

PALAEOECOLOGY OF HARD SUBSTRATE FAUNAS FROM THE CRETACEOUS QAHLAH FORMATION OF THE OMAN MOUNTAINS

by MARK A. WILSON *and* PAUL D. TAYLOR

ABSTRACT. Skeletal encrusters and carbonate hardgrounds are rare in siliciclastic sands and gravels because of high levels of abrasion and sediment movement. An exception to this is the Maastrichtian Qahlah Formation of the Oman Mountains, a sequence of coarse siliciclastic sediments deposited on a shallow marine shelf above wavebase and at an equatorial palaeolatitude. This unit contains intercalated carbonate hardgrounds and other hard substrates which were encrusted and bored. The hard substrates, comprising carbonate and silicate clasts, calcareous bioclasts (mollusc shells and coral fragments) and wood, supported a diverse encrusting and boring fauna dominated in biomass by the oyster *Acutostrea*. There are twelve bryozoan species and at least two serpulid worm species, most living cryptically. Other encrusters on exposed surfaces include the agglutinated foraminiferan *Placopsilina* and several species of colonial corals. Borings in the carbonate clasts and shells are predominantly those of bivalves (*Gastrochaenolites*), with subsidiary clionid sponge (*Entobia*) and acrothoracican barnacle (*Rogerella*) borings. The woodgrounds are thoroughly bored by teredinid bivalves (*Teredolites*). Of the common substrate types, carbonate hardground clasts support the greatest number of taxa, followed by chert clasts, with limestone rockground pebbles being depauperate. Clast composition and relative stability probably explain these differences. Individual clasts probably had variable and typically long colonisation histories. Detailed palaeoecological interpretation is constrained by taphonomic loss, time-averaging and clast transportation and reorientation. Evidence from the Qahlah Formation shows that tropical rocky-shore biotas in the Cretaceous were not impoverished as previously believed.

KEY WORDS: Cretaceous, encrusters, borings, palaeoecology, rocky-shore, Arabia.

SKELETAL encrusters are usually uncommon in high-energy marine environments characterised by coarse siliciclastic sedimentation (Daly and Mathieson 1977). Physical abrasion by silicate grains quickly destroys calcareous skeletons through scouring and rolling. Encrusters in these environments tend to be either cryptic, inhabiting recesses such as vacated borings or undersurfaces, or have especially robust and resistant skeletons (Wilson 1987). The Qahlah Formation of the Oman Mountains provides an exception. This Maastrichtian deposit contains thick beds of gravel with, at one locality in particular, several different types of clasts, ranging from wood to chert cobbles, limestone rockground pebbles, carbonate hardgrounds and calcareous shells, which host a surprising variety and abundance of skeletal encrusters and endoliths.

Two other unusual features make the Qahlah hard substratum biotas particularly worthy of study. The first is the presence in this dominantly siliciclastic sequence of intercalated carbonate hardgrounds colonised by encrusting and boring organisms. Such hardgrounds are normally associated with subtidal limestones, not siliciclastic sands and gravels (Wilson and Palmer 1992). Secondly, the Qahlah was deposited close to the palaeoequator, thereby providing a rare glimpse of a tropical, Cretaceous rocky-shore community (*sensu* Johnson 1988) and permitting comparisons to be made with higher latitude communities described from elsewhere in the world (Surlyk and Christensen 1974; Wilson 1986; Bryan 1992; Zít and Nekvasilová 1996; Johnson and Baarli 1999).

Palaeoecological studies of hard substrates benefit from the fact that colonisers of individual substrates retain their original spatial relationships to the substrate and to one another, opening the way for analyses of, for example, oriented growth, microhabitat selection and competitive overgrowth. Nevertheless, interpretation of the dynamics of the original living community is hampered by severe limitations. In most

cases it is impossible to know if specific encrusters were contemporary. Time-averaging of hard substratum assemblages operates at two hierarchical levels: the borers and encrusters visible on individual clasts can be time-averaged, but additional between-clast time-averaging is inevitable. Selective preservation is also a major problem, not only because soft-bodied organisms are rarely present as fossils (even bioimmuration will not preserve flaccid components of encrusting biotas), but also because some substrates are more stable than others. (In the case of the Qahlah, igneous clasts exfoliate rapidly when weathered, whereas the surfaces of chert and carbonate clasts survive much longer.) Borings in clasts are palaeoecologically problematical because we often cannot tell if they were excavated in the depositional environment where they were recovered, or elsewhere at a time during their transportation history. Even the orientation of clasts with respect to their colonising biota can be difficult to discern because of likely movement before final burial, except for boulder-sized clasts which are more likely to remain stable and consequently preserve a clear ecological zonation of their biotas (e.g. Surlyk and Christensen 1974), and erosion at the outcrop as in the Qahlah of Jebel Huwayyah.

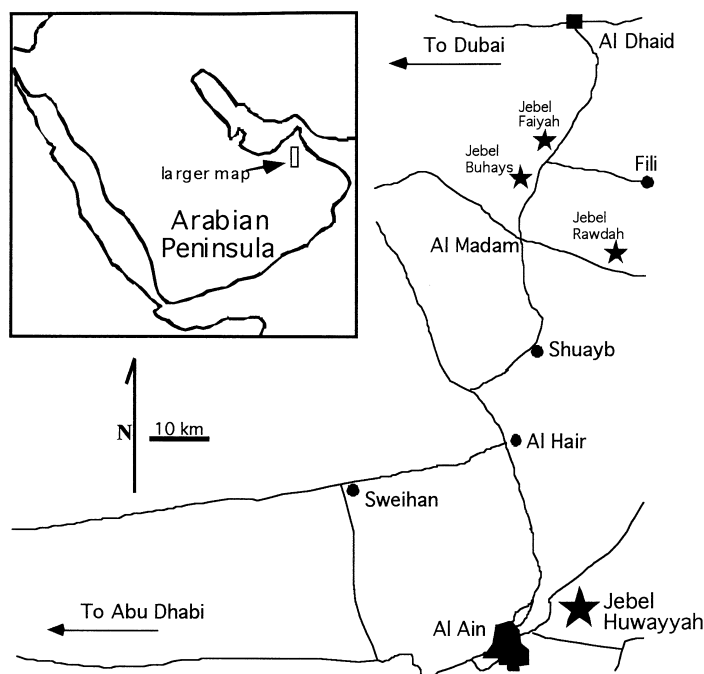
The objectives of this study are to describe the composition and palaeoecology of hard substratum biota in the unusual setting of the Qahlah Formation. Particular areas of focus are the variations in colonisation of different clast types, and the effects of the highly abrasive environment on the biota and its preservation. We also use the Qahlah fauna to illustrate some limitations of hard substratum palaeoecological studies, particularly those concerning potentially highly mobile substrates such as clasts, shells, and fragments of wood.

GEOLOGICAL SETTING

The Qahlah Formation is a series of transgressive sediments resting unconformably on the Semail Ophiolite and exposed in several disjunct outcrops on the flanks of the western Oman Mountains (Text-fig. 1). It is irregular in thickness, ranging from a few metres at the north-western end of Jebel Faiyeh in the eastern United Arab Emirates, to over 140 m at its type section in Oman. Conformably overlying the Qahlah are shallow-water carbonates of the lower Simsima Formation (Maastrichtian), rich in molluscs, echinoids and corals. The Qahlah is primarily composed of grain-supported sands, gravels and boulders derived from the obducted ophiolite. At most localities the predominant clast type is serpentinitised peridotite, with lesser amounts of chert, gabbro and basalt. Silty limestone units are locally developed in the studied section at Jebel Huwayyah, including some which are recognizable as hardgrounds from the presence of borers and encrusters. The Qahlah is considered to be Maastrichtian because of the occurrence of the agglutinated foraminiferan *Loftusia* (Nolan *et al.* 1990; Alsharhan and Nasir 1996).

Palaeoenvironmental interpretations of the Qahlah Formation vary, but all authors agree that it represents transgressive, shallow-marine, high-energy sedimentation. Skelton *et al.* (1990) hypothesized that the Qahlah was deposited as part of a fan delta spread over eroded remnants of the Semail Ophiolite. Smith *et al.* (1995) suggested an open marine, tidally-influenced environment, and Alsharhan and Nasir (1996) concluded that the Qahlah was formed in a nearshore to beach setting following a retreating cliff line of the ophiolite. Significant variations in thickness over short distances were noted by Vennin *et al.* (1999) who identified both matrix-supported, debris flow and clast-supported, grain flow conglomerates in the Qahlah. Our observations at Jebel Huwayyah of the diverse marine fauna, planar and trough cross-bedding (Pl. 1, fig. 1), and numerous truncation surfaces support, for this locality at least, the deltaic and tidal-channel models of Skelton *et al.* (1990) and Smith *et al.* (1995), with the sediments almost certainly derived from an adjacent high-relief ophiolitic coastline in the manner described by Alsharhan and Nasir (1996). This depositional system is at least partly analogous to the present deposition of ophiolite debris from cliffs in the shallow, subtropical Gulf of Oman on the eastern side of the Musandem Peninsula (see El-Sayed 1999). It is also a rocky-shore environment in the sense of Johnson (1988).

The main study site, Jebel Huwayyah, close to the city of Al Ain (UAE), is a plunging anticline known locally as 'Fossil Valley' (Text-fig. 1). The Semail Ophiolite is unexposed here but is assumed to be present not very far below the most basal exposures of the Qahlah Formation, which can be seen on the eastern limb of the anticline near the nose of the fold (N24°17'88", E55°51'48"). The Qahlah attains a thickness of about 34 m at Jebel Huwayyah. The upper part of the Qahlah Formation consists of muddy



TEXT-FIG. 1. Map showing the location of the main study site, Jebel Huwayyah, and other outcrops of the Qahlah Formation in the United Arab Emirates/Oman border region.

carbonate sands rich in *Loftusia*. These *Loftusia* Beds were interpreted by Smith *et al.* (1995) as representing extremely shallow-water, back bar or lagoonal deposits formed below wave-base in a protected environment.

Bored and/or encrusted rock clasts have been observed only at Jebel Huwayyah, and this is the only locality with *in situ* carbonate hardgrounds (Pl. 1, fig. 2). Apart from some examples of bored wood collected at Jebel Bu Milh (N24°28.11', E55°54.89'), no evidence of colonisation of hard substrates was found at any of the other Qahlah localities (Jebel Rawdah, Jebel Thanais, Jebel Buhays, Jebel Aqabah, Jebel Faiyah). No determination has been made of the proportion of clasts from Jebel Huwayyah which are colonised but it is estimated to be a very small percentage of the total clasts present (probably less than 1 per cent). The majority of the pebbles and cobbles weathering free on the shallow slopes of the jebel are barren.

MATERIAL AND METHODS

Fieldwork and sampling in the Qahlah and overlying Simsima Formations was undertaken in eight locations (see Smith *et al.* 1995) during three visits to the Oman Mountains (1992, 1995, and 1999) by parties from The Natural History Museum, London (BMNH). A total of 181 encrusted and bored clasts of various compositions were collected and brought back for further study using optical microscopy, scanning electron microscopy, and thin-sectioning. Whenever possible, way-up arrows were marked on *in situ* clasts at the time of collection. However, erosional dislodgment of clasts and downslope movement precluded this for most of the clasts. Each clast was classified according to its lithologic composition, its three primary axes were measured, the identities of the encrusters and/or borers present were recorded, together with their locations (e.g., on outer clast surface or in a recess, on the upper or lower side of the clast), and skeletal overgrowth relationships were logged.

Most of the specimens used have been registered into the palaeoecology collection at the NHM (prefixed PEI), but some are in the bryozoan (BZ) or coral (AZ) collections.

HARD SUBSTRATES IN THE QAHLAH

Types of hard substrate

There are six common types of hard substrate in the Qahlah Formation, all encrusted and/or bored to varying degrees: silicate clasts, *in situ* carbonate hardgrounds, carbonate hardground clasts, limestone pebbles, calcareous bioclasts, and wood.

Silicate pebbles, cobbles and boulders. The dominant clasts at most Qahlah localities were derived from the Semail Ophiolite during its initial obduction onto the Arabian continental margin in the Late Cretaceous (Nolan *et al.* 1990; Alsharhan and Nasir 1996; Searle and Cox 1999). The most common of these silicate pebbles and cobbles comprise serpentinised peridotite, but there are also pebbles and cobbles of dark brown to black gabbro, and white to grey leucogranite, most of which form angular to subangular clasts. Boulder-sized clasts occur occasionally, for example at Jebel Faiyah. However, boulders are absent and igneous rocks constitute only a minority of clasts at the main study site of Jebel Huwayyah where most clasts consist of very fine-grained, red-brown chert cobbles with rounded to subrounded shapes (Pl. 1, figs 3–4). These cherts may have been derived from the Hawasina Group (Mamdoul Shebl, pers. comm. March 1999).

All encrusters found on silicate clasts occur on the cherts; none was found on igneous rocks. This may in part be a taphonomic artefact since the igneous clasts are weathered deeply and tend to exfoliate. In contrast, the chert clasts are virtually inert and their encrusted surfaces are thus in good condition.

Thin crusts of bladed calcite marine cement partly cover the surfaces of some chert clasts. These crusts are approximately 0.2 mm thick and consist of palisades of crystals flaring outwards toward their termini. Examples of skeletal organisms growing over these inorganic crusts (Pl. 1, fig. 5) prove that the cements were formed before final clast burial. The crusts may be equivalent to the ‘thin rim of fibrous calcite spar’ previously noted by Alsharhan and Nasir (1996, p. 234) on clasts in the Qahlah. They are here interpreted as early marine cements.

The borings in the Qahlah hard substrates were formed entirely by chemical and mechanical borers which required a calcareous substrate; thus none of the silicate clasts is bored.

Carbonate hardgrounds (in situ). Carbonate hardgrounds are defined as ‘synsedimentarily lithified carbonate sea-floors that became hardened *in situ* by the precipitation of a carbonate cement in the primary pore spaces’ (Wilson and Palmer 1992, p. 3). Three levels of hardground development, each 5–20 cm thick, are found within the Qahlah section at Jebel Huwayyah. In contrast with many hardgrounds described elsewhere (see Wilson and Palmer 1992), none of the Qahlah hardgrounds forms continuous, unbroken platforms; instead, all are considerably localised. The lowest is poorly exposed approximately

EXPLANATION OF PLATE 1

Figs 1–2. Field photographs. 1, small-scale cross-bedding in calcareous siltstones and cobbles weathering loose from the outcrop; scale bar divided into cm. 2, surface of hardground showing deeply eroded *Gastrochaenolites* and scalloped relief; field of view approximately 20 cm wide.

Figs 3–5. Encrusted chert cobbles. 3, BMNH PEI 321; dense encrustation of abraded and disarticulated shells of the oyster *Acutostrea*; $\times 0.9$. 4, BMNH AZ 2527; encrusting pseudosolitary (*Brachyphyllia* sp.) and bored sheet-like (*Actinacis parvistella* Oppenheim, 1930) corals; $\times 0.7$. 5, BMNH PEI 322; bryozoan *Conopeum* overgrowing a thin crust of early calcite cement; $\times 3$.

Fig. 6. Bored carbonate hardground cobble with *Gastrochaenolites* deeply eroded; BMNH PEI 323; $\times 0.8$.

All field photographs and specimens are from the Qahlah Formation (Maastrichtian), Jebel Huwayyah, Oman Mountains.



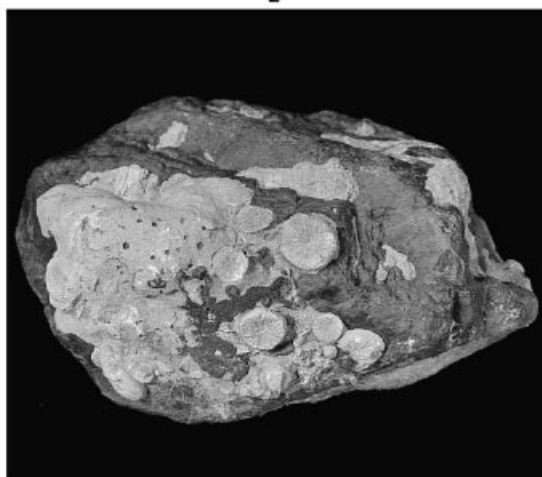
1



2



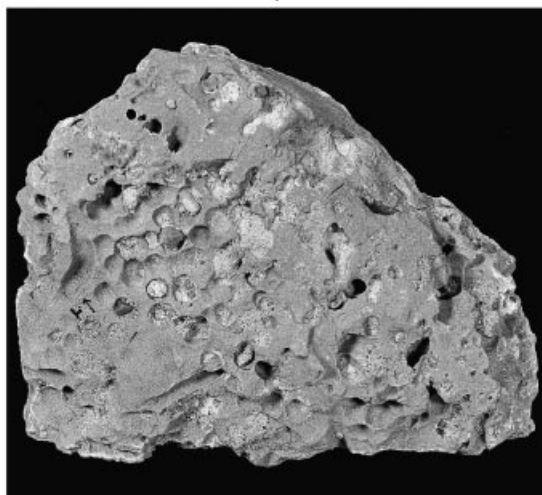
3



4



5



6

5 m above the base of the section, near the middle of Unit 2 of Smith *et al.* (1995, p. 101), and is characterised by deeply eroded *Gastrochaenolites* on the upper surface. The second is approximately 16 m above the section base measured as Unit 7 in Smith *et al.* (1995, p. 101). The third is approximately 23 m above the section base at Unit 9 of Smith *et al.* (1995, p. 101). Each is composed of very silty micrite containing angular grains of olivine, feldspars, micas, pyroxenes, chert and calcareous bioclasts. The matrix is a partially peloidal micrite, some of which has been neomorphosed to microspar. All of these hardgrounds (Pl. 1, fig. 2) are bored on their upper surfaces by bivalves (producing *Gastrochaenolites*), and encrusted by oysters (*Acutostrea*), and/or serpulids and foraminifera (*Placopsilina*).

The Qahlah hardgrounds are similar to hardgrounds described in a siliciclastic-carbonate sequence in the Eocene of southern Spain by Martinius and Molenaar (1991). In both cases the hardgrounds formed by the precipitation of an early carbonate fringing cement in sandy and silty sediments. The Spanish hardgrounds had an earlier nodular stage, whereas the Qahlah hardgrounds formed directly as beds, as was common under the 'Calcite Sea' conditions of the Cretaceous (Wilson and Palmer 1992).

Carbonate hardground clasts. Many carbonate hardground fragments are found in the Qahlah Formation. These clasts, which range from pebble- to cobble-sized (Pl. 1, fig. 6), vary in shape because they were broken in a variety of ways, and also because many contain partially-filled prelithification burrows (Pl. 2, fig. 1) which eroded preferentially to leave hollows and deep cavities. Like the *in situ* hardgrounds, the clasts are formed of very silty micrite with a partially peloidal matrix. They appear to have been locally derived from hardgrounds which were broken up on the sea-floor by storms and migrating tidal channels charged with, for example, mobile clasts of chert.

The hardground clasts have numerous encrusters, both on their outer surfaces and within cavities. They also contain many borings, especially *Gastrochaenolites* (Pl. 1, fig. 6). Some of the burrowed clasts are partly filled by a poorly-lithified, chocolate-brown mudstone which may contain small, branching burrow systems cast in calcite (Pl. 2, fig. 1). These burrows are identified as *Arachnostega* (Bertling 1992; Fürsich *et al.* 1994), a trace fossil possibly made by a polychaete annelid. *Arachnostega* is normally found within the sediment infill contained between the two valves of a bivalve. Fürsich *et al.* (1994) attributed its occurrence in bivalves as due to differential preservation where the sediment was protected from compaction. This would also be true for the sediment which fills lithified burrows in the hardground clasts from the Qahlah.

A small number of carbonate clasts are encrusted yet unbored and have rougher, more granular surfaces than is typical (Pl. 3, fig. 4). These were probably incompletely lithified at the time of colonisation, firm enough to be encrusted but insufficiently cemented for colonisation by the *Gastrochaenolites* producing borer, and represent 'firmgrounds' (Goldring 1995).

Older limestone pebbles. Well-rounded pebbles of grey micrite, pelmicrite and occasionally oomicrite are relatively common in the Qahlah Formation at Jebel Huwayyah (Pl. 2, fig. 3). They are apparently scattered through much of the formation. The micrite is virtually featureless, except for occasional layers

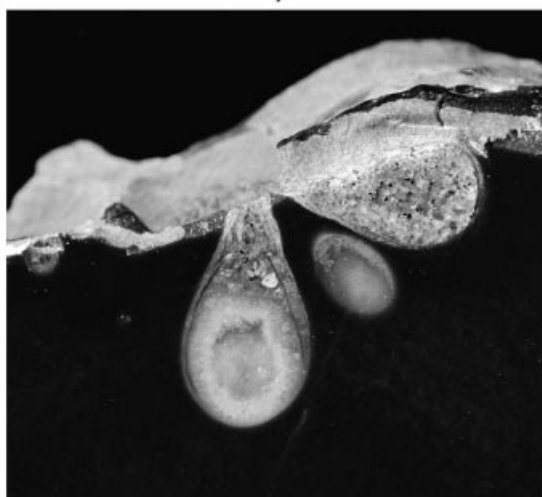
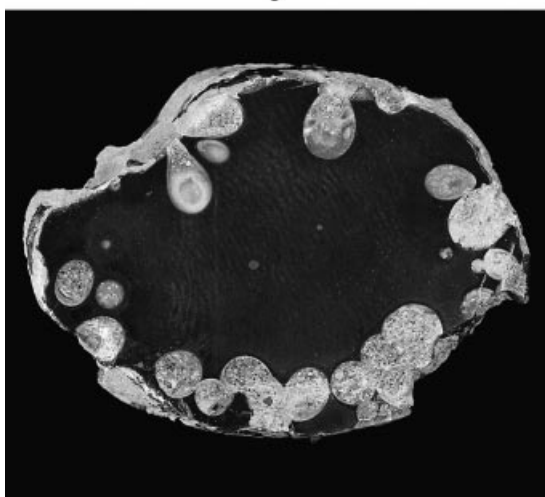
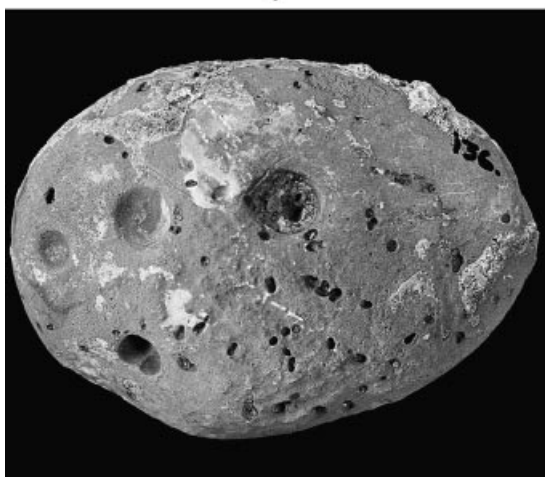
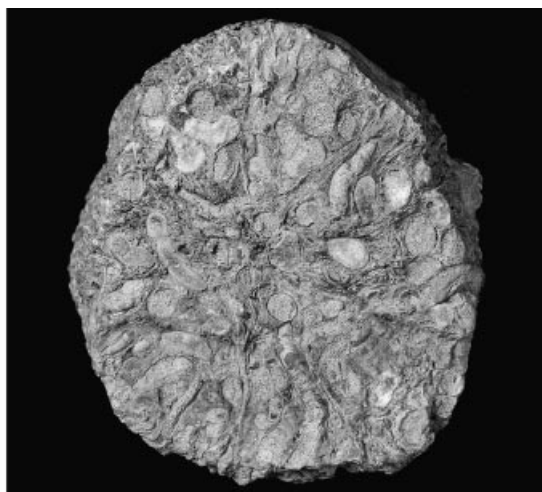
EXPLANATION OF PLATE 2

Fig. 1. Pre-lithification burrow in fractured carbonate hardground clast with wall encrusted by the bryozoan *Bullaconopeum nodosum* Taylor, 1995, and overlain by a calcite cast (centre right) of *Arachnostega*, a narrow burrow made in the soft sediment which subsequently infilled the original large burrow; BMNH BZ 3173; $\times 3.6$.

Fig. 2. Packed *Teredolites* visible in a transversely fractured piece of fossil wood; BMNH PEI 324; $\times 1.3$.

Figs 3–6. Bored limestone rockground pebbles. 3, BMNH PEI 325; variably truncated borings visible on exterior of pebble; $\times 1.6$. 4, BMNH PEI 326; pebble broken through area with closely-spaced *Gastrochaenolites*; $\times 2$. 5–6, BMNH PEI 327; cut and polished pebble. 5, *Gastrochaenolites* around pebble perimeter variously filled by sediment and calcite; $\times 2.4$. 6, detail showing *Gastrochaenolites* with *in situ* shell (centre) with a second, truncated example on the right; $\times 6.8$.

All specimens are from the Qahlah Formation (Maastrichtian), Jebel Huwayyah, Oman Mountains.



of peloids, small isolated ostracod valves, a few uniserial foraminiferans, and calcispheres. The matrix is cut by numerous calcite veins and stylolites of at least two diagenetic generations. Unlike the silty micrites of the hardgrounds, these allochthonous carbonates clearly did not form contemporaneously with the deposition of the Qahlah gravels. Instead, they are derived from older limestones, apparently deposited in a low-energy, deep marine carbonate environment. Unfortunately there are no age indicators in these pebbles, and they do not clearly match any described limestones from the region. They may possibly be derived from 'calcilutites', 'Upper Triassic reef limestones' and 'white crystalline limestone' found as large clasts in the complex Batinah mélange above the Semail ophiolite in the northern Oman Mountains (Robertson and Woodcock 1983).

Almost all these older limestone pebbles contain the bivalve boring *Gastrochaenolites* (Pl. 2, figs 3–6). They have fewer encrusters than the other clasts; only five encrusting taxa are recorded from the limestone pebbles (Table 2). Reasons for the depauperate encrusting biota may include the small surface area of the pebbles, their relatively smooth surfaces which provide few protected microhabitats, and the greater disturbance resulting from the higher mobility of these small clasts compared to the larger silicate and hardground cobbles.

Calcareous bioclasts. The Qahlah Formation gravels also contain numerous cobbles and pebbles derived from animals with robust calcareous skeletons. The most common are clusters of oysters, followed by fragmented to intact rudists, colonial corals and acteonellid gastropods. These clasts, because of their calcareous composition, contain numerous borings. Encrusters (e.g. oysters fouling coral surfaces) are present but in surprisingly small numbers, especially when compared with the carbonate hardground clasts.

Wood. Finally, pieces of wood are common in the Qahlah, especially in the *Loftusia* Beds at Jebel Huwayyah (units 9–12 of Smith *et al.* 1995, p. 101). The wood ranges from small pebble-sized fragments to logs up to 2 m long and 0.25 m in diameter. Probably coniferous in origin, the wood has been diagenetically altered and replaced in complex ways. It was first thoroughly bored by teredinid bivalves (Pl. 2, fig. 2), which left densely-packed, calcite-lined tunnels (*Teredolites longissimus* Kelly and Bromley, 1984) varying in diameter and morphology. The wood was subsequently buried in silty micrite, similar to that forming the hardgrounds, which filled the *Teredolites* borings. Early calcite cements then precipitated in cavities in the wood, often nucleated from the calcite tube linings left by the teredinids. Much of the wood itself was displaced by the calcite, and some was later silicified. The preservational style corresponds to either the 'well-preserved log-ground' or 'relict log-ground' categories defined by Savdra *et al.* (1993).

The surfaces of the wood fragments are not well preserved, and only one encrusted specimen has been observed. This is an oyster growing over the top of, and therefore postdating, *Teredolites*.

Clast size statistics

Three types of clast are most commonly encrusted and bored: carbonate hardgrounds, cherts, and older limestones. The number of analysed clasts in each category, and their mean cuboid volumes are given in Table 1. On average, carbonate hardground clasts are slightly larger than the chert clasts, and both are cobble grade and considerably larger than the older limestone clasts, which are entirely of pebble grade. Surface areas potentially available for encrustation and boring therefore differ substantially between the pebble-grade older limestone clasts and the predominantly cobble-grade carbonate hardground and chert clasts.

ENCRUSTING BIOTA

Twenty-seven encrusting taxa have been recognised on the Qahlah clasts. Their taxonomy and general distribution patterns are summarised in Table 2 and displayed in Text-fig. 2. A total of 103 skeletal overgrowths were recorded among these encrusters. Overgrowth patterns involving taxa with ten or more encounters are listed in Table 3.

TABLE 1. Statistics of analysed cobbles in the three most common lithologic categories. The cuboid volumes were calculated by multiplying three mutually perpendicular diameters and therefore overestimate the true volumes of the clasts.

Clast type	Number	Average cuboid volume
Carbonate hardground	87	326 cm ²
Chert	48	214 cm ²
Older limestone	29	55 cm ²

Oysters

The cementing oyster *Acutostrea* (Pl. 1, fig. 3; Pl. 3, fig. 1) is the most common encruster on the Qahlah clasts. It is found on a higher proportion of clasts than any of the other encrusters, and is probably the most abundant encruster in terms both of area occupied and skeletal biomass. Oysters apparently favoured the upper-facing surfaces of the clasts, but are occasionally found on cryptic undersurfaces, especially in concavities where pre-lithification burrows are exposed by clast breakage. Individuals on upper surfaces of carbonate hardground cobbles are often densely aggregated (Pl. 3, fig. 1), their cemented valves covering all of the available substrate space and their juxtaposed edges raised (cf. Düringer 1985; Wilson *et al.* 1998). Only rarely were the oysters articulated when collected; in the great majority of cases the right valves are missing and the interiors of the left valves visible and sometimes fouled by other organisms. Typically, all the oysters in each dense cluster are of a similar size, indicating colonisation from a single spatfall or closely-spaced spatfalls. Very rarely, small oysters foul the interior surfaces of left valves of larger oysters, implying successive spatfalls at significantly different times.

Acutostrea is often penetrated by *Gastrochaenolites* and *Entobia* borings. Conversely, the oyster can be found growing over or within borings of *Gastrochaenolites*, indicating that boring by *Gastrochaenolites* and encrustation by *Acutostrea* did not succeed one another in a fixed sequence. Because these oysters are the largest and most abundant encrusters in this assemblage, they have the highest number of recorded overgrowths. However, they are successful overgrowers in only 35 per cent of observed encounters with other encrusters. This low value may not be a reliable indicator of a lack of success in competitive interactions for two reasons. First, it is impossible to tell how many smaller encrusters (e.g. foraminifers and bryozoans) were completely overgrown by the thick shells of the oysters and therefore go unnoticed. Second, the majority of the observed overgrowths entail small encrusters, such as *Placopsilina* and bryozoans, fouling the interior surfaces of oyster left valves, clearly signifying encrustation after death and decay of the soft tissues of the oysters rather than spatial competition between living organisms.

Acutostrea is equally common on chert and hardground clasts, but is rare on the older limestone pebbles. This could be because these smaller clasts were more often disturbed by currents, either removing oyster colonists at an early stage, or preventing colonisation altogether.

Foraminifera

The two foraminifers found on the Qahlah clasts are identified as *Nubeculinella* and *Placopsilina*. *Nubeculinella* is a calcareous, multilocular encruster found only infrequently on hardground and chert clasts in crevices and cavities. The best examples are preserved by bioimmuration when overgrown by oysters, suggesting that they may have been more abundant in the living community but have been mostly removed by pre- and post-depositional processes including recent weathering of clasts on the surface of the outcrop.

Much more common in the Qahlah is the agglutinating foraminifer *Placopsilina* (Pl. 3, fig. 3; Pl. 4, fig. 1; see Hodgkinson 1992 for a discussion of the taxonomy of this genus). Indeed, in terms of numbers of individuals, *Placopsilina* may be the most abundant of all encrusters in the Qahlah. Close examination of the test surface reveals that *Placopsilina* agglutinated small grains of sediment usually less than 50 µm in diameter but of variable size. The similarity of the grains utilised with the lithified silty micrite encrusted

TABLE 2. Encrusting taxa identified on the three most common clast types. Numbers are percentages of each clast type with the particular encruster. These data refer only to colonised clasts, which are a small fraction of the total clasts in the Qahlah Formation.

Taxa	% hdgd clasts	% chert clasts	% limestone clasts
Oysters			
<i>Acutostrea</i>	55.2	60.4	10.3
Bryozoans			
<i>Conopeum</i>	34.5	45.8	10.3
<i>Bullaconopeum</i>	6.9	0	0
<i>Wilbertopora</i>	2.3	0	0
<i>Biaviculigera</i>	6.9	2.1	0
<i>Onychocella</i>	1.2	0	0
<i>Pelmatopora</i>	3.5	0	0
<i>Leptocheilopora</i>	1.2	0	0
<i>Tecatia</i>	23.0	0	0
<i>Balantiostoma</i>	8.1	0	0
<i>Voigttopora</i>	5.8	0	0
' <i>Berenicea</i> '	4.6	0	0
Foraminifera			
<i>Placopsilina</i>	59.8	41.7	6.9
<i>Nubeculinella</i>	1.2	4.2	0
Corals			
unidentified	1.2	2.1	0
<i>Brachyphyllia</i>	0	29.2	0
<i>Columnastrea</i>	2.3	16.7	0
? <i>Goniopora</i>	1.2	0	0
? <i>Pleurocora</i>	0	4.2	0
<i>Actinacis</i>	0	6.3	0
<i>Monticulastrea</i>	0	2.1	0
Rudists	1.2	4.2	3.5
Calcareous algae			
coralline alga	9.2	4.2	0
' <i>Solenopora</i> '	3.5	0	0
'Worms'			
terebellid	4.6	4.2	0
serpulids	34.5	62.5	13.8
Brachiopods			
<i>Discinisca</i>	0	2.1	0

often makes it difficult to see the foraminiferans against their background (Pl. 3, fig. 3). *Placopsilina* is found in roughly similar percentages on both chert and hardground clasts. However, it is rare on the older limestone pebbles. *Placopsilina* often encrusted eroded borings, and is the dominant taxon in about 41 per cent of overgrowth encounters. Although *Placopsilina* is found most frequently in cryptic microhabitats, including erosional hollows, vacated borings and pre-cementational burrows, a significant minority (c. 44 per cent) of occurrences are on outer surfaces of clasts, occasionally with densely aggregated tests piled one on top of the other. Many of the delicate *Placopsilina* tests display pristine preservation on the outside of the clasts, suggesting colonisation just prior to final burial, thereby avoiding abrasion. A similar situation was apparently the case with at least some foraminifer-encrusted clasts in the Upper Cretaceous of eastern Bohemia (Žítt and Nekvasilová 1991). Alternatively, the foraminifers may have lived interstitially on stable clasts below the sediment-water interface, although this idea is not supported by the fact that in examples where the way-up when collected is known, in six cases the foraminifer was only on the upper side of the clast and in no cases was it found only on the underside. There is no morphological

TABLE 3. Overgrowth patterns of the five encrusters with more than 10 encounters with other encrusters.

Taxa	Number of encounters	% of encounters on top
<i>Tecatia</i>	12	83
<i>Conopeum</i>	37	68
serpulids	20	65
<i>Placopsilina</i>	29	41
<i>Acutostrea</i>	54	35

evidence for special adaptations of their tests to resist high-energy conditions, as described for fistulose polymorphinids of the Late Cretaceous and Early Tertiary by Pozaryska and Voigt (1985).

Bryozoans

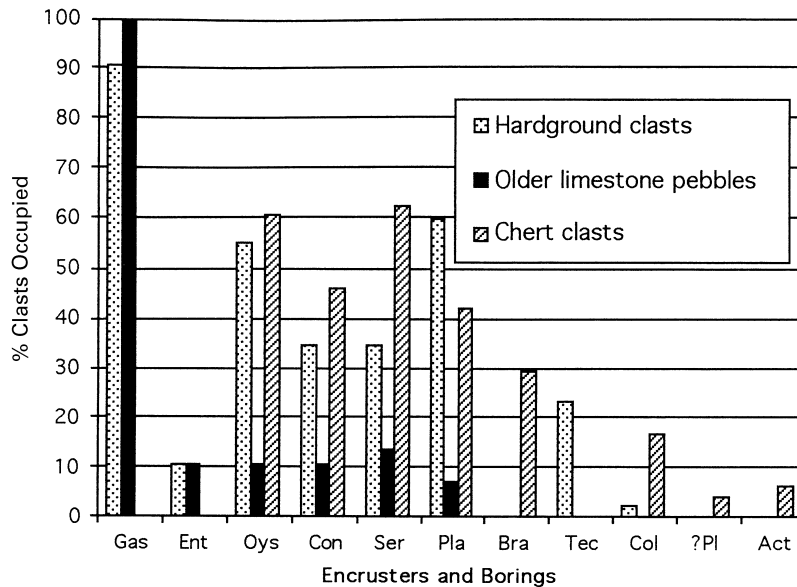
With 12 species, bryozoans are the most diverse major taxonomic group present in the Qahlah hard substrate assemblage. However, their numerical abundance and biomass are small. Most are cryptic in habit. Nine species of cheilostome bryozoans and three species of cyclostomes have been identified; systematic descriptions of most of these species can be found in Taylor (1995). With three exceptions, all of the bryozoan species have multiserial, sheet-like colonies (Pl. 1, fig. 5; Pl. 2, fig. 1; Pl. 4, figs 2, 4, 6). The exceptions are *Tecatia* (Pl. 4, fig. 3) and *Voigttopora* with uniserial, runner-like colonies, and the colony bases of an unidentified erect cyclostome. The two encrusting architectures utilise substratum space in contrasting ways (see Taylor 1999 and references therein): sheets have densely packed zooids and employ a confrontational (or phalanx) strategy in spatial competition, whereas runners have a fugitive (or guerilla) strategy and survive by dispersing their zooids widely across the substratum. The Qahlah assemblage contains a higher diversity of sheets than runners, as is the case in most hard substratum assemblages of bryozoans from the Ordovician to the present-day.

A cheilostome species tentatively referred to *Conopeum* (Pl. 4, fig. 2) is the most abundant bryozoan in the Qahlah, with colonies sometimes attaining a moderately large size (20 mm diameter) and occasionally showing multilamellar growth. Colonies of *Conopeum* can be found in both cryptic microhabitats (vacated borings and pre-cementational burrows) and on clast surfaces, although they are more common in the former (13 vs. 8 occurrences) and it is possible that even those on clast surfaces lived on cryptic undersides.

Another relatively common bryozoan is *Tecatia* (Pl. 4, fig. 3). This gymnocystidean ascophoran has uniserial colonies consisting of very small and delicate zooids. Colonies of *Tecatia* are characteristically damaged and disrupted: colony origins have not been found; most specimens comprise small, irregular clusters of zooids, and there is often evidence of skeletal breakage and sometimes of subsequent repair. The latter indicates that colonies were damaged during life, as is commonly the case in uniserial encrusting bryozoans (Taylor, 1988, 1990a). *Tecatia* frequently overgrows valves of *Acutostrea* but this apparent association may be an artefact caused by the greater visibility of this tiny bryozoan when on a smooth and uniform shell than a rough and heterogeneous clast where the grains can be of a similar size to the zooids of the bryozoan. This bryozoan shows a strong preference for cryptic microhabitats, with 11 indisputably cryptic occurrences and only three on outer clast surfaces. Examples of *Tecatia* fouling interior surfaces of the cemented left valves of *Acutostrea* in a seemingly exposed location may have been sheltered by the upper, right valves if these remained articulated after oyster death.

Corals

With the exception of a few corals encrusting carbonate hardground cobbles, all of the encrusting corals were found on chert cobbles in the *Loftusia* Beds, apparently deriving from a coral bed estimated to be less than 2 m from the top of the Qahlah but not seen *in situ*. Many of the coral-encrusted chert cobbles (Pl. 1,



TEXT-FIG. 2. Graphical distribution of boring and encrusting taxa on the three primary clast types. Each taxon is found on at least 10 per cent of one clast type. Gas, *Gastrochaenolites*; Ent, *Entobia*; Oys, oysters; Con, *Conopeum*; Ser, serpulids; Pla, *Placopsilina*; Bra, *Brachyphyllia*; Tec, *Tecatia*; Col, *Columnastrea*; ?Pl, *?Pleurocora*; Act, *Actinacis*. Numbers of each clast type: carbonate hardground, 87; chert, 48; older limestone, 29.

fig. 3) contrast with those typical of the Qahlah in having a yellow colour, suggesting a higher degree of surface oxidation than is typical, possibly pointing to a longer period of exposure on the sea-bed. All the corals present are colonial, although one of them (*Brachyphyllia* sp.) is pseudosolitary, i.e. usually found only as single corallites representing immature colonies. Often only one surface, presumed to be the upper surface, of the chert clast is encrusted but this is not always the case. Corals tend to dominate the chert cobbles on which they are present, sometimes attaining a relatively large size. Oysters, serpulids and occasionally *Placopsilina* may be associated with these coral-encrusted cobbles but bryozoans appear to be totally lacking.

Serpulids

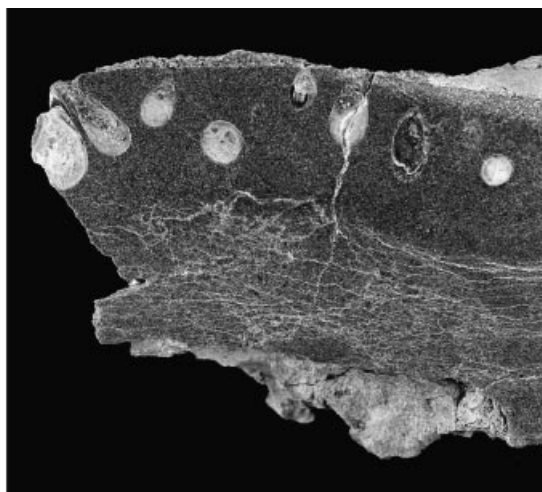
Serpulid worms (Pl. 3, fig. 4; Pl. 4, fig. 4), of which at least two species may be present judging from tube morphology, are moderately common on all clast types. However, they never form dense clusters unlike serpulids on some other Mesozoic hard substrates (e.g. Taylor 1990b, fig. 2F). Their distribution is almost

EXPLANATION OF PLATE 3

- Fig. 1. Dense colonization of cobble upper surface by disarticulated *Acutostrea*; BMNH PEI 328; $\times 0.4$.
 Fig. 2. Vertically sectioned and polished cobble with *Gastrochaenolites*; BMNH PEI 329; $\times 1.9$.
 Fig. 3. *Placopsilina* individuals aggregated close to the entrance of a pre-lithification burrow; BMNH PEI 330; $\times 4.5$.
 Fig. 4. Coiled serpulids encrusting a ?firmground cobble; BMNH PEI 331; $\times 3$.
 Fig. 5. Valve of a rudist (*?Dictyoptychus*) cemented to a cobble surface; BMNH PEI 332; $\times 1.7$.
 Fig. 6. Lithophagid bivalve occupying *Gastrochaenolites* boring; BMNH PEI 333; $\times 3.2$.
 All specimens are carbonate hardground cobbles from the Qahlah Formation (Maastrichtian), Jebel Huwayyah, Oman Mountains.



1



2



3



4



5



6

identical to that of the oyster *Acutostrea* and the bryozoan *Conopeum*. Serpulids are most common on the chert clasts and least common on the older limestone pebbles.

Others

Too few examples of other encrusters are present to draw any conclusions about their preferences for particular substrate types or locations on those substrates. Preservation of these rarer encrusters is sometimes dependent on bioimmuration, overgrowth by oysters and protection of the overgrown organism beneath the oyster shell until exposed by removal of the shell from its substrate (Taylor 1990c). Bioimmuration is useful in serving to indicate the presence of otherwise unpreserved encrusters, and in hinting at their abundances in the living community (Wilson and Taylor 1996).

Several examples of agglutinating worm tubes, mostly bioimmured, have been found (Pl. 4, fig. 5). These straight to curved tubes consist of platy grains of sediment, averaging about 100 μm in diameter but varying in exact size and in shape, agglutinated to form a tube adherent to the substratum. The tubes may be straight or curved and are about 0.5 mm in width. Species belonging to a considerable number of modern polychaete families have the ability to incorporate sediment in their tubes, including the Sabellariidae, Sabellidae, Oweniidae, Alvinellidae, Pectinariidae, Terebellidae, Trichobranchidae, Apistobranchidae, Longostomatidae, Chaetopteridae, Arenicolidae, Maldanidae and Capitellidae (C. J. Glasby, pers. comm. November 1999). It is impossible to determine to which (if any) of these families the Qahlah tube-builder belonged to, although the likelihood is that it came from either the Order Sabellida or Terebellida.

Although not encrusting in the sense of being cemented to the substratum, discinid brachiopods can be significant sessile components of hard substratum communities but are often only preserved when bioimmured (Taylor and Todd 1990). A single example of a tiny discinid has been found in the Qahlah: the brachiopod was revealed when an oyster became detached from a chert pebble substrate, leaving the brachiopod still adhering to the substrate.

Two types of crustose algae can be distinguished: the first has a featureless, lamellar surface; the second, tentatively referred to as '*Solenopora*' has a surface consisting of a honeycomb of minute, polygonal apertures (Pl. 4, fig. 6). Most examples of these algae encrust carbonate hardground clasts but the lamellar coralline alga is occasionally found on chert clasts.

BORING BIOTA

Gastrochaenolites

Carbonate hardground cobbles and older limestone pebbles both tend to be profusely bored by bivalves, leaving the characteristic trace fossil *Gastrochaenolites* (Pl. 1, figs 1, 6; Pl. 2, figs 3–6; Pl. 3, figs 2, 6). It is difficult to assign the borings to an ichnospecies: some have the overall morphology of *G. lapidicus* Kelly and Bromley, 1984 whereas others resemble *G. turbinatus* Kelly and Bromley, 1984, but the majority are

EXPLANATION OF PLATE 4

Fig. 1. Agglutinating foraminiferan *Placopsilina* on a carbonate hardground cobble; BMNH PEI 334; $\times 16$.

Fig. 2. Part of a colony of the sheet-like cheilostome bryozoan *Conopeum* on a carbonate hardground cobble; BMNH PEI 335b; $\times 42$.

Fig. 3. Typically damaged zooids of the uniserial, runner-like bryozoan *Tecatia* on a carbonate hardground cobble; BMNH PEI 335a; $\times 40$.

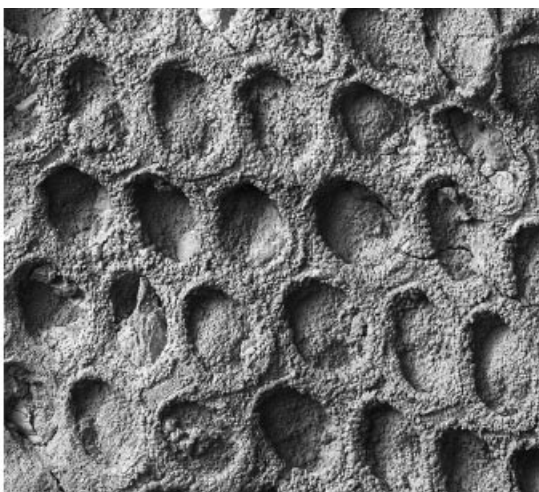
Fig. 4. Reciprocal overgrowth between a serpulid worm tube and the bryozoan *Conopeum* on a carbonate hardground cobble; the outer edge of the serpulid tube can be seen overgrowing the bryozoan near the top of the figure, whereas to the right and in the centre the bryozoan overgrows the serpulid; BMNH PEI 335b; $\times 11$.

Fig. 5. Agglutinating worm tube on a chert clast preserved by bioimmuration and exposed after removal of an overgrowing oyster shell (remnants of which visible in lower right); BMNH PEI 336; $\times 15$.

Fig. 6. Bryozoan *Conopeum* (lower left) overgrowing a coralline alga ('*Solenopora*') on a carbonate hardground cobble; BMNH PEI 337; $\times 45$.



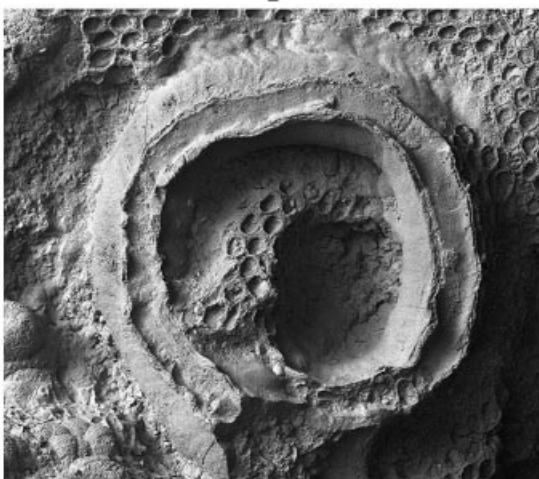
1



2



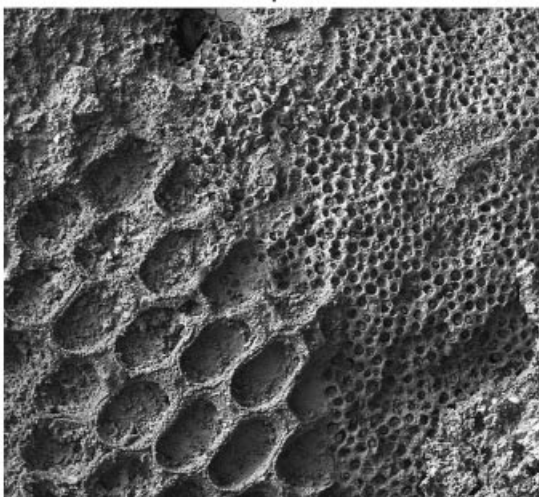
3



4



5



6

too eroded for the ichnospecies to be determined. Not surprisingly, *Gastrochaenolites*, and indeed any other recognisable boring are lacking from the chert cobbles. The condition of *Gastrochaenolites* varies greatly but many are deeply eroded and truncated (Pl. 1, fig. 2; Pl. 2, figs 3, 6). Relatively few borings are uneroded and complete. Among these more intact borings are examples in which the shell of the borer (or a subsequent nestling species of bivalve) is preserved *in situ* (Pl. 2, fig. 6; Pl. 3, fig. 6), and a few with calcareous boring linings. Individual clasts usually contain *Gastrochaenolites* exhibiting varying states of preservation. This shows that erosional truncation of the borings occurred concurrently with the production and occupation of the boreholes, and was not an exclusively late stage process occurring at the end of clast colonisation. Where the density of *Gastrochaenolites* is very high, especially in some older limestone pebbles, the clast may be weakened with fracturing occurring at this position.

Most of the *Gastrochaenolites* present in the carbonate hardground cobbles, and all of those in the older limestone pebbles, can be attributed to the activities of gastrochaenid bivalves, judging from examples with *in situ* shells. However, some of the borings in carbonate hardground clasts (Pl. 3, fig. 6) are occupied by a lithophagid bivalve which is presumed to be the trace maker and not simply a secondary occupant nestling in a boring created by another bivalve (cf. Wilson 1986). Lithophagids also account for most or all of the occupied *Gastrochaenolites* present in the bored corals.

Carbonate hardground clasts with *Gastrochaenolites* tend to be bored on both the upper and lower surfaces, although there is a slight tendency for upper surfaces to be more intensely bored. While most *Gastrochaenolites* penetrate outer, exposed clast surfaces, some are cryptic, boring through the walls of pre-lithification burrows.

We cannot be certain that the *Gastrochaenolites* in the older limestone pebbles were excavated in the Qahlah depositional environment or at some point earlier in their transportation history. They may be remanié fossils from an earlier system, possibly as far back as the 'Early Triassic reef limestone' found in the Batinah mélange overlying the Semail ophiolite in northern Oman (Robertson and Woodcock 1983, p. 2).

Teredolites

These borings, specifically *Teredolites longissimus*, are of course found only in the woodgrounds in the Qahlah Formation (Pl. 2, fig. 2). The tunnels vary in diameter, are densely packed in the wood, and are lined with calcite. Pallets found in some of the borings enable some of the trace makers to be identified as the teredinid bivalve *Nausitora* sp. (Evans 1997).

Rogerella

The barnacle boring *Rogerella* is rare in the Qahlah and found only in the older limestone pebbles. As with the *Gastrochaenolites* borings in these older limestone pebbles, it is possible that they were excavated in the clasts before they were transported into the Qahlah depositional environment.

Entobia

The clionid sponge boring *Entobia* is comparatively rare in the Qahlah ichnofauna and was not a routine borer of hardground cobbles. It is found only within *Gastrochaenolites* borings in the hardground clasts, on a few older limestone pebbles, and penetrating shells including bioclasts (rudists and acteonellid gastropods) and, sometimes profusely, in oysters cemented to other clasts.

Gnathichnus

This ichnogenus consists of an ideally pentaradiate pattern of grooves formed in hard substrates by the teeth of grazing echinoids (Bromley 1975). One clear example of *Gnathichnus* has been observed on the left valve of an oyster encrusting a carbonate hardground cobble, apparently representing the first example of echinoderm boring or scraping from a Late Cretaceous rocky-shore (cf. Lescinsky *et al.* 1991, p. 137). It is doubtful whether such shallow grooves would be discernible on the irregular surface of the clasts.

Therefore, the impact of grazing echinoids on the hard substratum community, and on erosion of the clasts, is difficult to gauge but the possibility must be considered that echinoids were significant agents of bioerosion in the Qahlah, supplementing the physical erosion caused by scour and tumbling.

DIVERSITY ON DIFFERENT CLAST TYPES

The three principal clast types in the Qahlah Formation of Jebel Huwayyah are carbonate hardground cobbles, chert rockground cobbles and limestone rockground pebbles. Of the 27 'taxa' recognised as encrusters of Qahlah clasts (Table 2), 22 species (81 per cent) are recorded on hardground cobbles, 16 species (59 per cent) on chert cobbles, and five species (19 per cent) on limestone pebbles. The greater overall diversity of hard substrate colonisers present on the hardground and chert cobbles relative to the limestone pebbles may be in part related to surface area available for colonisation (however, see below); a more compelling explanation is the comparative stability of cobbles relative to pebbles: high degrees of physical disturbance by overturning and rolling are likely to have hindered colonisation of the limestone pebbles by many species.

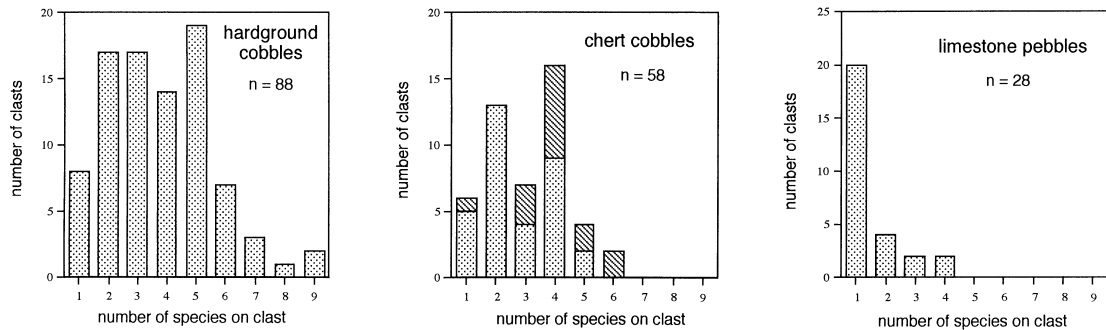
Considering the diversity of colonisers (encrusters and borers) on individual clasts belonging to the three main types (Text-fig. 3), there is a striking difference between the numbers of colonisers on the limestone pebbles relative to the hardground and chert cobbles. The great majority of limestone pebbles have only one taxon, which is invariably *Gastrochaenolites*, with a small number of pebbles colonised by 2–4 taxa, and a mean value of 1.5 taxa per clast. Individual hardground cobbles are colonised by up to nine taxa, although the majority host between two and five taxa, with a mean value of 3.8 taxa. Up to six taxa were recorded on individual chert cobbles, although colonisation by 2–4 taxa was the norm (mean value 2.6 taxa). Diversity on individual hardground cobbles is therefore slightly greater than that on chert cobbles, especially if the 'atypical' coral-encrusted cobbles occurring near the top of the Qahlah are excluded. There is no strong relationship between the surface areas of the clasts and species richness per clast. The linear correlation coefficient (r^2) between species richness and surface area on the limestone pebbles is 0.005, which is very insignificant. Coefficients for species richness on the chert (0.103) and carbonate hardground cobbles (0.097) also show no statistical correlation. Therefore, surface area is not the principal determinant of diversity. The presence of borers only in the hardground cobbles accounts for some of these diversity differences but the greater number of bryozoans on the hardground cobbles is another contributory factor: most of these bryozoans are cryptic species exploiting vacated borings and the walls of pre-cementational burrows in the cobbles.

Three recent studies of modern encrusting communities produced conflicting views of the effects of substrate composition on epibenthic community development. Connell (2000) showed that encrusters on sandstone and concrete substrates in Sydney Harbour, Australia, were not significantly different in taxonomic composition or abundance. Bavestrrello *et al.* (2000), however, presented evidence that one hydroid species prefers to recruit on carbonate rather than quartz-rich substrates in the Mediterranean. Glasby (2000) used settlement panels in Sydney Harbour to demonstrate that substrate composition and surface orientation can interact in complex ways for epibenthic organisms. This means that generalizations about substrate effects can only be made with caution, which is a view supported by the Qahlah Formation data presented here.

COMPARISONS WITH OTHER HARD SUBSTRATE FAUNAS

The Qahlah fauna is one of very few 'rocky-shore' communities recorded from the Late Cretaceous. In their review of rocky shores through time, Johnson and Baarli (1999, p. 269) stated that 'coeval diversities of rocky-shore biotas at some low latitudes are substantially impoverished . . .'. The single fossil assemblage in their database from a palaeolatitude of less than 30 degrees (southern Spain; González-Donoso *et al.* 1983) contained only one species. The 27 encrusting and five boring taxa described here from the nearly equatorial Qahlah are significant additions to the rocky-shore fossil record, and represent the first evidence that Late Cretaceous rocky shore community diversity was relatively high in tropical latitudes.

The Qahlah Formation is virtually unique in its composition and depositional environment. There are



TEXT-FIG. 3. Diversities of colonisers (encrusters and borers) on individual clasts belonging to the three main types. Bars for the chert cobbles are subdivided with the upper, hatched portion representing cobbles from the coral bed.

very few well-exposed ophiolites, and even fewer with an overlying sediment consisting of ophiolitic clastics deposited in shallow, tropical marine waters. The closest sedimentological analogue would be the Pakhna Formation (Miocene) on Cyprus, which in part consists of a mix of ophiolitic clasts, carbonates, and bioclastic debris. Most of this unit was deposited as mass flows in deeper water, however, and encrusters or borers on the cobbles have not been recorded (Eaton and Robertson 1993).

The nearest palaeontological analogue to the Qahlah Formation encrusters and borers is the Lower Cretaceous (Upper Aptian) Faringdon Sponge Gravel in southern England. Like the Qahlah, the Faringdon Sponge Gravel contains thick beds of cobbles and pebbles deposited under tidal influence in shallow, high-energy waters (Krantz 1972). The Faringdon Sponge Gravel also contains carbonate and silicate clasts. The carbonate cobbles and pebbles are mostly clayey micrite and calcareous claystone; the silicate clasts are quartzite and a few bits of rhyolite (Wilson 1986). Like the Qahlah, the carbonate clasts are usually thoroughly bored by *Gastrochaenolites*, sometimes with bivalve shells still intact. Unlike the Qahlah, the Faringdon cobbles and pebbles have a more diverse ichnofauna, including abundant borings by sponges (*Entobia*) and 'worms' (*Maeandropolydora* and *Trypanites*).

The encrusting fauna on the Faringdon clasts is also about twice as diverse in species richness and abundance compared to the Qahlah assemblages (Wilson 1986). There are 23 encrusting bryozoan species from the Faringdon, compared with 11 from the Qahlah. Placopsilininid foraminiferans and *Nubeculinella* are common on both the Faringdon and Qahlah clasts, but Faringdon also has three other foraminiferan species. Faringdon has four serpulid species compared to the two that are recognisable in the Qahlah. The Faringdon clast-encrusting fauna also contains abundant calcareous sponges, which are thus far unknown in the Qahlah. Conversely, the Qahlah encrusters include at least seven species of coral, whereas there are no corals in the Faringdon.

The reasons for the diversity and abundance differences between the Faringdon and Qahlah clasts can be several. The Faringdon calcareous cobbles are so thoroughly bored with *Gastrochaenolites* that they had a network of intersecting tunnels which housed a diverse cryptic fauna protected from abrasion (Wilson 1986). The Qahlah cobbles also appear to have experienced more abrasion than their Faringdon counterparts, as shown by the greater truncation of *Gastrochaenolites*. The higher levels of abrasion would have not only eliminated many encrusters, but also removed shallow borers such as *Entobia*. The lack of corals in the Faringdon shows that there were some significant palaeoenvironmental differences with the Qahlah, but much of the diversity variance may be due to taphonomic factors.

Bryan (1992) described a fauna on sandstone cobbles from the Maastrichtian Prairie Bluff Formation in south-central Alabama, USA. These cobbles host a low-diversity assemblage of encrusters dominated by cementing bivalves (mostly oysters), serpulids, and cheilostome bryozoans. The encrusters are found mostly on the sides of the cobbles (most of the bryozoans) and the top surface of the cobbles (most of the cemented bivalves), suggesting that they were stable after colonisation and buried in deep, quiet waters. The Prairie Bluff cobble fauna is thus contemporary with the Qahlah fauna, but very different in its depositional environment.

Another cobble- and boulder-dwelling fauna contemporary with the Qahlah Formation was described by Surlyk and Christensen (1974) from the Upper Cretaceous of Scania, Sweden. The clasts in the Scania deposit are composed of gneiss derived from exposed bedrock along a Cretaceous rocky coast. The encrusting fauna (there are no borings) is diverse and abundant. Like the Prairie Bluff cobbles of Bryan (1992), the encrusters are found in distinct zones, indicating that the clasts were no longer moving after they were colonised. The enclosing transgressive sediments suggest that these cobbles and boulders, like their Prairie Bluff counterparts, were occupied in considerably lower energy waters than the Qahlah clasts.

Zítt (1992) analyzed an Upper Cretaceous gravel sequence and its biota in central Bohemia. The clasts are, like the Qahlah, dominantly igneous pebbles and cobbles (gneisses in this case) and oyster bioclasts. Encrusting diversity is considerably lower than the Qahlah; it includes two foraminifer species, two serpulid species, and six species of attaching bivalves. Zítt (1992) also noted the taphonomic difficulties of studying a gravel-dwelling fauna, including most importantly the potential mixing of clasts from different environments, and their consequently more complex colonisation history.

Both Lescinsky *et al.* (1991) and Johnson and Baarli (1999) have provided useful reviews of Late Cretaceous rocky-shore biotas which need not be repeated here. These reviews permit typical and atypical characteristics exhibited by the Qahlah biota to be identified in the context of the broader picture which is emerging for rocky-shore biotas of this age. Encrusting groups including oysters, serpulid worms, agglutinating foraminifera and bryozoans, together with the ichnogenera *Gastrochaenolites* and *Entobia* are shared between the Qahlah and most other Late Cretaceous rocky-shore biotas. Scleractinian corals as well as bryozoans are more diverse in the Qahlah than elsewhere, although for bryozoans this may be, at least in part, an artefact of a lack of taxonomic work. While it is difficult to draw any firm conclusions from the absence of taxa (Lescinsky *et al.* 1991) in these assemblages, it is nevertheless worth mentioning some common components of Late Cretaceous rocky-shore assemblages yet to be found in the Qahlah. Cemented spondylid and atretid bivalves have not been recorded on clasts in the Qahlah. Also absent are thecidean and craniid brachiopods, which is surprising because they are typically associated with low- to mid-latitudes and cryptic habitats.

CONCLUSIONS

The Maastrichtian Qahlah Formation of Oman and the United Arab Emirates contains a remarkably wide variety of hard substrates, including silicate clasts, *in situ* carbonate hardgrounds, carbonate hardground clasts, older limestone pebbles, calcareous bioclasts, and wood. These hard substrates hosted a unique assemblage of shallow, tropical, marine encrusting and boring organisms. The Qahlah hard substrate faunas can be categorised as robust skeletal encrusters (oysters and corals), cryptic encrusters (bryozoans and serpulids found on undersides, within vacated borings or prelithification burrows) and endolithic taxa (bivalves, sponges and barnacles). Delicate agglutinated foraminifera are found anomalously on exposed surfaces, sometimes covering truncated borings. These foraminifera may have recruited quickly enough to maintain a presence on the clast exteriors despite the abrasion, or they may less likely have lived interstitially on stable clasts below the sediment-water interface.

The Qahlah hard substrate assemblage is a rare example of a tropical rocky-shore community surviving from the Late Cretaceous. It adds significantly to the growing historical narrative of this ecosystem (e.g. Johnson and Baarli 1999), and promises to be especially useful in subsequent work on latitudinal diversity gradients and recovery from the end-Cretaceous mass extinction.

Acknowledgements. Fieldwork for this research was made possible by a generous grant to the NHM from ADCO (Abu Dhabi), negotiated and administered by Peter Whybrow for the NHM. Additional support came from the Luce Fund for Distinguished Scholarship at The College of Wooster. We are very grateful for the collecting efforts and field assistance of Andrew Smith, Andy Gale, Noel Morris and Phil Crabb, as well as the hospitality of Professor A. Alsharhan and other staff in the Geology Department, UAE University, Al Ain. Particular thanks go to Rosemarie Baron-Szabo for identifying the corals, and to Noel Morris and Richard Hodgkinson for help with the bivalves and foraminifers respectively. Sian Evans kindly allowed us to use some findings from her unpublished PhD research on wood-boring bivalves. We thank Rachel Wood and Tim Palmer for their useful reviews of this manuscript.

REFERENCES

- ALSHARHAN, A. S. and NASIR, S. J. Y. 1996. Sedimentological and geochemical interpretation of a transgressive sequence: the Late Cretaceous Qahlah Formation in the western Oman Mountains, United Arab Emirates. *Sedimentary Geology*, **101**, 227–242.
- BAVESTRELLO, G., BIANCHI, C. N., CALCINAI, B., CATTANEO-VIETTI, R., CERRANO, C., MORRI, C., PUCE, S. and SARA, M. 2000. Bio-mineralogy as a structuring factor for marine epibenthic communities. *Marine Ecology Progress Series*, **193**, 241–249.
- BERTLING, M. 1992. *Arachnostega* n. ichnogen – burrowing traces in internal moulds of boring bivalves (Late Jurassic, northern Germany). *Paläontologische Zeitschrift*, **66**, 177–185.
- BROMLEY, R. G. 1975. Comparative analysis of fossil and recent echinoid bioerosion. *Palaontology*, **18**, 725–739.
- BRYAN, J. R. 1992. Origin and paleoecology of Maastrichtian rockground and chalk facies in south-central Alabama. *Palaos*, **7**, 67–76.
- CONNELL, S. D. 2000. Floating pontoons create novel habitats for subtidal epibiota. *Journal of Experimental Marine Biology and Ecology*, **247**, 183–194.
- DALY, M. A. and MATHIESON, A. C. 1977. The effect of sand movement on intertidal seaweeds and selected invertebrates at Bound Rock, New Hampshire, USA. *Marine Biology*, **43**, 45–56.
- DURINGER, P. 1985. Stratégie adaptative de la croissance de *Placunopsis ostracina* Schlotheim, épizoaire du Muschelkalk supérieur (Trias germanique, Est de la France). *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, **1985**, 1–22.
- EATON, S. and ROBERTSON, A. H. F. 1993. The Miocene Pakhna Formation, southern Cyprus, and its relationship to the Neogene tectonic evolution of the eastern Mediterranean. *Sedimentary Geology*, **86**, 273–296.
- EL-SAYED, M. I. 1999. Tidal flat rocks and sediments along the eastern coast of the United Arab Emirates. *Carbonates and Evaporites*, **14**, 106–120.
- EVANS, S. 1997. The palaeoecology of marine driftwood with special reference to the wood-boring bivalves. Unpublished PhD thesis, Imperial College, 315 pp.
- FÜRSICH, F. T., PALMER, T. J. and GOODYEAR, K. L. 1994. Growth and disintegration of bivalve-dominated patch reefs in the Upper Jurassic of southern England. *Palaontology*, **37**, 131–171.
- GLASBY, T. M. 2000. Surface composition and orientation interact to affect subtidal epibiota. *Journal of Experimental Marine Biology and Ecology*, **248**, 177–190.
- GOLDRING, R. 1995. Organisms and the substrate. 151–180. In BOSENCE, D. W. J. and ALLISON, P. A. (eds). *Marine palaeoenvironmental analysis from fossils. Geological Society, London, Special Publication*, **83**, 272 pp.
- GONZÁLEZ-DONOSO, J. M., LINARES, D., MARTÍN-ALGARRA, A., REBOLLO, M., SERRANO, F. and VERA, J. A. 1983. Discontinuidades estratigráficas durante el Cretácico en el Penibético (Cordillera Bética). *Estudios Geológicos (Madrid)*, **39**, 71–116.
- HODGKINSON, R. L. 1992. ‘*Placopsilina*’ *cenomana* d’Orbigny from France and England and the type species of *Placopsilina* d’Orbigny, 1850 (Foraminifera). *Bulletin of the British Museum (Natural History), Geology Series*, **48**, 1–8.
- JOHNSON, M. E. 1988. Why are ancient rocky shores so uncommon? *Journal of Geology*, **96**, 469–480.
- and BAARLI, B. G. 1999. Diversification of rocky-shore biotas through geologic time. *Geobios*, **32**, 257–273.
- KELLY, S. R. A. and BROMLEY, R. G. 1984. Ichnological nomenclature of clavate borings. *Palaontology*, **27**, 793–807.
- KRANTZ, R. 1972. Die Sponge-Gravels von Faringdon (England). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **140**, 207–231.
- LESCINSKY, H. L., LEDESMA-VÁZQUEZ, J. and JOHNSON, M. E. 1991. Dynamics of Late Cretaceous rocky shores (Rosario Formation) from Baja California, Mexico. *Palaos*, **6**, 126–141.
- MARTINIUS, A. W. and MOLENAAR, N. 1991. A coral-mollusc (*Goniaraea-Crassatella*) dominated hardground community in a siliciclastic-carbonate sandstone (the Lower Eocene Roda Formation, southern Pyrenees, Spain). *Palaos*, **6**, 142–155.
- NOLAN, S. C., SKELTON, P. W., CLISSOLD, B. P. and SMEWING, J. D. 1990. Maastrichtian to Early Tertiary stratigraphy and palaeogeography of the central and northern Oman Mountains. 495–519. In ROBERTSON, A. H. F., SEARLE, M. P. and RIES, A. C. (eds.). *The geology and tectonics of the Oman region. Geological Society, London, Special Publication*, **49**, 849 pp.
- POZARYSKA, K. and VOIGT, E. 1985. Bryozoans as substratum of fossil fistulose Foraminifera (Fam. Polymorphinidae). *Lethaia*, **18**, 155–165.
- ROBERTSON, A. H. F. and WOODCOCK, N. H. 1983. Genesis of the Batinah mélange above the Semail ophiolite, Oman. *Journal of Structural Geology*, **5**, 1–17.
- SAVDRA, C. E., OZALAS, K., DEMKO, T. H., HUCHISON, R. A. and SCHEIWE, T. D. 1993. Log-grounds and the ichnofossil

- Teredolites* in transgressive deposits of the Clayton formation (Lower Paleocene), western Alabama. *Palaios*, **8**, 311–324.
- SEARLE, M. and COX, J. 1999. Tectonic setting, origin, and obduction of the Oman ophiolite. *Geological Society of America Bulletin*, **111**, 104–122.
- SKELTON, P. W., NOLAN, S. C. and SCOTT, R. W. 1990. The Maastrichtian transgression onto the northwestern flank of the Proto-Oman Mountains: sequences of rudist-bearing beach to open shelf facies. 521–547. In ROBERTSON, A. H. F., SEARLE, M. P. and RIES, A. C. (eds). The geology and tectonics of the Oman region. *Geological Society, London, Special Publication*, **49**, 846 pp.
- SMITH, A. B., MORRIS, N. J., KENNEDY, W. J. and GALE, A. S. 1995. Late Cretaceous carbonate platform faunas of the United Arab Emirates-Oman border region. *Bulletin of the Natural History Museum, London (Geology)*, **51**, 91–119.
- SURLYK, F. and CHRISTENSEN, W. K. 1974. Epifaunal zonation on an Upper Cretaceous rocky coast. *Geology*, **2**, 529–534.
- TAYLOR, P. D. 1988. Colony growth pattern and astogenetic gradients in the Cretaceous cheilostome bryozoan *Herpetopora*. *Palaeontology*, **31**, 519–549.
- 1990a. The impact of the SEM in studies of living and fossil bryozoans. 259–280. In CLAUGHER, D. (ed.) Scanning electron microscopy in taxonomy and functional morphology. *Systematics Association, Special Volume* **41**, 315 pp.
- 1990b. Encrusters. 346–351. In BRIGGS, D. E. G. and CROWTHER, P. R. (eds). *Palaeobiology: a synthesis*. Blackwell Scientific Publications, Oxford, 608 pp.
- 1990c. Preservation of soft-bodied and other organisms by bioimmuration – a review. *Palaeontology*, **33**, 1–17.
- 1995. Late Campanian–Maastrichtian Bryozoa from the United Arab Emirates-Oman border region. *Bulletin of the Natural History Museum, London (Geology)*, **51**, 267–273.
- 1999. Bryozoa. 623–646. In SAVAZZI, E. (ed.) *Functional morphology of the invertebrate skeleton*. Wiley, Chichester, 706 pp.
- and TODD, J. A. 1990. Sandwiched fossils. *Geology Today*, **6**, 151–154.
- VENNIN, E., BARRIER, P., SOUDET, H. J., BIDEAU, T. and PROUDHON, B. 1999. Architecture of Maastrichtian carbonate deposits of the United Arab Emirates and Oman Sultanate border region. *Bulletin des Centres de Recherches Exploration-Production Elf Aquitaine*, **22** (for 1998), 71–95.
- WILSON, M. A. 1986. Coelobites and spatial refuges in a Lower Cretaceous cobble-dwelling hardground fauna. *Palaeontology*, **29**, 691–703.
- 1987. Ecological dynamics on pebbles, cobbles, and boulders. *Palaios*, **2**, 594–599.
- OZANNE, C. R. and PALMER, T. J. 1998. Origin and paleoecology of free-rolling oyster accumulations (ostreoliths) in the Middle Jurassic of southwestern Utah, USA. *Palaios*, **13**, 68–76.
- and PALMER, T. J. 1992. Hardgrounds and hardground faunas. *University of Wales, Aberystwyth, Institute of Earth Studies Publications*, **9**, 1–131.
- and TAYLOR, P. D. 1996. Ordovician bioimmurations and skeletalization of hard substratum communities through geological time. *Geological Society of America, Abstracts with Programs*, **28** (7), 290–291.
- ZÍTT, J. 1992. A new occurrence of Upper Cretaceous epibionts cemented to the rocky substrates and bioclasts (locality Radim, Czechoslovakia). *Casopis pro Mineralogii a Geologii*, **37**, 145–154.
- and NEKVASILOVÁ, O. 1991. Epibionts cemented to rocky bottom and clasts in the Upper Cretaceous of Zelezné Hory Mountains (Czechoslovakia). *Casopis Národního Muzea, Rada Přírodovědná*, **156**, 17–35. [Dated 1987 but published in 1991].
- and NEKVASILOVÁ, O. 1996. Epibionts, their hard-rock substrates, and phosphogenesis during the Cenomanian–Turonian boundary interval (Bohemian Cretaceous Basin, Czech Republic). *Cretaceous Research*, **17**, 715–739.

MARK A. WILSON

Department of Geology
The College of Wooster
Wooster, Ohio 44691, USA
e-mail mwilson@acs.wooster.edu

PAUL D. TAYLOR

Department of Palaeontology
The Natural History Museum
London SW7 5BD, UK
e-mail pdt@nhm.ac.uk

Typescript received 24 January 2000

Revised typescript received 26 May 2000