HARDGROUNDS AND HARDGROUND FAUNAS

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Front cover photograph. Middle Jurassic coelobite fauna growing on the roof of a cavity excavated beneath a hardground described by Palmer and Fürsich (1974). Serpulid worms and *Berenicea*-type bryozoans typically dominate such cavity faunas. Compare with typical Jurassic upward-facing surfaces, such as those in Figures 32 and 39. Width of view is 6 mm.

ECOLOGY AND PALEOECOLOGY OF HARDGROUND FAUNAS

TEMPORAL TRENDS IN HARDGROUND COMMUNITIES

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INTRODUCTION

Hardgrounds, synsedimentarily lithified carbonate sea-floors, are fascinating geological and biological systems. They are found throughout the Phanerozoic in sufficient numbers to be geologically useful, yet well-preserved examples are scarce enough to be of unusual interest. Hardgrounds formed under a fairly consistent set of physical parameters, so we can use them to estimate ancient sedimentation and erosion rates, oceanic geochemistry, and tectonic and eustatic changes in sea level. The consistent physical environment offered by hardgrounds also enables us to plot the patterns of evolution of various organisms which became adapted to these hard substrates. These evolutionary patterns can be studied at the clade or community levels. Well-preserved hardground faunas also give us opportunities to analyze a paleoecosystem with an accuracy not possible in most other fossil assemblages.

This paper is primarily designed to introduce geologists to the study of hardgrounds by providing a survey of their common features and faunas, along with a thorough citation of the relevant literature. We have written this paper for a Paleontological Society workshop on hardgrounds, but we hope it is also useful outside these brief classroom moments. We are paleontologists and carbonate sedimentologists, and this paper shows our mix of interests. Those topics we know well we elaborate; those topics we are less familiar with we refer the readers to other literature. We do not consider this paper to be the definitive text on hardgrounds, but view it instead as a guide to their study through the work of dozens of experts.

For the past few years we have been accumulating a large collection of hardground samples, both lithologic and paleontologic, in the Department of Geology at The College of Wooster. We are also assembling a library of hardground-related papers and books. Any interested geologist is invited to visit Wooster and examine these collections, and we are always soliciting additional donations of rocks, fossils and reprints.

We encourage other members of the geological community to study, or at least notice, hardgrounds and their associated fossils. There is much useful geological information encoded within ancient hardgrounds, and simply recognizing them is a start toward understanding their development and evolution.

Where possible, fossils and rocks figured in this work have been given numbers. "OSU" refers to specimens housed in the Department of Geological Sciences at Ohio State University; "C/W" is the prefix for specimens stored at The College of Wooster.

Finally, a major portion of these notes is devoted to an extensive bibliography of lithologic substrate studies. Most of the citations in the text can be found in this large compendium starting on page 61. There are some citations used here, though, which do not directly concern lithologic substrates; these are listed in the "Additional References Cited" section beginning on page 129.

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HARDGROUNDS: PHYSICAL FEATURES AND PROCESSES

Hardgrounds Proper

Sedimentological definition.--Hardgrounds are synsedimentarily lithified carbonate sea-floors that became hardened *in situ* by the precipitation of a carbonate cement in the primary pore spaces. To the sedimentologist studying Recent carbonate sediments, the term describes the consequence of the precipitation of cement within a soft sediment on the sea floor, contemporaneously with or soon after deposition (Bathurst, 1975; Bromley, 1975a). Essentially, sedimentation and cementation occur in the same submarine environment, giving rise to a hard sea-floor which may then be colonized by a fauna and flora that show adaptations to hard-substrate dwelling. Ideally, the term should be used for the same circumstances when applied to the ancient record, but it is not always certain that the cementation of the surface of a unit necessarily took place in the same submarine environment in which the bed was originally deposited. Cementation episodes, for example, may also represent intervals of exposure to meteoric waters or burial, with colonization and renewed sedimentation following resubmergence or erosion. Only detailed study of cement textures and fabrics, and maybe trace-elements and isotopes, can distinguish such cases from true hardgrounds formed by synsedimentary submarine cementation.

Paleontological concerns.--To the student of the faunas of ancient hard substrates, the details of the environment of substrate cementation or the precise timing of substrate hardening relative to colonization may or may not be important, depending on the type of study. Primary descriptions of community composition, species interactions, succession, or spatial distributions do not necessarily require the elucidation of the substrate's cementation history. Comparative studies, however, in which hardground faunas of different ages are compared in order to determine long term evolutionary trends in community composition and structure, require maximum information about environments of cementation and colonization in order to ensure that the communities being compared across the ages come from as similar environments as possible (Palmer, 1982; Wilson and Palmer, 1990).

Just as sedimentological detail may or may not be of concern to the student of hardground faunas, so the faunas may or may not be of concern to the hardground sedimentologist. The principal reason why sedimentologists ignore the fauna at their peril, however, is that it is often the fauna that unequivocally points the finger at the lithified character of the original sediment surface. Although many hardgrounds show a characteristic mineral staining (most commonly by iron minerals) at or just below their surface, which can draw attention to the surface in outcrop, this is not always present (particularly in coarser-grained lithologies). In the absence of such staining it is the presence of the boring and encrusting fauna alone that testifies at the macroscopic level to the originally hard character of the surface.

Early hardground studies and terminology.--Bromley, whose major paper in 1967 heralded the modern era of English language hardground studies, has outlined the early history of hardground research and discussed the usages of some of the terms under which hardgrounds have been known in the past (Bromley, 1975a). The term "hardground" derives from oceanographic studies, at a time when sea-floor sediments were sampled from wax attached to the weight on the end of a sounding line. A hardground was a hard sea floor that returned no sediment. The term was adopted in the geological literature for an intraformational hard surface. The synsedimentary origin of the lithification has particularly been stressed since the acceptance by the English-speaking world in the late 1960's that cements could precipitate on the floors of Recent seas (e.g. Shinn, 1969), and that a period of emergence, though often resulting in cementation, was not the only process by which shallow water carbonate sediments could be lithified.

Hardgrounds represent intervals of time during which sedimentation did not take place, cement precipitated, and specialized faunas flourished. Many of the earlier terms under which hardgrounds have been mentioned stress this gap in time and interruption in sedimentation. Thus the term "discontinuity surface" for a minor break in the stratigraphic column (ranking lower than an disconformity), which includes hardgrounds as well as some other junctions between minor lithostratigraphic units, stresses the omission of sediment (e.g. Jaanusson, 1961). The term "omission surface", renewed by Bromley (1975a), is virtually synonymous, being a surface exposed at the sea floor for a brief period of time between two intervals of sedimentation. It should be stressed, however, that although synsedimentary cement precipitation is a process that has often occurred during such sedimentary hiatuses, in neither of these two terms is such lithification part of the strict definition, whereas in the term "hardground" it is.

The time break represented by hardgrounds has often permitted episodes of erosion, and hardgrounds themselves often show truncation of fossils (Figure 1), grains, and early cements at their surfaces. The importance of solution to such erosion processes increases with depth, at least in Recent seas, and has been termed "subsolution" by Heim (1958). Thus some hardgrounds may represent "subsolution surfaces". In North America, significant observations were made on Middle Ordovician hardgrounds in the Upper Mississippi Valley region by Sardeson (1898, 1914), Prokopovic (1955), and Weiss (1954, 1958). The latter two authors considered dissolution (= corrosion) to have been particularly important in determining the character of these surfaces, and called them "corrosion surfaces" or "corrosion zones". Although recent evidence has shown that submarine dissolution of aragonite occurred in Ordovician hardgrounds (Palmer et al., 1988), the features that were attributed to dissolution by Weiss (1958) are preomission burrows, excavated in the hardground bed before lithification, but preserved as open galleries by cementation within the host sediment (Palmer, 1978). These Champlainian hardgrounds, however, are locally smoothly polished by scour and physical abrasion (corrasion) from shoals of soft sediment that swept around on their surfaces (Figure 2). The term "corrasion surface" is thus occasionally encountered.

Other Marine Hard Substrates

Biogenic hard substrates.--True hardgrounds provide only one of the several types of hard substrate that are studied by paleontologists with an interest in the identity and paleoecology of the faunas in such environments. By far the most abundant hard substrates in modern and most ancient seas are provided by dead shells and other bioclastic debris, and in some cases by the skeletons of the living biota as well. Most skeletons of marine benthos from oxic sea-bottoms show some evidence of surface colonization, and the majority of studies that have involved hard-substrate-dwelling species have been made on biogenic substrates (see Alexander and Brett, 1990). These are not dealt with here. Reefs constructed by frame-building skeletal organisms particularly tend to have a diverse associated epifauna. Reefs often provide sites for extensive development of contemporaneous cement, precipitated directly from the surrounding sea-water, which may partially or completely fill primary cavities within the reef, and which may also cement soft sediment that settles within the reef interstices. Thus within many reef bodies only some of the available hard substrate is of primary biogenic origin: the rest is inorganic and is directly comparable to true hardground. To the encrusting and boring fauna and flora of the primary framework and of the reef-rock, the organic or inorganic origin of the substrate is probably of no great importance (though there may be differences in hardness, erosion resistance, and organic content). Studies of the associated faunas of reefs have not generally distinguished between those boring and encrusting forms that colonize biogenic hard substrate (endobionts and epibionts) and those that infest and attach to early cemented material (endoliths and epiliths).

Rockgrounds and unconformities.--True hardgrounds representing rapid *in situ* cementation prior to deposition of the next bed of sediment show no evidence of a biostratigraphic break across the surface. But surfaces that were hardened in one environment and then exposed to sea-floor processes as a result of transgression or erosion of overlying strata may show biostratigraphic evidence of a hiatus and thus constitute discontinuity surfaces, disconformities or unconformities on which a rich fauna may have flourished before sediment buried the surface. These colonized unconformable surfaces are often referred to as "rockgrounds" (Fürsich, 1979). Rockgrounds show a variety of lithologies above and below the surface. Faunas appear to be most diverse when the underlying lithology is a limestone (e.g. the Mississippian/Jurassic contact in southwest England, see Figure 3; Hölder and Hollmann, 1969; Fürsich, 1979) because chemically-boring endoliths are only found in carbonate substrates. Rockgrounds and other aspects of rocky shores have been discussed and cataloged by Johnson (1988a, 1988b, 1992).

Rockgrounds resulting from transgression across former land surfaces often do not show good preservation of an encrusting fauna because of their high energy nature, being overlain by conglomerates or other abrasive, high-energy deposits. However, sometimes the large clasts themselves are sites for epilith colonization, and may show differences in faunal composition on tops, sides, and bottoms of cobbles and boulders (Wilson, 1987, and references therein).

Young rockgrounds, representing short intervals of geologic time and bounded by similar sediments deposited in similar environments but cemented during a geologically-brief time when different conditions prevailed, may be difficult to tell from true hardgrounds without close petrographic study. Particularly, some described ancient hardgrounds may actually represent hitherto unrecognized intervals of emergence and meteoric cementation. In 100 million years time, the rockground junction between Holocene and Pleistocene carbonates, seen so widely in the Caribbean today, may well be mistaken for a synsedimentary hardground by some sedimentological novice who fails to closely examine the cements.

Hiatus concretions.--A third category of hard substrate that has been the subject of several faunal studies is hiatus concretions (Voigt, 1968). These are exhumed, early-diagenetic carbonate-cemented nodules and concretions, often showing septarian cracking, that grew a few centimeters to meters below the sediment/water interface, predominantly (but not exclusively) in organic-rich, fine-grained, clastic sediments. Such concretions, normally occurring at discrete horizons and sometimes coalescing to form more continuous nodular layers, are common features of many mudrocks but usually show no signs of exhumation. In some cases, however, erosion of overlying soft sediment has exposed the concretions so that they lay on the sea floor as a lag. Sometimes many generations of reburial, further growth, and re-exhumation can be recognized. Such hiatus concretions represented islands of hard substrate in an inhospitable sea of soft sediment and are often heavily bored and encrusted. Hiatus concretion faunas have been described from the Ordovician (Wilson, 1985a), Devonian (Baird, 1976, 1978, 1981), Jurassic (Voigt, 1968; Hallam, 1969; Kazmierczak, 1974; Baird and Fürsich, 1975; Fürsich, 1979; Hesselbo and Palmer, 1992), and Cretaceous (Kennedy and Klinger, 1972; Kennedy and Garrison, 1975a, b; Kennedy et al., 1977).

Formation of hardgrounds

It was only at the end of the 1960's that sea-floor cementation of carbonate sediments became accepted as a widespread phenomenon in Recent and ancient shelf seas. Since that time, extensive research on the sea floor diagenetic environment has led to a general understanding of the processes involved in synsedimentary cementation, and of the variations on the theme that are encountered across space and time. They have been summarized in several review articles and recent textbooks (e.g. Bathurst, 1971; Bromley, 1978; Longman, 1980; James and Choquette, 1983; Tucker and Wright, 1990). It is beyond the scope of these notes to discuss sedimentological details of hardground formation processes, but the main points are summarized below

Rates of hardground lithification.--Cementation of some hardgrounds probably occurred rapidly, particularly in calcite-precipitating seas (see below), with enough cement to confer rigidity being precipitated within years or tens of years. Others may have taken one or two orders of magnitude longer than this. All hardgrounds represent something of a break in sedimentation, though we suspect that the lengths of time represented by the most rapidly formed hardgrounds are no longer than those represented by many bedding planes in sequences without synsedimentary cementation. Clearly rates of lithification will have been influenced by matters such as sediment porosity and permeability, rates of pore water exchange, supply of ions to precipitation sites, replenishment of the overlying seawater with dissolved calcium and bicarbonate ions, and character of the substrate on which cement crystals nucleated. Lithification of mudstones and wackestones, with their low permeabilities, may be expected to have taken place much more slowly than that of highly-permeable grainstones and rudstones. Today, cementation within reefs to produce reef rock is particularly rapid because of the rapid pumping of seawater through reef porosity in high energy reefal environments, whereas formation of lithified crusts in deep-sea oozes probably takes many thousands of years.

Cement minerals.--The carbonate minerals that cement hardgrounds are calcite (LMC), magnesian calcite (HMC), and aragonite. Holocene shallow-water hardgrounds are cemented by aragonite and/or HMC. Passing into deeper water, calcite becomes predominant, with the proportion of magnesium falling with depth, reflecting falling temperatures (Schlager and James, 1978). The predominance of aragonite and HMC in shallow water hardground cements seems also to have been true for the Tertiary (though Tertiary shallow water hardgrounds are poorly known), and for the Pennsylvanian, Permian and (maybe) the Triassic, based on similarities in composition between early marine cements and marine ooliths of the same age. However, early marine cements of these ages have invariably been altered to LMC in diagenesis and their original compositions must be inferred from relict textures and trace element signatures (aragonite inclusions or high Sr in altered aragonite, for example; Sandberg, 1983, 1985). Hardgrounds of other ages are cemented by LMC, which was almost certainly the original composition of the sea-floor cements. This important matter of the changing composition of early marine cements across the Phanerozoic is referred to more fully below.

Cement supply.--For carbonate hardground cements to grow, Ca^{++} and CO_3^{--} ions must be supplied in sufficient concentrations. The carbonate is mostly in solution as the HCO_3^- ion, which is one of the ions resulting from the dissolution of carbon dioxide in water. Seawater contains abundant dissolved CO_2, from the lithosphere, the atmosphere, and from respiration of marine organisms. Much hardground cement probably results from flushing of large volumes of seawater through the sediment pores. Locally within organic-rich sediments, particularly in finer-grained settings with reduced permeability and flushing, bacterial respiration processes may result in localized concentrations of bicarbonate which may promote carbonate precipitation. Bacterial bicarbonate generation is often more stressed in studies of the early diagenesis of clastic sediments (such as may give rise to hiatus concretions) than in carbonates, in which seawater saturation is the general rule. Some studies (e.g. Jeans, 1980), however, have stressed its role in hardground formation.

In deeper Recent seas, aragonite bioclasts on or just below the sea-floor may go into solution and supplement the supply of dissolved ions for calcite cementation. This process happened much more extensively in ancient calcite-precipitating seas, even in shallow water

(Palmer et al., 1988), and may represent an important additional source of cement that is not widely recognized in many ancient shallow water hardgrounds.

Growth of cement.--Hardgrounds that precipitate from circulating seawater need large amounts of water to pass through the sediment. To yield a single volume of cement, on the order of 50,000 volumes of water are probably required. Seawater circulation is most efficient through the uppermost few centimeters of the sediment, falling off downwards. Thus cementation is most complete just below the seafloor, often forming a crust of a few cm thickness, whose degree of cementation lessens downwards eventually passing down into uncemented sediment. Local permeability differences (often related to bioturbation of the initial soft sediment) may result in patchy cementation (Marshall and Ashton, 1980).

Hardgrounds that cement from internally-generated carbonate resulting from bacterial respiration of organic matter (see Curtis, 1977) will also tend to be concentrated in layers just below the sediment surface because they are dependent on diffusion of oxygen (either as free O_2 or as sulfate ions) from overlying seawater. Layers may again be patchy or may occur as discrete nodules that enlarge and coalesce as a result of permeability heterogeneities or concentrations of organic matter, possibly reflecting relict bioturbation texture. Erosive events affecting such layers before the growing nodules have had time to coalesce may winnow away soft sediment and leave a lag of exhumed nodules. Sometimes, hardgrounds pass laterally into such cobble horizons. They are common in Jurassic limestones and Cretaceous chalks (Kennedy and Garrison, 1975a; Fürsich, 1979; Bromley and Gale, 1982; Gale et al., 1987).

Cementation by calcite resulting from aragonite dissolution may be confined to the region immediately adjacent to the dissolving bioclast, particularly in finer-grained lithologies in which pore-water flushing is reduced. Local centers of growth around aragonite grains may enlarge and coalesce to form continuous cemented layers in sediments initially rich in aragonite fauna. This may be a significant way of cementing low permeability sediments. In coarser-grained, more permeable sediments, ions released from aragonite dissolution will mix with sea water to supplement the general dissolved bicarbonate pool. For further discussion and details of early calcite cement derived from aragonite dissolution, see Wilson et al. (1992) and references therein.

Cement petrography.--The fabrics of the early cements in hardgrounds are variable. The most easily recognized type is an isopachous rind of crystals growing perpendicular to the surface of the grains. Aragonite crystals in such rinds are acicular (Figures 4, 5 and 6), whereas LMC and HMC crystals are typically more stubby or bladed, or may have a micritic form (Figure 7). However, individual crystal shapes may be strongly influenced by the shape and orientations of the crystals that make up the allochems on which they seed. In Ordovician hardgrounds, for example, early LMC cements growing on ostracods and trilobites (which are made up of a pallisade of rod-like calcite crystals growing with their C-axes perpendicular to the skeletal surface) grow by syntaxial enlargement of the skeletal crystals to form a rim cement of acicular calcite, superficially resembling aragonite (Figure 8). In all calcite sea hardgrounds, early cements tend to form large, rapidly-grown syntaxial rims on echinoderms (e.g. Purser, 1969), which tend to be thicker along the C-axis direction (Figures 9 and 10). Many Ordovician and Jurassic hardgrounds developed in grainstones that were almost entirely made up of echinoderm debris, and nearly all the early cement is of this kind.

Rim cements are most clearly developed in grainstone fabrics with good porosity. Rim thicknesses diminish over a distance of 10 - 20 centimeters down from the hardground surface, reflecting the reduction in sea-water circulation, but even in the upper parts of hardground profiles, significant volumes of primary pore space may remain after completion of marine cementation. Pore spaces in the upper parts of hardgrounds often show fine sediment geopetally or completely filling remaining primary porosity (Figure 9). This internal sediment overlies the early cement and has probably filtered down from the sea bed or been carried in by an interstitial meiofauna, though some workers have suggested that it is a primary precipitate (Reid et al., 1990). In the absence of internal sediment, late diagenetic (usually blocky calcite) cements overlie the early cements (Figure 11). The junction between the two cement generations is sometimes marked by a pyrite-rich zone (Figure 12). This probably reflects passage of the hardground through the sulfate reduction zone as it became buried beneath accumulating sediment.

Hardgrounds developed in finer-grained lithologies seldom show unequivocal early cement fabrics on account of the small pore sizes. Cements are micritic. Micrite cements, however, may also lithify grainstones or sediments with even larger pore spaces: they are very common in reefs, for example. The micrite may grow as a thin rim around the grains, or occupy large volumes. In the latter case, it usually has a clotted or peloidal appearance in which discrete spheroidal aggregates of micrite crystals, up to about 60 microns across, can be distinguished (Figure 13). Recent micrite cements are HMC (Figure 14), but those forming in calcite seas were probably LMC (Figure 15). In the absence of contemporaneous borings cutting through them, it is often difficult to recognize then as cements. A bacterial involvement has been implicated in their origin (Chafetz, 1986).

Associated mineralization.--Hardground surfaces, and the walls of burrows and borings that descend from them, are often mineral stained (Figure 16). Iron minerals such as pyrite (which readily oxidizes to limonite in weathered sections) are most common in shallow water hardgrounds. The hardgrounds in Cretaceous chalks are frequently phosphatized or glauconitized (Jarvis, 1980, 1992). Deeper-water hardgrounds sometimes show staining by manganese minerals (Prescott, 1988; Allouc, 1986b). Mineral staining may be related to sea floor or shallow burial diagenetic processes that take place in the presence of concentrations of organic matter at the hardground surface or just below it in microborings.

Mineral staining of this kind is often the most conspicuous feature that hardgrounds show in the field, and is sometimes used as a diagnostic field criterion for hardgrounds. However, care must be taken to seek corroborating faunal evidence, since some ancient seabeds may show mineral staining similar to that exhibited by hardgrounds, yet show no evidence whatsoever of boring or encrusting. In the absence of both faunal and petrographic evidence of early marine cements, these may be called "firmgrounds" (Fürsich, 1979), a rather subjective term that hardground workers often use for a surface that they suspect would have become rigid enough to support a boring and encrusting fauna if only a little more time for sea floor cementation had elapsed (see also Crane and Goldring, 1991, and Bromley and Goldring, 1992).

Erosive and Diagenetic Processes Influencing Hardground Appearance

Effects of preomission burrows.--Soft sea-bottoms were frequently burrowed prior to the onset of lithification. Open, three-dimensional dwelling galleries similar to those produced in the Recent by some burrowing decapod crustaceans and enteropneusts (Figure 17) have been common in shallow shelf carbonates since the Ordovician (Bromley, 1967; Kazmierczak and Pszczolkowski, 1969; Fürsich and Palmer, 1975; Palmer, 1978). Hardground cementation proceeded in the sediment around such burrows, eventually preserving them as open galleries with hardened walls, which penetrated the hardground and often descended as far as the loose sediment below the cemented crust (Figure 18). Burrows of this sort are particularly common in Jurassic and Cretaceous hardgrounds, but it must be stressed that they belong to the pre-omission fauna (*sensu* Bromley, 1975a), not to the hardground fauna itself. If the hardground grew by nodule enlargement and coalescence, then the shapes of the burrows may gradually have become more tortuous and distorted as continuing burrowing activity became confined to the diminishing amount of soft sediment between the growing nodules. Such burrows provided additional microhabitats on hardground surfaces. Their hardened walls often support a community of cavity-dwellers (coelobites), and further excavation of soft sediment beneath the hardground crusts may allow them to open into small caves (see Voigt, 1987).

Preomission burrows may also facilitate sea water circulation and cementation within the sediment. The sediment is invariably better cemented at the burrow walls than further in, and cemented burrows sometimes extend as hardened tubes down into the soft sediment below the base of the crust. Decay of organic matter associated with such burrow walls may liberate HCO_3^- in an alkaline environment, leading to enhanced cementation.

Tepees and crust expansion.--Crusts may expand laterally and buckle due to horizontal stresses set up by cement growth (Figures 19 and 20), forming tepee structures and crust overthrusts (Shinn, 1969; Fürsich, 1979). Currents and organisms may be able to excavate the soft sediment beneath the crust, forming small caves and overhangs. The hardened roofs of such cavities, formed by the lower surfaces of the crusts, are often colonized. Such features are particularly common in Ordovician and Jurassic hardgrounds (Palmer and Fürsich, 1974; Brett and Liddell, 1978).

Sediment scour.--Growing hardgrounds may be overlain by a thin layer of uncemented sediment in which the grains are being jostled around too much (by currents or organisms) to become cemented together. Such sediment, and other material introduced from nearby uncemented areas, may move around on the crust surface, abrading and smoothing it by scour (Figure 21). Occasionally this scouring sediment is preserved on the top of hardground surfaces as a set of starved ripples (Figure 22). Some hardground surfaces become very smooth and planar by such erosion, and show considerable truncation of pre-omission features such as burrows and large fossils incorporated into the lithified sediment (Figures 1 and 18; see Palmer, 1978). This is not a feature of all hardgrounds, however, and the details of surface relief, smoothness, undulation, and presence of overhangs, re-entrants, and cobbles are unique to any particular lithified surface (Fürsich, 1979). They reflect the style and patchiness of the cementation process, the degree of burrowing before and during cementation, the thickness and degree of expansion of the hardening crust, and the nature and timing of erosive processes while cementation was proceeding and after its termination.

Spatial Distribution of Hardgrounds

Depth of formation.--Hardgrounds form across a considerable range of water depths, from sea level, through the shallow subtidal (on shelves and ramps), into slope and basinal settings. The great majority of ancient hardgrounds whose faunas have been studied probably formed (judging from associated lithofacies) in shallow subtidal settings (likely depths from sea level to several tens of meters; perhaps a bit deeper for some Cretaceous chalk examples) in low latitudes. Deeper water hardgrounds (e.g. Wendt, 1971) tend to have lower diversity faunas which have not attracted so much attention from paleontologists. There has, though, recently been a surge of interest in deeper water hardgrounds cemented with methane-derived carbonate and associated with chemosynthetic communities (Roberts et al., 1987, 1988, 1989; Beauchamp and Savard, 1992; Paull et al., 1992).

Areal extent.--Some ancient hardgrounds cover many thousands of square kilometers and may be used for lithostratigraphic correlation (e.g. Bromley and Gale, 1982). Such hardgrounds often form the upper surfaces of typical shelf or ramp carbonate shallowing-upward cycles, though they may be diachronous. Many hardgrounds, however, have a much more limited geographic distribution, and die out across a few tens or hundreds of meters. Such smaller scale hardgrounds often represent the consequence of introducing a well-sorted carbonate sand body of limited extent into an overall environment conducive to rapid marine carbonate precipitation. Kendall and Schlager (1981, p. 193) made a useful distinction between hardgrounds which are "facies selective" (and hence of limited areal extent) and those which are "widespread" across facies. Some unusual hardgrounds, like those underlying Cretaceous chemosynthetic cold-seep communities in the Canadian Arctic, can be less than three meters in diameter (Beauchamp and Savard, 1992).

Stratigraphy of Hardgrounds

Hardgrounds are surfaces where complex geochemical, biological and sedimentological events have taken place. One of the primary processes in the development of a hardground, though, is the simplest: the net accumulation of sediment is reduced to virtually zero. The typical hardground represents a sedimentary hiatus -- an interval of time during which "normal" sedimentation has stopped. Hardgrounds thus have temporal significance in a package of sedimentary rocks. They have the potential for use in stratigraphy as correlative "marker beds" or as time-stratigraphic boundaries in the developing field of sequence stratigraphy.

Hardgrounds, in combination with nodular beds, marl seams and flint horizons, have been used in the lithostratigraphy of Cretaceous chalks and related units in Europe (Bromley and Gale, 1982, Francis, 1984, and Gale et al., 1987) and other carbonates in North America (Rose, 1970). These "marker bed" correlations can be highly detailed and accurate; in many cases they are superior to biostratigraphical schemes (Gale et al., 1987). Hardgrounds have been used less frequently in other systems for stratigraphic correlation beyond a few nearby localities. Notable exceptions include correlation of carbonates in the Devonian of western Canada (Stoakes, 1980) and the Jurassic of Europe (Purser, 1969) and India (Fürsich et al., 1991, 1992), as well as current work in the Ordovician of North America (Siewers and Sandberg, 1992). In each case hardgrounds have proven their correlative value as generally synchronous surfaces which cross facies boundaries. Since the lithologies vary along these surfaces, the expression of the hardgrounds vary as well. Faunal content will, of course, differ considerably along an extensive surface which crosses into different environments. Hardgrounds on carbonate shoals may be replaced by reworked concretions in offshore siliciclastics (Fürsich et al., 1992). Sandberg and Siewers (1992) found in the Ordovician of Nevada and Utah that shelf and upper slope carbonate hardgrounds give way to phosphatic firmgrounds in middle and lower slope settings. Hardgrounds, though, are not always directly correlative between facies. For reasons given below, Martire (1992) noted that deep water hardgrounds in the Jurassic of northern Italy frequently do not correlate with condensed sections on the coeval shelves.

Hardgrounds and related horizons, such as reworked concretions and condensed layers, are usually associated with the beginning of transgressive pulses characterized by fairly rapid flooding events (Fürsich et al., 1991, 1992; Martire, 1992; Sandberg and Siewers, 1992). Hardgrounds can thus be used plot changes in relative sea level. Although previous workers had noted the relationship between transgressions and hardgrounds, Kendall and Schlager (1981) provided the most detailed conceptual framework for understanding the effects of sea level changes on carbonate deposition. They recognized a variety of carbonate responses to sea level changes, including "facies selective" and "widespread" hardgrounds (Kendall and Schlager, 1981, p. 193) at the bases of transgressive sequences. Many geologists are now considering hardgrounds and related horizons in the new terminology of sequence stratigraphy. The hardground surfaces which bound transgressive-regressive cycles are thus often sequence or parasequence boundaries (Sarg, 1988). The complexities of this sequence stratigraphic approach are still becoming evident. For example, Martire (1992) demonstrates that while slope and shelf sedimentation diminishes during sea level highstands, deep-water sedimentation can actually increase because bottom current activity is reduced and pelagic sediments can accumulate. The opposite can happen during lowstands. Hardgrounds on shelves and slopes would thus form during highstands (given the necessary sedimentological and geochemical conditions), while hardgrounds and other omission surfaces would form in deep waters during lowstands. Hardgrounds would not, then, be correlative between these deep and relatively shallow environments. Nevertheless, when such geological conditions are taken into account, sequence stratigraphy provides chronostratigraphic frameworks of unprecedented resolution. Hardgrounds are often critical elements in their construction.

Hardgrounds Over Time

The recognition that, over the Phanerozoic, periods of shallow marine LMC precipitation (Calcite Seas) have alternated with periods of aragonite (and subsidiary HMC) deposition (Aragonite Seas), is probably the major discovery in the field of shallow marine carbonate diagenesis in the past few years (Sandberg, 1975, 1983; MacKenzie and Pigot, 1981; Wilkinson et al., 1985). Proposed reasons for the fluctuations have stressed the influences of varying amounts of dissolved CO_2 and Mg^{++} ions in the carbonate-precipitating waters upon carbonate precipitation (both of these are thought to vary in accordance with sea-floor spreading and subduction rates), but there is no consensus about driving mechanisms. The field evidence that many ancient hardgrounds did indeed have original calcite cements is strong, however, because the early cements grow syntaxially on echinoderms and other calcite bioclasts (e.g. Wilkinson et al., 1982, 1985; Wilson et al., 1992). Early aragonite cements could not have done this. Furthermore, the early calcite cements are often cut by borings, and do not show any of the hallmarks of later diagenetic alteration of aragonite mentioned above. Since the overwhelming majority of ancient hardgrounds that have been described come from calcite seas, hardground sedimentologists and paleontologists should be circumspect about making too many uniformitarian assumptions based on what is known of hardground formation in Recent aragonite seas.

Supplementation of dissolved carbonate from aragonite dissolution, the fact that calcite precipitates at lower concentrations than aragonite, and the greater rate of growth of calcite cements growing syntaxially on calcite substrates such as echinoderm ossicles are all reasons why hardgrounds may be expected to be more common and faster growing in calcite than in aragonite seas. Certainly it appears that hardgrounds are significantly more common at some times during the fossil record than at others, even allowing for different overall volumes of carbonate sediment. Hardgrounds seem particularly abundant in Ordovician, Jurassic and Cretaceous rocks (all calcite seas), and particularly scarce in the Pennsylvanian, the Permian and the Tertiary (aragonite seas) (Wilson and Palmer, 1990). The correlation between high sea-level stands and calcite seas has been stressed by some workers (Walker and Diehl, 1985; Wilson and Palmer, 1990). High sea levels further increased the areas of low latitude carbonate-accumulating epeiric seas in which hardgrounds were most likely to form. The sudden abundance of hardgrounds and other manifestations of early marine cementation such as intraformational conglomerates (which are mainly broken-up hardgrounds) in the late Cambrian and, particularly, the Ordovician, probably results from the co-occurrence of a significant oceanographic event (the shifting of oceanic chemistry into calcite sea mode) with the radiations of calcitic organisms, particularly echinoderms (Walker and Diehl, 1985; Palmer and Wilson, 1990; Wilson et al., 1992; Sprinkle and Guensburg, 1992). Ordovician shallow marine carbonates contain vast quantities of calcite single-crystal echinoderm ossicles on which marine calcite cements grew particularly rapidly, thus speedily forming hardgrounds. Indeed, by nature of their skeletal structure, echinoderms promoted the rapid and widespread production of the very substrates on which they thrived and radiated evolutionarily.

Figure 1. Erosion of hardground surface; orthocone nautiloid within sediment truncated by erosion of hardground. Middle Ordovician of Iowa.

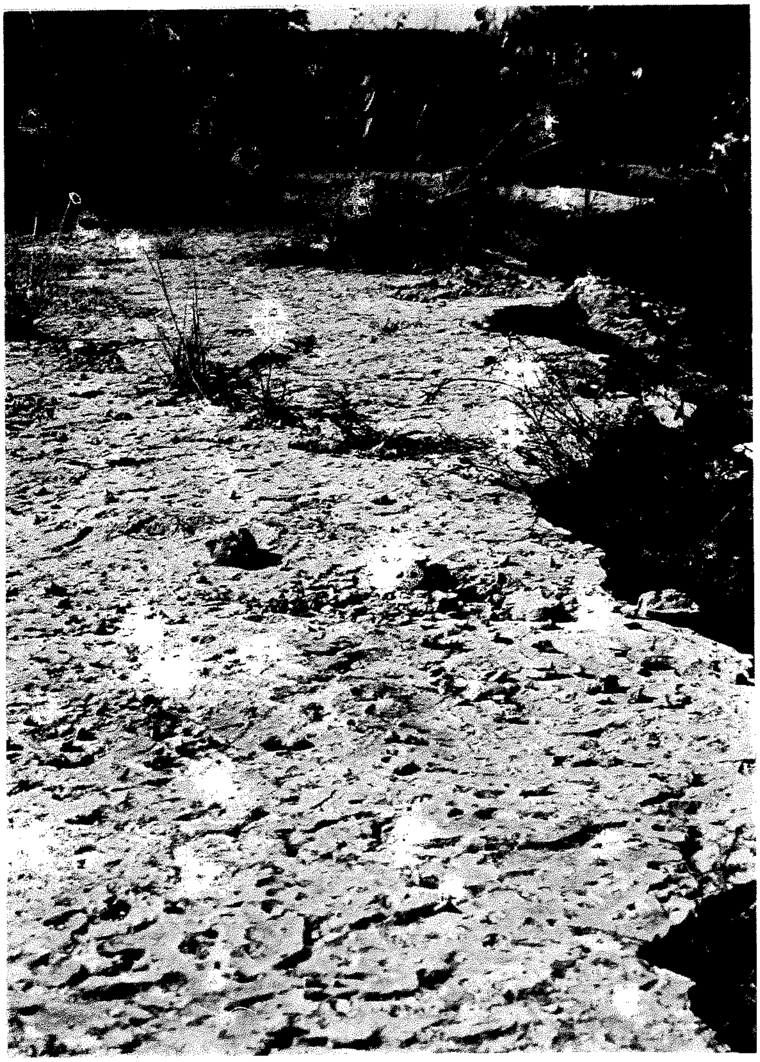

Figure 2. Extensive, smooth, abraded hardground surface showing truncation of pre-omission burrows at the hardground surface. Middle Ordovician of Iowa.

Figure 3. Jurassic rockground in cross-section. This Lower Carboniferous limestone was exposed on the sea floor in the Middle Jurassic (Bajocian) and eroded, encrusted and bored. Borings visible here include the cylindrical *Trypanites* and the vase-shaped *Gastrochaenolites*. Note that the borings cut through the late diagenetic calcite vein in the center. Specimen C/W-79-1, Mendip Hills, Somerset County, England; x1.6.

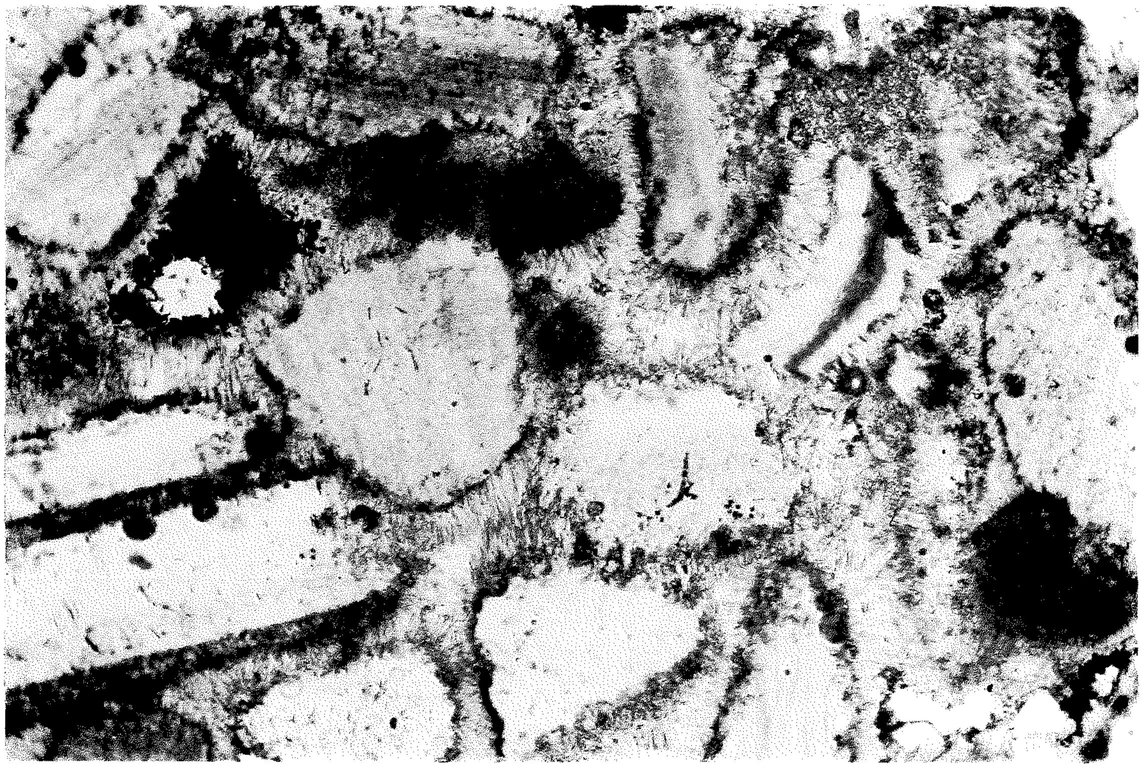

Figure 4. Acicular aragonite marine cement. Hardground, Recent, Persian Gulf. Width of field is 1.1 mm.

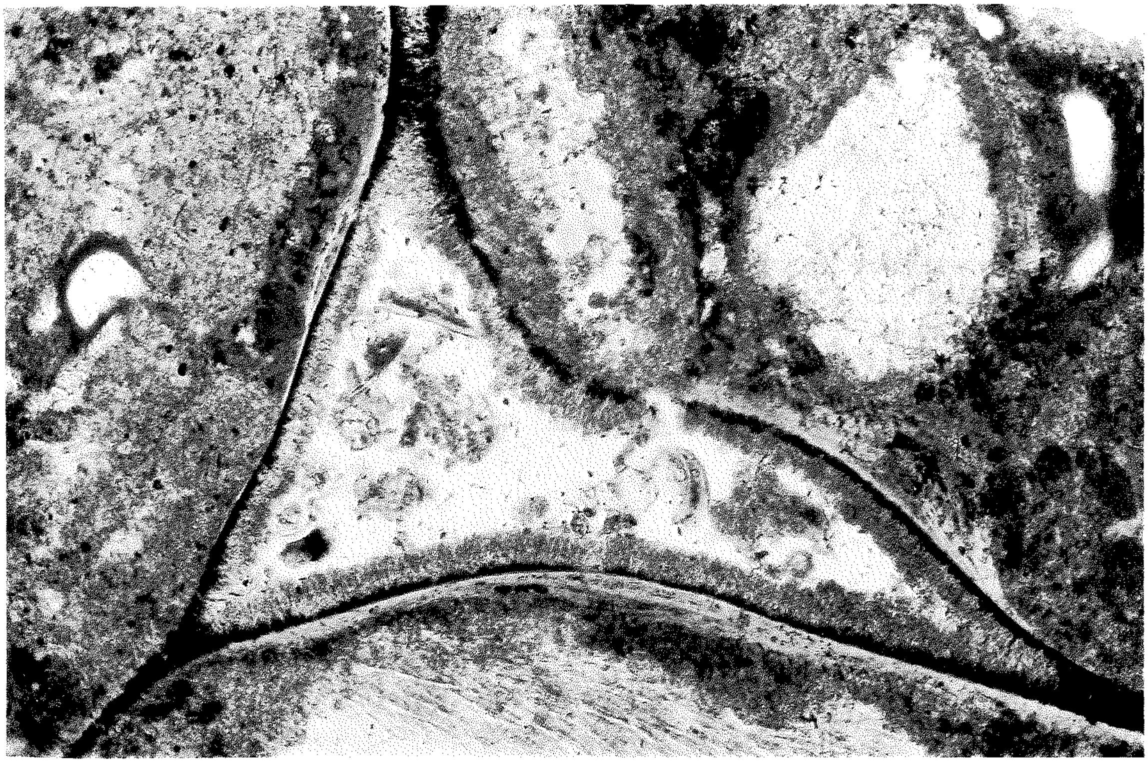

Figure 5. Pallisade of acicular aragonite marine cement. Hardground, Recent, San Salvador Island, The Bahamas. Width of field is 1.1 mm.

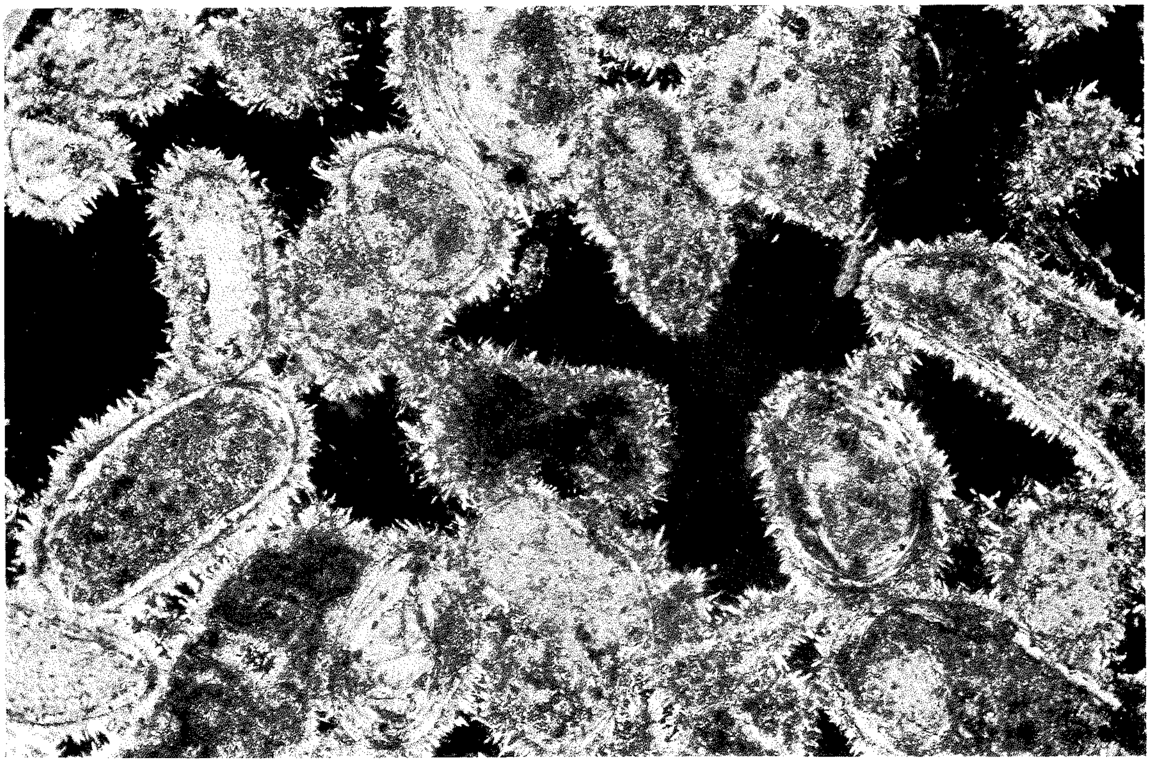

Figure 6. Acicular aragonite early marine cement. Hardground, Recent, San Salvador Island, The Bahamas. Width of field is 1.1 mm.

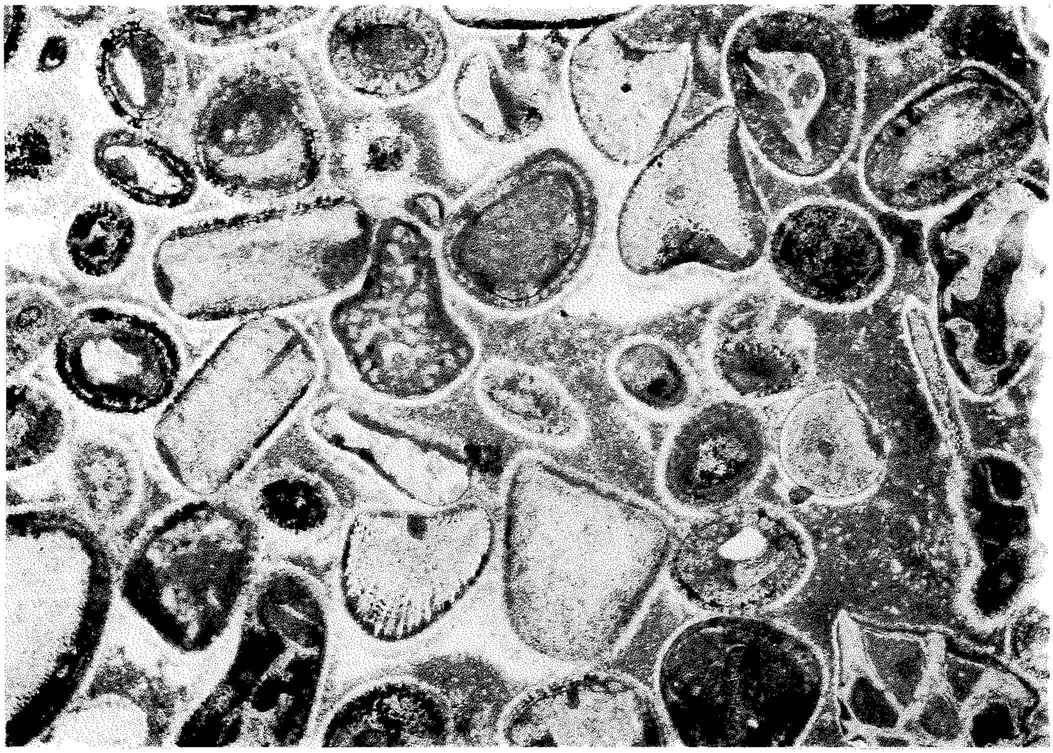

Figure 7. Marine isopachous LMC cement; remaining pore space partially filled with geopetal micrite and later LMC cement. Hardground, Middle Jurassic of Normandy, France. Width of field is 4.4 mm.

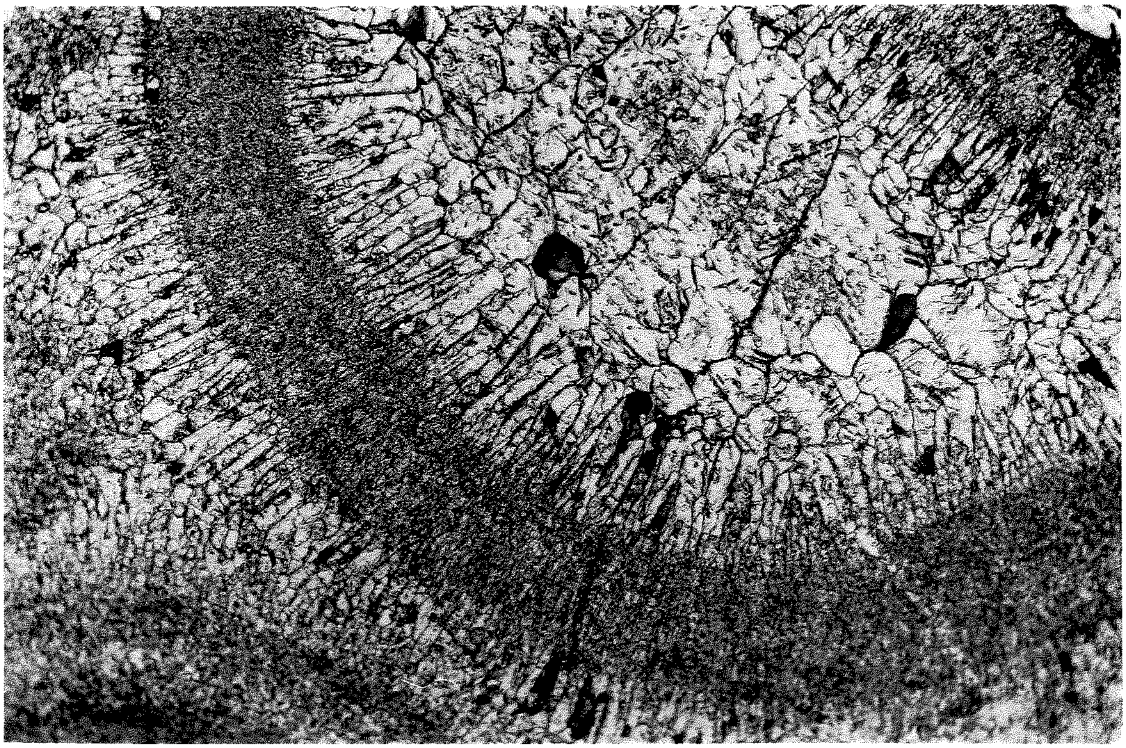

Figure 8. Marine, isopachous, fibrous, calcite (probably LMC) cement growing syntaxially on trilobite fragment. Acetate peel of intraformational conglomerate, Early Ordovician, Kanosh Shale, Millard County, Utah. Width of field is 1.1 mm.

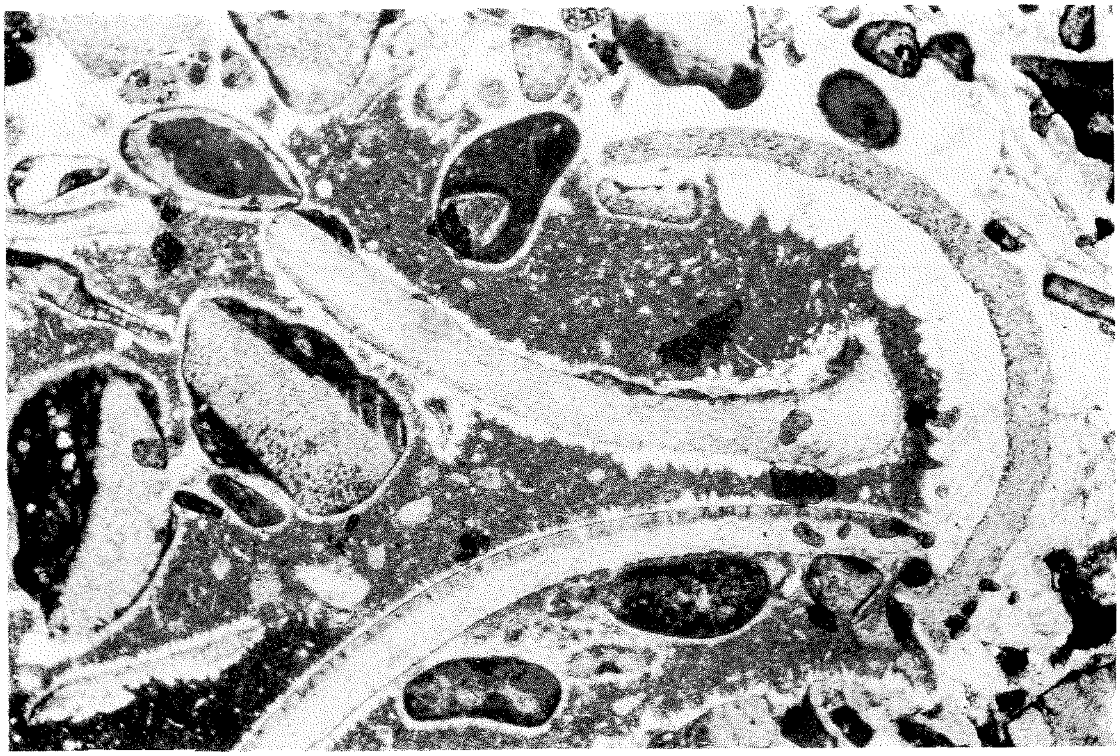

Figure 9. Marine isopachous LMC cement overlain by interstitial micrite. Note that the early cement grew syntaxially on an echinoderm fragment (bow-shaped grain on right). Hardground, Middle Jurassic of Normandy, France. Width of field is 4.4 mm.

Figure 10. Close-up of same hardground as that illustrated in Figure 9 showing syntaxial nature of early cement on echinoderm (left) and drusy scalenohedral form on polycrystalline grains. Width of field 1.1 mm.

Figure 11. Early, non-ferroan, scalenohedral, marine LMC cement overlain by later diagenetic, ferroan, equant LMC cement (stained blue by potassium ferricyanide). Middle Jurassic of Lincolnshire, England. Width of field is 4.4 mm.

Figure 12. Drusy, isopachous, LMC marine cement overlain by later diagenetic LMC cement. The two cement generations are separated by a pyrite-rich zone which probably reflects passage of the sediment through the Sulfate Reduction Zone as burial proceeded. Hardground, Middle Jurassic of Normandy, France. Width of field is 4.4 mm.

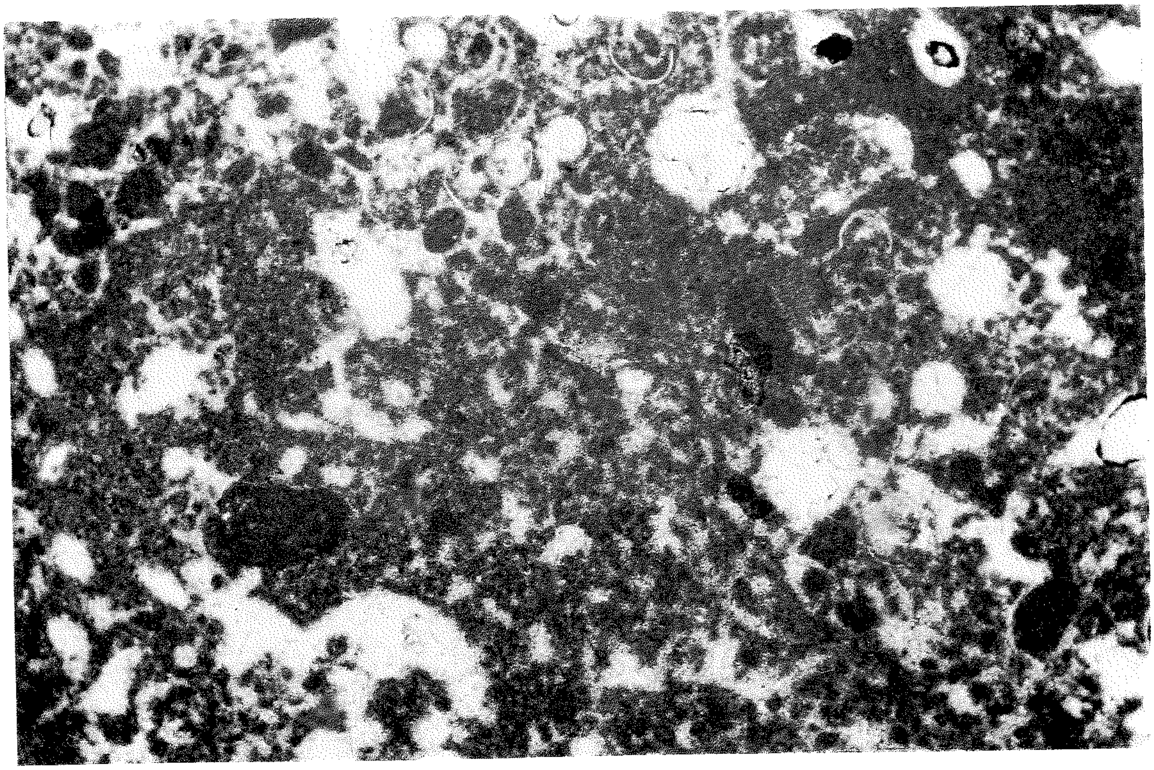

Figure 13. Peloidal ?LMC marine cement; pore space filled by late diagenetic calcite. Marine cemented reef rock, Upper Jurassic, England. Width of field is 2.7 mm.

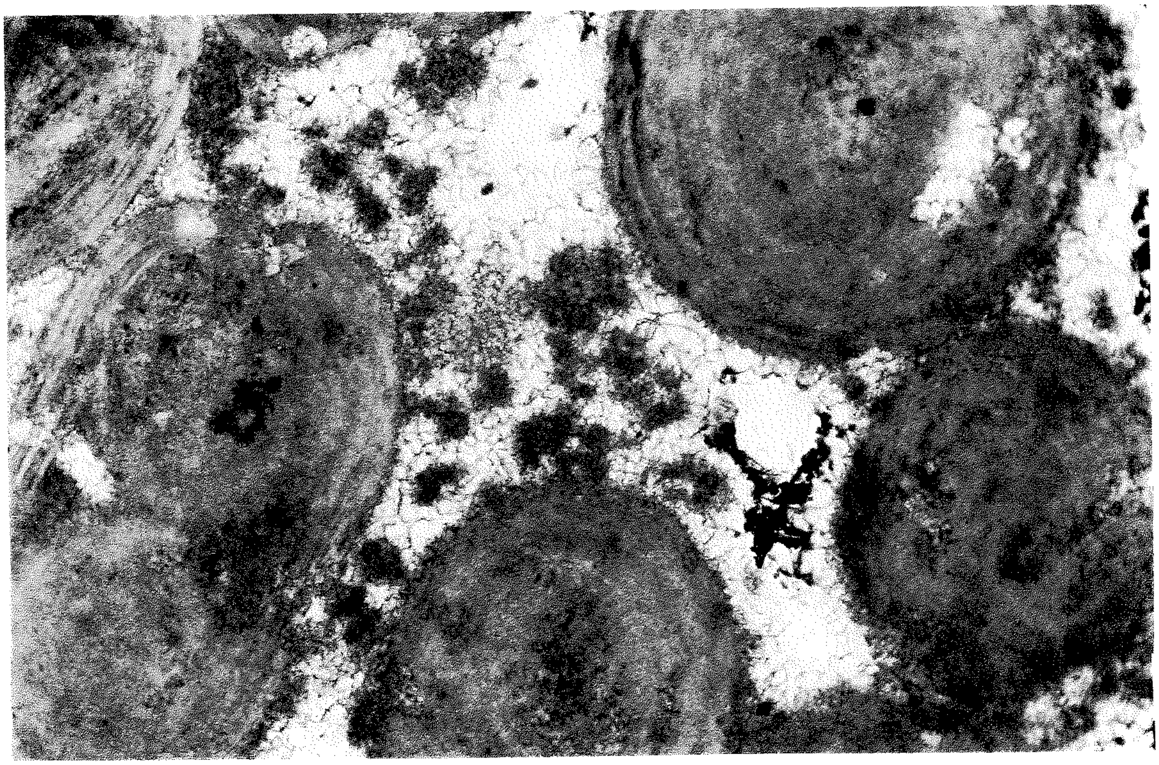

Figure 14. Peloidal and drusy, probably HMC, marine cement. Hardground, Recent, Persian Gulf. Width of field is 1.1 mm.

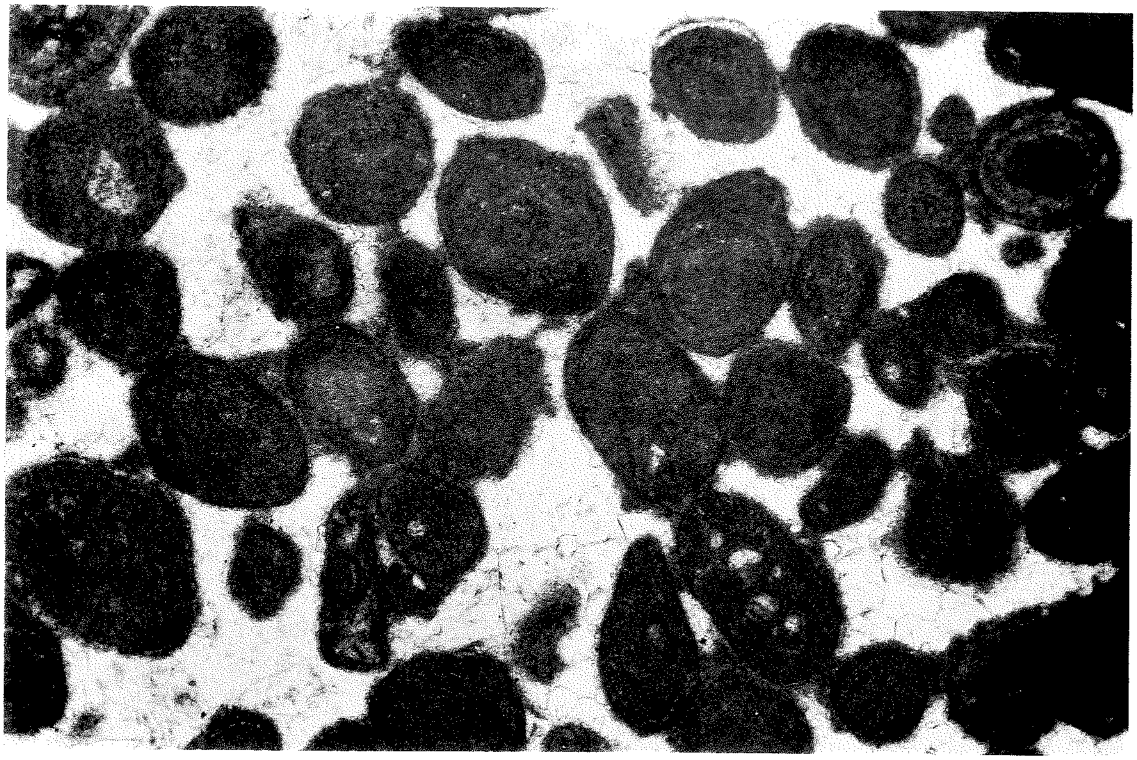

Figure 15. Micrite meniscus cement; pore spaces filled by late diagenetic calcite. Beachrock, Middle Jurassic, Madagascar. Width of field is 2.7 mm.

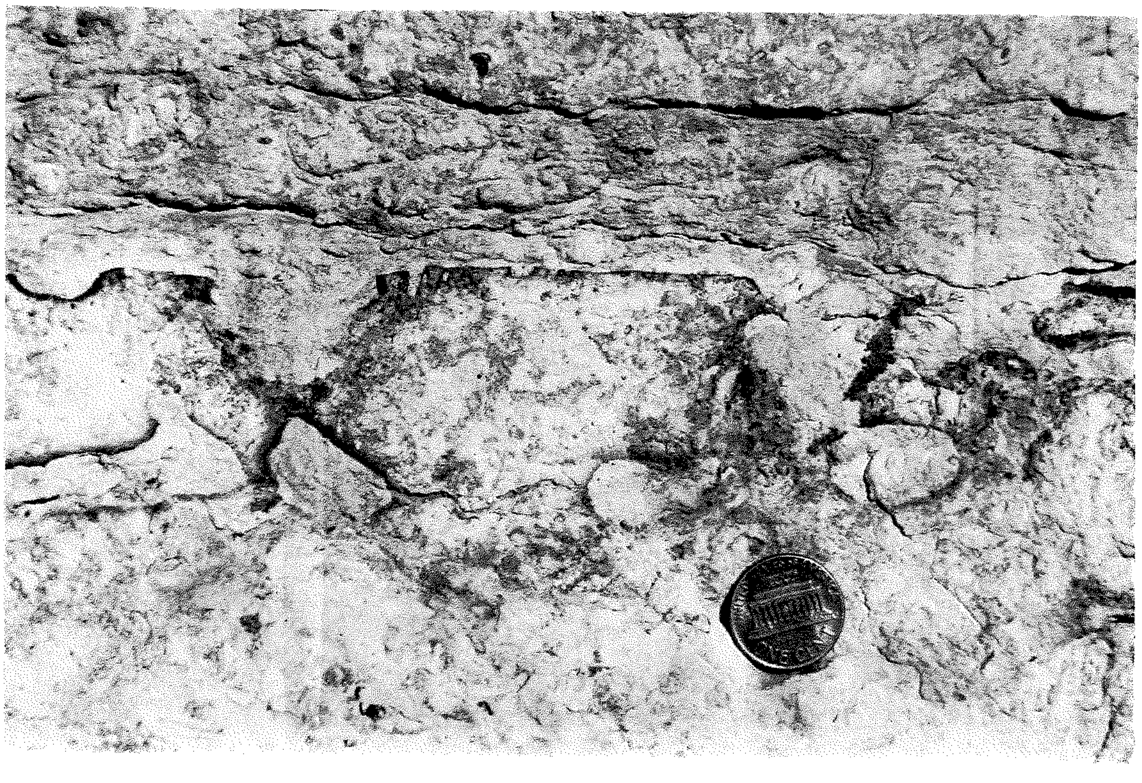

Figure 16. Vertical section across hardground in the field showing pyrite-rich rim along the surface itself, as well as within the small *Trypanites* and the large pre-omission burrows that penetrate it. Middle Ordovician of Iowa.

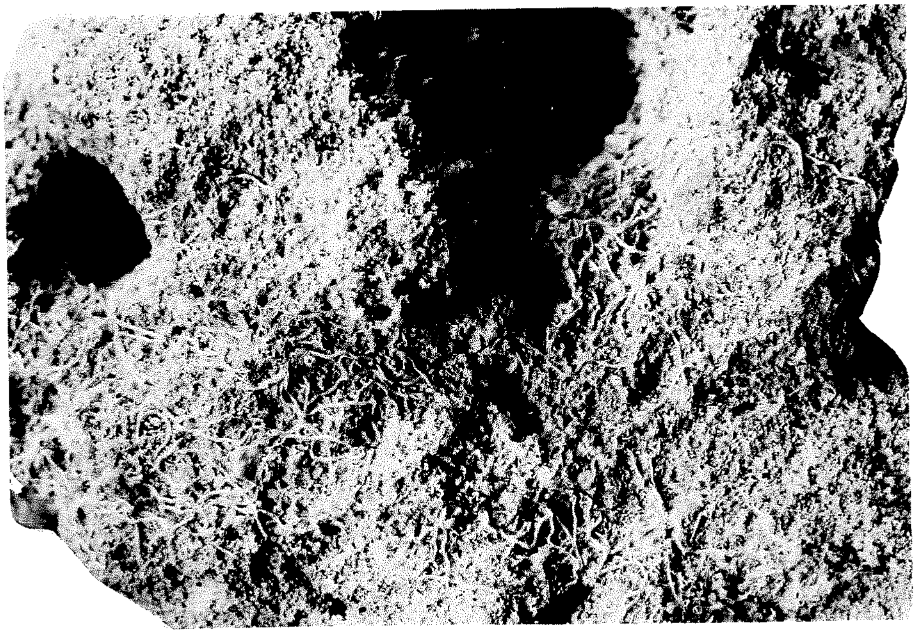

Figure 17. Plan view of the underside of a modern hardground. The large holes are burrows formed in the sediment before lithification. The small tubes are those of encrusting serpulid polychaetes. Specimen C/W-135-1, Norman's Pond Cay near Lee Stocking Island, The Bahamas; x1.

Figure 18. Pre-omission crustacean burrows preserved in an open condition at hardground surface by early marine cementation of the surrounding host sediment. Middle Jurassic of England.

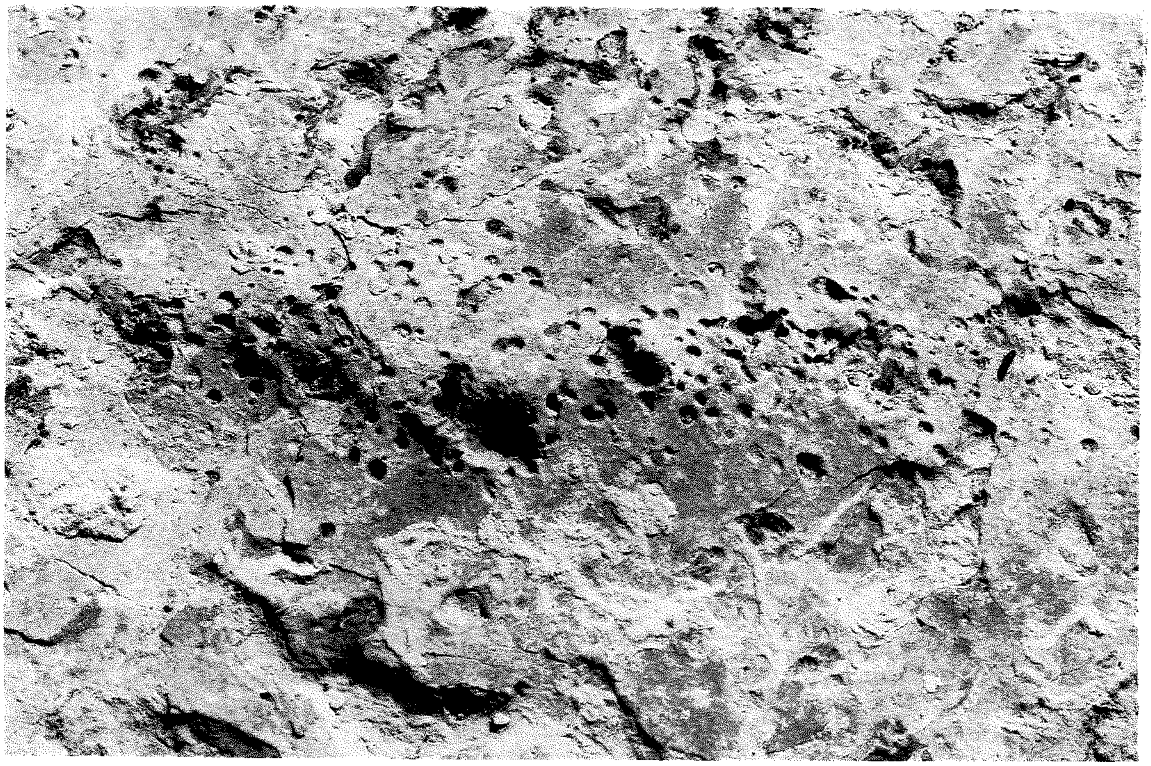

Figure 19. Raised hummock (small teepee structure) on hardground surface showing truncation of burrows. Middle Ordovician of Iowa.

Figure 20. Oblique view of structure in Figure 19.

Figure 21. Scoured, encrusted and bored Silurian hardground. The light patches near the scale are trepostome bryozoans. Brassfield Formation, northern Adams County, Ohio.

Figure 22. Starved ripples on Early Ordovician hardground surface. The ripples are the darker crescent shapes perpendicular to the staff. Wah Wah Formation, near Ibex, Confusion Range, Millard County, Utah, USA.

COMMON FOSSILS ON CARBONATE HARDGROUNDS

Fossil Preservation on Carbonate Hardgrounds

Hardgrounds represent significant intervals of non-deposition, and thus inevitable erosion, in the sedimentary record. The exposed remains of organisms associated with these hard substrates were commonly subjected to considerable scour and dissolution. The skeletons of encrusting organisms often suffered the greatest erosive abuse, with only the most robust surviving; nestlers were usually plucked from all but the most deeply-recessed cavities, and even borings were often eroded into near-oblivion, sometimes with only the distal-most portions of the excavations surviving. Properly assessing a hardground fossil community, like all fossil communities, requires an adequate understanding of the taphonomic processes that have taken place. Often some of the most important paleontological information will be recovered from fossils that are mere stumps of their former glory. Sometimes strongly abraded encruster skeletons are encrusted by later generations, which may indicate the amount of time involved in community development and the pattern of ecological succession (see Brett and Liddell, 1978, and Wilson, 1985a).

Occasionally hardground communities are buried quickly by fine-grained sediments and preserved in extraordinary detail. These hardground *lagerstätten* provide detailed glimpses into the structure of the original communities, since most skeletonized hardground occupants are preserved in place. There is yet no hardground equivalent of the Burgess Shale, but there are some beautifully preserved faunas. Most notable are the Ordovician echinoderms of Brett and Liddell (1978; see Figure 23) and Guensburg (1984, 1992; see Figure 24), the Devonian rhombiferans and edrioasteroids of Koch and Strimple (1968) and Bell (1975; see back cover), the Jurassic crevice fauna of Palmer and Fürsich (1974; see front cover and Figure 30), and the Cretaceous bryozoans of Voigt (1974, 1987, 1988).

There have been no published studies on the relative abundance of soft-bodied organisms on and in carbonate hardgrounds. Some idea of the preserved/non-preserved ratios can be gathered from studies of other modern hard substrates, such as the work with coral encrusters by Rasmussen and Brett (1985), but we cannot apply these observations with much confidence to ancient hardgrounds. Soft-bodied encrusters and nestlers were present on ancient hardgrounds, but the evidence they left is indirect at best. Sometimes skeletonized encrusters are found with raised edges as if they began to overgrow another organism which has not been preserved. Sometimes barren patches in an otherwise densely encrusted fossil hardground will evoke thoughts of missing non-skeletonized occupants. Only rarely do soft-bodied encrusters leave direct evidence, and that has thus far been through "bioimmuration", a process by which skeletonized encrusters rapidly overgrow and replicate on their undersurfaces soft-bodied organisms (see Taylor, 1990, and Taylor and Todd, 1990, for recent reviews of bioimmuration). Sometimes soft-bodied animals encrusted living substrates on hardgrounds such as bryozoans and were then embedded within the developing skeletons (Palmer and Wilson, 1988). Other more clever ways of detecting soft-bodied hardground occupants may be devised in the future.

Common Encrusting Hardground Fossils

The following is a brief annotated listing of the common fossils found encrusting carbonate hardgrounds. Most hardgrounds go unrecognized in the field because the fossils associated with them are not usually noticed. We hope to increase the number of recorded hardgrounds by improving the abilities of geologists to distinguish the often esoteric fossils associated with them. Often the best preserved specimens of hardground-dwelling groups are found on other hard substrates, such as shells, cobbles or rockgrounds, so we have included below some non-hardground references.

Algae.--Calcareous and fleshy algae are among the most common encrusters on modern hardgrounds and other marine hard substrates (see Table 1). Evidence of algae on ancient hard substrates, though, is uncommon. The earliest known encrusting algae are bangiophyte red algae described from "locally stabilized" peritidal carbonate sediment surfaces between 1250 and 750 million years old in northern Canada (Butterfield et al., 1990). Algae such as *Renalcis, Serligia* and *Epiphyton* are found on hardground surfaces and within archaeocyathid cavities of the North American Lower Cambrian (Kobluk and James, 1979; Kobluk, 1981a, 1981b). Brett et al. (1983) figure and briefly described a hardground-dwelling *Renalcis*-like spongiomorph alga from the Upper Cambrian of Montana and Wyoming. Algae are then virtually unknown on the remainder of Paleozoic hardgrounds. Halleck (1973, p. 243) interpreted "clods" on a Silurian hardground as algally-formed, but our examination of these structures showed them to be cemented sediment from the walls of burrows developed in a unit above the hardground. Calcareous algae reappear on Jurassic (Goldring and Kazmierczak, 1974) and Cretaceous (Voigt, 1959, 1974) hardgrounds, but are never common. We have observed calcareous algae on Tertiary and Quaternary hardgrounds, but these have not been described in the literature. The rise of calcareous algae in the Late Mesozoic may be an effect of the Mesozoic Marine Revolution as many diverse algal groups developed resistant skeletons in the face of escalating herbivory (Steneck, 1983).

Foraminiferans.--The tests of foraminiferans are, of course, usually very small. They are noted on most hardgrounds only after examination with a hand lens or microscope. A notable exception is the Late Cenozoic encrusting rotaliid *Homotrema*, which is usually numerous, large, and a gaudy red or purple. The color of *Homotrema* is persistent in subrecent and Pleistocene samples, even when other shell colors have faded. Other hardground-dwelling foraminiferans are quite inconspicuous; most are found in crevices, borings, eroded burrows and other cryptic areas. A few, such as *Nubeculinella* and *Bullopora* of the Jurassic and Cretaceous, have calcareous shells which usually stand out against the rocky background, but many others have agglutinated tests made of carbonate grains and quartz silt, making them virtually invisible on a lithologic substrate. Among the latter are *Lapillincola, Bdelloidina* and *Acruliammina* of the Cretaceous. An agglutinated encrusting foraminiferan was noted by Kobluk and James (1979) within archaeocyathid cavities in the Lower Cambrian of Labrador. Among the earliest foraminiferans encrusting a lithologic substrates are small calcareous tests on cobbles from the Pennsylvanian of midcontinental North America (West and Palmer, 1983). Various encrusting foraminiferans are described from cobbles and hardgrounds of Europe by Hofker (1965), Kaever (1974), Wilson (1986a,b), Hercogová (1988) and Zitt and Nekvasilová (1991b). Voigt (1970a) analyzed the commensal habits of some Upper Cretaceous encrusting foraminiferans, as did Bromley and Nordmann (1971); Voigt and Bromley (1974) did the same with Cretaceous and Recent species.

Sponges.--Encrusting sponges and similar forms are difficult to recognize under the best of circumstances, and fossil sponges clinging to eroded hardgrounds are virtually impossible to identify with confidence. (We are, like many paleontologists, indebted to Keith Rigby for his continual willingness to analyze sponge material we send him.) Encrusting sponges are not common on ancient hardgrounds, undoubtedly for taphonomic reasons. Boring sponges are ubiquitous on many lithologic and shell substrates; they are covered separately under "common hardground borings" below. Kobluk (1981b) describes cavity-dwelling sponges from the Lower Cambrian of western North America. Wilson et al. (1992) found the encrusting sponge *Patellispongia* on Early Ordovician hardgrounds of western North America. Calcareous-walled sponges and sclerosponges become common on Jurassic and Cretaceous cobbles and hardgrounds (particularly as coelobites), as noted by Fürsich (1974), Palmer and Fürsich (1981), Palmer (1982), Wilson (1986a) and Nekvasilová and Zitt (1988). Demosponges are common today on shallow-water and deep-water hardgrounds (Messing et al., 1990).

Corals.--These are relatively common encrusters on hardgrounds from the Silurian through the Recent. The oldest encrusting coral on hardgrounds may be the problematic *Protarea* (possibly a heliolitid) of the midcontinental North American Upper Ordovician (Palmer, 1982). Westphal (1974) mistakenly described an eroded crinoid holdfast from the Middle Ordovician as an encrusting coral (see Brower and Veinus, 1978, p. 388). Paleozoic hardground-dwelling tabulate and rugose corals are recorded from the Silurian by Halleck (1973), the Devonian by Koch and Strimple (1968) and Hecker (1935, 1960, 1983), and the Mississippian by Palmer (1982). Mesozoic corals are rare on hardgrounds, which may not be surprising because of the frequent diagenetic loss of the aragonitic skeletons of scleractinians. Only one scleractinian coral (*Thamnasteria*) is known from Jurassic hardgrounds of Europe, and a single indeterminate octocoral is found on Cretaceous hardgrounds in Texas (Palmer, 1982). Martinius and Molenaar (1991) detail the development of encrusting scleractinian corals on unusual mixed siliciclastic-carbonate sandstone hardgrounds of the Spanish Eocene. Other ancient hard substrates, especially shells and rockgrounds, are commonly encrusted with corals (see, for examples, Baird, 1976; Johnson and Baarli, 1987). It is also undoubtedly the case, especially in the Pleistocene and Recent, that carbonate hardgrounds provided the initial hard substrates for massive coral reefs (Crame, 1980; Thomassin and Coudray, 1981). The rapid and abundant growth of the coral reefs quickly obscures their hardground-dwelling roots.

Brachiopods.--This is a problematic group on hardgrounds, especially those from the Paleozoic. Since their shells are so abundant in surrounding sediments, brachiopods were almost certainly common on most shallow marine hard surfaces, either attached by pedicles or resting unattached in hollows and crevices. Only those brachiopods, though, which cemented a valve to the substrate have left a significant record on hardgrounds. It is possible to detect the etched borings left by brachiopod pedicles on hard substrates (Bromley and Surlyk, 1973), but these delicate and small features have not yet been found on carbonate hardgrounds. Paleozoic hardground-encrusting brachiopods are present on Middle and Upper Ordovician and Silurian hardgrounds of North America (Palmer and Palmer, 1977; Brett and Liddell, 1978; Bodenbender et al., 1989; St. John and Wilson, 1991; Halleck, 1973), and the Devonian of eastern Europe (Hecker, 1935, 1960, 1983), but rare for the remainder of the Paleozoic. Mesozoic and Cenozoic encrusting brachiopods are mostly craniid acrotretids (Nekvasilová, 1982, 1986; Zitt and Nekvasilová, 1990, 1991a, 1991b) and thecideidinids (Fürsich, 1974; Palmer and Fürsich, 1974; Revert and Pajaud, 1975).

Bryozoans.--By far the most common and diverse group on Paleozoic hardgrounds, bryozoans deserve star status in most hardground studies. Unfortunately, though, their systematics can be very difficult for non-specialists to decipher, so they are most commonly treated by us and others with either questionable generic names or with morphologic/ecologic labels such as "minute pimples" or "erect bifoliate" and so forth. We are continuing to work on the systematics of hard-substrate bryozoans because of their importance in the early radiation of the phylum (Taylor and Larwood, 1991; Taylor and Wilson, 1993).

The earliest hardground-dwelling bryozoans are four trepostome species found on Lower Ordovician surfaces in western North America (Wilson et al., 1992). They include *Nicholsonella* (Figure 25)and *Dianulites*, both with recrystallized walls which may indicate skeletons composed originally of high-magnesian calcite. These early bryozoans are mostly simple crusts and radial mounds with virtually no zooidal polymorphism. Middle Ordovician hardgrounds have the highest diversity of bryozoans, including abundant trepostomes (Figures 26 and 27), cyclostomes and jointed ptilodictyid cryptostomes, most with higher degrees of zooidal polymorphism (Palmer and Palmer, 1977; Brett and Liddell, 1978; Palmer, 1982; Brett and Brookfield, 1984; Siewers, 1988). Upper Ordovician hardgrounds and limestone cobbles also have numerous bryozoans (Figure 28), but their diversity is lower because some trepostomes (especially massive forms like *Amplexopora*) apparently excluded many other forms (Wilson, 1985a; Bodenbender et al., 1989; St. John and Wilson, 1991). Silurian hardground bryozoans are not well studied, but they are common (Ettensohn et al., 1977). Later Paleozoic bryozoans are relatively scarce on hardgrounds, probably because they consist mostly of fenestellids and other forms with small holdfasts.

Bryozoans are common again on Jurassic and Cretaceous hardgrounds, although they never reach the dominance they had in the Early Paleozoic (see Palmer, 1982, for summary). They include a diversity of types, mostly cyclostomes, from erect forms (e.g. *Terebellaria* and *Ceriocava*) to sheets (e.g. *Reptomultisparsa*, which is often assigned to the form-genus "*Berenicea*") to encrusting runners (e.g. *Stomatopora*). Voigt (1973, 1974, 1987, 1988) described some beautiful bryozoans from Late Cretaceous hardgrounds in Europe.

Cenozoic hardground-dwelling bryozoans are poorly known. We have seen them on hardgrounds from the Eocene through the Recent, but they are usually cryptic and rare.

Echinoderms.--Among the most spectacular hardground-dwelling fossils are the echinoderms, which reach their peak diversity on hard substrates in the Early Paleozoic. The holdfasts of what are probably tiny stemmed echinoderms first appear on hardgrounds in the Middle Cambrian of Greenland (Frykman, 1980; Ineson, 1988). Probable eocrinoid holdfasts are common on Upper Cambrian hardground surfaces in Montana and Wyoming (Brett et al., 1983; see Figure 29) and on somewhat younger Upper Cambrian hardgrounds in Nevada (Wilson et al., 1989). Stemmed echinoderms become abundant and diverse on hardgrounds in the Early Ordovician. Wilson et al. (1992) and Guensburg and Sprinkle (1992) describe Early Ordovician hardground-dwelling eocrinoids and crinoids from Utah and Nevada. Eocrinoid holdfasts are so common on some of these hardgrounds that they cover large patches with forests of truncated stumps (Figure 25). The diversity of Middle Ordovician holdfasts is also noted by Palmer and Palmer (1977), Brower and Veinus (1978), Brett and Liddell (1978), Lewis (1982), Brett and Brookfield (1984) and Guensburg (1992). Echinoderm holdfasts decline in diversity and abundance on hard substrates in the Upper Ordovician, but they are still common (Palmer, 1982; Wilson, 1985a; St. John and Wilson, 1991). Echinoderm holdfasts are easily found on some Silurian hardgrounds (Halleck, 1973; Franzen, 1977) but they become increasingly rare in younger Paleozoic rocks, with the notable exception of the spectacular complete rhombiferans (including cemented holdfasts) described by Koch and Strimple (1968; see back cover). Stemmed echinoderms with holdfasts cemented on hardgrounds are not common in the Mesozoic and Cenozoic, but they have been recorded from the Triassic (Palmer, 1982; Hagdorn, 1983) and the Jurassic (Fürsich, 1974; Palmer and Fürsich, 1974; Palmer 1982). Holdfasts are notoriously difficult to systematically analyze, but work by Franzen (1977), Brett (1981) and Lewis (1982) has provided a framework for assessing the paleoecology and life habits of stemmed echinoderms from the morphology of their holdfasts.

Edrioasteroids are also common on Paleozoic hardgrounds and other hard substrates. The mechanism by which edrioasteroids fixed themselves to a hard substrate is mysterious (see Bell, 1976), and evidence suggests that it was not as firm as the cementation of stemmed echinoderm holdfasts (Wilson, 1985a). There is thus a probable taphonomic bias against the preservation of edrioasteroids on hardgrounds because they were easily removed by various physical and biological processes after death. Nevertheless, edrioasteroids are occasionally preserved on hardgrounds in large numbers, probably as the result of storm burials. Brett et al. (1983, p. 285) mention a "large edrioasteroid" which may be associated with Upper Cambrian hardgrounds in Montana and Wyoming. Guensburg and Sprinkle (1992) record edrioasteroids (edrioasterids and isorophids) on hardgrounds from the Early Ordovician of Utah, and they are common on Middle Ordovician hardgrounds of eastern Canada (Brett and Liddell, 1978; Brett and Brookfield, 1984; see Figure 23). Upper Ordovician hardgrounds and cobbles have fewer edrioasteroids, but when they are found it is usually in large numbers (Wilson, 1985a). They are common on strophomenid brachiopod "pavements" of the Cincinnatian in North America (Meyer, 1990), which may have been early-cemented surfaces. The Iowa Devonian hardgrounds of Koch and Strimple (1968) and Bell (1975) have many well-preserved edrioasteroids, as do the Mississippian cobbles of Smith (1983).

Tube-dwelling "worms".--"Worm" is a terrible classification term because it covers so many often fundamentally different organisms, but it is a convenient category for paleontologists to lump together several groups of elongated, apparently limbless invertebrates about which we know little. We will here discuss three disparate groups under this rubric. All leave some form of skeletal tube fixed to hardgrounds and other hard substrates and all were probably sessile filter-feeders.

Cornulitids are small, tapering, calcitic tubes found encrusting a variety of hard substrates in the Early and Middle Paleozoic. They usually have a small initial coil and strong concentric ornamentation. Most workers believe they were probably annelids (Fisher, 1962), but a case has been made to include them among the mollusks (Blind, 1972). A systematic paleoecological study of the group was done by Richards (1974). He unfortunately never found them on hardgrounds, so he wrote that they never lived on these surfaces. They are, though, common on Upper Ordovician hardgrounds of the Cincinnatian (Bodenbender et al., 1989; St. John and Wilson, 1991) and we have seen them on Silurian hardgrounds as well.

Sphenothallids are small phosphatic (apatitic), free-standing tubes found from the Early Ordovician to the Permian. They often left shiny black holdfasts, sometimes called "*Dawsonia cycla*", on shells, cobbles and hardgrounds. These holdfasts were slightly inflated and hollow with a dorsal ring-like attachment from which the free tube extended. After death the holdfast collapsed, leaving a flat, wrinkled disk with a central collar. (Sphenothallid holdfasts are sometimes misidentified or attributed to other organisms. For example, Frey (1989, fig. 7.4) suggested that sphenothallid holdfasts on nautiloid conchs were likely the "attachment sites" of the dendroid graptolite *Mastigograptus*.) Given enough space, sphenothallids formed gregarious groups on hardground surfaces (Bodenbender et al., 1989). Van Iten et al. (1992) recently described some complete *Sphenothallus* tube systems from the Carboniferous of North America. The authors showed that some sphenothallid species produced clonal, branching colonies, and that their wall structure resembles that of conulariids and other scyphozoans. The current debate is whether sphenothallids are indeed more closely related to cnidarians (promoted by Van Iten et al., 1992) or annelid or other "worms" (a position held by Feldmann et al., 1986).

Serpulids are tube-dwelling polychaetes still living today. Their calcitic tubes first appear on hardgrounds in the Triassic and become nearly ubiquitous on hardgrounds through the rest of the Mesozoic and Cenozoic (Palmer, 1982). Modern serpulids are classified by features in their soft anatomy unrecognizable in the fossil record, so most ancient serpulids are given generic names reflecting features of their tubes, such as *Pentaserpula*, *Dorsoserpula* and so on. Serpulids were often but by no means always cryptic in habit, tending to heavily encrust overhangs and the sides of crevices in hardgrounds (Figures 17, 30 and 31). This pattern was stressed for a Jurassic occurrence by Palmer and Fürsich (1974) and is still common today (see Table 1). Almost all the references to Mesozoic and Cenozoic hardgrounds listed in the bibliography mention the abundance of encrusting serpulid tubes. "Spirorbid" tubes are recorded on hardground surfaces back to the Devonian (Palmer, 1982). These Paleozoic "spirorbids" need closer study now that the morphologically similar vermiform "gastropods" are coming to be recognized as an important Upper Paleozoic encrusting group (Weedon, 1990).

Bivalves.--Encrusting bivalves on hardgrounds are an almost exclusively Mesozoic phenomenon, with the exception of *Limanomia* of the Devonian and Mississippian (Palmer, 1982). Oysters, such as *Lopha*, *Exogyra* and *Liostrea*, become the dominant encrusters on many Jurassic hardgrounds in Europe and North America (Palmer, 1982; see Figures 32, 33 and 34). In some horizons they accumulated in thick rinds so that the original hardground is nearly lost beneath their shells (see Palmer and Fürsich, 1974 and Nielson, 1990, for examples). Sometimes the oysters grew so thickly that individuals could not reach full size and often had deformed shapes. Non-oyster encrusting bivalves, such as *Atreta* (a dimyid) *Eopecten*, and *Plicatula*, are also common on Jurassic hardgrounds (Fürsich, 1979; Gruszczynski, 1979, 1986; Harper and Palmer, 1993). Encrusting bivalves in the Cretaceous continue to be abundant on hardgrounds and other lithologic hard substrates (Voigt, 1959; Nekvasilová and Zitt, 1988; Zitt and Nekvasilová, 1991b; Bryan, 1992). Cenozoic hardgrounds have far fewer encrusting bivalves, but they are occasionally present (Martinius and Molenaar, 1991).

Graptolites.--A surprising addition has been recently made to the lists of hardground-dwelling organisms. Mitchell et al. (1993) describe the first complete colony of a crustoid graptolite (*Bulmanicrusta*?), which was found on a hardground fragment from the Cincinnatian of Ohio (Figure 35). The specimen has a runner-type colony form and numerous thick-walled small vesicles ("graptoblasts") at the ends of the branches. So far the specimen is unique, but we expect that further examples will be found once paleontologists begin looking for them.

An odd form sometimes attributed to graptolites is also occasionally found on Upper Ordovician hardgrounds, cobbles and shells. It is a set of thin, carbonaceous black tubular strands known as *Chaunograptus*, which was treated as a graptolite by Ruedemann (1947). There is no recent description of the genus and the specimens we have seen show no clear thecae. Nevertheless, the *Treatise* (Bulman, 1970) suggests that *Chaunograptus* is synonymous with the "aberrant crustoid" *Hormograptus*. We suspect the affinities of *Chaunograptus* may be closer to *Sphenothallus*. Mierzejewski (1986) regarded the genus as a hydroid.

Common Hardground Borings

An organism "bores" when it excavates a hard substrate by cutting through it by chemical and/or mechanical means (Figure 36). Borings are formed on virtually all marine hard substrates, including shells, cobbles and rocks of many lithologies, as well as on carbonate hardgrounds. Macroborings in hardgrounds have been well studied, from their earliest appearance in the Lower Cambrian (James et al., 1977) through the Cenozoic and Holocene (see, for examples, Bromley and D'Alessandro, 1989, and Bromley and Asgaard, 1992). Since borings are the last faunal features to succumb to erosional scour, they are the most common criterion for recognizing ancient hardgrounds. In this section we briefly list and describe the four most common boring ichnogenera found on carbonate hardgrounds. There are many other borings found on hardgrounds, but these are the forms most commonly seen.

Trypanites.--Mägdefrau (1932) described *Trypanites* as a simple, unbranched, cylindrical, mostly straight boring with a single opening (Figures 3, 36 and 37). *Trypanites* is almost always excavated perpendicularly to the hardground surface. From our observations, most *Trypanites* have diameters of about 2 mm, but they can range from 0.5 to 3.0 mm; lengths of this boring can at times exceed 15 cm, but they are usually less than 5 cm long. Extended discussions of the ichnotaxonomy of *Trypanites* can be found in Müller (1956), Bromley (1972), Elias (1980), and Pemberton et al. (1988). *Trypanites* is the most common Paleozoic hardground trace fossil. It is a feature of Lower Cambrian hardgrounds (James et al., 1977) but it is thus far absent on Middle and Upper Cambrian surfaces as well as those of the Lower Ordovician. It reappears in great numbers in the Middle and Upper Ordovician and is found sporadically on hardgrounds from the Silurian to the Holocene. *Trypanites* was probably created by several different organisms, from sipunculids (Rice, 1969; Pemberton et al., 1980) to polychaetes (Kobluk and Nemcsok, 1982) to barnacles (Warme, 1975; Watkins, 1990). During their heyday in the Middle and Upper Ordovician, these borings were preferentially made on the tops of small topographic highs (Figures 19 and 20) and along slab edges on hardground surfaces (Brett and Liddell, 1978, Brett and Brookfield, 1984; Siewers, 1988; Bodenbender et al., 1989).

Petroxestes.--This ichnogenus is a shallow to deep, elongate boring with rounded ends and parallel sides in plan view; it is up to 30 mm long and 4 mm wide (Figure 38). Pojeta and Palmer (1976) originally described these structures as the facultative borings of the modiomorphid bivalve *Corallidomus.* Wilson and Palmer (1988) formally named the ichnogenus, illustrating its occurrence in skeletal substrates, cobbles and hardgrounds. *Petroxestes* is common on Cincinnatian hardgrounds, but is often misinterpreted as the distal end of a *Diplocraterion* burrow (e.g. "*Corophiodes* cf. *luniformis*" in Osgood, 1970, pl. 61, fig. 5). *Petroxestes* is often the only surviving evidence of many Cincinnatian hardgrounds. When a hardground exposure is large enough, *Petroxestes* will show a clumped distribution which may have been controlled by the degree of cementation of the sediment substrate. Virtually all *Petroxestes* are known from the Upper Ordovician Cincinnatian Group, but we recently found the boring in prasoporid bryozoans from the Middle Ordovician Lexington Limestone (Grier Limestone Member) of central Kentucky.

Gastrochaenolites.--This boring, described in detail by Kelly and Bromley (1984), is a clavate boring with a single entrance (Figures 3 and 39); some forms had a calcareous lining, particularly in the posterior part of the boring. *Gastrochaenolites* ranges in size from less than one cm to over 10 cm deep and 5 cm wide and is usually constructed perpendicular to the substrate surface. Most of these borings were made by bivalves, particularly the lithophagids, gastrochaenids, and pholads. *Gastrochaenolites* appears first in the Triassic (J.G. Carter, personal communication) and is abundant in Jurassic, Cretaceous, Tertiary and Quaternary hardgrounds and other hard substrates. In confined substrates, such as cobbles, *Gastrochaenolites* may intersect and form elaborate tunnel systems, usually with a variety of encrusting and nestling organisms inside (Voigt, 1973, 1974; Baluk and Radwanski, 1977; Wilson, 1986a, b).

Entobia.--This large ichnogenus covers many of the borings of endolithic sponges such as *Cliona*, *Cliothosa* and *Siphonodictyon.* It is most commonly a series of small swollen chambers (camerae) connected by thin canals to other chambers and multiple apertures (Figure 40); Jurassic *Entobia* appears to be non-camerate. The ichnotaxonomy of *Entobia* is complex; Bromley (1970), Bromley and D'Alessandro (1984, 1989) are the best sources for details of both the classification of *Entobia* and its formation. Evidence for sponge boring seems to extend back into the Lower Cambrian (Kobluk, 1981c), but earlier forms often required other ichnogenera to accommodate them. The small, possibly sponge-formed, rosette borings in Paleozoic and Mesozoic hardgrounds badly need more study. Sponges only become a major bioerosive factor in the Middle Mesozoic. Today clionid sponges bore calcareous substrates at extraordinary rates, producing dramatic rates of bioerosion and sediment production (Neumann, 1966; Cobb, 1969; Rützler, 1974, 1975) and destroying countless carbonate hardgrounds in the process.

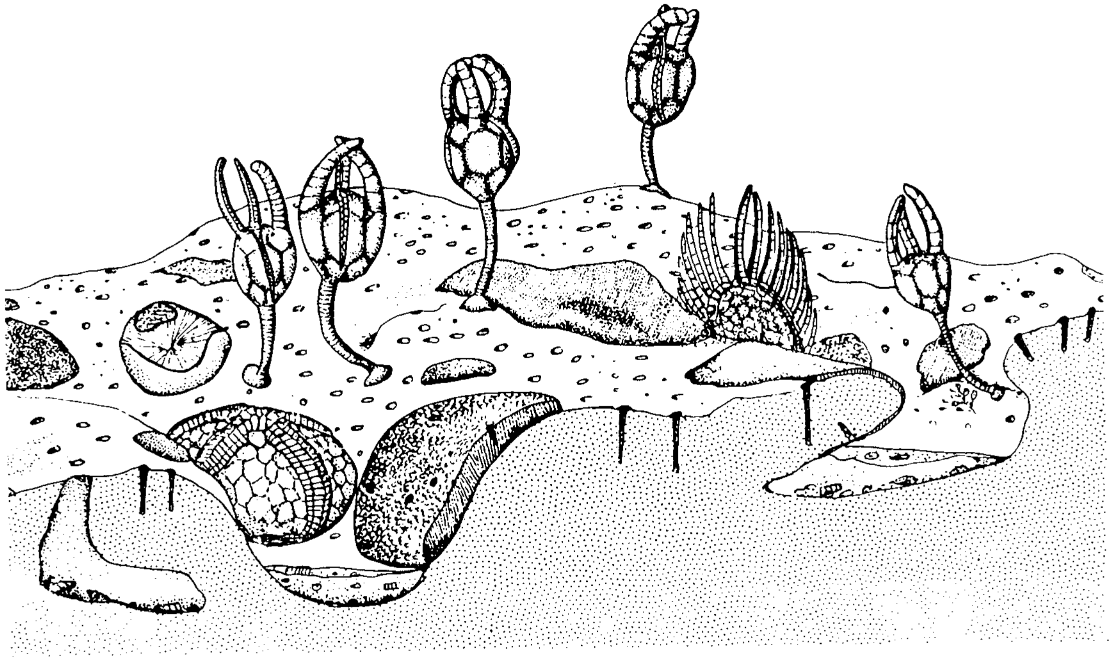

Figure 23. Detailed reconstruction of a Middle Ordovician hardground community described by Brett and Liddell (1978). Illustrated organisms include encrusting bryozoans, *Hybocystites eldonensis, Edriophus levis, Amygdalocystis*, an eroded holdfast (*Cleiocrinus?*) and *Trypanites* borings. Reproduced from Figure 9 of Brett and Liddell (1978) with permission of the Paleontological Society.

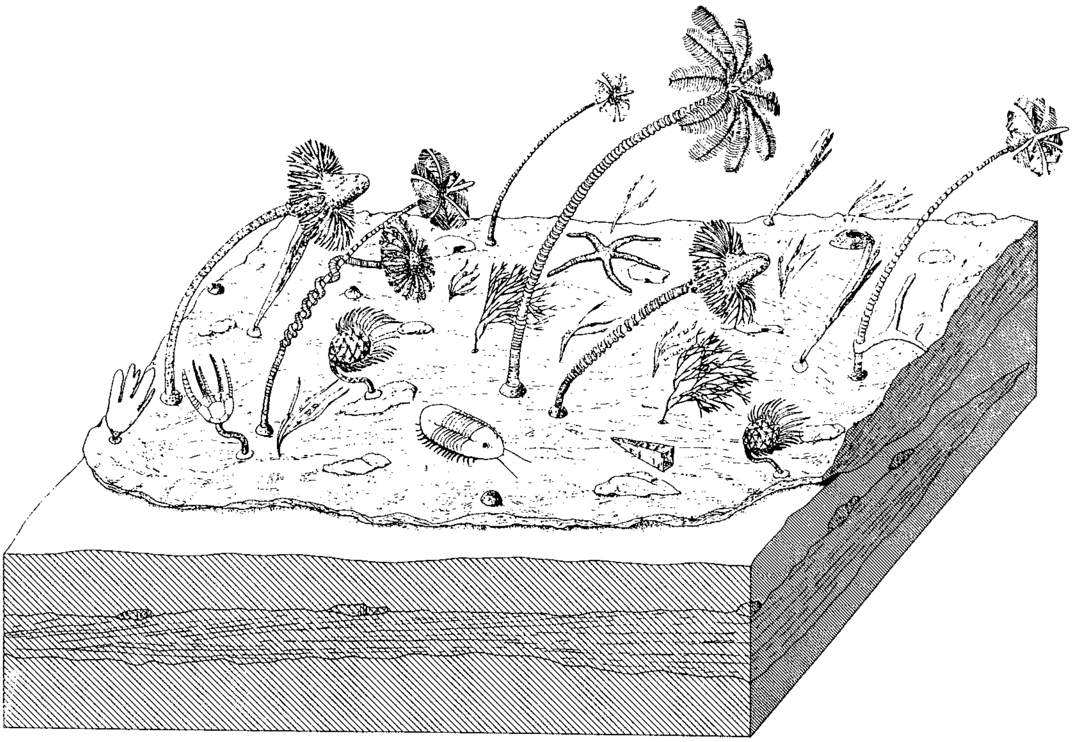

Figure 24. Block diagram of a Middle Ordovician hardground (Lebanon Formation, central Tennessee) and some of its associated fauna. Figure drawn by Tom Guensburg; crinoids fully discussed in Guensburg (1992). The silhouette diagram below identifies the figured organisms: **a**=*Reteocrinus polki*, **b** =*Tryssocrinus endomitus*, **c** =*Gustabilicrinus plektanikaulos*, **d** =*Hybocrinus bilateralis*, **e** =*Oklahomacystis trigonis*, **f**=*Columbicrinus crassus*, **g**=*Reteocrinus variabilicaulis*, **h**=small crinoid holdfast, **i**=*Cleiocrinus tesselatus* holdfast, **j**=*Salteraster grandis*, **k**=bifoliate bryozoans (three species), **l**=arthrostylid bryozoan, **m**=*Homotelus* sp., **n**=conulariid skeleton, **o**=trepostome bryozoan, **p**=*Doloroides* sp. (brachiopod) cluster. For scale, *Columbicrinus* had a height of about 35 cm. Reproduced from Figure 16 of Guensburg (1992) with permission of the Paleontological Society.

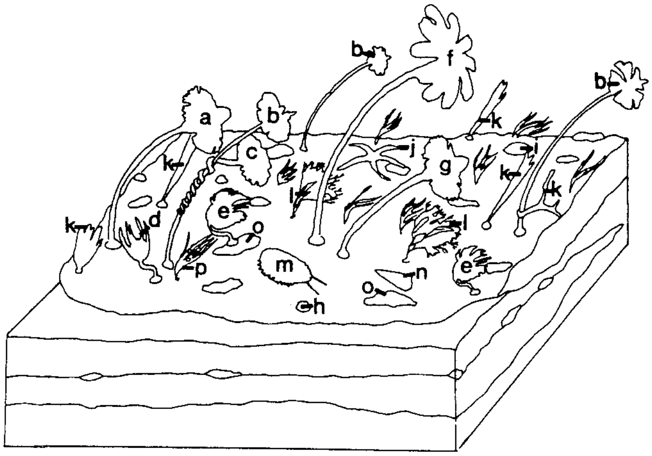

Figure 25. Eocrinoid holdfasts encrusting the bryozoan *Nicholsonella* on a Lower Ordovician hardground. See Wilson et al. (1992) for a full description of this hardground and its fauna. Specimen C/W-98-8, Kanosh Shale, near Ibex, Confusion Range, Millard County, Utah; x2.

Figure 26. Trepostome bryozoan on a Middle Ordovician hardground. The triradiate ridges are typical of many massive bryozoan colonies on hardgrounds. Specimen C/W-129-1, Point Pleasant Limestone, Bradford, Bracken County, Kentucky, USA; x2.5.

Figure 27. Trepostome bryozoans encrusting a Middle Ordovician hardground. Specimen C/W-15-1, Lebanon Limestone, Rutherford County, Tennessee, USA; x2.

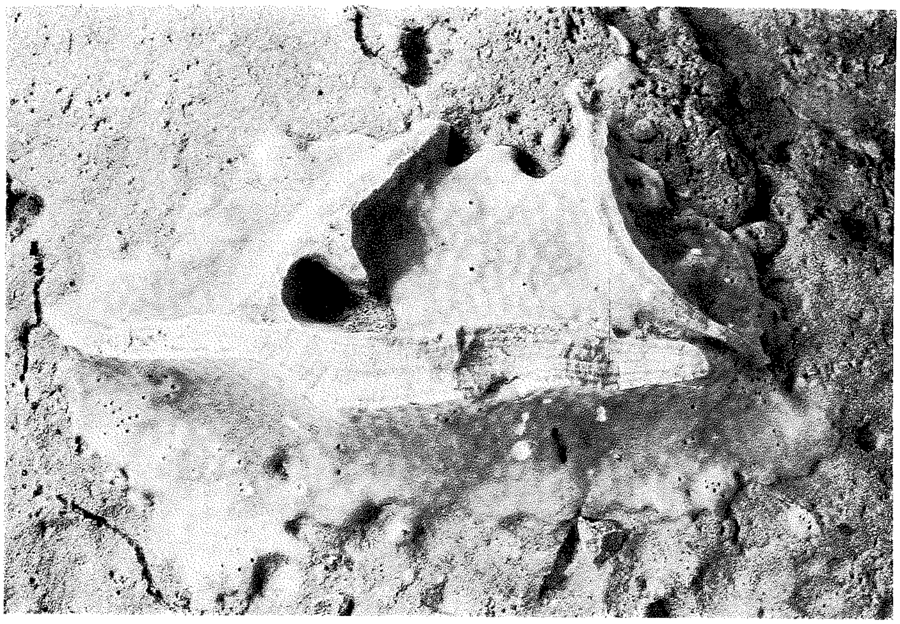

Figure 28. Large trepostome bryozoan (*Amplexopora*) on an Upper Ordovician hardground. Note also the numerous small borings in the bryozoan which have raised lips, indicating they were made while the bryozoan was still alive and growing. See Bodenbender et al. (1989) for a description of this hardground and its fauna. Specimen C/W-6-1, Dillsboro Formation, near Dillsboro, Dearborn County, Indiana, USA; x0.6.

Figure 29. Echinoderm holdfasts (probably of eocrinoids) on an Upper Cambrian intraformational conglomerate hardground. See Brett et al. (1983) for a full description of this hardground and its fauna. Specimen C/W-47-1, Snowy Range Formation, south of Red Lodge, Carbon County, Montana, USA; x1.6.

Figure 30. Middle Jurassic coelobite fauna growing on the roof of a cavity excavated beneath the hardground described by Palmer and Fürsich (1974). Serpulid worms and *Berenicea*-type bryozoans typically dominate such cavity faunas. Compare with typical Jurassic upward-facing surfaces, such as those in Figures 32 and 39. Width of view is 3 mm.

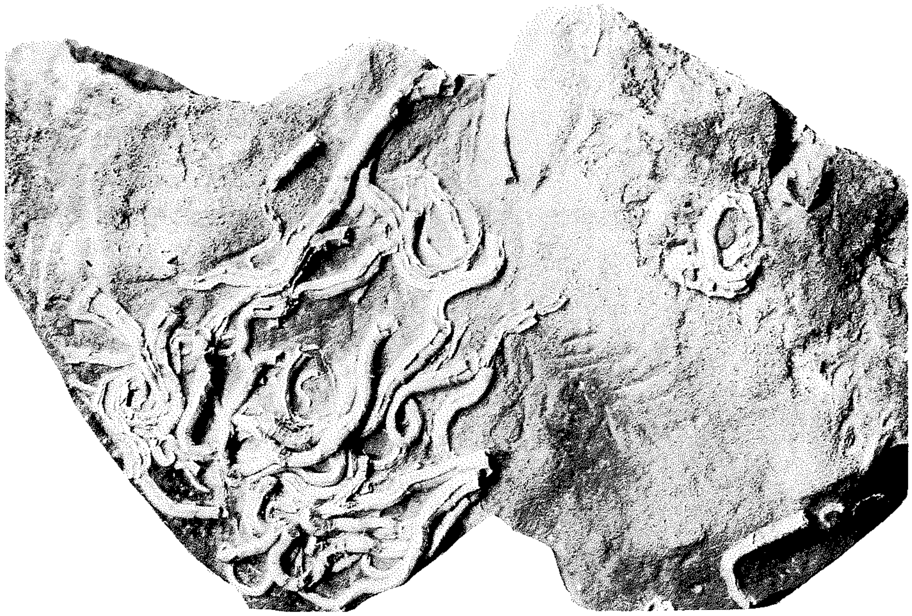

Figure 31. Serpulid tubes (probably *Dorsoserpula*) on the underside of a Jurassic hardground. Note the fairly consistent orientation of the openings. C/W-138-1, Snowshill Quarry near Moreton-in-Marsh, England; x1.8.

Figure 32. Bivalves (oysters and dimyids) encrusting a hardground surface. Middle Jurassic of Normandy, France. Coin is 24 mm in diameter.

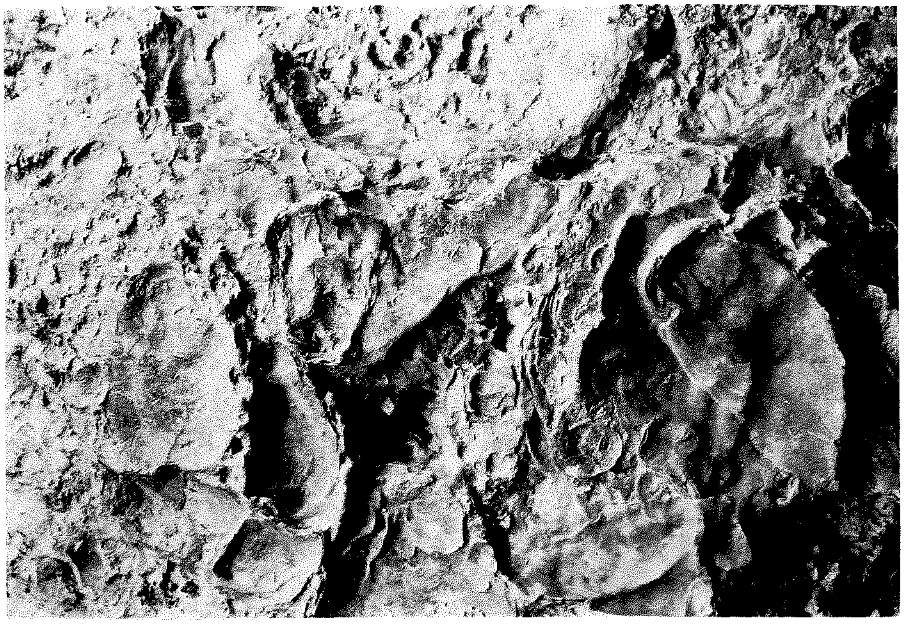

Figure 33. Oysters on a Jurassic hardground. Specimen C/W-77-1, Upper Bathonian, Old Cement Quarry, Ranville, Normandy, France; x1.

Figure 34. Oysters (*Liostrea strigilecula*) and *Gastrochaenolites* borings in plan view on a Middle Jurassic hardground. Specimen C/W-136-1, Carmel Formation, near Gunlock, Washington County, Utah, USA; x0.6.

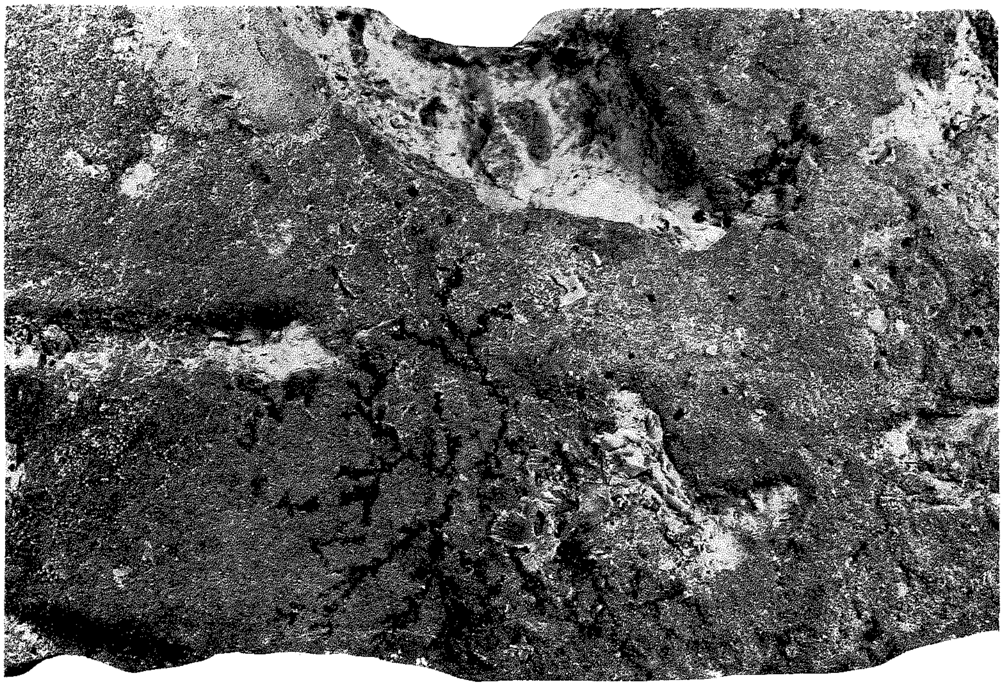

Figure 35. The crustoid graptolite *Bulmanicrusta?* sp. on an Upper Ordovician hardground. The crustoid is the dark set of runners in the lower center of the photograph. The small black disks scattered across the right side of the slab are isolated graptoblasts. Note also the trepostome bryozoan in the upper left and the runner-type bryozoan *"Proboscina" auloporoides* in the center and left. See Mitchell, Wilson and St. John (1993) for full description. Specimen OSU 47297, Bull Fork Formation, Caesar Creek Lake, Warren County, Ohio, USA; x1.

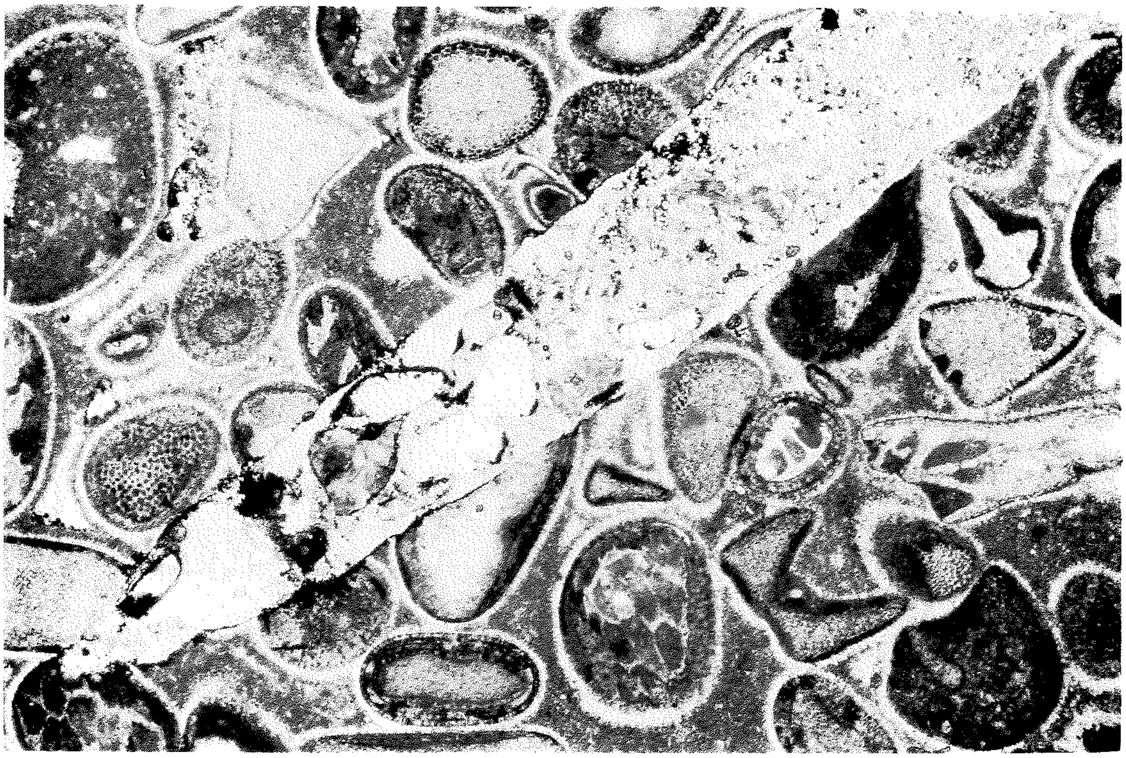

Figure 36. Same specimen as in Figure 7. Grains, marine cement and geopetal micrite cut by *Trypanites*. Hardground, Middle Jurassic of Normandy, France. Width of field is 4.4 mm.

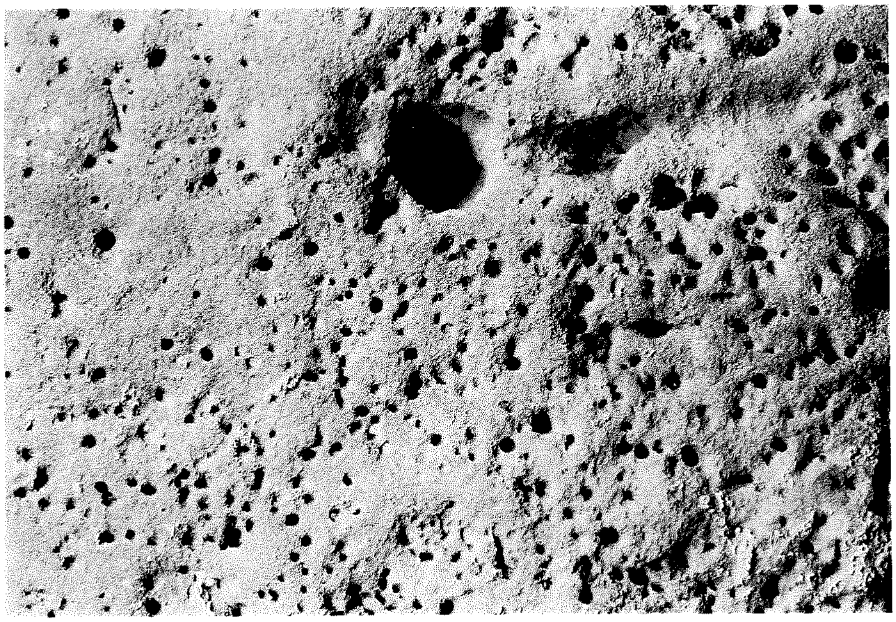

Figure 37. Plan view of *Trypanites* borings (the scattered small holes) in an Upper Ordovician hardground. The large cavity at the top of the photograph is a burrow formed in the soft sediment before lithification of the hardground. The sediment filling this burrow has been preferentially eroded away. Specimen C/W-43-1, Liberty Formation, Oliver Township, Adams County, Ohio, USA; x1.

Figure 38. Plan view of the boring *Petroxestes* on an Upper Ordovician hardground. See Wilson and Palmer (1988) for description. Specimen C/W-128-1, Bull Fork Formation, Caesar Creek Lake, Warren County, Ohio, USA; x1.

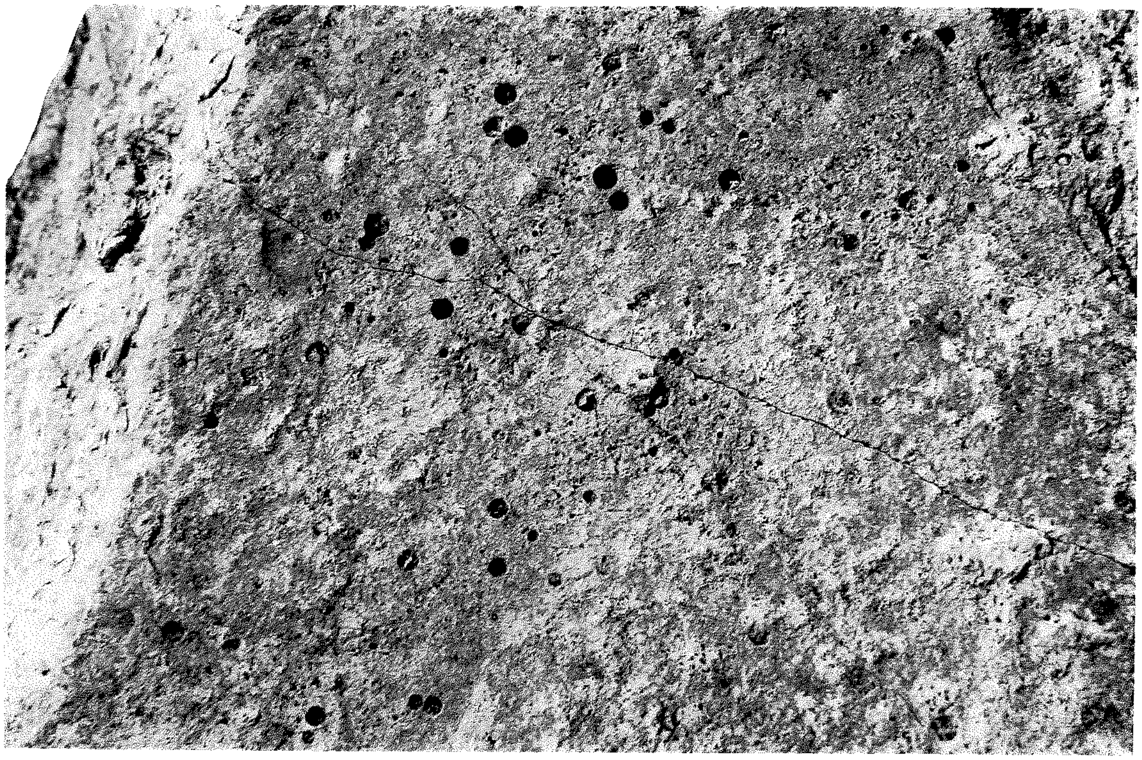

Figure 39. Smooth, eroded hardground surface perforated by bivalve borings. Middle Jurassic of Normandy, France. Width of field is 30 cm.

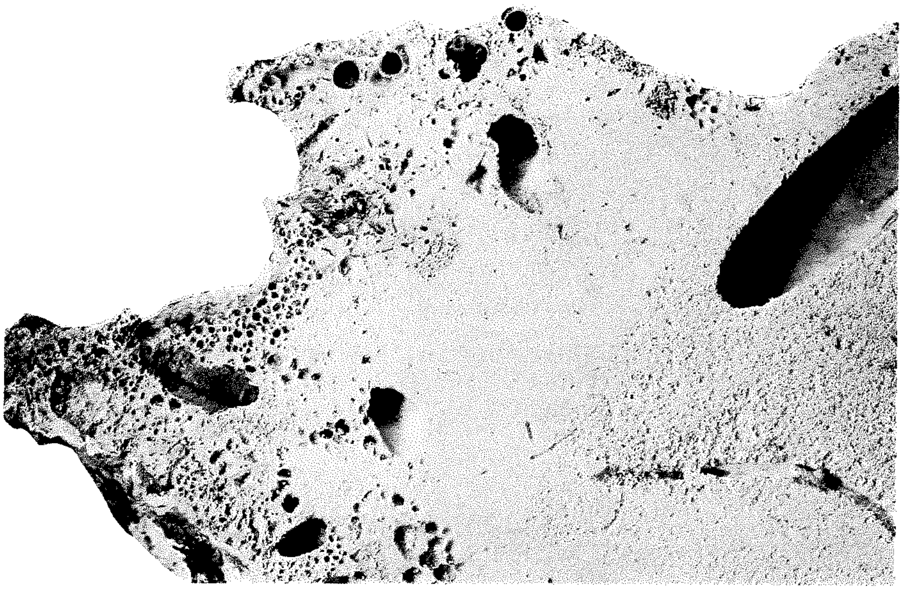

Figure 40. Cross-section of modern bored and encrusted carbonate eolianite. Large hole in the upper right was produced by the bivalve *Lithophaga*; holes in the center were probably drilled by polychaetes; the network of small holes on the left side was excavated by the sponge *Cliona*. The shell-rimmed holes at the top are cross-sections of vermetid gastropods which encrusted the upper surface. Specimen C/W-137-1; North Point, San Salvador Island, The Bahamas; x1.

ECOLOGY AND PALEOECOLOGY OF HARDGROUND FAUNAS

Some Ecological Adaptations of Hardground Faunas

Hardgrounds were usually stable, high energy, well oxygenated environments with a good supply of food for the suspension feeders that constituted the great proportion of their faunas. However, the hydraulic energy of the environment presented the fauna with a number of attachment and stability problems that required adaptive morphological solutions, and recurring patterns of such adaptations can be seen in unrelated groups of hardground inhabitants of different ages. Cementation and infaunalization by boring or nestling are the criteria by which ancient hardground faunas are defined (see above) and these two habits are themselves part of the panoply of adaptations for dealing with the rigors of hard substrate life. These and other adaptations which are considered below, are not, of course, exclusive to hardground faunas but apply to hard substrate dwelling generally.

Problems with the physical environment.--Buffeting by currents, and scour and abrasion by sediment held in suspension or moving by traction are the principal physical hazards to hardground dwellers. Borers avoid both problems. Firm cementation resists buffeting but may involve a rigidity that increases the abrasive effects of scour. Many cementers are very low growing with large areas of attachment, or present a streamlined, rounded profile to currents sweeping across the sea-bed (e.g. many bryozoans, tabulate corals, edrioasteroids, inarticulate brachiopods). Taller rigid organisms have areas of attachment which expand at the bottom where they adhere to the substrate and where the bending moment is greatest (many bush-like and fenestellid bryozoans); sometimes these are buttressed like the bases of tree-trunks (as in fenestellids). The tallest tiers of the hardground community often combine expanding attachment discs with articulations or flexible stems so that they may bend with the surging currents like trees in the wind (stalked echinoderms, ptilodictyid bryozoans, soft corals).

Scour is also countered by streamlined profiles, and by thick exoskeletons, though, as we argue below, it was probably increasing predation pressure that drove the move towards more and thicker skeletons in the Mesozoic. A consequence of erosion resistance in Mesozoic encrusters is the building up of thick layers of shells, particularly oysters and serpulid tubes, on some Mesozoic hardgrounds ("biogenic layers" of Palmer and Fürsich, 1974). Flexible elastic periostraca, and surface ornaments that slow down corrasive laminar flow immediately adjacent to encrusting skeletons, may also be expected to reduce scour effects.

Effects of any sort of damage, both physical and biological (see below), are mitigated in modular organisms in which death of individuals does not mean death of the colony, so that both reproduction and regeneration may still occur. Corals and bryozoans (probably the most successful of all hardground-inhabiting groups) are examples. Indeterminate growers with good regeneration and repair capabilities, such as sponges, are also favored.

Many hardgrounds occur in sequences in which there is abundant evidence of storm activity, during which the consequences of both buffeting and abrasion are particularly severe. Storms also move shoals of soft sediment around on hardground surfaces, smothering colonized areas and exposing new ones. Such an environment may favor small, rapidly-growing, opportunistic, weedy species with brief generation times (such as spirorbid serpulids, encrusting foraminiferans, runner-type bryozoans).

Problems from encounters with other species.--Borers and encrusters cannot flee the predatory and competitive attentions of other species, though borers, as we have seen, may find refuge in their excavations and hand them over to small nestling and encrusting coelobites after their deaths. Shallow borings become increasingly vulnerable to attack as groups with the ability to rasp away the rock substrate, such as fishes, echinoids, and grazing mollusks, become more abundant. We are currently studying the effects of the

Mesozoic Marine Revolution with its radiations in many durophagous groups (Vermeij, 1977) on boring habits and diversities.

Among encrusters, some of the morphological stratagems that help deal with the rigors of the physical environment, such as exoskeletons and thick shells, are also likely to be effective against predators. This is a field that would benefit from experimental work. Harper (1991) has shown that cementation in bivalves confers advantages by limiting the abilities of potential predators to maneuver the prey. Serpulids developed a range of ornaments through the Mesozoic, which may have something to do with attack. The triangular profile of some upward-facing serpulids (interestingly, not so common in coelobitic forms), may make it difficult for crabs to pinch and crush the tube. Coelobitic hardground faunas become well differentiated in the Mesozoic compared with earlier times (Palmer and Fürsich, 1974; Brett and Liddell, 1978; Wilson and Palmer, 1990); cavity dwelling is an effective way of side-stepping predation (Jackson, 1977).

Modularity, indeterminate growth, and weediness (small size, abundance, and rapid growth) are as effective in dealing with biological as with physical depredations, and also increase handling times thus offering less reward for a unit of predatory effort. Extensive work has been undertaken on morphological and chemical strategies designed to cope with the extreme competition for space that can occur on limited hard substrates (see Jackson, 1977a, 1977b, 1979, 1981, 1983; Buss, 1986).

Ecological Succession and Community Replacement on Hardgrounds

One of the attractive features of studying hardground faunas is knowing that, despite the many other vagaries of paleontological data, the fossil encrusters and borings are at least *in situ*. It is highly unlikely that an encruster or boring was transported into a hardground assemblage without leaving obvious evidence. This stability has led some paleontologists to attempt to decipher "ecological succession" or "paleoecologic succession" on ancient hardgrounds (Goldring and Kazmierczak, 1974; Gruszczynski, 1979, 1986; Walker and Diehl, 1986). In a review of this topic, Miller (1986) pointed out various misunderstandings of the original biological definition of ecological succession. Such succession is defined as biotic changes in community composition and structure in which organism-organism interactions are most important (Miller, 1986, p. 227). Most paleontological studies of "ecological succession" have actually been of *community replacement* (Hoffman and Narkiewicz, 1977; Johnson, 1977) in which community turnover is controlled by environmental changes rather than organismal interactions. True ecological succession is thus *autogenic*, or controlled by organisms within the community, and community replacement is *allogenic*.

Ecological succession.--Since succession on hard substrates is primarily controlled by competition for living space on these generally two-dimensional surfaces, we can study the preserved overgrowth relationships among encrusters to approximate the patterns of ecological change. Unfortunately this technique only works as an approximation because it is almost always impossible to tell if an encruster was overgrowing another living encruster or its dead skeleton. Brett and Liddell (1978) were able to suggest a sequence of encrusters on Middle Ordovician hardgrounds because earlier generations were often highly abraded before the next generation was established (Figure 41). They did not claim this as an ecological succession because the causes could well have been allogenic. So far there is only one documented scenario of an autogenic ecological succession on an ancient hard substrate. Wilson (1985a) described a succession of bryozoans, cornulitids, crinoids and edrioasteroids on a set of cobbles from the Upper Ordovician (Cincinnatian) of Kentucky. Even though these cobbles are not part of a traditional hardground, the fossils which encrust them are the same as those found on contemporaneous Cincinnatian hardgrounds. Succession on the cobbles was probably similar to that which occurred on the hardgrounds, but a significant difference was the relative sizes of the available substrates.

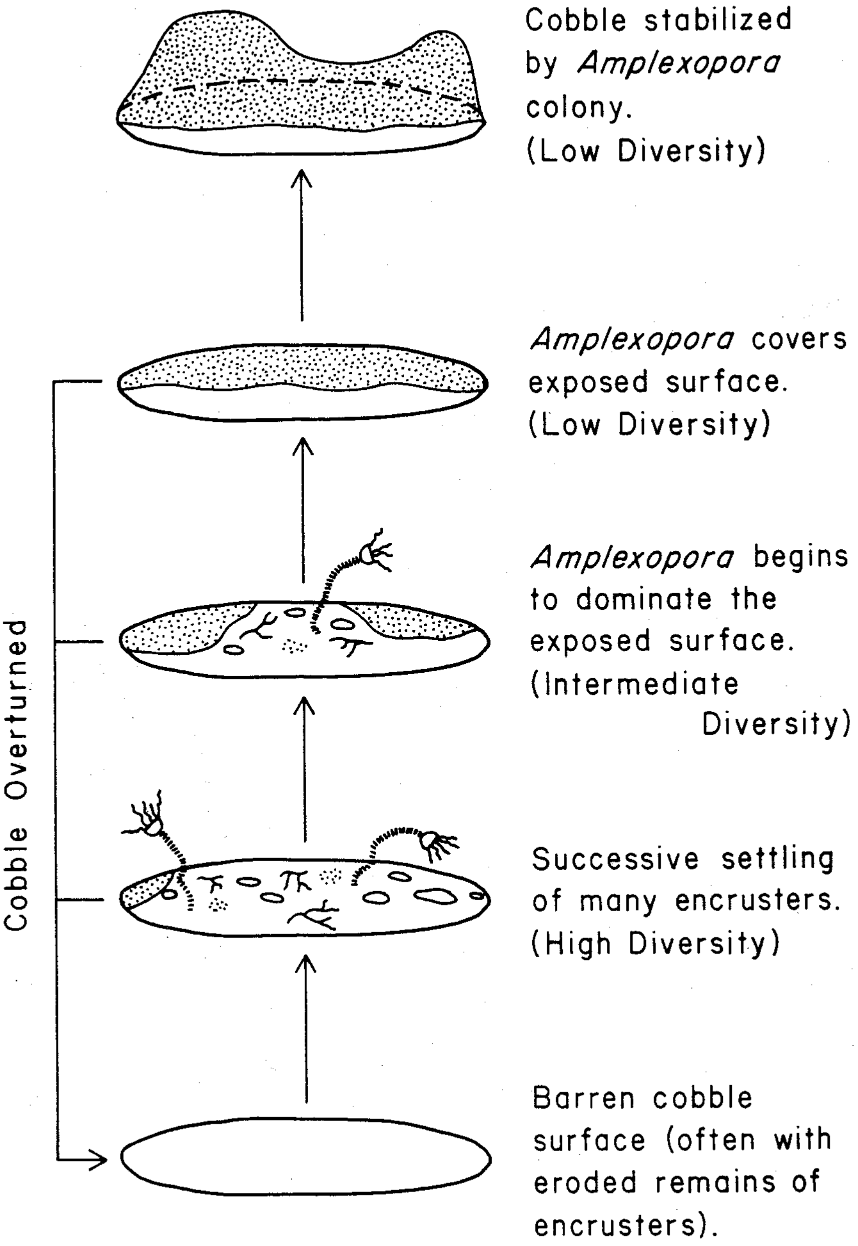

Figure 42. Encrusting community succession on cobbles from the Upper Ordovician of northern Kentucky. Note that the overturning events maintain high diversity unless the trepostome bryozoan *Amplexopora* produces a colony massive enough to stabilize the cobble. Reproduced from Figure 2 of Wilson (1985) with permission of the American Association for the Advancement of Science.

TEMPORAL TRENDS IN HARDGROUND COMMUNITIES

The First Marine Hard Substrate Communities

Marine hard substrates form distinct, easily defined environments that are usually first recognized by their encrusting or boring fauna. In this section we present a summary of the earliest hard substrate faunas, whether on traditional carbonate hardgrounds, other inorganic surfaces, or shells. We want to examine the origins of the distinctive hard substrate communities which become so common and pervasive from the Middle Ordovician until today. The initial exploitation of the hard substrate niche was slow and measured, and later evolution of these communities was marked by similar conservatism.

Precambrian.--Marine hard substrates have been present for as long as there have been seas, but finding evidence that a particular surface was exposed on the ocean floor is usually laborious. Since the primary clues to this exposure are the remains of encrusting and boring organisms, recognizing hard substrates in their absence is especially difficult. Precambrian rocky shores are fairly well known (Johnson, 1988a, 1988b, 1992), but evidence of hard substrate organisms is understandably rare. Extensive stromatolites have been noted on various rock surfaces; the earliest known grew on brecciated komatiite flows between 3300 and 3500 million years ago (Byerly et al., 1986). Bangiophyte red algae are described from "locally stabilized" peritidal carbonate sediment surfaces between 1250 and 750 million years old (Butterfield et al., 1990). The earliest described endoliths are from 1700 million year old stromatolites in northern China (Zhang and Golubic, 1987). Bengston and Zhao (1992) recently described endoliths and possible predatorial borings in tubes of the earliest skeletal animal, *Cloudina*, from the latest Precambrian of China. We expect, though, that with closer observations borings will be found to be considerably older.

Lower Cambrian.--Hard substrate dwellers in the earliest Paleozoic are thus far known only from archaeocyathid reefs and associated hardgrounds. Kobluk (1981b) described middle Lower Cambrian encrusters from framework cavities within archaeocyathid patch reefs of western Nevada. The preserved community consists mostly of calcified algae (especially *Renalcis* and *Epiphyton*), sponges, juvenile archaeocyathids and a few rare problematic forms. A more diverse archaeocyathid-cavity community was described by Kobluk & James (1979) from the upper Lower Cambrian of Labrador. That community is similar to the earlier version but also contains some agglutinated foraminiferans, evidence of endolithic sponge boring (Kobluk, 1981c), and the earliest macroboring, the cylindrical excavation *Trypanites* (James et al., 1977). *Trypanites* has also been found in Lower Cambrian hardgrounds in Scotland (Palmer, 1982).

Middle Cambrian.--Hardgrounds are briefly described from the Middle Cambrian of Greenland by Frykman (1980) and Ineson (1988). These surfaces probably formed from the early diagenetic replacement of cyanobacterial mats with phosphate minerals. Some of these hardgrounds display numerous small ?echinoderm holdfasts on their upper surfaces, which represent the earliest hardground encrusters. The holdfasts are not yet described, but they resemble those of eocrinoids. The Middle Cambrian hardgrounds show no evidence of boring.

Upper Cambrian.--Brett et al. (1983) described an encrusting community on a sequence of Upper Cambrian hardgrounds developed on carbonate flat pebble conglomerates in Montana and Wyoming (Figure 29). The preserved community contains large numbers of echinoderm holdfasts (probably of eocrinoids according to Guensburg & Sprinkle, 1992, p. 409) and some small lumps of spongiomorph algae and probable stromatolites. Similar eocrinoid-encrusted hardgrounds are also known from the Upper Cambrian of Nevada (Wilson et al., 1989). There is little evidence yet for macroboring in Upper Cambrian hardgrounds. Chow & James

(1992, p. 119) mention and briefly figure "*Trypanites*-like borings" which apparently truncate crystals in Upper Cambrian oolitic hardgrounds in western Newfoundland. Further examination of these specimens is needed to distinguish them from similar eroded burrows.

Lower Ordovician.--Carbonate hardgrounds become extraordinarily common in the Ordovician, and it is during the early part of this period that hard substrate communities diversify and begin to assume a character they retain for the remainder of the Paleozoic. Guensburg & Sprinkle (1992) note dozens of echinoderm species from the Tremadoc-Arenig of the western United States. Many of these echinoderms, including eocrinoids, crinoids and edrioasteroids, were attached to carbonate hardgrounds. Wilson et al. (1992) describe and interpret a diverse Arenigian hardground community from Utah (Figure 25). The primary inhabitants of these hardgrounds were stemmed echinoderms of at least four types, including eocrinoids and crinoids. These echinoderms were at times so common that they formed dense thickets of stems and crowns. Bryozoans, represented by four species, make their first appearance on hard substrates in this community. One rare sponge was also noted. The Utah hardgrounds also show the first polarization of the encrusting species between those which preferred upward-facing surfaces and those more commonly found under overhangs and within crevices. Despite the abundance of carbonate hardgrounds in the Lower Ordovician, there is no convincing evidence of macroborings at this time. The structures described by Lindström (1979a) in Arenigian hardgrounds of Sweden appear to be exhumed burrow systems. The *Trypanites* borings detailed by Orviku (1940, 1960) and Jaanuson (1961) are sometimes cited as "Lower Ordovician" but are actually Llanvirnian-Llandeilian (Middle Ordovician).

Middle Ordovician.--Hardground communities reach a peak of abundance and diversity in the Middle Ordovician and take on a general structure they will maintain through the remainder of the Paleozoic. Among the earliest hardgrounds in this interval are the Llanvirnian-Llandeilian "discontinuity surfaces" described by Orviku (1940, 1960) and summarized by Jaanuson (1961) in the Baltics and Scandinavia. These units have no described encrusters, but they are thoroughly bored by *Trypanites*. Blackriverian hardgrounds in Tennessee have diverse echinoderm and bryozoan encrusting faunas, as well as numerous *Trypanites* borings (Guensburg, 1984, 1992; Siewers, 1988; see Figures 24 and 27). Trentonian hardgrounds in Ontario hosted dozens of encrusters, including over two dozen echinoderm and bryozoan species and rare cornulitids, and were abundantly perforated by the now common *Trypanites* (Brett & Liddell, 1978; Brett & Brookfield, 1984; see Figures 23 and 41). Palmer & Palmer (1977) and Palmer (1978) described in detail a single Trentonian hardground surface in Iowa which had a similar diversity of echinoderms, bryozoans, *Trypanites*, and what appears to be the first sponge boring on a hardground (*Cicatricula*).

Summary and analysis.--Marine hard substrate communities developed in a slow, step-wise fashion. The earliest organisms to exploit this niche were, predictably, bacteria and algae in the Precambrian. The most commonly preserved Early Cambrian marine hard substrates were the skeletons of archaeocyathids, and it is here we find the first macroborings (*Trypanites*) and skeletonized encrusters. These organisms, though, are thus far found only in cryptic spaces in archaeocyathid patch reefs; exterior surfaces apparently did not host these organisms. There are several possible explanations: (1) predatory or grazing activities deterred these organisms from the exposed surfaces; (2) these communities preferred the gloomy light and reduced current of the internal cavities; (3) living tissue or other activities of the archaeocyathid hosts inhibited epibiont settlement; or (4) we have not looked hard enough for epibionts on archaeocyathid exteriors.

With the extinction of archaeocyathids, hard substrate communities nearly disappear. Rare eocrinoids are virtually the only encrusters in the Middle and Late Cambrian. Macroborings are simply unknown until the Middle Ordovician. Much of this pattern is certainly due to the scarcity of persistent hard substrates in the later Cambrian. Carbonate hardgrounds become abundant only near the end of the Cambrian and the beginning of the Ordovician, and extensive shell layers make their first appearance in the Middle Ordovician. The hardground communities of the latest Cambrian and the Early and Middle Ordovician thus record the origination and diversification of new groups onto hard substrates with few or no ancestors from the earlier equivalents of the niche. The appearance of many vast carbonate hardgrounds in the Cambro-Ordovician may have played a fundamental role in the evolutionary radiation of these groups, especially bryozoans and echinoderms.

Carbonate Hardgrounds and Faunal Radiations

The rapid formation of cemented carbonate substrates on shallow marine platforms changed the benthic environment dramatically. Tracts of soupy, unstable carbonate mud were transformed quickly into extensive rocky sea floors stretching for tens or even hundreds of kilometers from the shallowest subtidal zone seaward. Sessile and vagrant benthic organisms which were adapted to soft sediments were then confined to surrounding patches of still-mobile muds, silts and sands as the hardened sea floor was occupied by borers and encrusters of many varieties. The transition from soft-sediment to hardground communities is often recorded as a change in the trace fossils from burrows to borings and from infaunal and semi-infaunal body fossils to epifaunal encrusters (Goldring and Kazmierczak, 1974). An interesting question is whether the rapid development of hardgrounds on the carbonate shelves of the Early Paleozoic facilitated the evolutionary radiations of groups which were adapted to hard substrates, especially since shelly hard substrates were rare. A fascinating corollary question is whether some of these organisms actually facilitated the development of those hardgrounds and thus their own radiations. And since Early Paleozoic carbonate hardground formation was primarily (but not entirely) a shallow water phenomenon, the study of these radiations may provide data to test the onshore-offshore origination hypotheses for marine clades (Jablonski and Bottjer, 1990).

The key interval to test these hypotheses is the Early Ordovician, when the primary hardground dwellers of the Paleozoic (stemmed echinoderms and bryozoans) undergo their extensive radiations in shallow marine carbonate environments. We think that it is not a coincidence that this is also the time when carbonate hardgrounds and intraformational conglomerates derived from hardgrounds reach their peak abundances worldwide. We shall examine, then, an Early Ordovician hardground interval briefly assessed by Palmer and Wilson (1990), and then studied in detail by Wilson et al. (1992).

The Kanosh Shale and echinoderm facilitation of hardground formation.--The Kanosh Shale is a thick (172 meters at its type section) sequence of interbedded shales and limestones of Early Ordovician (Late Arenig) age in west-central Utah, North America. In 1989 Tom Guensburg visited its type section in the Confusion Range and noticed fragments of a hardground, one of which he sent to us. We visited the site the next year and, with more time, found dozens of carbonate hardground horizons in the Kanosh, each separated by thin layers of shale. Some of the hardgrounds were rich with cobbles; all of them had significant amounts of fine echinoderm skeletal debris in their matrices. The hardground surfaces were covered with holdfasts of rhipidocystid eocrinoids and crinoids, and what proved to be the earliest bryozoans on carbonate hardgrounds (or any hard substrate). Oddly, though, there were no borings, not even the usually ubiquitous *Trypanites*.

Many of the hardgrounds near the base of the formation are intraformational conglomerates rich in micritic cobbles, some of which were apparently encrusted and rolled about on the seafloor before incorporation in the hardground. These intraformational hardgrounds become rarer up section. Petrographic analysis of the hardgrounds showed that the most common early cement was syntaxial calcite, very large interlocking crystals of which grew from echinoderm ossicle debris. From these observations, we (Palmer and

Wilson, 1990b; Wilson et al., 1992, p. 24) developed the following scenario for hardground development in the Kanosh (summarized in Figure 43):

1. *Development of early diagenetic carbonate nodules in fine-grained siliciclastics.*--The shales and silty shales of the Kanosh were deposited under normal marine conditions in an intrashelf basin. The sediments were burrowed by a variety of infaunal organisms and there was a diverse but often sparse epifauna of orthid and lingulid brachiopods, ostracodes and trilobites. Carbonate nodules probably precipitated and grew in these sediments by two mechanisms. One is sulfate-reducing bacterial respiration, which yielded increased HCO_3^- levels and $CaCO_3$ precipitation (Curtis, 1977). The second is the dissolution of aragonitic shells in the sediments with immediate reprecipitation of calcite. In either case, these early diagenetic nodules preserved sedimentary features, such as trace fossils and fecal pellets, that were later lost during compaction of the surrounding sediments.

2. *Storm current winnowing and cobble lag deposits.*--Periodic storm currents swept away large amounts of unconsolidated fine-grained sediments in some parts of the depositional basin. Diagenetic carbonate nodules were exhumed and formed lag deposits on the sediment surface. These lags also included fossil debris, especially of ostracodes, brachiopods, nautiloids and gastropods.

3. *Encrustation of cobble lags.*--The exhumed cobbles represented the first extensive hard substrates on this basinal sea floor. They were encrusted by large numbers of stemmed echinoderms, trepostome bryozoans and a few sponges.

4. *Accumulation of echinoderm debris.*--The echinoderms disarticulated upon death and released vast quantities of ossicles. These ossicles were sorted by storm currents into local concentrations with cobbles and other skeletal debris including, most importantly, aragonitic nautiloid and gastropod shells.

5. *Early marine cementation of hardgrounds.*--Two cementation processes then took place on the Kanosh sea floor. Both undoubtedly occurred together in most situations. Calcite cement precipitated directly from sea water (see Tucker and Wright, 1990 for review), and calcite cement was derived from the dissolution of aragonitic shells, primarily nautiloids and gastropods, within the sediments. The single-crystal nature of the abundant echinoderm debris facilitated rapid lithification through the formation of extensive syntaxial cements.

6. *Intraformational conglomerate formation.*--The cemented crusts thus formed were subjected to episodes of violent erosion and break-up during storms, which produced further cobble horizons. These in turn became attachment sites for more echinoderms and bryozoans, and so the cycle was repeated.

Echinoderm debris was a controlling factor in the rapid and extensive development of the Kanosh hardgrounds. The hardgrounds themselves, in turn, formed the bulk of the hard substrates required by these echinoderms. The Kanosh echinoderms thus taphonomically facilitated the widespread growth of their critical habitat by the single-crystal nature of their abundant ossicles (which acted as nuclei for rapid calcite precipitation) under the chemical conditions of the Ordovician Calcite Sea. The abundant trepostome bryozoans on these hardgrounds played no apparent role in their development, but they did take advantage of the widespread marine hard substrates they offered. The Kanosh Shale may provide the first evidential links between hardgrounds and the early radiation of stemmed echinoderms and bryozoans.

Hardgrounds and early echinoderm radiation.--Actually plotting the evolutionary details of evolutionary radiations and their relationship to hardgrounds requires systematic and stratigraphic work on a larger scale. Guensburg and Sprinkle (1992) have begun this process with echinoderms. They gathered an extensive collection of echinoderms from the coeval Ninemile Shale and Fillmore Formation (Tremadoc-Arenig) of Nevada and Utah. The Fillmore is a storm-dominated, inner shelf unit with numerous intraformational conglomerates and carbonate hardgrounds. The Ninemile is an outer shelf to upper slope deposit characterized by low energy calcareous shales and no hardgrounds. There is thus a nearly complete inner shelf to outer shelf gradient preserved in these units. They collected at least 46 echinoderm species, most of which are undescribed. Their data supports the predicted onshore origination pattern for crinoids of the Paleozoic Evolutionary Fauna (Sepkoski and Sheehan, 1983) and Guensburg and Sprinkle (1992, p. 409) specifically cite the "extrinsic influence" of the shallow shelf hardgrounds in this radiation pattern. More work is now needed to extend these observations down into the latest Cambrian and up into the Middle Ordovician to further develop the evolutionary patterns.

Hardgrounds and early bryozoan radiation.--Taylor and Larwood (1990, p. 228) wrote that "bryozoan evolution has not been played out in an environmental vacuum". As yet little is known about the early history of the Bryozoa. The oldest known bryozoans are briefly described by Hu and Spjeldnaes (1991) from the Lower Ordovician (Tremadoc and Early Arenig) of China. These bryozoans, which apparently include trepostomes and a form intermediate between trepostomes and cryptostomes, are fragmentary and occur entirely in well-sorted biosparites. Hu and Spjeldnaes (1991, p. 183, punctuation corrected) tantalizingly write, "The impression gathered from the fossil material, and the Recent analogues, is that the bryozoans grew on a fairly hard, but not cemented, bottom and were ripped up, fragmented and transported to their place of deposition by occasional heavy storms". The authors then mention that Lower Ordovician bryozoans seem to have been as a group more selective of bottom conditions than their descendants, citing their discontinuous occurrences worldwide. Hu and Spjeldnaes (1991, p. 183) also point out that the Arenigian bryozoans of the Balto-Scandian area often have large concave attachment bases. They attribute these bases to growth on a sedimentary substrate being slowly undermined by erosion. We suggest that a more likely explanation is that these bryozoans had attachments for growth on carbonate hardgrounds, which we predict are likely present in all Lower Ordovician carbonate sequences. Hardgrounds have not been described from these bryozoan-bearing sections in China and the Baltic, but no one has yet specifically looked for them. The later Arenig hardgrounds of the Kanosh Shale in Utah (described above) support a dense accumulation of trepostome bryozoans, and they were unknown until recently. It is possible that the extensive hard substrates offered by the widespread carbonate hardgrounds of the Early Ordovician triggered an adaptive radiation among the developing Bryozoa, allowing them to spread widely from local areas. As with echinoderms, there is an opportunity here for detailed work tracing the environmental context of bryozoan evolution, and hardgrounds may well be a critical factor.

Composition of Hardground Communities Through Time

Carbonate hardgrounds represent a well-defined set of depositional environments which have remained fairly constant in their physical features through geologic time. Since their associated communities have been thus constrained by similar environmental factors for the Phanerozoic, we can study the long-term evolution of a community with relatively few environmental variables. This was first done by Palmer (1982), who collected faunal data from Paleozoic and Mesozoic shallow water, upward-facing carbonate hardgrounds. Wilson and Palmer (1990) provided a brief update of this work. We present here a summary of these studies along with more updated information.

Hardground faunas have changed substantially since the Early Paleozoic. Figure 44 is a graph of the diversity and general composition of hardground faunas in the Paleozoic and Mesozoic. The hardground-dwelling species have been divided into three groups. The first includes those encrusters that have external soft tissues that could not be entirely enclosed by a mineralized skeleton. Echinoderms, with their soft epidermis, free-walled stenolaemate bryozoans, such as the trepostomes and some cyclostomes, and anthozoans have exposed soft tissues. The second group is defined by those encrusters with true exoskeletons capable of protecting all the soft parts of the animal. This includes serpulid worms, bivalves, and most cyclostome bryozoans. The third group of hardground organisms contains those organisms capable of boring into the calcareous substrate. Borers on hardgrounds are diverse, including polychaete, sipunculid and phoronid worms, bivalves, echinoids, barnacles and sponges.

Paleozoic communities.--The earliest hard substrate and hardground communities and their possible origins have been described separately above. The pattern for Paleozoic hardground communities is well established by the Middle Ordovician. The dominant occupants of Middle Ordovician and Late Ordovician hardgrounds were free-walled trepostome and cyclostome bryozoans, followed by a variety of echinoderms, including edrioasteroids, crinoids, eocrinoids and cystoids. Corals, brachiopods and other miscellaneous encrusters are rare on Ordovician hardgrounds. Borings consist mainly of the small, ubiquitous *Trypanites* and the occasionally abundant bivalve boring *Petroxestes*. Silurian through Pennsylvanian hardground communities are considerably less diverse than their Ordovician counterparts (although also less studied), with the most apparent decline in the rigid erect, mound-like and lamellate trepostome bryozoans. Foraminiferans and corals become moderately important in Devonian communities. Borings are still mainly the simple *Trypanites*. Pennsylvanian hardgrounds are very rare, so faunal diversities appear low. No hardground faunas have been described from the Permian.

In summary, Early Paleozoic hardground communities are diverse and dominated by encrusters with exposed soft tissues. Middle and Late Paleozoic communities appear less diverse, mainly because they are considerably less common, and show a modest increase in the proportion of encrusters with true exoskeletons. Borings are common, simple and small.

Mesozoic communities.--Triassic hardgrounds are not common, but there are enough encrusters to note the increase in attaching bivalves that are characteristic of Mesozoic hardground communities. The first *Gastrochaenolites* boring is also known from the Triassic (J. G. Carter, 1978 and personal communication). Jurassic and Cretaceous hardgrounds are common and they possess a diversity of occupants. Serpulid worms, bivalves (especially oysters) and fixed-walled cyclostome bryozoans are the most common encrusters. Most of these possessed true exoskeletons. The diversity of borings, now including the large excavations of bivalves and echinoids, has increased considerably.

Cenozoic communities.--Tertiary hardground communities are poorly described, even though there are several well-preserved examples in the Eocene and Miocene of North America and Europe. Because there have been no complete taxonomic surveys of these communities, we cannot include them in the statistical data on diversity. Studies of Paleogene and Neogene borings on carbonate substrates demonstrate the continuing diversity increase among endolithic bivalves and polychaete worms (Macarovici, 1969; Radwanski, 1970; Roniewicz, 1970; Watkins, 1990). Encrusters on ancient Cenozoic hardground surfaces have not been systematically described, but our observations of Eocene specimens suggest that cheilostome bryozoans are the most commonly preserved organisms, followed closely by fixed-wall cyclostome bryozoans, serpulid worms and oysters. Nearly all the Cenozoic encrusters have true exoskeletons.

A modern "hardground" community.--There have been a number of published investigations of modern hard substrate communities (see Buss, 1986, for a review). Unfortunately, they do not fit our requirements of a tropical or subtropical environment and an inorganic carbonate substrate. The researchers studying modern warm-water encrusters and borers have concentrated on reef communities and other utilizers of biogenic substrates, while those investigating organisms on non-carbonate substrates have been working in temperate climates. We therefore present here a preliminary survey of a modern tropical "hardground" community on an inorganic carbonate substrate, a submerged beachrock. This substrate is not a "hardground" by definition, but it is as close to a true hardground as we can easily get in the Recent.

In June 1988, we visited the subtidal shelf of Fernandez Bay on the western side of San Salvador Island, The Bahamas. We mapped a profile from the high-tide mark seaward to the end of the exposed rocky shelf, which was marked by a coral reef. At no point was the water deeper than two meters. We collected large slabs of the beachrock along the subtidal portion of the measured profile and recorded the encrusting and boring species from each sample, along with their relative proportions and their position on the upper or undersurfaces of the slabs (Figure 45). Table 1 gives the faunal and floral lists.

The hard substrate forming the seafloor at Fernandez Bay is a flooded Holocene beachrock; for discussion of the beachrock on San Salvador Island, see Bain (1989a, b). The rock has the typical beachrock petrology of carbonate sand cemented by isopachous aragonitic cement. It is exposed on the subtidal seafloor as large sheets, approximately 25 cm thick, gently dipping seaward. Crevices and underhangs are formed when the edges of sheets are eroded.

The most prominent encrusters on the upper surfaces of the modern hardground are green, brown and red algae. Of these, only one species, the coralline red alga *Neogoniolithon affine*, is skeletonized enough to be preserved in situ in the typical hardground fossil record. The other mostly fleshy algae are not usually preservable. The only evidence we may find of them on a fossil hardground is a pattern of microborings and etchings. The skeletonized encrusting animals include rare anthozoans and an occasional serpulid tube. There are thus only five preservable encrusters, 18.5% of those recorded, on the upper surfaces of this hardground.

Encrusting organisms are also found on the undersurfaces of the hardground. Algae are considerably less common than on the upper surfaces. Where present, they are confined to the exposed edges of the slabs, as are the corals. The deeper recesses are occupied mostly by foraminiferans, serpulids and one demosponge species. Thirteen encrusting animal and algal species, two-thirds of those present on the slab undersurfaces, are preservable.

The borings of five species are found in the Fernandez Bay hardground slabs. Polychaete borings are the most common, followed by sponge, barnacle and bivalve borings.

The details of this study, including work on four additional hardground localities on San Salvador, will be presented in a later paper.

Evolutionary Trends in Hardground Communities

A current question in evolutionary theory at the community level is whether modern organisms are any "better" adapted to their physical and biological environments than their ancient counterparts. Basic Darwinian natural selection theory proposes that in the struggle for survival, adaptive improvements are continually favored within lineages. Van Valen (1973) pointed out that the improvements of one species will affect many others within the same ecosystem. As a consequence, the biological environment for almost any species is continually deteriorating because of evolutionary improvements in other species to which it is ecologically bound (predators, competitors and prey). Vermeij (1987, p. 4) has expressed this concept as the hypothesis of *escalation*, whereby modern organisms, although they have histories of continual adaptations, are no better adapted to their biological environments than their ancient counterparts were to theirs. To avoid extinction, organisms must continually respond to their deteriorating biological environments with adaptations, or they must find a refuge from the selective pressure. To adequately test the escalation hypothesis, ecosystems must be examined in which the physical environment has remained relatively constant through long periods of time, so that the observed evolutionary changes in the associated organisms may be due, at least in part, to escalating systems of biological adaptation within the communities. Hardground communities, with their well-defined physical conditions and extensive fossil record, are appropriate paleontological subjects for this test.

True exoskeletons.--The most prominent faunal change in the hardground encrusting communities is the pattern of dominance by organisms with exposed soft tissues over those with true exoskeletons in the Paleozoic followed by a complete reversal of the relationship in the Mesozoic and Cenozoic (Figure 44). It has been earlier noted that true exoskeletons provide scour resistance in the abrasive hardground habitat (Palmer and Palmer, 1977) and are a much more effective armor against grazers and other predators (Palmer, 1982). The abundance of encrusters with exposed soft tissue on Paleozoic hardgrounds demonstrates that true exoskeletons were not required for the physical conditions of hardground dwelling, so their Mesozoic dominance must be due to changing biological conditions. Those changes are now well documented as the "Mesozoic Marine Revolution" (Vermeij, 1977, 1978, 1987) in which many grazing and predatory marine groups appeared. Encrusters with true exoskeletons were favored in the biologically abrasive environments of the Jurassic, Cretaceous and Cenozoic. An additional benefit to these encrusters was the increased resistance to physical abrasion, but this was apparently not the controlling factor of their evolution.

Infaunalization.--Mesozoic hardgrounds show a dramatic increase in the proportion of boring species within the communities (Figure 44). The most common borings are those produced by lithophagid and gastrochaenacean bivalves. An increase in the number and diversity of infaunal organisms in soft sediment faunas has been correlated with the rise of predators in the Mesozoic (Stanley, 1977; Thayer, 1979, 1983). Since the hardground infaunalization trend mirrors that of the soft substrates, it is most likely a direct consequence of increased predation as well. We are currently investigating the details of this response by examining the radiation of all hard substrate macroborers across the Mesozoic. Morton (1990) has discussed a similar hypothesis that increased predation beginning in the later Mesozoic forced the radiation of bivalves which bore into living coral.

Cavity-dwelling.--Cracks, crevices, borings and other cryptic areas found associated with most hardgrounds. Such habitable cavities can develop on or in carbonate hardgrounds in a variety of ways, including: soft-sediment burrows exhumed in the hardground (Fürsich and Palmer, 1975; Voigt, 1987); undercut ledges and overhangs (Brett and Liddell, 1978; Brett and Brookfield, 1984); early diagenetic crystallization pressures (Fürsich and Palmer, 1979); and borings (Wilson, 1986). Organisms that occupy cryptic spaces are termed *coelobites* (Ginsburg and Schroeder, 1973).

Many hardground faunas show distinct polarization between organisms inhabiting upper, exposed surfaces and those living in cryptic environments. In the Middle Ordovician community studied by Brett and Brookfield (1984), the upper faunas are diverse, including mound-like, arborescent and ptilodictyid bryozoans, echinoderms, and numerous *Trypanites* borings. The undersurfaces of ledges, however, are occupied by low diversity assemblages of mostly laminar ceramoporid and cystoporate bryozoans, with the runner-like "*Stomatopora*" common. Jurassic hardground faunas are also highly polarized (Palmer and Fürsich, 1974; Fürsich, 1979). Upper, exposed surface faunas contain dozens of encrusters and borers, while cryptic faunas, including foraminiferans, sponges, brachiopods, laminar and runner-type bryozoans, serpulid worms and some bivalve species, are still numerous but less diverse Figure 46). Modern hardground communities have the same distinct polarization between dwellers on upper and lower surfaces. The data from Fernandez Bay (Table 1) shows the obvious restriction of most algae to exposed upper surfaces, and most polychaetes and foraminiferans to the cryptic regions. Almost twice as many species are found on the upper surfaces than on the lower. When only the skeletonized organisms (those with asterisks in Table 1) are counted, however, 13 encrusting species are coelobites, whereas only 5 are living on the upper surfaces.

The diversity of coelobite faunas appears to have increased through the Paleozoic, Mesozoic and into the Cenozoic. Much of this diversity increase may be due, though, to better preservation and larger numbers of hardgrounds with cryptic spaces that have been described from the Mesozoic. As discussed earlier, the amount of cryptic niche space available increased dramatically in the Mesozoic with the increase in infaunalization. Boring bivalves in particular created numerous large borings that, when empty, served as cryptic habitats for a variety of encrusters, nestlers and other borers (Wilson, 1986).

Van Valen (1973) and Vermeij (1987) have shown that the exploitation of refuges may be one of the responses of organisms to intolerable levels of evolutionary escalation. The pattern of cryptic and exposed hardground community polarization found here, however, does not document a general move into spatial refuges in such a climate, although a retreat may have occurred before our record begins. The abundance of modern coelobites on the Fernandez Bay hardgrounds suggests that the cavities serve as important refuges for sessile animals from algal overgrowth, but additional studies of modern hard substrate ecosystems are necessary to support this hypothesis.

Tiering.--Since preserved hardground faunas are dominated by fixosessile filter-feeders, there is only a limited range of ways in which niche space is likely to have been divided up between the different species. Specialization in different particle sizes may have been practiced, but it is difficult to see how information on this can be retrieved. It is easier, however, to get some idea of specialization for feeding at different levels above the surface since the positions of the feeding organs can be inferred or directly observed in most hardground-dwelling species. The dividing up of the space above the substrate into a number of levels within which feeding specialization occurs is called "tiering" (Ausich and Bottjer, 1982) but is akin to the vertical zonation that is seen amongst the plants within terrestrial communities, and has long been recognized by terrestrial ecologists (e.g. Elton, 1966).

Palmer and Fürsich (1974) first drew attention to the establishment of different feeding levels on hardground surfaces, identifying one infaunal and four epifaunal zones in a Jurassic hardground community (Figure 46). Not surprisingly, cavity-dwelling encrusters in the limited space on the undersurfaces of hardgrounds only displayed the lower-growing levels, as there was no room for the taller species.

Palmer (1982) later gave estimates of the distance of feeding levels above the substrate for all the hardground species discussed in his compilation of Cambrian to Cretaceous hardground faunas and their community evolution (Figure 47). He was able to show that, at least as represented by this single criterion, available niche space was rapidly exploited as hardground communities diversified in the Ordovician, and that all subsequent ages of hardground community have been represented by a full range of epifaunal tiers.

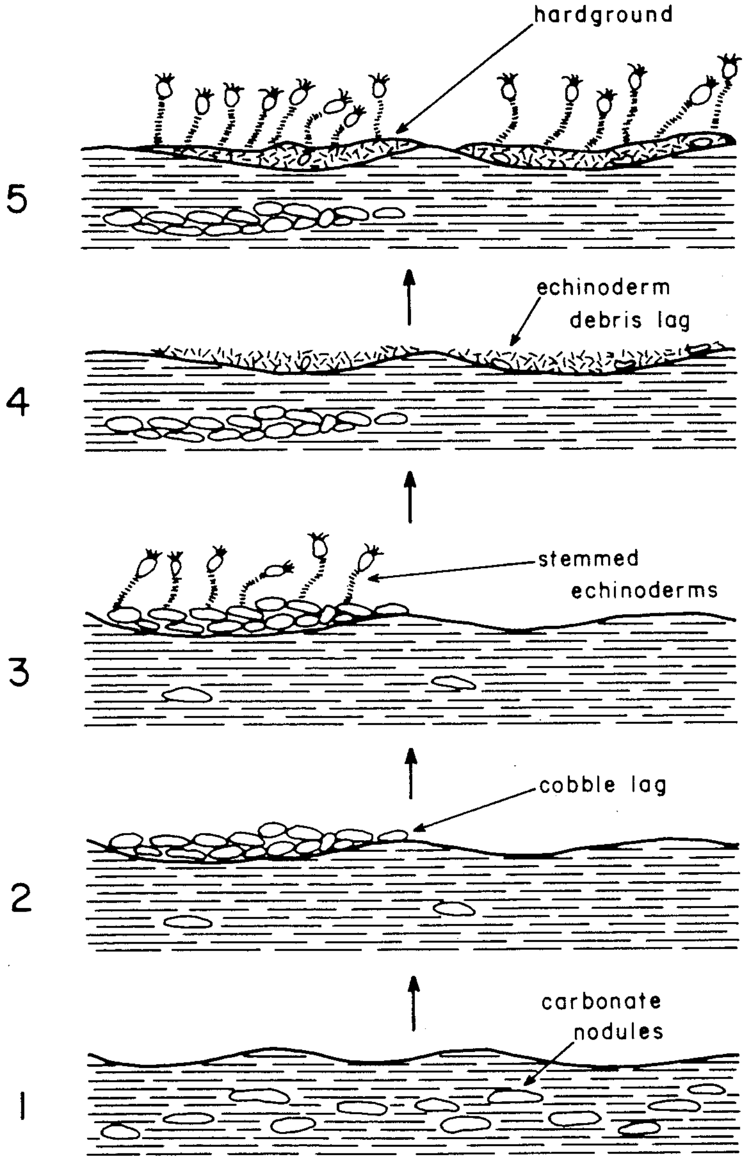

Figure 43. Proposed steps for the origin of carbonate hardgrounds in the Kanosh Shale (Early Ordovician) of west-central Utah. 1=Development of early diagenetic carbonate nodules in fine-grained siliciclastics. 2=Storm current winnowing and formation of cobble lags. 3=Encrustation of the cobbles by stemmed echinoderms. 4=Accumulation of echinoderm debris in lag deposits. 5=Early marine cementation of hardgrounds and the settlement of additional stemmed echinoderms. Reproduced from figure 3 of Wilson et al. (1992) with permission of the editors of *Lethaia*.

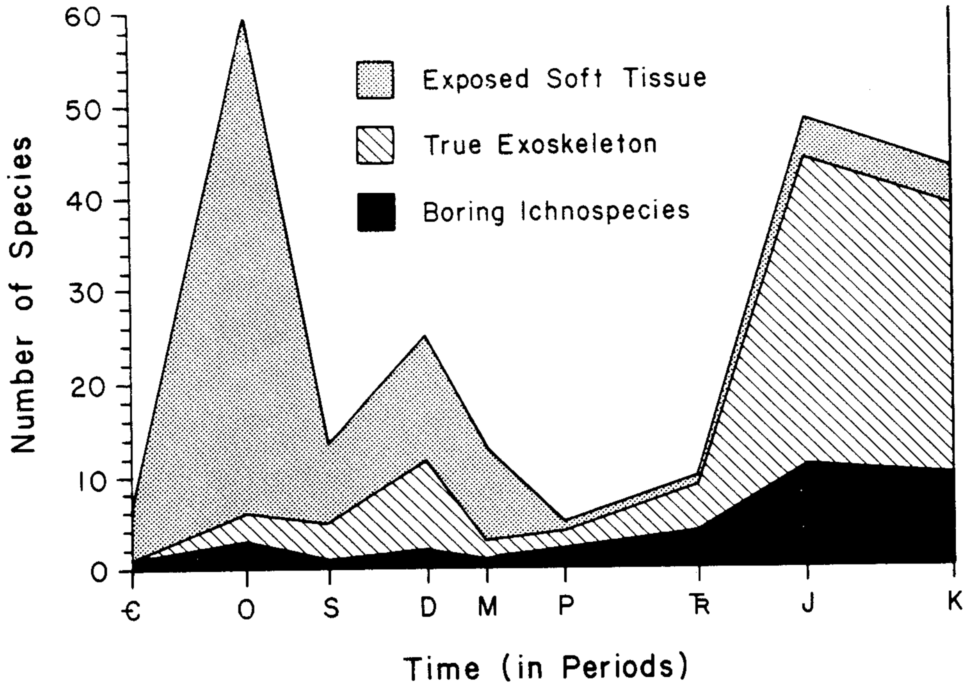

Figure 44. Diversity and general composition of hardground faunas in the Paleozoic and Mesozoic. Reproduced from figure 2 of Wilson and Palmer (1990) with permission from the Paleontological Society.

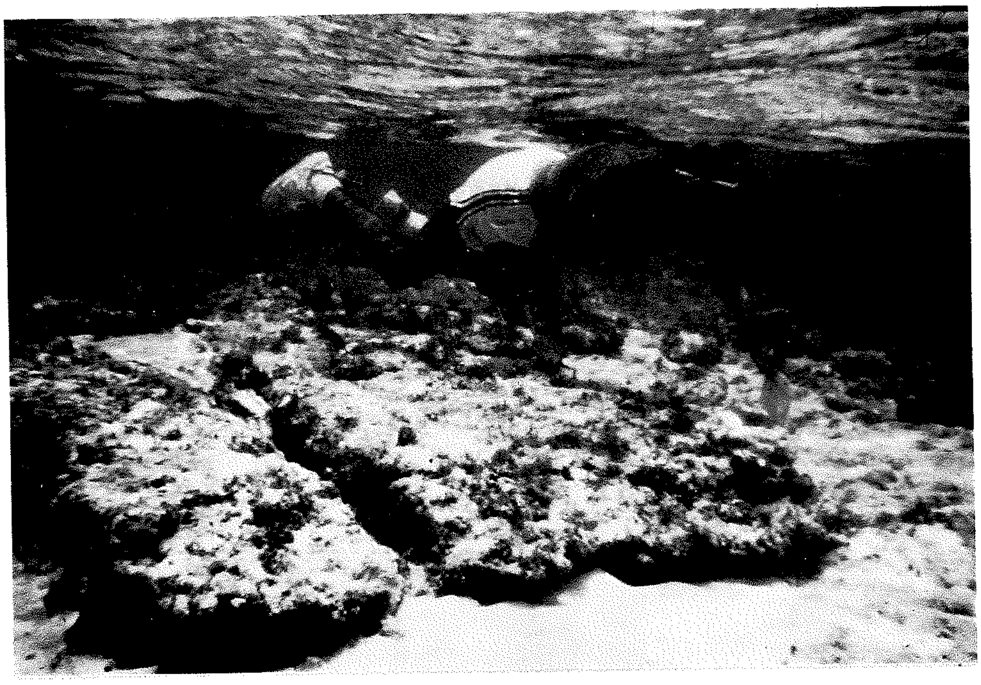

Figure 45. Exhumed Holocene beachrock slabs, Fernandez Bay, San Salvador Island, The Bahamas.

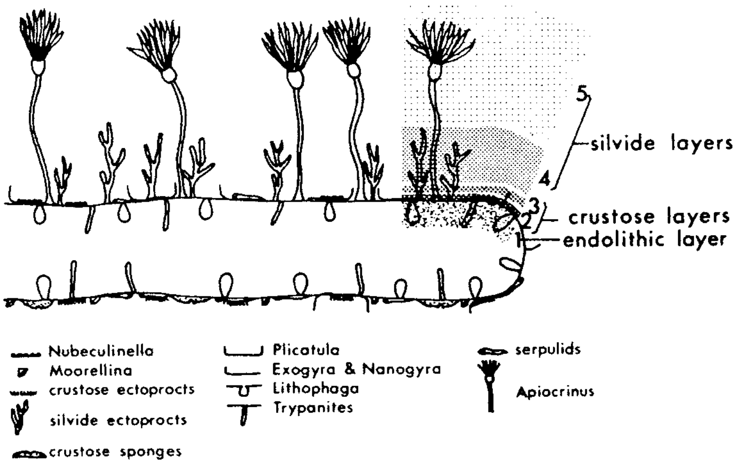

Figure 46. Ecological stratification on surfaces of a Middle Jurassic hardground. Endolithic and crustose layers occur on the upper surfaces as well as in the cavities beneath. The silvide layers are on the upper surfaces only. Reproduced from text-figure 3 of Palmer and Fürsich (1974) with permission of the Palaeontological Association.

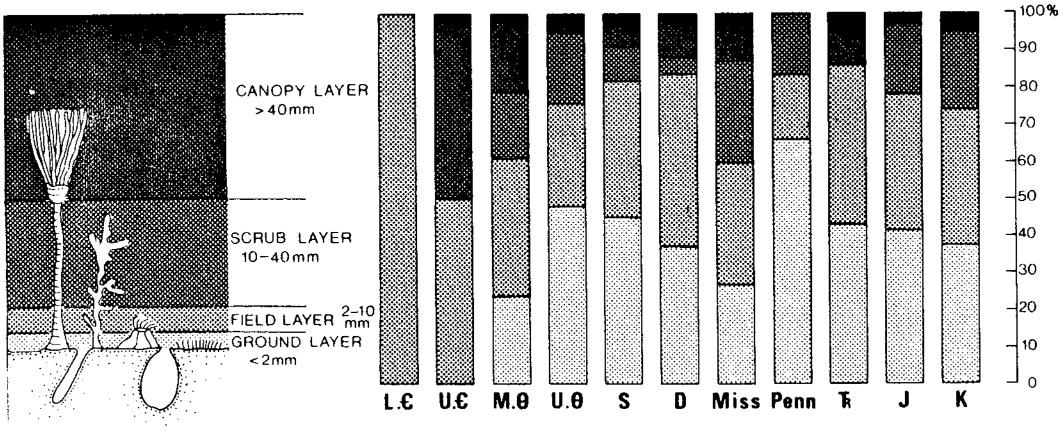

Figure 47. Relative proportions of hardground species of different ages which suspension-feed at different levels above the substrate. Reproduced from figure 9 of Palmer (1982) with permission of the editors of *Lethaia*.

Table 1. Species recorded from a modern subtidal carbonate hardground in Fernandez Bay, San Salvador, The Bahamas. Asterisks indicate those species likely to leave an *in situ* record on a fossil hardground.

SPECIES PRESENT:	UPPER SURFACES	UNDERSURFACES
Chlorophyta:		
Acetabularia crenulata	Rare	
Anadyomene stellata	Abundant	
Caulerpa racemosa	Rare	
Cladophoropsis membranacea	Common	
Dictyosphaeria cavernosa	Common	
Halimeda favulosa	Rare	
Penicillus capitatus	Rare	
Udotea flabellum	Rare	
Valonia ventricosa		Rare
Chlorophyte sp. A	Rare	
Phaeophyta:		
Dictyota divaricata	Common	
Lobophora variegata	Rare	
Padina sp.	Abundant	
Sargassum sp.	Rare	
Phaeophyte sp. A	Rare	
Phaeophyte sp. B	Rare	
Rhodophyta:		
Gracilaria verrucosa	Common	
Laurencia microcladia	Common	Rare
**Neogoniolithon affine*	Abundant	Abundant
Foraminifera:		
**Homotrema rubrum*		Abundant
Porifera (non-boring):		
Ircinia felix		Rare
Demosponge sp. A	Rare	
Demosponge sp. B	Rare	
Demosponge sp. C	Rare	Common
Demosponge sp. D	Rare	
Anthozoa:		
**Astrangia solitaria*		Abundant
**Diploria strigosa*		Rare
**Gorgonia* sp.	Rare	
**Montastrea annularis*	Rare	Rare
**Porites porites*		Rare
Hydrozoa:		
**Millepora alcicornis*	Rare	
Polychaeta (tube-dwelling):		
**Filograna implexa*		Common
**Hydroides parvus*		Common
**Spirorbis formosus*		Common
*Serpulid sp. A	Rare	Rare
*Serpulid sp. B		Common
*Spirorbid sp. A		Rare
*Terebellid sp. A (agglutinated tube)		Common

Ascidacea:		
Eudistoma obscuratum	Rare	Common
Boring forms:		
Porifera --		
**Cliona dioryssa*	Common	Rare
Bivalvia --		
**Gastrochaena hians*	Rare	
Polychaeta --		
**?Hypsicomus elegans*	Common	Common
**Eunice vittata*	Common	Common
Cirripedia --		
**Lithotrya dorsalis*	Rare	Rare
TOTAL NUMBER OF SPECIES	32	18
NUMBER OF ENCRUSTERS	27	18
NUMBER OF PRESERVABLE ENCRUSTERS	5	13
NUMBER OF BORERS	5	4

CONCLUSIONS AND OPPORTUNITIES FOR FUTURE WORK

Ancient hardground faunas are attractive to paleontologists for two reasons: First, fossils are preserved *in situ* on hardgrounds, so their distribution on the surface and proximity to neighbors reflects their original spacing in life. This makes them appropriate for various types of paleoecological analysis. To this could be added the fact that many hardgrounds show episodes of scour, which killed or removed much of the encrusting fauna and some of the superficial borers, thus creating a fresh and pristine surface for recolonization. Many hardgrounds are thus effectively not time-averaged, so spacing relationships and species interactions are quite likely to reflect vital encounters. Second, hardgrounds are particularly characteristic of shallow, tropical and sub-tropical, fully marine, carbonate-precipitating conditions, thus maximizing the comparability of the faunas when compared in long-term, community evolution studies. These conditions of formation can usually be tied down precisely using petrographic and associated lithofacies criteria.

The size of the bibliography which follows this text gives an indication of the number of studies that have been carried out on hardgrounds. Most of these only mention hardgrounds and their faunas in passing, usually when the hardgrounds have merely been one facies encountered in a wider study of a sedimentary unit or its fauna. More focused studies on hardground faunas have usually concentrated on one or more of five principal aspects, which are summarized below:

Community description.--The most obvious thing to ask about a hardground fauna is its exact composition. Unfortunately, hardground faunas usually contain examples of poorly-known or undescribed taxa, often belonging to groups which require considerable expertise for identification. As a result, many identifications cannot be made to the specific or even the generic level. The variety of undescribed small encrusting bryozoans on some Ordovician hardgrounds (e.g. Palmer and Palmer, 1977) is a case in point. Furthermore, some hardground dwellers are represented only by proximal attachment structures (such as bryozoan and pelmatozoan holdfasts) which play no part in taxonomy. Borings in particular are seldom identified to the ichnospecific level. Nevertheless, the recognition of the range of taxa which make up the hardground community is clearly the essential starting point for ecological and evolutionary stories, and much primary description of hardground faunas of different ages remains to be done. Many such studies consist of faunal lists; others have supplemented basic identifications with elegant reconstructions of how hardground communities must have appeared in life (e.g. Koch and Strimple, 1968; Halleck, 1973; Brett and Liddell, 1978; Guensburg, 1992; see Figures 23 and 24 and the back cover).

Spatial distribution of species.--The distribution of the fauna on a hardground surface often shows that certain species had preferences for certain microenvironments. On the Ordovician hardgrounds studied by Palmer and Palmer (1977) and Brett and Liddell (1978), for example, *Trypanites* was preferentially distributed on raised bosses and mounds where, presumably, water circulation was better. Hardgrounds that are perforated by pre-omission burrows or undercut by cavities have a distinctive fauna of coelobites that are not found on the upward-facing surfaces (Wilson and Palmer, 1990, and references therein). The characteristic nature of the coelobitic community in the Jurassic has been used to interpret the complex diagenetic history of ferruginous oncoliths (Palmer and Wilson, 1990a); many similar applications of such living relationships are possible.

Hardgrounds are also suitable for studies of the distributions of individuals within populations. Many populations show marked clumping, such as the bryozoans recorded by Palmer and Palmer (1977) and the sphenothallids studied by Bodenbender et al. (1989). Such clumps are not usually associated with any obvious physical feature on the hardground surface, and probably reflect a biological preference for close association with conspecifics.

Species interaction.--Space is limited on hard substrates generally, and with increasing community maturity, individuals are more likely to interfere with neighbors. Attempts to recognize patterns of dominance in interactions between pairs of individuals on hardground surfaces (e.g. Palmer and Palmer, 1977) have not been particularly successful, mainly because numbers of observed interactions on particular hardgrounds have been small, and because of the uncertainty that overgrowth interactions took place while both individuals were alive. A related matter that would repay closer study is the possibility of interaction between skeletonized encrusters and their soft-bodied neighbors. Ordovician bryozoans, for example, often show large indentations of their growing margins, or raised edges, steps or terraces, that suggest an encounter with a neighbor that was not preserved. It is possible that some cases would show details of the encounters preserved as a bioimmurations (see Taylor, 1990). As a general rule, Paleozoic hardgrounds have a much lower percentage of cover by preserved fauna (around 2 to 20%) than do Mesozoic and later hardgrounds (which have around 50 to 100% cover). This difference suggests that soft-bodied faunas may have been much more important on Paleozoic hardgrounds.

Ecological succession.--Competition for space in a maturing hardground community leads to species interaction and change in total species composition. Some attempts have been made to describe details of such ecological succession on hardground surfaces (e.g. Halleck, 1973; Goldring and Kazmierczak, 1974; Gruszczynski, 1979, 1986; Wilson, 1985a), but there is much scope for further work in this area. As stated earlier, care must be taken to distinguish true community succession from changing community composition as a result of the gradually changing character of the physical environment. Goldring and Kazmierczak's (1974) work, for example, documented changes in the nature of the fauna as surfaces hardened up through a firmground stage to a rigid hardground, a process now termed community replacement (Hoffman and Narkiewicz, 1977; Johnson, 1977; Miller, 1986).

Temporal distribution of species.--Finally, one of the primary goals of paleontology is to describe the evolutionary history of organisms and their changing ecological relationships through time. Hardground faunas are uniquely suited to this type of study for the reasons outlined above. This type of large-scale analysis requires systematics for the evolutionary connections, paleoecology to sort out the living relationships, and sedimentology to interpret the living environments. We have done some initial work on the evolution of hardground communities (Palmer, 1982; Wilson and Palmer, 1990) and will continue to add to our compilations, but we hope that this text has inspired others to approach this topic in new ways with fresh ideas. There is much left to do.

BIBLIOGRAPHY OF LITHOLOGIC SUBSTRATE STUDIES

This bibliography is intended as an aid for those people studying lithologic substrates and the organisms that inhabit them. Most of the citations used in this paper are listed here; the references to articles which do not cover hard substrates are compiled separately beginning on page 129 ("Additional References Cited"). Although many references to recent hard substrate environments are presented, the primary emphasis here is paleontological. Please note that this listing does not contain studies concerning the encrustation or boring of purely biotic substrates, nor does it attempt to cover all studies of modern encrusters. Each article included here has some immediate paleobiological or evolutionary interest. For the most part, abstracts, theses, dissertations and local guidebook articles are not listed in this bibliography unless they are unusual or rare studies not published elsewhere. We have made every attempt to insure the spelling is correct in these citations, but critical marks in non-English references are sometimes missing. This is especially the case with articles from eastern Europe. Occasionally annotations are attached to references to explain the inclusion of papers which may not appear from their titles to concern lithologic substrates.

This bibliography is updated continually. If you are interested in a more recent version, contact one of the authors. Any comments, suggestions, corrections, or additions should also be sent to Mark Wilson.

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_____, _____, _____, _____ and L.E. Kaufman. 1991.
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1748.	De Maillet
1832.	Anonymous (M.J. Desnoyers?)
1846.	De La Beche, H.T.
1850.	Caillaud, F.
1854.	____.
1858.	Godwin-Austen, R.
1863.	Hébert, D.E.
1872.	____.
1874.	Kupffer, A.
1875.	____.
1882.	Chamberlin, T.C.
1896.	Andersson, J.G.
1897.	Munier-Chalmas, M.
1898.	Sardeson, F.W.
1908.	____.
1909.	Bather, F.A.
1911.	Leriche, M.
1913.	Heim, A.
1914.	Sardeson, F.W.
1917.	Barrows, A.L.
1917.	Klüpfel, W.
1922.	Trueman, A.E.
1924.	Heim, A.
1929.	Ehrenberg, K.
1929.	Voigt, E.
1932.	Mägdefrau, K.
1935.	Hecker, R.F.
1935.	Cayeux, L.
1937.	Mägdefrau, K.
1938.	Bucher, W.H.
1940.	Orviku, K.
1945.	Jillson, W.R.
1946.	Ellenburger, F.
1947.	____.
1948.	____.
1948.	Záruba, Q.
1950.	Jones, O.T. & W.J. Pugh
1952.	Mayer, G.
1953.	Calembert, L.
1954.	Weiss, M.P.
1955.	Avnimelech, M.
1955.	Prokopovich, N.
1955.	Yonge, C.M.
1956.	Herrman, A.
1956.	Muller, A.H.
1957.	Dvorak, J.
1958.	Heim, A.
1958.	Warburton, F.E.
1958.	Weiss, M.P.
1958.	Yonge, C.M.
1959.	Radwanski, A.
1959.	Voigt, E.
1960.	Hecker, R.F.
1960.	Orviku, K.
1961.	Jaanusson, V.
1962.	Häntzschel, W.
1962.	Hodgkin, N.M.
1962.	Hollmann, R.
1962.	Klein, V.
1962.	Pietzsch, K.
1962.	Reid, R.E.H.
1963.	Addicott, W.O.
1963.	Clapp, W.F. & R. Kenk
1963.	Lindström, M.
1963.	Yonge, C.M.
1964.	Hollman, R.
1964.	Purdy, E.G.
1964.	Radwanski, A.
1965.	Barnes, C.R.
1965.	De Groot, K.
1965.	Hofker, J.
1965.	Radwanski, A.
1966.	Freeman, T.
1966.	Gevirtz & Friedman
1966.	Jahnke, H.
1966.	Milliman, J.D.
1966.	Neumann, A.C.
1966.	Pianovskaya & Hecker
1967.	Bromley, R.G.
1967.	Driscoll, E.G.
1967.	Evans, J.W.
1967.	Fischer & Garrison
1967.	Lutze, G.F.
1967.	Radwanski, A.
1968.	Bromley, R.G.
1968.	Choquette, P.W.
1968a.	Evans, J.W.
1968b.	____.
1968c.	____.
1968.	Fabricius, F.H.
1968.	Jaccarini, V., et al.
1968.	Kazmierczak & Pszczolkowski
1968.	Koch, D.L. & H.L. Strimple
1968.	Macintyre, I.G., et al.
1968.	Masuda, K.
1968a.	Radwanski, A.
1968b.	____.
1968.	Roniewicz, E. & P. Roniewicz
1968.	Taft, W.H. et al.
1968.	Voigt, E.
1969.	Allen, R.C., et al.
1969.	Ansell, A.D. & N.B. Nair
1969.	Carriker, M.R. & E.H. Smith
1969.	Cobb, W.R.

1969.	Craig, A.K., et al.
1969.	De Groot, K.
1969.	Fannin, N.G.T.
1969.	Garrison, R.E. & A.G. Fischer
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1969.	Hallam, A.
1969.	Hölder, H. & R. Hollmann
1969.	Kazmierczak & Pszczolkowski
1969.	Macarovici, N.
1969.	Masuda, K. & Y. Matsushima
1969.	Milliman, J.D., et al.
1969.	Purser, B.H.
1969.	Radwanski, A.
1969.	Rice, M.E.
1969.	Richards & Shabica
1969.	Seilacher, A.
1969.	Shinn, E.A.
1969.	Taylor, J.C.M. & L.V. Illing
1969.	Warme & Marshall
1969.	Wendt, J.
1969.	Zankl, H.
1970.	Ansell, A.D.
1970.	Bartlett, G.A. & R.G. Greggs
1970.	Bromley, R.G.
1970.	Evans, J.W.
1970.	Juignet, P.
1970.	Kennedy, W.J.
1970.	Radwanski, A.
1970.	Roniewicz, P.
1970.	Rose, P.R.
1970.	Sabine, P.A.
1970a.	Voigt, E.
1970b.	_____.
1970.	Warme, J.E.
1970.	Wendt, J.
1971.	Bathurst, R.G.C.
1971.	Bromley & Nordmann
1971.	Felder, P.J.
1971.	Felder, W.M.
1971.	Fürsich, F.T.
1971.	Jackson, J.B.C., et al.
1971.	Jenkyns, H.C.
1971.	Kendall, A.C. & M.E. Tucker
1971.	Milliman, J.D.
1971.	Perkins, B.F.
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Back cover illustration. Reconstruction of an Upper Devonian hardground (Mason City Member, Shell Rock Formation) and some of its associated fauna. Figure drawn by D.L. Koch; echinoderms described in Koch and Strimple (1968). Illustrated organisms include *Adocetocystis williamsi* (the large rhombiferans), the edrioasteroid *Agelacrinites hanoveri*, *Aulopora* (runner-type colonial coral), *Pachyphyllum* (small colonial rugose coral in foreground), and *Trypanites* borings. Reproduced from Plate 1 of Koch and Strimple (1968) with permission of the Iowa Department of Natural Resources, Geological Survey Bureau.