

Paleoecology and Evolution of Marine Hard Substrate Communities: An Overview

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INTRODUCTION

Hard substrates, including hardgrounds, cobbles/boulders, and skeletons of organisms, present unique opportunities for the study of community paleoecology and evolution. Because remains of hard substrate encrusting and endolithic organisms are buried or embedded in their life sites, problems of post-mortem transport and assemblage mixing, which complicate many paleocommunity studies, are reduced. Thus, hard substrate fossil assemblages permit examination of ecological details, such as spatial distribution, overgrowth competitive interactions, and community succession. This theme issue of PALAIOS encompasses a series of papers on hard substrate paleocommunities and the biotic and physical factors controlling their preservation, ecology, and evolution. Certain of these contributions were first presented at a symposium on this general subject at the Fourth North American Paleontological Convention, held August 13, 1986, in Boulder, Colorado.

This paper summarizes the general evolutionary history of hard substrate communities through the Phanerozoic, and reviews some of the factors appearing to have controlled their diversity and structure that are discussed by authors of the present symposium. Obviously there have been major advances in knowledge of hard substrate biotas in the past 15 years, and this research paves the way for broader synthetic studies of paleoecology and evolution of these communities.

TEMPORAL PATTERNS IN HARD SUBSTRATE COMMUNITIES

During the past 10–15 years, paleoecological study of hard substrate biotas has greatly accelerated. In a recent unpublished compilation of literature, Mark Wilson included 118 titles of hardground and related studies published in the past 19 years alone; this contrasts with a total of about 70 such papers published previously. This proliferation of research has resulted in a substantial increase in our understanding of the

ecology and evolution of these communities, which had been largely ignored in an earlier period.

Specifically, a rather detailed chronology of changes in hard substrate biotas now exists (see Palmer, 1982; Segars and Liddell, this volume; and Kobluk, this volume, for overviews of hardground and cryptic faunas, respectively). The oldest representatives are cavity-dwelling or coelobitic encrusters (Kobluk, 1981a,b, 1985), and cylindrical boreholes in Early Cambrian archeocyathid reefs and associated hardgrounds (Kobluk and James, 1979; Kobluk et al., 1978). These earliest biotas were followed by relatively low-diversity encrusting pelmatozoan and ?algal assemblages (Brett, Liddell, and Dershtler, 1983) in the Late Cambrian. Low-diversity assemblages of borings, pelmatozoan holdfasts, and rare bryozoans appear to persist into the Early Ordovician (Tremadocian to Arenigian; Jaanusen, 1961; Lindstrom, 1963; Mergl, 1983, 1984). Thus, very sparse, limited assemblages characterize hardgrounds for the first 100 million years of the Phanerozoic. This observation raises the intriguing question of why hardgrounds, which should have been present in shallow carbonate shelf environments throughout the Proterozoic, were so late to be colonized by skeletonized organisms, as compared with contemporary soft substrate environments.

Hardgrounds are particularly abundant, worldwide, in the Middle to Late Ordovician, possibly because of peculiarities of ocean-water chemistry, coupled with the still relatively minor bioturbation of sediments (Wilkinson et al., 1982; Walker and Diehl, 1985). Moreover, the Middle Ordovician saw a great adaptive radiation of both hardground and shell-encrusting animals, with the appearance of a host of new groups of holdfast-bearing pelmatozoans, tube-dwelling annelids, and, particularly, encrusting bryozoans of four orders (Palmer and Palmer, 1977; Brett and Liddell, 1978; Brett and Brookfield, 1984; Palmer, 1982). The first rock-boring bivalves evolved by the Late Ordovician, although they were not important until the Mesozoic (Pojeta and Palmer, 1976); at the same time, encrusting faunas became well established on large skeletal substrates, on hiatus concretions, and on pebbles (see Wilson, 1985, 1987). For the first time in the Middle Ordovician there is evidence for slight differentiation between cryptic, coelobi-

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ONLINE

The Pull of the Recent Analogue

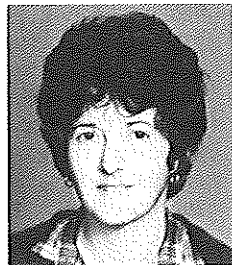
Paleoecology is particularly susceptible to interpretations that are heavily based on what can be observed in recent ecosystems. Just as the "pull of the recent" may affect paleontological analyses because there is so much more information about evolution, diversity, etcetera, for modern organisms, the "pull of the recent analogue" inevitably shapes ideas about how organisms were ecologically related to one another and to their physical environments throughout the history of life.

Modern ecology generates expectations regarding species diversity and guild structure within each level of the Eltonian pyramid, as well as body size distributions and behavioral correlates of habitat and food resources for herbivores and carnivores. In the vertebrate record, we look for familiar patterns in assemblages of land animals and judge the validity of our samples against these expectations. An "unusual distribution of species"—many large vertebrate herbivores but no small ones, for instance—is typically blamed on taphonomic biases or other sampling problems. This may be true, but a factual observation is thereby dismissed as a sampling problem *because* it does not fit our expectations based on recent ecosystems. The result is that present ecological structures are subtly imposed on the past, and we are prevented from seeing how the past might have been different.

How do we loosen the bonds of this dependency on the present? The objective approach to the question of "large herbivores only?" should include hypotheses concerning both taphonomic biases and real ecological information. In order to support ecological hypotheses, we are forced to account for taphonomic biases. This is not an impossible task, for it is becoming clear that taphonomic processes leave discernable evidence on organic remains, and that many biases are patterned rather than idiosyncratic. Taphonomic indicators within single assemblages provide a basis both for judging post-mortem processes that have interacted with the organic remains and for assessing how ecological information is biased. Comparison of multiple samples from different taphonomic contexts helps to distinguish whether presence/absence or other features of fossil assemblages are effects of ecological or taphonomic causes. The "isotaphonomic approach" samples faunas and floras with similar taphonomic biases to compare through time.

There is great potential for learning new things about ecological history for all types of organisms if research emphasis shifts toward more rigorous taphonomic analysis and away from uncritical (or unconscious) "top-down" application of recent analogues. We cannot separate ourselves from our own realm and the ideas it provides, nor would we want to. The Recent gives us our only opportunity to observe ecological and taphonomic processes at work and to compare contemporaneous life and death assemblages. But we can strengthen the objectivity with which we regard ecosystems of the past and reduce the "pull of the recent analogue" on paleoecology. Perhaps there *were* no small vertebrate herbivores during particular geological intervals since such herbivores evolved, and perhaps their diversity relative to large herbivores *has* fluctuated widely in tune with other physical or biotic factors. This is the kind of information that is only available in the fossil record. If paleoecological research is to achieve the strength and credibility it deserves in the arenas of ecological and evolutionary theory, then it is imperative that we seek greater independence from the Recent, that we learn to understand paleontological evidence more on its own terms.

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tic, and exposed upper surface communities (Brett and Liddell, 1978; Kobluk, 1980, 1981c). Palmer (1982) has noted that an equilibrium diversity and general structure of hard substrate communities was established in the Middle Ordovician and remained relatively little changed, despite changes in the constituent taxa, throughout the remainder of the Paleozoic.

Evidence for spatial competition among ancient marine hard substrate biotas comes from study of overgrowth networks among Silurian bryozoans from North America (Liddell and Brett, 1982), England, and Gotland (Taylor, 1984). Several studies have documented cryptic communities on the under-surfaces of Silurian and Devonian coral and stromatoporoid heads, which closely resemble modern cryptofaunas in diversity and general guilds of organisms (Spjeldnaes, 1975; Kershaw, 1980; Liddell and Brett, 1981; Carthew, 1986; Segars and Liddell, this volume).

Relatively little is known of Late Paleozoic hard substrate communities, in part because, for unknown reasons, few marine hardgrounds have been documented from this interval of geologic time. Suchy and West's paper (this volume), dealing with encrusting cryptic communities on Pennsylvanian chaetetids, is a welcome contribution in this area and seems to document the persistence of cryptic community structure first established in the Silurian (Segars and Liddell, this volume).

The great Permo-Triassic extinctions clearly had a major effect on hard substrate communities, as evidenced by the fact that Mesozoic encrusting communities have markedly different compositions than do middle Paleozoic counterparts (Palmer, 1982). The magnitude and dynamics of this extinction event are difficult to assess, however, because of the general lack of knowledge of encrusting biotas in the Late Permian and Early Triassic. Palmer has documented major changes in the modes of life of encrusting organisms beginning in the Triassic. In particular, the much greater abundance of deep boring bivalves and sponges in the Mesozoic hardgrounds parallels the trend toward deeper invasion of soft substrate areas by infaunal organisms (Ausich and Bottjer, 1982; Thayer, 1983). Wilson (1987) has further noted that the greater availability of crevices and crypts produced by deep boring organisms fostered an adaptive radiation of nestling and cryptic organisms in Mesozoic cobble faunas. Increased thickness of skeletons of Mesozoic, as contrasted with Paleozoic epifaunal encrusters, is consistent with the predictions of Vermeij's (1977, 1987) model of intensified predation pressure in the Mesozoic; indeed, this "Mesozoic marine revolution" may have also triggered the above-mentioned trend toward deeper boring and its attendant effects. The Jurassic Period appears to have been another time in earth history when, as in the Middle Ordovician, hardgrounds were particularly well developed, and again, peculiarities of oceanic chemistry such as a high Mg/Ca ratio and high $P(\text{CO}_2)$ have been suggested as agents favoring calcite cement precipitation (Sandberg, 1983). Jurassic hardground faunas have been well documented (Kazmierczak and Pszczolkowski, 1968; Roniewicz and Roniewicz, 1968; Hallam, 1969; Palmer and Fürsich, 1972; Gruszczynski, 1979, 1986; Fürsich, 1979). These papers clearly document that the general diversity and guild structure observed in modern hardgrounds were established by the Jurassic. Hardgrounds and reworked carbonate/phosphate nodules were well developed in Late Cretaceous

chalks, and tend to be deeply riddled with borings of clionid sponges and bivalves (Voigt, 1959; Bromley, 1967, 1970, 1972; Kennedy and Garrison, 1975 a,b; Kennedy and Klinger, 1972; Thomsen, 1977). As in the Middle Ordovician, worldwide eustatic sea-level rise in the Late Cretaceous inundated continental areas and favored preservation of rocky intertidal encrusting communities which display zonation resembling that seen in modern rocky shorelines (Surlyk and Christensen, 1974).

Detailed studies of Cenozoic hardgrounds are surprisingly rare (but see Pedley and Bennett, 1985). Understanding of modern hard substrate biotas, particularly those on skeletal substrates, however, has increased substantially during the past 15 years (see Jackson, 1977a,b, 1979a,b, 1981; Jackson and Buss, 1975; Jackson and Winston, 1982). The taphonomy of modern hard substrate biotas has been largely ignored until recently, but progress is being made (Liddell and Ohlhorst, this volume; Kobluk, this volume; Rasmussen and Brett, 1985, 1986). Results of these taphonomic studies are both encouraging and discouraging: on the one hand, the skeletonized, and thus preservable, portion of the fauna represents only a small fraction of the total community (usually < 40% of species richness and < 15% of total area originally covered by encrusters). On the other hand, the skeletonized component appears to record a distinctive early successional community; thus, comparisons of hard substrate biotas through time are probably based on comparable samples, all biased toward early successional seres (Rasmussen and Brett, 1985, 1986).

CONTROLS ON DIVERSITY AND STRUCTURE OF HARD SUBSTRATE COMMUNITIES

Several themes that emerged from the NAPC symposium relate to controls on the diversity and structure of hard substrate communities. First, several papers document succession (*sensu* Goldring and Kazmierczak, 1974) in these communities. Carthew (1986) observed successional sequences, controlled in part by overgrowth dominance networks, among bryozoans encrusting Silurian stromatoporoids, while Kauffman (1986) noted up to five successional seres on single shell islands from the Cretaceous. Surprisingly, Suchy and West (this volume) find little evidence for succession or competitive overgrowth dominance among encrusters in Pennsylvanian cryptic communities. This observation presents a challenge to most hypotheses based on study of recent cryptic biotas, which would predict intense spatial competition in the very limited spaces available under chaetetid sponges. Finally, Rasmussen and Brett (1985, 1986) found that succession influenced the taphonomy of cryptic biotas. Not only are the preservable relicts of cavity and coral-undersurface communities biased toward early successional groups, but also, later climax faunas, dominated by demosponges, may to some extent eradicate the record of these earlier skeletonized organisms. The influence of this bias is particularly severe in stable, undisturbed environments of larger reefal cavities; this leads directly to the second major theme.

Many authors of the symposium stressed the role of disturbance in limiting or promoting diversity. Wilson (1985, 1987), for example, found that disturbance in the form of abrasion and

impacts keeps rolling stone biotas in a low state of succession and therefore of moderate diversity; however, he also noted that, through the Phanerozoic, cobble faunas have adapted to this stress, either directly, or indirectly, as a result of other environmental changes, by developing nestling modes of life and/or thicker skeletons. In contrast, Kobluk and Lysenko (1986, 1987) have recently suggested that cryptic organisms living under boulders in tropical reef settings are somewhat *more* resistant to destruction during large storms than are exposed encrusters, because of their sheltered habitat. Kobluk and Lysenko proposed a unique model in which cobble-pebble encrusters provide a reservoir that facilitates recolonization in the general environment following storm disturbances. Carthew (1986) documented disturbance effects among Silurian corals and the organisms which encrusted them. Storm disturbance effects were not inferred in Kauffman's examples of Cretaceous shell islands but the role of disturbance by a fluctuating anoxic/oxic boundary was found to be critical in limiting diversity and controlling patterns of colonization. Finally, Liddell and Ohlhorst (this volume) postulate that physical disturbance in the form of sedimentation is of some importance in producing zonation of modern encrusting faunas in fore-reef hard substrate environments. They find, however, that the change from high to low physical disturbance into deeper water has relatively little effect on the diversity of encrusters.

Longer-term biotic disturbance may have been a key factor in directing the evolution of hard substrate biotas. Thus, Palmer (1986) concludes that intensified predation may have led not only to thicker shells but also deeper boring among Mesozoic bivalves inhabiting hardgrounds (also see Vermeij, 1987); Wilson (1987) comes to a similar conclusion for cobble-dwelling faunas.

As a final point, several authors note the evolutionarily conservative nature of hard substrate communities. Suchy and West's Pennsylvanian undersurface communities resemble those of the Silurian and Devonian (Segars and Liddell, this volume). Elements of much more ancient upper surface encrusting faunas, such as sclerosponges, certain brachiopods, spirorbids, and certain cyclostome bryozoans, survive as relicts in Recent cavity habitats (Jackson et al., 1971; Vermeij, 1987). It is possible that there is an evolutionary progression of organisms from upper to protected lower surfaces in hard substrate settings. In this view, cavity faunas are evolutionary relicts reminiscent of deep-sea faunas in the model of onshore innovation/offshore migration proposed recently by Sepkoski and Sheehan (1983; see also Jablonski et al., 1984).

PROSPECTIVES

Where do we go from here? First, some basic documentation is still needed in several areas, despite the multiplicity of detailed case studies that have appeared in recent years. This is particularly so in the gap areas, such as the Late Paleozoic, from which hardgrounds seem to be rare but where other types of hard substrate such as corals and shells are available. (We also need to consider this temporal distribution of hardgrounds; why, for example, are they so common in the Early Paleozoic carbonate shelves, but seemingly so uncommon in geologically similar settings of the Carboniferous?) Another

gap, ironically, is the Cenozoic, including the Recent, where our knowledge of hardground biotas is surprisingly poor (perhaps it is destined to stay that way—most of the best extant hardgrounds seem to be in the Persian Gulf!). Moreover, a general lack of quantitative data on species richness, diversity, and percent coverage of encrusters presently hampers temporal comparisons among hard substrate communities. Future studies should endeavor to collect such information in a consistent manner.

We also need to build up a much better data base on non-hardground-encrusting communities, such as those on corals, which can be more easily controlled for comparable environments than can hardgrounds, by attention to the biofacies distribution of the hosting skeletal substrates. One could, for example, make comparative studies of communities developed on related taxa of corals or shells and examine encrusting assemblage evolution in the larger context of the biofacies to which they belong.

Perhaps more importantly, we need to begin applying some of our knowledge of hard substrate biotas in paleoenvironmental and evolutionary studies. In paleoecology many possible avenues of research exist; we need more studies of encrusting organism interactions. Can competitive networks be more rigorously documented? Do they differ in stable *vs.* ephemeral environments? What morphological adaptations do encrusting organisms display for spatial competition or avoidance of overgrowth? The elegant bryozoan studies of Taylor (1984) and Lidgard (1985, 1986) are breaking new ground in this area.

There is great potential in the application of hard substrate assemblages to paleoenvironmental studies. Diversity and taxonomic composition of hard substrate encrusters may provide a very sensitive index of gradients in oxygen, turbidity, and light intensity. An excellent case study along these lines is Baird's (1981) documentation of diversity gradients in encrusting epizoans on hiatus concretions down a Devonian paleoslope. Kauffman's (1986) research on shell islands may similarly permit reconstruction of oxygen gradients. Also related to this point is the potential utility of endolithic microborings on shell substrates. Algal borings can provide important indicators of light penetration and, therefore, of paleobathymetry (Golubic et al., 1975; Budd and Perkins, 1980); or, where depth can be established independently, of water clarity. Recent work in microendoliths in the Devonian and Jurassic (Vogel et al., 1987) indicates considerable potential for this type of study.

Finally, we need to place hard substrate studies in a broader evolutionary perspective, comparable to other marine communities. Evolutionary adaptations of encrusting organisms need to be studied over broad ranges of time and environment. The question of the late appearance of hard substrate communities deserves further attention. Likewise, we need to consider the assumption of evolutionary conservatism in hard substrate communities. Are we seeing a type of community level stasis, and, if so, why? Are cryptic habitats refugia (cf. Jackson et al., 1971), or, as Kobluk and James (1979) have suggested, crucibles of new evolutionary innovation? It is certainly timely (if also trendy) to evaluate the effects of mass extinctions on hardground and shell ground communities. Indeed, many of the famous extinction boundary beds are hardgrounds; yet few if any studies have compared in detail the changes in hardground

faunas immediately above and below these boundaries. Were they synchronous with extinctions in soft substrate and pelagic settings? More or less severe? It is also important to compare cryptic and non-cryptic hard substrate biotas in terms of extinction and evolutionary patterns.

In summary, there are many avenues for future research in hard substrate communities. The documentation phase of study is well under way, although with much left to do, but synthetic evolutionary and ecological approaches have scarcely been attempted. There is room for considerable development in this field in the near future and it promises to yield many new insights into ancient environments, paleoecology, and evolutionary patterns.

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The concept of the vast extension of our world in time, one which grew from investigations seeded in the seventeenth century, has surely been no less revolutionary than the concept of vast stellar space emerging after Copernican astronomy appeared during the century preceding. However, outside a relatively small community, which includes most practitioners, historians, and philosophers of science, many conservationists and writers of science fiction, and a growing number of artists and poets, the idea of geological time as often as not has been greeted with indifference, skepticism, or downright hostility.

—Claude Albritton