ECOLOGY OF SPONGE REEFS FROM THE UPPER BATHONIAN OF NORMANDY

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ABSTRACT. *Platychonia magna* (d'Orbigny), a lithistid sponge previously regarded as a calcisponge (*Cupulospongia magna*), forms small bioherms in rocks of Upper Bathonian age (sub-zone of *Clydoniceras hollandi*), at Saint-Aubin-sur-Mer on the Normandy coast. In addition to the main frame-builder, four subsidiary faunal groups are preserved. These are: (i) encrusting organisms which attached to the sponge fronds and gave the reef additional strength; (ii) byssate and pedically attached filter-feeding nestlers; (iii) vagile strollers which predated, scavenged, or grazed; (iv) borers. The encrusters may be further subdivided into a low diversity assemblage on the upper sides of the *Platychonia* fronds, and a high diversity assemblage on their undersides. The reefs are envisaged as having grown in the lower photic zone, below normal wave-base but above that reached during storms. The fauna and habitat of the reefs are compared with those of Upper Jurassic lithistid sponge reefs in southern France and Germany, and with those of Middle and Upper Jurassic sponge accumulations in Great Britain.
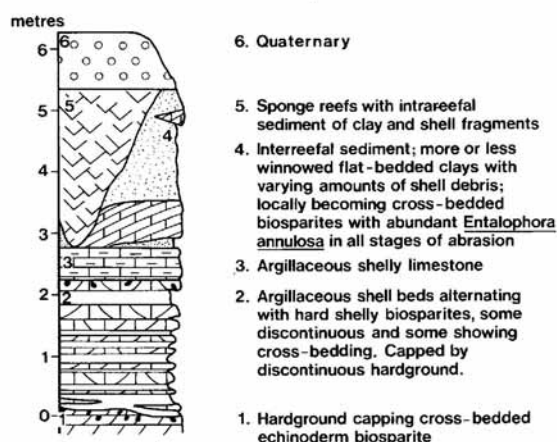
The *Platychonia magna* fronds underwent early diagenetic loss of their original hyaline silica skeleton, together with early lithification of the fine sediment which permeated their canals after death. This appears to be a common occurrence in fossil lithistids.

THERE are two localities in the Upper Bathonian of the region north-west of Caen, Normandy, where the sponge widely referred to as *C. magna* d'Orbigny forms *in situ* patch reefs. The best known of these localities is at Saint-Aubin-sur-Mer, where excellent exposure of the sponges in the low cliff at the west end of the village allow detailed examination. The other locality is on the foreshore just east of Luc-sur-Mer, 4 km east-south-east of Saint-Aubin. Exposure and preservation of the sponge bodies here, however, is inferior to that at Saint-Aubin, and the work for this account has been restricted to the latter site. The stratigraphic horizon at which the reefs are developed lies in the sub-zone of *Clydoniceras hollandi*. It is thus roughly equivalent to the bottom part of the Forest Marble Formation of the Dorset coast (Arkell 1930).

The Normandy Upper Bathonian as a whole is largely developed as cross-bedded biosparites (Fily 1978) containing a diverse fauna. Locally, more clayey and marly beds occur which also contain a rich fauna. Commonly these beds overlie hardgrounds, and have been interpreted as representing a relatively sudden deepening (and return to clastic sedimentation) after formation of the hardground in shallow water (e.g. Fily 1974). Whilst this may indeed be part of the story, the fine clastic sediment is always obviously pelleted when protected from compaction inside shells. It is obvious that its accumulation has primarily been effected by the pelleting and baffling actions of the extensive suspension feeding fauna immediately above the hardground, rather than solely by fines settling out of suspension in deeper, quieter water.

The over-all nature of the fauna is entirely marine, and all major marine invertebrate groups are represented. Algal oncoliths are also common. It seems clear that Upper Bathonian sedimentation took place beneath a relatively shallow, clear sea with good water circulation. This sea abutted against the shore of the Armorican Massif to the south and west, but north-west of Caen there is no evidence of significant clastic input from this or any other region during Upper Bathonian times.

The reef bodies at Saint-Aubin rest on cross-bedded biosparites with thin marl partings. They are in turn overlain by cross-bedded biosparites (seen better above the reefs at Luc) which constitute

CLIFF SECTION EAST OF THE FAULT
ST. AUBIN - SUR - MER, NORMANDY

metres

6. Quaternary

5. Sponge reefs with intrareefal
   sediment of clay and shell fragments

4. Interreefal sediment; more or less
   winnowed flat-bedded clays with
   varying amounts of shell debris;
   locally becoming cross-bedded
   biosparites with abundant Entalophora
   annulosa in all stages of abrasion

3. Argillaceous shelly limestone

2. Argillaceous shell beds alternating
   with hard shelly biosparites, some
   discontinuous and some showing
   cross-bedding. Capped by
   discontinuous hardground.

1. Hardground capping cross-bedded
   echinoderm biosparite

TEXT-FIG. 1. Section through the lower part of the Upper Bathonian, as seen east of the fault in the low cliff at Saint-Aubin-sur-Mer, Calvados, France.

the Calcaire de Langrune. The sediments within the reef horizon are described more fully in the next section. Text-fig. 1 shows the stratigraphic section through the reefs as seen at Saint-Aubin.

The whole of the Upper Bathonian of the Normandy coast constitutes a classic area of French palaeontology. Many of d'Orbigny's types came from there and from the inland exposures of the same beds. The first full description of the sponges at Saint-Aubin, together with a list of many of the associated fossils, was given by Eudes-Deslongchamps (1864). Subsequently, they have received little attention in the literature. Mercier (1931) discussed the detailed stratigraphic succession at Saint-Aubin and described the faulting which downthrows the sponge bodies to the level of the foreshore at the west end of the cliff. His measured sections were figured in a later work (Mercier 1932). More recently, Fürsich and Palmer (1979) have used the section at Saint-Aubin to interpret the form of the sponge reefs at Luc, and have discussed the effects of early diagenetic compaction on the reefal and inter-reefal sediments. The only previous attempt to define the environment in which the reefs grew has been that of Fily and Rioult (1978). They concluded that the sponges could only grow in the sheltered troughs between submarine dunes at the edge of the North Armorican carbonate platform.

The purpose of this paper is to describe the total invertebrate fauna of the sponge reefs, and to discuss its distribution and ecology within the reef bodies. The differences between the sponge-reef fauna and that of the underlying beds are also discussed, and comparison is made with other Jurassic sponge reefs and their associated faunas. To our knowledge, this is the first Middle Jurassic sponge reef to be so described.

GROWTH AND MORPHOLOGY OF THE REEF BODIES

Present-day and original form of the reef bodies

About a dozen sponge-reef bodies are exposed in the low cliff (Falaise du Câtel) at Saint-Aubin, over about 50 m between the west end of the concrete sea defences and a track down to the beach through a cutting in the cliff. Their tops have been truncated and overlain by Quaternary deposits

(text-figs. 1 and 2) but, just west of the track, a fault downthrows the reef bodies to the west, and their tops and the overlying sediments can be seen. The individual reef bodies reach a height of 2·55 m. The most typical form has a pointed base in section, and expands upwards to a width of 2–4 m (text-fig. 2). Adjacent bodies usually join up at the top to form a more or less continuous layer. It seems most likely that the growing reef bodies were elongate structures which have been cut across by the section of the cliff.

The angle of expansion suggests that the reefs would have been rather unstable had they been standing proud of the sea floor. It seems more likely that growth of each body was initiated at one point, and that the colony expanded outwards as it grew up to keep pace with sediment accumulation. In the latter stages of growth, the mature colonies must have joined up to form a largely continuous meadow. A few of the bodies, however, do not expand upwards; they form columns or broad-based mounds.

Sediment associated with the reef bodies

The sediment associated with the reefs falls into two categories: that between the individual sponge fronds within a single reef body (the intra-reefal sediment), and that between adjacent reef bodies (the inter-reefal sediment).

The intra-reefal sediment is largely composed of clay (Pl. 1, fig. 1). It is apparently amorphous and unbedded. However, where best protected from post-depositional compaction and disturbance (e.g. inside fossils), it is entirely pelleted. The fine-grained clastic material in suspension was no doubt concentrated into faeces and pseudofaeces by the suspension feeders in the reef. In this compacted form it then settled out in the slack-water micro-environments amongst the sponges. Indeed this self-sedimentation of the reef (cf. the same phenomenon in modern oyster reefs—see Lund 1957), may have been a frequent cause of death amongst the sessile interstitial fauna. Within the intra-reefal mud are myriads of shell fragments and whole shells, of which micromorphic brachiopods are the best-preserved single category (see below).

TEXT-FIG. 2. The sponge reefs in the low cliff at Saint-Aubin-sur-Mer. Adjacent reef bodies have grown upwards and outwards as sediment has accumulated around them and have eventually coalesced.

The inter-reefal sediment is more varied than that within the sponge bodies, depending on the amount of winnowing it has undergone. It varies from a fairly pure clay with abundant bioclastic fragments, through a clay-rich limestone, to pure biosparite. Bedding is usually planar and poorly to moderately developed in the more clay-rich lithologies (text-fig. 2), but well developed (planar or cross-bedded) in the biosparites. The bioclastic material that makes up these thin planar or thicker lensoid units in the inter-reefal sediment is largely made up of the fronds of erect bryozoans (Pl. 1, fig. 2). Many specimens have the very delicate zoecial apertures well preserved, and have clearly not been greatly rolled or abraded. By far the most abundant species is *Entalophora annulosa*, which is considered to have grown in closely packed meadows between the sponge patches. *Multisparsa lamellosa* is also common.

The more clayey inter-reef sediment is again pelleted where seen inside shells, and much of the shell debris within it appears to have been derived from the reef bodies. A strong biological control over both the supply and the accumulation of the sediment is again envisaged. There is no infauna in the inter-reef muds, but such a fauna would be expected to have been largely aragonitic. Skeletons originally of aragonite, it seems, are virtually never represented in either the reef or the inter-reef material.

The sponge bodies as reefs

Since we believe that the sponge bodies, although clearly three-dimensional now, did not stand as thickets more than a few centimetres to decimetres high on the original sea floor, there are those who would deny us the right to call them 'reefs'. We follow the definition of Heckel (1974), who lists as characteristic of reefs that they have a potential wave resistance, and exert some control over the surrounding environment. The sponge fronds were skeletally rigid, cemented to one another, and seem (as discussed above) to have influenced both the supply and the accumulation of the surrounding sediment. They may therefore continue to be regarded as reefs, as they have been for the past century.

PHYSICAL CONSTRUCTION OF THE REEF

The fauna within the reef, whether loose in the intra-reef mud or still attached to the sponge fronds, has been closely examined. Relative abundances of the species present have been assessed either objectively (by counting), or subjectively (estimation of whether rare, occasional, common, or abundant). Subjective estimates were used for the loose material in the reef mud, and for the attached serpulid worms where it was difficult to separate adjacent individuals. Species counts of the remainder of the attached fauna were obtained from a randomly selected $10\,000$ cm^2 of sponge frond surface. Half of this value was accounted for by the upper sides of the fronds, and half the undersides.

We have distinguished five faunal elements which together comprise the whole reef community. These are now discussed further:

EXPLANATION OF PLATE 1

Fig. 1. A sponge reef at Saint-Aubin, Normandy. The plate- and cup-shaped sponge fronds form a rigid framework whose interstices are filled with fine-grained sediment. Hammer is 33 cm long.

Fig. 2. Bryozoan-rich shell hash with abundant *Entalophora annulosa*, typical of the winnowed inter-reefal sediment, × 2.

Fig. 3. Thin section of calcisponge on the lower surface of a *Platychonia magna* frond. The original calcite skeletal material (dark) is now surrounded by a cement of clear calcite, × 40.

Fig. 4. Thin section of a *Platychonia magna* frond. The light regions are the desmas, originally of hyaline silica, which have been replaced by sparry calcite during diagenesis. The dark material is sediment which is infilling the original pores, × 40.

PLATE 1
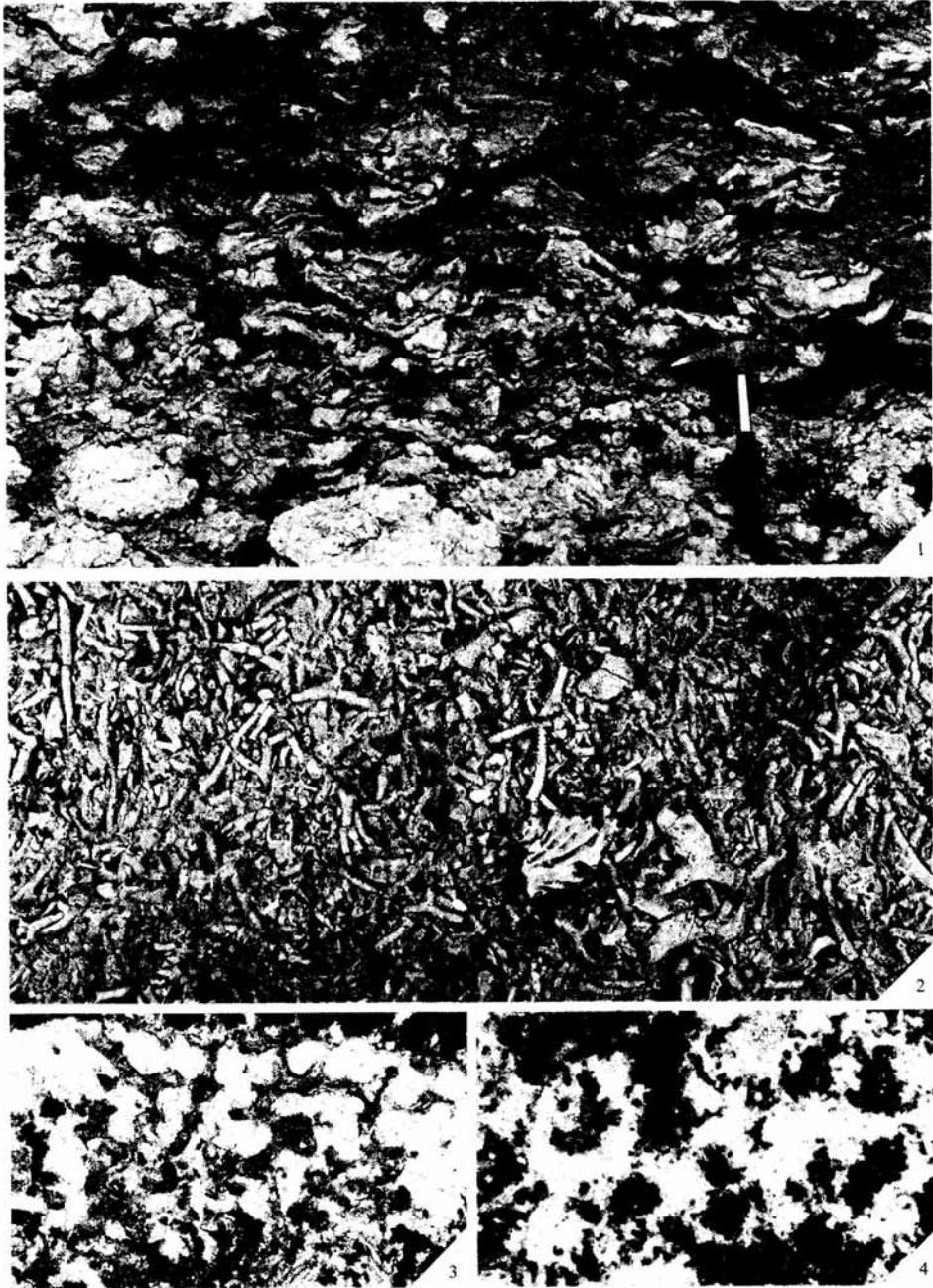
PALMER and FURSICH, Jurassic sponge reefs from Normandy

Principal frame-builder

The sponge which was called *Cupulospongia magna* by d'Orbigny (1850), is usually cupuliform or auriform in shape, and ranges up to a diameter of about 35 cm. Most individuals in the Saint-Aubin reefs, however, are no longer than 15 cm across (Pl. 1, fig. 1). Successive generations of the sponge settled on conspecific adults and firmly cemented themselves to form a rigid reef structure. The fact that most of the reef bodies expand upwards suggests that successive generations crowded in and occupied all the space provided by the established individuals. It is not clear whether the sponge spat could only settle on dead regions of the pre-existing generation, or whether they could settle and attach on individuals covered with living tissue. Furthermore, the possibility of some individuals being budded off asexually from established adults cannot be discounted.

De Laubenfels (1955, p. E104) listed *Cupulospongia* among unrecognizable supposed sponges, its fine structure having been described too insufficiently to allow it to be placed satisfactorily in any of the orders of the Porifera. Informally, the sponge reefs at Saint-Aubin have always been known as calcisponge reefs (e.g. Fily and Rioult 1978), the assumption being that C. belonged to this class. Although now preserved in calcite, the preservation of the *Cupulospongia* skeleton differs greatly from that of undoubted encrusting calcisponges which are abundant subsidiary frame-builders and thus closely associated with the former. In the encrusting calcisponges, the original microstructure of the skeleton can still be observed (Pl. 1, fig. 3). In contrast, the *Cupulospongia* skeleton is heavily recrystallized and is preserved as calcite cement (Pl. 1, fig. 4). No features of the original fine structure can be seen. This preservational difference seems to indicate replacement of an original opaline silica skeleton by calcite. The geometry of this skeleton is identical to that of sponges described, for example, from the Upper Jurassic sponge reefs of the Swabian or French Jura as lithistid sponges. The over-all shape of *C. magna* is very similar to Zittel's (1878) lithistid genus *Platychonia*, as has been pointed out by Thevenin (1923). Thin-sections show a microstructure very similar to that shown in calcified *Platychonia* from the English Inferior Oolite by Sollas (1883), who first described the replacement of sponge silica by calcite. We therefore feel that the frame-builder of Saint-Aubin was a lithistid sponge for which the appropriate name is *Platychonia magna* (d'Orbigny). The peculiar diagenesis is discussed more fully below.

Subsidiary frame-builders

The basic framework provided by the *P. magna* fronds has been heavily encrusted by a wide variety of smaller filter-feeding organisms with calcitic skeletons. These are listed in Table 1, which gives some quantitative information on their relative abundance. On some of the fronds, thick biogenic layers (commonly up to 5 mm, locally exceeding 10 mm) have been built up as successive generations of the encrusters have overgrown one another. As in modern coral patch reefs, such layers contribute greatly to the physical strength of the reef body. Today, a major contributor in this respect are the encrusting coralline algae (e.g. Purdy 1963; Bathurst 1971), and algae are also known to form thick encrusting rinds in other Jurassic sponge reefs (e.g. Gaillard 1971; Schrammen 1924; Hiller 1964; Nitzopoulos 1974). In the Saint-Aubin reefs, however, there is no indication of algae on the sponges themselves, even though bivalve shells with oncolitic algal coverings are occasionally found associated with the sponges. The environmental implications of this are discussed in a later section.

The most conspicuous group of encrusters are the bivalves (Table 1), which are dominated numerically by *Atreta retifera*. This species occupies the niche which is more usually filled by oysters in the Jurassic, both on organic and inorganic hard substrates. Nevertheless, *A. retifera* is abundant both in the Saint-Aubin reefs, and also on Bathonian hardgrounds in Normandy. One of us has argued before (in Hudson and Palmer 1976) that ostreine oysters radiated in the early Jurassic to occupy hard substrates in marginal environments. They are thus a prominent component of the English Bathonian where eurytopic species thrive, and over-all species diversities in southern England are low as a result of relatively poor water circulation on an extensive, shallow platform (Palmer 1979). The Normandy Bathonian, in contrast, yields much higher diversities and many

TABLE 1. Faunal elements of the sponge reef and their distribution within the reef. Figures refer to the numbers of individuals on 5000 cm² of the upper surface of *Platychonia magna* fronds, and 5000 cm² of under surface. r = rare; o = occasional; c = common; a = abundant.

	Under surface and cavities	Upper surface	Loose in intra reefal mud		Under surface and cavities	Upper surface	Loose in intra reefal mud
PORIFERA:				**BRACHIOPODA:**			
Platychonia magna				Micromorphic terebratellid			a
calcisponge sp. A	10		o	Micromorphic terebratulid with striations			a
calcisponge sp. B	1			*Rioultina triangularis*	up to 3/cm²		c
calcisponge sp. C	19			*Dictyothyris coarctata*			r
calcisponge sp. D	22		o	*D. coarctata*, micromorphic juveniles			a
calcisponge sp. E	8		r	*Flabellothyris flabellum*			r
calcisponge sp. F	18			*Eudesia cardium*			r
calcisponge sp. G	29			*Disculina hemispherica*			r
Blastinia ornata	37		r	*Crania ponsorti*	4		o
Enaulofungia sp. A	13			**BRYOZOA:**			
Enaulofungia sp. B	1		r	*Terebellaria ramosissima*			c
Enaulofungia sp. C	2		r	*Ripisoecia conifera*			c
Enaulofungia sp. D	16			*Mesenteripora undulata*	45		r
? *Oculospongia* sp.	21		r	*Reptomultisparsa* sp.			r
Peronidella pistilliformis	7		o	*Apsendesia cristata*	1		o
Eudea cribraria	20		c	*Entalophora annulosa*			o
Elasmostoma palmatum	1		r	*Multisparsa lamellosa*			r
Limnorea mamillosa	5		c	*Ceriocava corymbosa*			o
Corynella tuberosa			c	Unidentified 'stick bryozoan'			o
Corynella sp.	2			*Idmonea triquetra*			o
Trachyphlyctia helvelloides	1		r	*Stomatopora dichotoma*	14		
Neuropora spinosa	108		o	*Stomatopora dichotomoides*	4		
Neuropora sp., erect form	15		a	*Hyperosopora typica*	94		
				bereniciform sp. A	47		
ANTHOZOA:				bereniciform sp. B	4		
Thamnasteria sp.		1		bereniciform sp. C	9		r
				bereniciform sp. D	8		r
ANNELIDA:				bereniciform sp. E	12		
Serpula (*Tetraserpula*) *tricarinata*	r			bereniciform sp. F	26		
S. (*Cycloserpula*) *gordialis*	r			bereniciform sp. G	6		
S. (*Cycloserpula*) *filaria*	a						
S. (*Cycloserpula*) sp. A	o			**ECHINODERMATA:**			
S. (*Dorsoserpula*) sp. A			r	*Psephechinus morieri*			r
S. (*Dorsoserpula*) sp. B	c			*Gymnocidaris pustulosa*			o
Spirorbula sp.	up to 10/cm²			starfish plates			r
boring worms	0	r					
CRUSTACEA:							
acrothoracican borings	c						
BIVALVIA:							
Atreta retifera		1042	r				
Spondylus consobrinus	14						
Plicatula sp.	11		r				
Lopha costata	22		o				
Nanogyra sp.	3		r				
Chlamys (*Chl.*) *viminea*			a				
Plagiostoma sp.			c				
Trichites sp.			r				
Lithophaga sp.	c	r					

stenotopic groups thrived. The environment was much more fully marine, with less violent fluctuations in the whole suite of variable physical parameters. *Atreta*, then, may have been the stenotopic equivalent of the eurotopic ostreine oysters.

The oysters which do occur in the Saint-Aubin reefs are members of more fully marine groups (Lophinae; Exogyrinae) and are not present in large numbers. A few large *Plicatula* (probably *P. fistulosa* Morris and Lycett), and *Spondylus consobrinus* Deslongchamps (Pl. 2, fig. 11) are also found.

The most diverse encrusting group represented is the calcisponges (Pl. 2, figs. 3–6). At least twenty-two species are present, which are nearly exclusively confined to the lower surfaces of the principal frame-builder. In the past, calcisponges (and indeed most sponges) have often been described purely on grounds of their over-all shape. Thus, correct identification, for which the fine structure of their skeleton is often necessary, has been severely hampered. In the present case only those whose external features were highly characteristic could be identified with certainty. The remainder has been listed informally in order to illustrate the diversity of the group.

The majority of the calcisponges are adpressed encrusting forms (e.g. calcisponge spp. A–G, ?*Oculospongia*, *Blastinia ornata*). Among erect forms, the branching *Peronidella pistilliformis*, *Limnorea mammillosa*, and *Eudea cribraria* are relatively common. More rarely, blade-shaped forms occur such as *Trachyphlyctia helvelloides* and *Elasmostoma palmatum*. *Corynella tuberosa*, although a relatively large, knob-shaped form, had only a very small attachment area. This might be the reason why it was not found in life position, indicating some degree of disturbance of the biotope which dislocated such forms relatively easily.

The commonest encrusting sponge is *Neuropora spinosa* (Pl. 2, fig. 7), which frequently grows in clusters. Walter (1969) included *N. spinosa* (Lamouroux) amongst the Heteroporidae (Bryozoa) following Bassler (1953), on account of the fact that '*Neuropora* present des lunaria comme certains Heteroporidae . . .' (Walter 1969, p. 176). He further, however, acknowledged the considerable doubt in this assignment. Earlier, Canu (1910) had considered that some species of the genus (including those placed by Walter in synonymy with *N. spinosa*) were hydrozoans. Morphology and fine structure, however, make it more likely that *N. spinosa* is a sclerosponge. The same view has been adopted by Kaźmierczak and Hillmer (1974) for the Cretaceous *N. pustulosa* which, like the Bathonian form, possesses stellate veinules and resembles the recent sclerosponge *Ceratoporella nicholsoni* (Hartman and Goreau 1970). The *Neuropora* in the Saint-Aubin sponge reefs range in growth form from encrusting to mammillate to spinose to erect branching. All variations are found, and doubtless individual growth form was moulded by micro-environmental factors.

Next in diversity after the sponges, but more abundant in absolute numbers, are the cyclostome bryozoans (Pl. 2, figs. 8, 9, 12). Those that remain *in situ* on the sponge fronds are mainly closely adpressed stomatoporiform, prosobosciniform, and bereniciform types. The multilamellar *Mesenteripora undulata* is also found growing in dome-like colonies up to 1 cm high (Pl. 2, fig. 9). Additionally, the zoaria of several erect forms are commonly found in the intra-reefal mud. The taxonomy of the Normandy Bathonian Bryozoa has recently been considered by Walter (1969), who points out that initially encrusting (bereniciform) zoria may give rise at a later ontogenetic stage to a variety of erect forms (bilamellar fronds, tubes, or rods) thus complicating identification. For the present

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EXPLANATION OF PLATE 2

Figs. 1–7. Epifaunal species found in the intra-reefal mud within the sponge reefs at Saint-Aubin. 1, *Dictyothyris coarctata* juvenile, × 30. 2, unidentified micromorphic terebratulid, × 20. 3, *Blastinia ornata*, × 6. 4, *Eudea cribraria*, × 3. 5, *Corynella tuberosa*, × 2. 6, *Limnoria mamillosa*, × 2. 7, *Neuropora spinosa*, × 3. Figs. 8–12. Epifaunal species encrusting the undersides of *Platychonia magna* fronds. 8, bereniciform bryozoan sp. E, × 3·5. 9, *Mesenteripora undulata*, × 9. 10, *Rioultina triangularis*, × 22. 11, *Spondylus consobrinus*, × 6. 12, *Spirorbula* sp. on bereniciform bryozoan sp. E, × 16.

PLATE 2
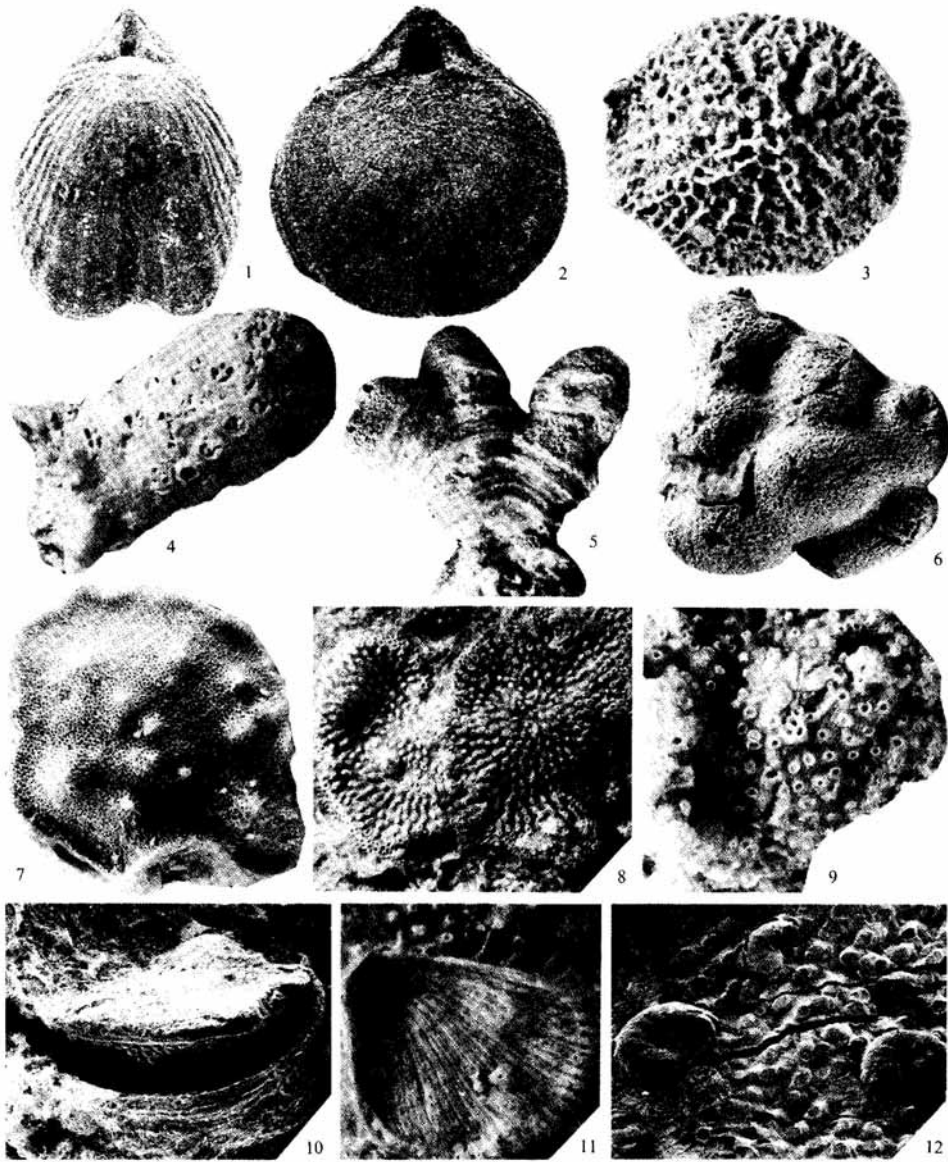
PALMER and FURSICH, Jurassic sponge reefs from Normandy

study, all bryozoan identifications have been made on the basis of external morphology, which Walter states to be very much under ecological control. However, we have found that individuals which could not immediately be fitted into one or other of our categories were virtually never encountered, and we saw no examples of adnate individuals in the process of producing erect fronds of any sort. Perhaps all the adnate forms were species which did not produce erect fronds.

The bivalves, sponges, and bryozoans were the most important contributors of additional cementing material to the original framework, but there were two additional groups represented by abundant individuals of very small size. Amongst the brachiopods are rare craniids (*Crania ponsorti*) which are occasionally seen in life position, but which are better represented by loose brachial valves in the intra-reef sediment. In contrast, the thecideacean *Rioultina triangularis* is very abundant as articulated and pedicle valves attached to *Platychonia* fronds and other shell debris (Pl. 2, fig. 10), and as disarticulated valves in the intra-reef mud.

Serpulid worms are rather less conspicuous than on other hard substrates (e.g. hardgrounds—see Palmer and Fürsich 1974) of Bathonian age. Many individuals are present, but they are dominated by a tiny *Spirorbula* sp. (Pl. 2, fig. 12), which we have not seen in the English Bathonian. Perhaps, as in the case of *Atreta* and oysters considered above, *Spirorbula* is a more stenotopic ecological equivalent of more eurytopic serpulids found in more marginal areas.

The most poorly represented encrusters are the corals. One badly preserved *Thamnasteria* was seen. However, there is no trace of many aragonite components which are known to have been present, such as the inner shell layers of the spondylid and plicatulid bivalves. The single coral thus seems to represent a preservational quirk, and encrusting corals may have been more common during life.

Nestling epibenthos

This group includes the pedically attached brachiopods and the byssate bivalves which were sessile filter-feeders during life, and which became detached from their substrates after death by decay of their organic organs of attachment (the organohesive fauna of Palmer 1979). They were collected in varying numbers by washing and sieving the intra-reef mud.

The brachiopods are dominated in numbers by myriads of micromorphic individuals which are most common in the 0·5–2·0-mm size range. Three species, all of them Terebratulida, predominate. One of them (Pl. 2, fig. 1) was identified by Eudes-Deslongchamps (1862–1886) as the juvenile form of *Dictyothyris coarctata*. The affinities of the other two species are not immediately obvious. One is a terebratellidinid, almost as wide as long, and usually rather flattened dorso-ventrally. These dimensions preclude it from being the juvenile stages of *Digonella digona*, which is over-all one of the most common Normandy brachiopods, and whose juvenile stages were discussed by Eudes-Deslongchamps (1885). It is doubtless the 'toute petite Terebratelle lissé non encore décrite' previously mentioned from the sponge reefs (Eudes-Deslongchamps 1864). It does not get much larger than the 2-mm stage. The third species (Pl. 2, fig. 2) also unrepresented by larger forms, is a terebratulidinid with light-coloured longitudinal striations in the shell, and a brachial valve that is almost circular in plan.

The abundance of the micromorphic forms should be seen in the context of the rarity of the larger forms of pedically attached brachiopod, which are so common elsewhere in the Normandy Upper Bathonian. *Eudesia cardium, Flabellothyris flabellum, Dictyothyris coarctata, Digonella digona,* and *Disculina hemispherica* occur only rarely in the reefs, and are all much more common in the inland exposures of the marls which are the lateral equivalent of the reef facies exposed on the coast. Even more striking is the apparent total absence of rhynchonellids and the species of *Avonothyris* which are very abundant in the laterally equivalent beds, as well as above and below the reef horizons. Clearly there was something about the reefs that such brachiopods did not like. Perhaps there was too much competition for food and space from the many species of encruster. Alternatively, perhaps they were easily smothered by fine sediment being stirred up during storms, and settling out in the slack water amongst the sponge fronds. Under such conditions, selection would favour opportunistic micromorphic species which spent a relatively high proportion of their

life span as larvae, and which could settle, grow, and produce the next generation between successive disturbing events. Small size may also be viewed as an adaptation to cavity dwelling.

The byssally attached bivalves are also rather poorly represented in comparison with their abundance in other Middle Jurassic epifaunal associations. *Chlamys viminea* and *Plagiostoma* sp. are the only representatives. Again, forms common in the surrounding beds (such as *Radulopecten vagans*) are absent, and the same ecological control as affected the brachiopods no doubt affected the byssate bivalves also. Possibly the two species that do occur in any abundance were able to release themselves form their byssus, move to escape encroaching sediment, and re-attach.

Certain of the byssate nestling groups common in other Middle Jurassic deposits had a shell composed entirely of aragonite (arcids) or had only a thin calcitic outer shell layer (mytilids). It cannot be ruled out that members of these groups were present, but suffered diagenetic dissolution.

Vagile epibenthos

This group may again have suffered diagenetic depletion, with the possible loss of aragonitic gastropods and chitons. Echinoderms therefore dominate, and include occasional starfish ossicles (probably *Astropecten cotteswoldiae* Wright). Much more striking are the large tests of *Gymnocidaris pustulosa* which are frequently found wedged into crevices within the reef. This is probably the species responsible for the echinoid tooth marks seen on many of the shells (Bromley 1975). Arthropods are represented by rare unidentifiable decapod claws.

Borers

Borings of worms, acrothoracic barnacles, and bivalves all occur. The first two categories are most common in shells and the calcitic encrusting material on the *Platychonia* fronds. *Lithophaga*, however, is frequently found in crypts excavated in the fronds themselves and was probably the excavater. This throws an important light on the diagenetic history of the sponges, and is mentioned again later in the text.

TROPHIC STRUCTURE OF THE REEF

The great majority of the reef species are suspension feeders which presumably subsisted on zoo- and phytoplankton, and organic detritus. One or two of the vagile forms may have been algal grazers or scavengers. There is little evidence, however, of either algae, or of an extensive fauna of algal grazers. This may be partly a result, as we have discussed, of the absence of aragonitic fossils, and thus we cannot draw conclusions about primary productivity from the absence of grazing forms such as gastropods. Similarly, the higher trophic levels (likely to have included gastropods, crustaceans, fish, and various soft-bodied invertebrates) seem to be completely absent. We would expect a community with such a high diversity at the primary consumer level to have included a variety of forms at higher trophic levels, but unfortunately the evidence is just not available.

DISTRIBUTION PATTERN OF THE EPIFAUNA ON THE PRIMARY FRAMEWORK

Even the most casual study of the faunal distribution on the primary framework reveals that it is not random. Both faunal density and diversity are considerably lower on the upper surfaces of the *Platychonia* fronds than on the lower surfaces (Table 1). On upper surfaces, only the plicatulid bivalve *Atreta retifera* occurs along with some rare borings made by worms and *Lithophaga*. In contrast, the lower surfaces are heavily encrusted by calcisponges, sclerosponges, serpulids, *Spirorbula*, the cemented brachiopods *Rioultina triangularis* and *Crania ponsorti*, the bivalves *Spondylus consobrinus*, *Plicatula*, *Lopha costata*, and *Nanogyra*, as well as by a host of adnate bryozoans. They usually form a thick biogenic layer, locally exceeding 10 mm in thickness. Boring annelids and *Lithophaga* also occur more frequently on lower than on upper surfaces. The only

occasions when members of the undersurface fauna (especially calcisponges) are found on upper surfaces appear to have been when the latter formed floors of cavities resulting from the overgrowth of the next *Platychonia* generation. As mentioned above, it is also likely that the micromorphic brachiopods lived in the cavities, their size making them suitable for this habitat.

In addition to this obvious faunal polarization some members of both the upper and the lower surface fauna are preferentially orientated with respect to the vertical position (text-fig. 3). This is particularly well displayed by *Atreta retifera* whose dorso-ventral axis usually points downslope and whose hinge line occupies a horizontal position. The thecideacean brachiopod *Rioultina triangularis* shows a similar orientation on the lower surface, its beak pointing preferredly upslope.

Less clear is the orientation pattern of *Spirorbula* sp., where the aperture of the adult frequently points in a horizontal direction. Some organisms which are too rare to be subjected to statistical treatment nevertheless exhibit preferred orientation. This is the case, for example, in *Spondylus consobrinus*, where five out of eight specimens showed an orientation like *Atreta*.

Frequently, encrusters occur in clusters of conspecific individuals, as in *Neuropora spinosa*, *Rioultina triangularis*, *Spirorbula*, *Lithophaga*, boring annelids, and *S.* (*Cycloserpula*) *filaria*. The advantages on hard substrates of such a distribution pattern have recently been discussed by Palmer and Palmer (1977).

The polarization of encrusters on large Jurassic sponges has been noted before (e.g. Fritz 1958; Hiller 1964; Gaillard 1971; Wagenplast 1972; Gaillard and Pajaud 1971; Nitzopoulos 1974; for English summary see Gwinner 1976). These authors noted that hexactinellid and lithistid sponges which build up the famous Upper Jurassic sponge reefs of Franconia, Swabia, and the Swiss and French Jura, were covered on their upper surfaces by a calcareous crust which proved to be of blue-green algal origin (stromatolites and Aphanostromata—Nitzopoulos 1974). Within this algal
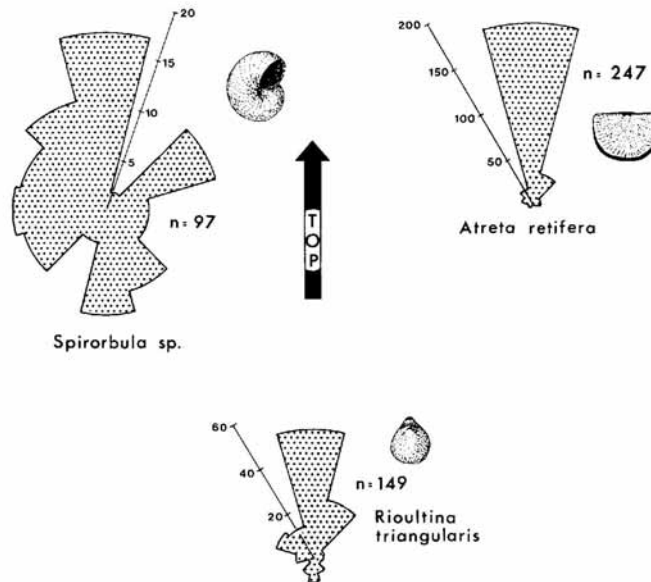
TEXT-FIG. 3. Orientation with respect to the vertical of three species of encrusting organisms on fronds of *Platychonia magna* in the sponge reefs at Saint-Aubin.

layer, encrusting foraminifera, particularly *Nubeculinella*, were frequently found. The lower surfaces of these sponges were, in turn, often densely covered by a fauna consisting of calcisponges, *Neuropora*, *Crania*, thecideid brachiopods, bivalves (particularly *Spondylus*), and serpulids, the latter furnishing the highest numbers of individuals. Most elements of the lower surface fauna were, however, not strictly confined to this habitat, but also occurred, if only rarely, on upper surfaces. The fact that dead and overturned bowl- and plate-shaped sponges showed the same faunal polarization indicates that the distribution pattern was not caused by activities of the host sponge but by environmental factors, and that the epifauna settled on the siliceous sponges only after their death (e.g. Fritz 1958; Ziegler 1964; Gaillard and Pajaud 1971). Polarization of encrusting fauna into an upper surface community and a coelobiontic community is a widespread phenomenon. It has been encountered in modern coral reefs (e.g. Garrett, Smith, Wilson, and Patriquin 1971; Jackson, Goreau, and Hartman 1971; Vasseur 1974, 1977) as well as in submarine caves of the Mediterranean (Riedl 1966), in Jurassic (Palmer and Fürsich 1974) and Ordovician hardgrounds (Brett and Liddell 1978), and on Palaeozoic corals and stromatoporoids (Spjeldnaes 1975). In all these cases differences in light intensity, turbulence, and food supply seem to have been the main abiotic factors governing the faunal distribution. In addition, biotic factors, particularly competition, may be responsible for faunal polarization, restricting some faunal elements to the seemingly less favourable cryptic habitat. It is interesting to note that the major groups of the modern cryptofauna occupied this habitat at least since the Jurassic: The dark community within Bermuda patch reefs contains, as does that of the Saint-Aubin reefs, ectoprocts, *Spondylus*, serpulids, and sponges. Recent thecideid brachiopods such as *Thecidellina* and *Lacazella* favour cryptic habitats (Hartman and Goreau 1970; Pajaud 1970; Logan 1977) as do their Jurassic relatives such as *Moorellina* and *Rioultina*. The sclerosponges are typical members of modern reef cryptofaunas (e.g. Hartman and Goreau 1970; Vacelet 1967a) as was *Neuropora spinosa* in the Jurassic. The same is true of calcisponges, common members of both Recent and ancient cryptofaunas (e.g. Vacelet 1967b; Jackson *et al.* 1971). Some faunal groups seem to have shown a preference for the cryptic habitat since Jurassic times only: sclerosponges are an abundant and diverse element of the Triassic calcisponge/coral reefs of the Cassian Formation (Dolomites, Northern Italy) where they act as subsidiary frame-builders by no means confined to cavities (Fürsich and Wendt 1977). In the same reefs, the cemented *Thecospira tyrolensis* does not live in cavities, in contrast to the related *Rioultina* and *Moorellina* with a similar over-all shape and life habit which are known since the early Jurassic.

Vacelet (1967b) interpreted a modern cryptofauna of pharetronid calcisponges as a relict fauna, whereas Hartman and Goreau (1970) regarded it as part of a widespread and diverse benthic assemblage, which is usually confined to the lower photic zone. The latter view can be confirmed in the light of the available information, especially as the typical undersurface fauna of Upper Jurassic sponge reefs, although being found mainly in this habitat, occasionally occurs on upper surfaces as well (see Wagenplast 1972, p. 50). This probably reflects the fact that those reefs grew in depths of at least 50 m and probably down to 100 m (Gwinner 1976), where the light influx and turbulence was very low. Only when extending their range into shallower and better-illuminated waters they remained confined to cavities. This seems to have been the case in the Saint-Aubin sponge reefs.

Wagenplast (1972) and Gaillard and Pajaud (1971) explain the confinement of the undersurface fauna to its habitat in terms of interspecific competition. Algal growth on the upper surface of sponges form Upper Jurassic reefs prevented any other faunal elements apart from foraminifera from settling there, thus confining them to the lower surfaces. Gaillard and Pajaud (1971) in particular argue that at the depth of growth of the Oxfordian sponge reefs from the southern French Jura (in the lower photic zone), thecideaceans should be indifferent with regard to settlement on upper or lower surfaces. The fact that even there they are restricted to lower surfaces could only be explained in terms of interspecific competition with algae which still managed to grow at those depths (as evidenced by the presence of calcareous crusts).

In the Saint-Aubin sponge reefs, there are no indications of algal growth on the upper surfaces of the sponges. Of course, they might have been present but left no trace in the fossil record. The

high density of *Atreta* on many upper surfaces, however, seems to rule out a dense algal cover. It seems more likely that, in addition to the factors mentioned already, the rate of sedimentation (e.g. in form of faecal pellets) might have forced elements of the fauna which could not cope with it to colonize the lower surfaces. This was obviously not the case with *Atreta*, whose elevated ventral margin may have helped with access to the higher parts of the water column.

Discussion of faunal orientation

The orientation which is so well displayed by several species (text-fig. 3) might also be related to sediment influx. On inclined surfaces it is advantageous for cemented bivalved animals to keep the dorso-ventral axis pointing downslope, thus preventing fine-grained sediment from entering the mantle cavity when the valves are opened and allowing easier cleaning (Surlyk and Christensen 1974). Such an orientation has been found both on upper (*Atreta*) and lower surfaces (*Rioultina*, *Spondylus*). According to the argument employed here, there should be no advantage in a preferred orientation on horizontal surfaces: significantly *Atreta* is randomly orientated where more or less horizontal plate-shaped sponges are colonized.

In the case of *Rioultina* there is an additional advantage in such an orientation. Having to dispose of waste products through the front of the commissure line (the position of the exhalant current), pseudofaeces can be prevented from re-entering the shell in the lateral inhalent currents.

The reason for the admittedly less pronounced orientation of *Spirorbula* is not clear. Serpulids are known to grow upwards (e.g. Seilacher 1960), but in the spiral *Spirorbula* the aperture changes position during growth. The preferred apertural orientation normal to the slope might be a compromise between avoiding sediment to enter the shell by turning the aperture away from the top, and achieving a favourable feeding position by turning towards the top.

CHANGE OF FAUNA AND FACIES AS A RESULT OF REEF GROWTH

One purpose of our work has been to record the change in facies, faunal composition, diversity, and abundance brought about by the growth of the sponge reefs. For this, the abundance of the fauna of the reef, the inter-reef mud, and the two main lithofacies underlying the reef (see inset in text-fig. 4) has been assessed in a semi-quantitative way distinguishing between rare, occurring, common, and abundant forms. The faunal diversity is the number of species recorded, whilst the semi-quantitative abundance data were processed in the same way as in Fürsich (1975). This involves assigning an arbitrary value of 4 to the record of any given species regarded as abundant, 3 to that of any regarded as common, 2 to that which is occasional, 1 to that which is rare, and 0 to an absentee. The total value plotted is the sum of the abundance ratings of all the species in the ecological group in question, divided by the number of species in the group (diversity). The resultant figure only has a meaning when used in comparison with another that has been obtained from comparable units used in the same way. It is designed only to give an impression of changing quality. Text-fig. 4 illustrates the change of diversity and abundance of the different ecological groups around the sponge reefs.

The frame-builder *Platychonia magna* occurs in all the four units analysed in this way, its abundance increasing from scattered individuals to the solid masses forming the reef framework. Within the inter-reef mud, too, it forms small clusters. The vast majority of individuals occur in life position. Encrusting calcisponges similarly reach their maximum diversity and abundance within the reefs, thus demonstrating their close relationship to the frame-builder. The same is true of a number of other groups such as the sclerosponges, serpulids, boring worms, boring and cemented bivalves, micromorphic and cemented brachiopods, and encrusting bryozoans. The fact that these groups occur also outside the reefs, although there in lower numbers of species and individuals, can be explained partly by the scattered occurrence of *Platychonia* in these beds providing a suitable substrate for colonization. A hardground with numerous undercuts and cavities on top of bed 2 also provided an ideal habitat for the cryptofauna otherwise restricted to the undersurfaces of *Platychonia*. More importantly, the lateral faunal differentiation between the inter-reef mud and
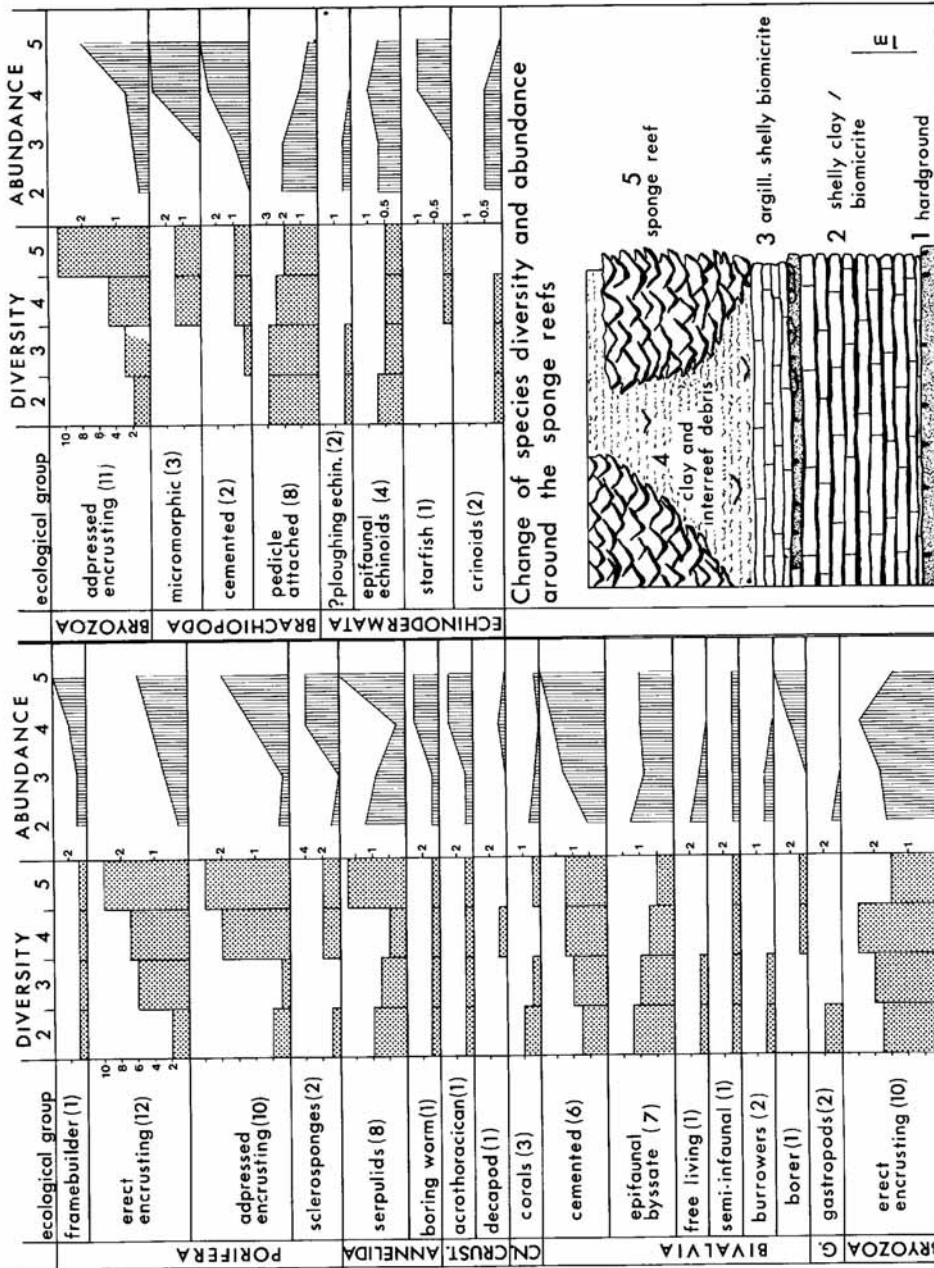
TEXT-FIG. 4. Changes in species diversity (number of species) and species abundance of the main ecological groups in all the higher taxa represen as the level of the sponge reefs is approached. For details of the method used to assess abundance, see text.

the reefs is blurred by the transport of reef elements into the neighbouring habitat. The distribution pattern of corals and gastropods has almost certainly been altered by diagenetic processes reducing their numbers due to solution of aragonitic shells followed by collapse of the moulds. The same process might explain why burrowing bivalves are so rare and why epifaunal byssate bivalves are less widespread in the reef than in the underlying beds, although the former provides the ideal habitat for a nestling epifauna.

The lack of rhynchonellids within the reef has already been commented upon. Generally, the diversity and abundance of pedically attached brachiopods—apart from the micromorphs—decreases towards the reef, which is surprising. Their distribution pattern may have been influenced by biological factors such as competition which excluded them from the reef biotope.

The abundance of encrusting serpulids, epifaunal byssate bivalves, and pedically attached brachiopods indicates that substrates below the level of the reefs were generally fairly firm. Large amounts of skeletal material and shell debris mixed with a varying degree of mud created a firm ground on which a suspension-feeding epifauna flourished. Several times, hardgrounds formed during periods of reduced sedimentation and stable bottom conditions. Occasionally the energy level increased, ripping up, for example, the hardground on top of bed 2 and reworking it into pebbles which were then heavily encrusted.

The growth of the sponge reefs finally led to a differentiation of the biotope into reef bodies, and patches of clay and inter-reef debris between them. The sponge reefs seem to have decreased the turbulence level, and finer material, particularly in the form of faecal pellets, could settle out of suspension within slack-water areas within and between the reefs. Within the inter-reef mud, erect encrusting bryozoans reach their maximum abundance and diversity. Whereas some of them might be derived from the patch reefs, the majority (above all *Entalophora annulosa*, which is very abundant whilst being rare in the reef itself) colonized this protected habitat, probably in dense meadows.

ENVIRONMENTAL CONSIDERATIONS

Evidence concerning the depth of water and the predominant current regime under which the sponge reefs grew, comes from both palaeontological and sedimentological considerations. Lithistid sponges themselves, although once considered deep-water indicators, have now long been recognized as having occupied shallow habitats. For example, a range of species, including *Platychonia*, was described by Sollas (1883) from the Inferior Oolite of Dorset. These beds are oolitic, condensed, limonite rich, with abundant algal activity and show every sign of having been deposited in thoroughly shallow-water conditions (Gatrall, Jenkyns, and Parsons 1972).

The shapes of the *Platychonia* fronds do not appear to be particularly massive, and do not suggest that they needed to withstand frequent strong wave-surge. Morphologically the bowl- and plate-shaped fronds are reminiscent of the coral growth-forms found on the fore-reef slope in Caribbean reefs, ranging in depths from about 15 to 70 m (e.g. Goreau and Hartman 1963). However, too much importance should not be attached to this similarity, since the shape of coral colonies is dictated as much by the level of incident light, as by hydraulic energy (Graus and Macintyre 1976). There is no evidence that *Platychonia* supported symbiotic zooxanthellae or was light dependent. Evidence for depth of growth from the occurrence of other algal structures, however, may be informative. It has already been stated that algal crusts of the sort found commonly in Upper Jurassic hexactinellid and lithistid reefs (e.g. Gaillard 1971) are absent. Similarly, there is no sign of crustose coralline algae which are so important in Recent coral reefs (e.g. Goreau 1963). Crustose corallines today are found in water down to depths of some 200 m (Adey and Macintyre 1973). However, absence from the Normandy reefs, and indeed their considerable rarity in Bathonian limestones of the Anglo-Paris basin generally, is certainly not due to excessive water depths. Rather it reflects the general rarity of crustose coralline rhodophytes at that time. Only the solenopores, which built massive dome-like structures in the English Bathonian, are commonly found. The rhodophyte groups which are so important today in reef-cementing niches were only

just starting their adaptive radiation in the Middle Jurassic, and did not start an explosive radiation until the Cretaceous (Wray 1971).

The absence in the Saint-Aubin reefs of the algal layers such as are found in the Upper Jurassic sponge reefs may again not mean that the water depth was too great. The crusts, produced by sediment trapping on what were probably blue-green algae, were a post-mortem phenomena (Gaillard 1971), and seem to have built up over a considerable period of time, either on the upper surfaces of specimens in life position, or on the undersides of overturned specimens. If the living fronds of the *Platychonia* at Saint-Aubin only died as they became overgrown by younger fronds, then light-dependent epibionts would have been excluded from their surfaces.

The presence of oncolites in beds laterally equivalent to the reefs, and the presence of some oncolites actually in the reef body (probably washed in from outside) suggests growth in the relatively shallow photic zone. The presence of a scleractinian coral on top of one of the sponge fronds, and the faunal polarization involving groups whose larvae are today known to be negatively phototactic supports this view.

The sedimentological evidence also points to such moderate depths. The inter-reefal sediment is locally winnowed and cross-bedded, whereas elsewhere it is predominantly a bioclastic clay. Similarly all stages of abrasion of the delicate bryozoans are present. Some have clearly been buried almost instantly, whereas others have undergone considerable taphonomic attrition. Such a state of affairs points strongly towards storm activity, in an environment which was usually quiet, but which occasionally experienced considerable current activity—i.e. below normal but above storm wave-base.

Recently, Fily and Rioult (1978) have suggested that these sponge reefs were restricted to sheltered troughs between submarine dunes at a critical point between the inner and the outer regions of the north Armorican carbonate platform. They suggested that such precise ecological requirements were rarely satisfied and that was the reason why calcisponge reefs are so rare in the fossil record. However, we have now shown that these bodies are not unique calcisponge accumulations, but lithistid bodies no more unusual than any other lithistid reef in the fossil record. Furthermore, we are not convinced that the inter-reef material represents dunes which were in existence before the reef bodies started to grow in the troughs. It is not a single cross-bedded unit as is a dune, but a complex of poorly and well-winnowed beds of highly variable grain size, only the coarser beds in which are cross-bedded. Additionally it contains large amounts of transported shells of species which are only found *in situ* in the reef bodies themselves. It seems much more likely that the sponge bodies grew upwards as sediment accumulated around them, and that the nature of this sediment was strongly influenced by the reefs themselves. Thickets of erect bryozoans locally colonized the inter-reefal areas. Periodically storm activity churned up the inter-reefal sediment and its epifauna and sometimes even caused smothering of the sponges by loose sediment. The reefs as we visualize them having looked during life are shown in text-fig. 5.

We do not envisage a widely different macro-environment for the beds beneath the reef horizon (beds 2 and 3 in text-fig. 1). Again the alternation of muddy bioclastic sediments, and more clearly winnowed, cross-bedded shell hashes is reminiscent of periodic storm activity. The discontinuous hardground at the top of bed 2, which passes into cobbles, may also have been ripped up by an episode of severe current activity before it became wholly rigid. The presence of rare *P. magna* individuals at all levels below the main reef horizon suggests that at no time during the deposition of the sequence were conditions unsuitable for sponge growth. Perhaps, then, the establishment of the large reef bodies on the top of bed 3 (text-fig. 1) was due rather to a biological event than to any significant change in the environment. Possibly the coincidence of a heavy sponge spatfall and a relatively long period of minimum current disturbance, allowed establishment of a series of rigid, slightly elevated *P.* mounds, which were able to withstand subsequent storm activity. They then began to influence the nature of sedimentation in their vicinity, both by providing bioclastic material and the baffle action which allowed it to accumulate, and to grow upwards and outwards as sediment accumulated around them.

Bathonian sponge reef communities

upper surface of Platychonia   lower surface of Platychonia
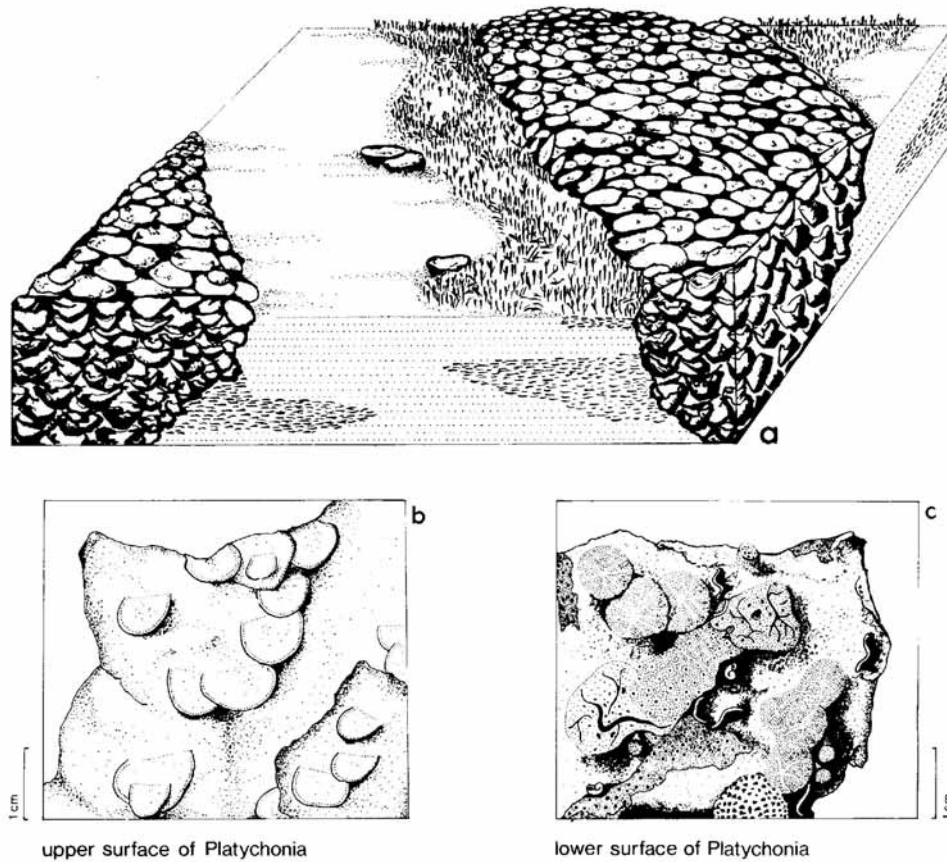
TEXT-FIG. 5. Diagrammatic block-reconstruction of the Saint-Aubin sponge reefs as they appeared during life.

DIAGENESIS OF THE REEF FRAMEWORK

The desmas of the *Platychonia* fronds, which were originally composed of opaline silica, are now shown by staining to consist of low magnesium calcite. This calcite has the form typical of void-filling cement (Pl. 1, fig. 4) and thus appears to have grown radially into voids which remained after the dissolution of the siliceous spicules. This preservation is commonly found in siliceous sponges, and where silica is present, it is mainly due to secondary silicification of the calcified sponges (Hiller 1964). The change of silica to calcite is generally thought to have taken place as early diagenetic replacement. Studying Upper Jurassic sponge reefs in Swabia, Fritz (1958), and later Hummel (1960) and Aldinger (1961) envisaged a rapid mummification of the sponge skeletons due to carbonate precipitation caused by decaying organic sponge tissue. Rauff (1893-1894) had previously

suggested that the pore space within the sponge was filled with lime mud after decay of the soft parts; then, after lithification, solution of the siliceous skeleton, followed by deposition of calcite, took place. Earlier on, Sollas (1877a, b) and Hinde (1887-1912) had noticed the replacement, without, however, speculating on the timing of this process. Rauff's view has also been adopted by Ziegler (1964) and Wagenplast (1972) who emphasized that macerated skeltons were quite stable and could, for some time, survive intact on the sea floor.

Examination of thin sections of *Platychonia* fronds from Saint-Aubin reveals that the sponge canals are filled with a peloidal micrite (Pl. 1, fig. 4). This must originally have moulded itself around the siliceous spicules, either as an early clotted micrite cement or as a passive sediment fill which subsequently became lithified. Either way, it was rigid when the siliceous sponge skeleton dissolved, as is indicated by the well-preserved, uncollapsed nature of the desma moulds which subsequently became occupied by void-filling cement. This much seems clear from the fabrics of the cements themselves.

Support for this diagenetic sequence, and information on the timing of some of its steps, are provided by examination of the borings. The *Platychonia* fronds are commonly bored by *Lithophaga*, and occasionally by worms. *Lithophaga* today is a chemical borer which uses a calcium complexing agent (Jaccarini, Bannister, and Micallef 1968). It is thus confined to calcareous substrates. Similarly, Jurassic *Lithophaga* is only found in calcareous substrates, and Jurassic worm borings have the same distribution. In the Upper Jurassic sponge literature no bivalve borings are mentioned, and an extensive search for any borings in the sponge reefs of the Franconian and Swabian Alb by one of us (F. T. F.) yielded only negative results. We infer in this case that the sileceous meshwork of the sponges was unsuitable for chemical borers, and was still present at burial. At Saint-Aubin, however, it appears that filling and hardening of the canals, and dissolution of the sponge desmas, occurred prior to boring. It was thus cemented carbonate replicas of the sponge fronds, rather than the sponges themselves, that were so attacked. Thin-section study confirms this. The borings cut sharply across the canal filling, and in many cases became filled at a later stage by the same generation of void-filling cement which filled the desma moulds. Often, individual cement crystals of this cement occupy both mould and boring. Similarly, the borings are sometimes filled by the fine silt of the intra-reefal sediment. At the sharply incised edges of such borings, this silt passes into the desma moulds which must therefore have been open voids. It therefore seems that the final cement growth within the desma moulds was the only stage in the complex diagenetic history of these sponges which occurred after burial.

COMPARISON WITH OTHER JURASSIC SPONGE REEFS

The Upper Jurassic algal/sponge reefs (Franconian and Swabian Alb, Swiss and French Jura)

In contrast to the Saint-Aubin patch reefs, these Upper Jurassic algal/sponge 'reefs' are much larger structures which attained considerable elevations on the ancient sea floor. They have been described in detail by Dorn (1932), Roll (1934), Fritz (1958), Hummel (1960), Hiller (1964), Paulsen (1964), Wagenplast (1972), Gaillard (1971), Nitzopoulos (1974), and Gwinner (1976). They consist of a number of species of hexactinellid and lithistid siliceous sponges together with a high percentage of algae (stromatolites and 'calcareous crusts') which grew preferentially on top of sponges and form the main reef builders. The sponges are bowl-, funnel-, or plate-shaped; rarely cylindrical forms occur. Although not forming a rigid framework (and therefore not reefs *sensu stricto*), most are preserved in life position. This, together with the lack of any reef debris, indicates their growth in a low energy environment below wave base. Generally they are thought to have lived between 50 and 100 m depth, possibly a bit more, i.e. very low in the photic zone. Where these algal sponge reefs are part of a shallowing sequence hexactinellids, which form the bulk of the sponges in the deeper parts, are gradually replaced by lithistids which predominate in the shallower regions (to be then replaced by corals). Even there, depth of sponge growth was considerably greater than in the Bathonian of Normandy where occasional disturbance by wave action or storms is noted.

The Upper Jurassic algal/sponge 'reefs' carry a distinct cryptofauna which does not seem, however,

to have been as strictly confined to lower surfaces as in the Bathonian reefs, probably due to the position in the low photic zone.

The so-called Lochenschichten, particularly those from the Lochengründle near Balingen (Oxfordian, Swabian Alb) resemble the Bathonian patch reefs to a greater extent. There, siliceous sponges are found within a marly sequence where they formed biostromes. Associated with the sponges is a micromorphic fauna of ammonites, belemnites, and particularly brachiopods. In addition, stick-like bryozoans are quite common and might have formed patches or meadows between the sponge beds.

The shallow-water 'sponge reefs' of the Aalenian, Bajocian, and Oxfordian of England

Sponges, usually growing in low thickets, locally form a conspicuous component of the benthic epifauna in the Inferior Oolite (Bajocian) of the Dorset coast. At Shipton Gorge near Burton Bradstock a rich fauna of calcisponges including *Peronidella, Enaulofungia, Limnorea, Oculospongia*, and *Eudea* (see Hinde 1887–1912, p. 191) is associated with corals, numerous bryozoans, echinoderms, and small brachiopods (*Crania, 'Thecidea'*) (Walford 1889). In addition, fragments of siliceous sponges occur. Most likely the calcisponges, together with the encrusting brachiopods and bryozoans, formed again a shade-loving cavity community, but no details of the faunal distribution are available from the literature. A similar sponge bed has been recorded by Wethered (1891) from the Aalenian Pea Grit (Inferior Oolite) near Cheltenham. There, calcisponges and bryozoans together with shell debris and numerous belemnites form a layer within an argillaceous bed. A different composition characterizes the autochthonous sponge bed from the Inferior Oolite at Burton Bradstock on the Dorset coast. The sponges are mainly hexactinellids and some lithistids (among them *Platychonia*), whilst calcisponges are rare (Hinde 1887–1912), although quite diverse (Richardson 1920).

The sponges in the Hambleton Oolite (Oxfordian) of the Hackness Hills, Yorkshire, occur associated with cerioid and branching corals which form small patch reefs (Wilson 1949). Calcisponges are very common and probably formed part of the cryptofauna of the reef.

CONCLUSIONS

The Upper Bathonian sponge reefs at Saint-Aubin, Normandy, are built up of the lithistid sponge *Platychonia magna* (d'Orb.), whose individuals are cemented on to each other and form a rigid structure. On this primary framework, many encrusting organisms act as subsidiary framebuilders strengthening the structure.

The organisms which colonized the primary framework after the death of the sponges show a pronounced differentiation into a low diversity upper surface community now represented by *Atreta retifera*, and a diverse cavity community consisting of crustose bryozoans, encrusting brachiopods, *Spirorbula*, serpulids, *Lopha, Plicatula*, calcisponges, and sclerosponges (text-fig. 5).

Among the encrusters *Atreta, Rioultina, Spondylus*, and *Spirorbula* show preferred orientation on inclined sponge surfaces which can be explained in terms of adaptation to life in this crowded environment.

The dissolution of silica and the lithification of sediment filling the canals within the *Platychonia* fronds was a synsedimentary event which is evidenced by the presence of chemically boring bivalves.

The growth of the sponge reefs caused a distinct differentiation of the environment, enabling erect bryozoans to form meadows on a comparatively low-energy shelly inter-reef mud (text-fig. 5). In addition, diversity and abundance of various ecological groups show a distinct change both vertically up to the reef and laterally away from it.

The Normandy sponge reefs formed in shallow, but not highly agitated waters which were periodically affected by storms. Their environment is thus comparable to that of sponge beds occurring in the Bajocian and Oxfordian of England, but different from that of the well-known Upper Jurassic algal/sponge 'reefs' of central Europe which formed at greater depth.

Reef-like structures of siliceous sponges are not confined to the lower shelf, but extend into very shallow water. This is in agreement with Wiedenmayer (1977) who described Recent shallow-water demosponges (although no lithistids) from the western Bahamas.

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