THE ECOLOGY OF A MIDDLE JURASSIC HARDGROUND AND CREVICE FAUNA

by T. J. PALMER *and* F. T. FÜRSICH

ABSTRACT. The base of the Bradford Clay (Bathonian) at Bradford-on-Avon, Wiltshire, was a hardground. Soft lime-sand below the hardground was washed out to form crevices, the walls and the floor of which also became lithified. The hardground and the crevices were colonized by encrusting and boring organisms, which polarized into: (i) an upper-surface community dominated by oysters, *Apiocrinus* and *Nubeculinella* and (ii) a crevice community, dominated by *Serpula* (*Cycloserpula*), encrusting ectoprocts, and *Moorellina*.

Similar ecological distributions are known from other formations, and are attributed to differences in light and turbulence, which in turn influenced competition for space and food.

AROUND Bradford-on-Avon, Wiltshire, the Forest Marble Formation (Upper Bathonian) is about 24 m thick (Green and Donovan 1969); the basal 3 m or so consists of well-sorted, cross-bedded oobiosparites. Above this, about 3·5 m of clay alternating with thin limestone partings, first described by William Smith (1816) as 'Clay above the Upper Oolite', soon became known as the Bradford Clay. It achieved fame on account of the rich fossil bed frequently found at its base. Ammonites of the genus *Clydoniceras* have been found in the Bradford Clay which allow it to be placed in the *hollandi* Subzone of the *discus* Zone (Stinton and Torrens 1968).

Smith (1816) realized that the fossils in the basal shell bed of the Bradford Clay had in life been associated with the top surface of the underlying limestone, and that the clay had buried this fauna. It is the nature of this surface and its fauna which forms the subject of this paper. Several previous accounts have been published (e.g. Smith 1817; Cunnington 1859; Woodward 1894), and also Periam (Periam, C. E. 1956, The Jurassic rocks of mid-Wiltshire. Unpublished Ph.D. thesis, University of Reading), but these have tended to stress the species which became separated from their substratum after death, and are now found loose in the base of the clay. Equally important members of the community were the forms which lived firmly cemented to the sea bottom or which bored into it. Except for the conspicuous *Apiocrinus*, this element has been largely ignored.

Good exposures in the lower part of the Bradford Clay have been very rare since the old brick pits in which it was quarried passed out of work. However, the basal shell-bed and the underlying limestone have recently been re-exposed at two localities:

(i) The old Canal Quarry (ST 826600) (text-fig. 1), where about 5 m² of the top of the limestone are exposed at the back of the quarry. The overlying clay may also be seen here.

(ii) Springfield, Bradford (ST 831609), 1100 m to the NNE., where a further 5 m² of the limestone top, as well as 2·5 m of the overlying clay, were temporarily visible in the summer of 1972. In addition, the contact between the limestone and the overlying Bradford Clay could be followed in vertical section for about 100 m towards the north.
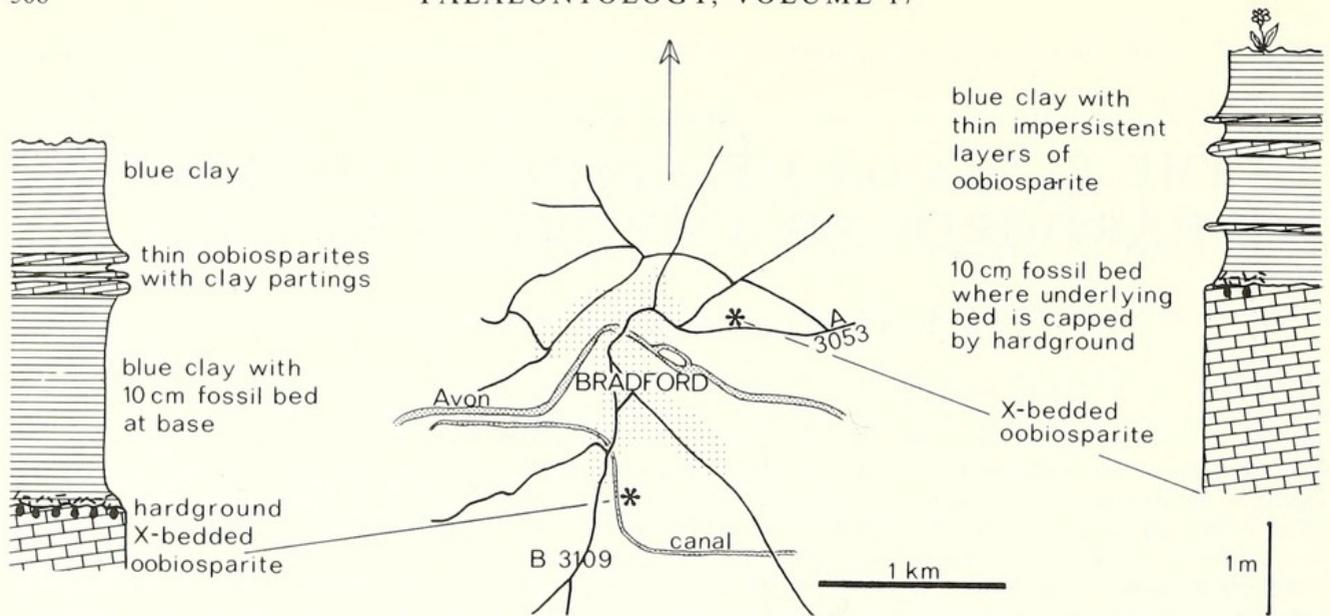
TEXT-FIG. 1. Localities and sections in the Bradford Clay at Bradford-on-Avon.

The top of the limestone at both localities is an intra-formational hardground with an associated boring and encrusting fauna. The northern exposure at Springfield showed the hardground fauna and shell-bed derived from it, dying out northward over 10 m. There is no sign of the hardground having been removed by erosion before the deposition of the clay, and it seems likely that it was developed only patchily over the area where it is now seen.

The hardground is also undermined by crevices, which cut back beneath it for up to 25 cm. These crevices measure up to 5 cm from roof to floor, and are filled with clay and shell debris.

Registration of material. Figured specimens are housed in the Oxford University Museum.

THE DEVELOPMENT OF THE HABITAT

The limestone beneath the clay is a light-brown, cross-bedded oobiosparite locally passing into lenses composed largely of disarticulated and broken shell material. Brachiopods, echinoids, and ectoprocts are common, and bivalves are well represented by pectinids and oysters. The bed has every appearance of having been deposited in current-swept, fully marine conditions.

The top of this oobiosparite is a hardground: synsedimentary calcium carbonate cementation of the lime-sand produced a rocky bottom, rather than a bottom that was merely compacted and firm. This assumption is supported by the following observations:

(i) Well-developed overhangs, rigid enough not to collapse under their own weight (text-fig. 2).

(ii) Encrustation on upper and lower surfaces, especially by oysters and serpulids (Pl. 76, fig. 1; Pl. 77, fig. 9).

(iii) Borings cutting through sediment particles (Pl. 75, fig. 2; text-fig. 2).

(iv) Occasional bored and encrusted pebbles, of the same lithology as the top of the limestone, found at the base of the overlying clay.

Recent hardground formation

The occurrence of early diagenetic lithification of carbonate sediments in Recent environments has been reviewed by Bathurst (1971): cementation in a shallow, but permanently submerged, environment is found in parts of the Bahamas (Taft *et al.* 1968), and over wide areas of the Persian Gulf (Shinn 1969; Taylor and Illing 1969). A similar depositional environment has already been proposed for the Upper Bathonian of the Bradford region by Green and Donovan (1969). The similarity between the Bradford hardground and those in the Persian Gulf is striking.

Description of the Bradford hardground and its similarity to Persian Gulf examples

(i) The upper surface of the hardground at Bradford is irregular, with a succession of flat hummocks separated by gullies up to 1 m or so across. The floors of the gullies are lithified, and their sides often recessed back under the adjoining high areas, so that crevices are formed (text-fig. 2). The roofs of these crevices are formed by thin layers of sediment 5 to 15 m thick, both top and bottom of which are encrusted and bored. It seems as if these layers are the result of cementation having occurred in thin zones, as in the Persian Gulf (Shinn 1969; Taylor and Illing 1969). The soft sediment beneath the lithified layers was removed by currents or animals to form the cavities (cf. Shinn 1969, p. 124).

(ii) Both top and bottom surfaces of the hard layers are pitted with irregular holes up to 3 cm across, whose sides are also encrusted. These are almost certainly the burrows of crustaceans which excavated open dwelling systems in the soft lime-sand, before lithification became too far advanced. The undersurfaces of Persian Gulf hardgrounds are also irregular, due to differential cementation around burrows.

(iii) Small cracks, up to 1 mm wide and now filled with sparry calcite, cut across some of these thin cemented layers. These probably represent fractures, formed as a result of intergranular growth of cement crystals (cf. Shinn 1969, p. 128 and fig. 18).

(iv) The frequency with which the crevices occur suggests that it was easy for either currents or vagile animals to remove soft sediment from below the lithified layers. It may be that these layers were developed only locally in the sediment (below). Alternatively, major breaks in an extensive crust may have occurred, perhaps as a result of the same intergranular crystalline growth postulated in (iii) above. In either case, removal of the underlying soft sediment would have been facilitated.

(v) A patchy development of the lithified layers is supported by the observation that the hardground is locally discontinuous over the whole area studied. Alternatively, the lithified layer may have formed here, but become covered by a layer of soft sediment which protected it from colonization (cf. Shinn 1969, p. 115).

(vi) If the gullies and crevices were formed by removal of soft sediment from between and under pieces of lithified layer, then lithification must have occurred in more than one episode, and perhaps continuously. This is so because the floors and sides of the cavities are themselves hardened and encrusted. Furthermore, the cemented sediment which forms these cavity floors contains fossils, such as *Apiocrinus*, which were associated with the overlying hardground. After death, these crinoids and other hardground fauna tended to accumulate in the cavities, together with sediment trapped in this far less turbulent microenvironment. Subsequent cementation of the walls of these cavities, as well as the floor deposits, provided a new

settlement area for the hardground fauna and, consequently, led to further intensive encrustation and boring.

The history of formation of the Bradford hardground is summarized in text-fig. 2 (cf. Fürsich 1971, fig. 3).

THE FAUNA AND ITS ECOLOGY

Faunal types and their distribution

The collections made at the two exposures contain nearly all the species considered typical of the Bradford Clay by earlier workers (e.g. Woodward 1894; Periam 1956). The total fauna may be divided into three types on ecological and preservational criteria:

(i) Vagile benthos including several species of micromorphic gastropods, asteroids, and the regular echinoid '*Cidaris*' *bradfordensis* Wright.

(ii) Bysally and pedically attached fixosessile benthos, usually attached in life to some hard substrate such as a piece of shell or the hardground. This group includes the bivalves *Lima* (*Plagiostoma*) sp., *Oxytoma costatum* (Townsend), and *Radulo-pecten vagans* (J. de C. Sowerby), as well as the brachiopods usually considered diagnostic of the Bradford Clay and its supposed stratigraphic equivalents (see Elliott 1973). These include *Dictyothyris coarctata* (Parkinson), *Avonothyris bradfordensis* (Davidson), *Eudesia cardium* (Lamark), *Digonella digona* (J. Sowerby), *Crypto-rhynchia bradfordensis* (S. Buckman), and other small rhynchonellids. Periam (1956) gives a more detailed account of the brachiopods from the Canal Quarry. Neither he nor the present authors have found *E. cardium*, but it has been collected extensively in the past. Also tentatively included in this group are small corals of the *Anabacia* type which were probably free-living in the adult stage. The fauna of these two groups may now be found loose in the cavities, or in the shell-bed above the hardground.

(iii) Cemented and boring fixosessile benthos which required a hard, cemented surface. This surface was provided either by pieces of shell material, or by the extensive hardground whose physical and chemical properties were equivalent to those of shell material. This is the fauna with which we are most concerned here; because

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TEXT-FIG. 2. Diagrammatic history of cementation and colonization of the Bradford hardground:

(*a*) Deposition of lime-sand.

(*b*) Crustaceans excavated burrow systems; discontinuous lithification of a thin layer of sediment began at or near the sediment/water interface.

(*c*) Lithification continued; the bottom surfaces of these lithified layers were exposed by removal of the underlying uncemented sediment.

(*d*) The exposed hard surfaces were colonized by boring and encrusting animals. Periods of shell accumulation on the hardground alternated with periods of bioerosion, during which boring activity removed some encrusting shell material (Pl. 75, fig. 4). The floors of the crevices started to lithify.

(*e*) Shell material derived from the hardground accumulated within crevices. Eventually, clay deposition buried the hardground and its associated fauna.

The rectangular insets on the left of the figure show the growth of cement around the grains; sediment passes from loose → lightly cemented → well cemented.

clay sedimentation

colonisation

upper surface

lower surface = crevice roof   gully floor   crevice floor

erosion

burrowing and selective cementation

deposition

cementation
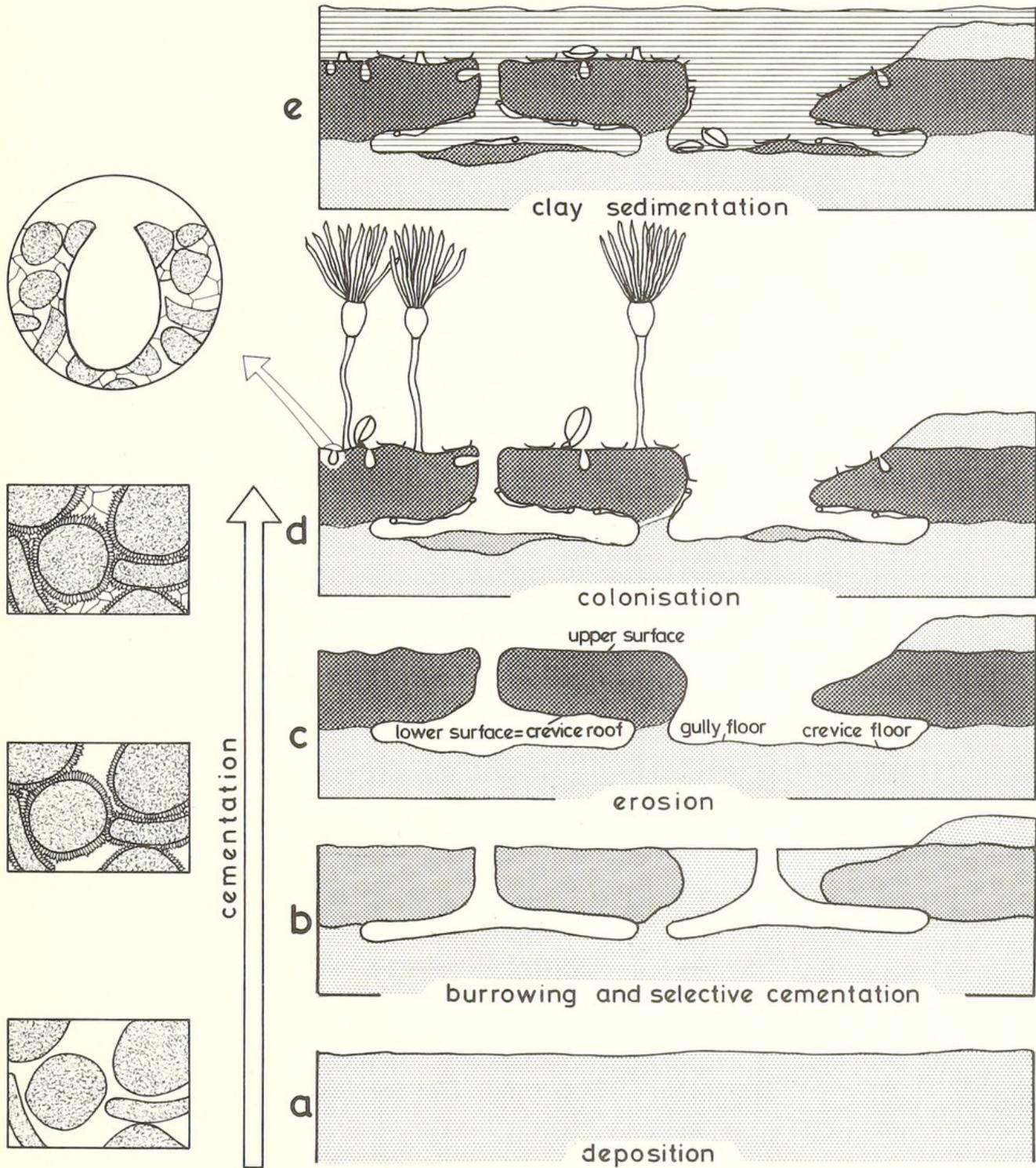
of its attached nature, it is preserved in life position, and is therefore more suitable for palaeoecological study than faunas which became detached after death.

Species distribution of the boring and encrusting fauna

The encrusting and boring fauna can be further subdivided into two groups, the first of which is composed of species which preferred to live on the upper surfaces of the hardground, and the second of those forms which preferred the under surface of the lithified layers, provided by the crevice roofs. It has not been possible to collect for close examination the faunas of the crevice floors. As far as can be determined from cursory examination in the field, these resemble the crevice roof faunas, but

TABLE 1. Table showing distribution of encrusting and boring species on the Bradford hardground. Note preference of arborescent forms and bivalves for upper surface, and preference of serpulids, encrusting ectoprocts, and thecidaceans for lower surface. *r* = rare; *o* = occasional; *c* = common; *a* = abundant.

	GROUP	SPECIES	UPPER SURFACES (r o c a)	LOWER SURFACES (r o c a)
ENCRUSTING	Foraminifera	Nubeculinella sp.	▨	
	Porifera	Limnoria sp.		▨
	Serpulidae	Serpula (Cycloserpula) sp. 1		▨
		Serpula (Cycloserpula) sp. 2	▨	▨
		Serpula (Tetraserpula) sp.		▨
		Serpula (Dorsoserpula) sp. 1		▨
		Serpula (Dorsoserpula) sp. 2	▨	
	Bivalvia	Liostrea wiltonensis (Lycett)	▨	
		Liostrea hebridica (Forbes)	▨	▨
		Exogyra crassa (Smith)	▨	▨
		? Nanogyra nana (J. Sowerby)	▨	▨
		Lopha gregaria (J. Sowerby)	▨	▨
		Plicatula fistulosa (Morris & Lycett)	▨	
		Plicatula sp. 2		▨
	Ectoprocta	Plagioecia sp.	▨	▨
		Mesenteripora sp.		▨
		Stomatopora dichotoma (Lamouroux)		▨
		Collapora sp.	▨	
		Terebellaria ramosissima (Lamouroux)	▨ ? ▨	
	Brachiopoda	Moorellina sp.		▨
	Crinoidea	Apiocrinus parkinsoni (Schlotheim)	▨	
BORING	Porifera	borings of Cliona sp.	▨	
	"Vermes"	Trypanites sp.	▨	▨
	Bivalvia	Lithophaga sp.	▨	
	Cirripedia	Acrothoracican borings	only in shell debris	
	Phoronida	Talpina ramosa (Hag.)	▨	

r o c a　　r o c a

pass into typical upper surface faunas as the crevice floor passes laterally into the exposed floor of the gullies (text-fig. 2). These preferences are outlined below, and summarized in text-fig. 4.

Protozoa; Foraminifera; *Nubeculinella* sp. (Pl. 76, fig. 3). This adherent calcareous foraminifera is extremely abundant on the hardground, always on the upper surface. It thrived both on the cemented sediment itself and on the shells attached to it.

Porifera; *Limnoria* sp. (Pl. 77, fig. 4). This calcisponge occurs on lower surfaces only. Specimens are usually small and poorly preserved, and seldom obvious to the naked eye.

'*Cliona*' sp. Irregular borings up to 2 mm diameter of the ichnogenus *Entobia* are abundant in the shells encrusting the upper surface of the hardground. The raised margins of *Exogyra* valves seem to have been particularly susceptible to attack. Similar borings also occur commonly in the loose shell debris overlying the hardground.

'Vermes'; *Trypanites* sp. (Pl. 75, fig. 1). Borings in the form of simple tubes between 1 and 3 mm diameter, inclined at various angles to the perpendicular, are assigned to this ichnogenus. They appear to be equally common on both lower and upper surfaces.

Annelida; *Serpula* (*Cycloserpula*) spp. Two species of this subgenus are found on lower surfaces. The first is relatively uncommon and is characterized by having started its growth in a flat spiral for 4 or 5 whorls (Pl. 77, fig. 8), before taking up an irregular path. The second form is abundant and grew in an apparently random path from its earliest stages (Pl. 77, fig. 9). Occasionally, a large form (2–3 mm diameter) is found growing in approximately straight lines on upper surfaces. It invariably occurs near the edge of an overhang, and probably represents a different growth form of the species so abundant on the lower surface.

Serpula (*Dorsoserpula*) spp. Two species occur; they are mutually exclusive on lower and upper surfaces respectively. The former is common, growing up to 3 mm diameter. It is nearly circular in cross-section and the median dorsal keel is prominent (Pl. 77, fig. 3). The other species is also common, and is triangular in cross-section. It usually grows to no more than 1·5 mm high and 2 cm long. It occurs both on bare hardground and on associated shell material.

Serpula (*Tetraserpula*) sp. (Pl. 77, fig. 2). One species of *Tetraserpula* is common on under surfaces, but is not found on upper surfaces. It is easily recognized by its circular cross-section (up to 2 mm across), and the three prominent longitudinal keels. On the older part of the test, these keels subtend a series of sharp projections about 1 mm long.

Taken together, serpulids account for the largest proportion of the crevice roof fauna. On some roofs they appear to account for over 90% of the covered surface. In contrast, the upper surface forms are not only less common, but also smaller.

Arthropods; Cirripedia. Small acrothoracian borings occur occasionally in loose *Apiocrinus* ossicles, but have not been recognized in the hardground itself, or in the shells attached to it. No conclusions can be drawn about their life preferences.

Bivalvia; *Liostrea*. Two species of this genus are found attached to the hardground: *L. wiltonensis*, a large solitary form, is found rarely on the upper surfaces. The other species, which resembles *Liostrea hebridica* in overall shape, occurs occasionally on both surfaces.

'*Exogyra*' (Pl. 76, fig. 4). The large *E. crassa* (Smith), which was first recorded from this horizon by Smith (1816), is everywhere abundant over the upper surface of the hardground. There are also many small forms, some of which may be referable to *Nanogyra nana* which Periam (1956) records from the Canal Quarry. Alternatively, they may be no more than the young stages of *E. crassa*. *Exogyra* is occasionally found on the under surfaces of overhangs, but always near the outside edges.

Lopha gregaria. This species occurs commonly on the top surface, where it prefers small depressions, such as those provided by the remains of crustacean burrows. It is occasionally found on the outside edges of the under surfaces of overhangs.

Plicatula. *P. fistulosa* occurs commonly on the upper surfaces (Pl. 76, fig. 4), where it is usually found in small clusters. It is also found occasionally growing amongst the branches of arborescent bryozoans. A second species of *Plicatula* is found exclusively on crevice roofs (Pl. 77, fig. 7). It is larger than *P. fistulosa*, more adpressed to the substratum, and less spinose in the attached valve. It appears to have preferred to colonize the bare hardground, rather than a surface which was already covered by a biogenic layer of calcium carbonate.

Lithophaga sp. (Pl. 75, figs. 2, 3). This boring form is abundant on both surfaces, with a slight preference for the upper.

It is bivalves, particularly '*Exogyra*', which dominate the hardground's upper surface.

Bryozoa; Ectoprocta. Three crustose ectoprocts occur on the hardground. The first two, *Mesenteripora* sp. (Pl. 77, fig. 5) and *Stomatopora dichotoma* (Pl. 77, fig. 1), are confined to the crevice roofs where they usually occur in close association with the serpulids and other shell material. They colonized the bare hardground less frequently. The third form, *Plagioecia* sp. (Pl. 77, fig. 6) occurs similarly, and is also found occasionally on upper surfaces, where it displays a marked substrate preference for *Apiocrinus* holdfasts.

Fragments of arborescent ectoprocts are common in the shell debris above the hardground. The roots of one of these (*Collapora* sp.) are occasionally seen on upper surfaces (Pl. 76, fig. 2). The other, *Terebellaria ramosissima*, is not found *in situ*. It seems likely, however, that it was also attached to the upper surface in a similar way.

Together with the serpulids, ectoprocts are a major element of the crevice roof fauna.

Phoronida. Ramose borings (*Talpina ramosa* Hag.), attributed to phoronids (Voigt 1972), are very abundant in bivalve shells on both surfaces, and also in loose shell debris (Pl. 75, fig. 5).

Brachiopoda; Thecideacea; *Moorellina* sp. (Pl. 77, fig. 4). Cemented brachiopods assigned to the genus *Moorellina* abound on the crevice roofs only. They appear to thrive equally on the bare hardground and on other shell material, but prefer the outer regions of the crevices to the inner recesses.

Echinodermata; Crinoidea; *Apiocrinus parkinsoni* (Schlotheim) (Pl. 76, fig. 5). Black holdfasts of *Apiocrinus* abound on the upper surface of the hardground. Occasionally, complete specimens are found, lying flat and fully articulated along the hardground. Holdfasts are never found on undersurfaces.

Community ecology

The top and bottom surfaces (= crevice roofs) of the hardground each have a distinct association of species wherever they have been observed. The associations may be regarded as two distinct communities: on the upper surface of the hardground is an oyster/*Apiocrinus* community, and on the roofs and, probably, floors of the crevices is an serpulid/ectoproct community. The former is characterized by the presence of *Apiocrinus*, *Lopha*, *Plicatula fistulosa*, *Liostrea wiltonensis*, *Serpula* (*Dorsoserpula*) sp. 1, *Nubeculinella*, *Cliona*, and the arborescent ectoprocts *Collapora* and *Terebellaria ramosissima*. The crevice community is characterized by two species of *Serpula* (*Cycloserpula*), the crustose ectoprocts *Mesenteripora*, *Stomatopora*, *Plagioecia* (which also occurs occasionally on upper surfaces), the calcisponge *Limnoria*, a second species of *Plicatula*, and abundant *Moorellina*. Other species are represented in both communities.

The two communities not only contain different members, there is also a difference

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Boring fauna in the Bradford hardground and associated shell material.

Fig. 1. Polished section through lower surface biogenic layer, with abundant *Lithophaga* borings and occasional *Trypanites* sp. (arrowed), (J 40033), × 2·4.

Fig. 2. Section through *Lithophaga* sp. in crypt on upper surface; truncation of grains (arrowed) shows bed was cemented before boring occurred, (J 40034), × 6·3.

Fig. 3. Enlargement of section in fig. 1 through lower surface endolithic layer, showing *Lithophaga* borings cutting through older borings (arrowed) which indicates more than one generation of boring activity, (J 40033), × 5.

Fig. 4. Polished section through upper surface biogenic layer showing *Lithophaga* crypt truncated and overgrown by oyster (arrowed), (J 40035), × 6·5.

Fig. 5. Phoronid borings in *Oxytoma costatum* (Townsend), (J 40036), × 2·5.

PLATE 75
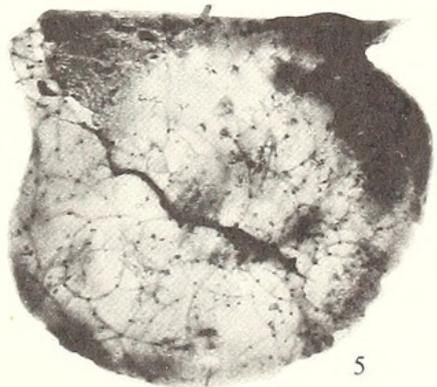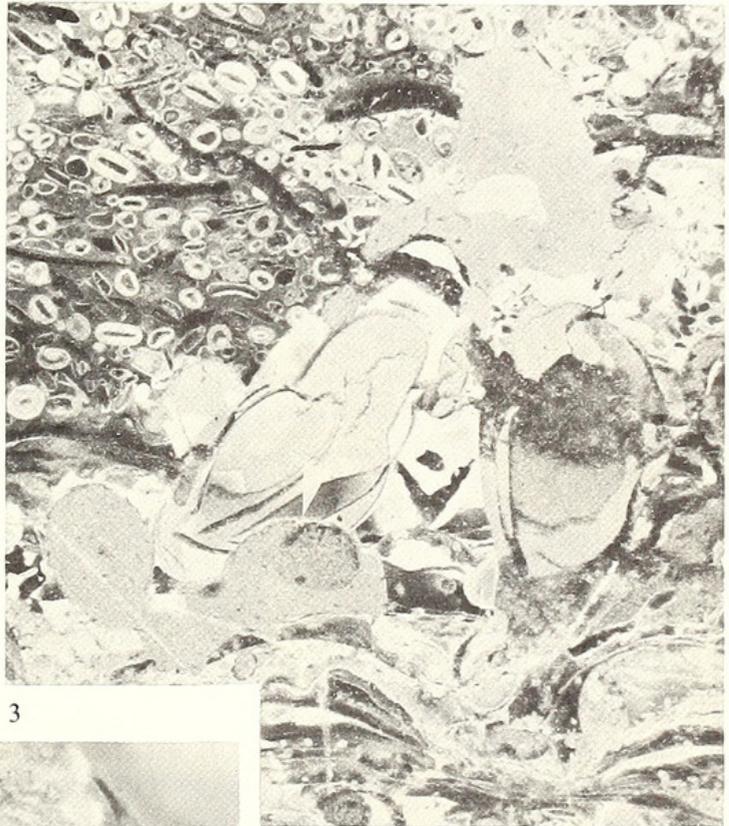
PALMER and FÜRSICH, Middle Jurassic hardground

in growth forms. The cavity community is dominated by members which are closely adpressed to the substrate, as might be expected in a small space of restricted height. In contrast, the oyster/*Apiocrinus* community contains forms, such as *Apiocrinus* itself and the arborescent ectoproct *Collapora*, which extended upwards to exploit food at different heights above the hardground. Altogether, five different levels at which exploitation occurred can be distinguished (text-fig. 3). This vertical stratification is analogous to that noted by Elton (1966) for terrestrial woodland. In the substrate itself is an endolithic layer, corresponding to Elton's soil layer; on top of the substrate, in order of increasing height, come the two encrusting layers, analogous to ground and field layers, and the two silvide layers, analogous to shrub and canopy layers.
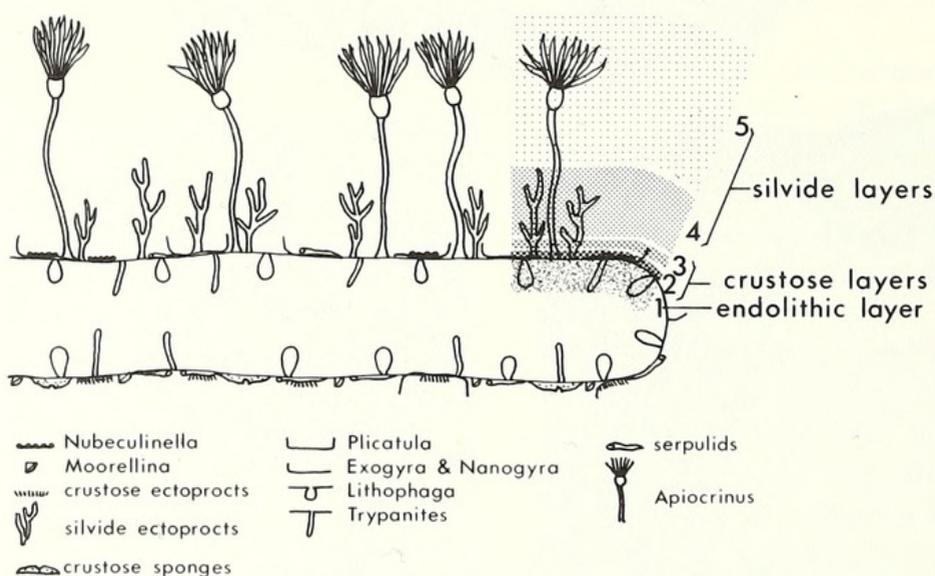
TEXT-FIG. 3. Ecological stratification on hardground surfaces. Endolithic and crustose layers occur on the upper surface of the Bradford hardground, as well as in the cavities beneath. The silvide layers are confined to the upper surface.

The cemented and boring forms were preserved in life position after death and their life preferences are clear. It seems probable that the other elements of the fauna which did not remain in life position after death also had similar life preferences. Many Recent asterozoa, for example, favour the protection offered by cavities and overhangs. However, it seems likely that *Cidaris* with its large primary spines, was

EXPLANATION OF PLATE 76

Elements of the upper surface oyster/*Apiocrinus* community of the Bradford hardground.

Fig. 1. Oysters heavily bored by *Lithophaga* sp., (J 40037), × 1·7.

Fig. 2. Root of silvide ectoproct *Collapora* sp., (J 40038), × 20.

Fig. 3. Encrusting foram *Nubeculinella* sp. on oyster, (J 40039), × 20.

Fig. 4. *Exogyra crassa* (Smith) and *Plicatula fistulosa* (Morris and Lycett), (J 40032), × 1·8.

Fig. 5. *Apiocrinus* holdfast, (J 40040), × 1.

Fig. 6. Section through hardground and overlying thick biogenic layer (junction arrowed); biogenic layer is composed of oysters (dark), which have been bored by *Lithophaga* (light, with rounded bottoms), (J 40041), × 2·1.

PLATE 76
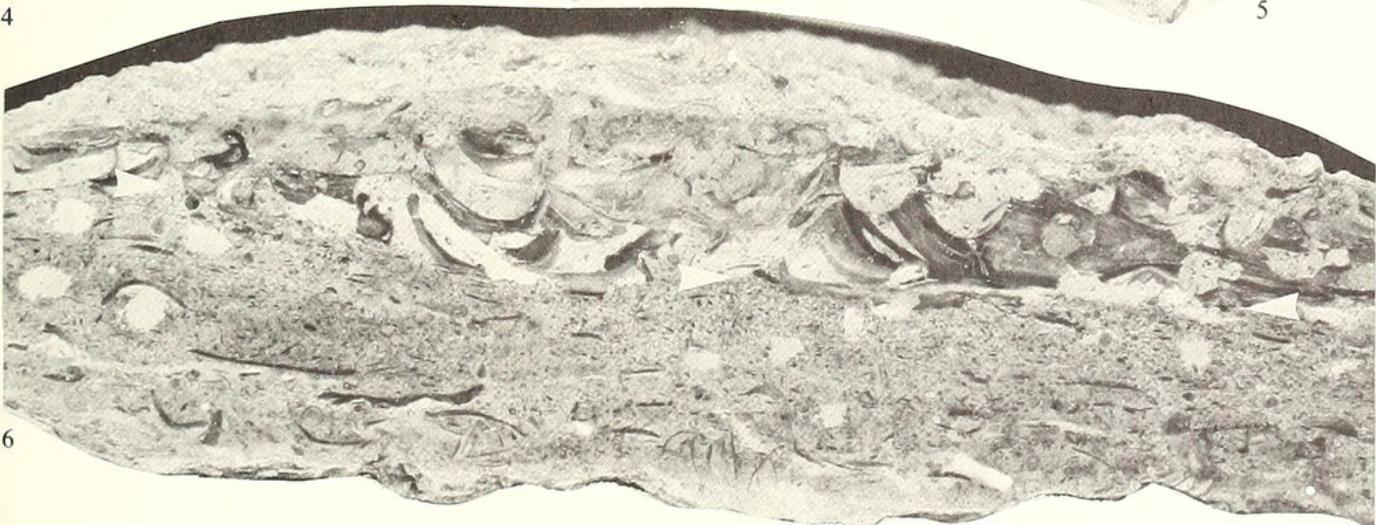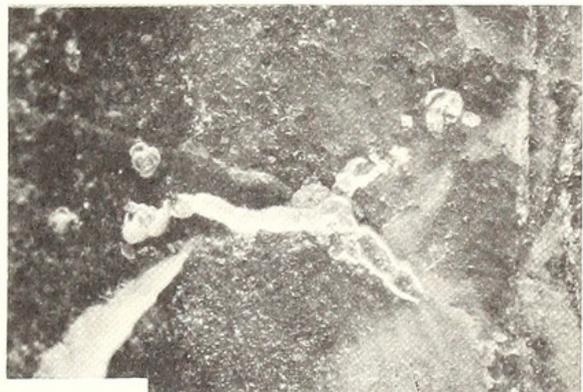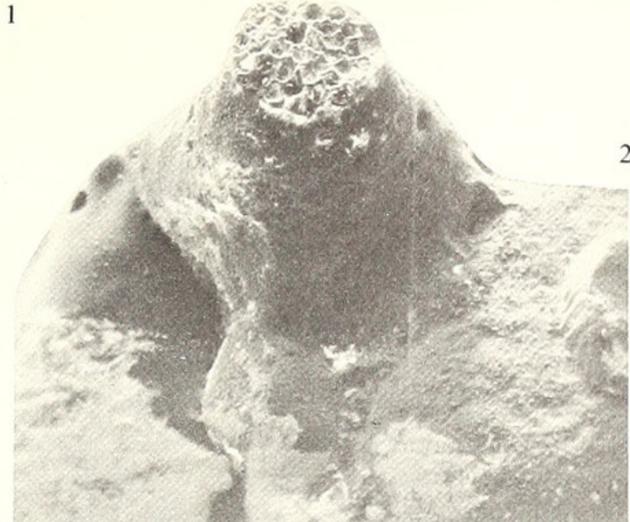
PALMER and FÜRSICH, Middle Jurassic hardground

unsuitable to cavity dwelling, and was active on the top surface of the hardground. Similarly, it is unlikely that the pedically attached brachiopods were confined to lower surfaces. They were too bulky for small cavities, and also occur commonly elsewhere where there is no evidence of there having been cavities of any sort (e.g. Elliott 1973).

In addition to a preference for either top or bottom surfaces the crevice-living *Plicatula* is almost always found on the bare hardground rather than on older layers of serpulids and ectoprocts. The only biogenic material on which it grew was other *Plicatula*. Thus, on crevice roofs there is evidence of some sort of ecological succession, with *Plicatula* being the first species to colonize a newly exposed surface, but being replaced by a fauna dominated by serpulids, ectoprocts, and *Moorellina*. A similar succession is not obvious on the upper surface, where oysters may build up a biogenic layer, up to 2 cm in thickness (Pl. 76, fig. 6). However, it seems that oyster growth at any one point was not a continuous process: sections through the oyster layer frequently show *Lithophaga* crypts, of which only the bottom quarter or so remain (Pl. 75, fig. 4). The inference is that the material in which the upper part of the crypt was located, has been eroded away. At the present day, it has been estimated that bioerosion in limestone can account for the removal of between 2 and 10 mm of sediment per year (Warme *et al.* 1971). A similar figure, applied to the Bradford oyster layer in a single season of spatfall, could easily account for the truncation of the *Lithophaga* borings. When the next heavy spatfall occurred the truncated crypts were smothered, and the thickness of the oyster layer again increased.

At the time when the Bradford hardground was swamped by the first influx of the overlying clay, the oyster layer was undergoing a marked bioerosive phase. Nearly all the oysters seen are represented by their attached valves only, and most are heavily bored by ctenostomes and clionids. In places, truncated *Lithophaga* borings abound (Pl. 76, fig. 1). The most abundant encrusting form alive at this time was the foraminifer *Nubeculinella*.

Although the nature of the two communities which inhabited the hardground are very different, they are similar in diversity. Seventeen species occur on each community, and to each community, eight species are exclusive (Table 1). The main difference between the two is biomass. We have already noted the crustose nature of the members of the serpulid/ectoproct community, as opposed to the more arborescent forms on top, but the former are also considerably smaller. Consequently,

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EXPLANATION OF PLATE 77

Elements of the lower surface serpulid/ectoproct community of the Bradford hardground.

Fig. 1. Ectoproct *Stomatopora dichotoma* (Lamouroux), (J 40042), × 4·7.

Fig. 2. *Serpula* (*Tetraserpula*) sp., (J 40043), × 2·2.

Fig. 3. *Serpula* (*Dorsoserpula*) sp. 1, (J 40044), × 2·5.

Fig. 4. Thecideacean *Moorellina* sp. (left) and encrusting calcisponge (right), (J 40045), × 13.

Fig. 5. Ectoproct *Mesenteripora* sp., (J 40046), × 14.

Fig. 6. Ectoproct *Plagioecia* sp., (J 40047), × 4.

Fig. 7. Attached valve of *Plicatula* sp., (J 40048), × 1·5.

Fig. 8. *Serpula* (*Cycloserpula*) sp. 1, (J 40049), × 4·6.

Fig. 9. General view of serpulids, (J 40031), × 1·8.

PLATE 77
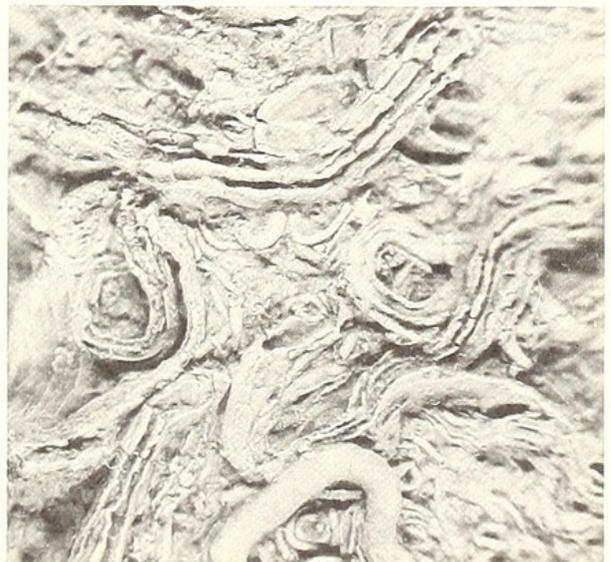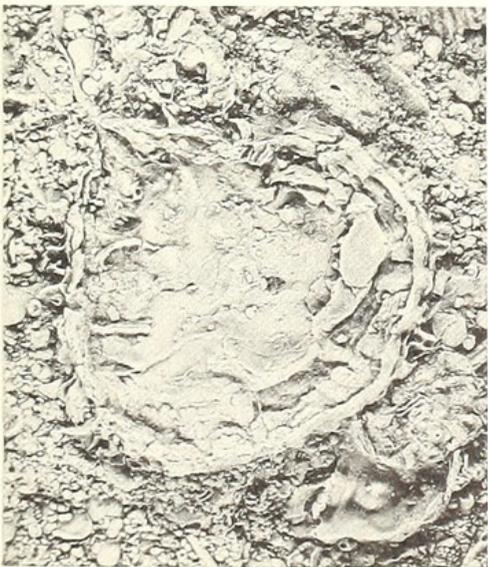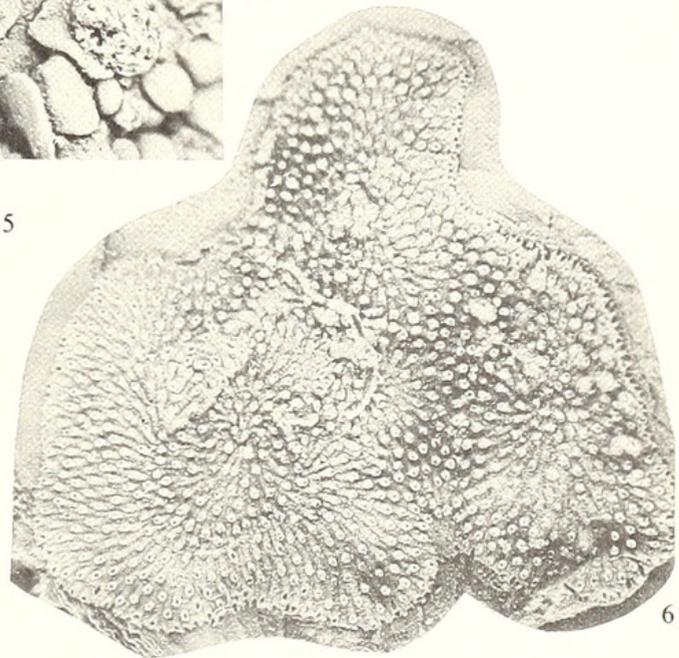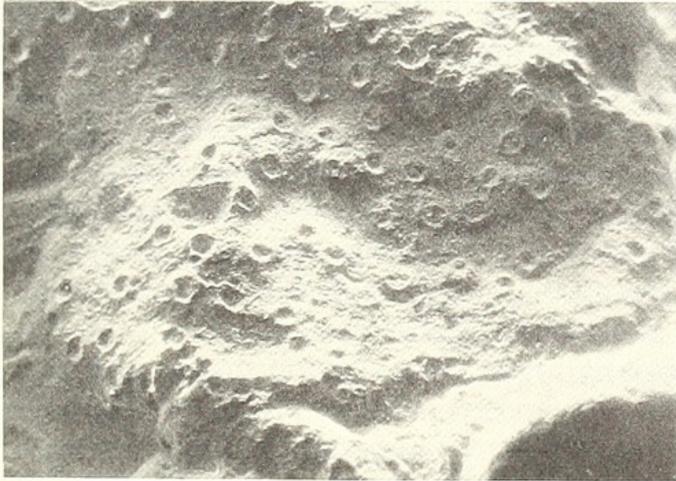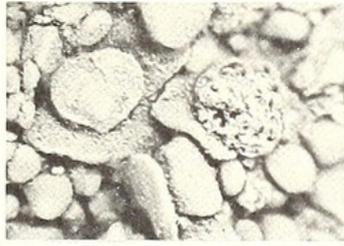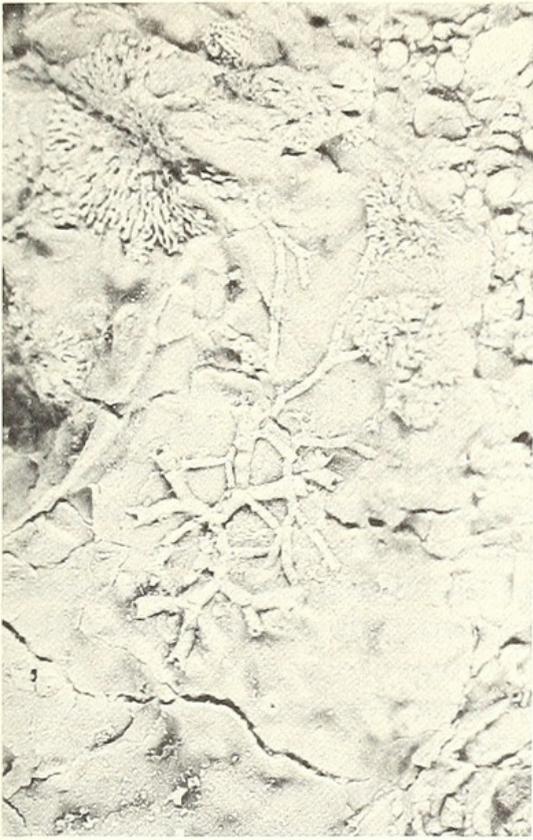
PALMER and FÜRSICH, Middle Jurassic hardground

the biogenic layer of oysters and *Apiocrinus* on the upper surface is always thicker than that composed of *Plicatula*, ectoprocts, and serpulids on the lower, in spite of the top's greater rate of bioerosion.

DISCUSSION

Factors responsible for the distribution of the hardground fauna

The polarization of the Bradford hardground fauna into an upper surface oyster/*Apiocrinus* community and a crevice serpulid/ectoproct community is attributed to three abiotic factors: cavity size, light intensity, and degree of turbulence. Linked to these are biotic factors, such as competition for space and competition for food.

Reidl (1966) has given an extensive review of the faunas found in submarine caves in the Mediterranean. He has discussed the nature of the faunas, and also the variations in biotic and abiotic factors within the cave microenvironment which affect the faunal distribution.

Hartman and Goreau (1966) have discussed the importance of encrusting sponges in the cryptic habitats within Jamaican reefs, and Jackson *et al.* (1971) discussed sponge/thecidacean brachiopod communities found on the undersides of foliaceous corals, and on the insides of caves, in pantropical reefs. Jackson *et al.* also mentioned the occurrence of cheilostome ectoprocts and serpulids in these habitats, and stressed the relative paucity of bivalves, which are common on other parts of the reef. Garrett *et al.* (1971), however, recorded that the attached valves of *Spondylus americanus* are extremely common in the 'gloomy' cavities in Bermuda patch reefs, where *Chama macerophylla*, *Isognomon radiatus*, and *Lithophaga nigra* are also found. Bermudan gloomy and dark cavities are also colonized by sponges, ectoprocts, and serpulids.

The size of a cave determines the size of its fauna. Forms like *Apiocrinus* were far too big to grow in the small cavities of the Bradford hardground. The same is true to some extent of the arborescent bryozoans and some large oysters.

The light intensity in crevices is substantially lower than that on upper surfaces. Within crevices the ceiling and the back form the darkest parts and therefore provide an ideal settlement area for shade-loving forms. Many larvae of the marine sessile epibenthos can distinguish between light of various intensity for settlement (Riedl 1966, p. 348). In the Bradford hardground fauna, the preference of serpulids and crustose ectoprocts for undersurfaces may partly be due to this fact. Recent ectoprocts are known to show a zonation according to light intensity in caves, and Gautier (1961) describes three species from the western Mediterranean which are particularly shade-loving. Unfortunately, no observations are available on the distribution of Recent serpulids as a function of light intensity.

Turbulence is the third important abiotic factor influencing the distribution of this hardground fauna. The degree of turbulence is far lower in crevices (especially small ones) than on the sea floor, even in a high-energy environment (Riedl 1966, p. 276). Consequently, faunal elements which prefer a quiet environment are found in the crevices (cryptophilic forms), whereas other members of the fauna which prefer a high-energy environment are found on the current-swept sea floor (acrophilic forms). Most oysters of the Bradford hardground fauna belong to the latter group.

Even when found in the cavities, they prefer edges and well-exposed overhangs (above).

Competition for space, an important biotic factor, is correlated with light intensity. Low light intensity results in a decrease of the algal cover and the epiphyton (Riedl 1966, p. 370). On upper surfaces with a high light intensity, fast-growing algae threaten to overgrow other sessile benthos. In crevices with a low light intensity this danger is far less pronounced, and crustose serpulids and ectoprocts suddenly become competitive and dominate the fauna. This may well have been the case in the Bradford hardground, though no evidence of an algal cover has been preserved. On upper surfaces, only relatively large crustose forms (e.g. *Exogyra crassa*, very large specimens of *Cycloserpula*) or silvide forms (e.g. *Apiocrinus* and arborescent ectoprocts) were able to compete with algal growth. Also competitive are very small crustose forms with a very short life-cycle (Riedl 1966). The mass occurrence of the encrusting foraminifer *Nubeculinella* on upper surfaces is therefore well in agreement with observations in the Recent. Boring organisms, like *Cliona*, *Lithophaga*, and some polychaetes, which are common on upper surfaces of the Bradford hardground, also compete successfully and are found in great numbers even under a dense algal cover in the Recent (Riedl 1966, p. 370). This is because there is less danger of their being overgrown by encrusting forms, which are excluded by the dense algal cover.

Competition for food, another biotic factor, is correlated with turbulence. In Recent caves there is a distinctive zonation of the benthonic filter-feeders according to their filtering capacity (Riedl 1966, p. 394): at the entrances passive filter-feeders predominate, but these are replaced by half-passive and finally by active filter-feeders towards the back parts of caves. The fact that all forms found on crevice roofs in the Bradford hardground are active filter-feeders is not, therefore, surprising.

Turbulence is also responsible for the biomass differences (expressed by the thickness of shell layers) between upper and lower surfaces of the Bradford hardground. The 'Konsumationszeit' (the time in which the fauna filters the water content of a cave of a given size) is shorter the smaller is the cave (Riedl 1966, p. 392). The relatively small Bradford hardground cavities could only support a low biomass density.

In conclusion, it becomes apparent that a combination of several biotic and abiotic factors was responsible for the polarization of the Bradford hardground fauna. It is difficult to decide which of the factors discussed above governed the distribution of a particular faunal element. We assume that in most cases several factors were responsible for distributions on the hardground.

Further evidence for polarization of communities on hard surfaces

The Bradford situation is not unique and a similar situation occurs in the White Limestone (Middle Bathonian) at Foss Cross quarry, Calmsden (SP 056091), where a crevice system is locally present below an extensive layer, about 3–5 cm thick, of cemented lime-sand. The lower surface is colonized by an almost identical fauna to that at Bradford, except that the calcisponge is more abundant. The upper surface, however, is encrusted only by *Liostrea* and *Nanogyra* sp. and bored only by *Lithophaga*. *Apiocrinus*, *Nubeculinella*, and arborescent ectroprocts are absent so that the diversity of the upper surface fauna is lower than at Bradford. Bysally attached

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bivalves and pedically attached brachiopods, associated with the hardground at Bradford are also absent. The absence of the diagnostic brachiopods seems to be the general rule in the Oxfordshire–North Cotswolds province of the Middle Bathonian; they probably preferred the offshore regions, where the water was clearer and better circulated, to the nearshore regions which were more lagoonal, and contained much suspended lime-mud.

The Foss Cross hardground is continuous around the whole quarry (about 150 m) but cavities are only developed locally. Elsewhere, however, the hardground is penetrated by open burrow systems. Presumably, these were excavated when the surrounding sediment was still soft, and were preserved in an open condition as cementation proceeded (see Shinn 1969). The walls of these open burrows are encrusted by *Moorellina*, an encrusting calcisponge, *Plagioecia* sp., *Serpula* (*Cycloserpula*) sp., and *Stomatopora* sp. Presumably, conditions of light and water circulation inside these burrow systems were similar to those in the hardground crevices.

Another example of an apparent cavity fauna is from the Middle Bathonian at Tytherley Farm Lane, Wiltshire (ST 769594). A single piece of limestone (H. S. Torrens collection HT 1153), about 3 cm thick and 100 cm² in area, is encrusted on both sides. The orientation may be determined from a geopetal fill in one of the *Lithophaga* crypts. The upper surface is encrusted by large oysters, *Plicatula* sp., *Atreta* sp., and small crustose *Isastraea*. The lower surface is covered with encrusting calcisponges. *Moorellina* sp., and *Serpula* (*Cycloserpula*) sp. *Lithophaga* borings penetrate the hardground from both sides.

Synsedimentary lithification of thin layers of carbonate sand with subsequent colonization of both the top and the bottom surfaces, has been described from the Middle Jurassic of the Paris Basin by Purser (1969). Although he does not discuss details of the respective faunas of the two surfaces, Purser does illustrate a bottom surface which is crowded by *Serpula* (*Cycloserpula*) sp. and bored by *Lithophaga*.

Outside the Middle Jurassic, this preference of serpulids for undersurfaces has also been noted. Hallam (1969) figures serpulids on undersurfaces from the Coinstone (Lower Lias) of Dorset, and Kennedy and Klinger (1972) note a similar preference in the Cretaceous of South Africa. Voigt (1959) in his discussion of Upper Cretaceous hardgrounds, mentions examples (e.g. from the Maastricht region) with a rich encrusting and boring fauna from both upper surfaces, and from burrow and crevice walls. However, he does not differentiate between the two faunas.

Hardgrounds in the Corallian of central England have also been studied by one of us (F. T. F.). An example from Cothill quarry (SP 467997) again shows a clear polarization of top surface and crevice-dwelling faunas.

We have also observed a similar phenomenon in Jurassic patch reefs, where the top and the bottom of the corals or coralline sponges which constitute the bioherm, support different communities. The large knolls of *Isastraea* in the Corallian of England and northern France support a fauna dominated by ectoprocts and serpulids on the lower surfaces, whereas the upper surfaces are colonized primarily by bivalves.

Similarly, in the Bathonian sponge reefs at St. Aubin, Calvados, *Atreta* and arborescent ectoprocts are dominant on top of the sponges, whereas the familiar association of crustose ectoprocts, *Moorellina* sp. and small sponges, as well as a *Spirorbis*, predominate underneath.

A similar polarization of faunas on upward- and downward-facing calcareous substrates is known from the Palaeozoic. Koch and Strimple (1968) describe a discontinuity surface with crevices from the Upper Devonian of Iowa. The upper surfaces support *Spirorbis*, edrioasteroids, *Aulopora*, stromatoporoids, together with *Trypanites* borings, whereas the under surfaces support cystoids, ?*Aulopora* and *Trypanites* (additional information from C. R. C. Paul, pers. comm.). We have also seen a massive stromatoporoid in Mr. J. M. Hurst's collection from the Silurian of Gotland, where *Spirorbis* seems to be confined to the lower surface, whilst tabulate corals, ectoprocts, and *Trypanites* borings occur on the upper surface.

In conclusion it would seem that the distinction between exposed surface encrusting and boring faunas, and those dwelling in cryptic crevices, has been maintained at least from the Silurian. This distinction applies to inorganic substrates (such as a hardground or a pebble), and to organically formed substrates (such as scleractinians or foliaceous calcisponges). In the example from Bradford the upper surface fauna is an *Apiocrinus*/oyster dominated community whilst the crevice community is dominated by serpulids and encrusting ectoprocts, with *Moorellina*, *Plicatula*, and encrusting calcisponges.

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T. J. PALMER and F. T. FÜRSICH
Department of Geology and Mineralogy
University of Oxford
Parks Road
Oxford OX1 3PR