Modern sponge bioherms of the Great Bahama Bank

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ABSTRACT

Bioherms are described which occur in the grapestone facies northwest of Joulters Cays with its associated oolitic shoals (north of Andros Island). Some species of sponges, chiefly hadromerids, are believed to be responsible for early lithification based on the evidence of preliminary investigations in situ; *Spheciospongia vesparium* (LAMARCK) is by far the most important of these species. The lithified plates are later colonized by serpulids, encrusting coralline algae and bryozoans, scleractinians which occasionally build up conspicuous tall structures together with special adventitious sponges. Other colonists of these bioherms are diverse sponges and alcyonarians belonging to species common in the coralgal facies of the platform margin.

ZUSAMMENFASSUNG

Die beschriebenen lebenden Schwammriffe sind in der «grapestone»-Fazies nordwestlich der Joulters Cays und der dahinter liegenden oolithisch-sandigen Untiefen (nördlich der Insel Andros) weit verbreitet. Einige Arten, hauptsächlich hadromeride Schwämme, deren Basis das unverfestigte Sediment durchdringt, sind wahrscheinlich für die Frühphasen der Lithifizierung des durch sie gebundenen Sediments verantwortlich. Dafür sprechen erste Feldbeobachtungen. *Spheciospongia vesparium* (LAMARCK) ist weitaus die wichtigste dieser Arten.

Die lithifizierten Platten werden während ihrer Bildung und ihres Wachstums von Serpuliden, inkrustierenden Kalkalgen und Bryozoen sowie von Steinkorallen besiedelt. Sie bilden gelegentlich, unter Mitwirkung besonderer, sonst nicht häufiger Schwämme, turmartige Bauten. Die auffälligsten Besiedler der Bioherme sind mannigfaltige, ziemlich eurytopische Schwämme und Alcyonarien, die auch in der «coralgal»-Fazies des Plattformrandes häufig sind.

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A. INTRODUCTION

I. Significance

Up to 25 years ago studies of ancient reefs have proceeded with little input from investigations on modern reefs. Earlier geological studies of modern reefs were very few. Such research was intensified in the 1950's, beginning largely in the Pacific, but gradually expanding to the detailed examination of reefs in many parts of the tropical world oceans (JONES & ENDEAN 1973-1977; CAMERON et al. 1974; TAYLOR 1977).

The major lines of current research on modern reefs can be outlined as follows:

1. Geographic distribution and geomorphology.
2. Environmental parameters which determine morphology and distribution.
3. Detailed analyses of species composition and abundance versus position on the reef; studies of morphologic variation within and between coral species of different portions of the reef.
4. Grain size and grain composition of sediments surrounding reefs.
5. Submarine diagenesis.

Practically all these studies describe modern reefs which are coral or coral-algal reefs. The major reef building organisms in the modern world are the hermatypic scleractinian corals and the calcareous red algae. There are certain important limitations in applying all this information on modern coral-algal reefs to the study of ancient reefs. In particular, corals are acutely sensitive to environmental parameters such as salinity and temperature. Thus, all modern coral reefs are confined to regions of the carbonate shelves of the world which possess normal open ocean salinities, and which have the high turbulence and oxygenation required for the metabolism of diverse coral communities. The potential environment for their development is limited to positions along platform margins or shorelines facing onto relatively large bodies of open marine waters. Furthermore, modern coral-algal reefs can be used as direct analogues for ancient reefs only as far back as these organisms were the sole dominant reef-building taxa: that is, to the middle to late Mesozoic (NEWELL 1971).

Many ancient bioherms were constructed by various marine invertebrates other than corals. Though much information on modern coral-algal reefs can be extrapolated to fossil non-coral reefs, well founded correlations of modern and ancient reef communities and structures are frequently inadequate or tentative. Functional roles, community structures, abundance-diversity relationships and morphologic variations may be very different in reefs whose major taxa have different ecologic strategies than corals and red algae. It is unlikely that other types of reefs will occur in exactly the same environments as modern coral-algal reefs. Many non-coralgal reefs probably occupied portions of carbonate platforms with hydrologic and sedimentologic parameters different from those along platform margins. Recognition of such distributional patterns in modern settings would be extremely important for both paleogeography and paleoecology. Types of carbonate diagenesis may be quite different in non-coralgal reefs, if indeed they occupy positions on the platform other than the marginal setting. Information on any aspects of non-

coralgal reefs would greatly advance our ability to understand ancient reef complexes.

Bioherms and biostromes partly or wholly constructed by sponges were not infrequent during the geological past, particularly in Paleozoic and Mesozoic times. Interest in their study has recently intensified, chiefly following the discovery of modern representatives of calcareous groups with rigid skeletons (see RIGBY 1971; TERMIER & TERMIER 1975). Compared to these calcareous groups (collectively called "ischyrosponges" by TERMIER & TERMIER), siliceous sponges with rigid or firm skeletons (lithistids, dictyonine hexactinellids, occasionally haplosclerid demosponges) played a subordinate role as reef builders (as in the well-known Permian reefs of Texas and Tunisia, see FINKS 1960; NEWELL et al. 1976; TERMIER, TERMIER & VACHARD 1977; WIEDENMAYER 1977b).

There are two facies types in the European Jurassic, which can, in my opinion, be regarded as likely analogues of the Bahamian sponge bioherms. Both are relatively well described, but still poorly understood as to paleoecological interpretation and mechanism of formation.

In the case of the sponge "reefs" of the Upper Jurassic of Southern Germany, lithistids and dictyonine hexactinellids abound, but are not true framework builders. The other postulated fossil analogue is the Hierlatz or Broccatello facies, consisting of bodies of crinoidal and ammonite-gastropod-brachiopod biosparites, biosiltites and biomicrites, which are scattered in Tethyan carbonate sequences. They are most abundant in the Lower Jurassic, but range into the Upper Jurassic (JENKYNS 1971; BERNOULLI & JENKYNS 1974, p. 139 under c).

In both instances, isolated sponge spicules and cherts formed from these are extremely abundant in the basinal limestones adjoining the bioherms. Many of these spicules were probably derived from non-lithistid demosponges living on the bioherms. Some of these may have been responsible, in part, for rapid lithification and accretion of the sedimentary substrate. The community structures in the bioherms, as opposed to those of the interbiohermal basins, suggest that continuous rapid lithification of the growing surface of the bioherms was needed by many of the taxa not engaged in lithification but nevertheless important as source of sediment, both to the bioherms themselves and, more especially, to the adjoining basins. This applies particularly to the Broccatello of the Arbostora Swell (= Lugano Swell, Canton Ticino, Switzerland; see WIEDENMAYER 1963, 1967; KÄLIN & TRÜMPY 1977), and to the grey, pelagic, spiculitic-cherty limestone of the adjoining basins (Lombardic Kieselkalk Formation, see BERNOULLI 1964, Fig. 18; KÄLIN & TRÜMPY 1977, Pl. 10).

A discussion of these fossil analogues will be forthcoming in another article, scheduled to appear in the Proceedings of the International Sponge Biology Colloquium in Paris, December 1978.

II. The discoveries

During the last nine years, scientists of the Institute for Marine Sciences (Pompano Beach, Florida) under the direction of Conrad D. Gebelein (University of California at Santa Barbara) and David M. Carter (Miami, Florida) have been

conducting research on the sedimentology, ecology, geochemistry and diagenesis of the modern carbonate sediments of the Great Bahama Bank (Fig. 1). While the main thrust of these studies has been towards an understanding of the highly restricted marine and tidal flat facies to the west of Andros Island, studies have also been undertaken on: 1. the oolite shoals north of Andros Island; and 2. the chemical, sedimentologic and ecologic nature of the transition from the platform margin
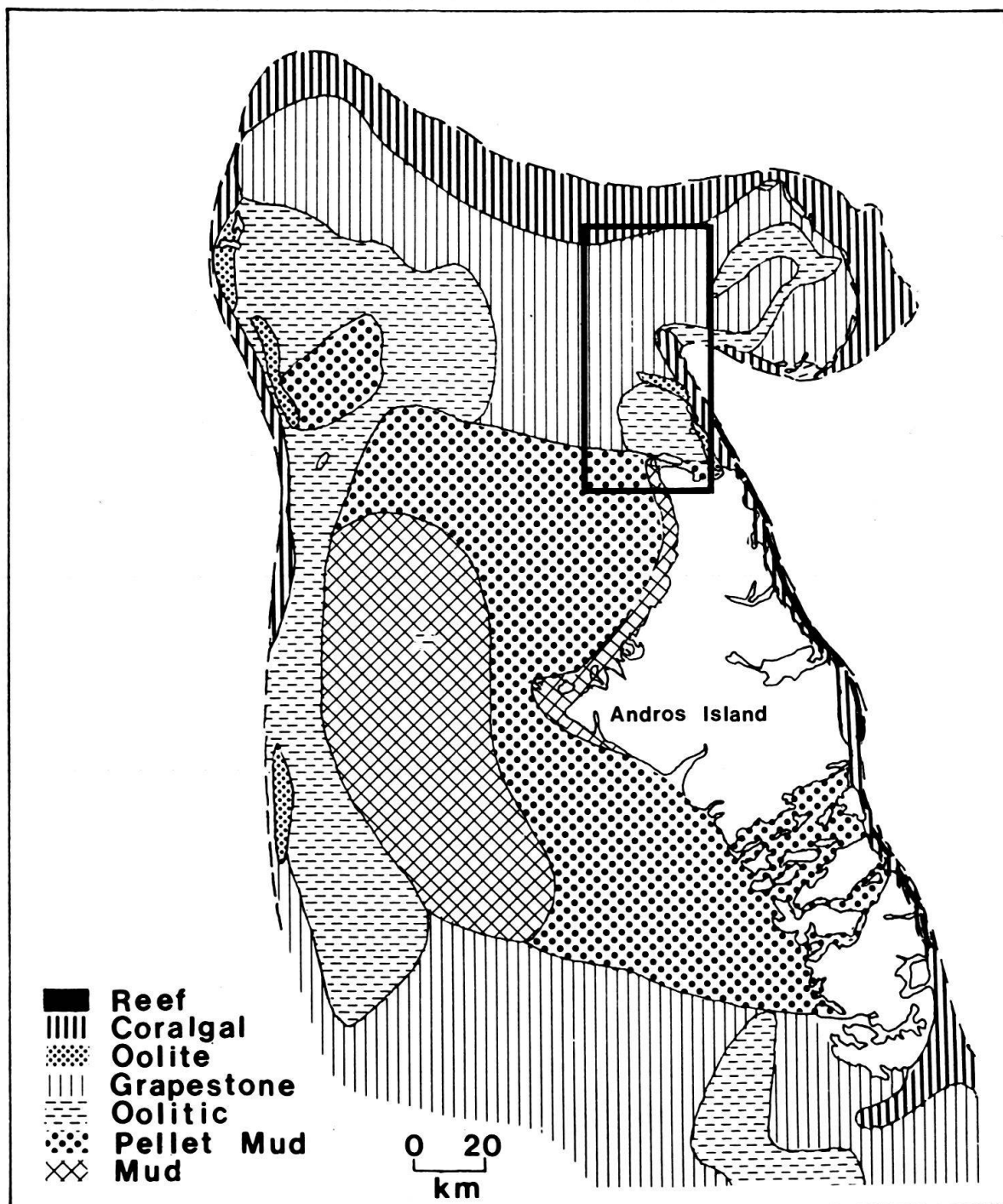

Fig. 1. Distribution of lithofacies on the Great Bahama Bank, from GEBELEIN (1974). Area in rectangle enlarged in Figures 2 and 3.

to the interior. In the course of these studies, detailed observations of the sea floor have been made over an area of the Great Bahama Bank larger than 2,400 km².

Preliminary results of these investigations were published by GEBELEIN (1974). (For an earlier account of the sediments of this area, see PURDY & IMBRIE 1964.)

In particular, these observations have led to the recognition of two types of reefal and biohermal structures previously unknown from the modern world: bryozoan reefs, and sponge reefs and bioherms. Preliminary observations on both types of reefs were made during 1975. The data on species composition, sedimentology and diagenesis, and distribution of these two types of structures gathered in that short period indicate that: 1. each reef type was previously undescribed from modern carbonate environments; 2. each has a specific environment of formation, different from coralgal reefs; 3. each has a correspondingly distinct sedimentology and diagenetic history; 4. each is likely to provide important analogues for the study of ancient bryozoan and sponge reefs.

A preliminary report on the bryozoan reefs was published by CUFFEY et al. (1977).

B. THE SPONGE BIOHERMS

I. Preliminary observations on distribution, morphology and structure

According to the first observations by Gebelein (unpublished, research proposal to the National Science Foundation, Washington, of March 15, 1976), made during a cruise in summer 1975, the sponge bioherms occupy a specific hydrodynamic environment on the platform, covering a very large area in great numbers (Fig. 2). Platform margins are characterized by currents which keep sand-sized materials in nearly constant motion (oolite deposits). At a rather well-defined line moving towards the platform interior, currents decrease in velocity and become unable to move sand-sized particles, although fines are still very effectively winnowed. This decrease in current velocity marks the onset of grapestone deposits on the Bahama Bank. Moreover, grapestone deposits which occur at positions with the highest current flows not capable of moving sand-sized materials have the greatest amounts of intergranular cement. That is, this environment represents one in which the maximum amount of water percolates through the pore systems without moving the grains themselves. It is in this hydrodynamic environment that sponge bioherms appear to be most abundant.

The abundance of the bioherms appears to decrease further onto the Bank, as current velocities decrease further: both the abundance of sponges and the amount of cementation decrease along the same lines. More information on this sedimentary environment is found in GEBELEIN (1977, p. 56-61). Therein, the following brief description of the sponge bioherms is given:

"In areas with high abundances of cemented grapestone, small biostromes and bioherms (1-5 m across, up to 2 m high) occur. These mounds have a rich surficial biota of [green algae,] sponges, alcyonarians, red algae, forams, molluscs and corals (in about that order of abundance). Preliminary investigations of the internal structure of these mounds reveal that they are composed of sand and silt sized sediment trapped within and around non-boring sponges. The sediments are
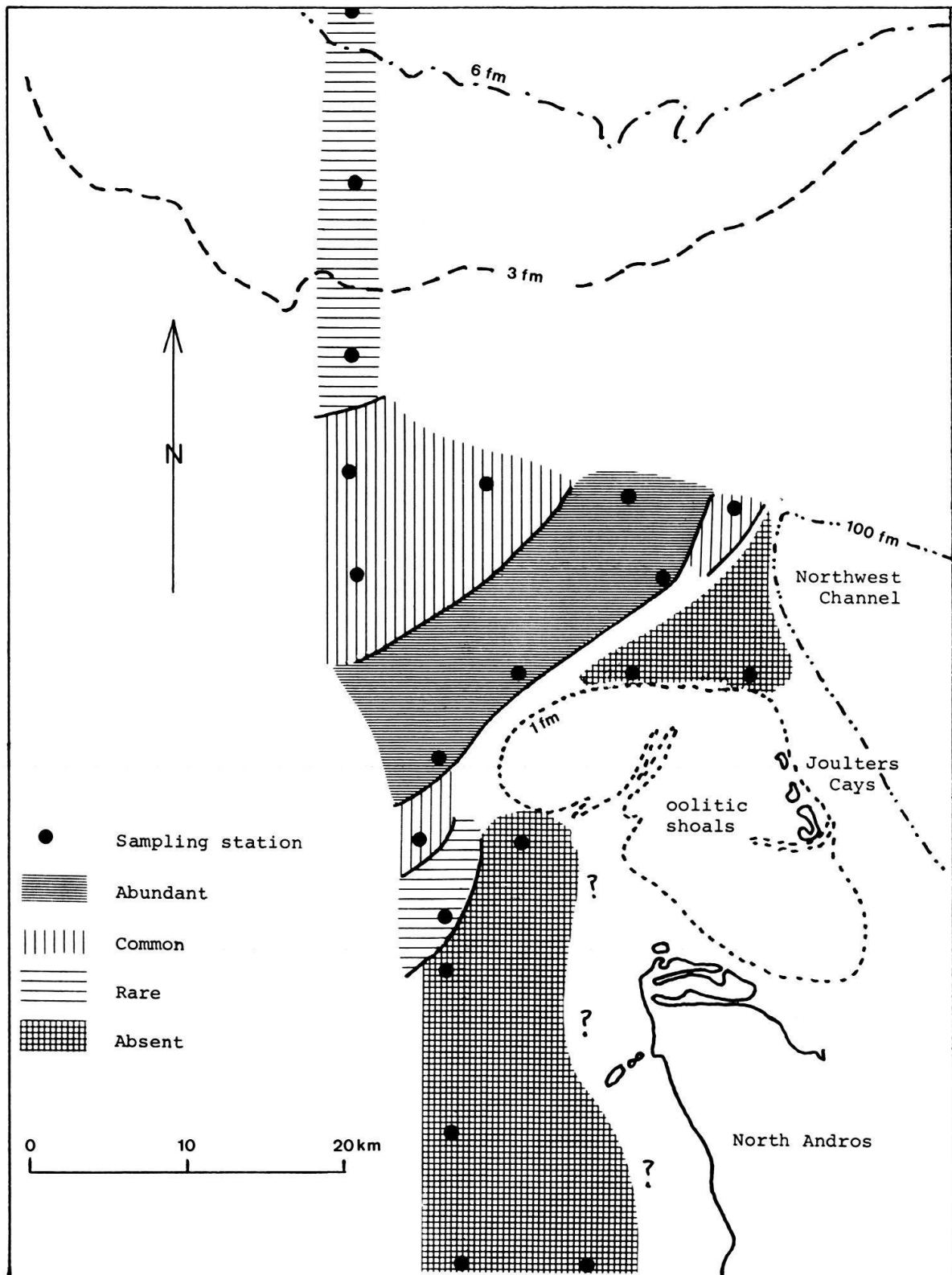
Fig. 2. Relative abundance of sponge bioherms, according to sampling obtained by C.D. Gebelein and associates during a cruise in summer 1975.

subsequently lithified by acicular and micritic aragonite. Living sponges occur deep within the bioherms (up to 2 m below the surface) and generate a complex pattern of inter-connected voids. These sponge bioherms apparently are unique in the Holocene and may be analogous to some Mesozoic sponge bioherms."

From limited sampling in 1975, Gebelein (unpublished NSF proposal) found that "the bioherms are composed of lithified grapestone sands, with variable portions of finer-grained material. Our samples show no evidence of either a coral or Pleistocene limestone core. The sands which compose the bioherms are nearly identical to the sands around the bioherms. Probing of the surrounding sediments reveals a total sediment thickness over the Pleistocene of 1 to 3 m. While numerous lithified zones are preserved in these sediments, the relief on the Pleistocene is negligible. Thus the possibility of growth of the bioherms over a Pleistocene high is eliminated."

"In general, the rock is very porous, with intricate systems of connecting voids, making a honeycombed pattern. Some of these voids have been filled with finer sands or muddy material. Borers and cryptic encrusters are quite common. Crude layering, 1-2 cm thick, is observed on some slabs of the bioherms."

Gebelein summarized his knowledge of the ecology and structure of these bioherms as follows: "1. They are not related to underlying bedrock highs; 2. they are forming at the present time; 3. sponges appear to be the major, and possibly the sole, agent of upbuilding of the bioherms; 4. they have a distinctive internal fabric which apparently relates to their mode of upbuilding and lithification; 5. the mounds are unique in the modern world; 6. the bioherms may be analogous to some (but not all) sponge bioherms in the geologic record."

II. Subsequent studies

a) Objectives, limitations and prospects

A new research project was begun in September, 1976, with Conrad D. Gebelein, Roger J. Cuffey (Pennsylvania State University) and the writer as principal investigators to study both types of bioherms in detail. For the sponge bioherms, the objectives were formulated as follows:

1. Determine, in quantitative fashion, the distribution of sponge bioherms on the northeastern portion of the Great Bahama Bank.
2. Determine the parameters which control the distribution of sponge bioherms and their constituent faunas.
3. Determine the nature of and variation in community composition of bioherms over the study area.
4. Determine the nature of the internal structure of the bioherms in the study area, including their framework, internal sedimentation and diagenesis.
5. Develop a model to describe the growth and structure of modern sponge bioherms.

Unfortunately, various difficulties in organizing cruises, aggravated by the sudden and premature death of C. D. Gebelein in March, 1978, plus unfavourable weather conditions, imposed serious limitations on scheduled field work and its

evaluation. The first trip to the sponge bioherms was confined 1½ days, with 3 stations occupied at random during stormy weather and poor visibility. The second trip (6 stations) was more profitable, but strong winds still prevented a meaningful selection of stations.

Therefore, few contributions can be made now to the first two points in the list of research objectives given above. The data presented below refer mainly to point 3. The objectives outline under 4 are part of the doctoral research program (dissertation) of Miss Debbie Bliefnick (University of California, Santa Cruz), who took part in both cruises. Nevertheless, an attempt at objective 5, to develop a model to describe the growth and structure of modern sponge bioherms, based on our preliminary field data, is presented in the concluding part of this paper.

Further research with regard to this last point (and partly towards point 4) centers on biological sections of sediment-binding, lithified, and endolithic sponges, and on microscopic examination (including scanning electron microscopy) of sediment and bioherm samples for tissue and spicules of sponges. This research is now in progress and will be presented in another paper.

b) The field evidence

1. Descriptions of the stations and their communities

The taxonomy of sponges is generally in accordance with WIEDENMAYER (1977a), except for some revisions in the Keratosa following consultation of R. W. M. VAN SOEST's manuscript (see 'references'). A full documentation is deposited in the Natural History Museum Basel. The stations are numbered consecutively (numbers 1 and 2 refer to stations at a coral patch reef and among bryozoan reefs, respectively, which are not described). See Figure 3 for location of stations 6–11. For stations 3–5, only LORAN fixes are given. Their position can be found on new navigation charts of the Great Bahama Bank with the grid of the LORAN radio-navigation system.

Station 3, December 6, 1976, LORAN fixes 26.50 (3L5)/11.75 (3L1)

Small flat bioherms, 5–20 cm high, ca. 20–100 cm in diameter are frequent. Some are partly or wholly buried under loose sediment. The surrounding loose sediment bottom shows abundant *Callianassa* burrows and mounds, a comparatively sparse vegetation of *Thalassia, Rhipocephalus* and *Penicillus,* with interspersed grazers and half buried benthonic animals: the holothurians *Actinopyga* and *Holothuria,* the echinoid *Clypeaster,* the bivalve *Pinna,* and a dark brown sabellid worm. The only sponge found in this environment (rare) is *Haliclona molitba* DE LAUBENFELS, which lives attached to *Thalassia.*

The bioherms support a diverse community of alcyonarians (see Table 2, with several species of plexaurids) and sponges (see Table 1). Felted algae, chiefly *Cladophora fuliginosa,* are abundant. A pale brown didemnid tunicate was noted, but no corals.

The sponges are mostly massive (except for the encrusting *Lissodendoryx sigmata* ?), usually well separated except for rare aggregates of 2–3 species, and grow
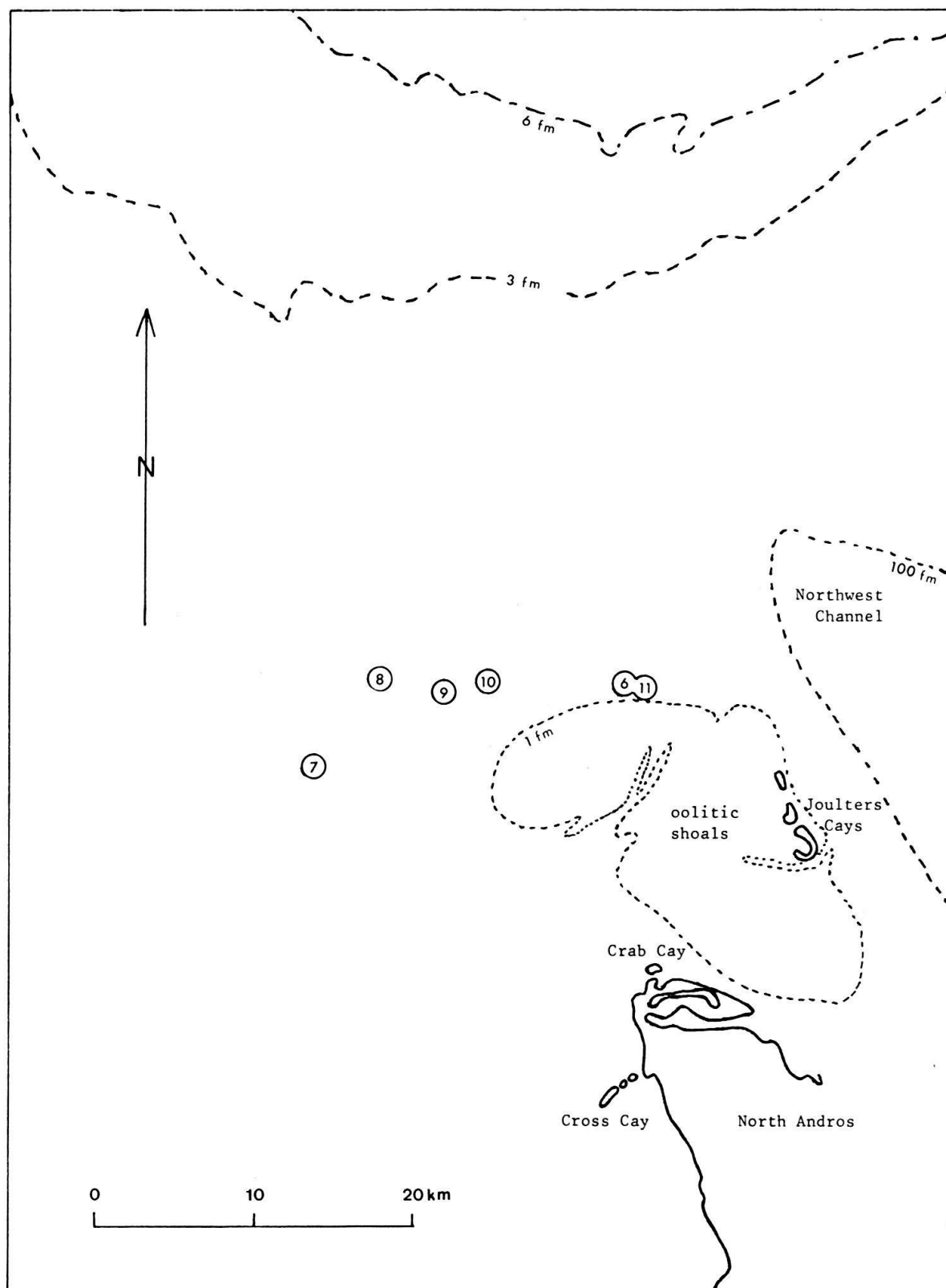
Fig. 3. Index map with stations 6-11.

on the bare bioherm rock, occasionally on dead alcyonarian stalks. *Lissodoryx sigmata* ? tolerates thin covers of loose sediment, with the aid of fistulose processes, with or without terminal oscules, protruding. Individuals of *Spheciospongia vesparium* habit *b* (juveniles of the species) seem to tolerate sediment covers 2–5 cm thick. Their buried thick and fleshy base around the axial atria is packed with sediment. Some specimens collected seemed to be attached to buried bioherm rock. Whether other aggregates can survive without firm attachment, merely anchored by the weight of the incorporated sediment, as noticed earlier near Bimini, could not be ascertained.

Samples of the bioherms brought on deck showed many oscular chimneys of this species (habit *b*) protruding from the rock surface, with intervening algal felt in some samples so thick as to hide the oscules. Upon breaking the samples they were found to contain widespread caverns parallel to and 1–2 cm below the surface, 1–10 mm high, communicating with the epilithic oscular chimneys and containing the same purplish black choanosome and presumably endopinacoderm. These caverns are interpreted as the atria within the broadening and coalescent massive bases of the juveniles, which while growing under the sediment surface incorporated more and more sediment between and on them, thus aiding or actively promoting cementation. One sample (Fig. 4) had a cemented layer 2–3 cm thick above the sponge-lined cavernous layer with fine upright canals between the endolithic sponge portion and the surface. The impression here was that the choanosome had retracted downward, leaving the top layer cemented and devoid of living sponge tissue. The rock around the caverns is penetrated by the choanosome of the same blackish color, for about 2–5 mm. The fabric of the rock in this penetrated area looks cellulose or alveolate in section, with sediment grains filling the fleshy interstices between the aquiferous canals. This fabric seems to be identical with that in the choanosome of isolated specimens surrounded by unindurated sediment. The texture of deeper levels of bioherm rock is more densely packed, but still porous.

Some broken samples of the bioherms showed other internal caverns, more irregular in shape, though sometimes forming more or less continuous thin layers below the endolithic atria of *Spheciospongia*. They contain a pale yellowish drab sponge with soft, very open-work choanosome. This has since been identified in a preliminary way (spicule slide) as *Timea* sp., a genus little known in the West Indies. This endolithic form seems to communicate with short, thin and fragile fistules of the same color observed on the bottom while diving, but this connection could not be confirmed with the samples at hand.

Station 4, December 7, 1976, Loran fixes 26.10 (3L5)/11.65 (3L1)

The situation is much the same as at the previous locality, but the sponge fauna is less diverse, and *Spheciospongia vesparium* habit *b* is rare or inconspicuous (oscular protuberances hidden in algal cover).

The community on the bioherms comprises relatively diverse alcyonarians (see Table 2, with several large forms of plexaurids), moderately diverse sponges (Table 1), and 3 species of corals (Table 3).

The sponges are again rarely crowded. Miss Debbie Bliefnick, diving at the same time near by, reported a knoll of corals and sponges 3–4 feet high.

Locality 5, December 7, 1976, LORAN fixes 26.11 (3L5)/11.70 (3L1)

It is situated within a large grass patch with few scattered bioherms in the same size range as before. Some are buried, judging from alcyonarians surrounded by loose sediment. Some large knolls with conspicuous coral heads were noticed from the boat. The following community was observed in the grapestone sediment with *Callianassa*-burrows, between the bioherms:

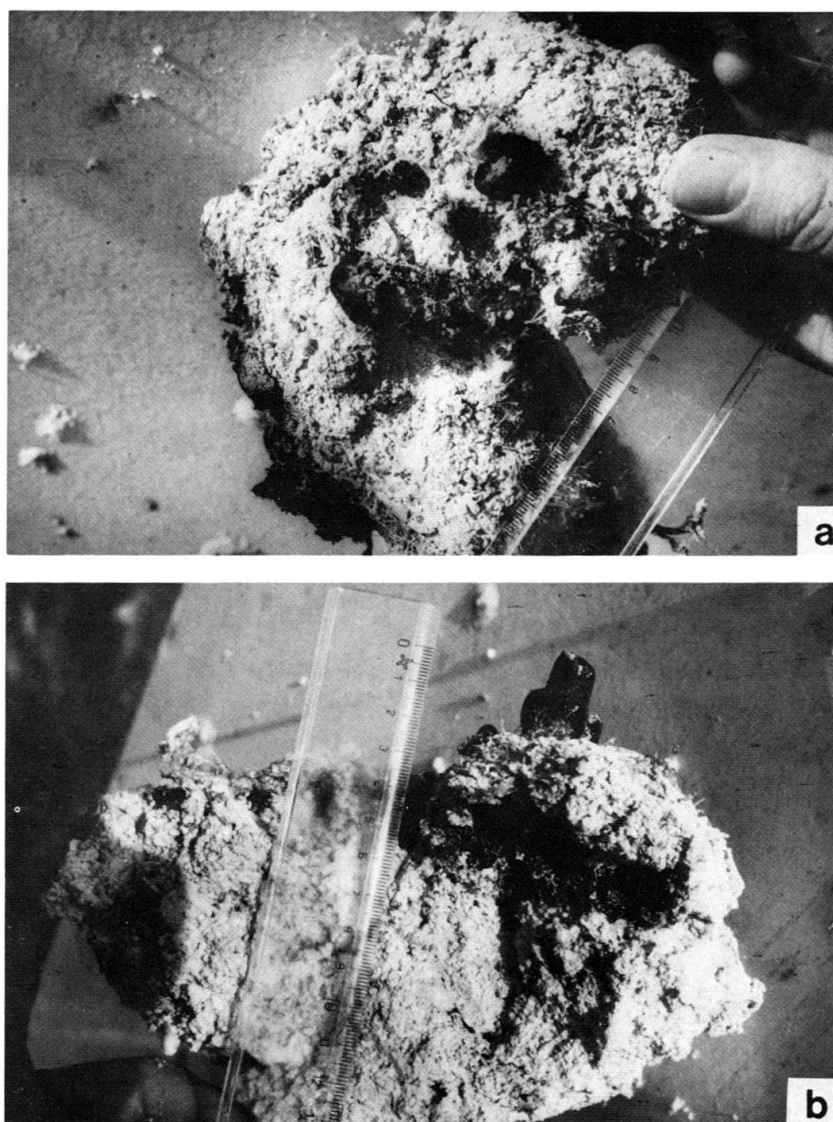| Vegetation	Scleractinian	Echinoderms
Thalassia (medium to sparse)	*Manicina areolata*	*Actinopyga*
Penicillus		*Holothuria*
Rhipocephalus	Sponge	*Tripneustes*
Udotea	*Haliclona molitba* (on *Thalassia*)	*Clypeaster*
Avrainvillea		

Fig. 4. Fragment of small young bioherm at station 3, photographed on deck after collecting.
a = Top view with group of epilithic chimneys of *Spheciospongia vesparium* habit b. b = Transverse fracture showing epilithic chimneys and endolithic portions of the same sponge.

The community on cemented patches and bioherms is comparable in diversity to that of station 4. Plexaurids are relatively rare. The sponges *Tedania ignis* and *Microciona spinosa* ?, both rare, were not seen at other stations.

The presence of *Anthosigmella varians* is remarkable. The specimens seen and collected here have an unusually long fistulose or digitate shape and their thicker bases, when surrounded by sediment, are packed solid with grains as in *Spheciospongia vesparium* habit *b*. Both sponges are known regularly to inhabit loose sediment substrates. They are also known to possess rock-burrowing properties. More important in this context is their little known property of binding sediment in their choanosome, especially its lower portions. *Siphonodictyon siphonum* is another sponge known to have such properties.

The occurrence of *Spheciospongia* both loose or only with the basopinacoderm firmly attached to the buried bioherm rock, with its choanosome packed with sediment grains (Fig. 5) and also partly endolithic, at the same locality, seems to eliminate penetration of the rocky substrate by boring alone. This probably equally applies to *Timea* sp. and by inference also to *Anthosigmella* and *Siphonodictyon.*

Station 6, July 16, 1977; 78° 7½′ W, 24° 22¾′ N

Depth 3 m. The bottom is largely unconsolidated, with *Callianassa*-mounds, sparse *Thalassia* and *Penicillus.* The most conspicuous grazers are the echinoderms *Holothuria, Actinopyga* and *Clypeaster.* The most common sponge is *Spheciospongia vesparium* habit *a*. Specimens are mostly massive, hemispherical to ellipsoidal, to cake-shaped. Some are terraced. A few are sprawling, buried under a cemented sediment crust, with oscules barely protruding. The massive specimens are usually single, frequently implanted in loose sediment with an obtuse-conical base incorporating sediment and coarser debris. Clumps of up to 4 such massive sponges were noted. One terraced specimen dissected under water revealed continuous layers of the choanosome packed with sediment grains extending inward from the terraces, presumably reflecting stages of inhibited growth. Other large specimens are growing on small lithic plates of the same lateral extent as the sponge (Fig. 6).

Much less common and conspicuous are patches of *Spheciospongia vesparium* habit *b* mostly covered by clusters of soft brown algae (*Laurencia* sp.). The sponges are barely visible by their almost level ocular margins. Digging out of some specimens revealed the buried portions consisting of short branching tubes (atrial ducts) which, except for the atrial linings, are packed with sediment and quite rigid and are therefore presumably at least partly cemented.

The only other sponges found implanted in loose sediment were some specimens of *Hyrtios proteus* (= *H. cavernosus:* WIEDENMAYER (1977a), in part, here corrected in accordance with VAN SOEST, in press, who examined my specimens J 967 and 968 and confirmed the revised identification).

Fig. 5. A specimen of *Spheciospongia vesparium* habit *b* photographed in situ at station 5.

a = Undisturbed, viewed from top. Most of the surface is covered by soft brown algae, *Briareum asbestinum*, and sediment. b = Dug out and turned on its side, showing heavy sediment crust around base. c = View of bottom after removing the base. Note the incorporated, vaguely layered sediment.
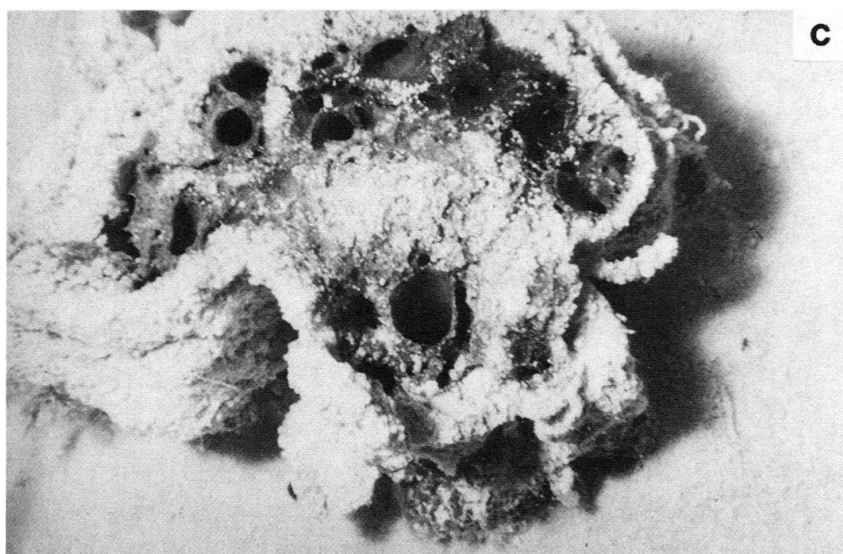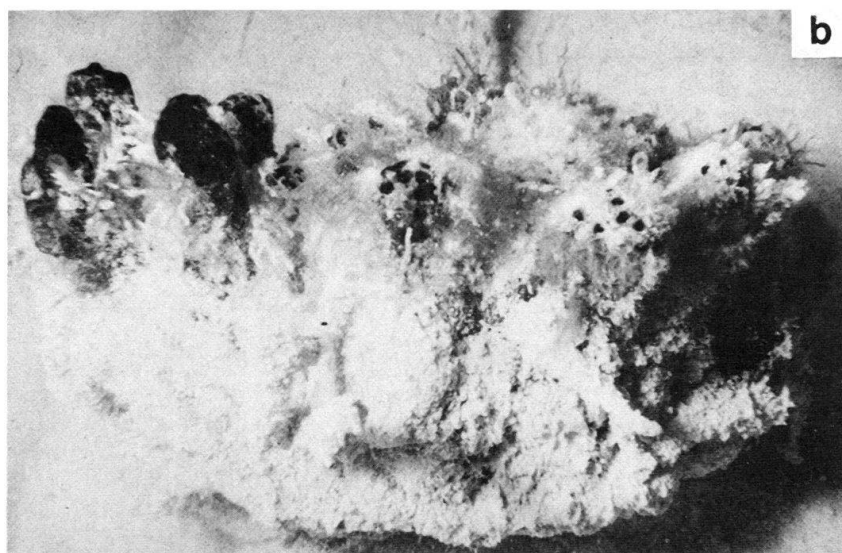
Fig. 6. Small bioherm at station 6, almost completely covered by massive specimens of *Spheciospongia vesparium* habit *a* in a cluster (2 isolated specimens are visible in the background). An *Ircinia felix* is visible on the left middle. The dead *Clypeaster* on the right is ca. 12–15 cm long. Inbetween, attached to the side of the middle one of the large Spheciospongias is the orange sponge *Ulosa ruetzleri*.

About equally abundant (10–20 per 100 m²) and interspersed with the massive spheciospongias are small cemented plates to mounds (bioherms), 0.2 to ca. 1 m in diameter, with a relief of up to 15–20 cm (Fig. 7).

Among the epilithic organisms on the bioherms, the green algae *Microdictyon* sp. and *Cladophora fuliginosa* are most abundant. Other algae are long soft browns, chiefly *Laurencia* sp. and rare *Sargassum* sp. Alcyonarians (Table 2) are dominated by plexaurids (chiefly *Eunicea*). Corals (Table 3) are more common and diverse than at previous stations, while sponges (Table 1) are moderately diverse.

Spheciospongia vesparium forma *b* is chiefly endolithic, with oscula barely protruding among the *Microdictyon* and hence easily overlooked. It was noticed only in one photograph of the bioherms. Particularly interesting is a specimen of *Porites astreoides* which was growing directly on a massive *Spheciospongia*, without rigid attachment to lithic substrate. Similar instances were observed at other localities.

Station 7, July 17–18, 1977; 78°26½′ W, 25°19¾′ N

Depth 5 m, current at surface 10 cm/sec. The turbidity was relatively high, the visibility ca. 15 m. The community of soft bottom with *Callianassa* mounds between bioherms is characterized by sparse to medium *Thalassia*, the algae *Penicillus* and

Fig. 7. Larger bioherm at station 6. Massive specimens of *Spheciospongia vesparium* habit *a* on middle left and in background. The algal cover in the foreground is mostly *Microdictyon* sp. The foreground is ca. 2 m wide.

Rhipocephalus, the echinoderms *Clypeaster*, *Holothuria*, *Actinopyga* and the bivalve *Pinna carnea*. The sponge *Haliclona molitba* is rare, attached to *Thalassia*. Some specimens of *Hyrtios proteus* and *Anthosigmella varians* forma *varians*, and one specimen of *Tethya crypta* were noted. All had their buried bases packed with coarse-grained sediment.

Spheciospongia vesparium again dominates, but massive specimens are much less common than at station 6, while habit *b* is common. The bases of such specimens are again buried and packed with sediment; they are commonly not branched, but are in the shape of cushions. Their undersides within the loose sediment is often attached to buried lithic plates, the extent of which and of the endolithic sponge caverns could not be ascertained. Examples in my collection are J970, 971 and 975. The latter was found adjacent to a small, slightly elevated flat bioherm infested by the same form (Fig. 9).

The cemented areas (bioherms) are irregular in size, shape and distribution (see Fig. 8). They are 10 cm to 2.5 m in diameter, of little relief, often lacunose, partly or wholly buried. They are largely covered by the green algae *Microdictyon* sp. and *Cladophora fuliginosa*. Other epilithic algae are long soft browns *(Laurencia, Dictyota)*, felted browns and reds (among the latter, *Amphiroa fragilissima* dominates), and encrusting corallines. Among the alcyonarians (Table 2), species of *Pseudopterogorgia* dominate while plexaurids are uncommon. Corals (Table 3) are represented by 4 forms. The epilithic sponge community (Table 1) is characterized by several species not present or rare at other stations.

Legend for 100 m² – Squares No. 1–8 (Fig. 8, 12, 13, 25, 34).

Sponges

Spongia spp.

Ircinia felix

Ircinia strobilina

Aplysina fistularis, chiefly f. fulva

Aplysina cauliformis

Dysidea etheria

Aiolochroia crassa

Haliclona molitba

Ulosa ruetzleri

Higginsia strigilata

Anthosigmella varians f. incrustans

Spheciospongia vesparium form a

Spheciospongia vesparium form b

Tethya crypta

Chondrilla nucula

Gorgonacea

Briareum asbestinum

Plexaurids

Pterogorgia anceps

Pseudopterogorgia spp.

Gorgonia

Corals (Scleractinia and Milleporina)

Porites porites furcata

Porites porites clavata (commonly blue)

Massive scleractinians
  1. Siderastrea radians
  2. Siderastrea siderea
  3. Porites astreoides
  4. Dichocoenia stokesi

Millepora alcicornis

General, algae

Bioherms with some relief, covered by Microdictyon and Cladophora

Buried to level (portions of) bioherms (not used when bioherm is extensively inhabited by Spheciospongia vesparium b). Broken outlines denote estimated contours

Higher portions of bioherms built up by (dead) corals, usually encrusted by Goniolithon

Long delicate browns (Laurencia etc.) on bioherm rock
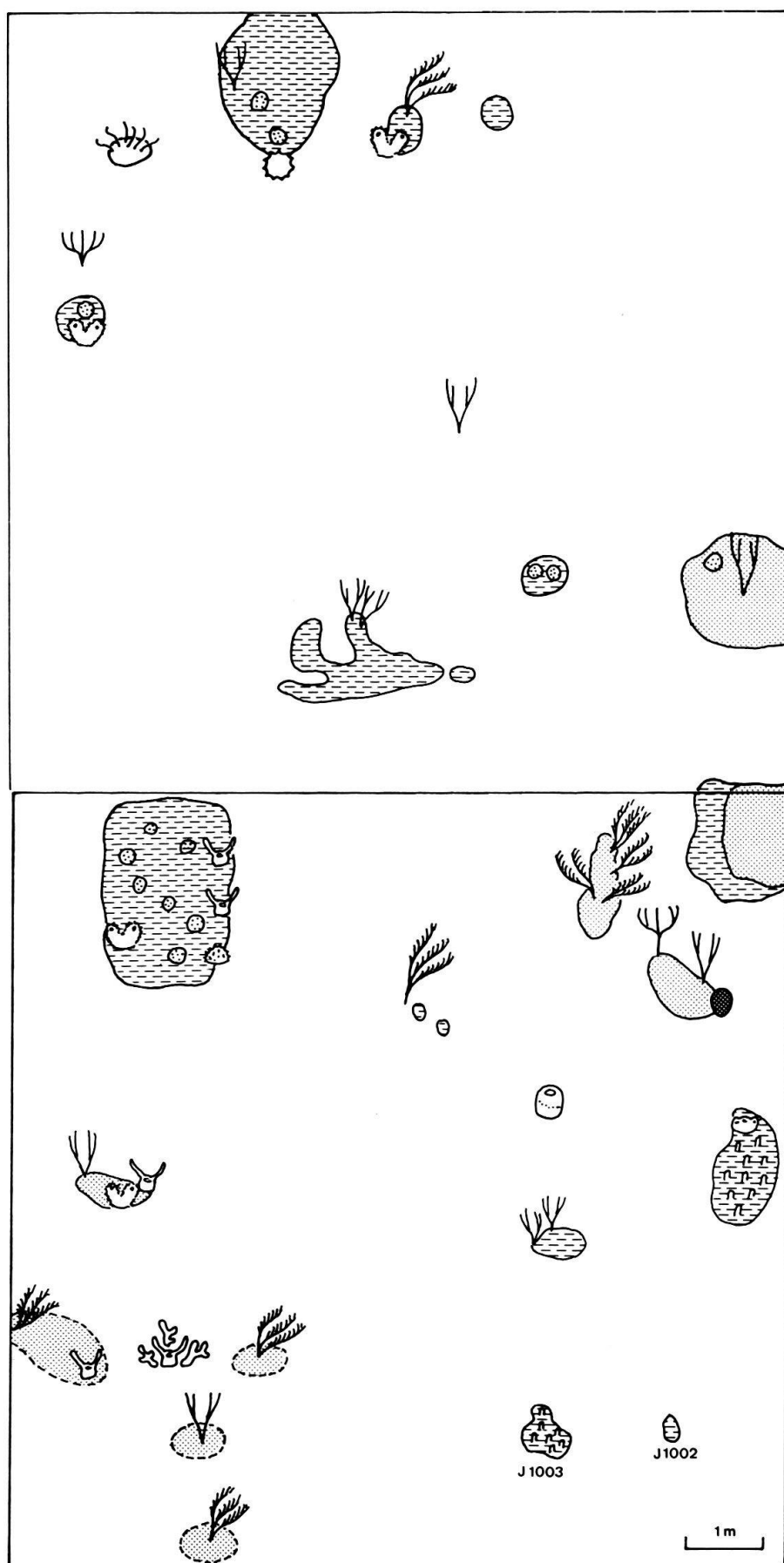
Fig. 8. 100 m²-squares No. 1 (below) and 2 (above), station 7.
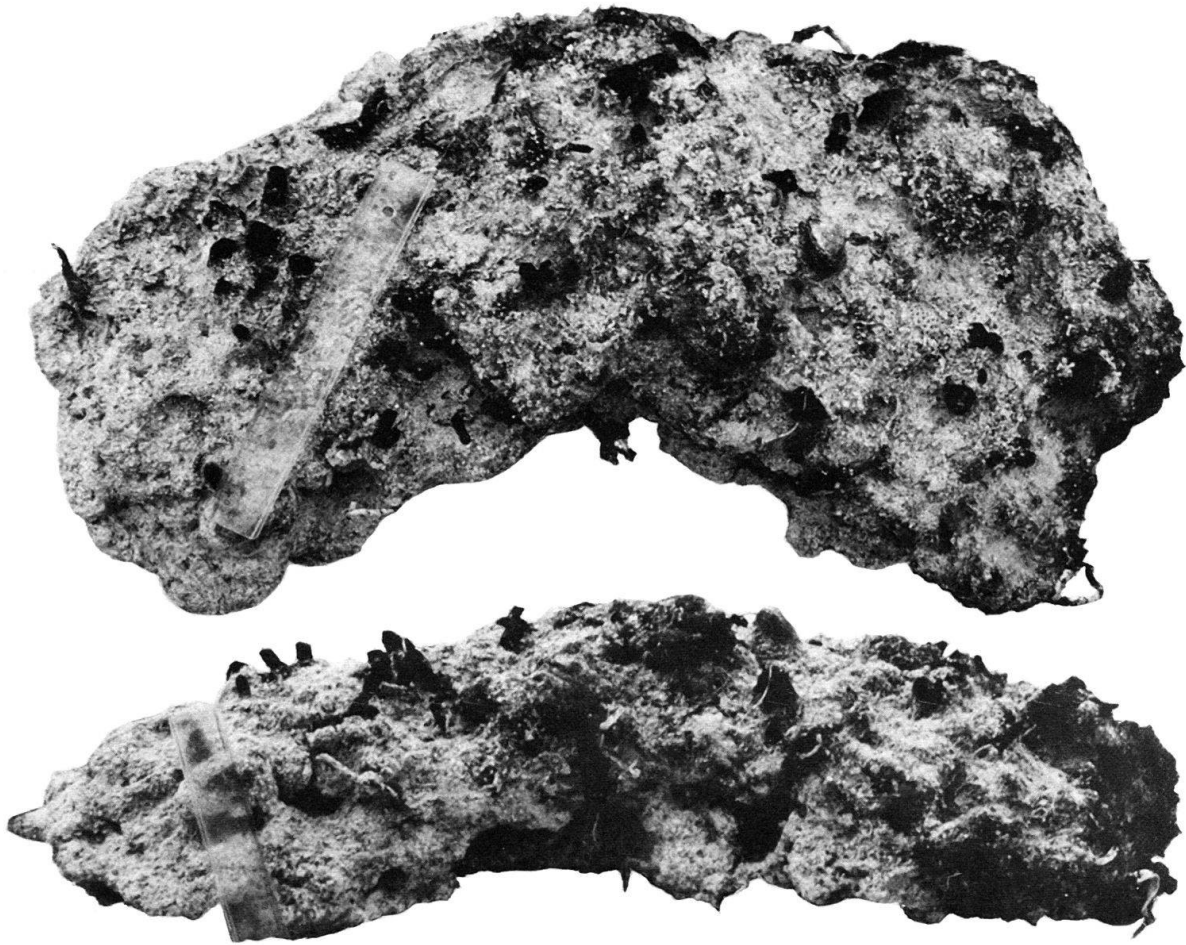
Fig. 9. Small cemented plate (embryonic bioherm) from station 7 (J1003, Fig. 8, square 1), photographed on deck after collecting, with conspicuous free chimneys of *Spheciospongia vesparium* habit *b*.

a = Top view. A small *Siderastrea radians* is fixed to the center of the right half. The plastic scale is 22 cm long. b = Side view.

Several of the slightly elevated cemented plates with dense algal cover were found to contain abundant *Spheciospongia vesparium* habit *b*, with the characteristic epilithic chimneys. One such plate was sampled (Fig. 9). The interior is rather compact, without extensive endolithic atrial cavities. The atria seem to be concentrated at the surface, half covered by algal felt incrusted with sediment, half embedded in the peripheral lithic portion but with occasional thin ducts extending inwards. The rock is variably porous, vaguely stratified with more friable porous layers and thicker, more solid, better cemented portions. The more porous portions seem to be impregnated by sponge choanosome, possibly by more than one species, but this remains to be confirmed by microscopic investigation. The bottom is stiffened by an ochre-brown thin binding coat, presumably calcareous, and by different kinds of serpulid tubes, of which the thinnest ones are often very prolific, in places packed almost solid. Accessory are patches of *Homotrema*.

Two tall, pinnacle-shaped bioherms were noted (Fig. 10, 11). The taller one (Fig. 10) was not examined closely. The smaller, slender one (Fig. 11) was taken on deck and broken up. *Haliclona podatypa*, a brown crumbly sponge, which was

1   Porites astreoides

2   Porites porites clavata (blue)

3   Ircinia strobilina

    Chondrilla nucula, light brown, encrusting

    Briareum asbestinum

    Dysidea etheria

    Hyattella intestinalis (LAMARCK): VAN SOEST
    = Spongia cerebriformis: WIEDENMAYER

    Haliclona (Reniera?) podatypa

    Sabellid worm

    Amphiroa fragilissima

    Microdictyon sp.

    encrusting coralline alga

    unidentified bivalve
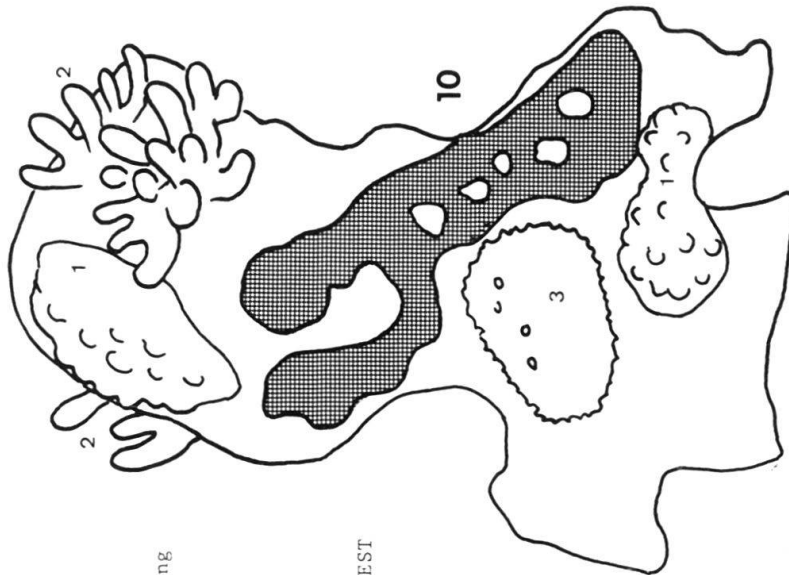
Fig. 10. Tall bioherm observed at station 7, sketched under water. Height 1–1.2 m. Not drawn are interstitial *Microdictyon*, *Briareum asbestinum*, *Ircinia felix*.

Fig. 11. Other tall bioherm from station 7, sketched on deck. Height 63 cm. The interstitial surface, over extensive areas of *Haliclona podatypa*, is covered by algal felt.

F. Wiedenmayer
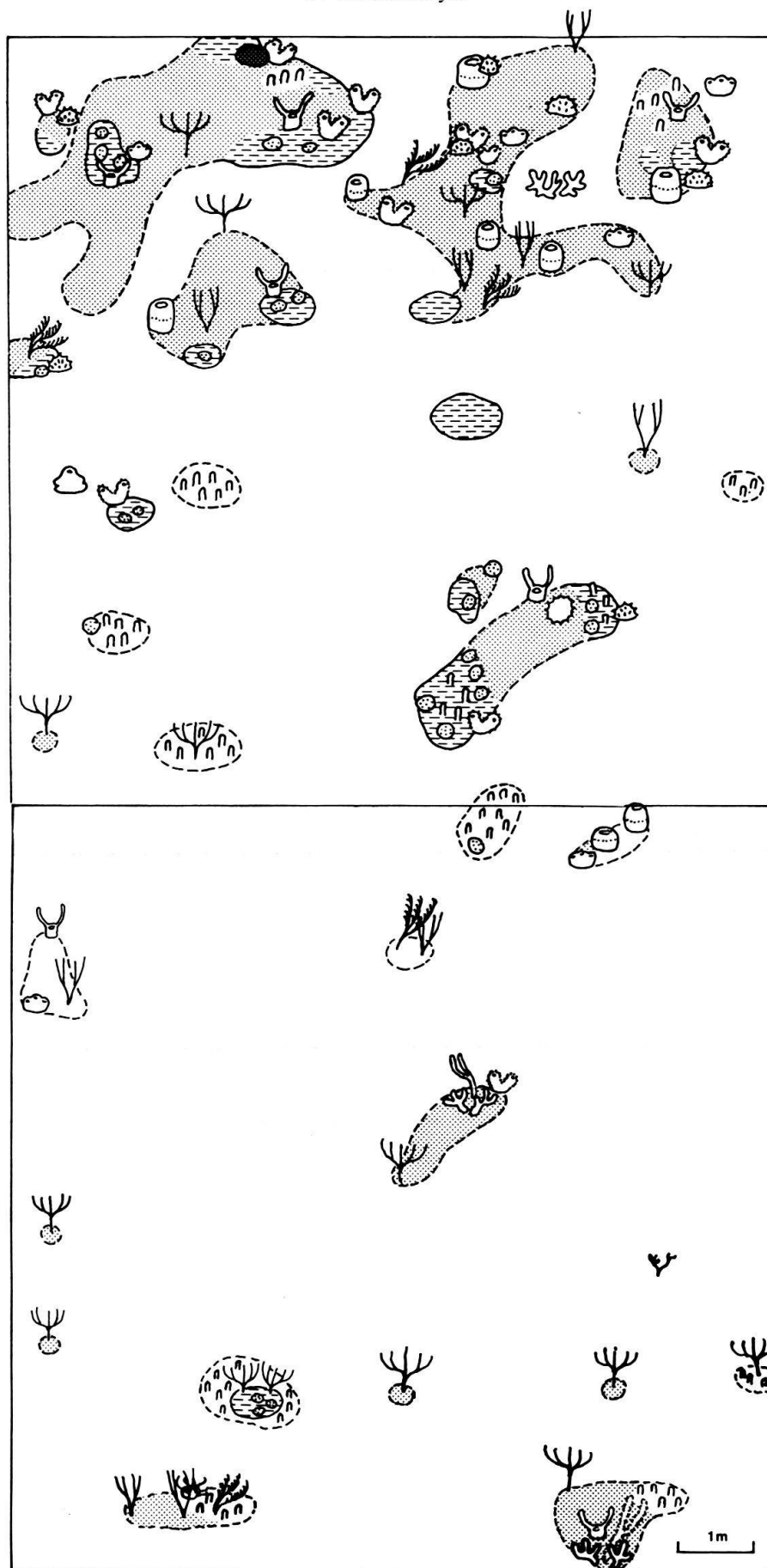
Fig. 12. 100 m²-squares No. 3 (below) and 4 (above), station 8. See page 714 for legend.
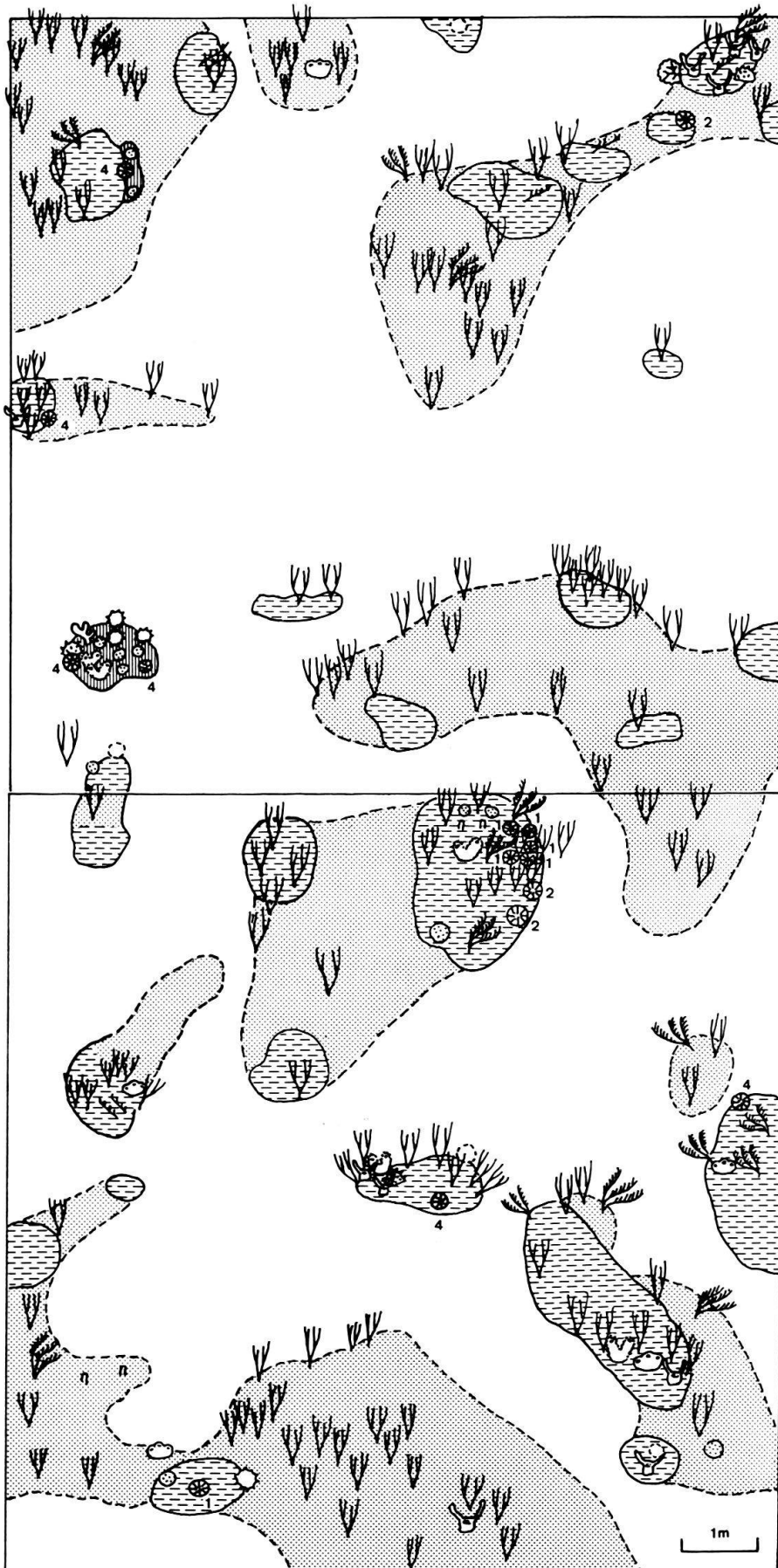
Fig. 13. 100 m²-squares No. 5 (below) and 6 (above), station 9. See page 714 for legend.

Fig. 14. Station 9. Patch of flat bioherm barely emerging above sediment surface, with surface beset by *Microdictyon* and alcyonarians. One naturally uprooted alcyonarian colony (left foreground), with free branches partly still alive, is becoming rapidly buried. The black sponge is *Spongia pertusa*. Diver's knife for scale in foreground.

visible only in small patches on the surface (large areas being covered by algal felt), was found to permeate extensive peripheral portions of the rocky pinnacle. The core of the pinnacle is quite dense compared to flat bioherms, but did not show macroscopic evidence of scleractinians, hence can be assumed to have formed by cementation of grapestone sand. This is made all the more likely by the presence of roots of algae or marine grass encased in the core. Transverse fractures reveal a vague zonation: outwards from the largely solid core follows a zone of porous rock with interstitial sponge choanosome and irregularly distributed tangled serpulids of various sizes. Then, out to the surface follows the grossly cavernous sponge choanosome with variable amounts of incorporated grapestone sand and serpulids. Some serpulids can be seen in the periphery of the solid core. Numerous large borings of *Lithophaga* further confuse the zonation of the periphery. Some of the borings are partly hollow, partly filled by sponge choanosome, packed serpulids, *Homotrema* and/or encrusting coralline algae; others are completely filled with younger, partly cemented grapestone.

Haliclona podatypa has been described only from 2 localities from a few specimens (WIEDENMAYER 1977a, p. 90) and hardly anything is known of its ecology. It cannot be excluded, pending microscopic examination of our samples from this pinnacle, that this sponge has boring properties (though unlikely for this genus), and that it settled on the pinnacle after its formation.

Station 8, July 18–19, 1977; 78°23¾′W, 25°22¾′N

Depth 4.5 m, surface current 25 cm/sec. The soft-bottom community is similar to that of previous stations. The cemented areas are also comparable to those of station 7, in prevailing low relief, irregularity of distribution, size and shape, and in epilithic community (e.g. relatively low frequency of gorgonians; see Figure 12 with squares No. 3 and 4). They can be classed as follows:

1. Buried plates, ca. 20 cm thick, containing *Spheciospongia vesparium* habit *b*, covered with barren sand, only the oscular chimneys sticking out.
2. Similar plates, but with the enlarged bases of individual sponges (habit *b*) more or less free, beset with algal felt, some sediment, occasionally habit *a* of the same sponge.
3. Plates with 10–15 cm relief, beset with *Cladophora* or *Microdictyon*. *S. vesparium* habit *b* may be present or not.
4. Higher structures, in the shape of towers or clubs, of bioherm rock, capped by corals *(Porites astreoides, P. porites clavaria)*.

The alcyonarian community of the bioherms is comparable to that of the previous station. Corals are restricted to the genus *Porites*. The community of adventitious epilithic sponges (Table 1, C) is comparable to that of station 5 in its 7

Fig. 15. Station 9. Exceptionally tall bioherm capped by an unidentified coral. The foreground is extensively encrusted with *Briareum asbestinum* (polyps mostly retracted, except for the side to the left of the pinnacle). The pinnacle is ca. 30 cm high.

eurytopic species. Like at station 5, the remaining 2 species are rare in this environment.

Though some specimens of *Spheciospongia vesparium* habit *a* and one specimen each of *Tethya crypta* and *Hyrtios proteus* were seen implanted in loose sediment, the epilithic (and partly endolithic) sponges dominate. Most characteristic and abundant is *S. vesparium* habit *b* with cushion-shaped bases fixed to cemented plates. These enlarged bases are partly or wholly buried and packed with sediment, sometimes lithified, or more or less free, beset with soft brown algae. One small cemented area with only one epilithic chimney of this sponge, was dug out and also photographed on deck. The structure was about as deep as it was wide (15 cm), conical with narrowing base. While being removed from the sand it split along a more porous layer parallel to and 5 cm below the surface. The top part consisted partly of sponge choanosome packed with sand grains. The atrium of the sponge could be seen to descend into the lower, otherwise wholly lithified portion. The porous layer separating the 2 portions contained many serpulids.

Other specimens photographed had more extensive bases, and were thus transitional to habit *a* of the same species. These were packed with sediment, sometimes lithified, covered with a mat of algal felt and *Perophora viridis*, which obviously traps sediment and presumably helps the sponge to incorporate it. Incipient growth of *Microdictyon* marks the transition to the more stable bioherm type densely covered by this green alga and *Cladophora*.
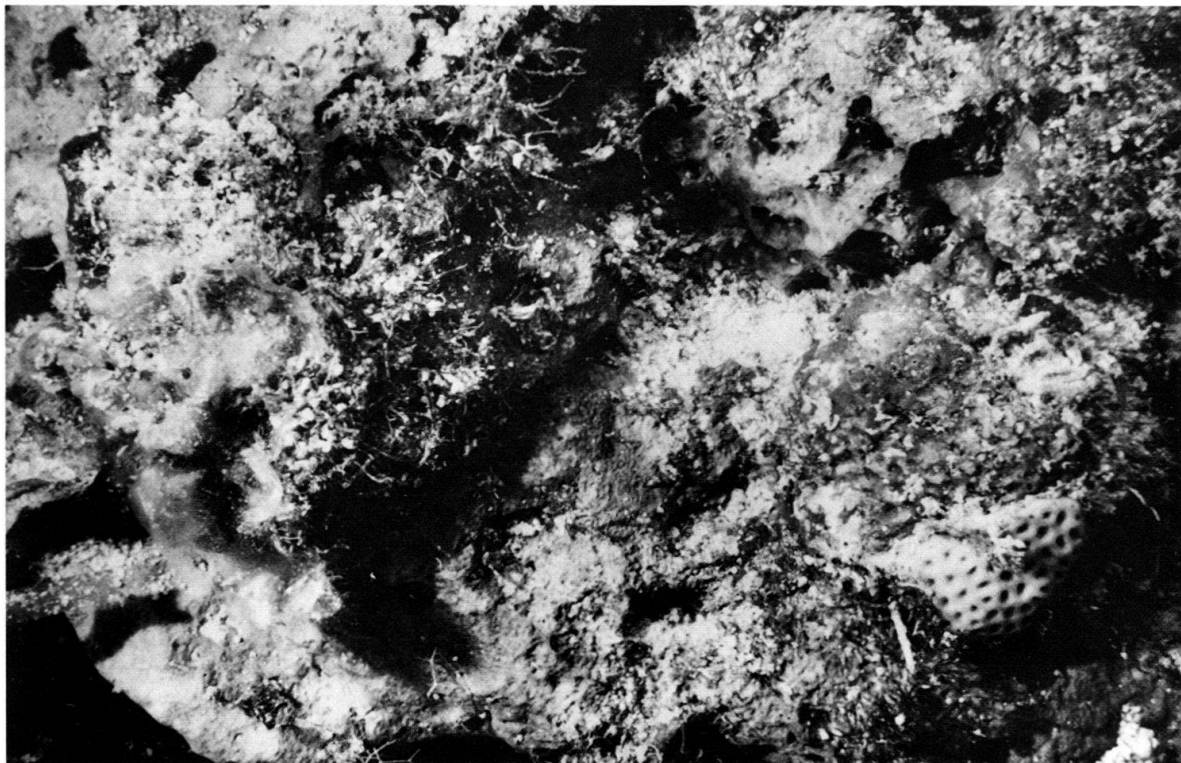
Fig. 16. Station 9. Detail from the overhanging side of a bioherm, thoroughly encrusted by a pink coralline alga. Other, less prominent algae are *Padina sanctaecrucis* (at mid height near left margin), *Cladophora fuliginosa* and *Amphiroa fragilissima*. The coral near the lower right corner is *Siderastrea radians*. Field 144 × 216 mm.

Station 9, July 20–21, 1977; 78°21¼′ W, 25°22¼′ N

Depth 3.5 m, surface current (flood-tide) 19 cm/sec. The soft-bottom community with *Callianassa* and sparse to moderately dense *Thalassia* is restricted by an extensive development of lithified plates (Fig. 13, 14). Also distinctive, in comparison with previous stations, is the luxuriant growth of gorgonians, with plexaurids dominating and *Pterogorgia* virtually absent. Plates with a cover of *Microdictyon* and *Cladophora*, with a relief of ca. 10–25 cm, are commonly 1–3 m² large, but, if connecting portions buried under sand are taken into account, the total areas are much larger. *Spheciospongia vesparium* habit *b*, with its epilithic portions frequently hidden among the green algae, is much more frequent than drawn in squares 5 and 6, both in buried and in slightly elevated plates. Some bioherms are exceptionally tall, up to 2–3 m long and 1 m high, usually capped by massive corals or sponges (Fig. 15). Their lower sides are often overhanging, and, where not overgrown by sponges, *Briareum* or corals, have lithic surfaces encrusted by a thin, pink coralline alga, with variable admixtures of algal felt, *Microdictyon*, *Padina* and sertulariids (Fig. 16).

The alcyonarian community is dominated by very abundant and diverse plexaurids. *Pterogorgia anceps*, almost ubiquitous elsewhere, is absent. Corals (Table 3) and adventitious epilithic sponges (Table 1, C) show the highest diversity of all stations.

Fig. 17. Station 9. Upper side of a trench dug trough one of the bioherms. The flat surface bears algal felt *(Cladophora)* and alcyonarians. Field 144 × 216 mm.

One of the cemented structures was opened by means of a small trench (60 cm long, 30 cm wide) dug with picks and crowbar. Its surface (Fig. 17) is generally flat, covered with sparse to moderately dense *Cladophora* and other felted algae. There are some deep furrows lined with an encrusting pink coralline alga (*Goniolithon* ?). The plate was found to be 35–40 cm thick. The uppermost portion, 5–10 cm thick, was conspicuously cavernous, with thick serpulids and borers. Deeper portions are more compact, though always more or less porous. A vague, often discordant stratification was observed, caused by more porous layers. Some of these are light brown and are locally associated with tangled masses of a very fine serpulid. One deeper area showed irregular cavernosities with ragged, unlined walls, reminiscent of the smaller, less mature plates with endolithic portions of sponges.

Fig. 18. Station 10. A cluster of *Spheciospongia vesparium* habit *b* in situ, viewed from top, their surface being covered by algal felt and trapped sediment, leaving only the oscules free. Field 144 × 216 mm.
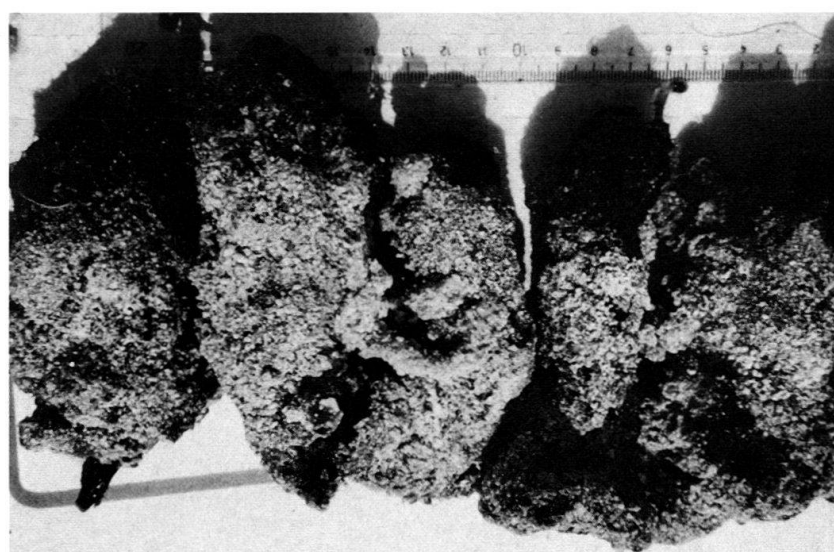
Fig. 19. Station 10. Crowded erect tubes of *Spheciospongia vesparium* habit *b*, implanted in the sediment, which they incorporate. Their bases are beginning to coalesce. Photographed on deck after collecting.

Station 10, July 22-23, 1977; 78° 19¾′ W, 25° 22¾′ N

Depth 3 m at low tide; surface current (flood-tide) 31 cm/sec. The communities, both of soft bottom and of cemented areas, are rather diverse. One type of soft-bottom community is similar to previous stations, with large *Callianassa* mounds, medium *Thalassia*, *Penicillus* and grazing echinoderms. *Spheciospongia vesparium* habit *a* is rare. Habit *b* of this species occurs here and there in patches. Individuals and groups are often covered by a mat of soft brown algae, very fine branching corallines *(Amphiroa)*, *Perophora viridis*, trapped sediment, and by *Batophora* (Fig. 18). Some of these patches are crowded, with individuals coalescent and buried, sediment-packed portions beginning to lithify into solid plates (Fig. 19).
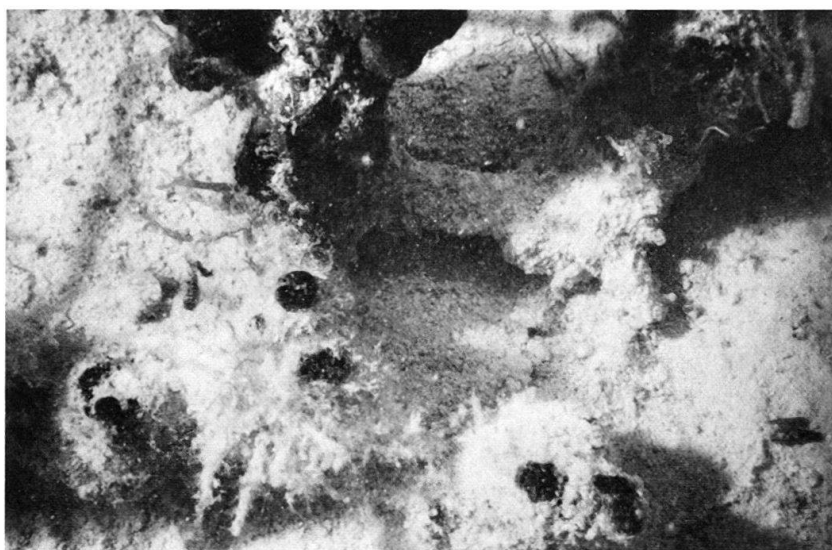
Fig. 20. Station 10. Top view of cluster of *Spheciospongia vesparium* habit *b* in situ, but with sediment removed to show connecting buried tubular stolons which are beginning to get lithified. Field 144 × 216 mm.
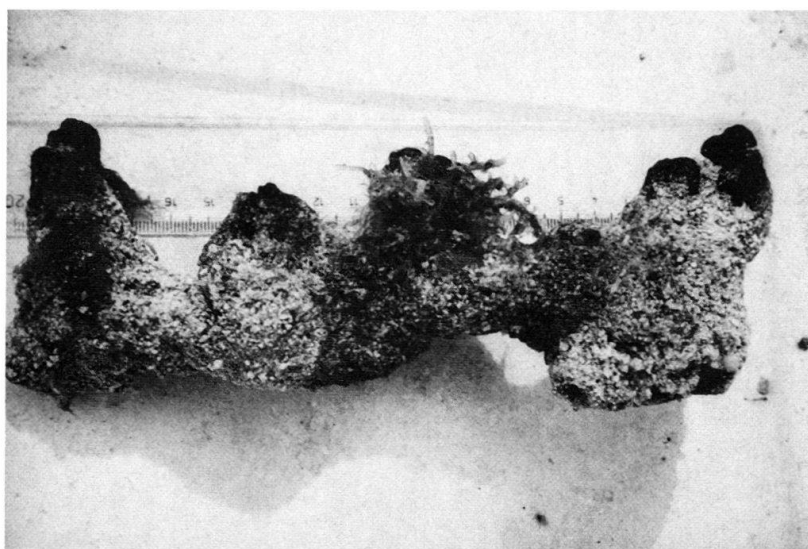
Fig. 21. Station 10. Side view of a stoloniferous specimen of the same form, photographed on deck after collecting.

Another observed habit is that having branched tubular portions buried in the loose sediment, often in the form of stolons below and parallel to the surface (Fig. 20, 21). The walls of these tubes (containing the atria and communicating with the free chimneys) are packed with sediment which is often partly cemented. Free chimneys are sometimes exceptionally tall, and are often encrusted by *Briareum*. *Microdictyon* sometimes begins to grow on such colonies. Some of the buried portions had masses of partly indurated sediment around the atrial stolons, which were agglutinated by an unidentified blue and yellow-green sponge. Here again, transitions to young cemented plates could be observed, with *Briareum* and *Microdictyon* on top, and tangled serpulids and agglutinated worm tubes on the bottom (Fig. 22, 23). The
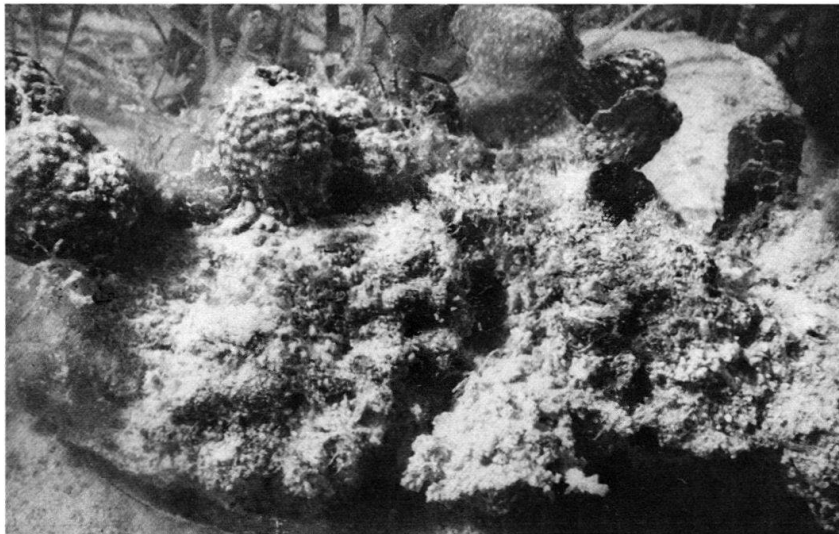
Fig. 22. Station 10. Early stage of bioherm formation. Side view of a cluster of *Spheciospongia vesparium* habit *b* in situ, with its free surface, except the oscules, covered by *Briareum asbestinum* and algal felt. The buried portions of the host sponge are surrounded by an unidentified blue to green sponge agglutinating sediment supposedly in the process of cementation. Field 144 × 216 mm.

Fig. 23. Station 10. Bottom of the same specimen, coated with an ochre colored diaphanous film, very finely tangled serpulids and some agglutinated worm tubes. Field 144 × 216 mm.

impression was gained from some samples that lithification starts along the bottom of the buried sponge choanosome, possibly aided by serpulids. Some of these buried portions, however, were noted to overlie buried lithified plates to which they may have been attached.

Much rarer are patches with *Anthosigmella varians* forma *varians*. Here again, buried portions may be extensive and packed with sediment with bottoms encrusted by serpulids, but lithification was not observed.

Other sponges of this community are *Hyrtios proteus* (frequent, implanted in loose sand, which is incorporated into its base) and *Tedania ignis* in depressions and among loosely lying *Porites porites furcata*. One unidentified black sponge, largely covered by algal felt and sediment, was found to be fixed to a small boulder, presumably dead coral, encrusted by *Goniolithon* and serpulids. Similarly, a buried dead *Porites porites* and a buried *Clypeaster* shell seemed to play the role of "Micro-bioherms" and indicate that many conspicuous epilithic invertebrates in this environment are ubiquitous and largely independent of the nature and hardness of the lithic substrate.

The mature cemented plates in this area are between 30 cm and 4–5 m in greatest extension, more or less irregularly scattered. Plates with some relief (up to 20 cm) and a cover of *Microdictyon* are the rule, level or buried plates are rare here.

Fig. 24. Station 10. Detail of a typical adventitious epilithic community on the edge of a mature, stabilized sponge bioherm. Curly *Microdictyon* (green alga), upper left corner and upper margin, middle; *Aplysina fistularis*, above center left; *Ircinia felix*, lower left corner and right margin; *Spirastrella coccinea* in recessed, shady parts and lower left; *Briareum asbestinum*, upper right center; *Porites astreoides*, lower right corner. Remaining interstices bear algal felt and branching coralline algae. Field 144 × 216 mm.

Higher structures with massive corals occur, some capped by *Porites porites clavaria,* but are mostly small. Gorgonians are not as frequent as at station 9, with plexaurids and gorgoniids about equally represented. *Pterogorgia anceps* is again absent. The presence of *Gorgonia ventalina,* otherwise restricted to the coralgal habitat, is remarkable. Corals (Table 3) are almost as diverse as at station 9. Like *Siderastrea siderea* and *Diploria strigosa* at station 9, *Meandrina meandrites* constitutes an exotic, stenotopic element extending on the bank from the coralgal habitat. The community of adventitious epilithic sponges (Fig. 24, Table 1, C) is only slightly less diverse than at station 9.

Square No. 7 (Fig. 25) was sketched where the cemented plates with *Microdictyon* and *Cladophora* were particularly frequent.

A somewhat different community was also encountered at this station. The *Callianassa* mounds, though frequent, are considerably smaller than seen elsewhere.
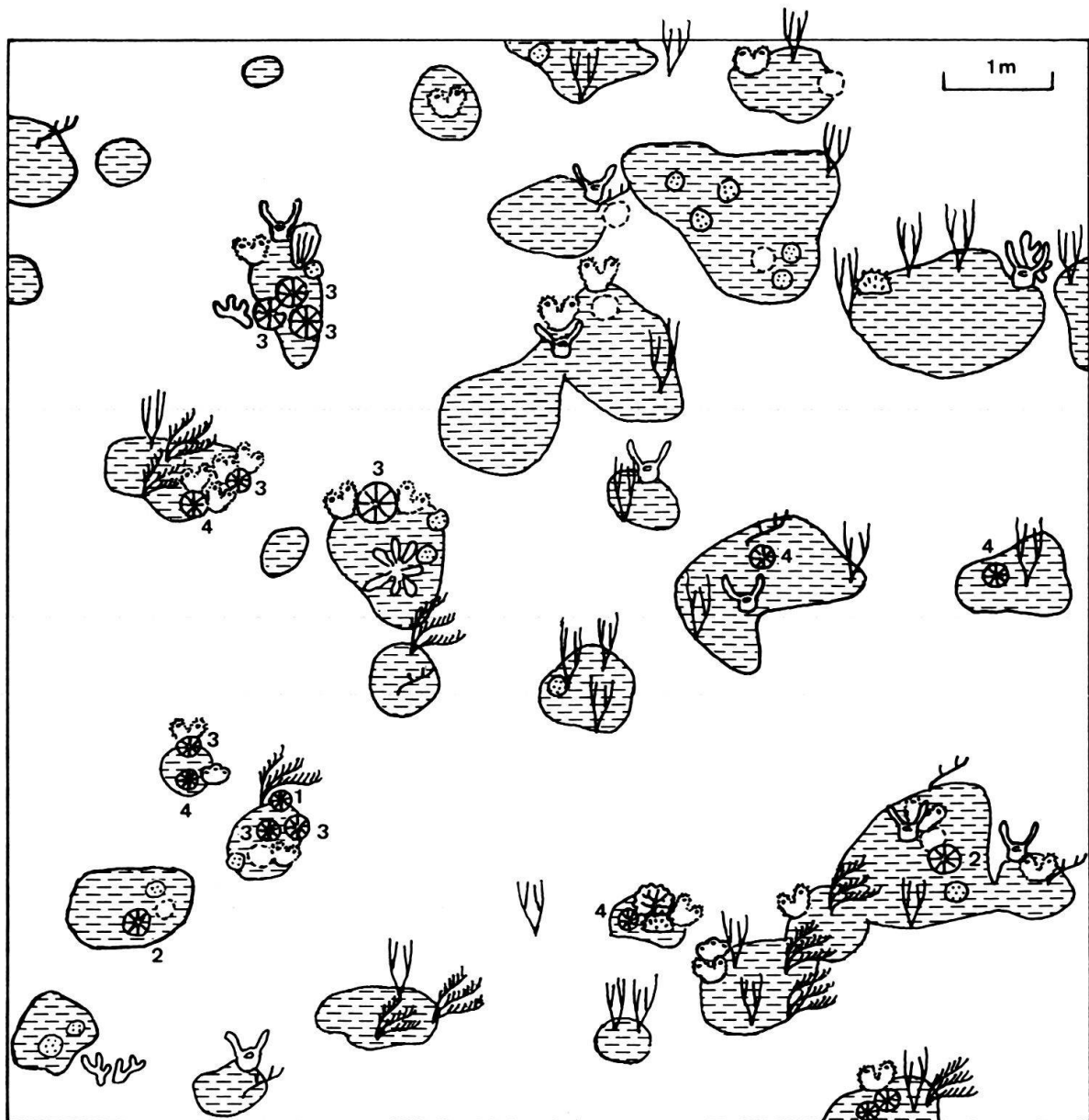
Fig. 25. 100 m²-square No. 7, station 10. See page 714 for legend.

Thalassia is rather sparse, especially over some areas with frequent *Penicillus* and *Rhipocephalus*, and a distinctive *Caulerpa (C. serrulata)*. The only other benthonic invertebrates first noted while diving were rare stunted gorgoniids, frequent *Ircinia felix* and *Spheciospongia vesparium* habit *b* in clusters. These are covered by tangled soft brown algae and felted green algae. After removal of the algae such a patch with clustering sponges was dug out (Fig. 26, 27) and seen to belong to the surface of a buried lithic plate with a tapering, obtusely conical base. It was brought on deck for sampling (Fig. 28, 29). Removal of the felted algae on top and exposure of transverse sections revealed the presence throughout the upper portion of a yet
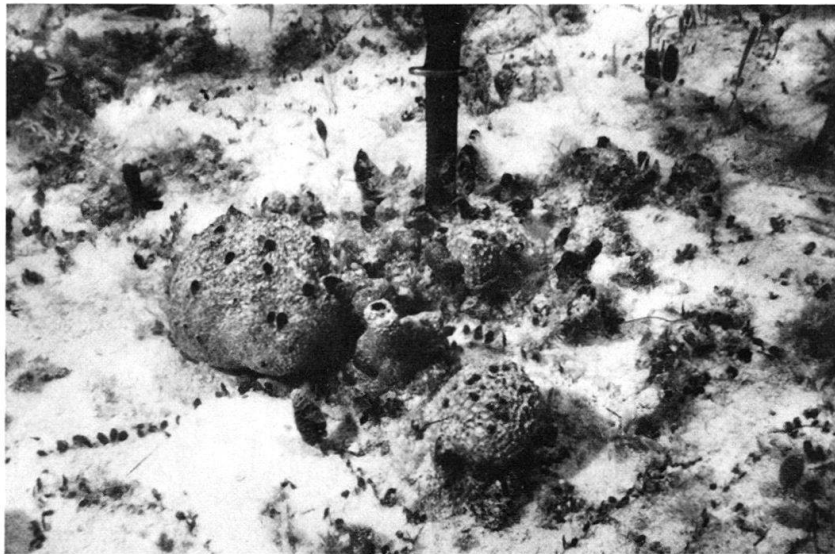
Fig. 26. Station 10. Cluster of sponges on an immature, semilithified bioherm which is mostly buried, with its surface level with the surrounding sediment. Its extent is merely indicated by the epilithic sponges: *Spheciospongia vesparium* habit *b* around center, with diver's knife for scale; *Ircinia felix* to the left and below. The stringy green alga is *Caulerpa serrulata*.
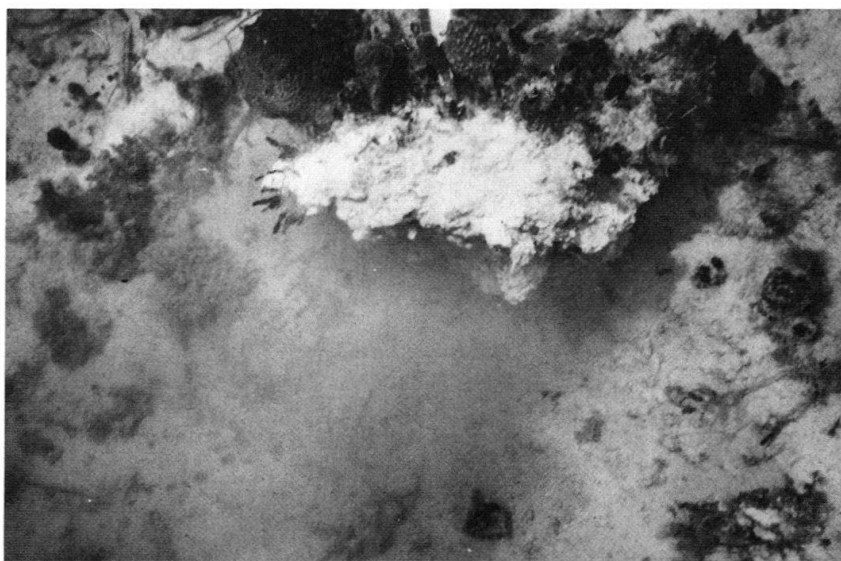
Fig. 27. The same bioherm as Figure 26, but extracted from the sediment and laid on its side.

unidentified light grey sponge penetrating the interstices between the endolithic portions of *Spheciospongia vesparium* habit *b*, down to a level 4–5 cm below the surface. The choanosome of the intimately aggregated sponges (Fig. 30) contains much sand, which is partly cemented, judging from the firmness during sectioning. The underlying barren grapestone is poorly cemented, porous and crumbly. The interface is sharp and the immediately underlying layer is cavernous and marked by abundant serpulids. These also occur scattered in the choanosome and deeper in the barren grapestone, but seem to be concentrated in at least one layer below the sponge-rock interface.

Station 11, July 24–25, 1977; adjacent to station 6

Depth 3 m, surface current (flood-tide) 30 cm/sec. The soft-bottom community is distinctive. *Callianassa* mounds are mostly small. *Thalassia* is sparse to absent, often aligned in a reticulate pattern. *Penicillus* is frequent, other algae are *Acetabularia, Batophora, Halimeda, Caulerpa*, soft browns. The level sediment surface is covered everywhere by a flocculant algal mat, and the tunicate *Perophora viridis* is abundant, virtually ubiquitous (also on bioherms). The level sediment surface is stable enough to support a fairly common purple colonial tunicate (presumably a didemnid, possibly a botryllid). Other colonial tunicates seen on grass blades were *Ecteinascidia turbinata* and a light brown didemnid. Other characteristic invertebrates were *Pinna carnea* and *Oreaster reticulatus*. Several isolated gorgonians were observed, one of which, a *Pterogorgia anceps*, was found to be fixed to a flat bioherm cobble about 10 cm wide. Gorgonians seen isolates among the bioherms here and at other stations may have been similarly fixed.

Fig. 28. The same bioherm as Figure 26 photographed on deck (top view). The plastic scale is 22 cm long.

The only sponges noted in this community were *Spheciospongia vesparium* habit *a* and *Anthosigmella varians* forma *varians*, the former more frequent. Smaller specimens of the former are conical to cushion-shaped above the sediment and are commonly covered by felted green algae, soft brown algae and *Batophora*, with a veneer of trapped sediment. *Briareum* was seen encrusting on some specimens, and, in one instance, a small *Porites astreoides* was growing on such a sponge. Larger specimens of *S. vesparium* are approximately hemispherical. One such specimen was sectioned and dug out (Fig. 31). The implanted base, obtusely conical, was encrusted with partly cemented sand, reinforced by sediment-agglutinated worm tubes. The basal choanosome was seen, upon sectioning, to contain much sand up to the level of the surrounding sediment, packed in layers parallel to the lower surface. This seems to indicate that the sponge was growing rhythmically, with pauses marked by incorporation of surrounding sediment and (yearly?) growth stages with choanosome relatively free of sediment.

Anthosigmella varians forma *varians* occurs isolated, or with *Spheciospongia vesparium* habit *a*, in one instance associated with an unidentified black sponge.
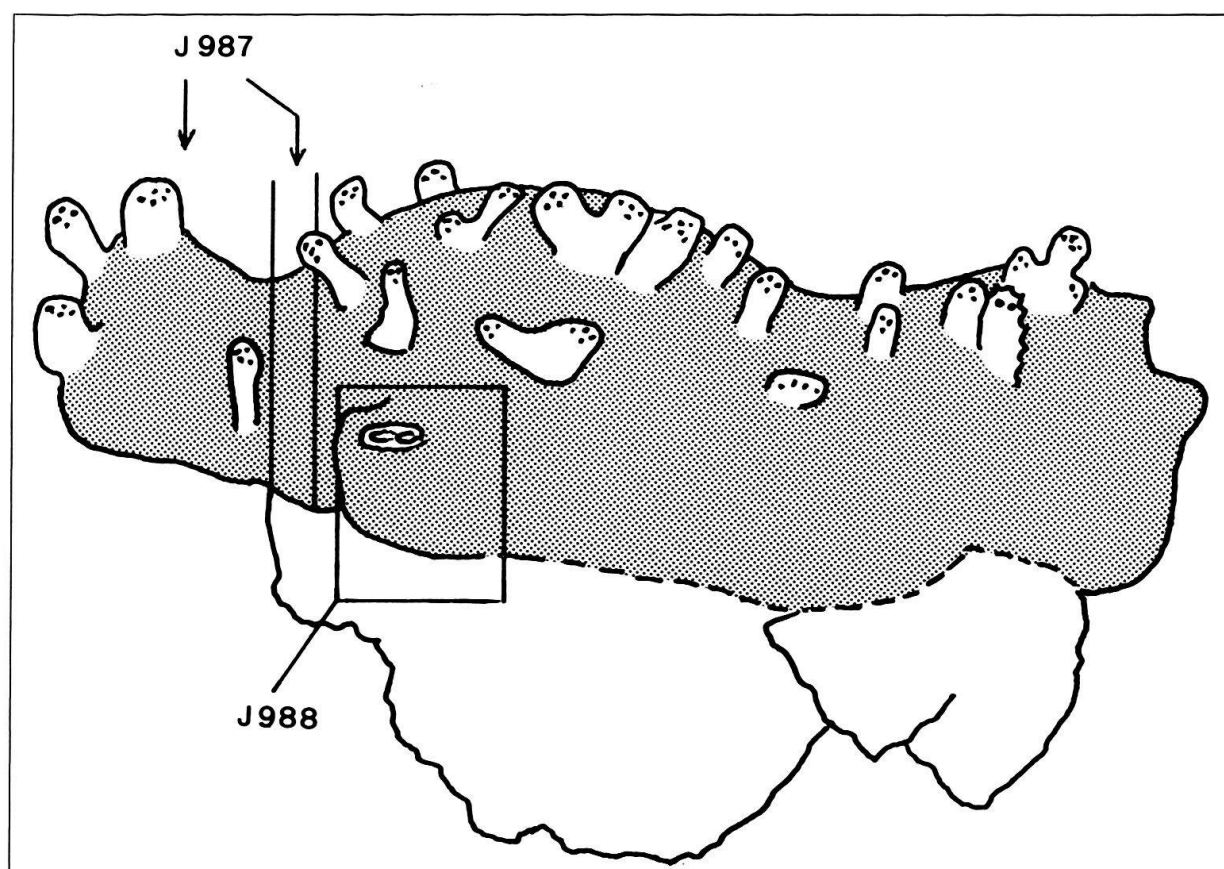
Fig. 29. The same bioherm sketched from the lower side on Figure 28, with location of samples taken for microscopic examination. The white structures on top are epilithic chimneys of *Spheciospongia vesparium* habit *b* with apical oscula. One such chimney, containing a subdivided atrium, is broken off (within area J988). One young specimen of *Ircinia felix* is situated near the right margin (a larger specimen of this species, which was fixed to the right margin, is not drawn). Shaded is an unidentified light grey to beige sponge permeating the whole top part of the bioherm between the branched ducts of *Spheciospongia*. White below is porous bioherm rock devoid of sponges.
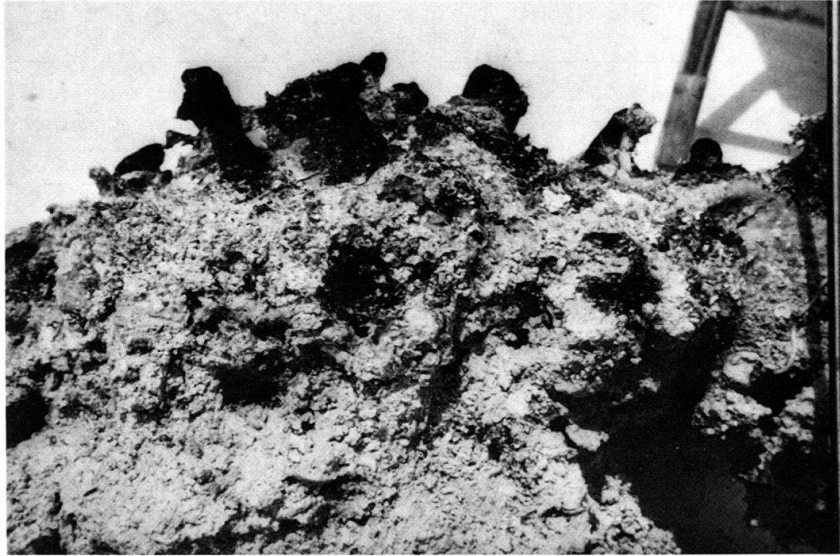
Fig. 30. The same bioherm as Figure 26, transverse section through the top part. The lighter portion over much of the lower third is more thoroughly though weakly cemented, and macroscopically devoid of sponge. The upper portion, which is permeated by an unidentified sponge, shows beginning cementation around the buried black atrial ducts (center and right middle) of *Spheciospongia vesparium* habit *b*, which connect with the free chimneys at the surface. Field 155 × 233 mm.

Portions of these sponges are usually buried and packed with sediment, especially in the base. In some cases, the buried portions were found to be very extensive, the incorporated sediment showing incipient cementation to form a lithic plate (Fig. 32). A similar structure was collected (Fig. 33), in which the sponge (also yellow) may belong to yet another species. This sample showed a segregation of a lower, purely lithic portion from an upper, sponge-infested portion, similar to J 987–988 of the previous station (Fig. 30), though less distinct. The interface is again marked by prolific tangled serpulids, though serpulids are also scattered in the cavernous, purely lithic base.

The bioherms are concentrated in different areas, of which 2 sorts were noted. One type is that sketched in square No. 8 (Fig. 34), with intervening level soft bottom of the type described above. *Microdictyon* and *Cladophora* are not so abundant on the plates as before: other felted green and brown algae dominate. Though the relief is commonly around 10 cm, much of the surface of the plates is covered with sediment. Many oscular chimneys of endolithic *Spheciospongia vesparium* habit *b* were seen protruding (not drawn on square No. 8). Some of these sponges are transitional to habit *a*. There are many *Porites porites furcata* lying freely on the level bottom between bioherms, also rubble and blocks of detached bioherm material. Many of these are probably buried and serve as holdfasts for the seemingly free gorgonians.

Fig. 31. Station 11. A massive specimen of *Spheciospongia vesparium* habit *a* implanted in sediment. Diver's knife with inch marks as scale.

a = Undisturbed; b = vertical section showing layered sediment incorporated by base; c = view of bottom after extraction, with base cut off.

The bioherms of the other type are surrounded by virtually barren, shifting sand, except for prolific *Batophora* on rubble. The bioherms are irregularly distributed, 0.2–1 m across, with strong relief, often up to 60–70 cm (Fig. 35, 36). Sponges and corals are more prolific than ever before; *Microdictyon, Cladophora, Batophora,* encrusting *Goniolithon,* brown algae and *Briareum* cover the interstices and much of the surface of *Spheciospongia vesparium* habit *a* (again transitional to habit *b*). *Pseudopterogorgia acerosa* dominates, often in very tall colonies. The most frequent coral is *Porites astreoides.* The most frequent sponge is *Spheciospongia vesparium* habit *a.* The epilithic chimneys of habit *b* of the same species are common but
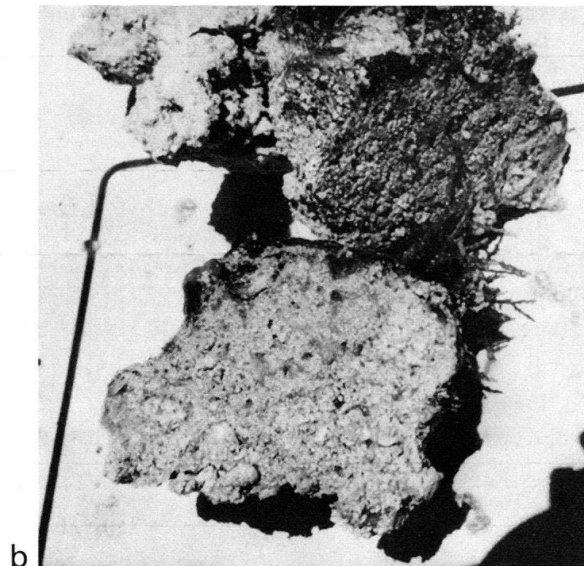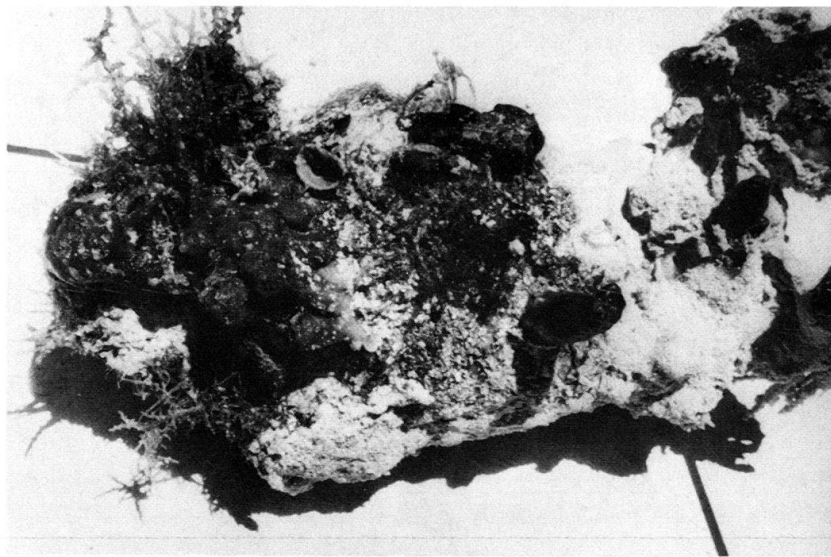
Fig. 32. Station 11. Incipient lithification in a massive specimen of *Anthosigmella varians,* photographed on deck after collecting. The main part, which was buried, is packed and encrusted with sediment. Free portions are limited to isolated knobby and digitate protuberances, partly covered by algae.

a = Oblique view of top. Field 155 × 233 mm. b = Transverse section; field 155 × 155 mm. The irregularly lacunose appearance is caused by the canal system of the sponge.
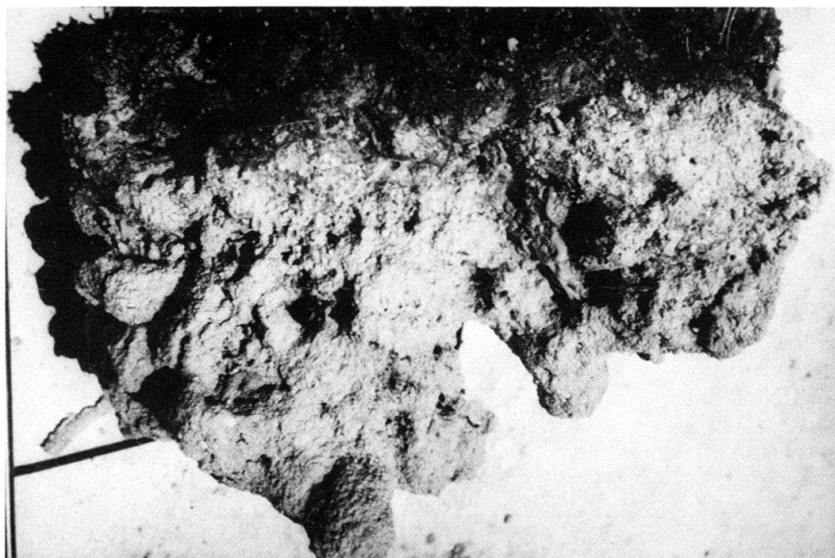
Fig. 33. Station 11. Embryonic bioherm photographed on deck after collecting, side view. Field 155 × 233 mm. The grossly cavernous base is well cemented and macroscopically devoid of sponge. An unidentified yellow endolithic sponge occupies a layer about 1 inch thick below the surface, which bears a dense cover of algae.

inconspicuous. An unidentified purplish black, rubbery, lipostomous sponge is encrusting large areas. The same species was also noted at station 7 and on patch reefs east of Joulters Cays.

There are indications of relatively high turbulence: the shifting barren sand between bioherms, the high and irregular relief of the bioherms with margins steep to overhanging, the sediment immediately surrounding sometimes sloping away from the bioherm (Fig. 35), occasional fringes of rubble and *Porites porites furcata* (Fig. 36) and general frequency of large debris.

One headsized bioherm from this site was brought on deck and broken up. The surface was covered by *Briareum asbestinum*, *Porites astreoides* and diverse algae; it showed signs of borers. The interior is cavernous, the lithic portions showing variable degree of cementation. The cavernosities are commonly well-rounded with sharp margins, and some are clearly borings of *Lithophaga*. Much of the interior is permeated by sponge choanosome, both interstitially in the porous lithic portions, and lining or partly filling the caverns. There seem to be 2 species of sponges present, one light grey to beige, more extensive and more thoroughly permeating the lithic parts, the other brown, lining the cavernosities and extending into the intervening rock through peculiar sharp interstices reminiscent of *Cliona* borings. The former may be primarily endolithic and instrumental in lithification, but this remains to be investigated by appropriate microscopic technique.

2. Summary and conclusions

The occurrences of identified sponge species at all stations with bioherms are compiled in Table 1, those of gorgonians in Table 2 and those of corals in Table 3.

Table 1: *Occurrence of identified sponge species at stations 3-11.*

Sponges	Stations								
	3	4	5	6	7	8	9	10	11
A *Spheciospongia vesparium* habit *a*	- +	- +	+ +	+ +	+ -	+ +	- +	+ -	+ +
Spheciospongia vesparium habit *b*	+ +	- +	+ +	+ +	+ +	+ +	- +	+ -	- +
Anthosigmella varians forma *varians*	- -	- -	+ -	- -	+ -	- -	- -	+ -	+ -
B **Hyrtios proteus*	-	-	-	x	x	x	x	x	-
Haliclona molitba	x	-	x	-	x	x	-	-	-
*Tethya crypta	-	-	-	-	x	x	-	-	-
*Siphonodictyon siphonum	-	-	x	-	-	-	-	-	-
Tedania ignis	-	-	-	-	-	-	-	x	-
C *Ircinia felix*	x	x	x	x	x	x	x	x	x
I. strobilina	x	x	x	x	x	x	x	x	x
Aplysina fistularis[1]	x	x	x	x	x	x	x	x	x
Dysidea etheria	x	x	x	x	x	x	x	x	x
Spongia spp.[2]	x	x	x	-	x	x	x	x	-
Ulosa ruetzleri	x	-	x	x	-	x	x	x	x
Chondrilla nucula[3]	-	-	x	x	-	x	x	x	x
Aiolochroia crassa	-	x	-	-	-	–	x	x	x
Pandaros acanthifolium	x	-	-	x	-	-	x	-	-
*Anthosigmella varians forma *incrustans*	-	-	-	x	-	-	-	x	x
Hyattella intestinalis[4]	-	-	-	-	x	-	-	-	x
Hyrtios cavernosus[5]	-	-	-	-	-	-	x	-	x
Aplysina cauliformis	x	-	-	-	-	x	-	-	-
Spinosella vaginalis forma *vaginalis*	-	-	-	-	x	-	x	-	-
S. vaginalis forma *armigera*	-	x	-	-	x	-	-	-	-
Lissodendoryx sigmata	x	-	-	-	-	-	x	-	-
Spirastrella coccinea	-	-	-	-	-	-	-	x	x
Thorecta horridus[6]	-	-	-	-	-	-	x	-	-
Verongula "ardis" (rigida)[7]	-	-	-	-	-	-	-	x	-
Haliclona compressa	-	-	-	-	x	-	-	-	-
*Haliclona podatypa[8]	-	-	-	-	x	-	-	-	-
Tedania ignis	-	-	x	-	-	-	-	-	-
Microciona spinosa ?	-	-	x	-	-	-	-	-	-
Higginsia strigilata	-	-	-	-	-	x	-	-	-

[1]) Four forms of this species were observed: 1. forma *insularis* DUCHASSAING & MICHELOTTI, name reintroduced by VAN SOEST (in press) = formae *fistularis* and *aggregata* sensu WIEDENMAYER (1974, 1977a); 2. forma *fulva;* 3. stoloniferous form; 4. appendiculate form.

[2]) *Spongia pertusa* HYATT: VAN SOEST (in press) = *S. tubulifera:* WIEDENMAYER (1977a). Stations 3, 4, 10. *Spongia obscura.* Station 5. *Spongia tubulifera* sensu VAN SOEST (in press), non WIEDENMAYER (1977a). Stations 9, 10. Species of *Spongia* at stations 7 and 8 were not identified.

[3]) Light brown, encrusting.

[4]) Sensu VAN SOEST (in press) = *Spongia cerebriformis:* WIEDENMAYER (1977a).

[5]) = *caracasensis* (CARTER): VAN SOEST (in press).

[6]) The generic attribution to *Thorecta* in WIEDENMAYER (1977a) is inappropriate according to P.R. Bergquist (personal communication). Colleagues G.J. Hechtel, K. Rützler and R.W.M. van Soest have expressed their doubts to me that this species belongs to the Keratosa.

[7]) *Verongula rigida* (DUCHASSAING & MICHELOTTI), name reintroduced by VAN SOEST (in press).

[8]) According to Dr. van Soest (personal communication), the Bahamian material attributed by me to this species is not conspecific with de Laubenfels' type specimen in the US National Museum.

Table 2: *Occurrence of Gorgonacea at stations 3-11 (same order as sponges, group C).*

	3	4	5	6	7	8	9	10	11
Plexaurids	x	x	x	x	x	x	x	x	x
Pseudopterogorgia spp.	x	x	x	x	x	x	x	x	x
Briareum asbestinum	x	x	x	–	x	x	x	x	x
Pterogorgia anceps	x	x	x	x	x	x	–	–	x
Gorgonia ventalina	–	–	–	–	–	–	–	x	x

Table 3: *Occurrence of corals at stations 3-11 (same order as above).*

	3	4	5	6	7	8	9	10	11
Porites astreoides	–	x	–	x	x	x	x	x	x
P. porites furcata	–	x	–	x	x	x	x	x	x
Siderastrea radians	–	x	–	x	x	–	x	x	x
Porites porites clavaria	–	–	–	–	x	x	x	x	x
Dichocoenia stokesi	–	–	–	x	–	–	x	x	x
Millepora alcicornis	–	–	–	x	–	–	x	x	x
Manicina areolata	–	–	x	x	–	–	–	–	–
Siderastrea siderea	–	–	–	–	–	–	x	–	–
Diploria strigosa	–	–	–	–	–	–	x	–	–
Meandrina meandrites	–	–	–	–	–	–	–	x	–

The sponges of group C in Table 1 are adventitious to the bioherms, i.e. secondarily epilithic (in contrast to group A) and generally ubiquitous to hard substrates. The degree of ecological tolerance (recurrence) shows traits consistent with distribution at Bimini (WIEDENMAYER 1977a, Tables 42, 45), in the 3 most eurytopic forms. The 6 most eurytopic sponges are in accord with the lagoonal habitat at Bimini (Table 42, especially *Dysidea etheria*), but the others are more reminiscent of the outer fauna (Table 45). The bioherms belong to a special habitat, while the distributional data in Tables 42 and 45 are ecologically much more complex. However, *Ulosa ruetzleri* (relatively rare at Bimini) and *Chondrilla nucula* (light greyish brown, encrusting, not quite comparable to habit *a* or *b* at Bimini) seem to be much more characteristic of the eastern parts of the Great Bahama Bank.

Explanation of Table 1

A = Species burrowing and binding loose sediment, associated with lithification. Left sides of columns: specimens implanted in loose sediment and associated with beginning lithification (small, immature buried plates); right sides of columns: specimens associates with mature plates and mounds.

B = Species found on soft sediment bottom. Those marked by an asterisk tend to bind sediment, but lithifications was not observed.

C = Epilithic species on mature bioherms, in the order of degree of recurrence over all stations (presumed ecological tolerance; cf. WIEDENMAYER (1977a, Table 42, p. 208; Table 45, p. 220); in both, the order is inversed with respect to the present table). The species marked with an asterisk also have endolithic portions: *Anthosigmella varians* forma *incrustans* is known to have burrowing properties on hard substrates (hence is secondarily endolithic); *Haliclona podatypa* is assumed to be primarily endolithic, like *Spheciospongia vesparium* and *Anthosigmella varians* forma *varians*, but initial stages of internal cementation, though likely from the distribution of serpulids, cannot be proven.

The sponge *Spheciospongia vesparium* (Table 1, group A) is present at all stations in at least 2 of the 4 forms generally encountered (i.e. habit *a* or *b*, implanted in loose sediment or epilithic [partly endolithic] on bioherms). This confirms the important role of this sponge in formation of the bioherms. Other, yet unidentified sponge species are often found to be intimately associated with *Spheciospongia vesparium* habit *b*. Being almost always confined to sediment interstices or wholly endolithic and often light grey to beige, they are particularly inconspicuous and apt to be overlooked. Microscopic investigations and field observations might show that this association is the rule and important in the formation of bioherms.

The intake of adjacent sediment by Spheciospongias into their choanosome seems to be complex. On preliminary field evidence this intake, though seemingly centripetal in early stages, is essentially vertical in 2 different mechanisms in relation to the sediment/water interface, as explained below.
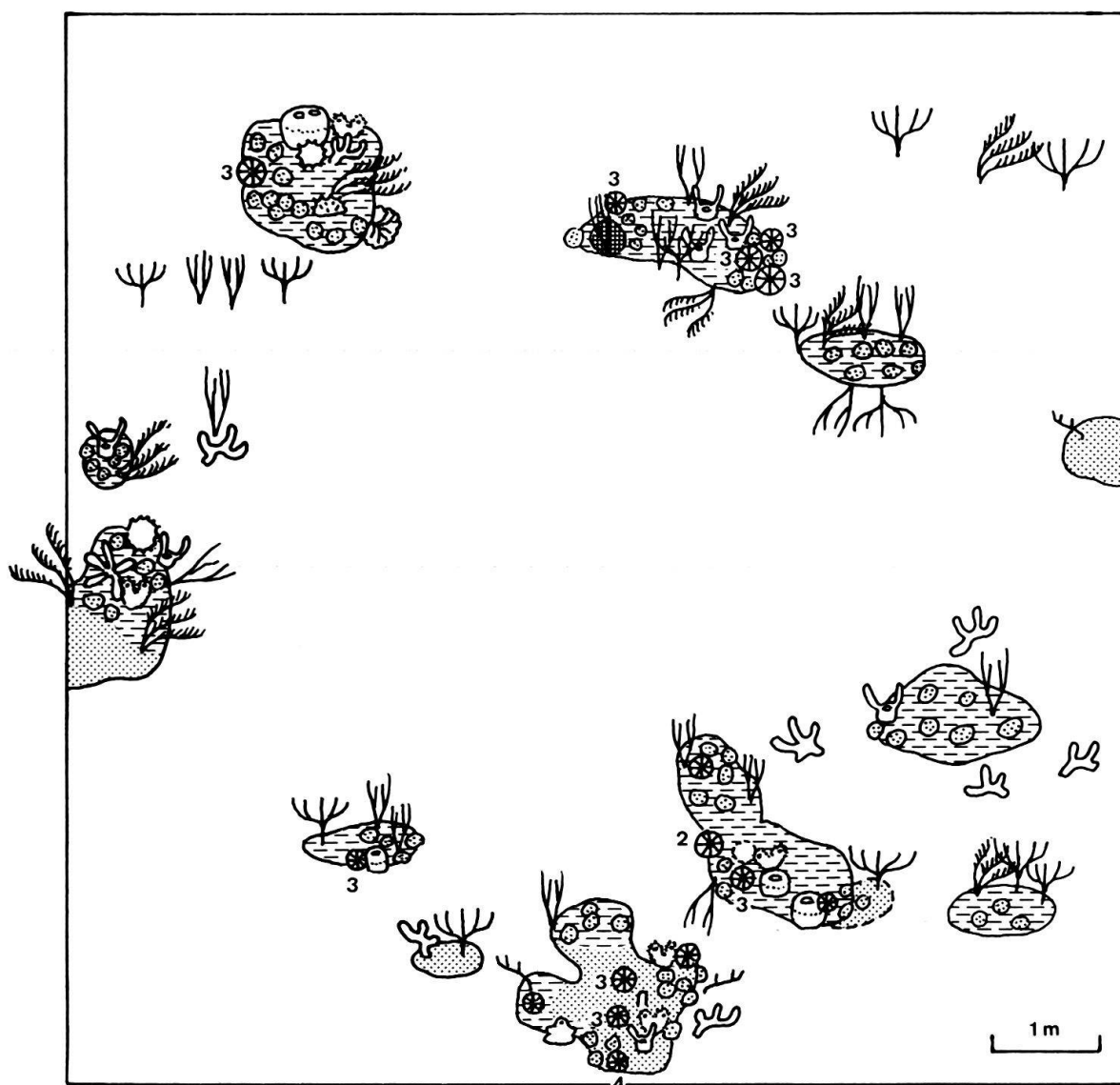

Fig. 34. 100 m²-square No. 8, station 11. See page 714 for legend.

One type of intake is through the base, i.e. by portions of the sponge buried in sediment. It seems to be associated with soft-bottom burrowing, i.e. with growth under the sediment surface. Such growth seems to be directed chiefly downward in massive specimens and is probably rhythmic, as suggested by the dissected specimen at station 11 (Fig. 31). In habit *b* of this species, growth and lithification of buried portions seem to be less predictable from the free portions. The commonly vertical free tubes containing the atria and oscula may continue into the sediment vertically, or branching in several directions. Stolons below the sediment surface, connecting neighbouring individual atria, seem to be frequent, sometimes in 2 stories. Lateral
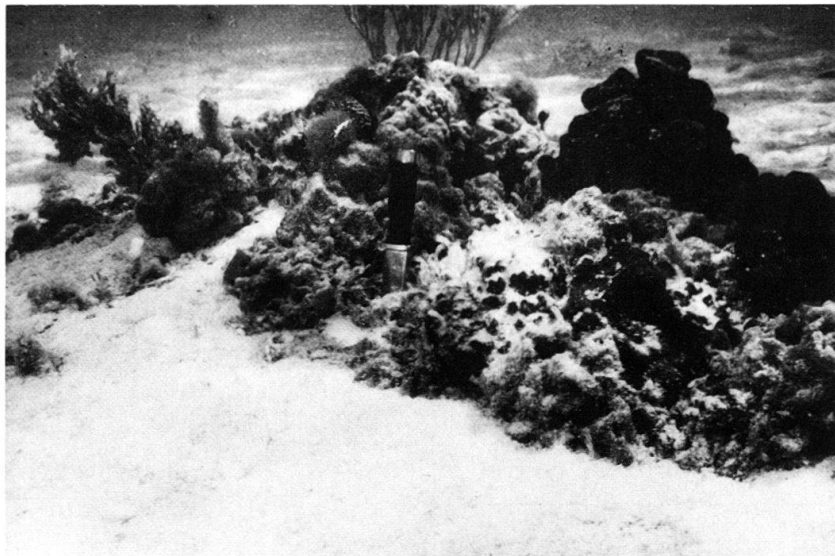

Fig. 35. Station 11. Prominent bioherm with prolific and diverse community. Diver's knife for scale. Note barren sediment sloping towards the left foreground.
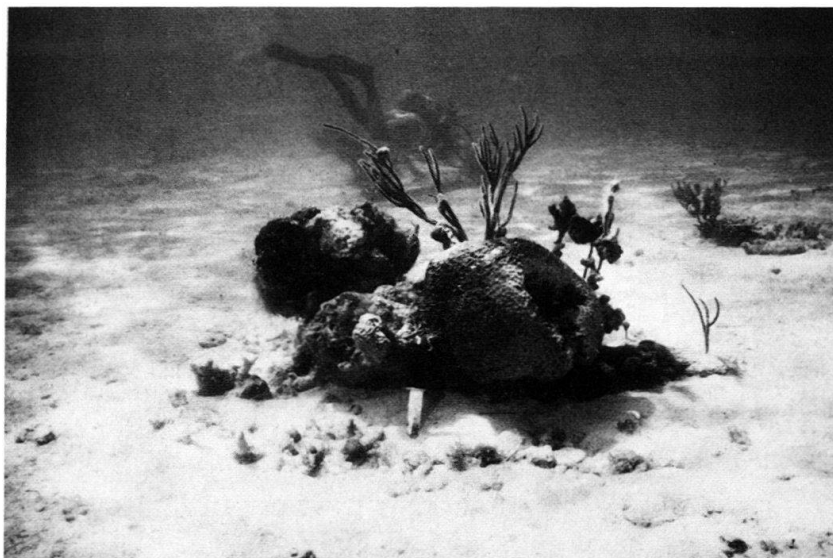

Fig. 36. Station 11. Bioherms of the same type, with a large *Ircinia strobilina* in the foreground. Diver's knife for scale. Note the fringe of rubble and *Porites porites.*

expansion of the sponge body also occurs, both below and above the sediment surface, most commonly at the level of the surrounding sediment surface, producing continuous or lacunose cushions.

Some specimens of habit *b* of this species showed crowded, erect, sediment-packed buried tubes with a tendency to coalesce along their base. Frequently, buried portions of habit *b*, in which sediment accumulation and cementation has not yet progressed to formation of lithic plates, but has accrued well beyond the outer limits of this sponge's choanosome, are surrounded by choanosome of other species yet to be identified. They are presumably adapted to interstitial life in the sediment, but probably need initial attachment to portions of the young host sponge with which they are always in direct contact in this phase. (They may pass into endolithic existence upon thorough cementation in mature plates, and may thereby loose contact with the original host sponge.) By agglutinating the intervening sediment between buried atrial ducts and in the lacunae of buried choanosome of the host sponge, these interstitial sponges seem to play a key role in formation of the lithic plates. A particularly good exemple is that in Figures 29, 30. The sediment-packed choanosome of these epibiotic sponges, which is totally buried, is thoroughly cavernous as a rule, when extensively developed. Very similar structures were observed in deeper parts of lithified plates, with or without choanosome.

Bottoms of such buried sponge portions are commonly encrusted by abundant serpulids and sediment-agglutinated worm tubes of various sizes. There is also invariably a rusty brown diaphanous film of unknown nature. The aspect is identical to that of roofs of thin cavernous layers in cemented plates, of such plates' bottoms, and of the sponge/rock interface of the immature bioherm of Figures 26-30.

It should be added that such buried sponge portions, without or with weak cementation, were rarely found to rest on loose sediment, but that most were flimsily attached to flat surfaces of buried lithic structures. From the jagged bottoms of such structures (Fig. 27, 29) and from their fabric (with or without endolithic sponge portions) one can conclude that they represent more mature, earlier stages of sponge-infested sediment, once closer to the surface.

The other fundamental type of sediment intake by *Spheciospongia vesparium* is through its top. Portions of these sponges above the surrounding sediment surface are commonly covered by felted green algae, soft brown algae and a veneer of trapped sediment, except for vertical or overhanging sides in large specimens. Among the felted algae the prolific tunicate *Perophora viridis* is frequently present. Its branching and anastomosing stolons probably help to bind sediment.

Encrusting epizoans, chiefly *Briareum* and other sponges like *Ulosa ruetzleri*, are not infrequent in this stage and might promote lithification. In a few cases, even small corals were found attached to such sponge surfaces.

Flat portions close to the level of the surrounding sediment, i.e. the typical cushion-shaped parts in habit *b*, usually have the thickest sediment veneer of this sort. In some cases the contrast is apparent between sediment-encrusted basal parts and actively growing apical parts of chimneys, which are mostly free of sediment. Here, at the transition between sediment-encrusted and free sponge surface, incorporation of sediment grains can often be observed. The sediment encrusting the tops in veneers is commonly somewhat finer than that adhering to and incorpo-

rated into the bottoms, where whole mollusk shells and their fragments are frequent. There are definite indications of stratification parallel to the surface, i.e. of rhythmic growth. Patterns of growth, however, remain to be thoroughly investigated, chiefly by cross-sectioning.

Relatively low, terraced specimens of habit *a*, like those at station 6, showed some stratified sediment in the upper choanosome upon sectioning, in relation with the terraces at the surface, attesting to lateral growth of the steep, sediment-free portions over the terraces. In taller massive specimens, however, intake of sediment does not seem to occur above surrounding sediment level; but whether this is a rule must await sectioning of further massive specimens.

While thin veneers of relatively fine sediment on higher portions (especially with habit *a*) reflect protracted sedimentation from frequently stirred up fines in suspension, the thicker sediment covers on deeper parts (cushions of habit *b*) are probably largely due to episodic transport along the bottom of coarser, more voluminous fractions of surrounding sediment. The extensive buried portions of some mature lithic plates, as at station 9, are indicative of sediment volumes involved in such transports.

The variability in shape of individuals of *Spheciospongia vesparium* habit *b* and of their aggregates, and in their relation to the sediment/water interface and to epibiotic organisms, makes it difficult to assess the influence of rate and grading of sedimentation on growth patterns of the sponge. Habits *a* and *b*, as provisionally distinguished, though intergrading, are more likely ontogenetic stages than ecophenotypes. This is corroborated by the high degree of recurrence of both habits next to each other at all stations (which, in the case of ecophenotypes, would have to be explained with sudden, even if subtle, mosaic-like differences in sedimentary environment and hydrodynamics). More indicative of ontogenetic segregation of the 2 habits is the lack of significant departures in other Bahamian environments (e.g. shallow and sheltered parts of the Bimini Lagoon). As long as the life history of the species is not well-known (including habit *c* in WIEDENMAYER 1977a, and the relation to the boring species *S. othella*, see RÜTZLER 1974), discussions of growth patterns is very difficult.

In partial contradiction to the doubts expressed above as to ecophenotypic segregation, the hypothesis might be advanced that some clusters of habit *b* are prevented from transition to habit *a* because of a slightly depressed location among the irregular overall relief created by *Callianassa* and other sediment dwellers, perhaps also in slight differences of vegetation and hydrodynamics. They would thus be prone to repeated burial and thereby to become nuclei of bioherm formation. Specimens of habit *a* would represent ecophenotypes of a more exposed, perhaps more turbulent micro environment, either on loose sediment (where an ecological differentiation could be inferred already for larvae settling at different levels among the *Callianassa* mounds) or on bioherms: here endolithic/epilithic specimens of habit *b* could pass into habit *a* during periods of higher relief and longer intervals between reburial; recolonization by larvae, however, is equally likely).

In comparing various small specimens of *S. vesparium* habit *b* and *Anthosigmella varians* forma *varians*, it is likely that cementation begins in the buried portions, particularly around the base. Supporting this view is the circumstance that sediment

intake by the free tops is much less in evidence in massive Anthosigmellas. The frequency of buried, but epilithic sponges or their portions occurring on flat surfaces of buried lithic structures, with a sharp interface between sediment-packed sponge and rock, is a further argument in favour of this interpretation. Whether lithification begins in the choanosome of these sponges or along their underside, perhaps aided by serpulids and other encrusting organisms, or by interstitial, sediment-agglutinating epizoic sponges, is open to question.

Many cemented plates (Fig. 26-30) give the impression that they grew exclusively under constant sediment cover. Others, like those at station 3 and at station 7, (Fig. 9) which had considerable relief in situ, are likely to have grown at least partly above the surrounding sediment surface: The endolithic caverns of *S. vesparium* habit *b*, sometimes of considerable horizontal extent, are always near the upper surface, with a poorly cemented cover no thicker than 2-3 cm. From these peripheral endolithic caverns, terete atrial ducts lead vertically or obliquely into deeper lithic portions. It could be surmised that the young sponge spreads laterally along the sediment surface forming cushions with upper surfaces becoming covered by algae and finer sediment; the surfaces gained some relief while cementation started early along the bottoms. Upon successive burial by drifting coarser sediment, it will adapt by building up its oscular chimneys. After a certain accumulation of sediment, it might grow laterally again, and the cycle might repeat itself. Peripheral endolithic atria with lateral extent would gradually collapse with progressive lithification and eventually form thin porous layers, perhaps still containing sponge choanosome. The vague stratification observed in fractured and cut bioherms, in association with serpulids and spreading sponge choanosome, might be explained with such cyclic accretion.

Increase of relief in later stages might be explained by lateral expansion of the plates (by coalescence of neighbouring ones?), colonization by prolific stiff green algae, gorgonians, corals and massive sponges: such communities would tend to promote turbulence and thus sediment removal around the edges of the plates. Corals and encrusting coralline algae would tend to create differences in relief within the plates. Where these differences and the marginal relief remain moderate, depressed areas on the plates could become covered again by exceptional volumes of drifting sediment (after storms). Endolithic Spheciospongias, apparently not uncommon even in mature bioherms, could produce vertical bioherm accretion by pushing their oscular chimneys through the new sediment cover essentially with the same cyclic mechanism as before. This interpretation might explain the comparative rarity of relief above 30 cm and the thickness of 35-40 cm of the mature plate at station 9, most of which under surrounding sediment level.

Rocky pinnacles are likely to be formed in different ways. One plausible mechanism is vertical accretion by corals. Another one, though rare, is that suggested by the pinnacle in Figure 11: *Haliclona podatypa* may be credited with the habit of constructing its own lithic support by centripetal transport of sediment grains, initially along its base, later, with increasing relief, perhaps chiefly by trapping from suspension by means of the covering algal felt and epizoans. Alternatively, periodic overgrowth of its coat of corallines and serpulids might be considered as a more likely lithifying mechanism in this case.

Samples and photographs are not sufficient at present to overcome the general difficulties in explaining patterns of lithification and accretion of plates and in assessing degrees of consistency in such mechanisms. Considerably more field work will be needed for careful observations and sampling of initial stages, immature plates and large, mature plates. In particular, the latter will need sectioning to their base and search for primarily endolithic sponges.

III. Further investigations needed

Because the original objectives of the research project have not yet been met in their entirety due to the shortcomings in field work to date, considerably more study is needed to understand the Bahamian sponge bioherms. Most desirable are investigations on quantitative aspects of distribution in the northeastern portion of the Great Bahama Bank, coupled with observations and sampling of the parameters controlling distribution (hydrodynamics, depth, suspended and bottom sediment, associated benthic communities). Equally important are in-depth probes of various bioherms by dissecting and core drilling.

Eventually, other potential areas should be investigated for sponge bioherms. We suspect that they might also occur in the grapestone facies to the west of the southern end of Andros Island. Furthermore, much of the lithification of modern carbonate sediments in the area of Yellow Bank (to the southeast of New Providence), which was described by TAFT et al. (1968), may be caused by sponges.

REFERENCES

BERNOULLI, D. (1964): *Zur Geologie des Monte Generoso (Lombardische Alpen).* – Beitr. geol. Karte Schweiz [N.F.] *118.*

BERNOULLI, D., & JENKYNS, H. C. (1974): *Alpine, Mediterranean, and Central Atlantic Mesozoic facies in relation to the early evolution of the Tethys.* In: DOTT, R. H., Jr., & SHAVER, R. H. (Ed.): *Modern and ancient geosynclinal sedimentation.* – Spec. Publ. Soc. econ. Paleont. Mineral. *19,* 129–160.

CAMERON, A. M., CAMPBELL, B. M., CRIBB, A. B., ENDEAN, R., JELL, J. S., JONES, O. A., MATHER, P., & TALBOT, F. H. (Ed.) (1974): *Proceedings of the Second International Symposium on Coral Reefs* (2 vol.). – The Great Barrier Reef Committee, Brisbane.

CUFFEY, R.J., FONDA, S.S., KOSICH, D.F., GEBELEIN, C.D., BLIEFNICK, D.M., & SOROKA, L.G. (1977): *Modern tidal-channel bryozoan reefs at Joulters Cays (Bahamas)*. In: TAYLOR, D.L. (Ed.): *Proceedings, Third International Coral Reef Symposium* (vol. 2, p. 339-345). - Rosenstiel School of Marine and Atmospheric Sci., Univ. Miami.

FINKS, R.M. (1960): *Late Paleozoic sponge faunas of the Texas region. The siliceous sponges.* - Bull. amer. Mus. nat. Hist. *120/*1.

GEBELEIN, C.D. (1974): *Guidebook for modern Bahamian platform environments; field trip, annual meeting.* - Geol. Soc. Amer., Boulder, Colorado.

— (1977): *Guidebook for modern Bahamian platform environments* (2nd ed.) - Inst. Marine Sci., Pompano Beach, Florida, and Univ. California, Santa Barbara.

JENKYNS, H.C. (1971): *Speculations on the genesis of crinoidal limestones in the Tethyan Jurassic.* - Geol. Rdsch. *60*, 471-488.

JONES, O.A., & ENDEAN, R. (Ed.) (1973-1977): *Biology and geology of coral reefs* (4 vol.). - Academic Press, New York, London.

KÄLIN, O., & TRÜMPY, D.M. (1977): *Sedimentation und Paläotektonik in den westlichen Südalpen: Zur triasisch-jurassischen Geschichte des Monte Nudo-Beckens.* - Eclogae geol. Helv. *70/*2, 295-350.

NEWELL, N.D. (1971): *An outline history of tropical organic reefs.* - Amer. Mus. Novitates *2465.*

NEWELL, N.D., RIGBY, J.K., DRIGGS, A., BOYD, D.W., & STEHLI, F.G. (1976): *Permian reef complex, Tunisia.* - Brigham Young Univ. Geol. Stud. *23/*1, 75-112.

PURDY, E.G., & IMBRIE, J. (1964): *Carbonate Sediments, Great Bahama Bank. Guidebook for field trip No. 2, Geological Society of America Convention, November, 1964, Miami, Florida.* - Geol. Soc. Amer., Boulder, Colorado.

RIGBY, J.K. (1971): *Sponges and reef and related facies through time.* - In: Proc. North amer. paleont. Conv. Chicago, Pt. J, 1374-1388.

RÜTZLER, K. (1974): *The burrowing sponges of Bermuda.* - Smithson. Contr. Zool. *165.*

SOEST, R.W.M. VAN (in press): *Marine sponges from Curaçao and other Caribbean localities. Part I. Keratosa.* - Stud. Fauna Curaçao.

TAFT, H.W., ARRINGTON, F., HAIMOVITZ, A., MacDONALD, C., & WOOLHEATER, C. (1968): *Lithification of modern marine carbonate sediments at Yellow Bank, Bahamas.* - Bull. marine Sci. *18/*4, 762-828.

TAYLOR, D.L. (Ed. 1977): *Proceedings, Third International Coral Reef Symposium* (2 vol.). - Rosenstiel School of Marine and Atmospheric Sci., Univ. Miami.

TERMIER, H., & TERMIER, G. (1975): *Rôle des éponges hypercalcifiées en paléoécologie et en paléobiogéographie.* - Bull. Soc. géol. France (7), *17/*5, 803-819.

TERMIER, H., TERMIER, G., & VACHARD, D. (1977): *Monographie paléontologique des affleurements permiens du Djebel Tebaga (Sud Tunisien).* - Palaeontographica (A) *156/*1-3, 1-109.

WIEDENMAYER, F. (1963): *Obere Trias bis mittlerer Lias zwischen Saltrio und Tremona.* - Eclogae geol. Helv. *56/*2, 529-640.

— (1967): *Broccatello d'Arzo.* In: PRUVOST, P., & RUTSCH, R.F. (Ed.): *Léxique stratigraphique international* (vol. I/7c, p. 66-69). - Centre National de la Recherche Scientifique, Paris.

— (1974): *Recent marine shallow-water sponges of the West Indies and the problem of speciation.* - Verh. natf. Ges. Basel *84/*1, 361-375.

— (1977a): *Shallow-water sponges of the western Bahamas.* - Birkhäuser, Basel (Experientia Supplementa *28*).

— (1977b): *The Nepheliospongiidae Clarke 1900 (Demospongea, Upper Devonian to Recent), an ultraconservative, chiefly shallow-marine sponge family.* - Eclogae geol. Helv. *70/*3, 885-918.