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## 4.8 Reefs and Carbonate Build-ups

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### Introduction

Definition has always been a prominent issue in reef studies, at the heart of which has been the struggle to integrate two perspectives, one based on modern and the other on fossil structures. Although modern reefs provide important insights into processes, they can be misleading as gross analogues because of the way in which they have been affected by Quaternary glacioeustatic events — events that cannot be assumed to have applied to all reefs and build-ups throughout the geological record. It is appropriate here to be pragmatic and accept, *de facto*, all features that have been regarded as reefs and build-ups to date (Scholle *et al.* 1983; James & Macintyre 1985; Scoffin 1987). While no simple definition unites them all, there is a logical (if sometimes indirect) thread that connects them. For a succinct discussion of reef types, see James & Macintyre (1985, p. 22). Fig. 1 summarizes the principal organic contributors to reefs and build-ups through geological time.

Criteria mentioned in most reef definitions include one or more of the following: *organic framework*, *raised relief*, *wave resistance*, *photic zone restriction*, and *tropical (or warm water) distribution*. In practice, the only structures that can be *observed* to fulfil all these criteria are modern tropical coral reefs. All other structures that have been regarded as reefs and build-ups, past or present, usually show (or have been interpreted as showing) *either* evidence of framework, *or* raised relief, *or* both. Generally, if any distinction between reefs and

build-ups is made at all, reefs are usually thought of as showing evidence of framework as well as relief ('ecological reefs' (Fig. 2B)), whereas build-ups can also be used for relief structures without (observable) framework. Criteria other than framework and relief have come to be regarded as secondary, and may or may not be met in the identification of a particular reef or build-up.

However, even this simple approach leaves problems. Various fossil structures have come to be called reefs simply because their features *seem* to include framework or relief, in the absence of clear evidence to the contrary. Moreover, the search for Recent analogues of all the different fossil structures now included in reefs and build-ups has generated interest in Recent biogenic structures other than tropical coral reefs, notably deep- and cold-water coral banks, lithoherms, and carbonate mounds (Cairns & Stanley 1981; Mullins *et al.* 1981; Scholle *et al.* 1983; James & Macintyre 1985). These have also become part of the broad notion of reefs and build-ups.

### Principal reef criteria

*Framework.* The consensus is that framework (Fig. 3) consists of three biogenic components: (1) closely packed, primary *in situ* accumulations or intergrowths of rigid macro-organisms (typically corals, branching coralline algae, rudistid bivalves, stromatoporoids) further bound together by (2) a secondary framework of *in situ* encrusting and

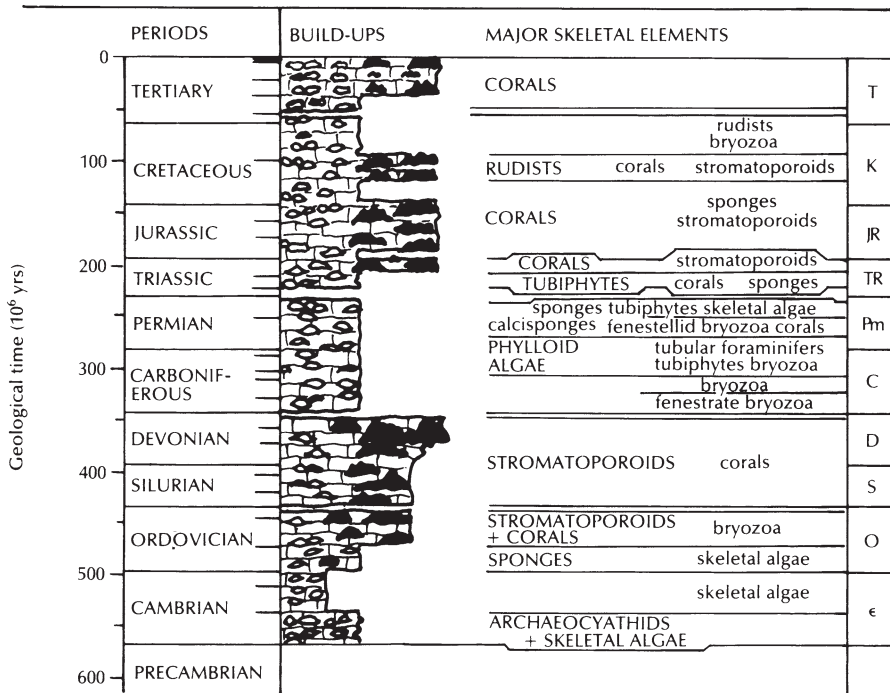


Fig. 1 Idealized stratigraphic column showing major organic contributors to reefs and build-ups through the Phanerozoic. Block symbols represent framework structures, and open symbols represent structures without framework ('reef mounds'). Gaps indicate times when there appear to have been no framework structures, and times when there were no build-ups at all. Note that many authors would regard skeletal algae as being similar in importance to corals in the Tertiary. (After James in Scholle *et al.* 1983, by permission from the American Association of Petroleum Geologists.)

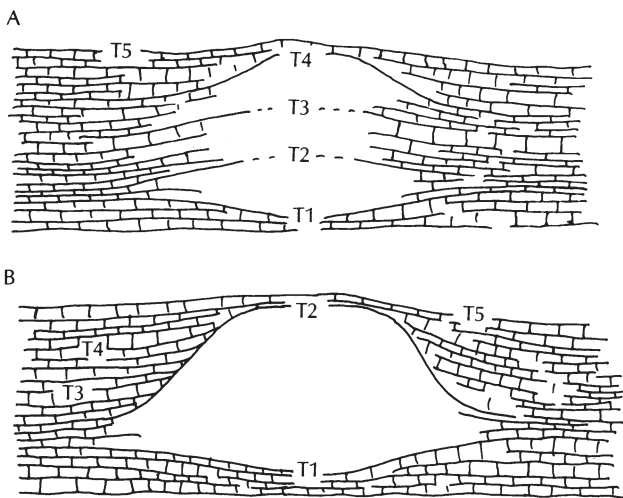


Fig. 2 Schematic difference between A, a stratigraphic reef and B, an ecological reef. Successive time planes are indicated by 'T' symbols. Stratigraphic reefs may also contain ecological phases, as in the lowest and uppermost reefal units in A. (After James in Scholle *et al.* 1983, by permission from the American Association of Petroleum Geologists.)

cementing organisms (typically coralline algae, bryozoans, and encrusting foraminifera and sheet-like corals); and (3) infilling material, trapped within this rigid structure, consisting of sediment whose origins may be from either the framework itself or beyond it. There are also numerous infilling organ-

isms, usually smaller than the main framework contributors, both encrusting and free-living, many of them (*coelobites*) occupying caves, cavities, and overhangs (*cryptic habitats*). Much sediment infill is also postlithification.

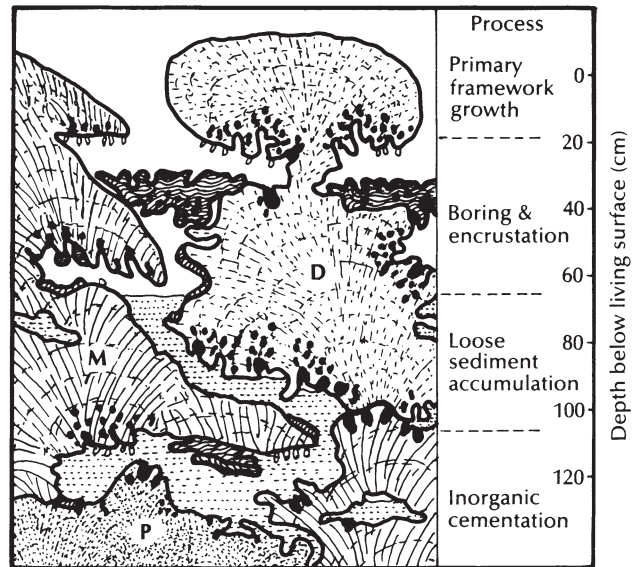
This rigid framework model, however, is an idealized end-member of a whole spectrum of 'frameworks'. Different processes of sedimentation and preservation result in an intergradation of prominence between the above three framework components. Large branching or mound-like organisms may be sparse or absent, leaving encrusting and cementing organisms like coralline algae to build up structures on their own (Bosence 1983; Scholle *et al.* 1983), as in the largely algal Bermuda cup reefs. Encrusters can also bind sediment ranging in grain size from fine mud and silt (as in stromatolites) to cobbles of broken, worn, and transported material, or other accumulations of biogenic clasts like rhodoliths. If the clastic material consists of large, relatively unworn coral fragments, it may be hard to distinguish the finally preserved rock from a true *in situ* framework of macro-organisms. At another extreme (and probably more abundant than the idealized framework model), dense stands or accumulations of organisms can occur without any apparent binding organisms, e.g. the coral beds of the British Carboniferous and many facies of rudistid reefs. In the case of lithoherms, early diagenesis has a significant constructional role not

unlike a framework built by organic encrusters, but in this case, primary structure consists almost entirely of sediment; the organic component consists of secondary colonizers.

While a true framework is usually considered to be a relatively permanent feature, frameworks of non-rigid organisms are also very important as constructive agents, although they usually break down before preservation. Structures of this kind, built up by sediment-trapping marine grasses, occur in the inshore areas of the Florida Keys (Scholle *et al.* 1983; James & Macintyre 1985, Bosence *et al.* 1985). Delicate branching corals, crinoids, and organisms whose preservable skeletal elements are held together by soft tissues (such as many sponges and octocorals) can also have a similar sediment-trapping role, but usually break down into fragments and spicules before preservation. The environment of such non-rigid frameworks is generally less favourable to cementing organisms than that of rigid frameworks, so the resulting rock contains large amounts of sediment in relation to primary organisms. Even with rigid frameworks, however, the final proportion of framework in the resulting rock can be surprisingly reduced to shadowy remnants where they have suffered extensive *in situ* contemporaneous destruction by boring organisms (such as endolithic algae, clionid sponges, and various bivalves). Diagenetic processes can also destroy framework.

Thus the concept of framework, like that of reefs, has become broad, and takes into account both frameworks that are preserved and those that are not. The end-product may be a structure with relief but no apparent framework, a framework with raised relief, or a framework without true relief (i.e. a laterally developed *in situ* growth or biostrome). There are also relief-features to consider that may never have had any framework at all, as discussed next.

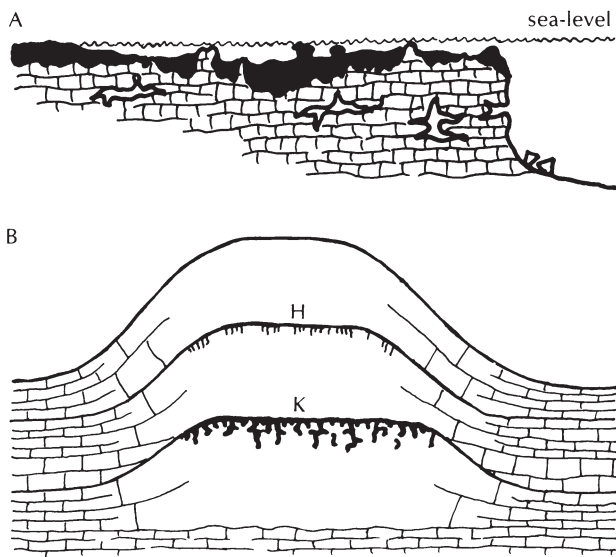
*Relief.* For fossil build-ups, the identification of relief is usually an inference derived from the observation of a facies discontinuity that marks the limits, ideally, of a bioconstructional formation. Relief is inferred if this discontinuity has a mound- or ridge-like geometry, and (in theory at least) it results from the ability of framework organisms to maintain net growth against the agents of destruction and transport. In many cases, moreover, it is difficult to conceive what other primary sedimentary process could cause the commonly observed steepness of sedimentary dips. Problems arise from



**Fig. 3** Vertical cross-section through part of a Bermuda lagoonal patch reef, showing framework structure and internal processes. Capital letter symbols indicate primary framework of scleractinian corals, here consisting of three genera (D, *Diploria*; M, *Montastrea*; P, *Porites*). Secondary framework (laminated pattern) consists of coralline algae above, Bryozoa in middle cavities, and *Agaricia* coral in lower cavity. The encrusting foraminiferan, *Homotrema*, lines undersides of overhangs. Sediment infill is shown by horizontal stipple. Bioerosion is denoted in black: mainly by bivalves like *Lithophaga* (larger holes) and clionid sponges (smaller holes); not to scale. (After Scoffin 1987.)

this, however:

- 1 Some of the relief and its flank-slope steepness may be due to antecedent structure (Fig. 4, and discussed below).
- 2 There are relief features that contain no clear framework. This might be because framework has not been preserved, or because the build-ups were shaped primarily by contemporaneous hydrodynamic factors or early diagenesis. (Such features can also be colonized by organisms as they grow, giving the illusion of framework.)
- 3 Postlithification erosion can 'create' or enhance primary relief. It is not always easy to distinguish a discontinuity surface which is due to stratigraphical disconformity from a syndepositional interface between framework and flanking facies, especially when identification of framework is uncertain. Similarly, the present-day surface of land erosion can also 'create' reef-like relief in ancient deposits, and this is not easy to distinguish from the exhumation of ancient syndepositional features. Although emphasis has been placed on the recognition of talus blocks to infer syndepositional relief,



**Fig. 4** Composite structure and antecedent surfaces as factors in reef relief (not to scale). A, Recent model showing Holocene reef growth as a veneer, 0–10 m thick (black), overlying disconformity in karst-eroded, pre-Holocene reef limestones. (After Braithwaite 1987.) B, Fossil reef structure composed of a stacked series of reef phases separated by discontinuities; lower discontinuity (K) is a karstic erosion surface, while upper discontinuity (H) is a hardground. (After James & Macintyre 1985.)

this kind of evidence can be misleading. Blocks at the foot of modern deep fore-reef slopes in the Caribbean, previously taken to be modern and syndepositional, might well be residuals derived from subaerial erosion of older reef limestones during pre-Holocene low sea-level stands. Many ancient talus deposits might therefore have originated in analogous fashion. Better knowledge of Pleistocene–Holocene karstic phenomena and the erosional history of modern reef complexes (below) has stimulated a search for intraformational palaeo-karstic surfaces in fossil build-ups (Fig. 4). This has revealed that at least part of the apparently contemporaneous relief of some supposed build-ups may actually be due to cyclical alternation of deposition of prograding carbonates with emergence and karstic erosion.

4 Another possible cause of 'pseudo-relief' is that of sharp syndepositional interfaces between different communities and facies. Where the relative lateral extent of these interfaces persists, waxing and waning through time, a mound-like geometry can develop, although at the time of deposition, one facies may not have projected significantly more than another above the sea floor ('stratigraphic

reefs': Fig. 2A). Other postdepositional factors, such as diagenesis and relative compaction, may also account for 'pseudo-relief' or exaggerate primary relief.

Even in modern environments, reef relief, though readily observed, is not a simple phenomenon. It is certainly not always attributable to framework or sediment-trapping organisms. Hydrodynamic influence can be as important as the direct role of organisms, or more so, as in the growth of columnar stromatolites, and in the linear carbonate mud mounds of Florida Bay (now regarded as partial analogues of Carboniferous Waulsortian reefs; Bridges & Chapman 1988).

A great deal of apparent relief, moreover, can be ascribed to underlying, antecedent topography (Fig. 4). This is now beyond doubt for most modern coral reefs, for which glacioeustatic events have been especially important. Shallow drilling and radiometric dating show that in both scale and detailed topography, much of their relief still matches the dissected and cavernous morphology of pre-existing platforms formed by underlying, older reef limestones. These were evidently exposed subaerially during glacioeustatic regressions, especially during the last 140 000 years, and subjected to karstic erosion. Since then, the Holocene transgression has drowned the resulting topographies, and renewed modern growth has contributed only a veneer (varying from a few centimetres to about 10 m or more) which often scarcely masks these older features (Fig. 4A). Recognition of this took a surprisingly long time and was hindered by: (1) the lithological similarity between modern and older limestones; and (2) the fact that some of the older limestones were prograded to approximately the same sea-level as today, so the uppermost features of modern reefs are in fact partly contemporary and partly fossil.

Implications of this for the study of fossil reefs are as follows: (1) they may similarly have been affected by intraformational, erosional histories (Fig. 4B) that are not immediately obvious and might still be unrecognized; and (2) the most informative modern analogue for fossil reefs is not the gross structure and relief of modern reefs, since this is usually a composite of numerous phases which may go back to the Early Tertiary or before. Rather, it is the Holocene veneer alone that provides the most direct clues for a single phase reef-growth model. However, even this has limitations as a general case for the fossil record, because it represents a relatively short term response to transgressive conditions. It

must be adapted to take account of the probable effects of static or regressive sea-levels, as well as different rates of sea-level change and the vertical component of any tectonic movement that affected the foundations.

Even without eustatic influence in the history of a build-up, the ecological preference of many benthic organisms for sea-floor highs (like submarine horsts, scarps, and volcanoes), as well as the greater rates of carbonate deposition on such features, points to a general likelihood of an antecedent factor in almost any carbonate complex.

In order to relate relief in fossil build-ups to that of modern reefs, physical scale must also be considered. Many modern coral reefs are extensive complex structures many kilometres across with a whole mosaic of carbonate facies. True framework is highly localized, not necessarily at the seaward rim of such complexes, and usually accounts for much less surface area and volume than bioclastic sediments, oolites (e.g. Bahamas), and evaporites. This facies complexity appears to reflect immaturity, because Holocene submergence and growth recovery has been so recent, and this is another constraint to be considered in using modern reefs as fossil analogues.

Although some fossil build-ups are also seen as complexes (e.g. the Devonian of the Canning Basin), many are defined purely with respect to a local outcrop of a framework or relief feature, perhaps only metres across (e.g. the Silurian of the British Wenlock). The best analogues for such structures are not complete reef complexes like modern atolls, which are tens of kilometres across, nor even platform reefs like those of the Australian Great Barrier Reef complex, but rather the separate small-scale constructional features within these carbonate systems. The lagoonal patch reefs of Bermuda, which are just one of a whole range of features within its atoll-like complex, are much more comparable in scale and structure to reefs of the British Wenlock.

Similarly, there is confusion of scale in the use of 'lagoon' in reef studies, which might denote anything from the shallow (less than 5 m) sheet of water that covers many modern reef flats, to the large and relatively deep (up to 70 m or more) areas that lie within atoll rims or between barrier reef complexes and their mainland. It follows that 'fore-reef' and 'back-reef' concepts also have various meanings. It is probably best to think of reef relief as a fractal phenomenon — similar topographic patterns repeated within themselves on different scales (e.g. compare atolls, faros, and microatolls).

### Other criteria

Remaining criteria are secondary, often introduced in support of a particular reef interpretation. Although such criteria apply to modern coral reefs, there also exist modern bioconstructional features and other possible analogues of ancient build-ups that occur: (1) below wave base; (2) below the photic zone; (3) in deep and cold water; and (4) in high latitudes. Many kinds of largely algal build-up, sometimes combined with bryozoans, occur in temperate latitudes, and there exists a whole suite of different deep- and cold-water coral banks (Cairns & Stanley 1981; Mullins *et al.* 1981; Bosence 1983; Scholle *et al.* 1983; James & Macintyre 1985; Scoffin 1987).

Common arguments for inferring wave influence are: (1) relief as an indication of wave resistance; and (2) zonation of communities as a response to sharp environmental gradients caused by the breakwater-like effect of a positive feature close to sea-level. But relief is equivocal evidence, as already discussed, and zonation can occur in deeper-water structures. Conversely, modern small surface patch reefs of a size comparable to many fossil build-ups are often too small to show either real zonation or any clear fore-reef and back-reef differences. In view of the popular use of reefs and build-ups as palaeoclimatic and palaeogeographical indicators, it is therefore also worth noting that their occurrence (defined broadly) in the geological record is not a reliable reflection of temperature, climate, latitude, water depth, or wave energy, even when corals or algae are prominent.

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## 4.9 Encrusters

P. D. TAYLOR

### Introduction

Encrusting animals and plants are important colonizers of marine hard substrata today (Jackson 1983), and are well represented in the Phanerozoic fossil record. Interest in modern encrusters is linked both to their commercial importance as foulers of man-made structures (e.g. ship's hulls and offshore oil platforms), and to the fact that encrusting communities on artificial settlement panels are excellent subjects for studies of competition and ecological succession. Encrusters are also attractive subjects for palaeoecological studies because they retain their original spatial relationships to the substratum and to one another, thus allowing the inference of life orientations and interactions. Furthermore, the substrata used by encrusters are often discrete and of a size suitable for collection in the field and transportation back to the laboratory for detailed study.

Communities living on hard substrata are usually dominated by sessile organisms which include *endobionts* (boring into the substratum) and *epibionts* (attaching to the surface of the substratum). The epibionts comprise organically-attached (e.g. pedically-attached brachiopods, bysally-attached bivalves) and cemented forms. Many organisms have cemented bases or holdfasts which anchor more extensive erect parts (e.g. crinoids, arborescent bryozoans). However, the term 'encruster' is here restricted to organisms of low profile which are cemented to the substratum across a large part of their basal surfaces. Organisms cementing to small substrata which they quickly outgrow to rest freely on the sea bed (e.g. gryphaeate oysters, many

stromatoporoids) are excluded from this definition of encrusters, although, as with erect organisms, they may intergrade with typical encrusters.

Encrusting animals are characteristically suspension feeders, capturing particulate food from the water column. Being sessile as adults, they are dependent for colonization on a free-swimming larval stage. Those individuals whose larvae settle successfully and survive immediate post-settlement mortality are termed *recruits*.

### Taxonomic composition and morphology of encrusters

The following groups generally dominate modern encrusting biotas: algae, foraminifera, sponges, coelenterates, bryozoans, brachiopods, bivalves, serpulid polychaetes, ascidian tunicates, and barnacles. Apart from ascidians, all of these groups contain at least some species with mineralized skeletons, and therefore have good preservation potential. Even soft-bodied encrusters are occasionally preserved as fossils by *bioimmuration*, i.e. when overgrown by other encrusters and left as natural moulds on their undersides.

It is useful to classify encrusting animals according to aspects of their growth and form that determine how they use and compete for substratum space. A fundamental distinction is between solitary and colonial forms. Solitary forms typically grow to a fixed size and shape (determinate growth), whereas colonial forms, which grow by the asexual budding of modular units (zooids), are often highly irregular in size and shape (indeterminate growth), may suffer partial mortality (death of some but

not all zooids in the colony), and undergo fission into several parts or fusion with other colonies (Section 4.6).

Encrusters commonly found as fossils are shown in Fig. 1. Solitary encrusters fall into two main morphological groups: forms with a subcircular outline shape which grow centrifugally from an encompassing growing zone, and linear forms which grow in straight, curved, or spirally coiled lines from an apical growing zone. Subcircular forms are often bivalved or multiplated, and are well equipped to defend their margins against lateral overgrowth by other encrusters. Many linear forms can change growth direction and 'migrate' significantly across the substratum, but they have poorly defended flanks which are vulnerable to lateral overgrowth.

Colonial encrusters also fall into two main morphological groups (Jackson 1979): *sheets* (Fig. 2A), which are 'two-dimensional' colonies, with closely-packed zooids, which spread across the substratum by zooidal budding from an encompassing growing zone; and *runners* (Fig. 2B), which are 'one-

dimensional', branching colonies which grow by budding zooids from numerous growth tips. Sheet-like colonies are highly committed to defending and winning substratum space from other encrusters (*confrontational* or *phalanx* strategy). Runners, by contrast, are vulnerable to lateral overgrowth, but distribute their zooids across wide areas of the substratum (*fugitive* or *guerilla* strategy); this enables them to locate patches of substratum (*spatial refuges*) where the probability of mortality is lower and in which some zooids may survive (see also Section 4.6).

Points to note in the geological history of encrusters (Fig. 1) are the major radiation of encrusters in the Ordovician, the scarcity of encrusters in the Late Palaeozoic, and the Mesozoic radiation of the modern encrusting biota, with the late appearance of acorn barnacles.

### Encruster-substratum relationships

Modern communities of encrusters are best known from intertidal and shallow subtidal habitats, and

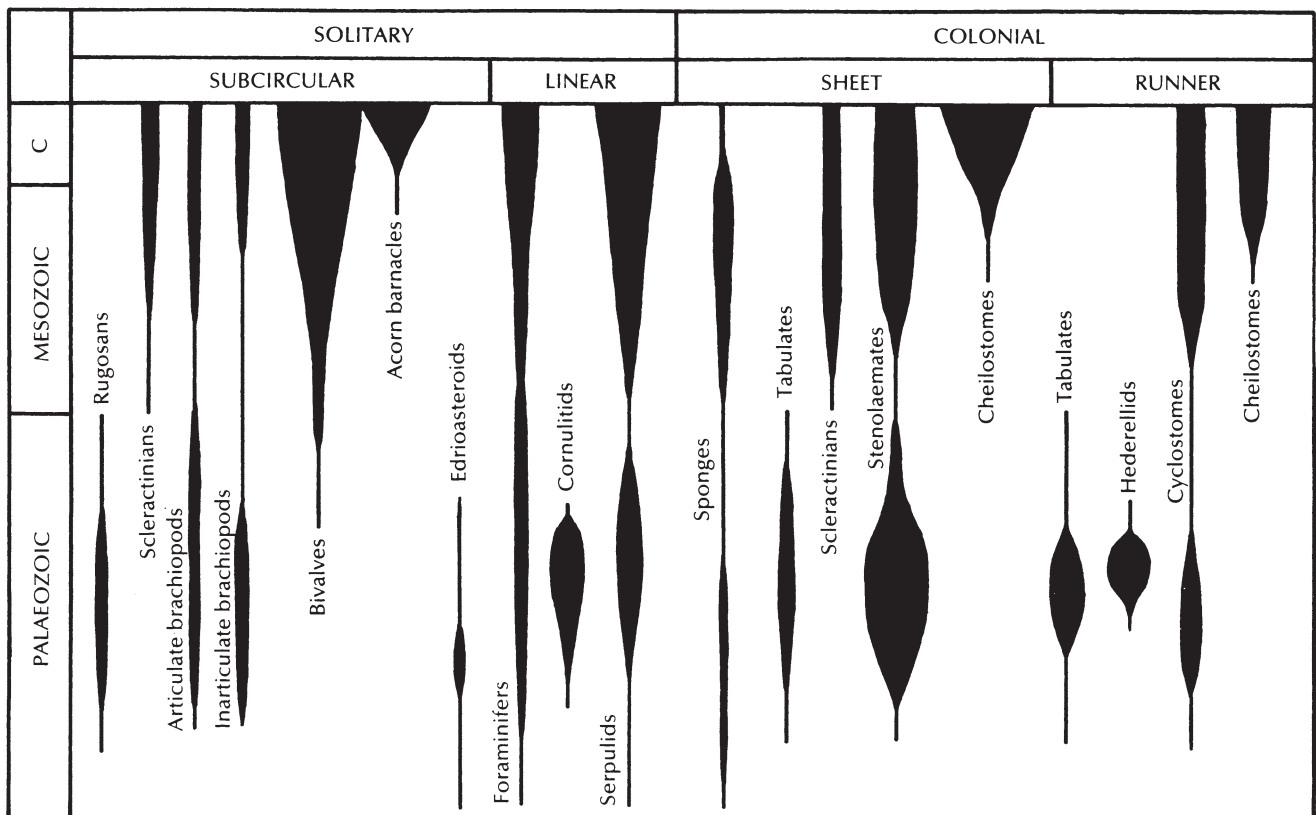
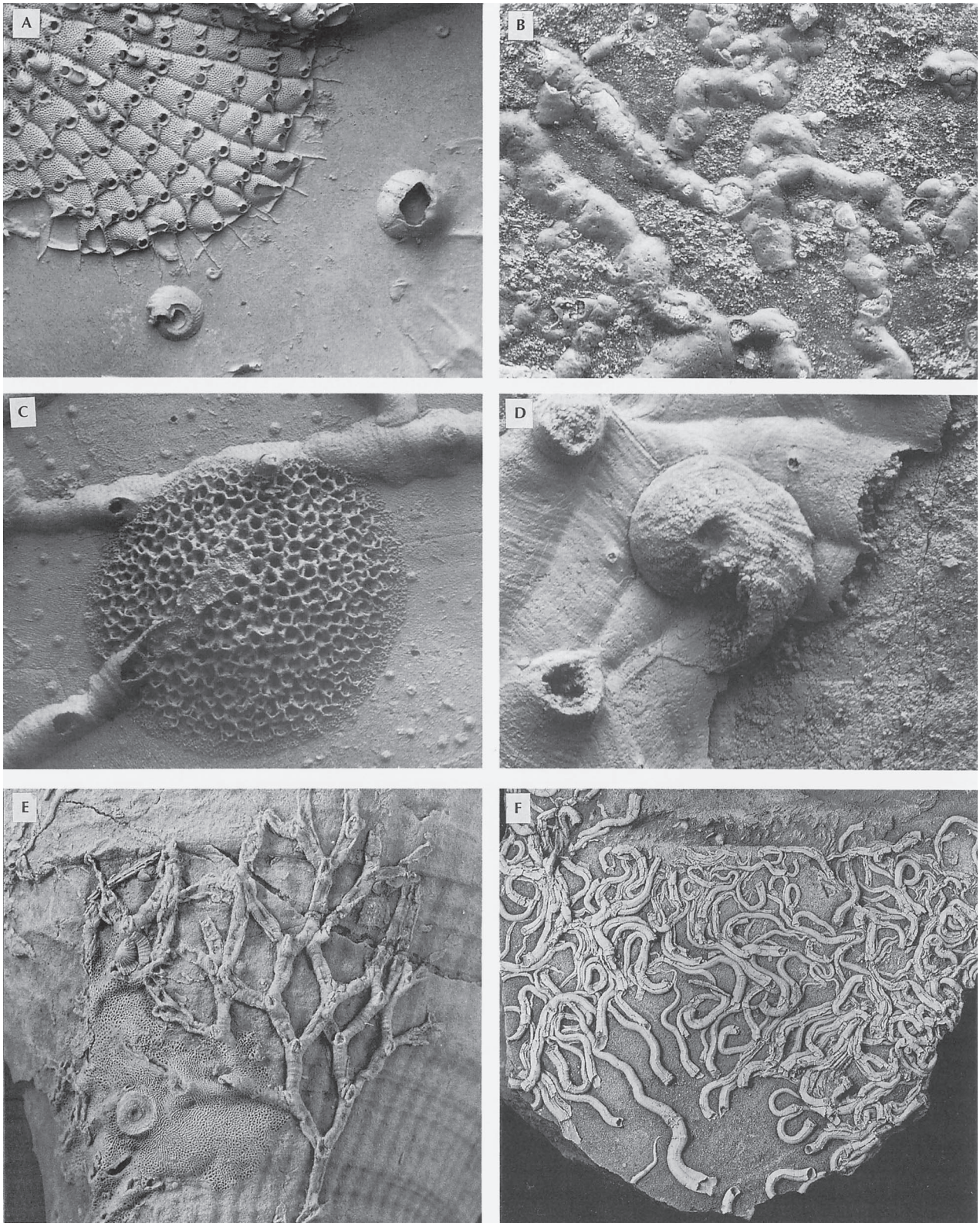


Fig. 1 Stratigraphic distribution and morphological classification of the principal taxonomic groups of encrusting animals represented in the fossil record. Line thickness gives a very approximate indication of the importance of each group in encrusting assemblages. The category 'stenolaemates' includes encrusting cyclostome, cystoporate, and trepostome bryozoans.



**Fig. 2** Encrusting animals and their interactions. A, Sheet-like cheilostome bryozoan *Schizoporella* growing towards a polychaete tube *Spirorbis* and a small barnacle; Recent, Adriatic Sea ( $\times 10$ ). B, Linear growth-form in encrusting foraminifers *Nubeculinella*; Upper Jurassic, Normandy, France ( $\times 42$ ). C, Reciprocal overgrowth between a sheet-like sponge and a runner-like cyclostome bryozoan; the upper part of the sponge is overgrowing the branch flanks of the bryozoan, but a branch of the bryozoan is overgrowing the sponge at the bottom left; Upper Cretaceous, Norfolk, U.K. ( $\times 14$ ). D, *Spirorbis* fouling the surface of the cyclostome bryozoan *Sagenella*; Silurian, Gotland, Sweden ( $\times 57$ ). E, Runner-like tabulate *Aulopora*, partly overgrown by the basal holdfast of a cryptostome bryozoan, encrusting the epitheca of a solitary rugose coral; Silurian, Gotland, Sweden ( $\times 3$ ). F, Dense encrustation of serpulid polychaetes on a cobble; Middle Jurassic, Gloucestershire, U.K. ( $\times 1.4$ ).



include communities attached to rocks, shells and skeletons of living and dead animals, macroalgae, and artificial substrata (e.g. pier pilings). Organisms which attach to living plants are termed *epiphytes*; those attached to living animals are termed *epizoans*. Epiphytic communities of nearshore macroalgae have been extensively studied, but macroalgal epiphytes have yet to be recognized in the fossil record. Epizoid communities can be found at the present day on a wide variety of hosts, particularly sessile animals (e.g. large epifaunal bivalves, undersides of corals). Colonization by epizoans can be advantageous or disadvantageous to the host animal. For example, some Recent bivalves gain from the camouflage provided by epizoans, but it has been shown that certain epizoans increase drag and therefore the probability of dislodgement. The term 'epizoan' should be applied only to encrusters whose hosts were alive at the time of encrustation, although inference of life association can be extremely difficult in fossils (one of the few reliable criteria is epizoan-induced modification of host growth pattern; Section 4.14).

Encrusted skeletal substrata are very common in the fossil record and range from intact, *in situ* skeletons of probable living hosts, to fragmented, transported, and *remanié* skeletal debris. The condition of encrusted substrata can provide useful information on depositional environments, particularly on the occurrence of episodic sedimentation and reworking. Among studied hard substrata are: Palaeozoic stromatoporoids, which frequently harbour encrusting biotas on the cryptic undersides of their coenostea; cavities in reefs occupied by *coelobionts*; and Cenozoic molluscan shell gravels in which the concave inner surfaces of bivalves may be particularly well encrusted. In environments normally hostile to epibenthos, as in some muddy deposits, the rare substrata provided by the shells and bones of nektonic animals (e.g. cephalopods, marine reptiles) constitute important *habitat islands* for sessile species which often form dense encrustations.

Abiotic substrata for encrusting organisms range from rocky shorelines to hardgrounds, pebbles and cobbles, and even coarse sandy sediments. Colonization of ancient rocky shorelines has seldom been recognized, but a good example occurs in the Upper Cretaceous of Sweden where Surlyk & Christensen (1974) described zonation in encrusted boulders of Precambrian gneiss. Hardgrounds formed by early lithification of carbonate sediments are better known as substrata for encrusters (Palmer 1982).

Hardground morphology determines the types of habitats they provide. Upper surfaces may be planar or hummocky, and the hardground can be undercut, broken-up, or penetrated by burrows excavated before the sediment was lithified. Hummocky Ordovician hardgrounds commonly lack encrusters on the hummocks but are colonized by bryozoans and other encrusters between the hummocks. Undercut and burrowed hardgrounds commonly show a polarization of encrusters between exposed upper surfaces and cryptic undersides or burrow walls. Trends through the Phanerozoic in hardground assemblages have been towards: (1) greater diversity of cryptic inhabitants of hardgrounds; (2) replacement of encrusters on hardground surfaces by borers; and (3) an increase in the proportion of encrusters with exoskeletons. These trends may reflect the increasing influence of grazing predators.

Clasts of widely ranging size and derived from various sources (including broken-up hardgrounds, and exhumed concretions — 'hiatus concretions') frequently support encrusting biotas. While the surfaces of cobbles and pebbles in high energy environments may be very stressful habitats, cavities and vacated borings in these clasts can act as important refuges for encrusters. On the microscopic scale, the larvae of many encrusters preferentially settle in cracks and crevices (*rugophilic* behaviour).

Encrusters of *in situ* substrata may be found to exhibit orientated growth, e.g. the commissures of encrusting bivalves and brachiopods often point downslope, presumably allowing unwanted particles to be more easily expelled.

### Competition, aggregation, succession, and disturbance

Living space is often a limiting resource which is actively competed for by organisms inhabiting hard substrata today. Even when free space appears to be present (as in most fossil assemblages), the chance juxtaposition of encrusters may cause interference competition. A great deal of research has been published on spatial competition among living encrusters (see Buss 1986), and there is much controversy about its influence on community composition relative to such factors as composition of the larval pool, disturbance, and predation. Encrusters compete for space by overgrowing the margins (lateral overgrowth) or settling on the surfaces (fouling) of other encrusters, by releasing toxic chemicals, or by prising competitors off the sub-