

# Early Bashkirian Rugosa (Anthozoa) from the Donets Basin (Ukraine). Part 6. The Family Aulophyllidae Dybowski, 1873

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## ABSTRACT

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Seven genera (one new), belonging to four subfamilies, seven named species (six new), four species left in open nomenclature and two specimens included in this paper as unnamed Aulophyllidae are described from strata ranging from the lowermost Bashkirian Limestone D<sub>5</sub><sup>10</sup> to the lower Bashkirian Limestone F<sub>1</sub>. A new genus: *Voragoaxum* and six new species: *Dibunophyllum medium*, *Dibunophylloides columnatus*, *D. paulus*, *D. similis*, *Voragoaxum cavum* and *Rozkowskia lenta* are introduced. Comparison of the ontogeny of the earliest Bashkirian species of *Nina* Fedorowski, 2017a and *Dibunophylloides* Fomichev, 1953 suggest the derivation by descent of the Family Bothrophyllidae from the Subfamily Dibunophyllinae. This means that true bothrophylla are absent in the Mississippian strata of the Western European Province and, perhaps, in the contemporaneous strata of other areas as well.

**Key words:** Donets Basin; Rugosa (Aulophyllidae); Bashkirian; Taxonomy; Phylogeny; Relationships.

## INTRODUCTION

This paper follows my earlier contributions dealing with the early Bashkirian Rugosa of the Donets Basin (Text-fig. 1). For the introductory data the reader is referred to the first paper of the series (Fedorowski 2009a). Detailed descriptions of stratotypes of particular stages and substages established in the Donets Basin have been recently published by Poletaev *et al.* (2011) and are not repeated here. Fedorowski and Ogar (2013) published a detailed description of a new section of the Voznesenskian stratotype at the Berestovaya River mouth. Fedorowski (2017a) summarized the geological data of the Limestone Groups D, E, F (Text-figs 2–4), which have yielded various rugose corals, including those described in the present paper.

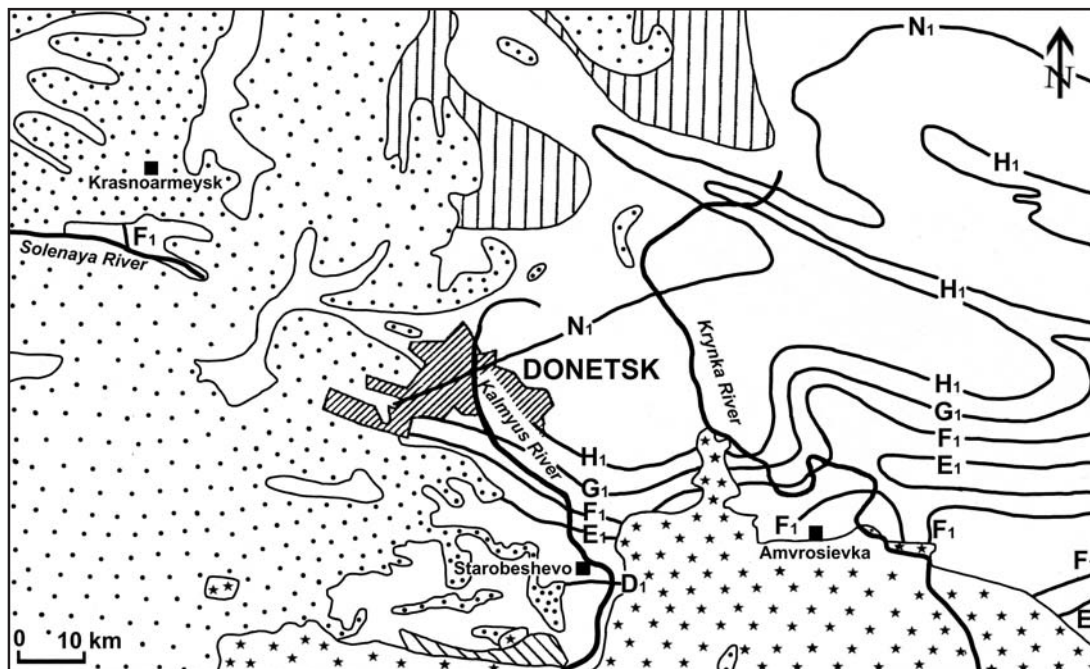
Four taxa are left in open nomenclature. Their questioned identification reflects both the incom-

pleteness of the material and the occurrence in *Zakowia?* sp., *Spirophyllum?* sp. 1 and *Spirophyllum?* sp. 2 of some characters disagreeing with diagnoses of those genera. The question mark applied to the name *Arachnolasma* reflects its uncertain generic status. In addition to those four species left in open nomenclature, four specimens are described and illustrated as unnamed Species 1 and Species 2. The characters of those specimens, aulophyllid in general, do not follow the diagnoses of any of the existing genera. The omission of these six unnamed taxa would lead to an apparent reduction of the taxonomic variability of the Rugosa during the deep early/late Carboniferous faunal turnover. Thus that option is not followed.

Following Hudson (1936) and Fedorowski (1997a) only the cardinal and the counter major septa are considered as protosepta. As in my earlier papers, the term “primary septa” refers here to the innermost



Text-fig. 1. General map of Ukraine showing the approximate position of the study area (copied from Fedorowski 2009a)



Text-fig. 2. Vicinity of the town of Donetsk. General positions of individual Limestone Groups (D to N). All Carboniferous deposits left in white (provided by Dr. N.P. Vassilyuk, copied from Fedorowski 2009a)

parts of septa, created within septal pockets prior to secretion of the sclerenchymal sheets. These primary septa are described in the part of the paper devoted to the microstructure of septa.

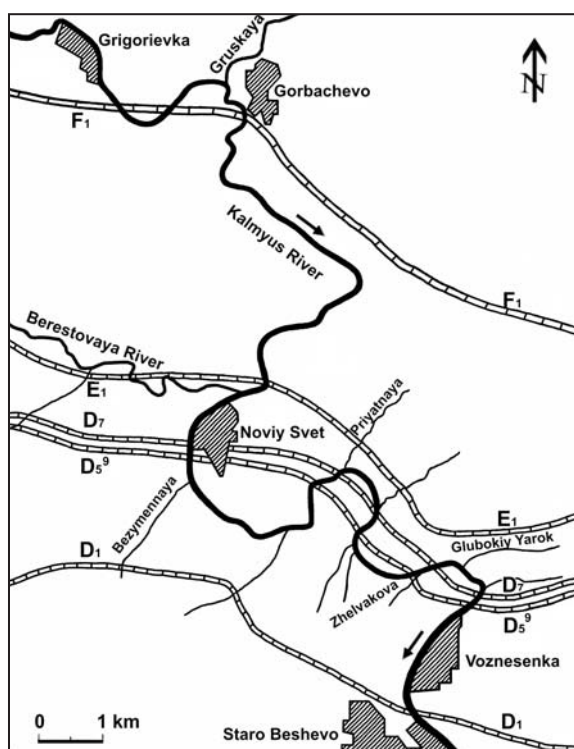
The corals described in this paper are housed in the Institute of Geology, Adam Mickiewicz University in Poznań (collection acronym UAM-Tc/Don.1).

**NEW ENGLISH TERM: Grape-like dissepiments**

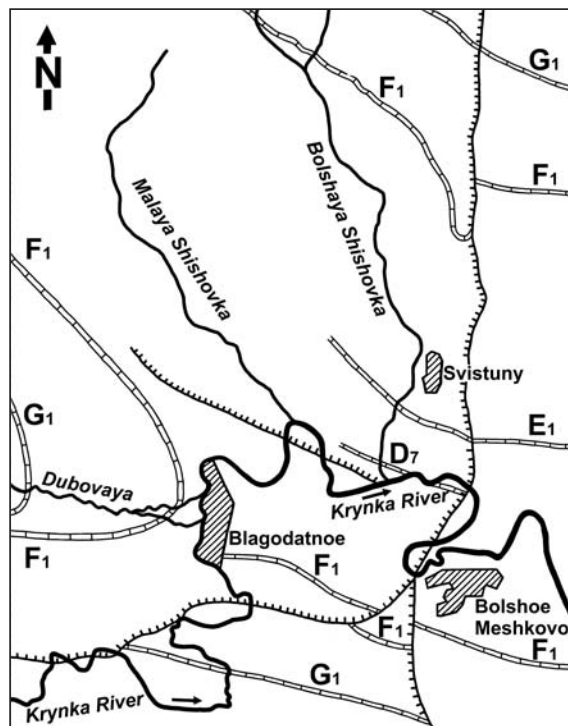
– very small dissepiments, attached to septa at the corallite periphery in a way that imitates bunches of grapes. This term is here translated from the Russian term *grozdevidnyi*, commonly applied by Fomichev (1953). Such dissepiments resemble pseudonaotic septa, but differ from them by being attached to continuous septa. Dissepiments of that arrangement were not recognised by Hill (1981).

**MATERIAL AND METHODS**

The specimens described in this paper belong to the collection gathered by Dr. N.P. Vassilyuk, Professor Emeritus of the Donetsk Polytechnic, Ukraine during many years of her fieldwork. The material has been offered to me for both investigation and housing. The generally extreme rarity of the early Bashkirian Rugosa is the reason why some taxa are named here despite the small number of specimens available for study. Nevertheless, only taxa represented by specimens with at least part of the early and mature growth stages preserved have been named. Taxa represented



Text-fig. 3. Outcrops along the Kalmyus River, south of the town of Donetsk. The most important ravines (balkas) are named. Distribution of Limestone Groups D to F drawn as bands with brick ornaments (provided by Dr. N.P. Vassilyuk, copied from Fedorowski 2009a)



Text-fig. 4. Outcrops along the Krinka River, south of the town of Donetsk. The most important ravines (balkas) are named. Distribution of Limestone Groups D to F drawn as bands with brick ornaments (Provided by Dr. N.P. Vassilyuk, copied from Fedorowski 2009a)

by single, incomplete specimens are left in open nomenclature, but are described and illustrated when their macroscopic morphology is well preserved. Images of poorly preserved corallites are augmented by computer drawings based on large magnifications of images. Specimens for thin sections and peels were cut with a 0.05 mm thick wire.

**SYSTEMATIC PALAEOLOGY**

Order Stauriida Verrill, 1865  
 Suborder Aulophyllina Hill, 1981  
 Family Aulophyllidae Dybowski, 1873  
 Subfamily Aulophyllinae Dybowski, 1873  
 Genus *Zakowia* Fedorowski, 1971  
 (Type species *Zakowia sanctaerucensis*  
 Fedorowski, 1971)

*Zakowia?* sp.  
 (Text-fig. 5)

**MATERIAL:** One fragment of specimen UAM-Tc.

Don.1/166. Probably mature growth stage. Small sector of corallite crushed. Two peels and one transverse thin section available for study. 2.5 mm thick remnants of specimen too short for reliable longitudinal section.

**DESCRIPTION:** Major septa radially arranged, slightly thickened in tabularium next to dissepimentarium. In ontogenetically earlier growth stage (Text-fig. 5A), almost all major septa disconnected from their axial lamellae. Rare major septa continuous, meeting inner margin of cardinal septum that extends to corallite axis. Counter septum indistinguishable in length and thickness from adjacent major septa. Minor septa (Text-fig. 5A, B) differentiated in length; in cardinal quadrants well developed, some reaching thick inner wall; in counter quadrants very short; from some septal loculi absent. Rare septa interrupted by small lonsdaleoid dissepiments at periphery of counter quadrants. Axial structure based on inner margin of cardinal septum. Septal lamellae in early mature growth stage (Text-fig. 5A) numerous, supplemented by rare extra septal lamellae. In more advanced growth stage (Text-fig. 5B), axial structure reduced to very few septal lamellae and some inner margins of continuous major septa. Cardinal fossula either absent or very shallow. Dissepimentarium in counter quadrants reaches almost 1/2 corallite radius in width, reduced towards cardinal septum to less than 1/3 corallite radius. Dissepiments varying in size, irregular and herringbone. Lonsdaleoid dissepiments small and reduced to very few.

**REMARKS:** Specimens of *Zakowia* have not been described since the introduction of that genus (Fedorowski 1971, p. 30). Thus their appearance in stratigraphically younger strata (Limestone F<sub>1</sub>, Blagodatnian Substage, late early Bashkirian) is worth documenting in spite of being represented by a single, incomplete corallite. The questionable assignment of that corallite to *Zakowia* results from its insufficient preservation rather than lack of the main diagnostic characteristics. Its morphology is simplified by comparison to the Brigantian species from the Holy Cross Mountains in Poland (Fedorowski 1971, figs 8A<sub>2</sub>– B<sub>1</sub>; 9A–C). That simplification concerns the axial structure and the dissepimentarium. The latter is most important. Lonsdaleoid dissepiments occur in the Donets Basin specimen, whereas a grape-like peripheral dissepimentarium is observed in the Polish species. *Zakowia?* sp. resembles *Zakowia sanctaecrucensis* Fedorowski, 1971, the type species of the genus, in having a long cardinal septum, constituting the basis for the axial structure. However, that structure in *Zakowia?* sp. is

much narrower and simpler than in the type species, being more similar in size to the axial structure in *Z. parva* Fedorowski, 1971. The latter species differs from both the type species and the Donets Basin specimen in having the cardinal septum shortened and the cardinal fossula well developed. The latter character makes questionable the co-generic position of *Z. parva* with both the type and the Donets Basin species.

**OCCURRENCE:** Volnukhino Village, left bank of Luganchik River. Limestone F<sub>1</sub>, Mandrykinian Stage, Blagodatnian Substage, late *Bilinguites*–*Cancelloceras* ammonoid Biozone, *Pseudostaffella pre-gorskyi*–*Staffelleformis staffelleformis* foraminiferal Biozone, *Idiognathodus sinuosus* conodont Biozone. Late early Bashkirian.

Subfamily Amygdalophyllinae? Grabau in Chi, 1935

**REMARKS:** The position of the Subfamily Amygdalophyllinae within the Family Aulophyllidae (Hill 1981) is generally accepted. However, that solution appears questionable when the substantial isolation of the eastern Australian seas from the European and northern African seas in Mississippian times is taken into account. That isolation, proposed long ago and repeated much later (Fedorowski 1981, 2008) was supported by Webb (1994, 2000). It puts into doubt the true relationships of the rugose coral taxa described from those distant areas. This statement also concerns the Australian *Amygdalophyllum etheridgei* Dun and Benson, 1920 and the European-north African species included in the genus. i.e., *Amygdalophyllum* Dun and Benson, 1920 (e.g., Fedorowski 1970; Semenoff-Tian-Chansky 1974; Żołyński 2000). Poty's (2007, p. 243) opinion is most advanced in that respect. He mentioned "*Lophophyllum*" sp. of Poty (1989) from the Hastarian (lower Tournaisian) strata of Belgium and the late Tournaisian *Cyathoclisia* Dingwall, 1926 as possible ancestors of *Amygdalophyllum* and wrote (Poty 2007, p. 243) "It [i.e., *Amygdalophyllum*] could quite arise from a representative of these taxa before it spread at the end of the Tournaisian." That recognition suggests an almost worldwide migration of *Amygdalophyllum* from the Dinant-Namur Basin in Belgium at least in the first instance. Unfortunately, the data published by Poty (2007) are not convincing enough for acceptance of his concept. An unquestionable and direct connection between the eastern Australian and the European-north African seas, allowing coral larvae to cross such an enormously large distance, forms the first condition necessary

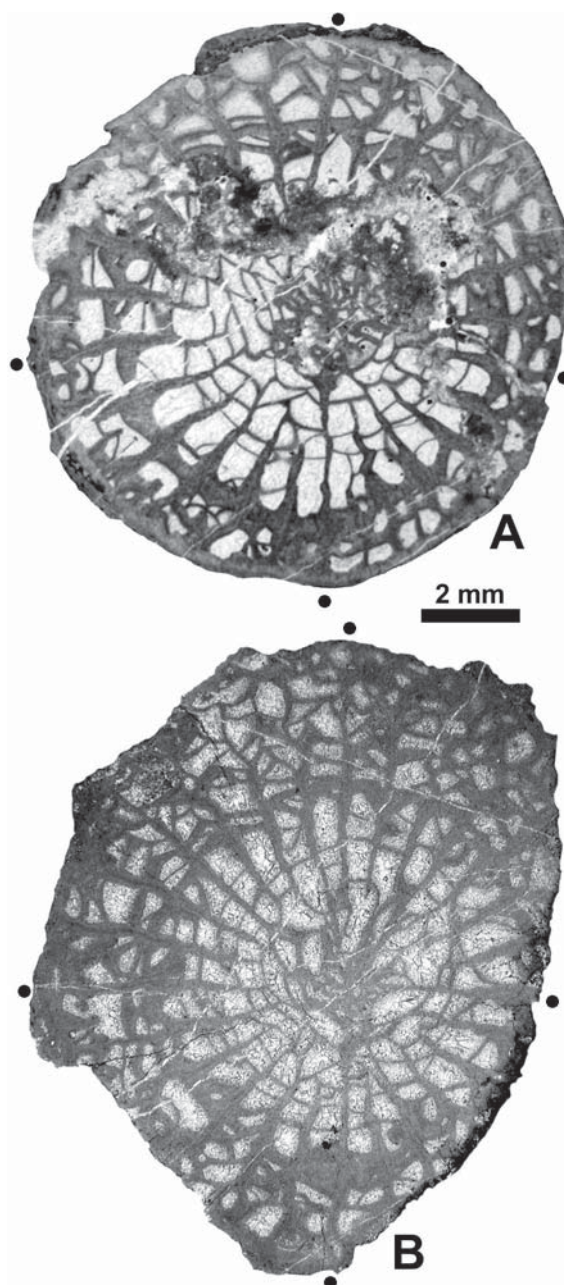
for accepting that relationship. Closely comparable ontogenies and microstructure of septa in species of the Amygdalophyllinae present in both Australia and western Europe forms the second condition. Nothing like that is available from the literature data. Thus, the genus *Spirophyllum* Fedorowski, 1970, related to the European-north African Aulophyllidae, is here questionably included in the Subfamily Amygdalophyllinae because a more suitable subfamily is not available at the moment and a new subfamily is not proposed.

Genus *Spirophyllum* Fedorowski, 1970  
 (Type species *Spirophyllum sanctaecrucense*  
 Fedorowski, 1970)

EMENDED DIAGNOSIS: Dissepimented, solitary Rugosa; incipient colonies may occur; axial structure consists of free septal lamellae, complex pseudocolumella with contiguous septal lamellae incorporated and axial tabellae; extra septal lamellae absent; cardinal septum may meet median lamella; tabularium normal; tabulae incomplete, typically forming axial column-like bunches; dissepimentarium with rare lateral dissepiments and common grape-like dissepiments at periphery; microstructure of septa finely trabecular.

REMARKS: The emended diagnosis of the genus *Spirophyllum* differs slightly from its original diagnosis, published almost half a century ago (Fedorowski 1970, p. 571). Two reasons make both the emendation and the discussion necessary: 1. the taxonomic value and the discussion necessary: 1. the taxonomic value of the biform tabularium of Weyer (1972); and 2. the extra septal lamellae of Fedorowski *et al.* (2007). The first character was not interpreted clearly enough and the second was not named at the time when the genus *Spirophyllum* was introduced.

The biform tabularium is based on the so-called Positions I and II of the tabulae, established by Sutherland (1965) for Silurian taxa. The opposite inclination of two parts of tabulae, recognized by Sutherland (1965) in corals with the minor septa contrasting, was shown to be of truly important taxonomic value through the reinvestigation and redefinition by Weyer (1972). He documented the occurrence of such peculiar tabulae not only in the non-dissepimented corals, but also in both solitary and colonial dissepimented taxa. The term “biform tabularium” introduced by Weyer (1972) in opposition to the normal tabularium, i.e., consisting of one way directed tabulae, is now accepted as an important qualitative difference.



Text-fig. 5. *?Zakowia* sp. Specimen UAM-Tc.Don.1/166. Transverse thin section (A) and peel (B). Mature growth stage. For stratigraphic position see text. Scale bar corresponds to both images

The understanding of the biform tabularium has been further developed by Fedorowski *et al.* (2007), who established the difference between the clinotabulae, an important character recognized by Minato and Kato (1965) for the Family Waagenophyllidae Wang, 1950, and the biform tabularium. Fedorowski *et al.* (2007, p. 43) introduced the term “extra septal lamellae” for the lamellae in an axial structure

corresponding to minor septa. Those lamellae were known for almost two centuries from the illustration of *Turbinolia fungites* Fleming, 1828, the type species for *Aulophyllum* Milne Edwards and Haime, 1850, but they remained unnamed and not distinguished from normal septal lamellae, i.e., those corresponding to major septa.

The preceding remarks allow one to contest the original content of *Spirophyllum* and *Amygdalophyllum* established by Fedorowski (1970) and justify the differentiation and grouping proposed herein. This grouping is not a formal revision of the genus *Spirophyllum*. It only points to the morphological diversity of species formerly included in *Spirophyllum* and allows the characters diagnostic for the emended *Spirophyllum* to be established. Thus, only the Polish species described by Fedorowski (1970) are considered. Species of that genus introduced since then (e.g., Rodríguez 1984; Wu and Zhao 1989; Berkowski 2002; Chwieduk 2005; Ogar *et al.* 2013) are either not discussed or only briefly commented.

The following morphological variants (taxa?) among the species mentioned can be established. The holotype and all specimens included in both subspecies of *S. sanctaecrucense* contain only normal septal lamellae in their axial structures and possess a normal tabularium. Their axial columns are discontinuous. The same is true for *S. clisium* Fedorowski, 1970, *S. densum* Fedorowski, 1970, *S. regulare* Fedorowski, 1970, *Amygdalophyllum axophylloides* Fedorowski, 1970 and *Amygdalophyllum* aff. *inopinatum* (Etheridge, 1900). The Polish specimens of *Spirophyllum histiophylloides* (de Groot, 1963) also belong to that group, but a new species name should be introduced for them. The Spanish specimens, originally described by de Groot (1963, p. 64) as *Koninckophyllum histiophylloides*, have been revised by Fedorowski (2004, p. 98), who transferred them to the genus *Mirka* Fedorowski, 1974, a position accepted herein. Thus, only the species listed above and *S. geminum* (see below) are now considered to belong to the genus *Spirophyllum sensu stricto*.

*Spirophyllum divisum* Fedorowski, 1970 possesses the main features of *Spirophyllum* proper, but differs from it in having a continuous axial column, similar to that in the genus *Dibunophyllum*. Thus, it may represent a different subgenus.

*Spirophyllum perditum* Fedorowski, 1970 has a normal tabularium, but it incorporates some extra septal tabellae in its axial structure. During the early growth stage its pseudocolumella is solid and complex, resembling *S. sanctaecrucensis*. However, in advanced maturity the pseudocolumella forms a

dense spire of septal lamellae supplemented by axial tabellae to surround a thin median lamella. Even that rudimentary structural element disappears from some specimens. The difference in the two qualitative characters may appear adequate for the distinction of its bearers at subgeneric level.

*Spirophyllum nexilis* (Vassilyuk, 1964), *S. multilamellatum* (de Groot, 1963) of Fedorowski (1970) and *S. complexum* Fedorowski, 1970 form a group of species possessing extra septal lamellae in their axial structures and biform tabularia. Extra septal lamellae are absent from the revised Spanish specimens of *Koninckophyllum multilamellatum* and the biformity of their tabularia is either uncertain or absent. Thus, the co-specific position of the Polish and Spanish specimens has been already questioned (Fedorowski 2004, pp. 111, 112). I now exclude the Polish specimen from the Spanish species, but continue to accept the position of that Spanish species in *Spirophyllum*.

*Spirophyllum geminum* Fedorowski, 1970 is morphologically similar to the group of *Spirophyllum sensu stricto* and is accepted herein as being co-generic with *S. sanctaecrucense*. However, this is the only species in the collection showing a potential to produce intracalicular offsets. That kind of offsetting is closely comparable to the rejuvenation as discussed recently in the case of *Bothrophyllum* (Fedorowski 2016). The process, named “multiple rejuvenation”, was probably initiated by an environmental stress causing the polyp to divide its body into several offset-like structures in order to survive. The multiple rejuvenation ends with immature daughter individuals, considerably differing from the intracalicular (peripheral) offsetting, such as in *Diphyphyllum* Lonsdale, 1845. The latter leads to the formation of regular, sometimes large colonies. The name “incipient colony”, proposed already for the offsetting *Spirophyllum* (Fedorowski 1970, p. 600) seems proper for all individuals offsetting that way irrespective of their taxonomic position. An incipient colony should be distinguished from the protocolony of Fedorowski and Ogar (2013), in which lateral offsetting leads to the formation of the “lost structures” of Fedorowski (1978). Such lost structures may appear several times during a given protocorallite growth.

All taxa characterized above were derived from the identical deposits of two neighbouring outcrops in the Holy Cross Mountains (Poland). Specimens identified as different species of *Spirophyllum* and several other genera (Fedorowski 1970, 1971) are commonly found next to each another. The same is true for numerous dissepimented solitary corals other than those described in the papers cited, and for

many non-dissepimented corals and colonial rugose coral taxa collected from those outcrops and yet undescribed. The corals are accompanied by abundant crinoid ossicles, brachiopods, trilobites, pelecypods, bryozoans, rare goniatitids and algae. All specimens belonging to those taxa are worn, as has been already stated (Fedorowski 1971, pp. 17–20). The terms “tempestites” or “turbidity current deposits” were not in use when that paper was written, but this was what I had in mind. Thus, not only the specimens of *Spirophyllum*, but all fossils derived from the localities mentioned above are bioclasts. They were probably carried by turbidity currents as suggested by the lack of traces of erosion. The mixture of all the so-called coral “faunas” of Hill (1938–1941), i.e., the *Cyathaxonia* fauna, the *Caninid–Clisiophyllid* fauna, and the *reef coral* fauna confirms that deduction. That interpretation also explains both the extreme richness and diversification of the fauna and the occurrence of several species of the same genera mixed together in the rocks to form a time-average assemblage.

*Spirophyllum?* sp. 1  
(Text-fig. 6)

**MATERIAL:** Two transverse and one longitudinal thin sections of specimen UAM-Tc.Don.1/167 and one longitudinal thin section of specimen UAM-Tc.Don.1/168, both without rock material left after thin sectioning. Macroscopic morphology well preserved. Microstructure of septa diagenetically altered.

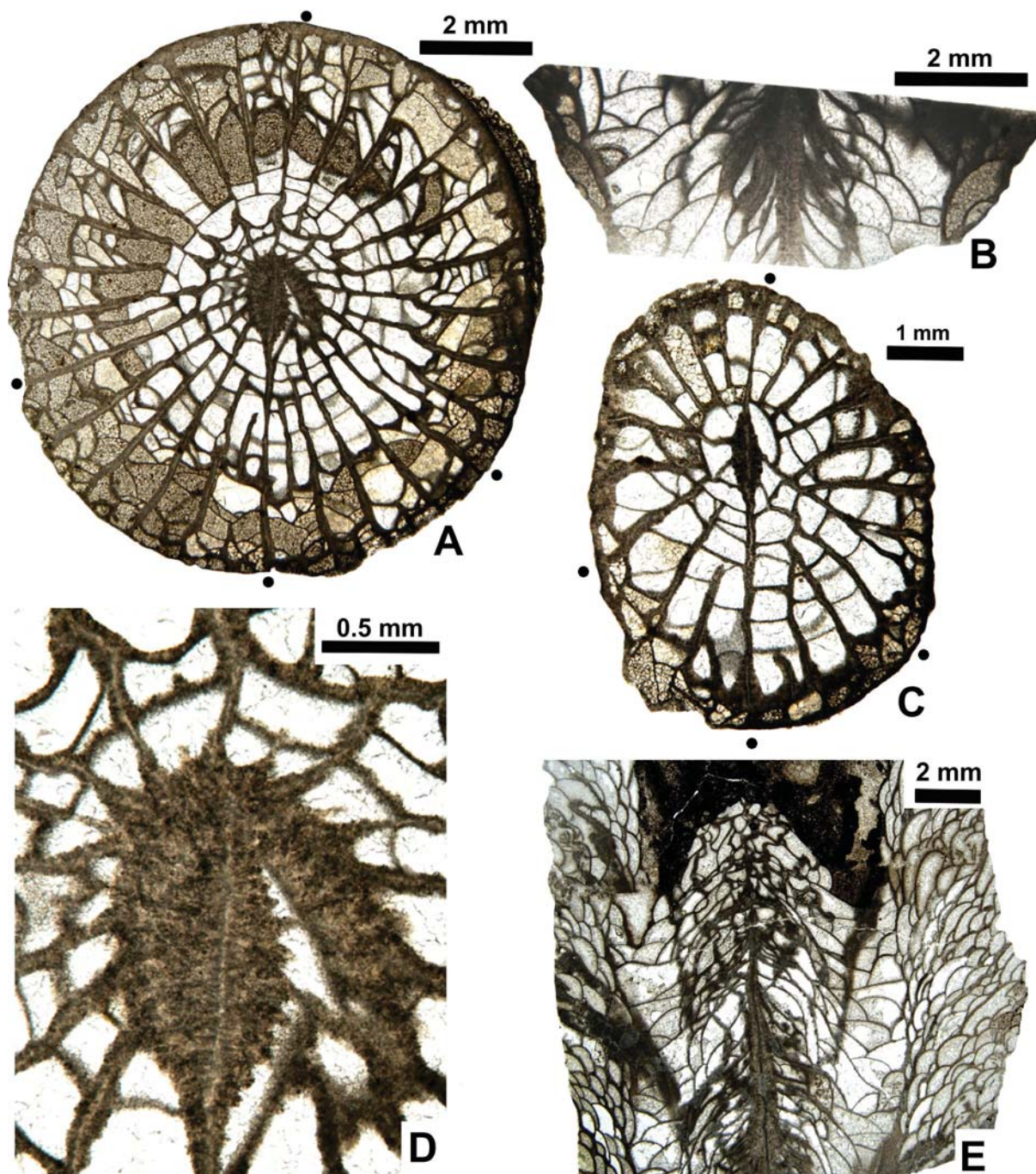
**DESCRIPTION:** Morphology of late neanic/early mature growth stage of the specimen UAM-Tc.Don.1/167 with n:d value 29:6×4 mm (Text-fig. 6C) resembles comparable growth stage of *Dibunophyllum*. Axial septum well developed with middle part thickened. Four inner margins of longest major septa incorporated in that thickened part marking the early stage of formation of complex pseudocolumella. Major septa in counter quadrants semi radially arranged, accelerated in increase (six and seven vs. four in each cardinal quadrant), most leaving the axial area free. Minor septa present in most septal loculi. Cardinal fossula distinct. Dissepiments regular when in single row, irregular in size when two or three rows present in some loculi.

In mature growth stage of that specimen with n:d value 23:10.0×9.5 mm (Text-fig. 6A) major septa long, continuous. Last major septa inserted in cardinal quadrants consist of long fragments in tabularium and short fragments at periphery of dissepimenta-

rium. Inner margins of some major septa incorporated directly in pseudocolumella (Text-fig. 6D, left). Other terminated within thickness of axial tabella located close to pseudocolumella, but their septal lamellae incorporated in pseudocolumella (Text-fig. 6D, right). Few thick extra septal lamellae traced in pseudocolumella and in thickness of axial tabella mentioned. Median lamella of pseudocolumella elongated towards and united with cardinal septum. Direct connection of median lamella to counter septum less obvious, but probable (Text-fig. 6A, D). Cardinal fossula indistinct. Minor septa restricted to peripheral dissepimentarium; better developed in cardinal quadrants, in counter quadrants very short, hardly recognizable. Dissepimentarium slightly more than 1/4 corallite radius in width. Dissepiments differentiated in size and arrangement. Almost regular between major and minor septa, large and irregular directly above minor septa, herringbone in inner dissepimentarium. Innermost dissepiments in counter quadrants commonly elongated towards major septa. Their inner parts reach lateral surfaces of septa whereas outer parts rest on underlying dissepiments. The position described distinguishing those dissepiments from the lateral dissepiments of Hill (1981), attached to the lateral surfaces of both sides of septa. Their occurrence makes the dissepimentarium / tabularium border indistinct, i.e., the development of the disstabularium of Fedorowski (2016).

In longitudinal section of specimen UAM-Tc.Don.1/167 (Text-fig. 6B), taken from the early mature growth stage, i.e., between the transverse sections illustrated in Text-fig. 6A and C, the dissepiments differentiating in size, arranged in steep rows. Tabulae incomplete. Peripheral tabellae convex, dissepiment-like. Inner tabellae elongated steeply towards pseudocolumella, most of them strongly thickened by sclerenchyme.

The longitudinal thin section of corallite UAM-Tc.Don.1/168, taken from its cylindrical, mature part and calice resembles *Amygdalophyllum* (= *Spirophyllum*) *nexilis* Vassilyuk, 1964 (Vassilyuk 1964, pl. 6, fig. 3b) in morphology. Corallite slightly more than 15 mm wide (external wall corroded). Incomplete depth of calice 7.5 mm. Axial column elevated 2.8 mm above calice floor. Dissepimentarium 1/3 of corallite radius in width. Dissepiments differentiated in size, arranged steeply, inner row vertical. Tabulae incomplete. Elevated peripheral tabellae anastomose with horizontal and dissepiment-like peripheral tabellae. Inner tabellae differentiated in length, elevated towards pseudocolumella. Some lateral lamellae border fragments of axial column. Most of densely packed



Text-fig. 6. ?*Spirophyllum* sp. 1. A-D – Specimen UAM-Tc.Don.1/167. Transverse thin sections, except for B and E. A – mature growth stage, B – longitudinal thin section, C – late neanic/early mature growth stage, D – enlarged from A to show pseudocolumella consisting of median lamella and septal lamellae laterally contiguous. E – Specimen UAM-Tc.Don.1/168. Longitudinal thin section. For stratigraphic position see text. Scale bars indicate enlargements of individual images

axial tabellae pass gently into middle tabellae, which are longer, less steeply elevated and arranged looser than the axial tabellae that form axial structure.

REMARKS: Only the scarcity of the late Bashkirian

Rugosa legitimizes the inclusion of specimen UAM-Tc.Don.1/168 represented by a single longitudinal section in this paper. It most probably represents a species different from the other specimen included in *Spirophyllum*? sp. 1, but it is included in that species



in order to reduce the number of incompletely documented taxa. Its morphology resembles some longitudinal sections of *Spirophyllum* (e.g., Fedorowski 1970, text-fig. 12: 2b; pl. 3, fig. 7).

Specimen UAM-Tc.Don.1/167 resembles most species of *Spirophyllum sensu lato* in the morphology of the longitudinal section. Also, the inner margins of its major septa tend to spire. The morphology of the pseudocolumella with thick extra septal lamellae incorporated and the morphology of the dissepimentarium distinguish that corallite from all species of *Spirophyllum* described so far. Comparable characters allow it to be considered as a relative of *Spirophyllum* but the differences suggest its position in a new genus, not introduced here.

**OCCURRENCE:** Kalmyus River Area, Solenaya River Bank near Novo-Troitskoe Village. Limestone F<sub>1</sub>, Mandrykinian Stage, Blagodatnian Substage, late *Bilinguites–Cancelloceras* ammonoid Biozone, *Pseudostaffella pregorskyi–Staffelleformis staffelleformis* foraminiferal Biozone, *Idiognathodus sinuosus* conodont Biozone. Late early Bashkirian.

*Spirophyllum?* sp.2  
(Text-fig. 7)

**MATERIAL:** Two specimens UAM-Tc.Don.1/169 and UAM-Tc.Don.1/239. Lower part of calice preserved in second corallite, neanic growth stage preserved in both. Microstructure of septa destroyed by diagenesis. Six thin sections, eight peels and six polished surfaces available for study.

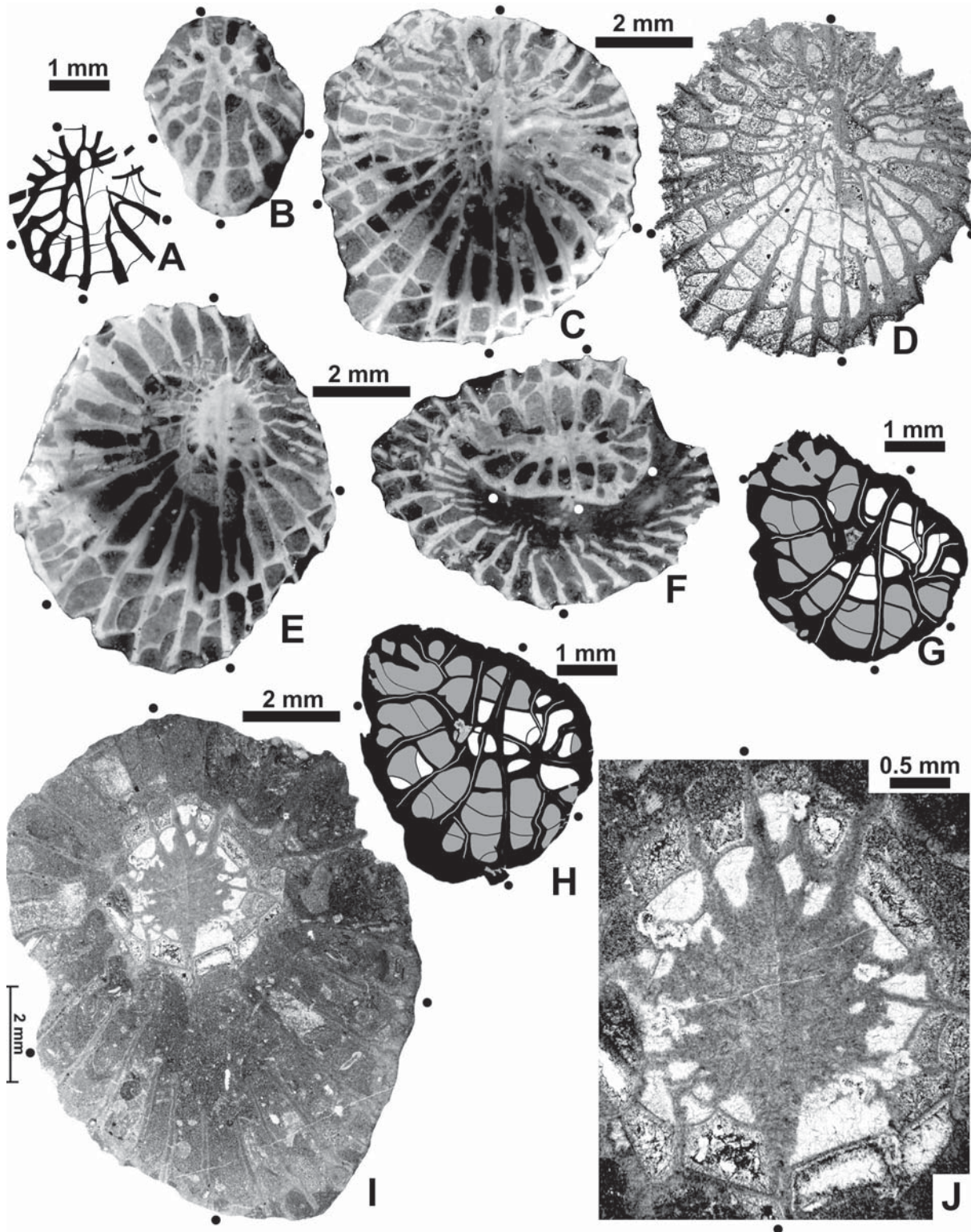
**DESCRIPTION:** In neanic growth stage of specimen UAM-Tc.Don.1/169 (Text-fig. 7A, B) with n:d value 19:3.0×2.6 mm (both diameters incomplete), major septa zaphrentoidally arranged, those of counter quadrants prevailing in number. Axial septum present; its middle part thickened to form monoseptal pseudocolumella. Cardinal fossula distinct. Minor septa and dissepimentarium not developed yet. Neanic growth stage of specimen UAM-Tc.Don.1/239 (Text-fig. 7G, H) differs from specimen UAM-Tc.Don.1/169 in n:d values (17:4.0×3.0 mm and 17:4.2×4.0 mm). Also, the arrangement of its major septa is irregular. Irregularity resulted mostly from attachment to substrate and partly from diagenetic alterations.

In mature growth stage of specimen UAM-Tc.Don.1/169 (Text-fig. 7C–F) with maximum n:d value 28:7.0×7.5 mm (both diameters incomplete), major septa thickest in outer tabularium and inner dissepimentarium, thin in their inner parts, but their inner margins thickened when incorporated in the sclerenchymal thickening of tabulae. Most major septa reach pseudocolumella. Axial septum continued to occur, but its median lamella connected with cardinal septum closer than with counter septum. Inner morphology of pseudocolumella destroyed by diagenesis. Its outline slightly wavy; some inner margins of major septa and remnants of incorporated septal lamellae suggesting a complex structure typical of *Spirophyllum*. Minor septa eroded together with most of the dissepimentarium. Cardinal fossula indistinct, or absent, not dips into dissepimentarium. Dissepiments irregular. Rejuvenation confirms zaphrentoid arrangement of major septa in neanic growth stage and length of cardinal septum indistinguishable from other major septa in calice (Text-fig. 7F, lower).

The mature morphology of specimen UAM-Tc.Don.1/239, documented by transverse section above calice floor (Text-fig. 7I), with n:d value 29:8.6×10.8 mm (both diameters very incomplete), resembles *Dibunophyllum*. Arrangement of septal lamellae and sections of axial tabellae suggest occurrence of axial column. However, pseudocolumella incorporating contiguous septal lamellae (Text-fig. 7J) typical for *Spirophyllum*. Median lamella of pseudocolumella disconnected from cardinal septum only above calice floor. Slight and not clearly documented depression next to short cardinal septum may suggest occurrence of septal fossula.

**REMARKS:** The morphology of the immature growth stage and the arrangement of the major septa in the mature growth stage with the cardinal septum dominating and the cardinal fossula marked by the underdevelopment of the last pair of major septa are features closely comparable to *Spirophyllum?* sp. 1. The mature morphology of both species differs from that of the type species to an extent adequate for their distinction at a genus level. The similarity of *Spirophyllum?* sp. 2 (Text-fig. 7) to *Dibunophylloides columnatus* sp. nov. (Text-fig. 17) may either be incidental, or it may suggest a relationship between those two taxa. Only a more complete collection would solve that question.

**OCCURRENCE:** Kalmyus River Area, Solenaya River Bank, Novo-Troitskoe Village. Limestone F<sub>1</sub>, Blagodatnian Substage, *Bilinguites–Cancelloceras* ammonoid Biozone, *Pseudostaffella pregorskyi–Staffelleformis staffelleformis* foraminiferal Biozone, *Idiognathodus sinuosus* conodont Biozone. Late early Bashkirian.



Text-fig. 7. *Spirophyllum* sp. 2. Transverse thin sections except when stated otherwise. A-F – Specimen UAM-Tc.Don.1/169. A, B – neanic growth stage (A – peel with drawing, B – polished surface), C-F – mature growth stage, F – rejuvenescence (C, E, F – polished surfaces). G-J – Specimen UAM-Tc.Don.1/239. G, H – neanic growth stage (drawings), I – mature growth stage, above calice floor except axial area and dissepimntarium, J – enlarged from I to document complex pseudocolumella with septal lamellae incorporated. For stratigraphic position see text. Scale bars located between two adjacent images correspond to both; those to right of image apply only to that image

## Subfamily Dibunophyllinae Wang, 1950

EMENDED DIAGNOSIS: Solitary and/or fasciculate Aulophyllidae; cardinal septum shortened; cardinal fossula indents dissepimentarium; axial structure invariably present in early ontogeny; may disappear in advanced maturity; median lamella monoseptal derived from axial septum; pseudocolumella closer connected to cardinal than to counter septum when axial septum divided; axial column appear in some genera; tabularium uniform, may be indistinctly bifurcated when minor septa enter tabularium; microstructure of septa trabecular.

GENERA ASSIGNED: *Arachniophyllum* Smyth, 1915 (maybe synonym of *Dibunophyllum*), *Arachnolasma* Grabau, 1922, *Biphyllum* Fedorowski, 1971; *Caninostroton* Easton, 1943; *Copia* Vassilyuk and Kozyreva, 1974; *Corwenia* Smith and Ryder, 1926; *Dibunophyllum* Thomson and Nicholson, 1876; *Dibunophylloides* Fomichev, 1953; *Eostroton* Vaughan, 1915; *Koninckinaotum* Fedorowski, 1971; *Mirka* Fedorowski, 1974; *Koninckophylloides* Gorskiy, 1978; *Koninckophyllum* Thomson and Nicholson, 1876; *Slimoniphyllum* Kato and Mitchell, 1961; *Turbinatocaninia* Dobrolyubova, 1970 (genera with question mark may belong to another subfamily or subfamilies of the Aulophyllidae).

REMARKS: The content of the Family Aulophyllidae Dybowski, 1873 proposed by Hill (1981), mostly acceptable at subfamily level, is not discussed in detail herein. Only the position in that family of two subfamilies is doubtful. The Subfamily Heterocaniniinae Hill, 1981 with two Praetethys genera incorporated, is restricted to that area and should perhaps be elevated to family rank. Doubts concerning the Subfamily Amygdalophyllinae are discussed above. The remarks that follow are restricted to the Subfamily Dibunophyllinae.

The question of the diagnostic characters and the independent status of the genus *Arachnolasma* Grabau, 1922 has been recently discussed (Fedorowski 2015) and is not repeated herein. Its redefinition is badly needed. The taxonomic status of the weakly colonial genus *Caninostroton* Easton, 1943, revised by Webb (1987), remains uncertain. The enormous variability of its axial structure from simple or non-existing, to so complex as to contain extra septal lamellae exceeds all criteria accepted here for classification within the Aulophyllidae. The position of *Cystilophophyllum* Fomichev, 1953, included by Hill (1981, p. F365) in the Dibunophyllinae

with a question mark, remains questionable. Its relationship to the Bothrophyllidae, suggested recently (Fedorowski 2017a), is closer than to any other existing family. However, it may belong to a separate subfamily of that family. *Diaschophyllum* Semenoff-Tian-Chansky, 1974 (Semenoff-Tian-Chansky 1974, pl. 29, figs. 6, 7, text-figs 53, 54) is another genus, the taxonomic position of which is doubtful. Its tabularium which is concave at the periphery, constitutes its main distinguishing feature, whereas its morphology in the transverse section can easily be compared with *Dibunophyllum pseudoturbinatum* Stuckenbergh, 1904 and several other species of *Dibunophyllum*. Moreover, the tabellae forming the axial column and the tabellae adjacent to them are identical to those in the genus *Dibunophyllum*. The restriction of this genus to the incomplete mature growth stage of the holotype and a very short longitudinal thin section of that corallite, do not allow a reliable conclusion. The morphology of the fragment illustrated by Semenoff-Tian-Chansky (1974, pl. 29, fig. 7) has been either deformed by diagenesis or is pathologic. The synonymy of *Diaschophyllum* with *Dibunophyllum* is here suggested as possible. *Faberolasma* Bykova, 1974 requires an additional ontogenetic study in order to reconstruct its true relationship. Its characters established so far point towards the Family Palaeosmiliidae Hill, 1940 or Ekvasophyllidae Hill, 1981 rather than the Aulophyllidae.

*Haplolasma* Semenoff-Tian-Chansky, 1974 is another genus requiring careful revision. That name has been applied by several authors from various countries on the basis of the morphological similarity of mature growth stages. (e.g., Poty 1981; Wu and Zhao 1989; Fan *et al.* 2003; Rodríguez *et al.* 2004; Aretz 2011; Khaksar and Khaksar 2014). Moreover, some new species, based on the similarity of the mature growth stages, were introduced into that genus. Such a similarity does not prove the relationship. Only a close similarity of the early ontogeny is decisive in corals of such mature morphology. Thus, the discussion on *Haplolasma* must be postponed until the early ontogeny in *Caninia subibicina* McCoy, 1851, the type species of that genus, is studied in detail. The peculiar ontogeny of *Haplolasma parvicarinatum* Semenoff-Tian-Chansky, 1974 differs considerably from the ontogeny of genera in both the Family Cyathopsidae and the Family Aulophyllidae. The aulos (in the sense of Fedorowski 2009b), persisting in that species for a few millimetres of the corallite growth (Semenoff-Tian-Chansky 1974, text-fig. 78) makes at least that species of *Haplolasma* a member of a new family.

*Heintzella* Fedorowski, 1967 was documented by Fedorowski *et al.* (2007) as a member of their new family Kleopatrinidae. *Katranophyllum* Kropacheva in Degtyarev and Kropacheva, 1972, another incompletely studied genus, is known from one transverse and one longitudinal thin section, taken from an unknown part of the corallite. Hill (1981, p. F368) questionably suggested its synonymy with either *Dibunophyllum* or *Debaophyllum* Zhang in Jia *et al.*, 1977. It resembles *Dibunophyllum* only in possessing the axial column. However, that column is rather of the *Aulophyllum*-kind, whereas the morphology of the dissepimentarium in *Katranophyllum* does not resemble any member of the Family Aulophyllidae. Both the morphology and the geographic position (southern Fergana) suggest the relationship of *Katranophyllum* with some far Asiatic taxa, such as *Nagatophyllum* Ozawa, 1925. Its comparison to *Debaophyllum* will be possible only when both those genera become documented adequately for the discussion. *Nagatophyllum* Ozawa, 1925 belongs to a fauna that is either endemic for the Hida and the Akiyoshi Limestones of Japan, or related to the faunas of eastern Australia and, perhaps, the Fergana Area in Central Asia. The morphology of its axial structure, similar to that in *Dibunophyllum*, is here considered as a homeomorphic structure, developed independently from that in *Dibunophyllum*.

*Koninckophyllum* Thomson and Nicholson, 1876, *Koninckinaotum* Fedorowski, 1971 (synonymized by Hill 1981, p. F368 with *Koninckophyllum*, with which I disagree), *Koninckophylloides* Gorskiy, 1978 and *Neokoninckophyllum* Fomichev, 1953 constitute a group of taxa similar to each other in lacking an axial column at any growth stage and in possessing a simple pseudocolumella. The first three of those genera may belong to the Subfamily Koninckophyllinae Wang, 1950, synonymized by Hill (1981) with the Dibunophyllinae. The genus *Neokoninckophyllum* has been left in the revised Family Neokoninckophyllidae Fomichev, 1953 (Fedorowski *submitted*).

The genus *Orygmophyllum* Fomichev, 1953 belongs to the Family Neokoninckophyllidae (Fedorowski *submitted*). The ontogenetically earliest growth stage studied so far (Fomichev 1953, pl. 18, fig. 11a) show the cardinal and the counter septa equal to the adjacent major septa in length and the axial corallite area free from major septa. Those characters are contrary to the diagnosis of the Family Aulophyllidae. Sando (1965) questionably identified as *Orygmophyllum* the fasciculate species "*Lithostrotion*" *whitneyi* Meek of White (1875) from the early Pennsylvanian of the United States. He established its suspected syno-

nymy and included *Orygmophyllum* within the Family Lithostrotionidae d'Orbigny, 1852. Both the synonymy and those identifications are rejected.

*Sestrophyllum* Fomichev, 1953 is the Carboniferous coral genus possessing everted calices. Hill (1981, p. F370) mentioned that character in her diagnosis of *Sestrophyllum* but did not elevate its taxonomic position to the family level. My attitude to that genus, based on both the restudy of Fomichev's (1953) collection and the unpublished study on the Smithsonian Institution collection derived from the Pennsylvanian and Permian strata of SW Texas suggest the necessity for separation of *Sestrophyllum* at the family level.

The position of the genus *Spirophyllum* Fedorowski, 1971 is discussed above. It may belong to the Family Aulophyllidae but not to the Subfamily Dibunophyllinae. The genus *Mirka* Fedorowski, 1974, synonymized by Hill (1981, p. F370) with *Spirophyllum*, should be retained within the Family Aulophyllidae. The latter position is suggested by its long and mono-septal median lamella, by the rotation of the inner margins of major septa and by the occurrence of the axial column. The characters listed make its position within the Subfamily Clisiophyllinae Nicholson and Lyddeker, 1889 almost equally possible as that in the Dibunophyllinae.

The independent status of the genus *Yakovleviella* Fomichev, 1953 has been put in doubt (Fedorowski 2016). The same is true for species named as *Yakovleviella* from various areas (e.g., Wu and Zhao 1989; Chwieduk 2014). The taxonomic position of the genus *Yuanophylloides* Fomichev, 1953 is discussed in a separate report (Fedorowski *submitted*). That genus and some North American taxa named as *Neokoninckophyllum* (e.g., Moore and Jeffords 1945; Cocks 1970) are in that paper included in the Family Neokoninckophyllidae.

*Turbinatocania* Dobrolyubova, 1970 with type species *Caninia okensis* Stuckenberg, 1904 exhibits some features identical with those of the Family Bothrophyllidae as discussed recently (Fedorowski 2017a). However, its close relationship to the Family Aulophyllidae established by Dobrolyubova (1970) is not questioned. Also, its position within the Dibunophyllinae (Hill 1981) is followed.

Dobrolyubova (1948, 1960) discussed *C. okensis* in terms of its phylogeny and eventually selected it as the type species of her genus *Turbinatocania* Dobrolyubova, 1970. She did not revise Stuckenberg's (1904) specimens, but all her specimens included in that species are topotypes. Unfortunately, Dobrolyubova (1948, 1960, 1970) failed to select the lectotype for *C. okensis*. Thus, Ivanovsky's (1987, p.

30, pl. 17, fig. 1a, b) selection of the lectotype, called the holotype by him, must be accepted as formal and must be followed. That incomplete specimen (No. 38/336), preserved in the mature growth stage, is comparable to some almost complete topotypes, investigated by Dobrolyubova (1948, 1960). The compilation of the morphological features of the lectotype and Dobrolyubova's topotypes show that the diagnostic characters of *Turbinatocania okensis* are established well enough to become a reference to similar and/or related taxa.

Dobrolyubova (1970, p. 130) included in *Turbinatocania* the following species (generic names as applied by species authors): *Campophyllum sinzovi* Stuckenberg, 1904; *Caninia okensis* Stuckenberg, 1904; *Rhodophyllum slimonianum* Thomson, 1874; *Turbinatocania besputensis* Dobrolyubova, 1970; and *T. toporovensis* Dobrolyubova, 1970. Two species of that list are disputable. *Campophyllum sinzovi* has been questionably synonymized with *T. okensis* (Ivanovsky 1987, p. 30). Only the revision of the original material can solve the question of its taxonomic position. *Rhodophyllum slimonianum* was revised by Kato and Mitchell (1961), who established the new genus *Slimoniphyllum* for that species. This would mean the priority of *Slimoniphyllum* over *Turbinatocania*, if Dobrolyubova's (1970) suggestion concerning *slimonianum* is accepted. However, *S. slimonianum*, known from the Brigantian strata in Britain (Kato and Mitchell 1961) and Poland (Fedorowski 1971) possesses a shortened counter septum located in the counter fossula. Those two characters are adequate for distinguishing between *Turbinatocania* and *Slimoniphyllum*. Thus, only three species included by Dobrolyubova (1970) in *Turbinatocania*, i.e., *Caninia okensis*, *Turbinatocania besputensis* and *T. toporovensis* are known to represent that genus in the Moscow Basin.

Dobrolyubova (1970) failed to take in mind *Campophyllum concaveum* Thomson, 1893, renamed by Lewis (1931, p. 236) as *Caninia concavea*. Lewis (1931, pl. 8, fig. 4a–c) selected the neotype for that species and illustrated it in two transverse sections and one longitudinal section of the mature growth stage. The axial structure is present up to the early mature growth stage and the “caninoid” morphology in the ontogenetically advanced growth stage, suggest the possibility of that Brigantian species being a member of *Turbinatocania*. Thus, the roots of *Turbinatocania* may not be eastern, but western European.

Two specimens of *Turbinatocania* from the Besputa River bank (limestone layer “b”) near the Toporovo Village (Dobrolyubova 1960, pl. 5, figs

1a–zh, 2a–z in the Russian alphabet) show characters intermediate between Dibunophyllinae and Bothrophyllidae in possessing the counter, but not the cardinal septum connected with the median lamella. Both those specimens were re-illustrated by Dobrolyubova (1970, pl. 47, fig. 1a–zh, pl. 48, fig. 1a–z in the Russian alphabet) under the new species name *Turbinatocania toporovensis* and were supplemented by illustrations of two other specimens from the same limestone layer (Dobrolyubova 1970, pl. 47, fig. 2a, b; pl. 48, fig. 2a–d in the Russian alphabet). The first of those newly illustrated specimens resembles the dibunophyllids more closely than the bothrophyllids, whereas the morphology of the second with its elongated counter septum and short cardinal septum, located in the open cardinal fossula, could be readily included in the Family Bothrophyllidae, if the entire morphology of that specimen is not taken in mind. This question is briefly discussed in the Considerations below.

To sum up: The content of the Subfamily Dibunophyllinae proposed here differs considerably from that established by Hill (1981). New data achieved since the publication of her Treatise are one of the reasons for that difference. My different attitude to the value of individual diagnostic characters and my attempt to eliminate unimportant morphological similarities treated as proof of the relationships, is the second and the most important reason.

Genus *Dibunophyllum* Thomson and Nicholson, 1876  
(Type species *Dibunophyllum muirheadi* Thomson and Nicholson, 1876; selected by Gregory 1917, p. 232; see Hill 1938–1941, p. 65 for supplementary data)

DIAGNOSIS: Solitary Dibunophyllinae with long median lamella pointing towards and/or connected with cardinal septum; axial column composed of axial tabellae and regular septal lamellae continuous up to calice floor inclusively; extra septal lamellae absent (slightly modified after Fedorowski 2015, p. 246).

REMARKS: The reason for the emendation of the diagnosis established by Hill (1938–1941, p. 65) and repeated by her later (Hill 1981, p. F361) is explained in my earlier paper (Fedorowski 2015) and not repeated here. Also, the reader is referred to that paper for a more comprehensive discussion on that genus and its relationships. The reason for the exclusion of *Dibunophyllum finalis* Vassilyuk, 1960 from *Dibunophyllum* is discussed under the remarks to that

species. In contrast to other papers in the series devoted to the early Bashkirian Rugosa from the Donets Basin, the synonymy and the species content of the genus *Dibunophyllum* are not established. That decision resulted from the impossibility of making them complete and credible in this paper. The morphology and the ontogeny of typical representatives of that genus were widely discussed (Hill 1938–1941; Fedorowski 1971; Semenoff-Tian-Chansky 1974) and the diagnostic characteristics of typically built *Dibunophyllum* do not cause doubts. However, species either peripheral to and/or atypical for that genus are numerous. Some of them tend towards *Arachnolasma* by possessing a narrow axial structure and thickened median lamella. The axial column in some other species tends to disappear, making them similar to either *Adamanophyllum* Heritsch, 1941 or *Yuanophylloides* Fomichev, 1953. Some other species (e.g., *Dibunophyllum lonsdaleoides* Vassilyuk, 1960) known from the Donets Basin and Poland (Fedorowski 1971) developed lonsdaleoid dissepiments, lacking from the typically built dibunophylla. A list of synonyms of such morphologically differentiated taxa, proposed without an analysis based on their types, would be misleading.

The North American species included in *Dibunophyllum* by Newell (1935), Moore and Jeffords (1945), Cocke (1970) and some other American authors have been already excluded from *Dibunophyllum* by Fedorowski (1971, 2015) and Fedorowski and Ogar (2013). However, a much more elaborate analysis, based on the type collections, would be required in order to establish the reliable taxonomic positions of those North American “dibunophylla”.

*Dibunophyllum medium* sp. nov.  
(Text-figs 8 and 9)

? e.p. 1960. *Dibunophyllum turbinatum* McCoy; Vassilyuk, p. 132.

? e.p. 1960. *Dibunophyllum dobroljubovae* Vassilyuk, p. 138.

ETYMOLOGY: *Lat. medius* – transitional – after its morphology transitional between *Dibunophyllum bipartitum* and *Dibunophylloides*.

HOLOTYPE: Specimen UAM-Tc.Don.1/170.

TYPE LOCALITY: Kalmyus River Area, Bezymennaya Ravine (Balka).

TYPE STRATUM: Limestone D<sub>5</sub><sup>10</sup>. Early Voznesenskian Substage. Early *Homoceras*–*Hudsonoceras* am-

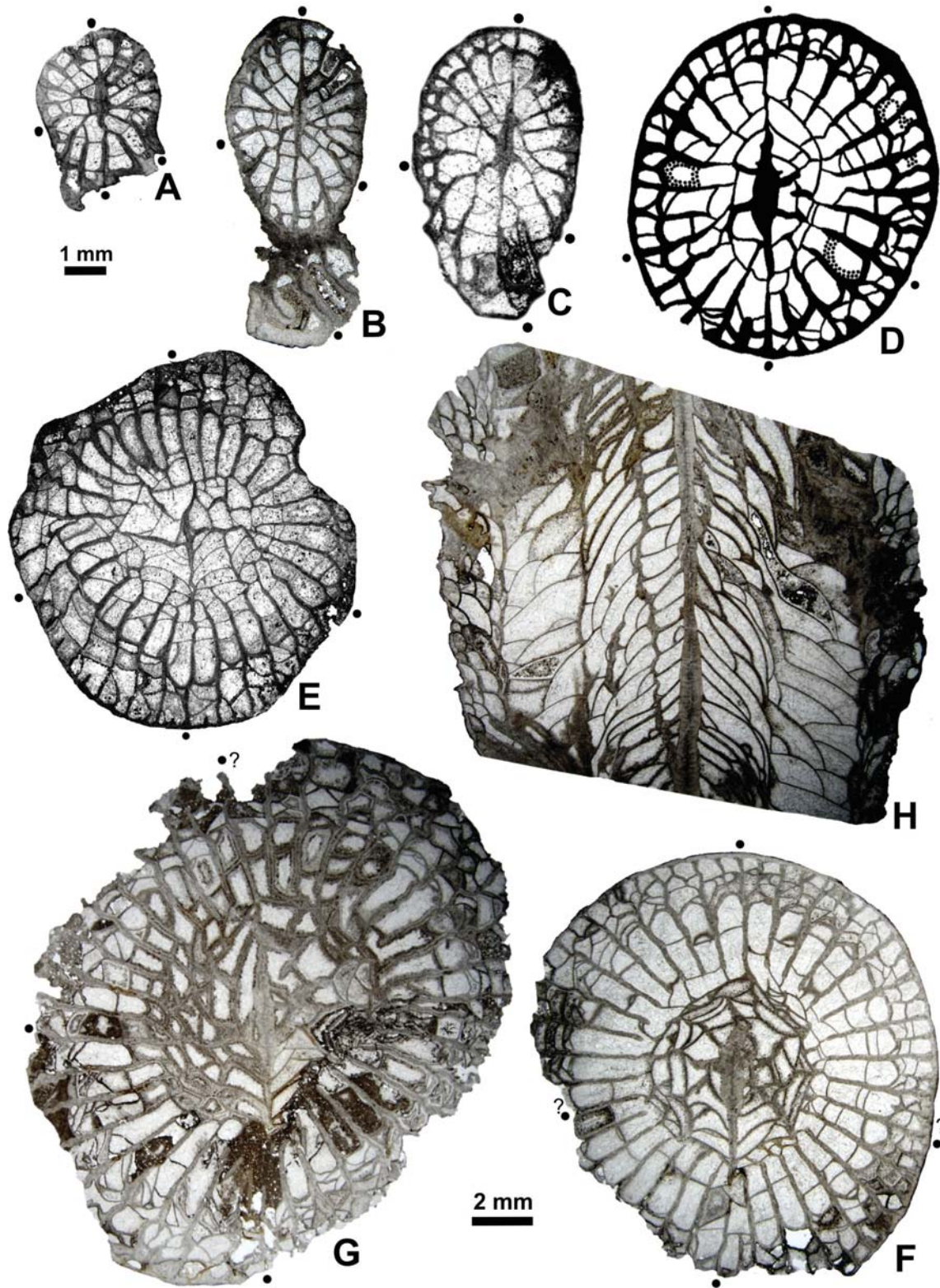
monoid Biozone, early *Plectostaffella bogdanovkensis* foraminiferal Biozone, early *Declinognathodus noduliferus* conodont Biozone. Closely above the base of the Bashkirian.

DIAGNOSIS: *Dibunophyllum* with thickened median lamella, commonly united with cardinal and counter septa; septal lamella 4–8 in number, mostly united with inner margins of major septa; minor septa intersect 1/3–3/4 width of the dissepimentarium that occupies 1/6–1/4 corallite radius; 32–39 (most commonly 34–36) major septa at 11–19 mm (most commonly 12–14 mm) mean corallite diameter.

MATERIAL: Holotype UAM-Tc/Don.1/170 and 14 paratypes UAM-Tc.Don.1/171–185. Corallites in various stage of preservation. Holotype almost complete. Only brephic growth stage and calice missing. Two corallites with lower parts of calices and three with talons preserved. Most corallites restricted to long fragments, cylindrical in shape, i.e., in the mature growth stage. All corallites sectioned. Internal structure of most corallites well preserved, some a little crushed. Fragments of most specimens corroded but not eroded. One overgrown by a bryozoan colony.

DESCRIPTION OF HOLOTYPE: Corallite growth direction changed three times. Its length approximately 4.5 cm when curvature ignored and 7.0 cm when measured along its convex side. Corallite surface ornamented by growth striae. Septal furrows either absent or extremely shallow. Attachment structure (talon) strong, developed at cardinal septum side of corallite as documented in transverse thin section (Text-fig. 8A–C). Ontogenetically earliest part preserved (Text-fig. 8A; n:d value 16:4.8×3.0 mm), with minor septa not recognized and dissepimentarium lacking, represents neanic growth stage. Most major septa attached to axial septum, those of counter quadrants accelerated in increase over cardinal quadrants (5:2 and 4:3, respectively). Median lamella long and much thicker than peripheral parts of axial septum.

Approximately 0.7 mm and 1.2 mm of further corallite growth, measured at concave and convex side respectively, with n:d values 19:5.5×3.4 mm (talon excluded) and 20:7.0×4.5 mm (Text-fig. 8B, C), first few dissepiments appear at counter side of corallite. That earliest dissepimentarium, comprising one row of dissepiments, extends towards cardinal septum at left side of picture (Text-fig. 8C). Short minor septa appear in corallite lumen when dissepiments well developed. Remaining morphology similar to the afore described one. Insertion of major septa in counter



Text-fig. 8. *Dibunophyllum medium* sp. nov. Specimen UAM-Tc.Don.1/170. Holotype. Transverse thin sections, except when stated otherwise. A, B – neanic growth stage, C-E – late neanic to early mature growth stage (C – peel, D – peel with drawing), F, G – mature growth stage (G above calice floor in some loculi), H – longitudinal thin section. For stratigraphic position see text. Scale bar below A corresponds to A-D. Scale bar between G and F corresponds to E-H

quadrants accelerated. Counter lateral septa remain considerably short. This part of corallite growth arbitrary accepted as late neanic.

Approximately 2.4 mm of further corallite growth with n:d value 24:8.6×7.8 mm (Text-fig. 8D), axial septum remains complete with median lamella strongly thickened. However, arrangement of major septa becomes radial and inner margins of most of them, except four, separate from axial septum. Those four inner parts of major septa thicken to form septal lamellae, weakly connected to remaining parts of major septa. Those lamellae and axial tabellae constitute earliest axial structure and, perhaps, axial column. Complete ring of dissepiments and minor septa present in all loculi allow one to consider the described morphology as early mature.

Rapid thinning of all skeletal structures within approximately 2 mm of further corallite growth (n:d value 30:13.5×12.5 mm) and reduction of axial structure to median lamella, two septal lamellae and a few sections of axial tabellae (Text-fig. 8E) resulted perhaps from unfavourable extrinsic conditions. Morphology changed again within a few millimetres of mature corallite growth (n:d value 34:15.5×14.5 mm; Text-fig. 8F). Major septa radially arranged, almost equal in length, with the quadrants of septa undistinguishable. Cardinal septum shortened, in indistinct cardinal fossula. Median lamella thick, disconnected from both protosepta. Its thinner extension penetrating cardinal fossula. Almost all of eight septal lamellae separated from inner margins of major septa. Those lamellae and sections of axial tabellae forming a classic dibunophyllid axial structure confirmed by axial column in longitudinal section (Text-fig. 8H). Minor septa differentiated in length. Shortest restricted to peripheral row of dissepiments, longest approach inner margin of dissepimentarium, 1/5–1/4 corallite radius in width. Dissepiments regular and herringbone. Moderately thick median lamella remains disconnected from cardinal septum to advanced mature growth stage (Text-fig. 8G) with n:d value 38:20.0×14.8 mm (slightly deformed) and close to calice floor with n:d value 38:20.0×18.0 (not illustrated). However, median lamella meets counter septum at that advanced growth stage. Several septal

lamellae join inner margins of corresponding major septa and twist around pseudocolumella like those in *Clisiophyllum* McCoy, 1849 (Text-fig. 8G, left).

Longitudinal section (Text-fig. 8H) clearly three partite. Dissepiments globose, slightly differentiated in size, arranged in steep rows; inner row vertical. Peripheral tabellae differentiated in length with some spanning entire distance between dissepimentarium and axial column, others dissepiment-like. Axial column clearly isolated from peripheral tabularium by peripheral, almost vertical parts of long axial tabellae resting on one another. Lateral tabellae of axial column short and rare.

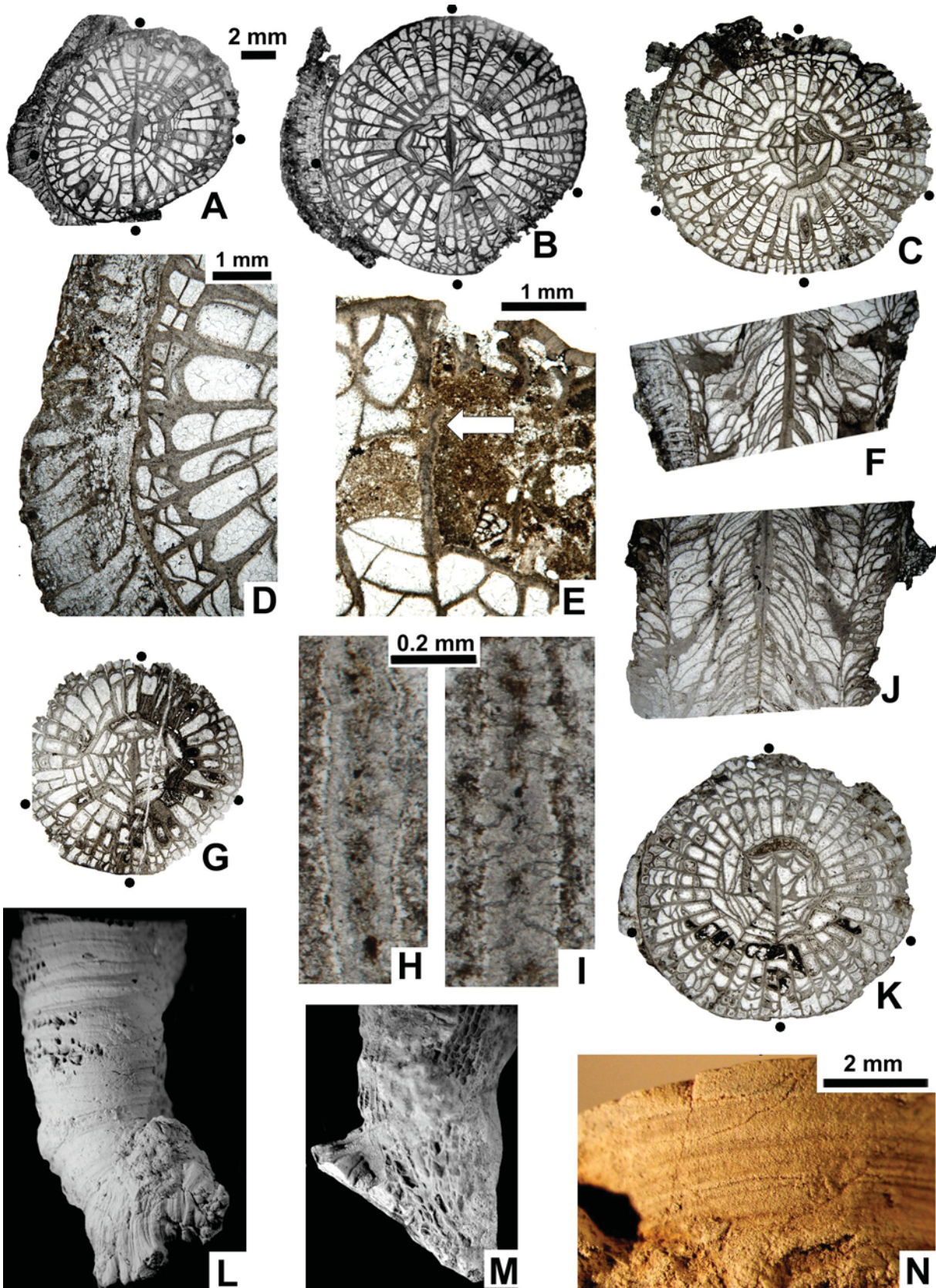
Microstructure of septa destroyed by diagenesis to various extent. In some septa (Text-fig. 9H, I) large isolated bunches of fibrils, accompanied by wavy shape of peripheral surfaces of septa suggest trabecular microstructure. However, size of those bodies much larger than in other dibunophyllids, may suggest recrystallization and artificial enlargement of some trabeculae on cost of others.

**INTRASPECIFIC VARIABILITY:** The morphology of individual growth stages of the holotype, its axial structure in particular, differs considerably. However, only its simplified morphology (Text-fig. 8E) and most advanced growth stage (Text-fig. 8G) find no counterparts among the paratypes. The morphology of the remaining growth stages of the holotype, particularly that illustrated in Text-fig. 8F, is reflected in the particular growth stages of the paratypes in both transverse (Text-fig. 9A–C, G, K) and longitudinal (Text-fig. 9F, J) sections. Differences in thickness and length of median lamella, in continuous axial septum and more or less advanced reduction in length of minor septa are deviations from the holotype slight enough to make a detailed description unnecessary.

Corallites with early growth stages preserved display strong talons (Text-fig. 9L, M) and external surface smooth with septal furrows recognized as delicate imprints rather than true depressions (Text-fig. 9L, N). One corallite is overgrown at one side by a bryozoan colony (Text-fig. 9A–D, F). The same corallite (Text-fig. 9C, upper, E) displays either mechan-

Text-fig. 9. *Dibunophyllum medium* sp. nov. Paratypes, except H, I. Transverse thin sections except when stated otherwise. A–F – Specimen UAM-Tc.Don.1/171. A–C – early to advanced mature growth stage; shallow rejuvenation in C (upper), D – enlarged from B to demonstrate differentiation in length of minor septa and overgrowth by bryozoan colony, E – enlarged from C; major septum (arrow) replaces external wall, F – longitudinal thin section. G, N. Specimen UAM-Tc.Don.1/177. G – early mature growth stage, N – corallite surface; septal furrows absent. H, I – Specimen UAM-Tc.Don.1/170. Holotype. Remnants of trabeculae in major septa. J, K – Specimen UAM-Tc.Don.1/173. J – longitudinal thin section, K – mature growth stage. L – Specimen UAM-Tc.Don.1/184. Side view of corallite early growth stage with strong talon; extremely shallow septal furrows in upper part. M – Specimen UAM-Tc.Don.1/172. Side view of corallite early growth stage with strong talon. For stratigraphic position see text. Scale bar between A and B corresponds to all images except when indicated →





ical destruction or a shallow and local rejuvenation. The left skeleton is bordered by a peripheral part of the major septum at one side (Text-fig. 9E, arrowed) and by a new external wall from the remaining part.

REMARKS: Vassilyuk (1960) identified as *Dibunophyllum turbinatum* McCoy, 1851 and *D. dobrolyubovae* Vassilyuk, 1960 many specimens collected from various sites and strata in the Donets Basin, starting from the late Viséan Zone  $C_{1f}$  and ending with the early Bashkirian Limestone  $D_6$  (Vassilyuk 1960, occurrences, pp. 134 and 140, respectively). Unfortunately, only mature growth stages of the specimens derived from the late Viséan and the Serpukhovian strata were illustrated by her (Viséan specimens: Vassilyuk 1960, pls. 32; 33; 34, figs 1, 1e; 36, figs 2–2c, respectively). Some of the Serpukhovian specimens (Vassilyuk 1960, pl. 33, figs 1d, 1e; pl. 34, figs 1, 1a–1c) resemble the corallites described here in n:d value, but most of them are larger and they differ from the specimens described here in the morphology of the axial structure both in transverse and longitudinal sections. Those differences and the lack of data on Vassilyuk's (1960) early Bashkirian specimens make the introduction of a new species more rational than the inclusion of the early Bashkirian corals in any of the species questionably and in part included here in the synonymy of *D. medium*. Analysis of the *Dibunophyllum* species described from the Donets Basin (Vassilyuk 1960, 1964 and this paper) documents a continuous phylogenetic lineage of the *Dibunophyllum* species in that basin ending so far with *D. medium*.

OCCURRENCE: As for the holotype.

Genus *Dibunophylloides* Fomichev, 1953

(Type species *Cyathoclisia simmetrica*

Dobrolyubova, 1937; subsequent designation by Fomichev 1953, p. 393)

EMENDED DIAGNOSIS: *Dibunophyllum*-like, solitary, dissepimented corals with axial column absent from the mature growth stage or earlier; septal lamellae commonly short and restricted in number to very few; monoseptal median lamella connected to cardinal and counter septa up to early mature growth stage or up to mature calice floor; rarely and temporarily separated from protosepta in advanced mature growth stage; cardinal fossula indistinct; tabularium normal; dissepimentarium consists of regular and herringbone dissepiments.

REMARKS: The diagnosis of *Dibunophylloides* established by Fomichev (1953, p. 393) contains quantitative and descriptive characters making its emendation necessary. The common appearance of *Dibunophylloides* in clusters allowed Fomichev (1953) to suggest a possible simple colonial growth form of the Donets Basin specimens. He wrote in his diagnosis: "Some of them may form small colonies (?), composed of a restricted number of cylindrical-conical corallites" [translated here from Russian]. That suggestion has not been supported by offsetting specimens present in his collection. Only maturation and offsetting involving at least three generations of corallites constitute true colonies (Fedorowski 1970, 1978; Fedorowski and Ogar 2013). Nothing like that exists among the corals described by Fomichev (1953), making his supposition untenable. However, de Groot (1963, p. 66) considered the colonial growth form of *Dibunophylloides* as proven. She wrote "He [i.e., Fomichev] proposed the genus *Dibunophylloides* for these corals, which differ from *Corwenia*, according to Fomichev, chiefly in comprising **also** (boldface my) solitary corals." Thus, she reversed the original meaning of *Dibunophylloides* by Fomichev in order to include in *Corwenia* both the solitary (*Amandophyllum* Heritsch, 1941; *Sestrophyllum* Fomichev, 1953; *Dibunophylloides*) and colonial (*Heritschioides* Yabe, 1950) corals. That approach, rejected by Fedorowski (2004, p. 107) and herein, allowed her to name some colonial species from northern Spain as *Corwenia symmetrica* [sic] (Dobrolyubova, 1937) and *Corwenia longiseptata* (Fomichev, 1953). Rodríguez (1984) followed de Groot (1963) in describing some of his specimens as *Corwenia longiseptata* (Fomichev, 1953). All Spanish fasciculate colonies included by de Groot (1963) and Rodríguez (1984) in various species of *Corwenia*, and only those colonies, were grouped by Fedorowski (2004, p. 108) in one species *Corwenia cantabrica* de Groot, 1963. Also, the synonymy by de Groot (1963) and Rodríguez (1984) at both the genus and the species level were rejected – an approach that is also followed herein.

The designation of *Cyathoclisia simmetrica* Dobrolyubova, 1937 by Fomichev (1953) as the type species of *Dibunophylloides* definitely solves the question of the growth form of that genus as solitary. The sketch of the type specimen and the early (not the earliest) ontogeny of the type species (Dobrolyubova 1937, pl. 19, figs 9 and 10, respectively) leave no doubts in that matter. The solitary growth form of the Bashkirian species of *Dibunophylloides* is confirmed by the morphology of their early growth stages and/

or the talon (Text-figs 10A–C, 11F, 14A–J, 15H, 17A–E). The invariability of that character is further documented by the early ontogeny of the Moscovian topotype of *D. longiseptatus* (Text-fig. 13A–I).

The morphology of the axial structure in both transverse and longitudinal sections is crucial for the distinction between *Dibunophyllum* and *Dibunophylloides*. “*Cyathoclisia*” *symmetrica* and its synonym “*C.*” *myatshkovensis* Dobrolyubova, 1937 as suggested by Fomichev (1953) and supported herein, are more distant from *Dibunophyllum* than the Donets Basin specimens. Major septa in the transverse thin sections of the type species are mostly continuous and radially arranged approaching or meeting the thin axial septum directly, i.e., without septal lamellae being separated (Dobrolyubova 1937, pl. 19, figs 11–13). The axial tabellae in the longitudinal section are densely packed and short, and pass gently into convex and looser peripheral tabellae (Dobrolyubova 1937, pl. 19, fig. 14). The axial column is absent from all longitudinal sections of the Moscow Basin specimens illustrated (Dobrolyubova 1937, pl. 19, figs 7, 8, 14) including the tiny corallite described by Dobrolyubova and Kabakovich (1948, pl. 16, figs 6–8). The characters of the type species of *Dibunophylloides* listed makes it different from all Donets Basin specimens included in that genus by Fomichev (1953) and in this contribution. The axial column occurs in the early growth stages of the latter specimens and short septal lamellae are developed. The morphological differences between the Moscow Basin type species and the Donets Basin species may suggest a different subgeneric status of the latter.

Not only *Dibunophylloides* but also *Amandophyllum* Heritsch, 1941 differs from *Dibunophyllum* in the absence of the axial column. Thus *Amandophyllum* would have a priority over *Dibunophylloides* if those two genera are synonymized. The morphological similarity mentioned has been confirmed by my own unpublished reinvestigation of Heritsch’s (1936, 1941) collection housed in Graz, Austria. Several incomplete specimens included by Heritsch (1936) in the genera *Clisiophyllum*, *Dibunophyllum*, *Corwenia* and *Palaeosmilina*, and specimens identified by Felser (1937) as *Dibunophyllum* belong to the same genus and possibly to the same species. They were already synonymized with *Clisiophyllum* (= *Amandophyllum*) *carnicum* Heritsch, 1936 (Fedorowski 1971, p. 112). The occurrence of *Amandophyllum carnicum* and its synonyms in the early Permian strata of the Carnic Alps fix its incorporation into the Tethys Realm of Fedorowski (1986, fig. 1). The name “Tethys” has been rather unfortunately applied in that paper and should

be replaced by “Palaeotethys” or “Palaeotethian”. However, the replacement of the name does not change my original idea of two rugose coral kingdoms or realms existing from the late Carboniferous till the end of the Permian. The stratigraphic and palaeogeographic position of *Amandophyllum* excludes its connection with the species of the Subfamily Dibunophyllinae. At first, *Amandophyllum carnicum* appeared in the Palaeotethys Realm, i.e., on the eastern shelves of Pangea long after the disappearance of *Dibunophylloides* from both the Moscow and the Donets basins before the end of the Moscovian. Secondly, the assemblage of Pangea in the meantime precluded any connection between the rugose coral faunas from the western shelves of that supercontinent and the Palaeotethys. That isolation of the realms took place not later than in the early Gshelian (Fedorowski 1981, 1986, 1997b). Thus, *Amandophyllum* is treated here as homeomorphic with *Dibunophylloides*.

SPECIES CONTENT: *Cyathoclisia symmetrica* Dobrolyubova, 1937 (non Fomichev, 1953; non de Groot, 1963); *Dibunophyllum bolli* Rodríguez, 1984; *Dibunophyllum finalis* Vassilyuk, 1960; *Dibunophylloides columnatus* sp. nov.; *Dibunophylloides longiseptatus* Fomichev, 1953 (non de Groot, 1963; non Rodríguez, 1984); *Dibunophylloides paulus* sp. nov.; *Dibunophylloides similis* sp. nov.; *Koninckophyllum gentisae* de Groot, 1963 (= *Dibunophyllum? gentisae* de Groot, 1963 of Fedorowski 2004).

*Dibunophylloides paulus* sp. nov.

(Text-figs 10 and 11)

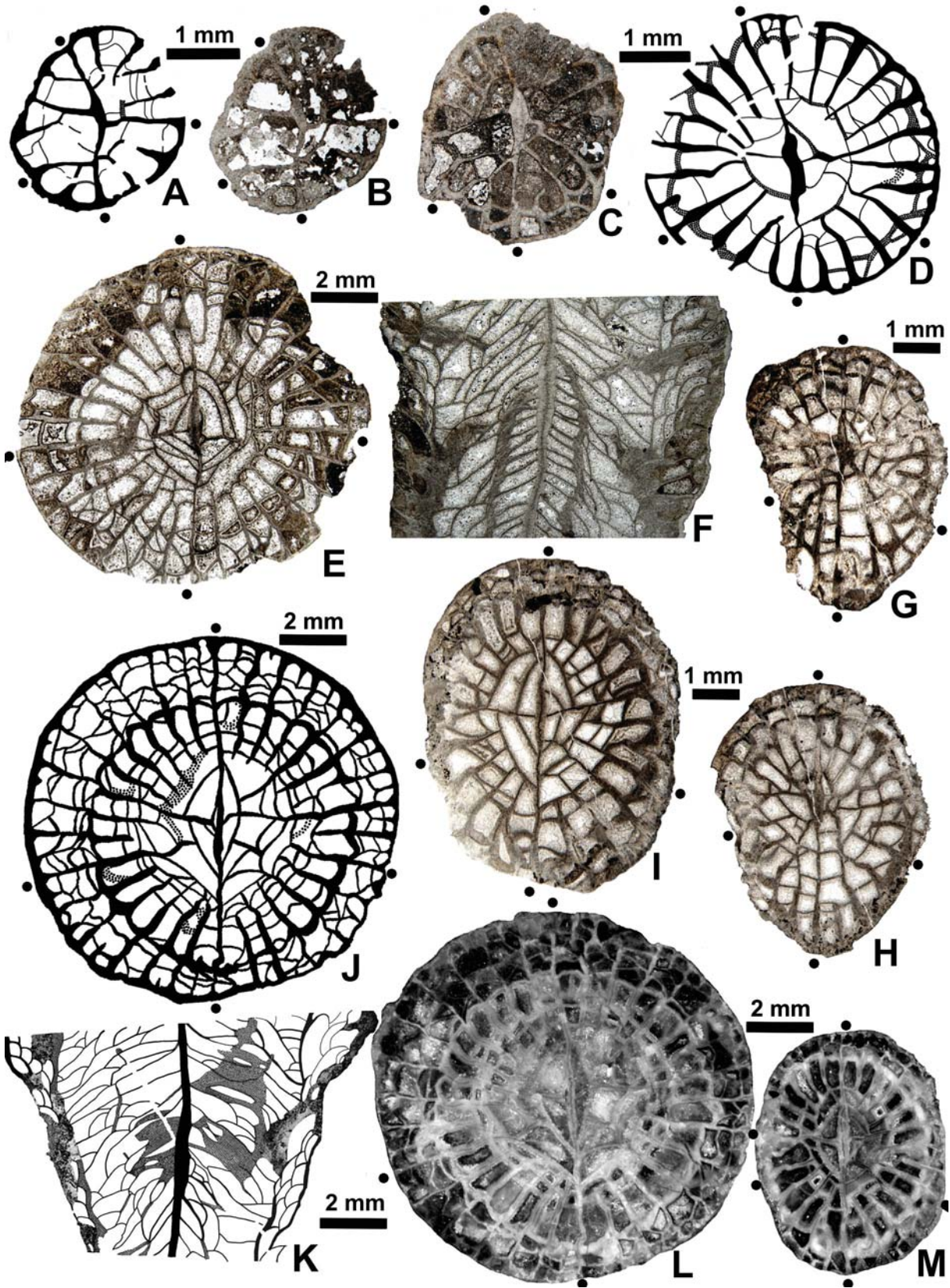
ETYMOLOGY: *Lat. paulus* – small, tiny – named after the tiny size of the corallite.

HOLOTYPE: Specimen UAM-Tc.Don.1/186.

TYPE LOCALITY: Kalmyus River Area, north of the Voznesenka Village.

TYPE STRATUM: Limestone D<sub>5</sub><sup>10</sup>. Early Voznesenskian Substage. Early *Homoceras*–*Hudsonoceras* ammonoid Biozone, early *Plectostaffella bogdanovkensis* foraminiferal Biozone, early *Declinognathodus noduliferus* conodont Biozone. Closely above the base of the Bashkirian.

DIAGNOSIS: *Dibunophylloides* with a maximum n:d value 31:10.0 mm; major septa radially arranged; mi-



nor septa restricted to peripheral dissepimentarium that occupies 1/3 of corallite radius or less; cardinal fossula indistinct; axial structure in transverse section loose with 2–6 septal lamellae.

**MATERIAL:** Holotype UAM-Tc.Don.1/186 preserved in a long fragment including neanic growth stage with talon and mature growth stage, but no calice. Twenty three paratypes, nos. UAM-Tc.Don.1/187-209. Corallites incomplete. Several with calices preserved although most crushed. Skeletons commonly with iron oxide intra-skeletal infillings. Poorly preserved fragments illustrated by drawings when required. 22 thin sections and 28 peels available for study.

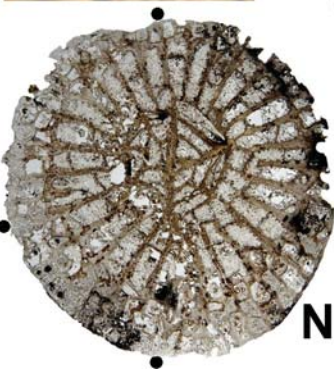
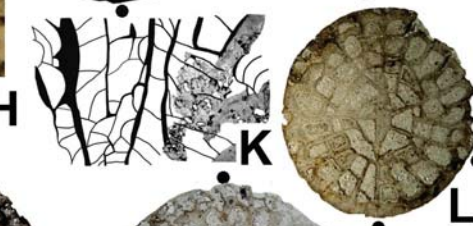
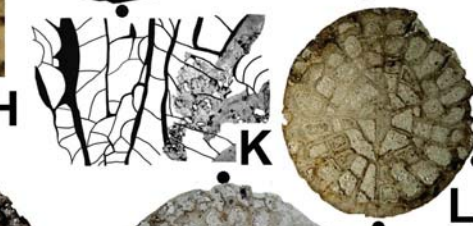
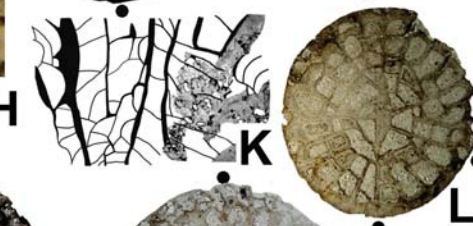
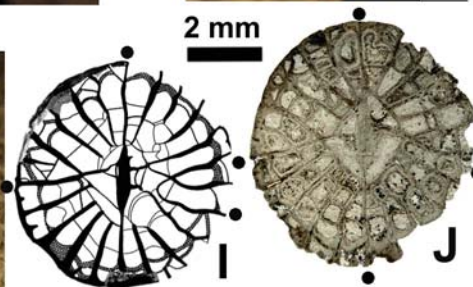
**DESCRIPTION OF HOLOTYPE:** In neanic growth stage (Text-fig. 10A, B) with n:d value 14:2.6×2.4 mm, major septa irregularly differentiated in length. Asymmetry in their arrangement emphasized by curved axial septum. That asymmetry lasting until mature growth stage. Middle part of axial septum thickened to form pseudocolumella. Minor septa and dissepimentarium absent. One incomplete row of irregular dissepiments appearing after 0.8 mm of corallite growth with n:d value 19:4.0×3.2 mm (Text-fig. 10C). Major septa at that growth stage, considered late neanic, remain irregularly differentiated with their length reduced towards both cardinal and counter side of axial septum. Pseudocolumella thicker than in younger growth stage. Minor septa not seen in corallite lumen. In early mature growth stage with n:d value 23:5.2×4.8 mm (Text-fig. 10D) all major septa radially arranged, most shortened to approximately 2/3 of corallite radius. Only two elongated to meet thick, irregular, elongated median lamella connected with very thin ended cardinal septum and thin counter septum. Minor septa present in some septal loculi as protuberances of external wall. One row of concave dissepiments in some loculi and/or 2–3 dissepiments in herringbone pattern in other loculi. In fully mature growth stage with n:d value 31:10.0 mm (Text-fig. 10E) major septa remain radially arranged and most of them approximately 2/3 corallite radius in length. Septal lamellae of two major septa, perhaps alars, meeting median lamella thinner than in the earlier growth stage, but remaining connected to cardinal

and counter septa. Those two septal lamellae and few sections of tabellae form loose axial structure. Minor septa very short, in most loculi hardly distinguishable, absent from some. Dissepimentarium approximately 1/3 of corallite radius in width. Dissepiments herringbone and regular, convex towards periphery. Inner wall not marked by sclerenchymal thickenings.

In longitudinal section (Text-fig. 10F) dissepiments differentiated in length, mostly long, arranged in steep rows, inner row vertical. Tabulae incomplete, at periphery short, convex. Periaxial and axial tabellae elongated. In ontogenetically earlier corallite growth, axial tabellae densely packed to imitate axial column. Impression of development of axial column intensified by sections of longest major septa, bordering inner area of tabularium in lower part of section. However, direct connections of innermost tabellae to periaxial tabellae and absence of lateral tabellae, bordering axial column proper (Fedorowski *et al.* 2007, fig. 21b) proves absence of that structural element. Nevertheless, the arrangement of innermost tabellae resembles axial column in *Dibunophyllum medium* closely enough to accept that arrangement as a modification of dibunophyllid axial column.

**INTRASPECIFIC VARIABILITY:** Paratype UAM-Tc.Don.1/206 closely resembles the holotype in mature morphology (Text-fig. 10H) and in n:d value (30:11×10.5 mm). Five septal lamellae in the axial structure in the paratype instead of two in the holotype, cardinal fossula slightly better accentuated and thickened inner wall are the main differences of that paratype from the holotype in the mature growth stage. Also, its longitudinal section follows the main features of the holotype by possessing an axial column-like structure in the early growth stage that disappeared during further corallite growth (Text-fig. 10K, lower and upper, respectively). Some tabulae in the advanced growth stage are complete with additional tabellae attached to their surfaces. Incomplete tabulae consist of long tabellae. All tabulae in mature growth stage, i.e., upper in section, are directed upward at approximately 50° towards the continuous section of pseudocolumella. Immature growth stage of paratype discussed, with measured n:d values 25:7.0×6.0 mm and 22:5.6×4.6 mm (Text-fig. 10G, H,

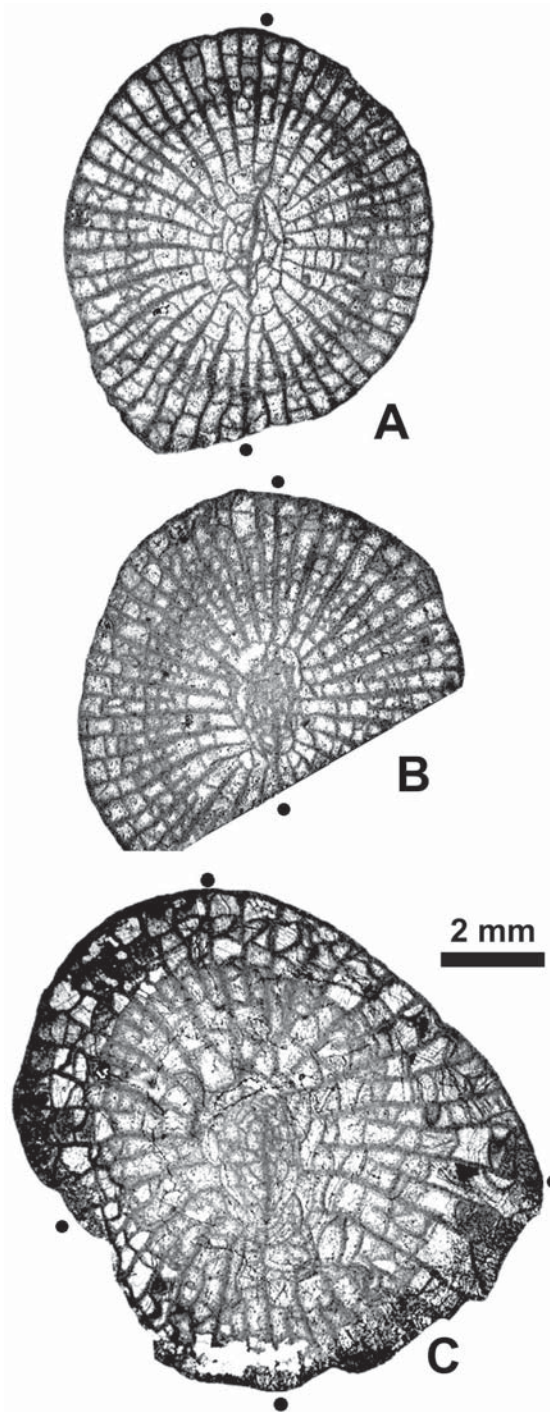
← Text-fig. 10. *Dibunophylloides paulus* sp. nov. Transverse thin sections except when stated otherwise. A-F – Specimen UAM-Tc.Don.1/186. Holotype. A, B – late neanic growth stage (A drawing from B), C, D – early mature growth stage (D – peel with drawing), E – mature growth stage, F – longitudinal thin section. G-M – Specimen UAM-Tc.Don.1/206. Paratype. G, J, I, M – successive late neanic to early mature growth stages (M – polished surface), H, L – mature growth stage (H – peel with drawing, L – polished surface), K – longitudinal section (peel with drawing). For stratigraphic position see text. Scale bars located between two adjacent images correspond to both; those to right of image apply only to that image



I, M, respectively), differs from that in the holotype by zaphrentoid arrangement of the major septa.

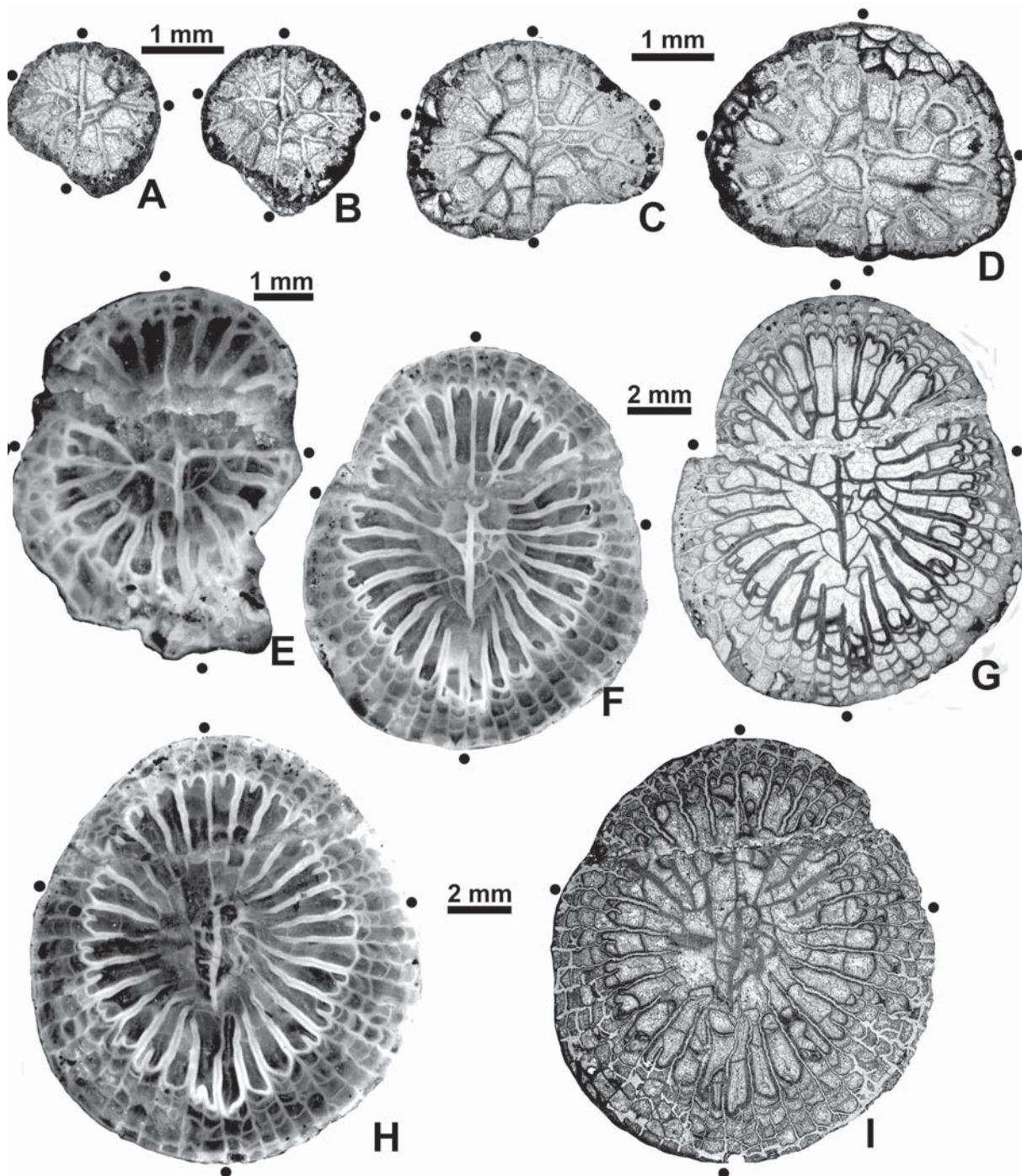
Paratype UAM-Tc.Don.1/192 with n:d value 30:9.0 mm and 28:8.0×7.2 mm (Text-fig. 11N, O) possesses an axial structure in transverse section most closely resembling that in *Dibunophyllum*. Its thin ended cardinal septum, broken by squeezing, remains long and connected to median lamella. Longitudinal section (Text-fig. 10K) taken from an early growth stage deformed by attachment structures and precipitation with iron minerals. Tabulae in the lower part of section incomplete, resembling the axial column. In upper part either complete or composed of long, flat tabellae. Both parts typical of *Dibunophylloides* despite deformation. Another paratype with strong talon (Text-fig. 11F) differs from holotype and remaining paratypes in simplified morphology and tiny diameter of its early cylindrical part (Text-fig. 11I, J, L; n:d value 24:6.5×6.0 mm). Its position in the discussed species is suggested by characters resembling the immature growth stage of the holotype, in radial arrangement of major septa leaving the axial area free, in long and thick pseudocolumella and its unrecognizable cardinal fossula. Thickening of its median lamella greater than in any mature specimen included here in *D. paulus*, resembles that structure in corallites tentatively named as *Arachnolasma?* sp. (see below).

Most corallites studied, including all derived from Zhelvakova Balka (Ravine), are flattened by pressure. Calices (Text-fig. 11A, B, D, G, H, M) and smooth external surfaces with only growth striae, but no septal furrows (Text-fig. 11A–C, E, F) preserved in several corallites. N:d values measured in reasonably preserved calices: smallest 23:5.9 mm in cylindrical part of corallite (Text-fig. 11C), 28:8.8×7.8 mm, 28:11.5 mm (calice margin), 26:8×6 mm (be-



Text-fig. 12. *Dibunophylloides longiseptatus* Fomichev, 1953. Transverse sections. A, B – Specimen 476. Holotype. Lobov Yar, Limestone M<sub>5</sub>, Late Moscovian. C – Specimen 241/37. Paratype. Kamyshevakh River, left bank, 2 km below Babivki Village, Limestone M<sub>6</sub>, late Moscovian. Peels taken from rudiments of specimens left after thin sectioning. Compare Fomichev (1953, pl. 27, figs 8a, 9). Scale bar between A and B corresponds to all images

← Text-fig. 11. *Dibunophylloides paulus* sp. nov. Paratypes. A – Specimen UAM-Tc.Don.1/187. Calice of crushed corallite. B – Specimen UAM-Tc.Don.1/188. Calice and partly preserved external wall of squeezed corallite. C – Specimen UAM-Tc.Don.1/209. External view; extremely shallow septal furrows in the middle. D, E – Specimen UAM-Tc.Don.1/190. D – partly preserved calice of slightly deformed corallite, E – corallite surface; growth striae well preserved; extremely shallow septal furrows in upper part. F, I, J, L – Specimen UAM-Tc.Don.1/207. F – side view of early growth stage with strong talon, L, I, J – successive transverse sections (J, L – thin sections, I – peel with drawing). G – Specimen UAM-Tc.Don.1/189. Incomplete calice. H – Specimen UAM-Tc.Don.1/193. Remnants of calice. M – Specimen UAM-Tc.Don.1/191. Squeezed calice. K, N, O – Specimen UAM-Tc.Don.1/192. K – slightly eccentric longitudinal section (drawing on peel), N, O – transverse thin sections; advanced (N) and early mature (O) growth stage. For stratigraphic position see text. Scale bar between I and J corresponds to all pictures



Text-fig. 13. *Dibunophylloides longiseptatus* Fomichev, 1953. Specimen UAM-Tc.Don.1/241. Topotype. Lobov Yar, Limestone M<sub>5</sub>, late Moscovian. Transverse thin sections except when stated otherwise. A-D – early to late neanic growth stage, E – late neanic/early mature growth stage, F-I – mature growth stage (E, F, H – polished surfaces, I – peel). Scale bars located between two adjacent images correspond to both; those to right of image apply only to that image

neath calice), 28:9.5×7.5 mm (incomplete calice), and 23:5.6×4.8 mm (below calice). Axial structure in calice with median lamella dominating and with up to six septal lamellae present, resembles axial struc-

tures in calices of *Dibunophyllum*. Also, cardinal septum slightly thinner than the adjacent major septa appears shortened when its inner margin is broken by squeezing (Text-fig. 11G, H, M).



REMARKS: *Dibunophylloides paulus* is the stratigraphically earliest representative of that genus in the Donets Basin, occurring in beds of the same age as *Dibunophyllum medium*. That occurrence and its suspected influence on the reconstruction of the phylogeny are discussed in the Considerations. *Dibunophylloides paulus* differs from the Moscovian type species in possessing more obvious dibunophyllid features. Two species of *Dibunophylloides* from the Donets Basin described by Fomichev (1953, pl. 27, figs 2–11; Text-fig. 12a–c) closely resemble one another in the morphology and in the n:d values. Thus, *Dibunophylloides symmetricus* (Dobrolyubova, 1937) of Fomichev (1953) has been synonymized here with *D. longiseptatus* Fomichev, 1953. That species differs from the Moscow Basin type species in the bilateral rather than radial arrangement of the major septa and, first of all, in septal lamellae separated from the major septa (Text-figs 12, 13).

OCCURRENCE: Holotype UAM-Tc.Don.1/186 and paratype UAM-Tc.Don.1/206 see type locality. Paratype UAM-Tc.Don.1/207 from the Kalmyk River Area, Bezymennaya Balka (Ravine). Paratypes UAM-Tc.Don.1/187–205 from the Kalmyk River Area, Zhelvakova Balka (Ravine). All specimens from Limestone D<sub>5</sub><sup>10</sup>. Early Voznesenskian Substage. Early *Homoceras*–*Hudsonoceras* ammonoid Biozone, early *Plectostaffella bogdanovkensis* foraminiferal Biozone, early *Declinognathodus noduliferus* conodont Biozone. Closely above the base of the Bashkirian.

*Dibunophylloides finalis* (Vassilyuk, 1960)  
(Text-figs 14 and 15)

1953. *Lophophyllum* cf. *grabaui* Chi; Fomichev, p. 271, pl. 16, fig. 4.

1960. *Dibunophyllum finalis* Vassilyuk, p. 146, pl. 36, fig. 2.

EMENDED DIAGNOSIS: *Dibunophylloides* with median lamella thin; septal lamellae short, united with inner margins of major septa when latter elongated, 4–8 in number; dibunophyllid axial structure in transverse section persists to maturity, but axial column absent; cardinal fossula barely recognizable; minor septa restricted to peripheral dissepimentarium that occupies up to 1/3 of corallite radius; 30–39 (most commonly 30–32) major septa at 10–23 mm (most commonly 11–13 mm) corallite diameter.

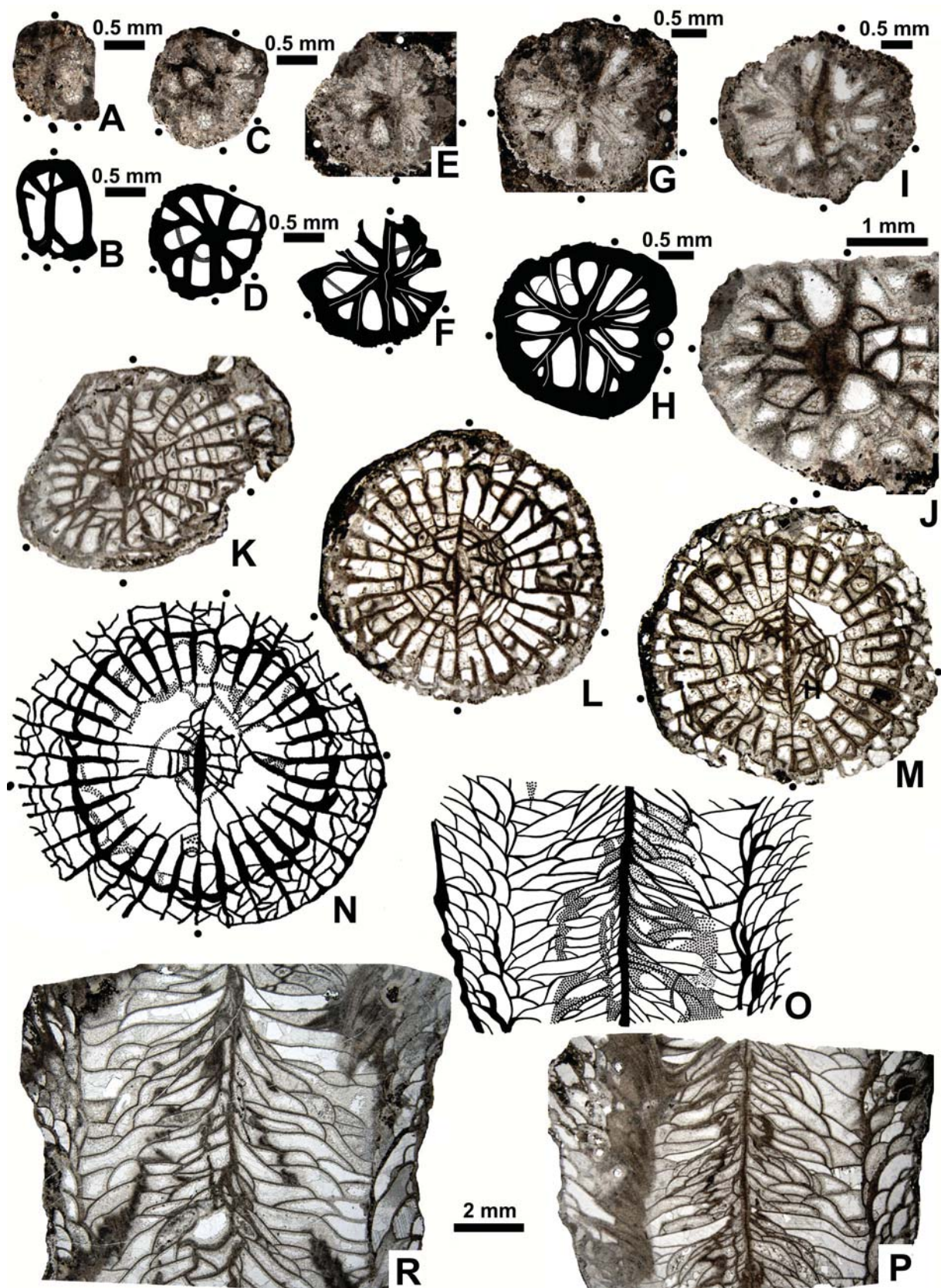
MATERIAL: Holotype restudied but not re-illustrated. 11 incomplete corallites UAM-Tc.Don.1/210–

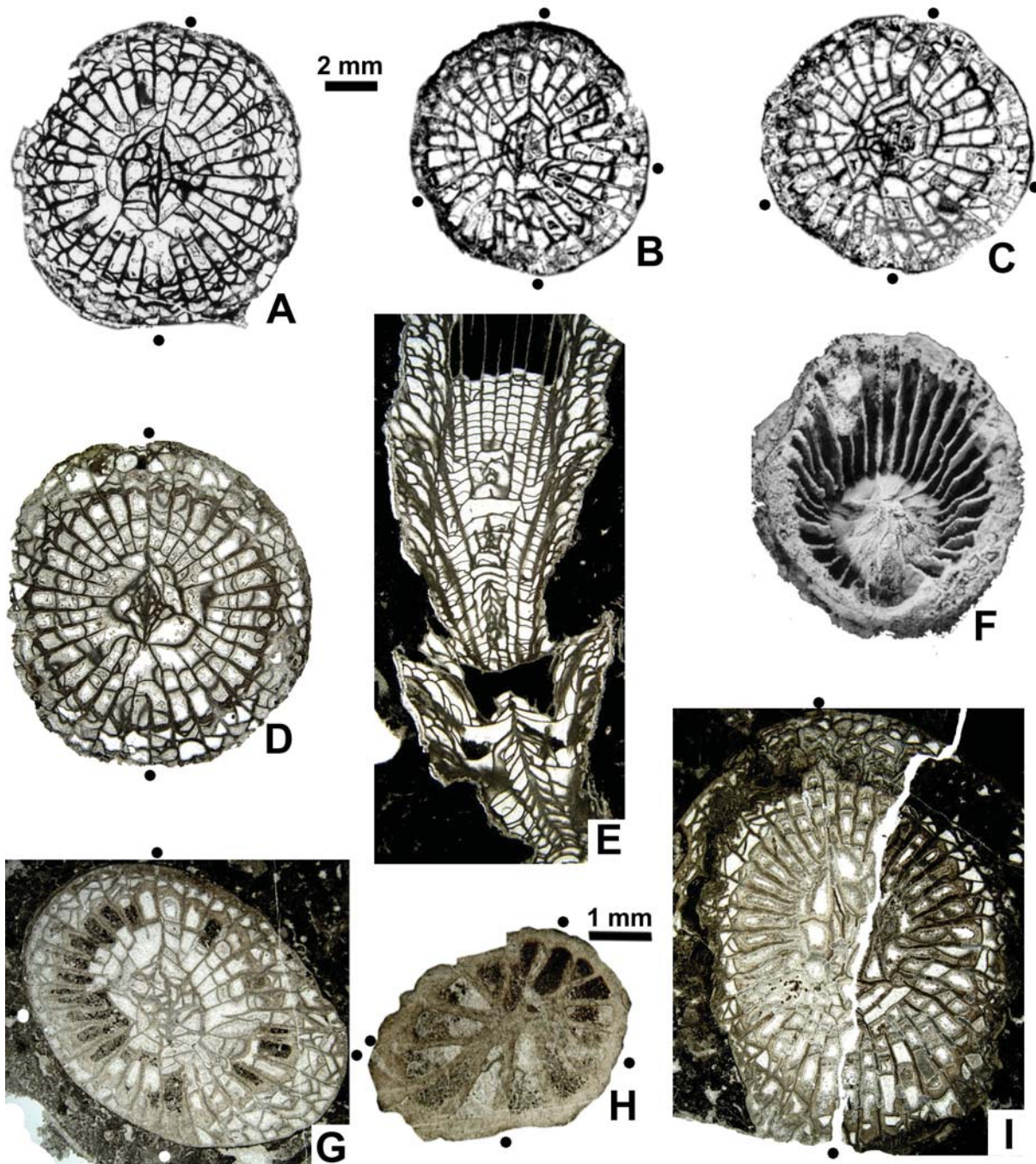
220. One corallite with calice and two with early growth stages preserved. All corallites sectioned. 16 thin sections and 21 peels available for study.

DESCRIPTION: The calice preserved in a single specimen (Text-fig. 15F). N:d value at its margin 30:12.6×11.6 mm. Calice floor irregularly dome-shaped, lacking distinct axial cone. The highest point of the calice top extends for approximately 12 mm above the deepest part at dissepimentarium/tabularium boundary, not exposed in the figure. Median lamella united with counter septum and with curved cardinal septum to form axial septum elevated very slightly above the surface of the calice floor. Septal lamellae *sensu stricto* absent, but inner margins of some elongated major septa approach or meet axial septum. Cardinal fossula marked by shallow depression in calice floor (Text-fig. 15F, lower).

Early ontogeny in one corallite almost complete (Text-fig. 14A–K). Brephic growth stage (Text-fig. 14A, B) with seven major septa at 1.2×1.0 mm corallite diameter. Counter-lateral septa appeared prior to alar septa as indicated by the underdevelopment of the left alar septum. Direction of early corallite growth (neanic stage) changes twice, both times in the alar septal plane. That atypical curvature resulted in the underdevelopment of quadrants of septa at concave corallite side: right quadrants in the early neanic growth stage (Text-fig. 14C–H) and left quadrants in the late neanic/early mature growth stage (Text-fig. 14J, K). Second, stronger curvature resulted in apparent elongation of major septa in right quadrants. Peripheral fragments of those septa cut out from Text-fig. 14J (right). Axial septum dominates during entire early ontogeny.

In neanic growth stage (Text-fig. 14C–J) major septa in counter quadrants increase in number faster than in cardinal quadrants. Successive n:d values: 9:1.4 mm, 11:2.0×1.6 mm, 15:2.5×2.3 mm, 17:3.0×2.5 mm, 19:3.2×7.0 mm. Elongation of corallite in late neanic growth stage (Text-fig. 14J, right) resulted from strong curvature. Inner part of axial septum corresponds to pseudocolumella, which thickens successively to reach its peak in late neanic growth stage (Text-fig. 14J). Minor septa absent from corallite lumen, not recognized in thickness of external wall. Dissepimentarium absent. Morphology of neanic growth stage exposed by thin section of another specimen (Text-fig. 15H) closely resembles advanced neanic growth stage of specimen described here in detail (Text-fig. 14G, H), but it has a larger diameter and its n:d value (15:4.2×3.4 mm) differs slightly from that in the afore described specimen.





Text-fig. 15. *Dibunophylloides finalis* (Vassilyuk, 1960). Transverse thin sections except when stated otherwise. A, D. Specimen UAM-Tc. Don.1/212. Mature growth stage. B, C, F. Specimen UAM-Tc.Don.1/213. B, C – mature growth stage (peels), F – calice. E – Specimen UAM-Tc.Don.1/214. Longitudinal thin section. Deep rejuvenation of early mature corallite. G – specimen UAM-Tc.Don.1/215. Mature growth stage. H, I – Specimen UAM.Tc.Don.1/216. H – neanic growth stage, I – mature growth stage. For stratigraphic position see text. Scale bar between A and B corresponds to all images except H

← Text-fig. 14. *Dibunophylloides finalis* (Vassilyuk, 1960). Transverse thin sections except when stated otherwise. A-P – Specimen UAM-Tc. Don.1/210. A, B – brephic growth stage, C-J – neanic growth stage (B, D, F, H – drawings from A, C, E, G respectively), K – late neanic/early mature growth stage, L-N – successive sections of mature growth stage (N – drawing on peel image), O, P – longitudinal sections at distance of approximately 0.8 mm (O – drawing on peel image, P – thin section). R – Specimen UAM-Tc.Don.1/204. Longitudinal thin section. For stratigraphic position see text. Scale bar between P and R corresponds to all images except A-J

In early mature growth stage of corallite described in detail (Text-fig. 14K), with n:d value 23:8.6×5.6 mm, major septa begin to differentiate in length with some meeting axial septum. Inner part of axial septum, corresponding to pseudocolumella, begin to thin. Incomplete dissepimentarium appears at that growth stage, but minor septa remain absent from corallite lumen.

In mature growth stage (Text-fig. 14L–N) with n:d values 30:9.5×9.3 mm, 31:10.4×9.6 mm and 32:12.6×11.0 mm, major septa radially arranged, in tabularium slightly thickened starting from thickened inner wall, in dissepimentarium thin. Shape of major septa similar in mature growth stage of all corallites studied (Text-figs 14M, N; 15A–D, G, I), but their length differs both during corallite growth and between corallites. In earlier mature growth of completely studied corallite (Text-fig. 14L) some major septa elongate to approach axial septum and to participate in formation of axial structure, that is in this transverse thin section identical to typical *Dibunophyllum*. In course of corallite growth (Text-fig. 14M, N), septal lamellae in axial structure become isolated and width of that structure reduced. Similar trend is observed in most other corallites, although their axial structures are narrower (Text-fig. 15A–D, G). That trend ends with axial structure reduced to axial septum and few short septal lamellae (Text-fig. 15I; Vassilyuk 1960, pl. 31, fig. 2 [holotype]).

Most morphological characters of mature growth stage of corallites studied resemble one another: cardinal and counter septa directly and permanently connected to median lamella; cardinal septum shortened in only one corallite (Text-fig. 15A, D). Cardinal fossula hardly recognizable, dipping slightly into dissepimentarium. Minor septa thin, restricted to peripheral-most dissepimentarium that occupies 1/4 of corallite radius in most to 1/3 in holotype and one other corallite in this collection (Text-fig. 15I). Dissepiments irregular and herringbone.

In longitudinal sections of the mature growth stage (Text-fig. 14O–R) axial column lacking even though axial structure appears in transverse thin sections (see above). All tabulae incomplete. Three sectors of tabularium can be distinguished: 1. innermost sector, very narrow, composed of dissepiment-like tabellae elevated steeply towards and attached to pseudocolumella to form discontinuous axial column comparable to early growth stage of rejuvenated corallite (Text-fig. 15E, lower); 2. long tabellae, arranged less steeply than axial tabellae, form middle sector of tabularium. They either rest on one another, or inter-finger with peripheral tabellae. Peripheral margins of

middle lamellae may curve down to form a kind of wide, interrupted axial column. That arrangement of middle tabellae early recognizable in some corallites, but hardly if at all distinguishable in others (Text-fig. 14O, P vs. R). 3. tabellae in peripheral sector short, horizontal or only slightly elevated, interfinger with middle tabellae. Dissepiments globose, differentiated in length. Some may be as long as to constitute entire width of dissepimentarium (Text-fig. 14R, lower right), most moderate in size or small, arranged in 2–4 steep rows, inner row vertical.

REMARKS: *Dibunophylloides finalis* has been introduced on the basis of five specimens, but Vassilyuk (1960, p. 145) wrote: "... only one – large cylindrical corallite with the lower part broken apart, whereas the remaining ones – fragments." [translated here from Russian]. Thus, the species was originally represented by the mature growth stage of the holotype only, known from one transverse and one longitudinal thin section. That specimen wider (23 mm) than all but one corallite described in this paper, possesses more numerous major septa (36) and has a wider dissepimentarium. Fortunately, its longitudinal thin section documents the lack of an axial column. The description in this paper of several specimens derived from areas adjacent to the type area and from the same stratigraphic level (Limestone F<sub>1</sub>) as the holotype supplements the knowledge of that species. Three new findings are considered most important: 1. the early ontogeny closely resembles that in *Dibunophyllum* in the zaphrentoid arrangement of the major septa; 2. remnants of an axial column are present in the longitudinal section of the early ontogeny and they disappear in the course of growth; 3. the presence of a dibunophyllid axial structure in the mature transverse section, reduced step by step up to almost an axial septum alone (holotype and Text-fig. 15I herein). All those characters combined reflect both a close relationship to *Dibunophyllum* and the difference from it in qualitative characters.

From the early Bashkirian taxa known to me, only *Arachnolasma djihaniense* Semenov-Tian-Chansky, 1974 from western Sahara displays the morphology in the transverse section similar to the holotype of *D. finalis*. However, the continuous axial column present in the longitudinal section of the holotype of *A. djihaniense* excludes that specimen from *Dibunophylloides*, whereas the paratype of that north African species is known only from a transverse thin section.

OCCURRENCE: Holotype: Kalmyus River Area, Panska Gora near Amvrosievka Village, drilling

core, depth 478.3–483.7 m. Limestone E<sub>2</sub>. Specimens described here: UAM-Tc.Don.1/214, 216: Kalmyus River Area, Fenino Village, Limestone E<sub>1</sub>; UAM-Tc.Don.1/219, 215: Amvrosievskiy Kupol (locality imprecise), Limestone E<sub>1</sub><sup>1</sup> and Limestone E<sub>2</sub>, respectively. All specimens from the early Feninian Stage, Olmezovian Substage. Early *Reticuloceras*–*Bashkortoceras* ammonoid Biozone, early *Semistaffella variabilis*–*S. minuscularia* foraminiferal Biozone, early *Idiognathoides sinuatus* conodont Biozone. UAM-Tc.Don.1/210–213, 217, 220: Olkhovaya River Area, Vodyanoy Khutor, Limestone F<sub>1</sub>; UAM-Tc.Don.1/218: Uspenskiy Khutor, Limestone F<sub>1</sub><sup>1</sup>. Early Blagodatnian Stage, Mandrykinian Substage. Middle *Bilinguites*–*Cancelloceras* ammonoid Biozone, early *Pseudostaffella peregorskiy*–*Staffelleformes staffelleformis* foraminiferal Biozone, early *Idiognathodus sinuosus* conodont Biozone. Early Bashkirian.

*Dibunophylloides similis* sp. nov.

(Text-fig. 16)

HOLOTYPE: Specimen UAM-Tc/Don.1/221.

TYPE LOCALITY: Kalmyus River Area. Voznesenka Village.

TYPE HORIZON: Limestone D<sub>7</sub><sup>3</sup>. Early Voznesenskian Substage. Svita C<sub>1</sub><sup>s.g.</sup>. *Homoceras*–*Hudsonoceras* ammonoid Biozone, *Plectostaffella bogdanovkensis* foraminiferal Biozone, *Declinognathodus noduliferus* conodont Biozone. Closely above the base of the Bashkirian.

ETYMOLOGY: *Lat. similis* – similar, resembling – after its similarity to *Nina dibimitaria* Fedorowski, 2017a.

MATERIAL: Holotype UAM-Tc.Don.1/221 and four paratypes UAM-Tc.Don.1/134, 135, 222, 223. Brephic and neanic growth stages lacking from all specimens. One specimen preserved as thin section with no rock material left. Holotype most complete with a late neanic/early mature up to advanced mature growth stage preserved, slightly crushed in advanced growth stage. Eight thin sections and 13 peels available for study.

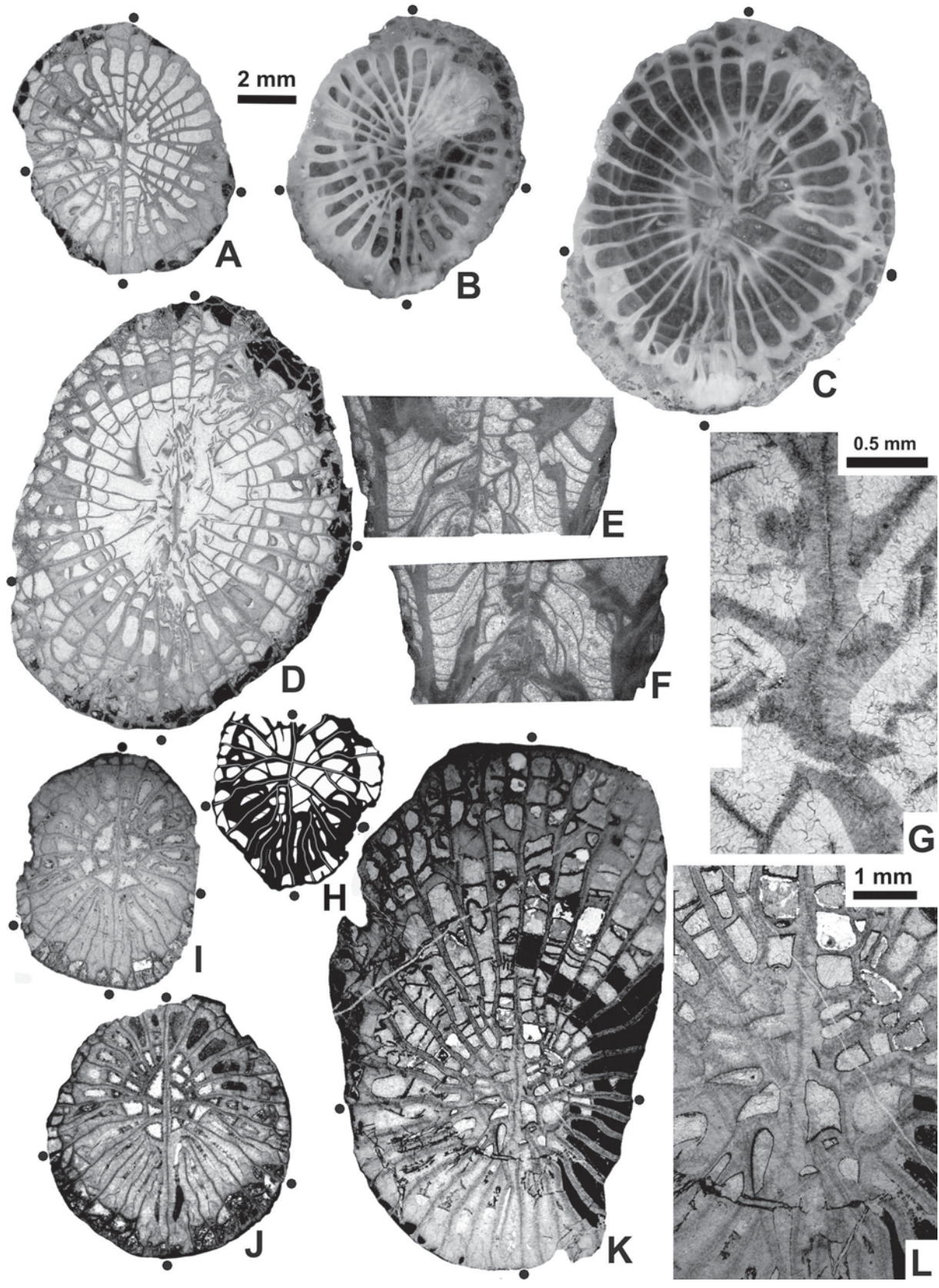
DIAGNOSIS: *Dibunophylloides* with maximum n:d value 40:16.0×12.2 mm; major septa straight; their tabularial part in cardinal quadrants thicker than those in counter quadrants; axial septum straight;

pseudocolumella slightly thickened; cardinal fossula narrow, dips into dissepimentarium; minor septa restricted to most peripheral part of dissepimentarium. Axial tabellae convex, widely spaced.

DESCRIPTION: In late neanic/early mature growth stage of holotype with n:d value 30:9.2×7.2 mm, 32:10.0×7.6 mm and one paratype with n:d value 22:6.1[incomplete]×5.2 mm, 24:8.4×6.4 mm (Text-fig. 16A, B and H, I, respectively), major septa bilaterally arranged. Axial septum almost straight and not thickened, intersects entire corallite diameter to form symmetry axis. Alar septa and two (Text-fig. 16H–J) to several (Text-fig. 16A, B, K) major septa meet axial septum. In major septa attached to axial septum calcite fibrils directed towards that septum (Text-fig. 16G, L), proving the monoseptal character of pseudocolumella. Counter-lateral septa at this growth stage and in early mature growth stage (Text-fig. 16C, J, K) shorter than adjacent major septa, inclined towards axial septum and meeting its lateral surface. Minor septa short, not recognized in some septal loculi. Dissepimentarium may be temporarily and in part replaced by sclerenchyme (Text-fig. 16B, lower left; K, lower).

Advanced mature growth stage preserved only in holotype (n:d value 40:16.0×12.2 mm). Several major septa continue attachment to middle part of axial septum, thickened there to form pseudocolumella (Text-fig. 16D, G). Presence of continuous axial septum in holotype possible to decipher by putting together its broken fragments. Minor septa seen only at most peripheral part of dissepimentarium when thin external wall preserved. Dissepiments regular and herringbone. Dissepimentarium approximately 1/4 of corallite radius in width. In longitudinal section (Text-fig. 16E, F), taken from the late neanic/early mature growth stage between Text-fig. 16B and C, dissepimentarium consists of 1–2 rows of small dissepiments, arranged in almost vertical rows. Tabulae incomplete, almost horizontal in short peripheral parts, steeply elongated upwards to meet either median lamella or inner tabellae that form a kind of irregular axial column. That arrangement best accentuated in slightly eccentric section (Text-fig. 16F). In exactly centric section (Text-fig. 16E) weak axial column recognizable in lower, ontogenetically early part. Some tabulae in upper part of that centric section meet axial septum directly. Thus, general arrangement of tabularium resembles that in *D. paulus* and *D. finalis*.

REMARKS: *Dibunophylloides similis* is poorly represented. Also, the corallites included in that species as paratypes differ in their stratigraphic occurrences



(see below). Both those factors may suggest that it is a morphotype rather than a true, genetically tied species. However, the morphology of the late neanic/early mature growth stage, similar in all specimens, is used here to legitimize the proposed identification. That early growth stage is at the same time strikingly similar to the corresponding growth stage in *Nina dibimitaria* Fedorowski, 2017a. Such a similarity allows us to consider the possibility of the relationship between the late Dibunophyllinae and the early Bothrophyllidae as discussed in the Considerations below.

The morphology mentioned, the bilateral rather than radial arrangement of the major septa, the minor septa strongly reduced in length and the arrangement of the tabulae in the longitudinal section distinguish *D. similis* from the type species. The last two characters distinguish it from *D. longiseptata* Fomichev, 1953. Details in the morphology of the tabularium, i.e., the inner tabellae convex and loosely arranged but not flat and densely packed as in *D. paulus* and *D. finalis* and the dibunophyllid morphology of the axial area less well accentuated in the transverse sections are the main difference of *D. similis* from the latter two species.

**OCCURRENCE:** Kalmyus River Area, Voznesenka Village. Holotype UAM-Tc.Don1/221 and Paratype UAM-Tc.Don.1/223: Amvrosievskiy Kupol, Limestone D<sub>7</sub><sup>3</sup>. Paratype UAM-Tc.Don.1/135: Nikolaevka Village, Limestone D<sub>6</sub>. Paratype UAM-Tc.Don.1/222: Popovaya Balka (Ravine), Limestone D<sub>7</sub><sup>5</sup>. All specimens from Svita C<sub>1</sub><sup>s</sup><sub>g</sub>, early Voznesenskian Substage. *Homoceras*–*Hudsonoceras* ammonoid Biozone, *Plectostaffella bogdanovkensis* foraminiferal Biozone, *Declinognathodus noduliferus* conodont Biozone. Paratype UAM-Tc.Don.1/134: Blagodatnoye Village, Malaya Shishovka Ravine (Balka), Limestone E<sub>1</sub><sup>nizhn.</sup>. Svita C<sub>2</sub><sup>b</sup><sub>a nizhn.</sub>, earliest Feninian Substage. *Reticuloceras*–*Bashkortoceras* ammonoid Biozone, *Semistaffella variabilis*–*S. minuscularia* foraminiferal Biozone, *Idiognathoides sinuatus* conodont Biozone. Early Bashkirian.

*Dibunophylloides columnatus* sp. nov.  
(Text-figs 17 and 18)

**HOLOTYPE:** Specimen UAM-Tc.Don.1/224.

**TYPE LOCALITY:** Kalmyus River Area. Voznesenka Village.

**TYPE HORIZON:** Limestone D<sub>7</sub>, early Voznesenskian Substage. Early *Homoceras*–*Hudsonoceras* ammonoid Biozone, early *Plectostaffella bogdanovkensis* foraminiferal Biozone, early *Declinognathodus noduliferus* Biozone. Closely above the base of the Bashkirian.

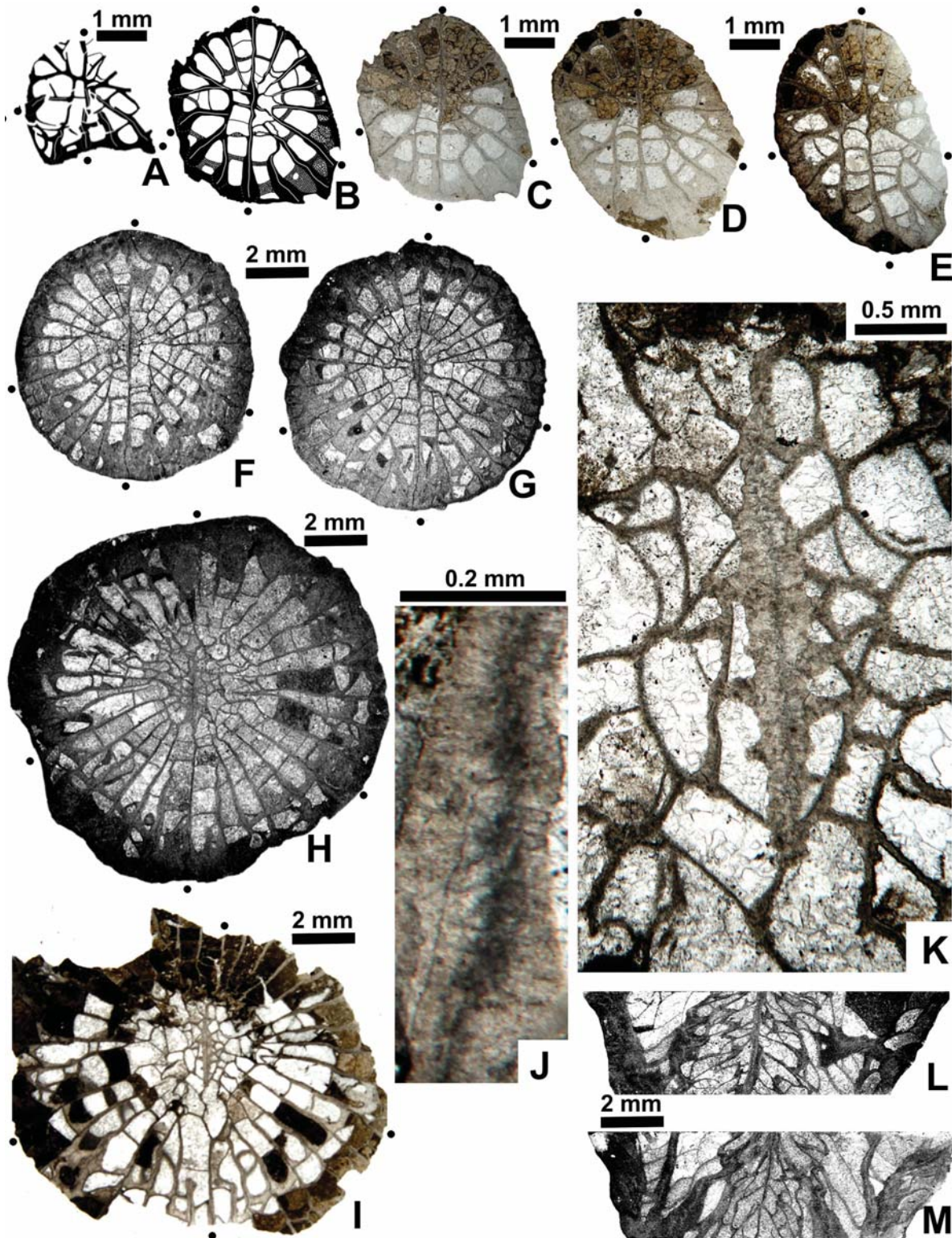
**ETYMOLOGY:** Named after the distinctly thickened pseudocolumella present permanently up to calice floor.

**MATERIAL:** Holotype UAM-Tc.Don.1/224 preserved from early neanic to late mature growth stage. Brephic growth stage and calice lacking. Microstructure diagenetically altered. Five paratypes UAM-Tc.Don.1/225–229, all squeezed in mature growth stage, but their main characters recognizable. Two paratypes with late neanic/early mature growth stage well preserved.

**DIAGNOSIS:** *Dibunophylloides* with n:d value 35:14 mm (holotype) up to 44:16.5 mm (mean value) in the largest paratype; inner margins of major septa wavy; several meet pseudocolumella; short septal lamellae separated from some inner margins of major septa; pseudocolumella long, thick; minor septa vary in length with some almost crossing narrow dissepimentarium; cardinal fossula distinct; inner tabellae sigmoidal, densely packed.

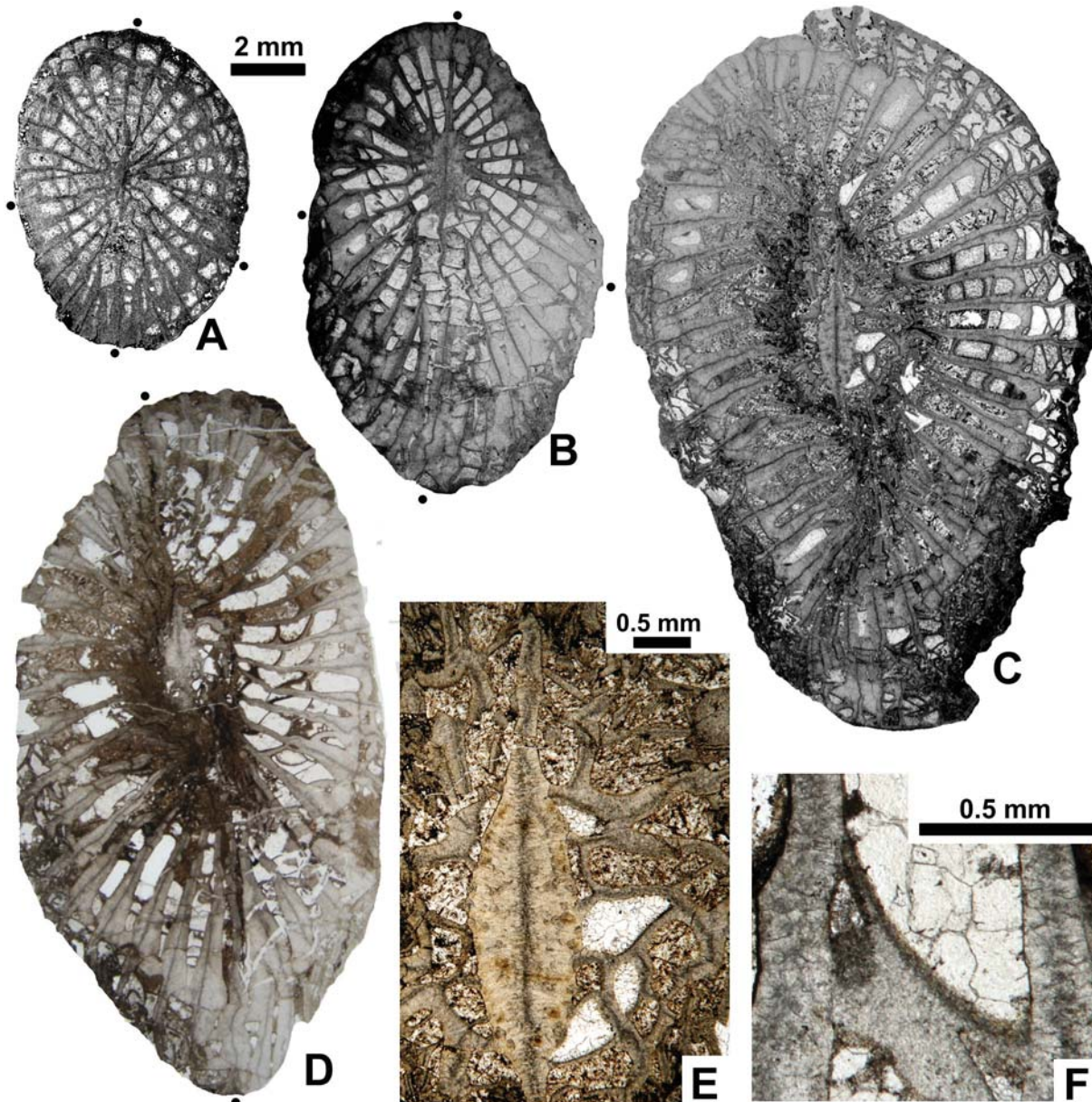
**DESCRIPTION OF HOLOTYPE:** In early to late neanic growth stage, with n:d values 12:2.5 mm, 17:4.0×3.0 mm and 18:5.0×3.0 mm (Text-fig. 17A–E), major septa bilaterally arranged with axial septum as axis of symmetry. Individual quadrants of major septa recognizable due to slight underdevelopment of last inserted major septa. Alar pseudofossulae absent. Alar septa and 2–3 longest major septa reach axial part of thickened axial septum, i.e., pseudocolumella. Counter-lateral major septa meet axial septum, whereas last pair of major septa inserted in cardinal quadrants bent outwards cardinal septum and join

← Text-fig. 16. *Dibunophylloides similis* sp. nov. Transverse thin sections except when stated otherwise. A–G – Specimen UAM-Tc.Don.1/221. Holotype. A, B – late neanic/early mature growth stage, C – early mature growth stage, D – mature growth stage, E, F – longitudinal sections approximately 0.8 mm apart, G – morphology of pseudocolumella (B, C – polished surfaces, E, F – peels). H–J – Specimen UAM-Tc.Don.1/134. Paratype. H – late neanic/early mature growth stage (peel with drawing), I, J – early mature growth stage. K, L – Specimen UAM-Tc.Don.1/135. Paratype. K – mature growth stage; great width of dissepimentarium (upper in picture) apparent, resulted from obliqueness of section, L – axial area enlarged from K. For stratigraphic position see text. Scale bar between A and B corresponds to all images except G and L.



Text-fig. 17. *Dibunophylloides columnatus* sp. nov. Specimen UAM-Tc.Don.1/224. Holotype. Transverse thin sections except when stated otherwise. A-E – early to late neanic growth stage (B – drawing on C), F, G – early mature growth stage (peels), H, I – mature growth stage (H – peel), J – microstructure of septum diagenetically altered, K – axial part of corallite (enlarged from I), L, M – longitudinal sections; L – centric, M – 1.0 mm apart from L (peels). For stratigraphic position see text. Scale bars located between two adjacent images correspond to both; those to right of image apply only to that image





Text-fig. 18. *Dibunophylloides columnatus* sp. nov. Paratypes. Transverse thin sections except when stated otherwise. A – Specimen UAM-Tc.Don.1/225. Late neanic/early mature growth stage (peel). B, C, E – Specimen UAM-Tc.Don.1/226. B – late neanic/early mature growth stage, C – mature growth stage; crushed, E – axial structure (enlarged from C). D, F – Specimen UAM-Tc.Don.1/227. D – mature growth stage; crushed, F – microstructure of septa altered diagenetically. For stratigraphic position see text. Scale bar between A and B corresponds to images A-D

preceded pair of major septa making cardinal fossula wide. First dissepiments, mostly filled with sclerenchyme appear in some septal loculi. Minor septa not recognized.

In early mature growth stage (Text-fig. 17F, G), with n:d values 27:8.5×8.0 mm and 27:9.0 mm, major septa semi radially arranged with inner margins starting to wave. Axial septum remains as symmetry axis. Strong underdevelopment of last major septa inserted

makes all quadrants of septa clearly distinguishable. Minor septa thin, restricted to peripheral dissepimentarium. Dissepimentarium complete. Dissepiments regular in single row, herringbone in 2–3 rows.

In mature growth stage (Text-fig. 17H, I), with n:d values 34:12.2 mm and 35:14 mm (incomplete in Text-fig. 17I), major septa radially arranged. Cardinal and counter septa remain connected to long, thickened pseudocolumella; connection with cardi-

nal septum stronger. Several major septa either meet pseudocolumella with their thin, twisted inner margins or septal lamellae separated from them. Length of septal lamellae varies from short blades not incorporated in median lamella to blades long and wavy (Text-fig. 17K). Minor septa short and thin. Cardinal fossula well developed, slightly narrowing axially. Dissepimentarium up to 1/4 of corallite radius in width. Dissepiments irregular and herringbone.

Morphology exposed in two surfaces of one longitudinal cut, made between transverse cuts as illustrated in Text-fig. 17G and H, differs in spite of there being only 1 mm distance between them. Axial tabellae in both less convex and arranged denser than peripheral tabellae of incomplete tabulae. However, in slightly eccentric section inner tabellae flatter, longer and elevated steeper than in the axial section and area occupied by them narrower (Text-fig. 17M and L, respectively). Well defined axial column absent from both, but some inner tabellae in axial cut rest on underlying tabellae alike those in axial column. Dissepiments long, arranged in two rows. Microstructure of septa (Text-fig. 17J) damaged by diagenesis. Some bunches of crystalline fibrils may be remnants of trabeculae but this suggestion is unsupported.

**INTRASPECIFIC VARIABILITY:** All paratypes (Text-fig. 18A–F) larger than holotype, their major septa in tabular parts of cardinal quadrants and their pseudocolumellae thicker and minor septa longer. Those differences and similarities of paratypes to one other may suggest their separate specific status. However, immature growth stages, perhaps late neanic/early mature, resemble comparable growth stages of holotype in arrangement of major septa, direct connection of cardinal and counter septa with thick pseudocolumella and cardinal fossulae distinct. Also inner margins of their major septa wavy (Text-fig. 18E), dissepimentaria narrow, consisting of herringbone dissepiments, resemble those in holotype. Squeezing of mature growth stages excludes preparation of good longitudinal sections.

**REMARKS:** The inner margins of the major septa wavy, approaching and/or reaching the pseudocolumella; the occurrence of septal lamellae, the thick pseudocolumella; the permanent and well developed cardinal fossula and the pseudocolumella connected more closely to the cardinal than to the counter septum are characters distinguishing *D. columnatus* from all other species of *Dibunophylloides* described so far. *Dibunophylloides columnatus* is most similar and most closely related to *D. similis*.

**OCCURRENCE:** Kalmyus River Area. Holotype UAM-Tc.Don.1/224: Voznesenka Village, Limestone D<sub>7</sub>. Paratype UAM-Tc.Don.1/226: Zhelvakova Balka (Ravine), Limestone D<sub>5</sub><sup>10</sup>. Paratype UAM-Tc.Don.1/227: Bezymennaya Balka (Ravine), Limestone D<sub>5</sub><sup>11</sup>. Paratypes UAM-Tc.Don.1/225, 228, 229: Bezymennaya Balka (Ravine). Limestone D<sub>6</sub>. Early Voznesenskian Substage. Early *Homoceras*–*Hudsonoceras* ammonoid Biozone, early *Plectostaffella bogdanovkensis* foraminiferal Biozone, early *Declinognathodus noduliferus* Biozone. Closely above the base of the Bashkirian.

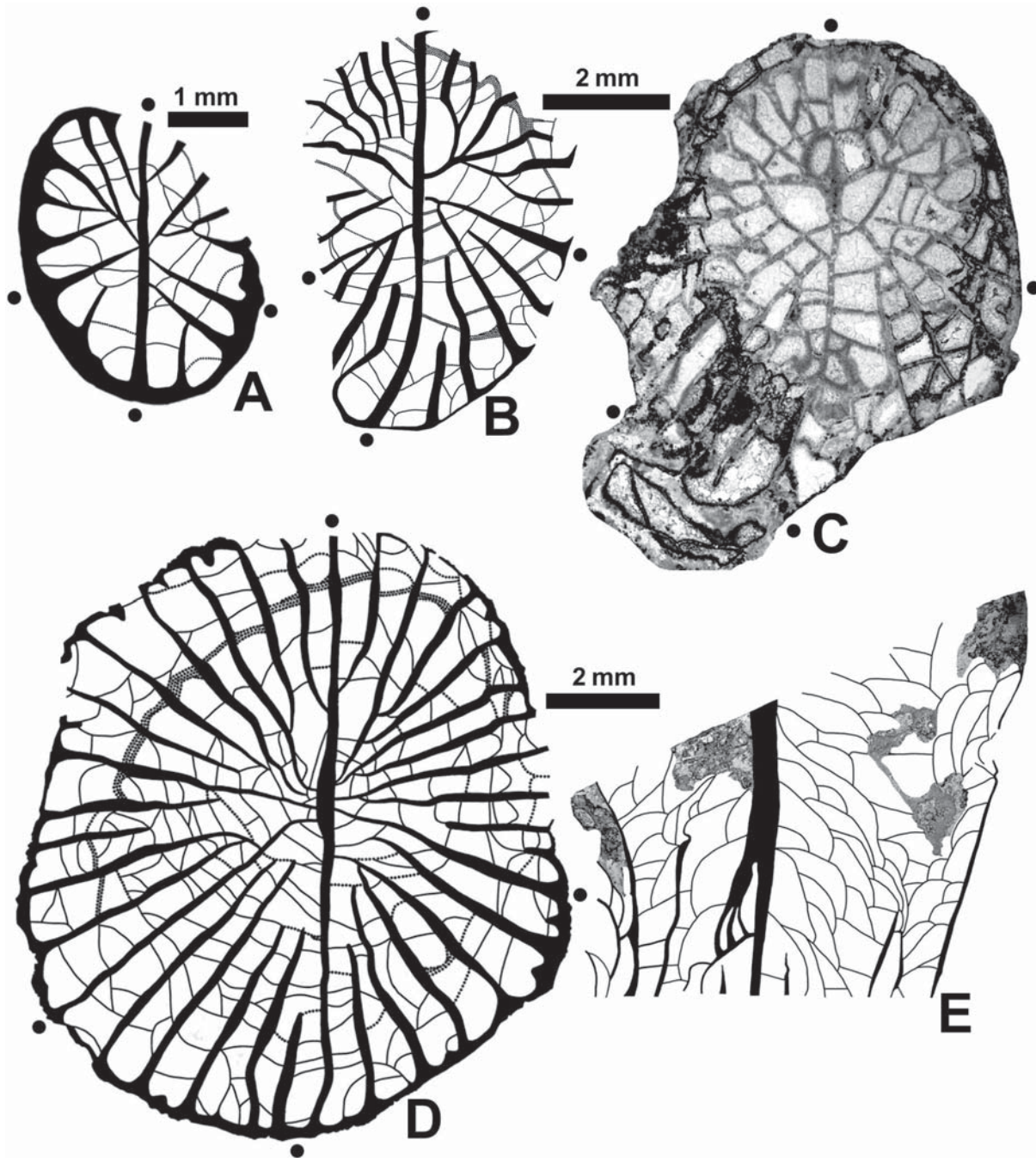
*Dibunophylloides* sp.

(Text-fig. 19)

**MATERIAL:** Single corallite UAM-Tc.Don.1/240. Most of early ontogeny and mature growth stage preserved. Calice lacking. Microstructure of septa destroyed by diagenesis. One thin section and five peels available for study.

**DESCRIPTION:** Early neanic growth stage oval due to lateral attachment to substrate (Fig. 19A). N:d value 18:4.0×3.2 mm. Major septa arranged bilaterally in clearly recognizable quadrants. Strong axial septum forms symmetry axis. Number of major septa in counter quadrants (5) prevails over cardinal quadrants (3). Counter-lateral septa shortest, middle septa in counter quadrants longest. In cardinal quadrants alar septa prevail in length. Last major septa inserted remain underdeveloped. Cardinal fossula well developed. Minor septa not recognized in thickness of external wall. Dissepiments absent.

Late neanic growth stage with n:d values 24:6.5×4.5 mm (Text-fig. 19B) approximately 1.3 mm above the afore described section remains oval, only slightly curved at bottom of strong talon. The next growth stage, with n:d value 26:9.0×6.0 mm (including talon), considered early mature (Text-fig. 19C). Arrangement of septa remains distinctly bilateral, despite deformation caused by talon. Counter-lateral septa short, but free ended. Only middle major septa in counter quadrants and either alar or middle septa in cardinal quadrants attach axial septum, remaining major septa free ended. Cardinal fossula well developed, alar pseudofossulae recognizable. First very short minor septa present in some septal loculi. Dissepimentarium of 1–3 rows of regular and herringbone dissepiments. Dissepimentarium/tabularium boundary in counter quadrants marked by thickening of inner row of dissepiments, in cardinal



Text-fig. 19. *Dibunophylloides* sp. Specimen UAM-Tc.Don.1/240. A, B – early and late neanic growth stage, C – transverse thin section, late neanic/early mature growth stage, D – mature growth stage, E – longitudinal section (A, B, D, E – drawings on peels). For stratigraphic position see text. Scale bars located between two adjacent images correspond to both; those to right of image apply only to that image

quadrants that boundary unrecognizable (disstabilarium).

In mature growth stage (n:d value 35:10.2×11.5 mm) morphology similar to that described above (Fig. 19D). Longest major septa located in middle part of counter quadrants. Alar septa longest in cardinal

quadrants, but third pair of major septa inserted in these quadrants second longest. Counter-lateral septa short, attached to strong axial septum. Six other major septa in counter quadrants and alar septa attached to slightly thickened part of axial septum, i.e., mono-septal pseudocolumella. Septal lamellae not formed.

Cardinal fossula and alar pseudofossulae easily recognizable. Minor septa only as knobs on external wall. Dissepimentarium in counter quadrants 1/4–1/3 of corallite radius in width. In cardinal quadrants indistinguishable from sections of peripheral tabellae (distabularium). Dissepiments interseptal, large, slightly irregular or in loose herringbone pattern.

In longitudinal section dissepiments large, in almost vertical rows. Tabulae incomplete, variable in size and arrangement. Peripheral tabellae flat or slightly convex when inner wall thickened; those forming distabularium more convex, contact with dissepimentarium in various way (Text-fig. 19E, left and right, respectively). Some axial tabellae large, resting on underlying tabellae in a way typical for lateral tabellae. A fragment of axial column developed that way in ontogenetically younger part of corallite. Remaining tabellae vary in size from very long to short and bubble-like that prevail. Pseudocolumella continuous, strong.

REMARKS: The morphology of the specimen discussed resembles the morphology of *Nina* Fedorowski, 2017a more strongly than any other species of *Dibunophylloides* described so far. It could be included in *Nina*, if the presence of an incomplete axial column in the longitudinal section and the typical dibunophyllid morphology in the early mature growth stage are not established. That similarity would have made *Dibunophylloides* sp. closer to the Dibunophyllinae/Bothrophyllidae intermediate species rather than *D. similis*, if occurring early enough. Its occurrence in Limestone F<sub>1</sub> may only suggest a long lasting morphological inconsistency occurring parallel to the more rigid morphology of *Dibunophylloides* in the Donets Basin.

OCCURRENCE: Kalmyus River Area. Volnukhino Village, left bank of Luganchik River, Limestone F<sub>1</sub>. Mandrykinian Stage, Blagodatnian Substage, late *Bilinguites*–*Cancelloceras* ammonoid Biozone, *Pseudostaffella pregorskyi*–*Staffelleformis staffelleformis* foraminiferal Biozone, *Idiognathodus sinuosus* conodont Biozone. Late early Bashkirian.

Genus *Arachnolasma* Grabau, 1922

(Type species *Lophophyllum sinense* Yabe and Hayasaka, 1920; by subsequent designation of Grabau 1922, p. 59)

REMARKS: The independent generic position of *Arachnolasma* is commonly accepted by various au-

thors (e.g., Yu 1933; Volkova 1941; Wu 1964; Dobrolyubova and Kabakovich 1966; Fedorowski 1971; Semenoff-Tian-Chansky 1974; Hill 1981; Igo and Adachi 2000; Rodríguez *et al.* 2013b). Unfortunately, the characters included in the diagnosis established by Hill (1956, p. F288) and repeated later (Hill 1981, p. F361) are mostly quantitative rather than qualitative. Such a diagnosis does not follow the ICZN requirements. That failure has been already pointed out in the brief discussion on the genus *Arachnolasma* (Fedorowski 1971, p. 92), which ended with the conclusion that it is valid.

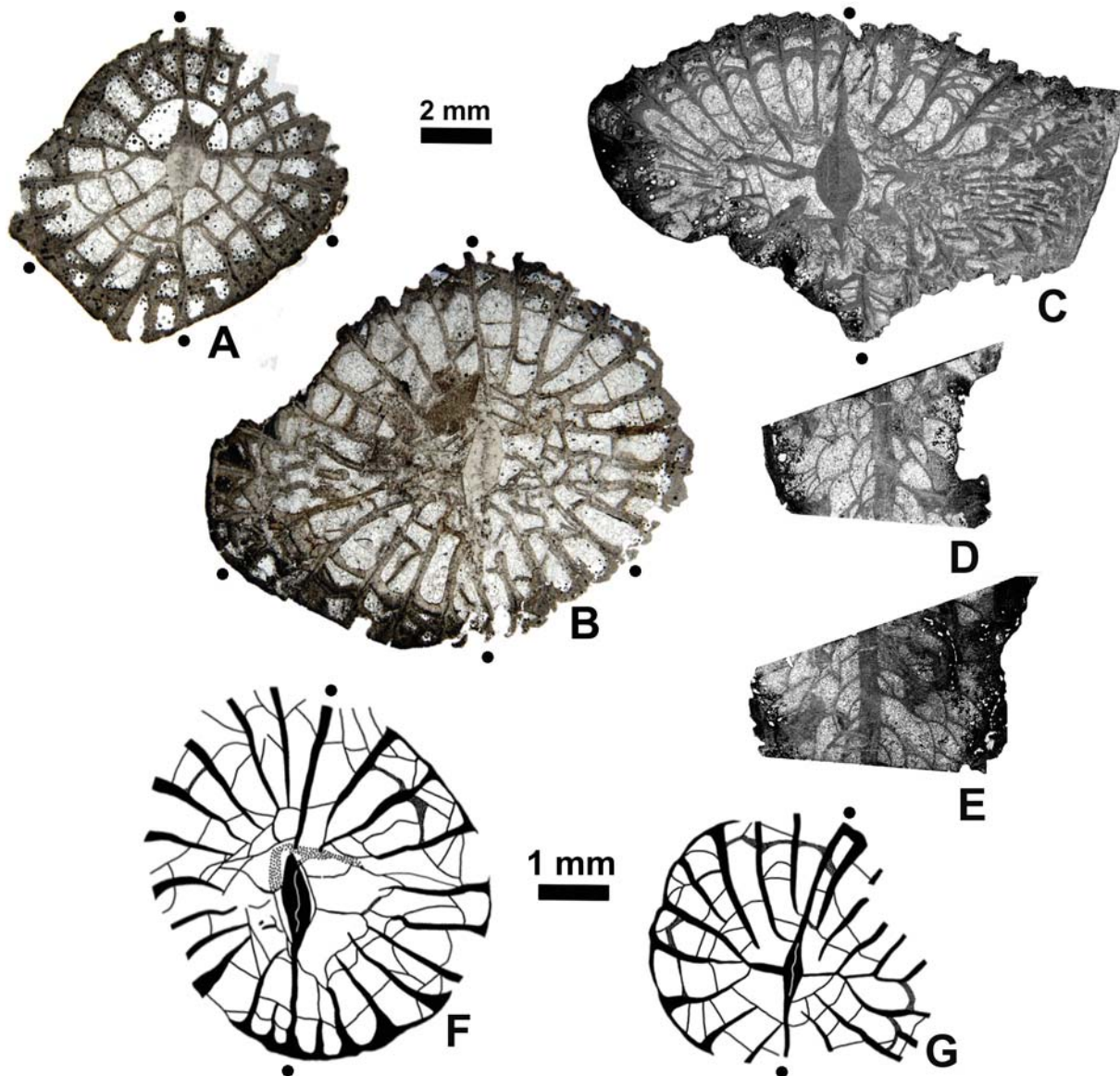
My recent attitude to the question of the independent generic status of *Arachnolasma* (Fedorowski 2015, pp. 246–249) concluded as follows: “The occurrence of a continuous axial column in the longitudinal sections, always present in the type species of *Dibunophyllum* and in other unquestionable species of that genus vs. the absence or incompleteness of such a column in *Arachnolasma*, accompanied by a very narrow axial structure in the transverse section, may serve as qualitative criteria for distinguishing between those two genera. *Arachnolasma kamyschnense* Dobrolyubova and Kabakovich, 1966 may serve as an example of *Arachnolasma*, if the criteria mentioned are accepted”. However, *A. kamyschnense* cannot replace the Chinese species as the type for *Arachnolasma*, since the type species for that genus, i.e., *Lophophyllum sinense* Yabe and Hayasaka, 1920 was derived from the upper Viséan strata of China. A single specimen illustrated by Yabe and Hayasaka (1920, pl. 6, fig. 2a–g) documents the morphology of the mature growth stage as seen in the transverse thin sections, but the very oblique and eccentric longitudinal section does not document either the occurrence or absence of the axial column. The large variability of the Chinese specimens included in that species by Yu (1933, 1937) and by subsequent Chinese authors excludes the selection of rigid diagnostic, i.e., qualitative characters of that genus based solely on literature data.

*Arachnolasma?* sp.

(Text-fig. 20)

MATERIAL: Two incomplete corallites UAM-Tc.Don.1/209 and UAM-Tc.Don.1/230. Both altered diagenetically. One squeezed in advanced mature growth stage and in calice. Two thin sections and eight peels available for study.

DESCRIPTION: In the earliest preserved growth stage of specimen UAM-Tc.Don.1/209 (Text-fig.



Text-fig. 20. *?Arachnolasma* sp. A-E – Specimen UAM-Tc.Don.1/230. A, B – transverse thin sections, late neanic/early mature and mature growth stages respectively, C – transverse section below calice floor, advanced mature growth stage (peel), D, E – longitudinal sections approximately 0.8 mm apart (peels), D – centric, E – slightly eccentric. F, G. Specimen UAM-Tc.Don.1/209. Transverse sections with peels and drawings. F – early mature growth stage, G – late neanic/early mature growth stage. For stratigraphic position see text. Upper scale bar corresponds to A-E, lower corresponds to F, G.

20G), with n:d value 20:4.0×3.5 mm, major septa irregular in length, but only two connect with thick, monoseptal pseudocolumella. Quadrants of major septa impossible to establish. Axial septum curved, making arrangement of major septa asymmetrical. Minor septa absent, first irregular dissepiments appear in counter quadrants. In more advanced growth stage of that specimen (early mature?), with n:d value 23:5.6×5.0 mm (Text-fig. 20F), major septa radially

arranged, almost equal in length except for cardinal septum that meets thick pseudocolumella and long counter septum that closely approach pseudocolumella. Remaining major septa leave large axial area free, although some very thin skeletal structures in that area may be septal lamellae as suggested by their radial position. Advanced diagenesis does not allow one to establish those features with certainty. Minor septa not recognized. Dissepimentarium absent from

cardinal quadrants, consists of two to four rows of flat herringbone dissepiments in counter quadrants.

In the earliest preserved growth stage of specimen UAM-Tc.Don.1/230 (Text-fig. 20A), with n:d value 23:5.5×4.7 mm (incomplete) arrangement of major septa in cardinal and counter quadrants differ. Those of cardinal quadrants shorten sequentially from long alar septa to shortest major septa adjacent to cardinal septum. Inner margins of most major septa in cardinal quadrants meet either pseudocolumella or cardinal septum. Only last inserted pair free. Most major septa in counter quadrants short, those next to counter septum shortest. Only three major septa in counter quadrants join lateral surface of very thick pseudocolumella. “Middle dark lines” of cardinal and counter septa contiguous with that of pseudocolumella document the occurrence of axial septum. In several septal loculi, first minor septa and dissepiments appear.

Last major septa inserted remain underdeveloped in early mature growth stage (Text-fig. 20B), making quadrants of major septa distinct. Length of earlier inserted major septa differentiated. Some of them meet lateral surface of thick pseudocolumella. “Middle dark line” of cardinal and counter septa continue to join that “line” in very thick, almond-shaped pseudocolumella up to advanced mature growth stage (Text-fig. 20C). Short minor septa recognizable in some septal loculi. Cardinal fossula absent. Preserved fragment of dissepimentarium consists of several rows of herringbone dissepiments. Inner row thickened to form inner wall.

Longitudinal section (Text-fig. 20D, E) made from early corallite growth stage between transverse sections A and B. Pseudocolumella thick, straight. Dissepiment-like inner tabellae widely spaced. Lower margins of most rest on underlying tabellae; some interfinger with convex periaxial tabellae. Thus, complete axial column absent. Dissepimentarium destroyed by erosion or corrosion.

REMARKS: The specimens described differ considerably from one another in both n:d value and morphology. They have been described under a common generic name in order to avoid multiplication of poorly supported names. Only their stratigraphic position closely above the base of the Bashkirian and the phylogenetic value of taxa of that age legitimize their description and illustration. The name *Arachnolasma* is applied to them with a question mark because of the uncertain status of that genus and the morphology of the specimens, which is rather distant from that of the type species of that genus. The typical dibunophylid axial structure is not developed, but elongation of

some inner margins of the major septa connected to the lateral surface of the very thick pseudocolumella and the morphology of the axial area of the second corallite described may be accepted as the axial structure and the incomplete axial column.

OCCURRENCE: Kalmyk River Area. UAM-Tc.Don.1/230: Voznesenka Village. UAM-Tc.Don.1/209: Bezymennaya Balka (Ravine). Both specimens from Limestone D<sub>5</sub><sup>10</sup>, early Voznesenskian Substage, early *Homoceras*–*Hudsonoceras* ammonoid Biozone, early *Plectostaffella bogdanovkensis* foraminiferal Biozone, early *Declinognathodus noduliferus* Biozone. Closely above the base of the Bashkirian.

#### Genus *Voragoaxum* gen. nov.

ETYMOLOGY: Combined from *Lat. vorago* – vortex and *axis* – axis – after the major septa twisted around the pseudocolumella in the axial corallite area.

TYPE SPECIES: *Voragoaxum cavum* sp. nov.

DIAGNOSIS: Solitary, dissepimented corals; early growth stage zaphrentoid; in maturity major septa continuous, spirally arranged, meeting but not entering monoseptal pseudocolumella derived from axial septum; cardinal septum permanently long on convex corallite side; microstructure of septa probably finely trabecular.

SPECIES CONTENT: Monotypic.

REMARKS: The early ontogeny and the arrangement of the major septa, twisting around the pseudocolumella in *Voragoaxum* gen. nov. resemble those in the genus *Cyathoclisia* Dingwall, 1926 (Dingwall 1926, pl. 2, figs. 8–10), first described from the late Tournaisian of Britain, but known from several areas of Europe, such as the Tournaisian and Viséan of the Donets Basin (Vassilyuk 1960), Tournaisian of the Northern Urals (Sayutina 1973), Ivorian of Belgium (Poty 1981), Chadian of the Island Rügen, Germany (Weyer 1993) and from the present author’s undescribed collection (late Tournaisian of the Cracow Region, Poland). According to Dr. Dieter Weyer (review of the present paper) “*Cyathoclisia* is restricted to the Tournaisian” and “German occurrences are all upper Ivorian”. The mature morphology of *Cyathoclisia* with the complex axial structure, a shortened cardinal septum beneath the calice floor in transverse section, a deep cardinal fossula, often

widened axially and bordered by a few pairs of major septa, and long, often contratingent or contraclined minor septa, form a set of important characters distinguishing *Cyathoclisia* from the mature morphology of *Voragoaxum* gen. nov. The similarities and differences mentioned may suggest either derivation of *Voragoaxum* from *Cyathoclisia* by neoteny or its derivation from another taxon, unknown to me at this moment. The first option is excluded. Extreme simplification of the complex and specialized morphology of *Cyathoclisia* would be required to achieve the simple morphology of *Voragoaxum*.

*Spirophyllum* Fedorowski, 1970, which appeared late in the Viséan and continued to exist up to the early Moscovian in Spain (de Groot 1963; Rodríguez 1984; Fedorowski 2004), is another potential ancestor of *Voragoaxum*. However, like *Cyathoclisia*, extreme simplification of *Spirophyllum* would be required in order to attain the morphological level of *Voragoaxum*. All those reductions should be recognizable in the evolution of *Spirophyllum*, but they are not. The Donets Basin *Spirophyllum?*, described in this paper, suggests a different trend in the development of that group of corals in the Eastern European Province (see description above). The Famennian specimen from the Holy Cross Mountains (Poland), questionably included in *Spirophyllum* by Berkowski (2002) and the Tournaisian specimen from Pomerania (Poland), questionably included to that genus by Chwieduk (2005), are homeomorphic to *Spirophyllum* as has been stated already by both cited authors.

The Tournaisian *Lophophyllum* sp. Gorskiy, 1932 is the next option available. The brief revision of *Lophophyllum subtortuosum* Gorskiy, 1932 and of two unnamed species introduced by Gorskiy (1932), made on the basis of peels taken from his originals is at present accepted for publication (Fedorowski 2017b). That brief revision allows the suggestion of a possible relationship of the paratype of *Lophophyllum subtortuosum* to the specimens included here in *Voragoaxum*. The gap in the occurrence between *L. subtortuosum* and *Voragoaxum* (Viséan and Serpukhovian) is equally as long as that between *Voragoaxum* and *Cyathoclisia*. Thus that factor can be omitted from further discussion. However, that ancestry, if occurring, is not close enough to include all the specimens discussed in the same genus.

*Voragoaxum cavum* sp. nov.  
(Text-figs 21 and 22)

HOLOTYPE: Specimen UAM-Tc.Don.1/231.

TYPE LOCALITY: Kalmyus River Area. Voznesenka Village.

TYPE STRATUM: Limestone D<sub>7</sub><sup>3</sup>, early Voznesenskian Substage, early *Homoceras*–*Hudsonoceras* ammonoid Biozone, early *Plectostaffella bogdanovkensis* foraminiferal Biozone, early *Declinognathodus noduliferus* conodont Biozone. Closely above the base of the Bashkirian.

ETYMOLOGY: *Lat. cavus* – empty – after the deep depression of the calice near the dissepimentarium/tabularium boundary and only the axial area elevated.

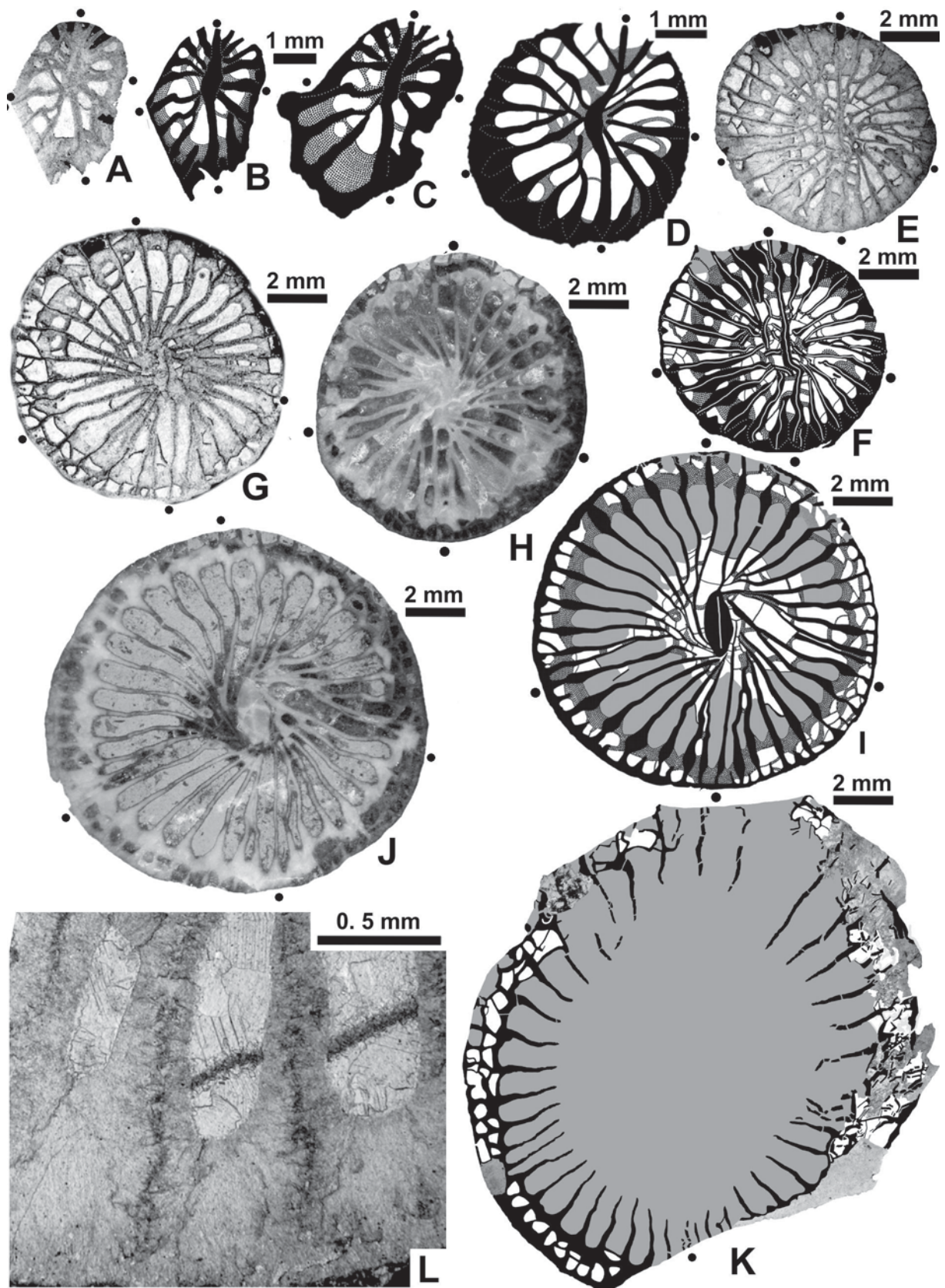
DIAGNOSIS: *Voragoaxum* with 40 major septa at up to 22×19 mm diameter near calice margin; minor septa reduced to external row of dissepiments; 1–3 rows of irregular dissepiments.

MATERIAL: Two specimens, but only holotype well preserved and almost complete. Paratype UAM-Tc.Don.1/232 with peripheral parts corroded, early growth stages lacking, calice crushed.

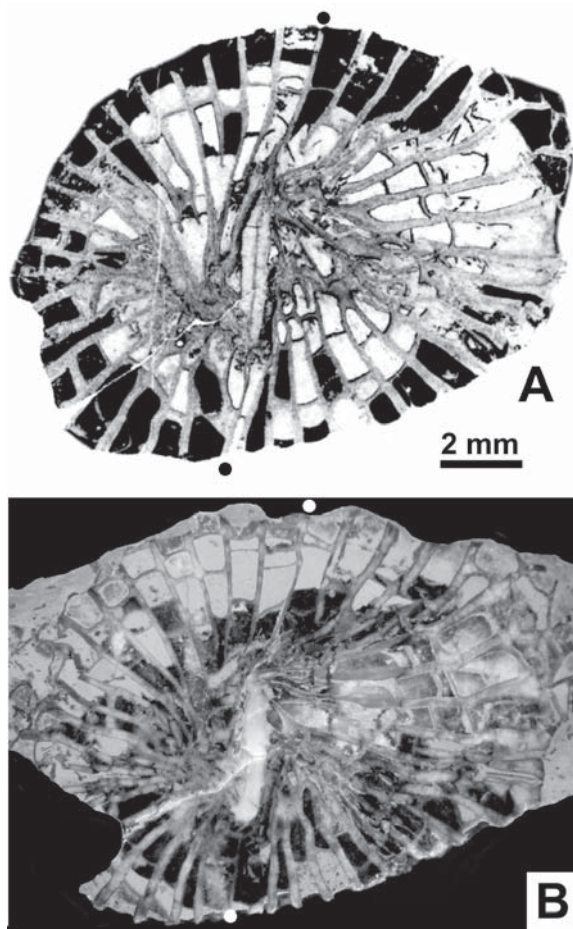
DESCRIPTION: Holotype widely conical, approximately 16–17 mm long when measured along convex side. Septal ribbing very shallow. Calice 21.5×18.2 mm in diameter with 40 thin, short major septa in its upper part (Text-fig. 21K). Infillings of calice: calcite in areas sectioned beneath calice floor (white in the photographs) and mud above calice floor (Text-fig. 21I–J) suggest both high elevation of circumaxial calice area around pseudocolumella and deepest part of calice at dissepimentarium boundary.

Ontogenetically earliest growth stage investigated (Text-fig. 21A–C) with n:d value 17: 3.4×2.4 mm and 17: 3.8×2.4 mm, oblique due to attachment to substrate. Major septa zaphrentoidally arranged. Most of them attached to axial septum. Cardinal septum side of axial septum curved to its widening axial part, i.e., future pseudocolumella. Alar septa undistinguishable by length and thickness. Counter-lateral septa shortest of major septa in counter quadrants. Minor septa absent from both corallite lumen and external wall.

In section made approximately 2 mm higher, above the attachment scars, with n:d value 20:4.0×3.6 mm, major septa start to twist. Minor septa not recognizable and dissepimentarium absent. This morphology (Text-fig. 21D) is considered the oldest neanic. First minor septa become recognizable and first few dissepiments appear with corallite n:d value 26:7.4×7.2 mm (Text-fig. 21E, F). Appearance of those two skel-







Text-fig. 22. *Voragoaxum cavum* sp. nov. Specimen UAM-Tc. Don.1/232. Paratype. A – transverse thin section, B – polished surface. Both mature growth stage. For stratigraphic position see text. Scale bar corresponds to both

etal elements with other skeletal elements resembling earlier morphology, characterizes intermediate neanic/earliest mature growth stage. Major septa long; some meet axial septum other connected to adjacent major septa. Axial septum elongated directly to counter septum, but curved at border of future cardinal septum. Twisting of major septa becomes more obvious shortly after complete dissepimentarium formed, i.e., with n:d value 30:9.5×9.0 mm (Text-fig. 21G, H). Cardinal and counter septa remain connected with just formed pseudocolumella, but both curve away from middle part of axial septum. Minor septa differenti-

ated in length, most very short and thin, absent from septal loculi where dissepiments underdeveloped. Dissepimentarium restricted to one row of dissepiments in most septal loculi and two rows of irregular dissepiments in other loculi. Inner wall strong, formed by sclerenchymal thickening of inner margins of dissepiments supplemented by thickened parts of major septa at tabularium/dissepimentarium boundary.

Section with peel made approximately 1.5 mm on concave and 3 mm on convex side of further corallite growth and approximately 1.5 mm above polished surface (Text-fig. 21I, J) with n:d values 36:12.7 mm and 36:13.0 mm, respectively, show morphology partly below and partly above the calice floor. Thin and straight cardinal septum intersects cardinal fossula, bordered by the last pair of underdeveloped major septa inserted. Inner margin of cardinal septum extends to middle part of almond-shaped, monoseptal pseudocolumella. Counter septum longer than cardinal septum but equally thin, surrounds pseudocolumella and meets its lateral surface close to its cardinal septum side. Remaining major septa twist around pseudocolumella with longest approaching lateral surface of pseudocolumella, but not penetrating it. All major septa are almost equally thin, except for their parts thickened at the tabularium/dissepimentarium border. Alar septa marked by underdevelopment of last pair of major septa inserted in counter quadrants. Minor septa remain short and thin. In upper part of calice (Text-fig. 21K) with n:d value ?44:18.5×15.5 mm (both incomplete), major septa become strongly shortened, thin, radially arranged and almost equal in length. Cardinal septum may be slightly shortened, but incompleteness of corallite makes this statement uncertain. Minor septa and dissepimentarium remain as described above.

Only one incomplete and slightly squeezed corallite is accepted as paratype (Text-fig. 22A, B). Direct connection of protosepta to pseudocolumella and the elongated rather than almond shape of pseudocolumella are the main differences of that specimen from the holotype. Direction of all major septa located left of pseudocolumella to its counter septum side and all major septa of opposite quadrants directed toward cardinal septum side of pseudocolumella closely resembling the holotype. Although accepted as a paratype, that corallite may belong to separate species.

← Text-fig. 21. *Voragoaxum cavum* sp. nov. Transverse sections. A-L – Specimen UAM-Tc. Don.1/231. Holotype. A-D – neanic growth stage (A, B – thin section with drawing, C, D – peels with drawings), E, F – transverse thin section, late neanic/early mature growth stage (F – drawn on E), G, H – early mature growth stage (G – thin section, H – polished surface), I, J – mature growth stage, above calice floor in part (I – peel with drawing, J – polished surface), K – middle part of calice (peel with drawing), L – Microstructure of septum destroyed by diagenesis. For stratigraphic position see text. Scale bars located between two adjacent images correspond to both; those to the right of image apply only to that image.

OCCURRENCE: Kalmyus River Area, Voznesenka Village. Holotype: Limestone D<sub>7</sub><sup>3</sup> and paratype: Limestone D<sub>7</sub><sup>6</sup>. Early Voznesenskian Substage. Early *Homoceras–Hudsonoceras* ammonoid Biozone, early *Plectostaffella bogdanovkensis* foraminiferal Biozone, early *Declinognathodus noduliferus* conodont Biozone. Closely above the base of the Bashkirian.

Subfamily Rozkowskiinae Fedorowski, 1970  
(Type genus *Rozkowskia* Fedorowski, 1970)

EMENDED DIAGNOSIS: Solitary, dissepimented; early growth stage dibunophyllid; in mature growth stage major septa radially arranged in all quadrants; cardinal fossula shallow; pseudocolumella consisting of monoseptal median lamella with cone-shaped inner tabellae incorporated; tabularium normal; microstructure of septa trabecular.

GENERA INCLUDED: Monotypic, but inclusion of some north African species probable.

REMARKS: Fedorowski (1970, p. 604) distinguished a new Family Rozkowskiidae for the solitary dissepimented rugose corals with pseudocolumella composed of median lamella and axial parts of tabellae. Hill (1981, p. F355) synonymized that family with the Subfamily Amygdalophyllinae Grabau in Chi, 1935 of the Family Aulophyllidae Dybowski, 1873. Hill's (1981) general idea of the inclusion of *Rozkowskia* in the Family Aulophyllidae is accepted herein, but the synonymy proposed by her is not. The origin and morphology of the pseudocolumella in *Amygdalophyllum* Dun and Benson, 1920 forms the main criterion for distinguishing that genus from the remaining Aulophyllidae at subfamily level. The same should be applied to *Rozkowskia*, the pseudocolumella of which differs from all remaining Aulophyllidae. Thus, the earlier introduced family rank for *Rozkowskia* is here lowered to subfamily level and the Subfamily Rozkowskiinae is included in the Family Aulophyllidae.

The Australian *Amygdalophyllum vallum* Hill, 1934 resembles the species of *Rozkowskia* in the inner morphology of the pseudocolumella. It differs in possessing shorter major septa and long minor septa entering the biform tabularium. The occurrence of that species in a province almost totally isolated from most of the Mississippian rugose coral provinces (Fedorowski 1981, 2008; Denayer and Webb 2015) puts in doubt its position within the Rozkowskiinae. Dr. J. Denayer in his critical review of this paper

wrote: "it is a genuine *Amygdalophyllum*, even if not well preserved". Thus, the question of the relationship of *A. vallum* is left open.

The species described by Semenoff-Tian-Chansky (1974) from northern Africa and included by him in *Amygdalophyllum*, especially *A. cf. vallum* Hill, 1934 and *A. turbophylloides* Semenoff-Tian-Chansky, 1974 resemble *Rozkowskia* in having axial parts of the tabulae cone-shaped, highly elevated and closely approaching the pseudocolumella composed of median lamella and contiguous septal lamellae in its main part. Most of the tabellae cones are slightly separated from the pseudocolumella (Semenoff-Tian-Chansky 1974, pl. 33, figs. 5, 6; pl. 34, figs 5, 6; pl. 35, fig. 5). However, some innermost margins of tabulae and inner margins of some major septa are incorporated into the pseudocolumella (Semenoff-Tian-Chansky 1974, pl. 32, figs 2, 3; pl. 36, figs 1, 3). In contrast to *Rozkowskia*, the pseudocolumella of which incorporates a few long inner parts of tabulae, closely attached to each other, only the uppermost parts of tabulae may be incorporated in the pseudocolumella of the African "*amygdalophylla*" discussed. Thus, only one tabula is shown by a given transverse section of those species as forming a part of the pseudocolumella. This and the incorporation of the septal lamellae in addition to the innermost parts of the axial tabellae constitute the main distinguishing characters of the African "*amygdalophylla*". Both that morphology and the occurrence of *Amygdalophyllum etheridgei* Dun and Benson, 1920 in the Australian Province, almost totally isolated from the Western European Province as mentioned above, allow the suggestion of a new generic name for those northern African taxa. They resemble *Rozkowskia* closer than other co-existing genera and may belong to the Subfamily Rozkowskiinae.

Genus *Rozkowskia* Fedorowski, 1970  
(Type species *Rozkowskia compacta* Fedorowski, 1970)

DIAGNOSIS and REMARKS: See under Subfamily.

*Rozkowskia lenta* sp. nov.  
(Text-figs 23 and 24)

HOLOTYPE: Specimen UAM-Tc.Don1/235.

TYPE LOCALITY: Amvrosievskiy Kupol, Amvrosievka Village.

TYPE STRATUM: Limestone E<sub>1</sub><sup>verkh</sup>, Svita C<sub>2</sub><sup>b</sup><sub>a</sub><sup>nizhn</sup>. Feninian Substage, *Reticloceras*–*Bashkortoceras* (R<sub>1</sub>) ammonoid Biozone; *Semistaffella variabilis*–*S. minuscularia* foraminiferal Biozone, *Idiognathodus sinuosus* conodont Biozone. Late early Bashkirian.

ETYMOLOGY: *Lat. lentus*, -a, -um – late. Named after the occurrence of this species later than the remaining species of the genus.

MATERIAL: Holotype specimen UAM-Tc.Don.1/235, preserved in the mature growth stage. Inner morphology well preserved, but microstructure of septa altered by diagenesis. Two transverse thin sections and one longitudinal thin section of holotype available for study. Two paratypes UAM-Tc.Don.1/233, 234, each represented by one transverse thin section of mature growth stage.

DIAGNOSIS: *Rozkowskia* with n:d value 33:14.2 mm (holotype) to 38:17.5 mm; major septa amplexoid, closely approach pseudocolumella along tabulae surfaces; thickest in thickened inner wall; cardinal septum continues into median lamella, shortened only in calice; counter septum only meets pseudocolumella; minor septa differentiated in length, in some loculi interrupted; dissepimentarium 1/2–1/3 of corallite radius in width.

DESCRIPTION: Thick, smooth external wall comprising bases of major and minor septa strongly and equally thickened to form septotheca (Text-fig. 24A). Small amounts of sclerenchyme may locally supplement septotheca. Bases of septa thin inward from external wall so much as to become separated from the remaining parts of some minor septa (Text-figs 23B, right; 24B). Thinning of major septa in peripheral dissepimentarium conspicuous but they remain continuous. Major septa thickest in inner dissepimentarium and peripheral tabularium, thin toward corallite axis, except when meeting upper surfaces of thickened tabulae along which they become thickened by sclerenchyme. Alar septa undistinguishable by length or thickness.

Both protosepta continuously long up to calice floor. Cardinal septum in outer tabularium only slightly thinner than adjacent major septa, thin abruptly inward to form thread-like blade, connected directly to median lamella of thick pseudocolumella (Text-fig. 23A, B, D). It becomes slightly shortened immediately above calice floor (Text-fig. 23C). Counter septum attached to pseudocolumella, but not meeting median lamella, terminating at pseudo-

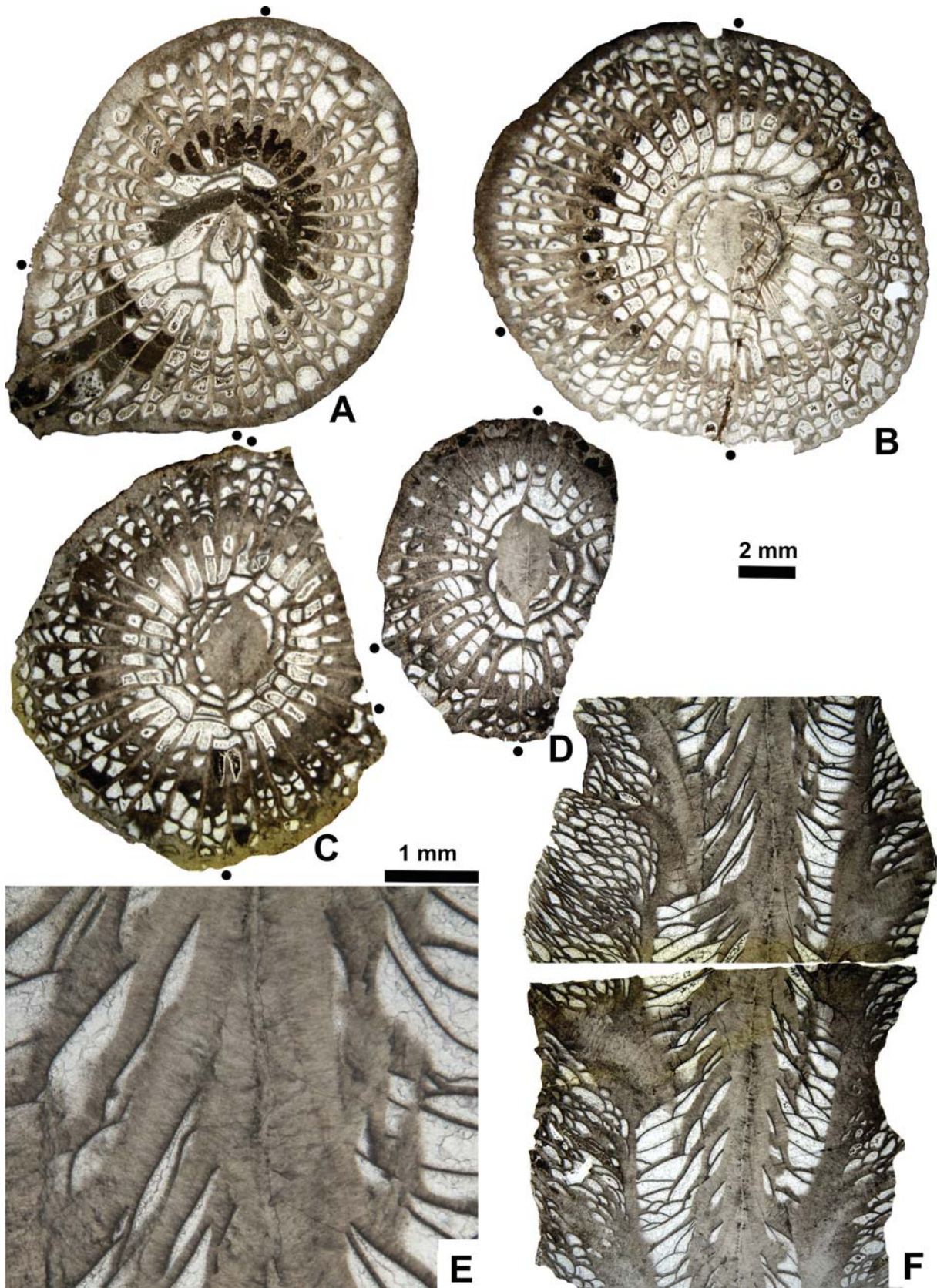
columella surface (Text-fig. 23B–D). Counter septum in one paratype seems to be connected with median lamella (Text-fig. 23A). Nevertheless, direct connection of median lamella to cardinal septum, and leading role of that septum in formation of axial structure, typical for most Aulophyllidae, occurs in all corallites studied. Cardinal fossula inconspicuous and shallow as documented by its very slight dip into dissepimentarium (Text-fig. 23A–D).

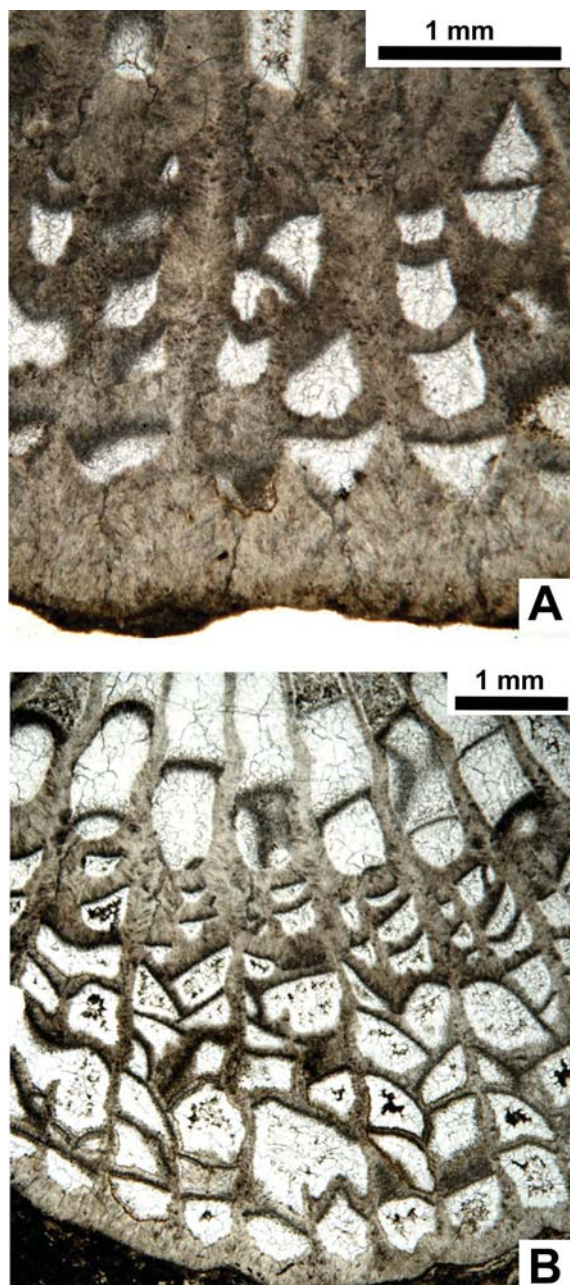
Minor septa vary in length and morphology within the same transverse section irrespective of growth stage. Longest in counter quadrants where some reach inner margin of dissepimentarium in holotype and one paratype (Text-fig. 23D, B). In remaining parts of dissepimentarium shortened. In some loculi broken into segments either restricted to peripheral dissepimentarium or reaching tabularium (Text-fig. 24A, B).

Pseudocolumellae in individual corallites vary in thickness, being thinnest in one paratype (Text-fig. 23A). That section, made partly above calice floor, may suggest dependence of thickness of pseudocolumella on corallite growth stage. Pseudocolumella invariably consists of median lamella derived from inner margin of cardinal septum, surrounded by thick inner parts of tabulae that form steep cones elevated towards and meeting median lamella. Interrelation mentioned is best documented in longitudinal section (Text-fig. 23E). Major septa not incorporated in pseudocolumella although inner margins of some join its surface (Text-fig. 23B–D) as a result of their amplexoid character.

In early maturity dissepimentarium narrowest near counter septum (Text-fig. 23D), widens during corallite growth, reaching almost 1/2 of corallite radius. Dissepiments between major and minor septa in irregularly herringbone pattern where minor septa shortened. Small lonsdaleoid dissepiments appear where minor septa interrupted. Sclerenchymal thickening of innermost dissepiments supplements thickened parts of major septa and thick inner margins of longest minor septa to form distinct inner wall.

In longitudinal section (Text-fig. 23F), dissepiments small, globose, arranged in rows sloping down at approximately 45°. Tabulae incomplete. Peripheral tabellae thin, comparatively short, flat or slightly convex, elevated inwards at approximately 30–45°. Most of inner tabellae long and strongly thickened, all elevated steeper than peripheral tabellae, those close to median lamella steepest. Most steeply elevated axial tabellae strongly thickened, constitute cones incorporated into pseudocolumella (Text-fig. 23E, F).





Text-fig. 24. *Rozkowskia lenta* sp. nov. Transverse thin sections. A – Specimen UAM-Tc.Don.1/235. Holotype. Septotheca. Minor septa fragmented and continuous. Dissepimentarium narrow. B – Specimen UAM-Tc.Don.1/233. Paratype. Minor septa fragmented. Dissepimentarium wide. For stratigraphic position see text

Microstructure of septa diagenetically altered so as to preclude reliable reconstruction. Long crystalline fibrils extending from middle line of septum obliquely towards its surface (Text-fig. 24A) suggest strong recrystallization.

REMARKS: *Rozkowskia lenta* sp. nov. closely resembles the type species in the arrangement of tabulae in the longitudinal section. It differs from that species in its smaller diameter and number of septa, the major septa being amplexoid and, most important, in the narrower and much less complex dissepimentarium with small lonsdaleoid dissepiments, where the minor septa are interrupted. *Rozkowskia lenta* differs from *R. parva* Fedorowski, 1970 by having the major septa long, amplexoid, closely approaching the pseudocolumella, by the minor septa differentiated in length and interrupted, and by the morphology of the dissepimentarium. It differs from both Polish Brigantian species in possessing the cardinal septum permanently connected to the median lamella of the pseudocolumella.

OCCURRENCE: Kalmyus River Area, Amvrosievka Village. Limestone E<sub>1</sub><sup>verkh.</sup>. Early Feninian Substage, *Reticuloceras*–*Bashkortoceras* ammonoid Biozone, *Semistaffella variabilis*–*S. minuscularia* foraminiferal Biozone, *Idiognathoides sinuatus* conodont Biozone. Early Bashkirian.

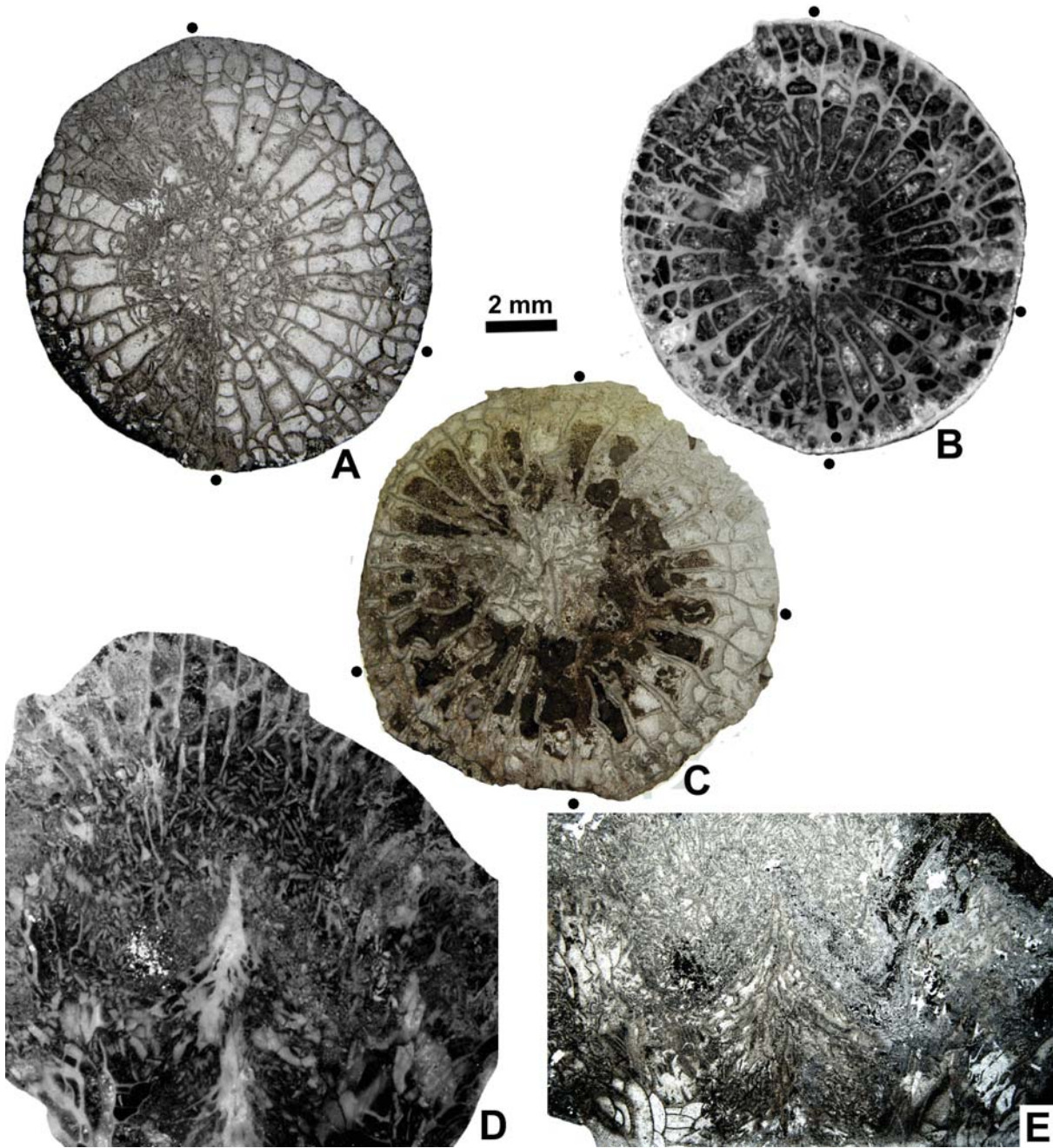
#### Unnamed Aulophyllidae

REMARKS: Three specimens in the collection, all derived from lower Bashkirian strata, have no relatives at genus level either among the taxa described earlier or herein. The stratigraphic positions of those specimens, potentially valuable for the evolution of the Aulophyllidae legitimize their brief, illustrated description as a supplement to the knowledge of the Bashkirian representatives of the family.

Species No. 1  
(Text-fig. 25)

DESCRIPTION: Two specimens, both crushed. Specimen UAM-Tc.Don.1/237 with n:d value 29:12.0 mm preserved only as thin section made in its tab-

← Text-fig. 23. *Rozkowskia lenta* sp. nov. A – Specimen UAM-Tc.Don.1/233. Paratype. Transverse thin section. Mature growth stage. B – Specimen UAM-Tc.Don.1/234. Paratype. Transverse thin section. Mature growth stage. C–F – Specimen UAM-Tc.Don.1/235. Holotype. C, D – transverse thin sections. Advanced and early mature growth stage respectively, E, F – longitudinal thin sections; E – enlarged from F to demonstrate cone-like arrangement of innermost tabulae attached to median lamella to form pseudocolumella. For stratigraphic position see text. Scale bar between B and F corresponds to all images except E



Text-fig. 25. Unnamed Aulophyllidae. Species No. 1. A, B, D, E – Specimen UAM-Tc.Don.1/236. A – transverse thin section, B – polished surface; both mature growth stage, D, E – longitudinal sections (D – polished surface, E – thin section). C – Specimen UAM-Tc.Don.1/237. Transverse thin section, mature growth stage, partly in calice. For stratigraphic position see text. Scale bar between A and B corresponds to all images

ularium above calice floor (Text-fig. 25C) without rock material left. Only mature growth stage with n:d value 34:11.5 mm and 34:13 mm preserved from specimen UAM-TcDon.1/236. Upper part of its calice broken and pressed down (Text-fig. 25D, E). External wall 0.2–0.4 mm thick, almost smooth. Major septa radially arranged, all equally thin around, approach

closely or reach inner margin of long cardinal septum (Text-fig. 25A, B). Counter septum indistinguishable by length and thickness from adjacent major septa. Minor septa reach 1/3 to 1/2 of dissepimentarium width. Cardinal fossula indistinct, dips slightly into dissepimentarium. Axial structure in transverse section distinct, variable. Morphology seen in longitudi-

dinal polished section (Text-fig. 25D) allows one to link that variability to the thickness of the sclerenchymal thickening of the tabulae. Rare, inconsistent extra septal tabellae occur when axial structure is more complex. Tabularium consists of incomplete tabulae. Peripheral tabellae horizontal (Text-fig. 25E, lower left). Middle tabellae long, elevated at approximately 45° towards corallite axis. Only innermost tabellae turn abruptly upwards to meet section of inner margin of cardinal septum. Those parts covered by sclerenchyme. Some vertically arranged tabellae resemble lateral tabellae, but the occurrence of the axial column cannot be proven. Dissepimentarium occupies 1/4–1/3 of corallite radius. Dissepiments in transverse sections herringbone and regular; in longitudinal section mostly small, rather flat when long, arranged steeply; inner row vertical.

REMARKS: Radial arrangement of the major septa, formation of the axial structure around the inner margin of the cardinal septum and the appearance of rare extra septal lamellae allow comparison to *Nervophyllum* Vassilyuk, 1959. However, the ephemeral appearance of rare extra septal lamellae and the uncertain appearance of the axial column prevent their assignment to that genus. *Dibunophylloides* or a new genus would be another alternative.

OCCURRENCE: Both specimens from the Kalmyk River Area. Specimen UAM-Tc.Don.1/237: Svistun Village, Bolshaya Shishovka Balka (Ravine), Limestone E<sub>1</sub>, Feninian Substage, *Reticuloceras*–*Bashkortoceras* ammonoid Biozone, *Semistaffella variabilis*–*S. minuscularis* foraminiferal Biozone, *Idiognathoides sinuatus* conodont Biozone. Specimen UAM-Tc.Don.1/236: Amvrosievskiy Kupol, Sevastianovka Village, Medovaya Balka (Ravine), Limestone E<sub>8</sub><sup>3</sup>, Manuilovian Substage, *Bilinguites*–*Cancelloceras* ammonoid Biozone, *Pseudostaffella antiqua* foraminiferal Biozone, *Neognathodus askynensis* conodont Biozone. Early Bashkirian.

Species No. 2  
(Text-fig. 26)

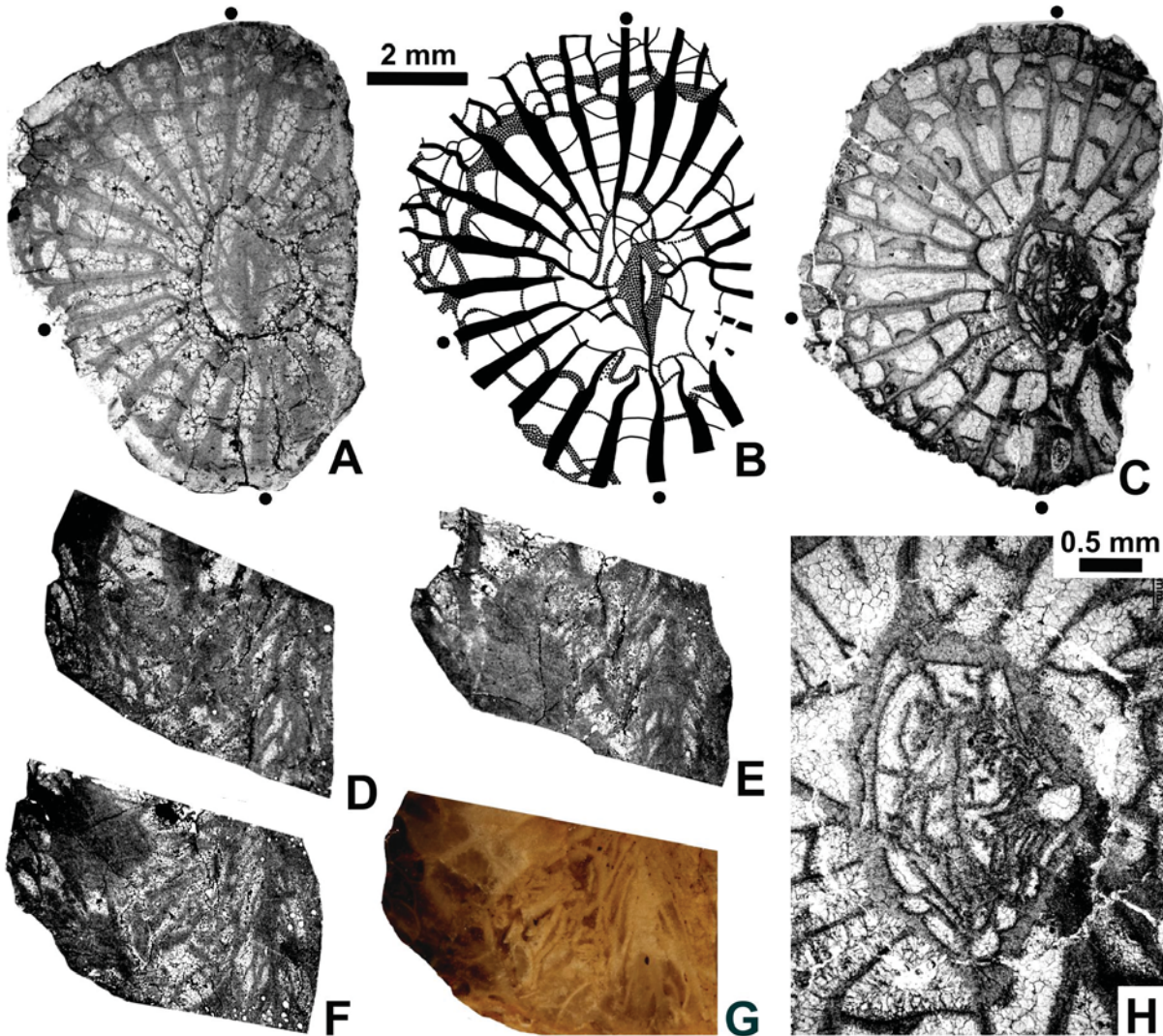
DESCRIPTION: One incomplete specimen UAM-Tc.Don.1/238. Early growth stage and calice lacking. Peripheral part eroded. Internal morphology slightly damaged by diagenesis, but all main features preserved. N:d value 24:9.6×7.2 mm (incomplete). Major septa semi-radially arranged, in tabularium wedge-shaped; in early growth stage (Text-fig. 26A, B) more

distinctly; dissepimental parts of major septa thinner and slightly wavy, but boundary between their peripheral and inner parts not sharp despite inner wall thickened. In early growth stage, inner margins of major septa thin, most free, some twisted, terminate within very thick sclerenchymal sheet of inner tabellae. Cardinal septum elongated into long median lamella covered by thick sclerenchyme at left side (Text-fig. 26A, B). Right side of pseudocolumella at some distance from strongly thickened inner tabella. Counter septum meets sclerenchymal circumaxial sheet, but does not meet pseudocolumella at that growth stage. Minor septa reach inner margin of narrow dissepimentarium in both transverse sections illustrated, spanning approximately 2 mm of corallite growth. In more advanced growth stage (Text-fig. 26C, H), axial area of corallite surrounded by thick periaxial tabellae that form a kind of isolated axial structure, consisting of monoseptal pseudocolumella connected to both protosepta, several septal lamellae and numerous axial tabellae occurring between lamellae. Inner margins of major septa either terminated in sclerenchymal thickening of thick tabula or free. Cardinal tabular fossula either lacking or very shallow.

Three peels and one polished section representing longitudinal section (Text-fig. 26D–G, respectively), made approximately 1 mm apart. Peripheral and middle parts of tabulae broken by squeezing. Nevertheless, tripartite structure clearly demonstrated. Dissepimentarium occupies approximately 1/4 of corallite radius. Dissepiments differentiated in length, arranged in 2–4 rows at approximately 50° or steeper. Tabulae incomplete. Peripheral and middle tabellae elongated, elevated at approximately 40° towards narrow axial column occupying approximately 1/6 of corallite diameter. Pseudocolumella distinct. Axial tabellae long, in 2–3 rows, elevated very steeply towards pseudocolumella, rest on underlying axial tabellae to form axial column.

REMARKS: The single and very incomplete specimen does not allow a comprehensive comparison. It has been described and illustrated as the stratigraphically youngest corallite in the Donets Basin unquestionably possessing an axial column. That character makes it related to *Dibunophyllum*, whereas the variable and rather peculiar morphology of the axial structure in transverse section distinguishes it from the latter genus and all other known genera.

OCCURRENCE: Kalmyk River Area, Fenino Village. Limestone F<sub>1</sub>. Blagodatnian Substage, *Bilin-*



Text-fig. 26. Unnamed Aulophyllidae. Species No. 2. Specimen UAM-Tc.Don.1/238. A-C, H – transverse sections, mature growth stage. A, B – peel and drawing, C – thin section, H – axial structure enlarged from C. D-G – Successive longitudinal sections through corallite axis. D-F – peels, G – polished surface. For stratigraphic position see text. Scale bar between A and B corresponds to images A-G

*guites–Canelloceras ammonoid Biozone, Pseudostaffella pregorskyi–Staffelleformes staffelleformis* foraminiferal Biozone, *Idiognathodus sinuosus conodont Biozone*. Late early Bashkirian.

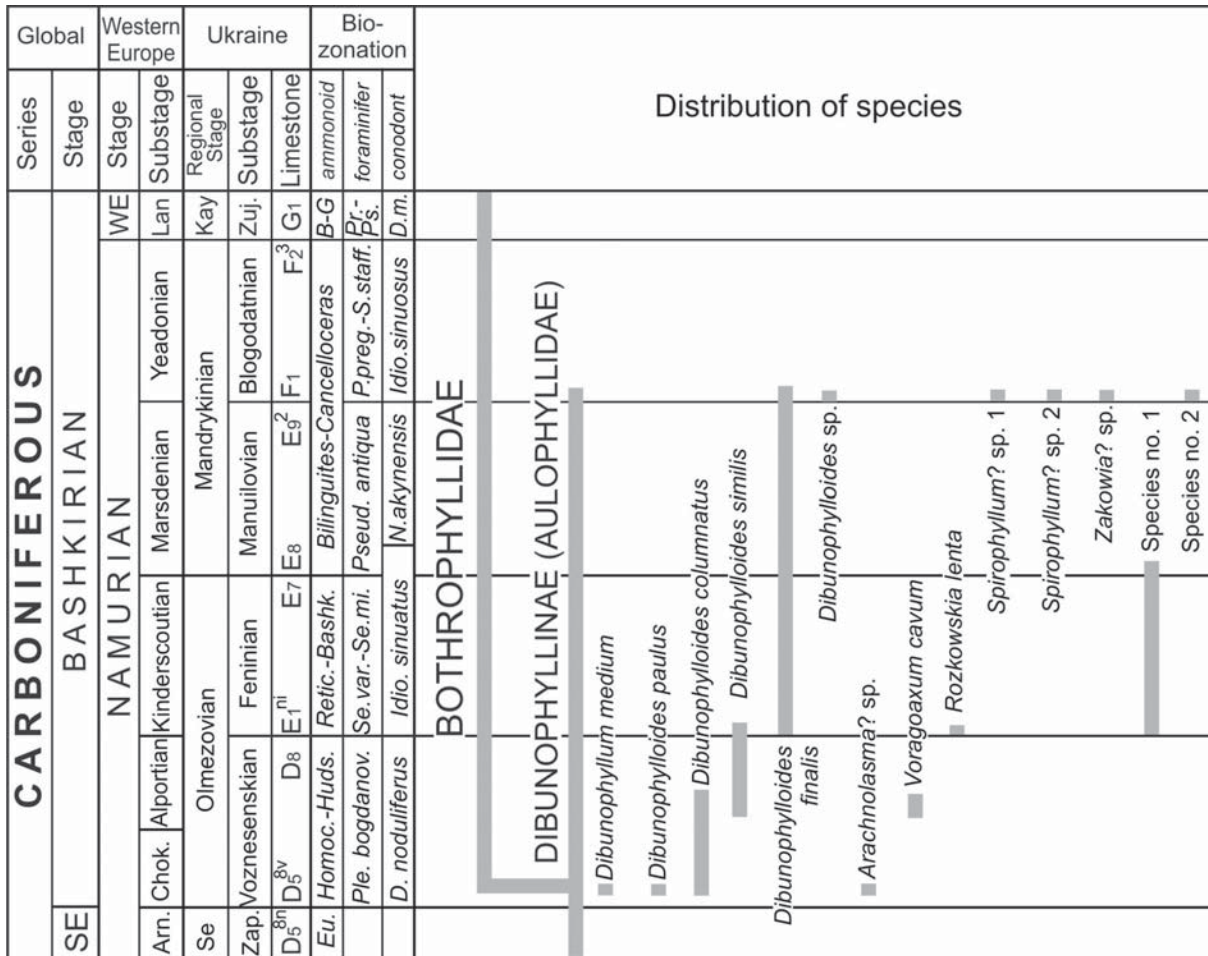
#### CONSIDERATIONS

At least three characters of the fauna described demand more general remarks: the stratigraphic occurrence of some genera lasting longer than established previously, the relationships of taxa within the Subfamily Dibunophyllinae and the relationship vs. similarity to Bothrophyllidae of advanced

Dibunophyllinae. The stratigraphic position closely above the base of the Bashkirian of most taxa described herein legitimizes such considerations despite the small number of specimens investigated.

Four typically Viséan genera: *Dibunophyllum* Thomson and Nicholson, 1876; *Rozkowskia* Fedorowski, 1970; *Spirophyllum* Fedorowski, 1970; and *Zakowia* Fedorowski, 1971 are described here from Bashkirian strata. The occurrence of *Dibunophyllum* in the early Bashkirian (Rodríguez *et al.* 2013a) and up to the early middle Bashkirian (Fedorowski *et al.* 2012), and of *Spirophyllum* up to the middle or late Moscovian (de Groot 1963; Fedorowski 1970, 2004) has been reported previously, but the remaining two





Text-fig. 27. Distribution of studied species. Abbreviations: Ammonit. – Ammonitida, Alport – Alportian, Arn – Arnsbergian, *Bashk.* – *Bashkortoceras*, *B-G* – *Brannoceras*–*Gastrioceras*, Choki – Chokierian, Conodon. – Conodonta, *D.* – *Declinognathodus*, *D.m* – *Declinognathodus marginodosus*, *Eu* – *Eumorphoceras*, Foraminif. – Foraminiferida, *Homoc.* – *Homoceras*, *Huds.* – *Hudsonoceras*, *Idio.* – *Idiognathoides*, *Idg.* – *Idiognathodus*, *Kay* – *Kayalskian*, *Lan* – *Langsetian*, *N.* – *Neognathodus*, *P. preg.* – *Pseudostaffella pregorskyi*, *Ple. Bogdanov.* – *Plectostaffella bogdanovkensis*, *Pr.-Ps* – *Profusulinella primitiva*–*Pseudostaffella gorskyi*, *Pseud.* – *Pseudostaffella*, *Retic.* – *Reticuloceras*, *S. staff* – *Staffeleiformes staffeleiformis*, *Se* – *Serpukhovian*, *Se. var.* – *Semistaffella minuscularia*, *We* – Westphalian, *West.* – Western, *Zap* – Zapaltyubinskian, *Zuj* – Zujevian

genera were up to now known only from their first descriptions. The identification of *Zakowia*, based on a single, incomplete corallite may be considered disputable despite the presence of the main diagnostic characters in the corallite fragment available for study. Thus, the identification was left in open nomenclature and with a question mark. The identification of *Spirophyllum* is questionable for two reasons: the inadequate representation and the morphology suggesting a separate subgeneric status of the Donets Basin specimens. However, the close relationship of them to the Brigantian type species of *Spirophyllum* seems real.

The extension in the Donets Basin of the genus *Dibunophyllum* into Bashkirian strata has been sug-

gested by Vassilyuk (1960), who described the new species *D. finalis* from Limestone E<sub>2</sub>, i.e., the early *Reticuloceras*–*Bashkortoceras* ammonoid Biozone. The occurrence of that species has been extended here into Limestone F<sub>1</sub>, i.e., the middle *Bilinguites*–*Cancelloceras* ammonoid Biozone. However, *D. finalis* does not exhibit the main character of *Dibunophyllum*, i.e., the permanent axial column in the longitudinal section. Thus, it has been transferred here to the genus *Dibunophyloides* Fomichev, 1953 (see above).

*Dibunophyllum*, typical of the late Viséan (Brigantian), extends into Serpukhovian strata in several areas including the Donets Basin [e.g., Hill 1938–1941; Vassilyuk 1960, 1964; Semenov-Tian-Chansky

1974; ?Boll 1985; Aretz 2011; Rodríguez *et al.* 2013b; ?Cózar *et al.* 2014 (not illustrated)]. The Bashkirian occurrences of *Dibunophyllum* are either not illustrated (Cózar *et al.* 2014) or insufficiently known except for those described by Rodríguez *et al.* (2013a) from the early Bashkirian of Morocco. The single, incomplete corallite from the d'Hassi Kerma Formation (Algeria), described by Semenoff-Tian-Chansky (1974, p. 97, pl. 37, figs 7–9) as *Dibunophyllum* sp. B belongs to *Dibunophylloides* as suggested by its tabularium composed of bubble-like tabellae with the axial column absent. Its early growth stage resembles the comparable growth stages of the early Bashkirian species of *Dibunophylloides* described here. The single, incomplete specimen described by Fedorowski *et al.* (2012) from the early late Bashkirian strata of the Sverdrup Basin as *D. bipartitum craigianum* (Thomson, 1874) possesses a wide axial column and its morphology closely resembles that of the Scottish early Serpukhovian type species (Zone 3 according to Hill 1938–1941, p. 78). Thus it can be considered the youngest representative of *Dibunophyllum* known so far, documenting the range of *Dibunophyllum* up to late Bashkirian.

*Dibunophyllum* undoubtedly crossed the Serpukhovian/Bashkirian boundary in the Donets Basin as documented by *Dibunophyllum medium* sp. nov. (Limestone D<sub>5</sub><sup>10</sup>). *Dibunophylloides paulus*, co-occurring with *D. medium* would have been ideal as an example of a direct derivation from *D. medium*, i.e., *Dibunophylloides* from *Dibunophyllum*. However, characters typical of *Dibunophylloides* occur in the Brigantian *Amandophyllum delicatum* Fedorowski, 1971 from Poland, *Dibunophyllum bolli* Rodríguez, 1984 and *Dibunophyllum bipartitum cantabricum* Boll, 1985, the two latter from the Serpukhovian strata in Spain. Those stratigraphically early appearances of *Dibunophylloides* morphology do not put in doubt the direct derivation of that genus from *Dibunophyllum*, as suggested by Fomichev (1953) and supported here. The early species of *Dibunophylloides* listed would have found their Viséan ancestor or ancestors among the *Dibunophyllum* species common at that time. On the other hand, the direct ancestor/descendant relationship between *Dibunophyllum medium* and *Dibunophylloides paulus* would be difficult to question. Thus, two interpretations are possible: 1. the iterative evolution during the Brigantian–Serpukhovian to earliest Bashkirian time with *Dibunophyllum* as the source genus; 2. homeomorphy to *Dibunophylloides* of the pre-Bashkirian *Dibunophyllum* taxa listed above. The first option is suggested here.

The permanent occurrence of the axial column in

*Dibunophyllum* forms the most important and commonly the only qualitative character differing that genus from *Dibunophylloides* and from those species of *Arachnolasma*, in which the axial column is not developed (e.g., Yu 1937; Fedorowski 1971). Thus, grouping in *Dibunophyllum* of species possessing and lacking the axial column may be suggested as an alternative. However, that alternative would change the well defined genus *Dibunophyllum* into a taxonomic waste basket and is therefore rejected.

The occurrence of the *Voragoaxum*-like axial structure in the late Tournaisian specimens of the Kirghiz Steppe (Gorskiy 1932) may suggest their ancestry to *Voragoaxum* (Fedorowski 2017b). The specimen most similar to *Voragoaxum* possesses not only the axial area *Voragoaxum*-like, but also the minor septa free ended. However, its tabularium is biform. That character puts in doubt its direct relationship to the species from the Donets Basin within the frame of the same genus, but does not exclude a more distant relationship within the frame of the same family. Thus, distant roots of *Voragoaxum* among Tournaisian taxa, morphologically similar to that from the Kirghiz Steppe, is considered here as possible. Besides, the morphology and ontogeny of *Voragoaxum*, different from those in other Aulophyllidae, may suggest its separate subfamily position. The Tournaisian specimen from the Kirghiz Steppe may find its place as a separate genus within the frame of such a subfamily.

Some morphological similarities of the early Bashkirian species of the Family Bothrophyllidae to the contemporaneous taxa of the Subfamily Dibunophyllinae, suggesting the relationship of those two families, were briefly discussed recently (Fedorowski 2017a). That discussion is supplemented here by the data derived from the early Bashkirian species of *Dibunophylloides*. The neanic to the early mature morphology in taxa of both families is crucial for the discussion. In both families the strong axial septum occurs early in the ontogeny, but its modifications during late ontogeny differ, forming the first distinction between them. In the Dibunophyllinae, the axial septum is divided into the cardinal septum, the counter septum and the median lamella. That division is commonly permanent, but temporarily returns to the continuous axial septum in rare species. The return mentioned is more common in the Serpukhovian and the early Bashkirian representatives of *Dibunophyllum* from the Donets Basin than it is in the Viséan species of that genus elsewhere. The axial septum is almost invariably continuous in *Dibunophylloides*. Besides, the median

lamella in the Dibunophyllinae is more closely related to the cardinal than to the counter septum. In contrast to the Dibunophyllinae, the axial septum in most Bothrophyllidae is divided only in two parts: the shorter part of the cardinal septum and the longer part of the counter septum. The separate median lamella, if occurs, is derived from an axial part of the counter septum and is either ephemeral during the mature corallite growth (*Bothrophyllum* Trautschold, 1879) or its occurrence is restricted to the neanic growth stage (*Gshelia* Stuckenbergh, 1888).

In *Dibunophyllum*, i.e., one of the two genera most important for this discussion, septal lamellae are well developed and are attached to, but not incorporated within, the median lamella. Those lamellae are stronger and commonly more numerous in the late Viséan and Serpukhovian *Dibunophyllum* species than they are in some earliest Bashkirian species of *Dibunophylloides* (Text-figs 10, 11), another genus important for this discussion. Moreover, septal lamellae in the late Bashkirian and Moscovian species of *Dibunophylloides* in the Donets Basin are strongly reduced in number and strength (Text-figs 12, 13, 19). Separated septal lamellae are practically absent from the Moscovian type species of that genus in the Moscow Basin. Most major septa in that species are continuous, either reaching the axial septum or staying slightly short of it.

Similarities in some skeletal features of the Subfamily Dibunophyllinae to those of the Family Bothrophyllidae can be considered as supportive for the thesis of the relationship of those families, but are inadequate for proving that relationship firmly. Only taxa intermediate between families compared can play such a role. Two species, i.e., *Nina dibimitaria* Fedorowski, 2017a and *Dibunophylloides similis* sp. nov. are crucial in that respect. The holotypes and some paratypes of those two species were derived from the same Limestone D<sub>7</sub><sup>3</sup>. Most other paratypes of both species are slightly younger and one paratype of *D. similis* is slightly older (Limestone D<sub>6</sub>) than all other specimens of both species (see Occurrences). The late neanic/early mature growth stages of specimens belonging to those two species are strikingly similar (Fedorowski 2017a, text-figs 13A–C, 14A in *N. dibimitaria* vs. Text-fig. 16A, B, H–J in *D. similis*). Differences between them appeared only in the mature growth stages and in the longitudinal sections. The early ontogeny of *D. longiseptatus* Fomichev, 1953 (Text-fig. 13A–D) from the Moscovian Limestone M<sub>5</sub> confirms the similarity discussed as constant. Those new data allow the acceptance of a close relationship of *Dibunophylloides*

to *Nina* Fedorowski, 2017a. Moreover, this means either the relationship by descent of the Pennsylvanian Bothrophyllidae from the Dibunophyllinae, or an incorrect identification of *Nina* as a member of the Family Bothrophyllidae (Fedorowski 2017a). The first option is selected here with one restriction: the suborder position of the Family Bothrophyllidae appears uncertain as a result of its derivation suggested here. That derivation excludes the Family Bothrophyllidae from the Suborder Caniniina as provisionally accepted (Fedorowski 2017a), whereas its morphology is rather distant from many members of the Suborder Aulophyllina, the genus *Aulophyllum* Milne Edwards and Haime, 1850 in particular. Whether it should be included in the Suborder Aulophyllina, or whether a separate suborder should be erected for the Families Bothrophyllidae and Neokoninckopyllidae Fomichev, 1953, remains an open question.

The suggested relationship stays in obvious opposition to the content and derivation of the Family Bothrophyllidae summarized by Hill (1981). That relationship allows for the following solution: the late Tournaisian to Serpukhovian “bothrophylla”, common in the Western European Province and present in some other areas as well, may have been derived from cyathopsid species similar to *Caninophyllum* Lewis, 1929. Should they be grouped in a new subfamily of the Family Cyathopsidae Dybowski, 1873, or do they belong to a separate family, remains an open question. Whatever the decision in that question will be, the Mississippian European and far Asiatic “Bothrophyllidae” are considered here as homeomorphs of the Family Bothrophyllidae in the meaning accepted in this paper.

The discussion of *Bothrophyllum* or *Bothrophyllum*-like coral faunas from other areas, such as the Urals, Novaya Zemlya, and the Chinese Microcontinents, Iran and the Western Interior Province of North America is omitted from this paper. The existing data on the late Serpukhovian/early Bashkirian rugose coral faunas from those areas known to me are not precise enough for the reliable comparison to the Donets Basin bothrophyllids and dibunophyllids of that age. Nevertheless, the value of those areas as centres creative of species of the Pennsylvanian rugose coral faunas cannot be neglected. Yet, the Donets Basin and/or its vicinity is suggested here as one of the main creative areas for new species of the Rugosa in early Bashkirian times.

**SUMMARY:** The lithology of the late Viséan to the late early Bashkirian strata of the Donets Basin is characterized by many limestone intercalations of the

Limestone D and E Groups, reflecting the location of the basin closest to the open sea at that time and dependent on sea level fluctuations. Poletaev *et al.* (2011), followed by Fedorowski (2017a), considered that period as the transgressive phase of deposition. The shelves of the open sea, i.e., the source area of marine ingressions, secured the stable environmental conditions necessary for the continuous development of coral and other faunas, whereas members of those faunas migrating together with marine ingressions must have coped with a changeable environment. Conditions like those were perhaps suitable for both the extermination of some taxa and the creation of new ones. The period of time we are dealing with in the present paper, i.e., the late Serpukhovian/early Bashkirian, was the period of the strongest rugose coral fauna deterioration during the Carboniferous (Fedorowski 1981). This means the disappearance of a majority of the Mississippian rugose coral taxa and the strong reduction in the number of specimens of the taxa that survived in refugia such as the Donets Basin or northern African basins. That global factor resulted in coral collections being sporadic and represented by a very few specimens of both surviving and new taxa. Thus, one can expect inconsistent characteristics and ephemeral appearance of new taxa. This question is briefly discussed in my previous paper (Fedorowski 2017a) and herein in the case of the Families Bothrophyllidae and Aulophyllidae, but will be elaborated in detail in a paper concluding the cycle of papers devoted to the early Bashkirian corals of the Donets Basin. New data on the early Bashkirian Dibunophyllinae and Bothrophyllidae allow me to suggest: 1. a separate family position for the Mississippian rugose coral taxa traditionally included in the Family Bothrophyllidae; and 2. the derivation by descent of the Bothrophyllidae *sensu stricto* from the early Bashkirian Dibunophyllinae. This evolutionary lineage leads to the Moscovian type genus *Bothrophyllum* and to younger representatives of the Family Bothrophyllidae.

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