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Palaeoecology and evolution of marine hard substrate communities

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Abstract

Marine organisms have occupied hard substrates since the Archaean. Shells, rocks, wood and sedimentary hardgrounds offer relatively stable habitats compared to unconsolidated sediments, but the plants and animals which inhabit them must develop means to gain and defend this premium attachment space. Hard substrate communities are formed by organisms with a variety of strategies for adhering to and/or excavating the substrates they inhabit. While mobile grazers, organically attached and even soft-bodied organisms may leave evidence of their former presence in ancient hard substrate communities, a superior fossil record is left by sessile encrusters with mineralised skeletons and by borers which leave trace fossils. Furthermore, encrusters and borers are preserved in situ, retaining their spatial relationships to one another and to the substrate. Spatial competition, ecological succession, oriented growth, and differential utilisation of exposed vs. hidden substrate surfaces can all be observed or inferred. Hard substrate communities are thus excellent systems with which to study community evolution over hundreds of millions of years. Here we review the research on modern and ancient hard substrate communities, and point to some changes that have affected them over geological time scales. Such changes include a general increase in bioerosion of hard substrates, particularly carbonate surfaces, through the Phanerozoic. This is, at least in part, analogous to the infaunalisation trends seen in soft substrate communities. Encrusting forms show an increase in skeletalisation from the Palaeozoic into the Mesozoic and Cenozoic, which may be a response to increasing levels of predation. Hard substrate communities, considering borers and encrusters together, show a rough increase in tiering through the Phanerozoic which again parallels trends seen in soft substrate communities.

This extensive review of the literature on living and fossil hard substrate organisms shows that many opportunities remain for large-scale studies of trends through time at the community and clade levels. Palaeontologists will especially benefit by closer integration of their work with that of neontologists, particularly in aspects of ecology such as larval recruitment, competition and succession.

Keywords: Hard substrates; Encrusters; Borers; Bioerosion; Ecology; Palaeoecology; Evolution

1. Introduction

Modern and ancient marine environments abound in substrates that are sufficiently firm and consolidated to be bored and encrusted. These hard substrates range in scale from coarse sand particles, to vast

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expanses of lithified seabed. They include the skeletons of living and dead organisms as well as rock clasts. Areas of otherwise barren seabed may be opened up for colonisation by a diverse array of organisms when hard substrates are present. Nowhere is this more vividly illustrated than by the rich communities developing on shipwrecks and other artificial 'reefs' which prove so attractive to recreational divers. Naturally occurring hard and firm substrates lie at the nucleus of many benthic communities, both at the present day and in the geological past. In turn, the skeletal remains of organisms living in these communities are used as hard substrates by other organisms in a process known as 'taphonomic feedback' (Kidwell and Jablonski, 1983). Hard substrates play crucial roles in numerous marine biological and geological processes, including initial colonisation of the seabed and sedimentation.

From the perspective of palaeoecology, studies of hard substrate assemblages offer the important advantage that the organisms cemented to and boring into hard substrates generally retain their original positions on the substrate after fossilisation. Therefore, it is possible to investigate the living spatial distributions and orientations of organisms from their fossil remains. For example, distributions of species can be quantified relative to exposed and hidden surfaces, and their orientations compared with inferred current directions. Furthermore, the relationships between different colonisers on the same hard substratum can be studied, allowing interpretations of ecological succession and competitive interactions to be made. For example, careful investigation of an encrusted and bored brachiopod shell may yield information on the autecology of the brachiopod, including life orientation, feeding current patterns and symbionts, as well as the sequence of colonisation by borers and encrusters before and after the host's death, their preference for particular locations on the host shell, and how they interacted with one another during life. Hard substrates provide unique opportunities for observing competition between individuals in fossil material and for tracing competition between clades over geological timescales (McKinney, 1995a).

This review sets out to summarise the main areas of research on the palaeoecology of marine hard substrates. The literature on this topic is far too extensive for a comprehensive review and our coverage is consequently weighted towards our personal interests and expertise in hardgrounds, bioerosion, and bryozoans. We have paid particular attention to related studies on modern hard substrate communities which, although often neglected by palaeontologists who may not have easy access to marine biological journals, offer important insights into processes that must have operated in the geological past, as well as underscoring constraints on the extent to which ancient hard substrate communities can be interpreted. While the present, as always, provides an essential key to the past, the fossil record of hard substrate communities opens a unique window into the long-term evolution of such communities, especially epibionts (Lescinsky, 1996b), and permits investigation of how they have responded to such important global changes as mass extinctions and the switch between aragonite and calcite seas.

After a general introduction to the diversity of marine hard substrates and the lifestyles of organisms colonising them, we go on to discuss: (1) terminology; (2) communities on biotic substrates; (3) ecological patterns and processes in modern hard substrate communities; (4) the geological history of hard substrate communities; (5) palaeoecological themes; (6) evolutionary trends; and (7) the geological utility of hard substrate communities.

2. Hard substrate diversity

Modern marine hard substrates include biogenic (shells, wood, bones) and abiogenic materials (rocks of various origins), and anthropogenic structures such as wharves, boat hulls, concrete shore defenses, 'artificial reefs' usually created for fishery purposes (e.g., Collins and Jensen, 1996; Lam, 2000; Svane and Petersen, 2001), and plastic debris drifting in the ocean (e.g., Winston et al., 1997). Ancient hard substrates are nearly the same, with some historical changes in abundance and distribution of substrate types, such as with wood, shells and hardgrounds, and, of course, the lack of anthropogenic objects.

2.1. Biogenic hard substrates

"Shells" as understood here include any mineralised tissues of invertebrates, whether external in life

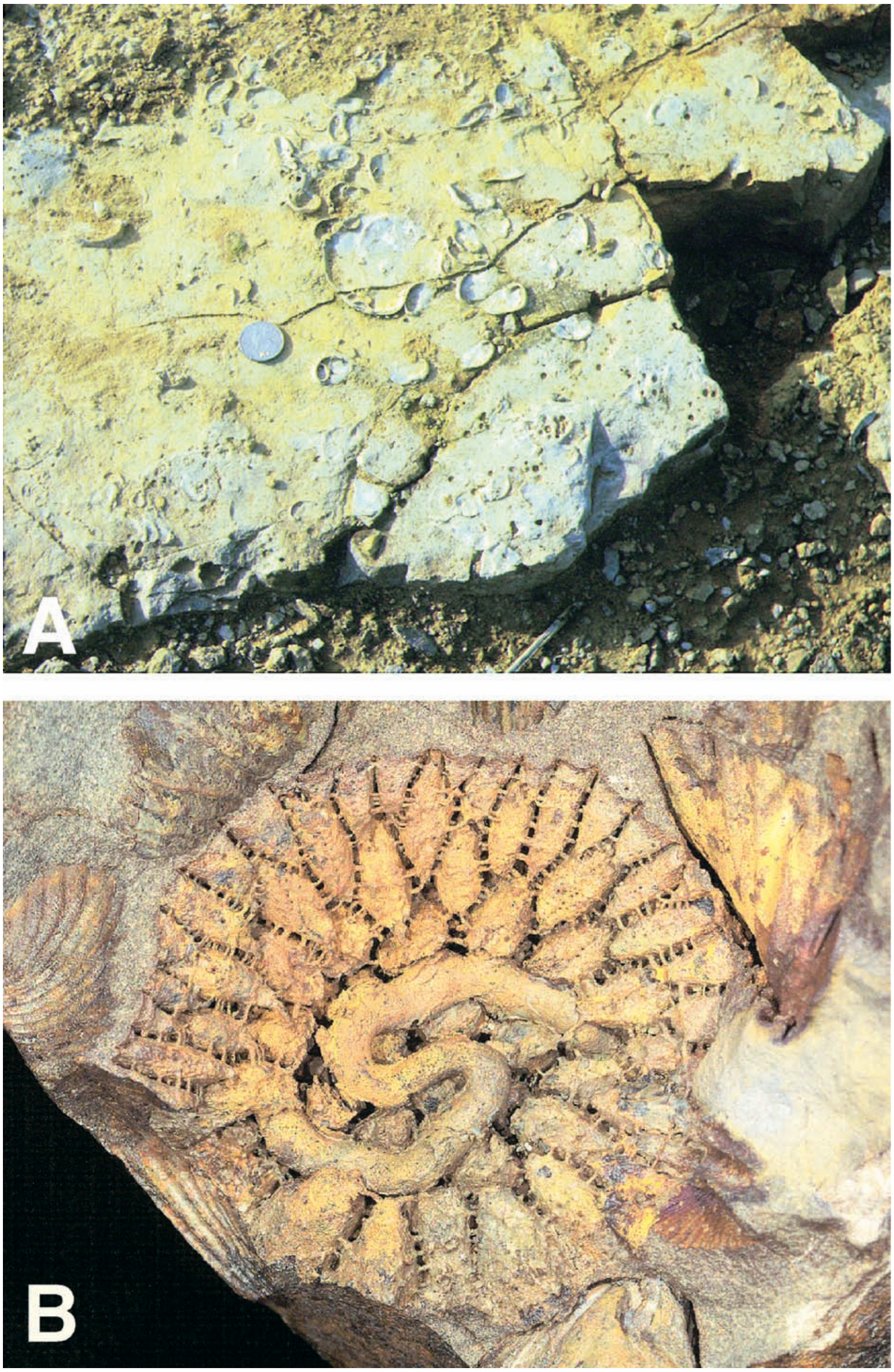


Fig. 1. Abiotic and biotic hard substrates exhibiting different modes of faunal colonisation. (A) Field photograph of a hardground encrusted by oysters and bored; coin is about 25 mm in diameter; Jurassic, Bathonian, White Limestone Fm., Foss Cross Quarry, Gloucestershire, England. (B) Decalcified specimen of the coral *Pleurodictyum* containing the sinuous mould of the embedded 'worm' *Hicetes* that grew at the same time as the coral; × 2.8; Devonian, Daun, Eifel, Germany.

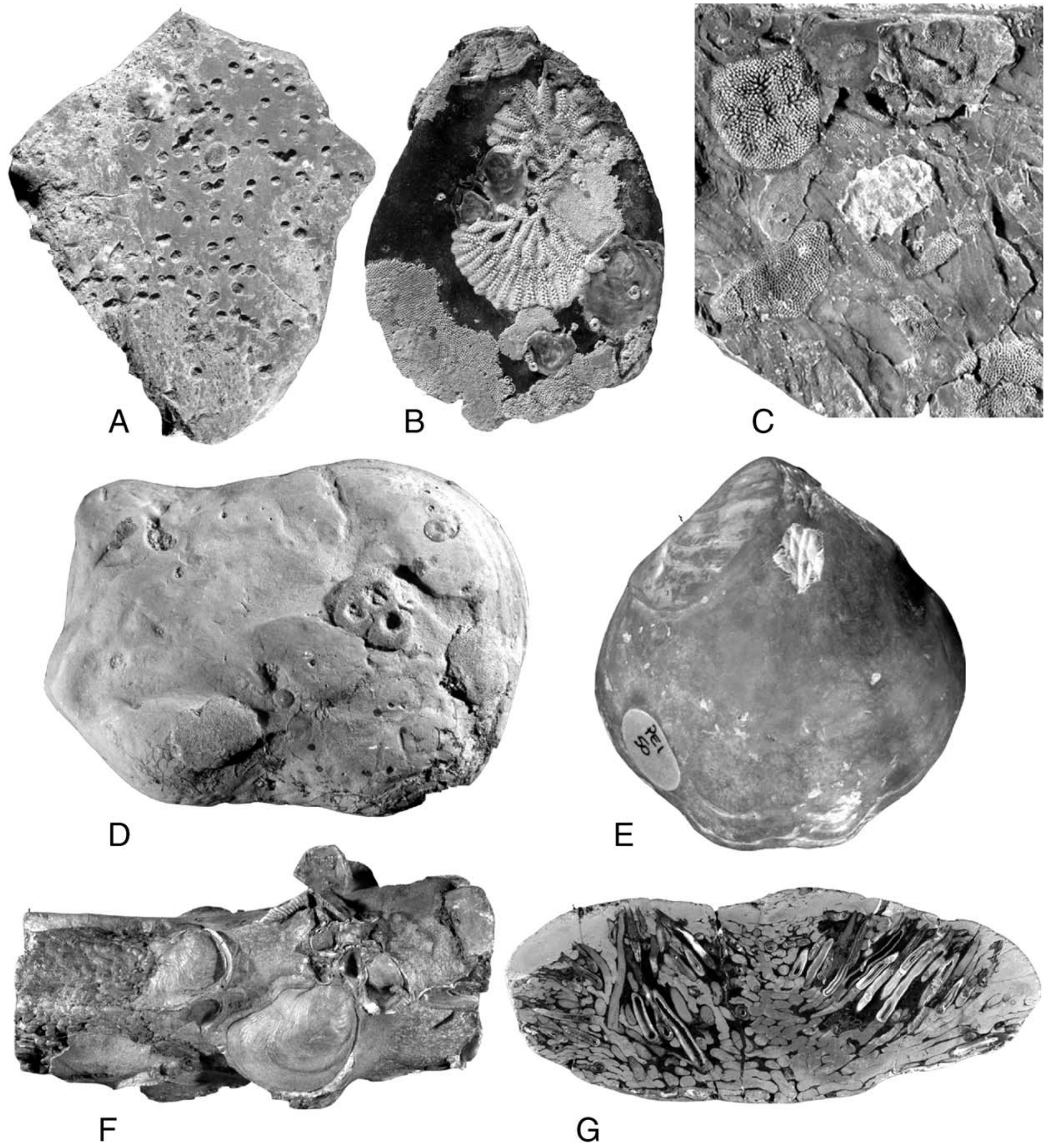
(e.g., bivalves, gastropods and brachiopods) or internal (e.g., echinoderms, some bryozoans and cephalopods). External shells can be encrusted or bored while the host animal is still alive (e.g., Ward and Thorpe, 1991; Berkman, 1994). In addition, shell growth around another living organism may lead to embedment (Fig. 1B). A living host introduces several elements into the structure of a shell-dwelling hard substrate assemblage. The host may be infaunal for part or all of its life history, reducing the opportunities for colonisation. Some shelled animals are partially infaunal, leaving one portion of the shell exposed to encrustation and boring: Watson (1982) and Keough (1984) discuss Jurassic and Recent examples, respectively. Some animals have an organic membrane over the outer parts of the shell, such as the molluscan periostracum, which may dissuade epizoans by physical or chemical means (Bottjer, 1981). Some organisms are sessile benthic, providing a relatively stable substrate, whereas others are vagrant benthic or nektonic, forcing any successful colonisers to adapt to movement of the host (see Schmitt et al., 1983; Landman et al., 1987). Even shells remaining after the death of the shell-producer host can still biotically move if they are secondarily inhabited by another organism, such as when a hermit crab occupies a gastropod shell (Stachowitsch, 1980; Al-Ogily and Knight-Jones, 1981; Brooks and Mariscal, 1986). We may expect to find hard substrate communities on the exposed portions of shells which had still-living hosts or secondary occupants, but not on internal shells of living animals or on shells of sediment-dwellers.

Shells which are "dead" and not secondarily occupied can be encrusted and bored on all exposed surfaces, including those once on the interior of the animal or otherwise covered by flesh (Fig. 2B). The existence of an encruster or boring initiated on an interior surface is a strong indication that the shell producer was dead at the time of colonisation, as discussed by McKinney (1995b). Dead shells begin to decompose physically, producing changes in the hard substrates available to colonisers. Many aragonitic bivalve shells, for example, lose their external lustre and become "chalky" in time after death, producing changes in the substrate which may be expected to attract or repel particular encrusting and boring species. Dead shells are also easily disturbed in high-energy environments and quickly buried under high sedimentation conditions, so hard substrate communities may have only limited opportunities to colonise them. Shells in soft-sediment environments can serve as important "benthic islands" for hard substrate communities (Hattin, 1986; Zuschin and Pervesler, 1996; Zuschin et al., 1999).

Wood is a special type of organic hard substrate (Fig. 2F,G). In the marine realm wood can be: (1) living and in situ, as with the roots and trunks of mangrove trees (Sutherland, 1980); (2) in situ and dead (submerged forests, for example); (3) floating, and potentially hosting a characteristic driftwood community of encrusters and borers (see Noda, 1981; Wignall and Simms, 1990; Evans, 1999); or (4) waterlogged and submerged. Different types of wood will have varying consistencies and resistances to decomposition, producing varying boring and encrusting assemblages. Woody substrates, like shells, also change significantly with time after death. The removal of bark, for example, dramatically modifies the surface available for colonisation. Plant-derived amber is an unexpected marine hard substrate. Nevertheless, several instances of amber bored by pholadid bivalves in marine environments are known (Bandel et al., 1997; Jeffery, personal communication).

Fig. 2. Examples of bored, encrusted and grazed hard substrates. (A) Fragment of an Ordovician hardground upper surface with numerous *Trypanites* borings and sparse encrusting bryozoans and pelmatozoan holdfasts (top); × 0.7; Arenig, Volkhov Fm., Zheltjaki Unit, Kolchanovo, nr Volkhov, Russia. (B) Internal surface of Pliocene bivalve shell densely encrusted after death by bryozoans, oysters and *Spirorbis*; × 1; Pliocene, Nukumaru Limestone, Nukumaru Beach, nr Wanganui, New Zealand. (C) Part of the underside of a stromatoporoid encrusted by a cryptic fauna including bryozoans (e.g., *Ceramopora*, upper left) and the cemented brachiopod *Liljevallia* (top right), × 1.1; Silurian, Wenlock, Upper Visby Beds, Lickershamn, Gotland, Sweden. (D) Bored and encrusted hiatus concretion; × 0.9; Upper Ordovician, Kope Fm., Newport, KY, USA. (E) Heavily bioeroded ventral valve of the brachiopod *Epithyris*; grazing by echinoids has destroyed the shell entirely in one area, exposing the white sediment infill, while leaving a small crescent (top left) of unaffected shell; × 1.4; Jurassic, Bathonian, White Limestone Fm., Gilbraltar Quarry, Oxfordshire, England. (F) Oysters encrusting a log of fossil wood; × 0.4; Eocene, London Clay, Wokingham, Berkshire, England. (G) Sectioned piece of fossil wood riddled with the bivalve boring *Teredolites*, many lined and some filled with sediment but others with calcite; × 0.3; Eocene, London Clay, Kent, England.

Bones and teeth are the internal skeletal elements of vertebrates. Bones, of course, vary in their structure and composition, which affects the organisms attempting to colonise these surfaces. There have been relatively few studies of marine communities colonising vertebrate remains, notable exceptions being: Allison et al. (1991) on organisms encrusting Recent whale bones; Grange and Benton (1996) on Jurassic crocodile bones; Underwood et al. (1999) on microborings in Cretaceous fish teeth; and Kues (1983) on a bryo-



zoan encrusting a Cretaceous ceratopsian dinosaur skull. White (1978) even figures an auloporid tabulate coral encrusting the bony head of a Devonian fish. Bioerosion of bird bones is discussed by Davis (1997), and Hutchinson and Frye (2001) describe pitting on the surfaces of Cenozoic turtle shells which may be induced by fouling bacteria, fungi or metazoans.

Reefs are a special type of biogenic hard substrate community. We use here the broad definition of reefs as "discrete organic carbonate structures that develop topographic relief upon the sea floor" (Wood, 2001a, p. 162), and recognise that they promote in situ carbonate production at a higher rate than the sediments which surround them (Wood, 1999). Reef systems are complex and have a spectacular geological history. We cannot cover them in detail here, but fortunately they have been well reviewed in the past two decades. Good general palaeoecological

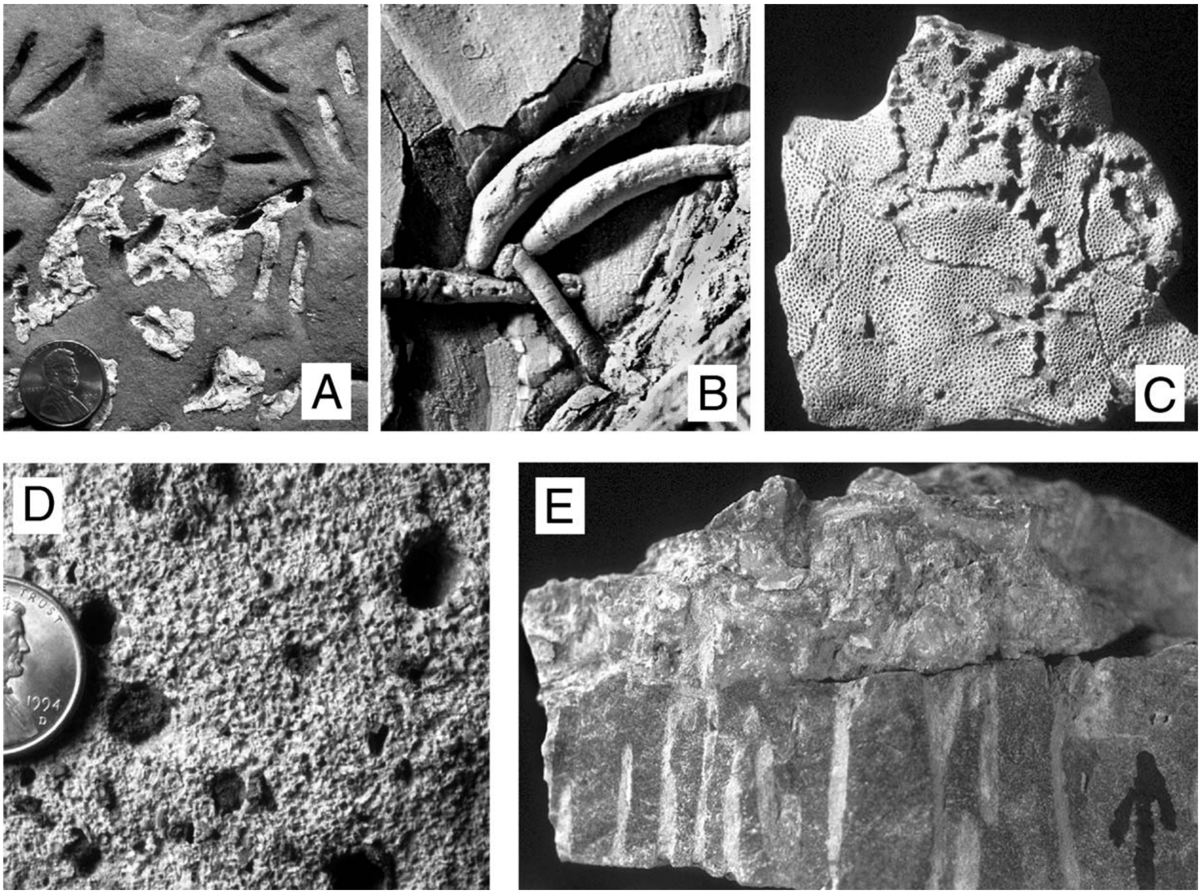


Fig. 3. Borings and a 'pseudoboring' (bioclaustration). (A) The facultative bivalve boring *Petroxestes pera* in an Upper Ordovician limestone hardground from southern Ohio, USA (see Wilson and Palmer, 1988); coin is 1.9 cm in diameter. (B) Casts of the boring *Palaeosabella* exposed on the inner shell of the bimineralic bivalve *Caritodens demissa*, Upper Ordovician, northern Kentucky, USA; the borer cut through the outer calcitic shell layer into the inner aragonitic layer, ending its excavation; the boring later became filled with calcite cement and the aragonite shell layer dissolved away, leaving these casts; borings are approximately 1 mm wide at their widest points. (C) Stellate pits of the bioclaustration *Catellocaula vallata* hosted by the trepostome bryozoan *Amplexopora persimilis* from the Upper Ordovician of Ohio, USA (see Palmer and Wilson, 1988); × 2.5. (D) Plan view of *Gastrochaenolites anauchen*, possibly a bivalve boring, in a limestone cobble from the Upper Carboniferous of Arkansas, USA; the rough texture of the surface between the large *G. anauchen* borings was produced by numerous acrothoracican barnacle borings (see Wilson and Palmer, 1998); full coin is 1.9 cm in diameter. (E) Vertical section through a carbonate hardground penetrated by *Trypanites* borings (infilled by paler sediment) and encrusted on its upper surface by a thick trepostome bryozoan; Upper Ordovician of northern Kentucky, USA; × 1.

references include the books by Fagerstrom (1987) and Wood (1999); recent discussions of the history of reefs are summarised in Wood (2001b); the value of diverse reef types for palaeoclimatic studies is assessed by Kiessling (2001); and coral reef ecology is reviewed by Knowlton and Jackson (2000). Many of our following discussions of bioerosion and encrustation on hard substrates will include materials from reefs of many ages and kinds.

2.2. Abiogenic hard substrates

Natural abiogenic marine hard substrates comprise rocks of diverse origin, composition, shape and size. The simplest are rocky shelves and subtidal cliffs, including caves and other cavities with rocky walls. These surfaces remain in situ until broken up by erosion. They are referred to in the literature as "rockgrounds" and more broadly as "rocky shores". Ecological zonation on modern rocky shores has been well studied (Lewis, 1964), while Johnson and co-workers have led research on ancient rocky shores (see Johnson, 1988a,b, 1992; Johnson and Baarli, 1999, for discussion and review). Virtually every major rock type is exposed somewhere in the open ocean. A very important distinction for encrusting and boring organisms is between limestones (primarily calcium carbonate) and other rock types. Limestones can be more easily reduced or modified by chemical means, especially by various borers using acids and chelating agents. Besides chemical composition, the friability of rock surfaces is important to colonising organisms. A loosely cemented sandstone, for example, erodes easily, making an unstable attachment surface. Other rocks may contain high concentrations of heavy metals, particularly copper, which may potentially discourage colonisation. Whereas the majority of rocks are colonised on the seabed, floating pumice can be colonised by corals, pedunculate barnacles and other organisms (Jokiel, 1989; Donovan, 1999).

Hardgrounds (Figs. 1A, 2A and 3A,E) are in situ rocky surfaces formed by the contemporaneous submarine cementation of seafloor sediment (see Wilson and Palmer, 1992, for review). They are usually limestones, although some are carbonate-cemented quartz sandstones. Most hardgrounds today are cemented by aragonite, whereas most in the geo-

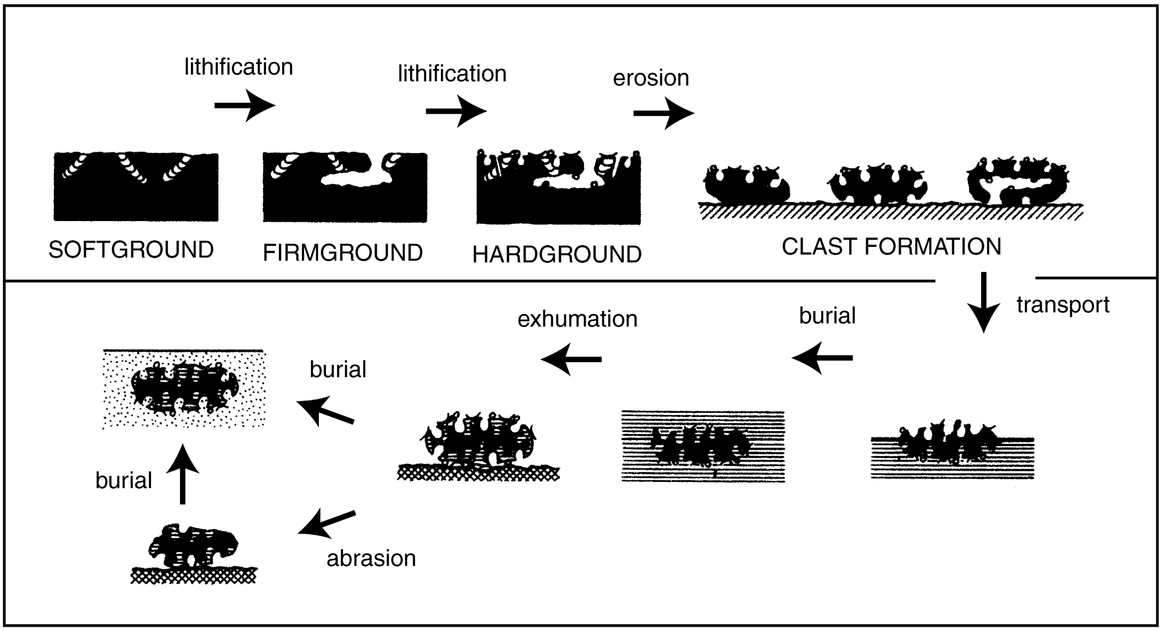


Fig. 4. Genesis of bored and encrusted clasts based on studies of Upper Jurassic carbonates in Poland. After Chudzikiewicz and Wieczorek (1985).

logical past had low-magnesium calcite as the primary cement. Hardgrounds are most common in tropical and subtropical shallow carbonate environments (Dravis, 1979; Wilson and Palmer, 1992). However, they are also known in deep-water chalks and other carbonate oozes (Kennedy and Garrison, 1975a; Bromley and Gale, 1982). Organisms encrust and bore carbonate hardgrounds much as they would any exposed limestone. Exposed beachrocks are often encrusted and bored, and they are sometimes described as "hardgrounds" (e.g., Clari et al., 1995), but since they are not synsedimentarily cemented on the seafloor, they are better classified as rockgrounds. "Firmgrounds" may be precursors of hardgrounds or may remain of intermediate consistency and hence colonisable by both boring and burrowing organisms (e.g., West et al., 1990, Fig. 13). Related to hardgrounds are reworked concretions (Fig. 2D), a subset of which are hiatus concretions showing evidence of exhumation, encrustation and/or boring, followed by burial with renewed growth of the concretion. The complex genetic history of some hard substrates (Fig. 4) offers opportunities for multiple generations of different colonists.

Hydrothermal vents on spreading centres produce a special type of rocky substrate. Exhalations of mineral-rich super-heated water form chimneys of various metal sulfides, often many meters high. These chimneys, and the surrounding seafloor basalts, can support a distinctive hard substrate community dominated by large tubeworms and ultimately sustained by chemosynthetic bacteria (see Tunnicliffe, 1991; Little et al., 1998). Regions of shallow water hydrothermal vents may also harbour rich communities of sessile organisms: Morri et al. (1999) recorded a total of 212 species at sites ranging from 2 to 90 m depth associated with such vents in the Aegean.

Methane hydrates can form rocky seafloors by the cementation of sediment in a matrix of water ice and methane (see Hovland et al., 1987). Bacterial decomposition of the methane under certain geochemical conditions can lead to the precipitation of carbonate cements and crusts. These substrates form around gas seeps in near-freezing temperatures at depths exceeding 500 m. They are sometimes termed "cold seeps" and can support hard substrate communities, sometimes similar to those formed around hydrothermal vents (e.g., Barry et al., 1996). Carbonate chimneys associated with cold seeps at about 220 m depth off southeastern New Zealand grow up to 90 cm in height and support hard substrate communities including encrusting bryozoans and borers (Orpin, 1991). Methane hydrates are extraordinarily common in deeper shelf environments. Current estimates are that they contain more stored carbon than all other fossil and living reservoirs combined (Paull et al., 1992). Cold seep deposits and faunas are now well known in the rock record (Beauchamp et al., 1989; Campbell and Bottjer, 1993; Campbell et al., 1993; Kelly et al., 1995).

All rocky substrates, including cliff faces, hardgrounds, hydrothermal vent chimneys and methane hydrates, can be fragmented by erosion. The loose pieces then become clasts of varying mobility, depending on their sizes and the energy of their depositional environments. The movement of these clasts, of course, dramatically affects the hard substrate communities attempting to colonise them (Wilson, 1985, 1987; Lee et al., 1997, Wilson and Taylor, 2001a,b). Large clasts in soft-sediment environments, such as dropstones from icebergs, can, like isolated shells, serve as benthic islands for encrusters (Oschmann, 1990).

3. Colonisation of hard substrates

Fossil hard substrate assemblages preserve mostly the sessile (fixed) components of the original communities, particularly encrusting and boring organisms. Encrusters living on these substrates were attached by cementation during life. In modern organisms, cementation is achieved using various organic compounds, including glycoproteins, polysaccharides and mucopolysaccharides (Abbott, 1990; Langer, 1993, p. 243). However, mineral cements can also contribute significantly to fixation on hard substrates. For example, Harper (1992, 1997) has shown how the crystallisation of spherulitic calcite between the periostracum of bivalves and the substrate binds the shell to the substrate. This 'extrapallial cement' may superficially resemble a diagenetic precipitate in morphology. Some encrusting bivalves switch from organic fixation to cementation during their development (e.g., Harper and Palmer, 1993). The durability of cementation to hard substrates varies—while some

Table 1
Major taxonomic groups of animals containing species with mineralised skeletons that encrust fossil hard substrates

Taxonomic group	Range (as encrusters)	Remarks	References
Foraminiferans	Ordovician–Recent	Various genera of calcareous and agglutinating benthic foraminiferans encrust hard substrates. Most are post-Palaeozoic, although it is likely that some problematical Palaeozoic encrusters (e.g., *Allonema*) are foraminiferans. Loosely attached foraminiferans may also be found (e.g., Cossey and Mundy, 1990).	Adams, 1962; Wilson, 1986b; Langer, 1993
Sponges	Cambrian–Recent	Sponges are undoubtedly under-represented as encrusters in the fossil record; however, forms with fused or closely interlocked spicules, or with mineralised basal skeletons (e.g., archeocyathans, stromatoporoids, chaetetids) can be common.	Wood et al., 1992; Molineux, 1994; Rigby and Mapes, 2000
Corals	Cambrian–Recent	Most major groups of corals include encrusting representatives. Coralliths are formed by encrusting corals that encapsulate rolling substrates (e.g., Dullo and Hecht, 1990).	Marek and Galle, 1976; Webb, 1993; Miller, 1996; Young, 1999; Helm, 2000
Brachiopods	Ordovician–Recent	Cementation has evolved independently in several groups of brachiopods, both inarticulates and articulates. Encrusting articulates include the tiny thecideans of the post-Palaeozoic as well as diverse larger Palaeozoic genera.	Cowen and Rudwick, 1967; Pajaud, 1974; Bassett, 1984; LaBarbera, 1985; Brunton and Mundy, 1988; Copper, 1996
Bryozoans	Ordovician–Recent	Palaeozoic encrusting bryozoans comprise mainly trepostomes and cystoporates, with occasional cyclostomes; post-Palaeozoic examples comprise cheilostomes and cyclostomes.	Taylor, 1984b; Lee et al., 1997; Taylor, 1999
Hederellids	Silurian–Carboniferous	This predominantly Devonian group of runner-like colonial encrusters is commonly assigned to the cyclostome bryozoans but their true affinity is problematical.	Sparks et al., 1980; Wilson and Taylor, 2001b
Bivalves	?Carboniferous–Recent	Several groups of bivalves have independently evolved a cemented habit, including the oysters (Ostreidae) and at least 9 other families. Most encrusting bivalves range from the Jurassic onwards.	Nicol, 1978; Harper, 1991; Harper and Palmer, 1993; Harper et al., 1996; Damborenea, 2002
Gastropods	Cretaceous–Recent	Vermetids are the main group of encrusting gastropods and are common in the Neogene. Vermiform 'gastropods' from the Palaeozoic may not be true molluscs (Weedon, 1990).	Morton, 1965; Savazzi, 1999a
Unstalked barnacles	Eocene–Recent	Verrucomorph barnacles are present in the Cretaceous, but the main group of 'acorn' barnacles—balanomorphs—does not become common until the Upper Eocene.	Schram, 1986; Foster, 1987; Foster and Buckeridge, 1987; Donovan, 1988
Serpulid/ spirorbid worms	Ordovician–Recent	Polychaetes with calcareous tubes first become abundant in the Mesozoic. The true affinities of Palaeozoic examples, notably supposed *Spirorbis* often recorded from the Silurian and Devonian, remain unclear.	Rzhavsky, 1994; Weedon, 1994; Savazzi, 1999c
Cornulitids	Ordovician–Carboniferous	The taxonomic affinity of these tubular, serpulid-like encrusters is not known.	Richards, 1974a,b
Sphenothallids	Cambrian–Permian	These attached tubes are either phosphatic or carbonaceous. The affinities of the worm-like organisms which formed them are unknown.	Bodenbender et al., 1989; Van Iten et al., 1992; Neal and Hannibal, 2000
Edrioasteroids	Cambrian–Carboniferous	Edrioasteroids had limited mobility but occur in assemblages of permanently cemented encrusters.	Bell, 1976; Smith, 1983; Meyer, 1990
Pterobranch hemichordates	Cambrian–Recent	Several Palaeozoic groups of pterobranchs, including crustoids, form encrusting colonies, as does the long-ranging extant genus *Rhabdopeura*.	Chapman et al., 1995; Mitchell et al., 1993

Table 2
Ichnogenera associated with hard substrates

Ichnogenus	Range	Remarks	References
Calcidelatrix Mägdefrau, 1937	Jurassic–Cretaceous	Lobed rosette-like boring.	Kennedy, 1970; Plewes, 1996
Caulostrepsis Clarke, 1908	Devonian–Recent	Pouch-shaped or ear-shaped borings or embedments produced by a gallery bent in a U-shape; single entrance. Modern spionid (polydorid) polychaetes make incipient *Caulostrepsis.*	Bromley and D'Alessandro, 1983; Aitken and Risk, 1988; Fürsich et al., 1994; see also Sato-Okoshi and Okoshi, 2000 for spionid boring mechanism
Centrichnus Bromley and Martinell, 1991	Cretaceous–Recent	Byssal etchings of anomiid bivalves.	Bromley and Martinell, 1991
Cicatricula Palmer and Palmer, 1977	Ordovician–Jurassic	Radiating etched canals; canals subdivide and anastomose, producing a net-like pattern. Usually found on hardgrounds and possibly made by sponges.	Palmer and Palmer, 1977; Fürsich, 1979
Clionoides Fenton and Fenton, 1932	Devonian	Tubular borings with irregular branching; attributed to sponges.	Sparks et al., 1980; Fagerstrom, 1996
Clionolithes Clarke, 1908	Ordovician–Carboniferous	Rosette boring branched from elongate origin.	Clarke, 1921; Plewes, 1996
Dendrina Quenstedt, 1849	Ordovician–Cretaceous	Rosette trace with a single point of origin; branches anastomose.	Hofman and Vogel, 1992
Dictyoporus Mägdefrau, 1937	Ordovician–Cretaceous	Network of anastomosing branches.	Mägdefrau, 1937; Plewes, 1996
Entobia Bronn, 1838	Jurassic–Recent	Single or numerous chambers excavated in calcareous substrates; connected to surface by apertures. Made at the present day by clionid sponges.	Bromley, 1970; Bromley and D'Alessandro, 1984, 1989; Mikulás, 1992; Fürsich et al., 1994
Feldmannia Casadío et al., 2001	Eocene	Small, teardrop-shaped cavities connected by irregular tunnels on oyster valves; likely an embedment structure and not a boring.	Casadío et al., 2001
Filuroda Solle, 1938	Devonian–Jurassic	Irregular tubes with rare branching and anastomosing.	Plewes, 1996
Gastrochaenolites Leymarie, 1842	Ordovician–Recent	Clavate borings; aperture narrower than main chamber and may be circular, oval, or dumb-bell shaped; main chamber may vary from subspherical to elongate. Usually made by bivalves which may be preserved in situ (see Savazzi, 1999b).	Kelly and Bromley, 1984; Wilson and Palmer, 1988; Ekdale and Bromley, 2001
Globodendrina Plewes et al., 1993	Jurassic	Fan-like branching tubes from one side of globular chamber; main chamber with agglutinated chimney; a foraminiferan boring.	Plewes et al., 1993 (see Vénec-Peyré, 1996 for a general review of bioeroding foraminiferans; and Vogel et al., 1987 for other rosette borings)
Gnathichnus Bromley, 1975	Triassic–Recent	Stellate, often pentameral scrape marks made by some species of regular echinoids.	Bromley, 1975; Michalík, 1977 (as the junior synonym *Roderosignus*); Nicosia, 1986; Breton et al., 1992
Helicotaphrichnus Kern et al., 1974	Eocene–Recent	Helical borings made by spionid (polydorid) polychaetes in the columella of gastropod shells occupied by hermit crabs.	Kern et al., 1974; Kern, 1979
Leptichnus Taylor et al., 1999	Cretaceous–Recent	Groups of closely spaced small, shallow and typically elliptical pits excavated in calcareous substrates. Attributable examples are made by cheilostome bryozoans, each pit corresponding to a single zooid.	Taylor et al., 1999

Table 2 (*continued*)

Ichnogenus	Range	Remarks	References
Maeandropolydora Voigt, 1965	Cretaceous–Pleistocene	Long, sinuous to contorted galleries with two or more apertures.	Bromley and D'Alessandro, 1983; Zítt and Mikulás, 1994
Oichnus Bromley, 1981	Cambrian–Recent	Circular or subcircular predatory borings in shells; made by gastropods, octopods or unknown predators.	Bromley, 1981, 1993; Nielsen and Nielsen, 2001
Palaeosabella Clarke, 1921	Ordovician–Cretaceous	Unbranched, cylindro-clavate borings.	Clarke, 1921
Petroxestes Wilson and Palmer, 1988	Ordovician–Miocene	Shallow to deep boring with elongate outline and rounded base.	Wilson and Palmer, 1988; Pickerill et al., 2001
Podichnus Bromley and Surlyk, 1973	Carboniferous–Recent	Pedicle etchings of articulate brachiopods comprising a circular cluster of small holes increasing in size and obliqueness outwards.	Bromley and Surlyk, 1973; Michalík, 1977; Vogel et al., 1987; Alexander, 1994
Radulichnus Voigt, 1977	Jurassic–Recent	Parallel sets of straight to curved scrape marks forming scoop-like depressions. Incipient examples at the present-day represent gnawing traces made by the radulae of chitons and gastropods.	Voigt, 1977; Kase et al., 1998
Ramosulcichnus Hillmer and Schulz, 1973	Cretaceous	'Worm' borings in belemnites.	Hillmer and Schulz, 1973
Rogerella Saint-Seine, 1951	Devonian–Recent	Pouch-shaped borings produced at the present day by acrothoracican barnacles. Other names applied to acrothoracican borings are *Brachyzapfes*, *Simonizapfes* and *Zapfella*.	Lambers and Boekschoten, 1986; Baird et al., 1990; Abletz, 1993
Ropalonaria Ulrich, 1879	Ordovician–Cretaceous	Ramifying tunnels with periodic expansions and openings to the surface putatively made by ctenostome bryozoans. Various other ctenostome borings have been named, some as trace fossils but others as body fossils, including *Iramena*, *Orbignyopora*, *Penetrantia*, *Pennatichnus*, and *Pinaceocladichnus*. The total range of ctenostome borings is Ordovician–Recent.	Pohowsky, 1978; Vogel et al., 1987; Smyth, 1988; Mayoral, 1988b, 1991
Spirichnus Fürsich et al., 1994	Jurassic	Cylindrical spiral borings (0.5 mm wide) branching at irregular intervals.	Fürsich et al., 1994
Talpina von Hagenow, 1840	Devonian–Recent	Narrow curved, branching tunnels connected to the surface by apertures. Attributed to colonial species of phoronid worms.	Voigt, 1975; Bromley and D'Alessandro, 1987; Abletz, 1994; Fürsich et al., 1994
Teredolites Leymerie, 1842	Jurassic–Recent	Tubular, clavate borings in wood, sometimes with calcareous linings. Some contain the shells of the trace-making bivalve.	Bromley et al., 1984; Kelly and Bromley, 1984; Savrda et al., 1993; Savrda and Smith, 1996; Evans, 1999
Tremichnus	Ordovician–Jurassic	Circular to elliptical parabolic embedment pits in crinoid columnals, commonly with associated swelling of the stem.	Brett, 1985; Feldman and Brett, 1998
Trypanites Mägdefrau, 1932	Cambrian–Recent	Cylindrical, unbranched boring; length up to 50 times width. Some Ordovician examples described by Kobluk and Nemcsok (1982) contain scolecodonts suggesting that the borings were made by polychaete worms.	Bromley, 1972; Kobluk et al., 1978; Kobluk and Nemcsok, 1982; Kelly and Bromley, 1984; Cole and Palmer, 1999
Vermiforichnus Cameron, 1969	Devonian–Jurassic	Arcuate to sinuous cylindrical borings with protuberances where direction changes; senior synonym of *Cunctichnus*.	Cameron, 1969; Sando, 1984; Lescinsky, 1995; Plewes, 1996

encrusters are effectively bonded permanently to their substratum (and typically remain attached in fossil material), others may fall off before (e.g., Igic, 1984) or after burial and fossilisation (e.g., Walker, 2001, p. 144). Such loss of encrusters must be borne in mind when undertaking palaeoecological studies of hard substrates. Many invertebrate phyla include encrusting species with mineralised skeletons. These are summarised in Table 1. Traces of soft-bodied encrusters are occasionally preserved in the fossil record through the processes of bioimmuration (overgrowth) and epibiont shadowing (Section 8.5).

Non-encrusting organisms can be cemented to hard substrates in the same way as encrusters, as in some scleractinian cup corals which have a small basal attachment supporting a predominantly erect growth (e.g., Hillmer and Scholz, 1991). Alternatively, they may be organically attached using specific structures, e.g., many bivalves are anchored by the byssus and brachiopods by the pedicle. Mussels have byssal threads with sticky tips containing adhesive proteins known as '*Mytilus* foot proteins' (Floriolli et al., 2000). Organically attached forms are prone to dropping-off the substrate during fossilisation but occasionally leave trace fossils indicating their former presence, notably *Podichnus* produced by brachiopod pedicles (Bromley and Surlyk, 1973). Instances of organically attached animals being fossilised more-or-less in life position have also been recorded (e.g., Richards, 1972; Walker and Diehl, 1985; Harland and Pickerill, 1987; Hattin and Hirt, 1986; Harper and Pickerill, 1996; Peters and Bork, 1998). Cemented holdfasts anchor many echinoderms, arborescent bryozoans and octocorals to hard substrates; some are provided with diverging root-like prolongations, others having a more simple dimple- or volcano-shape after loss of the erect parts (e.g., Franzén, 1977; Palmer and Palmer, 1977; Brett, 1981; Zítt and Nekvasilová, 1993). There are also numerous instances of organisms which initially cement to small substrates and rapidly outgrow these substrates, as in the case of some corals (Scrutton, 1998) serpulid worms (Savazzi, 1999c) and bryozoans (Rosso, 1996) that adopt free-living or free-lying ecologies.

Boring organisms inhabiting holes in hard substrates are sedentary but not always strictly sessile in that many are able to move about freely within their borings. As noted below, boring is accomplished by secretion of low pH chemicals and/or mechanical rasping. The hole left by the boring organism is an ichnofossil, although in some groups (e.g., clionid sponges, ctenostome bryozoans) where the borer remains stationary within this hole, the boring so exactly moulds the external shape of the organism that it has been treated as a body fossil (e.g., Pohowsky, 1978). In some cases, a body fossil of the boring organism is present within the ichnofossil, especially bivalve shells preserved in the boring *Gastrochaenolites*. Radtke et al. (1997) provided a comprehensive bibliographical overview of borers and bioerosion, while Vermeij (1987, Table 5.2) tabulated the taxonomy and geological ranges of mobile rock boring animals. Table 2 summarises the main ichnogenera of macroscopic borers that have been named (see also

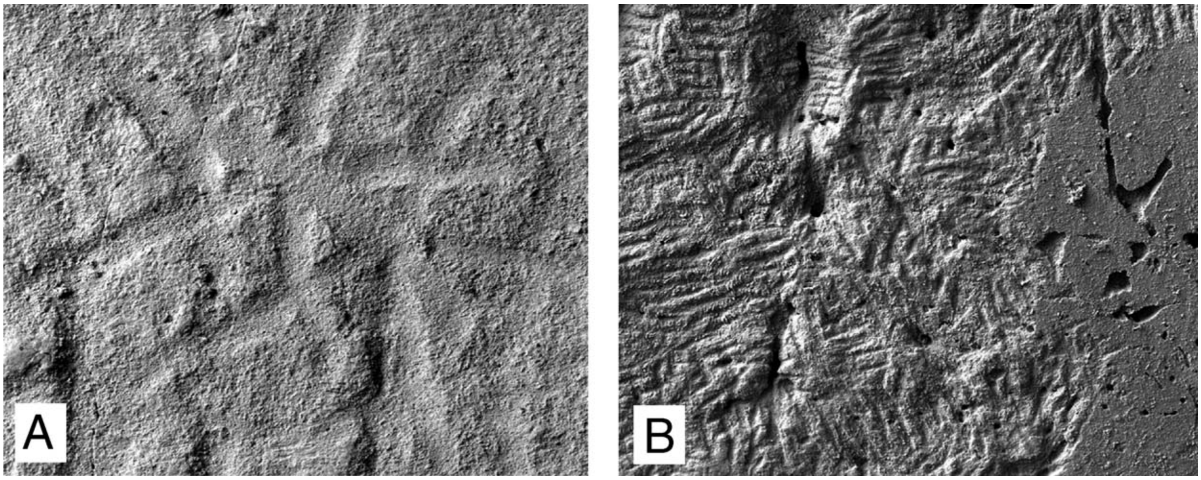


Fig. 5. Scanning electron micrographs of fossil grazing traces. (A) *Gnathichnus*, a superimposed complex of stellate traces inferred to have been made by the radula of an echinoid on a brachiopod shell; × 24; Jurassic, Bathonian, White Limestone Fm., Daglingworth, Gloucestershire, England. (B) *Radulichnus*, parallel scratches inferred to have been made by the radula of a gastropod or chiton on a bivalve shell; note ungrazed but bored area of shell on the right; × 45; Pliocene, Waccamaw Formation, Shallotte, near Wilmington, NC, USA.

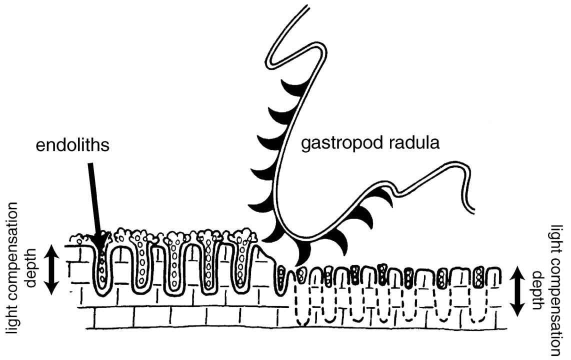


Fig. 6. Bioerosion of a carbonate substrate resulting from a combination of boring by endoliths and grazing by a molluscan radula. After Schneider and Torunski (1983).

Perry and Bertling, 2000, Table 1). Related to borings are embedment fossils where the growth of a host skeleton is distorted by the presence of another organism (e.g., Radwanski and Baluk, 1997).

A third major component of hard substrate communities is vagile (mobile) animals. These include permanent residents that cling to and move across the surface of the substrate (e.g., chitons), and temporary visitors such as fishes. Direct evidence for the presence of these animals in fossil communities is poor compared to encrusters and borers, although some vagile animals leave trace fossils on the surfaces of hard substrates, notably the ichnogenera *Gnathichnus* (Bromley, 1975; Figs. 2E and 5A) and *Radulichnus* (Voigt, 1977; Fig. 5B) produced, respectively, by the grazing activities of echinoids and molluscs (chitons and gastropods; Fig. 6), and homing scars of gastropods (Bongrain, 1995). The combination of grazing and boring can be a potent bioerosional force accounting for the destruction of significant volumes of hard substrates (Fig. 7). Body fossils of vagile animals can sometimes be found loose in the sediments associated with hard substrates, together with those of organically attached members of the hard substrate community (e.g., Johnson and Ledesma-Vázquez, 1999).

Communities of animals and plants living attached to hard substrates in the sea are often referred to as fouling (or biofouling) communities (see Wahl, 1989). Most fouling organisms colonise hard substrates via a free-living juvenile or larval stage which develops into the sessile adult through metamorphosis. Larval settlement on hard substrates should be distinguished from recruitment, a term used to describe only those individuals surviving metamorphosis, i.e., settling larvae minus individuals suffering early mortality. Clustering or aggregation of organisms recruited to hard substrates is often observed in the Recent and in the fossil record (Section 8). Aggregation is a pattern which can be produced by a variety of different processes, including differential early mortality of those individuals settling more distantly from others, variations in the surface topography of the substratum which attract larvae to particular areas, limited substrate availability, and active selection by larvae of sites close to adults of the same species. The last of these processes is referred to as gregarious behaviour, a term frequently misused in the palaeontological literature for aggregation arising from any process. Aggregation plays a key role in the formation of certain types of reefs founded on hard substrates (e.g., Bosence, 1979b).

Living space is often at a premium in hard substrate communities and represents the limiting resource for population growth in many species. Active competition for space commonly results in the overgrowth of one individual by another (Section 6.2). Fossil hard substrate assemblages reveal skeletal overgrowths, some of which may be due to competition between two living individuals, but others to a living individual growing over the surface of a dead individual. Overgrowths are of two main types: (1) lateral overgrowth occurs when two individuals contact each others' edges as they grow across the

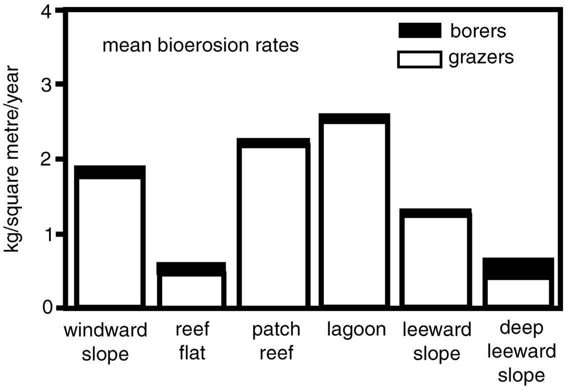


Fig. 7. Mean bioerosional rates by borers and grazers in different environments at Lizard Island on the Great Barrier Reef, Australia. After Kiene and Hutchings (1994).

substratum; (2) fouling overgrowth results from the settlement of the larva of one individual on the surface of an another, previously established individual. It may be difficult to distinguish these two types of overgrowth in fossils if the exact point of origin of the overgrowing individual cannot be ascertained, e.g., when the material being studied consists of a section which is unlikely to intersect the precise origin of the overgrowing encruster. Overgrowth may cause the death (mortality) of the overgrown organism or may be non-fatal. For example, overgrowth of the exoskeletal tube of a serpulid worm need not cause death of the worm if the aperture remains open to allow continued access by the tentacle crown of the worm to the water column, and the bases of erect organisms are sometimes overgrown with no obvious detrimental effects on the erect parts (e.g., Fletcher and Day, 1983). Survival in these circumstances is sometimes referred to by marine biologists as epizooism. Colonial animals typically exhibit partial mortality—death of some individuals (zooids) in the colony but survival of the colony as a whole. Incomplete overgrowth of a colony is a common cause of partial mortality.

Stratigraphic principles (e.g., Choi, 1984; Gibson, 1992) can be applied to the analysis of spatial relationships and short-term ecological succession among encrusters and borers, particularly as seen in vertical sections through hard substrate assemblages. The principle of superposition means that encrusters at the bottom of the pile (i.e., close to the substratum) are older than those above them. Vertically oriented thin sections are often used to reveal superposition sequences (e.g., Hölder, 1972; Taberner and Bosence, 1985). The caveat to this method is that underlying encrusters, especially colonial animals, may have continued to live at the substratum surface elsewhere (off the plane of section) and can therefore be partly contemporaneous with overlying encrusters. Consequently, it is more accurate to state that overlying encrusters cannot be older than those beneath (unless undercutting and encrustation of cavity roofs has occurred). Continuing the stratigraphical analogy for borers, these are equivalent to igneous intrusions in that they crosscut the sequence of encrusters. An important difference, however, is that intrusions are normally emplaced from beneath whereas borings tend to penetrate from above, having entered the substrate from the exterior. Nevertheless, the relative chronology of encrusters and borers can be easily determined using the principles applied in geology, e.g., a borer cutting encruster A but covered by encruster B must postdate encruster A but antedate encruster B. Good examples of such relationships between borers and encrusters can be found in Hölder (1972) and Wilson et al. (1998a,b). Sometimes alternating layers of individuals belonging to two different encrusting species resemble cyclic sedimentary strata and prove contemporaneity between the species concerned which lived in symbiosis (e.g., Powell, 1991).

4. Terminology

A large number of terms have been used to categorise organisms colonising hard substrates, some

Table 3
Terminology for organisms colonising hard substrates

Substrate	Colonist					
	Animal (sclerozoan)		Plant (sclerophyte)		Any organism (sclerobiont)	
Rock	lithozoan	epilithozoan endolithozoan	lithophyte	epilithophyte endolithophyte	lithobiont	epilithobiont endolithobiont
Wood	xylozoan	epixylozoan endoxylozoan	xylophyte	epixylophyte endoxylophyte	xylobiont	epixylobiont endoxylobiont
Plant	phytozoan	epiphytozoan endophytozoan	phytophyte	epiphytophyte endophytophyte	phytobiont	epiphytobiont endophytobiont
Animal (living)	zoozoan	epizoozoan endozoozoan	zoophyte	epizoophyte endozoophyte	zoobiont	epizoobiont endozoobiont
Any organic hard part (dead or alive)	skeletozoan	episkeletozoan endoskeletozoan	skeletophyte	episkeletophyte endoskeletophyte	skeletobiont	episkeletobiont endoskeletobiont

See text for explanation of how the terms are derived.

depending on the type of substrate colonised (e.g., animal, plant, rock), others describing the spatial location of colonist on or in the substrate, and yet others alluding to whether the colonist is an animal or a plant. With such a plethora of possibilities (see West, 1977; Walker and Miller, 1992), including plurals, adverbs and terms which refer collectively to two or more of the categories, it is hardly surprising that considerable inconsistency of usage has developed, particularly between palaeontologists and neontologists. The terms in common use tend to be compounds of two roots, as in 'epizoan' in which 'epi-' refers to the position (surface) and '-zoan' to the type of organism (animal). Even with such a straightforward term as this, however, there is potential for confusion because the '-zoan' part of the name could signify that either the colonising organism or the substrate it colonises is an animal. Nomenclatorial confusion is often traceable to such subject vs. object inconsistencies.

For the purpose of this review, a set of terms (Table 3), first proposed by Taylor and Wilson (2002), is applied as far as possible. Each of the terms consists of a compound derived from two or three roots, the last always referring to the identity of the colonising organism (i.e., animal = 'zoan', plant = 'phyte', or either = 'biont'). Preceding this is a root derived from the type of substrate: rock = 'litho', wood = 'xylo', living plant = 'phyto', living animal = 'zoo', and any organic hardpart of unknown or uncertain status, living or dead = 'skeleto'. A prefix can be added to indicate the spatial location of the colonist, either on the surface ('epi') or within the substrate ('endo'). A new collective term—*sclerobiont*—is coined for all organisms inhabiting any kind of hard substrate. The term encompasses encrusters adpressed closely to the surface of the substrate, sessile organisms which are cemented or organically anchored to the substrate surface but grow away from it into the water column, borers which enter the substrate from its perimeter and penetrate to various depths within, and vagile organisms living on or habitually visiting the surface of the hard substrate. *Sclerozoans* are animal sclerobionts, and *sclerophytes* plant sclerobionts.

Certain terms commonly encountered in the literature on hard substrates deserve comment. *Epizoan* is generally used by neontologists, along with the synonymous epizoite (e.g., Hughes, 1979), for organisms (animal or plant) attached to a living host animal, a habit referred to as 'epizooism'. Palaeontologists have, however, often designated as epizoans organisms attached to demonstrably dead animal substrates, to plant substrates (e.g., Brasier, 1975; De Burgh and Fankboner, 1979; Ivany et al., 1990), or even to inorganic substrates (e.g., Baird, 1981). The term *epizoobiont* here replaces epizoan. *Epiphyte* is the plant equivalent of epizoan for any organism using a plant as its substrate. It has been used in marine settings for organisms encrusting kelp or seagrasses, and in terrestrial environments for ferns, orchids etc growing on the branches of living trees. Even if the host plant is not preserved, fossil marine epiphytes are occasionally recognisable by the impression (substratum bioimmuration, see Section 8.5) of the host plant on their attachment surfaces. Misuse of the term epiphyte includes application of '-phyte' to the colonising organism rather than the substrate (e.g., Ghosh, 1997). The term *epiphytobiont* here replaces epiphyte.

Walker and Miller (1992) used the term *epibiont* for organisms, respectively, fouling the surface of organic substrates and *endobiont* for organisms boring into organic substrates, regardless of whether the substrate was dead or alive at the time of colonisation. These terms remain useful as long as it is appreciated that they are object-based, 'biont' in this case referring not to the coloniser but to the substrate (cf., for example, Gutt and Schikan, 1998). However, it should be noted that marine biologists (e.g., Wahl, 1989) typically restrict the term epibiont to organisms attached to surfaces of living hosts. *Cryptobiont* is a positional term describing organisms colonising hidden surfaces such as concave undersides of bivalve shells or cavities in rocks and reefs. Assemblages of cryptobionts have been referred to as 'cryptos' (e.g., Wood et al., 1996). *Coelobiont* is used almost synonymously with cryptobiont (e.g., Kobluk, 1981a). *Basibiont* is occasionally used to describe a living substratum hosting a fouling community (e.g., Wahl, 1989; Laudien and Wahl, 1999).

Symbiosis is a term for any permanent or semi-permanent association between two individuals of different species. Because many sclerobionts are sessile, they are prone to forming symbioses with other sclerobionts that colonise the same substratum, as well as with the host substrate if this is a living animal or plant. Symbioses can be subdivided into three types according to the relative effects of the symbionts on one another: (1) *parasitism* is when one symbiont benefits (often trophically) by living in association but the other loses; (2) *mutualism* is when both symbionts benefit; and (3) *commensalism* is when one benefits but the other incurs neither a loss nor a benefit. Biologists measure benefits and losses in terms of either fecundity (reproductive output) or relative population growth when the symbionts are in and out of association. Neither of these measures is available to palaeontologists working on fossil symbioses. Consequently, as discussed by Darrell and Taylor (1993), when describing fossil symbioses the terms parasitism, mutualism and especially commensalism should be used with extreme caution or avoided altogether. The fossil record can provide good evidence on the antiquity and longevity of symbioses (e.g., Darrell and Taylor, 1993, for corals; Savazzi, 2001, for bivalves), as well as *specificity* and *obligacy*, but not on their overall beneficial or detrimental effects. Specificity refers to the identity of the taxa involved, with a species specific association indicating that only one species is colonised by the symbiont, and obligacy to whether the species concerned is found in symbiosis exclusively (obligate), preferentially (facultative) or only occasionally (incidental). Wahl and Mark (1999) concluded that most marine zoobiotic and phytobiotic relationships were non-obligatory and non-specific. Some symbioses involve a host species transporting the other symbiont, a phenomenon called *phoresis* (e.g., Lawn, 2002).

5. Communities on biotic substrates

5.1. Phytobiota

Macroalgae and seagrasses (marine angiosperms) today often support diverse phytobiotic (‘epiphytic’) communities of animals and plants. Some members of these communities possess mineralised—and consequently fossilisable—skeletons. Nevertheless, phytobiotic assemblages are seldom recognised in the fossil record. This can be explained by the typical nonfossilisation of the plant substratum (e.g., Brasier, 1975) which not only means that the nature of the original substratum must be inferred but also that the phytobionts lose their support and are prone to transport and destruction. Adaptations of the phytobionts themselves for coping with the hazard of breaking when the plant substratum flexes include weak or incomplete mineralisation (e.g., Hayward, 1980), further diminishing their fossilisation potential. Conversely, other adaptations of phytobionts may have potential utility in recognising their identity as epiphytes, e.g., bryozoans with frontal tubercles (Voigt, 1993a) and basal stilts (Voigt, 1993b). The skeletons of phytobionts found on beached drifts of floating *Sargassum* contribute significant amounts of carbonate sediment to shoreline deposits in Bermuda (Pestana, 1985). There is good reason to believe that careful study of some ancient beach deposits may reveal fossils of phytobiotic species. Attachment to floating algae is potentially important in the dispersal of phytobionts at the present day (Highsmith, 1985) and was likely so in the geological past.

Although we are unaware of any studies of ancient phytobiont assemblages of fleshy macroalgae, a brief mention of research on modern communities is included here to illustrate some more general points about encrusters and their relationships to living substrates. Seed and O’Conner (1981) have thoroughly reviewed the ecology of macroalgal phytobionts. These communities are more common in the low intertidal and shallow subtidal than they are in the high intertidal, their diversity tends to be higher on brown algae (e.g., *Fucus*, *Macrocystis*, *Sargassum*) and red algae (e.g., *Solieria*, *Bryothamnion*) than on green algae (Hayward, 1980; Winston and Eiseman, 1980), and phytobiont abundance is greatest in regions of high water flow and turbulence but low silt loading. Microhabitat differentiation can be evident on individual algal fronds (Hayward, 1980), with some species of phytobionts recruiting preferentially in troughs or on concave surfaces. Furthermore, zonation of phytobionts along the length of the frond is common, paralleling gradients in frond flexibility, ambient current velocity and age of the frond surface. Brumbaugh et al. (1994) showed that preferential recruitment of the bryozoan *Membranipora membranacea* to the younger, proximal part of kelp fronds was apparently cued by the relatively undamaged condition of the algal tissues in this region. Because distal parts of fronds are constantly lost by erosion, colonies recruiting in proximal areas could reach an ultimate size three orders of magnitude greater than distal recruits. Low levels of specificity by macrofauna for particular algal species were found in an Arctic fiord by Lippert et al. (2001).

Competition for space can result in complex networks (Seed and O'Conner, 1981; Fig. 2). Various types of interaction are possible between phytobionts and their macroalgal host substrates. Photosynthetic activity of the alga may be depressed by the presence of phytobionts (Oswald et al., 1984; Cancino et al., 1987), frond deterioration accelerated (Dixon et al., 1981), and fronds damaged by fish and echinoid preying on the phytobionts (Bernstein and Jung, 1979; Scheibling et al., 1999). In addition to using macroalgae as substrates for attachment, some phytobionts have been shown to take up organic carbon from their hosts, suggesting a trophic interaction (De Burgh and Fankboner, 1979).

Phytobiotic communities of high diversity (e.g., Borowitzka et al., 1990) often develop on modern seagrasses. Some of these phytobionts have been shown to influence the growth of their host significantly. For example, encrustation by the bryozoan *Calpensia* causes rhizomes of the Mediterranean seagrass *Posidonia* to grow faster and higher above the sediment while weakening them and potentially increasing the probability of breakage (Romero Colmenero and Sánchez Lizaso, 1999). Foraminifera living on seagrass in Western Australia show microzonation along the leaves, with some species being aggregated close to serpulid worm tubes (Semeniuk, 2000).

Fossilised seagrasses from the Eocene of Florida are encrusted by the polychaete worm *Spirorbis* together with foraminiferans, barnacles and bryozoans (Ivany et al., 1990). Silicified stems and roots of seagrasses in the Maastrichtian of the Netherlands—among the oldest examples of seagrasses in the fossil record (den Hartog, 1970)—support a biota dominated by bryozoans (Voigt, 1981). Although the leaves are never silicified, unequivocal evidence of encrustation of leaves is present in the form of substratum bioimmurations (Taylor, 1990)—impressions of the venation patterns of the leaves are preserved as natural moulds on the undersides of the phytobionts. Other examples of seagrass phytobionts identified entirely from the existence of bioimmured impressions come from the Neogene of central America (Cheetham and Jackson, 1996) and the Eocene of the Paris Basin (Taylor and Todd, 2001). Langer (1993) described similar patterns on the undersides of Recent foraminiferans adhering to seagrasses.

A good example of fossil phytobionts preserved in situ on their plant substrates has been described by Kelber (1987) from the German Triassic. Here, terrestrial plants in a non-marine setting are encrusted by small coiled worm tubes attributed to *Spirorbis*.

Calcareous algae include two groups of rhodophytes—solenoporaceans and corallinaceans—with extensive fossil records. Examples of phytobionts associated with these algae at the present day include diatoms and foraminiferans (Freiwald, 1993). Rhodoliths (sometimes called "maërl") are free-living structures formed by non-geniculate coralline algae (see Foster, 2001, which is an excellent recent review). Rhodoliths are often found in thick beds, and they are distributed through a variety of shallow marine environments, including tropical, temperate and even polar. Some rhodoliths are made completely of coralline algae, whereas others nucleated on hard objects, such as broken pieces of coral, shells, pebbles, or fragments of other rhodoliths (Freiwald and Henrich, 1994), enveloping the substrate as they grew (e.g., Akpan and Farrow, 1984, pl. 1). Often more than one species of algae forms the rhodolith framework. Rhodoliths and rhodolith-like forms have a long fossil record, going back as far as the Cambrian (Copper, 1994), although they are uncommon before the Cenozoic when coralline algae rose in importance. They are useful for palaeoenvironmental interpretations because their shapes can be related to hydraulic energy (Bosence, 1983), with the caveat that other environmental factors may be involved (Marrack, 1999). The slow, laminar growth of rhodoliths makes them potentially valuable isotopic recorders of climate change over time (Frantz et al., 2000).

Microbes of various types can form elevated features on hard substrates, especially extensive rockgrounds and hardgrounds. Stromatolites are microbial structures (microbialites) with internal laminations; thrombolites are microbial masses with clotted internal textures (Aitken, 1967; see also Riding, 1999; Shapiro, 2002). Stromatolites were especially common on the exposed upper surfaces of intertidal and subtidal rockgrounds in the Precambrian, extending back to 3.3–3.5 billion years ago (Byerly et al., 1986). The bacterial mats which formed stromatolites flourished in the Precambrian, apparently because of a combination of distinctive physical conditions (Melezhik et al., 1997) and a lack of grazers (Seilacher, 1999). Stromatolites today are found only in highly restricted environments, such as hypersaline bays (Seilacher, 1999). Thrombolites range from the Neoproterozoic (Aitken and Narbonne, 1989) to the Recent (Moore et al., 1984). They were common in the Cambrian and Ordovician (Kennard and James, 1986) and the Devonian (Shapiro, 2002), but rarer though present in every other Phanerozoic system. Thrombolites have a much more varied environmental distribution than stromatolites, being found in cryptic spaces such as cavity walls (e.g., Taylor and Palmer, 1994) as well as on exposed surfaces (Riding, 2000). Phosphatic microbial mats originally attributed a bryozoan origin have been described from the Ordovician by Niedermeyer and Langbein (1989). Microbial buildups commonly incorporate metazoans which contribute to the overall structure (e.g., Crowley and Zenger, 1975; Pisera, 1996).

5.2. Xylobiota

Wood occurs in marine environments as terrestrially derived logs transported out to sea and as in situ mangroves. Both types may be colonised by encrusting and boring xylobionts. In the case of transported logs, colonisation can occur when the wood is floating or after it has become waterlogged and sunk to the seabed. It is also possible for colonisation of xylic substrates to occur after burial and re-exposure prior to coalification of incipient coal seams (Bromley et al., 1984).

The most spectacular examples in the fossil record of colonisation of floating wood are provided by *Pentacrinus* from the Lower Jurassic. Aggregations of this pseudoplanktonic crinoid are inferred by Simms (1986) to have hung down from large pieces of floating driftwood, although Brett et al. (1997) have argued that the occurrence of multiple generations of crinoids points to colonisation of sunken logs on the sea floor.

Two groups of pholadacean bivalves—teredinids (‘shipworms’) and pholadids (‘piddocks’)—are well known for boring into wood in Mesozoic–Recent marine environments (Fig. 2G). Boring may be exclusively for the purpose of creating a protected domicile for the suspension feeding bivalve, or to obtain nutrition through digestion of the cellulose (see Turner and Johnson, 1971). Calcite linings are often present in teredinid borings (Savrda and Smith, 1996) and sometimes these are all that remains in fossil material after taphonomic decay of the wood substrate and loss of the aragonitic shells (Evans, 1999).

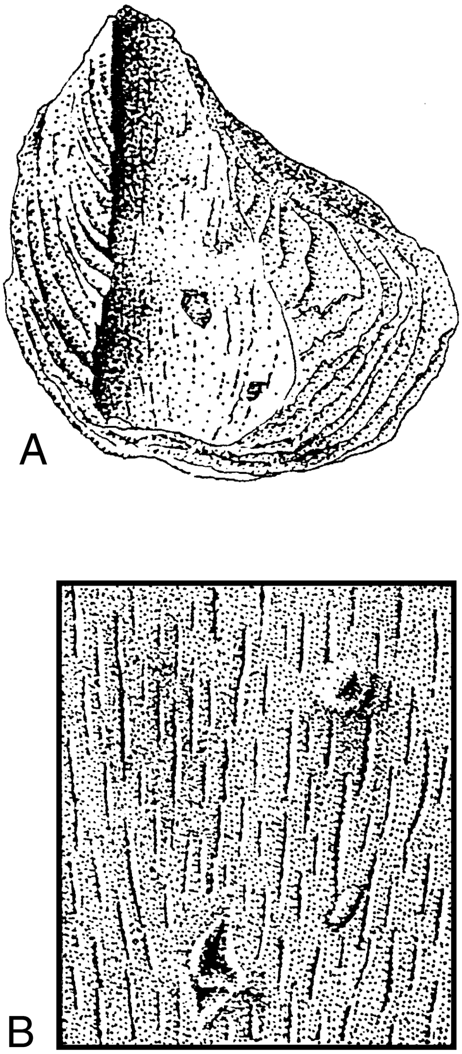


Fig. 8. Mould bioimmurations of mangroves on the attachment areas of oysters. (A) Concave attachment area of the French Eocene oyster *Ostrea uncifera*. (B) Detail of mangrove root impression on the attachment area of a Recent mangrove oyster from New Caledonia. After Plaziat (1970).

Oysters sometimes foul wood (Fig. 2F), especially mangrove wood. Fossil and subfossil examples of mangrove oysters have been recognised in the fossil record in the absence of the mangrove themselves by the natural moulds (substratum bioimmurations) of the wood preserved on the attachment areas of the oysters (Plaziat, 1970; Kendrick and Morse, 1990; Fig. 8).

5.3. Zoobiota

The term zoobiont, equivalent to epizoan plus endozoan as used by previous authors, here refers to animals and plants which colonise living animals. In the context of the fossil record, zoobionts are invariably associated with hosts possessing exoskeletons. An important problem when dealing with these fossils is how to determine whether the host was alive or dead at the time of colonisation. Criteria for distinguishing between living and post-mortem colonisation are discussed below (Section 5.4). However, it is clear that in many fossils this issue will be unresolvable or at the very least contentious. For these cases, the more neutral term skeletobiont, applicable to encrusters and borers colonising any organic hard substrate, animal or plant, dead or alive, should be used.

Present-day zoobionts are known in association with a wide range of marine animal hosts. Those attached to unmineralised parts of host animals, such as sea snakes and whales (see Key et al., 1995 and references therein), are of less direct palaeontological relevance and will not be considered further. Among marine vertebrates, modern turtle carapaces often host a range of zoobionts, including algae, hydrozoans, bivalves, barnacles and tunicates (e.g., Frazier et al., 1992). However, loss of the epidermal scutes to which the zoobionts are attached would jeopardise any potential fossil record of in situ turtle zoobionts (encrusting oysters and echinoid grazing traces (*Gnaathichnus*) have been recorded as post-mortem associates on Jurassic turtle carapaces by Meyer, 1994). Ephemeral substrates, including tunicates, sponges and octocorals, support rich and diverse assemblages of zoobiotic bryozoans off southern Australia (Hageman et al., 2000). Such substrates do not usually survive into the fossil record but the basal attachment structures of the bryozoans involved may provide diagnostic evidence of their former presence.

The extent to which modern animals ‘tolerate’ or are able to rid themselves of zoobionts and phytobionts varies. Some host animals produce bioactive chemicals—antifouling substances—to prevent or discourage fouling (e.g., Thompson, 1985), whereas others are able to shed outer layers of their body tissue in order to rid themselves of fouling organisms (e.g., Barthel and Wolfrath, 1989; Winston and Håkansson, 1989) or react by proliferating skeletal tissue to embed the fouler. Colonisation by zoobionts and phytobionts, however, is not always disadvantageous to the host (Wahl, 1989) and in some instances their presence is actively encouraged by host behaviour (e.g., decorator crabs) or morphology (e.g., the bivalve *Spondylus*, see Section 5.3.2). Here, the presence of a fouling community may function in defence of the host against predators. From a palaeontological perspective, such beneficial interactions serve to underscore the danger of concluding that zoobionts are necessarily a burden to the living host and therefore parasitic.

5.3.1. Brachiopod-hosted communities

Zoobionts on living brachiopods have been studied from several modern environments and provide important evidence for the interpretation of the encrusters and borers which can be extremely common on fossil brachiopods (see Section 5.4.4). Among inarticulate brachiopods, *Lingula* may be colonised by a zoobiotic community of barnacles, algae, anemones, bryozoans and polychaetes (Hammond, 1984). Almost all of these are located at the anterior end of the shell, the only site readily available for settlement in this infaunal brachiopod, and occur equally on

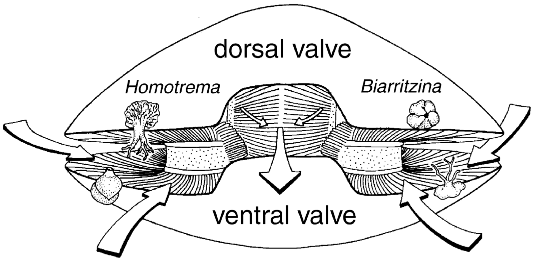


Fig. 9. Relationship between the distribution of attached foraminiferans and feeding currents of the Recent brachiopod *Tichosina floridensis* Cooper from Florida. After Zumwalt and Delaca (1980).

dorsal and ventral valves. Tubes of the worm *Polydora* open adjacent to the inhalant setal funnel of the host *Lingula* in a position where poaching of the brachiopod's food is a possibility. Damage to and distortion of the anterior commissure, potentially recognisable in fossils, was observed in two thirds of the colonised *Lingula* shells studied by Hammond (1984).

Articulate brachiopods are more commonly cited as hosts for zoobionts (e.g., d'Hondt, 1984; Fagerstrom, 1996). Mapping of seven species of foraminiferans encrusting the Floridian brachiopod *Tichsina floridensis* by Zumwalt and Delaca (1980) revealed a concentration close to the commissure but statistically indistinguishable numbers in the inhalant and exhalent areas of the host (Fig. 9). Consequently, although feeding by the foraminiferans may benefit from increased current velocities and particle flux near the brachiopod commissure, there is no evidence of food poaching. Barnes and Clarke (1995) have described mainly sponges, bryozoans and polychaetes encrusting the Antarctic brachiopod *Liothyrella uva*. The area covered by these zoobionts increased from less than 20% on the smallest to more than 50% on the largest hosts, and species richness also increased with brachiopod size, while the average area of shell encrusted decreased slightly with depth of collection. These high coverage values were attributed to the long lifespan of the host brachiopods. Some evidence was found of encrusting bryozoans growing across the commissure, blocking feeding, and apparently causing brachiopod mortality.

5.3.2. Mollusc-hosted communities

The shells of living epifaunal molluscs form important substrates for many zoobionts. The diversity and density of these 'molluscobiotic communities' varies according to host species and environment. Among bivalves, oysters and scallops are particularly prone to biofouling, and this can be a major problem for commercial shellfisheries (e.g., Korringa, 1954; Igic, 1972; Thangavelu and Sanjeevaraj, 1988), especially through the shell weakening effects of boring sponges and spionid polychaetes. While the periostracum of the mollusc shell is known or believed to deter fouling in some species (Bottjer, 1981), damage to this often thin organic covering is common and may account for the existence, for example, of heavily fouled individuals of the gastropod *Astraea heliotropium* on the Otago Shelf, New Zealand (PDT, personal observation). As with other sclerobiotic communities (see Section 6.1), nutrient levels have been hypothesised to play an important role in determining the degree of fouling of living molluscs (Voight and Walker, 1995).

Research on zoobiotic communities colonising bivalve shells has provided insights into the effects fouling organisms can have on living hosts. Observations of in situ *Mytilus edulis* showed that unfouled shells were preferred as prey by the starfish *Asterias rubens*, with shells fouled by hydrozoans and algae better protected against predators than barnacle-fouled shells (Laudien and Wahl, 1999). Conversely, zoobionts on mussels (*M. edulis* and *M. californianus*) can increase drag forces and therefore lead to dislodgment and death (Witman and Suchanek, 1984). A dramatic illustration of the effect of frondose algae on living host substrates is the report by González et al. (2001) of the stranding of more than two million individuals of the scallop *Agropecten* on a Chilean beach in March 1999. The stranding took place during a period of strong wave action and was facilitated by the algae which increased the probability of dislodgement. However, such catastrophic effects may only apply to large zoobionts such as kelp and barnacles; zoobionts which do not increase vertical relief appreciably may have no appreciable influence on dislodgement. Another study (Laihonen and Furman, 1986) found that encrustation by barnacles had no significant effect on the growth rate of *M. edulis*. The barnacles themselves, however, grew faster on living than on dead shells, suggesting a commensal relationship with the host mussel.

The Queen Scallop (*Chlamys opercularis*) is encrusted by the sponge *Suberites* in an apparently mutualistic association. Sponge encrustation protects the bivalve from predation by starfish, probably by reducing the adhesion of the tube feet, and the sponge in return is protected from predatory nudibranchs by the mobility of the swimming mollusc (Pond, 1992; see also Bloom, 1975). Another scallop (*Chlamys varia*) is encrusted by a different, much larger sponge (*Halichondria*) which also hinders starfish predation, in this case not only through its effects on tube foot adhesion but also by making the valve margins almost inaccessible beneath the enveloping sponge (Forester, 1979). There is also speculation that sponges encrusting scallops provide additional predator deterrence as a result of their toxicity, while crellid sponge encrustation of *Chlamys asperrima* apparently prevents endolith infestation and allows the scallop to secrete a thinner shell than that found in individuals lacking a sponge covering (Pitcher and Butler, 1987). Survival in natural habitats of sponge-encrusted individuals of *C. asperrima* has been shown to be greater than unencrusted individuals (Chernoff, 1987). Individuals of the Antarctic scallop *Adamussium colbecki* are often encrusted by the hydroid *Hydractinia angusta* which can eat the tube feet and pedicellariae of echinoids grazing algae on the shell surface. The hydroid may thereby limit the damage caused to the shell of its host by grazing (Cerrano et al., 2000).

In the spinose bivalve *Spondylus americanus*, which is preyed upon by gastropods, crustaceans and fishes, Feifarek (1987) presented experimental evidence that the spines alone are not effective against predators but that they encourage shell colonisation by a sponge-dominated zoobiotic community which does provide protection against predators. Enhanced fouling has been reported for a second species of *Spondylus* (*S. regis*), whereas ribbed bivalves show no effect (Jones, 2001). However, naturally rugose shells of another bivalve (*Chama pellucida*) attract a greater coverage of encrusters than do smooth shells of the same species (Vance, 1978). Removal of the dense zoobiotic covering on *C. pellucida* increases predation by *Pisaster giganteus* which is less able to detect encrusted individuals.

Fouling of the periwinkle *Littorina littorea*, particularly by algae, may increase drag on the snail and decrease growth rate, possibly because the snail has to expend more energy holding onto the substrate (Wahl, 1996). Conversely, fouling by the bryozoan *Alcyonidium* of another gastropod, the whelk *Burnupena papyracea*, has a beneficial effect on the host, protecting it from predation by rock lobsters (Barkai and McQuaid, 1988). Cerith gastropod shells from seagrass meadows in Brazil are rarely colonised by zoobionts when empty, whereas shells of living gastropods and shells occupied by hermit crabs are more often colonised, the former usually by oysters and the latter by polychaetes (Creed, 2000). Shells of living molluscs can provide rare hard substrates on muddy seabeds for corals and other sclerobionts (e.g., Nishihira, 2001).

Shells of living *Nautilus* often support zoobiotic communities (Landman et al., 1987), with up to 92% of shells colonised, although the low surface coverage (< 1%) is not thought to present a significant problem for the host cephalopod. Among the commonest encrusters are bryozoans, foraminiferans, serpulids, barnacles and the tubular scyphozoan *Stephanoscyphus*. Whereas bryozoans are the principal zoobionts on *N. belauensis*, serpulids dominate on two other species, *N. pompilius* and *N. scrobiculatus*. The umbilicus appears to be the preferred site of colonisation, possibly because of the high flow into this region of water containing entrained larvae and planktonic food particles when the animal is swimming. The black area and apertural margin are generally free of zoobionts, as might be predicted given the presence of soft tissues here, and the thick periostracum of *N. scrobiculatus* seemingly deters zoobionts. Colonisation of live animals contrasts with that seen in drift shells where density of encrustation may be much greater and distributions more random.

5.3.3. Arthropod-hosted communities

The mobility of most arthropods, together with the periodic shedding of the exoskeleton (ecdysis) and the complexity of the exoskeleton, make zoobiotic communities colonising arthropods of special interest.

As they pass beyond the age of final moulting, horseshoe crabs accumulate "a striking variety of hitchhikers" (Grant, 1998, p. 14), including barnacles, bryozoans, oysters, sponges and serpulid worms. Many of these zoobionts must become submerged in the sediment when the crabs burrow during rest periods, although the barnacles may occupy an elevated position on the crown of the carapace. Several studies—most recently Key et al. (2000) and Patil and Anil (2000)—have found greater encrustation of male than female individuals of the horseshoe crab *Tachypleus gigas*, possibly because females spend more of their time burrowing, including egg laying. Encrusting bryozoans are more common in this species on the dorsal than the ventral surface, and on the prosoma than the opisthosoma. Whereas 77% of *T. gigas* individuals were found by Key et al. (1996) to be bryozoan-encrusted, another horseshoe crab (*Carcinoscorpius rotundicauda*) from Singapore was unfouled, a pattern attributed to the fact that the

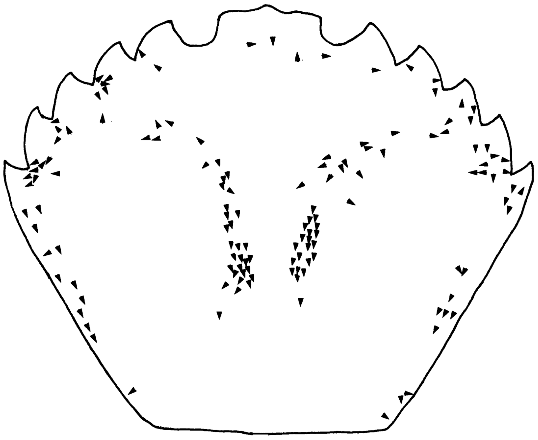


Fig. 10. Orientation of barnacles on the carapace of the Recent crab *Carcinus maenus* from Wales. The cirral nets of the barnacle face predominantly backwards, towards the exhalent respiratory currents of the crab. After Heath (1976).

second species spends more time in brackish waters. A detailed analysis (Dietl et al., 2000) of the zoobionts on *Limulus polyphemus* showed that different taxonomic groups had very different patterns of distribution. This was explained by variations in larval settlement behaviour often influenced by current flow over the crab's body. Few zoobionts were present on smooth-surfaced areas prone to abrasion during movement of the host through sediments. Apertures of the serpulid worm *Filograna* are predominantly oriented posteriorly, facing into a zone of current eddies which may have facilitated their ability to capture food particles.

Populations of true crabs may support diverse communities of zoobionts. For example, Colodey et al. (1980) recorded 53 taxa living on only 7 crabs (*Cancer irroratus*) from the Gulf of St Lawrence. Predictably, newly moulted crabs were less encrusted, and larger individuals hosted greater numbers of zoobionts. The distribution of zoobionts on this crab was determined mostly by the presence or absence of setae: few zoobionts occur in setose areas apparently because these are sites where detritus accumulates. Barnacles encrusting another crab (*Carcinus maenus*) are found only in the grooves and depressions on the

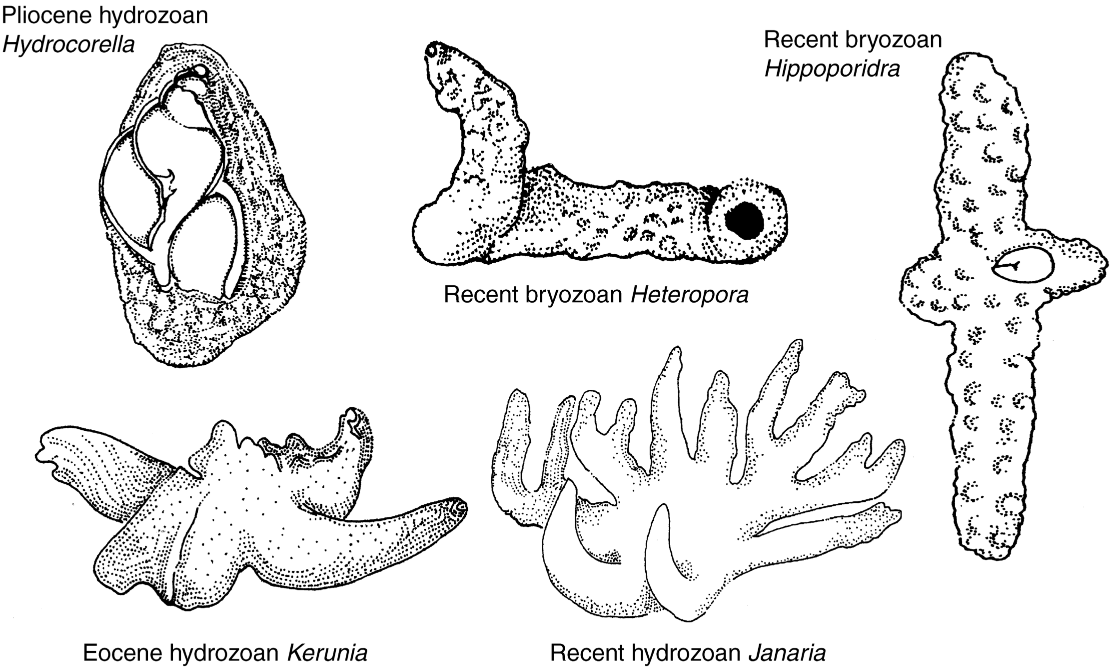


Fig. 11. Massive encrusters on gastropod shells known or inferred to have been occupied by hermit crabs. These colonial bryozoans and hydrozoans completely envelop the shell, sometimes growing long branches (*Kerunia*, *Janaria* and *Hippoporidra*) and extending the helicospiral coiling of the gastropod shell (*Heteropora*). After Walker (1992).

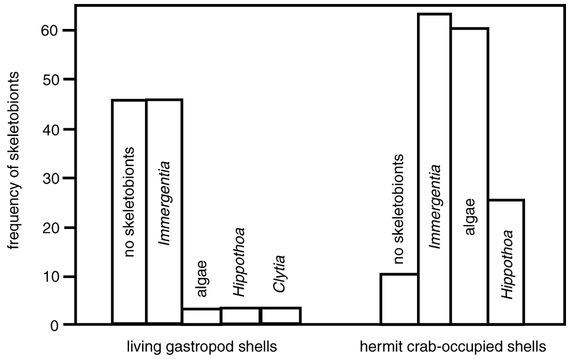


Fig. 12. Differences in skeletobiont colonisation of *Olivella biplicata* shells (25–30 mm size class) containing living gastropods and those occupied by the hermit crab *Pagurus granosimanus*, from Bodega Harbor, California, USA. *Immergentia* is a boring ctenostome bryozoan, *Hippothoa* (more correctly *Celleporella*) an encrusting cheilostome bryozoan, and *Clytia* a hydrozoan. After Walker (1988).

dorsal carapace, sites of preferential larval settlement (Heath, 1976). Non-random orientation of the barnacles is evident, with the cirral nets face predominantly backward towards the flow of exhalent respiratory currents generated by the host crab (Fig. 10). Another study (Cadée, 1991) of zoobionts on the same crab found a strong preference of the bryozoan *Conopeum reticulum* for the cryptic, ventral side of the shell, a weak dorsal preference by the bryozoan *Electra pilosa*, and no preference by barnacles. The presence of zoobionts in the eyes and their sockets may lead to eye loss or overgrowth, both obviously harmful to the host. Key et al. (1996) recorded more foulers on the ventral than dorsal surface in the blue crab (*Callinectes sapidus*), and confirmed the greater fouling of female than male crabs which is probably because female crabs spend a longer time in deeper waters of more fully marine salinity.

Hermit crabs are a group of crustaceans which typically inhabit the shells of dead gastropods but may also be found living a mobile existence in serpulid tubes, scaphopods, and man-made objects, as well as a sessile life in fixed worm tubes (Schuhmacher, 1977; Gherardi, 1996). Because they are unable to maintain tenanted shells in the same way as an animal secreting its own shell, a very different and frequently dense and diverse community of zoobionts may live in association with hermit crabs, some species encrusting the shell surface, some boring into the shell and yet others cohabiting the shell lumen with the hermit crab (e.g., Jensen and Bender, 1973; Stachowitsch, 1980). 'Pagurized' shells occupied by hermit crabs show several characteristic features (Walker, 1988, 1992, 1995). These include massive encrustation (Fig. 11) extending evenly over the external shell surface and into the shell interior, the presence of distinctive zoobionts in the region of the shell aperture, and abrasion marks ('pagurid facets') on the base of the shell caused by dragging along the substratum. Communities colonising hermitted shells may be more diverse than those on vacant shells (Fig. 12). This is because the crabs prevent shells from being buried and hence allow a greater time for the fouling community to develop (Conover, 1979). In some instances, tangible benefits have been demonstrated for both the hermit crabs and its symbionts. For example, the stinging cells of sea anemones and hydroids living on hermitted shells protect the crabs from predatory octopus (e.g., Brooks and Mariscal, 1985), while by living with a hermit crab the anemones and hydroids receive protection from attacks by echinoids and polychaetes (Brooks and Gwaltney, 1993), i.e., the symbiosis is mutualistic. However, another study (Buckley and Ebersole, 1994) showed that the presence of symbiotic hydroids actually increased the vulnerability of hermit crabs to predation by blue crabs. The contrasting results of studies

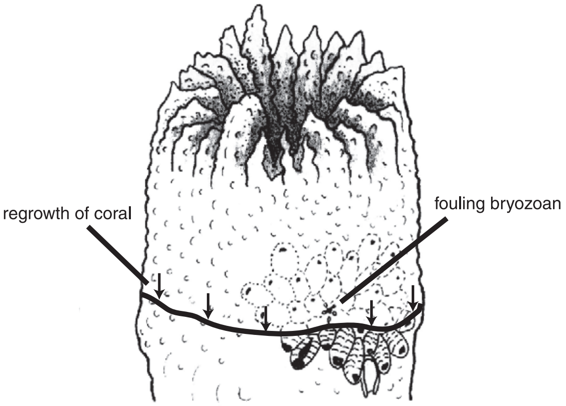


Fig. 13. Overgrowth of bryozoan *Puellina* fouling a corallite of the Recent Mediterranean scleractinian *Hoplangia*, unequivocal evidence that the two were life associates. After Harmelin (1990).

Table 4
Criteria for distinguishing between life and post-mortem skeletobiont colonisation of biotic hard substrates (see also Lescinsky, 1995, Table 1)

Criterion	Inferred condition of host	Reliability	Remarks	Examples
Skeletal intergrowth and interlayering	Living	Absolute	Skeletal intergrowth and interlayering both indicate unequivocally that the host was live at the time of colonisation.	'Caunopores'—intergrowths between stromatoporoids and tabulate corals (Young and Noble, 1989); fouling barnacles overgrown by gastropods (Boekschoten, 1967); cornultids and gastropods (Morris and Felton, 1993); solitary scleractinian corals embedded in cheilostome bryozoan colonies (Cadée and McKinney, 1994)
Distortion or other reaction of host skeleton	Living	High	Cornulitids are often reported to have caused damage to host brachiopod shells.	Ammonites (Merkt, 1966); brachiopods (Schumann, 1967; Chatterton, 1975; Sparks et al., 1980; Peters, 1995); crinoids (Franzén, 1974; Feldman and Brett, 1998)
Encruster growth halting at a growth line in host	Living	High	Termination of encruster growth is inferred to have occurred because of the same perturbation which caused the host to produce a growth check.	Brachiopods (Ager, 1961; Lescinsky, 1995)
Preferred orientation or distribution of skeletobionts relative to host morphology	Living	Variable	While such patterns may indeed signify a response to the activities of a living host, it is also possible that they are post-mortem features caused by the orientation of a dead substrate to ambient flow regimes and to the sediment/water interface.	Hosts: cephalopods (Baird et al., 1989); bivalves (Trueman, 1942; Morris and Rollins, 1971; Bottjer, 1982; Hattin, 1986; Villamil et al., 1998); brachiopods (Schumann, 1967; Morris and Rollins, 1971; Richards, 1974a,b; Alexander and Scharpf, 1990; Meyer, 1990; Gibson, 1992; Fagerstrom, 1996); crinoids (Brett and Eckert, 1982; Peters and Bork, 1998); Corals (Sando, 1984)
Size distribution of skeletobionts along host	Living	High	Skeletobionts attached to a living and growing host will show a pattern of average size increase towards the older part of the host as this was available for colonisation first.	Gabbott (1999)
Modified skeletobiont growth pattern	Living	High	Unusual, candelabra-like growth of branching auloporid corals on brachiopod shells is evidence of concurrent growth of encruster and host (Fig. 15).	Alvarez and Taylor, 1987 (see also Pitrat and Rogers, 1978, text-Fig. 1)
Denser colonisation of older parts of host	Living	Variable	Being available for a longer period of time should lead to denser colonisation of older parts of living hosts.	Bordeaux and Boyajian, 1991
Skeletobionts colonising internal and/or soft tissue surfaces of host	Dead	High	Skeletal surfaces invested by soft tissues are usually inaccessible to skeletobionts (Fig. 2B).	Belemnite guards (Pugaczewska, 1965; Hölder, 1972); brachiopods (Pitrat and Rogers, 1978)
Host specificity	Living	Variable	Skeletobiont larva using a biological cue to settle on a living host, or only those individuals settling on such hosts successfully recruiting.	Gastropods: Baird et al., 1990; ammonites: Seliacher, 1982

Table 4 (*continued*)

Criterion	Inferred condition of host	Reliability	Remarks	Examples
Growth from one valve to another across the commissure of a bivalved host	Dead	Very high	This pattern of skeletobiont growth would seal the valves shut and prohibit host feeding.	
Lack of growth across commissure	Living	Variable	Gaping of the shells after death is possible, diminishing the applicability of this criterion.	Brachiopods (Ager, 1961)
Dense/heavy skeletobiont colonisation	Dead	Variable	Different hosts are able to tolerate different degrees of skeletobiont colonisation but relatively few survive heavy fouling.	

such as these provide a salutary warning to palaeontologists attempting to infer the advantages and disadvantages experienced by participants in fossil associations. Sometimes a single phytobiont or zoobiont monopolises the entire surface of the substrate provide by the hermitted shell. In such cases, the symbiont may not only produce a very thick encrustation which strengthens the shell, but can also grow outwards from the shell aperture in the form of a helicospiral tube, mimicking the shape of the gastropod shell and providing an enlarged chamber for the hermit crab to occupy (Taylor, 1996). Modern examples of this type of symbiont are known among coralline red algae (Zuschin and Piller, 1997), sponges (Sandford and Kelly-Borges, 1997), hydrozoans (Cairns and Barnard, 1984) and bryozoans (Taylor, 1994) (Fig. 11). It has been hypothesised that these bulky symbionts benefit the hermit crab by protecting it against various types of predators as well as removing the necessity for shell exchange as the crab outgrows its home.

Key and Barnes (1999) investigated fouling of Antarctic *Glyptonotus antarcticus*, a large marine isopod of particular interest as a trilobite analogue. Just under half of the individuals in their sample were fouled by bryozoans and/or serpulids, with as many as 12 bryozoan colonies per host isopod. No significant differences were found between encrustation of dorsal and ventral surfaces but fouling was greater on particular parts of the host, especially the fused pleon and telson. Bryozoans evidently use their isopod hosts as a refuge from the ice scour that renders rock surfaces in these shallow water habitats a less attractive option as a substrate.

5.3.4. Other zoobiotic communities

Large and diverse zoobiotic communities are typically associated with colonial corals in tropical reefs, and also deep-water corals such as *Lophelia* (Jensen and Frederiksen, 1992; Zabala et al., 1993; Freiwald and Wilson, 1998). A colonial lifestyle with its inherent plasticity in growth and form, together with the incidence of partial mortality, especially in older parts of colonies where a ‘dead zone’ or necromass may be developed, explains the widespread colonisation of colonial corals by zoobionts. Plasticity allows for zoobionts to be accommodated within the structure of the colony, while partial mortality permits zoobionts to overgrow or bore into individual corallites or groups of corallites without bringing about death of the colony as a whole.

A cool-water, solitary scleractinian coral—*Caryophyllia*—commonly attaches to the calcareous tubes of the free-living polychaete *Ditrupa* (Wilson, 1976). The majority of corals settle on the concave side of the curved tube, at first living symbiotically with the host but ultimately killing the host as the weight of the coral forces the tube into the sediment and buries the tube aperture. However, the coral itself survives while the tube progressively disintegrates through the action of boring algae and fungi. Harmelin (1990) described two solitary scleractinian corals from Mediterranean caves which become fouled and overgrown by sponges, bryozoans and serpulids but are able to extend their tissues basally to envelop these epizoans in new skeleton (Fig. 13). Likewise, healthy, active parts of the deep-water colonial coral *Lophelia* are able to respond to fouling organisms by enveloping them in layers of sclerenchyme, whereas older and inactive parts of colonies acquire a biofilm associated with Fe–Mn precipitation and host a diverse zoobiotic community of encrusters and borers (Freiwald and Wilson, 1998).

Stebbing's (1971) study of the zoobionts ('epizoites') of the seaweed-like bryozoan *Flustra* from Wales demonstrated zonation of species along the flattened branches of the host, with some zoobionts apparently favouring the basal (oldest) parts of branches and others the terminal (youngest) parts. Modern bryozoans with large, erect colonies can support very high diversities and biomasses of zoobionts (e.g., Rao and Ganapati, 1980; Bradstock and Gordon, 1983). These are frequently concentrated in the basal parts of colonies, regions which may constitute inactive necromass or be exoskeletal and hence vulnerable to colonising zoobionts. Similarly, Barnes (1994) found zoobionts to be significantly commoner on the rear, exoskeletal surfaces of two Antarctic bryozoan species. He also demonstrated differences in species composition of the zoobiotic community between: (1) the front and rear surfaces; (2) the two host species; and (3) according to depth, with the area colonised by zoobionts being a factor of six or more greater in shallow (40 m) than deep water (150 m). A detailed study of the spatial distributions of epibionts colonising the branches of the erect, articulated bryozoan *Cellaria* in the Adriatic Sea was undertaken by McKinney and Jaklin (2000). Young (distal) branches were found to be characterised by foraminiferans, algae and sponges, intermediate branches by hydroids, annelids, ctenostome bryozoans and ascidians, and old (proximal) branches by cheilostome and cyclostome bryozoans. Larval settlement behaviour may be responsible for at least some of this patterning. The sessile vermetid gastropod *Serpulorbis squamigerus* recruits preferentially onto the surfaces of encrusting cheilostome bryozoans belonging to several species in southern California (Osman, 1987). While the gastropods may obtain benefit during early growth stages from the bryozoans in the form of camouflage against predators and a refuge from competitors for space, no measurable disadvantage could be detected for the fouled bryozoans.

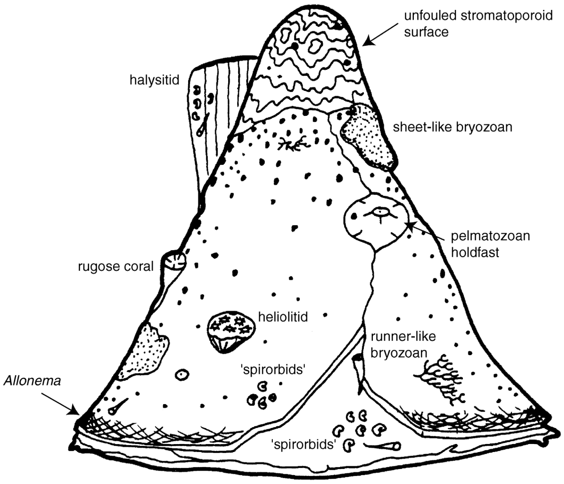


Fig. 14. Skeletobionts colonising a high dome-shaped stromatoporoid from the Silurian Upper Visby Beds of Gotland, Sweden. After Nield (1986b).

5.4. Fossil skeletobionts

Shells and other invertebrate skeletons belonging to various taxonomic groups are the most common hard substrates encountered in the fossil record. Many of these skeletobiotic assemblages developed while the host was still alive, i.e., they are zoobiotic. Others, however, represent post-mortem colonisation of the shells of dead animals, and yet others are mixtures of organisms that colonised when the host was alive and after it had died. Distinguishing between life and post-mortem skeletobiotic associations has been a major focus of many palaeoecological studies. Several criteria with varying degrees of certainty can be used to infer whether colonisation occurred before or after death of the host (see Holland, 1971; Lescinsky, 1995). These are summarised in Table 4.

5.4.1. Sponge-hosted skeletobionts

Fossil sponges are often found to support assemblages of skeletobionts. These communities can be rich and diverse. For example, Palmer and Fürsich (1981) identified more than 40 species encrusting the Middle Jurassic sponge *Platychonia magna* from a reef in Normandy, France. Palaeozoic stromatoporoids commonly served as hard substrates for bryozoans, 'worms', cemented brachiopods, corals and crinoids, and often contain the boring *Trypanites* (e.g., Kershaw, 1980; Nield, 1986b; Copper, 1996; Lebold, 2000; Figs. 2C and 14). The undersides of Carboniferous chaetetid sponges may host cryptic skeletobionts, including cemented brachiopods (*Sinuatella*), bryozoans, foraminiferans, *Spirorbis*, and the borings *Caulostrepsis* and *Rogerella* (Suchy and West, 1988; Brunton and Mundy, 1988).

5.4.2. Cnidarian-hosted skeletobionts

Among corals, both solitary (e.g., Baird and Brett, 1983; Sando, 1984) and colonial (e.g., Housa and Nekvasilová, 1987; Oschmann, 1989; Manceñido and Damborenea, 1990; Bertling, 1994; Copper, 1996) forms can be bored and/or encrusted. Several groups of bivalves bore into post-Palaeozoic corals, the best known of which belong to the genus *Lithophaga* (see Kleemann, 1994b). A tube-forming 'worm', *Hicetes* (Fig. 1B), lives within the coralla of the Devonian coral *Pleurodictyum*, almost 100% of corals from the Hamilton Group containing one such tube (Brett and Cottrell, 1982). The phosphatic conical shells of conulariids, generally regarded as scyphozoan cnidarians, occasionally hosted skeletobionts (Harland and Pickerill, 1987).

5.4.3. Bryozoan-hosted skeletobionts

Large erect or semierect bryozoans are frequently encrusted and bored. Fouling of basal parts of such colonies commonly takes place while the colony is still alive—such regions were often devoid of actively feeding zooids and are poorly defended. Palaeozoic trepostome and cystoporate bryozoans sometimes contain the boring *Trypanites*, especially conspicuous in dome-shaped colonies (e.g., Kobluk and Nemcsok, 1982). Arborescent bryozoans were also utilised as substrates by organically attached skeletobionts (e.g., Richards, 1972; Harper and Pickerill, 1996). According to Thomsen (1977), encrusting bryozoans from Danian mounds in Denmark preferred to attach to erect bryozoans with smooth rather than ridged surfaces. Pozaryska and Voigt (1985) made a detailed study of fistulose foraminiferans attached to erect and vagile bryozoans of Upper Cretaceous and Palaeocene age. They concluded that attachment could occur to both dead and living bryozoans, the foraminiferans benefiting from the provision of a sheltered substrate in high-energy environments.

5.4.4. Brachiopod-hosted skeletobionts

As epifaunal suspension feeders, it is not surprising that brachiopods frequently play host to assemblages of other suspension feeders, both borers and encrusters (Fig. 15). This is particularly true in the Palaeozoic where brachiopods are major components of the marine fossil record (e.g., Ager, 1961; Hoare and Steller, 1967; Schumann, 1967; Richards, 1972; Hurst, 1974; Chatterton, 1975; Pitrat and Rogers, 1978; Anderson and Dimitracopoulos, 1980; Kesling et al., 1980; Sparks et al., 1980; Spjeldnaes, 1984; Alvarez and Taylor, 1987; Alexander and Scharpf, 1990; Meyer, 1990; Brice and Mistiaen, 1992; Gibson, 1992; Lescinsky, 1995, 1996a, 1997; Peters, 1995; Fagerstrom, 1996; Roark, 1997). However, skeletobionts can also be found on Mesozoic (e.g., Brookfield, 1973; Michalík, 1977) and Cenozoic (e.g.,

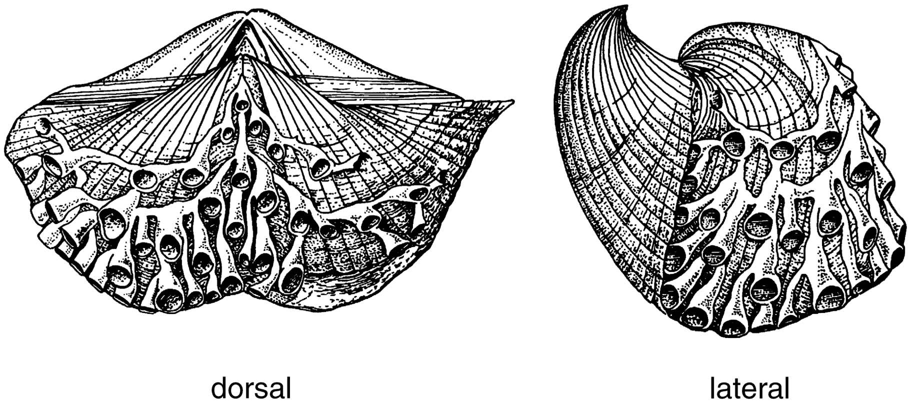


Fig. 15. Candelabra-like growth pattern of the tabulate coral *Aulocystis commensalis* on the brachiopod *Spinocyrtia clintoni*, the coordinated growth of encruster and host almost certainly signifying a life association (see Alvarez and Taylor, 1987). Devonian, Traverse Group, Michigan, USA. After Pitrat and Rogers (1978).

Brunton and Hiller, 1990; Taddei Ruggiero, 1999) brachiopods.

In a predominantly disarticulated population of the Devonian brachiopod *Spinocyrtia* from the Hamilton Group, Brett and Bordeaux (1990) found ‘fresh’ encrusters to be less abundant on the most corroded/abraded shells, leading them to conclude that degree of encrustation is not necessarily a good indicator of shell residence time on the seabed. A related study (Bordeaux and Brett, 1990) showed substrate specificity for particular brachiopod taxa by skeletobionts: brachiopods having non-punctate shells without spines or frills were found to be the most heavily encrusted. Alexander and Scharpf’s (1990) detailed study of encrusters on Ordovician brachiopods from the Dillsboro Formation of Indiana also demonstrated substrate selectivity, with punctate and coarsely ribbed brachiopods being less favoured by at least some species of epibionts. In common with some other studies, species of large brachiopods were found to be more often encrusted than small species. Surface area considerations as well as host longevity can often explain this kind of pattern.

The distributions of encrusters on Palaeozoic brachiopod shells have been used by many palaeontologists to infer the life attitudes and feeding current patterns of the host animals. For example, cornulitids which disturbed shell growth in the host brachiopod *Paraspirifer bownockeri*, and were therefore life associates, grew preferentially towards the lateral commissure. This has been taken to indicate that the incurrents of the brachiopod, potentially of benefit to the cornulitid, approached the shell laterally rather than medially (Peters, 1995).

5.4.5. Mollusc-hosted skeletobionts

By virtue of the good preservation potential of their shells and their typically epifaunal habit, calcitic bivalves, especially oysters and pectinids, provide among the most preservable hard substrates for fossil skeletobionts. Examples of bivalve-hosted skeletobionts have been described from the Palaeozoic (Trueman, 1942), Mesozoic (Seilacher, 1954; Pugaczewska, 1970; Taylor, 1979b; Mayoral and Sequeiros, 1981; Bottjer, 1982; Hattin, 1986; Hary, 1987; Hollingworth and Wignall, 1992; Fürsich et al., 1994; Villamil et al., 1998; Bien et al., 1999; Fürsich and Pandey, 1999; Moosleitner, 2000) and Cenozoic (Boekschoten, 1967; Miller and Alvis, 1986; Aitken and Risk, 1988; Watkins, 1990a,b; Bishop, 1988, 1994; Mayoral and Reguant, 1995; Velcescu, 1999). These include not only sessile species but also occasional examples of bioerosional traces left by associated motile species. For example, traces made by capulid gastropod on pectinid shells have been reported from the Miocene onwards (Bongrain, 1995).

An interesting example has been described by Baird et al. (1990) of a Devonian platyceratid gastropod (*Naticonema*), presumed to have been a coprophagous symbiont of crinoids, bored by acrothoracican barnacles and encrusted by bryozoans. Relative chronology is given by the observation that the bryozoans sometimes overgrew the borings, but were more often cut by them. Platyceratids from the Ordovician of Cincinnati were fouled by cornulitids during life, as indicated by reciprocal overgrowth (Morris and Felton, 1993), and some also appear to have barnacle borings (Felton, personal communication).

Fossil cephalopods with external shells occasionally support sclerobionts which either colonised the shells while the host animal was alive or after it died. A good example of inferred life associations occurs between the Ordovician–Devonian orthoconic nautiloids and colonial bryozoans (notably *Spatiopora*), problematica (*Reptaria*) and corals (*Alveolites*) described by Baird et al. (1989). Distinct orientation patterns, with apertures pointing forwards, may be present in *Reptaria* colonies encrusting nautiloids. Orthoconic nautiloids from the Ordovician of South Africa were colonised by inarticulate brachiopods and cornulitids (Gabbott, 1999), and Prokop and Turek (1983) described a Silurian orthocone with no fewer than 17 attached crinoids. An unusual example of a hydrozoan (*Delheidia*) totally enveloping a small nautiloid was described from the French Miocene by Lozouet and Maestrati (1992). It is unclear whether this represents growth on a dead but floating shell, or on a shell that had rolled along the seabed.

Merkt (1966) has described Jurassic ammonites fouled by oysters and serpulids on one side and evidently responding by adjusting the trajectory of shell growth in order to maintain a vertical attitude in the water column. A Triassic *Ceratites* studied by Meischner (1968) was colonised by the cemented bivalve *Placunopsis* in several phases, partly while the ammonoid was still alive and partly after death.

Seilacher (1982) has argued that ammonites and nautiloids from the Early Jurassic Posidonia Shale of Germany were colonised by sessile organisms both when the host animal was alive, and while the dead shell was floating in a vertical orientation. This view contrasts with Kauffman's (1981) interpretation of the same material as representing benthic islands colonised on a muddy sea floor. Support for Kauffman's hypothesis is from ammonites bearing encrusters on one side only (the upper side). A comparable problem of benthic vs. planktonic colonisation is posed by spheroidal colonies of the ?hydrozoan *Parkeria* from the mid-Cretaceous which totally envelop ammonite substrates (Wilmsen, in preparation). This is well seen in the magnificent illustrations of Carpenter and Brady (1869) who, however, regarded *Parkeria* as an arenaceous foraminiferan and the ammonite substrate as the early chambered test. Some Upper Cretaceous ammonite shells bear the 'home scars' of limpets that apparently colonised living host animals (Kase et al., 1994, 1998), and fed on algae growing on the shell surface, leaving grazing traces (*Radulichhnus*). The clearest examples of entirely post-mortem colonisation of fossil cephalopods can be seen when moulds rather than shells themselves are encrusted and bored (e.g., Macchioni, 2000). Post-mortem boring and grazing of ammonites and nautiloids has been well described in a Maastrichtian fauna from Western Australia (Henderson and McNamara, 1985), and in Jurassic faunas in Tunisia (Rakús and Zítt, 1993) and Italy (Nicosia, 1986).

Boring and encrustation of belemnite guards (e.g., Pugaczewska, 1965; Hölder, 1972; Hillmer and Schulz, 1973; Mariotti, 2002) was also a post-mortem phenomenon, although Seliacher (1968) has argued that some acrothoracican barnacles bored into living belemnites through a thin covering of soft tissue that invested the guard. An unusual occurrence of small solitary corals attached to belemnite guards has been described from the Jurassic of Sicily by Mariotti (2002). Many of the belemnite guards are coated by a black film (?manganese) which is lacking on the corals, suggesting that the guards may have been buried and exhumed prior to their colonisation by the corals.

Hyoliths, a problematical group included here among molluscs for convenience, may host skeletobionts. Marek and Galle's (1976) study of the Devonian hyolith *Pterygotheca* from the Czech Republic provides the best example. Most specimens of *Pterygotheca* have their more convex sides covered by a tabulate coral, *Hyostragulum*. The presence of this life associate led Marek and Galle to interpret hyoliths as sedentary animals which rested with the convex side of the shell uppermost (dorsal). Specificity of encrustation of *Hyolithes* by prasoporid bryozoans has also been observed in the Ordovician Trenton Group of New York and Lexington Limestone of Kentucky (Brett, personal communication, 2002).

5.4.6. Arthropod-hosted skeletobionts

Trilobites are not noted for hosting epibionts, but a few examples have been recorded (see Brandt, 1996). For example, Taylor and Brett (1996) described articulated examples of the Silurian trilobite *Arctinurus* with the dorsal exoskeleton colonised by microcommunities of small encrusters and pedically attached brachiopods that apparently associated with the living trilobite. Brandt (1996) found that encrustation on a sample of *Flexicalymene* from the Cincinnati area occurred only on the largest trilobites which probably represent individuals in their terminal moult stage. Schumacher et al. (1998), working with the same Ordovician trilobite genus, interpreted as symbionts some encrusting bryozoans, cornulitids and inarticulate brachiopods, with ramose bryozoan colonies seemingly taking advantage of the feeding currents of the host. Small crinoid holdfasts and an inarticulate brachiopod were found attached to a fragmentary specimen of *Selenopeltis* (Budil and Saric, 1995) and bryozoans to the exuvia of *Dalmanitina* (Kácha and Saric, 1995), both from the Ordovician of Bohemia, while the bryozoan *Corynotrypa* has been described encrusting a cephalon of the trilobite *Calyptaulax* from the Irish Ordovician (Clarkson and Tripp, 1982).

5.4.7. Echinoderm-hosted skeletobionts

Crinoid stems may be encrusted or bored either during life or after death (Donovan and Lewis, 1999; Klikushin, 1996; Kovacsik, 1997; Feldman and Brett, 1998). Colonisation of the stem during life may elicit renewed growth of stereom, producing swollen or distorted columnals (e.g., Franzén, 1974; Peters and Bork, 1998). In the case of stem encrustation, a life association can sometimes be inferred by symmetrical growth of the fouling organism around the entire circumference of the stem (Hudson et al., 1966; Brett and Eckert, 1982; Peters and Bork, 1998; Wyse Jackson et al., 1999), indicating that the stem was upright when fouled. For example, Hudson et al. (1966) described columnals of Irish Carboniferous crinoids encrusted circumferentially by two tabulate corals (*Cladochonus* and *Emmonsia*) which lived attached to the stems of the living hosts. On the other hand, encrustation of articulation facets points to post-mortem association (e.g., Rakús and Zítt, 1993; McGee and Watkins, 1994; Feldman and Brett, 1998). Skeletobionts attached to the stems of living crinoids may have benefited from access to higher suspension feeding tiers (Peters and Bork, 1998).

Skeletobionts are common on some post-Palaeozoic echinoids (e.g., Müller, 1969; Nebelsick, 1996; Nebelsick et al., 1997). Most apparently represent post-mortem colonisation, although the robust spines of regular echinoids can become densely encrusted while the host animal is still alive. A significant proportion of irregular echinoids in the Upper Cretaceous Chalk of northwest Europe, especially the genus *Echinocorys*, is encrusted by bryozoans, sponges, foraminiferans, serpulids, bivalves and craniid brachiopods (e.g., Schmid, 1949; Müller, 1969; Cross and Rose, 1994). As the host echinoids were infaunal during life, tests bearing skeletobionts had to be exhumed onto the seabed and colonised before disarticulation.

5.5. Conchicole symbionts

Vermeij (1987) used the term conchicole to refer to animals inhabiting empty shells, particularly of gastropods. The best-known conchicoles at the present day are hermit crabs, although several other groups have also been recorded living in mollusc shells (see Vermeij, 1987, Table 8.1). The fossil record of in situ hermit crabs and other conchicoles is meagre; however, inhabited gastropod shells may support distinctive assemblages of skeletobionts which are of value in showing: (1) that the shell was occupied by a conchicole and was not vacant or still inhabited by the gastropod maker; and (2) the likely taxonomic identity of the conchicole.

A large number of symbionts are associated with some Recent hermit crab species; for example, McDermott (2001) found 31 symbionts living with *Pagurus longicarpus*. Massive encrustations distributed evenly over surfaces of fossil gastropod shells have been recorded back to the early Palaeozoic. Examples are found among hydrozoan cnidarians (Allman, 1872; Douvillé, 1908; Olivero and Aguirre-Urreta, 1994), anthozoan cnidarians (Kase, 1986; Darrell and Taylor, 1989) and bryozoans (e.g., Buge and Fischer, 1970; McNamara, 1978; Morris et al., 1991; Aguirre-Urreta and Olivero, 1992; Taylor, 1994; Kidwell and Gyllenhaal, 1998). By analogy with modern symbioses between bryozoans and gastropods or between bryozoans and hermit crabs (see Taylor, 1994, p. 168), those examples in which the encruster either grows over the lips of the gastropod shell and onto internal surfaces normally covered by mantle tissue when the gastropod is alive, or extends outwards from the aperture to form a helicospiral tube-like extension to the gastropod living chamber, are likely to have been tenanted by a conchicole. Given the dominance today of hermit crabs as conchicoles, coupled with the fact that hermit crab body fossils range back to the Lower Jurassic, there is a reasonable probability that any post-Triassic examples of such encrusters will have been hermit crab symbionts. Supporting evidence for symbiosis with a hermit crab is sometimes available from the knowledge that modern examples of the same taxa are obligate hermit crab symbionts (e.g., the bryozoan *Akatopora circumsaepta* in New Zealand, see Taylor, 1994), from the occurrence of other associates (especially the trace fossil *Helicotaphrichnus*, see below), and wear facets on the base of the shell caused by dragging (e.g., Palmer and Hancock, 1973; Kidwell and Gyllenhaal, 1998). For Palaeozoic examples, the identity of the conchicole/s is unclear, although other groups of arthropods and worms, including sipunculans, are likely candidates (e.g., Morris et al., 1991).

Boring skeletobionts may be associated with conchicole-occupied gastropod shells. The trace fossil, *Helicotaphrichnus commensalis* Kern et al., 1974, is a groove-like excavation in the columella produced by a spionid polychaete which is an obligate symbiont of hermit crabs. This ichnogenus has been recorded from Eocene to Recent (Kern et al., 1974; Kern, 1979; Darrell and Taylor, 1989; Walker, 1992; Taylor, 1994; Kidwell and Gyllenhaal, 1998). Ctenostome bryozoan and acrothoracican barnacle borings, as well as cheilostome bryozoan etchings (*Lepptichnus*, see Taylor et al., 1999), frequently infest fossil gastropod shells inferred to have been occupied by hermit crabs; Walker (1992) gives a comprehensive review.

'Recycling' of fossil gastropod shells by Recent hermit crabs (Walker, 2001; Barnes, 2001) complicates palaeoecological interpretation in that fossil conchicoles potentially may have been associated not only with different shell occupants, but also with occupants that lived at widely different times.

6. Ecology of modern hard substrate communities

The literature on the ecology of modern hard substrate communities is vast. In part, this is not only because of their economic significance (e.g., as sources of commercial shellfish) but also because hard substrates, particularly in the intertidal, have formed important experimental sites for ecological studies of recruitment and community succession (Underwood, 2000). It is impossible here to do justice to the work on modern hard substrate ecology. Rather, we focus on aspects having a bearing on palaeoecological studies of fossil hard substrates, giving a few examples to illustrate these points. An important lesson to be learned from the Recent is that a myriad of physical and biological factors influence the development of modern hard substrate communities, some fairly predictable in their effects but others more obscure. Not only are many of these factors 'invisible' to the palaeoecologist, but complex interactions between individual factors may render it impossible to infer the processes that actually structured ancient hard substrate communities. Some appreciation of the ecology of modern hard substrates is absolutely essential for palaeontologists embarking on studies of ancient hard substrates.

Important review papers covering this topic or dealing with specific aspects, include: Jackson (1983), Branch (1984), Buss (1986), Woodin and Jackson (1979), Bishop (1989), Menge and Branch (2000), Witman and Dayton (2000) and Knowlton and Jackson (2000).

6.1. Settlement and recruitment

Hard substrates in the sea are usually colonised through the settlement of free swimming larvae from the plankton. As already mentioned above (Section 3), the term *recruitment* refers to the organisms which survive immediate post-settlement mortality (see Keough and Downes, 1982; Osman and Whitlatch,

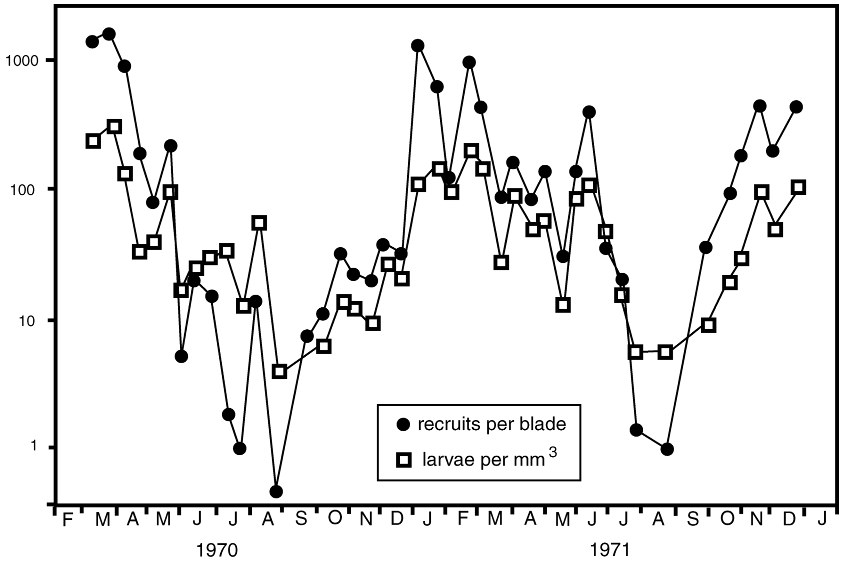


Fig. 16. Bimonthly averages (logarithmic scale) of larval abundance of *Membranipora membranacea* plus recruited colony densities of this bryozoan on the kelp *Macrocystis pyrifera* in California. After Yoshioka (1982).

1995), potentially becoming established in the community. Because individuals suffering such early mortality are rarely fossilised, studies on ancient hard substrate communities effectively deal with recruits and recruitment patterns rather than settlers and settlement patterns. The significance of recruitment to subsequent community development and structure is evident in such studies as that of Bingham (1992) who examined the epifauna growing on red mangrove roots in Florida. Differential larval recruitment was found to be more important in determining species distributions than the physical factors acting upon either larvae or adults. Butler's (1991) work on sessile invertebrates colonising *Pinna* shells, pier pilings and settlement panels in South Australia showed that communities were structured more by the heavy recruitment of poor competitors than by subsequent dominance of substrate space by good competitors. The enormous variability in rates of recruitment (e.g., Yoshioka, 1986) are at least partly responsible for the heterogeneity or patchiness characteristic of many hard substrate communities. Jackson (1984) found that cryptic communities on the undersides of individual corals in Jamaica developed largely independently of one another.

The importance of variations in larval supply ('supply-side ecology') to community composition and development is becoming increasingly evident (see Caley et al., 1996, and references therein). Substantial variations in larval abundance occur in time (Fig. 16) and at all spatial scales. Many benthic invertebrates have seasonal patterns of reproduction, releasing large numbers of larvae at particular times. Mass spawning is a well-known characteristic of reef corals, with multiple species displaying short, coordinated pulses of egg and sperm release and hence peaks in larval abundance (Richmond, 1997). Commonly, invertebrate larvae cannot feed (i.e., they are non-planktotrophic, see Jablonski and Lutz, 1983) and are incapable of spending more than a day or so in the plankton before they are forced to settle. Therefore, recruitment of particular species onto hard substrates may take place for only a limited period of time during each year (e.g., Maturo, 1959), with different species showing different peak times of recruitment (e.g., Brown and Swearingen, 1998). Recruitment may also occur at different rates depending on when the substrate first becomes available for colonisation (e.g., Igic, 1972). In many settlement panel studies, the season of panel deployment has been shown to have a large effect on which species recruit, in turn profoundly influencing subsequent community development (e.g., Sutherland and Karlson, 1977; Van Dolah et al., 1988; Nandakumar, 1996; Lam, 2000). Superimposed on annual variations are variations between years. For instance, Haderlie (1970) found dramatic differences in the density of barnacles recruiting onto settlement panels in two successive years in Monterey Harbor, California. Such findings caution against palaeontologists attempting to explain differences in species patterns on ancient hard substrates in terms of substantial environmental changes through time.

Spatial variations in recruitment may be equally dramatic. Again, the short interval of motility of many larvae is an important factor causing spatial heterogeneity in recruitment. The presence of a source population of adults close to a newly available hard substrate will greatly increase the likelihood of recruitment onto that surface. The proximity of natural hard bottom habitats plays an important role in the colonisation by sessile organisms of ships' hulls sunk off South Carolina and, a factor is even more important than the amount of time the ships had been available to colonisers Georgia (Wendt et al., 1989). Carter et al. (1985) found that distance from hard bottom areas providing the source of colonisers appeared to be an important factor in community development on artificial reefs. Lack of a nearby source population may explain some instances in the fossil record where shells apparently suitable for colonisation are neither encrusted nor bored.

Oceanographic factors can have a major effect on larval abundance. For example, during periods of high upwelling, larval abundance (and recruitment) may decline both in barnacles (Roughgarden et al., 1988) and bryozoans (Yoshioka, 1982). Note, however, that high biomasses of suspension feeders often develop in phytoplankton-rich, upwelling regions, (Witman and Dayton, 2000) and correlate with increased nutrient levels (e.g., Huang et al., 1999). Making simple correlations between suspension feeders and nutrient levels is as unwise in the fossil record as it is at the present day unless supported by independent evidence. On a regional scale (South Carolina–northern Florida), Wenner et al. (1983) found that the invertebrate community diversity of hard bottoms showed no clear pattern according to depth or latitude but seemed to depend on habitat complexity.

The work of Judge and Craig (1997) using tapered pipes placed in the subtidal off Long Island, New York, showed increases in both recruitment and growth of barnacles and the hydroid *Obelia* over a 5-month period in fast compared to slow flow. In contrast, a rare study of deep-water hard substrates (Mullineaux, 1988) deployed manganese nodules at a depth of 1240 m in the Santa Catalina Basin off southern California. After 7 weeks, the nodules had been colonised by a fauna dominated by foraminiferans, with a greater settlement of larvae on surfaces in low flow regimes. Recruitment patterns may also be influenced by shading. Baird and Hughes (2000) studied the differences in recruitment on settlement panels placed beneath fronds of the tabular coral *Acropora hyacinthus* and those placed in the open at Lizard Island, Great Barrier Reef. Corals, filamentous algae and coralline algae recruited less often on the plates placed beneath the corals, whereas bryozoans recruited four times more abundantly on the shaded plates. The reduction in ambient current velocity, increased sedimentation and lower light intensity associated with understory kelp environments influence recruitment patterns of sessile animals in varying ways (Duggins et al., 1990).

Larval behaviour can be another major factor determining recruitment patterns. Many larvae show very specific preferences in where they settle depending on such factors as the physical and chemical condition of the substrate surface (e.g., Roberts et al., 1991), the presence of existing colonisers (both of microscopic and macroscopic scale), colour (Pomerat and Reiner, 1942), and especially orientation. Marine hard substrates vary in wettability (the tendency to induce spreading of a liquid on the surface), with materials such as glass being wettable and wax unwettable. Larvae often prefer non-wettable over wettable substrates (e.g., Mihm et al., 1981). Glasby (2000) deployed settlement panels of sandstone, concrete and wood in Sydney Harbour to investigate the effects of panel composition and orientation on fouling communities. Assemblages developing on the wooden panels were always found to be significantly different from those on the lithic panels. The uniqueness of the communities on the wooden panels was partly but not entirely due to the presence of the wood-boring bivalve *Bankia*. Among lithic substrates, composition can influence larval settlement. For example, Bavestrello et al. (2000) found that planulae of the hydroid *Eudendrium* settled preferentially on carbonate rather than quartzose substrates. In contrast, Connell (2000) found that pontoon composition (sandstone or concrete) did not affect the communities developing in Sydney Harbour. Recruitment of sessile species to hard substrates may depend on the heterogeneity and structure provided by existing colonists. This was demonstrated experimentally by Bros (1987) using settlement panels in Tampa Bay, Florida: the presence of barnacle shells (living or dead) increased recruitment significantly.

Wahl (1989) recognised four main stages in the establishment of fouling communities on hard substrates (Fig. 17). During the first stage, which can occur within a minute of the substrate being immersed, dissolved macromolecules are adsorbed onto the substrate surface, causing biochemical conditioning. Bacterial colonisation follows after about an hour, and is succeeded within about a day by unicellular eukaryotes, including diatoms, which secrete mucus as a cement. Finally, larger, multicellular organisms colonise the surface, often after about 1 week of immersion.

The presence of biofilms has a significant influence on recruitment (Wieczorek and Todd, 1998; Hamer and Walker, 2001). For example, larvae of the bryo-

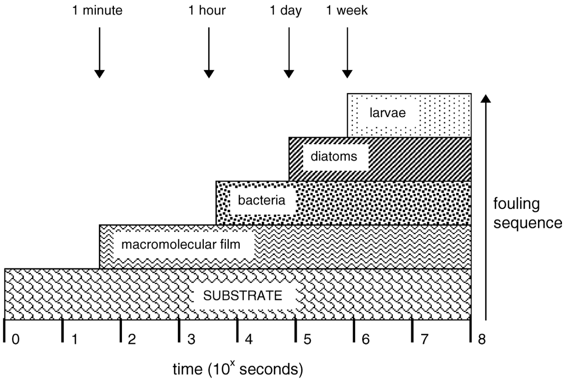


Fig. 17. Schematic development of marine biofouling communities with time. A macromolecular film develops first on newly immersed substrates which are then colonised successively by bacteria, diatoms and the larvae and spores of larger organisms. Based on Wahl (1989).

zoan *Bugula* preferentially settle on substrates coated by primary films of detrital particles, bacteria and diatoms rather than clean substrates (Brancato and Woollacott, 1982; Kitamura and Hirayama, 1987). Successful recruitment by corals may require the presence of crustose coralline algae (Morse et al., 1996). Larvae of some species are gregarious (e.g., Patzkowsky, 1988; Toonen and Pawlik, 2001), exhibiting a tendency to settle close to adult conspecifics in response to a chemical cue. In other instances, aggregation is due to different factors. For example, Keen (1987) showed that aggregated settlement of larvae of the scyphozoan *Aurelia aurita* was not due to gregarious behaviour but was related to substrate heterogeneity: locations where hydrodynamic shear stress was low attracted more settlers. Depressions and elevations on the surface of the substrate very often influence recruitment, with some species recruiting in greater numbers into crevices and others onto mounds. Walters and Wethey (1991), for example, found preferential recruitment of the larvae of arborescent ascidian and bryozoan species in crevices on algal fronds. They attributed this to the protection provided against predators and dislodgement by physical disturbance during the vulnerable early phases of growth immediately after settlement. However, a co-occurring species of encrusting bryozoan settled preferentially on elevations, a behaviour possibly explained by the height advantage so gained in spatial competition. A study of the distributions of common encrusting bryozoan species on disarticulated bivalve shells off the Isle of Man showed considerable overlap between species, although some species did exhibit tendencies to occur more commonly on rough instead of smooth shell surfaces (Ward and Thorpe, 1989).

Numerous studies (see references in Glasby and Connell, 2001, p. 132) have demonstrated that substrate orientation has an extremely strong effect on recruitment patterns. In an early study, Pomerat and Reiner (1942) found that two bryozoan species settled in greatest numbers on undersides of glass plates, whereas a barnacle showed no preference. Maturo (1959) also found greater settlement of bryozoans onto undersides of ceramic tiles which he attributed to the silting of upper surfaces. Coralline algae dominate upper surfaces of rocks in the intertidal and subtidal of Signy Island, Antarctica, whereas encrusting animals are almost entirely restricted to undersides (Barnes et al., 1996). For most bryozoan species in this community, the proportion of colonies on upper rock surfaces initially increased with depth, possibly reflecting decrease in light intensity and hence the likelihood of overgrowth by coralline algae, before diminishing with greater depth as silting of upper surfaces became important in the lower current flow regimes pertaining here. Fairfull and Harriott (1999) found conspicuous differences between the organisms colonising upper and lower surfaces of settlement panels placed in 7 m of water in a subtropical setting in eastern Australia. Upper panel surfaces were dominated by algae, whereas lower surfaces were dominated by bryozoans, ascidians and sponges. Differential recruitment of spirorbid worms to shaded lower surfaces may result from the negative response of the larvae to light (Saunders and Connell, 2001). Horizontal and gently sloping surfaces throughout the rocky subtidal tend to be covered by macroalgae in contrast to vertical surfaces where suspension-feeding invertebrates dominate (Barnes, 1995; Witman and Dayton, 2000). Reasons for this contrast, which may be greater in temperate than tropical environments, include differences in light levels, sedimentation rates, and degree of protection from physical and biological disturbance. With respect to the last factor, for example, grazing echinoids are known to experience difficulty attaching to steep faces, making invertebrate communities on these surfaces less susceptible to being grazed (Sebens, 1985). Bivalve shells commonly show major differences in encrustation and boring patterns on the convex and concave surfaces (e.g., Bosence, 1979a, pl. 52, Figs. 9 and 10). McKinney (2000) studied bryozoans encrusting disarticulated bivalves from the Adriatic and found that species with large, sheet-like colonies were commoner on convex outer surfaces whereas species with small colonies tended to settle on concave inner surfaces that provided cryptic habitats.

6.2. Competition

Sessile organisms colonising hard substrates potentially compete with one another for living space, for food and, in the case of plants and zooxanthellate corals harbouring photosymbionts, for light (Buss, 1986). Many biologists (e.g., Paine, 1984) consider competition to be very important in community ecology whereas others (e.g., Simberloff, 1982) question its role. Most research on hard substrate communities has been directed towards spatial competition because this is relatively easy to observe and quantify (Buss, 1990; Nandakumar and Tanaka, 1993). Spatial competition is also of most relevance to the palaeoecologist as its results can be preserved as 'frozen behaviour' in fossil material (see Section 8.3).

An early review of competition in sedentary marine animals was published by Knight-Jones and Moyse (1961, p. 72) who noted that: "The great majority of such animals are plankton feeders and their competition for food is rather like the competition of land plants for carbon dioxide". In other words, competition for food does not occur as this is a superabundant, non-limiting resource. While possibly true in some habitats, there is now good evidence that organisms on hard substrates can reduce the food resources available to their competitors (see Okamura et al., 2001). For example, working with experimental boxes deployed at 40 m depth on a Jamaican reef, Buss and Jackson (1981) found that high densities of sessile suspension-feeders caused a measurable depletion in planktonic food resources. There is also evidence that competition for food along the margins of neighbouring encrusting suspension feeders may retard the growth rates of competitors less able to acquire food particles, thereby making them more likely to lose in competition for substrate space (Buss, 1980; McKinney, 1992, 1993). Zajac et al. (1989) presented evidence that adults and juveniles of resident species are able to deplete the food available to new colonists and hence lower recruitment rates.

Substrate space is very often a limiting resource for sessile organisms. Even when there is uncolonised space available on the substrate, the growth of neighbouring organisms may bring them into direct contact and force a competitive encounter. Competition for space occurs both within (intraspecific) and between (interspecific) species. There are several possible outcomes, most notably: (1) complete overgrowth by a superior spatial competitor, generally resulting in death of the inferior competitor; (2) incomplete overgrowth by a superior competitor; (3) stand-off in which no clear competitive dominant emerges but both competitors potentially have their further growth impeded; (4) reciprocal overgrowth with one competitor winning along part of the line of contact but the other winning elsewhere. Incomplete overgrowth (2) often entails the death of some but not all zooids in a colonial animal (partial mortality), with a potential reduction in reproductive fitness. Individuals of the worm *Spirorbis* may be incompletely overgrown by bryozoans leaving the aperture protruding through the bryozoan colony and the worm still able to feed (Stebbing, 1973a; Keen and Neill, 1980; Lopez Gappa, 1989). Stand-offs (3) between species are frequent in some hard substrate communities. For example, the majority of encounters between four species of colonial ascidians growing on settlement panels in Langston Harbour, England, resulted in stand-offs (Schmidt and Warner, 1986). Among encrusting sponges, which cover in excess of 40% of substrate space in a New Zealand rock wall community studied by Ayling (1983), stand-offs were the most frequent spatial interactions. Similarly, Aerts (2000) found standoffs to be more common than overgrowths in coral–sponge interactions. Instances have also been recorded of complete overgrowth resulting in a period of enforced dormancy of the overgrown organism followed by renewed activity after detachment of the overgrowing organism (Sebens, 1986; Todd and Turner, 1988).

Mechanisms for winning and/or defending substrate space from conspecific and allospecific competitors are diverse (see Lang, 1973; Buss, 1986). They include morphological adaptations, many reflected in the skeleton and hence fossilisable, and chemical adaptations which are unlikely to leave any clear trace in the fossil record. Important morphological correlates of competitive success are growth rate, spinosity (Stebbing, 1973b), size and thickness. Ability to lift growing edges off the substrate (Stebbing, 1973b), to undercut (as in the bivalve *Anomia*) or to crush competitors, production of outgrowths (e.g., bryozoan stolons), and tentacular contact in cnidarians (Bruno and Witman, 1996) can also be important. Namikawa et al. (1992) showed that colonies of the hydroid *Stylactaria* living on gastropod shells developed polymorphic zooids (tentaculozooids) more frequently when in contact with the bryozoan *Celleporella*. Touching the tentaculozooids elicited retraction of bryozoan lophophores, possibly because of nematocyst discharge, and was hypothesised to have aided the hydroid during competition for substrate space. The inarticulate brachiopod *Discinisca* living in the intertidal zone of Panama uses modified lateral setae as well as movements of the shell to abrade the tissues of adjacent sponges and bryozoans competing for space (LaBarbera, 1985).

In an early study of chemical factors, Jackson and Buss (1975) extracted homogenates from the tissues of 11 sponge and colonial ascidian species from a coral reef in Jamaica. Many of the homogenates had deleterious effects on four species of bryozoans with which they were tested but not on two serpulids, a brachiopod and a bivalve. These effects included inhibition of bryozoan feeding, death of zooids and of entire colonies. Such allelopathic reactions may have a role in competition for substrate space. Allelopathy was also demonstrated by Bak and Borsboom (1984) who found that exudates of the Antillean reef anthozoan *Condylactis* significantly reduced algal biomass accumulating on experimental glass slides. A study of competition for space between two species of scleractinian corals and three of ‘soft corals’ (alcyonacean octocorals) on the Great Barrier Reef found that allelopathy was manifested by tissue necrolysis induced by species of each group on the other (Sammarco et al., 1985).

The ability of larvae to recruit onto spatial refuges where their probability of being overgrown is diminished can be important. For example, Rubin (1985) found that the serpulid *Pomatoceras triqueter* readily overgrew colonies of the 32 bryozoan species which recruited onto settlement panels he deployed off Plymouth, England. Many of the bryozoan species, however, were able to avoid overgrowth by preferentially settling onto serpulid tubes or by growing onto them as adults. Therefore, serpulid tubes functioned as refuges for these bryozoans. Small-sized shells form refuges from intraspecific competition for hydroids living symbiotically with hermit crabs (Buss and Yund, 1988). By virtue of their reduced surface area, small substrates are more likely to be completely covered by a species before superior competitors can settle. Grosberg (1981) found that the colonial ascidian *Botryllus* won the majority of competitive encounters for space with other sessile animals at Woods Hole, MA, and that larvae of subordinate competitors consequently settled preferentially away from *Botryllus*. Subordinate spatial competitors growing on the giant kelp in California may settle on older blades and thereby avoid competition with the dominant bryozoan *Membranipora* which mainly grows on younger blades (Bernstein and Jung, 1979). Conversely, a potent competitor in reefal environments, the hydrozoan *Millepora*, actively detects and overgrows neighbouring gorgonians (Wahle, 1980). Buss (1981b) showed how gregarious behaviour by larvae of the bryozoan *Bugula turrita* resulted in aggregations of colonies which were better able to compete for space with another bryozoan.

Factors not always directly controlled by the organisms may also influence competitive interactions, notably the angle of encounter between the growing edges of competitors (Jackson, 1979). Poorly defended lateral flanks of bryozoan colonies are vulnerable to overgrowth compared with distal growing edges where active budding takes place; some colonies may even redirect their growth in order to encounter competitors ‘head-on’ (Buss, 1981a). Symbionts can also have an important effect on the performance of sessile organisms competing for space. Osman and Haugness (1981) demonstrated dramatic improvements in the success of colonies of the bryozoan *Celleporaria brunnea* in overgrowth interactions with other species when the *C. brunnea* colonies hosted the symbiotic hydroid *Zanclea* which could sting competing species (and predators). Another bryozoan, *Rhynchozoon larreyi* from the Red Sea, similarly benefits in winning substrate space by harbouring *Zanclea* as a symbiont (Ristedt and Schuhmacher, 1985).

At the community level, the complexities of competition for substrate space mean that relationships are not always expressible as simple competitive hierarchies, i.e., species A overgrows both species B and C, and species B overgrows species C, thereby defining a simple ranking in competitive ability from A to B to C. Instead, they may take the form of a competitive network (Buss and Jackson, 1979) in which no single species is dominant: i.e., species A overgrows species B, species B overgrows species C but species C overgrows species A. For example, Sebens’ (1986) study of sessile communities on subtidal vertical rock walls in Massachusetts over a 2-year period revealed a basically hierarchical competitive structure complicated by some reversals and numerous standoffs. Lopez Gappa (1989) also found an essentially hierarchical structure between encrusting bryozoans on settlement panels, as did Barnes and Lehane (2001) for South Atlantic boulder communities. In contrast, an example of a competitive network was found by Rinkevich et al. (1993) in a study of sessile invertebrates on a Red Sea reef. Four common species (a scleractinian coral, an alcyonarian coral, a hydrocoral and a sponge) formed a network in which overgrowth, allelopathy, necrosis and bleaching reactions were all involved. Russ (1982) explained competitive hierarchies in terms of backloops in essentially hierarchical systems arising from the absence of clear competitive dominance. The term 'transitivity' has been used to indicate the extent of deviation from a perfect competitive hierarchy and is quantifiable using an index of transitivity (Rubin, 1982; Tanaka and Nandakumar, 1994). Jackson (1981), in a review of competitive interactions between bryozoans and other organisms, underlined how subtle and complex interactions can be, and advised caution in the interpretation of even the simplest patterns.

Intraspecific spatial competition more often results in stand-offs or ties than interspecific competition (e.g., Karande and Swami, 1988), presumably because of the matching competitive abilities of the two protagonists. Indeed, in the case of colonial animals the tissues of the two individuals may even fuse to form a chimaera (e.g., Craig, 1994). Such fusion between different individuals is termed 'autosyndrome' in contradistinction to 'homosyndrome' referring to fusion between different parts of one individual. Barnes and Rothery (1996) found that intraspecific competition for space in an Antarctic bryozoan community was more likely to result in overgrowth when the competing colonies were on the upper than lower surfaces of rocks. They explained this pattern by the greater likelihood of colonies on undersides being closely related because of the weaker currents not carrying sibling larvae away.

The bryozoan *M. membranacea* produces stolons when competing for space with conspecifics (Harvell and Padilla, 1990; Padilla et al., 1996). These outgrowths are induced by the presence of neighbouring conspecifics and act to slow their rate of growth. Unmineralised stolons are also effective in blocking interspecific overgrowths among various other bryozoans (Osborne, 1984; Tzioumis, 1994).

The results of numerous studies of interspecific competition for space have revealed a general competitive hierarchy according to major animal group in the sequence: colonial tunicates (ascidians) and sponges>bryozoans>serpulid worms and barnacles (e.g., Gordon, 1972; Russ, 1982; Keough, 1999; Barnes and Lehane, 2001). Some studies have found an overall competitive dominance of colonial over solitary encrusters, whereas others have shown the reverse to be true. According to Jackson (1977) colonial animals are superior competitors for hard substrate space because their indeterminate growth permits continuous lateral substrate occupation and also because they are less prone to fouling.

A latitudinal cline in relative overgrowth dominance between cheilostome and cyclostome bryozoans has been suggested by Barnes and Dick (2000b). Whereas cheilostomes win most encounters in low and mid latitudes, cyclostomes fare better in high latitudes.

A recent review of competition between sponges and algae on coral reefs (McCook et al., 2001) noted that static observations are often made of algae overgrowing corals but that these do not necessarily prove that the algae are killing the corals. Instead, they may be overgrowing coral tissues damaged by predators, sedimentation, bleaching, etc. Aerts (2000) found that damage (lesions) in reef corals increased their susceptibility to overgrowth by sponges.

The intuitively attractive notion of a strong positive correlation between competitive ability and abundance is not always supported. Poor competitors for substrate space sometimes dominate on ephemeral and disturbed hard substrates because they often exhibit higher rates of recruitment than better spatial competitors (e.g., Jackson and Winston, 1982). Sebens (1986) found that cleared areas were colonised first by species which ranked low in the competitive hierarchy. Karande and Udhayakumar (1992) studied five species of cheilostome bryozoans colonising settlement panels suspended in Bombay Harbour over periods of 30 and 60 days. Overgrowth ability did not correlate with species abundance; in fact, the two least competitive species were the most abundant. Similarly, for bryozoans encrusting rocks in Alaska, the most abundant species were found to be low- or mid-ranked competitors (Barnes and Dick, 2000a), while the dominant bryozoan species in an Antarctic encrusting community wins fewer than 20% of interactions for space with other species (Barnes and Clarke, 1998). At Signy Island in the Antarctic, tunicates and sponges are the dominant competitors but bryozoans and polychaete worms are the most abundant encrusting groups present (Barnes et al., 1996).

Competitive interactions between encrusters and borers are poorly understood. Smyth (1988), however, noted the susceptibility of the boring ctenostome bryozoan *Penetrantia* to overgrowth by coralline algae.

6.3. Biofouling

The living surfaces of sessile organisms are often settled upon by the larvae (or other dispersal propagules) of other organisms. Such biofouling can be followed by successful growth of the settler across the surface of the host, sometimes completely smothering and killing the host. Therefore, organisms often exhibit strong reactions against being fouled, employing both mechanical and chemical defences. Mechanical mechanisms may also be used. These include mucus production in corals and the pincer-like structures found in echinoderm pedicellaria and some bryozoan avicularia (see Wahl, 1989). Many marine animals produce biologically active chemicals, some potentially having an anti-fouling function. The survey conducted by Uriz et al. (1991) on Mediterranean species showed the highest levels of such activity in sponges, bryozoans and tunicates. Antifungal and antibacterial activity was regarded as particularly important in discouraging fouling. If the formation of a bacterial film is prevented, then settlement of larvae of larger organisms which preferentially settle on such films may also be prevented. In this connection, a study of antibacterial activity through secondary metabolite production and fouling in four bryozoan species from Tasmania (Walls et al., 1993) showed that the two bryozoans with the highest levels of antibacterial activity were the least fouled. Despite the existence of potent antifouling defences, biofouling is often observed, especially on exoskeletons (e.g., Rubin, 1985), on lesions (e.g., Palumbi and Jackson, 1982), and on older parts of colonial animals where the zooids are senescent. Fungal fouling of bryozoan colonies has been hypothesised to stimulate self-overgrowth in some species (Sterflinger and Scholz, 1997).

Wahl and Mark (1999) concluded that most macrofouling species were facultative and non-specific rather than obligate, species-specific colonisers of living substrates. Among the most conspicuous biofoulers in temperate environments is the small polychaete worm *Spirorbis*. This genus is also often recorded in the fossil record as a biofouler (e.g., Gibson, 1992). Keen and Neill's (1980) study of encrusting communities on concrete blocks in the intertidal of Vancouver, Canada, found that even though blocks displayed a large amount of unoccupied primary space, *Spirorbis* recruited in considerably higher densities onto the surfaces of existing colonists, such as bryozoans and other serpulids, than it did on unoccupied substrate space. The biofouling ability of *Spirorbis* is counterbalanced by its tendency to be overgrown by spatial competitors (e.g., Gordon, 1972).

6.4. Disturbance, grazing and predation

Disturbance effects nearly all marine hard substratum communities and can be caused by physical or biological agents including predation. It has long been recognised that disturbance can act to regulate diversity by preventing a competitively dominant species from achieving a total monopoly (e.g., Paine, 1971). Sousa (1979a,b) undertook a now classic study of the effects of disturbance on communities inhabiting boulders subject to overturning through wave action. He found that small boulders which were overturned frequently supported low diversity communities, large, infrequently overturned boulders also had low diversities, whereas boulders of intermediate size exhibited the highest diversity in accordance with the "intermediate disturbance hypothesis". Two types of disturbance (Connell and Keough, 1985) of different severity are recognised by marine ecologists: Type I disturbances where the damaged patch remains surrounded by survivors belonging to the original community, and Type II disturbances where the patch becomes isolated from existing communities. Whereas patches resulting from Type I disturbances can be recolonised by vegetative growth of the organisms around, Type II disturbance patches tend to become recolonised by opportunistic species, mostly through larval recruitment.

Physical disturbance can be caused by storms, most notably hurricanes and typhoons which have devastating effects on tropical benthic communities (see Knowlton and Jackson, 2000, p. 403). Ice scour is another agent of disturbance impacting on shallow subtidal habitats in Arctic latitudes (Barnes, 1999).

Grazing predators are an important source of disturbance in many hard substrate communities. Breitburg's (1985) research using caged and uncaged settlement panels off Santa Barbara, CA, showed how only algal crusts, diatom/cyanobacterial films and short-lived filamentous algae became abundant on substrates exposed to high levels of grazing by echinoids and asteroids. On ungrazed substrates, other algae and sessile invertebrates were also common and overall diversity was higher. Grazing not only reduced diversity by physically removing species, but it also favoured some tolerant species which inhibited the recruitment of other species. For example, grazer-resistant coralline algal crusts precluded recruitment of bryozoans and polychaetes (Breitburg, 1984). A very different effect of herbivorous grazers (limpets and chitons) was found by Van Temelen (1987) in a rocky intertidal community in California. Here removal of algae by the grazers was important in allowing recruitment of barnacles. Day's (1983) study of settlement panels on the Great Barrier Reef showed how grazing on filamentous algae by herbivorous fishes also scraped off sessile animals and allowed the faster-growing algae to monopolise space. Grazing fishes significantly altered the composition of bioeroding communities of sponges and "worms" without changing the total rate of bioerosion on dead corals from the Great Barrier Reef (Sammarco et al., 1987). Kiene and Hutchings' (1994) bioerosional experiments led them to hypothesise that grazing modifies the ecological succession of endoliths by constantly exposing bare substrate that can be colonised by early successional boring species, thereby preventing the development of a 'mature' community of borers.

The rock lobster *Jasus lalandii* was identified by Barkai and Branch (1988) as a 'keystone' species controlling the communities developing on hard substrates in southern Africa. Exclusion of this crustacean allows mussels to dominate the community whereas an algal cover develops when it is present. Early successional cyclostome bryozoans were preyed upon by the asteroid *Patiria* in southern California, causing acceleration in the rate of succession towards a community diverse in the competitively dominant cheilostome bryozoans (Day and Osman, 1981).

Among numerous studies of the interplay between grazing predators and competitors in shaping hard substrate communities, Russ (1980) studied settlement panels placed in the subtidal of Victoria, Australia, leaving some of the panels accessible to grazing fishes but caging others to exclude the fishes. Caged panels became dominated within 7 months by two highly competitive ascidian species, whereas removal by fishes of newly settled ascidians led to higher diversities on the uncaged panels. The polarity of competitive dominance in overgrowth between two coralline algae is reversed by depth-related differences in the intensity of grazing by limpets (Steneck et al., 1991).

6.5. Succession

The pattern of ecological succession on hard substrates is determined by the interplay of recruitment, competition and disturbance (including predation). In a pioneering study, Osman (1977) identified five major factors important in the development and distribution of hard substrate communities on rocks: (1) larval selectivity; (2) seasonal fluctuations in larval abundance; (3) interactions within and between species; (4) substrate size; and (5) disturbance (rock overturning). Much interest has been focused on the extent to which succession is predictable, and whether it ever converges on a single, stable 'climax community' as in the classic models developed for terrestrial vegetation (see Greene and Schoener, 1982; Turner and Todd, 1993).

Sutherland and Karlson (1977) deployed ceramic settlement panels off Beaufort in North Carolina and found that panel undersides converged towards an equilibrium diversity of 10 species after 21/2 to 31/2 years. However, the pattern of succession varied greatly according to when the panels were first submerged, both on monthly (i.e., seasonally) and yearly (i.e., interannually) scales. Larval recruitment patterns were variable, and established colonists tended to inhibit (e.g., McGuinness, 1988) rather than pave the way for later colonists. Most colonists lived for less than a year and were usually replaced by different species. Sutherland and Karlson contrasted this pattern of succession with the classical succession seen in terrestrial plant communities, attributing the differences to: (1) the short-lived adults; (2) the fact that the colonists do not prepare the substrate for later arrivals; and (3) the lack of stored seeds of successional species. Longer-term findings from the Beaufort study prompted Sutherland (1981) to develop the concept of multiple stable points: resident communities which succeed in resisting recruitment over the short term may be ephemeral over the longer term because of the continued recruitment of other species, overgrowth, sloughing off and senility.

In contrast to the results of Sutherland et al., Keough and Butler (1983) found no evidence of an equilibrium species diversity among animals attached to shells of the bivalve *Pinna* at Edithburgh, South Australia. Here, the variance in number of species on individual shells was extremely high. A study by Turner and Todd (1993) using settlement panels at intertidal sites in NE Scotland for 5–6 month periods found no evidence of a predictable order of colonisation; rather, the changing patterns of species on the panels appeared to be the result of seasonal variations in the availability and abundance of larvae (i.e., due to supply-side variability).

A study of settlement panel colonisation in Puget Sound, Washington showed a clear species–area effect, larger panels supporting a greater number of species (Schoener and Schoener, 1981). Diversity on individual panels was found to increase steeply for the first ten weeks of immersion, during which time extinction rates were negligible, before leveling-off for the next 80 weeks of study (Fig. 18). Other studies of species–area effects on hard substrates include McGuinness (1987) and Maughan and Barnes (2000).

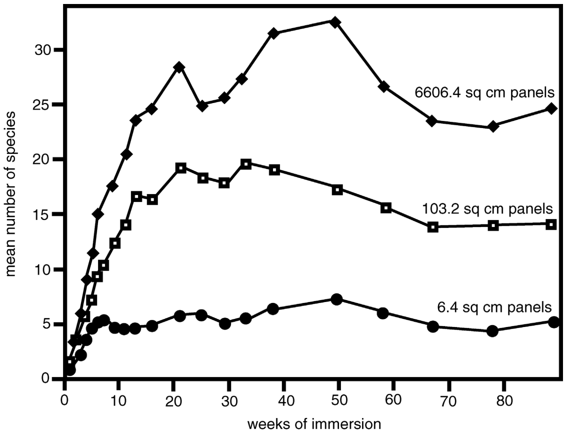


Fig. 18. Species colonisation curves for settlement panels of three different sizes deployed at about 1 m below sea level in Puget Sound, Washington, USA, showing a strong species-area effect. After Schoener and Schoener (1981).

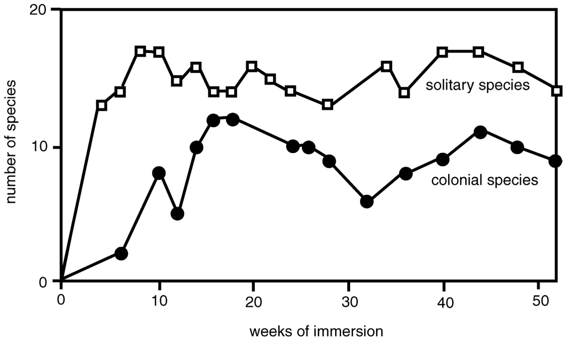


Fig. 19. Species colonisation curves for solitary and colonial species on settlement panels in the Bay of Santa Marta, Colombian Caribbean. After Garcia and Salzwedel (1995).

Superior spatial competitors, not surprisingly, may increase through time at the expense of early, poorly competitive colonists. For example, Jackson (1977) deployed settlement panels in cryptic settings in Jamaica and showed how initial dominance by serpulids, which are poor spatial competitors in this habitat, changed to sponge dominance after 14 months of immersion.

Garcia and Salzwedel (1995) used asbestos panels to study the succession of fouling organisms in the Caribbean off Colombia, focusing particularly on the

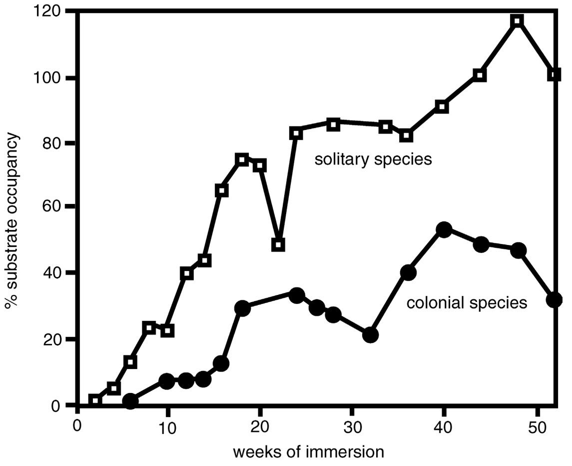


Fig. 20. Area colonisation curves for solitary and colonial species on settlement panels in the Bay of Santa Marta, Colombian Caribbean. Total coverages of more than 100% are possible because of epizooism. After Garcia and Salzwedel (1995).

relative colonisation by colonial and solitary species. Diversity on the panels reached a plateau of about 25 species after 10–16 weeks of submergence, a level maintained for the 52 weeks of the study. The diversity plateau was attained more rapidly by solitary species than it was by colonial species (Figs. 19 and 20). The sessile epibenthic species colonising lava fields of different ages (17, 55 and several thousand years) around a volcano in the Kuril Islands were studied by Oshurkov and Ivanjushina (1992). They found an increase in species richness between the 17- and 55-year lavas but a slight decline between the latter and the ancient lava.

In contrast to findings from the tropics, studies in temperate environments (Shin, 1981; Schoener and Schoener, 1981; Greene and Schoener, 1982) have usually shown a switch during succession from colonial to solitary species (Fig. 21). This pattern is largely explained by the fact that individuals of the solitary species are typically longer-lived, and are able to form dense aggregations through gregarious larval settlement (Greene et al., 1983).

Depth can be an important correlate of successional variations. Hirata (1987) studied the colonisation over 3 years of settlement panels placed at depths of 1, 2.5, 4 and 5.5 m in Nabeta Bay, Japan. Three successional stages could be recognised: Stage 1 was characterised by the barnacle *Balanus* and spirorbid worm *Dexiospira*, Stage 2 by the ascidian *Diplosoma*, and Stage 3 by the oyster *Crassostrea*. Panels at the deepest station failed to reach stage 3 during the 3-year period of study. Diversity rose steeply for 2 to 6 months after panel immersion to about 10 species and then leveled out in panels from the two shallower depths whereas it declined somewhat in the two deeper stations. Pisano and Boyer (1985) found that colonisation by bryozoans of settlement panels placed at 15 m in the Ligurian Sea followed a similar pattern but was slower than panels deployed at 3 m depth. In contrast, colonisation rates were found to be lower in shallow (5–8 m) than in deeper (25 m) water sites off Signy Island in the Antarctic (Stanwell-Smith and Barnes, 1997; Fig. 22). Relative to temperate and tropical environments (Fig. 23), low recruitment and slow growth in the cold-waters of the Antarctic meant that after 15 months an

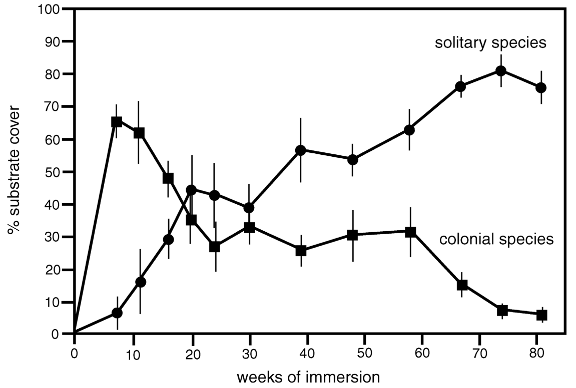


Fig. 21. Trends in the relative coverage through time of solitary and colonial species on settlement panels deployed at 1–1.3 m below sea level at Bremerton, WA, USA. After Greene and Schoener (1982).

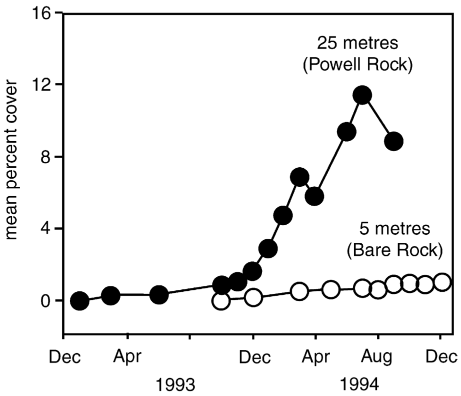


Fig. 22. Changes in the percentage cover of organisms during two years on settlement panels deployed at two different depths off Signy Island, Antarctica. After Stanwell-Smith and Barnes (1997).

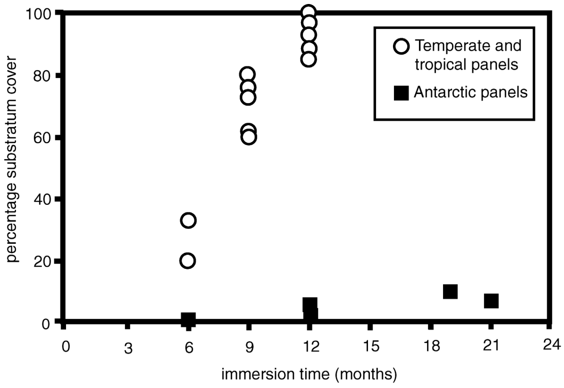


Fig. 23. Differences in the colonisation of sublittoral settlement panels deployed in the Antarctic compared with temperate and tropical stations. After Stanwell-Smith and Barnes (1997).

average of less than 2% of the surface of panels submerged at 5 m were covered, and less than 6% of those submerged at 25 m. Depth also played a significant role in succession on 8 year old lava grounds at Jan Mayen where Gulliksen et al. (1980) found that communities at depths of less than 15 m resembled those of old lava grounds more than did communities from deeper sites. This they attributed to the more severe physical conditions limiting community complexity in shallow waters.

Seabed characteristics may influence the composition of hard substrate communities, at least those developing on settlement panels. In a 1-year study off South Carolina, Van Dolah et al. (1988) found that colonial species (colonial ascidians and hydroids) dominated on panels placed above hard bottoms whereas solitary species (solitary ascidians and barnacles) were dominant on panels above sandy bottoms. It is not unreasonable to surmise that natural substrates, including ancient examples, will show similar patterns.

The effect of a single taxon on substrate characteristics and future development is well illustrated by Gulliksen's (1980) work in a fiord in Norway. After a heavy settlement of the large solitary ascidian *Ciona* in 1974, sediment accumulation on the rock surface increased and with it the abundance of infaunal organisms to the detriment of epifaunal species.

A study of shallow marine bioerosion off Rhodes (Bromley et al., 1990) deployed marble blocks. These were rapidly colonised by endolithic algae which attracted grazing chitons and echinoids. Boring sponges did not become visible until year 2 of the study, and after 5 years the blocks were deeply bioeroded.

7. Ancient hard substrate communities

7.1. Precambrian communities

Precambrian hard substrate communities are surprisingly common, although of the expected low diversity.

7.1.1. Encrusters on inorganic hard substrates

Many stromatolites were initiated on intertidal and subtidal rocky substrates. An example would be the 3.3–3.5 Ga stromatolites of the Fig Tree Group in South Africa, which formed directly on silicified komatiitic lava flows (Byerly et al., 1986). The bacterial mats adhered very closely to the contours of the surfaces, forming structures which mirrored surface irregularities for at least the first few layers. Precambrian stromatolites grew luxuriously, probably in part because there were few if any macroinvertebrate grazers to limit their distribution (Seilacher, 1999). Butterfield (2000, p. 387) described late Mesoproterozoic bangiacean red algae which grew as filaments attached to "firm" and possibly hard substrates in a shallow marine sequence of the Hunting Formation of Somerset Island, Arctic Canada. These algae may be the earliest known examples of complex multicellularity; they possess holdfasts and stood erect above the substrate.

7.1.2. Encrusters on organic hard substrates

The earliest known example of epibiosis (biofouling) is found in stromatolites of the Mesoproterozoic Gaoyuzhuang Formation in northern China (Seong-Joo et al., 1999). These are coccoid microfossils of chamaesiphonalean cyanobacteria which settled in large numbers on the cyanobacterial sheaths of the stromatolite builders. Seong-Joo et al. (1999) suggest that this epibiosis represents either an early adaptation to competition for attachment space, or it is evidence for a specialised mutualism between the host and epibiotic bacteria.

7.1.3. Cryptic hard substrate communities

Turner et al. (1993) describe reefs from the Neoproterozoic formed of calcareous microfossils. From the roofs of cavities within these structures hung a clotted micritic organism similar to *Renalcis*.

7.1.4. Bioerosion

Fossils of endoliths have only recently been discovered in Precambrian rocks (Campbell, 1982; Knoll et al., 1986, 1989; Zhang and Golubic, 1987; Al-Thukair and Green, 1988; Green et al., 1988). These are, in all cases, microorganisms which have excavated very small cavities in sedimentary grains such as ooids or in the laminae of stromatolites. Some of them appear to have been photosynthetic, much like many modern microbial endoliths (Golubic et al., 1975). The first apparent predatory borings are described from the late Precambrian (Bengtson and Zhao, 1992). These are simple round holes in the tubular mineralised skeletons of *Cloudina*.

7.2. Cambrian communities

Hard substrate communities in the Cambrian are considerably more diverse than those of the Precambrian, but they are still impoverished compared to Ordovician and later assemblages. Stromatolites are still present on hard surfaces, as they will be throughout the Phanerozoic under environmental conditions which generally excluded grazers (Monty, 1981). Late Cambrian encrusting communities show a jump in diversity, albeit small, with the appearance of early adherent echinoderms.

7.2.1. Encrusters on inorganic hard substrates

Frykman (1980) briefly described "crater-like" encrusters, early pelmatozoans of some type, from Middle Cambrian hardgrounds in Greenland. From the same hardgrounds, Palmer (1982) recorded indeterminate acrotretid brachiopods. Brett et al. (1983) described an upward-facing hardground community from the Upper Cambrian of Montana and Wyoming which includes abundant pelmatozoan holdfasts (probably of a single crinoid species), a *Renalcis*-like alga, and isolated plates of an edrioasteroid, a carpoid, and two other unidentifiable echinoderms.

7.2.2. Encrusters on organic hard substrates

Episkeletobionts are rare in the Cambrian. There are a few inarticulate brachiopods and eocrinoids found on arthropod fragments (Lescinsky, 2001). Daley (1996) described solute echinoderms attached to trilobite fragments which may themselves have been cemented into the seafloor.

7.2.3. Cryptic hard substrate communities

Lower Cambrian cryptic communities are surprisingly common and diverse. The cryptic spaces are found in archaeocyath and radiocyath reefs, within calcified microbial mounds, in pockets underneath early cemented carbonate sediments, and underneath skeletal debris (Kobluk and James, 1979; Kobluk, 1981a,b,d, 1985; Rees et al., 1989; James and Gravestock, 1990; Fröhler and Bechstädt, 1992; Wood et al., 1993; see for review the paper by Zhuravlev and Wood, 1995). These early cryptic biotas included cyanobacteria, archaeocyaths, sponges, possible sponge borings, and various problematica, many of which are found only in cryptic spaces. Cambrian cavities tend to be smaller than those found in later systems, and they were quickly filled with sediment and early cements. Nevertheless, the diverse cryptic inhabitants showed possible competition for space (through overgrowths) and significant taxonomic and structural differences from their counterparts on exposed surfaces. Among the archaeocyaths, for example, exposed surfaces have solitary ajacicyathids and numerous irregular, branching forms, whereas the crypts have solitary irregulars and solitary chambered forms (Zhuravlev and Wood, 1995). Presumably, these early cryptic organisms were exploiting the same advantages of cavity-dwelling as modern cryptobionts: refuge from most predators and reduced environmental stresses in general.

7.2.4. Bioerosion

Bioerosion in the Cambrian consisted almost entirely of small, simple, rounded holes excavated into skeletons and hardgrounds. These traces are rare, implying that bioerosion was an insignificant geological process in the Cambrian. Conway Morris and Bengtson (1994) reviewed the array of borings known in Cambrian skeletons, demonstrating that some, especially those in brachiopods, were almost certainly excavated by predators. Microborings in Middle Cambrian trilobite cuticle, apparently formed by boring algae and cyanobacteria, are illustrated and briefly discussed by Geyer and Malinky (1997). Runnegar (1985) described microscopic, long, unbranched tunnels and short vertical holes in Cambrian mollusc shells which appear to have been excavated by photosynthetic endolithic algae. The cylindrical macroboring *Trypanites* is known from numerous Lower Cambrian hardgrounds, but is strangely rare in Middle and Late Cambrian and Early Ordovician hard substrates (James et al., 1977; Palmer, 1982). Chow and James (1992, p. 120) briefly described and illustrated "*Trypanites*-like borings" which truncate cement crystals in an Upper Cambrian hardground in Newfoundland, but the full shape and size of these excavations is unknown. Kobluk (1981b) described microscopic scalloped-shaped excavations and associated carbo-

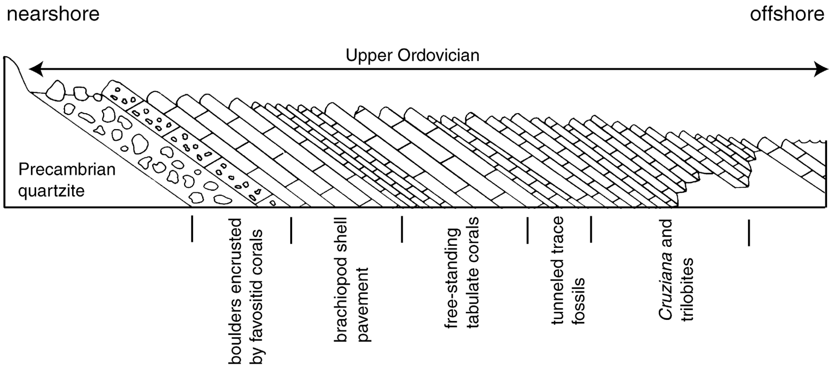


Fig. 24. Stratigraphic transect across a Late Ordovician rocky shoreline near Churchill, Manitoba, Canada, showing biotic zonation. After Johnson et al. (1988).

nate chips in archaeocyathan cavity walls in the Lower Cambrian of southern Labrador. These are similar to traces made by endolithic sponges, such as the modern *Siphonodictyon* and *Cliona*.

7.3. Ordovician communities

The Ordovician was a golden age for epizoans on hard substrates, at least for those which left skeletal evidence. Much of the increased abundance and diversity of Ordovician hard substrate organisms is due to the increase in hard substrate availability since the Cambrian.

7.3.1. Encrusted inorganic hard substrates

Carbonate hardgrounds reach their peak abundance in shallow marine environments largely due to the prevailing Calcite Sea conditions which facilitated early aragonite dissolution and synsedimentary calcite cementation (see for review Wilson and Palmer, 1992). Even rocky shores can be well preserved in Ordovician deposits (Jones and Pugh, 1950; Mergl, 1983; Harland and Pickerill, 1984; Kobluk, 1984; Johnson and Baarli, 1987, 1999; Johnson et al., 1988; Johnson and Rong, 1989; Fig. 24). Hardgrounds often support diverse communities (Fig. 25). Many bryozoan genera encrusted hardgrounds

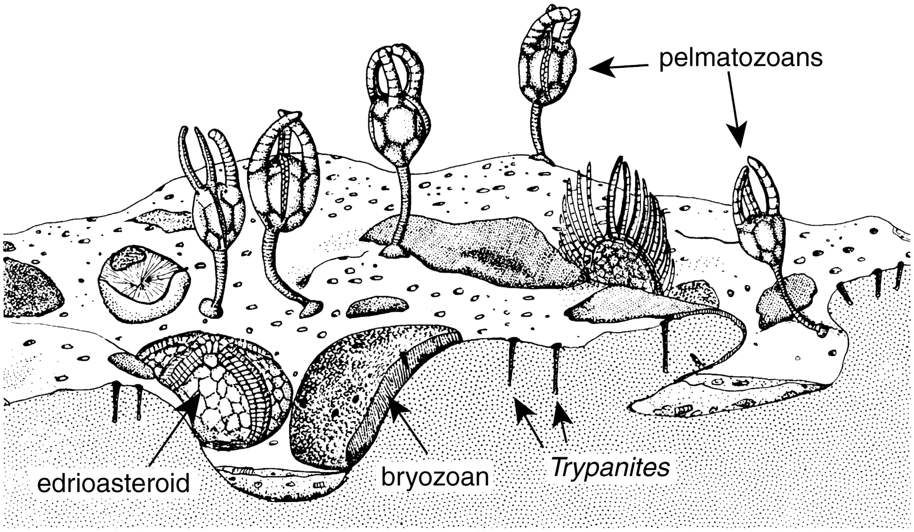


Fig. 25. Reconstruction of an Ordovician hardground community from near Kirkfield. Ontario, Canada. After Brett and Liddell (1978).

and associated cobbles, especially cyclostomes (see, for example, Wilson, 1985; Taylor and Wilson, 1994) and trepostomes (see, for examples, Brett and Brookfield, 1984; Wilson, 1985). Encrusting echinoderms also dramatically increase in diversity and abundance on Ordovician hardgrounds (Guensburg and Sprinkle, 1992). These include edrioasteroids (Brett and Liddell, 1978; Palmer, 1982; Wilson, 1985; Guensburg, 1988; Meyer, 1990), crinoids (Brett and Liddell, 1978; Guensburg, 1984, 1992) and other pelmatozoans (Guensburg, 1991; Guensburg and Sprinkle, 1992; Wilson et al., 1992). Additional encrusting organisms on Ordovician hardgrounds, cobbles and other rocky substrates are sphenothallid worms (Bodenbender et al., 1989; Neal and Hannibal, 2000), cornulitids (Wilson, 1985), corals (Palmer, 1982; Johnson and Baarli, 1987; Johnson et al., 1998; Elias and Young, 2000), articulate and inarticulate brachiopods (Palmer, 1982), crustoid graptolites (Mitchell et al., 1993), and problematica (Mergl, 1984, for which see Taylor, 1984a).

7.3.2. Cryptic hard substrate communities

Ordovician cryptic encrusting and boring communities have been well described. The most common cavities are within bryozoan reefs (Cuffey, 1974; Kobluk, 1980, 1981c) and underneath hardground ledges (Brett and Liddell, 1978). These cavities are considerably larger than their Cambrian counterparts, and in many cases they appear to have remained open for long periods. Encrusters include numerous bryozoans, stalked echinoderms and calcareous algae. Many cavities also housed worm-like endolithic organisms which produced the boring *Trypanites* (Fig. 3E). Interestingly, the Ordovician cryptic communities are remarkably similar to those found on the adjacent exposed hard substrates, showing at best only a weak polarity between these environments.

7.3.3. Encrusted organic hard substrates

Hard substrates provided by shells are more common in Ordovician deposits than in their Cambrian equivalents (Kidwell, 1994). The encrusting taxa on these organic hard substrates are virtually the same as those on hardgrounds, cobbles and rocky shores. The most commonly encrusted shells are those of brachiopods (Morris and Rollins, 1971; Richards, 1972, 1974a; Alexander and Scharpf, 1990; Lescinsky, 1995; Lescinsky, 1996a) and trilobites (Clarkson and Tripp, 1982; Kácha and Saric, 1995; Brandt, 1996; Budil and Saric, 1995; Taylor and Rozhnov, 1996). Because most mollusc shells were aragonitic in the Ordovician, encrusters are often found on their early cemented internal and external moulds (Waddington, 1980; Palmer et al., 1988; Wilson and Palmer, 1992; Gabbott, 1999), but some are found on calcitic bivalves (Morris and Felton, 1993). The skeletons of rugose corals are also often encrusted (Elias and Buttler, 1986; Harland and Pickerill, 1987). Articulate brachiopods have been found attached to trepostome bryozoans (Richards, 1972; Harper and Pickerill, 1996) and conulariids (Harland and Pickerill, 1987), and inarticulate brachiopods are found on algae and graptolites (Botting and Thomas, 1999). Soft-bodied encrusters of the Ordovician have been preserved through epibiont bioimmuration (see Section 8.5) on mollusc shells. Ordovician epibiont bioimmurations include what appear to be hydroid cnidarians (Wilson et al., 1994). Also in the Ordovician of upper midwestern North America are cavities in trepostome bryozoan skeletons formed when the bryozoan grew up and around an encrusting, soft-bodied, stoloniferous animal, forming the trace fossil *Catellocaula* through bioclaustration (Palmer and Wilson, 1988; Fig. 3C).

7.3.4. Bioerosion

Ordovician bioerosion was more common, and the bioeroders more diverse, than their Cambrian counterparts. Nevertheless most Ordovician borings are simple, small holes. *Trypanites* (Fig. 2A and 3E) is the most common boring ichnogenus, found abundantly in hardgrounds (Byers and Statsko, 1978; Kobluk et al., 1978; Brett and Liddell, 1978; Palmer and Palmer, 1977; Palmer, 1982; Wilson and Palmer, 1992; Dronov et al., 1996), cobble-size reworked concretions (Wilson, 1985, 1987), rocky shores (Desrochers and James, 1988), and massive skeletons such as those of trepostome bryozoans (Opalinski and Harland, 1980; Kobluk and Nemcsok, 1982) and rugosan corals (Elias, 1980, 1986). Probable sponge borings have also been recorded from the Ordovician, but they are rare (Palmer and Palmer, 1977; Lindström, 1979; Kobluk, 1981c; Pickerill and Harland, 1984). The first bivalve borings (*Petroxestes*, formed by mytilids) are also known from the Ordovician, but they are thus far only locally common in the upper midwest of

North America (Pojeta and Palmer, 1976; Wilson and Palmer, 1988; Fig. 3A). An unusual macroboring, representing the first occurrence of the ichnogenus *Gastrochaenolites*, has been recently described by Ekdale and Bromley (2001) (see also Ekdale et al., 2002) from Ordovician (Volkhovian) hardgrounds in Sweden. This vase-shaped trace (*G. oelandicus*) is thus far found in only one formation. The trace-maker is unknown, but it almost certainly was not a bivalve.

Felton (personal communication to M.A.W.) has recently found what appear to be acrothoracican barnacle borings in Ordovician platyceratid gastropods almost identical to those described from the Devonian by Baird et al. (1990). Durophagy is known from the Ordovician, such as the shell breakage recorded from the Cincinnatian (Alexander, 1986), but predatory borings have been difficult to distinguish. Lescinsky and Benninger (1994) pointed out how pressure solution can produce structures resembling predator traces, and the ubiquitous *Trypanites* borings sometimes cut through shells in cemented sediments, forming holes easily mistaken for predator drillings (see Bucher, 1938; Kaplan and Baumiller, 2000, with alternative interpretations given respectively by Richards and Shabica, 1969; Wilson and Palmer, 2001; the borings in Cameron, 1967, are also not likely to have been those of predators). Carriker and Yochelson (1968) attribute a particular type of round hole in Ordovician brachiopod shells to a soft-bodied epibiont, not a predator.

Ctenostome bryozoan borings are a special type of ichnofossil in which the zooids of the colony immersed themselves in a calcareous shell through etching. These borings are very common on shallow marine shells in the Ordovician, particularly on strophomenid brachiopods (Pohowsky, 1974, 1978; Mayoral, 1991). Microbioerosion is also known from Ordovician shells (Hessland, 1949; Kobluk and Risk, 1977; Olempska, 1986; Elias and Lee, 1993), skeletal grains (Klement and Toomey, 1967) and limestones (Kobluk, 1984; Podhalanska, 1984; Podhalanska and Nõlvak, 1995).

7.4. Silurian communities

Hard substrate communities in the Silurian continued the themes from the Ordovician. Encrusters were still dominated by bryozoans and echinoderms, particularly crinoids, and borings were mostly simple *Trypanites*.

7.4.1. Encrusted inorganic hard substrates

Encrusting communities have been described from carbonate hardgrounds (Halleck, 1973; Franzén, 1977; Cherns, 1980), cobbles (Kissling, 1973; Jones et al., 1979), and rocky shore substrates (Bridges, 1975; Cherns, 1982; Johnson and Baarli, 1987; Keeling and Kershaw, 1994; Rong and Johnson, 1996; Calner and Säll, 1999; Rong et al., 2001; Johnson et al., 2001). They differ little from their Late Ordovician counterparts, except that encrusting tabulate corals are more diverse and foraminiferans first appear upon them (Palmer, 1982; Wilson and Palmer, 1992).

7.4.2. Encrusted organic hard substrates

Encrusted organic hard substrates include abundant shells (see, for examples Franzén, 1974; Hurst, 1974; Watkins, 1981; Liddell and Brett, 1982; Prokop and Turek, 1983; Spjeldnaes, 1984; Turek, 1987; Watkins and McGee, 1998; Lebold, 2000) and stromatolites (Cherns, 1982). Silurian episkeletobionts are most commonly reported from crinoids (Franzén, 1974; Brett and Eckert, 1982; Liddell and Brett, 1982; Watkins and McGee, 1998; Peters and Bork, 1998), molluscs (Holland, 1971; Prokop and Turek, 1983; Turek, 1987), bryozoans (Taylor and Brett, 1996), brachiopods (Hurst, 1974; Watkins, 1981), stromatoporoids (Kershaw, 1980; Nield, 1986a,b; Carthew, 1987; Segars and Liddell, 1988; Lebold, 2000) and trilobites (Taylor and Brett, 1996). Episkeletobionts are also reported as bioclaustrations in crinoids (Brett, 1978; Eckert, 1988). The first cementing articulate brachiopods appear on Silurian shells (Cowen and Rudwick, 1967; Nield, 1986a).

7.4.3. Cryptic hard substrate communities

The cryptic faunas of the Silurian are similar to those of the Ordovician (Scoffin, 1972; Spjeldnaes, 1975; Kershaw, 1980). Bryozoans dominate the communities (Fig. 2C), which are most commonly found on the undersides of stromatoporoids, tabulate corals, and larger bryozoans, but articulate brachiopods and cornulitids may also be prominent encrusters.

7.4.4. Bioerosion

Bioerosion in the Silurian was also similar to that of the Ordovician. Macroborings consist primarily of *Trypanites* excavated into hardgrounds (Halleck, 1973; Cherns, 1980; Pemberton et al., 1980) and stromatoporoids (Kershaw, 1980; Nield, 1984; Segars and Liddell, 1988). *Petroxestes*, originally known only from the Upper Ordovician of the North American midwest, has recently been described in Lower Silurian stromatoporoids in eastern Canada (Tapanila and Copper, 2002). Microbioerosion is represented by endolithic rhodophytes and eubacteria (Kazmierczak and Golubic, 1976; Campbell et al., 1979; Campbell, 1980; Bundschuh et al., 1989; Bundschuh and Balog, 2000) and microborings in mollusc shells (Liljedahl, 1986).

7.5. Devonian communities

7.5.1. Encrusted inorganic hard substrates

Encrusted and bored inorganic hard substrates are less common in the Devonian than they were in the Silurian and Ordovician, but they are still present. These surfaces include carbonate hardgrounds (Hecker, 1935, 1983; Koch and Strimple, 1968), pebbles and cobbles (Fannin, 1969; Tucker, 1971, 1973; Baird, 1976, 1978, 1981; Landing and Brett, 1987) and rocky shores (Dvorak, 1957; Playford and Lowry, 1966).

7.5.2. Encrusted organic hard substrates

Devonian encrusting communities are better known on shells than any other hard substrate. These communities are no longer dominated by bryozoans and echinoderms, although they are still common (see Solle, 1968; Koch and Strimple, 1968; Franzén, 1974; Alvarez and Taylor, 1987; Brice and Mistiaen, 1992; Gibson, 1992). ‘Spirorbid’ worms, hederellids and tabulate corals are more abundant as encrusters on shells (Ager, 1961; Hoare and Steller, 1967; Kiepura, 1965, 1973; Marek and Galle, 1976; Brassel, 1977; Pitrat and Rogers, 1978; Kesling et al., 1980; Sparks et al., 1980; Bonem, 1982; Brett and Cottrell, 1982; Alvarez and Taylor, 1987; Bordeaux and Brett, 1990; Brice and Mistiaen, 1992; Grimm, 1998). Stromatoporoids provided large surfaces for encrusters (Cockbain, 1984). Encrusting brachiopods and bryozoans have recently been noted on Devonian oncoids in western North America (Rodriguez and Gutschick, 2000).

7.5.3. Cryptic hard substrate communities

Few Devonian cryptic assemblages are thus far definitely known. Liddell and Brett (1981) described *Spirorbis*, *Hederella* and the brachiopod *Heteralosia* encrusting the undersides of coral heads from the Middle Devonian of Michigan. Copper (1996) described cemented atrypid brachiopods from underneath tabulate corals and stromatoporoids. It is also possible that the *Trypanites* borings, preserved in solution-opened joints at the Silurian–Devonian disconformity in Ontario, are Devonian in age (Kobluk et al., 1977).

7.5.4. Bioerosion

Devonian macroborings are still relatively small and dominated by *Trypanites* (Pemberton et al., 1980, 1988) and the similar but distally clavate *Palaeosabella* (Cameron, 1969; Thayer, 1974). Acrothoracican barnacles borings make their appearance in the shells of platyceratid gastropods (Baird et al., 1990) and brachiopods (Rodriguez and Gutschick, 1977); they are also known in oncoids (Rodriguez and Gutschick, 2000). Ctenostome bryozoan borings are described in brachiopod shells by Richards (1974b), Pohowsky (1978) and Vogel et al. (1987). “Sponge” borings in shells and carbonate rocks are reported in older literature (Fenton and Fenton, 1932; Solle, 1938) and in Vogel et al. (1987), but their origins are still unclear. Microborings in the Devonian are still mostly attributed to algae and/or fungi (Kobluk and Risk, 1974; Vogel, 1987; Vogel et al., 1987). What are almost certainly predatory borings, attributed to gastropods, have been reported in Middle Devonian brachiopod shells (Rodriguez and Gutschick, 1970; Smith et al., 1985; Leighton, 2001) and blastoids (Baumiller, 1993). For a review of Phanerozoic predatory boring, see Kowalewski et al. (1998, 2000), Harper et al. (1998, 1999), and Leighton (2001).

7.6. Carboniferous communities

Until recently, encrusting and boring organisms were considered relatively rare on hard substrates in the Carboniferous (Wilson and Palmer, 1992; Alvarez and Taylor, 1987). Lescinsky (1997), however, made the point that common and low-diversity Carboniferous hard substrate communities may have been overlooked in favour of the rare "spectacular" examples, although low primary productivity could have contributed to a genuine scarcity (Lescinsky, 1994). According to Nicol (1978), the first cemented bivalves appeared in the Early Carboniferous.

7.6.1. Encrusted inorganic hard substrates

Encrusting tabulate corals have been described on Upper Carboniferous rockgrounds (Webb, 1993) from Arkansas, and Lower Carboniferous edrioasteroids are known from cobbles in Britain (Smith, 1983) and hardgrounds in Kentucky (Sumrall, 2001). Dix and James (1987) described bryozoan/microbial bioherms on a karstic limestone surface. Palmer (1982) recorded from Carboniferous carbonate hardgrounds encrusting foraminiferans, rugose corals, tabulate corals, "worm" tubes, bivalves, fenestellid and fistuliporid bryozoans, hederellids, blastoids, edrioasteroids and crinoids. Carbonate hardgrounds, though, are rare in the Carboniferous.

7.6.2. Encrusted organic hard substrates

Epibionts in particular are now well known from this interval. Spiriferid brachiopod substrates in North America are often encrusted by trepostome, fenestellid and ctenostome bryozoans, hederellids, cornulitids, edrioasteroids, foraminiferans, and brachiopods (Nelson and Bolton, 1980; Powers and Ausich, 1990; Lescinsky, 1997). Legrand-Blain and Poncet (1991) describe a similar assemblage of encrusters on brachiopods from Algeria, with the addition of calcareous algae and tabulate corals. Demosponges served as hard substrates for bryozoans, "worm" tubes, rugose corals and articulate brachiopods (Gundrum, 1979). Demosponges were themselves significant epibionts in some muddy substrates where shells provided the only hard substrate (Molineux, 1994). Attached vermiform gastropods, which appear to be convergent with vermetids, make their first appearance on Lower Carboniferous stromatolites in Great Britain (Burchette and Riding, 1977). Note, however, that Weedon (1990) considered these fossils not to be gastropods. Cemented bivalves appear first in the Lower Carboniferous (Nicol, 1978). Episkeletobionts are also known on crinoid stems (Powers and Ausich, 1990; Donovan and Lewis, 1999; Wyse Jackson et al., 1999), rugose corals (Condra and Elias, 1944; Sando, 1984; Nakazawa, 2001), bivalves (Trueman, 1942; Kammer et al., 1987), bellerophontids (Taylor, 1985), brachiopod spines (Billing, 1991), fenestrate bryozoans (Condra and Elias, 1944) and cephalopods (Seilacher, 1963). A "loosely attached" and apparently mobile foraminiferan is known from biogenic substrates in England (Cossey and Mundy, 1990) and North America (Toomey, 1972).

7.6.3. Cryptic hard substrate communities

Bonem (1977) describes a diverse Pennsylvanian cryptic community in biohermal cavities. It again contains abundant, diverse bryozoans, along with rugose and tabulate corals and *Trypanites* borings. Suchy and West (1988) found numerous attached brachiopods, bryozoans, calcareous worm tubes, rugose corals, and the borings *Rogerella* and *Caulostrepsis* underneath the overhangs of Pennsylvanian chaetetid colonies.

7.6.4. Bioerosion

Borings are also more common in Carboniferous hard substrates than were originally estimated (Wilson and Palmer, 1992). Predatory borings and other signs of predation in brachiopod shells, probably produced by gastropods, are now well known (Ausich and Gurrola, 1979; Alexander, 1981; Baumiller et al., 1999), as are "non-predatory" holes made by platyceratid gastropods in crinoids (Baumiller, 1990). Acrothoracican barnacle borings are common in brachiopod shells (Ettensohn, 1978; Lescinsky, 1997) and limestone cobbles (Webb, 1993, 1994). The earliest known *Gastrochaenolites*, apparently constructed by mytilid bivalves, is found in the Upper Carboniferous rockgrounds in Arkansas (Webb, 1994; Wilson and Palmer, 1998; Fig. 3D), and *Caulostrepsis* is present in Upper Carboniferous rockgrounds of Utah (Loope, 1994) and Kansas (West and Palmer, 1983). Microborings are thus far not common in the Carboniferous; the ichnogenera *Eurygonum* and *Scolecia*, probably produced by cyanobacteria, are possibly known from the Lower Carboniferous of Utah (Vogel, 1991; Glaub et al., 1999).

7.7. Permian communities

Hard substrate communities are poorly known in the Permian.

7.7.1. Encrusted inorganic hard substrates

Carbonate hardgrounds have yet to be documented in the Permian (Wilson and Palmer, 1992). A rocky shore with encrusting bryozoans has been described by Herrmann (1956), and Runnegar (1979) described a shelly fauna probably associated with a rocky shore.

7.7.2. Encrusted organic hard substrates

Rare encrusters on Permian shells include cyclostome bryozoans (Taylor, 1985), serpulids, productacean brachiopods and "oyster-like bivalves" (Newell and Boyd, 1970).

7.7.3. Cryptic hard substrate communities

Calcified microbial layers have been reported from cavities in Permian *Tubiphytes* bioherms (Flugel, 1977), and foraminiferans and calcareous algae are found on cements within reef framework cavities (Mazzullo and Cys, 1979; Toomey and Cys, 1979). Wood et al. (1994, 1996) dramatically challenged current images of the Permian Capitan Reef of Texas and New Mexico by showing that most of the calcareous sponges formed pendants in cavities rather than upright exposed pillars. These cavities also contained bryozoans, rugose corals, crinoids, and calcareous algae.

7.7.4. Bioerosion

Permian borings described in the literature were produced by barnacles (Schlaudt and Young, 1960; Simonsen and Cuffey, 1980), thallophytes (Balog, 1996; Weidlich, 1996), cyanobacteria/cyanophyta (Glaub et al., 1999; Vogel et al., 1999), sponges (Weidlich, 1996), polychaetes (Teichert, 1945; Newell and Boyd, 1970), brachiopod pedicles (Alexander, 1994), and predatory gastropods (Kowalewski et al., 2000).

7.8. Triassic communities

Triassic hard substrate communities are scarcely more diverse and abundant than their Permian counterparts, and stand in marked contrast to the diverse mollusc-dominated assemblages of the Jurassic and Cretaceous.

7.8.1. Encrusted inorganic hard substrates

Encrusters, such as bivalves, crinoids, bryozoans, serpulids and brachiopods, are known primarily from carbonate hardgrounds (Jahnke, 1966; Wendt, 1970; Hagdorn and Mundlos, 1982; Hagdorn and Simon, 1983; Zwenger, 1987, 1988) and cobbles (Kostecka, 1978).

7.8.2. Encrusted organic hard substrates

Brachiopod (Michalík, 1976, 1977; Taylor and Michalík, 1991) and mollusc shells are found encrusted in the Triassic (Kieslinger, 1925; Seilacher, 1954; Meischner, 1968; Aigner, 1977, 1979; Ziegler and Michalík, 1980; Duringer, 1985; Marquez-Aliaga et al., 1986; Blendinger, 1991), but they are rarely common. Stiller (2001) recorded a Middle Triassic fauna from China that includes encrusting serpulids and bivalves associated with crinoids.

7.8.3. Cryptic hard substrate communities

There appear to have been no descriptions of Triassic cryptic communities. They certainly must have been present in Triassic reefs.

7.8.4. Bioerosion

Triassic borings are rare compared to those in other systems, although they do include the type species of the ubiquitous ichnogenus *Trypanites* (Mägdefrau, 1932; Müller, 1956; Bertling, 1999a). Triassic reefs have bivalve borings (Kleemann, 1994a). A brachiopod fauna in Slovakia is bored by acrothoracican barnacles and "worms" (Taylor and Michalík, 1991), and it has the echinoid grazing trace *Gnathichnus* (Michalík, 1977). Microborings which were probably produced by cyanobacteria or algae are found in a variety of shell substrates (Schmidt, 1990, 1992, 1993; Glaub and Schmidt, 1994; Balog, 1996; Vogel et al., 1999).

7.9. Jurassic communities

Hard substrate communities return to the fossil record in great abundance and diversity during the Jurassic, and they are very different from their Palaeozoic equivalents. Fossils on hard substrates have not been this common since the Late Ordovician. This flowering of encrusters and borers is due in part to the proliferation of carbonate hardgrounds during these Calcite Sea times (Palmer et al., 1988; Wilson and Palmer, 1992). Taphonomy plays a role as well with the new abundance of thick, attaching bivalves and deep bivalve borings which are more easily preserved (and discovered) than their earlier counterparts. Coral, sponge, bivalve and microbial reefs also become important in shallow, warm Jurassic seas, providing abundant attachment space for hard substrate organisms (Wood, 1993; Fürsich et al., 1994; Fookes, 1995; Bertling and Insalaco, 1998).

7.9.1. Encrusted inorganic hard substrates

Carbonate hardgrounds provided extensive marine hard substrates in the Jurassic, and thus show the highest diversity of encrusters and borers. Cementing oysters and oyster-like bivalves, such as *Eopecten*, and *Plicatula*, become very common on all marine hard substrates (see, for example, Merkt, 1966; Kauffman, 1978, 1981; Harper and Palmer, 1993; Villamil et al., 1998; Wilson et al., 1998a,b). Oysters and oyster-like bivalves are particularly common on many Jurassic hardgrounds (Fig. 1A), often producing thick crusts (Palmer and Fürsich, 1974; Andersson, 1979; Fürsich, 1979; Gruszczynski, 1979, 1986; Fürsich and Oschmann, 1986; Kershaw and Smith, 1986; Valenzuela et al., 1992; Garcia, 1993; Harper and Palmer, 1993; Wilson and Palmer, 1994). Encrusted and bored rockgrounds are also fairly common in the Jurassic. Some of the best known are the Carboniferous limestone substrates that formed rocky shorelines during the Jurassic in southern Wales and England. The eroded upper surfaces are encrusted by corals and oysters, and contain the borings *Gastrochaenolites* and *Trypanites* (Johnson and McKerrow, 1995; Cole and Palmer, 1999). Similarly encrusted and bored Jurassic karst surfaces in limestones are known in northwestern Germany (Helm, 1998) and Scotland (Farris et al., 1999). Encrusted and bored carbonate pebbles and cobbles, including exhumed concretions, are also described from the Jurassic (Voigt, 1968a; Hallam, 1969; Kazmierczak, 1974; Baird and Fürsich, 1975; Andersson, 1979; Fürsich, 1979; Kelly, 1980; Chudzikiewicz and Wieczorek, 1985; Palmer and Wilson, 1990; Fürsich et al., 1992; Hesselbo and Palmer, 1992).

7.9.2. Encrusted organic hard substrates

Encrusted shells are very common in the Jurassic. The encrusters are nearly the same is on the inorganic hard substrates, including foraminiferans, sponges, serpulids, oysters, and oyster-like bivalves (e.g., Schindewolf, 1934; Adams, 1962; Pugaczewska, 1970; Hölder, 1972; Taylor, 1979b; Fürsich, 1980; Hary, 1987; Machalski, 1989; Palmer and Wilson, 1990; Feldman and Brett, 1998; Ziegler and Michalík, 1998). The trepostome bryozoans of the Palaeozoic have given way to cyclostomes (e.g., Taylor, 1979b; Sequeiros and Mayoral, 1980; Mayoral and Sequeiros, 1981; Taylor and Wilson, 1999), and attaching echinoderms are now reduced to locally abundant crinoids (e.g., Nicosia, 1986; Rakús and Zítt, 1993). Soft-bodied fossils preserved through epibiont bioimmuration are becoming increasingly better known from the Jurassic. These include ctenostome bryozoans and probable hydroids on oyster valves (Todd, 1993), and ctenostomes on wood substrates (Evans and Todd, 1997).

7.9.3. Cryptic hard substrate communities

Jurassic hardgrounds and other lithologic hard substrates were sometimes partially dissolved, cracked, dissected, bored, or undercut on the ancient seafloor, forming a variety of marine cryptic spaces. The ceilings and walls of smaller cavities, such as those formed beneath undermined hardground slabs, on cobble bases or in exhumed burrows, supported a distinctive cryptic encrusting fauna of sponges, serpulids, oysters, plicatulids, bryozoans, and thecideide brachiopods (Palmer and Fürsich, 1974; Fürsich and Palmer, 1975; Kershaw and Smith, 1986; Palmer and Wilson, 1990; Wilson, 1998; Baker and Wilson, 1999). Cryptic faunas similar to those on inorganic substrates are found on the interiors of mollusc shells (e.g., Gaillard and Pajaud, 1971), within caves in coral reefs (e.g., Taylor and Palmer, 1994), on the undersurfaces of sponge reefs (Palmer and Fürsich, 1981), and on coral fronds (Manceñido and Damborenea, 1990; Bertling, 1994).

7.9.4. Bioerosion

Bioerosion also gradually takes on a modern aspect in the Jurassic (Fürsich et al., 1994). Reefs show high degrees of bivalve boring, with increasing levels of "worm" and sponge boring (Pisera, 1987; Garcia et al., 1989; Bertling, 1999b), and mollusc shells are bored by polychaetes, sponges and bivalves (Hillmer and Schulz, 1973; Mayoral and Sequeiros, 1981). Carbonate hardgrounds are primarily bored by bivalves (Wilson and Palmer, 1992; see also Neto de Carvalho and Farinha, 2001). Numerous predatory borings in Jurassic shells have also been described (see Harper and Wharton, 2000; Kowalewski et al., 1998). Limestone rockgrounds are bored by bivalves and "worms" in Britain (Johnson and McKerrow, 1995; Cole and Palmer, 1999) and Poland (Radwanski, 1959). The first wood-boring bivalves appear in the Jurassic (Kelly, 1988; Evans, 1999; Schlirf, 2000). Microborings in Jurassic shells and coral skeletons are well described (Gatrall and Golubic, 1970; Gehring, 1986; Glaub, 1988, 1994; Glaub and Schmidt, 1994; Glaub and Bundschuh, 1997; Hary, 1987; Kolodziej, 1997; Vogel et al., 1999). Shells heavily grazed by echinoids can be found in the Jurassic (Fig. 2E).

7.10. Cretaceous communities

Cretaceous hard substrate communities are similar in structure to their antecedents in the Jurassic, but they are even better known because of the wider variety of hard substrates found encrusted and bored. The same taphonomic advantages of Calcite Sea preservation, thick calcitic bivalve shells, and deep borings, continue into the Cretaceous from the Jurassic.

7.10.1. Encrusted inorganic hard substrates

Encrusted and bored cobbles and rockgrounds are especially common in the Cretaceous. Igneous and silicic metamorphic rock substrates, which were exposed in high-energy, shallow marine settings (Fig. 26), are described as heavily encrusted by serpulids, oysters, rudistids, spondylids, cyclostome and cheilostome bryozoans, scleractinian corals, foraminiferans, sponges, and thecideide and craniid brachiopods (Záruba, 1948; Pietzsch, 1962; Pianovskaya and Hecker, 1966; Surlyk and Christensen, 1974; Zítt and Nekvasilová, 1989, 1990, 1991a–c, 1992, 1993, 1994, 1996; Nekvasilová, 1982, 1986; Crampton, 1988; Hercogová, 1988; Nekvasilová and Zítt, 1988; Asgaard and Bromley, 1991; Lescinsky et al., 1991; Zítt, 1992a; Johnson and Hayes, 1993; Johnson et al., 1996; Sanders, 1997; Stilwell, 1997; Zítt et al., 1997a,b, 1999; Wilson and Taylor, 2001a). Limestone rockgrounds are encrusted as heavily as their igneous and metamorphic rock counterparts, and are in addition bored by bivalves, barnacles, worms, and clionid sponges (Gonzalez-Donoso et al., 1983; Ellis, 1983; Mikulás, 1992; Zítt, 1992b; Voigt et al., 1994). Phosphatic rockgrounds, hardgrounds and cobbles are similarly encrusted and bored (Kennedy and Garrison, 1975a,b; Delamette, 1989, 1990; Pomoni-Papaioannou and Solakius, 1991; Bryan, 1992; Pomoni-Papaioannou, 1994; Zítt and Mikulás,

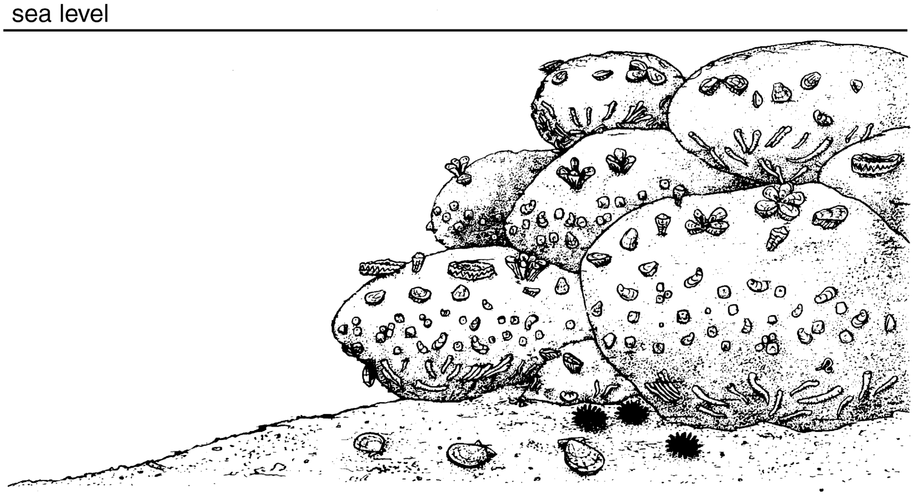


Fig. 26. Reconstruction of the Late Cretaceous rocky shoreline community at Ivö Klack, Sweden. Boulders of Precambrian gneiss are encrusted by a variety of sclerobionts. These are zoned, with serpulids predominating on boulder undersides and spondylid bivalves on uppermost surfaces. After Surlyk and Christensen (1974).

1994). Carbonate hardgrounds are abundant in the Cretaceous, extending from shallow-water, high-energy limestones (see Palmer, 1982; Wilson and Palmer, 1992; Tripathi and Lahiri, 2000) to deep-water, low-energy chalks (see Bromley, 1967, 1968; Bromley and Gale, 1982). Encrusting and boring communities on these hardgrounds are virtually identical to those on rockgrounds, especially limestone rockgrounds (Voigt, 1959, 1974; Lewy, 1985; Garrison et al., 1987).

7.10.2. Encrusted organic hard substrates

Shell-encrusting faunas in the Cretaceous are mostly described from large bivalve shells, particularly oysters and inoceramids, as well as belemnite guards and ammonites. The encrusters include cheilostome and cyclostome bryozoans, oysters and serpulids (see, for example, Pugaczewska, 1965; Carter, 1968; Cuffey et al., 1981; Bottjer, 1982; Hattin, 1986; Lehmann and Wippich, 1995). Cryptic Cretaceous faunas, as described below, have been found on the undersurfaces of rudistid bivalves and corals (Housa and Nekvasilová, 1987), and semi-cryptic encrusting foraminiferans are known from bryozoan substrates (Pozaryska and Voigt, 1985). Sponge-on-sponge encrusting has been described from Cenomanian lithistid sponge mounds (Kauffman et al., 2000). Preservation of soft-bodied encrusters by bioimmuration is becoming increasingly better known from the Cretaceous. The bioimmured fossils include hydroids (Taylor, 1988; Jarms and Voigt, 1994), ctenostome bryozoans (Voigt, 1968b; Todd et al., 1997), and even seagrass (Voigt, 1981).

7.10.3. Cryptic hard substrate communities

The hard substrate fauna on calcareous cobbles is often polarised between a high-energy assemblage on the exteriors and a low-energy assemblage on the interiors of borings (Wilson, 1986a,b; Pitt and Taylor, 1990). Cryptic faunas, primarily cyclostome and cheilostome bryozoans, foraminiferans, serpulids and thecideide and craniid brachiopods, are found in cemented and exhumed thalassinoid burrow systems (Hofker, 1965; Voigt, 1973b, 1987, 1988).

7.10.4. Bioerosion

Borers include the by now common acrothoracican barnacles, bivalves, clionid sponges, polychaetes, and bryozoans (Joysey, 1959; Schlaudt and Young, 1960; Voigt, 1973a; Ghare, 1982; Henderson and McNamara, 1985; Bien et al., 1999). Drill holes, probably made by from predatory gastropods, into bivalve and gastropod shells are described from the Albian by Taylor et al. (1983). Similar borings occur in Santonian echinoids (Cross and Rose, 1994) and Cretaceous brachiopods (Harper and Wharton, 2000; Fig. 27). Some unusual features associated with bioerosion on Cretaceous shells are the traces of limpet grazing on ammonites (Akpan et al., 1982; Kase et al., 1994, 1998) and foraminiferans clustered around the papillae of clionid sponges (Bromley and Nordmann, 1971; Voigt and Bromley, 1974). An interesting controversy has developed around perforations in the conchs of Cretaceous ammonites: are they bite marks from mosasaurs (Kauffman and Kesling, 1960; Tsujita and Westermann, 2001) or limpet homing scars (Kase et al., 1998; Seilacher, 1998)? We believe that the case is stronger for the mosasaur bite interpretation. Microborings are well described from Cretaceous shells (Taylor, 1971; Glaub and Bundschuh, 1997; Hofman, 1996; Hofman and Vogel, 1992) and even fish teeth (Underwood et al., 1999). *Podichnus*, the boring produced by brachiopod pedicles, is found on some Cretaceous shell surfaces (Bromley and Surlyk, 1973; Nekvasilová, 1975, 1976), as is the echinoid grazing trace *Gnathichnus* (Breton et al., 1992). Wood-boring

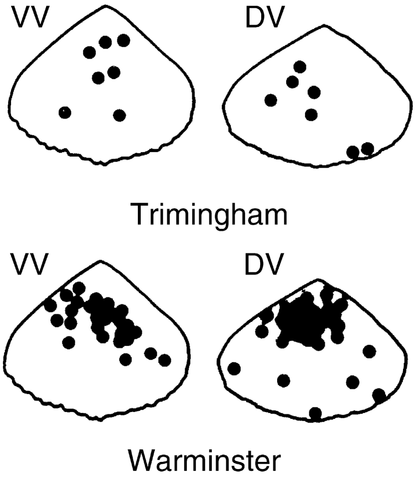


Fig. 27. Location of predatory boreholes in ventral valves (VV) and dorsal valves (DV) of British Cretaceous brachiopods from the Maastrichtian of Trimingham, Norfolk, and the Albian/Cenomanian of Warminster, Wiltshire. After Harper and Wharton (2000).

bivalves diversify and increase in abundance in the Cretaceous (Bromley et al., 1984; Kelly, 1988; Crampton, 1990; Savrda and King, 1993; Mikulás, 1993; Mikulás et al., 1995; Evans, 1999), all forming borings of the ichnogenus *Teredolites*.

7.11. Cenozoic communities

Hard substrate fossil assemblages of the Cenozoic resemble very closely those of the Holocene.

7.11.1. Encrusted inorganic hard substrates

The most prominent Cenozoic hard substrate communities in the literature are those of carbonate rocky shores, which are often intensely bored and occasionally encrusted. These assemblages are well studied because they provide critical information about sea level changes in the climatically volatile Tertiary and Quaternary. Clionid sponge, bivalve, polychaete worm and barnacle borings have been well described from carbonate littoral cliffs and ramps in the Eocene of Poland (Roniewicz, 1970), the Eocene of Iraq (Hanna and Al-Radwany, 1993), the Miocene of Poland (Radwanski, 1964, 1965, 1967, 1968a,b, 1969, 1970, 1977; Baluk and Radwanski, 1977), the Miocene of Spain (Martin et al., 2001), the Miocene of Bulgaria (Koyumdzhsieva, 1976), the Miocene of the Czech Republic (Mikulás and Pek, 1995), the Miocene of Brazil (Fernandes and Assis, 1980), the Miocene and Pliocene of Portugal (da Silva et al., 1999), the Pliocene of Egypt (Aigner, 1983, but see Hamza, 1983, for reasons why it may be post-Pliocene), the Pliocene of southern California (Watkins, 1990a,b), the Pliocene of Greece (Bromley and Asgaard, 1993a,b), the Plio-Pleistocene of Italy (Bromley and D'Alessandro, 1983, 1984, 1987), the "post-Pliocene" of Egypt (Hamza, 1983), and the Pleistocene of Mexico (Libbey and Johnson, 1997). Rocky shore borings and encrusters are also described from non-carbonate substrates, such as Miocene and Pliocene *Gastrochaenolites* in slates in Australia (Bolger and Russell, 1983; note that they termed the borings *Trypanites*), vermetid gastropod and bryozoan biostromes on Miocene dacites in Spain (Betzler et al., 2000), serpulid, bryozoan and foraminiferal biostromes on metamorphic basement in the Miocene of Austria (Friebe, 1994), pholadid bivalve borings in Pliocene siltstones of Mexico (Ledesma-Vazquez and Johnson, 1994), and various Late Pleistocene encrusters and borers on andesites in Mexico (Johnson and Ledesma-Vázquez, 2001). For a review of Upper Pleistocene rocky shores, see Johnson and Libbey (1997); for a review of rocky shores in the Phanerozoic, see Johnson and Baarli (1999). Associated with rocky shores are cobble and boulder beds, which were often bored and encrusted in the Cenozoic (e.g., Domènach et al., 2001). Pebbles and cobbles of limestones and calcareous sandstones are found heavily bored by bivalves and polychaetes in the Eocene of Croatia (Babic and Zupanic, 2000). A late Eocene basaltic pebble and cobble rockground in New Zealand was described by Lee et al. (1997). These clasts are encrusted by an extraordinary diversity of skeletal organisms, including coralline algae, serpulids, bivalves, foraminiferans, brachiopods, and over 70 species of cheilostome and cyclostome bryozoans. Carbonate cobbles and boulders are heavily bored by clionid sponges and bivalves in the Miocene of Spain (Doyle et al., 1998). Cuffey and Johnson (1997) found andesite pebbles and cobbles thickly encrusted with a cheilostome bryozoan in the Pliocene of Mexico, and Kidwell and Gyllenhaal (1998) described similar cheilostome encrustation of Pliocene gastropod shells and crystalline rock clasts. Aguirre and Jiménez (1997) assessed hard-substrate encrusters and borers from diverse boulders in the Plio-Pleistocene of Spain. Johnson and Ledesma-Vázquez (1999) described a fauna of encrusting oysters, corals and coralline red algae on andesite and granite boulders in the Pleistocene of Mexico.

7.11.2. Encrusted organic hard substrates

Encrusters on Cenozoic shells are very common, but published studies of them are surprisingly few. Notable examples include foraminiferans on Eocene shells (Adams, 1962); cyclostome bryozoans on Eocene bivalves, echinoids and brachiopods (McKinney et al., 1996); bryozoans, barnacles and serpulids on Oligocene bivalves (Velcescu, 1999); oysters on Miocene gastropods (Hladilová and Pek, 1998); bryozoans and barnacles on Pliocene gastropods and bivalves (Boekschoten, 1967); bryozoans, serpulids and barnacles on Pliocene bivalves (Mayoral and Reguant, 1995); cheilostome bryozoans on Plio-Pleistocene disarticulated bivalve shells (Bishop, 1988, 1994); barnacles on numerous Plio-Pleistocene hard substrates (Donovan, 1988, 1989); calcareous algae, bryozoans, foraminiferans and serpulids on Pleistocene corals (Martindale, 1992); barnacles, bryozoans, serpulids and corals on Pleistocene molluscs (Miller and Alvis, 1986); and cheilostome bryozoans, foraminiferans, tubiculous polychaetes and small borings in Late Cenozoic articulate and inarticulate brachiopods (Brunton and Hiller, 1990).

7.11.3. Cryptic hard substrate communities

Curiously, published studies on Cenozoic fossil cryptic faunas are rare. Martindale (1992) examined "calcified epibionts" in Pleistocene coral reef cavities, and Barrier et al. (1996) described encrusting communities on the sides and undersides of boulders in Pleistocene deep-sea environments.

7.11.4. Bioerosion

Bored shells are very common in the Cenozoic, with the main culprits being clionid sponges, bivalves, polychaetes, phoronids, ctenostome bryozoans and acrothoracican barnacles. Notable studies describe borings in Eocene mollusc shells (Abletz, 1993, 1994), Oligocene–Miocene corals and molluscs from the West Indies (Pleydell and Jones, 1988), molluscs in the Polish Miocene (Baluk and Radwanski, 1977) and Argentine Miocene (Farinati and Zavala, 2002), Miocene capulid gastropod scars on pectinids in France (Bongrain, 1995), Pliocene polydorid borings in bivalves in Japan (Watanabe and Noda, 1995), gastropod "homing scars" on other gastropods (Noda, 1991), lithophagid bivalve borings in Eocene and Oligocene corals of Florida and the Caribbean (Krumm and Jones, 1993; Krumm, 1999), ctenostome bryozoan borings in Pliocene bivalve shells in Spain (Mayoral, 1988a,b), echinoid grazing traces on shells and limestone pebbles in the Pliocene of Spain (Martinell, 1982); plus a variety of borings in Pliocene corals (Bromley and D'Alessandro, 1990) and brachiopods (Taddei Ruggiero, 1999), lithophagid bivalve borings in Pleistocene corals in the British West Indies (Jones and Pemberton, 1988), sponge, bivalve and polychaete borings in Pleistocene corals on Jamaica (Perry, 2000), sponge, bryozoan, polychaete and gastropod borings in Pleistocene mollusc shells (Miller and Alvis, 1986), and diverse borings in Pleistocene brachiopods (Taddei Ruggiero and Annunziata, 2002) and early Holocene bivalve shells (Martinell and Domènech, 1981). The monograph by Radtke (1991) is a thorough analysis of Palaeogene microborings in a variety of hard substrates. Wood-boring bivalves reached their full diversity by the Cenozoic (Hoagland and Turner, 1981; Evans, 1999). Numerous studies of Cenozoic wood-boring bivalves and their traces include Palaeocene teredinids in Iraq (Elliot, 1963) and North America (Cvancara, 1970; Savrda, 1991; Savrda et al., 1993), Eocene *Teredolites* in England (Hugget and Gale, 1995), and Miocene wood-boring bivalves in Korea (Noda and Lee, 1989). Predatory borings and examples of durophagy are commonplace in Cenozoic molluscan shells. Drilling behaviour entered what Kowalewski et al. (1998) call the "Cenozoic Phase" in the Late Cretaceous. Gastropods are the primary drillers, and they have a significant effect on the morphology and distribution of their prey. Examples of published studies include gastropod predation on Eocene echinoids (Gibson and Watson, 1989), stomatopod predation on gastropods in the Miocene (Baluk and Radwanski, 1996), drilling predation on Miocene molluscs (Kelley, 1988; Hoffmeister and Kowalewski, 2001; Verde, 2001), durophagous and drilling predation among Pliocene molluscs (Boekschoten, 1967), and naticid gastropod drilling of bivalves, gastropods, and barnacles in the Pleistocene (Miller and Alvis, 1986).

8. Palaeoecology of ancient hard substrate communities

8.1. Spatial distributions

Numerous studies have focused on the spatial distributions of organisms colonising fossil hard substrates ranging in scale from single brachiopod shells to large expanses of rockgrounds and hardgrounds. It is a relatively simple matter to map sclerobiont distributions, especially on flat, two-dimensional surfaces (e.g., Surlyk and Christensen, 1974, Figs. 3 and 4; Fürsich, 1979, Fig. 17; Nebelsick et al., 1997, Fig. 2A), or to record frequencies of skeletobionts within defined sectors of regularly shaped biotic substrates, such as brachiopod shells (e.g., Sparks et al., 1980; Alvarez and Taylor, 1987; Alexander and Scharpf, 1990). Statistical tests can then be applied to determine whether the distribution is random or non-random (i.e., spaced or clumped), and to quantify the proportion of the surface occupied by particular taxa of sclerobionts. Variations in the distributions of sclerobionts on different surfaces of a single substratum can also be evaluated; for example, quantitative or qualitative differences in colonisation of upper and lower surfaces can be investigated.

Aggregation has been shown for putative spirorbid worms (Nield, 1986b) and the cemented brachiopod *Liljevallia* (Nield, 1986a) encrusting Silurian stromatoporoids from Gotland, with individual brachiopods often found to foul the remains of disarticulated conspecifics from earlier generations. Palmer and Palmer (1977) mapped the surface of an Ordovician hardground in Iowa and found strongly clumped distributions in several of the taxa colonising the upper hardground surface. In the case of *Trypanites*, individual borings were found to be clustered on low hummocks and present in much lower densities on the surrounding flat regions (see also Brett and Brookfield, 1984). The oyster *Nanogyra* was found to have a clustered distribution on a Jurassic hardground mapped by Kershaw and Smith (1986). Clustering has also been reported by Fürsich (1979) on European Jurassic hardgrounds.

Gibson (1992) found that the Devonian worm *Spirorbis laxus* showed a strong preference for low areas between grooves on brachiopod shells. Mapping of skeletobionts on Upper Cretaceous bivalve shells from Delaware revealed non-random patterns of distribution, notably with the borings *Entobia* and *Gastrochaenolites* concentrated on parts of shells of high relief where sediment cover was likely to be minimal (Bien et al., 1999). Bishop's exemplary study of encrusting bryozoans on the concave inner surfaces of disarticulated Pliocene bivalves showed that *Cribrilina puncturata* recruited preferentially to what would have been the highest point of the shell interior when the shell was resting in a stable, convex-up position on the sandy sea floor (Fig. 28). This pattern could be explained by the geonegative bryozoan larvae creeping up the inside of the shell until they reached the highest position before becoming fixed and undergoing metamorphosis. In this location, clogging of the tentacle crowns and mechanical damage by entrained particles of sediment would be minimised. Sando's (1984) analysis of epibiont distribution on horn-shaped rugose corals demonstrated the preference of most species for concave sides and distal parts of their hosts. This pattern was taken to support the notion that such horn corals lived prostrate on the seabed with the concave surface uppermost. Bryozoans were recorded by Brandt (1996) as preferentially encrusting the sagittal axis of the semi-infaunal Ordovician trilobite *Flexicalymene*. This is the highest part of the dorsal exoskeleton and was probably held above sediment surface during life.

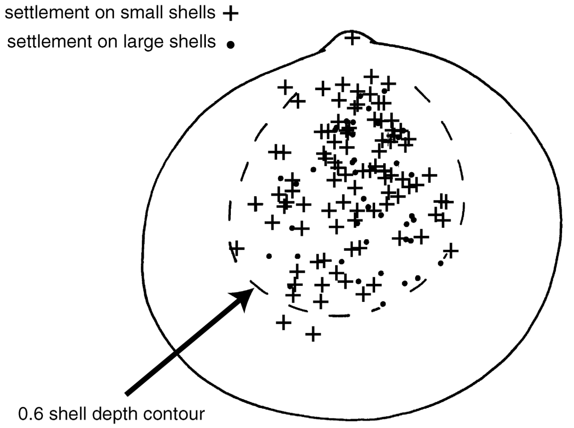


Fig. 28. Recruitment pattern of the bryozoan *Cribrilina puncturata* on the concave interiors of small (27–31 mm high) and large (43–47 mm high) shells of the bivalve *Glycymeris* from the Pliocene Red Crag of Brightwell, Suffolk, England. Note the concentration of bryozoan colonies in areas of the shell which would have been highest above the seabed in shells oriented convex upwards. After Bishop (1988).

Polarisation of sclerobionts between upper and lower surfaces has been discussed by Palmer and Fürsich (1981) with particular reference to their own work on a Jurassic sponge reef in Normandy, France. Plates of the large demosponge *P. magna* hosted on their undersides a diverse encrusting fauna of smaller sponges, serpulids, cemented bivalves, thecidean brachiopods and bryozoans. In contrast, sponge upper surfaces were almost entirely encrusted by one bivalve, *Atreta retifera*. The main factor inferred by Palmer and Fürsich (1981) to have caused such strong polarisation was the difference in sedimentation, mostly in the form of faecal pellets, with encrusters on lower surfaces being those unable to cope with sediment. Other Jurassic sponges show a similar

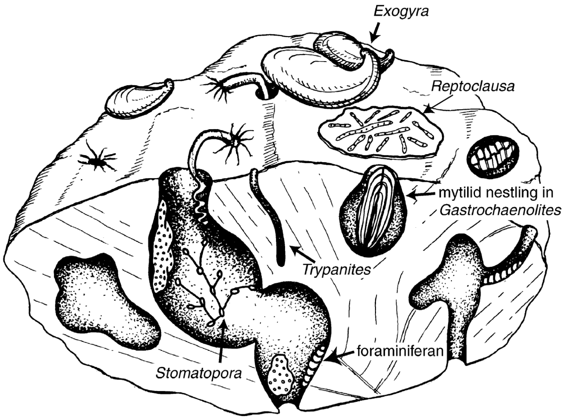


Fig. 29. Reconstruction of an early Cretaceous cobble dwelling community from Faringdon, England. Robust encrusters, including the oyster *Exogyra* and bryozoan *Reptoclausa*, encrust exposed outer surfaces, whereas the cryptic habitats provided by borings (*Gastrochaenolites* and *Trypanites*) support more delicate encrusters, such as foraminiferans and the runner-like bryozoan *Stomatopora*. After Wilson (1986a).

polarisation of encrusting skeletobionts, with the distributions of thecideans and bryozoans strongly biased towards undersurfaces (e.g., Pajaud, 1974, Table 1). Martindale (1992) described Recent and Pleistocene reefs in Barbados where exposed surfaces have thick crusts of coralline algae whereas cryptic surfaces are covered by thin algal crusts, bryozoans, foraminiferans and serpulid worms. The lower, oral surface of both Miocene and Recent dead echinoid tests is more densely encrusted than the upper, aboral surface (Nebelsick et al., 1997).

Hardground faunas also commonly show polarisation. In Jurassic hardgrounds, the upper surface is generally dominated by cemented bivalves, erect bryozoans, the crinoid *Apiocrinus* and the foraminiferan *Nubeculinella*, whereas underhangs are colonised by serpulids, calcareous sponges, thecidean brachiopods and encrusting bryozoans (Fürsich, 1979). Palmer and Fürsich (1974) have described a particularly good example of polarisation on a hardground from the Bathonian of Bradford-on-Avon, England. The number of species recorded from the upper surface and cavity roofs of this hardground is exactly the same but their identities are mostly different. The biomass on the upper surface is much greater because many of the species here are large arborescent animals which fed at higher tiers ('silvide layers') than the exclusively low-level ('crustose layers') suspension feeders on the cavity roofs. Another British Middle Jurassic hardground containing precementational burrows was found to show differences between colonisation of

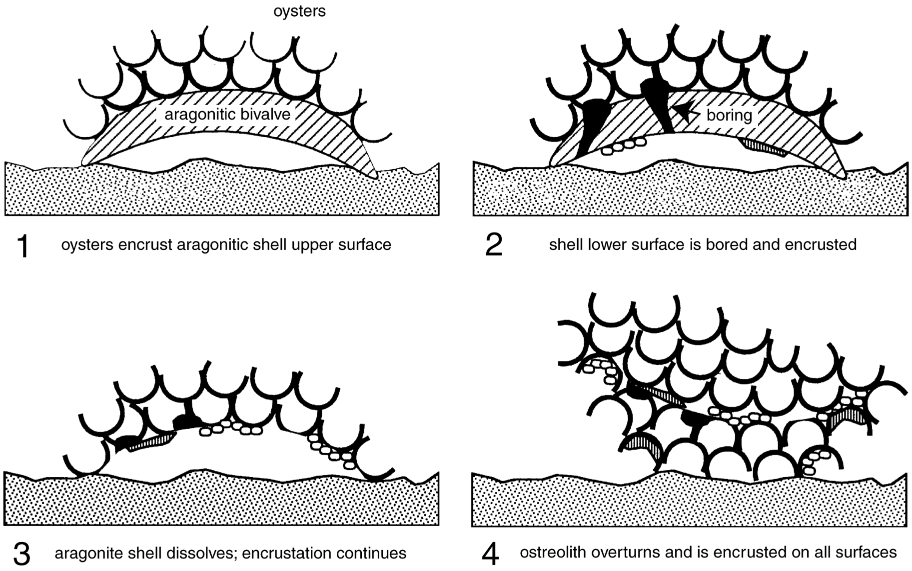


Fig. 30. Genesis of ostreoliths (free-lying oyster balls) from the Middle Jurassic Carmel Formation of Utah, USA. Frequent rolling ensured no faunal polarisation. After Wilson et al. (1998a,b).

the upper hardground surface, burrow floors and burrow roofs (Kershaw and Smith, 1986). Oysters and borings covered the upper hardground surface, burrow roofs were occasionally densely encrusted by serpulids, but floors were devoid of encrusters. Examples of polarisation may also be seen in pebble- and cobble-encrusting biotas (e.g., Bryan, 1992). Striking differences in the biotas colonising exposed outer surfaces of cobbles and cryptic interiors of vacant borings were recorded by Wilson (1986a) in a study of hard substrates in a high energy Cretaceous environment (Fig. 29). The lack of polarisation in other such biotas has been inferred to indicate rolling of the clasts (e.g., Lee et al., 1997). Extreme cases of distributional homogeneity are represented by rolling hard substrates that became totally encapsulated by a single species of encrusting sclerobiont. Examples include rhodoliths formed by coralline algae (e.g., Bosence, 1983), coralliths by corals (e.g., Glynn, 1974; Dullo and Hecht, 1990), ectoproctoliths (or bryoliths) by bryozoans (e.g., Nebelsick, 1996), and ostreoliths by oysters (e.g., Wilson et al., 1998a,b; Fig. 30).

Palaeozoic stromatoporoids and similar large, free-lying colonial organisms may show differences in the encrusters and borers colonising the exposed upper and cryptic lower surfaces. Kershaw's (1980) study of non-reefal Silurian stromatoporoids from Gotland revealed the presence of delicate encrusters on the gently concave undersides, cryptic surfaces made available for colonisation by sediment scouring. Upper surfaces contained a profusion of *Trypanites* borings, generally more robust encrusters and crinoid holdfasts (Fig. 31). In another study of Silurian stromatoporoids, Lebold (2000) found that number of epibiont occurrences decreased inwardly from the outer edges of the stromatoporoids on both upper and lower surfaces.

Concavo-convex Palaeozoic brachiopods often show different degrees of encrustation of the two valves. In a Devonian assemblage, Bordeaux and Brett (1990) found that convex valves, which they supposed to have rested on the seabed when the host was alive, were more heavily encrusted than the concave valves, possibly reflecting reorientation after death of the brachiopod. An extensive analysis by Lescinsky (1995) of epibiont distributions on concavo-convex brachiopods (excluding productids) from the Ordovician and Devonian showed that epibionts were more common on convex than concave valves. Many of the brachiopods could be shown to have been alive when encrusted, leading Lescinsky to suggest that living brachiopods rested on the seabed with the convex valve uppermost, the opposite of conventional wisdom (but see Leighton, 1998; note also that encrusters commonly grow towards the brachiopod commissure, supporting a concave-upwards life orientation as growth downwards towards the sediment seems less likely). Biconvex brachiopods may also show differential encrustation patterns apparently reflecting the life orientation of the host, as in the case of the Devonian species *P. bownockeri* where encrusters are commoner on brachial valves that are thought to have been oriented upwards after pedicle atrophy (Kesling et al., 1980).

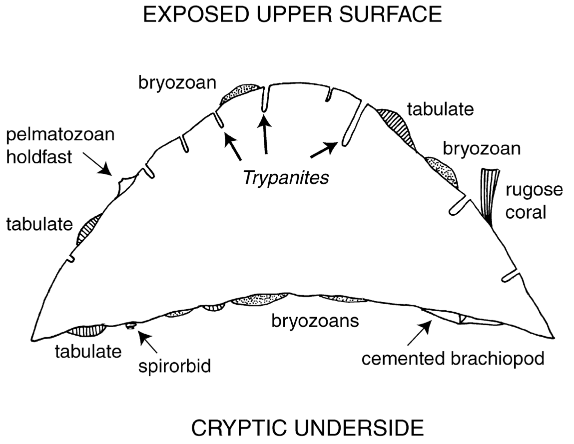


Fig. 31. Polarisation of skeletobionts encrusting and boring the exposed upper surface and cryptic underside of a hypothetical stromatoporoid, shown in vertical section, from the Silurian of Gotland, Sweden. After Kershaw (1980).

The distribution of *Podichnus*, a trace fossil made by brachiopod pedicles, on the surfaces of individuals of the Carboniferous brachiopod *Leiorhynchoidea* was studied by Alexander (1994). Most *Podichnus* were located close to the anterolateral incurrent regions of their hosts and none were observed on the shell posterior. The beaks of the living host shells were interpreted to have been buried in sediment and fouled by larvae that behaved rheotaxically. A comparison can be made with trigoniid bivalves, some of which are semi-infaunal leaving only the posterior-posteroventral region of the shell exposed for colonisation (Villamil et al., 1998). Watson (1982)

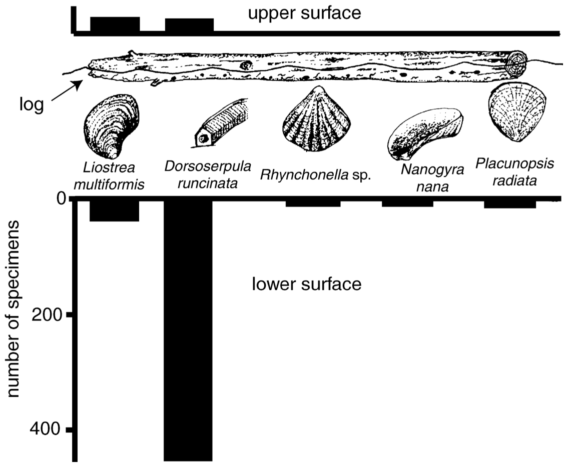


Fig. 32. Polarisation of xylobionts attached to a 3.5-m-long piece of Upper Jurassic driftwood from the Kimmeridge Clay of Dorset, England. The sparsely colonised upper surface contrasts with the more densely colonised lower surface where the serpulid worm *Dorsoserpula runcinata* is particularly abundant. After Wignall and Simms (1990).

described clustering of attached individuals of the inarticulate brachiopod *Discinisca* around the posterior margins of the bivalve *Dacryomya* from the Jurassic. The brachiopods are interpreted to have exploited the feeding currents of their semi-infaunal hosts by attaching in this location above the sediment–water interface.

Wignall and Simms (1990) have described an example of polarisation of xylobionts attached to a plank of Jurassic driftwood. There is a marked contrast between the upper surface of the wood, colonised by small numbers of oysters and serpulids, and the lower surface where serpulids in particular are much more abundant (Fig. 32). Both floating wood and drifting ammonite shells sometimes preserve sclerobionts (bivalves, brachiopods, crinoids and lepadomorph barnacles) which hung pendently from their undersides (Wignall and Simms, 1990).

A Cretaceous rocky shore in southern Sweden contains large boulders of gneiss which show a clear vertical zonation of encrusters (Surlyk and Christensen, 1974). Boulder undersides are dominated by serpulids, vertical faces by oysters and an inarticulate brachiopod (*Crania*), and upper faces by a cemented spondylid bivalve (Fig. 26). Barrier et al. (1996) studied a deep-sea section in the Pleistocene of Italy containing encrusted boulders. Upper surfaces of these boulders were found to be either devoid of encrusters or colonised by isolated gorgonian and scleractinian corals, whereas the sides of the boulders were densely encrusted, especially by serpulids and bryozoans.

Non-random spatial distribution patterns on a larger scale can be seen in some ancient rocky shore deposits. This is well illustrated by the study of

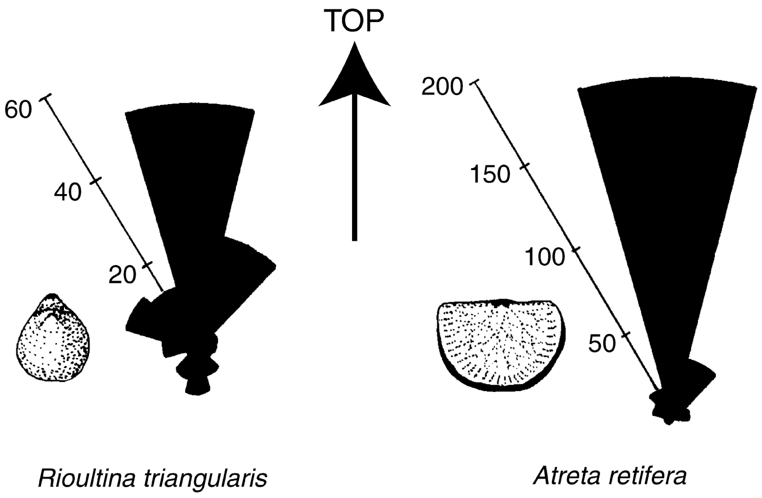


Fig. 33. Orientations with respect to the vertical of the thecideidine brachiopod *Rioultina triangularis* and the bivalve *Atreta retifera* encrusting fronds of the sponge *Platychonia magna* from a Middle Jurassic sponge reef at St. Aubin-sur-Mer, Normandy, France. After Palmer and Fürsich (1981).

Johnson and Ledesma-Vázquez (1999) on a Pleistocene rocky shore in Mexico where both lateral and vertical variations are apparent. For example, a high-energy outer rocky shore habitat contained an upper zone colonised by *Modiolus* and a lower zone by *Codakia*. A small outcrop of diorite in Inner Mongolia formed an island in the Silurian sea, fringed by rocky shoreline deposits which, only on the inferred leeward side of the island, contain stromatoporoids in growth position, many cemented directly to the diorite substrate (Johnson et al., 2001).

8.2. Orientations

Non-random orientation of sclerobionts on hard substrates is often evident. Alignment of encrusters may occur with respect to: (1) other encrusters; (2) way-up; (3) topological features on the surface of the substrate; and (4) in biotic substrates, functionally important morphological features of biotic substrates.

Strongly preferred orientations with respect to the vertical were found, in the study mentioned above (Section 8.1), by Palmer and Fürsich (1981) for a bivalve (*A. retifera*) and a brachiopod (*Rioultina triangularis*) encrusting inclined plates of the Jurassic reef-building sponge *P. magna*. In both cases, the dorsoventral axis pointed downslope (Fig. 33), thereby decreasing the likelihood of sediment entering the valves. Fürsich (1979) reported a similar downslope orientation for *Atreta* on inclined hardground surfaces (e.g., pseudoanticlines formed by warping during cementation), whereas flat hardgrounds usually failed to show any evidence of a preferred orientation in this bivalve. Another cemented bivalve, *Spondylus*, shows a clear pattern of orientation on Cretaceous rockgrounds and boulders in Bohemia (Zítt and Nekvasilová, 1994, 1996), with umbones positioned in the upper left quadrants of the encrusted substrates. Boulders in Sweden colonised by Late Cretaceous encrusters include inarticulate brachiopods showing strong downslope orientation (Surlyk and Christensen, 1974). Jurassic thecidean brachiopods cemented to conical corals are oriented with their commissures directed towards the base of the corals (Housa and Nekvasilová, 1987; Fig. 34). Downslope orientation has also been noted in the bivalve *Placunopsis matercula* cemented to the large bivalve *Plagiostoma* [*Lima*] *lineata* in the German Triassic (Seilacher, 1954), and in the inarticulate brachiopod *Orbiculoidea papyracea* pedically attached to ammonites from the German Lower Jurassic (Seilacher, 1982). Perhaps the oldest occurrence of downslope orientation, termed 'slopelet line docking' by Struve (1980), occurs in the Silurian brachiopod *Liljevallia gotlandica* encrusting the undersides of stromatoporoids (Nield 1986a).

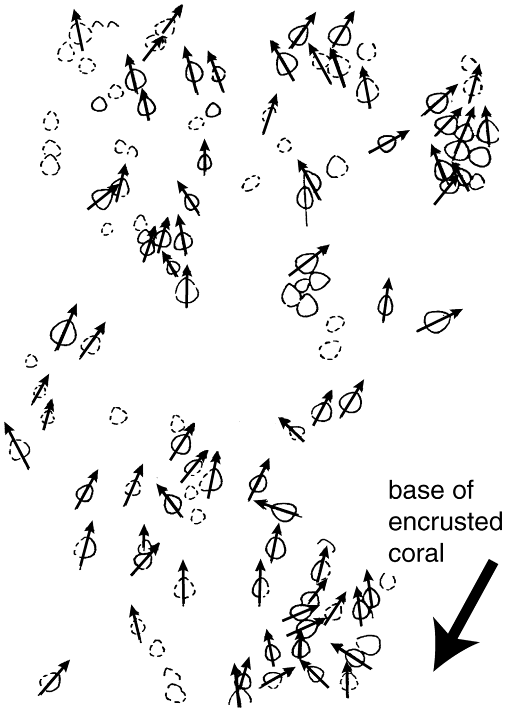


Fig. 34. Orientation of thecideidine brachiopods cemented to a Jurassic coral from the Tithonian of Stramberk, Czech Republic. Arrows point posteriorly along the median septum. After Housa and Nekvasilová (1987).

Upward growth of encrusters on dead echinoid tests has been observed by Nebelsick et al. (1997), while diverse orientation patterns on tests from the Cretaceous were shown by Schmid (1949). A bimodal pattern was found by Simms (1986) for the orientation of small cemented bivalves (*Plicatula*) encrusting the stems of Jurassic *Chladocrinus*: most of the bivalves had their commissures facing towards or away from the crown of the host crinoid, with fewer oriented laterally.

In Palaeozoic orthoconic nautiloids, Baird et al. (1989) documented growth of the colonial problematicum *Reptaria* towards the shell aperture, and alignment of the monticules of the bryozoan *Spatiopora* parallel to the long axis of the cephalopod shell. These patterns were interpreted as responses of the encrusters to water flow induced by swimming of living hosts.

Clustered individuals of the edrioasteroid *Stalticodiscus milleri* attached to cobbles in the Carboniferous of England exhibit a parallel orientation of their anterior–posterior axes at 90° to the inferred ambient current direction (Smith, 1983). Unlike most encrusting sclerobionts, edrioasteroids were not strictly immobile but could apparently swivel and reorient themselves after attachment, raising the possibility of an active response to changes in current direction or host orientation.

Cornulitids frequently grow in subparallel or fan-like orientations towards the commissures of the brachiopods or bivalves which they encrust, often following the grooves in the shell surfaces (e.g., Schumann, 1967; Morris and Rollins, 1971; Hurst, 1974; Fig. 35). The usual explanation for this pattern is that the cornulitids benefited from the feeding or respiratory currents of the living host.

Duringer (1985) documented radially oriented growth in densely spaced populations of the Triassic encrusting bivalve *Placunopsis ostracina*. Four-leafed clover patterns (Fig. 36), in which the umbones of four individuals are touching, were found to be common. It was inferred that such radial patterns developed when the density of larval recruits was high because the bivalves reoriented themselves to maximise perimeter/area ratio. In contrast, low recruitment densities caused bivalves to become oriented with respect to ambient current flow, thereby resulting in parallel alignment.

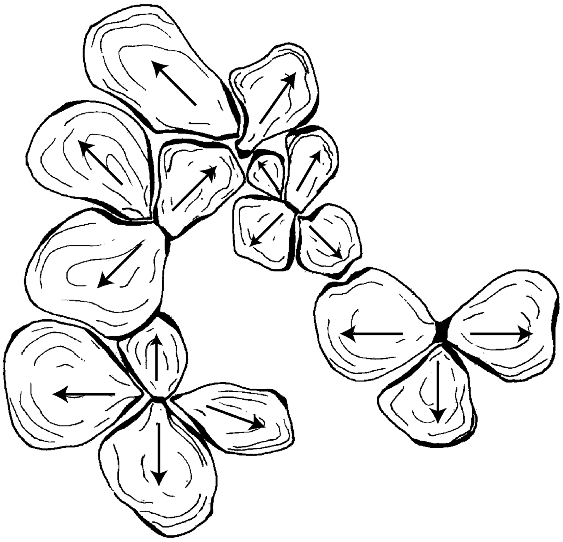


Fig. 36. Four-leaved clover pattern of growth in the cemented Triassic bivalve *Placunopsis ostracina* from the Muschelkalk of eastern France. After Duringer (1985).

Non-random distributions and orientations of skeletobionts on Cretaceous *Inoceramus* were inferred by Hattin (1986) to indicate that living individuals of these large bivalves formed important habitat islands on a soupy sea floor. Elongation of encrusting oysters towards the commissure of the host, and alignment of acrothoracican barnacle borings along growth lines of the host, were both observed.

8.3. Competition

Direct competition among species can be difficult enough to demonstrate among living species (see Section 6.2), and it is often nearly impossible to

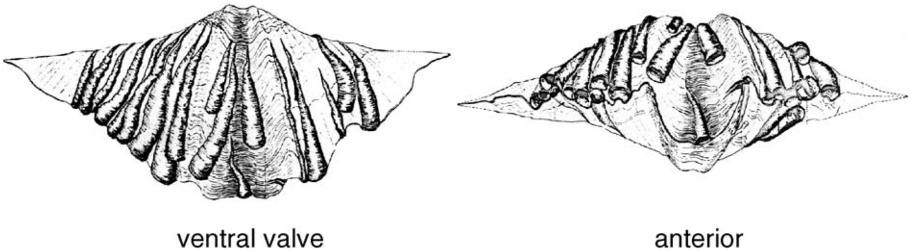


Fig. 35. Growth of cornulitids between the folds and towards the anterior commissure of the host brachiopod *Mucrospirifer reidfordi* from the Upper Devonian of Canada. After Schumann (1967).

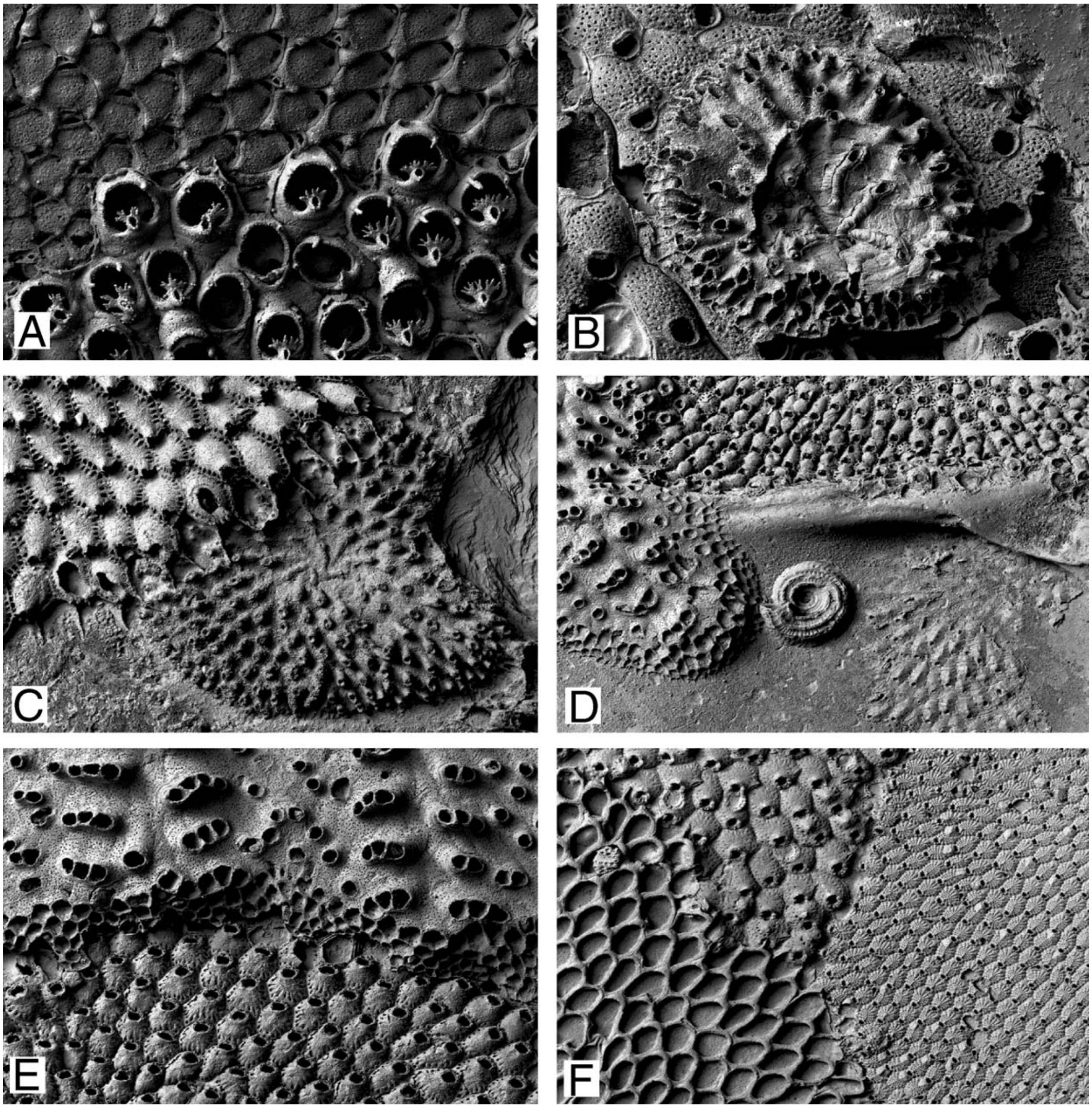


Fig. 37. Scanning electron micrographs showing examples of skeletal overgrowths and fouling among Cenozoic bryozoans and other encrusters. (A–E) Pliocene, Nukumaru Limestone, Nukumaru Beach, nr Wanganui, New Zealand. (A) cheilostome bryozoan *Chaperiopsis* (bottom) overgrowing another cheilostome *Micropora* (top), × 28. (B) Cyclostome bryozoan *Liripora* fouling the surface of cheilostome bryozoan *Emballotheca*, × 33. (C) Cheilostome bryozoan *Escharoides* (top left) overgrowing cyclostome bryozoan *Liripora* (bottom right), × 13. (D) Internal surface of cemented valve of disarticulated oyster fouled by *Spirorbis* (centre) and cheilostome bryozoan *Celleporella* (lower right), and overgrown by cyclostome bryozoan *Desmediaperoecia* (upper left) and a cheilostome (top), × 13. (E) Cyclostome bryozoan *Desmediaperoecia* (top) overgrowing cheilostome bryozoan (bottom), × 18. (F) Interactions between three genera of cheilostome bryozoans encrusting a shell; *Aplousina* (lower left) is beginning to overgrow *Escharina* (top centre) and *Puellina* (right), whereas the contact between *Escharina* and *Puellina* suggests a stand-off with neither genus overgrowing the other; × 5; Pliocene, Waccamaw Formation, Shallotte, nr Wilmington, North Carolina, USA.

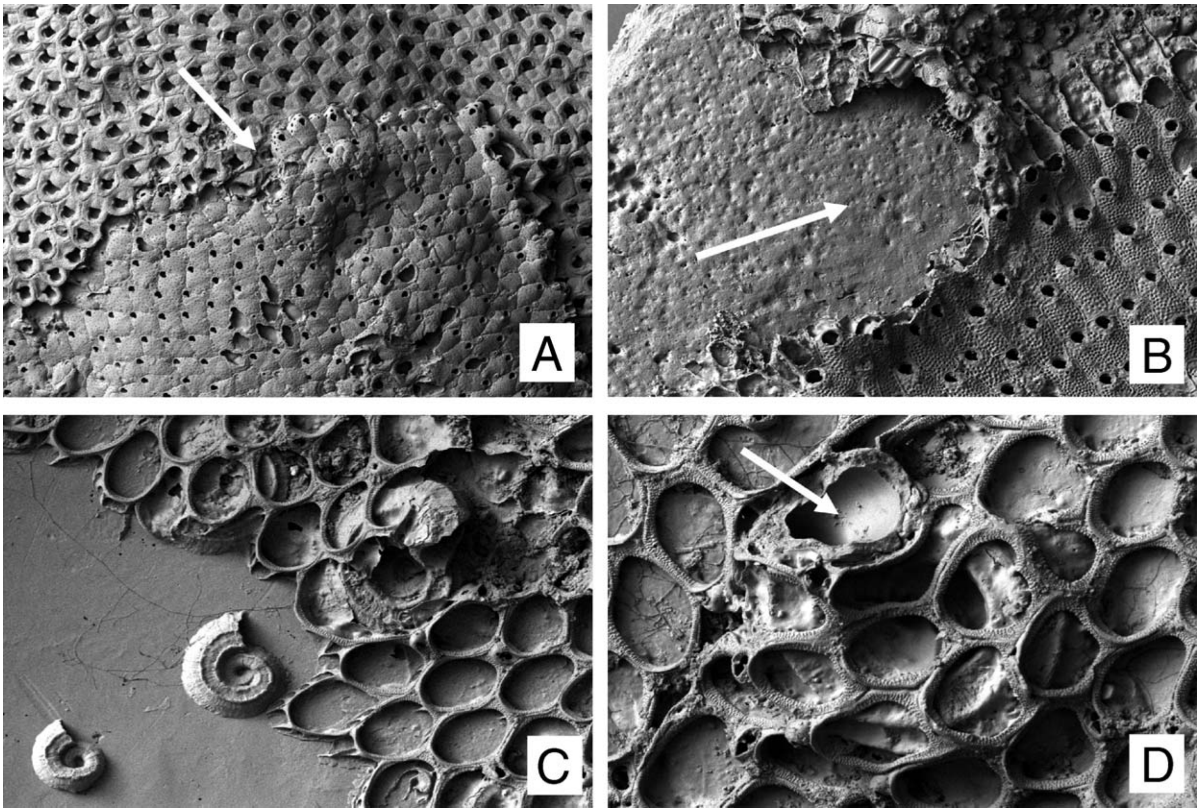


Fig. 38. Scanning electron micrographs of skeletal overgrowths among fossil bryozoans and other encrusters. (A) Reciprocal overgrowth at the junction between colonies of two cheilostome bryozoans, *Floridina* (top) and *Trypostega* (bottom); left of the arrow *Floridina* overgrows *Trypostega* whereas right of the arrow *Trypostega* overgrows *Floridina*, a relationship which proves that the two bryozoans were alive at the same time; × 10; Pliocene, Waccamaw Formation, Shallotte, nr Wilmington, North Carolina, USA. (B–D) Pleistocene, Kupe Fm, Mowhanau, nr Wanganui, New Zealand. (B) Arrow indicating position of non-preserved sclerobiont, around part of the perimeter of which two cheilostome bryozoan colonies (top right and top left) have formed a rampart, × 13. (C) Cheilostome bryozoan *Ellisina* (top right) progressively overgrowing individuals of *Spirorbis*, × 18. (D) older part of the same colony of *Ellisina* with a *Spirorbis* almost entirely overgrown apart from the tube aperture, suggesting that the worm may have remained alive ('epizooism'), × 28.

deduce in most fossil assemblages. There are distinct advantages, however, in studying competition on hard substrate communities. One of the primary limiting resources for these communities was often living space, and sessile skeletal encrusters, and to some extent borers, can show competitive interactions through overgrowths, raised margins, changed growth directions, and other features preserved in fossils (Figs. 37 and 38). Encrusting and boring communities have an easily discernible stratigraphy (see Section 3) where we can at least establish a sequence of biotic and physical events. The actual timing of these events, though, and whether they represent living interactions are the primary difficulties palaeontologists face when attempting to sort out ancient competitive and successional systems.

In this review of competition in the fossil record of hard substrate communities, we are not including various symbiotic relationships such as those noted between Silurian corals and stromatoporoids (Kershaw, 1987; Young and Noble, 1989), Devonian worms, chaetetids and stromatoporoids (Zhen and West, 1997), Cretaceous worms and scleractinian corals (Voigt and Lafrenz, 1973), Mesozoic and Tertiary hydroids and serpulids (Scrutton, 1975), Miocene polychaetes and scleractinian corals (Baluk and

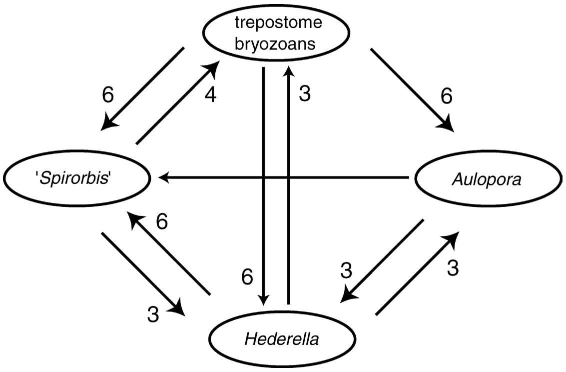


Fig. 39. Skeletal overgrowths observed among four common encrusters on shells of the brachiopod *Anathyris phalaena* from the Lower Devonian of NW Spain. Arrows point towards the overgrown taxon, and numbers indicate the observed frequency of overgrowth. After Alvarez and Taylor (1987).

Radwanski, 1997), and Neogene scleractinian corals and cheilostome bryozoans (Cadée and McKinney, 1994). We are also not including intraspecific competition such as that described by Kidwell and Gyllenhaal (1998) on Pliocene ectoproctoliths.

The most common spatial relationship between potentially competing encrusters on hard substrates is the growth of one over the other. The dilemma is trying to deduce whether the two organisms were alive at the time one overgrew the other (live–live interaction), and thus potentially competitive. McKinney (1995a,b) and Fagerstrom et al. (2000) have each provided useful discussions of the ways in which live–live interactions can be discerned in fossil material. The most conclusive evidence consists of: (1) changes in the skeletons (such as raised margins, spine development, or altered growth direction) at the margins where the organisms interacted, followed with lesser confidence by (2) skeletal modifications in only one of the organisms, and (3) lack of erosion or sediment between the top of the overgrown and base of the overgrower. Reciprocal overgrowth (e.g., Lescinsky, 1993, Figs. 2F and 38A) is another sure indication that both organisms were alive but such 'draws' provide no information on competitive dominance unless the areas overgrown by each competitor are compared. Extant hard substrate encrusters are known to compete for space without leaving clear evidence for it in their skeletons (Fagerstrom et al., 2000), dead encrusters can have pristine skeletons when encrusted by later organisms, and overgrowing encrusters can develop skeletal modifications to the physical characteristics of the substrate they are covering that do not indicate a live–live interaction. Unequivocal competitive interactions among encrusters are seldom demonstrable in the fossil record; see the arguments in McKinney (1995a,b) and the study of recent epibionts on live and dead scallop shells by Lescinsky (1993). Fagerstrom et al. (2000, p. 20) reached a similar conclusion: "Prudence suggests that without skeletal distortion in one or both competitors, live–dead association is more probable than competition." This may be true for encrusters on long-lived substrates but it is less likely for more ephemeral substrates where colonising organisms have roughly equivalent lifespans to the age of the substrate. Statistically significant overgrowth patterns where some taxa are consistently more overgrown than others may be used in a probabilistic way to determine competitive dominance (McKinney, 1995b) even if specific interactions cannot be categorised with certainty as either live–live or live–dead. This is because overgrowth of dead organisms adds noise to the data that can diminish the degree of dominance of one taxon over another but does not reverse the direction of competitive dominance.

Three studies provide good evidence of competition in the fossil record. Liddell and Brett (1982) studied the interactions of Silurian bryozoans on the calyces of crinoids. Inflated growth forms and upturned margins among these bryozoans are an

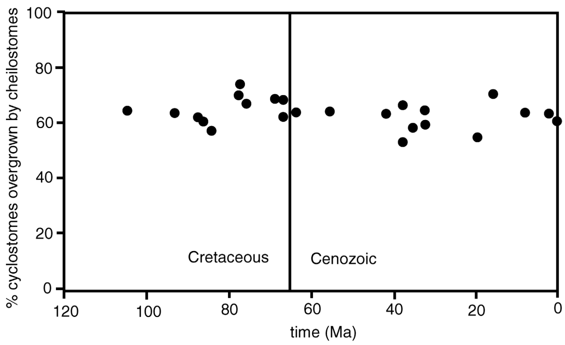


Fig. 40. Constancy through geological time in the proportion of cheilostome overgrowths of cyclostomes as shown by data from 24 fossil assemblages. After McKinney (1995a).

indication of direct competition for space. Taylor (1984b) demonstrated again with Silurian encrusting bryozoans a variety of growing-edge effects as the results of competition. Thirdly, Lescinsky (1993), in a study of Carboniferous epibionts on brachiopods, showed a few competitive interactions among encrusting bryozoans and worms. Several other studies have recorded skeletal overgrowths between species (Palmer and Palmer, 1977; Taylor, 1979b; Alvarez and Taylor, 1987; Hollingworth and Wignall, 1992) or stand-offs (Alexander and Scharpf, 1990; Kidwell and Gyllenhaal, 1998). Network diagrams can be used to express the realationships found (Fig. 39). Wilson (1998) studied overgrowths among species encrusting Jurassic hardground cavities and found an inverse correlation between overgrowth index and the coverage of substrate space, a relationship also seen in some modern communities (see Section 6.2).

A unique and outstanding study of long-term competition among encrusters is McKinney's (1995a) analysis of overgrowths between cyclostome and cheilostome bryozoans. McKinney looked at 24 Albian–Holocene assemblages, each with 50 or more skeletal overgrowths involving a cyclostome and a cheilostome, and found that, regardless of geological age, cheilostomes won approximately two-thirds of their encounters with cyclostomes (Fig. 40). Therefore, there has been no escalation in the competitive dynamics between these two clades through 100 million years of geological time.

Putative adaptations for dealing with competition for substrate space are mentioned above (Section 6.2). Two basic strategies may be distinguished: confrontational and fugitive. An example of these contrasting strategies can be seen among Jurassic encrusting cyclostome bryozoans. Most of these belong either to the confrontational form-genus *Berenicea*, or the fugitive genus *Stomatopora* (Taylor, 1979a; Bertling, 1994). The former has compact, subcircular colonies with a circumferential growing edge able to engage spatial competitors and potentially overgrow them, whereas the latter has branching colonies which bud zooids over a wide area of the substrate but are prone to overgrowth of the undefended branch flanks. A runner-like, fugitive colony-form is also epitomised by the Palaeozoic tabulate coral *Aulopora* (see Helm, 2000).

8.4. Succession

"Succession" in palaeoecology is used for two different concepts. One is a biologically controlled (or autogenic) ecological succession in which the species composition and structure of a community changes over time within the same physical environment. The classic succession on a cleared field, from grasses to forest, represents an autogenic succession if the physical environment has remained the same. Autogenic successions are controlled by recruitment, competition, predation, etc. A physically controlled (allogenic) succession is one in which the community changes in response to a changing environment. The succession of an intertidal community into a subtidal one with a gradually increasing sea level would be an example of allogenic succession. Recruitment and competition still play strong roles in allogenic successions, but the primary controls are environmental changes.

Autogenic successions are very difficult to demonstrate in the fossil record because we can rarely be certain that the environments have remained constant (see McCall and Tevesz, 1983; Walker and Diehl, 1986, for discussions). Fossil assemblages on hard substrates, however, are again useful because these

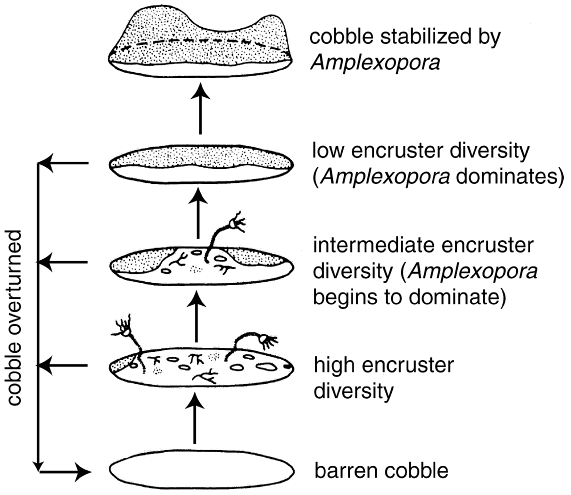


Fig. 41. Disturbance and community development on cobbles from the Upper Ordovician Kope Formation of Kentucky, USA. Unless cobbles are disturbed by overturning, a competitive dominant, the bryozoan *Amplexopora*, eventually monopolises substrate space. After Wilson (1985).

organisms have been preserved in situ and often with some aspects of colonisation sequences through overgrowths. Wilson (1985) demonstrated an autogenic succession of encrusters on Ordovician cobbles sitting on top of a muddy substrate (Fig. 41). The cobbles were occasionally overturned by storm currents, killing the encrusters on the top surfaces and exposing new space for encrusters on the bottoms. The result was a collection of cobbles with various frequencies of overturning, and thus various stages of an autogenic succession of encrusters. In this case, runner-type cyclostome bryozoans like *Corynotrypa* and *Cuffeyella* were the opportunistic early colonisers, followed by cornulitids, crinoids, ceramoporid bryozoans, and a final massive trepostome bryozoan (*Amplexopora*) which was apparently the climax form, or at least the last preserved climax form.

Working with the epibiota on the Devonian brachiopod *Spinocyrtia iowensis*, Ager (1961) was able to determine a colonisation sequence of the worm *Spirorbis* followed by the colonial problematicum *Hederella*, then the sheet-like bryozoan *Paleschara*, and finally the tabulate coral *Aulopora*. Some Tunisian Jurassic ammonites encrusted by foraminiferans, worms and crinoid holdfasts were later bored by acrothoracican barnacles, as indicated by the occurrence of borings into articulation facets of disarticulated, dead crinoids (Rakús and Zítt, 1993). The epibionts of Jurassic crinoids from the Crimea showed a typical colonisation sequence of small oysters, followed in turn by serpulid worms, bryozoans, sponges and corals, and algal crusts (Klikushin, 1996). In a study of encrusted shells of the bivalve *Pycnodonte* from the Cretaceous of Arkansas, Bottjer (1982) inferred a colonisation sequence of: (1) the worm boring *Trypanites* plus *Pycnodonte* juveniles; (2) the sponge boring *Entobia* plus the foraminiferan *Bullopora*; and (3) cheilostome bryozoans. Hattin and Hirt (1986) studied the epibionts attached to Turonian *Inoceramus* shells from Kansas and were able to infer a sequence of colonisation of: (1) bivalves (*Pseudoperna* and ?*Placunopsis*); (2) serpulids; (3) scalpellomorph barnacles; and (4) acrothoracican barnacles and bryozoans. Mayoral and Reguant's (1995) study of Pliocene bivalves from Spain showed how the predominantly infaunal bivalve *Glycymeris insubrica* was colonised during life by worms, producing the ichnogenera *Caulostrepsis* and *Maeandropolydora*, followed after death by bryozoans and boring sponges (*Entobia*), and finally a more diverse community containing bryozoans barnacles, serpulids, and boring bivalves and phoronids.

Allogenic successions are much more common in the fossil record of hard substrate communities. For example, hardground communities can develop through several stages in response to early diagenetic cementation of the substrate (Goldring and Kazmierczak, 1974; Gruszczynski, 1979, 1986; Walker and Diehl, 1986; Goldring, 1995), cave faunas can change over time with increasing sedimentation and restriction of the environment (Wilson, 1998), and reefs and bioherms respond to changes in sea levels and climate (Toomey and Cys, 1979; Crame, 1980; Williams, 1980; Nakazawa, 2001). Physical changes primarily control these successions, but biotic interactions such as larval recruitment strategies and competition are still critical. The complex nature of the physical and biological factors, though, makes it nearly impossible to distinguish one set from another. The interaction of colonisation and physical abrasion on bored clasts has been modelled by Babic and Zupanic (2000).

8.5. Bioimmuration, xenomorphism and epibiont shadowing

Bioimmuration, preservation resulting from organic overgrowth, provides a window into the soft-bodied and weakly mineralised components of hard substrate communities which are normally not fossilised (see reviews by Taylor, 1990; Taylor and Todd, 2001). The most basic type of bioimmuration—an epibiont mould bioimmuration—consists of an imprint of an overgrown epibiont on the underside of the organism that lived on the same substratum and overgrew it (Fig. 42), for example, a hydroid impression on the attachment scar of an oyster. Epibiont cast bioimmurations may be produced if the epibiont mould between the overgrowing organism and its substrate is infilled with diagenetic minerals. Fouling organisms with hard skeletons may carry a mouldic impression of the substrate on their attached surfaces, known as a substratum bioimmuration. A final type of bioimmuration is a bioclaustration (Palmer and Wilson, 1988) or pseudoboring, formed when a soft-bodied fouling organism becomes embedded in the skeleton of its host. In contrast with other bioimmurations, bioclaus-

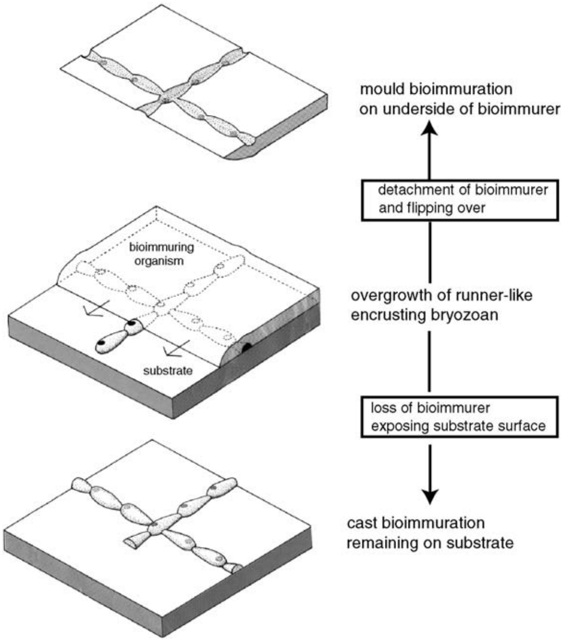


Fig. 42. The formation of bioimmured fossils as illustrated diagrammatically by the overgrowth of a soft-bodied, runner-like bryozoan (centre diagram). The bioimmuring organism (e.g., an oyster) carries a mould bioimmuration of the bryozoan on its underside (upper diagram). A cast bioimmuration may be left adhering to the substrate after removal of the bioimmurer if the mould of the bryozoan has been filled by diagenetic minerals (lower diagram). After Taylor and Todd (1990).

trations have sometimes been given ichnotaxonomic names. For example, Radwanski and Baluk (1997) erected the ichnotaxon *Clavatulicola evaephilus* for bioclaustrational furrows in the Miocene gastropod *Clavatula* which were formed in response to the presence of a soft-bodied symbiont. Parabolic embedment pits—*Tremichnus* (Brett, 1985; Feldman and Brett, 1998)—in crinoids are also bioclaustrations. Chatterton (1975) described, as *Burrinjuckia spiriferidophilia*, open-ended tubes formed within the brachial valves of some Devonian brachiopods apparently in response to the presence of a suspension feeding symbiont. These too can be classified as bioclaustrations.

Attachment areas of oysters, bryozoans, foraminiferans and serpulids may carry impressions of plant substrates that prove their origin as phytobionts (= epiphytes) (e.g., Langer, 1993). Sclerobionts that colonised diagenetically unstable substrates, notably aragonitic mollusc shells, or substrates prone to decay (e.g., wood; Evans and Todd, 1997), otherwise lost to the fossil record, can also be preserved if bioimmured. However, most interest in bioimmuration has focused on soft-bodied epibionts. Examples of bioimmured ctenostome bryozoans, hydroids and pterobranch hemichordates (*Rhabdopleura*) are common in the Jurassic and Cretaceous rocks of northwest Europe particularly (see Taylor, 1990; Todd et al., 1997). These colonial animals make good subjects for bioimmuration because their small-sized zooids can be rapidly overgrown before post-mortem deterioration. Each bioimmured fossil records the condition of the colony over a period of time as zooids become progressively overgrown. Upright structures, such as peristomes and erect branches, are flattened down against the substrate parallel to the local direction of overgrowth. Permineralisation of soft parts by pyrite or phosphate often accompanies bioimmuration (e.g., Todd and Taylor, 1992), possibly facilitated by the enclosed microenvironment of the sandwiched epibiont. Exceptional preservation of articulated animals (stalked barnacles) and soft parts of skeletonised organisms (e.g., brachiopod setae) may also result from bioimmuration (Taylor and Todd, 2001). Because the process of bioimmuration resembles the action of a moving flatbed scanner in making an incremental recording, it is potentially possible to use bioimmurations to investigate short-term succession on hard substrates: the youngest parts of the bioimmurer sample the sclerobiont community at an earlier successional stage than the older parts.

Xenomorphism is the term given to replication of substrate topography on the upper surface of encrusters. Most examples of xenomorphism have been described in cemented bivalves (e.g., Lewy, 1972; Hary, 1987; Lehmann and Wippich, 1995; Damborenea, 2002, text-fig. 45) and brachiopods (e.g., Richards, 1972, pl. 1, Figs. 2 and 3; Sparks et al., 1980, pl. 11, Fig. 4; Baird and Brett, 1983, Fig. 4F; Bassett, 1984). In the case of diagenetically unstable aragonitic substrates, the xenomorph may represent an identifiable replicate of the substrate. Xenomorphism in bivalved encrusters is dependent on the upper valve maintaining a constant distance during growth from the lower, cemented valve so that a tight fit between the valves is conserved at the shell margin. Therefore, any features on the substrate which are replicated in negative by the lower valve are passed on in positive relief to the upper valve.

The term ‘epibiont shadow’ was introduced by Palmer et al. (1993) for the subtle outlines of soft-bodied encrusters which occasionally remain on the substrate surface after loss of the encrusters themselves. These result from the effects that the encrusters have on the substrates they cover. Epibiont shadows of soft-bodied ctenostome bryozoans from the Upper Jurassic are formed because the bryozoan zooids protected the shell substrate beneath them from attack by microendoliths whereas the shell all around the zooids was bored and is noticeably whiter in the fossils. Small-scale erosion of the bored shell may leave the shadows upstanding.

8.6. Taphonomy

Palaeontologists should always be aware of those parts of the record they are *not* seeing. Rasmussen and Brett (1985) examined the modern cryptic encrusting biotas in submarine caves and on the undersides of ledges offshore of St. Croix, Virgin Islands. They showed that, at least with modern communities, large taphonomic losses occur on the way to preservation. Up to 85% of original area covered is lost, and up to 62% of original species richness. It is not only the non-preservation of soft-bodied forms which accounts for this deficit, but later successional forms may erase traces of the earlier colonists. In addition, the early successional species in this community tended to have mineralised skeletons whereas later species did not. Therefore, the fossil record would be biased towards the former. A taphonomic study by Zuschin et al. (1999) (see also Zuschin and Pervesler, 1996) in the Adriatic demonstrated the expected loss of organisms such as ascidians, anemones and demosponges in the death assemblage, as well as vagile forms with articulated skeletons. Another study in the Adriatic (Nebelsick et al., 1997) modeled the taphonomic processes effecting the tests of dead echinoids and noted how soft-bodied hydrozoans, sponges and ascidians would be lost to the fossil record.

Of the 30 invertebrate and algal species inhabiting a modern rocky intertidal environment in Mexico, 70–80% were found to have the requisite mineralised skeletons to become fossilised (Hayes et al., 1993). In the case of encrusted pectinid shells collected from near San Juan Island, Washington, Lescinsky (1993) found that external surfaces of live bivalves were dominated by sponges and agglutinated worms, both having a low preservation potential, plus some barnacles. Little indication of these symbionts is likely to survive into the fossil record. By contrast, the encrusting biota on dead shells consisted predominantly of serpulid worms and bryozoans having good preservational potentials. McKinney (1996) studied encrusters on disarticulated bivalve shells from Bogue Sound, North Carolina, recording the species identifiable before and after hypochlorite treatment which removed those species not expected to survive fossilisation. Bleaching reduced the 23 taxa to 8, with the loss not only of encrusting sponges but also of erect species which formed the highest tiers of suspension feeders in the living community. The area of valve encrustation declined by up to 25%.

Phases of erosion which commonly effect hardgrounds will remove encrusters with thin skeletons and truncate borings (Fürsich, 1979). Encrusting bivalves and brachiopods normally lose their upper valves after death (e.g., Zítt and Nekvasilová, 1996), taking with them any fouling organisms. Babic and Zupanic (2000), in a study of Croatian Eocene clasts, have highlighted the erosional loss of shallow borings in high-energy environments and its effect on the preserved endolithic assemblage.

Very little experimental taphonomy has been conducted using epibionts, although an abstract by Michel (1986) did report differential loss of particular groups when subjected to physical and chemical destruction.

9. Phanerozoic trends in hard substrate communities

Since hard substrate communities have a fossil record extending far back into the Precambrian, we can outline a series of trends in their composition and ecology. There are distinct advantages for this type of analysis with these fossils because they are almost entirely in situ, at least with respect to their substrates. The attached skeletal fossils retain their spatial relationships within the community, although their temporal relationships are often in doubt (see, for example, Wilson and Taylor, 2001a). The encrusted and bored hard substrates themselves are generally consistent through the Phanerozoic, although they change in relative abundances. Most of the hard substrate communities in the fossil record are on calcareous shells and carbonate hardgrounds, with a small number on siliciclastic and silicate rockgrounds, wood, and (rarely) methane hydrate-cemented sediments.

9.1. Bioerosion intensity and style

The first recorded bioerosion consists of very small cavities excavated by microbial endoliths in ooids and stromatolites. They are in many cases almost identical to the microborings produced by modern bacteria (Golubic et al., 1975). These earliest endoliths were at least in part photosynthetic like their recent counterparts, and so they favoured exposed substrates in shallow waters. Microboring communities change in composition over time, but they retain a remarkable uniformity in their physical expression and ecological requirements.

Macroborings, on the other hand, have changed dramatically through the Phanerozoic. Domichnial (dwelling) borings appear in Lower Cambrian as the simple, cylindrical *Trypanites*, which was probably produced by many worm-like organisms over time (Kobluk et al., 1978). These borings are the most common in the Palaeozoic, penetrating calcareous shells, hardgrounds, and carbonate rockgrounds (Palmer, 1982; Wilson and Palmer, 1992). Other borings appear in the Palaeozoic, such as *Petroxestes* (Fig. 3A), *Palaeosabella* (Fig. 3B), *Rogerella*, *Gastrochaenolites* (Fig. 3D) and various "sponge" borings, but they are rare. Mesozoic macroboring is very different in intensity and style. Bivalve borings, especially *Gastrochaenolites*, are abundant on carbonate hard substrates from the Jurassic to the Recent, as are sponge borings such as *Entobia* and grazing traces like *Gnathichnus*. Borings become so common that the substrates themselves are rapidly degraded, especially in tropical and subtropical environments (see for Jurassic examples Andersson, 1979; Chudzikiewicz and Wieczorek, 1985; Gruszczynski, 1986; Garcia et al., 1989; Fürsich et al., 1994; Wilson and Palmer, 1994; Bertling, 1999b). This infaunalisation on hard substrates may be a response to the rise of predators known as the Mesozoic Marine Revolution (Vermeij, 1977, 1978, 1987). The equivalent infaunalisation within soft substrates has been thoroughly discussed (Stanley, 1977; Thayer, 1979, 1983), but this hard substrate pattern in the Mesozoic needs further elucidation (Morton, 1990; Wilson and Palmer, 1992). In the Cenozoic, bioerosion rates are especially high on carbonate substrates, with the main borers being bivalves (Kleemann, 1996), sponges (see Bromley and D'Alessandro, 1984) and polychaete worms (see Bromley and D'Alessandro, 1983). Perry and Bertling (2000) examined Mesozoic to Recent trends in macroboring in coral reefs, concluding that overall intensity of boring has increased through time. They also described marked changes in the composition of boring communities: bivalves and 'worms' initially dominated (at least until the Late Cretaceous) but were of secondary importance to sponges from the Early Miocene onwards. For additional information on marine bioerosion through the Phanerozoic, see Bromley (1994) and Kiessling et al. (1999).

Putative predatory borings are a more complex story through time because they are not always clearly distinguished from other borings. The first reported predatory borings are simple round holes in *Cloudina* skeletons of the Late Precambrian (Bengtson and Zhao, 1992). There are similar holes in Cambrian brachiopod shells which appear to be predatory (Conway Morris and Bengtson, 1994). It has proven very difficult to distinguish predatory from domichnial borings in the Ordovician (see Richards and Shabica, 1969; Kaplan and Baumiller, 2000; Wilson and Palmer, 2001). In fact, the earliest post-Cambrian predatory borings may be the work of naticid-like gastropods in the Devonian (see Leighton, 2001). Predatory borings increase in abundance and diversity in the Carboniferous (Baumiller et al., 1999), a trend which continues through the Mesozoic and Cenozoic. For a review of Phanerozoic predatory boring and the associated controversies, see Kowalewski et al. (1998), Kowalewski (2000), Harper et al. (1998, 1999), Hoffmeister and Kowalewski (2001), and Leighton (2001).

9.2. Encrusters

As would be predicted, encrusting assemblages on organic and inorganic hard substrates increase dramatically in diversity, niche utilisation, and abundance from the Cambrian into the Ordovician, and even more so from the Early to the Middle Ordovician (Palmer, 1982; Palmer and Wilson, 1992; Lescinsky, 2001). Thereafter, encrusters show two distinct peaks of diversity and abundance. Those on upward-facing, shallow water carbonate hardgrounds peaked in diversity and abundance in the Late Ordovician and the Jurassic–Cretaceous (Palmer, 1982; Palmer and Wilson, 1992). These peaks are coincident with the bimodal abundance of hardgrounds during "calcite sea" times and so may represent a significant sampling bias. Encrusters on organic hard substrates peak in species richness during the Silurian–Devonian and the Jurassic. Lescinsky (2001) points out that this pattern may be biased by preferential description of high-diversity assemblages during these intervals, but nevertheless it accords with our experience in the field. More work is necessary to better delineate these diversity patterns. We especially need detailed studies of encrusting assemblages in the Carboniferous, Permian and Triassic.

Carbonate hardground encrusters show an increase in external skeletalisation from the Palaeozoic through the Mesozoic (Palmer, 1982; Wilson and Palmer, 1992). Examples include trends in the dominant bryozoans (from groups like trepostomes, where the colony surface was invested by soft tissues, to most cyclostomes and cheilostomes with mineralised outer walls), in the reduction of adpressed echinoderms such as edrioasteroids, and in the appearance of abundant and well-skeletalised encrusting bivalves, brachiopods and serpulid worms in the Mesozoic. This increase in skeletal protection may have been a response to rising levels of predation, especially during the Mesozoic Marine Revolution. Hardground communities also show a rough increase in tiering, especially if borings are considered. Later Palaeozoic hardgrounds, for example, have more erect bryozoans such as fenestrates than their middle and early Palaeozoic equivalents. Jurassic and Cretaceous hardgrounds, though, have fewer erect forms and tend to be dominated by low encrusters like oysters and plicatulids. These same hardgrounds, however, also often have deeper tiers of diverse borings than any preceding them.

Lescinsky (2001) has provided the best summary of historical trends in epibiont communities, most of which are consistent with those outlined above on hardgrounds. Epibionts on shells are better known than hardground encrusters in the crucial intervals of the later Palaeozoic–early Mesozoic and the Cenozoic. Lescinsky (1997), for example, showed that with careful study of many bulk samples, diversity trends can be delineated. He postulated that peaks in epibiont diversity may be related to high levels of nutrient supply and hence productivity. Taylor and Michalík (1991), in a rare study of Triassic skeletobionts, demonstrated that most of the common encrusting groups of the Mesozoic appeared by at least the Late Triassic.

9.3. Cryptic hard substrate communities

Marine cryptic hard substrate communities have been in existence nearly as long as their exposed hard substrate counterparts. Cryptic spaces provide additional living space and a refuge from most predators and physical disturbance. The price cryptic organisms pay for this habitat includes less light and sometimes lower levels of nutrients (Gischler and Ginsburg, 1996). Cryptic spaces have varied in their type, availability and abundance over time, and thus cryptic fossil communities will have irregular distributions through the geologic record. Cambrian crypts were most often in archaeocyath reefs and algal mounds, and they tended to be small and ephemeral. Ordovician through Early Carboniferous cavities were primarily formed under hardgrounds and large, massive skeletons like those of tabulate corals and stromatoporoids. Pennsylvanian and Permian reefs provided a large amount of cryptic space within their frameworks, hosting a significant portion of their total diversity. The Middle and Late Mesozoic showed again the importance of hardgrounds for providing cryptic space on carbonate shelves. Modern coral reefs today may have between 30% and 75% of their volume taken up by cavities, and the surface area of these cavities may be two to three times that of the exposed portions of the reef (Logan et al., 1984; Kobluk and van Soest, 1989; Gischler and Ginsburg, 1996). An endoscopic study of cavities in Red Sea reefs revealed a sponge-dominated community of filter feeders that had a far greater biomass than the community of filter feeders on the reef surface (Richter et al., 2001). Cryptic organisms are thus prominent in the history of hard substrate communities.

One of the most interesting historical questions to ask about cryptic communities is whether they have served as ecological refuges for formerly open-dwelling organisms. That is, have they housed relict forms which have disappeared from exposed environments? That may be the case with modern "hypercalcified" sponges, which are sometimes thought to be relicts from the Mesozoic (Vacelet, 1983, 1991). Taylor and Palmer (1994) described the preserved sessile fauna on the walls of exhumed Jurassic caves in western France. They found thrombolitic structures and abundant calcified demosponges, calcisponges, thecideidine brachiopods, serpulids, cyclostome bryozoans, and cemented bivalves. The microbes which formed the thrombolites in the Jurassic were present in open and cryptic spaces; today they are confined to caves, meaning they could be considered relict. The other organisms, though, may have always been cryptic and thus not truly relict today. Thecideidine brachiopods, for example, were common in Jurassic caves and other cavities (Taylor and Palmer, 1994; Wilson, 1998) and are just as common today in similar habitats (Harmelin et al., 1985).

9.4. The effects of calcite and aragonite seawater chemistry

It is now clear that some ancient seas had significantly different chemistries with respect to calcium carbonate dissolution and precipitation. Some intervals in the past, notably the early Palaeozoic and the middle to later Mesozoic, were characterised by low-magnesium calcite inorganic precipitation ('Calcite Seas'), which contrasts with the aragonite and high-magnesium calcite inorganic precipitation ('Aragonite Seas') we see from the middle Palaeozoic through the early Mesozoic and the Cenozoic (Wilkinson et al., 1985; Wilkinson and Given, 1986; Morse and Mackenzie, 1990; Lowenstein et al., 2001). The significance for this review is that Calcite Sea conditions facilitated the rapid and widespread formation of carbonate hardgrounds as well as the contemporaneous dissolution of aragonitic shells in shallow tropical seas (Palmer, 1982; Palmer et al., 1988; Wilson and Palmer, 1992; Wilson et al., 1992; Cherns and Wright, 2000; Fig. 43).

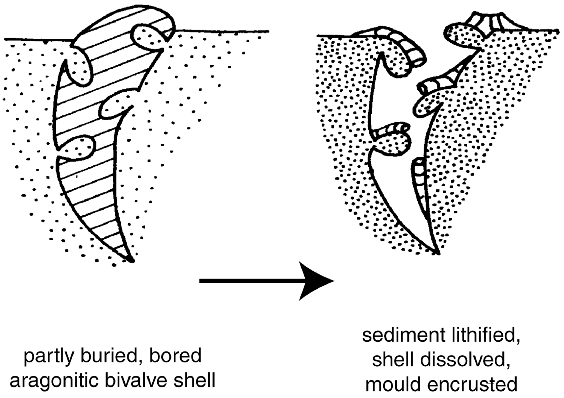


Fig. 43. Early diagenetic cementation, aragonite shell dissolution and encrustation of moulds typical of Calcite Seas. After Palmer et al. (1988).

9.4.1. Abundance of carbonate hardgrounds over time

Carbonate hardgrounds formed rapidly and extensively in shallow, warm seas during Calcite Sea times, especially the Ordovician and the Jurassic (Palmer, 1982; Wilson and Palmer, 1992). In contrast, Aragonite Sea intervals have very few carbonate hardgrounds. There are at least 100 papers describing carbonate hardgrounds from the Ordovician, for example, and not a single paper about a Permian carbonate hardground.

There is a correlation between the rapid increase in the abundance and extent of carbonate hardgrounds in the Early Ordovician and the evolution of attaching echinoderms (Wilson et al., 1989, 1992; Guensburg and Sprinkle, 1992; Wilson and Palmer, 1990, 1992; Rozhnov and Palmer, 1996). It is possible that the pervasive lithification of carbonate sediment seafloors at this time provided a selective pressure for echinoderms which could attach to hard substrates, and thus the hardgrounds dramatically widened the hard substrate niche long before shelly substrates became common. The echinoderm stereom structure also promoted rapid substrate cementation. There may be a similar story for the Early Ordovician radiation of bryozoans. Some of the earliest bryozoans have large attachment bases (Hu and Spjeldnaes, 1991); Wilson and Palmer (1992) suggested that these bases are adaptations for attachment to hardgrounds.

9.4.2. Skeletal biomineralogy and taphonomy

The invertebrate faunas recovered from Calcite Sea intervals are dominated by those with calcitic skeletons (Stanley and Hardie, 1998, 1999; Wilkinson, 1979) or aragonitic skeletons with outer calcite layers (Harper et al., 1997). It is difficult to test the hypothesis that the invertebrate shelly fauna in Calcite Seas had evolved calcitic shells as an adaptation to the prevailing seawater chemistry because their aragonitic-shelled contemporaries were preferentially dissolved and thus not often preserved (and see also the "thermal potentiation" argument of Carter et al., 1998). We can note, though, that many of the aragonitic molluscs we do find from Calcite Seas were infaunal and/or had thick periostraca (e.g., Pojeta, 1971), meaning that their shells were somewhat protected from the aragonite-dissolving seawater.

One taphonomic advantage of Calcite Sea geochemistry occurs when a calcitic epibiont encrusts an aragonitic shell with a soft-bodied encruster between them. The soft-bodied organism may be bioimmured within the base of the calcitic epibiont and then revealed when the aragonitic host shell is dissolved (Wilson et al., 1994). Many soft-bodied encrusters are now known only through bioimmurations in overlying skeletons (see Taylor, 1990, for review).

10. Geological utility of hard substrate communities

Extensive exposed hard substrates, such as hardgrounds and rockgrounds, often represent significant breaks in the sedimentary record. Their recognition, then, is important to sedimentological and stratigraphic studies. When there are few lithological differences above and below such a horizon, as in a carbonate sequence with hardgrounds, palaeontological criteria are often the only indicators of the hiatus.

10.1. Recognising sequence boundaries

Carbonate hardgrounds are commonly formed when sedimentation rates are very low and bioturbation is at least temporarily diminished (Wilson and Palmer, 1992). These conditions may occur near the end of a transgressive cycle in a carbonate sequence, producing a hardground as the maximum flooding surface. Fürsich et al. (1991, 1992) showed that hardgrounds and reworked concretions were critical to understanding the basinal history of a Jurassic sequence in western India. Fookes (1995) used such hardgrounds to sort out the sequence stratigraphy of an Upper Jurassic reef complex in eastern France. He could recognise the surfaces because they were "perforated" by "cylindrical bioerosions" (probably *Trypanites*), and because of pervasive mineralisation by what appears to be authigenic glauconite (Fookes, 1995, p. 136). Wilson et al. (1998a,b) used a similar bioeroded and encrusted surface (though not a hardground) to detect an otherwise unknown interglacial eustatic sea-level change in Late Pleistocene (Eemian) coral reefs of the Bahamas. This disconformity had gone unrecognised because the sediments and fossils are so similar above and below it; it was only revealed when blasting exposed large *Gastrochaenolites*. Hesselbo and Palmer (1992) demonstrated that a regional discontinuity within Lower Jurassic marine mudstones was marked by bored and encrusted septarian concretions. The hiatus associated with these hard substrates included three ammonite subzones. The same horizon has been the subject of a recent debate as to whether or not they represent a sea level fall (Hallam, 1999; Coe et al., 2000). Siggerud et al. (2000) demonstrated the utility of bored limestone pebbles for interpreting wave-ravinement surfaces within an Eocene transgressive systems tract in northeastern Spain.

10.2. Identifying and estimating magnitudes of sea level change

Hard substrate communities, particularly on bioeroded carbonate rocky shores, are very useful for estimating the magnitude of sea level changes. Wilson et al. (1998a,b) showed that an erosional surface and subsequent reef developed upon it indicated a sea level fall and rise of several meters in the Late Pleistocene. Various workers have deduced numerous tectonically produced local sea level changes in the Holocene by examining patterns of bioerosion and encrustation, particularly by light-sensitive coralline algae (Laborel, 1979a,b; Papageorgiou et al., 1993; Laborel and Laborel-Deguen, 1994, 1995; Pirazzoli et al., 1994, 1996; Laborel et al., 1994, 1999; Sartoretto et al., 1996). Such work in the Mediterranean has been especially important for detecting and estimating the magnitude of historical seismic events (Papageorgiou et al., 1993; Pirazzoli et al., 1994), which has immediate applications in archaeology. Distinctive assemblages of sessile organisms, including barnacles, can be used to recognise the positions of ancient intertidal zones and hence to chart sea-level changes (Baker et al., 2001).

11. Summary

Hard substrates of organic and inorganic origin are locally abundant in the geological record. Many preserve components of the ancient communities which colonised them, especially encrusters that were cemented permanently to the surface of the substrate and borers excavating holes into the substrate. These fossil sclerobionts are preserved in situ, retaining their original spatial relationships to the substrate and to one another, thereby eliminating one major factor—displacement—constraining any research that attempts to interpret ancient ecology from fossil evidence. Most studies of hard substrate palaeoecology have been concerned with material from a single stratigraphic horizon and locality. The literature base that has accumulated over approximately the past 50 years is very scattered and tends to be somewhat anecdotal in scope. As a rule, little or no reference is made to neontological work on the ecology of modern hard substrates. Consequently, hard substrate palaeoecology contains few of the insights that knowledge of modern communities can potentially provide.

This review of hard substrate palaeoecology has revealed various general themes, several worthy of further study. While many strategies for utilising hard substrates have long geological histories, the taxa employing these strategies have changed through time, and the relative importance of different modes of life (e.g., encrustation vs. boring) have also varied. The details of such temporal patterns are not well documented, nor has there been much testing of the causal processes responsible for the patterns.

Future research on hard substrate palaeoecology should also include bed-by-bed sampling to document geologically short-term changes in sclerobionts and their interactions with one another. This appears not to have been previously attempted, even though such studies could address important issues of long-term (in an ecological sense) stability of in situ communities and the changing dynamics of ecological interactions through intervals of geological time. Extinction, survival and restructuring of hard substrate communities during mass extinctions deserves particular attention in view of interest concerning the extent to which mass extinctions have shaped the evolution of life on Earth.

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