ZOOGEOGRAPHY AND EVOLUTION IN THE OCTOCORALLIAN FAMILY GORGONIIDAE[1]

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ABSTRACT

The predominance of Gorgoniidae and Plexauridae in the shallow-water alcyonarian fauna of the West Indian and warm-water east Pacific regions is noted. The family Gorgoniidae is briefly characterized and its subdivisions down to genus defined. The subfamily designations Gorgoniinae and Lophogorginae are established. The nature of spiculation and external morphology is described and the significance of certain features in establishing an evolutionary sequence is explained. At the present time, two distinct lines of evolution can be detected within the family: one, well established and differentiated, characterized by simple spindle sclerites, centered as a whole in the American tropics but the most generalized species of world-wide warm-water distribution; and a second, less clearly differentiated but closely paralleling the development of the first, characterized by modified spicules, and limited to the Antillean region. The modern distribution is interpreted with the help of palaeogeography, which reveals Tertiary marine seaways through Central America. During the period of interoceanic communication, the homogeneous Atlantic-Pacific gorgonian population probably consisted of spindle-bearing species which had begun to undergo differentiation of branching pattern and were at the "anastomosed fan" level; spicular differentiation toward disk spindles had probably commenced also, since some Atlantic species have disk spindles nearly as well developed as those of typical Pacific Eugorgias. As the Pliocene wore on and interoceanic communication came to an end, the Gulf-Caribbean area apparently suffered changes in conditions that caused all but the hardiest species, or those in areas still reasonably favorable for gorgonian growth, to die out. In the subsequent ages, there has arisen from the small nucleus of undifferentiated species that survived, an entire new lineage which has flourished and now occupies as dominant a position in the shallow Caribbean waters as the relatively unchanged group from whose ancestors it arose still does in the eastern Pacific. It has followed much the same road of morphological development, but the physiological adjustment that the isolated eastern segment of the fauna achieved in the struggle for survival was accompanied by modification of spicule type from which developed the scaphoid sclerites that characterize all members of the lineage. That it is a newer group than the spindle lineage is suggested by the low level of differentiation between species. In the West Indian region the old spindle lineage now occupies a subordinate position and has not continued to develop as it has on the west coast of the Americas, where an extensive array of species has evolved.

Perhaps nowhere else in the world have the gorgonian corals at-

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tained such a prominent place in the coral reef fauna as they have in tropical American waters. Upon the Indo-Pacific reefs, which one thinks of as representing the very pinnacle of coral reef development, they are a minor element, largely replaced by their less elegant, though more ponderous, relatives, the Alcyonacea (Nutting, 1924, page 56). But on almost any reef or rocky bottom from Bermuda to Bahia, sea-fans and whips may be found in countless thousands, often comprising the most spectacular feature of submarine topography down to a depth of ten fathoms or so[2]. Likewise from La Paz to Peru they flourish, although true reefs appear not to be developed in this region (Galtsoff, 1950, page 27).

These vast gorgonian "sea-gardens" of the tropical Americas are made up almost exclusively of species belonging to but two families, the Gorgoniidae and the Plexauridae[3]. Certain peculiarities in the distribution of the gorgoniid genera prompted an investigation aimed at explaining these phenomena, and in the pages that follow I shall set forth the results and conclusions of this search. Before proceeding farther, however, it might be well to summarize the features considered in the classification of the Gorgoniidae, for the benefit of those not acquainted with the group, and to define my concept of the genera under consideration for those who are.

Since the earliest days of binominal systematics, when the Gorgoniidae included (as a genus: Linnaeus, Pallas, Ellis & Solander; as a family: Blainville; as an order: Lamouroux) practically all horny Octocorallia, the family has been restricted more and more until now it includes only those forms in which the calcareous spicules are less than 0.3 mm. in length, sculptured with regularly disposed girdles of complicated tubercles ("warts"), the anthocodiae are relatively unarmed, at most with but a few characteristically shaped flat rods *en chevron* beneath each tentacle, the horny axial cylinder is weakly loculated if at all, and is perforated by a relatively narrow, chambered central chord, and in which the branchlets are usually quite slender, with a thin cortex.

The basic spicule type, the symmetrical spindle with transverse belts of wart-like tubercles (Fig. 1, a), has been modified in various ways, and these modifications are the recognized criteria for the major sub-

[2]A. Agassiz, 1895, pp. 236, 237 (Bermuda); Nutting, 1895, p. 192 (Bahamas); Nutting, 1919, pp. 109-110 (Barbados); Hartt, 1870, p. 209 (Brazil).

[3]The genus *Muricea*, commonly considered the type of another family, actually belongs in the Plexauridae and has little to do with the other "Muriceidae" which are not reef-dwelling forms.

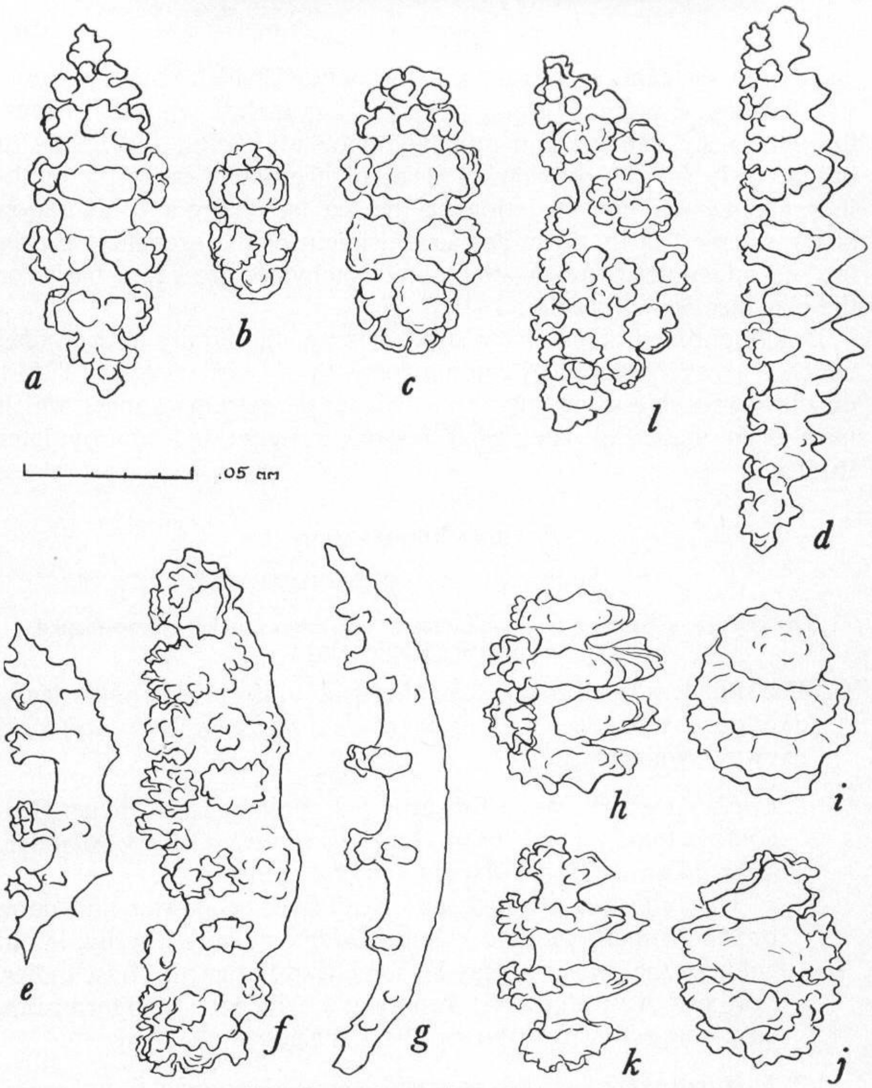


FIGURE 1. Gorgoniid spicule types.

a. Typical spindle of *Pacifigorgia media* (Verrill).
b, c. Short and long capstans of *Pacifigorgia media* (Verrill).
d. Unilaterally spined spindle of *Leptogorgia stheno* (Bayer).
e. Scaphoid of *Gorgonia flabellum* Linnaeus.
f. Scaphoid of *Pterogorgia guadalupensis* Duchassaing & Michelin.
g. Scaphoid of *Antillogorgia acerosa* (Pallas).
h-j. Disk-spindles of *Eugorgia rubens* Verrill. Profile and two oblique views.
k. Disk-spindle of *Leptogorgia viminalis* (Pallas) [=*L. virgulata* (Lamarck)]. Profile view.
l. Bent spindle of *Pacifigorgia media* (Verrill). Compare with true scaphoids, figs. e-g.

All figures drawn to the same scale, x420.

division of the family. The habit of branching, which shows progressive development from simple or sparsely branched whip-like forms, through bushy, pinnate and reticulate-flabellate facies, and finally to broad, leafy fronds, provides a series of characters useful in establishing generic limits. Variations in the size, sculpture and coloration of the spicules, in the form and arrangement of the branches, and in the secondary development of the coenenchyme, provide a basis for the classification of species.

Briefly outlined below is the subdivision of the family Gorgoniidae which is here recognized. A comparison with my earlier paper (1951) on the nomenclature of this group will reveal certain changes which have been made for zoological reasons brought to light by later studies.

Family Gorgoniidae

Subfamily Lophogorgiinae

The spicules are only straight spindles or derivatives, never canoe-shaped scaphoids (Klammern).

A. The spicules are all straight spindles with uniformly, symmetrically developed tubercles, and often also blunt spindles (capstans), likewise symmetrical.

1. *Lophogorgia* H. Milne Edwards & J. Haime, 1857. Type, *Gorgonia palma* Pallas, 1766 = *Gorgonia flammea* Ellis & Solander, 1786 [Cap de Bonne-Espérance], by monotypy.

   The branches are long and whip-like, or shorter and more or less distinctly pinnate, oriented in one plane, or bushy; in old colonies the branches may be somewhat flattened. [East Indies, northern Australia, west America, Caribbean, Mediterranean, east, south and west Africa; 30+ species.]

2. *Pacifigorgia* F. M. Bayer, 1951. Type, *Gorgonia stenobrochis* Valenciennes, 1846 [west coast of Central America], by original designation.

   The branchlets anastomose to form a fan-like network, in one plane. The spicules are capstans and simple spindles; the latter, if curved, never have the tubercles of the convex side reduced or absent (Fig. 1, l). [West coast of Mexico and Central America, including the Galápagos; Trinidad; Brazil; about 15 species.]

3. *Phycogorgia* H. Milne Edwards & J. Haime, 1850. Type, *Gorgonia fucata* Valenciennes, 1846 [west coast of Central and South America], by original designation.

   The branches are flat, foliate fronds with a lamellar axis. The spicules are blunt capstans. [Mazatlán to Chile.]

B. The characteristic spicules are spindles with the transverse girdles of tubercles fused to form disks, more or less eccentrically placed on the long axis of the spicule due to asymmetrical development (Fig. 1, h-j).

1. *Eugorgia* A. E. Verrill, 1868. Type, *Leptogorgia ampla* Verrill, 1864 [Margarita Bay, Lower California], by subsequent designation, Verrill, 1868, p. 386.

   The principal type of sclerite is the disk-spindle (the "double-wheels" of Verrill's descriptions); ordinary spindles with symmetrical sculpture are present in small numbers in some species. The anthocodiae are unarmed. [West coast of the Americas from southern California to Peru; 9 species.]

While this paper was in press, material of a *Eugorgia*-like gorgonian with anastomosing branches was received from Dr. Cadet Hand of the University of California. These specimens may justify the establishment of a new genus at the *Gorgonia-Pacifigorgia* level of development, and certainly suggest a continuing divergence of the disk-spindle offshoot in a direction similar to that taken by the spindle and scaphoid lines.

2. *Leptogorgia* H. Milne Edwards & J. Haime, 1857. Type, *Gorgonia viminalis* Milne Edwards & Haime, 1857 = *G. viminalis* Esper, 1791, ? = *G. viminalis* Pallas, 1766, = *Plexaura viminea* Valenciennes, 1855, = *G. virgulata* Lamarck, 1815 [in dem Hafen bey Charlstown in Süd-Carolina], by subsequent designation, Verrill, 1868, p. 387.

   The shorter spindles show more or less complete fusion of the tubercles of the transverse girdles into disks (Fig. 1, k). Near the branch tips, long spindles with tubercles unilaterally developed as smooth, conical processes (Fig. 1, d) are common; in the inner layer of cortex there are symmetrical spindles. The anthocodiae have a weak crown. [Southeastern states, Gulf of Mexico, Caribbean; 4 species.]

Subfamily GORGONIINAE

In addition to straight spindles there are modified forms, more or less canoe-shaped in profile, with the tubercles of the convex side undeveloped (scaphoids, Klammern or crampons; Fig. 1, e-g); disk-spindles are never present.

A. The coenenchyme may be somewhat flattened but it is not developed as broad expanded flanges with zooids in a groove along the edge, nor as querciform leaves.

1. *Antillogorgia* F. M. Bayer, 1951. Type, *Gorgonia acerosa* Pallas, 1766, by original designation [West Indies]. [= *Pterogorgia* of many authors, but not of Ehrenberg.]

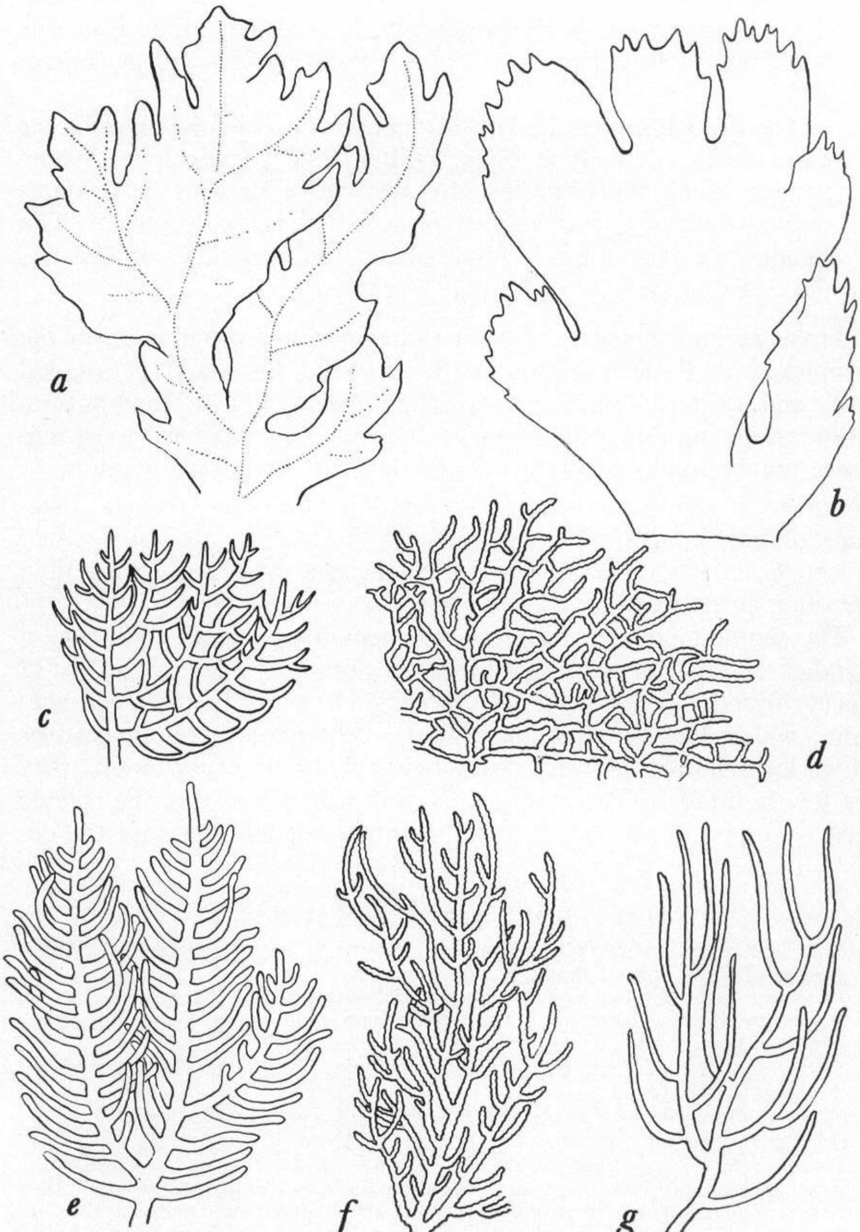
   The branchlets are pinnately disposed and more or less strictly in one plane. The major branches are in one plane or not, colonies often forming large, feathery bushes. The spicules are spindles and slender scaphoids. [Exclusively West Indian; 5 species.]

2. *Gorgonia* Linnaeus, 1758. Type, *Gorgonia flabellum* Linnaeus, 1758 [West Indies], by subsequent designation, Verrill, 1868, p. 386. [= *Rhipidigorgia* Valenciennes, 1855. Type, *G. flabellum* Linnaeus, 1758, by subsequent designation, Verrill, 1868, p. 385. In an earlier paper, I erroneously attributed this type designation to Bielschowsky, suggesting that the name could have been saved by a different choice. Obviously, however, the situation was already out of her hands, and the responsibility rests with Verrill.]

   The branchlets anastomose to form reticulate, fan-like colonies from which free twigs sometimes issue at right angles. The spicules are in the form of symmetrical spindles and stout scaphoids. [Exclusively West Indian; 1 certain, 2 doubtful species.]

B. *Phyllogorgia* H. Milne Edwards & J. Haime, 1850. Type, *Gorgonia dilatata* Esper, 1806 [das Meer des südlichen America], by original designation. [= *Hymenogorgia* Valenciennes.]

   In this genus the horny axis is loosely reticulated but the coenenchyme is greatly expanded, filling in the meshes to form thin, flat fronds suggestive of oak leaves. The spicules are spindles and stout scaphoids. [Brazil; 1 species.]


a
b
c
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e
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g

C. *Pterogorgia* Ehrenberg, 1834. Type, *Gorgonia anceps* Pallas, 1766 [Mare Americanum], by subsequent designation, Milne Edwards & Haime, 1850, p. lxxx. [= *Xiphigorgia* Milne Edwards & Haime, 1857.]

The branching pattern in this genus is lax, openly whip-like or more bushy, depending upon habitat. The coenenchyme is expanded along the branches into two, three or four thin, longitudinal flanges into the edges of which the zooids retract. The spicules are very coarsely tuberculate, stubby spindles and scaphoids. [Exclusively West Indian; 3 species.]

These gorgoniid genera show a rather uniform progression in the complexity and specialization of the colonial form and of skeletal units, and it is most tempting to speculate therefrom as to their natural relationships, although the complete absence of palaeontological evidence reduces such speculations to the level of considered opinion.

The most significant feature of gorgonian colonies, from a systematic standpoint, is their spiculation, for the sclerites are less likely to reflect the effects of certain ecological factors upon the colony than are other structures.

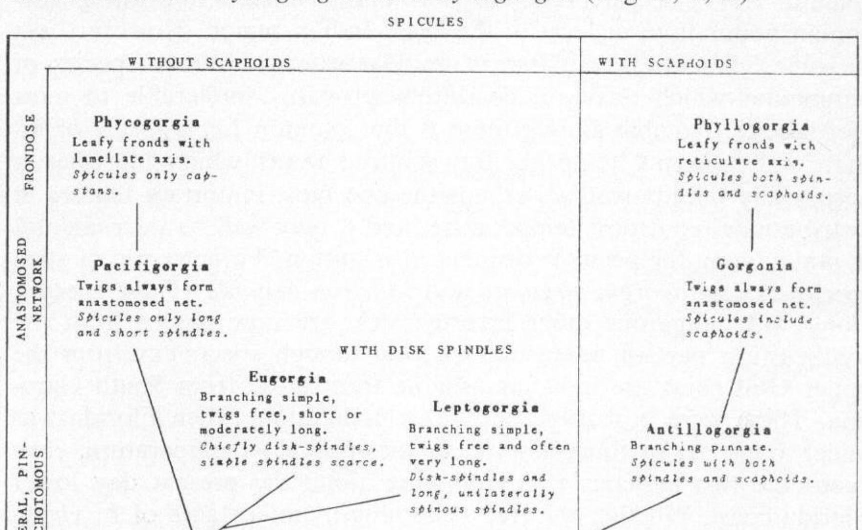
The simple monaxial rod more or less pointed at both ends (*i.e.*, a spindle) and ornamented with tubercles, spines or ridges, is a type of spicule found throughout the Octocorallia (except in the Coenothecalia, which lack spicules altogether). Although there are species which lack spindles in every order and probably in every family, they are few in number. The almost universal presence of this one spicule type is viewed as an indication of a primitive condition, and the de-

FIGURE 2. Branching patterns of gorgoniids.

a. *Frondose* with a weakly anastomosed, reticulate axis. One genus, *Phyllogorgia,* of the scaphoid lineage.
b. *Frondose* with lamellar axis. One genus, *Phycogorgia,* of the spindle lineage.
c. *Reticulate,* derived from the close-pinnate type. One genus, *Gorgonia,* of the scaphoid lineage.
d. *Reticulate,* derived from the open-pinnate type. One genus, *Pacifigorgia,* of the spindle lineage.
e. *Close-pinnate.* All species of *Antillogorgia* and some *Lophogorgia.*
f. *Open-pinnate.* Many species of *Lophogorgia,* some of *Eugorgia.*
g. *Simple lateral* or *whiplike.* Certain species of *Leptogorgia, Lophogorgia* and *Eugorgia* produce this type of colony. Its basic ramification may follow either a lateral (*i.e.,* very open pinnate) or dichotomous pattern; the end twigs may be greatly elongated. The branching of *Pterogorgia* (=*Xiphigorgia*) also follows this simple plan.

velopment of various modifications as representing evolutionary progression. These modifications, in the Gorgoniidae, are essentially four: (1) shortening of the axis with the number of tubercle whorls reduced to two, with terminal clusters (Fig. 1, b, c); (2) unilateral development of the tubercles of one side to form conical or spine-like processes (Fig. 1, d); (3) terminal bending of the axis, in one plane, to form a spicule canoe-shaped in profile with the tubercles of the convex side reduced or absent (Fig. 1, e-g); (4) the fusion of the tubercles to form disks (Fig. 1, h-k).

Superimposed on the spicular features is the gross morphology of the colony as a whole. This may reflect the effects of the external environment, especially of currents and wave action, although there are certain basic characteristics which apparently are never modified by the environment. Thus, a *Gorgonia* or a *Pacifigorgia* will always form a reticulate colony by anastomosis of the branches, though external factors may largely determine the size of the meshes, the diameter of the twigs, the growth of free lateral twigs at right angles to the plane of branching, or the production of secondary fans from the main flabellum. In general, the colonial form increases in complexity from a simple whip, through openly branched (Fig. 2, e-g) to reticulate forms (Fig. 2, c, d), ultimately reaching the frondose development characteristic of *Phyllogorgia* and *Phycogorgia* (Fig. 2, a, b).



In the representation given above, the genera are arranged in order of complexity of growth form, from the simple, open pattern of *Lophogorgia* to the leafy fronds of *Phycogorgia* and *Phyllogorgia*. The right half of the diagram shows the scaphoid-bearing genera of the Atlantic, the left half the spindle genera of predominantly Pacific distribution. Perhaps the divisions appear to be founded on relatively minor variations, still it is even more obvious that the only alternative, to treat all of these genera as mere variations within an all-inclusive *Gorgonia,* would be a century's stride backward from reality.

Virtually nothing is known about the environmental factors which govern the distribution of Gorgonacea, although something can be inferred from a comparison with the stony corals. A suitable solid support is required (only a few deep-sea species can adapt themselves to life upon both rocky and muddy bottoms) and if it is not present, planulae presumably will not develop (Cary, 1914, page 84). The chemical composition of the seawater is unquestionably important in restricting gorgonian distribution, and the variations in salinity, oxygen content, and other critical factors, which gorgoniids can tolerate are probably about the same as for hermatypic scleractinians, the distribution of which roughly corresponds to that of the Gorgoniidae in general. Heavy sedimentation is not conducive to a flourishing gorgonian population, at least in the West Indian region. However, just as some Scleractinia can live in muddy water, there are species of gorgonians which thrive in conditions probably intolerable to most reef species. Notable among these is the common *Leptogorgia* of inshore waters from Chesapeake Bay south to Texas, which flourishes in perpetually muddy water. Perhaps the one most important feature in distributional control is temperature, and it may well be instrumental in maintaining the peculiar disjunct distribution characteristic of such species as *Leptogorgia virgulata* and *Muricea pendula*. These species, along with numerous other invertebrates, are now absent from the southeastern part of peninsular Florida though specimens from the upper Gulf coast are indistinguishable from those from South Carolina. These were probably continuous populations when Florida was under water, even though some factor, probably temperature, now keeps the two moieties from rejoining along the present day lower Florida coast. Whether the free-swimming planula-stages of *L. virgulata* and *M. pendula* are of sufficiently long duration for offspring of the Gulf populations to become established on the Carolina coast, and thus contribute genetically to the populations of that region, is unknown.

The Recent distribution of gorgoniids is rather narrowly limited. With the exception of *Lophogorgia,* which occurs also on both coasts of Africa, in the Mediterranean, and in the East Indies as well as in the Americas, it is exclusively a tropical American family. The scaphoid-bearing group of species is restricted to the West Indian region, while the group lacking scaphoids is principally west American. As nearly as I have been able to determine, there are about 27 species of *Lophogorgia,* 22 of which occur on the Pacific coast. Since the African and East Indian species do not occur in American waters, they will not be considered further. This genus alone of all gorgoniids now enjoys a wide distribution, but even it is nowhere rich in species except on the west coast of Central America. The known gorgoniid genera displaying any degree of specialization are exclusively tropical American, both Atlantic and Pacific. One possible conclusion to be drawn from this observation is that a relatively primitive *Lophogorgia* was once widespread, but has continued to flourish and differentiate only in those regions particularly suited to its development, the Americas. Of course, it is also possible that all of the genera were formerly of wider occurrence, but have lately died out except in American waters. Were this the case, however, we should expect to find traces of the other genera along with *Lophogorgia* in widely separated localities. Perhaps we shall, but since the days of great explorations have come to a close without their being found, their discovery now seems improbable.

There appear to be upwards of 60 recognizable species of Gorgoniidae at present living on the two coasts of the Americas and in the adjacent islands. Most striking is the fact that all of the species characterized by the peculiar canoe-shaped spicules called scaphoids are confined to the Caribbean area. Similarly, those species with strongly modified disk-spindles and few symmetrical spindles are found only on the Pacific coast, while those with the disk-spindles moderately developed and abundant unilaterally spinous spindles are entirely Atlantic. The genus *Pacifigorgia,* especially well developed in the Gulf of California and Panama Bay, has been found only in the eastern Pacific, with a single exception—which occurs in Trinidad.

A preliminary tally shows that on the Pacific coast there are 22 species of *Lophogorgia,* 14 of *Pacifigorgia,* 9 of *Eugorgia,* and 1 of *Phycogorgia,* whereas in the Atlantic *Lophogorgia* is represented by only 5 species and *Pacifigorgia,* by a single relict species. The strictly

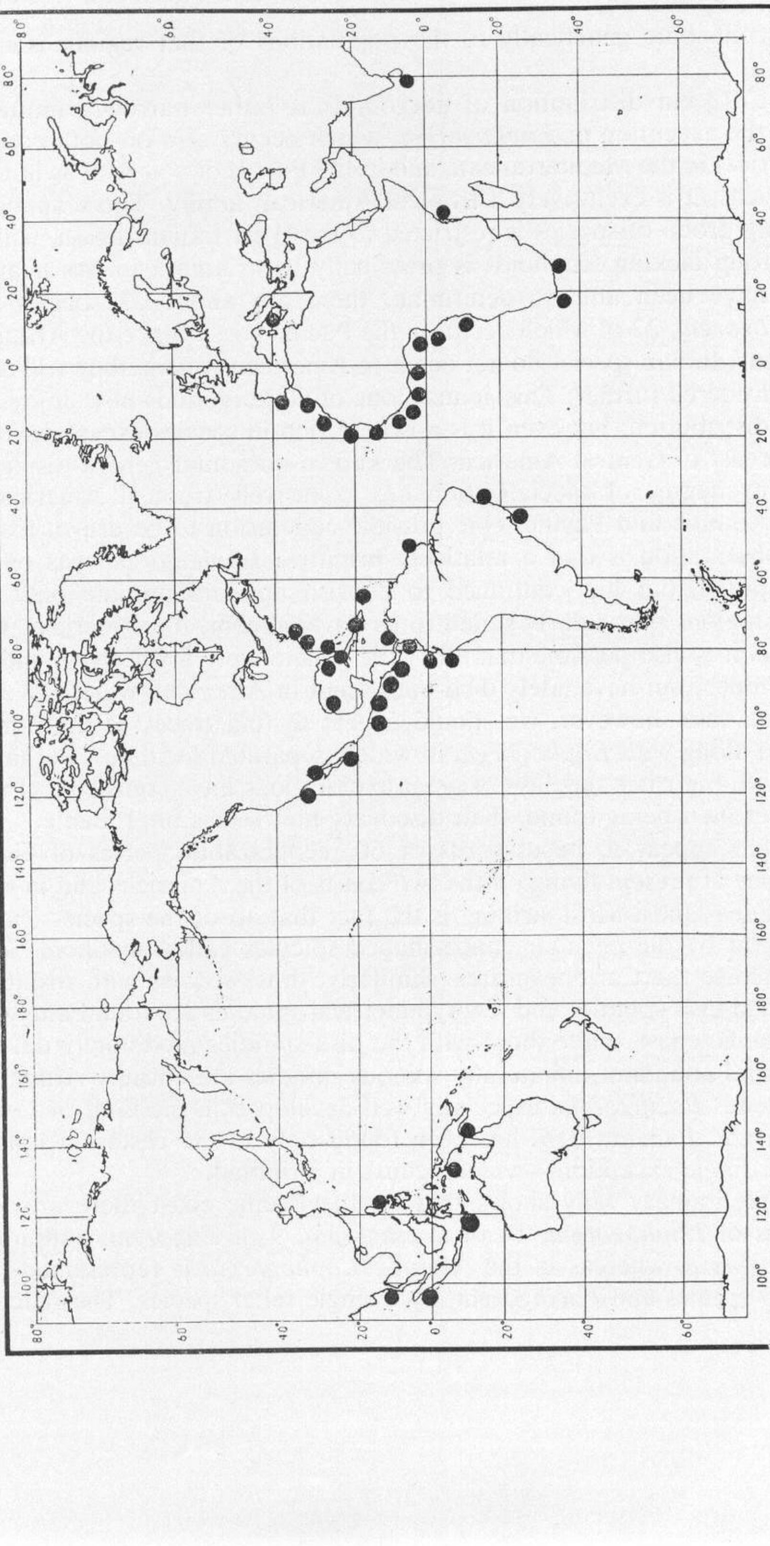


FIGURE 3. Geographical distribution of the gorgoniid genus *Lophogorgia*.

Atlantic genera *Antillogorgia, Gorgonia, Phyllogorgia, Pterogorgia* and *Leptogorgia* are represented by 4, 1, 1, 3 and 4 species, respectively.

Even though there is no published palaeontological evidence to assist in the interpretation of these observations, the palaeogeography of the Caribbean region is significant. Schuchert (1929) points out that there was open communication between Atlantic and Pacific (and thus the faunas were potentially continuous) in two places at different times. The earlier of these was the Panama-Costa Rica marine portal, which opened late in the Eocene and finally closed at the end of the Miocene, a period perhaps in excess of 30 million years (Knopf, 1949). Evidence is conflicting, however, and it is thought possible that the Panama-Costa Rica area was emergent during most of the Oligocene, so that the oceanic portal may only have been open during the late Eocene and again in Miocene time. Perhaps more significant to the present study is the later, more northerly Tehuantepec portal. Of it Schuchert says, "However, another but short-lived marine portal came into existence, this time to the north of Central America across the Isthmus of Tehuantepec. It was certainly open during early Pliocene time and probably also during the late Miocene, permitting the marine faunas of the Gulf of Mexico to spread west and thence north into southern California." (Page 341.)

A recent communication by Durham, Arellano and Peck (1952), read before the annual meetings of the Geological Society of America, denies the existence of any Tehuantepec seaway in the Cenozoic. Dr. Wendell P. Woodring tells me that he has never accepted the idea of a portal at the Isthmus of Tehuantepec, but that interoceanic communication across the Panama-Costa Rica region during the Tertiary is a certainty. For the purposes of marine faunal interchange, and probably also of ecological alteration in the Caribbean and the Gulf of Mexico, the portal in lower Central America is entirely adequate.

Let us consider what is known of the modern distribution of gorgoniid genera in the light of the palaeogeographical picture. Since the species at the lowest level of development, which we refer to by the generic name *Lophogorgia,* are still generically undifferentiated on the two sides of Central America, it is inescapable that they represent a once continuous population for there is no possible way they could have spread from the one ocean to the other after the final, complete emergence of Central America. The same holds true for the genus *Pacifigorgia,* which represents a more advanced grade of specialization, but in this case there is only one relict species in the Atlantic though fourteen still persist in the Pacific. From this it is possible to conclude that a newly evolved, more specialized, less tolerant group was all but wiped out in the Atlantic by changed conditions resulting from closure of the portals. If the more highly developed, foliate *Phycogorgia* had come into existence while there was still free interoceanic communication, the Caribbean population did not survive the conditions accompanying isolation from the Pacific segment.

The spatial and temporal distribution of some scleractinian genera serves to substantiate the observations outlined above. The genus *Acropora,* which has numerous Pacific species, is represented in the Caribbean by only three; and *Pocillopora,* likewise a prominent reef form of the Indo-Pacific area, including the warm-water East Pacific, is now entirely absent from the Antillean region. Both genera are better represented in the Tertiary deposits of the Antilles and southeastern United States, showing that one genus has suffered regression to some extent in this area, while the other has died out entirely. About the Acroporas Prof. John W. Wells (personal communication) has the following to say: "It would appear that there was a wider diversity of species in the Tertiary in the West Indies, and that some species-groups, still flourishing in the Pacific, have died out." Other genera showing similar distributional patterns could be mentioned.

Leptogorgia and *Eugorgia* are closely related genera both of which have modified spicules in which the transverse whorls of tubercles are solid disks instead (Fig. 1, h-k); however, since *Leptogorgia* has highly characteristic, unilaterally spined spindles (Fig. 1, d) which *Eugorgia* lacks, it seems likely that it represents a new offshoot of the *Eugorgia* stock, each genus now having diverged from the ancestral type. The scaphoid-bearing genera, *i.e.*, the entire subfamily Gorgoniinae, are absolutely restricted to the waters of the western Atlantic. Extensive collections from the Gulf of California and the Bay of Panama have failed to yield a single specimen which has scaphoid spicules. Neither has any scaphoid species been recorded in the literature from the Pacific coast, and the few references from the Australian region appear to be based upon a misinterpretation of spindles as scaphoids. The late Professor G. Stiasny (1951, pages 32, 49, 50) recently recorded *Pterogorgia peruana* Stiasny and *Pterogorgia* sp. (now *Antillogorgia*) from the coast of Peru, but it should be observed that these records, like those of *Phycogorgia fucata* (Valenciennes) and *Gorgonia stenobrochis* Valenciennes (now *Pacifigorgia steno-*

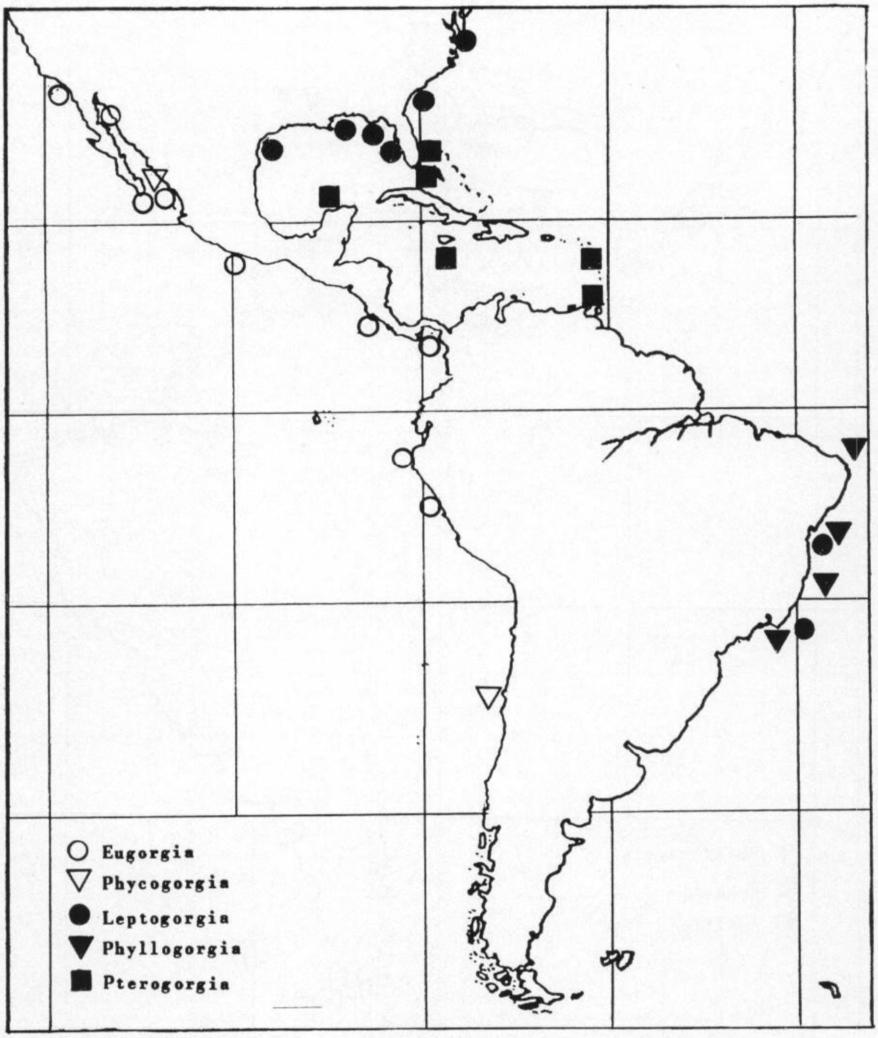


FIGURE 4. Geographical distribution of the gorgoniid genera *Eugorgia, Phycogorgia, Leptogorgia, Phyllogorgia,* and *Pterogorgia.*

brochis) from New Zealand, which he also perpetuates, are based upon very old material gathered in times when the mixing of labels was a commonplace. It is most improbable that these specimens grew where their labels indicated, and their appearance in the literature at this late date is not considered a serious threat to any suggestions advanced

FIGURE 5. Geographical distribution of the gorgoniid genera *Pacifigorgia, Gorgonia* and *Antillogorgia.*

in the present paper.

It is a most inviting conclusion that the scaphoid genera evolved from remnants of the older spindle group after the final closure of the Tehuantepec Portal. It seems almost beyond question that circulation of water in the Gulf of Mexico and Caribbean Sea was changed, perhaps radically, by the closure of the portals, and other features of the physical environment probably changed with it. Such changes may well have been sufficiently far-reaching to cause the regression of even the stable genera and to stimulate the production of new evolutionary trends through the selection of mutations better adapted for survival in the new surroundings. It is interesting to note that the grades of development within the (presumably younger) scaphoid lineage are almost exactly parallel with those of the older, simple spindle lineage, and that the species are not only fewer in number but less clearly defined. At the simplest level of colonial form (*Antillogorgia*) there are but four, perhaps five, good species (though a number of others have been described). Of the more advanced, reticulate form, only one species is at present recognized, though there appear to be incipient species which critical study may enable us to distinguish accurately. It is impossible to assign systematic significance to the various growth forms of *Phyllogorgia,* and only a single species can be recognized. *Pterogorgia* (the *Xiphigorgia* of most authors) appears to be an early divergent offshoot of the scaphoid line. It contains three closely related species that are restricted to the Antillean region.

An interesting parallel can be drawn between this apparent evolutionary series in the Gorgoniidae and that of some fossil scleractinians as described by Lang (1938). This author held that a number of well-established genera of corals which cut across geological time also spanned more than one evolutionary line. In short, these genera represented the members of different lineages at similar levels of evolutionary development. Thus, a given species in genus "A" could be more closely related to a contemporary species in another genus, "B," than to a third placed in genus "A" but which actually belongs to a different lineage in a higher stratum. Lang proposed to retain these polyphyletic "genera" as a matter of convenience, under the name "genomorph," written in braces between the true generic and specific names. Since the gorgoniid scaphoid lineage is apparently derived from, and younger than, the spindle lineage, and is now isolated from it by a geographical barrier which may be taken to represent time, the evolutionary trends within this modern group seem to approximate closely the situation described in the fossil corals. There was a time in the history of gorgoniid nomenclature when externally similar but unrelated species were placed in the same genus, a situation which thus takes on the character of genomorphs. For example, Valenciennes (1855) established the genus *Rhipidigorgia* for a number of net-like species (not all gorgoniids), and for a time this name was used by Verrill for both the Atlantic and Pacific reticulate Gorgoniidae which have been shown to be generically distinct and evolving separately. If we used the genomorph system of retaining the old genera, we should have to write *Gorgonia* [*Rhipidigorgia*] *flabellum* Linnaeus and *Pacifigorgia* [*Rhipidigorgia*] *adamsii* (Verrill). It would obviously be pointless, indeed unthinkable, to use any sort of genomorphic nomenclature to preserve antiquated generic concepts which modern methods of investigation have shown to be groundless. Such a system may be useful to palaeontologists, but its application in systematic zoology is questionable.

In review, we have seen that the family Gorgoniidae comprises two virtually parallel lines of development, each clearly showing three major evolutionary grades and some minor divergences. One of these lines, which we have called the "scaphoid lineage," is restricted to the tropical western Atlantic, has relatively few and poorly differentiated species, and is thought to represent a newly developing group. The other line, the so-called "spindle lineage," is found in warm seas around the world, has numerous (especially on the Pacific coast of the Americas) species which are more clearly defined, and is thought to represent an older stock from which the scaphoid lineage has developed. The presence of the most generalized genus of Lophogorgiinae on both shores of the Americas can be explained most satisfactorily in terms of an Atlantic-Pacific oceanic portal, which geologists consider certain. The recession of all advanced Lophogorgine types in the Caribbean to a single relict species, and the establishment of an entirely new line of evolution are attributable to the influence of ecological changes brought on by closure of the portal.

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In the present day, when so much of real value is being written about such theoretical aspects of biology as evolution, one hesitates to add to the mass of worthy literature any observations not solidly based on confirmable fact. So much of zoogeography depends upon the vagaries of collectors, and so much of palaeogeography depends upon the interpretation of fossil evidence, that it may seem foolhardy to reconstruct with their help the possible evolution of a group which itself lacks a good fossil record. Should these suggestions prove invalid, as well they may, still their refutation may cause someone to learn something new and all will not have been lost. For the encouragement, helpful criticisms and patience of the following friends and colleagues I am most grateful: Fenner A. Chace, Lawrence B. Isham, J. Brookes Knight, Alfred R. Loeblich, Harding Owre, Gilbert L. Voss, and Donnell B. Young. I am also greatly indebted to Prof. John W. Wells of Cornell, and W. P. Woodring of the U. S. Geological Survey, for up-to-date palaeontological and geological information regarding the West Indian region.

REFERENCES

Agassiz, Alexander
1895. A visit to the Bermudas in March, 1894. Bull. Mus. comp. Zool. Harv., *26* (2): 205-281, pls. 1-30.

Bayer, Frederick M.
1951. A revision of the nomenclature of the Gorgoniidae (Coelenterata: Octocorallia), with an illustrated key to the genera. J. Wash. Acad. Sci., *41* (3): 91-102, 14 figs.

Cary, Lewis Robinson
1914. Observations upon the growth-rate and oecology of gorgonians. Pap. Tortugas Lab., *5* (182): 79-90, pls. 1-2.

Durham, John Wyatt, A. R. V. Arellano and Joseph H. Peck, Jr.
1952. No Cenozoic Tehuantepec seaways (abstract). Bull. geol. Soc. Amer., *63* (12, pt. 2): 1245. (Also published in the Program of the 1952 annual meetings, Geological Society of America, page 33.)

Ehrenberg, Christian Gottfried
1834. Beiträge zur physiologischen Kenntniss der Corallenthiere im allgemeinen, und besonders des rothen Meeres, nebst einem Versuche zur physiologischen Systematik derselben. Abhandlungen der Königlichen (preussischen) Akademie der Wissenschaften zu Berlin. Aus dem Jahre 1832. Erster Theil, pp. 225-380.

Ellis, John, and Daniel Solander
1786. The natural history of many curious and uncommon zoophytes, collected from various parts of the globe by the late John Ellis, Esq. F. R. S. Pp. xii+208, 63 pls. London. M. DCC. LXXXVI.

Esper, Eugenius Johann Christoph
1788-1830. Die Pflanzenthiere in Abbildungen nach der Natur mit Farben erleuchtet nebst Beschreibungen. In der Raspeschen Buchhandlung, Nürnberg. Vols. 1-3; Fortsetzung, vols. 1-2; 428 col. pls.
1791. Theil 2, pp. 1-96.
1806. Fortsetzung, Theil 2, pp. 25-48.

Galtsoff, Paul Simon
1950. The pearl oyster resources of Panama. Spec. sci. Rep. U.S. Fish Wildl. Serv. 28: 1-53, 28 figs.

Hartt, Charles Frederick
1870. Geology and physical geography of Brazil. Scientific results of a journey in Brazil by Louis Agassiz and his travelling companions. Fields, Osgood, & Co., Boston, xxiii+620 pp.

Knopf, Adolph
1949. Time in earth history. Genetics, paleontology, and evolution, part 1: geological time. Princeton University Press, pp. 1-9.

LAMARCK, JEAN BAPTISTE PIERRE ANTOINE DE MONET DE
1815. Suite des polypiers corticifères. Mem. Mus. Hist. nat., Paris, *2:* 157-164.

LANG, WILLIAM DICKSON
1938. Some further considerations on trends in corals. Proc. Geol. Ass. Lond., *49:* 148-159, figs. 25-28, pl. 7.

LINNAEUS, CAROLUS
1758. Systema naturae per regna tria naturae . . . Editio decima, reformata. Tomus 1. Pp. 824. Holmiae.

MILNE EDWARDS, HENRI, AND JULES HAIME
1850. A monograph of the British fossil corals. Part 1, Introduction; corals from the Tertiary and Cretaceous formations. Palaeontographical Society, London. Pp. i-lxxxv+1-71, pls. 1-11.
1857. Histoire naturelle des coralliaires ou polypes proprement dits. Volume 1. A la Librairie Encyclopédique de Roret, Paris. Pp. i-xxxjv+1-326, pls. A1-B2 (8 in all).

NUTTING, CHARLES CLEVELAND
1895. Narrative and preliminary report of the Bahama Expedition. Bull. Lab. nat. Hist. State Univ. Iowa, *3* (1&2): i-vi+(2)+1-252, 19 unnumbered pls.
1919. Barbados-Antigua Expedition. Narrative and preliminary report of a zoological expedition from the University of Iowa to the Lesser Antilles under the auspices of the Graduate College. Univ. Iowa Studies in nat. Hist., *8* (3): 1-274, 50 pls.
1924. Fiji-New Zealand Expedition. Narrative and preliminary report of a scientific expedition from the University of Iowa to the South Seas. Univ. Iowa Studies in nat. Hist., *10* (5): 1-369, 56 pls.

PALLAS, PETER SIMON
1766. Elenchus zoophytorum sistens generum adumbrationes generaliores et specierum cognitarum succinctas descriptiones cum selectis auctorum synonymis. Apud Franciscum Varrentrapp, Hagae Comitum. Pp. i-xvj+28+1-451.

SCHUCHERT, CHARLES
1929. Geological history of the Antillean region. Bull. geol. Soc. Amer., *40:* 337-360, 9 figs.

STIASNY, GUSTAV
1951. Alcyonides et gorgonides des collections du Muséum National d'Histoire Naturelle (II). Mem. Mus. Hist. nat., Paris, Nouvelle Série (A), *3* (1): 1-80, pls. 1-22.

VALENCIENNES, ACHILLE
1846. *In:* Abel Dupetit-Thouars. Voyage autour du monde sur la frégate la Vénus, pendant les années 1836-1839. Atlas de zoologie; zoophytes, pls. 1-15.
1855. Extrait d'une monographie de la famille des Gorgonidées de la classe des Polypes. Comptes Rendus Acad. Sci. Paris, *41:* 7-15.

VERRILL, ADDISON EMERY
1864. List of the polyps and corals sent by the Museum of Comparative Zoölogy to other institutions in exchange, with annotations. Bull. Mus. comp. Zool. Harv., *1* (3): 29-60.
1868. Critical remarks on halcyonoid polyps in the Museum of Yale College, with descriptions of new genera. Amer. J. Sci., *45:* 411-415.
1868-1871. Review of the corals and polyps of the west coast of America. Trans. Conn. Acad. Sci., *1:* 377-567, pls. 5-10.