

Part 2.



The Problem of Corals Species

Up to the end of the 80's of the XIX century the problem of species was absent in coral descriptions. Taxonomic or identification works were conducted on the basis of single specimens or a very sparse series of samples. It is quite natural and especially revealing that the investigation of variability in these animals was almost impossible. Lack of knowledge about variability resulted in description of "new" species, which very often were only local variants, nevertheless they received a taxonomic status. Other identifications were conducted only by way of comparison with specimens identified earlier, and it was rather difficult to identify species without a described sample at hands (Studer, 1901). The presently recognized problem of coral identification due to very wide variability of their morphological features appeared only with investigation of large collections, which give the opportunity to compare similar samples within a series.

For the first time we knew properly about the variability of corals. The collections of the Challenger expeditions were actually the first to contain representative series of many species, reported by J. Quelch (1886). He wrote that for most genera he presented, little or nothing was known about the early stages growth of the corals, colonial or solitary. J. Quelch mentioned that information about coral ontogenesis and their variability could be obtained in the future. Naturalists will be well informed on these issues when they collect and study types of coral variability. In the same work this researcher wrote about the necessity of critical comprehension of data on ancient Rugosa in connection with modern corals, and vice versa. He wrote that comparison is an essential part of characterization of main groups of modern and fossil corals (1886, p. 8).

S. Pace (1901) showed in *Turbinaria* that many morphological features and growth forms of corals which were used for distinguishing species in a given coral group, in fact have only a secondary value, especially colony shape, and in most cases reflect environmental effects. On the other hand, not all variations between two variants (in any of a variety of genera) are simply expressions of adaptive modification. According to Pace's opinion (he mentioned experimental observations of three species of clearly-distinguishable *Turbinaria*, inhabiting the same place), some variations of specimens, living close to each other, cannot be explained by environmental conditions but have a hereditary nature. This author underlined that determination of the limits of variability of any species is not an easy task, especially if investigation is not based on the materials of museum collections. In the case with corals it becomes a very difficult problem.

In conclusion, speaking on the problem of species, S. Pace wrote that everyone who studies nature not only in museums or laboratories, but also in the field, will inevitably face facts which will leave him face to face with the question, which always arises: "What are species?" This question, which cannot be answered satisfactorily until taxonomical investigations are conducted at a higher level,

when a large series of specimens and other data, collected as a result of special observations and facilitating the solution of this problem, residing in the familiar word “species”, are available for zoologists.

The main arguments on the problem of species started after the work of G. Bernard (1903, 1905, 1906) who refused to use Linneaus nomenclature and used a taxonomical unit named “local shape.” Such an attack on the existing classification of corals demonstrates the importance of the problem in full as early as at the beginning of coral taxonomy, but unfortunately, as it was correctly noted by J. Veron and M. Pichon (1976), such works add very little to our knowledge of coral taxonomy. Bernard’s works were subjected to criticism immediately after publication (Gardiner, 1904; Bedot, 1907; Vaughan, 1907; and others).

F. Wood-Jones (1907), highlighting the investigation of living corals in their habitats, pointed out difficulties in establishing the meaning of growth form as a species feature. Various vegetative forms of the same species can be produced by different environmental conditions, and very dissimilar coral forms of the same species, formed under the effect of extremely different conditions, can be found at the same atoll. However, conditions intermediate between those that produce extreme colony variants exist in various parts of an atoll, and intermediate coral growth forms can be found in such places. He did not make an attempt to classify genetic coral growth forms, but he believed that every coral could have any colony form, since vegetative form is a result of the type of fission characteristic of polyps. In Wood-Jones’ opinion, various types of fission, though typical for certain growth forms, are not unchangeably fixed, and variations of vegetative growth forms cannot be taken as species-specific.

The first critical review of coral classification (only for one genus) we found was that by G. Brook (1893). He reviewed schemes of J. Dana, H. Milne-Edwards and J. Haime, and C. Klunzinger and found that they were based only on the form of colonies, and many sub-divisions of coral types overlapped each other in distinguishing features. Brook, when describing and classifying *Acropora*, took into account differences in colony form, and small-scale skeleton variations, especially in corallites. He underlined that variation in polyp morphology between corals should be considered.

T. Vaughan (1907) was the first who indicated the problem of coral species. Not emphasizing any one concept of species, he pointed out that this problem is of biology as a whole. This researcher critically reviewed views of Gardiner and Bernard and noted that even the system of local shapes of these authors cannot be considered completely preposterous, as in certain cases when working with large series of specimens, this method can help to estimate the limits of variability. Vaughan especially underlined the importance of investigation of intra-specific variability for coral taxonomy. “As we know, coral variations are great and complicated. If we get to know their limits, we shall have to know

the limits of variability of different species” (Vaughan, 1907, p. 4). Species definition is given in the same place: “A species is a group of individuals connected by common intergrading features and separated from the other individuals by distinct gaps”. Underlining again the importance of knowledge about variability of intra-specific skeleton elements of corals, Vaughan wrote that any theory of species can be correct if identification of a species is based on knowledge of the pattern of variability.

As it can be seen, immediately after the formulation of the biological concept of species, coral taxonomists were offered a theoretical basis supported by a practical work on the description and classification of the corals of Hawaii. Unfortunately, during the following decades, up to the present time, these statements were not used by coral taxonomists except in very rare cases.

N.N. Yakovlev (1904, 1913, 1956) wrote again about the uncommon variability of corals, their “unlimited capacity to change, vary, adapt to requirements of the environments,” and the necessity to take into account this variability when classifying modern and fossil corals. He urged paleontologists to take care to study a sufficiently large number of specimens of the same shape, underlining that even modern coral division to species is highly subjective and obviously not natural as it is not in any other groups of animals. This outstanding expert in *Rugosa* underlined that in order to have a full notion of species variability it is necessary to have a considerable amount of material to establish a connection between individuals belonging to the same species.

Up to the 1950’s some taxonomists held the opinion of Bernard, others – that of Vaughan, and the majority took an intermediate position. Investigations were mainly carried out on the basis of small coral groups from separate collections. Previously distinguished and considered valid features and studies, based only on investigation of hard skeleton, were rejected, and many species were considered synonymous. Various systems of “shapes” and “facies” were offered, up to naming different part of a colony by different names. But all arguments and were concentrated on the multiplicity of growth forms and variability of corals. They served as the main obstacle for coral classification in the majority of works. A necessity arose to place “previous” species in synonymy, or to revise the principles of classification of whole coral groups.

Studying reef corals and their variability, J. Hoffmeister also faced the problem of their identification. In this connection he devoted a special part of his work to the problem of species (Hoffmeister, 1925). Mentioning that this problem is of biology as a whole, he underlined its uncommon acuteness in such a variable living form as corals, which are strongly affected by environmental influences. Pointing to insufficient knowledge on species evolution, Hoffmeister wrote that the term “species” could be used in a more or less artificial manner for the purpose of classification. In his opinion in coral taxonomy the definition of species made by T. Vaughan can be

used, and we have to obtain as clear and full a picture of our main object as it is possible in order to complete our classification. “If our knowledge about corals were greater and we knew the limits of variability of every species, than we would have been able to use Linneaus’s system as it is, without any problems” (1925, p. 5).

Speaking about problems of species identification, T. Vaughan mentioned that if a given specimen is sufficiently far from a known and described species by a complex of initially observed features, we give it other species name. Other researchers can consider that this species is not so different as to require giving it a different name. Hoffmeister asked the polemic question: “Who is right?” He showed for *Pavona* as an example that in a large series of specimens a high degree of variability of features can be observed. When there is a long series of graded forms, the extreme forms of the series can be especially different, and nevertheless they should be referred to the same species. It often happens that two clearly different species are in fact series members, connected by forms with intermediate features. Instead of giving new species names to two forms which seem to be intermediate, or naming them as variants, Hoffmeister offered to use some symbols. These symbols had to show an attitude of a researcher to a sampling, and to give the opportunity to determine its position in the nomenclature. If, for example, some problems arise with identification of specimens, possessing a combination of *Leptoria gracilis* and *L. phrygia* features, and their appearance is close to the latter species, we can identify them as *L. phrygia* → *gracilis*. From the logic of such a definition, in Hoffmeister’s opinion, it can be clear what features are variable in the given case. This researcher believed that this taxonomic method not only gives the notion of a taxon, but also informs a researcher about the trend of evolutionary variations. Hoffmeister continued the discussion about the problem of species, holding the same points of view, in a separate article (Hoffmeister, 1926).

Perhaps J. Umbgrove (1939, 1940) was the first who followed Vaughan in the study of corals, but a real systematic work with a considerable collection of corals from the Great Barrier Reef of Australia was carried out by C. Crossland (1952). He noticed again extraordinary variability of these animals not only in the growth form, but also in features which were considered fundamental structures, such as the number of septal cycles, and even in very fine components of septal ornamentation. Crossland called for care when applying data, found for one genus, to some other taxa members without criticism and publication of arguments. In his opinion, it is necessary to be especially careful with some details, which seem to not be significant, but in one group they are a basis for specific difference, and in the other group they can be fixed and do not show any variation. Showing that many species are in fact only ecological variations, this author called for us to determine the limits of these variations, typical for every species, and until these limits have been established, it is not possible to make conclusions on their taxonomic category. Crossland considered that it is possible to attribute ecological variants to

different species in order to make it convenient for future investigators. In his opinion, it is better to consider them variations, but not species, and to give them different names than to integrate them initially and to separate them afterwards. Unfortunately Crossland did not participate in the expedition to the Great Barrier Reef, and that is why variability of some corals was not always properly reflected in his works. On the whole, the work of this researcher remains very important even now and remains within the sight of specialists, involved in the study of corals, and especially in their taxonomy.

Publications of A.B. Ivanovsky (1975, 1976, 1978) are devoted to principles of coral systematics in general, and Rugosa in particular. In these papers he emphasizes that a biological species is an objective notion, not dependent on the fact of whether it is fossil or modern, when and what conception of it was elaborated, and that it is necessary to use the same principles of systematization of organisms in paleontology and neontology. Ivanovsky thought that underestimation of intraspecific variability was the weakest point in the classification of fossil corals. He stated that when identifying specific and intraspecific affiliation it is necessary first of all to introduce a definition of variability; only after that is it possible to constate a zoological population and an appropriate category for paleontological material. In the opinion of this author, when systematizing Rugosa it is necessary to be guided by the following principles:

1. Phenons of the same stratigraphical horizon can be different species or a result of intraspecific variation.
2. Subspecies can be established only regarding allopatric populations.
3. It is practically impossible to distinguish sibling species in paleontology.

Species of the same genus can be identified on the basis of morphological differences of mature growth stages with obligatory verification of ecological criteria in case of substantial variation of one morphological feature or minor morphological variations of a complex of features. Species of different genera, which develop in parallel, differ by ontogenetic process. Forms (morpha) can be established on the basis of partial morphological deviations of mature growth stages of corals inhabiting the same areas, and statistical methods are very important for their verification.

The problem of species and intraspecific variability was considered in a special chapter of a paper of J. Veron and M. Pichon (1976), in which a critical investigation of the taxonomy of Scleractinia from the Great Barrier Reef of Australia was conducted based on long-term underwater observations and well labeled samples of huge series of corals. When considering the history of the species problem for scleractinians, these researchers noted that T. Vaughan's opinion is the first in many new trends of coral taxonomy, but unfortunately he had few followers. Veron and Pichon considered in detail the

concept of “ecomorphose”, introduced by Laborel (intraspecific skeletal variations determined by environmental factors), and showed that this notion was not clearly defined and was most often applied to groups of individuals and populations inhabiting homogenous conditions. They also do not consider the term “ecotype”, as it was understood by Wijsman-Best, as a good one for characterization of skeletal variations of reef-building corals.

In order to avoid incorrect interpretations of their own position, these researchers offered the concept of “ecomorphs.” “Ecomorph is hereby defined as “intraspecific skeletal variations phenotypically and/or genotypically, determined in response to specific ecological conditions.” Veron and Pichon understood quite well that their concept of ecomorph had its limitation and did not help to solve the problems of taxonomy, but they hoped that it would improve somehow the existing situation. They stressed that the concept of ecomorph had the same problems as the notion of “ecotype”, and these problems were mentioned by Mayr. “Ecotype is not good because it is unusually intermittent, rarely well delineated, often polyphyletic and always abundant inside ecotypical variability.” As Veron and Pichon wrote, variations happen because it is hardly possible to find homogenous environmental conditions, and that is why a homogenous population has variation as well, in coral reefs. Even polyps of the same colony are subjected to the effect of different light, hydrodynamic, and sedimentation conditions, as well as to the effect of commensals or parasites. Therefore, variations, determined in these cases, are quite likely phenotypic, which can be frequently observed in different parts of the same colony. Maximizing the study of intraspecific variability of corals, these scientists established its limits for every species by three successive methods.

1. One large colony with more than one microhabitat, located lower, higher and at the same level was under study; the limits of variability of such a colony were established with various degree of variability between the central and peripheral colony parts.
2. The limits of growth form variability in the same biotope were determined.
3. Variability between interconnected biotopes was determined.

Later J. Veron (1995), analyzing various species concepts (Dobzhansky, 1935; Simpson, 1944; Paterson, 1981; Cracraft, 1987; Templeton, 1989), concluded that the majority of taxonomists and paleontologists accepted Simpson’s concept of population. The evolutionary species concept (Simpson, 1944) is, by default, the concept of most taxonomists and paleontologists, where species are envisaged as populations, or groups of populations that have had a common evolutionary history. Species are held together by developmental, genetic and ecological constrains, not just heredity. This is the nearest any general concept comes to operational coral taxonomy. As a concept, however, it is insignificant, contributing almost no guidance as to what are acceptable criteria for taxonomic decisions.

Y.I. Tesakov (1974, 1978) paid much attention to the problem of species and in especially to investigation of fossil tabulate corals. He showed that the quantity of identified species and intraspecific subdivisions greatly depends on the concept of species accepted by a researcher, as well as from the available material and methods of study. Tabulata can be completely investigated from the position of biological species using population analysis, as well as biological, paleontological, ecological, biometrical and even genetic methods. In his opinion, tabulata hierarchy – a colony, population generation and inhabitants, population, subspecies – as a species subdivision, fully reflects the structure of biological species. Emphasizing the variability of tabulata, Tesakov showed clearly that with the increase of quantity of material studied, the variability of features can be revealed more completely, every species possesses certain features with their values. That is why it is necessary to establish the scope of species variability, and after that to establish its range.

“Taxonomists are inclined to believe that problems they face when studying their objects are the most difficult in comparison with those of the other investigation objects. Probably coral specialists are the exception, but the permanence of these problems and their visible intensification in the process of coral investigation history serve as a circumstance which seems to deserve a detailed discussion.” B. Rosen wrote these words in a review (Rosen manuscript, 1971) devoted to the problem of species for Scleractinia. Based only on English language publications, he considered all known concepts of species and intraspecific subdivisions, as well as simple systematic reviews, and came to the conclusion that corals are very difficult for identification, and the problem has not become much easier than 70 years ago. In his opinion, these are the following reasons for the difficulties.

1. No two corals can be absolutely similar, and it is very difficult to distinguish intraspecific variations from interspecific ones.
2. Limitations in collection. Large collections are often an inaccessible ideal, whereas collections of separate fragments are of little interest and unimportant.
3. Coral researchers know very little (especially in the past) about the biology of living corals, that is why they were not careful when naming them.
4. Species are based on skeletal morphology, and soft tissue is not taken into consideration.
5. Corals genetics have not been studied, which is why these is no basis for a strong theory of species for them.

Rosen formulated the key conclusions of his review in the form of questions.

1. Does every distinctly observable coral represent a separate species, even if the observed difference is the result of habitat?

2. If not, then where is a boundary between variations within one species and variations between different species?
3. What is the source of variability, especially for the growth forms?
4. Can Linneaus's system be applied to corals, and if not, what is an alternative? (This question practically contains at least three separate disputed problems: species concept for corals, type concept in the procedure of classification, and limitations of binomial nomenclature.)
5. What is a species for corals? (Previously morphological concept of species was accepted by the majority of biologists).

Thus, the issue of unusual intraspecific variability and its limits for every specific taxon or population was always extremely essential in the problem of coral species. Researchers, who had large collections and great experience of living coral observations, could clearly see that without understanding of the variability pattern it was impossible to identify either modern or fossil corals. "A sound theory of species" for corals was formulated by Vaughan in the very beginning of the past century, and it was similar to the biological species concept which appeared two years earlier. At the same time it was emphasized that the question was not in application of various species concepts, but in a single biological approach while studying corals.

In our work we do not deal with species as such. We study individuals, samples and series of samples, and combine them in groups of phenotypically similar specimens – phenones. Phenones, gathered in one place, can represent various species or intraspecific differentiates. In order to have an option of alternatives, it is necessary to study thoroughly individual variability, having analyzed it completely, qualitatively and quantitatively. The variability of corals is especially high and diverse, and "if we know its limits, we shall be able to know the limits of different species" (Vaughan, 1907). Values of some features can vary 10-30 times even within the same population (Tesakov, 1978; Latypov, 1980; Latypov, 1984).

No matter how high the variability is of different populations of individuals inhabiting the same biotope, two alternatives can be revealed after its comprehensive analysis. Value complexes of several series features can be arranged in certain limits, being connected by a full row of transitions, and peculiarities and variations of individual development are similar fundamentally and in details in all samples; or value complexes of several series features have evident gaps, and peculiarities and variations of individual development have distinctions of kind. In the first case individual communities represent a system of potentially interbred populations, relating to the same species and representing a pattern of intraspecific variability of features. In the other case we have a right to consider

communities of individuals with gaps as reproductively isolated populations, since gaps in their feature complexes and ontogenetic peculiarities could be easily seen both in one and in various habitats.

Even at a very high degree of features variation, intraspecific variation will have its specific limits. In this case variation in values of features is continuous. In some populations they will form connective series, and the greater the sampling there is, the more regular and continuous these series are. Interpopulation variations will be connected between each other with a full row of features value transitions. In the compared phenones a value of every feature, if they belong to the same species, will be positioned between the value extremes of their variability without gaps in values of qualitative and quantitative features. For example, the width of branch ends of different *Stylophora pistillata* colonies can be 10-20 and 60-70 mm, the distance between branches – 5-10 or 30-40 mm. In a representative sample maximal and minimal values of these features have successive transitions. The fact that these are continuous variations of features is confirmed by coefficients of fatty acids composition proportion, which differ by fractions of a percent (Fig. 8, 9, Table 1).

Properties of phenones, belonging to different species, will necessarily have qualitative and quantitative gaps for one or several features, no matter whether these are peculiarities of morphology or percentage ratio of fatty acids composition.

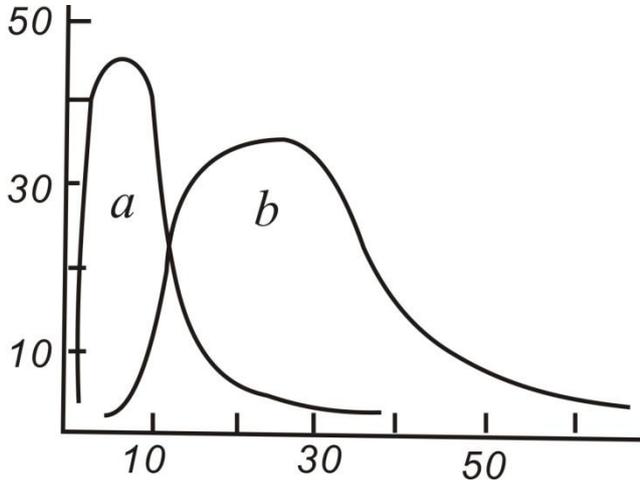


Fig. 8. Distribution of the number of specimens according to the modal size of branch ends of *Pocillopora damicornis* (a) and *P. verrucosa* (b). It can be well-seen that sizes of thickenings of branch ends of the both species are partially overlap, but one of the species includes mainly branches of up to 10 mm thickness, whereas another species – up to 15-30 mm. Axis of abscissa shows sizes of branch ends; and axis of ordinates - occurrence frequency.

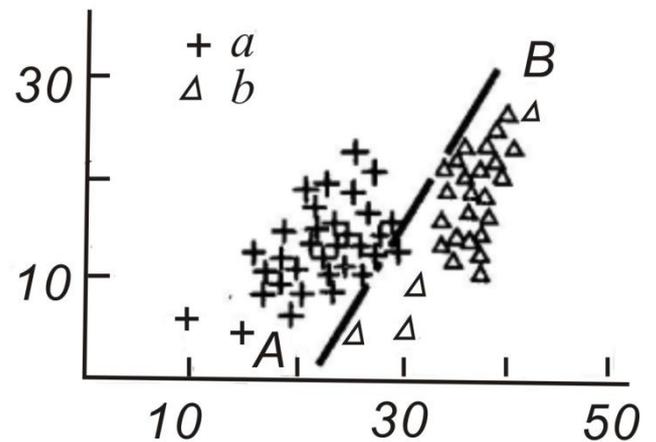


Fig. 9. Division of two *Pocillopora* species according to the ratio of branch diameter to the number of corallites per area unit of a branch. a – *P. damicornis*; b - *P. verrucosa*; AB – a line of the best division. Axis of ordinates shows branch diameter, and axis of abscissa – number of corallites per area unit.

In this case variations of features values, their gaps and peculiarities will not have only modifying character, but will also show differences in biology of carriers of such variations, determined by discrete gene pool which form various phenotypes together with environments. Different *Pocillopora* species have distinctions in branches width, in a number of corallites per area unit, which partially overlap. They have an evident gap in the frequency of laying floors (the first ones laid them 4-5 times oftener), differ by the presence and absence of verrucosa bifurcation on main branches, and proportions of some fatty acid compositions differ by 2-3 fold (Fig. 8, 9; Table 1).

Table 1. Proportion of fatty acids composition in various scleractinian species.

A	B	C	D	E
14:0	2.4	2.3	2.8	2.5
16:0	21.5	30.4	30.9	29.0
16:1	2.3	2.1	2.0	2.5
18:0	7.5	8.0	5.9	4.9
18:1	8.2	8.8	9.4	11.3
18:2 ω 6	1.3	11	0.5	0.7
18:4 ω 3	5.9	4.8	2.2	2.5
20:1	2.9	4.3	1.3	1.7
20:2	0.5	0.5	0.5	0.4
20:3 ω 6	3.0	5.6	5.2	6.4
20:4 ω 6	6.1	3.3	2.3	2.1
20:4 ω 3	1.4	2.1	3.0	3.1
20:5 ω 3	5.2	3.0	1.7	1.8
22:4 ω 6	4.5	2a	1.0	0.9
22:5 ω 6	0.2	0.3	0.2	0.4
22:5 ω 3	0.9	0.9	1.1	1.1
22:6 ω 3	22,7	24,3	28,5	25,3

Note: A – names and composition of fatty acids; B – *Pocillopora damicornis*; C-D – *P. verrucosa*; E- *Stylophora pistillata*. It can be well seen that quantitative and qualitative variations in fatty acids composition in representatives of the same species have modification character, and such variations in different species have quantitative and qualitative gaps.

While working with corals having extraordinary variability of practically all features and, as a rule, polytypic species, a question often arises whether differences between samples (populations) are great enough to consider them as different species. In such cases it is useful to carry out statistical investigations. At that, absolute values of some features do not give unequivocal results because of the very high scattering, whereas the ratio of two measurements often give either more information or more satisfactory results. Thus, branch diameter of *Pocillopora* corals from a large sample varied from 1 to 36 mm, their length – from 18 to 110 mm, the number of corallites per surface area unit – from 10 to 64. At the same time the sample could be divided into two parts. One set of corals had longer and thinner branches (rarely longer than 20 mm) with fewer corallites, whereas other corals had

considerably shorter and thicker branches (thickness as a rule 20-40 mm) with a greater number of corallites. The diagrams allowed us to identify clearly two species - *P. damicornis* and *P. verrucosa* - according to these features (See Figs. 8, 9). Using the known principles and methods of population taxonomy in zoology and in studying corals (Mayr, 1971; Tesakov, 1978; Latypov, 1984), it is possible to solve taxonomic problems of any difficulty, and it is better not to trust in “peculiarities” of the object of study, but to rely on the data of population analysis and intraspecific variability.

In 1998 the book “The principles and methods of the CNIDARIAN classification” (Latypov et al. 1988) was published. This book presents the basic results of more than 20 years of investigations in the systematics and taxonomy of the cnidarians, which is a difficult subject for taxonomy. The modern ideas about the criteria for taxon definition for the fossil and recent corals, actinians, and hydroids are presented. Morphologic and genetic differences and the taxonomic value of ethological and ecological characteristics are considered. Using numerous examples, the significance of the various features, definition of the limits of their variability, and methods of the resolving the inevitable problems which take place in the identification and classification of Cnidaria, are shown.

2.1 The Reef Builders - Hard Corals

The reef-building corals are colonies of replicated polyps, each with a structure similar to that of an anemone, but with two important additions; they build a hard skeleton of calcium carbonate and their tissues contain single celled symbiotic plants called zooxanthellae. Corals are primitive marine animals with a simple body structure. At the top of each individual coral, called a polyp, is a crown of tentacles (Fig. A) arranged in groups of six, which wave in the water and act as a food trap. Extended polyps have an anemone-like appearance. In the middle of the tentacles is a flat oral disc and in its centre the mouth, a slit-like aperture which is the animal's only opening to the environment. Beneath it lays a narrow channel, the stomodeum, which in turn leads to a single large body cavity, the coelenteron.

Fleshy plates (mesenteries) radiate in from the wall of the body column towards the central axis of the polyp. Within the body cavity, digestion is accomplished on the surfaces of specialized filaments or mesenteries, which secrete enzymes that quickly reduce ingested prey to its components. Most corals are, therefore, potentially efficient predators, although many other types of feeding seem to have developed for meeting their energy requirements. The common characteristic of this group is the secretion of a basal skeleton of calcium carbonate as the mineral aragonite. The skeleton of the polyp is called a corallite. It has a basal plate, from which arise partitions called septa. The septa alternate in position with the fleshy mesenteries. From the centre of the plate a structure called the columella may extend up into the corallite. The skeletal walls support the polyp, and they are variously formed by the

outer edges of the septa or by extensions between the septa. New polyps are budded off by division of a mature polyp or separately from between the polyps.

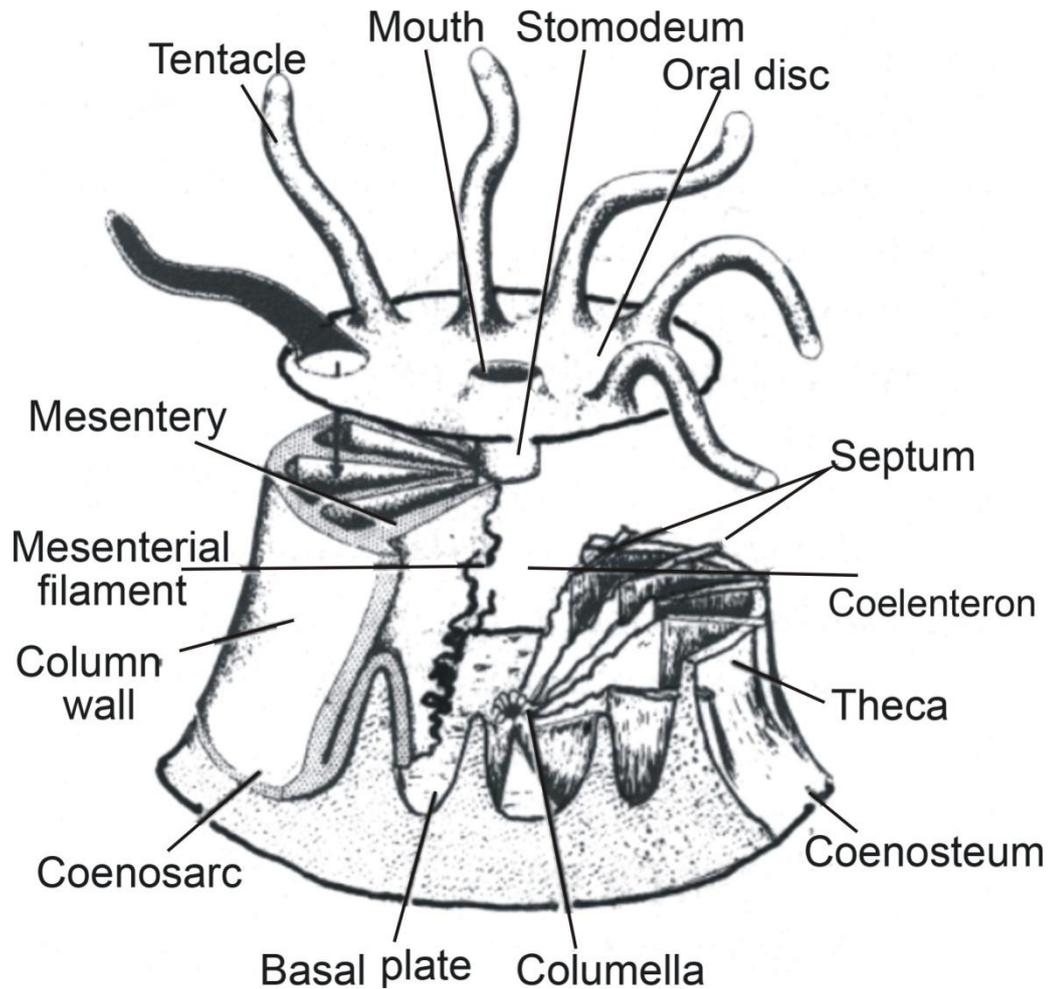


Fig. A. A schematic view of a polyp, showing its main features.