

Particular qualities of identification and taxonomy of some scleractinian

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Publication History

Received: 20 February 2015

Accepted: 19 March 2015

Published: 25 March 2015

Citation

Latypov YuYa. Particular qualities of identification and taxonomy of some scleractinian. *Species*, 2015, 13(40), 29-41

ABSTRACT

Is a brief history of the taxonomy scleractinian genera *Porites* and *Turbinaria*, common in all reefs Indo-Pacific. Discusses the morphology and terminology of the skeleton of the coral and their taxonomic history. Are audited signs to identify those corals.

Key words: *Porites*, *Turbinaria*, Scleractinian, Taxonomy, Signs, Morphology, Terminology.

1. INTRODUCTION AND TACSONOMIC HISTORY

Scleractinian genera *Porites* and *Turbinaria* distributed on all reef Indo-Pacific. They are found in all reef zones from littoral baths palm-size up to the maximum depth (40-45 m) base reef slopes. Especially in time of reproduction and the ability to get rid of muddy sediment, may be one of the main factors in the success of this corals at high latitudes and in turbid eutrophicated waters, where they compete with algae for area and light (Tomascik and Sander, 1974; Terry, *Fish Channel.com*; SKM, 2009).

1.1. Genus *Turbinaria*

The generic name "*Turbinaria*" for funnel-shaped Dendrophyliidae was offered for the first time by L. Oken (1815), but almost for a half a century it was not recognized among taxonomists of that time. A year later J. B. Lamarck (1816) did not accept this name, including the most typical turbinarians *Madrepora crater* Pallas and *M. cineraccens* Ellis & Solander (in the current interpretation *Turbinaria mesenterina*) and 4 other species in the *Explanaria* genus. Two other species – *T. palifera* and *T. stellulata* – were attributed by him to the *Astraea* genus. A. Schweigger (1820) accepted Lamarck's generic name "*Explanaria*", but gave it his own definition and introduced only two species – *E. crater*

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and *E. cinerascens*. Only in the classical work of Milne-Edwards and Haime (1849), in which a new classification for all corals was validly offered, funnel-shaped Dendrophylliidae with a well developed spongy columella were returned, and this time forever, to their generic name *Turbinaria*. Later on coral researchers mainly accepted the content offered earlier of this genus with the addition of some remarks and new species (Verrill, 1865; Klunzinger, 1879; Studer, 1880; Duncan, 1884; Quelch, 1886; Bourne, 1888; Ortmann, 1890). At the very end of the 19th century the fundamental multivolume monograph of H. Bernard "Catalogue of Madreporaria" was published, devoted to the investigation and revision of all the corals kept in the British Museum of Natural History (Bernard, 1896). A good proportion of the second volume of this monograph is devoted to *Turbinaria*. Bernard critically analyses the early taxonomic history of this genus and considers in detail strong and weak points in his opinion of the *Turbinaria* taxonomy of the previous researchers. Actually Bernard was the first to make an attempt to take account of the data on intra-species variability in coral taxonomy. Taking into account peculiarities of corallite construction (structure) and distinctions in colony shapes, he subdivided all known 80 *Turbinaria* species into 9 non-taxonomic groups from funnel-shaped through foliate and laminae to bifacial ones, and referred more than 20 species to synonyms. At present Bernard's monograph also remains a fundamental work, being a well illustrated catalogue of *Turbinaria* species, supplied with valuable remarks on their morphology, history and distribution. From the theoretical methodological point of view, it was one of the very first publications containing the idea of intra-species variability in corals.

Modern coral taxonomists have not have any doubts about the status of the genus *Turbinaria*. However, its composition has sometimes been revised. Revisions were mainly relocations of some species to synonyms of other species, described earlier, more rarely – to later or newly described species (Gravier, 1911; Crossland, 1941, 1952; Yabe and Sugiyama, 1941). New species were described, old species were re-described and their validity or synonymy was discussed again (Wells, 1954, 1958; Nemenzo, 1962; Scheer and Pillai, 1974). Veron and Pichon (1979), based on the great amount of available information and taking into account the fact that more than a half of nominal *Turbinaria* species are found in Australia, not only described these corals, but also to a great extent revised the entire genus. They stressed that *Turbinaria*, despite their seeming simplicity, remain to be corals difficult to identify, since they do not have any conservative skeletal characteristics and have extremely broad variation both in the fine skeletal structure of the calice and in the colony growth form.

1.2. Genus *Porites*

In the early 19th Century H. Link (Link, 1807) proposed the name "*Porites*" for the genus, which, in his opinion, included branching corals, covered with star-shaped orifices scattered throughout the surface. These were two species – *Porites polymorphus* and *Porites damicornis*. The latter was later re-identified as *Pocillopora damicornis*. Establishment of boundaries and intragenus structure of *Porites* was hampered due to insufficient knowledge of the morphology and systematics of scleractinian as a whole. The taxonomy was often based only on differences in colony shape or in corallite sizes and the number of tentacles per polyp. J. Dana (1846) for the first time characterized the *Porites* genus correctly, relying on the complex of features, representing a number of corallite structure peculiarities: such as the presence of pali and septal denticles arranged in concentric rows, etc. Later on, as facts were accumulated, descriptions of new *Porites* species appeared without the revision of species described earlier. This resulted in an insufficiently justified increase in the number of species.

This was the situation by the beginning of the 20th Century, when Bernard (1903, 1905, 1906) produced a monographic revision of the genus *Porites* and the entire Poritidae family. The first detailed description of the morphology of Poritidae was an undoubted advantage of his work. Characterizing the family as a whole, the author noted that the pattern of corallite structure is common for *Porites* and *Goniopora* genera: porous septa ascending from epitheca are united by synapticular rings and form a reticular wall, whereas a circle of synaptacula surrounds the columella and fossa (central space). In his opinion, these genera differ by the fact that *Goniopora* has 24 septa, whereas *Porites* has 12, and septa of the third cycle almost are not developed at all in *Porites*. Bernard revised the family's taxonomy, being guided by peculiarities of corallite morphology and geographic localization of every form. He mentioned that the Poritidae, and most of all, the *Porites* genus, are characterized by a large amount of minor morphological variations. Ornamentation, shape and sizes of corallite elements vary even within the same colony. Trying to cover all variants of corallite architecture, Bernard gave a great number of descriptions of *Porites* species, which were actually ecomorphs, and differed only by one or two minor morphological features. In the process, he rejected the Linnaean nomenclature and the term "species" with reference to corals, replacing it by the term "local form". Bernard's studies concurred with the beginning of the discussion on the problem of species for corals and partially provoked it. T. Vaughan (1907) wrote that Bernard divided *Porites* and *Goniopora* into as many species as was possible, however, investigation of the limits of their intra-species variability was the key to identification of the Poritidae and other Scleractinian species. Vaughan (1907, 1918) completely reviewed the intra-generic taxonomy of the Poritidae, and produced the description of 35 species of *Porites* from the Indo-West Pacific and synonymised many species described earlier, including some "local forms" of Bernard. Thus, two tendencies in the classification of both the Poritidae and all scleractinian were established. One of them lay in raising morphological distinctions, often-minor ones, to the rank of species features. Another one was the investigation of the variability of features and establishment of its intra-species (and intra-generic) limits. However, most researchers held an intermediate point of view.

At present the genus *Porites* includes not less than 122 species names (Veron, 1986; Foster, 1986). The taxonomic structure of the genus has not been finally established. Both Bernard's local forms and actual species, which have been subjected to synonymization up to the present time, are included in it. Definition of species, as a rule, has been impeded by indistinct diagnostics. This is caused by the following factors: 1) the absence of clear and convenient ways of describing skeletal structure features for taxonomic analysis; 2) a wide variation of skeleton elements; 3) an insufficient evaluation of the taxonomic value of these features.

As usual, these authors gave a lot of attention to the analysis of intra-species variability of skeletal characteristics and growth forms of coral colonies from different biotopes, but unfortunately, they did not try to estimate somehow the taxonomic value of one or another feature. The wide variation of morphological characteristics described by these authors, who practically extend from one description to another, makes it difficult, as well as for *Porites* and *Turbinaria*, to identify many species, despite beautiful and numerous coral photos.

Common poritid and dendrofylliid allowed us to explore the site and assemble the extensive material on the variability of these coral from of Spratly Islands to Seychelles and Mauritius (Latypov, 1986, 1993, 2003a, b, 2007, 2009, 2011). Having some experience in the study of modern and fossil corals, having studied the morphology described in detail scleractinian (Latypov, 1982, 1984, 2014; Latypov and Long, 2010), we offer an improved, partially expanded vocabulary to describe the morphology and characteristics, as well as the most significant taxonomic characteristics identified in the course of their functional and taxonomic evaluation.

2. TERMINOLOGY, MORPHOLOGICAL AND TAXONOMIC FEATURES

The analysis of morphology and the structure of skeletal elements of a corallites and a colony as a whole for *Turbinaria* have not been made on the modern level until the present, not to mention the absence of a taxonomic estimation of featured value. Below we provide a more detailed description and analysis of morphological and taxonomic features of these corals. A number of terms for characterization of skeletal elements of *Turbinaria* and *Porites* are introduced for the first time.

2.1. Corallite

Turbinaria corallites have a conical and cylindrical-conical shape. They project over the coenosteum surface more or less, and in some colony areas, corallites can be embedded. In many *Turbinaria* a uniform orientation of corallites in rows parallel with the upper colony margin can be traced, in some species this is not distinct, and in the others it can be totally absent or be observed only at the very edge of a colony. The shape and size of corallite cones, the degree of their tilting on the colony surface and the height of their projection over the coenosteum are variable even within the same colony, and still more variable on intra- and interspecies levels. They can be elongated and regularly conical, inclined with one side shortened and another side elongated, low widely conical and cylindrical, or very high. Size and shape of the upper margin of the calice – an orifice, usually called “aperture” in *Turbinaria* – is variable in the same way. Aperture sizes can vary within the same colony by a factor of 2.5-3 times, and its shape – from regularly round to narrow elliptical to slit-like. The density of corallites (their number per colony area unit), which together with corallite shape and their size can serve in a number of cases as a taxonomic feature at the inter-species level, can be considered the most stable morphological feature. The synapiculate wall of all *Turbinaria* species is similar in its structure and differs only by its thickness, with variations within the same colony which are comparable with interspecies variations and do not allow us to use this feature at the species level.

The corallites of the *Porites*, as a rule, closely adjoin each other, and have a polygonal shape in cross-section (cerioid polyps). *Porites rus*, *P. densa* and *P. lichen*, in which a small amount of coenosteum is situated between rows of corallites, are the exception. Corallites of these species often have a round shape. *Porites* coenosteum morphologically seems to be a many-rowed (reticular) corallite wall (see the following section). The wall composing of many rows (reticular wall) along the entire perimeter of corallites is a stable feature, and in this case, it has a taxonomic importance at the species level together with some other features. In the other *Porites* species corallite walls become reticular only in the corallite corners and between corallites at the colony margin. Thus, the presence of coenosteum, developed in various degrees in *Porites* species, is not a qualitative feature and seemingly is not a basis for recognition of monospecies subgenera within the genus *Porites*.

2.2. Septa

The septa of *Turbinaria* are well developed vertical thin laminae of different lengths: from less than a half of a corallite radius to two thirds of a corallite radius. Lateral septal surfaces are ornamented with different densities of granules, denticles or spines. Axial septal margins can be either almost smooth or dentate with fine spines, granules, saw-shaped denticles or large variously shaped wide teeth with flat tips. Such features as septal length, degree of granulation of the lateral surface and more rarely dentition on the axial margin both separately or especially in combination with each other can be used as interspecies differences. The number of septa and the nature of insertion of new septa in different parts of the colony, and especially in different species, are the most variable features. The total number of septa in *Turbinaria* varies from 12 to 64. Numerous measurements show that more than 24-36 septa can be observed only in two species – *T. patula* and *T. stellulata*, and only in single cases in very large corallites and not in every colony. More than 36 septa can be found only in *T. peltata* in separate vertically protruding corallites having a diameter which is twice that of the other corallites of the colony. The majority of corallites of this species (92%) have no more than 24 septa. The bulk of corallites of all *Turbinaria* species (88%) have 16-18 septa in three incomplete cycles.

The configuration plan of the septa and topography of insertion of new higher cycle septa older than the second cycle, uniting *Turbinaria* as a whole with their similarity, differ by a rather large diversity of morphological characteristics. Septa can be oriented radially in all six sextants or only in opposing ones, and in the main sextant they can be plumose. First cycle septa can differ by their sizes from the other septa, or be equal to them. The directive septum can be detached from the neighboring higher cycle septa by a fossulate formation, and differs very little from them. Septa can have an arrangement similar to the Pourtales plan (Pourtales, 1871) with two to three cycles, but they do not differ by orders and can have a clear cyclicity of insertion of regular higher cycle septa, and pronounced first cycle septa. The reason for such diversity is the following. Growth of *Turbinaria* colonies takes place at their upper peripheral margin. Along this peripheral margin new corallites are formed, and mainly two cycles of septa are established in them. So, the structure of the septal apparatus of every separate corallite takes place already

at this stage. New septa are produced mainly in entocoelic cavities (Bernard, 1896; Wells, 1956), and that is why, as in many Scleractinia with the accented bilateral symmetry, the first septa of the third and fourth cycles can be laid only between mesenteries of corresponding cycles. Since the growth of most corallites and formation of their septal apparatus takes place mainly earlier, and the increase of corallite sizes or appearance of new corallites is limited by neighboring polyps, sets of septa of the third and later cycles are not completed. Insertion of several higher cycle septa of the first series of the third cycle rarely includes more than four to six septa, and only in newly budding corallites or corallites increasing their diameter.

These peculiarities of the formation of the mesenterial and septal apparatus explain the fact that the bulk of corallites of all *Turbinaria* species usually have 16-18 septa. This is also a reason for uniformity of sizes of all septa of all cycles and interseptal intervals, which only grow uniformly or remain unchanged. For the same reason the septal orientation similar to Pourtales Plan, when septa of the higher cycles (fifth, fourth) have to fuse with the lateral surface of the lower cycle septa (fourth, third), can be present or absent. The Pourtales Plan is not clearly observed in *Turbinaria* species. Firstly, they have no septa of the fourth cycle, except for *T. peltata*. Secondly, new inserted septa of the third cycle become closer, not fusing, or fuse with neighboring septa by their axial ends, but do not fuse with the lateral surface of the earlier cycle septa. Besides, in *Turbinaria* septa of the second and third cycles fuse, whereas according to the Pourtales Plan axial ends of the second cycle septa and their lateral surface remain free. Peculiarities of higher cycle septal insertion and their morphology together with different septal lengths create different structures of septal apparatus for *Turbinaria*. There are four types of insertion and orientation of the septal apparatus (Fig. 1):

1. Septa along the entire calice are oriented radially with a tendency toward spiral twisting. The first and second cycles differ by length, and the insertion of new septa does not occur or is observed only in single corallites (Fig. 1-2).
2. Septa are oriented radially in the directive sextants. Cycles differ very little. Septa which are the closest to the directives, become closer, and sometimes fuse at the point of connection with columella. Insertion of septa of the third cycle is observed in the minority of corallites (Fig. 1-3).
3. Septa in the opposite quadrants are radial, and in the directive they are plumose. Higher cycle septa neighboring to the main septa fuse by their axial ends. Insertion of septa of the first series of the third cycle is developed in the majority of corallites (Fig. 1-4).
4. Septa in the opposite quadrants are radial, whereas in the directive they are plumose. Higher cycle septa neighboring to the lower cycle septa fuse on their lateral surface in the axial end. Insertion of septa is not limited to either the peripheral margin of the colony or by the cycle of their formation, and can be observed in all places of a colony (Fig. 1-5).

All studied *Turbinaria* are characterized by one of these types of formation of septal apparatus with their variations in septal length, number, degree of merging of axial ends of septa (Fig. 2), being next to the directive septa, and the character of granulation of septal surfaces. Peculiarities of septal insertion and their morphology, despite their considerable variability, in certain complex combinations, are species-specific and quite limited by qualitative and quantitative bounds with gaps between species, which allows us to elaborate appearance diagnoses and schemes of construction of septal apparatus, offered below with their description.

Septa of *Porites* are radial barriers, dividing a corallite cavity into interseptal spaces (loculi). Internal and upper (distal) margins of septa are distinguished. The septa of the *Porites* consist of one row of trabeculae. Typically for the *Porites* the porosity of the septa is the result of combining depressions on the surfaces of neighboring trabeculae and of fall-out of some sclerodermites (growth interval Bendukidze and Chikovani, 1962).

The free upper ends of septal trabeculae are called septal denticles (Wells, 1956). The sizes and shapes of septal denticles in the corallites of the *Porites* vary from thin, slightly ornamented, rod-shaped denticles to irregularly branched denticles (Fig. 3, f). If a septum bears more than one denticle, then internal ones (which are close to the corallite center) are usually rod-shaped, whereas outer ones (which are placed near the wall) are irregularly shaped and thickened peripherally. In Bernard's opinion (1905), in the corallites of *Porites* all trabeculae are parallel to each other. As a result both septal and wall denticles are arranged vertically. Other researchers (Crossland, 1952; Veron and Pichon, 1982), after Vaughan (1907), consider that septal trabeculae diverge from the wall at a very acute angle. As a result septal denticles are inclined towards the corallite center. However it can be seen in tangential sections of corallite tubes (for example in *P. solida*, *P. australiensis*, *P. lobata*, *P. lutea*, *P. rus*, and *P. densa*) that septal and wall trabeculae are parallel to each other for a distance of not less than 12-15 mm of a corallite tube's length: this corresponds approximately to 10 years of living and skeletal building by a polyp. The point of merger of septal trabecula with wall trabecula was not found by the author in such sections. In any case, trabeculae remain parallel in corallite tube for a considerable length. Septal denticles are oriented vertically without an evident incline towards the corallite center (Fig. 3, f).

At the same time spike-like outgrowths, inclined towards the corallite center, are often observed along the septal margin. This may be explained in the following way. Septal trabeculae are arranged at a small distance from each other, and connected by horizontal cross connections, which are formed in points of contact between neighboring trabeculae. If internal trabeculae grow slower than outer septal trabeculae, then the free ends of horizontal connections can be seen along the septal margin. They are inclined towards the corallite center, often almost horizontal, and spike-like (*Goniopora stokesi*, *Porites densa*) or irregular and scale-shaped (*Porites lichen*). Scale-shaped outgrowths inclined towards the corallite center are often visible on the wall too. A scale-shaped projection can be seen in a tangential section of a corallite to be only the initial stage of formation of a horizontal cross connection between the wall and septum. It is not the end of a septal trabecula and, therefore, is not a septal denticle. Swellings, not connected with septal trabeculae, and not being denticles, can be sometimes be found on horizontal interseptal cross connections (Fig. 4 B).

In the Poritidae septa are sometimes bifurcate or trifurcate - split into two to three branches between the outer septal denticle and the wall (Fig. 5). In this case the septum becomes wedge shaped. Septal denticles at the point of dividing are always tangentially thickened and of irregular shape (Fig. 3 f, 5). The distal septal margin of the Poritidae is more or less inclined towards the corallite center, and the corallite depth depends on it. In some species the distal septal margin is almost horizontal throughout the entire colony (*P. rus*, *P. cylindrica*), and the outer denticles are at the same level with the septal denticles. As a result calices are not pronounced. The same thing is observed near the growth margin of most *Porites* colonies. Near the wall septa are connected by an outer synapticular ring (see Fig. 5). This ring is often not complete. In corallites with a deep calice the ring is, as a rule, fragmentary and merges with the wall, whereas in shallow corallites it is almost complete and is away from the wall. The inner synapticular ring, in its turn, connects septa at the base of pali-like septal denticles (see Fig. 5) and can often be incomplete. No uniformity in the development of these synapticular rings, which could have been used as a feature to distinguish species, was observed. The degree of development of rings varies greatly within the same colony, and is obviously connected only with the level of skeleton calcification.

Internal septal margins are fused bilaterally symmetrically according to the Pourtales plan (Fig. 6) in all *Porites* species treated here. Lateral septal pairs and the dorsal septum are always detached. The ventral septum and two neighboring septa of the second order which compose a ventral triplet of septa can have free or fused internal margins (Fig. 6). Fusion of septa of the ventral triplet is used as an important taxonomic feature of the genus *Porites* (Bernard, 1905; Vaughan, 1907, 1918; Veron and Pichon, 1982; etc.). Bernard (1905) and Veron and Pichon (1982) propose that these septa can be fused by different ways, including a horizontal cross connection between internal septal margins (Fig. 6 b). However this cross connection is often a fragment of the internal synapticular ring or a result of intergrowth of lateral surfaces of well-calcified septal trabeculae, when carinae – vertical rows of granules - are developed on their lateral surfaces. In such cases every septum of a triplet retains a complete number of trabeculae, and such a triplet probably should not be considered fused.

It is an accepted point of view that pali are located at the internal septal margins of corallites in *Porites* – vertically arranged trabecular projections, developed between the internal septal margin and the corallite axial zone (Vaughan, 1907, 1918; Vaughan and Wells, 1943; Wells, 1956; Veron and Pichon, 1982). However, it can be clearly seen on a corallite tangential section that “pali” are not detached from the septum, and that is why they do not correspond to the definition of the term “pali”, given by Vaughan and Wells (see Fig. 6). The terms “internal septal denticle” or “pali-like denticles” are preferable to consider. Such denticles differ from the neighboring denticles only by their height and diameter (Foster, 1986). The number of pali-like denticles varies in a random way. Sometimes pali-like denticles are not developed on one or more septa, including the septa of ventral triplet. Corallites with incomplete sets of pali-like denticles can be found irregularly throughout the entire colony.

2.3. Columella

In all *Turbinaria* the columella is well developed and often occupies about one third of a calice. It is usually deeply embedded in the calice. It is usually a spongy but rather dense structure, formed by vertical irregular laminae, variously bent and interlacing with each other. Sometimes laminae are long and smooth, if so then they are clearly spirally twisted. If laminae are not numerous, they can be arranged in one row between the directive septa and even merge in a styliform column. In most *Turbinaria* columella formation starts after a corallite is no longer at the peripheral margin of a colony. Neighboring corallites, depending on their sizes and age, can have a large hilly columella or a row of linearly elongated twisting laminae. That is why it is necessary to be especially careful using morphological features of columella construction for taxonomic purposes at the species level.

The columella in *Porites* corallites is an axial structure in the form of a simple trabecula, similar in thickness to septal and wall trabeculae. The free tip of a columella can be poorly developed (in the form of a tubercle or a vesicle), or it can have the form of a rod or a lamina, granulated to various degrees (see Fig. 3 f).

2.4. Colony

Whereas it is rather easy to recognize colony forms of all *Turbinaria* as a whole, it is not always possible to distinguish unambiguously one or another colony form at the species level. Bernard noted that all *Turbinaria* at their initial growth stage have a crateriform colony. Our observations on numerous Indo-Pacific reefs confirm this conclusion. Small colonies of different *Turbinaria* (with a height of 25-30 mm and diameter of 30-50 mm) have a crater form of different proportions depending on biotope. Under the conditions of limited illumination at the base of the reef slope such craters have a widely conical shape and become almost flat (Fig. 7, 8).

The following forms of *Porites* colonies are usually recognized: massive with a smooth surface, massive with protrusions at the colony base or along the entire surface, incrusting, plate-like, submassive with columnar elevations or branches; ramose or branching, branching with a flat base, irregularly branching, etc. (Bernard, 1905; Vaughan, 1907, 1918; Crossland, 1952; Veron and Pichon, 1982; Latypov and Dautova, 1996). Various colony forms are frequently found within the same species, for example, in *P. lichen*. Many of these forms are only variants of the main growth forms of *Porites* colonies, since the development of three types of the key vertical elements – columnar protrusions, plates and branches - is connected with the shape of the growth area or conditions of living and development of a colony. It is more convenient to carry out the analysis of colony form variations taking into account growth proportions, proposed by Marfenin (1987) for the description of *Acropora* colony morphology (Fig. 9).

The initial stage for all forms is an incrusting colony, with maximal sizes which usually do not exceed several centimeters in diameter and three to five mm thick (Fig. 9 A). If vertical growth is absent, the colony remains as an incrusting colony, with a growth index which is usually

close to 0 (Fig. 9 B). An incrusting colony is usually not only the initial developmental stage, but can also be the result of the effect of ecological factors, for example, the lack of light (Tytlyanov and Latypov, 1991). An incrusting colony follows the shape of substrate, for example, fouling a dead branch of *Acropora* (Fig. 9 C). When the rates of horizontal and vertical growth are comparable, a massive colony is formed, growth occurring throughout the entire surface occupied by soft tissues (Fig. 9 D).

As it grows, a massive colony steadily acquires a round form. Living tissue gradually dies at the periphery of a massive colony, i. e. at the place of the colony attachment to the substrate. Deposition of aragonite stops here. The colony grows only vertically and horizontally (laterally). The same thing happens with asymmetrical colonies. A so-called “microatoll” (Fig. 9 D) is an ecotypical modification of a massive colony. In the central part of the colony soft tissues die due to the damaging effect of environmental factors at low tides. Growth continues laterally and results in the formation of “microatolls” with a diameter of several meters and a height of less than one meter. Microatolls with a height of 20 cm and a diameter of 1.8 m were found at Bai Tu Long Archipelago in Vietnam by the author. The location of such colonies was confined to the intertidal reef zones – coastal channel and reef flat.

Development of vertical elements is connected to the presence of local growth zones. On an encrusting colony primary swellings are formed, then they produce laminae (from a band shaped growth zone), or columnar projections and branches (from an apical growth zone). Branches or columnar elevations can be of different lengths due to correlation of the rates of the lateral and apical growth. Proportions of the thin columnar projections on *P. lichen* remind one branches, but they are not the same. They are chaotically divided into several unequal portions, and clear dichotomous branching is absent. Single- or multi-layered epitheca is usually formed at the base of columnar, branching, lamellar and massive Poritid colonies. This phenomenon is of environmental, not genetic nature, and is connected to the growth of colonies in sandy and silty environments (Crossland, 1952).

2.5. Wall of colonies *Porites*

A porous wall is a typical feature of the *Porites* family corals. In the *Porites* walls are formed by vertical elements – trabeculae, connected by horizontal cross connections – synapticalae (synapticulotheca, see Fig. 3). The porosity of the wall relates to the fact that trabeculae are situated at some distance from each other, which is equal to their diameter or less. If wall trabeculae are placed close together, the wall still remains porous due to the presence of depressions on trabecular surfaces. A wall can be multirowed or single-rowed, and in the latter case it is formed by one row of trabeculae (see Fig. 3 c). A part of a wall trabecula, protruding over the upper synaptical ring, is called a wall denticle. Denticles have a rod-shape or irregular shape, and as a rule, are granulated. In *Alveopora* wall denticles can be absent, if wall trabeculae do not protrude over wall synapticalae. In this case the wall margin is smooth. Granules are the ends of radial crystals forming a trabecula, and look like spines, small or large thorns, etc. (see Fig. 3 f). Very different granules shapes can be observed within the same *Porites* colony. It is difficult to express quantitatively the degree of granulation of skeletal elements. Probably using the following terms will be quite satisfactory: abundant granulation, weak granulation, or granulation absent.

A single-rowed wall can be straight (if trabeculae are located along a straight line), or zigzag (if trabeculae are displaced from each other in a radial direction, Fig. 3 c). The outline of a corallite with a single-rowed wall is polygonal: in cross-section it is an elongated polygon with unequal sides (Fig. 4 A). In corallite corners the wall can consist of several rows of trabeculae, and becomes reticular there (multirowed, Fig. 3 d). In the opinion of Bernard (1905), this occurs due to the fact that the distance between corallites is farther than usual. Costal trabeculae of the primary corallite are able to develop and to be imbedded in the wall. If the distance between corallites even greater, then additional rows are imbedded along the entire wall.

Vaughan (1907, 1918) showed that the theory of Bernard was based on the incorrect supposition that all trabeculae in the corallite ascend parallel to each other. In fact septal trabeculae are inclined towards the corallite center and are joined to the wall trabeculae at a very small angle. If corallites are drawn together very closely, only the internal part of the septum is developed. If the outer part of the septum is also developed, corallites turn out to be separated by a spongy tissue called coenosteum (Vaughan, 1907). It is necessary to note that the points of view of Bernard and Vaughan virtually coincide: a multirowed wall is a result of development of septacostal trabeculae, which becomes possible when corallites are at some distance from each other. Species such as *P. densa* and *P. lichen* have mainly a multi-rowed corallite wall: groups of four to ten corallites are separated from each other by coenosteal ridges, analogous to a multi-rowed wall by its construction. One particular type of wall was described by Gardiner (1898) under the name “trimurate”. This term is still being used (Veron and Pichon, 1982, and others). But already Bernard (1905) rightly noted that the wall in this case has a single row, and the illusion of two additional rows is created by well-developed outer synaptical rings of neighboring corallites (see Fig. 5).

The following designations have been used for describing the construction of a corallite wall: narrow, thin, pointed, wide, thick, etc. (Bernard, 1905; Vaughan, 1907, 1918; Crossland, 1952; Veron and Pichon, 1982). Such designations may be subjective, and it is difficult to use them for identification of material in collections. Besides, the wall thickness usually varies within the same colony depending on the degree of calcification of the skeleton at different sites on the colony surface. That is why, when describing the walls of the Poritidae, the author recommends indicating the number of trabecular rows forming the wall instead of its thickness.

Depending on how high the distal septum margin is where it joins the wall, the wall can be low or high (Fig. 4 b). If the septum margin and the wall are the same height, i. e. the tips of septal and wall denticles are at the same level, the calice is not pronounced. Wall height and wall denticles, calice depth, as well as the sizes of other vertical elements of the corallite, can be connected with the environmental conditions the colony lived in (Foster, 1979; 1980). That is why such morphological features as wall height, height of wall denticles and septal denticles, columella height, etc. cannot be used for diagnostics at any taxonomic level. It is preferable to use more stable features of a qualitative nature,

which represent a combination of several morphometric characteristics (Tesakov, 1974). For example, wall denticles are higher than septa denticles or at the same level with them.

3. VARIABILITY OF A PORITID CORALLITE AND THE CHOICE OF TAXONOMICALLY IMPORTANT FEATURES FOR INTER-SPECIES DIAGNOSTICS

The form and structure of corallite elements and colony are traditional diagnostic features of Scleractinian taxa of various ranks. Variations of morphological characteristics of Scleractinian are rather broad (Bernard, 1905; Vaughan, 1907, 1918; Gravier, 1911; Crossland, 1952; Veron and Pichon, 1976; Tesakov, 1978; Latypov, 1984; etc.). Poritid corals, especially *Porites*, are some of the most variable scleractinian. It seems as if it is impossible to find two similar corallites in the same *Porites* colony. One can observe that corallites on the upper part of a colony and near its growing margin, facing the substrate, are the most different. Colony fragments of any *Porites* species, taken from its different parts, can be completely attributed to different species. Broad variability of characteristics have hampered taxonomic investigations of Scleractinia during the entire time they have been studied, and made Bernard (1905) abandon Linnaean nomenclature when describing the Poritidae.

A. Foster (1979, 1980, 1985, 1986) investigated intra-colony and intra-species variability of a great number of quantitative and qualitative characteristics of Caribbean scleractinian. When studying the taxonomy of fossil Poritidae of the Caribbean basin, Foster (1986) first of all points out that fossil Poritidae, as well as modern ones, are characterized by the absence of discrete qualitative features and such a broad variability that it is very difficult to characterize them. Having established generic affiliation of the collected colonies by traditional qualitative and quantitative characteristics, she established the boundaries of species within these genera using a multi-dimensional statistical method. The data obtained by stratigraphy and population analysis were used with this purpose. The applied mathematical methods allowed her to compare features not separately but in a complex, to estimate the importance of separate features for species differentiation and in such a way to discuss their importance for classification.

In some cases Foster followed a traditional approach to the selection of some features for the analysis. Thus, construction of a corallite wall is used by her as a meristic characteristic “wall width” (mm), and is included in the statistical analysis with this definition together with the other features. However if we consider this feature as a qualitative one, i. e. the presence or absence of a wall reticulum (single or multiple rows of the wall), we will have a discrete qualitative characteristic of a species.

4. CONCLUSION

The intricacy of taxonomic structures of *Porites* and *Turbinaria* cannot be eliminated by a detailed redescription of species. First of all, it is necessary to examine the construction of such elements this corals skeleton, the peculiarities of which can be used as species features, then to choose the most taxonomically important ones from all possible features and to follow a unified pattern of their presentation.

In any case, the original opinion about the similarities or differences between taxa is done based on the absence or presence of the unfilled gap in those or other signs, identifying and comparing the specific characteristics of each taxon. Then it turns out what biological reasons cause the differences and similarities of signs. And based on the facts of discreteness phenotypes, identified between the two sets of signs, one could argue about the reproductive isolation of each type. In conclusion, it remains to be said that both the ambiguity of the evidence leads to unnatural growth of their variability and the limits of taxa, so clearly marked sign clearly limits its variability within the species and allows to define the gap (morphological, ethological, biochemical or genetic) between taxonomic signs and identify them correctly.

DISCLOSURE STATEMENT

There is no financial support for this research work from the funding agency.

ACKNOWLEDGEMENT

Authors are thankful to Tatyana Chernenko for the pictures *Turbinaria*.

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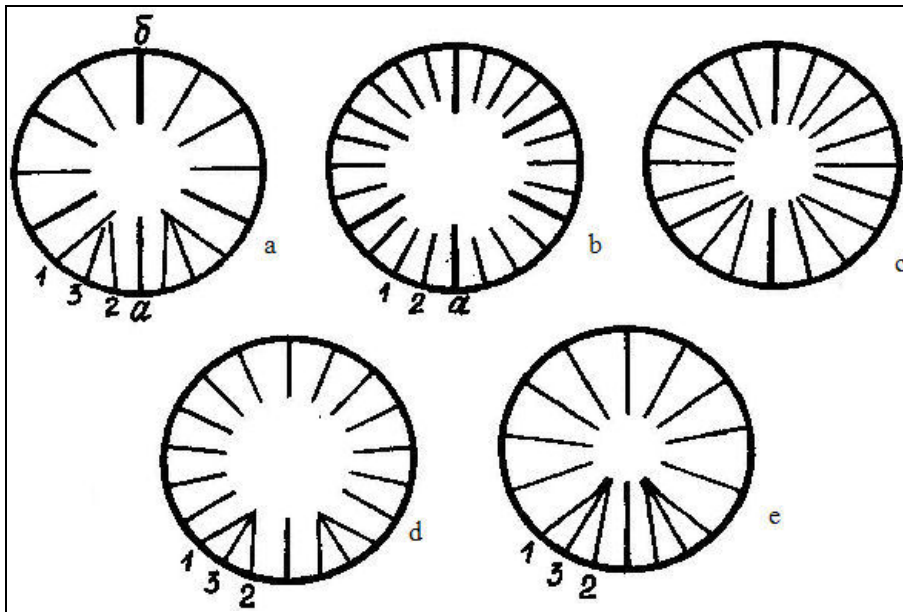


Figure 1

The order insertion septa of various cycles (a); 1, 2, 3 - partitions of the first, second and third cycles, protosepta are allocated by fatter; insertion and orientation of septa: b - on the first type, c - on the second type (it is advanced three incomplete cycles of the septa, again inserted methasepta approach the axial ends), d - on the third type (it is advanced three incomplete cycles of the septa, again inserted septa merge axial the ends), e - on the fourth type (it is advanced three incomplete cycles of septa).

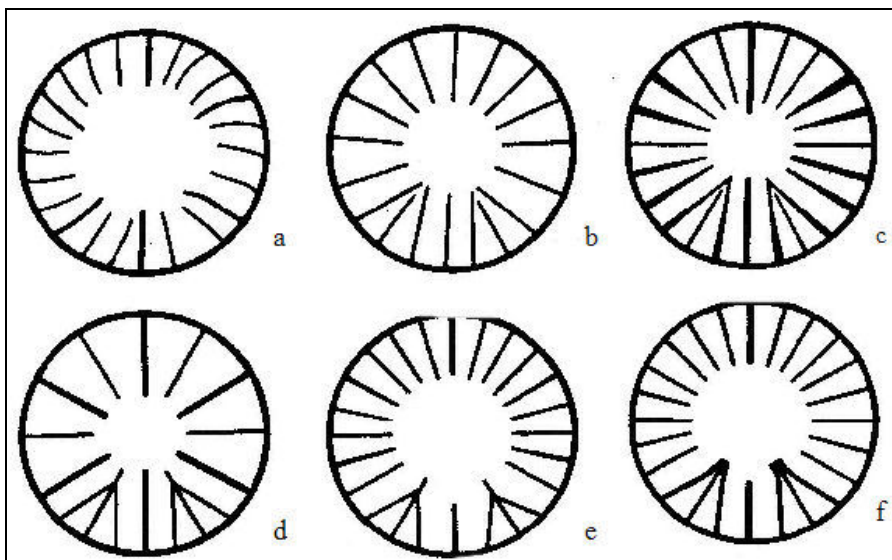


Figure 2

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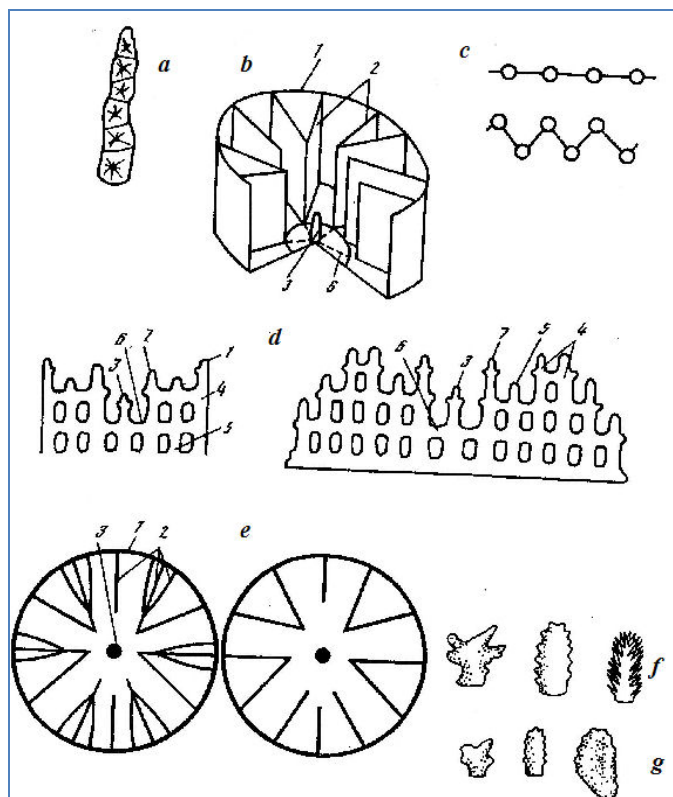


Figure 3

Schema of structure a poritid corallites and its basic elements. *a* - simple trabeculae, *b* - the schema of a structure *Porites* corallites, *c* - single-row direct and zigzag corallite walls, cross-section, *d* - corallite of *Porites*, tangential section (on: Bernard, 1905), *e* - a septal configuration corallites of *Goniopora* (at the left) and *Porites*, *f* - various forms denticles of a *Porites* septa, *g* - various forms of a columella in *Porites* corallites. By figures are designated: 1 - wall, 2 - septa, 3 - columella, 4 - wall trabeculae, 5 – septal trabeculae, 6 - radii, 7 – paliform denticles.

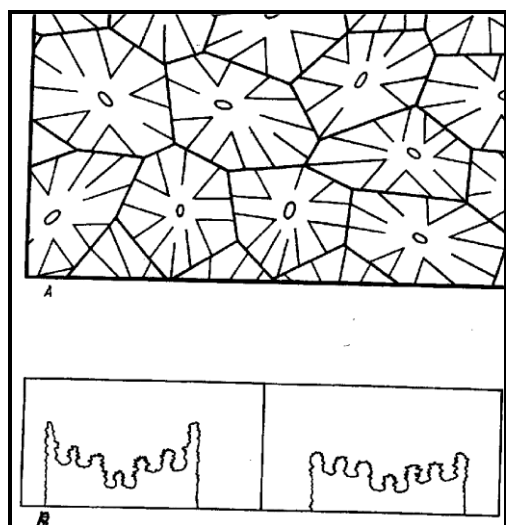


Figure 4

Orientation of septa in a *Porites* corallites (A), (B) - a corallite with high (at the left) and low (on the right) walls, tangential section

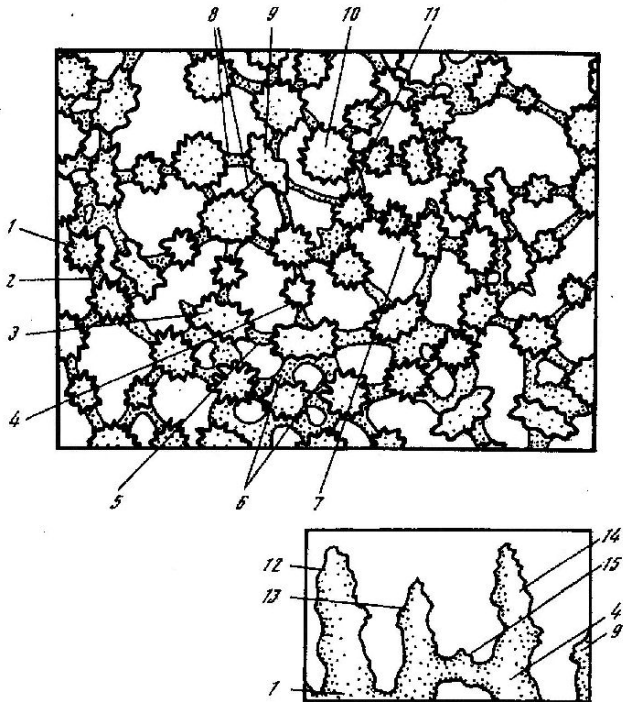


Figure 5

Cross-section section a *Porites* corallite (from above); a structure of septum, tangential section (from below). By figures are designated: 1 - wall trabeculae, 2 - wall synapticulae, 3 - expanded wall a denticle of septum, 4 - septal trabecula, 5 - wall (external) a synapticular ring, 6 - the split septum, 7 - not split septum, 8 - radii, 9 - columella, 10 - an internal septal trabecula, 11 - palar (internal) synapticular ring, 12 - wall denticles, 13 - septal denticle, 14 - paliform denticles, 15 - swelling on the crosspiece between septal trabeculae

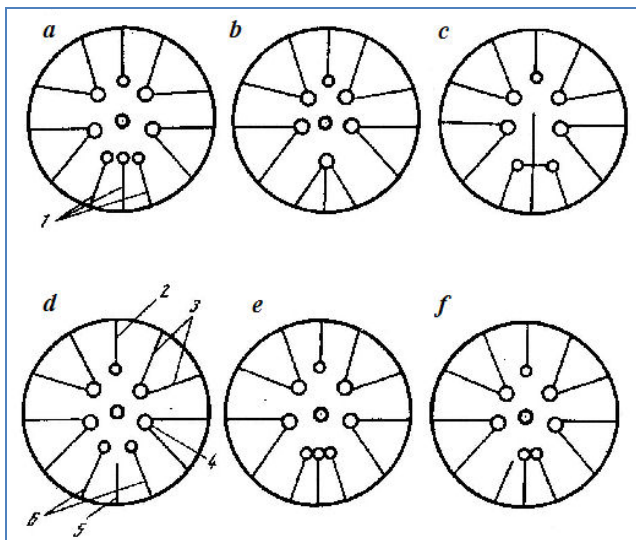


Figure 6

Variants of association of septa at *Porites* corallites. Fused (two top on the right) and not fused triplets. By figures are designated: a – ventral triplet, b – dorsal directive septa, c – lateral pair septa, d – paliform denticle, e – ventral directive septa, f – lateral septa of triplet

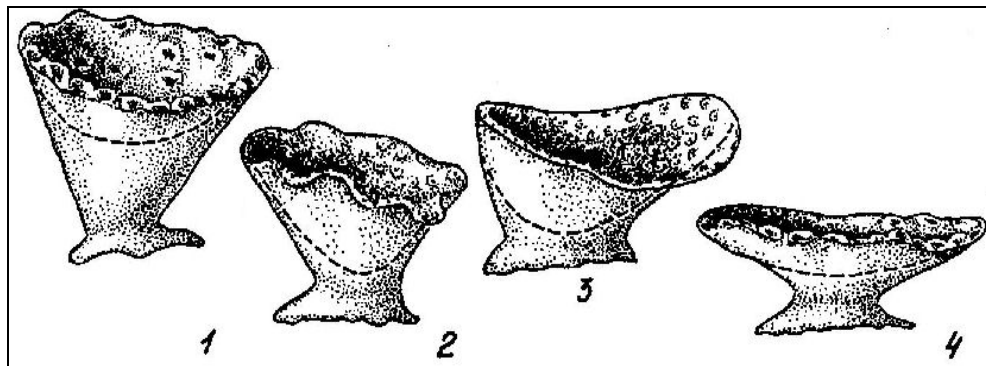


Figure 7

Initial growth phases of *Turbinaria* colonies. 1 – *Turbinaria peltata*, low part of reef slope, depth 9 m; 2 – *T. bifrons*, a site too, reef slope, depth 5 m; 3 – *T. radicalis*, reef slope, depth 6 m; 4 – *T. peltata*, depth 35 m. The dashed line designates a configuration and depth of a calyx

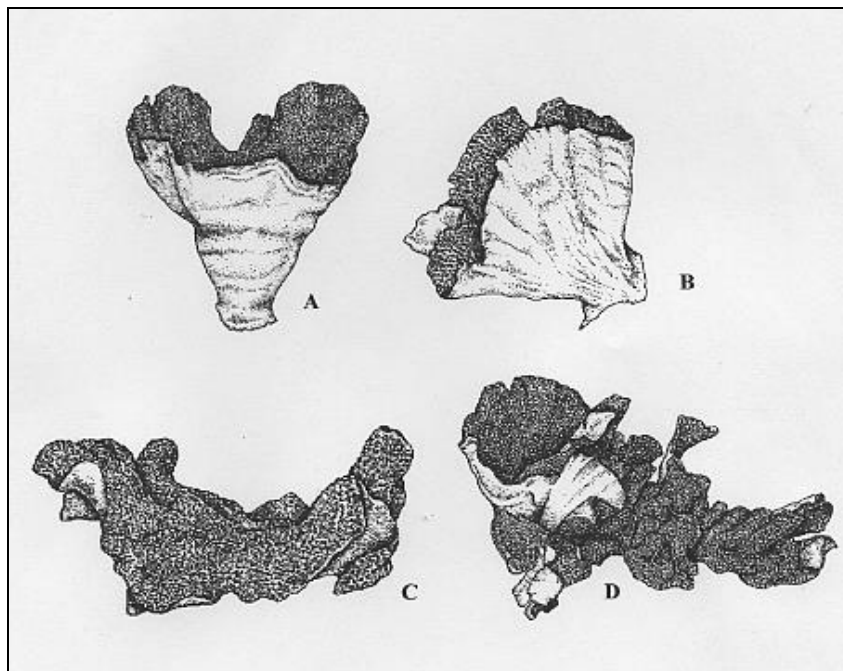


Figure 8

Forms of *Turbinaria* colonies. a – funnel-form *Turbinaria crater*, depth 9 m; b – funnel festoon-form *T. mesenterina*, dept 11 m; c – bifacial *T. bifrons*, depth 12 m; d – plate-encrusting *T. contorta*, depth 6 m.

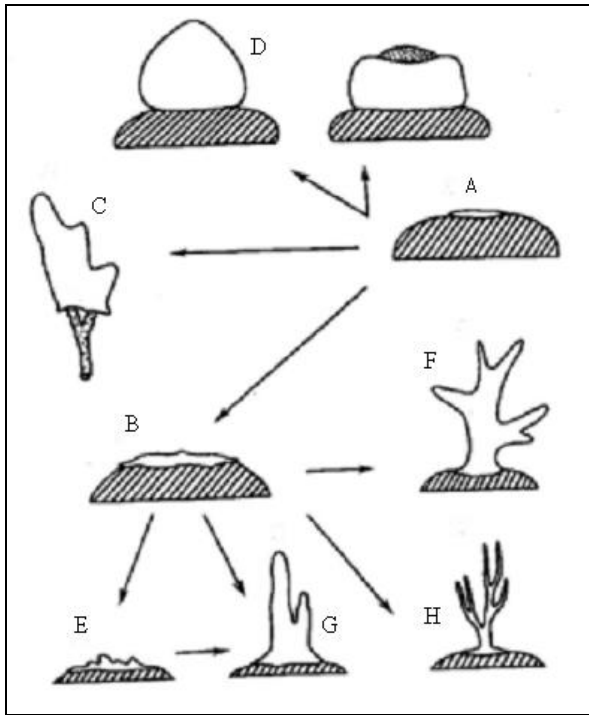


Figure 9
Forms of poritid colonies and possible parities between them. Explanatories in the text