

Early Bashkirian Rugosa (Anthozoa) from the Donets Basin (Ukraine). Part 5. The Family Bothrophyllidae Fomichev, 1953

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ABSTRACT:

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Four genera (one new, one questionable), seven named species (five new) and five taxa left in open nomenclature are described from uppermost Serpukhovian (Limestone D₅³) to middle Bashkirian (Limestone G₁¹) strata. A new genus: *Nina* and the new species: *Bothrophyllum kalmyussi*, *B. gorbachevensis*, *Nina donetsiana*, *N. dibimitaria* and *N. magna* are introduced. The genus *Cystilophophyllum* Fomichev, 1953 is redefined and transferred to the Family Bothrophyllidae. Three general topics discussed in the Considerations are: 1. The taxonomic value of the microstructure of the septa and the necessity for a distinction between that character and diagenetic alterations; 2. Depositional conditions, under which the rugose coral skeletons were deposited; 3. The similarity of skeletal constructions vs. relationships in some taxa of the Subfamily Dibunophyllinae Wang, 1950 and the Family Bothrophyllidae Fomichev, 1953. The lack of final conclusions in the matter of the relationships is due to the incompleteness and restricted number of specimens studied herein and the incomplete investigations of a great majority of the earlier described bothrophyllid taxa.

Key words: Late Mississippian; Early Pennsylvanian; Bothrophyllidae; Taxonomy; Microstructure vs. diagenesis; Relationships vs. similarity.

INTRODUCTION

Whereas the series of my papers dealing with the rugose corals from the Donets Basin (Fedorowski 2009a, b, 2016; Fedorowski and Vassilyuk 2011; Fedorowski and Ogar 2013) were devoted chiefly to the early Bashkirian taxa, corals investigated in this paper also include a latest Serpukhovian specimen (holotype of *Bothrophyllum berestovensis* Vassilyuk, 1960) and some earliest Zhuyevskian specimens (*Bothrophyllum gorbachevensis* sp. nov. and *Cystilophophyllum kalmiussi* Fomichev, 1953). Most specimens were derived from the Limestone Groups D₆ and D₇. Thus, the title of the series has not

been changed. The Limestone Groups mentioned belong to the strata located close to the Mississippian/Pennsylvanian boundary. This stratigraphic position makes the fauna important for the interpretation of the evolutionary relationships of some early to late Carboniferous and Permian rugose corals.

Representatives of the Family Bothrophyllidae are common in the Carboniferous strata of the Donets Basin (Fomichev 1953; Vassilyuk 1960; Ogar 2009), starting from the uppermost Serpukhovian Limestone D₅³ (*Bothrophyllum berestovensis* Vassilyuk, 1960) and ending with the lower Gzhelian Limestone O₆ (*Bothrophyllum conicum* Ogar, 2009). A few specimens described in this paper from the Limestones F₂



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

and G_1 are included in *Bothrophyllum* Trautschold, 1879. Those positions make them the stratigraphically earliest species of that genus as emended by Fedorowski (2016). The genus *Cystilophophyllum* Fomichev, 1953 was transferred from the Family Lophophyllidae Grabau, 1922 to the Family Bothrophyllidae with some doubts (see remarks). The content of the latter family accepted here closely resembles that of Hill (1981, p. 344). Small differences are discussed with remarks on the family.

The preservation of the specimens is not good (see Material and Methods). The incompleteness and restricted number of specimens, augmented by their morphological variability, make solutions proposed in this paper subjective to some extent. However, new formal names are introduced only when the nearly complete ontogeny in at least one representative of a given morphotype is studied. Some specimens, obviously different from the holotype of *Nina donetsiana* sp. nov., are described as variants. This inconsistent procedure is applied to specimens derived from the lowermost Bashkirian strata (Limestones D_6 and D_7). Rugose corals of that age are extremely restricted in the world and that period of time (*Homoceras*–*Hudsonoceras* ammonoid Biozone) is crucial for the understanding of the Pennsylvanian and Permian evolution of those corals (Fedorowski 1981).

This paper follows earlier contributions by the author dealing with the early Bashkirian Rugosa of the Donets Basin. For introductory data, the reader is referred to the first paper of the series (Fedorowski 2009a).

Following Hudson (1936) and Fedorowski (1997), only the cardinal and the counter major septa are considered as the protosepta. The term “primary septa” refers herein to the innermost parts of the septa, cre-

ated within the septal pockets prior to the secretion of the sclerenchymal sheets.

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

MATERIAL AND METHODS

The specimens studied were collected by Dr. N.P. Vassilyuk, Professor Emeritus of the Donetsk Polytechnic, Ukraine, during many years of her field investigations and have been offered to me for both study and housing. The specimens were originally labelled in accordance to the indexes of the Limestone from which they were derived. Thus the Limestone indexes, constant for many decades, have priority over “Horizons” [= Stages] and “Suites” and are mentioned as first in the Occurrences. The Limestone indexes are supplemented by data derived from the study of Nemyrovska (1999) and the stratigraphic summary of Poletaev *et al.* (2011).

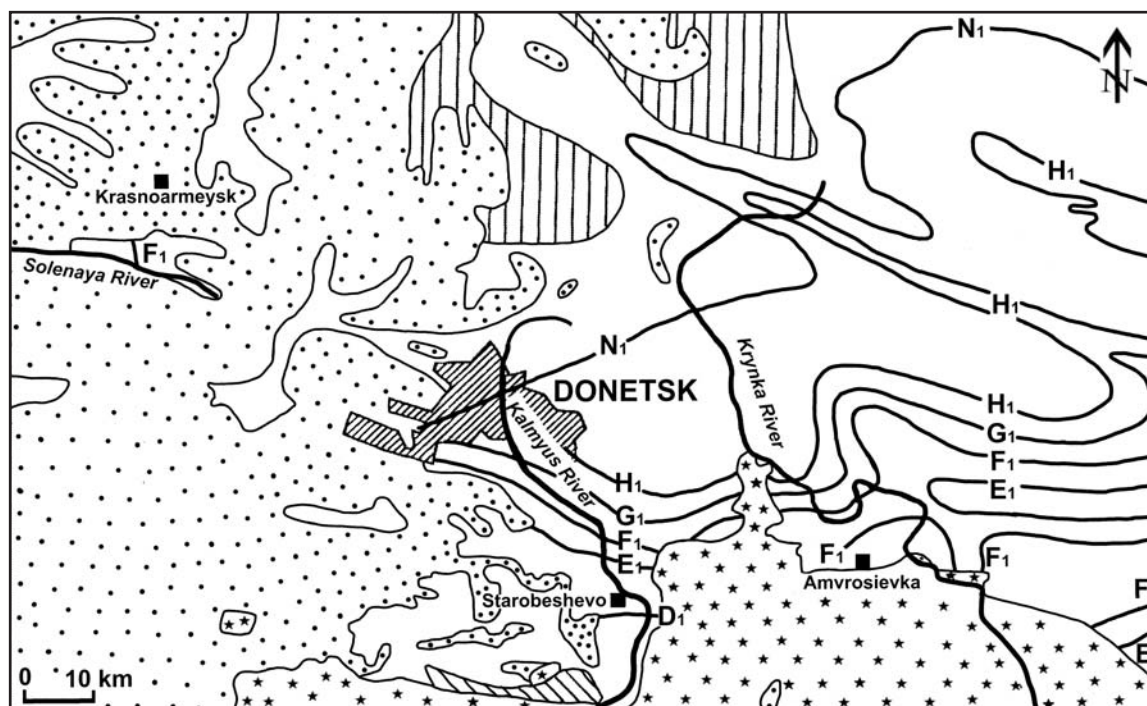
The detailed study of the present collection is supplemented by my restudy of the holotype of *Bothrophyllum berestovensis* Vassilyuk, 1960 and by my earlier reinvestigations of Fomichev’s (1953) collection. Those reinvestigations allow a direct comparison of the taxa described in this paper to the earlier described ones.

All coral specimens described herein were worn, fractured and/or slightly eroded during transport. They were also subjected to further diagenetic changes after deposition. The latter led to the corrosion of their peripheries and internal squeezing, sometimes so strong as to make some specimens hardly determinable. The corallites affected most strongly are not investigated in detail.

Traditional methods of thin sectioning and peeling are applied in most instances. Characters inadequately demonstrated in the images are supplemented by computer drawings based on highly enlarged images.

GEOLOGICAL SETTING

The history of the recognition and content of the Bashkirian Stage is available from the earliest of a series of papers dealing with the rugose corals of the Donets Basin (Fedorowski 2009a). Detailed descriptions, faunal contents and some historical details of the Mississippian, Pennsylvanian and lower Permian (Cisuralian) stratotypes in that basin have been pub-



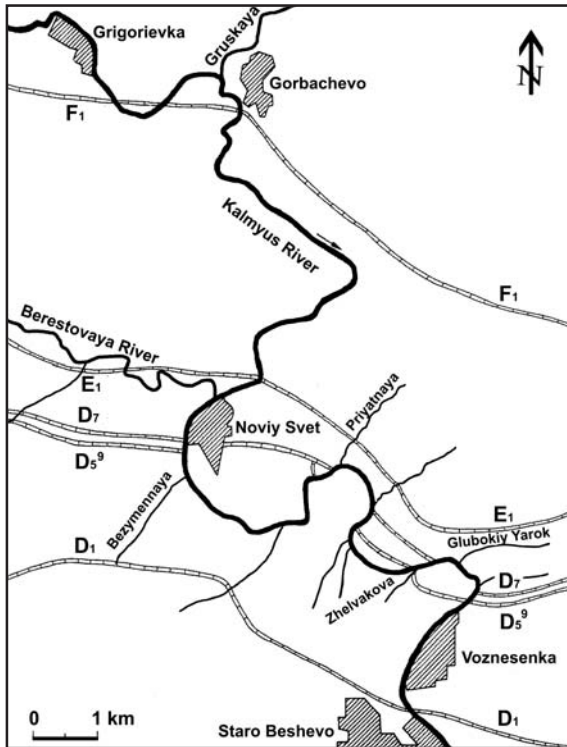
Text-fig. 2. Map of the vicinity of the town of Donetsk showing the general positions of individual Limestone Groups (D to N). All Carboniferous deposits left in white. Provided by Dr. N.P. Vassilyuk, after Fedorowski (2009a)

lished by Poletaev *et al.* (2011). A detailed description of the most important new locality of the lowermost Bashkirian (Berestovaya River Mouth) was given by Fedorowski and Ogar (2013). Thus, this chapter is restricted to a summary of the distribution of taxa described herein and to a few statements, most of which were compiled on the basis of Poletaev *et al.* (2011) and a few on the basis of my own field notes.

1. Most of the specimens and species described herein were collected from the Limestones D_6 to D_7^8 . These are: *Nina berestovensis* (Vassilyuk, 1960), *N. donetsiana* sp. nov., *N. magna* sp. nov. and *Nina* sp. 1. The Limestone Group D constitutes limy intercalations within one of the thickest (more than 500 m) and stratigraphically longest lasting series of the Serpukhovian and Bashkirian deposits in the Donets Basin (Novolyubivskian and Zapaltyubinskian [Serpukhovian], and Voznesenskian [Bashkirian] Substages). Beds of limestones, which were deposited within a thick series of differentiated clastic deposits, differ greatly from each other in both thickness (0.1 m to 2 m exceptionally; commonly much less than 1 m) and lithology (Poletaev *et al.* 2011, figs 7–10). The coral-bearing intercalations are grainstones and packstones composed of small crinoid ossicles, fragments of bryozoan colonies, complete and broken shells of smaller Foraminifera, various

calcareous algae and unidentified shell fragments, belonging perhaps to brachiopods and molluscs. Almost all of the Limestones D are further subdivided into two to several lower rank intercalations that bear their own numbers (e.g., D_5^8). Several second rank intercalations are composed of a few limestone beds (e.g., D_5^{8v}).

2. The examples of the Limestones cited above were selected on purpose. The first of them (D_5^8) was proposed by Nemyrovska (1999, fig. 36) as marking the top level of the Serpukhovian strata; Poletaev *et al.* (2011, figs 9, 10) subdivided the Limestone D_5^8 into a lower (*nizhnyi*, D_5^{8n}) that terminated the deposition of the Serpukhovian strata, and an upper (*verkhnyi*, D_5^{8v}) that began the deposition of Bashkirian strata (Poletaev *et al.*, p. 59, fig. 10). The number of the lower rank intercalations of the Limestone D group increases upwards through the series of strata, with the Limestones D_5 up to D_7^8 constituting the most numerous and most densely packed intercalations. In addition, the limy beds in that part of the series are separated mostly by argillaceous deposits, whereas the sandy intercalations are reduced to only a few thin layers. This kind of lithology suggests a prevailing marine regime, described by Poletaev *et al.* (2011, p. 59) as the transgressive part of the Bashkirian transgressive-regressive megacycle.



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, after Fedorowski (2009a)

3. Only two specimens are described here from the Limestone E₁, subdivided by Poletaev *et al.* (2011, fig. 11) into three thin (approximately 0.4 m each) limestone layers: the lower (*nizhnyi*) that yielded one specimen of *Nina dibimitaria* sp. nov., the middle (*srednyi*) and upper (*verkhnyi*) layers, from which *Nina* sp. 2 was collected. Moreover, Vassilyuk (1960) described three new species from these Limestones, i.e., *Adamanophyllum incertus* (E₁^{nizh}), *Lytvophyllum dobroljubovae* (E₁–E₆) and *Dibunophyllum finalis* (E₂). Limestone E₁^{nizh} initiated the deposition of the Feninian Substage strata. The stratigraphic proximity of all three Limestone E intercalations, their lithological character (grainstones similar to those of the Limestone D₇ group) and their position within the argillaceous deposits suggest that they represent the transgressive subcycle mentioned above.

4. The Blagodatnian Substage in the type area (Krynka River) begins with a 12 m thick bed of grainstone, indexed as Limestone F₁ (Poletaev *et al.* 2011, fig. 13). Corals occur in that limestone, but they belong to taxa not considered herein. Three specimens identified as *Bothrophyllum kalmyussi* sp. nov., and

two specimens, identified as *Cystilophophyllum* sp. and ?*Siedleckia* sp. were collected from Limestone F₂ of the Kalmyus River Area. That group of limestones (F₂) in both the Kalmyus River and the Krynka River areas is represented by a few thin (commonly less than 0.5 m each) limestone layers scattered through the clastic deposits with sandstones and aleurites prevailing. Poletaev *et al.* (2011, fig. 13) estimated a thickness of 220 m for the Blagodatnian Substage. Corals from the Limestone F group were earlier described by Fomichev (1953), who introduced two new species (“*Stereophrentis*” *mandrykinensis* and *Bothroclisia crassiseptatum*) and illustrated two other specimens of uncertain affinities.

5. Two species, i.e., *Cystilophophyllum kalmyussi* Fomichev, 1953 described by that author from the Limestone G₁, redescribed here from the same layer although from a different area, and *Bothrophyllum gorbachevensis* sp. nov., are stratigraphically the youngest taxa investigated herein. According to Poletaev *et al.* (2011, fig. 14), the Limestone G₁ begins the deposition of the Zhuyevskian Substage, i.e., the lowest Kayalskian Stage of the upper Bashkirian. Thick series of clastic deposits with sandstones prevailing and with several thin limy intercalations (G₁¹–G₄¹) belong to the regressive part of the Bashkirian megacycle of Poletaev *et al.* (2011).

To sum up: the fragmented and commonly eroded nature of the coral specimens and the lithology of the deposits briefly characterized above strongly suggest that these coral specimens were transported, worn, segregated and deposited as clasts. The living area of the coral fauna, its environment, richness and the true taxonomic diversity of the corals remain unknown, but were perhaps much larger than the established here on the basis of the remnants available for the study.

SYSTEMATIC PALAEOONTOLOGY

Order Stauriida Verrill, 1865

Suborder Caniniina Wang, 1950

Family Bothrophyllidae Fomichev, 1953

(Type genus *Bothrophyllum* Trautschold, 1879)

EMENDED DIAGNOSIS: Solitary dissepimented corals; in neanic growth stage axial septum present, major septa zaphrentoidally arranged; after late neanic and/or early mature growth stage protosepta varying in length constantly for individual genera; loose axial structure, if present, never forming a continuous axial column; in advanced maturity axial area commonly free; tabularium convex: normal,

biform and/or disstabilium (new term introduced by Fedorowski 2016); microstructure of septa finely trabecular.

GENERA ASSIGNED: *Bothrophyllum* Trautschold, 1879; *Gshelia* Stuckenberg, 1888; *Timania* Stuckenberg, 1895; *?Caninophyllum* Lewis, 1929; *Pseudotimania* Dobrolyubova and Kabakovich, 1948; *Bothroclisia* Fomichev, 1953; *?Cystilophophyllum* Fomichev, 1953; *?Yakovleviella* Fomichev, 1953; *Hornsundia* Fedorowski, 1965; *Siedleckia* Fedorowski, 1975; *Nina* gen. nov.

REMARKS: Large dissepimented solitary rugose corals, occurring through the Carboniferous and Permian, are among the most common and most frequently described Rugosa. Those of the Tournaisian and Viséan from Europe, investigated since the early 19th century and mostly revised afterwards, received a fairly accurate taxonomy. In contrast to the former, the taxonomy of many Serpukhovian and stratigraphically younger dissepimented solitary taxa remains controversial. Differences in their identifications resulted both from difficulties in collecting complete large solitary specimens and from their superficial investigations. Thus, two most important features, i.e., the complete ontogeny and the microstructure of septa of many species remain unknown. Also, many unrelated and/or distantly related solitary dissepimented taxa reached the so-called “caninoid stage”, i.e., shortening of the major septa that make axial areas free. That similarity in advanced maturity, commonly disregarded, forms the next important misleading factor. The papers by Dobrolyubova (1937, pl. 12, figs 3–7), Dobrolyubova and Kabakovich (1948, pl. 13, figs 12–17), Fomichev (1953, pl. 19, fig. 3a–d in Russian alphabet) and Fedorowski (1965, fig. 1: 1–16; 1975, fig. 5a–g) can be used as examples of differences in the early morphology, leading to the morphological similarity in advanced maturity of some bothrophyllid genera.

The genus *Bothrophyllum* Trautschold, 1879 and related and/or similar taxa have already been discussed (Fedorowski 2016). Thus only the genus *Cystilophophyllum* Fomichev, 1953, conditionally included here in the Family Bothrophyllidae and genera omitted from that paper mentioned, are briefly discussed herein.

Hill (1981) considered the taxonomic position of *Siedleckia* Fedorowski, 1975 disputable. Her suggestion of its possible synonymy with *Bothrophyllum* was based on the lack of the earliest growth stages from the type species of *Siedleckia*. However, the

cardinal and the counter septa, shortened in that species after the late neanic growth stage (Fedorowski 1975, fig. 5b–f) prove its independent generic status. The position of *Siedleckia* within the Family Bothrophyllidae is less obvious as the occurrence of the axial septum in the earliest growth stage has not been proven. However, the long cardinal and counter septa almost meeting at the corallite axis in the earliest growth stage studied (Fedorowski 1975, fig. 5a) may suggest the occurrence of the axial septum in an ontogenetic growth stage only slightly less advanced than the one illustrated. Thus, the position of *Siedleckia* within the Family Bothrophyllidae is more probable than its transfer to any other existing family.

The major part of the content of the Family Bothrophyllidae proposed by Hill (1981) is accepted herein. It should only be stated that the type species of *Caninella* Gorskiy, 1938 has not been supplemented by complete topotype specimens. A brief discussion and new illustrations provided by Kossovaya *et al.* (2016, pp. 12, 13, fig. 8: 1–6) clarified some details omitted by Gorskiy (1938) from his description and not seen from his poor picture, but did not solve the fundamental question, i.e., the morphology of the neanic and the early mature growth stages. The Donets Basin specimens included in that genus by Fomichev (1953) do not solve the problem either (for a wider discussion see Fedorowski 2016). An occurrence of the lateral dissepiments in the type species of *Caninella pulchra* Gorskiy, 1938, highly evaluated by Kossovaya *et al.* (2016) does not help. Such dissepiments occur in the type species of *Bothrophyllum* Trautschold, 1879 (e.g., Dobrolyubova 1937, pl. 11, fig. 2; pl. 14, fig. 2; pl. 14, fig. 3; 1940, pl. 5, fig. 5). They are recognizable in the advanced growth stage of *Siedleckia* Fedorowski, 1975 (pl. 4, fig. 4b) and are especially well developed in the peculiar corallite described by Stevens *et al.* (2012) from the Pennsylvanian of California. Thus, *Caninella* remains an insufficiently known taxon of unknown taxonomic position. *Calmiussiphyllum* Vassilyuk, 1960, another insufficiently known genus, included by Hill (1981, p. F346) in the Family Bothrophyllidae, is characterized by a key-hole cardinal fossula and long, contrajunct and contrajunct minor septa. It may belong either to the Family Palaeosmiliidae Hill, 1940 or to the Family Heterocaniidae Hill, 1981, but it does not belong to the Bothrophyllidae. Reasons for the allocation of *Cystilophophyllum* in the Bothrophyllidae and its suggested relationships, are discussed with that genus.

The diagnostic characters of the genera included in the Family Bothrophyllidae form a kind of differ-

entiated net. Thus, it seems more reasonable to discuss individual sets of characters occurring in particular genera described below rather than to introduce a wide discussion at the family level.

Genus *Bothrophyllum* Trautschold, 1879
(Type species *Turbinolia conica* Fischer von
Waldheim, 1830=1837)

SYNONYMY: See Fedorowski (2016).

SPECIES CONTENT: See Fedorowski (2016) + *Bothrophyllum kalmyussi* sp. nov. and *B. gorbachevensis* sp. nov.

DIAGNOSIS: Solitary Bothrophyllidae; axial septum present during entire neanic growth stage; inner margins of several major septa approaching corallite axis up to early maturity; in late maturity may leave axial area free; cardinal septum equal to average major septa; counter septum long up to the early mature growth stage or longer, may be equal to other major septa in advanced maturity; cardinal fossula indistinct; loose indistinct axial structure composed of inner margins of major septa and axial tabellae, may be gradually reduced during growth; tabularium biform and/or disstabularium; microstructure of septa finely trabecular (after Fedorowski 2016).

REMARKS: The concept of the genus *Bothrophyllum* and its diagnosis depends on the evaluation of particular characteristics by individual authors (e.g., Dobrolyubova 1937, 1940, 1948; Dobrolyubova and Kabakovich 1948; Fomichev 1953; Semenov-Tian-Chansky 1974; Fedorowski 1975; Poty 1981; Kossovaya 2001; Ogar 2009). The comprehensive discussion on the type species of *Bothrophyllum*, i.e., *Turbinolia conica* Fischer von Waldheim, 1830=1837, supplemented by the discussion on the possible relationships of that genus to some *Bothrophyllum*-like corals (Fedorowski 2016), allows reduction of the remarks that follow to a few statements. 1. Well documented ontogenetic and microstructural data are absent from the majority of the taxa so far included in *Bothrophyllum*. 2. The inadequate documentation of taxa derived from geographically distant localities and the very long time (Tournaisian to Artinskian) of

the apparent occurrence of the genus *Bothrophyllum*, makes doubtful the relationships of many species included in that genus by various authors (see synonymy in Fedorowski 2016). 3. The extremely wide intraspecific variability proposed by Dobrolyubova (1937) in her redescription of *Bothrophyllum conicum* legitimizes to some extent a broad definition of that genus applied by subsequent authors. My recent analysis (Fedorowski 2016), based in part on the toptype material, has allowed for the reduction of the intraspecific variability of the type species, to establish the characters most important for the genus, and to emend its diagnosis, as cited above.

Bothrophyllum kalmyussi sp. nov.
(Text-figs 4 and 5)

HOLOTYPE: Specimen UAM-Tc/Don.1/115.

TYPE LOCALITY: Left bank of the Kalmyus River, west of the Gorbachevo Village.

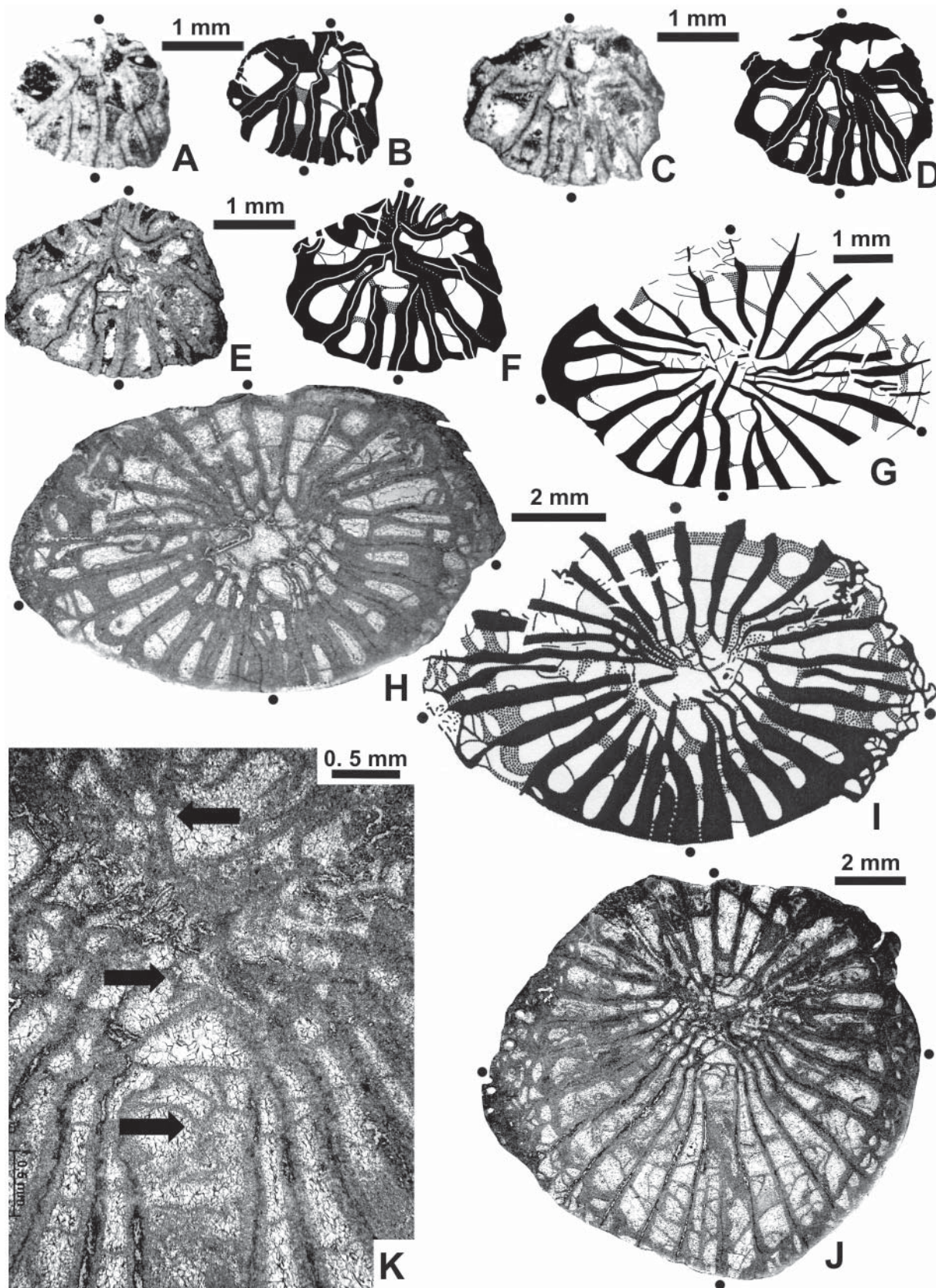
TYPE STRATUM: Limestone F₂. Blagodatnian Substage, Suite C₂^b_a verkh. *Pseudostaffella pregorskyi*–*Staffelleiformes staffelleiformis* foraminiferal Biozone, *Idiognathodus sinuosus* conodont Biozone, *Bilinguites*–*Cancelloceras* ammonoid Biozone. Middle Bashkirian.

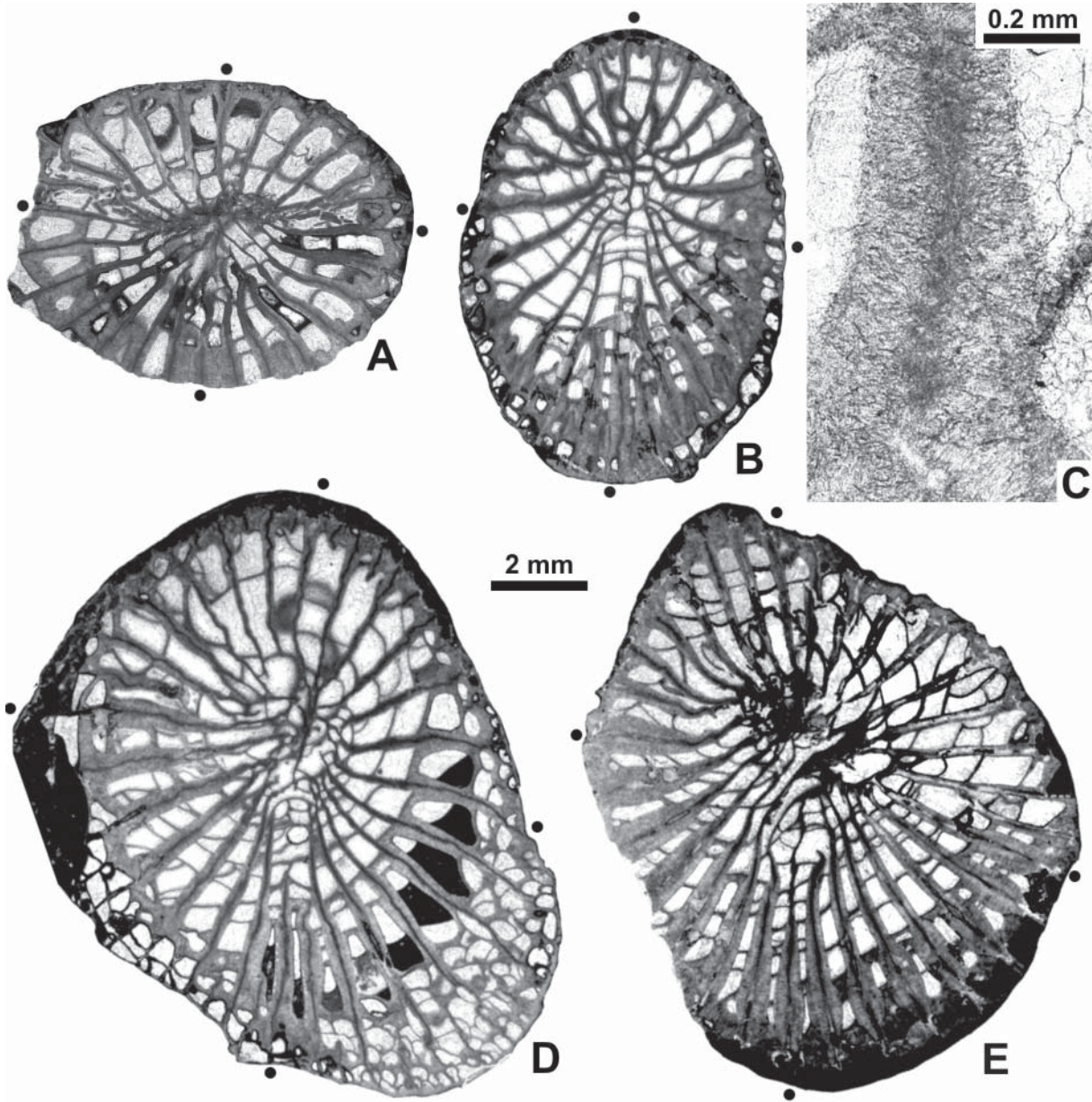
ETYMOLOGY: Named after the Kalmyus River crossing the type area.

DIAGNOSIS: *Bothrophyllum* with n:d value 31:13.0 mm. Major septa closely approaching, some reaching corallite axis; those of cardinal quadrants bending over long cardinal septum; cardinal fossula deep, resembling key-hole; minor septa extending to tabularium when dissepimentarium narrow.

MATERIAL: Three corallites. Holotype UAM-Tc/Don.1/115 with most of the peripheral parts eroded. Early growth stage preserved, but calice lacking. Earliest growth stage slightly diagenetically altered. Mature growth stage squeezed a little (three thin sections and six peels). Both paratypes represented by transverse thin sections only. Paratype UAM-Tc/Don.1/116 well preserved (three thin sections).

Text-fig. 4. *Bothrophyllum kalmyussi* sp. nov. Specimen UAM-Tc/Don.1/115. Holotype. Transverse sections. A-F – neanic growth stage (thin sections and corresponding drawings), G – late neanic/early mature growth stage (polished surface with drawing), H, I – early mature growth stage (peel and drawing), J – mature growth stage (peel), K – fragment of J enlarged to document fragments of elongated cardinal septum (two lower arrows) and long counter septum (upper arrow). For stratigraphic position see text. Protosepta and alar septa marked by dots when recognizable. Scale bars common for two adjacent pictures are located between them, those corresponding to a given picture located in its upper right →





Text-fig. 5. *Bothrophyllum kalmyussi* sp. nov. Paratypes. Transverse thin sections. A – Specimen UAM-Tc/Don.1/117. Late neanic/early mature growth stage morphologically corresponding to the holotype (Text-fig. 4G). B-E – Specimen UAM-Tc/Don.1/116. B, D, E – early to late mature growth stage, C – diagenetically altered major septum; bunches of calcite fibrils interpreted as remnants of trabeculae. For stratigraphic position see text. Protosepta and alar septa marked by dots. Scale bar in the middle of figure corresponds to all pictures except for C

Paratype UAM-Tc/Don.1/117 slightly squeezed (one thin section).

DESCRIPTION OF HOLOTYPE: Early neanic growth stage (Text-fig. 4A–F) with successive n:d values ?10:2.0 mm, ?10:2.5 mm, and ?14:2.8 mm. Both the number of septa and the corallite diameter uncertain due to diagenetic alteration, but the main generic features: zaphrentoid arrangement of major

septa and occurrence of axial septum recognizable. N:d values of late neanic and early mature growth (Text-fig. 4G–I) 23:6.5×4.1 mm and 29:11.0×6.5 mm, respectively. Both diameters reduced by corrosion. Smaller corallite diameter additionally reduced by squeezing. Major septa almost equal in length, semi-radially arranged. In late neanic growth stage (Text-fig. 4G) most major septa approaching corallite axis. Cardinal septum elongated to corallite axis. Periaxial

fragment of counter septum broken. In early mature growth stage (Text-fig. 4H, I) narrow axial area free from major septa. Cardinal septum remaining longer than adjacent major septa, but strong leftward bend of its inner margin camouflages its true length. Counter septum crossing corallite axis with its thin inner part. Minor septa not observed, may be eroded. Dissepiments irregular when preserved.

Mature morphology (Text-fig. 4J) with n:d value 31:12.5×11.5 mm, differs considerably from earlier growth stages. Most major septa approach, some reach corallite axis. Those of cardinal quadrants bend over cardinal fossula. Inner margins of some major septa meet over cardinal fossula, some others connected by sections of tabulae to make cardinal fossula closed. Cardinal septum slightly thickened at periphery, long, almost reaches corallite axis with its very thin inner margin. Discontinuity of cardinal septum apparent, resulting from its low extension above tabula. Only sections cut immediately above tabulae appear in picture (Text-fig. 4K). Thin inner margin of counter septum extends to corallite axis. Alar septa indistinguishable by length. Alar pseudo-fossulae absent. Minor septa cross dissepimentarium when narrow. Dissepiments regular, angular and pseudo-herringbone. Inner wall thickened.

INTRASPECIFIC VARIABILITY: One of the two paratypes (Text-fig. 5A), restricted to a single transverse thin section of the immature growth stage (n:d value 26:8.8×7.0 mm), closely resembles the immature growth stage of the holotype (Text-fig. 4G). The second paratype represented by three transverse, slightly oblique thin sections (Text-fig. 5B, D, E), resembles the mature growth stage of the holotype in most characters. It differs by n:d values being smaller (24:11.0×7.6 mm, 28:14.2×10.6 mm, 31:13.5×10.3 mm), by minor septa restricted to the dissepimentarium when wide (Text-fig. 5D, lower right) and by inner margins of major septa in cardinal quadrants only bent above the long cardinal septum, but do not meet above the cardinal fossula. Its distabularium accentuated slightly better than in the holotype. Hardly recognizable bunches of calcite fibrils (Text-fig. 5C) may suggest a trabecular microstructure.

REMARKS: *B. kalmyussi* sp. nov. resembles *B. conicum* (Fischer von Waldheim, 1830=1837), the type species for the genus from the Moscovian strata of the Moscow Basin, in the main diagnostic characters. The mature characteristics of both the holotype and the more completely preserved paratype of *B. kalmyussi* (Text-figs 4J; 5D, E) are most closely comparable to

the advanced growth stage of the neotype of *B. conicum* (Ivanovsky 1987, pl. 1, fig. 1a), considered early mature (Fedorowski 2016). It also resembles the early mature growth stage of the specimen illustrated by Dobrolyubova (1937, pl. 3, fig. 7; pl. 4, fig. 1) and the early mature growth stage of the Gzhelian specimen from the Donets Basin, illustrated by Ogar (2009, pl. 1, fig. 7). It differs clearly from the type species and the remaining specimens mentioned above in the length and the arrangement of the major septa in both the early mature and the advanced mature growth stages, in the length of the minor septa, restricted to the dissepimentarium, in the diameter and the number of septa being much smaller, and in the n:d value.

B. kalmyussi follows to some extent the “evolutionary” scheme of development within the genus *Bothrophyllum*, based on the length of the minor septa (Dobrolyubova 1948). This question was widely discussed recently (Fedorowski 2016). Characters of *B. kalmyussi* allow to consider it as one of the stratigraphically earliest species possessing a set of characters typical of *Bothrophyllum*.

OCCURRENCE: As for the holotype.

Bothrophyllum gorbachevensis sp. nov.
(Text-fig. 6)

HOLOTYPE: Specimen UAM-Tc/Don.1/118.

TYPE LOCALITY: Left bank of the Kalmyus River, west of the Gorbachevo Village.

TYPE STRATUM: Limestone G₁¹. Lower Zhuyevskian Substage, Suite C₂^b. *Profusulinella primitiva*–*Pseudostaffella gorskyi* foraminiferal Biozone, early *Branneroceras*–*Gastrioceras* ammonoid Biozone. Early late Bashkirian.

ETYMOLOGY: Named after the Gorbachevo Village, near which the specimens were collected.

DIAGNOSIS: *Bothrophyllum* with n:d value near calice floor 35:15.5 mm; major septa tapering axially, in cardinal quadrants sequentially shortened; axial area free from septa approximately 1/5 corallite diameter wide; cardinal septum longer than 2–3 last inserted pairs of major septa; counter septum slightly elongated; cardinal fossula narrow, indistinct; minor septa meeting tabularium when dissepimentarium narrow; tabularium bifiform when minor septa extend to it.

MATERIAL: Two fragmentary, worn corallites. Holotype UAM-Tc/Don.1/119 with immature growth stage preserved. Mature growth stage slightly crushed. Squeezing of axial area makes longitudinal sectioning useless for study. Calice destroyed. Two transverse thin sections and seven peels available for study. Paratype UAM-Tc/Don.1/120 squeezed. Its main diagnostic characters recognizable (one peel). Only holotype described in detail.

DESCRIPTION: External surface almost smooth with delicate growth striae. Septal furrows hardly recognizable or absent. Advanced neanic growth stage, with n:d value 21: 5.0×4.4 mm, zaphrentoid, asymmetrical. Axial septum recognizable (Text-fig. 6A, B). Alar septa dominating in cardinal quadrants, counter-lateral septa short. Cardinal fossula and alar pseudofossulae indistinct. No dissepiments.

Morphology changing considerably within 3.3 mm of corallite growth. In latest neanic or earliest mature growth stage (Text-fig. 6C) with n:d value 28:10.0×9.4 mm, major septa wedge-shaped, sequentially shorten in all quadrants, leaving narrow axial area free. Cardinal septum longer than the last pair of major septa inserted, but not highly elongated. Counter and alar septa dominating in length. Cardinal fossula inconspicuous, narrow. Presence of minor septa uncertain. No dissepiments.

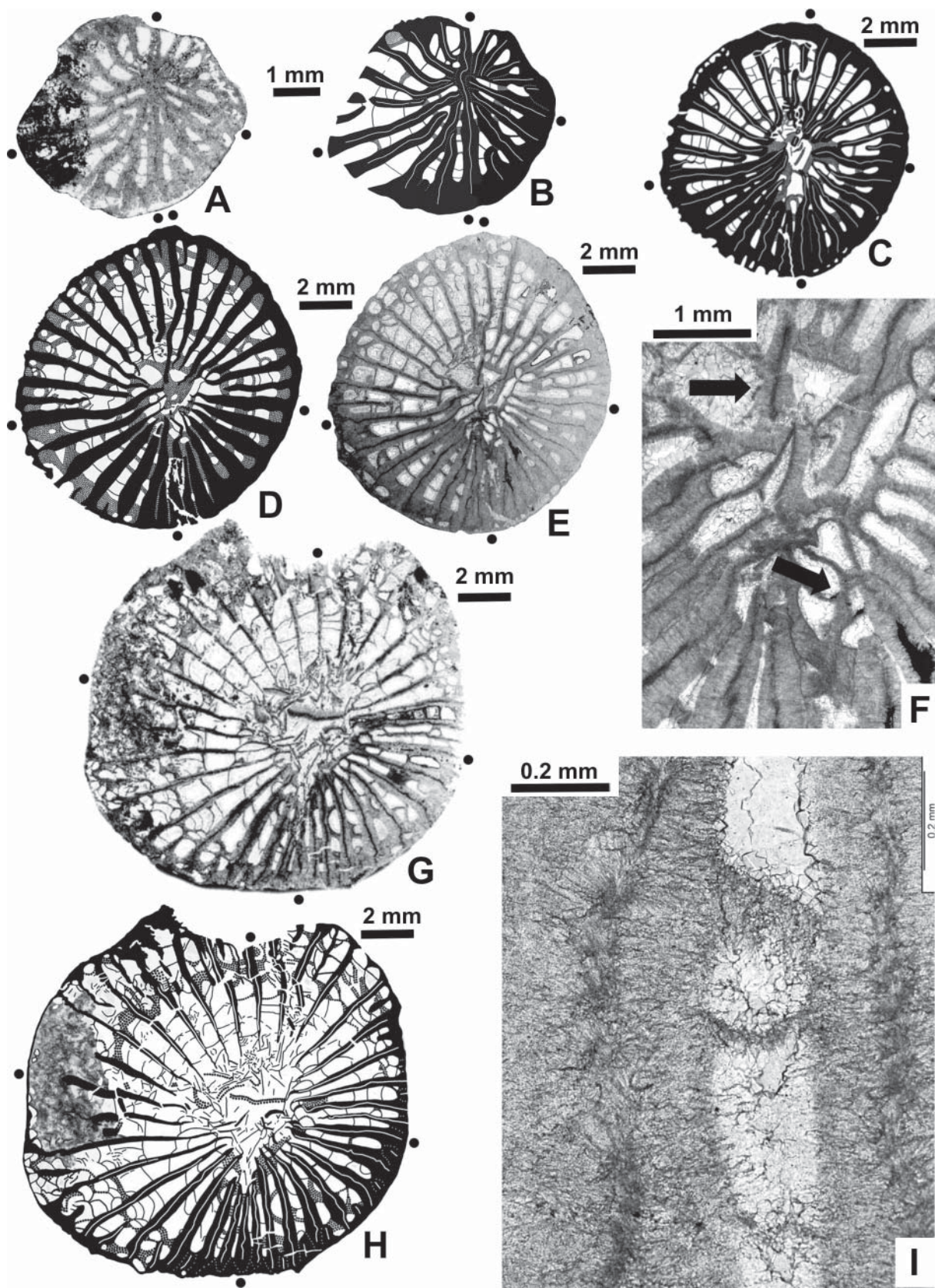
During approximately 4.5 mm of further corallite growth with n:d value 31:11.5×10.3 mm (Text-fig. 6D, E), major septa remaining long, closely approaching corallite axis. Counter and alar septa dominating in length. Major septa in cardinal quadrants thicker than those in counter quadrants, sequentially shortened towards cardinal septum. Their thin inner margins inclining towards cardinal septum to form tent-like structure supplemented by sections of tabulae. Cardinal septum with inner margin thin and bent (Text-fig. 6F, lower arrow), approximately equal in length to middle septa of cardinal quadrants. Cardinal fossula indistinct. Major septa in counter quadrants almost radially arranged, middle of them the longest, but only counter septum extending to corallite axis. Minor septa present in most loculi, hidden in external wall where dissepiments absent. Dissepimentarium incomplete, present in most loculi. Its appearance arbitrarily accepted here as the

earliest limit of mature growth stage. Dissepiments mostly regular. Inner wall thick. Disorderly arranged sections of peripheral parts of tabulae in counter quadrants suggest presence of disstabularium.

In mature growth stage (Text-fig. 6G, H), n:d value 34:15.8×14.8 mm up to approximately 38:16.8 mm near calice floor (crushed, not illustrated). Major septa thinner than in early mature growth stage, but similar in arrangement. Two last pairs of major septa slightly shorter from very thin-ended cardinal septum. Thread-like thin inner part of counter septum approaching corallite axis. Cardinal fossula narrow, hardly recognizable. Axial area free from major septa approximately 1/7 corallite diameter wide. Minor septa restricted to dissepimentarium, longest in counter quadrants, where dissepimentarium widest, reaching up to 1/4 corallite diameter. Dissepiments regular when dissepimentarium restricted to one row, herringbone and pseudo-herringbone when wide. Bulbous dissepiments in some loculi. Microstructure diagenetically altered in most septa, reasonably well preserved in fragments (Text-fig. 6I). Separate bunches of calcite fibrils differentiated in width. The largest in middle part of left septum perhaps enlarged by recrystallization on cost of sclerenchymal sheets. Bunches in lower part of the same septum much smaller, whereas those in right septum altered to irregular half-fans.

REMARKS: *B. gorbachevensis* sp. nov. to some extent resembles *B. conicum* (Fischer von Waldheim, 1830=1837) and other representatives of that genus from the type area. The main characters in common, i.e., the axial septum present in the neanic growth stage, the counter septum elongated, the cardinal septum not shortened, and the disstabularium present in the counter quadrants, are of a generic rather than specific value. The sequential shortening of the major septa in the cardinal quadrants in both *B. conicum* and *B. gorbachevensis* is the most important character in common at species level. *B. gorbachevensis* differs from both *B. conicum* and *B. pseudoconicum* Dobrolyubova, 1937 in a smaller diameter and lower number of septa, a different n:d value, straight and long major septa, closely approaching the corallite axis and in the underdevelopment of the cardinal fossula.

Text-fig. 6. *Bothrophyllum gorbachevensis* sp. nov. Specimen UAM-Tc/Don.1/118. Holotype. Transverse sections. A, B – neanic growth stage (peel and drawing respectively), C – latest neanic or earliest mature growth stage (drawing), D, E – early mature growth stage (drawing and thin section respectively), F – axial part of E enlarged to show inner margins of cardinal and counter septa (lower and upper arrow respectively), G, H – mature growth stage (thin section and drawing respectively), I – microstructure of septa. For stratigraphic position see text. Protosepta and alar septa marked by dots. Scale bars correspond to closest pictures →



B. gorbachevensis is more advanced in its bothrophyllid characteristics than *B. kalmyussi* sp. nov. derived from earlier strata (Limestone F₂) of the same locality. It resembles *B. kalmyussi* in the diameter, the number of septa, the n:d value, and in the short length of the minor septa, but differs distinctly in the arrangement of the major septa in both early and advanced maturity.

OCCURRENCE: As for the holotype.

Genus *Nina* gen. nov.

NAME DERIVATION: Named after the first name of Dr. Nina Pavlovna Vassilyuk, Professor Emeritus of the Donetsk Polytechnic, an outstanding Ukrainian coral specialist, to honour her scientific achievements.

TYPE SPECIES: *Nina donetsiana* sp. nov.

DIAGNOSIS: Bothrophyllid coral with zaphrentoid arrangement of septa in neanic growth stage; axial septum either continuous or divided into cardinal and counter septa; both protosepta remaining long up to calice floor inclusively; major septa differentiated in length; protosepta, alar septa and/or middle major septa in individual quadrants approaching/meeting corallite axis; cardinal fossula typically present, may be inconspicuous; tabularium normal; microstructure finely trabecular.

REMARKS: The new genus *Nina* resembles *Bothrophyllum* in the following characters: 1) the cardinal septum long or at least equal to completely developed major septa in cardinal quadrants; 2) the axial column absent in longitudinal sections; 3) the tabulae incomplete; and 4) the finely trabecular microstructure of septa. The most important characters distinguishing *Nina* from *Bothrophyllum* are: 1) the axial septum recognizable or well developed up to the early mature growth stage or permanently; 2) the length of major septa not in order of insertion, but inclined towards the longest, middle major septa in individual quadrants; 3) the tabularium normal; thick inner wall precluding the formation of a disstabularium; and 4) the dissepimentarium simple with pseudo-neotic structures absent. The similarities and differences mentioned above allow the consideration of *Nina* as a close relative of *Bothrophyllum*. Its early appearance in the stratigraphic column (latest Serpukhovian/earliest Bashkirian), an easy communication between the Donets and the Moscow Basins,

and the occurrence in the middle and the lower upper Bashkirian strata of the Donets Basin of the two new *Bothrophyllum* species introduced in this paper, make *Nina* a potential ancestor of *Bothrophyllum*.

The grouping of major septa in all quadrants of the septa, obvious in the type species and in most other species of *Nina*, may be weakly accentuated and/or absent from the individual quadrants in some specimens of *N. berestovensis*, making them similar to *Bothrophyllum*. Species with a permanent axial septum resemble the genus *Dibunophyllum* Thomson and Nicholson, 1876 (see discussion on *N. dibimittaria* sp. nov. and Conclusions). These two examples illustrate the wide spectrum of characters proposed here for *Nina*. Such a morphological variability is perhaps too large for the definition of a single genus. However, it was accepted here for two reasons: 1. Most specimens investigated were derived from the lowermost Bashkirian strata and the holotype specimen of *N. berestovensis* was collected from the uppermost Serpukhovian deposits. This period of time was recognized long ago (Fedorowski 1981), and generally accepted since, as the largest evolutionary turnover in the phylogeny of the Carboniferous Rugosa. Large morphological variability and the instability of characters should be considered normal for such a period in rugose coral evolution. 2. The specimens available for study are restricted in number and commonly fragmented. Thus, lumping of morphologically similar species in one genus and a broad definition proposed for the new species, is accepted here as taxonomically the most reasonable. The wide morphological variability of the specimens studied, documented as completely as possible, should help in the revision of their taxonomy when new material is collected.

The occurrence of species potentially belonging to *Nina* is uncertain outside the Donets Basin. Literature investigations allows one to point out only two species, i.e., *Pseudotimania* sp. of Kato and Gupta (1989), and *Orygmophyllum* sp. of Wu and Zhao (1989). The stratigraphic position of the Himalayan specimen is uncertain. Kato and Gupta (1989, p. 404) mentioned an "...either late Viséan or early Namurian age", but did not exclude "an Upper Carboniferous age...". *Pseudotimania* sp. is illustrated by two transverse thin sections (Kato and Gupta 1989, pl. 2, figs 4, 5), belonging perhaps to the late neanic and the early mature growth stages. The morphology in both of these growth stages corresponds to *Nina* in the main diagnostic characters. Thus *Pseudotimania* sp. is accepted here as a potential member of the new genus.

Orygmophyllum sp. of Wu and Zhao (1989, p. 96,

fig. 51), derived from the lowermost Weiningian of South China, is represented by a single transverse thin section. It displays some characters in common with *Nina berestovensis* and may belong to *Nina*, but a formal synonymy of this poorly preserved Chinese specimen with the Donets Basin species and genus is not proposed.

The derivation of *Nina* is uncertain. “*Pseudocaninia*” *longiseptata* Lewis, 1931 is the only species known to me that fulfils some diagnostic characters of *Nina*, i.e., the occurrence of the axial septum that may last in some specimens up to the late neanic growth stage (Lewis 1931, p. 230) and a grouping of the major septa around the middle major septa in each quadrant. Both these characters are weakly accentuated and the cardinal septum in some transverse sections illustrated by Lewis (1931) looks shortened. Unfortunately, the suggestions above are given exclusively on the basis of the published literature, but nevertheless this relationship seems doubtful, especially as there may have not even been a connection between the western and eastern European coral sites during the late Serpukhovian times (Fedorowski 2015, 2016).

Nina donetsiana sp. nov.
(Text-figs 7 and 8)

HOLOTYPE: Specimen UAM-Tc/Don.1/119.

TYPE LOCALITY: Kalmyk River Area, Voznesenka Village.

TYPE HORIZON: Limestone D₇³. Lower Voznesenskian Substage, Suite C₁^s_g. *Plectostaffella bogdanovkensis* foraminiferal Biozone, *Declinognathodus noduliferus* conodont Biozone, *Homoceras–Hudsonoceras* ammonoid Biozone, earliest Bashkirian.

ETYMOLOGY: Named after the sedimentary basin, in which it occurs.

MATERIAL: Seven specimens. Holotype UAM-Tc/Don.1/119 almost complete, but with calice flattened and mature growth stage crushed in part. Six paratypes: UAM-Tc/Don.1/120, 121, 162–165. All incomplete worn corallites, with only fragments of their mature growth stages preserved. All specimens diagenetically altered. Twelve thin sections and 23 peels available for study. In addition to specimens definitely included in that species, two informal variants are distinguished and described. Reasons for their distinction explained in Remarks. All specimens

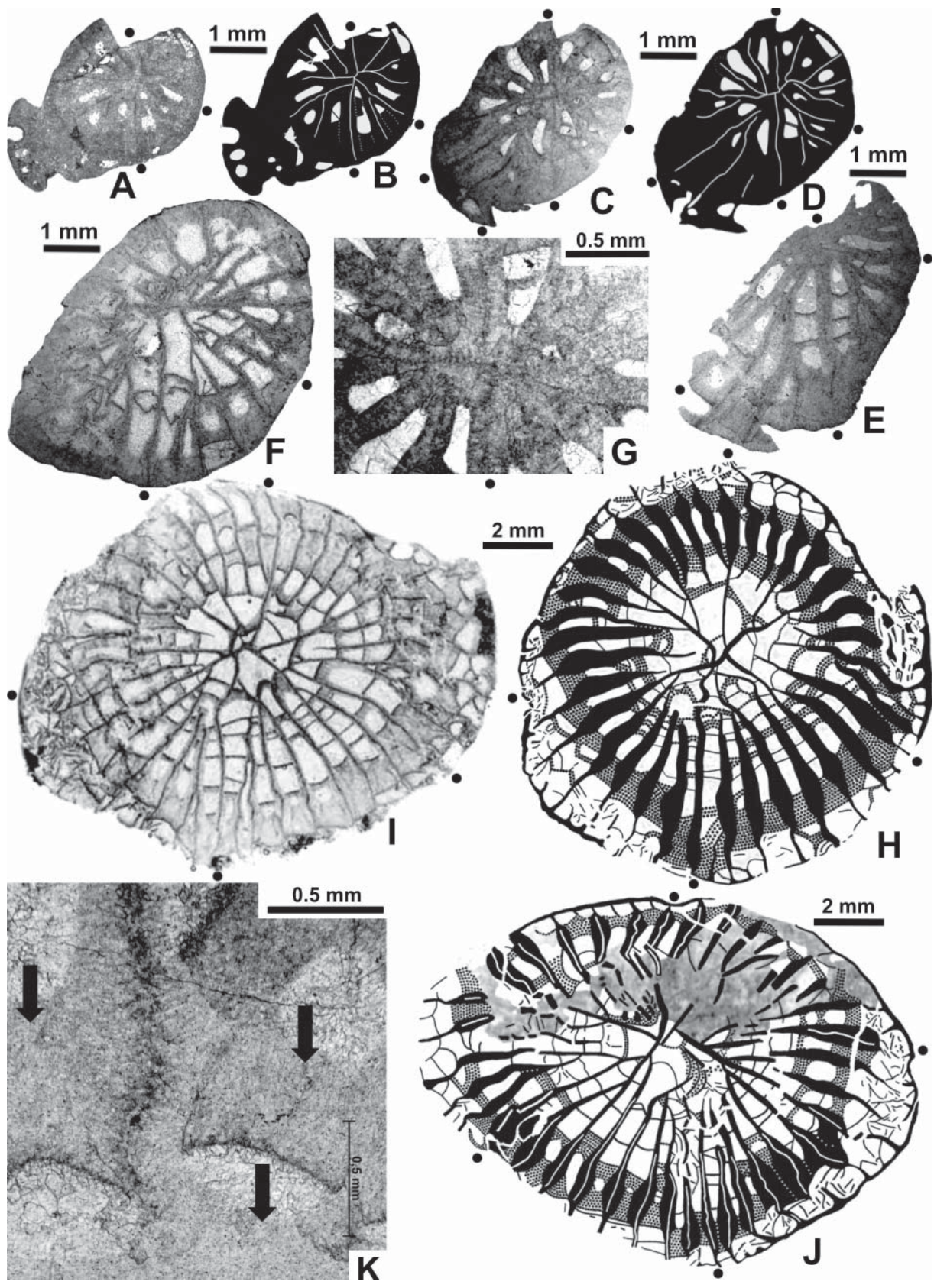
listed may have been originally included by Vassilyuk (1960) in her species *Bothrophyllum berestovensis* (see Remarks on *Nina berestovensis* below).

DIAGNOSIS: *Nina* with n:d value 36:13.0 mm (holotype) and up to 39:13.2 mm (paratypes); axial septum, or long protosepta meeting longest major septa near corallite axis; major septa straight, at peripheral tabularium thickened; minor septa restricted to outer dissepimentarium.

DESCRIPTION OF HOLOTYPE: In early neanic growth stage (Text-fig. 7A–D) major septa thick, zaphrentoidally arranged, slightly more numerous in counter than in cardinal quadrants. Protosepta reaching corallite axis, but their “dark middle lines” (primary septa) not meeting directly (Text-fig. 7G, enlarged from C). Small displacement illustrates the irregularity of the axial septum but not its absence. Cardinal fossula weakly marked in early growth stage, becoming well developed in more advanced neanic growth stage (Text-fig. 7E, F).

In early mature growth stage (Text-fig. 7H) major septa thickened along most of their length except for tapering inner margins; thickest in wide inner wall. Length of major septa differentiated. Protosepta long. Cardinal septum reaching corallite axis to join inner margins of longest major septa, i.e., left alar septum and middle major septa of particular quadrants. Counter septum long, thin, meets axial part of longest major septum of right counter quadrant, but extends directly to corallite axis during further corallite growth (Text-fig. 7I, J). Counter-lateral major septa shortest in counter quadrants, reaching lateral surfaces of counter septum. Minor septa hardly recognizable as short slats or protuberances of external wall. Dissepimentarium varying in width from one row of dissepiments adjacent to cardinal septum to 1/4 corallite radius (Text-fig. 7H, J). Dissepiments regular and herringbone. Strong thickening of inner wall remaining consistent irrespective of width of dissepimentarium.

Morphology of more advanced mature growth stage (Text-fig. 7I, J) similar to that described above. Further differentiation in length of major septa and connection of inner margins of several of them to longest major septa in all quadrants being the most important changes. Arrangement of adaxial margins of longest major septa in individual transverse sections varying. Cardinal septum remaining long, but squeezing of corallite and breaks of some major septa making its total length uncertain. Fragment of septum near corallite axis (Text-fig. 7J) may or may



not belong to the cardinal septum. Counter septum long, permanently reaching corallite axis, but its inner margin not thickened. Microstructure of septa described in the Considerations as an example of the state of preservation and diagenetic alterations.

INTRASPECIFIC VARIABILITY: All paratypes (Text-fig. 8A–H) resemble the holotype in their main diagnostic characters. However, their morphological similarity to each other is closer than to the holotype. Counter septum with inner margin thickened, dominates the remaining major septa and forms the most important difference of all paratypes from the holotype. Grouping of major septa around the major septum longest in each quadrant of septa less clearly accentuated in the paratypes than in the holotype. One of the paratypes (Text-fig. 8G) differs from all remaining specimens, holotype included, by the greater total length of the major septa with most approaching, but only three reaching the corallite axis. Moreover, the n:d value of that corallite (32:10.8 mm mean) differs from the holotype and the remaining paratypes (37:11.5 mm, 39:13.2 mm). Variety in diameters and n:d values may be due to incomplete-ness of corallites. Location of individual transverse sections against the specimen's growth stages and their shape (conical vs. cylindrical) remain unknown.

The very short remnants of the holotype specimen, left after transverse thin sectioning, preclude the making of a longitudinal section. Thus, the longitudinal section of the paratype (Text-fig. 8A) is accepted here as typical for the species despite being slightly eccentric and destroyed by squeezing in its axial part. Dissepiments strongly differentiated in size, arranged in steep rows. Very long, almost vertical dissepiments supplemented by much smaller, globose bubbles. Tabulae incomplete, elevated gently towards the corallite axis, thus resembling those in *Bothrophyllum*.

REMARKS: Since this species is selected as the type for the genus, the remaining species are compared to it. Two variants described below possibly represent two new species. They demonstrate some characters in common with *N. donetsiana*, but those similarities are not close enough to accept them as co-specific.

To distinguish them temporarily as variants of that species, but not formal subspecies, meets two targets: it avoids the creation of the multiplication of poorly represented taxa, and increases the morphological variability of the bothrophyllid taxa in the *Homoceras–Hudsonoceras* ammonoid Biozone.

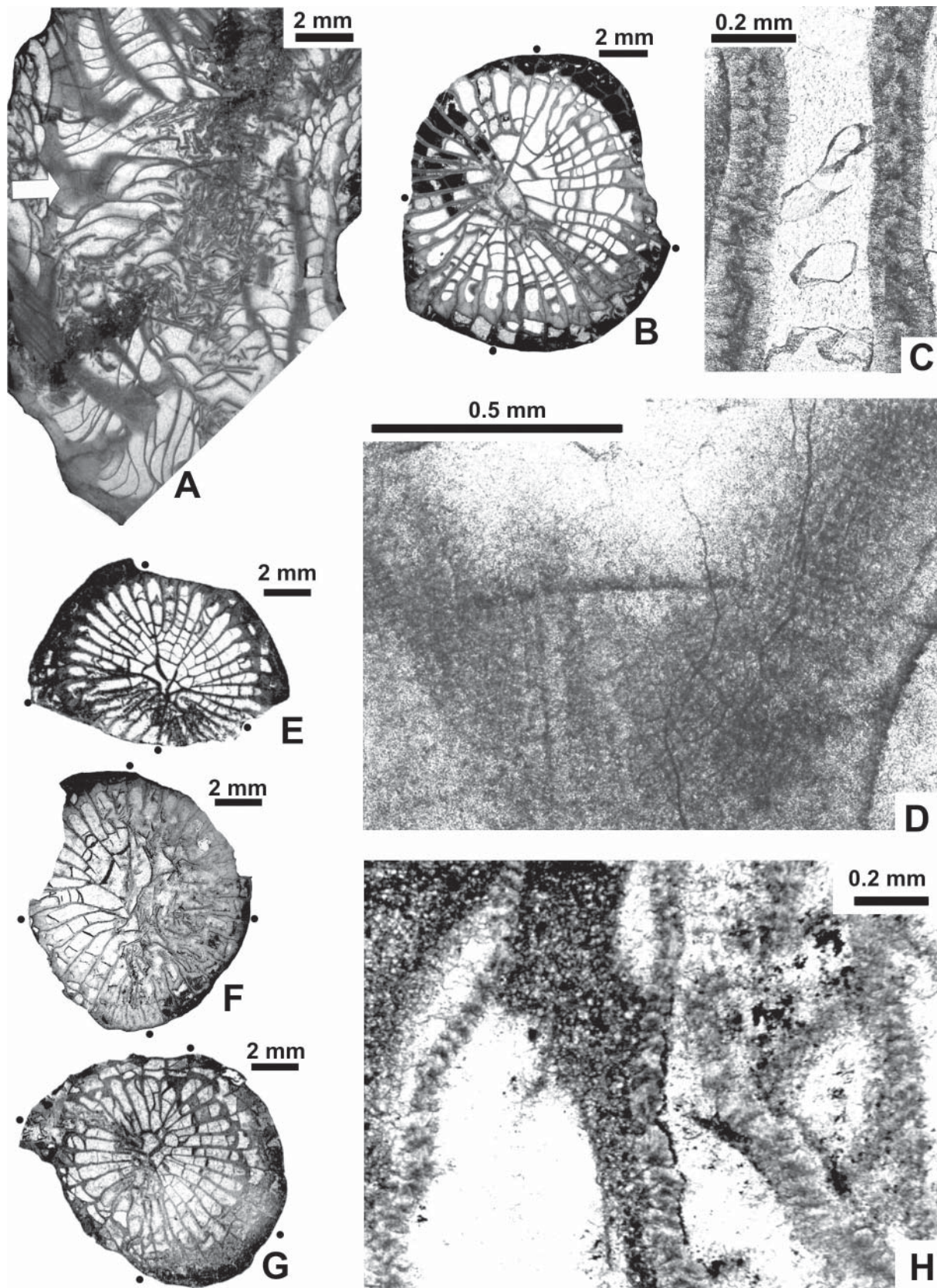
OCCURRENCE: As for the holotype.

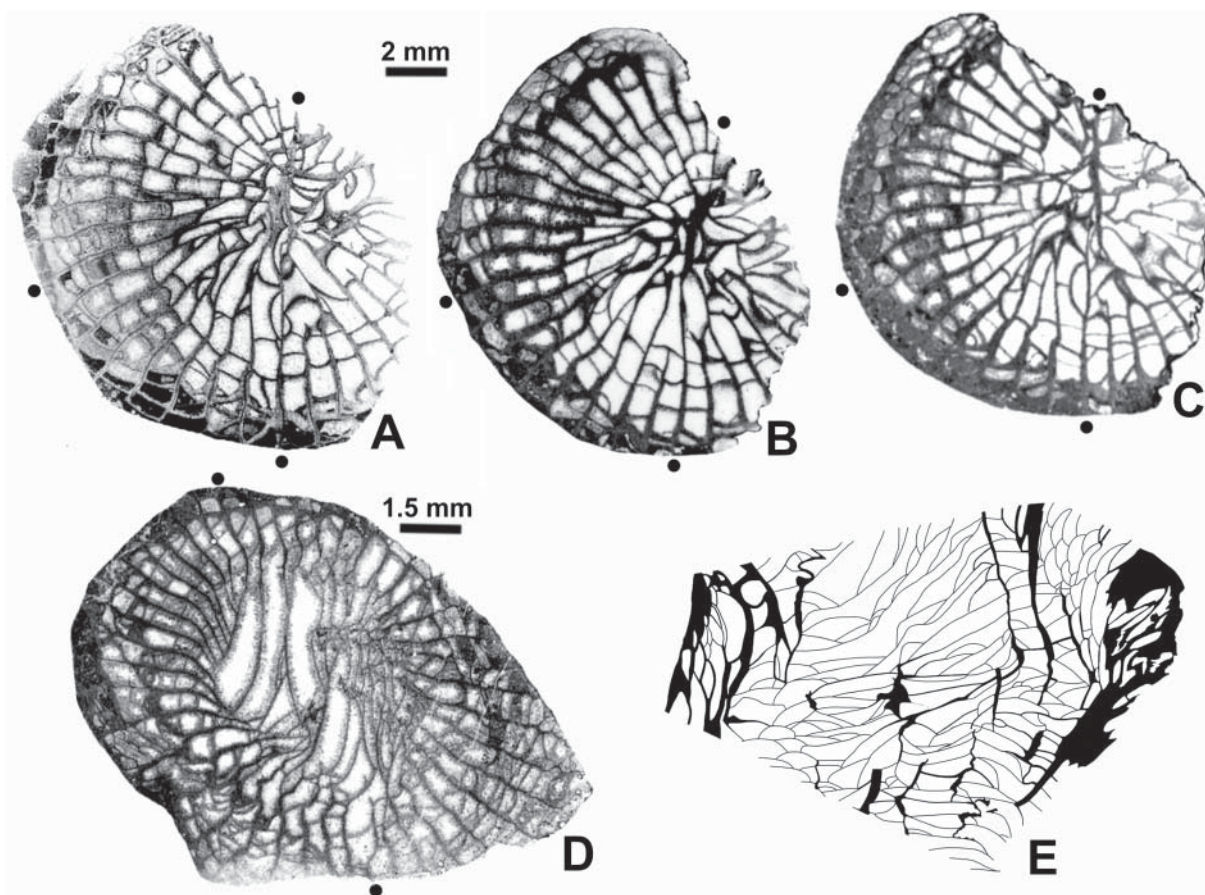
Variant 1 (Text-fig. 9). Specimen UAM-Tc/Don.1/122. Kalmyus River area, Amvrosievskiy Kupol, Nikolaevka Village, Limestone D6 (remaining data as for the holotype). Two thin sections and eight peels available for study. Corallite incomplete. Early growth stage lacking. In earliest preserved growth stage (Text-fig. 9A–C) with approximately 37 major septa at 15 mm in the largest corallite diameter preserved, major septa long, most approaching corallite's axial area, some meeting thickened axial septum (Text-fig. 9A, B) or inner part of very long counter septum when axial septum divides. Both protosepta very long at that growth stage (Text-fig. 9C). Counter septum extending well beyond corallite axis. Cardinal septum extending beyond inner margin of counter septum at its left side. Cardinal fossula absent. Minor septa appearing as short slats in peripheral part of dissepimentarium occupying approximately 1/5 corallite radius. Dissepiments mostly regular. Sclerenchymal coating of inner wall thin or absent.

Morphology changing greatly in upper part of corallite preserved (Text-fig. 9D) with n:d value of oblique section 43:18×14 mm (shorter diameter incomplete). Major septa thin, most of them shortened and equal in length, leaving an approximately 3×5 mm wide axial area free. All major septa, including protosepta, amplexoid. Immediately above tabulae surfaces major septa elongated as documented by their slats attached to transverse sections of tabulae. Below tabulae protosepta and alar septa equal in length to adjacent major septa. Cardinal fossula distinguishable. Minor septa restricted to most peripheral part of corallite. Dissepiments mostly regular.

In longitudinal section (Text-fig. 9E) dissepiments differentiated in size, longest where corallite curved, arranged in steep rows, vertical at inner dissepimentarium margin. Tabulae incomplete gently convex in

← Text-fig. 7. *Nina donetsiana* sp. nov. Specimen UAM-Tc/Don.1/119. Holotype. Transverse thin sections except when stated otherwise. A–D – early neanic growth stage (A – peel, B, D – drawings), E, F – late neanic growth stage; cardinal fossula well developed, G – axial area of C enlarged to document arrangement of inner margins of protosepta and longest major septa, H – early mature growth stage (drawing on picture taken from polished surface), I, J – mature growth stage; variety in arrangement of inner margins of septa in H–J, K – microstructure of septum and thick inner wall diagenetically altered; suspected remnants of trabeculae in primary septum (“dark middle line”). For stratigraphic position see text. Protosepta and alar septa marked by dots when recognizable. Scale bars common for two adjacent pictures are located between them, those corresponding to a given picture located in its upper right





Text-fig. 9. ?*Nina donetsiana* sp. nov. *Variant 1*. Specimen UAM-Tc/Don.1/122. Kalmyus River area. Amvrosievskiy Kupol, Nikolaevka Village, Limestone D₆ (for remaining data see holotype). Transverse sections except when stated otherwise. A-C – early mature growth stage, D – mature growth stage (A – thin section, B-D – peels), E – longitudinal section (peel with drawing). Protosepta and alar septa marked by dots when recognizable. Scale bar between A and B corresponds to all pictures except D

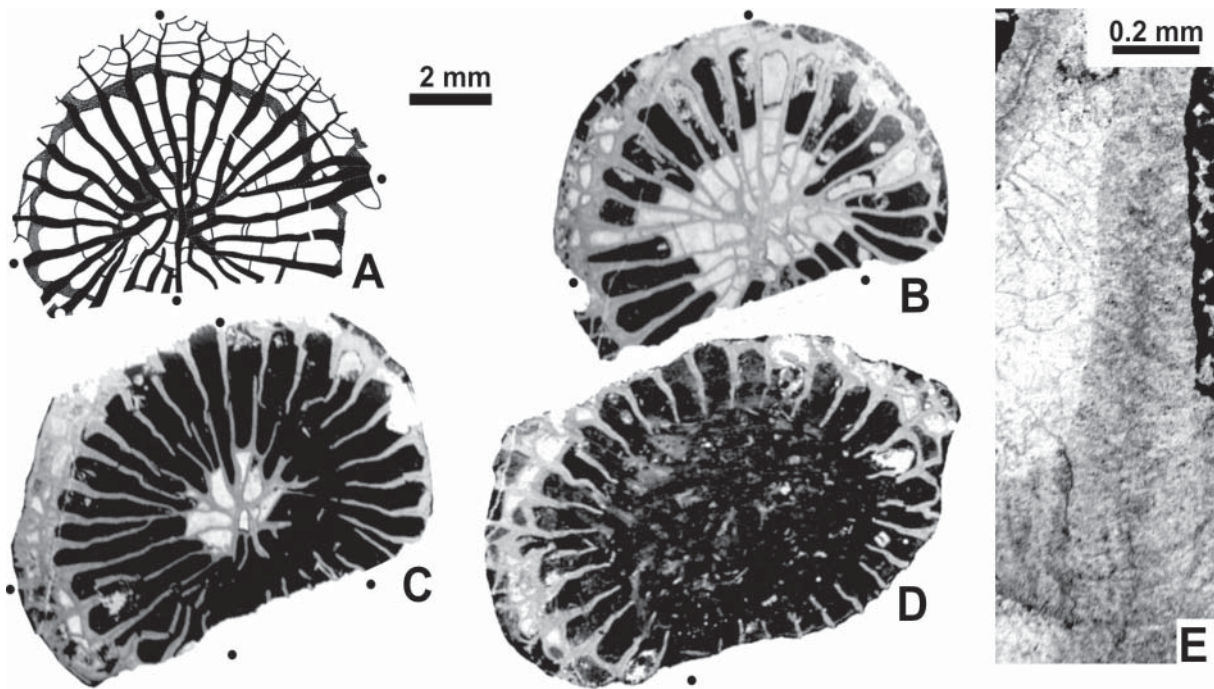
lower half of corallite, slightly concave in its upper part. Inner tabellae in lower part and most in upper part longer than peripheral tabellae; some peripheral tabellae dissepiment-like in shape.

Early mature growth stage of this variant resembling the paratypes of *N. donetsiana* in the great length and thickening of the inner margin of the counter septum. Extremely large length of its protosepta in the early mature growth stage distinguishes it from all specimens of that species. Equal shortening of all major septa in the advanced growth stage and rapid changes in shape of the tabulae, perhaps resulting from extrinsic factors, which affected the change of

corallite growth, and a larger number of major septa (43 vs. 36 in the holotype) forms additional distinguishing characters of the variant described.

Variant 2. (Text-fig. 10). Specimen UAM-Tc/Don. 1/123. Kalmyus River area, Voznesenka Village, Limestone D₇³ (remaining data as for the holotype). Two thin sections and four peels available for study. Peripheral fragment of calice, hosting cardinal septum and adjacent major septa broken apart, making length of cardinal septum in calice uncertain. Directly below calice floor (Text-fig. 10A) with n:d value approximately 30:9.5 mm, the major septa

← Text-fig. 8. *Nina donetsiana* sp. nov. Paratypes. A-D – Specimen UAM-Tc/Don.1/120. A – longitudinal thin section squeezed axially, B – transverse thin section, mature growth stage, C – transverse thin section; differentiated diagenetic alteration of microstructure in two adjacent major septa, D – longitudinal thin section, enlarged from B; everted fan of remnants of trabeculae perpendicular to growth lines that follow depression and axialward elevation of major septum (arrow in A). E – Specimen UAM-Tc/Don.1/121. Transverse thin section. Mature growth stage. F – Specimen UAM-Tc/Don.1/163. Transverse thin section. Mature growth stage. G, H – Specimen UAM-Tc/Don.1/162. G – Transverse section (peel). Mature growth stage, H – Transverse thin section. Microstructure of septa diagenetically altered. For stratigraphic position see text. Protosepta and alar septa marked by dots when recognizable. Scale bars correspond to individual pictures



Text-fig. 10. ?*Nina donetsiana* sp. nov. Variant 2. Specimen UAM-Tc/Don.1/123. Kalmyus River Area, Voznesenka Village, Limestone D₇³ (for remaining data see holotype). Transverse sections, mature growth stage. A – just below calice floor (peel with drawing), B – lower part of calice (thin section), C – middle part of calice (peel), D – upper part of calice (peel), E – microstructure of septum. Protosepta and alar septa marked by dots. Scale bar between A and B corresponds to all figures except E

differentiated in length, most inclined towards and grouped around longest middle septa in individual quadrants. Longest major septa meet axial septum. Minor septa corroded together with peripheral dissepimentarium. Most remaining dissepiments heringbone, some regular.

Identical arrangement of major septa lasting up to middle part of calice with axial part highly elevated (Text-fig. 10B, C) and with n:d value approximately 30:10 mm. Axial part of counter septum temporarily thickened (Text-fig. 10B). Length of cardinal septum uncertain. It may be already separated from counter septum. Very short minor septa recognizable in some loculi. Inner wall thickened by sclerenchyme up to middle part of calice. In upper part of calice with n:d value 32:14.0×7.8 mm (Text-fig. 10D), all major septa short, thin, equal in length except for shortened cardinal septum. Microstructure of septa diagenetically altered. Remnants of bunches of calcite fibrils recognizable in peripheral parts of some septa (Text-fig. 10E).

The variant described resembles *N. donetsiana sensu stricto* in the arrangement of major septa, very short minor septa and a narrow dissepimentarium. It differs in smaller dimensions, different n:d value, and, most important, in the grouping of major septa persisting up to the calice inclusively and the corallite's axial area elevated high above the peripheral parts of the calice.

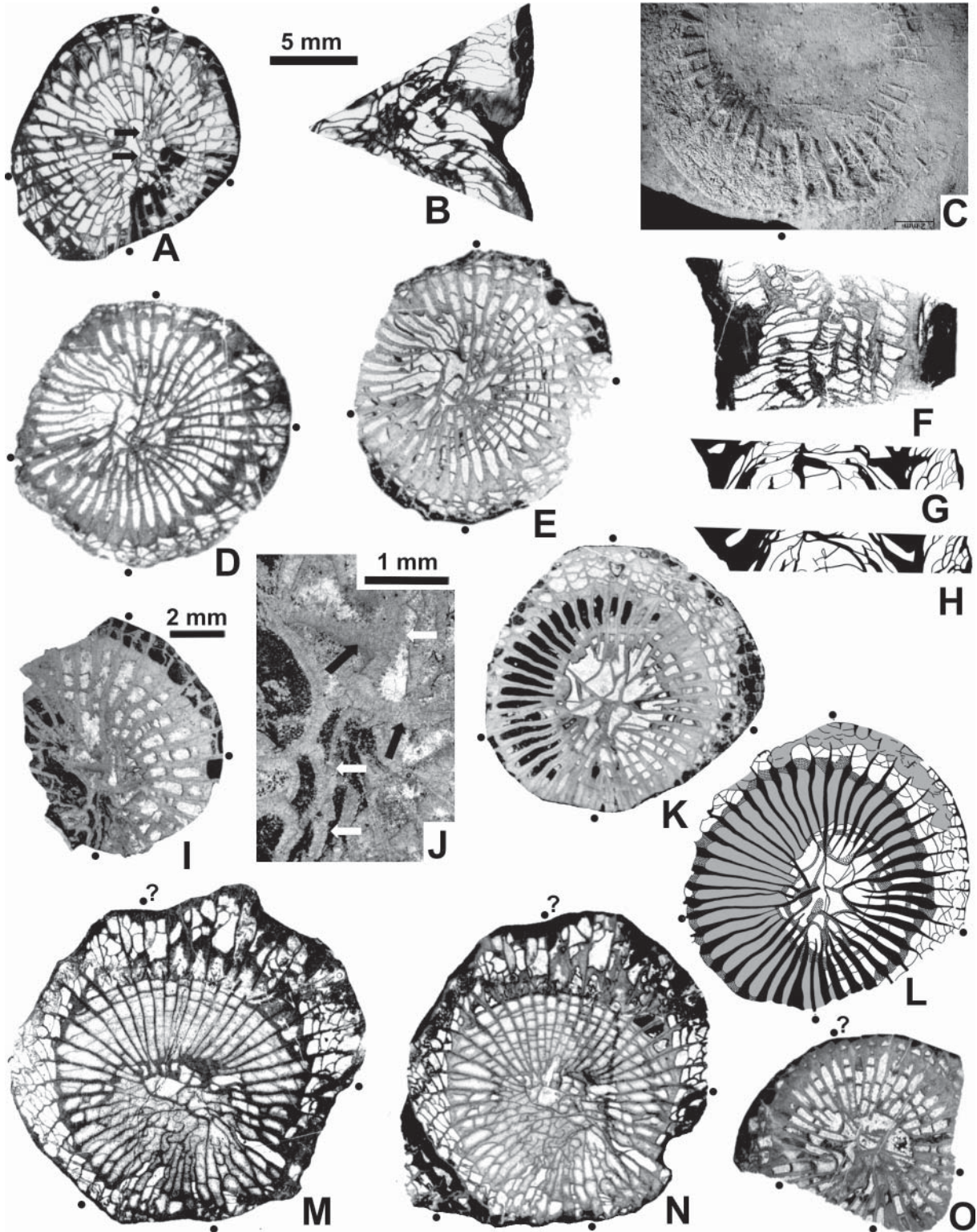
Nina berestovensis (Vassilyuk, 1960)
(Text-figs 11 and 12)

1960. *Bothrophyllum berestovensis* sp. nov.; Vassilyuk, p. 65, pl. 14, fig. 2.

1983. *Bothrophyllum berestovensis*; Vassilyuk in Aizenverg *et al.*, pl. 28, fig. 6.

MATERIAL: Holotype (restudied) No. 1405/6 preserved as a small corallite fragment of mature growth stage, supplemented by one transverse and one longi-

Text-fig. 11. *Nina berestovensis* (Vassilyuk, 1960). Transverse thin sections except when stated otherwise. A, B – Specimen no. 1405. Holotype. Housed in the Donetsk Polytechnic, Ukraine. A – mature growth stage; inner margins of protosepta marked by black arrows, B – longitudinal thin section (original of Vassilyuk 1960, pl. 14, fig. 2a, b). C-F – Specimen UAM-Tc/Don.1/124. Hypotype. C – upper part of weathered, incomplete calice, D, E – mature growth stage, F – longitudinal section. G-L – Specimen UAM-Tc/Don.1/125. Hypotype. G, H – longitudinal sections; G – centric, H – eccentric (both peels with drawings), I – early mature growth stage, J – axial area enlarged from I; lower white arrow →



points to fragmented cardinal septum with its inner margin meeting long major septum, upper white arrow points to axial part of counter septum; black arrows point to thickened axial parts of major septa longest in counter quadrants, K, L – mature growth stage; below calice floor in middle and right part left white (L – polished surface with drawing). M, N – Specimen UAM-Tc/Don.1/126. Hypotype. Mature growth stage, O – Specimen UAM-Tc/Don.1/127. Hypotype. Early mature growth stage. For stratigraphic position see text. Protosepta and alar septa marked by dots. Scale bar between A and B corresponds to all specimens except I and J

tudinal thin section (Vassilyuk 1960, pl. 14, fig. 2a, b; Text-fig. 11A, B). Hypotypes: Six incomplete, worn corallites Nos. UAM-Tc/Don.1/124–129. Only mature growth stages of all corallites available for study with incomplete calices preserved in two of them. Skeletons diagenetically altered. External surfaces and dissepimentaria often eroded and/or corroded. Some corallites flattened and partly crushed. Several badly crushed specimens, probably belonging to this species, supplement this study without being numbered and mentioned in description. 16 thin sections and 20 peels available for study.

EMENDED DIAGNOSIS: *Nina* with n:d value 44:13.2 mm (holotype) up to 50:21.0 mm (largest hypotype); major septa thin, slightly thickened near the inner wall, closely approaching, rarely meeting corallite axis; cardinal septum hardly distinguishable; cardinal fossula indistinct or absent; minor septa restricted to most peripheral part of dissepimentarium that reaches up to 1/3 corallite radius, commonly less.

DESCRIPTION: Large variability of morphological characters. Protosepta long in all corallites studied, including holotype (Text-fig. 11A). Vassilyuk (1960, p. 65) considered cardinal septum short. However, she misidentified underdeveloped major septum left of cardinal septum with the latter. That short septum and two short major septa right of cardinal septum support new interpretation. Cardinal septum in holotype approaching corallite axis without meeting long, thin counter septum (Text-fig. 11A, lower and upper arrows, respectively). Protosepta in mature growth stage of most hypotypes permanently separated from one another (Text-fig. 11I–O), but temporarily meeting in some (Text-figs 11D, E; 12D, E). Close approaching of protosepta to one another may in part result from squeezing (Text-fig. 12C). In some growth stages of specimen UAM-Tc.Doc.1/125 (Text-fig. 11I, J) protosepta meeting axial margins of the longest major septa.

Major septa arranged almost radially (Text-fig. 11A, K, L) with some irregularities such as their increased density in some corallite fragments, accompanied by undulation (Text-fig. 11M, N, lower left) or reduced thickness and length (Text-figs 11D, E; 12D, both left). Most major septa thin and straight with their parts next to dissepimentarium slightly (Text-figs 11A, M, N; 12A, D) to greatly (Text-fig. 11D, E) thickened. Greater thickening in these parts of septa accompanied by greater thickening of inner wall; in other parts rather thin. Dissepimental parts of major septa thin, slightly undulated in some corallites.

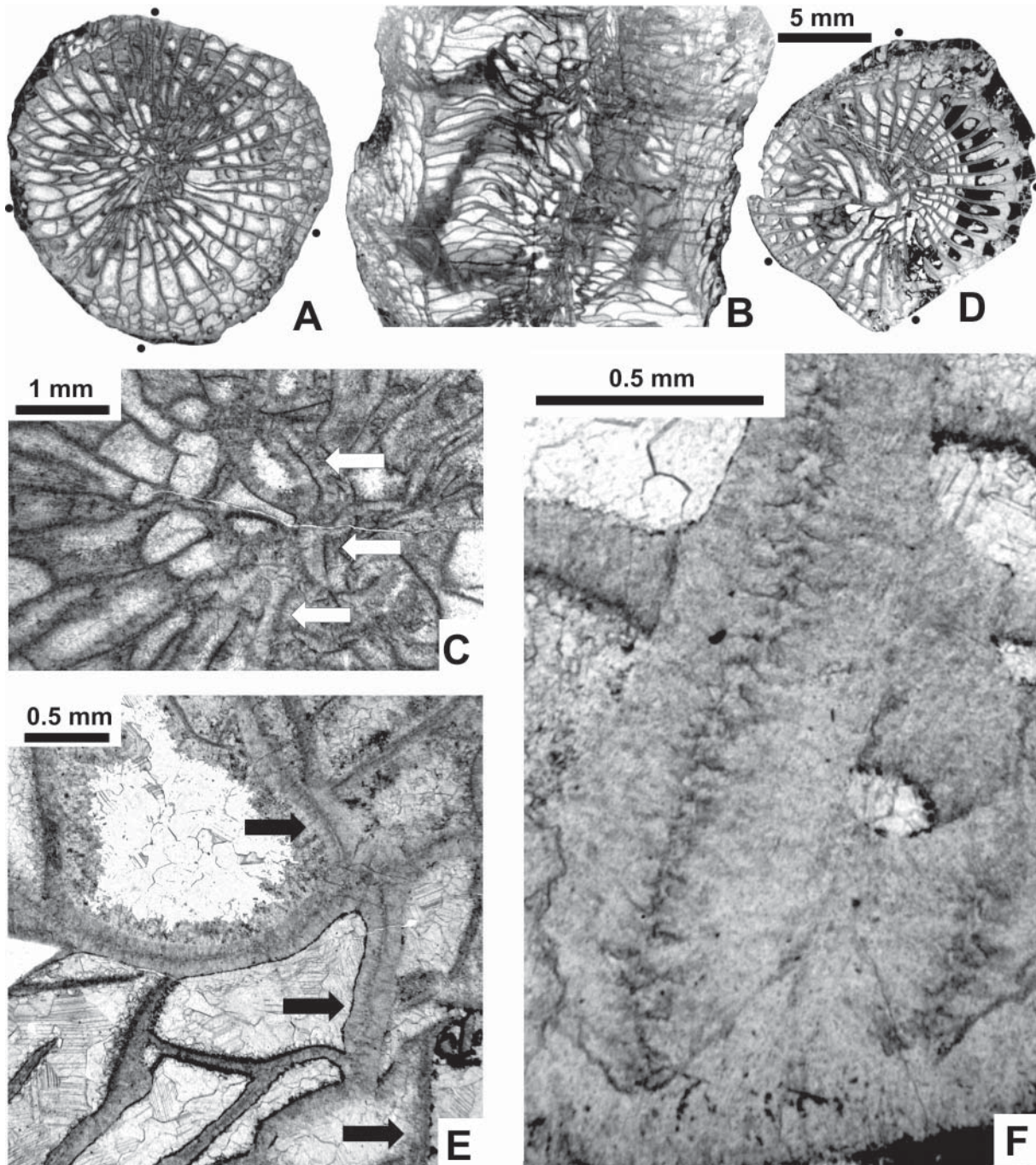
Minor septa thin, restricted to peripheral dissepimentarium; not recognizable from some septal loculi (Text-fig. 11M, lower left). Microstructure of septa destroyed by recrystallization; may have been finely trabecular as suggested by arrangement of crystalline fibrils within primary septa (Text-fig. 12F).

Occurrence of cardinal fossula in holotype uncertain (dissepimentarium eroded). In hypotypes cardinal septal fossula recognizable (Text-fig. 11L, N) or absent (Text-fig. 11D, E). Tabular, i.e., true cardinal fossula perhaps absent as documented by lack of its dipping into dissepimentarium in all better preserved fragments of corallites and in calice (Text-figs 11C–E, M; 12A).

Dissepimentarium in transverse sections varying in width from 1/6 corallite radius during earliest growth stages available for study to 1/4 in mature parts. Wider dissepimentarium apparent, resulting from obliqueness of sections (Text-fig. 11M, N, upper). Dissepiments mostly regular. Herringbone and/or irregular dissepiments only in widest dissepimentaria. In longitudinal section tabulae incomplete, generally dome-shaped, elevated indistinctly in some and strongly in other corallites (Text-fig. 11F vs. Text-fig. 11G, H, respectively); tabulae in holotype s-shaped at periphery (Text-fig. 11B). Inner tabellae elevated towards section of elongated counter septum. Dissepiments differentiated in size, arranged in steep rows. Inner row almost vertical. Inner wall thickened.

REMARKS: The very incomplete holotype of *Bothrophyllum berestovensis* is the only specimen derived from the uppermost Serpukhovian Limestone D₅³ (Vassilyuk 1960, p. 66). All other specimens included by her in that species were collected from the lowermost Bashkirian strata. The transverse thin section of one specimen, collected from the Limestone D₇³, was illustrated by Vassilyuk (in Aizenverg *et al.* 1983, pl. 28, fig. 6), but not described. Its morphology resembles the holotype. The remaining specimens derived from the Limestone D₇³, described herein, belong to the original collection of Vassilyuk (1960). Unfortunately, they have not been specified by numbers allowing their recognition as paratypes. Thus, they are described here as hypotypes.

Vassilyuk (1960) did not distinguish between the morphology of the holotype and the paratypes. This would not be important if: a) the holotype was derived from the early Bashkirian strata as were the remaining specimens; and b) the particular specimens were pointed out and illustrated by her as demonstrating the characters described. Unfortunately, none of



Text-fig. 12. *Nina berestovenski* (Vassilyuk, 1960). A-C – Specimen UAM-Tc/Don.1/128. Hypotype. A – transverse thin section, mature growth stage, B – longitudinal thin section, C – corallite axial area enlarged from A; lower arrow points to inner margin of cardinal septum, two upper arrows point to fragmented inner margin of counter septum. D-F – Specimen UAM-Tc/Don.1/129. Hypotype. D – transverse thin section, mature growth stage, E – corallite axial area enlarged from D; two lower arrows point to fragmented inner margin of cardinal septum, upper arrow points to inner margin of counter septum, F – diagenetically altered microstructure of major (left) and minor (right) septa and their connection to external wall. For stratigraphic position see text. Protosepta and alar septa marked by dots. Scale bar between B and D corresponds to figures A, B, D; that corresponding to given picture located in its upper left

these preconditions were fulfilled, whereas several characters of the Bashkirian specimens differ from the holotype. The wide morphological variability of

the specimens suggest a possibly different taxonomic status at the species level for some of them. However, a formal introduction of new species, based on such

restricted and incomplete material, is considered unwise. Several characters either omitted by Vassilyuk (1960) from the description, or interpreted by her in a way different from the results of this study, makes the emendation of her diagnosis necessary. This first of all concerns the length of the cardinal septum in the holotype and the hypotypes. It is not shortened, as she wrote, but permanently long above the calice floor. My evaluation of the shortening *versus* the permanent elongation of the cardinal and the counter septa is discussed in the revision of the genus *Bothrophyllum* (Fedorowski 2016) and is not repeated herein. Much earlier those characters were accepted by Fomichev (1953) as the major criteria for distinguishing separate genera and subgenera among the bothrophyllid corals.

N. berestovensis differs from *N. donetsiana* sp. nov. in having a larger diameter of the corallites and a larger number of the septa, in the poorly developed grouping of major septa in most quadrants of septa, and in the cardinal fossula being either absent or very inconspicuous. All those characters together form a set of features making the transfer of *B. berestovensis* to *Nina* questionable. However, its direct relationship to *B. conicum* is much less probable, therefore the creation of a new genus or subgenus, based on such an incomplete material is not reasonable.

OCCURRENCE: All specimens from the Kalmyus River area. Holotype 1405: Voznesenka Village, Limestone D₅³, upper Zapaltyubinskian Substage, Suite C₁^s_f. Latest Serpukhovian. Hypotype UAM-Tc/Don.1/128: Amvrosievskiy Kupol, Nikolaevka Village, Limestone D₆. Remaining hypotypes: Voznesenka Village, Limestone D₇³. All hypotypes from the Voznesenskian Substage, Suite C₁^s_g, *Plectostaffella bogdanovkensis* foraminiferal Biozone, *Declinognathodus noduliferus* conodont Biozone, *Homoceras–Hudsonoceras* ammonoid Biozone. Earliest Bashkirian.

Nina dibimitaria sp. nov.
(Text-figs 13 and 14)

HOLOTYPE: Specimen UAM-Tc/Don.1/130.

TYPE LOCALITY: Kalmyus River Area. Voznesenka Village.

TYPE HORIZON: Limestone D₇³. Voznesenskian Substage, Suite C₁^s_g. *Plectostaffella bogdanovkensis* foraminiferal Biozone, *Declinognathodus noduliferus*

conodont Biozone, *Homoceras–Hudsonoceras* ammonoid Biozone, earliest Bashkirian.

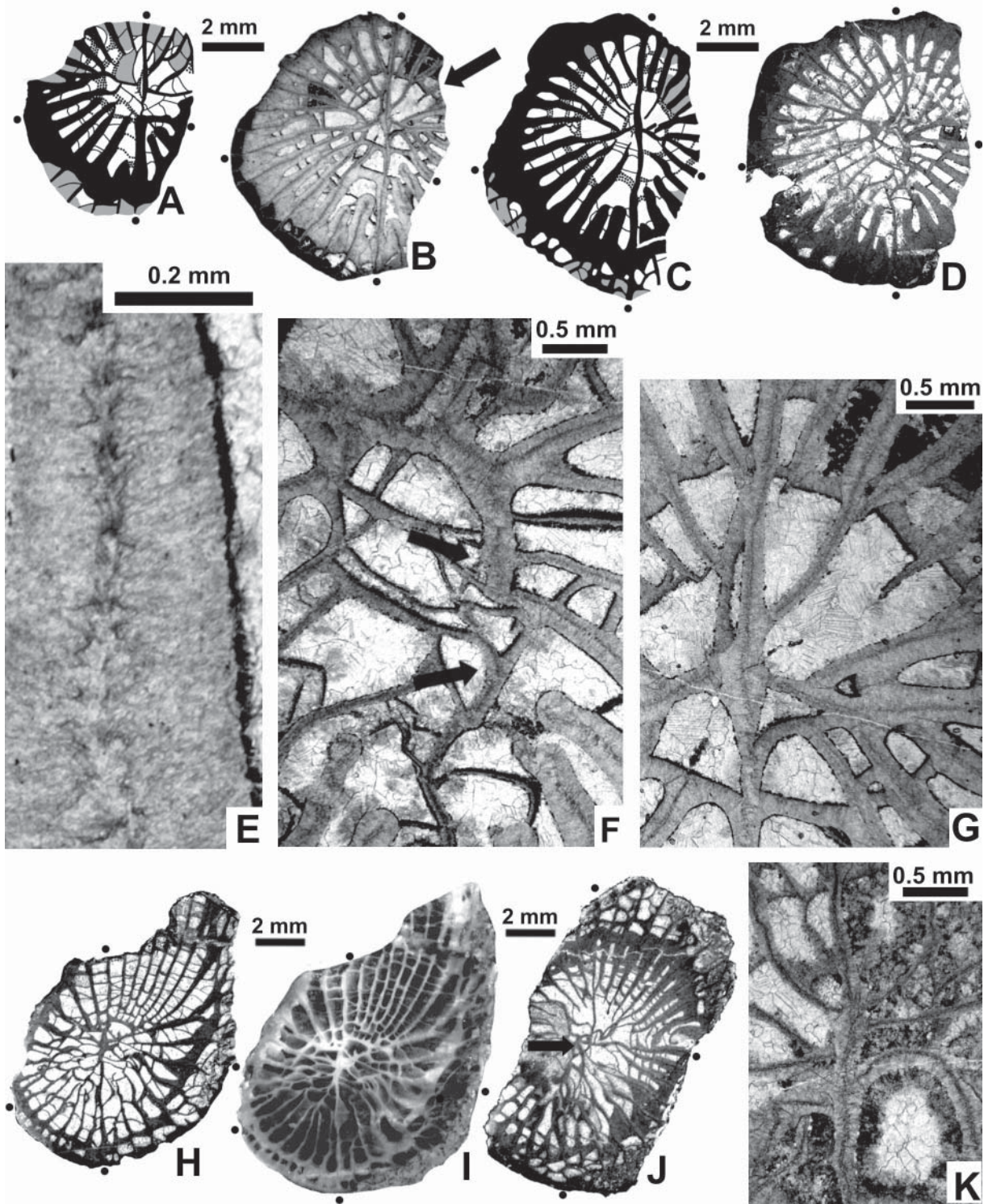
ETYMOLOGY: Name composed of first syllable of the genus *Dibunophyllum* Thomson and Nicholson, 1876 and *lat. imitari* – to imitate, to copy – after the similarity to *Dibunophyllum* in the early growth stages seen in transverse section.

DIAGNOSIS: *Nina* with n:d value 34:10.5 mm (holotype), 29:9.0 mm to 36:14.2 mm (paratypes); strong axial septum lasting to early maturity or longer; cardinal and counter septa remaining very long when separated; cardinal fossula well developed; minor septa short; dissepimentarium 1/5–1/4 corallite radius wide.

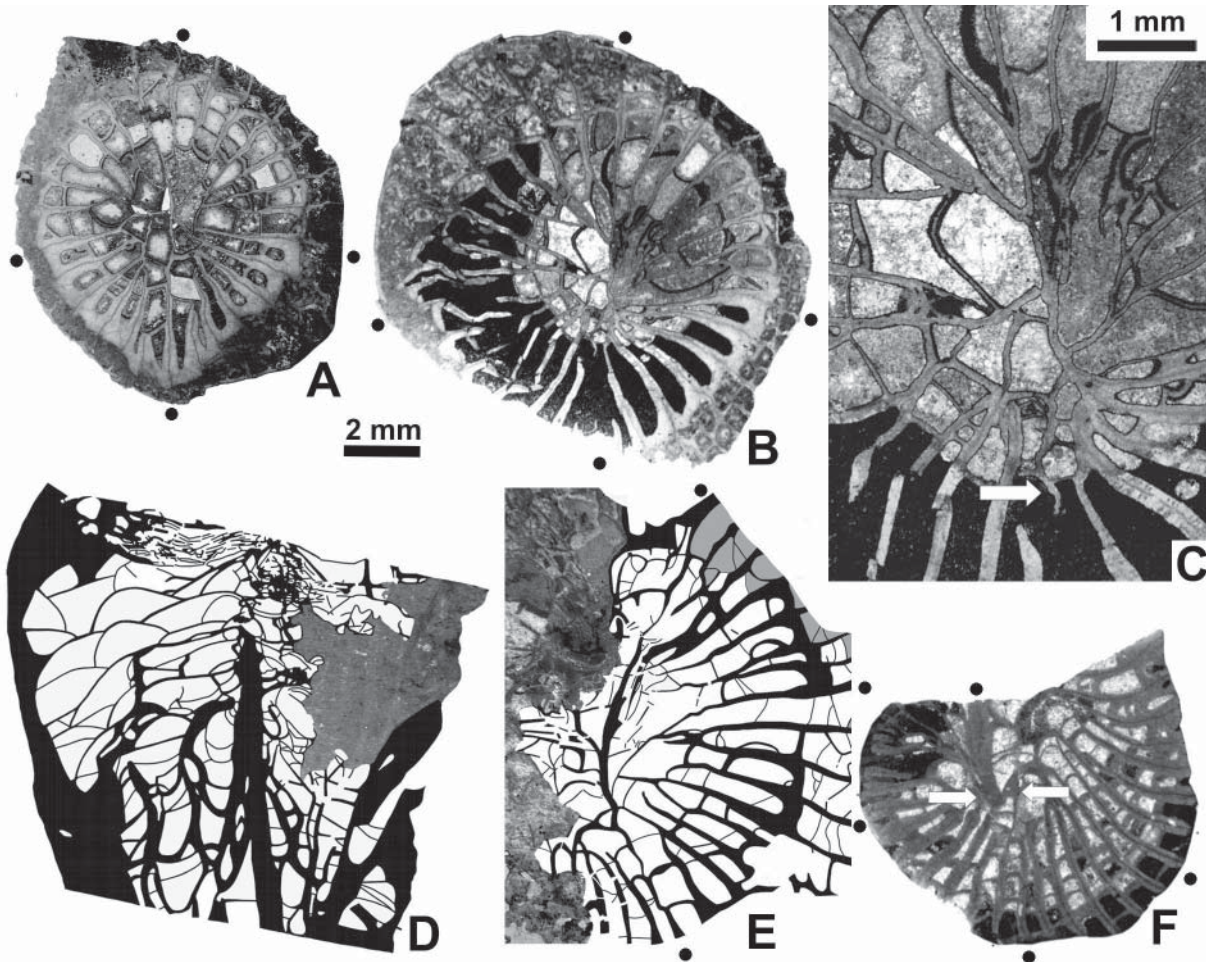
MATERIAL: Five incomplete specimens. Holotype UAM-Tc/Don.1/130. Paratypes: UAM-Tc/Don.1/131–133, 136. Corallites fragmented, partly squeezed. Thus only one longitudinal thin section from partly preserved corallite UAM-Tc/Don.1/136 could be made. Eight thin sections and 15 peels available for study.

DESCRIPTION OF HOLOTYPE: Late neanic to early mature growth stage (Text-fig. 13A–C) resembling comparable growth stages of some Serpukhovian dibunophyllids from the Donets Basin (Fedorowski in press): two last pairs of major septa in cardinal quadrants underdeveloped, whereas inner margins of at least two other major septa attached to strong axial septum (Text-fig. 13G). In mature growth stage (Text-fig. 13D) both protosepta closely approaching corallite axis. Wavy, thin inner margin of cardinal septum closely approaching but does not meeting thick, curved inner margin of counter septum. Both protosepta meeting inner margin of long major septum at a distance of approximately 0.1 mm from one another (Text-fig. 13F, lower and upper arrow, respectively). Inner margins of major septa differentiated in length, shape and arrangement (Text-fig. 13D, F). Last pair of major septa adjacent to cardinal septum remaining underdeveloped to mark cardinal septal fossula. Occurrence of tabular fossula indicated by slight dipping into dissepimentarium, recognizable starting from late neanic/early mature

Text-fig. 13. *Nina dibimitaria* sp. nov. Transverse sections. A–G – Specimen UAM-Tc/Don.1/130. Holotype. A–C – late neanic to early mature growth stage (A, C peels with drawings), D – mature growth stage, E – advanced diagenetic alteration of microstructure of major septum, F – enlarged axial part of D; lower arrow points to inner margin of cardinal septum, upper arrow points to thick septal body: either axial extension of counter septum, or longest major →



septum of left counter quadrant, G – fragment of B (arrow) enlarged to demonstrate strong axial septum and peculiar, fossula imitating arrangement of major septa. H-J – Specimen UAM-Tc/Don.1/131. Paratype. Mature growth stage; arrow in J points to inner margin of cardinal septum (H, J – peels, I – polished surface). K – Specimen UAM-Tc/Don.1/132. Paratype. Axial area of corallite enlarged to demonstrate strong axial septum and differentiation in length of major septa. For stratigraphic position see text. Protosepta and alar septa marked by dots when recognizable; in enlarged images not marked. Scale bar between two pictures corresponds to both, bar corresponding to a given picture located in its upper right



Text-fig. 14. *Nina dibimitaria* sp. nov. Paratypes. Transverse thin sections except when stated otherwise. A-C – Specimen UAM-Tc/Don.1/133. A – early mature growth stage, B – mature growth stage; above calice floor except circumaxial and upper right (whitish infillings), C – axial area enlarged from B to show extremely long counter septum entering cardinal fossula. D-K – Specimen UAM-Tc/Don.1/136. D – longitudinal section, E – mature growth stage, squeezed in part; axial septum thickened in middle part, F – early mature growth stage (peel); arrows point to extremely long cardinal (right) and counter (left) septa, (D, E – peels with drawings). For stratigraphic position see text. Protosepta and alar septa marked by dots when recognizable. Scale bar between A and B corresponds to all images except C

growth stage (Text-fig. 13A) and onwards. Strange arrangement of major septa emphasized by development of cardinal fossula-like and cardinal septum-like structure in right counter quadrant (Text-fig. 13G, upper right). Microstructure of septa destroyed by advanced diagenesis (Text-fig. 13E). Dissepimentarium incomplete, herringbone when present. Inner wall strong, composed of thickened major septa, supplemented by sclerenchymal thickenings of inner dissepiments. Minor septa either absent or very short; destroyed by erosion.

Fragments of corallite left after transverse thin sectioning too short for longitudinal section. However, lack of densely packed sections of axial tabellae in transverse sections, typical for dibunophyllid corals, allow one to exclude the occurrence

of an axial column. Longitudinal section of paratype derived from type locality and type horizon (Text-fig. 14K) accepted as typical for the species. Strong, thick rod in ontogenetically younger part of corallite corresponding to axial septum. Abrupt thinning of that rod and its apparent disappearance from upper part of section resulting from corallite curvature. Transverse section made above longitudinal section (Text-fig. 14J) proving constant occurrence of axial septum. Tabulae incomplete, assembled from convex bubble-like tabellae at periphery and more flat tabellae in axial corallite part. Axial column absent. Arrangement of tabulae typical of the Bothrophyllidae, and similar to that in *Bothrophyllum conicum* (Fischer von Waldheim, 1830=1837).

INTRASPECIFIC VARIABILITY: In the early mature growth stage of two paratypes, both derived from the type locality (Text-fig. 13H, I, K), axial septa thin, but easily recognizable. Early growth stage of one paratype, also derived from the type locality (Text-fig. 14F) differs from comparable growth stage of all remaining specimens by having counter and cardinal septa separated. Inner margin of cardinal septum reaches corallite axis, whereas strongly thickened inner margin of counter septum extends almost to cardinal fossula (Text-fig. 14I, right and left arrows respectively). This kind of temporary separation of protosepta is interpreted here as a result of their too large elongation. Similar arrangement of inner margins of protosepta occurs in mature growth stage of another paratype. Inner margins of protosepta in that corallite do not meet, but extend parallel to one another for a distance of approximately 0.3 mm (Text-fig. 13J, arrow). Cardinal septum in this paratype varies in thickness along its length with middle part very thin, hardly distinguishable from sections of tabulae, but with peripheral and inner margins thickened. That paratype differs from remaining specimens in strong thickening of major septa in right cardinal and right counter quadrant, making it asymmetrical. Also, it differs by a distinctly sequential shortening of the major septa in right counter quadrant and by cardinal fossula hardly recognizable or absent (Text-fig. 13J). Axial septum, thin and twisted in early mature growth stage of paratype derived from younger strata (Limestone E₁) (Text-fig. 14A) resembles inner margins of cardinal and counter septa in holotype, but differs from axial septum in comparable growth stage of other paratypes. Mature growth stage of that paratype, with n:d value 32:13.0×11.0 mm (diameter incomplete), resembles the mature growth stage of the holotype in the arrangement of major septa. Immediately above calice floor, cardinal septum shortened (Text-fig. 14B, C), but its very long counter septum penetrating distinct cardinal septal fossula, suggesting occurrence of axial septum until very advanced ontogeny.

REMARKS: *Nina dibimitaria* differs from the type species and from the remaining species described in this paper in possessing an axial septum either permanent or with cardinal and counter septa almost in contact with each other (see above). The morphology in transverse thin sections of the early growth stages of this species makes it similar to the genus *Dibunophyllum*, as suggested by its name. However, the continuous axial column, i.e., the main diagnostic character of *Dibunophyllum* is absent in *N. dibimitaria* as documented by the longitudinal section.

Besides, the occurrence of the axial column can be deduced in transverse sections from densely packed sections of tabellae near the corallite axis, contrasting to their loosely arranged sections at the peripheral tabularium. Nothing like that is observed in the transverse sections of the corallites identified here as *N. dibimitaria*.

The long lasting thickening of the axial septum, resulting in the formation of a rod-like body, is similar in longitudinal section to the pseudocolumella of the genus *Koninckophyllum* Thomson and Nicholson, 1876. However, the structure and arrangement of tabulae in *N. dibimitaria* differ from those in *Koninckophyllum*. The similarity of *N. dibimitaria* to the Subfamily Dibunophyllinae Wang, 1950 is discussed in the Considerations below.

OCCURRENCE: For occurrence of the holotype see above. Paratypes UAM-Tc/Don.1/131, 132 and 136 the same occurrence as the holotype. Paratype UAM-Tc/Don.1/133 Krynka River Area, Amvrosievskiy Kupol, Limestone E₁^{verkh.}. Lowermost Feninian Substage, Suite C₂^b_{a nizhn.} *Semistaffella variabilis*–*S. minuscularia* foraminiferal Biozone, *Idiognathoides sinuatus* conodont Biozone, *Reticuloceras*–*Bashkortoceras* ammonoid Biozone. All specimens from the early Bashkirian.

Nina magna sp. nov.
(Text-figs 15 and 16)

1983. *Neokoninckophyllum nipponense* Kato; Vassilyuk in Aizenverg *et al.*, pl. 28, fig. 8.

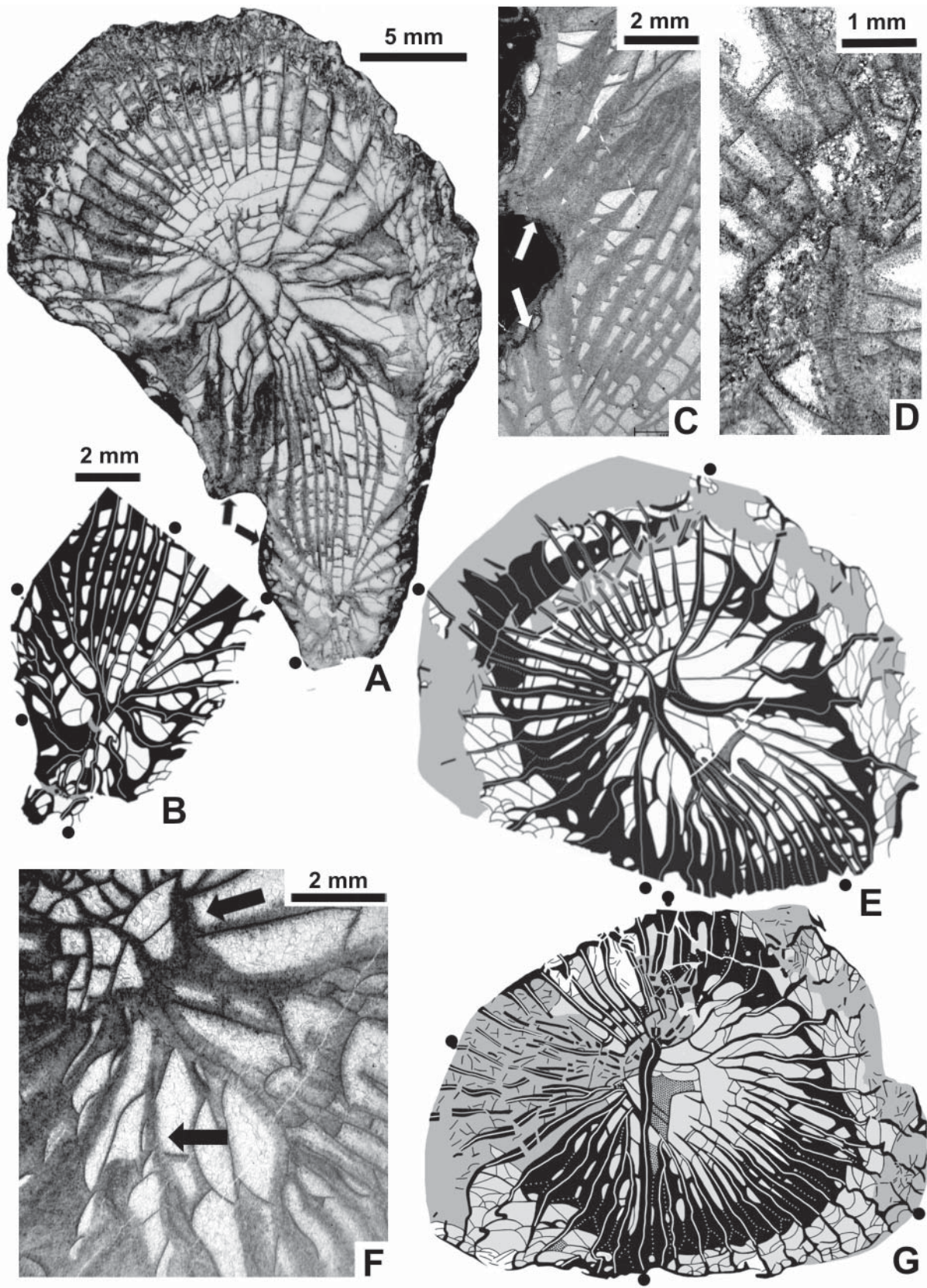
HOLOTYPE: Specimen UAM-Tc/Don.1/137.

TYPE LOCALITY: Kalmyus River Area. Voznesenka Village.

TYPE HORIZON: Limestone D₇⁵. Lower Voznesenskian Substage. Suite C₁^s_{g.} *Plectostaffella bogdanovkensis* foraminiferal Biozone, *Declinognathodus noduliferus* conodont Biozone, *Homoceras*–*Hudsonoceras* ammonoid Biozone, earliest Bashkirian.

ETYMOLOGY: *Lat. magnus, a, um* – large; after the size of the corallites being larger than other representatives of the genus described so far.

DIAGNOSIS: *Nina* with n:d value 46:24×18 mm (holotype) to 53:23×21 mm (largest paratype); major septa closely approaching corallite axis, their tabu-



larium/dissepimentarium boundary parts thick, inner margins tapering; protosepta may be separated in advanced maturity; cardinal septum dominating when axial septum divides; minor septa restricted to outermost periphery; cardinal fossula well developed.

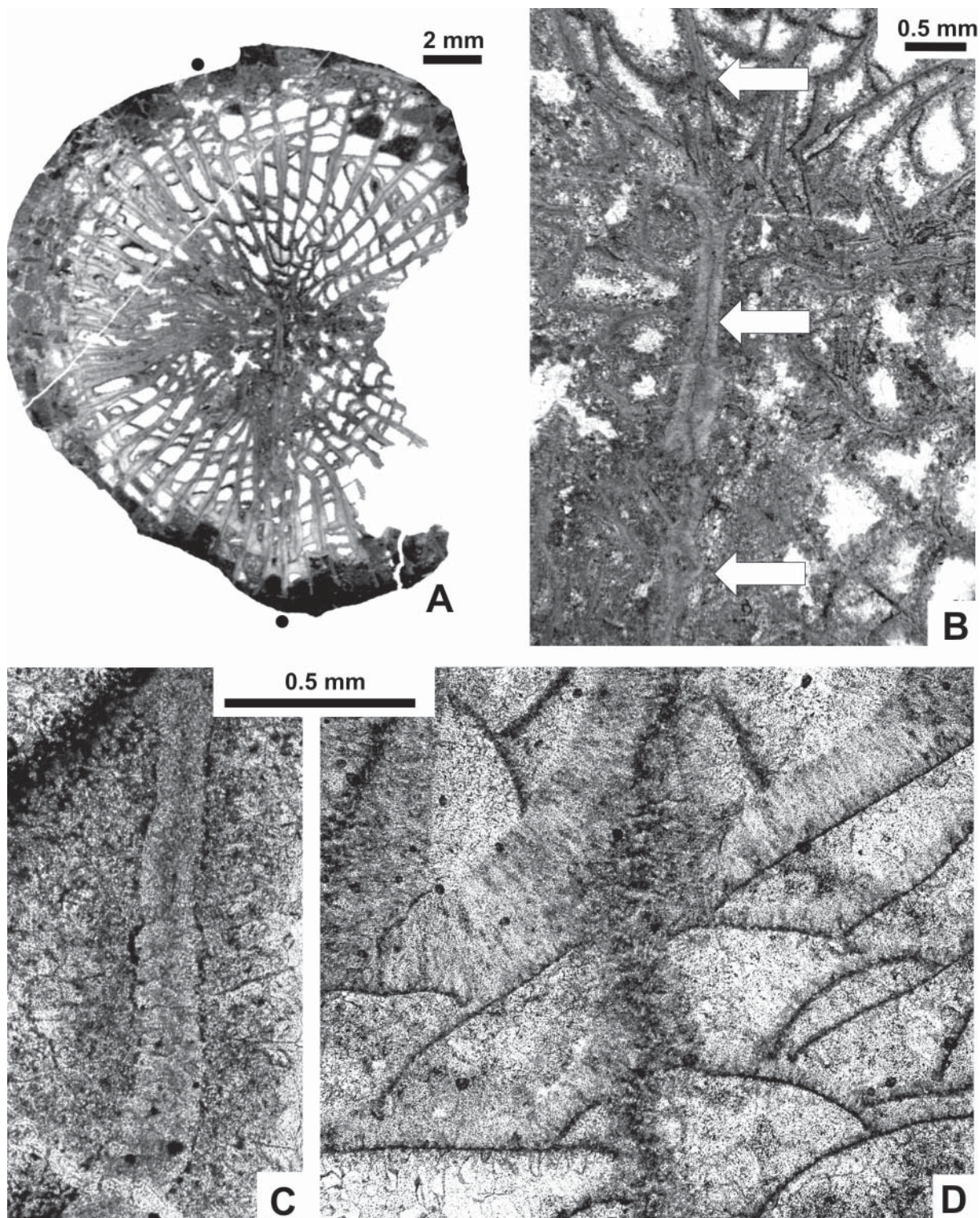
MATERIAL: Holotype UAM-Tc/Don.1/137 represented by three thin sections with no rock material left. One oblique thin section of curved holotype incidental (Text-fig. 15A). Those of more advanced growth stage (Text-fig. 15B, C) oriented better. Seven paratypes Nos. UAM-Tc/Don.1/138–144. All specimens fragmented, partly eroded. Their axial and/or peripheral parts crushed to various extent, but main diagnostic features recognizable in all specimens. Squeezing and erosion make their true diameters unknown; always larger than mentioned in diagnosis and description based on measurements of preserved fragments.

DESCRIPTION OF HOLOTYPE: Oblique section showing both neanic and early mature growth stages (Text-fig. 15A, lower and upper respectively) with oblique longitudinal section in the middle. Obliqueness of section resulting in different growth stages exposed: left cardinal and left counter quadrant, ontogenetically more advanced than quadrants in lower right part of pictures (Text-fig. 15A, lower, B). These representing advanced neanic growth stage and early neanic growth stage, respectively. Major septa in cardinal quadrants zaphrentoidally arranged, successively reduced in length from long alar septa towards long cardinal septum; seven major septa in left, four in right quadrant. (Text-fig. 15B, upper left; orientation as in A). Zaphrentoidal arrangement and direct connection of inner margins of seven major septa in left counter quadrant well demonstrated; only counter-lateral septum in that quadrant separated from remaining major septa. Right counter quadrant poorly preserved, consisting perhaps of three major septa. Cardinal septum, located in distinct key-hole cardinal fossula, extends to corallite axis. Its connection with long, thin counter septum broken. However, inner margins of protosepta with their “middle dark lines” pointing towards one another, suggesting presence of axial septum.

Obliqueness of thin sections, reduced sequentially (Text-fig. 15A, E, G), camouflaging some details of morphology. This concerns disappearance of axial septum. Cardinal and counter septa remaining long (counter septum longer), but inner margins of both attached to major septa longest in left cardinal and counter quadrants (Text-fig. 15E, F). Direct connection of some of those longest major septa imitating axial septum. Most major septa, except for cardinal, counter and longest major septa in quadrants thin-ended, staying off corallite axis, leaving axial area almost free. All major septa greatly thickened at tabularium / dissepimentarium boundary. Cardinal fossula well developed beginning in early mature growth stage. Its “separate” occurrence in two areas of one thin section (Text-fig. 15A and C, arrows) apparent, resulting from curvature of corallite and position of cardinal septum on concave side of corallite.

Near calice floor (Text-fig. 15G) with n:d value 46:24×18 mm (diameter reduced by corrosion), major septa irregularly differentiated in length and shape. Most similar to those in earlier growth stage, but some thin. Left sector occupied by those thin septa squeezed (Text-fig. 15G, left, shadowed). Cardinal septum strongly dominating in length and thickness, intersecting corallite axis and probably meeting counter septum as indicated by small, thick septal remnant attached to its inner margin (Text-fig. 15D). Middle major septum in right cardinal quadrant equal to other major septa in length. Elongation of middle major septa in remaining quadrants and inclination of other major septa towards them hardly recognizable. Minor septa thin, seldom crossing more than two rows of dissepiments. Not seen when peripheral dissepimentarium destroyed. Middle part of oblique section (Text-fig. 15A) allowing one to establish the main characters of tabularium and dissepimentarium. Tabulae incomplete, consist of convex tabellae, elevated axial-wards at low angle. No axial structure present. Short minor septa suggesting normal tabularium, whereas major septa contiguous laterally near dissepimentarium border in most loculi and thick inner wall present in remaining loculi, suggesting absence of distabularium. Best preserved fragments of dissepimentarium occupying approximately 1/5 corallite radius. Dissepiments regular, irregular and pseudo herringbone. In oblique longitudinal section

← Text-fig. 15. *Nina magna* sp. nov. Specimen UAM-Tc/Don.1/137. Holotype. A – oblique thin section exposed by random cut of rock; cardinal septum marked by arrows, B – neanic growth stage (lower part of A, enlarged; drawing), C – cardinal septum (arrows) at corallite concave side (enlarged from A), D – axial part of thick, long cardinal septum (enlarged from G), E – slightly oblique thin section succeeding A, mature growth stage, F – axial part of corallite (enlarged from E; protosepta indicated by arrows, G – well oriented transverse thin section, approximately 1 mm above E, mature growth stage. For stratigraphic position see text. Protosepta and alar septa marked by dots when recognizable. Scale bar above A corresponds to A, E, G; bar corresponding to a given picture located in its upper right or above



Text-fig. 16. *Nina magna* sp. nov. Transverse thin sections. A-C – Specimen UAM-Tc/Don. 1/138. Paratype. A – mature growth stage, squeezed in part, B – corallite axial area enlarged from A; cardinal septum long, thick, counter septum thinner, approach inner margin of cardinal septum, C – microstructure of septum; rounded segments correspond perhaps to recrystallized trabeculae enlarged on cost of thin sclerenchymal cover. D – Specimen UAM-Tc/Don. 1/137. Holotype. Remnants of trabeculae in dissepimental and peripheral tabular parts of major septum. Protosepta marked by dots. For stratigraphic position see text. Scale bars common for two adjacent pictures are located between them, those corresponding to a given picture located in its upper right

globose, arranged in almost vertical rows (Text-fig. 15A, middle). Microstructure of septa trabecular. Twisted row of trabeculae, occupying almost entire width of thin part of septa in dissepimentarium and narrow fragment of thickened tabularial part (Text-fig. 16D, lower and upper, respectively). Irregular shape of trabeculae resulting from their partial recrystallization. Recrystallization of major septa in paratype more advanced (Text-fig. 16C). Remnants of trabeculae expanded by recrystallization to entire width of inner, periaxial part of major septum.

INTRASPECIFIC VARIABILITY: All paratypes squeezed in axial and in some other parts of corallites (e.g., Text-fig. 16A, B), but characters most important for identification preserved. N:d values in adequately preserved corallites at: UAM-Tc/Don.1/140 – 42:24×16 mm, UAM-Tc/Don.1/138 – 50:19.5 mm (in cardinal/counter septa plan), UAM-Tc/Don.1/141 – 50:26×21 mm, UAM-Tc/Don.1/144 – 53:23×21 mm. All diameters incomplete. Paratypes closely resembling holotype in long lasting axial septa, in long cardinal septa, with their axial parts thickened, in inner margins of major septa tapering, in short, thin minor septa and in morphology of cardinal fossulae, dipping distinctly into dissepimentaria. However, major septa in all paratypes longer than the mean length of major septa in holotype, closely approaching, some meeting axial part of cardinal septum (Text-fig. 16B). Wedge-shaped thickenings of tabular parts of major septa in all paratypes less accentuated than that in the holotype, but adequate for exclusion of both biform tabularium and distabularium.

REMARKS: The oblique thin section of the holotype of *Nina magna* (Text-fig. 15A) was illustrated by Vassilyuk (in Aizenverg 1983, pl. 28, fig 8) and named *Neokoninckophyllum nipponense* Kato. Unfortunately, neither a description nor comments on the rugose corals were provided in the original reference. Thus, the reasons for Vassilyuk's identification remain unknown and are not discussed. *N. magna* differs from the type species *N. donetsiana* in the cardinal septum dominating, in the cardinal fossula more distinct and in the corallite diameters and the number of septa much greater. The latter characters distinguish *N. magna* from most species of *Nina*. Only *N. berestovensis* possesses comparable features. However, the cardinal septum in the mature growth stage of *N. berestovensis* is hardly distinguishable from adjacent major septa and its cardinal fossula is inconspicuous or absent, allow the separation of that species from *N. magna*. *N. dibimitaria*,

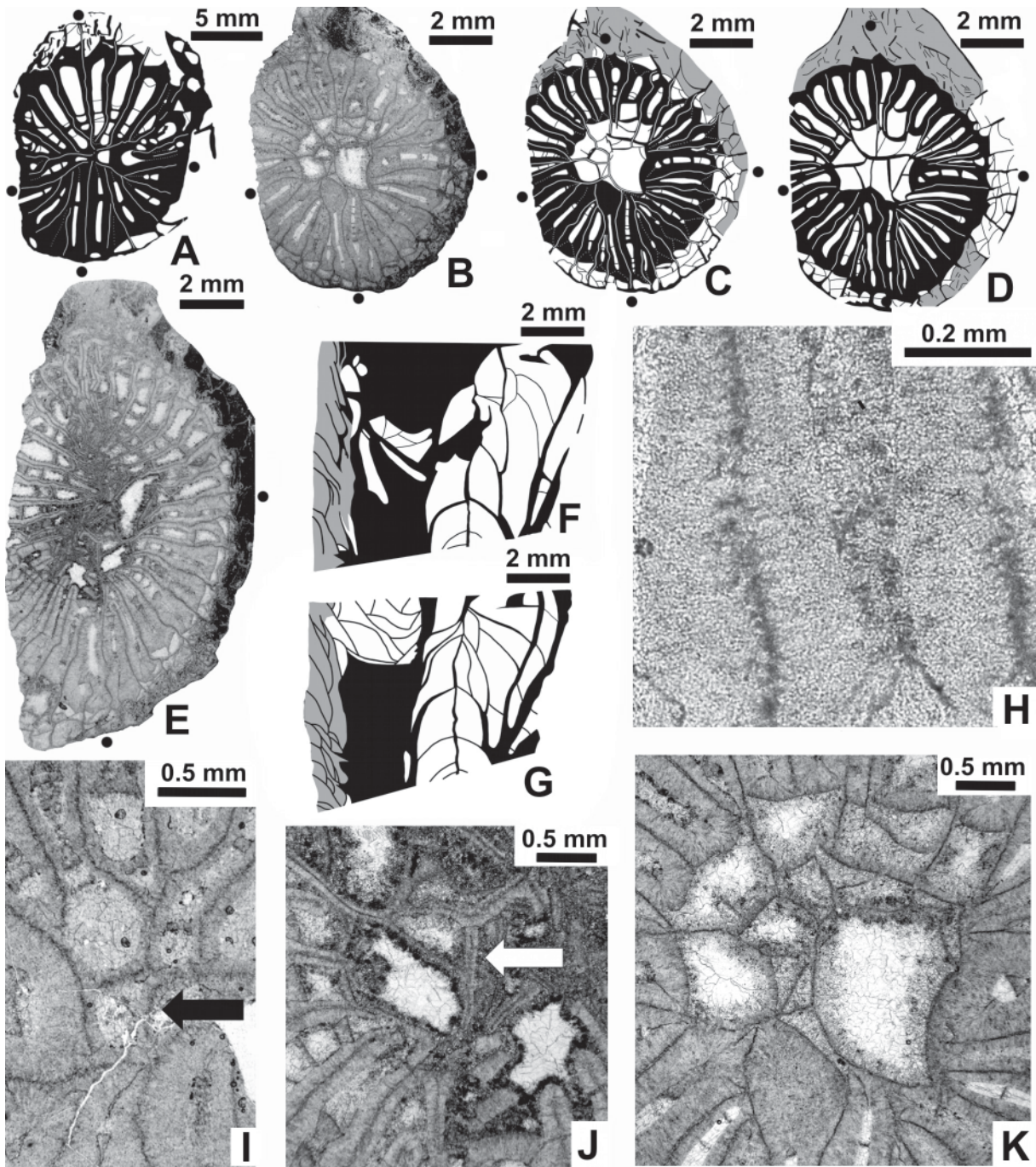
characterized by a well-developed cardinal fossula, resembles *N. magna* in that feature, but differs from it in the cardinal septum thin and not dominating, and the corallite diameters and number of septa much smaller. However, those two species may be most closely related among the species of *Nina* described so far.

OCCURRENCE: All specimens from the Kalmyus River Area. Holotype UAM-Tc/Don.1/137 (Limestone D₇⁵). Paratype UAM-Tc/Don.1/144 (Limestone D₇²). Paratypes UAM-Tc/Don.1/141, 143 (Limestone D₇³), all from Voznesenka Village. Paratypes UAM-Tc/Don.1/139, 142 (Limestone D₆), Amvrosievskiy Kupol, Nikolaevka Village. Paratype UAM-Tc/Don.1/140 (Limestone D₇⁵), left bank of Popovaya Ravine [Balka]. Paratype UAM-Tc/Don.1/138 (Limestone D₇⁸), Glubokiy Yarok Ravine [Balka]. All specimens from the lower Voznesenskian Substage, Suite C₁^s, *Plectostaffella bogdanovkensis* foraminiferal Biozone, *Declinognathodus noduliferus* conodont Biozone, *Homoceras–Hudsonoceras* ammonoid Biozone. Earliest Bashkirian.

Nina? sp. 1
(Text-fig. 17)

MATERIAL: Single, incomplete specimen UAM-Tc/Don.1/145. Earliest growth stage and calice lacking. Mature growth stage squeezed, but its main diagnostic characters distinguishable. Four transverse thin sections and nine peels available for study.

DESCRIPTION: In ontogenetically earliest growth stage preserved (late neanic or early mature), with n:d value 21:6.5×5.5 mm, all septa in tabularium strongly thickened. Cardinal septum thickest. Cardinal and counter protosepta and four longest major septa meeting in corallite axis (Text-fig. 17A). “Dark middle lines” of protosepta disconnected, perhaps due to diagenetic alterations (Text-fig. 17I). Thus, occurrence of axial septum uncertain. Counter-lateral septa inclined towards counter septum, shorter than next major septa inserted. Length of most major septa not in sequence of their insertion, but cardinal septal fossula and alar pseudofossulae recognizable. Minor septa not traced. Dissepimentarium present in a few loculi adjacent to counter septum; consisting perhaps of two rows of delicate dissepiments (broken). Dissepiments in cardinal quadrants of septa either absent or connecting adjacent major septa; minor septa absent from those loculi.



Text-fig. 17. *Nina* sp. 1. Specimen UAM-Tc/Don.1/145. Transverse thin sections, except when stated otherwise. A – late neanic/early mature growth stage (peel with drawing), B-D – mature growth stage (C – thin section with drawing, D – polished surface with drawing), E – advanced mature growth stage (squeezed), F, G – longitudinal sections; centric (F) and slightly eccentric (G) (peels with drawings), H – microstructure of two adjacent major septa with remnants of trabeculae, I-K – corallite axial area in particular growth stages, I – late neanic growth stage with axial septum (arrow) approached and met by longest major septa, J – enlarged from E; arrow points to inner margin of cardinal septum connected to united inner margins of longest major septa, K – enlarged from B; very thin inner margins of major septa, protosepta included, hardly distinguishable from section of tabulae. Protosepta and alar septa marked by dots when recognizable. For stratigraphic position see text. Scale bars correspond to individual pictures

In mature growth stage (Text-fig. 17B-E) with n:d values 29:11.0×7.0, 29:13.5×8.5 and 35:15.5×8.0

mm (smaller diameters incomplete), thickening of major septa tripartite: 2/3 length in tabularium very

strong and equal in thickness around corallite transverse section, thin in dissepimentarium and inner tabularium. Only rare and very thin inner margins of major septa elongated to corallite axial area (Text-fig. 17K). Both reduced thickness of primary septa and diagenetic alteration making their distinction from sections of tabulae difficult. Middle part of cardinal septum remaining thickest; temporarily meeting long counter septum to form axial septum (Text-fig. 17D). Minor septa differentiated in length from swellings of thin external wall to distinct structures, intersecting peripheral ring of dissepiments. Dissepimentarium adjacent to cardinal septum reduced to one row of regular dissepiments. Presence of true, tabular cardinal fossula documented by reduction of dissepimentarium width and by sections of tabulae adjacent to cardinal septum more numerous than in other septal loculi. Widest dissepimentarium preserved consisting of two to four rows of thin-walled, large, herringbone dissepiments. Dissepiments in longitudinal sections long, dipping down steeply (Text-fig. 17F, G). In two surfaces of longitudinal cut, 0.4 mm apart, tabulae in right (counter septum) side widely spaced, either complete or consisting of two tabellae, steeply hemispherically elevated towards longitudinal section of thin axial septum. Some axial tabellae resting on underlying ones to form a kind of axial column. Tabulae in left (cardinal septum) side consist of more tabellae than in opposite corallite side. Their downward arrangement at periphery and elevation towards axial septum in inner parts proving presence of cardinal fossula.

Greatly elongated cardinal septum in advanced mature growth stage (Text-fig. 17E, J) recognizable despite squeezing. Length of counter septum uncertain. Some major septa elongated to corallite axis and joining inner margin of cardinal septum (Text-fig. 17J). Major septa remaining strongly thickened in tabularium, but their great difference in thickness between innermost and other tabularial parts disappeared (Text-fig. 17E). Microstructure of septa altered diagenetically to various extent. Remnants of very fine trabeculae preserved in some parts of major septa (Text-fig. 17H).

REMARKS: The peculiar arrangement of the sclerenchymal thickenings of the major septa in the mature growth stage and the morphology in the longitudinal section with the tabulae widely distributed and steeply arranged with some tabellae resting on the underlying ones, distinguishes the corallite described from all species of *Nina*. The possible appearance of lateral tabellae make its generic identification

doubtful. The morphology in the longitudinal section points towards dibunophyllid corals. However, the morphology in the early mature growth stage, the arrangement and differentiation in length of the major septa in the mature growth stage, with the middle major septa in all quadrants longest, and the cardinal septum permanently long, are characters typical of *Nina*, to which this specimen is temporarily assigned.

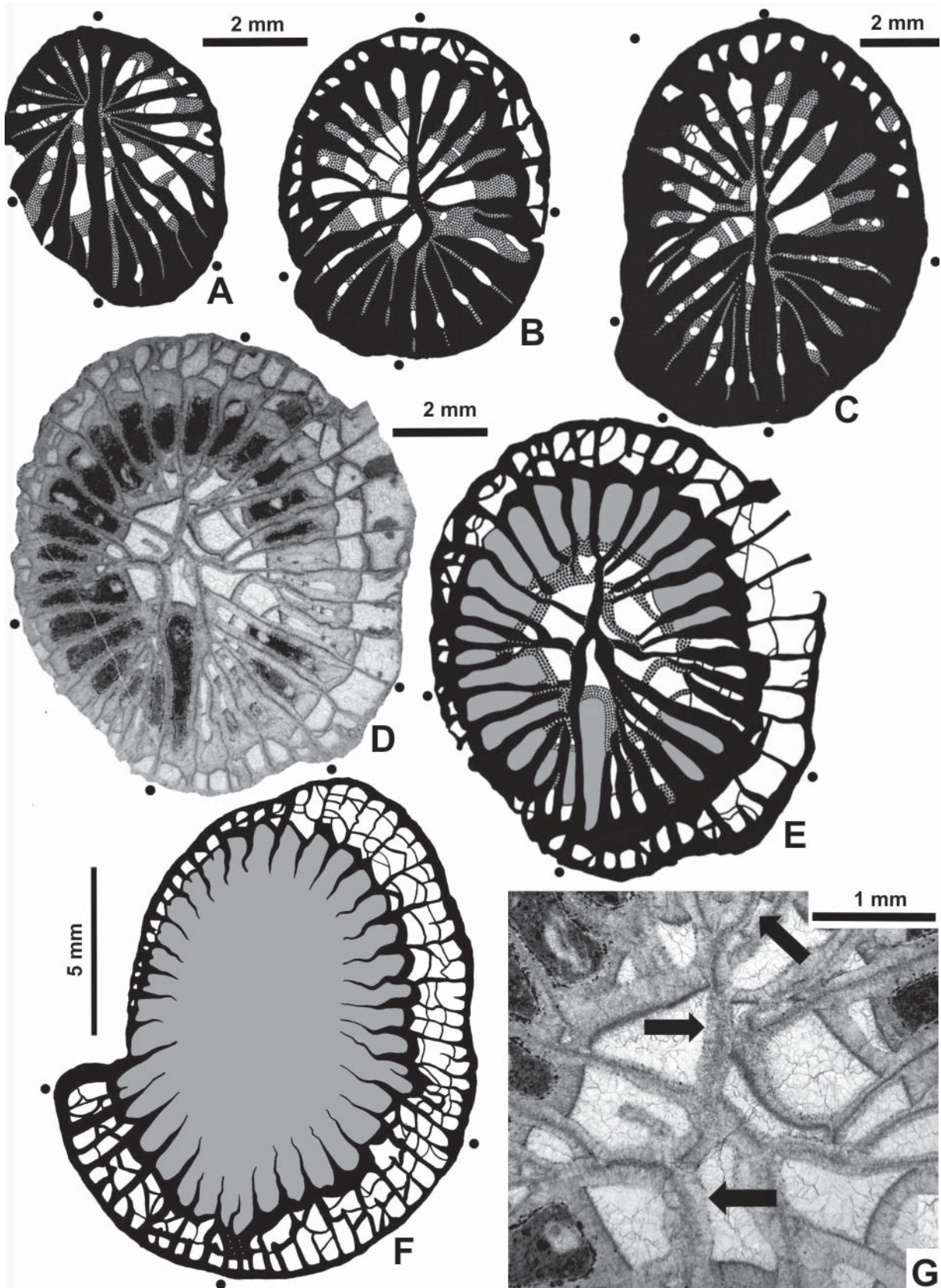
OCCURRENCE: Kalmyus River Area, Voznesenka Village, Limestone Group D₇ (band not specified). Lower Voznesenskian Substage, Suite C₁^s, *Plectostaffella bogdanovkensis* foraminiferal Biozone, *Declinognathodus noduliferus* conodont Biozone, *Homoceras–Hudsonoceras* ammonoid Biozone. Earliest Bashkirian.

Nina sp. 2
(Text-fig. 18)

MATERIAL: Single, almost complete corallite UAM-Tc/Don.1/146 embedded in packstone, partly weathered out. Specimen worn, but most of its thin external wall preserved. Six peels and one transverse thin section available for study. Fragments of corallite left between transverse sections too short for preparation of longitudinal section.

DESCRIPTION: Specimen widely horn-shaped, approximately 20 mm long and 18.0 mm wide at calice margin. Its oval shape original. Calice approximately 12 mm deep (not exposed from inside). External wall 0.2 mm thick, almost smooth, bearing delicate growth striae and traces of very low and flat interseptal ridges.

In late neanic to early mature growth stage with n:d value 23:5.5×4.5, 23:6.5×5.0 and 25:7.0×5.3 mm (Text-fig. 18A–C), corallite symmetry bilateral with axial septum as symmetry axis. Major septa long. In cardinal quadrants shortening sequentially towards cardinal septum starting from long alar septa. Most reaching inner margins of adjacent major septa. In counter quadrants middle major septa longest, counter-lateral septa comparatively short inclined towards and attached to counter septum, last pairs of septa sequentially shorter towards alar septa. Arrangement described makes cardinal fossula and alar pseudo-fossulae easily distinguishable. In earliest growth stage observed (Text-fig. 18A) first dissepiments appearing in thick peripheral sclerenchyme next to first few, short minor septa. In course of approximately 4 mm growth, measured along convex and 1



mm along concave corallite surface, with n:d values listed above, arrangement of major septa remaining similar to afore described growth stage. Appearance of completely developed minor septa and one row of dissepiments in counter quadrants (Text-fig. 18B, C) suggesting early maturity of that growth stage.

Corallite reaching its mature morphology within approximately 2.5 mm further growth along its convex side, 2 mm along its concave side, and with n:d value 31:10.2×9.0 mm. In transverse section made mostly below, but partly above calice floor (Text-fig. 18D, E) major septa in tabularium reduced in thickness by comparison to earlier growth stages, but remaining wedge-shaped and thin in dissepimentarium. Their thickest parts supplementing sclerenchymal thickening of external wall. Number of major septa in cardinal quadrants (six each) smaller than in counter quadrants (eight and nine). Their arrangement in cardinal quadrants pinnate, with alar septa longest and last inserted shortest. In counter quadrants middle major septa remaining longest, counter-lateral septa and last pairs of septa inserted shortest. All longest septa attached to continuous axial septum. Asymmetrical position of cardinal and counter septa (Text-fig. 18E, G) resulting in bent axial septum. Minor septa reaching inner wall when dissepimentarium very narrow, remaining restricted to single row at periphery when dissepimentarium wider. Cardinal fossula marked by its slight dipping into dissepimentarium. Alar pseudofossulae well developed. Occurrence of true, tabular alar fossulae uncertain but possible as indicated by number and shape of tabulae sections next to alar septum in right counter quadrant.

In middle part of calice (Text-fig. 18F) with n:d value 36:15.0×12.4 mm, major septa short, slightly wavy, wedge shaped in tabularium. Cardinal septum and last inserted major septum in right quadrant located in septal loculi dipping into dissepimentarium. This proving occurrence of both cardinal fossula and right alar fossula. Shallow rejuvenation of left corallite side and lack of dissepiments next to major septum last inserted in left counter quadrant making occurrence of left alar fossula uncertain. Minor septa varying in length from short slats incorporated into external wall to long, terminated in strong, sclerenchymal thickening of inner wall. Dissepimentarium

differentiated from non-existing to occupying almost 1/3 corallite radius (Text-fig. 18F, middle left and right, respectively).

REMARKS: The main features of the specimen discussed, such as the axial septum long lasting and the major septa longest in the middle of the counter quadrants, are typical of *Nina*. The specimen differs from the type species of the genus in the axial septum permanent and the zaphrentoid arrangement of the major septa lasting up to the mature growth stage. It differs from all remaining species of *Nina* in the arrangement of the major septa in all quadrants, in the minor septa strongly differentiated in length, and in the occurrence of the alar tabular fossula.

OCCURRENCE: Amvrosievskiy Kupol, Bolshaya Shishovka Ravine [Balka]. Limestone E₁^{verkh}, Feninian Substage, Suite C₂^b_a nizhn. *Semistaffella variabilis*–*S. minuscularia* foraminiferal Biozone, *Idiognathodus sinuosus* conodont Biozone, *Reticuloceras*–*Bashkortoceras* (R₁) ammonoid Biozone. Late early Bashkirian.

Genus *Cystilophophyllum* Fomichev, 1953

(Type species *Lophophyllum* (*Cystilophophyllum*) *kalmiussi* Fomichev, 1953, p. 274)

EMENDED DIAGNOSIS: Solitary; lonsdaleoid dissepiments appearing at advanced mature growth stage; cardinal septum similar in length to adjacent pair of major septa; counter septum may remain longer than adjacent major septa; monoseptal pseudocolumella derived from axial septum, commonly reduced in mature growth stage; tabularium normal and disstabularium; tabulae incomplete, elevated at periphery and towards pseudocolumella when present, horizontal in axial part when pseudocolumella absent; microstructure of septa trabecular.

REMARKS: Fomichev (1953) followed Carruthers' (1913) concept of the genus *Lophophyllum* Milne Edwards and Haime, 1851, in considering it a dissepimental genus. This approach allowed Fomichev (1953) to identify several dissepimental species derived from the Limestones G to M of the Donets

← Text-fig. 18. *Nina* sp. 2. Specimen UAM-Tc/Don.1/146. Transverse sections. A – late neanic growth stage, B, C – early mature growth stage, D, E – mature growth stage; above calice floor dark (D) and shadowed (E), F – lower part of calice; above floor shadowed (A-C, E, F – peels with drawings), G – enlarged from D to document occurrence of axial septum; lower arrow cardinal, upper arrow counter septum. For stratigraphic position see text. Protosepta and alar septa marked by dots. Scale bars common for two adjacent pictures located between them, those corresponding to given picture located in its upper right

Basin as *Lophophyllum*. In most of those species the dissepiments are interseptal, but lonsdaleoid dissepiments appear in the advanced mature growth stage of some corallites. Bearers of the latter character were separated by Fomichev (1953, p. 274) in the new subgenus *Cystilophophyllum*, here elevated to genus level. *C. kalmiussi* Fomichev, 1953 is the type and remains the only named species of the genus. Fomichev (1953, p. 274) characterized his new subgenus as follows: "The pseudocolumellae in those taxa are united with the counter septum, allowing the author to include them into the genus *Lophophyllum* Mn. Edw. et H. They deserve a separation into a different subgenus *Cystilophophyllum* since septa in typical *Lophophyllum* Mn. Edw. et H. meet the external wall." [Translated here from Russian].

Neither Fomichev's (1953) approach to the genus *Lophophyllum*, nor his emendation (p. 260) of the Family Lophophyllidae Grabau, 1928 is accepted here for one main reason, either unknown at his time, or forgotten, i.e., the absence of dissepiments in *Lophophyllum konincki* Milne Edwards and Haime, 1850, the type species of that genus. The lack of dissepiments in five syntypes of that species was first established by Lecompte (1955) in his introductory revision, then accepted by Fedorowski (1974, p. 442), who re-examined those syntypes, confirmed by Hill (1981, p. F333), who selected the lectotype, and further discussed by Fedorowski (1989, p. 309). Although all syntypes are silicified corallites, known only from their external shapes and calices, and none of them is sectioned, the broken fragment of the lectotype documents the absence of dissepiments.

The original documentation of *C. kalmiussi* (Fomichev, 1953, pl. 16, figs 6–11) is poor. Fomichev (1953, p. 276) listed six specimens, all derived from the Limestone G₁¹ (late Bashkirian) and from the same locality in the Donets Basin. Five of these corallites were illustrated by Fomichev (1953, pl. 16, figs 6–10) and one, not illustrated by him, is illustrated in the present paper (Text-fig. 19A–C). Three paratypes are very incomplete, illustrated by one transverse section each. One of those thin sections (Fomichev 1953, pl. 16, fig. 7) illustrates the early neanic growth stage with the axial septum present. Only the holotype is documented by four thin sections: one longitudinal and three transverse thin sections. The latter illustrate the late neanic/early mature and the advanced mature growth stages. The longitudinal thin section covers the lowermost part of the calice and the subcalicinal area of the corallite (Fomichev 1953, pl. 16, fig. 6a–g in Russian alphabet). Only the thin sections mentioned, but not the rock material of the speci-

mens illustrated by Fomichev (1953), were available for the restudy at the time of my visit to the VSEGEI Museum in 1969. Thus, only one paratype was peeled and illustrated here (see Material). A single, very incomplete specimen derived from the Limestone M (Moscovian), described and illustrated as the holotype of *Cystilophophyllum* (?) sp. nov. (Fomichev 1953, p. 277, pl. 16, fig 11) is omitted from the discussion.

Specimens from the new collection, investigated herein, are incomplete as well (see Material). However, their derivation from the Limestone G₁ allows their treatment as supplementary to the original documentation of the species and genus.

As mentioned above, the dissepimental species included by Fomichev (1953) in the genus *Lophophyllum* and in *Cystilophophyllum* have nothing in common with the type species of the genus *Lophophyllum*. Also, they differ distinctly from the dissepimental genus *Eostroton* Vaughan, 1915, introduced for primitive Mississippian taxa. That koninckophyllid genus is characterized by a narrow dissepimentarium, composed of regular interseptal dissepiments, by a permanent, strongly thickened median lamella, derived from the axial septum, but free from protosepta beginning in early maturity, and by a long cardinal septum, intersecting the narrow cardinal fossula. Those characters distinctly contrast to the characters of *Cystilophophyllum* (see Description) that displays a strong similarity to the genera included in the Family Bothrophyllidae, *Gshelia* Stuckenberg, 1888 in particular. This similarity includes the nature of the early ontogeny, the distribution of sclerenchymal thickenings of the major septa, the morphology of the cardinal fossula and the trend to achieve a caninoid morphology at maturity. Derivation of the pseudocolumella from the axial septum in both genera is proven (Dobrolyubova 1940, pl. 16, figs. 4–7; Text-figs. 19A, D, E; 20A, B), but the connection of the pseudocolumella to particular protosepta is uncertain. It is more closely connected to the cardinal septum in most specimens of *Gshelia rouilleri* Stuckenberg, 1888 investigated in detail (Dobrolyubova 1940, pl. 17, fig. 6; Fedorowski in Fedorowski and Goryanov 1973, fig. 19: 1a–g, 2a–e). A similar connection is observed in *Cystilophophyllum* sp. (Text-fig. 21A), but in the early growth stage of the holotype and in one paratype of *C. kalmiussi*, the pseudocolumella is more closely connected to the counter septum (Fomichev 1953, pl. 16, figs 6a, 11).

Some of the corallites investigated here (e.g., Text-fig. 19F) resemble certain transverse thin sections of *Yakovleviella lissitzini* Fomichev, 1953 (e.g., Fomichev 1953, pl. 19, fig. 3g). Unfortunately, the

uncertain status of the latter genus (see Fedorowski 2016 for details) excludes the indisputable comparison of it to any taxon displaying a similar morphology. The development of the lonsdaleoid dissepiments at the periphery, considered by Fomichev (1953) as the main difference between *Cystilophophyllum* and *Lophophyllum*, constitutes the main difference of the former genus compared to all genera included herein in the Family Bothrophyllidae. Thus, its similarity to the bothrophyllid genera is much closer than its difference, making its inclusion in the Family Bothrophyllidae more probable than its relationship to any other existing family. The definition of *C. kalmiussi* accepted here is perhaps too broad. However, only such an approach to the incomplete material seems appropriate.

Cystilophophyllum kalmiussi Fomichev, 1953
(Text-figs 19 and 20)

1953. *Lophophyllum* (*Cystilophophyllum*) *kalmiussi*; Fomichev, p. 274, pl. 16, figs 6–10.

EMENDED DIAGNOSIS: *Cystilophophyllum* with 32–35 major septa at 16–20 mm corallite diameter.

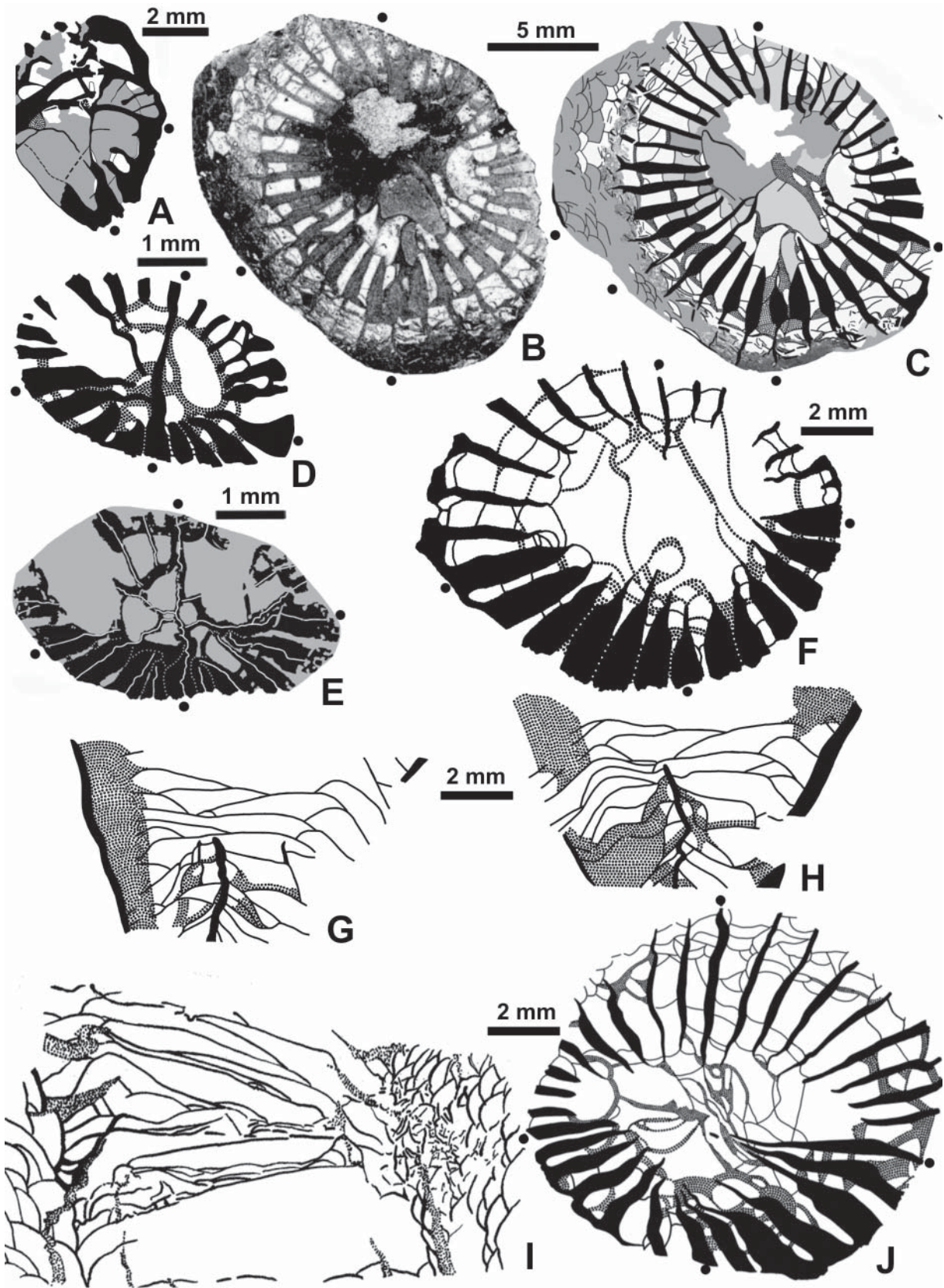
MATERIAL: Thin sections of types restudied in the VSEGEI Museum. One incomplete paratype Nr. 5030/869b peeled from three surfaces. Two of those peels illustrated (Text-fig. 19A–C). Third corresponds to squeezed part of specimen. Ontogenetically earliest growth stage preserved, partly destroyed by diagenesis. Mature growth stage best preserved in interseptal part of tabularium; peripheral part mostly eroded and crushed; circumaxial area free from septa partly dolomitized (white), partly recrystallized in two phases: calcitic (light shade) and calcitic enriched with iron (dark shade in Text-fig. 19C).

All seven specimens here identified as *C. kalmiussi* (UAM-Tc/Don.1/147–153) incomplete, worn and corroded corallites, incorporated in brownish grainstone. Dissepimentaria of some completely or in part destroyed. Identification of such specimens may be considered uncertain. Microstructure of septa diagenetically altered in most, less altered parts of some corallites remain. In addition to three peels of paratype, eight thin sections and 14 peels of supplementary material available for study.

SUPPLEMENTARY DESCRIPTION: Morphology of early growth stage uncertain, neanic growth stage of holotype missing. In earliest growth stage illus-

trated by Fomichev (1953, pl. 16, fig. 7) with n:d value approximately 22 (24):5.1×4.0 mm, major septa differentiated in length, those of cardinal quadrants longer, but not thicker than those of counter quadrants, most approach axial septum. Counter-lateral septa short, inclined towards and attached to counter septum. Morphology described differing from both rejuvenated paratype illustrated herein (Text-fig. 19A) and most completely preserved corallite from new collection (Text-figs 19D, E; 20A, B). Major septa differentiated in length and thickness by quadrants and within quadrants of septa in both latter corallites. Presence of axial septum joined by elongated alar septa, common for all three specimens discussed and closely comparable to early growth stage of *Bothrophyllum* Trautschold, 1879. Middle major septa in all quadrants of late neanic growth stage of newly collected corallite elongated (Text-figs 19E, 20B), resembling comparable growth stage in *Nina*.

In mature growth stage all major septa distinctly shortened in all corallites studied by Fomichev (1953) and herein. Those of cardinal quadrants thin in dissepimentarium, strongly thickened in tabularium, wedge-shaped inward from inner wall, with inner margins ending thin (Text-figs 19B, C, F, J; 20C). In mature growth stages of individual corallites cardinal septum varying in length. In holotype and some paratypes shortened in other paratypes and some specimens described here, hardly distinguishable from adjacent major septa in length and thickness (Fomichev 1953, pl. 16, figs 8, 10; Text-fig. 19J). Cardinal septum in some corallites (Text-figs 19C, F; 20C) greatly thickened in tabularium, but that thickened part shorter than thicker parts of adjacent major septa. Thin inner part of that cardinal septum equal in length to adjacent major septa. Counter septum in earliest growth stage of holotype and in one paratype (Fomichev 1953, pl. 16, figs 6a, 9) elongated to corallite axis, but equal to adjacent major septa in remaining paratypes illustrated by Fomichev (1953, pl. 16, figs 8, 10) and herein (Text-fig. 19B, C). However, diagenetic alterations make length of counter septum uncertain in all paratypes. Counter septum remains slightly longer than adjacent major septa in holotype (Fomichev 1953, pl. 16, fig. 6v in Russian alphabet) and in specimens described herein (Text-figs 19F, J; 20C). Erosion of peripheral parts of most paratypes and of specimens investigated herein makes length of minor septa uncertain. Fomichev (1953, p. 275) described them in certain growth stages of the holotype as follows: “Thin minor septa seen here and there within dissepimentarium”. “Minor septa not preserved”. “Minor septa preserved in some



parts. They, alike major septa, isolated from external wall by large lonsdaleoid dissepiments. In subzone with minor septa present, dissepiments oblique, partly herringbone.” [Translated here from Russian]. Minor septa absent from part of dissepimentarium preserved in paratype illustrated here (Text-fig. 19B, C) and from narrow remnants of one newly studied corallite (Text-fig. 19J), but some very short minor septa occur at very peripheral part of another corallite (Text-fig. 20D). Pseudocolumella distinct in early mature growth stage of holotype, absent from its mature growth stage, and from comparable growth stage of all paratypes and specimens described here (Fomichev 1953, p. 16, figs 6b, 8–10; Text-figs 19B, C, F, J; 20C herein). Fomichev (1953, p. 275) described the pseudocolumella as follows: “Thin, plate-like pseudocolumella, united with counter septum, occurs in the middle of the section” and “...presence of strong pseudocolumella characteristic for early growth stages and its disappearance [typical] for mature growth stage...” [Translated herein from Russian]. Eroded, corroded and/or squeezed peripheral parts of all corallites investigated by Fomichev (1953) and herein makes determination of exact width and morphology of dissepimentarium uncertain. Presence of lonsdaleoid dissepiments documented best in the paratype illustrated here (Text-fig. 19B, C). Illustrations provided by Fomichev (1953) do not support his description (p. 275) of the dissepimentarium, the occurrence of pseudonaotic septa in particular. He wrote: “...wide belt of dissepimentarium; large dissepiments in the peripheral area of which break septa, whereas oblique dissepiments (commonly herringbone) occur in the inner area; grape-like [= pseudonaotic] tissue present.” [Translated here from Russian].

In longitudinal section of holotype made through lower part of calice and subcalicinal part of corallite (Fomichev 1953, pl. 16, fig. 6g in Russian alphabet), dissepiments mostly destroyed. Large, globose in best preserved part. Tabulae incomplete, anastomosing. Their elevation and dense arrangement may have resulted in part from squeezing. Paratypes not sectioned longitudinally. In longitudinal section of early growth stage of one corallite from the collection studied here (Text-fig. 19G, H) tabulae incomplete, elevated to section of either axial septum or pseudo-

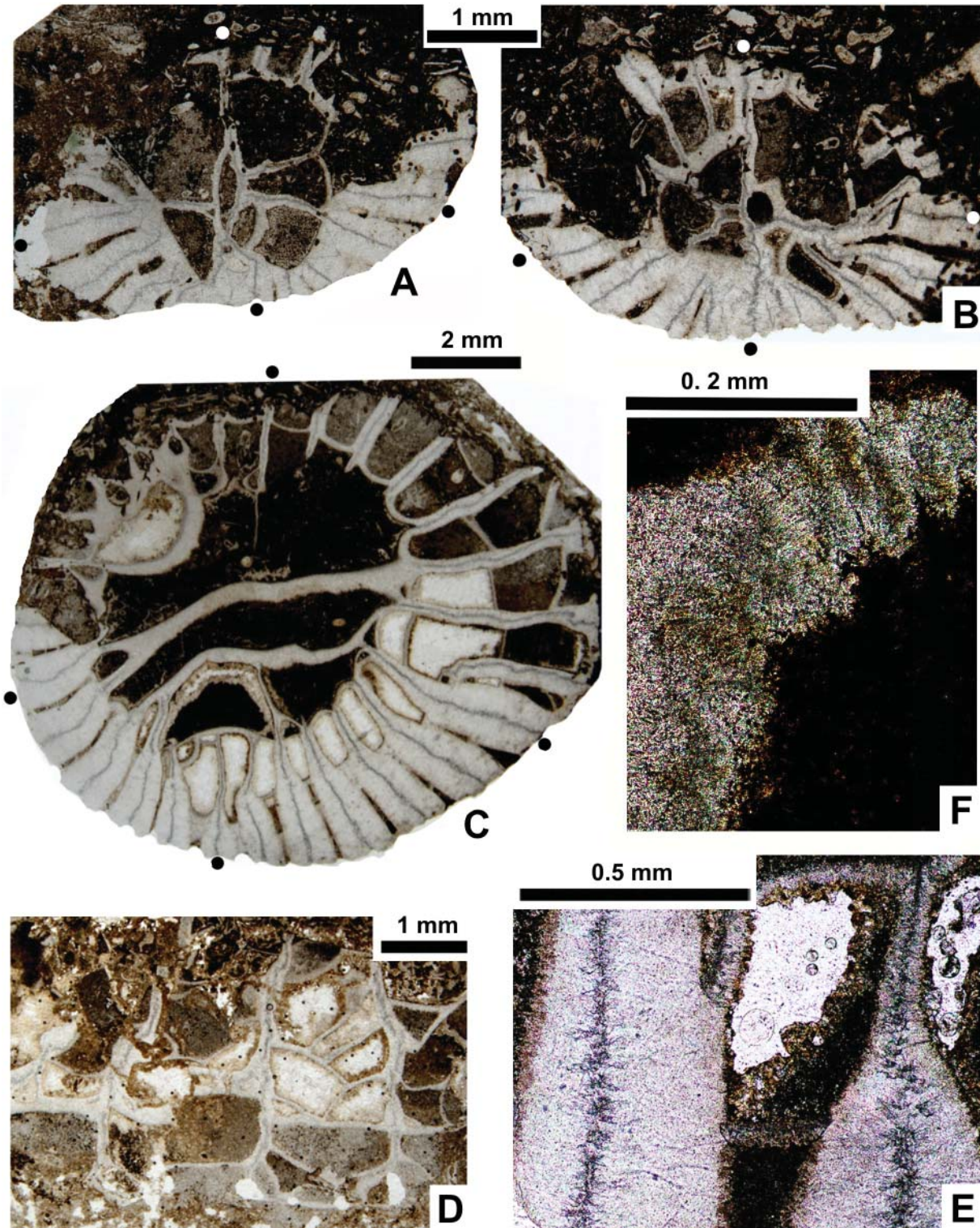
columella. Tabulae flat and horizontal in corallite axis, anastomose with downturned peripheral tabulae, when pseudocolumella reduced. In fully mature growth stage (Text-fig. 19I) arrangement of tabulae similar to those above pseudocolumella in young corallite. Dissepimentarium in that mature corallite wide. Dissepiments arranged in steep rows. Their size differs irrespective of position within dissepimentarium. Large dissepiments present at periphery of right side and next to tabularium in left side of corallite (Text-fig. 19I). Tabularium/dissepimentarium interrelation in paratype studied here and in best preserved hypotype (Text-fig. 19B, C, J, respectively) closely resembles that of *Nina*, i.e., normal in cardinal quadrants and disstabularium in counter quadrants.

Remnants of very fine trabeculae recognizable in some better preserved septa (Text-fig. 20E). Bodies following zig-zagged “dark line” in obliquely longitudinal section of septum (Text-fig. 20F) interpreted here as remnants of trabeculae strongly enlarged by recrystallization. Thus, microstructure of septa in *Cystilophophyllum* is considered trabecular, but size of trabeculae remains unknown.

REMARKS: The poor preservation and fragmentary condition of all specimens studied by Fomichev (1953) and herein makes the identifications somewhat uncertain. However, sets of morphological data for individual specimens leave little doubt as to their relationship at genus level. Most paratypes described by Fomichev (1953, pl. 16, figs 8–10) and herein (Text-fig. 19A–C) and the supplementary specimens (Text-figs 19D–J; 20A–E) resemble the holotype closely enough to accept them as co-specific. The corallite morphologically most distant from the holotype, described by Fomichev (1953), was an unnamed, poorly preserved new species, for which the illustration is inadequate for a comprehensive comparison and discussion. For remaining discussion see remarks on the genus above and *Cystilophophyllum* sp. below.

OCCURRENCE: Type collection: All specimens 400 m north of the railroad bridge across the Kisilichnaya Ravine (Balka), Limestone G₁¹. Specimens described herein: UAM-Tc/Don.1/147, 149–152. Kalmyus River Area, Larino Village, Obetochnaya Ravine [Balka]. Specimens UAM-Tc/Don.1/148, 153, 154.

← Text-fig. 19. *Cystilophophyllum kalmiussi* Fomichev, 1953. A-C – Specimen 5030/869b. Paratype. Transverse sections. A – neanic growth stage (peel with drawing), B, C – mature growth stage (peel, C – drawing from B). D-H – Specimen UAM-Tc/Don.1/147. D, E – late neanic growth stage (drawings; D – peel, E – thin section = Text-fig. 20B), F – mature growth stage (polished surface with drawing), G, H – longitudinal sections 0.5 mm apart (peels with drawings). I – Specimen UAM-Tc/Don.1/148 – longitudinal thin section with drawing. J – Specimen UAM-Tc/Don.1/150 – mature growth stage (peel with drawing). For stratigraphic position see text. Protosepta and alar septa marked by dots when recognizable. Bars between two pictures correspond to both, bar corresponding to given picture located in its upper right or above



Text-fig. 20. *Cystilophyllum kalmiussi* Fomichev, 1953. Transverse thin sections except F. A-E – Specimen UAM-Tc/Don.1/147. A, B – late neanic growth stage, C – mature growth stage, D – mature growth stage; remnants of dissepimentarium and minor septa, E – cardinal septum (right) and major septum adjacent to it from left; different shape of sclerenchymal thickenings of those septa and probable remnants of trabeculae in their middle. F – Specimen UAM-Tc/Don.1/148. Longitudinally oblique thin section of major septum with probable remnants of trabeculae (upper right). For stratigraphic position see text. Protosepta and alar septa marked by dots when recognizable. Scale bars common for two adjacent pictures located between them, those corresponding to given picture located in its upper right

Kalmyus River Area, Menchugovo Village. All specimens from Limestone G₁, lower Zhuyevskian Substage, Suite C₂^b, early *Profusulinella primitiva*–*Pseudostaffella gorskyi* foraminiferal Biozone, early *Branneroceras*–*Gastrioceras* ammonoid Biozone. Early late Bashkirian.

Cystilophophyllum sp.
(Text-fig. 21A–C)

MATERIAL. One incomplete specimen UAM-Tc/Don.1/155 embedded in finely grained, brownish grainstone. Early growth stages lacking. Remaining fragment of corallite corroded and squeezed to a various extent. Only best preserved parts illustrated. Three transverse thin sections and one peel available for study.

DESCRIPTION. In ontogenetically earlier growth stage illustrated (Text-fig. 21A), at least partly below calice floor (whitish interseptal infillings), major septa much thicker in cardinal than in counter quadrants. Their thickening at dissepimentarium/tabularium boundary not sharp. Axial area free from major septa approximately 1/5 of corallite diameter wide. Cardinal septum thick, shortened. Counter septum equal to adjacent major septa in length and thickness. Alar septa indistinguishable. Cardinal fossula narrow, bordered by two major septa, equal in length to remaining major septa. Minor septa varying in length from restricted to periphery to entering tabularium, absent from some loculi (Text-fig. 21C). Pseudocolumella monoseptal, elongated, thickest in middle part, connected with cardinal septum (Text-fig. 21A) by thin, irregular extension. Dissepimentarium mostly interseptal (Text-fig. 21A, C). Dissepiments herringbone above minor septa and pseudo-herringbone between them and major septa. Lonsdaleoid dissepiments rare and only at very peripheral corallite part.

Morphology immediately above calice floor (Text-fig. 21B) similar to that described above. Counter septum slightly thinner than adjacent major septa and disconnection of cardinal septum from pseudocolumella forming the only difference. Cardinal fossula dipping into dissepimentarium; character not seen in earlier growth stage, eroded in that corallite area.

REMARKS: The specimen described here differs from all specimens accepted here as *C. kalmyussi* except for one paratype (Fomichev 1953, pl. 16, fig. 9). The main differences of these two specimens

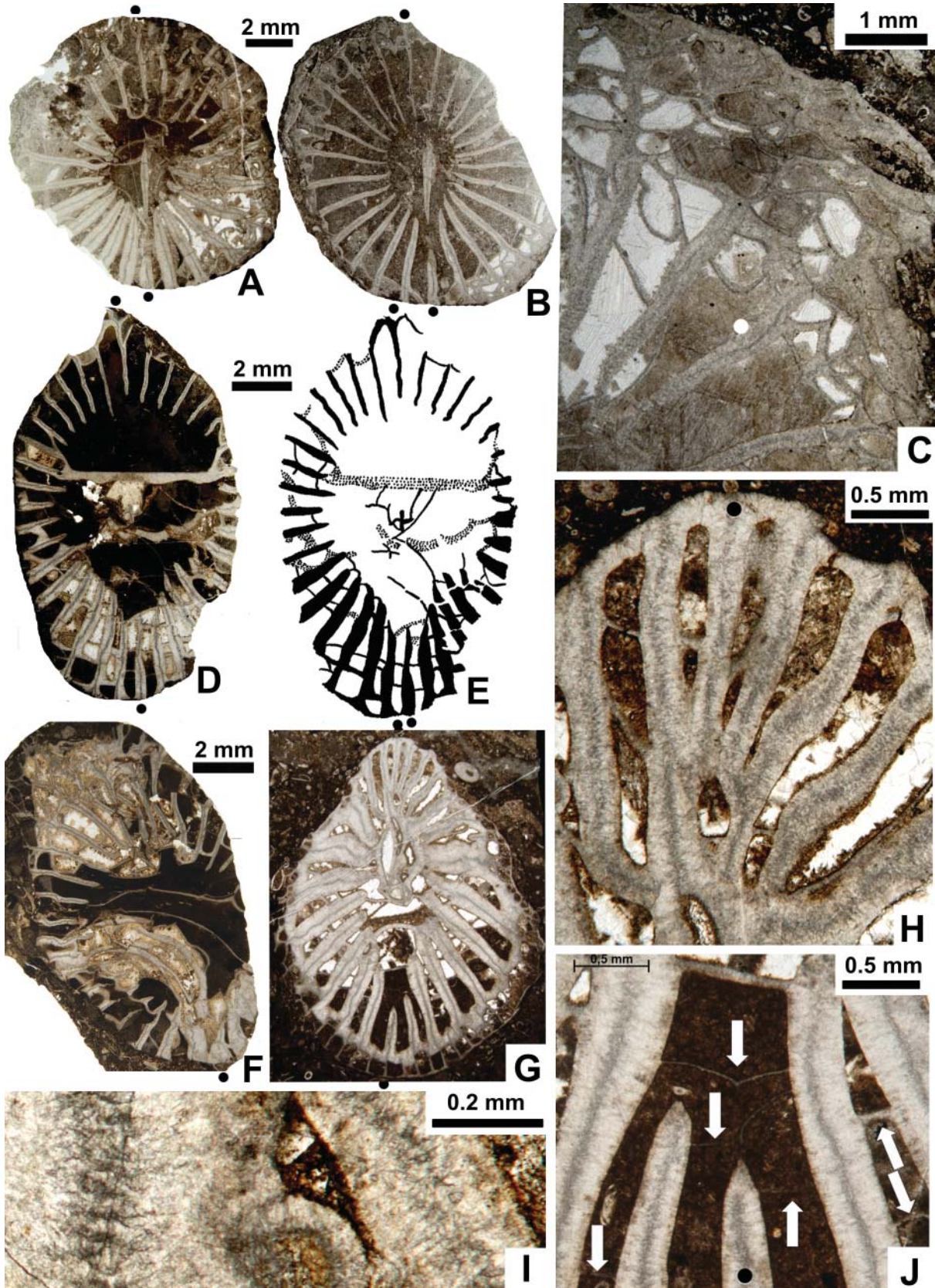
from the remaining corallites concern the shape and length of the major septa, clear shortening of the cardinal septum and a differentiated length of the minor septa, some of which penetrate the tabularium. The specimen described here differs from Fomichev's paratype in the shape of the cardinal fossula. Also, its pseudocolumella is stronger, lasting up to the calice inclusively. The latter character, combined with the stratigraphic position (Limestone F₂), earlier than all other corallites included in *Cystilophophyllum* so far, place the corallite described here in an ancestral position for the genus, if the connection of its pseudocolumella to the cardinal septum, i.e., opposite to that in the holotype of *C. kalmyussi*, is not taken into consideration. That connection may point towards the Dibunophyllinae as an ancestral taxon for the specimen described here as *Cystilophophyllum* sp., i.e., its generic identification may be incorrect. However, a more suitable taxon for that specimen is not available. Its ancestral position to *Gshelia*, apparently suggested by the close connection of its pseudocolumella to the cardinal septum, is not considered possible.

OCCURRENCE: Kalmyus River Area. Watershed between Lozovaya and Sukhaya Olkhovka ravines [balkas]. Limestone F₂. Blagodatnian Substage, Suite C₂^b. *Pseudostaffella pregorskyi*–*Staffelleformis staffelleformis* foraminiferal Biozone, upper *Bilinguites*–*Cancelloceras* ammonoid Biozone. Late middle Bashkirian.

Incertae sedis taxa
Genus *Siedleckia* Fedorowski, 1975
? *Siedleckia* sp. 1
(Text-fig. 21D–J)

MATERIAL: Two specimens UAM-Tc/Don.1/156 and 157, embedded in thin grained, brownish grainstone. Both found during cutting of rock samples. Thus, only three slightly oblique transverse thin sections available for study.

DESCRIPTION: In thin section of the ontogenetically earliest growth stage preserved (specimen UAM-Tc/Don.1/157; Text-fig. 21G), major septa in tabularium thickened, next to counter septum less so, in dissepimentarium thin. Last pair of major septa inserted in counter quadrants equal in length to adjacent major septa, including alar septa. Thus, quadrants of major septa weakly recognizable. Arrangement of major septa extraordinary: their length in particular quad-



rants reduced towards short cardinal and long counter-lateral septa. Cardinal septum thinner and much shorter than most major septa in cardinal quadrants. Counter septum shortened, bordered by long counter-lateral septa (Text-fig. 21G, H), left of which either originally or diagenetically split along some length, imitating sections of tabulae in that part (Text-fig. 21H). Inner margin of that major septum and inner margins of three other major septa attached to it, forming a kind of loose axial structure. Cardinal fossula open, very slightly dipping into single row of dissepiments. Occurrence of very delicate tabulae (Text-fig. 21J, arrowed) documenting position above calice floor of cardinal fossula and remaining parts of corallite, including those infilled with mud. Minor septa in cardinal quadrants intersecting dissepimentarium. Their thick inner margins extending slightly into tabularium. Those from counter quadrants probably eroded. Dissepimentarium best developed in middle part of cardinal quadrants, consisting of 2–3 rows of irregular dissepiments.

Second corallite preserved in two transverse sections. Both representing growth stage more advanced than the previously described specimen. Main characters of ontogenetically less advanced growth stage of second specimen (Text-fig. 21D, E), i.e., occurrence of weak axial structure and major septa arranged in hardly recognizable quadrants, reminiscent of those in first specimen. Remaining characters, i.e., major septa thinning towards counter septum, free axial area wide, and cardinal septum only slightly shorter than adjacent major septa, constituting main differences of this growth stage from specimen described above.

In ontogenetically most advanced growth stage of second specimen (Text-fig. 21F), only short cardinal septum and major septa closest to it remaining thickened. Slight shortening of counter septum recognizable despite damage in that part of corallite. Axial structure absent. Sections of tabulae in middle part of corallite suggesting their completeness and hemispherical shape. Peripheral part of corallite squeezed and partly eroded. In small preserved fragment dissepimentarium herringbone. Minor septa not seen. Microstructure of septa diagenetically altered (Text-fig. 21I), preserved as flat fans of crystalline fibrils.

REMARKS: The incompleteness of the specimens available for study excludes both their comprehensive description and an indisputable identification not only at species, but also at genus level. The remaining fragments expose a mixture of characters: shortened cardinal and counter septa typical of *Siedleckia* and a moderately weak axial structure. The strong elongation of the counter-lateral septa in the earliest growth stage described, can be roughly compared to the corresponding septa in *Arctophyllum* Fedorowski, 1975. The mixture of characters mentioned makes impossible any suggestion of the relationship of the specimens discussed. Their weak axial structure points towards dibunophyllids as a hypothetical ancestor, whereas the shortening of both protosepta in the mature growth stage contradicts such a possibility and suggest their ancestral position for either *Arctophyllum* or *Siedleckia*.

OCCURRENCE: Kalmyus River Area. Gorbachevo Village. Limestone F₂. Blagodatian Substage, Suite C₂^b_a. *Pseudostaffella pregorskyi*–*Staffelleformis staffelleformis* foraminiferal Biozone, upper *Bilinguites Cancelloceras* ammonoid Biozone. Late middle Bashkirian.

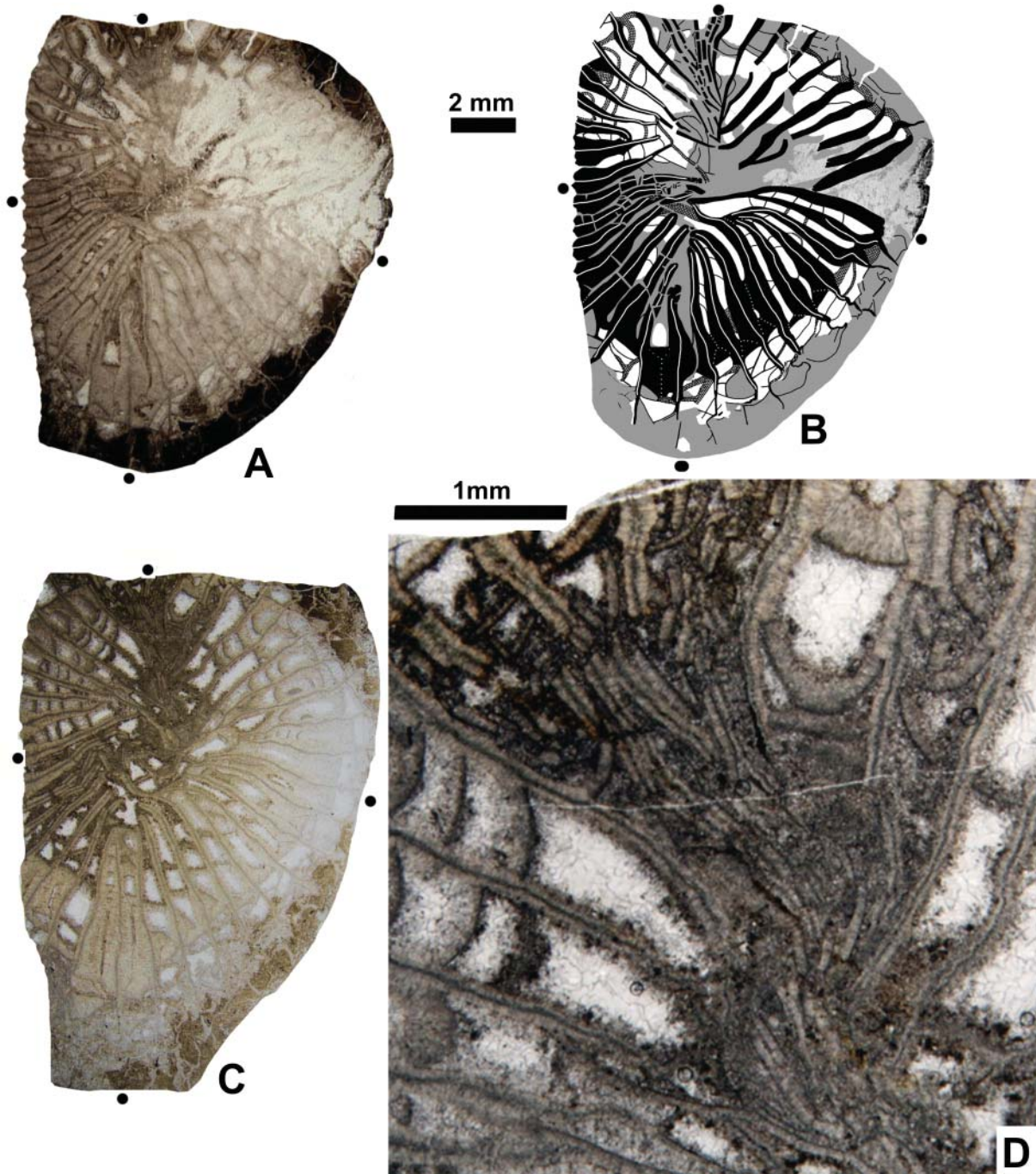
?*Siedleckia* sp. 2
(Text-fig. 22)

1983. *Siedleckia mutafii* (Gorskyi); Vassilyuk in Aizenverg *et al.*, pl. 28, fig. 5.

MATERIAL: Single, incomplete, worn specimen UAM-Tc/Don.1/158 embedded in brownish grainstone. Portions of corallite recrystallized and/or crushed, other fragments well preserved. Squeezing, corrosion at periphery and recrystallization makes measurements incomplete and uncertain. Two thin sections and one peel available for study.

DESCRIPTION: Diameter of preserved part of corallite skeleton 17.0×11.5 mm and 16.0×11.8 mm. Major septa long, 39 or 40 in number, inconsistently differentiating in length. Those of counter quadrants more

← Text-fig. 21. **A–C** – *Cystilophophyllum* sp. Specimen UAM-Tc/Don.1/155. Transverse thin sections, mature growth stage. A, B – above calice floor in most parts, C – fragment of dissepimentarium documenting lonsdaleoid dissepiments. **D–J** – ?*Siedleckia* sp. Transverse thin sections (slightly oblique). D–F – Specimen UAM-Tc/Don.1/156. Mature growth stage. G–J – Specimen UAM-Tc/Don.1/157. Transverse thin section (oblique). G – Early mature (upper and left) and mature (lower and right) growth stage. H – counter septum shortened; continuous “middle line” of curved right counter-lateral septum documents its elongation, I – possible remnants of trabeculae in two adjacent major septa, J – cardinal fossula; sections of thread-like thin and hardly seen tabulae (arrows) document its position beneath calice floor despite being infilled with strange matrix (H–J enlarged from G). For stratigraphic position see text. Protosepta marked by dots when recognizable. Bars between two pictures correspond to both, bar corresponding to given picture located in its upper right



Text-fig. 22. ?*Siedleckia* sp. 2. Specimen UAM-Tc/Don.1/158. Transverse thin sections. A-C – mature growth stage, D – counter septum and major septa adjacent to it; enlarged from C. Mutual positions, length and thickness of major septa in right counter quadrant approximate. For stratigraphic position see text. Protosepta marked by dots when recognizable. Bars between A and B corresponds to all illustrated specimens

numerous than major septa in cardinal quadrants. All major septa thickened in tabularium; more so in ontogenetically younger growth stages (Text-fig. 22A, B). Thickening strongest near cardinal septum, reduced sequentially towards counter septum. Major septa in counter quadrants and right cardinal quadrant, lo-

cated near or in middle of quadrants longest, approaching and/or reaching corallite axis. Major septa in cardinal quadrants either bent above or inclined towards short cardinal septum, but their inner margins free. Cardinal septal fossula open. Counter septum and four adjacent pairs of major septa squeezed and

fragmented (Text-fig. 22C, D), making description of their length impossible. Analysis in large magnification of individual fragments of crushed major septa and their comparison to better preserved major septa in counter quadrants, suggesting shortened counter septum. Corrosion and diagenetic damage of peripheral parts of corallite making length of minor septa and width of dissepimentarium unknown. Minor septa absent from inner dissepimentarium consisting of regular and herringbone dissepiments.

REMARKS: The poorly preserved corallite, described above, is included in this paper only because one of the thin sections illustrated here (Text-fig. 22A, B) has been illustrated earlier by Vassilyuk (in Aizenverg *et al.* 1983, pl. 28, fig. 5), but has not been described in the original paper. Thus, supplementary illustrations and a brief description may help in the determination of its taxonomic position. The mixture and inconsistency of characters of ?*Siedleckia* sp. 2 may be indicative of an intermediate taxonomic position. The shape of its cardinal fossula resembles that in *Pseudotimania* Dobrolyubova and Kabakovich, 1948, the differentiation in length of its major septa points towards *Nina* gen. nov., whereas the shortening of both protosepta is typical of *Siedleckia*.

The species name applied by Vassilyuk (in Aizenverg *et al.* 1983) is not accepted and the generic name applied by her is questioned. The species *Caninia mutafii* was introduced by Gorskyi (1938) for the incomplete and poorly preserved corals from the Moscovian strata of Novaya Zemlya. Fedorowski (1975, p. 51) accepted that species, established some of its characters in common with three incomplete specimens from the late Carboniferous of the Bjørnøya and found the main features of *C. mutafii* comparable on the genus level to the mature growth stage of *Siedleckia bjornoyana* Fedorowski, 1975, the type species of the genus. Consequently, the occurrence of *Siedleckia mutafii* has been extended to the Bjørnøya. However, the Novaya Zemlya specimens differ clearly from the Donets Basin corallite in the radial arrangement, length and shape of the major septa, most of which, except for the shortened protosepta, are equal in length and remain far from the corallite axis.

OCCURRENCE: Kalmyus River Area, Voznesenka Village. Limestone D₇. Lower Voznesenskian Substage, Suite C₁^s_g. *Plectostaffella bogdanovkensis* foraminiferal Biozone, *Declinognathodus noduliferus* conodont Biozone, *Homoceras–Hudsonoceras* ammonoid Biozone. Earliest Bashkirian.

CONSIDERATIONS

Microstructure and diagenesis

The microstructure of the septa is generally accepted as a character very important for the classification of the Scleractinia. Only identical or closely comparable microstructure of the septa documents the relationships within that subclass. Nothing like that is observed in the rugose coral studies. The microstructural studies in this subclass are rare, incomplete and have brought more controversies rather than solutions. Reasons for the controversies vary. In my opinion the most important among them are: 1. Disregarding the diagenetic alterations. The summary by Oekentorp (2001) and some remarks by myself (Fedorowski 2003) may form an introduction to the discussion on this topic. 2. Disregarding the difference between the microstructure of the innermost parts of septa, inserted prior to the formation of the sclerenchymal sheets and the microstructure of those sheets. The former, called the “middle dark lines” in the old literature and considered by myself as primary septa, varies, whereas the latter, if secreted, is always composed of calcite fibrils parallel to each other. The occurrence of two kinds of microstructure in most septa of the Rugosa does not mean two phases of their formation as stated by Stolarski (2003). They only reflect a change in the orientation of growth of the crystalline fibrils from radial to parallel. That change in the growth direction depends on the shape of the septal pockets that either kept their “bulbous” character long, or flatten laterally at a more or less early period of secretion of a given septum. Huge monacanthine trabeculae, like those in the Devonian genus *Neaxon* Kullmann, 1965, appeared when the distances between the centers of calcification are long, whereas more or less tiny trabeculae appeared in the second case. Thus, the size of trabeculae depends on the distances between the calcification centers and the shapes of septal pockets. Those two factors cannot be incidental, but must have been genetically controlled, making the microstructure in the Rugosa constant for a taxon and taxonomically important. 3. Disregarding the shape of the upper margins of septa and the orientation of the trabeculae, always growing perpendicular to that margin. This issue was raised and discussed long ago (Fedorowski 1974), but remains disputable (e.g., Stolarski 2003).

The remarks that follow do not pretend to solve any of the important questions raised above, but may be useful for a more comprehensive discussion on

the microstructure and diagenesis of septa in the Rugosa. The similarity in many skeletal details of the Subclass Scleractinia to those in the Rugosa formed a basis for making the relationship between those subclasses accepted. This in turn should allow transferring into the Rugosa the fundamental characters of the Scleractinia, the microstructure of septa being of the greatest taxonomic value. Thus, a close similarity of the microstructure of at least species and genera of the rugose corals should be considered as fundamental for their relationships. However, the phenomena observed in the transverse sections of *Nina donetsiana*, supplemented by data derived from other species of that genus, and the other genera described herein, apparently contradict this thesis. Not only in adjacent major septa (Text-fig. 8C), but also in the primary septa observed in various species and genera, the microstructure differs along their length (Text-figs 5C, 6I, 7K, 8C, 10E, 16C, D, 17H, 18E). Thus, the different microstructure present in the same septum appears to make that character not only curious but also useless taxonomically. Therefore, should the use of the microstructure of septa in the Rugosa be abandoned and instead macro-morphological and ontogenetic criteria be applied in generic and species identifications? The answer is no. These differences in the microstructure of the septa have been determined herein to have resulted due to diagenetic alterations of the original microstructure of septa. The narrow width of the primary septa ("dark middle lines") and tiny bunches of calcite fibrils in better preserved parts of septa, allow one to consider the microstructure of septa in species considered here as finely trabecular. This kind of trabecular microstructure is confirmed by the longitudinal section with the original arrangement of growth lines and trabeculae preserved (Text-fig. 8D). The similarity in trabecular remnants and similar diagenetic alterations, observed in most instances, suggest the finely trabecular microstructure of septa typical for the family Bothrophyllidae.

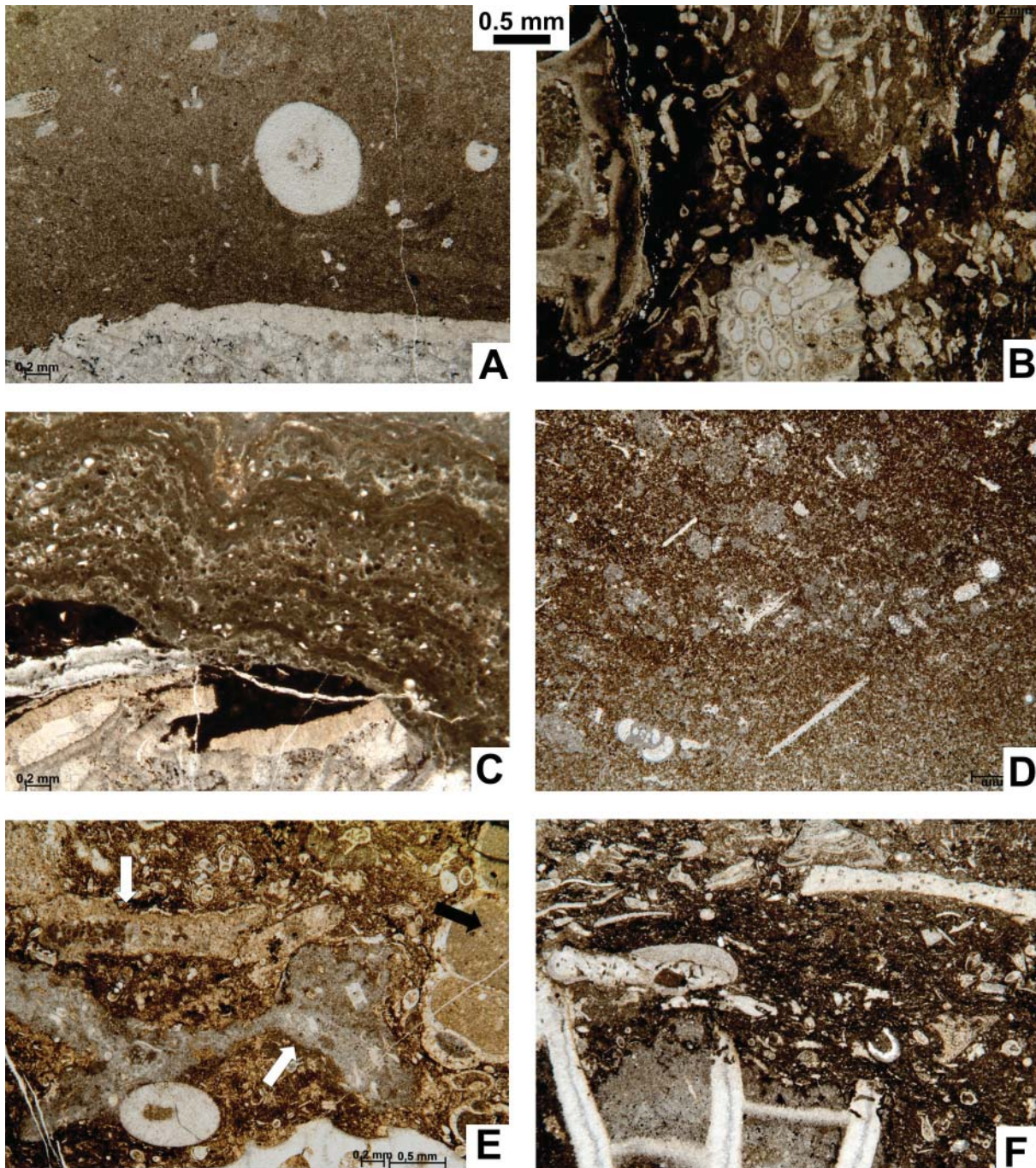
The latter conclusion requires special attention to two kinds of the "microstructure" observed. The first one appears either along the entire length of the major septa or occurs only in their thin inner parts. Bunches of fibrils are absent from the "middle dark lines" of such septa (Text-figs 12F, 13E), being replaced by rhombohedrons. This "microstructure" prevails in the major septa of all taxa investigated here and is interpreted as the result of recrystallization leading to the formation of large solid crystals of calcite, but not in the form of crystalline fibrils. Total dissolution of the primary septa, with no remnants of the trabeculae

left as centres of the crystallization may have been the reason for such recrystallization.

The second kind of microstructure, apparently negating the conclusion of it being common for the entire family Bothrophyllidae, is only sporadic. This "microstructure", best seen in the paratype of *Nina donetsiana* (Text-fig. 8H), is observed in part of the major septum of another paratype of that species (Text-fig. 8C, right septum, lower) and in the paratype of *Nina magna* (Text-fig. 16C). It differs considerably from the original or altered microstructures of septa. Distinct, large fans of calcite fibrils and/or flattened bodies consisting of radial crystalline fibrils, may either lack sclerenchymal sheets (Text-fig. 8H), may be covered by narrow sheets (Text-fig. 8C, right septum), or may be covered by thick sheets as in Text-fig. 16C, where the original microstructure is barely recognizable. The two major septa adjacent to one another in *Bothrophyllum gorbachevensis* (Text-fig. 6I) with some bunches of large crystalline fibrils clearly separated from each other, with some others arranged in fans. Most parts of the septa lacking crystalline fibrils in their "middle dark lines" (Text-fig. 6I) can be pointed out as intermediate between the two "microstructures" described in this and the preceding paragraph.

The discussed examples leave little or no doubts to both, the original, trabecular microstructure of septa postulated above and the secondary, diagenetically altered images seen in most primary septa. The occurrence of bunches of fibrils exclusively in the narrow "middle dark lines", and their absence from the sclerenchymal sheets of septa from the inner and the external wall (Text-figs 5C, 6I, 7K, 12F, 13E, 16C, D, 17H, 20E, 21) indirectly prove this suggestion. Only the trabeculae, acting as the nuclei for recrystallization, allow an organization of the diagenetically altered fibrils. The one-way growing calcium carbonate crystals in dissepiments and tabulae were demonstrated independently by Wells (1969) and Sorauf (1970). The recrystallization of those skeletal structures and external walls never lead to the formation of fibril bunches.

The interpretation of the microstructure in septa of the Rugosa differs (e.g., Semenov-Tian-Chansky 1974; Fedorowski 1974, 2002; Oekentorp 2003; and this paper). These differences are not discussed. However, I consider both the facts illustrated and their interpretation to be useful for both the understanding of the difference between the original microstructure of septa in the Rugosa and diagenetic alterations of that microstructure. Such recognition in turn is necessary for making the taxonomy in that subclass of corals close to natural classification.



Text-fig. 23. Rugose corals yielding deposits. A – Specimen UAM-Tc/Don.1/159. Voznesenka Village. Limestone D₇⁵. Sandy wackestone with rare skeletal remnants, mostly resistant crinoid ossicles; coral skeleton at the bottom. B – Specimen UAM-Tc.Do.1/160. Voznesenka Village. Limestone D₇³. Algal grainstone; small fragments of algae dominating; crinoid ossicles, fragments of bryozoan colonies rare and unrecognizable detrital particles; coral skeleton at left. C – Specimen UAM-Tc/Don.1/161. Voznesenka Village. Limestone D₇⁶. Mudstone and fragmented coral skeleton overgrown by calcareous algae. D – Specimen UAM-Tc/Don.1/139. Amvrosievskiy Kupol, Nikolaevka Village. Limestone D₆. Sandy grainstone with rare foraminifers (some fragmented) and fragments of algae. E – Specimen UAM-Tc/Don.1/157. Gorbachevo Village. Limestone F₂. Grainstone/packstone composed mainly from fragments of various algae (white arrows) with crinoid ossicle (lower left) and gastropod shell (black arrow). F – Specimen UAM-Tc/Don.1/147. Larino Village, Obetochneya Ravine [Balka]. Limestone G₁¹. Grainstone composed mainly from undetermined particles with fragments of algae and foraminifer shell; intraskeletal loculi of coral filled in with matrix different from surrounding deposits, corroded together with septa sticking out from it

Taphonomy and diagenesis

All corallites described in the present paper are worn specimens. This makes considerations on their living conditions unsupported. Also, the recapitulation of distances they were transported prior to becoming deposited are unknown. All illustrations (Text-fig. 23A–F) should be treated as random examples of the organic content of the limy intercalations illustrated. They differ considerably in both the richness and the diversification of the organic remnants (Text-fig. 23A, D vs. B, E). Coral skeletons are commonly the largest bioclasts within the samples. Reasons for such a domination were discussed recently (Fedorowski 2015).

Only a single coral specimen is overgrown by algae (Text-fig. 23C). The overwhelming absence of epibionts excludes the long time exposure on a sea floor of nearly all coral skeletons studied and suggests their permanent burial. Almost all coral skeletons are broken by squeezing. That deformation is in several samples advanced so that their diagnostic characters are destroyed.

Recrystallization, and sometimes replacement by dolomite or silica, are further diagenetic processes within the limestone layers. Most skeletons are altered to an extent excluding their identification in part or totally (Text-fig. 23E, upper and lower white arrows, respectively). The infillings of a well-preserved shell of a gastropod and of some rugose coral skeletons (Text-fig. 23E, black arrow, F, respectively) differ from the surrounding deposits clearly enough to suggest the transportation of those bioclasts after becoming infilled by mud. The transportation and deposition of heavy, infilled bioclasts with much lighter, small fragments of other organic remnants, is difficult to explain.

Similarity in characters vs. relationships

Similarity in characters. The relationships and a suspected derivation of the genus *Bothrophyllum* Trautschold, 1879 were discussed recently (Fedorowski 2016) and are not repeated here. The remarks that follow in this subchapter are restricted to two topics: 1. The appearances of characters in some species, which are strange for a family to which they belong. 2. Relationships of the taxa described in this paper.

Two taxa are discussed here in the context of the first point: *Turbinatocaninia* Dobrolyubova, 1970 and *Nina dibimitaria* sp. nov. The position of *Turbinatocaninia* in the Subfamily Dibunophyllinae, established by Hill (1981), is accepted here. An occurrence of the axial column early in the ontogeny, lasting sometimes up to the early mature growth stage

(Dobrolyubova 1970, pl. 46, fig. 1z in Russian alphabet) in two indisputable species of *Turbinatocaninia*, i.e., *T. okensis* Stuckenberg, 1904 (type species) and *T. besputensis* Dobrolyubova, 1970, is the character clearly pointing towards the Dibunophyllinae. Thus, the concept of Dobrolyubova (1970) of the derivation of *Turbinatocaninia* from *Dibunophyllum* is well supported and is followed herein. *Turbinatocaninia toporovensis* Dobrolyubova, 1970 (Dobrolyubova 1970, pls 47, 48) differs from the remaining two species in possessing an elongated counter septum and a thin median lamella either connected to that septum or free. Also, the weak, interrupted axial structure, documented only in some transverse sections, is connected with the counter septum in the holotype and one paratype (Dobrolyubova 1970, pl. 47), but that connection is either extremely weak and short lasting or absent from the remaining paratypes. In one of the paratypes, the counter septum is elongated up to advanced maturity (Dobrolyubova 1970, pl. 48, fig. 2a–d in Russian alphabet). That character and lack of the axial column are typical of the Family Bothrophyllidae but not for the Subfamily Dibunophyllinae.

Lack of the main dibunophyllid features and the literal and formal approach to the taxonomic rules would allow the transference of *T. toporovensis* to the Family Bothrophyllidae and even to the genus *Bothrophyllum*. This, in turn, would make the Family Bothrophyllidae a phylogenetically late offspring and a continuation of the Aulophyllidae phylogenetic line. That concept, although attractive and theoretically solving a disputable question of the relationships between Mississippian and Pennsylvanian bothrophyllids (Fedorowski 2016), is not suggested at least in the case of *Turbinatocaninia*. All morphological features of *T. toporovensis*, other than the two mentioned, follow the diagnosis of *Turbinatocaninia*. Also, the morphology of *T. besputensis* is intermediate between *T. toporovensis* and *T. okensis*, i.e., two indisputable dibunophyllid species. Thus, the bothrophyllid characters present in *T. toporovensis* are treated herein as morphological structures developed in that species independently and without any connection to the bothrophyllids.

Nina dibimitaria is the taxon trending towards *Dibunophyllum* in the morphology of its late neanic/early mature growth stage. Moreover, this species occurs in the area and time hosting representatives of the latter genus (Vassilyuk 1960; Fedorowski in press). Structures repeated after *Dibunophyllum*, i.e., the long lasting axial septum, commonly thickened in its axial part and joined by the inner margins of several major septa to imitate the dibunophyllid axial structure, last

in that species up to the early mature growth stage inclusively. Such an arrangement of septa, misleading at first glance, can be corrected as a morphological repetition when the morphology of the axial area of corallites, exposed by transverse sections, is studied carefully. In corals with the axial column present, sections of tabulae are invariably denser near the corallite axis than they are in the peripheral parts of the tabularium. Nothing like that occurs in the specimens included here in *N. dibimitaria*. Also, the longitudinal section does not show an axial column. However, the possibility of the Dibunophyllinae-Bothrophyllidae relationship is tentatively accepted. This question is further discussed on the basis on the study of the earliest Bashkirian dibunophyllids from the Donets Basin (Fedorowski in press).

Repetition of morphological solutions is not unique and not restricted to the examples discussed. On the contrary, repetitions of various skeletal structures are common in organisms as primitive as the rugose corals. It is enough to mention an axial column present in the middle Devonian *Hamaraxonia* Berkowski and Weyer, 2012, closely comparable to the axial column in the Viséan *Dibunophyllum*. A very far phylogenetic distance between those two genera makes the repetition of that skeletal structure obvious.

To conclude: The genus *Turbinatocania* represents a phylogenetically advanced taxon of the Subfamily Dibunophyllinae. It secreted some skeletal structures similar to those typical of the Family Bothrophyllidae. However, the occurrence of those structures neither requires elimination of their bearers from the Subfamily Dibunophyllinae nor suggests their relationship to the Family Bothrophyllidae. Contrary to the former, the *Dibunophyllum*-like structure in *Nina dibimitaria* either repeats a part of the skeletal solution introduced earlier by *Dibunophyllum* species, or inherited those structures. This topic is left open for the time being.

Relationships. Most of the corals studied herein are fragmented, diagenetically altered, and few in number, whereas the investigation of the very rare latest Serpukhovian and earliest Bashkirian rugose corals is commonly inadequate for satisfactory comparisons, therefore the remarks that follow should be treated as possibilities rather than solutions.

Nina gen. nov. comprises four named species and two specimens left in the open nomenclature. The mature morphologies of those taxa differ distinctly from each other. *Nina donetsiana*, the type species for the genus and *Nina berestovensis* (Vassilyuk, 1960) are most similar to the genus *Bothrophyllum*, reflected in the original inclusion by Vassilyuk

(1960) of the latter species in *Bothrophyllum*. Also, those two species, *N. berestovensis* in particular, resemble "*Pseudocania*" *longiseptata* Lewis, 1931, mentioned in the remarks on the genus *Nina* as a potential ancestor of that genus. That suggestion is poorly supported and cannot be considered proven.

The type species of *Nina magna* in turn was first identified by Vassilyuk (in Aizenverg *et al.* 1983) as *Neokoninckophyllum nipponense* Kato, 1959. Indeed, it superficially resembles these Japanese corals derived from the *Millerella* foraminiferal Biozone. The characters in common are: the cardinal septa long, the cardinal fossula hardly distinguishable, the dissepimentarium wide and the tabularium convex, consisting of incomplete tabulae (Kato 1959, p. 265, pl. 1, figs 1–8). However, none of the Japanese specimens exhibits a differentiation in length of the major septa typical of *Nina* and their early ontogeny is unknown. Kato (1959, pp. 267, 268) discussed several possibilities of the relationship of his corals to those from other regions. His special attention was directed to the corals described by Moore and Jeffords (1945) from the Bashkirian strata of Texas and Oklahoma. Those and other North American "*Neokoninckophyllum*" species (e.g., Cocks 1970) share several morphological characters with the Japanese species and with some Bashkirian corals from the Donets Basin (Fedorowski in press). However, they do not belong either to *Nina* or to *Neokoninckophyllum*.

The multidirectional variety of the characters in *Nina* can be interpreted as either suggesting a polyphyletism of that genus, i.e., the incorrect identification of some species, or as the instability of characters, common in taxa at the beginning of their existence. The material studied does not allow a positive answer to that question, but the second possibility is considered as more probable. Also, none of the existing taxa can be indicated with adequate conviction as ancestral for *Nina*. *Caninophyllum* Lewis, 1929 seems to be the only possibility for the time being. Hill (1981) considered the relationship of *Bothrophyllum* and *Caninophyllum* proven, but Fedorowski (2016) put in doubts the ancestral status of that genus for *Bothrophyllum*. Those doubts must be extended to *Nina*, if the latter two genera are related as accepted here.

The stratigraphic position of *Nina* and the supposed relationship should make *Nina* ancestral for *Bothrophyllum*. Two Bashkirian taxa of the latter genus described herein should play an intermediate role between *Nina* and *Bothrophyllum*. Unfortunately, none of the species of *Nina* from the Voznesenskian Substage can assume that role. The morphology of

some of them (*N. berestovensis*, *N. magna*) is too advanced for their being ancestral for the morphologically simpler *Bothrophyllum* species described here, whereas the characters of the other species (*N. dibimitaria* in particular) are obviously not on the trend leading to *Bothrophyllum*. Only *Nina* sp. 2 from the Feninian Substage (Limestone E₁) may be indicated as potentially ancestral. Unfortunately, such a role of that single corallite can be treated as merely a possibility.

The position of *Cystilophophyllum* within the phylogenetic line of the Family Bothrophyllidae is disputable. The occurrence of the axial septum early in the ontogeny, the great length of the cardinal and counter septa, the character of the sclerenchymal thickenings of the major septa and the morphology of the tabularium, the occurrence of the disstabilarium in particular, are bothrophyllid characters. They prevail so much over the temporary appearance of a pseudocolumella in some specimens, that the position of *Cystilophophyllum* within the Family Lophophyllidae Grabau, 1928 suggested by Fomichev (1953) cannot be followed. Besides, the pseudocolumella present in *Cystilophophyllum* resembles that in *Gshelia* Stuckenberg, 1888, the position of which within the Family Bothrophyllidae seems unquestionable. Elongation of the middle major septa in all quadrants, established in the late neanic growth stage of one corallite of *C. kalmiussi* studied here in adequate detail, cannot point to *Nina* as an undisputable ancestor for *Cystilophophyllum*, but it allows a consideration of such a possibility. The development of lonsdaleoid dissepiments, unique among the Bothrophyllidae, makes *Cystilophophyllum* an easily distinguishable genus, if that feature is preserved. However, that character leaves *Cystilophophyllum* outside of the main phylogenetic line of the Bothrophyllidae, the taxa of which tend to make their dissepimentarium complex, including formation of the pseudonaotic septa.

Possibilities in the relationships mentioned above, rather than rigid suggestions, are more relevant to the actual level of the investigation of the corals resembling, related and/or belonging to the genus *Bothrophyllum* and to the Family Bothrophyllidae. *Bothrophyllum* as the nominative genus must be considered firstly and it has been redescribed in the separate paper (Fedorowski 2016). Unfortunately, more problems than solutions were raised in that paper. Most of those problems have resulted from the unsatisfactory level of the investigations. Superficial descriptions based sometimes on a single or on two thin sections taken from an unknown part of a corallite, common in rugose coral papers up to now, cannot solve any problem.

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