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Taxonomical problems of the Heliolitida

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ABSTRACT. Systematic position of group is accepted by the beginning scientist after the teacher or after the leader in the field of studying of this group of corals. But the lowest categories (species and genera) are established by him, first of all, on a regional material. Long-term study of heliolitids of Central Tajikistan and their comparison with heliolitids from other regions shows faunistical peculiarity of each region. Ambiguity of treatment of the same morphological features as a result takes place. The situation becomes complicated by parallelism of development between some taxa of the Heliolitida and wide variability of features of many species. Standardization of arrangement of coenenchyme because of parallelism of development results in occurrence of forms with a similar structure, but with a different genetic basis. So we can tell now that the main problem in definition of taxa of the Heliolitida is the heterogeneous genus *Heliolites*.

KEYWORDS: Paleozoic corals, Variability, Autotomy, Taxa definition, Middle Asia.

1. Introduction

Taxonomical problems of the Heliolitida include such aspects, as discussion about a rank of group and difficulty of an establishment of the taxa within the Heliolitida. At the hearth of these problems lies an interpretation ambiguity of the same morphological features by various researchers. Interpretation ambiguity of the same morphological features depends on individual point of view, material that every investigator has, and a degree of the study of group. The other trouble of the taxa definition in the Heliolitida is standardization of arrangement of coenenchyme due to parallelism of development. Also wide variability of features could take place among some taxa of the Heliolitida. Variability of the species *Propora speciosa* (Billings) will be considered below as an example.

2. The rank of Heliolitida

A question about the rank of Heliolitida is the question about its independence from the Tabulata or the others Coelenterata. Many investigators consider heliolitids as a part of Tabulata (Dixon, 1974; Lin Baoyu & Chow Xinghu, 1977; Hill, 1981; Noble &Young, 1984; Young & Noble, 1990; Scrutton, 1997; Chatterton et al., 2008). In means the rank of Heliolitida should be lower than the rank of Tabulata. It can be mentioned here that the rank of Heliolitida is interpreted differently - from the family to the subclass (Bondarenko, 1992; Ospanova, 2010). Sokolov (1955, 1962) analyzed relationship of the Heliolitida with other groups of Coelenterata (Tabulata, Hexacoralla, Rugosa, Alcyonaria, and Hydrozoa). He established the differences and independent development of that group of corals from other groups of Coelenterata. He concluded that the Heliolitida is a separate taxon that is equal to the Tabulata and Rugosa in rank. Long-term study of heliolitids of Central Tajikistan confirms his point of view. The concept of the sum of common features has been used by me (Ospanova, 2010) for comparison of the Heliolitida with other groups of Paleozoic corals (Tabulata and Rugosa) and determination of its position within the common system of corals. The Tabulata, Heliolitida and Rugosa as a result included into one subclass Paleosclerocoralla (Ospanova, 2007a) as related orders. I support point of view of Ivanovsky (1990) about common classification system for ancient and modern corals. If we make common classification system for ancient and modern corals, the rank of such subdivisions as Tabulata, Heliolitida or Rugosa must be not higher than order. On the other hand, their rank cannot be lower than order owing to big capacity of these groups. Thus, it seems well proved that the rank of the Heliolitida is the order.

3. Individual point of view

Individual point of view depends on scientific school to which paleontologist belongs, and a private experience in group studying. Some Canadian researchers (for example, Dixon, 1974; Noble & Young, 1984) following Hill (Hill & Stumm, 1956) considered the Heliolitida as the family. And they come to consider this group of corals as the order (Dixon et al., 1986; Young & Noble, 1990; Dixon, 1998) after new Treatise of Hill (1981) or as suborder (Chatterton et al., 2008) according to Scrutton's classification (Scrutton, 1997). Many Russian and Chinese researchers (for example, Bondarenko, 1971; Mironova, 1974; Leleshus, 1975; Ospanova, 1978; Li & Lin, 1982; Kim & Salimova, 2007) following Sokolov (1962) consider heliolitids as the subclass. Sokolov (1971) has in the sequel proposed the subclass Tabulata (Tabulatomorpha) with three super-orders: Tabulata s. str., Heliolitoidea and ?Chaetetoidea. Bondarenko (1992) has used this rank in her "System of Heliolitoidea" following Sokolov (1971). However she considers that group of corals as the subclass at the present time (Bondarenko, 2003). As a rule, the beginning scientist holds the opinion of his teacher. Only private experience allows him to have another opinion.

Taxa	Features
Superorder **Heliolitoidea**	Polymorphism + fixing number of septa
Orders	Macrostructure of skeletal tissue of vertical elements; *variants of heteromorphous components*
Order **Coccoseridida:** superfamilies	Texture of skeletal tissue; arrangement of heteromorphous components; *degree of stereoplasmatic filling of corallites*
families	variant of texture + aureole; *presence of axial structures in corallites*
subfamilies	*arrangement of heteromorphous components*
tribes	*orientation of trabecula and bacula*
Order **Proporida:** families	Presence or absence of crowns, aureoles and diadems around the corallites
subfamilies	*combination of heteromorphous components*
Order **Khangailitida:** superfamilies	Constancy or inconstancy of structure of skeletal elements in a cyclomorphosis; shape of colonies + presence of crowns, aureoles and diadems around the corallites
families	variation of structure of skeletal tissue; arrangement of heteromorphous components; arrangement of corallites; presence or absence of aureoles and diadems
Order **Heliolitida:** families	Arrangement of central parts of corallites; presence or absence of crowns, aureoles and diadems
genera	Density of corallites disposition in coenenchyme; number and type of septa; variants of symmetry; axial structure; shape of tabula; appearance of new structures in the cyclomorphosis
species	Numerical diagnostics

Table 1. Taxonomical criteria used in the system of Bondarenko (1992). Characteristics used in system, but not listed Bondarenko in an anticipating part, are italicized.

Such investigators as Nicholson (1876), Sardeson (1896) and Bondarenko (1978, 1987b) considered the colonies of the Heliolitida as polymorphic. They supposed that coenenchyme is not lateral or sole enlargement of polyps but small true

Taxa	Features
Order **Heliolitida:**	Presence of coenenchyme, fixing number of septa, vertical or inclined-up orientation of septa
Suborders (**Coccoseridina, Proporina, Heliolitina**)	Type of coenenchyme and its development trend
families	Morphogenesis (asto-phylogenesis); mode of decrease of stereoplasma; arrangement of walls and septa; presence of aureole; arrangement of tabula as auxiliary feature
genera	Density of corallites disposition in coenenchyme; shape of corallites; septal apparatus; axial structure; shape of tabula; structure of walls; type of folding of corallites' cavities; aureole; texture; cyclomorphosis; arrangement of coenenchyme; branchy form of colonies
species	Density of corallites disposition in coenenchyme; numerical diagnostics; insignificant qualitative varieties

Table 2. Taxonomical criteria used for description of the heliolitids of Central Tajikistan.

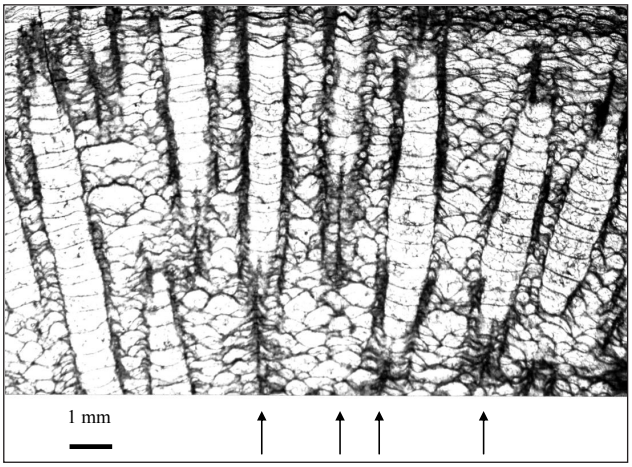

Figure 2. Autotomy of corallites in *Oskaria islamovi* Ospanova; autotomic seams are shown by arrows. Oblique section of the holotype IGEES 605-11 (Turkestan-Alaj mountain oblast, Nuratau mountains, south mountainside of Merishkor; Upper Silurian, Ludlovian, the Dal'an formation). Author's collection (1978).

polyps. Bondarenko uses a special terminology in order to show differences between coenenchyme and zooids' tissue. She calls that as *heteromorphous components* (1978, 1982) or *heterolites* (1987b). She distinguishes between them cystolites, eucystolites, and siphonolites (Bondarenko, 1978), and also protolites (Bondarenko, 1980), prosiphonolites, parasiphonolites (Bondarenko and Minzhin, 1980), and siphonotella (Bondarenko, 1982), and also paraprotolites (Bondarenko, 1987b). New system of the Heliolitoidea has been formulated by Bondarenko (1992) with the using new terminology. Two tables are given here as examples of the various individual points of view on definition of the taxa of the Heliolitida. The taxonomical criteria used in system of Bondarenko are summarized here in the Table 1. The taxonomical criteria used for the description of the heliolitids of Central Tajikistan are summarized in the Table 2.

It can be seen from the Table 2 that we consider coenenchyme only as connecting intermediate tissue between polyps. Most researchers held this opinion. Between them are Lindström (1899), Sokolov (1955) and Beklemishev (1964).

4. Taxonomical value of morphological characters depending on material

Comparison of heliolitids of Central Tajikistan with those of other regions (Baltic region, Ural, Kazakhstan, Mongolia, and others) shows that unique (specific) fauna is characteristic for every region (Ospanova, 2003). Complexes of species or degree of variability of cosmopolitan species can differ from each other. So each paleontologist establishes taxonomical value of characters, leaning against an own material. Two examples will be considered below.

Such feature as type of folding of corallites' cavities is mentioned in the Table 2. Study shows that for Ordovician and Silurian heliolitids of Central Tajikistan broad development of autotomy is characteristic. On the bases of that, the using of the term ***autotomy*** in relation to the Heliolitida has been defined more exactly by me. This term was firstly used by Bondarenko (1987a). She supposed that small part (or some parts) which disjoined from margin of parent corallite can grow and transform into new corallite ("metacorallite"). Parent corallite can also exist or transform into heterolites (i.e. coenenchyme). However, individuality is present in the other animals after autotomy. And also Lindström (1899) showed (in heliolitids with tubular coenenchyme) that such parts cannot change into mature corallites. So autotomy in the Heliolitida is such separation of small parts from the periphery of parent polyp when its individuality is present (Ospanova, 2007b). Study shows that these parts cannot transform into new corallites or tubules of coenenchyme, but they can form additional wall of corallite (Figs 1, 2). In Central Tajikistan autotomy occurs in representatives with vesicular coenenchyme. It can be added that

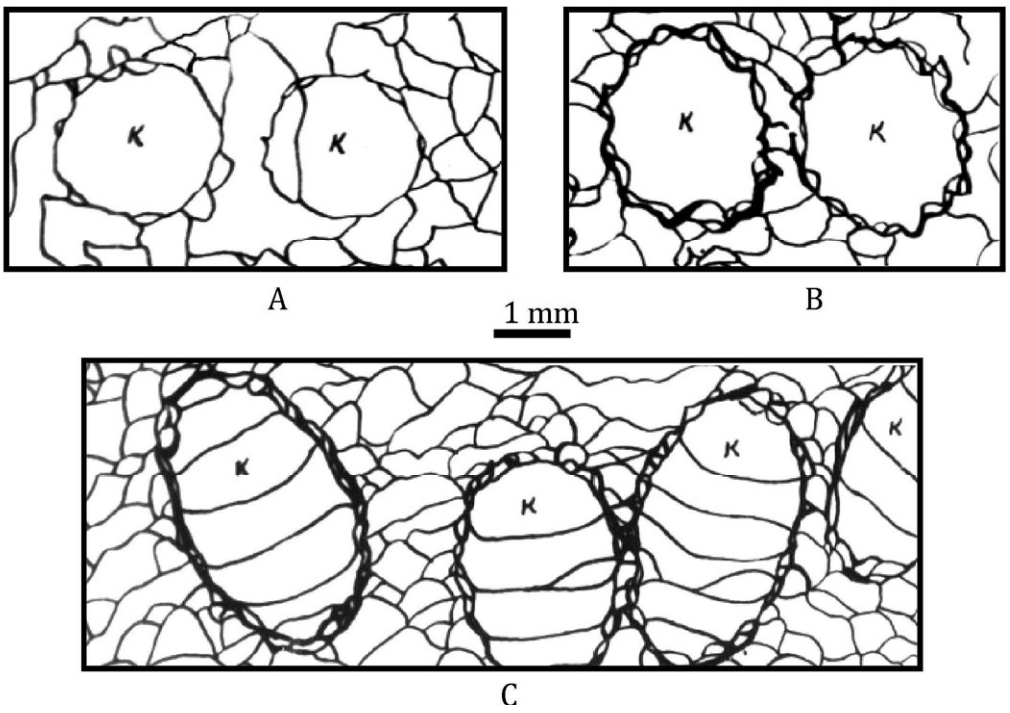

Figure 1. Autotomy of corallites in *Rotalites nuratensis* (Chekhovich). A: Initial stage of the astogenesis of colony; autotomy is no intensive, and cavities plicated slightly and irregularly (cross-section of a specimen IGEES 605-59). B, C: Later stages of the astogenesis of colonies; autotomy is more intensive and cavities plicated more intensively (B: Cross-section of the specimen IGEES 603-26. C: Oblique section of the specimen IGEES 605-63). Turkestan-Alaj mountain oblast, Nuratau mountains, south mountainside of Merishkor; Upper Silurian, Ludlovian, the Dal'an formation). Author's collection (1978).

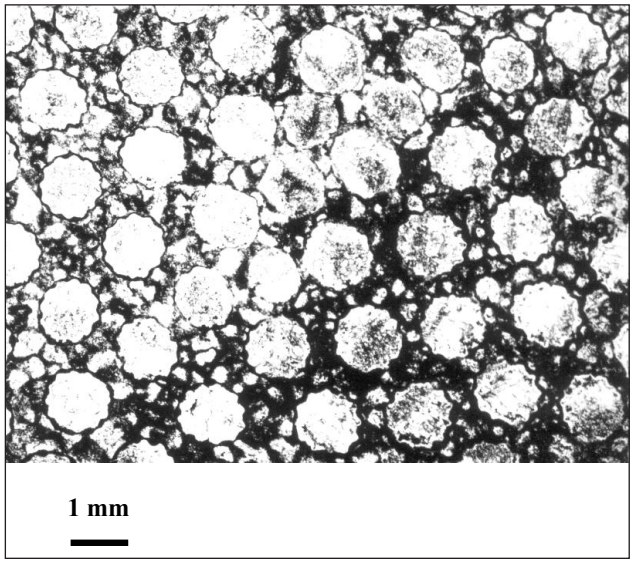

Figure 3. Undulatory type of plicated cavities of corallites in V*orupora exigua* (Billings). In dark zone are aureole-like structures. Cross-section of a specimen IGEES Sh-2-29 (west area of Zeravshan mountain, hole Shakhriomon, section Shakhriomon-2; Upper Ordovician, upper Ashgillian, Minkuchar beds). Author's collection (1986).

this feature has not been noticed by Leleshus at allocation of the genus *Rotalites* (Leleshus, 1974).

Partial or total transformation of corallite into coenenchyme was called as metatomy (Ospanova, 2007b). Autotomy in the Heliolitida can intensify folding of cavities of corallites (Fig. 1). Based on it, four types of longitudinal folding of cavities of corallites have been established by me (Ospanova, 2009): undulatory (Fig. 3), septate (Fig. 4), autotomic (Figs 1, 2) and coenenchyme-dependent (Fig. 5). They have been used as additional morphological feature for diagnostics of taxa of the Heliolitida of Central Tajikistan. It can be added here that longitudinal folding of cavities and walls of corallites studies in cross-sections and cross folding of cavities and walls of corallites studies in longitudinal cuts of coralla.

Scrutton (1993) has distinguished two species of *Propora* based on their different strategy of growth. Comparison of shape and internal structure of coralla from some localities allowed him to establish these species. Thus he used growth-form of colonies as additional taxonomical characteristic. This example demonstrates also that each researcher establishes taxonomical value of features, leaning, first of all, against a regional material.

Peculiarity of fauna of each region is connected with various environmental conditions in different parts of the basin. Repeated visiting of the same sections convinces us that eventually different parts of a biotope are exposed to erosion.

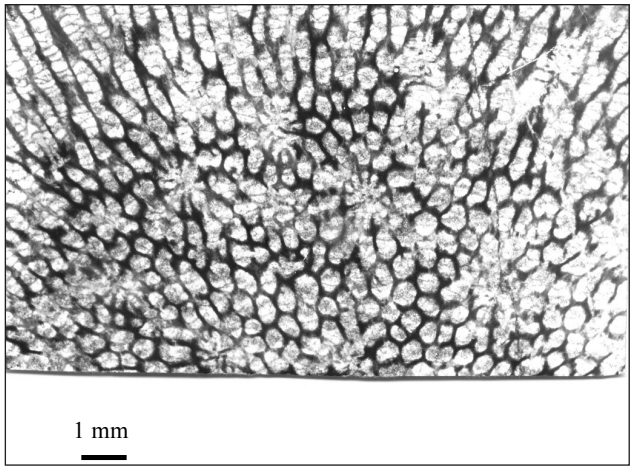

Figure 4. Septate type of folding of corallites' cavities in Bondarenkolites olgae Kim. Oblique section of a specimen IGEES 19-72 (Zeravshan mountain, Zinzinlban ravine; Lower Devonian, Emsian, the Khodzhakurgan Formation). Author's collection (1986).

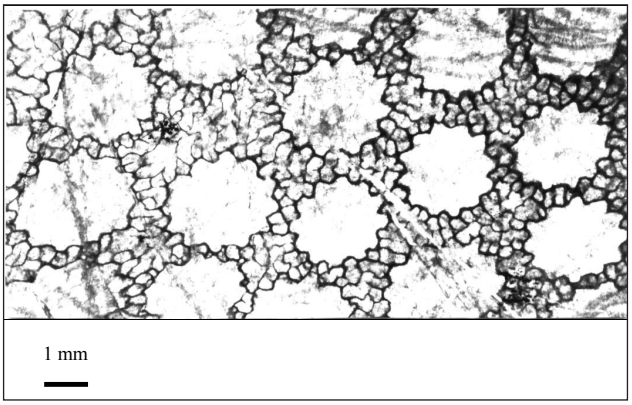

Figure 5. Coenenchyme-dependent type of folding of corallites' cavities in *Ducdonia interrupta* Leleshus. Cross-section of a specimen IGEES 18-85 (Zeravshan-Gissar mountain oblast, Obi-Hundy mountain, the Upper Kashka-Dar'a, left side of mouth Farab ravine, bed 18; Lower Silurian, upper Llandovery-lower Wenlock, stratigraphic analogues of beds H, I of Daurich mountain). Author's collection (1979).

They can contain various organic forms. So I have come to conclusion about necessity of repeated visiting of the same sections after some time (Ospanova, 2003).

5. Degree of the study of variability on an example of the species *Propora speciosa* (Billings)

Distribution and variability of the species *Propora speciosa* (Billings) have been studied by Bondarenko and Minzhin (1981). They showed that this species has global distribution. It occurs on Upper Ordovician of Canada, Central Mongolia, Scandinavia and Baltic region. Biozone of the species corresponds to Ashgillian (Members 2 and 6 of the Ellis Bay Formation, Anticosti Island, Canada; beds 5a and 5b of Norway; the Pirgu and Porkuni Stages of Estonia; upper strata of Middle Tsagandel and Upper Tsagandel beds of Mongolia). Colonies of *Propora speciosa* make two phylozones: lower and upper. Coralla with corallites' diameter of 1,3-2,2 mm make lower phylozone (lower part of the Ellis Bay Formation, Canada; the Pirgu Stage of Estonia; the Khangai Horizon of Central Mongolia, beds 6, 7). Coralla with corallites' diameter of 2,2-3,2 mm make upper phylozone (upper part of the Ellis Bay Formation, Canada; the Porkuni Stage of Estonia; beds 5b of Norway).

In Middle Asia the species *Propora speciosa* has been established by me (Ospanova, 1984). Representatives of this species have been defined before as *Propora* cf. *bacillifera* Lindström, *P. bacillifera* Lindström, *P.* aff. *magna* Sokolov (Leleshus, 1966; Muftiev et al., 1971; Lavrusevich, 1972; Lavrusevich et al., 1972) or as *Proporella rubanovi* Leleshus (Leleshus, 1975).

20 specimens of the species have been studied. Moreover some exemplars of *Propora speciosa* from the collection of Apekin (Kitab State Geological Reserve) were also examined. Therefore the ranges of corallites maximum sizes have been defined more exactly. Our coralla make four morphogroups and corallites' diameter varies from 1,8-2,2 mm to 4,0-4,5 mm. Some conclusions from this study are resulted more below (Ospanova, 2001):

1) One new region as Middle Asian (Tajikistan and Uzbekistan) of the distribution of *Propora speciosa* (Billings) is found.

2) Our researches confirm the data of Bondarenko and Minzhin (1981) about wide variability of the species *P. speciosa.* We can distinguish four morphogroups with different morphometric characteristics in our region.

3) Archalyk beds (we have found the first species in these beds) correspond to middle part of Ashgillian stage while Minkuchar beds correspond to upper part of Ashgillian stage. Archalyk beds can be stratigraphically compared with lower part of the Ellis Bay Formation of Canada, the Pirgu Stage of Estonia, and beds 5a of Norway and with beds 6, 7 of the Khangai Horizon of Central Mongolia. Minkuchar beds can be stratigraphically compared with upper part of the Ellis Bay Formation of Canada, the Porkuni Stage of Estonia, and beds 5b of Norway. Furthermore they can

be compared with the White Head Formation (Ordovician) of East Canada (peninsula Gaspe) after Bolton (1980).
4) Superior range of variability of the species *Propora speciosa* was determined. It is not equal with 3,2 mm as supported by Bondarenko and Minzhin (1981) but with 3,5-3,8 mm after Dixon (1974) and with 4,0-4,5 mm according to our data.
5) *Proporella rubanovi* Leleshus is younger synonym of *Propora speciosa* (Billings). So the genus *Proporella* is younger synonym of the genus *Propora*.

Thus, the cumulative data about morphology of the species *Propora speciosa* from different regions is a proof of the species high study level. Rather more through studies can help to confirm the allocation of the taxa of Heliolitida and to estimate the age of deposits precisely. Besides, the study of *P. speciosa* from our region shows its peculiarity: gigantism of skeletal elements is characteristic for some representatives of species.

6. Standardization of arrangement of coenenchyme due to parallelism of development

The main problem of the definition of taxa in Heliolitida is the genus *Heliolites*. The forms with *Heliolites*-like tubular coenenchyme could appear in next ways: (1) decrease of stereoplasma at some Coccoseridina with solid trabecular-bacular skeleton of colonies; (2) transformation of vesicular coenenchyme to tubular or vesicular-tubular one.
1) Sokolov (1962) supposed that some genera of Heliolitida descend from the Protaraeida (= Coccoseridina now). He considered well proved the relationship between these two groups. He has established following trend of development: *Protaraea - Estonia - Acidolites; Acidolites - Heliolites* ; *Heliolites - Stelliporella.*
2) Transformation of vesicular coenenchyme to tubular or vesicular-tubular one is characteristic for such families of heliolitids as Plasmoporidae Wentzel, 1895; Aviceniidae Ospanova, 1986; Ducdoniidae Ospanova, 1989; Khangailitidae Bondarenko, 1992; Hemiplasmoporidae Bondarenko, 1992; Helioplasmolitidae Ospanova, 1998; Wormsiporidae Ospanova, 1999. As a result, many forms have a similar structure but different genetic basis. It can be added that some heliolitids can take secondary similarity with the genus *Heliolites* (*Paraheliolites*). I have studied the variability of the species *Pachycanalicula opaca* Dubatolov, 1963 from Zinzilban-section, Lower Devonian, Emsian, the Khodzhakurgan Formation (Uzbekistan, Zeravshan-Gissar mountain oblast). 105 samples were examined. Study shows that thinning of skeletal elements led to occurrence of coralla with *Paraheliolites*-like arrangement. So we can see secondary similarity with the genus *Heliolites* (or *Paraheliolites*) in this case. I consider that mention on the genus *Paraheliolites* in Zinzilban section is erroneous.

The genus *Heliolites* includes at time 180-200 species (Bondarenko, 1992). Heterogeneous character of the genus *Heliolites* is obvious.

7. Conclusions

1) It seems well proved that the rank of the Heliolitida is the order.
2) Faunistical peculiarity of each region can cause interpretation ambiguity of the same morphological features of the Heliolitida. The study of variability of species can help to define the taxa more accurately and estimate the age of deposits precisely.
3) Transformation of vesicular coenenchyme to tubular or vesicular-tubular one is characteristic for many taxa of the heliolitids. Heliolitid morphotype could also appear owing to decrease of stereoplasma among some Coccoseridina with solid trabecular-bacular skeleton of colonies. As a result, many forms have *Heliolites*-like structure at a different genetic basis.
4) Heterogeneous character of the genus *Heliolites* is obvious. So researches must give more attention to the problem of the genus *Heliolites*.

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