LIDIA M. ULITINA

ASTOGENY IN SOME COLONIAL RUGOSA

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Differentiation of corallite morphology and ability and rate of gemmation observed in colonies of *Veraephyllum sytovae*, *Evenkiella cincta* and *Minussiella beljakovi* have been regarded as a manifestation of polymorphism. Three corallite morphes in a colony have been distinguished: protocorallite, mature corallites and immature, underdeveloped corallites.

K e y w o r d s: Coral colony, astogeny, polymorphism, Rugosa, Paleozoic.

Lidia M. Ulitina, Paleontological Institute, Academy of Sciences of USSR, Maronovsky per. 26, Moscow 117049, USSR. Received: June 1981.

INTRODUCTION

Most rugose colonies have all corallites of the same structure. The colonies are generally monomorphic except for the protocorallite which is morphologically similar to hysterocorallites but differs from them in its origin. However, some colonial Rugosa have a marked differentiation of corallites. Along with ordinary corallites growing to maturity and producing daughter corallites, they develop unique smaller immature forms that bud off from the parent-corallite and either remain immature throughout the colony's development or cease to grow earlier. Fedorowski (1978) introduced the term "lost structure" to describe a similar kind of corallites. The term was ment to denote nonviable daughter corallites of solitary corals genetically capable of lateral gemmation. It seems to be more reasonable to refer to all such underdeveloped forms as immature corallites.

The astogeny of some tetracorals reveals another feature essentially typical of tabulatomorphic corals but hardly known in rugosans. It involves the alternation of light and dark zones associated with reproductive

cycles and also shows up in more or less widely spaced horizontal skeletal elements. The immature corallites and alternating light and dark zones are confined to certain growth stages in the colony. In both cases regular changes in the corallite structure can be observed.

This paper deals with the astogeny of three genera *Evenkiella* Soshkina, 1955; *Veraephyllum* Ulitina, 1980 and *Minussiella* Bulvanker, 1952, from the Great Late Basin, western Mongolia. The first two genera come from Wenlock deposits of the Khutsin-Bulak locality and *Minussiella* from Eifel limestones north of Lake Khara-Us-Nur.

All corals were studied for the astogeny of neanastic and ephebastic stages. The protocorallite ontogeny could not be studied because of the inadequate preservation of the colonies. The collection is housed at the Paleontological Institute, Academy of Sciences USSR, Moscow.

DESCRIPITION

Astogeny of *Veraephyllum sytovae* Ulitina
(fig. 1)

Dense dendroid colonies are made of large cylindrical and conical corallites. The colonies developed by lateral gemmation and, rarely, division.

Neanastic stage. The neanastic stage features an intense gemmation of protocorallites and initial hysterocorallites which grew almost at right angles to the protocorallite. The base of the colony was formed by morphologically mature corallites having a well-developed septal apparatus, long septa of two orders. The corallites, 25 to 30 mm in diameter, numbered $(36—38) \times 2$ septa.

Ephebastic stage. What makes this stage remarkable is the development, in addition to ordinary corallites, of numerous immature, permanently underdeveloped forms. The parental corallites produced as many as 6 offsets at the same time or almost simultaneously. Some of them were bound to remain small, 3 to 6 mm in diameter. Some ceased to grow before the development of the entire colony terminated. The inner structure of small immature corallites is simple and uniform, displaying scarce, fairly large dissepiments, some with a slight axial and peripheral differentiation. Most offsets gradually increased in size to attain a diameter of 6 to 12 mm, but these, in turn, never produced new corallites. Their structure is more complex, the dissepimental tissue showing a pronounced differentiation, the septal apparatus consisting of sporadic short septa of two orders that are basically confined to the peripheral zone and only slightly project into the axial part. At the ephebastic stage, mature, gemmating corallites have a diameter of 15 to 35 mm. Their septa are discontinuous, particularly in the peripheral part, with small septa sporadically. The main distinction of ephebastic corallites as compared to those at the neanastic stage is their septal degradation. So, the younger stages
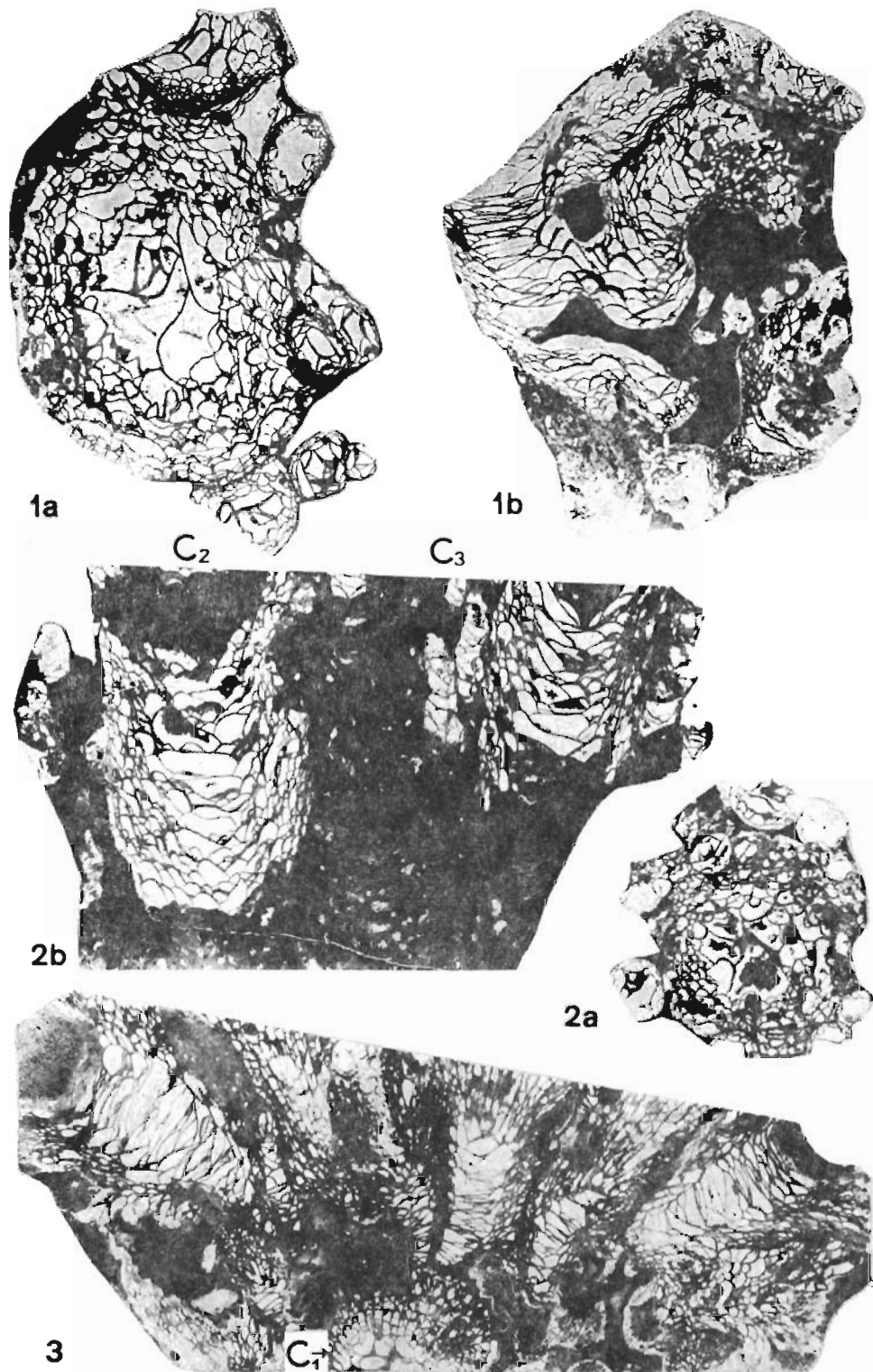
Fig. 1. *Veraephyllum sytovae* Ulitina, Western Mongolia, Great Lake Basin, Khutsinbulak; Silurian, Wenlock: *1.* Holotype, No 3294/6024, ×1.5: *a* cross-section, *b* longitudinal section. *2.* Specimen No 3294/6025, ×1.5: *a* cross-section, *b* longitudinal section, lateral increase; C_2 mature corallite, C_3 immature corallite; ephebastic stage. *3.* Specimen No 3294/6030, ×1.5: longitudinal section; protocorallite (C_1); neanastic stage. (After Ulitina 1980: pls. 3 and 4).

feature a fully-developed septal apparatus, while the ephebastic stage of
the astogeny is associated with discontinuous, partially reduced septa.

Thus, the *V sytovae*, colonies display a great morphological variety
in the structure of individual corallites. There are (1) neanastic mature
corallites with a well-developed septal apparatus; (2) ephebastic mature
corallites with degraded septa, and (3) immature corallites at different
early stages of blastogeny.

Astogeny of *Evenkiella cincta* Ulitina
(fig. 2)

The growth of massive colonies was entirely due to lateral gemmation.
The base of the colony was formed by large corallites encircled with
numerous (up to 20) small ones.

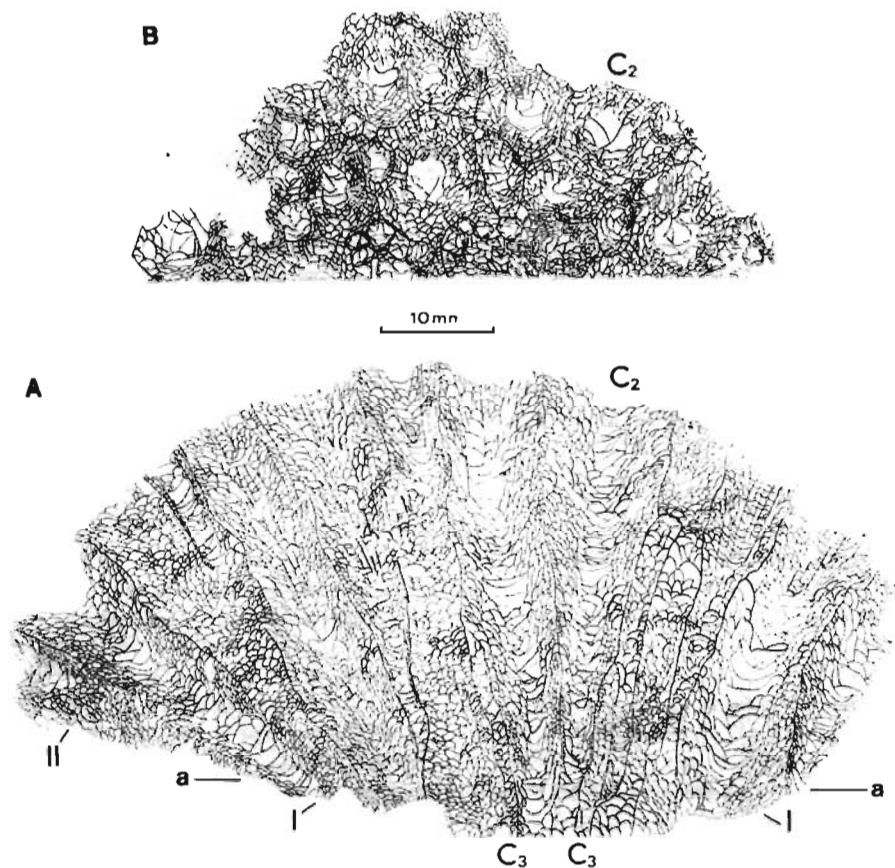*Neanastic stage.* The most intense gemmation was associated with the

Fig. 2. *Evenkiella cincta* Ulitina, holotype No 3294/6012: *a* longitudinal section; *b* cross-section; $\times 2$. *I* neanastic stage, *II* ephebastic stage; *a—a* location of cross-section shown; C_2 mature corallites, C_3 immature corallites (after photo in Ulitina 1980: pl. 3).

early development of the colony. Corallites gemmating from the protoco-
rallite and initial hysterocorallites sharply diverged from the main line of
the colony growth. These new offsets fall into two groups: (1) the ordinary
corallites which grew, developed their skeletal elements, reached morpho-
logical maturity and produced more daughter organisms, and (2) the uni-
que underdeveloped corallites.

Ephebastic stage. The transition from the neanastic to the ephebastic
stage is gradual without a distinct boundary. The gemmation, though at
a drastically lower rate than that observed at the neanastic stage, shows
two distinct levels. Immature corallites are scarce. The corallites of the
colony display a size differentiation, the neanastic immature offsets never
exceeding 2 mm in diameter. Rarely, some immature corallites abruptly
grew larger and started developing their skeletal elements typical of ma-
ture specimens.

Thus, the *E. cincta* colonies feature two types of corallites: (1) mature
ones with a well-developed septal apparatus and (2) immature ones having
short or no septa.

Astogeny of *Minussiella beljakovi* Bulvanker
(figs. 3 and 4)

Dense dendroid colonies developed by lateral gemmation and accidental
lateral rejuvenescence.

Neanastic stage. The base of the colony displayed intense gemmation.
The offsets, diverging at almost right angles to the colony's growth direc-
tion, grew rapidly and reached maturity to produce offsets. Corallites were
tightly packed which accounts for their polygonal or rounded-polygonal
cross-section. Morphologically mature corallites had well-developed septa
of two orders with a length of up to 2/3 to 3/4 of their radius. Peripheral
parts of septa adjoin the corallite wall.

Ephebastic stage. With the colony growth, the corallites became less
crowded, cylindrical in shape and, more and more frequently, circular in
cross-section. Gemmation was much less intense than at the neanastic
stage, displaying three levels. Beside the normally developed daughter
corallites, there was a growing number of immature ones. They appeared
both peripherally and inside the colony, two to three at a time. The daugh-
ter corallites inside the colony show no regular pattern of disposition with
respect to the parent corallite, while at the periphery they tend to grow
closer to the colony surface and to diverge outwardly. There were some
forms of immature corallites that existed concurrently with all the others
until the end of the colony's growth and ceased to develop prior to the
death of the parent corallites.

The ephebastic stage of certain corallites displays larger and less dense horizontal skeletal elements (tabulae and dissepiments) and a poorly pronounced septal apparatus with septa cut off peripherally by lonsdaloid dissepiments.

A wider spacing of skeletal structures is usually confined to certain post-gemmating levels, which may be due to the energy-consuming reproductive process. These zones in *M. beljakovi* may be compared with the light zones in tabulatamorphic corals. The light and dark zones in tabulate and heliolitoid corals are associated with vegatative and sexual reproduction respectively. In *M. beljakovi* colonies, the wider spacing of skeletal structures follows the gemmation.

The development of immature corallites together with the appearance of light zones at the ephebastic stage accounts for a great morphological diversity of *M. beljakovi* corallites. The septal apparatus was highly varied in mature corallites. Their septa were either (a) continuous, long, stretching out from the walls, or (b) discontinuous, in particular at the corallite periphery, some growing only at the boundary of the tabulae and
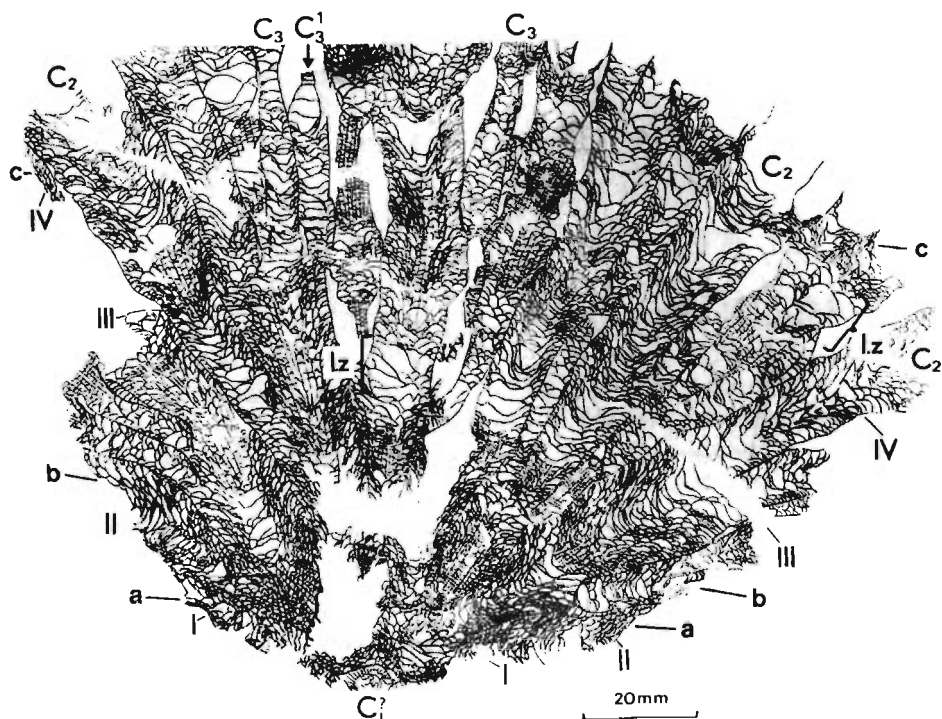

Fig. 3. *Minussiella beljakovi* Bulvanker, No 4061-2, ×1: longitudinal section. *I* neanastic stage, *II—IV* ephebastic stage; lz light zones; *a, b, c* location of cross-sections shown in fig. 3; C_1 protocorallite; C_2 mature corallites; C_3 immature corallites, C_3^1 immature corallites, or lost structures according to Fedorowski (1978), (after Ulitina 1980).

dissepiments, or (c) totally underdeveloped, with horizontal elements of a markedly larger size.

Thus, one can distinguish between three types of corallites in a *M. beljakovi* colony: (1) mature corallites having well-developed septa, (2) mature corallites with their septa discontinuous or lacking, and (3) immature corallites, small throughout their astogeny, having either no septa or a poorly developed septal apparatus.
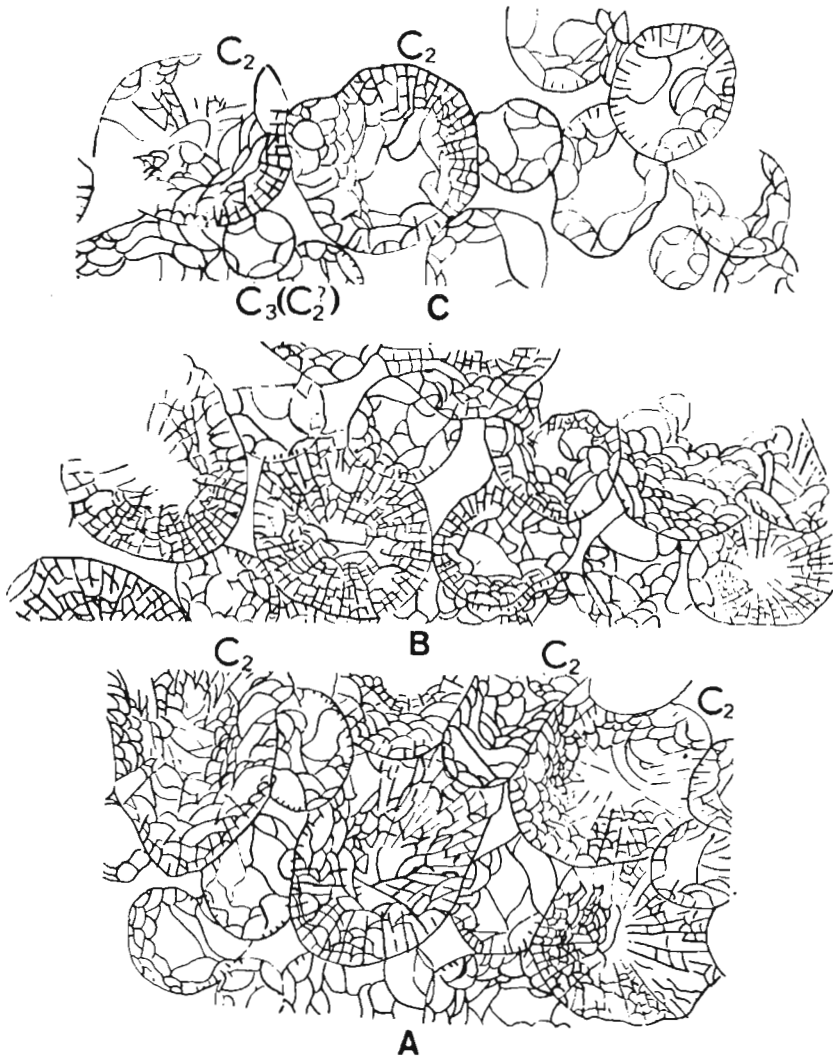

Fig. 4. *Minussiella beljakovi* Bulvanker, No 4061-2; cross-section of the specimen: *a* neanastic stage, slide No 4061-2,6; *b* the beginning of neanastic stage, slide No 4061-2,7; *c* section at the light zone of ephebastic stage, slide No 4061-2,17 (after Ulitina 1980).

PATTERNS OF ASTOGENY IN SOME COLONIAL RUGOSA
Polymorphism

The study of astogeny in the colonies of *Veraephyllum* Ulitina, *Even-kiella* Soshkina and *Minussiella* Bulvanker has revealed a common peculiarity, that is a distinct differentiation of their offsets. Among the ordinary and normally developing corallites were smaller, immature forms. As a rule, immature corallites were to remain so until the end of the colony's growth, with a few ceasing to develop earlier on. In the colonies under study, immature corallites appeared at different astogenetic stages. In the dendroid colonies of *Veraephyllum sytovae* Ult. and *Minussiella beljakovi* Bulvanker they were associated with the ephebastic stage alone. In massive colonies of *Evenkiella cincta* Ulitina the immature forms chiefly appeared at the early, neanastic stage of the colony development. Besides, part of *E. cincta* corallites remains underdeveloped for a long time and then reaches maturity surprisingly quickly. Soshkina (1959) has also recorded this feature of *Evenkiella* in *E. helenae* Soshkina colonies described from the Llandovery of Siberia. The appearance of immature corallites in the astogeny of the colony may be due to genetic causes. Even if we assume that their appearance was influenced by the envrionment, still it was only some species and genera that responded to the environmental impacts by developing immature forms and this, again, suggests their being genetically determined.

Some species of the Devonian genus *Hexagonaria* Gürich also feature variations in the structure of corallites. *H. arctica* (Meek) reveals two types: gemmating corallites and non-gemmating ones having a constant diameter and probably producing planulae (Ulitina 1974). Minato and Rowett (1967) suggested that Rugosa might have polyps of two generations (sexual and asexual). Dobrolyubova (1958) described the structural non--uniformity in the colonies of Carboniferous *Lonsdaleia* corals.

All the above cases of corallite differentiation in the colonies may be regarded as a manifestation of polymorphism, recurring in rugosans throughout the Paleozoic. Polymorphism is one of the forms of colony development observed in Anthozoa. But rugosans more often exhibited a different trend, that is the merging of corallites. Here, the level of coloniality was manifested by the variety of colonies ranging from the dendroid types whose daughter polyps were only connected with the parent corallite at the time of gemmation to the massive ones with corallites tightly sticking to one another so that their gastrovascular cavities could join over the calicular edge throughout the colony. The most advanced within this trend of rugosan colony development were asteroid, thamnasteroid and aphroid colonies, in which some corallites displayed lack of separating walls and a complete merging of their gastrovascular cavities (Oliver 1968; Coates and Oliver 1973). Polymorphism is the next step in

raising the level of coral coloniality. Among the Palaeozoic corals the most conspicuous polymorphism can be observed in heliolitids. "By complexes of different morphs one can distinguish dimorphism, trimorphism, tetramorphism and so on, that is a varying degree of polymorphism" (Bondarenko 1978: 23). The rugose corals under study display trimorphism expreseed in the presence of a protocorallite, mature corallites and immature, underdeveloped corallites.

MORPHOLOGICAL VARIETY OF CORALLITES IN A COLONY AND ITS PATTERNS

A morphological variety of corallites has been observed in the astogeny of *Minussiella* and *Veraephyllum.*

Both *M. beljakovi* and *V. sytovae* display three morphological types: (1) mature corallites having well-developed septa, (2) mature corallites with septa discontinuous or lacking and (3) immature corallites with septa lacking or poorly-developed, at different initial stages of blastogeny, remaining small throughout the astogeny.

The differentiation of corallites in rugose colonies has been discussed earlier. Dobrolyubova (1958: 27) gave a detailed description of a varied corallite structure in the massive colonies of *Lonsdaleia rossica rossica* Stuck from the Tarussa and Steshev horizons, Serphukhovian Stage, Lower Carboniferous, Moscow Basin. She recognized four types: "1) normal corallites having an axial column characteristic of a given species; 2) *Thysanophyllum*-like corallites with the central part containing nothing but tabulae or tabulae together with the tip of an elongated septum, probably the cardinal one; 3) corallites featuring no vesicular tissue, but a great number of short or, on the contrary, long septa extending up to the corallite centre and, finally, 4) corallites whose vesicles (buds) slightly increase in size to insert short septa and then to degenerate and disappear." The fourth type is another example of Fedorowski's "lost structures" in ordinary colonies which we recognize not as a separate type but as immature corallites that ceased their development before the rest of the colony did.

The morphological diversity in the corallite structure is quite natural, being associated with different stages of the colony growth. The study of this diversity is expedient for the understanding of the intracolonial variability and the updating of the classification.

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REFERENCES

[BONDARENKO, O. B.] БОНДАРЕНКО, О. Б. 1978. Полиморфизм у палеозойских табулятоморфных кораллов. — Палеонт. ж., **2**, 23—35.

COATES, A. G. and OLIVER, W. A. 1973. Coloniality in Zoantharian Corals. *In*: Animal colonies, 3—27.

[DOBROLYUBOVA, T. A.] ДОБРОЛЮБОВА, Т. А. 1958. Нижнекаменноугольные колониальные четырехлучевые кораллы Русской платформы. — *Тр. Палеонт. Ин. АН СССР*, **70**, 1—224.

FEDOROWSKI, J. 1978. Some aspects of coloniality in rugose corals. — *Palaeontology*, **21**, 1, 177—224.

[IVANOVA, E. A., SOSHKINA, E. D., ASTROVA, G. G., IVANOVA, V. A.] ИВАНОВА, Е. А., СОШКИНА, Е. Д., АСТРОВА, Г. Г., ИВАНОВА, В. А. 1955. Фауна ордовика и готландия нижнего течения р. Подкаменной Тунгуски, ее экология и стратиграфическое значение. — *Тр. Палеонт. Ин. АН СССР*, **56**, 118—128.

MINATO, M. and ROWETT, C. L. 1967. Modes of reproduction in rugose corals. — *Lethaia*, **1**, 175—183.

PEDDER, A. E. H., JACKSON, J. H. and PHILIP, G. M. 1970. Lower Devonian biostratigraphy in the Wee Jasper region of New South Wales. — *J. Paleontol.*, **44**, 2, 206—251.

OLIVER, W. A. Jr., 1968. Some aspects of colony development in corals. — *Ibidem*, **42**, 5, II, 16—34.

[ULTINA, L. M.] УЛИТИНА, Л. М. 1974. Рост массивных колониальных ругоз (на примере Hexagonaria Gürich, 1896). *In*: Б. С. Соколов (ed.), Древние Cnidaria, **1**. — *Тр. Ин. Геол.-Геоф. АН СССР сибир. отд.*, **201**, 172—179.

—   1980. Некоторые закономерности колониального развития ругоз. — *Палеонт. ж.* 2, 32—43.

LIDIA M. ULITINA

ROZWÓJ KOLONII U NIEKTÓRYCH RUGOSA

Streszczenie

Zróżnicowanie morfologii koralitów i ich zdolności pączkowania w koloniach *Veraephyllum sytovae* Ulitina, *Evenkiella cincta* Ulitina i *Minussiella beljakovi* Bulvanker zostały tu zinterpretowane jako przejaw polimorfizmu. Wyodrębniono trzy postaci koralitów w kolonii: protokoralit, dojrzałe korality i niedojrzałe, niedorozwinięte korality.