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Diversity and bathymetric distribution of lithistid sponges in the tropical western Atlantic region

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Abstract.—Nineteen species of lithistid sponges (Porifera: Demospongiae), representing 13 genera, eight families, and four suborders are reported from the tropical western Atlantic region, including three new records of occurrence: *Discodermia verrucosa* Topsent, *Corallistes* cf. *undulatus* Lévi & Lévi, and *C.* cf. *nolitangere* Schmidt. This inventory of the biodiversity and bathymetric distribution of these sponges is based on the results obtained from 36 expeditions and more than 450 submersible transects. The objective of these expeditions was the collection of marine organisms for discovery of biologically active compounds with pharmaceutical potential. The taxonomic diversity and distribution thus noted contrasts with the results of previous reports which describe more specific regional faunas. Lithistids are dominant components of hard-bottom habitats at depths greater than 150 m in the tropical western Atlantic region.

Sponges are an important part of all marine benthic communities, yet sponge classification is still very much in a state of flux and evolutionary relationships are unclear (Bergquist 1994), despite recent advances in the use of biochemical and molecular data in phylogenetic analyses.

Lithistid sponges, a polyphyletic group within the Demospongiae, are of particular interest to science as they are thought to represent relict forms of an ancestral sponge fauna from which many living sponges evolved (Reid 1967). There are only about 50 extant genera compared to the approximately 150 genera that were abundant during the Mesozoic era (250–60 mybp) (see Lévi 1991). Apart from the proliferation of *Discodermia* in the tropical Atlantic, *Theonella* in the Indo-Pacific, *Aciculites* in the southwest Pacific, and *Corallistes* in each of these oceans (Kelly-Borges 1998), most remaining genera are only known from one or two species, or from dredged fragments.

The lithistids differ from other demosponges in that they are composed of articulated siliceous desma spicules that, in most species, render the sponge body solid and rock-like. The sponges were originally recognized as a single group, the Order Lithistida, due to the possession of this type of spicule. There is a tremendous diversity of morphology in the desma skeleton, where ornamentation and articulation of these spicules can be important indicators of relatedness within and between genera (Schrammen 1910, see Kelly 2000).

Clues to the familial and ordinal relationships of lithistids with each other and with non-desma-bearing sponges are rare. The most significant morphological clue in some genera lies in the presence of megasclere and microsclere spicules that resemble those of extant non-desma-bearing sponges. In the case of lithistid genera that contain asterose and sigmaspire microscleres, the phylogenetic affinity with non-lithistid Astrophorida and Spirophorida, respectively, seems relatively certain and is

supported to some extent by 18S and 28S rDNA (Kelly-Borges & Pomponi 1994, McInerney et al. 1999). However, in genera that lack these indicator microscleres, affinity is impossible to assess as the resemblance of the megascleres to those of other non-lithistid demosponges is only superficial, and the spicule types are not homologous (Kelly 2000). Some lithistids such as *Vetulina* do not contain any megascleres other than sphaeroclone desmas, and affinity is virtually impossible to determine, if it indeed exists, other than with the use of 18S and 28S rDNA sequence comparisons and palaeontology.

Lithistids are of particular interest in biomedical research because they are the source of a variety of chemical compounds with pharmaceutically-relevant biological activity. For example, a number of compounds with therapeutic potential have been isolated from *Discodermia* spp., including the anticancer compound discodermolide (ter Haar et al. 1996), the antifungal compound discodermide (Gunaskera et al. 1991), and the anticancer compound polydiscamide (Gulavita et al. 1992). Lithistids are valuable living marine resources that may provide clues to the evolution of sponges and biogeographic events in the past, and it is important to inventory their diversity and distribution in regions of the world where they occur.

Two important regional lithistid faunas are known: the continental shelf and slope fauna of the tropical western Atlantic region (Schmidt 1870, 1879, 1880; van Soest & Stentoft 1988) and the seamount fauna of the southwest Pacific, including the Norfolk Ridge (Lévi & Lévi 1983, 1988; Lévi 1991) and northern New Zealand (Kelly et al. 1999, 2001; Kelly 2000). In both these locations, lithistid sponges are dominant components of the communities (Reed & Pomponi 1997), but the nature and composition of the communities differ considerably. Research on the New Caledonian end of the Norfolk Ridge has revealed a rich and unique fauna that represents a "window into the Cretaceous world," an era when these genera were very abundant and more widely spread (Lévi 1991). Living species of fossil genera *Iouea* and *Aulaxinia,* discovered on these remote Norfolk Ridge seamounts, are little changed from their fossil relatives that existed millions of years previously (Lévi 1991, Lévi & Lévi 1988). In northern New Zealand, similar faunas exist on northern seamounts and sand banks (Kelly et al. 1999, Kelly 2000).

The deep-water environments of the tropical western Atlantic region are not as well-documented as they are in the southwest Pacific, despite the richness of the lithistid fauna in the region (Pomponi et al. 1996, Reed & Pomponi 1997), and the fact that there have been several oceanographic research expeditions to the region (*Porcupine*—Carter 1874, 1876; *Argo*—Higgin 1877; *Fish Hawk*—Wilson 1902; *Blake*—Schmidt 1879, 1880). Descriptions of the Jamaican (Lehnert & van Soest 1996), Bahamian (Maldonado & Young 1996), and Barbados (van Soest & Stentoft 1988) deep-water lithistid faunas are based on only one or two scuba, submersible, or dredge collections. Other records of occurrence of lithistids have been noted through reports of new chemicals discovered with biomedical significance (e.g., Gunasekera et al. 1991, Gulavita et al. 1992), chemosystematics studies (Kerr & Kelly-Borges 1994, Kelly-Borges et. al. 1994), and molecular systematics studies (Kelly-Borges & Pomponi 1994).

This study is the result of a compilation of data from 36 expeditions and 450 submersible dives conducted throughout the tropical western Atlantic region (Pomponi et al. 1996, Reed & Pomponi 1997) by Harbor Branch Oceanographic Institution (HBOI) from 1984 to 2000 for the purpose of discovery of novel, marine-derived chemicals with biomedical potential. Based on this experience, we have observed that sponges are a dominant and complex component of deep-water communities, just as they are in shallow-water communities. The

objectives of this study were to provide an inventory of the diversity and bathymetric distribution of lithistid sponges in the tropical western Atlantic region, based upon the combined results of these expeditions, and to compare these to other known lithistid faunas.

Methods

Shallow-water sponges were collected by scuba, and deep-water sponges were collected with the *Johnson-Sea-Link* and *Clelia* manned submersibles which are capable of diving to −914 and −305 m, respectively. Each submersible is equipped with a multifunctional manipulator arm which enables the collection of specimens by either a claw, suction tube, or scoop. Samples were generally obtained intact, except for extremely fragile or brittle sponges. All samples were documented by in situ 35-mm photographs and/or videotapes, which are archived at HBOI.

Taxonomic voucher specimens were preserved in 70% ethanol and are archived in the Harbor Branch Oceanographic Museum (HBOM). Sponges were identified after histological preparation using the method described by Kelly-Borges et al. (1994). Morphological, taxonomic, and station data are stored in a custom Microsoft Access® relational database.

Results

Twenty-five species of lithistids were previously reported from the tropical western Atlantic region (van Soest & Zea 1986, van Soest & Stentoft 1988, Pisera 1999, table 1). This study increases the number of valid species to 28, representing 18 genera and 9 families (Table 1), by adding three new records of occurrence: *Discodermia verrucosa* Topsent, 1928 (HBOM catalog number 003:00914); *Corallistes* cf. *undulatus* Lévi & Lévi, 1983 (HBOM catalog number 003:00974); and *C.* cf. *nolitangere* Schmidt, 1870 (HBOM catalog number 003:00975).

The depth distribution was categorized into five zones (0–60 m; 61–150 m; 151–300 m; 301–600 m; and 601–914 m), based on the general geomorphology of the shelf edge in most of the sites that were sampled (from Reed and Pomponi 1997). Lithistids were most commonly found in the following habitats: 0–60 m, caves and rock ledges often in turbid locations; 61–150 m, steep fore reef, rock slope and vertical walls; 151–300 m, steep (45–70°) rocky slopes often with sediment and rubble or 1–5 m high boulders; 301–914 m, rock outcrops on mud or sand slopes (5–50°), rock pinnacles and boulders to 10 m high, and vertical rock walls.

In general, the families Corallistidae and Theonellidae dominate the collections (Fig. 1). The greatest number of lithistid specimens occurs in the 300 and 600 m zones (data not shown), due primarily to the concentration of Corallistidae found within this depth range.

0–60 m zone.—Lithistids were rarely collected from the 0–60 m zone, in contrast to their occurrence in shallow water in the southwest Pacific. *Discodermia dissoluta* is found rarely in shallow water, but occurs on the fore reef escarpment, in crevices between coral heads, or on rock ledges at depths of 16–37 m. *Amphibleptula madrepora* was collected once, at 15 m from a deep crevice off the island of St. Vincent in the eastern Caribbean. *Petromica ciocalyptoides* was collected twice at depths of 15 and 24 m from the fore reef slope and caves at Los Hermanos, Venezuela.

61–150 m zone.—*Discodermia polydiscus* is the dominant lithistid in the 61–150 m zone (Fig. 1). *Corallistes* cf. *nolitangere* was collected on boulders and rock ledges from Mona Island off Puerto Rico at 146 m, *Neopelta perfecta* was collected at 116 m on a rock outcrop off the southwest coast of Grenada, and *Scleritoderma cyanea* was collected on rock slopes and outcrops from Honduras (northwest coast of Utila) at 141 m.

151–300 m zone.—*Corallistes typus* and

Table 1.—Valid species of lithistids reported from the tropical western Atlantic region, with depth range and location of all species reported in this study.

Suborder, family, & species	Other studies[a]	Depth range and distribution (This study)
Suborder Tetracladina		
Family Theonellidae		
Theonella atlantica van Soest & Stentoft, 1988	+	
Discodermia dissoluta Schmidt, 1880	+	16–137 m, Bahamas (San Salvador, Grand Bahama Island, Egg Island, Rum Cay); Curacao; Bonaire; Puerto Rico
D. polydiscus Du Bocage, 1869	+	91–217 m, Bahamas (Grand Bahama Island, Andros, New Providence Island, Chub Cay)
D. cf. *verrucosa* Topsent, 1928		224 m, Barbados
Family Phymaraphinidae		
Racodiscula asteroides Zittel, 1878	+	613–736 m, Bahamas (Great Inagua, San Salvador)
R. clava (Schmidt, 1879)	+	
Suborder Dicranocladina		
Family Corallistidae		
Corallistes typus Schmidt, 1870	+	144–736 m, Bahamas (Acklins, Egg Island, Eleuthera, Little San Salvador, Mayaguana, Mira por Vos, Rum Cay, San Salvador, Great Inagua); Belize; Jamaica; Puerto Rico; St. Croix; Guadaloupe; Martinique; St. Vincent; Barbados
C. paratypus van Soest & Stentoft, 1988	+	447–549 m, Jamaica; Belize
C. tubulatus van Soest & Stentoft, 1988	+	
C. cf. *undulatus* Lévi & Lévi, 1983		378 m, Bahamas (San Salvador)
C. cf. *nolitangere* Schmidt, 1870		145–182 m, Puerto Rico (Mona Island)
Family Neopeltidae		
Neopelta perfecta Schmidt, 1880	+	116 m, Grenada
Macandrewia clavatella (Schmidt, 1870)	+	177 m, southeast Gulf of Mexico (off southwest coast of Florida)
Daedalopelta nodosa Schmidt, 1879	+	452 m, Bahamas (Rum Cay)
Suborder Rhizomorina		
Family Scleritodermidae		
Aciculites cribrophora (Schmidt, 1880)	+	534 m, Bahamas (Joulters Cay)
A. higginsi Schmidt, 1879	+	
Scleritoderma paccardi Schmidt, 1879	+	438–552 m, Bahamas (San Salvador, Great Inagua)
S. cyanea van Soest & Stentoft, 1988	+	141–536 m, Bahamas (Andros); Turks and Caicos; Curacao; Honduras (Utila)
Amphibleptula cf. *madrepora* Schmidt, 1879	+	15 m, St. Vincent
Setidium objectum Schmidt, 1879	+	

Table 1.—Continued.

Suborder, family, & species	Other studies[a]	Depth range and distribution (This study)
Family Siphonidiidae		
Siphonidium ramosum (Schmidt, 1870)	+	
Leiodermatium lynceus Schmidt, 1870	+	208–614 m Bahamas (Chub Cay); Martinique; Belize
L. pfeifferae (Carter, 1873)	+	
Gastrophanella implexa Schmidt, 1879	+	181 m, Puerto Rico (Mona Island)
Suborder Sphaerocladina		
Family Vetulinidae		
Vetulina stalactites Schmidt, 1879	+	220 m, Martinique
Family Desmanthidae		
Desmanthus incrustans Topsent, 1889	+	
Lithobubaris tenens Vacelet, 1969	+	
Family Petromicidae		
Petromica ciocalyptoides (van Soest & Zea, 1986)	+	15–24 m, Venezuela (Los Hermanos)

[a] Lehnert & van Soest 1996; Maldonado & Young 1996; Pisera 1999; Schmidt 1870, 1879, 1880; van Soest & Stentoft 1988; van Soest & Zea 1986.

Discodermia polydiscus are most abundant in the 151–300 m zone (Fig. 1). *Corallistes typus* is often found on vertical rock walls, and on mud and sand slopes with boulders and rock outcrops. *Discodermia polydiscus* is found on steep rock and rubble slopes. Less common were *Gastrophanella implexa* in Puerto Rico (south coast of Mona Island), *D. verrucosa* in Barbados (southwest of the island, on Trader Bank), and *Leiodermatium lynceus* and *Vetulina stalactites* in Martinique. These were commonly found on rock and sand slopes with boulders or rock outcrops. *Macandrewia clavatella* was collected only once, at 177 m in the Gulf of Mexico, off the southwest Florida shelf on a cobble, gravel slope.

301–600 m zone.–The 301–600 m zone is dominated by the Corallistidae, including *Corallistes typus* throughout the entire depth range and region (Fig. 1). *C.* cf. *undulatus* was found on a rock slope at 378 m in the Bahamas (off San Salvador Island), and *C. paratypus* was found only in Jamaica and Belize on mud and sand slopes with boulders. *Scleritoderma cyanea* and *S. paccardi* were also found throughout the depth range and region. Both *Daedalopelta nodosa* and *Aciculites cribrophora* were collected on rock slopes in the Bahamas, at Rum Cay at 452 m, and north of Andros Island at 534 m, respectively. *Leiodermatium lynceus* occurred at 208 m at Cap Enrage, Martinique. Until Pisera (1999) described new material, *Setidium objectum* was only known from one specimen dredged off Havana from a depth range of 234–441 m. This new material was collected off Miami and the Bahamas, between 429–516 m. We have not encountered this species as yet in our collections.

601–914 m zone.–The number of lithistids decreased in the 601–914 m zone, dominated again by *Corallistes typus* (Fig. 1). *Leiodermatium lynceus* was collected in the Bahamas (Chub Cay), and *Racodiscula asteroides* was found on vertical rock walls and steep rock slopes only in this depth

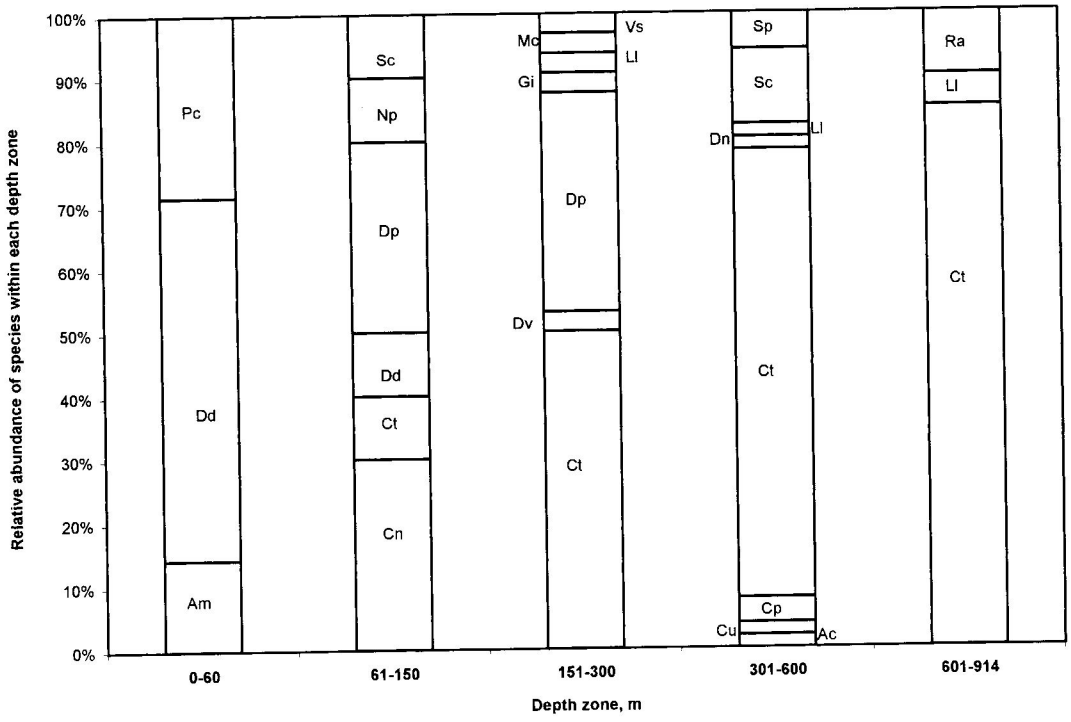

Fig. 1. Bathymetric distribution and relative abundance of lithistid species in the tropical western Atlantic region, based upon 450 submersible transects during 36 expeditions to different locations from 1984–2000 (n = 120 lithistid sponge specimens). Ac, *Aciculites cribrophora,* Am, *Amphibleptula* cf. *madrepora,* Cn, *Corallistes* cf. *nolitangere,* Cp, *C. paratypus,* Ct, *C. typus,* Cu, *C.* cf. *undulatus,* Dn, *Daedalopelta nodosa,* Dd, *Discodermia dissoluta,* Dp, *D. polydiscus,* Dv, *D.* cf. *verrucosa,* Gi, *Gastrophanella implexa,* Ll, *Leiodermatium lynceus,* Mc, *Macandrewia clavatella,* Np, *Neopelta perfecta,* Pc, *Petromica ciocalyptoides,* Ra, *Racodiscula asteroides,* Sc, *Scleritoderma cyanea,* Sp, *S. paccardi,* Vs, *Vetulina stalactites.*

zone and exclusively in the southeastern Bahamas (Great Inagua and San Salvador Islands).

Discussion

Of the 28 species of lithistids reported for the tropical western Atlantic, 19 were collected during this study (Table 1). Although more than 500 specimens of lithistid sponges have been collected from this region during our expeditions, only 120 have been identified to species. The remaining sponges consist predominantly of unidentified samples of the same species, but several new species are known and are the subject of revisionary research in progress by one of us (MK). The evaluation of relative abundance within each depth zone is based upon the 120 samples identified to species (Fig. 1). Data (not presented) on the abundance and distribution of more than 500 specimens identified to family suggests that the abundance of these species reflects the abundance of lithistid specimens in the tropical western Atlantic region. Further taxonomic revisionary work is unlikely to adjust the general patterns of distribution to any great extent, except by increasing the biodiversity inventory of species within each ecological/bathymetric zone.

It should be noted that the family Theonellidae may be over-represented in our collections, particularly in the 61–150 and 151–300 m zones, because of the focus of biomedical research on the genus *Discodermia* (e.g., ter Haar et al. 1996). However,

personal observations support our data that *Discodermia* and *Corallistes* are the two dominant genera within these depth ranges (Fig. 1). Both the diversity and bathymetric distribution of lithistids reported in this study contrast with other studies of lithistid sponges in the tropical western Atlantic (van Soest & Stentoft 1988, Maldonado & Young 1996). As previously reported (van Soest & Stentoft 1988), two of the three sponge facies in Barbados were dominated by lithistids: the *Corallistes typus/Gastrophanella implexa/Amphibleptula madrepora* facies at 137–172 m, and the *Vetulina stalactites/Amphibleptula madrepora/Scleritoderma* sp. facies at 208–324 m. In contrast, *G. implexa* and *A. madrepora* were identified only once during this study, at 181 and 15 m, respectively. Similarly, *Vetulina stalactites* was not a major component of the lithistid fauna in any depth zone at any location, and both *S. paccardi* and *S. cyanea* occurred only at greater depths, between 401 and 552 m, with one exception: *S. cyanea* was identified once at 141 m. *Corallistes typus* dominated both the 151–300 and 301–600 m zones (representing 59% and 73%, respectively, of all lithistids). *Discodermia dissoluta* was the dominant lithistid in the 0–60 m zone in this study and also occurred in the 61–150 m zone (Table 1, Fig. 1), but was not reported at all by van Soest & Stentoft (1988). These differences are undoubtedly due to the more precise sampling method (scuba and submersible vs. dredging) as well as the location, number, and depth of stations sampled (more than 450 submersible transects from 30 to 914 m throughout the tropical western Atlantic in this study vs. only two transects between 90 and 324 m off Barbados by van Soest & Stentoft (1988)). *Corallistes, Discodermia, Racodiscula, Scleritoderma,* and *Vetulina* were reported as the most abundant lithistids in a single submersible transect from 91 to 531 m off New Providence Island, Bahamas (Maldonado & Young 1996), however, *Racodiscula* occurred only at greater depths in this study, *Vetulina* was a minor component of the 151–300 m zone, and *Scleritoderma* spp. represented only 16% of the lithistid fauna in the 301–600 m zone and 8% of the lithistids identified in the depth range studied by Maldonado and Young (1996).

The diversity of lithistids represented in this study contrasts quite markedly with that of the southwest Pacific regions of the Norfolk Ridge and northern New Zealand. In the tropical western Atlantic, Theonellidae and Corallistidae dominate the fauna in terms of numbers of species, particularly of the genera *Discodermia* and *Corallistes* (Table 1). In the southwest Pacific region, *Corallistes* is also the most speciose genus, but *Discodermia* is represented by only one species. In addition to *Corallistes, Herengeria* and *Iouea* are added to the Corallistidae, and *Callipelta* and *Homophymia* are added to the Neopeltidae in the southwest Pacific. None of these genera is represented in the tropical western Atlantic. In both the southwest Pacific and our study area, *Macandrewia* and *Neopelta* are rare (Lévi 1991, Kelly 2000).

The southwest Pacific is also noted for the presence of genera from two additional suborders and one family of lithistids that are absent from the tropical western Atlantic. Suborder Helomorina, represented by *Costifer wilsoni* Lévi (1993) and the Family Phymatellidae (Suborder Tetracladina: *Aulaxinia, Reidispongia,* and *Neosiphonia*) are only known from the New Zealand-New Caledonian region. Species of *Pleroma* in the Suborder Megamorina are abundant in northern New Zealand and on the Norfolk Ridge seamounts. *Lyidium torquila* Schmidt, 1870, recorded from the West Indies and believed to be synonymous with *Pleroma,* is considered unrecognizable.

The tropical western Atlantic is noted for the presence of *Vetulina stalactites,* the only living representative of the Suborder Sphaerocladina, and for the occurrence of the genus *Racodiscula* (Suborder Tetracladina: Family Phymaraphinidae).

In terms of bathymetric distribution, a

similar pattern can be seen where Corallistidae are most abundant between 300 and 600 m in the southwest Pacific. These communities are extremely diverse with many species of bryozoans, hydroids, brachiopods, echinoderms, solitary corals and gorgonians. In northern New Zealand, the same lithistid communities are common on rocky sand-banks in waters of just over 100 m deep (Kelly 2000). The tropical western Atlantic deep-water lithistid communities are frequently co-dominated by sponges of the Class Hexactinellida ("glass sponges") and the demosponge orders Astrophorida, Haplosclerida, and Halichondrida (Reed & Pomponi 1997).

The lithistid fauna of the tropical western Atlantic is significant, both in the composition which differs substantially from the lithistid fauna of the southwest Pacific, and in the dominance of these sponges in hard-bottom habitats at depths greater than 150 m. Revisions in progress will undoubtedly add new taxa to the 28 species presently known from this region, particularly in terms of new genera, and will contribute to a better understanding of the taxonomic diversity of the group as a whole.

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