoliths of actinopterygians may be concentrated with respect to other skeletal elements. However, fish remains are frequently overlooked due to their small size, and perhaps because they are frequently disarticulated. Reptile remains on the other hand are frequently large, where isolated limb bones may be several tens of centimetres long. Such remains are easily recognized, and in several years of collecting I have discovered many more skeletons of marine reptiles than I have fish.

It is difficult to accurately assess the true abundance of individual taxa within the vertebrate palaeocommunity. Problems arise in determining the best way to count remains, and also in determining the longevity of individual taxa. An attempt to assess the relative abundance of the major reptile groups is given in text-fig. 8.1.

PRESERVATION OF THE VERTEBRATE FAUNA

Vertebrates have been found in all of the facies types represented in the Oxford Clay, but the style of preservation varies according to the facies in which they occur. Two main factors control preservation. The post-death, pre-burial environment determines the state of the carcass when it reaches the sea floor, and may determine the way in which it is scavenged or decomposed. The post-burial environment controls the physical and chemical processes of fossilization.

A few vertebrate fossils are produced during the life of an individual. The teeth of fish and reptiles are shed at frequent intervals; in the case of some large sharks it is estimated that a tooth is shed each day. Many



TEXT-FIG. 8.1. Relative abundance of Oxford Clay marine reptiles in museum collections. Original data set represents over one thousand accessions. After Martill (1986).

isolated teeth show large wear facets, indicating that the tooth was shed as it no longer performed well in the jaw. Fish-eating vertebrates also drop faecal pellets rich in phosphate from dissolved fish bone. These have a high preservation potential as the dissolved phosphate rapidly precipitates to lithify the faecal pellet. Such coprolites are abundant in the Lower Oxford Clay, and may contain small fish remains or cephalopod hooklets.

Post-death, pre-burial environment. The time between death and burial is a crucial episode in the fossilization process. This is when scavenging and break up of the carcass takes place, and when microbial breakdown of the soft tissues occurs. Exposure of the skeleton due to biodegradation also renders the carcass vulnerable to disarticulation by current activity. Many of the larger marine reptiles from the Lower Oxford Clay are disarticulated due to intense scavenger activity, probably from large hybodont sharks, the teeth of which are often found close to reptile skeletons. Isolated bones are also common, these probably have fallen from rotting carcasses floating at the surface.

Post-burial environment. After burial of a skeleton (articulated or disarticulated) diagenetic processes occurring within the sediment begin to take place in and around the bones. In many cases the first process is the formation of a thin layer of pyrite (FeS_2) on the outer surface of the bone and lining many cavities within it. After the initial phase of mineralization there is commonly a second phase in which non-ferroan calcite is precipitated. In some cases this forms a concretion around the bone, but it may also form in cavities within the bone as a discrete layer on top of the pyrite. If the calcite does not completely fill the cavity another layer of pyrite sometimes forms followed by a later ferroan calcite. Later still small crystals of sphalerite and baryte can form, the latter being rather rare. Usually the first pyrite to precipitate fills most of the cavities and prevents the bone from compacting under the weight of sediment. However many bones are apparently 'watertight', and are not filled with minerals in the initial stages of burial. Such bones are usually crushed flat and extensively fractured. They then become filled with ferroan calcite only. Very occasionally bones that have no internal mineralization are found in concretions and are able to resist compaction. Unfortunately the Oxford Clay concretions are extremely hard and it is very difficult to extract the bones without damaging them.

Pyrite in the Lower Oxford Clay is only metastable at normal room temperatures and humidities. Any heavily pyritized specimens should be kept dry and in a stable environment. They may then last for several tens of years before any serious deterioration is observed. It may be necessary to seek expert advice if pyrite rot threatens a rare or valuable specimen.

COLLECTING OXFORD CLAY VERTEBRATES

The diverse nature of the Oxford Clay vertebrate fauna necessitates the adoption of a number of collecting strategies according to the type of fossil sought. A number of methods have been successful over the past few years in the Peterborough district.

Phosphatic and calcareous micro-vertebrates. Bulk sampling of the Oxford Clay for micro-fossils will usually yield a few isolated teeth and scales. However in some shell beds natural winnowing has concentrated the micro-vertebrates by a factor of one hundred. In particular a shell bed at the junction of the *jason* and *coronatum* zones is rich in micro-vertebrates. Collect several kilograms of shell bed and break down manually in a bucket of warm water. Pass this through a coarse sieve to remove belemnites, larger shells and wood. The coarse residue can then be passed through a 5 mm sieve. This residue may contain the occasional large tooth or otolith, so check it before throwing it away. Now pass the sample that passed through the 5 mm sieve through a 250 micron sieve. This is where you lose all the clay material down the drain. The remaining residue will contain a large proportion of comminuted shell material and micro-vertebrates, and will appear whitish-grey. Inspect this for otoliths and collect them. Now place the residue in a bath of 10% acetic acid for an hour or until most of the shell debris has dissolved. The residue will be very much reduced in volume, but will contain an abundance of micro-vertebrates and a considerable portion of pyritised shell material. Picking of the micro-vertebrates can be made even easier by repeatedly swishing the residue around in an evaporating basin. Pyrite should go to the bottom at the centre and the micro-vertebrates lie over the pyrite. The micro-vertebrates can then be pipetted out. I do not recommend separation in heavy liquids as most of the cheaper liquids are highly carcinogenic. Ward (1981) gives an excellent method for bulk processing of silts and clays for micro-vertebrates.

Complete marine reptiles. It is still possible to collect reasonably complete skeletons of marine reptiles. Finding them can be difficult, but the task is made easier by observing the following procedures.

1. Examine all concretions lying around the floor of the pit and on spoil dumps.
2. If one of these concretions contains part of an articulated skeleton examine the floor of the pit for an area where the excavator has gone too deep. At Peterborough the digger operators try to avoid digging up the concretions.
3. Look around the hole for bone shards. These weather yellow after only a few weeks' exposure.
4. If bone fragments occur, follow the drag marks made by the bucket of the drag line until they pass close to one of the holes where a concretion has been removed.
5. Get on your hands and knees and examine every surface available. You may have to bail water out of the holes in wet summers.

While this does not guarantee success, it offers the best opportunity for a short visit. On longer visits to the pits I simply take an organized walk across the floor of the pit so that I cover all of the newly exposed beds.

Isolated bones not in situ. The spoil dumps in the bottom of the pit usually comprise a mixture of clay and old bricks from the top of the pit, and dark blue/grey clay from the base of the pit. Spoil dumps of this latter material frequently yield fragmentary skeletons after weathering.

9. FISH

by DAVID M. MARTILL

FISH remains are abundant in the Lower Oxford Clay, though they are often fragmentary. The more resistant elements such as teeth, scales and the fin spines of elasmobranchs occur most frequently. Articulated remains are less common, mainly due to the break up of the clay by mechanical diggers. Fine articulated specimens can sometimes be obtained in the basal paper shales of the Lower Oxford Clay, and also in some of the larger septarian concretions. Only isolated fragments have been found in the Middle and Upper Oxford Clay, where they are relatively scarce.

The fish fauna was extensively studied by Woodward during the latter part of the last century and the beginning of this century (Woodward, 1886, 1888, 1889, 1890, 1892a,b, 1896, 1897, 1928, 1929), but was largely ignored until the 1970s. More recently, isolated discoveries receive attention as and when they are made (Ward & McNamara, 1977; Martill, 1989; Thies, 1983).

A number of fish have elaborate dentitions for specialized diets. These teeth can be diagnostically useful, and many elasmobranch taxa are based solely on dentitions. This has of course led to problems as many fish have distinct teeth in different parts of the jaw, and so several species based on isolated teeth may later prove to be from a single taxon. The classification here follows Thies (1983), Maisey (1975) and Patterson (1965).

Class CHONDRICHTHYES

The class Chondrichthyes are the cartilaginous fish, and include the sharks, skates, rays and chimaeras. These fishes frequently shed large numbers of highly resistant teeth during their life span, and as such are relatively common finds. A number of sharks have elaborate fin and head spines which are frequently well preserved. Micropalaeontological residues commonly contain small neoselachian teeth and a variety of dermal denticles.

Subclass ELASMOBRANCHII
Order HYBODONTIFORMES
Family HYBODONTIDAE
Genus *HYBODUS*
Hybodus obtusus Agassiz
Plate 36, figs 1, 5, 8

Description. Trunk fusiform and elongate, two dorsal fins each preceded by a single elaborate fin spine. Fin spines with longitudinal grooves and

ridges laterally, and two medial rows of posterior denticles. Anterior fin spine larger than posterior. Teeth conical to multicuspidate with larger central cusp, cusps moderately striated. Dermal denticles low domes with prominent ribbing.
Range. Found throughout the Oxford Clay from Weymouth to Scarborough.
Remarks. Isolated teeth of *Hybodus* are frequently found associated with large marine reptile skeletons and suggest that the sharks may have been scavengers.

Hybodus dawni Martill
Plate 36, fig. 3

Description. *Hybodus* in which the dorsal fin spines are coarsely ribbed.
Range. Known only from the Lower Oxford Clay of Peterborough.
Remarks. Only a single dorsal fin spine of this highly distinct species is known.

Genus *ASTERACANTHUS*
Asteracanthus ornatissimus Agassiz
Plate 36, figs 2, 4, 9, Plate 37, fig. 4

Description. Hybodont shark in which the dorsal fins are preceded by a single large fin spine. Fin spines highly ornamented with lateral stellate tubercles in rows, sometimes fusing to form ridges apically. Posterior margin with two rows of hooked denticles medially, often alternating. Base of fin spine lacking ornamentation, highly fibrous. Cephalic spines smooth with lateral keels and hooked extremity, placed anteriorly on

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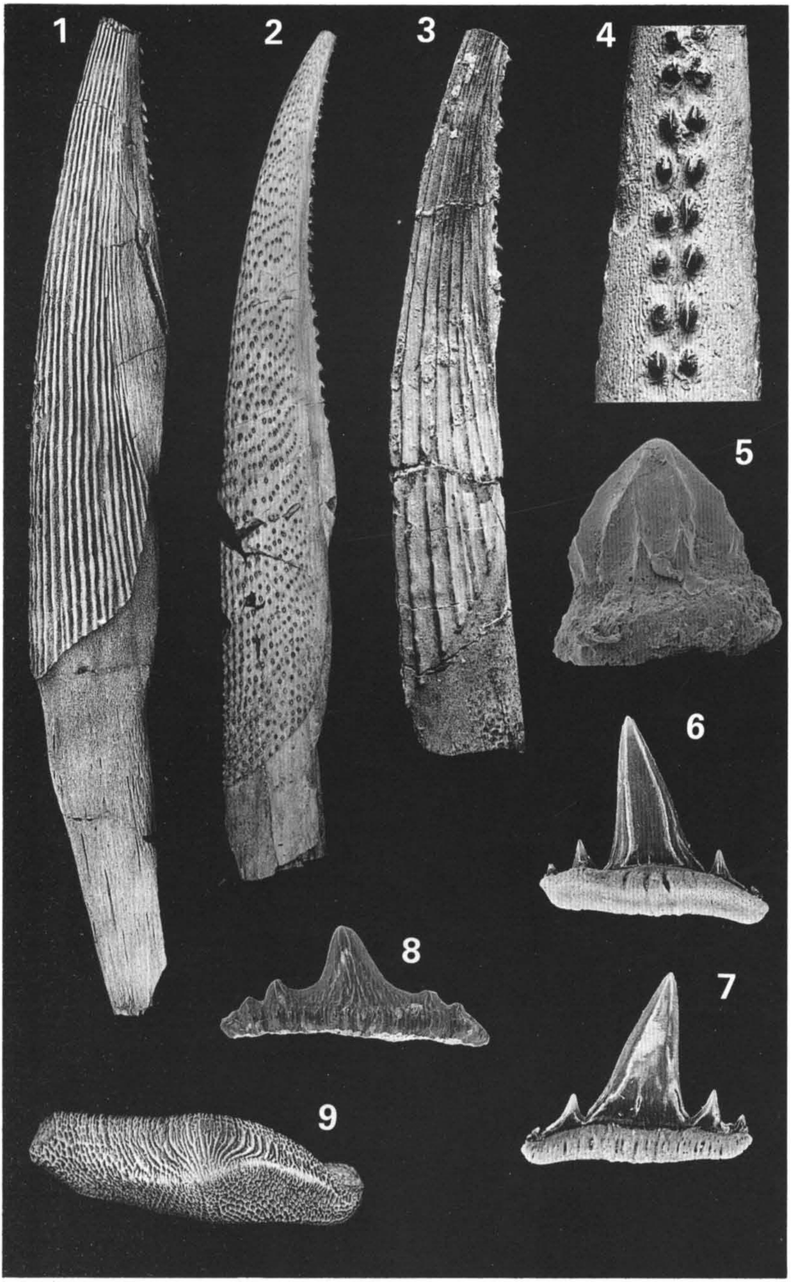
EXPLANATION OF PLATE 36

Fig. 1. *Hybodus obtusus*, dorsal fin spine. Lower Oxford Clay, Peterborough, ×0·5.
Fig. 2. *Asteracanthus ornatissimus*, dorsal fin spine, Lower Oxford Clay, Peterborough, approximately ×0·5.
Fig. 3. *Hybodus dawni*, dorsal fin spine, Lower Oxford Clay, Peterborough, approximately ×0·75.
Fig. 4. Posterior margin of *Asteracanthus ornatissimus* dorsal fin spine, ×1.
Fig. 5. Dermal denticle of hybodont shark, ×20.
Fig. 6a,b. *Sphenodus longidens*, tooth, Middle Oxford Clay, Woodham, Buckinghamshire, a, lingual view, b, labial view, both ×2.
Fig. 7. *Hybodus obtusus*, tooth, labial view, Lower Oxford Clay, Peterborough, ×1·2.
Fig. 8. *Asteracanthus ornatissimus*, tooth in occlusal view, Lower Oxford Clay, Peterborough, ×1.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triradiate base. Teeth dorso-ventrally compressed, sub-quadrate anteriorly, becoming arcuate posteriorly, median axial ridge, frequently with worn surface, from which radiate fine striations, oral surface reticulate.
Range. Lower to Upper Oxford Clay. Also known from Kimmeridge Clay.
Remarks. *Asteracanthus* is probably the most common macrovertebrate found in the Oxford Clay.

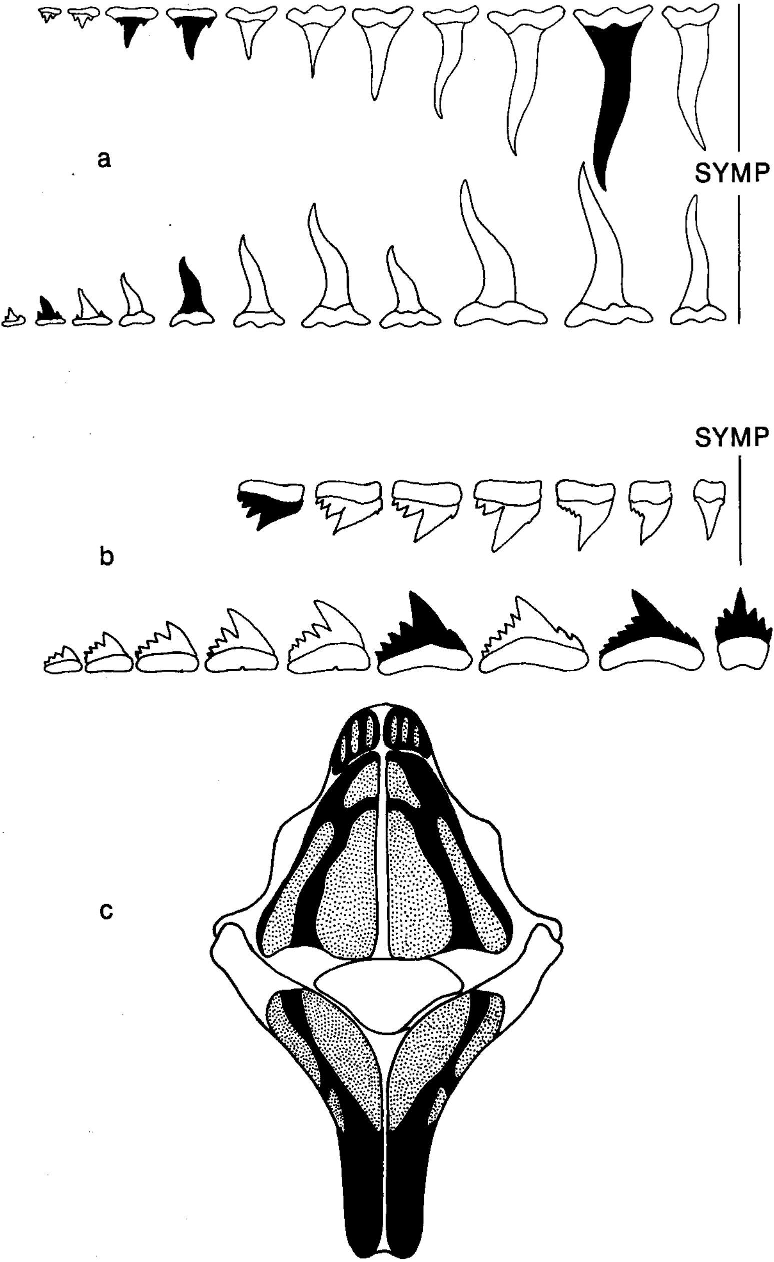
Asteracanthus acutus Agassiz
Text-fig. 9.2

Description. Dorsal fin spines of hybodont type characterized by lateral ornament comprising both vertical ribbing and tubercles.
Remarks. The holotype of this species was originally held in the collections of the Bedford Museum, but is now lost. Agassiz (1837–44) records the locality as Castle Mills, east of Bedford. The holotype, and possibly only record of this specimen was found in 'clays above the Cornbrash'. This might be interpreted as Kellaways Clay or the base of the Lower Oxford Clay. Many specimens of *A. ornatissimus* show some faint ribbing on the lateral margins of the fin spine (Martill, 1989; pl. 1, fig. c), thus *A. acutus* may simply be an extreme variant of *A. ornatissimus*.

Superorder SQUALOMORPHII
Order HEXANCHIFORMES
Suborder HEXANCHOIDEI
Family HEXANCHIDAE
Genus *NOTIDANUS*
Notidanus muensteri Agassiz
Plate 38, fig. 4

Description. Teeth laterally compressed, multicuspidate, lateral teeth with anterior cusp usually larger, but sometimes with small subsidiary cusp anterior to the highest cusp. Cusps generally inclined posteriorly. Root long, laterally compressed, blade-like. Symphysial teeth bilaterally symmetrical.
Range. Lower to Upper Oxford Clay. Recorded over most of the outcrop.
Remarks. *Notidanus* is a form-genus for laterally compressed multicuspidate teeth from hexanchid sharks. Three other species of *Notidanus*

TEXT-FIG. 9.1. Dental variation in Oxford Clay chondrichthyan fishes. **a**, *Sphenodus*, shaded teeth represent forms recorded from the Oxford Clay. **b**, *Notidanus*, the shaded teeth have been recorded from the Oxford Clay and described a distinct species. **c**, Upper and lower dental plates of a chimaera. **a** and **b** based on Schweizer (1964), **c** after Kemp (1984).


a
SYMP
SYMP
b
c

have been described from the Oxford Clay, but the great variability of shark teeth within a single jaw suggests that the teeth may all be from the same taxon, but from different parts of the jaws. The other taxa described are *N. serratus* Fraas, 1855, and *N. daviesi* Woodward, 1886.

Order SQUALIFORMES
Family PROTOSPINACIDAE
Genus *PROTOSPINAX*
Protospinax muftius Thies
Plate 38, fig. 7

Description. Small selachians with reduced dorsal fin spines, teeth with well developed median cusps, two or three lateral cusps developed.
Range. Isolated teeth known only from the Lower Oxford Clay of Bedfordshire and Cambridgeshire. Complete fully articulated specimens of *Protospinax* are well known from the Solnhofen Limestone of Bavaria, West Germany.
Remarks. Only found in residues prepared for micropalaeontological study.

Superorder GALEOMORPHI
Order HETERODONTIFORMES
Family HETERODONTIDAE
Genus *PARACESTRACION*
Paracestracion falcifer Wagner
Plate 39, fig. 5

Description. Finspines up to 8 cm high with lateral tubercles. Smooth enamel cap with irregular lower margin and faint horizontal striae. Anterior margin acute, posterior margin obtuse.
Range. *Paracestracion* is known from the Lower Oxford Clay to the Kimmeridge Clay, but only a single specimen has been collected from the Lower Oxford Clay to date.
Remarks. A lack of articulated material from the Lower Oxford Clay leaves the taxonomy of its small shark teeth in some doubt. It is highly

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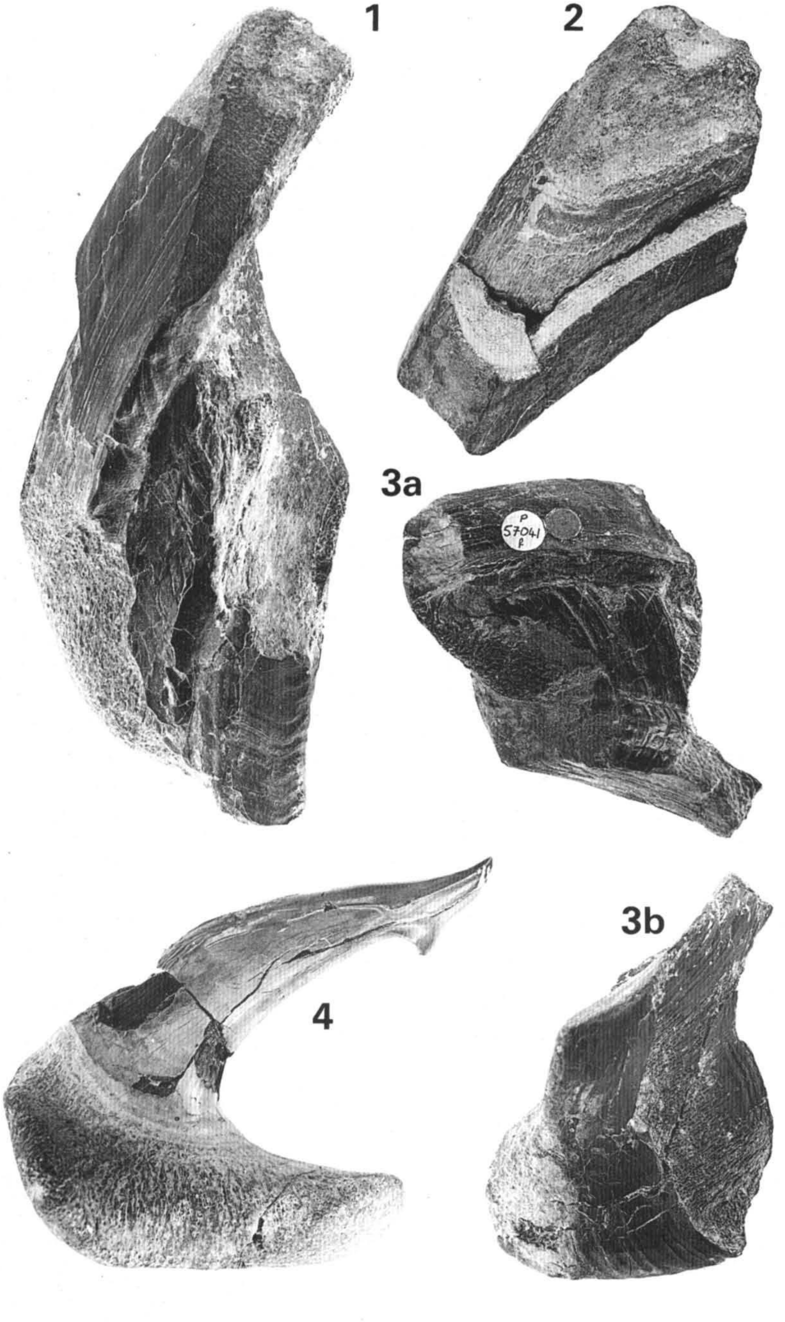
EXPLANATION OF PLATE 37

Fig. 1. *Brachymylus altidens*, right mandibular plate, Lower Oxford Clay, Peterborough, × 1.
Fig. 2. *Pachymylus leedsi*, right palatine plate, Lower Oxford Clay, Peterborough, × 0·8.
Fig. 3a,b. *Brachymylus altidens*, left vomerine plate, Lower Oxford Clay, Peterborough, a, oral surface, b, wear surface, both × 1.
Fig. 4. *Asteracanthus ornatissimus*, cephalic spine, Lower Oxford Clay, Peterborough, × 0·75.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3b
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likely that teeth referred to *Heterodontus* sp. are congeneric with *Paracestracion* (see below).

Genus *HETERODONTUS*
Heterodontus sp.
Plate 38, figs 1, 2

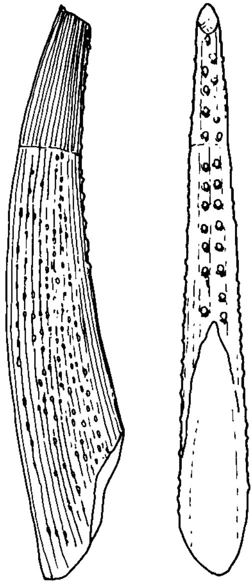
Description. Teeth with anteriorly sloping crown, becoming multicuspidate posteriorly, usually with a large median cusp flanked by one to three smaller lateral cusps. Occlusal crest on median and lateral cusps. Prominent basal flange.
Range. Only recorded from micropalaeontological preparations from the Lower Oxford Clay of Peterborough and Bedford.
Remarks. See *Paracestracion* above.

Order ORECTOLOBIFORMES
Family BRACHILURIDAE
Genus *PALAEOBRACHAELURUS*
Palaeobrachaelurus bedfordensis Thies
(not figured)

Description. Teeth with mesiodistal primary cusp. Pronounced basal projection of crown labially. Hemiaulacorhize root.
Range. Known only from the Lower Oxford Clay of Bedfordshire and Buckinghamshire.
Remarks. Very abundant in residues prepared for micro-vertebrate examination.

Family *INCERTAE SEDIS*
Genus *ORECTOLOBOIDES*
Orectoloboides pattersoni Thies
Plate 38, fig. 5

Description. Teeth small, crown with well developed median cusp and smaller lateral cusps. Strong median ribs on labial surface of all cusps. Root hemiaulacorhize, frequently with two medio-internal foramina. Labial-basal crown projection tongue shaped.
Range. *Orectoloboides pattersoni* is the earliest record of a genus known previously only from the Barremian to Cenomanian.
Remarks. Relatively common in micro-vertebrate residues from Peterborough and Bedford. This taxon is easily distinguished from other micro-shark teeth by the distinctive projections on the labial surface of the cusps.



TEXT-FIG. 9.2. Dorsal fin spine of *Asteracanthus acutus* Ag. Probably Lower Oxford Clay of Bedfordshire. Based on a figure in Agassiz (1837–1844). Approximately ×0·75.

Family ORTHACODONTIDAE
Genus *SPHENODUS*
Sphenodus longidens (Agassiz)
Plate 36, fig. 6, 7

Description. Relatively large (commonly up to 3 cm high), antero-posteriorly compressed, erect, slender teeth, placed centrally on anterior margin of horizontally expanded root.
Range. A specimen from Peterborough, Cambridgeshire, is probably from the Lower Oxford Clay. Definitely known from the Middle Oxford Clay of Woodham, Buckinghamshire.

Superorder BATOIDEA
Order RAJIFORMES
Suborder RHINOBATOIDEI
Family RHINOBATIDAE
Genus *SPATHOBATIS*
Spathobatis werneri Thies
Plate 38, fig. 3

Description. Small teeth, wider than long, with lingual and labial basal crown projections. Strong occlusal crest. Root holaulacorhize. Arc shaped in apical view with more or less definite indentation in place of crown tip.

Range. Known only from micro-vertebrate residues from the Lower Oxford Clay of Bedfordshire and Cambridgeshire.

Remarks. If the assignment of these teeth to the rays is correct they are amongst the oldest known of the order.

Subclass HOLOCEPHALI
Order CHIMAERIFORMES
Suborder CHIMAEROIDEI
Family CHIMAERIDAE

Chimaeras or rabbit fish are chondrichthyans with a short rounded snout. Diphycercal tail. Anterior dorsal fin preceded by slender fin spine, above large pectorals. Living taxa have a poison gland connected to the fin spine. Posterior dorsal fin low, elongate, extending from just behind anterior dorsal fin to a position anterior to tail fin. All have elaborate crushing dentitions.

Genus *ISCHYODUS*
Ischyodus egertoni (Buckland)
Plate 38, fig. 6

Description. Mandibular dental plate with narrow symphysis, external thickening along oral margin. Oral margin deeply sinuous. Palatine dental plate with four tritors, two median, one inner, one outer.

Range. Known from the Lower Oxford Clay of Peterborough, and probably the Middle Oxford Clay of Oxfordshire. Also recorded from the Kimmeridge Clay of Weymouth, Dorset, and Boulogne, France.

EXPLANATION OF PLATE 38

Figs 1, 2. *Heterodontus* sp., 1, tooth in lingual view, 2, tooth in oblique view, Lower Oxford Clay, Peterborough, × 30.

Fig. 3. *Spathobatis werneri*, tooth, occlusal view, Lower Oxford Clay, Peterborough, × 30.

Fig. 4. *Notidanus muensteri*, tooth, Lower Oxford Clay, Peterborough, × 1·2.

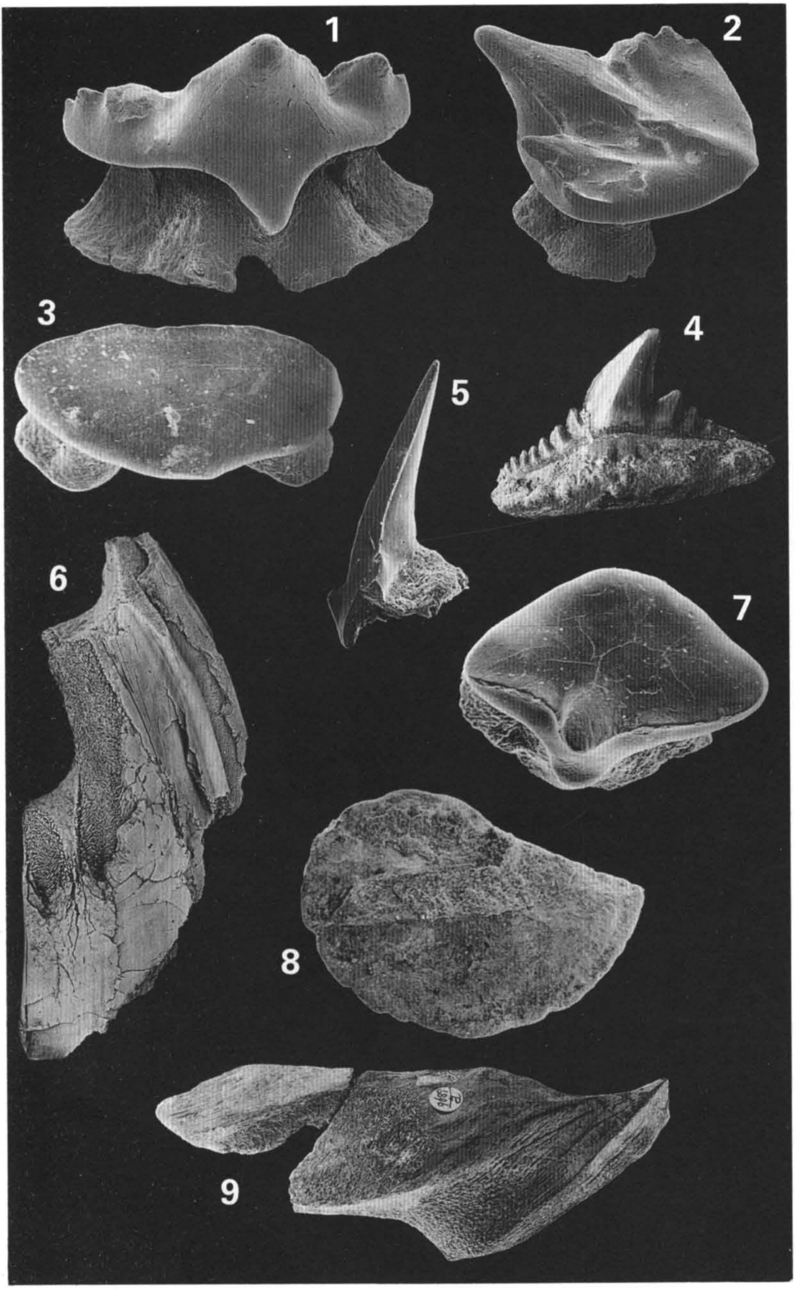
Fig. 5. *Orectoloboides pattersoni*, ?symphisial tooth, lateral view, Lower Oxford Clay, Peterborough, × 30.

Fig. 6. *Ischyodus egertoni*, left mandibular dental plate, occlusal surface, Lower Oxford Clay, Peterborough, × 1.

Fig. 7. *?Protospinax* sp., tooth, occlusal view, Lower Oxford Clay, Peterborough, × 30.

Fig. 8. Otolith of indeterminate actinopterygian, Lower Oxford Clay, Peterborough, × 10.

Fig. 9. *Ischyodus beaumonti*, right mandibular dental plate, occlusal view, Lower Oxford Clay, Peterborough, × 0·5.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Ischyodus beaumonti Egerton
Plate 38, fig. 9

Description. Palatine dental plate with posterior inner tritor large, median tritor not extending anteriorly as far. Outer tritor elongate.
Range. Known from the Lower Oxford Clay of Peterborough and the Kimmeridge Clay of Weymouth, Dorset, and Boulogne, France.

Family CALLORHYNCHIDAE

Chimaeras with flexible, hook-like, elongated snout in living forms. First dorsal fin high, preceded by high, slender spine projecting beyond tip of fin. Posterior dorsal fin just posterior to pelvic fins, moderately high.

Genus *BRACHYMYLUS*

Brachymylus altidens Woodward
Plate 37, figs 1, 3a,b

Description. Mandibular plate with sub-quadrate outline, laterally compressed. Oral surface with three tritoral areas arising from single body of tritoral dentine. Post oral border parallel to symphysial border. Oral border between posterior outer and symphysial tritors. Median tritor occupies posterior half of oral surface only. Inner surface excavated to expose compact base of tritoral dentine.
Range. Known only from the Lower Oxford Clay of Peterborough.

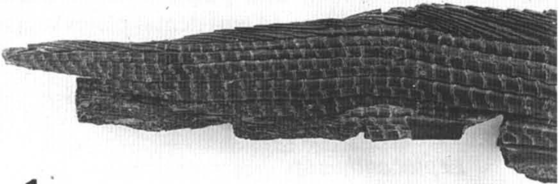
Genus *PACHYMYLUS*

Pachymylus leedsi Woodward
Plate 37, fig. 2

Description. Dental plates large. Mandibular plate with prominent beaks, median tritors narrow, posterior outer tritor divided into three small areas. Palatine plate with sharp blade like edge, median tritor occupying one-third width of plate.
Range. Known only from the Lower Oxford Clay of Peterborough.

EXPLANATION OF PLATE 39

Fig. 1. *Caturus* cf. *porteri*, fin rays, Lower Oxford Clay, Peterborough. Approximately ×1.
Fig. 2. *Hypsocormus tenuirostris*, jaws with caniniform teeth, Lower Oxford Clay, Peterborough, ×0·5.
Fig. 3. *Heterostrophus phillipsi*, almost complete skeleton lacking only caudal fin, Lower Oxford Clay, Chickerell, Dorset, ×0·75.
Fig. 4. *Leptacanthus* sp., dorsal fin spine, Lower Oxford Clay, Peterborough. Approximately ×0·5.
Fig. 5. *Paracestracion falcifer*, dorsal fin spine, Lower Oxford Clay, Peterborough, ×1.



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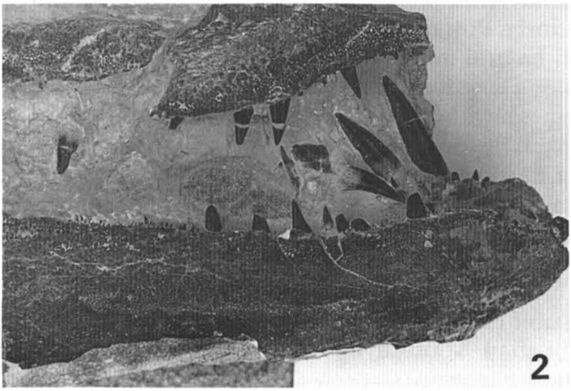

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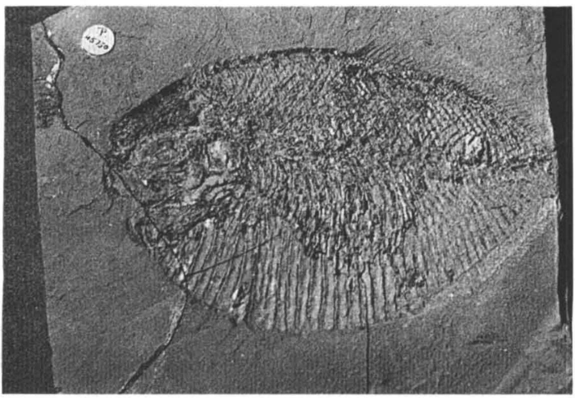

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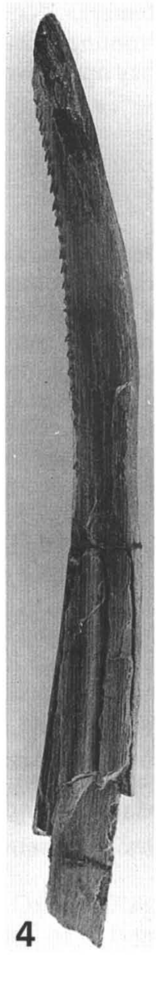

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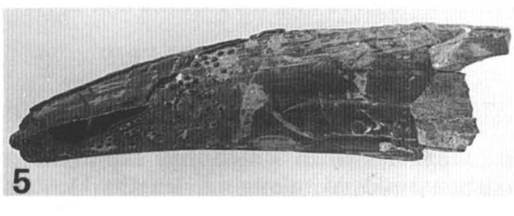

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Remarks. Known only from mandibular and palatine dental plates. Prominent beaks of large mandibular (up to 14 cm) dental plates suggest they may have been used for prising molluscs from the sea floor.

Family *INCERTAE SEDIS*
Genus *LEPTACANTHUS*
Leptacanthus sp.
Plate 39, fig. 4

Description. Long slender finspines with triangular cross section, apex of triangle points anteriorly. Posterior margin ornamented with single row of hooked denticles. Lateral margins of finspine smooth, or with faint striations running along length of spine.
Range. Chimaera spines have been recorded from the Lower Oxford Clay of Christian Malford, Wiltshire, and Peterborough, Cambridgeshire.
Remarks. Chimaera finspines have not yet been found in association with dental plates in the Lower Oxford Clay. It is most likely that finspines called *Leptacanthus* belong to one of the genera known by dental plates. A single complete chimaeroid (*Ischyodus*) was described by Woodward (1892), but this specimen is now lost.

A fin spine of possible chimaeroid affinities is known from the Lower Oxford Clay of Christian Malford in which there are two rows of denticles on the posterior margin.

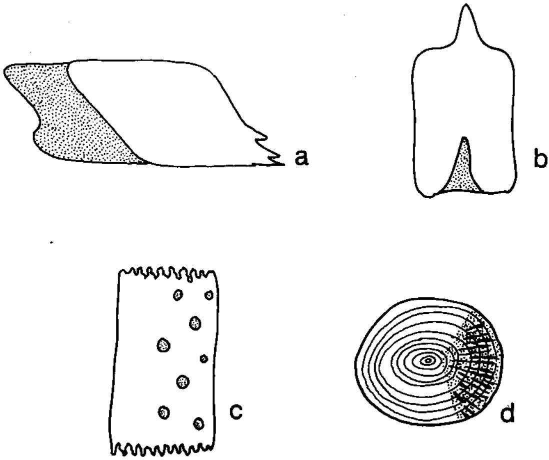
Chimaera finspines are extremely rare in the Oxford Clay. The rarity may be a true reflection of their abundance compared to the number of dental plates found. Unlike selachians, chimaeras do not shed their dental plates. An individual will produce six dental plates in its lifetime, but only one finspine. If finspines are only found in males, then the relative abundance of spines to dental plates will again be reduced.

Class OSTEICHTHYES
Subclass ACTINOPTERYGIA
Family PALAEONISCIDAE

Palaeoniscids are actinopterygian fishes with enamel coated scales, anteriorly placed orbits and a maxilla with a narrow, elongate anterior process. Palaeoniscids were the dominant fishes during the Upper Palaeozoic, but most groups became extinct at the end of the Triassic. Only a few genera survived into the Jurassic and Cretaceous.

Genus *COCCOLEPIS*
Coccolepis sp.
(not figured)

Description. Maxilla slender anteriorly, rapidly becoming broader posteriorly about midway along its length. Dentary with straight



TEXT-FIG. 9.3. Morphology of fish scales commonly found in isolation. **a**, diamond shaped with coating of shiny black or dark brown enamel; various species of *Lepidotes*. **b**, elongate, smooth scale with dorsal peg and ventral socket; *Heterostrophus* sp. and some scales of *Aspidorhynchus* sp. **c**, elongate scales with tuberculate enamel surface, complex suture on dorsal and ventral margins; *Mesturus leedsi*. **d**, round scale with annular growth rings, thin enamel coating posteriorly, sometimes tuberculate; larger specimens of *Caturus* sp. perhaps *Osteorachis leedsi*.

dentigerous border, slightly curved ventral margin, sharply pointed anteriorly. Teeth simple cones, slightly recurved. Preoperculum sub-oval, thin, slightly broader ventrally. Operculum elongate dorso-ventrally, with straight posterior margin, anterior margin sinuous.
Range. Known only from the Lower Oxford Clay of Christian Malford, Wiltshire.
Remarks. *Coccolepis* appears to be extremely rare in the Oxford Clay, but this may in part be due to its small size, so that it may have been overlooked.

Family GYRODONTIDAE

Deep bodied, rounded, laterally compressed fishes. Skull bones highly ornamented, dentition modified for crushing, pectoral fins above pelvics. Scales ganoid.

Genus *MESTURUS*
Mesturus leedsi Woodward
Plate 41, figs 6, 7, text-fig. 9.3c

Description. Pycnodont fish with highly ornamented skull bones and tuberculate scales. Premaxilla with three prehensile teeth, dentary with

four. Vomerine and splenial dentition globident with apical tubercle and crimped margin. Oral surface of vomer forming flat table. Scales united dorsally and ventrally by complex suture.
Range. Lower Oxford Clay of Peterborough.
Remarks. A graphic account of the initial discovery of this elegant fish is given by Leeds (1956) giving the impression that it is extremely rare. Isolated skull bones with slightly hooked tubercles are possibly referable to *Mesturus*. The scales are easily identified by the complex sutures.

Family SEMIONOTIDAE
Genus *LEPIDOTES*
Plate 40, fig. 1, text-fig. 9.3a, 9.4

Large fusiform ganoid fishes (possibly up to 1 m long) scales with thick diamond shaped enamel coatings. Centrally placed dorsal fin. Skull bones may be highly ornamented.

Lepidotes macrocheirus Egerton
Plate 41, fig. 2, text-fig. 9.4

Description. Parietals less than half as long as frontals, which are three times as long as broad, united in the midline with an almost straight median suture. Principal flank scales usually serrated posteriorly.
Range. Lower Oxford Clay of Christian Malford, Wiltshire, and Peterborough, Cambridgeshire.
Remarks. Difficult to distinguish from *L. latifrons* without well preserved skull material.

Lepidotes latifrons Woodward
Plate 41, figs 3, 4, text-fig. 9.4

Description. All external bones tuberculate or rugose, parietals unequal, usually half length of frontals. Frontals twice as long as broad, united by irregular median suture. Dentigerous portion of dentary slender, becoming slightly broader at the symphysis. Marginal teeth styliform, slender, erect. Inner teeth rounded, robust, on long pedicles. Flank scales large, smooth, quadrate, becoming elongate, diamond shaped posteriorly.
Range. Known definitely only from the Lower Oxford Clay of Peterborough, but scales of *Lepidotes* sp. are common at most localities

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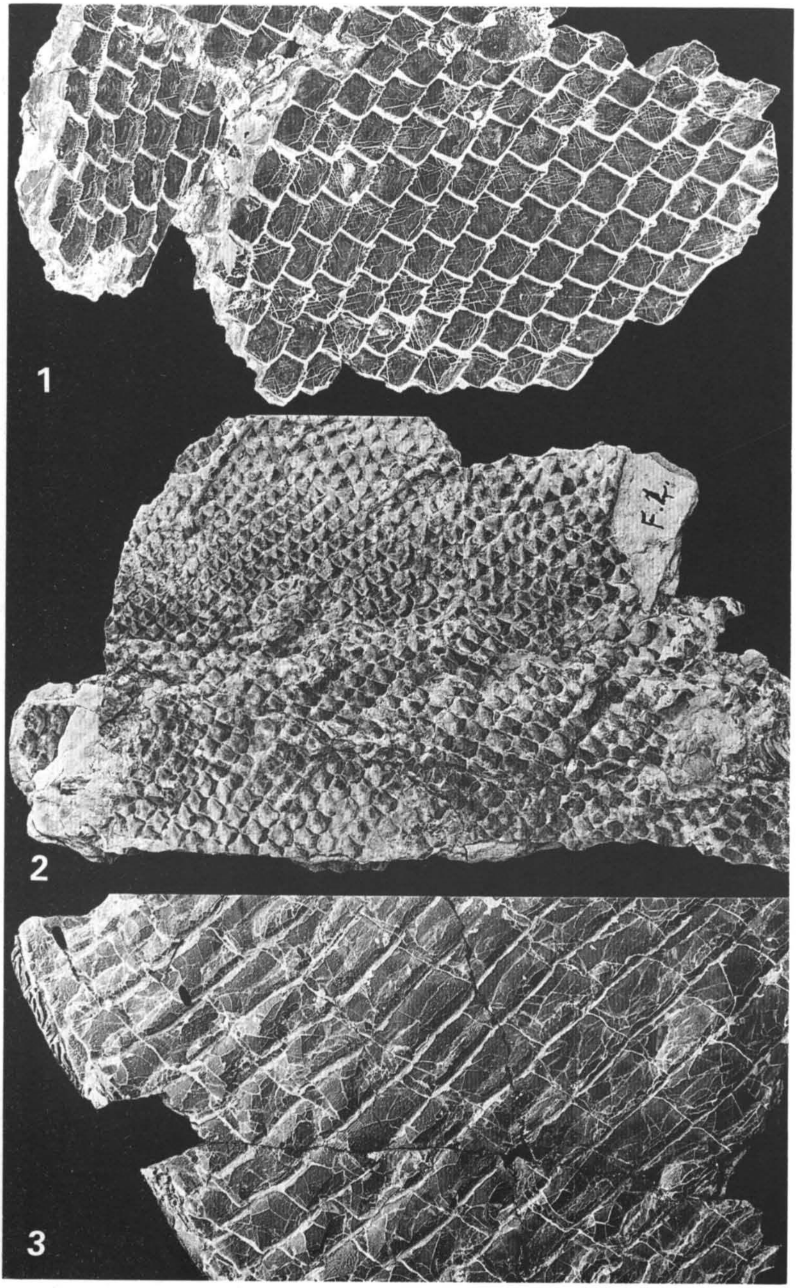
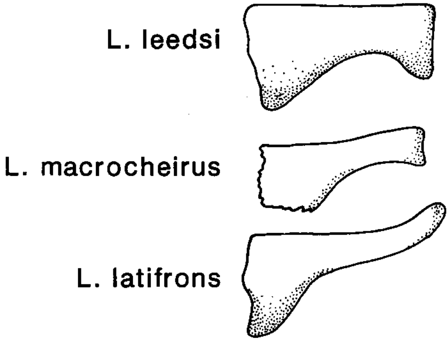
EXPLANATION OF PLATE 40

Fig. 1. Scales of *Lepidotes* sp.
Fig. 2. Scales of *Caturus* sp.
Fig. 3. Scales of *Heterostrophus phillipsi*. All Lower Oxford Clay, Peterborough.





TEXT-FIG. 9.4. Differences in lower jaw morphology of Oxford Clay species of *Lepidotes*. Based on Woodward (1895).

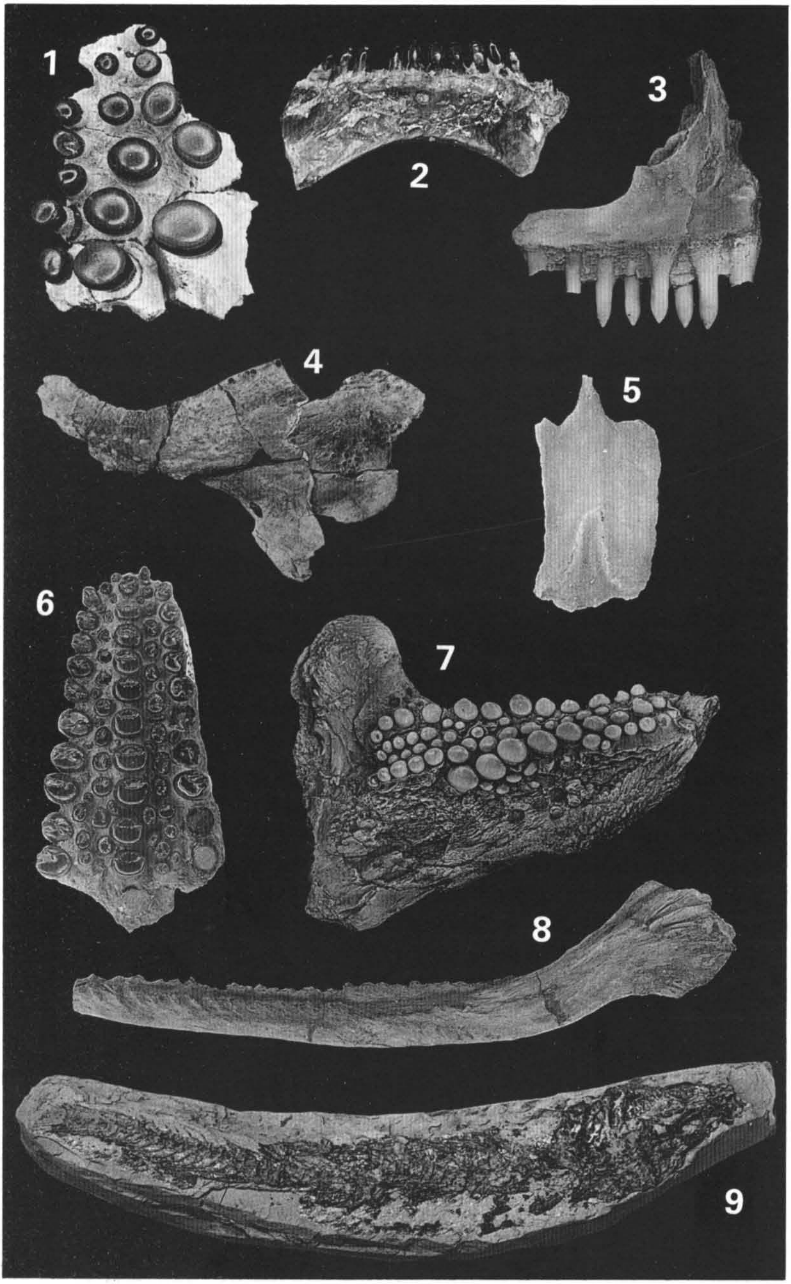
where Lower Oxford Clay is exposed. Isolated scales also known from the Middle and Upper Oxford Clays.

Lepidotes leedsi Woodward
Text-fig. 9.4

Description. *Lepidotes* in which the external skull bones are only lightly rugose or tuberculate, opercular elements almost smooth, but with occasional patches of tuberculation. Dentary short, robust, almost flat, with inferior border deeply curved. Teeth oval, median teeth on short pedicles, sometimes with apical tubercle on crown.
Range. Lower Oxford Clay of Peterborough, Cambridgeshire. Also known from the Kimmeridge Clay of Dorset.

EXPLANATION OF PLATE 41

Fig. 1. *Lepidotes* sp., dentition, Lower Oxford Clay, Peterborough, ×1.
Fig. 2. *Lepidotes macrocheirus*, right lower jaw, Lower Oxford Clay, Peterborough, ×1.
Fig. 3. *Lepidotes latifrons*, maxilliary dentition, Lower Oxford Clay, Peterborough, ×1.
Fig. 4. *Lepidotes latifrons*, left lower jaw, Lower Oxford Clay, Peterborough, ×0·5.
Fig. 5. *Heterostrophus* sp. single scale, Lower Oxford Clay, Peterborough, ×1·6.
Fig. 6. *Mesturus leedsi*, vomerine dentition, Lower Oxford Clay, Peterborough, ×1.
Fig. 7. *Mesturus leedsi*, splenial dentition, Lower Oxford Clay, Peterborough, ×1.
Fig. 8. *Leedsichthys problematicus*, gill raker, Lower Oxford Clay, Peterborough, ×1·5.
Fig. 9. *'Leptolepis' macrophthalmus*, Oxford Clay, Peterborough, ×0.5.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TEXT-FIG. 9.5. Vertebra of *Osteorachis leedsi* Woodward. Lower Oxford Clay, Peterborough, approximately. × 1.

Remarks. A rather poorly known member of the genus. Generally much smaller than *L. macrocheirus* or *L. latifrons*.

Genus *HETEROSTROPHUS*
Heterostrophus phillipsi Woodward
Plate 39, fig. 3, Plate 40, fig. 3
Plate 41, fig. 5, text-fig. 9.3b

Description. A deep bodied fish, rounded anteriorly, laterally compressed. External skull bones ornamented with tubercles and rugae. Strong pectoral fins, very small pelvics. Caudal fin robust, fan shaped. Dorsal and anal fins extended posteriorly, almost uniting with caudal fin. Scales ganoid, united with scale dorsally by elongate pointed peg.
Range. Known from the Lower Oxford Clay of Peterborough, Cambridgeshire, and Chickerell, Dorset.

Family CATURIDAE

Elongate fusiform fishes, external bones feebly ornamented. Teeth large and evenly spaced on dentary, finer and closely spaced on maxilla, small and densely distributed on inner bones. Well developed gular plate, prominent branchiostegal rays. Caudal fin deeply forked.

Genus *CATURUS*

Remarks. *Caturus* is probably the most common bony fish macro-fossil encountered in the Oxford Clay.

Caturus porteri Rayner
Plate 39, fig. 1, Plate 40, fig. 2

Description. A caturid in which the depth of the dentary below the most posterior tooth is one-quarter the length of the dentigerous border. Teeth of the dentary fine, gently recurved, closely spaced. Gular plate with prominent centre of ossification, 20 or more branchiostegal rays.
Range. Known from the Lower Oxford Clay of Peterborough and Whittlesey, Cambridgeshire, Calvert, Oxfordshire, Milton Keynes, Buckinghamshire, and Christian Malford, Wiltshire.

Caturus sp.
Plate 42, text-fig. 9.3d

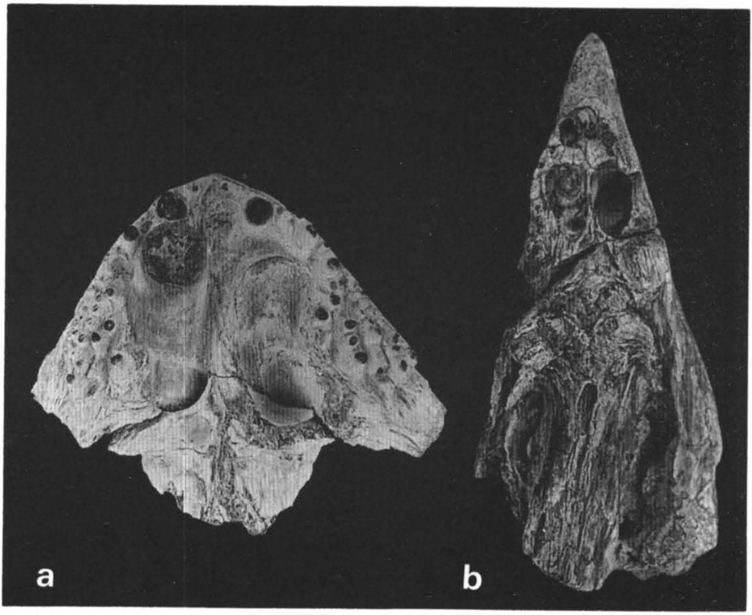
Description. A second species of *Caturus* is indicated by the presence of a caturid-like dentary in which the depth of the dentary at the posterior tooth is one-quarter the length of the dentigerous border as in *C. porteri*, but where the teeth are evenly spaced, large, robust, slightly recurved lingually, and with expanded roots.
Range. Only reported from the Oxford Clay of Whittlesey, Cambridgeshire (Martill, 1985).

Genus *OSTEORACHIS*
Osteorachis leedsi Woodward
Text-fig. 9.5

Description. Right parietal twice as broad as left. Frontals large, approximately equal size, united by wavy, median suture. Squamosals large, tapering anteriorly to an acute point. Mandible long, slender, with numerous large robust teeth in a single row. Splenial well developed, producing broad ledge on inner side of dentary with numerous small teeth. Hypocentra and pleurocentra well developed, almost bilaterally symmetrical. Both are arcuate with well developed articulatory facets.
Range. The genus *Osteorachis* is well known from the Lower Jurassic of southern England where two species are recognized. *O. leedsi* is only known from the Lower Oxford Clay of Peterborough, where it is very rare and poorly known.
Remarks. *O. leedsi* may prove to be identical to the large, but as yet undescribed, *Caturus* shown in Plate 7. Resolution of this awaits further study.

Family PACHYCORMIDAE

Streamlined fusiform fishes, elongate rostrum composed of single bone with teeth. Teeth pointed, usually round in cross section. Pectoral fins large, scythe-like. Pelvic fins very small or absent. Caudal fin deeply



TEXT-FIG. 9.6. Rostrum and dentition of *Hypsocormus*. **a**, *H. leedsi* Woodward, **b**, *H. tenuirostris* Woodward. Both Lower Oxford Clay, Peterborough.

forked. Fin rays slender, branching in some genera. Scales cycloid, thin, sometimes with layer of ganoin posteriorly. Some genera reach gigantic proportions.

Genus *SAUROPSIS*

Sauropsis longimanus Agassiz

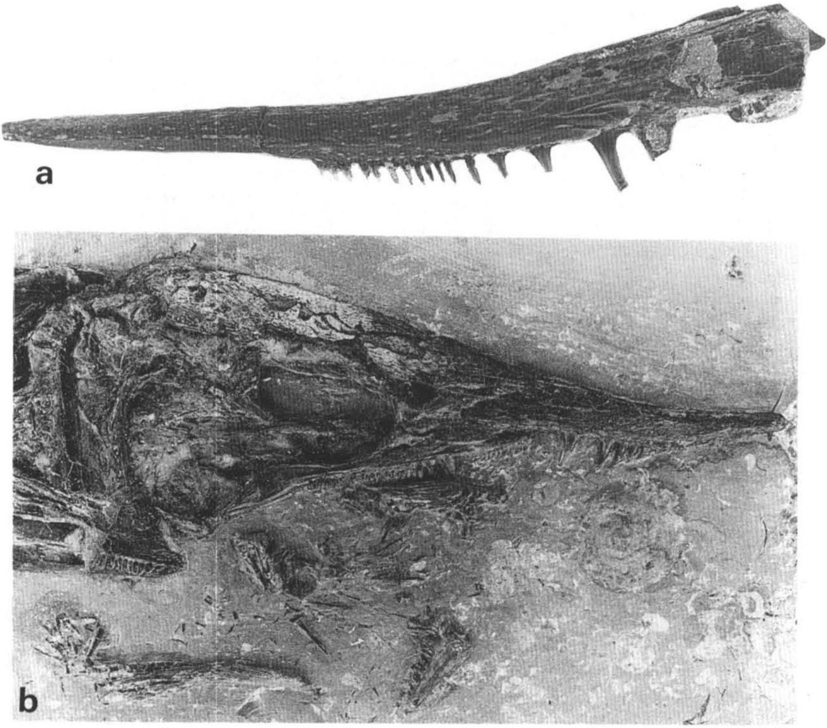
(not figured)

Description. Elongate, fusiform pachycormid. Relatively large skull. Teeth small, well spaced, rostrum not developed. Pectoral fins very elongate, sickle-shaped. Fin rays bifurcate towards extremity. Dorsal fin partly opposed to anal fin. Small pelvic fins mid-way between pectorals and anal fin, which is extended. Caudal fin deeply forked. Scales minute, well developed lateral line.

Range. Only known from the Lower Oxford Clay of Christian Malford, Wiltshire. *Sauropsis* is well known from the Solnhofen Limstone (L. Tithonian) of Bavaria, West Germany.

EXPLANATION OF PLATE 42

Caturus sp. skull and anterior portion of trunk, Lower Oxford Clay, Peterborough, approximately life size.



TEXT-FIG. 9.7. *Aspidorhynchus*. **a**, rostrum of *Aspidorhynchus* sp. showing prominent dentition, Lower Oxford Clay, Peterborough, ×3. **b**, Skull of *Aspidorhynchus eodus* in calcareous shale from the Lower Oxford Clay of Christian Malford, Wiltshire. ×1.

Remarks. An extremely rare fish in the Lower Oxford Clay. A single specimen is held in the NHM, London.

Genus *ASTHENOCORMUS*
Asthenocormus sp.
Plate 44

Description. An elongate (up to 2 metres) pachycormid with disproportionately small, deeply forked caudal fin. Dentary elongate, becoming broad posteriorly without teeth. Skull one-quarter length of body to base of

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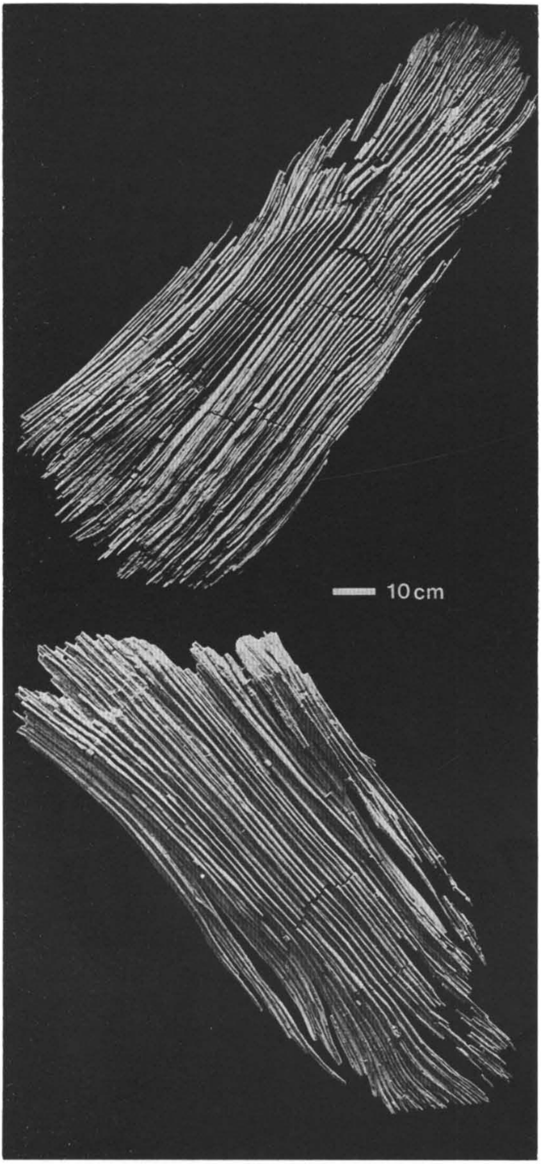
EXPLANATION OF PLATE 43

Leedsichthys problematicus, caudal fin, Lower Oxford Clay, Peterborough.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tail. Elongate ceratohyals with staple-like ceratobranchials along entire length. Pectoral fins elongate, scythe-like. Fin rays bifurcate without articulation. Pelvic fins present but small, situated just beneath pectorals.

Range. *Asthenocormus* has been recorded from Dogsthorpe (one complete skeleton and one well preserved skull) and Orton (single pectoral fin) brick pits at Peterborough, Cambridgeshire (Martill, 1985). A number of complete specimens have been reported from the Solnhofen Limestone (Lower Tithonian) of Bavaria, West Germany.

Remarks. The stomach contents of the complete specimen from Dogsthorpe brick pit included portions of '*Leptolepis*'-like fish indicating prey size up to 10 cm long.

Genus *LEEDSICHTHYS*
Leedsichthys problematicus Woodward
Plate 41, fig. 8, Plate 43

Description. Fish of gigantic proportions (possibly greater than 10 metres). Skull bones massive, irregular and often difficult to identify. Fin rays with fibrous texture bifurcate repeatedly. Ribs massive. Gill rakers with V shaped ramus with serrated edges. Rakers may be devoid of teeth or may have up to 50 needle-like, laterally compressed teeth arranged in a single row.

Range. Known from the Lower Oxford Clay of Peterborough, Cambridgeshire, and Stewartby, Bedfordshire. Also known from the Callovian of Normandy, France, and the Kimmeridgian of Dorset.

Remarks. Although *Leedsichthys* was a gigantic fish it was most likely planktivorous, with the gill apparatus functioning as a food sieve (Martill, 1988).

Genus *HYPSOCORMUS*
Hypsocormus leedsi Woodward
Text-fig. 9.6a

Description. A fusiform pachycormid with blunt rostrum bearing two large caniniform teeth up to 3 cm long, surrounded by smaller conical teeth.

Range. Known definitely only from the Lower Oxford Clay of Peterborough, Cambridgeshire.

EXPLANATION OF PLATE 44

Asthenocormus sp. nov. Ventral view of skull. Lower Oxford Clay (*jason* Zone), Dogsthorpe Brick Pit, Peterborough, ×0·5.

Hypsocormus tenuirostris Woodward
Plate 39, fig. 2, text-fig. 9.6b

Description. *Hypsocormus* with elongate rostrum bearing two gigantic caniniform fangs and numerous smaller teeth.
Range. Known definitely only from the Lower Oxford Clay of Peterborough. The genus *Hypsocormus* has been obtained from other localities but specimens lack the diagnostic rostrum.
Remarks. Easily distinguished from *H. leedsi* due to the sharp pointed nature of the rostrum.

Family ASPIDORHYNCHIDAE
Genus *ASPIDORHYNCHUS*
Aspidorhynchus eodus Egerton
Text-fig. 9.7a,b

Description. Long slender fish with narrow, elongate rostrum projecting well beyond dentary and predentary. lateral body scales elongated dorso-ventrally, one row especially so. Scales lack ganoin. Dorsal fin placed posteriorly above anal fin. Caudal fin small, strongly forked. The closely related *Vinctifer* from the Cretaceous of Brazil may reach one metre in length, but Oxford Clay specimens are generally smaller than this.
Range. Known from the Lower Oxford Clay of Christian Malford, Wiltshire, and Peterborough, Cambridgeshire.
Remarks. Isolated rostral and predentary bones are relatively common.

Actinopterygians of uncertain relationship
Genus '*LEPTOLEPIS*'

The genus *Leptolepis* has become a 'dumping ground' for small primitive teleost fishes. It is likely that several taxa belonging to a number of genera are present within this category.

'*Leptolepis*' *macrophthalmus* Egerton
Plate 41, fig. 9

A number of fish from the Lower Oxford Clay of Christian Malford, Wiltshire, Peterborough, Cambridgeshire, and from the Argile de Dives of Normandy, France, have been referred to *Leptolepis*. The genus *Leptolepis* has been extensively reviewed due to the key position attributed to these fishes in early teleost evolution. The Oxford Clay '*Leptolepis*' are rarely well enough preserved for detailed relationships to be established. For this reason it is best to refer to Egerton's *L. macrophthalmus* as '*Leptolepis*' *macrophthalmus*.

Genus PHOLIDOPHORUS

Pholidophorus sp.
(not figured)

Description. Fusiform, trunk not much deepened, head relatively large. External bones smooth, or very lightly ornamented with rugae and tuberculations. Prominent branched sensory canal on suborbital and preorbital plates. Maxilla arched, oral margin convex with very small teeth; mandibular teeth slightly larger. Scales broader than deep, sometimes serrated. Pectoral fins slightly larger than pelvics.
Range. Lower Oxford Clay of Christian Malford, Wiltshire, and Peterborough, Cambridgeshire.
Remarks. A number of specimens have been placed in this genus, but their true affinities remain to be established.

OTOLITHS

Plate 38, fig. 8

Otoliths are small calcareous bodies found in the inner ear of fishes. Of the three types of otolith, *leganalith*, *sacculith* and *utriculith*, sacculiths are the largest and commonest elements to be found. They are sometimes large enough to be picked from residues without the aid of a microscope. Isolated otoliths are abundant in residues prepared for micropalaeontological examination, especially in those prepared from the finer shell beds. Some specimens may show etched surfaces; evidence of having passed through the guts of larger piscivorous fish and reptiles (Fitch & Brownell, 1968). Although otoliths may be sufficiently distinct to enable specific identifications to be made (Stinton, 1975), no Oxford Clay fish have been found with otoliths within the auditory bullae, accordingly otoliths are not further subdivided here.

10. MARINE REPTILES

by DAVID M. MARTILL

THE Oxford Clay has yielded the skeletons of numerous marine reptiles and also a few pterosaurs which may have been semi-aquatic like puffins and gannets. Marine reptiles are relatively abundant in the Lower Oxford Clay, and appear to be most common in the Peterborough district (fig. 8.1). By far the most frequently encountered remains are isolated vertebrae, which can sometimes be a problem to identify. Fortunately vertebrae may vary in form from one taxon to another (fig. 10.1). They also vary considerably according to their position along the vertebral column. Pointers to look for to aid identification are the positioning of facets for the attachment of ribs, neural and haemal arches, and the shape of the centrum. It is not usually possible to identify marine reptiles to the species level on the basis of vertebrae alone.

Fragments of ribs are very common, and although of little diagnostic value, it can be possible to identify the higher taxonomic categories from the shape of the cross-section and the form of the articulation with the vertebra if it is present (fig. 10.2). Isolated teeth may also be useful (fig. 10.3), and can usually be identified to generic level. In the pliosaurs caniniform teeth may reach lengths of over 40 cm, whereas in the ichthyosaur *Ophthalmosaurus* they may be absent altogether.

ICHTHYOSAURS

All described ichthyosaurs from the Oxford Clay have been referred to the genus *Ophthalmosaurus*. Two species have been recognized, but there are a few fragmentary scraps that suggest a third species of a distinct genus may be present. This should be looked out for. Phillips (1871) lists *Ichthyosaurus dilatus* Phillips and *I. thyreospondylus* Owen, from the Oxford Clay of Oxfordshire. Phillips' species is based on a row of vertebrae, and must be considered invalid. The occurrence of *I. thyreospondylus*,

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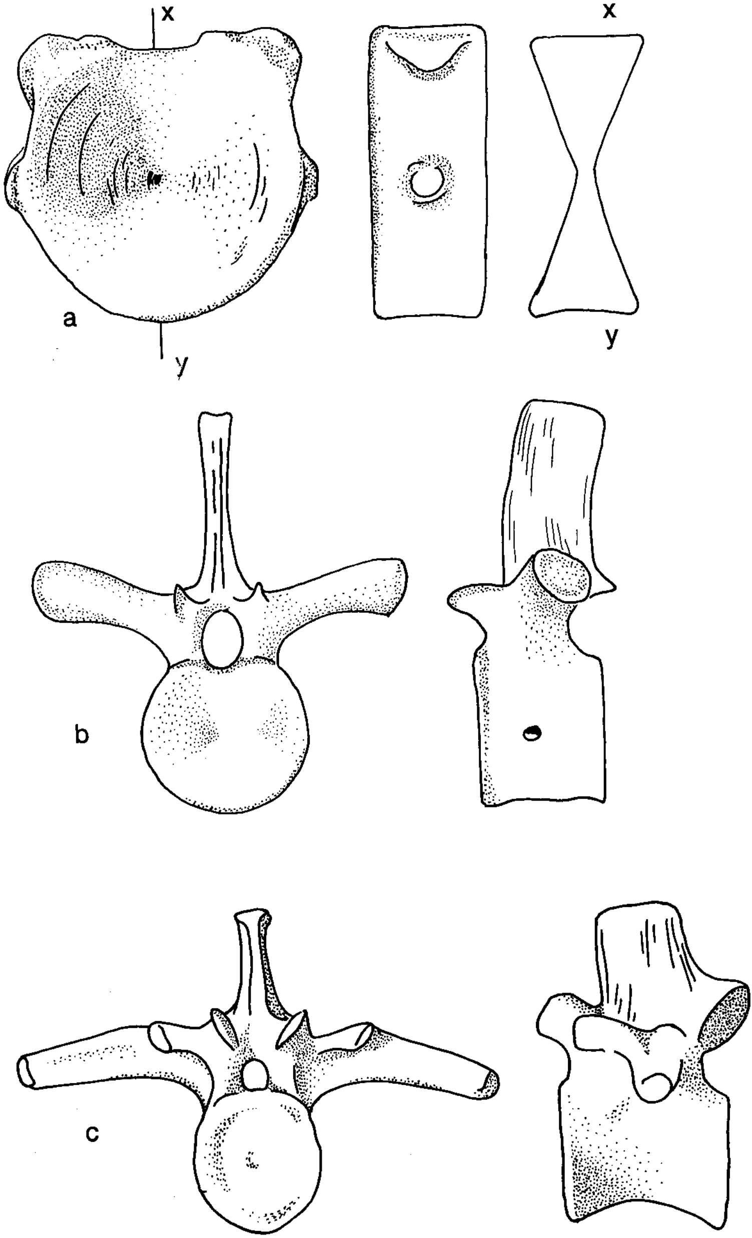
TEXT-FIG. 10.1. Morphology of marine reptile thoracic vertebrae. **a**, Ichthyosaur anterior thoracic centrum. Note the neural arch and spine are not fused to the centrum, and that the ribs articulate with the centrum only. **b**, Plesiosaur mid thoracic vertebra from adult. Here the neural arch and spine is fused to the body of the centrum; notice that the ribs articulate with the neural arch, and not with the centrum. **c**, Mid thoracic centrum and neural arch of crocodilian; ribs articulate with the neural arch.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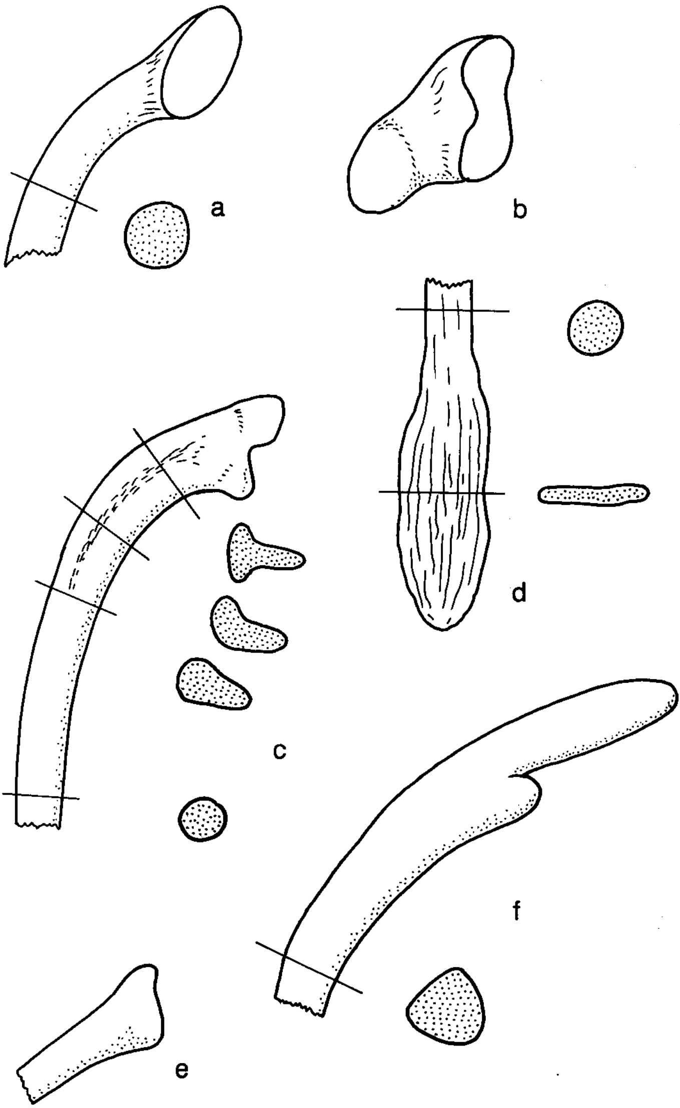

TEXT-FIG. 10.2. Variation in rib morphology of Oxford Clay marine reptiles. **a**, Articulation of sauropterygian thoracic rib. **b**, Pliosaurian cervical rib. **c**, Ichthyosaurian thoracic rib with cross-sections. **d**, Distal end of old adult ichthyosaurian thoracic rib. **e**, Articulation of ichthyosaurian caudal rib. **f**, Articulation of crocodilian rib.

a Kimmeridgian species of doubtful validity, is also based on isolated vertebrae. Thus the genus *Ichthyosaurus* is not certainly known outside the Lias. Important contributions to the osteology of Oxford Clay ichthyosaurs can be found in Andrews (1910–13), Appleby (1956, 1958), and Seeley (1874b). Martill (1987) discussed aspects of ichthyosaur taphonomy using specimens from the Oxford Clay.

Order ICHTHYOSAURIA
Family OPHTHALMOSAURIDAE
Genus *OPHTHALMOSAURUS*
Text-fig. 10.3i,j, 10.4

Ophthalmosaurus is an ichthyosaur characterized by an elongate rostrum, usually lacking dentition, although teeth are sometimes present in the distal part of the tooth groove. These are usually small and often do not erupt above the tooth groove. *Ophthalmosaurus* was up to 5 metres long.

Even in old individuals the bones of the skull and the vertebral column remain unfused. This frequently results in the complete disarticulation of the skull, resulting in many isolated bones. This is a sharp contrast to the usually complete skulls of ichthyosaurs from the Lower Lias of southern England.

Commonly found elements include rib fragments (round cross-section distally, L shaped cross section proximally, double articulation with vertebral centrum), paddle bones (phalanges: round discs of bone with flat faces and irregularly ossified edges), vertebrae (circular, deeply amphicoelous, two prominent facets dorsally, double lateral facets for ribs).

Two species of *Ophthalmosaurus* are found in the Oxford Clay. *O. icenicus* Seely, and *O. monocharactus* Appleby. It is only possible to distinguish between the two species when the coracoids are present.

Ophthalmosaurus icenicus Seeley
Text-fig. 10.5a

Description. *Ophthalmosaurus* in which the coracoids have posterior and anterior notches.

Range. Well known from the Lower Oxford Clay of Peterborough, Cambridgeshire, Stewartby, Bedfordshire, and Bletchley, Buckinghamshire. *Ophthalmosaurus* sp. indet. is known from the Lower Oxford Clay of Weymouth, Dorset, Christian Malford, Wiltshire. It is also recorded from the Upper Oxford Clay of Warboys, Cambridgeshire.

Ophthalmosaurus monocharactus Appleby
Text-fig. 10.5b

Description. Distinguishable from *O. icenicus* by having only a single notch in the coracoids.

Range. Recorded only from the Lower Oxford Clay of Peterborough, Cambridgeshire (Appleby 1958).

PLESIOSAURS

Representatives of both plesiosaur superfamilies are abundant in the Lower Oxford Clay (text-fig. 10.6, 10.8). The long-necked plesiosaurs are represented by the families Cryptoclididae and Elasmosauridae, while the short-necked Pliosauroidea are represented by four genera all belonging to the family Pliosauridae. The Oxford Clay pliosaurs were among the largest known carnivorous marine reptiles. Some of the larger species may have reached a mass comparable to the large terrestrial carnivorous dinosaurs such as *Tyrannosaurus* and *Albertosaurus*. Contributions to the osteology of plesiosaurs can be found in Andrews (1895a,b,c,d, 1896, 1897, 1909a, 1910, 1911, 1910–13), Lydekker (1888b, 1890), Seeley (1874a, 1877), Smellie (1915, 1916). Important recent accounts of plesiosaur taxonomy can be found in Tarlo (1960) and Brown (1981). Charig and Horrell (1971) give an account of a spectacular specimen scientifically excavated from Fletton, Peterborough.

Subclass SAUROPTERYGIA
Order PLESIOSAURIA
Superfamily PLESIOSAUROIDEA
Family ELASMOSAURIDAE
Genus *MURAENOSAURUS*
Muraenosaurus leedsii Seeley
Text-fig. 10.3g

Description. It is difficult to distinguish isolated fragments of the various plesiosaur genera. The genus *Muraenosaurus* is characterized by the possession of teeth with numerous longitudinal ridges. There are usually between 19 and 22 teeth in each dentary and only five teeth in the premaxilla. There are 44 platycoelous cervical vertebrae. The clavicles are highly reduced, or may be entirely absent. *M. leedsii* is characterized by

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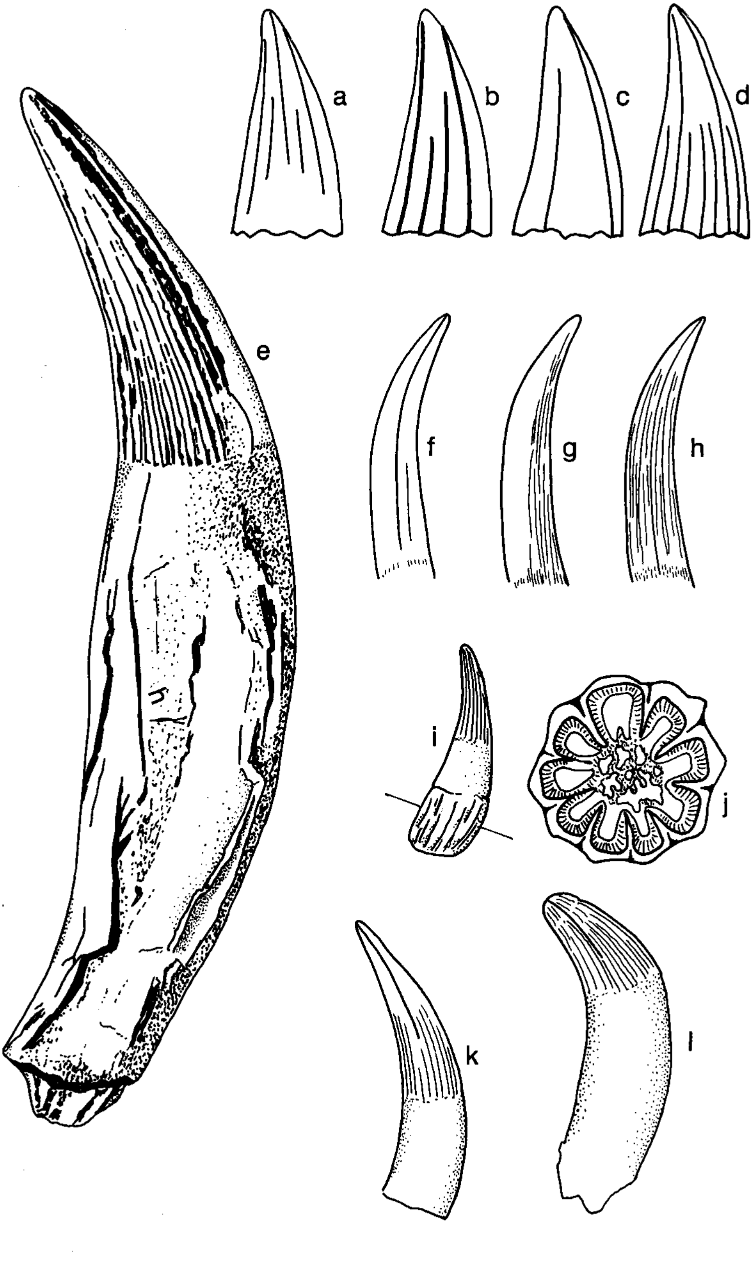
TEXT-FIG. 10.3. Teeth of marine reptiles from the Oxford Clay. **a**, *Simolestes vorax*. **b**, *Liopleurodon ferox*. **c**, *Pliosaurus andrewsi*. **d**, *Peloneustes philarchus*. **e**, Complete tooth of *Liopleurodon ferox*. **f**, *Cryptoclidus eurymerus*. **g**, *Muraenosaurus* sp. **h**, *Tricleidus seeleyi*. **i** and **j**, *Ophthalmosaurus* sp. with cross section through base, **k**, *Steneosaurus* sp. **l**, *Metriorhynchus* sp., posterior tooth. Based on Andrews (1910, 1913), Tarlo (1960), and Brown (1981). Drawn approximately life size.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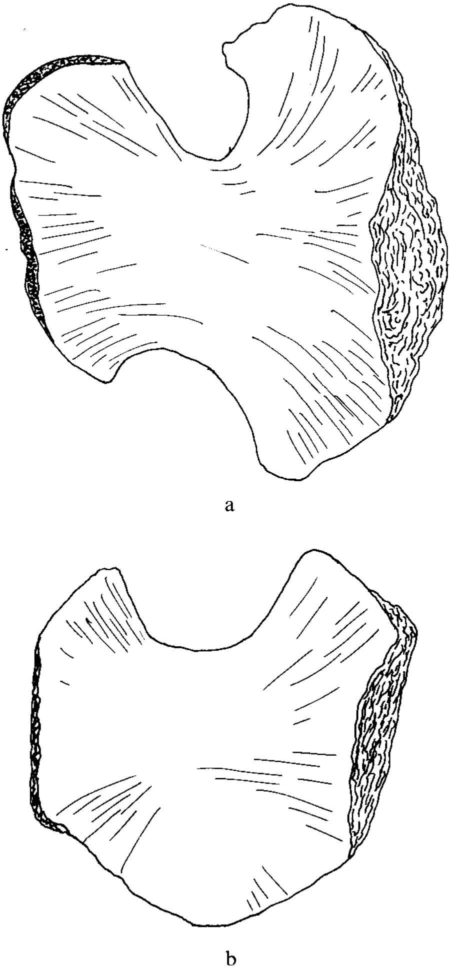
TEXT-FIG. 10.4. Restoration of *Ophthalmosaurus* sp. by J. G. Martin.

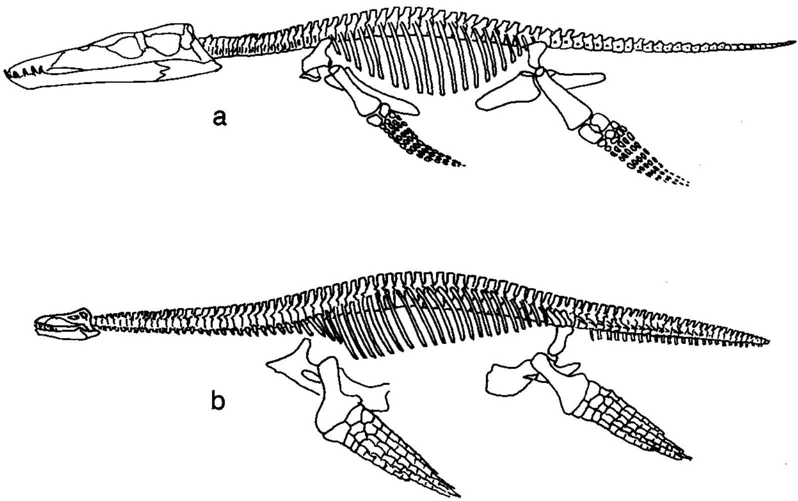


TEXT-FIG. 10.5. Coracoids of *Ophthalmosaurus* spp. **a**, *O. icenicus* with anterior and posterior notches. b, *O. monocharactus* with anterior notch only.

having cervical ribs without an anterior flange. Brown (1981) records a maximum length of 5·2 metres.

Range. Known only from the Lower Oxford Clay of Peterborough, Cambridgeshire. Specimens referable to *Muraenosaurus* sp. indet. are known from the Lower Oxford Clay of Bedfordshire.

Remarks. This is a relatively common plesiosaur in the Peterborough district. It is known from juvenile, adult and old adult skeletons.



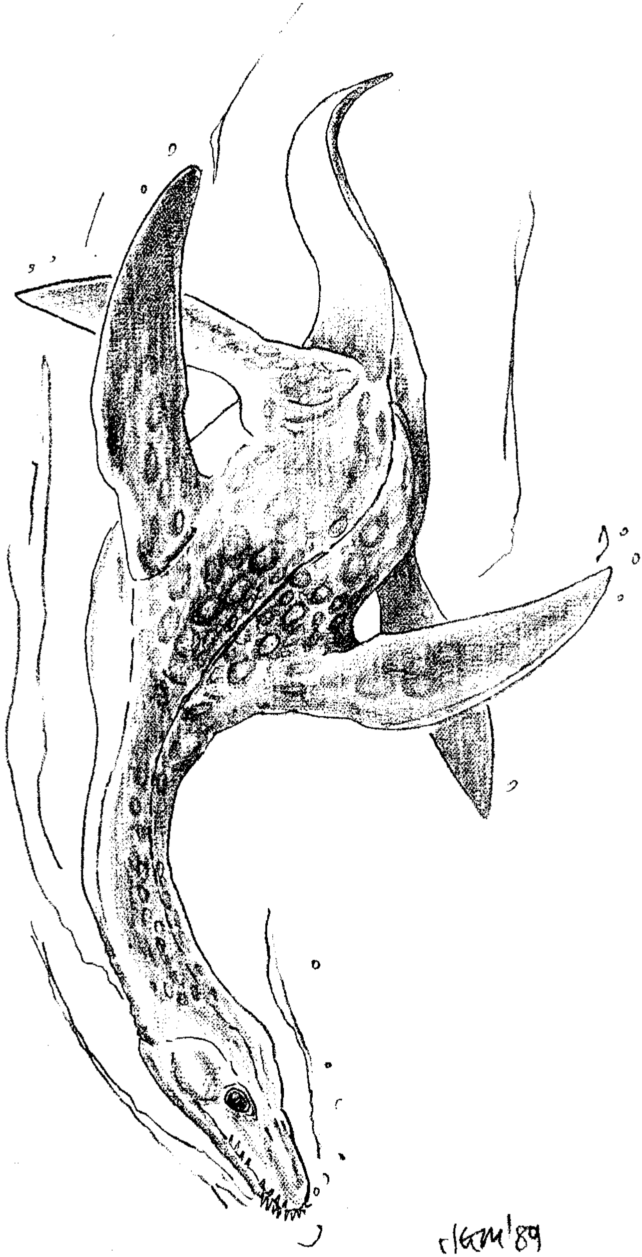
TEXT-FIG. 10.6. Skeleton reconstructions of Oxford Clay sauropterygians. **a**, *Liopleurodon*, after Tarlo (1960). **b**, *Cryptoclidus*, after Andrews (1910).

Muraenosaurus beloclis Seeley
Text-fig. 10.3g

Description. This species of *Muraenosaurus* is distinguished from *M. leedsii* by the presence of an anterior flange on the cervical ribs. Brown (1981) suggests a length of 2·5 m for an adult specimen.
Range. Known only from the Lower Oxford Clay of Peterborough, Cambridgeshire.
Remarks. Very few specimens of this plesiosaur are known. As there is little accurate stratigraphic data on the source of the specimens it is not known if the two species of *Muraenosaurus* coexisted.

Genus *TRICLEIDUS*
Tricleidus seeleyi Andrews
Text-fig. 10.3h

Description. *Tricleidus seeleyi* is the only species in the genus *Tricleidus*. The teeth are ornamented by longitudinal ridges, but the ridges are finer than in *Muraenosaurus*. There are only 17 teeth on each dentary, and 5 teeth on the premaxilla. Brown (1981) records a minimum of 26 cervical amphicoelous vertebrae.
Range. Known only from the Lower Oxford Clay of Fletton, near Peterborough, Cambridgeshire.



TEXT-FIG. 10.7. Restoration of *Cryptoclidus eurymerus*, by J. G. Martin.

Remarks. The rarest of the elasmosaur plesiosauroids from the Oxford Clay.

Family CRYPTOCLIDIDAE
Genus *CRYPTOCLIDUS*
Text-fig. 10.3f, 10.7

Cryptoclidus is the most common of the plesiosaurs found in the Oxford Clay. Isolated vertebrae probably attributable to this genus are relatively common over much of the outcrop.

Cryptoclidus eurymerus (Phillips)
Text-fig. 10.7

Description. These are typical long necked plesiosaurs. They have slender, elongate, gently recurved teeth in which ornament is lacking or reduced. There are usually between 24 and 26 teeth on the dentary, and 6 teeth on the premaxilla. There are generally 32 cervical vertebrae. In *C. eurymerus* the teeth are characterized by two prominent axial ridges which meet over the tip of the tooth. Between these two ridges on the lingual face of the tooth are 4–7 finer ridges which only extend two-thirds of the way up the tooth.
Range. Recorded from the Lower Oxford Clay of Peterborough, Cambridgeshire, and the Bedfordshire district. Possibly known also from the basal Oxford Clay of Lincolnshire.
Remarks. One of the best known of all plesiosaurs. This is a very common animal, and is known from numerous specimens representing all stages of development from juveniles to old adults.

Cryptoclidus richardsoni (Lydekker)
(not figured)

Description. This species can only be distinguished from *C. eurymerus* if the forelimbs are preserved. In *C. richardsoni* the humerus is less expanded antero-distally. The radius has a concave anterior border and the ulna is almost square.
Range. The exact horizon from which the only known specimen of *C. richardsoni* comes is in doubt. However Brown (1981) records the locality as a brick pit between Weymouth and Chickerell. The clays here extend from the Jason Zone (M. Callovian) to the Cordatum Zone (L. Oxfordian).
Remarks. Only a single specimen of this very rare plesiosaur is known, but it is possible that much of the fragmentary material from the Weymouth area may be assigned to *C. richardsoni*.

Superfamily PLIOSAUROIDEA

Pliosaurs were the giant carnivores of the Oxford Clay seas. Fragmentary remains indicate animals in excess of 15 metres long. They had dentitions modified for a number of feeding strategies. Some of the smaller species were probably teuthoid and fish feeders, whilst the larger species were capable of dispatching other large marine reptiles. At least one pliosaur, *Simolestes*, was able to bite chunks from prey by combining the bite of a rosette shaped symphysis with a rapid rotation of the body on its long axis (Taylor, 1987). Complete pliosaurs are rare, perhaps reflecting their true relative abundance, but isolated teeth are fairly common.

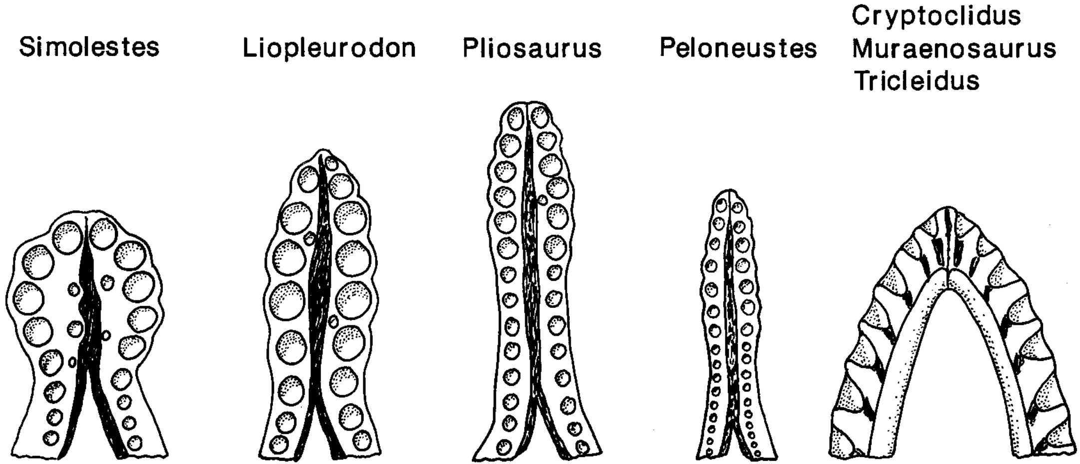
The teeth of pliosaurs are sharply pointed, strongly ribbed and robust. They are easily distinguished from the teeth of the long necked plesiosaurs by their more massive appearance. Oxford Clay pliosaur teeth have a round cross-section, while the teeth of Kimmeridge Clay pliosaurs generally have triangular cross-sections. The genera can be distinguished by the number of teeth present at the symphysis of the jaws (text-fig. 10.8).

Family PLIOSAURIDAE
Genus *LIOPLEURODON*
Liopleurodon ferox Sauvage
Text-fig. 10.3b,e

Description. A large pliosaur, probably in excess of 15 metres long. The mandibular symphysis is elongate with six caniniform teeth. The teeth have several prominent, widely spaced ridges extending almost to the tip of the crown, between which are ridges reaching only halfway up the tooth crown.
Range. *Liopleurodon* has been recorded from the Lower Oxford Clay of Peterborough, Cambridgeshire, and Bedfordshire. The holotype was found near Boulogne, France.
Remarks. The skull of *Liopleurodon* may have been up to 3 m long, making it the largest known marine reptile, and possibly the largest carnivorous reptile. A specimen in excess of four metres in length, probably referrable to *Liopleurodon* sp. was discovered during preparation of this book. It contains a variety of elements within the stomach region, including numerous cephalopod hooklets, small phosphatic 'pebbles' and possible fish teeth.

Liopleurodon pachydeirus (Seeley)
(not figured)

Description. Distinguished from *Liopleurodon ferox* by the possession of finer ridges on the teeth. The ridges are closely spaced on the inner



TEXT-FIG. 10.8. Lower jaw symphysial morphology of Oxford Clay sauropterygians. Based on Tarlo (1960) and Brown (1981).

surface. There are about 8 evenly spaced ridges on the outer surface of the tooth.
Range. Recorded from the Oxford Clay of Great Gransden, Cambridgeshire, and Peterborough, Cambridgeshire.
Remarks. This species appears to be rarer than its close relative *L. ferox*.

Genus *SIMOLESTES*
Simolestes vorax Andrews
Text-fig. 10.3a

Description. Large pliosaur in which the mandibular symphysis is short and the terminal caniniform teeth are developed into a large rosette. The teeth of *Simolestes* are similar to those of *Liopleurodon*, but with shorter and fewer enamel ridges.
Range. Lower Oxford Clay of Peterborough.
Remarks. *Simolestes vorax* is one of the most spectacular marine reptiles from the Oxford Clay. The rosette of symphysial teeth was probably used for tearing large chunks of flesh from its prey, or for biting chunks out of larger ammonites.

Genus *PELONEUSTES*
Peloneustes philarchus (Seeley)
Text-fig. 10.3d

Description. Small pliosaurs in which the mandibular symphysis is elongate, with 14 pairs of teeth. The anterior 6 or 7 teeth are large and caniniform. The teeth possess longitudinal ridges reaching half-way up the crown.
Range. Lower Oxford Clay of Peterborough, Cambridgeshire.
Remarks. *Peloneustes* is very difficult to distinguish from *Pliosaurus*.

Genus *PLIOSAURUS*
Pliosaurus andrewsi Tarlo
Text-fig. 10.3c

Description. A large pliosaur in which the mandibular symphysis is elongate, bearing up to 12 pairs of teeth. Teeth with few fine enamel ridges.
Range. Lower Oxford Clay of Peterborough, Cambridgeshire, and possibly Middle Oxford Clay, Great Gransden, Cambridgeshire.
Remarks. Possibly a large form of *Peloneustes*, see above.

MARINE CROCODILES

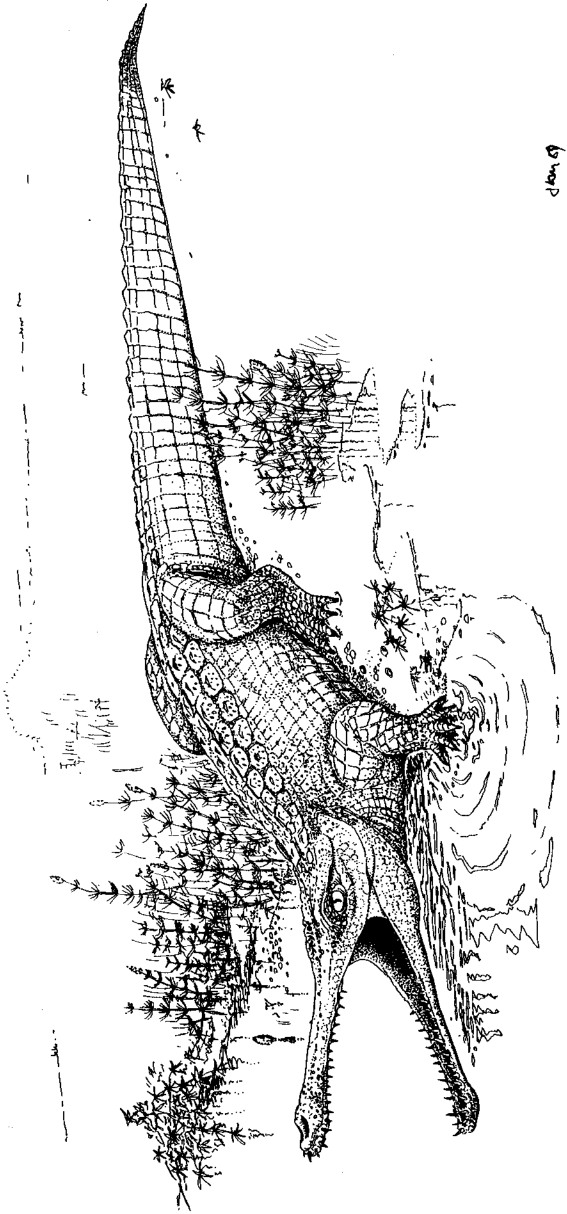
Marine crocodilians are an important part of the Oxford Clay marine reptile fauna. Two genera are currently recognized, the slender snouted *Steneosaurus*, and the more massively snouted *Metriorhynchus* (text-fig. 10.9, 10.10, 10.11). Both were well adapted to a marine existence. By far the majority of specimens come from the Peterborough district, but there are documented occurrences from the Bedfordshire/Buckinghamshire area. They are relatively abundant in the basal parts of the Lower Oxford Clay at Peterborough, where a number of specimens have been found containing stomach contents. These have included cephalopod hooklets and pebbles of quartzite (Martill 1986b). Accounts of Oxford Clay crocodilian anatomy can be found in Andrews (1909b, 1910–1913), Lydekker (1890c), Mateer (1974) and Phizackerley (1951). More recently Adams-Tresman (1987a and b) has reviewed the status of Lower Oxford Clay crocodiles.

Class ARCHOSAURIA
Subclass CROCODILIA
Order MESOSUCHIA
Family TELEOSAURIDAE
Genus *STENEOSAURUS*
Steneosaurus leedsi Andrews

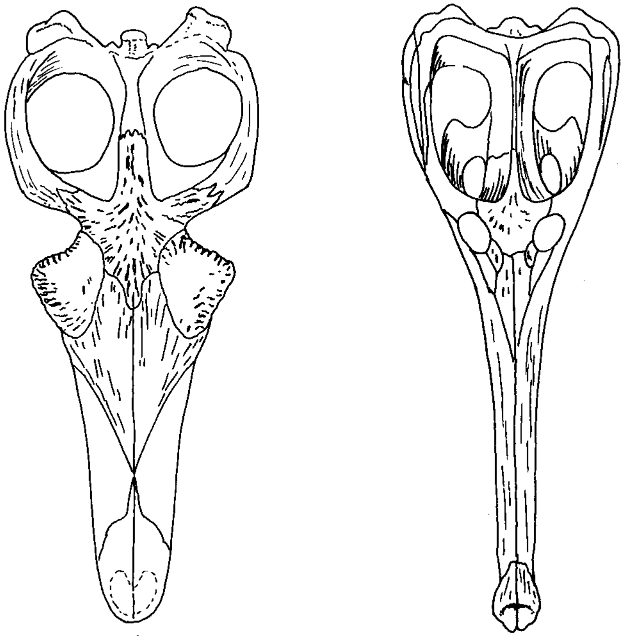
Description. Crocodilian well adapted for marine existence (text-fig. 10.9). Skull with elongate rostrum, numerous sharp, robust teeth with lateral keels. Upper jaw with 45–46 teeth on each side, lower jaw with 43–44 teeth on each side. Back covered with thin, ornamented bony scutes. Sharp downward flexure of vertebral column at end of tail. Trunk vertebrae with broad transverse processes with which double headed ribs articulate. Centrum longer than wide, with height approximately equal to width.
Range. Well known from the Lower Oxford Clay of Peterborough, Cambridgeshire. *Steneosaurus* sp. is recorded from most of the large brick making areas situated on the Lower Oxford Clay outcrop.
Remarks. A large marine crocodilian, *Steneosaurus* can be distinguished from *Metriorhynchus* (see below) by the presence of numerous dorsal scutes, a more reduced anterior limb, and a more lightly built skull with long slender rostrum (text-fig. 10.10).

Steneosaurus durobrivensis Andrews
(not figured)

Description. As for *S. leedsi*, but upper jaw with approximately 34 teeth on each side, lower jaw with approximately 31 teeth on each side. The rostrum is generally shorter than that of *S. leedsi*, but the skull has proportionally larger orbits. Scutes larger with shallower ornament than *S. leedsi*.
Range. Lower Oxford Clay of Peterborough.



TEXT-FIG. 10.9. Restoration of *Steneosaurus* sp. by J. G. Martin.

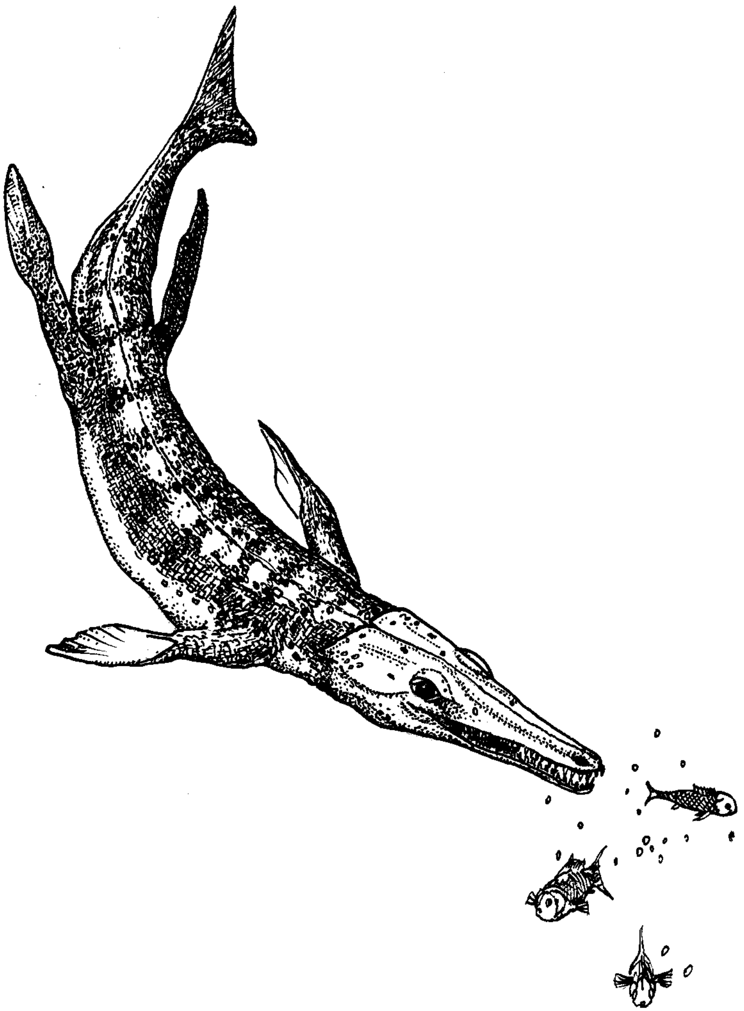


TEXT-FIG. 10.10. Crocodilian skull morphologies. *Steneosaurus* (b) has a long slender rostrum, whereas that of *Metriorhynchus* (a) is blunt and more robust.

Family GEOSAURIDAE
Genus *METRIORHYNCHUS*
Text-figs. 10.10, 10.11
Metriorhynchus brachyrhynchus Deslongchamps
(not figured)

Description. Crocodiles well adapted for a marine existence. Limbs reduced to flippers, probably incapable of use on land except for breeding excursions. Tail with downward flexure. Skull with elongate rostrum, but generally broader than that of *Steneosaurus*. Nares almost unite with premaxilla, resulting in very short maxillary symphysis. Skull bones may be highly rugose. Lacks dermal armour.

Range. Lower Oxford Clay of Peterborough, Cambridgeshire. *Metriorhynchus* sp. is recorded from the Lower Oxford Clay of Buckinghamshire. Isolated crocodilian teeth assignable to either *Metriorhynchus* sp. or *Steneosaurus* sp. can be found from Weymouth to Scarborough. *Metriorhynchus* is also known from the Oxfordian of Normandy, France.



TEXT-FIG. 10.11. Restoration of the marine crocodile *Metriorhynchus* sp. by J. G. Martin.

Metriorhynchus superciliosus Deslongchamps
(not figured)

Description. As for *M. brachyrhynchus* but with extended maxillary symphysis.
Range. Well known from the Lower Oxford Clay of Peterborough, Cambridgeshire.

11. TERRESTRIAL REPTILES

by DAVID M. MARTILL

ALTHOUGH the Oxford Clay is a fully marine deposit containing a diverse offshore marine invertebrate fauna, a considerable number of terrestrial reptiles have been discovered over the last one hundred years. Most of these discoveries have been of isolated bones from large dinosaurs, presumably dropped from floating carcasses that have drifted out to sea from nearby landmasses. There are a few reports of almost complete skeletons of dinosaurs, and a number of accounts of small pterosaur bones. Martill (1988a) gave a review of all known discoveries of terrestrial vertebrates from the Oxford Clay and attempted to determine the stratigraphic position of the individual specimens. There are no records of mammalian remains from the Oxford Clay, despite their abundance in slightly older non-marine sediments on the Midlands platform.

For accounts of Oxford Clay terrestrially derived faunas see Galton (1985), Charig (1981), Hulke (1887), Leeds (1956), Lydekker (1888a, 1890b, 1893), and Martill (1984, 1988a). Martill (1988a) gives an extensive bibliography on Oxford Clay dinosaurs.

Subclass DINOSAURIA
Superorder SAURISCHIA
Order SAUROPODOMORPHA
Suborder SAUROPODA
Family DIPLODOCIDAE
Genus *CETIOSAURISCUS*
Cetiosauriscus stewarti Charig
Text-fig. 11.1b,e

Description. A diplodocid sauropod. Dorsal vertebral centra anteroposteriorly compressed. Caudal vertebrae with straight chevrons anteriorly, becoming boat-shaped posteriorly. Humerus relatively short, with thick deltoid crest. Femur long and slender. Tooth crowns spatulate with cylindrical root.

Range. Lower Oxford Clay of Peterborough.

Remarks. A single specimen of this dinosaur comprising portions of the pelvic girdle, hind limb, fore limb, caudal and some dorsal vertebrae. Three isolated teeth of a sauropod have also been referred to this taxon.

Family *INCERTAE SEDIS*
Genus ORNITHOPSIS
Ornithopsis leedsi Hulke
(not figured)

Description. Ischium long and slender with antero-ventral projection. Pubis massive, becoming thickened towards distal end, with foramen present proximally.
Range. Probably *calloviense* Zone, Kellaways Sand Formation, Peterborough.
Remarks. A single specimen comprising portions of pelvic girdle and vertebrae. It was discovered last century during the digging of a well at Peterborough gasworks. The skeleton may still remain to be excavated.

Suborder THEROPODA
Infraorder CARNOSAURIA
Family MEGALOSAURIDAE
Genus *EUSTREPTOSPONDYLUS*
Eustreptospondylus oxoniensis Walker
(not figured)

Description. A large, up to 7 m long, but lightly built carnivorous dinosaur. Vertebrae elongate, cervicals and anterior dorsals strongly opisthocoelus, scapula small, humerus slender, pubis straight and rod like with a terminal expansion. Teeth laterally compressed, keeled with fine serrations.
Range. Known only from the Middle Oxford Clay *athleta* Zone, Summertown brick pit, near Oxford.
Remarks. The most complete dinosaur known from the Oxford Clay.

Genus *METRIACANTHOSAURUS*
Metriacanthosaurus parkeri (von Huene)
(not figured)

Description. Megalosaurid with elongate neural spines. Femur slender with lesser trochanter placed proximally, pubis with expanded foot, cnemial process of tibia with strong upward projection.
Range. There is some doubt as to the exact horizon from which this specimen was obtained, however, a specimen of *Gryphaea dilatata* found adhering to the specimen suggests an Upper Oxford Clay source. The only known specimen, consisting of three dorsal vertebrae, right ilium, portions of left and right ischia, left and right pubes, right femur and proximal part of left femur, was found at Weymouth, Dorset.
Remarks. The relationship of the genus *Metriacanthosaurus* is in some doubt. Although it has been assigned to the Megalosauridae, the elongate neural spines perhaps suggest an association with the Spinosauridae.

Subclass ORNITHISCHIA
Order ORNITHOPODA
Family HYPSILOPHODONTIDAE
Genus? *DRYOSAURUS*
(not figured)

Remarks. A single limb bone appears to indicate the presence of an early hypsilophodontid dinosaur in the allochthonous fauna.

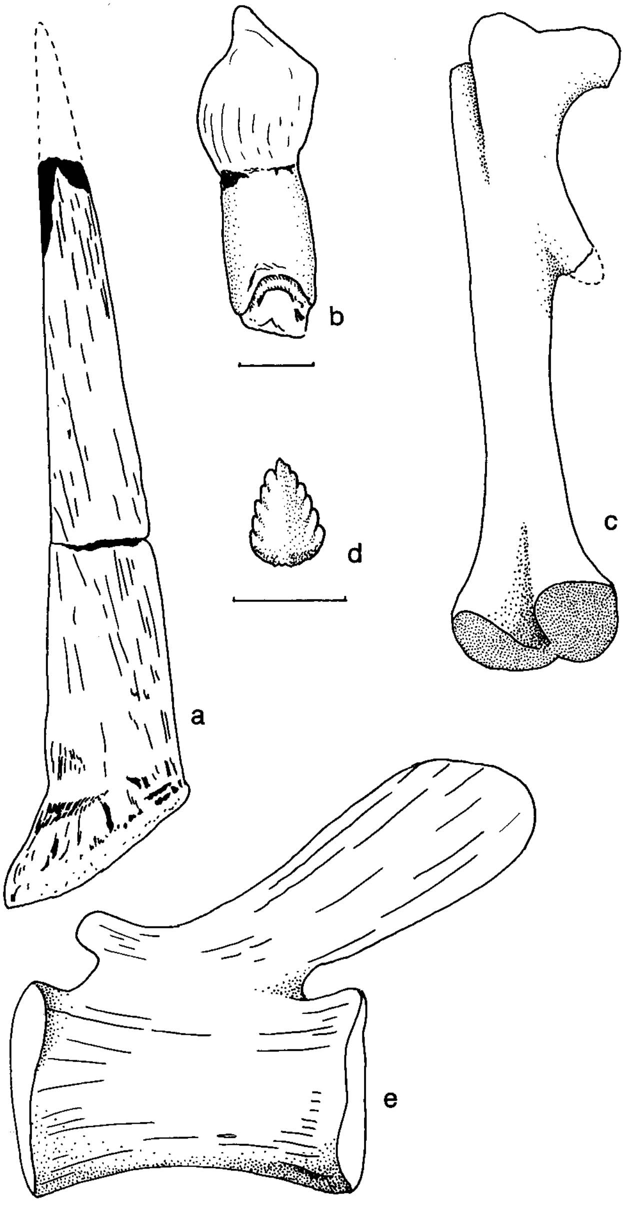
Family CAMPTOSAURIDAE
Genus *CALLOVOSAURUS*
Callovosaurus leedsi (Lydekker)
Text-fig. 11.1c

Description. Femur in which the greater trochanter is proportionally narrow, lesser trochanter expanded antero-posteriorly and flattened transversely. Distal end unexpanded with shallow anterior intercondylar groove.
Range. Known only from the Lower Oxford Clay of Peterborough, Cambridgeshire.
Remarks. A single, well preserved limb bone of a camptosaurid dinosaur is all that is known of this dinosaur.

Order STEGOSAURIA
Family STEGOSAURIDAE
Genus *LEXOVISAURUS*
Lexovisaurus durobrivensis (Hulke)
Text-fig. 11.1a

Description. Stegosaur in which the dermal armour comprises a series of elongate, subtriangular plates arranged along the back. There are two parasacral spines, and possibly a number of caudal spines.
Range. Lower Oxford Clay of Peterborough and Bedford, possibly Weymouth. Also known from the Argiles de Dives, Normandy, France.
Remarks. A small stegosaur with dermal plates, para-sacral and caudal spines. Known from several fragmentary specimens in England and France. May be closely related to the African *Kentrurosaurus*.

TEXT-FIG. 11.1. Dinosaurs from the Oxford Clay. **a**, Dermal spine from the stegosaur *Lexovisaurus* sp. **b**, Tooth probably from the sauropod *Cetiosauriscus* sp. **c**, Femur of *Callovosaurus leedsi*. **d**, Tooth of the ankylosaur *Sarcolestes leedsi*. **e**, caudal vertebra from the sauropod *Cetiosauriscus stewarti*. All scale bars 1 cm.


a
b
c
d
e

Order ANKYLOSAURIA
Family NODOSAURIDAE
Genus *SARCOLESTES*
Sarcolestes leedsi Lydekker
Text-fig. 11.1d

Description. A small ankylosaur in which the teeth are laterally compressed, with finely serrated lateral keels.
Range. Lower Oxford Clay of Peterborough.
Remarks. Only a single specimen is known of this dinosaur. Isolated fragments of dermal armour found in the Lower Oxford Clay of Whittlesey, Cambridgeshire, are probably attributable to *Sarcolestes*.

PTEROSAURS

Only fragmentary remains of pterosaurs have been discovered in the Oxford Clay. Two species of *Rhamphorhynchus* have been recognized, but the material is of little diagnostic value. Fragments have been found in the Lower and Middle Oxford Clays (Phillips 1871; Leeds 1956; Wellnhofer 1978).

Subclass PTEROSAURIA
Order RHAMPHORHYNCHIODEA
Family RHAMPHORHYNCHIDAE
Genus *RHAMPHORHYNCHUS*
Rhamphorhynchus jessoni Lydekker
and *R. bucklandi* Phillips
(not figured)

Description. Wing bones elongate, slender, thin-walled, hollow tubes.
Range. *R. jessoni* from the Middle Oxford Clay, Cambridgeshire. *R. bucklandi* Oxford Clay (probably Middle Oxford Clay), St Clement's, Oxfordshire. Fragmentary remains of *Rhamphorhynchus* sp. wing bones have been found in the Lower Oxford Clay at Peterborough.
Remarks. Pterosaur bones are extremely fragile, and as such their preservation potential is low. Remains of only four individuals are known.

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APPENDIX 1. FAUNAL LIST FOR THE OXFORD CLAY

INVERTEBRATES

BIVALVES
Anisocardia (*Anisocardia*) *tenera* (J. Sowerby)
Atreta sp.
Bositra buchii (Roemer)
Camptonectes (*Camptonectes*) *auritus* (Schlotheim)
Chlamys (*Chlamys*) *bedfordensis* Duff
Corbulomima macneillii (Morris)
C. mosae (d'Orbigny)
Dacromya acuta de Loriol
Discomiltha lirata (Phillips)
Entolium (*Entolium*) *corneolum* (Young and Bird)
E. (*E.*) ?*orbiculare* (J. Sowerby)
Eonomia timida Fursich & Palmer
Exogyra sp.
Grammatodon (*Grammatodon*) *minimus* (Leckenby)
G. (*G.*) *concinnus* (Phillips)
G. (*G.*) *clathratus* (Leckenby)
G. (*Cosmetodon*) *keyserlingii* (d'Orbigny)
Gryphaea (*Bilobissa*) *dilobotes* Duff
G. (*B.*) *lituola* Lamarck
G. (*B.*) *dilatata* J. Sowerby
Isocyprina (*Isocyprina*) *roederi* Arkell
Isognomen (*Isognomen*) *promytiloides* (Arkell)
Lopha (*Actinostreon*) *marshii* (J. Sowerby)
Meleagrinella braamburiensis (Phillips)
Mesosaccella morrisi (Deshayes)
Modiolus (*Modiolus*) *bipartitus* J. Sowerby
Myophorella (*Myophorella*) *irregularis* (Seebach)
M. (*M.*) *caytonensis* Duff
Neocrassina (*Pressastarte*) *ungulata* (Lycett)
N. (*P.*) *calvertensis* Duff
Nicaniella (*Trautscholdia*) *carinata* (Phillips)
N. (*T.*) *phillis* (d'Orbigny)
Nuculoma pollux (d'Orbigny)
N. kathrynae Duff
Oxytoma (*Oxytoma*) *inequivalve* (J. Sowerby)
Palaeonucula triangularis Duff
P. calliope (D'Orbigny)
Parainoceramus subtilus (Lahusen)
Pholadomya (*Bucardiomya*) *protei* (Brogniart)
Pinna (*Pinna*) *mitis* Phillips
P. (*P.*) *lanceolata* J. Sowerby
Plagiostoma argillacea (Phillips)
Pleuromya alduini (Brogniart)
P. uniformis (J. Sowerby)
Plicatula (*Plicatula*) *fistulosa* Morris & Lycett
Protocardia (*Protocardia*) *striatula* (J. de C. Sowerby)
Pteroperna pygmaea (Dunker)
Radulopecten scarburgensis (Young and Bird)
R. fibrosus (J. Sowerby)
Rollierella minima (J. Sowerby)
Solemya woodwardiana Leckenby
Thracia (*Thracia*) *depressa* (J. de C. Sowerby)
Trigonia (*Trigonia*) *elongata* J. de C. Sowerby

GASTROPODS AND SCAPHOPODS
Amberleya meriani (Goldfuss)
Bathrotomaria reticulata (J. Sowerby)
Dicroloma bispinosum (Phillips)
D. trifida (Phillips)
D. sp.
Procerithium damonis (Lycett)
Prodentalium calvertensis Palmer
Scaphopod gen. et sp. undetermined

AMMONITES
Alligaticeras (*Alligaticeras*) *alligatum* (Leckenby)
A. (*A.*) *rotifer* (Brown)
A. (*Properisphinctes*) *bernensis* (de Loriol)
A. (*P.*) *matheyi* (de Loriol)

Binatisphinctes binatus (Leckenby)
B. comptoni (Pratt)
B. hamulatus (Buckman)
Cadoceras compressum (Nikitin)
C. durum (Buckman)
C. milaschevici (Nikitin)
Calliphylloceras demidoffi (Rousseau)
Cardioceras (*Cardioceras*) *buckowskii* Maire
C. (*C.*) *cordatum* (J. Sowerby)
C. (*C.*) *costicardia* Buckman
C. (*Pavloviceras*) *praecordatum* Douville
C. (*P.*) *scarburgense* (Young and Bird)
Chamoussetia funifera (Phillips)
Creniceras crenatum (Bruguiere)
C. renggeri (Oppel)
Distichoceras bicostatum (Stahl)
Erymnoceras coronatum (Bruguiere)
E. argoviense (Jeannet)
Euaspidoceras acuticostatum (Young and Bird)
E. baneanum (d'Orbigny)
E. douvillei (Collot)
E. hirsutum (Bayle)
Grossouvria (*Grossouvria*) cf. *leptoides* (Till)
G. (*G.*) *sulcifera* (Oppel)
G. (*Klematosphinctes*) *vernoni* (Young and Bird)
G. (*K.*) sp. A
G. (*K.*) sp. B
G. (*Poculisphinctes*) *poculum* (Leckenby)
Hecticoceras (?*Lunuloceras*) cf. *lugeoni* (de Tystovitch)
H. (*Orbignyceras*) *pseudopunctatum* (Lahusen)
H. (*Putealiceras*) *bonarellii* de Loriol
H. (*P.*) *puteale* (Leckenby)
H. (*Sublunuloceras*) *lonsdali* (Pratt)
Homeoplanulites cardoti (Petitclerc)
H. difficilis (Buckman)
Indosphinctes patina (Neumayr)
Kosmoceras (*Gulielmiceras*) *jason* (Reinecke)
K. (*G.*) *medea* (Callomon)
K. (*Kosmoceras*) *kuklikum* (Buckman)
K. (*K.*) *spinosum* (J. de C. Sowerby)
K. (*Lobokosmokeras*) *phaeinum* (Buckman)
K. (*L.*) *proniae* Teisseyre
K. (*Zugokosmokeras*) *grossouvrei* Douville
K. (*Z.*) *obductum* (Buckman)
K. (*Z.*) *posterior* Brinkman
Longaeviceras laminatum (Buckman)
L. placenta (Leckenby)
L. staffinense Sykes
Lytoceras adeloides Kudern
Macrocephalites tumidus (Reinecke)
Ochetoceras (*Campylites*) *delmontanum* (Oppel)
O. (*Campylites*) sp.
Pachyceras (*Pachyceras*) cf. *crassum* Douville
P. (*P.*) *lalandeanum* (d'Orbigny)
P. (*Tornquistes*) *leckenbyi* Arkell
Paralcidia glabella (Leckenby)
Peltoceras (*Peltoceras*) ex grp. *athleta* (Phillips)
P. (*Peltoceratoides*) *williamsoni* (Phillips)
P. (*Peltomorphites*) *hoplophorus* (Buckman)
P. (*P.*) *subtense* (Bean)
Perisphinctes (*Perisphinctes*) sp. A
Pseudopeltoceras chauvinianum (d'Orbigny)
P. famulum Spath
Quenstedtoceras henrici (R. Douville)
Q. lamberti (J. Sowerby)
?*Q. paucicostatum* (Lange)
Reineckeia (*Collotia*) cf. *collotiformis* (Jeannet)
R. (*C.*) *oxyptychoides* Spath
R. (*C.*) *spathi* Bourquin
R. (*Reineckeia*) *anceps* (Reinecke)
Scaphitodites navicula Buckman
Sigaloceras (*Catasigaloceras*) *anterior* (Brinkman)
S. (*C.*) *enodatum* (Nikitin)
S. (*C.*) sp. A

TEUTHOIDS
Belemnopsis bessina (d'Orbigny)
Belemnopsis depressa (Quenstedt)
Belemnotheutis antiquus Pearce
Cylindroteuthis puzosiana (d'Orbigny)
Hibolithes hastata Montfort
Lagonibelus beaumontiana (d'Orbigny)
Mastigophora brevipinnus Owen
Pachyteuthis abbreviata (Miller)
?*Romaniteuthis* sp.
Trachyteuthis sp.

NAUTILOID
Paracenoceras calloviense (Oppel)

FORAMINIFERA
Ammobaculites agglutinans (d'Orbigny)
A. coprolithiformis (Schwager)
A. suprajurassica (Schwager)
Brotzenia cf. nuda (Terquem)

B. parastelligera Hofker
B. stelligicostata (Bielecka & Pozaryski)
Bullpora rostrata Quenstedt
Citharina flabellata (Guembel)
C. implicata (Schwager)
C. serratocostata (Guembel)
C. tharinella
Citharinella moelleri (Uhlig)
C. nikitini (Uhlig)
Cyclogyra liasina (Terquem)
Dentalina bicornis Terquem
D. cuneiformis Terquem & Berthelin
D. digitata Paalzow
D. filiformis (d'Orbigny)
D. guembeli Schwager
D. pseudocommunis Franke
D. torta Terquem
D. turgida Schwager
D. vetusta d'Orbigny
Eoguttulina liassica (Strickland)
Epistomina mosquensis Uhlig
E. nuda Terquem
E. stellicostata Bielecka & Pozaryski
E. stelligera (Reuss)
Frondicularia franconica (Guembel)
F. moelleri Uhlig
F. nikitini Uhlig
F. pseudosulcata Barnard
Guadryina sherlocki (Battenstaedt)
G.? sp. 2 Lutze
Guttulina pera Lalicker
Lagena sp.
Lenticulina ectypa (Loeblich & Tappan)
L. ectypa (L & T) *costata* Cordey
L. major (Bornemann)
L. muensteri (Roemer)
L. plebeia (Terquem & Berthelin)
L. quenstedti (Guembel)
L. subalata (Reuss)
L. tricarinella (Reuss)
L. varians (Bornemann)
Lingulina cernua Terquem
L. longiscata (Terquem)
L. laevissima (Terquem)
L. nodosaria (Terquem)
Marginula batrakiensis (Mjatliuk)
Marginulina ectypa (Loeblich & Tappan)
M. glabra d'Orbigny
Milliamina jurassica (Haeusler)
Miliospirella sp.
Nodosaria corallina Guembel
N. hortensis Terquem
N. metensis Terquem
N. opalina Bertenstein
Nubeculinella bigoti Cushman
Ophthalmidium strumosum (Guembel)
O. stuifense (Paalzow)
Paalzowella feifeli (Paalzow)
Planularia anceps
P. beierana (Guembel)
P. eugenii (Terquem)
P. filosa (Terquem)
P. protracta (Bornemann)
P. suturalis (Terquem)
Pseudolamarckina rjasenensis (Uhlig)
Pseudonodosaria humilis (Bornemann)
P. radiata (Barnard)
P. tenuis (Bornemann)
P. vulgata (Bornemann)
Quinqueloculina sp.
Rheophax helveticus (Hausler)
Saracenaria oxfordiana Tappan
Spirillina infima (Strickland)
Subdelloidina sp.
Textularia jurassica (Guembel)
Triplasia acuta Bartenstein & Brand
T. althoffi (Bartenstein)
T. kimeridiensis (Bielecka & Pozaryski)
Tristix triangularis Barnard
T. oolithica (Terquem)
Trochammina globigeriniformis (Parker & Jones)
T. squamata Parker & Jones
Vaginula contracta (Terquem)
Verneuilinoides tryphera Loeblich & Tappan

COELENTERATES
Protulophila gestroi Roverto
Trochocyathus magnevillianus Michelin

BRYOZOA
Arachnidium smithii (Phillips)
Hyporosopora spp.
Plagioecia sp.
Ropalonaria? arachne (Fischer)
Stomatopora spp.

BRACHIOPODS
Acanthorhynchia lorioli (Rollier)
Aulacothyris bernadina (d'Orbigny)
Cererithyris? oxoniensis (Davidson)
Lingula craneae Davidson
Orbiculoidea latissima (Sowerby)
Rhynchonelloidella socialis (Phillips)

ANNELIDS
Genicularia vertebralis (J. de C. Sowerby)
'*Serpula*' *sulcata* J. de C. Sowerby
Serpula sp.

ARTHROPODS

CRUSTACEANS
Eryma mandelslohi von Meyer
Eryon sublevis Carter
Glyphaea rostrata Carter
G. stricklandi Bean
Goniochirus cristatus Carter
Magila dissimilis Carter
M. levimana Carter
Mecochirus pearcei Meloy
Pagurus sp.
Pseudastacus? *serialis* Carter

OSTRACODS
Cytherella fullonica Jones and Sherborn
Eucytherura (*Vesticytherura*) *costaeirregularis* Whatley
E. (*V.*) *scottia* Whatley
Galliaecytheridea postrotunda Oertli
Glabellacythere reticulata Whatley
G. nuda Wienholz
Lophocythere interrupta interrupta Triebel
L. scabra bucki Lutz
Nophrecythere cruciata cruciata (Triebel)
N. cruciata alata (Whatley)
N. cruciata intermedia (Lutze)
N. cruciata oxfordiana (Lutze)
Palaeocytheridea parabakirovi Malz
Pedicythere anterodentina Whatley
Pleurocythere caledonia Whatley
P. borealis carinata Whatley
Praeschuleridea batei Whatley
Progonocythere multipunctata Whatley
Pseudohutsonia hebridica Whatley
Pseudoperissocytheridea parahieroglyphica Whatley
Schuleridea triebeli (Steghaus)
Terquemula flexicosta lutzei (Whatley)
Vernoniella sequana Oertli

CIRRIPEDES
Pollicepes concinnus Morris
P. planulatus Morris

ECHINODERMS
Anchistrum issleri (Croneis)
A. gamma Hodson et al.
A. monochordata Hodson et al.
Disaster granulosus (Goldfuss)
Eosalenia sp.
Isocrinus fisheri (Forbes)
Ophiochiton? *pratti* (Forbes)
Ophiomusium weymouthiense (Damon)
Rhabdotites divergens Hodson et al.
R. bifidus Hodson et al.
R. tridens Hodson et al.
Theelia wessexensis Hodson, Harris and Lawson

TRACE FOSSILS
Mycelites enameloides Martill
Ophiomorpha sp.
Thalassinoides sp.

VERTEBRATES

ELASMOBRANCHS
Asteracanthus acutus Agassiz
A. ornatissimus Agassiz
Heterodontus sp.
Hybodus obtusus Agassiz
Hybodus dawni Martill
Notidanus muensteri Agassiz
Orectoloboides pattersoni Thies
Palaeobrachaelurus bedfordensis Thies
Paracestracion falcifer Wagner
Protospinax muftius Thies
Spathobatis werneri Thies
Sphenodus longidens (Agassiz)

CHIMAERAS
Brachymylus altidens Woodward
Ischyodus egertoni (Buckland)
Ischyodus beaumonti Egerton
Leptacanthus spp.
Pachymylus leedsi Woodward

ACTINOPTERYGIANS
Aspidorhynchus eodus Egerton
Asthenocormus sp.
Caturus porteri Rayner
Caturus sp.
Coccolepis sp.

Heterostrophus phillipsi Woodward
Hypsocormus leedsi Woodward
H. tenuirostris Woodward
Leedsichthys problematicus Woodward
Lepidotes latifrons Woodward
L. leedsi Woodward
L. macrocheirus Egerton
'*Leptolepis*' *macrophthalmus* Egerton
Mesturus leedsi Woodward
Osteorachis leedsi Woodward
Pholidophorus sp.
Sauropsis longimanus Agassiz
Otoliths

ICHTHYOSAURS
Ophthalmosaurus icenicus Seeley
O. monocharactus Appleby

LONG NECKED PLESIOSAURS
Cryptoclidus eurymerus (Phillips)
C. richardsoni (Lydekker)
Muraenosaurus beloclis Seeley
M. leedsii Seeley
Tricleidus seeleyi Andrews

PLIOSAURS
Liopleurodon ferox Sauvage
L. pachydeirus (Seeley)
Peloneustes philarchus (Seeley)
Pliosaurus andrewsi Tarlo
Simolestes vorax Andrews

CROCODILES
Metriorhynchus brachyrhynchus Deslongchamps
M. superciliosus Deslongchamps
Steneosaurus durobrivensis Andrews
S. leedsi Andrews

DINOSAURS
Callovosaurus leedsi (Lydekker)
Cetiosauriscus stewarti Charig
Dryosaurus sp.
Eustreptospondylus oxoniensis Walker
Lexovisaurus durobrivensis (Hulke)
Metriacanthosaurus parkeri (von Huene)
Ornithopsis leedsi Hulke
Sarcolestes leedsi Lydekker

PTEROSAURS
Rhamphorhynchus bucklandi Phillips
R. jessoni Lydekker

APPENDIX 2. LIST OF OXFORD CLAY FOSSIL LOCALITIES

Compiled by David M. Martill

This list is not comprehensive, but includes currently active pits, coastal sites, and a number of sites of historical importance. A few of the active sites have yielded complete skeletons in recent years despite the highly mechanized nature of the workings. Invertebrates are generally abundant at all of the sites.

It will be apparent that most vertebrates from the Oxford Clay have been, and still are, found in the active brick pits. IT CANNOT BE TOO HIGHLY STRESSED THAT THESE WORKINGS ARE PRIVATE PROPERTY, AND ARE DANGEROUS. Permission must always be obtained to visit them, and conditions of entry rigorously observed.

1. Peterborough, Buntings Lane Borrow Pit. Rubbish dump. TL 200957. Kellaways Beds and basal Lower Oxford Clay. Vertebrates reasonably common.
2. Peterborough, Dogsthorpe Brick Pit. Recently abandoned. TF 210020. Kellaways Beds/Lower Oxford Clay Junction, up to *E. coronatum* Zone. Vertebrates reasonably common in basal Lower Oxford Clay. Arthropods abundant in top of *K. jason* Zone and base of *E. coronatum* Zone.
3. Peterborough, Orton Brick Pit. Active. TL 170940. Lower Oxford Clay *K. jason* Zone to *E. coronatum* Zone.
4. Peterborough, Yaxley Brick Pit. Disused. TL 180930. Lower Oxford Clay *K. jason* Zone to basal *P. athleta* Zone. A boulder clay filled glacial channel on the south side of the pit yields abundant derived Middle Oxford Clay fossils.
5. Peterborough, Norman Cross Brick Pit. Disused. TL 175917. Lower and Middle Oxford Clay. *S. calloviense* Zone to high in the *P. athleta* Zone.
6. Whittlesey, Kings Dyke. Numerous disused brick pits at TL 237970, 230975, 243975. Lower Oxford Clay, *S. calloviense* Zone to basal *P. athleta* Zone.
7. Whittlesey, Active brick pit. TL 247975. Lower Oxford Clay, *S. calloviense* Zone to basal *P. athleta* Zone.
8. Whittlesey, Active brick pit. TL 250967. Lower Oxford Clay to base of poorly fossiliferous Middle Oxford Clay.
9. Maxey Gravel Pit. Cambridgeshire. Active. Floor of pit sometimes Lower Oxford Clay, otherwise Cornbrash. TF 135075.
10. Other Gravel pits in north Cambridgeshire, especially near Baston. TF 110130. Floor of pit frequently exposes Lower Oxford Clay, probably *E. coronatum* Zone.

11. Warboys Brick Pit, Cambridgeshire, TL 308818. Disused, Upper Oxford Clay with abundant pyritised invertebrates. Large *Gryphaea* sp. with epifaunas. Disconformity and associated breccia with Ampthill Clay above.
12. St Ives, Cambridgeshire. Disused Clay pits. TL 326715. Age undetermined. May show uppermost Oxford Clay with base of Elsworth Rock. Needs further investigation.
13. Caldecotte Lake, Simpson, Milton Keynes, Buckinghamshire. Formerly exposed Lower Oxford Clay of *E. coronatum* Zone. Vertebrates were relatively abundant. SP 892352.
14. Stewartby, Bedfordshire. Old pits at TL 015415. Working pit at TL 030420. Lower Oxford Clay. Kellaways beds sometimes exposed in drainage sumps.
15. Vale of Marston, Bedfordshire. Numerous old pits. TL 005425, SP 965405. Lower Oxford Clay.
16. Kempston, near Bedford. Old pits. TL 036450. Lower Oxford Clay.
17. Bletchley Brick works, Buckinghamshire. SP 855315. Lower and Middle Oxford Clay, *K. jason* Zone to high in the *P. athleta* Zone. All highly fossiliferous (see Callomon 1968 for detailed section).
18. Calvert Brick Works, Oxfordshire. Active brick pit at SP 695234. Numerous disused pits in area are either flooded or used for waste disposal. Lower to basal Middle Oxford Clay (see Callomon 1968 for detailed section).
19. Woodham, Bucks. Old brick pit, now completely filled with waste, nothing visible. SP 708185. Middle and Lower Oxford Clay with Lamberti Horizon (see Hudson and Palframan 1969).
20. Summertown, near Oxford. Old pits in Middle Oxford Clay. SP 510090.
21. Christian Malford, Wiltshire. Old borrow pits by side of railway (no exposure), ST 956775. Probably top of Middle Oxford Clay (see Page this volume). One of the most famous Oxford Clay localities.
22. Chickerell Brick yard, near Weymouth, Dorset. Disused. SY 644797.
21. The Fleet, Tidmoor point, Dorset. Very small cliff of Middle Oxford Clay. Pyritised fossils are abundant in the beach gravel. SY 643786.
23. Furzy Cliff at the foot of Jordans Hill, Weymouth, Dorset. Coastal exposure. SY700818. Upper Oxford Clay.
24. Castle Cliff, Scarborough, Yorkshire. No access. TA 052892.
25. Cayton Bay, Yorkshire. Sea cliffs. TA 070843.
26. Stanton Harcourt, Oxfordshire. SP 410050. Base of old gravel pits, and borrow pits in gravel pits converted to rubbish tips. Excellent outcrops of Middle Oxford Clay, Lamberti Horizon and base of Upper Oxford Clay.
27. Ashton Keynes, Wiltshire. SU 055950. Base of active gravel pits. Lower Oxford Clay of unusual oil shale facies, and Middle and Upper Oxford Clay. Profuse ammonites with original aragonite shells on pyrite internal moulds.

APPENDIX 3. COLLECTIONS OF OXFORD CLAY FOSSILS

Below is a selection of United Kingdom museums which hold collections of Oxford Clay vertebrates. Many of the museums have only a small portion of their material displayed. If you wish to use the collections for comparative purposes be sure to arrange to see the collections in advance.

Bath. Bath Museum of Geology, 18 Queen Square, Bath, Avon, BA1 2HP. Telephone (0225) 28144. Some Christian Malford material, including a crocodilian skull.

Bristol. Bristol City Museum and Art Gallery, Queens Road, Bristol, BS8 1RL. Telephone (0272) 299771. Some fish from the Christian Malford locality. Unfortunately a large portion of the Bristol collection was destroyed by enemy action in 1940.

Cambridge. Sedgwick Museum of Geology, University of Cambridge, Downing Street, Cambridge, CB2 3EQ. Some marine reptile material and fragmentary dinosaur bones.

Cardiff. National Museum of Wales. Cathays Park, Cardiff, CF1 3NP. Telephone (0222) 397951. Some marine reptile material, not currently displayed.

Glasgow. Hunterian Museum, University of Glasgow, G12 8QQ. Telephone (041) 330 4221. Part of the Leeds collection, including an almost complete *Cryptoclidus* skeleton.

Leicester 1. Leicestershire Museums and Art Gallery, New Walk, Leicester, LE1 6TD. Telephone (0533) 554100. Large collection of fragmentary skeletons of marine reptiles. Good selection of *Ophthalmosaurus* material. Some material on display.

Leicester 2. Leicester University, Department of Geology, University Road, Leicester, LE1 7RH. Telephone (0533) 554455. Large number of marine reptiles in concretions. Three almost complete skeletons of *Ophthalmosaurus*. Some type and figured material.

Liverpool. Department of Geology, University of Liverpool. Isolated pieces of fish and marine reptiles displayed in department foyer.

London. Natural History Museum, Cromwell Road, South Kensington, SW7 5BD. Telephone (071) 938 9123. The greater portion of the Leeds collection is housed here. Unfortunately only an *Ophthalmosaurus* and a baby *Cryptoclidus* are currently displayed.

Nottingham. Natural History Museum, Wollaton Hall, Wollaton Park, Nottingham, NG8 2AE. Telephone (0602) 281333. Fragmentary marine reptile material.

Oxford. University Museum, Parks Road, Oxford, OX1 3PW. Telephone (0865) 272950. Almost complete skeleton of *Eustreptospondylus* on display.

Peterborough. Peterborough City Museum, Priestgate, Peterborough, Cambridgeshire, PE1 1LF. Telephone (0733) 43329. Extensive collections made by J. Phillips during the early part of this century. Almost complete crocodilian and *Cryptoclidus* on display. New material arriving on regular basis.

There are good collections of Oxford Clay vertebrates in the USA, New York, AMNH; Germany, Stuttgart, Frankfurt and Tübingen; France, Paris; and Sweden, Upsaala. By far the best collections of the marine reptiles from a visual point of view are in Germany at the Senckenberg Museum, Frankfurt, and the Institute for Geology and Palaeontology at the University of Tübingen, in Tübingen.

SYSTEMATIC INDEX

This index has been compiled such that higher taxa, genera, subgenera and species, as well as species within genera and subgenera may be consulted. Plate numbers are in bold typeface.

The Jurassic Oxford Clay, the major source of brick clay in the United Kingdom, contains a diverse and exceptionally well preserved fauna. Historically it has provided the basis for Brinkmann's now classic work on ammonite evolution, and furnished the Leeds brothers with the finest collection of marine reptiles ever assembled. Only now have descriptions of the entire fauna been available in a single volume. The introduction describes the geological setting and discusses aspects of the palaeoecology. Ten chapters deal with all the major macroinvertebrate groups, some of the microinvertebrates, and the famous vertebrate fauna. Useful appendices provide the collector with a list of important fossil localities and the locations of museums with collections of comparative material. In addition, an up to date list of Oxford Clay taxa and a comprehensive bibliography of Oxford Clay palaeontology are provided.

This book is a definitive guide to our current knowledge of Oxford Clay faunal diversity. It is an essential purchase for all those interested in Jurassic palaeontology.

Also in this series

Field Guides to Fossils No. 1: *Fossil Plants of the London Clay.* M. E. Collinson. Palaeontological Association, London, 1983. 121 pp., including 3 tables and 242 text-figs. (£7·95), paperback, ISBN 0-901702-26-9.

Field Guides to Fossils No. 2: *Fossils of the Chalk.* Edited by A. B. Smith. Palaeontological Association, London, 1987. 306 pp., including 59 plates. (£11·50), paperback, ISBN 0-901702-36-6.

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PALAEONTOLOGICAL ASSOCIATION

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