

Early Bashkirian Rugosa (Anthozoa) from the Donets Basin, Ukraine. Part 3. On the genera *Cyathaxonia* Michelin, 1847 and *Barytichisma* Moore and Jeffords, 1945

JERZY FEDOROWSKI¹ AND NINA P. VASSILYUK²

¹*Jerzy Fedorowski, Institute of Geology, Adam Mickiewicz University, Maków Polnych 16, Pl-61-606 Poznań, Poland. E-mail: Jerzy@amu.edu.pl*

²*Nina P. Vassilyuk, Artioma 58, Donetsk, Ukraine.*

ABSTRACT:

Fedorowski, J. and Vassilyuk, N.P. 2011. Early Bashkirian Rugosa (Anthozoa) from the Donets Basin, Ukraine. Part 3. On the genera *Cyathaxonia* Michelin, 1847 and *Barytichisma* Moore and Jeffords, 1945. *Acta Geologica Polonica*, **61** (2), 133–152. Warszawa.

The genus *Cyathaxonia* Michelin, 1847 is determined to be one of only two possible genera belonging in the family Cyathaxonidae Milne Edwards and Haime, 1850. This detailed study of a new species, *Cyathaxonia nodosa*, proves the origin of the columella independent of major septa, as demonstrated in crossed nicols. The inner margins of the major septa retreat from the corallite axis in the late neanic growth stage. The presence of a circulotheca is considered to be an important feature of this genus. *Barytichisma* represented by *Barytichisma* sp. is placed in the family Stereophrentidae Fomichev, 1953.

Key words: *Cyathaxonia*; *Barytichisma*; Taxonomy; Morphology; Relationships.

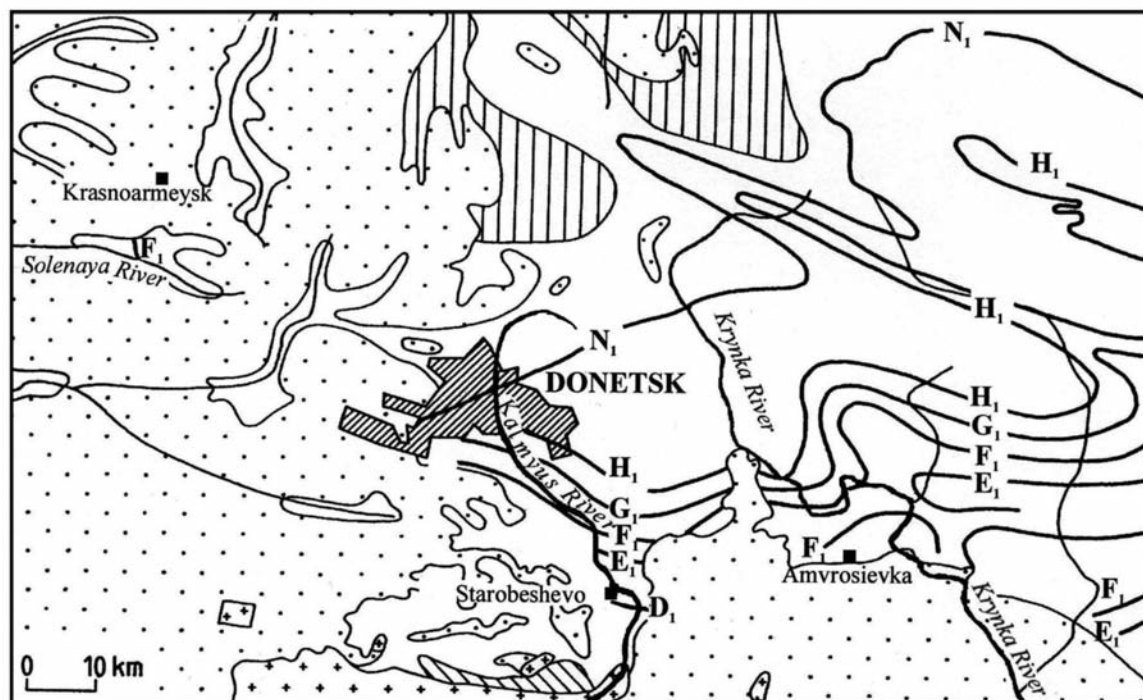
INTRODUCTION

The present paper is the third in a series devoted to the description of Bashkirian rugose corals from the Donets Basin, Ukraine (Text-fig. 1). The two species treated in the paper are restricted to a very few localities (see occurrences) and to the F₁ group of Limestones. This F₁ group, Lower Bashkirian in age, corresponds to the upper *Bilinguites-Cancelloceras* ammonoid Biozone, the *Pseudostaffella praegorskyi-Staffelleformis stafelleformis* foraminiferal Biozone, and the *Idiognathodus sinuosus* conodont Biozone, the boundaries of which are not identical. However, those small differences in the boundaries are unimportant for the topic of the present paper. The geographic location of the F₁ group of Limestones in the vicinity of the Donets Basin, i.e., the study area, is

shown on Text-fig. 2. For the details mentioned, the history of the investigation, and the geological setting, see Fedorowski (2009a, b).



Text-fig. 1. General map of Ukraine showing approximate position of the study area. Upper frame North



Text-fig. 2. Vicinity of the town of Donetsk. Generalized positions of individual Limestone Groups (D to N). Carboniferous deposits left in white (after J. Fedorowski (2009a), provided by N.P. Vassilyuk). Upper frame North

SYSTEMATIC PALAEOONTOLOGY

Order Stauriida Verrill, 1865

Family Cyathaxonidae Milne Edwards and Haime,
1850

Genus *Cyathaxonia* Michelin, 1847

TYPE SPECIES: *Cyathaxonia cornu* Michelin, 1847.

1847. *Cyathaxonia* J. L. H. Michelin, p. 257.
 1895. *Cyathaxonia* Michelin 1846; Stuckenber, p. 24 (*cum synonym.*)
 1906. *Cyathaxonia*; Vaughan, p. 316
 1909. *Cyathaxonia cornu* Michelin; Faurot, p. 75.
 1913. *Cyathaxonia* Mich.; Carruthers, p. 53.
 1925. *Cyathaxonia* Michel. [27] 1846; Soshkina, p. 89.
 1928. *Cyathaxonia* Michelin; Grabau, p. 117.
 1928. *Cyathaxonia* Michelin 1846; Soshkina, p. 375
non 1929. *Cyathaxonia*; Dutertre, p. 127 (= *Axisvacuus* Fedorowski, 2009)
 1932. *Cyathaxonia* Michelin 1846; Soshkina, p. 254
 1934. *Cyathaxonia* Michelin; Vojnovsky-Krieger, p. 30
 1935. *Cyathaxonia* Michelin; Grove, p. 367.
 1936. *Cyathaxonia* Michelin 1846; Dobrolyubova, p. 91.
 1938. *Cyathaxonia* Michelin 1847; Demanet, p. 34.

- 1938-1941. *Cyathaxonia* Michelin; Hill, p. 194 (*cum synonym.*)
 1942. *Cyathaxonia* Michelin, 1847; Hudson and Fox, p. 120
 1944. *Cyathaxonia* Michelin 1847; Easton, p. 29 (*cum synonym.* of *C. tentilla*).
 1951. *Cyathaxonia* Michelin, 1846; Gorsky, p. 46
 1951. *Cyathaxonia cornu* n. subsp.; Schindewolf, p. 101.
 1953. *Cyathaxonia* Michelin 1846 em. Mn. Edw. et H., 1850; Fomichev, p. 54.
 1960. *Cyathaxonia* Michelin 1846; Vassilyuk, p. 156.
 1961. *Cyathaxonia* Michelin 1847; Fontaine, p. 73.
 1964. *Cyathaxonia* Michelin 1847; Vassilyuk, p. 87.
 1964. *Cyathaxonia* Michelin 1847; Wu, p. 26.
 1966. *Cyathaxonia* Michelin, 1846; Pyzhyanov, p. 267
 1968. *Cyathaxonia* Michelin, 1847; Fedorowski, p. 210.
 1969. *Cyathaxonia* Michelin 1847; Rózkowska, p. 52 (*cum synonym.*)
 1975. *Cyathaxonia* Michelin, 1847; Weyer, p. 937.
 1977. *Cyathaxonia* Michelin 1847; Jia *et al.*, p. 124.
 1977. *Cyathaxonia* Michelin 1847; Khoa, p. 318.
 1977. *Cyathaxonia* Michelin; Sando, p. 53 (*cum synonym.* pp. 53, 54, 56).
 1979. *Cyathaxonia* Michelin 1847; Degtjarev, p. 45

1979. *Cyathaxonia* Michelin 1847; Li and Liao, p. 20.
1981. *Cyathaxonia* Michelin 1847; Poty, p. 16.
1981. *Cyathaxonia* (*Cyathaxonia*) sp.; Weyer, p. 5.
1982. *Cyathaxonia*; Yang and Fan, p. 63.
1983. *Cyathaxonia* Michelin 1847; Cao *et al.*, p. 54.
1983. *Cyathaxonia* Michelin 1847; Yu *et al.*, p. 64.
1984. *Cyathaxonia* Michelin (1847); Rodríguez, p. 165.
1984. *Cyathaxonia* (*Cyathaxonia*) sp. Weyer, Photo 4, fig. 3.
1984. *Cyathaxonia* (*Cyathocarinia*) n. sp.; Weyer, Photo 4, fig. 4; Text-fig. 6:2.
1986. *Cyathaxonia* (*Cyathocarinia*); Weyer, Pl. 2, fig. 12.
1989. *Cyathaxonia* Michelin 1847; Wu and Zhao, p. 38.
1990. *Cyathaxonia* Michelin 1847; Rodríguez and Kullmann, p. 22.
1993. *Cyathaxonia cornu* Michelin, 1847; Weyer, text-fig. 3, Pl. 5, figs 2, 3.
1994. *Cyathaxonia* Michelin, 1847; Weyer, p. 184.
1995. *Cyathaxonia* Michelin, 1847: Lin Baoyu *et al.*, p. 373.
1999. *Cyathaxonia* Michelin 1847; Rodríguez and Kullmann, p. 27.
2000. *Cyathaxonia* Michelin, 1847; Igo and Adachi, p. 43.
2001. *Cyathaxonia* Michelin, 1847; Fedorowski, p. 100.
2002. *Cyathaxonia* Michelin, 1847; Berkowski, p. 19.
2003. *Cyathaxonia* Michelin 1848; Fan *et al.*, p. 266.
2003. *Cyathaxonia* Michelin, 1847; Fedorowski, p. 60.
2003. *Cyathaxonia* Michelin, 1847; Weyer, p. 102.
2005. *Cyathaxonia* Michelin, 1847; Chwieduk, p. 416.

EMENDED DIAGNOSIS: Small, solitary, non-dissepimented; major septa meet axially in early ontogeny and form a circulotheca at a more advanced growth stage with their inner margins reaching a basally secreted columella which projects high in calice; minor septa contratingent; tabularium biform; microstructure of septa finely trabecular.

REMARKS: *Cyathaxonia* Michelin, 1847 is one of the most easily recognizable genera among the latest Devonian and Carboniferous Rugosa. Its unique diagnostic features are present only in *Cyathocarinia* Soshkina, 1928. The only difference between those

two genera is the presence of carinae in the latter genus. However, in some specimens of *Cyathaxonia* a few flanges or low swellings are present on some septa (e.g., Pl. 1, fig. 2d, e; Pl. 2, fig. 5b). Such specimens can be interpreted as intermediate between the strongly carinated and the non-carinated corallites, making the independent generic status of *Cyathocarinia* questionable. That status has already been questioned by some scientists (e.g., de Groot 1963; Sando 1977; Hill 1981; Rodríguez and Kullmann 1999). We do not take a position on this question, so neither the type of *Cyathocarinia* nor other species included in that taxon are here synonymized with *Cyathaxonia*.

All genera included by Hill (1981) in the family Cyathaxoniidae, other than *Cyathaxonia*, bear only a superficial similarity to that genus. *Lophotichium* Moore and Jeffords 1945 and *Epiphanophyllum* Ilina, 1970, included by her in that family, were correctly transferred by Weyer (1972) to his new family Lophotichiidae. The Silurian *Columnaxon* Scrutton 1971, placed by Hill (1981) in the Cyathaxoniidae, was originally included in the family Lindstroemiidae Počta 1902 (Scrutton 1971). This latter idea was supported by the occurrence in that genus of contratingent minor septa and a circulotheca, called an aulos at that time. However, the 'columella' of *Columnaxon*, derived from the inner margin of the counter protoseptum, has nothing in common with the true columella of *Cyathaxonia* and should be called a pseudocolumella. This suggests that *Columnaxon* should be placed in a different family.

Weyer (1980, 2005) recognized the difference in the development of the axial structure in *Cyathaxonia* and *Columnaxon*, as opposed to its development in *Lindstroemia* Nicholson and Thomson, 1876, so he introduced a new subfamily Columnaxoninae Weyer, 1980. He, however, included it in the family Cyathaxoniidae on the basis of the presence of a circulotheca. That idea is clearly demonstrated in one of his more recent papers (Weyer 2001, p. 73) in which he included the subfamilies Cyathaxoninae, Columnaxoninae, Laccophyllinae and Taralasmatinae in the family Cyathaxoniidae. We do not follow that idea, as discussed below. Also, Weyer's (2005) 'lineage' of *Laccophyllum/Hamarophyllum – Antilacca – Columnaxon* is not accepted by us. This 'lineage' serves only as an example of the increase in the morphological complexity of some non-dissepimented Silurian and Devonian Rugosa through time. However, two of them (*Columnaxon* and *Antilacca*) possess the counter protoseptum elongated whereas most, but not *Antilacca*, possess the circulotheca. Also, occurrences of the gen-

era included in that 'lineage' are not stratigraphically sequential and their geographic positions are so scattered that direct relationships seem very unlikely. The stratigraphically much earlier occurrence of the morphologically more complex *Columnaxon* (in the Ludlow) than the much simpler *Antilacca* (in the Upper Emsian–?Lower Eifelian) and the lack of a circulotheca in the latter genus, are additional arguments against the reality of that lineage. A theoretically possible trend towards morphological simplification cannot be applied in this case if the morphologically simplest genus, *Laccophyllum*, is accepted as a starting point for the lineage.

We fully accept the taxonomic elevation of *Columnaxon* to a higher taxonomic level as proposed by Weyer (1980). In fact, we would increase that elevation to that of an independent family not connected with the Cyathaxoniidae. The content of Columnaxoninae, proposed by Weyer (2005, p. 7), should be treated as provisional until the relationships between the relevant taxa are firmly documented. That documentation should include information on the microstructure of the septa and the geographic occurrence of species. The distribution of all species should reflect free communication and thus be compatible with the Late Silurian and Devonian palaeogeography.

Cyathaxonella Stuckenberg, 1895 was also included by Hill (1981) in the family Cyathaxoniidae. The state of preservation of the type specimen and the only representative of that genus, however, is poor and it cannot be sectioned (Ivanovskiy 1987, p. 13). Thus, its morphology cannot be re-investigated and no topotypes have ever been collected. The large size of the type specimen (4 cm in length and 1.8 cm in the diameter) is one of the characters distinguishing that genus from *Cyathaxonia*. However, Stuckenberg (1895, p. 26) stated that the morphology of the columella in *Cyathaxonella* was the only character distinguishing his possibly non-dissepimented genus from *Cyathaxonia*. He described that columella as 'composed of radially arranged and slightly curved plates' [translated herein from Russian] and illustrated such a columella on his plate 6, figure 5a. If that observation and the picture are accurate, the axial structure in *Cyathaxonella* is totally different from that in *Cyathaxonia*. Unfortunately, there is no possibility of verifying that difference, so *Cyathaxonella* is not considered here.

The preceding discussion suggests that the content of the family Cyathaxonidae Milne Edwards and Haime 1850 (in our meaning) is restricted to the genera *Cyathaxonia* and *Cyathocarinia*, if those two are not subgenera or synonyms. Thus, the approach taken

here is opposed to the broad concept of that family proposed by Weyer (2001), as mentioned above. The reconstructed morphology of *Cyathaxonia*, including a highly elevated columella, differs substantially from that of taxa possessing an empty circumaxial structure. Fedorowski (1997) has already noted that difference in a reconstruction of the probable physiology of *Cyathaxonia* and *Syringaxon*. Such long-lasting morphological and physiological differences as those between *Cyathaxonia*/*Cyathocarinia* on the one side and circulothecate corals on the other, must have been genetically controlled at a level higher than subfamily.

Also, a trend towards an amplexoid mature morphology, observed in some taxa possessing the circulotheca in the early growth stages (e.g., *Schindewolfia* Weissermel, 1943; *Silesamplus* Fedorowski, 2009), is absent from both *Cyathaxonia* and *Cyathocarinia*. The columella is invariably present in those genera (or genus?) during the entire history of their occurrence, i.e., from the Famennian (Rózkowska 1969; Chwieduk 2005) to the Middle Artinskian (Soshkina 1925) and Upper Artinskian (Kossovaya 2007).

In contrast to the presence of a columella in *Cyathaxonia* and *Cyathocarinia*, which is unique in morphology and derivation, contratingent minor septa and biform tabularia are common among the non-dissepimented corals of Silurian and Devonian age (e.g., *Syringaxon* Lindström, 1882; *Laccophyllum* Simpson, 1900; *Boolelasma* Pedder, 1967; *Columnaxon* Scrutton 1971; *Sutherlandinia* Weyer, 1972; *Muenstraia* Weyer, 2001). Some forms extend into the Early Carboniferous (e.g., 'Permian' of Hudson 1943, 1944, 1945, that may belong to *Laccophyllum*) or are definitely Carboniferous (*Claviphyllum* Hudson 1942; *Silesamplus* Fedorowski 2009). Thus, presence of contratingent minor septa and a biform tabularium must be considered taxonomically important only in conjunction with other morphological, microstructural, and palaeogeographic data. Most of the corals listed above and several other genera possess circumaxial structures. However, there are genera such as *Claviphyllum*, *Muenstraia* and the Carboniferous and Permian family Lophotichiidae Weyer, 1972 that developed a biform tabularium and contratingent or free minor septa, but not a circumaxial structure. Thus, the columella, in contrast to all the other characters listed, appears to be the only stable morphological structure in the genera and families considered. Therefore, the family Cyathaxoniidae is unique and not related to other taxa at a level lower than suborder.

The early skeletogenesis has been documented in only a few genera developing a biform tabularium and contratingent, or in some cases, free minor septa.

All such genera pass through a brephic growth stage characterized by about six major septa meeting at the corallite axis with contratingent minor septa absent. Such an early growth stage is known from *Cyathaxonia* (Faurot 1909, text-figs 4–7; Weyer 1993, text-fig. 4:1a, b; and Pl. 1, Fig. 1a, b; Text-fig. 3A, B herein) and in several circulothecate taxa, including *Syringaxon* (Fedorowski 1965, text-fig. 1:1; Berkowski 2008, pl. 8, fig. 2a), *Metrixaxon* Glinski, 1963 (Fedorowski 1965, text-figs 2, 3) and *Schindewolfia* (Berkowski 2008, pl. 9, fig. 2a, b). It was also documented in representatives of the family Lophotichiidae including *Lophotichium* Moore and Jeffords, 1945 (Fedorowski 1987, text-fig. 54:1a–c), *Paraduplophyllum* Wu and Zhou, 1982 (Fedorowski 1987, text-figs. 75:3a–g), its subgenus *P. (Vacoa)* Fedorowski, 1987 (text-figs 81:1a–c, 83:9a–c), and *Assimulia* Fedorowski, 1987 (text-figs 60:3a–d, 71:1a–c). The biform tabularium and contratingent minor septa other than those at the counter protoseptum, may appear as late as in the early mature growth stage (e.g., *Muenstraia* Weyer, 2001, pl. 1, figs 1b, 2d; text-fig. 2d), documenting the necessity of complete studies of those and other solitary, non-dissepimented corallites in order to establish their correct taxonomic positions.

As indicated above, early skeletogenesis is known in only a small number of genera possessing a biform tabularium (not all mentioned in the list above) and minor septa which are either contratingent (most), or only contraclined, but free. Nevertheless, that character appears in different taxa at different growth stages, making their close relationship doubtful. This information allows recognition of several informal groups of taxa:

1. Taxa possessing a columella, contratingent minor septa, and rhopaloid major septa, the inner margins of which remain in lateral contiguity, i.e., the same way as they are in a circulotheca. Only *Cyathaxonia* and *Cyathocarinia* fit these characteristics.

2. Taxa possessing most characters indicated above, but lacking a columella. The microstructure of septa is unknown from most type species. It was established as finely trabecular in a Polish specimen included in *Syringaxon* (Fedorowski 2009a, fig. 4B, C), but this cannot be extended to the entire family Laccophyllidae. The same is true for coarsely trabecular microstructure seen in the calice of *Boolelasma* Peder, 1967 from the Emsian of Morocco (Berkowski 2008, pl. 1, fig. 6c) and trabecular microstructure of septa in *Schindewolfia* Weissermel, 1943 (Berkowski 2008, pl. 2, fig. 2a) from the same age and area. The

latter two taxa were included by Weyer (2001) and Berkowski (2008) in different subfamilies placed in turn in different families, the Protozaphrentidae and Cyathaxoniidae, respectively. Both of those families were included by them within the suborder Cyathaxoniina Spasskiy 1977.

Our position concerning the subfamilies included in the family Cyathaxoniidae was discussed above. The family designation of individual genera by both Weyer (2001) and Berkowski (2008) and the relationships of particular subfamilies, questioned in part by Berkowski (2008, pp. 33, 34), are not discussed here. However, the morphologically simple *Protozaphrentis* Yu, 1957, which has underdeveloped minor septa and a probably normal tabularium, has very little in common with the morphologically complex taxa included by Weyer (2001) and Berkowski (2008) in the family Protozaphrentidae. The simple morphology of *Protozaphrentis* differs distinctly from that of *Cyathaxonia*. Thus, we question the position of the family Protozaphrentidae within the suborder Cyathaxoniina, as we do the content of that suborder as proposed by both Weyer (2001) and Berkowski (2008). The relationships between taxa included in that suborder by the authors mentioned are more complex and require a re-consideration, especially in the context of the microstructure of septa, morphology of the tabularium, formation of the circulotheca vs. other axial and circumaxial structures, peripheral splitting of septa, and development of minor septa. Also, placement of dissepimented taxa within the suborder Cyathaxoniina seems inappropriate.

3. Taxa of this group can in general be characterized by features attributed to the family Lophotichiidae. They bear such characters as long contratingent and/or contraclined minor septa and biform tabularia, thus resembling the subfamily Sutherlandiniinae, which was included by Weyer (2001) and Berkowski (2008) in the suborder Cyathaxoniina. Morphological similarity between *Lophotichium* Moore and Jeffords, 1945 and *Sutherlandinia* Weyer, 1972 is only superficial, whereas the main features of both genera are distinct from that in *Cyathaxonia* at the suborder level.

Being clearly distinct from all other Rugosa at the family and genus level, representatives of *Cyathaxonia*, which extend over a very long time span (Late Famennian-Late Artinskian), are strikingly similar to one another irrespective of their age. Specimens possessing septa more or less clearly carinated, i.e., identified as *Cyathocarinia*, accompany the non-carinated ones since their earliest recorded occurrence (Rózkowska, 1969). Bodies called “jagged projections”, probably

representing indistinct carinae, were mentioned by both Carruthers (1913) in *C. cornu* Michelin, 1847 and by Vaughan (1906) in his species *C. rushiana*. None of the distinguishing characters introduced by Vaughan (1906, pp. 316, 317 and foot notes) for his species, are of a diagnostic value. This species was accepted by several authors mainly on the basis of Carruthers' (1913) recognition of its oval columella. Distinguishing characters of *C. rushiana* have been rather inconsistently applied by other authors. For instance, Smith (1931) identified as *C. cf. rushiana* a Bashkirian specimen from South Wales, despite it being the size of the smaller species *C. cornu* and possessing a columella of uncertain shape. Moreover, the columella may vary in its shape and outline, as demonstrated in the present paper.

Reduction in the length of the minor septa in the course of phylogeny was mentioned as important by Smith (1931, pp. 9, 10) and supported by de Groot (1963, p. 25). Unfortunately, Smith (1931) referred to the length of the minor septa in the calice, i.e., where they became shortened, irrespective of their stratigraphic position. They are very long in some Upper Moscovian specimens described by de Groot (1963), contradicting her own and Smith's (1931) position. This is also true for the Moscovian and Gshelian specimens described by Fomichev (1953) and for some specimens described herein (Pl. 2, Fig. 1b; Text-fig. 5D, F). Accepting that character, de Groot (1963) rejected the following characters as taxonomically important: presence or absence of carinae, length and shape of specimens, and thickness of the septa and the external wall (called 'epitheca' by her). Such an approach leaves almost no character to be used for a species distinction. We list those characters in order to stress difficulties in distinguishing between species.

Several authors (e.g., Khoa 1977; Sando 1977; Rodríguez and Kullmann 1999) discussed nearly all the characters present in *Cyathaxonia* and came to the conclusion that at least some of those characters are different in different species. Unfortunately, evaluation of the differences varies from paper to paper showing clearly that rigid characters for the distinction between species of *Cyathaxonia* have not yet been established.

Fomichev (1953) discussed most of the older papers dealing with species truly belonging to *Cyathaxonia* and other species belonging to other genera and families incorrectly bearing that name. He also introduced several new species of *Cyathaxonia*, mostly Moscovian and Gshelian in age. A few specimens described by him were derived from the Upper Bashkirian Prikamsk Stage (Limestone H), therefore stratigraphically close to the species described here (in Limestone F). His discussion was comprehensive and

need not be repeated, but none of his new species were investigated completely enough to form an indisputable basis for their distinction. For instance, weak carinae are mentioned by Fomichev (1953) to occur in all species except for *C. kapustini*, a species represented by two small, poorly preserved fragments, and *C. archangelskyi intermedia*, which also is poorly represented. Both of those taxa are omitted from this discussion. Differences between Fomichev's (1953) remaining species, as pointed out by him, are: the shape and size of the columella, the thickness of the external wall, the thickness of the major and minor septa, the slightly different angle between the major and contrasting minor septa, and the diameter and number of septa. Most of these characters are unimportant and occur in various combinations in individual groups of specimens identified by Fomichev (1953) as species. Besides, it is not quite certain whether or not identical growth stages were compared by him. One of us (J.F.) restudied Fomichev's (1953) specimens briefly and a long time ago, but did not revise them in detail. Although it is likely that some of the species should be placed in synonymy, we do not have a rigid basis to make a determination. These specimens were not restudied by Rodríguez prior to his publishing a synonymy of *Cyathaxonia cornu* (Rodríguez 1984, p. 165), so we cannot accept his synonymy.

Difficulty in identification of species of *Cyathaxonia* is well illustrated by the work of Rodríguez (1984) and Rodríguez and Kullmann (1990, 1999) on specimens from Bashkirian to Podolskian (Middle/Upper Moscovian) strata in Spain. Illustrations of the Spanish specimens identified by those authors as *Cyathaxonia cornu* Michelin closely resemble Late Tournaisian and Early Viséan specimens of that species from several other European countries. The question arises, however, whether is this an extremely long-lasting species or a genetically distinct species which produced similar appearing skeletons? This is a fundamental question that cannot be solved on purely palaeontological data which, of course, must be taken into consideration. Nevertheless, the existence of the same species extending from the late Famennian into the Gshelian (see synonymy of Rodríguez and Kullmann 1990, p. 22) or Upper Artinskian (Kossovaya (2007) seems very unlikely, especially when the Serpukhovian/Bashkirian crisis in rugose coral evolution is considered.

Thus, several points must be made clear: (1) The fundamental basis for the distinction between species of *Cyathaxonia* has not been established either in previous works or in this paper. Many species have been introduced with the result that several of them appear

to be synonyms; (2) The opposite situation, i.e., the existence of a single species for more than 80 million years is very unlikely. It only proves a lack of methods allowing a distinction between species of *Cyathaxonia*, but not the identity of palaeontological objects studied; (3) Only a few specimens of *Cyathaxonia* have been investigated adequately enough for unquestionable comparison. Some features, including the external morphology and microstructure of the external wall, the microstructure of the septa and columella, the intraspecific variability, and the step by step description of the ontogeny allowing a precise comparison of individual growth stages, are missing from the vast majority of descriptions; (4) Comparison between the specimens described in this paper and earlier inadequately described species has resulted in the introduction of a new species. This has been done mostly because the inclusion of those specimens in any of the existing species must be preceded by a synonymy of the most similar species. Such a synonymy, which would suggest a close relationship, would be superficial until a re-investigation of type collections of such species is made. Such a condition is impossible for us to fulfill. For the same reason the species content of the genus *Cyathaxonia* was not included in this paper.

A complete synonymy of the genus has not been published in any paper known to us. We have made an attempt to complete it as much as possible, but there are almost certainly papers omitted by us. Also, we refer to earlier papers when possible (*cum synonymicum*). Several papers not cited, especially old ones, are to be found in citations in those other papers. In some papers specific names are cited, but not the generic names. Such papers, however, may contain references important enough to be mentioned. Papers in which the name *Cyathaxonia* was only mentioned but specimens not illustrated, were omitted from the synonymy. Thus, the overall geographic and stratigraphic distribution and the species content of the genus may be larger than cited.

Cyathaxonia nodosa sp. nov.
(Pls 1–4, Text-figs 3–6A, B)

HOLOTYPE: UAM-Tc.Don.1/79.

TYPE HORIZON: Limestone F₁¹, Upper Mandrykinian Horizon, Blagodatnian Subhorizon, upper Lower Bashkirian.

TYPE LOCALITY: Kalmyus River area, Menchugovo Village.

ETYMOLOGY: Lat. *nodosus*, *a*, *um* – full of nodes – after numerous swellings on interseptal ridges.

DIAGNOSIS: *Cyathaxonia* with n:d values of 18:4.6 to 20:5.8; interseptal ridges bear distinct swellings; major septa reach columella which occupies 1/6–1/8 corallite diameter and appears in late neanic growth stage; minor septa meet major septa at 3/4–4/5 the latter length; cardinal protoseptum is almost equal to remaining major septa; septotheca up to 0.8 mm thick.

MATERIAL: Holotype UAM-Tc.Don.1/79, fourteen paratypes UAM-Tc.Don.1/80, 82–94, and nine unnumbered specimens were available for study. The corallite surfaces and the macro-morphology of their mature parts are well preserved, except for the upper parts of their deep calices which are either missing or flattened in most corallites. The microstructure of the septa is altered diagenetically. That alteration precludes recognition of the primary septa in most instances. However, rudiments of the original microstructure remain in some septal fragments. Tips of all specimens, including the holotype, are missing. The ontogenetically earliest part of the holotype preserved, 1.0 mm in the mean diameter (Pl. 1, Fig. 1a; Text-fig. 4A), is strongly corroded and burrowed, suggesting bioerosional and diagenetic reasons for the incompleteness of this and other specimens. The external surfaces of most specimens are well preserved and do not show destruction resulting from transportation. The measured length of corallites (10 mm to almost 30 mm) is approximate because of the incompleteness mentioned. Thirty-three thin sections and thirty-five peels were available for study.

DESCRIPTION OF THE HOLOTYPE: The corallite is 11.3 mm long and has 18:4.6 n:d value above the calice floor (Text-fig. 3). Its 0.6 mm-thick septotheca bears deep septal furrows and distinct interseptal ridges armed with swellings (Pl. 1, figs 1i, j). A detailed description of the latter bodies in the holotype and the paratypes is given below.

In the ontogenetically earliest growth stage preserved (Pl. 1, Fig. 1a, b; Text-fig. 4A, B), the inner margins of the strongly thickened major septa approach the corallite axis, but their direct connection is uncertain due to the diagenetic alteration (Pl. 3, Fig. 1a, b). The minor septa are absent from the corallite lumen at this stage, but their furrows occur on the corallite surface. The first minor septa appear in the corallite lumen next to the counter protoseptum and the counter-lateral septa at a corallite n:d value of 12:1.9 mm (Pl. 1, Fig. 1c; Text-fig. 4C). The distal extensions of

the major septa are unequal as are their diagenetic alterations (Pl. 3, Fig. 1b–d). Remnants of trabeculae (Pl. 3, Fig. 1c) suggest that only the longest major septa meet at the corallite axis. However, the protosepta do not dominate in length and their retreat from the corallite axis is not delayed compared to the remaining long major septa. The cardinal protoseptum is long and thick at an early growth stage (Pl. 1, Fig. 1c–f; Text-fig. 4C–G). Only in the calice does it become slightly shorter and thinner than the adjacent major septa. Its inner margin, however, remains extended to the circulotheca (Pl. 1, Fig. 1h; Text-fig. 4I).

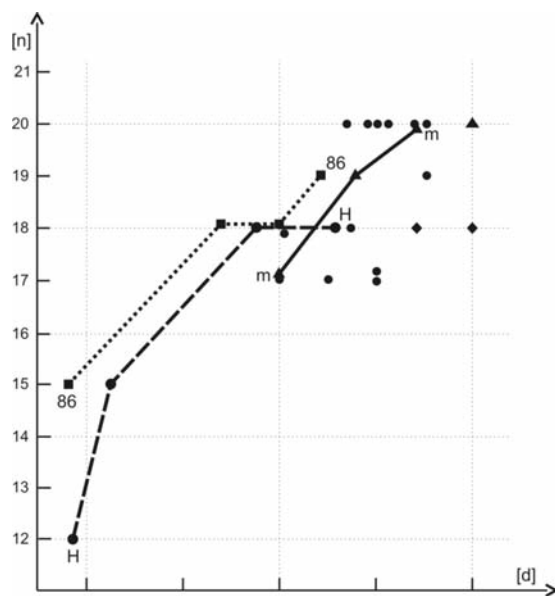
The formation of the circulotheca begins when an unequal retreat of the major septa from the corallite axis occurs. The septa are replaced by sclerenchyme that probably does not form a cone at the very beginning of its appearance in the corallite axis. This is suggested by the absence of isogyre lines = polarization brush (Pl. 3, Fig. 1e). The poorly developed isogyre lines in the next thin section (Pl. 3, Fig. 1f, axial right), made 0.4 mm above the previous one, indicates a rearrangement of crystalline fibrils towards a cone-shaped mass within that distance of corallite growth. That transformation took place at an advanced neanic/early mature growth stage, when some loculi sectioned were already above the calice floor (Pl. 1, Fig. 1f). The complete, narrow columella, well demonstrated by isogyre lines, appears only at the early mature growth stage when most loculi are cut above the calice floor (Pl. 1, Fig. 1g; Pl. 3, Fig. 1g). A complete and clearly distinguishable circulotheca is absent at that growth stage. It becomes fully developed higher in the calice (Pl. 1, Fig. 1h) where the columella, well documented by isogyre lines (forming a cross), reaches its final width of 0.7×0.9 mm and attains a slightly oval outline (Pl. 3, Fig. 1h).

Both major and minor septa are strongly thickened during the entire early growth of the corallite (Pl. 1, Fig. 1a–f; Text-fig. 4A–F). A slight reduction in their thickness begins only at the late neanic/early mature growth stage and is best accentuated in the calice (Pl. 1, Fig. 1f–h; Text-fig. 4G–I). This and the diagenetic alterations camouflage the precise level of the appearance of individual minor septa in the corallite lumen. These septa are always inserted next to the wide peripheral parts of the major septa at the cardinal protoseptum side, appearing at the very beginning like the lateral extensions of the major septa. The borders between the major and minor septa are commonly irregular and distinguished mainly by a different arrangement of crystalline fibrils on both sides of the borderline (Pl. 1, Fig. 1c–e). The complete number of minor septa is established only when the entire septo-

genesis is finished (Pl. 1, Fig. 1h; Text-fig. 4I), i.e., in the calice.

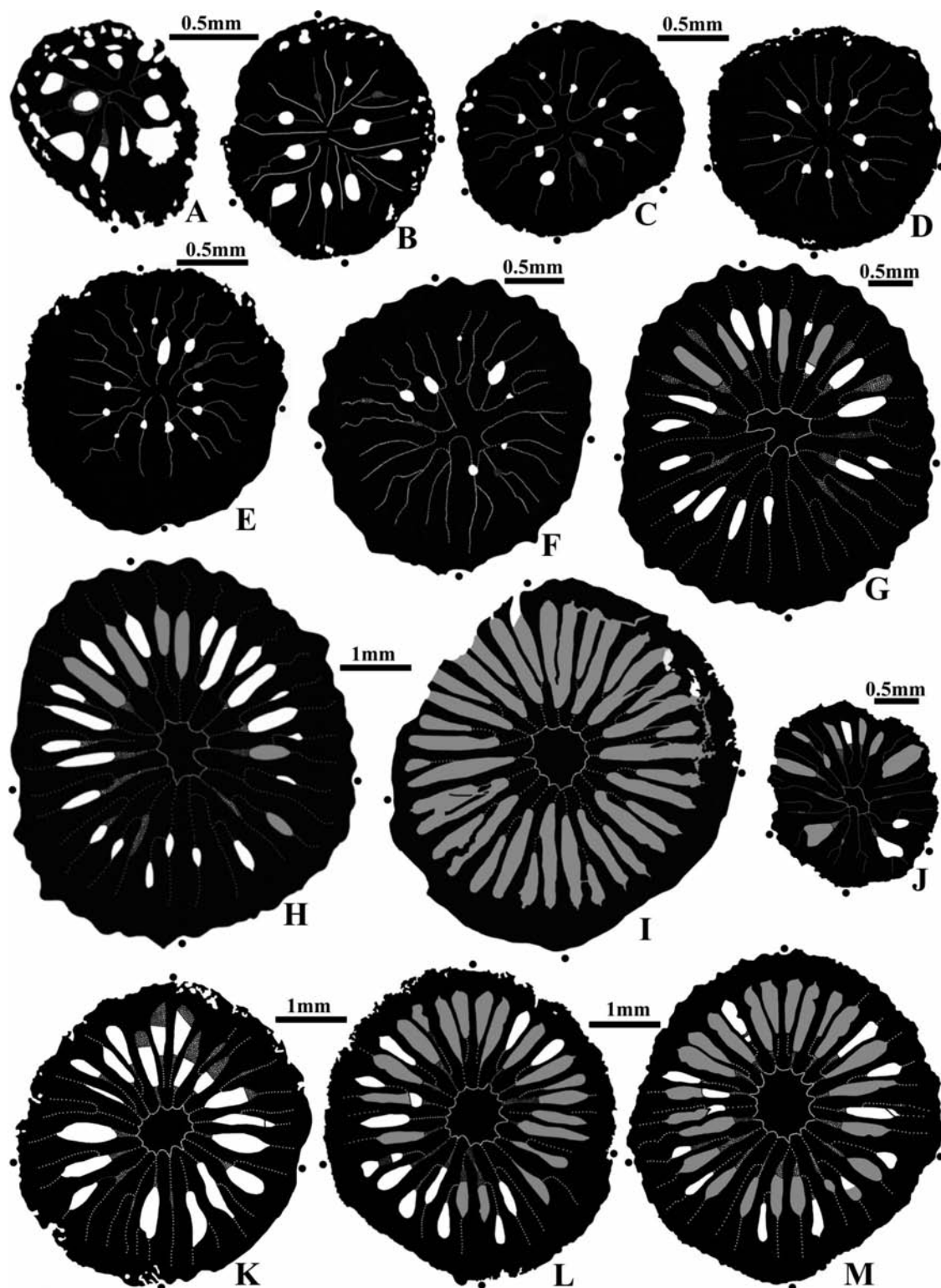
The length of the minor septa and their thickness and isolation from the major septa depends on both the growth stage and position within the corallite lumen. This process is well illustrated by the successive transverse sections (Pl. 1, Fig. 1e–h; Text-fig. 4E–I). The first inserted minor septa in each quadrant become the thinnest and the longest in later growth stages, reaching nearly up to $\frac{3}{4}$ the length of the major septa. The last inserted minor septa reach only $\frac{1}{2}$ the length of the adjacent major septa or less. That relationship continues up into the calice (Pl. 1, Fig. 1h, left; Text-fig. 4I, left).

INTRASPECIFIC VARIABILITY: Mature corallites (Pl. 1, Figs 2a–e, 3; Pl. 2, Figs 1–5; Text-figs 4L, M; 5B–D, F, H–L), except for two specimens, described separately as *Cyathaxonia* sp. (Text-fig. 6C–J), differ from the holotype in individual characters rather than in sets of characters. Thus, the morphologically closest groups of individuals cannot be clearly established. The same seems to be true for the measurements (Text-fig. 3). Some differences in the septal pattern do not show any trend in that character (e.g.: 1/79 (holotype) 4+4+4+4, 1/82 – 4+5+5+4, 1/85 – 5+5+4+4, 1/86 –

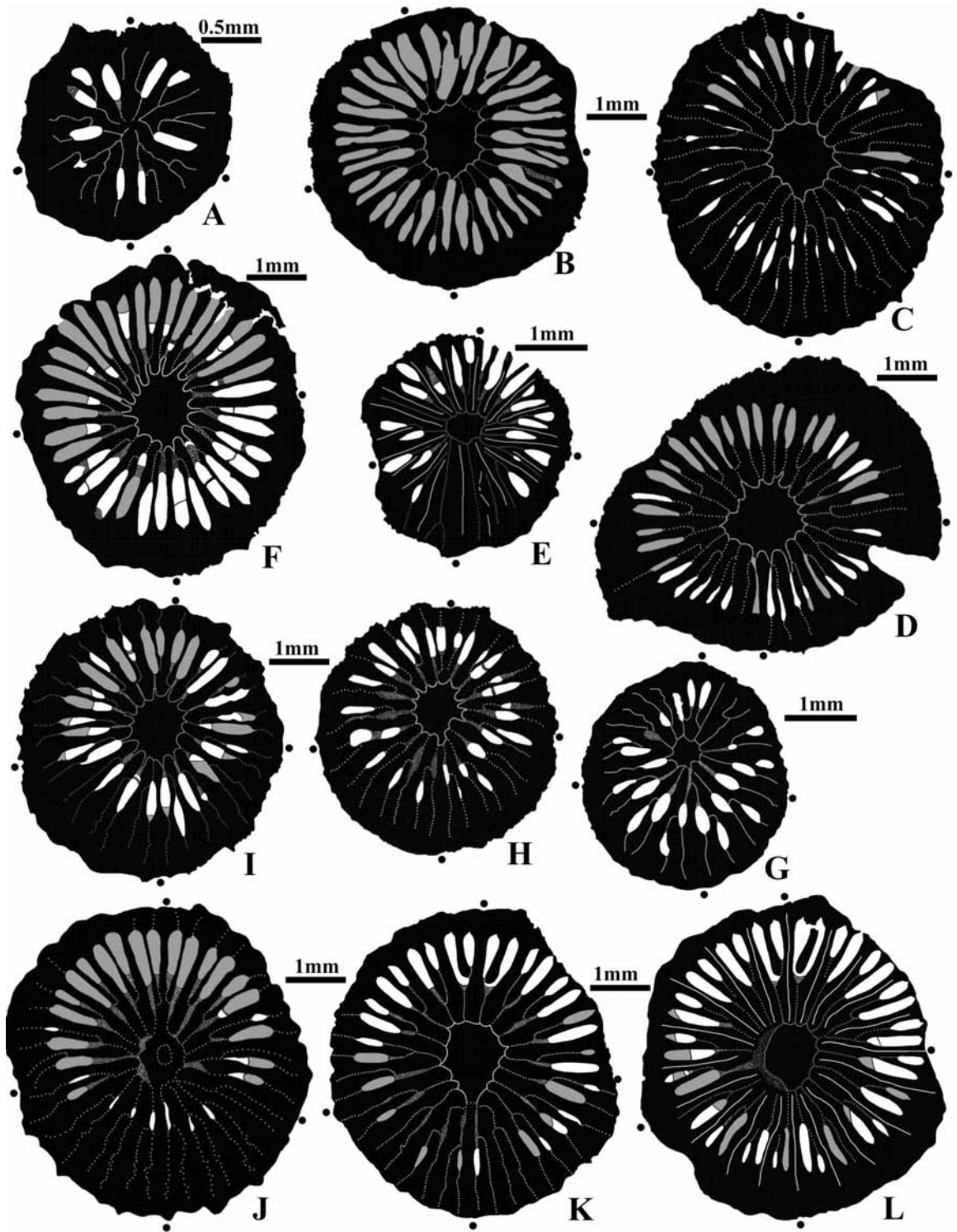


Text-fig. 3. Numerical data provided by specimens of *Cyathaxonia*. Ordinate (n) – number of major septa. Abscissa (d) – corallite diameter in mm. *C. nodosa*: Dashed line, marked **H** both ends, join values of particular measurements of the holotype. Dotted line, marked **86** shows the same for the specimen UAM-Tc.Don.1/86. Solid line, marked **m** – mean n:d value for the species. Dots not connected by lines correspond to n:d values of mature growth stages of remaining measured corallites. *Cyathaxonia* sp. Diamonds – n:d values of specimen UAM-Tc.Don.1/95. Triangle n:d value of specimen UAM-Tc.Don.1/81

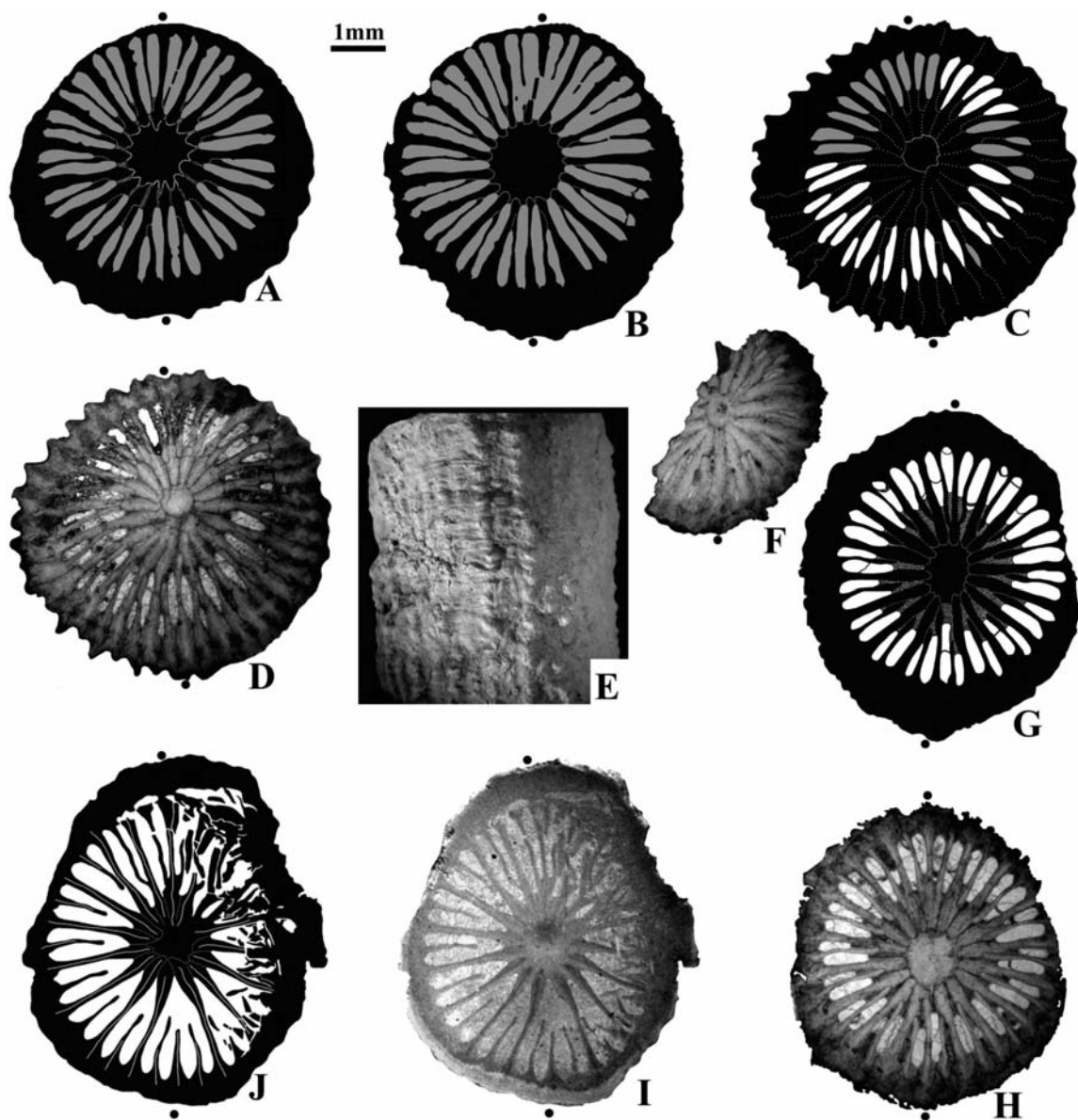
CARBONIFEROUS RUGOSA FROM THE DONETS BASIN, UKRAINE



Text-fig. 4. *Cyathaxonia nodosa* sp. nov. A-I – UAM-Tc.Don.1/79, holotype, Menchugovo Village, Limestone F₁, Upper Mandrykinian Horizon, Blagodatnian Sub-horizon, upper Lower Bashkirian, transverse thin sections; A-F – early to late neanic growth stage; G – early mature growth stage; H, I – mature growth stage; above calice floor in some (H) and in all septal loculi (I). J-M – UAM-Tc.Don.1/86, paratype, Novo Troitskoe Village, stratigraphic position as the holotype, transverse thin sections; J, K – early mature growth stage, L, M – mature growth stage; above calice floor in most loculi, note flanges on some septa. *Remarks to Text-figs 4, 5.* Cardinal protoseptum at the bottom. Protosepta and alar septa marked by dots. Scale bars located between two adjacent pictures correspond to both; those right to the picture correspond only to it



Text-fig. 5. *Cyathaxonia nodosa* sp. nov., paratypes, transverse thin sections of mature growth stage, except when stated. A, B – UAM-Tc.Don.1/84, locality and horizon as the holotype; A – late neanic growth stage, B – above calice floor. C, D – UAM-Tc.Don.1/82, locality and horizon as the holotype, above calice floor in some (C) and most (D) loculi. E, F – UAM-Tc.Don.1/88, Novo Troitskoe Village, stratigraphic position as the holotype; E – late neanic/early mature growth stage, F – above calice floor in most loculi. G–I – UAM-Tc.Don.1/87, Novo Troitskoe Village, stratigraphic position as the holotype; G – early mature growth stage, H – just beneath calice floor, I – above calice floor in some loculi; note rare flanges on some septa. J – UAM-Tc.Don.1/85, locality and horizon as the holotype, above calice floor in counter quadrants. K, L – UAM-Tc.Don.1/94, Novo Troitskoe Village, stratigraphic position as the holotype, just beneath calice floor in most loculi; further remarks see Text-fig. 4



Text-fig. 6. **A, B** – *Cyathaxonia nodosa* sp. nov., UAM-Tc.Don.1/80, paratype, Novo Troitskoe Village, stratigraphic position as the holotype, transverse thin sections, mature growth stage. **C–J** – *Cyathaxonia* sp.: **C, D** – UAM-Tc.Don.1/81, locality and horizon as the holotype, above calice floor in some loculi; **E–J** – UAM-Tc.Don.1/95, locality and horizon as above; **E** – corallite surface, weak nodulation of interseptal ridges; **F–J** – transverse sections (**I, J** peels), minor septa free beneath calice floor in advanced mature growth stage (**I, J**); *Note*. Cardinal protoseptum at the bottom. Protosepta and alar septa marked by dots in transverse sections. Scale bar corresponds to all images

5+5+4+3. Counter quadrants at top, protosepta cardinal and counter omitted) However, the number of specimens is too small to provide reasonable statistics. Here, individual features in the sections are compared with reference to the growth stage of the corallites.

The cardinal protoseptum in most corallites is long but not dominant in the late neanic growth stage (Pl. 2, Fig. 3a; Text-fig. 5A), resembling that of the protoseptum in the holotype. In the early mature growth stage that protoseptum may be either stronger than adjacent

major septa and more clearly connected to the columella (Pl. 1, Fig. 3; Pl. 2, fig. 4; Text-figs 4J, K; 5J, K) or (rarely) a little shortened (Text-fig. 5G). That growth stage commonly corresponds to the corallite skeleton cut just below the calice floor in some and just above it in the other septal loculi. However, the length of the cardinal protoseptum changes during growth, as exemplified by the corallites cited above. Those corallites possessing a long protoseptum in their early growth may have a clearly shortened one at maturity, which

may reach only the peripheral part of the inner ring of the margins of the rhopaloid major septa (Pl. 2, Fig. 5a; Text-fig. 4 L, M vs 4J, K). Contrary to that sequence, the cardinal protoseptum, shortened slightly at early maturity, may increase in length during growth, up to almost reaching the length of the adjacent major septa (Text-fig. 5I vs 5G). In that respect it resembles both the holotype and most paratypes (Pl. 1, Fig. 1h; Pl. 2, Figs 1a, b, 3b; Text-figs 4I; 5B–D, F). In some specimens the cardinal protoseptum is equal in length and thickness to that of the remaining major septa (Pl. 1, Fig. 3 Pl. 2, Fig. 4; Text-fig. 5J–L) or it may be slightly thinner (Pl. 1, Fig. 2a, b; Text-fig. 6A, B).

The length of the counter protoseptum is much more constant than that of the cardinal protoseptum in both the holotype and the paratypes. It reaches the columella beginning at the latest neanic or earliest mature growth stage similar to that of the adjacent major septa (Pl. 1, Figs 1f–h, 2a,b; Pl. 2, Figs 1a, b, 3b, 4, 5a; Text-figs 4G–I, K–M; 5B–L; 6a, B).

The major and minor septa are thickened in the early growth stages of all corallites, but that thickening is less advanced in most of the paratypes than it is in the holotype (Pl. 1, Figs 1a–e; Text-fig. 4A–F vs Pl. 2, Fig. 3a; Text-figs 4J, 5A). The septa in the cardinal quadrants commonly remain thickened longer than those in the counter quadrants and are slightly delayed in their insertion (Pl. 1, Fig. 2a, b; Pl. 2, Fig. 3a; Text-figs 4J, K; 5A, E). The thin sections made exactly along the growth lines proves the reliability of the above statement as well as the depth of the calices, which are shallower in the cardinal quadrants. The calice depth is slightly irregular, but the septal loculi adjacent to the counter protoseptum are always the deepest and those closer to the cardinal protoseptum, but not the cardinal fossula, are the shallowest. However, the cardinal fossula is not deep. The loculi between the major and the adjacent contratingent minor septa are always shallowest at the periphery, resulting from the Position I of Sutherland (1965).

The major septa continue to reach the columella up to the upper part of the calice. Their number is constant in the fully mature parts of specimens, i.e., beginning at the calice floor, and their length, except for the cardinal protoseptum, is equal. These characters make recognition of individual quadrants possible only by comparison to the earlier growth stages.

Recognition of the level of insertion of the minor septa in the paratypes is difficult for the same reason as it is in the holotype. The easily recognizable insertion of those septa next to the counter protoseptum is the only exception in both cases. Also, an increase in the length of the minor septa in the paratypes is simi-

lar to that described in the holotype. Thus, their true length is exposed only in transverse sections made well above the calice floor. The length of the fully developed minor septa does not exceed $\frac{3}{4}$ the length of the major septa. In the early mature growth stage of one specimen, the minor septa adjacent to the counter protoseptum are comparatively short (Pl. 1, Fig. 2a; Text-fig. 5K, L). That character, as well as the dominance of the cardinal protoseptum, separates the specimen discussed from the remaining corallites, whereas another specimen, possessing a dominant cardinal protoseptum, but long counter-lateral minor septa (Pl. 2, Fig. 4; Text-fig. 5J), allay it with the other corallites. Thus, both are included here in *C. nodosa*. The same is true for the corallite in which the counter-lateral minor septa in maturity are relatively long (Pl. 2, Fig. 1b; Text-fig. 5D).

The length of the minor septa is to some extent related to the width of the circumaxial interseptal sclerenchyme. They cross the interseptal loculi free from the sclerenchyme and terminate within it. The circumaxial, interseptal sclerenchyme is commonly wider in the early growth stages than upwards in the calice. That reduction may be considerable (Text-figs 4K–M; 5G–I) or slight (Text-fig. 5C, D, K, L).

All major and minor septa widen at the periphery so as to become laterally contiguous to form the septotheca. That kind of external wall was originally present in all corallites, but in some parts of corallites it may have been totally altered diagenetically.

The width and outline of the columella differ both at different growth stages of individual corallites and between corallites. It is invariably narrowest at the beginning of formation and reaches its maximum width at the calice floor. That width is constant along most of the calice, i.e. until the columella becomes cone-shaped.

The outline of the columella reflects the regularity or irregularity of the circulotheca, resulting from the inter-relationships between those two skeletal elements. The inner margins of the major septa intrude into the peripheral part of the columella that may in turn extend slightly between those margins and pass into sclerenchymal infillings of the incomplete circulotheca (a term introduced by Fedorowski 2009a). That inter-relationship is best seen at the early level of formation of the columella, as documented in the holotype (Pl. 3, Fig. 1f, g) and one paratype (Pl. 4, Fig. 1c), but may be recognized in more advanced growth stages as well (Pl. 3, Figs 1h, 2, 3; Pl. 4, Fig. 2a). Thus, the outline of the columella is never smooth, but it is generally oval (Pl. 1, Fig. 2a, b; Pl. 2, Figs 3b, 5a; Text-figs 4M, 5F, I). However, it may be circular (Pl. 1, Fig. 1h; Text-figs 4I, L; 5C, G, J), elongated towards the cardinal

protoseptum (Pl. 1, Fig. 3; Text-fig. 5K), irregular (Pl. 1G; Text-figs 4G, H; 5B) or slightly widened in the alar septa plan (Pl. 2, Fig. 1b; Text-figs 4K; 5D). Such a wide variability makes that feature taxonomically unimportant.

The cone- or fan-shape arrangement of crystalline fibrils is well documented by isogyre lines (=polarization brush). That phenomenon reflects not only that arrangement, but also the level of development of the columella, its width, and the increase in thickness when the specimen is adequately preserved. A cross of four shades is always recognizable (Pl. 3, Figs 1f–h, 2, 3; Pl. 4, Figs 1d, 2a, b), but increments of crystalline fibrils, documenting their inconsistent growth, is exceptional in the material studied (Pl. 4, Fig. 2b).

MICROSTRUCTURE OF SEPTA: The microstructure of septa is diagenetically altered in all septa in all corallites. The diagenetic alteration has commonly resulted in the total destruction of the primary septa documented by an absence of ‘dark lines’, extension of the crystalline fibrils from the middle part of septa, and their arrangement within the septa oblique to their surfaces (Pl. 3, Fig. 5). Also, the disorderly arranged crystals in the septotheca are diagenetic in the origin.

In one transverse section of the early growth stage of the holotype (Pl. 3, Fig. 1c) and in some transverse sections of the paratypes (Pl. 4, Figs 1a, b, 2a), chains of closely packed, irregularly outlined dots occur along the middle parts of several major septa. Those dots are interpreted as very fine and densely packed trabeculae, arranged in a single row and probably stained with iron compounds. The rows of suspected trabeculae occupy 1/10 to 1/7 width of those major septa.

PROTUBERANCES ON SEPTA: The lateral surfaces of septa are smooth in a large majority of the specimens. However, there are septa in some specimens which bear lateral thickenings as seen in transverse sections (Pl. 1, Fig. 2d, e; Pl. 2, Fig. 5b). Those protuberances are never well enough developed to be called flanges which are present in typical representatives of the genus *Cyathocarinia* Soshkina 1925, but they certainly are primary, rather than diagenetic in origin. The advanced diagenetic alterations preclude the recognition of their microstructure. Nevertheless, their occurrence again blurs the difference between *Cyathaxonia* and *Cyathocarinia*.

NODES: The occurrence of nodes has been observed in all specimens. Thus, it is here considered as taxonomically important, although their more or less strong development was perhaps environmentally controlled.

Also, swellings along particular ridges may differ. They are weaker on the interseptal ridges corresponding to the loculi between contratingent minor and adjacent major septa in most specimens observed (Pl. 1, Figs 1i, j, 2c; Pl. 2, Figs 2, 3c, d). However, those differences may be hardly recognizable in some (Pl. 1, Fig. 2c) and extremely strong in some others (Pl. 2, Fig. 3c, d). Swellings range in development from irregular low protuberances in some corallites and in early growth of all specimens, through a combination of protuberances and knobs (Pl. 1, Figs 1i, j, 2c) to mostly knobs or distinct nodes (Pl. 2, Fig. 3c, d). The swellings, which are always solid, rather than tubular, may appear along the same growth line, as is evident in the holotype specimen with the undulose/ribbed margin (Pl. 1, Fig. 1f, g; Text-fig. 4G, H).

REMARKS: Lower Bashkirian species of *Cyathaxonia* have not been described from western Europe or North Africa, except for a single poorly preserved specimen from the “Middle Coal Measures” (= *Donetzoceras aegiranum* ammonite Biozone) of South Wales, identified by Smith (1931) as *Cyathaxonia* cf. *rushiana* Vaughan. Also, we cannot point to any eastern Asiatic species to have been collected from well established, Lower Bashkirian strata. Thus, *C. nodosa* fills the gap between the Lower and Upper Carboniferous species of *Cyathaxonia*.

OCCURRENCE: Kalmyus River Area, Menchugovo Village. Limestone F₁¹ (16/24-32); Kalinin Quarry. Limestone F₁¹ (16/33-43); Solenaya River Area, Novo-Troitskoe Village, Limestone F₁¹ (16/86, 206-209). Upper Mandrykinian Horizon, Blagodatiian Subhorizon, upper Lower Bashkirian.

Cyathaxonia sp.
(Text-figs 3, 6C–J)

MATERIAL: Two incomplete specimens: UAM-Tc.Don.1/81 with only the upper part of the calice remaining from thin sectioning and UAM-Tc.Don.1/95 without the tip or the calice, but with a 8.5mm-long skeletal fragment preserved. Three thin sections and four peels were prepared.

DESCRIPTION: The thin section of specimen UAM-Tc.Don.1/81 (Text-fig. 6C, D) exposes the corallite morphology near its calice floor. It cuts some septal loculi above (Text-fig. 6C, shadowed) and some below the calice floor. The n:d value 20:5.8 mm places that specimen among the widest corallites of *Cyathaxonia*

studied here (Text-fig. 3). The cardinal protoseptum, cut below the last tabula, is thinner and shorter than the adjacent major septa. The rhopaloid, inner parts of the major septa, except for the cardinal protoseptum, are in lateral continuity so that the complete circulotheca occupies almost 1/3 of their length. The counter protoseptum does not differ from the remaining major septa. The contratingent minor septa attach to the lateral surfaces of the major septa at or just above the peripheral limit of their rhopaloid parts, i.e., at about 2/3–3/4 the length of the major septa. The cardinal fossula, if present, must be shallow, short, and narrow as suggested by a transverse section. It is hardly distinguishable from septal loculi occupied by tabulae in the Position II of Sutherland (1965). The columella occupies only 1/9 of the corallite radius, being one of the narrowest among the known specimens of *Cyathaxonia*. These sets of characters suggest a separate species status for this specimen. Thus, it is here briefly described and illustrated, but not named.

The external surface of corallite UAM-Tc.Don.1/95 resembles that of specimens of *C. nodosa* sp. nov. with weakly developed protuberances on interseptal ridges rather than knobs (Text-fig. 6E). Also, the morphology at the earliest growth stage preserved (Text-fig. 6F) and at the early maturity (Text-fig. 6 G, H) resembles that in specimens of *C. nodosa* that have a slightly shortened cardinal protoseptum, an oval columella, and an incomplete circulotheca with a wide sclerenchymal ring. The only difference at that growth stage is that the minor septa reach rather than attach to the lateral surfaces of the major septa. However, that difference is camouflaged by the sclerenchyme and is hardly recognizable at a low magnification. The n:d value of that corallite (Text-fig. 3) differs slightly from that of both the largest specimens and the mean value of *C. nodosa*.

The advanced mature growth stage, exposed by a section made just below the calice floor (Text-fig. 6I, J), with n:d mean value 18:6.0 mm, differs distinctly from all previously described species of *Cyathaxonia* in that almost all of the minor septa are free, slightly rhopaloid, and reach less than 1/2 the corallite radius. Only the counter-lateral minor septa are attached to the counter protoseptum to form a triad, and 2–3 minor septa adjacent to the latter remain contratingent at that growth stage. The length of the cardinal protoseptum, the distal end of which is thin, is only approximately 1/3 the corallite radius. It is shorter than the adjacent minor septa. The counter protoseptum does not differ from the adjacent major septa. The rhopaloid thickenings of the latter are oval in shape with the inner margins terminating at the 6 mm-wide columella. The pe-

ripheral parts of these thickenings grade smoothly into the thin middle parts of major septa. The circulotheca is mainly complete with narrow sclerenchymal infillings. The columella and the circulotheca together occupy approximately 1/3 of the corallite diameter. The major and the minor septa are strongly expanded at the periphery to form the septotheca.

The free minor septa are the most important distinctive character of the corallite described, whereas the remaining characters could be included in the intraspecific variability of *C. nodosa*. The shape of the inner margins of the major septa and the columella, which is narrower than in any specimen of the latter species, are the only remaining major differences. However, the free minor septa are perhaps different enough for distinction of a new genus, not proposed here for a single, incomplete specimen.

OCCURRENCE: UAM-Tc.Don.1/81 – Kalmyus River Area, Menchugovo Village. Limestone F₁¹ (16/24–32); Kalinin Quarry. Limestone F₁¹ (16/33–43); UAM-Tc.Don.1/95 – Solenaya River Area, Novo-Troitskoe Village, Limestone F₁¹. Upper Mandrykinian Horizon, Blagodatiian Subhorizon, upper Lower Bashkirian.

Family Stereophrentidae Fomichev, 1953
Genus *Barytichisma* Moore and Jeffords, 1945

TYPE SPECIES: *Barytichisma crassum* Moore and Jeffords, 1945.

Synonyms:

? e.p.1953. *Thecophyllum* Fomichev, p. 175.

? 1986. *Eoamplexocarinia* Wang and Yu, p. 662.

EMENDED DIAGNOSIS: Slightly curved conico-cylindrical Stereophrentidae with thick external wall; major septa pinnately arranged and axially confluent in early stages, radially arranged and amplexoid at maturity; cardinal protoseptum shortened; cardinal fossula distinct; counter protoseptum slightly longer than or equal to adjacent major septa; tabularium uniform; microstructure of septa trabecular.

REMARKS: All of the main diagnostic characters of the genus, except for the microstructure, were described and illustrated by Moore and Jeffords (1945). Unfortunately, the unpublished revision by one of us (JF) of the type material was based exclusively on specimens and peels; thin sections that might have established the microstructure were impossible to make.

Weyer (1965) and Sando (1965) independently revised another species of *Barytichisma*, i.e., *Amplexus zaphrentiformis* White 1876. Based on those studies and a detailed description by Sando (1975) of *Zaphrentis* (= *Barytichisma*) *amsdenensis* Branson and Greger 1918 on the ontogeny and variability within individual species of *Barytichisma*, that genus can be considered well established.

In contrast to Sando (1965), who did not mention possible members of *Barytichisma* outside North America, Weyer (1965) included the Donets Basin *Thecophyllum* Fomichev, 1953 in the synonymy with that genus. He even included (with a question mark) one of Fomichev's (1953) specimens in *Barytichisma zaphrentiforme*. Indeed, the specimen he selected bears some characters of immature *Barytichisma*. The problem is, however, that several Upper Viséan to Moscovian taxa are similar in their neanic growth by possessing a long cardinal protoseptum and a strongly accentuated alar pseudofossulae. Some of those taxa also possess slightly amplexoid major septa which are generally shortened in the axial area both beneath and above a tabula. *Amplexizaphrentis* Vaughan, 1906 is best known among such taxa. Thus, we do not accept Weyer's (1965) re-identification of that Fomichev's specimen.

Fedorowski (2009c, in his discussion on *Axisvacuus*) provisionally accepted the original description of the holotype of *Thecophyllum lebedevi* Fomichev, 1953 of shortening of the cardinal protoseptum at maturity. That position is followed here and a part of that genus was included, with restriction, in the synonymy of *Barytichisma*, whereas some paratypes of that species were considered members of *Axisvacuus* (Fedorowski 2009c, p. 285) and were left aside this discussion.

The differences in the microstructure between *Amplexizaphrentis* Vaughan, 1906 and *Barytichisma*, discussed in detail by Weyer (1965), are omitted from consideration herein. Judging from the descriptions by Weyer, supported by his own illustrations, there were diagenetic alterations but not original microstructures showing differences between species and genera.

Weyer (1965, p. 455) described the microstructure of septa in *B. zaphrentiforme* as "typically lamellar with a dark middle line, corresponding to that described by Kato (1963) as fibro-normal or fibro-lamellar" (roughly translated here from German). Enlarged illustrations (Weyer 1965, pl. 2:2a,b) exhibit diagenetic alterations in both the external wall, probably septothecal in the origin, and the major septa. Primary parts of the latter ("dunkelem Medianstreif" of Weyer 1965, p. 455) are irregular with a few bunches of crystalline fibrils elongated into the stere-

oplasmic sheets. Those bunches may be remnants of diagenetically altered trabeculae, but the microstructure cannot be considered truly known. Sando (1965) did not study the microstructure in specimens he restudied, but the septothecal nature of the external walls of his specimens is obvious from his illustrations (Sando 1965, pls 2:5, 7, 8; 3:19).

Specimens included in *Barytichisma* in the present paper exhibit some diagenetic alterations (Pl. 5, Figs 1h, 2c) similar to those illustrated by Weyer (1965). Thus, their original microstructures may have been similar as well.

All species included in the genus *Barytichisma* on the basis of adequate studies possess amplexoid major septa although their shortening beneath tabulae is variously developed. Judging from the illustrations published by Moore and Jeffords (1945, text-fig. 111), of sections made close to the upper surfaces of tabulae in the holotype of the type species, *B. crassum*, that shortening apparently is weak. Paratypes of *B. crassum* and specimens identified originally as *B. callosum* Moore and Jeffords, 1945 possess obviously shortened and radially arranged major septa at maturity. *Barytichisma repletum* (Moore and Jeffords 1945, text-fig. 114c) and *Zaphrentis amsdenensis* Branson and Greger, 1918 (Sando 1975, pl. 3:123, 14), the most advanced species described prior to the present paper, exhibit distinct shortening of major septa in maturity. In the case of *B. zaphrentiforme* (White, 1876), only some corallites or restricted parts of the corallites show well-developed amplexoid morphology (e.g., Weyer 1965, text-fig. 2e; pls 1:2d; 2:1c). *Barytichisma* sp., especially the specimen UAM-Tc.Don.1/96, is the most advanced in the reduction in the length of the major septa among all species of the genus so far described (Pl. 5, Fig. 1f; Text-fig. 7D).

The strong reduction in the length of the major septa in *Barytichisma* sp. is very similar to that shown in the genus *Eoamplexocarinia* Wang and Yu, 1986, introduced by those authors for early Upper Carboniferous corals of the Dongtulinhe Group from the Jinghe Province, Xinjiang, China. The mature morphology of the holotype of the type species of that Chinese genus (Wang and Yu 1986, pl. 1:7a, b) also resembles that of the *Axisvacuus* both in the transverse and longitudinal sections. Unfortunately, early growth stages of that and other corals included in *Eoamplexocarinia* were neither described nor illustrated. Also, illustrations of specimens other than the holotype are so poor that details of the morphology are difficult to check. The length of the cardinal protoseptum, critical for distinguishing between *Barytichisma* and *Axisvacuus*, was mentioned in the original diagnosis of *Eoamplexo-*

carinia of Wang and Yu (1986) as "a little short". This can be only suspected from the illustrations provided (Wang and Yu 1986, p. 662, pl. 1:7a; 9a, b). Besides, it is uncertain whether the slightly shortened major septa illustrated by those authors in the holotypes of *E. typica* (lower in the picture) and *E. crassiseptata* (upper in the picture) are really the cardinal protosepta. We accept the first option and provisionally include *Eoamplexocarinia* in the synonymy with *Barytichisma*.

Barytichisma sp.
(Pl. 5, Text-fig. 7)

MATERIAL: Two incomplete corallites. UAM-Tc.Don.1/96 with earliest ontogeny and the calice missing. Specimen UAM-Tc.Don.1/97 consists of a partly broken calice. Both specimens are diagenetically altered, but remnants of the primary microstructure remain in some major septa. Three thin sections and eight peels were available for study.

DESCRIPTION: In the more complete specimen UAM-Tc.Don.1/96, n:d value 29:8.0–8.5 mm in the late neanic growth stage increases to 29:11.7 mm at maturity. The mean thickness of the external wall to the mean width of the tabularium in the late neanic growth stage (1:3.3) increases to 1:4.1 at maturity. Those two growth stages differ considerably in their morphology.

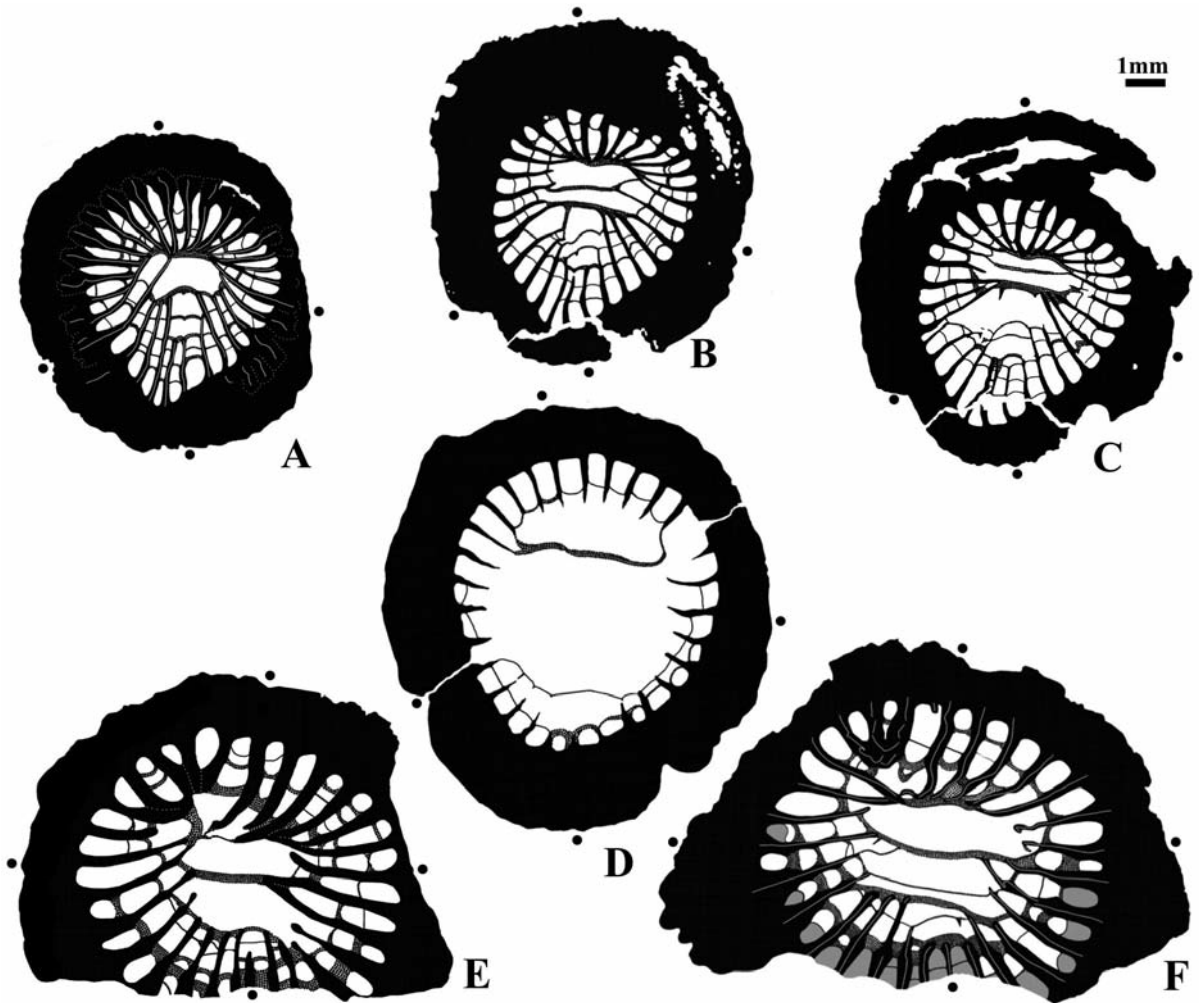
In the late neanic growth stage (Pl. 5, Fig. 1a, c–e, Text-fig. 7A–C), the arrangement of the major septa resembles that in the genus *Amplexizaphrentis* Vaughan, 1906. The major septa in the counter quadrants are slightly shorter and thicker than those in the cardinal quadrants. The former are almost equal in length, joining each other at their inner margins, forming an arch opening towards the cardinal quadrants. Their peripheral parts are thicker than those in the cardinal quadrants. The counter protoseptum is minimally longer than the counter-lateral septa. Only the last pair of major septa in the counter quadrants remain underdeveloped during the entire late neanic growth stage. The amplexoid alar septa are elongated only in earlier corallite growth (Pl. 5, Fig. 1a, c; Text-fig. 7A) and when being sectioned close to a tabula surface (compare left and right sides in Pl. 5, Fig. 1d, e; Text-fig. 7B, C). Thus, the alar pseudofossulae are not always clearly recognizable.

All major septa in the cardinal quadrants are directed towards the counter protoseptum, with their inner margins free from one another, unless connected by sections of tabulae. Their amplexoid character is ac-

centuated by differentiated length in particular transverse sections (Pl. 5, Fig. 1a, c–e; Text-fig. 7A–C). The cardinal protoseptum is less amplexoid than the remaining major septa. Thus its length varies slightly by comparison to that of adjacent major septa, and its shortening is generally not prominent. A distinct cardinal fossula widens slightly peripherally. (Pl. 5, Fig. 1d, e; Text-fig. 7B, C). The arrangement and shape of sections of tabulae, arching above the cardinal protoseptum in the ontogenetically earliest growth stage observed (Pl. 5, Fig. 1a, c; Text-fig. 7A), suggest an extension of that fossula behind the corallite axis. The fossula may extend up to the inner margins of major septa in the counter quadrants. With further growth, its length is reduced to 2/3–3/4 of the corallite radius as demonstrated by sections of tabulae, flat in the corallite axial area, free from major septa (Pl. 5, Fig. 1d, e; Text-fig. 7B, C). The minor septa are unrecognizable in the corallite lumen and the external wall at this growth stage.

At maturity (Pl. 5, Fig. 1f; Text-fig. 7D) the major septa become distinctly shortened and reduced in thickness. The cardinal protoseptum remains slightly shortened, but it is hardly recognizable because the shortest major septa in the cardinal quadrants reach only 0.25 mm in length. The cardinal fossula is unrecognizable at this growth stage (Pl. 5, Fig. 1f; Text-fig. 1D), from which it may be absent. The counter protoseptum is indistinguishable from adjacent major septa in length and thickness. The longest major septa in the counter quadrants, including the suspected counter protoseptum, reach 0.7 mm in length. The alar septa are indistinguishable from the adjacent major septa and alar pseudofossulae are absent. Connection of inner margins of some major septa by sections of tabulae make that stage very similar to *Amplexocarinia* Soshkina, 1925.

The n:d value 28:12.0 mm determined just beneath the calice in the specimen UAM-Tc.Don.1/97 closely resembles that in the specimen UAM-Tc.Don.1/96, but the morphology of the former corallite retains some juvenile characteristics, i.e., a comparatively long major septa, almost up to the calice floor slightly advanced towards a radial arrangement, and the shape of the cardinal fossula closely resembling that in the immature growth stage in the other specimen (Pl. 5, Fig. 2a, b; Text-fig. 7E, F). The slightly elongated counter protoseptum in the corallite UAM-Tc.Don.1/97 is another difference, whereas minor septa are absent from the corallite lumen, although their furrows occur on the surface. Their absence from the external wall in this and in the earlier described specimen may be apparent, resulting from an advanced



Text-fig. 7. *Barytichisma* sp. A-D – UAM-Tc.Don.1/96, Kalmyus River area, Gorbachevo Village, Gruzskaya Ravine (Balka), Limestone F₁², Upper Mandrykinian Horizon, Blagodatnian Subhorizon, upper Lower Bashkirian; A-C – neanic growth stage, D – mature growth stage; E, F – UAM-Tc.Don.1/97, mature growth stage; *Note*. Cardinal protoseptum at the bottom. Protosepta and alar septa marked by dots in transverse sections. Scale bar corresponds to all images

diagenetic damage. That supposition is to some extent supported by the morphology of the external wall of the specimen UAM-Tc.Don.1/96 (Pl. 5, Fig. 1b), but it cannot be considered as proven.

The strange shape of three major septa in the counter quadrants, left of the counter protoseptum in the picture (Pl. 5, Fig. 2a, b; Text-fig. 7E, F, upper left), is here considered pathological. It may reflect recovery from an injury or an activity of a parasitic organism. Unfortunately, the corallite is not preserved completely enough to establish a true reason for that character.

MICROSTRUCTURE AND DIAGENESIS: The microstructure in the septa has been diagenetically altered to various degrees. There is almost nothing left from the original microstructure in some septa (Pl. 5, Fig.

1h), whereas dark bunches of crystalline fibrils, interpreted here as remnants of trabeculae, remain in some septa (Pl. 5, Fig. 2c, g). They may form short chains in some major septa in which most parts have been intensely altered by diagenesis (Pl. 5, fig. 1g upper and lower, respectively). The primary microstructure of the external wall is almost completely destroyed (Pl. 5, Fig. 1b). Thus, neither connections of the major septa to the external wall, nor the occurrence of minor septa within the wall has been observed with adequate reliability.

The involvement of diagenesis was not studied by us in detail. Thus, individual steps are not described. However, the difference in the photographs taken with parallel vs. crossed nicols is important. The apparently smooth lateral surface of the major septum, as seen with parallel nicols (Pl. 5, Fig. 2c), suggest only

a moderate amount of diagenetic alteration. However, the photograph taken with cross nicols shows long calcite crystals, extending from the corallite axis well behind the boundary between the septum and the inorganic calcite (arrow in Fig. 2c), seen with parallel nicols (Pl. 5, Fig. 2d, upper left). Thus, the primary septum, the sclerenchymal sheets of that septum, and the secondary and purely inorganic infilling of the interseptal loculum underwent a common, deep recrystallization.

REMARKS: The cardinal fossula, well developed in the premature growth stages, and a permanently shortened cardinal protoseptum are the main characters distinguishing *Barytichisma* sp. from *Amplexocarinia* Soshkina, 1928 and *Axisvacuus* Fedorowski, 2009. The first of the specimens described here differs from the type species of *Barytichisma* in the extremely reduced length of the major septa at maturity and the possession of a counter protoseptum equal to that of other major septa in length and thickness. This protoseptum is more or less clearly elongated in all North American species. The second specimen described resembles the North American species more closely in both elongation of that protoseptum and in longer length of the remaining major septa.

The elongated counter protoseptum is probably absent from "*Thecophyllum*" *lebedevi* Fomichev, 1953, a species from the Donets Basin that also possesses a thick external wall although not as thick as in *Barytichisma* sp. This, as well as much more distinctly shortened major septa in *Barytichisma* sp. and some differences in the n:d value, allows differentiation between the Donets Basin species, presuming that "*T.*" *lebedevi* belongs to *Barytichisma* as discussed by Fedorowski (2009b, p. 289).

Description of two incomplete specimens, that also differ in some morphological details, may be questioned. The following reasons support our decision: (1) The specimen UAM-Tc.Don.1/96 is complete enough to demonstrate the immature and mature morphology, with the former typical for the genus and the latter totally different from that of all other known species of *Barytichisma*; (2) The second specimen closely resembles North American species in mature morphology and may appear useful for palaeogeographic reconstructions; (3) The rugose coral taxa of the *Pseudostaffella praegorskyi* or *Idiognathodus sinuosus* biozones are very rare all over the World, making every enrichment to the knowledge in that fauna valuable; (4) Further demonstration of the occurrence of *Barytichisma* in the Donets Basin is useful for the comparison of the relationship of the rugose coral

fauna from that basin to the rugose coral fauna of similar age in Texas and Oklahoma, USA.

OCCURRENCE: Kalmyus River Area, *Gorbachevo Village*, Gruzskaya Ravine (Balka). Limestone F₁² (Specimens UAM-Tc.Don.1/96, UAM-Tc.Don.1/97). Upper Mandrykinian Horizon, Blagodatnian Subhorizon, upper Lower Bashkirian.

SUMMARY

(1) This taxonomic paper is one of a series of papers leading to as complete a knowledge of the Lower Bashkirian rugose coral fauna of the Donets Basin as possible;

(2) Analysis of the main characteristics of taxa previously included in the family Cyathaxoniidae Milne Edwards and Haime, 1850 allows rejection of most of them from that family, so that the family apparently is restricted to only two taxa, *Cyathaxonia* Michelin, 1847 and *Cyathocarinia* Soshkina, 1925. This conclusion is mainly supported by the origin of the columella. This character is unique and is restricted to the many species of these genera which lived in various different environments and were present almost world-wide for more than 80MY. Such a persistent feature must be accepted as a first rank taxonomic character;

(3) Closely spaced series of thin sections prepared through the neanic growth stage has allowed confirmation of the typical rugosan increase of septa which meet at the corallite axis early in ontogeny. It also allowed recognition of the early steps of formation of the columella, which is exclusively sclerenchymal and appears independent of the septa. During the first step in the formation of the columella, tabulae-like sclerenchyme replace the inner margins of the major septa which retreat from the corallite axis. Soon after, the sclerenchyme forms a cone-shaped body. Those two steps are demonstrated by the absence of isogyre lines (= polarization brush) from the first secreted layer of crystals and their appearance approximately 0.4 mm higher;

(4) In contrast to the unique columella that allows an easy identification of specimens at the family level, identification of both genera and species is difficult. Different authors have had very different approaches to their taxonomy. The question of either synonymy or an independent status of *Cyathaxonia* and *Cyathocarinia* is left open;

(5) Two incomplete specimens, identified as *Barytichisma*, but left in open nomenclature, are included in the paper to demonstrate the wider differentiation of that mostly North American genus in Europe than previously documented. Those two specimens may represent different species.

Acknowledgements

We are indebted to Dr. Calvin H. Stevens, San Jose State University, California, USA, for discussion and linguistic corrections and to Professor Ian D. Somerville from School of Geological Sciences, University College Dublin, Ireland for his very careful critical reading and several important suggestions. We thank Mrs. Marta Bartkowiak MSC from the Institute of Geology, A. Mickiewicz University for making thin sections and peels. The accomplishment of this paper was possible due to the support of the Adam Mickiewicz University and grant 0541/p04/2001/20 of the Polish Committee of Scientific Research.

REFERENCES

- Berkowski, B. 2008. Emsian deep-water Rugosa assemblages of Hamar Laghdad (Devonian, Anti-Atlas, Morocco). *Palaeontographica. Abteilung A*, **284** (1–3), 17–68.
- Carruthers, R.G. 1913. *Lophophyllum* and *Cyathaxonia*: Revision notes on two genera of Carboniferous corals. *Geological Magazine*, n.s. **5**, **10** (2), 49–56.
- Chwieduk, E. 2005. Late Devonian and early Carboniferous Rugosa from Western Pomerania, northern Poland. *Acta Geologica Polonica*, **55** (4), 393–443.
- Faurot, L. 1909. Affinités des tétracoralliaires et des hexacoralliaires. *Annales de Paléontologie*, **4**, 69–108.
- Fedorowski, J. 1965. Lindstroemiidae and Amplexocariniidae (Tetracoralla) from the Middle Devonian of Skaly, Holy Cross Mountains, Poland. *Acta Palaeontologica Polonica*, **10**, 335–363.
- Fedorowski, J. 1987. Upper Palaeozoic rugose corals from southwestern Texas and adjacent areas: Gaptank Formation and Wolfcampian corals. Part I. *Palaeontologia Polonica*, **48**, 1–271.
- Fedorowski, J. 1997. Remarks on the palaeobiology of Rugosa. *Geologos*, **2**, 5–58.
- Fedorowski, J. 2009a. Morphogenesis and taxonomic value of the circum-axial skeleton in Rugosa (Anthozoa). *Lethaia*, **42**, 232–247.
- Fedorowski, J. 2009b. Early Bashkirian Rugosa (Anthozoa) from the Donets Basin, Ukraine. Part 1. Introductory considerations and the genus *Rotiphyllum* Hudson, 1942. *Acta Geologica Polonica*, **59** (1), 1–37.
- Fedorowski, J. 2009c. Early Bashkirian Rugosa (Anthozoa) from the Donets Basin, Ukraine. Part 2. On the genera *Axisvacuus* gen. nov. and *Falsiamplexus* Fedorowski, 1987. *Acta Geologica Polonica*, **59** (3), 283–317.
- Fomichev, V.D. 1953. Rugose corals and the stratigraphy of the Middle and Upper Carboniferous and Permian deposits of the Donets Bassin. *Trudy Vsesoyuznogo Nauchno-issledovatel'skogo Geologorazvedochnogo Instituta*. 1–622, Leningrad. [In Russian]
- Groot, G.E. de. 1963. Rugose corals from the Carboniferous of northern Palencia (Spain). *Leidse Geologische Mededelingen*, **29**, 1–123.
- Hill, D. 1981. Supplement 1, Rugosa and Tabulata. In: Teichert, C. (Ed.), *Treatise on Invertebrate Paleontology*, Part F. Coelenterata, 1–762. Geological Society of America and University of Kansas Press; Boulder, Colorado and Lawrence, Kansas.
- Hudson, R.G.S. 1943. On the Lower Carboniferous corals: *Rhopalolasma bradbournense* (Wilmore) and *Rhopalolasma rylstonense* sp. nov. *Quarterly Journal of the Geological Society of London*, **99**, 81–92.
- Hudson, R.G.S. 1944. Lower Carboniferous corals of the genera *Rotiphyllum* and *Permia*. *Journal of Paleontology*, **18** (4), 355–362.
- Hudson, R.G.S. 1945. On the Lower Carboniferous corals *Permia capax* and *P. rota* n. spp. *Proceedings of the Leeds Philosophical and Literary Society*, **4**, 285–298.
- Ivanovsky, A.B. 1987. Rugosa, described by A.A. Stuckenberg (1888-1905). Nauka, pp. 1–44. Moskva. [In Russian]
- Kato, M. 1963. Fine skeletal structures in Rugosa. *Journal of the Faculty of Sciences, Hokkaido University, Series 4 Geology and Mineralogy*, **11**, 571–630.
- Khoa, N.D. 1977. Carboniferous Rugosa and Heterocorallia from boreholes in the Lublin Region (Poland). *Acta Palaeontologica Polonica*, **22**, 301–404.
- Kossovaya, O.L. 2007. Ecological aspects of upper Carboniferous – lower Permian ‘*Cyathaxonia* Fauna’ taxonomic diversity (the Urals). In: Hubmann, B and Piller, W.E. (Eds), *Fossil corals and Sponges*, Proceedings of the 9th International Symposium on Fossil Cnidaria and Porifera, Graz, 2003. *Österreichische Akademie der Wissenschaften, Schriftenreihe der Erdwissenschaftlichen Kommissionen*, **17**, Vienna, 383–405.
- Moore, R.C. and Jeffords, R.M. 1945. Description of Lower Pennsylvanian corals from Texas and adjacent states. *University of Texas Publications*, **4401**, 77–208.
- Rodríguez, S. 1984. Corales rugosos del Carbonifero del este de Asturias. Ph.D. thesis published by Departamento de Paleontología, Universidad Complutense de Madrid. Doctoral theses collection no. 109/84, 1–328.
- Rodríguez, S. and Kullmann, J. 1990. Hornförmige Einzelkorallen (Rugosa) aus spätoberkarbonischen

- Flachwasser-Ablagerungen des Kantabrischen Gebirges (Nordspanien). *Palaeontographica, Abteilung A*, **210**, 19–40.
- Rodríguez, S. and Kullmann, J. 1999. Rugose corals from the upper member of the Picos de Europa Formation (Moscovian, Cantabrian Mountains, NW Spain). *Palaeontographica, Abteilung A*, **252** (1–3), 23–92.
- Rózkowska, M. 1969. Famennian tetracoralloid and heterocoralloid fauna from the Holy Cross Mountains (Poland). *Acta Palaeontologica Polonica*, **14** (1), 1–187.
- Sando, W.J. 1965. Revision of some Paleozoic coral species from western United States. *U.S. Geological Survey Professional Paper*, **503-E**, 1–39.
- Sando, W.J. 1975. Coelenterata of the Amsden Formation (Mississippian and Pennsylvanian of Wyoming). *U.S. Geological Survey Professional Paper*, **848-C**, C1–C31.
- Sando, W.J. 1977. The status of coiled protocoralla in some Mississippian horn corals. *Palaeontology*, **20** (1), 47–58.
- Scrutton, C.T. 1971. Palaeozoic coral faunas from Venezuela. I. Silurian and Permo-Carboniferous from the Mérida Andes. *Bulletin of the British Museum (Natural History). Geology*, **20** (5), 183–227.
- Smith, S. 1931. Some Upper Carboniferous corals from South Wales. *Summary of Progress of the Geological Survey for 1930*, **3**, 1–13.
- Soshkina, E.D. 1925. Les coraux du Permien inférieur (étage d'Artinsk) du versant occidental de l'Oural. *Bulletin de la Société des Naturalistes de Moscou, Section Géologique*, **33**, 76–104.
- Stuckenberg, A.A. 1895. Corals and bryozoans from the Carboniferous deposits of the Urals and Timan. *Trudy Geologicheskogo Komiteta*, **10**, 1–244. [In Russian and German]
- Sutherland, P.K. 1965. Rugose corals of the Henryhouse Formation (Silurian) in Oklahoma. *Oklahoma Geological Survey, Bulletin* **109**, 1–92.
- Vaughan, A. 1906. Faunal lists and account of the faunal succession and correlation. In: C.A. Matley and A. Vaughan, The Carboniferous rocks at Rush (County Dublin). *Quarterly Journal of the Geological Society of London*, **62**, 295–322.
- Wang Zhengji and Yu Xueguang 1986. Early Late Carboniferous rugose corals from Jinghe of Xinjiang. *Acta Palaeontologica Sinica*, **25** (6), 662–677.
- Weyer, D. 1965. Über *Amplexus zaphrentiformis* White, 1876 (Pterocorallia, Oberkarbon, Pennsylvanian). *Geologie*, **14** (4), 449–463.
- Weyer, D. 1972. Zur Morphologie der Rugosa (Pterocorallia). *Geologie*, **21** (6), 710–737.
- Weyer, D. 1980. Zur Kenntnis seltener Petraiidae (Anthozoa, Rugosa) aus dem amerikanischen Obersilur. *Zeitschrift für geologische Wissenschaften*, **8** (9), 1209–1216.
- Weyer, D. 1993. Korallen aus dem Obertournai und Unter-visé der Inseln Hiddensee und Rügen. *Abhandlungen und Berichte für Naturkunde*, **16**, 31–69.
- Weyer, D. 2001. *Muenstraia*, ein neues Rugosa-Genus (Anthozoa) aus dem Obersilur und Unterdevon. *Mitteilungen aus dem Museum für Naturkunde in Berlin, Geowissenschaftliche Reihe*, **4**, 71–82.
- Weyer, D. 2005. *Antilacca*, ein neues Rugosa-Genus aus dem mitteleuropäischen Unterdevon. *Abhandlungen und Berichte für Naturkunde*, **28**, 5–21.

Manuscript submitted: 18th May 2010

Revised version accepted: 15th March 2011

PLATES 1-5

PLATE 1

Cyathaxonia nodosa sp. nov.; Kalmyus River area

- 1** – UAM-Tc.Don.1/79, holotype, Menchugovo Village, Limestone F₁, Upper Mandrykinian Horizon, Blagodatnian Subhorizon, upper Lower Bashkirian, transverse thin sections, except when stated. 1a-e – early to late neanic growth stage; 1f – early mature growth stage; 1g, h – mature growth stage; 1i, j – external view showing nodular interseptal ridges.
- 2** – UAM-Tc.Don.1/80, paratype, Novo Troitskoe Village, stratigraphic position as the holotype. 2a, b, d, e – transverse thin sections, mature growth stages with protuberances on some septa (2d, 2e enlarged); 2c – external view showing nodular interseptal ridges.
- 3** – UAM-Tc.Don.1/94, paratype, locality and horizon as above, transverse thin section, mature growth stage, beneath calice floor in most loculi.

Cardinal protoseptum at the bottom. Protosepta and alar septa marked by dots. Scale bars located between two adjacent pictures correspond to both; those right to the picture correspond only to it

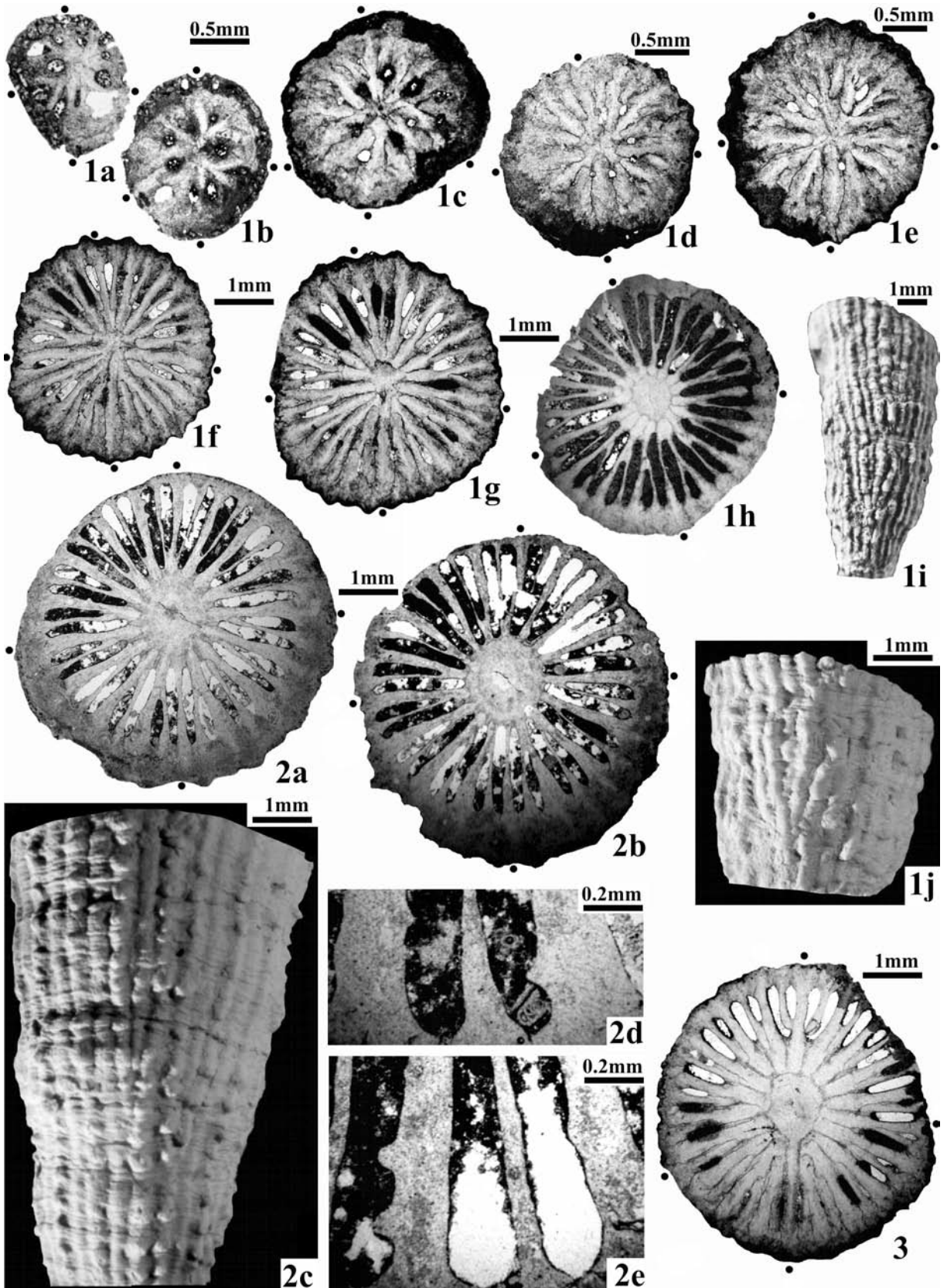


PLATE 2

Cyathaxonia nodosa sp. nov.; paratypes, Kalmyus River area

- 1 – UAM-Tc.Don.1/82, locality and horizon as the holotype. 1a, b – transverse thin sections, mature growth stage; 1c – longitudinal thin section.
- 2 – UAM-Tc.Don.1/83, Novo Troitskoe Village, stratigraphic position as the holotype, external view of early growth stage. Strongly nodular interseptal ridges present only above tip.
- 3 – UAM –Tc.Don.1/84, locality and horizon as the holotype. 3a – late neanic growth stage; 3b – mature growth stage, above calice floor in most loculi; 3c, d – external view showing strongly nodular interseptal ridges; 3d enlarged to demonstrate relationships of nodules to growth lines.
- 4 – UAM-Tc.Don.1/85, locality and horizon as the holotype, transverse thin section, mature growth stage, above calice floor in loculi of counter quadrants.
- 5 – UAM –Tc.Don.1/86, Novo Troitskoe Village, stratigraphic position as the holotype, transverse thin sections. 5a – mature growth stage; 5b – protuberances on some septa.

Cardinal protoseptum at the bottom. Protosepta and alar septa marked by dots. Scale bars located between two adjacent pictures correspond to both; those right to the picture correspond only to it

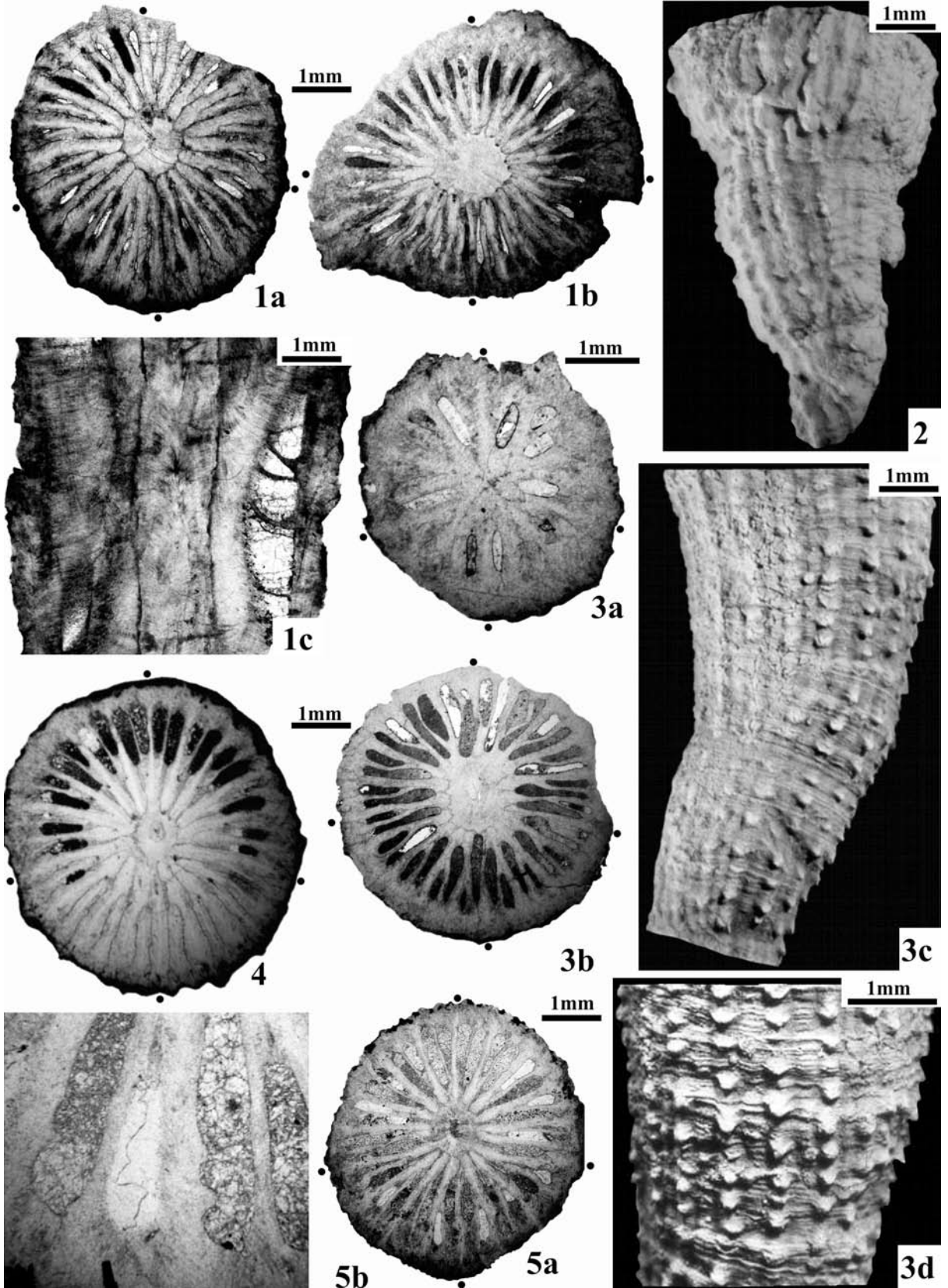
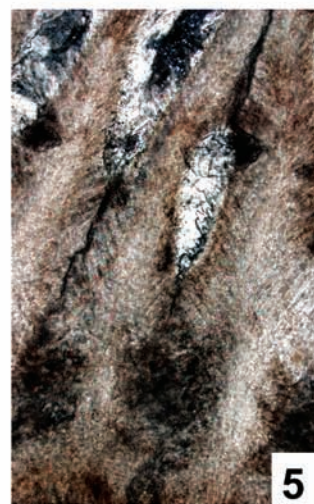
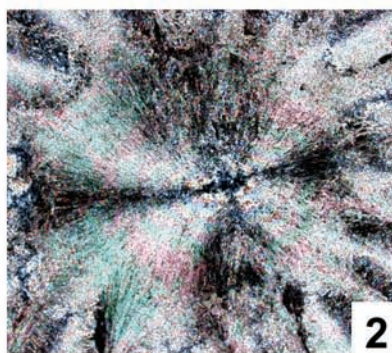
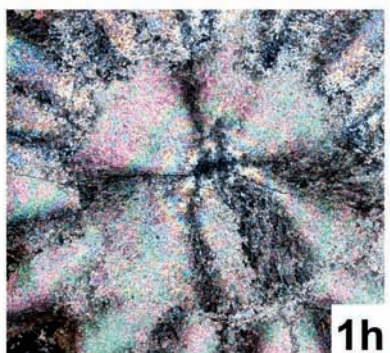
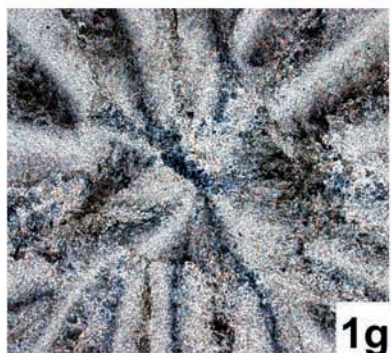
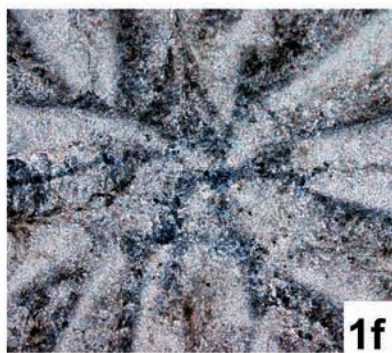
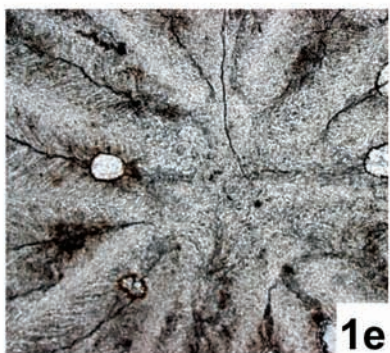
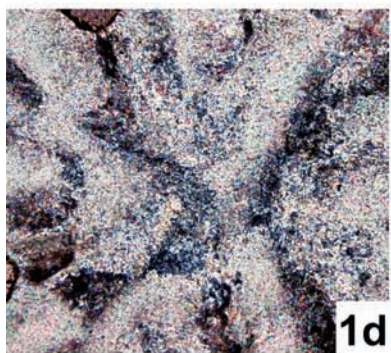
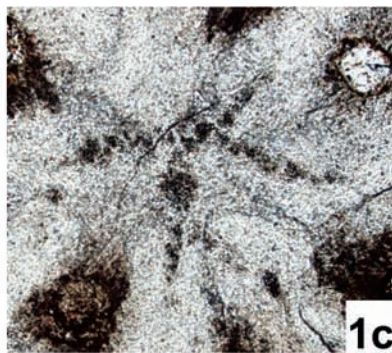
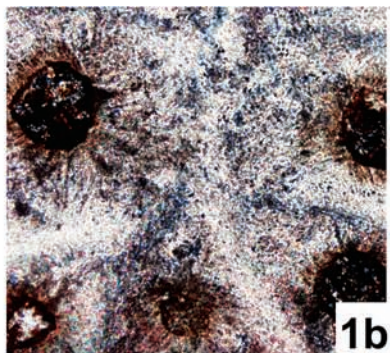
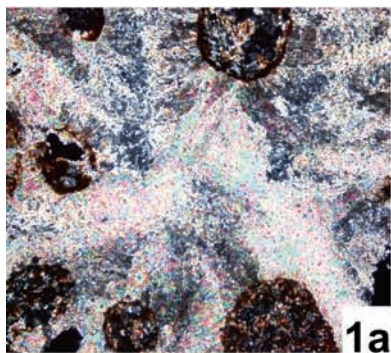


PLATE 3

- 1-4** – *Cyathaxonia nodosa* sp. nov.; 1 – UAM_Tc.Don.1/79, holotype. 1a-e – early to late mature growth stage; major septa approach corallite axis; note rudiments of fine trabeculae in 1c and slight retreat of some major septa from corallite axis in 1e (compare Pl. 1, Fig. 1a-e; Text-fig. 1A-F); 1f – early mature growth stage; beginning of conical columella shown by deformed isogyre lines (= Pl. 1, Fig. 1f = Text-fig. 1G); 1g – mature growth stage; narrow columella, but isogyre lines (=crystallization brush) easily recognizable (= Pl. 1g, Fig. 1g = Text-fig. 1H); 1h – mature growth stage, lower part of calice; columella remains comparatively narrow. 2 – UAM-Tc.Don.1/86, paratype, mature growth stage. 3 – UAM-Tc.Don.1/87, paratype, Novo Troitskoe Village, stratigraphic position as the holotype, mature growth stage. 4 – UAM-Tc.Don.1/82, paratype, longitudinal thin section, fan-shaped arrangement of crystalline fibrils.
- 5** – *Cyathaxonia* sp., UAM-Tc.Don.1/81, Kalmyus River area, Menchugovo Village. Limestone F₁, Upper Mandrykinian Horizon, Blagodatnian Subhorizon, upper Lower Bashkirian, transverse thin section, arrangement of crystalline fibrils in strongly diagenetically altered septa resembles that in columella; primary septa unrecognizable.

Transverse thin sections, except when stated; axial parts of corallites, except Fig. 5; Crossed nicols; Horizon and locality not repeated when explained in earlier plates



0.1 mm

PLATE 4

Cyathaxonia nodosa sp. nov.

Transverse thin sections, axial parts of corallites, crossed nicols, except when stated. Paratypes. Horizon and locality not repeated when explained in earlier plates

- 1 – UAM-Tc.Don.1/84; 1a, b – late neanic growth stage, remnants of fine trabeculae. 1a – parallel nicols; 1b – turned 90° left by comparison to 1a; 1c – near the end of neanic growth stage; 1d – mature growth stage.
- 2 – UAM-Tc.Don.1/88, Novo Troitskoe Village, stratigraphic position as the holotype. 2a – early mature growth stage; remnants of fine trabeculae apparent in most major septa, columella narrow; 2b – advanced mature growth stage, columella wide, demonstrating both growth lines and crystalline fibrils.

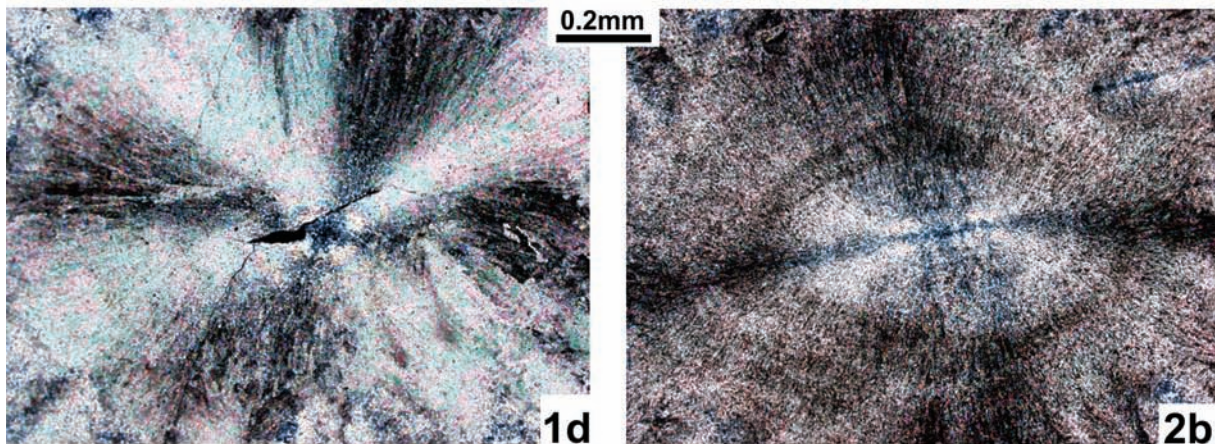
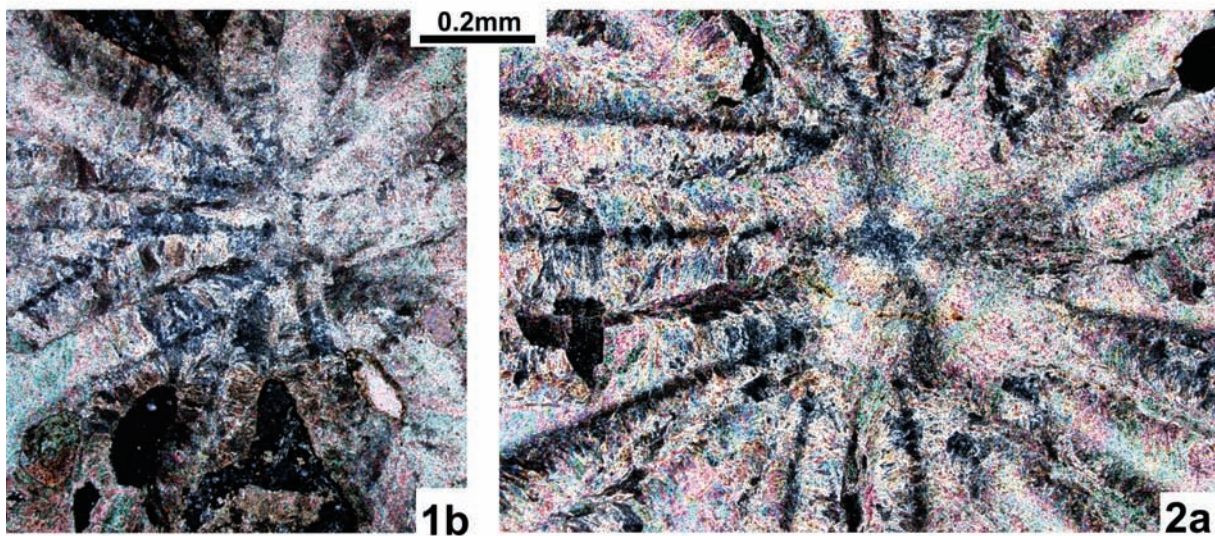
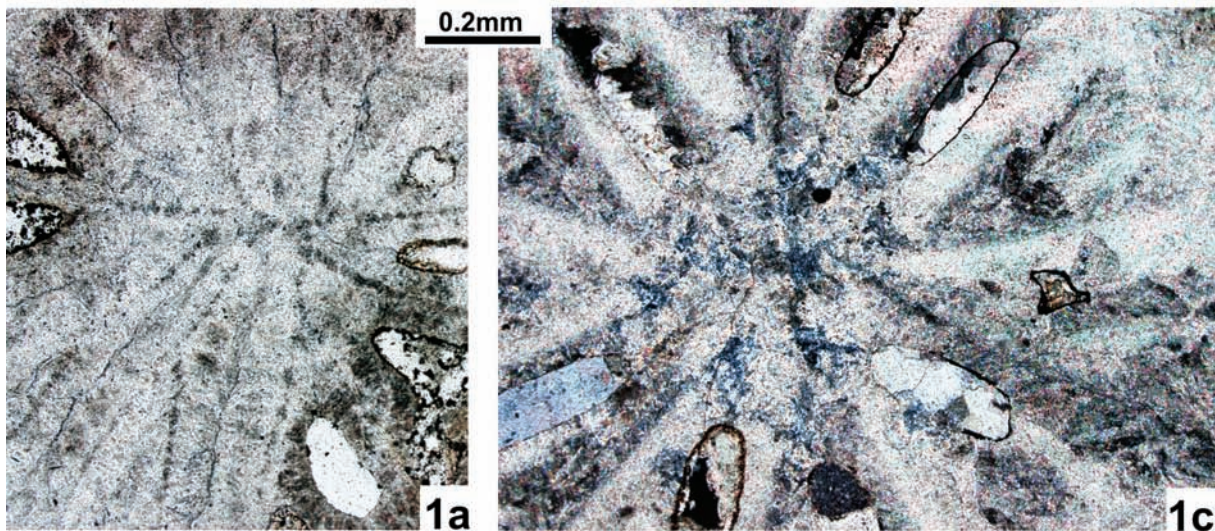


PLATE 5

Barytichisma sp. transverse thin sections

- 1** – UAM-Tc.Don.1/96, holotype, Kalmyus River area, Gorbachevo Village, Gruzskaya Ravine (Balka), Limestone F₁², Upper Mandrykinian Horizon, Blagodatnian Subhorizon, upper Lower Bashkirian. 1a, c-e – successive sections of neanic growth stage; 1b – part of fig. 1a (arrow) enlarged to show diagenetic alteration of septa and external wall; 1f – mature growth stage; 1g, h – major septa documenting differentiated diagenetic alterations (parallel nicols).
- 2** – UAM-Tc.Don.1/97, locality and horizon as above. 2a, b – mature growth stage; 2c, d – major septum documenting differentiated diagenetic alterations (c – parallel, d – crossed nicols).

Cardinal protoseptum at the bottom. Protosepta and alar septa marked by dots. Scale bars located between two adjacent pictures correspond to both; those right to the picture correspond only to it

