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About Symmetry of Paleozoic Corals and Its Relation with the Gravity

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Abstract*:* The symmetry as morphological feature of Paleozoic corals can have in some cases taxonomic value, in other cases it is considered only as an integral characteristic of the population. Symmetry of corallites is evaluated by the shape of their cross section, but the number and location of septa can also be taken into account. Symmetry of corallites of the Tabulata, Heliolitida and Rugosa can change not only at different representatives, but also in the astogenesis of the same colony or in the ontogenesis of solitary forms. Talking about the symmetry of corallites in massive colonies is possible only if their sides are equal. By analogy with the cellular structures of biological tissues, the term "corallite adjacency" for massive colonies is proposed. The formation of the main types of symmetry of Paleozoic corals is inseparably linked with the origin of these groups. The small sizes of the ancient initial forms prove that not adult polyps were subjected to calcification. Larvae or planula-like organisms, representing a reduced stage of development of Corallomedusa (pedomorphosis), settled to the bottom and gave rise to the first calcite polyps, which were bent by their own weight or sea currents. The early coloniality of heliolitids could be associated with the subsidence of a group of genetically homogeneous planules, unlike the Rugosa and Tabulata. Shafranovsky has developed the Curie symmetry principle, indicating that the elements of the organism's symmetry may not fully coincide with the symmetry of the environment or may not coincide with it. Symmetry of corallites and colonies of Paleozoic corals is connected with symmetry of the gravity. A phylogenetic implication shows that tetragonal symmetry is the most ancient and was inherent in the ancestors of corals. We should take into account the rule of Shafranovsky (everything that grows and moves horizontally and obliquely has bilateral symmetry; everything that, being attached, grows vertically, has radial symmetry) studying coral symmetry.

Keywords: Paleosclerocoralla, auloporoidity, calcification, septogenesis, phylogeny, Shafranovsky’s rule.

1. Introduction

The same morphological characteristics can have different classificatory value for different taxa. This applies to both high taxa (orders) and low rank taxa (genera and species). And different ontogenetic development of relative taxa can serve as significant criterion for its definition and allocation. For example, cyclomorphosis is specific for different relative genera and species (Bondarenko, 1985; Ospanova, 2019a). Symmetry as one of morphological characteristic can also play different role in separate cases. In some cases, this feature is considered as having the taxonomic value, in other cases only as an integral characteristic of a population. For example, different type of septa insertion serves for many investigators as one of the arguments for opposition of the Rugosa and Scleractinia (Oliver, 1980, et al.). Investigators believe that lateral attachment of the larvae causes bilateral symmetry of the Rugosa, and axial attachment of the larvae causes radial symmetry of the Scleractinia (Il'ina, 1984; Bondarenko, 1987a, et al.). Symmetry of corals can change in the process of individual development. So the swimming larvae of modern corals have always well-defined bilateral symmetry, but at the adult animals, which are attached to substrate the septa arrangement is radial (Krasnov& Kostina, 2003). In this case, symmetry is considered only as the integral characteristic of the population.

The taxonomic ambiguity of the symmetry puts on the agenda the question: whether there are general rules to which the symmetry of organisms obeys, or each case individual is?

2. Study Methodology and Material

There are two methods of study of development of corals: 1 – observation of development of individual corallite (both solitary and in colonies) during its total growth beginning from the initial stages; 2 – observation of group of corallites (in colony or among solitary corals of one species in biotope) presented at different stages of individual development. In the first case, we get an idea of the ontogenetic development of individual corallite. In the second case, we get the idea of the structure of the colony (astogenesis) or the integral population characteristics. We have used both methods at study of morphology of the Heliolitida.

In preparation of material for the study, we used the method of oriented sections. It consists in the covering by series of cuts all parts of the colony, which can differ from each other in structure: the base of the colony, the mature stages of growth, the center, the periphery. For this, in the polishing laboratory, we directly marked future cuts on the polypary with a felt-tip pen, and only after that the material was sawn. Longitudinal sections crossed the entire colony from the base up; the number of cross sections from one colony was not limited and was determined by its size. All stone material that was available was ground up in order to obtain a complete picture of variability under the future microscopic study. In total, at least 8000-10000 thin sections from different regions (Tajikistan, Estonia, Uzbekistan, Russia, Kazakhstan etc.) were examined and studied by us.

When working in the field, layer-by-layer sampling from geological sections was carried out.

3. Symmetry of Corallites at Paleozoic Corals

The symmetry of corallites is evaluated by the shape of their cross section, but the number and location of septa can also be taken into account.

A) Symmetry of corallites of the Tabulata. The bases of corallites have a conical and auloporoid shape, respectively, rounded and elliptical cross-sectional shapes. In the first case, the symmetry is radial, in the second (curved cone) – bilateral. In fasciculate colonies, vertically growing corallites have cylindrical shape and radial symmetry.

In massive colonies, corallites acquire polygonal outlines in cross section due to their close location; the number of their faces is determined by the number of surrounding corallites. By analogy with the cellular structures of biological tissues (Maresin, 1990), we call this quantitative indicator a **corallite adjacency**. Talking about the symmetry of corallites in massive colonies is possible only if their sides are equal. The adjacency of corallites in massive colonies varies from 3 to 11 (rarely 12). High adjacency (8-12) is noted in the colonies, where the corallites are strongly differentiated in size and the large corallite is surrounded by a series of small ones (like in *Lecfedites*). The lowest adjacency (3) is characteristic of corallites in the early stages of their development. If corallites are uniform in size, their adjacency is 5-6.

Kim (1974) indicated the presence of bilateral symmetry connected with the pinnate arrangement of septa at the Ordovician *Agetolites* and in the Silurian Theciidae. And bending corallites of Alveolitidae have bilateral symmetry, too.

The tetragonal form of corallites is noted in Tetradiida, some Syringoporida (the family Tetraporellidae) and Halysitida.

Polygonal corallite shape in massive colonies, caused by squeezing, masks true symmetry. The development of septa may be affected by the development of porosity. In general, the number of septa in the Tabulata ranges from 1 to 24 (32). Nevertheless, 12-ray symmetry, most pronounced in the Heliolitida, may be present in the Tabulata, too. For example, in *Thamnopora apparata*, irregularly developed coarse protrusions of the walls are taken as septal formations. And only in the very upper part 12 thin well-developed septa appear in the cups, almost reaching the axis (Yanet, 1965). In addition, 12 fossilized tentacles are found in fossil *Favosites* (Copper, 1985; Copper & Plusquelles, 1993).

B) Symmetry of corallites of the Heliolitida. Corallites of the Heliolitida have the most pronounced 12-ray symmetry, which occurs sporadically in the Tabulata. It is expressed in the constant presence of 12 septal formations or 12 folds of walls. In the early stages of immature corallite growth (the hystero-neanic stage), the number of septa may be less than 12. Elements of septal symmetry appear at more mature stages of development.

In addition to 12 septa, 12 wall segments can be counted in some heliolitids (*Plasmoporella*, *Vorupora*, sometimes *Squameolites*, *Helioplasmolites*, *Veraepora*, etc.). In some heliolitids (*Syringoheliolites*, *Linhuangites*, etc.), the septal plates bend, sequentially leaning against each other and growing together (Bondarenko, 1971). As a result, an axial channel appears in the center of corallite, as in *Syringopora*, and dissepiment-like structures in the amount of 12 near the walls. The number of coenenchymal tubes adjacent to corallites varies from 12 to 24; that is associated with the number of exothecal outgrowths of corallite walls (Ospanova, 1978). Exothecal outgrowths can develop as a continuation of septa into the coenenchyme or as ridges of the external folds. The binding of outgrowths of one corallite with each other or with outgrowths of adjacent corallites leads to the appearance of tubes in representatives with vesicular coenenchyme. If there are 12 outgrowths, an aureole of 12 tubes appears; if the ridges of the folds are crowned with two exothecal outgrowths, the potential number of coenenchymal tubes near corallites increases to 24.

So, the influence of symmetry of corallites of the Heliolitida can extend to the coenenchyme. The formation of the aureole of 12 tubes around *Plasmopora* cups, when exothecal outgrowths are a direct continuation of septa, was considered by Lindström (1899) as a type of cup reduplication. Bondarenko (1983, 1987b) compares aureole structures with the cormidia of modern Cnidaria (“colonies within the colonies”).

The rarely encountered 6-ray symmetry of corallites in the *Oskaria* genus that we have allocated (Ospanova, 1983) from the Upper Silurian of the Turkestan-Alai mountain region, associated with the development of 6 septal trabeculoids (the term was introduced by Bondarenko, 1987b), is more likely to be an exception.

C) Symmetry of corallites of the Rugosa. Among three groups of Paleozoic corals, the most pronounced bilateral symmetry is characteristic of the Rugosa. The bilaterality of corallites of the Rugosa is expressed both in the bending of their lower parts and in the character of septa insertion – at four points about four primary septa in the sequence established by Kunth. Bilaterality can be emphasized by the two-sided symmetrical structure of axial formations. Bilaterality is better expressed in solitary rugoses in comparison with colonial. Analyzing the septogenesis of the Rugosa, Heliolitida and Tabulata and emphasizing the relationship of the external form and internal structure, we came to the conclusion that *the more conservative the external form, the more conservative septogenesis* (Ospanova, 2013b). The initial stages of growth of the solitary Rugosa, characterized by a curved conical shape, are the most stable and most conservative (only the proximal angle changes); therefore, the clearest observance of the Kunt rule is precisely for solitary Rugosa. Colonial rugoses are more inherent in the cylindrical shape of corallites, which have radial symmetry, and the curved conical shape is preserved in their protocorallites.

There is tetragonal symmetry in some representatives. The cystiphore corals *Goniophyllum* and *Araeopoma* are interesting; they have the form of tetrahedral pyramids with caps (Ivanovsky, 1965). The tetrapod division can occur at Rugosa. If the *Rhizophyllum* larvae settled on algae, the growing corals could acquire an irregular, worm-like shape (Stolarski, 1993).

4. Formation of the Basic Types of Symmetry of Paleozoic Corals

The formation of the symmetry types is inseparably linked with the origin of groups.

The relationship between the Tabulata, Heliolitida and Rugosa is recognized by all researchers, but the degree of relationship and the character of phylogenetic binding are disputed. We analyzed a set of basic morphological features of these three groups (18 features) and have concluded that they originated from one common ancestor (presumably Corallomedusa) by the way of pedomorphosis (Ospanova, 1995, 2003b, 2010). The scenario of the origin of Paleozoic corals, which we proposed, well explains all the features of these groups: the later appearance of skeletal remains of corals in geological sections compared with the beginning of general calcification in the Early Cambrian, the small sizes of the oldest representatives, the structural diversity, differentiation of corallites in size and the different complexity of the structure of groups. Therefore, we have included them in one subclass Paleosclerocoralla Ospanova, 2007 of the class Anthozoa (Ospanova, 2007, etc.). The conclusion obtained as a result of using the concept of the sum of common features agrees well with the data obtained in the study of cyclomorphosis of these groups (Ospanova, 2019a).

One of the common features inherent in these three groups of corals is the auloporoidity, which Sokolov (1955) considered as the evidence of its relationship. This sign strongly pronounced at the Tabulata and Rugosa, but Sokolov believed that it should be present in the Heliolitida, too. The auloporoidity is the curvature of the conical bases of corallites in the initial stage of growth (the structure inherent in the genus *Aulopora*). We have shown that auloporoidity is not so much an indicator of relationship, as it indicates the generality of the processes to which Paleozoic corals underwent at the beginning of their formation (Ospanova, 2013a). The small sizes of the ancient initial forms prove that not adult polyps were subjected to calcification. Larvae settled to the bottom and gave rise to the first calcite polyps, which were bent by their own weight or sea currents. Among the reasons causing the appearance of bilateral symmetry in sessile primary radial animals, Beklemishev (1964) calls the presence of mechanical force (strong currents, lateral attachment, or one-way food intake), acting perpendicular to the direction of gravity. In this case, the greater stability of the body is achieved by the curvature of the axis, leading to the appearance of bilateral symmetry. Rozhnov (2014) considers that direct or remote soft-bodied rugose coral ancestors had a planula-like body shape and paired ventral and, probably, dorsal mesenteries. They were benthic, crawling on the ventral side, and fed on bottom semi-decomposed organic matter. The plane of symmetry of the Rugosa corallites, which is marked by the cardinal and counter septa, coincides with the plane of larval symmetry, which is marked by the position of the cardinal septum and the attachment scar on the same side of corallite.

It can be added here that appearance of septa, similar to rugoses, is also observed at the Tabulata (Kim, 1974). In *Thecia*, the first septum also appeared on the lying side of corallite, almost simultaneously with it the opposite septum, and then two lateral septa, shifted towards the first septa. The similarity of septogenesis is important not only to state the affinity of two groups of corals but also to understand that bilateral symmetry of the Rugosa was acquired in the process of evolution (Ospanova, 2013b). In ontogenesis of the Rugosa, the cardinal and counter septa appear firstly, then two lateral and immediately adjacent to them (or simultaneously with them) two neighboring with the counter (Il'ina, 1984). Most likely, here we are dealing with recapitulation: the sequence of the appearance of protosepta in the ontogenesis of the Rugosa reflects the evolutionary sequence of their appearance. The appearance of the first four septal folds is due to the inheritance of ancestral symmetry. Their location was not strictly symmetric; because of the curvature of the coral in the initial stages of growth the lateral septa were shifted to the cardinal one. Compensatory and symmetrical with respect to the lateral septa, two more septal folds appeared – nearby to the opposite septum. We called this process **the symmetrization of the primary partitions of the Rugosa**.

The constant presence of epitheca between corallites of the Tabulata and Rugosa indicates that solitary forms were subjected to primary calcification. The presence of epitheca only at the base of the Heliolitida colonies may indicate that their transition to coloniality coincided with skeletonization or somewhat preceded it. Coloniality of heliolitids could be associated with the subsidence of a group of genetically homogeneous planules, when growing polyps did not secrete the walls between them, but still represented rather weak integration into the colony. In the future, the formation of colonies could begin from one founding individual, carrying the genes of coloniality. It could give rise to either protocorallite or protocoenenchyme. In the last case, the larva that settled on the substrate could develop into a faceless stolon in which corallites appeared. Bondarenko (1971, 1975) considered that colonies with vesicular coenenchyme can probably develop from protocoenenchyme. Bondarenko was engaged in the search for protocorallites of heliolitids, but in most cases we are talking about the alleged protocorallites due to the simultaneous appearance of a coenenchyme (Fig. 1). The presence of a layer of fine-bubble coenenchyme under "protocorallite" is considered by her as a possible protocoenenchyme. If the underlying layer of the coenenchyme is primary, can one speak of protocorallite in this case?

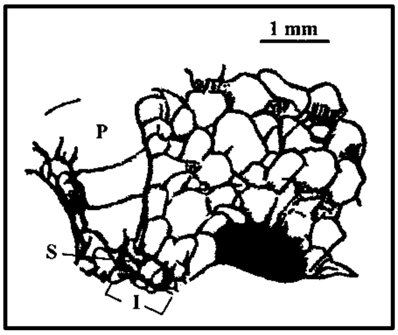

Figure 1. Protocorallite (p) of *Laminoplasma tuberosa* (Lindström, 1899): longitudinal section; s – septa, I – phylastic stage, where protocorallite, according to Bondarenko, is oriented horizontally. Silurian, Upper Wenlock of Gotland. From the work of Bondarenko & Stasinska, 1976.

It is appropriate to recall here that representatives of some solitary rugoses and heterocorals could construct the so-called paracolonies, the formation of which began with the union of tissues of several (up to 16) protocorallites without any observable genetic barrier (Weyer, 2016). It is known from the experiments on modern corals that with the mechanical connection of two adult individuals of the same species of different forms, an “alienation zone” arises between them – a piece of dead tissue. It can be assumed from this that immunological barriers in the early stages of growth are still poorly developed, in contrast to adult individuals, which allowed protocorallites of rugoses and heterocorals to build paracolonies. In that rate, the immunological barrier at the stage of development of the planules could be so low that did not prevent their integration in colony at the Heliolitida (recall that we are talking about genetically homogeneous planules). The presence of coenenchyme around corallites of the Heliolitida determined the radial symmetry of corallites (see Fig. 4).

When auloporoid habit is replaced by cylindrical, bilateral symmetry can transform into radial (Tabulata and Rugosa).

5. Principles of Symmetry

According to the Curie symmetry principle (1966), the body retains those symmetry elements that coincide with the symmetry elements of the environment. Gravity has the symmetry of a cone, with its apex directed toward the center of the earth. The cross section of the cone is a circle having, as you know, radial symmetry. Therefore, corallites and coral colonies having the circle in cross section (cylinders, discs, hemispheres, cones, conoids) will also have radial symmetry. The cross-sectional shape of curved corallites is an ellipse, bilateral symmetry is characteristic of it. Therefore, bending corallites, including the auloporoid structure, are characterized by bilateral symmetry. Violation of the radial symmetry of corallites in massive colonies occurs due to their compression, as a result of which they acquire a prismatic shape. We can speak about the symmetry of prismatic corallites if their sides (and, accordingly, the angles) are equal to each other. Otherwise, it is more correct to talk about the adjacency of corallites.

Studying the symmetry of natural objects, Shafranovsky (1985) established an empirical regularity that we call the Shafranovsky's rule (Ospanova, 2019b): *everything that grows and moves horizontally and obliquely has bilateral symmetry; everything that, being attached, grows vertically, has radial symmetry*. For example, the crown of a vertically growing tree has radial symmetry, while horizontally and obliquely growing branches, as well as leaves, have bilateral symmetry. The same applies to corals: in the initial stages of growth, when the corallites bend, that is, grow horizontally or obliquely, their cross sections are oval, accordingly, symmetry of such corallites is bilateral; when corallites grow vertically and have rounded cross sections, their symmetry transforms into radial. The same goes for larvae symmetry: they have bilateral symmetry because they swim horizontally, and a polyp should have radial symmetry because it grows vertically. This can be represented by the diagram (Fig. 2).

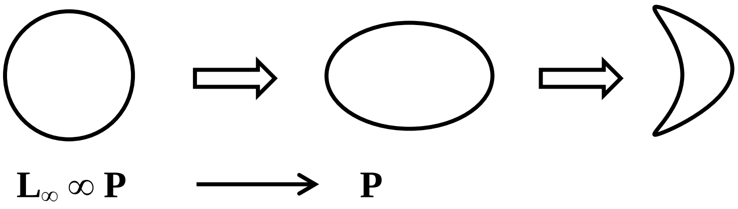

Figure 2. The scheme of transformation of radial symmetry into bilateral when the shape of the cross section is changed.

Shafranovsky (1985) explains his rule as follows: deviating from the vertical axis of the cone L_∞, a rectilinearly moving object inevitably follows along one of the countless planes of symmetry of the cone, which is imprinted on it, as required by the Curie symmetry principle. He also points out that according to this principle it is necessary to take into account both the structure of the environment, and the movement of the studying object relative to this environment, and the movement of the environment relative to the object. For example, moving objects can develop or maintain radial symmetry if they actively swim in all directions. So, radial symmetry in moving Metazoa develops due to active swimming in all directions (like Medusa). Shafranovsky also writes that in the marine environment, radial-beam symmetry does not impede the directional swimming of the animal, but at the bottom, everything moving, crawling, growing horizontally or obliquely will have only one type of symmetry: this is bilateral symmetry with the single plane P.

If the body is in suspension in a liquid or gaseous, the gravity for it is compensated by the uniform and comprehensive pressure of the liquid or gas. The impact of such environment can be likened to the symmetry of a sphere – $\infty L_\infty \infty P$. Such environment should give rise to forms close to spherical (Shafranovsky, 1985). Corallites of the Heliolitida, surrounded by coenenchyme, are similar to cylindrical bodies placed in the liquid (Fig. 3). The equable pressure of the coenenchyme from different sides contributes to the preservation of their radial symmetry $L_\infty \infty P$ (Fig. 4), which with the full development of septa or folds of walls in an amount of 12 has the formula $L_{12}\,12P$.

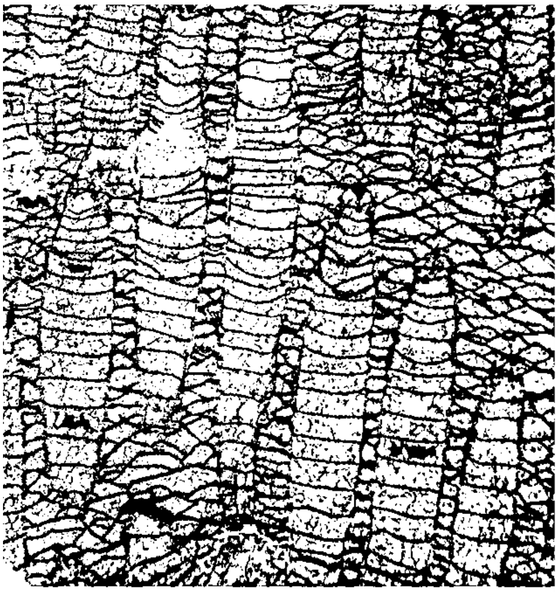

Figure 3. *Vorupora exigua* (Billings, 1865); specimen No. 387-75: longitudinal section; corallites are similar to cylindrical bodies placed in the liquid (the middle part of the Zeravshan ridge, the left board of Archa-Majdan River, gorge Zakhona, Voru section, bed 13; Upper Ordovician, Upper Ashgill, Minkuchar beds). Collected by V.L.Leleshus, 1976. The scale is not respected.

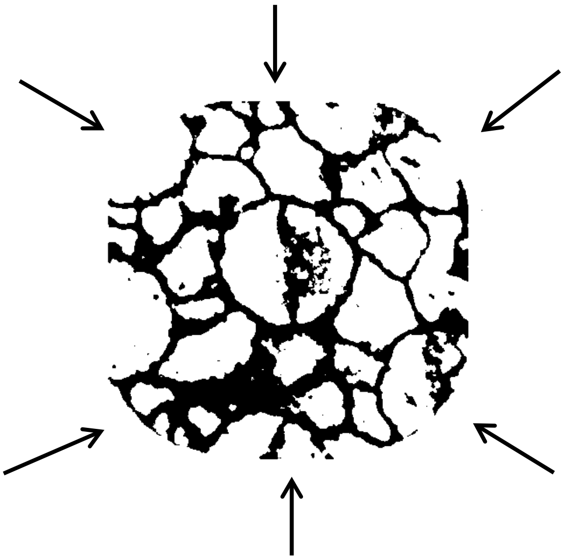

Figure 4. *Vorupora exigua* (Billings, 1865); specimen No. 387-90: cross section; corallite (in the center) is surrounded by coenenchyme on all sides; so, we can suppose that it experiences uniform pressure (shown by arrows) from different sides (the middle part of the Zeravshan ridge, the left board of Archa-Majdan River, gorge Zakhona, Voru section, bed 13; Upper Ordovician, Upper Ashgill, Minkuchar Abeds). Collected by V.L.Leleshus, 1976. The scale is not respected.

Developing the Curie symmetry principle further, Shafranovsky pointed out that three options are possible for organisms: 1 – the symmetry elements of the organism coincide with the symmetry elements of the environment (the Curie symmetry principle); 2 – only part of the elements coincides; 3 – the symmetry elements of the body do not coincide with the symmetry elements of the environment (the body forms its own symmetry). Without going into an analysis of these cases, we note only that corals as benthic animals obey the first option.

The effect of gravity on coral growth and coral symmetry is not always taken into account. Typically, when studying corals, such environmental factors are considered as temperature, sedimentation of terrigenous material, the presence of currents, illumination, and depth, but not gravity. These factors change rapidly over time, while the constant effect of gravity is less noticeable and often not taken into account. For example, some authors exclude environmental control on growth rhythm in some Alveolitidae, in contrast to Favositidae, and specify that causes of differences between individual corallites remain unknown (Zapalski et al., 2012). Zoning implies synchronism of changes, that is, it is formed due to the synchronism of changes in areas located on the continuation of each other. For example, in heliolitids, changes cover both corallites and the coenenchyme located between them (Ospanova, 2019a). Bottoms are usually located perpendicular to the direction of growth of the coral. If corallite grows vertically (as at Favositidae), the bottoms are deposited horizontally, that is, perpendicular to the direction of growth of the coral and to the vertical axis of the cone (symmetry of gravity). Such a position is most stable in this situation as the compensating ("neutralizing") effect of gravity. Since the effect of gravity is compensated, seasonal influence comes to the first plane; therefore the zoning of growth manifests itself. In curving corallites (alveolitoid structure), some bottoms located perpendicular to the direction of growth of corallites, and some bottoms, under the influence of gravity, are located not perpendicular to the direction of growth of corallite, but inclined to it. Thus the bottoms in the adjacent corallites appear strongly displaced relative to each other. As a result, the rhythm of growth is violated, veiled.

6. Symmetry and Phylogenetic Implications

As the review shows, the shape of corallites and the symmetry associated with it could be diverse. Three main types of symmetry at Paleozoic corals are outlined: bilateral, radial (12-ray symmetry is a type of radial) and tetragonal. Evasions are associated with a specific lifestyle and are rare.

The formation of the bilateral type of symmetry in the Rugosa is considered above. The oldest "auloporoid" form of corallites of the Tabulata (that is, inherent in the genus *Aulopora*) is also characterized by bilateral symmetry. Radial symmetry is observed in cases when the auloporoid form of corallites is replaced by the cylindrical one. At the same time, the tetragonal shape of corallites may indicate the ancestral symmetry. Earlier, we briefly considered such integral characteristic of Paleozoic corals as the multiplicity of certain features by four (Ospanova, 2003a). One of its manifestations is expressed in the tetrahedral form of corallites of some Tabulata (Fig. 5) and Rugosa.

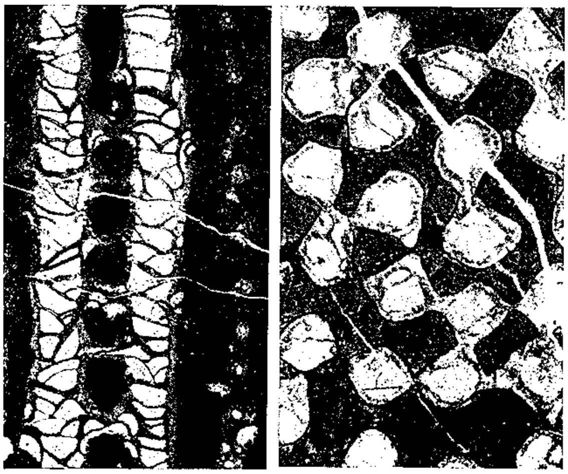

Figure 5. *Hayasakaia tsengi* Sokolov, 1955; longitudinal (left) and transverse (right) sections; the tetrahedral shape of the corallites in the transverse section is clearly visible (South China, Sichuan; Lower Permian, Chisya horizon).From the work of B.S.Sokolov, 1955. The scale is not respected.

According to Sokolov (1955), the genus *Tetraporella* descended from *Palaeofavosites*: even a slight divergence of the *Palaeofavosites* corallites should lead to elongation of the pores into the tubes. In turn, the genus *Palaeofavosites* descended from lichenariids.

The question of the genesis of the porosity of the Tabulata was examined in detail by us (Ospanova, 1998). It is obvious that it is impossible to understand from Sokolov’s scheme how exactly the angular pores appeared in *Palaeofavosites*, which lichenariids developed along the entire perimeter of corallites. It is also unclear how *Tetraporella* could have a tetrahedral form of corallites if the *Palaeofavosites* had a multifaceted shape (adjacency from 3 to 9-11). In addition, the genus *Palaeofavosites* first appeared in the upper Middle Ordovician and *Tetraporella* in the lower Middle Ordovician (Sokolov, 1955, 1962; Preobrazhensky, 1979, 1982; Chudinova, 1986; Khayznikova, 1989, et al.). Therefore, we can rather assume that not *Palaeofavosites* gave rise to the genus *Tetraporella*, but the genus *Tetraporella* was the forerunner of the genus *Palaeofavosites*. If we take this line of development, the presence of pores initially only in the corallite corners of Favositida is well explained: the porosity of favositids arose as a result of the transformation of fasciculate colonies of *Tetraporella* with a free arrangement of corallites into massive (cerioid) colonies of *Palaeofavosites,* while the corner connecting tubes were reduced, being replaced by angular pores. A continuation of this development trend is the subsequent shift of pores from corners to the walls of corallites; it led to the emergence of new taxa – the genera *Mesofavosites*, *Favosites*, *Multisolenia,* etc. However, some representatives of Tetraporellidae retained corner connecting tubes (see Figure 5).

Corallites of cerioid colonies have a polygonal cross-sectional shape, which is associated with their close arrangement. Fasciculate and massive tabulates colonies have the ability of interchangeability, and the shape of corallites changes accordingly. During the transformation of massive colonies into fasciculate polygonality disappears and corallites become rounded in cross-section. There are colonies of mixed type with areas of both massive and fasciculate structures. In this case, polyhedral (in areas of massive arrangement) and cylindrical corallites (in areas with a free disposition) are observed. Therefore, the ancestor of *Tetraporella* cannot be either *Palaeofavosites* or any other massive colonial coral. Without stopping in detail, we note only that the genus *Tetraporella* is associated with auloporids, which had a tetrahedral corallite form (Ospanova, 1998). The tetramerity of *Tetraporella* corallites is not acquired, but indicates ancestral symmetry. The inability of corallites to preserve their polygonality during the disintegration of massive colonies, the existence of initially solitary forms with a square cross-section of corallites among different groups of corals (*Goniophyllum* and *Araeopoma* in rugoses, solitary tetradiids among the Tabulata), as well as the antiquity of the appearance of the trait (lower Middle Ordovician) and its stability (conservation tetramerities in representatives of the Tetraporellidae family throughout the Paleozoic) indicate the independence of this feature. Chudinova (1986) also paid attention to the antiquity of the tetragonal form of corallites.

It should be noted that Sokolov (1955) who proposed the scheme Lichenariida (Billingsariidae) – *Palaeofavosies – Tetraporella*, never considered the question of the origin of porosity of the Tabulata finally resolved. He emphasized the absence of a direct link between lichenariins and favositins. So, the point of view of Sokolov (1955, 1962) on the origin of syringoporids from favositids, as it is clear from the foregoing and as established by the studies of Chudinova (1986), is not confirmed.

Preservation of the ancestral tetragonal symmetry was possible in cases when corals maintained a solitary form of existence, that is, did not transform into massive cerioid colonies, or the arrangement of corallites in the colony remained relatively free (fasciculate and hemi-massive colonies). Tetradiids and halysitids built hemi-massive colonies, according to our classification (Ospanova, 2010), and they can preserve the tetragonal form of corallites.

Bassler (1950) associated the tetrahedral shape of corallites of the Tetradiida with the tetrahedral division of corallites, but the two- and three-dimensional division of tetradiids, noted by Sokolov (1955), does not determine the trihedral shape of corallites. Therefore, it is more correct to say that division did not violate the tetragonal form of corallites. It also emphasizes the primacy of the tetragonal symmetry.

Wright (1971) leads a phylogenetic line (within the Rugosa) from *Goniophyllum* through *Araeopoma* to *Rhizophyllum* and further to *Calceola*. In this case, the tetragonal form of corallites is lost and is replaced by a semiconical (shoe-like). The flattening of one of the sides is associated with the fact that the coral lay at the bottom, lifting only the mouth of the calyx. Wright considers the Conulata as the alleged ancestor of Calceolidae. If this assumption is based on the tetragonal form of the corallites of both, then what is about tabulates having a similar form of corallites? Our idea of the antiquity of the tetrameric feature is consistent with the opinion of modern zoologists. Most zoologists believe that protocnidaria had 4-ray symmetry, expressed in the appearance of 4 hollow tentacles and a square cross-section of the stomach (Stepan’yants, 1988). This means, that to one degree or another, 4-ray symmetry must manifest itself in descendants. At Paleozoic corals, it persists in solitary forms or in representatives with a more or less free arrangement of corallites.

The presence in Paleozoic corals of such integral characteristic as a multiplicity by four testifies in favor of the 4-ray symmetry of the ancestor (Ospanova, 2003a). However, this trait is not always clearly expressed, was not manifested in all species and could easily be violated due to the formative overlay. Therefore, most likely, tetramerity was transferred to the Tabulata, Rugosa and Heliolitida not directly from the ancestor with 4-ray symmetry, but through a series of additional morphological transformations (pedomorphosis – transition to sedentarity – calcification) (Ospanova, 2005).

Sokolov (1955, p. 269) pointed out that for the septal formations of the most ancient tabulates “the most characteristic is the development according to the plan of four, eight, sixteen, twenty and twenty four rows; a multiple of six is dominant since the end of the Ordovician." At the Rugosa, the retreat from 4-ray symmetry occurs at the beginning of their formation: when the corallites bend, the second pair of septa shifts to the main one (which is also observed in tabulates with well-developed septa), and the body turns out to be unevenly folded. Coral in general is characterized by the paired appearance of mesentery. The next pair of septa appeared where the body was smooth – near the opposite septa. Thus, the multiplicity of four was violated (symmetrization of the primary partitions of the Rugosa), but the primary 4-ray symmetry did not disappear without a trace and was manifested in the fact that the septa were inserted at 4 points, in 4 quadrants. From the statement of Sokolov it is clear that deviation from tetramerity occurred at the Tabulata more gradually.

7. Conclusions

The study of the symmetry of Paleozoic corals not only supplements their general morphological characteristics, but also helps to restore phylogenetic relationships in some cases. Tracing the formation of the main types of coral symmetry allows us to judge the origin of the groups. Thus, the tetragonal symmetry of Tetraporellidae corallites could not arise during the transformation of massive Favositida colonies into semi-massive Syringoporida colonies, as was previously thought. This contradicts the totality of factors (the antiquity of the appearance of the trait and its conservatism; the nature of the manifestation; non-preservation of the polygonality of corallites when replacing massive colonies with fasciculate). The data complex indicates that four-ray symmetry could be inherent in the ancestors of coral (presumably Corallomedusa). In total, the symmetry of corals was determined not only by heredity, but also depended on the symmetry of the environment (Curie symmetry principle). Among many environmental factors, gravity plays a leading role in the formation of the symmetry of organisms. Therefore, for a more well-founded evaluation of the taxonomic significance of features, the effect of gravity should be taken into account. The effect of gravity is most fully investigated by Shafranovsky; therefore we must take into account the Shafranovsky's rule when studying coral symmetry.

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