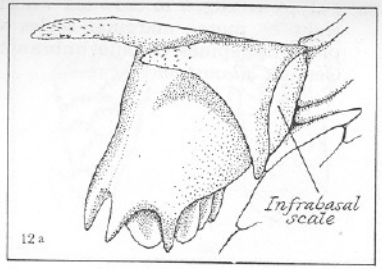
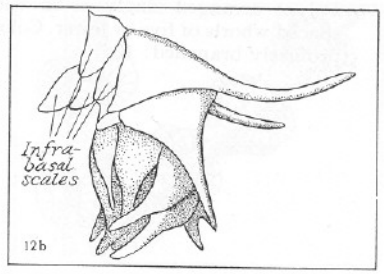
12a. One pair of small infrabasal scales between basal scales and stem scales; no adaxial buccal scales: Genus *Calyptrophora*



12b. Several pairs of small infra-basal scales lie between basal body scales and scales of stem rind; vestigial adaxial buccal scales present: Genus *Arthrogorgia*



Genus **Callogorgia** Gray, 1858

Callogorgia Gray 1858, p. 286. (Type species, *Gorgonia verticillata* Pallas, by monotypy.)
Caligorgia, Deichmann 1936, p. 158.

Calligorgia and *Caligorgia* are quite inadmissible variant spellings; the latter was introduced by Wright & Studer in the 'Challenger' Report (1889) and so gained wide usage. It must be dropped.

Distribution. This genus has a virtually cosmopolitan distribution, although most of its species belong to the Indo-Pacific region. Two species occur in the West Indies, one of them also in the Mediterranean. One species has been described from the Antarctic and two from cold waters in the North Pacific.

Species of *Callogorgia* characteristically inhabit considerable depths, down to 2472 meters, but in the Gulf of Mexico, the common *Callogorgia verticillata* has been taken as shallow as 20 fathoms.

94 **Callogorgia verticillata** (Pallas), 1766

(Fig. 96)

Gorgonia verticillata Pallas 1766, p. 177. (Mare Mediterraneum, Atlanticum.)
Caligorgia verticillata, Deichmann 1936, p. 159, pl. 25 figs. 5–9, pl. 26 fig. 6. (Cuba, Jamaica, and the Windward Islands.)

This species has been described by Deichmann, so it will suffice here only to give a figure and to note that *C. verticillata* has clavate polyps (Fig. 96 b) with strongly sculptured scales (Fig. 96 c) numbering 8–10 in each abaxial row and a low operculum composed of scales with several radial ridges but no terminal tooth (Fig. 96 d), whereas *C. gracilis* (Milne Edwards & Haime) has nearly cylindrical polyps with almost smooth scales numbering 4–7 in each abaxial row, and a tall, conical operculum composed of scales with a strong apical tooth. *C. gracilis* has not yet been found in water as shallow as has *C. verticillata*.

Material. One specimen from the Campeche Bank, Gulf of Mexico, 21°17′ North, 91°18′ West, in 20 fms., *Oregon* sta. 1048, 13.V.1954 (USNM 50527). Also a number of USNM specimens from deeper water (100–250 fms.) off the Florida Keys (44131, 44159, 44160, 44161), Cay Sal Bank (50185), the northern coast of Cuba (10104), and off Surinam, east of Paramaribo, 75–80 fms. (51257).

Distribution. In the West Indian region, from the Florida Keys to Surinam; also the Mediterranean Sea and probably the eastern part of the Atlantic.

Family **CHRYSOGORGIIDAE** Verrill, 1883

Diagnosis. Holaxonia with axis heavily calcified, its core solid, not cross-chambered; layers concentric, smooth, rarely undulated (one genus); calcification not radial. Sclerites of rind and of polyps in the form of rods or needles, in many species modified into thin scales or plates, with granular or aculeate ornamentation; calcification concentric, no cruciform pattern under polarized light. Basal disk calcareous, simple and adherent to solid objects, or root-like for securing the colony in mud.

Remarks. Inasmuch as this deep-water family has been thoroughly covered by Deichmann (1936), treatment here is limited to a key to the genera.

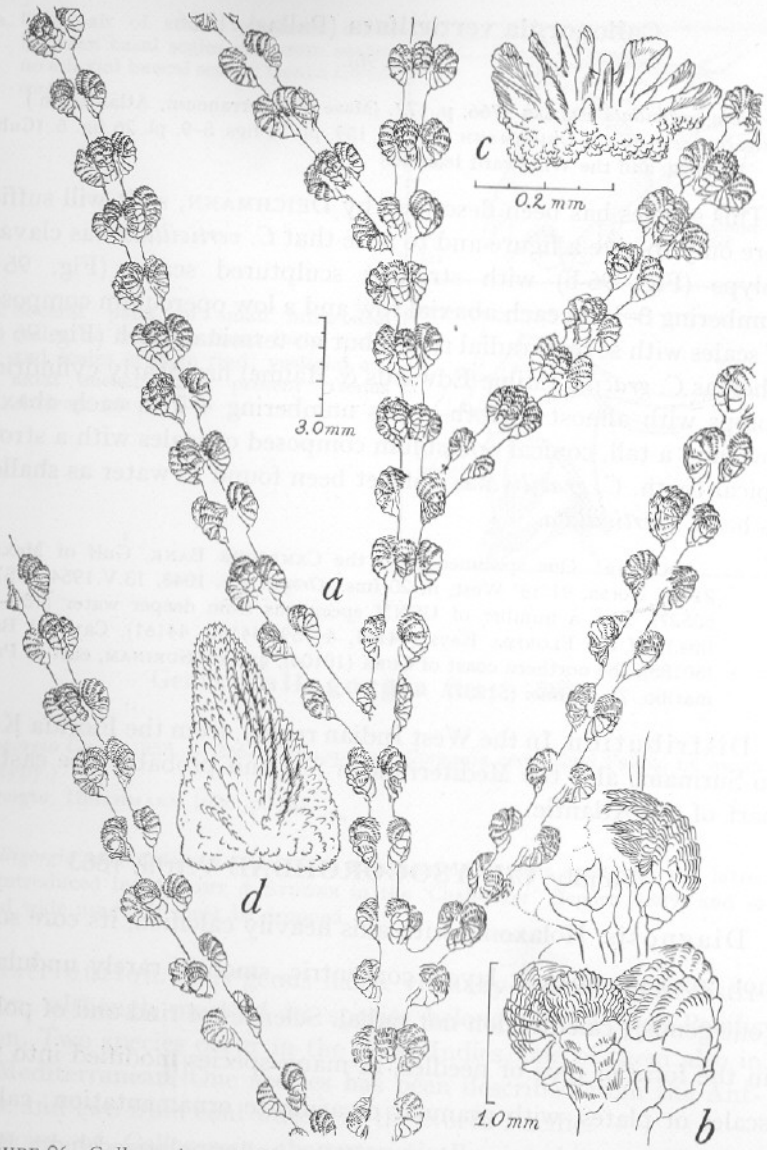


FIGURE 96. *Callogorgia verticillata* (Pallas); a specimen from the Florida Keys (USNM 44159): *a*, part of a branch (enlarged as indicated by 3.0 mm. scale); *b*, whorls of polyps (enlarged as indicated by 1.0 mm. scale); *c*, abaxial body scale (enlarged as indicated by 0.2 mm. scale); *d*, opercular scale (at same magnification as *c*.)

KEY 25

KEY TO THE GENERA OF CHRYSOGORGIIDAE

1a. Polyps without an operculum of eight large plates: 2

1b. Polyps with an operculum of eight triangular plates: Genus *Chalcogorgia* Bayer

2a. Colonies unbranched: Genus *Radicipes* Stearns

2b. Colonies branched: 3

3a. Polyps closely crowded, sometimes in two rows: Genus *Trichogorgia* Hickson

3b. Polyps widely scattered, on all sides or uniserial: 4

4a. Branchlets dichotomizing several times: 5

4b. Branchlets simple, unilateral: 6

5a. Colonies sympodial, usually with a zigzag main trunk: Genus *Chrysogorgia* Duchassaing & Michelotti

5b. Colonies monopodial, with a long, straight main trunk: Genus *Metallogorgia* Versluys

6a. Branchlets arising from the outside of a main stem coiled in an upright spiral. Spicules as plates and spindles: Genus *Iridogorgia* Verrill

6b. Branchlets arising from one side of a straight main setm not spirally twisted. Spicules as irrgular bodies: Genus *Pleurogorgia* Versluys

In the West Indies the Family **ISIDIDAE** Lamouroux, 1812, occurs exclusively in deep water, and therefore is not considered here. See DEICHMANN 1936, p. 237.

Order **PENNATULACEA** Verrill, 1865

Diagnosis. Unbranched colonial octocorals consisting of a primary polyp that elongates to produce a barren proximal stalk, which anchors the colony in a soft substrate, and a polypiferous distal rachis from which secondary polyps arise. Gastric cavity of primary polyp divided into two primary and two secondary longitudinal canals by fleshy partitions at the center of which a more or less calcified horny axial rod usually is produced. Secondary polyps dimorphic. Spicules in the form of smooth, cylindrical or three-flanged rods or needles, rarely tuberculated; or small scales or plates.

Remarks. The order Pennatulacea is not conspicuously represented in the shallow waters of the West Indian region, and since its species are adapted for life on sandy or muddy bottoms they are not to be expected in the reef community. In the western Atlantic, two species of *Renilla* are found intertidally, and could occur in sandy areas associated with reefs. One species of *Virgularia* has been trawled at moderate depths in a number of localities along the Gulf and southeast coasts of the United States, and may be expected in favorable localities throughout the Caribbean area.

Since a complete treatment of the western Atlantic pennatulids is found in DEICHMANN's monograph of 1936, only a few species likely to be encountered in shallow water are mentioned here.

Suborder ***SESSILIFLORAE*** Kükenthal, 1915

Family **RENILLIDAE** Gray, 1860

Diagnosis. Pennatulacea with a slender stalk lacking an axial rod, and a broad, flat frond bearing dimorphic polyps on the upper surface only. Spicules in the form of three-flanged rods or needles.

Genus **Renilla** Lamarck, 1816

Renilla LAMARCK 1816, p. 428. (Type species, *Renilla americana* Lamarck = *Renilla reniformis* (Pallas), by monotypy.)
Renilla, DEICHMANN 1936, p. 257.

Diagnosis. As for the family.

Distribution. From Cape Hatteras to the Straits of Magellan, and from California to Chile; endemic amphi-American.

The species of the Atlantic coast of the southeastern United States is *Renilla reniformis* (Pallas), which also extends into the Antilles. *Renilla mülleri* Kölliker occurs along the Gulf and Caribbean coasts of the mainland south to Brazil. As far as I know, *R. reniformis* does not enter the Gulf of Mexico and *R. mülleri* does not occur outside of it to the northward.

95 **Renilla reniformis** (Pallas), 1766

Pennatula reniformis PALLAS 1766, p. 374. (Mare Americanum.)
Renilla reniformis forma *typica* DEICHMANN 1936, p. 259. (North and South Carolina; northern Florida.)

Diagnosis. Frond cordate, not conspicuously wider than long; stalk longer than the radius of the frond, projecting distinctly beyond the notch in which it is inserted. Spicules of stalk shorter than those of the frond. Color rose or pale purple. Some specimens with frond white or yellow and stalk deep purple.

Material. CURAÇAO: Westpunt Baai, in sand near rampart wall, 2.5 m., J. S. Zaneveld, 27.XII.1958, 2 specimens in alcohol (USNM 51276), one with pale violet frond and purple stalk, the other pale yellow with purple stalk; cast ashore, J. S. Zaneveld, 16.IX.1956, 2 spec. in alcohol (USNM 51275), one with pale violet frond and purple stalk, the other with yellow frond and purple stalk. (Both have the frond unusually broad and the stalk unusually short, almost as in *R. mülleri*, but this difference appears to be due in part to the state of contraction; the spicules are quite typical of *reniformis*.) Plaja Djerimi, sandy shore, 11.XII.1948 (USNM 50669). Santa Marta Baai, 7.XII.1958; Vaersen Baai, 25.XI.1958 and 6.I.1959 (USNM 51304); Piscadera Baai, 21.II.1959 (USNM 51303); all collected by J. H. Stock (Amsterdam). Caracas Baai (?), IV.1955, spec. in alc. (USNM 51274). ST. MARTIN: Little Bay, in sand, 1 m., J. H. Stock, 2.II.1959, purple (Amsterdam).

The collections of the U.S. National Museum contain a number of specimens from various localities on the North American coast, including NORTH CAROLINA (43256, 49594), SOUTH CAROLINA (43212, 43251, 50132), and FLORIDA (49723).

Distribution. Southeast coast of the United States from Cape Hatteras to Florida; Antilles; east coast of South America.

Remarks. Specimens from northern localities, especially the eastern coast of the United States, tend to be pale in color, whereas those from the South American coast are usually a much darker purple. The former are referred by DEICHMANN (1936) to forma *typica*, and the latter to forma *americana* Lamarck. These color forms seem to be inconsistent, since specimens from the Antilles may be either uniformly dark purple, or pale (yellowish or purplish white) with a deep purple stalk, and retention of names for them seems to serve no useful purpose.

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96 **Renilla mülleri** Kölliker, 1872

(Fig. 97)

Renilla Mülleri Kölliker 1872, p. 106, pl. 20 figs. 172, 176. (Mazatlan; Desterro, Brazil.)

Renilla mülleri, Deichmann 1936, p. 258. (Gulf of Mexico; Venezuela; Brazil; Chile; west coast of Central America.)

Renilla mülleri, Bayer 1959, p. 31, fig. 14 (Surinam.)

Diagnosis. Frond reniform, broader than long; stalk short, usually less than the radius of the frond, not conspicuously projecting beyond the notch in which it is inserted. Spicules of the stalk about as long as those of the frond. Color white to deep purple.

Material. Several specimens from the Gulf of Mexico, between Apalachee Bay and the coast of Texas (USNM 49575, 49633, 49680, 49681, 49743, 49810). Five lots from Surinam, in 10–28 fathoms (USNM 50826–50830).

Distribution. Continental shore of the Gulf of Mexico and Caribbean south to Brazil; west coast of Central America to Chile.

Family **KOPHOBELEMNIDAE** Gray, 1860

Diagnosis. Bilateral seapens commonly of clavate form with tendency toward radial symmetry. Autozooids in more or less distinct ventral and lateral longitudinal rows, leaving a dorsal streak naked. Siphonozooids distributed between the autozooids everywhere on the rachis except along the dorsal streak. Axial rod well developed.

Remarks. This family comprises two genera, both of which are represented in the western Atlantic. *Kophobelemnon* Asbjörnsen, an inhabitant of cold or deep water from the Grand Banks south to the latitude of Virginia, in 215 to 2369 fathoms (mostly deeper than 500 fathoms), is characterized by three-flanged, twisted rods, often with tubercles and serrated edges; *Sclerobelemnon* Kölliker occurs in warm, shallow water in the Caribbean area where it

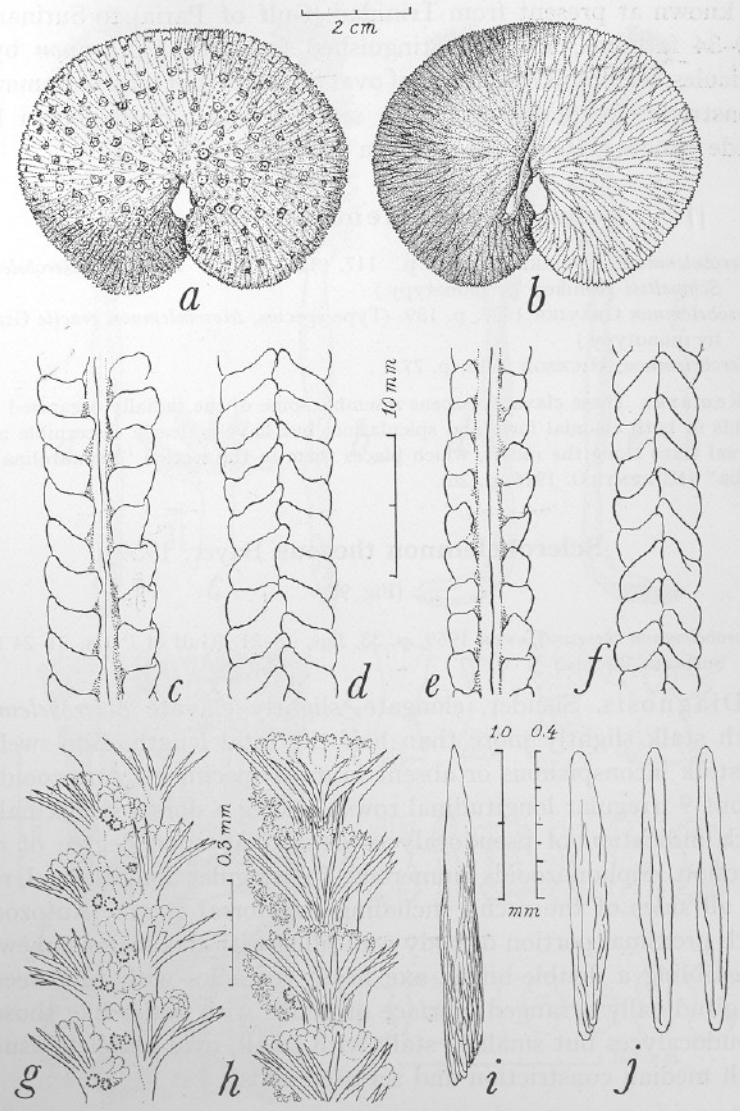

Figure 97. *Renilla mülleri* Kölliker, from Surinam: *a*, dorsal view; *b*, ventral view. *Virgularia presbytes* Bayer, from Surinam: *c* and *e*, dorsal view; *d* and *f*, ventral view. *Stylatula diadema* Bayer, from Surinam: *g*, ventral view, and *h*, lateral view of part of rachis of type; *i*, large needle from the supporting fan; *j*, smaller, 3-flanged rods from supporting fan. (Enlargement as indicated by scales.)

is known at present from Trinidad (Gulf of Paria) to Surinam in 30–34 fathoms, and is distinguished from *Kophobelemnon* by its spicules, which take the form of oval platelets that may be somewhat constricted medially and have serrated ends. Both genera have wide ranges outside the western Atlantic.

Genus **Sclerobelemnon** Kölliker, 1872

Sclerobelemnon Kölliker 1872, p. 117, 131. (Type species, *Sclerobelemnon Schmeltzii* Kölliker, by monotypy.)
Mesobelemnon Gravier 1907, p. 159. (Type species, *Mesobelemnon gracile* Gravier, by monotypy.)
Sclerobelemnon, Hickson 1916, p. 77.

Remarks. These clavate seapens resemble some of the radially organized veretillids in both colonial form and spiculation, but have a clearly discernible naked dorsal tract along the rachis, which places them in the section "Pennatulina biserialia" (Kükenthal 1915, p. 26).

97 **Sclerobelemnon theseus** Bayer, 1959

(Fig. 98)

Sclerobelemnon theseus Bayer 1959, p. 33, figs. 18–21. (Gulf of Paria, 31–24 fms.; Surinam, 30 fms.)

Diagnosis. Slender, elongate, slightly clavate *Sclerobelemnon* with stalk slightly more than half the total length. End-swelling of stalk inconspicuous or absent in most specimens. Autozooids in about 9 irregular longitudinal rows, leaving a dorsal streak naked, with indication of pseudocalyces dependent upon degree of contraction. Siphonozooids numerous, in irregular longitudinal rows on all sides of the rachis including the dorsal streak. Autozooids with proximal portion of body wall filled with flat scales somewhat resembling a double-bitted axe head, tentacles with tiny needles longitudinally arranged; surface of rachis with scales like those of pseudocalyces but smaller; stalk with small, oval platelets usually with median constriction and serrated ends.

Description. See Bayer 1959, p. 33.

Material. The type series. Trinidad, Gulf of Paria, 31–34 fms., *Albatross* sta. 2121–2122, holotype (USNM 50954) and 19 paratypes (7072); Surinam, *Coquette* sta. 226, 30 fms., paratype (50955), and one other specimen trawled off Surinam (50956).

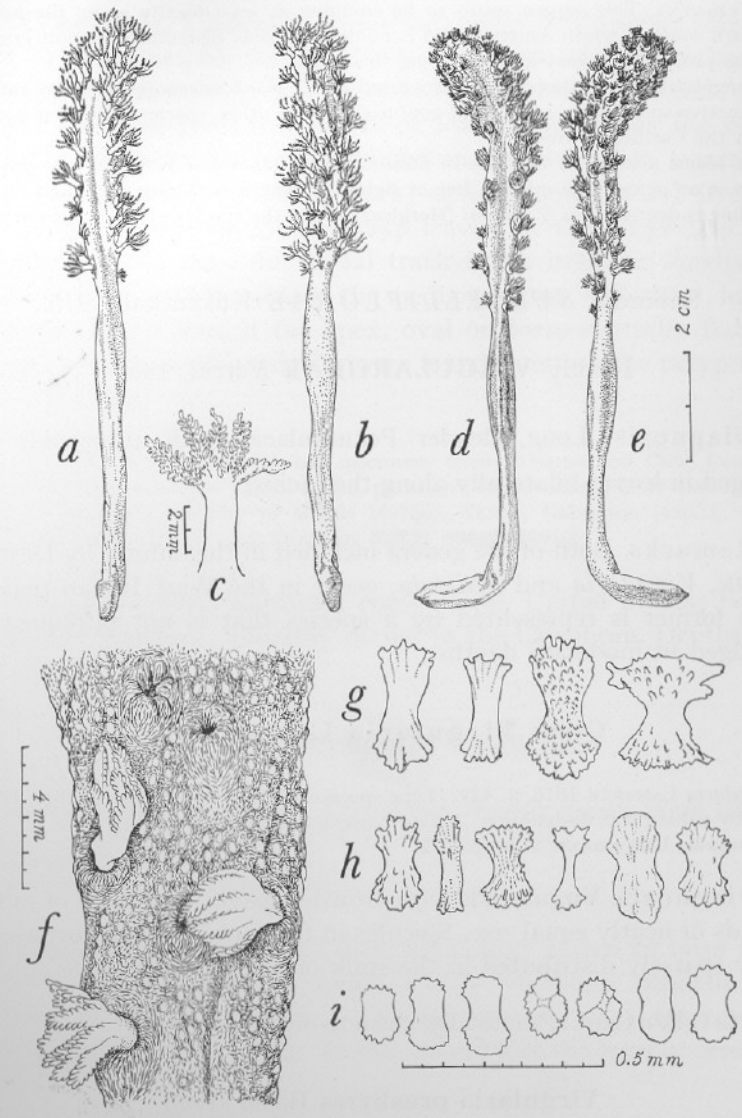

Figure 98. *Sclerobelemnon theseus* Bayer: *a*, dorsal, and *b*, ventral view, and *c*, autozooid of paratype from Surinam; *d*, dorsal, and *e*, ventral view, *f*, part of rachis showing expanded autozooids and pseudocalyces of retracted individuals, *g*, scales from pseudocalyces, *h*, scales from surface of rachis, and *i*, platelets from stalk of holotype from Trinidad. (*a–b* and *d–e* drawn to the same scale, as indicated at *e*; *c* and *f–i* as indicated.)

Remarks. This seapen seems to be common at least locally along the northeastern coast of South America, and is no doubt widely distributed on soft ground in the proper bathymetric range along this coast.

Sclerobelemnon theseus can be recognized by its *Kophobelemnon*-like form and its distinctive spiculation, and can be confused with no other species at present known from the Caribbean area.

As seems also to be the case in *Sclerobelemnon schmeltzii* Kölliker from Japan, there is no perceptible midline free of siphonozooids in *S. theseus*, although such a midline is described in *S. burgeri* (Herklotz) and in the species of *Kophobelemnon*.

Suborder ***SUBSELLIFLORAE*** Kükenthal, 1915

Family **VIRGULARIIDAE** Verrill, 1868

Diagnosis. Long, slender Pennatulacea with autozooids arranged in leaves bilaterally along the rachis.

Remarks. Both of the genera included in this family by Deichmann, *Virgularia* and *Stylatula*, occur in the West Indian region. The former is represented by a species that is not infrequently dredged in moderate depths.

Genus **Virgularia** Lamarck, 1816

Virgularia Lamarck 1816, p. 429. (Type species, *Pennatula mirabilis* Müller 1776, by subsequent designation: Milne Edwards & Haime, 1850.)
Virgularia, Deichmann 1936, p. 272.

Diagnosis. Virgulariids with crowded leaves composed of autozooids of nearly equal size. Spicules in the form of small corpuscles very sparsely distributed in the stalk or absent entirely.

Distribution. Practically cosmopolitan.

98 **Virgularia presbytes** Bayer, 1955

(Fig. 97)

Virgularia spec. Deichmann 1936, p. 274. (Corpus Christi, Texas.)
Virgularia presbytes Bayer 1955, p. 295, figs. 1, 2a–e. (Cape Canaveral, Florida; Mobile, Alabama; Galveston and Corpus Christi, Texas, 9–32 fms.)

Diagnosis. Virgularias with thick, fleshy polyp leaves composed of 13–30 autozooids united by the full length of their anthosteles, showing no distinct projecting calyces and without marginal tubercles; leaves in pairs fused more or less completely on the ventral side of the rachis but well-separated on the dorsal side, leaving free a distinctly grooved dorsal track; siphonozooids in 2–7 irregular, crowded rows between the polyp leaves, in the larger specimens extending out onto the dorsal track in an irregular longitudinal row or field on either side of the median groove. Axis stout, in cross section round toward the apex, oval or dorso-ventrally flattened toward the base. No spicules were found in either the polyp leaves or the rachis.

Material. The original specimens from Florida, off Cape Canaveral, 9 fms. (holotype USNM 50143, paratypes 49755); and USNM material from Alabama, vicinity of Mobile (49758), Texas, Galveston (43023), Corpus Christi (43214), and Surinam (50821–50824, 50910).

Distribution. Southeast coast of the United States; Gulf of Mexico; Surinam; probably occurs in the Caribbean. Depths from 9–32 fathoms.

Genus **Stylatula** Verrill, 1864

Stylatula Verrill 1864b, p. 30. (Type species, *Stylatula elongata* Verrill 1864, non Gabb, by subsequent designation: Kükenthal 1915.)
Stylatula, Kükenthal 1915, p. 67.
Stylatula, Deichmann 1936, p. 269.

Diagnosis. Virgulariids with autozooids united to form ridge-like or distinctly foliate polyp leaves supported beneath by a "fan" or "plate" of stout, radiating spicules that may project beyond the margin of the leaves. Spicules in the form of prismatic needles.

Remarks. There appear to be at least four distinctly different species of *Stylatula* in tropical western Atlantic waters. Since they may be locally common in shallow water throughout the area, the following key, based upon information contained in Kölliker's monograph (1870–72) and upon the examination of a limited amount of material, is offered as a provisional guide for their separation.

KEY 26

PROVISIONAL KEY TO THE WESTERN ATLANTIC SPECIES OF *Stylatula*

1a. Siphonozooids lateral on the rachis in the leaf axils, not on the leaves: 2

1b. Siphonozooids in rosettes on the lower surface of the polyp leaves near their ventral end. Autozooids 25–30, in alternating double rows; bodies of autozooids without spicules. 8–12 pairs of leaves in 2 cm. of rachis. Spicular plate with 8–12 large spines: *Stylatula diadema* Bayer

2a. Autozooids 15 or fewer in each leaf: 3

2b. Autozooids 26 or more in each leaf; 9 pairs of leaves in 2 cm. of rachis. Spicular plate with 7–8, sometimes up to 12, large spines: *Stylatula antillarum* Kölliker

3a. Each leaf with a single row of 3–7 distinctly separated autozooids joined only in their lowest parts; tentacles and body walls of autozooids often with spicules. 3–4 pairs of polyp leaves in 2 cm. of rachis; 10–12 large, spinelike spicules in the supporting plate: *Stylatula elegans* (Danielssen)

3b. Each leaf with a single row of 7–8 (up to 12 according to Kölliker) autozooids fused together except for a short, free, distal calycular part; tentacles and body walls devoid of spicules. 6–8 pairs of polyp leaves in 2 cm. of rachis; 4–5 large, spinelike spicules in the supporting plate (my observation of the types in the British Museum; according to Kölliker, 7–8 spines, based upon the same material): *Stylatula brasiliensis* (Gray)

99 **Stylatula diadema** Bayer, 1959

(Fig. 97)

Stylatula diadema BAYER 1959, p. 38, fig. 17 (Surinam.)

Diagnosis. Slender *Stylatula* with 8–12 pairs of polyp leaves in 2 cm. of rachis. Autozooids 25–30 in each leaf, arranged in alternating double row near middle of leaf, becoming a single zigzag row dorsally and ventrally. Supporting plate with 8–12 large needles 2.2–2.7 mm. long, and numerous smaller needles. No spicules in tentacles and body walls. Spicules in rachis arranged in two narrow lateral bands from which the spicules of the supporting plates extend. Siphonozooids placed on lower surface of polyp leaves, in one or two circles or rosettes near the ventral end of the leaves. Axis stiff, rounded-quadrangular, with a shallow groove along each side.

Description. See BAYER 1959, p. 38.

Material. The USNM type series, from four *Coquette* localities off SURINAM: sta. 2, 15 fms.; sta. 144, 14 fms.; sta. 188, 15 fms.; and sta. 191, 14 fms.; 11.V.–10.VI.1957 (holotype 50834; paratypes 50833, 50835).

Remarks. The peculiar location of the siphonozooids serves to distinguish *Stylatula diadema* from all species of the genus heretofore described.

ECOLOGY

The distribution of alcyonarians in diverse habitats is obviously controlled by the physiological requirements of the organisms themselves, and they will occur wherever the environment satisfies these requirements. Unfortunately, little experimental work has been performed upon alcyonarians, so the bulk of knowledge in this field is assumed from work on other anthozoans or depends upon observations on the distribution of various species under diverse ecological situations. The important limiting factors are temperature, salinity, light, and depth. Concomitant factors are the nature of the substrate and sedimentation.

LIMITING FACTORS

Temperature

The only work done on the temperature relations of alcyonarians is that of CARY (1918) who determined the upper limit of tolerance for twelve species growing on the reefs around the Dry Tortugas. He found that the various species were killed by one hour's exposure to temperatures between 34.5° and 38.2° C. The most resistant of the species studied was *Briareum asbestinum* (Pallas), which died after exposure to 38.2° C., and the least resistant were the plexaurids, all of which succumbed to 34.5°–35.0° C. The gorgoniids were intermediate with death temperatures between 37.0° and 37.5° C. CARY found no constant relationship between respiration rate and resistance to high temperatures. The most heat-resistant species, *Briareum asbestinum*, had the lowest rate of respiration, contrary to the situation found in madrepores by MAYER (VAUGHAN & WELLS 1943, p. 56), but the gorgoniids showed the highest rate of respiration, and resistance to high temperature exceeded only by *Briareum*.

In the peripheral populations of a tropic-derived fauna it is naturally the annual minimum water temperature that controls distribution and not the maximum. It has been pointed out by students of coral reefs that hermatypic corals make vigorous growth only in areas with a minimum water temperature not less than 20°C. (= 69°F.) in the coldest part of the year. Since most of the shallow-water alcyonarians in the West Indian region are members of the reef community, we can safely assume that they will conform to the temperature requirements of coral reefs in general, even though we know almost nothing about the requirements of the alcyonarians themselves. Most species must be able to withstand a few degrees less than the minimum temperature required for reef growth or they could not exist in Bermuda where the minimum surface temperature is 66°F. (= 18.9°C.) (FUGLISTER 1947, p. 23), and even in the vicinity of Miami, Florida, surface temperature may be as low as 19.58°C. =(67.3°F.) in mid-winter (Voss & Voss, 1955, p. 207).

Reasonably healthy reef growth occurs at Bermuda, and the alcyonarian component consists of typical Antillean species. VERRILL (1907) reports seventeen species, which represent less than 25% of the Antillean fauna. On the continental shore, the West Indian gorgonian fauna stops roughly at Jupiter Inlet at the northern border of Palm Beach County, perhaps in part because the necessary solid bottom does not prevail north of that point, but no doubt in part also because the warm waters of the Florida Current swing offshore at about that point on the coast. Because of the resultant drop in temperature, a faunal break occurs on the coast of Florida at about Palm Beach, which is therefore a critical area from a zoogeographic standpoint. It would be most instructive to have detailed collections of gorgonians from a number of localities between Miami and Jupiter Inlet, with observations on water temperatures during the cold months.

On the West coast of Florida, Antillean species extend northward in greatly reduced numbers to Alligator Harbor and vicinity, but along this coast the bottom is generally inhospitable to gorgonians, being sandy, and it is difficult to separate the effects of temperature from those of the poor substrate.

North of Palm Beach to the vicinity of the Virginia Capes and Chesapeake Bay, the shallow water fauna is very distinctive, being virtually limited to three species, *Leptogorgia virgulata*, *L. setacea*, and *Lophogorgia hebes*. In slightly deeper water, *Muricea pendula* and *Telesto fruticulosa* also occur. Of these, the first two, and probably also the third, have a disjunct distribution omitting south Florida and resuming along the Gulf coast to extend southward to the reefs of Brazil. The last two species seem to be restricted to the northern part of this range and are characteristic of the so-called Carolinian fauna that has an isolated arm in the northern Gulf of Mexico. These species, which tolerate both low temperatures (less than 45°F. minimum at the mouth of Chesapeake Bay) and low salinities, are not restricted by the maximum temperatures in the tropical part of their range, but according to present records they do not range out into the Antillean islands and must be excluded from that area by some other factor. Their distribution seems intimately tied to the continental shore. Too little collecting has been done along the coastline between Corpus Christi, Texas, and the reefs of Brazil to provide any clear picture of the distributional behavior of the alcyonarians occurring in that region.

The temperature requirements of species typical of deeper waters certainly differ widely from those of reef-dwelling species, but probably are sufficiently narrow to restrict distribution to a limited bathymetric range.

Salinity

Very few species of alcyonarians can be found in waters subject to fluctuations in salinity. Along the southeastern coast of the United States *Leptogorgia setacea* and *L. virgulata* inhabit inshore waters of salinity less than that of the adjacent sea. In Chesapeake Bay, for instance, *L. setacea* has been found generally over the lower half of the Bay or as far north as the mouth of the Potomac River, where bottom salinity was 17.2‰. *Leptogorgia virgulata* has not been recorded from areas of such low salinity although it, too, occurs within Chesapeake Bay. Both species are known also to inhabit purely marine environments.

In areas where coral reefs are best developed, the surface salinity

averages 36‰, but madrepores normally living under these conditions can endure appreciably higher and lower concentrations for short periods. At the Dry Tortugas, experimental work showed that reef corals could tolerate water reduced to 80% of the normal 36.01‰ concentration for 24 hours without ill effects, and concentrations from 110% to 133% of normal salinity for 12 hours (VAUGHAN & WELLS 1943, p. 58). There is no reason to assume that alcyonarians have the same tolerances as reef corals and it remains for experimental work to determine what their capacity is in this regard.

Illumination

Alcyonarians are affected by light in the same way that reef corals are, and for the same reason. Reef-dwelling species are, without known exception, heavily infested with symbiotic algae, the zooxanthellae, which require light for processes of photosynthesis. In the case of madrepores, experimental work has shown that the algae are not essential to the coral, which can live for some months in complete darkness as long as food is provided (YONGE & NICHOLLS 1931). It is therefore not clear whether the algae are indeed the factor limiting the distribution of reef corals to depths receiving sufficient light for photosynthesis. A more intimate relationship has been demonstrated between certain alcyonarians and their zooxanthellae (GOHAR 1940, 1948). In these cases, the algae are necessary to the nutrition of the alcyonarians, which die if deprived of light even though food is provided, and which thrive in light even though starved. No experimental work has been done on the relationship of zooxanthellae to the reef-dwelling Gorgonacea of the West Indian region.

Depth of water

The bathymetric distribution of alcyonarians seems to follow phylogenetic lines, some families being restricted to moderate depths, others to intermediate ranges, and still others to the deep seas. The reef-dwelling species ordinarily do not quite reach the low tide level, since they cannot tolerate exposure to air for any

appreciable period. Therefore, for any given species, the minimum depth limit at mean low tide is about equal to the average height of the colony; some species adjust their height and growth form to the depth in which they grow, forming broad, bushy colonies in very shallow water, and tall, slender ones in depths allowing maximum growth.

The genera and species of the reef environment usually do not descend very far below it. Their place is taken by other genera and species with greater bathymetric ranges, from 25 or so fathoms down to 300 or 400. At the lower end of this range, the characteristically abyssal groups assume dominance and continue downward to great depths (the deepest record is 6250 meters for a species of *Umbellula* taken by the 'Galathea' Expedition).

The West Indian region is only moderately rich in alcyonarians, with a total of about 196 species [1], of which some 75, or 38% of the total, are inhabitants of the reefs and shallow waters less than 25 fathoms in depth. Most of these species belong to two families, the Plexauridae and the Gorgoniidae, and are large and conspicuous forms, thus assuming a disproportionately prominent place in the reef community. It is impossible to state how this proportion of shallow-water to deep-water species in the West Indies compares with another warm-water fauna, such as that of the East Indies, because no other fauna has been investigated in sufficient detail. The 'Siboga' and the 'Snellius' Expeditions, both of which explored the East Indies, collected primarily by dredging, and although much work was done in depths of less than 50 meters, the dredge is not adaptable to sampling the reef community proper and it must be assumed that this segment of the fauna remains largely uninvestigated.

A valid comparison of the reef-dwelling components of the alcyonarian faunas of the West Indies and the East Indies cannot yet be made because the East Indian shallow-water fauna has not been extensively sampled by hand collecting, whereas a large proportion of the West Indian collections was taken by hand. However,

[1] Compiled from DEICHMANN (1936) for the deep-water groups, and from the present report for the shallow-water families; some additional records from BAYER (1952, 1955, and 1957).

it is instructive to note that of about 445 species (Stolonifera, Telestacea, Alcyonacea and Gorgonacea) collected by the 'Siboga' Expedition, 263 (59%) were taken at depths shallower than 50 meters. Of the 445 species, 235 were Gorgonacea, representing about 56% of the fauna, which is a very low proportion when compared with the West Indies where about 85% of the total fauna of 196 species belong to the Gorgonacea. Since the predominant reef forms in the East Indies are alcyonaceans, which are poorly represented in the Caribbean, a better comparison may be had if we restrict ourselves to the Gorgonacea. Following this procedure, we find that 100 of the 235 species of Gorgonacea were collected in less than 50 meters, or 42% as compared with 41% in the Antilles. In the East Indies a greater proportion of the total alcyonarian fauna inhabits shallow

TABLE 1

COMPARISON OF THE PROPORTION OF SHALLOW-WATER SPECIES IN THE ALCYONARIAN FAUNAS OF THE EAST AND WEST INDIES

	EAST INDIES (Siboga Collection)		WEST INDIES	
	Total Species	Species in Less than 50 meters	Total Species	Species in Less than 50 Meters (or 25 Fathoms
Stolonifera	14	11 (79%),	...	.....
Telestacea	8	5 (63%)	7	4 (57%)
Alcyonacea	188	147 (78%)	9	0 (0)
Gorgonacea	235	100 (42%)	167	68 (41%)
Scleraxonia	39	29 (74%)	9	5 (56%)
Holaxonia	196	71 (36%)	158	63 (40%)
Acanthogordiidae	14	4 (29%)	2	0 (0)
Paramuriceidae	81	40 (49%)	41	0 (0)
Plexauridae	13	10 (76%)	37	31 (84%)
Gorgoniidae	4	2 (50%)	34	31 (91%)
Ellisellidae	21	12 (57%)	11	0 (0)
Chrysogorgiidae	25	0 (0)	11	0 (0)
Primnoidae	25	1 (4%)	14	1 (7%)
Isididae	13	2 (15%)	8	0 (0)
Pennatulacea	...	.....	13	3 (23%)
	445	263 (59%)	196	75 (38%)

water than in the West Indies, but the proportion of shallow-water Gorgonacea is about the same. The apparent dominance of alcyonarians on Atlantic reefs is due to the profusion of a rather small number of conspicuous species, whereas in the East Indies a greater proportion of a richer but less conspicuous fauna inhabits shallow water. (Table 1)

Nature of the Substrate

Work by CARY (1914) indicates that the planulae of gorgonians are similar to those of corals in requiring a rough, solid bottom for attachment. Young colonies were invariably found growing in small depressions in the coral rock. The suitability of the substrate is thus of prime importance to these sessile animals, and is one of the major factors controlling their distribution. This is clearly demonstrated by comparing the southwest coast of Florida with the Florida Keys, the former having a predominantly sandy bottom, the latter with vast tracts of solid reef rock. Dense fields of gorgonians are found covering the rocky bottoms along the Keys, but only scattered outcrops of rock along the sandy west coast can support gorgonians and other sessile reef animals. Although solid support is essential to gorgonians in the turbulent upper layers of water, it is not required by certain species living in deep or quiet waters. One entire order, the Pennatulacea, characteristically inhabits only soft bottoms of sand or mud, into which the fleshy, stalk-like lower end of the colony is inserted. A few gorgonians, notably chrysogorgiids and isidids, are able to form a basal attachment suitable to the substrate, spreading and rootlike if the bottom is soft, a simple calcareous disk if it is rocky. A small number of species belonging to families that usually require solid support have been found growing unattached on the soft sea floor. One of the first records of this kind was *Filigella gracilis* described by GRAY (1868). COWLES (1930, p. 332) mentioned the discovery of gorgonians, which he called *Leptogorgia virgulata*, growing unattached in Chesapeake Bay; STIASNY (1939, p. 301) described a West African genus (*Filigorgia*) with three species showing no evidence of attachment, and recently BAYER (1952, p. 186–188)

reported three new species of *Eugorgia* (now transferred to *Leptogorgia*) that live free on sandy bottom. In some species, colonies have been found with a minute base of attachment fixed to small shells while the majority show evidence of growth at both ends, and in others such as *Leptogorgia setacea*, colonies are as frequently found free as attached. It seems probable that if the settling planula of any of these species attaches to a large enough object it will grow in the usual fixed position, but if no large objects are available and it is obliged to attach to a tiny shell, sand grain, or other minute object, it will eventually topple over and lie prone, then commencing to grow at both ends. Since it has been observed that if normally attached specimens of gorgonians are detached they necrose and soon die from abrasion on the sea floor, it follows that the species growing free on the bottom are either not subjected to fatal abrasion or are resistant to any abrasion that may occur.

Octocorallia as Members of the Reef Community

As has already been pointed out in the remarks on bathymetric distribution, a considerable proportion of the alcyonarian fauna in both Atlantic and Pacific Oceans inhabits reef and shoal-water situations. Although the percentage of species living in less than 50 meters appears to be greater in the East Indian fauna in the West Indian (see Table 1), the families characteristic of this habitat in the West Indies are represented by large, conspicuous, colorful forms that in many places overshadow the madrepores in both size and numbers. The octocorals therefore have greater prominence in the Atlantic reef community than they enjoy in the Indo-Pacific, where this habitat is occupied by families of drab, inconspicuous (but often large) species that closely resemble madrepores in build. In both geographic regions, characteristic micro-communities have developed around the various alcyonarians in the reef assemblage. The intimacy of relationship between the various members of the alcyonarian micro-community and their hosts ranges from the fortuitous, in which a fish may hide among the branches of a gorgonian, to parasitism, in which copepods invade the gastrodermal canals and live there permanently.

Parasites

The best-known parasites of octocorals are the copepods of the family Lamippidae, as described by Zulueta (1908, 1910). Barnacles of the order Ascothoracica are not infrequent parasites of Gorgonacea, especially in deeper waters; the relationship of barnacle to host is unknown in the case of *Balanus galeatus*, which attaches to the axial rod of gorgonians and lives imbedded in the soft tissues. The young of certain pycnogonids enter the polyps of gorgonians and remain encysted there for some time (Stock 1953, p. 307). The large, reef-dwelling Alcyonacea of the western Pacific are often found to have large snails of the genus *Rapa* living imbedded in their tissues, often with no communication to the outside except through the gastric cavities of the alcyonarian polyps, which bring water for respiration; the source of nutrition is unknown.

Symbionts

So far as is known, all reef-dwelling alcyonarians contain unicellular algae, the zooxanthellae, living intracellularly in the entoderm. As Yonge & Nicholls (1931) pointed out, the zooxanthellae of madrepores are not necessary to the life of the coral, but those of at least a few alcyonarians are required in nutrition (Gohar 1940, 1948). There is also some evidence that certain species of Gorgonacea with especially abundant zooxanthellae have lost most, if not all, of their nematocysts, and with them the power to feed. Moreover, with feeding unnecessary, the need for digestive tissues fades and the glandular areas of the septal filaments may be much reduced. Conversely, the species with few zooxanthellae may have especially abundant nematocysts and well-developed digestive structures, indicating dependence on external sources of food (Bayer 1954).

Commensals

The host relationships of a variety of invertebrates associated with octocorals are little known, but since they are obviously

intimate and to a large extent obligatory, the organisms involved may for convenience be classed as commensals.

COELENTERATES. *Hydrichthella epigorgia* Stechow, a hydroid, lives on the Japanese shallow-water plexaurid *Anthoplexaura dimorpha* Kükenthal.

CTENOPHORES. KOMAI (1922) has reported the presence of the sessile ctenophore *Coeloplana* on colonies of *Dendronephthya* in Japan. The present author observed plexaurid gorgonians heavily infested with related ctenophores in the Palau Islands in 1955 and in the Florida Keys in 1960.

POLYCHAETES. Deep-water primnoids commonly are infested with polychaetes, which cause a malformation of the scale-like spicules of the gorgonian host. *Acanthogorgia* and *Corallium* produce coenenchymal flaps, runways or tunnels under stimulation by the polychaetes, but the spicules themselves are not modified. In *Anthogorgia*, the worms inhabit the stem canals, and in *Echinogorgia* they have been found living in deep grooves formed in the thick, fleshy rind.

CRUSTACEANS. Anomuran crustaceans of the families Porcellanidae and Chirostylidae are often found clinging to gorgonian colonies, the former in shallow water, the latter in greater depths. In the western Pacific, a spider crab, *Xenocarcinus depressus* Miers, lives among the branches of the shallow-water gorgonian *Melithaea*, which it mimics precisely in color. In Florida, a shrimp, *Tozeuma carolinensis*, which ordinarily inhabits eelgrasses, has also been found inhabiting colonies of *Pseudopterogorgia*, where it takes on a special color phase (VOSS 1957).

MOLLUSKS. Three species of the gastropod genus *Cyphoma* are conspicuous associates of *Pseudopterogorgia*, *Plexaura*, *Plexaurella*, and related gorgonians in the West Indies. Their spotted mantles, which completely cover the shell, provide effective camouflage in spite of bright coloration. The feeding habits of *Cyphoma* are unknown, so its relationship to the host is not clear. Its eggs are deposited in gelatinous capsules on the surface of the gorgonian branches. A related snail, *Simnia*, lives upon *Leptogorgia* and *Gorgonia* in the Atlantic and upon various genera of Gorgonacea in the Pacific. The large 'egg cowry' of the Pacific lives in association

with the massive alcyonaceans of shallow waters, and several related genera of snails have similar habits.

In cold waters, gorgonians are often infested with primitive, worm-like mollusks of the order Solenogastres. They have been found in abundance on primnoid corals from the Antarctic, and upon *Acanthogorgia* and *Paramuricea* in northern waters.

EPIZOA. A number of invertebrates depend upon gorgonians for support. It is common to find the hydrocoral *Millepora* growing on the exposed axis of various species in the western Atlantic. The millepore apparently never settles on healthy gorgonians, but once it gains a foothold on the accidentally exposed axis it rapidly spreads, killing the gorgonian before it. Several kinds of echinoderms, notably Ophiuroidea and Crinoidea, regularly cling to healthy gorgonians. Of these, the basket star (*Astrophyton muricatum*) is especially conspicuous in the tropical Atlantic, where it lives inextricably entwined among the branches of *Pseudopterogorgia* and other gorgonians of the reef community. Littoral crinoids of the order Comatulida in both Atlantic and Indo-Pacific regions commonly utilize gorgonians for support, but the degree to which they are dependent upon the coral is unknown.

OTHER ASSOCIATIONS. It is well known that certain species of reef-fishes regularly take refuge among the branches of gorgonians, with which they blend perfectly. Notable among these is the trumpet-fish (*Aulostomus*), which lurks among sea-plumes in wait for its prey. In the Pacific, the so-called shrimp-fish (*Centriscus*) may resort to gorgonians for protection when pursued, but they will also hide among the branches of stony corals or the long spines of sea urchins.

OCTOCORALLIA AS REEF-FORMERS

The role of alcyonarians as formers of reef limestone has been investigated by CARY, both in the Dry Tortugas (1918) and Samoa (1931). In the western Atlantic, virtually all reef-dwelling alcyonarians are members of the gorgonacean families Gorgoniidae and Plexauridae, whose calcareous skeleton takes the form of minute mesogloeal spicules. The average spicule content of twelve species was found to be 27.4% of the wet weight of the colonies,

and the average weight of spicules per square yard, based on twenty samples, was 2.1225 pounds. Records for five years showed that one-fifth of the total gorgonian fauna is destroyed annually, releasing one ton of limestone per acre in the form of spicules. Many of these spicules would be swept away by currents or dissolved, but a substantial proportion would still be available for incorporation in the general reef mass.

No Gorgonacea were found on the reefs at Tutuila, Samoa, where four species of Alcyonacea were the dominant alcyonarians. The spicule content of these four species averaged 8.73%, 9.48%, 22.783%, and 35.58% of the wet weight. It is not necessary for these alcyonaceans to die before their spicules become available for incorporation in the reef mass since those in the basal part of the colonies become cemented together to form solid spicule rock, which remains in place. The spicule rock formed by alcyonarians was found to be harder and more durable than the skeletons of most madrepores, which it often covered and protected from the disintegrative forces operative on the reef.

The contribution made to the reef mass by alcyonarians on both Atlantic and Pacific reefs is therefore found to be considerable, and imparts to them an importance in reef formation that is generally unappreciated.

ZOOGEOGRAPHY

The West Indian Region

As defined by Hummelinck (1940, p. 24; 1953, p. 2), the *West Indies proper* include all of the Antilles, the Bahamas, the Florida Keys, the Islands of the Caribbean, and the Bermudas. The great insular arc of the Antilles is subdivided into the Greater Antilles, extending from Cuba to Puerto Rico inclusively, and the Lesser Antilles, extending from the Virgin Islands to Trinidad and Aruba. The Lesser Antilles are further divided into a Windward Group (Bovenwindse Eilanden, Islas de Barlovento, Isles sur le Vent) consisting of the islands from the Virgins to Grenada, and a Leeward Group (Benedenwindse Eilanden, Islas de Sotavento, Isles sous le Vent) including those from Los Testigos to Aruba and Los Monges, at the mouth of the Gulf of Maracaibo.

Faunistically, extensions of the *West Indian region* reach into the Gulf of Mexico and up the east coast of Florida, and south along the northeast coast of South America to the reefs of Brazil. Since it is quite impossible to draw any hard and fast boundary between the fauna of the Gulf of Mexico and the southeastern coast of the United States and that of the West Indies proper, those areas are included in the present treatment. Moreover, the available information on the alcyonarian fauna of Brazil is also included, since so little is known of that interesting region.

The accompanying map (Fig. 99) shows the general location of localities from which the material used in this study was collected. From this it will be seen that numerous samplings have been made along the southeastern coast of the United States, especially around the peninsula of Florida. The shores of the Gulf of Mexico, with the exception of western and northwestern Florida and the coast of

Texas, have been rather poorly investigated and are far from well known even in those regions most thoroughly collected.

Among the islands of the West Indies, the Lesser Antilles (the Windward Group in the sense of HUMMELINCK) are the most thoroughly known and provide the greatest number of collecting localities in the present study.

Extensive collections have been made in the Bahamas, especially in the vicinity of New Providence, Bimini, and Andros, but even these are incomplete, owing to the fact that most of them result

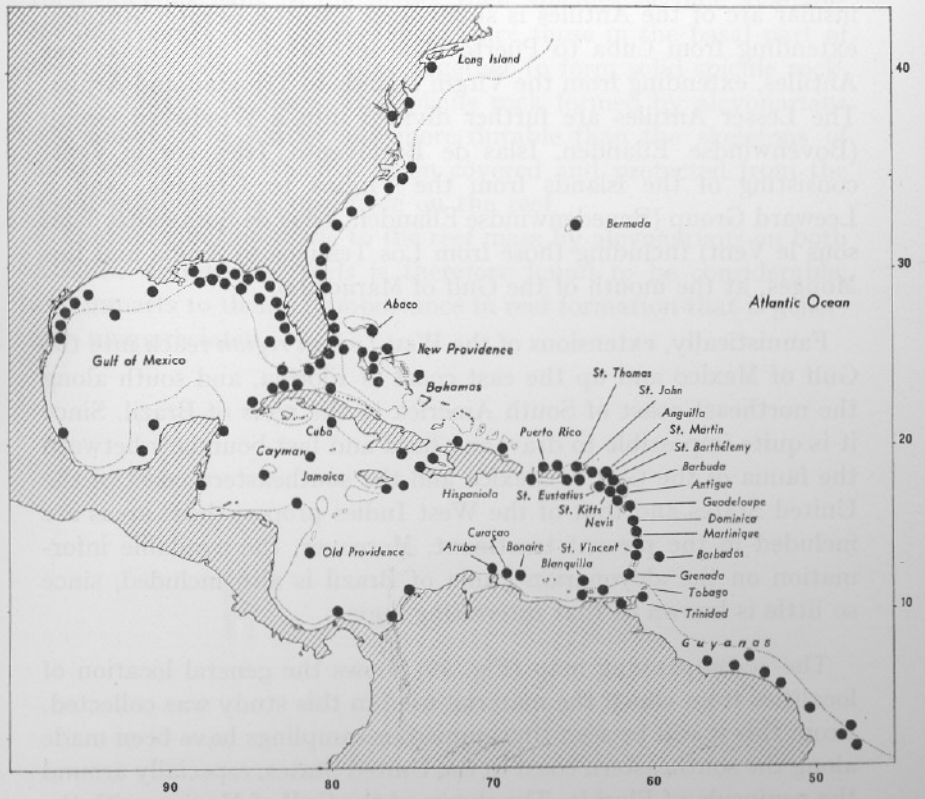

FIGURE 99. Approximate positions of western Atlantic localities represented in the material used for the present study.

from short stays in well known places rather than from intensive collecting around many of the islands.

Almost nothing is known of the shore fauna of the Greater Antillean islands, although several exploratory vessels have worked the deeper waters around them. The reefs along the coast of Yucatan, Honduras and Panama are a conspicuous and vexing zoogeographic gap, as are the banks and small islands of the western Caribbean.

The Caribbean coast of South America has been little explored and the number of shallow-water octocorals reported is pitifully small. The Netherlands islands off the Venezuelan coast have been collected rather well, but the adjacent mainland, which probably supports a somewhat different gorgonian fauna, has not.

Except for records provided by some recent fisheries investigations by the exploratory vessels 'Coquette' and 'Oregon', the coast of South America south and east of Trinidad forms another troublesome gap in our faunal knowledge. A few older collections from this area have been reported, rather inadequately, by STIASNY (1951). The gorgonian fauna of the Brazilian coast has been studied by VERRILL (1912), but thorough collecting is still needed even in this region.

THE OCTOCORAL FAUNA OF THE WARM WESTERN ATLANTIC

The octocoral fauna of the tropical and subtropical parts of the western Atlantic amounts to about 195 species, not a rich fauna when compared with that of the Indo-Malayan region, where the number of alcyonaceans alone may exceed this number, but it is without doubt the most spectacular one to be found anywhere in the world. This results from the preponderance of large, colorful gorgonians in the reef fauna, which produce the fantastic 'Sea Gardens' of the Bahamas, the Florida Keys, and the upper part of the Antillean chain. This fauna is made up mostly of species belonging to two families, the Gorgoniidae and the Plexauridae, which account for 51 of the 54 species reported from reef habitats, and 62 of the 75 species living in depths of 24 fathoms or less. The species that this study has found to be valid are listed in Table 2, which indicates their general occurrence throughout the geographic region under consideration.

TABLE 2

GEOGRAPHICAL DISTRIBUTION OF SHALLOW-WATER OCTOCORALLIA IN THE WARM WESTERN ATLANTIC

Systematic List

* species occurring in less than 25 fathoms but not in reef habitat

† species occurring in more than 25 fathoms

× specimens studied in present paper

\+ record from literature

		Geographical regions																								
		Atl. coast to E. Florida	E. Florida to Dry Tortugas	West coast of Florida	Northern Gulf of Mexico	E. coast of Mex. & C. Amer.	Bermuda Islands	Bahama Islands	Greater Antilles: Cuba	Greater Antilles: Hispaniola	Greater Antilles: Puerto Rico	Greater Antilles: Jamaica	Cayman Islands	Lesser Antilles: Windward Group	Lesser Antilles: Leeward Group	Old Providence	North coast of S. America	Guyana	Brazil
	TELESTACEA																		
	Telestidae																		
†1	*Telesto corallina*	–	–	–	–	–	–	–	×	–	–	–	–	–	–	–	–	–	–
†2	*Telesto operculata*	–	–	–	–	–	–	–	×	–	–	–	–	×	×	–	–	–	–
*3	*Telesto riisei*	–	×	–	–	–	–	–	–	×	–	×	–	×	–	–	–	×	×
*4	*Telesto flavula*	–	+	–	×	–	–	–	–	–	–	–	–	–	–	–	–	–	–
*5	*Telesto sanguinea*	×	×	–	×	–	–	–	–	–	–	–	–	–	–	–	–	–	–
*6	*Telesto fruticulosa*	×	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
†7	*Telesto nelleae*	×	–	–	–	–	–	–	×	–	–	–	–	–	–	–	–	–	–
	ALCYONACEA																		
	Alcyoniidae																		
*8	*Nidalia occidentalis*	×	×	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–
	Nephtheidae																		
†9	*Eunephthya nigra*	×	×	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
†10	*Neospongodes portoricensis*	–	–	–	–	–	–	–	×	–	–	×	–	–	+	–	–	–	–
	GORGONACEA (Scleraxonia)																		
	Briareidae																		
11	*Briareum asbestinum*	–	×	–	–	×	–	×	×	+	–	–	–	×	–	×	–	–	–
	Anthothelidae																		
12	*Iciligorgia schrammi*	–	×	–	–	–	–	×	×	–	×	–	–	–	–	–	–	–	×
†13	*Anthothela tropicalis*	–	–	–	–	×	–	–	–	–	–	–	–	–	–	–	–	–	+
†14	*Tripalea clavaria*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
*15	*Diodogorgia nodulifera*	–	×	–	–	×	–	+	+	–	×	–	–	×	–	–	+	–	–
16	*Erythropodium caribaeorum*	–	×	–	–	–	–	×	–	–	–	–	+	×	–	–	–	–	–
†17	*Titanideum frauenfeldii*	×	–	–	–	–	–	–	×	–	–	–	–	–	–	–	–	–	–
*18	*Anthopodium rubens*	+	–	–	×	–	–	–	–	–	–	–	–	–	–	×	–	–	–
	GORGONACEA (Holaxonia)																		
	Keroeididae																		
†19	*Lignella richardii*	–	–	–	–	–	–	–	–	–	–	–	–	×	–	–	–	–	–
	Acanthogorgiidae																		
†20	*Acanthogorgia aspera*	–	–	–	–	–	–	+	–	–	+	–	–	+	–	–	–	–	–
	Plexauridae																		
21	*Plexaura homomalla*, typical form	–	×	–	–	×	×	×	–	–	–	×	×	×	–	–	–	–	–
21a	*Plexaura homomalla*, forma *kükenthali*	–	×	–	–	–	–	×	–	–	–	×	–	–	–	×	–	–	–
†22	*Plexaura nina*	–	–	–	–	–	–	×	–	–	–	–	–	–	–	–	–	–	–
23	*Plexaura flexuosa*	–	×	–	–	×	+	×	–	–	–	×	×	×	×	–	–	–	–
24	*Pseudoplexaura porosa*	–	×	–	–	×	×	×	–	–	–	×	×	+	×	–	–	–	–
25	*Pseudoplexaura flagellosa*	–	×	–	–	–	×	–	–	–	–	×	×	×	×	–	–	–	–
26	*Pseudoplexaura wagenaari*	–	×	×	–	–	×	–	–	–	–	×	×	×	×	–	–	–	–
27	*Pseudoplexaura crucis*	–	–	–	–	–	–	–	–	–	–	–	×	–	–	–	–	–	–
28	*Eunicea laxispica*	–	–	–	–	–	–	×	–	–	×	–	–	×	–	–	–	–	–
†29	*Eunicea pinta*	–	–	–	–	–	–	×	–	–	–	–	–	–	–	–	–	–	–
30	*Eunicea palmeri*	–	×	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
31	*Eunicea mammosa*	–	×	–	–	×	×	×	×	–	–	–	×	×	×	×	–	–	–
32	*Eunicea succinea*, typical form	–	–	–	–	+	–	–	–	–	–	–	–	×	×	×	–	–	–
32a	*Eunicea succinea*, forma *plantaginea*	–	×	–	–	–	–	–	–	–	–	–	–	×	×	–	–	–	–

TABLE 2 (*Continued*)

Systematic List

* species occurring in less than 25 fathoms but not in reef habitat

† species occurring in more than 25 fathoms

× specimens studied in present paper

\+ record from literature

		Geographical regions																	
		Atl. coast to E. Florida	E. Florida to Dry Tortugas	West coast of Florida	Northern Gulf of Mexico	E. coast of Mex. & C. Amer.	Bermuda Islands	Bahama Islands	Greater Antilles: Cuba	Greater Antilles: Hispaniola	Greater Antilles: Puerto Rico	Greater Antilles: Jamaica	Cayman Islands	Lesser Antilles: Windward Group	Lesser Antilles: Leeward Group	Old Providence	North coast of S. America	Guyana	Brazil
33	*Eunicea fusca*	–	–	–	–	×	×	+	–	–	–	×	–	–	–	–	–	–	–
34	*Eunicea laciniata*	–	–	–	–	×	×	×	–	–	–	×	–	–	–	–	–	–	–
35	*Eunicea tourneforti*, typical form	–	–	–	–	×	×	×	–	–	–	×	–	–	–	–	–	–	–
35a	*Eunicea tourneforti*, forma *atra*	–	–	–	–	×	×	×	–	–	–	×	–	–	–	–	–	–	–
36	*Eunicea asperula*	–	–	–	×	–	–	–	–	–	–	–	–	–	–	–	–	–	–
37	*Eunicea clavigera*	–	–	–	–	×	×	×	–	–	–	×	–	–	–	–	–	–	–
38	*Eunicea knighti*	–	–	–	×	–	–	–	×	–	–	–	–	–	–	–	–	–	–
39	*Eunicea calyculata*, typical form	–	–	–	–	×	×	×	–	–	–	×	–	–	–	–	–	–	–
39a	*Eunicea calyculata*, forma *coronata*	–	–	–	–	×	×	×	–	–	–	×	–	–	–	–	–	–	–
40	*Eunicea* sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
41	*Muriceopsis sulphurea*	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	×
42	*Muriceopsis flavida*	–	–	–	–	–	–	×	×	+	–	×	–	×	×	×	–	–	–
†43	*Muriceopsis petila*	–	–	–	–	–	–	×	×	–	–	–	–	×	×	×	–	–	–
44	*Plexaurella dichotoma*	–	–	–	–	×	+	×	×	–	–	+	×	×	×	×	–	–	×
45	*Plexaurella nutans*	–	–	–	–	–	–	×	–	–	–	–	×	×	+	×	–	–	–
46	*Plexaurella grandiflora*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	×
47	*Plexaurella grisea*	–	–	–	–	×	–	×	–	–	–	–	–	×	+	×	–	–	–
48	*Plexaurella pumila*	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	×
49	*Plexaurella fusifera*	–	–	–	–	–	–	–	×	–	–	–	–	×	+	×	–	–	–
50	*Muricea muricata*	–	–	–	–	–	–	–	×	+	–	–	–	×	×	×	–	–	–
51	*Muricea atlantica*	–	–	–	–	–	–	×	×	–	–	–	–	×	+	×	–	–	–
†52	*Muricea pinnata*	–	–	–	–	–	–	–	×	–	–	–	–	×	+	×	–	–	–
*53	*Muricea laxa*	–	–	–	–	–	+	–	×	×	–	–	–	×	+	×	–	–	–
54	*Muricea elongata*	–	–	–	–	–	–	–	×	+	–	–	–	×	+	×	–	–	–
*55	*Muricea pendula*	×	–	–	×	–	–	–	–	×	–	–	–	×	+	×	–	–	–
	Gorgoniidae																		
56	*Lophogorgia sanguinolenta*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
57	*Lophogorgia violacea*	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–
†58	*Lophogorgia barbadensis*	–	–	–	–	–	–	–	–	–	–	–	–	×	+	–	–	–	×
*59	*Lophogorgia cardinalis*	–	–	–	–	–	–	–	×	–	–	–	–	–	–	–	–	–	–
60	*Lophogorgia punicea*	–	×	×	–	–	–	–	–	–	–	–	–	–	–	–	–	+	×
61	*Lophogorgia hebes*	×	+	×	–	–	–	–	–	–	–	–	–	–	–	–	–	–	×
62	*Lophogorgia miniata*	–	–	–	–	–	–	–	–	–	–	–	–	×	+	–	–	–	–
63	*Lophogorgia* sp.	–	–	×	–	–	–	–	–	–	–	–	–	–	–	×	–	–	–
64	*Lophogorgia* sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	×
65	*Pacifigorgia elegans*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	×
*66	*Leptogorgia virgulata*	×	–	–	×	×	–	–	–	–	–	–	+	–	–	–	–	–	×
*67	*Leptogorgia setacea*	×	–	–	×	×	–	–	–	–	–	–	–	–	–	–	–	–	–
*68	*Leptogorgia medusa*	–	–	–	×	×	–	–	–	–	–	–	–	–	–	–	–	–	–
†69	*Leptogorgia stheno*	–	–	–	×	×	–	–	–	–	–	–	–	–	–	–	–	–	–
*70	*Leptogorgia euryale*	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–
71	*Pseudopterogorgia bipinnata*	–	–	–	–	–	–	×	×	–	–	–	–	×	–	–	–	–	–
72	*Pseudopterogorgia kallos*	–	×	–	–	–	–	–	×	–	–	–	–	–	–	–	–	–	–
73	*Pseudopterogorgia rigida*	–	×	×	–	–	–	–	×	–	–	–	+	+	+	–	–	–	–
74	*Pseudopterogorgia blanquillensis*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
75	*Pseudopterogorgia acerosa*	–	×	×	–	–	×	+	×	+	×	–	×	–	–	–	–	–	–
76	*Pseudopterogorgia americana*	–	×	×	–	–	×	×	×	–	–	–	×	–	–	–	–	–	–
77	*Pseudopterogorgia hummelincki*	–	–	–	–	–	–	–	–	+	×	–	–	–	–	–	–	–	–
*78	*Pseudopterogorgia elisabethae*	–	–	–	–	–	–	–	×	–	–	–	–	–	–	–	–	–	–
*79	*Pseudopterogorgia albatrossae*	–	–	–	–	–	–	–	–	–	–	–	×	–	–	–	–	–	–
*80	*Pseudopterogorgia navia*	–	–	–	–	–	–	–	×	–	×	–	–	–	–	–	–	–	–
†81	*Pseudopterogorgia hystrix*	–	–	–	–	–	–	–	×	–	–	–	–	–	–	–	–	–	–
*82	*Pseudopterogorgia marcgravii*	–	–	–	–	–	–	–	×	–	–	–	–	–	–	–	–	–	×

TABLE 2 (*Continued*)

Systematic List	Atl. coast to E. Florida	E. Florida to Dry Tortugas	West coast of Florida	Northern Gulf of Mexico	E. coast of Mex. & C. Amer.	Bermuda Islands	Bahama Islands	Cuba	Hispaniola	Puerto Rico	Jamaica	Cayman Islands	Windward Group	Leeward Group	Old Providence	North coast of S. America	Guyana	Brazil
	Geographical regions: Greater Antilles; Lesser Antilles																	
83 *Gorgonia flabellum*, typical form	–	+	–	–	×	–	×	–	×	–	–	–	×	–	–	–	–	–
83a *Gorgonia flabellum*, forma *occatoria*	–	–	–	–	–	–	×	–	×	–	–	–	×	–	–	–	–	–
84 *Gorgonia ventalina*	–	×	–	–	–	×	×	×	×	×	×	–	×	×	×	–	–	–
85 *Gorgonia mariae*, typical form	–	–	–	–	–	–	×	×	×	×	×	–	×	×	×	–	–	–
85a *Gorgonia mariae*, forma *cymosa*	–	–	–	–	–	–	–	–	×	×	–	–	×	–	–	–	–	–
85b *Gorgonia mariae*, forma *plumosa*	–	–	–	–	–	–	–	–	–	×	–	–	×	–	–	–	–	–
86 *Phyllogorgia dilatata*	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	×
87 *Pterogorgia citrina*	–	×	–	–	×	+	×	–	–	–	×	–	×	×	–	–	–	–
88 *Pterogorgia anceps*	–	×	×	–	×	–	×	–	–	–	×	–	–	+	–	–	–	–
89 *Pterogorgia guadalupensis*	–	×	–	–	–	–	–	–	–	–	–	–	×	×	–	–	–	–
Ellisellidae																		
*90 *Ellisella barbadensis*	–	×	–	×	+	–	–	×	–	–	–	–	+	–	–	–	×	×
*91 *Ellisella elongata*	–	–	–	×	+	–	–	–	–	–	–	–	+	–	–	–	×	×
†92 *Nicella schmitti*	–	–	–	–	×	–	–	–	–	–	–	–	–	–	–	–	–	–
†93 *Nicella guadelupensis*	–	+	–	–	×	–	–	×	–	×	–	–	×	–	–	–	–	–
Primnoidae																		
*94 *Callogorgia verticillata*	–	×	–	–	×	–	–	×	–	–	+	–	+	–	–	–	×	–
PENNATULACEA																		
Renillidae																		
*95 *Renilla reniformis*	×	×	–	–	–	–	–	–	–	–	–	–	×	×	–	–	–	–
*96 *Renilla mülleri*	–	–	–	×	–	–	–	–	–	–	–	–	–	–	–	+	×	+
Kophobelemnidae																		
*97 *Sclerobelemnon theseus*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	×	×	–
Virgulariidae	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
*98 *Virgularia presbytes*	–	×	–	×	–	–	–	–	–	–	–	–	–	–	–	–	×	–
*99 *Stylatula diadema*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	×	–
Total number of species and forms reported	12	54	17	16	24	18	32	29	8	19	23	10	59	26	9	8	12	19

* species occurring in less than 25 fathoms but not in reef habitat

† species occurring in more than 25 fathoms

× specimens studied in present paper

\+ record from literature

DISTRIBUTION BY REGION

The Atlantic seaboard

The coast of New Jersey, Delaware, Maryland and Virginia, including Delaware and Chesapeake Bays, has been investigated with some degree of intensity, at least locally, and the shallow-water octocorallian fauna proves to be very limited. Only *Leptogorgia setacea* and *L. virgulata* are reported from localities in Chesapeake and Delaware Bays; the latter species was reported

years ago (as *L. tenuis*) from the 'Bay of New York' but I have seen no specimens from so far north collected in recent times.

The waters off the Carolinas have been sampled rather thoroughly, chiefly at moderate depths, by the 'Albatross' and the 'Fish Hawk', and more recently by the 'Silver Bay' and the 'Bowers'. Localities in North Carolina are located mainly in the vicinity of Cape Hatteras, Cape Lookout (including Beaufort and Morehead City), New River, and Cape Fear (near the city of Wilmington). From this region come *Telesto fruticulosa, T. nelleae, Titanideum frauenfeldii, Muricea pendula, Leptogorgia virgulata, Lophogorgia hebes,* and *Renilla reniformis*. *Leptogorgia setacea* undoubtedly occurs, but is not present in the collections before me. *Anthopodium rubens,* which was originally reported from Ft. Macon, North Carolina, has not subsequently been found in this region, probably being overlooked due to its modest and inconspicuous little colonies.

In South Carolina, localities are in the vicinity of Myrtle Beach, Winyah Bay, Charleston, and Port Royal. Collections from this area include *Telesto sanguinea, Nidalia occidentalis, Titanideum frauenfeldii, Leptogorgia virgulata,* and *Renilla reniformis*. The absence of *Leptogorgia setacea, Lophogorgia hebes,* and *Muricea pendula* is no doubt due to inadequate collecting.

The available collections contain few specimens from localities along the coast of Georgia. Those present come mostly from the vicinity of Savannah and Brunswick. From shallow warer come *Leptogorgia virgulata* and *Renilla reniformis*; further collecting can be expected to yield several additional species. Offshore dredgings in deep water have brought up *Eunephthya nigra* and *Eunicella modesta,* which are briefly treated in this paper as representatives of their respective genera.

From a faunal standpoint, the east coast of Florida, or at least that part of it from Fernandina south to Cape Canaveral, cannot be separated from Georgia and the Carolinas. In shallow and moderate depths, *Telesto sanguinea, Nidalia occidentalis, Titanideum frauenfeldii, Muricea pendula, Leptogorgia setacea* and *Renilla reniformis* occur, while in deep water *Eunephthya nigra* and *Eunicella modesta*

are extremely abundant. A deep-littoral representative of a characteristic tropical reef-dwelling genus, *Muriceopsis*, appears as a transitional element; this is a new species, *M. petila*, whose distribution is as yet imperfectly known. *Ellisella barbadensis*, also a West Indian species, has been dredged off St. Augustine.

The coast of Florida between Cape Canaveral and Palm Beach has been poorly explored for octocorals but presumably conforms more or less closely with the region to the north.

Just north of Palm Beach, the Florida current (Gulf Stream) swings offshore, causing a rather distinct faunal break. South of this boundary, shallow-water West Indian species appear on the rocky outcrops near shore and down to depths of 25 or 30 fathoms. *Telesto riisei, Nidalia occidentalis, Titanideum frauenfeldii, Iciligorgia schrammi, Diodogorgia nodulifera, Eunicea calyculata, Muricea elongata, Lophogorgia cardinalis, L. punicea, Leptogorgia stheno, Pterogorgia anceps, P. citrina,* and *Renilla reniformis* have all been reported. *Pseudopterogorgia* and some plexaurids occur abundantly on the rocky ledges at Palm Beach, Lake Worth and Boynton, but unfortunately are not represented in the collections available for study at this time.

In the vicinity of Miami, the shallow-water octocoral fauna is purely West Indian. Collections from shallow dredging and shore-collecting off Miami, Biscayne Key, and Cape Florida include *Telesto riisei, T. sanguinea, Nidalia occidentalis, Briareum asbestinum, Erythropodium caribaeorum, Plexaura flexuosa, P. homomalla* forma *kükenthali, Pseudoplexaura porosa, Eunicea tourneforti, Muriceopsis flavida, Muricea laxa, Plexaurella dichotoma, Leptogorgia stheno, Pseudopterogorgia acerosa, P. bipinnata, P. kallos, P. rigida, P. elisabethae,* and *Pterogorgia anceps*. Many more species certainly are present.

The Florida Keys, beginning with Soldier Key at the entrance of Biscayne Bay and extending south and west to the Dry Tortugas, some 70 miles west of Key West, is a chain of islands exceptionally rich in gorgonian corals. The northern islands in this chain, Soldier Key, Ragged Keys, and Elliott Key together with the intervening passes such as Caesar's Creek, and the adjacent reefs, notably

Triumph Reef and Bache Shoal, have been very diligently collected by marine biologists from the University of Miami Marine Laboratory. The several larger and many smaller islands to south and west also have been rather thoroughly collected over a long period of time but probably not so intensively as have the upper Keys. The following list, incomplete though it certainly is, gives the commonest species and some of the localities at which they have been collected (indicated by abbreviations, arranged approximately in geographical sequence from northeast to southwest).

List of Octocorallia from Localities in the Florida Keys

Abbrevations of localities:

BP = Big Pine Key
C = Caesar's Creek
E = Elliott Key (with Bache Shoal and Triumph Reef)
KL = Key Largo
KV = Key Vaca
KW = Key West
LV = Lignum Vitae Lake
M = Mangrove Key, NE of Key West
Rag = Ragged Keys
Rod = Rodriguez Key
SP = Salt Pond Key, NE of Key West
Sol = Soldier Key
SL = Sombrero Light
T = Dry Tortugas and nearby banks

(Species indicated with an asterisk come from shallow-water dredging.)

*Telesto sanguinea** (KL)
*Nidalia occidentalis** (SL)
Briareum asbestinum (Sol, Rod, LV)
*Iciligorgia schrammi** (E, T)
*Diodogorgia nodulifera** (E)
*Titanideum frauenfeldii** (T)
Plexaura flexuosa (Sol, Rag, Rod, T)
Plexaura homomalla, typical (Rod, E)
Plexaura homomalla f. *kükenthali* (C)
Pseudoplexaura flagellosa (M, KW)
Pseudoplexaura porosa (E, Rod, KW,T)
Pseudoplexaura wagenaari (Rag, C, E, KW)
Eunicea asperula (C, KW)
Eunicea calyculata (Sol)
Eunicea knighti (Sol)
Eunicea laciniata (E)
Eunicea mammosa (C, Rod, KW, T)
Eunicea palmeri (Sol, C, KW)
Eunicea tourneforti (Sol)
Muriceopsis flavida (E)
Plexaurella dichotoma (S, KL, T)
Plexaurella fusifera (KV, T)
Plexaurella nutans (Sol, T)
Muricea atlantica (Sol, E, KL, T)
Muricea elongata (Rag, E, C, T)
*Muricea laxa** (T)
*Lophogorgia cardinalis** (T)
Lophogorgia punicea (T)
Pseudopterogorgia acerosa (Sol, C, KW, T)
Pseudopterogorgia americana (Sol, KW, T)
Pseudopterogorgia bipinnata (Rod, T)
Pseudopterogorgia rigida (T)
Gorgonia ventalina (KL, T)
Pterogorgia anceps (Sol, C, BP, KW)
Pterogorgia citrina (Sol)
Pterogorgia guadalupensis (KW)

The Gulf of Mexico

The distribution of octocorals in the Gulf of Mexico has been discussed briefly elsewhere (BAYER 1954, 1958). The abyssal species show a characteristically wide distribution. The deep littoral fauna is mainly West Indian, and most if not all of its elements may be expected to turn up in the Gulf as dredging operations bring in more and more new records. However, the shallow-water fauna has two distinct elements, the West Indian, which invades from the south, and the Carolinian, which forms a disjunct pocket along the northern Gulf coast from northwest Florida to Texas. The Carolinian species present in the northern Gulf are *Anthopodium rubens*, *Muricea pendula*, *Lophogorgia hebes*, *Leptogorgia virgulata*, and *L. setacea*. *Muricea pendula* has been collected off Laguna Beach, Florida, off Louisiana, and off Padre Island, Texas, but not off the coast of peninsular Florida. *Lophogorgia hebes* occurs along most if not all of the Gulf coast of Florida and west to Texas; its distribution in the western Gulf and Caribbean is not known, but it occurs in Brazil (as *Leptogorgia rubropurpurea* Verrill). *Leptogorgia virgulata* and *L. setacea* have a similar distribution but apparently do not extend very far south of Fort Myers on the Florida coast; both are known from Brazil. They seem to be the only shallow-water gorgonians along much of the northern Gulf coast.

The West Indian representatives are *Pseudoplexaura wagenaari*, *Eunicea asperula*, *E. calyculata*, *E. knighti*, *Plexaurella grisea*, *P. fusifera*, *P. nutans*, *Muricea elongata*, *M. laxa*, *Pseudopterogorgia acerosa*, *Pterogorgia anceps*, and *Ellisella elongata*. Although several of these species reach as far north as Tampa, Florida, only *Eunicea knighti*, *Muricea elongata* and *Ellisella elongata* are known to occur in the region of Apalachee Bay. The two species of *Telesto* common along west Florida, *T. sanguinea* and *T. flavula*, seem to be restricted to continental shores for they have not been recovered from West Indian localities.

The mainland coast of Central America

The least known part of the area covered in this paper is the mainland coast of the Caribbean. Except for a few dredgings off the Canal Zone and in the Gulf of Darien, which yielded *Diodogorgia nodulifera* and *Nicella schmitti*, and the records of *Eunicea tourneforti* from Belize (British Honduras), *Lophorgorgia miniata* from Puerto Colombia, *Telestio riisei* from Guanta (Venezuela), and *Pseudopterogorgia bipinnata* from Cumaná, nothing is known of the composition of the alcyonarian fauna. The few indications just noted suggest that it is typically West Indian at both shallow and moderate depths, but any faunal peculiarities remain to be demonstrated.

West Indian localities

The octocorals of Bermuda, the northernmost frontier of the West Indian fauna, have been studied in some detail by VERRILL (1907) and DEICHMANN (in Ms). The collections in the U.S. National Museum contain the following Bermudian species: *Plexaura homomalla*, *P. flexuosa*, *Pseudoplexaura porosa*, *P. flagellosa*, *P. wagenaari*, *Eunicea calyculata*, *E. clavigera*, *E. fusca*, *E. tourneforti* f. *atra*, *Muricea atlantica*, *Pseudopterogorgia acerosa*, *P. americana*, *Gorgonia ventalina*, *Pterogorgia citrina*.

Large numbers of the more conspicuous gorgonians have been collected at several localities in the Bahamas. The largest number of species on the following list comes from New Providence and the adjacent small cays, Long Island and Hog Island. Smaller collections are present from Abaco, Andros, Bimini, Cat Cay, Eleuthera, Orange Key, Rum Cay, the lower end of the Tongue of the Ocean, and Watling's Island. Thorough collecting at these localities presumably would yield the same species recorded from New Providence.

LIST OF OCTOCORALLIA FROM LOCALITIES IN THE BAHAMAS

Abbreviations of localities:

Ab = Abaco	N = New Providence, Long and Hog Is.
An = Andros	O = Orange Key
B = Bimini	R = Rum Cay
C = Cat Cay	T = Tongue of the Ocean
E = Eleuthera	W = Watling's Island (San Salvador)

(Species indicated with an asterisk were dredged at shallow or moderate depths.)

Briareum asbestinum (An, E, N)
*Iciligorgia schrammi** (C)
Plexaura flexuosa (B, N, W)
Plexaura homomalla, typical (An, N, W)
Plexaura homomalla f. *kükenthali* (N)
*Plexaura nina** (T)
Pseudoplexaura laevigata (N)
Pseudoplexaura porosa, typical (B, N, R)
Pseudoplexaura ramosa (N)
Eunicea calyculata (N)
*Eunicea clavigera** (C)
Eunicea laxispica (N)
Eunicea mammosa (Ab, An, B, N, R)
*Eunicea pinta** (T)
Eunicea tourneforti (N)
Muriceopsis flavida (B, N, R)
*Muriceopsis petila** (C, T)
Plexaurella dichotoma (N)
Muricea atlantica (N)
Muricea elongata (N)
*Muricea laxa** (C)
Muricea muricata (B, N)
Pseudopterogorgia acerosa (N)
Pseudopterogorgia americana (An, N, R)
Pseudopterogorgia bipinnata (N, R)
Pseudopterogorgia elisabethae (N)
*Pseudopterogorgia hystrix** (T)
*Pseudopterogorgia navia** (O)
Gorgonia flabellum (N, W)
Gorgonia ventalina (N, R, W)
Pterogorgia anceps (N)
Pterogorgia citrina (B, N)

Collections of octocorals from localities in the Greater Antilles are strangely few. The limited material available suggests that the reef fauna has a composition much like that of the Florida Keys, but additional species could be expected and some faunal differences between the north and south coasts of the major islands are not unlikely. Such zoogeographic features will be revealed only after comprehensive field work has been done on all coasts of the islands in question.

The collections available to me contain the following species from localities in Cuba, mostly toward the western end of the island (species dredged at moderate depths are indicated by an asterisk): *Telesto operculata**, *Telesto nelleae**, *Neospongodes portoricensis**, *Briareum asbestinum*, *Iciligorgia schrammi**, *Titanideum frauenfeldii**, *Plexaura flexuosa*, *Eunicea mammosa*, *Muriceopsis flavida*, *Plexaurella dichotoma*, *Plexaurella fusifera*, *Muricea atlantica*, *Muricea muricata*, *Muricea laxa**, *Lophogorgia cardinalis**, *Leptogorgia setacea*, *Pseudopterogorgia americana*, *Pseudopterogorgia bipinnata*, *Pseudopterogorgia elisabethae**, *Pseudopterogorgia kallos*, *Pseudopterogorgia rigida*, *Gorgonia mariae*, *Gorgonia ventalina*, *Pterogorgia anceps*, *Ellisella barbadensis*, *Nicella guadalupensis*, and *Riisea paniculata*.

Very few specimens are available from the island of Hispaniola. I have seen: *Telesto riisei*, *Plexaura flexuosa*, *Pseudoplexaura porosa*, *Pseudopterogorgia acerosa*, *Pseudopterogorgia navia*, *Gorgonia flabellum* and *Gorgonia ventalina*.

Work around Puerto Rico by the U.S. Fish Commission steamer 'Fish Hawk' provides a better sampling of octocorals: *Telesto corallina**, *Telesto riisei*, *Neospongodes portoricensis**, *Iciligorgia schrammi**, *Diodogorgia nodulifera**, *Plexaura flexuosa*, *Plexaura homomalla*, *Eunicea calyculata*, *Eunicea laxispica*, *Eunicea tourneforti*, *Muriceopsis flavida*, *Pseudopterogorgia acerosa*, *Gorgonia mariae*, *Gorgonia ventalina*, and *Riisea paniculata**.

Records from Jamaica are disappointingly few; these include: *Telesto riisei*, *Plexaura homomalla*, *P. flexuosa*, *Pseudoplexaura porosa*, *P. flagellosa*, *Eunicea mammosa*, *E. tourneforti*, *Plexaurella dichotoma*, *P. nutans*, *Muricea atlantica*, *M. pinnata **, *Pseudopterogorgia acerosa*, *P. americana*, *P. albatrossae **, *Gorgonia ventalina*, *Pterogorgia anceps*, *P. citrina*.

The material studied for this report contains specimens from many islands of the Lesser Antilles', although in no case is a very large number of species recorded from any one island.

The localities on the Windward Group represented, followed by the number of species from each, are as follows:

Anegada (1)
Anguilla (6)
Antigua (2)
Islote Aves (1)
Barbados (14)
Barbuda (1)
Dominica (4)
Grenada (1)
Guadeloupe (5)
Saba Bank (7)
St. Barthélemy (5)
St. Christopher (7)
St. Eustatius (8)
St. John (7)
St. Lucia (2)
St. Martin (3)
St. Thomas (5)

Amongst the collections from these 17 localities, *Plexaura flexuosa* occurs most frequently, being present in 8 (or 47%); *Plexaurella dichotoma*, *Gorgonia mariae*, and *Pterogorgia citrina* are next, with 6 occurrences out of 17 (or 35%); *Briareum asbestinum*, *Eunicea tourneforti*, and *Pseudopterogorgia americana* are present from 5 of the islands (or 29%); *Eunicea succinea*, *Muriceopsis flavida*, *Gorgonia ventalina*, and *Pseudopterogorgia acerosa* from 4 (or 25%); *Muricea muricata* from 3 (18%); *Gorgonia flabellum* from 2 (12%); and *Erythropodium caribaeorum*, *Plexaura homomalla*, *Eunicea calyculata*, *Eunicea fusca*, *Eunicea mammosa*, *Plexaurella grisea*, *Muricea elongata*, *Muricea atlantica*, *Muricea laxa*, *Pseudoplexaura ramosa*, *Pseudopterogorgia hummelincki*, *Lophogorgia barbadensis*, and *Renilla reniformis* are the least abundant, each coming from only one (6%) of the islands represented. I have no doubt that all of these species (and more) occur at all of the places mentioned above as well as on every other island in the Lesser Antilles; the absence of certain species from a given locality tends only to reflect their relative rarity or the difficulty of collecting them. Thus we can say that, e.g., *Eunicea calyculata* either lives in a habitat that is difficult of access, or is relatively uncommon in the gorgonian population, whereas *Plexaura flexuosa* occurs in numbers almost everywhere and is practically certain to be encountered.

The islands of the Leeward Group, off the coast of Venezuela, support an alcyonarian fauna that is West Indian in composition although somewhat attenuated in number of species. The collections studied amount to 22 species.

In the following list, A = Aruba, Bon = Bonaire, C = Curaçao, Bl = Blanquilla, and F = Los Frailes.

Telesto riisei (C)
Plexaura flexuosa (A, Bl, Bon, C)
Plexaura homomalla (Bon, C)
Pseudoplexaura wagenaari (F)
Eunicea clavigera (C)
Eunicea mammosa (Bon)
Eunicea succinea (Bl, C)
E. succinea f. *plantaginea* (Bl)
Eunicea tourneforti (C)
Muricea muricata (C)
Muriceopsis sulphurea (A)
Muriceopsis flavida (F)
Lophogorgia hebes (A?)
Pseudopterogorgia acerosa (Bon, C, F)
Pseudopterogorgia americana (A, Bon, C)
Pseudopterogorgia blanquillensis (Bl)
Gorgonia flabellum (Bon)
Gorgonia ventalina (A, Bon, C)
Pterogorgia anceps (A)
Pterogorgia citrina (A, Bon, C)
Pterogorgia guadalupensis (C)
Renilla reniformis (C)

The South American coast

Of particular interest is the material obtained during exploratory fisheries operations off the coast of the Guianas and Brazil by the 'Coquette' in 1957 and the 'Oregon' in 1957 and 1958. The presence of *Iciligorgia schrammi, Diodogorgia nodulifera, Ellisella barbadensis* and *E. elongata* shows that the offshore (but still relatively shallow-water) fauna has a decidedly West Indian flavor and is possibly only an extension of the Antillean fauna. At somewhat greater depths (50–150 fms.), the occurrence of such genera as *Thesea, Muricea, Ellisella* and *Callogorgia* indicates that West Indian faunal affinities persist also in this bathymetric range. (See BAYER, 1959).

The reef fauna of Brazil contains an endemic element consisting of such species as *Phyllogorgia dilatata* and *Plexaurella grandiflora*, and a non-endemic western Atlantic element typified by *Leptogorgia virgulata* and *Lophogorgia hebes*, which extend northward to the vicinity of Cape Hatteras on the North American coast. The geographical limits of the endemic component are not known.

DISTRIBUTION OF GENERA AND SPECIES

Order **TELESTACEA**

Family **Telestidae**

Genus *Telesto*. In the West Indies the order Telestacea is represented by a single genus, of which only one species is found at about low tide level. This is *Telesto riisei*, which ranges from southern

Florida through the Florida Keys and the Antilles south to the coast of Brazil. The remaining species, which may prove to be subgenerically or even generically distinct, are found at moderate depths, tow of them along the coast of the Carolinas, two of them in the Gulf of Mexico. The common species in the Florida Keys, *Telesto sanguinea*, has not yet been reported from the Antilles proper, where it is replaced by the very different *T. corallina*.

Order **ALCYONACEA**

Family **Nidaliidae**

Genus *Nidalia*. This is the only alcyonacean genus that approaches the bathymetric region covered by this paper. It has been found from South Carolina to the Dry Tortugas, the Gulf of Mexico (1 record from the Texas coast), and the Barbados. The absence of records off Cuba and Hispaniola indicate a lack of dredging in those regions and not a discontinuity of distribution.

Family **Nephtheidae**

None of the members of this family invade the reefs and shallow waters in the West Indies. The distribution of *Neospongodes portoricensis* corresponds with that of other Antillean alcyonarians from the same bathymetric range, while *Eunephthya nigra* belongs to a cold water group that demonstrates equatorial submergence.

Order **GORGONACEA**

Family **Briareidae**

Genus *Briareum*. The single West Indian species of this genus occurs commonly from the Dry Tortugas and Florida Keys through the Bahamas, Greater Antilles, and Lesser Antilles as far south as Barbados. I have been unable to discover any differences, generic or specific, between *Erythropodium polyanthes* and *Briareum asbestinum*. Moreover, since at least some of the Indo-Pacific species

of *Solenopodium* are generically indistinguishable, *Briareum* can no longer be considered an endemic Caribbean genus.

Family **Anthothelidae**

Genus *Anthothela*. Until the present time, *Anthothela* has been represented in the Atlantic by a single species occurring from the Grand Banks south to Fernandina, Florida, in deep water. A distinctly different species has now been recorded from the Gulf of Mexico, also in deep water, which proves to be a new species closely related to the eastern Pacific *Anthothela pacifica* (Kükenthal), forming with it an eastern Pacific – western Atlantic twin-pair of species. The genus is also represented in the eastern Atlantic, and in the Indo-Pacific from east Africa to Hawaii and the Galapagos.

Genus *Iciligorgia*. The Caribbean species is common at moderate depths from Palm Beach, Florida, to Dominica. The West Indian genus *Iciligorgia* is very closely allied to the Indo-Pacific genera *Semperina* and *Solenocaulon*.

Genus *Tripalea*. The anatomical features of this genus render it quite unique, and the few records of its occurrence indicate that it is endemic in the western Atlantic. The single species, *T. clavaria*, is known from the eastern coast of South America between 23° South and 37° South.

Genus *Diodogorgia*. Material at hand indicates that this genus is represented in the western Atlantic by a single species which ranges from Palm Beach, Florida, south to Montserrat and the southern shore of the Caribbean. It probably occurs throughout the Antilles and around the rim of the Caribbean. Stiasny has described a species from the west coast of Africa (1939, p. 174), but so far the genus seems confined to the Atlantic.

Genus *Titanideum*. One species in the western Atlantic, occurring between Cape Hatteras and the Straits of Florida; it apparently does not extend very far into the Antilles. If this species follows the Carolinian disjunct pattern of distribution it may be expected in the northern part of the Gulf of Mexico, but extensive trawlings by the 'Pelican' and 'Oregon' in this area have failed to disclose its presence there.

Genus *Erythropodium*. From the southern tip of Florida to the northernmost of the windward Lesser Antilles and the western Caribbean. This genus has nothing to do with the Indo-Pacific species assigned to it by various authors, and is endemic in the Caribbean area.

Genus *Anthopodium*. Known from only two localities: Fort Macon, North Carolina, and the coast of Texas. It probably conforms to the Carolinian disjunct pattern since it has not been found in Florida. Its nearest relative is *Callipodium*, of the Panamic province.

Family **Keroeididae**

Genus *Lignella*. The West Indian representative of this family differs so widely from typical *Keroeides* that it is necessary to separate it as a distinct genus, which is endemic in the western Atlantic. Members of the genus *Keroeides* proper are distributed from the East Indies to Hawaii.

Family **Acanthogorgiidae**

No members of this family occur in shallow water in the West Indies. The western Atlantic species are found off Nova Scotia and the Grand Banks in depths of 170 to 677 fathoms, and in the West Indies, 75 to 400 fathoms.

Family **Plexauridae**

Genus *Plexaura*. Although a number of Indo-Pacific species have been referred to this genus from time to time, it is quite clear that they are all generically distinct and require reallocation. The present studies indicate the validity of three species, one of them with a named growth forma. *Plexaura homomalla* and *Plexaura flexuosa* have practically identical ranges, including Bermuda, southern Florida the Keys, the Antilles and the Caribbean islands. *Plexaura homomalla* forma *kükenthali* has been found off Miami, Florida, in the Bahamas, and at Old Providence in the Caribbean, and probably has a range identical with that of the typical form. *Plexaura nina*

is a deep-water (36 fathoms) species closely related to *P. homomalla*, which is known only from the type locality in the Bahamas.

Genus *Pseudoplexaura*. This genus is also completely endemic in the West Indian region. *P. porosa* is recorded from Bermuda, the Florida Keys and Dry Tortugas, Bahamas, Lesser Antilles, Jamaica, and Curaçao; *P. flagellosa* is known from Bermuda, the Florida Keys, Lesser Antilles, Jamaica, and possibly Curaçao; *P. wagenaari* occurs in Bermuda, the Florida Keys, west coast of Florida, and the Lesser Antilles south to the Venezuelan Islands; *P. crucis* is known as yet only from the Virgin Islands but probably will be found throughout the Antilles.

Genus *Eunicella*. No representatives of this genus are found in shallow water in the West Indies. Off the eastern coast of the United States, two species are found at depths between 276 and 440 fathoms.

Genus *Eunicea*. This genus includes some of the most important reef-dwelling gorgonians of the western Atlantic. The most widely distributed species extend from Bermuda south to the Leeward Group of the Lesser Antilles, including the Florida Keys, Bahamas, and the Caribbean islands. These include *Eunicea tourneforti* and its slender forma *atra*, *E. calyculata*, *E. clavigera*, *E. laciniata*, and *E. fusca*. Most of the remaining species, which do not extend to Bermuda, have similar ranges over the Antillean region, except for *Eunicea knighti*, which is restricted to the west coast of Florida and the Keys. From records presently available, it seems that no species of *Eunicea* extends south to Brazil.

Genus *Muriceopsis*. Of the reef-dwelling species of *Muriceopsis*, one, *M. flavida*, extends from southern Florida and the Bahamas south to Curaçao, and the other, *M. sulphurea* (= *humilis*), is common on the South American mainland but becomes scarce through the Lesser Antilles and northward to Puerto Rico.

Genus *Plexaurella*. Of the six species recognized herein, one extends from Bermuda to Brazil (*P. dichotoma*), two seem to be limited to the Brazilian fauna (*P. grandiflora*, *pumila*), and the others are more or less purely Antillean. The genus is strictly endemic in the western Atlantic.

Genus *Muricea*. This is the only amphi-American genus of shallow-water plexaurids; none of the species occurs in both oceans.

When the Panamic fauna is adequately investigated, it will probably be found that one or more twin-pairs exist in the two regions. *Muricea pendula* is the only representative of the genus extending into cool water; it has a disjunct Carolinian distribution, extending from Texas to northwest Florida, and along the coast of the Carolinas. The common species *M. atlantica* and *M. muricata* have a typical Antillean distribution, with *M. atlantica* occurring in Bermuda. *Muricea elongata* and *M. laxa* appear to be common in the vicinity of the Florida Keys, but not much is known of their distribution outside of this area. *Muricea pinnata* is at present known only from a single locality in the Caribbean Sea.

Family **Gorgoniidae**

Genus *Lophogorgia*. This is the most widely distributed of all gorgoniid genera, being practically circumtropical. In the western Atlantic, at least one species, *L. punicea*, extends from Florida to Brazil. The others are apparently restricted either to the northern or the southern half of this range. *Lophogorgia hebes* has a typical disjunct Carolinian distribution, *L. cardinalis*, *L. miniata*, *L. barbadensis*, and *L. sanguinolenta* seem to be Antillean, and *L. purpurea* South American. Additional records are required to clarify the distribution of these species.

Genus *Pacifigorgia*. The distribution of this genus is amphi-American, with numerous species in the Panamic province but only one in the western Atlantic. It has already been suggested that *P. elegans* is a relict of the period when Central American portals permitted a continuous trans-American fauna, surviving only in those regions that suffered the least change of environmental conditions after final closure of the last portal.

Genus *Leptogorgia*. All evidence indicates that this genus is endemic in the western Atlantic. The common *Leptogorgia virgulata* and *L. setacea* of the eastern seaboard of the United States extend south to Brazil, probably following the continental coast; no records of either species can be substantiated from Antillean localities. Three additional species have been described from the Gulf of Mexico.

Genus *Pseudopterogorgia*. The West Indian members of this genus, referred in the past to *Pterogorgia* (sensu Bielschowsky, Kükenthal, et al.) and *Antillogorgia* (Bayer), are not generically separable from the Indo-west-Pacific species for which *Pseudopterogorgia* originally was established, although it does appear that ten of the twelve West Indian species form a group of species distinct from the other two plus four from the Indo-Pacific. In spite of the fact that the genus is not endemic in the West Indies, a group of species somewhat divergent from their Indo-Pacific relatives has certainly developed there and assumed a rôle of major importance among the reef-dwelling gorgonians. *Pseudopterogorgia bipinnata*, *P. blanquillensis*, and possibly *P. rigida* are more closely related to the Indo-Pacific group of species and may form with them a recognizable subgenus. Of the nine remaining species, two (*acerosa* and *americana*) extend as far north as Bermuda, six are found generally through the Antilles, and one (*marcgravii*) is at present known only from Brazil. *P. acerosa* penetrates northward into the Gulf of Mexico, certainly as far as Tampa, and probably into Apalachee Bay, and has been taken also in the Gulf of Campeche.

Genus *Gorgonia*. This well known genus occurs throughout the West Indian region, from Bermuda and southern Florida through the Antillean arc to Trinidad. Available record indicate that both Linnaean species, *G. flabellum* and *G. ventalina*, occur together in the Bahamas, Florida Keys, and Antilles; it appears that only *G. ventalina* occurs in Bermuda. The third species of the genus, *G. mariae*, is restricted to the northern part of the Antillean chain, from Cuba to St. Eustatius.

Genus *Phyllogorgia*. The one species of this genus is not certainly known from any locality outside of Brazil, but was reported from Guadeloupe by Milne Edwards & Haime (1857). It would probably have been noticed more recently if it actually occurs in the Antilles.

Genus *Pterogorgia*. The three species of the genus are virtually sympatric but *P. citrina* seems to be the only one of them that reaches Bermuda, and *P. anceps* the only one found along the west coast of Florida.

Family **Ellisellidae**

In comparison with the East Indian region, the tropical western Atlantic is poor in members of this family. Three genera, *Ellisella* (= *Scirpearia*), *Nicella*, and *Riisea*, are present; the four additional genera that make up the family are exclusively Indo-west-Pacific in their distribution. *Riisea* appears to be endemic in the West Indies. Both *Ellisella* and *Nicella* occur on both sides of the Atlantic but are not so well represented on the west coast of Africa as the literature might indicate. Contrary to Kükenthal's belief, the genus *Ellisella* does occur on the Pacific coast of Mexico and accordingly is the only genus of the family known to have a practically circumtropical distribution: western Atlantic, eastern Atlantic, Mediterranean, Red Sea, Indian Ocean, East Indies, western Pacific, and eastern Pacific.

In the West Indies, most ellisellids inhabit moderate to considerable depths and only a few extend within range of shallow water diving equipment, whereas a number of East Indian species occur just below low tide mark.

Order **PENNATULACEA**

Many members of this order enjoy wide geographical ranges and those from great depths may be cosmopolitan. Of the pennatulacean genera included in this treatment, *Renilla* is of particular interest because of its endemic amphi-American distribution. Two species, *Renilla reniformis* and *R. mülleri*, occur on both Atlantic and Pacific coasts of the Americas, the latter without any discernible regional differentiation. Unfortunately, collection records are not sufficiently complete to reveal whether or not the populations are continuous around the southern tip of South America. Such a case seems unlikely.

The genus *Sclerobelemnon*, which has only recently been detected in the Caribbean area, is otherwise known from the Red Sea, Indian Ocean, Japan, the Philippines and Australia.

The virgulariid genera *Virgularia* and *Stylatula* are widely distri-

buted in both the Atlantic and Indo-Pacific. At least one species of *Stylatula, S. elegans,* occurs in both northern Atlantic and northern Pacific, and other species may prove to be similarly widespread once synonymies have been clarified adequately.

Faunistic Regions

The western Atlantic warm-water fauna is unified by the broad distribution of the common *Leptogorgia virgulata* and *L. setacea,* which extend from the Virginia Capes south to the reefs of Brazil. Within this vast geographic area, several faunal subdivisions are more or less clearly defined:

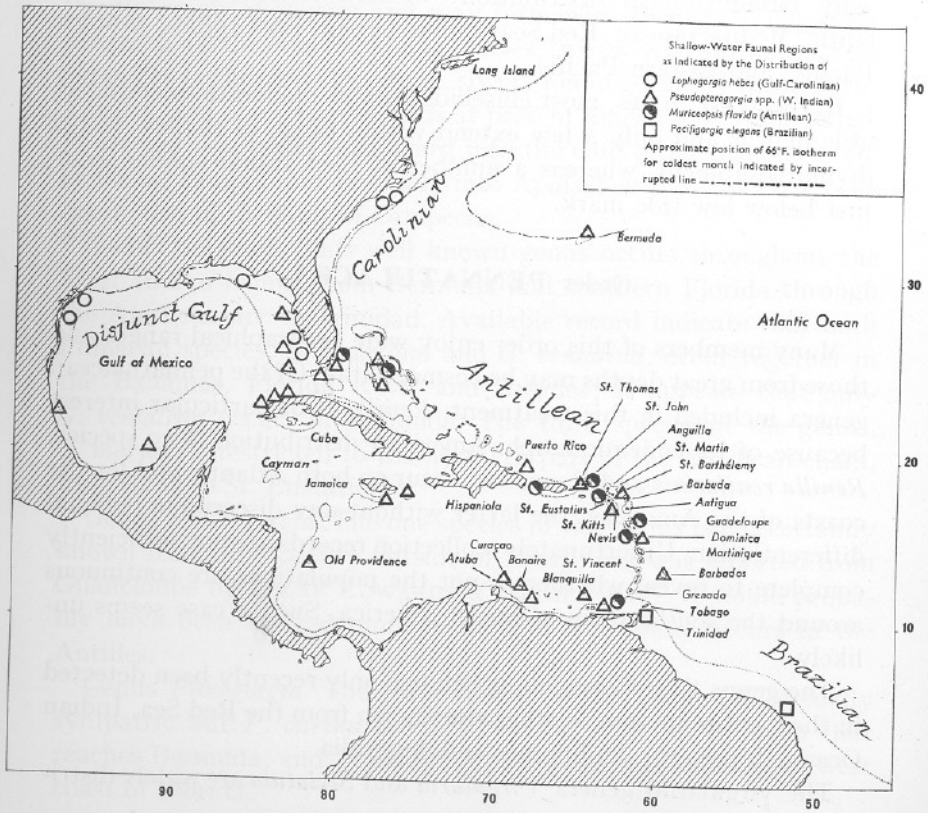

Figure 100. Shallow water faunal regions.

1. *Carolinian:* The Atlantic coast from the Virginia Capes to Georgia or east Florida. (*Telesto fruticulosa, T. nelleae, Titanideum frauenfeldii.*)

2. *Disjunct Gulf – Carolinian:* The Carolinian region plus the northern shore of the Gulf of Mexico, distinctly separated by more or less of the Florida peninsula. (*Muricea pendula.*)

3. *West Indian:* The islands of the West Indies, the Caribbean Sea, southern Florida, and Bermuda. (*Antillogorgia acerosa, A. americana, Gorgonia ventalina, Plexaura flexuosa.*)

4. *Antillean:* The Antillean islands from Trinidad to Cuba, and including the Florida Keys and Bahamas. (*Diodogorgia nodulifera, Iciligorgia schrammi, Gorgonia flabellum, Pterogorgia anceps.*)

5. *Brazilian:* The coast of the Guianas to the reefs of Brazil. (*Muriceopsis humilis, Phyllogorgia dilatata.*)

Adequate data are not now available to permit the recognition of any clear-cut smaller faunal areas. The broad faunal areas are indicated on the accompanying map. (Figure 100)

Comparative Distribution of the Deeper-water Fauna

Although species occurring at depths greater than 25 fathoms are for the most part not included in this report, it is desirable to summarize briefly their distributional characteristics in order to draw comparisons with the shallow-water population. Seasonal temperature fluctuations are much reduced as depth increases, and it is accordingly no surprise to learn that the genera and species living at depths of 25–100 fathoms exceed the geographical bounds of their shallow-water relatives. In the Gulf of Mexico the paramuriceids and ellisellids characteristic of the Antillean islands continue northward from the Tortugas around the rim of the Gulf basin wherever suitable bottom occurs within the requisite depth range. Even the great discharge of silt-laden fresh water from the Mississippi River seems not to affect the distribution of gorgonians below 25 fathoms, for dredgings off the delta mouth by the 'Oregon' have revealed a typical West Indian assemblage. (Figure 101)

Relationships of the Western Atlantic Alcyonarian Fauna

The faunas of the West Indian region (or the warm-water west Atlantic) and the Panamic region (warm-water east Pacific) are closely related. As pointed out above, the families Gorgoniidae and Plexauridae are common to the shallow waters of both areas and, since species of both families are elsewhere uncommon or even rare, are virtually characteristic of them.

As I have elsewhere pointed out (1953), the genus *Lophogorgia* has several species in the Panamic and West Indian regions whereas other genera are more or less restricted to one area or the other. Thus, *Leptogorgia* is limited to the Atlantic, and its counterpart

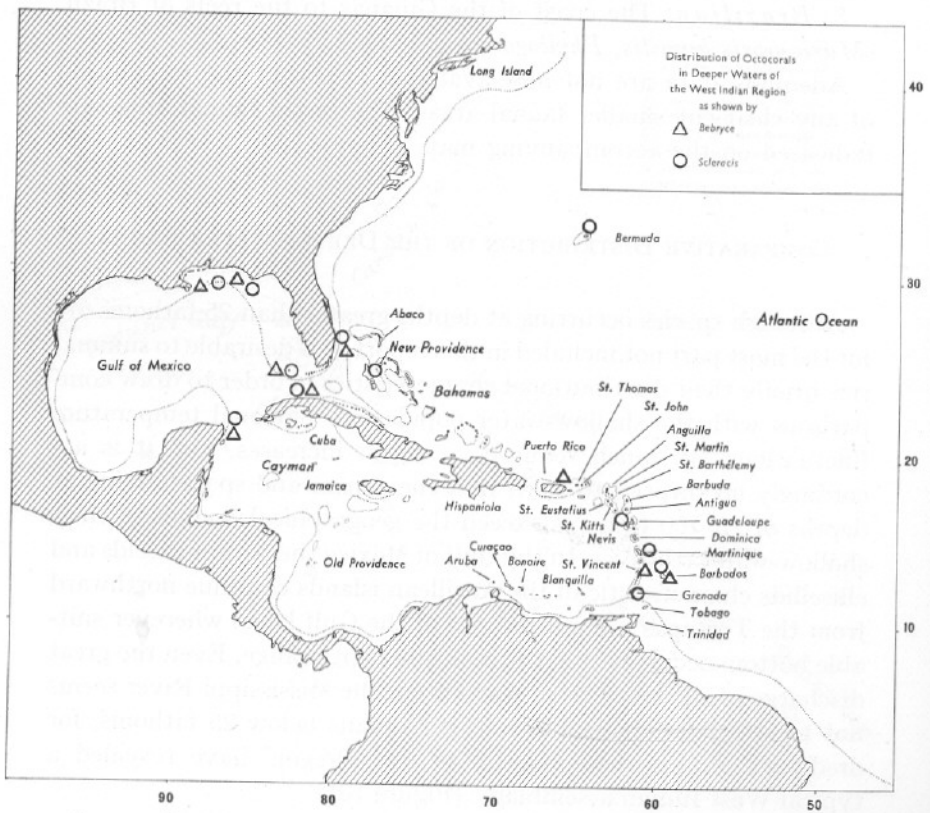

Figure 101. Distribution of typical deeper water West Indian Octocorallia.

Eugorgia to the Pacific; *Pacifigorgia* has numerous species in the Panamic fauna, but one relict appears in Trinidad and Brazil.

Among the Plexauridae as herein recognized, one genus, *Muricea*, is represented both in the West Indies and in the Panamic-Californian region, whereas all the other shallow-water genera are restricted either to the Atlantic or the Pacific. *Plexaura*, *Plexaurella*, *Eunicea*, and *Muriceopsis* are endemic in the Atlantic, and *Psammogorgia* is limited to the Pacific coast.

The former faunal confluence of the two areas is clearly indicated by the distribution of the gorgonians, but even more clearly by that of the pennatulid genus *Renilla*, a warm shallow-water group that has two species common to the two oceans, one of which shows subspecific differentiation.

If we tabulate the distribution of the two predominant shallow-water families of the western Atlantic, the strong independence of the fauna becomes clear. (Table 3)

Table 3

Zoogeographic Relationships of West Indian Gorgoniidae and Plexauridae

	Gorgoniidae		*Plexauridae*	
	Species (34)	Genera (7)	Species (35)	Genera (6)
Endemic western Atlantic . . .	34 (100%)	4 (57%)	35 (100%)	5 (83%)
West Atlantic and Panamic (= 'Amphi-American')	0	1 (14%)	0	1 (17%)
West Atlantic and East Atlantic (= 'Amphi-Atlantic')	0	0	0	0
West Atlantic and Indo-Pacific (including circumtropical) . .	0	2 (29%)	0	0

It has been shown that the West Indian fauna contains six genera and thirty four species of Plexauridae and seven genera and thirty three species of Gorgoniidae, of which 67% of the genera and 100% of the species are endemic in the western Atlantic. Let us now see what percentage of the genera and species of these families as a whole occurs in the western Atlantic region. Using Kükenthal's monographs (1919, 1924) as a basis, we find a total of 13 genera and

103 species of Plexauridae, and 9 genera and 86 species of Gorgoniidae. (Table 4)

TABLE 4

GEOGRAPHICAL DISTRIBUTION OF THE GENERA AND SPECIES OF GORGONIIDAE AND PLEXAURIDAE

	Gorgoniidae		*Plexauridae*	
	Species (86)	Genera (9)	Species (103)	Genera (13)
Endemic western Atlantic . . .	34 (40%)	4 (44%)	35 (34%)	5 (38%)
Eastern Atlantic	9 (10%)	1 (11%)	5 (5%)	1 (7.7)
Mediterranean	1 (1.2%)	1 (11%)	2 (2%)	1 (7.7%)
Indo-West Pacific	6 (7%)	1 (11%)	46 (45%)	5 (38%)
Endemic eastern Pacific	32 (37%)	2 (22%)	14 (14%)	1 (7.7%)

For the sake of comparison, let us prepare a table of the zoogeographic affinities of some gorgonians from that part of the continental shelf lying between 25 and 150 fathoms in depth. The reef genera of the Plexauridae and Gorgoniidae invade this region to only a small extent, and the members of its typical families, the Primnoidae, Paramuriceidae, and Ellisellidae, correspondingly do not approach the reef habitat.

Because the present account does not consider these families of deeper waters, we must go to the literature for the necessary data, depending mainly upon the work of KÜKENTHAL (1919, 1924) and DEICHMANN (1936). As examples for tabulation, we may take the Primnoidae and the Ellisellidae (= Gorgonellidae), the former with its species concentrated in the deeper waters of the continental shelf and slope and in the abysses, and the latter in the shallower parts of the bathymetric zone under discussion. In her monograph of the western Atlantic Alcyonaria, DEICHMANN (1936) lists two ellisellid genera in the West Indies, viz. *Scirpearia* (properly *Ellisella*) and *Nicella*, and I have recently transferred the genus *Riisea* from the Chrysogorgiidae to the Ellisellidae (BAYER 1955), bringing the total to three. The Indo-Pacific genus *Junceella* as recorded in the Atlantic (DEICHMANN 1936, p. 204) seems to be based upon an *Ellisella* with unusually asymmetrical spicules, or upon an error of labelling, or both (BAYER 1958, p. 384, 386). Three others genera,

also of the Indo-Pacific region, complete the family. The Primnoidae, following the same author, is represented in the Atlantic by seven genera. (Table 5)

TABLE 5

ZOOGEOGRAPHIC RELATIONSHIPS OF WEST INDIAN ELLISELLIDAE AND PRIMNOIDAE

	Ellisellidae		*Primnoidae*	
	Species (10)	Genera (3)	Species (16)	Genera (7)
Endemic western Atlantic . . .	10 (100%)	1 (33%)	12 (75%)	0
West Atlantic and Panamic (= 'Amphi-American')	0	0,	0	0
West Atlantic and East Atlantic (= 'Amphi-Atlantic')	0	0	4 (25%)	0
West Atlantic and Indo-Pacific (including circumtropical) . .	0	2 (66%)	0	7 (100%)

In the West Indian region we find less generic endemism in the gorgonian families of the deeper waters than in those of shallow-water habitats. Among the ellisellids, a family with strong affinity for the shallower waters, a single monotypic genus is restricted to the warm western Atlantic. On the other hand, the genera of Primnoidae, a family with strong affinity for the deeper waters, show no endemism in the western Atlantic and even the percentage of species endemic there is low if compared with that of other families. It is apparent that the Atlantic Ocean forms a barrier to trans-Atlantic migration of alcyonarians living in moderate depths, but not to those of the deeper waters.

AMPHI-AMERICAN AND AMPHI-ATLANTIC DISTRIBUTION

The amphi-American element in the West Indian fauna obviously must consist of only those genera and species that have persisted unchanged since the interruption of a continuous Atlantic-Pacific American fauna. This element is represented in shallow water by the genera *Muricea* (Plexauridae), *Lophogorgia* and *Pacifigorgia* (Gorgoniidae), and *Renilla* (Pennatulacea) with its species *reniformis* and *mülleri;* of these, the genus *Lophogorgia* is circumtropical rather

than strictly amphi-American. In deeper waters the picture is clouded by lack of reliable information on the Pacific coastal fauna, although the genera *Telesto, Anthothela, Swiftia, Thesea, Callogorgia, Plumarella,* and probably others, occur on both Atlantic and Pacific coasts of the Americas. Most, if not all, of these genera are circumtropical rather than amphi-American.

Correspondingly, any amphi-Atlantic elements must represent genera or species that are or were distributed continuously between the two areas, or that have remained stable since continuity existed. In shallow water, only two genera, *Lophogorgia* and *Telesto,* are definitely common to both sides of the Atlantic, and both of them are circumtropical genera. The only reported shallow-water amphi-Atlantic species, *Lophogorgia sanguinolenta,* appears from all indications to be two distinct species. The fact that no members of this large circumtropical genus occur on both sides of the Atlantic indicates that there is now little or no faunal interchange and that the areas have been isolated, at least as far as gorgonians are concerned, for a long time. It appears that a truly amphi-Atlantic element exists only in the deep-water fauna, among species of the Primnoidae and perhaps also the Paramuriceidae and Anthothelidae.

Thus, we have a definite amphi-American element in the shallow-water Octocorallia, but no demonstrable amphi-Atlantic fauna; in deeper water there certainly are both amphi-American and amphi-Atlantic elements and, although their extent is not known, they probably are not large.

TETHYAN DISTRIBUTION

Tables 3 and 5 and the foregoing discussion have shown that there is no strictly amphi-Atlantic element in the shallow-water gorgonians, and only a small one among the deeper-water forms. The genera common to the eastern and western shores of the Atlantic are mostly circumtropical rather than amphi-Atlantic, and since many of them are warm-water groups, they have no possible migration route from ocean to ocean. Consequently, they have at present a highly discontinuous distribution, groups of species being isolated in the western Atlantic, eastern Atlantic-Mediterranean,

Indo-West Pacific, and eastern Pacific by continental land masses, the East Pacific Barrier, and the Atlantic Barrier.

EKMAN (1953, p. 40) points out that the warm-water fauna of the western Atlantic has a somewhat closer relationship with the Indo-Pacific than has that of the Pacific coast of the Americas. Although it is not correct as stated by EKMAN that no species of Gorgonellidae (= Ellisellidae) occur along the western shores of America, a number of paramuriceid genera, e.g., *Bebryce, Villogorgia,* and *Placogorgia,* which are otherwise circumtropical, do show such a distribution. Others, such as *Swiftia,* definitely occur on both American coasts as well as in the Indo-West Pacific. In contrast, the genus *Corallium* skips the western Atlantic but occurs from the eastern Atlantic through the Mediterranean, Indian Ocean, Malay Archipelago and Japan, east to Hawaii and Guadelupe Island off the Mexican coast.

As suggested by STIASNY (1936, p. 39–42), this discontinuity certainly finds its best explanation in the Tethys Sea, a great body of water that girdled nearly the entire earth until the time of the middle Tertiary and made possible the existence of a continuous circumtropical Tethys fauna.

The strongest manifestation of the Tethyan distribution is found in the warm-water alcyonarians living at moderate depths, many of which have groups of species in both Atlantic and Indo-West Pacific which must have been isolated since sometime toward the middle or end of the Tertiary, but which still clearly retain their generic identity.

The high degree of generic and specific endemism in tropical American reef alcyonarians is indicative of profuse development of the two predominant families in this area, and the low amphi-American element suggests that the Atlantic and Pacific American faunas have reached their present state of development in rather recent times, i.e., since the closure of the Central American portals. The West Indian reef fauna is therefore a young fauna, but one with its heritage in the Tethys. The West Indian shelf, slope, and deep-sea alcyonarian fauna owes its characteristics not only to the old Tethys Sea with its continuous circumtropical fauna, but also to the more stable conditions at greater depths, which have not stimulated evolution beyond the specific level.

SUMMARY

The alcyonarian fauna of the West Indies is prolific and conspicuous and has been known for many years, with the natural result that a great many more species have been described than actually exist. The deep-water fauna, which received little attention prior to the work of VERRILL, was thoroughly reviewed by DEICHMANN in 1936. The shallow-water and reef fauna was the subject of a series of extensive papers by KÜKENTHAL and his collaborators, KUNZE, MOSER, RIESS, BIELSCHOWSKY, and TOEPLITZ, but this ambitious study appears to have been based upon inadequate collections and its usefulness is seriously limited by the number of synonyms and misidentifications that it contains. No comprehensive survey of the fauna exists, and there is no satisfactory guide for the identification of specimens.

This paper, which was prepared at the request of Dr. P. WAGENAAR HUMMELINCK, Secretary of the Stichting 'Natuurwetenschappelijke Studiekring voor Suriname en de Nederlandse Antillen' (Foundation for Scientific Research in Surinam and the Netherlands Antilles), forms such a guide and at the same time reviews the fauna to the extent permitted by the collections in hand and the literature. With Dr. HUMMELINCK's collection of West Indian octocorals serving as a nucleus, the pertinent material in the collections of the U.S. National Museum was critically revised and correlated with the literature in order to gain an accurate picture of the known fauna. As a result of this study, it was possible to recognize 75 species of alcyonarians belonging to the orders Telestacea, Alcyonacea, Gorgonacea, and Pennatulacea inhabiting the reefs and shallow waters of the warm western Atlantic. An additional 21 species from deeper water are also included for comparative purposes or because they inhabit the transitional zone just below

the region of active reef growth. Seventeen species and a few growth forms are described as new to science. Each species is diagnosed and illustrated with drawings of the details of spiculation and, in the case of new or especially common species, photographs of the colonial form. Taxonomic keys with couplets illustrated for clarity are provided to facilitate the identification of specimens. The species described in this paper are arranged as indicated in the Table of Contents (p. 3–7).

A total of 96 species are described from the region including the Bermudas, the southeastern coast of the United States, the Bahamas and Antilles, and the east coast of South America south to the reefs of Brazil. Of these, 52 species occur in the reef habitat proper or closely associated with it, and another 23 species occur in depths of 25 fathoms or less. The orders Telestacea, Alcyonacea, and Pennatulacea are togehter represented by only 13 species within the bathymetric limits set forth, the remaining 83 belonging to the order Gorgonacea. The littoral and reef-dwelling representatives of the last-named order belong for the most part to the two families Plexauridae and Gorgoniidae, which include 35 and 34 species respectively. When the shallow-water alcyonarian fauna is added to the deep-water fauna as reported by DEICHMANN, a total of 196 species is revealed for the area. This is a fauna of only modest proportions when compared with that of the East Indies, where some 445 species (exclusive of Pennatulacea) were obtained by the 'Siboga' Expedition, but nevertheless, the gorgonians are the dominant sessile animals on many of the reefs of Florida, the Bahamas, and the Antilles. This dense population consists chiefly of about a dozen species, all the others being rare or of local occurrence, so it appears that the reef fauna is rich in individuals but poor in species.

The distribution of alcyonarians is influenced by a variety of factors, among them salinity, temperature, illumination, depth of water, and character of the bottom. It is not possible to single out any one factor as the most important, since they all interact closely, but there is no doubt that temperature is one of the most influential.

Although temperature requirements and tolerations have not been determined experimentally for alcyonarians, they can reasonably be assumed to parallel more or less closely those of the principal reef-formers. It has been observed that formation of reefs does not take place in waters that drop below 68°F. for any appreciable period during the winter. Since active growth of reefs occurs at Bermuda, the northernmost limit of the West Indian fauna, its annual minimum temperature of 66°F, may be taken as the limit for reef formation in the West Indian area. Tropical alcyonarians occur up to this minimum isotherm of both coasts of Florida.

Most alcyonarians are stenohaline and require salinities within the range found in the open sea. However, the occurrence of a few species, such as *Leptogorgia setacea* of the southeastern coast of the United States, in the brackish inshore waters of bays and river mouths indicates that a limited degree of euryhalinity does occur in the Octocorallia.

A rough and solid bottom is apparently as necessary for the attachment of gorgonian planulae as it is for those of madrepores, and the importance of this requirement is clearly demonstrated on the west coast of Florida, where reef communities gain a foothold only on the scattered solid outcrops on an otherwise broad, sandy shelf. A few species of Gorgonacea are known to live unattached, the colonies apparently doing so in some cases because no suitable objects were available for attachment, in others because they were broken loose from their original solid support but continued to live in a prone position. Certain deep-water gorgonacean groups (families Chrysogorgiidae and Isididae) that inhabit areas with a scarcity of solid material are able to adapt the form of their holdfast to the conditions present at the time of metamorphosis, producing either a calcareous basal disk for attachment to shells and stones, or a branched, rootlike process for anchoring the colony firmly in a muddy bottom. The pennatulaceans, which are adapted for life on soft bottoms, require either sand or mud and therefore are not found closely associated with reef communities.

The octocorals of the reefs are restricted bathymetrically to the upper 25 fathoms of water, perhaps because of their symbiotic zooxanthellae, which require sunlight for the process of photo-

synthesis, but the physiological relationships of zooxanthellae and their coelenterate hosts are in general less clearly understood in the octocorals than in the madrepores, so the cause of the bathymetric-photic correlation cannot be stated in general terms. Obviously, the vertical distribution of those octocorals that are dependent upon their zooxanthellae for nutrition is governed by the physiological requirements of the algae. In those octocorals that are nutritionally independent of their zooxanthellae (as appears to be generally the case among scleractinian corals) other ecological factors must limit bathymetric distribution.

In the West Indies, almost all of the shallow-water octocorals, which represent 38% of the total known fauna, belong to the two families Plexauridae and Gorgoniidae. Very few members of these families extend downward below 25 fathoms, and very few members of the deep-water families venture into water shallower than this. In the East Indies, where a rich tropical alcyonarian fauna exists, 59% of the species taken by the 'Siboga'-Expedition lived in depths shallower than 50 meters, but this fauna is inordinately rich in groups poorly represented in the West Indies, where 85% of the species are gorgonaceans. In both regions, somewhat more than 40% of the gorgonaceans occur in depths less than 50 meters.

The alcyonarians are an important component of the reef community, perhaps more so in the West Indies than elsewhere in the tropics because of the great profusion of a few conspicuous forms in the reef habitat. They provide shelter and sustenance for a wide array of casual associates, epizoa, commensals, and parasites, ranging from other coelenterates to fishes. Moreover, when they die they liberate great quantities of calcareous spicules which are then available for incorporation into the general mass of the reef.

The alcyonarian fauna of the warm parts of the western Atlantic shows a high degree of endemism and only indistinct subdivision into smaller faunal regions. It is possible to distinguish a Carolinian fauna occupying the southeastern coast of the United States, with part of its species occurring only along the Atlantic coast and part

of them with isolated populations in the northern Gulf of Mexico. At least three species follow the continental coast more or less continuously from the Carolinas to Brazil. This is basically a continental fauna and its species do not range out into the West Indian islands.

The fauna of the West Indies is essentially an insular fauna and it suffers depletion wherever it invades continental coasts. The largest number of reef dwelling species seems to occur in the northern islands of the Lesser Antilles, the Greater Antilles, and the Florida Keys. At the present time, more species are known from the last-named locality than from the islands of the Greater Antilles, but it has certainly been more thoroughly explored. Intensive collecting will probably reveal an even larger number of species in the northeastern part of the Antilles. Antillean species extend along both coasts of Florida northward to about the 66°F. minimum surface isotherm, but their number is sharply diminished. A small group of the hardiest species reaches Bermuda, which is the northernmost outpost of the West Indian fauna.

Records indicate that the Antillean fauna becomes attenuated also toward the southern islands of the Lesser Antilles, and the Leeward Group along the coast of South America has a fauna comparable in many respects with that of Bermuda. However, the fauna of Bermuda is restricted by the low temperature of the water during midwinter (66°F), a limiting factor that does not exist at the low latitude of the Leeward Islands. The fauna must instead be restricted by other ecological factors, perhaps imposed by the proximity of the continental coast.

The alcyonarian fauna of the reefs of Brazil, although composed largely of West Indian genera – *Plexaurella*, *Muriceopsis*, *Lophogorgia* – shares few species, perhaps no more than three or four, with the Antillean region to the north, and is probably the most distinct of the subregions of the western Atlantic.

Within the broad limits of the warm western Atlantic faunal region, extending from Bermuda south to Brazil, we can distinguish an insular Antillean fauna centered in the northeastern part of the Antilles; a continental Carolinian fauna along the southeastern

Atlantic seabord, some of its species with disjunct populations in the Gulf of Mexico and some following virtually the entire coastline from the Carolinas to Brazil; and a Brazilian fauna extending northward along the South American coast as far as Trinidad.

The presence in the West Indies of Alcyonarian genera known also in the tropical Indo-West Pacific can be explained only on the basis of former faunal continuity. The presence of a small amphi-American element clearly points to the existence of a continuous East Pacific–West Atlantic (or trans-American) fauna during the past, and the high level of endemism in the West Indian region suggests a subsequent rapid development of a new fauna from remnants of the old, left behind after closure of the Central American seaways. The distribution of modern alcyonarians corroborates the former existence of a great equatorial sea, the Tethys, that permitted circumtropical distribution of marine animals, which geology tells us existed during much of Earth's history between the Cambrian and the Tertiary.

POST SCRIPT

During the many months this volume has been in press, many new specimens and new observations have become available to me, requiring more or less extensive revisions at several points in the text. Such alterations must obviously result in some inconsistencies in the general discussions, and I hope that the most obvious of these have been corrected. For those that have escaped, I beg the reader's indulgence. I would like to take this opportunity to express once again my sincere appreciation to the Editor, Dr. P. WAGENAAR HUMMELINCK, and to the publishers Messrs. MARTINUS NIJHOFF, for their continued patience and willing assistance whereby my wishes have been transformed into type. Without them, this book could not have come into being.

SUGGESTIONS FOR FURTHER STUDY

It has been shown in the foregoing pages that the characters upon which the classification of octocorals depends – e.g., the ramification and general form of the entire colony, the size, shape and color of the spicules, and the development of anthocodial armature in the polyps – are subject to a degree of variation and intergradation that imposes an uncomfortably large element of doubt upon the resultant system. These perplexities will be dispelled only when the influence of the environment upon the morphological features of the colonies is fully understood. Even large suites of specimens from many localities fail to provide such understanding, and it is now becoming obvious that only through an experimental approach will the answers to many questions be found. The West Indian region – i.e., southern Florida, the Bahamas and Antilles – provides one of the richest grounds in the world for reef-dwelling gorgonians, with several marine laboratories at which experiments in controlled ecology could readily be undertaken.

By the simple technique of transplanting young colonies on tiles, some of the easily recognized forms – e.g., *Pseudopterogorgia acerosa* and *P. americana*, *Pterogorgia anceps* and *Pt. citrina*, *Plexaura flexuosa* and *P. homomalla*, *Plexaurella dichotoma*, and *Muricea muricata* – could be moved about from one situation to another, where the principal environmental factors, including current, temperature, salinity, and light, could be measured and recorded and their effects upon the growing colonies determined. It is known that currents have a marked effect upon the branching of reef corals, millepores, and calcareous algae (ABE 1937, p. 309) and they probably exert a similar influence upon the growth form of gorgonians. However, the influence of environmental factors upon the size and shape of the skeletal spicules of octocorals is as yet completely unknown, but possibly could be determined by repeated examination of the spicules formed at the growing tips of colonies transplanted into habitats with selected environmental characteristics, and comparison with samples taken before they were moved. The resultant information would be invaluable in defining the limits of ecological variation within species and could well provide a new and solid foundation for the identification and classification of the Octocorallia.

Until studies of this kind are undertaken to determine valid means of defining species and their ecological variants, classification of the octocorals will remain subject to changes imposed by the differing taxonomic interpretations employed by various workers, and instability inevitably will prevail.

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