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CAVITY-DWELLING SPONGES IN A SOUTHERN CARIBBEAN CORAL REEF AND THEIR PALEONTOLOGICAL IMPLICATIONS

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ABSTRACT

The cryptobiontic (cavity-dwelling) sponges from 32 growth framework reef cavities were collected over the depth range 12 m to 43 m along the leeward side of Bonaire, Netherlands Antilles. The resulting sample of 1,245 specimens comprised 92 species, which showed a peak in species diversity at about 18 m depth. Of the 79 species that show significant restriction of their depth ranges in this study, most are known elsewhere to have different or greater depth ranges. However, 17 cryptobiontic sponge species in Bonaire appear to be depth restricted. This suggests that there may be a depth zonation of some cryptobiontic sponges, and opens up the possibility that with more study, cryptobiontic sponges may be of some use in ancient reefs as a paleoenvironmental tool. The presence of 10 species of endolithic sponge over a broad depth range shows that sponge bioerosion in the cavities is widespread, although it does not appear to be intensive. Based upon the amount of preservable skeletal material produced by sponges in these reef cavities, it appears that as much as 97% of the cryptobiontic sponge sample would be lost during fossilization, leading to the conclusion that the fossil record of cryptobiontic sponges may be a very poor representation of their actual importance in fossil reef cavity systems.

Cavities are a prominent feature of modern reefs, and include the spaces and surfaces under rubble, the undersurfaces of skeletal organisms such as corals, the interiors of vacated borings, the shaded undersides of overhangs, and framework cavities. Together these cavities may make up an important part of the volume of a reef, exceeding 50% in some cases, and provide surface area for colonization by organisms that may be equal to, or greater than, the area of the (exposed) reef surface (Garrett et al., 1971; Logan et al., 1984).

Among the groups that have been studied from cryptic habitats (cryptobionts) are: molluscs (bivalves and gastropods: Kobluk and Lysenko, 1985), brachiopods (Logan, 1975; 1977; Noble et al., 1976; Saunders and Thayer, 1987), corals (Wells, 1972; Zibrowius, 1976; Dinesen, 1982; 1983; Kobluk and Lysenko, 1987a; 1987b), bryozoans (Cuffey, 1972; 1978; Ryland, 1974; Jackson, 1979; Kobluk et al., 1988), various worm groups (Peyrot-Clausade, 1974; Videtich and Macintyre, 1979; Macintyre et al., 1982), and sponges (discussed below). Others that have received less attention, but that are known to be cryptobiontic are protozoans, bacteria, foraminifers, and hydrozoans (Rooney, 1970; Kobluk, 1981a; Palumbi and Jackson, 1982).

Sponges, one of the most important of modern reef-dwelling groups, are important contributors to the reef biomass. For example, Hartman (1977) estimates, using data from Reiswig (1973), that in some situations, such as on the north coast of Jamaica, sponge biomass may actually be greater than that of scleractinian corals and octocorals. In some reefs, particularly at depth, they comprise the main reef-building group (Lang, 1974; Lang et al., 1975).

Sponges have long been known as inhabitants of all types of cavities (Hartman, 1969; 1977; Pouliquen, 1970; Vacelet and Vasseur, 1977), and are found to have been cryptobiontic (cavity-dwellers) in ancient reefs and other hard substrates as well (Palmer and Fürsich, 1974; 1981; Kobluk, 1981b; Schäfer, 1984). However,

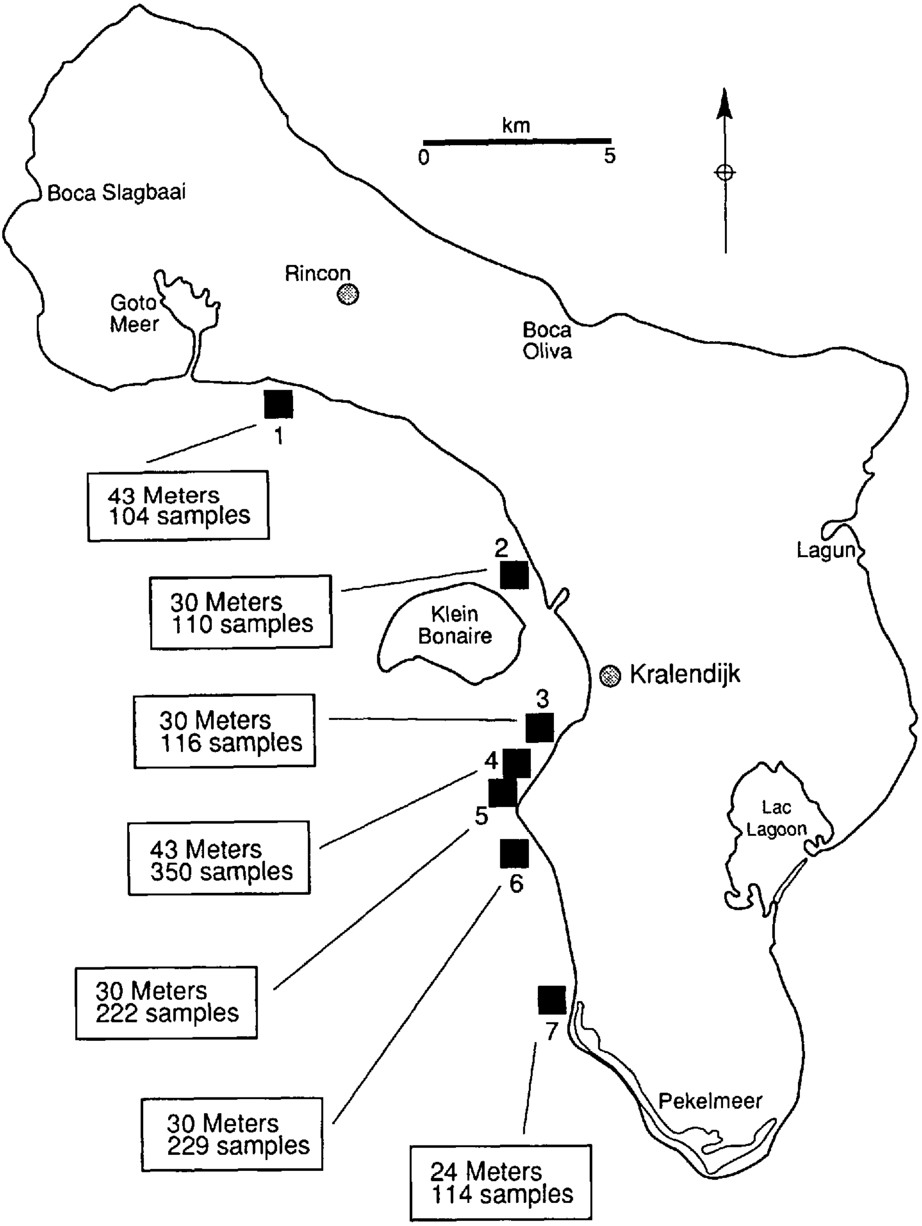

Figure 1. Map of Bonaire, Netherlands Antilles, showing the locations of the seven sites where transects were placed to collect the cavity-dwelling sponge specimens for this study. The maximum depth of each of the transects and the total number of sponge specimens collected along the transects are shown in the boxes on the left.

there are no studies of cryptobiontic sponges from Caribbean reef cavities where large numbers of specimens have been identified systematically over a substantial depth range. It is the purpose of this study to describe for the first time, a large collection of cryptobiontic sponges made systematically from growth framework cavities in a southern Caribbean coral reef over a broad depth range, and to attempt to relate their distribution to water depth.

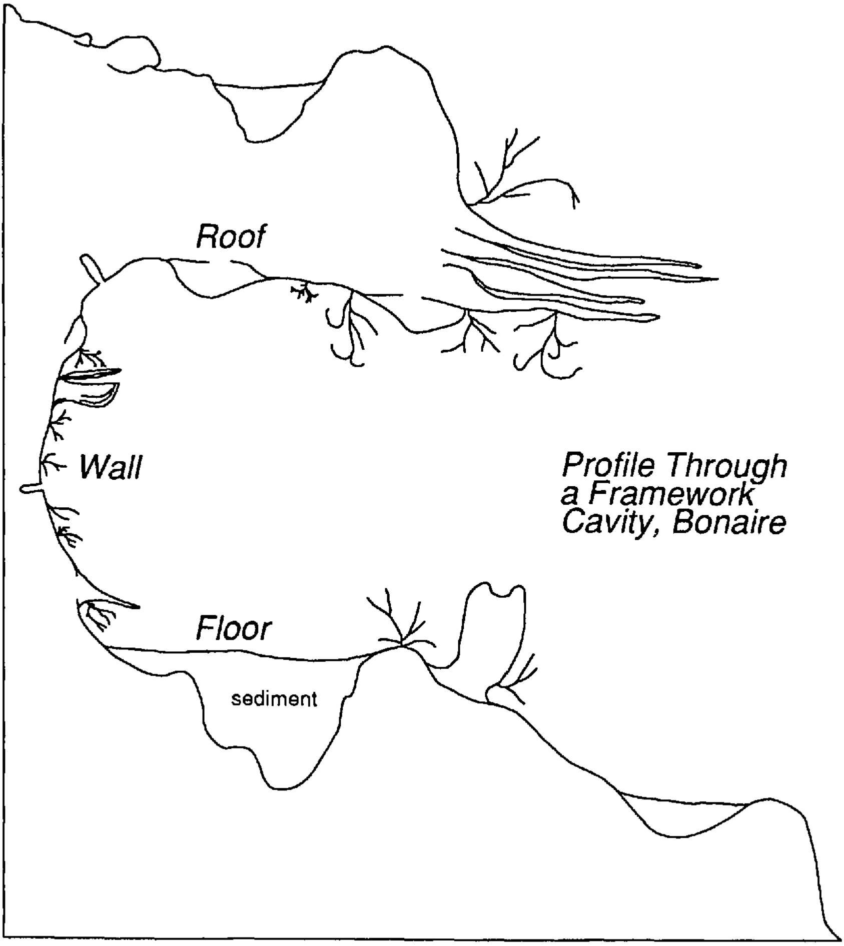

Figure 2. Profile through a generalized growth framework cavity as seen on the leeward reef of Bonaire. These cavities reach a maximum of about 1 m in depth, and 1 m in height.

Location, Material and Methods

A total of 1,245 sponge specimens, representing 92 species (Table 1) were collected from 32 reef growth framework cavities in May and June 1984, at seven sites along the leeward side of Bonaire (Fig. 1). The reefs of Bonaire are described in Scatterday (1974), Kobluk and Lysenko (1984), and van Duyl (1985). At each site specimens were collected at depths of 12 m, 18 m, 24 m, and 43 m when growth framework cavities (Fig. 2) could be found. In some areas along the leeward side of Bonaire the coral reef does not extend to 43 m depth, so that samples could not be gathered from that depth everywhere; in other areas accessible growth framework cavities could not be found even at 30 m depth. Taken together, however, the collection represents all depths, although the sample size at 43 m depth is small in comparison to shallower samples, due to the difficulties in repetitive diving to those depths and the more limited number of sample sites available.

Figure 1 shows the maximum depth sampled at each site, and the total number of samples retrieved at each of the seven sites.

In each of the 32 cavities investigated, a sample from every sponge visible to SCUBA divers was collected and bagged in sea water; the cavity interior walls and roof also were sampled by removing, and bringing to the surface, as much of the rock substrate as possible. At the surface, sponges not seen underwater (e.g., in small crevices not visible to the divers), and those found to be endolithic within the rock, were sampled. The specimens were preserved in alcohol.

The diversity indices presented in the text and in Figure 5 were calculated using the following: Species Richness is just the number of species; Margalef Diversity $(S - 1)/[\log(N)]$ where $S =$ the

Table 1. Taxonomic listing of the cavity-dwelling (cryptobiontic) sponges recovered from reef framework cavities in Bonaire

- Class Demospongiae
  - Order Homosclerophorida
  - Family Plakinidae
    - Plakortis angulospiculatus (Carter 1882)
  - Order Astrophorida
  - Family Pachastrellidae
    - Dercitus sp.
  - Family Geodiidae
    - Erylus formosus Sollas 1887
  - Order Desmophorida
  - Family Desmanthidae
    - Desmanthus incrustans (Topsent 1889)
  - Family Theonellidae
    - Discodermia dissoluta Schmidt 1880
  - Order Chondrosida
  - Family Chondrosiidae
    - Chondrilla nucula Schmidt 1870
  - Order Hadromerida
  - Family Clionidae
    - Cliona amplicavata Rützler 1974
    - Cliona schmidti (Carter 1871)
    - Cilona janitrix Pang 1971
    - Cliona vermifera Hancock 1867
    - Cliona delitrix Pang 1971
    - Anthosigmella varians (Duch. and Mich. 1864)
    - Spirastrella coccinea (Duch. and Mich. 1864)
    - Spirastrella sp.
    - Diplastrella megastellata Hechtel 1965
  - Family Placospongiidae
    - Placospongia melobesioides Gray 1867
  - Family Suberitidae
    - Pseudosuberites sp.
    - Terpios cf. fugas Duch. and Mich. 1864
    - Terpios sp.
  - Order Incerta 1
  - Family Tethyidae
    - Aaptos aaptos (Schmidt 1864)
  - Order Incerta 2
  - Family Jaspidae
    - Jaspis sp.
  - Order Halichondrida
  - Family ?Halichondriidae
    - Halichondria? sp.
    - Didiscus oxeata Hechtel 1983
    - Myrmekioderma reiswigi (Diaz, Alvarez and Van Soest 1987)
    - Myrmekioderma styx De Laubenfels 1953
    - Topsentia roquensis Diaz, Alvarez and Van Soest 1987
  - Family Hymeniacidonidae
    - Dictyonella ruetzleri (Wiedenmayer 1977)
    - Dictyonella sp.
    - Hymeniacidon sp.
  - Order Axinellida
  - Family Axinellidae/Bubaridae
    - Hymerhabdia sp.
    - Ptilocaulis marquezi (Duch. and Mich. 1864)
  - Dragmaxia ? sp.
  - Family Raspailiidae
    - Ectyoplasia ferox (Duch. and Mich. 1864)
    - Eurypon laughlini Diaz, Alvarez and Van Soest 1987
    - Tricheurypon viridis (Topsent 1889)
  - Order Agelasida
  - Family Agelasidae
    - Agelas clathrodes (Schmidt 1870)
    - Agelas conifera (Schmidt 1870)
    - Agelas sceptrum (Lamarck 1814)
    - Agelas dispar Duch. & Mich. 1864
    - Agelas sp.
  - Order Poecilosclerida
  - Family Microcionidae
    - Clathria affinis (Topsent 1889)
    - Clathria bulbotoxa Van Soest 1984
    - Clathria echinata (Alcolado 1984)
    - Clathria spinosa (Wilson 1902)
    - Rhaphidophlus venosus (Alcolado 1984)
    - Rhaphidophlus cf. minutus Van Soest 1984
    - Pandaros acanthifolium Duch. and Mich. 1864
  - Family Hymesdesmiidae
    - Hymesdesmia agariciicola Van Soest 1984
    - Hymedesmia palmatichelifera Van Soest 1984
    - Phorbas amaranthus Duch. and Mich. 1864
  - Family Myxillidae
    - Acarnus souriei (Levi 1952)
    - Damiria testis Topsent 1925
    - Hemitedania baki Van Soest 1984
  - Family Desmacididae
    - Iotrochota birotulata (Higgin 1877)
    - Holopsammia helwigi (De Laubenfels 1936)
    - Monanchora arbuscula (Duch. and Mich. 1864)
  - Family Hamacanthidae
    - Neofibularia nolitangere (Duch. and Mich. 1864)
    - Biemna sp.
    - Merlia normani Kirkpatrick 1903
  - Order Haplosclerida s.l. (including Petrosida)
  - Family Chalinidae sensu De Weerdt 1986
    - Acervochalina molitba De Laubenfels 1950
    - Halclona implexiformis (Hechtel 1965)
  - Family Niphatidae
    - Niphates erecta Duch. and Mich. 1864
    - Niphates sp. Van Soest 1980
  - Family Callyspongiidae
    - Callyspongia fallax Duch. and Mich. 1864
    - Callyspongia vaginalis (Lamarck 1814)

Table 1. Continued

Callyspongia armigera (Duch. and Mich. 1864)
Family Petrosiidae
Petrosia weinbergi Van Soest 1980
Petrosia pellasarca (De Laubenfels 1934)
Xestospongia aff. muta (Schmidt 1870)
Xestospongia sp.
Family Oceanapiidae
Aka coralliphaga (Rützler 1975)
Aka/Metschnikowia sp.
Calyx podatypa (De Laubenfels 1934)
Order Dictyoceratida
Family Thorectidae
Hyrtios violacea (Duch. and Mich. 1864)
Ircinia felix (Duch. and Mich. 1864)
Ircinia strobilina (Lamarck 1814)
Ircinia cf. campana ? (Lamarck 1814)
Smenospongia cerebriformis (Duch. and Mich. 1864)
Smenospongia sp.
Order Dendroceratida
Family Aplysillidae
Chelonaplysilla erecta (Keller 1891)
Aplysilla sp. aff. sulfurea Schulze 1878
Halisarca sp. 1
Halisarca sp. 2
Order Verongida
Family Aplysinidae
Aplysina fistularis (Pallas 1766)
Aplysina archeri (Higgin 1877)
Aplysina fulva (Pallas 1766)
Aplysina cauliformis (Carter 1882)
Verongula rigida (Esper 1794)
Family Aplysinellidae
Pseudoceratina crassa (Hyatt 1877)
Order Incerta
Keratose ?excavating sponge
Class Calcarea
Subclass Calcinea
Order Leucettida
Family Leucettidae
Leucetta imberbis (Duch. and Mich. 1864)
Order Clathrinida
Family Clathrinidae
Clathrina sp.

number of species in the sample from each depth, N = total number of individual sponges at each depth; the log is base 10 logarithm); Odum Diversity (the average number of species represented by each individual) S/N.

All of the material used in this study is deposited in the collections of the Zöologisch Museum, Instituut voor Taxonomische Zoölogie, Amsterdam.

SPONGE FAUNA, HABITAT AND ECOLOGY

All cryptic sponge species encountered in Bonaire are listed in Table 1 in taxonomic order. The following species merit comment, either because they are of taxonomic interest, or because they represent new records.

Dercitus sp.

This species is incrusting, and invades holes left by other organisms boring into calcareous substrates (simulating an endolithic habit), a feature also described for the related Indo-Pacific *Dercitus simplex* (Carter, 1880). The Bonaire form differs from *D. simplex,* and from the Mediterranean *D. plicatus* (Schmidt, 1868), in spicule sizes; oxea (few) 650–760 μm by 22–25 μm, calthropes of widely different shapes and sizes, including dichotriaene-like variations: rays 35–220 μm by 4–30 μm; acanthorhabds (resembling straight *Cliona*-type spirasters) averaging 12 by 1 μm; thicker growth forms of these are sanidasters 18–20 μm by 2 μm (resembling *Thoosa* microscleres). It is likely that this is an undescribed species. Another *Dercitus* species from the Caribbean is *D. lististinus* (Schmidt, 1880) (Topsent, 1927 = *Pachastrella*; De Laubenfels, 1936 = *Tachataxa*); possibly a third Caribbean species exists.

Dercitus differs marginally from *Pachastrella* in possessing sanidasters instead of metasters (asymmetrical amphiasters), and perhaps in the possession of only a few oxeotes instead of numerous ones; both share the calthropes of widely different sizes. A synonym of *Dercitus* is *Stoeba.*

Erylus formosus Sollas, 1888

The specimen conforms to Sollas' description and differs from Wiedenmayer's (1977) specimens in having a larger category of oxytylasters (up to 55 mm), next to the smaller chiasters. For this reason Pulitzer-Finali (1986) erected a new species, *E. bahamensis,* to include Wiedenmayer's material. A second new species erected in *Erylus* by Pulitzer-Finali (l.c.), viz. *E. clavatus* is quite obviously conspecific with the present *E. formosus.*

Desmanthus incrustans (Topsent, 1889)

This is an incrusting sponge, and is microhispid due to its projecting styles. The spiculation consists of characteristically small basal desmata: rhabd averaging 120 by 11 μm; styles erect on the basal desma-reticulation: 340–510 μm by 3.5–8 μm. Although described only once from the Caribbean, this seems not uncommon in the cavity habitat. Indo-Pacific records of the species (Vacelet, Vasseur and Levi, 1976) are probably the related *D. topsenti* Hentschel, 1912, which has larger styles and desmata.

Discodermia dissoluta Schmidt, 1880

A common inhabitant of holes and caves, characterized by the combination of ectosomal discotriaenes (disc diameter 160 μm, rhabd 110 μm), it has a subectosomal region free of desmata, supported by radiating bundles of flexuous oxeotes (up to 900 μm by 8 μm), a choanosomal desma-reticulation (desma-rhabds up to 300 μm), and numerous acanthorhabds (possibly in two size categories: 55 μm and 15 μm). This species shows the phenomenon of reduction of the desma-reticulation in peripheral regions also observed in Indo-Pacific *Theonella swinhoei* Gray, 1867. The ectosomal discotriaenes often appear obscured or absent due to their thinness and complete cover of acanthorhabds. This feature leads us to suspect that the recently erected genus *Desmahabana* Alcolado, 1986, with type species *D. violacea,* is a junior synonym of the present species.

Cliona janitrix Pang, 1971

The spicules are 160–225 μm by 5–10 μm, short and relatively thick; many points are slightly jagged, and a few are attenuated.

Cliona delitrix Pang, 1971

This occurs as a thin film over the substrate with papillae of about 8 mm in diameter. The tylostyles have a wide axial termination with sizes averaging 300 μm by 6 μm.

Anthosigmella varians (Duch. and Mich., 1964)
Spirastrella sp.

This species grows as a thin crust, which is now black (this may be due to contact with verongids). The spicules long, thin tylostyles (300–380 μm by 2–4 μm), with annulated tyles, and spirasters which are somewhat compact and short-shafted with branching spines (5–12 μm by 2–4 μm, possibly in a larger and a smaller category). This form might be an extreme representative of the cosmotropical species complex known under the name *S. cunctatrix* Schmidt, 1862.

Diplastrella megastellata Hechtel, 1965

Although reported only very infrequently, this proves to be a common inhabitant of reef cavities. The spiculation is very characteristic, consisting of robust tylostyles, sphaerasters of 30 μm diameter and spirasters of 12–15 μm. The genus bridges the gap between *Spirastrella* and *Timea* of the "families" Spirastrellidae and Timeidae.

Pseudosuberites sp.

An incrusting species with a (halichondroid) tangential ectosomal skeleton, as is characteristic for the genus. The choanosomal skeletal consists of vague columns and is mostly confused, halichondroid; subdermal spaces are well-developed. The spicules are exclusively tylostyles (410–560 μm by 6–12 μm), with small tyles and fusiform shafts (thickest in the middle). The genus was so far represented in the West Indian region by *P. melanos* De Laubenfels, 1936a, a black colored incustation with much smaller spicules (125 μm to 285 μm by 3–6 μm). A third, still undescribed *Pseudosuberites* is the one mentioned in a checklist of Curaçao sponges (van Soest, 1981); it differs from *P. melanos* in being golden in color. The Curaçao *Pseudosuberites* occurs under shallow-water (1 m) coral rubble and has tylostyles of 170 μm to 300 μm by 3–4 μm.

Terpios cf. *fugax* Duch. and Mich., 1864

The thin incrustation has the characteristic thin tylostyles (133–300 by 2–5 mm) in whispy bundles, erect on the substrate, with points directed outwards. The tyles are quadrilobate and very much compressed, and look like nail-heads. This species has been reported widely and it is probable that many records are unjustified. The same applies to the genus name. If the genus *Terpios* is considered to include also large, massive forms, or even forms without quadrilobate tylostyle heads, then delimitation towards the genus *Suberites* is difficult. We prefer *Terpios* to comprise only the incrusting forms with quadrilobate tyles. A consequence, however, is that the common *T. aurantiaca* (Duch. and Mich., 1864) (senior synonym of the widely recorded West Indian *T. zeteki* De Laubenfels, 1936b) cannot be maintained in *Terpios* but should be transferred to *Suberites*.

Terpios sp.

A specimen that differs from *T. fugax* by being transparent in spirit, and having longer and thicker tylostyles (250–400 μm by 5–7.5 μm), which have the same characteristic quadrilobate tyles. Several species of *Terpios* have been described by Cudhassaing and Michelotti (1864); these remain unfortunately obscure through the lack of adequate descriptions and the poor condition of the type material (some loose crumbles) (van Soest et al., 1983).

Aaptos cf. *aaptos* (Schmidt, 1864)

Grows greyish-orange thick crusts, that are rough to the touch. The architecture is radiate with fusiform styles with wide axial canals as the only spicules. Size categories: 800–1,300 by 20 mm, 300–600 μm by 15–25 μm, and 200–220 μm by 3–4 μm (the latter only in the peripheral region). This sponge has been reported from widely diverging parts of the world (Mediterranean, West Indies, Indo-West Pacific). The variability reported is wide enough to assume that there are several species, but at present these cannot be discriminated.

Jaspis sp.

This sponge forms a red (?) incrustation. The ectosomal crust of asters is carried by a tangential layer of small oxea. Subdermally microcavernous (very regularly), in between a subtangential skeleton of larger oxea. The spiculation consists of two size catgories of oxea, the larger with stair-stepped apices (510–690 μm by 4–8 μm and 78–195 μm by 1.5–4 μm), and oxysphaerasters (10–14 μm, with 8–12 rays).

A second West Indian species of *Jaspis* (s.s.) has smaller microxea and thin-rayed oxyasters (not oxysphaerasters) with only 6–8 rays. The type species of *Jaspis,* i.e., the Mediterranean *Vioa johnstoni* Schmidt, 1864, has smaller oxea (400 μm by 8 μm and 70 μm by 1–2 μm) and larger oxyasters (10–28 μm, 6 rays). These three forms are closely related.

Confusion exists in the literature over the true nature of *Jaspis.* Many species have been included, which are in reality reduced *Stelleta* or *Penares,* because they have the characteristic radiate architecture of huge oxea. It is clear that proper *Jaspis* are not at all related to these genera (although judged solely on their spicule complement this might seem otherwise). Examples of such misplaced *Jaspis* from the West Indies are *Jaspis pudica* Widenmayer, 1977, and *Jaspis colombiana* Wintermann-Kilian and Kilian, 1984.

?*Halichondria* sp.

Forms incrustations with a tangential ectosomal skeleton and a confused choanosomal skeleton; technically the spicules are oxea, some straight but many are strongly curved, with wide axial canals and ragged stair-stepped points. The spicule size is variable: 50–250 μm by 1–11 μm (possibly in two size categories). The specimen shows affinities with the Red Sea species *Anacanthaea nivea* Row, 1911 in the peculiar spicule endings, but differs from it in the absence of the peculiar surface grooves. A revision of Halichondrid genera is necessary to understand the significance of these similarities.

Didiscus oxeata Hechtel, 1983

Common in the cavity habitat. Junior synonyms are *D. flavus* van Soest, 1984a, and *D. habanensis* Alcolado, 1984.

Myrmekioderma reiswigi (Diaz, Alvarez and van Soest, 1987)

Recent studies have brought to light that spination of oxea is quite variable in *Myrmekioderma,* and may be absent. This compels assignment of this species to a widened genus *Myrmekioderma.*

Myrmekioderma styx De Laubenfels, 1953

The three species *D. oxeata, E. reiswigi* and *M. styx* are all very similar in appearance, sharing the characteristic sinuous surface channels and yellow-orange color. It is quite possible that *Topsentia gyroderma* Alcolado (1984) also belongs in this series; it apparently lacks any microscleres or acanthose conditions in the megascleres (Alcolado, in litteris), thus it cannot be synonimized with any of the three, although it is certainly not a *Topsentia.*

Topsentia roquensis Diaz, Alvarez and van Soest, 1987

This form is common in the cavity habitat.

Hymeniacidon sp.

Forms thin incrustations in which the ectosomal skeleton is doubtfully developed and the choanosomal skeleton is confused. The spicules are large, straight styles, with blunt apices, 800–1,000 μm by 11 μm. This combination of characters is not known in any described Caribbean sponge.

Dictyonella ruetzleri (Wiedenmayer, 1977)

The species needs comparison with *Ulosa hispida* Hechtel, 1965. As argued elsewhere (van Soest, in press), the genus *Ulosa* De Laubenfels, 1936, in which this species was originally placed, is not the correct genus, as the type specimen has a different ('chalinid') architecture. *Dictyonella* Schmidt, 1868, seems the proper assignment for the present species and for *hispida,* although further comparisons are necessary (e.g., with *Scopalina* Schmidt, 1862).

Dictyonella sp.

Specimens differ from *D. ruetzleri* in details of the skeletal architecture. They are narrowly- but irregularly-meshed, and spongin is present only sparingly, while foreign material is abundant. The styles are similar to those of *D. ruetzleri* (300–400 μm in length).

Hymerhabdia sp.

This comprises an incrustation with choanosomal skeleton of confused bundles of styles, which are arranged perpendicular to the substrate near the base of the sponge; they are straight, occasionally flexuous, 550–1,200 μm by 5–15 μm. Next to these there is a basal layer of strongly curved or angulated oxea, with wide axial canals and hastate/stair-stepped apices.

The genus is barely differentiated from *Bubaris* Gray, 1867, which has proper sinuous strongyles/oxea, instead of merely strongly arched ones. *Uplexoa* De Laubenfels, 1936a (type species the New Zealand *Bubaris oxeata* Dendy, 1924) was erected to receive species like the present one, with oxeote basal spicules, to differentiate them from the stylote basal spicules in the type of *Hymerhabdia* (i.e., the Atlantic deep-water *H. oxytruncata* Topsent, 1904). In view of the instability of spicule apices in this group, it seems superfluous to recognize *Uplexoa* as generically distinct.

Ptilocaulis marquezi (Duch. and Mich., 1864)

A massively-incrusting specimen that conforms in skeletal details (architecture and spicule form and size) with ramose specimens of this species. *Ptilocaulis gracilis* Carter, 1883, is a junior synonym of this species.

Dragmaxia sp.

A thin crust with easily detachable ectosome containing tangentially strewn styles (800–1,050 μm by 10–21 μm) and long whispy trichodragmata (up to 220 μm long). The choanosome is cavernous with a loose skeleton of vague bundles. This species is certainly new to science. It was already listed by van Soest (1981) from Curaçao and presumably by Wintermann-Kilian and Kilian (1984 as *D. variabilis* Whitelegge, 1907) (no descriptions given). The generic assignment is somewhat uncertain, because the present material also answers to the definition given for the genus *Dragmatella* Hallmann (1917), with type *Desmacella aberrans* Topsent, 1892; it is assumed that this is a reduced *Desmacella.*

Agelas dispar Duch. and Mich., 1864

It appears that there are two color forms of this species in the West Indian region, viz. orange (Van Soest, 1981) and brown (Widenmayer, 1977; Zea, 1987), but further data are lacking. To date the brown form has not been found on Bonaire.

Agelas sp.

Thin incrustations deviating from the known species of *Agelas* in their habit (which could be a juvenile stage of any of the above listed species), and the large size of the spicules (up to 300 μm by 10 μm, with up to 23 verticils of spines). They may belong to *A. schmidti* sensu Zea, 1987 (spicule size range up to 309 μm, verticil number up to 18) or *A. conifera* (spicule size range up to 299 μm, verticil number up to 23: Zea, 1987).

Clathria affinis (sensu Topsent, 1889)

Van Soest (1984a) transferred *Hymeraphia affinis* Topsent, 1889, to *Clathria.* However, *Microciona affinis* Carter, 1880 probably also belongs to *Clathria* but is not conspecific. If these suspicions prove to be correct, then the present species will need a new name.

Clathria echinata (Alcolado, 1984)

Junior synonym: *C. simpsoni* Van Soest, 1984a.

Rhaphidophlus venosus (Alcolado, 1984)

Junior synonym: *Raphidophlus raraechelae* Van Soest, 1984a.

Rhaphidophlus cf. *minutus* Van Soest, 1984a

The specimen differs from the type in the shape of the toxa, which are straight-angled instead of softly and deeply curved. Other spicule sizes and categories are conforming.

Holopsammia helwigi De Laubenfels, 1936

Lobate, with fine conulose surface, and purplish in color. The ectosome is a detachable membrane containing a reticulation of sand grains enclosing meshes of 50–120 μm. Choanosome, a reasonably well-organized system of longitudinal tracts of sand grains lying close together (less than 100 μm), here and there interconnected by similar sand tracts. Spongin cements the sand grains, but is inconspipuous. Among many broken spicules there are proper thin strongylote oxea, about 100–120 μm by 1–2 μm. Earlier suggestions (van Soest, 1984a) that specimens such as this are attributable to *Desmapsamma anchorata* (Carter, 1882) are incorrect, as it is a clearly distinct species (see also Gomez-Lopez and Green, 1984).

Monanchora arbuscula (Duch. and Mich., 1864)

Junior synonyms: *M. unguifera* (De Laubenfels, 1953 as *Echinostylinos*) and *M. barbadensis* Hechtel, 1965. Reexamination of the lectotype of *Pandaros arbusculum* (ZMA POR. 1728) revealed that it is conspecific with ramose specimens of what is currently known as *Monanchora barbadensis* Hechtel (van Soest, 1984a), and not with *Ptilocaulis* sp. aff. *spiculifera* contended by Wiedenmayer, 1977, followed by van Soest et al., 1983. A spicule mount made from the lectotype shows abundant microscleres (unguiferate chelae and reduced sigmatose chelae).

Biemna sp.

The specimen does not conform to the published descriptions of other West Indian *Biemna* species (i.c. *B. tubulata* sensu van Soest, 1984a = *B. caribea* Pulitzer-Finali, 1986; *B. microstyla* De Laubenfels, 1950), and *Biemna* sp. sensu Pulitzer-Finali, 1986). Its spiculation includes larger sigmata (up to 60 μm) many of which are in dragmata, next to smaller (20 μm), likewise in dragmata, and three sizes of microxea/rhaphides (40 μm, 100 μm and 190 μm).

Merlia normani Kirkpatrick, 1908

This sclerosponge turns out to be a common (10 samples) species in reef cavities. Previously it was found on the Curaçao reefs in its deficient growth form (van Soest, 1984b), and in Bonaire in its calcareous growth form (Kobluk and Lysenko, 1984); in the present material both the calcareous and the deficient growth forms are represented.

Niphates erecta Duch. and Mich. (1864) + *Niphates* sp. indet.

These species are very common in the cryptic habitat. *N. erecta* is readily recognized by its purplish grey, hispid, normally branching, occasionally incrusting habit. The distinctness of the species has recently been questioned from different sides. Are amorphously incrusting specimens answering to the general description of *N. erecta* merely incrusting growth stages, which occur frequently, especially in the cryptic habitat, or should these be considered a separate species (*N. amorpha* Wiedenmayer, 1977)? Specimens with many sigmata of both growth forms have also been given separate specific status: *N. recondita* (Wiedenmayer, 1977 as *Sigmadocia*), and *N.* (*Gelliodes*) *sosia* Pulitzer-Finali, 1986). Relatively smooth, white branches are distinguished as *N. alba* Van Soest, 1980 (junior synonym: *Protophlitaspongia antillarum* Pulitzer-Finali, 1986). To this complex we can now add dark-brown (in spirit) lobate forms with a very tough, almost hard consistency; the skeleton presents an irregular system of very thick (up to 500 μm) fibers, much coarser than normal. At first the specimen was mistaken for *Xestospongia proxima* (Duch. and Mich., 1864), but the structure of the ectosome with irregular meshes enclosed by thick spicule tracts precludes this. It is clear that the West-Indian *Niphates* species are in need of revision.

Xestospongia sp. aff. *muta* (Schmidt, 1870)

The material consists of incrusting fragments conforming in their spiculation to *X. muta*: strongyles of 380 μm by 18 μm.

Xestospongia sp.

Irregular white fistulose-tubular mass with oxea up to 400 by 12 mm. This species was reported before from Curaçao (Van Soest, 1981 as *Xestospongia* sp.). It seems to be an undescribed species (see reviews of the genus in Zea and Rützler, 1983, and Zea and van Soest, 1986).

Aka/Metschnikowia ?sp.

This may be an excavating sponge, with a dark purple color in spirit, that fills cavities of 1–2 mm in diameter in calcareous substrates; it is a slimy organic mass containing loosely strewn acanthose oxea-strongyles of 60–100 μm by 1–3 μm. The genus *Aka* (senior synonym of *Siphonodictyon* Bergquist, 1965 (cf. de Weerdt and Van Soest, 1985; Rützler and Stone, 1986) normally has smooth oxea, although *A. trachys* De Laubenfels, 1954, also has spined ones. It is uncertain whether the latter and the present material are congeneric with *Aka.*

Calyx podatypa (De Laubenfels, 1934)

This species is difficult to assign to a genus (in the past it has been assigned to *Haliclona* and *Pachypellina*), because it unites a *Haliclona*-type of choanosomal reticulation with *Oceanapia*-characteristics such as the possession of a distinct ectosomal crust of tangential oxea and randomly oriented choanosomal spicule tracts.

Ircinia cf. *campana* (Lamarck, 1814)

Incrusting reddish lamellae which may represent incipient *I. campana.* It is difficult to identify *Ircinia* species with certainty when they do not exhibit their characteristic growth form.

Smenospongia cerebriformis (Duch. and Mich., 1864)

This material was originally identified with *Smenospongia aurea* (Hyatt, 1875) (massive, cone-shaped, with prominent trunate conules, stiff, with square-meshed skeleton of amber-colored stratified fibers, occasionally pithed) that has been compared exhaustively with the type specimens of *Spongia cerebriformis* Duch. and Mich. (1864). This has resulted in the conclusion that both are synonymous, with the latter name having priority. A few pithed fibers are present in the type specimens of *S. cerebriformis* (overlooked in a recent redescription by Van Soest (1978) as *Fasciospongia*). Since Bergquist (1980) reserved *Rasciospongia* for sponges with detritus-cored primary fibers, it seems best to retain *Smenospongia* as valid, though closely related, based on the absence of such detritus, and the presence of aerophobic (color-change) properties.

Smenospongia sp.

This is more finely conulose than *S. cerebriformis,* and does not turn black in preservation. It is tempting to assign these specimens to Smenospongia echina De Laubenfels (1936a), which is likewise less conspicuously connulose. However, the latter species has a finer reticulation of thin dark-colored spongin fibers between the main fibers, a situation not found in our specimens. Another possibility is the species known as '*Coscinoderma*' *musicalis* (Duch., and Mich., 1964), only known from a single old-collection specimen (van Soest, 1978). In this specimen there are also occasional pithed fibers.

Aplysilla sp. aff. *sulfurea* Schulze, 1878

Very thin sulfur-yellow conulose incrustations, very common also outside caves, e.g., on the bases of branching corals. The species is aerophobic (turns dark purple out of the water). Whether this is really conspecific with *A. sulfurea* from the Eastern Atlantic and the Mediterranean remains to be demonstrated.

Halisarca sp. II

Dark purple (spirit), forming a slippery incrustation that lacks the characteristic star-shaped oscules of the previous species.

Ordo incerta

Keratose ?excavating sponge.

Forms dark purple invasions (endolithic ?) in coral, that lack any spicules. It is likely that it originally was yellow and that an aerophobic color change has occurred. This type of excavation has been known for some years among sponge workers, but was never properly described for lack of easy diagnostic characters. Its existence is here merely mentioned to draw attention to it.

Leucetta imberbis (Duch. and Mich., 1864)

This is *Leucetta floridana* of De Laubenfels, 1953.

Clathrina sp.

Identical to Wiedenmayer's (1977) *C. coriacea,* but probably not conspecific with eastern Atlantic populations of this species. The identification of *Clathrina* species is at present not really possible through lack of comparative studies.

Depth Distribution

Only 13 of the 92 species (14%) found in the cavities range from 12 m to 43 m depth; 9 species (9.9%) appear restricted to about 12 m depth, 11 (12%) are restricted to 18 m depth, 12 (13%) are restricted to about 24 m depth, 8 species (8.8%) are restricted to 30 m, and only 1 species (1.1%) was at 43 m depth (although it may occur deeper as well). The depth distributions of many species are very restricted (Figs. 3, 4), some being found at only one depth (Fig. 4); in almost all cases these are rare or uncommon sponges. It appears that a large number of these species actually have broader depth ranges than represented by these data (van Soest, unpublished data); they would probably have been found at other depths in a large sample. However, 17 of the cryptic sponge species appear (at present) to be depth restricted (Fig. 4). Although tentative, this suggests that there may be some depth zonation of cryptic sponge species, and that there is at least some potential cryptic sponges that may be useful in ancient reefs as a paleoenvironmental tool, in particular as a depth indicator.

Diversity and Abundance

The cryptobiontic sponge sample is dominated by *Niphates erecta* (17.4% of all specimens) and *Ectyoplasia ferox* (7.7%). Of the remaining species, only 13 have an abundance of 2% or more of the sample (Table 2). Most species are therefore very uncommon or rare, so that although the species diversity is moderately high, the assemblage is dominated by a small proportion (16%) of the species.

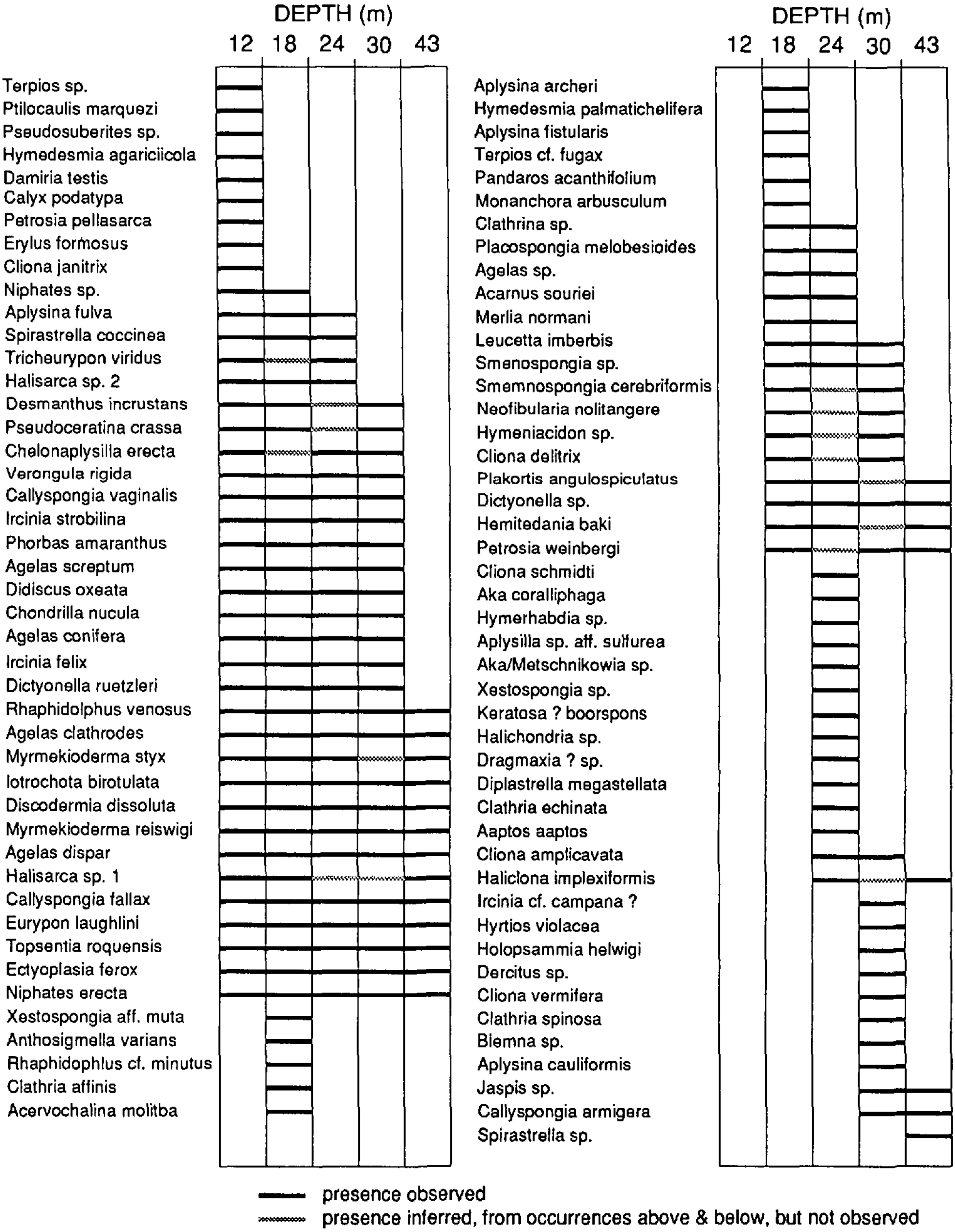

Figure 3. Depth ranges of the sponge species identified from cavities in this study. The solid black bars indicate that the species was found at that depth; grey bars indicate that although not actually found at that depth, the species is probably present.

The simplest measure of diversity, the Species Richness is the number of species in a sample. Figure 5A shows that the Species Richness increases from 12 m to 18 m depth and declines from 18 m to 43 m depth. However, Species Richness gives the same weight to all species, so that a very rare species (e.g., *Ptilocaulis*

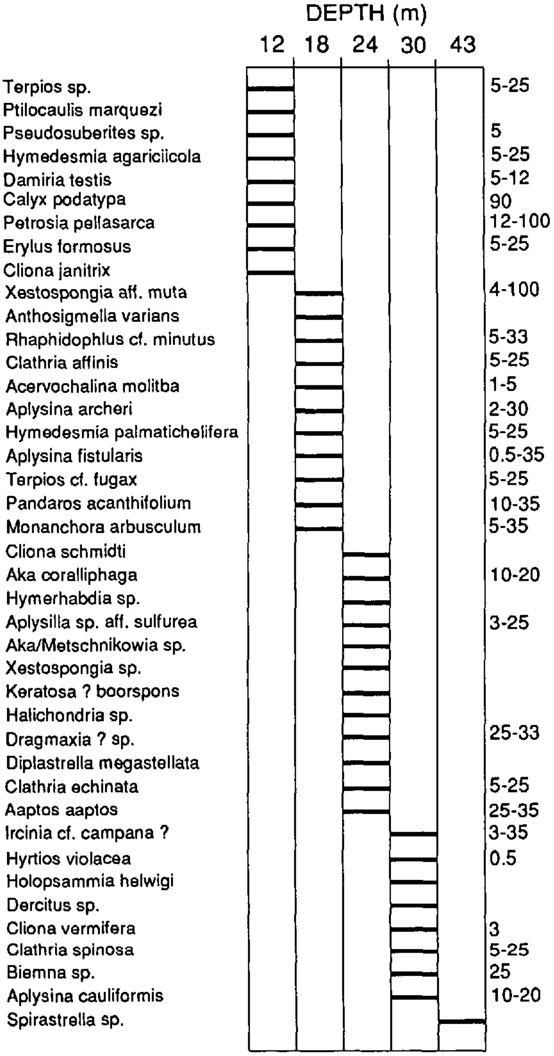

Figure 4. The distribution of the 41 sponge species with the narrowest depth ranges (i.e., found at only one sample depth). The numbers on the right are the depth ranges (meters) of some of the species known to have broader or different depth ranges than found in this study (van Soest, unpublished data). Although most of these sponges are rare to uncommon, the occurrence of some apparently depth-restricted species may indicate that some species of cryptic sponge have potential value as paleoenvironmental and paleoecological indicators in ancient reefs.

marquezi) receives the same measure of importance as a very common one (e.g., *Niphates erecta*).

To help overcome the problem inherent in the uneven weighting of rare and common species, two other measures of diversity, Margalef Diversity, and Odum Diversity, were also calculated. Margalef Diversity is a logarithm-based diversity index that has as a premise the empirical assumption that the minimum abundance in a sample or population is shared by the greatest number of species; this is true for the Bonaire cryptic sponges (Table 2). The Margalef Diversity index, therefore,

Table 2. Number of specimens of each species of cryptobiontic sponge identified from Bonaire at each depth (Species are arranged by first appearance and depth range)

Depth (meters):	12	18	24	30	43	Total	Depth (meters):	12	18	24	30	43	Total
Terpios sp.	1					1	*Aplysina archeri*		7				7
Ptilocaulis marquezi	1					1	*Hymedesmia palmatichelifera*		3				3
Pseudosuberites sp.	1					1	*Aplysina fistularis*		3				3
Hymedesmia agariciicola	1					1	*Terpios* cf. *fugax*		2				2
Damiria testis	1					1	*Pandaros acanthifolium*		2				2
Calyx podatypa	1					1	*Monanchora arbusculum*		2				2
Petrosia pellasarca	2					2	*Clathrina* sp.		1	3			4
Erylus formosus	2					2	*Placospongia melobesioides*		1	2			3
Cliona janitrix	2					2	*Agelas* sp.		1	2			3
Niphates sp.	2	2				4	*Acarnus souriei*		1	1			2
Aplysina fulva	1	2	7			10	*Merlia normani*		3	7			10
Spirastrella coccinea	1	2	1			4	*Leucetta imberbis*		7	10	3		20
Tricheurypon viridus	1		1			2	*Smenospongia* sp.		4	1	1		6
Halisarca sp. 2	2	7	18			27	*Smenospongia cerebriformis*		2		4		6
Desmanthus incrustans	1	2		1		4	*Neofibularia nolitangere*		1		1		2
Pseudoceratina crassa	1	11		1		13	*Hymeniacidon* sp.		1		3		4
Chelonaplysilla erecta	1		3	1		5	*Cliona delitrix*		1		3		4
Verongula rigida	2	2	9	4		17	*Plakortis angulospiculatus*		6	2		1	9
Callyspongia vaginalis	2	6	6	1		15	*Dictyonella* sp.		2	2	1	2	7
Ircinia strobilina	3	5	3	2		13	*Hemitdedania baki*		1	1		1	3
Phorbas amaranthus	3	7	2	1		13	*Petrosia weinbergi*		3		10	2	15
Agelas sceptrum	3	9	10	3		25	*Cliona schmidti*			4			4
Didiscus oxeata	4	28	34	12		78	*Aka coralliphaga*			4			4
Chondrilla nucula	8	7	6	3		24	*Hymerhabdia* sp.			3			3
Agelas conifera	9	32	16	8		65	*Aplysilla* sp. aff. *sulfurea*			2			2
Ircinia felix	11	13	18	7		49	*Aka/Metschnikowia* sp.			2			2
Dictyonella ruetzleri	15	14	16	9		54	*Xestospongia* sp.			1			1
Rhaphidolphlus venosus	1	11	13	8	1	34	*Keratosa ? boorspons*			1			1
Agelas clathrodes	1	9	13	7	2	32	*Halichondria* sp.			1			1
Myrmekioderma styx	1	6	1		1	9	*Dragmaxia ?* sp.			1			1
Iotrochota birotulata	1	4	2	6	1	14	*Diplastrella megastellata*			1			1
Discodermia dissoluta	1	2	6	2	3	14	*Clathria echinata*			1			1
Myrmekioderma reiswigi	1	1	1	1	1	5	*Aaptos aaptos*			1			1
Agelas dispar	2	21	21	6	2	52	*Cliona amplicavata*			2	1		3
Halisarca sp. 1	2	8			1	11	*Haliclona implexiformis*			1		1	2

Table 2. Continued

Depth (meters):	12	18	24	30	43	Total	Depth (meters):	12	18	24	30	43	Total
Callyspongia fallax	5	28	24	4	3	64	*Ircinia* cf. *campana ?*				1		1
Eurypon laughlini	8	11	16	5	5	45	*Hyrtios violacea*				1		1
Topsentia roquensis	11	10	14	10	4	49	*Holopsammia helwigi*				5		5
Ectyoplasia ferox	16	34	31	11	4	96	*Dercitus* sp.				1		1
Niphates erecta	42	84	64	24	3	217	*Cliona vermifera*				1		1
Xestospongia aff. *muta*		1				1	*Clathria spinosa*				1		1
Anthosigmella varians		1				1	*Biemna* sp.				1		1
Rhaphidophlus cf. *minutus*		1				1	*Aplysina cauliformis*				1		1
Clathria bulbotoxa		1				1	*Jaspis* sp.				1	3	4
Clathria affinis		1				1	*Callyspongia armigera*				1	1	2
Acervochalina molitba		1				1	*Spirastrella* sp.					1	1

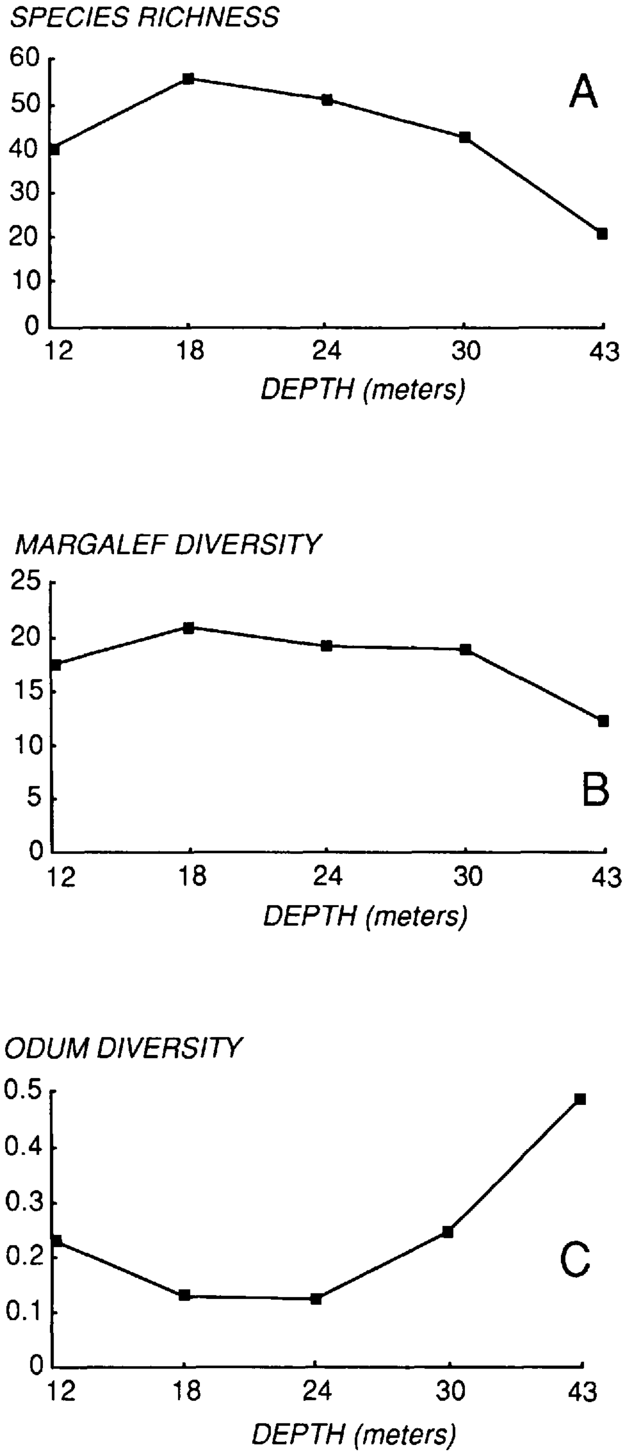

Figure 5. Species diversity versus depth (meters) for Bonaire cavity-dwelling sponges. A) Species Richness (the number of different species) versus depth. B) Margalef Diversity versus depth. C) Odum Diversity (the average number of species represented by each individual) versus depth.

helps to reduce the impact of unimportant and rare species. Figure 5B shows that Margalef Diversity increases to 18 m depth, and declines below 18 m, a similar trend to that seen in the Species Richness (Fig. 5A).

The Odum Diversity index expresses the average number of species represented by each individual specimen (sponge in this case); an Odum index value of 1 would mean that each specimen is of a different species, and that there are as many species as there are individuals. In the case of the cryptobiontic sponges from Bonaire, the Odum Diversity index decreases from 12 m depth to 18 to 24 m depth, and increases in deeper water (Fig. 5C). This could be interpreted to mean that from the shallow to intermediate depths the cryptic sponge species are, on average, represented by progressively more individual sponges. At even greater depths, however, the species are represented by progressively fewer sponges. Alternatively, if the population density of sponges in the cavities were assumed to be more or less the same through the entire depth range of the study, then the Odum index would be showing that from shallow to intermediate depths the number of species tends to increase, and in deeper water, the number of species tends to decline. This latter alternative is in agreement with the trends of Species Richness and Margalef Diversity values with depth. It appears, therefore, that with increasing depth (starting at 12 m) the Bonaire cryptobiontic sponges reach their highest diversity at approximately 18 m depth, and decline in diversity below 18 m at least as far as 43 m depth.

Endolithic Sponges

Five species of *Cliona* (*C. amplicavata, C. schmidti, C. vermifera, C. janitrix, C. delitrix*), *Aka coralliphaga, Aka/Metschnikowia* ? sp. (*Aka* is *Siphonodictyon* of other authors), *Anthosigmella varians,* and one specimen of an unidentified keratose sponge, were found as endoliths (borers) in the walls or roofs of cavities. These sponges probably are more abundant than the number of specimens recovered indicates, due to the limited sampling of the wall and roof rock of many cavities. The depth distribution of the endolithic sponges is shown in Figure 6.

The clionid sponges are widely known as endoliths. *Cliona schmidti* has a global distribution, having been reported from the Indo-Pacific, Mediterranean, Red Sea, and Atlantic (summarized in Pang, 1973a, 11). *C. vermifera* is known from the Indo-Pacific, Mediterranean region, and the Caribbean (Pang, 1973a, 15), *C. janitrix* is more restricted in distribution, having been found only in the Mediterranean and Jamaica previously (Topsent, 1932; Pang, 1973a). *C. delitrix* is even further restricted in distribution, and is currently known only from the Caribbean region (Pang, 1973a). *Cliona amplicavata* was reported as endolithic in Bermuda (Rützler, 1974). It should be kept in mind, however, that the apparent cosmopolitan distributions of some clionid sponges should be treated with caution, as they may be a reflection of a lack of morphological characters to distinguish between similar closely related forms, and also a lack of sufficient comparisons.

The presence of these sponges in reef cavities over a broad depth range shows that bioerosion by sponges in reef cavities is widespread; however, its importance within cavities compared to bioerosion by other groups such as algae and bivalves is unknown, as is the importance of sponge bioerosion compared to its very significant effect in more exposed reef surface habitats.

Controls on Cryptobiontic Sponge Distribution

Sponges are sessile attached filter feeders, and as such depend upon water flow to deliver adequate dissolved and particulate nutrients (Reiswig, 1981). Because

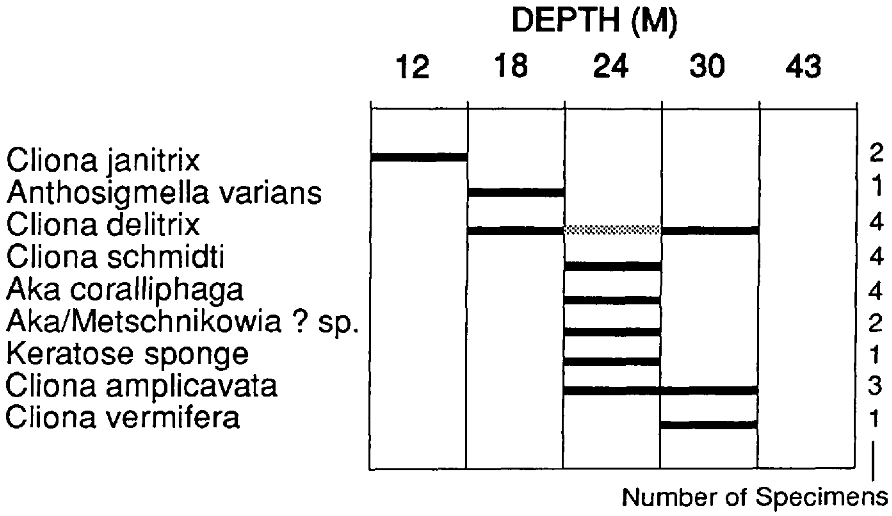

Figure 6. Depth distribution of the nine species of endolithic (boring) sponge found in Bonaire reef cavities. *Spirastrella varians* is an excavating sponge, but bores only to "root" itself, and then overgrows the surface of the substrate. The absence of endolithic sponges at 43 m depth is almost certainly due to the comparatively small sample from that depth.

most cavities are by their nature at least somewhat enclosed and restricted, water flow within them may be reduced, or even almost non-existent in the deepest recesses. This has important implications for some cryptobiontic groups such as the sponges, which must rely entirely upon the water flow within cavities. Wilkinson and Vacelet (1979) have shown that reduced water flow has the effect of reducing sponge growth, so that there may be a direct relationship between the size and abundance of sponges in cavities, and the rate of water interchange.

Some sponges, including certain species of *Cliona* such as *C. aprica, C. langae,* and *Anthosigmella varians* (found in Bonaire cavities) also have photosynthetic symbionts (de Laubenfels, 1950; Pang, 1973b, and J. C. Lang, pers. comm., *in* Wilkinson, 1983; Rützler, in press). The most important of these symbionts in sponges are photosynthetic cyanobacteria (Wilkinson, 1981), which are reported in Caribbean *Neofibularia nolitangere* by Rützler (in press), which although rare, is found in Bonaire reef cavities. As a result these sponges can behave like hermatypic corals in that they require light (Sara and Liaci, 1964). Such sponges often prefer brightly-lit rather than shaded habitats (Pang, 1973b), thereby helping to explain why such species are not common in the Bonaire cavities. The observation that some sponges have photosynthetic symbionts indicates that light probably is one control on the presence or absence, and probably the distribution, of many sponges in cryptic habitats as it is for other groups of organisms. The picture is complicated, however, as many sponges without photosynthetic symbionts are also found in cavities.

Sponges are known to be sensitive to both continuous and intermittent sedimentation which has the effect of clogging canals and reducing pumping rates (Reiswig, 1971; Gerrodette and Flechsig, 1979). This sensitivity to sedimentation is probably an important control on sponge distribution in general, and without doubt has some effect on sponges in cryptic habitats. Wilkinson (1983) concludes from this that sponges are as a result not common on the floors of caves. This is generally true, in that sponges in cavities tend to prefer the walls and roofs, where sedimentation is usually less intensive than on the floor. Cryptic sclerosponges and sphinctozoans in particular, appear to be sensitive to sedimentation. Hartman (1973) found *Ceratoporella* on the undersurfaces of ledges in Jamaica where sedimentation was high (see also Dustan and Sacco, 1983). Fagerstrom (1984) suggests from this evidence that depth (and turbulence) may not be the prime control on the distribution of sclerosponges and sphinctozoans, but rather the comparatively low turbidity of cryptic habitats.

We have seen numerous examples in Bonaire of demosponges (many of the encrusting species reported in this study) that live on the walls of cavities, and that are covered or partly covered in deposits of fine silt, and of (unidentified) sponges in cavities at depths of 61 m and 73 m that are similarly covered, and also that live on the sediment-covered floors of cavities (D. R. Kobluk, unpublished observations). Therefore, although sedimentation may be an important control on sponges in cavities, it is not so important, at least in some areas, that all sponges are excluded from even parts of cavities where sedimentation is high. To speculate, sedimentation rates may be a factor in determining which species can live where in a cavity, and in which cavities, so that its most important role may be as a determinant in the species composition of cavity-dwelling sponge assemblages. The intolerance of sclerosponges for high sedimentation rates and turbidity may help to explain why, although sclerosponges (*Merlia normani*) are present in Bonaire reef cavities, they are not as common as in some other reefs (e.g., Jamaica).

Among the most important problems that all sessile organisms have to deal with is finding available space for settlement and for growth, and defending that space. This results in intense competition, which is especially evident in cryptic habitats where available substrate is always very limited (Jackson, 1977a; 1977b; 1979; Jackson and Buss, 1975; Buss, 1980). Jackson and Winston (1982) found, that at least in the shaded habitat under foliaceous corals, sponges are the most effective overgrowth competitors, and therefore can increase their available space by taking over space occupied by others. Other organisms compete with sponges by having higher recruitment rates that allow them to become established earlier, so that in cryptic habitats under expanding substrates (such as growing corals) the older areas of the substrate become dominated by the sponges whereas the less effective overgrowth-competitive groups dominate in the newer areas (Jackson and Winston, 1982). Choi (1984) outlined successional stages for cryptobionts living under rubble in the Florida reef tract, and illustrated that the cryptic sponges are intermediate to late stage colonizers, following some algae, a few species of bryozoan, foraminifers, serpulids, and some molluscs. The overgrowth strategies of sponges are not limited to the overgrowth of other kinds of organisms, however. They overgrow one another, thereby increasing the space available to them, but are able in some cases to maintain themselves and the space they occupy, even if being overgrown. Rützler (1970) showed in an experiment using artificial cavities, that one way cryptobiontic sponges have dealt with the problem of competition among themselves and certain other groups for limited space in cryptic habitats is by epizoism.

Although there may be a link between predation and a cryptobiontic lifestyle for sponges, such a relationship has not been clarified. The inference is that living in cavities in one way or another provides protection from some predators. Without doubt some cavities will exclude certain predators (for example, by the predator being too large to enter) and so provide some advantage to cryptobionts within. However, there are known predators on sponges, and some of these are cryptobiontic or casually cryptobiontic. Graham (1955) lists molluscs that feed on sponges, including several that Kobluk and Lysenko (1985) documented from within growth framework cavities in Bonaire; Guida (1976) showed that even the well-protected clionid sponges have specific predators such as molluscs, echinoderms, and crustaceans, all of which have cryptobiontic representatives.

Cryptic Sponges in Ancient Reefs

Rare evidence of sponges in reefs and reef mounds has been found in the early Cambrian, but most sponges in the earliest Paleozoic appear to have been level-bottom dwellers (Fagerstrom, 1984). Only in the Ordovician did sponges become significant contributors to reefs and mounds (Pitcher, 1964; Rigby, 1966; Toomey, 1970; Pratt and James, 1982). This parallels the history of sponges in general in the early Paleozoic, wherein sponges appear not to have been very diverse or common until the Ordovician (Rigby, 1976). The sponges (including the stromatoporoid sponges) have either been important biotic elements in, or the constructors of, reefs and mounds in the Silurian (Mori, 1968; Manten, 1971; Stearn, 1975; Kershaw, 1981), and the Devonian (Klovan, 1964; Krebs, 1974). In the Permian and Triassic sphinctozoans were the most important sponges in reefs (Bain, 1968; Rigby, 1971; Toomey and Cys, 1979; Zankl, 1968). Sponges were also significant in reefs and mounds in the Jurassic (Flügel and Steiger, 1981; Palmer and Fürsich, 1981), the Cretaceous (Heckel, 1974), as well as much of the Cenozoic (Heckel, 1974, and James, 1983, for summaries). Sponges also were present in some Mississippian and Pennsylvanian mounds, but only locally, and do not appear to have been important contributors (Heckel, 1974).

The fossil record of cryptobiontic sponges in reefs is very sparse. There are, however, a few studies that show cryptobiontic sponges were, or probably were, present. For example, Schäfer (1984) found sponges in Triassic reef cavities in Austria, and Palmer and Fürsich (1981) described an abundant and diverse cryptic sponge fauna, comprising calcisponges, in a Jurassic reef. Kobluk and James (1979) reported clusters of spicules in cavities in patch reefs from the early Cambrian, and Kobluk (1981b, 1981c) found evidence supporting the presence of cryptic endolithic sponges in early Cambrian and Middle Ordovician reefs and mounds.

The poor fossil record of cryptobiontic sponges in general, and cryptobiontic reef-dwelling sponges in particular, may be reflecting, in part, the same preservational biases that affect the surface-dwelling sponges. Hartman (1977) expressed it well when he referred to the slow growth rate and low average skeleton to tissue ratio of sponges as a whole as being a factor in explaining the low concentrations of siliceous spicules in reef sediments. If taken as a group, sponges produce far more soft, non-preservable tissue than preservable hard parts (even the siliceous hard parts are unstable—see Rützler and Macintyre, 1978).

The sclerosponges and spinctozoans, so common in some cryptic habitats today, are considered to have been exposed surface-dwellers in reefs and hardgrounds in the ancient (Fagerstrom, 1984), although at least one Late Cretaceous sclerosponge is now known from a cryptobiontic habitat (Reitner and Engeser, 1987). Fagerstrom (1984) expressed the view that the current cryptic habit of sclerosponges and sphinctozoans may have been a comparatively late development, arising from competition with the hermatypic scleractinian corals.

Rasmussen and Brett (1985) used the assumption of complete non-preservability of non-skeletonized organisms to show that about 62% of the cryptic biota in marine caves in St. Croix would not be preserved as fossils. Of these, most important (in areal coverage of cryptic substrates) were the non-skeletonized or poorly-skeletonized demosponges (up to 54% areal coverage). The skeleton-secreting sclerosponges covered 10%–11% of the surface area in deeper caves. The resulting fossil cryptic sponge assemblage would be almost exclusively sclerosponge, and would give the impression that sponges were cryptic only in deeper water cavities, and that they were either very rare or absent from shallow water cavities. In comparison to other reef-dwelling groups with hard skeletons, such as scleractinian corals, the sponges probably are grossly under-represented in most ancient reefs.

Evidence of sponges may be preserved in the following ways: 1) boreholes if they are endolithic species, 2) rare body fossils, 3) spicules, and 4) preserved skeletons, if they are calcareous or silicate skeleton-secreting forms. Borings produced by endolithic sponges are difficult to recognize in ancient substrates, are susceptible to modification or erasure during diagenesis, and can be confused with microborings produced by other groups; this may in part account for why there are so few reports of them (for examples see: Elias, 1957; Poulsen, 1967; Tucker, 1973; Palmer and Palmer, 1977; Lindström, 1979; Kobluk, 1981b; 1981c; Pickerill and Harland, 1984). Body fossils of sponges are uncommon in most ancient reefs. Some workers suggest this is because most sponges are, and were, largely soft tissue, and the spicules of many, comprising amorphous biogenic silica, are susceptible to solution (see Hartman, 1977 for a discussion). Only some groups of sponges secrete, or secreted, calcareous skeletons (e.g., modern and ancient sclerosponges, and the ancient stromatoporoids) that are easily preservable, so that when present, these tend to dominate most fossil assemblages.

In Bonaire only 0.8% of the sample of cryptobiontic sponges were firmly attached massive carbonate skeleton-secreting (*Merlia normani*) or potentially massive skeleton-secreting (non-calcareous form of *Merlia*; see Vacelet, 1980 and van Soest, 1984b for descriptions of, and the possible significance of skeleton-deficient *M. normani*); under 1.7% were endolithic (*Cliona, Spirastrella,* and *Aka*) and produced preservable boreholes. Of the remaining sponges with ‾∨‾ skeletons, such as the lithistids (e.g., *Discodermia dissoluta* and *Desmanthus incrustans* in the Bonaire cavities) the skeletons are not likely to be preserved in place. Following the approach of Rasmussen and Brett (1985), as much as 97.5% of the cryptobiontic sponge sample could be lost during fossilization.

CONCLUSIONS

With increasing depth (starting at 12 m) the cryptobiontic sponges in reef cavities in Bonaire, N.A., reach their highest diversity at approximately 18 m depth, and decline in diversity below 18 m at least as far as the limits of this study at 43 m depth. The cryptobiontic assemblage is dominated by *Niphates erecta* (17.4% of the specimens) and *Ectyoplasia ferox* (7.7%). Only 13 of the species have an abundance of 2% or more of the sample. As a result, most species are very uncommon or rare; although the species diversity is moderately high, the assemblage is dominated by a small number (15 species = 16%) of species.

Only 13 of the 92 species in the collection were found through the entire 12 m to 43 m depth range of the study; 9 species occur at only about 12 m depth, 11 at 18 m depth, 12 at 24 m depth, 8 at 30 m depth, and 1 species was found only at 43 m depth (it may occur deeper as well). Most of these are known from other published work to have different or broader depth ranges; however, 17 of the cryptobiontic sponge species in this study appear to be depth restricted. Although tentative, this suggests that there may be some depth zonation of cryptic sponge species, at least in reef framework cavities, and that there is at least some potential that cryptic sponges can be useful in ancient reefs as a paleoenvironmental tool.

Five species of *Cliona, Aka coralliphaga, Aka/Metschnikowia* ? sp., *Anthosigmella varians,* and one specimen of an unidentified keratose sponge, were found as endoliths (borers) in the walls or roofs of cavities. The presence of these sponges over a broad depth range shows that bioerosion by sponges in framework reef cavities in Bonaire is widespread, although it may not be intensive. However, its importance compared to bioerosion by other groups within cavities is unknown, as is the importance of sponge bioerosion in cavities compared to its importance in more exposed surface habitats in reefs.

The fossil record of cryptobiontic sponges in reefs is very sparse. There are, however, a few studies that show that cryptobiontic sponges were, or probably were, present. The poor fossil record of cryptobiontic reef-dwelling sponges may be reflecting in part the same preservational biases that affect the surface-dwelling sponges.

In Bonaire less than 1% of the sample of cryptobiontic sponges were carbonate skeleton-secreting (*Merlia normani*) or potentially skeleton-secreting (non-calcareous form of *Merlia*; under 2% were endolithic (*Cliona, Spirastrella,* and *Aka*) and produced preservable boreholes. Therefore, as much as 97% of this cryptobiontic sponge sample could be lost during fossilization, indicating that the fossil record of cryptobiontic sponges may be a very poor representation of the importance of sponges in ancient reef cavities.

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