Early Bashkirian Rugosa (Anthozoa) from the Donets Basin, Ukraine. Part 1. Introductory considerations and the genus *Rotiphyllum* Hudson, 1942

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ABSTRACT:

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The present paper is the first in a series devoted to the Early Bashkirian Rugosa (Anthozoa) from the Donets Basin. The history of investigation and current status of Early Bashkirian stratigraphy is discussed in the context of the Donets Basin strata. Corals of that time interval are extremely rare worldwide and those from the Donets Basin have never been described in detail. Four of the five species described are new: *Rotiphyllum asymmetricum* sp. nov., *R. latithecatum* sp. nov., *R. simulatum* sp. nov., and *R. voznesenkae* sp. nov. Two species are left in open nomenclature. The synonymy, species content and critical review of species potentially belonging to the genus *Rotiphyllum* are reviewed.

Key words: Rugosa (Anthozoa); *Rotiphyllum*; Systematics; Early Bashkirian; Donets Basin, Ukraine.

INTRODUCTION

Rugose corals, diverse and widespread in the Late Viséan, became greatly impoverished during the Serpukhovian and disappeared from most areas of the world in the *Homoceras, Reticuloceras* and early *Gastrioceras* zones. The Donets Basin (Ukraine), the Cantabrian Mountains (northern Spain), restricted areas in North Africa, western North America and South China hosted the rugose coral survivors and newcomers appearing in the latter zones. Thus the Early Bashkirian Rugosa are of special value for the Pennsylvanian Carboniferous–Permian cycle of rugose coral evolution (Fedorowski 1981).

Despite the relative taxonomic diversity of the early Bashkirian Rugosa in the Donets Basin, only five species and two forms left in open nomenclature were described from that area so far (Fomichev 1953; Vass-ilyuk 1960). A few other Bashkirian species from the basin were listed and/or illustrated by Vassilyuk (1960, 1975; in Ayzenverg *et al.* 1983, 1987; in Poletaev *et al.* 1990) and Vassilyuk and Polyakova (in Poletaev *et al.* 1988). The present paper is the first in a series devoted to a monographic treatment of the Early Bashkirian Rugosa from the Donets Basin.

All specimens studied were collected during many years by Dr. N.P. Vassilyuk, Professor Emeritus of the Donets Polytechnic. She also provided stratigraphical and geographical data included in the labels of individual specimens, and made preliminary identifications of some species. She will co-author those subsequent papers of the series in which her preliminary identifications are confirmed. A few specimens, all belonging to one species, were provided by Dr. V. Ogar, from the Kiev State University. He will co-author the paper dealing with his material.

Only the collecting areas, such as villages and/or ravines (Balka), but not the exact localities of particular specimens are mentioned in the Occurrences and shown in Text-figs 1–4. Such an approach to the material resulted from the absence of detailed lithological sections of individual ravines. Fortunately, only one intercalation of a given limestone occurs in particular ravines, allowing an adequate location of individual specimens studied.

The geological setting, described in the present paper, will not be repeated in subsequent papers unless new important data appear. The locality register and lists of species derived from individual localities will be published in the final paper of the series.

Genera and species described in particular papers included in the series are discussed in detail, whereas remarks on families are introduced only when necessary. The synonymy and species content is provided for each genus. None of those is complete. The incompleteness resulted from the uncertain taxonomic positions of quite a few taxa, revision of which was impossible for the purpose of this paper. Synonymies of taxa are questioned when the illustrations do not allow a satisfactory identification.

In the section 'Species included', generic names from the original descriptions are given. Subsequent descriptions of particular species are not mentioned when their identifications are accepted, whereas species names applied to specimens morphologically different from the types are listed with the names of their authors. Thus, lists of synonyms include more items than the section 'Species included'. Species left in open nomenclature are omitted from both lists.

Depository of all specimens studied: Institute of Geology, A. Mickiewicz University in Poznań, Poland. Collection number: UAM-Tc.Don.1.

HISTORY OF THE BASHKIRIAN STAGE AND ITS LOWER LIMIT

The name 'Bashkirian' was first introduced by Semikhatova (1934), who investigated the middle Carboniferous deposits of the Povolzhe area. She established the difference between Moskovian deposits of the Moscov Basin and those of her study area and found the latter to be stratigraphically older. Thus, she divided the middle Carboniferous into two parts. The lower part she referred to as the 'Bashkirian beds', with its type section established in the Mountainous (Gornaya) Bashkiria, in the South Urals. Throughout this and subsequent papers the terms lower, middle and upper Carboniferous are used when referring to the traditional three-fold Russian subdivision of the System, and terms Mississippian and Pennsylvanian in the case of reference to the standard subdivision.

Rotai (1944) agreed with Semikhatova's (1934) general idea, but he considered the faunal content of the Bashkirian type section inadequate for characterization of the stage and also that the lower and upper boundaries were uncertain. He therefore proposed the Donets Basin succession, namely the part that begins with the bottom of Limestone Group F_1 and ranges to the top of Limestone K_3, as the type section of the lower Middle Carboniferous, and named it the Kayalskian Stage. The concept of Rotai (1944) was not widely accepted. Also not accepted was his correlation of the Kayalskian Stage with Western European Westphalian A + B. Nevertheless, Nemyrovska (1999) regarded the Kayalskian as the equivalent of the Cheremshansky and Melekessky horizons of the Russian Platform (in her nomenclature), while Menning *et al*. (2006) equated it with the standard Russian Arkhangelskian Stage. The lower and upper limits of the Kayalskian accepted by those authors (Limestones G_1 and K_2) respectively disagreed with those proposed by Rotai (1944). Menning *et al*. (2006) correlated the Kayalskian Horizon with the Langsettian (Westphalian A) and the lower part of the Duckmantian (Lower part of Westphalian B), which also disagrees with the original concept of Rotai (1944). Neither of those boundaries is truly precise. Nevertheless the Kayalskian Horizon is tentatively accepted herein and is shown in Table 1 with the boundaries sug-


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

Text-fig. 2. Vicinity of the town of Donets. Generalized positions of individual Limestones (D to N). Carboniferous deposits left in white. Provided by Dr. N.P. VASSILYUK
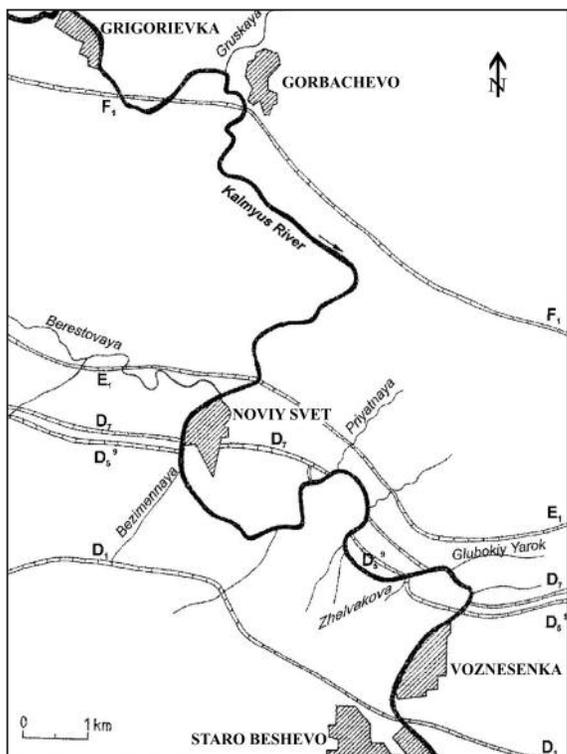
Text-fig. 3. Outcrops in the Starobeshevo Village area, south of the town of Donets. Locations of ravines (balka) exposing Limestones D to F. Provided by Dr. N.P. Vassilyuk
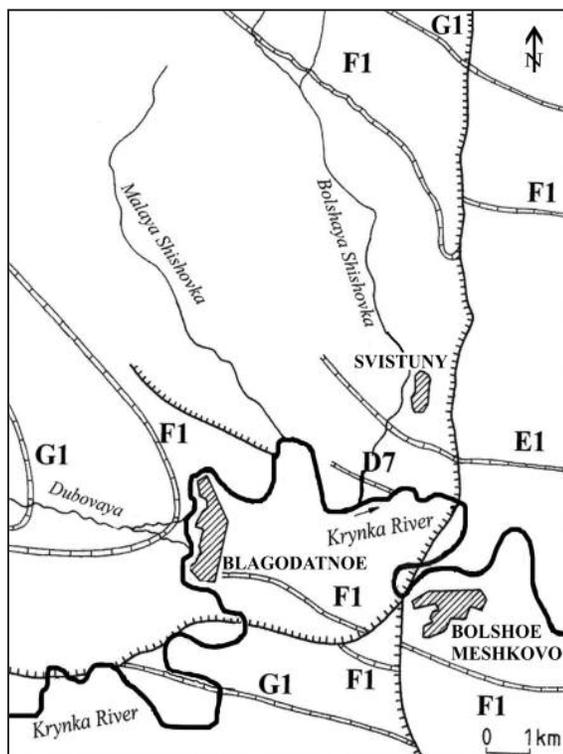
Text-fig. 4. Outcrops along Krynka River and its tributes, east of the town of Donets. Tectonically affected Limestones D to G. Provided by Dr. N.P. Vassilyuk

Distribution of *Rotiphyllum* species

Column headers:

Global			Central & West Europe		Russia		Ukraine		Biozonation		
Series	Stage	Time	Stage	Substage	stand. Stage	c. Substage	Horizon	Subhorizon	Limestone	Ammonitida	Foraminiferida	Conodonta

Stratigraphic content (PENNSYLVANIAN / BASHKIRIAN):

- **WESTPHALIAN** — Duckmantian (B), Langsettian (A)
- **NAMURIAN** — Chokier./Alportian (A), Kinderscoutian (B), Marsdenian (B), Yeadonian (C)
- **BASHKIRIAN** — Syuranian (A D_5^8–D_8; E_1^0–E_7), Krasnopolyanian, Severokel., Mandrykinian, Akavasskian (Askynba., Prikamian), Arkhangelskian (Cheremshanskian, Melekesskian)
- Russia stages: Voznesenskian, Feninian, Manuilovian (E_8–F_2), Blagodatnian, Zujevian (G_1–H_3), Kayalskian, Makejivkian (H_4–I_1), Krasnodonian (I_2–K_1)

Biozonation — Ammonitida:
- Homoceras – Hudsonoceras
- Reticuloceras – Bashkortoceras
- Bilinguites – Cancelloceras
- Branneroceras – Gastrioceras
- Diaboloceras – Axinolobus

Biozonation — Foraminiferida:
- Plectostaffella bogdanovikensis
- Semistaffella variabilis – S.minuscularia
- Pseudostaffella antiqua
- P.praegorskyi – Staffel. staffel.
- Profusulinella primitiva – Pseudostaffella gorskyi
- Profusulinella rhombiformis
- Verella spicata – Aljutovella tikhonovitchi

Biozonation — Conodonta:
- Declinognathodus noduliferus
- Idiognathoides sinuatus
- Neognathod. askynensis
- Idiognathodus sinuosus
- Declinognathodus marginodosus

Species ranges:
- *R.voznesenkae* (D_7)
- *R. abnormae* (E_1^{IV}–G_1)
- *R. asymmetricum* (E_1^{IV}–G_1)
- *R.latithecatum* (F_1)
- *R.simulatum* (G_{1-4})
- *Rotiphyllum* sp.2 (F_1)
- *Rotiphyllum* sp.1 (G_1)

Time scale: 312–320 Ma

Table 1. Litho- and biostratigraphic schemes of the Bashkirian Stage in Eastern Ukraine with references to the Russian and western European standards, and the vertical ranges of the *Rotiphyllum* species studied. Abbreviations: Chokier. – Chokierian, *Neognathod. – Neognathodus, P – Pseudostaffella, S. – Semistaffella,* Severokel. – Severokeltmenian, *Staffel. staffel. – Staffelleformes staffelleformis*

gested by Nemyrovska (1999) and Menning *et al*. (2006) because the present paper is not devoted to a revision of Bashkirian stratigraphy.

In January 1974, the Interdepartmental Stratigraphical Committee of the former USSR lowered the base of the Bashkirian Stage to the base of the *Reticuloceras* Zone and introduced a new stage, the Serpukhovian Stage, as the top unit of the Lower Carboniferous. The stratotype of the Bashkirian was eventually proposed by Semikhatova and Einor (1977) along the Askyan River in the former type area, i.e. the South Urals of Bashkiria. A modified concept of the Bashkirian Stage was then accepted by the 1978 International Carboniferous Congress. The research effort of Russian geologists and scientists from other countries who co-operated with them was since then focused mostly on a detailed study of the South Urals sections.

The base of the Bashkirian Stage was shifted down again by the Subcommission of Carboniferous Stratigraphy in 1983 in order to synchronize the lower/upper Carboniferous boundary in Europe with the Mississippian/Pennsylvanian boundary in North America. That new boundary corresponds to the Arnsbergian/Chokierian or the *Eumorphoceras/Homoceras* boundary in the ammonoid zonation of the Western and Central European Namurian. It also approximates the boundary between the Staroutkinskian or Yuldybaevskian (Kulagina and Pazukhin 2002) and Bogdanovskian substages in the South Urals, and the boundary between the Zapaltyubian and Voznesenskian substages in the Moscov and Donets Basins.

This newly proposed definition of the base of the Bashkirian Stage corresponds approximately to the entry of the conodont *Declinognathodus noduliferus*. However, according to Kullmann and Nikolaeva (2002, p. 781) (confirmed by Professor J. Kullmann, written communication, November 2003), this conodont species is facies-controlled and its appearance may be diachronous. The first appearances of *Homoceras* and *D. noduliferus* differ in several areas and therefore boundaries based on these two biomarkers are not equivalent. Titus *et al*. (1997), who first found homoceratids in North America (Nevada), established the entry of *Isohomoceras subglobosus* slightly below the first appearance of *D. noduliferus*. The lower limit of the Bashkirian is thus differently treated by conodont and ammonoid specialists. The differences in the placing of this boundary are very slight and do not significantly affect the distribution of the rugose corals. However, the most recent correlation charts, i.e., Menning *et al*. (2006) and Kossovaya *et al*. (2006), differ in the placement of the Serpukhovian/Bashkirian boundary in Central Russia and the Donets Basin. The former authors extended the up-

per limit of the Serpukhovian to the upper limit of the Voznesenskian, whereas the latter authors included that substage in the Bashkirian. The latter concept is accepted herein (Table 1).

Since the Southern Urals, but not the Donets Basin, is the type area for the Bashkirian, the stratigraphical subdivision of the Southern Urals succession must be taken into account in the interpretation of the equivalent succession in the Donets Basin. Unfortunately, the proposal by Kulagina and Pazukhin (2002) is difficult to apply to the Donets Basin strata irrespective of the fossil group used. In addition, the ammonoid-based correlation with the Western European substages is imprecise. Thus, the boundaries indicated in tables published by Nemyrovska (1999) and Fedorowski and Vassilyuk (2001) should be treated as preliminary. The same will most probably be true for Table 1 herein. Controversies concerning the chronological ranges of individual substages and biozones, as well as the differently treated correlation of individual substages, etc., present in the most recent summaries (Meanning *et al*. 2006; Kossovaya *et al*. 2006) leave no doubt that the Bashkirian stratigraphical framework needs many further adjustments. Such obvious errors as the position of the Akavasskian Substage above the Askynbashian Substage in fig. 3 of Menning *et al*. (2006) emphasizes the urgent need for such a revision. In view of this uncertainty, three subdivisions, namely the Russian standard, the central Russia and the Ukrainian, plus the approximate ranges of the ammonoid, foraminiferal and conodont biozones, are included in Table 1 in order to minimize misunderstandings.

Of the ammonoid, foraminifera and conodont biozonations used for standard correlations, the ammonoid zonation was found to be the most constant, albeit the ranges of the ammonoids are differently interpreted by different authors (see discussion below). Thus, the ammonoid zonal scheme is accepted here as primary, with the foraminiferal zonation being supplementary and the limits of the conodont zones treated as approximate in comparison with the limits of both the ammonoid and foraminiferal zones. The biozonations are omitted from fig. 3 of Menning *et al*. (2006), whereas Kossovaya *et al*. (2006) repeated the ammonoid, foraminiferal and conodont zonations in the standard part of their table 4.8, but omitted ammonoids from most of the regional biostratigraphic subdivisions, based mainly on the Foraminifera, Conodonta and Rugosa, with some other groups of fossils added where available.

The question of the base of Bashkirian was discussed above. The different concepts of the base of the *Reticuloceras* zone by Ruzhencev and Bogoslavskaya (1978), on the one hand, and by Ramsbottom and Saunders (1985), followed by Kullmann (2002), Kullmann and

Nikolaeva (2002), on the other, is the next question. In this paper the opinion of the latter authors is accepted, i.e. the *Homoceras-Hudsonoceras* Zone is extended to the upper limit of the Alportian. The range of *Declinognathodus noduliferus* postulated by Nemyrovska (1999) for the Donets Basin seems to be correlative with such a limit.

The above solution allows the Voznesenskian Subhorizon in the Donets Basin to be equated with the Chokieran–Alportian substages, i.e. the *Homoceras-Hudsonoceras* Zone. Such a solution was already accepted by Nemyrovska (1999), by Fedorowski and Vassilyuk (2001) and indirectly by Kullmann and Nikolaeva (2002) and is followed in the present paper. It makes the Voznesenskian Subhorizon an approximate equivalent of the Bogdanovskian Substage in the South Urals, with the limits mentioned above. However, the Voznesenskian equates with only the lower part of the Syuranian, when the Russian standard is considered.

The lower limit of the *Reticuloceras-Bashkortoceras* Zone is important in the context of the Limestone groups "D" and "E" yielding the rugose coral faunas. Fedorowski and Vassilyuk (2001, fig. 1) placed that lower limit at the entry of the Limestone E_1^{IV} subgroup, whereas Nemyrovska (1999) indirectly proposed to begin it with Limestone D_7^6, by making that limestone intercalation equivalent to the lower limit of the Krasnopolyanian Substage. The absence in the collection of rugose corals from the Limestones $E_1^{II, III}$ and their occurrence in Limestone E_1^{IV} was used by Fedorowski and Vassilyuk (2001) in support of their suggestion concerning the lower limit of the *Reticuloceras-Bashkortoceras* Zone. However, an interpretation based on occurrences of Rugosa cannot be decisive. The restudy by Efimenko (2006) of the Chorna Skelya (Black Rock) section allowed him to prove the identity of Limestone E_1^{I} with Limestone D_8 and the occurrence in Limestone E_1^{II} of *Eostaffella postmosquensis* and *Plectostaffella varvariensis*, typical of the Kammennogorskian Subhorizon, i.e., the upper part of the Syuranian Horizon in the Urals. Those findings allowed Efimenko (2006) to re-name the former Limestone E_1^{II} as E_1^0 and to place it at the lower limit of the Feninian Subhorizon in the Donets Basin. Efimenko's (2006) suggestions were used herein to equate the lowermost limestone intercalations of Limestone group E with the lower limit of the *Reticuloceras-Bashkortoceras* (R1) Zone (Table 1).

The upper part of the *Reticuloceras* zone and the R1/R2 boundary causes even more problems than its lower limit. It is discussed as important for the stratigraphic positions of the corals studied herein and in the subsequent papers on the Early Bashkirian Rugosa from the Donets Basin. Ramsbottom and Saunders (1985) equated the R1/R2 boundary (*Reticuloceras-Bashkortoceras/ Bilinguites-Cancelloceras*) with the beginning of the Marsdenian, whereas Ruzhencev and Bogoslavskaya (1978) and Kullmann and Nikolaeva (2002) elevated that boundary to the middle of the Marsdenian. The latter option opens the question of the upper limit of the Kamennogorskian Substage from the South Urals and its correlation with both the Krasnopolyanian and the Severokeltmenian substages in central Russia and the Western European stages. The position of Kullmann and Nikolaeva (2002) is therefore not accepted in this paper for the time being and the *Bilinguites-Cancelloceras* biozone is accepted as shown in Table 1 with the proviso that the correlation of individual substage boundaries be considered approximate. The *Reticuloceras-Bashkortoceras* ammonoid Zone in such a situation equates only with the Kinderscoutian in western and central Europe and its approximate equivalents in Russia and the Donets Basin as shown in Table 1.

According to Nemyrovska and Alekseev (1994) and Nemyrovska (1999), the Severokeltmenian and Prikamian substages equate with the Akavasskian and Askynbashian substages in the South Urals respectively. A similar position was accepted in Russia as standard, except for a much shorter temporal extension of the latter (Kossovaya *et al.* 2006, table 4.8). Kulagina *et al.* (2001) documented an occurrence of *Cancelloceras elegans* and *Bilinguites superbilinguis* with the Akavassian foraminifer *Pseudostaffella antique* in the Bolshoi Kizil section, Chelyabinsk Region, South Urals. The latter foraminiferal species was shown by Kossovaya *et al.* (2006) as standard for the Akavassian in Russia, with the *Pseudostaffella pregorskyi-Staffellaeformes staffellaeformis* biozone equating with the standard Askynbashian Substage, its central Russian equivalent Prikamian Substage and the Ukrainian Blagodatnian Subhorizon. All those correlations are tentatively accepted in this paper (Table 1).

In this interpretation, the Yeadonian appears in its traditional position, i.e., end-Namurian as shown in the Ratified Series and Stage Subdivision of the Carboniferous System (Newsletter on Carboniferous Stratigraphy, 2008, vol. 22, p. 2) and is correlated herein with the upper part of the *Bilinguites/Cancelloceras* Zone. A similar position and correlation can be found in both the recent Russian study (Kossovaya *et al.* 2006) and the summary by Menning *et al.* (2006), albeit the former does not refer to the western and central European subdivisions, and the biozonation is omitted from the latter. Table 1 includes all those correlations with the provisos mentioned above.

The coral collection treated in this and the subsequent papers of the series are restricted almost exclusively to the Olmezovian and Mandrykinian horizons, i.e. Limestones D_5^8–G, and consequently the correlation

of the individual substages and biozones of younger strata are not discussed in detail. The compilation of figure 3 of Menning *et al*. (2006) and table 4.8 of Kossovaya *et al*. (2006) shows the recent stratigraphical interpretation of that part of the Bashkirian stratigraphy in Central and Western Europe, the Donets Basin and western part of the Russian Federation.

The situation discussed above resulted in the following solutions: (1) Boundaries in Table 1 are treated here as approximate rather than certain. The same is true for mutual correlations of the ammonoid, conodont and foraminiferal biozones and their relation to the substages or subhorizons. (2) All specimens described were linked first of all with particular beds of limestones subdivided and numbered in accordance to the scheme generally accepted and applied to the Donets Basin strata. This provides a fixed stratigraphical position for each coral specimen within the succession irrespective of the subdivision into biozones and substages. (3) As a result, only the letters of the limestone intercalations and names of the Ukrainian subhorizons are mentioned in the occurrences. Their approximate equivalents are to be found in Table 1.

GEOLOGICAL SETTING

The summary of the stratigraphic succession in the Donets Basin (Nemyrovska 1999) and the sequence stratigraphy of the Serpukhovian to Moscovian of several areas, including the Donets Basin (Izart *et al*. 2002), allow the reduction of this chapter to a few general remarks and some statements concerning mainly the rugose coral occurrences. Such a position resulted also from my limited personal studies on the Donets Basin geology, restricted to two visits to that geologically complex area.

The Donets Basin, initiated in the Mid Devonian, is situated at the NE limit of the Ukrainian Shield and was considered the rift area (Izart *et al*. 2002, p. 145). Global sea-level changes and continuous but variable subsidence of the area resulted in cyclic, marine and continental sedimentation, characteristic of paralic coal basins. In general, however, 'The downwarp was entirely compensated by sedimentation' (Nemyrovska 1990, p. 6). The central part of the basin yields thicker deposits and more numerous limestone intercalations than those in its marginal parts. Although sedimentation was generally cyclic, the development of limestone intercalations occupied no more than 1–2 % of the entire volume of otherwise siliciclastic deposits (Einor 1996). Large and long lasting carbonate platforms did not develop, but thick-bedded organodetrital limestone intercalations, yielding rich and diverse

faunas occurred during the Early Carboniferous, especially during the Late Viséan and Early Serpukhovian (see Vassilyuk 1964; Ayzenverg *et al*. 1983, 1987 for references). This corresponds to the transgressive peak (Izart *et al*. 2002, p. 147). The same authors noted 'a lowstand near the base of Bashkirian' and 'high transgression in the Donets Basin' during that stage.

The Carboniferous deposits of the Donets Basin were studied by many geologists and palaeontologists for utilitarian and scientific purposes (see Poletaev *et al*. 1990; Einor 1996; Nemyrovska 1999; and Izart *et al*. 2002 for main references) and consequently several stratigraphic schemes were proposed. The subdivision into three series, each further subdivided into the numbered 'svity' (suites) was most commonly accepted. However, the subsequent changes in the original numbering made that scheme misleading. The Lower Carboniferous was originally subdivided into five suites (C_1^1 –C_1^5) (e.g. Fomichev 1953). The fifth of those suites was renamed C_2^0 when the lower boundary of the Bashkirian was moved down to the base of the *Reticuloceras* Zone. This, however, became misleading again after a further shifting of this boundary down to the base of the *Homoceras* Zone. For instance, Poletaev *et al*. (1990, fig. 3) included the Voznesenskaya Formation (as they called it) into C_1^4, i.e. the Lower Carboniferous Series. Nemyrovska (1999, p. 7) avoided that question by writing 'lower part of the C_2^0 Suite', but such an approach does not solve the problem. The Voznesenskian Substage (or Subhorizon in the Ukrainian nomenclature) is here accepted as equivalent to the Chokieran–Alportian substages, i.e. the *Homoceras-Hudsonoceras* Zone (see preceding chapter).

Fortunately for the correlation of occurrences, particular limestone intercalations or series of limestones intercalated between diverse clastic deposits were designated by capital letters. Where necessary, series or groups of limestones were numbered with the lower and upper indexes, e.g., D_4, D_5^{1-12}, etc. This allows much more precise correlation of the fauna and strata within the Donets Basin than other subdivisions established so far, and it is consequently adopted herein. The lithology of individual groups of limestones yielding corals treated in the present paper, was briefly described by Nemyrovska (1999, pp. 7–10).

Specimens studied in this and the subsequent papers of the series were derived mostly from the outcrops along Kalmyus and Solenaya Rivers, southeast and northwest of the town of Donets respectively (Text-figs 2, 3). Some specimens came from the Krynka River area (Text-figs 2, 4). Outcrops were located in small tributaries or ravines ('Balka') to those rivers, some of which were seasonal streams.

SYSTEMATIC PALAEONTOLOGY

Subclass Rugosa Milne Edwards and Haime, 1850
Order Stauriida Verrill, 1865
Family Antiphyllidae Ilina, 1970
Genus *Rotiphyllum* Hudson, 1942

TYPE SPECIES: *Densiphyllum rushianum* Vaughan, 1908, by subsequent designation of Hudson (1942, p. 257).

1849. *Cyathaxonia* Mccoy, p. 6 non Michelin 1847, p. 257.
e.p. 1851. *Zaphrentis* Milne Edwards and Haime, p. 326 non Rafinesque and Cliford 1820, p. 234.
1883. *Densyphyllum* Thomson, p. 150 non *Densiphyllum* Dybowski 1873, p. 392.
? 1883. *Fasciculophyllum* Thomson, p. 153.
? 1883. *Centrocellulosum* Thomson, p. 157.
e.p. 1882. *Zaphrentis* Miller, p. 620 non Rafinesque and Cliford 1820, p. 234.
e.p. 1891. *Zaphrentis* Miller, p. 10 non Rafinesque and Cliford 1820, p. 234.
1906. *Densiphyllum* Vaughan, p. 318 non Dybowski 1873, p. 392.
e.p 1908. *Zaphrentis* Carruthers, p.24 non Rafinesque and Cliford 1820, p. 234.
1908. *Densiphyllum* Vaughan, p. 459 non Dybowski 1873, p. 392.
e.p. 1909. *Zaphrentis* Douglas, p. 576 non Rafinesque and Cliford 1820, p. 234.
1909. *Densiphyllum* Dybowski, p. 578 non Dybowski 1873, p. 392.
e.p. 1910. *Zaphrentis* Wilmore, p.569 non Rafinesque and Cliford 1820, p. 234.
e.p. 1911. *Zaphrentis* Reynolds and Vaughan, p.372 non Rafinesque and Cliford 1820, p. 234.
1915. *Densiphyllum*; Smyth, p. 556 non Dybowski 1873, p. 392.
1920. *Zaphrentis* Smyth, p. 19 non Rafinesque and Cliford 1820, p. 234.
e.p. 1924. *Zaphrentis* Garwood and Goodyear non Rafinesque and Cliford 1820, p. 234.
? 1925. *Stereolasma* Soshkina, p. 84 non Simpson 1900, p. 205.
1937. *Meniscophyllum* Dobrolyubova, p. 16 non Simpson 1900, p. 199.
1938. *Zaphrentoides (Zaphrentoides)* Schindewolf, Pl. 45:3 non Stuckenberg 1895, p. 38
e.p. 1938-1941. *Zaphrentis* Hill, p. 135 non Rafinesque and Cliford, 1820,p. 234.

1942. *Rotiphyllum* Hudson, p. 257.
1942. *Fasciculophyllum* Thomson; Hudson, p. 258.
1942. *Fasciculophyllum* Thomson; Hudson and Fox, p. 105.
e.p. 1942. *Rotiphyllum* Hudson; Hudson and Fox, p. 106
1942. *Centrocellulosum* Thomson; Hudson and Fox, p. 108.
1943a. *Rotiphyllum* Hudson, p. 23.
non 1943b. *Rotiphyllum* Hudson, p. 136.
e.p. 1944. *Rotiphyllum* Hudson, p. 356.
e.p. 1944. *Rotiphyllum* Hudson; Easton, p. 32.
e.p. 1952. *Fasciculophyllum* Schindewolf, p. 177 non Thomson 1883, p. 153.
e.p. 1952. *Claviphyllum* Schindewolf, p. 195 non Hudson 1942, p. 262.
e.p. 1953. *Stereophrentis* Fomichev, 1953, p. 141.
1953. *Parastereophrentis* Fomichev, 1953, p. 162.
e.p. 1953. *Allotropiophyllum* Fomichev, p. 167 non Grabau 1928, p. 130.
? 1956. *Rotophyllum* (*sic !*); Davis, p. 33.
non 1957. *Rotiphyllum* Hudson; Easton, p. 623
non 1958. *Rotiphyllum* Hudson; Easton, p. 20.
non 1960. *Rotiphyllum* Hudson; Langenheim and Tischler, p. 112.
non 1960. *Rotiphyllum* Hudson; Sando, p. 171.
1961. *Rotiphyllum* Hudson; Fontaine, p. 61.
1963. *Rotiphyllum* Hudson; De Groot, p. 8.
1963. *Zaphrentites* De Groot, p. 37 non Hudson 1941, p. 309.
e.p. 1975. *Rotiphyllum* Hudson; Wyer, p. 758.
non 1976. *Rotiphyllum* Hudson; Guo, p. 67.
? 1977. *Stereolasma* Wu, p. 112 non Simpson 1900, p. 205.
? 1977. *Rotiphyllum* Hudson; Wu, p. 112.
? 1978. *Zaphrentites* Wang *et al*., p. 110 non Hudson 1941, p. 309.
? 1978. *"Zaphrentis"* Gorsky, 1978, p. 65 non Rafinesque and Cliford 1820, p. 234.
1981. *Rotiphyllum* Hudson; Poty, p. 14.
1982. *Rotiphyllum* Hudson; Weyer, p. 56
? 1982. *Homalophyllites* Yang and Fan, p. 59 non Easton 1944, p. 42.
? 1982. *Stereolasma* Fan (in Yang and Fan), p. 60 non Simpson 1900, p. 205.
1984. *Rotiphyllum* Hudson; Rodriguez, p. 121.
e.p. 1984. *Allotropiophyllum* Rodriguez, p. 214 non Grabau 1928, p. 130.
1984. *Rotiphyllum* Hudson; Weyer, Fig.8:5, 6.
? e.p. 1984. *Zaphrentoides* Xu, p. 183 non Stuckenberg 1895, p. 38.
non 1985. *Rotiphyllum* Hudson; Sando and Bamber, p. 27.
? 1985. *Rotiphyllum* Hudson; Wu and Zhang, p. 109.
e.p. ? 1986. *Rotiphyllum* Hudson; Wang and Yu, p. 658.

? 1986. *Meniscophyllum* Wang and Yu, p. 658 non Simpson 1900, p. 199.

1989. *Rotiphyllum* Hudson; Wu and Zhao, p. 44.

1990. *Rotiphyllum* Hudson; Fedorowski, p. 297.

1990. *Zaphrentites* Rodriguez and Kullmann, p. 26 non Hudson 1941, p. 309.

1991. *Protoheterelasma* (?) Pelhate, Conil, Vuillemin and Meilliez, p. 244.

1992. *Pseudoallotropiophyllum* Peng *et al*., p. 131.

1993. *Rotiphyllum* Hudson; Weyer, p. 41 (with synonymy of particular species).

non 1994. *Rotiphyllum* Hudson; Poty and Hannay, p. 57.

1994. *Fasciculophyllum* Thomson; Poty and Hannay, p. 58 non Thomson, p. 153.

? 1997. *Bradyphyllum* Grabau; Goreva and Kossovaya, pl. 2, fig. 9.

1999. *Rotiphyllum* Hudson; Rodriguez and Kullmann, p. 80

2001. *Duplophyllum* Wang *et al*., p. 273 non Koker 1924 p. 21.

2002. *Duplophyllum* Wang and Sugiyama, pl. 4, figs. 1, 2 non Koker, 1924, p.21.

? e.p. 2003. *Calophyllum* Fan *et al*., 239 non Dana 1846, p. 183.

? e.p. 2003. *Groenlandophyllum* Fan *et al*., p. 241 non Flügel 1973, p. 11.

e.p. 2003. *Parastereophrentis* Fan *et al*., p. 278 non Fomichev 1953, p. 162.

2005. *Rotiphyllum* Hudson; Chwieduk, P. 426.

SPECIES INCLUDED (in alphabetical order of species names): *Parastereophrentis abnormis* Fan, 2003; *Rotiphyllum asymmetricum* sp. nov., *Rotiphyllum charlestonense* (Thomson) of Hudson and Fox, 1943; *Cyathaxonia costata* Mccoy, 1849 (= *Zaphrentis costata* of Hill, 1938-1941); *Parastereophrentis crassiseptata* Fan, 2003; *Rotiphyllum crassiseptatum* Wu and Zhao, 1989; ?*Rotiphyllum cuneatum* Wu, 1977; *Centrocellulosum cylindricum* Thomson, 1883 of Hudson, 1942; *Centrocellulosum densothecum* Thomson, 1883 of Gregory, 1917 and Hudson, 1942; *Rotiphyllum diutinum* Fedorowski, 1990; "*Zaphrentis*" *dobroljubovae* Gorsky, 1978; *Fasciculophyllum dybowskii* Thomson, 1883 of Gregory, 1917 and Hudson, 1942; *Rotiphyllum exilae* De Groot, 1963; *Zaphrentis granularis* Thomson of Hill, 1938-1941; *Pseudoallotropiophyllum hubaiense* Peng *et al*., 1992; *Rotiphyllum* (*Centrocellulosum*) *intermedium* Thomson, 1883 of Hudson, 1942 and Hudson and Fox, 1943; *Parastereophrentis invalida* Fomichev, 1953; ?*Allotropiophyllum irregulare* Fomichev, 1953; *Meniscophyllum jingheense* Wang and Yu, 1986; *Zaphrentis junctoseptata* Smyth, 1920; *Rotiphyllum latithecatum* sp. nov.; *Fasciculophyllum magnifi-*

cum Thomson of Hudson, 1942; ?*Stereolasma minima* Soshkina, 1925; e.p. *Parastereophrentis minor* Fan, 2003; *Densiphyllum nodosum* Smyth, 1915; *Zaphrentis omaliusi* Milne Edwards and Haime, 1851; *Zaphrentites paralleloides* De Groot, 1963; ?*Groenlandophyllum pulchrum* Fan, 2003; *Densiphyllum rushianum* Vaughan, 1908; *Rotiphyllum simulatum* sp. nov.; *Fasciculophyllum thomsoni* Hudson and Fox, 1943; *Parastereophrentis virgata* Fomichev, 1953; *Rotiphyllum voznesenkae* sp. nov.; ?*Calophyllum xizangense* Fan, 2003; ?*Groenlandophyllum xizangense* Fan, 2003; ?*Groenlandophyllum yunzhugense*, Fan 2003 "*Zaphrentis*" *zilimi* Gorsky, 1978.

DIAGNOSIS: Antiphyllinae with major septa meeting near corallite axis. Cardinal protoseptum reaching corallite axis along cardinal fossula in all growth stages. Counter protoseptum commonly thicker and slightly longer than adjacent major septa. Tabularium typically normal, sometimes weakly biform in some septal loculi. Microstructure of septa trabecular (after Fedorowski 2004, p. 79, slightly modified).

REMARKS: The very long stratigraphical range, with some gaps in the occurrences, and the wide geographical distribution of the species included here in the genus *Rotiphyllum*, may suggest that we are dealing with a morphotype rather than a true genus. However, the latter option, although probable, cannot be proven on the basis of the existing data.

The morphology of the tabularium was diagnosed here slightly differently than before (Fedorowski 2004). The need for that modification was caused by the well preserved specimens described below as *Rotiphyllum voznesenkae* sp. nov. The tabularium is biform in several septal loculi of mature parts in that species (Text-figs $14A_{4,5}$; $15B_2$), whereas it is normal in all septal loculi during the early growth stages and in some septal loculi of mature growth of the same specimens. Such an inconsistent development of the biform tabularium cannot be treated as diagnostic for a new genus or subgenus, but it indicates a possibility of divergence.

Papers dealing with illustrated but not described species belonging probably to *Rotiphyllum* were omitted from the synonymy and such species were not added to the list of species. Also, the reader is referred to Weyer (1974, 1975, 1977, 1982) and Fedorowski (1987, 2004) for more comprehensive discussion. The synonymy proposed by Weyer (1975) is only in part accepted here. Fedorowski (1987) discussed that question already with remarks on *Monophyllum* Fomichev, 1953.

The discussion that follows is restricted to poorly known species, the taxonomic position of which can be

either accepted or questioned on the basis of the published illustrations and/or descriptions. In several instances the characters described and illustrated do not allow a firm identification of taxa as either *Rotiphyllum* or the new genus that will be introduced in the next paper of this series (Fedorowski, in press 1). Such taxa are discussed here as well.

Rotiphyllum sp. of Guo 1976 is not accepted as belonging to *Rotiphyllum* because it displays carinae (Guo 1976, pl. 40.4), whereas *Allotropiophyllum* sp. of that author (Guo 1976, p. 75, pl. 41.12) possesses pinnately arranged major septa and a cardinal protoseptum meeting other septa in the corallite axis up to the lower part of the calice. Such a protoseptum is diagnostic for *Rotiphyllum* but not for *Allotropiophyllum* in its original concept by Grabau (1928). The Early Permian taxon *Allotropiophyllum* sp. of Guo (1976) may thus be the stratigraphically youngest representative of *Rotiphyllum* known so far.

Two specimens (Jia *et al.* 1977) identified as *Stereolasma* Simpson, 1900 and *Rotiphyllum* Hudson, 1942 exhibit some characters of the latter genus, but illustrations of those specimens do not allow identification of the main diagnostic characters. In contrast, the probably Serpukhovian specimen from the Guizhou area (south China), identified by Wang (1978, pl. 29, fig. 9) as *Zaphrentites parallelus* (Carruthers) shows characters of both *Rotiphyllum* and *Zaphrentites*. Unfortunately, the single transverse section illustrated cannot be conclusive. It probably represents an ontogenetically early growth stage, when the morphology of those two genera is identical.

Gorsky (1978) described two new species, '*Zaphrentis*' *zilimi* and '*Z.*' *dobroljubovae* and, in open nomenclature,'*Z.*' ex gr. *delanouei* M. Edwards *et* J. Haime, 1851'. All these taxa were based on a single transverse section each. Despite such inadequate material, all are listed in the synonymy above. They possess long cardinal septa and the remaining major septa are arranged in the *Rotiphyllum omaliusi*-like manner. The Pennsylvanian occurrence, in addition to the morphology, makes their position within *Rotiphyllum* much more probable than within *Zaphrentites* Hudson, 1941.

At least some of several specimens included by Degtjarev (1979) in *Bradyphyllum* Grabau, 1928, *Hapsiphyllum* Simpson, 1900 and *Monophyllum* Fomichev, 1953 (Degtjarev 1979, pl. 45, fig. 7; pl. 49, fig. 3; pl. 46, fig. 7 and pl. 49, fig. 4 respectively) probably belong to *Rotiphyllum*. One of them (Degtjarev 1979, pl. 45, fig. 8) may belong either to that genus or in *Barytichisma* Moore and Jeffords, 1945. None of the specimens mentioned was illustrated and described in sufficient detail for an unequivocal generic assignment and consequently none was included in the synonymy.

Jia *et al*. (1984) described several species included by them in *Zaphrentoides* Stuckenberg, 1895. Illustrations of most of these species are too incomplete or too poor for an accurate identification. Their *Zaphrentoides delanouei* (Edwards and Haime, 1851), illustrated in both an early and probably mature growth stage (Jia *et al*. 1984, pl. 18, fig. 9), exhibits characteristics similar to those of *R. omaliusi* and was included here in the synonymy of *Rotiphyllum*.

Neither the description nor the illustration by Wu and Zhang (1985, pl. 2, fig. 9) of their *R. rushianum* (Vaughan) is adequate for a firm identification of their specimen as *Rotiphyllum*. However, its much younger stratigraphical position (Aoqu Group, Late Pennsylvanian or Early Permian) and differences in morphology exclude the Chinese specimen from that European Viséan species.

Homalophyllites sp. and *Stereolasma shengzhanense* Yang and Fan, 1982 from the Viséan of Tibet are certainly not members of those endemic North American Tournaisian and Middle Devonian genera respectively. They may belong to *Rotiphyllum*, but the illustrations available for checking the original descriptions, are inadequate for a firm identification.

Rotiphyllum and *Meniscophyllum* of Wang and Yu (1986) may belong to *Rotiphyllum*, although their illustrations (Wang and Yu 1986, pl. 1, figs 1–5) are inadequate for an unequivocal determination. Some of their specimens seem to possess an axial area permanently free from septa in maturity, but all of them are incompletely illustrated. This is particularly true for their *Rotiphyllum monophylloides* (Fomichev), which possesses a small axial area free of septa, but it is not certain whether this feature is permanent or temporary. This species is therefore only provisionally included here in *Rotiphyllum*. Illustrations of *Lytvolasma bradyphylloidea* Wang and Yu, 1986 seem to show an absence of the narrow, triangular cardinal fossula that is typical of *Lytvolasma,* but appear to show the presence of a long cardinal protoseptum. This taxon may belong to *Rotiphyllum* if the presence of the latter character is proven.

Revision of the plesiotype of *Meniscophyllum* by Easton (1944), and the restudy by Fedorowski (1990) of additional material from the Mississippi Valley region, have shown the distinctive characters of that endemic North American genus, which have nothing in common with those of the specimen included in it by Wang and Yu (1986). Also, many other Chinese specimens identified by various authors as *Meniscophyllum*, including '*Meniscophyllum*' *kansuense* Grabau, 1928, do not belong in that genus. An incorrect concept of the genus *Meniscophyllum* by Grabau (1928, p. 140, pl. 4, fig. 4a-e), was followed by several Chinese and other coral specialists, including Hill (1981). The specimen illustrated by Grabau (1928)

shows a superficial similarity to *Meniscophyllum* only when sectioned above a calice floor. Its slightly rhopaloid major septa of the counter quadrants extend higher into the calice than those of the cardinal quadrants and form a moon-like structure when cut above the last tabula. The early ontogenetic morphology of the Chinese specimen suggests that Grabau's (1928) '*Meniscophyllum*' *kansuense* belongs either to *Bradyphyllum* Grabau, 1928 or (more probably) to a new genus.

Specimens included by Peng *et al*. (1992) in *Stereolasma, Zaphrentites* and *Pseudoallotropiophyllum* may belong to *Rotiphyllum*, whereas *Bradyphyllum* and *Barrandeophyllum* Počta, 1902 of Peng *et al*. (1992) belong most probably to a new genus. Unfortunately, the illustrations provided by those authors do not allow a firm decision to be taken. Thus, only two species of Peng *et al*. (1992) were assigned here to definite genera. The diagnosis of and remarks on *Pseudoallotropiophyllum* (Peng *et al*. 1992, p. 150) substantiate characters shown in the illustrations (Peng *et al*. 1992, pl. 13, figs 8, 9) which closely resemble those of some *Rotiphyllum*. This new genus of Peng *et al*. (1992) was therefore included here in the synonymy of *Rotiphyllum*.

The specimen from the Kasimovian deposits of Northern Timan, identified by Goreva and Kosovaya (1997, pl. 2, fig. 9) as *Bradyphyllum bellicostatum* Grabau shows characters of *Rotiphyllum*. Unfortunately, the single transverse section illustrated by those authors, taken from an unknown part of the corallite, does not allow precise generic assignment of this taxon.

The same is true for the specimen from the Moscovian/Kasimovian boundary beds of the Picos de Europa, northwestern Spain, identified by Villa *et al*. (1993) as *Rotiphyllum* sp. Although this section shows the main characters of *Rotiphyllum*, the ontogenetically more advanced growth stage may show features of a new genus. Another specimen of the same authors and from the same area and age (Villa *et al*. 1993, pl. 3, fig. 2), identified as *Bradyphyllum* sp., was sectioned partly below (most counter quadrants) and partly above the calice floor and it is therefore oriented incorrectly. The short septum at the bottom of the picture is not the cardinal protoseptum as identified by those authors, but instead is the last major septum of the left counter quadrant. The true cardinal protoseptum, located lower right in the picture cited, remain long above the calice floor. This specimen therefore belongs to *Rotiphyllum*.

Most species described recently by Chinese authors under various generic names were included in the synonymy of *Rotiphyllum* with restrictions. Illustrations of several of them were either incomplete or did not show diagnostic features adequately. Detailed analysis of such taxa is omitted from this paper because more information concerning the morphology of the immature *vs.* mature stage must be obtained prior to final generic assignments. Some species, such as *Duplophyllum* sp. A of Wang *et al*. (2001, figs 6.4–6.6) and Wang and Sugiyama (2002, pl. 4, figs 1, 2), exhibit all the characters typical of *Rotiphyllum*, including a long cardinal protoseptum in the calice. Also, the Late Tournaisian or Early Viséan (Shihuadong Formation) specimen of the latter authors, possessing a long cardinal protoseptum, belongs to *Rotiphyllum* rather than to *Zaphrentites* as identified by them. Consequently, the genus *Rotiphyllum* or *Rotiphyllum*-like corals occurred in China from the Late Tournaisian or Early Viséan up to and including the Early Permian.

Fan *et al*. (2003) created several species displaying rotiphylloid characters but included them in various genera (see synonymy). Most of those species were il-

Species name	N:d values	Major septa	Minor septa	Counter septum	Cardinal fossula	Axial column	External wall
abnormae Fan, 2003	22-24: 5.5-6	Pinnately arranged	Absent from margin	Equal to Cl	Distinct, walls parallel	High, narrow	1/5-1/3 radius
asymmetricum sp.n.	25-26:6.5-8	Asymmetrical	Absent*	Thicker than Cl	Inconspicuous in most	High, eccentric	1/7-1/5 radius
latithecatum sp.n.	23-24:7-9.5	Rhopaloid	Absent from margin	Slightly elongated	Inconspicuous	Low, narrow	1/3-½ radius
simulatum sp.n.	24-26:7.5-9	Rhopaloid	Biformly reduced	Thicker, longer than Cl	Distinct, walls parallel	High, concave axially	1/7-1/5 radius
voznesenkae sp.n.	21-24: 8-10.5	Radially arranged	Very short strips	Equal to Cl	Distinct, triangular	Low, narrow	1/10-1/6 radius
Rotiphyllum sp.1	30:10.5	Radially arranged	In corallite wall	Equal to Cl	Long, narrow	Strong, wide	1/5 radius
Rotiphyllum sp.2	24:7	Pinnately arranged	Absent*	Thicker, longer than Cl	Key hole	Higher near K-septum	1/3 radius

* Absent means that calice margin is not preserved and minor septa are absent from corallite lumen

Table 2. Main characters of particular species of the *Rotiphyllum* studied

lustrated in a way that made their generic assignment doubtful. This concerns both photographs that are not always sufficiently complete to show all the diagnostic characters clearly and idealized drawings. Taxa identified by Fan *et al*. (2003) as *Parastereophrentis* were illustrated completely enough to either include them in *Rotiphyllum* or to suggest their probable affinity. Moreover, some well-illustrated specimens described by these authors, resemble Donets Basin specimens closely enough to include the latter in the Chinese species (see remarks below on *Rotiphyllum abnormae* Fan, 2003). The close morphological similarity between the Early Bashkirian specimens from the Donets Basin and the Chinese specimens from the 'lower' and 'upper part of Upper Carboniferous Series' (Fan *et al*. 2003, p. 280) may be homeomorphic, but such an option cannot be proven on the basis of existing data.

The holotype and one paratype of '*P.*' *minor* Fan (in Fan *et al*. 2003, pl. 22, figs 3, 5 respectively) belong to *Rotiphyllum* and closely resemble *R. abnormae* in morphology, but differ in much smaller diameters and numbers of septa. Nevertheless, the synonymy of those two species is here accepted as possible. The corallite of "*P.*" *minor*, illustrated by those authors in plate 22, figure 4, possesses a triad and belongs to a different genus and family from the holotype.

Specimens described by Fan *et al*. (2003) as *Groenlandophyllum pulchrum, G. yunzhugense, G. xizangense* and *Calophyllum xizangense* do not show the characters of the genera to which they were referred, but instead fit the diagnosis of the genus *Rotiphyllum*. However, illustrations of those specimens do not allow their unequivocal generic identification and they were therefore only questionably included in the list of species above.

Chwieduk (2005) described two species of *Rotiphyllum* from the early Tournaisian deposits of Polish Pomerania. Although left in open nomenclature, both those species are mentioned here as showing the main characteristics of *Rotiphyllum* and thus being one of the oldest representatives of that genus.

Main characters of all species described herein are compiled in Table 2.

Rotiphyllum abnormae (Fan, 2003)
(Text-figs 5, 6)

2003. *Parastereophrentis abnormis* Fan, p. 280. pl. 22, figs 1, 2.
? 2003. *Parastereophrentis qingshuigouensis* Fan, p. 279, pl. 22, figs 8, 9.
?e.p. 2003. *Parastereophrentis minor* Fan, p. 279, pl. 22, figs 3,5 (only).

MATERIAL: Seven specimens (UAM-Tc.Don.1/1-7). Some almost complete, with lower parts of calices preserved. Some slightly crushed and/or corroded. Sixteen thin sections and thirteen peels were available for the study.

DIAGNOSIS: *Rotiphyllum* typically with 22-24 major septa and 5.5-6.0 mm corallite diameter at calice floor; external wall 1/5-1/3 corallite radius thick with shallow septal furrows; major septa pinnately arranged; counter protoseptum equal to counter-lateral septa in length; minor septa absent from corallite lumen and its external wall including calice margin.

INTRASPECIFIC VARIABILITY: Some differences discussed may perhaps extend beyond the range acceptable for a species. One character – an 'additional' septum is difficult to classify.

Most specimens (Text-fig. 5A-D) resemble each other in both early ontogeny (Text-fig. $5A_{1-5}$, B_{1-3}, C_1, D) and in mature morphology (Text-fig. $5A_6$, B_4), if the 'additional' septum (see below) in one of the latter is not considered. One specimen (Text-fig. $6A_{1-5}$) resembles the remaining corallites in the pinnate arrangement of the major septa, the easily recognizable cardinal fossula and the well developed alar pseudofossulae, but it is much larger (29:8.5 mm). Also, the sclerenchyme is almost totally reduced from its axial part (Text-fig. $6A_{5, 6}$) and the external wall is relatively thin, bearing mainly delicate growth striae with virtually non-existent septal furrows (Text-fig. $6A_1$).

The major septa in another fragmentary and doubtful specimen (Text-fig. 6B) are either terminated on the section of the tabula (Text-fig. 6B, left) or do not meet directly in the corallite axis. The first of those characters may suggest an amplexoid character of the major septa, whereas the second was almost certainly caused by diagenesis. The dimensions of that corallite correspond to those of the typically built corallites when its long diameter, resulting from the obliqueness of the section, is reduced.

A kind of split of the counter protoseptum, or the existence of an additional septum contratingent to it, is observed in the calice of an otherwise typically built corallite (Text-fig. $B_{4, 5}$). Neither the weak septal grooves nor the diagenetically altered external wall offer information allowing a rigid classification of that additional septum. The lack of an extra groove between the counter protoseptum and the left counter-lateral septum (Text-fig. $5B_5$) may suggest the contratingent minor septum status of that skeletal body. On the other hand, however, the smooth interior of the calice rim of a morphologically very similar
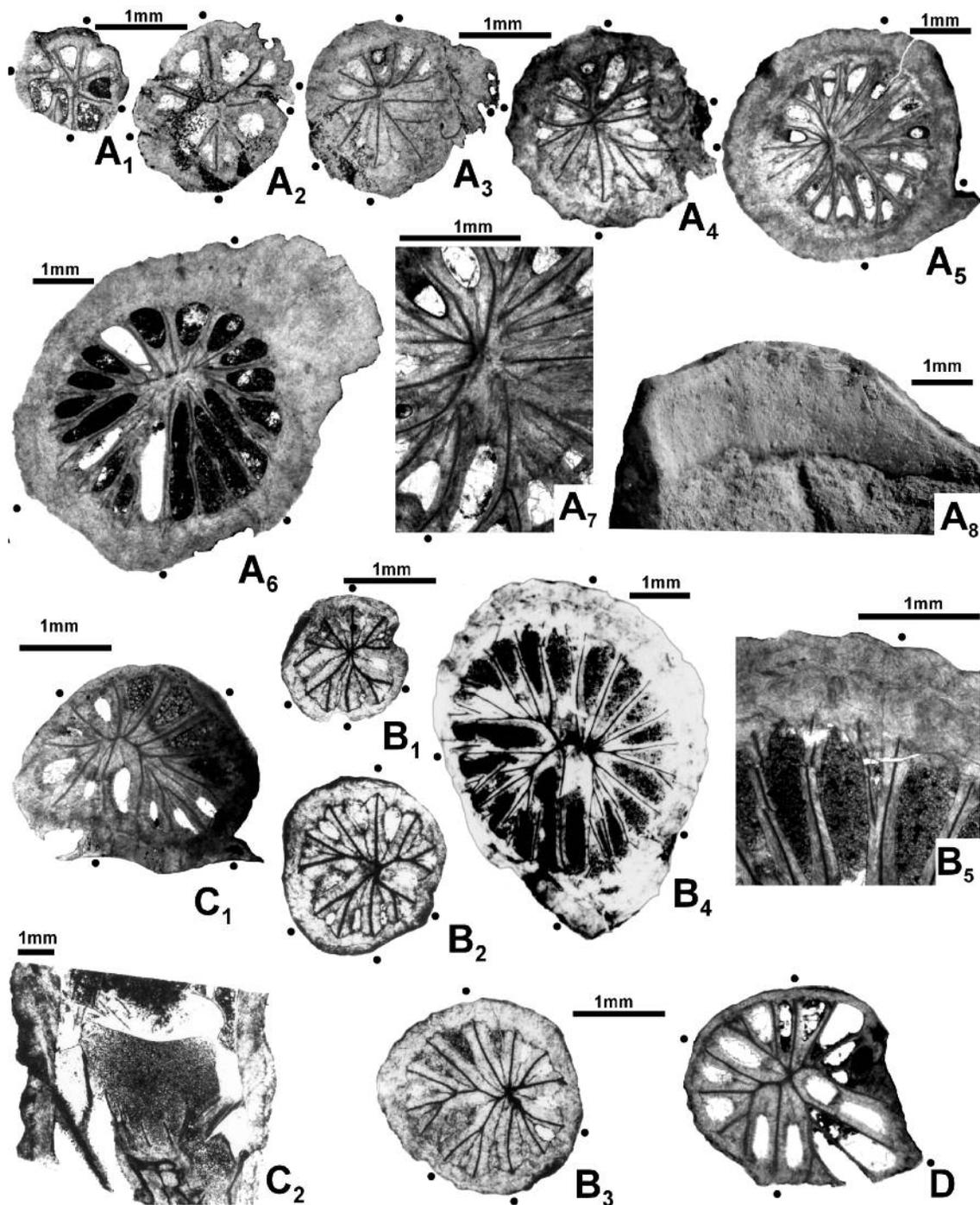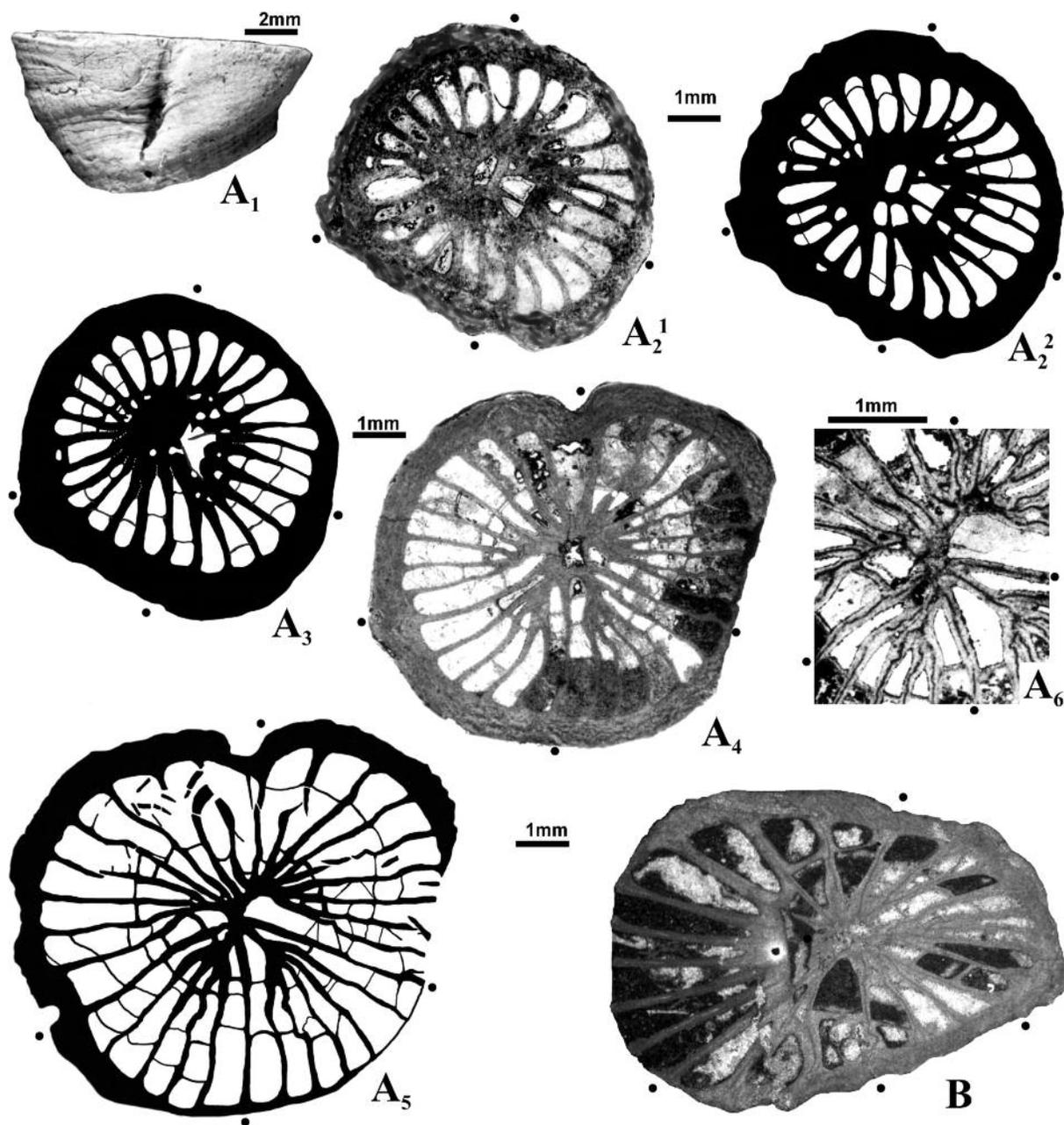
Text-fig. 5. *Rotiphyllum abnormae* (Fan, 2003). **A** – Specimen UAM-Tc.Don.1/1. A_{1-4} – successive sections, neanic growth stage, A_5 – late neanic or early mature growth stage, A_6 – mature growth stage, above calice floor at periphery, A_7 – Axial part of figure A_5 – enlarged to show unequal differentiation in length of primary major septa, A_8 – smooth inner surface of calice floor. **B** – Specimen UAM-Tc.Don.1/2. B_{1-3} – neanic growth stage, B_4 – mature growth stage, above calice floor at periphery, B_5 – additional septum at counter protoseptum. **C** – Specimen UAM-Tc.Don.1/3. C_1 – late neanic growth stage, C_2 – longitudinal section. **D** – Specimen UAM-Tc.Don.1/4 late neanic growth stage

Transverse thin sections, except when stated. Scale bars are common to two or more pictures when adjacent to each other. Protosepta and alar septa are marked by dots. Cardinal septum at the bottom. Computer drawings supplement corresponding photographs when necessary. Both bear the same main numbers, but are distinguished by upper indexes 1 and 2. Parts of individual corallites shadowed in drawings when cut above a calice floor. Positions of individual specimens are indicated in the Occurrences of particular species

corallite, (Text-fig. $5A_8$), suggests a total absence of blades of the minor septa. Thus, such a sudden insertion of the comparatively long minor septum inside the calice, can hardly be accepted. The very restricted data do not allow the suggestion of a relationship of the specimens discussed either to '*Rotiphyllum*' *axiferum* Hudson, 1943 from the Lower Viséan of Britain or to other species displaying the rotiphylloid length and arrangement of the major septa, but possessing contratingent minor septa at the counter protoseptum. Thus, only the occurrence of this phenomenon is reported.

The longitudinal section is known from a single, slightly eccentric section (Text-fig. $5C_2$). The trapezoid shape of the tabulae, with slightly concave middle parts and nearly vertical peripheral parts, correspond to those characters in other species of the genus.

Text-fig. 6. *Rotiphyllum abnormae* (Fan, 2003) **A** – Specimen UAM-Tc.Don.1/5. A_1 – side view; injured and recovered external wall, $A_{2, 3}$ – late neanic growth stage (peels), $A_{4, 5}$ – mature growth stage; just beneath calice floor (A_4, peel) and partly above calice floor at periphery, A_6 – enlarged axial part of A_5. **B** – Specimen UAM-Tc.Don.1/6. Mature growth stage; Additional explanations see Text-fig. 5

ONTOGENY: The earliest neanic stage known, with 7 major septa and 1.1 mm corallite diameter (Text-fig. $5A_1$), displays the arrangement of the protosepta, the alar and counter-lateral septa typical of most rugose corals. The seventh major septum appeared in the left cardinal quadrant. Further increase in the major septa and their length was irregular in all specimens studied (Text-fig. $5A_{2-5}$, B_{1-3}, C_1, D). In all those corallites one or two quadrants remain underdeveloped during the neanic growth stage. The protosepta do not dominate in most corallites and are commonly located asymmetrically. Such an asymmetry resulted perhaps from various kinds of attachment to the substrate, causing differently oriented growth of the corallites. Also, individual major septa inserted early in the septogenesis may stay short, whereas the ontogenetically younger ones are longer, i.e., the length of the major septa does not correspond to the sequence of their insertion. That character occurs in most specimens studied, but it is especially strongly accentuated in the late neanic growth stage of one of them (Text-fig. $5A_7$). All those characters are considered secondary and taxonomically unimportant.

In the specimen tentatively included in the species discussed, the asymmetry of the late neanic growth stage resulted in temporary development of the alar fossula (Text-fig. $6A_2$). This fossula disappeared within 1 mm of the corallite growth. The slightly shortened, rhopaloidally thickened alar septum and the first two septa in the right cardinal quadrant appeared in its place (Text-fig. $6A_3$). The long length of the alar septa in the mature growth stage (Text-fig. $6A_{4-6}$) suggest the ephemeral nature of both immature arrangements of the major septa described above.

DISCUSSION: A comparison of the Donets Basin and Chinese specimens in terms of their stratigraphical positions can only be approximate. '*Parastereophrentis*' *abnormis* came from the 'lower part of the Upper Carboniferous Guanpo Formation' in the Western Yunnan region (Fan *et al*. 2003, p. 100), whereas its suspected synonym, "*P*." *qingshuigouensis*, was mentioned by Fan *et al*. (2003) as present in the 'upper part of Upper Carboniferous Dingjiazhai Formation'. In some tables published by those authors '*Fusulinella-Fusulina*' (p. 174) and '*Fusulinella-Fusulina* to *Triticites* Time' (p. 181) were indicated as Late Pennsylvanian. Thus, all the Chinese specimens may be much younger than the Donets Basin ones, with the oldest being of Moscovian age. This makes the conspecificity of the Chinese and Donets Basin specimens doubtful. Nevertheless, the close morphological similarity between the specimens illustrated here (Text-fig. $5A_6$, B_4) and those of Fan *et*

al. (2003, pl. 22, fig.1b) cannot be ignored. The number of septa in the Chinese specimens is slightly smaller than in the most advanced Donets Basin specimens, but such a difference may be accepted as intraspecific.

The holotype and one paratype of '*Parastereophrentis*' *minor* Fan, 2003 may also be conspecific with *R. abnormae*. Both are smaller and possess less numerous major septa, but the arrangement of those septa, lack of minor septa and the large thickness of the external wall make them closely comparable to the species discussed. The paratype of that species (Fan *et al*. 2003, pl. 22, fig. 4a) belongs to a different genus and family. It possesses long Km septa forming a triad with the counter protoseptum. That specimen may be the stratigraphically youngest representative of the lineage including the British '*Rotiphyllum*' *axiferum* from the Lower Viséan. The species *Rotiphyllum abnormae* is similar to *R. voznesenkae* sp. nov. in the lack of the elongated counter septum, and to the Spanish species *R. exile* De Groot, 1963 in the inconsistent arrangement of the major septa and the secretion of an eccentric axial stereocolumn in some specimens. The strong underdevelopment of the minor septa, absent from the corallite lumen, and the very thick external wall, are characters distinguishing *R. abnormae* from both species mentioned, whereas the incipient tabular biformity established in *R. voznesenkae* constitutes an additional distinction from *R. abnormae.*

The largest corallite in the collection, mentioned above as a potentially different species, is broadly horn-shaped, with the cardinal protoseptum located on the convex side. It was bitten by a fish or a cephalopod and recovered, as indicated by the growth striae present in the depression (Text-fig. $6A_1$).

OCCURRENCE: China, Yunnan Province: Guangpo and (?) Dingjiazhai Formations, Upper Carboniferous and Baoshan County, Sisuo Formation, Lower part of Upper Carboniferous. Donets Basin: Krynka River Area: bank of Bolshaya Shishovka Ravine (Balka), Svistuny Village, Limestone E_1^{IV} (Specimen UAM-Tc.Don.1/3), Lower Feninian Subhorizon. Solenaya River Area: Novo-Troitskoe Village, Limestone F_1 (Specimens UAM-Tc.Don.1/1, 7) and Kalmyus River Area: Gorbachevo Village, Limestone F_1^2 (Specimens UAM-Tc.Don.1, 2, 4, 5), Lower Blagodatian Subhorizon. Amvrosievskiy Kupol, Limestone G_1^4 (Specimen UAM-Tc.Don.1/6), Lower Zujevian Subhorizon. All Lower Bashkirian.

Rotiphyllum asymmetricum sp. nov.
(Text-figs 7, 8)
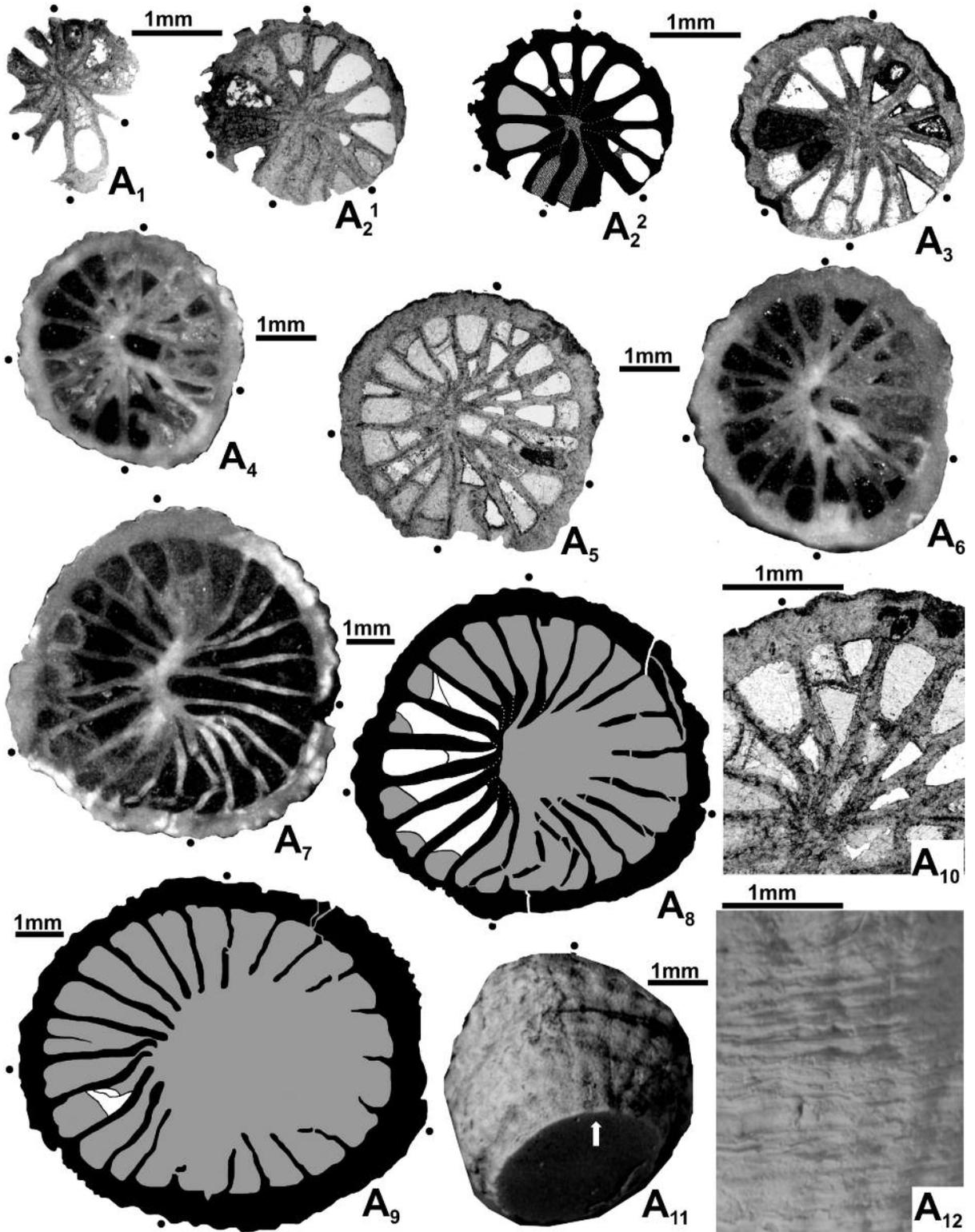
Text-fig. 7. *Rotiphyllum asymmetricum* sp. nov. **A** – Specimen UAM-Tc.Don.1/8. Holotype. A_{1-3} – early neanic growth stage, A_{4-6} – late neanic growth stage, A_7 – mature growth stage, A_8 – mature growth stage; mostly above calice floor, A_9 – middle part of calice, A_{10} – counter quadrants of A_5 enlarged to show additional septum at counter protoseptum, A_{11} – corallite surface documenting position of cardinal protoseptum (arrow and dot), A_{12} – strong growth striae and shallow septal furrows on mature corallite surface; Additional explanations see Text-fig. 5

HOLOTYPE: Specimen UAM-Tc. Don.1/8, illustrated in Text-fig. 7A$_{1-12}$. Six thin sections and five peels were studied.

TYPE LOCALITY: Kalmyus River Area, Grigorievka Village, Shirokaya Ravine (Balka).

TYPE HORIZON: Shales between Limestones E$_1$^{IV} and E$_1$^{V}. Lower Feninian Subhorizon

ETYMOLOGY: Greek (Latinized) *asymmetricus* – asymmetrical – after asymmetry in the arrangement of major septa.
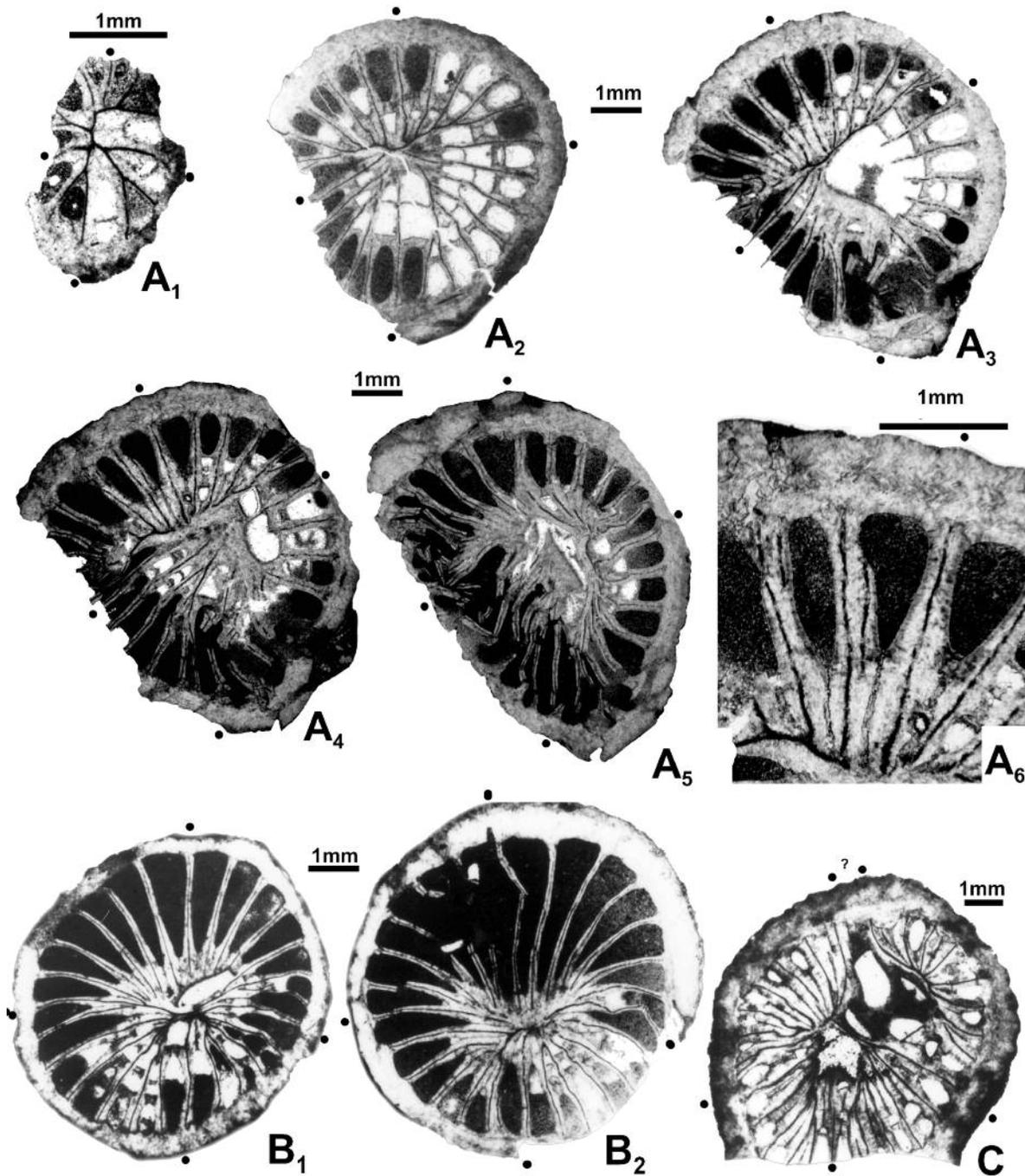
Text-fig. 8. *Rotiphyllum asymmetricum* sp. nov. **A** – Specimen UAM-Tc.Don.1/9. Paratype. A$_1$ – neanic growth stage, A$_2$ – late neanic-early mature growth stage, A$_{3-5}$ – mature growth stage; above calice floor at periphery, A$_6$ – fragment of A$_4$ enlarged to show duplications of "middle dark lines" of some major septa. **B** – Specimen UAM-Tc.Don.1/10. Paratype. B$_{1, 2}$ – mature growth stage; above calice floor at periphery. **C** – Specimen UAM-Tc.Don.1/11. Paratype. Strongly deformed arrangement of major septa; Additional explanations see Text-fig. 5

MATERIAL: Seven specimens, the holotype (UAM-Tc.Don1/8) and six paratypes (UAM-Tc.Don1/9-14). Some specimens almost complete. Microstructure diagenetically altered. Twenty thin sections and fifteen peels were available for study.

DIAGNOSIS: *Rotiphyllum* with external wall 1/5-1/7 corallite radius thick; n:d value at calice floor 25-26:6.5-8.0 mm; counter protoseptum slightly thicker than counter-lateral septa; inner margins of major septa joined at convex side of corallite to form arch; minor septa absent from corallite lumen.

DESCRIPTION OF THE HOLOTYPE: The corallite, approximately 17 mm long, is curved in the alar septa plane. Its up to 0.75 mm thick external wall constitutes 1/5 or less of the corallite radius. Growth striae are more conspicuous in the mature part of growth (Text-fig. $7A_{12}$). The inconspicuous septal grooves in the advanced neanic growth stage (Text-fig. $7A_{11}$) prove the location of the cardinal protoseptum on the lateral side of the corallite.

The arrangement of the major septa in the earliest growth stage preserved (Text-fig. $7A_1$) is regular. In this early growth stage the cardinal protoseptum is located on the convex corallite side, intersecting the cardinal fossula. The inner margins of the protosepta meet each other. Major septa are grouped in regular quadrants: two in each cardinal and three in each counter quadrant. The latter quadrants dominate in volume.

The two transverse sections that follow (Text-fig. $7A_{2,3}$) were cut from the straight part of the corallite growth, whereas the remaining ones (Text-fig. $7A_{4-9}$) were cut from its laterally curved growth part. The radial arrangement of the major septa in the straight part of growth is regular and typical for the genus, with the cardinal fossula inconspicuous and just above a tabula filled up with sclerenchyme (Text-fig. $7A_2$). The lateral curvature caused the re-arrangement of the major septa, with the development of a false cardinal fossula on the concave side (Text-fig. $7A_{4-7}$, right) and with the inner margins of the major septa on the convex side arranged into an arch open towards the false fossula. This arrangement persists up to the middle part of the calice (Text-fig. $7A_{8,9}$). The calice floor remains elevated higher at the convex than at the concave corallite side. The irregular length and arrangement of some major septa (Text-fig. $7A_{4,7}$) additionally camouflages the position of the cardinal protoseptum, which is recognizable in transverse sections when new major septa are inserted (Text-fig. $7A_{5,6}$).

Minor septa are absent from both the external wall and the corallite lumen, but slight protrusions of the inner surface of the external wall suggest their original occurrence within the wall. Unfortunately the microstructure of the external wall is completely destroyed by diagenesis, precluding proof of that suggestion. An ephemeral skeletal body, perhaps septal in the microstructure, was inserted at the counter protoseptum (Text-fig. $7A_3$), resembling the contratingent minor septum. This or a similar body appeared twice more during the growth of the corallite. It is attached to the counter-lateral septum initially (Text-fig. $7A_{5,10}$) and then appears as a short, free body, located close to the counter protoseptum in the calice (Text-fig. A_8). The provenance of that body (bodies ?) remains unknown.

INTRASPECIFIC VARIABILITY: The position of the cardinal protoseptum against the corallite curvature commonly determines the arrangement of the major septa and should be considered when the intraspecific variability is discussed. Two transverse sections (Text-fig. $8B_{1,2}$) of a corallite with the cardinal protoseptum located on the concave side, atypical for *Rotiphyllum*, illustrate that well. The major septa in the cardinal quadrants are shorter than those in the counter quadrants. Their thickened inner margins meet together to form an arch concave towards the long counter protoseptum and counter-lateral septa. The well developed cardinal fossula is intersected by the cardinal protoseptum, which approaches the counter protoseptum in a manner typical of the genus and species discussed. The ratio between the number of septa and the corallite diameter of the larger thin section of that corallite (26:7.0 mm) also follows the diagnosis. A small, eccentric disconnection of the inner margins of the major septa in the periaxial area of the ontogenetically younger growth stage (Text-fig. $8B_1$, right) is here considered taxonomically unimportant. Much larger disconnections of a similar kind occur in two other paratypes (Text-fig. $8A_3$ [right], C). All those disconnections were classified here as pathological.

One paratype (Text-fig. $8A_{1-6}$) displays septal arrangements in particular growth stages that are hardly comparable to each other. In the earliest ontogeny observed (Text-fig. $8A_1$), the cardinal protoseptum joined the major septa of the left cardinal quadrant, imitating the last septum of that quadrant. The next thin section looks regular until the highly variable numbers of major septa in particular quadrants are calculated (Text-fig. $A8_2$). The cardinal protoseptum, located on the convex corallite side, intersects the distinct cardinal fossula and approaches the counter protoseptum. Alar pseudofossulae are distinguishable.

The reason for the pathological re-arrangement of the major septa during further corallite growth (Text-fig. $8A_{3-5}$) was not established. The inner margins of several

major septa (Text-fig. $8A_3$, upper right) were suddenly disconnected. The disconnection disappeared step by step during further growth (Text-fig. $8A_{4, 5}$), but a thick sclerenchymal framework, connecting the inner margins of major septa located opposite the axially free major septa, was more consistent. The same is true for the highly irregular arrangement and number of septa in individual quadrants.

The ephemeral doubling of 'middle dark lines' of two major septa in the specimen discussed (Text-fig. $8A_4$ [upper], A_6), is worth attention as its next incomprehensible feature. The relationship of those additional 'dark lines' to the regular 'dark lines' (i.e., the primary septa) precludes diagenetic alteration: Both 'dark lines' are surrounded by the common sclerenchyme and hence both existed duringt the polyp's lifetime and can be interpreted as temporary double folding of septal pockets.

One specimen, represented by a single thin section (Text-fig. 8C), reveals an obviously pathological arrangement of the septa. Its major septa are grouped and their inner margins connected in distinct quadrants, leaving a large, irregular area free from septa. This free area seems to include the loculus in which the counter protoseptum should be located, whereas the protoseptum appears to be divided into two forks along its entire length. The inner margin of each fork is bent in the opposite direction (Text-fig. 8C, upper). The main diagnostic characters of this specimen, including the long cardinal protoseptum, correspond to the diagnosis of the genus *Rotiphyllum*. It is larger than all other corallites of *R. asymmetricum* (n:d value 28:8.1 mm) and was therefore only tentatively included in that species.

DISCUSSION: *R. asymmetricum* is perhaps most closely related to the Donets Basin specimens of *R. abnormae*. It differs from them in the slightly larger numbers of septa and corallite diameters, the much thinner external walls and the development of an arch formed from the inner margins of major septa connected to each other irrespective of the quadrants of major septa, but corresponding to the corallite curvature.

This arch resembles a similar character developed by the endemic North American Tournaisian genus *Meniscophyllum* Simpson, 1900, re-investigated by Easton (1944) and Fedorowski (1990). The latter author described and illustrated the ontogeny of that genus, but not its microstructure, which was diagenetically altered in his specimens. Both revisions of the genus allow it to be excluded from further consideration in the present paper.

OCCURRENCE: Kalmyus River Area: Grigorievka Village, Shirokaya Balka (Ravine), shales between Limestones E_1^{IV} and E_1^{V} (UAM-Tc.Don.1/8, holotype), Lower Feninian Subhorizon. Gorbachevo Village, Limestone F_1^2 (Specimens UAM-Tc.Don.1/9, 10, 11), Lower Blagodatnian Subhorizon. Amvrosievskiy Kupol, Limestone G_1^4 (Specimen UAM-Tc.Don.1/12), Lower Zujevian Subhorizon. Solenaya River Area: Novo-Troitskoe Village, Limestone F1 (Specimens UAM-Tc.Don.1/13, 14), Lower Blagodatnian Subhorizon.

Rotiphyllum latithecatum sp. nov.
(Text-figs 9, 10)

HOLOTYPE: Specimen UAM-Tc. Don.1/15, illustrated in Text-fig. $9A_{1-15}$. Six thin sections and eleven peels were studied.

TYPE LOCALITY: Solenaya River Area, Novo Troitskoe Village, Sazanova Ravine (Balka).

TYPE HORIZON: Limetone F_1, Lower Blagodatian Subhorizon.

ETYMOLOGY: Lat. *latus* – wide, *theca* – cover – after wide external wall.

MATERIAL: The holotype (UAM.Tc.Don.1/15), almost complete (Text-fig. $9A_1$); and four paratypes (UAM.Tc.1/16-18). One (Text-fig. $10A_{1-7}$) with the lower part of the calice and the apex preserved, the other three incomplete. Microstructure diagenetically altered. Nineteen thin sections and nineteen peels were available for study.

DIAGNOSIS: *Rotiphyllum* with 23–24 major septa at 7.0–9.5 mm corallite diameter; major septa thickened adaxially; counter protoseptum slightly longer and/or thicker than counter-lateral septa; cardinal fossula inconspicuous; minor septa absent from corallite lumen and external wall including calice margin; thickness of external wall 1/3-1/2 corallite radius.

DESCRIPTION OF THE HOLOTYPE: The corallite, horn-shaped in early ontogeny, becomes almost straight and regularly widened in further growth (Text-fig. $9A_1$). The surface of the very thick external wall bears delicate septal furrows and growth striae. The thickness of the external wall differs within a given cross section. It also increases in the course of growth from 0.7 mm in the late neanic growth stage, immediately above the attachment, to 2.0 mm locally at 7.5 mm corallite diameter, i.e., just beneath the calice floor. That thickness is slightly reduced above the cal-
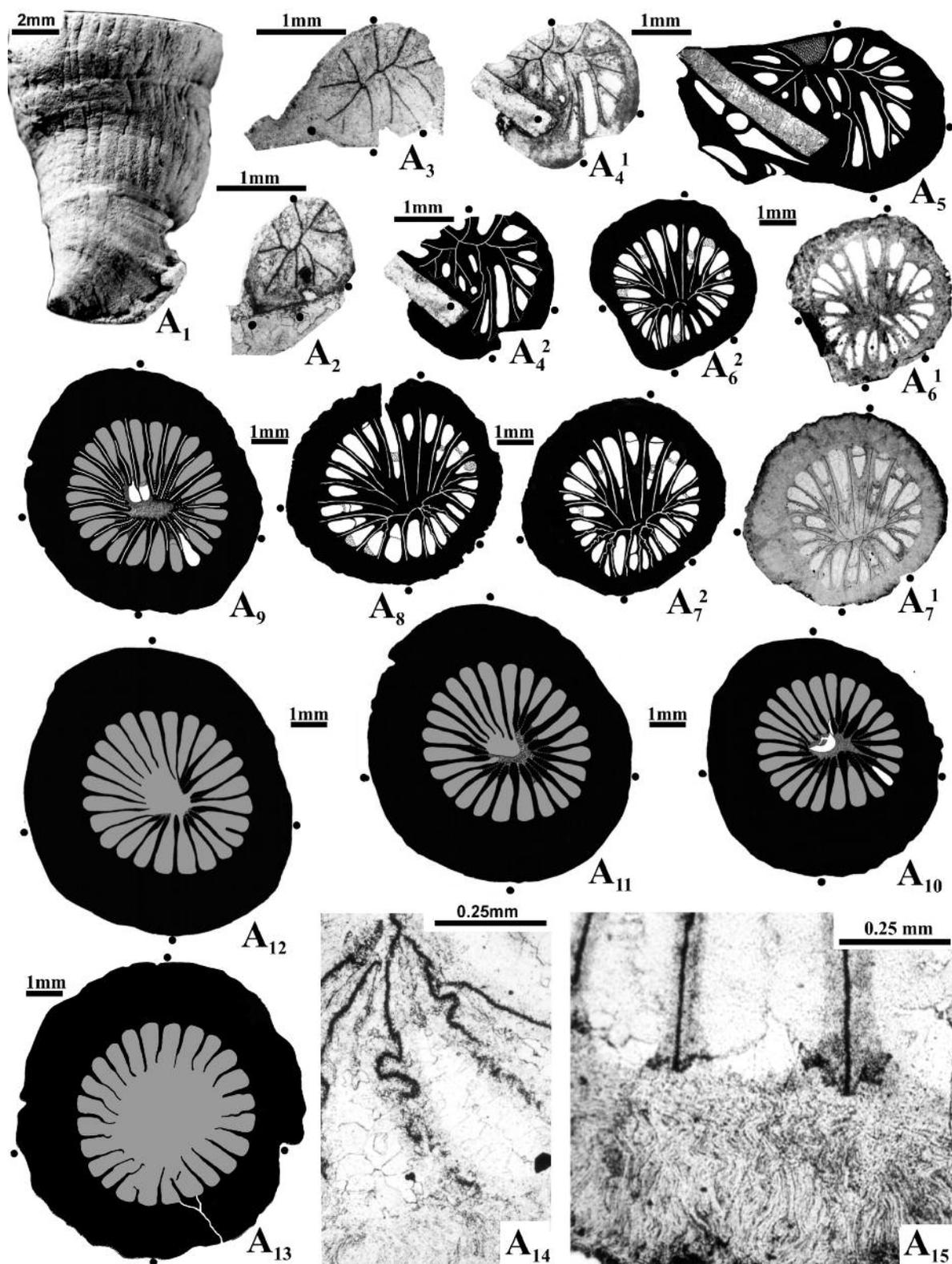
Text-fig. 9. *Rotiphyllum latithecatum* sp. nov. **A** – Specimen UAM-Tc.Don.1/15. Holotype. A_1 – side view, A_{2-5} – neanic growth stage, A_{6-8} – late neanic/early mature growth stage, $A_{9,10}$ – mature growth stage; parts sectioned above calice floor shadowed, A_{11} – above calice floor except for inner portions of several septa connected by sclerenchyme, $A_{12, 13}$ – middle and upper part of calice, A_{14} – diagenetically altered major septa, A_{15} diagenetically altered external wall; Additional explanations see Text-fig. 5

ice floor, where the external wall is 1.8 mm thick at 8.5 mm corallite diameter.

The zaphrentoid arrangement of the major septa is deformed by the attachment to a brachiopod shell. This deformation, slight at the very beginning of growth (Text-fig. $9A_{2, 3}$), became advanced when the corallite surrounds a part of the shell (Text-fig. $9A_{4, 5}$). The location of the cardinal protoseptum on the laterally convex side, but outside the attachment, resulted in the asymmetry of the septal arrangement during further corallite growth (Text-fig. $9A_{6-10}$).

The major septa opposite the attachment and just above it are strongly differentiated by quadrants in their length and number (Text-fig. $9A_{4-8}$). The counter protoseptum and major septa in the counter quadrants, short at the level of the attachment (Text-fig. $9A_{4, 5}$), become elongated and increase in number above that level (Text-fig. $9A_{6-8}$) The counter protoseptum and
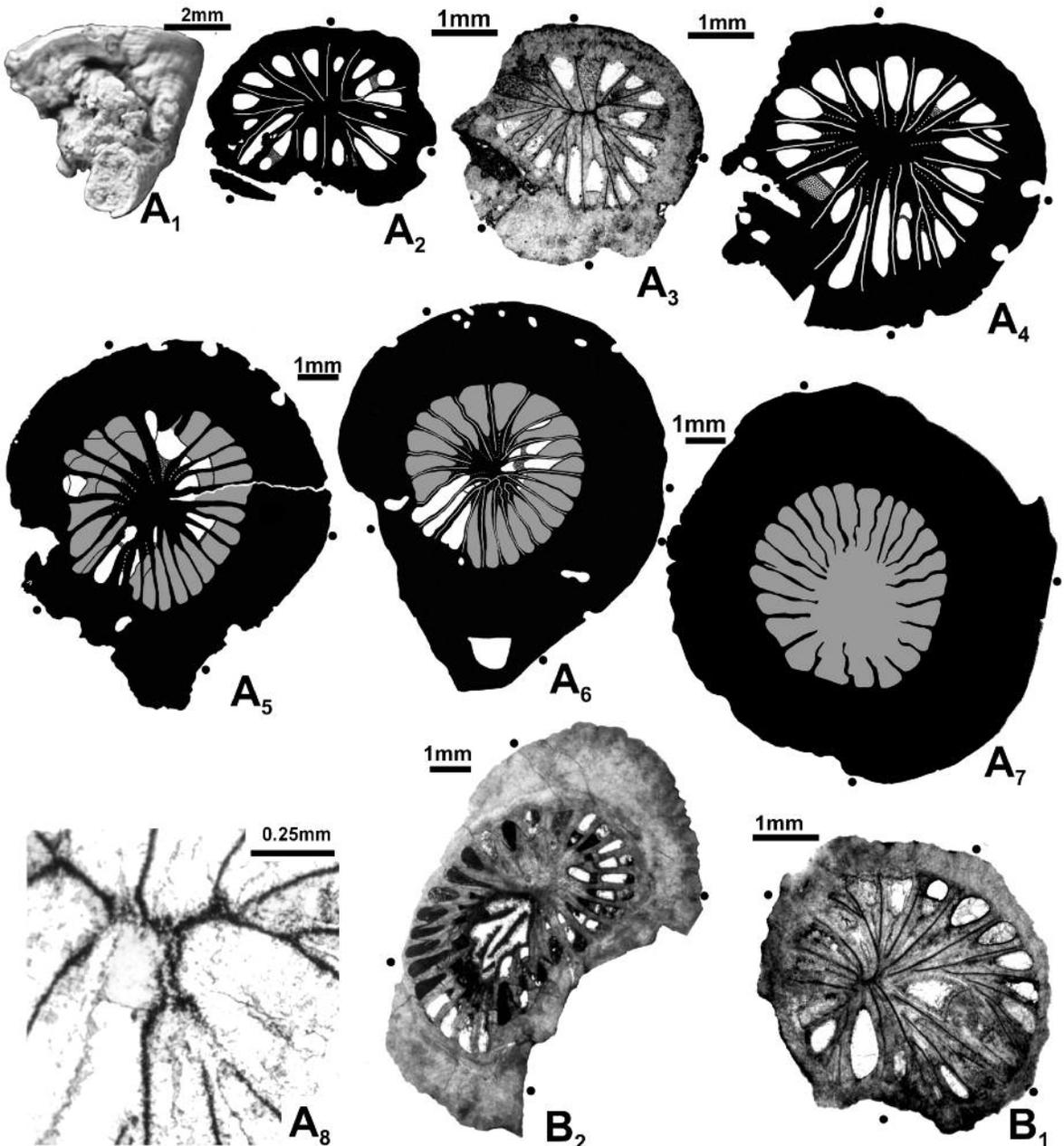
Text-fig. 10. *Rotiphyllum latithecatum* sp. nov. **A** – Specimen UAM-Tc.Don.1/16. Paratype. A_1 – attachment scars, $A_{2, 3}$ – neanic growth stage, A_4 – late neanic/early mature growth stage, $A_{5, 6}$ – mature growth stage; note holes left by boring organisms (A_{4-6}), A_7 – middle part of calice, A_8 – arrangement and diagenetic alterations of inner margins of major septa; enlarged axial part of fig. A_3. **B** – Specimen UAM-Tc.Don.1/17. Paratype. B_1 – neanic growth stage, B_2 – strongly deformed mature growth stage; Additional explanations see Text-fig. 5

counter-lateral septa dominate strongly over the remaining major septa of counter quadrants that shorten irregularly towards the alar septa. The 'middle dark lines' of the dominant major septa are free axially. In this growth stage, all major septa in the cardinal quadrants, including the cardinal protoseptum and the alar septa, are shorter than most of the major septa of the counter quadrants. Their 'middle dark lines' (i.e., the primary septa) unite to form an arch concave towards the longest septa of the counter quadrants (Text-fig. $9A_{6-8}$). The 'middle dark line' of the cardinal protoseptum is bent towards the adjacent major septum and is united with its 'middle dark line'. Thus, that protoseptum is hardly distinguishable from the fully developed last pair of major septa (Text-fig. $9A_8$). The same is true for the alar septa. The sclerenchymal cover of the inner margins of the major septa, stronger in the counter quadrants, camouflages the asymmetry in the arrangement of septa.

The disconnection of the middle lines of septa on the cardinal protoseptum side of the corallite (Text-fig. $9A_{9, 10}$) is here arbitrarily taken as marking the mature growth stage. Most septal loculi were sectioned just above the calice floor (shadowed). Only the axial corallite part, filled in with sclerenchyme, is elevated. The asymmetry in the arrangement of the major septa became accentuated at this growth stage by their stronger and longer-lasting sclerenchymal cover on the right-hand side of the corallite (Text-fig. $9A_{10-12}$). It disappears step by step parallel to the reduction in length of the major septa (Text-fig. $9A_{12, 13}$). The short major septum in the right-hand cardinal quadrant (Text-fig. $9A_{12}$) is not a newly inserted septum. It was inserted much earlier in the growth of the corallite, but becomes temporarily shortened for an unknown reason. The counter protoseptum, which strongly dominates during the early growth stages, becomes thin and equal to the adjacent major septa in length. The cardinal protoseptum stays permanently long and slightly rhopaloidally thickened in the lower and middle part of the calice(Text-fig. $9A_{11, 12}$). In the upper part of the calice (Text-fig. $9A_{13}$), all major septa become thin. The dominant role of the cardinal protoseptum is accentuated there by shortening of the two major septa adjacent to it. Minor septa are absent from the corallite lumen beneath the calice and from more than three-quarters of the the calice depth preserved.

INTRASPECIFIC VARIABILITY: The early growth stages in both paratypes possessing that part of the skeleton preserved are similar to each other and to that of the the holotype (Text-fig. $10A_{2-4}$, B_1). The asymmetry in the arrangement of the major septa in one of the paratypes (Text-fig. $10B_{1, 2}$) was caused by the attachment to the substrate. However, the arrangement of the major septa in the late neanic growth stage of both paratypes is opposite to that in the holotype. This difference depends on the attachment of the given corallite to the substrate and on the position of the protosepta against the curvature of the corallite. It is therefore taxonomically unimportant.

The stereocolumn connecting the inner margins of the major septa in the paratypes is narrower than in the holotype. It is centric in the mature growth stage (Text-fig. $10A_{5, 6}$, B_2), but longer lasting than that in the holotype. Also, the 'middle dark lines' (i.e., the primary major septa) of the cardinal quadrants remain connected much longer in the paratypes illustrated (Text-fig. $10A_6$) than in the holotype, being in that respect comparable to its late neanic growth stage (Text-fig. $9A_{7, 8}$). The number of septa in one paratype, larger in the ontogenetically earlier than in the more advanced growth stage (Text-fig. $10A_5$ *vs.* $10A_6$) and an ephemeral shortening of two major septa adjacent to the counter protoseptum, constitute curious features. The 'middle dark lines' of septa adjacent to the counter protoseptum, are free. The morphology of the lower part of the calice in this paratype (Text-fig. $10A_7$) is closely comparable to that of the holotype.

The mature morphology of the other paratype illustrated (Text-fig. $10B_2$) demonstrates pathology in the arrangement of the major septa and the shape of the corallite, resulting from its strong and long-lasting attachment to the substrate. The shape of the corallite became kidney-like and the arrangement of the septa strongly asymmetrical, with those of the cardinal quadrants thin. The latter character disagrees with that of the holotype, but it was considered less important than the characters in common. Diagenetic alterations (see below) hindered the classification of this specimen.

MICROSTRUCTURE AND DIAGENESIS: The advanced diagenesis destroyed all details in the microstructure of the primary major septa and the external wall of all specimens included in this species. The very narrow diameters of the primary major septa (approximately 0.01 mm) suggest that the original microstructure was either fibro-normal or very finely trabecular. Small disconnections in some septa of one paratype (Text-fig. $10A_8$) are diagenetic in nature and cannot be accepted as indicative of a trabecular microstructure.

The peripheral margins of most of the major septa are broadly wedge-shaped (Text-fig. $9A_{15}$), but they are attached to the inner surface of the external wall rather

than truly dip into it. Such a relationship suggests a long-lasting aseptal growth in the upper parts of calices. The nuclei of the minor septa, if originally present within the external wall, were totally destroyed by diagenetic alterations that transformed the original microstructure of the external wall into the zig-zag transverse layers (Text-fig. $9A_{14,15}$). The strong curvature of some of the major septa, with parts of them fragmented (Text-fig. $9A_{14}$), is another result of the diagenesis. The diagenetic fragmentation and partial dissolution of the major septa may be either on a large scale (Text-fig. $10B_2$, lower left), or this character may be recognizable only under a high magnification (Text-fig. $10A_3$ *vs.* $10A_8$, axial part).
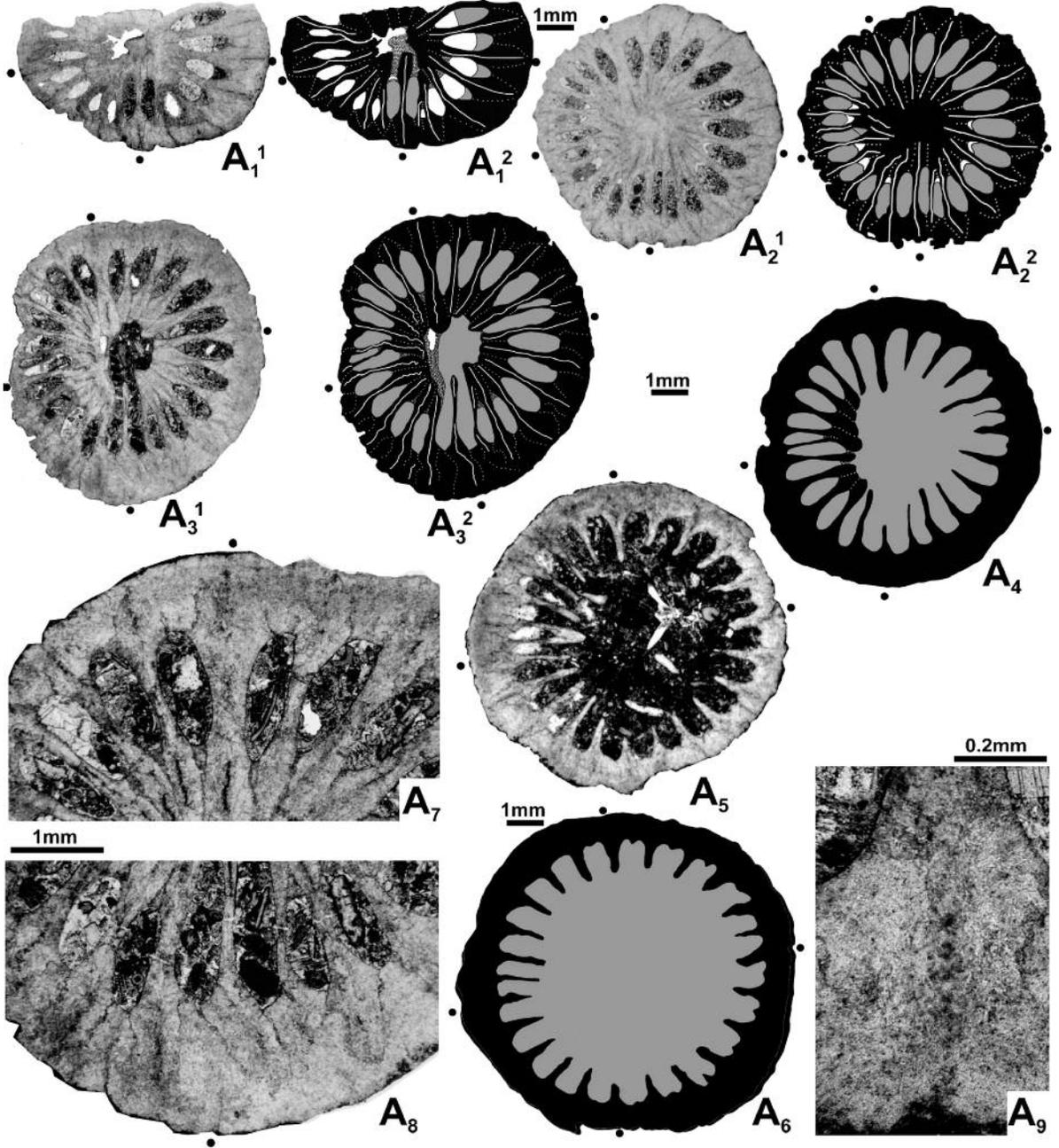
Text-fig. 11. *Rotiphyllum simulatum* sp. nov. **A** – Specimen UAM-Tc.Don.1/19. Holotype. A_1 – late neanic/early mature growth stage; deep cardinal fossula sectioned above calice floor, A_2 – mature growth stage; above calice floor at periphery, A_3 – mature growth stage, inner margins of major septa elevated above calice floor, A_{4-6} – successive sections from middle to upper part of calice, $A_{7, 8}$ – morphology of septotheca next to counter (upper) and cardinal (lower) protosepta, A_9 – rudiments of trabeculae in major septum embedded in external wall; Additional explanations see Text-fig. 5

DISCUSSION: *R. latithecatum* is most closely related to the Donets Basin representatives of *R. abnormae* (Fan, 2003). All specimens of both species came from similar stratigraphic levels and some from the same locality. It differs from the latter species in possessing an extremely thick external wall, in lacking recognizable minor septa, and in smaller numbers of septa at corresponding corallite diameters. The remaining Donets Basin species of *Rotiphyllum* are morphologically more distant from *R. latithecatum* and are not discussed.

OCCURRENCE: Solenaya River Area: Novo Troitskoe Village, Sazanova Ravine (Balka), Limestone F_1 (the holotype UAM-Tc.Don.1/15 and the paratype UAM-Tc.Don.1/16). Kalmyus River Area: former Kalinin's Quarry, Limestone $F_1{}^1$ (the paratype UAM-Tc.Don.1/17), Gorbachevo Village, Limestone $F_1{}^2$ (the paratype UAM-Tc.Don.1/18). All specimens from the Lower Blagodatnian Subhorizon.

Rotiphyllum simulatum sp. nov.
(Text-figs 11, 12)

HOLOTYPE: Specimen UAM-Tc. Don.1/19, illustrated in Text-fig. $11A_{1-9}$. Four thin sections and three peels were studied.

TYPE LOCALITY: Kalmyus River Area, Gorbachevo Village.

TYPE HORIZON: Limestone G_4, Lower Zujevian Subhorizon.

ETYMOLOGY: Lat. *simulo* – to look like, to imitate – after resembling *Monophyllum* Fomichev, 1953 and *Neaxon* Kullmann, 1965.

MATERIAL: The holotype (UAM-Tc.Don.1/19), from which four thin sections and three peels were prepared (no material left), and five paratypes (UAM-Tc.Don.1/20-24). Three of them (Nos UAM-Tc.Don.1/20, 21, 22) preserved in thin sections only. Nine thin sections and six peels were available for study.

DIAGNOSIS: *Rotiphyllum* with n:d value near calice floor 24:7.5 mm to 26:9.0 mm; major septa rhopaloid; their inner margins included in strong stereocolumn, elevated high in calice; above calice floor form circumaxial, incomplete ring; counter protoseptum slightly thicker and longer than adjacent major septa; minor septa biformly reduced.

DESCRIPTION OF THE HOLOTYPE: The slightly in-
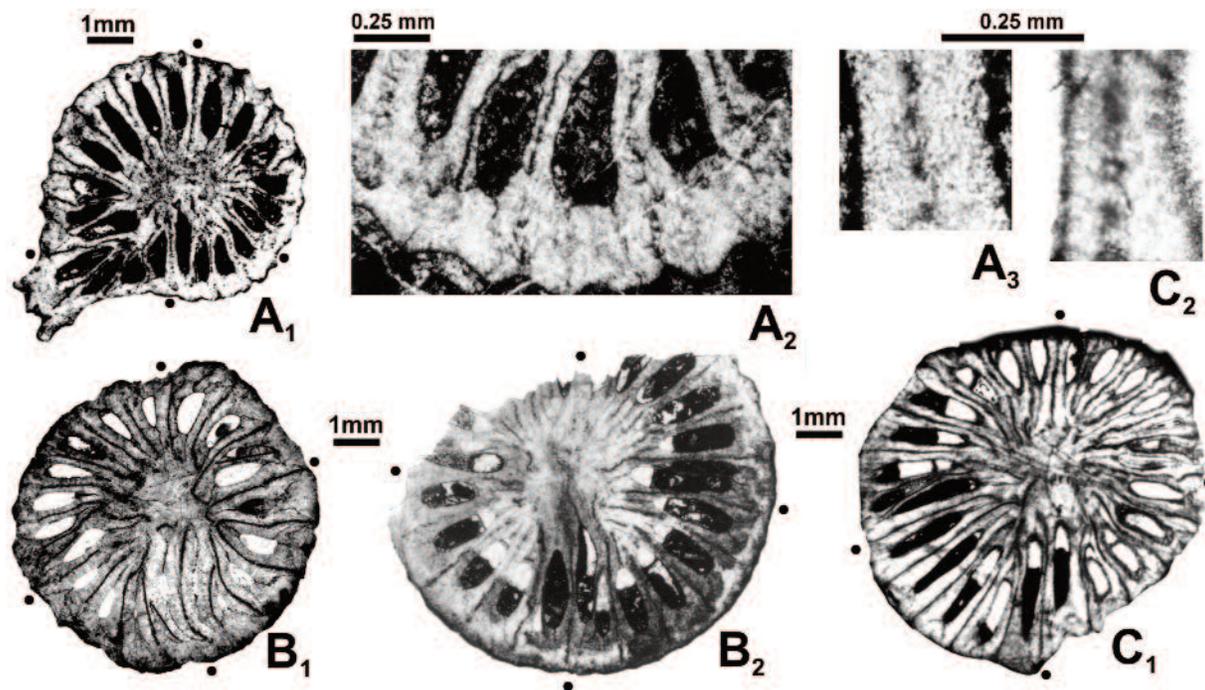
Text-fig. 12. *Rotiphyllum simulatum* sp. nov. **A** – Specimen UAM-Tc.Don.1/20. Paratype. A_1 – late neanic/early mature growth stage, A_2 – septothecal external wall, A_3 – rudiments of trabeculae in major septum. **B** – Specimen UAM-Tc.Don.1/21. Paratype. B_1 – late neanic growth stage, B_2 – mature growth stage; above calice floor at periphery. **C** – Specimen UAM-Tc.Don.1/22. Paratype. C_1 – mature growth stage; partly above calice floor at periphery, C_2 – rudiments of trabeculae in major septum; Additional explanations see Text-fig. 5

complete transverse section of the lowermost part of the corallite preserved (Text-fig. $11A_1$) represents the late neanic/early mature growth stage. The arrangement of the rhopaloid major septa is almost radial in all quadrants, with their 'middle dark lines' separated from each other. The cardinal protoseptum is slightly longer but thinner than the remaining major septa of the cardinal quadrants. It intersects the deep cardinal fossula, sectioned already above the calice floor. The wide stereocolumn is solid. The opening in the corallite axis resulted from destruction.

The mature growth stage (Text-fig. $11A_2$), with n:d value 22:6.8 mm, differs only slightly from the preceding morphology of the corallite. The counter protoseptum becomes thicker and slightly longer than the adjacent major septa. All septal loculi were here sectioned above the calice floor, proving a high elevation of the stereocolumn. The inner margins of the rhopaloid major septa do not meet in the corallite axis. The axial area is completely filled with sclerenchyme.

The highly elevated circumaxial area in the advanced mature growth stage, with n:d ratio 24:7.4 mm (Text-fig. $11A_3$), resembles the circulotheca of Fedorowski (in press 2). The dominating counter protoseptum, thicker than in the preceding growth stage, remains longer than the adjacent major septa (Text-fig. $11A_{3, 7}$). The long, but thin cardinal protoseptum is located in the break of the circulotheca-like structure, i.e., in the rudiment of the former cardinal fossula. The occurrence of biformly reduced minor septa is best developed in this growth stage (Text-fig. $11A_{7, 8}$).

All thin sections were cut exactly along growth lines. Thus, the longer-lasting rhopaloid character and greater length of the major septa on the left-hand side of the calice (Text-fig. $11A_{4, 5}$) are primary features, but perhaps pathological. The counter protoseptum remains most prominent, whereas the cardinal protoseptum is already shortened in that part of the calice. In the upper part of the calice, with n:d value 24:9.2 mm, the major septa become almost equal in length and thickness (Text-fig. $11A_6$).

INDIVIDUAL VARIABILITY: All paratypes are incomplete and hence the following remarks cannot be considered a comprehensive discussion of the subject. The neanic growth stage (n:d value 22:4.7) was observed in only one paratype (Text-fig. $12B_1$). Its morphology corresponds closely to the neanic growth stage of other *Rotiphyllum* investigated in detail, including those in the present paper. The mature morphology of this specimen (Text-fig. $12B_2$) closely resembles that of the holotype (Text-fig. $11A_2$), but the specimen is larger (n:d value 26:8.6 mm) than the holotype at a corre-

sponding growth stage. The other two paratypes illustrated (Text-fig. $12A_1$, C_1) represent perhaps the late neanic/early mature growth stage. They differ from each other and from the holotype in diameters and n:d values (21:5.7 mm and 26:7.2 mm), but display all the main morphological characteristics of the species, including the dominant counter protosepta, the biformly reduced minor septa, and the very wide stereocolumn highly elevated above the calice floor.

MICROSTRUCTURE AND DIAGENESIS: Although the microstructure of the septa is strongly diagenetically altered in all corallites, its rudiments can be recognized in fragments of their septa. The trabeculae (Text-figs $11A_9$, $12A_3$, C_2) are very fine, perhaps only 0.13-0.17 mm wide, but rather widely spaced. This suggests the appearance of narrow primary septa, covered by sclerenchymal sheets several times thicker.

DISCUSSION: None of the here described species resembles *R. simulatum* closely enough to make a discussion of its differences from them necessary. The circulotheca-like structure in the calice of this species resembles the circumaxial structures in the genera *Syringaxon*, Lindström, 1882 and *Neaxon* Kullmann, 1965. The latter genus lacks contratingent minor septa, thus being more similar to *R. simulatum*. However, the circumaxial structure in the genera mentioned appears early in ontogeny and is permanent, whereas in *R. simulatum* it forms only an intermediate step in the reduction of rhopaloid major septa. Besides, the rotiphylloid early ontogeny in the latter species and the coarsely trabecular microstructure of the septa in *Neaxon* (Różkowska 1969, p. 58) preclude a relationship between *R. simulatum* and that genus.

The counter protoseptum of the species discussed, thicker and slightly longer than the remaining major septa, is common within the genus *Rotiphyllum*. This character points towards the genus *Monophyllum* Fomichev, 1953, as suggested by Fedorowski (1987, pp. 67, 68, text-figs 22–24). *R. simulatum* most closely resembles the Spanish species *Rotiphyllum exile* De Groot, 1963 (revised by Fedorowski 2004, p. 80, pl. 1, figs 2–4; pl. 4, figs 1-4) in the number of septa and diameters of corallites, in possessing cardinal and counter quadrants almost equal in the numbers of septa, in the elongated counter protoseptum, the biformly reduced minor septa, and an almost radial arrangement of the major septa at maturity. However, elongation of the counter protoseptum in *R. exile* is accentuated much earlier in ontogeny, its major septa are either non-rhopaloid or only very slightly rhopaloid, while the rotiphylloid arrangement of the major septa lasts longer
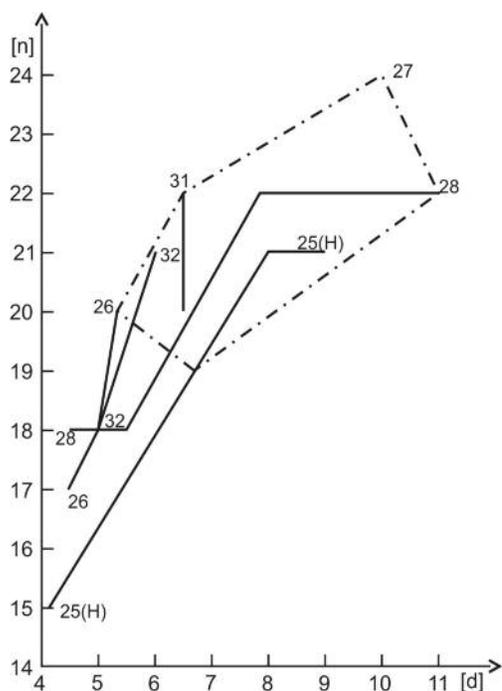
Text-fig. 13. *Rotiphyllum voznesenkae* sp. nov. Numbers of major septa (n) *vs*. corallite diameters (d) of individual specimens. Lines, marked by collection numbers of specimens, join individual n:d values measured. Values corresponding to mature growth stages of specimens surrounded by broken lines to show the intraspecific variability

than in *R. simulatum*. These characters, together with the slightly stronger development of the minor septa in calices of some specimens of *R. exile* (e.g. De Groot 1963, pl. 1, figs 1d, 2d), suggest the distinction of the Donets Basin specimens. The difference in the occurrence: Upper Moscovian in Spain, *versus* Lower Bashkirian in the Donets Basin, supports such an opinion. The small differences in morphology of both species and the easy communication between the areas of their occurrence may suggest an ancestor/descendant relationship between them.

OCCURRENCE: Kalmyus River Area, Gorbachevo Village, Limestone G_2 (UAM-Tc.Don.1/21, 22, 23, paratypes) and Limestone G_4 (UAM-Tc.Don.1/19, holotype and UAM-Tc.Don.1/20, 24, paratypes), Lower Zujevian Subhorizon.

<div align="center">

Rotiphyllum voznesenkae sp. nov.
(Text-figs 13–16)

</div>

HOLOTYPE: Specimen UAM-Tc. Don.1/25, illustrated in Text-fig. $14A_{1-10}$. Three thin sections and eleven peels were studied.

TYPE LOCALITY: Kalmyus River area, Voznesenka Village.

TYPE HORIZON: Limestone D_7, Lower Voznesenskian Subhorizon.

ETYMOLOGY: Named after the village of Voznesenka, from the vicinity of which the holotype and most paratypes were collected.

MATERIAL: The holotype (UAM-Tc.Don.1/25) and 15 paratypes (UAM-Tc.Don.1/26-39). Calices in most specimens and mature growth parts in some corallites flattened by compaction. Early growth stages and surfaces of most corallites well preserved. For n:d values of representative specimens see Text-fig. 13. Twenty-five thin sections and thirty peels were available for study.

DIAGNOSIS: *Rotiphyllum* with maximum 24 major septa at 10.5 mm corallite diameter, commonly 21–22:8.0–9.0 mm; some major septa may withdraw from corallite axis below tabulae; minor septa very short; tabularium in several loculi biform; external wall 1/10–1/6 corallite radius thick with distinct septal grooves.

DESCRIPTION OF THE HOLOTYPE: The corallite is 27 mm long and slightly curved in the cardinal/counter protosepta plane, with the cardinal protoseptum located on its convex side. Its flattened calice is 13 mm deep and 10.3 mm wide at the margin. An attachment scar was absent from the corallite since its 1.8 mm diameter, i.e. the earliest growth stage preserved. Septal furrows are deep and growth striae are well preserved in most parts of the surface, offering an opportunity to study the increase in septa. An alteration in the insertion of major and minor septa was established when transverse sections were compared to septal furrows and growth striae (Text-fig. $14A_{7, 8}$).

In the neanic growth stage, with n:d value12 (13): 2.3×2.8 mm and 16:3.6×4.2 mm (Text-fig. $14A_{1, 2}$), the major septa are pinnately or rotiphylloidally arranged. Counter quadrants are accelerated in the increase in septa and occupy more than one half of the corallite volume. The cardinal fossula and alar pseudofossulae are recognizable. Minor septa are not yet present inside the external wall and in the corallite lumen, but their furrows are developed.

The n:d value increases during the mature growth stage from 19:7.8×7.0 to 22: 9.4×8.0 nearby the calice floor (Text-fig. $14A_{3-6}$). The major septa become nearly radially arranged, with the pinnate pattern accentuated mainly by a slight underdevelopment of the last septa in quadrants and the occurrence of alar pseudofossulae.

Counter quadrants dominate over cardinal quadrants in volume and in possessing one or two more major septa (including the alar and counter-lateral septa), but not in the length of the major septa. None of the major septa dominates in length and/or thickness, but the inner margin of some may be slightly rhopaloid. The cardinal pro-
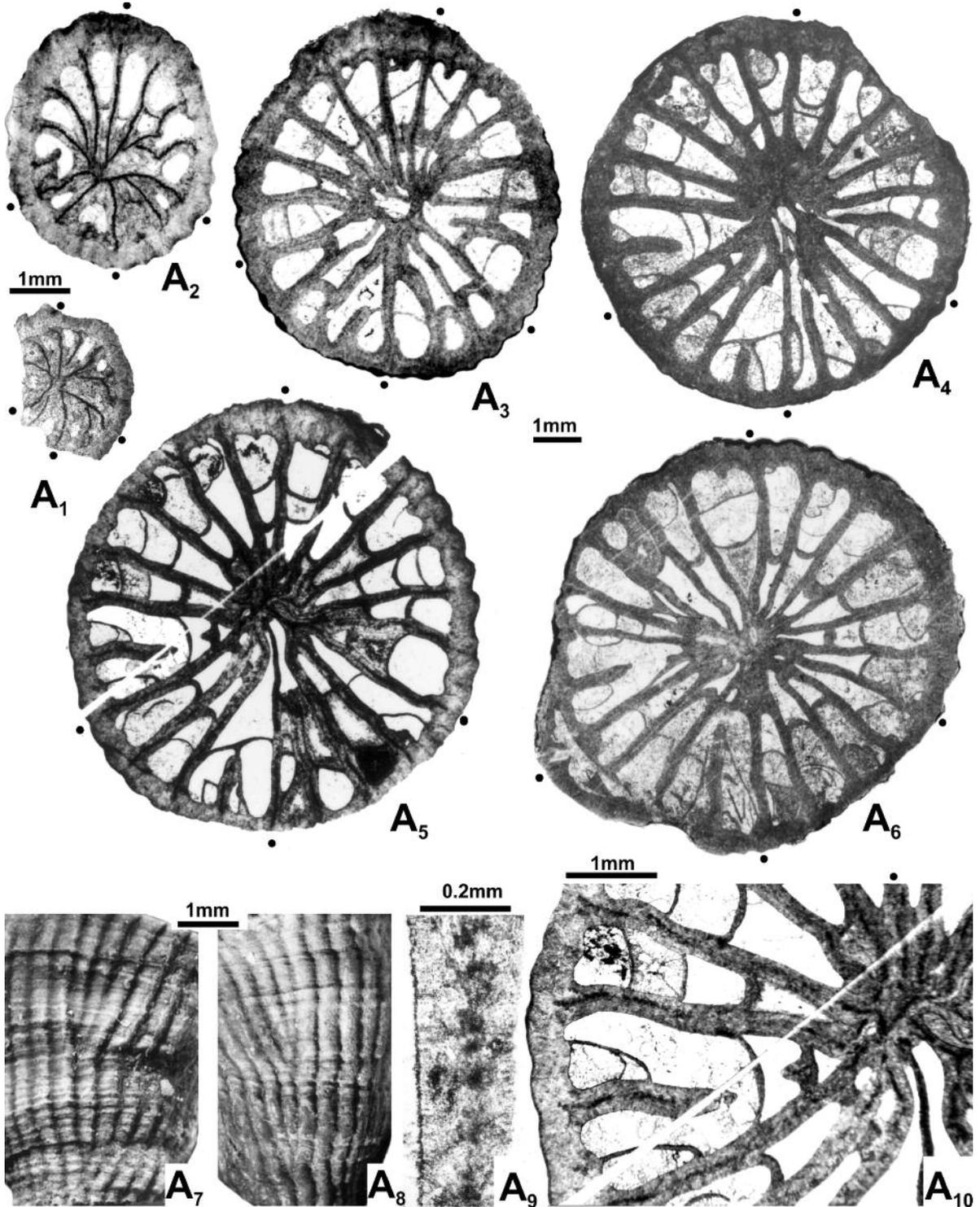
Text-fig. 14. *Rotiphyllum voznesenkae* sp. nov. **A** – Specimen UAM-Tc.Don.1/25. Holotype. $A_{1,2}$ – neanic growth stage, A_{3-6} – mature growth stage ($A_{3,4,6}$ peels), $A_{7,8}$ – increase of septal furrows, A_9 – trabecular microstructure of major septum, A_{10} – part of figure A_5 enlarged to show biform tabularium at periphery and morphology in corallite axis; Additional explanations see Text-fig. 5
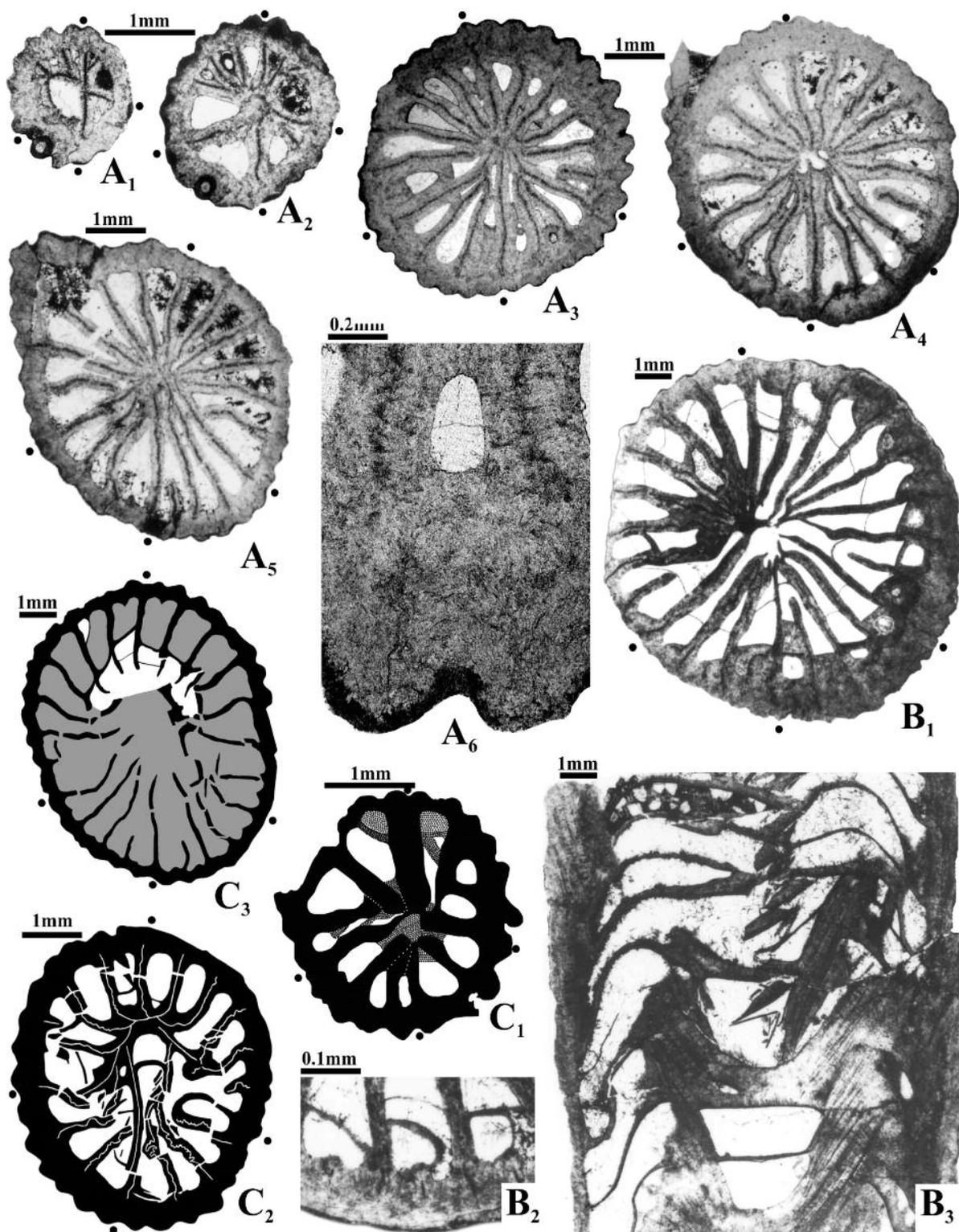
Text-fig. 15. *Rotiphyllum voznesenkae* sp. nov. **A** – Specimen UAM-Tc.Don.1/26. Paratype. $A_{1,2}$ – neanic growth stage, A_{3-5} – mature growth stage, A_6 – microstructure of external wall and major septa with rudiments of trabeculae. **B** – Specimen UAM-Tc.Don.1/27. Paratype. B_1 – mature growth stage, B_2 – longitudinal section of mature growth stage, B_3 – fragment of external wall and biform peripheral parts of tabulae. **C** – Specimen UAM-Tc.Don.1/28. Paratype. C_1 – late neanic growth stage, C_2 – late neanic/early mature growth stage, C_3 – mature growth stage sectioned mostly above calice floor; Additional explanations see Text-fig. 5
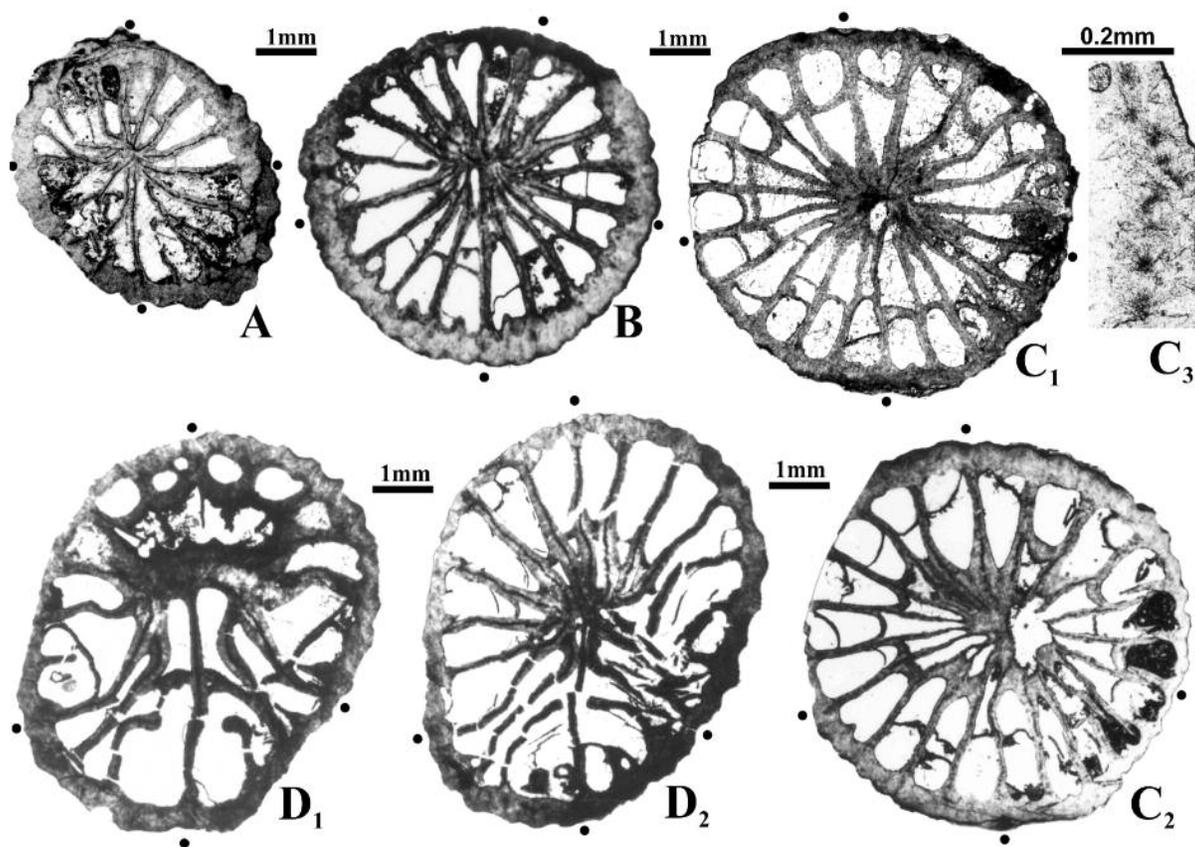
Text-fig. 16. *Rotiphyllum voznesenkae* sp. nov. **A** – Specimen UAM-Tc.Don.1/29. Paratype. Early mature growth stage. **B** – Specimen UAM-Tc.Don.1/30. Paratype. Mature growth stage. **C** – Specimen UAM-Tc.Don.1/31. Paratype. $C_{1,2}$ – mature growth stage, C_3 – trabecular microstructure of major septum. **D** – Specimen UAM-Tc.Don.1/32. Paratype. D_1 – late neanic or early mature growth stage, D_2 – mature growth stage; Additional explanations see Text-fig. 5

toseptum is the thinnest major septum in some parts of the corallite growth (Text-fig. $14A_{4,5}$). Both protosepta and most major septa approach the corallite axis, but are not united by their inner margins. Secretion of the sclerenchyme is slight. Consequently, the axial column, comprising mostly the inner margins of the major septa, is narrow and may disappear temporarily below tabulae when the deposition of sclerenchyme is weakest (Text-fig. $14A_3$). Both the cardinal fossula and alar pseudofossulae are well marked by distinct underdevelopment of the last major septa in quadrants. The alar pseudofossulae may in fact be true tabular fossulae, as documented by the larger number of sections of tabulae within them than in the adjacent septal loculi.

Most minor septa form only small swellings of the 0.4 mm thick corallite wall (Text-fig. $14A_{10}$). Their microstructure is recognizable mainly by the arrangement of crystalline fibrils. Only the minor septa adjacent to the counter protoseptum are slightly more elongated in some sections of the mature growth stage (Text-fig. $14A_{3, 6}$).

Sections of tabulae, attached to the inner margins of the longest minor septa on one side and to the lateral surfaces of adjacent major septa on the other, document an occurrence of a biform tabularium in several, but not all septal loculi (Text-fig. $14A_{3-6}$). Such an inconstant occurrence of this character may have resulted from the underdevelopment of minor septa. Also, it is not shown when a section is cut just beneath a tabula in a given septal loculus. The indistinct difference between Position I and II is the next factor making recognition of the biform tabularium difficult. As shown by one paratype, the biform tabularium may poorly be exposed in the longitudinal section (Text-fig. $15B_3$), being at the same time easily recognizable in peripheral parts of the transverse section of the same specimen (Text-fig. $15B_{1, 2}$).

INTRASPECIFIC VARIABILITY: The ontogenetically early occurrence of the axial septum is shown in one paratype (Text-fig. $15A_1$). However, the same transverse section exhibits either a pathology in the underdevelopment of the left alar septum, recognizable only in the corallite wall, or partial diagenetic damage of that sec-

tor of the corallite. This phenomenon is very short-lasting and the alar septum in question appears as long and strongly thickened in the next transverse section, only 0.4 mm above the previous one (Text-fig. $15A_2$). An atypical arrangement and insertion of the major septa in the early growth of the corallite discussed was perhaps caused by a foreign body incorporated in the external wall (Text-fig. $15A_{1,2}$, lower left). The mature morphology of this paratype (Text-fig. $15A_{3-5}$) resembles the equivalent growth stage of the holotype, except for much smaller dimensions (Text-fig. 13) and an almost total absence of minor septa in the external wall. The lack of those septa in the corallite lumen resulted in its normal tabularium. The minor septa are much better developed in the paratype UAM-Tc.Don.1/30 (Text-fig. $16B_1$). They do not extend far from the external wall, but are long enough to make the biform arrangement of peripheral sections of tabulae recognizable in several loculi (Text-fig. $15B_{1,2}$).

The paratypes discussed so far and some other ones (Text-figs $15A_{1-5}$, C_{1-3}, 16A-D) constitute a group of corallites generally smaller than the holotype in diameter but possessing a similar number and arrangement of major septa. They also differ from the holotype in weaker development of the cardinal fossula and alar pseudofossulae. The latter are absent from one of them (Text-fig. $16C_{1,2}$).

Most corallites included in this species are either immature individuals or their mature parts were flattened, sometimes strongly, preventing precise measurements. Thus, there is a bias in the n:d value (Text-fig. 13) because only well preserved parts of particular corallites were measured. The holotype belongs to the largest specimens, with only two paratypes being slightly larger, and four possessing slightly more numerous major septa (Text-fig. 13). The mature morphology of the largest paratype (Text-fig. $15B_1$) resembles closely that of the mature part of the holotype, except for more numerous major septa in the counter quadrants. The slight axial disintegration of the inner margins of the major septa closely resembles that in some parts of growth of the holotype (Text-fig. $14A_3$) and is considered temporary. It resulted from the amplexoid nature of the major septa, shown by thickenings of the upper surfaces of the inner parts of tabulae in the longitudinal section (Text-fig. $15B_3$). A slight and temporary disintegration of the major septa was also observed in some other corallites, exposing a small open axial area in some transverse sections (Text-fig. $15A_4$). This character may thus be considered a common feature in the species discussed.

A group of specimens possessing cardinal protosepta dominating in length display another distinguishing character: a kind of half-aulos formed from the united inner margins of the major septa (Text-figs $15:C_2$, $16D_1$). This structure resembles those developed by the Tournaisian *Hapsiphyllum* Simpson, 1900 and *Meniscophyllum* Simpson, 1900 from the Mississippi Valley Province of North America, but it is only analoguous to those structures and does not indicate a relationship. More advanced growth stages of both specimens discussed (Text-figs $15C_3$, $16D_2$) allow them to be regarded as variants of *R. voznesenkae*. The morphology of corallites intermediate between those specimens and the holotype confirms such an interpretation (Text-fig. 16A).

Acceleration in the insertion of major septa in counter quadrants occurs in all specimens investigated and in all growth stages, starting from early ontogeny through the late neanic growth stage (Text-figs $14A_{1,2}$, $15A_{1,2}$, C_1). This character differs slightly in the course of growth of individual corallites. Also, individual quadrants may not be equal in the number of septa.

Only one specimen was sectioned longitudinally (Text-fig. $15B_3$). Complete tabulae in this corallite are widely spaced (3 in 5 mm corallite growth). Their peripheral segments rise steeply upwards from the external wall and then curve more or less distinctly axialwards, passing into horizontal or slightly sagging axial segments. A few hemispherical peripheral tabellae-like bodies, interpreted here as sections of the tabulae in Position I, also occur.

MICROSTRUCTURE AND DIAGENESIS: Diagenesis in both the compaction and re-crystallization is advanced in all corallites studied. It is revealed by the zigzag or oblique arrangement of crystalline fibrils within the external wall (Text-figs $14A_{10}$, $15A_6$, B_2) and by solid 'middle dark lines' of septa. However, some fragments of septa show remnants of the original microstructure (Text-figs $14A_9$, $15A_6$, $16C_3$). In all such fragments fine trabeculae are recognizable. Both their slightly different diameters and distances between them may have resulted from the diagenesis.

DISCUSSION: Two characters of the species described, both inconspicuous, i.e., the incipient biformity of the tabularium and the temporary disintegration of the inner margins of the major septa, are important. Such a combination distinguishes this species from all remaining species of *Rotiphyllum* described here. The counter protoseptum equal to adjacent septa in length allows this evolutionary trend to be distinguished from that leading towards *Monophyllum* Fomichev, 1953. The temporary disintegration of the inner margins of major septa may lead towards a new genus that will be introduced in the paper that follows. A more comprehensive treatment of this matter will be given in the remarks on that new genus.

The incipient biformity of the tabularium may point to the single specimen from the Moscovian Sierra Corrisa Limestone in the Palencia Province of Spain, identified by De Groot (1963) as *Bradyphyllum* (?) sp. no. 2 and re-illustrated by Fedorowski (2004, pl. 1, fig. 6) as *Genus and species indeterminata*. Its immature growth stage (De Groot 1963, pl. 1, fig. 1a, b) shows characters
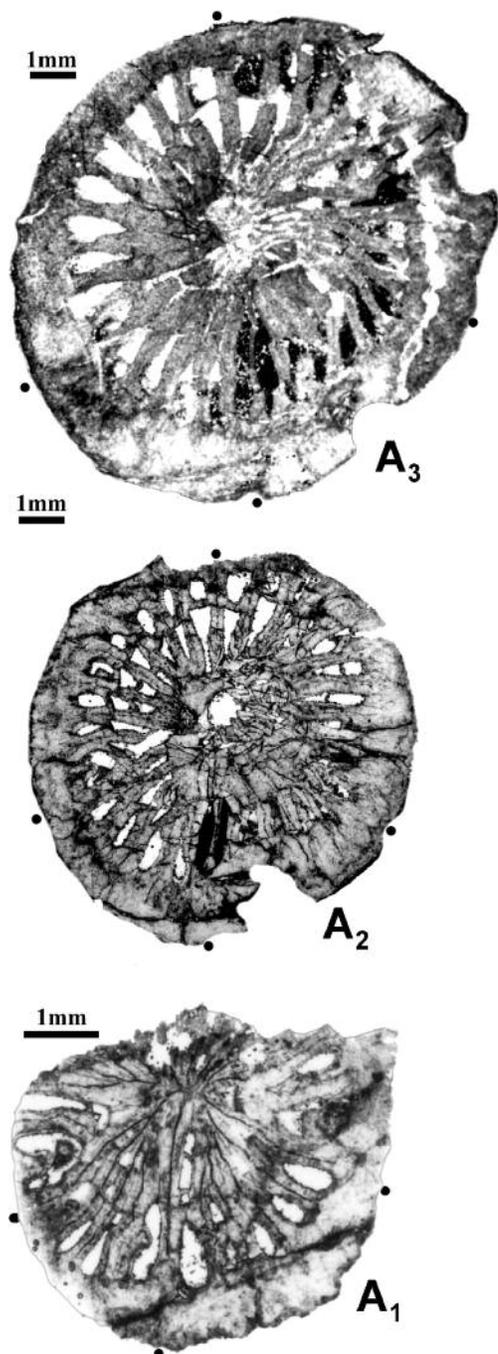
of *Rotiphyllum*, being closely comparable to the corresponding growth stage of *R. voznesenkae*. However, its counter septum is elongated and the major septa are permanently shortened at maturity (De Groot 1963, pl. 1, fig. 6c; Fedorowski 2004, pl. 1, fig. 6).

OCCURRENCE: Kalmyus River Area. Voznesenka Village, Limestone Group D_7, Lower Upper Voznesenskian Subhorizon. The holotype UAM-Tc.Don.1/25 and paratypes UAM-Tc.Don.1/33, 34 from Limestone D_7 (undivided). Remaining paratypes, UAM-Tc.Don.1/35-39 from shales immediately overlying Limestone D_7 [7].

Rotiphyllum sp. 1
(Text-fig. 17)

MATERIAL: One almost complete specimen UAM-Tc.Don.1/40 with the calice flattened and septa slightly crushed by compaction. Two thin sections and four peels were available for study.

DESCRIPTION: In the neanic growth stage (Text-fig. $17A_1$), with n:d value 23:4.0 mm when measured perpendicular to the protosepta plane, the arrangement of the major septa is typical of the genus, with the cardinal protoseptum dominating in length and crossing the corallite axis to meet the counter protoseptum. Major septa in all quadrants are pinnately arranged, with the 'middle dark lines' of most of them united. Minor septa are not yet developed.

In the mature growth stage (Text-fig. $17A_{2,3}$), with n:d value 30:10.5 mm, the radially arranged major septa closely approach, but not meet the corallite axis. Many are laterally contiguous in the middle and inner sectors of their length, but their inner margins are pointed. The cardinal protoseptum is the thinnest septum of all, but it is not shortened despite being sectioned above the last tabula of the long, narrow cardinal fossula. The counter protoseptum does not differ in length and thickness from the counter-lateral septa. Minor septa can be traced in better preserved parts of the 1.2 mm thick external wall and are seen as small knobs in some septal loculi. The microstructure of septa was diagenetically damaged. Some of the best preserved septa show probable rudiments of fine trabeculae.

DISCUSSION: This poorly preserved corallite was described only because very few specimens of rugose corals are known so far from Limestone G (see Fomichev 1953, Prilozheniye). Its mature morphology differs from that of the remaining species of *Rotiphyl-*

Text-fig. 17. *Rotiphyllum* sp. 1. Specimen UAM-Tc.Don.1/40. A_1 – neanic growth stage, $A_{2,3}$ – mature growth stage; Additional explanations see Text-fig. 5

lum described so far in possessing a kind of circumaxial ring of laterally contiguous major septa that approach the corallite axis with their pointed margins. They neither meet there directly nor join the sclerenchymal cover. The lack of the stereocolumn, and the presence of an axial area free from major septa only be-

low a tabula (Text-fig. 17A$_2$) are features reminiscent of *R. voznesenkae*. The extremely thin cardinal protoseptum, crowded and slightly wavy major septa and scarcely recognizable minor septa form a set of features distinguishing the specimen discussed from other species of the genus.
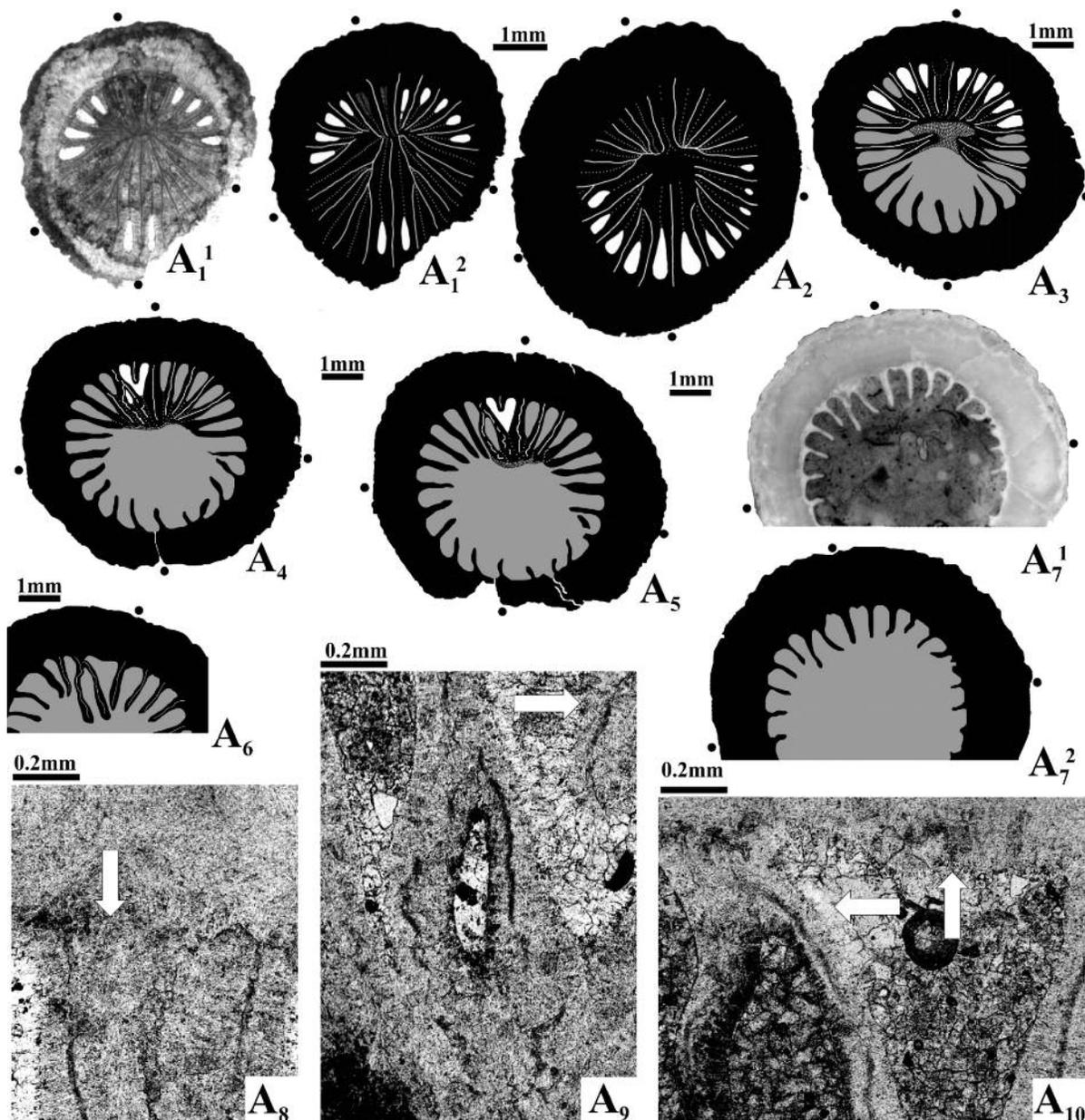
Text-fig. 18. *Rotiphyllum* sp. 2. Specimen UAM-Tc.Don.1/41. A$_{1,2}$ – Late neanic to early mature growth stage, A$_{3,8}$ – Mature growth stage sectioned immediately above calice floor in cardinal quadrants. Modifications of counter-lateral septum begins (A$_3$ upper, A$_8$ arrow). A$_{4,9}$ – Lower part of calice; only loculus hosting peripheral fragment of modified, left counter-lateral septum is sectioned beneath calice floor (white). Enlarged fragment of that loculus (A$_9$) shows peripheral (arrow) and inner (right fork) remnants of the counter-lateral septum. A$_5$ – Approximately 0.4 mm above A$_4$; peripheral and inner margins of first major septum in left counter quadrant and inner fragment of left counter-lateral septum united. A$_6$, $_{10}$ – Inner margins of afore mentioned two septa free (A$_6$). Peripheral fragment of counter-lateral septum disappeared (A$_{10}$, right arrow). Its inner fragment is shifted towards external wall (A$_{10}$, left arrow). A$_7$ – Middle part of calice. Peripherally thickened, left counter-lateral septum attached back to external wall (upper left); Additional explanations see Text-fig. 5

OCCURRENCE: Kruchik Ravine (Balka), Limestone G_1, Lower Zujevian Subhorizon.

Rotiphyllum sp. 2
(Text-fig. 18)

MATERIAL: One specimen, UAM-Tc.Don.1/41,with the tip missing, but with the major part of the calice preserved. Six thin sections and two peels were available for study.

DESCRIPTION: The specimen is horn-shaped, with the cardinal protoseptum located on its concave side. Such a location is atypical in the genus *Rotiphyllum*. This feature alone is not, however, critical to its generic affiliation. The external wall, covered with delicate septal grooves and growth striae, is up to 1.6 mm thick in the middle part of the calice and 0.8–1.0 mm near its floor. Major septa in the earliest growth stage preserved (Text-fig. $18A_1$), with n:d value 22:4.7 mm, are strongly thickened and laterally contiguous either along their entire extent or in their inner segments. Those of the cardinal quadrants are longer than those of the counter quadrants and are less regularly arranged. The cardinal protoseptum dominates in length and thickness. It approaches the counter protoseptum behind the corallite axis. One alar septum, and the penultimate major septa in the cardinal quadrants, are almost as long as the cardinal protoseptum. They reach the counter-lateral septa. Other major septa in the cardinal quadrants, including one alar septum, are much shorter than those mentioned above.

Major septa in the counter quadrants shorten regularly, starting from the counter-lateral septa and ending with the last pair inserted. Their inner margins form a kind of arch above the cardinal quadrants. Minor septa are absent from both the corallite lumen and the external wall. The thickness of the latter (one millimetre) is equal to the length of the counter protoseptum.

The morphology near the calice floor, with n:d value 23:5.5 mm (Text-fig. $18A_2$), is similar to that described above. However, the major septa in that growth stage become regularly pinnately arranged in all quadrants. The cardinal protoseptum remains longer than 2–3 pairs of the adjacent major septa, but it does not reach or approach the counter protoseptum. The arrangement of 'middle dark lines' (i.e., the primary major septa) imitates the adaxially widened cardinal fossula and alar pseudofossulae. However, all those fossulae and the circumaxial area of the corallite are filled in with sclerenchyme. In contrast to the earlier growth stage, all major septa in counter quadrants are laterally contiguous along their entire extent, whereas openings appeared in peripheral parts of septal loculi in cardinal quadrants. Some of those loculi are filled in with matrix, i.e., they were sectioned above the calice floor.

The section 0.5 mm above the previous one, with n:d value 24:7.0 mm, was cut above the calice floor in the cardinal quadrants (Text-fig. 18_3). This is the highest level of the calice possessing the last pair of major septa in counter quadrants somewhat underdeveloped, thus allowing recognition of the alar pseudofossulae. The next two transverse sections were cut above the calice floor, except for the loculus left of the counter protoseptum (Text-fig. $18A_{4,5}$). This protoseptum dominates by being more strongly thickened than the other major septa. The major septa thin and shorten step by step in both directions, starting from the counter protoseptum towards the cardinal protoseptum. The latter protoseptum, although short, is not the shortest (Text-fig. $18A_{3-5}$).

A peculiar modification of one counter-lateral septum is worth mentioning although it is not of taxonomic significance. The process starts from a hardly recognizable separation of the peripheral-most fragment of the septum in question (Text-fig. $18A_{3,8}$ [arrow]). Only 0. 4 mm higher in the corallite growth (Text-fig. $18A_{4,5,9}$ [arrow]) that separated fragment becomes a short, but easily recognizable septum, whereas the counter-lateral septum becomes attached to the next major septum. At the beginning of the process (Text-fig. $18A_{4,9}$), the inner segments of those two septa look like a longitudinally split septum. Then (Text-fig. $18A_{5,10}$) a strange fabric appeared in the slit between two arms of the 'fork', documenting its section above the calice floor. The process ends with two forks that are free axially (Text-fig. $18A_6$). The total number of major septa remains the same and equal (11) in both directions from the cardinal protoseptum to the counter protoseptum, if either two forks or a short septum are included in the calculation (Text-fig. $18A_{4,5}$). The short septum adjacent to the counter protoseptum is thus nothing but an ephemeral fragment of the counter-lateral septum, the remaining part of which forms the also ephemeral fork mentioned above. The short septum disappears well below the calice margin (Text-fig.$18A_{6,10}$ [right arrow]). Simultaneously to the disappearance of the short septum, the right fork, i.e. the former counter-lateral septum, approaches the external wall (Text-fig. $18A_{10}$ [left arrow]) and then reaches it (Text-fig. $18A_7$) However, the bases of the counter-lateral septum and its neighbouring major septum remain closely attached.

The phenomenon described is interpreted as an anomaly in the formation and operation of septal pockets that secreted the counter-lateral septum and the major septum adjacent to it. The former pocket of the counter-lateral septum was reduced to a bubble on the inner margin of

the external wall, while an extra fold of the adjacent septal pocket appeared simultaneously. That extra fold became free axially and expanded peripheral-wards until two regular septal pockets became re-constructed and a normal counter-lateral septum became secreted.

DISCUSSION: The neanic morphology of the specimen discussed and the great thickness of its external wall resemble those features in *R. latithecatum*. Also, its n:d value resembles those of the smallest specimens of that species, to which it is probably related. It differs distinctly from *R. latithecatum* and from all other *Rotiphyllum* in its peculiar shape of the calice floor and in the arrangement of the major septa at maturity.

OCCURRENCE: Solenaya River Area, Novo Troitskoe Village, Limestone F_1, Lower Blagodatnian Subhorizon.

CONCLUSIONS

1. A brief discussion on the history of investigation of the Bashkirian Stage, its substages and individual biozones has show the lack of generally acceptable standards. Such a situation caused difficulty in establishing the rigid stratigraphic positions of the individual species described. The occurrence of the corals in particular limestones is here considered the best method for establishing the sequence of their appearance.

2. Neither the morphology nor the sequence of appearance of the individual taxa allows a phylogenetic lineage within the genus *Rhotiphyllum* to be established. Only some species may be grouped in possibly related pairs. It is therefore possible that most species were immigrants. Unfortunately, the very limited knowledge of the Early Bashkirian and Late Serpukhovian coral faunas precludes reasonable suggestions of their origins.

3. Despite diagenetic alterations of most specimens, it was possible to establish some microstructural data, all of which suggest a very finely trabecular septal microstructure. This and the typically rotiphylloid early ontogeny of all species, including those left in open nomenclature, proves their close relationship.

4. The generic name *Rotiphyllum* was not applied so far to the Carboniferous corals of the Donets Basin, albeit some species belonging to that genus were described under different generic names (see the synonymy of the genus).

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