Caribbean Journal of Science, Vol. 41, No. 3, 492-507, 2005

Caribbean Shallow-water Black Corals (Cnidaria: Anthozoa: Antipatharia)

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Abstract.—Our aim is to provide a complete key and guide to the species of black corals from the Caribbean reefs at depths shallower than about 100 m. The key to the species is mostly based on colonial features that are recognized in the field, although some closely related species can only be differentiated by microscopic skeletal features. Each species is illustrated with one or more photos showing the size and shape of the colony; many photos were taken in the natural environment to facilitate underwater identification. Additionally, a short description is provided of each species and their microscopic diagnostic characters are illustrated with the aid of the Scanning Electron Microscope (SEM). Fifteen black coral species are found in relatively shallow-water in the Caribbean, Gulf of Mexico, and other parts of the tropical western Atlantic; these belong to the families Myriopathidae [*Tanacetipathes hirta* (Gray), *T. tanacetum* (Pourtalès), *T. barbadensis* (Brook), *T. thamnea* (Warner), and *Plumapathes pennacea* (Pallas)]; Antipathidae [*Antipathes lenta* Pourtales, *A. rubusiformis* Warner and Opresko, *A. furcata* Gray, *A. umbratica* Opresko, *A. atlantica* Gray, *A. gracilis* Gray, *A. caribbeana* Opresko, *Stichopathes lutkeni* Brook, and *S. occidentalis* (Gray)]; and Aphanipathidae [*Rhipidipathes colombiana* (Opresko and Sánchez)]. We hope that this guide will facilitate research on black corals on Caribbean reefs, where population surveys are urgently needed to evaluate or modify conservation policies.

KEYWORDS.—**Black corals, Antipatharia, coral reef, *Tanacetipathes, Antipathes, Stichopathes, Rhipidipathes, Plumapathes*.**

INTRODUCTION

Black corals (order Antipatharia in the class Anthozoa of the phylum Cnidaria) are important long-lived, habitat forming, sessile benthic suspension feeders (Grigg 1965; Lewis 1978; Parrish et al. 2002). Dense populations of these corals have been found in both the tropical western Atlantic and southwest Pacific (e.g., Warner 1981; Grange 1985; Sánchez 1999). Many Caribbean reefs harbor large populations of black corals, particularly on the outer reef slopes (Sánchez et al. 1998; Guzmán and Guevara 1999; Sánchez 1999), where shaded inclined substrata are more likely to be settled by black coral larvae (Grigg 1965; Oakley 1988). Black corals are everywhere in the Caribbean, usually at depths below 20 m, but reefs with high levels of suspended particulate matter and seston allow the settlement of black coral larvae as shallow as 5 m [e.g., Trinidad (Warner 1981); Bocas del Toro, Panama (Guzmán and Guevara 1999)].

Although studies on the ecology of black corals are scarce (e.g., Grigg 1965; Grange 1985), there are many important papers on the associated fauna. The number of black coral-associated-species is considerable, and includes copepods (Hume 1992), brittle-stars (Stewart, 1998), shrimp (Criales 1980; Spotte et al. 1994; Vargas 2000; Wirtz et al. 2001) and crabs (Shih and Mok 1996; Wirtz et al. 2001). Many of these commensal organisms are species-specific, demonstrating the importance of black corals in providing habitat and enhancing the diversity of other invertebrate groups.

Black corals have been harvested for

many years for the jewelry trade (Grigg 2001). Northern latitudes of the Caribbean have had established black coral fisheries and jewelry industries for many years (e.g., Cayman Islands, Cuba, and Mexico; see Castorena and Metaca 1979; Guitart et al. 1997), and in some localities there are still abundant black coral populations at relatively shallow depths (e.g., Banco Chinchorro: Mexico; see Padilla and Lara 2003). Black corals are protected by international treaties (e.g., CITES) restricting their exploitation and exportation/importation. Given the limited and complex genetic flow among black coral populations over long distances, as inferred by molecular markers (Miller 1997, 1998), as well as the low growth rates of black corals (Newton and Bak 1979; Oakley 1988), longevity seems to be the key factor for population maintenance. Consequently, overexploitation of black corals without proper management, particularly that targeting the largest/oldest colonies, could easily lead to local population extinction. Unfortunately, there is little information on "shallow-water" black coral populations in the Caribbean and it is not possible to diagnose the current state of their populations. Surveys of the black corals throughout the Caribbean region are urgently needed to estimate the status of the populations on coral reefs and to document the distribution of species.

Black corals are differentiated from other corals by their spiny, proteinaceous, skeletal axis, which may be black or various shades of brown, and by their small polyps with six simple (unbranched) tentacles, six internal primary mesenteries, and 0, 4 or 6 secondary mesenteries. Calcareous elements, such as spicules or sclerites, are not present in either the axis or soft tissue. The skeletal part of the colony is referred to as the corallum and, depending on the species, the corallum can grow as an unbranched, upright stalk that may be straight, irregularly twisted or spirally curved; or as a regularly or irregularly branched tree-like structure that may be bushy, flabellate, very symmetrically branched and pinnate, or bottle-brush in shape. Antipatharian polyps range in size from about 0.5 mm to a maximum of about 9 mm, as measured across the surface in the direction of the branch axis, and they are generally not more than a few millimeters tall. A single colony, which in some species can reach several meters in height, may possess tens of thousands of polyps. The polyps are round or elongated or compressed in the direction of the axis of the branch; in most species they are arranged in a single series on one lateral side of the axis. This side is referred to as the anterior side of the corallum, and the opposite side as the posterior side. The polyp tentacles are contractile but not retractile, i.e., they are considerably shorter when the polyps are not actively feeding, but they cannot be withdrawn into the oral cavity. When fully expanded the tentacles of some species are many times longer than the height of the polyp body and end in a very narrow tip; however, in other species the tentacles are short and blunt, with a rounded tip. The color of living colonies is often white or grayish, but it can also be yellow, green, orange, brown or even deep red. The underlying axial skeleton can be various shades of reddish-brown, brown, or black. The axial spines vary considerably in size and shape depending on the species. In some cases they are only small rounded knobs not more than 0.02 mm in height and only visible at the tips of the smallest branchlets; in others they are triangular or conical and thorn-like, whereas in still others they are cylindrical and needle-like and up to about 1 mm in height. The surface of the spines can be smooth or covered to varying degrees with small papillae or tubercles. The tip of the spines can be simple or multiply divided, and in some cases can even have an antler-like appearance. The spines are often larger on the side of the axis on which the polyps occur, and these are referred to as polypar spines; those on the opposite side of the axis are referred to as abpolypar spines.

The classification of the black corals has for many years been complicated by the description of numerous species from incomplete specimens and by the lack of a clearly defined taxonomic hierarchy at the genus and family level. For a long time all species were placed in a single family, the An-

tipathidae. However, today six families are recognized: Antipathidae, Schizopathidae, Cladopathidae, Leiopathidae, Myriopathidae, and Aphanipathidae (Opresko 2001, 2002, 2003, 2004). Families are separated on the basis of internal and external characteristics of the polyps and, in a more limited sense, by the shape, arrangement and development of the axial spines. In the Cladopathidae the polyps lack secondary mesenteries and in the Leiopathidae the polyps contain six secondary mesenteries. In all other families the polyps possess six primary and four secondary mesenteries. The Schizopathidae is characterized by polyps elongated in the direction of the branch and having a transverse diameter of 2 mm or more. Most species in the Schizopathidae, Cladopathidae and Leiopathidae occur in deep water, and are therefore not included in this guide. Species that are found in relatively shallow-water in the Caribbean and western Atlantic belong to either the Antipathidae, Myriopathidae, or Aphanipathidae.

Our aim is to provide a complete guide to the "shallow-water" black corals present in Caribbean reefs. As noted above, "shallow-water" is a relative term, and here refers to depths of 20 to about 100 m; black corals are only rarely found at shallower depths in the Caribbean, but in places such as Bocas del Toro, Panama, they do occur as shallow as 10 m on certain reefs. Our specific goals are: (1) to present a key to the species that is based as much as possible on colonial field characters; however, some closely related species can only be differentiated by microscopic skeletal features; (2) to describe the diagnostic features of each species, illustrated with the aid of the Scanning Electron Microscope (SEM); and (3) to show some images of the different species in their natural environment to facilitate underwater identification.

Materials and Methods

The key was based on SEM and drawings from specimens deposited and available at the National Museum of Natural History (NMNH, USNM), Smithsonian Institution; the British Museum of Natural History (BMNH); the Rosenstiel School of Marine and Atmospheric Science (RSMAS, UMML), University of Miami; and the Museum of Comparative Zoology (MCZ), Harvard. In addition, photographs of most specimens were added to each species description, some taken during the during the 2003-Invertebrate Workshop (Smithsonian Institution, Bocas del Toro, Panama) and from other areas of the Caribbean using SCUBA. Consequently, much of the material presented here is predominantly illustrative in nature. It is also the first time that this group of species is presented according to the recently updated classification of the Antipatharia (see Opresko 2001, 2002, 2003, 2004). Additional revisions to the classification, particularly as they pertain to the family Antipathidae, are still in progress.

Species Key

1a. Coral forming long unbranched, whip-like colonies ---------- 2
1b. Coral forming branched and/or pinnulated colonies. ---------- 3
2a. Living colony reddish brown in color ---------- ---------- *Stichopathes lutkeni* Brook
2b. Living colony yellowish-green in color ---------- ---------- *Stichopathes occidentalis* (Gray)
3a. Colony (stem and branches) with pinnules of uniform size, and arranged on the axis in a pinnate or bottle-brush pattern ---------- 4
3b. Colony irregularly bushy or fan-shaped; without pinnules --------- 5
4a. Stem and branches with simple pinnules in 2 rows ---------- ---------- *Plumapathes pennacea* (Pallas)
4b. Stem and branches (when present) with pinnules (some with subpinnules) arranged in 4-6 rows around axis (bottle brush appearance) ---------- 13
5a. Colony fan-shaped, branches mostly in one plane. ---------- 6
5b. Colony bushy, branchlets not in one plane ---------- 9
6a. Smallest branches more than 2 cm, linear, elongate, most reaching

to the top of the corallum; branching dichotomous ---------- *Antipathes furcata* Gray (young colonies of about 20 cm or less in height)

6b. Smallest branchlets short, usually less than 1 cm; irregularly bilateral ---------- 7

7a. Spines less than 0.1 mm ---------- 8

7b. Spines greater than 0.2 mm ---------- *Rhipidipathes colombiana* (Opresko and Sánchez)

8a. Living polyps grayish white, sometimes greenish ---------- *Antipathes atlantica* Gray

8b. Living polyps orange or red-orange ---------- *Antipathes gracilis* Gray

9a. Branches generally directed vertically; mature colonies usually >20 cm in height ---------- 10

9b. Branches in all directions; mature colonies usually <20 cm tall ---------- 11

10a. Colony up to 1 m or more; branching from all sides and extending to various heights and often curved downward ---------- *Antipathes caribbeana* Opresko

10b. Colony usually less than 0.5 m; branching dense, with straight, stiff, elongate branchlets, most reaching to the top of the corallum ---------- *Antipathes furcata* Gray (older colonies >20 cm in height)

11a. Colony with very thin branchlets (usually less than 0.5 mm) ---------- 12

11b. Colony with thick branchlets (mostly 0.5 mm or more in diameter) ---------- *Antipathes umbratica* Opresko

12a. Colony with single holdfast; spines smooth ---------- *Antipathes lenta* Pourtalès

12b. Colony with multiple holdfasts; spines papillose ---------- *Antipathes rubusiformis* Warner and Opresko

13a. Primary pinnules long, with only a few subpinnules near the proximal end closest to the point of origin ---------- 14

13b. Primary pinnules with subpinnules along more than half of the length ---------- 15

14a. Spines usually less than 0.13 mm ---------- *Tanacetipathes hirta* (Gray)

14b. Spines usually greater than 0.13 mm (up to 0.3 mm) ---------- *Tanacetipathes barbadensis* (Brook)

15a. Subpinnules mostly on one side of primary pinnules ---------- *Tanacetipathes tanacetum* (Pourtales)

15b. Subpinnules bilaterally arranged on two sides of primary pinnules ---------- *Tanacetipathes thamnea* (Warner)

Species Account

Family Antipathidae Ehrenberg, 1834

The family Antipathidae is characterized by polyps of variable size (from about 1-3 mm in diameter), usually with very long tentacles ending in a narrow tip (as seen in living, fully expanded polyps; however, when preserved the tentacles can be considerably shorter). The spines are simple, triangular in lateral view, often laterally compressed, smooth or papillose, and sometimes knobbed or multiply forked at the apex. The corallum can be bushy or fan-shaped (*Antipathes*), or consist of only a single elongated, straight or spirally curved stalk (*Cirrhipathes* and *Stichopathes*).

Antipathes lenta Pourtalès, 1871 (Fig. 1)

Small, sparsely and irregularly branched colonies, usually less than 15 cm high, with thin branches rarely more than 0.5 mm in diameter. Branches up to 15 cm long; branch angles very wide (45-90°); branches spaced at varying distances apart (mostly 1-2 cm apart). Spines short, triangular, smooth, 0.05-0.09 mm tall and 0.07-0.12 mm wide at their base; arranged in 6-9 axial rows with 15-40 spines per cm in each row. Polyps variable in size, maximum transverse diameter about 1 mm; arranged in a single series, 1-2 mm apart, with 5-6 polyps per centimeter. Color of living colonies white or grayish. Found mostly at depths of 20 to 100 m. Known from Venezuela north to the Gulf of Mexico.

Antipathes rubusiformis Warner and Opresko, 2004 (Fig. 2)

Colonies low and spreading, usually less than 10 cm high and 50 cm wide, with mul-

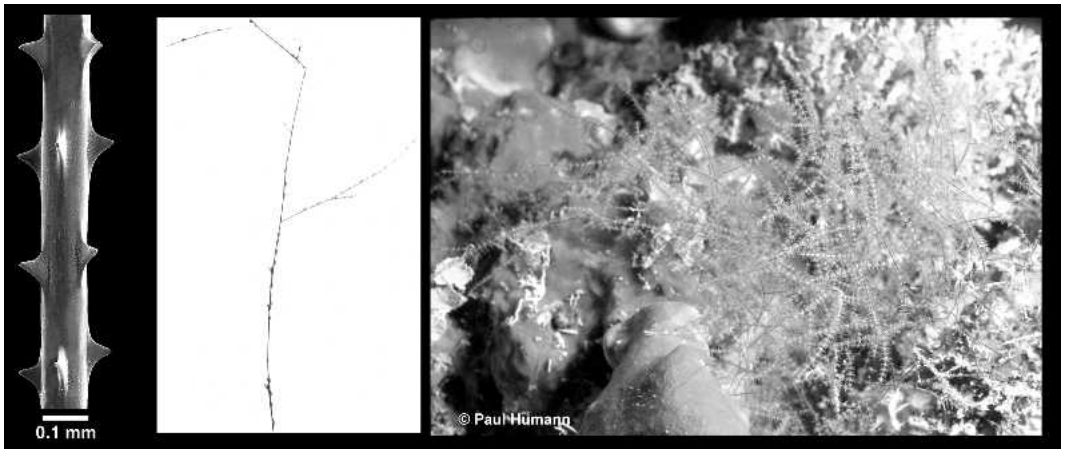

FIG. 1. SEM of the axis (USNM 91418), lectotype (MCZ 61447), and living colony of *Antipathes lenta* Pourtalès, 1871. (*In situ* photo copyright© Paul Humann)

tiple holdfasts and no distinct stem. Branchlets thin, not more than 0.6 mm in diameter and up to 10 cm long, extending out in all directions (branch angles close to 90°) and spaced 10-15 cm apart. Spines short, triangular, papillose, up to 0.11 mm tall. Polyps 0.5-1.0 mm in transverse diameter, arranged in a single series, with 7-8 polyps per cm. Tentacles up to 3.5 mm long when fully expanded. Colonies yellowish in color when alive. Found on ceiling of overhangs, in about 20-30 m. Known only from Jamaica.

Antipathes umbratica Opresko, 1996 (Fig. 3)

Branched colonies, low and spreading laterally; usually less than 20 cm high, with thick branches 0.5-1 mm in diameter. Branches up to 15 cm or more in length; branch angles very wide (usually > 75°); branches spaced varying distances apart (mostly 0.5-1.0 cm). Spines relatively large, triangular, papillose, up to 0.24 mm tall; arranged in 8-10 axial rows. Polyps 0.9 to 1.2 mm in transverse diameter; arranged in a single series, about 0.5 mm apart, with 6-7

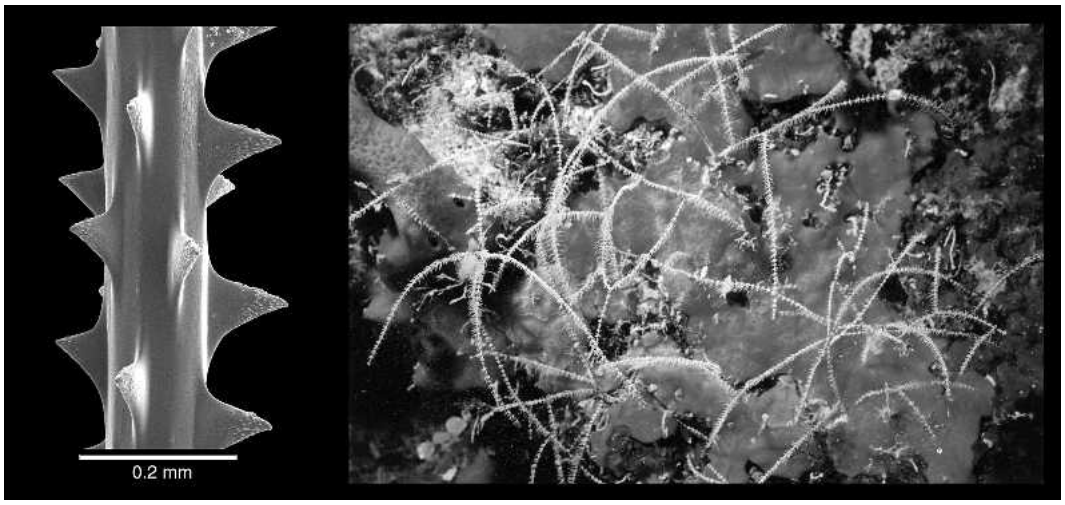

FIG. 2. SEM of the axis from the holotype (BMNH 2000.1844), and living colony of *Antipathes rubusiformis* Warner and Opresko, 2004 (Jamaica; *in situ* photo courtesy of George F. Warner).

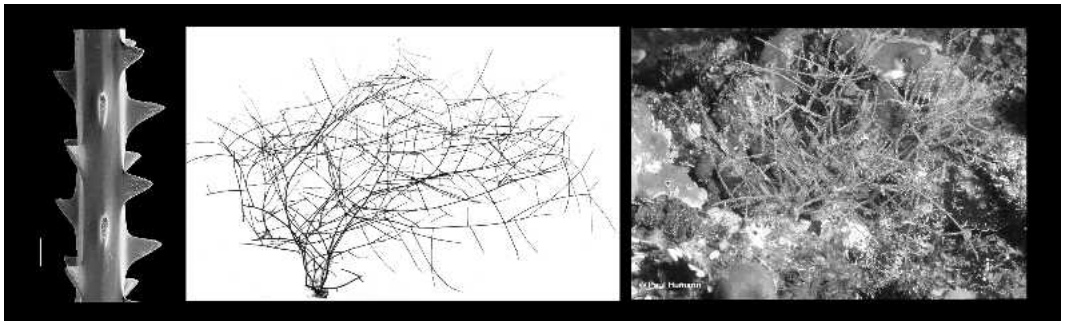

FIG. 3. SEM of the axis and holotype (USNM 94388) (scale = 0.1 mm), and living colony of *Antipathes umbratica* Opresko, 1996. (*In situ* photo copyright© Paul Humann)

polyps per centimeter. Color of living colonies white, light yellow, or reddish brown. Found in caves and under ledges at depths of 25-40 m. Known from Honduras north to the Bahamas.

Antipathes furcata Gray, 1857 (Fig. 4)

Small colonies (less than ~20 cm in height) fan-shaped, branched mostly in one plane; with very long, straight, ascending branches. Larger colonies (20-40 cm in height) densely branched, in a thick plane with numerous overlapping branches. Branches directed upward and away from the centre, with most reaching to the top of the corallum; branch angles very narrow, 30° or less. Spines short, triangular, smooth, 0.05-0.1 mm tall and 0.07-0.1 mm wide at their base; arranged in 6-8 rows with 30-40 spines per centimeter in each row. Spines occasionally bifid or forked. Polyps 0.7-1.0 mm in transverse diameter; arranged in a single series on one side of branches; 6-8 polyps per centimeter. Colonies white in color when alive. Found at depths of 15 to about 70 m. Known from Colombia north to the Bahamas.

Antipathes atlantica Gray, 1857 (Fig. 5)

Large, often densely branched, fan-shaped colonies, 0.5 m or more in height.

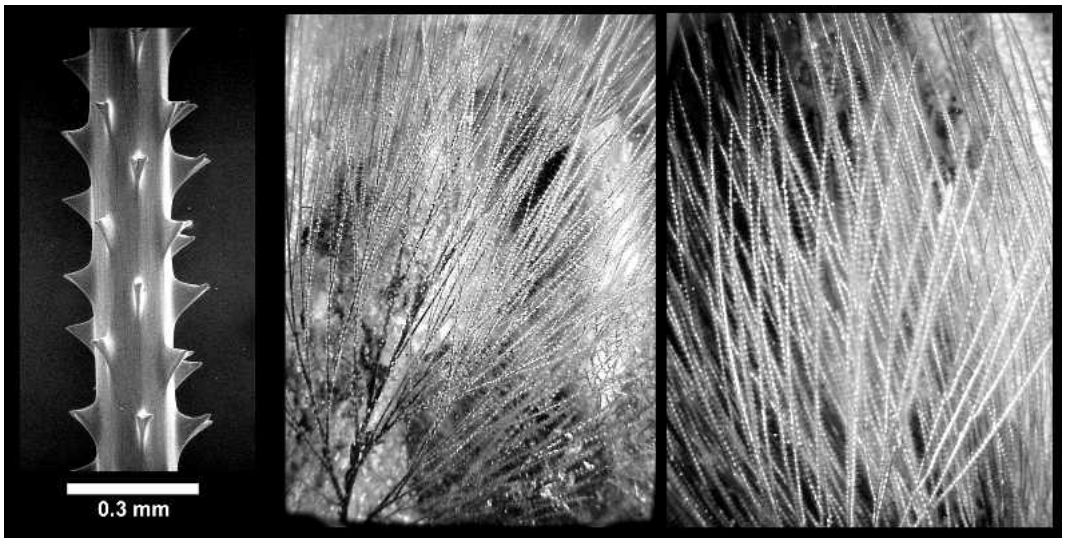

FIG. 4. SEM of the axis, and living colonies *Antipathes furcata* Gray, 1857 (Colombia, Santa Marta, Punta de Betin, 25 m, INVEMAR collection).

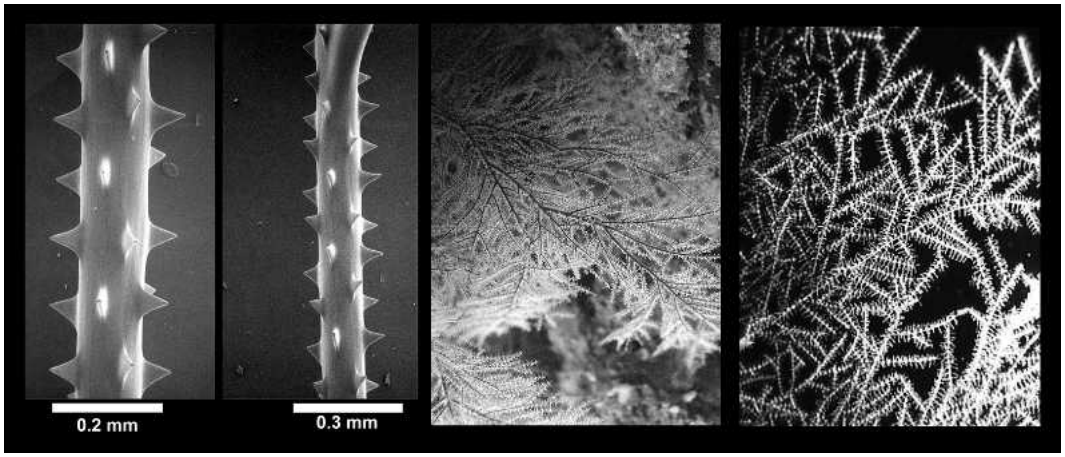

FIG. 5. SEMs of the axis, and living colonies (Bahamas, Cat island, 20-30 m) of *Antipathes atlantica* Gray, 1857.

Branching to the 8th or 9th order; branches sometimes anastomosing. Smallest branchlets straight or slightly curved, usually less than 1 cm long; arranged bilaterally along the sides of the branches. Spines short, triangular, smooth, mostly 0.05-0.07 mm tall, and about equally as wide at their base; arranged in 7-8 rows with 35-50 spines per centimeter in each row. Polyps 0.6-1.0 mm in transverse diameter; arranged on the branchlets in a single series and usually present on only one side of the corallum. Living colonies greyish-white or greenish in color.

This species is often difficult to distinguish from *A. gracilis* Gray except by the color of the living polyps. Found on deep reefs at depths of about 20 to 100 m. Known from Colombia north throughout the Caribbean. This species has been important commercially, the main axis of the largest colonies is suitable for jewelry. This species was commonly observed in the vicinity of Bocas del Toro (e.g., Crawl Key) below 15 m depth.

Antipathes gracilis Gray, 1860 (Fig. 6)

Large, strongly branched, fan-shaped colonies, 0.5 m or more in height. Primary branches often very distinct, curved or sinuous and some extending upward from near the base of corallum. Branching to the 8th or 9th order; branches sometimes anastomosing. Smallest branchlets straight or slightly curved, usually less than 1.5 cm; arranged bilaterally along the sides of the branches. Spines short, triangular, smooth, mostly 0.05-0.07 mm tall and about equally as wide at their base; arranged in 7-8 rows with 30-50 spines per centimeter in each row. Polyps 0.6-1.0 mm in transverse diameter; arranged on the branchlets in a single row and mostly confined to only one side of the corallum. Living colonies orange or reddish-orange in color. Note: this species is often difficult to distinguish from *A. atlantica* Gray except by the color of the living polyps. Found on deep reefs at depths of about 20 to 100 m. Known from Colombia north throughout the Caribbean and in Gulf of Mexico. This species has been important commercially, the main axis of the largest colonies is suitable for jewelry. This species was also observed in Crawl Key, Bocas del Toro, Panama.

Antipathes caribbeana Opresko, 1996 (Fig. 7)

Large bushy colonies branched to the 10th order or more, 1 m or more in height. Branches linear, elongate, with narrow distal branch angles (30-45°). Smallest branchlets straight or slightly curved, 0.15-0.30 mm in diameter (excluding spines) and 10 cm or more in length without becoming branched. Spines conical to subcylindrical in appearance; flared out distally and proximally at junction with axis; covered with small knob-like or cone-shaped tubercles over apical one-half to three-

FIG. 6. SEM of the axis (type, BMNH), and living colonies (Bocas del Toro, Panama, 20 m) of *Antipathes gracilis* Gray, 1860. The width of the axis at the bottom of SEM (not including the spines) is 0.1 mm.

quarters of surface. Polypar spines 0.08-0.16 mm tall; abpolypar spines 0.06-0.12 mm. Narrow conical secondary spines sometimes present on branches 0.4 mm or more in diameter. Polyps about 1.0 mm in transverse diameter with an interpolypar space of 0.3-0.5 mm; arranged on smallest branchlets in a single series with 6-10 polyps per centimeter. Polyps on larger branches and stem less regularly distributed, sometimes occurring on all sides of the axis. Living colonies brownish in color with translucent tentacles. Found especially on vertical wall faces at reef edge in areas of strong currents, at depths of 30 to about 100 m. Known from Colombia north to the Bahamas (abundantly observed in Crawl Key, Bocas del Toro, Panama). This

FIG. 7. SEM of the axis (USNM 94379), and living colonies (Bocas del Toro, Panama, 20 m) of *Antipathes caribbeana* Opresko, 1996.

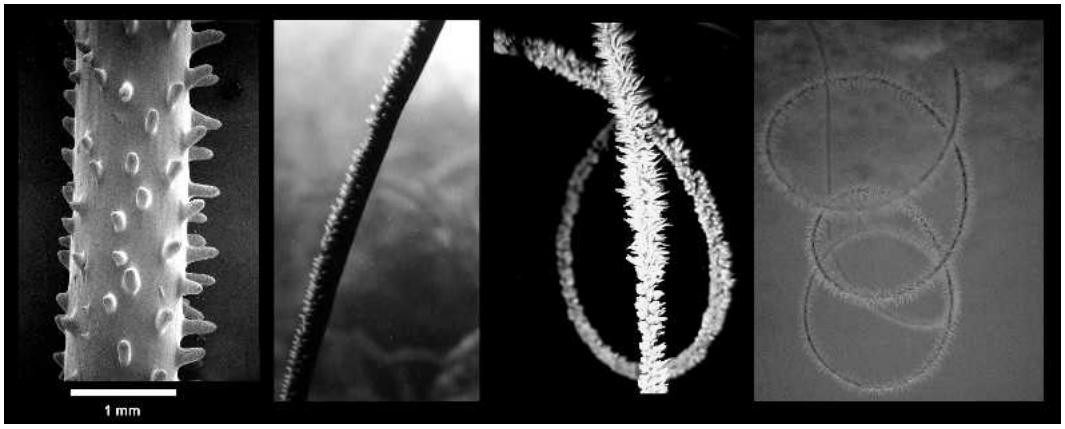

FIG. 8. SEM of the axis, and living colonies (Bocas del Toro, Panama, 25 m) of *Stichopathes lutkeni* Brook, 1889.

species has been important commercially, the main branches of large colonies are suitable for jewelry.

Stichopathes lutkeni Brook, 1889 (Fig. 8)

Corallum unbranched, 80 cm or more in height; lower part of stem straight or curved, upper part spiral (in large colonies). Spines conical to subcylindrical; covered with small knob-like or cone-shaped tubercles. Polypar spines up to 0.34 mm tall; abpolypar spines up to 0.25 mm. Spines arranged in 13 or more rows, with 25-30 spines per centimeter in each row. Polyps about 1.4 mm in transverse diameter; arranged in a single series and very crowded. Colonies usually orange or reddish brown with translucent-white tentacles. Usually found at depths greater than 20 m. Known throughout the Caribbean. This species was commonly observed in the vicinity of Bocas del Toro below 15 m depth.

Stichopathes occidentalis (Gray, 1860) (Figs. 9 & 10)

Corallum unbranched, 1 m or more in height; lower part of stem straight or curved, upper part spiral (in large colonies). Spines conical to subcylindrical; covered with small knob-like or cone-shaped tubercles. Polypar spines up to

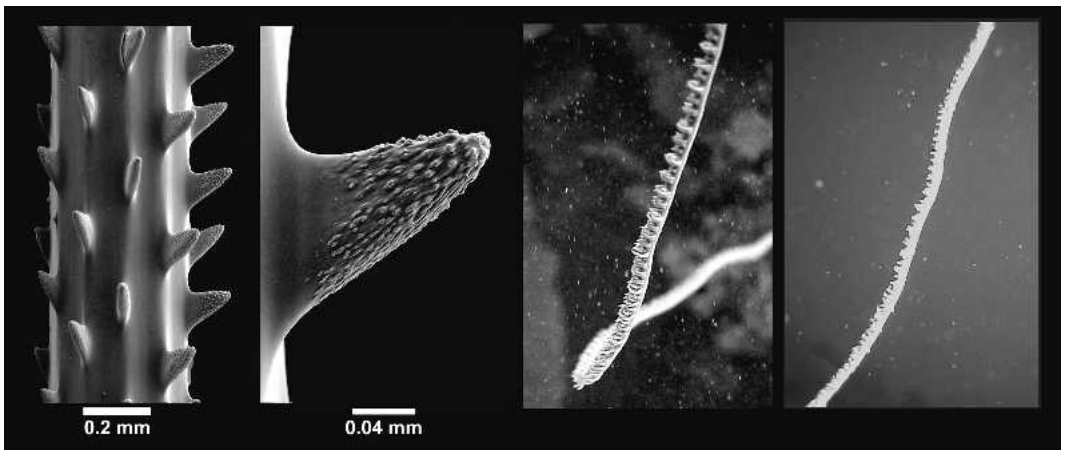

FIG. 9. SEM of the axis and single spine from the type (USNM 100386), and living colonies (Bocas del Toro, Panama, 25 m) of *Stichopathes occidentalis* (Gray, 1860).

FIG. 10. Colonies of *Stichopathes occidentals* (Gray) on the coral reef slopes of the Rosario islands, off Cartagena, Colombia (20-40 m).

0.18 mm tall (Fig. 9); abpolypar spines up to 0.07 mm. Polyps about 1.4 mm in transverse diameter; arranged in a single series and very crowded together. Living colonies yellowish green. Usually found at depths greater the 20 m. Known throughout the Caribbean, it can be one of the most abundant species on outer coral reef slopes (e.g., Fig. 10).

Previous type descriptions of *S. occidentalis* (Gray, 1860, and Brook, 1889) indicated that spines were triangular and laterally compressed with a smooth surface; however, recent re-examination of the type specimen by SEM (Fig. 9) revealed that the polypar spines are distinctly papillose, and similar to those of *S. lutkeni*, except smaller. The type of *S. occidentalis* is a dry specimen; therefore, information on the size of the polyps and color of the living colonies is not available; however, based on spine size and morphology, it is very likely that the common yellowish-green *Stichopathes* on the reefs of the Caribbean is *S. occidentalis*. Bocas del Toro (e.g., Crawl Key) reefs present abundant sympatric populations of both *S. lutkeni* and *S. occidentalis*.

Family Myriopathidae Opresko, 2001

The family Myriopathidae is characterized by polyps 0.5 to 1.0 mm in transverse

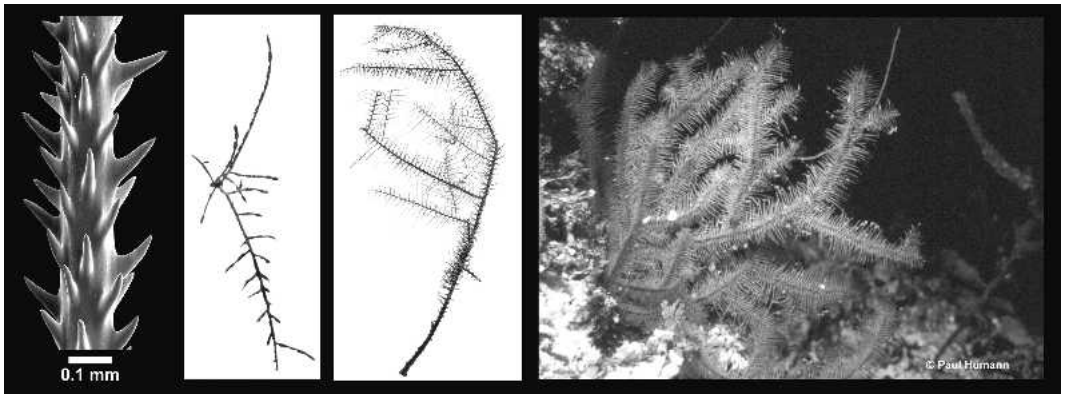

FIG. 11. SEM of the axis (USNM 77481), branch pinnules, and colonies of *Tanacetipathes hirta* (Gray, 1857). (*In situ* photo copyright© Paul Humann)

diameter; short tentacles with a rounded tip; acute, conical to blade-like spines up to 0.3 mm tall on the smallest branchlets or pinnules; and cylindrical, simple, forked or antler-like spines on the larger branches and stem. The family contains five genera of which two, *Tanacetipathes* and *Plumapathes*, occur in the western Atlantic.

Tanacetipathes hirta (Gray, 1857) (Fig. 11)

Sparsely branched, pinnulated colonies; usually less than 0.5 m in height. Branching to the 3rd or 4th order; branches usually arising laterally at right angle to the lower branches. Stem and branches with 4-6 rows of primary pinnules, arranged biserially and in alternating groups of two or three along the length of the axis. Posterior primary pinnules usually 2-3 cm long and 2-6 times longer than anterior primary pinnules. Secondary pinnules usually confined to posterior (abpolypar) side of basal section of primary pinnules; tertiary pinnules few in number (1-3) and restricted to posterior side of those secondaries nearest the base of each primary. Spines smooth, conical to sub-cylindrical, with acute apex, often distally inclined; 0.07-0.13 mm tall on polypar side of the axis and 0.03-0.10 mm on the abpolypar side of the axis. Polyps in a single series, 0.7-0.8 mm in transverse diameter, with 10-12 polyps per centimeter. Living colonies grayish in color. Found at depths of 25 to 400 m. Known from Brazil north to the Gulf of Mexico.

Tanacetipathes tanacetum (Pourtales, 1880) (Fig. 12)

Small, simple, pinnulated colonies (rarely branched), usually less then 20 cm in height. Branches, when present, usually arising from near base of stem. Stem and branches with 4-6 rows of primary pinnules, arranged biserially and in alternating groups along the length of the axis. Posterior primary pinnules usually 1.0-2.5 cm long. Primary pinnules typically with two, and sometimes three orders of subpinnules. Four or more secondary pinnules arranged mostly uniserially on posterior (abpolypar) side of primaries; tertiary pinnules occurring uniserially on abpolypar side of secondary pinnules. Quaternary pinnules sometimes present on tertiaries. Spines smooth, conical, with acute apex, often distally inclined; 0.13-0.3 mm tall on polypar side of the axis. Polyps in a single series, 0.6-0.8 mm in transverse diameter, with 10-13 polyps per centimeter. Color of living colonies grayish. Found on deep reefs usually at depths greater than 50 m. Known from Brazil north to the Gulf of Mexico.

Tanacetipathes barbadensis (Brook, 1889) (Fig. 13)

Young colonies less than about 30 cm, simple, unbranched, but pinnulate; larger colonies sparsely branched and 50 cm or

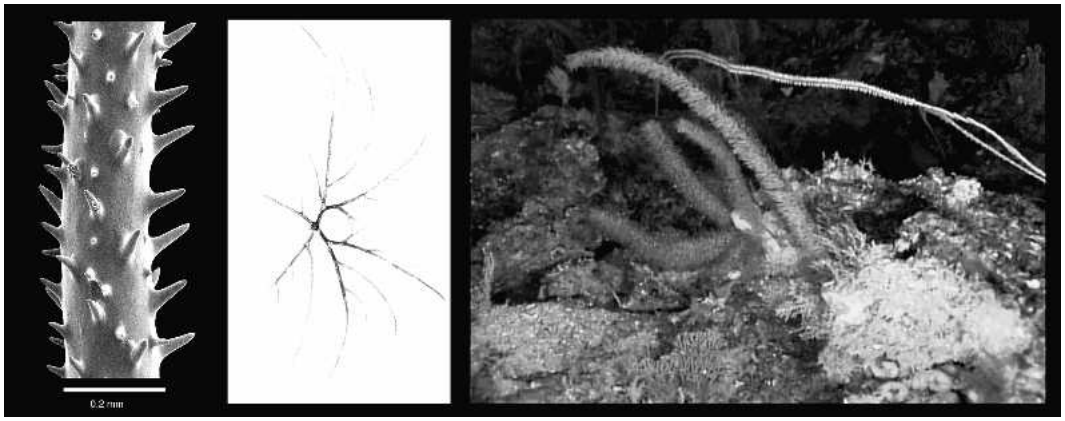

FIG. 12. SEM of the axis of a syntype (MCZ 57361), branch pinnules, and colonies of *Tanacetipathes tanacetum* (Pourtalès, 1880). (*In situ* photo courtesy of Peter Etnoyer, and NOAA)

more in height. Branches sometimes as long as stem. Stem and branches with 4-5 rows of primary pinnules arranged biserially, with two-three rows on each side, and in alternate groups of two or three on opposite sides of axis. Posterior primary pinnules up to 6 cm long and slightly longer than anterior primary pinnules. Secondary pinnules usually confined to the posterior (abpolypar) side of primary pinnules; tertiary pinnules on posterior (abpolypar) side of those secondaries nearest the base of each primary. Subpinnulation often limited to only one or two secondaries near base of posterior primaries. Tertiary pinnules sometimes absent. Spines smooth or slightly papillose, subcylindrical, acute; often distally inclined; up to about 0.28 mm tall on polypar side of the axis. Polyps in a single series, about 1 mm in transverse diameter. Living colonies grayish or brownish in color. Found mostly at depths of about 30 to 100 m. Known from Brazil north to the Bahamas Islands.

Tanacetipathes thamnea (Warner, 1981)
(Fig. 14)

Sparsely branched, densely pinnulated colonies; mostly 20-40 cm in height (young colonies without branches). Branching irregular but tending to be planar; lower order branches sometimes as long as stem. Stem and branches mostly with four (up to six) rows of primary pinnules, arranged biserially, and also in alternating groups consisting of one pinnule from each row. Pos-

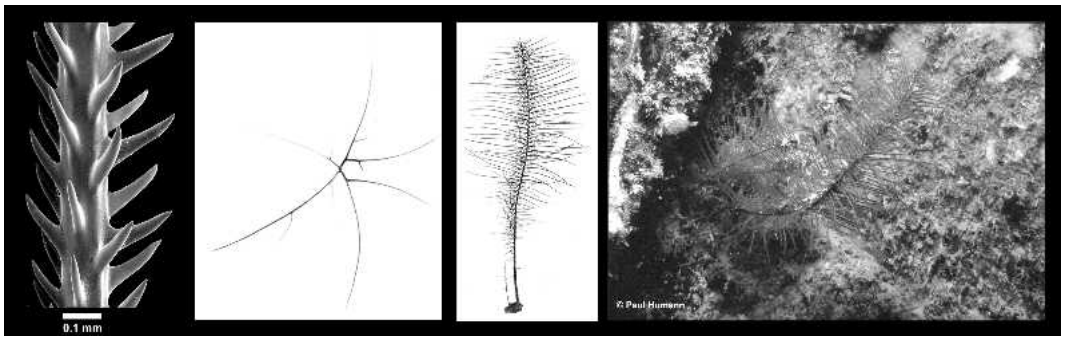

FIG. 13. SEM of the axis (USNM 92278), branch pinnules and dry colony (UMML 7.946), and living colony of *Tanacetipathes barbadensis* (Brook, 1889). (*In situ* photo copyright© Paul Humann)

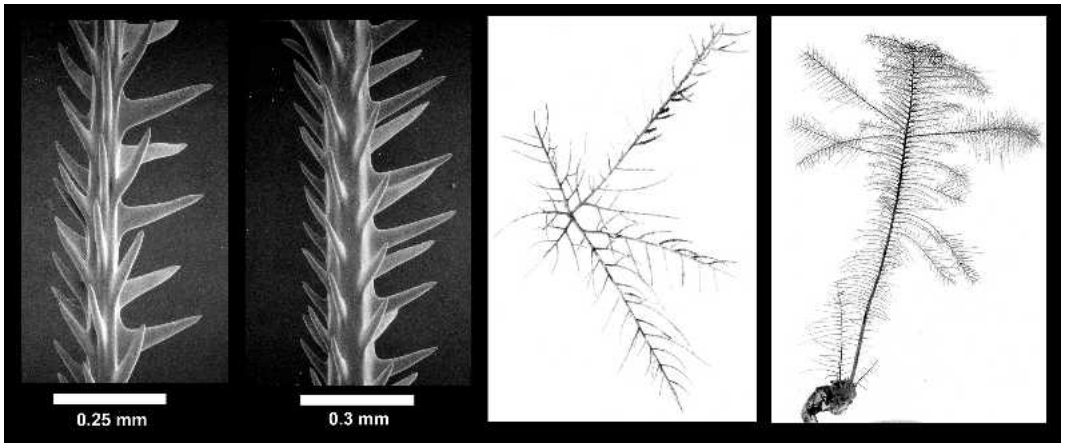

FIG. 14. SEMs of the axis (USNM 92583), branch pinnules, and dry colony (UMML 7.1130) of *Tanacetipathes thamnea* (Warner, 1981).

terior primary pinnules up to 2.5 cm long and slightly longer than anterior primary pinnules. Secondary pinnules usually numerous, 5-10 per centimeter, often arranged biserially and alternating; tertiary pinnules on posterior (abpolypar) side of those secondaries nearest the base of each primary. Spines smooth, subcylindrical, acute; often distally inclined; 0.09-0.21 mm tall on polypar side of the axis and 0.05-0.19 mm on the abpolypar side of the axis. Polyps in a single series, 0.5-0.65 mm in transverse diameter, with 10-17 polyps per centimeter. Color of living colonies not reported. Found at depths of about 30 to 100 m. Known throughout the Caribbean north to the Bahama Islands.

Plumapathes pennacea (Pallas, 1766)
(Fig. 15)

Large, sparsely to densely branched, pinnulated colonies, 0.5 m or more in height. Branching irregular but tending to be in one plane; lower order branches one-half as long as stem or longer. Stem and branches with two anterolateral rows of simple filiform pinnules up to 6 cm long (usually 2-4 cm long). Pinnules in opposite rows arranged alternately with members of each row spaced 1-3 mm apart. Spines smooth to very faintly papillose, subcylindrical, acute; distally inclined; up to 0.35 mm tall on polypar side of the axis and up to 0.15 mm tall on abpolypar side of axis. Spines on

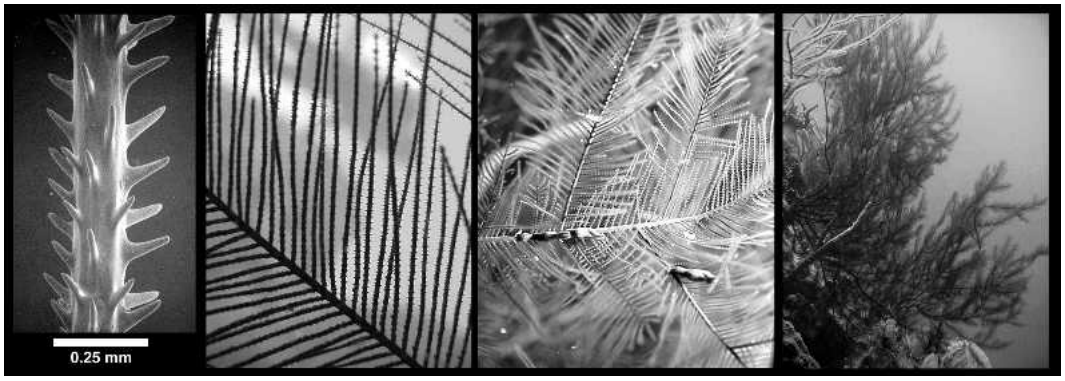

FIG. 15. SEM of the axis (USNM 92976), and living colonies (color photos: Cat Island, Bahamas, 25 m) of *Plumapathes pennacea* (Pallas, 1766) (black and white photo courtesy of Pat Collin).

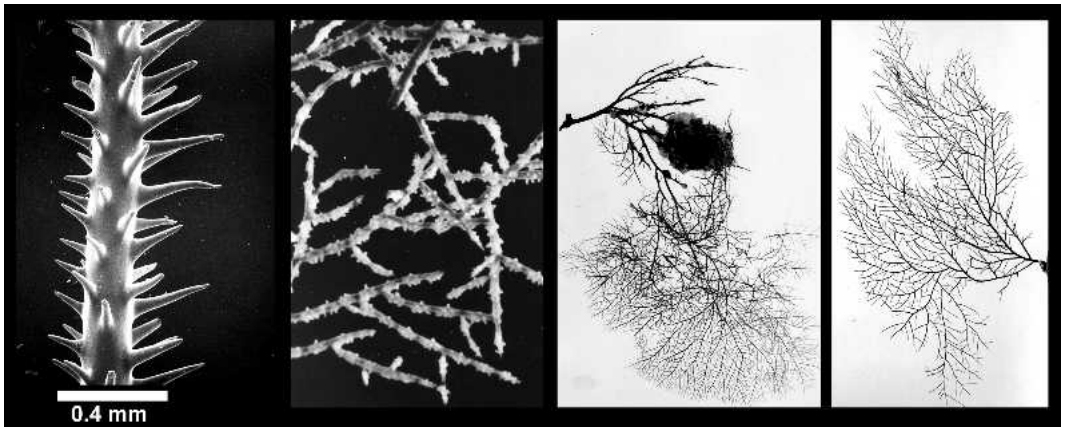

FIG. 16. SEM of the axis (USNM 92983), close-up of branchlets and dry holotype (USNM 96512) and paratype of *Rhipidipathes colombiana* (modified from Opresko and Sánchez, 1997).

pinnules arranged in 7-10 longitudinal rows with 35-70 spines per centimeter in each row. Polyps 0.45-0.8 mm in transverse diameter; arranged in a single series, with 10-13 polyps per centimeter. Color of living colonies grayish or orange-brown. Found at depths of 20 m or more. Known from Brazil north to the Bahamas. This species is important commercially, the main branches of large colonies are suitable for jewelry.

Family Aphanipathidae Opresko, 2004

The family Aphanipathidae is characterized by polyps 0.5-1.3 mm in transverse diameter and with short subequal tentacles, and by tall, conical to cylindrical spines which are often covered with small conical tubercles. Most species in the family occur at depths greater than 100 m, and only one species falls in the category of "shallow-water" fauna discussed in this paper.

Rhipidipathes colombiana (Opresko and Sanchez, 1997) (Fig. 16)

Small fan-shaped colonies, branched to 9th order or more, usually less than 25 cm in height. Major branches distinct, relatively long (up to one-half or more of total height of corallum); irregularly curved or sinuous; occasionally overlapping and adhering. Highest order, unbranched branchlets arranged bilaterally, usually irregularly alternate, occasionally uniserial, rarely subopposite; usually 8-10 per centimeter; inclined distally, straight or curved; some projecting slightly out of polypar side of corallum; typically 3-6 mm in length and spaced 1-9 mm apart. Spines long, needle-like, acute, smooth; unequal in size around circumference of axis. Polypar spines on branchlets typically 0.20-0.30 mm from midpoint of base to apex; abpolypar spines 0.10-0.18 mm. Polypar spines anisomorphic, i.e., slightly larger in the area of the polyps. Spines generally decreasing in size on larger branches and stem. Spines on branchlets spaced 0.18-0.31 mm apart (4-6 per mm) and arranged in 7-8 axial rows along the length of the branchlets and branches. Polyps small, usually 0.55-0.65 mm in transverse diameter (from proximal side of proximal lateral tentacles to distal side of distal lateral tentacles) and spaced 0.27-0.36 mm apart. Polyps on branchlets arranged in single row on one side of corallum, usually with 9-10 per centimeter. Polyps on larger branches and stem less crowded and arranged less regularly. Color of living colonies dark yellow or ocher. Found at depths of 18-60 m. Known only from Colombia (Rosario islands-Cartagena and Santa Marta).

Acknowledgments.—Special thanks to Rachel Collin (STRI-Smithsonian) who coordinated and directed the Invertebrate Workshop at Bocas del Toro, Panama, and encouraged the writing of this paper. Paul

Humann, Peter Etnoyer, George F. Warner, and Pat Collin kindly provided underwater photos of some of the species studied. J. A. Sánchez acknowledges a postdoctoral fellowship from the National Museum of Natural History (NMNH) of the Smithsonian Institution (2002-2003). Assistance and advice from the staff of the SEM laboratory at the NMNH (Scott Whitaker and Susan Braden), the Invertebrate Zoology Department at the NMNH (Stephen D. Cairns and F. M. Bayer), the British Museum of Natural History (S. Halsey), the Museum of Comparative Zoology, Harvard (A. Johnston), the Rosenstiel School of Marine and Atmospheric Science, University of Miami (N. Voss), and INVEMAR, Santa Marta, Colombia (Sven Zea, Juan M. Díaz, and Jaime Garzón-Ferreira) are especially appreciated and gratefully acknowledged.

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