# Croonian Lecture: *Evolution and Symmetry in the Order of the Sea-pens.*

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## 1. *On Radial and Bilateral Symmetry in the Animal Kingdom.*

In a general survey of the animal kingdom two kinds of body symmetry are found—the bilateral and the radial. In many cases, genera, families, and even classes of animals show some structural departures from the completely radial or bilateral symmetry; in others, there is a combination of the two symmetries, as when an outer body form of radial symmetry covers bilaterally symmetrical organs, and, further, there is now conclusive evidence that in the course of the evolution of certain groups of animals one form of body symmetry has been supplanted by the other. With all the varieties of form and structure adapted to the different conditions of life, and with all the complexities of development and organisation due to phylogeny, there are but few examples of animals that are completely bilateral or completely radial as regards all their organs, but the dominance of one or other of these symmetries is, in most cases, so far pronounced that any animal can be placed in its proper group on this method of classification.

It is not possible to give in a few words a comprehensive definition of what is meant by the two symmetries; but if attention is confined for the moment to such types as the earthworm or a fish on the one hand, and to a polyp or a jelly-fish on the other hand, a basis for a definition may be found for each of the two symmetries. Thus, a bilaterally symmetrical animal is one in which the principal organs and appendages of the body are arranged in pairs on either side of a median vertical plane. Such an animal exhibits an anterior and a posterior extremity, a dorsal and a ventral surface, and a right and left side. And a radially symmetrical animal is one in which the principal organs and appendages of the body are arranged symmetrically on radial lines or planes proceeding from a common centre or a common axis. Radially symmetrical animals may be spherical or oval, dome- or disc-shaped, or cylindrical in form, and they do not exhibit anterior and posterior extremities, dorsal and ventral surfaces, nor right and left sides.

Animals that are bilaterally symmetrical are usually free, and propel their bodies actively through the medium in which they live by powerful muscular movements of the body wall or of the appendages. Animals that are radially

symmetrical, on the other hand, are usually either sedentary in habit, or have a floating or drifting habit with the aquatic plankton.

There is clearly an intimate association between the symmetry and the habit. An animal that is active and moves rapidly from place to place in search of food or shelter must be bilaterally symmetrical. The animal has been constructed by the forces of Nature in the same way as man constructs his railway trains, steamships, and aeroplanes, with a view to rapidity of progress combined with economy of power.

An animal that is sedentary or drifting in habit, one that does not use its muscles for driving its body through the water, through the air, or on the surface of the earth, does not need this exquisite balance of parts on a median vertical plane. It may be any shape that is not inconsistent with the conditions of the environment, as we see in variations of shape and ramification of corals and sponges. But, provided that the forces that act upon it and the food upon which it preys come to it with equal intensity from all directions, it has a tendency to assume a more or less perfect radial symmetry.

We can see the influence that habit has had in determining the symmetry of the body in the evidence of phylogeny afforded by the embryonic development of several kinds of animals.

Thus, the Crustacea are, as a rule, animals with perfectly bilateral symmetry of the body, and they are bilaterally symmetrical from the early embryonic stages until adult life is reached, and all the time they are active and free. But in the order Cirripedia we find a series of forms in which the bilateral symmetry of the external shell is gradually obscured until we reach the almost perfect radial symmetry of such a genus as Coronula. The nauplius and the cypris larval stages of these Cirripedes are free and, like other Crustacea, bilaterally symmetrical, and it is only in the adult and sedentary stage that the tendency to the assumption of a secondary radial symmetry shows itself.

Again, in the Echinodermata we find a dominant radial symmetry, associated in many of the Crinoidea with a sedentary habit, and in the forms that are not strictly sedentary the movements are slow and indeterminate in direction. The embryological evidence that the Echinoderms have passed through, in their phylogeny, firstly a free bilaterally symmetrical stage is almost conclusive; but it is even of greater interest to find that in some of the Holothuroidea, a group in which the movements in a definite direction of the body are assisted by a more powerful development of muscles in the body wall, several genera—such as the Elasipoda—exhibit a very pronounced return to a bilateral symmetry of the body.

In comparing the animals that show a dominant radial symmetry and are sedentary or drifting in habit with those that show a dominant bilateral symmetry and are free and active in their movements, it may be observed that the former are far more variable in external form and in the number and arrangements of their organs than the latter.

If we take such a form as Hydra as an example of a sedentary animal, or Aurelia as an example of a drifting animal, with radial symmetry, it is found that, within the limits of what is at present regarded as a simple species, profound variations in the important organs are of frequent occurrence. In Hydra the number of tentacles and the number and form of the gonads vary within a wide range in any collection of the same species taken from the same locality. In Aurelia* and in Eucope† there are numerous variations to be found, when a large collection of specimens is examined, in the number and arrangement of the gonads, the gastric pouches, the radial canals, the sense organs, and the tentacles, and if we add to these variations in the important organs the minor variations in size, colour, length, or size of the parts, etc., which are reckoned of some importance in systematic description, the variability of these forms is found to be of great importance. If we compare the extent of these variations with the variations seen in a typical bilaterally symmetrical animal such as an earthworm or a crayfish a great difference is observed. Thousands of specimens of a species of earthworm may be examined without finding any variations in the number or position of the gonads, of the œsophageal pouches, or of the principal blood-vessels. Similarly, variations in the number or form of the appendages of a crayfish are very rarely met with, and major variations in the viscera are so rare that only a few isolated cases have been recorded.

Many other examples could be quoted to illustrate this point of difference between radially symmetrical and bilaterally symmetrical animals, but a great many instances could also be brought forward which seem to be exceptions to what we might otherwise call a biological rule.

I have frequently been impressed, in my systematic work on Cœlenterata, with instances of the rigidity of certain characters in some species or genera or even larger groups of these radially symmetrical organisms. The colour of the spicules of *Tubipora musica* is always red, there is always a blue colour in the corallum of Heliopora, the spicules of Eunicella are always torch-shaped, *Paragorgia arborea* is always dimorphic, there are always eight mesenteries in the Alcyonarian polyps and never more than eight tentacles.

These characters, which in other genera and orders are very variable

* Ehrenberg, 'Abh. k. Ak. Wiss.,' Berlin, 1835.

† Agassiz and Woodworth, 'Bull. Mus. Comp. Zool.,' Cambridge, 1896.

indeed, seem to have become rigid or invariable in the cases quoted. No reason can, at present, be given to account for this rigidity of certain characters in a few of the many thousands of sedentary individuals and colonies, but they cannot be put forward as a controversion of the general statement that sedentary animals are usually more variable as regards their principal organs than animals that are free and active in their movements.

It is not surprising that bilaterally symmetrical animals should be less variable than radially symmetrical animals. In order to secure the greatest possible efficiency of movement in any direction it is necessary that the organs should be equally poised on either side of the median plane. Any variation of an organ on one side of the plane, unless balanced by an exactly equivalent variation of the corresponding organ on the other side, would produce deviation of direction in movement. An increase of the median unpaired structures of the dorsal side would require some compensating change in the structure of the unpaired or paired structures of the ventral side, variations in size or form of the anterior end would require some modification of the structure at the posterior end, if the mechanical economy is to be maintained. There are many kinds of variation, therefore, which, in bilaterally symmetrical animals, would materially interfere with the chances of survival of the variant in the struggle for existence, but would not, at any rate to the same extent, interfere with the chances of a radially symmetrical sedentary or drifting animal.

Moreover, it can be understood that many kinds of sedentary and drifting animals have need of powers of variation and accommodation of form which are not required by animals that are active.

In most cases, sedentary animals begin life as free swimming or floating larvæ. These larvæ settle down in positions of various environmental conditions, and there they remain for life or perish.

Considerable powers of variations or plasticity in growth are therefore of immense advantage to a species for accommodation to the various and the variable conditions of the environment.

A sedentary animal that does exhibit considerable variability and accommodation has obviously a better chance of survival than one that is more rigid in its development and growth.

With an animal that is capable of vigorous muscular movements through its medium such variability has not the same essential value, for within limits it can escape from unfavourable environments and seek others that are better suited to its more rigid characters. Sedentary animals are either solitary or colonial in habit. Those that are solitary are almost invariably radially symmetrical, but those that are colonial, although showing radial

symmetry as regards the individual of which the colony is composed, exhibit a great variety of form as regards the colony as a whole.

The study of the form of animal colonies is one of the most difficult, but at the same time most interesting, studies within the range of biological science, but at present very little progress has been made, and the solution of many of the problems that it affords is quite obscure. But we can see that in the formation of full-grown colonies there is a prevalent tendency to the construction of a radially symmetrical shape. Among the Madreporarian corals, for example, we find many examples of the solidly constructed Meandrinas, Siderastræas, etc., and of the ramose Pocilloporas and Seriatoporas that are spherical or hemispherical in shape. Among the Alcyonaria we find the club-shaped Alcyonium colonies, the mushroom-shaped Sarcophytums, the cylindrical Juncellas and the symmetrical bush-shaped colonies of such as species as *Chrysogorgia flexilis*. Among the sponges we find the spherical masses of Suberites, Tuberella and Tethea, and the horn-shaped Euplectella. Among the Polyzoa we find the beautiful funnel-shaped colonies of Retepora, the spherical masses of Cellepora and the disc-shaped colonies of Lagenipora.

In many other examples, however, the colony is not strictly radial in symmetry, as, for example, the flabellate forms of Gorgonia, the plicate forms of Madrepora and Millepora, and countless other varieties of branching and encrusting growth.

The general principle that seems to underlie the growth of these colonies is a tendency to assume a radially symmetrical form subject to modifications within a wide range, in adaptation to the variable conditions of the environment.

Thus, if the larva of one of these organisms settles down in shallow water in an open space where the necessary food may drift towards it from any point of the compass, it will, in the formation of its colony, send out branches of equal length in all directions, and thus assume a spherical shape; if it settles down in a narrow space between two massive rocks or corals, where the food from two directions is cut off, the shape of the colony will tend to become oval or flat. If the larva settles on a spot where the sea currents or wave actions are strong the branches will be strong and tend to anastomose; if it settles in deeper water where such are less powerful, the branches grow more delicately and do not anastomose. An interesting variety of such adaptation to conditions is seen in the genus Stylaster, one of the genera of hydroid corals that extends from shallow water to great depths of the ocean. The general form assumed by colonies of this genus is that of a fan, the main branches radiating from the base in one plane give rise to a large

number of delicate branches which fill in the spaces between the main radii and frequently anastomose. As in all shallow water corals, however, the form of the colony is subject to great variations.

The polyps of Stylaster are arranged in cycles of five or six individuals—the Dactylozooids—with one larger individual—the Gasterozooid—in the centre of the cycle, and each of these cycles is protected by a calcareous cup which is called the calyx.

In the shallow-water species, such as *Stylaster eximius*, the calices are situated on the sides of the branches, that is to say, with the mouths of the cups facing in a direction parallel with the plane of the flabellum. In some of the deep-sea species, such as *S. umbonatus* and *S. minimus*, the calices are all situated on one surface of the branches, that is to say, with the mouths of the cups facing in a direction at right angles to the surface of the flabellum. It seems probable that the former arrangement is an adaptation to life in the strong varying currents and wave action of shallow water, and the latter to life in comparatively quiet water, with a gentle current flowing mainly in one direction, such as we find in some localities in deep water.

It is not necessary to refer to further examples of the great variability of external form, mode of growth, and method of ramification of the sedentary colonies of animals. They are well known to systematists interested in the various orders of the Porifera, Cœlenterata, Polyzoa, and Tunicata, but it must be remarked that the range of variability is by no means the same in all cases. In some genera, such as Millepora, the range is very wide. We find flat encrusting forms, plicate forms, fan-shaped branching forms, forms with thick anastomosing branches, and forms with delicate, not anastomosing, branches, of shrubby aspect. The anatomical structures of the polyps that build up all these manifold kinds of colony are found, on careful examination, to be identical.

In other genera, such as Meandrina, solid more or less spherical or oval colonies only are found; in others, such as Juncella, long cylindrical colonies; in others, such as Seriatopora, branching bushy colonies; and in many other genera flat laminate colonies following the contours of their support.

The shape assumed by a full-grown colony is not, therefore, entirely due to individual adaptation to the surrounding conditions. There is undoubtedly a genetic influence tending to produce a type of growth for each genus of a family, but this influence allows departures from the exact model of the type within certain ranges, which vary in extent in different genera.

Allowing for differences of this kind in the plasticity of growth, however, all the colonial and sedentary genera exhibit greater variation of shape than

the active bilaterally symmetrical genera of the animal kingdom, and minor variations of shape cannot be used with any confidence for the diagnosis of species.

In the building up of the colonial organisation, the various methods of growth bring the individual polyps into a position in the water where they will receive during their vigorous lifetime the most abundant supply of food and, in some cases, of light. In such positions the food upon which the polyps feed will usually come, not from one direction only, but with greater or less frequency from all directions, and it is therefore to their advantage that the tentacles, of approximately equal length, should radiate from a common centre, where the mouth is situated. Upon the arrangement of the tentacles the whole symmetry of the body depends, and it is found that, whatever shape the colony as a whole may have assumed in adaptation to its environment, the radial symmetry of the tentacles, of the hard protective skeletal structures of these polyps, and of certain other organs of the body, is maintained.

But although the structure of the individual polyp and of the hard parts, such as the pores, calices, septa, cells (of Polyzoa), etc., are rightly regarded by systematists as more reliable than the form of the colony for the diagnosis of species, even these are liable to considerable variation in detail, according to their position on the colony.

The great variability that is observed in most of the species of colony-forming animals may be associated with their sedentary or stationary habit of life. It is only in a few cases, such as Pelagohydra, Cristatella, the Salps, and a few others that we find that the colony as a whole has the power of moving by its own efforts from place to place. In the order of the sea-pens, if we may judge from the character of the muscles, and from the direct evidence of observation of a few genera, every colony has the power of forcing its way into the sand by its own muscular movements. It seems probable that their movements are more powerful and rapid than the movements of any other colony of animal zooids.

Now, as Döderlein* has pointed out, the power of movement is correlated with plastic variability. When a species for any reason becomes less active in its movements—and he quotes *Bosmina coregoni* and *Daphnia hyalina* among others as examples of this—it tends to become much more variable. His view is summarised in the statement: "Die Höhe des Vagilität bei verschiedenen Thiergruppen muss in umgekehrtem Verhältniss Stehen zur Zahl der auf dem gleichen Gebiete vorhandenen adaptiven Formen."

Similarly, if in the evolution of a group of animals there has been an

* Döderlein, L. 'Zeitschr. für Morphologie,' vol. 4, p. 441 (1902).

increase in power of movement (vagility), there has also been in all probability a diminution in the number of adaptive forms, or, in other words, a decrease in plastic variability. And the increase in power of movement is accompanied by a change from a previous radial symmetry to a more and more pronounced bilateral symmetry of the parts.

Moreover, if we consider individual characters, we find that many of them, which are extremely variable in the forms which show radial symmetry, and are sedentary or show slight signs of movement, become rigid or less variable in the more active forms with bilateral symmetry. Characters which are determined in the former by external forces become genetic in the latter.

2. *On Symmetry and Variation in the Pennatulacea.*

The general statement that forms the substance of the introductory part of this lecture, namely, that radially symmetrical forms of animals are more variable than bilaterally symmetrical forms, is so difficult to prove absolutely, owing to a variety of complications in special cases, each of which requires separate consideration, that it would be of interest to discover whether in any one order which affords examples of genera showing both kinds of symmetry the radially symmetrical genera are more variable than those with bilateral symmetry. We find such an order in the Pennatulacea, an order which includes forms that are almost completely radially symmetrical, such as Veretillum, and forms such as Pennatula, that are bilaterally symmetrical.

At the time of the publication of the 12th edition of Linnæus' 'Systema Natura' (1768), eight species of the sea-pens were known, seven being described under the generic name Pennatula, and one (the deep-sea *Umbellula encrinus*) under the name Vorticella.

These species were included by Linnæus in his sub-class Zoophyta, a group of organisms which, notwithstanding the researches of Peysonnell and of John Ellis, were still regarded by Linnæus to be partly of the nature of animals and partly of the nature of plants: "Zoophyta composita Animalcula, in bivio Animalium Vegetabiliumque constituta . . . Stirps vegetans, metamorphosi transiens in florens Animal."

From the time of Linnæus and the final settlement of the Pennatulacea as an order of the Alcyonaria in the animal kingdom, little progress was made until the "Challenger" and subsequent scientific expeditions sent home their deep-sea booty. For most of the sea-pens are found to be inhabitants of deep or very deep sea-water, and it is only by the appliances carried by the great national deep-sea expeditions that they can be captured in large numbers and variety. The richest collection so far obtained is that of the

Dutch "Siboga" Expedition in the waters of the Malay Archipelago, which I have had the privilege to examine and describe.*

In the early days of the investigations of sea-pens, when one or two specimens from a single locality were all that a naturalist could examine, and the range of variation within a specific group could not be determined, there appeared to be a much greater discontinuity than actually occurs in nature, and in the course of time a large number of generic and specific names were suggested which have since been suppressed or submerged.

The result of the examination of the collection of sea-pens made by the naturalists of the "Siboga" Expedition and of other large collections in the British and Dutch Museums has led to the conclusion that many of the genera and species of previous writers are but local varieties of genera and species that have already been described, and further that the degree of variability is much greater in those forms that exhibit radial symmetry than in those which are bilaterally symmetrical.

In order to make this point clear it is necessary to call attention to one or two features of the Pennatulid colony.

The body of a sea-pen consists of a colony of trimorphic or quadrimorphic zooids, which in the most familiar genus Pennatula has the external form of a feather.

The first-formed zooid or "oozooid" becomes profoundly modified in the course of its development to form the rachis and quill (or "stalk," as it is called in the terminology of the Pennatulacea) of the feather and all the other zooids (with a few exceptions), which are formed by gemmination from the oozoid, are borne by the rachis. Of the secondary zooids one group—the autozooids—exhibit the typical alcyonarian characters and alone bear generative organs; and it is the arrangement of these autozooids on the rachis that gives us the external signs of the symmetry of the colony.

In a bilaterally symmetrical genus such as Pennatula the autozooids are arranged in rows on opposite sides of the rachis, leaving two broad tracks, extending from the base to the apex, free from autozooids. These two tracks on the rachis that do not bear autozooids are known as the dorsal and ventral tracks and they can be distinguished from one another by the order of succession of the autozooids in the rows. In a radially symmetrical genus such as Veretillum or Cavernularia, on the other hand, the autozooids are scattered quite irregularly all round the surface of the cylindrical rachis and there is no trace either of a dorsal or of a ventral track free from autozooids.

Between these two kinds of sea-pens we find a series of genera that are intermediate in character as regards their symmetry. In Echinoptilum, for

* Hickson, S. J., 'Siboga Expeditie,' "LXXVII. Pennatulacea," 1916.

example, the autozooids are distributed all over the rachis except along a short and narrow groove on one side.

In Sclerobelemnon there is usually a well-marked dorsal track free from autozooids, but in some specimens one or, more rarely, more than one autozooid occurs in the course of the dorsal track. And in this genus there is no trace of a ventral track. In Anthoptilum there is always a complete dorsal track but usually very little trace of a ventral track. And finally in Pteroeides, Pennatula and some other genera both tracks are always present and always free from autozooids.

Deeply imbedded in the tissues of the rachis and stalk there is usually found a long calcified rod, known as the axis. It is always present in bilaterally symmetrical genera, but it may be absent or incomplete in some of the radially symmetrical genera.

In the walls of the zooids and in the surface tissues of the rachis and stalk there are usually found numerous calcareous spicules. The shape and size of these spicules are usually regarded as of the greatest importance in the diagnosis of genera and species, but although they are of great value as accessory characters in recognising some forms, and particularly in the bilaterally symmetrical genera, they are so variable, both in form and size, in others that they may be most unrealiable for systematic work.

It is unfortunate that owing to the deep-sea habits of the sea-pens we know very little about their powers of movement and habit. Rumphius,* in 1705, stated that the *Sagitta marina alba* (probably a species of Virgularia), found at low tide on the shores of Amboyna, burrows deeper and deeper into the sand as the tide ebbs, and Darwin relates that the sea-pens (probably a species of Stylatula) found off the coast of Patagonia, "when touched or pulled, suddenly drew themselves in with great force, so as nearly or quite to disappear." The huge *Osteocella septentrionalis* of British Columbia is said to writhe like a worm when it is caught, and there are scattered observations that in an aquarium Pteroeides will bore with its stalk into the sand and draw itself upright. But these observations were all made on bilaterally symmetrical sea-pens and we are still without information, by direct observation, about the activities and habits of the radially symmetrical forms.

We know then from direct observation that the sea-pens, unlike other Alcyonarian colonies, can move through the sand in which they burrow and that in some cases these movements are rapid and powerful and therefore must be due to muscular contraction.

We do not know from observation that the movements of the bilaterally

* Rumphius, 'D'Amboinsche Rariteitkamer,' 1705.

symmetrical forms are more rapid and more powerful than the movements of the radially symmetrical forms; but, judging from the arrangement and development of the muscles, it seems very probable that they are.

The difference in variability between the radially symmetrical and the bilaterally symmetrical sea-pens may be seen in almost all the important characters upon which the classification is based.

The axis is present in all the bilaterally symmetrical Pennatulacea. In such genera as Pennatula, Pteroeides and Scytalium for example every specimen that has been examined has been provided with an axis extending from one end of the colony to the other. Moreover, in all the specimens of Pennatula and of Pteroeides that I have examined the axis is always circular in section, tapering at each end to a fine point, and in all the specimens of Scytalium and Funiculina the axis is four-sided (square with rounded angles in section). There seem to be no variations from these characters in any species. In some of the intermediate genera such as Umbellula and Virgularia, for example, the axis is complete but is sometimes four-sided and sometimes circular in section. In the classification recently suggested by Kükenthal the species of the genus Umbellula are arranged in groups according to the possession of a round or a quadrangular axis. In the genus Virgularia most of the species that have been described have a cylindrical axis, but in *V. rumphii* and in *V. gustaviana* the axis is sometimes cylindrical and sometimes four-sided. In the radially symmetrical Pennatulacea the axis varies greatly in length or may be absent. In the genera Actinoptilum, Echinoptilum and Renilla no trace of the axis has yet been found. Of these genera the last two named show signs of incipient bilateral symmetry but are, nevertheless, more closely related in their general anatomy to the Veretillidæ than to the higher forms of Pennatulacea. In the genus Lituaria one species (*L. australasiæ*) shows an incomplete axis, in the other two species the axis is complete but, as the number of specimens of these species that have been examined is as yet very small, it is quite possible that there is considerable variation in this respect in each of the three species. It is interesting to note too that in *L. phalloides*, according to Fowler, the complete axis is associated with an incipient bilateral symmetry. In the genus Veretillum the axis is very variable. In two species (*V. malayense* and *V. tenue*) the axis is said to be complete, but as only five specimens have at present been examined, it may be a variable character. In *V. cynomorium*, of which a very large number of specimens have been examined, the axis is incomplete and varies considerably in length.

In the genus Cavernularia, which is, perhaps, the most typically radially symmetrical of all the sea-pens, the axis is extraordinarily variable. Of this

genus, five species have been described without any axis; in five species the axis is incomplete or variable, and in three species the axis is said to be complete. In the description of *Cavernularia habereri* from Japanese waters, Balss states that, on examining a number of specimens, some were found to have a short axis of variable length, and others to have no axis at all. As the axis in this species is found to be variable, even in specimens from the same locality, it seems probable that the length of axis cannot be taken as a sound specific character even in the diagnosis of a species of this genus.

As regards the shape of the axis in these forms, the evidence is, perhaps, not sufficient to justify any general conclusions. It has been described as round in section, square, square with fluted sides, and in one species at least (*L. hicksonii*) it is square above and round in section below.

The axis then seems to be a character which is variable both in length and shape in the radially symmetrical Veretillidæ, but attains to its full length in forms that show an incipient bilateral symmetry, as in *Lituaria phalloides*, and its full length and definite shape in the higher forms of Pennatulids, or to disappear entirely from all specimens that show an incipient bilateral symmetry, as in the genera Echinoptilum and Renilla. It is clearly an unreliable character for systematic purposes in the Veretillidæ, but may be a reliable character in other families.

The calcareous spicules that occur in the wall of the rachis and in the body wall and tentacles of the zooids have for many years been relied upon to afford good characters for the diagnosis of the species of the Pennatulacea, but the development of our knowledge of these characters shows that there are differences in the degree of variability of the spicules similar to those found in the case of the axis. In the genus Pennatula, for example, the spicules found in the rachis and zooids are always long, narrow spindles, showing three longitudinal curved flanges (the "dreiflügelig" spicule of Kükenthal). They vary in length according to position, and they vary in number and thickness according to position and according to the species, but they are always three-flanged. In the genus Pteroeides the spicules, although varying in length and thickness according to the position and species, are always smooth, long rods or spindles without the three flanges. Again, to take one more example from the higher bilaterally symmetrical genera, in the genus Scytalium the spicules are always very small, flat discs (about 0·05 mm. in diameter), round, oval, or dumb-bell-shape in outline.

In other families of bilaterally symmetrical sea-pens, we find examples, such as Virgularia, in which there are never any spicules in the rachis or zooids, and Stylatula, in which spicules are always present in a certain position in the colony. In another genus, Umbellula, with less pronounced

bilateral symmetry, spicules are entirely absent in some species, but present and very variable in others.

In the radially symmetrical Veretillidæ the spicules are so variable that they afford very unreliable characters either for generic or specific diagnosis. In Veretillum itself the spicules of the rachis are nearly all thin, flat plates or rods, but their size and outline shape are so variable, even in a single preparation, that it is difficult to find any common characters. They may be of almost any size up to a maximum of about 0·25 mm. in length. Some are round or oval discs with serrate edges, some are oval or dumb-bell-shaped, divided by a line into two parts, technically known as twins, others divided into four parts by crossed line (the quadruplets), then there are straight rods, spindles, and others of quite irregular outline.

In a careful investigation of the *Veretillum cynomorium* of the Mediterranean Sea, Niedermeyer* finds that "Die äussere Form der Spicula ist ausserordentlich variabel, und man kann wohl sagen dass sich kaum zwei gleiche vorfinden."

The variability of these spicules in form and size is paralleled by their variability in number. In some specimens of a species the spicules are so scarce that they may be overlooked, in others they may be very numerous. Moreover, in some parts of the rachis of a single colony they may be crowded together, and in other parts very scarce.

In Lituaria we also find a great variety in the distribution and shape of the spicules. Many varieties of flat plates and rods are found, similar to those of Veretillum, but, in addition, we usually find a number of thick double-star or "capstan" spicules, which occur in no other genus of the order.

In the wide-spread genus Cavernularia most of the spicules in some species are straight, flat rods, but forked or branched forms and spindles are sometimes abundant. Kükenthal and Broch† have placed a species into a separate genus (Cavernulina) on the ground of the variability of its spicules, and state, "mit voller Sicherheit," that such a variation does not occur in Cavernularia. But this statement is not in accordance with the previous investigations of Kölliker‡ nor of Balss,§ who states, in his description of *C. habereri*, that the spicules are so extraordinarily variable that they are not adapted for species diagnosis.

* Niedermeyer, 'Zool. Anz.,' vol. 43, p. 263 (1913).

† Kükenthal and Broch, 'Wiss. Ergeb. d. Deutschen Tiefsee-Expedition "Valdivia,"' 1911.

‡ Kölliker, 'Abh. Senckenb. Ges.,' 1870.

§ Balss, 'Abh. K. Bayr. Akad. d. Wiss.,' Supplementband, 1910.

A remarkable illustration of the variability of the spicules of this genus was obtained by the examination of four specimens obtained by the "Siboga" Expedition. These specimens were all dredged up at the same time in the anchorage at Amboyna, and, although they vary in length from 40 mm. to 113 mm., there can be no doubt that they belong to the same species. A preparation of the cortex of the rachis of the two larger specimens shows a dense felt-work of spicules, and, when these are teased out, it is found that the great majority of them are flat rods with round bifurcated extremities; but, in addition, there are many twins, triplets, and other varieties. In the two smaller specimens, however, the spicules are much less densely clustered, and the predominating type is a small, flat rod without bifurcated extremities. An even more remarkable illustration, however, was found in the examination of a number of specimens of *Sclerobelemnon burgeri* from the same dredging in the Molo Strait. This species, although it usually exhibits an incipient bilateral symmetry, is so closely related to Veretillum that some specimens are almost exactly intermediate in character between the two genera. The spicules of the rachis are, as in Veretillum, thin, flat plates with a great variety of outline; but the majority of them are irregularly round, oval, or dumb-bell-shaped, frequently divided by lines into twins, triplets, quadruplets, and multiplets, but rod- or spindle-shaped spicules are scarce. With so much variety in the spicules of a single specimen there was found great variation from one specimen to another. In one of two specimens from the same station, of approximately the same size, the spicules were few in number, and the larger ones 0·4 mm. in diameter, and in the other the spicules were numerous, and the larger ones only 0·04 mm. in diameter. This difference between the two specimens is so striking that, according to the general practice of systematists, they would undoubtedly be placed in distinct species, but fortunately there are 60 other specimens of various sizes from the same locality, and an examination of these shows that no two specimens are alike as regards the spicular armature, and that there are many intermediate cases between the two that were first mentioned. There can be no doubt therefore that in *S. burgeri* we have an example of a species in which the spicules are so variable that they cannot be regarded as being of any value for the separation of species.

The presence or absence of spicules in the expansible parts (anthocodiæ) of the autozooids has been used by some authors to distinguish genera from one another. Thus Kölliker distinguished the genus Clavella from Lituaria by the presence of spicules in the anthocodiæ of the former and their absence in the latter, but the only known species of the old genus Clavella resembles *L. phalloides* so closely in other respects that it cannot be

separated generically from it. In a species described recently by Thomson and Simpson* from the Indian Ocean under the name *L. hicksoni*, there are no spicules in the tentacles. In a species described by Balss from Japan, under the name *L. habereri*, there are numerous spicules in the tentacles. In other respects the two species are so much alike that it is difficult to separate them, and, as regards the spiculation of the tentacles, we find an intermediate condition in specimens from the Malay Archipelago, in which spicules are occasionally present in the tentacles, but usually absent. In the genus Veretillum spicules are said to be present in the anthocodiæ of *V. cynomorium*, but are absent in that position in the other four species.

Similarly with respect to the presence of spicules in the cortex of the rachis. A genus (Policella) was established by Gray† in 1870, and more fully described by Kölliker in 1872. In Kölliker's description great stress was laid on the character of the absence of spicules in the rachis, to distinguish the genus from Veretillum. On making an examination of the Gray's type specimen, however, he found a considerable number of large spicules in the rachis. Marshall and Fowler‡ found no spicules in the rachis of two specimens of *P. manillensis* from the Indian Ocean, but a few calcareous bodies in that position in a new species they named *P. tenuis*. In a specimen from the Malay Archipelago, which in other respects closely resembles the *P. tenuis* of Marshall and Fowler, I could find no trace either of formed spicules or of calcareous bodies. With the failure of this character, the genus Policella has become merged with Veretillum.

No such wide variations as regards the variations in the distribution of spicules are found in the higher bilaterally symmetrical Pennatulids. In Pennatula, Pteroeides, or Scytalium, the presence of spicules in the rachis is a constant character; in Virgularia their absence is a constant character. In any one species of the species that have spicules in the rachis, spicules are either present or absent in the body-wall or the tentacles of the anthocodiæ. For example, spicules occur in the tentacles of *P. naresi*, but do not occur in the tentacles of any one of the many specimens of *P. murrayi* that I have examined. In *S. balssii* there are numerous spicules in the body-wall of the anthocodiæ and in the tentacles, but in *S. martensii*, of which I have had over a hundred specimens to examine, spicules are only found quite at the base of the body-wall, and never in the tentacles.

This character, however, is one that must be used with some caution for

* Thomson and Simpson, 'Indian Alcyonaria,' Calcutta, Part II, 1909.

† Gray, 'Catalogue of Sea-pens, British Museum,' 1870.

‡ Marshall and Fowler, 'Trans. Roy. Soc. Edinb.,' vol. 33 (1887).

systematic purposes, even in the higher Pennatulids, as it is possible that differences may be found in some cases in the spicular armature of young and old colonies. Thus Grieg has shown that, in young colonies of *Funiculina quadrangularis*,* spicules are present in the tentacles of the young, but not in the tentacles of the old colonies. In other cases the spicules seem to be more numerous and widely distributed in the older colonies than in the younger ones.

Moreover, if the spicules of any particular part of the rachis, such as the dorsal track, the calyx of the siphonozooids, the outer border of a leaf, or the tentacles be examined in a number of specimens of a given species, it will be found that they are constantly of the same form and approximately of the same size, although occasionally local variations are found in the number and size of the spicules in the zooids, due perhaps to local environmental conditions. An interesting example of such a local variation in the spicules was found in the examination of three specimens of *P. fimbriata* from the coast of Timor and two specimens of the same species from the Kei Islands. The species is an interesting one, as being intermediate in many respects between the two genera Leioptilum and Pennatula, and one of the distinguishing features given by previous authors of the genus Leioptilum is that spicules are confined to the margins of the leaves, whereas in Pennatula they are more evenly distributed throughout the whole leaf. In two specimens of *P. fimbriata* from the Kei Islands the spicules are confined to the margins of the leaf as in Pennatula, but in the three specimens from Timor these marginal spicules are supplemented by others, extending almost to the base of the leaf. The spicules of the Timor specimens, moreover, are much larger and more numerous throughout the colony than in the specimens from the Kei Islands. Many other instances, probably, could be found of local variations of the spicular armature of the higher Pennatulids, but such instances ought not to obscure the much more impressive fact of the constancy of these characters in specimens taken from a single locality, and the remarkable similarity, in most cases, as regards this character, seen in specimens from distant localities, when the higher Pennatulids are compared with the radially symmetrical Veretillidæ.

There is one more character frequently used in systematic treatises that may be briefly referred to before passing on to a more general statement. If a large number of specimens of a species of Pennatula from a single locality be carefully measured, it will be found that the ratio of the length of stalk to length of rachis is fairly constant. For example, in 38 specimens of *P. phosphorea*, var. *candida*, from the Mediterranean Sea, the ratio of

* Grieg, 'Bergens Museums Aarbog,' 1896.

stalk-length to rachis-length was about 1 : 1·5, the range extending to 1 : 1·9 and 1 : 0·8. In nine specimens of the same species, var. *variegata*, from the coast of Denmark, the range extended from 1 : 1·86 to 1 : 1·13. In 33 specimens of *P. pearceyi* from the coast of East Africa, the range extended from 1 : 1·7 to 1 : 3·2 (Kükenthal and Broch). In six specimens of *P. murrayi* from the coast of Timor, the range extended from 1 : 3·6 to 1 : 5·5, and in four specimens of the same species from the Kei Islands from 1 : 2 to 1 : 4. All the specimens of *P. phosphorea* were obtained in shallow water (150 metres), the specimens of *P. pearceyi* in deep water (693–1134 metres), the deep-sea forms in this case having a shorter stalk.

The specimens of *P. murrayi* from Timor were obtained in shallow water (112 metres), and those from the Kei Islands in deep water (310–397 metres), the deep-sea forms in this case having a longer stalk.

A consideration of these ratios and others that have been worked out leads to the conclusion that, even in the genus Pennatula, the stalk-rachis ratio is not a very reliable character for the determination of species, and, further, it seems to indicate that the rachis is much more variable in deep-sea species than in shallow-water species. Whether the relatively short stalk in specimens of *P. murrayi* from deep water is to be correlated with depth or with the character of the sea bottom is a matter that requires further investigation. Nevertheless, through all the conflicting evidence afforded by these measurements, it seems that the specimens of a given species living under the same conditions of depth and sea bottom have in this genus, at least, a ratio of length of stalk to length of rachis that varies within a small range from a common average, and this conclusion is confirmed by the measurements I have made of 30 specimens of *S. martensii* from the same locality off the coast of Timor, in which the length of the stalk was about 4½ times the total length of the colony. In the radially symmetrical Veretillidæ it is difficult to obtain trustworthy estimates of this ratio, because specimens seem to suffer more from contraction during preservation than specimens from the genera with a complete axis. Neidermeyer found, however, that in *V. cynomorium* no two species possessed the same ratio of length of stalk to length of rachis, and my own impression, from the study of this family, is that the character is much too variable, even in specimens from the same locality, to be of any value for systematic purposes.

Having now discussed in some detail the differences observed in the variability of certain individual characters, it is necessary to turn to the characters as a whole of the genera and species to ascertain if their study confirms the conclusion already indicated. It might be anticipated that if the individual characters in any one group are more variable than in another

there would be greater difficulty in determining the generic and specific limitations in the former than in the latter, and that there should be, also, a greater discontinuity between genera and species of the former, that are less variable, than there is between the forms that are more variable.

This is exactly what we do find in the order of the sea-pens. In the higher groups with very pronounced bilateral symmetry there is seldom any difficulty in assigning a specimen to its proper genus. In the family Pennatulidæ, for example, there are four well known genera: Pennatula, Leioptilum, Acanthoptilum, and Scytalium. Pennatula stands out distinctly from the others in the character and distribution of the spicules, the arrangement of the spicules to form the so-called calyx teeth, in the shape and texture of the leaves, and in several other characters. The only difficulty in this case arises in the species *P. fimbriata*, in which, as previously mentioned, the arrangement of the spicules on the leaves is in some specimens intermediate between Pennatula and Leioptilum. Leioptilum, with its closely set leaves with thick margins, is also quite distinct, Scytalium with its minute flat spicules can always and at once be separated from the other genera, and Acanthoptilum with its fan-shaped arrangement of flanged spicules in the leaves and minute disc-shaped spicules in the calices is equally distinct. In the family Pteroeididæ, also the three genera Pteroeides, Sarcoptilum, and Gyrophyllum are quite distinct. Each genus is distinguished by several well-marked characters, and there are no intermediate forms.

In the Veretillidæ, on the other hand, the generic groups are very indistinct, as is particularly well shown in the instability of most of the generic names. Clavella has been merged with Lituaria, Policella with Veretillum, Sarcobelemnon, Stylobelemnon, Fusticularia, and Cavernulina, with Cavernularia, and the characters which are used for the separation of the four remaining genera, Lituaria, Veretillum, Cavernularia, and Actinoptilum, are admittedly very variable and unsatisfactory. Lituaria differs from Veretillum only in the presence of the capstan or double-star spicules, and in some specimens of Lituaria these spicules are not very abundant, and are always supplemented by flat plate-like spicules similar to the prevailing type in Veretillum. Veretillum is closely related to Cavernularia, although the autozooids are usually larger in the former than in the latter, and the spicules of Cavernularia are usually rod-shaped or forked. Actinoptilum is separated from Cavernularia by the presence of verrucæ for the autozooids, a character which is very variable, and depends to a considerable extent upon the method of preservation.

Moreover, there are connecting links between the Veretillidæ and the related families with incipient bilateral symmetry. A few rare specimens

of Echinoptilum without any ventral track bridge the gap between the Echinoptilidæ and the Veretillidæ, and some specimens of *Sclerobelemnon burgeri* can only with difficulty be separated from Veretillum.

As regards the separation of generic groups into species, there are throughout the group endless difficulties owing to the want of agreement among the authorities as to a working plan for recognising the difference between "species" and "variety." These difficulties are the same as those that are met with in nearly all the classes both of the animal and vegetable kingdoms, and do not call for special comment. Nevertheless, in the study of a large collection of Pennatulacea a very great difference is observed in the facility with which specimens of the higher families and of the lower families can be confidently assigned to their specific groups.

In the genus Pennatula, for example, some of the species, such as *P. grandis, P. fimbriata, P. murrayi, P. naresi,* and *P. phosphorea*, are quite distinct, and can be recognised by several well-defined characters. In Scytalium three of the six species are well defined, and of the others our knowledge is not yet sufficient to enable a judgment to be given as to whether they are well-defined species or not.

Even in Virgularia, a widespread genus of which a very large number of species and specimens have been examined and described, several of the species can be easily recognised on careful examination. In the Veretillidae, however, difficulties of arranging specimens in defined specific groups are practically insuperable. When a large number of specimens are obtained from one locality they are found to exhibit so much variation that overlapping of several described species may be discovered, and the present-day classification is extremely unsatisfactory. Moreover, in the genus Echinoptilum, with incipient bilateral symmetry, the characters that are used to separate the six species that have been described are so unsatisfactory that it seems quite probable that these species will prove to be only local varieties of one widely distributed but very variable species. It would take too much time and space to analyse more fully the specific grouping of the order. Such an analysis would involve the discussion of some exceptional cases such as that afforded by the genus Pteroeides in which the species appear to overlap as in the radially symmetrical forms. It is only to be taken as an expression of opinion based on a long study of a very large collection of specimens of sea-pens that with the evolution of a bilateral symmetry and increased power of movement the specific groups tend to become better differentiated.

### 3. *On the Classification of Sedentary Animals.*

The difficulties that are found in separating the radially symmetrical Pennatulacea into defined specific groups are met with even in a more pronounced degree in the study of the corals, in the sub-orders of Alcyonaria, and in some other groups of sedentary animals; and it may even be suggested that, as our knowledge of the range of variation increases, the conclusion will be reached that, in some cases at least, the evolution of those discontinuous groups which are commonly recognised as "species" does not occur in nature. In some of the genera of sedentary Cœlenterata, such as Millepora, Tubipora, and Stylaster, and in some sedentary Foraminifera such as Sporadotrema and Polytrema, with a very wide geographical distribution in shallow water, very careful examination of a large number of specimens and an analysis of all possible characters that would be used in classification show very little if any evidence of the existence of discontinuous specific groups. There are differences between specimens from different localities in the mode of branching, in colour, in the size of the zooids, and in the arrangement of the zooids on the colonies, but these characters are found to be so variable when a number of specimens are examined from the same locality that it is impossible to use them in the definition of species. Similarly Bernard, in preparing his monumental catalogue of the Madreporaria in the British Museum, found the difficulties of maintaining the old or establishing new species so great that he abandoned the orthodox binomial system and grouped the specimens according to their growth forms and geographical distribution, "The task of establishing genetic species," he writes, "is practically hopeless in such a case as Porites."* And Wood Jones† after a careful study of the different forms assumed by the corals on a reef writes, "There is no doubt that a great number of our museum-made species are mere vegetative varieties, produced in response to the demands of the environment."

Nor are the difficulties of determining species confined to the sedentary Cœlenterata, as we see, for example, in the statement made by Gregory‡ in his introduction to the catalogue of the Jurassic Bryozoa, that he came reluctantly to the conclusion "that there are no true genera among Cyclostomata but only certain convenient artificial groups of species." It might be urged in reply to these expressions of opinion, and to many others of a similar kind that have not been quoted, that, unless the anatomy of the zooids and their connections with one another are as carefully studied as the skeletal structures, the conclusions are based on insufficient evidence. There

* Bernard, 'Catalogue of Madreporaria, Brit. Mus.,' V, p. 27 (1905).

† Wood Jones, 'Proc. Zool. Soc.,' 1904, p. 555.

‡ Gregory, 'Catalogue of Jurassic Bryozoa, Brit. Mus.,' 1896, p. 21.

are many practical difficulties in the investigation of a large number of examples of the soft and perishable tissues of these organisms, difficulties which are insuperable in the case of the extinct genera; but it seems improbable that a well-marked discontinuity in the structure of the mesenteries, tentacles, body wall and other parts of the zooids would leave no corresponding impressions on the hard parts as they are built up.

A thorough investigation of the soft parts is, however, most desirable, whenever it is possible, to test the accuracy of the conclusions derived from the study of the hard parts, and we have already a valuable contribution to our knowledge in this direction in the investigations of Mr. Matthai on the anatomy of certain Astræid corals. Mr. Matthai* gives a list of 10 different characters of the hard parts of these corals which are usually regarded by systematists as of value in their schemes of classifications and comes to the conclusion that none of them have any constant value "and therefore the distinctions based upon them would be arbitrary," but he finds that "any species whose limits had once been settled by the study of both polyps and hard parts can be recognised later from the hard parts alone." With the admitted variability of the hard parts, it is not clear how this recognition of the species can be made; but it does not appear to me that the author of this valuable contribution to our knowledge has been able to prove from his investigations that the soft parts of these corals are less variable than the hard parts.

In an examination I made some years ago of both the hard and soft parts of a large number of specimens of the genus Millepora, obtained from many different localities both in the East and in the West Indies, I† found that the soft parts gave no assistance in the determination of species. But what may be true of one genus or family may not be true of another, and it is quite possible that in some kinds of sedentary animals, and more particularly in some forms of floating and drifting animals, there may be true genetic species. The causes that have brought about, in the course of evolution, the discontinuity which, in the bilaterally symmetrical animals, enables us to recognise distinct species are so numerous and involved that it would be presumptuous to assert that they can never affect animals that do not move about by their own muscular effort. In fact the existence of specific groups in the higher plants, every bit as well defined as in the higher animals, should be sufficient to convince any one that causes leading to discontinuity may affect all kinds of sedentary organisms. In the course of my systematic work on Cœlenterata, I have come across several instances

* Matthai, 'Trans. Linn. Soc.,' vol. 17, p. 1 (1914).

† Hickson, 'Proc. Zool. Soc.,' 1898.

in which there seem to be distinct specific differences between groups of specimens belonging to the same genus. For example, the two species *Alcyonium digitatum* and *A. glomeratum* appear to be quite good species. They are found close together in some parts of the waters of the British coast (*e.g.*, the south coast of Cornwall), and the first-named species, which is by far the most abundant, exhibits a wide range of variation in form, colour, and spiculation. Nevertheless, I have not yet found a single variety of *A. digitatum* among the many hundreds I have examined that could possibly be mistaken for *A. glomeratum*, or any other species of the genus. But even if it be established that specific discontinuity does occur in some genera of sedentary animals, it does not follow that such discontinuity occurs in all or even in a majority of them, and the evidence, so far as it goes at present, tends to show that it is exceptional rather than universal.

In attempting to make a scientific classification of any group of animals it is found that the characters of the greatest value are those that are least variable; but characters that are very variable in one family or genus may be much less variable in another family, and it is therefore necessary, before a suggested scheme of classification can be regarded as stable, to ascertain the range of variation of the characters it is proposed to use.

Thus in the shrimp Hippolyte the character "colour" is so variable that it cannot be used in specific diagnosis, but in the crayfish Astacus (Potamobius) the red colour of the chelæ of *Astacus flaviatilis*, and the pale colour of the chelæ of *A. pallipes* are invariable characters, supported by others, for distinguishing the species.

In the sea-anemone *Metridium marginatum* only 33 per cent. of 131 adult specimens exhibited the arrangement of mesenteries which is regarded as normal for the species, but in *Actinia equina* only 4·24 per cent. showed variations from the normal arrangement of the mesenteries. In *A. equina*, therefore, the arrangement of the mesenteries is a much more reliable character for specific diagnosis than it is in *Metridium marginatum*.

Some years ago* I suggested the use of the term "plastic" for characters that are variable within the species and "rigid" for characters that are fixed, or show only a small percentage of variations. The term "plastic" suggests that the characters are to some extent moulded or modified in the course of their development by external forces, and that the exact form that they exhibit in the adult must be due in large measure to the environment. There seems to be no doubt that this is true of many of the plastic characters of sedentary animals, although it may be difficult to prove to be true in the case of some of the variable characters of the higher bilaterally

* 'Reports of British Association,' 1903, p. 680.

symmetrical animals. But characters that are rigid and are not, therefore, subject to fluctuations caused by external forces must be genetic, they are characters transmitted as such by heredity. It is on the rigid characters, therefore, rather than on the plastic characters, that we must rely for a scientific basis for the diagnosis of species. But in the groups of radially symmetrical animals with which we have been dealing more particularly in this lecture, it has been shown that there is a larger proportion of plastic characters than in the bilaterally symmetrical animals, and, moreover, that many of the characters that are plastic in one genus may be rigid in another. The first step therefore in a scientific classification of these animals is to find out the degree of plasticity of the characters it is proposed to use for the diagnosis of each genus and species. Until this is done, the classification can only be regarded as provisional. But the practical difficulty that so often occurs in systematic work is that the number of specimens available is so small that no reliable estimates can be formed of the plasticity of the characters they exhibit, and the question arises, What should be done with isolated specimens of which the plasticity of the characters cannot be determined? It seems to me that if a new specimen differs from previously described specimens of a known species only by one character that is known to be very variable in the genus, it should not be regarded as a new species, but be regarded as a plastic variety of the nearest known species, and if it is desired to call attention to some peculiarity of the plastic form, an additional name should be given to it to indicate this peculiarity. In order to avoid the term "variety," which is so frequently applied in higher animals and plants to genetic variations, I have used the term "facies" to signify a variety which is probably purely plastic in character. Thus, in *Millepora alcicornis*, I have used the expressions facies *ramosa*, facies *plicata*, facies *verrucosa*, etc., for various forms of growth or surface markings, the peculiar features of which are almost certainly caused by the external environment; and in the Foraminifer *Sporadotrema cylindrica* I have used geographical terms, such as facies *providentiæ*, facies *amirantiæ*, etc., for specimens differing from one another in plastic characters that cannot be easily described by a single word.

To use either of the terms "variety" or "sub-species" in these cases would be entirely misleading, for, as they are commonly used with reference to both the higher animals and plants, they imply genetic differences. Thus, an albino mouse or an albino stock is a variety that breeds true. Mammals with long hair, instead of the short hair that is normal for the species, produce offspring that are long-haired, and plants that have cut leaves instead of the entire leaf that is normal for the species produce offspring with

cut leaves. But, so far as we can judge from circumstantial evidence, the offspring of a plicate *M. alcicornis* or a verrucose *M. alcicornis* would only produce plicate or verrucose offspring if the external conditions of their growth were the same as those of the parents.

The advantage of using some such word as "facies," instead of "variety" or "sub-species," to express these plastic variations in the sedentary forms of animal life is conclusive, but I would specially urge its adoption because of the tendency shown by some systematists, weary perhaps of the number of different forms of their specimens, simply to mention the name of the species to which they refer them without description. In this way a great deal of valuable information about the plasticity of species is withheld. The tendency there is to provide distinct specific names for local environmental forms has undoubtedly led to a great confusion in our system, and this confusion has, in its turn, tended to discourage systematic work in many groups of sedentary animals. New species are founded, and in a few years merged with others. However carefully the descriptions are made, there is little prospect of the system proposed remaining stable for any length of time, and the result is that it is becoming increasingly difficult to get any one to undertake a systematic description of a large collection of these groups. The advantage of the system of proposing new specific names for specimens differing from others only by certain plastic characters, however, must be acknowledged. It has at least placed on record detailed facts regarding these characters, and provided many excellent figures for future investigations. By the system I have suggested of using the species in a more comprehensive way, and describing the "facies" as frankly a local environmental form, there may be, I hope, a prospect of the revival of detailed analysis of collections.

### 4. *Evolution of the Pennatulacea.*

In the study of the order of the sea-pens, we find a series of forms showing at the one end of the scale almost complete radial symmetry, and at the other end a well marked bilateral symmetry. Moreover, as I have shown, it is among the radially symmetrical that we find that overlapping of genera and species, due to the wide range of variation of plastic characters, which makes systemic work so difficult, and among the bilaterally symmetrical forms that we find, on the whole, well defined genera and species. The question arises, then, whether this series represents the general outlines of the evolution of the order, *i.e.* from radial symmetry to bilateral symmetry, or *vice versâ*, or whether a centrally placed form such as Protoptilum represents the most primitive sea-pen from which the radially symmetrical forms

have been derived by degeneration on the one hand, and the higher bilaterally symmetrical forms by differentiation and specialisation on the other. In the earlier writings of Kölliker, Studer, Wilson, Jungersen, and Bourne, the view is expressed that the Pennatulacea are derived from a bilaterally symmetrical stock, and such genera as Bathyptilum or Protoptilum are regarded as the most primitive genera of recent sea-pens.

It is to Kükenthal* that we owe the first definite suggestion that it is the radially symmetrical Veretillidæ that are the most primitive, and with his view I am in agreement.

The principal reasons in favour of Kükenthal's view may be summarised as follows :—

(1) The general structure of the colony of the radially symmetrical Pennatulacea is simpler than that of the bilaterally symmetrical ones. In the latter we find the two kinds of zooids, autozooids and siphonozooids, distributed all over the surface of the rachis without any definite arrangement in rows or leaves. It is difficult to believe that, in the evolution of the sea-pen from its Alcyonacean ancestry, there could have arisen by some great mutation that very definite and orderly arrangement of these zooids on each side of the rachis, that we find in such genera as Pennatula and Scytalium, and still more difficult to conceive a reason for a subsequent change of this arrangement unless accompanied by some very definite change of habit.

(2) In passing through the series leading from radially to the bilaterally symmetrical sea-pens, we find an increasing differentiation in the structure of the colony. Such definite organs as the radial canals of Virgularia and Osteocella, the specially differentiated zooids, which I have called "mesozooids," of Pteroeides and some species of Pennatula, and that peculiar type of spicule known as the three-flanged or "dreiflügelig" spicule, do not occur at all in the Veretillidæ, nor in any known genus of the other groups of Alcyonaria.

(3) The axis of the higher Pennatulacea is a skeletal structure which has no homology with any structures found in the other orders of Alcyonaria. It must have arisen within the Pennatulid stem as an organ adapted to the needs of a free colony, with an elaborate and powerful set of muscles. We should expect to find, therefore, this structure to be better developed in the higher forms with the more powerful muscles than in the more primitive forms, in which the muscular system is not so well developed. If we accept the view that the radially symmetrical forms are the most primitive, this is exactly what we do find. As already mentioned, it is only in

* Kükenthal, W., 'Verhandl. VII. Internat. Zool. Congress. Graz,' p. 563 (1910).

the genera Cavernularia (some species), Actinoptilum, Echinophilum, and the aberrant Renilla, that we find that the axis is absent, and in Cavernularia (some species), Veretillum, and Lituaria that we find it incomplete.

(4) In the study of the Veretillidæ, Kükenthal discovered that the system of endodermal canals in the rachis has a closer resemblance to that of the other Alcyonacea than that of any of the higher sea-pens.

(5) In this connection, a small piece of evidence, but not an unimportant one, is found in the genus Lituaria, a genus closely allied to Veretillum, but occasionally showing incipient bilateral symmetry in the presence of a short groove on one side of the rachis free from autozooids, similar to the groove seen in Echinoptilum, and more rarely in Actinoptilum. In this genus only, we find, interspersed with other spicules of the types found in other Veretillidæ, a number of thick spicules of the shape of a dumb-bell, with sharp tubercular spines standing from each side of the swollen extremities. This type of spicule, known as the twin star ("doppelsternige," Kölliker) or "capstan" spicule, is not found in any other genus of the Pennatulacea, but is a common type in the Alcyonacea. This fact is significant, because the Pennatulid spicules, except in Lituaria, are quite different to those found in the Alcyonacea. The thin flat flakes of Veretillum, the smooth flat rods of Cavernularia, the smooth cylindrical rods of Umbellula and Pteroeides, and more particularly the remarkably specialised three-flanged spicule of Pennatula and several other genera, are quite peculiar to the Pennatulacea, and could not be confounded with any type of spicule found in the other Alcyonaria. The conclusion seems to be inevitable that the types of radially symmetrical Pennatulacea are not degenerate, but do represent the nearest approach to the ancestral type of which we have any knowledge.

The evidence in favour of the view that the radially symmetrical Pennatulacea are the most primitive appears to me so strong that it is worth while to consider how they arose from the Alcyonacean stock. Such consideration must necessarily be purely speculative, because at present no species has been discovered that can be regarded as intermediate in structure between the Pennatulacea and the other orders of the Alcyonaria and because the ontogeny of the Pennatulacea so far as it is known does not really shed any light on the matter. There seems to be little doubt that the ancestral form of the sea-pens was colonial in habit. At any rate there is no evidence derived from embryology or morphology to show that the origin of the stock dates back to the original solitary Alcyonarian polyp. If we are justified in making this assumption, as all previous writers have done, there are two hypotheses as to the further evolution. Either the Pennatulacea are derived directly from a

sedentary Alcyonarian colony or indirectly through a floating or drifting stage. In either case the ancestry must have been radially symmetrical.

It seems probable from the little knowledge we possess of the natural history of the sea-pens that they are all capable of boring into the sand or mud at the bottom of the sea by the muscular movement of the stalk, and the difficulty of deriving them directly from the sedentary ancestry is that the body wall of such Alcyonarians is not provided with muscles capable of any such movements. There must have been between the absolutely sedentary ancestry and the more active burrowing Pennatulid an intermediate stage with some powers of muscular movement, and it may be suggested that this stage was a floating or drifting colony. The transition from a sedentary to a floating habit is not difficult to understand. The feeble musculature of the endoderm of Alcyonarians, which is used for contracting the cœlenteric cavities under certain unfavourable conditions, such as removal from the sea-water or exposure at low tide, could readily be adapted to slow pulsations sufficient to keep a colony afloat in running water and particularly so if it were supplemented by the ciliary action of the ectoderm. Moreover, an Alcyonarian showing a dimorphism of the zooids such as we find in Sarcophytum and Anthomastus, in which a flow of water through an elaborate plexus of canals in the substance of the colony is produced by the action of the siphonozooids, would be a more favourable form for adaptation to such a pelagic mode of life than the heavier monomorphic forms. In all the sedentary Alcyonaria about which we have information on the point the cilia supported by the ectoderm cells of the larva are lost when the fixation takes place. There is no record of a ciliated ectoderm covering the colony in any species. In the Pennatulacea, on the other hand, Kölliker* originally pointed out, there are certainly patches or tracts of cilia on the ectoderm of the rachis, although they appear to be absent on the stalk. My view, therefore, is that there was a stage in the evolution of the Pennatulacea when the colony became free from its sedentary habit and was dimorphic and ciliated. If this transition actually occurred, it would not be exceptional in the animal kingdom. The remarkable hydrozoan *Pelago hydra*, discovered by Dendy, was undoubtedly derived from a sedentary ancestry, and there is good reason to believe that the Salps and Doliolum were independently derived from sedentary Tunicates. It is unlikely that in this stage the axis was developed, as a heavy skeletal structure of this character would be of little use for the attachment of muscles such as would be used for pulsating movements, and its weight would impair the flotation power. The shape of the body, in

* Kölliker, 'Anat. System. Beschreibung der Alcyonarien,' p. 424 (1872).

conformity with other floating forms, would probably have shown a perfect radial symmetry, and, from the ancestral history, it would have probably had an outline like a top or pear. Without referring to certain changes of internal structures, which it is much more difficult to understand, we may suppose that, at the time this intermediate form was assuming the full Pennatulid characters, it was in form not unlike a Cavernularia, and succeeded, at times, in obtaining an insecure foothold in the sand. This suggestion is supported by the fact that *C. malabarica*, as related by Fowler,* is the only species of the order that has been found washed ashore in great numbers after a storm.

The habit and structure of the Pennatulid stock being thus established, the further evolution followed the main lines of increased powers of deep, rapid burrowing in the sand, accompanied by a completion of the development of the muscles and a gradual change to an almost complete bilateral symmetry of the colony as a whole.

This conception of the evolution of the Pennatulacea, which I have ventured to bring forward, seems to me to give a satisfactory explanation of two difficulties that are met with in the alternative hypothesis of a bilaterally symmetrical ancestry. It is very difficult to understand why a bilaterally symmetrical colony provided with an axis and with powers of burrowing deeply in the sand should lose the axis and become radially symmetrical. It has been suggested that the Veretillidæ are degenerate, but I cannot see that there is a shadow of evidence to support this view. They are not parasitic, sedentary, nor cryptic in habit, and there is no reason for supposing that in any structural characters they show signs of retrogressive evolution. The only ground for the assertion is that they show greater variation than the bilaterally symmetrical families, but, although it is undoubtedly a fact that degenerating organisms and structures are more variable than others that are not degenerating, it does not follow that, because organisms or structures are very variable, they are consequently degenerate or degenerating.

As I have attempted to show in the earlier part of this lecture, the great range of variation seen in the radially symmetrical Pennatulacea is to be associated not with the idea of degeneration, but rather with their feeble powers of movement and their radial symmetry.

* Fowler, G. H., 'Proc. Zool. Soc.,' 1894, p. 376.