

## Some remarks on diagenesis of rugose coral skeletons

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**Abstract.** Rugose coral microstructure exhibits striking similarity to that in the Scleractinia. The main difference lies in the mineral composition: calcitic in the former and aragonitic in the latter. Calcitic skeletons of the Rugosa are commonly better preserved than those in the Scleractinia, and therefore some of them have been interpreted as unaltered, a position rejected in this paper. The dual nature of septa, which commonly consist of a primary trabecular septum and secondary fibrous sheets, results in differently expressed diagenetic alterations in comparison to other structural elements.

It has been postulated that both early and advanced diagenesis may, in some circumstances, be distinguished in the Rugosa. In most instances the early diagenetic features were destroyed by the post-burial alterations. Replacement and recrystallization are the most important processes among the advanced chemical alterations. Both may either facilitate the recognition of original macro- and microstructures or obscure them. Surface replacement by silica promotes perfect preservation of shape and inner morphology, whereas pervasive replacement may destroy both. Selected replacement by hematite may help in exposing the trabecular microstructure of septa, whereas deep replacement may destroy the entire morphology. Physical alterations, such as crushing and flattening of skeletons are always destructive. They result from compaction, and their scale depends on skeletal morphology and on the relationship between the rate of infilling of intra-skeletal spaces and the accumulation of surrounding sediment.

Pre-burial events, such as overgrowth and penetration by borrowing organisms, their holdfasts or roots may aid in the recognition of early diagenesis, but may also lead to substantial pre- or post-burial skeletal alteration, resulting sometimes in total destruction. This depends mostly on the pH of pore fluids.

**Key words:** Rugosa, diagenetic alterations.

### Introductory considerations

The occurrence of diagenetically unaltered rugose coral skeletons seems very unlikely. Thus, rather than attempting to detect the presence of dia-

genetic alterations, we should be investigating the degree of alteration that has occurred. Unfortunately, this is not widely recognized. Fossils from some areas (for instance, some rugose coral taxa from the Permian deposits of Timor Island) have commonly been considered to be unaltered (Schindewolf 1942; Schouppé & Stacul 1955; Sorauf 1984). Neither this, nor the opposing opinion, suggesting replacement by calcite of the original aragonitic skeleton (Oekentorp 1984) can be supported. Such opposite opinions, published in the same journal (Oekentorp 1984 *versus* Sorauf 1984), result from differing approaches to the problem of coral diagenesis and differing interpretations of features observed. I quote this example to stress the need for extensive investigations in this matter.

The growth rates of epidermal rugose coral skeletons differ, depending on the genetic makeup of a given taxon, the growth stage involved and environmental conditions. Irrespective of local conditions, however, coral growth is continuous and cannot be interrupted by retreat of the body of the polyp or colony from part of its skeleton. Interrupted skeletogenesis cannot be renewed without being clearly marked. A self re-colonization of a skeleton is not uncommon, especially in colonial species. In each such instance the temporarily abandoned skeleton is easy to recognize, either because it has been subjected to more advanced diagenesis or its inter-skeletal spaces have been filled with the sediment, or both. An overgrowth by strange organisms of such temporarily exposed skeletons was also observed.

Macro- and microstructures resulting from the process of organic skeletogenesis should be defined prior to a discussion of their diagenetic alterations. The Scleractinia, and also probably the Rugosa, did not secrete an outermost protective layer of the skeleton, comparable to the molluscan *periostracum*. Thus, only restricted areas of their skeletons, i.e., those covered directly by polyp bodies, were protected against extrinsic factors. Major parts of the skeletons of solitary and colonial taxa were exposed to bioerosion and physical and chemical stress – factors commonly not considered to be active during an individual animal life time. The great variability in morphology and size of the Rugosa, superimposed on the environments in which they lived and their life habits constitute the next set of conditions affecting the differentiation of diagenetic processes altering their skeletons.

Skeletogenesis in the Scleractinia and most probably in the Rugosa is common for all skeletal elements in that they are secreted by ectodermal calicoblasts. This process may be clearly differentiated, however, when secretion of septa and structures derived from septa are compared to that of the remaining skeletal elements. External walls, tabulae and dissepiments were secreted by calicoblasts of the flat or weakly folded basal disc of the polyp and/or its walls, whereas secretion of the septa was more complex. As a rule, two steps are observed in the formation of septa, which were secreted in septal pockets, i.e., narrow folds of the ectoderm developed between mesenteria. The so called “dark line” was secreted during the first step of secretion. In most instances it consists

of skeletal micro-elements called trabeculae (Pl. 1, fig. 3). Genesis of the “dark line” in the Rugosa is one of the subjects discussed by me in the separate paper. The “dark line” can, in short, be called a primary septum and its secretion was possible only when the septal pocket was narrow. Once the pocket widened, partly because of the secretion of the primary septum, the second step of septal secretion began. This step ended with secretion of the so-called secondary sheets of septa or stereoplasmic growth layers – nontrabecular skeletal elements that cover the primary septa. A stereoplasmic growth layer expanded also towards the remaining skeletal elements (Schouppé & Stacul 1955, 1959). All such secondary thickenings were originally composed of crystalline fibrils oriented parallel to the surface of a given skeletal element. The differentiation of the microstructure of septa leads to more complexity in their diagenetic alteration than occurs in other parts of the skeleton.

Microstructural stability in the middle rank taxa (families and orders) requires special attention. As summarized by Roniewicz & Morycowa (1993), this character is commonly applied to the taxonomy of the Scleractinia. In contrast, the microstructure of the septa and external wall is commonly omitted from the taxonomy of the Rugosa. This may have resulted from both limited knowledge of the microstructure itself and inadequate recognition of the diagenetic alterations affecting it. Original microstructures in the Rugosa have sometimes been considered to be secondary, as Oekentorp (1980) interpreted the so-called “Stirn-zonen” or diagenetic alterations have been misinterpreted as original microstructures (e.g. Schindewolf 1942). In contrast to Rodriguez (1989) who claimed the microstructure in the Rugosa variable within a single corallite I maintain the position of it being constant at least in middle rank taxa (genera and families). The origin of the microstructure was undoubtedly controlled by the calicoblasts. Thus, its random pattern seems unlikely. Sorauf (1996) summarized both results and doubts in skeletal structure of Phanerozoic corals and pointed out a high rank (order) level character of the microstructure in the Scleractinia. I do not see any reason to consider it less important in the Rugosa. This question is not developed in the present paper, which is devoted to an overview of some aspects of the diagenetic alteration in rugose coral skeletons.

Despite mineral differences – calcite (low and high magnesium calcite were recognized or postulated) in the Rugosa *versus* aragonite in the Scleractinia – details of the skeletal microstructure in these two subclasses are similar to a large degree. This has been already pointed out by Kato (1963). According to the supporters of the thesis of a direct derivation by descent of the Scleractinia from the Rugosa, such an analogy favours their interpretation. Contrary to that position, the difference in mineralogy constitutes one of the key arguments against a direct relationship between those two subclasses. It is always pointed out by the supporters of a distant relationship between those taxa and the derivation of the Scleractinia from a non-skeletal ancestor (Oliver 1980). Some students (Oekentorp 1984; Wendt 1991) suggested that the mineralogy of the rugose coral ske-

**Plate 1**

**Fig. 1.** Gen. et sp. nov. 1. Glass Mountains, SW Texas, USA. Upper Guadalupian, Bell Canyon Formation. Perfectly preserved calice,  $\times 5$ .

Gen. et sp. nov. 1. Glass Mountains, południowo-zachodni Texas, USA. Formacja Bell Canyon, górny gwadalup. Doskonale zachowany kielich,  $\times 5$ .

*Wannerophyllum cristatum* (Gerth). Timor Island, Upper Permian. Fanning microstructure of septum,  $\times 75$ .

*Wannerophyllum cristatum* (Gerth). Wyspa Timor. Górny perm. Wachlarzowa mikrostruktura septum,  $\times 75$ .

**Fig. 3.** *Disphyllum geinitzi* Smith & Lang, 1935. Holy Cross Mountains, Poland. Givetian. Monacanthine trabeculae in longitudinal section,  $\times 150$ .

*Disphyllum geinitzi* Smith & Lang, 1935. Góry Świętokrzyskie. Żywet. Trabekule monakantowe w przekroju podłużnym,  $\times 150$ .

**Fig. 4.** *Lophophyllidium* sp. Glass Mountains, SW Texas, USA. Lower Cisuralian, Wolfcampian. Transverse section of the septum. Recrystallized trabeculae (middle) and stereoplasmic growth layers,  $\times 50$ .

*Lophophyllidium* sp. Glass Mountains, południowo-zachodni Texas, USA. Dolny cisural, wolfkamp. Poprzeczny przekrój septum. Przekryształizowane trabekule (w środku) i złożki okrywowe septum,  $\times 50$ .

**Fig. 5.** *Heterophyllia* sp. Holy Cross Mountains, Poland. Upper Viséan. Several generations of palisade and mosaic cements shown by means of the cathodoluminescence technique,  $\times 40$ .

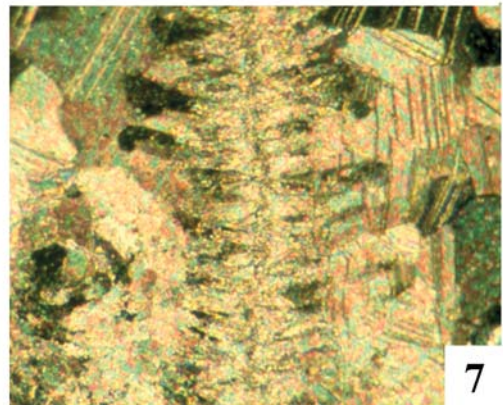
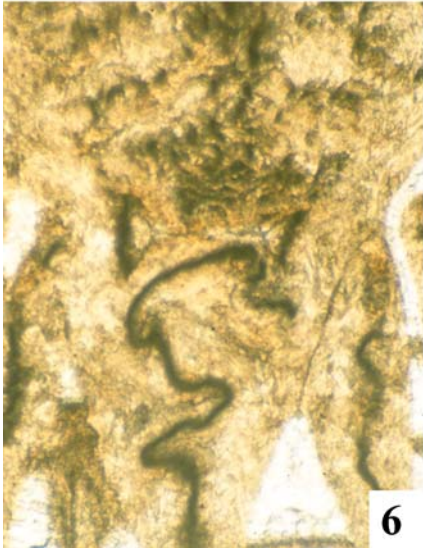
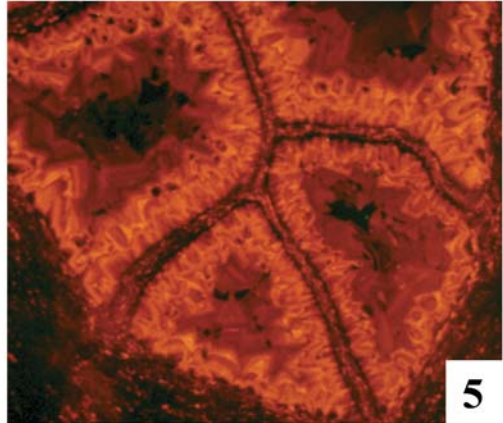
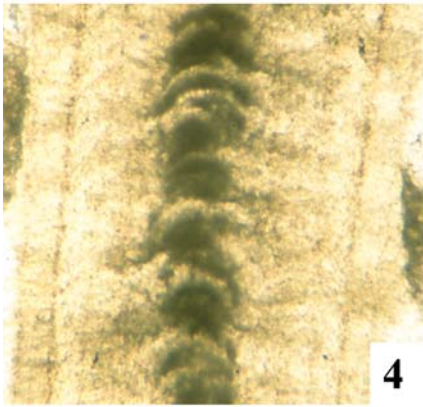
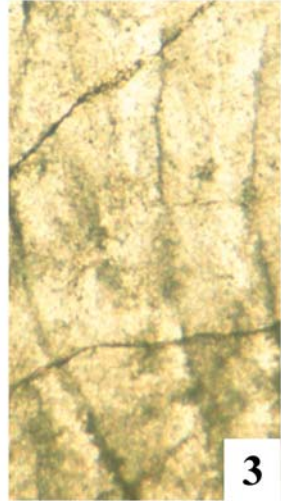
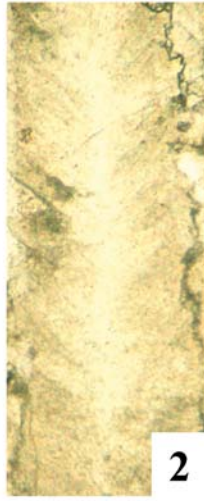
*Heterophyllia* sp., Górny wizen. Góry Świętokrzyskie. kilka generacji cementów palisadowych i mozaikowych w katodoluminescencji,  $\times 40$ .

**Fig. 6.** *Lophophyllidium* sp. Glass Mountains, SW Texas, USA. Middle Guadalupian, Roadian. Transverse section. Trabeculae in septal lamellae incorporated in the columella and strongly curved "dark line" of the counter septum,  $\times 30$ .

*Lophophyllidium* sp. Glass Mountains, południowo-zachodni Teksas, USA. Środkowy gwadalup. Trabekule w lamellach septalnych włączonych w kolumellę oraz powyginana „ciemna linia” septum przeciwległego,  $\times 30$ .

**Fig. 7.** *Protowentzelella* sp. Hornsund area, Vestspitsbergen, Cisuralian, probably Sakmarian. Transverse section. Palisade cement continuing orientation of septal biocrystallites. Mosaic cement developed both sides of palisade cement,  $\times 50$ .

*Protowentzelella* sp. Hornsund, Vestspitsbergen. Cisural, zapewne sakmar. Przekrój poprzeczny. Cement palisadowy naśladuje orientację oryginalnych kryształów. Cement mozaikowy zapełnia pozostałe przestrzenie na prawo i lewo od palisadowego,  $\times 50$ .



leton is secondary and was supposedly originally aragonitic. A comparison of preservation of the skeletons of the Scleractinia and Rugosa does not support such a thesis. Lack of pseudomorphs after aragonite is only an additional argument. In the vast majority of scleractinians the skeletons, which undoubtedly were originally aragonite, have been completely destroyed diagenetically, whereas rugose coral skeletons, hundreds of millions of years older, are commonly very well preserved. The primary low magnesium calcite mineralogy of their skeletons is perhaps the most probable explanation of that fact.

## Initial diagenesis

In view of observations on the Recent Scleractinia (Sorauf & Cuiff 2001), it seems reasonable to accept that initial diagenesis started during the life time of individual rugose coral organisms. In the Rugosa, however, the presence of low magnesium calcite, a mineral diagenetically more stable than aragonite, has made initial diagenetic alterations less obvious and difficult, often impossible to recognize. In contrast to the Scleractinia, data dealing with that problem are absent from the rugosan literature. Moreover, empirical proof of diagenetic alterations taking place during the life time of individual specimens are impossible to obtain. Whereas the recognition of diagenetic alterations in the living Scleractinia skeletons is only a matter of application of an appropriate technique, one cannot be certain when the observed alterations actually took place in the Rugosa. Nevertheless, some deductions concerning initial diagenesis in the latter subclass are possible.

By analogy with the Scleractinia, initial diagenesis in the Rugosa can be divided into two steps: pre- and post-burial. The earliest pre-burial diagenesis in the latter subclass affects the external wall perhaps soon after its secretion. In contrast to the Scleractinia, the vast majority of the Rugosa possessed entire external walls uncovered by the polyp's body and exposed to a variety of pre-burial diagenetic processes from the very beginning. Pre-burial, diagenesis of remaining skeletal structures of the Rugosa, covered by the polyp that rested on them in the calice, was perhaps slightly postponed in comparison to that in the external wall. Those inner structures were protected by both the external wall at the periphery and the body of the polyp from the calice side. This protection particularly concerns bioerosion. In the part of the skeleton distant from the calice, diagenetic processes acted irrespective of its exposure or burial, but the results differ and are characteristic for each environment. Biogenic destruction and abrasion prevailed in exposed skeletons and chemical processes were most dominant in those that were buried. Pre- and post-burial processes occurred in sequence, however, and should be carefully analysed in that respect. Skeletal increase in calices did not influence the diagenesis of previously secreted skeletal elements, nor did the diagenesis of skeletal elements below the calice change the mineralogy and skeletogenesis of the newly secreted structures.

The second phase of initial diagenesis in rugose coral skeletons, i.e. the shallow burial stage, may be documented by differences in the degree of alteration in ontogenetically younger and older parts of corallites and colonies. Pre-burial processes in the ontogenetically younger parts of the Rugosa cannot be detected directly, but may in some instances be deduced. For instance, horn corals supplied with well developed talons or attachment scars inhabited high energy regimes, which are characterised by a low rate of sediment accumulation. Thus, their extended exposure above a sea floor is likely. Bioerosion or overgrowth may also indicate such exposure. Those characters, combined with a successively decreasing degree of diagenesis toward the calice may provide indirect proof of pre-burial diagenesis, replaced successively by the shallow burial stage in the last example. All such proofs should be applied to any analysis with care, because none can be treated as decisive.

Diagenesis may also follow a step by step burial of a corallite that grew upward in conditions of moderate sediment accumulation. Such a process is superimposed on earlier diagenetic effects and the two processes are indistinguishable. Therefore, distinction between lack of sedimentation and moderate sediment accumulation may be deduced only from the shape of a given corallite or colony, whereas the boundary between initial and moderately advanced diagenesis in individual rugose coral skeletons is commonly unrecognizable. In large solitary corals that grew for several years, the difference in the degree of diagenetic alteration in ontogenetically earlier and later parts of skeletons is sometimes more obvious than in short-lived individuals. The same is true for some large colonies. Unfortunately, advanced diagenesis commonly destroys all sights of early diagenesis, causing equal alteration of the entire skeleton. It may also appear that the skeleton in the calice shows greater diagenetic alteration than that below the calice. Such a situation provides evidence of post-burial changes, discussed below.

Although rigid boundaries between individual stages of diagenesis of the rugose coral skeletons are indistinguishable, the following characteristics may be useful. *Initial diagenesis*: crystalline fibrils remain recognizable in trabeculae and in non-trabecular skeletons. *Moderately advanced diagenesis*: Remnants of trabeculae and growth layers of non-trabecular structures are recognizable, but crystalline fibrils were recrystallized. *Advanced diagenesis*: Original microstructure of all structural elements became unrecognizable. Chevron and/or zig-zag structures may appear.

I know of no method of detecting or measuring the degree of diagenesis of skeletal elements prior to development of infilling cement. Palisade or columnar cements that follow a pattern of diagenetically altered crystals in skeletons (Pl. 1, fig. 5) suggest that the diagenesis of the latter preceded the infillings. Those original skeleton crystals, altered perhaps in the second phase of early diagenesis, formed matrices for the first generation of cement. More or less equal diagenetic alterations of both original skeletal crystals and palisade (columnar) ce-

ments (Pl. 1, fig. 7) may indicate contemporaneous recrystallization of original crystals and palisade cements. Crystallization of the latter may also have caused early diagenetic alterations of the original crystals. This second step of early diagenesis most probably resulted from chemical reactions between skeletal material and fluids penetrating interskeletal spaces. The influence of compaction seems unlikely. The question of the extent to which the degree of diagenesis of individual parts of a skeleton depended on early diagenesis remains open. This question has not been considered to date in rugose coral studies.

Although some skeletal structures in the Rugosa may be temporarily or permanently in contact during early ontogeny, the complete skeletal infilling of a corallite inside is seldom observed. The great majority of the Rugosa built a comparatively light skeleton with interskeletal spaces occupying much more room within the external walls than all skeletal elements combined (Pl. 1, fig. 5; Pl. 2, fig. 6). This prevalence of interskeletal spaces made some skeletons comparatively light. This is especially true for flat, massive colonial taxa that may have floated over a great distance without being damaged or abraded. Such a factor is seldom considered when pre-burial changes in rugose coral taxa are analysed in terms of diagenetic alterations. The process of infilling of the interskeletal spaces may have begun during the pre-burial phase, but was fully developed only after the skeleton was buried.

### Some examples of advanced diagenesis

*Cementation.* Two main types of infilling cements are commonly distinguished in the interskeletal spaces of rugose corals: *palisade* or *columnar cement* (Pl. 1, fig. 5, middle) and *drusy mosaic cement* (Pl. 1, fig. 7, left and right; Pl. 2, fig. 7). The palisade (columnar) cement formed the first generation of infilling cements. Its calcite crystals grew perpendicular to individual structural elements, in a sense continuing the organically controlled crystallization. The C-axes of individual crystals of palisade cement are always longest. Thus, it forms palisade-like or columnar rows of long crystals, as indicated by the etymology of its name. This is an early diagenetic cement that may have been developed in several phases as revealed by CL studies (Pl. 1, fig. 5). In very narrow interskeletal spaces it may be the only cement developed.

Drusy mosaic cement fills spaces left by palisade cement. The C-axes of the crystals in mosaic cement are not precisely oriented. The growth direction of these crystals depends on their crystallization strength and on the space available. Their size and arrangement in the section differ considerably, resulting in a mosaic-like image. The number of crystallization phases in this type of cement (Pl. 1, fig. 5) depends on both the space available and the volume and chemical composition of pore fluids, which may vary in such a way that crystallization may either cease or be intensified.

The growth of mosaic cement may, in some instances, be so extensive that it causes destruction of primary corallite structural elements. Such events are seldom attributed to secondary processes, although they may lead to considerable morphological and taxonomic misinterpretation when not recognized. Destruction of the axial parts of septa (Pl. 2, figs. 7, 10), for instance, may be interpreted as original shortening – a diagnostic character for some taxa. Such alteration may have resulted from incomplete infilling of the axial parts of inter-tabular areas during the first phase of crystallization. A renewed supply of supersaturated pore fluids would cause crystallization of drusy mosaic cement. Also, the described alteration may have resulted from a change in the pH of the supplied pore fluids. Dissolution of parts of septa adjacent to empty space is most likely in such a situation. The crystallization of quartz in some destroyed areas may provide evidence of such alteration.

The infillings of interskeletal spaces vary in time of occurrence and, less frequently, in composition. The reason for such variability remains unknown. A simple dependence on the intensity of pore fluids flow, although probable in some instances, is certainly inadequate as a general explanation. Why, for instance, do the intraskeletal spaces of Middle Carboniferous colonial corals remain nearly empty today in the Moscow Basin? Their burial in the calcareous mud and occurrence in limestone cannot be considered inappropriate for a supply in  $\text{Ca}^{2+}$  ions. The overpressured beds may be an explanation. Also, early diagenetic bituminous infilling of interskeletal spaces may in rare instances cause them to remain empty. The Upper Devonian and Lower Carboniferous Rugosa from Polish Pomerania (Pl. 2, fig. 3) may constitute an example. Dissolution is much less likely in those corals, because their skeletons remain untouched by that process in all instances observed.

*Compaction.* Despite the fact that we do not recognize the reason for variation in the rate of infilling of interskeletal space, some results of incomplete infillings can be analysed in terms of diagenetic processes. The more or less advanced flattening of a coral, resulting in breakage (Pl. 2, fig. 6) or total destruction of its skeleton, is the most obvious symptom of compaction. The advancement of that process depends on several factors, the most important of which are: the morphology of the skeleton and its resistance to pressure, depending on the strength of individual components of the skeleton and their mutual arrangement; the intensity of interskeletal space infillings; the orientation of a corallite or colony (perpendicular or parallel to the acting stress); the rate of accumulation of the enclosing sediment with respect to both the rate of infilling of interskeletal spaces and the rate of lithification of the surrounding matrix. Curious taphonomic and taxonomical interpretation may result if those factors are not taken into consideration.

The analysis by Ivanovsky (1989) of two genera from the Upper Carboniferous deposits of the Moscow Basin forms a good example. He analysed small horn corals included by him to the genus *Paracania*, possessing strong, radial-

## Plate 2

**Fig. 1.** *Lophophyllidium* sp. Glass Mountains, SW Texas, USA. Lower Cisuralian, Wolfcampian. Borings through the silicified external wall,  $\times 12$ .

*Lophophyllidium* sp. Glass Mountains, południowo-zachodni Texas, USA. Dolny cisural, wolfkamp. Wiercenia skrzemionkowanej ściany zewnętrznej,  $\times 12$ .

**Fig. 2.** *Paraduplophyllum (Vacoa) vermiculare* Fedorowski, 1987. SW Texas, USA, Cisuralian, Wolfcampian. Surface morphology altered by crystallization of silica,  $\times 15$ .

*Paraduplophyllum (Vacoa) vermiculare* Fedorowski, 1987, południowo-zachodni Teksas. Dolny cisural, wolfkamp. Morfologia powierzchni zniszczona przez krystalizację krzemionki,  $\times 15$ .

**Fig. 3.** Gen. et sp. indet. Pomerania, northern Poland. Transverse section. Early diagenetic bituminous infilling of interskeletal spaces,  $\times 8$ .

Gen. et sp. indet. Pomorze. Przekrój poprzeczny. Wczesno-diagenetyczne wypełnienie przestrzeni międzyskieletowych bituminami,  $\times 8$ .

**Fig. 4.** *Paraduplophyllum (Vacoa) vermiculare* Fedorowski, 1987. SW Texas, USA, Cisuralian, Wolfcampian. Peripheral parts of the skeleton incompletely replaced by silica and partly dissolved,  $\times 8$ .

*Paraduplophyllum (Vacoa) vermiculare* Fedorowski, 1987, południowo-zachodni Teksas, USA, cisural, wolfkamp. Peryferyczne części szkieletu nie w pełni zastąpione przez krzemionkę i częściowo rozpuszczone,  $\times 8$ .

**Fig. 5.** *Paraduplophyllum (Vacoa) vermiculare* Fedorowski, 1987. SW Texas, USA, Cisuralian, Wolfcampian. Silica replaced the original skeleton completely,  $\times 8$ .

*Paraduplophyllum (Vacoa) vermiculare* Fedorowski, 1987, południowo-zachodni Teksas, USA, cisural, wolfkamp. Krzemionka całkowicie zastąpiła oryginalny szkielet,  $\times 8$ .

**Fig. 6.** Probably a plerophyllid rugose coral. Donets Basin, Ukraine. Lower Bashkirian. Delicate skeleton flattened by compaction,  $\times 6$ .

Zapewne przedstawiciel Plerophyllidae. Basen Doniecki, Ukraina. Dolny baszkir. Delikatny szkielet spłaszczony przez kompaktację,  $\times 6$ .

**Fig. 7.** *Euryphyllum troldfjordense* Fedorowski & Bamber, 2001. Ellesmere Island, Canadian Arctic Archipelago, Upper Guadalupian. Large crystals of mosaic cement deformed morphology of the periaxial area of the corallite,  $\times 20$ .

*Euryphyllum troldfjordense* Fedorowski & Bamber, 2001. Wyspa Ellesmere, Kanadyjski Archipelag Arktyczny. Górny gwadalup. Wielkie kryształy cementu mozaikowego zdeformowały morfologię przyosiowej części koralita,  $\times 20$ .

**Fig. 8.** *Soshkineophyllum turgidiseptatum* (Tidten, 1972). Melville Island, Canadian Arctic Archipelago, Upper Guadalupian. Remnants of small trabeculae in the middle area and stereoplasmic growth layers altered to zig-zag structure,  $\times 60$ .

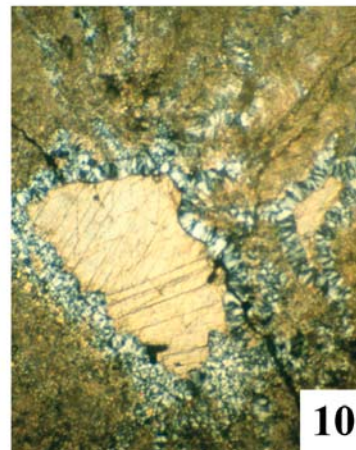
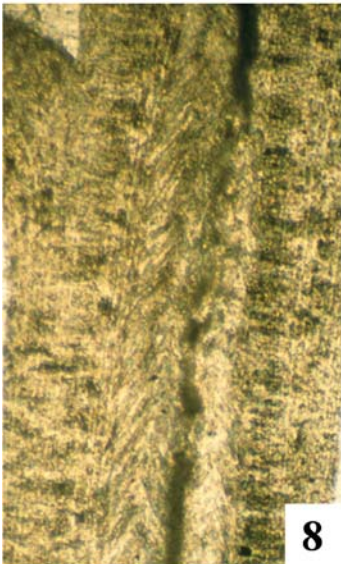
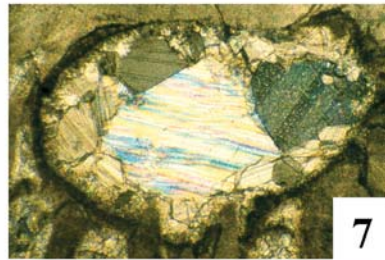
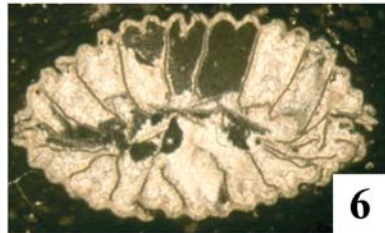
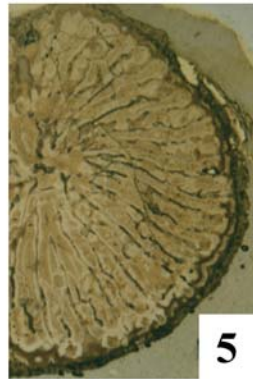
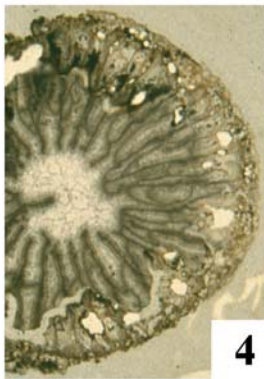
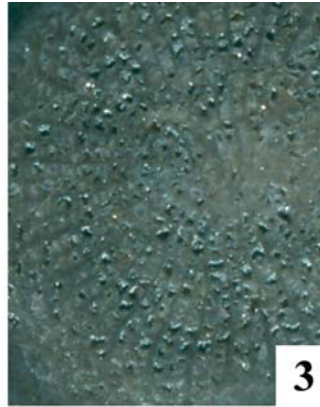
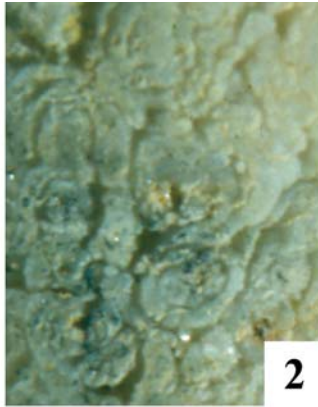
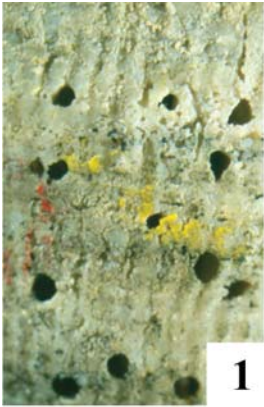
*Soshkineophyllum turgidiseptatum* (Tidten, 1972). Wyspa Melville, Kanadyjski Archipelag Arktyczny. Górny gwadalup. Resztki drobnych trabekul w części środkowej oraz złogi pokrywowe zmienione do struktury zygzakowatej,  $\times 60$ .

**Fig. 9.** “*Diphyphyllum*” *mutabile* Kelly, 1942. Alberta, Canada. Upper Tournaisian. Transverse section. Hematite stained trabeculae,  $\times 80$ .

“*Diphyphyllum*” *mutabile* Kelly, 1942. Alberta, Kanada. Górny turnej. Przekrój poprzeczny. Trabekule przesycone hematytem,  $\times 80$ .

**Fig. 10.** *Euryphyllum troldfjordense* Fedorowski & Bamber, 2001. Ellesmere Island, Canadian Arctic Archipelago, Upper Guadalupian. Large crystals of mosaic cement damaged inner margins of major septa in the corallite axis,  $\times 20$ .

*Euryphyllum troldfjordense* Fedorowski & Bamber, 2001. Wyspa Ellesmere, Kanadyjski Archipelag Arktyczny. Górny gwadalup. Wielkie kryształy cementu mozaikowego zniszczyły wewnętrzne końce septów osiowej części koralita,  $\times 20$ .



ly arranged septa beneath the calices and a comparatively thick external wall, and found them undeformed except for the calices, which were flattened in some. In contrast, *Gshelia*, another abundant coral from the same beds, is as a rule, strongly flattened. The difference in observed preservation led Ivanovsky (1989) to the conclusion that *Gshelia* is a coral lacking an external wall.

When greatly advanced, the forms of deformation discussed above make palaeontological investigations difficult or impossible. Thus, the palaeobiological and stratigraphic value of strongly deformed Rugosa may be greatly reduced or non-existent. Nevertheless, such fossils are not useless and can be utilized for several analyses. Some examples are as follows: the arrangement of inorganic versus original crystals, the disintegration and shifting of crystals within a corallite, the sequence of cement infillings and the relation of cements to original skeletal elements, the substitution by other minerals, the presence or absence of sediments in interskeletal spaces beneath the calice, and others. Some of these are briefly discussed below.

*Replacement* is one of the most common diagenetic alterations observed in corals, and silica is the most common compound to replace calcite in rugose coral skeletons. It penetrated corallites mostly in the form of the silica free solution flow, but may then crystallize into quartz. Iron compounds, mainly hematite, are perhaps second in abundance. The process of substitution by these minerals may, in some instances, improve the value of coral skeletons for scientific investigations, but may also lead to the destruction of data. Permian rugose corals from the Glass Mts. and the Guadalupe Mts., southwestern Texas, are excellent examples. Surface replacement by silica of external walls and structural elements within calices resulted in perfect preservation of these fossils. Acid treatment excavates their external characters and calice morphology without ruining the original mineralogy of their inner skeletal elements (Pl. 1, fig. 1). Unfortunately, extensive silicification may lead to total destruction of the microstructure first and of several macro-morphological characters later (Fedorowski, 1987). Numerous rugose coral specimens from southwestern Texas have been reduced in scientific value because silica penetration was so deep that it camouflaged their inner morphology (Pl. 2, fig. 5). Also, the crystallization of silica may eventually destroy both the internal and surface characters of a specimen, making it inadequate for study of any kind (Pl. 2, fig. 2).

Environmental marine conditions during Early and Middle Permian time in present-day SW Texas were rather peculiar. Silicious Spongiae constituted one of the most common elements of the benthic faunas, flourishing together with calcareous Spongiae during limestone accumulation. The elevated pH of pore solutions resulted in *post mortem* decomposition of their skeletons into silica enriched fluids, which in turn reduced the pH locally. The resulting surplus of silica lead to substitution by its compounds of skeletons buried in slowly accumulated sediment nearby. Perfectly preserved brachiopods from that area were monographed by Cooper & Grant (1972–1977) and some rugose corals were described or mentioned and illustrated by Fedorowski (1986, 1987, 1993).

Complete replacement of calcite by hematite in skeletal structures, and extended infilling by that mineral of interskeletal spaces cause damage to rugose coral skeletons. Such alterations may go so far as to make investigation impossible. Although advanced alterations are well-known, little attention is paid to the slight replacement by iron compounds of individual parts of rugose coral skeletons, even though minimal replacement may help greatly in establishing some microstructural details. Hematite may replace individual fibrils of trabeculae early in diagenesis and resist further diagenetic alterations, such as, for instance, recrystallization of calcite (Pl. 2, fig. 9). Such substitution makes it possible to reconstruct the main microstructural characters from small fragments of septa, although almost the entire septal apparatus may have been damaged by recrystallization.

*Bioerosion.* Rugose coral skeletons, like skeletons of other organisms, were subjected to bioerosion when exposed on the sea floor or only slightly covered with sediment. Penetration of skeletons, mostly of their external walls (Pl. 2, fig. 1), may have taken place both before and after silicification of the external walls. This is indicated by the shape and infillings of holes made by sponge rhizoids and other organisms. The occurrence of holes may have resulted in differential preservation of the inner parts of skeletons. The following extreme processes may serve as an example: In a comparatively low pH environment with a limited supply of silica supersaturated solution, the calcitic inner skeleton may be partly (Pl. 2, fig. 4) or completely dissolved after the silicified external shell has been burrowed through. An inadequate supply of silica supersaturated solution would prevent replacement by the silica and all skeletal structures but the external shell would be lost. Fossils subjected to this process have very low scientific value (Pl. 2, fig. 5). In an environment similar to that mentioned above, but with abundant supply of silica supersaturated solution, its flow through holes would greatly accelerated the process of replacement.

Replacement and mechanical damage by compaction are the most obvious, eye-catching diagenetic processes, but they are not the most important in the Rugosa. Re-mineralization within carbonates, particularly dolomitization, and re-crystallization of calcitic microstructures are the most common alterations observed in that group. Also, the latter processes may lead to total destruction of the microstructure and to severe changes in the macro-morphology when advanced.

*Recrystallization.* Septa, the microstructurally most compact skeletal elements in the Rugosa, provide a good basis for discussion of some forms of diagenetic alteration. In a sense, the dual microstructure of most septa (primary septa mostly trabecular and septal sheets fibro-lamellar) forces us to differentiate between their respective types of diagenetic alteration. The order in which different types of alteration occurs is often difficult to establish. The common absence of recognizable ultrastructure in trabeculae suggests that the process begins in the primary septa.

There remains little doubt that trabecular microstructures underwent re-crystallization in most Rugosa. The shape, plus the arrangement of long C-axes in crystals that replaced original calcite fibrils, are all that is commonly left of altered trabecula. Such replacement imitates the original trabeculae at the microscopic level, because recrystallized calcite refracts light in the same way as was done by the original calcite fibrils. Thus, the image seen under the microscope may obscure both diagenetic alterations in the primary septa and moderately advanced diagenetic processes in the septal sheets (Pl. 1, fig. 4). Our attention is attracted mainly by such advanced diagenetic alterations as the appearance of zig-zag structures (Pl. 2, fig. 8), first described as original by Schindewolf (1942) in some external walls of solitary corals. They were afterwards reinterpreted by Oekentorp (1980) as diagenetic alterations, resulting from the re-crystallization of elongated primary calcite fibrils under increased pressure caused by compaction. Webb & Sorauf (2002) offered different explanation of that event. According to those authors an early diagenetic transformation from the high magnesium into the low magnesium calcite was responsible for deformations discussed. Moreover, Webb & Sorauf (2002, p. 415) wrote: "Hence, zig-zag microstructure may serve as a proxy for diagenetically altered HMC [high magnesium calcite] coral skeletons, and such HMC skeletons may serve as indicators of the high Mg/Ca ratios that have been implicated as the cause of aragonitic seas." Although the authors pointed out several examples to support their interesting interpretation and I may add additional one (Fedorowski & Bamber 2001), existing data remain inadequate for accepting the interpretation as proven. There occur many more taxa, contemporaneous with the mentioned ones, sometimes derived from the same beds, that do not show zig-zag microstructure.

Diagenetic deformation of individual parts of septa may eventually result in crystallographic unification of their primary and secondary parts (Pl. 1, fig. 2). At the beginning of the process, the trabecular microstructure of the primary septum becomes irregularly feather-like. Diagenetically altered microstructure having that appearance was considered to be primary by Semenoff-Tian-Chansky (1974), who named it "mésoplasme". Such weakly altered primary septa were covered at that stage by lamellar-fibrous septal sheets with individual crystals oriented perpendicular to the lateral surface of a septum. Further diagenetic alteration led towards the unification of the microstructure of the septa mentioned above. The long crystal axes (C-axes) of primary septa and secondary sheets of the septa became reoriented to form common fan-like structures directed obliquely towards the lateral surfaces of the septa (Pl. 1, fig. 2).

The advanced diagenetic alterations may have begun in the zone of trabeculae (primary septum) and were afterwards extended to the secondary sheets of the septa (Rodríguez 1989). The opposite option, i.e., the expansion of diagenetic alteration from the surface deeper into the septum, is also an acceptable possibility. In such an instance, the trabecular fibrils would have recrystallized in the matrix formed by earlier altered septal sheets. More advanced diagenesis of the

septal sheets, observed in several instances (Pl. 2, fig. 8), suggests the second option, but both are probably possible.

The degree of diagenetic alterations may differ not only between specimens collected from the same bed, but also within the framework of a single specimen as described above, and occasionally within individual structural elements, especially the septa. Regularities in the timing and cause of diagenetic processes may sometimes be deduced. More often, however, they are unrecognizable or are, perhaps, not recognized. It may happen, for instance, that diagenetic alteration is more advanced in particular parts of a specimen than it is in others (e.g., at the periphery or on one side of a specimen, in the primary septa or in their secondary sheets). Such precisely located diagenetic alterations allow deduction of the sequence in which they occurred and of the factor causing them. There are also examples, however, in which the results of diagenetic processes are unpredictable. For instance, recognizable trabeculae may have survived in a specimen that had been hollowed by boring organisms, re-crystallized, and dolomitized. Neither the reasons for such selective diagenetic activity nor their sequence may be determined in such instances.

*Other changes.* Strong curvature of the primary septa with no effect on the secondary sheets of the septa (Pl. 1, fig. 6) is one of peculiarities of diagenetic alteration within rugose coral skeletons. Such deformation, described earlier by Oekentorp (1980) may involve all or almost all inner margins of major septa in a given specimen or it may affect only some of the septa. Moreover, such deformed septa may be located adjacent to undeformed septa and may be either longer or shorter than the latter. At first glance, compaction seems to be the only possible cause for such deformation. That concept, however, requires reduction in volume of the entire specimen without alteration of the mutual relationships of its individual skeletal elements. It also requires reduction in the diameter of the specimen with no change in the microstructure of its external wall. Neither of these alternatives is possible and neither has been observed. In addition, neither alternative explains the selective deformation of septa. Having no explanation for that phenomenon, I simply draw attention to its presence without comment.

Summing up these brief remarks, it should be pointed out that the level of preservation of a rugose coral skeleton or, strictly speaking, the degree of advancement in its diagenetic alteration, depends on several factors. Most important of these are: the stability of the mineral constituting the skeleton, the length of the pre-burial exposure above the sea floor, the abundance of epibionts and boring organisms, the pH of the sediment and pore solutions in subsequent diagenetic stages, the physical conditions, i.e. the relationship between the rate of sediment accumulation and the rate of infilling of intra-structural spaces within the coral, the position of the specimen within the sediment, and tectonic events. All those factors may cause significant alterations, which may subsequently affect the taxonomy when they are not investigated or are misinterpreted.

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## Kilka uwag o diagenizie szkieletów koralowców Rugosa

### Streszczenie

Istnienie niezmiennych diagenetycznie szkieletów koralowców Rugosa, za jakie część badaczy (Schouppé & Stacul 1955, 1959; Sorauf 1984) uważała koralowce ze środkowego i górnego permu Wyspy Timor, nie wydaje się prawdopodobne. Zatem nie tyle zmiany diagenetyczne jako takie, ile stopień ich zaawansowania powinny być przedmiotem badań. Scleractinia, a zapewne również Rugosa, nie wytwarzają najbardziej zewnętrznej, ochronnej warstwy szkieletu, analogia *periostracum*. Znaczne części ich zewnętrznych szkieletów, chronionych ciałem jedynie w najmłodszych fazach wzrostu osobników i kolonii, są zatem poddawane oddziaływaniu biotycznych i abiotycznych czynników środowiska wkrótce po wytworzeniu.

Pomimo zasadniczo tych samych mechanizmów wydzielania węgla wapnia przez kalikoblasty ektodermy, wszystkie Scleractinia i Rugosa inaczej budowały tabule i dissepimenta, a inaczej septa i struktury septopochodne. W pierwszym przypadku sekrecja miała miejsce na płaskiej lub w różnym stopniu wypukłej powierzchni dysku bazalnego i ścian bocznych polipa. W drugim w początkowo wąskich, a następnie poszerzonych kieszeniach septalnych. W tych szerokich kieszeniach były tworzone pokrywy septów o mikrostrukturze włóknistej, nałożone na struktury trabekularne septum, wytworzone w wąskiej kieszeni. W skutek dwoistości budowy septów ich diageneza przebiega w sposób bardziej złożony, niż diageneza pozostałych struktur.

Wydaje się, iż podobnie jak w przypadku Scleractinia (Sorauf & Cuiff 2001) wstępne fazy diagenetyzacji mogły zachodzić już za życia Rugosa. Mogły jednak być mniej zaawansowane niż u Scleractinia i trudniej dostrzegalne ze względu na bardziej stabilny budulec – nisko magnezowy kalcyt zamiast aragonitu. W literaturze rugozowej nie pojawiły się jeszcze próby przeprowadzenia dowodu diagenetyzacji na tak wczesnym etapie, jak u Scleractinia. Zróżnicowanie zaawansowania diagenetyzacji szkieletów Rugosa jest łatwiej dostrzegalne w taksonach osobni-

czych cechujących się koralitami rosnącymi w ciągu kilku lat oraz w równie długowiecznych taksonach kolonijnych.

Nie jest mi znana metoda umożliwiająca stwierdzenie drogą pomiaru czy i o ile diagenaza elementów szkieletowych wyprzedzała rozwój cementów wypełniających przestrzenie pomiędzy elementami szkieletowymi. Kryształy cementów palisadowych, niejednokrotnie rozwinięte zgodnie na kryształach wytworzonych przez epidermę (Pl. 1, fig. 7), mogą sugerować wcześniejsze zdiagnozowanie kryształów organicznych. Te zmienione diagenetycznie kryształy stanowiły następnie matryce dla pierwszej generacji cementów. Wydaje się, iż wczesnych zmian diagenetycznych raczej nie należy przypisywać kompaktacji. Były one zapewne powodowane oddziaływaniem roztworów krążących w przestrzeniach między szkieletowych na węglanowe komponenty szkieletów. Struktury wewnętrzne, chronione przez ścianę zewnętrzną z jednej, a kielich z drugiej strony, ulegały początkowo znacznie mniejszym przeobrażeniom niż ściana. W szczególności nie dotykała ich bioerozja. Diagenaza w częściach koralita oddalonych od kielicha mogła zachodzić niezależnie od pogrzebienia lub odsłonięcia, choć w obydwu przypadkach miała zapewne nieco odmienny przebieg, a jej rezultaty były typowe dla środowiska, w jakim przebiegała. Bioerozja i abrazja przeważały jeśli szkielet był odsłonięty a procesy chemiczne przeważały po pogrzebaniu.

Nie zagrzebane lub płytko zagrzebane szkielety koralowców często były penetrowane przez różne organizmy wierzące (Pl. 2, fig. 1). Kształty i wtórne wypełnienia otworów wskazują, iż penetracja mogła zachodzić zarówno po, jak i przed skrzemionkowaniem zewnętrznych części okazów. Istnienie otworów mogło również powodować różne skutki. W warunkach zakwaszonego środowiska, przy niedoborze żeluz krzemionkowego, nie dochodziło do zastępowania węglanu wapnia przez krzemionkę, lecz do zupełnej lub częściowej destrukcji oryginalnego szkieletu. Liczne takie mumie występują w kolekcjach chemicznie wypreparowanych skamieniałości z permu Glass Mts w południowo-zachodnim Teksasie.

Przytłaczająca większość koralowców wytwarza szkielety azurowe. Przestrzenie międzyszkieletowe zajmują przeważnie nieporównanie więcej miejsca, aniżeli wszystkie razem wzięte elementy szkieletowe. Przestrzenie międzyszkieletowe są jednak stopniowo zapełniane kolejnymi generacjami cementów wypełniających. Proces ten może rozpoczynać się przed pogrzebaniem. W większości zachodzi jednak dopiero po pogrzebaniu. Wyróżnia się dwa podstawowe rodzaje cementów wypełniających: *cement palisadowy* i *cement mozaikowy*. Cement palisadowy tworzy pierwsze generacje cementów wypełniających. Kryształy tego cementu są zawsze ustawione prostopadłe do powierzchni organicznych elementów strukturalnych, w pewnym sensie kontynuując krystalizację organiczną (Pl. 1, figs. 5, 7). Kryształy cementu palisadowego mają osie C zawsze znacznie dłuższe od pozostałych. Stąd etymologia nazwy. Jest to cement

wczesno-diagenetyczny, zwykle krystalizujący w kilku fazach. (Pl. 1, fig. 5) Może całkowicie wypełniać wąskie przestrzenie między organicznymi elementami strukturalnymi.

Cement mozaikowy (Pl. 1, fig. 5, 7) wypełnia przestrzenie pozostałe po wykrystalizowaniu cementu palisadowego. Orientacja długich osi kryształów tego cementu nie jest jednoznacznie zdefiniowana. Wynika to z różnego usytuowania kierunków wzrostu kryształów uzależnionych od kształtu, rozmiarów i położenia wypełnianych przestrzeni. Różne usytuowanie tych osi względem płaszczyny przekroju oraz różne rozmiary kryształów dają w polu widzenia mikroskopu obraz mozaiki. Również ten cement krystalizuje w wielu fazach, których liczba zależy od rozmiarów wypełnianej przestrzeni oraz stężenia roztworów. Rozwój cementu mozaikowego może niekiedy powodować znaczne destrukcje organicznych elementów strukturalnych, nie zawsze rozpoznawalne jako wtórne. Na przykład destrukcja osiowych części septów (Pl. 2, figs. 7, 10) może być uznana za ich skrócenie, co w niektórych taksonach ma znaczenie diagnostyczne. Przyczyny takich zmian nie były dotychczas dyskutowane, a ich skutki są bądź nie rozpoznawane, bądź nie brane pod uwagę, w wyniku czego tworzono błędne interpretacje morfologiczne, taksonomiczne i filogenetyczne.

Tempo wypełniania przestrzeni między strukturami organicznymi jest bardzo zróżnicowane, a przyczyny tego zróżnicowania, poza banalnym stwierdzeniem stopnia nasycenia krążących roztworów i możliwości ich strącania, przeważnie pozostają nie zbadane. Niekiedy brak wypełnień lub destrukcja fragmentów szkieletu (Pl. 2, fig. 3) może być wiązany z penetracją bituminów lub z nadciśnieniem roztworów porowych. Nie znając w pełni przyczyn zróżnicowanego tempa wypełniania przestrzeni międzyskieletowych koralowców można jednak analizować niektóre ich skutki, z których część bez wątpienia mieści się w definicji procesów diagenetycznych. Zmiażdżenie, pokruszenie lub przynajmniej spłaszczenie skamieniałości jest najłatwiejszym do stwierdzenia przejawem procesu kompaktacji (Pl. 2, fig. 6). Jego intensywność i zaawansowanie zależy od tempa wypełniania przestrzeni międzyskieletowych, od morfologii wewnętrznej koralita oraz wynikającej z niej odporności na nacisk, od ułożenia okazu względem siły nacisku (prostopadle/równoległe), a także od tempa narastania nadkładu i jego masy zarówno w stosunku do tempa wypełniania przestrzeni międzyskieletowych koralitów, jak i do tempa lityfikacji otaczającego je osadu.

Septa zbudowane z dużych trabekul mogą zachować ślady pierwotnej mikrostruktury nawet w przypadku nieznacznej rekrystalizacji lub substytucji (Pl. 1, fig. 3). Rekrystalizacja zwykle uszkadza mikrostrukturę, natomiast substytucja może wywoływać zarówno skutki negatywne, jak i pozytywne. Dzięki zastąpieniu krzemionką jedynie najbardziej zewnętrznych części szkieleatów można uzyskać idealne skamieniałości, zachowujące zarówno morfologię zewnętrzną (Pl. 1, fig. 1), jak i mikrostrukturę szkieletu (Pl. 2, fig. 6). Dalsze zaawansowanie substytucji prowadzi jednak do częściowego (Pl. 2, fig. 4), a nawet do niemal zu-

pełnego zatarcia nie tylko mikrostruktury, ale również wielu szczegółów makromorfologicznych (Pl. 2, fig. 5). Liczne skamieniałości koralowców Rugosa o doskonale zachowanej morfologii zewnętrznej, utrwalonej w wyniku tak głębokiej substytucji, mają ograniczoną wartość taksonomiczną, ponieważ ich struktury wewnętrzne zatraciły większość cech morfologicznych. Postępująca diagenезa krzemionki zastępującej kalcyt, a następnie krystalizującej, niszczy w końcu również cechy zewnętrzne okazu, czyniąc go całkowicie nieprzydatnym do badań (Pl. 2, fig. 2).

Zupełne zastępowanie kalcytu hematytem powoduje zwykle uszkodzenia uniemożliwiające badania. Niewielkie zażelazienia mogą być natomiast pomocne w badaniach. Hematyt może zastępować częściowo włókienka kalcytu w trabekulach, niemal nie poddając się następnie dalszej diagenезie, co umożliwia odtworzenia mikrostruktury z niewielkich fragmentów septów (Pl. 2, fig. 9).

Dwoistość pierwotnej budowy septów wymusza różnicowanie zmian diagenetycznych. Zwykle uważa się, iż diagenезie ulegają najpierw trabekule, ponieważ ultrastruktura trabekul koralowców kopalnych – poszczególne włókienka i ich pęczki – jest przeważnie nierozpoznawalna (Pl. 1, figs. 3, 4). Niewątpliwie mikrostruktury takie uległy rekrytalizacji i po trabekuli pozostał tylko jej zarys oraz układ długich osi kryształów (włókienek) w jej obrębie, odmienny od układu kryształów w złogach okrywowych. Układ ten nadal powoduje intensywniejsze wygaszanie światła i zaciemnienie obrazu w obrębie trabekul (Pl. 2, fig. 8). Ten narzucający się obraz tuszuje zarówno zmiany diagenetyczne septów pierwotnych, jak i niezbyt zaawansowane zmiany diagenetyczne w septalnych złogach okrywowy (Pl. 1, fig. 4). Uwagę zwraca dopiero bardziej zaawansowana rekrytalizacja, prowadząca do powstania struktur zygzakowatych w obrębie złogów okrywowych (Pl. 2, fig. 8).

Deformacje diagenetyczne mikrostruktur septalnych mogą prowadzić do zatarcia różnic ich genezy. Septum pierwotne (trabekularne) przybiera nieregularną postać pierzastą (Pl. 1, fig. 2). Długie osie poszczególnych kryształów w zdiagenezowanych trabekulach ulegają reorientacji. Wraz z kryształami przekrytalizowanych złogów okrywowych kierują się wachlarzowato ku bocznym powierzchniom septów. Mikrostruktury takie są niejednokrotnie uznawane za pierwotne.

Swoistym wynikiem diagenезy septów jest sfalowanie ich części trabekularnych bez deformacji złogów okrywowych (Pl. 1, fig. 6). Deformacji tej mogą ulegać wszystkie lub prawie wszystkie wewnętrzne końce septów I rzędu niektórych Rugosa, albo tylko niektóre septa, dłuższe lub krótsze od tych, które deformacji nie uległy. Nie mając poglądu na prawdopodobną genezę tego zjawiska pozostawiam je bez komentarza.

Stan zachowania szkieletów koralowców zależy zatem od stabilności minerału budującego szkielet, okresu ekspozycji przed pogrzebaniem w osadzie, chemizmu osadu i wód porowych w kolejnych stadiach diagenезy, intensywności

krążenia roztworów i ich chemizmu oraz warunków fizycznych, a w szczególności tempa narastania osadów w stosunku do wypełniania przestrzeni pomiędzy makroelementami szkieletowymi koralita lub kolonii, pozycji okazu w osadzie oraz wydarzeń tektonicznych. Wszystkie te czynniki, a także działalność organizmów, szczególnie wierzących lub zakorzeniających się, mogą powodować znaczące zmiany, przekładające się następnie na nieporozumienia taksonomiczne.