

COELOBITES AND SPATIAL REFUGES IN A LOWER CRETACEOUS COBBLE-DWELLING HARDGROUND FAUNA

by MARK A. WILSON

ABSTRACT. A diverse hardground fauna of encrusters, nestlers and borers has been found on calcareous cobbles in the Lower Cretaceous (Upper Aptian) Faringdon Sponge Gravel of south-central England. The bulk of the fauna consists of coelobites that inhabited the vacated borings of bivalves. These coelobites often clustered near the cavity openings, apparently to escape epifaunal predators and physical abrasion, and to avoid sedimentary infilling of the cavity interiors. The few encrusting species common on the outside surfaces are robust and apparently adapted to abrasion resistance. Some species, notably the serpulid *Glomerula gordialis*, had a growth strategy that exploited the advantages of cavity-dwelling as juveniles and the resources available on the outside cobble surfaces as adults. The fauna thus shows adaptations to life in cavities and to existence on a mobile hardground in a high energy environment. The increase in hardground boring in the Upper Palaeozoic and Mesozoic may have caused a general increase in hardground faunal diversity by providing more niche space for coelobites.

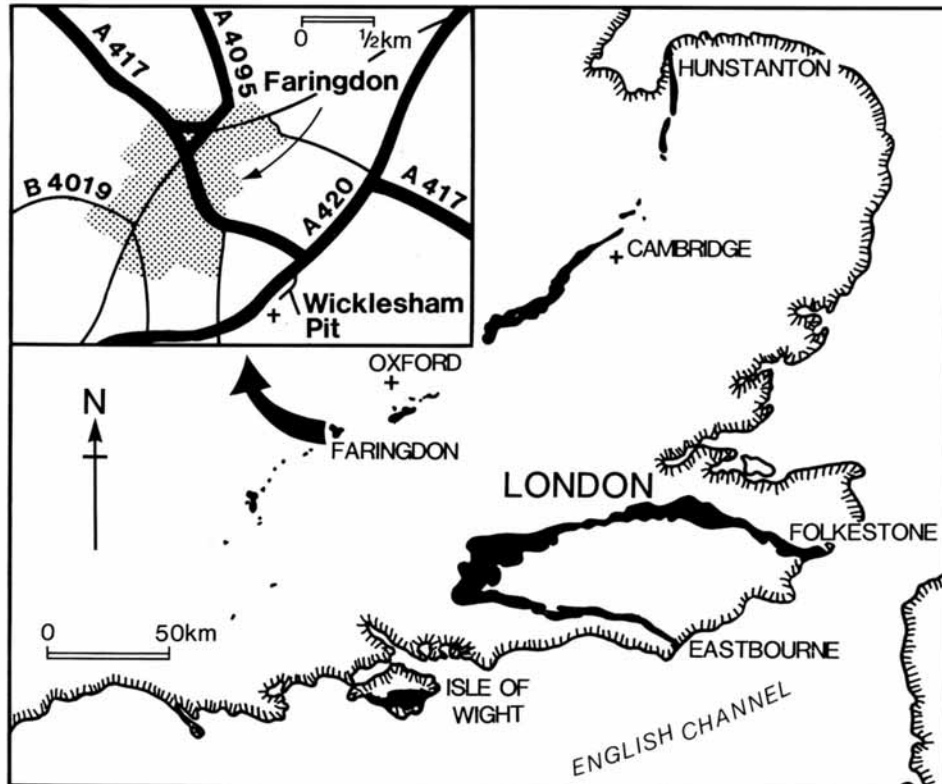
COELOBITES, or cavity-dwelling organisms (Ginsburg and Schroeder 1973), form discrete communities that first appear in Lower Cambrian rocks and are common today (Kobluk 1981a, Choi 1984). Epizoans on pebble, cobble, or boulder substrates ('mobile hardgrounds') also range from the Lower Palaeozoic (at least as early as the Ordovician) to the Recent (Wilson 1985, Osman 1977). Organisms from both types of communities usually experience high levels of competition, especially for living space. When these organisms are occasionally fossilized in life positions, they become valuable tools for reconstructing ancient ecological systems and for charting evolution in well-defined niches.

An extraordinarily diverse fauna of encrusting, nestling and boring invertebrates has been found preserved on and in heavily bored calcareous claystone and siltstone cobbles from the Faringdon Sponge Gravels (Lower Greensand; Lower Cretaceous) at Faringdon, England. The fossils are in life positions within the cavities and on the outer cobble surfaces, and so show adaptations spanning the coelobite and mobile hardground niches. Broadly, the cavities were spatial refuges from the physical and biological rigours inherent in living on a cobble in a highly disturbed gravel environment.

LOCALITY AND STRATIGRAPHY

The fossiliferous cobbles were collected from the 'Red Gravel' of the Faringdon Sponge Gravel in an interval between 5.5 and 8.5 metres above the disconformable contact with Oxfordian limestones of the Corallian Group, in the Wicklesham gravel pit at the south-east edge of Faringdon, Oxfordshire, England (national grid reference SU 293943; lat. 51° 41' 20" N, long. 1° 34' 45" W; text-fig. 1).

Faringdon fossils have attracted scientific attention for centuries. The first published reference to them is found in the museum catalogue by Lhwyd (1699). Mantell (1838, 1844) discussed the fossils in some detail, but it was Austen (1850) who produced the first comprehensive study of the Faringdon Sponge Gravel. He (Austen 1850, p. 459) was also the first to note the bored cobbles, referring to them as '... fragments of secondary calcareous rocks, much eaten out by perforating animals'. Meyer (1864) established the internal stratigraphy of the Sponge Gravel, naming the lowermost unit the 'Yellow gravel' and the overlying ferruginous sediments (where the fossiliferous cobbles used in this study are found) the 'Red gravel'. Melville



TEXT-FIG. 1. Location of the Wicklesham Pit, Faringdon, where the fossiliferous cobbles were collected. The solid pattern is the outcrop of the Lower Greensand in southeastern England (after Casey 1961).

(1941, p. 11) proposed using the term 'Sponge Gravel' for both the Yellow and Red gravels. This usage has been followed by all subsequent authors.

The Faringdon Sponge Gravel is placed in the *Parahoplites nutfieldensis* Zone of the Upper Aptian (Casey 1961).

PALAEOENVIRONMENT

The fossil-bearing cobbles are scattered throughout the top three metres of the gravels. They are interspersed with sand and gravel and are not confined to discrete layers. They also do not show any preferential orientation. The cobbles are spherical to oblate and range in size from 2 to 10 cm in the longest dimension, with the most common size at approximately 8 cm. They are composed of fine-grained sediments ranging from calcareous clay to coarse silt in a calcareous matrix, with a few specimens of oolitic limestone. All of the studied cobbles have a carbonate content of at least 40% by weight. The presence of encrusting organisms and borings on all surfaces, and the occurrence of exterior encrusters that were abraded and then regenerated or had their space reoccupied, shows that these cobbles were rolled (and subjected to abrasion) during inhabitation.

In addition, there are a variety of encrusted cobbles composed of either quartzite or rhyolite, although the latter is rare. There are also bored and encrusted phosphatic fragments of reworked Jurassic ammonites. Only the calcareous cobbles are considered in this study because they have an approximately constant composition and are consistently bored.

One calcareous claystone cobble contained within its matrix the ammonite *Prorاسenia bowerbanki* (kindly identified by H. G. Owen). This indicates that at least some of the cobbles were derived from the lower Kimmeridge Clay or Upper Oxfordian clays and siltstones, which had long been suspected (Arkell 1947).

In the most thorough palaeoenvironmental analysis of the Faringdon Sponge Gravel, Krantz (1972) concluded that these sediments were deposited in narrow channels during an Early Cretaceous transgression. The gravel was continually reworked in its upper layers, probably by tidal currents. Bridges (1982) presents a palaeogeographic reconstruction of southeastern England during the late Upper Aptian showing the probable sediment sources for the Faringdon Sponge Gravel and related units.

METHODS

Three hundred cobbles were collected from the top three metres of the Faringdon Sponge Gravel. Some were removed from the gravel pit wall, but most were collected loose on a shelf below the interval excavated by quarrymen. One hundred cobbles were randomly selected and washed with water and detergent to loosen the sand and gravel filling the borings. Each cobble in this collection was then carefully broken apart and the identity and location of the encrusting species recorded. Location on the cobble was listed as one of four areas: (1) outer surface, (2) interior surface within 2 mm of the boring opening, (3) interior surface deeper than 2 mm from the boring opening, and (4) inside-to-outside, for those forms that grew from within a boring onto the outside surface. Because of the probable loss of encrusting specimens during the breaking process, only the presence, and not the numerical density, of a species could be recorded from each cobble. Nestling species were recorded only if their shells were trapped within a boring in such a way that they could not have been washed in.

The remaining 200 cobbles were washed and broken apart in the same manner as the first 100, but only to search for rare species that may not have been recorded in the numerical census.

Representative specimens of the bryozoans are deposited in the British Museum (Natural History) collections (BMNH D55420-38), as are the nestling bivalves (BMNH LL31824-31) and the foraminiferans (BMNH P51734-9). Samples of the cobbles and the remaining species are deposited in the Oxford University Museum (OUMK 37751-93).

RESULTS

From the entire collection of 300 cobbles, 37 encrusting, 5 nestling and 1 boring species were recorded, along with 8 ichnospecies (Table 1). Table 1 also contains the results of the census of the random sample of 100 cobbles. It should be noted that the results in Table 1 are for statistical comparison only. Some species that in this study were 'entirely inside' are found on the exteriors of some cobbles housed in the British Museum (Natural History). Table 2 is derived from Table 1 and shows the ranked percentage of the encrusting species recorded inside the borings, excluding those species found on less than 5% of the cobbles.

THE FAUNA

Ichnofossils. The most common ichnofossils, homes for most of the encrusters, are the clavate *Gastrochaenolites* borings recently described by Kelly and Bromley (1984). Over 90% of these borings are referred to *G. lapidicus* (Pl. 53, fig. 4). A few *G. lapidicus* specimens still possess a calcareous lining, and fewer still contain poorly preserved bivalves of the Subfamily Lithophaginae.

TABLE 1. Species recorded from the calcareous claystone cobbles of the Faringdon Sponge Gravel. See text for complete descriptions. The statistical columns contain the results of the detailed census of 100 cobbles. The numbers represent the percentage of cobbles in or on which the particular species was found. Those specimens recorded 'near opening' were within 2 mm of the outer lip of a boring. Those listed as 'inside to outside' extended from a boring onto the outer cobble surface.

Cobble-Dwelling Species	Life Habit	Exterior		Interior		Inside to Outside	
		Near Opening	Deep Inside	Near Opening	Deep Inside	Near Opening	Deep Inside
FORAMINIFERA:							
Family Placopsilinidae, sp. A	Encrusting, agglutinated	2	22				
<i>Acruliammina</i> sp. A	Encrusting, agglutinated						
<i>Belloidina</i> cf. <i>B. vincentownensis</i> Hofker	Encrusting, agglutinated						
<i>Bullopore</i> sp. A	Encrusting, calcareous	8					
<i>Nubeculinella</i> cf. <i>N. bigoti</i> Cushman	Encrusting, calcareous						
PORIFERA:							
<i>Neuropora hemispherica</i> Canu & Bassler	Encrusting, lamellar	14		1			
<i>Barroisia anastomosans</i> (Mantell)	Erect, encrusting base			2		1	
<i>Corynella foraminosa</i> (Goldfuss)	Erect, encrusting base	2		7			
BRYOZOA:							
<i>Stomatopora calypso</i> (d'Orbigny)	Encrusting, runner-type			1		6	
<i>Stomatopora</i> sp. A	Encrusting, runner-type	7		26		32	2
S. sp. B	Encrusting, runner-type					1	
S. sp. C	Encrusting, runner-type					1	
<i>Proboscina</i> <i>coarctata</i> Canu & Bassler	Encrusting, runner-type			7		15	1
<i>P. cornucopia</i> (d'Orbigny)	Encrusting, ribbon-type	4					
<i>P. parvula</i> Canu & Bassler	Encrusting, ribbon-type						
<i>P.</i> sp. A	Encrusting, ribbon-type						
<i>P.</i> sp. B	Encrusting, ribbon-type	3		1		10	
<i>Berenicea grandipora</i> Canu & Bassler	Encrusting, ribbon-type			3		11	
<i>B. orbijera</i> (Canu & Bassler)	Encrusting, sheet-like	3		4			
<i>B. spissa</i> (Gregory)	Encrusting, sheet-like	13		23		17	3
<i>B. haimi</i> (sensu Gregory 1899)	Encrusting, sheet-like					1	
<i>B.</i> sp. A	Encrusting, sheet-like	3		2		2	
	Encrusting, sheet-like	1		2		2	

<i>Ceripora collis</i> (d'Orbigny)					
<i>Multirescis mammilosa</i> Canu & Bassler					
<i>Discosparsa fecunda</i> (Vine)					
<i>Tholopora virgulosa</i> Gregory					
<i>Idmonea denticulata</i> (Canu & Bassler)					
<i>Reptoclausa hagenowi</i> (Sharpe)					
<i>Semimulticaeva</i> sp. A					
' <i>Meliceritites semiclausa</i> ' Gregory					
<i>Meliceritites haimana</i> d'Orbigny					
ANNELIDA:					
<i>Fluctularia sharpei</i> Ware					
<i>Proliserpula faringdonensis</i> Ware					
<i>Propomatoceros gracilis</i> Ware					
<i>Glomerula gordialis</i> (Schlotheim)					
BIVALVIA:					
Subfamily Mytilinae, sp. A					
Subfamily Lithophaginae, sp. A					
<i>Exogyra</i> sp.					
<i>Lopha diluviana</i> (Linné)					
BRACHIOPODA:					
<i>Cyclothyris depressa</i> (J. de C. Sowerby)					
<i>C. lepidia</i> Owen					
<i>Gemmarcula aurea</i> Elliott					
<i>Praelongithyris praelongiforma</i> Middlemiss					
ICHTHOFOSSILS:					
<i>Macandropolydora sulcans</i> Voigt					
<i>Gastrochaenolites lapidicus</i> Kelly & Bromley					
<i>G. clunifomis</i> Kelly & Bromley					
<i>G. turbinatus</i> Kelly & Bromley					
Sponge Boring A					
Sponge Boring B					
<i>Trypanites</i> sp. A					
<i>Trypanites</i> sp. B					
Encrusting, mound-like	10	3	1		
Encrusting, mound-like	6	11	1		
Encrusting, mound-like	2	2	1		
Encrusting, ribbon-type	15	1	1		
Encrusting, sheet-like		1			
Encrusting, mound-like					
Erect, encrusting base					
Erect, encrusting base					
Encrusting	2	4	1	2	
Encrusting					
Encrusting	5	4	4	4	
Encrusting, partly erect		19	23	25	
Nestling					
Boring					
Encrusting	6	3			
Encrusting					
Nestling					
Nestling					
Nestling					

TABLE 2. Percentage of encrusting species found inside the borings (excluding those species found in less than 5% of the cobbles). Based on the data from Table 2.

Placopsilinid sp. A	100%	
<i>Bullopore</i> sp. A	100%	
' <i>Stomatopora calypso</i> '	100%	Entirely inside
' <i>Proboscina</i> ' sp. B	100%	
<i>Glomerula gordialis</i>	100%	
<i>Stomatopora</i> sp. A	90%	
' <i>Proboscina</i> ' <i>coarctata</i>	85%	
' <i>Proboscina</i> ' sp. A	79%	
<i>Corynella foraminosa</i>	78%	Usually inside
<i>Flucticularia sharpei</i>	78%	
' <i>Berenicea</i> ' <i>orbifera</i>	77%	
<i>Propomatoceros gracilis</i>	71%	
<i>Tholopora virgulosa</i>	67%	
<i>Exogyra</i> sp.	33%	
<i>Discosparsa fecunda</i>	29%	Usually outside
<i>Reptoclusa hagenowi</i>	12%	
<i>Neuropora hemispherica</i>	7%	

These were apparently the original borers. Sponge borings A and B are shallow systems of ramifying tubes, possibly produced by the holdfasts of larger poriferans (Pl. 53, fig. 7). *Trypanites* sp. A is a relatively straight, cylindrical tube with a diameter of approximately 3 mm. *Trypanites* sp. B is a curved cylindrical tube, approximately 5 mm. in diameter, with an expanded chamber at its terminus (Pl. 53, fig. 6). *Maeandropolydora sulcans* Voigt, a wandering cylindrical tube between 1 and 2 mm. in diameter (Pl. 53, fig. 2), was recently redescribed by Bromley and d'Alessandro (1983).

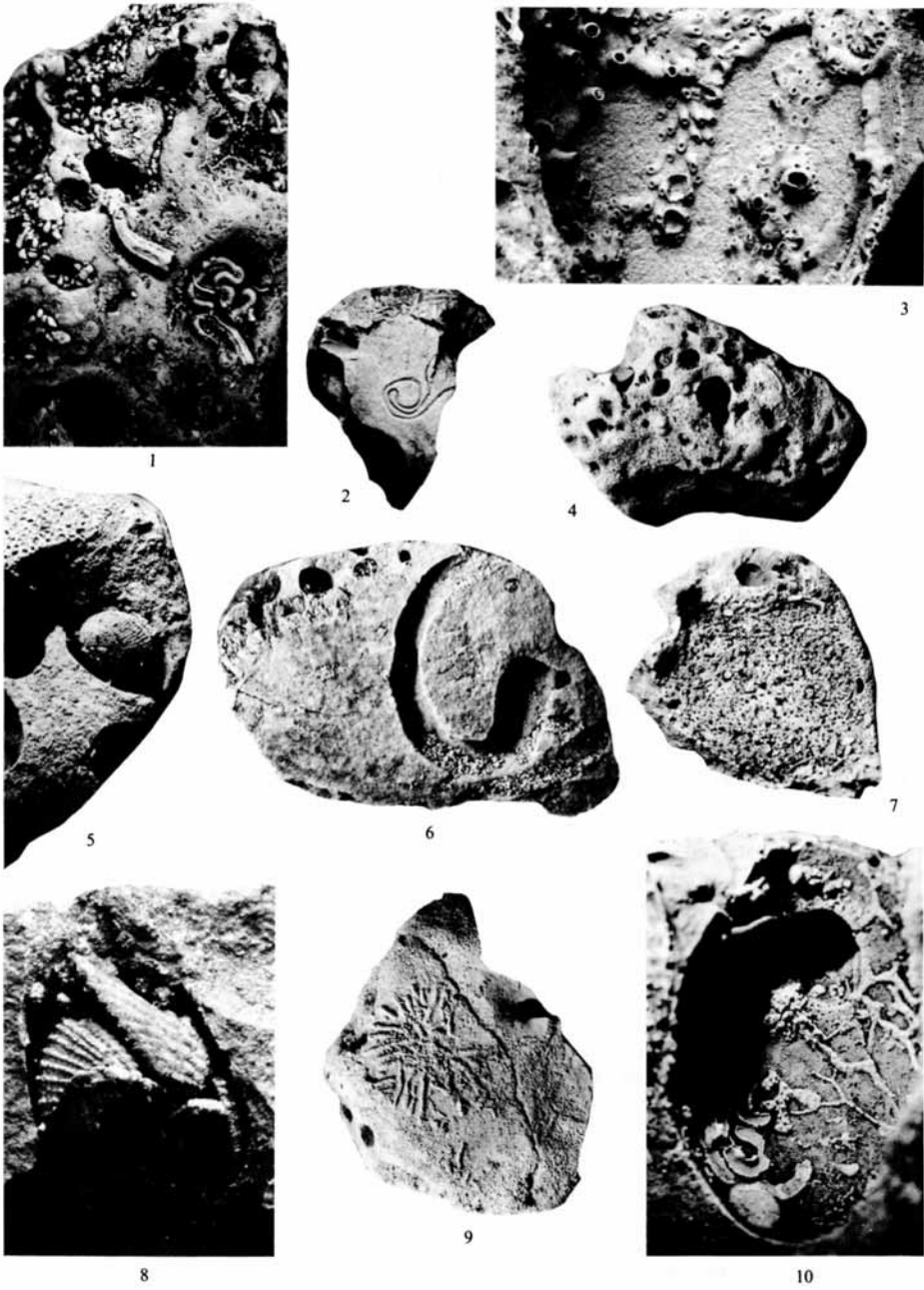
Foraminiferida. One new genus and three new species of adherent foraminiferans from this fauna are described in Wilson (1986).

Porifera. *Neuropora hemispherica* (a sclerosponge; see Kazmierczak and Hillmer 1974) is the most common poriferan. *Barroisia anastomosans* and *Corynella foraminosa* are found as juveniles.

Bryozoa. All of the lettered species in Table 1 are new and will be described in a taxonomic paper on the Faringdon bryozoans by L. J. Pitt and P. D. Taylor. Those taxa in quotation marks are species noted by Canu and Bassler (1926); their correct classification has not yet been determined. The bryozoan life-habits are taken from the colony shapes discussed by Taylor (1984).

EXPLANATION OF PLATE 53

Figs. 1-10. Fauna on cobbles in the Faringdon Sponge Gravel. 1, *Flucticularia sharpei* Ware extending from within a boring (*Gastrochaenolites lapidicus* Kelly and Bromley) to the cobble surface (centre), *Glomerula gordialis* (Schlotheim), and another *F. sharpei* within a boring (lower right), OUM K.37753, $\times 1$. 2, *Maeandropolydora sulcans* Voigt boring, OUMK 37751, $\times 0.7$. 3, *Stomatopora* sp. A (left) and '*Proboscina*' sp. B within a *G. lapidicus* boring, BMNH D55422, $\times 15$. 4, Complete cobble with *G. lapidicus* borings, OUMK 37757, $\times 0.6$. 5, *Cylothyrus lepida* Owen nestling within a *G. lapidicus* boring, OUMK 37752, $\times 2$. 6, *Trypanites* sp. B in a broken cobble, OUMK 37756, $\times 1$. 7, Sponge boring A, OUMK 37755, $\times 1$. 8, Bivalve of the Subfamily Mytilinae (sp. A) nestling between the valves of another mytilinan within a *G. lapidicus* boring, BMNH LL31824, $\times 8$. 9, *Reptoclusa hagenowi* (Sharpe) encrusting the exterior of a cobble, BMNH D55420, $\times 0.8$. 10, *G. lapidicus* boring interior with '*Proboscina*' sp. B (centre), *Glomerula gordialis* (lower left), and *Stomatopora* sp. A (upper right), BMNH D55421, $\times 2$.



WILSON, Lower Cretaceous cobble-dwelling fauna

Annelida. The serpulid tubes are classified according to the scheme proposed by Ware (1975).

Bivalvia. The most common nestler is a small, well-ornamented mytilid that apparently fits no described genus (Pl. 53, fig. 8). Hölder (1972) found similar bivalves nestling in borings excavated in Jurassic belemnite rostra. A few rare specimens of a smooth-shelled boring bivalve were found *in situ*, but their poor preservation precluded generic identification. The attachment scars of *Exogyra* and *Lopha* are common on the cobble outer surfaces, as would be expected, but some whole shells were also found attached to the interiors of the borings.

Brachiopoda. Nestling brachiopods are common in the borings, but they are difficult to extricate as whole shells. The rhynchonellid *Cyclothyris* (Pl. 53, fig. 5) is the most abundant, followed by the terebratulids *Gemmarcula* and *Praelongithyris*.

FACTORS CONTROLLING THE DISTRIBUTION OF COELOBITE AND COBBLE-DWELLING FAUNA

Modern coelobites

Marine coelobite faunas in the Recent are physically controlled by relative levels of light and food. Garrett *et al.* (1971, p. 657) recognized three cavity-dwelling assemblages controlled by light availability. The 'open', 'gloomy', and 'dark' communities show the expected decrease in algal abundance with decreasing light, but they also show concurrent increases in bryozoan and encrusting foraminiferan abundance. The bryozoans and foraminiferans may be benefiting from the lower level of space competition with algae in the darker cavity recesses.

Food resources are a function of the size of the cavity and the number and type of openings into it. A large cavity will contain a relatively large amount of suspended food. Small cavities contain smaller amounts of food and thus the 'Konsumationszeit' (the time in which the fauna filters the water content of a cavity; Reidl 1966) is shorter in smaller cavities. The larger and more numerous the connections between the cavity and the open water, the more quickly these food resources can be replaced. Reidl (1966) showed that modern cavity-dwellers are often distributed with the passive filter-feeders clustered near cavity openings and the active (and more efficient) filter-feeders in the recesses where the water is less turbulent and partially depleted of its original food content.

Interspecific competition is a well-known phenomenon in modern coelobite faunas. Jackson (1977), Choi (1984) and others have shown that in general, solitary encrusters are usually the pioneers on a new substrate, but they are later outcompeted for living space by colonial organisms. Predation, while not rare, is uncommon in coelobite faunas (Jackson 1977).

Fossil coelobites

Fossil cavity-dwelling assemblages show evidence that food and light availability were also basic controls of their distribution. The known record of Palaeozoic coelobite faunas was summarized by Kobluk (1981a), and the most diverse Mesozoic coelobite fauna was described by Palmer and Fürsich (1974). Although there appears to be no evidence of algal growth, Palmer and Fürsich (1974) proposed that the serpulids and bryozoans in their Jurassic crevice-dwelling fauna were abundant because low levels of light excluded algae. They also showed a zonation in which active filter-feeders dominated the crevice roof fauna, which would have had the lowest ambient levels of suspended food.

An additional physical factor that limits fossil coelobite faunas is the sedimentary infilling of the cavities (Kobluk 1981a, 1985). The influx of sediment would kill the encrusting organisms by either burying them or restricting the flow of water in the cavities.

The biological factors that controlled fossil coelobite faunas have been difficult to demonstrate. Direct evidence of interspecific competition among these organisms has not been shown. Hölder (1972), Palmer and Fürsich (1974), Kobluk and James (1979), and Kobluk (1985) have shown some

indistinct successions in fossil coelobite faunas that can be alternatively interpreted as overgrowth patterns resulting from interspecific competition.

Modern cobble-dwellers

Recent marine epifaunal cobble-dwelling communities are primarily controlled by physical disturbance. Osman (1977) showed that the encrusting organisms are continually subject to local catastrophes when the cobble is overturned or abraded. This high level of disturbance produces diverse communities in which the top competitors for space are prevented from occupying the entire surface of the substrate.

When disturbance frequencies are low, modern epifaunal cobble-dwelling faunas experience the same high levels of interspecific competition as the coelobite faunas, with the same resulting pattern of colonial dominance over solitary forms. The competition on these open substrates, though, may be lessened by predation, which may act as a 'biological disturbance' to reduce the abundance of the top space competitor (Paine 1974).

Fossil cobble-dwellers

Wilson (1985) showed that an epifaunal bryozoan, edrioasteroid, and crinoid community inhabiting Ordovician cobbles was subjected to the same physical disturbances and levels of interspecific competition noted by workers in the Recent. The resulting pattern of high diversity on disturbed substrates was in agreement with the conclusions of Osman (1977) and the dominance of colonial organisms over solitary on undisturbed cobbles matched Jackson's (1977) interpretations.

FACTORS CONTROLLING THE DISTRIBUTION OF THE FARINGDON FAUNA

The cobbles of the Faringdon Sponge Gravel provided two major habitats: the exterior surfaces and the interiors of the borings (text-fig. 2). The cobble fauna was thus controlled by a combination of physical and biological factors associated with cavity-dwelling and epifaunal encrustation.

Exterior encrusters

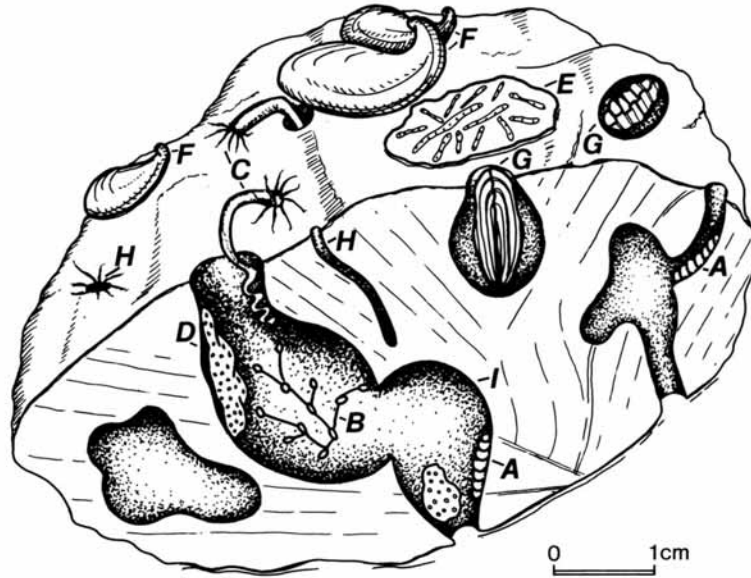
Those forms usually found on the exterior surfaces of the Faringdon cobbles are characteristically robust, heavy-shelled species (Table 2). The two most common exterior species, the bryozoan *Reptoclausa hagenowi* (Pl. 53, fig. 9) and the sclerosponge *Neuropora hemispherica*, produce low sheet-like colonies with large areas of attachment and no erect or protruding branches. *R. hagenowi* has an especially interesting morphology that combines concentrated zooids on radiating ridges with a large attachment surface. This form may have been advantageous in the high-energy gravel environment, since most of the zooids on ridge flanks would have been protected by ridge crests from direct impacts when the cobbles were rolled, and the sheet-like colony base would form a strong attachment surface.

There is undoubtedly some preservational bias behind the distribution of exterior species because robust fossils will survive the abrasive conditions longer than the more delicate forms. Abraded specimens are indeed common, but so are unworn encrusters. If other species had frequently inhabited the outside surfaces, more of their fossils would be expected to have survived post-mortem abrasion.

Interior encrusters (coelobites)

Every species in this fauna was found at least once on the inside of a boring, and most were found there predominantly (Table 2). Those encrusters that always occurred inside, including the juvenile stages of *Glomerula gordialis*, are characterized by relatively fragile skeletons and comparatively weak attachments. The bryozoans in this 'entirely inside' group do not include any sheet-like forms, but several runner-like and ribbon-like species are present (Pl. 53, figs. 3, 10).

Most of the interiors of borings were probably provided with through-flowing water currents



TEXT-FIG. 2. Reconstruction of the cobble-dwelling community at Faringdon. A, encrusting foraminiferan; B, *Stomatopora* (bryozoan); C, *Glomerula gordialis* (serpulid); D, '*Berenicea*' (bryozoan); E, *Reptoclausa hagenowi* (bryozoan); F, *Exogyra* (oyster); G, nestling mytilid (bivalve); H, *Trypanites* sp. A (ichnofossil); I, *Gastrochaenolites lapidicus* (ichnofossil).

because of the overlapping and interconnected cavities. Food resources would have thus been nearly as high inside the borings as in the outside water, although they may have been somewhat reduced by the higher concentration of filter-feeders.

The coelobites would have been limited by light availability and sediment influx. The deep interiors of the borings would have only received light reflected down the passageways, and so would be classified as 'gloomy' in the modern work of Garrett *et al.* (1971). Sediment infilling of the cavities, though, would have been a far greater limitation. All of the borings eventually filled with sand, and this was undoubtedly the factor that killed most of the preserved specimens. Siliciclastic sediment frequently entered the cavities during the period of inhabitation as shown by the number of encrusters overgrowing geopetal accumulations of sand and gravel.

There is little direct evidence of space competition preserved in the Faringdon fauna. Only twenty-six encounters between species (where one is superimposed on another) were recorded in the entire collection of 300 cobbles. In none of these encounters was there morphologic evidence of interference competition. There was also no consistent pattern in these overgrowths. However, these cobbles were certainly colonized by soft-bodied organisms that left no record. Tunicates and sponges, for example, routinely outcompete bryozoans and serpulids for living space on modern substrates (Jackson 1977; Osman 1977; Choi 1984). Interspecific competition was probably an important factor on the Faringdon cobble surfaces and within the borings, but its scale cannot even be estimated (see Rasmussen and Brett 1985).

The Faringdon coelobites could have thus exploited the bivalve borings as spatial refuges from the abrasive conditions in the high-energy gravel, and as probable refuges from predation and

competition on the exterior surfaces. The limitations of this coelobite life habit were reduced levels of food and light and the dangers of sedimentary infilling.

There were two methods by which the coelobites mitigated the limitations of cavity-dwelling. By living near the cavity openings (Table 1), some organisms retained the refuge from predators and abrasion, yet had greater resources of light and food-bearing currents than those forms deep in the borings. They would also survive the sedimentary infilling process considerably longer. Most of the coelobites in this study were found near the cavity openings, with the notable exceptions of species of the bryozoan '*Proboscina*' and the agglutinated foraminiferan placopsilinid sp. A.

A second method of escaping the limitations of coelobitic life was to live on both the interior and the exterior (Pl. 53, fig. 1). The convoluted shell of the serpulid *G. gordialis* is very commonly found starting as a contorted, thin-shelled tube inside a boring, and then growing out of the cavity onto the external cobble surface as a fairly robust, thick tube. This could be either a growth strategy adapted to the physical and biological rigours of epifaunal cobble-dwelling or a method of escaping progressive sedimentary infilling of the boring. The serpulids may have originally settled in this orientation to take full advantage of the food-bearing water currents, in a similar fashion to the cornulitids discussed by Schumann (1967). Occasionally other encrusters also show this inside-to-outside growth pattern, although at such a low frequency that it was probably due to luck rather than design.

IMPLICATIONS FOR HARDGROUND DIVERSITY THROUGH TIME

Mesozoic coelobite fauna have been shown to be more diverse than their Palaeozoic counterparts (Palmer 1982), although later work has narrowed that difference (Kobluk 1980, 1981a, 1981b, 1981c, 1985). With the exception of the work by Hölder (1972) and a brief mention by Voigt (1973), previous analyses of fossil coelobites have not considered the fauna within borings. It has been demonstrated in this study and in work on modern communities (R. C. Evans (1949), J. W. Evans (1967), and Warne (1970)) that vacant bivalve borings can be important niches for encrusting organisms. Since hardground boring increased dramatically in the Upper Palaeozoic and Mesozoic (Palmer 1982) as part of the general trend of bivalve infaunalization (Stanley 1977), we can predict that hardground diversity (including coelobites) will show a parallel increase. The comparatively high diversity of the Cretaceous cobble-dwelling hardground fauna from Faringdon clearly results from the availability of empty borings as a habitat for encrusting species. This evidence supports the hypothesis that higher frequency of boring was a contributing factor to the increase in hardground diversity.

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MARK A. WILSON
Department of Geology
The College of Wooster
Wooster, Ohio 44691
USA