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DO SPICULES IN SEDIMENTS REFLECT THE LIVING SPONGE COMMUNITY? A TEST IN A CARIBBEAN SHALLOW-WATER LAGOON

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ABSTRACT

We compared sponge spicules occurring in surface sediments with those of a living sponge community in a shallow-water reef environment of Bocas del Toro archipelago, Panama, with the goal of evaluating how faithfully spicular analysis reflects the living sponge community. Most megasclere morphotypes present in living species are also found in sediment. On the contrary, microscleres are underrepresented in the sediment samples. Apart from spicules that belong to taxa that live at present in the area, some morphotypes found in the sediment have no equivalent in the known living community. Forty species of living sponges have been recognized in the study area, but 9 (22%) do not produce mineral spicules and, therefore, are not recorded in sediment. Sediment spicules suggest the presence of 22 taxa, thus, loss of information in the process of fossilization is average to considerable, with most living taxa identified also with sediment spicules. Some morphotypes are abundant in sediment (i.e., ovoid spicules) even though the sponges bearing them are rare or absent, thus suggesting either preferential preservation or recent disappearances of taxa producing them. As transport did not play a significant role during the fossilization process, spicular analysis—when all limitations and constraints are considered—is a tenable tool in the reconstruction of former sponge communities, but not of the share of various sponge species. Spicular analysis may also help reveal the presence of cryptic and excavating species that are often overlooked in traditional studies.

INTRODUCTION

Since the Precambrian, sponges have been important members of coastal marine benthic ecosystems (Díaz and Rützler, 2001; Wulff, 2001; Gochfeld et al., 2007; Love et al., 2009). They provide structure and shelter for a wide array of other organisms, are themselves important food items, filter large quantities of water, and provide a vital role in the stability of reefs by gluing fragments of reef rubble together and, thus, providing a stable medium (=substrate) for the settlement of other organisms (Wulff, 1984).

Understanding changes in sponge communities over time is, therefore, of considerable interest. Sponges, however, rapidly disintegrate and rarely fossilize whole. Fortunately, their mineral skeletal elements called spicules are often preserved in sediments after the death and disintegration of the sponge organism, and spicules have characters potentially enabling the composition of a living sponge community to be reconstructed.

The general issues concerning fidelity of the fossil record have been studied in numerous papers (e.g., Schopf, 1978; Olszewski and Kidwell, 2007; Lloyd et al., 2012), but they never concentrated on sponges. While spicular analysis has successfully been used by paleontologists to explore the composition of ancient sponge faunas and their associated environments (e.g., Hinde and Holmes, 1892; Koltun, 1960; Reif, 1967; Mostler, 1990; Wiedenmayer, 1994; Pisera, 1997; Pisera et al., 2006, and references therein), the use of spicule assemblages as a proxy for inferring changes in more recent sponge communities has so far received little attention. Inoue (1984, 1985) used spicules in Holocene sediments to reconstruct changes in sponge communities in Sagami Bay (Japan), and freshwater sponge spicules preserved in Holocene lake sediments have been analyzed by Harrison et al. (1979), Hall and Herrmann (1980), Harrison (1988), Volkmer-Ribeiro and Turcq (1996), Gaiser et al. (2004), Parolin et al. (2007, 2008), and Volkmer-Ribeiro et al. (2007).

One major obstacle to the use of spicular analysis to reconstruct ancient sponge communities is that the relationship between living sponge communities and the assemblages of spicules in sediments has yet to be fully explored. The purpose of this paper is to reveal how faithfully sponge spicules in sediments reflect the living sponge community in a shallow marine lagoon in the southwestern Caribbean.

Limitations and Concerns of Spicular Analysis

Although some sponges possess only organic skeletons, most have skeletons composed of small, mineral elements made of opaline silica or calcium carbonate called spicules. The morphology and arrangement of spicules vary considerably and they are the basis for sponge classification. Some sponges may have solid, fused, or articulated skeletons that may be preserved intact, but most shallow-water tropical sponges, which belong principally to the class Demospongiae, have skeletons consisting of loose spicules that disintegrate rapidly following death. Spicules, thus, become incorporated into sediment and often form the main component of particulate silica on reefs (Rützler and Macintyre, 1978). As only those sponges that produce spicules have a good chance of being preserved as fossils, an important component of the living sponge community is lost in the process of fossilization. Furthermore, the presence of spicules in sediment that are not observed in nearby living sponges might arise in several ways, including incomplete sampling of natural special patchiness of temporal variability in living populations. The spicules may also reflect the former presence of living sponges that are unlikely to reoccupy the area owing to environmental change then.

The morphological types of sponge spicules, the number of spicule morphotypes, and the quantity of spicules can vary greatly among and within species. Although spicule types are taxonomically important they are not all constrained to clades, with some morphotypes repeated across families and even orders. Many sponge species produce several spicule types, and little is known about the proportions of different spicule types among species and within individuals of the same species. The size of the sponge individual also influences the number of spicules.

These conditions complicate the use of spicule assemblages to evaluate sponge diversity and species composition, and in fact make strict quantitative analysis impossible. Loose, disassociated spicules in surface sediment represent an unknown number of sponge taxa of unknown biomass. Additionally, selective preservation or the removal of spicules by postmortem transportation are likely biasing factors considering the small sizes of microscleres (10–150 micrometers) and

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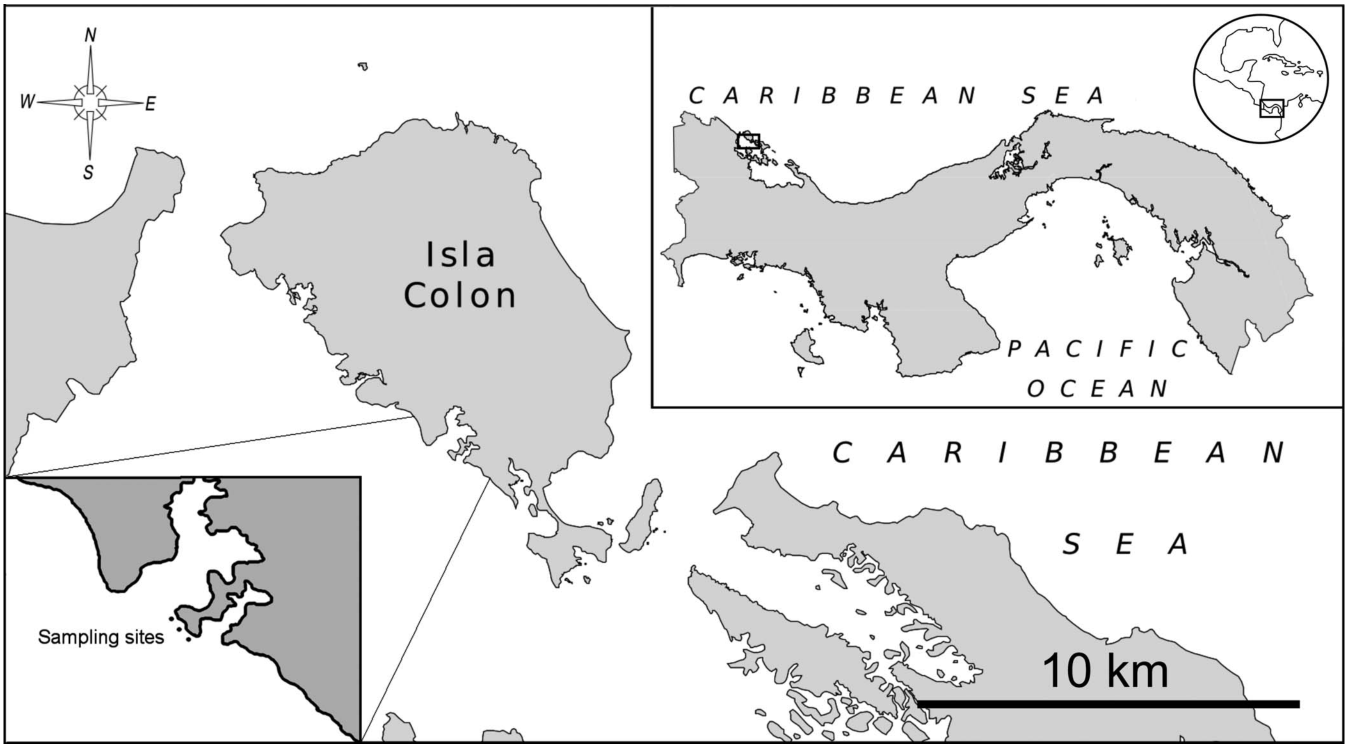

FIGURE 1—Schematic map of the study area.

natural waters that are undersaturated with respect to silica. Thus only a qualitative approach to spicular analysis of sponge communities seems reasonable (cf. Inoue, 1984).

MATERIAL AND METHODS

Setting

The Bocas del Toro archipelago, on the northwestern Caribbean coast of Panama, consists of a series of mangrove- and reef-fringed islands with lagoons having semirestricted exchange with the open Caribbean Sea and receiving large quantities of freshwater from the adjacent humid tropical mainland (Fig. 1). Of the 640 reef-associated sponge species that have been recorded in the wider Caribbean (Wulff, 2001), 130 have been found in the Bocas del Toro region (Guzmán and Guevara, 1998, 1999; Collin et al., 2005; Díaz, 2005; Díaz et al., 2007; Gochfeld et al., 2007). Of these, 106 have siliceous spicules.

The Casa Blanca reef (Fig. 1) lies in the Isla Cólon (Colon Island) within the Almirante Bay of the Archipelago and represents a diverse, well-developed patch reef (e.g., Collin et al., 2005). The coral-sponge community in this region has seen recent deterioration with reduced coral cover and increasing macroalgae due to various factors, with the latter including e.g., increasing concentrations of organic pollutants (Gochfeld et al., 2007).

Approach

A polygon was demarcated (9°21′35.9″N/82°16′38″W, 9°21′38.6″N/82°16′40.9″W, 9°21′41.5″N/82°16′43.6″W) within which three 5×5 m quadrats were randomly located at the Casa Blanca sandy patch reef. All three quadrats were at a depth of around 5–6 m. Surveys were made by SCUBA in June 2011. Three quadrats were used in the survey to reduce the influence of the patchiness in the sponge distribution. Within each quadrat the living sponge fauna was surveyed (by visual inspection and photography), living sponge samples of each recognized species collected, and a surface (1-cm-deep) sediment sample recovered by scoop to permit a comparison of living sponge and sediment spicule assemblages. For the terminology of spicule morphotypes used in this paper see Boury-Esnault and Rützler (1997) and Hooper and Van Soest (2002).

Living Sponge Survey

Within the three 25 m^2 quadrats, every individual sponge observed via SCUBA survey was identified to the lowest possible taxonomic level based on morphology (Guzmán and Guevara, 1998, 1999; Guzmán, 2003; Collin et al., 2005; Díaz, 2005; Gochfeld et al., 2007) and counted following the approach to determine physiological independence as proposed by Wulff (2001). Abundance of each sponge taxa within each quadrat was estimated volumetrically and by the number of individual sponges (herein termed biomass), and placed within five volumetric classes arbitrarily chosen by the authors but with respect to observed size distribution of sponge individuals in nature. Underwater photographs and voucher specimens were taken of some of the sponges for subsequent identification in the laboratory.

In the laboratory, samples of living sponges were macerated using two boiling cycles in concentrated household bleach, Clorox (5.95% sodium hypochlorite) to remove organic material including sponge fibers. Following this maceration, free spicules were recovered and placed on microscope slides for identification. Various spicule morphotypes were further studied using Scanning Electron Microscopy (SEM) to complete identification at the Institute of Paleobiology, Warsaw, Poland.

Spicules in Sediment Samples

In each quadrat a ~30 cm^3 sample of surface sediment was collected down to a depth of ~1 cm in the sediment from which 1 gram of dry sediment was further analyzed. The three sediment samples were subsequently dried, weighed, and macerated by treating them in 30% hydrogen peroxide to remove small particles of organic material and to help clean and separate sponge spicules, including microscleres up to

~150 micrometers in size (if possible) and megascleres that reach the size of centimeters (Van Soest et al., 2012). Nevertheless, the division into micro- and megascleres is not a strict one and there were some spicule morphotypes assigned as microscleres (e.g., geodiid sterrasters) having size within the megasclere range. Spicules were then handpicked from the dried residues under binocular microscope. Morphological spicule types were isolated, mounted on SEM stubs and identified using SEM. The spicule assemblages are deposited in the Institute of Paleobiology, Polish Academy of Sciences, Warsaw, under ZPAL Pf.24.

RESULTS

Living Sponge Diversity and Abundance

Forty living sponge species were recorded in the three quadrats in the Casa Blanca lagoon environment, which represents approximately a third of the 130 species that have ever been encountered alive across the Bocas del Toro archipelago by previous workers (Guzmán and Guevara, 1998, 1999; Guzmán, 2003; Collin et al., 2005; Díaz, 2005; Gochfeld et al., 2007; Tables 1–2). Thirty-one of these 40 species bear spicules and thus have potential to be recorded in sediments.

Living Sponge Biomass

The three largest biomass contributors in the quadrats were *Aplysina fulva*, *Amphimedon compressa*, and *Niphates erecta.* The above species of sponges, whose volumes varied from 6060 cm^3 to 7340 cm^3, were assigned to the fifth volumetric class and comprised 44% of all sponge biomass. In the next most voluminous class there were 11 sponge species assigned: *Mycale (Mycale) laevis*, *Verongula rigida*, *Chondrilla caribensis*, *Aplysina cauliformis*, *Cliona* sp., *Placospongia intermedia*, *Ircinia strobilina*, *Iotrochota birotulata*, *Monanchora arbuscula, Xestospongia muta*, and *Aiolochroia crassa* which constituted ~35% of a total sponge biomass. In this class the volume of sponges ranges from 910 cm^3 to 2380 cm^3. Seven smaller biomass constituents: *Cliona delitrix*, *Haliclona* sp., *Agelas* sp., *Neofibularia nolitangere*, *Ircinia* sp., *Spirastrella* sp., and *Neopetrosia rosariensis*, were placed in the third class of volume ranging from 270 cm^3 to 570 cm^3 (~6% of total biomass). The next nine sponge species: *Aplysina lacunosa*, *Mycale (Arenochalina) laxissima*, *Plakortis angulospiculatus*, *Ircinia felix*, *Mycale* sp., *Cliona varians*, *Clathria* sp., *Xestospongia* sp., and *Cinachyrella alloclada,* were placed in the second biomass class (~4% of total biomass) in which volume varied from 160 cm^3 to 200 cm^3. Finally, the biomass rapidly decreases (from 90 cm^3 to 10 cm^3) and the remaining ten sponge species, including: *Neopetrosia carbonaria, Niphates caycedoi*, *Lyssodendoryx (Lissodendoryx) colombiensis*, *Halichondria* sp., *Oceanapia peltata, Neopetrosia proxima*, *Dragmacidon reticulatum*, *Spongia* sp., *Tedania (Tedania) ignis*, and *Myrmekioderma* sp., had minor significance and were assigned to the first class and constitute hardly 1% of total sponge biomass.

Apart from the sponges discussed above, we found also 85 small individuals that belonged mostly to the first and second volumetric class, and to which taxonomic assignment was not established mostly due to their very small size. These individuals constituted about 10% of all sponge biomass.

Frequency of Spicule Types in Sediments

Spicules were dominated by monaxons, tetraxons, or polyactines that belong to nonlithistid demosponges—the highly distinctive spicules of lithistid and hexactinellid sponges were rare. Almost half of the spicules (49.4%) are sterrasters and/or selenasters (Table 3). The next most abundant morphological spicule types are oxeas and/or strongyles (18.7%), spherical microscleres (anthasters, spherasters), which comprise 4.6%, and styles (1.7%). All other types constitute <1% of the total spicule assemblage (Table 3).

We also included in our analysis the category broken (this constituted 21.9%) because we know that they are mostly fragments of monaxial spicules, and to a lesser degree, tetraxons, and thus they can be used in further analysis.

DISCUSSION

Caveats: Taxonomic Assignment of Sediment Spicules

The ovoid microsclere spicules called sterrasters and selenasters that dominate in the spicule assemblage (Figs. 2N–O) belong unambiguously to the sponge families Geodiidae (order Astrophorida) or Placospongiidae (order Hadromerida). More precise identification, however, was not possible under a binocular microscope because of their small size and similar morphology. The next most abundant types of spicules—oxeas and/or strongyles and styles (Figs. 2A–E)—occur in a very wide range of sponge families or even orders and, thus, cannot be assigned to any living sponge taxa in the local fauna. Three different morphotypes can nonetheless be distinguished within this group, and these undoubtedly belong to different taxa.

The spherical spicules from the next most abundant morphogroup—microsclere anthasters and spherasters (Figs. 2R, X)—may belong to the family Geodiidae (order Astrophorida), Spirastrellidae, Placospongiidae (order Hadromerida), and/or Chondrillidae (order Chondrosida). However, in the case of such ovoid spicules they cannot be differentiated more finely using a binocular microscope because of their morphological similarity and small size. There were at least two different types of spherasters present, however, and one type of anthaster microscleres.

Rarer spicule types, such as tylostyles (Figs. 2K–M), are equally difficult to assign to narrower taxonomic units because they may occur, for example, in Spirastrellidae, Suberitidae, Clionaidae, Crambeidae, and Microcionidae. At least three separate morphological types are present, however, most probably belonging to different species.

The long-shafted triaenes (Fig. 2H), which may belong to the family Geodiidae, were also observed in the sediment. There are two species of living geodiids reported from this region—*Geodia papyracea* and *Erylus formosus*—and the triaenes found in this study probably belong to *E. formosus* based on their size. This conclusion is supported by the presence of flat, discoidal microscleres called aspidasters (0.4% of spicule assemblage; Figs. 2P–Q) that closely resemble those occurring in living specimens of this species from Bocas del Toro (Díaz, 2005), although *E. formosus* was not found in our living surveys.

Besides triaenes of geodiid affinity, some other morphotypes were noted, for example, the long and slender dichotriaenes (Fig. 2G) that belong most probably to the family Pachastrellidae Carter, 1875. Moreover, some triods and oxeas with split ends that occur in this family were also found (Figs. 2C, W).

The rare sigma microscleres (Figs. 2S, Y) occur in a wide range of sponge families making their assignment to specific taxa untenable. In contrast, the calthrops (Fig. 2BB) can be more confidently assigned to the family Pachastrellidae, and some of them, such as the very characteristic triaenes with strongly branched clads as well as short-shafted dichotriaenes (with branched clades) (Figs. 2T–V, AA), undoubtedly belong to the pachastrellid genus *Triptolemma* Sollas, 1888 (order Astrophorida). They especially resemble those known from *Triptolemma endolithicum* Van Soest, 2009, an encrusting species that grows on lithistid demosponges of the genus *Corallistes* Schmidt, 1870. This species has been reported from the Colombian coasts of South America and the Southern Caribbean, but this is its first record in the Bocas del Toro region. We did not find characteristic microscleres from this species, but this may be because of their small size, dissolution, and sampling bias.

We also observed rare but characteristic tuberculated acanthoxeas (Fig. 2I) that clearly belong to *Alectona* Carter, 1879 (Alectonidae:

TABLE 1—Sponge species reported from Bocas del Toro region from Díaz, 2005; Collin et al., 2005; Guzmán and Guevara, 1998, 1999; and this study. Sponge spicules listed for family, or to a lower taxonomic level if the spicules are characteristic of the extant family. Bold = sponge species found in the sampling area during present study; Underlined = sponge species noted from Bocas del Toro for the first time; P. o. a. = present or absent; I. p. = if present (data from Hooper and Van Soest, 2002).

Order	Family	Species	Macrosclere spicules types	Microsclere spicule types
Verongida	Aplysinidae	***Aiolochroia crassa* (Hyatt, 1875)**	**no spicules**	
		***Aplysina lacunosa* (Lamarck, 1814)**	**no spicules**	
		***Aplysina fulva* (Pallas, 1766)**	**no spicules**	
		***Aplysina cauliformis* (Carter, 1882)**	**no spicules**	
		Aplysina insularis (Duchassaing & Michelotti, 1864)	no spicules	
		***Verongula rigida* (Esper, 1794)**	**no spicules**	
		Verongula reiswigi Alcolado, 1984	no spicules	
Dictyoceratida	Irciniidae	***Ircinia strobilina* (Lamarck, 1816)**	**no spicules**	
		***Ircinia felix* (Duchassaing & Michelotti, 1864)**	**no spicules**	
		***Ircinia* sp.**	**no spicules**	
		Ircinia campana (Lamarck, 1814)	no spicules	
		Dysidea etheria de Laubenfels, 1936	no spicules	
	Spongiidae	***Spongia* sp.**	**no spicules**	
		Spongia tubulifera Lamarck, 1814	no spicules	
		Spongia (Spongia) pertusa Hyatt, 1877	no spicules	
		Hyattella cavernosa (Pallas, 1766)	no spicules	
	Thorectidae	*Hyrtios proteus* Duchassaing & Michelotti, 1864	no spicules	
Haplosclerida	Petrosiidae	***Xestospongia muta* (Schmidt, 1870)**	**slightly curved oxeas, strongyles > 200 µm**	
		***Xestospongia* sp.**	**oxeas, sometimes styles, strongyles**	
		***Neopetrosia rosariensis* (Zea & Rützler, 1983)**	**oxeas, strongyles, styles > 200 µm**	
		***Neopetrosia proxima* (Duchassaing & Michelotti, 1864)**	**oxeas, stylote, strongylote forms**	
		Neopetrosia subtriangularis (Duchassaing, 1850)	oxeas	
		***Neopetrosia carbonaria* (Lamarck, 1814)**	**oxeas, styles, strongyles**	
		Petrosia (Petrosia) pellasarca (de Laubenfels, 1934)	oxeas (oxeote and strongylote) > 400, > 130, > 100 µm	centrangulate oxeas
		Petrosia (P.) weinbergi Van Soest, 1980	oxeas, strongyles	
	Phloeodictyidae	***Oceanapia peltata* (Schmidt, 1870)**	**oxeas**	**sigmas, toxas**
		Oceanapia nodosa (George & Wilson, 1919)	oxeas	
		Oceanapia oleracea (Schmidt, 1870)	strongyles	
		Siphonodictyon coralliphagum Rützler, 1971	short slender, curved oxeas, 100–200 µm	
		Siphonodictyon cf. *brevitubulatum* Pang, 1973	oxeas	
		Calyx podatypa (de Laubenfels, 1934)	oxeas	i. p., toxas
	Chalinidae	*Chalinula molitba* (de Laubenfels, 1949)	short vestial to cigar-shaped oxeas, 2–100 µm	
		Chalinula zeae de Weerdt, 2000	oxeas	
		***Haliclona* sp.**	**smooth diactines, oxeas, or strongyles, 80–250 µm**	**i. p., sigmas, toxas, raphides, or microxeas**
		Haliclona (Rhizoniera) curacaoensis (Van Soest, 1980)	oxeas	
		Haliclona (Reniera) implexiformis (Hechtel, 1965)	oxeas	
		Haliclona (R.) manglaris Alcolado, 1984	oxeas	
		Haliclona (R.) mucifibrosa de Weerdt et al., 1991	oxeas	
		Haliclona (R.) tubifera (George & Wilson, 1919)	oxeas	
		Haliclona (Halichoclona) vansoesti de Weerdt et al., 1999	slightly curved oxeas	
		Haliclona (Soestella) twincayensis de Weerdt et al. 1991	oxeas	
		Haliclona (S.) vermeuleni de Weerdt, 2000	slender oxeas	
		Haliclona (S.) caerulea (Hechtel, 1965)	oxeas	
		Haliclona (S.) piscaderaensis (Van Soest, 1980)	oxeas	
		Haliclona n.sp.	oxeas	
	Niphatidae	***Amphimedon compressa* Duchassaing & Michelotti, 1864**	**slightly bent oxeas, multitelescoped, or strongylote apices, 100–170 µm**	
		Amphimedon viridis Duchassaing & Michelotti, 1864	oxeas	
		Amphimedon erina (de Laubenfels, 1936)	oxeas	i. p., toxas
		***Niphates caycedoi* (Zea & Van Soest, 1986)**	**oxeas**	**stigmata, p. o. a.**
		***Niphates erecta* Duchassaing & Michelotti, 1864**	**oxeas**	

TABLE 1—Continued.

Order	Family	Species	Macrosclere spicules types	Microsclere spicule types
	Callyspongidae	*Callyspongia (Cladochalina) vaginalis* (Lamarck, 1814)		toxas
		Callyspongia (C.) armigera (Duchassaing & Michelotti, 1864)	no spicules	
		Callyspongia (Callyspongia) pallida Hechtel, 1965	oxeas	
		Callyspongia (C.) fallax Duchassaing & Michelotti, 1864		i. p., toxas
Spirophorida	Tetillidae	***Cinachyrella alloclada* (Uliczka, 1929)**	**long protriaenes, amphitriaenes, oxeas, fusiform, sharply pointed**	**sigmaspires**
		Cinachyrella apion (Uliczka, 1929)	oxeas, styles, amphitriaenes, protriaenes, tylostyles	sigmatas, raphides
Hadromerida	Spirastrelliadae	***Spirastrella* sp.**	**tylostyles**	**spirasters in two size categories**
		Spirastrella coccinea (Duchassaing & Michelotti, 1864)	tylostyles	spirasters
		Spirastrella hartmani Boury-Esnault et al., 1999	tylostyles	spirasters
		Spirastrella mollis Verrill, 1907	tylostyles	spirasters
		Diplastrella megastellata Hechtel, 1965	tylostyles	anthasters, oxyasters
	Suberitidae	*Terpios manglaris* Rützler & Smith, 1993	tylostyles with flattened-lobate or lumpy, wrinkled styles	
		Prosuberites laughlini (Díaz et al., 1987)	tylostyles	
		Suberites aurantiacus (Duchassaing & Michelotti, 1864)	tylostyles in two size categories	i. p., centrotylote microstrongyles
	Clionaidae	***Cliona delitrix* Pang, 1973**	**slightly curved tylostyles**	**spirasters or raphides**
		***Cliona varians* (Duchassaing & Michelotti, 1864)**	**tylostyles**	**anthosigmas**
		Cliona caribbaea Carter, 1882	tylostyles	toxas, spirasters
		Cliona tenuis Zea & Weil, 2003	tylostyles	spirasters
		Cliona aprica Pang, 1973	tylostyles	spirasters
		***Cliona* sp.**	**tylostyles**	**raphides or spirasters**
		Spheciospongia vesparium (Lamarck, 1815)	tylostyles	sigmaspires, spirasters
		Cervicornia cuspidifera (Lamarck, 1815)	styles, strongyles, tylostyles	spirasters
	Tethyidae	*Tethya* aff. *seychellensis* (Wright, 1881)	strongyloxeas, styles, spherasters, or oxyspherasters	tylosters, strongylasters, or oxyasters
		Tethya actinia de Laubenfels, 1950	styles	spherasters
	Theonellidae	*Discodermia dissoluta* Schmidt, 1880	desmas: massive tetraclones with branched and tuberculated zygomes and smooth rays, oxeas	slender fusiform and slightly curved or bent acantho- xeas (spines are hooklike), massive acanthorhabds
	Placospongiidae	***Placospongia intermedia* Sollas, 1888**	**tylostyles of two size classes**	**microscleres selenasters, spirasters, spherasters, and spherules**
Poecilosclerida	Crambeidae	***Monanchora arbuscula* (Duchassaing & Michelotti, 1864)**	**tylostyles**	**sigmatose chelae, spined microxeas**
	Microcionidae	***Clathria* sp.**	**tylostyles, styles, acanthostyles**	**isochelae and toxas with smooth or spined points**
		Clathria (Thalysias) venosa (Alcolado, 1984)	tylostyle, acanthotylostyles,	spirasters, toxas
		Clathria (T.) schoenus(de Laubenfels, 1936)	subtylostyles	isochelae, toxas
		Clathria (Clathria) microchela (Stephens, 1916)	acanthostyles, subtylostyles	isochelae
		Clathria (Microciona) echinata (Alcolado, 1984)	styles	isochelae
		Clathria cf. *(Microciona) ferrea* (de Laubenfels, 1936)	subtylostyles	isochelae, toxas
	Acarnidae	*Acarnus nicoleae* Van Soest et al., 1991	tylotes with swollen microspined bases, styles smooth, slightly curved at center, cladotylotes in two size classes	oxhorns, thin deeply curved and accolada toxas, palmate isochelae
	Raspaillidae	*Ectyoplasia ferox* (Duchassaing & Michelotti, 1864)	styles or acanthostyles, rhabdostyles	
	Desmacellidae	***Neofibularia nolitangere* (Duchassaing & Michelotti, 1864)**	**diactinal megascleres**	**sigmas, microxeas, raphides, commata**
		Biemna caribea Pulitzer-Finali, 1986	styles, 360–700 μm, abruptly bent near the rounded end	sigmas, microxeas, commata and raphides
	Mycalidae	***Mycale (Mycale) laevis* (Carter, 1882)**	**styles, subtylostyles, oxeas**	**aniso- and isochelae, rosettes, sigmas, toxas, raphides; microacanthoxeas**
		***Mycale (Arenochalina) laxissima* (Duchassaing & Michelotti, 1864)**	**spinulate, palmate anchorates, bihamates**	
		Mycale (Carmia) microsigmatosa Arndt, 1927	subtylostyles	anisochelae, sigmas
		Mycale (C.) magnirhaphidifera Van Soest, 1984	tylostyles	anisochelae, trichodragmatas
		Mycale (Aegogropila) carmigropila Hajdu & Rützler, 1998	subtylostyles	anisochelae, toxas
		Mycale (A.) citrina Hajdu & Rützler, 1998	subtylostyles	anisochelae, sigmas
		Mycale (A.) angulosa (Duchassaing & Michelotti, 1864)	subtylostyles	
		Mycale (A.) arndti Van Soest, 1984	subtylostyles	sigmas, rosetes
		Mycale cf. *(Aegogropila) americana* Van Soest, 1984	subtylostyles	anisochelae, sigmas
		***Mycale* sp.**	**(mycalo)styles, rarely replaced by oxeas**	**anisochelae**

TABLE 1—Continued.

Order	Family	Species	Macrosclere spicules types	Microsclere spicule types
	Coelosphaeridae	***Lyssodendoryx (Lissodendoryx) colombiensis* Zea & Van Soest, 1986**	**strongyles**	**sigmas, chelae**
		Lissodendoryx (L.) isodictyalis (Carter, 1882)	styles, tylotes	sigmas, chelae
	Tedanidae	***Tedania (Tedania) ignis* (Duchassaing & Michelotti, 1864)**	**tylostyles, styles, with smooth or microspined bases**	**raphides**
	Desmacididae	*Desmapsamma anchorata* (Carter, 1882)	slender oxeas	anchorate isochelae and sigmas
	Iotrochotidae	***Iotrochota birotulata* (Higgin, 1877)**	**styles or oxeas, or only strongyles**	**birotulas**
Chondrosida	Chondrillidae	***Chondrilla caribensis* Rützler et al., 2007**	**spherasters**	
		Chondrosia collectrix (Schmidt, 1870)	oxeas	sigmas, microxeas, commata, raphides
Halichondrida	Axinellidae	***Dragmacidon reticulatum* (Ridley & Dendy, 1886)**	**styles and/or oxeas, with telescoped tips**	**i. p., raphides in tightly packed trichodragmata**
		Ptilocaulis walpersi (Duchassaing & Michelotti, 1864)	styles in two size categories, occasionally oxeas or anisoxeas	
	Halichondriidae	***Halichondria* sp.**	**oxeas**	
		Halichondria (Halichondria) lutea Alcolado, 1984	oxeas	
		Halichondria (H.) magniconulosa Hechtel, 1965	oxeas	
		Halichondria (H.) melanadocia de Laubenfels, 1936	oxeas	
	Desmanthidae	*Petromica (Chaladesma) ciocalyptoides* (Van Soest & Zea, 1986)	monocrepid desmas, large, usually bent, oxeas, strongyloxeas and anisorhabds	
	Dictyonellidae	*Svenzea zeai* (Alvarez, Van Soest & Rützler, 1998)	short styles, with oxeote endings, oxeas	
		Scopalina ruetzleri (Wiedenmayer, 1977)	styles	
	Heteroxyidae	***Myrmekioderma* sp.**	**oxeas or acanthoxeas, strongyles, styles**	**raphides in trichodragmata**
Homosclerophorida	Plakinidae	***Plakortis angulospiculatus* (Carter, 1882)**	**diods centrotylote or with knobby-knotty centers, triods, sometimes calthrops**	**diactinal**
		Plakortis halichondrioides (Wilson, 1902)	oxeas	
		Plakinastrella onkodes Uliczka, 1929	nonlophose diods, triods, and/or calthrops, usually in 3 size classes	
		Oscarella sp.	no spicules	
Agelasida	Agelasidae	***Agelas* sp.**	**verticillate acanthoxeas and acanthostyles**	
		Agelas dispar Duchassaing & Michelotti, 1864	verticillate acantoxeas and acanthostyles	
		Agelas clathrodes (Schmidt, 1870)	verticillate acantoxeas and acanthostyles	
		Agelas conifera (Schmidt, 1870)	verticillate acantoxeas and acanthostyles	raphides
Astrophorida	Geodiidae	*Geodia papyracea* Hechtel, 1965	oxeas and plagio-, orthotriaenes	sterrasters, oxyasters
		Erylus formosus Sollas, 1886	triaenes (plagiotriaenes, orthotriaenes) and oxeas	microrhabds and aspidasters
Halisacrida	Halisarcidae	*Halisarca caerulea* Vacelet & Donadey, 1987	no spicules	
		Halisarca sp.	no spicules	
Dendroceratida	Darwinellidae	*Aplysilla glacialis* (Merejkowski, 1878)	no spicules	
		Chellonaplysilla erecta Tsurnamal, 1967	no spicules	
Calcarea		*Clathrina primordialis* (Haeckel, 1872)	no spicules	

TABLE 2—Species, spicule types and biomass of the investigated sponges. In the volumetric classes, column I, II, III, IV, or V denotes volumetric class (I = volume <21 cm^3, II = volume 21–140 cm^3, III = volume 141–240 cm^3, IV = volume 241–560 cm^3, V = volume >560 cm^3); number of sponges of each species\average volume of individuals in each class; the share of biomass of each species (given in percents) of a total investigated sponge biomass.

Species	Spicule types	Volumetric classes I	II	III	IV	V	% of all biomass
Amphimedon compressa	Slightly bent oxeas, multitelescoped or strongylote apices	11\110	50\4000	17\3230	-	-	15,80
Aplysina fulva	No spicules	28\280	74\5920	4\760	-	-	14,98
Niphates erecta	Oxeas	9\90	39\3120	15\2850	-	-	13,04
Mycale (Mycale) laevis	Styles, subtylostyles, oxeas, aniso- and isochelae, microsclere rosettes, sigmas, toxas, raphides; microacanthoxeas	27\270	24\1920	1\190	-	-	5,12
Verongula rigida	No spicules	4\40	13\1040	2\380	-	-	4,48
Chondrilla nucula	Spherasters	5\50	19\1520	1\190	-	-	3,79
Aplysina cauliformis	No spicules	3\30	7\560	5\950	-	-	3,31
Cliona sp.	Tylostyles, raphides, or spirasters	32\320	14\1120	-	-	-	3.10
Placospongia intermedia	Tylostyles of two size classes, microscleres selenasters, spirasters, spherasters, spherules	5\50	12\960	2\380	-	-	2.99
Ircinia strobilina	No spicules	1\10	4\320	5\950	-	-	2.76
Iotrochota birotulata	Styles or oxeas, or only strongyles, birotulas	1\10	3\240	5\950	-	-	2.58
Monanchora arbuscula	Tylostyles, sigmatose chelae, spined microxeas	6\60	6\480	3\570	-	-	2.39
Xestospongia muta	Oxeas, sometimes styles, strongyles	-	-	-	2\1040	-	2.24
Aiolocroia crassa	No spicules	2\20	4\320	3\570	-	-	1.96
Cliona delitrix	Slightly curved tylostyles, spiraster microscleres, or raphides	3\30	2\160	2\380	-	-	1.23
Haliclona sp.	Smooth diactines, oxeas or strongyles, 80–250 µm, i.p., microsclere sigmas, toxas, raphides, or oxeas	24\240	4\320	-	-	-	1.21
Agelas sp.	Verticillate acanthoxeas and acanthostyles	2\20	6\480	-	-	-	1.08
Neofibularia nolitangere	Diactinal megascleres, microsclere sigmas, microxeas, raphides, commata	-	3\240	1\190	-	-	0.93
Ircinia sp.	No spicules	-	4\320	-	-	-	0.69
Spirastrella sp.	Tylostyles, microsclere spirasters in two size categories	4\40	1\80	1\190	-	-	0.67
Neopetrosia rosariensis	Oxeas, strongyles, styles	-	1\80	1\190	-	-	0.58
Aplysina lacunosa	No spicules	1\10	0	1\190	-	-	0.43
Mycale (Arenochalina) laxissima	Spinulate, palmate anchorates, bihamates	-	-	1\190	-	-	0.41
Plakortis angulospiculatus	Diods, triods, sometimes calthrops, diactinal microscleres	3\30	2\160	-	-	-	0.41
Ircinia felix	No spicules	-	-	1\190	-	-	0.41
Mycale sp.	Mycalostyles, rarely replaced by oxeas, anisochelae microscleres	2\20	2\160	-	-	-	0.39
Cliona varians	Tylostyles, anthosigma microscleres	1\10	2\160	-	-	-	0.37
Clathria sp.	Tylostyles, styles, acanthostyles, microsclere isochelae, and toxas	1\10	2\160	-	-	-	0.37
Xestospongia sp.	Oxeas, sometimes styles, strongyles	-	2\160	-	-	-	0.34
Cinachyrella alloclada	Long protriaenes, amphitriaenes, oxeas, fusiform, sharply pointed, sigmaspire microscleres	-	2\160	-	-	-	0.34
Neopetrosia carbonaria	Oxeas, styles, strongyles	1\10	1\80	-	-	-	0.19
Niphates caycedoi	Oxeas, p.o.a. sigmata microscleres	-	1\80	-	-	-	0.17
Lyssodendoryx (L.) colombiensis	Strongyles, microsclere sigmas, chelae	-	1\80	-	-	-	0.17
Halichondria sp.	Oxeas	-	1\80	-	-	-	0.17
Oceanapia peltata	Oxeas, microsclere sigmas, toxas	6\60	-	-	-	-	0.13
Neopetrosia proxima	Oxeas, stylote, strongylote forms	1\10	-	-	-	-	0.02
Dragmacidon reticulatum	Styles and/or oxeas, with telescoped tips, i.p., raphides microscleres	1\10	-	-	-	-	0.02
Spongia sp.	No spicules	1\10	-	-	-	-	0.02
Tedania (Tedania) ignis	Tylostyles, styles, with smooth or microspined bases, raphide microscleres	1\10	-	-	-	-	0.02
Myrmekioderma	Oxeas or acanthoxeas, strongyles, styles, raphide microscleres	1\10	-	-	-	-	0.02
Unrecognized		48\480	37\2960	8\1520	2\1040	-	10.68

Hadromerida). They closely resemble those of *Alectona wallichii* Carter, 1874 (compare with Vacelet, 1999, and Pisera et al., 2006). This species was not previously reported in Bocas del Toro, which may be because alectonids are excavating sponges occupying chambers and cavities and can easily be overlooked (Rützler, 2002). Thus far, *A. wallichii* has been recorded only from Hawaii, Madagascar, and southern African coasts (Vacelet, 1999; Rützler, 2002), and this is the first occurrence in the Caribbean. Interestingly, *A. wallichii* was also recognized in the fossil record of Miocene of Portugal (Pisera et al., 2006) and Eocene of Australia (Łukowiak, 2013).

The characteristic amphitriaene spicules that belong to *Samus anonymus* Gray, 1867 (Fig. 2CC) of the monogeneric family Samidae Sollas, 1888 were relatively common. This is the first record of this species in the Bocas del Toro archipelago. *S. anonymus* is globally distributed and was earlier reported from northeastern Brazil, Australia, Sri Lanka, Singapore, Florida, Palau Islands, West Africa, Mediterranean, Colombia, and Curaçao (Van Soest et al., 2011). Samids are shallow-water excavating sponges making small holes and corridors in corals and coralline algae (Van Soest and Hooper, 2002) and, thus, because of their cryptic mode of life, may easily have been overlooked in previous surveys in Bocas.

Monaxons are not usually characteristic enough to be assigned to a particular taxon, but there are some exceptions such as the oxeas with tubercles on their tips that were observed in our sediment samples (Fig. 2F). They probably belong to the halichondrid *Myrmekioderma*. The species *Myrmekioderma rea* de Laubenfels, 1934 is known from

TABLE 3—Total numbers of spicule morphotypes found in the sediment, their taxonomic attribution if possible (in parenthesis), and their proportional abundance (%).

Spicule morphotype	Number of spicules	%
Sterrasters (Geodiidae) or selenasters (Placospongiidae)	9685	49.38
Oxeas or strongyles	3665	18.7
Anthasters or spherasters	903	4.6
Styles	331	1.69
Calthrops	196	1
Tylostyles	127	0.65
Acanthoxeas (*Alectona*)	87	0.44
Aspidasters (*Erylus*)	82	0.42
Amphitriaenes (*Samus*)	82	0.42
Triaenes	70	0.36
Branched triaenes (*Triptolemma*)	65	0.33
Triods	27	0.14
Discotriaenes	9	0.05
Anchorate basalia (hexactinellid)	2	0.01
Sigma microscleres	2	0.01
Sigmaspire microscleres	1	0.005
Broken (mostly monaxonic styles and oxeas)	4279	21.82

eastern and southern Caribbean (Puerto Rico, Venezuela, Bahamas, Barbados; Van Soest et al., 2011) but is here noted for the first time from Bocas del Toro region. Usually these sponges inhabit relatively deep water (46–83 m) (Díaz et al., 1993), in contrast to our finding them from a shallow water of 6 m depth. Such taxonomic assignment of subfossil spicules is supported by the fact that we also found a living specimen of this species during our study.

The small, pointed acanthoxeas (Fig. 2J) belong to the tetillid genus *Acanthotetilla* Burton, 1959, which has not previously been reported from this area, although *Acanthotetilla gorgonosclera* Van Soest, 1977, was reported from Barbados (compare with Van Soest and Rützler, 2002). The acanthoxeas found in the sediment are almost identical with those of *A. gorgonosclera* (see Van Soest, 1977).

The only lithistid demosponge spicules found were discotriaenes (0.05%) (Fig. 2DD), which were likely from the theonellid genus *Discodermia* du Bocage, 1869. They may belong to *Discodermia dissoluta* Schmidt, 1880, which is reported from Caribbean shallow waters (Van Soest et al., 2011).

Two surprising occurrences in our sediment samples were the toothed anchorate basalia (0.01%) (Fig. 2Z) of hexactinellid sponges, which are very similar to those occurring in the family Pheronematidae Gray, 1870 (Hexactinellida: Amphidiscophora). These spicules may belong to *Pheronema annae* Leidy, 1868, because these sponges were reported from the Caribbean and Northern Gulf of Mexico. These hexactinellids, however, inhabit rather deep waters from around 90 to 5000 m (Tabachnick and Menshenina, 2002). Their occurrence in the water few meters deep may reflect shoreward postmortem transportation of spicules via e.g., sponge grazers or onshore storm transport of entire sponges. Hurricanes do not affect the Bocas region.

We have found 95 taxonomically undetermined individuals that are assigned mostly to the first and second classes (except 8 individuals assigned to third class and 2 of fourth class). These individuals may belong to species other than those mentioned here, e.g., the encrusting taxa whose spicules have been observed in the sediment, but are not recognized in the living sponge community.

Thus, based on the spicule morphotypes found in sediment we can distinguish ~22 different sponge taxa including *Samus anonymus, Placospongia intermedia, Triptolemma endolithicum, Alectona wallichii, Pheronema annae, Discodermia dissoluta,* and probably *Myrmekioderma* sp., *Acanthotetilla gorgonosclera* and *Cinachyra* sp.. Additionally, at least two species of geodiids were recognized (probably *Erylus formosus* and *Geodia papyracea*). Other morphotypes of spicules indicate the presence of *Chondrilla caribensis* (and maybe one other taxon with spherical spicules), as well as one with anthasters (probably *Diplastrella megastellata*). The presence of three different morphotypes of both oxeas and tylostyles suggests the presence of at least six further sponge species. The presence of strongyles and styles and some spicules of the sponges belonging to the family Pachastrellidae were also observed.

Relationship between Living Sponges and Sediment Macroscleres and Ovoid Microscleres

Considering the calculated biomass of living sponges in the study area, oxeas and/or strongyles and styles are the types of spicules expected to be most abundant in the sediment because of the dominance of living biomass by *Amphimedon compressa*, *Niphates erecta,* and *Mycale (Mycale) laevis.* Such spicules comprise only ~20% of all nonfragmental spicules found in the sediment, however. This discrepancy may be due to the fragility of these relatively long, thin, and slender spicules, resulting in frequent breakage and, therefore, loss from our study. Indeed, most spicules in broken condition (Table 3) are probably fragments of monaxial spicules such as oxeas and/or strongyles, styles, and to a lesser degree, tetraxons. If those fragments were added to the clearly identifiable spicules of this type, then they would constitute 42% of the total sedimentary assemblage. One would then conclude that the most common sponges in the living assemblage are among the commonest spicule types in the sampled quadrats.

Even with this possible correction, however, the most abundant spicule morphotypes found in the sediment were sterraster and selenaster microscleres (49% of assemblage). The abundance of these spicule types does not correspond with the biomass of living sponges possessing these types, namely *Geodia papyracea* and *Placospongia intermedia*, which, although documented from the Bocas del Toro region by Díaz (2005) and Gochfeld et al. (2007), were either not found (*Geodia*) or moderately frequent (*Placospongia*, Table 2). The unexpected predominance of these ovoid-shaped spicules in sediment might have several causes, including lower rates of postmortem transportation out of the local habitat (e.g., Rützler and Macintyre, 1978), lower rates of postmortem destruction (e.g., owing to lower surface area to volume ratios than elongate spicules), and/or preferential removal of other spicule types by winnowing. This supposition of postmortem bias is supported by the fact that, in the studied area some additional spicule types that characterize these two sponge species are very rare from sediment (triaenes constitute only 0.4% of all spicules and tylostyles 0.7%). The abundance of those spicule types is thus more comparable to the relative abundance of these two genera among living sponges. Notably, as another factor in the overrepresentation of selenasters or sterrasters in sediment, both *Geodia* and *Placospongia* are characterized by extremely heavy (thick and dense) ectosomal armor formed by these spicules, respectively. This density of spicules exceeds that known in any other here-considered sponges. Thus, interpretation of the frequency of these spicule morphotypes in the sediment must be done with utmost caution.

A similar situation arises with aspidaster microscleres from the geodiid *Erylus formosus*. They were present in sediments but very rare (0.4%). Although the genus *Erylus* was not found during our study of living sponges, it was observed by other authors (e.g., Collin et al., 2005) in the study area. The most parsimonious explanation of our findings is that sponges bearing such spicules have been present in the past in the study area, and have only recently disappeared.

Tylostyles should be the third most abundant in the sediment, according to the biomass of living sponges, and so their frequency reflects more or less their biomass. Just like in the previous case, the frequency of spherasters belonging to *Chondrilla* sp. seems to correspond with the number of spherical spicules placed in the category anthasters and/or spherasters (the third most frequent). One must remember, however, that in this category are placed also spherical anthasters. These spicule types belong most probably to *Diplastrella*

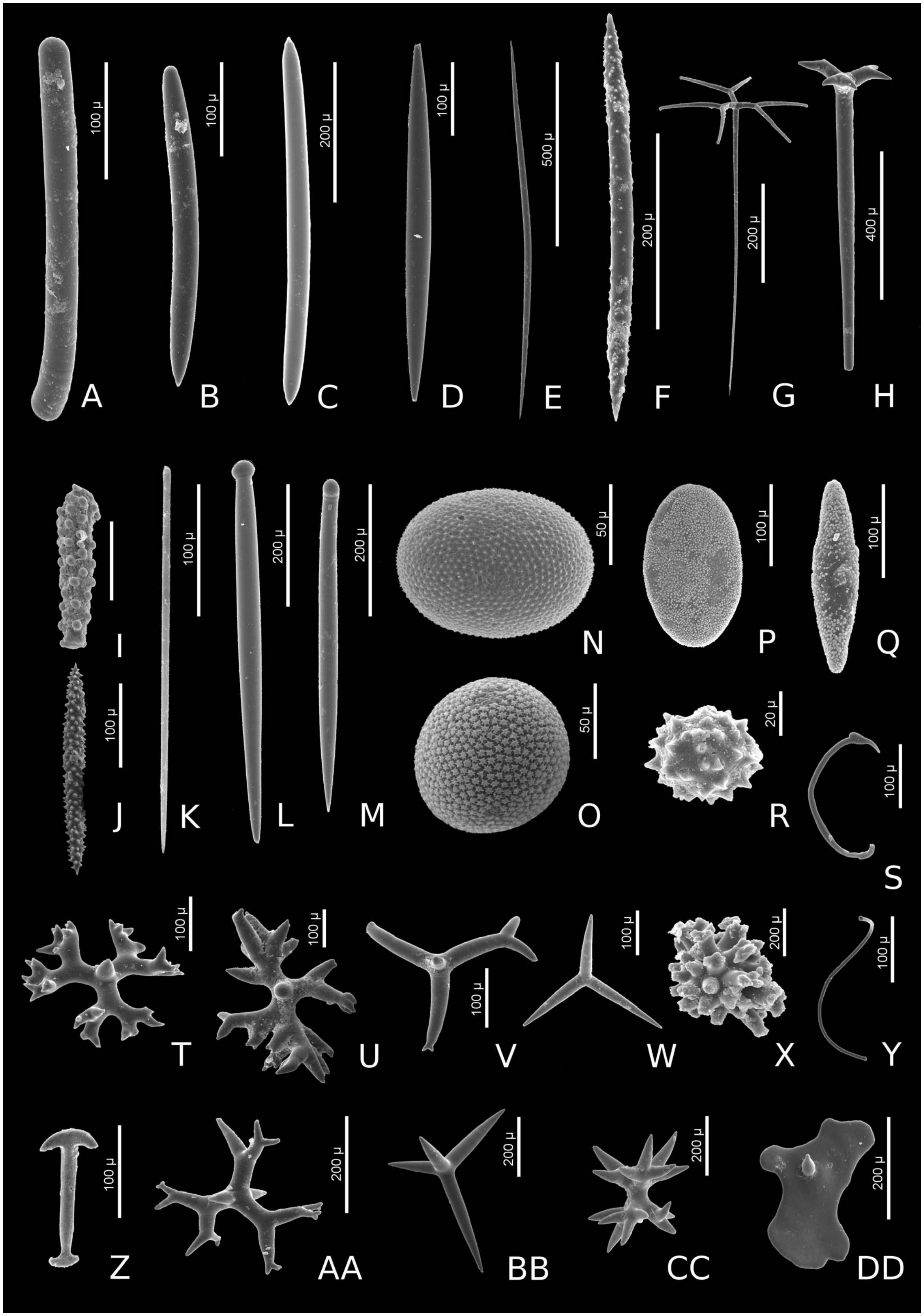

FIGURE 2—Spicule morphotypes present in sediments. A) Strongyle. B) Style. C) Oxea type I. D) Oxea type II. E) Oxea type III. F) Acanthoxea. G) Triaene type I. H) Triaene type II. I) Acanthoxea. J) Acanthoxea microclere. K) Tylostyle type I. L) Tylostyle type II. M) Tylostyle type III. N) Selenaster. O) Sterraster. P) Aspidaster type I. Q) Aspidaster type II. R) Spheraster. S) Sigma. T) Short-shafted triaene type I. U) Short-shafted triaene type II. V) Short-shafted triaene type III. W) Triod. X) Anthaster. Y) Sigmaspire. Z) Anchorate basalium. AA) Mesodichotriaene. BB) Calthrop. CC) Amphitriaene. DD) Discotriaene. Coll. number ZPAL Pf.24.

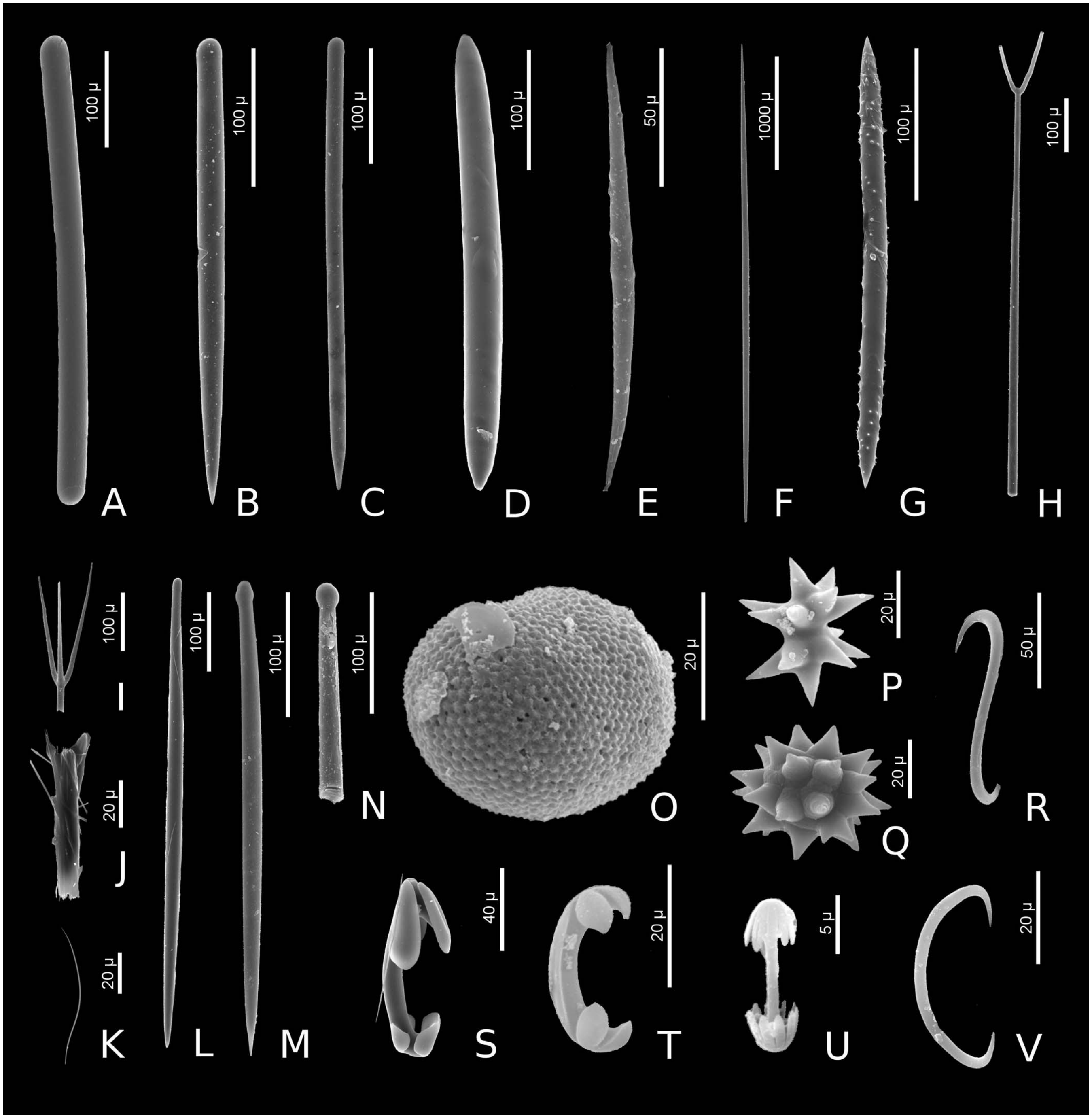

FIGURE 3—Spicule morphotypes present in living sponges. A) Strongyle. B) Style type I. C) Style type II. D) Oxea type I. E) Oxea type II. F) Oxea type III. G) Acantoxea. H) Diaene. I) Triaene. J) Raphide. K) Microxea. L) Tylostyle type I. M) Tylostyle type II. N) Tylostyle type III. O) Selenaster. P) Spiraster microsclere. Q) Spheraster. R) Sigmaspire. S) Anisochelae. T) Isochelae. U) Birotula. V) Sigma.

megastellata, which is known from Bocas del Toro but was not found during the present study. The other problem is that some tunicate ascidians have spicules with similar morphology and sizes (distinguishable only under scanning electron microscope; see for example Łukowiak, 2012) and may also be placed mistakenly in this category, further complicating the picture.

Spiraster microscleres that occur only in sponges of the third and fourth volumetric group do not reflect the situation in sediment because no spiraster spicules were found in the sediment during this study. The less frequent according to biomass are triods, calthrops, and triaenes that occurred only in the fourth category.

In the case of the amphitriaenes of *Samus*, acanthoxeas of *Alectona*, and triaenes of *Triptolemma*, the fact that these taxa were not recognized among living sponges can be explained by their cryptic and/or encrusting nature. The fact that lithistid discotriaenes were found in the sediment and not among living sponges may be associated with the general rarity of lithistids in shallow water. The presence of deep-water hexactinellid spicules in the sample is rather surprising, but can be explained perhaps by storm detachment and transport of living sponges from deeper water.

The frequency of occurrence of microscleres in sediment seems to be a separate case. Here, we treated ovoid and spherical spicules separately because of their suspected different behavior during the postmortem transport and deposition and their much larger size than typical microscleres. The rare appearance of microscleres (only one sigma and sigmaspire) may be the result of selective dissolution of this type of spicules because of their relatively high surface/volume ratio. Caribbean surface seawater down to 50 m is characterized by a pH of ~7.95 (Doney, 2006), which is sufficiently high for dissolution of amorphous sponge silica. The low frequency of microscleres may also be an effect of preferential winnowing and transport, due to their very small size; however, the transport seems not to play a significant role. Their small size may also cause their loss during maceration and washing of sediment samples, or their being overlooked even under the binocular microscope.

CONCLUSIONS

We have identified 23 different morphological types of spicules occurring in the living specimens that were found in the studied area, and 15 of them were also identified in the sediment samples (see Figs. 2–3). There are 4 morphotypes, however, that occur in the sediment but have no equivalents in living sponges recognized during the present study: euasters, sterrasters, discotriaenes, and anthasters. The sponges to which these types belong have been reported from the Bocas del Toro region by other authors, and thus their absence alive in our quadrats may follow only from spatial patchiness in sponge distribution. We have also found other spicule morphotypes—anchorate basalia, amphitriaenes, small acanthoxeas, and various plakinastrellid triaenes—that have no equivalents at all in the sponge fauna of the studied area, either encountered by us or by previous workers in the Bocas del Toro region.

The observed differences between the spicules generated by living sponges and those encountered in sediments may be explained by several biological and sedimentological factors that are not mutually exclusive. These include live-dead differences arising from small size, which promotes (1) selective removal in the face of dissolution, winnowing, and transport; (2) sampling bias in the sediment samples; (3) incomplete sampling of the living owing to patchiness in sponge communities or short-distance transport of sponges during storms; and also (4) recent disappearance of taxa in the living fauna bearing these spicule types, either under natural or anthropogenic forces.

Our investigation demonstrates that the frequency of various macrospicule types in the sediment reflects well the frequency of living sponges having a particular type of spicules. On the other hand, the frequency of microscleres in sediment is much lower compared to their frequency in the living sponge communities. One can speculate that their scarcity or absence is caused by their small size, which promotes their dissolution and/or winnowing, or by the sampling bias.

1. Forty species of living sponges from 28 genera were observed in surveys of three 5 × 5 m quadrats on Casa Blanca reef in Bocas del Toro. Of these, nine (22.5%) do not produce mineral spicules and are thus lost in the process of fossilization.

2. The most common spicule types in living sponges, according to frequency, are oxeas, strongyles, and styles. The most common spicule types in the sediment are small ovoid spicules (sterrasters and selenasters), oxeas, anthasters and/or spherasters, and styles. Less frequent are calthrops and tylostyles. This demonstrates that the frequency of various macrospicule types in the sediment reflects well the frequency of living sponges having a particular type of spicules. On the other hand, the frequency of microscleres in sediment is much lower (or they are even totally absent) compared to their frequency in the living sponge communities. One can speculate that it is caused by their small size that promotes their dissolution and/or preferential removal or the sampling bias.

3. Apart from spicules that belong to taxa living at present in the area, we have found also other types of spicules characteristic for sponges not found at all living at present in the area. Most probably this may be caused by a local extinction of the taxa producing this type of spicules, or the effect of patchiness in distribution of the sponges. Only four species have no equivalents in the living community but they may be hidden among 95 taxonomically undetermined small individuals. Spicular analysis is also a useful tool for revealing the presence of cryptic and excavating sponges that are otherwise difficult to spot, and thus overlooked in traditional faunistic studies.

4. Generally, most morphological types of megasclere found in living sponges had been recognized in the sediment, indicating that despite of the loss of information caused by nonpreservation of the species without mineral spicules, spicular analysis, when all limitations are considered, is a good tool in reconstruction of the taxonomic composition of former (subfossil) sponge assemblages, but not the frequency of various sponge species. Thus, it can be used to estimate diversity changes in sponge communities through time.

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REFERENCES

Alcolado, P.M., 1984, Nuevas especies de esponjas encontradas en Cuba [New species of sponges from Cuba]: Poeyana, v. 271, p. 1–22.

Alvarez, B., Van Soest, R.W.M., and Rützler, K., 1998, A Revision of Axinellidae (Porifera: Demospongiae) in the Central West Atlantic Region: Smithsonian Contributions to Zoology, v. 598, 1–47.

Arndt, W., 1927, Kalk- und Kieselschwämme von Curaçao: Bijdragen tot de Dierkunde, v. 25, p. 133–158.

Bocage, J.V. Barboza du, 1869 [1870], Eponges siliceuses nouvelles du Portugal et de l'île Saint-Iago (Archipel de Cap-Vert): Jornal de Sciencias mathematicas, physicas e naturaes, v. 2, p. 159–162.

Boury-Esnault, N., and Rützler, K., 1997, Thesaurus of sponge morphology: Smithsonian Contributions to Zoology, v. 596, p. 1–55, doi: 10.5479/si.

Boury-Esnault, N., Klautau, M., Bézac, C., Wulff, J., and Solé-Cava, A.M., 1999, Comparative study of putative conspecific sponge populations from both sides of the Isthmus of Panama: Journal of the Marine Biological Association of the United Kingdom, v. 79, no. 1, p. 39–50.

Burton, M., 1959, Sponges: *in* Scientific Reports, John Murray Expedition, 1933–34, v. 10, no. 5: British Museum (Natural History), London, p. 151–281.

Carter, H.J., 1874, Descriptions and figures of deep-sea sponges and their spicules from the Atlantic Ocean, dredged up on board H.M.S. 'Porcupine', chiefly in 1869; with figures and descriptions of some remarkable spicules from the Agulhas Shoal and Colon, Panama: Annals and Magazine of Natural History, v. 14, no. 79, p. 207–221, 245–257.

Carter, H.J., 1875, Notes Introductory to the Study and Classification of the Spongida. Part II. Proposed Classification of the Spongida: Annals and Magazine of Natural History, v. 16, no. 92, p. 126–145, 177–200.

Carter, H.J., 1879, On a new species of excavating sponge (*Alectona millari*) and on a new species of *Rhaphidotheca* (*R. affinis*): Journal of the Royal Microscopical Society, v. 2, p. 493–499.

Carter, H.J., 1882, Some sponges from the West Indies and Acapulco in the Liverpool Free Museum described, with general and classificatory remarks: Annals and Magazine of Natural History, v. 9, no. 52, p. 266–301, 346–368.

COLLIN, R., DÍAZ, M., NORENBURG, J., ROCHA, R., SANCHEZ, J., SCHULZ, A., SCHWARTZ, M., and VALDES, A., 2005, Photographic identification guide to some common marine invertebrates of Bocas Del Toro, Panama: Caribbean Journal of Science, v. 41, no. 3, p. 638–707.

DE WEERDT, W.H., 2000, A monograph of the shallow-water Chalinidae (Porifera, Haplosclerida) of the Caribbean: Beaufortia, v. 50, no. 1, p. 1–67.

DE WEERDT, W.H., RÜTZLER, K., and SMITH, K.P., 1991, The Chalinidae (Porifera) of Twin Cays, Belize, and adjacent waters: Proceedings of the Biological Society of Washington, v. 104, no. 1, p. 189–205.

DE WEERDT, W.H., DE KLUIJVER, M.J., and GOMEZ, R., 1999, *Haliclona (Halichoclona) vansoesti* n.sp., a new chalinid sponge species (Porifera, Demospongiae, Haplosclerida) from the Caribbean: Beaufortia, v. 49, no. 6, p. 47–64.

DÍAZ, C., 2005, Common sponges from shallow marine habitats from Bocas del Toro region, Panama: Caribbean Journal of Science, v. 41, p. 465–475.

DÍAZ, M.C., and RÜTZLER, K., 2001, Sponges: An essential component of Caribbean coral reefs: Bulletin of Marine Science, v. 69, no. 2, p. 535–546.

DÍAZ, M.C., ALVAREZ, B., and VAN SOEST, R.W.M., 1987, New species of Demospongiae (Porifera) from the national park 'Archipiélago de Los Roques', Venezuela: Bijdragen tot de Dierkunde, v. 57, no. 1, p. 31–41.

DÍAZ, M.C., POMPONI, S.A., and VAN SOEST, R.W.M., 1993, A systematic revision of the central West Atlantic Halichondrida (Demospongiae, Porifera). Part III: Description of valid species, *in* Uriz, M.-J., and Rützler, K., eds., Recent Advances in Ecology and Systematics of Sponges: Scientia Marina, v. 57, no. 4, p. 283–306.

DÍAZ, M.C., THACKER, R.W., RÜTZLER, K., and PIANTONI, C., 2007, Two new haplosclerid sponges from Caribbean Panama with symbiotic filamentous cyanobacteria, and an overview of sponge cyanobacteria associations, *in* Custódio, M.R., Lôbo-Hajdu, G., Hajdu, E., and Muricy, G., eds., Porifera Research: Biodiversity, Innovation and Sustainability, Série Livros 28: Museu Nacional, Rio de Janeiro, p. 31–39.

DONEY, S.C., 2006, The dangers of ocean acidification: Scientific American, v. 294, no. 3, p. 58–65.

DUCHASSAING DE FONBRESSIN, P., 1850, Animaux radiaires des Antilles: Plon Frères, Paris, p. 1–35.

DUCHASSAING DE FONBRESSIN, P., and MICHELOTTI, G., 1864, Spongiaires de la mer Caraïbe: Natuurkundige verhandelingen van de Hollandsche maatschappij der wetenschappen te Haarlem, v. 21, no. 2, p. 1X–124.

ESPER, E.J.C., 1791–1799, Die Pflanzenthiere in Abbildungen nach der Natur mit Farbenerleuchtet, nebst Beschreibungen: Zweyter Theil: Raspe, Nürnberg, p. 1–303.

GAISER, E.E., BROOKS, M.J., KENNEY, W.F., SCHELSKE, C.L., and TAYLOR, B.E., 2004, Interpreting the hydrological history of temporary ponds from chemical and microscopic characterization of siliceous microfossils: Journal of Paleolimnology, v. 1, p. 63–76.

GEORGE, W.C., and WILSON, H.V., 1919, Sponges of Beaufort (N.C.) Harbor and Vicinity: Bulletin of the Bureau of Fisheries, Washington, v. 36, p. 129–179.

GOCHFELD, D., SCHLÖDER, C., and THACKER, R.W., 2007, Sponge community structure and disease prevalence on coral reefs in Bocas del Toro, Panama, *in* Custódio, M.R., Lôbo-Hajdu, G., Hajdu, E., and Muricy, G., eds., Porifera Research: Biodiversity, Innovation, and Sustainability, Série Livros 28: Museu Nacional, Rio de Janeiro, p. 335–343.

GRAY, J.E., 1867, Notes on the Arrangement of Sponges, with the Descriptions of some New Genera: Proceedings of the Zoological Society of London, v. 1867, no. 2, p. 492–558.

GRAY, J.E., 1870, Notes on anchoring sponges (in a letter to Mr. Moore): Annals and Magazine of Natural History, v. 6, no. 34, p. 309–312.

GUZMÁN, H.M., 2003, Caribbean coral reefs of Panamá: Present status and future perspectives, *in* Cortés, J., ed., Latin American Coral Reefs: Elsevier Science, London, p. 241–274.

GUZMÁN, H.M., and GUEVARA, C.A., 1998, Arrecifes coralinos de Bocas del Toro, Panamá: II. Distribución, estructura, y estado de conservación de los arrecifes de las islas de Bastimentos, Solarte, Carenero y Colon: Revista de Biología Tropical, v. 46, no. 4, p. 889–912.

GUZMÁN, H.M., and GUEVARA, C.A., 1999, Arrecifes coralinos de Bocas del Toro, Panamá: III. Distribución, estructura, y estado de conservación de los arrecifes de las islas Pastores, Cristobal, Popa, y Cayo Agua: Revista de Biología Tropical, v. 47, no. 4, p. 659–676.

HAECKEL, E., 1872, Die Kalkschwämme. Eine Monographie in zwei Bänden Text und einem Atlas mit 60 Tafeln Abbildungen: G. Reimer, Berlin, v. 1, p. 1–484; v. 2, p. 1–418.

HAJDU, E., and RÜTZLER, K., 1998, Sponges, genus *Mycale* (Poecilosclerida: Demospongiae: Porifera), from a Caribbean mangrove and comments on subgeneric classification: Proceedings of the Biological Society of Washington, v. 111, no. 4, p. 737–773.

HALL, K.V., and HERRMANN, S.J., 1980, Paleolimnology of three species of freshwater sponges (Porífera: Spongilidae) from a sediment core of a Colorado semidrainage mountain lake: Transactions of the American Microscopical Society, v. 99, no. 1, p. 93–100.

HARRISON, F.W., 1988, Utilization of freshwater sponges in paleolimnological studies: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 62, p. 387–397.

HARRISON, F.W., GLEASON, P.J., and STONE, P.A., 1979, Paleolimnology of lake Okeechobee, Florida: An analysis utilizing spicular components of freshwater sponges (Porifera: Spongillidae): Notulae Naturae, v. 454, p. 1–6.

HECHTEL, G.J., 1965, A systematic study of the Demospongiae of Port Royal, Jamaica: Bulletin of the Peabody Museum of Natural History, v. 20, p. 1–103.

HIGGIN, T., 1877, Description of some sponges obtained during a cruise of the steam-yacht 'Argo' in the Caribbean and neighbouring Seas: Annals and Magazine of Natural History, v. 9, p. 291–299.

HINDE, G.J., and HOLMES, W.M., 1892, On the sponge-remains in the Lower Tertiary Strata near Oamaru, Otago New Zealand: Journal of the Linnean Society, Zoology, v. 24, no. 151, p. 177–262.

HOOPER, J.N.A., and VAN SOEST, R.W.M., ED., 2002, Systema Porifera: A Guide to the Classification of Sponges, vol. 1–2: Kluwer Academic/Plenum Publishers, New York, ISBN 0-306-47260-0, 1810 p.

HYATT, A., 1875, Revision of the North American Poriferae; with remarks upon foreign species: Part I, Memoirs of the Boston Society of Natural History, v. 2, p. 399–408.

INOUE, M., 1984, Correlation of the spicule assemblage in the sediment with the spicule assemblage of living sponges in Sagami Bay, Central Japan: Proceedings of Japan Academy, v. 60B, no. 6, p. 165–168.

INOUE, M., 1985, An examination of supply processes of sponge spicules to the sediment of the northeastern to eastern part of Sagami Bay: Annual Report of the Faculty of Education, Iwate University, v. 44, no. 2, p. 61–80.

KOLTUN, V.M., 1960, Spicule analysis and its application in geology: Izvestiya Akademii Nauk SSR, Seriya Geologicheskaya, v. 4, p. 96 (in Russian).

LAMARCK, J.B.P. DE MONET, COMTE DE, 1813–1814, Sur les polypiers empâtés. Suite du mémoire intitulé: Sur les Polypiers empâtés. Suite des éponges: Annales du Muséum national d'histoire naturelle, Paris, v. 20, no. 6, p. 294–312 (published 1813), 370–386, 432–458.

LAMARCK, J.B.P. DE MONET, COMTE DE, 1816, Histoire naturelle des animaux sans vertèbres, présentant les caractères généraux et particuliersde ces animaux, leur distribution, leurs classes, leurs familles, leurs genres,et la citation des principales espèces qui s'y rapportent: Verdière, Paris, v. 2, p. 1–568.

LAUBENFELS, M.W. DE, 1934, New sponges from the Puerto Rican deep: Smithsonian Miscellaneous Collections, v. 91, no. 17, p. 1–28.

LAUBENFELS, M.W. DE, 1936, A Discussion of the Sponge Fauna of the Dry Tortugas in Particular and the West Indies in General, with Material for a Revision of the Families and Orders of the Porifera: Carnegie Institute of Washington (Tortugas Laboratory Paper No. 467), v. 30, p. 1–225.

LAUBENFELS, M.W. DE, 1949, Sponges of the western Bahamas: American Museum Novitates, v. 1431, p. 1–25.

LAUBENFELS, M.W. DE, 1950, The Porifera of the Bermuda Archipelago: Transactions of the Zoological Society of London, v. 27, no. 1, 1–154.

LEIDY, J., 1868, Description of a new sponge: *Pheronema annae*: Proceedings of the Academy of Natural Sciences of Philadelphia 1868(6) Biological and Microscopical Department of the Academy of Natural Sciences, p. 9–10.

LLOYD, G.T., PEARSON, P.N., YOUNG, J.R., and SMITH, A.B., 2012, Sampling bias and the fossil record of planktonic foraminifera on land and in the deep sea: Paleobiology, v. 38, p. 569–584.

LOVE, G.D., GROSJEAN, E., STALVIES, C., FIKE, D.A., GROTZINGER, J.P., BRADLEY, A.S., KELLY, A.E., BHATIA, M., MEREDITH, W., SNAPE, C.E., BOWRING, S.A., CONDON, D.J., and SUMMONS, R.E., 2009, Fossil steroids record the appearance of Demospongiae during the Cryogenian period: Nature, v. 457, p. 718–721.

ŁUKOWIAK, M., 2012, First record of late Eocene ascidians (Ascidiacea, Tunicata) from southeastern Australia: Journal of Paleontology, v. 86, no. 3, p. 521–526.

ŁUKOWIAK, M., 2013, Reconstruction of "soft" demosponge fauna from the Eocene of southern Australia: Polish Academy of Sciences, Unpublished Ph.D. thesis, Warsaw, p. 1–199.

MEREJKOWSKI, C.S., 1877 (1878), Preliminary account on the sponges of the White Sea: Trudy St. Petersburg Obshestvo, v. 9, p. 249–270 (In Russian).

MOSTLER, H., 1990, Mikroskleren von Demospongien (Porifera) aus dem basalen Jura de nordlischen Kalkalpen: Geologisch-Palaeonologische Mitteilungen Innsburck, v. 17, p. 119–142.

OLSZEWSKI, T.D., and KIDWELL, S.M., 2007, The preservational fidelity of evenness in molluscan death assemblages: Paleobiology, v. 33, p. 1–23.

PALLAS, P.S., 1766, Elenchus Zoophytorum sistens generum adumbrations generaliores et specierum cognitarum succinctas descriptiones cum selectis auctorum synonymis: P. van Cleef, The Hague, p. 1–451.

PANG, R.K., 1973, The systematics of some Jamaican excavating sponges (Porifera): Postilla, v. 161, p. 1–75.

Parolin, M., Volkmer-Ribeiro, C., and Stevaux, J.C., 2007, Sponge spicules in peaty sediments as paleoenvironmental indicators of the Holocene in the upper Paraná river, Brazil: Revista Brasileira de Paleontologia, v. 10, p. 17–26.

Parolin, M., Volkmer-Ribeiro, C., and Stevaux, J.C., 2008, Use of spongofacies as a proxy for river-lake paleohydrology in Quaternary deposits of Central-Western Brazil: Revista Brasileira de Paleontologia, v. 11, no. 3, p. 187–198.

Pisera, A., 1997, Upper Jurassic siliceous sponges from the Swabian Alb: Taxonomy and paleoecology: Palaeontologia Polonica, v. 57, p. 1–216.

Pisera, A., Cachao, M., and Silva, C. da, 2006, Siliceous sponge spicules from the Miocene Mem Moniz marls (Portugal) and their environmental significance: Rivista Italiana de Paleontologia, v. 112, p. 287–299.

Pulitzer-Finali, G., 1986, A collection of West Indian Demospongiae (Porifera). In appendix, a list of the Demospongiae hitherto recorded from the West Indies: Annali del Museo civico di storia naturale Giacomo Doria, v. 86, p. 65–216.

Reif, W.-E., 1967, Schwammspicula aus dem Weissen Jura Zeta von Nattheim (Schwäbische Alb): Palaeontographica, v. 127, p. 85–102.

Ridley, S.O., and Dendy, A., 1886, Preliminary Report on the Monaxonida collected by H.M.S. 'Challenger': Annals and Magazine of Natural History, v. 18, p. 325–351, 470–493.

Rützler, K., 1971, Bredin-Archbold-Smithsonian Biological Survey of Dominica: Burrowing sponges, genus *Siphonodictyon* Bergquist, from the Caribbean: Smithsonian Contributions to Zoology, v. 77, p. 1–37.

Rützler, K., 2002, Family Alectonidae Rosell, 1996, *in* Hooper, J.N.A., and Van Soest, R.W.M., eds., Systema Porifera: A Guide to the Classification of Sponges, vol. 1: Kluwer Academic/Plenum Publishers, New York, p. 281–290.

Rützler, K., and Macintyre, I., 1978, Siliceous sponge spicules in coral reef sediments: Marine Biology, v. 49, p. 147–159.

Rützler, K., and Smith, K.P., 1993, The genus *Terpios* (Suberitidae) and new species in the "Lobiceps" complex, *in* Uriz, M.–J., and Rützler, K., eds., Recent Advances in Ecology and Systematics of Sponges: Scientia Marina, v. 57, no. 4, p. 381–393.

Rützler, K., Duran, S., and Piantoni, C., 2007, Adaptation of reef and mangrove sponges to stress: Evidence for ecological speciation exemplified by *Chondrilla caribensis* new species (Demospongiae, Chondrosida): Marine Ecology, v. 28, p. 95–111.

Schmidt, O., 1870, Grundzüge einer Spongien-Fauna des atlantischen Gebietes: Wilhelm Engelmann, Leipzig, p. iii–iv, 1–88.

Schmidt, O., 1880, Die Spongien des Meerbusen von Mexico (Und des caraibischen Meeres). Heft II. Abtheilung II. Hexactinelliden. Abtheilung III. Tetractinelliden. Monactinelliden und Anhang. Nachträge zu Abtheilung I (Lithistiden), *in* Reports on the dredging under the supervision of Alexander Agassiz, in the Gulf of Mexico, by the USCSS 'Blake': Gustav Fischer, Jena, p. 33–90, pls. V–X.

Schopf, T.J.M., 1978, Fossilization potential of an intertidial fauna: Friday Harbor, Washington: Paleobiology, v. 4, no. 3, p. 261–270.

Sollas, W.J., 1886, Preliminary account of the Tetractinellid sponges Dredged by H.M.S. 'Challenger' 1872–76: Part I. The Choristida: Scientific Proceedings of the Royal Dublin Society (new series), v. 5, p. 177–199.

Sollas, W.J., 1888, Report on the Tetractinellida collected by H.M.S. Challenger, during the years 1873–1876: Report on the Scientific Results of the Voyage of H.M.S. Challenger, 1873–1876: Zoology, v. 25, no. 63, p. 1–458.

Stephens, J., 1916, Preliminary Notice of some Irish Sponges. The Monaxonellida (Suborder Sigmatomonaxonellida) obtained by the Fisheries Branch of the Department of Agriculture and Technical Instruction, Ireland: Annals and Magazine of Natural History, v. 17, no. 99, p. 232–242.

Tabachnick, K., and Menshenina, L.L., 2002, Family Pheronematidae Gray, 1870, *in* Hooper J.N.A., and Van Soest, R.W.M., eds., Systema Porifera: A Guide to the Classification of Sponges, vol. 2: Kluwer Academic/Plenum Publishers, New York, p. 1267–1280.

Tsurnamal, M., 1967, *Chelonaplysilla erecta* n. sp. (Demospongiae, Keratosa) from Mediterranean Coast of Israel: Israel Journal of Zoology, v. 16, no. 1, p. 96–100.

Uliczka, E., 1929, Die tetraxonen Schwämme Westindiens (auf Grund der Ergebnisse der Reise Kükenthal-Hartmeyer), *in* Kükenthal, W., and Hartmeyer, R., eds., Ergebnisse einer zoologischen Forschungsreise nach Westindien: Zoologische Jahrbücher. Abteilung für Systematik, Geographie und Biologie der Thiere, Supplement, v. 16, p. 35–62.

Vacelet, J., 1999, Planktonic armoured propagules of the excavating sponge *Alectona* (Porifera: Demospongiae) are larvae: Evidence from *Alectona wallichii* and *A. mesatlantica* sp. nov.: Memoirs of the Queensland Museum, v. 44, p. 627–642.

Vacelet, J., and Donadey, C., 1987, A new species of *Halisarca* (Porifera, Demospongiae) from the Caribbean, with remarks on the cytology and affinities of the genus, *in* Jones, W.C., ed., European Contributions to the Taxonomy of Sponges: Sherkin Island Marine Station, Midleton, Ireland, p. 5–12.

Van Soest, R.W.M., 1977, A revision of the megacanthoxea-bearing tetillids (Porifera, Spirophorida), with a description of a new species, *in* Hummelinck, P.W., and Van der Steen, L.J., eds., Uitgaven van de Natuurwetenschappelijke Studiekring voor Suriname en de Nederlandse Antillen, No. 89. Studies on the Fauna of Curaçao and other Caribbean Islands, v. 53, no. 172, p. 1–14.

Van Soest, R.W.M., 1980, Marine sponges from Curaçao and other Caribbean localities. Part II. Haplosclerida, *in* Hummelinck, P.W., and Van der Steen, L.J., eds., Uitgaven van de Natuurwetenschappelijke Studiekring voor Suriname en de Nederlandse Antillen, No. 104. Studies on the Fauna of Curaçao and other Caribbean Islands, v. 62, no. 191, p. 1–173.

Van Soest, R.W.M., 1984, Marine sponges from Curaçao and other Caribbean localities, Part III, Poecilosclerida: *in* Hummelinck, P.W., and Van der Steen, L.J., eds., Uitgaven van de Natuurwetenschappelijke Studiekring voor Suriname en de Nederlandse Antillen, No. 112. Studies on the Fauna of Curaçao and other Caribbean Islands, v. 62, no. 191, p. 1–173.

Van Soest, R.W.M., 2009, New sciophilous sponges from the Caribbean (Porifera: Demospongiae): Zootaxa, v. 2107, p. 1–40.

Van Soest, R.W.M., and Hooper, J.N.A., 2002, Family Samidae Sollas, 1886, *in* Hooper, J.N.A., and Van Soest, R.W.M., eds., Systema Porifera: A Guide to the Classification of Sponges: Kluwer Academic/Plenum Publishers, New York, p. 99–101.

Van Soest, R.W.M., and Rützler, K., 2002, Family Tetillidae Sollas, 1886, *in* Hooper, J.N.A., and Van Soest, R.W.M., eds., Systema Porifera: A Guide to the Classification of Sponges: Kluwer Academic/Plenum Publishers, New York, p. 85–98.

Van Soest, R.W.M., Hooper, J.N.A., and Hiemstra, F., 1991, Taxonomy, phylogeny and biogeography of the marine sponge genus *Acarnus* (Porifera: Poecilosclerida): Beaufortia, v. 42, no. 3, p. 49–88.

Van Soest, R.W.M, Boury-Esnault, N., Hooper, J.N.A., Rützler, K., de Voogd, N.J., Alvarez de Glasby, B., Hajdu, E., Pisera, A.B., Manconi, R., Schoenberg, C., Janussen, D., Tabachnick, K.R., Klautau, M., Picton, B., Kelly, M., and Vacelet, J., 2011, World Porifera database, http://www.marinespecies.org/porifera/index.php, checked May 2013.

Van Soest, R.W.M., Boury-Esnault, N., Vacelet, J., Dohrmann, M., Erpenbeck, D., De Voogd, N. J., Santodomingo, N., Vanhoorne, B., Kelly, M., and Hooper, J.N.A, 2012, Global diversity of sponges (Porifera): PLoS ONE, v. 7, no. 4, p. e35105.

Verrill, A.E., 1907, The Bermuda Islands: Part V. An account of the Coral Reefs (Characteristic Life of the Bermuda Coral Reefs). Porifera: Sponges: Transactions of the Connecticut Academy of Arts and Sciences, v. 12, p. 330–344.

Volkmer-Ribeiro, C., and Turcq, B., 1996, SEM analysis of silicious spicules of a freshwater sponge indicate paleoenvironmental changes: Acta Microscópica, v. 5, p. 186–187.

Volkmer-Ribeiro, C., Ezcurra de Drago, I., and Parolin, M., 2007, Spicules of the freshwater sponge *Ephydatia facunda* indicate lagoonal paleoenvironment at the Pampas of Buenos Aires Province, Argentina: Journal of Coastal Research, v. 50, p. 449–452.

Wiedenmayer, F., 1977, Shallow-water sponges of the western Bahamas: Experientia Supplementum, v. 28, p. 1–287.

Wiedenmayer, F., 1994, Contribution to the knowledge of post-Paleozoic neritic and archibenthal sponges (Porifera): Schweizerische Palaeontologische Abhanlungen, v. 116, p. 1–147.

Wilson, H.V., 1902 [1900], The sponges collected in Porto Rico in 1899 by the U.S. Fish Commission Steamer Fish Hawk: Bulletin of the United States Fish Commission, v. 2, 375–411.

Wright, E.P., 1881, On a new genus and species of a sponge (*Alemo seychellensis*) with supposed heteromorphic zooids: Transitions of Irish Academy, v. 28, p. 13–20.

Wulff, J., 1984, Functional importance of biodiversity for coral reefs of Belize, *in* Palomares, M.L.D., and Pauly, D., eds., Too Precious to Drill: The Marine Biodiversity of Belize: Fisheries Centre Research Reports: Fisheries Centre, University of British Columbia, Vancouver, British Columbia, Canada, v. 19, no. 6, p. 52–56.

Wulff, J., 2001, Assessing and monitoring coral reef sponges: Why and how?: Bulletin of Marine Science, v. 69, p. 831–846.

Zea, S., and Rützler, K., 1983, A new species of *Xestospongia* (Porifera, Demospongea) from the Colombian Caribbean: Caldasia, v. 10, p. 817–831.

Zea, S., and Van Soest, R.W.M., 1986, Three new species of sponges from the Colombian Caribbean: Bulletin of Marine Science, v. 38, p. 355–365.

Zea, S., and Weil, E., 2003, Taxonomy of the Caribbean excavating sponge species complex *Cliona caribbaea C. aprica C. langae* (Porifera, Hadromerida, Clionaidae): Caribbean Journal of Science, v. 39, no. 3, p. 348–370.

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