PALAEOECOLOGICAL STUDIES IN THE GREAT OOLITE AT KIRTLINGTON, OXFORDSHIRE

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ABSTRACT. Middle Jurassic (Bathonian) limestones and clays at a quarry north of Oxford have yielded faunas, some of which are life assemblages, and others which have been transported before burial. Size distributions and articulation ratios are among the criteria discussed for distinguishing between the life and death assemblages.

The White Limestone, the lower of the two formations studied, consists of two facies: (*a*) limestones disturbed by burrowing molluscs, worms, and crustaceans which are interpreted as having lived in inter-tidal flats; and (*b*) channels cut into the inter-tidal deposits, which are either poorly fossiliferous or which contain an epifauna of terebratulid brachiopods (*Epithyris*) and mussels (*Modiolus*); the floors of these channels were sub-tidal.

The inter-tidal facies continues locally into the basal metre of the Forest Marble, but this higher formation is dominantly sub-tidal. The Forest Marble (in Oxfordshire) is distinguished from the White Limestone in containing an abundant epifauna (with a large proportion of oysters) and few signs of bioturbation. Shelly limestones and clays with lignite are the characteristic Forest Marble lithologies; one coral–*Epithyris* bed is present which contains a mixture of drifted and endemic forms.

KIRTLINGTON Old Cement Works (Grid reference: SP 494199) lies 10 miles north of Oxford on the east bank of the River Cherwell. It has been abandoned as a working quarry for about 40 years, but the exposures of the White Limestone and the lower part of the Forest Marble are still excellent, except on the long east face, where there has been considerable slipping of the beds with the formation of much scree material. The higher beds (the Cornbrash and the upper part of the Forest Marble) are only sporadically exposed and are not discussed in this work.

The most detailed account of the beds at Kirtlington is given by Arkell (1931, pp. 570–4), but he records only a few of the many lateral changes in thickness and lithology present, and there is little discussion of the relationships between lithology and fauna. Subsequent descriptions (Richardson *et al.* 1946, Arkell 1947, McKerrow and Baden-Powell 1953) have been based almost entirely on Arkell's (1931) account. Klein (1963, 1965) records channels in the Forest Marble at Kirtlington (1965, p. 176); he also records (pp. 187–8) thin graded beds, which he ascribes to storms in areas of tidal flats. Klein (1965, fig. 19, p. 190) shows that most of the channel directions in the Kirtlington area are towards the south-east, and he concludes (pp. 185, 191) that they are channels in a tidal flat. We agree with these conclusions with regard to the White Limestone, but we find no palaeontological or other evidence to suggest that the Forest Marble above the *fimbriatus–waltoni* Clay is intertidal.

STRATIGRAPHY

Only three beds below the Cornbrash can be traced with certainty through all parts of the Kirtlington quarry; these are:

1. A coral–*Epithyris* limestone (text-fig. 1, beds 3o, 4i, and 6j; Arkell 1931, p. 570, the Upper *Epithyris* Bed, bed 11).
2. The *Eomiodon* [*Astarte*] *fimbriatus–Bakevellia* [*Gervillia*] *waltoni* Clay, or, more

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briefly, the *fimbriatus–waltoni* Clay (text-fig. 1, beds 2o, 3l, 4e, and 6f; Arkell 1931, p. 572, bed 10).

3. An oyster–*Epithyris* marl immediately below the *fimbriatus–waltoni* Clay (text-fig. 1, beds 2n, 6e; Arkell 1931, p. 572, the Middle *Epithyris* Bed, bed 9). This bed is seen to pass laterally into a limestone with oysters in Profile 4 (bed 4d), and a limestone without oysters in Profile 3 (bed 3k).

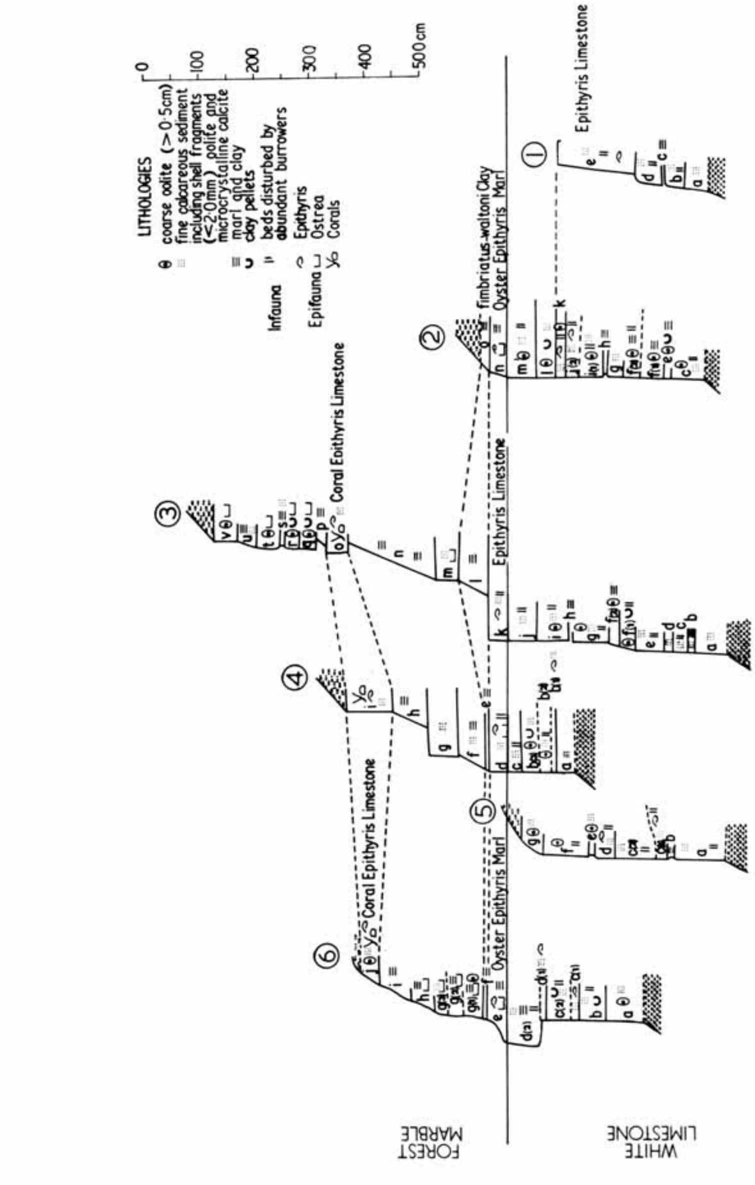
It is proposed to assign to the Forest Marble all the beds between the base of the oyster–*Epithyris* marl (and its equivalents: 2n, 3k, 4d, 6e) and the base of the Cornbrash, and the beds below this marl to the White Limestone. This is in accord with Arkell's (1931) usage, but not with later classifications (Richardson *et al.* 1946, Arkell 1947). The reasons for selecting this oyster–*Epithyris* marl as the base of the Forest Marble are many. It is the lowest bed in which oysters are abundant at Kirtlington, and oysters are seen to be characteristic of the Forest Marble throughout Oxfordshire. Arkell (1931, 1947), Richardson (1933, p. 49 et seq.), Richardson *et al.* (1946, p. 38 et seq.), and Worssam and Bisson (1961, p. 97) all record the abundance of oysters in the Forest Marble (which they subdivide into the Kemble Beds and the Wychwood Beds). Together with the oysters, there is a marked increase in the abundance of other epifaunal bivalves in the Forest Marble compared with the White Limestone, which suggests a marked change of environment. The Forest Marble clays contain much more lignite than those in the White Limestone; some also contain dinosaur remains (Arkell 1931, p. 572, Bed 10) and freshwater ostracods (Bate, 1965). The limestones in the White Limestone are usually oolites, much disturbed by burrowers (except for some channel fills), and some contain a large proportion of microcrystalline calcite in their matrices. Shell fragments make up most of the Forest Marble limestones, and when ooliths occur they are often merely a thin veneer of carbonate around shell fragments.

The flaggy nature of the Forest Marble has often been assumed to be a characteristic lithological feature of this formation. However, examination of the Great Oolite quarries in Oxfordshire shows that the limestones in the top three or so metres are always flaggy, whether they are shelly, bioturbated, or composed of microcrystalline calcite. Most old quarries, opened for building stone, were worked so that the Forest Marble and Lower Cornbrash were the highest beds exposed, but in the past 25 years many quarries wholly in the White Limestone have been opened for road metal and lime, and it is clear that weathering alone can be responsible for the flaggy nature of any type of Great Oolite Limestone.

It should be noted that though faunas play a part in the separation of the White Limestone and the Forest Marble, they are not of chronological significance in correlation. It is very probable that the transition from one environment to the other took place at different times throughout the Oxford area.

We have not attempted to subdivide either the Forest Marble or the White Limestone in this study, as these formations cannot be split into easily recognizable lithological members. In the absence of the Bradford Clay fauna, it is not possible to separate the Kemble Beds from the Wychwood Beds, either by lithology or by faunas (Arkell 1931, pp. 593–5; 1947, pp. 44–6); both are thus grouped as Forest Marble.

The distinction between the two subdivisions of the White Limestone, the Bladon Beds and the Ardley Beds (Arkell 1947, pp. 42–3), is based on the evolution of the gastropod *Aphanoptyxis ardleyensis* Arkell 1931 (spiral angle 10–12°; length less than



TEXT-FIG. 1. Six profiles at Kirtlington. For locations see text-fig. 2.

36 mm.), which grades upwards into *A. bladonensis* Arkell 1931 (spiral angle 23–26°; length in adult 60–70 mm.). This evolutionary change appears to be a reliable time indicator in the Oxford area, but, as the lithologies of the two sets of beds are often identical, they cannot be distinguished in the absence of *Aphanoptyxis*. At Kirtlington, the beds immediately below the oyster–*Epithyris* marl (text-fig. 1, beds 2l, m, 3i, j, 4b, c, 5g, 6c, d; i.e. beds 6–8 of Arkell 1931) have no *Aphanoptyxis* and cannot be definitely assigned to either the Ardley or Bladon Beds (see Arkell 1947, p. 57; '? Bladon Beds. Two bands of blue-hearted limestone with a marl parting'). It would seem best to use the occurrence of these species as zonal (i.e. time) indicators and not as diagnostic of formations.

There is a case for renaming the Forest Marble and the White Limestone with formation names based on a locality, but this should await further study of the Great Oolite Series around Oxford and a full description of the type localities of these formations.

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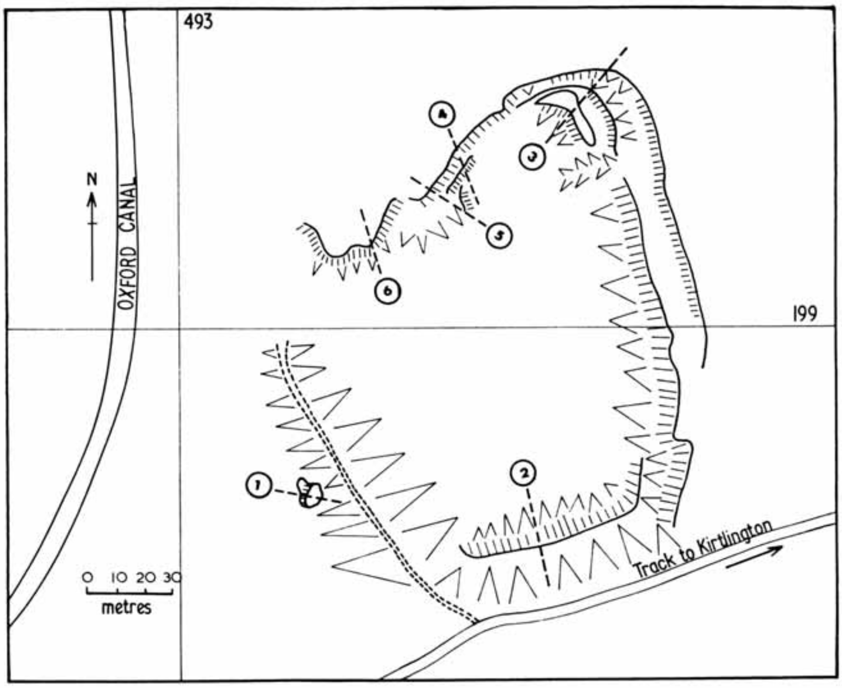
DESCRIPTION OF THE ROCKS AND FAUNAS

Six vertical profiles (text-fig. 2) were selected for the best exposures over maximum thicknesses of rock. The relationships between these profiles are shown in text-fig. 1.



TEXT-FIG. 2. Map of Old Cement Works, Kirtlington.

Profile 1 shows the rocks exposed on a pinnacle left by the quarrying operations in the south-west of the pit (text-fig. 2). All the rocks present are within the White Limestone.

There is strong evidence of burrowing activity in beds lb and ld (text-fig. 1), where very little sign of bedding is left within the limestones; coarse ooliths (0·5–2·0 mm. in diameter) and shell fragments are randomly mixed with finer ooliths and microcrystalline calcite. Some of the animals responsible for the disturbance of the bedding are preserved fossil (e.g. *Anisocardia*) and others can be recognized by their burrows or faecal trails (e.g. *Favreina*, Pl. 12, fig. 2), but there were probably others which left no diagnostic trace. (The genus *Favreina* Brönniman 1955, was founded for faecal trails of an anomuran crustacean; these consist of rods with a diameter of 1–2 mm., sculptured externally with longitudinal and transverse ridges and grooves.) Many of the burrows are vertical tubes 1–2 cm. in diameter lined with shell fragments and filled with fine limestone (Pl. 12, fig. 1); we consider it is likely that they were formed by terebelloid worms, but it is possible that they were formed by other burrowing organisms (perhaps ceriantthid sea anemones).

TABLE 1

Faunal and lithological details for the beds of Profile 1.

WHITE LIMESTONE	EPIFAUNA	INFAUNA	*Bedding disturbed*	*Bedding undisturbed*	*Epithyris*	*Modiolus*	*Oysters*	*Other epifauna*	*Anisocardia*	*Aphanoptyxis*	*Terebelloid worm tubes*	*Other infauna*	*Lignite*
1e●	A	O	Yes		Aws	Aws		*Lima* *Cucullaea* bryozoa	Ows		C	*Favreina*	
1d	O	C	Yes		Ows	Ows		echinoid spines	Cws		A	gastropods *Favreina*	
1c													
1b	O	C	Yes					bivalves			C	burrows bivalves *Favreina* C	
1a		O										*Nerinea*	

Key:
O = occurs.
C = common.
A = abundant.
w = whole shell.
s = single shell.
t = top of bed.
b = bottom of bed.
§ = coral *Epithyris* limestone.
† = *fimbriatus-waltoni* Clay.
* = oyster *Epithyris* limestone.
● = *Epithyris* limestone.

Similar bioturbation of sediments close to the low tide level is seen on the present-day Atlantic coast of America produced by the decapod *Callianassa* (MacGinitie 1934, Weimer and Hoyt 1964), and on the Dutch coast by *Arenicola* (van Straaten 1952).

Table 1 lists the fossils occurring in each bed of Profile 1. Bed 1a contains *Nerinea*; lithologically it is similar to beds 1b and 1d and it is considered that all these beds were laid down in a similar environment with an abundant infauna. *Turritella* (Yonge 1946)

EXPLANATION OF PLATE 8

Photograph of the south face of the Kirtlington Old Cement Works quarry, Oxfordshire.

is a burrower at the present day, and, from their faunal and lithological associations, we think that the turreted *Nerinea* and *Aphanoptyxis* also burrowed; however, this is by no means certain. A useful summary of the Mesozoic adaptive radiation of bivalves has recently been given by Stanley (1968).

The highest bed on the pinnacle (1e, text-fig. 1) is largely made up of specimens of the brachiopod *Epithyris* and the mussel *Modiolus*; some are whole shells, with valves attached, others are single valves. Some burrowing has occurred in this bed; terebelloid worm tubes are common and some burrowing molluscs are present.

Profile 2 (text-fig. 1) is on the south side of the quarry (text-fig. 2); its position is indicated on the elevation of the south face (Pl. 8). It should be noted that beds 2a, 2b, 2d, and 2j, while present in Plate 8, do not occur on the line of Profile 2. This is a reflection of the greater variability in the White Limestone at Kirtlington when viewed along a section extending from east to west; a fact which conforms with the suggestion that most of the channels in this area had a direction with a large north/south component.

Beds 2a, b, c contain a small amount of silt grade quartz (0·002%), but all the beds in this profile consist largely of terrigenous clay, shell fragments, ooliths, and microcrystalline calcite. Bed 2a is similar to bed 1a in containing a burrowing turreted gastropod, although the genus present is *Aphanoptyxis*, instead of *Nerinea*.

Beds 2k and 2i(2) are full of *Epithyris*; they continue across the south face of the quarry, merging eastwards into bed 2j and westwards into bed 1e (the Lower *Epithyris* Bed of Arkell 1931, 1947). In addition to the faunas recorded in Table 2, extensive collections were made from beds 2k and 2i(2) and their lateral equivalent, 1e (Table 8); some hundred pounds of rock was brought back to the laboratory and broken up to extract all the fossils present. The size distributions of the *Epithyris* and *Modiolus* collections from this bed are discussed in a later chapter.

Laminations of coarse and fine limestone with some clay pellets make up most of bed 2l, which rests on the *Epithyris* limestone; it is one of the few beds in the White Limestone that is not disturbed by burrowers. Bed 2m, which follows, is similar in gross lithology to 2l, but it has been bioturbated. This suggests that the deposition of beds 2l and 2m (together 90 cm. thick) occurred rapidly; then, during a subsequent pause in sedimentation, the infauna only disturbed the top 53 cm. (bed 2m).

Other beds at Kirtlington (e.g. 5c and 6c) and at Gibraltar Quarry (477185), 1½ miles south-west of Kirtlington Old Cement Works (where a large channel is well exposed), show that the *Epithyris* beds (like 2k) were laid down in channels, and it is suggested that the succeeding well-bedded (2l) and disturbed beds (2m) are part of a channel fill.

Bed 2n, the oyster–*Epithyris* marl, is the Middle *Epithyris* Bed of Arkell (1931, 1947). Although none of the shells seem to be in position of growth, the majority of the *Epithyris* are complete, but the *Ostrea* and *Modiolus* are largely single valves, suggesting variable resistance to disturbance by currents.

The *fimbriatus–waltoni* Clay (bed 2o) is not now well exposed at Kirtlington; in the south face it is only seen sporadically by digging into the grass at the top of the limestone face. It is recognized here by its dark colour and by the abundance of lignite. Arkell (1931, p. 572) records 'an impersistent layer of white pellets at the top' of this bed. Thirty metres north-east of Profile 2, some caliche-like nodules, similar to those recorded by Klein (1965, p. 177) and presumably similar to those seen by Arkell, are visible now, but we have not found them elsewhere at Kirtlington. They are best seen at the present time in the freshly exposed *fimbriatus–waltoni* Clay of Shipton Cement Works (475175), 2 miles south-west of Kirtlington quarry. Klein concluded that these indicate mud flats which were periodically exposed.

Profile 3 (Pl. 9) illustrates the largest complete section seen at Kirtlington; our measured section is in the north-east corner of the quarry (text-fig. 2 and Pl. 9) and includes the major portions of both the White Limestone and the Forest Marble. Table 3 lists the fauna in each bed; the thickness and some sedimentary features are given in text-fig. 1.

Beds 3a to 3j show a dominance of bioturbation similar to the White Limestone seen in Profiles 1 and 2 (though 3b(2) shows lamination), but no individual bed can be correlated with the south face of the quarry.

TABLE 2

Faunal and lithological details for the beds of Profile 2 (for key see Table 1).

	EPIFAUNA	INFAUNA	*Bedding disturbed*	*Bedding undisturbed*	*Epithyris*	*Modiolus*	*Oysters*	*Other epifauna*	*Anisocardia*	*Aphanoptyxis*	*Terebelloid worm tubes*	*Other infauna*	*Lignite*
FOREST MARBLE													
2o†	A							*Bakevellia* *Eomiodon* C					A
2n	A				Cw		Aw						
WHITE LIMESTONE													
2m	O	C	Yes		Cw				O			burrows	
21				Yes									
2k●	A	C	Yes		Aws	Cws	O	See Table 8	Os		A	See Table 8	O
2j	O	A	Yes	Yes	Os	Os		*Lima*	Os		A		
2i	O	C	Yes		Os	Os		echinoid spines *Pinna*	Cw	O	C	*Favreina*	O
2h	O	O				Os			Ow				O
2g	O	O				Os		echinoid spines	Ow			*Favreina*	
2f	O	O	Yes t			Os		*Bakevellia* trochids	Ow		O	*Favreina*	O
2e	O	O	Yes t	Yes b		Os		*Lima* echinoid spines					
2d	C	C	Yes b			Os	O	*Lima*	Ow			cardiids	O
2c	C	C	Yes			Cs			Cw		C	burrows C	O
2b	O	C	Yes					*Cucullaea*	Cw		C	burrows C	
2a	O	C				Cs		echinoid spines	Cw	O		burrows	O

Bed 3k is an *Epithyris* limestone with drifted single valves dominant; it occurs immediately below the *fimbriatus–waltoni* Clay and is equivalent to the oyster–*Epithyris* Marl (2n); it passes westwards into a limestone which contains oysters (4d), (see text-fig. 1). Many pounds of this bed were broken up in the laboratory; Table 9 lists the fauna obtained. Bed 3k is the lowest at Kirtlington with abundant oysters, and is taken as the local base of the Forest Marble.

EXPLANATION OF PLATE 9

Photograph of the north-east face of the Kirtlington Old Cement Works quarry, Oxfordshire.

In Profile 3, the *fimbriatus–waltoni* Clay (3l) can usually only be exposed by digging, and even then it is often in such a weathered state that none of the bivalve shells are preserved. The abundance of large (up to 20 cm.) pieces of lignite, the caliche-like

TABLE 3

Faunal and lithological details for the beds of Profile 3 (for key see Table 1).

	EPIFAUNA	INFAUNA	*Bedding disturbed*	*Bedding undisturbed*	*Epithyris*	*Modiolus*	*Oysters*	*Other epifauna*	*Anisocardia*	*Aphanoptyxis*	*Terebelloid worm tubes*	*Other infauna*	*Lignite*
FOREST MARBLE													
3v	C	O	Yes b				Aw	echinoid spines freshwater ostracods				burrows	O
3u													O
3t	C						Cws						
3s													
3r	C						Cws	freshwater and marine ostracods					O
3q	C						Cws	echinoid spines					O
3p													
3o§	A	O			As	As	Ow	See Table 10				See Table 10	
3n	C							*Bakevellia* C freshwater and marine ostracods *Cetiosaurus*				*Eomiodon* C	C
3m	C						Cws						
3l													
3k*	C	O	Yes		Awt Owb	Cws		See Table 9	Ow	O	C	*Favreina* gastropods C bivalves	
WHITE LIMESTONE													
3j	C	O	Yes		Ow	Ows		*Lima*	Ow			gastropods *Favreina*	
3i	C	C	Yes					coral			O	*Favreina* C/A gastropods	
3h								bivalves?				bivalves?	
3g	C	C	Yes		Os	Os		echinoid spines bivalves C	Os		O	*Corbis*	O
3f	C	O	Yes					echinoid spines *Cucullaea* *Bakevellia* C	Os			*Favreina* gastropods bivalves?	C
3e	A	O	Yes					echinoid spines *Cucullaea* bivalves, coral		O		gastropods A *Favreina*	O
3d	C			Yes				reptile tooth echinoid spines				*Favreina*	O
3c	C	O	Yes					echinoid spines coral *Cucullaea*; bivalves C					
3b	O					Os		echinoid spines					O
3a	C	C						echinoid spines gastropods A		O		*Trigonia* gastropods A	

nodules, and the record of the sauropod dinosaur *Cetiosaurus* (Arkell 1931, p. 572) suggest an intertidal swamp environment in which this large herbivore could wade and find sufficient food supply. Bate (1965) records freshwater ostracods in the *fimbriatus–waltoni* Clay; these had presumably drifted into the area to become mixed with the marine or semi-marine elements of the fauna (*Eomiodon fimbriatus*, *Bakevellia waltoni*, and other bivalves).

The succeeding clays and limestones in Profile 3 (3m–3v, but excluding 3o) nearly all contain abundant oysters; in the limestones, the oyster shells are usually fragmented and deposited with pectinids and other marine epifauna; in the clays, the shells are sometimes complete, but it is never certain that they are in growth position. The increase in the abundance of the epifauna in the Forest Marble is associated with a decrease in the bioturbation by infauna, which is so characteristic of the White Limestone. This oyster–pectinid epifauna may indicate a sub-tidal environment, and it is perhaps significant that we know of no occurrence of caliche-like nodules in any Forest Marble beds above the *fimbriatus–waltoni* Clay in Oxfordshire.

The coral–*Epithyris* limestone (bed 3o) differs from all the other beds at Kirtlington in having abundant corals in growth position (the few corals recorded in other beds are usually simple forms, and are often fragmented). *Isastrea* and *Thamnasteria* have two growth forms: either the corallum is hemispherical, with a flat base, or it consists of cylindrical branches 1–2 cm. in diameter; in both forms of corallum, all the compound corals have similar small (2–5 mm.) polygonal corallites. Table 10 lists the fauna obtained by breaking up many pounds of this bed in the laboratory. The terebratulids and bivalves in this bed appear to have drifted (see below), perhaps being trapped among the corals as currents carried them into the area. There is an unusually small proportion of burrowers. This bed accumulated when the substrate was sufficiently stable for coral growth to a height of 50–100 cm., but we are not clear whether any change in depth is involved compared with the remainder of the Forest Marble beds. The coral–*Epithyris* limestone is most easily examined on the boulders resting on the platform cut above bed 3k.

Profiles 4 and 5 are on the north face of the quarry (text-fig. 2 and Pl. 10). A fault downthrowing 115 cm. to the west occurs 8 m. east of Profile 4, lowering the oyster–*Epithyris* limestone (bed 4d, text-fig. 1 and Pl. 10) so that the platform formed at the top of bed 3k continues west at the top of bed 4g. Correlation in the field is also made difficult because beds 4e, f, g, and h are thinner than their equivalents in Profile 3 (3l, m, and n) so that the coral–*Epithyris* bed is only 155 cm. above the base of the *fimbriatus-waltoni* Clay (4e) in Profile 4. Beds 4e and 4f have been separated, although they may both correspond to bed 3l in Profile 3; the characteristic black colour of the *fimbriatus–waltoni* Clay is only present in a thickness of 6 cm. We are not certain whether the fine muddy limestone (4f) can be correlated with the upper part of bed 3l.

Profile 5 can be correlated with Profile 4 by the close similarity of bed 5g to bed 4b(3) (both are bioturbated with clay pellets at the top), and bed 5f is similar to 4b(1) in having numerous drifted shells of *Epithyris* and *Modiolus* in a matrix containing terebelloid worm tubes.

EXPLANATION OF PLATE 10

Photograph of the north face of the Kirtlington Old Cement Works quarry, Oxfordshire.

The faunas obtained from Profiles 4 and 5 are listed in Tables 4 and 5. They show a broad similarity to the profiles already described, but only the coral–*Epithyris* limestone, the *fimbriatus–waltoni* Clay, and oyster–*Epithyris* bed can be directly correlated with the other profiles.

TABLE 4

Faunal and lithological details for the beds of Profile 4 (for key see Table 1).

	EPIFAUNA	INFAUNA	*Bedding disturbed*	*Bedding undisturbed*	*Epithyris*	*Modiolus*	*Oysters*	*Other epifauna*	*Anisocardia*	*Aphanoptyxis*	*Terebelloid worm tubes*	*Other infauna*	*Lignite*
FOREST MARBLE													
4i§	A	O			As	As	Ow	See Table 10				See Table 10	
4h													
4g	O							trails				trails	
4f		C	Yes					coral			C		
4e†	C							pectinids C *Bakevellia* C				*Eomiodon* C	
4d*	A	C	Yes		Cw	Cw	Ow	See Table 9	Cw			*Natica* burrows C *Favreina*	
WHITE LIMESTONE													
4c			Yes										
4b	A	C	Yes b	Yes t	Cws b	Cws b					Cb	burrows Cb	
4a		O										bivalvia *Favreina*	

Profile 6 is in the north-west part of the quarry, on the side of the Cherwell valley; as a result of cambering, the thicknesses of the clay beds may be in error, but, as they are consistent along 20 m. of outcrop, this error is not likely to be very great. It is also probable that the coral–*Epithyris* limestone (6j, text-fig. 1 and Pl. 11) has slipped slightly, but its height above the *fimbriatus–waltoni* Clay corresponds well with Profile 4. There is no uncertainty about the thicknesses of the other limestones. The faunas are listed in Table 6. The White Limestone of Profile 6 is similar to the other White Limestone profiles, but bed 6c (and to a lesser extent 6d) shows clearly the relation between drifted shells of the epifauna (*Epithyris* and *Modiolus*) and the bedding; both beds have a concentration of shells towards the base (6c(1) and 6d(1)), suggesting a lag concentration in a channel.

The lower Forest Marble beds, from the oyster–*Epithyris* marl (6e) to the base of the coral–*Epithyris* limestone (6j), are all clays and marls. The absence of limestone (cf. Profiles 3 and 4, text-fig. 1) does not necessarily mean that there was a major lateral change in lithology; *some* limestones grade into *some* clays; a continuous range of carbonate content is known in the Oxfordshire Great Oolite (Sugden and McKerrow 1962).

The oyster–*Epithyris* marl (6e) contains abundant oysters, with subsidiary *Epithyris*; it is remarkable in that about 10% of the oysters have shallow irregular grooves on the interior of their valves (Pl. 12, fig. 3). Revelle and Fairbridge (1957, p. 281) report Dugal's (1939) observations on the erosion of the interior of modern *Venus* under anaerobic conditions, and they suggest that such features could result from (*a*) exposure above tide level, (*b*) oxygen-poor conditions in the water, or (*c*) bacterial decay after death.

In each case corrosion would appear to be due to a lowering of the pH by the production of organic catabolic acids. We have not seen this etching in any oysters in beds above 6e, and our interpretation is that these oysters became widespread at the base of the Forest Marble with slight deepening of the water, though the inter-tidal environment, charac-

TABLE 5

Faunal and lithological details for the beds of Profile 5 (for key see Table 1).

	EPIFAUNA	INFAUNA	*Bedding disturbed*	*Bedding undisturbed*	*Epithyris*	*Modiolus*	*Oysters*	*Other epifauna*	*Anisocardia*	*Aphanoptyxis*	*Terebelloid worm tubes*	*Other infauna*	*Lignite*
WHITE LIMESTONE													
5g													
5f	C	C	Yes		Cw	Cw		trails	Cw		Cb	trails	
5e	O	O		Yes				trails bivalves				trails bivalves	
5d	C	C	Yes		Cs			echinoid spines	Cw		C		O
5c	C	O	Yes		Cws b	Cws b		echinoid spines			O	gastropods *Favreina*	O
5b	O	O						echinoid spines *Bakevellia*				bivalves	O
5a	C	A						coral trails		A		gastropods C *Trigonia* C trails *Favreina* burrows C	O

TABLE 6

Faunal and lithological details for the beds of Profile 6 (for key see Table 1).

	EPIFAUNA	INFAUNA	*Bedding disturbed*	*Bedding undisturbed*	*Epithyris*	*Modiolus*	*Oysters*	*Other epifauna*	*Anisocardia*	*Aphanoptyxis*	*Terebelloid worm tubes*	*Other infauna*	*Lignite*
FOREST MARBLE													
6j§	A	O			As	As	Ow	See Table 10 also fish teeth				See Table 10	C
6i													
6h	O						Ows						O
6g	O			Yes b			Ows						
6f†	O							pectinids *Bakevellia*				*Eomiodon*	O
6e	C	O			Cw	Ows	Cws	*Lima* echinoid spines serpulids bryozoa	O			bivalves *Favreina*	
WHITE LIMESTONE													
6d	O	O		Yes				echinoid spines			O		
6c	O	O	Yes b	Yes t	Cb	Ct			Ob		Ot	bivalves b *Favreina* b	
6b	C	O	Yes t	Yes b	Cws	Cws		echinoid spines			Ot		
6a	O	O			Ows			echinoid spines			O	*Favreina*	

teristic of the White Limestone, continued locally after the first influx of oysters. These markings could have been made by predators (possibly gastropods), in which case they could result from chemical and/or mechanical abrasion. No suitable predators have, however, been found in this bed.

The *Epithyris*–oyster bed shows a lateral transition (within 90 m.) from a marl rich in oysters (6e, 2n) to a limestone with more abundant *Epithyris* and fewer oysters (4d), and finally to an *Epithyris* limestone with rare oysters (3k). Though this last bed (3k) is not as rich in *Epithyris* as beds 2k and 1e (Table 11, p. 76), it has a similar ratio of whole to single valves as well as a similar lithology; it was probably deposited in a similar channel to these White Limestone *Epithyris* beds.

THE *EPITHYRIS* AND *MODIOLUS* ASSEMBLAGES

Life and death assemblages

Much mixing of animals from different habitats has undoubtedly taken place at Kirtlington, for example:

(i) Transportation of faunas between greatly different habitats; e.g. the presence of freshwater ostracods in several Forest Marble clays which also contain oysters and other marine shells suggests fluviatile outflows into the sea.

(ii) Mixing at one locality: burrowers can mix dead shells of the epifauna and the infauna.

(iii) Lateral mixing of adjacent assemblages, e.g. the accumulation of *Epithyris* and bivalves among the corals in the coral–*Epithyris* bed.

There are several ways in which life and death assemblages may be distinguished:

(i) Broken and fragmented material. This is probably transported, though some shell banks may have been broken up almost *in situ*.

(ii) Epifauna showing no signs of wear and tear and including some young forms. These indicate a life assemblage (e.g. the *Epithyris* collection from the *Epithyris* bed 2k—text-fig. 3), and are either in place or have only been transported a very short distance.

(iii) Infauna in position of growth. This indicates a life assemblage; it occurs occasionally (e.g. the isolated vertical *Anisocardia*) in some of the White Limestone beds.

(iv) Infauna may show signs of transportation—single or broken valves, or (rarely at Kirtlington) randomly oriented bivalves with the valves in an open position.

Rock samples from the *Epithyris* limestone in the White Limestone (2k, 2j, and 1e) and at the base of the Forest Marble (3k), and from the coral–*Epithyris* limestone (3o), were broken up in the laboratory, and every possible shell extracted. The unbroken shells were measured, and the proportions of articulated shells noted (Table 11).

A low articulation ratio (i.e. the percentage of articulated valves in each collection) indicates transportation or disturbance under turbulent conditions. Before the valves of *Epithyris* can be separated, the teeth must be broken, whereas teeth in *Modiolus* are absent and the valves open after decay of the adductor muscles, and separate when the ligament either decays or is torn. Few *Modiolus* are found with their valves opened and connected, and it would appear that, in the three beds studied, the turbulence was such that, once the adductor muscles decayed, the valves were ripped apart unless the shell was already buried with the valves closed. There was certainly rapid burial of many of the *Epithyris* in these beds; the presence of calcite filling most of the interior of some of the shells points to burial before the pedicle had decomposed enough to let sediment enter through the pedicle opening.

Size-frequency distributions at Kirtlington

(i) The *Epithyris* limestone (beds 1e, 2j, and 2k).

Both the length and breadth distributions of whole (articulated) *Epithyris* have a strong negative skew (text-fig. 3), whereas a normal distribution is present in the single (disarticulated) pedicle valves. The means for the whole shells are significantly greater than for the single valves (Table 7). A similar pattern is obtained for *Modiolus* (text-fig. 3 and Table 7) where the maximum height of the shell was measured. Some *Anisocardia* were also collected; the majority were articulated and their height distribution has a strong negative skew.

TABLE 7

Numerical and statistical data for the *Epithyris* and *Modiolus* collections from some of the beds discussed in the text.

		Number of specimens	*Mean*	*Mode*	*Standard deviation*	*Standard deviation of the mean*
Epithyris (length of pedicle valve)						
Bed 3o:	WHOLE	37	20·74	20–24	7·2	1·183
	SINGLE	54	20·72	12–16	8·7	1·181
Bed 3k:	WHOLE	20	31·7	32–36	8·9	1·986
	SINGLE	13	20·38	—	11·5	3·194
Bed 1e/2k:	WHOLE	127	31·16	32–36	9·3	0·828
	SINGLE	52	25·93	16–20	9·1	1·266
Modiolus (maximum height)						
Bed 1e/2k:	WHOLE	35	24·46	24–28	4·6	0·777
	SINGLE	17	21·1	16–20	5·5	1·34

Significance of differences between means of sample pairs:

	Difference/standard deviation of difference (5% significance level: 1·96)	*Significance*
Epithyris		
Bed 3o: whole v. single	0·0012	None
Bed 1e/2k: whole v. single	3·456	Sign. (1%)
Bed 3o, whole v. Bed 1e/2k, whole	7·216	Sign. (1%)
Bed 3o, single v. Bed 1e/2k, single	3·009	Sign. (2%)
Modiolus		
Bed 1e/2k: whole v. single	2·445	Sign. (5%)

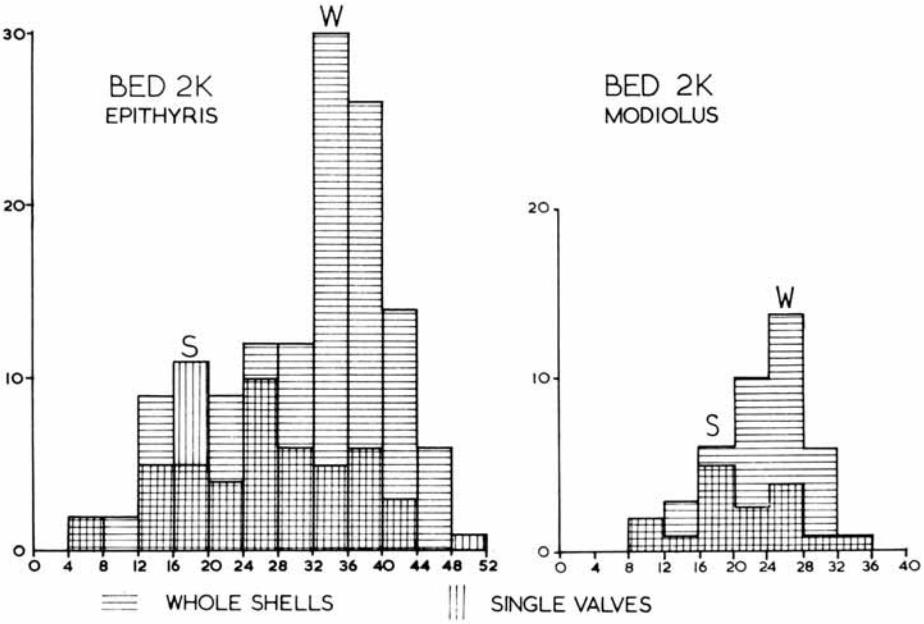
(ii) The *Epithyris* limestone at the base of the Forest Marble (3k).

Sample numbers for *Epithyris* and *Modiolus* were small, but the size-distributions (Table 7 and text-fig. 4) were similar to those in the White Limestone *Epithyris* bed (2k).

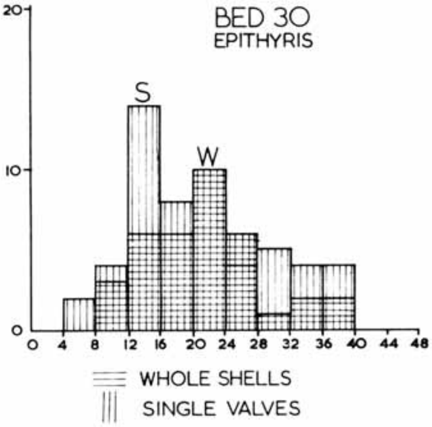
EXPLANATION OF PLATE 11

Photograph of the north-west face of the Kirtlington Old Cement Works quarry, Oxfordshire.

The *Anisocardia* distribution shows a strong positive skew, in contrast to the *Epithyris* limestone in the White Limestone.



TEXT-FIG. 3. Size distributions of *Epithyris* and *Modiolus* from bed 2k.



TEXT-FIG. 4. Size distributions of *Epithyris* from the coral–*Epithyris* bed (3o).

(iii) The coral–*Epithyris* limestone (3o).

Normal distributions are obtained for both whole and single valves of *Epithyris* (text-fig. 4). The latter show a tendency towards positive skewness. This bed contains very few whole specimens of *Modiolus*, while the single valves show a slight positively skewed distribution.

TABLE 8

Faunal list for beds 2k, 2j, and 1e with the total numbers collected for each item (in parentheses) and the Oxford University Museum registration numbers.

Annelida	INFAUNA	terebelloid worm tubes	(27) J28066–092
Brachiopoda	EPIFAUNA	*Epithyris oxonica* Arkell	
		whole shells (measured)	(127) J27516–642
		,, ,, (unmeasured)	(15) J27643–657
		single pedicle valves (measured)	(52) J27658–709
		single valves (unmeasured)	(58) J27710–867
Mollusca: Bivalvia	INFAUNA	Nuculacea *Nucula* sp.	J28041
		Cardiacea *Pterocardia* sp.	J28030
		Arcticacea *Anisocardia islipensis* (Lycett)	
		whole shells	(17) J27957–973
		left valves	(9) J27974–982
		right valves	(8) J27983–990
	EPIFAUNA	Mytilacea *Modiolus imbricatus* J. Sowerby	
		whole shells	(39) J27868–906
		left valves	(15) J27791–805
		right valves	(15) J27806–820
		Pinnacea *Trichites* sp.	J28033
		Pteriacea *Bakevellia* sp.	(2) J28031–032
		Pectinacea *Entolium* sp.	J28052
		Limacea *Lima* sp.	J28034
		Ostreacea *Ostrea* sp.	(2) J28039–040
		Exogyra sp.	(4) J28035–038
Gastropoda	INFAUNA	*Aphanoptyxis ardleyensis* Arkell	(7) J28042–048
		Natica sp.	(3) J28049–051
	EPIFAUNA	Nil	
Arthropoda	INFAUNA	*Favreina* sp.	(175) J28053
Echinodermata	EPIFAUNA	pseudodiadematid	J28054
		spines	(9) J28055–063
Vertebrata	EPIFAUNA	bone fragments	(2) J28064–065

Comparison of fossil and modern size-frequency distributions

Size-frequency distributions will depend on the interaction of populations of a given species with the environment, both in life (recruitment, growth, and mortality) and in death (turbulence, hydrodynamic properties of shells, rate of disarticulation, etc.). It is

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EXPLANATION OF PLATE 12

Fig. 1. Disturbed White Limestone (bed 3k) showing terebelloid tubes in transverse and longitudinal sections (×2).

Fig. 2. *Favreina* sp. (bed 3k); faecal remains of a burrowing anomuran crustacean (×10·5).

Fig. 3. *Ostrea* (*Liostrea*) *hebridica* (bed 6e) showing internal etching (×3).

Fig. 4. Unusual type of terebelloid tube (bed 2k) showing interior filled with shell fragments (×4).

of interest that the modes of *Epithyris* and *Modiolus* in the Kirtlington samples (Table 7) are all lower for the disarticulated shells than for the articulated shells; the smaller shells are clearly selectively transported.

TABLE 9

Faunal list for bed 3k with the total numbers collected for each item (in parentheses) and the Oxford University Museum registration numbers.

Coelenterata	EPIFAUNA	simple scleractinian	J28147
Annelida	INFAUNA	terebelloid worm tubes	(25) J28148–72
Bryozoa	EPIFAUNA	Cyclostomata (4 colonies)	J28176
Brachiopoda	EPIFAUNA	*Epithyris oxonica* (Arkell)	
		whole shells (measured)	(20) J27425–44
		,, ,, (unmeasured)	(6) J27445–50
		single pedicle valves (measured)	(13) J27451–63
		single valves (unmeasured)	(12) J27464–75
Mollusca: Bivalvia	INFAUNA	Nuculacea *Nucula* sp.	J28182
		Arcticacea *Anisocardia* sp.	
		whole shells	(4) J27907–10
		left valves	(17) J27911–27
		right valves	(12) J27928–39
		A. sp. (small shells)	J27940–4
		A. minima	J28184
		Pseudotrapezium sp.	J28183
		Lucinacea ? *Corbis*	(3) J28173–5
	EPIFAUNA	Arcacea	(5) J28177–81
		Mytilacea *Modiolus imbricatus* J. Sowerby	
		whole shells	(7) J27476–82
		left valves	(15) J27483–97
		right valves	(12) J27498–509
		fragments	(6) J27510–15
		Pteriacea *Bakevellia waltoni* (Lycett)	(20) J28185–204
		Pectinacea *Lima* sp.	J28205
		? *Lima*	J28206
		Ostreacea *Ostrea* sp.	J28207
Gastropoda	INFAUNA	*Aphanoptyxis* sp.	(4) J27423 J28208–10
		Natica sp.	(2) J28211–12
	EPIFAUNA	trochid	J28213
		Ataphrus comma (Lycett)	J28214
Arthropoda	INFAUNA	*Favreina* sp.	(6) J28215–20
Echinodermata	EPIFAUNA	spines	(4) J28221–4
Vertebrata	EPIFAUNA	bone fragments	(2) J28225–6

Unidentifiable gastropod and bivalve fragments are abundant.

The following evidence from living species has been taken mainly from temperate zone communities, as little information other than Craig (1967) is available on the biology of species in tropical or semi-tropical areas comparable to the environment of the Great Oolite Series. The life histories and the over-all patterns of survivorship in sessile benthonic bivalves and brachiopods are similar; they are discussed together below:

1. Much of the high juvenile mortality of the survivorship curve given by Deevey (1947) for a sessile benthonic invertebrate occurs in the pelagic larval stage, either

through predation (Paine 1963, Elliott 1950, Craig and Hallam 1963) or through factors such as loss in respiratory currents of adult bivalves (Thorson 1950).

2. On the abandonment of pelagic life, mortality is at once much reduced, though a high rate is maintained in the oyster (Walne 1961).

3. Site selectivity on the benthos is influenced by the presence of adult individuals of the same species on the substratum (Wilson 1958) or by the nature of the substratum itself (Rudwick 1961, Craig and Jones 1966). Mortality is low as compared with the pelagic phase, and may be further reduced by the double settling technique found in *Mytilus* and *Glottidia* (Bayne 1964, Paine 1963), where metamorphosis occurs away from the final position taken up in the colony.

4. Mortality after metamorphosis and in the young adult can be less than at any other time in the life history (Savage 1956, Rudwick 1962, Rowell 1960); but examples are known of high mortality at this stage (Hallam 1967, p. 33).

5. Later, mortality rises sharply as the pressure on the animal's resources increases with large size (Rowell 1960) and reproductive activity (Paine 1963), except in those cases where larger individuals cease to breed (Percival 1960).

6. Multimodicity will be introduced in size-frequency distributions by cyclic reproductive activity, particularly when the periods are long, e.g. seasonal reproduction in temperate zone species (Craig and Hallam 1963, Rudwick 1962, Sheldon 1965). In semi-tropical species, cyclic activity is present, though this may not have such a marked effect on size-frequency distributions.

Using the classification of mortality, growth, and recruitment of Craig and Oertel (1966), it is clear that a generalized bivalve or brachiopod population living in tropical or semi-tropical environments will exhibit (*a*) a 'tropical type' recruitment, (*b*) an 'increasing' mortality, and (*c*) a 'high to low' or 'very high to zero' growth-rate. Craig and Oertel predict a normal size-frequency distribution for the living members of a population with these characteristics (1966: experiments 20 and 23). The dead members of the population show a normal distribution in the case of a 'high to low' growth-rate, and a slight negative skew with a 'very high to zero' growth-rate.

Other factors will, however, alter the shape of such a distribution in a fossil population. First, with regard to the living sector some small shells may have been missed in breaking up the rock (however, we consider the methods employed here ensured that this error was reduced to a minimum—all our samples were extracted from the rock in the laboratory). Secondly, the distribution will be distorted by the presence of transported members of the populations that have not become disarticulated, and therefore cannot be distinguished from the living sector. The direction of this distortion is hard to predict, as it will depend on numerous factors such as the rate of disarticulation in different size groups. Physical actions, including transportation and selective fragmentation, will produce a variety of distributions (Menard and Boucot 1951, Lever 1958, Hallam 1967), some of which may have no similarity to the living population (van Straaten 1956, 1960).

Interpretation of the Kirtlington size distributions

The different distributions for whole and single *Epithyris* and *Modiolus* from the *Epithyris* limestone (text-fig. 3) suggest a mixture of living and transported populations in the cases of both genera.

The negative skew of the whole shells is an unusual distribution for living populations, but an analysis of living *Cardium* (Craig and Hallam 1963, text-fig. 5*a*) shows an approximation to the distribution of the whole shells from the *Epithyris* limestone, and the fact that the shells are articulated helps to confirm that they have suffered relatively little disturbance before burial. By contrast the normal distribution of the disarticulated shells is typical of transported populations (Craig 1967) and is, therefore, more a reflection of the post-mortem disturbance than of the population structure.

Two factors could be responsible for the negative skew of the whole shells:

1. The slowing down of growth in the older individuals, and
2. The accumulation of generations in the large sizes (cf. Craig and Hallam 1963, text-fig. 3).

But, until we know how long the animals lived after the growth-rates decreased and how many generations are present in our sample, we cannot tell which of these two effects is responsible for the negative skew.

Anisocardia from the same bed (1e, 2j and k) also have a negative skew in the size distribution of articulated shells. These appear to represent a living population burrowing on the floor and sides of the channel where the *Epithyris* and *Modiolus* were living.

Bed 3k did not yield large samples of *Epithyris* and *Modiolus* (Table 7 and text-fig. 4), but the fragmentation and articulation ratios point to a dominantly transported assemblage (Table 11). The positively skewed *Anisocardia* distribution suggests a living assemblage of these burrowers in this bed.

The coral–*Epithyris* limestone (3o) differs markedly from the other *Epithyris*-rich beds in that the *Epithyris* show normal distributions for both whole shells and single valves. The relatively few whole *Epithyris* suggest that this was dominantly a transported assemblage, though a small epifaunal population may have been present. Transportation of the shells into the area where corals were growing may have been due to the influence of the corals on currents near the sea floor. The sample of *Modiolus* shows a slightly positive skew. This might imply a death assemblage, but the fewer fragmentary shells suggest that the *Modiolus* were living nearer the corals than the majority of the *Epithyris*.

ECOLOGICAL INTERPRETATION

As a present-day equivalent to the Great Oolite environment at Kirtlington, the Bahama Banks offer the most useful comparison; not only are they similar in many physical and biological respects, but they have been well described in many recent publications (Newell *et al.* 1959, Purdy 1963, Craig 1967). The principal difference is in the lack of clastics on the Bahama Banks. Oolites are present in both environments, and so are corals, of similar form and distribution, associated with comparable epifaunas and infaunas. Both the corals and the ooliths indicate that Kirtlington had warm shallow seas with good connections to the open ocean, like the Bahamas. If the palaeolatitude proposed by Hargraves and Fischer (1959) is correct, then this would indicate that Oxford was about 30° north in the Middle Jurassic (Dr. J. C. Briden, personal communication); this compares with 25° north for the Bahamas and 25–30° north for the Persian Gulf. The Persian Gulf is another region of oolite formation, but this is in areas where high evaporation creates excessively hypersaline conditions (Evans *et al.* 1963); none the less some useful comparisons can be made with the Great Oolite (Kinsman 1963, Sugden 1963).

On the south margin of the Persian Gulf, Kinsman (1963) has described several profiles across tidal areas of the Trucial Coast. Coral and oolite sands, of a similar nature to those found at Kirtlington, are cut by channels up to a quarter of a mile wide; the surface of the sand flats range from sea level to a depth of 20 ft. and bases of channels can reach 40 ft. below sea level. The channels support prolific growth of the branching coral *Acropora*, while on the shallower sands there occurs a more patchy growth of corals, with intervening stretches of open sand. Growth within the coral colonies found on the sands is more limited than that of the channel assemblages; many of the coral heads are dead in the former environment.

The White Limestone

Klein (1963, 1965) deduced that the White Limestone environment was one consisting of meandering channels separated by inter-tidal mud-flats. Little sedimentation would occur between the channels, and the mud-flats are largely composed of old channel-fills. The faunas of the mud-flats were mainly burrowers, with the result that little bedding is left in these deposits, and their original deposition as channel-fill can only be surmised from the occasional epifaunal shell complete enough to be identified. This environment may correspond to that of Scarborough Beds (Farrow 1966), which also have an abundant infauna, but we find no evidence of a depth-controlled distribution of annelid and crustacean burrows.

The *Epithyris* beds (e.g. 2k, 3k) contain a rich epifauna (Tables 8 and 9) of *Epithyris*, *Modiolus*, and other bivalves, with subsidiary echinoids; the infauna consists mainly of *Anisocardia*, terebelloid worms, anomuran crustaceans (as indicated by the presence of *Favreina*), and *Aphanoptyxis*, any of which may be abundant in some beds. This community lived on a stable substrate on the floor and sides of channels. Ager (1965) suggests that terebratuloid morphology may be closely correlated to environment; he places forms (such as *Epithyris*) having broad folds, an elongated beak, and a large foramen in a shallow-water peri-reefal habitat, where the sediments include bioclastic calcarenites. There is thus some approximate correspondence between the channel-living *Epithyris* at Kirtlington and the habitat of other terebratuloids with a similar morphology.

Jones (1950) states that, in the Irish Sea at the present day, the *Modiolus* Community occurs in deeper water than the littoral *Mytilus* Community; if the Jurassic *Modiolus* lived in a similar environment, the channel floors of the White Limestone were covered at low tide (text-fig. 5, p. 79).

Tables 8, 9, and 10 show the faunas collected from three *Epithyris* limestones, together with their Oxford University Museum registration numbers. The distribution of epifaunal and infaunal species is given on the basis of Petersen's (1913) classification, and on Stanley's (1968) description of Mesozoic bivalve adaptive radiations. The proportions of each systematic group in the epifauna and infauna and the ratio between total epifauna and infauna are given in Table 11; this also shows articulation ratios for *Epithyris*, *Modiolus*, and *Anisocardia*. The articulation ratio is defined as the ratio of articulated shells to our estimate of the total population; we obtained this last figure by adding the number of articulated shells to half the total of single disarticulated valves.

The *Epithyris* beds in the White Limestone are channel deposits whose faunas are significantly different from the bulk of the White Limestone in the predominance of epifauna. Some of these channel deposits have a sharp base, e.g. beds 4b(1), 5c(1), and

6c(1), and appear to be lag deposits from which the fine material has been removed by currents. Other *Epithyris* beds (e.g. 1e, 2i(2)) merge downwards into a bioturbated deposit with an abundant infauna. It would appear that the base of the channel is sometimes blurred by the infauna living in the channel and burrowing into previously bioturbated material forming the sides and floor. A few beds (e.g. 2k) contain abundant epifauna and infauna together; some infauna therefore lived in the channels as well as in the tidal flats, though there is no direct evidence that they lived in exactly the same areas as the epifauna. The absence of infauna in some of the White Limestone beds which still have bedding preserved (e.g. 2l, 2j, and 2e) may be compared with Newell's (1959) observation that, in regions of rapidly shifting oolitic substrate, the infaunal *Tivela* Community is very sparse.

TABLE 10

Faunal list for bed 3o with the total numbers collected for each item (in parentheses) and the Oxford University Museum registration numbers.

Coelenterata	EPIFAUNA	*Cyathophora pratti* (Edwards)	(4) J28093–6
		Thamnasteria lyelli (Edwards and Haime)	(6) J28097–102
		Isastrea limitata (Michelin)	(5) J28103–7
		coral intermediate between *Isastrea* and *Thamnasteria*	J28108
		simple coral	J28143
Brachiopoda	EPIFAUNA	*Epithyris oxonica*, Arkell	
		whole shells (measured)	(37) J27000–36
		,, ,, (unmeasured)	(11) J27037–47
		single pedicle valves (measured)	(53) J27048–100
		single valves (unmeasured)	(246) J27101–346
Mollusca: Bivalvia	INFAUNA	Lucinacea *Sphaeriola* sp.	J28109
	EPIFAUNA	Arcacea arcids	(8) J28110–17
		cucullaeids	(3) J28118–20
		Mytilacea *Modiolus imbricatus* J. Sowerby	
		whole shells	(4) J27419–22
		left valves	(18) J27347–64
		right valves	(15) J27365–79
		fragments	(38) J27380–417
		Lithophaga fabella (J. A. Eudes-Deslongchamps)	J28142
		Pteriacea *Costigervillia* sp.	(2) J28121–2
		Pteroperna sp.	J28126
		Bakevellia waltoni (Lycett)	(3) J28123–5
		Pectinacea pectinids	(12) J28126–37
		Limacea *Lima cardiiformis* J. Sowerby	(3) J28138–40
		Ostreacea *Ostrea* sp.	J28141
Gastropoda	INFAUNA	? *Natica*	J28146
	EPIFAUNA	Nil	
Arthropoda	INFAUNA	*Favreina* sp.	J28227
Echinodermata	EPIFAUNA	spines	(2) J28144–5

The *Epithyris* limestone in Profiles 1 and 2 (1e, 2j, and 2k) extends for at least 40 m. The collections of *Epithyris*, *Modiolus*, and *Anisocardia* from this bed all have high articulation ratios (Table 11). The field evidence suggests that this is a channel deposit, where sedimentation, when it does occur, may be rapid. This model (text-fig. 5) fits with the palaeontological evidence: high articulation ratios in three varied animals (*Anisocardia* is a burrower; *Epithyris* and *Modiolus* are epifaunal) suggest rapid burial; negative skewed distributions (text-fig. 3) suggest little transportation; and the presence of many hollow *Epithyris* suggests burial before the tissues had decayed.

Table 11 also shows that 89% of the collection from this limestone is epifaunal, and that *Epithyris* and *Modiolus* are the dominant constituents, while the infauna consists

TABLE 11

Proportion of epifaunal and infaunal members of the faunas collected from beds 3o, 3k, and 2k, also showing the articulation ratios for *Epithyris* and *Modiolus* for each collection.

	No. of specimens	*% of epifauna or infauna*	*% of total fauna*		*Articulation ratio*
Bed 3o					
EPIFAUNA					
Epithyris	198	72·4	72·2	99·2	0·24
arcids	8	2·9	2·9		
cucullaeids	3	1·1	1·1		
Modiolus	41	14·9	14·9		0·10
Lithophaga	1	0·4	0·4		
Costigervillia	2	0·7	0·7		
Pteroperna	1	0·4	0·4		
Bakevellia	3	1·1	1·1		
pectinids	12	4·4	4·4		
Lima	3	1·1	1·1		
Ostrea	1	0·4	0·4		
Total	273				
INFAUNA					
Natica	1	50	0·4	0·8	
Sphaeriola	1	50	0·4		
Total	2				
Bed 3k					
EPIFAUNA					
Epithyris	39	41·5	30·7	74·0	0·69
arcaceans	5	5·3	3·9		
Modiolus	25	26·6	19·7		0·29
Bakevellia	20	21·3	15·8		
Lima	2	2·1	1·6		
Ostrea	1	1·0	0·8		
Ataphrus	1	1·0	0·8		
trochid	1	1·0	0·8		
Total	94				
INFAUNA					
Nucula	1	3·0	0·8	26·0	
Anisocardia (excluding very small shells)	22	66·7	17·3		0·22
? *Corbis*	3	9·1	2·4		
Pseudotrapezium	1	3·0	0·8		
Aphanoptyxis	4	12·1	3·2		
Natica	2	6·1	1·6		
Total	33				

TABLE 11 *continued*

	No. of specimens	*% of epifauna or infauna*	*% of total fauna*		*Articulation ratio*
Bed 1e/2k					
EPIFAUNA					
Epithyris	247	79·3	70·6	89·1	0·57
Modiolus	54	17·3	15·4		0·72
Trichites	1	0·3	0·3		
Bakevellia	2	0·6	0·6		
Entolium	1	0·3	0·3		
Lima	1	0·3	0·3		
Ostrea	2	0·6	0·6		
Exogyra	4	1·3	1·2		
Total	312				
INFAUNA					
Nucula	1	2·6	0·3	10·9	
Pterocardia	1	2·6	0·3		
Anisocardia	26	68·4	7·4		0·67
Aphanoptyxis	7	18·4	2·0		
Natica	3	7·9	0·9		
Total	38				

largely of *Anisocardia* and burrowing gastropods (Table 11). Terebelloid worms and anomuran crustaceans, represented by *Favreina* faecal material (see Table 8), are also present, though (as one animal produces thousands of faecal fragments) it is not practicable to count them.

The Forest Marble

(i) Oyster–*Epithyris* and Coral–*Epithyris* beds

The oyster–*Epithyris* marl (6e, 2n) passes laterally into the *Epithyris* limestone (3k, 4d), from which the fauna has been analysed (Tables 9, 11). *Epithyris* has high articulation ratios in this bed, but *Modiolus* and *Anisocardia* have low ratios. Bed 3k differs from bed 2k in that it does not clearly represent a channel (it passes laterally into a marl, and it can be correlated throughout the quarry); consequently, it could have had substantially slower rates of sedimentation. If the shells were exposed on the sea-floor for some period after death, one might expect the *Modiolus* to disarticulate more rapidly than *Epithyris*. The presence of drifted *Anisocardia* shows that sediments in which these burrowers lived were being eroded close by, and the low articulation ratios are in accord with the transportation of the shells after this erosion. At one point, many dozens of small *Anisocardia* (less than 3 mm.) occurred in a cluster; it was not possible to separate them from the matrix and no accurate count could be made. This clustering may be due to current action, but we have no understanding of the mode of life of very young *Anisocardia*.

Bed 3k shows considerable disturbance of the sediments; this may be linked with the fact that the proportion of infauna in this bed is over twice that in bed 2k. The proportions of individual genera in beds 2k and 3k are different (e.g. *Epithyris* is 30% in 3k and 70% in 2k, Table 11), but the species composition of both beds is very similar, except for the presence of arcaceans in bed 3k. Yonge (1961) suggests that arcaceans prefer clean shallow-water substrates, with coarse shell gravel; their presence in bed 3k may thus be linked with a more stable substrate than that present in the channel floor of bed 2k.

The Kirtlington coral–*Epithyris* bed may have formed in an environment similar to the Persian Gulf channels. The coral–*Epithyris* bed is absent in Gibraltar Quarry (477185), 1½ miles south-west of the Kirtlington quarry, and in Lower Greenhill Quarry (485178), 1½ miles south of Kirtlington. It (or a similar bed at a similar horizon) is present, however, at Shipton Cement Works (479175) half a mile further to the south-west. It is thus clear that this coral–*Epithyris* bed has an irregular lateral occurrence, which lends some support to the theory of a channel-controlled distribution.

Newell *et al.* (1959) have described coral environments in the Bahama Banks. The branching forms at Kirtlington suggest that they did not grow in excessively turbulent water, but at a depth of around 6 m. corresponding to the Plexaurid Community of Newell *et al.* Vaughan (1916) has stated that for shoal-water corals of Florida and the Bahamas there is a relation between the phenotypic nature of the coral mass and its environment, especially in relation to turbulence. He found that branching corals occurred in calmer water, and massive forms in more agitated conditions. The corals present at Kirtlington have been assigned to the genera *Isastrea*, *Thamnasteria*, *Cyathophora*, and *Stylina*; all of these genera can occur as massive hemispherical colonies, but only *Isastrea* and *Thamnasteria* develop long (up to 60 cm.) cylindrical branches (about 2 cm. in diameter, made up of 5-mm. polygonal corrallites). The coral–*Epithyris* bed contains both massive and branching forms of these two genera; the branching forms predominate. Hence we conclude that the immediate environment of the corals was neither completely calm nor excessively turbulent. The abundance of ramose corals suggests that they grew in a quiet environment.

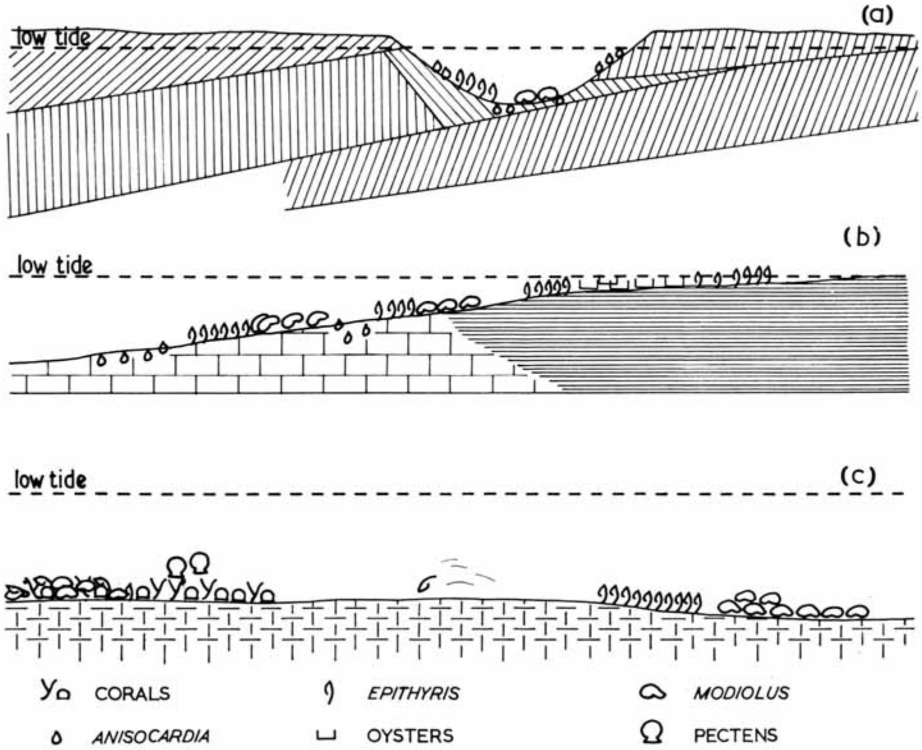
In the Bahamas, Newell's Plexaurid Community has a rock-pavement substrate, and is thus associated with a very reduced infauna; the coral–*Epithyris* bed also has a poor infauna; this may be an indication that the substrate was too hard for burrowers. Some *Anisocardia* and *Favreina* are present, but the dominant Kirtlington coral–*Epithyris* bed infauna consists of boring forms like *Lithophaga*.

The fauna of the coral–*Epithyris* bed (3o) is dominantly composed of epifaunal species (99·2%), and is very different from 2k and 3k in faunal composition (Tables 6, 10, and 11). The bulk of the shelly epifauna appears to have been transported into an area where corals were growing. This transportation is indicated by: low articulation ratios in *Epithyris* and *Modiolus*; normal distributions in both whole and single valves of *Epithyris* (text-fig. 4); and many small shell fragments. The corals are associated with a rich and diverse living fauna of bivalves such as the free-living, byssally attached, or cemented pectinids, and *Lima*, which are much less abundant in beds 3k and 2k.

The indigenous reef epifauna is not easily separated from those shells brought in by currents. Mujaji and Habe (1947) show that in some modern Japanese marine thanatocoenoses there is an abundance of species. The richness of species in bed 3o is another instance of a variety of animals living in slightly differing habitats being brought together by subsequent transportation. Bed 3o is like the remainder of the Forest Marble above bed 3k in the absence of *Anisocardia*; the substrate appears to have been unsuitable for burrowers apart from *Favreina* and the occasional gastropod.

(ii) The remaining Forest Marble beds

The Forest Marble limestones, other than beds 3k and 3o and their equivalents, have an abundant epifauna of oysters and pectinids (Tables 2, 3, 4, and 5). The infauna is very reduced and few of these limestones show signs of bioturbation. We are uncertain as to the precise form of shallow marine environment in which these beds accumulated, but, as there is no evidence of inter-tidal conditions, we would assume that there was slightly deeper water than during White Limestone times. In the case of the oyster–*Epithyris* bed (2n, 4d, and 6e), both genera occur together and most shells are complete; there is little doubt that they lived in the same area, though not necessarily closely intermingled. This area must have been marine, and we consider that



TEXT-FIG. 5. Interpretations of the environments represented by (*a*) the *Epithyris* limestone (bed 2k): *Epithyris* and *Modiolus* confined to channels with floors below low-tide level. *Anisocardia* also present. (*b*) The oyster–*Epithyris* limestone and clay (beds 2n, 3k, 4d, and 6e): oysters and *Epithyris* present on muddy substrates; *Epithyris*, *Modiolus* and *Anisocardia* on limy substrates. All below low-tide level. (*c*) The coral–*Epithyris* limestone (bed 3o): *Epithyris* and *Modiolus* transported into an area of more stable substrate where corals are growing and support a reef epifauna including pectens.

all the limestone beds (most of which contain pectinids and other bivalves in addition to oysters) were marine too.

The Forest Marble clays contain abundant lignite, and many of them also contain oysters and other bivalves. Some of them, like the *fimbriatus–waltoni* Clay (2o, 3l, 4e, and 6f), may have been formed in very shallow water in which the large herbivorous dinosaur *Cetiosaurus oxoniensis* Phillips could wade. The lignite could have come from vegetation growing nearby which provided a food supply for the dinosaurs. But other clays, some of which have a similar fauna to the Forest Marble limestones, may have been laid down in deeper water. The freshwater ostracods in four of these clays may have been derived from rivers flowing into the sea in this general area.

CONCLUSIONS

There are five broad lithological/faunal associations in the White Limestone and Forest Marble at Kirtlington.

1. The bioturbated limestones of the White Limestone, which show a wide range of sediment size from 5-cm. shells to microcrystalline calite; occasionally these may retain traces of bedding (e.g. bed 2l), but more usually the infauna has destroyed all trace of the depositional structures. We agree with Klein (1965) that these were tidal flats at the time of bioturbation, although the original sediments were probably deposited in migrating channels. This is suggested by the remains of epifauna which can be recognised in some less disturbed beds.

2. The *Epithyris* limestones, with or without *Modiolus* (e.g. beds 1e, 2k, 2i(2), and 6c), are often seen to have been deposited in channels (this is especially clear in Gibraltar Quarry). It is thought that all these epifaunal assemblages in the White Limestone lived in channels, which were cut in tidal flats, but were still holding water at low tide (text-fig. 5). Bed 3k, at the base of the Forest Marble, is completely sub-tidal, and is not part of any visible channel. It was laid down in a period of slow sedimentation, with intermittent erosion of the sea floor, exposing the infauna to the influence of transporting currents. The limestones pass laterally into oyster–*Epithyris* marls (beds 2n, 6e) where some of the oysters are internally etched, which might be due to exposure at low tide; the marl area may thus represent slightly shallower water than the limestone.

3. The Forest Marble limestones (excluding beds 3k and 3o and their equivalents) consist dominantly of oyster shells and other epifauna; they can easily be distinguished from the White Limestone by the scarcity of infauna and the lack of bioturbation. Although channels are present in the Forest Marble of other Oxfordshire quarries, none are clearly seen at Kirtlington, and there is no direct evidence of an inter-tidal environment. We think this epifauna lived in a shallow sub-tidal environment.

4. The coral–*Epithyris* bed (3o, 4i, and 6j) represents deposition on a stable substrate on which corals up to a metre high could grow (text-fig. 5). The sedimentation rate for this bed was very low, the currents were sufficient to transport brachiopods and bivalves, but not powerful enough to damage slender cylindrical coral; the substrate was unsuitable for burrowing bivalves. It is not possible to estimate any depth differences between beds 3o and 3k, nor do we see exposures of the area where the *Epithyris* and *Modiolus* were living before being drifted into the coral patches of bed 3o, but these epifaunal shells contemporaneous with bed 3o might have lived in peri-reefal environments similar to bed 3k. Comparisons with the Persian Gulf and the Bahamas suggest

that this bed may have been deposited in a shallow but sheltered region. No indications of channelling associated with bed 3o are visible in the field.

5. The Forest Marble clays are rich in lignite, and one (the *fimbriatus–waltoni* Clay, beds 2o, 3l, 4e, and 6f) has herbivorous dinosaur remains and freshwater and marine ostracods. We conclude that fringing swamps existed in or close to an area with rich vegetation. The *fimbriatus–waltoni* Clay contains caliche-like nodules, and the oyster–*Epithyris* marl has some oysters with internally grooved shells; these are indicators that the two basal clays of the Forest Marble may differ from the remainder in being intertidal.

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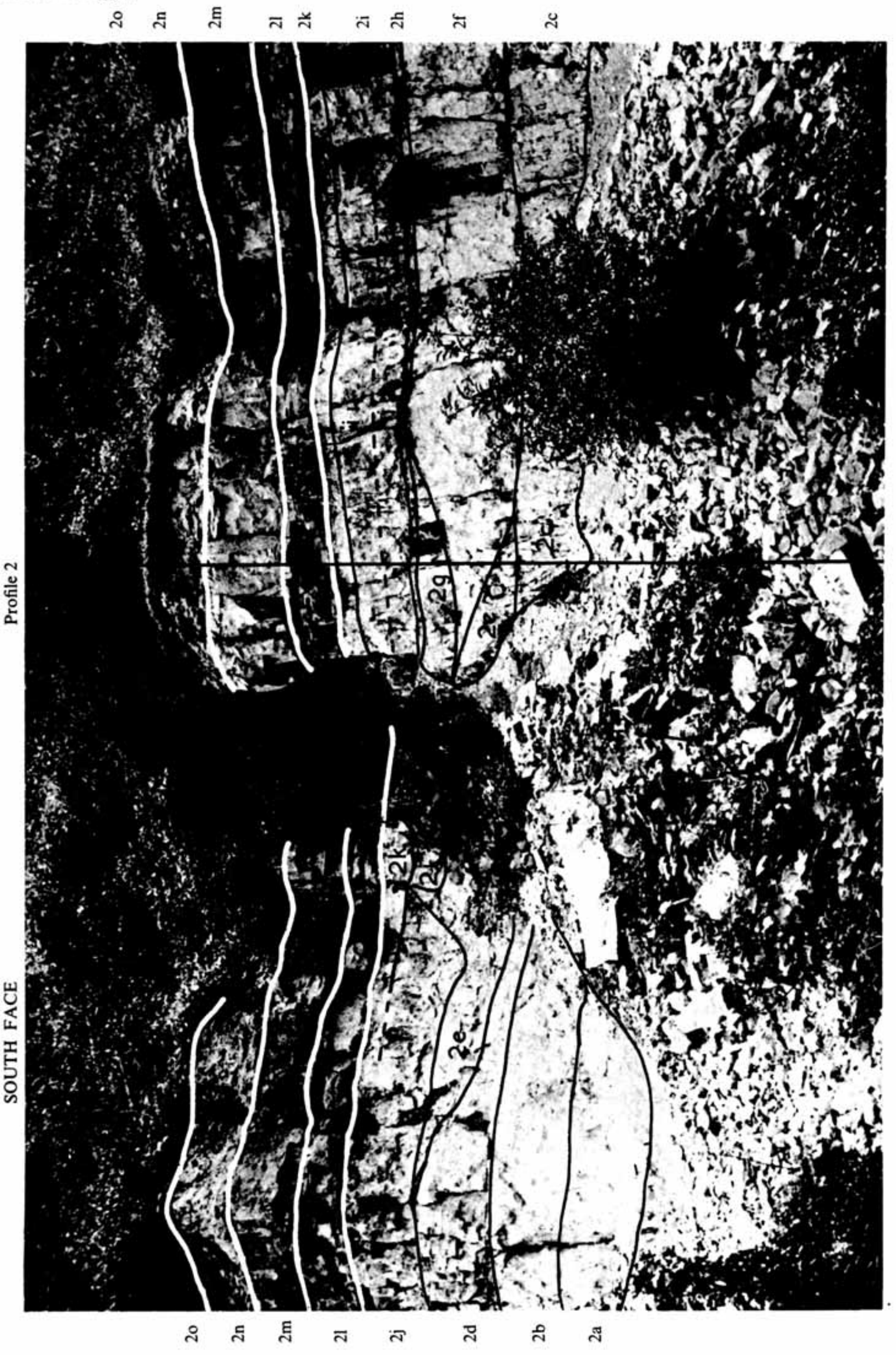
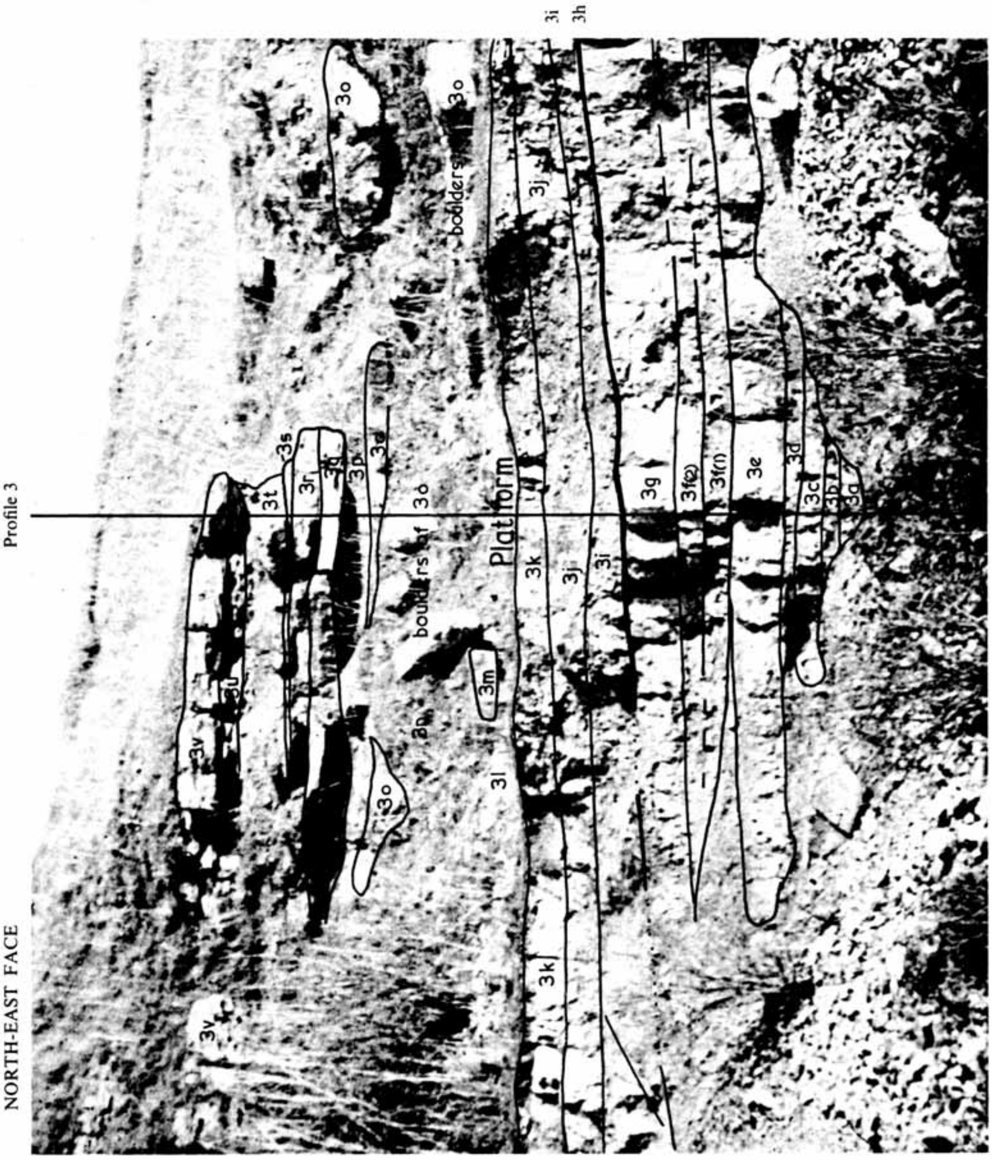


McKERROW, JOHNSON, and JAKOBSON, Great Oolite at Kirtlington



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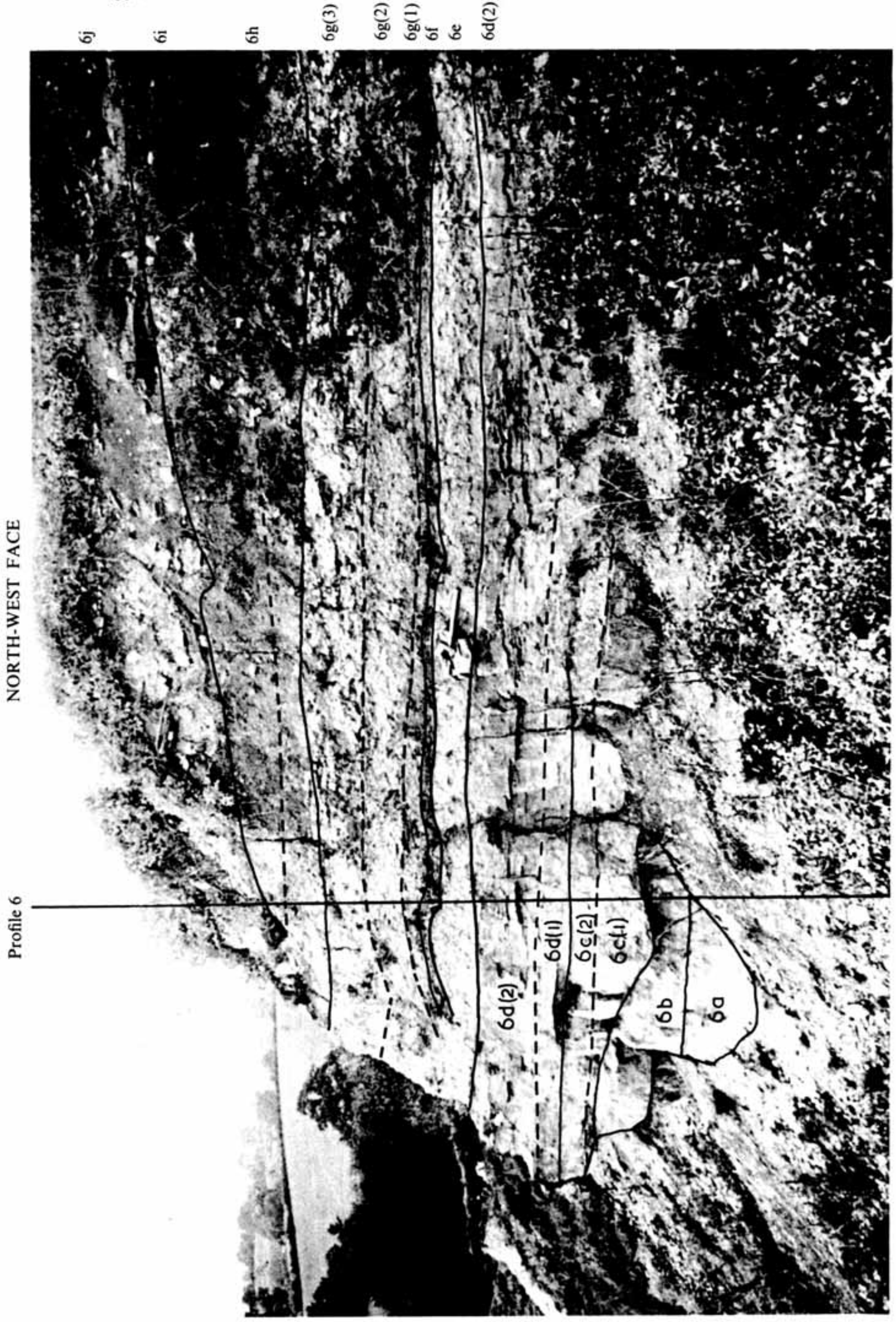
McKERROW, JOHNSON, and JAKOBSON, Great Oolite at Kirtlington

PLATE 11



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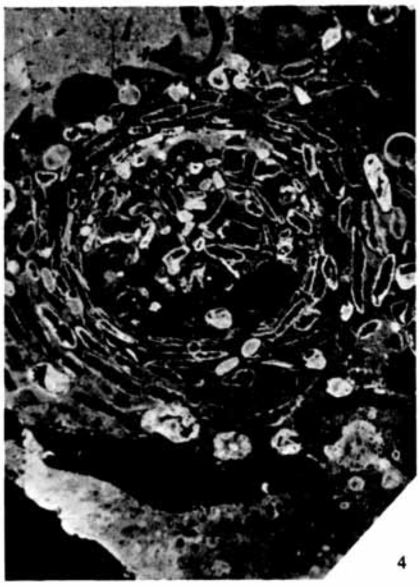
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