Colonial Organization in Octocorals

Frederick M. Bayer   University of Miami

ABSTRACT

This summary reviews the range of complexity of form resulting from vegetative reproduction of zooids in the anthozoan subclass Octocorallia (= Alcyonaria). Three sharply delimited octocoral groups are recognized: the order Coenothecalia (with only one surviving species), which have no spicules but produce a massive, madrepore-like skeleton; the order Pennatulacea, in which polymorphic colonies with hierarchical dominance are the rule; and all others (orders Stolonifera, Telestacea, Alcyonacea, and Gorgonacea), in which all degrees of colonial form and of zooidal integration are found, from simple, loosely united groups of monomorphic zooids arising from encrusting stolons (*Clavularia*), to highly integrated, dimorphic colonies whose component zooids share functions in such a way as to preclude independent existence.

It is considered that colonial integration is expressed both in the division of labor (e.g., feeding and digestion, water transport and circulation, sexual reproduction) between dimorphic types of zooids, and in the coordinated colonial functions such as anchoring and support, regularity of branching, and response to epizoites and commensals, which are shared among many or all of the zooids in a colony.

Although paleontological evidence is scanty, present interpretation of known fossils suggests that complex colonial forms similar to modern pennatulaceans with a high degree of colonial integration were already flourishing in Precambrian times. Several of the Recent groups are clearly recognizable in Tertiary deposits in various parts

Author's address: Rosenstiel School of Marine and Atmospheric Sciences, University of Miami, Miami, Florida 33149.

of the world. It seems likely that Octocorallia with diverse degrees of complexity and integration have been in existence over a long span of geological time.

INTRODUCTION

The octocorals are typically anthozoan in the structure of their zooids, which have a tubular pharynx (sometimes also called "esophagus" or "stomodaeum") extending from the mouth into the gastrovascular cavity, radial septa (called "mesenteries" by some authors) extending from body wall to pharynx and partitioning the gastrovascular cavity, and tentacles at the upper end of the column, positioned between the septa and surrounding the mouth. Among the anthozoans they are unique in having no more than eight septa and eight pinnately branched tentacles, one for each of the chambers formed by the septa. Most of them produce a calcareous skeleton, totally lacking in a few cases, mostly in the form of calcareous spicules (occasionally inseparably interlocked or solidly fused), rarely massive (Coenothecalia only). A thin proteinous cuticle is produced in many, if not all, stoloniferans and telestaceans, and a proteinous axial skeleton is found in all holaxonian Gorgonacea and in most Pennatulacea. Octocorals have a simple life history without any complex larval stages or alternation of generations, and all produce "colonies" vegetatively by budding from the sexually produced "founder" zooid (Fig. 1).

Although divided into six orders, the subclass Octocorallia shows only two clear lines of subdivision. One of these separates off the Coenothecalia, which produce a
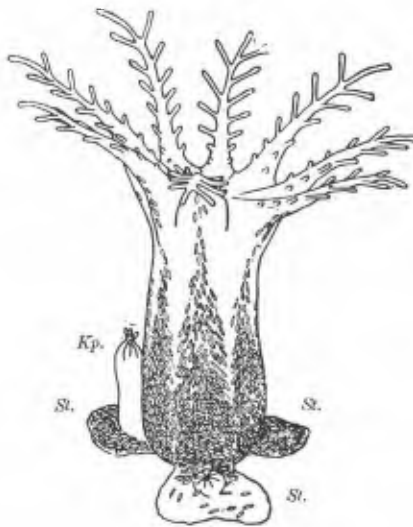

Figure 1

Young colony of *Anthoplexaura dimorpha* Kükenthal, with founder zooid and two vegetatively produced daughter zooids. (From Kinoshita, 1910.)

massive skeleton similar to that of scleractinians, not composed of fused spicules. The other line separates off the Pennatulacea, whose colonies are always dimorphic, asexually produced in a different way from that occurring in other groups, and adapted for life on a soft (sandy or muddy) substrate. The orders Stolonifera, Telestacea, and Gorgonacea (the latter with two suborders, Scleraxonia and Holaxonia) have highly characteristic colonial architecture in the "typical" species, but are linked by intergrading forms that make hard-and-fast ordinal and subordinal subdivision very difficult indeed.

In modern seas, the octocorals are a group of moderate diversity (on the order of 2000 species) and wide distribution. Lacking any protection against desiccation, they extend from roughly the level of mean low water down to abyssal depths (deepest recorded occurrence is an unidentified *Umbellula* at 6620 m; Madsen, 1956). Few species have any tolerance for reduced salinity, so the group is poorly represented in estuarine habitats, generally absent. Geographically, they occur from Arctic to Antarctic and around the world. They may form a conspicuous part of the marine environment as they do on reefs in the tropical Atlantic (order Gorgonacea) and Indo-west Pacific (order Alcyonacea), where in some localities they dominate the sessile community. The fossil record for octocorals is poor because few of them have skeletal structures suitable for preservation, but a number of finds (D'Achiardi, 1868; Bayer, 1955; Duncan, 1880; Hickson, 1938; Kugler, 1971) suggest that by the Tertiary the major groups as we know them were present and probably as well represented as they are now. Moreover, some problematical fossils from the Precambrian in Australia are strongly suggestive of pennatulaceans, and if they actually represent that group, then the most complex of all octocorals already existed over 500 million years ago (Glaessner, 1959, 1961).

Atlantic coral reefs are built for the most part by a few species of hermatypic scleractinians, but may support a community of perhaps 60–70 gorgonian species, some of which occur in vast numbers. By contrast, the soft corals are the important octocorals of Indo-Pacific reefs, where they compete with a scleractinian fauna of 200–300 species and do not form a conspicuous part of the reef community. With the possible exception of *Heliopora* (the blue coral), a few species of Alcyonacea (soft corals), and *Tubipora* (organ-pipe coral), they are not significant reef formers, although most of them contribute to the sediment through their calcareous spicules.

As in the scleractinian corals, the octocorals have developed an association with the unicellular algae known as zooxanthellae. This symbiotic association varies in its intimacy from cases in which the coelenterate apparently cannot exist without zooxanthellae (Gohar, 1940, 1948), having lost the ability to feed, to those in which feeding and digestion are still possible and the host can live without its algae (but probably do not do so in nature). Association with zooxanthellae is a preponderantly tropical phenomenon and obviously is confined to shallow water (although not exclusively to reefs). It has elsewhere been speculated that it was the development of the symbiotic relationship with zooxanthellae which enabled zoantharian corals to reach a sufficient size to produce reefs. Among the octocorals, however, some of the largest forms (e.g., *Paragorgia arborea, Primnoa reseda*) are not associated with zooxanthellae or with the reef habitat. It may be significant that one of these (*Paragorgia*) has dimorphic zooids that form a water-transport system, and that most of the tropical soft corals that reach large size have both zooxanthellae and a special water-transport system formed by siphonozooids. It should be noted, how-

Figure 2

Part of a colony of *Cornularia sagamiensis* Utinomi with two fully expanded polyps. (From Utinomi, 1955.)

ever, that large size is not always associated with dimorphism. In any case, symbiosis with zooxanthellae seems to have made reef formation possible by enhancing the ability of zoantharian corals to deposit $CaCO_3$, but the octocorals mostly have no potential in this direction, owing to the spicular nature of their skeletons. There is no evidence that zooxanthellae play any role in the calcification of spicules.

LEVELS OF COLONIAL ORGANIZATION AND INTEGRATION

Although colonial ontogeny is for the most part unknown and the stages in colonial complexity are inferred from the morphological evidence provided by the fully developed colonies, the increasing degrees of complexity and regularity show more and more inter-dependence of individual polyps, functional specialization, and more highly developed mechanisms controlling asexual reproduction, hence increasing degrees of colonial integration.

Levels of colonial organization range from quite simple to extremely complex. In the simplest forms, zooids are of only one kind and are not united laterally by thick layers of mesogloea. They reproduce asexually from stolonic outgrowths from the base by which they are attached to the substrate. Typical of this level are the members of

Figure 3

Clavularia hamra Gohar. A terminal part of the stolon, ribbon-like and showing three zooids of different ages. A bud is seen near the end. (From Gohar, 1948.)

the family Cornulariidae (Fig. 2) and some species of the family Clavulariidae (Fig. 3) in the order Stolonifera. Also included are some species now assigned to the order Telestacea, for example, a few species in the genus *Telestula* (Fig. 4). At this level of organization, the zooids are mostly tall and slender, cylindrical, or somewhat clavate. The fully developed individuals in a colony are of nearly uniform height, suggesting that the height of zooids is limited by a physiological or structural feature and may be genetically controlled.

Within the Stolonifera there also are species whose colonies are formed as above but with stolonic outgrowths proceeding laterally from the body wall of the zooids in addition to basally, so that new zooids arise at various levels above the substrate. When the zooids have reached a given height limit they produce lateral stolons, from which new zooids arise. The daughter individuals are physiologically interconnected via the solenia (entodermal canals) of both lateral and basal stolons, but the gastric cavities of adjacent zooids are not directly joined. This type of colonial structure is seen in some species of *Clavularia*, such as the type species of the genus, *C. viridis* Quoy and Gaimard (Fig. 5). Organizationally not very different from this condition is the colonial structure found in *Tubipora*, also allocated to the Stolonifera. Here the stolons are flat, expanded platforms extending between the zooids, containing a solenial network from which new polyps arise as the spacing between older zooids increases with upward growth. The platforms occur at rather regular intervals throughout the colony, and the
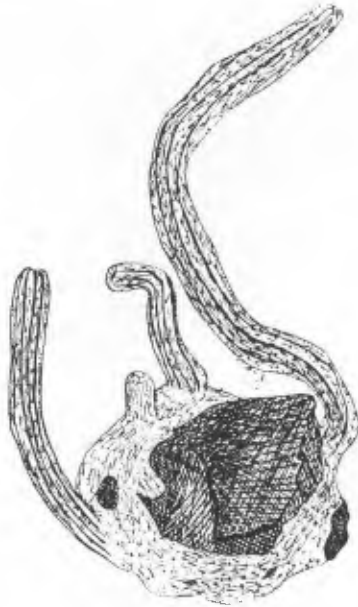
Figure 4

Telestula septentrionalis Madsen. Small colony without lateral daughter zooids. (From Madsen, 1944.)

lower ends of the elongated gastric cavities are sealed off by a succession of funnel-shaped tabulae as growth proceeds upward (Fig. 6).

The various species in the nominal order Telestacea have a range of organization comparable with that found in the Stolonifera just discussed. They have tall zooids, for the most part much taller than those of the Stolonifera, and they produce narrow, often anastomosing stolons adherent to the substrate, from which new zooids arise. In some, but not all, the lower part of the gastric cavity becomes partially filled in with mesogloea containing spicules and penetrated by entodermal canals communicating directly with the upper, functional part of the coelenteron. Tabulae are not formed as in *Tubipora*. The simplest telestaceans differ from the simple stoloniferans only in the infilling of the gastric cavity by spicule-containing mesogloea and in the form of the spicules. The more complex forms differ in the production of daughter zooids directly from the wall of the parent. No lateral stolons are produced as in *Clavularia* and *Tubipora*, but a conspicuous network of solenia is developed in the body walls of the zooids, and it is from this system that new zooids arise vegetatively. Two patterns of ramification (i.e., of budding) occur in this order: monopodial, in which tall axial zooids produce lateral daughters in a more or less regular pinnate arrangement (Fig. 7), sometimes to the third or fourth order of branching; and sympodial, in which each zooid produces one or two daughters of similar size from the distal part of the zooid wall just below the anthocodia, thus forming zigzag stems that dichotomize here and there to produce small, bushy colonies that have no dominant axial zooid (Fig. 8).

Figure 5
Clavularia viridis Q. and G. (From Thomson and Dean, 1931.)

The next level of colonial integration is the development of extensive coenenchyme, which unites adjacent zooids. In octocorals, coenenchyme is a common colonial mesogloea containing calcareous spicules, in which the gastrovascular cavities of the zooids are embedded. No boundary separates the coenenchyme of one zooid from that of its neighbors, and the gastrovascular cavities of adjacent zooids may lie very close together. Only the short distal part of each zooid, bearing the tentacles, remains independent of its neighbors. The coenenchyme is permeated by an anastomosing solenial system which serves to interconnect all the zooids of the colony. New zooids arise between the old individuals, developing from the superficial solenia, and become deeply embedded as the colony enlarges. Production of new zooids continues throughout the life of the colony, which thus contains zooids of various lengths. All members of the order Alcyonacea conform to this general plan, although the colonial form varies from massive, with more or less distinct lobes and plications, to arborescent, but even in the latter case (which may simulate gorgonaceans) the trunk and branches consist of bundles of very elongated zooids whose anthocodiae emerge on the branchlets at various levels in the colony.

Dimorphism of zooids appears for the first time in the order Alcyonacea. In all the groups mentioned heretofore, all zooids are exactly alike. Even the primary zooid arising from a fertilized egg is identical with the vegetative daughters. In the Alcyonacea, however, some of the zooids are anatomically quite different from the primary type, which is termed the "autozooid." These different individuals have an enormously developed
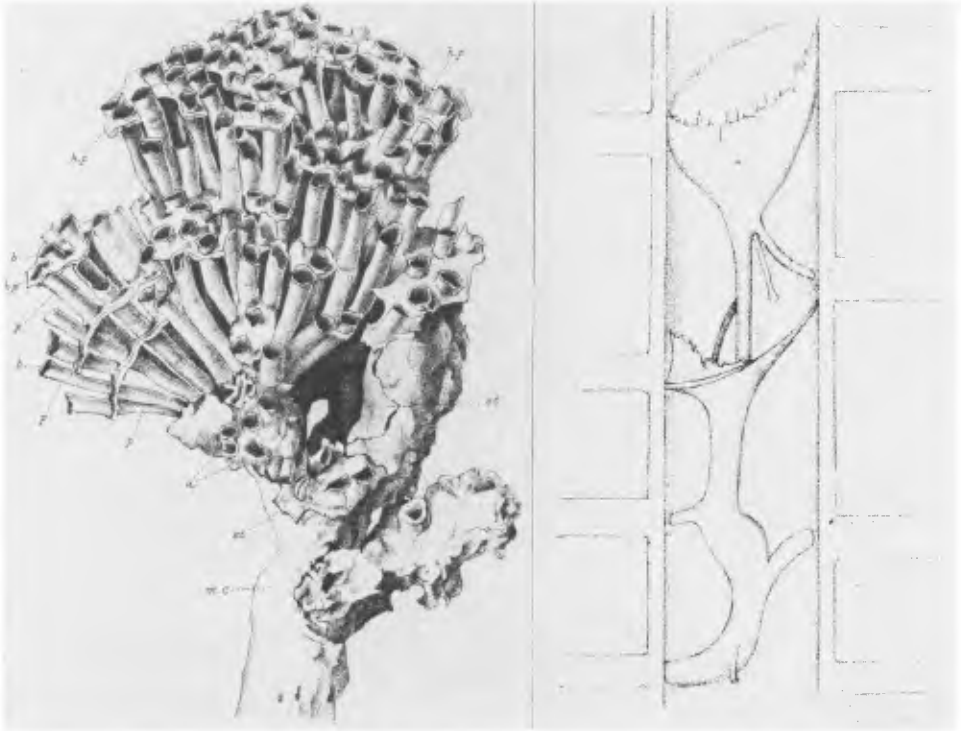
Figure 6

Tubipora musica Linn. a, Part of colony; b, diagram of tabulae. (From Hickson, 1883.)

siphonoglyph (i.e., ciliated groove along one edge of the pharynx), drastically reduced tentacles, and they bear gonads. These zooids, termed "siphonozooids," are specialized for moving water (by means of the siphonoglyph) and for reproduction. They have lost the ability to feed and to digest food, which are the function of the autozooids. The fact that all the branched, lobed, and arborescent alcyonaceans are monomorphic, whereas most of the large and massive forms are dimorphic, suggests that dimorphism arose out of a need to transport water more efficiently into the large colonial structure. Relegation of reproductive functions to the siphonozooids may be related to the abundance of water passing through them.

One group at present assigned to the Alcyonacea, the family Xeniidae, includes both monomorphic and dimorphic species, some of which seem to differ from one another in no other way. The colonies commonly are mushroom-shaped, with a sterile trunk and a rounded capitulum bearing the zooids, but in some species the trunk is subdivided into several lobes covered with zooids, and others are merely mat-like encrustations. All of the xeniids have peculiar, corpuscle-like spicules of very small size, entirely different from other alcyonacean spicules, and some species have the remarkable ability to pulsate the autozooids in unison, rhythmically opening and closing the tentacles. On the whole, this family is rather unlike the other alcyonaceans (Fig. 9).
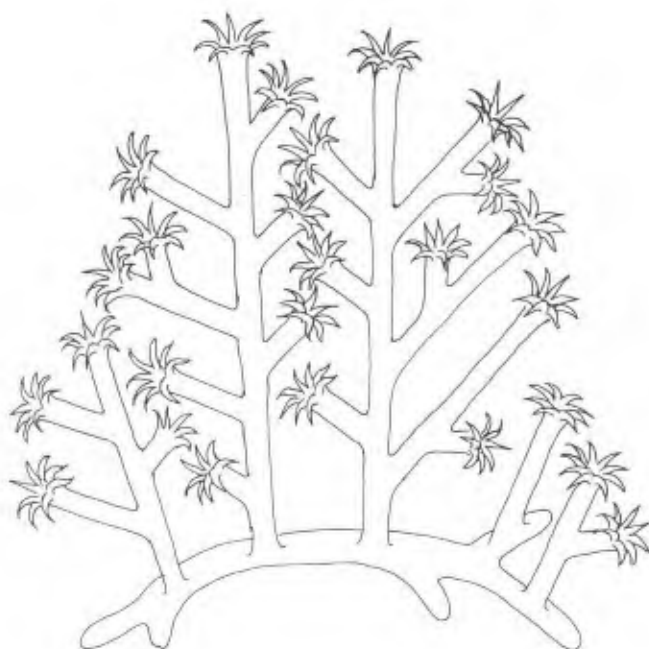
Figure 7
Telesto colony. Monopodial budding in pinnate arrangement. (Diagrammatic; original.)
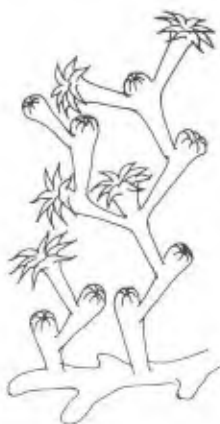

Figure 8
Pseudocladochonus colony. Sympodial budding in dichotomous arrangement. (Diagrammatic; original.)
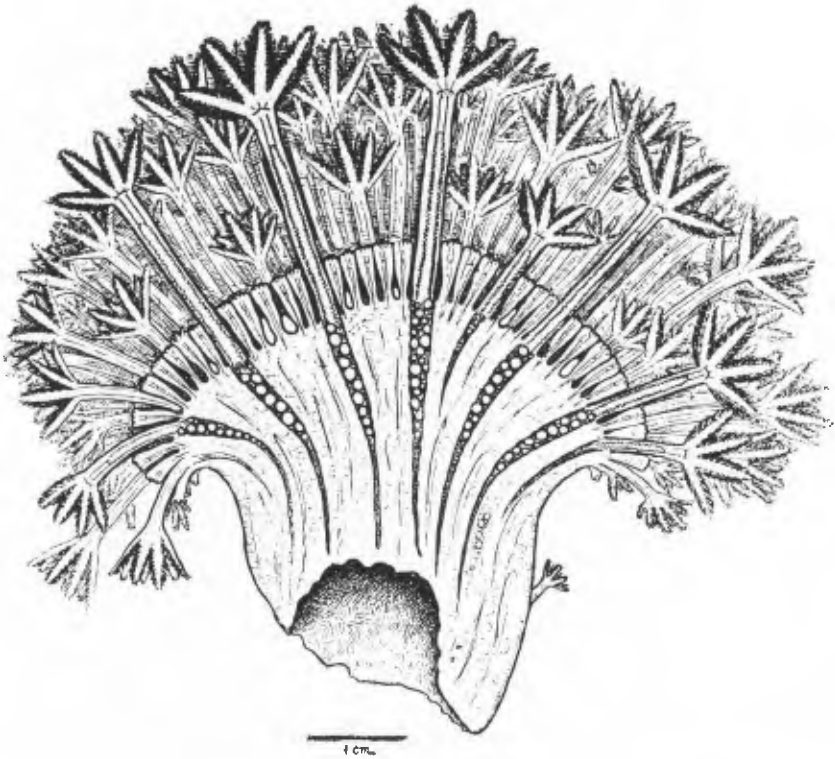
Figure 9

Colony of *Heteroxenia fuscescens* cut in half, to show the relation of the coelenteric cavities of the autozooids with gonads to those of the siphonozooids without. (From Gohar, 1940.)

The arborescent alcyonaceans fall into two groups on the basis of colonial structure. In the family Nephtheidae, colonies reach a large size, but the trunk is permeated by spacious gastrovascular canals and contains little coenenchyme. When the gastrovascular spaces expel their water, the entire colony collapses and shrinks to a much smaller size. Zooids are arranged in clusters at the ends of branchlets, and in some species the proximal ones form frilly or collar-like groups around the trunk. The arrangement of zooids on the branchlets, and the arrangement of the larger branches in the colony are characters that are used to subdivide the family, as they seem to follow consistent patterns (Figs. 10, 11, and 12).

In the family Siphonogorgiidae, the arborescent growth form is even more pronounced, the main trunk is narrower and more rigid, and the branches subdivided to a greater extent. The form of the colony and the arrangement of zooids on the branches is consistent within species.

In the remarkable family Maasellidae (= Fasciculariidae), the branches bearing zooids form a terminal tuft, and in contraction can be withdrawn as a group within the trunk, much as an actinian retracts its tentacles into the column (Fig. 13).

Figure 10
Diagram of divaricate branching in Nephtheidae. (From Thomson and Dean, 1931.)

Figure 11
Diagram of umbellate branching in Nephtheidae. (From Thomson and Dean, 1931.)

Figure 12

Diagram of glomerate branching in Nephtheidae. (From Thomson and Dean, 1931.)

Figure 13

Studeriotes longiramosa Kükenthal. Zooid-bearing branches retractile into trunk. (From Thomson and Dean, 1931.)

Figure 14
Gorgonia flabellum Linn. (From L. Agassiz, 1880.)

The most intimately integrated colonial organization in the order Alcyonacea is the remarkable species known as *Bathyalcyon robustum* Versluys. The fully developed colonies consist of a single giant autozooid in whose body wall are embedded numerous siphonozooids (Versluys, 1906; Bock, 1938). The gonads are located in the siphonozooids, which as usual have a very well developed siphonoglyph. The autozooid itself is sterile. Clearly, here is a case in which the siphonozooids function as "organs" of their vegetative parent; neither could exist without the other.

In the order Gorgonacea, colonies are predominantly arborescent, and colonial integration is demonstrated chiefly by the regularity of vegetative growth. Although the order is unified by the very consistent morphological form of the zooids, it is divided into two broad groups by the nature of the axial skeleton. The boundary between these two groups, the Scleraxonia and the Holaxonia, is still not agreed upon, and some workers remove the family Paragorgiidae from the order altogether. The zooids are laterally united by coenenchyme only basally (roughly half the length of the fully extended gastrovascular cavity, or less—often much less). The common colonial coenenchyme is supported on an axial structure composed of a horny proteinaceous material (gorgonin) that may be more or less extensively permeated by calcium carbonate—sometimes in the form of spicules, sometimes not. This axial skeleton, whatever its structure, is the product not of any individual zooids but of the colony as a whole. It is, in fact, a specialized part of the coenenchyme.

Division of labor, as reflected by dimorphism, is very rare in the Gorgonacea. It occurs only in the Scleraxonian families Coralliidae and Paragorgiidae, and the latter

Figure 15
Acanella arbuscula (Johnson). (From A. Agassiz, 1888.)

is considered by some to be alcyonacean rather than gorgonacean in its affinities. Nevertheless, *Corallium* must be considered a gorgonacean, and dimorphism certainly is the rule in this genus. The gonads are produced by the autozooids rather than by the siphonozooids. In *Paragorgia* functional specialization is apparently still in a formative state, as both autozooids and siphonozooids bear gonads, but with more in the latter.

In the holaxonian families of the Gorgonacea, which have an axial skeleton of scleroprotein with nonspicular calcareous deposits, increasing degrees of colonial integration are expressed in the increasing regularity of branching and occurrence of zooids. No functional specialization occurs, as far as is known. Branching is generally consistent in pattern but variable in details, which may be influenced by environmental factors such as water currents. In the more generalized types, the zooids are randomly distributed and branching is bushy—either pinnate or dichotomous. Orientation of the branches in a single plane, and location of the zooids on one side of the resulting flat colony, are colonial responses to unidirectional water movement.* The zooids are placed in a more favorable position to filter plankton from the passing current. Some flat colonies, as in the family Gorgoniidae, have zooids on both surfaces, and the branchlets may fuse into a quite regular network (Fig. 14). In other families, such as Paramuriceidae and Acanthogorgiidae, the zooids are either confined to one surface or are directed toward one surface.

*The same kind of flattening occurs in sponges, hydroids, hydrocorals, scleractinians, bryozoans, and in some species of algae.

Figure 16

Plumarella pourtalesii (Verrill). Pinnate branching, zooids biserial. (From Verrill, 1883.)

In three families having strong calcification in the axial skeleton, the Melithaeidae and Parisididae in the suborder Scleraxonia, and the Isididae in the suborder Holaxonia, the brittle, calcareous axis is interrupted by horny nodes that provide enough flexibility to withstand environmental turbulence (Fig. 15). This is clearly a colonial response to environmental forces. The modification is coenenchymal, not zooidal.

In one family, Primnoidae, with predominantly pinnate branching (Fig. 16), distribution of the zooids over the surface ranges from random through biserial and paired to regularly whorled. In any given species, the number of zooids in a whorl and the spacing of whorls along the branches varies only within circumscribed limits. Vegetative production of new zooids, either terminally or interstitially between older whorls, therefore is controlled with respect to time, place, and number and must be colonially, not zooidally, coordinated. In this family the sequence of branching may be very regular. In some species of *Calyptrophora*, for example, the first two branchings of the primary axis are dichotomous, in planes at right angles to each other, and in quick succession; subsequent branchings are unilaterally pinnate and in one plane. The result is two fan-like groups of parallel branches arising in parallel planes at the top of a supporting stalk. Members of the family Primnoidae, like gorgonaceans in general, are prone to infestation by a variety of commensals, predators, parasites, and epizooites, and some of the species show a colonial response to the foreign organism. Polychaete worms are common inhabi-
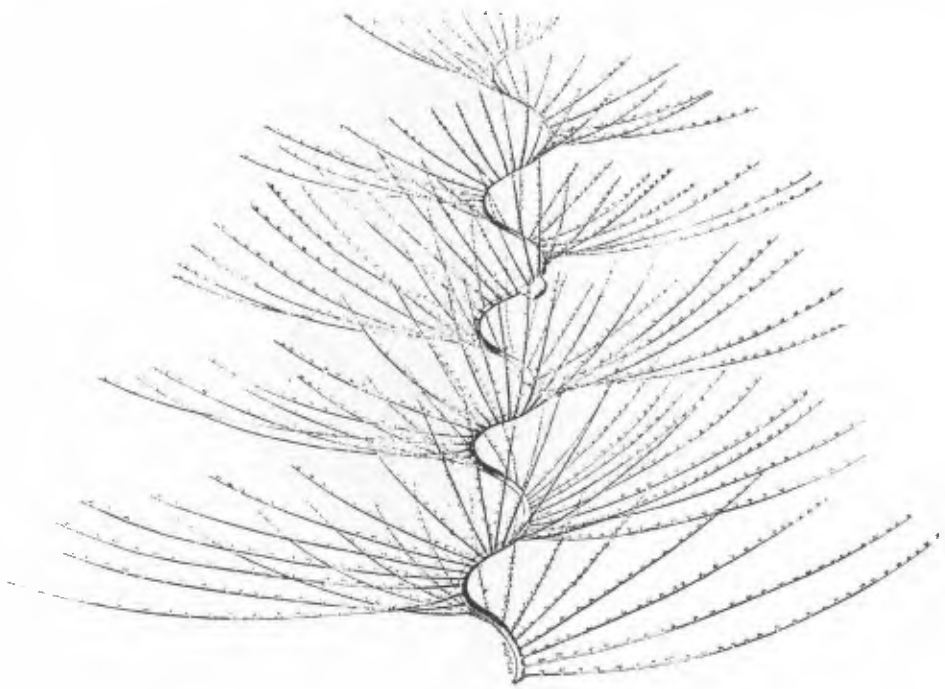
Figure 17
Iridogorgia pourtalesii Verrill. Unilateral spiral branching. (From A. Agassiz, 1888.)

tants of octocorals, and primnoids such as *Narella*, when infested with them, respond by producing enormously enlarged spicules in the affected region. The worm lives along the main axis, traveling along it between the zooids. Each zooid along the worm's path produces one or two broadly arched, flattened spicules that enclose a tunnel limiting the worm to a more or less definite path. This spicular modification is the same in all polyps, and the modified spicules are as distinctive for the given gorgonian species as are the normal ones. The gorgonian is in some degree protected from the polychaete, which itself is protected by the modified spicules. It is not known whether the worm is a commensal, parasite, or predator on the gorgonian, but it probably is not the last, as no damage to the zooids is evident. In other families, normally having spicules much smaller than in the primnoids, infesting polychaetes induce the growth of a web-like expansion of coenenchyme along the affected branch. The individual spicules are too small to be modified into protective structures, so the coenenchyme as a whole carries out this function.

Of all the holaxonian gorgonians, members of the family Chrysogorgiidae show the greatest regularity in branching. Most are inhabitants of deep water. The few exceptions show branching in one plane, similar to that seen in other families. Those living in deep, still water assume a multiplanar form arranged around an essentially spiral axis. Some are unbranched (genus *Radicipes*), but even in these, the long, whiplike colony
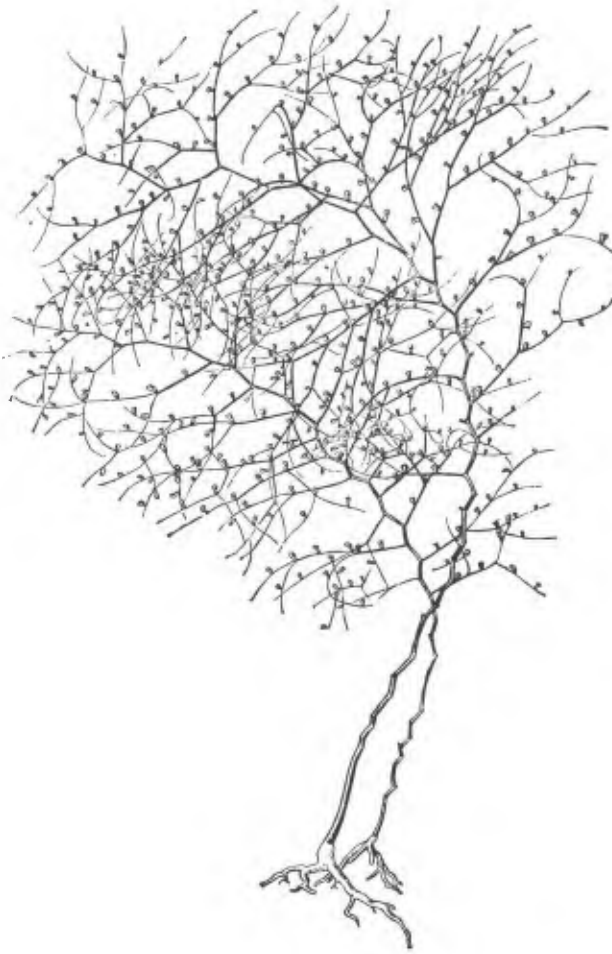
Figure 18

Chrysogorgia sp. Dichotomous branches arising spirally around main trunk. (From A. Agassiz, 1888.)

is spirally twisted—a form found also in other gorgonian families (Isididae and Ellisellidae) and in other coelenterates (e.g., Antipatharia). The branched forms may produce long, simple branchlets from the outer side of an ascending spiral main axis (*Iridogorgia*, Fig. 17). The branchlets are regularly spaced along the spiral, and the zooids are regularly spaced along the branchlets. More commonly, however, the main axis is a tighter spiral, producing a fixed number of lateral branches in each revolution. The direction of the spiral is clockwise in some species, counterclockwise in others; in some, one complete turn around the spiral brings the fourth branch directly above the first, but in other species, the first branch directly aligned with that at the beginning occurs at the completion of the second revolution, and very commonly this is the sixth. The lateral branches

Figure 19

Policella manillensis Kölliker. (From Kölliker, 1870–1872.)

then subdivide dichotomously a constant number of times, with a fixed number of zooids occurring between each dichotomy (Fig. 18).

Most members of the family Chrysogorgiidae inhabit soft bottom, where there are few solid objects for attachment. As the colonies are rather delicate, even small objects such as mollusk shells, bits of echinoid test, and the like are adequate supports. The holdfast established by the founding zooid eventually grows into a thickened, discoidal calcareous button to which is attached the proteinous axis. If the support is very small, the coenenchyme has the ability to produce branching, calcareous, root-like anchoring processes (Fig. 18) that penetrate the mud and hold the colony in position. This is covered by coenenchyme containing spicules, but no zooids are formed.

Among the octocorals, the pennatulaceans as a group are the most advanced in terms of colonial complexity, polymorphism, functional specialization of zooids, and colonial integration. In fact, the pennatulacean colony acts as a superorganism whose various kinds of zooids perform respiratory and circulatory, feeding and digestive, sexual, and locomotory functions.

Within the order Pennatulacea, several further intergrading levels of organization can

Figure 20
Sclerobelemnon schmeltzii Kölliker. (From Kölliker, 1870–1872.)

Figure 21
Renilla reniformis Pallas. (From Kölliker, 1870–1872.)

Figure 22

Umbellula lindahlii Kölliker. (From Verrill, 1885.)

be recognized. In the simplest, the daughter zooids (autozooids and siphonozooids) are arranged more or less generally around the primary individual (oözoöid), as in *Caver-nularia, Policella, Veretillum,* and a few other genera (Fig. 19). They become progressively more regularly arranged in the direction of bilaterality and in the relative positions of autozooids and siphonozooids. A longitudinal naked tract along the rhachis (body of the oözoöid) divides the other zooids into two lateral fields (Fig. 20) as in *Kophobelemnon, Sclerobelemnon,* and *Mesobelemnon,* and the zooids become limited to one face of a flattened colony (*Renilla*) (Fig. 21) or to the distal end of a tassel-like structure (*Umbellula*) (Fig. 22). In the latter arrangement, the tassels of zooids may be repeated as widely spaced pairs or whorls of zooids along the rhachis (*Chunella*).

In the biserial colonies, the autozooids are placed in more or less distinct transverse rows and more or less completely united by their bases to form flattened, leaf-like structures with a marginal fringe of zooids. The siphonozooids may be located on the sides of the autozooid leaves, between them, or in more or less restricted areas along the naked tract separating the two rows of leaves (Fig. 23). Further, each autozooid may produce sharply projecting spicules, probably defensive in function, always located in the same position.

In many (perhaps all) species of Pennatulacea, the colonies are capable of limited movement by means of the muscular and distensible proximal end of the stalk. Specimens

Figure 23
Pennatula rubra Ellis. (From Kölliker, 1870–1872.)

of *Renilla reniformis* (the sea pansy) can move from place to place by withdrawing the stalk from the substrate and reinserting it a short distance away, subsequently pulling the frond into a new position. Slender, rod-like forms, such as *Stylatula* and *Virgularia*, having a stiff, calcified axis that affords the colony little flexibility, nevertheless move up and down in the sandy or muddy substrate with the ebb and flow of the tide, as was reported more than 200 years ago by Rumphius (1705).

SUMMARY

The octocorals display a wide and virtually continuous range of colonial organization. In this one subclass are found extremely simple colonies founded by an individual produced from a fertilized egg and composed of asexually produced "daughters" exactly like itself and retaining a loose organic connection by way of a system of entodermal canals permeating the narrow, meandering stolons from which the individuals arise. Each of

these individual zooids is essentially an independent organism in spite of its organic connections with its vegetative siblings. No functional specialization has developed, and presumably every zooid retains the capacity for vegetative reproduction and could reestablish an entire colony. No two colonies are exactly alike, but distribution of stolons over the substrate always has the same pattern in any given species so the spatial relationships among zooids in different colonies have no more than a general similarity. Although each zooid is equipped to carry on all the vital processes, some advantages must result from the persistence of organic connection—such as the distribution among several (or all) individuals of food ingested by one or a few—to give colonial species a selective advantage.

At the other extreme, there are octocoral species whose colonies are highly organized and composed of functionally specialized individuals distributed in a very orderly sequence to form a structure highly characteristic for each species. In this case, the original founding zooid loses the ability to feed and take in water, never achieves the ability to reproduce sexually, and serves mainly as a support for its vegetative offspring. These are arranged in more or less orderly groups which, in the more complex forms, are serially repeated along much of the length of the rhachis (i.e., the body of the primary zooid); some of them are structurally modified to form a water-transport system through hypertrophy of the ciliated groove and reduction or loss of other structures, while others are adapted primarily for feeding and reproduction. Here, all the specialized zooids function together as a unit—a sort of superindividual—but cannot function alone. Within a species, all colonies are remarkably similar and the spatial relationships of their component individuals are always essentially the same. Between these two extremes—the simple stoloniferans and the complex pennatulaceans—there are innumerable subtle intermediates, but no one order includes the full range.

Two of the six orders stand clearly apart. The Coenothecalia, which has a long fossil history, is now represented by a single surviving species (*Heliopora coerulea*) and clearly is a relict. Although unmistakably octocorallian in anatomy, its skeleton is massive in the fashion of hermatypic scleractinians and its colonial organization is like that of scleractinians, with similar growth form. Its level of colonial integration is low. On the other hand, the Pennatulacea, with a high degree of colonial integration, is a rather diverse group with wide bathymetric and geographic distribution. Whether it was previously more prolific than now is impossible to say because of its fragmentary geological record, but it certainly was extant in the Eocene (*Graphularia*), and possibly in the Silurian (*Spirophyton, Alectorurus*) or even earlier (*Charnia, Rangea*; Glaessner, 1959, 1961). There are no known intermediates linking the Pennatulacea with any other order. A few gorgonaceans simulate certain of the simpler pennatulacean colonies, but they are unquestionable gorgonaceans and the resemblance is superficial. The order showing the most significant similarity to the Pennatulacea is the Telestacea, in some of which the tall axial zooid produces lateral daughters from its own body wall in a more or less regular organization. Even here the resemblance is superficial, as the axial zooids are not necessarily the sexual founder zooids (although one of them in each colony certainly is), the lateral daughters may also produce lateral daughters, all zooids are functionally monomorphic, the colonies have a low grade of integration, and the organization is basically Stoloniferan.

The orders Stolonifera, Telestacea, Alcyonacea, and Gorgonacea (with two suborders, Scleraxonia and Holaxonia) overlap to some extent so that drawing hard and fast boundaries between them is difficult. As these orders are based, in part, on aspects of colonial complexity, it follows that none has a very wide range in this character. The stoloniferans are at the lowest level, the monomorphic polyps reproducing vegetatively only from lateral stolons, never from the body walls. In certain species, these stolons arise from the body wall some distance above the substrate, so their condition approaches that found in the telestaceans, where the daughters arise directly from the parent body wall. In fact, there seems to be little justification for maintaining these two groups as separate orders.

In the arborescent genus *Coelogorgia*, the telestaceans overlap the arborescent alcyonaceans (e.g., *Siphonogorgia*), and more extensive anatomical research will be required to determine whether they are superficially or fundamentally similar in structure. In turn, the arborescent Alcyonacea overlap the arborescent scleraxonian Gorgonacea such as *Paragorgia*, which has been considered an alcyonacean on anatomical grounds (Verseveldt, 1940). Hence it seems unrealistic to consider the levels of colonial organization in these four orders from the standpoint of traditional classification. Two of the groups have no trace of functional specialization and are strictly monomorphic (except that the axial zooids in *Telesto* are longer than the laterals and thus might be considered a morphologically distinct type), one shows it to a more or less limited extent according to where its taxonomic limits are drawn, and one has a substantial number of genera with some or all species dimorphic and functionally specialized. Where dimorphism occurs, it commonly is in the form of zooids specialized for moving water through the colony, and thus is often found in groups having species whose colonies attain massive dimensions. Further, these same pumping zooids ("siphonozooids") may also assume the reproductive functions of the colony, leaving the autozooids with feeding as their principal activity. Such functional specialization does not always depend upon size, however. Some species whose colonies never reach large size (at most roughly 15 cm high and 15 cm in diameter) are dimorphic, whereas some that grow quite large (1 m or more) are not. The greatest degree of colonial integration is found in species whose colonies contain only a single autozooid in whose walls are embedded the numerous siphonozooids which control the hydrostatics of the parent autozooid and perform the reproductive functions. The aggregation of autozooid and siphonozooids behaves as a single biological entity.

A high level of colonial integration, or at least of coordinated vegetative growth, is achieved without the development of dimorphism. In most gorgonaceans, few of which show dimorphism, vegetative reproduction of the zooids proceeds in a manner that results in a colonial structure characteristic of the species. This could not occur without a control mechanism. In two families (Chrysogorgiidae, Primnoidae), colonial growth is so regular that zooids are arranged in a relationship to one another that varies only within rather narrow limits, the position of each branch in the colony is more or less rigidly predetermined, and extrazooidal tissues produce supporting structures that affix the entire colony to (or in) the substrate.

Although it is easy enough to postulate that in each species the zooids develop to a predetermined (genetically? physiologically? structurally?) height, extrazooidal growth

proceeds to a predetermined limit before zooidal replication occurs, and axial growth continues only for a certain distance before bifurcation or lateral ramification of the axis is triggered, it is less easy to imagine what forces cause ramification to follow a clockwise or counterclockwise spiral, why branches should be regularly aligned within these spirals, why adjacent branchlets should in some cases fuse when their courses intersect but in other instances remain free. The end result is that the zooids of a colony are deployed in the environment in the most effective arrangement for feeding, and situated with respect to one another in a manner that permits the most efficient distribution of nutriment. The control mechanism that brings it about must be a property of the colony as a whole, not of the individual zooids.

Although the ancestral octocoral probably was solitary, the advantages of coloniality must have been so great that the solitary state vanished completely. No undisputed trace of it exists in the Recent fauna, as the few putative examples of solitary forms (e.g., *Haimea*) eventually have been shown to be the primary founder zooids of colonial forms. The advantages of coloniality were probably related to reproduction, nutrition, and, perhaps, respiration. The largest octocoral zooids are rather small in comparison with a large actinian or even scleractinian zooid, and the average octocoral zooid is very small in this comparison. The female zooid is capable of producing several eggs, but their number is limited by the size of the adult, and of the eggs produced in one breeding season not all will mature and be fertilized (Grigg, 1970, p. 141). Thus a vegetative repetition of the adult increases its reproductive potential. This same repetition of adult zooids also increases the feeding capacity of the colony, especially if the colonial form places some of the individuals in positions more advantageous for capturing food than others. Moreover, the maintenance of gastrovascular connection between individuals permits many members of a colony to benefit when a few localized individuals feed.

Increasing colonial size, especially if massive coenenchyme is produced, raises problems of respiration because deeper-lying tissues are far removed from the surrounding seawater. The same interzooidal gastrovascular connections permit the distribution of water through-out the colony, and the development of zooids specialized for pumping water (siphonozooids with powerful ciliated groove) enhances this capacity.

REFERENCES

D'Achiardi, Antonio. 1868. Studio compartivo fra i coralli dei terreni terziari del Piemonte e dell' Alpi Venete. Ann. Univ. Toscane, *10*: 73–144, pls. 1, 2.

Agassiz, Alexander. 1888. Three cruises of the United States Coast and Geodetic Survey Steamer "Blake" . . . v. 2. Bull. Mus. Comp. Zool. Harvard, *15*: 1–220, figs. 195–545.

Agassiz, Louis. 1880. Report on the Florida Reefs. Mem. Mus. Comp. Zool. Harvard, *7*(1): (i–iv) + 1–61, pls. 1–22.

Bayer, F. M. 1955. Remarkably preserved fossil sea-pens and their Recent counterparts. Jour. Wash. Acad. Sci., *45*(9): 294–300, figs. 1, 2.

Bock, Sixten. 1938. The alcyonarian genus *Bathyalcyon*. Kungl. Svenska Vetenskapsakad. Handl. (Tredje Serien), *16*(5): 1–54, pls. 1, 2.

Duncan, P. M. 1880. A monograph of the fossil corals and Alcyonaria of Sind. Mem. Geol. Surv. India. Palaeont. Indica, *14*(1): 1–110, pls. 1–28.

Glaessner, M. F. 1959. Precambrian Coelenterata from Australia, Africa and England. Nature (London), *183*(4673): 1472–1473, fig. 1.

————. 1961. Pre-Cambrian animals. Sci. Am., *204*(3): 72–78, illustr.

Gohar, H. A. F. 1940. Studies on the Xeniidae of the Red Sea. Publ. Mar. Biol. Station Ghardaqa, *2*: 23–118, pls. 1–7, figs. 1–10.

————. 1948. A description and some biological studies of a new alcyonarian species *Clavularia hamra* Gohar. Publ. Mar. Biol. Station, Ghardaqa, *6*: 3–33, pls. 1–3.

Grigg, R. W. 1970. Ecology and population dynamics of the gorgonians, *Muricea californica* and *Muricea fruticosa*—Coelenterata: Anthozoa. Unpublished Ph.D. dissertation, Univ. Calif., San Diego. xvii + 261 p.

Hickson, S. J. 1883. The structure and relations of Tubipora. Quart. Jour. Micros. Sci., ns., *23*: 556–578, pls. 39–40.

————. 1938. An alcyonarian from the Eocene of Mississippi. Jour. Wash. Acad. Sci., *28*(2): 49–51, figs. 1–4.

Kinoshita, Kumao. 1910. Ueber die postembryonale Entwicklung von *Anthoplexaura dimorpha* Kükenthal. Jour. Coll. Sci. Imp. Univ. Tokyo, *27*(14): 1–[16], figs. 1–3.

Kölliker, Albert. 1870–1872. Anatomisch-systematische Beschreibung der Alcyonaria. Erste Abtheilung: die Pennatuliden. Abhandl. Senckenb. Naturf. Ges., *7*: 111–255, 487–602; *8*: 85–275, pls. 1–24.

Kugler, H. G. 1971. An enigmatic gorgonian remnant. Eclogae Geologicae Helvetiae, *64*(3): 635–636, pls. 1–3.

Madsen, F. J., 1944. Octocorallia. The Danish Ingolf-Expedition, *5*(13): 1–65, 1 pl.

————. 1956. *Primnoella krampi* n. sp. a new deep-sea octocoral. Galathea Rept., *2*: 21–22, fig. 1.

Rumphius, G. E. 1705. D'Amboinsche Rariteitkamer . . . Fr. Halma, Amsterdam, [28] + 340 + [43] p., frontisp., portr., 60 pls.

Thomson, J. A., and L. M. I. Dean. 1931. The Alcyonacea of the Siboga Expedition, with an addendum to the Gorgonacea. Siboga-Exped. Monogr., *13d*: 1–227, pls. 1–28.

Utinomi, Huzio. 1955. On five new stoloniferans from Sagami Bay, collected by His Majesty the Emperor of Japan. Jap. Jour. Zool., *11*(3): 121–135, figs. 1–11.

Verrill, A. E. 1883. Report on the Anthozoa, and on some additional species dredged by the "Blake" in 1877–1879, and by the U. S. Fish Commission Steamer "Fish Hawk" in 1880–82. Bull. Mus. Comp. Zool., Harvard, *11*(1): 1–72, pls. 1–8.

————. 1885. Results of the explorations made by the steamer "Albatross," off the northern coast of the United States, in 1883. U. S. Fish Comm. Rept., *1883*: 503–699, pls. 1–44.

Verseveldt, J. 1940. Studies on Octocorallia of the families Briareidae, Paragorgiidae and Anthothelidae. Dissertation, E. J. Brill, Leiden. [i–x] + 1–142 + 1–V p.

Versluys, J. 1906. *Bathyalcyon robustum* nov. gen. nov. spec. Zool. Anz., *30*(17/18): 549–553, figs. 1–4.