

Carbonate Borers—Their Role in Reef Ecology and Preservation¹JOHN E. WARME²

Abstract Studies of both modern and ancient reefs may benefit from focus not only on processes of reef construction and growth, but also on processes of their destruction and/or preservation.

Marine borers play an important role in the ecology of living reefs and associated habitats, and in the sedimentologic history of ancient reefs and reef-associated facies. Carbonate substrates of all kinds exposed on the shallow seabed are converted rapidly by borers into mud- and sand-size or coarser debris. Coral skeletons particularly are affected, with bioerosion commencing on the older parts of living skeletons and ceasing only if the substrates are buried, completely encrusted, or otherwise removed from reach of the borers.

Carbonate materials of living reefs are fixed, altered, and lost owing to processes that are both organic (skeletal precipitation, incrustation, boring) and inorganic (void-sedimentation, cementation). The difficulties or impracticalities of accurately delimiting the relative importance of these processes to calculate total carbonate budgets on modern reefs, and especially on ancient ones, can be met, in part, by careful inspection of small samples. Such samples commonly show that episodes of framework growth, incrustation, sedimentation, and cementation exhibit continuous or sporadic boring that may account for loss of most or all of the original framework although there is no loss in "reef" mass.

INTRODUCTION

The purpose of this paper is (1) to review briefly our knowledge of reef and limestone borers in tropical areas such as the Caribbean and to draw attention to recent literature on this subject; (2) to emphasize the importance of borers in the ecology, paleoecology, and preservation of reefs; and (3) to show, by way of examples, the usefulness of observing and understanding the role of borers in paleoecologic and sedimentologic interpretation.

The ultimate geologic record developing in many modern reefs encompasses the closely related processes of framework growth, framework boring, sedimentation in borings and other voids, incrustation, and cementation. These reef processes may occur in any order as a firm substrate becomes established, and in many examples may be repeated until the original framework becomes a minor proportion of the "reef" or is largely or completely destroyed and replaced by generations of filled and cemented borings and/or secondary framework growth.

With the use of cut slabs or thin sections, both modern and ancient reef samples can be profitably investigated for the sequence of events that gave rise to each sample, as illustrated, for instance, in Triassic Bavarian reefs (Zankl, 1971), in modern Bermudan algal cup reefs (Ginsburg and Schroeder, 1973), and in patch reefs (Scoffin and Garrett, 1974). These workers have carefully unraveled the history of selected samples. Because such multiple events appear to be so important in geologic reef formation, Schroeder and Zankl (1974) enumerated them and coined the phrase "dynamic reef formation" for them.

An important process in such reef dynamics is "bioerosion," a term proposed by Neumann (1966) for erosion by organism activities (e.g., boring, scraping, chewing). Herein, borers are defined as "organisms that penetrate hard substrates"; the resulting

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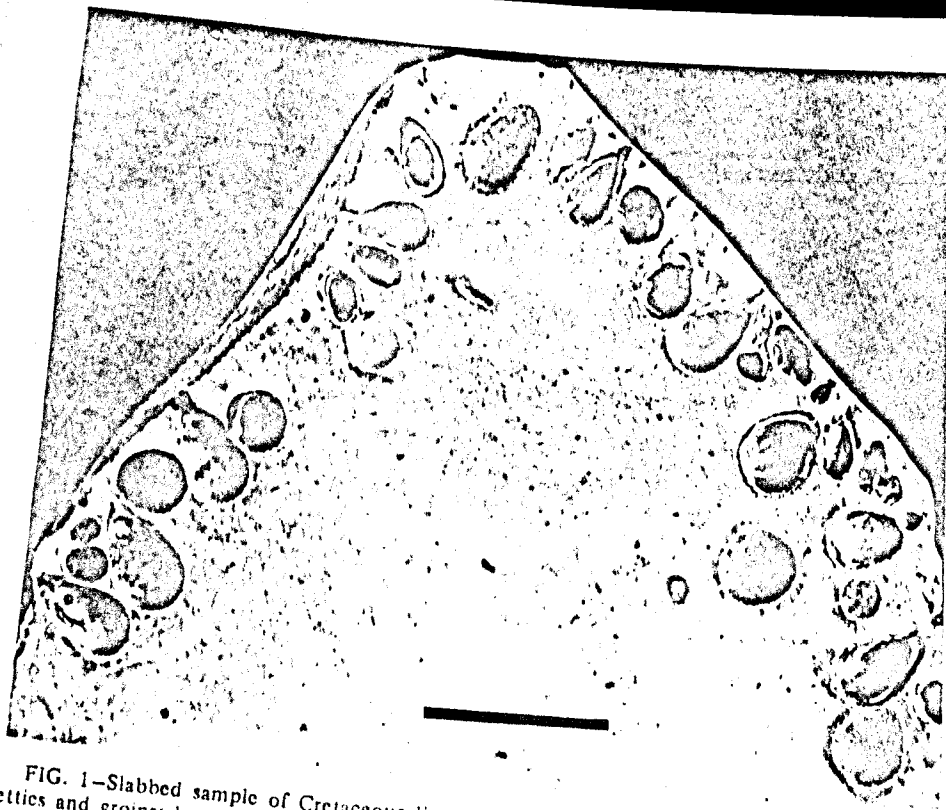


FIG. 1—Slabbed sample of Cretaceous limestone used as underlayment for Galveston, Texas, jetties and groins; bored by polychaetes (small tubes) and bivalves. Bivalve is *Diplothyra smythi*, an unusual member of family Pholadidae because it apparently occurs exclusively in calcareous shells or limestones. *D. smythi* can be used to calculate a rate of erosion for these rocks because its age can be ascertained by discrete annual growth stages (J. A. McCrevey and E. J. McIlhuron, unpub.). Small specimens are 1 year old, medium-sized ones 2 years old, and large ones 3 or more years old; after third year of growth they cease to bore. Bar scale equals 2 cm.

excavation is a "boring"; and distinctive borings may be preserved as a category of trace fossil. Bromley (1970), Frey (1973), and Warne (1975) discuss terms associated with rock and skeleton borers.

Results from investigations of modern Caribbean coral-algal reefs and Jurassic Moroccan scleractinian reefs strongly imply that carbonate substrates exposed to bioeroders may ultimately become reduced to a rubble unless bioerosion is arrested by another process, such as burial, submarine cementation, vigorous framework growth, or effective incrustation.

Borers create cavities of varied geometry, with boring diameters from a few micrometers to a decimeter or more. Most groups of borers actually dissolve little of the material excavated; rather, they produce mud- or sand-size and larger clasts for the local sedimentary regime. In fact, it is these clasts that commonly compose what is called "reef."

Past Work

Separate groups of borers have been studied in both reef and nonreef areas by many workers. Extensive reviews of all types of borers are provided by Clapp and Kenk (1963), Bromley (1970), and Warne (1975); one review specifically of microscopic algal and fungal borers is the work by Golubic et al (1975). Papers treating the whole

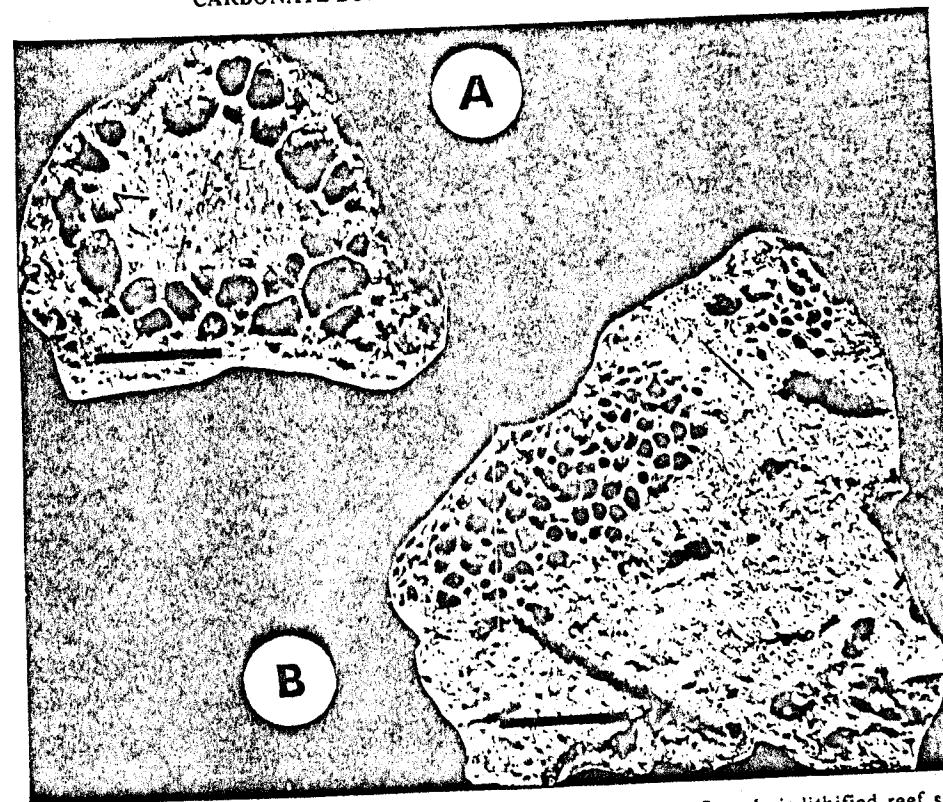


FIG. 2—A. Cut slab from deep forereef, Discovery Bay, Jamaica. Sample is lithified reef sand from 180 m depth, collected by submersible and dated at 11,910 years B.P. Entire periphery is bored by sponges, creating relatively large, roughly equidimensional cavities interconnected and bored by sponges, creating relatively large, roughly equidimensional cavities interconnected and connected to surface by very small, short passageways whose orifices are visible in cavities. Bar scale equals 2 cm. B. Similar broken slab from 165 m (9,490 years B.P.), showing smaller network of sponge borings (across upper left) and larger penetrations probably made by worms and crustaceans enlarging initial sponge borings. Bar scale equals 2 cm. (Specimen A = N-202 and B = N-232-H, courtesy L. S. Land.)

biota of reef borers, regardless of their taxonomic composition, include those by Gardiner (1902, 1903) for Indian Ocean reefs, Otter (1937) for the Great Barrier Reef, and Cloud (1959) for Saipan. James (1970) and Ginsburg and James (1974) emphasized the importance of borers in reef ecology, sedimentology, and aspects of reef preservation in the tropical western Atlantic. Yonge (1963) and Warne (1975) provide general reviews of borers that inhabit carbonates and reefs.

Bertram (1936) early recognized in the Red Sea that any slight damage to the protective envelope of live polyps on a coral head such as a parrot-fish bite, or other entry into the skeleton such as a vacated worm tube, provides opportunity for infestation by borers that could ultimately destroy the coral. He also observed that 90% of the "storm damage" to corals could be attributed to preliminary physical weakening of colony bases by borers. However, since then little work has been done toward a quantitative appraisal of the total effect of borers on reefs, and no estimate has been made, to my knowledge, of the budget for total material cycled through reef habitats by the work of borers and by the other processes contributing to reef dynamics. Recent work of Hein and Risk (1975) estimated that the work of borers on small, massive corals is exceedingly important. Their data indicated that bioerosion may have exceeded ske-

togenesis at the time their specimens were collected. On a practical scale, a realistic picture of seabed processes and their relative importance can be gained by recounting the sequences of events documented within such small, collectible samples.

The numerous papers on shell borers and the paleoecologic uses of their borings were amply summarized, along with new examples from the Dutch coast, by Boekschoten (1966), who also provided fossil examples from a Pliocene deposit (1967). Other papers summarize knowledge of borings in shells and other skeletons, as well as in wood, bone, and other natural materials (Clapp and Kenk, 1963; Bromley, 1970; Bishop, 1975; Warne, 1975).

BIOLOGY OF CARBONATE BORERS

Some limestone eroders are vagrant, such as grazing forms of echinoids, amphineurans, gastropods, and fish, but most are confined to their excavations and cannot begin anew if removed. New substrate is infested by free-swimming larvae. With few exceptions (see Goreau et al., 1969), dead substrates are colonized and more heavily attacked than those covered with coral polyps or lush growth. There is much debate and lack of documentation regarding rates of bioerosion and volumes of material removed. Neumann (1966) and Gygi (1975) reviewed and discussed earlier published work. Neumann (1966) also provided rates of penetration for the important Bermudan sponge borer *Cliona lampa*. These are estimated to be as high as 1 m/70 years, and at the same time significant volumes of material are removed. Similar calculations can be made from estimates of standing crop of borers per unit area or volume, from average longevity of the borers, and from the average size of the borings (Fig. 1). As emphasized by Robertson (1963, p. 11-12), rates of penetration vary depending on the kind, abundance, and vigor of the borers and the hardness, exposure, and other properties of the substrate.

In numerous locations investigated, both the diversity and abundance of borers are greater in shallow water near reef crests, especially in lagoons behind reefs, than deeper on the forereef. As an example, sponges are the only obvious borers below about 70 m off northern Jamaica, judging from samples collected with a research submarine (Fig. 2; Moore and Land, 1975; Hartman, this volume). This relationship appears to be real, rather than an artifact of the dearth of samples from deeper localities.

Most borers penetrate for protection. The endolithic mode of life is especially important for reef dwellers exposed to a diversity of predators, and is expressed not only by the many varied taxa of borers, but also by the heavily calcified skeletons, spines, stinging capabilities, escape mechanisms, and nocturnal habits of much of the reef biota. Bakus (1966) has discussed the obvious advantage of evolving cryptolithic (cavity dwelling) and endolithic habits to avoid predation by the ever-present reef fish. Dissection of dead reef rock or even of the bases of living corals invariably reveals an amazing variety of holes, galleries, and passageways which, although produced by the borers, harbor borers and nonborers alike. Thus, much of the biomass and diversity on reefs is not readily visible. For Pacific reefs, Odum and Odum (1955) documented the high proportion of reef biomass that occurs as endolithic algae alone.

Some bioeroders also penetrate for food. Intertidal and shallow subtidal browsers on epilithic and endolithic flora erode significant volumes of hard material; gastropods and chitons use their radulae and echinoids use both teeth and spines. Some vagrant species even become encased in their borings, or perhaps return to the same notch or crevice repeatedly, thus deepening it. Endolithic fungi also penetrate for food, seeking the organic matrix of skeletal material. In contrast, endolithic algae bore both organic and inorganic carbonate substrates. Finally, small holes are drilled by some octopuses, gastropods, and other groups, usually into shells to reach the soft parts of prey (see review by Bishop, 1975).

METHODS OF PENETRATION

The precise method of penetration is known for only a few species. Among them are shell-drilling gastropods (Carriker, 1969) that use...



FIG. 3—Colonial coral from Bajocian buildups at west end of Jebel Bou Kendill, near settlement of Karranto, High Atlas mountains of Morocco. Specimen is bored by at least 30 bivalves, probably similar to the modern genus *Lithophaga*, mostly with shells intact. Borings have been filled with fine-grained sediments and some have been rebored by other bivalves, thus illustrating rapid seafloor cementation. Dark rinds on borings and within shells are crystalline calcite cement; cement overlies sediment filling voids and provides geopetal indicators; arrow points upward. Bar scale equals 2 cm.

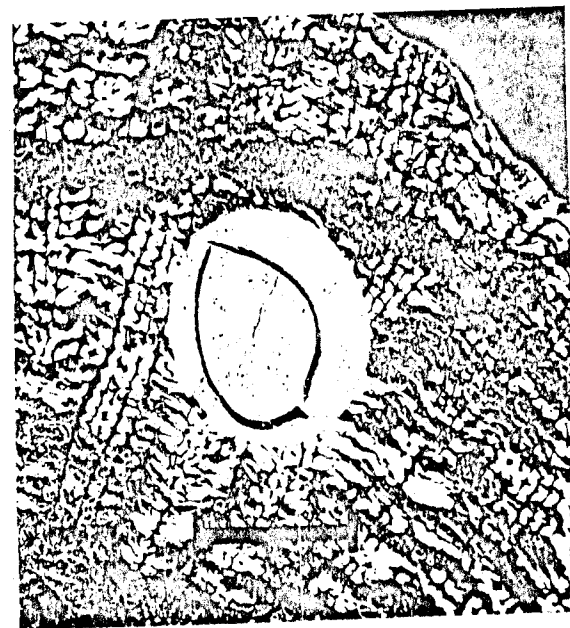


FIG. 4—Single bivalve boring, with shell of borer intact, in otherwise unexcavated sample of coral. Preparation same as Figure 3.

shell and mechanical means to rasp it away—an approach to the problem probably common to many borers. Creatures possessing such chemical aids are more abundant in the tropics where susceptible carbonates are widespread. A criterion for judging whether a borer uses chemical methods is whether or not it is restricted to calcareous substances; I am aware of no documentation of chemical penetration into siliceous or other rock or skeletal material that contains no carbonate.

The biochemical pathway for chemical borers is known for one species of the widespread low-latitude bivalve *Lithophaga* (Jaccarini et al, 1968), but the method of removing undissolved but loosened material from the boring is not clear; Yonge (1955) illustrated the use of ciliary currents for this purpose in another species of *Lithophaga*. The warm-water bivalve *Gastrochaena* also bores into carbonate material, and has a small, thin, delicate shell; it must use chemical means, but the process is unknown. Clionid sponges isolate chips of carbonate material, presumably using biochemical pathways, then transport them to an oscular opening where they are expelled. Such initial biochemical softening or excavation, with mechanical removal of whole frag-

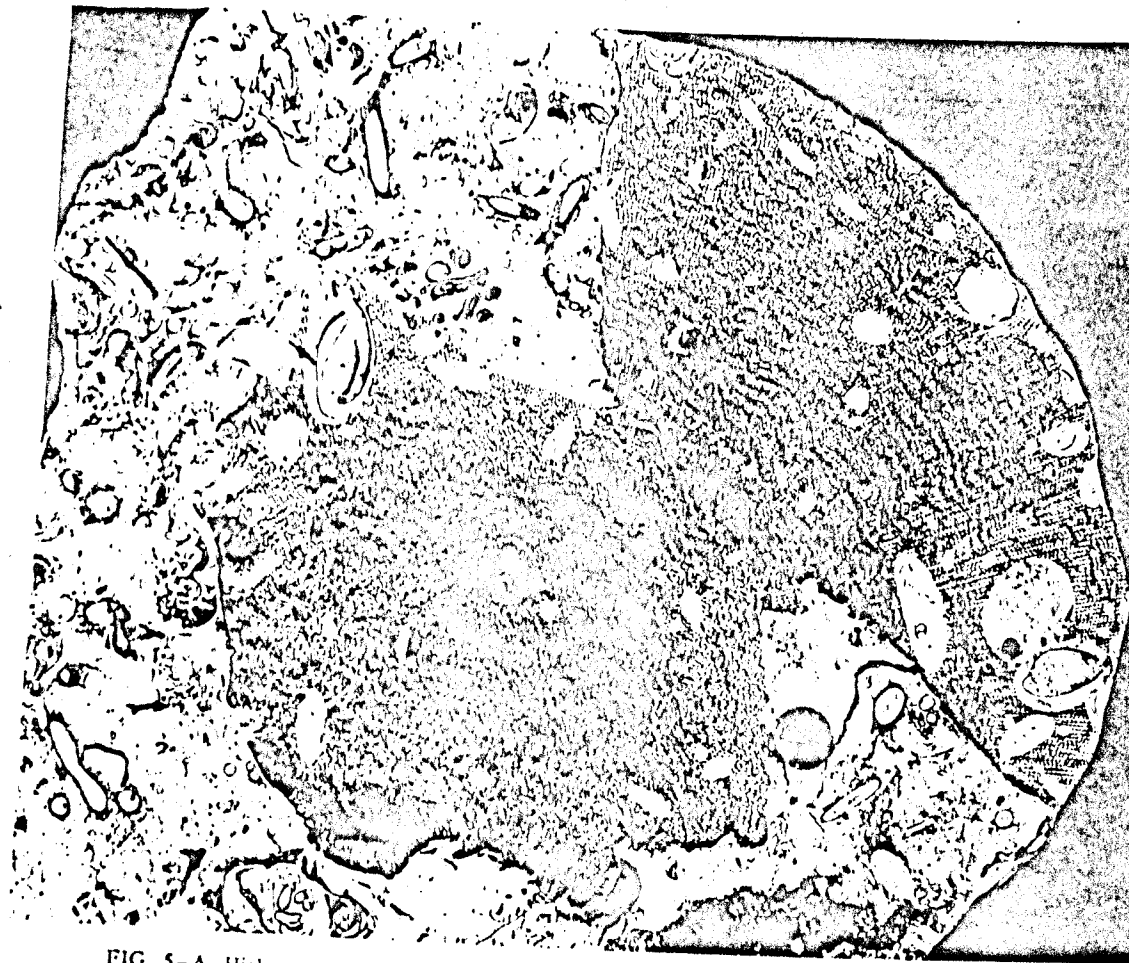


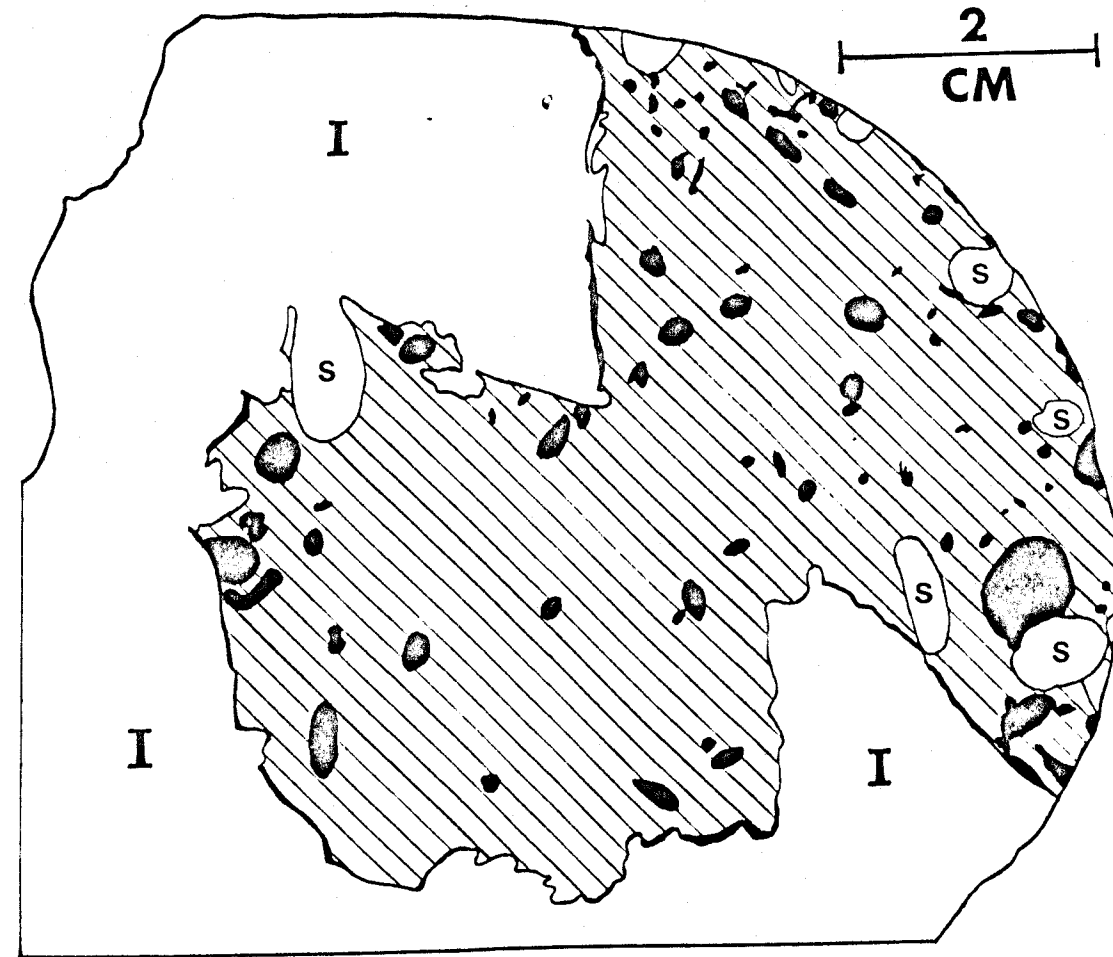
FIG. 5—A. High-contrast photograph of Bathonian coral colony. Colony is almost complete, with only partial peripheral destruction by borers or other erosion. Geopetal void fillings show top to be to right. Geometry and position of larger round or oval holes suggest bivalve borings; smaller round holes toward center of colony suggest polychaete or sipunculid penetration. Same locality and print preparation as Figure 3.

ments, appears to be metabolically economical for taxa possessing biochemical means of penetration. Forms more common in temperate and boreal latitudes, such as most species of pholadid bivalves, are predominantly mechanical borers (Warne, 1975). Their success and rates of penetration apparently depend on the physical hardness of the substrate compared with the hardness of their shells, spines, or other excavatory tools (Evans, 1968).

EVOLUTION OF BORING HABIT

Widespread boring of reef corals developed during the Mesozoic and Cenozoic. Although Paleozoic shell- and hardground-borers are documented (see references in the reviews of Clapp and Kenk, 1963; Bromley, 1970; Ziegler and Ginsburg, 1974; Warne, 1975), reef borers became important in the Triassic (Zankl, 1971) and were common by the Jurassic, as illustrated below.

Because much of the faunal diversity existing on modern reefs is endolithic and cytolithic, evolution of reef borers and the habitats that they generate has been important in the post-Paleozoic evolution of reefs, reef ecology, and reef biota.



B. Diagram of sample shown in A. Shows coral colony (lined); borings (black); borings with bivalve shells still in place (S); incrustation (possibly by algae) on undersurfaces (thickened peripheral sediments and cement (I)).

BRIEF TAXONOMIC SURVEY OF CARBONATE BORERS

Members of at least 13 invertebrate phyla are able to bioerode, as are some species of bacteria, algae, fungi, and fish. Only a brief review is included here of the most abundant and important groups occurring in reef areas: algae, fungi, sponges, sipunculids, polychaetes, mollusks, arthropods, echinoids, and fish. These taxa also encompass the groups that make excavations most likely to be identified in fossil reefs or other limestones. However, such unlikely groups as forams, nematodes, turbellarians, barnacles, and even "killer" clams (*Tridacna*) include species of borers that may be very abundant in some localities. The interested reader is referred to more detailed accounts by Yonge (1963), Bromley (1970), and Warne (1975).

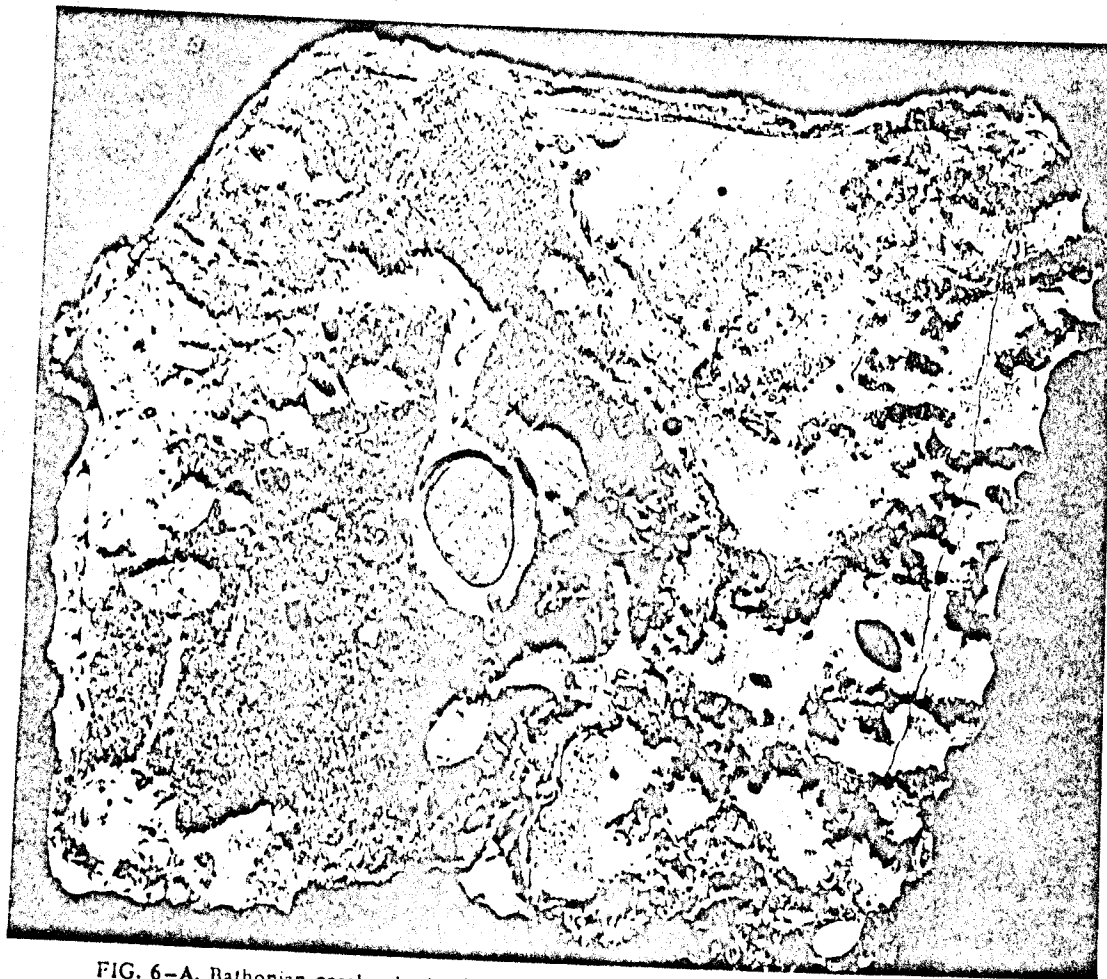
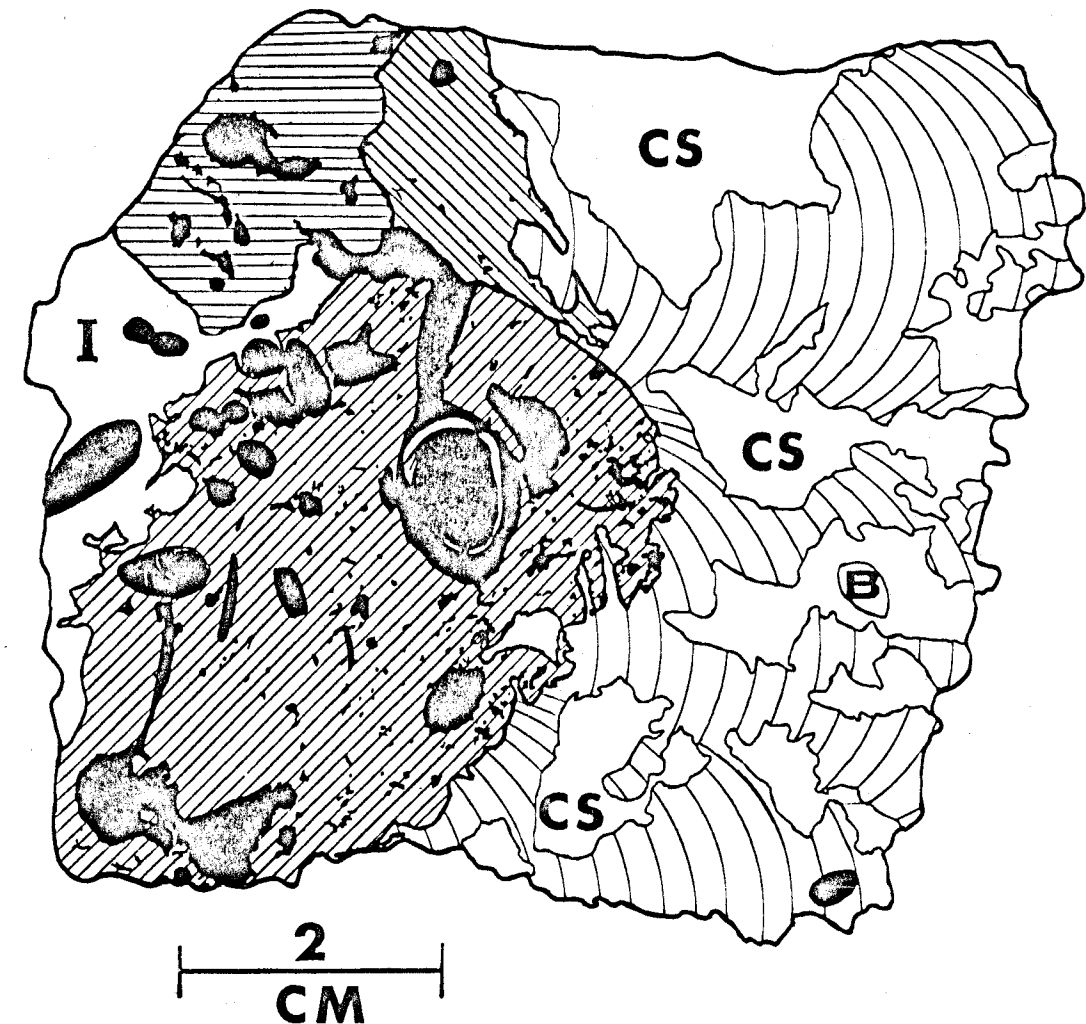


FIG. 6—A. Bathonian coral colonies from Jebel Assameur n'Ait Fergane, High Atlas, Morocco. Photograph prepared as in Figure 3. Bivalve shells remain in two borings. Irregular pattern of many borings, especially around periphery, suggests infestation by sponges or small worms. Opening of large bivalve boring in center (with shells in place) has been enlarged to surface by other eroders, a common circumstance in specimens from recent environments. Geopetal fillings suggest top was toward lower right.

Floral Microborers

Endolithic fungi and algae are exceedingly abundant and pervasive in reef areas, where they make microborings in live and dead coral, other skeletal material, and limestone. Golubic et al (1975) reviewed knowledge of these penetrants. As yet, however, little is known of the endolithic algae that live immediately beneath live coral polyps, penetrating upward into the skeleton almost as soon as it is secreted (Duerden, 1902; K. Lucas, 1974, personal commun.; Urish, 1976). Such activity must affect fluid migration, cementation, and diagenesis of coral skeletons, and also play an important role in initially weakening, or perhaps strengthening, of coral rock. Gatrall and Golubic (1970) illustrated fossil floral microborings and compared them with recent ones.



B. Diagram of sample shown in A. Three adjoining colonies (lined) all have bioeroded peripheries and extensive internal bored cavities (black). Encrusted and cemented layers on left (I) are bored, as are algal colonies (curved lines) with trapped and cemented fine-grained carbonate sediment (CS), which contained a brachiopod shell with internal sparry calcite (B).

Sponges (Phylum Porifera)

By far the most obvious and probably the most pervasive borers in tropical areas are the clionid sponges (discussed by Hartman, this volume). Many species exist, making more or less specific excavational patterns in calcareous skeletons and carbonate rocks. Alexandersson (1972) showed pits presumably made by microboring sponges in clasts as small as carbonate sand. As a group, the clionids appear to have wide depth and environmental tolerances, but also appear to bore only pure carbonate substrates.

By matching borings with spicules from which specific identifications must be made, Rutzler (1974) determined the patterns of penetration of different species of clionids in Bermuda, and provided potential paleoecologic guides as well as useful information for the identification of ancient borings.

Of sedimentologic importance, the clionid sponges are prodigious generators of clasts. Rutzler and Reiger (1973) estimated that only 2 to 3% of the material excavated goes into solution; the remainder is passed through the excurrent canal system and voided into the environment as chips with average diameters in the coarse-silt to fine-sand range. Because the sediments of most reefs are derived from the reefs themselves, these sponges are an important factor in the sediment budget. The chips have uniquely sculpted curved surfaces, making them easily identifiable, and the boring walls have matching surfaces (Pomponi, 1976). An estimate by Fütterer (1974) for Fanning Island lagoon (Line Islands) gave 30% of the sand-size and coarse-silt-size clasts as being derived from sponge borings, compared with 2 to 3% for samples from the Persian Gulf and northern Adriatic. Rutzler and Reiger (1973) provided an updated discussion of excavatory methods and sedimentary products of sponges. Another boring sponge that excavates large cavities in coral heads is *Siphonodictyon*, described from the Pacific and Caribbean; a third family (Spirostrellidae), related to the clionids, also excavates.

Sipunculid Worms (Phylum Sipunculida)

Sipunculids are marine worms; some species bore coral and carbonate material as well as other rock. They make straight or gently curved, smooth-walled, pencil-sized excavations into which they are tightly appressed. Warne (1975) illustrated several species found by Robertson (1963) to be prominent borers in south Florida. Samples collected in Yucatán and Jamaica show sipunculids to be very abundant in some localities, with almost every coral head or limestone fragment dismantled for study having split along one or more sipunculid borings. Gardiner (1902) and several subsequent workers have commented on the important role of these borers in penetrating reef rock and weakening it for erosion by physical processes. Rice and MacIntyre (1972) gave evidence for both mechanical and chemical methods of coral penetration by sipunculids.

Polychaete Worms (Phylum Polychaeta)

The erosional activities and boring morphology of the excavating polychaetes is not as well known in reef areas as are the more obvious sponges, bivalves, and echinoids. This circumstance arises in part because of the difficulty of separating wandering and nestling worms from the true borers in heavily bored coral rock. Because polychaetes exist in a bewildering spectrum of sizes and shapes, their borings also differ widely; polychaete habits generally are very poorly known. Many species appear to settle in previously made borings, pack them with sediment, construct lined or unlined coiled or wandering burrows in the sediment, and perhaps modify and expand the original borings (e.g., *Boccardia uncata* in Warne et al, 1971). A notable occurrence of coral-boring polychaetes is the Atlantic Palato worm *Eunice schemacephala*. Ebbs (1966) found the borings of this species, which infests the dead portions of coral heads in great numbers, to be packed with gray mud. Upon dissection, the worms' guts contained fresh-looking carbonate fragments that graded posteriorly into a similar gray mud,

seeming to illustrate an important degradational process. Gardiner (1902, p. 336) suggested that the polychaetes on reefs in the Indian Ocean were the "prime and most effective agent in the breaking down of coral rock," rotting the edges of reefs and turning the base of coral colonies into a sieve of holes. Most published descriptions of polychaete borings, however, are examples from terrigenous rock or calcareous shell rather than from coralgal substrates.

Bivalved Mollusks (Phylum Mollusca, Class Bivalvia)

Boring bivalves are ubiquitous in reef areas, with the two main genera (*Lithophaga*, *Gastrochaena*) being supplemented by numerous other borers, or nestling modifiers of borings, that may be important in some regions (e.g., species of *Petricola*, *Spengleria*, *Adula*; Warne, 1975).

The many species of *Lithophaga* are especially important because they are abundant, they leave distinctive borings, and their shells are robust enough to be preserved as fossils. Species of *Gastrochaena* have thin shells and more variable borings. Although the distributions of these and other bivalve carbonate borers are known, their spectrum of ecologies, boring morphologies, and substrates bored are not fully documented. Species of both *Lithophaga* and *Gastrochaena* secrete distinctive preservable linings of laminated carbonate on part or all of their borings. The linings are secreted most commonly after the animals reach maturity, but also when they are interfered with during growth by other borers or while they are approaching an external surface.

Arthropods (Phylum Arthropoda)

Several groups of arthropods are borers, including crabs, shrimp, and other crustaceans that nestle and excavate in various ways. The best known are the boring barnacles, of which the most common borers on tropical coasts are species of *Lithotrya*. They penetrate in great numbers upward under intertidal ledges (Ahr and Stanton, 1973) or at all angles in favorably exposed substrates.

Regular Echinoids (Phylum Echinodermata, Class Echinoidea)

Regular sea urchins (subclass Regularia) are obvious borers on many tropical shorelines, where, in places, they riddle intertidal rock with semipermanent burrows, commonly until only a delicate framework of substrate is left. Their teeth and spines are used for excavating. Similar activity takes place at subtidal depths, where bioerosion is accomplished by vast numbers of urchins that may be either vagrant or enclosed in a burrow. Echinoid borings have been mentioned by many workers (see Bromley, 1970; Warne, 1975), and their erosional importance is documented by Ogden (this volume). Echinoids also have been reported as predators on live coral, where they bite off both polyps and surficial layers of underlying skeleton (Bak and Van Eys, 1975). Bromley (1975a) documented fossil tooth scratches of echinoids.

Fish (Phylum Chordata, Class Pisces)

The fish best known as coral eaters and endolithic algae browsers are the tropical parrot fish (family Scaridae). Some species of Jamaican scarids forage in a tight school of 100 fish or more, creating an impressive underwater sight. Divers are familiar with the fine stream of sediment defecated by parrot fish, especially when they are alarmed and swim rapidly away. In a comprehensive review, Gygi (1975) presented data on the gut contents and sedimentologic significance of parrot fish, as well as new information for a Bermudan species. Estimates of sediment eroded and distributed over some reef areas average about 0.1 to 0.2 mm per year from this source alone.

Seven or more other fish groups also are known to transport calcareous fragments and thus perhaps bioerode in the process of ingestion (Bardach, 1961).

I know of no studies on the sizes, shapes, and surface textures of ingested grains, nor documentation of how these grains differ, if they do, from other calcareous debris on reefs.

HARDGROUNDS AND OTHER CARBONATE NONREEF SURFACES

Any carbonate surface can become colonized by borers, although "dead" surfaces are more susceptible than surfaces covered with live coral or other lush growth. Intertidal notches and carbonate cliff sapping provide prime examples of bioerosion on dead surfaces, where the work of borers is especially evident if a hammer is used to expose the endoliths (Vita-Finzi and Cornelius, 1973; Warne, 1975).

Carbonate hardgrounds and the borings by which they commonly are identified have been the subject of recent reviews by Perkins (1971), Ziegler and Ginsburg (1974), and Bromley (1975b). Their usefulness as stratigraphic markers and paleo-



FIG. 7—Two bioeroded coral colonies and layer of incrustation. From same locality and with same preparation as specimen in Figure 3. All visible coral surfaces are bioeroded. Coral on right has been attacked, mainly by sponges, until only ragged edge of skeletal material marks upper and right-hand colony boundaries. Coral on left shows superimposed and cross-cut bivalve borings, some with shells in place, strongly suggesting rapid seafloor cementation; most living bivalved borers do not penetrate voids or soft sediment, but change direction of boring or secrete a calcareous seal for protection. Overlying coral heads is a 1-cm-thick layer of encrusted sediments, tubes,

ecologic indicators in limestone sequences is enhanced by the distinctive bored surfaces they present. The multiple episodes and haphazard order of seafloor events, such as sedimentation, cementation, incrustation, boring, and erosion, have been unraveled in ancient examples of hardgrounds (see Purser, 1969; Bromley, 1975b; Kennedy, 1975; Kennedy and Garrison, 1975) and bored concretions (Kennedy and Klinger, 1972), just as they may be in reef rocks.

Although examples exist of extensive modern cemented and bored substrates (Taft et al, 1968; Shinn, 1969), most of these examples are from reefs (Ginsburg and Schroeder, 1973; Scoffin and Garrett, 1974) or other localities with vertical relief (Moore and Land, 1975). To my knowledge, no detailed studies have been undertaken on flat, horizontal, indurated, modern carbonate seabed to help explain the features exhibited by the extensive bored hardgrounds in the Mesozoic and Tertiary of Europe (Bromley, 1975b) and North America (Perkins, 1971; 1974).

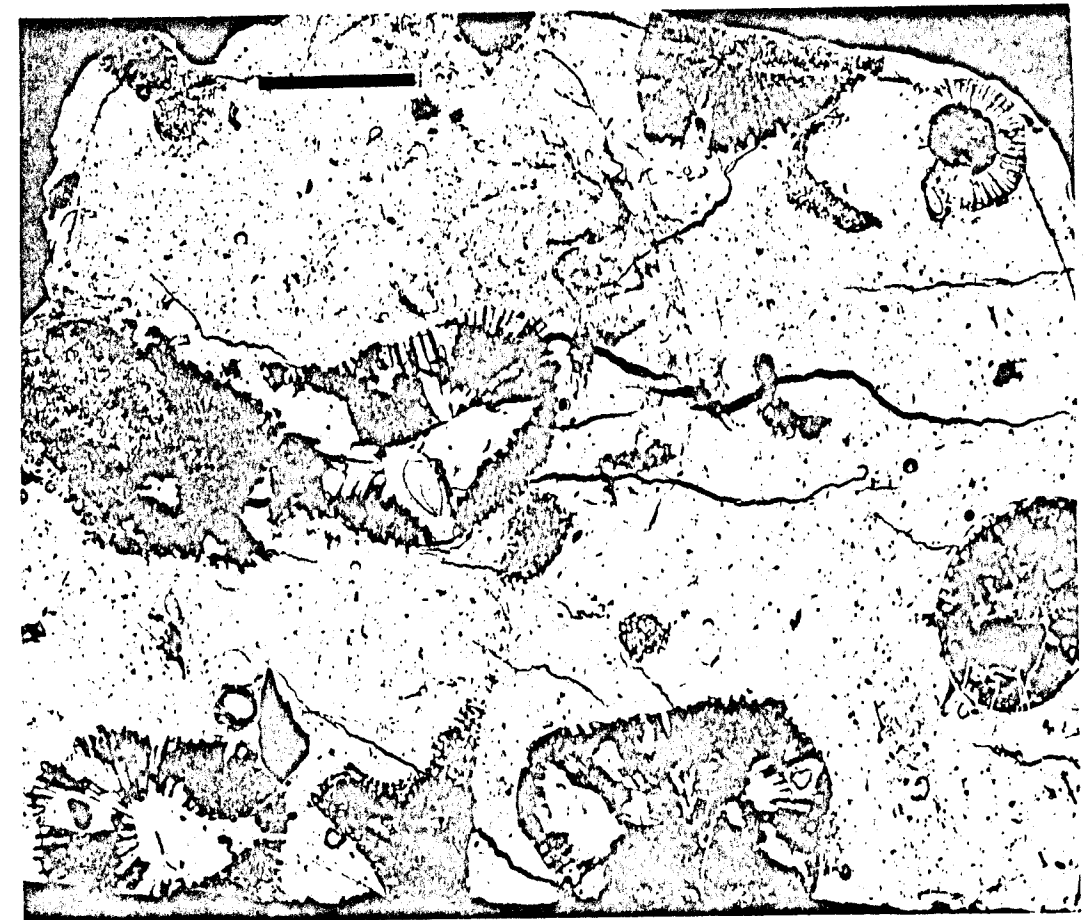


FIG. 8—Coral colony of branching small corallites. Same locality and preparation as Figure 6. Small-scale penetration by bivalves and other borers affects every corallite. Longitudinally oriented branch in lower center is completely bored (probably by sponges), replaced by spar in center, and either reduced to porous sieve or totally missing on periphery of branch. Their peripheral borings

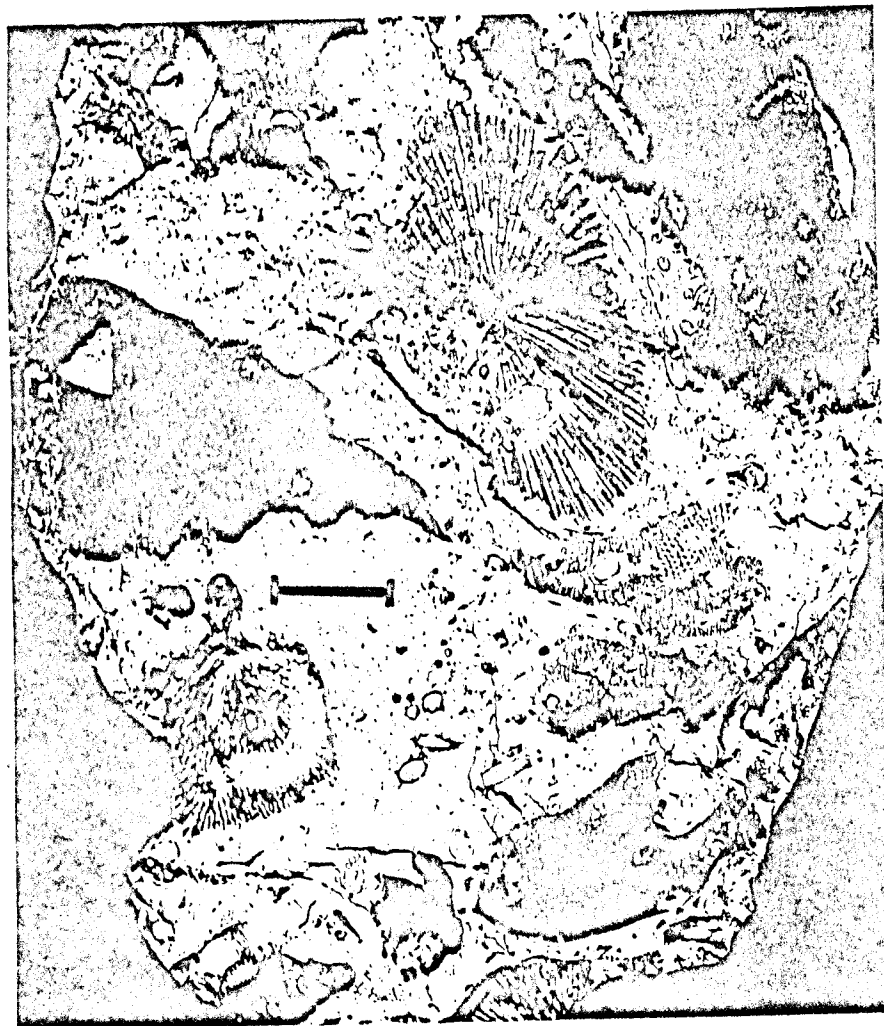


FIG. 9—Aggregation of colonial and solitary corals, probably preserved in approximate growth positions. Peripheries and interiors of all specimens are penetrated by smooth borings of bivalves and ragged holes probably made by sponges, polychaetes, and other borers. Interstices are filled with meandering and coiled tubes of encrusting worms and/or gastropods, as well as encrusting skeletal fragments and carbonate mud. Photo preparation and locality are same as for Figure 6. Bar scale equals 1 cm.

SIGNIFICANCE OF REEF BORERS

Reef Sculpting

Bioerosion plays an essential role in destroying dead or weakened coral and providing space for new growth on established reefs. Thus, while some of the framework elements of thriving reefs are growing, spreading, and proliferating, others are dying, succumbing to borers, and disintegrating. The work of individual borers is accomplished on a small scale; nevertheless, incessant boring, scraping, and chewing occurs as long as the substrate and the proper ecologic conditions exist. Owing to their vast numbers, the borers may in places be a dominant aspect of reef morphology.

Goreau and Hartman (1963) emphasized the role of borers in sculpting the reefs of northern Jamaica, particularly those on the quiet-water foreslope (30 to 60 m) where

the influence of the borers is not masked by the effects of vigorous physical energy. Many large specimens were weakened to the extent that the current from a diver's swim-fin was sufficient to break the colony from its base, and expose it to further attack. Scoffin and Garrett (1974) similarly remarked on the ease with which coral heads, even in shallow water, can be dislodged because of weakening by bioerosion.

Using X-ray radiographed slabs of coral heads collected in Florida, Hein and Risk (1975) estimated amounts of skeletogenesis from growth lines and of bioerosion from borings. They calculated a net loss of skeletal material for the specimens studied at the stage of life in which they were collected.

Borings in Reef Event-Sequences

The processes of framework growth, incrustation, sedimentation, and cementation all add to the volume and mass of reefs. Evaluation of the processes that remove material, such as boring, chemical solution, and physical erosion, is necessary in order to understand the growth history of any organic buildup. Recognition of bored or otherwise degraded surfaces provides important cross-cutting relationships (Fig. 3), yielding data on the amount, constancy, and pervasiveness of reef erosional episodes and other events that were involved in reef building. Multiple episodes of boring become a key to determining volumes of material eroded, just as unconformities are used in stratigraphy.

Borings which truncate filled and cemented voids or other borings provide evidence for rapid seafloor cementation (Figs. 3, 7). Another useful attribute of borings is that they provide prime sites for the development of geopetals as they become partially or wholly filled with sediment and/or cement (Figs. 3, 5, 6), and are used by many workers to determine the orientation of the substrate as the voids were being filled.

The relationships between these aggradational and degradational processes are apparent in well-exposed Bathonian reefs of the High Atlas mountains of Morocco. The Moroccan reefs are Tethyan in affinity, and can be regarded as fossil examples of proto-Caribbean scleractinian coral reefs. They are especially useful for analysis of sedimentologic event sequences in the reef habitat because many examples have escaped dolomitization and are superbly preserved (Warne et al, 1975; Warne, 1976).

The Jurassic examples (Figs. 3-9) show a spectrum of the proportions of original skeletal framework that have been removed (as represented by cross-sectional area), ranging from intact and almost unbored coral specimens to those that are fragmented and largely replaced by borings, cemented sediments, and incrustations. Although little attempt was made in the field to obtain a random sampling, the specimens are believed to be representative of the reefs, and most specimens slabbed for study are heavily bioeroded and encrusted.

Figures 3 through 9 illustrate progressively smaller proportions of framework and greater proportions of borings and other elements, and were chosen to illustrate the particular kinds of borings that they contain.

Fate of Reef-Erosion Products

The sedimentologic products of bioerosion by sponges, urchins, parrot fish, and a few other groups are obvious and documented; only a small amount of chemical solution occurs during bioerosion. Except for the fungal and algal microborers, the bulk of material removed by other borers also probably is in the form of clasts. The smaller clasts (mud and sand sized) were removed from the borings proper and the larger clasts were bounded and isolated by borings. This loose sediment can have several fates; it can fall and be directly incorporated into the abundant reef crevices and cavities; it can be moved aside to become interreef sediment or be even farther removed into oolite tracts or other environments; or, if sufficient relief exists, it may be moved downslope and completely out of the shallow reef system.

Erosion products that remain in or near the reefs initially have irregular and ragged perimeters, especially the larger clasts. The bored peripheries of such clasts in fact exhibit trace fossils, which commonly can be identified as such because of their dis-

tinctive geometries (Figs. 3-9). If they are incorporated into the reef by being covered or cemented, they become part of the reef structure (see Figs. 3-9).

Bored debris could be expected to collect easily and become cemented into buildups in deeper water, as well as in cavities or other protected places in shallow-water reefs (Figs. 7, 9). Because of the ubiquity of bioerosion on many reefs, the fate of perhaps a large proportion of calcified skeletons is to become a debris pile, composed of fragments of all sizes and shapes that fell and became trapped between the living frame builders; a similar future awaits a high proportion of the skeletonized living reef at any given time. Thus, only a small proportion of the corals of a fossil buildup are preserved precisely in situ, although they may have lived in close proximity to their final resting place before being toppled or otherwise moved.

As loose reef debris, whether prepared by bioerosion or by other processes, is redistributed by waves and currents, particularly those generated during storms, it assumes sedimentary bedforms on various scales. Evidence is accumulating that aggregations of coral that we call "reefs" grow in patches that are spit, bar, and even delta shaped in plan view (Maxwell, 1970; Garrett and Scoffin, 1976). Coarse debris mechanically aggregated as a bar or spit becomes a prime site for future reef growth, owing to its relief, its composition, and to the shoaling waves and currents bathing it. However, an obvious difficulty in separating the factors that control reef plan is that a bar or spit shape would become exaggerated by growth of the reef into the very currents that shaped the substrate before and during colonization (Maxwell, 1970; Maxwell and Swinchart, 1970).

DISCUSSION AND CONCLUSIONS

Most reefs are net exporters of carbonate material, generating all of the sediment on them as loose or incorporated clasts. The main sources of loose clasts are (1) articulated skeletons, mostly of mollusks and algae (Scoffin and Garrett, 1974), (2) physical erosion of hard surfaces by waves and currents, and (3) bioerosion. Of the last two factors, it is problematic which is more important simply through inspection of broken clasts. By weakening their substrates, the borers prepare it for physical damage; if physical damage fails to occur, bioerosion will continue, causing the same end result. The relations and relative importance of aggradational and degradational processes can be assessed on the basis of evidence from small manageable samples in order to arrive at a carbonate budget. An estimate made by Hein and Risk (1975) was for single coral heads in which only the factors of growth and bioerosion needed to be considered. Quantification should also be attempted in more complicated coral-algal rock where incrustation, cementation, and sedimentation were also factors. Although such quantification has not been accomplished, analysis of both modern and ancient scleractinian coral reefs shows that the borers are active, abundant, and important factors in cycling solid material through reef systems.

Inspection of fossil reefs shows that even those preserved with substantial relief may be composed mostly of fragments organized and cemented by processes other than framework growth. The Moroccan Jurassic samples studied were collected from fossil reefs that weather with up to 30 m of relief, not from flat biostromes. Nevertheless, very few large frame builders that create obvious relief on the seabed were preserved intact. Much of the volume of these buildups consists of encrusted and cemented debris, a large proportion of which occurs as infilling of space originally occupied by framework elements but subsequently bioeroded.

Aside from organic processes occurring on the reef surface and in some reef cavities, the reef builders have little or no effect on the bulk of the reef interior. Most modern reefs are simply thin veneers of organisms living on and attached to an edifice that may or may not mirror conditions and processes occurring today. Careful inspection of

recognition provides important tools for understanding reef history, ecology, and preservation.

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