PALAEOECOLOGY OF A BITUMINOUS SHALE—
THE LOWER OXFORD CLAY OF
CENTRAL ENGLAND

by K. L. DUFF

ABSTRACT. Quantitative palaeoecological studies, using triangular plots, rarefaction curves, trophic nuclei, trophic group composition, and Diversity Index, have allowed the definition of ten different biofacies within the Lower Oxford Clay (Upper Jurassic, Middle Callovian) of central England. Analysis of the distribution of these biofacies and seven lithofacies groups, has led to the recognition of the Lower Oxford Clay as a deepening-water sequence, in which two distinct environmental cycles are present. By comparison with other Mesozoic shale facies, the Lower Oxford Clay appears different in having its fauna dominated by infaunal deposit-feeders and by high-level ('pendent') epifaunal suspension-feeders; only the Upper Lias is comparable. Evolutionary changes are considered between Palaeozoic and Mesozoic deposit-feeder dominated assemblages, with siphonate bivalves occupying most of the niches previously held by articulate brachiopods.

PALAEOECOLOGICAL studies on clay sequences are of great importance in building up an understanding of Mesozoic environmental conditions. Most thick clay sequences seem homogeneous, but close inspection reveals many lithological and faunal variations capable of analysis. This is especially true of bituminous shale sequences, which until the work of Hallam (1960, p. 10), were usually thought of as homogeneous. Hallam showed that in the Blue Lias several lithologies, each with a characteristic fauna, could be recognized; only some lacked benthonic fossils, which had previously been considered a typical feature of bituminous shales. Since then other studies have been made on similar rock sequences, and it is the purpose of this paper to show the high variability, both in lithology and fauna, that exists within the Lower Oxford Clay.

STRATIGRAPHY

The Callovian deposits of England represent a transgressive marine phase after the lagoonal and estuarine conditions of the Bathonian, the base of the transgression being marked by the Upper Cornbrash, which passes upwards into the Kellaways Clay and Kellaways Rock. After the deposition of the Kellaways Rock, conditions appear to have stabilized, with deposition of a thick argillaceous sequence of bituminous shales, shaly clays, and more calcareous clays. The Yorkshire succession (text-fig. 1) differs in that it is developed in a more marginal facies, and has been well described by Wright (1968, p. 367): in this paper only the clay facies will be considered in detail. The Lower Oxford Clay has been defined by Callomon (1968, p. 265), and occupies the whole of the Middle Callovian together with the top subzone of the Lower Callovian and the lower part of the Upper Callovian (text-fig. 2). It consists of about 16–25 m of grey bituminous shaly clays with other minor lithologies developed within them (text-fig. 3). The biostratigraphy is further described elsewhere (Duff, unpublished Ph.D. thesis, Leicester University, 1974). The Lower Oxford Clay is of great importance for brickmaking, and is extensively quarried

North-east Yorks.	ZONE	Central & Southern England	STAGE
Yorkshire Oxford Clay	Mariae	U. Oxford Clay	L. Oxfordian
Hackness Rock	Lamberti	M. Oxford Clay	U. Callovian
	Athleta		
hiatus			
Langdale Beds	Coronatum	L. Oxford Clay	M. Callovian
hiatus	Jason		
Kellaways Rock	Calloviense	Kellaways Rock	L. Callovian
Shales of the Cornbrash	Macro-cephalus	Kellaways Clay	
U. Cornbrash		U. Cornbrash	
U. Deltaic Series	Discus	L. Cornbrash	U. Bathonian

TEXT-FIG. 1. Comparison of the lower part of the Upper Jurassic of Yorkshire and southern England, showing the development of a marginal facies in Yorkshire during Callovian times. After Wright (1968). All zones drawn to equal thickness, therefore the lithological sections are not to scale.

between Peterborough and Aylesbury. Higher parts of the Oxford Clay are more plastic, less bituminous, and not so easily used for brickmaking; consequently exposures are rarer.

The zonal divisions (text-fig. 2) have been considered by Callomon (1955, p. 254, 1964, 1968, p. 265), and are now widely accepted. Previous workers on the Oxford Clay have dealt mainly with the general stratigraphy of the formation, and paid scant attention to the Lower Oxford Clay itself (Woodward 1895, p. 5; Morley Davies 1916; Neaverson 1925; Arkell 1933, p. 341), although Brinkmann (1929, p. 28) and Callomon (1955, 1968) have dealt with that part of the formation in considerable detail. The only palaeoecological studies have been by Rutten (1956) and Hudson and Palframan (1969).

STAGES		ZONES	SUBZONE	DIVISION
OXFORDIAN	LOWER	Cardioceras cordatum	C. cordatum	UPPER OXFORD CLAY
			C. costicardia	
			C. bukowskii	
		Quenstedtoceras mariae	C. praecordatum	
			C. scarburgense	
CALLOVIAN	UPPER	Quenstedtoceras	lamberti	MIDDLE OXFORD CLAY
		Peltoceras athleta	Upper	
			Middle	
			Lower	
	MIDDLE	Erymnoceras coronatum	K. (Zugokosmoceras) grossouvrei	LOWER OXFORD CLAY
			K. (Zugokosmoceras) obductum	
		Kosmoceras jason	K. (Gulielmites) jason	
			K. (Gulielmites) medea	
	LOWER	Sigaloceras calloviense	S. (Catasigaloceras) enodatum	
			Sigaloceras calloviense	KELLAWAYS ROCK
			Proplanulites koenigi	
		Macrocephalites macrocephalus	M. (Kamptokephalites) kamptus	KELLAWAYS CLAY
			M. (Macrocephalites) macrocephalus	UPPER CORNBRASH

TEXT-FIG. 2. The zonal sequence of the Callovian and Lower Oxfordian stages of NW. Europe. After Callomon (1968).

NATURE OF THE FAUNA

The composition of the Lower Oxford Clay fauna has been considered elsewhere (Callomon 1968, p. 269); molluscs are very dominant, mostly cephalopods and bivalves. Other common macrofauna include gastropods, scaphopods, brachiopods, crustacea, annelids, and occasional echinoderms; a diverse and well-preserved vertebrate fauna has been described by several authors (Arkell 1933, p. 357). A faunal list of the macro-invertebrates is as follows:

POLYCHAETA

Genicularia vertebralis (J. de C. Sowerby)
Serpula sp.

CEPHALOPODA

'*Binatisphinctes*' *comptoni* (Pratt)
'*B.*' *fluctuosus* (Pratt)

CEPHALOPODA (*cont.*)

'*B.*' spp.
Choffatia spp.
Erymnoceras spp.
Hecticoceras spp.
Kosmoceras (*Gulielmiceras*) *gulielmi* (J. Sowerby)
K. (*Kosmoceras*) *baylei* Tintant
K. (*K.*) *grossouvrei* Douvillé
K. (*K.*) *nodosum* Callomon
K. (*Spinikosmoceras*) *aculeatum* (Eichwald)
K. (*Sp.*) *acutistriatum* Buckman
K. (*Sp.*) *castor* (Reinecke)
K. (*Sp.*) *pollux* (Reinecke)
K. (*Zugokosmoceras*) *enodatum* (Nikitin)
K. (*Z.*) *jason* (Reinecke)
K. (*Z.*) *medea* Callomon
K. (*Z.*) *obductum* (Buckman)
K. (*Z.*) *zugium* (Buckman)
Pseudocadoceras spp.
Reineckeia spp.
Sigaloceras calloviense (J. Sowerby)
Belemnopsis sulcata (Miller)
Belemnoteuthis antiquus Pearce
Cylindroteuthis puzosianus (d'Orbigny)

BIVALVIA

Anisocardia (*Anisocardia*) *tenera* (J. de C. Sowerby)
Bositra buchii (Roemer)
'*Entolium*' sp. nov.
Camptonectes (*Camptonectes*) *auritus* (Schlotheim)
Chlamys (*Chlamys*) sp. nov.
C. (*Radulopecten*) *fibrosa* (J. Sowerby)
C. (*R.*) *scarburgensis* (Young and Bird)
Corbulomima macneillii (Morris)
Discomiltha lirata (Phillips)
Entolium (*Entolium*) *corneolum* (Young and Bird)
Grammatodon (*Grammatodon*) *clathrata* (Leckenby)
G. (*G.*) *concinna* (Phillips)
G. (*G.*) *minima* (Leckenby)
G. (*G.*) *montaneyensis* (de Loriol)
Gryphaea (*Bilobissa*) sp. nov.
Isocyprina (*Isocyprina*) *roederi* Arkell
Meleagrinella braamburiensis (Phillips)
Mesosaccella morrisi (Deshayes)
Modiolus (*Modiolus*) *bipartitus* J. Sowerby

Myophorella (*Myophorella*) *irregularis* (Seebach)
Nanogyra nana (J. Sowerby)
Neocrassina (*Neocrassina*) sp. nov.
N. (*N.*) *ungulata* (Lycett)
Nuculoma sp. nov.
N. pollux (Raspail ex d'Orbigny)
Oxytoma (*Oxytoma*) *inequivalvis* (J. Sowerby)
Palaeonucula cottaldi (de Loriol)
Palaeonucula sp. nov.
Parainoceramus subtilis (Lahusen)
Pinna (*Pinna*) *mitis* Phillips
Plicatula (*Plicatula*) cf. *fistulosa* Morris and Lycett
Pleuromya alduini (Brongniart)
P. uniformis (J. Sowerby)
Protocardia (*Protocardia*) *striatulum* (J. de C. Sowerby)
Protocardia sp.
Pteroperna? pygmaea (Dunker)
Rollierella minima (J. Sowerby)
Solemya woodwardiana Leckenby
Thracia (*Thracia*) *depressa* (J. de C. Sowerby)
Trautscholdia phillis (d'Orbigny)

GASTROPODA

Dicroloma bispinosa (Phillips)
D. trifida (Phillips)
Pleurotomaria reticulata (J. Sowerby)
'*Procerithium*' *damonis* (Lycett)
Spinigera spinosa d'Orbigny

SCAPHOPODA

Prodentalium calvertensis Palmer

BRACHIOPODA

Lingula craneae Davidson
'*Orbiculoidea*' sp.
'*Rhynchonella*' sp.

CRUSTACEA

Mecocheirus pearcei M'Coy

ECHINODERMATA

Unidentified ophiuroids

The microfauna is more restricted than that of the Middle and Upper Oxford Clays, the foraminifera having been studied by Cordey (1962, 1963) and Barnard (1952, 1953), the ostracodes by Whatley (1970), and the coccoliths by Rood, Hay and Barnard (1971) and Rood and Barnard (1972). Apparently, the darker, more organic rich shaly clays of the Middle Callovian were less conducive to the development of a diverse benthonic microfauna than were the more calcareous clays of the Upper Callovian–Lower Oxfordian.
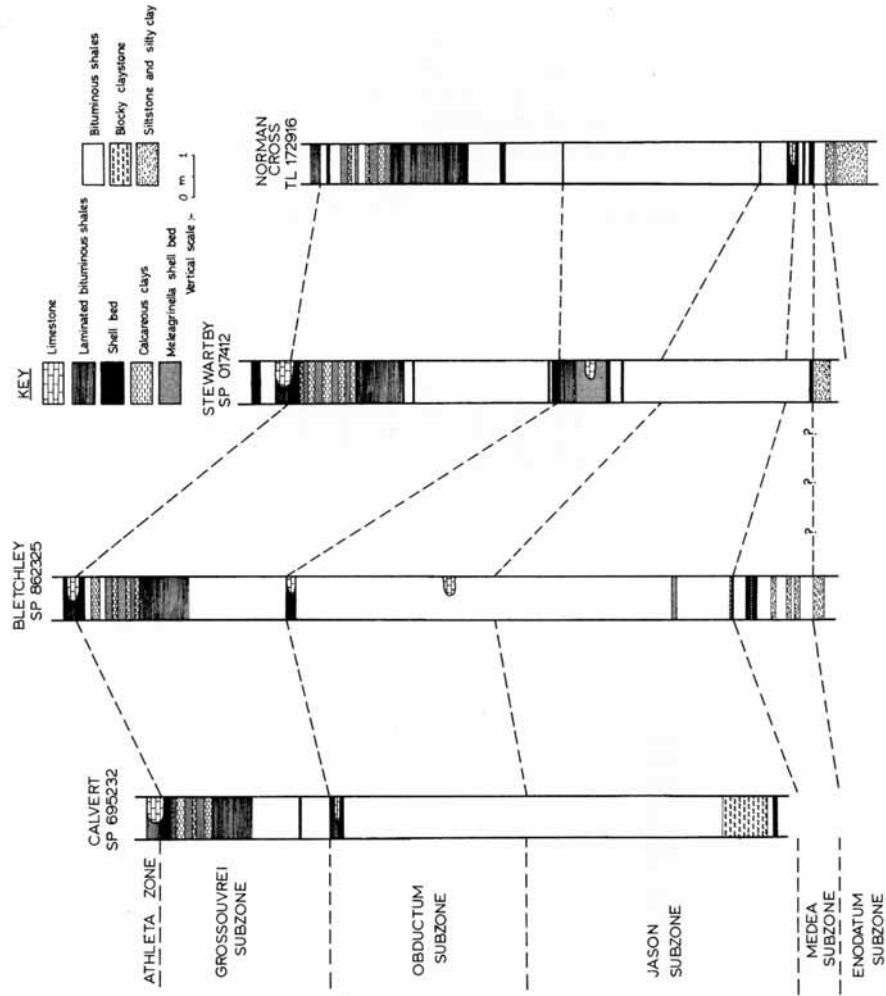
This paper is based on detailed studies made on the Lower Oxford Clay in 1970–

1971 at four brickpits in central England (text-fig. 4), collections coming from beds of Calloviense–Coronatum Zone age. The beds are well exposed in continuously accessible profiles, and are clearly marked off at the base by the sandy Kellaways Rock, and at the top by a concretionary limestone bed, the Acutistriatum Band (text-fig. 3); this marker horizon was shown by Callomon (1968, p. 272) to be the basal bed of the Athleta Zone. The palaeoautecology of the bivalves is summarized in Table 1.

TABLE 1. Life habits of the bivalve genera recognized in the Lower Oxford Clay of southern England.

Genera and feeding groups	Maximum shell length (mm)	Epifaunal				Infaunal						Taxonomic position
		Swimming	Free-living or cemented	Byssally attached	'Pendent'	Non-siphonate	Short siphons	Long siphons	Mucus-tube feeders	Byssally attached	Mobile	
Deposit-feeders												Superfamily
Palaeonucula	18·4										×	NUCULACEA
Mesosaccella	17·6										×	NUCULANACEA
Suspension-feeders												
Solemya	38·0							×				SOLEMYACEA
Grammatodon	28·0					×					×	ARCACEA
Modiolus	70·0			×								MYTILACEA
Pinna	82·4			×								PINNACEA
Pteroperna	15·3				×							PTERIACEA
Parainoceramus	72·5				×							PTERIACEA
Bositra	15·0				×							PECTINACEA
Oxytoma	39·8				×							PECTINACEA
Meleagrinella	33·7				×							PECTINACEA
Entolium	31·0	×										PECTINACEA
'Entolium' gen. nov.	12·3			×								PECTINACEA
Camptonectes	58·0			×								PECTINACEA
Chlamys	9·7			×								PECTINACEA
Radulopecten	76·0			×								PECTINACEA
Plicatula	26·8		×									PECTINACEA
Gryphaea	80·0		×									OSTREACEA
Nanogyra	11·2		×									OSTREACEA
Myophorella	88·0					×					×	TRIGONACEA
Discomiltha	47·0						×	×				LUCINACEA
Neocrassina	21·2					×					×	ASTARTACEA
Trautscholdia	12·5					×					×	ASTARTACEA
Protocardia	30·3						×				×	CARDIACEA
Anisocardia	25·0						×				×	ARCTICACEA
Isocyprina	20·0						×				×	ARCTICACEA
Rollierella	24·0						×				×	ARCTICACEA
Corbulomima	6·8					×				×		MYACEA
Pleuromya	71·0							×				PHOLADOMYACEA
Thracia	65·0						×	×				PANDORACEA

TEXT-FIG. 3. Lithological sections measured at the four quarries examined in central England.

The life habits of the benthonic invertebrates other than bivalves which occur in the Lower Oxford Clay are as follows:

Suspension-feeders: *Genicularia vertebralis* (epifaunal), *Serpula* sp. (epifaunal), '*Orbiculoidea*' sp. (epifaunal), '*Rhynchonella*' sp. (epifaunal), *Lingula craneae* (infaunal).

Deposit-feeders: *Procerithium damonis* (epifaunal), *Dicroloma bispinosa* (infaunal), *Dicroloma trifida* (infaunal), *Spinigera spinosa* (infaunal), *Prodentalium calvertensis* (infaunal).

Scavengers: *Mecocheirus pearcei*, ophiuroids.

Browsing herbivores: *Pleurotomaria reticulata*.

The methods of analysis used here are a combination of those introduced by both zoologists and palaeontologists, and have not previously been applied to Mesozoic clay deposits. Thus there is a lack of comparative data, and the Lower Oxford Clay has been compared only qualitatively with other Mesozoic sediments, especially clays.
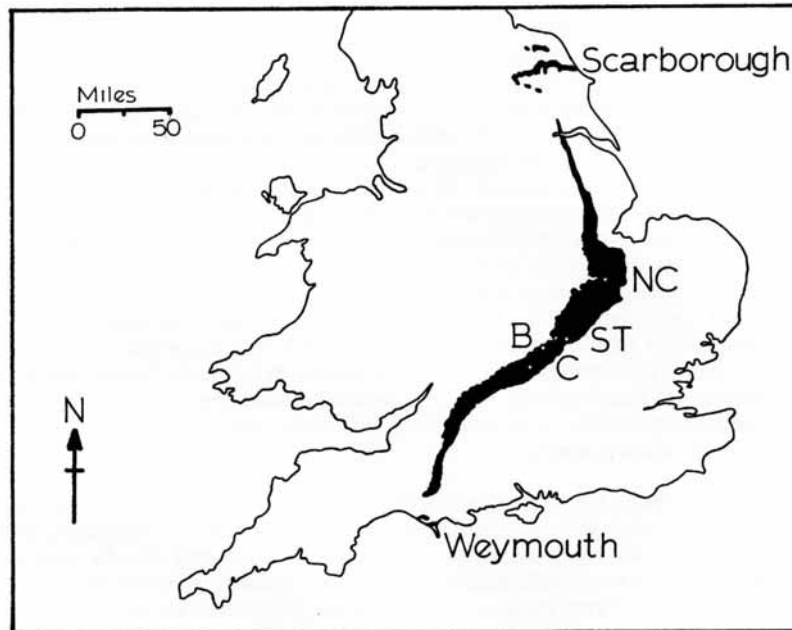
TEXT-FIG. 4. The outcrop of the Oxford Clay in Britain, showing the location of the major sections examined.

Preservation. The Lower Oxford Clay is notable for the preservation of original shell aragonite in the shales, especially in the bituminous shales; a feature caused by the impervious nature of the sediment (Hudson and Palframan 1969, p. 398). However, most of the material is crushed.

In some of the more porous lithologies, notably the shell beds, there has been replacement of the original aragonite by secondary calcite, precipitated from calcareous fluids moving through the rock, or by recrystallization of shell material *in situ*. A more notable post-depositional preservational change has been the growth of pyrite in many of the shell beds, and in local pockets within the shales. It appears that the porous shell beds have acted as 'aquifers' along which sulphide-rich fluids moved, and that when the pyrite was precipitated it became concentrated in the central parts of the shell beds. This is particularly noticeable in many of the Nuculacean shell beds, where the central part of the shell bed is strongly pyritized, with pyritization decreasing towards the margins. Many pyritized shells have had the shell material replaced by pyrite, rather than having had pyrite grow outward from the shell surface. Within the bituminous shales, many shells have developed pyrite overgrowths. The pyrite is usually rather patchily developed and often seems to be concentrated on aragonitic shells such as *Thracia, Pinna*, and *Palaeonucula* where it occurs as small patches on the shell surfaces. Hudson and Palframan (1969, p. 404) describe a comparable situation in the Middle and Upper Oxford Clay of Woodham, Bucks., where pyrite is patchily developed on the surfaces of bivalves preserved as clay moulds. They attribute the pyrite formation to local sulphate reduction by bacteria acting on the organic matrix of the dissolving shell. It is possible that the patchy pyrite developed on aragonitic shells in the Lower Oxford Clay formed in a similar manner, although the aragonite has not totally disappeared.

Another characteristic feature of the Lower Oxford Clay is the presence of concretionary limestones at certain levels (text-fig. 3). Dr. J. D. Hudson informs me of the existence of two phases of concretion development, one pre-compaction and the other post-compaction, each with distinctive carbon and oxygen isotopic compositions. The early pre-compaction concretions are septarian, and are found within the various Lower Oxford Clay bituminous shales and shell beds (text-fig. 3); they contain uncrushed fossils preserved in partially dissolved aragonite or secondary calcite. The later, post-compaction concretions occur as lenticular limestones within the Acutistriatum Band (text-fig. 3), and contain crushed fossils, usually preserved in secondary calcite. Both limestones are of diagenetic origin, and contain the same fauna as the enveloping shales.

Methods of analysis. At the four pits studied (text-fig. 4), the Lower Oxford Clay is up to 18 m thick, and worked in large open-cast pits by means of draglines, giving sloping faces for collections on which a continuous profile may also be measured. As the sections were measured, detailed counts were made of all the fossils found in each bed, collections being made over a horizontal distance of up to 2 m, and continuing until no new species appeared in the sample. In practice, collection ceased after about 2000 specimens had been counted, and when all the dominant species had appeared. In the case of beds over 50 cm thick, each 50 cm was then considered as a separate sample; this gave a method for evaluating the faunal similarity of different parts of the thicker units. In addition to these field counts (usually conducted on up to 2000 specimens), blocks from each sampled bed were taken back to the laboratory and broken up under more controlled conditions to check the accuracy of the field counts. While this sometimes revealed the presence of one or two
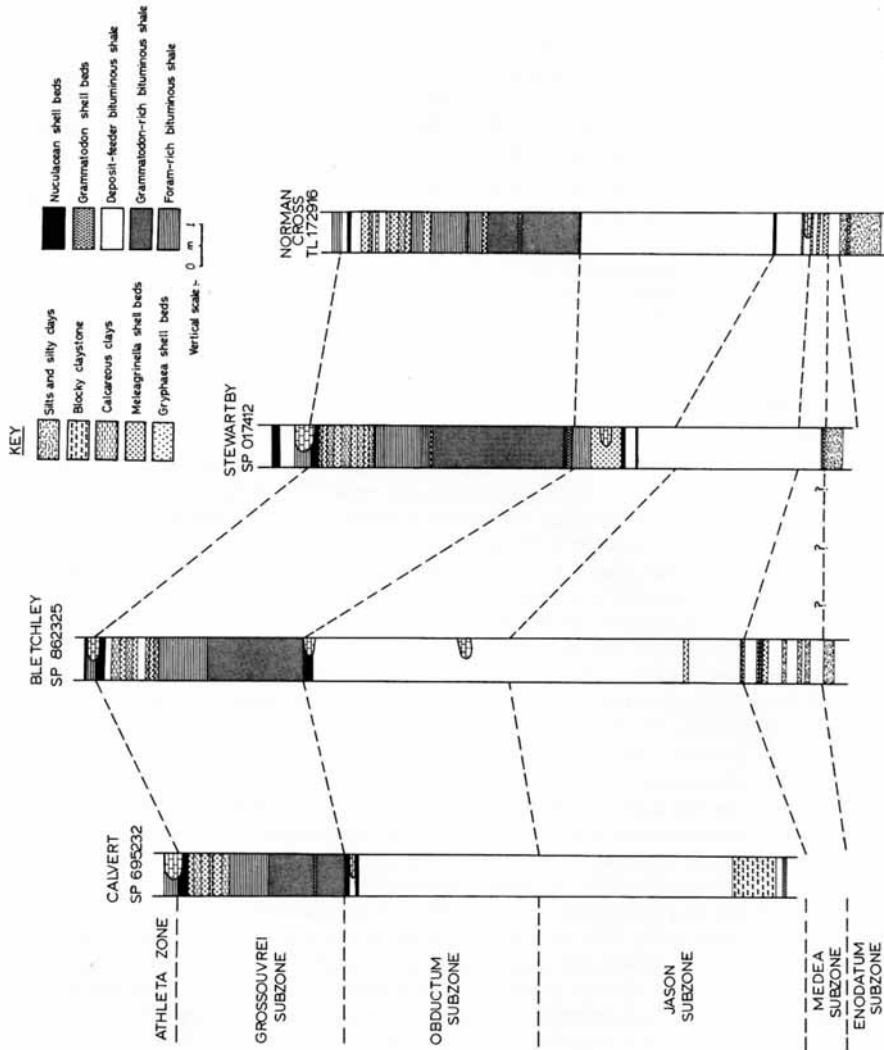
TEXT-FIG. 5. Distribution of the ten biofacies at each of the four Midlands quarries.

additional species (in small quantities), in most cases it merely confirmed the field counts, and so the analysis presented here is based on the field data only.

Analyses of the organic carbon and insoluble residue percentages of the samples are shown in Tables 2 and 3. The organic carbon content was determined volumetrically, the clay samples being treated with a solution of potassium chromate in phosphoric acid, and gives a measure of the amount of detrital organic matter available

TABLE 2. Organic carbon contents measured in the various Lower Oxford Clay biofacies.

Biofacies	N	Max	Min	Mean
Silts and silty clays	1	1·0	1·0	1·0
Deposit-feeder bituminous shales	10	3·5	2·1	2·9
Grammatodon-rich bituminous shales	2	6·1	3·4	4·8
Foram-rich bituminous shales	3	4·9	3·5	4·1
Nuculacean shell beds	1	1·8	1·8	1·8
Gryphaea shell beds	1	1·7	1·7	1·7
Meleagrinella shell beds	4	3·8	2·3	2·9
Calcareous clays	1	1·1	1·1	1·1

N = number of samples; Max = maximum observed value; Min = minimum observed value.

for collection by feeding organisms. The insoluble residue determinations give a measure of the amount of lime present in the sediment, either as cement or as original particles of shell or other carbonate. Organic carbon contents of over 3% in Recent mud deposits have been shown by Bader (1954, p. 40) to cause a diminution in bivalve diversity, with infaunal deposit-feeding protobranchs becoming dominant. The organic carbon contents of many of the Lower Oxford Clay samples (Table 2) show that they belong to this type of lithology, with an impoverished benthonic fauna. The degree of correlation between the organic carbon contents of Recent muds and fossil shales is uncertain, and it is not possible to tell whether or not the values obtained from compacted rocks are true reflections of the primary organic carbon content. Comparison of Bader's values with those from the Lower Oxford Clay suggests that in some cases, they are.

Most of the analysis was carried out on the benthonic fauna only, with the nektonic elements (such as the cephalopods) removed from consideration. However, before the nektonic elements were deducted, the relative percentages of nektonic predators and scavengers were calculated; in the bituminous shales they constitute 10–15% of the fauna. Having removed the nektonic elements, the data for the remaining benthos were recalculated to give percentages of epifaunal suspension, infaunal suspension, and deposit-feeders only. The reasons for using feeding groups were discussed by Rhoads *et al.* (1972, p. 1100), who suggested that it is sedimentary and hydrographical conditions which most closely control the distribution of bivalves, with sediment grain-size and texture, bottom turbidity, and food availability all being of importance in determining the spatial distribution of suspension and deposit-feeding bivalves. The status and mode of life of bivalve feeding groups in general have been studied by Stanley (1970). The ecological positions of the various bivalve genera are shown in Table 1.

The data for the bivalves was then further subdivided, because of the high proportion of epifaunal suspension-feeders such as *Bositra*, *Oxytoma*, *Meleagrinella*, *Parainoceramus*, and *Pteroperna* in some beds. It seems very likely that these genera

were not strictly benthonic, but lived byssally attached to organic matter at some distance above the sea floor, as there appears to be a lack of suitable benthonic attachment areas, and the genera show a tendency to occur in clusters. It is suggested that they were attached to algal fronds, probably not cemented to the sea floor, and which could be moved by currents; attachment to floating driftwood is also likely, as this material is characteristic of the bituminous shales, and is often associated with clusters of *Parainoceramus* and *Meleagrinella*. There is also the possibility that *Bositra* was pseudo-planktonic (Jefferies and Minton 1965). This group of genera is grouped together as 'pendent' epifaunal suspension-feeders, and as they tend to be rather abundant in the bituminous shales, thereby obscuring the relative importance of the more strictly benthonic elements, the bivalve percentages were recalculated to omit them. Consideration of the whole bivalve assemblage then shows the over-all faunal composition of a bed, the relative abundance of the strictly benthonic species being seen after the removal of the pendent species. The abundance of driftwood, frequently in large pieces, suggests that the bituminous shales were probably laid down fairly near shore, in a quiet-water environment, and where a large amount of suspended organic particles provided a rich food source for high-level suspension-feeders.

BIOFACIES ANALYSIS

Ten biofacies have been recognized within the Lower Oxford Clay of the Midlands, the major lithofacies groupings being subdivided by faunal content; the data are summarized in Table 3, while text-fig. 5 shows the distribution of each of these facies at the major pits. The data were then analysed in five ways to give a synthesis of the palaeoecology, the plots used being (*a*) triangular plots, (*b*) rarefaction curves, (*c*) trophic nuclei, (*d*) trophic group composition, (*e*) Diversity Index.

The triangular diagrams are based on bivalve feeding groups, the corners of the triangles representing 100% epifaunal suspension-feeders (ES), 100% infaunal suspension-feeders (IS), and 100% infaunal deposit-feeders (ID). Each sample has both the total bivalve fauna and the over-all benthonic fauna (excluding pendent genera) divided into these three groups, and may then be represented on the diagram by a single point. It can be seen from text-figs. 6 and 7 that each biofacies yields a group of points, all falling within a certain field of the triangle, with varying degrees of overlap.

The rarefaction curve method was conceived by Sanders (1968) as a means of comparing the diversities of different samples of benthonic organisms. He showed that most diversity measurements were affected by sample size, as individuals are added to a population at an arithmetic rate, while species are added at a decreasing logarithmic rate. The rarefaction method depends on the shape of the species abundance curve rather than the absolute number of specimens in a sample, and has the advantage that each sample generates a curve. The method of calculating and plotting rarefaction curves is described by Sanders (1968, p. 245). Each aquatic environment was shown by Sanders to have its own characteristic rate of species increment, with its rarefaction curves lying in a particular field. The curves generated by the various Lower Oxford Clay biofacies (text-fig. 8) agree closely with those
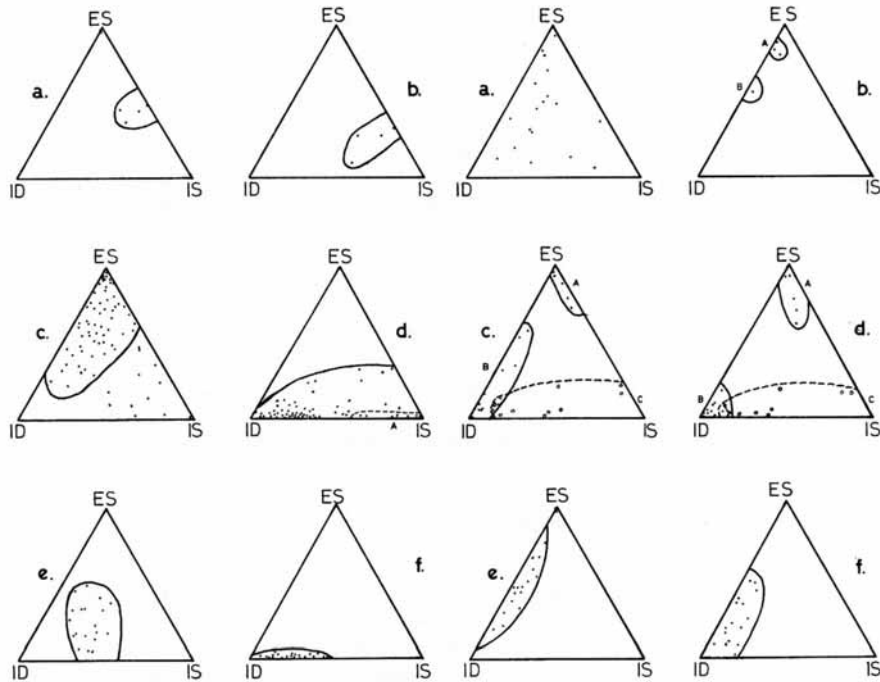
TEXT-FIG. 6. Triangular plots of bivalve feeding groups (ID, infaunal deposit; ES, epifaunal suspension; IS, infaunal suspension) for three of the biofacies. *a*, silts and silty clays, all bivalves; *b*, silts and silty clays, pendent bivalves removed; *c*, deposit-feeder bituminous shales, all bivalves; *d*, deposit-feeder bituminous shales, pendent bivalves removed; *e*, *Grammatodon*-rich bituminous shales, all bivalves; *f*, *Grammatodon*-rich bituminous shales, pendent bivalves removed.

TEXT-FIG. 7. Triangular plots of bivalve feeding groups for the remaining biofacies. *a*, foraminifera-rich bituminous shales, all bivalves; *b*, *Meleagrinella* shell beds, all bivalves (A); blocky claystone, all bivalves (B); *c*, shell beds (apart from *Meleagrinella* shell bed), all bivalves; *Gryphaea* shell beds (A), Nuculacean shell beds (B), *Grammatodon*-rich shell beds (C); *d*, shell beds (apart from *Meleagrinella* bed), pendent bivalves removed: *Gryphaea* shell beds (A), Nuculacean shell beds (B), *Grammatodon* shell beds (C); *e*, calcareous clays, all bivalves; *f*, calcareous clays, pendent bivalves removed.

generated by Recent Boreal shallow-water samples, and Hallam (1969, p. 11) placed England in his Boreal Province during Callovian times. However, the Boreal Province of the Jurassic is not necessarily equivalent to the Recent Boreal area.

The trophic nucleus of an assemblage or community is defined as the numerically dominant species which make up 80% of the fauna (Neyman 1967, p. 151). Analysis of the trophic nucleus helps clarify the relationships between the various members of the assemblage, notably in the relative abundance of the species, and the importance of deposit-feeders. The trophic nucleus of most communities consists of up to five species, although in some tropical marine environments high specific diversity

TABLE 3. A summary of the main faunal and lithological characteristics of the ten Lower Oxford Clay biofacies.

Biofacies	Lithology	Dominant faunal elements	Organic carbon %	Insoluble residue %
Silts and silty clays	Silts and silty clays	Cephalopods, *Pinna*, *Protocardia*, *Trautscholdia*, *Corbulomima*, *Meleagrinella*	1·0	93
Deposit-feeder bituminous shales	Dark olive-green shaly clays	Pendent epifaunal suspension-feeders (*Bositra*, *Meleagrinella*, and *Oxytoma*), together with *Palaeonucula* and *Mesosaccella*	2·9	90
Grammatodon-rich bituminous shales	Dark olive-green shaly clays	*Bositra*, *Oxytoma*, *Meleagrinella*, *Palaeonucula*, *Mesosaccella*, together with infaunal suspension-feeders such as *Grammatodon*, *Thracia*, and *Isocyprina*	4·8	90
Foram-rich bituminous shales	Light green, rather fissile, shaly clays	*Bositra*, *Parainoceramus*, *Mesosaccella*, *Corbulomima*, *Prodentalium*, foraminifers (*Brotzenia*)	4·1	87
Nuculacean shell beds	Shell concentrate	*Palaeonucula*, *Mesosaccella*	1·8	79
Grammatodon-rich shell beds	Shell concentrate in clay matrix	*Grammatodon*, *Isocyprina*, oysters, *Oxytoma*, *Discomiltha*, *Protocardia*, *Trautscholdia*, *Neocrassina*, *Myophorella*	—	80
Gryphaea shell beds	Shell concentrate	Gryphaeate oysters, bone fragments, cephalopods	1·7	82
Meleagrinella shell beds	Shell concentrate	*Meleagrinella*	2·9	69
Blocky claystone	Light grey plastic clay with dark streaks	*Bositra*, *Meleagrinella*, *Palaeonucula*, *Mesosaccella*, *Procerithium*, *Lingula*, *Solemya*	—	96
Calcareous clays	Light grey or grey-green, rather plastic, clay	*Palaeonucula*, *Mesosaccella*, *Discomiltha*, *Isocyprina*, *Myophorella*, '*Entolium*', *Genicularia*, oysters	1·1	74

greatly increases its size. Table 4 shows the over-all trophic nucleus of the whole benthonic fauna, whilst Table 5 shows the trophic nucleus discounting the pendent bivalves. Columns 7–9 of each table show the percentage of the various kinds of deposit-feeders within each biofacies.

As well as determining the size of the trophic nucleus, it is useful to examine the trophic group composition of each biofacies, a technique introduced, and later refined, by Turpaeva (1948). This method of determining the trophic relationships of all the benthonic invertebrates in an assemblage was shown by Walker (1972, p. 83) to be a useful method of ecological analysis. Turpaeva's work on the Recent faunas of the Barents Sea revealed several generalizations which apply to most Recent communities; Walker also showed that they could be applied to many Lower Palaeozoic communities, and the evidence from the Lower Oxford Clay suggests that they are also applicable to Mesozoic assemblages. Turpaeva chiefly showed that (*a*) each community is dominated by a single trophic group, (*b*) each of the dominant species in the trophic nucleus belongs to a different trophic group, (*c*) one species

TABLE 4. Trophic nuclei of each of the Lower Oxford Clay biofacies, all benthos included with percentages given of the dominant forms, and the diversities of biofacies and trophic nuclei, total number of species, and the proportions of deposit-feeders.

Biofacies	Position 1	Position 2	Position 3	Position 4	Position 5	Epifaunal deposit-feeders	Infaunal deposit-feeders	Percentage of deposit-feeders	Number in trophic nucleus	Diversity Index	Number of species
Silts and silty clays	Bositra 23·3	Corbulomima 19·4	Gryphaea 17·6	Procerithium 9·2	Palaeonucula 7·4	9·2	8·8	18·0	6	7·1	21
Deposit-feeder bituminous shales	Bositra 34·9	Meleagrinella 24·0	Procerithium 10·1	Mesosaccella 7·4	Dicroloma 5·2 Corbulomima 5·2	10·1	17·1	27·2	6	6·7	31
Grammatodon-rich bituminous shales	Procerithium 30·5	Mesosaccella 26·7	Bositra 12·9	Palaeonucula 8·0	Grammatodon minima 6·9	30·5	34·8	65·3	5	5·9	24
Foraminifera-rich bituminous shales	Meleagrinella 35·7	Bositra 19·6	Mesosaccella 19·1	Corbulomima 6·0	—	5·2	23·9	29·1	4	6·1	24
Nuculacean shell beds	Mesosaccella 47·0	Palaeonucula 28·2	Meleagrinella 10·4	—	—	7·8	75·4	83·2	3	5·2	19
Grammatodon-rich shell beds	Mesosaccella 30·1	Palaeonucula 13·6	Procerithium 13·5	Bositra 9·9	Grammatodon minima 8·1 Meleagrinella 7·4	13·5	44·0	57·5	6	6·1	24
Gryphaea shell beds	Gryphaea 62·2	Meleagrinella 9·8	Procerithium 4·1	Corbulomima 3·4	Grammatodon concinna 3·2	4·1	4·4	8·5	5	5·6	16
Meleagrinella shell beds	Meleagrinella 71·4	Mesosaccella 10·2	—	—	—	3·0	11·6	14·6	2	4·5	16
Blocky claystone	Meleagrinella 34·2	Bositra 24·2	Lingula 11·1	Palaeonucula 11·1	—	1·7	20·6	22·3	4	4·3	11
Calcareous clays	Mesosaccella 32·4	'Entolium' 14·4	Meleagrinella 14·0	Procerithium 12·4	Bositra 10·4	12·4	41·3	53·7	5	5·8	22

TABLE 5. Trophic nuclei of each of the Lower Oxford Clay biofacies, pendent bivalves removed, with percentages given of the dominant forms. Compare with Table 4.

Biofacies	Position 1	Position 2	Position 3	Position 4	Position 5	Epifaunal deposit-feeders	Infaunal deposit-feeders	Percentage of deposit-feeders	Number in trophic nucleus	Diversity Index	Number of species
Silts and silty clays	Corbulomima 28·5	Gryphaea 26·0	Procerithium 13·5	Palaeonucula 11·0	—	13·5	13·0	26·5	4	6·1	17
Deposit-feeder bituminous shales	Procerithium 25·2	Mesosaccella 19·1	Dicroloma 13·5	Corbulomima 13·4	Palaeonucula 11·6	25·2	44·2	69·6	5	6·1	26
Grammatodon-rich bituminous shales	Procerithium 36·9	Mesosaccella 32·4	Palaeonucula 9·6	Grammatodon minima 8·4	—	36·9	42·1	79·0	4	5·0	20
Foraminifera-rich bituminous shales	Mesosaccella 44·5	Corbulomima 13·8	Procerithium 12·1	Palaeonucula 10·5	—	12·1	55·7	67·8	4	5·4	14
Nuculacean shell beds	Mesosaccella 53·5	Palaeonucula 32·1	—	—	—	8·8	85·8	94·6	2	3·9	14
Grammatodon-rich shell beds	Mesosaccella 37·4	Palaeonucula 16·9	Procerithium 16·8	Grammatodon minima 10·0	—	16·8	54·7	71·5	4	5·0	19
Gryphaea shell beds	Gryphaea 71·4	Procerithium 4·7	Corbulomima 3·8	—	—	4·7	5·0	9·7	3	4·7	13
Meleagrinella shell beds	Mesosaccella 45·3	Corbulomima 25·6	Procerithium 13·5	—	—	13·5	51·7	65·2	3	4·5	13
Blocky claystone	Palaeonucula 28·2	Lingula 28·2	Solemya 13·4	Mesosaccella 13·4	—	4·2	52·2	56·4	4	3·7	8
Calcareous clays	Mesosaccella 43·2	'Entolium' 19·2	Procerithium 16·5	Palaeonucula 11·7	—	16·5	55·0	71·5	4	4·9	17
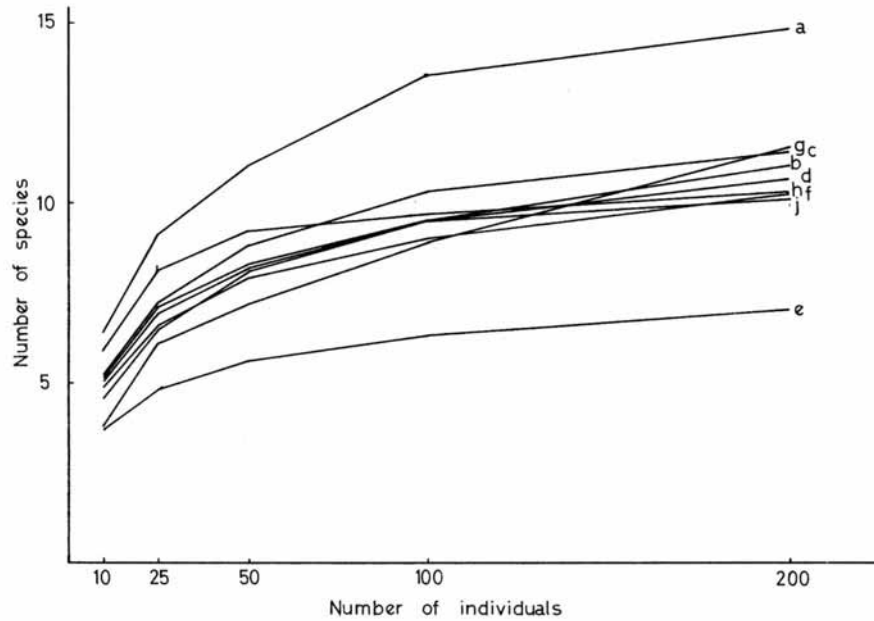
TEXT-FIG. 8. Rarefaction curves for the Lower Oxford Clay biofacies. *a*, silts and silty clays; *b*, deposit-feeder bituminous shales; *c*, *Grammatodon*-rich bituminous shales; *d*, foraminifera-rich bituminous shales; *e*, Nuculacean shell beds; *f*, *Grammatodon* shell beds; *g*, *Gryphaea* shell beds; *h*, blocky claystone; *j*, calcareous clays.

dominates each trophic group in the community. These generalizations led her to the conclusion that feeding competition is thus minimized. In most cases these generalizations appear to be valid, although Rhoads *et al.* (1972, p. 1101) showed the existence of heterogeneous trophic nuclei, in which habitat partitioning allows maximum use to be made of available food resources. In text-figs. 9–19 the trophic groups introduced by Turpaeva are used, as they represent the simplest and most clearly understood means of presenting the data. 'Swallowers' are infaunal deposit-feeders (*Palaeonucula*, *Mesosaccella*, *Dicroloma*), which feed by ingesting large quantities of sediment as they move through it; 'collectors' use organic detritus from the sediment surface, the category including epifaunal deposit-feeders (*Procerithium*), scavengers (*Meco-cheirus*, ophiuroids, cephalopods), and browsing herbivores (*Pleurotomaria*). 'Low-filterers' are low-level suspension-feeders, filtering food from the water immediately above the sea floor, and comprise *Lingula*, rhynchonellids, all infaunal suspension-feeding bivalves and some epifaunal bivalves (*Plicatula*, *Gryphaea*, *Modiolus*), together with *Genicularia* and serpulid worms. 'High-filterers' are high-level suspension-feeders, collecting food from some distance above the sea floor, and are represented by the pendent bivalves, together with *Pinna* and *Chlamys*.

Diversity Index is a parameter used by Ziegler *et al.* (1968, p. 4), and is defined as

$$\frac{\text{number of species}}{\text{log number of individuals}}$$

giving a relationship between the number of species present in an assemblage and the number of individuals counted; the parameter is strongly sample-size controlled, but gives a value which can be directly compared with values for Silurian communities given by Ziegler *et al.* Diversity Index values are incorporated in Tables 4 and 5.

Palaeoecological assumptions. In common with most other palaeoecological analyses, this study is concerned solely with the invertebrates with skeletons; no account is taken of the soft-bodied fauna which has left evidence only in the form of trace fossils. Johnson (1964, p. 119) showed that as many as 70% of the animals in some Recent communities are soft bodied. Occasionally, exceptional preservation allows recognition of some of the soft-bodied animals usually lost. Walker (1972, p. 85) suggested that by study of the abundance and nature of the trace fossils, it should be possible to obtain an estimate of the abundance of the soft-bodied fauna, but this is not a viable proposition in the Lower Oxford Clay, where trace fossils are rare. It is considered that the use of the term 'community' is not justified in palaeoecology, and that recurrent quantitative groupings of fossils should be referred to as associations. Local groupings not recurrent over wider areas are termed assemblages.

Recent ecological studies are based on the concept of biomass, which is defined as the weight of organisms per unit area sampled, usually expressed as gm/m^2.

As this measurement is based on the over-all weight of both soft parts and skeletal material, it is not applicable to palaeoecological work, and Walker (1972, p. 85) suggested the use of biovolume as a substitute. However, this method, also has difficulties, especially where there has been crushing of the fossils, and it is not readily applicable to the Oxford Clay assemblages. Simple numerical abundance has been used here, and as long as large enough samples are used, proves convenient. It must be remembered, however, that this method takes no account of biovolume or biomass, and so the bioenergetic relationships between the various species are not accurately represented. The problem is partially overcome by presenting the data as relative size histograms (text-figs. 9–19). As is discussed below, palaeoecological analysis is carried out at the generic level.

It has been assumed, at least for the shale facies (and most notably the bituminous shales), that the benthos is more or less indigenous, and that there has been little transport of shells in from elsewhere. The assumption is justified because articulated shells are common, although rarely in life position; there are roughly equivalent numbers of left and right valves in most samples; most bivalve species have rather fragile shells, but few show signs of physically induced breakage; complete articulated skeletons of ophiuroids, crustacea, and vertebrates are not uncommon (Schäfer 1972, p. 99 shows that the arms of ophiuroids begin to disintegrate within 15 hours of death, while crustacea are also rapidly disarticulated). In addition, there is very little evidence of current activity preserved in the sediment itself, as intercalations of coarser particles are extremely rare, and occur only as very thin films of sediment, whose thickness may be measured in fractions of a millimetre. There is also no

B

conspicuous orientation of skeletal remains, and no sign of shell concentrates (except
the shell beds). However, in contrast, the shells of many infaunal species, especially
Thracia depressa, *Pinna mitis*, and *Discomiltha lirata*, rest flat on bedding planes,
and so there must have been at least slight winnowing to exhume these shells from their
life positions. Schäfer (1972, p. 474) points out that such occurrences indicate the
presence of discontinuities, showing there to have been numerous short sedimentary
pauses within the Lower Oxford Clay. Rhoads and Young (1970) showed that in
many Recent shallow-shelf mud areas, the nature of the mud-water interface is sub-
stantially controlled by the activity of deposit-feeders, giving an uncompacted fluid
surface consisting mainly of faecal pellets ('seston'), which is very unstable in the
presence of weak bottom currents. As Rhoads (1973, p. 12) later pointed out, it
is only the uppermost 2–3 cm which becomes resuspended, and it seems unlikely
that this zone of disturbance would be great enough to exhume such deep burrowers
as *Thracia* and *Discomiltha*; clearly a mechanism more powerful than this is required
to lay bare the shells of such deep burrowers. However, thin sections of diagenetic
septarian concretions, from all the four major pits, show the presence of pyritized
pellets which Dr. J. D. Hudson considers to represent remnant seston. Thus, in this
respect, the Lower Oxford Clay is closely comparable with the Recent shallow-shelf
muds described by Rhoads and Young.

LOWER OXFORD CLAY ENVIRONMENTS

The Lower Oxford Clay is dominantly a series of dark bituminous shales, the fauna
being characterized by an abundance of infaunal deposit-feeders (*Palaeonucula* and
Mesosaccella) and pendent epifaunal suspension-feeders (*Bositra*, *Meleagrinella*,
Oxytoma, *Parainoceramus*, and *Pteroperna*). Although other epifaunal and infaunal
suspension-feeders occur throughout, they are rarely of numerical importance. In
common with other bituminous shales, such as parts of the Lias, the Lower Oxford
Clay fauna is very well preserved, including original aragonitic shells, and it seems
probable that most of the original skeletonized invertebrate fauna still remains.
There are, however, differences between the bituminous shales of the Lias and the
Oxford Clay, benthonic fossils being fairly common in the Oxford Clay, in direct
contrast to the Lias, where the only common fossils in such lithologies are cephalopods
and fish fragments (Hallam 1960, p. 10). This indicates that the bottom conditions
during Lower Oxford Clay times were not anaerobic, an important difference from
the Lias. The main characteristic of the Lias laminated bituminous shales is the
presence of uniform microscopic alternations of carbonaceous and calcitic-clay
laminae, which have remained undisturbed by burrowing organisms. Thin sections
of the Lower Oxford Clay do not show these laminations, and many benthonic
burrowers are present in the sediment, so it is clear that bottom conditions in the
Middle Callovian were less anaerobic than those prevailing in the bituminous shales
of the Lias. In so far as it has a fauna dominated by deposit-feeders and pendent
bivalves, the Oxford Clay differs from most other British shale facies; the Lower and
Middle Lias bivalve fauna (Hallam 1960, p. 28, 1967, p. 400; Palmer 1971, p. 62) has
a much higher proportion of suspension-feeders, and relatively few deposit-feeders,
as also do the faunas of the Kimmeridge Clay and the Gault (Price 1879, p. 60). The

only comparable formation is part of the Upper Lias (Melville 1956, p. 100). The bituminous shales seem comparable with parts of the 'dark-gray shale lithofacies' recognized by Scott (1970, p. 29) in the Lower Cretaceous of the United States, in particular his *Nuculana*-association, and these similarities will be discussed later.

The monotony of the shale sequence within the Lower Oxford Clay is most obviously broken by the various shell beds which occur at certain levels, often at the base of a subzone. Four types of shell bed have been recognized and described below but the most notable feature of all the types is that they contain the same species as the shales in which the shell bed occurs, only in greater abundance; thus Nuculacean shell beds occur within the deposit-feeder bituminous shales, while *Grammatodon* shell beds occur in the *Grammatodon*-rich bituminous shales. In the case of all the shell beds occurring within the clay facies, it seems most likely that they formed by concentration of shells *in situ*, due to slow deposition of sediment rather than by accumulation of shells transported in from elsewhere. This interpretation is supported in three ways, firstly, there is no reason to suspect marked shallowing of the sea (no oyster concentrations), secondly, the relative proportions of the species are similar to those of the shales, and thirdly, Brinkmann (1929) showed that whilst there was continuous evolution of shell features on ammonites during shale deposition, there was a marked discontinuity produced in the shell beds, indicating that a long period of time was represented by the thin shell beds. This is supported by the fact that most of the more important shell beds occur at subzonal boundaries (text-fig. 3). The controlling factor producing shell beds is obviously increased current activity, but the environmental factors producing this are not so readily apparent. Brinkmann's rates of ammonite evolution indicate that the sedimentary pause is unlikely to have been caused by storms, unless they were of sufficient strength to remove nearly 1 m of sediment. A more probable control is changes in sea-level, with recurrent phases of shallowing producing shell beds; if Hallam's (1967a) model of the geometry of the area of deposition of bituminous shales is accepted, then a change in sea-level of less than 1 m could bring the shoreline considerably closer, and increase the likelihood of stronger current activity. Schäfer (1972, p. 474) has shown that in the North Sea, shells are winnowed out of their life position by weak currents, which may or may not also move them laterally, and that if current activity at the depositional site is too small to move the shells, but too great to allow the settlement of suspended sediment, a bed consisting almost entirely of shells and shell fragments is formed with very little interstitial matrix. This appears to have been the case in the Lower Oxford Clay.

Despite the general homogeneity of the Lower Oxford Clay, several different facies may be recognized, characterized by lithological and faunal associations; these are grouped as biofacies associations. Palaeoecological analysis was carried out at the generic level, as most of the Lower Oxford Clay genera are represented by only one species, and, even where there is more than one species per genus, ecological differences are very small; where two species of the same genus occur together, niche partitioning between them is discussed at the relevant point. The various biofacies will now be considered.

Silts and silty clays. This alternation of silts and silty clays occurs within the transition beds from the Kellaways Rock to the Oxford Clay, and is characterized by infaunal

and epifaunal suspension-feeders (82% by number of the over-all benthonic fauna), infaunal and epifaunal species being of about equal importance (text-fig. 6a, b). Deposit-feeders are of minor importance, epifaunal and infaunal species being present in about equal quantities (Table 4). The high diversity of the trophic nucleus (Table 4) is also reflected in the position of the rarefaction curve for this facies (text-fig. 8), and in conjunction with the data of the trophic group composition (text-fig. 9), shows the domination of this facies by niche-separated filter-feeders. Pendent
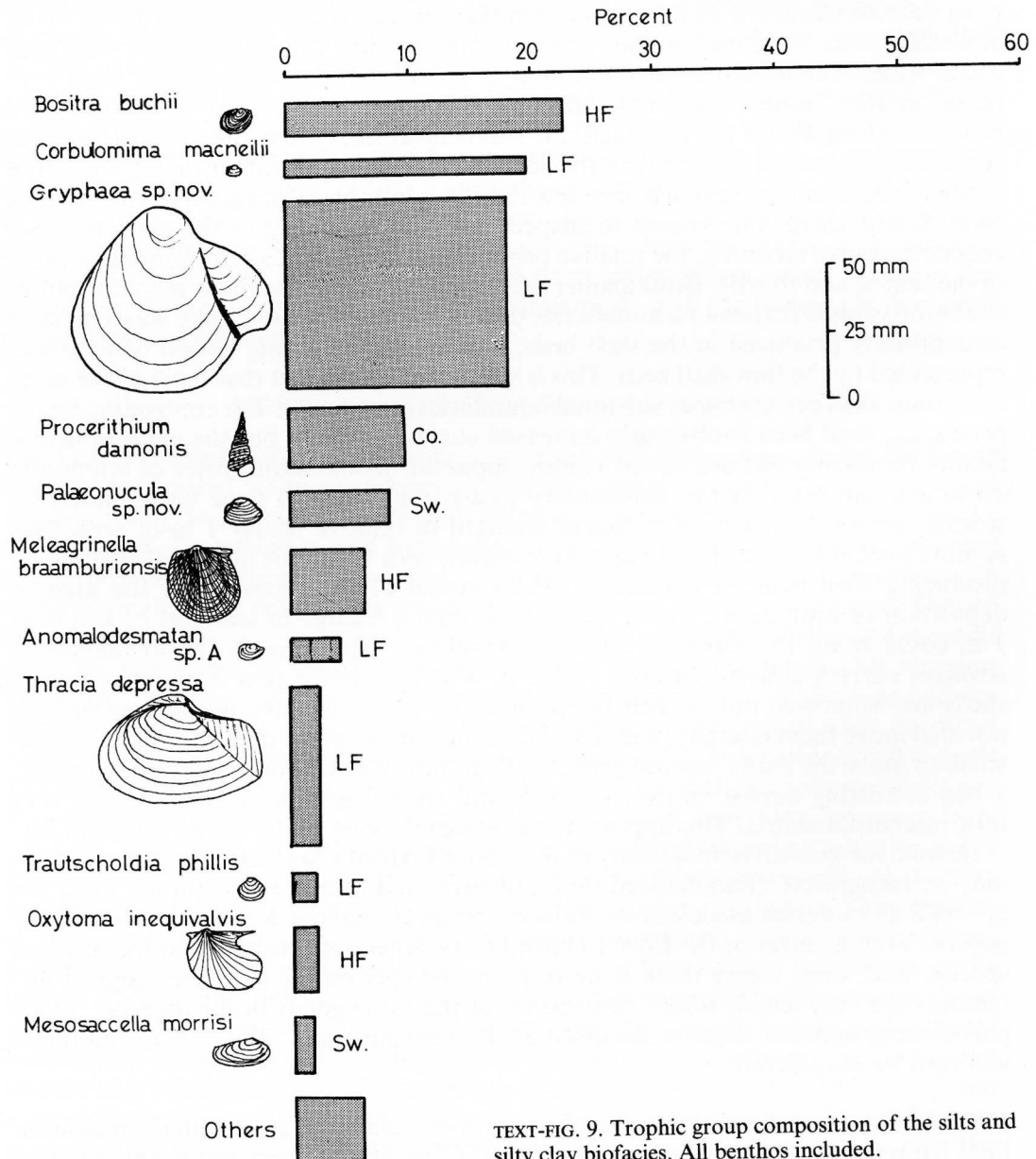
TEXT-FIG. 9. Trophic group composition of the silts and silty clay biofacies. All benthos included.

bivalves are of minor importance. The high aeration of the water, and presumably rich food supply, allowed the establishment of a diverse fauna, dominated by suspension-feeders, unlike any other seen in the Lower Oxford Clay. The low organic carbon content (1%) and abundant trace fossils (*Rhizocorallium* and indeterminate burrows, plus a high level of bioturbation) is further evidence of the high aeration and stronger current activity, and together with the small-scale cross-bedding, suggests deposition in shallow water, relatively near shore, a situation postulated by Farrow (1966) for *Rhizocorallium*-rich beds in the Bajocian of Yorkshire.

Bituminous shales. This facies is represented by well-laminated shaly clays with a high organic carbon content (3·0–4·7%) and a high insoluble residue content (90%), and comprises the bulk of the Lower Oxford Clay. Three biofacies may be recognized, deposit-feeder bituminous shales, *Grammatodon*-rich bituminous shales, and foraminifera-rich bituminous shales, the first two being mutually exclusive, while the latter is a foraminifera-rich variant of either of the first two. The trophic nuclei and diversity of the three biofacies may be compared from Tables 4 and 5, and the trophic group composition from text-figs. 10–13. Rarefaction curves (text-fig. 8) show how similar the diversity of each biofacies is, whilst the triangular plots (text-figs. 6c–7a) present convincing diagrammatic arguments for separating the biofacies.

The deposit-feeder bituminous shales occupy the largest part of the Lower Oxford Clay, and can be seen from text-fig. 10 to be dominated by pendent bivalves (*Bositra* and *Meleagrinella*); the truly benthonic fauna being dominated by deposit-feeders such as *Procerithium*, *Mesosaccella*, *Dicroloma*, and *Nuculoma*, and a few of the more tolerant infaunal suspension-feeders (*Corbulomima* and *Lingula*). There is also a wide
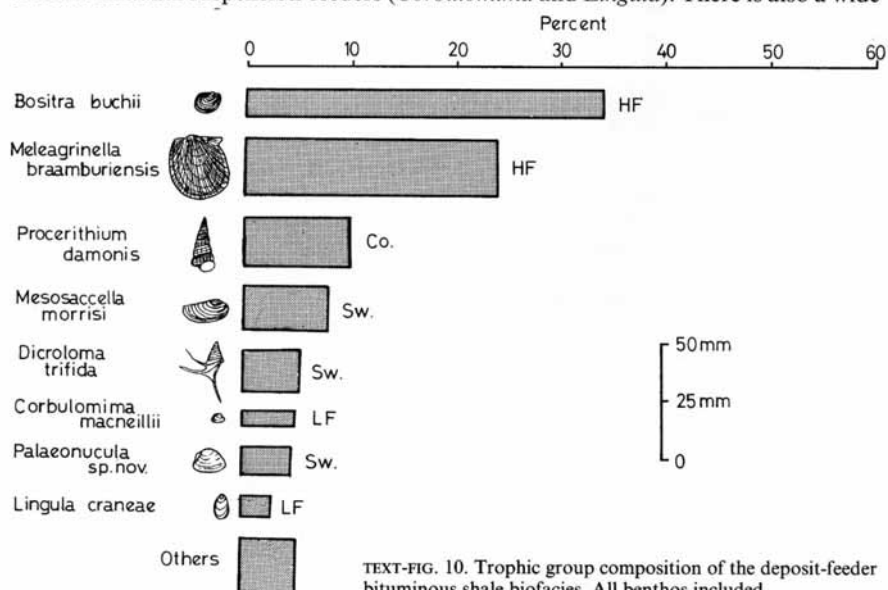
TEXT-FIG. 10. Trophic group composition of the deposit-feeder bituminous shale biofacies. All benthos included.
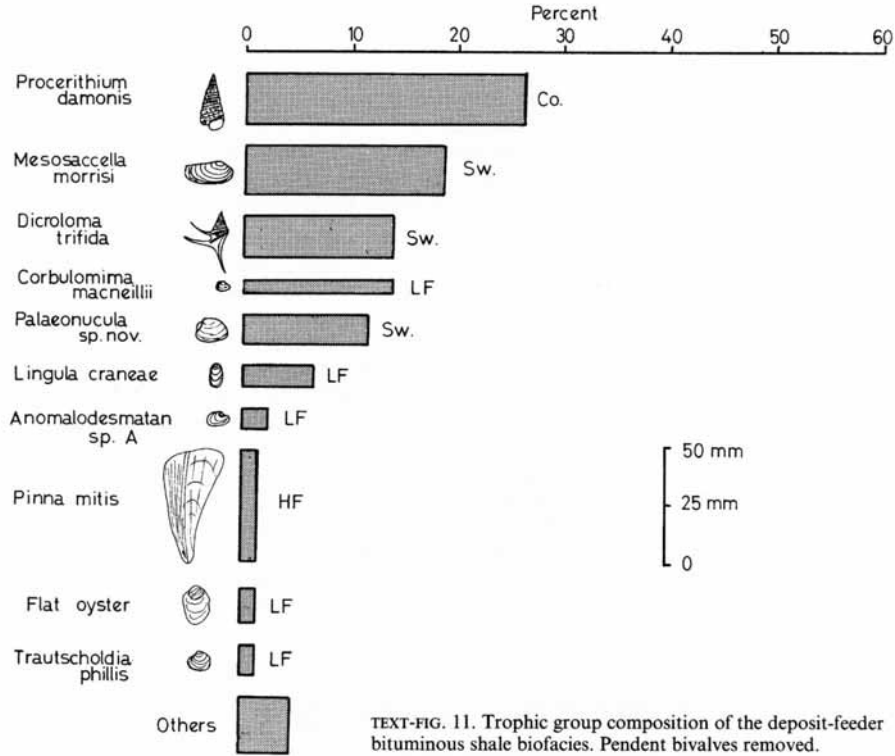
TEXT-FIG. 11. Trophic group composition of the deposit-feeder bituminous shale biofacies. Pendent bivalves removed.

diversity of infaunal and epifaunal suspension-feeders (twenty-three species, each less than 1% of the fauna), although they are not abundant. This biofacies seems to have been the least well aerated of the bituminous shales, with an impoverished benthonic fauna of tolerant deposit-feeders. The quiet nature of sedimentation, largely undisturbed by the activity of scavengers, is further evidenced by the presence of articulated crustacea and ophiuroids. Niche partitioning is not clearly developed in this biofacies (text-fig. 10), with two high-level suspension-feeders in positions 1 and 2, and three swallowers in positions 4, 5, and 7. This may be explained by postulating a superabundance of food (see below).

The trophic group composition (text-fig. 10) shows the facies to be dominated by two pendent bivalves, *Bositra buchii* and *Meleagrinella braamburiensis*: four of the next five positions are occupied by deposit-feeding bivalves and gastropods; and it is necessary to explain how such a fauna, using essentially the same food source, could survive. The abundance of pendent bivalves may be explained by there being a superabundance of suspended food, which allows two species of the same trophic group to coexist without deleterious effects on either. As Rhoads (1973, p. 2) has demonstrated, suspension-feeders are frequently excluded from assemblages in and on

a mud bottom, as the substrate is too unstable and creates problems of mantle-clogging. If, however, suspension-feeders are placed in racks above the sea floor, but within the zone of greatest turbidity (up to 3 m above the bottom), Rhoads showed that they thrive. It is probable that a similar situation prevailed during the deposition of the deposit-feeder bituminous shales, the pendent bivalves being attached to organic material within the zone of maximum turbidity (not necessarily 3 m thick in Callovian times), allowing use to be made of the superabundant food source. The truly benthonic fauna of this biofacies resembles the phenomenon of trophic group amensalism described by Rhoads and Young (1970, p. 173), in which one trophic group is excluded from a deposit either by nature of the substrate or by activity of other members of the fauna. The sea floor during deposit-feeder bituminous shale phases of deposition was not suitable for colonization by byssally attached suspension-feeders, and was dominated instead by deposit-feeders showing fairly well-developed niche partitioning. *Procerithium* is thought to have browsed more or less at the surface, on a probable algal film, while *Mesosaccella*, *Dicroloma*, and *Palaeonucula* burrowed through the sediment, ingesting it as they went. The coexistence of these three species again suggests a superabundance of deposited food material, although there could have been vertical separation of the three species within the sediment. Although Rhoads (1973, p. 16) showed that in Recent sediments of Buzzards Bay only 0·5–2·0% of the annual sediment supply of organic detritus on a soft-mud bottom was actually deposited permanently, the high organic carbon contents of the deposit-feeder bituminous shales suggests that transient amounts of organic material could have been greater in Middle Callovian times.

Text-fig. 6c–f shows that the *Grammatodon*-rich bituminous shales lie in a different field to the deposit-feeder bituminous shales, and have fewer pendent bivalves. The dominant species of this biofacies are deposit-feeders (*Procerithium* and *Mesosaccella*, together 57·2% of the fauna), with pendent bivalves less important (*Bositra* and *Meleagrinella* 15·8%). The most characteristic elements are infaunal suspension-feeding bivalves (*Grammatodon*, *Corbulomima*, *Thracia*, *Isocyprina*, and anomalodesmatan sp. A), which together make up 16·6%. Unlike the deposit-feeder bituminous shale, there is evidence for niche partitioning amongst the dominant species (text-fig. 12), but, as in the deposit-feeder shales, there is also a fairly diverse fauna of rarer suspension-feeders, thirteen species each less than 1% of the fauna.

The foraminifera-rich bituminous shales contain abundant foraminifers (*Brotzenia*) in a normal bituminous-shale type sediment. The trophic group composition (text-fig. 13) shows them to be related to the deposit-feeder bituminous shales, since they are dominated by pendent bivalves, with deposit-feeders in the next dominance positions. However, they also fall within the *Grammatodon*-rich bituminous shales, and form a wide spread on the triangular plot (text-fig. 7a). The only way in which they can be distinguished is by the presence of many foraminifers, which presumably had a localized distribution, since they are not confined to any stratigraphical level. Hence the foraminifera-rich bituminous shales do not really represent more than a local variation on the main twofold division of the bituminous shales, although they have a slight effect on the macrofauna in that, whenever foraminifers occur, scaphopods become very much more common; it has been shown that many scaphopods feed selectively upon foraminifers (Dinamani 1964, p. 4).

Percent
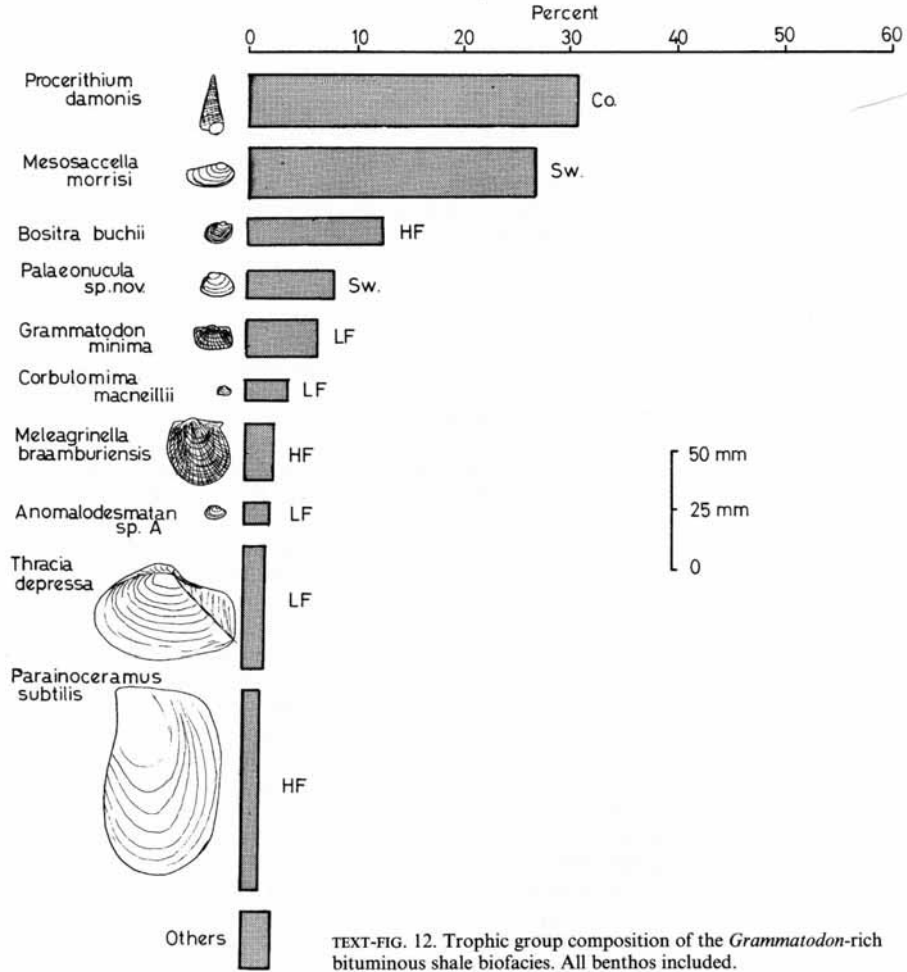
TEXT-FIG. 12. Trophic group composition of the *Grammatodon*-rich bituminous shale biofacies. All benthos included.

Shell beds. Four types of shell bed have been recognized in the Lower Oxford Clay. The relative diversities may be seen from the rarefaction curves (text-fig. 8), which show the low diversity of the Nuculacean shell beds as compared to the relatively higher diversities in the *Gryphaea* and *Grammatodon* shell beds. Comparison of the trophic nuclei (Tables 4 and 5), trophic group composition data (text-figs. 14–17), and the triangular plots (text-fig. 7*b–d*), graphically shows the differences in composition of the various shell beds. *Meleagrinella* shell beds are not shown on the triangular plots because of the difficulty of collecting accurate quantitative data, since *Meleagrinella* is so abundant.
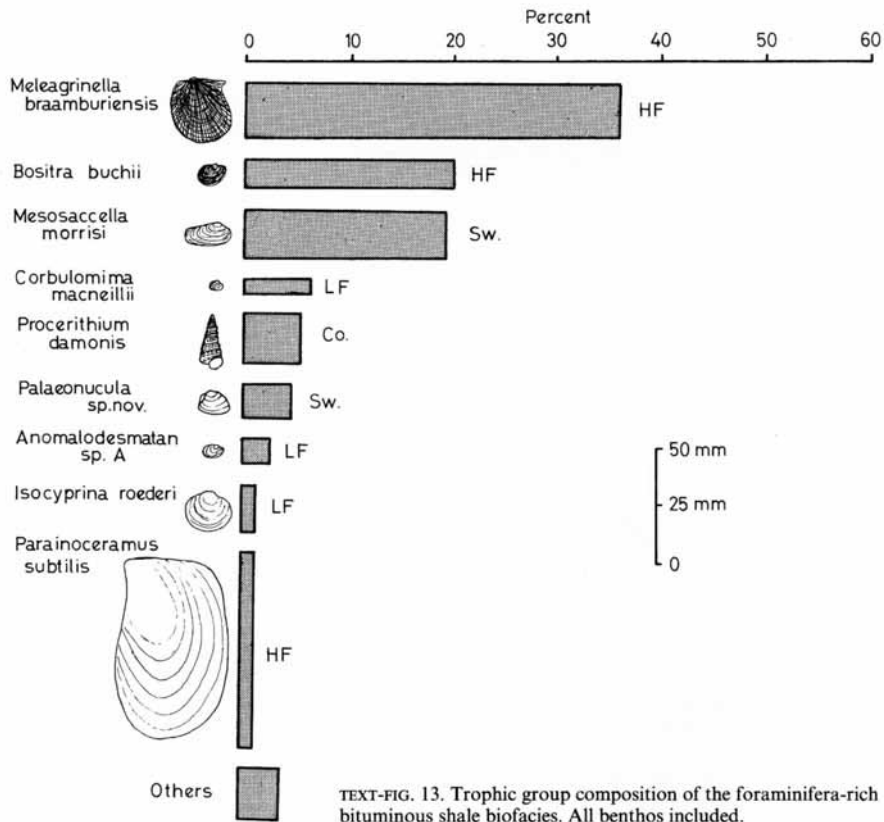
TEXT-FIG. 13. Trophic group composition of the foraminifera-rich bituminous shale biofacies. All benthos included.

The Nuculacean shell beds show the lowest dominance diversity of the shell beds; 75% of the fauna consist of infaunal deposit-feeding Nuculaceans. The next most abundant genera are *Meleagrinella* and *Procerithium* (18·2%), leaving the remaining 7% of the fauna distributed between fifteen species of infaunal and epifaunal suspension-feeders. The faunal composition (text-fig. 14) is grossly similar to that of the deposit-feeder bituminous shales, and these shell beds therefore represent pauses in deposition of normal deposit-feeder bituminous shale. This type of shell bed is often found at subzonal boundaries, and often contains abundant fragments of wood and bone, suggesting a significant pause in deposition.
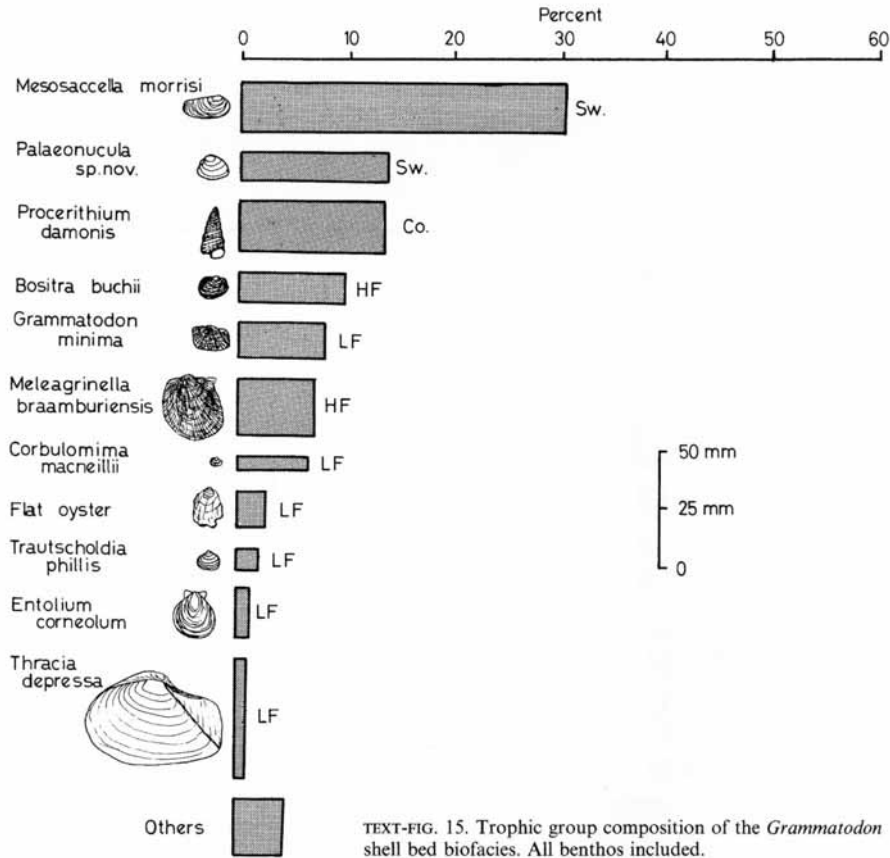
Grammatodon shell beds occur within the *Grammatodon*-rich bituminous shales, and have a similar trophic group composition (text-fig. 15), with deposit-feeders dominating, pendent species subordinate, and infaunal suspension-feeders such as *Grammatodon*, *Corbulomima*, *Trautscholdia*, and *Thracia* also characteristic. The
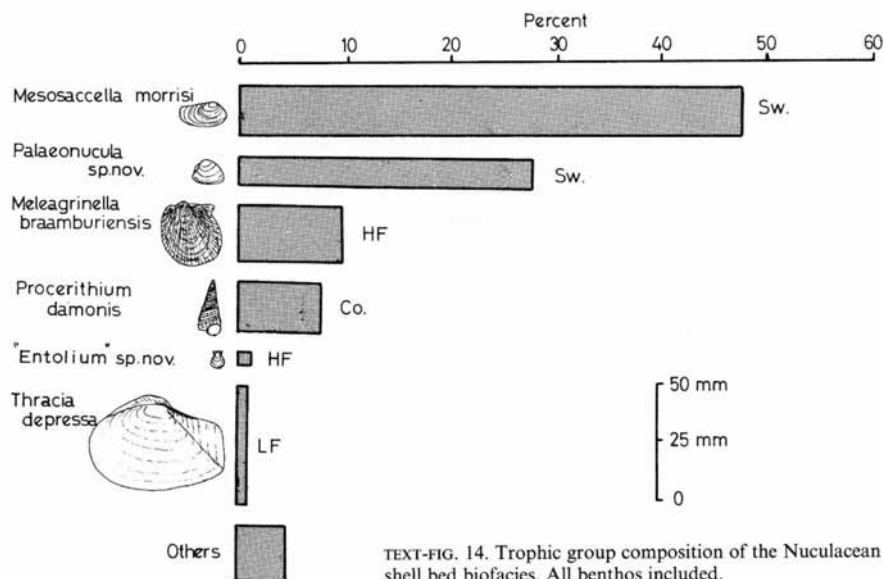
TEXT-FIG. 14. Trophic group composition of the Nuculacean shell bed biofacies. All benthos included.

triangular plots (text-fig. 7c, d) show the relationship between this and the preceding biofacies, indicating that there is some overlap. However, the two biofacies are easily distinguished by their faunal content and the surrounding lithology. This biofacies is also likely to be caused by slower sedimentation, and slight increase in current activity.

Gryphaea shell beds, like the two preceding types, are restricted to a particular lithology, the transition beds between the Kellaways Rock and the Oxford Clay. They, too, have a low dominance diversity, with *Gryphaea* 62·2% of the fauna (text-fig. 16), the remaining 37·8% being fairly evenly distributed between twelve species of suspension-feeder (28·7%) and three species of deposit-feeder (8·5%). Amongst the dominant species, there is evidence of niche separation, although in general the biofacies is characterized by suspension-feeders. The high oyster content places the field of this biofacies close to the epifaunal suspension-feeder corner of the triangle (text-fig. 7d, e). Again, the fauna is similar to that of the beds in which the shell beds occur, and the sediment seems to be another shell concentrate formed more or less *in situ*. There is, however, evidence to suggest that the fossils found in this biofacies may have been transported, as bivalves occur as disarticulated shells rather than articulated shells, many of the valves are fragmented, and there are disproportionate amounts of left and right valves. In addition, broken cephalopod fragments, reptile bones, and fish teeth are fairly common, and it seems likely that the *Gryphaea* shell beds represent a transported fossil assemblage. Facies associations (their occurrence in the silts and silty clays), and consideration of the mode of life of the various faunal

TEXT-FIG. 15. Trophic group composition of the *Grammatodon* shell bed biofacies. All benthos included.

elements, particularly the oysters, suggest that these were deposited in shallower water than the bulk of the Lower Oxford Clay, subject to wave-scouring at times.

Meleagrinella shell beds are largely confined to the upper part of the Grossouvrei Subzone, where they are interbedded with calcareous clays, and consist overwhelmingly of a concentration of broken and unbroken specimens of *Meleagrinella braamburiensis*. Accurate counts are difficult, and consequently the data in text-fig. 17 is less accurate than that of other biofacies. Over 70% of the fauna is *Meleagrinella*, the remainder consists of well niche-partitioned species occupying several habitats. Most of the shell beds are bounded above or below by burrowed surfaces, where fragments of the overlying bed are piped down into the bed beneath. Burrowed horizons are very rare elsewhere in the Lower Oxford Clay (except in the silts), and these may represent phases of slow or nil-deposition, with increased current activity.

TEXT-FIG. 16. Trophic group composition of the *Gryphaea* shell bed biofacies. All benthos included.
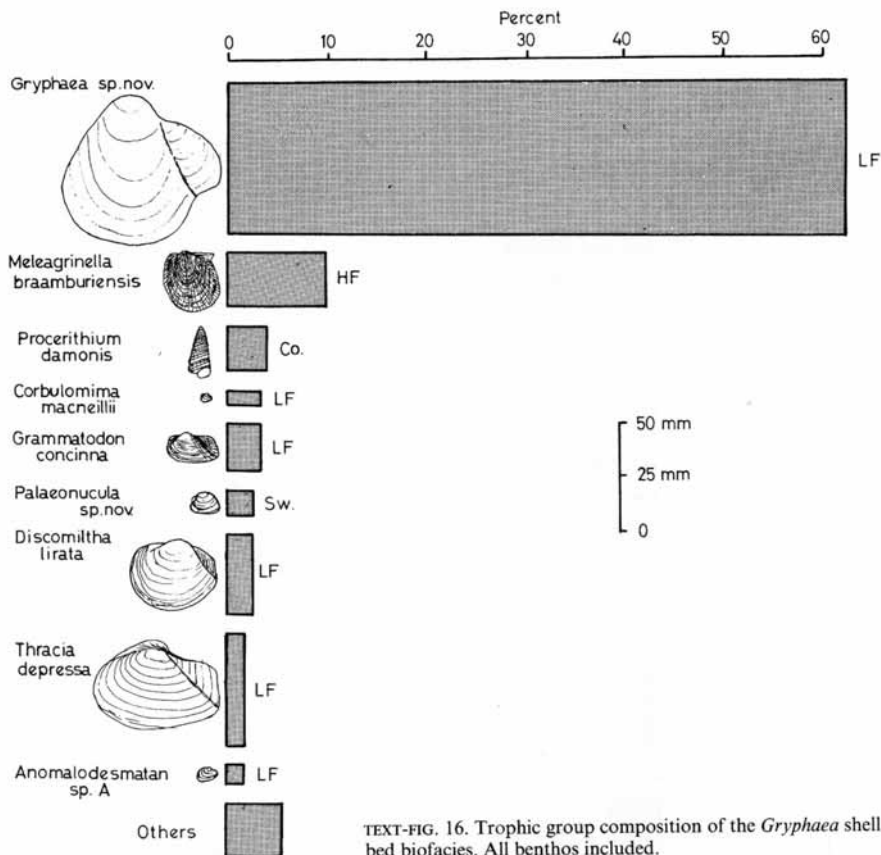
The overwhelming abundance of *Meleagrinella* is probably original, as the shells are too fragile to have withstood much post-mortem transport, and if the shell bed were current-concentrated, there would be more larger, heavier shells. To explain the numerous *Meleagrinella*, bearing in mind the inferred pendent mode of life of the genus, it is probable that there was a large amount of floating organic matter to which *Meleagrinella* may have been attached; the resulting environmental reconstruction may be comparable with the Recent *Sargassum*-dominated environments. However, this comparison is tentative, as most of the epifauna of *Sargassum* is soft bodied (Friedrich 1965, p. 198), and would leave no traces, and there is no direct evidence for large amounts of floating organic material in the Lower Oxford Clay, and its existence is deduced from the abundant thin-shelled byssally attached Pteriacea and Pectinacea in sediments such as bituminous shales, where the substrate would have been too soft to allow such animals to live on the sea floor.
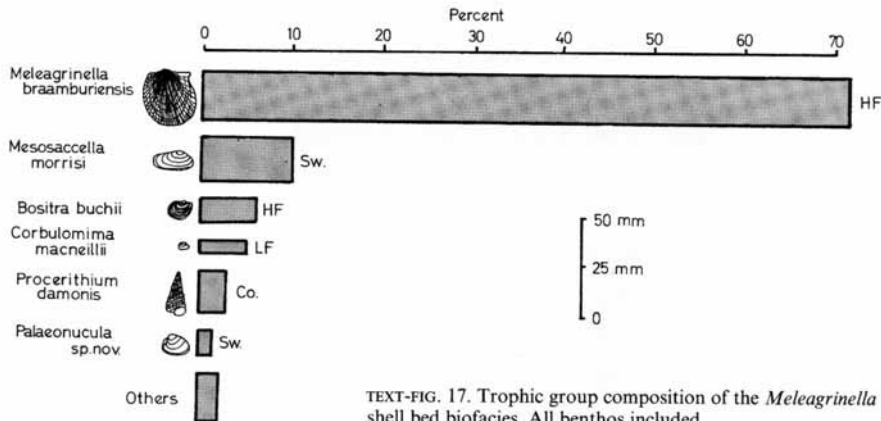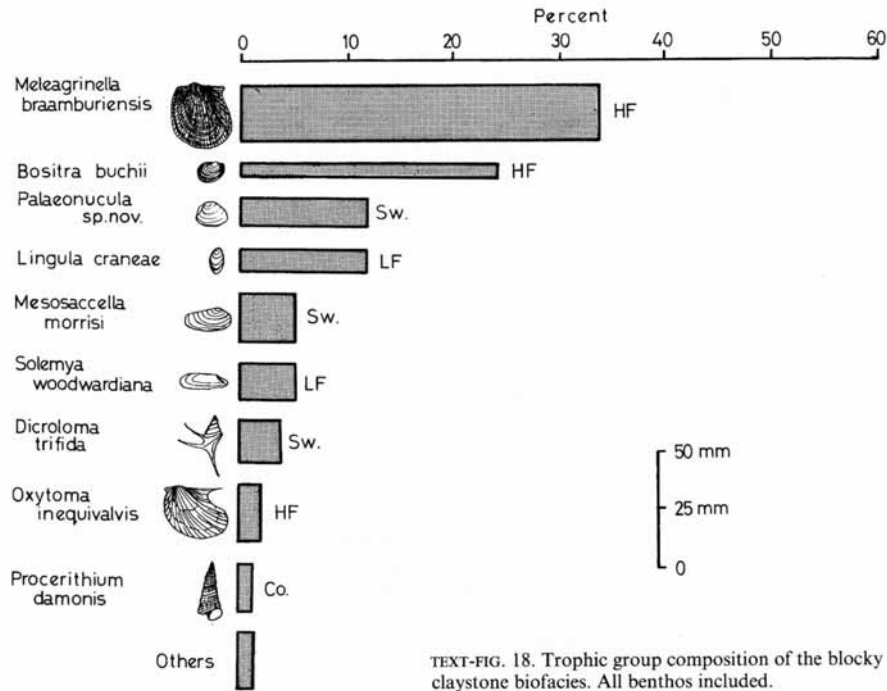
TEXT-FIG. 17. Trophic group composition of the *Meleagrinella* shell bed biofacies. All benthos included.

Blocky claystone. This lithology is known only from the Jason Subzone (Bed 3B) of Calvert. As with the deposit-feeder bituminous shales (within which it occurs), the first two dominance positions are occupied by pendent bivalves (58·4%), whilst the remainder of the fauna is dominated by an alternation of infaunal deposit and suspension-feeders, *Lingula* and *Solemya* being the characteristic members of the latter group (text-fig. 18). The total number of species found is small (only eleven), but there is a relatively high dominance diversity, with only two species less than 1% of the fauna. The lithology is a distinctive light grey, rather plastic, non-fissile clay, with many black organic fragments spread throughout it. Many of the *Lingula* are preserved upright in life position, unknown elsewhere in the Oxford Clay, which suggests that there was no deep scouring of the sea floor. The over-all trophic nucleus (Table 4) is similar to the normal bituminous shales, due mainly to the large content of pendent species, and it is not until these are removed (Table 5) that the unusual nature of the fauna becomes apparent.

Calcareous clays. This facies is restricted to the upper Grossouvrei Subzone, where it forms a regular alternation with the *Meleagrinella* shell beds with the junctions between the two always burrowed. The main characteristic of the calcareous clays is their high dominance diversity, with five species each more than 10% of the fauna (text-fig. 19), and a relatively large trophic nucleus (Table 4). The most abundant species is an infaunal deposit-feeder (*Mesosaccella*), the next two species being pendent bivalves ('*Entolium*' and *Meleagrinella*), which together make up 60·8% of the fauna. '*Entolium*' (a new genus to be described elsewhere) is the most characteristic faunal element, known only rarely from other facies; the polychaet worm *Genicularia* is also typical. Further analysis reveals that there is an approximately equal distribution of deposit and suspension-feeders (Table 4), with most of the suspension-feeders being pendent; infaunal suspension-feeders are not abundant (text-fig. 19), and the degree of aeration within the sediment was probably not great, in the same way as in the more calcareous Middle and Upper Oxford Clays. The low content of infaunal suspension-feeders is also apparent from the triangular plots

TEXT-FIG. 18. Trophic group composition of the blocky claystone biofacies. All benthos included.

(text-fig. 7e–f). The calcareous clays are rather rich in carbonate, and consequently have a low insoluble residue content (74%), together with a low organic carbon content (1·1%).

Relations between the biofacies. The over-all succession in the Lower Oxford Clay at the major pits examined in the Midlands (text-fig. 5) is generally similar, although there are local variations, especially at Stewartby and Calvert. Superimposed on these local variations in the details of the succession is a marked southward increase in thickness, the Enodatum–Grossouvrei Subzone succession being 12 m thick at Peterborough, and gradually increasing through 14 m at Stewartby, 17 m at Bletchley, to 18 m at Calvert. These thickness changes probably indicate greater distance from the shoreline or a submarine swell, with consequent decrease in the number and thickness of shell beds. This is particularly noticeable in the case of the shell bed which occurs at or just above the base of the Obductum Subzone at Peterborough and Stewartby; the shell bed is missing from the Bletchley section. Most of the thickness variation occurs within the Jason and Calloviense Zones (text-fig. 6), which thicken from 0·5 m at Peterborough to over 3·0 m at Calvert, suggesting that during the deposition of the initial subzones of the Oxford Clay, conditions were more variable, and controlled by local configurations of the sea floor. By the time of the Coronatum
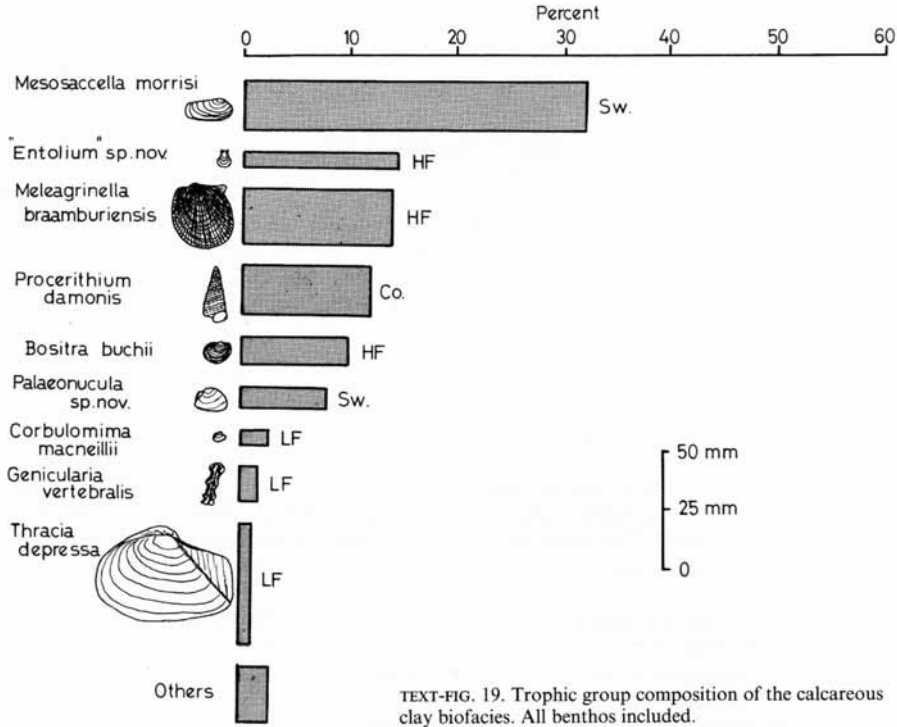
TEXT-FIG. 19. Trophic group composition of the calcareous clay biofacies. All benthos included.

Zone, conditions appear to have stabilized over the whole of the Midland area, giving a much more uniform thickness of Lower Oxford Clay.

The transition beds between the Kellaways Rock and the Oxford Clay are best developed at Peterborough and Bletchley, where they consist of an alternation of silts and silty clays, *Gryphaea* shell beds, and deposit-feeder bituminous shales. At Peterborough the transition beds occupy the whole of the Enodatum and Medea Subzones (0·5 m), but at Bletchley are restricted to the Medea Subzone (2·0 m), Kellaways Rock deposition having continued until the top of the Enodatum Subzone. At Stewartby the transition beds appear to be absent, a bipartite shell bed, the upper part a *Grammatodon* shell bed and the lower part a *Gryphaea* shell bed, rests directly on the silts of the Kellaways Rock, which are dated as Enodatum Subzone; deposit-feeder bituminous shales of the Medea Subzone follow these shell beds directly. Thus Kellaways Rock deposition ended earlier in the northern parts of the Midlands, and Oxford Clay did not reach the south Midlands until the end of Enodatum Subzone times; this suggests that the shoreline lay to the south during this time. There then appears to have been rather variable current activity, phases of shallowing and increased current activity giving *Gryphaea* shell beds, whilst in the intermittent quiet phases silts or bituminous shales were laid down. The bituminous shales indicate that

the influence of the offshore clay facies was greater at that time, and that distance from shore, and probably water depth, was gradually increasing. The transition beds are not exposed at Calvert, the pit ending in the Jason Subzone, although Callomon (1968, p. 287) records 10 ft of combined Medea and Enodatum Subzones in a borehole there.

Gradual recession of the shoreline during deposition of the transition beds eventually allowed the establishment of quiet water conditions in which bituminous shales were laid down. At Peterborough, Bletchley, and Calvert, this phase seems to have begun more or less at the start of Jason Subzone times, while at Stewartby similar conditions became established slightly earlier. At all the pits the lowermost few centimetres of the shales are markedly fossiliferous and contain the same species as the underlying shell beds, indicating the gradual dying out of the fauna of the preceding bed. There then followed thick dominantly deposit-feeder bituminous shales, which occupy the whole of Jason and Obductum Subzone time at Peterborough, Bletchley, and Calvert, with the exception of the 1-m band of blocky claystone near the base at Calvert. During this time bottom conditions were quiet, and water circulation probably poor, producing an impoverished benthonic fauna dominated by deposit-feeding bivalves and gastropods, with rare benthonic suspension-feeders. Living above the bottom and attached to postulated organic material were large numbers of pendent epifaunal suspension-feeding bivalves, chiefly *Bositra*, *Meleagrinella*, and *Oxytoma*. The suspension-feeder dominated fauna is unusual, and was probably caused by a superabundance of the suspended food source, as discussed above.

The general sequence seen in the Lower Oxford Clay of the Midlands, Kellaways Rock through transition beds to bituminous shales and then to more fossiliferous shales, adds substance to the suggestion of Hallam (1967a, p. 489) that bituminous shales are often laid down in relatively shallow water. Hallam suggested that near the base of transgressive sequences widespread bituminous shale deposition was characteristic, and that it was followed by more fossiliferous, deeper-water clays and shales, laid down as water circulation improved, and sediment oxygenation increased. The Kellaways Beds–Upper Oxford Clay sequence agrees with this model, the bulk of the Lower Oxford Clay representing the bituminous shale part of the cycle.

The presence of the 1-m band of blocky claystone near the base of the Jason Subzone at Calvert indicates that conditions were slightly different there during much of the Jason Subzone times, as the *Lingula*-rich blocky claystone fauna continues for most of the subzone. Both *Lingula* and *Solemya* have been considered by previous authors to be genera tolerant of poorly aerated water, and this, together with the low organic carbon content, the increased thickness, and reduced benthonic fauna, suggests that in the south Midlands area this part of the sequence was laid down more rapidly than the deposit-feeder bituminous shales and possibly in slightly deeper water.

At Stewartby the Obductum Subzone sequence is different to that seen at the other pits, a thin development of deposit-feeder bituminous shale, containing two very well-developed Nuculacean shell beds, being followed by a very thick *Meleagrinella* shell bed, and a development of foraminifera-rich bituminous shale. The combination of the two Nuculacean shell beds, being followed by a very thick *Meleagrinella*

shell bed, suggests that local current activity must have been increased at this time, probably on a local swell. The foraminifera-rich bituminous shale above the *Meleagrinella* shell bed shows a return to quieter and deeper water, with well-developed niche partitioning within the benthonic fauna.

Throughout the Midlands the end of the Obductum Subzone coincides with a widespread phase of slow deposition, marked by Nuculacean or *Grammatodon* shell beds. Brinkmann (1929, p. 81) showed that at Peterborough the shell bed at the top of the Obductum Subzone represents a significant pause in sedimentation, and it seems likely that a similar situation prevailed over much of the Midlands. This phase of condensed deposition is followed at all the pits by a similar succession in the Grossouvrei Subzone. The well-aerated conditions of the Nuculacean and *Grammatodon* shell beds persisted into the next phase of bituminous-shale deposition, giving a sequence of *Grammatodon*-rich bituminous shales, rich in infaunal suspension-feeders such as *Grammatodon*, *Isocyprina*, and *Thracia*. The start of the Grossouvrei Subzone sees the first appearance in the Oxford Clay of *Grammatodon minima*, and also marks the arrival of abundant *Isocyprina*. This event can be recognized at the same level in Dorset, and is useful for defining the base of the Grossouvrei Subzone. Phases of increased current activity during this time are marked by *Grammatodon* shell beds. As subsidence continued, and oxygenation of the water gradually decreased, the *Grammatodon*-rich bituminous shales were replaced by foraminifera-rich bituminous shales in which deposit-feeders became more abundant and infaunal suspension-feeders fewer, although the conditions which resulted in the deposit-feeder bituminous shales never became re-established.

Later, in Grossouvrei Subzone times, there was a renewed phase of shallowing, producing the characteristic alternation of calcareous clays and *Meleagrinella* shell beds, bringing the Middle Callovian to a close in southern England. As suggested above, this sequence must have been characterized by periodic explosions in colonization by organic matter, allowing dense *Meleagrinella* shell beds to accumulate, and producing many small non-sequences. Aeration in the calcareous clays must have been relatively good as they supported a diverse fauna of suspension-feeders, and there is a sudden increase in the abundance of tube-building annelid worms. Grossouvrei Subzone deposition was concluded over the whole area by a thick Nuculacean shell bed—the Comptoni Bed—which again represents a phase of increased current activity, and a pause in sedimentation. This part of the sequence is usually capped by a concretionary diagenetic limestone, the Acutistriatum Band, which is developed within a band of very bituminous foraminifera-rich shaly clay, and which represents the basal bed of the Athleta Zone.

Thus within a relatively thin sequence of Lower Oxford Clay (12–18 m), occupying just over two ammonite zones, there are two cycles of environmental conditions. Firstly, there is the deepening sequence from the Kellaways Rock through the transition beds into the deposit-feeder bituminous shales of the Jason–Obductum Subzones, with indications of shallowing towards the top, and secondly, the more balanced cycle of the Grossouvrei Subzone, which shows distinct deepening and shallowing phases, ending with a pronounced non-sequence.

C

COMPARISONS WITH OTHER FACIES

In view of the lack of comparable quantitative data from similar environments, comparisons must be limited to more qualitative observations, largely gleaned from the literature. In particular, the work of Melville (1956), Hallam (1960, 1967), Palmer (1966, 1966a, 1973), and Sellwood (1972) on the Lias, Hudson and Palframan (1969) on the Middle and Upper Oxford Clay, Price (1879) on the Gault, and Scott (1970) on the Lower Cretaceous of the United States, has been used for comparison of clay faunas, and shows the Lower Oxford Clay to be unusual because of its very high content of pendent epifaunal suspension-feeders and infaunal deposit-feeders. With the exception of Scott, no quantitative data was given, fossils merely being recorded, or being said to be rare, common, or occur, and thus direct comparison is difficult.

There is also the assessment of the relative importance of evolutionary and environmental changes when the palaeoecology of different ages is being compared. However, in this consideration all the rocks are of Jurassic or Lower Cretaceous age, and the importance of evolutionary changes appears minor; there is little change in the overall faunal composition, although there is much variation in the relative importance of species within it. Protobranch bivalves are known to be a slowly evolving group, so evolutionary effects in this protobranch-dominated assemblage are likely to have been small. In general terms it appears to be environmental conditions which have exercised the greater control over benthonic assemblages during Jurassic and Lower Cretaceous times.

The shales of the Oxford Clay have frequently been compared with the Lias, but this study shows many differences between the two deposits. Hallam (1960, p. 12) described the bituminous shales of the Blue Lias of Dorset and Glamorgan, and showed them to have a very high organic carbon content (3·9-8·0%), and a fauna consisting almost entirely of ammonites, fish scales, and bivalve spat, indicating that bottom conditions must have been anaerobic. Most of the fossils are preserved in the marls and limestone bands, which Hallam showed to be essentially of primary origin, although he later (1964) amended his views, but similarities with the Lower Oxford Clay are negligible, as in the Lias limestones there is a rich and varied fauna of normal infaunal and epifaunal suspension-feeders, while deposit-feeders and pendent bivalves are rare. It thus seems very likely that the limestone part of the Blue Lias rhythm was much better aerated than the Lower Oxford Clay, as it contains a much more varied fauna, including gastropods, brachiopods, and echinoderms.

Sellwood (1972) gives similar results on the Sinemurian–Pliensbachian Lias to those of Hallam (1960, p. 10), in so far as the fauna is dominated by infaunal and epifaunal suspension-feeders, with few deposit-feeders. Rocks of this age over most of Britain are clearly less bituminous and more well aerated than the bituminous shales of the Blue Lias, and contain many genera which are also characteristic of the Lower Oxford Clay, but again there is a lack of abundant pendent bivalves and deposit-feeders. The same is true of the Middle and Lower Lias described by Melville (1956, p. 74) from the Stowell Park borehole in Gloucestershire, pendent bivalves and deposit-feeders again not being abundant, the fauna being dominated by infaunal and epifaunal suspension-feeders. Palmer's (1973, p. 252) work on the upper parts of the Lower Lias in Gloucestershire shows a faunal list rather similar to that of the

Lower Oxford Clay, but again pendent bivalves and deposit-feeders are neither abundant nor widespread. The Middle Lias (Palmer 1966, 1966a; Hallam 1967) shows similar conditions to have prevailed during deposition of the more sandy shales.

The Upper Lias (Melville 1956; Hallam 1967) of Britain is probably the most similar deposit to the Lower Oxford Clay, consisting of dark shales and shaly clays with a sparse benthonic bivalve fauna, dominated by deposit-feeding Nuculaceans such as *Nuculana* and '*Nucula*', often with a pendent bivalve fauna of *Bositra radiata* and *Inoceramus dubius*. These shales, which are also rich in cephalopods and *Procerithium*, often contain local concentrations of comminuted fish debris, insect remains, and crustacea, emphasizing the similarity with the bituminous shales of the Lower Oxford Clay. Quantitative work on the fauna of the Upper Lias shales would be of interest for detailed comparisons with the Oxford Clay.

Hudson and Palframan (1969) have described the palaeoecology of part of the Middle–Upper Oxford Clay of the Midlands, and shown that there are clear differences between the fauna of this part of the Oxford Clay and the Lower Oxford Clay. The dark grey, well-laminated bituminous shales have been replaced by light grey, rather calcareous clays, often rich in fossils preserved as pyritic internal moulds, with no preserved aragonite. The Spinosum Clays (Athleta–Lamberti Zones) have a sparse benthonic fauna, dominated by shallow infaunal species (mostly deposit-feeders), with the epifauna characteristically rich in *Chlamys* and *Gryphaea*; other Pectinacea are locally common. Near the top, *Gryphaea* beds appear, alternating with the normal clay facies, and having, as well as common *Gryphaea lituola*, suspension-feeders dominating over deposit-feeders. However, these *Gryphaea* beds are not equivalent to those of the Lower Oxford Clay; they merely consist of a concentration of oysters (estimated at four per square foot) in slightly harder and more calcareous clay, and do not represent phases of non-deposition, although there must have been some slowing of sedimentation. The rest of the Spinosum Clays make up a sequence of quiet water muds similar to, but not equivalent to, the bituminous shales of the Lower Oxford Clay. The faunal density is also less than that of the Lower Oxford Clay, and there are none of the abundant *Bositra*, *Meleagrinella*, or *Oxytoma* so typical of the Middle Callovian. The abundance of *Astarte* s.l. in the Spinosum Clays suggests that the bottom sediments must have been fairly well aerated.

The Mariae Clays (Mariae Zone) are darker and more organic-rich than the Spinosum Clays, and have a different faunal composition. The benthonic fauna is reduced in variety, and is mostly infaunal, with *Dicroloma*, *Procerithium*, and Nuculacea abundant, and *Pinna* the only common suspension-feeder. This part of the Upper Oxford Clay is much more similar to the Lower Oxford Clay in faunal content, although the presence of pyritic ammonites is a notable difference and the shales are not well laminated. It seems likely, however, that during at least part of the Mariae Zone conditions were somewhat similar to those of the Lower Oxford Clay.

The fauna of the Gault Clay (Cretaceous, Albian) has been summarized by Casey (1966, p. 102), but a more comprehensive faunal list was given by Price (1879, p. 60), who charted the distribution of the bivalve fauna. Price recognized eighty-six bivalve species in the English Gault, fourteen of which are deposit-feeders, almost all species of '*Nucula*'. In spite of this apparently high diversity of deposit-feeding protobranchs,

they are not as abundant as they are in the Lower Oxford Clay, nor are there so many siphonate forms. There are, however, large swarms of *Inoceramus* throughout the Gault, and so in this respect there are close similarities with the Lower Oxford Clay. The main difference is in the greater diversity of infaunal and epifaunal suspension-feeders, especially deep burrowers. The Gault has long been divided into two lithological parts, the Upper Gault, consisting of light-coloured rather calcareous clay, while the Lower Gault is much darker, less calcareous, and is generally more similar to the Lower Oxford Clay, although it is not bituminous. Casey (1966, p. 105) records *Inoceramus* and Nuculacea (*Nucula* spp., *Acila*, and *Mesosaccella*) as the most abundant bivalves of the Lower Gault, with infaunal suspension-feeders becoming more abundant in the Upper Gault. Most of the molluscs preserved in the Lower Gault retain the original unaltered shell aragonite, although the cephalopods in particular, as well as some of the bivalves and gastropods, are usually pyritized. As in the Lower Oxford Clay, preservation of aragonite is related to the very impervious nature of the sediment.

Scott (1970) has described the palaeontology and palaeoecology of the Kiowa Formation (Lower Cretaceous, Aptian-Cenomanian) of Kansas, and recognized six lithofacies groupings, of which one, the dark-grey shale lithofacies, is comparable with the Lower Oxford Clay. It is a dark grey, fissile, well-laminated shale, with a general lack of small-scale sedimentary structures, and Scott believes the fossil assemblages to represent 'disturbed neighbourhood' and mixed-fossil assemblages. This lithofacies is characterized by the *Nuculana* association, dominated by *Nuculana*, *Yoldia*, *Nucula* (nuculaceans), *Breviarca* (Arcacea), *Pholadomya*, *Turritella*, *Drepano-cheilus*, and *Lingula*, which constitute 18–84% of the fauna; most of the remainder of the fauna is composed of a corbulid.

The other comparable lithofacies recognized by Scott is his shell conglomerate facies, which corresponds closely to the *Gryphaea* shell beds of the Lower Oxford Clay. Similarities include the high content of *Gryphaea* (51–100%), the common occurrence of calcitic shells, and the laterally discontinuous nature of the shell beds. There are, however, some sedimentary structures which suggest that the Kiowa shell conglomerates were deposited in very shallow water, possibly by storm-generated currents, and there is no direct evidence that this is the case for the Lower Oxford Clay *Gryphaea* shell beds.

Evolutionary changes—comparison with Palaeozoic and Recent assemblages. Deposit-feeder dominated assemblages occur in many argillaceous deposits, from the Ordovician to the present. In general trophic composition the assemblages are similar, but marked evolutionary changes have altered the structure of the younger ones, showing the importance of evolutionary changes over a long period. The main changes are in the composition of the suspension-feeding part of the fauna since the Lower Palaeozoic; bivalves having taken the place of the articulate brachiopods, as a result of the development of siphon formation (Stanley 1968, p. 224). The suspension-feeder groups present in the Lower Palaeozoic have also been replaced by more highly evolved superfamilies, leaving only the slowly evolving deposit-feeding Nuculoida as a conservative stock.

The most similar assemblages to those of the Lower Oxford Clay are the various

Lingula 'communities' described from the British and American Palaeozoic (Bretsky 1970, p. 61; Ziegler *et al.* 1968, p. 5; Craig 1955, p. 114). The data for these communities have been replotted by Walker (1972, pp. 87, 88, 90) to show the trophic structure of the assemblages, and it is clearly apparent that both the Ordovician and the Lower Carboniferous *Lingula* assemblages (described by Bretsky and Craig respectively), are dominated by deposit-feeders, and show well-developed niche partitioning. As in parts of the deposit-feeder bituminous shale biofacies, *Lingula* is an important constituent of the fauna, and occupies second place in the assemblage; the dominant species in both these Lower Palaeozoic assemblages is an infaunal nuculoid. In the Ordovician *Lingula* community described by Bretsky, third and fifth places are occupied by archaeogastropods, which functioned as epifaunal browsing herbivores. These elements are absent from the equivalent Mesozoic assemblages.

Ziegler *et al.* (1968) have described several 'communities' from the Silurian of the Welsh borderlands, the *Lingula* community being particularly relevant here. The commonest species is an epifaunal suspension-feeding brachiopod (*Camarotoechia*), with *Lingula* and *Palaeoneilo* (a nuculanid) occupying the next two positions; the epifaunal pterioid *Pteronitella* is also characteristic. This assemblage has a low diversity (Diversity Index 6·2), but shows a wide range of feeding types, although it differs from the other Palaeozoic *Lingula* associations in having a high content of filter-feeders; Walker (1972, p. 91) has suggested that perhaps this is not a true example of the *Lingula* assemblage. This *Lingula* community is usually developed in a more marginal facies, consisting mainly of sandstones, and so epifaunal suspension-feeders, such as *Camarotoechia*, are most abundant. Thus *Lingula* communities in general may be of varying type, and developed in several lithologies; only shale occurrences are of relevance here. The Diversity Index value for Ziegler's *Lingula* community (6·2) agrees well with the values from the Lower Oxford Clay (5·9–6·7 in the bituminous shales), in contrast to the other brachiopod-dominated Silurian communities, which have much higher diversities (D.I. 7·8–11·8) due to their low dominance diversity.

In general terms, there are close similarities between Palaeozoic and Mesozoic deposit-feeder dominated assemblages, notably in the abundance of infaunal deposit-feeding bivalves and infaunal suspension-feeding *Lingula*. In the Mesozoic, many of the niches originally occupied by brachiopods have been taken over by bivalves, many of the new superfamilies still being extant. One of the major differences between the Lower Oxford Clay and the Palaeozoic assemblages, is the lack of a rich fauna of pendent epifaunal suspension-feeding bivalves in the Palaeozoic, although they occur sporadically in some of the later assemblages (i.e. the *Posidonia* Band of Craig 1955, p. 112).

Recent offshore soft-mud communities have been described by many authors, and are broadly comparable with the Lower Oxford Clay assemblages, although there are differences. The silt-clay facies occupying the central axis of Buzzards Bay, Massachusetts (Sanders 1960; Rhoads and Young 1970; and Rhoads 1973) is dominated by deposit-feeders, both infaunal and epifaunal. Sanders identified the fauna as belonging to the *Nucula proxima–Nephthys incisa* community, with these two species (the latter a polychaet) making up 76% by number of the specimens collected. The

trophic nucleus consists of three deposit-feeders, *Nucula proxima* being the most abundant, and suspension-feeders are of minor importance; no pendent epifaunal suspension-feeding bivalves are known. The same is true of other offshore mud communities (Jones 1950, p. 308) which are usually dominated by deposit-feeding protobranchs and polychaets, usually with a conspicuous associated fauna of infaunal suspension-feeding bivalves. In this respect, the similarities with the various Lower Oxford Clay biofacies are many when the strictly benthonic fauna alone is considered, but, again, there is a noticeable lack of pendent suspension-feeders. The only known Recent assemblage with a high content of pendent epifaunal species is that found on *Sargassum* weed (Friedrich 1965, p. 198), but molluscs are not of great importance, only five species having been described from this habitat. Stanley (1972, p. 189) has recorded that many Recent species of *Pteria* attach preferentially to alcyonarian seawhips, a method of obtaining stable fixation in an agitated environment. Recent parallels for the mode of life postulated for the Oxford Clay pendent bivalves are not known, and this may be accounted for by evolutionary effects. Alcyonarians did not appear until the Jurassic, and gorgonaceans until the Cretaceous (Stanley 1972, p. 190), so it is possible that the lack of abundant rooted organic material during the Jurassic led to the colonization of floating or rooted organic material (including algae) by species that needed to live above, rather than on, a soft-mud substrate. Thus the Lower Oxford Clay bituminous shale assemblages were both of different structure and occupied slightly different environments to Palaeozoic and Recent offshore mud assemblages, a consequence of evolutionary, rather than environmental changes.

CONCLUSIONS

Hallam (1967a, p. 489) suggested that bituminous shales were relatively shallow-water deposits laid down in quiet, but not invariably stagnant water below wave base, in contrast to the deep-water 'barred basin' model postulated by earlier authors. The evidence deduced from the Oxford Clay appears to support this hypothesis, as there is a deepening sequence from the sands and silts of the Kellaways Rock, through the laminated bituminous shales of the Lower Oxford Clay, into the more massive calcareous clays of the Middle–Upper Oxford Clay. The many small-scale alternations of lithology within the Lower Oxford Clay indicate relatively shallow-water deposition, where a slight change in water depth could have a marked effect on hydrographic conditions.

Faunally, bituminous-shale sequences show variability through time, with Palaeozoic black shales either lacking benthonic elements (the graptolitic shales), or with a benthonic fauna dominated by deposit-feeding nuculoids and suspension-feeding linguloids. At various times pendent or benthonic byssally attached bivalves were fairly common, but were never as important as in the Mesozoic. In the European Jurassic, bituminous shales are particularly important in the Lower Hettangian, Lower Toarcian, and the Middle Callovian, and all tend to show a fauna consisting mainly of nuculoids and pendent bivalves. Recent organic-rich mud communities have rather more infaunal suspension-feeders and no pendent bivalves, but, again, nuculoids are numerically dominant. The role of the infaunal deposit-feeding protobranchs seems to have persisted more or less unchanged since the Lower Palaeozoic,

their mode of life (inhabiting quiet water muds in areas of environmental stability) needing little adaptive change. The replacement of brachiopods by bivalves as the dominant members of the epifauna after the Palaeozoic followed siphon formation in the Bivalvia, and marks the main change in the composition of the faunas of organic-rich shales since the Palaeozoic.

REFERENCES

ARKELL, W. J. 1933. *The Jurassic System in Great Britain.* Clarendon Press, Oxford.

BADER, R. G. 1954. The role of organic matter in determining the distribution of pelecypods in marine sediments. *J. mar. Res.* **13**, 32–47.

BARNARD, T. 1952. Foraminifera from the Upper Oxford Clay of Warboys. *Proc. Geol. Ass.* **63**, 336–350.

—— 1953. Foraminifera from the Upper Oxford Clay (Jurassic) of Redcliff Point, near Weymouth, England. Ibid. **64**, 183–197.

BRETSKY, P. W. 1970. Upper Ordovician ecology of the central Appalachians. *Bull. Peabody Mus. nat. Hist.* **34**, 150 pp., 44 pls.

BRINKMANN, R. 1929. Statistisch-Biostratigraphische Untersuchungen an Mitteljurassischen Ammoniten über Artbegriff und Stammesentwicklung. *Abh. Akad. Wiss. Göttingen Math. Phys. Kl.* N.F. **13** (3), 1–249, pls. 1–5.

—— 1929a. Monographie der Gattung *Kosmoceras.* Ibid. **13** (4), 1–124, pl. 1.

CALLOMON, J. H. 1955. The ammonite succession in the Lower Oxford Clay and Kellaways Beds at Kidlington, Oxfordshire, and the zones of the Callovian stage. *Phil. Trans. R. Soc.* **B. 239**, 215–264, pls. 2, 3.

—— 1964. Notes on the Callovian and Oxfordian stages. *C.r. Mém. Coll. Jurassique,* Luxembourg, 1962, 269–291.

—— 1968. The Kellaways Beds and the Oxford Clay. *In* SYLVESTER-BRADLEY, P. C. and FORD, T. D. (eds.). *The Geology of the East Midlands,* Leicester, 264–290.

CASEY, R. 1966. Palaeontology of the Gault. *In* SMART, J. G. O., BISSON, G. and WORSSAM, B. C. Geology of the country around Canterbury and Folkestone. *Mem. geol. Surv. G.B.* 102–113.

CORDEY, W. G. 1962. Foraminifera from the Oxford Clay at Loch Staffin, Isle of Skye, Scotland. *Senckenberg. leth.* **43**, 375–409, pls. 46–48.

—— 1963. The genera *Brotzenia* and *Voorthuysenia* (Foraminifera) and Hofkers classification of the Epistomariidae. *Palaeontology,* **6**, 653–657, pl. 93.

CRAIG, G. Y. 1955. The palaeoecology of the Top Hosie shale (Lower Carboniferous) at a locality near Kilsyth. *Q. Jl geol. Soc. Lond.* **110**, 103–119.

DAVIES, A. M. 1916. The zones of the Oxford and Ampthill Clays in Buckinghamshire and Bedfordshire. *Geol. Mag.* **53**, 395–400.

DINAMANI, P. 1964. Feeding in *Dentalium conspicuum. Proc. malac. Soc. Lond.* **36**, 1–5.

FARROW, G. 1966. Bathymetric zonation of Jurassic trace fossils from the coast of Yorkshire. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **2**, 103–151.

FRIEDRICH, H. 1965. *Marine Biology.* Sidgwick & Jackson, London.

HALLAM, A. 1960. A sedimentary and faunal study of the Blue Lias of Dorset and Glamorgan. *Phil. Trans. R. Soc.* **B. 243**, 1–44, pls. 1, 2.

—— 1964. Origin of the limestone–shale rhythms in the Blue Lias of England: a composite theory. *J. Geol.* **72**, 157–169.

—— 1967. An environmental study of the Upper Domerian and Lower Toarcian in Great Britain. *Phil. Trans. R. Soc.* **B. 252**, 393–445, pl. 20.

—— 1967a. The depth significance of shales with bituminous laminae. *Mar. geol.* **5**, 481–493.

—— 1969. Faunal realms and facies in the Jurassic. *Palaeontology,* **12**, 1–18.

HUDSON, J. D. and PALFRAMAN, D. F. B. 1969. The ecology and preservation of the Oxford Clay fauna at Woodham, Buckinghamshire. *Q. Jl geol. Soc. Lond.* **124**, 387–418, pls. 19, 20.

JEFFERIES, R. P. S. and MINTON, P. 1965. The mode of life of two Jurassic species of '*Posidonia*'. *Palaeontology*, **8**, 156–185, pl. 19.

JOHNSON, R. G. 1964. The community approach to palaeoecology. *In* IMBRIE, J. and NEWELL, N. D. (eds.). *Approaches to Paleoecology*, Wiley, New York, 107–134.

JONES, N. S. 1950. Marine bottom communities. *Biol. Rev.* **25**, 283–313.

MELVILLE, R. V. 1956. The stratigraphical palaeontology, ammonites excluded, of the Stowell Park borehole. *Bull. geol. Surv. G.B.* **11**, 67–139, pls. 2–8.

NEAVERSON, E. 1925. The zones of the Oxford Clay near Peterborough. *Proc. Geol. Ass.* **36**, 27–37.

NEYMAN, A. A. 1967. Limits to the application of the trophic group concept in benthic studies. *Oceanology*, *Acad. Sci. USSR*, **7**, 149–155.

PALMER, C. P. 1966. Note on the fauna of the Margaritatus Clay (Blue Band) in the Domerian of the Dorset coast. *Proc. Dorset nat. Hist. archaeol. Soc.* **87**, 67–68.

—— 1966a. The fauna of Day's shell bed in the Middle Lias of the Dorset coast. Ibid. 69–80, pls. 1–3.

—— 1971. The stratigraphy of the Stonehouse and Tuffley clay pits in Gloucestershire. *Proc. Bristol Nat. Soc.* **32**, 58–68.

—— 1973. The palaeontology of the Liassic (Lower Jurassic) clay pits at Stonehouse and Tuffley in Gloucestershire. *Geol. Mag.* **110**, 249–263, pl. 1.

PRICE, F. G. H. 1879. *The Gault*. Taylor & Francis, London.

RHOADS, D. C. 1973. The influence of bottom-feeding benthos on water turbidity and nutrient recycling. *Am. J. Sci.* **273**, 1–22, pls. 1, 2.

—— SPEDEN, I. G. and WAAGE, K. M. 1972. Trophic group analysis of Upper Cretaceous (Maestrichtian) bivalve assemblages from South Dakota. *Bull. Am. Ass. Petrol. Geol.* **56**, 1100–1113.

—— and YOUNG, D. K. 1970. The influence of deposit-feeding organisms on bottom-sediment stability and community trophic structure. *J. mar. Res.* **28**, 150–178.

ROOD, A. P. and BARNARD, T. 1972. On Jurassic coccoliths: *Stephanolithion*, *Diadozygus* and related genera. *Eclog. geol. Helv.* **65**, 327–342, pls. 1, 2.

—— HAY, W. W. and BARNARD, T. 1971. Electron microscope studies of Oxford Clay coccoliths. Ibid. **64**, 245–271, pls. 1–5.

RUTTEN, M. G. 1956. Depositional environment of Oxford Clay at Woodham clay pit. *Geologie Mijnb.* *N.S.* **18**, 344–346.

SANDERS, H. L. 1960. Benthic studies in Buzzards Bay. III. The structure of the soft-bottom community. *Limnol. Oceanogr.* **5**, 138–153.

—— 1968. Marine benthic diversity: a comparative study. *Am. Nat.* **102**, 243–282.

SCHÄFER, W. 1972. *Ecology and Palaeoecology of Marine Environments*. Ed. CRAIG, G. Y. Oliver & Boyd, Edinburgh.

SCOTT, R. W. 1970. Paleoecology and paleontology of the Lower Cretaceous Kiowa Formation, Kansas. *Paleont. Contr. Univ. Kansas*, *Art.* **52**, 94 pp., 7 pls.

SELLWOOD, B. W. 1972. Regional environmental changes across a Lower Jurassic stage-boundary in Britain. *Palaeontology*, **15**, 125–157, pls. 28, 29.

STANLEY, S. M. 1968. Post-Paleozoic adaptive radiation of infaunal bivalve molluscs—a consequence of mantle fusion and siphon formation. *J. Paleont.* **42**, 214–229.

—— 1970. Relation of shell-form to life habits in the Bivalvia (Mollusca). *Mem. geol. Soc. Am.* **125**.

—— 1972. Functional morphology and evolution of byssally attached bivalve mollusks. *J. Paleont.* **46**, 165–212.

TURPAEVA, E. P. 1948. The feeding of some benthic invertebrates of the Barents Sea. *Zool. Zh. Ukr.* **27**.

WALKER, K. R. 1972. Trophic analysis: a method for studying the function of ancient communities. *J. Paleont.* **46**, 82–93.

WHATLEY, R. C. 1970. Scottish Callovian and Oxfordian Ostracoda. *Bull. Br. Mus. nat. Hist. Geol.* **19**, 297–358, pls. 1–15.

WOODWARD, H. B. 1895. The Jurassic rocks of Britain. V. The Middle and Upper Oolitic rocks of England. *Mem. geol. Surv. G.B.*

WRIGHT, J. K. 1968. The stratigraphy of the Callovian rocks between Newtondale and the Scarborough coast, Yorkshire. *Proc. geol. Ass.* **79**, 363–399, pls. 10, 11.

ZIEGLER, A. M., COCKS, L. R. M. and BAMBACH, R. K. 1968. The composition and structure of Lower Silurian marine communities. *Lethaia*, **1**, 1–27.

K. L. DUFF

The Nature Conservancy Council
Foxhold House, Thornford Road
Crookham Common
Newbury, Berkshire, RG15 8EL